

EXTINCT PECCARY “*CYNORCA*” *OCCIDENTALE* (TAYASSUIDAE, TAYASSUINAE) FROM THE MIOCENE OF PANAMA AND CORRELATIONS TO NORTH AMERICA

BRUCE J. MACFADDEN,^{1,2} MICHAEL X. KIRBY,³ ALDO RINCON,⁴ CAMILO MONTES,⁴ SARA MORON,⁴ NIKKI STRONG,⁴ AND CARLOS JARAMILLO⁴

¹Florida Museum of Natural History, University of Florida, Gainesville, 32611-7800, <bmacfadd@flmnh.ufl.edu>; ²Division of Research on Learning (DRL/EHR), National Science Foundation, 4201 Wilson Boulevard, Arlington, Virginia 22230; ³Environmental Planning Group (EPG, Inc.), 4141 North 32nd Street, Phoenix, Arizona 85018; and ⁴Center for Tropical Paleocology and Archaeology, Smithsonian Tropical Research Institute, Balboa, Ancón, Panamá, Republic of Panamá

ABSTRACT—Recently collected specimens of the extinct tayassuine peccary “*Cynorca*” *occidentale* (and another indeterminant tayassuid) are described from new excavations along the southern reaches of the Panama Canal. Fossil peccaries were previously unknown from Panama, and these new tayassuid specimens therefore add to the extinct mammalian biodiversity in this region. “*Cynorca*” *occidentale* occurs in situ in the Centenario Fauna (new name) from both the upper part of the Culebra Formation and overlying Cucaracha Formation, thus encompassing a stratigraphic interval that includes both of these formations and the previously described and more restricted Gaillard Cut Local Fauna. “*Cynorca*” *occidentale* is a primitive member of the clade that gives rise to modern tayassuines in the New World. Diagnostic characters for “*C.*” *occidentale* include a retained primitive M1, reduced M3, and shallow mandible, and this species is small relative to most other extinct and modern tayassuine peccaries. Based on the closest biostratigraphic comparisons (Maryland, Florida, Texas, and California), the presence of “*C.*” *occidentale* indicates an interval of uncertain duration within the early Hemingfordian (He1) to early Barstovian (Ba 1) land mammal ages (early to middle Miocene) for the Centenario Fauna, between about 19 and 14.8 million years ago. Based on what is known of the modern ecology of tayassuines and previous paleoecological interpretations for Panama, “*C.*” *occidentale* likely occupied a variety of environments, ranging from forested to open country habitat mosaics and fed on the diverse array of available plants.

INTRODUCTION

IN 2007 THE Republic of Panama initiated a decade-long undertaking to widen and expand the Panama Canal. In so doing, these extensive excavations have uncovered important new exposures of diverse Neogene volcanic and sedimentary units. Within this sequence, previous studies have demonstrated that the continental Cucaracha Formation has yielded a significant fossil vertebrate assemblage, previously referred to as the Gaillard Cut Local Fauna (L.F.). So far as is known based on the mammals, the Gaillard Cut L.F. has entirely North American biogeographic affinities despite its proximity to South America (Whitmore and Stewart, 1965; Ferrusquía-Villafrancha, 1978; Tedford et al., 2004). Based on our recent fossil discoveries and biostratigraphic interpretations, the concept of the Gaillard Cut L.F. can no longer be applied to the entire mammalian faunal assemblage because it spans a significant stratigraphic interval. Therefore, following Tedford (1970), the early to middle Miocene land mammal assemblage in hereinafter designated the Centenario Fauna, of which the Gaillard Cut L.F. is a subset (as further described below).

MacFadden (2006) described the mammals from the Gaillard Cut L.F., *sensu stricto*, from the Smithsonian Institution collections made during the 1960s and 1970s (for a preliminary faunal list, see Whitmore and Stewart, 1965). Detailed locality and biostratigraphic data indicate that the original Gaillard Cut L.F. was collected from a geographically and temporally restricted area along the southern reaches of the Panama Canal. MacFadden (2006) described three orders (Carnivora, Artiodactyla, and Perissodactyla), including at least eight individual taxa of early to middle Miocene mammals (also see Stirton, in Woodring, 1957). In addition, during the 1970s, crews from Southern Methodist University screenwashed for micromammals along the Panama Canal.

These efforts yielded a new, extinct species of geomyoid, *Texomys stewarti* (Slaughter, 1981). Since these original discoveries, prospecting by groups from the Smithsonian Tropical Research Institute (STRI) and the University of Florida (UF) have added specimens to the original taxonomic list, as well as important specimens of the peccary described here.

The new specimens and associated biostratigraphic data described here: (1) enhance the morphological characterization of “*Cynorca*” as it is otherwise known from North America; (2) demonstrate that the previous Gaillard Cut L.F. now extends for a considerable stratigraphic interval, hence justifying the new name Centenario Fauna; and (3) provide evidence towards resolution of the enigmatic biostratigraphy of this assemblage from Panama. Although the fossil record reveals that peccaries were once more biogeographically widespread in the Americas, today they range from tropical to more arid habitats from southern North America, into Central America, and into lowland South America. As previous authors indicate (Woodburne, 1969; Wright, 1998; Harris and Liu, 2008), the clade that includes “*Cynorca*” *occidentale* also includes the extant peccary genera *Catagonus*, *Pecari*, and *Tayassu* (*sensu* Wilson and Reeder, 2005). Thus, the discovery of “*Cynorca*” *occidentale* from Panama provides evidence for the antiquity of the family Tayassuidae and subfamily Tayassuinae.

COMMENTS ON THE NOMENCLATURE OF “*CYNORCA*”

Similar to the complexity associated with the allocation of the extant species of Tayassuinae to their respective genera (e.g., Wilson and Reeder, 2005), the taxonomic and nomenclatural history of extinct species of peccaries is oftentimes confusing. It is beyond the intended scope of the current paper

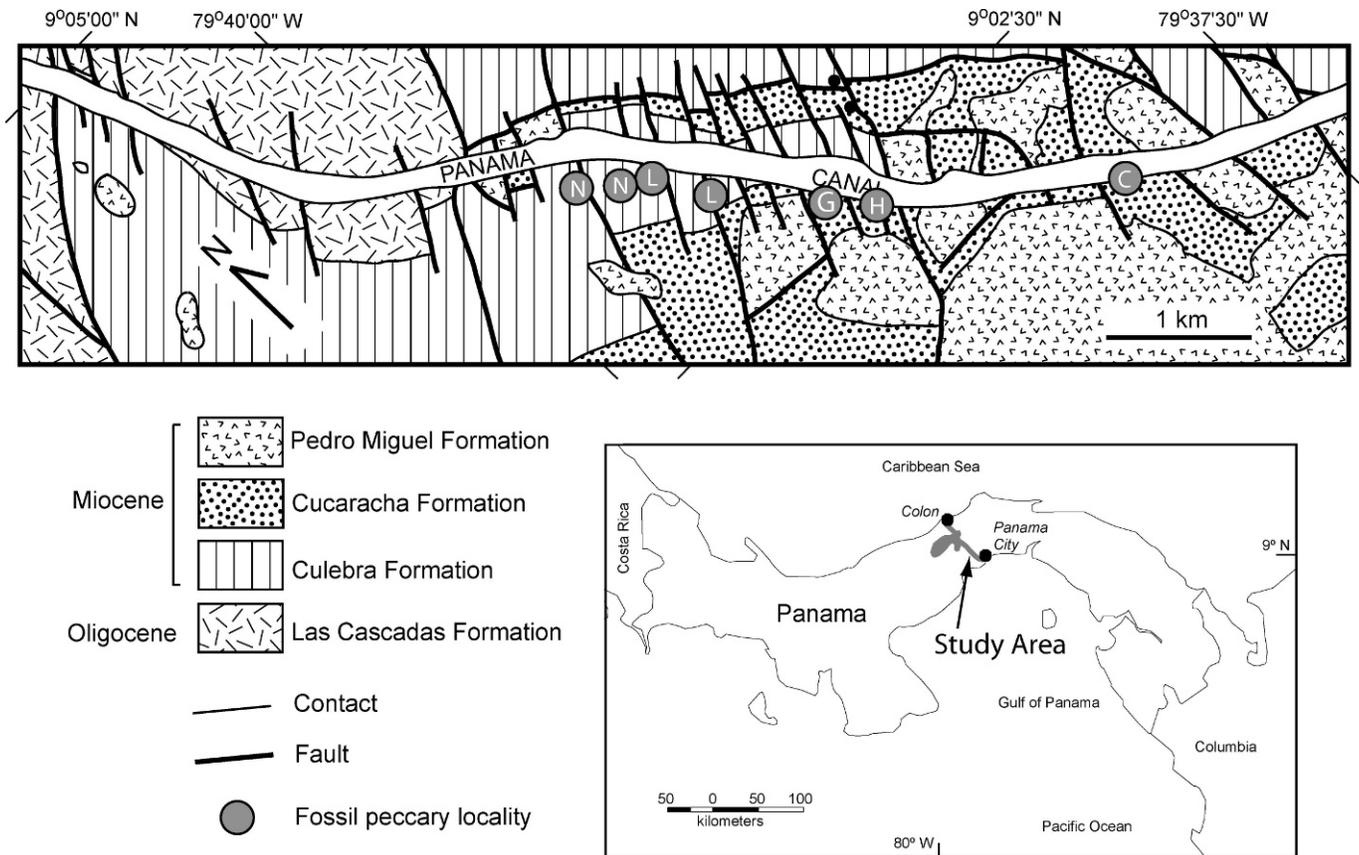


FIGURE 1—Geologic map of the Gaillard Cut portion of the southern reaches of the Panama Canal showing the fossil peccary localities (C = Centenario Bridge, H = Hodges Hill, L = Lirio, N = Lirio North), which also include many of those yielding the Centenario Fauna (also see SD Table 1). The original localities of Whitmore and Stewart (1965; also see MacFadden, 2005) are indicated by “G” (for Gaillard Cut L.F.). Geology modified from Stewart et al. (1980).

to provide a thorough analysis of Miocene tayassuid nomenclature; furthermore this has been carefully presented in previous studies (e.g., Woodburne, 1969; McKenna and Bell, 1997; Wright and Eshelman, 1987; Wright, 1998; Harris and Liu, 2008). Nevertheless, a brief explanation of the genus *Cynorca* Cope, 1867, its constituent species, and close relatives will provide the context and rationale for the discussion below.

Cope (1867) named *Cynorca* (“dog-whale”) based on an isolated canine tooth from the Calvert Cliffs of Maryland, although this genus has subsequently been used to include Miocene peccaries from numerous sites in North America. Woodburne (1969) allocated four species to the genus *Cynorca*, including the genoholotypic *C. proterva* Cope, 1867, *C. hesperia* (Marsh, 1871), *C. sociale* (Marsh, 1875), and a new species, *C. occidentale*. Wright (1998) recognized only two valid species of “*Cynorca*,” including *C. sociale* and *C. occidentale*. He uses *Cynorca* in quotes because: (1) of the undiagnostic nature of the type specimen and its species (*proterva*), and hence the genus should both be considered nomen dubium (also see McKenna and Bell, 1997); and (2) a cladogram of interrelationships of the species assigned to *Cynorca* indicates polyphyly, i.e., the tayassuid “*C.*” *sociale* lies outside the Tayassuinae and is most closely related to the extinct genera *Floridachoerus*, “*Thinohyus*” *siouxensis*, and *Hesperohyus*, whereas “*C.*” *occidentale* lies within this subfamily as a primitive outgroup to several extinct genera and the three extant genera. The taxonomy of extinct peccaries is thus quite complex and we choose to follow Wright (1998) in recognizing the two valid species *sociale* and *occidentalis*

within “*Cynorca*” until this nomenclatural problem is adequately resolved via a comprehensive phylogenetic analysis of fossil and modern Tayassuidae.

GEOLOGY, BIOSTRATIGRAPHY, CENTENARIO FAUNA, AND AGE CONSTRAINTS

Geology.—The peccary fossils were collected along the southern reaches of the Panama Canal (Fig. 1), which lies within a Tertiary structural and depositional basin (Coates and Obando, 1996; Coates, 1999). The fossils described here were found in two formations that crop out extensively along the Gaillard Cut (also called the Culebra Cut), including the predominantly marine Culebra Formation and the terrestrial Cucaracha Formation (Fig. 2). The Culebra Formation contains three members consisting of marine mudstone, sandstone, conglomerate, limestone, and lignite. Together, these represent a transgressive-regressive marine sequence with lagoonal, fringing reef, neritic, upper bathyal, and prograding deltaic environments (Woodring and Thompson, 1949; Kirby et al., 2008; Moron et al., 2008; Strong et al., 2008). Within the Culebra Formation, fossil peccaries have only been found in the uppermost member. The overlying Cucaracha Formation contains claystone, sandstone, conglomerate, and lignite, each with varying degrees of paleosol development (Retallack and Kirby, 2007; Moron et al., 2008; Strong et al., 2008). Together, these latter sediments represent a deltaic coastal plain environment that include mangrove, swamp, fluvial, woodland and dry tropical forested habitats (MacFadden and Higgins, 2004; Kirby et al., 2008; Moron et al., 2008; Strong et

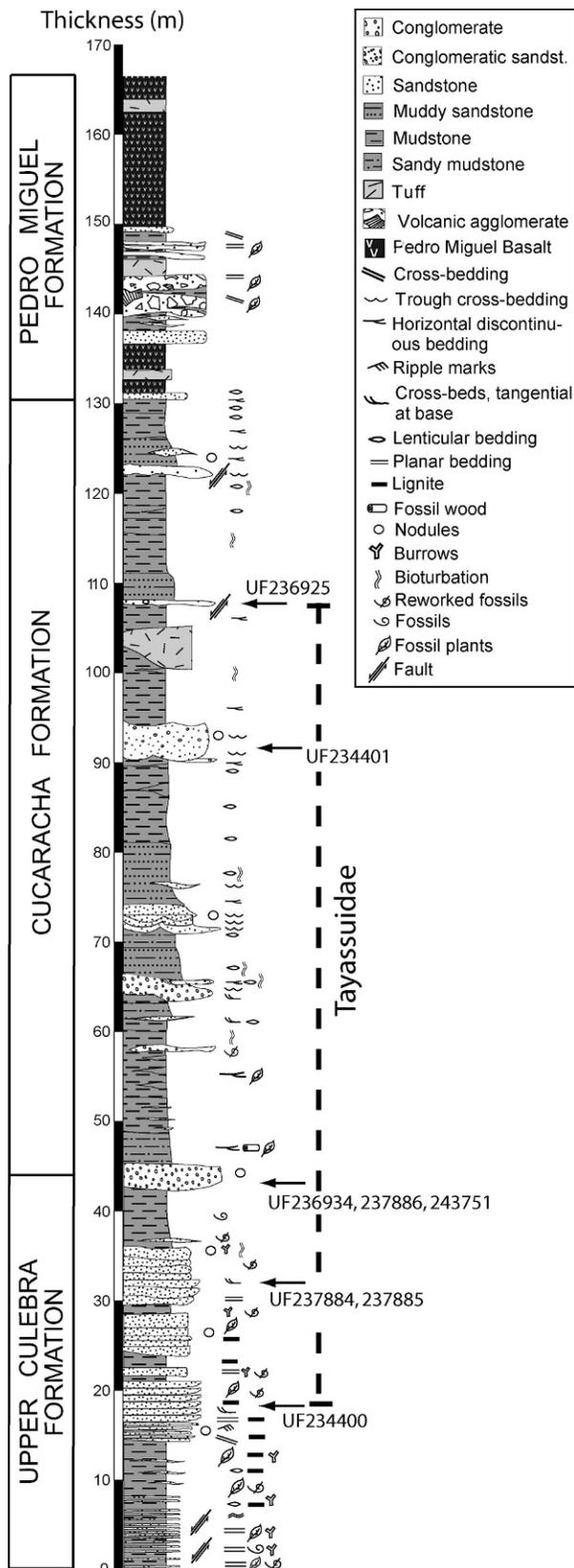


FIGURE 2—Composite stratigraphic section based on the Hodges Hill locality (locality H on Fig. 1) showing the stratigraphic positions and total biostratigraphic range of fossil peccary discoveries (also see SD Table 1). The correlated stratigraphic position of the Centenario locality in Fig. 1 is also shown on the Puente Centenario stratigraphic section of Retallack and Kirby (2007; Fig. 3A).

al., 2008). Peccary fossils have so far been found only in the lower two-thirds of the Cucaracha Formation, below a welded tuff marker bed that correlates to the 100–105 m zone in our composite stratigraphic section (Fig. 2). Underlying the Culebra Formation is the terrestrial Las Cascadas Formation, which contains agglomerate with tuffaceous claystone interbeds containing a recently discovered, and as yet undescribed, mammalian local fauna of probable Arikareean (late Oligocene/early Miocene) age (MacFadden and Rincon, pers. observ., 2009). The terrestrial Pedro Miguel Formation overlies the Cucaracha Formation and consists of basalt flows, tuffs, and interbedded paleosols and fine-grained sediments (Woodring and Thompson, 1949; Kirby et al., 2008; Moron et al., 2008; Strong et al., 2008).

The fossil peccaries have generally been found in siliciclastic, deltaic to fluvial sediments associated with nearshore, shallow-marine to terrestrial environments. Specifically, the peccary fossils from the uppermost Culebra Formation were found in volcanoclastic, clast-supported, pebble conglomerate to conglomeratic, medium- to coarse-grained sandstone. We interpret that these sediments were deposited in a coastal shallow-marine environment, based on the presence of shallow-marine fossils (mangrove wood, oysters, marine clams, terebratulid “shipworm” borings in wood, marine gastropods, crabs), marls, and intensity and type of bioturbation. Thus, the peccary fossils may have been transported into this marginal marine and deltaic environment as clasts. The peccary fossils from the Cucaracha Formation were found in thickly bedded, volcanoclastic, pebble-conglomeratic, medium- to coarse-grained sandstone beds that are interbedded with olive-gray claystone that show extensive paleosol development. We infer that the conglomeratic sandstone beds were deposited in a fluvial environment and the claystone beds formed in an associated floodplain environment (Retallack and Kirby, 2007; Kirby et al., 2008; Moron et al., 2008; Strong et al., 2008).

Biostratigraphy and the Centenario Fauna.—The peccary fossils provide additional information concerning the previously reported biostratigraphy of the Gaillard Cut L.F. (e.g., MacFadden, 2006). The new peccary material indicates that the Gaillard Cut L.F. actually extends from the Cucaracha Formation, where it was originally described by Whitmore and Stewart (1965), approximately 23 m below into the underlying Culebra Formation (Fig. 2). The stratigraphic interval containing peccary fossils is, therefore, approximately 85 m thick. The new peccary fossils thus extend downwards to the stratigraphic interval containing the Gaillard Cut L.F., and therefore fall outside of the definition of a “Local Fauna” to describe a stratigraphically and geographically restricted mammalian (or vertebrate) faunal assemblage (Tedford, 1970). We therefore herein name the Centenario Fauna from the southern reaches of the Panama Canal (Fig. 1), which takes its name from the new bridge completed in 2004 across the Gaillard Cut. Many of the fossils comprising the Centenario Fauna were collected as a result of the excavations for the bridge and subsequent excavations related to the expansion of the Panama Canal over the past several years. The Centenario Fauna has the following characteristics, so far as it is currently known: (1) it spans a total stratigraphic interval of 115 m (peccaries have been found in an 85-m thick subinterval) within the upper Culebra through middle Cucaracha formations (Fig. 2); (2) it yields a distinctive assemblage of at least 10 species within four orders of mammals, including Rodentia (*Texomys stewarti* Slaughter, 1981), Carnivora (*Tomarctus brevirostris* Cope, 1873,

Amphicyonidae Haeckel, 1866 or Hemicyonidae, indeterminate), Artiodactyla (*Merychochoerus matthewi* Loomis, 1924; “*Cynorca*” *occidentale* Woodburne, 1969; *Paratoceras wardi* Patton and Taylor, 1973), and Perissodactyla (*Anchitherium clarencei* Simpson, 1932; *Archaeohippus* sp. Gidley, 1906; *Menoceras barbouri* Wood, 1964; and *Floridaceras whitei* Wood, 1964); (3) based on comparisons with North American Land Mammal age (NALMA) biochronology, the Centenario Fauna mixes taxa diagnostic, or characteristic, of three early to late Miocene ages, i.e., late Arikareean (Ar4), Hemingfordian, and early Barstovian (Ba1; also see MacFadden, 2006, Fig. 17); and (4) all of the mammalian taxa are of North American biogeographic affinities, i.e., none are of South American origin. This definition and characterization of the Centenario Fauna is likely to change as more taxa are discovered during future field work at the new excavations along the Panama Canal.

Age constraints.—The age of the upper Culebra and Cucaracha formations, and hence the Centenario Fauna, is now constrained by several independent lines of evidence. Kirby et al. (2008) inferred that the uppermost Culebra Formation in this area of the Canal was 19.48 ± 0.41 Ma based on Sr-chemostratigraphic analyses of two marine bivalves collected 4 m below the top of the Culebra Formation, which is also within the stratigraphic interval where the peccary fossils were collected (Fig. 2). This age estimate thus suggests that the peccary fossils found in the upper Culebra Formation are about 19 Ma, which is about 1 million years older than “*C.*” *occidentale* found in North America. However, biostratigraphic evidence based on marine microfossils suggests a younger age for the upper Culebra Formation. Ostracodes from the upper Culebra Formation indicate correlation with planktonic foraminiferal zones N6 and N7 of Blow (1969; also van den Bold, 1972), which is 17.6 to 17.0 Ma in the time scale of Gradstein et al. (2004). In addition, benthic foraminifera from the upper Culebra Formation are correlated with the California Saucian benthic foraminifera stage by Blacut and Kleinpell (1969), currently dated between 24 and 17 Ma (Prothero, 2001). The stratigraphy and structural geology of the Gaillard Cut is sufficiently complex that alternative explanations for this discrepancy in geologic age of the upper Culebra Formation may be considered. One such explanation is that the upper part of the Culebra Formation has had differing amounts of erosion from place to place, such that one area may contain sediments that are 19.5 Ma, but another area may contain younger sediments that were not removed through erosion. Given the unconformity between the Culebra and Cucaracha formations and the deltaic nature of the sediments in the upper Culebra Formation, this explanation is plausible. The upper stratigraphic range of the peccary fossils is in the middle part of the Cucaracha Formation, which is stratigraphically below the welded tuff marker bed (Fig. 2). The middle part of the Cucaracha Formation remains undated, except for the other land mammal fossils. Taking these constraints, the Centenario Fauna (and the Gaillard Cut L.F. included as part of it) spans an interval of uncertain duration during the early to middle Miocene from latest Arikareean (Ar 4) through early Barstovian (Ba 1) age, sometime between 19.5 and 14.8 Ma (MacFadden, 2006; also see Tedford et al., 2004). Over the past several years we have tried, so far in vain because of a high degree of alternation, to produce radioisotopic age determinations for both the interbedded welded tuff marker horizon and the overlying Pedro Miguel basalts that potentially would provide independent age assessments for

the Centenario Fauna. Nevertheless, our ongoing geochemical studies continue to attempt resolution of this currently intractable problem of the upper temporal limits of the Centenario Fauna.

MATERIALS, METHODS, AND ABBREVIATIONS

The newly collected tayassuid fossils from Panama were compared with relevant collections housed at the following institutions: AMNH, American Museum of Natural History, New York; F:AM, Frick: American Mammals, part of the AMNH collection; MCZ, Museum of Comparative Zoology, Harvard University; UF, Florida Museum of Natural History, University of Florida, Vertebrate Paleontology Collection; UF-M, Florida Museum of Natural History, University of Florida, Mammalogy Collection; USNM, United States National Museum, Smithsonian Institution, Washington, D.C.

Other abbreviations—CRNHT, crown height, greatest measurement taken on labial lophs; L, left side; L.F., Local Fauna; M/m, upper/lower molar; Ma, Megannum, millions of years ago on the geological time scale; P, upper premolar; R, right side.

All data for specimens measured for this study are presented in SD Table 1. The taxonomy of the extinct Tayassuidae principally follows Wright (1998), cranial anatomy follows Getty (1975), dental topographic positions and orientations (distal, labial, lingual, and mesial) follow recent conventions proposed by Smith and Dodson (2003), tayassuid dental nomenclature and homologies follow Woodburne (1969), and biostratigraphy (relative to North America) follows Tedford et al. (2004).

SYSTEMATIC PALEONTOLOGY

- Class MAMMALIA Linnaeus, 1758
- Order ARTIODACTYLA Owen, 1848
- Family TAYASSUIDAE Palmer, 1897
- Subfamily TAYASSUINAE Palmer, 1897
- Genus “*CYNORCA*” Cope, 1867
- “*CYNORCA*” *occidentale* Woodburne, 1969
(Figs. 3–8; Supplementary Documents Table 1, 2)

Cynorca sp., Kirby and MacFadden, 2005, p. 195.

Cynorca sp., Retallack and Kirby, 2007, p. 669.

cf. *Cynorca* sp., Kirby, Jones, and MacFadden, 2008, p. 2.

Referred specimens.—Upper dentition: UF 234400, partial cranium, preserving the rostral and palatal regions with R & L P1–M3, upper Culebra Formation; UF 234401, R M2, Cucaracha Formation. Lower dentition: UF 237885, L partial mandible with m1–m2 from the upper Culebra Formation; UF 237884, L partial symphysis and mandible with m2, Culebra Formation; UF 236925, L distal portion of m2, Cucaracha Formation. (Also see three indeterminate specimens described below).

Geographic and Stratigraphic Location and Age.—As described above, these specimens of “*Cynorca*” *occidentale* were collected between 2003 and 2008 from several localities within the Gaillard Cut of the Panama Canal (Fig. 1; SD Table 1) and extend 73 m stratigraphically from the uppermost Culebra Formation to middle Cucaracha Formation (Fig. 2) within the Centenario Fauna; early to middle Miocene, probable age range from the early Hemingfordian (He 1) through the early Barstovian (Ba1) NALMA, about 19 to 14.8 Ma.

Diagnostic characters.—Taken together, the fossil peccary specimens from Panama preserve diagnostic tayassuid and/or

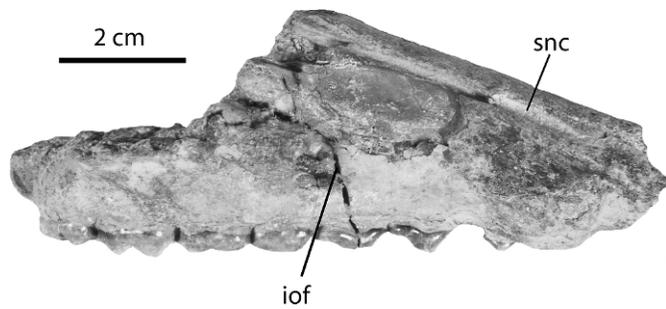


FIGURE 3—R lateral view of partial cranium (rostrum and palate) of UF 234400, “*Cynorca*” *occidentale* (also see Fig. 4.2 for palatal view). Abbreviations: iof, infraorbital foramen; snc, supraorbital nasal canal.

tayassuine characters, including posteriorly elongated maxilla that extends posterior to M3, supraorbital nasal canals (=supraorbital sulcus, *vide* Getty, 1975), and a tayassuid bunodont dentition with partially molarized premolars and a relatively simple dental pattern (Woodburne, 1969; Wright, 1998). The Panama specimens listed above are confidently allocated to the species “*Cynorca*” *occidentale* based on relatively small size and overall dental morphology, including retention of a P1, relative development (molarization) of the upper premolars (the lower premolars are not preserved in the Panama specimens), a reduced M3 relative to M2, and m2 that is transversely wider than m1. The Panama specimens have a relatively shallow mandible, similar in depth to specimens of “*C.*” *occidentale* from North America, and less deep than those assigned to, e.g., *Dyseoehyus* (*sensu* Woodburne, 1969).

Relative to primitive tayassuid taxa outside of the Tayassuinae (following Wright, 1998), including *Floridachoerus*, *Perchoerus*, and *Thinohyus*, “*C.*” *occidentale* from Panama is smaller, has a relatively reduced M3, the postdental process of the maxilla extends well posterior to M3, P4 has a metaconule, and the principal cusps of M3 are not separated by accessory cusps. Relative to its congener “*C.*” *sociale*, the Panama sample of “*C.*” *occidentale* is larger and has a relatively reduced M3. Relative to its most closely related sister-taxon *Dyseoehyus*, “*C.*” *occidentale* from Panama retains a P1, has a relatively reduced M3, a slightly more curved cheek tooth arcade, is slightly smaller than *D. fricki*, and significantly smaller than *D. stirtoni*. Relative to more derived tayassuines (e.g., *Prosthennops* and living peccaries [except for some individuals of *Pecari tajacu*]), “*C.*” *occidentale* from Panama is slightly to significantly smaller, has relatively unmolarized premolars, and a reduced M3.

Description.—Portions of the cranial morphology are preserved in UF 234400. Similar to extant peccaries, the snout region is characterized by nasals that slope towards the anterior of the skull (Fig. 3) and the presence of well-developed, continuous, and parasagittal supraorbital nasal canals, which house venous circulation. The infraorbital foramen, through which the infraorbital nerves and vessels emerge (Getty, 1975), lies dorsal to the mesial part of P4. In ventral view, the zygomatic arch (Fig. 4.2) is not flared as in some extinct peccaries (e.g., *Macrogenis*, see Wright, 1998, and *Mylohyus*, see Wright and Webb, 1984). Likewise in ventral view (Fig. 4.2), there are relatively large alveoli for the canines, which are not preserved in UF 234400, lateral to the mesial-distal (anteroposterior) line of the cheek teeth. Just anterior to the canine alveoli there is a weakly developed bony canal (sulcus) that in more advanced tayassuines accommodates the lower canines during occlusion. The P1 is small and separated from the P2 by a diastema (R = 4.9 mm; L =

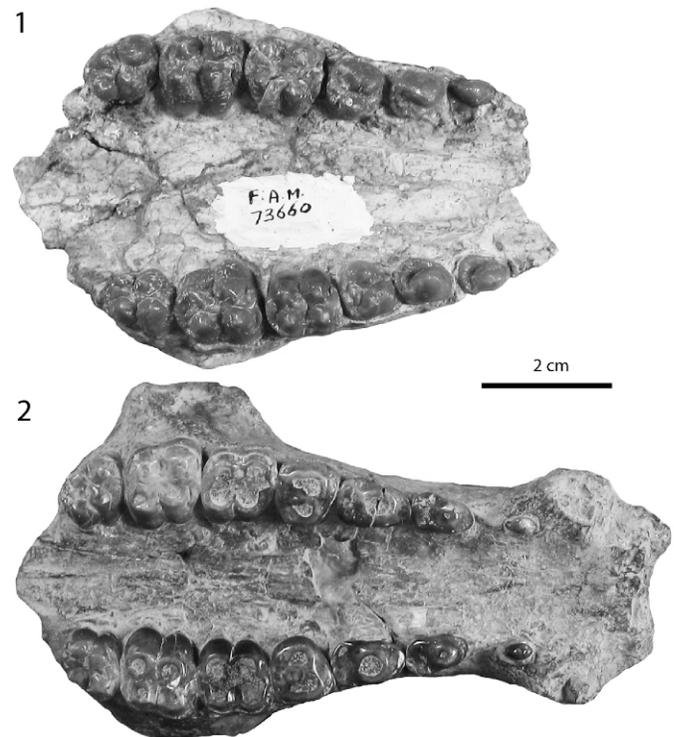


FIGURE 4—Comparisons of palatal views and cheek tooth dentitions of “*Cynorca*” *occidentale*, 1, F.A.M. 73660, holotype from the Barstow Formation, middle Miocene of California; 2, UF 234400 from the early to middle Miocene of Panama.

5.0 mm). Paired palatine foramina occur in the palate internal to P4. The postdental process of the maxillary (sensu Wright, 1998) extends posterior to the M3.

As preserved in UF 234400, which represents an adult with early to moderate wear (depending upon the particular tooth), the cheek tooth arcade is slightly curved (Fig. 4.2), whereas in more derived tayassuines this part of the dentition is straight and the corresponding R and L rows are relatively parallel, or subparallel, to each other. The P1 is small, conical, and consists of a single, transversely compressed principal cusp and a poorly developed, discontinuous cingulum (Fig. 5). The P2 and P3 are roughly oval-shaped and have a single principal cusp, probably the paracone (sensu Woodburne, 1969) in the mesial part of the tooth. The P3 is larger than the P2 (SD Table 2). In P2, a moderately to weakly developed crest runs distally from the principal cusp to the distal basin (talon) of the tooth. In both tooth positions the talon is relatively flat and lacks the development of distinct cusps. The cingulum is weakly developed or absent labially on P2 and lingually on the P3; these structures are moderately developed lingually on the P2 and labially on the P3. The P4 is subtriangular and consists of a twinned labial cusp (parametacone, sensu Woodburne, 1969) whose apex is not as high as the principal cusps developed in either P2 or P3. The protocone is smaller in occlusal cross-sectional area than that of the parametacone. The cingulum is absent lingually and moderately well developed labially.

The M1 and M2 are roughly square and consist of four principal cusps, i.e., the paracone and metacone labially, which are positioned mesial to the protocone and hypocone lingually. As evidenced by an isolated tooth, UF 234401 (Fig. 5.5), which is not as heavily worn as the more completely preserved palate (UF 234400), weakly developed crests

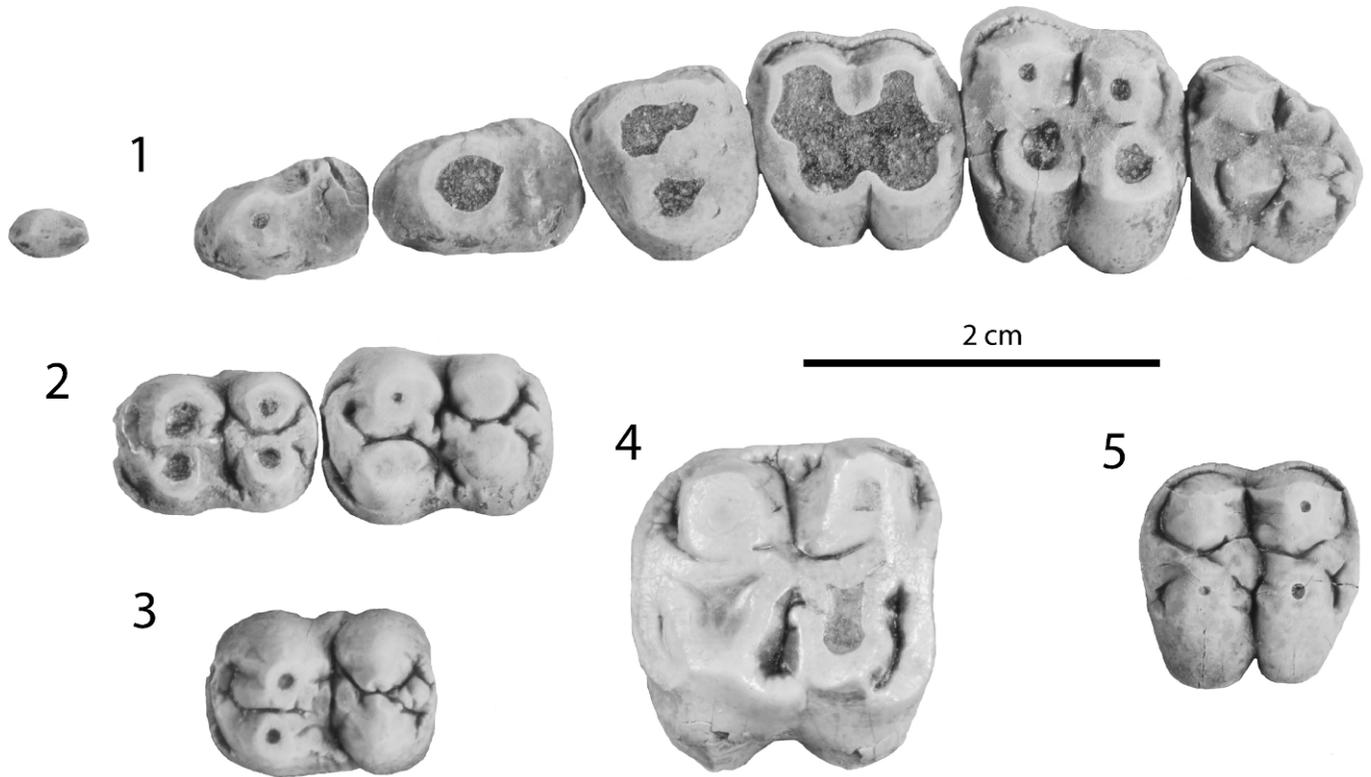


FIGURE 5—Dentitions and isolated teeth of extinct tayassuines from the early to middle Miocene, Panama Canal. 1, UF 234400, “*Cynorca*” *occidentale*, showing L P1–M3 (also see Fig. 4.2); 2, UF 237885, “*C.*” *occidentale*, L m1–m2 (also see Fig. 7.2); 3, UF 237884, “*C.*” *occidentale*, L m2 (also see Fig. 7.2); 4, UF 236034, tayassuid indeterminate, R M1 or M2; 5, UF 234401, “*C.*” *occidentale*, RM2.

(protoconule and metaconule, respectively) extend from the protocone and hypocone. The cingula are absent or poorly developed lingually, and relatively well developed mesially, labially, and distally. This upper molar morphology, consisting of four conical cusps and conules described above, which otherwise lack well-developed accessory cusps or other elaborations (e.g., well-developed enamel crenulations) seen in more advanced tayassuines, demonstrate a typical bunodont, or more specifically bunoselenodont, dental topography. The M2 is larger than the M1. In the M3, the paracone is situated more anterolabial than the other cusps in the tooth which results in a relatively rhomboidal outline relative to either the M1 or M2. The M3 dental cusp morphology is generally similar to those described for the M1 and M3. The cingulum in M3 is absent lingually and relatively well developed labially. As is characteristic for the species “*C.*” *occidentale*, the size of the M3 (Fig. 5.1) is reduced relative to either M1 or M2 (Wright, 1998). For example, the M3/M2-area ratios in the holotype of “*C.*” *occidentale* (F:AM 73660) and the referred specimen from Panama (UF 274400) range between 0.6 and 0.8, whereas for other extinct and extant tayassuines this ratio is characteristically ≥ 1.0 , indicating an unreduced M3 relative to M2 (raw measurements in SD Table 2). While “*C.*” *occidentale* is larger than its congener “*C.*” *sociale*, this genus is characterized by small size relative to most other extinct and extant tayassuines (Fig. 6), except for some smaller individuals of the modern *Pecari tajacu* (e.g., UF-M 13609).

With regard to the mandible and cheek tooth dentition, as represented in UF 237884 and 237885 (Fig. 7.1, 7.2), the mandible is relatively shallow, i.e., the depth below the m2 is, respectively, 20.0 and 20.5 mm (Fig. 8), similar to most other

specimens assigned to “*C.*” *occidentale* from North America and generally less deep than those assigned to *Dyseohyus* (sensu Woodburne, 1969). Of particular note, however, the Panama specimens are shallow relative to the holotype of “*C.*” *occidentale*, F:AM 73660 (Fig. 7.3). The interpretation of this difference in mandibular depth is discussed below.

Unfortunately, some of the most important characters of the lower cheek tooth dentition occur in the premolar dental pattern and morphology (corresponding to the degree of molarization seen in the upper premolars, see Wright, 1998),

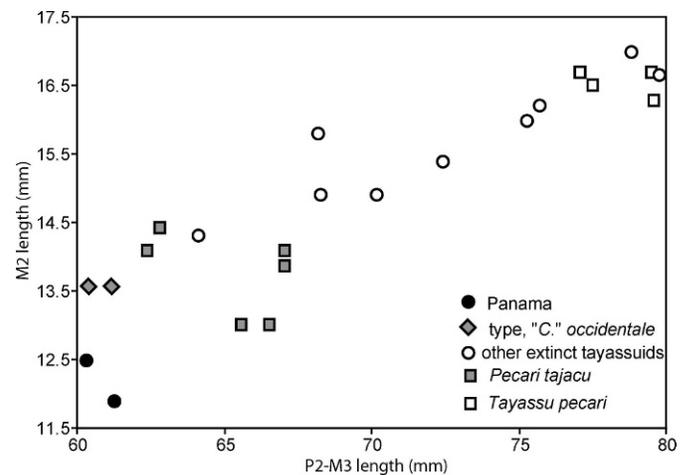


FIGURE 6—Plots of cheek tooth row length (P2–M3) versus mesial-distal length of M2 for relevant specimens of “*Cynorca*” *occidentale* from Panama, the holotype (F:AM 73660) from Barstow, California, other extinct tayassuine species, and the modern peccaries *Pecari tajacu* and *Tayassu pecari* (measurements taken from Table 1).

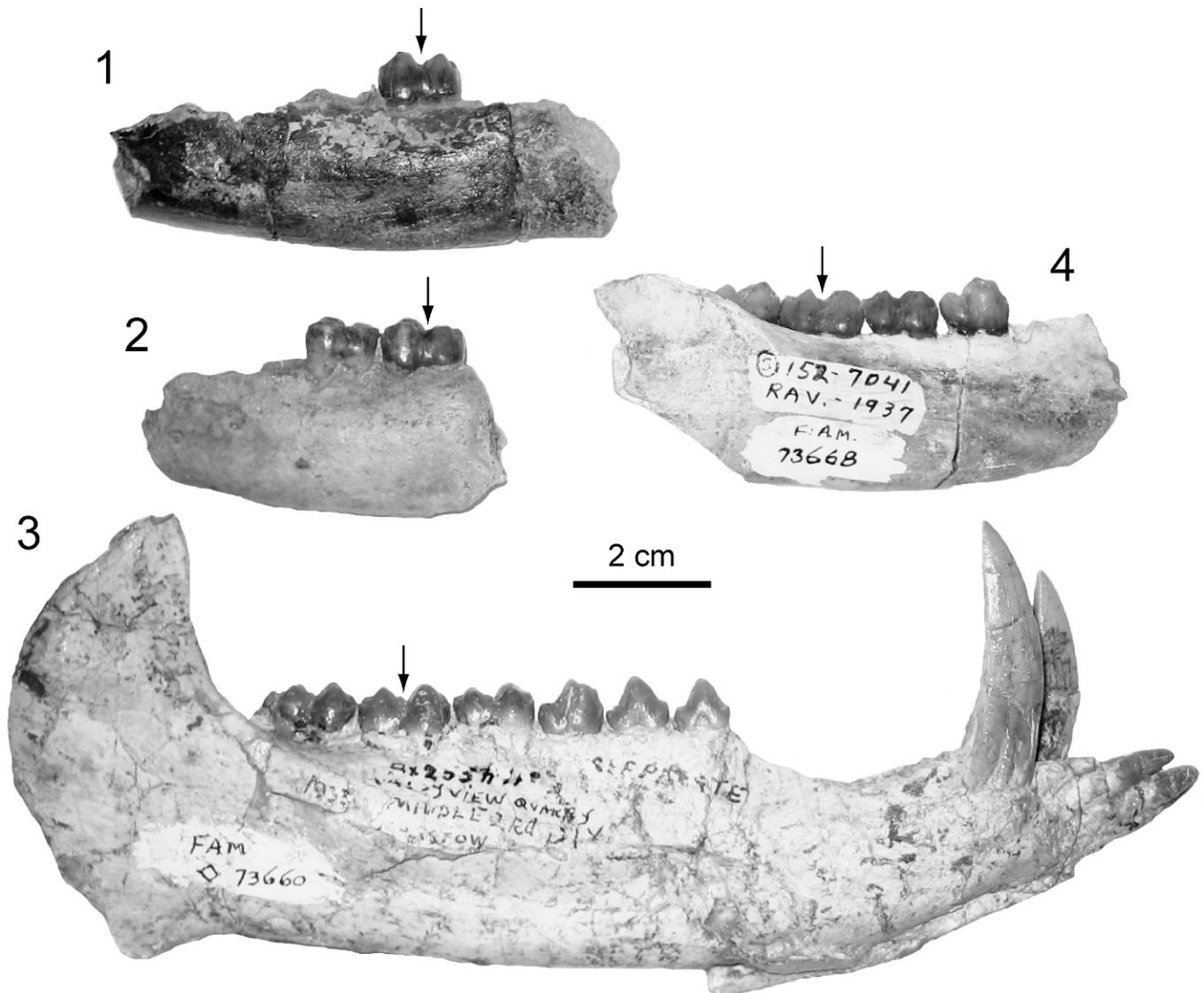


FIGURE 7—Selected mandibles of *Cynorca* *occidentale* showing general morphology and depth below the m2 (below arrow). 1. UF 237884 from Panama; 2. UF 237885 from Panama; 3. F:AM 73660 (holotype) from Barstow, California; 4. F:AM 73668 from early Hemingfordian near Lusk Wyoming. Also see Woodburne (1969) for more detailed locality descriptions for the latter two specimens.

which are not preserved in available specimens from Panama. The m1 and m2 are characterized by four principal cusps (Fig. 5.2), the mesially positioned protoconid and metaconid in the trigonid, and distally positioned hypoconid and entoconid in the talonid, forming a characteristic bunodont dental pattern (Woodburne, 1969; Wright, 1998). In the mesial part of the trigonid, a crest, the paralophid, is developed linguallally-labially and extends to the mesial portion of the protoconid. Another crest runs transversely in the middle of the tooth from the trigonid to the talonid. The cingulum is absent or relatively poorly developed linguallally, moderately well developed mesial-linguallally, and the distal portion of the tooth consists of a hypoconulid arising from the distal cingulum. As represented in UF 237885, the principal difference between the first two molars is that the m2 is considerably larger than the m1 (Figs. 5.2, 7.2; SD Table 1), in particular, the m2 is broader than the m1.

The Panama specimens described above are confidently allocated to the species *Cynorca* *occidentale* based on numerous characters of the overall dental morphology,

including relative development of the upper premolars and cheek tooth cusps, e.g., the reduced M3 relative to M2, and m2 that is broader relative to m1. Although not preserved in the type of *C.* *occidentale* (F:AM 73660), the P1 is present in UF 234400. With regard to size, *C.* *occidentale* from Panama is relatively small (e.g., mean M2 length of 12.8 mm [also see Wright, 1998]; mean R & L P2–M3 length of UF 234400 = 60.7 mm); and is essentially indistinguishable from the holotype of *C.* *occidentale* = 60.8 mm (also see other measurements in SD Table 1; Figs. 4, 6). Like that for the upper dentition, the dental proportions of the lower cheek teeth for *C.* *occidentale* from Panama are similar to those of this species from North America.

Family TAYASSUIDAE, indeterminant, or incertae sedis
(Figs. 5.4, 9)

Referred specimens and localities.—UF 236934, RM1 or M2; UF 243751, R tibia; UF 237886, upper tooth fragment; upper Culebra Formation (see Table 1).

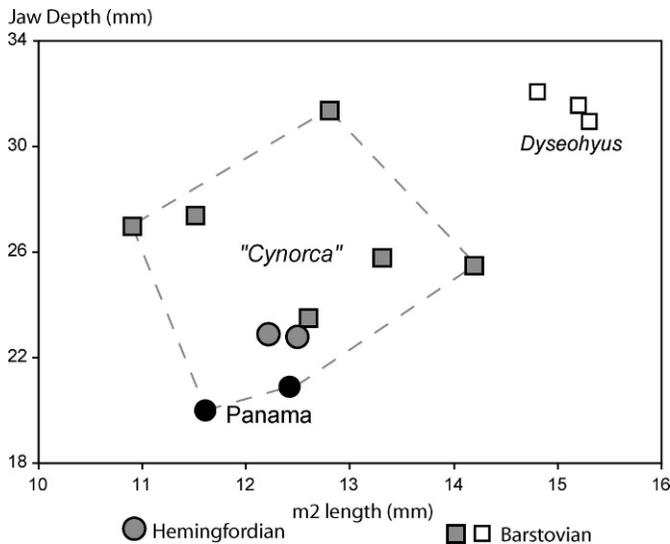


FIGURE 8—Plot of m2 mesial-distal length versus mandibular (jaw) depth below m2 for relevant specimens of “*Cynorca*” from Panama and North America.

Description and discussion.—Three additional specimens appear to be fossil peccaries from the Centenario Fauna, but for reasons described below, they represent indeterminate or uncertain taxonomic assignment. The first, representing a larger peccary tooth (UF 236934, Fig. 5.4) falls outside the range of size variation seen for “*C.*” *occidentale* described above. For example this specimen is larger and appears to be relatively shorter crowned than “*C.*” *occidentale* from the Centenario Fauna. It therefore could pertain to one of several potential tayassuine taxa (e.g., *Floridachoerus*, *Desmathyus*, *Dyseohyus* or *Prosthennops*) also known from the early to middle Miocene of North America (Wright, 1998). Given that this is an isolated tooth of an individual in advanced wear (which does not preserve important dental characters and lacks other morphological differentia), a definite taxonomic assessment of this peccary will await the recovery of additional material of this taxon, hopefully in the future.

The second specimen, UF 243751, represents a well-preserved R tibia of a small to medium sized mammal (Fig. 9). In general proportions and morphology of the proximal articular surface, development of the crest on the shaft, curvature of the shaft, and the distal surface that articulates with the astragalus, this tibia is distinctly artiodactyl (e.g., see Getty, 1975). This specimen therefore most likely pertains to either the protoceratid *Paratoceras wardi*, which is very common in the Centenario Fauna, or a peccary. Although no tibiae are known for *Paratoceras wardi* from

Panama, comparisons with the size of available astragali of this taxon relative to the distal trochlear region of UF 243751 indicate that UF 243751 is too large to be referred to that *P. wardi*. With regard to comparisons with North America, fossil peccaries are among the most common land mammals known from the Miocene Chesapeake Group in Maryland. Three fragmentary specimens from the Calvert Formation in the USNM collections, i.e., 413634, 413641, and 413643, preserve the proximal articular surface of the tibial head. Based on overall morphology and proportions, these are most probably tayassuid, although they were not collected in association with diagnostic dentitions, so specific allocations are ambiguous. In size these specimens compare favorably in length (35.1, 33.6, and 32.4 mm, respectively) and transverse width (32.8, 29.2, and 32.6 mm, respectively) with UF 243751 (34.3 mm, 37.8 mm) from Panama. Nevertheless, given the uncertain taxonomic allocation of the Calvert peccaries in the USNM collection, and the fact that now two taxa of tayassuids are known from the Centenario Fauna, specific allocation of UF 243751 is unwarranted at this time. It should also be noted that the possibility exists that this tibia represents an artiodactyl taxon not yet identified from the Centenario Fauna.

A third specimen (not illustrated), UF 237886, represents a small fragment of an upper cheek tooth (possibly deciduous) preserving two principal cusps. This specimen is most likely tayassuid, although given the poorly preserved nature of the specimen, even this is not certain.

Although these specimens are too poorly preserved, lack differentia, and/or taxonomically diagnostic comparative specimens, they nevertheless are placed on record here and indicate the presence of at least another tayassuid in the Centenario Fauna.

GENERAL DISCUSSION

Taxonomy and variation of “Cynorca” occidentale.—Excluding the three indeterminate specimens, based on overall morphology and size of the dentition, the other fossil peccary specimens from Panama are referred to “*C.*” *occidentale* (sensu Wright, 1998), which includes the concept of both *C. occidentale* and *C. proterva* in Woodburne (1969). Accordingly, based on the current study, we agree that there are few, if any, valid characters that can be used to distinguish “*C.*” *proterva* from “*C.*” *occidentale* (sensu Woodburne, 1969), and hence the latter name is used as described in Wright (1998). Having evaluated this matter, however, it should be noted that one character, i.e., depth of the mandibular ramus below m2, is greater in the type of *C. occidentale* (F:AM 73660) relative to the other specimens assigned to this species (SD Table 1; Figs. 7,8). Woodburne (1969, p. 312) noted the greater depth of the holotype of *C. occidentale* and other early Barstovian

TABLE 1—List of fossil specimens and locality data from the Centenario Fauna, early to middle Miocene of Panama.

UF Cat #	Description	Field #	Date collected	Locality	LOCALITY INFORMATION			
					UF Loc. #	Lat (°N)	Long (°W)	Formation
“<i>Cynorca</i>” <i>occidentale</i>								
234400	maxilla/palate with R & L P1–M3	PC0027	13-Aug-07	Lirio	YPA002	9.05475	79.65954	upper Culebra
234401	RM2	GC 13-3	20-Aug-03	Centenario Bridge	YPA003	9.03042	79.63519	Cucaracha
237884	mandible, symphysis with Lm1	PC 006	12-Jul-07	El Lirio North	YPA016	9.05261	79.65733	upper Culebra
237885	partial ramus with Lp4-m1	PC0027	13-Jul-07	El Lirio North	YPA016	9.05475	79.65954	upper Culebra
236925	posterior portion of Lm2	40212	5-Jun-08	Contractor’s Hill	YPA011	9.04815	79.64707	Cucaracha
tayassuid, indeterminate								
236934	M1 or M2	40177	2-Jun-08	El Lirio W (Hodges)	YPA012	9.04815	79.65389	upper Culebra
237886	partial upper tooth fragment	GC-12	17-Feb-07	El Lirio W (Hodges)	YPA012	9.05166	79.65584	upper Culebra
243751	R tibia	42087	13-Feb-09	El Lirio W (Hodges)	YPA012	9.04815	79.65389	upper Culebra

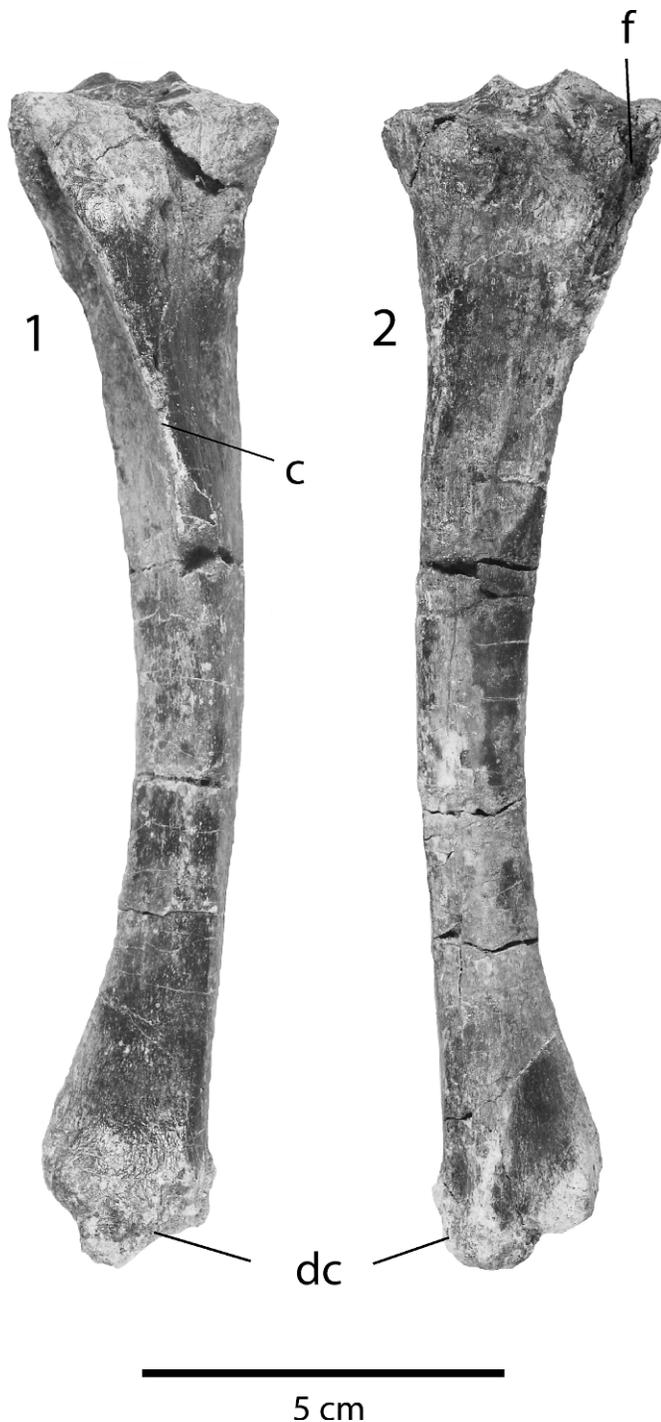


FIGURE 9—R tibia of Tayassuidae indeterminate, UF 243751, from upper Culebra Formation, Hodges Hill, Centenario Fauna, early to middle Miocene, southern Panama Canal. 1, cranial view; 2, caudal view. Abbreviations: c, crest; dc, distal cochlea; f, surface for articulation with head of fibula.

referred specimens as compared to other specimens assigned by him to this species. He interpreted this as intraspecific variation representing chronocline evolution within one species, i.e., late Hemingfordian specimens with shallow mandibles representing one variant and Barstovian specimens with the deep mandibles representing another variant. With the plethora of other known cranial and dental characters being indistinguishable within the concept of “*C.*” *occidentale*

as described above, Woodburne’s (1969) conservative approach of a single species to encompass the observed variation seems logical and is followed here. It also suggests a Hemingfordian, rather than a Barstovian, age for the “*C.*” *occidentale* from Panama relative to the biochronology of this species in North America.

Mammalian biostratigraphy of the Centenario Fauna.—Several of the land mammals previously described from Panama, e.g., the perissodactyls (*Archaeohippus* sp., *Anchitherium clarencei*, *Menoceras barbouri*, and *Floridaceras whitei*) show close morphological affinities with the middle Hemingfordian (late He1 through early He2) Thomas Farm L.F. of Florida. With the possible exception of the indeterminate tayassuid material described above, the referral of the other Panama peccary specimens to “*Cynorca*” *occidentale* therefore has the closest similarities to sites in North America, albeit other than Thomas Farm, where this species is absent. In particular, a close comparison exists between “*C.*” *occidentale* from Panama and the relatively abundant material described from the Calvert Formation of Maryland, which, based on in situ occurrences, come from beds 10 and 12 (Wright and Eshelmann, 1987). Although the entire Calvert Formation potentially spans an interval of uncertain duration from early Hemingfordian (He1) to the late Barstovian (Ba2), following the biostratigraphy of Tedford and Hunter (1984) and Wright and Eshelmann (1987), Tedford et al. (2004) interpreted bed 10 (and by inference, bed 12) of the Calvert Formation to be early Barstovian, no younger than the early late Barstovian (Ba2) age for overlying bed 14. This is likewise compatible with an early Barstovian occurrence for “*C.*” *occidentale* from other localities, including the Willacoochee Creek L.F., (listed as “*C.*” cf. “*C.*” *proterva* in Bryant, 1991) of Florida, Trinity River Pit I of Texas, and from the middle part of the Barstow Formation from California (Woodburne, 1969). Given the chronocline variation (e.g., as represented by the relative mandibular depths described above) and biochronological comparisons with North America, “*C.*” *occidentale* from Panama indicates either a Hemingfordian or early Barstovian age for the Centenario Fauna, somewhere between 19 and 14.8 Ma (also see Woodburne et al., 2006).

Tayassuine biogeography and paleoecology.—Two of the accepted modern tayassuine species, i.e., the Collared (*Pecari tajacu* [Linnaeus, 1758]) and White-lipped (*Tayassu peccari* Fisher de Waldheim, 1814) peccaries, are widely distributed biogeographically and inhabit a broad range of habitats. (A recently described new species, *P. maximus* Roosmalen et al. 2007 inhabits tropical rainforests of the southeastern Amazon, although its validity has recently been questioned [Gongora et al., 2007]. The remaining tayassuine species, *Catagomys wagneri* [Rusconi, 1930] lives in a restricted geographic area in the arid thorn forests and grasslands of the Chaco of central South America and feeds on legume seeds, roots, and cacti.) *P. tajacu* ranges from Arizona to Argentina, inhabits a wide variety of habitats including desert scrub, arid woodland, and rainforest, and feeds on cactus fruit, berries, fruit, rhizomes, and occasionally small invertebrates and vertebrates. Likewise, *T. peccari* ranges from southern Mexico to Argentina, and has generally similar dietary and habitat preferences to those of *P. tajacu*, although it tends to more frequently live in forested habitats (Nowak, 1999).

When they are present at a particular fossil locality in North America, Miocene peccaries are characteristically a rare element of the mammalian local fauna. An exception to this is the Calvert Formation, where tayassuids are the most common element of the mammalian faunal sequence (Wright

and Eshelmann, 1987; Tedford et al., 2004). This abundance of peccaries therefore raises the question of what the paleoecology of this region was like during the Miocene. Clearly it was coastal, but unfortunately Wright and Eshelmann (1987) declined to provide any additional insight or speculation about the paleoecology as it might relate to potential habitats for “*Cynorca*” *occidentale*. With regard to the terrestrial paleoecology of Panama during the Miocene, based on the sedimentology, Kirby et al. (2008) interpreted the uppermost portion of the Culebra Formation and the entire Cucaracha Formation to represent, respectively, deltaic distributary channels and mouth bars, and channel, marsh and flood-plain deposits, all of which suggest a coastal setting, potentially similar to the Calvert Formation of Maryland. In addition, studies of stable isotopes of mammalian tooth enamel from the Gaillard Cut L.F. (MacFadden and Higgins, 2004) and paleosols (Retallack and Kirby, 2007) of the Cucaracha Formation indicate potential habitats ranging from relative dense forests, to forest-woodland mosaics, to potentially more open woodlands. Using modern tayassuines as ecological analogs, “*Cynorca*” *occidentale* likely had the potential to exploit a wide range of coastal habitats and feed on a diversity of plants (and possibly small animals) during the middle Miocene in Panama, as it also did elsewhere in similar habitats in the southeastern and Atlantic coastal plain regions of North America.

SUMMARY AND CONCLUSIONS

Because of mostly fragmentary exposures in otherwise vegetated tropical areas to recover fossils, knowledge of extinct mammalian biodiversity from Central America is poor relative to other areas in the ancient New World tropics. The newly discovered specimens of the tayassuinae peccary “*Cynorca*” *occidentale* (and tayassuid specimens, indeterminate) advances our understanding of the extinct biodiversity of this region and demonstrates additional biogeographic and biochronological ties to corresponding faunas in North America. Curiously, the Centenario Fauna consists of a unique mixture of mammals representing three successive land mammal ages (Arikarean, Hemingfordian, and Barstovian) as these are defined in North America (Tedford et al., 2004). This paradoxical association, rarely found in North America, possibly represents the unique characteristics of land mammals located at the extremes of their known geographic ranges. Resolution of this temporal paradox will likely come if we are able to obtain independent age determinations from the stratigraphic sequence from which the Centenario Fauna was collected.

The Neogene exposures that crop out along the southern reaches of the Panama Canal have provided a unique window into our understanding of the vertebrate paleontology of Central America. Renewed excavations resulting from the construction of the Centenario Bridge and the expansion of the Panama Canal elsewhere along the Gaillard Cut, have resulted in a once-in-a-century opportunity to advance our understanding of the extinct biodiversity of this region. Along with these ongoing excavations over the next decade, there undoubtedly will be additional, interesting paleontological discoveries along the Panama Canal.

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