Journal of Vertebrate Paleontology
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ujvp20

New floridatragulines (Mammalia, Camelidae) from the early Miocene Las Cascadas Formation, Panama

Aldo F. Rincon [a] , Jonathan I. Bloch [a] , Catalina Suarez [b] , Bruce J. MacFadden [a] & Carlos A. Jaramillo [b]

[a] Florida Museum of Natural History, University of Florida, Gainesville, Florida, 32611, U.S.A.
[b] Smithsonian Tropical Research Institute, Box 0843-03092 No. 8232, Balbo, Ancon, Panama

To cite this article: Aldo F. Rincon, Jonathan I. Bloch, Catalina Suarez, Bruce J. MacFadden & Carlos A. Jaramillo (2012): New floridatragulines (Mammalia, Camelidae) from the early Miocene Las Cascadas Formation, Panama, Journal of Vertebrate Paleontology, 32:2, 456-475

To link to this article: http://dx.doi.org/10.1080/02724634.2012.635736

Journal of Vertebrate Paleontology 32(2):456–475, March 2012

ARTICLE

NEW FLORIDATRAGULINES (MAMMALIA, CAMELIDAE) FROM THE EARLY MIOCENE LAS CASCADAS FORMATION, PANAMA

ALDO F. RINCON,*,[1] JONATHAN I. BLOCH,[1] CATALINA SUAREZ,[2] BRUCE J. MACFADDEN,[1] and CARLOS A. JARAMILLO[2]
[1]Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, U.S.A., arincon@ufl.edu; jbloch@flmnh.ufl.edu; bmacfadd@flmnh.ufl.edu;
[2]Smithsonian Tropical Research Institute, Box 0843-03092 No. 8232, Balboa-Ancon, Panama, suarezs@si.edu; jaramilloc@si.edu

ABSTRACT—Early Miocene floridatraguline camels are characterized by having an elongate snout, shallow and narrow symphysial area, and relatively primitive dentitions. Their fossil record is restricted to subtropical assemblages including the Hemingfordian Thomas Farm Local Fauna (L. F.) in Florida, the Zoyotal L. F. in Mexico, and the Arikareean Castolon L. F. in Texas. Here we describe the first floridatraguline camels from the early Miocene Las Cascadas Formation, Panama Canal area, Central America. We describe two new species that are similar to *Aguascalientia wilsoni* from the Zoyotal L. F. in having (1) a primitive lower dental formula, (2) brachydont teeth, (3) an unusually elongate jaw with caniniform c1 and p1 that are well separated by a diastema, (4) a long and narrow mandibular symphysis, (5) lower molars with small intercolumnar pillars, (6) an m3 hypoconulid divided by lingual and labial selenes, and (7) no diastema between p2 and p3. *Aguascalientia panamaensis*, sp. nov., and *Aguascalientia minuta*, sp. nov., are represented by partial lower dentitions and isolated upper molars. Both new species are distinct from *A. wilsoni* in having (1) p1 and c1 similar in size, (2) less inflected paraconids on lower premolars, and (3) less reduced premolars. Interpreted primitive characters are similar to a small, unnamed camel from the earliest Miocene Buda L. F. of Florida (middle late Arikareean NALMA). The Las Cascadas fossil assemblage probably constitutes a distinctive Arikareean (Ar3–Ar4) faunal province characterized by the arrival of northern immigrants into a small continental basin connected with North American continental terrains.

INTRODUCTION

Since the construction of the Panama Canal at the beginning of the 20th century, and with recent ongoing expansion, mammal fossils have been collected that document a diversity of taxa with North American affinities that inhabited tropical areas during the early-middle Miocene at the southern-most extremes of their geographic ranges (Woodring, 1957, 1982; Whitmore and Stewart, 1965; MacFadden and Higgins, 2004; MacFadden, 2006, 2009; MacFadden et al., 2010; Uhen et al., 2010). The unique geographic position (Fig. 1A) of these faunas represents an opportunity to understand early Miocene terrestrial mammalian paleobiogeography prior to complete uplift of the Isthmus of Panama in the late Neogene (Coates and Obando, 1996). Outcrops of fossiliferous sediments representing a variety of geological settings, from shallow marine to continental (MacFadden, 2006; Kirby et al., 2008; MacFadden et al., 2010), are exposed along the southern part of the Panama Canal. Since 2004, crews from the Smithsonian Tropical Research Institute (STRI) and the Florida Museum of Natural history (FLMNH), in collaboration with the Panama Canal Authority (ACP), have been collecting new geological and paleontological data to better understand the origin and evolution of the Panamanian Isthmus. Large changes in vegetation have been well documented at the Oligocene–Miocene transition in the Central Great Plains, but their influence on tropical communities, mainly terrestrial mammalian herbivores, are still largely unknown (Pagani, 1999; Janis, 2000; Strömberg, 2002; Tipple and Pagani, 2010; Urban et al., 2010).

The Gaillard Cut stratigraphic sequence (Fig. 1B) encompasses a mosaic of environments including mangrove forest, forests, shallow marine, and transitional environments (Woodring, 1982; Retallack and Kirby, 2007). Recent collecting efforts have yielded new vertebrates from the transitional Culebra and continental Cucaracha Formations (MacFadden, 2006, 2009; Kirby et al., 2008; MacFadden et al., 2010; Uhen et al., 2010), as well as the marine Gatun Formation (Pimiento et al., 2010; Uhen et al., 2010). Based on previously collected (Whitmore and Stewart, 1965) and new fossil collections, MacFadden (2006, 2009) reported the presence of carnivores, artiodactyls, and perissodactyls from the Cucaracha Formation. Following Tedford et al. (1970), these fossil assemblages (also see Kirby et al., 2008), including those from the upper part of the Culebra Formation, were formally described as the Centenario Fauna (MacFadden et al., 2010). Although all of the mammals are known from the Miocene of North America, the Centenario Fauna does not obviously fit within the biochronological context of a specific North American Land Mammal Age (MacFadden, 2006). This problem has been exacerbated by the poorly constrained chronostratigraphic framework of the sequence, leading to a diversity of paradoxical interpretations (MacFadden and Higgins, 2004; MacFadden, 2006; MacFadden et al., 2010). Recent fieldwork in the underlying early Miocene Las Cascadas Formation (Woodring et al., 1984; Kirby et al., 2008; MacFadden et al., 2010) has yielded many new mammals that fill an important gap in a discontinuous tropical fossil record. The Las Cascadas fossil assemblage underlies the early Miocene Culebra Formation (Fig. 1B) and represents the oldest fossil vertebrate fauna found in southern Central America. The Las Cascadas Formation is composed of the oldest terrestrial deposits of central Panama, and probably registers the initial uplift of the Panamanian volcanic arc that was previously submerged (Fig. 1B). Mammals from the Las Cascadas Formation include the first immigrants from higher-latitude North American continental terrains that reached marginal tropical areas in the early Miocene. Because

---

*Corresponding author.

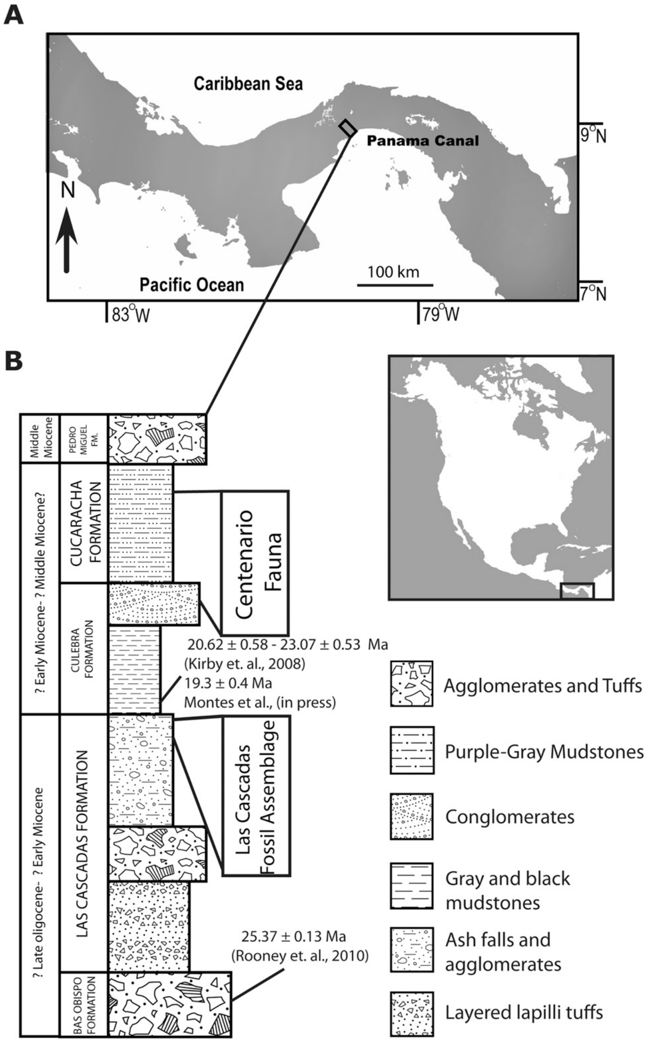

FIGURE 1. Location and stratigraphic position of camelid fossils from the Gaillard Cut, Panama Canal area. **A**, Map of North and Central America showing the location of the Panama Canal area and the Gaillard Cut; **B**, Stratigraphic section of the Gaillard Cut area showing the stratigraphic position of the Las Cascadas fossil assemblage and the Centenario Fauna. Modified from Kirby et al. (2008), MacFadden et al. (2010), and Montes et al. (2012).

fossil camels are extremely rare in the overlying Centenario Fauna (MacFadden et al., 2010), with known specimens still undescribed, it is somewhat surprising that the most common fossil remains collected to date in the fossiliferous intervals of the Las Cascadas Formation belong to new species of the bizarre and poorly understood floridatraguline camels (Rincon et al., 2010).

Among Camelidae (extant camels, llamas, and fossil relatives), the llama-like floridatragulines represent an aberrant group with unusually elongated snouts and unreduced dentitions. They have been reported exclusively from subtropical areas in northern Mexico, the Texas Gulf Coast and Florida (Fig. 2) during the early Miocene (Patton, 1969; Stevens et al., 1969; Stevens, 1977; Stevens and Stevens, 1989; Albright, 1998, 1999; Hulbert and Webb, 2001). The unique combination of Floridatragulinae morphological characters (White, 1940, 1942; Maglio, 1966; Stevens, 1977; Honey et al., 1998) has made it difficult to assess phylogenetic relationships. It has been related to several families within Artiodactyla, including Hypertragulidae (White, 1940, 1947), Protoceratidae (White, 1942), and Camelidae (Maglio, 1966). Although floridatragulines are now considered to be closely related to higher camels (Prothero and Emry, 1996), the limited fossil record for the group has led to ambiguity regarding their relationships to other North American camels (Prothero and Emry, 1996; Honey et al., 1998). Floridatraguline and nothokematine camels ("Nothokematinae" Honey et al., 1998) co-occur at least two localities (Albright, 1998, 1999). Although similar, nothokematines are distinctly different from floridatragulines in having more lingually inflected paraconids on p3–p4, a less developed overlap between the entoconulid and the hypoconulid of the m3 talonid, and lacking a caniniform p1 (Maglio, 1966; Patton, 1969; Frailey, 1978; Honey et al., 1998).

The first known species belonging to Floridatragulinae was referred to *Floridatragulus dolichanthereus* White, 1942, from the Hemingfordian Thomas Farm fossil site in Florida (Fig. 2). Because the morphology of *F. dolichanthereus* includes a strange mixture of primitive and derived characteristics, it was tentatively placed in the extinct artiodactyl family Hypertragulidae. Subsequent specimens recovered from Thomas Farm were referred to a new taxon *Hypermekops olseni* White, 1942, and also placed within the Hypertragulidae. Maglio (1966) synonymized *H. olseni* and *F. dolichanthereus* based on unpublished studies done by Bryan Patterson and further proposed a new camelid subfamily, Floridatragulinae Maglio, 1966, to include these taxa. Additional floridatraguline camels were described from the Hemingfordian Garvin Gully Local Fauna (L. F.) from Texas (Fig. 2), where three new specific designations were included in *Floridatragulus* (*F. nanus* Patton, 1969; *F. texanus* Patton, 1969; and *F. hesperus* Patton, 1969), suggesting that floridatraguline camels might represent an allocthonous element from the Great Plains Fauna (Patton, 1969). Further descriptions of Floridatragulinae taxa include *Aguascalientia* Stevens, 1977, from early middle Miocene Zoyotal L. F. in Mexico (*Miotylopus wilsoni* Dalquest and Mooser, 1974 = *Aguascalientia wilsoni* Stevens, 1977) and the early Miocene Arikareean Castolon L. F. in Texas (*Aguascalientia* sp., Stevens, 1977). To date, Floridatragulinae includes *Poebrotherium franki* Wilson, 1974, a primitive, small Chadronian camel with a slightly elongated rostrum from the Big Bend Area, Texas; the Arikareean and Hemingfordian *Aguascalientia* Stevens, 1977, from Texas and Mexico, respectively (Stevens and Dawson, 1969; Stevens, 1977; Stevens and Stevens, 1989); and *Floridatragulus* White, 1940 (White, 1940; Patton, 1969; Honey et al., 1998).

The distribution of Floridatragulinae during the early Miocene is restricted to subtropical areas in North America without any reliable northern counterparts (Wilson, 1942; Patton, 1969; Stevens et al., 1977; Wilson, 1984; Prothero and Emry, 1996; Albright, 1998, 1999), suggesting that they could have originated in the New World Tropics, probably descended from an oromerycid, as was suggested by Stevens (1977).

The present study focuses on two new camels from the Panama Canal area, offers a unique view of floridatraguline history in the tropics, and allows us to evaluate their relationship with other early Miocene faunas from the Gulf Coast, Florida, Texas, and Mexico (Simpson, 1930; White, 1940, 1942, 1947; Maglio, 1966; Patton, 1969; Dalquest and Mooser, 1974; Wilson, 1974, 1981; Stevens, 1977; Frailey, 1979). The new camels provide an opportunity to test previous biogeographic hypotheses (Stevens, 1977; Albright, 1998) by comparing Floridatragulinae fossils with other subtropical camelids such as the undefined small camelids from the Buda L. F. (Frailey, 1979); the small *Gentilicamelus* from the Brooksville 2 L. F. (Hayes, 2000) and additional poebrotherines from the Brule Formation in Nebraska.

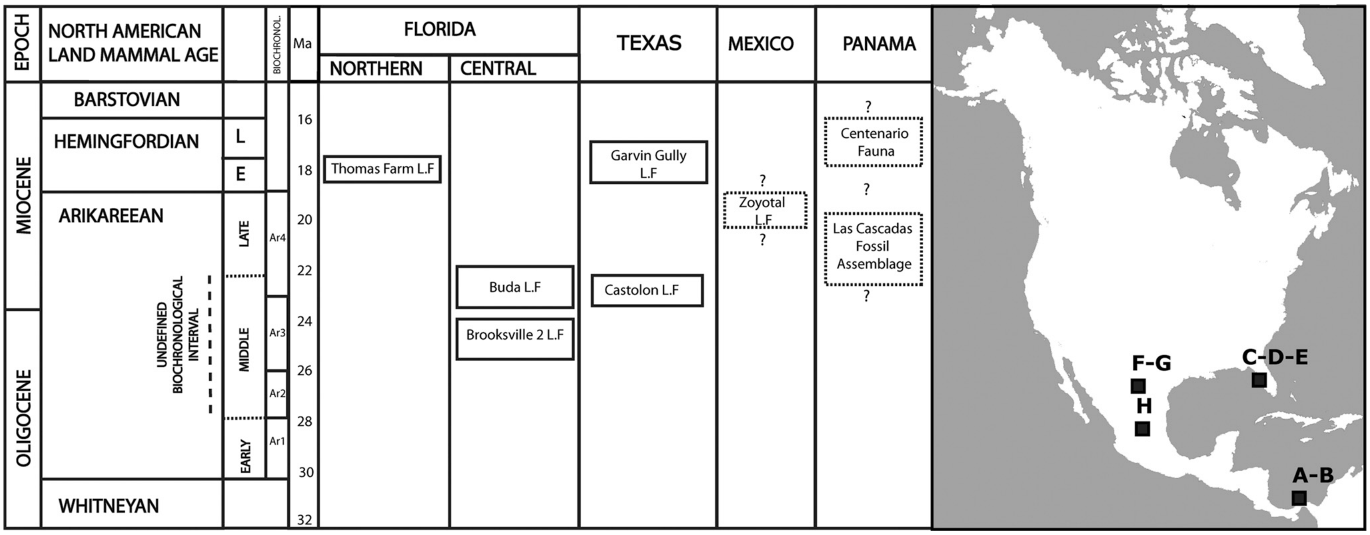

FIGURE 2. Location and biochronology of the camel-bearing fossil faunas discussed in this study. **A**, Las Cascadas fossil assemblage, Panama; **B**, Centenario Fauna, Panama (MacFadden et. al., 2010); **C**, Thomas Farm Local Fauna (L. F.), Gilchrist County, Florida; **D**, Brooksville 2 L. F, Hernando County, Florida (Hayes, 2000); **E**, Buda L. F., Alachua County, Florida (Frailey, 1979); **F**, Castolon L. F., Texas (Stevens, 1977); **G**, Garvin Gully L. F., Texas (Patton, 1969); **H**, Zoyotal L. F., Aguascalientes, Mexico (Stevens, 1977). Camelids from late Oligocene Brooksville 2 Local Fauna are of uncertain affinities, and no definitive floridatraguline camels have been recovered from localities below the Oligocene-Miocene boundary (~23 Ma). Chronostratigraphy and biochronology modified from Albright et al. (2008). **Abbreviations**: **Ar**, Arikareean Faunal Zone; **E**, early; **L**, late; **L. F.**, Local Fauna.

CONVENTIONS AND ABBREVIATIONS

The biochronology follows the late Oligocene–early Miocene biozonation developed in the Great Plains (Tedford et al., 1987, 2004; MacFadden and Hunt, 1998) and the subsequent recalibration proposed by Albright et al. (2008) for the Arikareean North America Land Mammal Age (NALMA). For the most part, dental terminology follows Gazin (1955). In accordance with this work, 'metaconule' will be used in place of 'posterior lingual cusp' (Fig. 3). The character is preferentially called metaconule for the Camelidae, because in ancestral artiodactyls (e.g., oreodonts) the hypocone disappears and its position is occupied by a large metaconule (Gazin, 1955; Miller and Wood, 1963; Patton, 1967). Additionally, we follow the terminology proposed by Smith and Dodson (2003) for the incisors. We follow Loring and Wood (1969) for the cusp and crest terminology of the deciduous dentition, which fundamentally differs from that of the permanent dentition in the retention of a homologous cusp equivalent to the hypoconule in the upper deciduous premolars.

Institutional Abbreviations—MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **TMM**, Texas Memorial Museum, Austin, Texas, U.S.A.; **UF**, Vertebrate Paleontology Collections, Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.

GEOLOGICAL SETTING

The stratigraphic sequence cropping out along the Gaillard Cut encompasses Eocene to middle-late Miocene volcanic, volcanosedimentary, and clastic units (Woodring and Thompson, 1949; Woodring et al., 1982; Kirby et al., 2008; MacFadden et al., 2010; Montes et al., 2012). This stratigraphic interval (Fig. 1B) represents one of the most complete and best-exposed Oligocene and Miocene volcanic sequences within the Central American arc (Rooney et al., 2010). The northern part of the Gaillard Cut is composed mainly of Eocene–early Miocene volcanic and volcaniclastic formations (Bas Obispo and Las Cascadas Formations), whereas the southern part is mainly characterized by shallow marine and volcaniclastic continental sequences of the Culebra and Cucaracha Formations (Kirby et. al, 2008). The Las Cascadas Formation is composed of andesitic flows and agglomeratic tuffs with cobbles of andesite and basalt set in a fine-grained

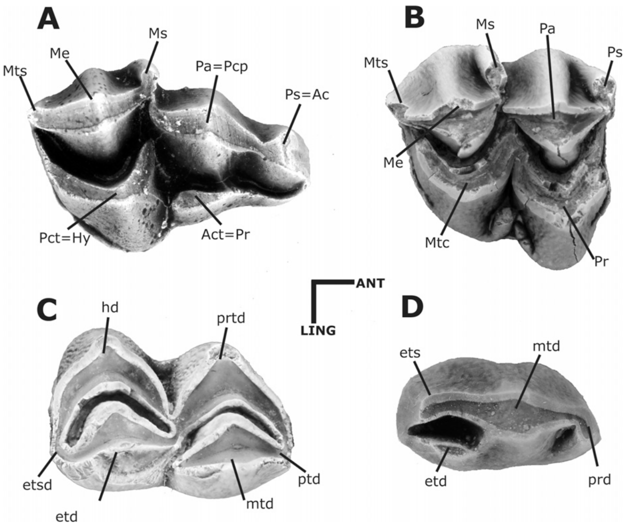

FIGURE 3. Diagram showing most of the dental cusp nomenclature applied to permanent and milk dentitions of camels in this study. **A**, right dP3; **B**, right M3; **C**, left m2; **D**, left p4. **Abbreviations**: **Upper dentition**: **Hy**, hypocone (**Pct**, posterior crescent); **Me**, metacone; **Ms**, mesostyle; **Mtc**, metaconule; **Mts**, metastyle; **Pa**, paracone (**Pcp**, principal cusp); **Pr**, protocone (**Act**, anterior crescent); **Ps**, Parastyle (**Ac**, anterior crest); **Lower dentition**: **etd**, entoconid; **etsd**, entostylid; **hd**, hypoconid; **mtd**, metaconid; **prd**: paraconid; **prtd**, protoconid; **ptd**, parastylid; **ANT**, anterior; **LING**, lingual. Modified from Loring and Wood (1969) and Gazin (1955).

tuffaceous matrix (Montes et al., 2012), which constitutes the main lithology associated with the vertebrate fossils. The structural complexity of the area, as well as the limited and ephemeral outcrops along the canal, restrict the exposures of the Las Cascadas fossiliferous interval to the northern part of the Gaillard Cut, where volcaniclastic sequences are more common and paleosols are well developed. The lower part of the Las Cascadas Formation is characterized by massive accumulations of volcanic rocks (mainly agglomerated breccias) and fluvial sediments. Conversely, the upper part of the Las Cascadas Formation is characterized by massive accumulations of volcanic blocks ranging from welded tuffaceus agglomerates to pyroclastic fall deposits and discrete intervals of fluvial sediments (Woodring, 1982; Kirby et al., 2008). The Las Cascadas Formation is overlain by the Culebra Formation and separated from it by a slightly angular unconformity (Montes et al., 2012). The overlaying volcaniclastic sequence is composed of the marine transgressive system of the Culebra Formation and the prograding sequence of the Cucaracha Formation (Kirby et al., 2008). Despite the abundance of volcanic material, efforts to date these rocks have been unsuccessful and the geochronology available for the section is restricted to Strontium (Sr^{87}/Sr^{86}) chemostratigraphy (Kirby et al., 2008) on calcareous biogenic shells and corals (Fig. 1B). Therefore, the upper Las Cascadas fossiliferous sequence represents an interval older than the lower part of the Culebra Formation, for which several dates have been published between 20.62 ± 0.58 and 23.07 ± 0.53 Ma (Kirby et al., 2008) and 19.3 ± 0.4 Ma (Montes et al., 2012). The lower boundary of the Las Cascadas Formation could be constrained by andesitic water-saturated arc lavas of the underlying Bas Obispo Formation dated using Ar^{40}/Ar^{39} age as 25.37 ± 0.13 Ma (Rooney et al., 2010; Farris et al., 2011). Therefore, the duration of the Las Cascadas Formation might span the late Oligocene to early Miocene (<25 Ma to >19.3 ± 0.4 Ma), likely representing the middle-to-late Arikareean NALMA sensu MacFadden and Hunt (1998) and Albright et al. (2008).

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order ARTIODACTYLA Owen, 1848
Suborder TYLOPODA Illiger, 1811
Family CAMELIDAE Gray, 1821
Subfamily FLORIDATRAGULINAE Maglio, 1966
Genus *AGUASCALIENTIA* Stevens, 1977

= *Miotylopus* (in part), Dalquest and Mooser, 1974.

Type Species—*Aguascalientia wilsoni* (Dalquest and Mooser, 1974) (= *Miotylopus wilsoni* Dalquest and Mooser, 1974).

Included Species—*Aguascalientia panamaensis*, sp. nov., and *Aguascalientia minuta*, sp. nov.

Distribution—Early Miocene (Arikareean) Castolon L. F. from Texas (Stevens, 1977); early Miocene (Hemingfordian) Zoyotal L. F. from Aguascalientes, Mexico (Dalquest and Mooser, 1974); and early Miocene (middle-to-late Arikareean) Las Cascadas Formation, Panama Canal area, Panama.

Emended Diagnosis—Smallest known floridatraguline. Further differs from other known floridatragulines in lacking a diastema between p2 and p3, having a shorter diastema between p1 and p2 that is similar or shorter than the combined length of m1–m2, slightly to strongly inflected bulbous paraconids on lower premolars, and having basal conical intercolumnar pillars on m1, m2, and variably developed on m3. Differs from *Floridatragulus nanus* Patton, 1969, in having m3 hypoconulid divided in two unequal selenes with additional cuspules variably present, and lacking a basal posterior cingulid. Differs from *Floridatragulus dolichanthereus* (= *Floridatragulus barbouri* White, 1947) in having less lingually inflected paraconids on lower premolars. Differs from *Floridatragulus texanus* (= *Floridatragulus hesperus* Patton, 1969) in having less reduced lower premolars, more prominent, bulbous, and lingually inflected paraconids on lower premolars, lacking labial cingular segments between protoconid and hypoconid on molars, and having a less developed posterolingual ridge on p3.

Discussion—When originally diagnosed, *Miotylopus wilsoni* was described as distinct in having very short premolars, lacking a first premolar and having strongly developed styles and ribs on the upper molars, but otherwise was similar to *Miotylopus brachygnathus* Schlaikjer, 1935, in being small and having brachydont teeth (Dalquest and Mooser, 1974). Stevens (1977) questioned the generic attribution of *M. wilsoni* based on the presence of a small and short crowned p1 (currently reduced to a badly preserved alveolus), bulbous and foreshortened premolars, and by transferring the deciduous dentition to a different larger camel. Unfortunately, neither Stevens (1977) nor the authors of the present study could locate the upper molars described by Dalquest and Mooser (1974) or the material referred to *Aguascalientia* sp. from the Delaho Formation (Stevens, 1977) in the *Aguascalientia* collection. After reviewing the fossil specimens and confirming the interpretations made by Stevens (1977) of *A. wilsoni*, the diagnosis of both the genus *Aguascalientia* (above) and the species *A. wilsoni* (below) is updated in order to take into account the morphology of the new Panamanian species described in this paper.

AGUASCALIENTIA WILSONI
(Dalquest and Mooser, 1974)

Holotype—TMM-41536-26, right and left dentary with left c1, left p3–m3, and right p4–m3 from the Zoyotal L. F. (Hemingfordian), Aguascalientes, Mexico (Dalquest and Mooser, 1974; Stevens, 1977).

Referred Specimens—TMM-41536-14, right dentary fragment with p2–m1; TMM-41536-30, right m2. *Aguascalientia* sp. from the Castolon L. F., Texas (Fig. 2); TMM-40693-25, left mandible fragment with partial m2 and complete m3.

Age and Distribution—Early Miocene (Hemingfordian) Zoyotal L. F. (Fig. 2), collected in a commercial rock quarry near the city of Aguascalientes, Mexico (Dalquest and Mooser, 1974; Stevens, 1977; Tedford et al., 2004); early Miocene (Arikareean) Castolon L. F. (Fig. 2), Big Bend Texas, U.S.A. (Stevens, 1977; Tedford et al., 2004).

Emended Diagnosis—Differs from all other species of *Aguascalientia* in having a smaller p1 than c1, prominent, bulbous, and strongly lingually inflected paraconids on lower premolars, shorter lower premolars relative to the molars, p2 distinctly smaller than p3, and less developed to absent styles and ribs on the lower molars. Differs from *A. panamaensis*, sp. nov., in having a shallower invagination on the talonid of m3, having shallower fossettids on lower molars, and lacking a small fossettid between the metaconid and hypoconid on p3. Differs from *A. minuta*, sp. nov., in being greater in size (similar to *A. panamaensis*, sp. nov.), having a shallower invagination on the talonid of m3, and lacking an enamel fold on the anterior fossettid of m2.

AGUASCALIENTIA PANAMAENSIS, sp. nov.
(Figs. 4–8, Table 1, Appendix 1)

Holotype—UF 236939, partial dentary with right c1-p3, m1-m3, left c1, and mandibular symphysis.

Paratypes—UF 254129, partial dentary with right c1, left i1-c1, left p2-p4 and mandibular symphysis; UF 254124, partial dentaries with right p3, right m1 (broken), left p2, left p4, left m2-m3, and mandibular symphysis.

Etymology—*Panama*–: named for the Republic of Panama, the country in which the fossils were recovered and –*ensis*, latin suffix for 'pertaining to,' or 'originating in.'

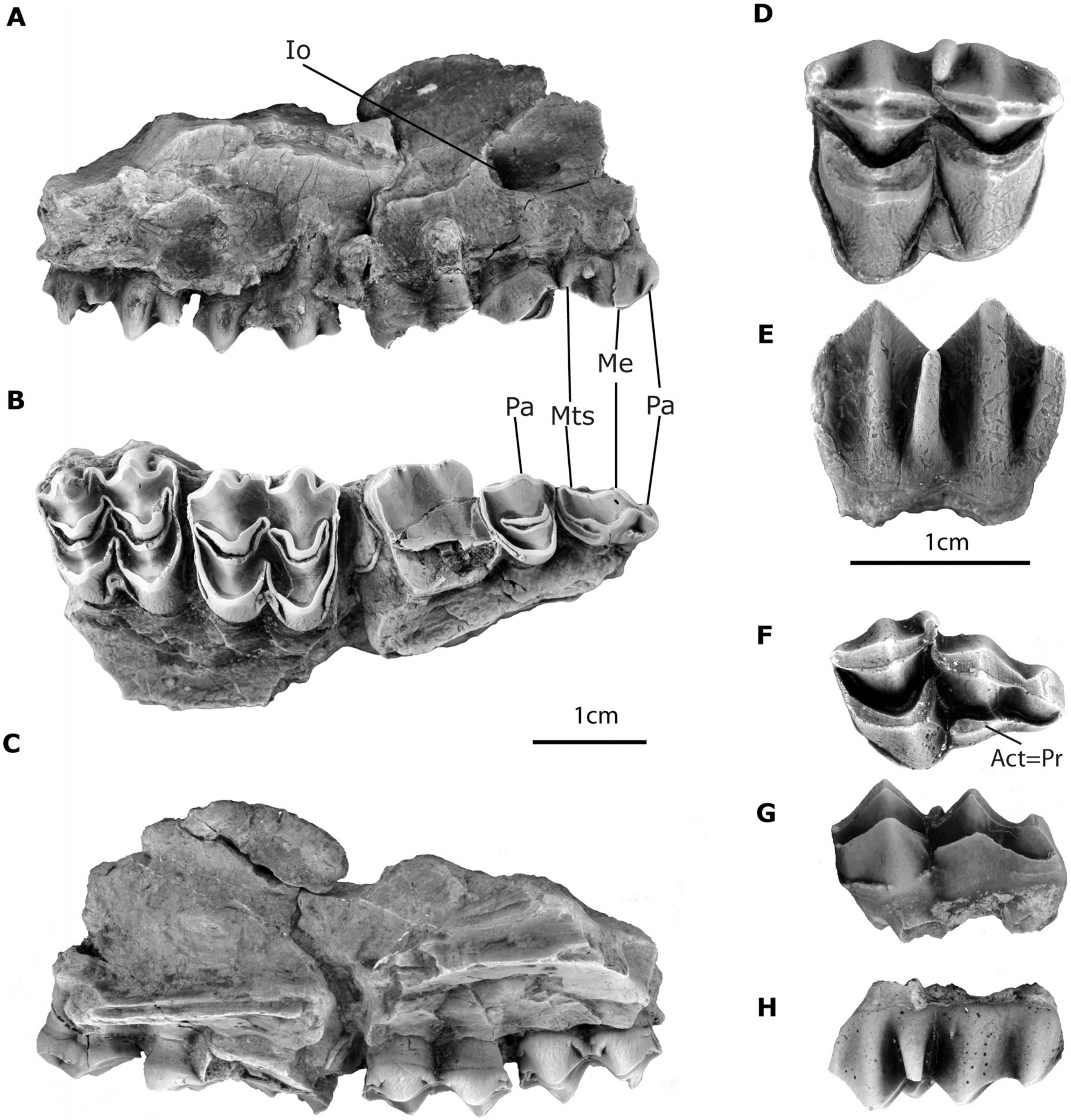

FIGURE 4. Upper dentition of *Aguascalientia panamaensis*. **A**, UF 254125, right maxilla with P3-M3, labial view; **B**, UF 254125, occlusal view; **C**, UF 254125, lingual view; **D**, UF 254115, left M3, occlusal view; **E**, UF 254115, labial view**;** **F**, UF 244156, right dP3, occlusal view; **G**, lingual view; **H**, labial view. **Abbreviations**: **Io**: Infraorbital foramen; **Me**, Metacone; **Mts**, metastyle; **Pa**, Paracone; **Pr**, Protocone (**Act**: Anterior crescent).

Referred Material—UF 254125, right maxilla with P3–M3; UF 244156, right dP3; UF 259878, right dP3; UF 254117, right M1; UF 244313, right M2 (broken); UF 246825, right M2 (broken); UF 246808, right M2 (broken); UF 257197, right M3; UF 244204, right M3; UF 254116, left M3; UF 254115, partial left M3; UF 245602, left M3; UF 259884, left c1; UF 244316, left p3; UF 254118, left p4; UF 254122, left m1; UF 254121, left m2; UF 246857, right M3; UF 246802, right and left dentary with left i3, p1, right c1–m2, and mandibular symphysis; UF 244288, left p3; UF 254127, left p3; UF 246803, left p3; UF 254120, left p4; UF 246836, left m2, m3; UF 254123, left m3; UF 254114, left m3 (broken); UF 257198, left m3; UF 254128, right distal humerus; UF 244202, left distal humerus; UF 244208, left astragalus; and UF 244163, right astragalus.

Locality and Horizon—Lirio Norte, Panama Canal area, Panama, Central America. Fossils were collected in the upper part of the Las Cascadas Formation (Fig. 1B), latest Oligocene to earliest Miocene, likely equivalent to the middle-to-late Arikareean NALMA (Fig. 2).

Diagnosis—Small floridatraguline that differs from all species of *Aguascalientia* in having a small fossettid between metaconid and hypoconid on p3; p1–c1 diastema longer than m2 length; and well-developed styles on lower and upper molars. Differs from *A. wilsoni* in having deeper fossettids on molars, less reduced premolars, and less lingualy inflected paraconids on lower premolars; having a relatively large caniniform p1; differs from *A. minuta*, sp. nov., in having a greater size, absence of enamel fold

TABLE 1. Summary of dental measurements (in mm) of *A. panamaensis*, sp. nov., from the Las Cascadas Formation.

Tooth position	N	Range	Mean	S	V
Lower dentition					
Ix(MDL)	6	4.6–5.53	5.16	0.339	6.57
Ix (APL)		2.84–3.14	2.97	0.122	4.11
c1 (APL)	6	5.16–5.68	5.324	0.205	3.86
c1 (TW)		3.68–3.90	3.81	0.083	2.18
p1 (APL)	3	5.86–7.04	6.56	0.621	9.48
p1 (TW)		3.52–4.06	3.85	0.289	7.51
p2 (APL)	4	9.88–11.57	10.49	0.741	7.06
p2 (TW)		4.42–4.61	4.50	0.097	2.17
p3 (APL)	9	10.16–11.55	10.58	0.552	5.22
p3 (TW)		4.31–4.53	4.42	0.103	2.34
p4 (APL)	5	9.06–10.11	9.61	0.352	3.66
p4 (TW)		5.05–5.62	5.34	0.252	4.72
m1 (APL)	3	9.80–10.90	10.16	0.501	4.93
m1 (TW)		6.14–7.28	6.597	0.559	8.48
m2 (APL)	4	13.22–15.16	13.85	0.887	6.40
m2 (TW)		8.47–9.82	9.01	0.585	6.49
m3 (APL)	5	17.96–19.83	18.58	0.850	4.57
m3 (TW)		9.32–9.98	9.55	0.316	3.30
Upper dentition					
P3 (APL)	1	10.43	10.43	–	–
P3 (TW)		5.65	5.65	–	–
P4 (APL)	1	7.78	7.78	–	–
P4 (TW)		8.37	8.37	–	–
M1 (APL)	2	10.08–12.58	11.3	1.810	16.01
M1 (TW)		11.18–11.96	11.57	0.551	4.76
M2 (APL)	2	13.28–14.26	13.77	0.692	5.03
M2 (TW)		13.75–15.11	14.43	0.962	6.66
M3 (APL)	6	13.5–14.71	14.13	0.463	3.26
M3 (TW)		14.67–15.74	14.87	0.598	4.02
RdP3 (APL)	2	11.28–11.43	11.35	0.106	0.93
RdP3 (TW)		7.16–7.44	7.30	0.198	2.71

Abbreviations: **MDL**, mesiodistal length; **APL**, anterior-posterior length; **TW**, transverse width; **S**, standard deviation; **V**, index of variance.

on the anterior wall of the posterior fossettid of m2, and absence of posterolingual crest on p3.

Description

Upper Dentition—In UF 254125 (Fig. 4A–C), the crowns P3 and P4 are preserved. P3 is elongate, trenchant, lacks external ribs, and has a strong metacone with an interrupted internal cingulum with small cuspules. The anterior crescent is weak, developed lingually over the anterior root, and bears small cuspules. The posterolingual crescent is also weakly developed and extends lingually from the base of the metacone toward the posterior margin, reaching the lingual part of the base of the metastyle. P4 is sub-molariform with a well-developed parastyle and metastyle. The metastyle is more prominent and recurved than the parastyle. All upper molars have strong stylar cusps on the anterior and posterior crests. The anterior half of each molar overlaps its posterior half buccally, resulting in a very prominent mesostyle and a deep recess anterior to it at the juncture of the paracone and metacone crests. A strong rib extends up each crest from the base of the crown to the tip of both the paracone and metacone (Fig. 4E). The shape of the crescents varies from an open V or U in the posterior molars (Fig. 4D), to a more closed V on M1. The apex of the accessory intercolumnar pillars (often double-limbed) usually coincides with the junction of the anterior and posterior crescents (Fig. 4D). Along the anterior and posterior margins of each molar is a faint and narrow cingulum that projects from just above the base of the crown and extends along the anterior or posterior basal part of each crescent. M1 and M2 are square whereas M3 has a posterior margin that is transversely reduced.

Deciduous Upper Dentition—Two isolated deciduous P3s (UF 244156 and UF 259878) are well preserved with a barely worn paracone, mesostyle, and well-developed hypocone (Fig. 4F–H). The crown of dP3 is brachydont and has similar proportions to that referred to *Gentilicamelus* (ACM 1846 in Loring and Wood, 1969:fig. 2D). The anterolingual margin has a discontinuous cingular segment dissected by a lingually expanded paracone, resulting in two anteriorly directed isolated valleys (Fig. 4F, G). A distinct mesostyle is well developed, increasing the molariform appearance of the posterior part of the tooth. The dP3 has well-developed labial ribs along the principal cusps and a strongly developed metastyle (Fig. 4H). A narrow, shallow cingular segment connects the posterior part of the hypocone with the distal part of the posterior crescent (Fig. 4G).

Mandible—Four well-preserved horizontal rami have been recovered (UF 236939, UF 254124, UF 254129, UF 246802). The lingual and labial surfaces are uniform below the tooth row and slightly concave below the diastemata (Figs. 5A, 6A). The lower dental formula is 3.1.4.3. The crown of p1 is separated by anterior and posterior diastemata from c1 and p2, respectively (Figs. 5A, B, 6A, B). The anterior-most diastema extends from the spatulate and procumbent i3 to the rather prominent ‘true’ canine (Fig. 6A, B). The i3–c1 diastema has an acute and sharp superior edge that is similar in length to that of the p3 crown (Fig. 6A, B). The length of the c1–p1 diastema varies between 75% and 100% that of the p2–p3 crowns, with the p1–p2 diastema usually longer. The superior edges of these diastemata are sharp and pinched below the edge forming a well-defined crest between the anterior teeth. The mandibular symphysis is completely fused and is long and shallow with no evidence of a suture (Figs. 5A, 6A, C). Posterior to the symphysis, the lingual and labial surfaces of the mandible become slightly concave, narrower, and deeper. A remarkable

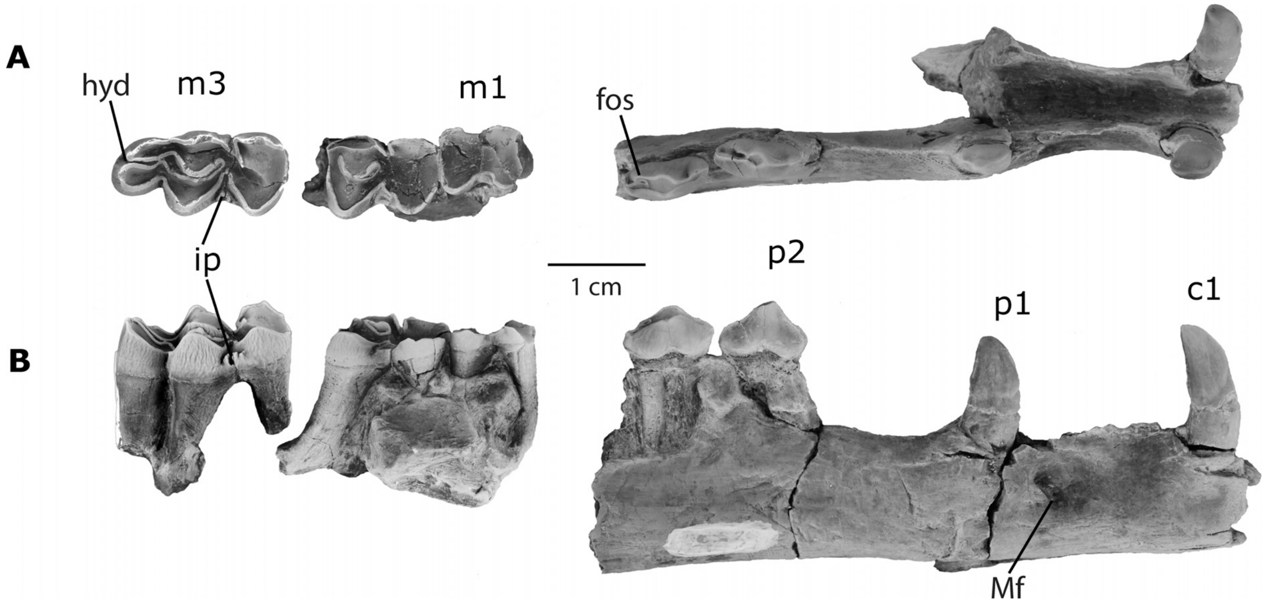

FIGURE 5. Lower dentition of *Aguascalientia panamaensis*, UF 236939 (holotype), partial dentary with right c1–p3, m1–m3, left c1, and mandibular symphysis. **A**, occlusal view; **B**, labial view. **Abbreviations**: **fos**, fossettid; **hyd**, hypoconulid; **ip**, intercolumnar pillar; **Mf**, mental foramen.

deepening of the mandible is evident beneath p2 and extends distally along the tooth row. The posterior edge of the symphysis projects below the inferior contour of the mandible at the level of the posterior edge of the mental foramen.

Lower Dentition—The complete dentition is not preserved in any of the specimens available for study; however, a complete dental formula is evident based on the referred associated material. UF 254129 provides the first evidence of the condition of the anterior lower dentition of *Aguascalientia* as well as the Floridatragulinae in general (Fig. 6A, B). The incisors are procumbent, spatulate, and progressively enlarged posteriorly. The lingual surface is concave, the labial surface is convex, with no crenulations or additional cusps. Although some wear is present on the occlusal surfaces of the incisors, the crowns are distally elongate with visible facets located along the anterior and posterior ends. Dentine is exposed on the occlusal wear surface as a fine band on the lingual and labial enamel (Fig. 7A–C). Lower canines are caniniform, similar in size to the first premolar, recurved, and transversely compressed (Figs. 5A, B, 6A, B). A small ridge on the basal antero-lingual part of the crown extends toward the apical antero-labial tip. A separate straight posterior ridge extends uniformly along the posterior edge of the crown (Fig. 7D). The p1 is transversely compressed, completely caniniform, single-rooted, and similar in size to c1 (Table 1). Similar to the canine, the anterior and posterior ridges are present but the anterior one is distinctly straight (Fig. 7E). The p2–p4 series (Figs. 6A–C, 8A, B) is characterized by elongate crowns. Although the p2 and p3 are similar in being double-rooted with an acute apex (metaconid) and trenchant edges, p2 is slightly longer, more transversely compressed, and has a less pronounced posterolingual crest than p3. The p3 also has a small fossettid between the metaconid and entoconid (Figs. 6A, C, 8A, B), absent on p2. The crown of p4 is wedge-shaped with a swollen posterior region. Apparently, most of the reduction in this tooth has occurred in the region of the protoconid, resulting in a shorter, high-crowned, and slightly bulbous tooth. The metaconid on p4 is high, the entoconid narrow, and the distal edge of the hypoconid slightly overlaps the metaconid. Two different crests connect the p4 metaconid with the entoconid and the hypoconid. Between these crests, a posteriorly opened lake is visible even in advanced wear stages (Fig. 6A, C). The posterior cusp of p4 is slightly narrower than the middle cusps. The lower molars are brachydont, with relatively deep anterior and posterior fossettids visible even in more advanced wear stages (Fig. 8C, D). The molars have discontinuous and overlapping crests with a distinctive metastylid and a metaconid crest well separated from the rest of the tooth, unless the tooth is highly worn. Intercolumnar tubercles are restricted to the basal part of the protoconid and hypoconid crests of m1 and m2 and are variably present on m3 (Figs. 5B, 8C, D). Parastylids are slightly developed along the m1 and m2 and barely discernible on the anterior crest of m3. Two ridges divide the hypoconulid of m3 (Figs. 5A, 8D). The lingual ridge is broader than the labial and in some specimens, with progressive wear, encloses a distinct invagination that can reach the distal basal segment of the crown.

Discussion and Comparisons—Fossils referred to *A. panamaensis* can be definitively attributed to the Floridatragulinae based on the following characteristics: (1) a complete lower dental formula, (2) brachydont teeth, (3) an unusually elongated jaw with 2 caniniform teeth (c1–p1) well-separated by a diastema, (4) a long and narrow mandibular symphysis, (5) reduced lower premolars, (6) small intercolumnar pillars present in the molars, and (7) a m3 hypoconulid divided by lingual and labial selenes. The horizontal ramus of the *A. panamaensis* mandible is slender and deep as in *A. wilsoni* Stevens, 1977, *F. dolichanthereus* White, 1942, and *F. texanus* Patton, 1969. The absence of a diastema between p2 and p3 in the lower series places the floridatragulines from the Las Cascadas Formation in the genus *Aguascalientia*. Moreover, the less inflected paraconids on the second and third premolars, presence of a fossettid posterior to the protoconid of the p3, and the presence of a first premolar that is completely caniniform and similar in size to the lower canine support the definition of a new species. These morphological characters are notably distinctive in the material referred to *A. wilsoni*, especially that of TMM-41536-14 and the holotype of *A. wilsoni*, where the paraconids of the second and third premolars are more bulbous and strongly inflected lingually (Stevens, 1977:fig. 16). Conversely, additional camelid fossils from the Buda Local Fauna

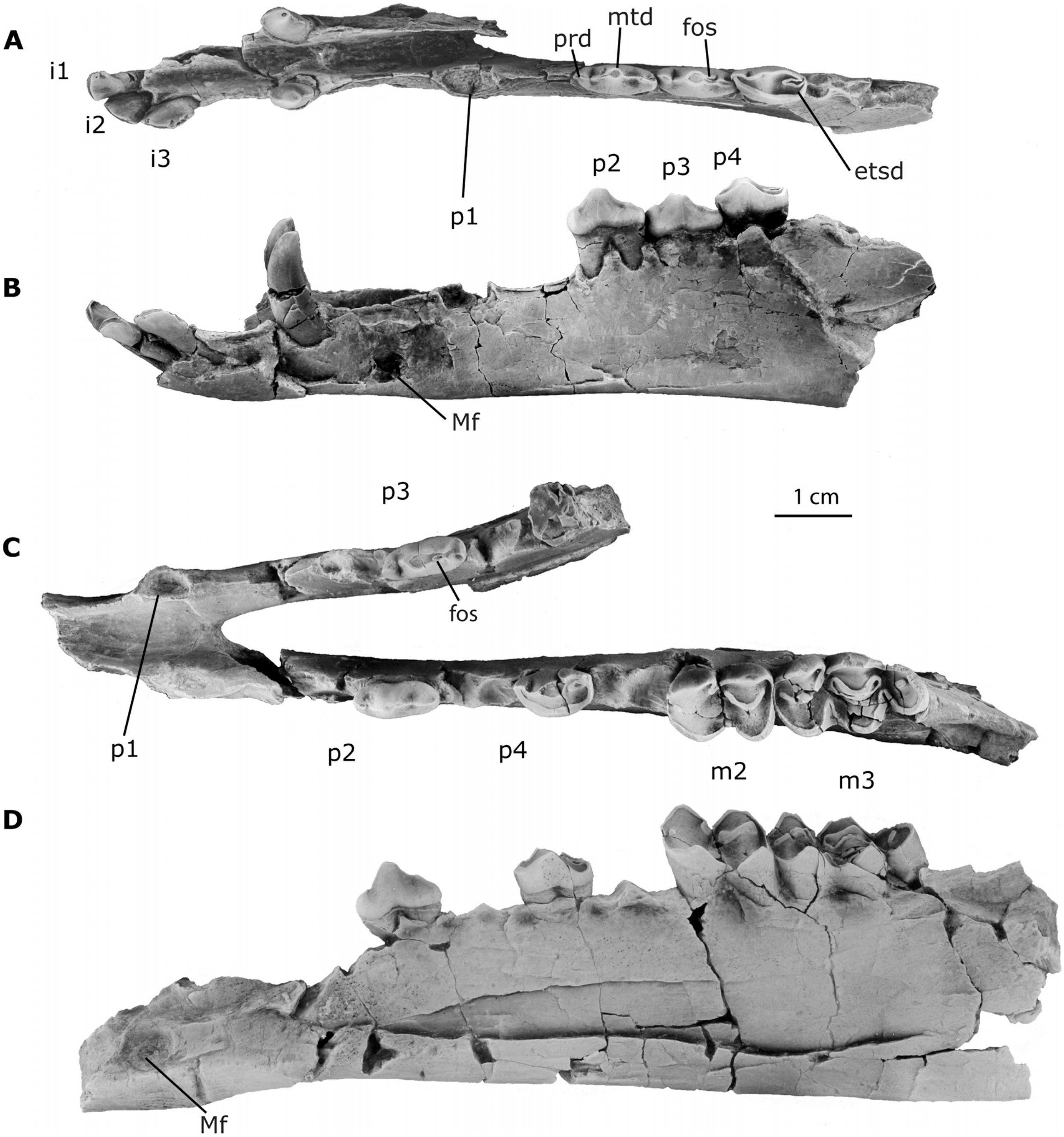

FIGURE 6. Lower dentition of *Aguascalientia panamaensis*. **A**, UF 254129 (paratype), partial dentary with right c1, left i1–p4, and mandibular symphysis, occlusal view; **B**, labial view; **C**, UF 254124 (paratype), right and left dentaries with right p3, right m1 (broken), left p2, p4, m2–m3, and mandibular symphysis, occlusal view; **D**, labial view. **Abbreviations**: **etsd**, entostylid; **fos**, fossettid; **Mf**, mental foramen; **mtd**, metaconid; **prd**, paraconid.

have more elongated, simple enamel patterns, and lack lingual stylids on p2–p3 (Frailey, 1979:153).

The morphology of the p4s of *A. panamaensis* is comparable to that of *A. wilsoni* (TMM-41536-26; Stevens, 1977:fig. 16), but differs from the latter in a less bulbous and less inflected paraconid. Additional comparisons were made with other Arikareean taxa such as the undefined genus from the Buda L. F. in Florida (Frailey, 1979:figs. 5, 8) where the paraconids are sharp and the premolar is more anteroposteriorly elongated. In addition, the morphology of the m3 hypoconulid of *A. panamaensis* varies from a deep invagination reaching the basal part of the tooth to shallower invaginations only evident in earlier wear stages. This latter feature could also be characteristic of protoceratids and other ruminants. In that case, the m3 of *A. panamaensis* could resemble that of *Prosynthetoceras* Frick, 1937, but is distinguishable on the basis of lacking the strong anterior cingulid and having an

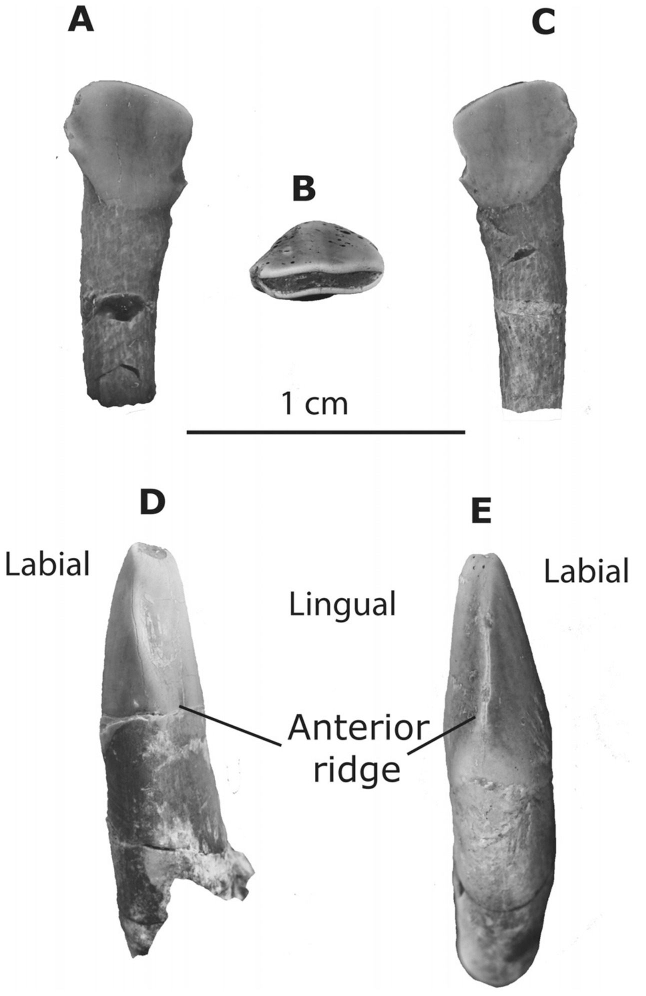

FIGURE 7. Detailed photographs of lower anterior teeth of *Aguascalientia panamaensis.* **A**, UF 254129, right i1, lingual view; **B**, occlusal view; **C**, labial view; **D**, UF 246802, right c1, anterior view; **E**, left p1, anterior view.

isolated paraconid during wear (Patton and Taylor, 1971). In addition, the small camels from the Buda L. F. possess an m3 that converges in some degree with that condition. The formation of a double enamel loop in the hypoconulid is accomplished by a slight posterior extension of the entoconid forming a deep cleft in the posterior part of the molar (Frailey, 1979:fig. 8).

The typical presence of additional cuspules forming the occlusal and lingual surfaces of the hypoconulid is quite variable and includes morphologies that are also integrated into the description of *Floridatragulus nanus* Patton, 1969 (TMM-40067-194, holotype), *F. dolichanthereus* White, 1940 (MCZ 3635, holotype), and partially *F. texanus* Patton, 1969 (TMM-31190-28, holotype). The intercolumnar pillars on the lower molars of *A. panamaensis* are characterized by basal and conical shapes clearly differing from the more robust and apically situated pillars on the molars of *F. nanus*, *F dolichanthereus*, and *F. texanus*. The pillars of *A. panamaensis* remarkably resemble the conical and basally restricted morphology present in the material from the Buda L. F. (Frailey, 1979:fig. 8).

The morphology of the upper deciduous dentition of the fossils referred to *A. panamaensis* suggests a more primitive shearing function for the anterior portion of the dP3 and a molar-like pattern characterizing the posterior portion (Loring and Wood, 1969). The species of *Aguascalientia* described here from the Las Cascadas Formation shows no evidence of the anterior portion of the deciduous upper third premolar becoming molariform. It is consistently composed of an anterior isolated crest with restricted occlusion inferred from little to no wear (Fig. 4F).

The morphology of the anterior portion of the dP3 associated with *A. panamaensis* (narrow and elongated primary cusp with a faintly visible development of the protocone) is comparable with that of Camelidae incertae sedis from the Thomas Farm L. F. (UF 216633) and Camelidae incertae sedis from Zoyotal L. F. (TMM-41536-21). The dP3 from the Zoyotal L. F. (TMM-41536-21) is characterized by a more pronounced cusp resembling the protocone, whereas the corresponding area for that of *A. panamaensis* is restricted to a barely worn basal ridge for which the morphology is not sufficient to confirm the presence of the paracone. In contrast, older camelids such as *Poebrotherium* sp. from Nebraska (UF 191834), *Gentilicamelus* sp. from the Arikareean Brooksville 2 L. F. of Florida (UF 175468), and also fossils from the Arikareean Buda L. F. (UF 22779) lack this cusp on the lingual side of the paracone.

AGUASCALIENTIA MINUTA, sp. nov.
(Figs. 9A, B, 10, and 11, Table 2, Appendix 1)

Holotype—UF 254113, paired mandibles with partial left p1–partial left p2, left p3–m3, right p1, right p4–m3, and partial mandibular symphysis.

Etymology—'*minuta*' from Latin: tiny, little, referring to the smallest representative of Floridatragulinae.

Referred Material—UF 259877, right M3; UF 246828 right c1, left c1–p2, p4–m1; UF 246833, partial canine; UF 254128, right humerus.

Locality and Horizon—Lirio Norte, Panama Canal area (Fig. 1), Panama, Central America; fossils were collected in the upper part of the Las Cascadas Formation (Fig. 1B), latest Oligocene to earliest Miocene, likely to be equivalent to the middle-to-late Arikareean NALMA (Fig. 2).

Diagnosis—Smallest known floridatraguline. Differs from all other species of *Aguascalientia* in having a shorter c1–p1 diastema than length of m2, and an enamel fold on the anterior part of the posterior fossettid of m2. Differs from *A. panamaensis* in lacking basal intercolumnar pillars on m3, and fossettid on p3. Differs from *A. wilsoni* in having deeper invagination on talonid of m3, c1 and p1 similar in size, relatively larger caniniform p1, and less developed medial crest on p3.

Description

Upper Dentition—Only one isolated M3 (UF 259877) can be referred to *A. minuta* (Fig. 9A, B). It is characterized by a prominent mesostyle with an anterior deep recess at the juncture of the paracone and metacone. Both the parastyle and metastyle are well expressed, although the metastyle is slightly less developed. A strong rib extends from the base of the crown to the tip of both the paracone and metacone (Fig. 9B). The anterior and posterior surfaces have weak cingular segments that project from just above the base of the crown and extend along the anterior or posterior basal portion of each crescent. Strong intercolumnar tubercles are present lingually between the protocone and metaconule (Fig. 9A).

Mandible—The ramus is slender and deep. Unfortunately, the holotype is badly broken in the symphysial and diastematal areas and the lingual and labial surfaces are highly compressed due to deformation (Fig. 11). The p1 and c1 are separated by a diastema of similar length to that of m1 (Fig. 11A). Anterior to p1, a partially preserved diastema of unknown length is present. The mandibular symphysis is completely fused. Although a complete premolar series was not found in association, the left ramus and

TABLE 2. Summary of dental measurement (in mm) on *A. minuta*, sp. nov.

Tooth position	N	Range	Mean	S	V
		Lower dentition			
c1 (APL)	2[a]	4.85	4.85	—	—
c1 (TW)		3.61	3.61	—	—
p1 (APL)	1	5.42	5.42	—	—
p1 (TW)		3.36	3.36	—	—
p2 (APL)	2[a]	10.2	10.20	—	
p2 (TW)		3.81 – 4.19	4.00	0.269	6.71
p3 (APL)	1	8.43	8.43	—	—
p3 (TW)		3.93	3.93	—	—
p4 (APL)	3	8.6 – 9.06	8.77	0.252	2.88
p4 (TW)		4.6 – 5.62	4.81	0.227	4.72
m1 (APL)	3	9.8 – 10.1	10.01	0.127	1.27
m1 (TW)		6.0 – 7.28	6.99	0.067	0.95
m2 (APL)	3	11.7 – 11.98	11.85	0.140	1.19
m2 (TW)		7.66 – 8.4	7.92	0.416	5.25
m3 (APL)	3	16.18 – 16.45	16.28	0.148	7.65
m3 (TW)		8.19 – 9.09	8.51	0.498	7.23
		Upper dentition			
M2 (APL)	1	12.20	12.20	—	—
M2 (TW)		12.24	12.24	—	—

Abbreviations: **APL**, anterior-posterior length; **TW**, transverse width; **S**, standard deviation; **V**, index of variance.
[a]Broken in *A. minuta* holotype.

alveoli clearly shows that the p2–p4 series is nearly continuous with a short and barely discernible p2–p3 diastema (Fig. 11B, C).

Lower Dentition—The lower dental formula is interpreted to be ?.1.4.3 with the dentary anterior to c1 as yet unrecovered (Figs. 10, 11). In UF 246828, the c1 is caniniform, oval, recurved, and transversely compressed. The lower c1 and p1 are similar in size and the p1 is more rounded and slightly lower-crowned (Fig. 10). A small ridge is present on the basal antero-lingual part of c1 that reaches the apex (Fig. 10B). The posterior ridge of the c1 is straight. In the holotype (UF 254113), the p1 is transversely compressed, caniniform, single-rooted, with faintly developed anterior and posterior straight ridges connecting the basal and the apical segments (Fig. 11A, B). The p2–p4 series is characterized by elongate crowns (Fig. 11E, F). The p2 is broken posteriorly, but it resembles p3 in having a well-defined metaconid and trenchant edges. It is also elongate and double-rooted. Whereas the p3 generally resembles p2, it differs in having a slightly developed lingually projected crest posterior to the metaconid. The p4 is slightly wedge-shaped with a swollen posterior region and a bulbous paraconid. Most of the reduction in this tooth has occurred in the region of the protoconid, resulting in a shorter and bulbous p4.

The lower molars are brachydont with relatively shallow anterior and posterior fossettids that are only visible during the initial wear stages (Fig. 11). They have discontinuous and overlapping crests that intersect after sufficient wear. The posterior crest merges first with the anterior crescent and secondly with the anterior crest when the occlusal surface is worn down. Intercolumnar tubercles are restricted to the basal parts of m1 and m2, but are absent on m3. No cingular segments are present on the lower molars. The molars are slightly bulbous and lack well-defined stylids. A prominent enamel fold is present along the antero-lingual occlusal segment of the posterior fossettid (Fig. 11D). Two ridges divide the hypoconulid of m3 and are separated by a prominent invagination that reaches the basal posterior portion of the talonid (Fig. 11A, E). A broad lingual ridge represents a distal continuation of the hypoconid; the labial ridge is a projection of the entoconid.

Discussion and Comparisons—As for *A. panamaensis*, *A. minuta* can be referred to the Floridatragulinae based on the

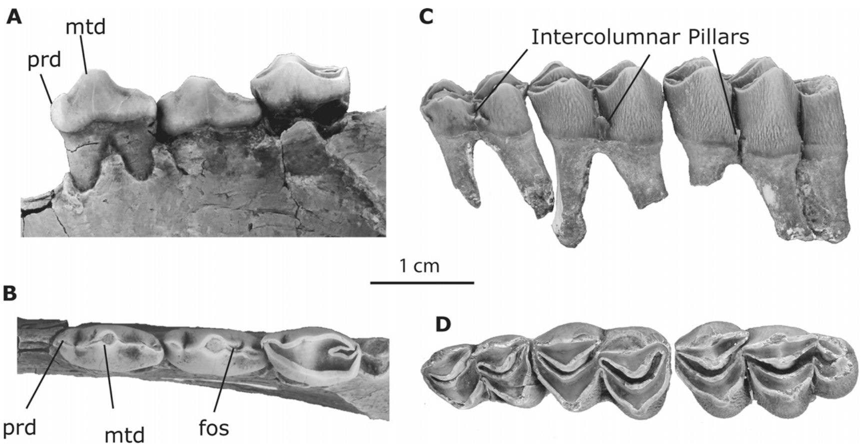

FIGURE 8. Detailed view of the lower dentition of *Aguascalientia panamaensis*. **A**, UF 254129, left p2–p4, labial view; **B**, occlusal view; **C**, composite of the lower molars of *A. panamaensis* (UF 254122, left m1 and UF 246836, left m2, m3), labial view; **D**, occlusal view. **Abbreviations**: **fos**, fossettid; **mtd**, metaconid; **prd**, paraconid.

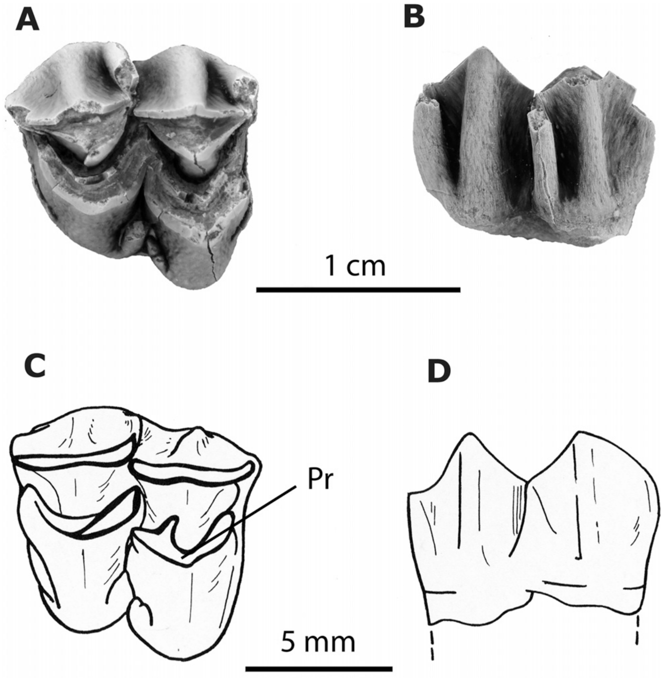

FIGURE 9. Comparison of upper molar morphology of *Aguascalientia minuta* from the Las Cascadas Formation, Panama, and an unidentified camelid from the Buda Local Fauna, Florida. **A**, *A. minuta*, UF 259877, right M3, occlusal view; **B**, labial view; **C**, Camelidae, gen. et sp. indet., UF 18384, left M3, occlusal view (reversed; modified from Frailey, 1979:fig. 8); **D**, labial view (reversed). Specimens are scaled to the same size for comparative purposes. **Abbreviation**: **Pr**, protocone.

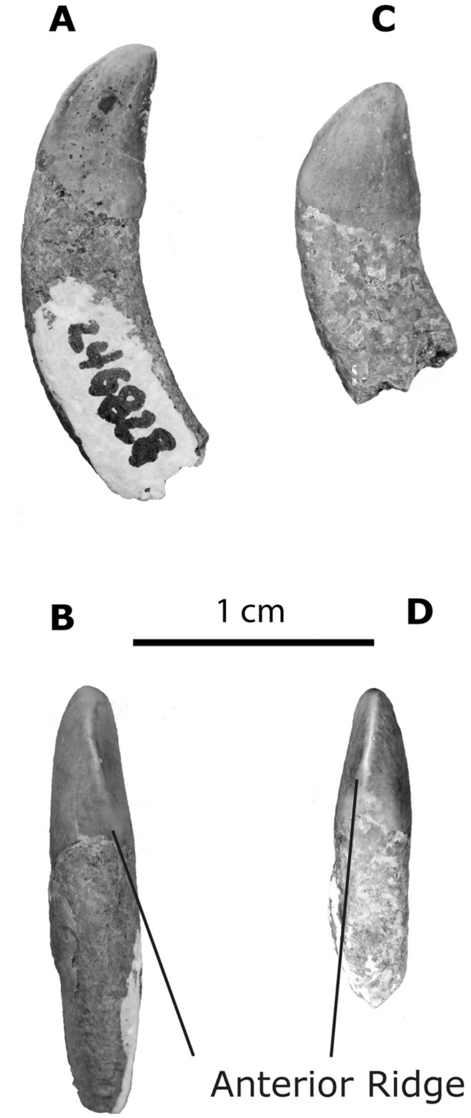

FIGURE 10. Detailed photographs of lower anterior teeth of *Aguascalientia minuta*. **A**, UF 246828, right c1, lingual view; **B**, anterior view**; C**, UF 246828, left p1, labial view; **D**, anterior view. Note the distinct anterior ridge on the canine of *A. minuta*.

following characteristics: (1) a complete lower dental formula, (2) brachydont teeth, (3) an unusually elongated jaw with two caniniform teeth (c1–p1) well separated by a diastema, (4) a long and narrow mandibular symphysis, (5) reduced lower premolars, (6) small intercolumnar pillars on the molars, and (7) an m3 hypoconulid divided by lingual and labial selenes. The lack of a significant p2–p3 diastema appears to be particularly diagnostic of *Aguascalientia*. The general morphology of the upper molar (UF 259877) is consistent with that of Floridatragulinae (Fig. 9A, B) and resembles that of the Hemingfordian *Floridatragulus*, *A. panamaensis*, and to some extent, the camelids from the middle Arikareean Buda L. F. (Fig. 9C), although it differs from the later in lacking a bifurcated protocone. Additionally, the lower molars are smaller than the smallest of *A. panamaensis* (Fig. 12A, B) and also fall outside the range of *A. wilsoni* from the Zoyotal L. F. Comparative body mass predictions based on dental and postcranial dimensions (Tables 3 and 4, respectively) demonstrate that *A. minuta* is the smallest floridatraguline known. Moreover, the lack of a well-developed fossettid located posterolingually to the protoconid on the p3 and the presence of the enamel fold on the m2 can be considered autapomorphies for the species. Similar to *A. panamaensis*, the talonid on the lower m3 of *A. minuta* has a continuous deep invagination reaching the basal part of the tooth with two well-developed grinding surfaces. The similar morphology and dimensions of *A. minuta* and material referred to *Aguascalientia* sp. from the Delaho Formation (TMM-49693-25; Stevens, 1977:table 12) could suggest a close relationship between these taxa, although the fragmentary nature of *Aguascalientia* sp. from Texas does not allow a more detailed comparison of the premolars.

The holotype (UF 254113) of *A. minuta* represents an adult individual in which the m3 is completely erupted. The morphology of the hypoconulid of *A. minuta* is similar to that of *A. panamaensis* with a divided hypoconulid where both the lingual and labial selenes are projections of the hypoconid and entoconid, respectively. It differs from that of *Floridatragulus dolichanthereus*, *F. texanus*, and *A. wilsoni* in having a more basal invagination on the talonid of m3.

PHYLOGENETIC ANALYSIS

To evaluate the phylogenetic relationships of *Aguascalientia panamaensis* and *A. minuta* within Floridatragulinae, we performed a cladistic analysis of nine camelid taxa and one oromerycid to represent the outgroup. Twelve dental characters were scored and used in the analysis, most of which were restricted to the lower dentition (Appendix 2). The ingroup includes the five floridatragulines recognized by Honey et al. (1998) (*Floridatragulus dolichanthereus*, *F. nanus*, *F. texanus*, *Aguascalientia wilsoni*, and *Poebrotherium franki*) and the two

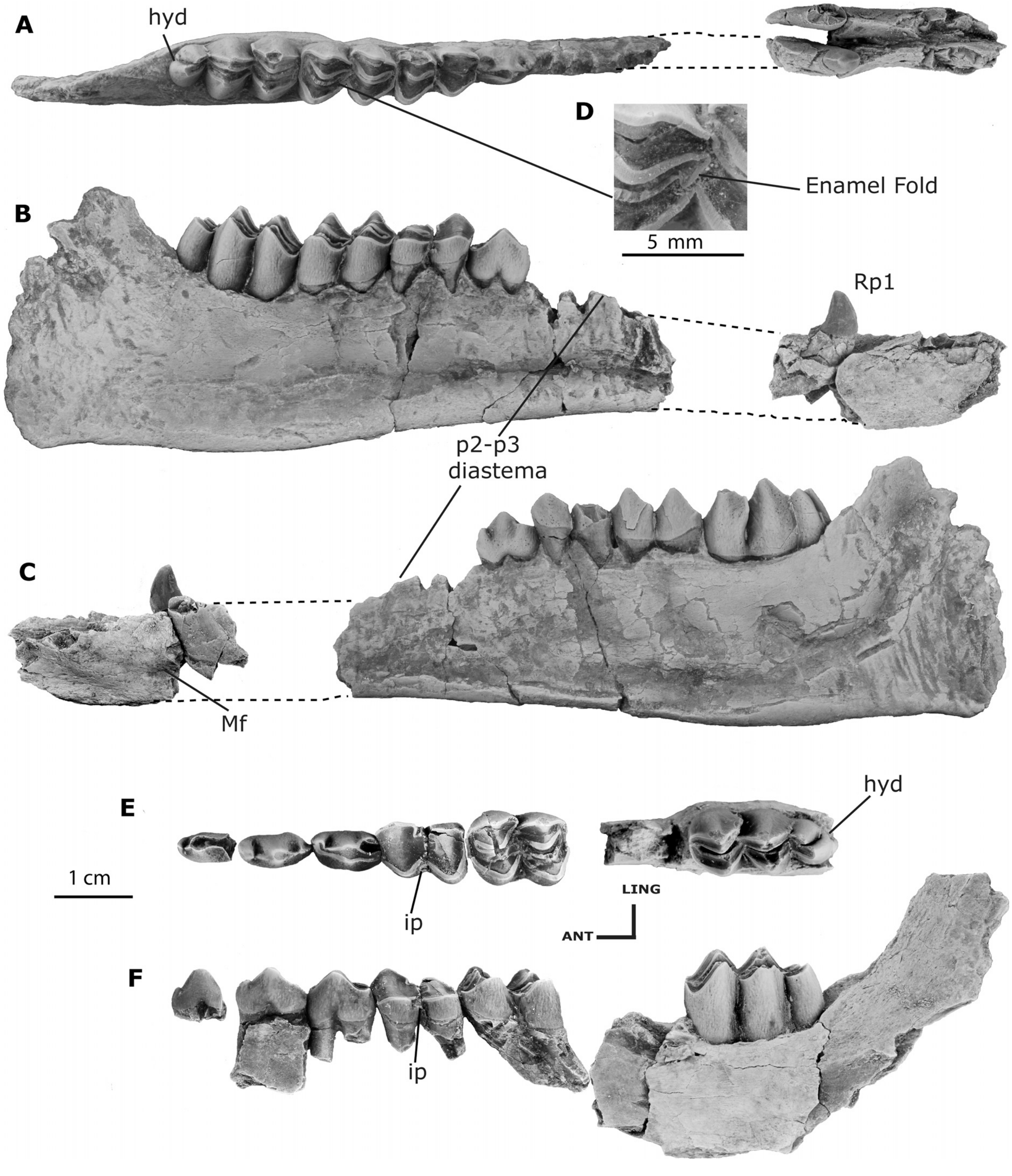

FIGURE 11. Lower dentition of *Aguascalientia minuta*, UF 254113 (holotype). **A**, right dentary with p1, p4–m3, and partial mandibular symphysis, occlusal view; **B**, labial view; **C**, lingual view; **D**, detail of the enamel fold on the anterior part of the posterior fossettid of m2, occlusal view (note different scale); **E**, left dentary with left p2–m3, occlusal view; **F**, labial view. **Abbreviations**: **hyd**, hypoconulid; **Mf**, mental foramen; **ip**, intercolumnar pillar.

new species of *Aguascalientia* from Panama (*A. panamaensis*, *A. minuta*). To assess the relationship of Floridatragulinae to more primitive camels, we also included the undefined small camelid from the Arikareean Buda L. F. in Florida and the late Eocene–early Oligocene *Poebrotherium* sp. from the Brule Formation, Nebraska (UF 191535). Finally, based upon the close relationship of Floridatragulinae and oromerycids proposed by Stevens (1977), the Chadronian *Eotylopus reedi* Matthew, 1910, from Wyoming was added as an outgroup. We believe that the inclusion of these taxa in our preliminary analysis not only provides a test for the position of the new species from Panama, but also offers an opportunity to evaluate alternative

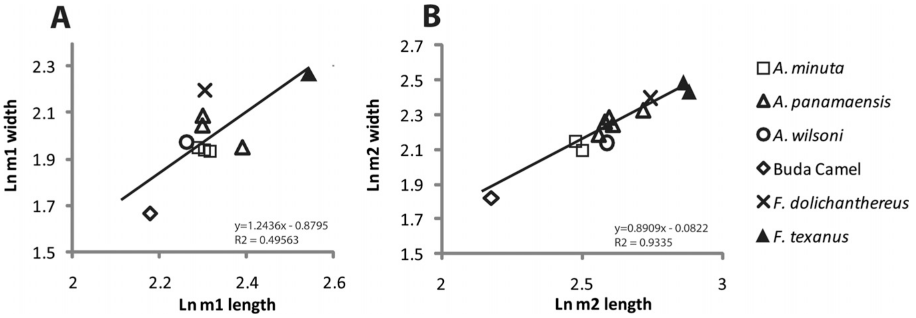

FIGURE 12. Bivariate plots of the natural logarithm of the anterior-posterior length versus maximum transverse width for relevant specimens of Floridatragulinae from Mexico (*A. wilsoni* Stevens, 1977), Texas (*F. texanus* Patton, 1969), Florida (*F. dolichanthereus* Wilson, 1942), and Panama (*A. panamaensis*, sp. nov., and *A. minuta*, sp. nov.), including the Camelidae, gen. et sp. indet., from the Buda Local Fauna (Frailey, 1979). **A**, lower first molar (m1); **B**, lower second molar (m2). Note that the m1 of *F. dolichanthereus* is somewhat wider relative to its length than that of other floridatragulines included in this plot.

hypotheses that have been proposed regarding the origins of Floridatragulinae.

Morphologic data were compiled from the literature (Matthew, 1910; White, 1942; Maglio, 1966; Patton, 1969; Stevens, 1977; Honey et al., 1998) and study of specimens. Cranial and postcranial characters were excluded from the analysis because *A. wilsoni*, *F. texanus*, *F. nanus*, the undefined camelids from the Buda L. F., and the new species from Panama are mostly known from partial lower dentaries. There are associated cranial fragments from Panama, but they do not contain any informative characters for a parsimony analysis. The data matrix (Appendix 3; Supplementary Data 1, available online at www.tandfonline.com/UJVP) includes dental characters that are unordered and weighted equally. Characters not known for a taxon were coded as missing. Data were compiled in Mesquite version 2.72 (Maddison and Maddison, 2009) and the data set was analyzed under the criterion of parsimony using the exhaustive algorithm of PAUP version 4.0b10 (Swofford, 2003). The analysis resulted in four equally most parsimonius trees (MPTs) with tree lengths of 22 steps, a consistency index (CI) of 0.818, a retention index (RI) of 0.833, and a homoplasy index (HI) of 0.182 (Fig. 13).

Despite considerable missing data for the lower dentition, our results support a monophyletic *Poebrotherium*, with Chadronian *P. franki* from Texas consistently the sister taxon of Chadronian *Poebrotherium* sp. from Nebraska in all of the MPTs (Node 2, Fig. 13) based on the shared absence of a lingual notch between the metaconid and the entoconid on lower molars.

The poorly known small camelid from the Buda L. F. (Frailey, 1979) falls out as the sister group to Floridatragulinae (Node 3). Although it lacks two of the unambiguous synapomorphies of the clade (7[1] and 9[1]; see below), it shares several unambiguous characteristics otherwise unique to Floridatragulinae, including (1) basally positioned and conical intercolumnar pillars on the lower molars (2[1]), (2) presence of a bilobed hypoconulid, with a basal invagination on the lower m3 (4[1]), and (3) a posteriorly open 'lake' on the p4 (10[1]). The Buda camelid also has a lingual notch between the entoconid and metaconid, a primitive character that is absent in *P. franki* and *Poebrotherium* sp. (Node 2), but also shared with the Floridatragulinae (Fig. 14). Although this result is interesting, relationships of this undiagnosed camel need to be further tested with a phylogenetic analysis that also includes a greater diversity of primitive camels (outside of the scope of the present study).

A monophyletic Floridatragulinae (Node 4, Fig. 13A), excluding the undiagnosed taxon from the Buda L. F., is supported by the following synapomorphies: (1) a mandibular symphysis ending beneath p1 (11[1], DELTRAN), (2) presence of a caniniform c1 (8[1], DELTRAN), (3) the presence of a p1–p2 diastema that is similar or longer than the crown of m2 (3[1/2], DELTRAN), (4) absence of a bifurcated protocone on the upper molars (7[1], unambiguous), and (5) moderately reduced lower premolar length relative to that of the molars (9[1], unambiguous). Within Floridatragulinae, our results support a monophyletic *Floridatragulus* (Node 6) supported by two unambiguous synapomorphies: (1) the p2–p3 diastema is longer than the p3 length (1[2]), and (2) an apically position and strong intercolumnar pillar between the hypoconid and hypoconulid on the lower molars (2[2]). Our results also suggest the possibility of a paraphyletic *Aguascalientia* with respect to *Floridatragulus*, with *A. panamaensis* as the sister taxon to all other floridatragulines.

In summary, our analysis suggests that Floridatragulinae is a monophyletic group, including two genera: *Aguascalientia* Stevens, 1977, and *Floridatragulus* White, 1942. However, without more complete fossils (including skulls) relationships between *A. wilsoni*, species of *Floridatragulus*, and the new forms of *Aguascalientia* from Panama are far from resolved and our results based on fragmentary dentitions should be regarded as preliminary. We note that although relationships within *Floridatragulus* are ambiguous, two of the MPTs (Fig. 13C, D) suggest that the Hemingfordian *F. texanus* and the poorly known *F. nanus* from Texas are sister taxa, descended from a common ancestor, with *F. dolichanthereus*, based on the development of a more apical invagination on the m3 talonid. Finally, and perhaps most interestingly, our results suggest that *A. panamaensis* could represent the most primitive floridatraguline, sharing plesiomorphic characters with the poorly known camel from the Buda L. F.

DISCUSSION

Although the geochronology of the Panama Canal section is not yet well resolved, *Aguascalientia panamaensis*, sp. nov., and *Aguascalientia minuta*, sp. nov., may be the oldest known floridatragulines. The primitive position of *A. panamaensis* seems to support this idea. Three of our MPTs (Fig. 13B, C, E) suggest that there is an increase in length of the p1–p2 diastema within the Floridatragulinae. Our analysis further suggests that the lower premolar length relative to that of the molars (Table 3 and Character 9) decreases through the evolutionary history of Floridatragulinae. The p2 demonstrates the greatest reduction and in its most derived state (*A. wilsoni*) is exceedingly small. The primitive condition is expressed in *A. panamaensis* and *A. minuta* from Panama with ratios around 0.72, whereas the values are closer to 0.5 in *A. wilsoni* (Table 3). This character is also evident in the presumably more primitive camelids from the Buda L. F. (Frailey, 1979), where ratios around 0.8 were obtained. This pattern in premolar reduction also suggests that *F. dolichanthereus* and *F. texanus* are more derived than *Aguascalientia* from Panama, exhibiting progressively more reduced posterior premolars, with p4 as the shortest premolar of the series and p2 the longest and isolated from other teeth by anterior and posterior diastemata. The lingual inflection of the paraconid on the lower premolars seems to be a homoplasic character for Floridatragulinae, with reduced paraconids in *F. texanus* and strongly inflected and bulbous morphologies in *A. wilsoni*.

TABLE 3. Comparative values of premolar reduction and predicted body mass along Floridatragulinae and the unnamed camels from the Buda Local Fauna.

Species	Distribution	Catalog number	Fauna	NALMA	p2–p3 APL (mm)	m1–m3 APL (mm)	Log (m1–m3 APL)	Body mass[a] (kg)	Reduction ratio (APLpremolar/APLmolar)
A. panamaensis	Panama	UF 254124	Las Cascadas	Ar3–Ar4?	29.03	39.62	1.597	47.99	0.73
A. minuta	Panama	UF 254113	Las Cascadas	Ar3–Ar4?	25.41	35.05	1.544	32.16	0.72
A. wilsoni	Mexico	TMM-41536-26, 41536-14	Zoyotal	He1	21.88	41.45	1.617	55.61	0.53
F. dolichanthereus	Florida	MZC 3636	Thomas Farm	He1	30.48	48.32	1.684	91.76	0.63
F. texanus	Texas	TMM-41536-26, 41536-14	Garvin Gully	He1	34.9	54.49	1.736	135.85	0.64
Camelidae inc. sed.	Florida	UF 19313, UF 18365, UF 18387, UF 18385	Buda	Ar3?	20.87	25.79	1.411	11.81	0.81

Ratio calculated based on the APL of the premolar series (p2–p4 APL in mm) and the APL of the molar series (m1–m3 APL in mm). Based on predictive equations from Janis, 1990. **Abbreviation**: **APL**, anterior-posterior length.

[a] Calculations based on linear regression for extant ungulates excluding Suines (From Janis, 1990). $r^2 = 0.941$, intercept $= -0.536$, slope $= 3.265$, percent standard error $= 45.9$, percent prediction error $= 31.9$.

Variation in body mass (Table 3) estimated on the basis of dental variables (Janis, 1990) supports *A. minuta* as the smallest species of *Aguascalientia*, with an estimated body mass of ~32 kg, whereas body mass predictions for *A. panamaensis* and *A. wilsoni* range between 47 and 55 kg, respectively. However, predictions based on postcranial dimensions (Gingerich, 1990; Scott, 1990) indicate that *A. panamaensis* had a body mass ranging between 10 and 14 kg (Table 4), likely comparable with the 10 kg reported for Musk Deer in Eisenberg (1981).

The morphology of the lower molars of *Aguascalientia* seems to be characterized by a basal invagination on the m3 talonid in the primitive forms (*A. panamaensis* and *A. minuta*) and a more apical morphology in *A. wilsoni*. The presence of strongly inflected and bulbous paraconids in *A. wilsoni* from Mexico seems to be a homoplasic character that could have evolved along with the premolar reduction in the genus. This pattern contrasts with that observed in *F. texanus*, which has moderately inflected paraconids on p3 and a complete reduction of the paraconid on p2.

Floridatragulinae may have originated from a basal camel probably closely related to those from the middle Arikareean Buda L. F. (Frailey, 1979). Camels from the Buda L. F. exhibit important floridatraguline plesiomorphies such as straight paraconids on the lower premolars, unreduced premolars, and upper molars with strong similarities to those of *A. panamaensis* and *A. minuta*. Unfortunately, many questions about the camelids from tropical and subtropical North America cannot be answered due to the fragmentary nature of the fossils. Consequently, in order to better understand the phylogenetic relationships of basal floridatragulines, the apparent paraphyletic nature of *Aguascalientia*, and also to clarify their connection to Camelidae, more complete material is required. Cranial and postcranial material would provide critical data to test some of the hypotheses presented here.

The relationship between the small *Aguascalientia* and the similarly sized *F. nanus* is unclear due to the fragmentary nature of the holotype (TMM-40067-194, isolated lower left m3). However, the morphology observed in the talonid of the m3 supports the relationship of this small floridatraguline with *F. texanus* (Fig. 13C, D) based on the shared morphology of the hypoconulid and intercolumnar pillars.

It is probable that the new material here described from the Las Cascadas Formation represents a middle-late Arikareean faunal assemblage (Ar3–Ar4; sensu Albright et al., 2008) based on the morphological states (e.g., premolar reduction, p1–p2 diastema length, development of the intercolumnar pillars on lower molars) observed in the floridatragulines from the Las Cascadas Formation and their previously discussed phylogenetic relationship within Floridatragulinae. Based on our cladistic analysis, we suggest that *Aguascalientia panamaensis* is intermediate between those camelids from the Arikareean Buda L. F. (Frailey, 1979) and the more derived floridatragulines from the early Hemingfordian Thomas Farm L. F. (White, 1942, 1947; Maglio, 1966; Hulbert and Webb, 2001), the Hemingfordian Garvin Gully L. F. (Patton, 1969), and the Hemingfordian Zoyotal L. F. (Stevens, 1977).

A possible middle to late Arikareean (Ar3–Ar4) age for Las Cascadas fossil assemblage can also be postulated by taking into account the morphology of the deciduous dentition present in *A. panamaensis*. Based on the progressive molarization pattern in deciduous teeth proposed by Loring and Wood (1969) for Oligocene-Miocene camels and by Miller and Wood (1963) for oreodonts, the morphology of the upper dP3 present in *A. panamaensis* seems to be more primitive than the morphology of other early Hemingfordian camels from Thomas Farm, where the anterior crescent encompasses a more apical continuous structure connecting the posterior crescent with the parastyle. In *A. panamaensis*, the anterior crescent is restricted to a basal isolated structure that is only connected with the parastyle during advanced wear. The upper deciduous dentition shows a less

TABLE 4. Predicted body mass for *A. panamaensis*, sp. nov.

Catalog number	Description	H4 (cm) (Scott, 1990)	Body mass (kg)	H5 (cm) (Scott, 1990)	Body mass (kg)	Parasagittal midshaft (cm) (Gingerich, 1990)	Body mass (kg)
UF 254128	R humerus	1.72	10.70	2.19	14.23	1.32	13.21
UF 244202	L humerus	1.62	9.14	—	—	—	—

Abbreviations: **H4**, transverse diameter measured from the lateral epicondyle to the medial condyle of the humerus; **H5**, transverse diameter measured from the lateral condyle to the medial condyle of the humerus. Parasagittal midshaft = parasagittal diameter at humerus midshaft. Based on predictive equations from Scott (1990) and Gingerich (1990).

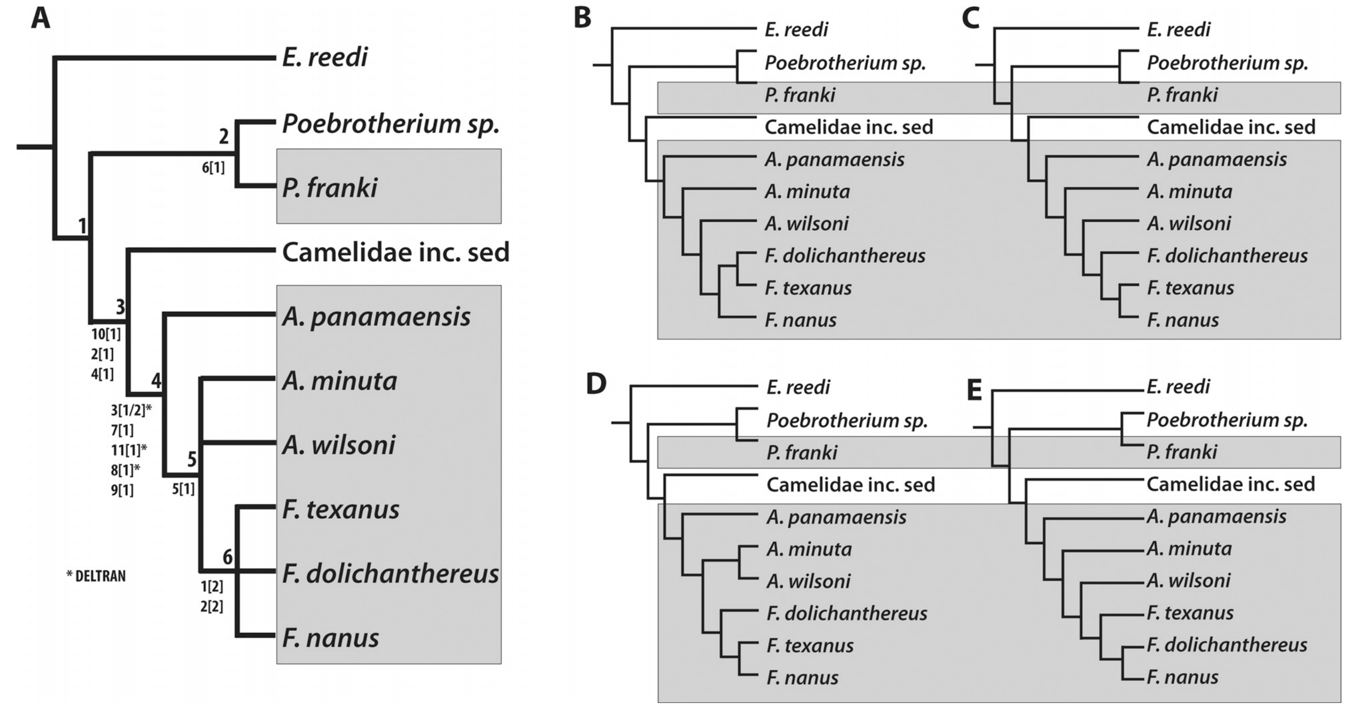

FIGURE 13. Hypothetical phylogenetic relationships of *Aguascalientia panamaensis*, sp. nov., and *A. minuta*, sp. nov., within Floridatragulinae based on 12 character matrix. **A**, strict consensus tree of the four most parsimonious trees resulted from the equal weighted exhaustive search (tree length = 22; CI = 0.818, RI = 0.833, HI = 0.182); **B**–**E**, equally single most parsimonious trees (MPTs) resulted from the parsimony analysis. At each node (bold numbers), each pair of numbers below represents, from left to right, character number, and the corresponding state (in brackets). Floridatragulinae sensu Honey et al. (1998) are shown in gray.

developed anterior crescent on the dP3 in Oligocene and Earliest Miocene camelids (e.g., UF 191834, *Poebrotherium* sp. from the Oligocene of Nebraska; UF 22779, camelid from the Buda L. F.; UF 175468, camelid from the Brooksville 2 L. F.), whereas in more derived camelids (e.g., UF 216633 from Thomas Farm L. F.), the upper third deciduous premolar is characterized by a more developed anterior crescent homologous to the protocone and a more reduced parastyle.

Although our phylogenetic analysis is preliminary, the presence of a lingual notch between the metaconid and the entoconid seems to be a plesiomorphic character for Floridatragulinae, probably grouping the small camelids from the Buda L. F., and perhaps other subtropical small early Arikareean camelids (e.g., those from Brooksville 2 L. F., Buda L. F., etc.), and even more derived forms such as the undescribed camels from the Centenario Fauna. Our interpretations reinforce the hypothesis proposed by Stevens (1977), in which *Aguascalientia* represents the most primitive floridatraguline that inhabited Central America and Texas during the early Miocene and larger floridatraguline camels (*Floridatragulus dolichanthereus* and *F. texanus*) represent derived clades also restricted to subtropical terrains during the Hemingfordian (Maglio, 1966; Patton, 1969; Stevens, 1977).

Assuming a tropical origin for Floridatragulinae, descendants of a basal stock of tylopods would have dispersed and inhabited southern tropical and subtropical terrains during the late Oligocene (Albright, 1999) and migrated into southern volcanic terrains formed during periods of intense volcanic activity (also see Kirby and MacFadden, 2005; Manz et al., 2011). These terrains may have been temporarily accessible near the time of the Oligocene–Miocene transition when extreme climate changes

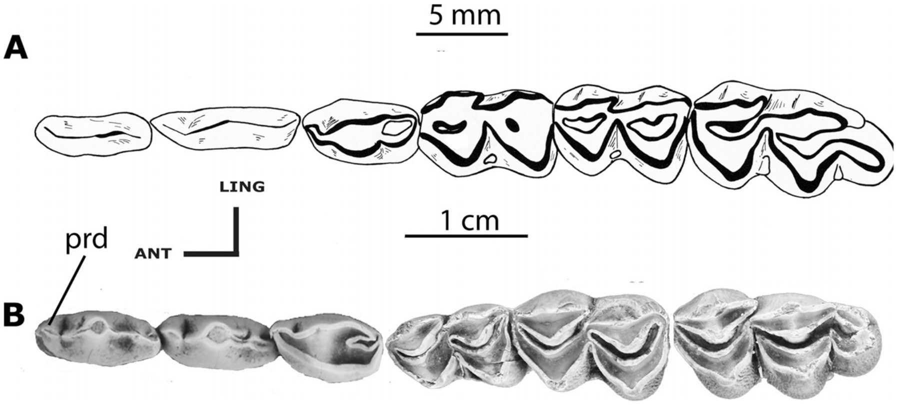

FIGURE 14. Comparison of lower dental morphology of *Aguascalientia panamaensis* from the Las Cascadas Formation, Panama, and an unidentified camelid from the Buda Local Fauna, Florida. **A**, Camelidae, gen. et sp. indet., composite including p2 (UF 19313), p3 (UF 18365), p4 (UF 18387), m1, m2 (reversed), and m3 (UF 18385), occlusal view. **B**, *A. panamaensis,* composite including p2–p4 (UF 254129), left m1 (UF 254122), and left m2, m3 (UF 246836). Specimens are scaled to the same size for comparative purposes. **Abbreviations**: **prd**, paraconid; **ANT**, anterior; **LING**, lingual.

were recorded in the ∂^{18}O and ∂^{13}C isotopic values of marine sediments (Zachos et al., 2001; Zachos et al., 2008) and vegetation changes in the Northern and Central Plains of North America occurring in the Oligocene (Strömberg, 2002, 2006) could have forced herbivore populations to migrate to marginal southern environments.

Finally, the wear pattern observed among the specimens belonging to both *A. panamaensis* and *A. minuta* is characterized by intense wear during early and late ontogenic states. This could be explained by a harsh diet, which probably included abrasive material associated with a dry or dusty environment with abundant volcanic material. This pattern is also present within the other Las Cascadas herbivorous mammals, including undescribed ungulates, such as horses, anthracotheres, and peccaries.

CONCLUSIONS

Floridatragulines are by far the most widely distributed early Miocene camels in tropical and subtropical North America terrains. The oldest specimens of *Aguascalientia* in Central America come from the Panama Canal basin that was clearly connected with Mexico, the Gulf Coastal Plain, and Florida. *Aguascalientia* representatives from Panama include two new species (*A. panamaesis*, sp. nov., and *A. minuta*, sp. nov.) from the Las Cascadas fossil assemblage. A middle to late Arikareean (Ar3–Ar4) age for the assemblage is tentatively proposed based on morphological changes inferred from a phylogenetic analysis that includes floridatragulines from the Las Cascadas fossil assemblage and other early to middle Miocene subtropical faunas from Florida, Texas, and Mexico. These morphological changes include (1) progressive development of the hypoconulid and intercolumnar pillar on lower molars, (2) overall reduction of the length of the premolar series, and (3) the gradual elongation of the anterior part of the skull inferred from the development of more elongated diastemata.

Despite the absence of well-preserved camelid material from the Buda L. F., some distinguishable Floridatragulinae characters suggest a close relationship between this small camelid and the more-derived *Aguascalientia* and, therefore, *Floridatragulus*. Stemming from this interpretation and the continuous presence of a notch between the metaconid and entoconid of the lower molars of Floridatragulinae and the small camelids from Buda L. F., a possible primitive tylopod ancestry could be postulated (Stevens, 1977) with floridatragulines split off from a southern oromerycid ancestor. However, in order to test this hypothesis, distinct oromerycid synapomorphies based on more complete cranial and postcranial material from the Panama Canal areas would be needed to clarify the relationship of these basal floridatragulines with Camelidae, Oromerycidae, or even other basal tylopods that were not considered here. However, this interpretation could explain the rarity of floridatragulines in other Neogene North American faunas when other camels, such as the high-crowned stenomylines and protolabines, were successfully exploiting more open habitats in the North American Miocene Great Plains.

ACKNOWLEDGMENTS

We thank J. Bourque, who prepared the specimens in the laboratory; T. Rowe and L. K. Murray (TMM) for access to relevant research collections; C. Montes, M. Vallejo, and F. Moreno (STRI) who helped in the collection of the specimens; and R. Hulbert Jr. for help with anatomical terminology and taxonomic nomenclature. C. Manz, L. Oviedo, E. Woodruff, F. Herrera, P. Morse, A. Hastings, J. Pardo, and J. Serrano read an earlier version of the manuscript and made helpful comments for its improvement. We thank the Panama Canal Authority (ACP) for assess to relevant fossil sites. This research was supported by UF Research Opportunity Grant; the U.S. National Science Foundation Partnerships in International Research and Education grant 0966884 (OISE, EAR, DRL), EAR 0824299, and EAR 0418042; STRI-Tupper Paleontological Fund; STRI-Panama Canal Authority Fund; and Ricardo Perez Toyota, Panama. This is a UF Contribution to Paleobiology number 641.

LITERATURE CITED

Albright, L. B., III. 1998. The Arikareean Land Mammal Age in Texas and Florida: Southern extension of the Great Plains and Gulf Coastal Plain endemism; pp. 167–183 in D. O. Terry Jr., H. E. LaGarry, and R. M. Hunt Jr. (eds.), Depositional Environments, Lithostratigraphy, and Biostratigraphy of the White River and Arikaree Groups (Late Eocene to Early Miocene, North America): Boulder Colorado. Geological Society of America Special Paper 325: 167–183, Boulder, Colorado.

Albright, L. B., III. 1999. Ungulates of the Toledo Bend Local Fauna (late Arikareean, early Miocene), Texas Coastal Plain. Bulletin of the Florida Museum of Natural History 42:1–80.

Albright, L. B., I., M. Woodburne, T. Fremd, C. Swisher, B. J. MacFadden, and G. R. Scott. 2008. Revised chronostratigraphy and biostratigraphy of the John Day Formation (Turtle Cove and Kimberly Members), Oregon, with implications for updated calibration of the Arikareean North American Land Mammal Age. Journal of Geology 116:211–327.

Coates, A. G., and J. A. Obando. 1996. The geologic evolution of the Central American isthmus; pp. 21–56 in J. B. C. Jackson, A. F. Budd, and A. G. Coates (eds.), Evolution and Environment in Tropical America. University of Chicago Press, Chicago, Illinois.

Dalquest, W. W., and O. B. Mooser. 1974. Miocene vertebrates from Aguascalientes, Central Mexico. Texas Memorial Museum, Pearce Sellards Series 21:1–10.

Eisenberg, J. F. 1981. The Mammalian Radiations. An Analysis of Trends in Evolution, Adaptation, and Behavior. The University of Chicago Press, Chicago, Illinois, 509 pp.

Farris, D. W., C. Jaramillo, G. Bayona, S. A. Restrepo-Moreno, C. Montes, A. Cardona, A. Mora, R. J. Speakman, M. D. Glascock, and V. Valencia. 2011. Fracturing of the Panamanian Isthmus during initial collision with South America. Geology 39:1007–1010.

Frailey, D. 1978. An early Miocene (Arikareean) fauna from northcentral Florida (the SB-1A local fauna). Occasional Papers of the Museum of Natural History, The University of Kansas, Lawrence, Kansas 75:1–20.

Frailey, D. 1979. The large mammals of the Buda Local Fauna (Arikareean: Alachua County, Florida). Bulletin of the Florida State Museum, Biological Sciences 24:1–173.

Frick, C. 1937. Horned ruminants of North America. Bulletin of the American Museum of Natural History 69:1–669.

Gazin, C. L. 1955. A review of the upper Eocene Artiodactyla of North America. Smithsonian Miscellaneous Collections 128:1–96.

Gingerich, P. D. 1990. Prediction of body mass in mammalian species from long bone lengths and diameters. The University of Michigan. Contributions from the Museum of Paleontology 28 (2):79–92.

Gray, J. E. 1821. On the natural arrangement of vertebrose animals. London Medical Repository 15:296–310.

Hayes, F. G. 2000. The Broksville 2 Local Fauna (Arikareean, Latest Oligocene): Hernando County, Florida. Florida Museum of Natural History 43(1):1–47.

Honey, J. G., J. A. Harrison, D. R. Prothero, and M. S. Stevens. 1998. Camelidae; pp. 439–462 in C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), Tertiary Mammals of North America. Cambridge University Press, Cambridge, U.K., and New York.

Hulbert, R. C., Jr., and S. D. Webb. 2001. Mammalia 5: artiodactyls; pp. 242–279 in R. C. Hulbert Jr. (ed.), The Fossil Vertebrates of Florida. University Press of Florida, Gainesville, Florida.

Illiger, C. 1811. Prodromus Systematis Mammalium et Avium Additis Terminis Zoographicis Utriusque Classis. C. Salfeld, Berolini, 301 pp.

Janis, C. M. 1990. Correlation of cranial and dental variables with body size in ungulates and macropodoids; pp. 255–299 in J. Damuth and B. J. MacFadden (eds.), Body Size in Mammalian Paleobiology: Estimation and Biological Implications. Cambridge University Press, Cambridge, U.K.

Janis, C. M., J. Damuth, and J. M. Theodor. 2000. Miocene ungulates and terrestrial primary productivity: where have all the browsers gone?

Proceedings of the National Academy of Sciences of the United States of America 97:237–261.

Kirby, M. X., and B. J. MacFadden. 2005. Was southern Central America an archipelago or a peninsula in the middle Miocene? A test using land-mammal body size. Palaeogeography, Palaeoclimatology, Palaeoecology 228:193–202.

Kirby M. X., D. S. Jones, and B. J. MacFadden. 2008. Lower Miocene stratigraphy along the Panama Canal and its bearing on the Central American peninsula. PLoS ONE 3(7):e2791.

Linnaeus, C. 1758. Systema Naturae per Regna tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentis, Synonymis, Locis, 10th edition. Laurentii, Slavi, Stockholm, 824 pp.

Loring, S. H., and A. E. Wood. 1969. Deciduous premolars of some North American Tertiary camels (Family Camelidae). Journal of Paleontology 43:1199–1209.

MacFadden, B. J. 2006. North American land mammals from Panama. Journal of Vertebrate Paleontology 26:720–734.

MacFadden, B. J. 2009. Three-toed browsing horse *Anchitherium* (Equidae) from the Miocene of Panama. Journal of Paleontology 83:489–492.

MacFadden, B. J., and P. Higgins. 2004. Ancient ecology of 15 million-year-old browsing mammals within C3 plant communities from Panama. Oecologia 140:169–182.

MacFadden, B. J., and R. M. Hunt Jr. 1998. Magnetic polarity stratigraphy and correlation of the Arikaree Group, Arikareean (late Oligocene-early Miocene) of northwestern Nebraska; pp. 143–165 in D. Terry, H. LaGarry, and R. M. Hunt, Jr. (eds.), Depositional Environments, Lithostratigraphy, and Biostratigraphy of the White River and Arikaree Groups (Late Eocene to Early Miocene, North America). Geological Society of America Special Paper 325.

MacFadden, B. J., M. Kirby, A. Rincon, C. Montes, S. Moron, N. Strong, and C. Jaramillo. 2010. Extinct peccary "*Cynorca*" *occidentale* (Tayassuidae) from the Miocene of Panama and correlations to North America. Journal of Paleontology 84:288–298.

Maddison, W. P., and D. R. Maddison. 2010. Mesquite: A Modular System For Evolutionary Analysis. Version 2.73. Available at http://mesquiteproject.org. Accessed December 2, 2010.

Maglio, V. J. 1966. A revision of the fossil selenodont artiodactyls from the middle Miocene Thomas Farm, Gilchrist County, Florida. Breviora 255:1–27.

Manz, C., E. Woodruff, and A. Rincon. 2011. Comparing the paleoecology of three subtropical to tropical Early Miocene faunas in the North American continent. [Presented at] Fourth Annual Meeting of the Southeastern Association of Vertebrate Paleontology. Florida Museum of Natural History, University of Florida Gainesville, Florida, 6–8 May 2011. Available at http://www.flmnh.ufl.edu/vertpaleo/SEAVPabstracts.pdf. Accessed May 7, 2011.

Matthew, W. D. 1910. On the skull of *Apternodus* and the skeleton of a new artiodactyl. Bulletin of the American Museum of Natural History 28:33–42.

Montes, C., A. Cardona, R. McFadden, S. E. Morón, C. A. Silva, S. Restrepo-Moreno, D. A. Ramírez, N. Hoyos, J. Wilson, D. Farris, G. A. Bayona, C. A. Jaramillo, V. Valencia, J. Bryan, and J. A. Flores. 2012. Evidence for middle Eocene and younger emergence in Central Panama: implications for Isthmus closure. Geological Society of America Bulletin. Posted online January 13, 2012; doi: 10.1130/B30528.1.

Miller, J. R., and A. E. Wood. 1963. The upper deciduous molars in mid-tertiary oreodonts (Mammalia, Merycoidodontidae). Journal of Paleontology 37:705–713.

Owen, R. 1848. Description of teeth and portions of two of two extinct anthracotheroid quadrupeds (*Hyopotamus vectianus* and *H. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N. W. coast of the Isle of Wight, with an attempt to develop Cuvier's idea of the classification of pachyderms by the number of their toes. Quarterly Journal of the Geological Society of London 4:104–141.

Pagani, M., K. H. Freeman, and M. A. Arthur. 1999. Late Miocene atmospheric CO2 concentrations and the expansion of C4 grasses. Science 285:876–879.

Patton, T. H. 1967. Oligocene and Miocene vertebrates from central Florida; pp. 3–10 in H. K. Brooks and J. R. Underwood (eds.), Miocene-Pliocene Problems of Peninsular Florida. 13th Field Trip, Southeastern Geological Society, Tallahassee, Florida.

Patton, T. H. 1969. Miocene and Pliocene artiodactyls, Texas Gulf Coastal Plain. Bulletin of the Florida State Museum, Biological Science 14:115–226.

Patton, T. H., and B. E. Taylor. 1971. The Synthetoceratinae (Mammalia, Tylopoda, Protoceratidae). Bulletin of the American Museum of Natural History 145:119–218.

Pimiento, C., D. J. Ehret, B. J. MacFadden, and G. Hubbell. 2010. Ancient nursery area for the extinct giant shark *Megalodon* from the Miocene of Panama. PLoS ONE 5(5):e10552.

Pratt, A. E. 1990. Taphonomy of the large vertebrate fauna from the Thomas Farm locality (Miocene, Hemingfordian), Gilchrist County, Florida. Bulletin of the Florida Museum of Natural History, Biological Sciences 35:35–130.

Prothero, D. R., and R. J. Emry. 1996. The Terrestrial Eocene-Oligocene Transition in North America. Cambridge University Press, New York, 688 pp.

Retallack, G. J., and M. Kirby. 2007. Middle Miocene global change and paleogeography of Panama. Palaios 22:667–669.

Rincon, A. F., J. Bloch, B. MacFadden, S. Suarez, and C. Jaramillo. 2010. New early Miocene camelids from the Las Cascadas Formation, Panama Canal, Central America. 70th Society of Vertebrate Paleontology Meeting, Pittsburgh, PA, USA, Program and Abstracts:151A. Available at http://www.vertpaleo.org/meetings/documents/SVP10Abstracts_WEB.pdf. Accessed October 8, 2010.

Rooney, T., P. Franceschi., and C. Hall. 2010. Water saturated magmas in the Panama Canal region: a precursor to Adakite-like magma generation. Contributions to Mineralogy and Petrology 161:373–388.

Schlaikjer, E. M. 1935. Contributions to the stratigraphy and paleontology of the Goshen Hole Area, Wyoming: new vertebrates and the stratigraphy of the Oligocene and early Miocene. Bulletin of the Museum of Comparative Zoology 76:97–189.

Scott, K. M. 1990. Postrcranial dimensions of ungulates as predictors of body mass; pp. 301–335 in J. Damuth and B. J. MacFadden (eds.), Body Size in Mammalian Paleobiology: Estimation and Biological Implications. Cambridge University Press, Cambridge, U.K.

Simpson, G. G. 1930. Tertiary land mammals of Florida. Bulletin of the American Museum of Natural History 59:149–211.

Smith, J. B., and P. Dodson. 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. Journal of Vertebrate Paleontology 23:1–2.

Stevens, M. 1977. Further studies of Castolon local fauna (early Miocene) Big Bend National Park, Texas. The Pearce-Sellards Series. Texas Memorial Museum 27:1–69.

Stevens, M. S., and J. B. Stevens. 1989. Neogene-Quaternary deposits and vertebrate faunas, Trans-Pecos Texas; pp. 67–90 in A. B. Busby and T. M. Lehman (eds.), Vertebrate Paleontology, Biostratigraphy and Depositional Environments, Latest Cretaceous and Tertiary, Big Bend Area, Texas. 49th Annual Society of Vertebrate Paleontology Meeting Guidebook.

Stevens, M. S., J. B. Stevens, and M. R. Dawson. 1969. New early Miocene formation and vertebrate local fauna, Big Bend National Park, Brewster County, Texas. The Pearce-Sellards Series, Texas Memorial Museum 15:1–53.

Strömberg, C. A. E. 2002. The origin and spread of grass-dominated ecosystems in the Late Tertiary of North America: preliminary results concerning the evolution of hypsodonty. Palaeogeography, Palaeoclimatology, Palaeoecology 177:59–75.

Strömberg, C. A. E. 2006. Evolution of hypsodonty in equids: testing a hypothesis of adaptation. Paleobiology 32:236–258.

Swofford, D. A. 2003. PAUP* 4.0. Sinauer Associates, Sunderland, Massachusetts.

Tedford, R. H. 1970. Principles and practices of mammalian geochronology in North America. Proceedings of the North American Paleontological Convention F:666–703.

Tedford, R. H., M. F. Skinner, R. W. Fields, J. M. Rensberger, D. P. Whistler, T. Galusha, B. E. Taylor, J. R. Macdonald, and S. D. Webb. 1987. Faunal succession and biochronology of the Arikareean through Hemphillian interval (Late Oligocene through Earliest Pliocene Epochs) in North America; pp. 153–210 in M. O. Woodburne (ed.), Cenozoic Mammals of North America. University of California Press, Berkeley California.

Tedford, R. H., L. B. Albright III, A. D. Barnosky, I. Ferrusquia-Villafranca, R. M. Hunt Jr, J. E. Storer, C. C. Swisher III, M. R. Voorhies, S. D. Webb, and D. P. Whistler. 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs); pp. 169–231 in M. O. Woodburne (ed.), Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology. Columbia University Press, New York.

Tipple, B., and M, Pagani. 2010. A 35 Myr North American leaf-wax compound-specific carbon and hydrogen isotope record: implications for C4 grasslands and hydrologic cycle dynamics. Earth and Planetary Science Letters 299:250–262.

Uhen, M. D., A. G. Coates, C. A. Jaramillo, C. Montes, C. Pimiento, A. Rincon, N. Strong, and J. Velez-Juarbe. 2010. Marine mammals from the Miocene of Panama. Journal of South American Earth Sciences 30:167–175.

Urban, M., D. Nelson, G. Jiménez-Moreno, J. Châteauneuf, A. Pearson, and F. Sheng. 2010. Isotopic evidence of C4 grasses in southwestern Europe during the Early Oligocene–Middle Miocene. Geology 38:1091–1094.

White, T. H. 1940. New Miocene vertebrates from Florida. Proceedings of the New England Zoological Club 18:31–38.

White, T. H. 1942. The Lower Miocene mammal fauna of Florida. Bulletin of the Museum of Comparative Zoology 92(1):1–49.

White, T. H. 1947. Additions to the Miocene fauna of North Florida. Bulletin of the Museum of Comparative Zoology 99: 497–515.

Whitmore, F. C., and R. H. Stewart. 1965. Miocene mammals and Central American seaways. Science 148:180–185.

Wilson, J. A. 1974. Early Tertiary vertebrate faunas, Vieja Group and Buck Hill Group, trans-Pecos Texas: Protoceratidae, Camelidae, Hypertragulidae. Texas Memorial Museum, Bulletin 23:1–34.

Wilson, J. A. 1984. Vertebrate fossil faunas 49 to 36 million years ago and additions to the species of *Leptoreodon* found in Texas. Journal of Vertebrate Paleontology 4:199–207.

Woodring, W. P. 1957. Geology and paleontology of Canal Zone and adjoining parts of Panama; description of Tertiary mollusks; gastropods; Trochidae to Turritellidae. US Geological Survey Professional Papers 306-A:1–239.

Woodring, W. P. 1982. Geology and paleontology of Canal Zone and adjoining parts of Panama; description of Tertiary mollusks; pelecypods, Propeamussiidae to Cuspidariidae; additions to families covered in P306-E; additions to gastropods; cephalopods. US Geological Survey Professional Papers 306–307:541–759.

Woodring, W. P., and T. F., Thompson. 1949. Tertiary formations of Panama Canal Zone and adjoining parts of Panama. American Association of Petroleum Geologists Bulletin 33:223–247.

Zachos, J. C., G. R. Dickens, and R. E. Zeebe. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature 451:279–283.

Zachos, J. C., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686–693.

Submitted July 6, 2011; revisions received September 22, 2011; accepted October 20, 2011.

Handling editor: Jessica Theodor.

APPENDIX 1. Dental measurements of *A. panamaensis*, sp. nov., and *A. minuta*, sp. nov., from Las Cascadas Formation, Panama. **Abbreviations**: **APL**, anterior-posterior length; **TWmx**, maximum transverse width; **TWHyd**, transverse hypoconulid width.

Taxon	UF catalog number	Tooth position	APL (mm)	TWmx (mm)	TWHyd
A. minuta	UF 259877	RM3	12.20	12.11	—
A. minuta	UF 254113	Lc1?	4.60	2.90	—
A. minuta	UF 246828	Lc1	4.85	3.61	—
A. minuta	UF 246828	Lp1	5.42	3.36	—
A. minuta	UF 254113	Lp2?	8.45	3.81	—
A. minuta	UF 246828	Lp2	10.20	4.19	—
A. minuta	UF 254113	Lp3?	8.36	3.50	—
A. minuta	UF 254113	Rp4	8.65	4.77	—
A. minuta	UF 254113	Lp4	8.60	4.60	—
A. minuta	UF 246828	Lp4	9.06	5.05	—
A. minuta	UF 254113	Lm1	9.92	6.98	—
A. minuta	UF 254113	Rm1	10.10	6.94	—
A. minuta	UF 246828	Lm1	9.80	7.07	—
A. minuta	UF 254113	Lm2	11.86	8.88	—
A. minuta	UF 246836	Lm2	11.70	8.91	—
A. minuta	UF 254113	Rm2	11.98	8.25	—
A. minuta	UF 254113	Lm3	16.21	8.19	5.51
A. minuta	UF 246836	Lm3	16.18	9.09	5.27
A. minuta	UF 254113	Rm3	~ 16.45	8.27	5.12
A. panamaensis	UF 259878	RdP3	11.28	7.44	—
A. panamaensis	UF 244156	RdP3	11.43	7.16	—
A. panamaensis	UF 254125	RP3	10.43	5.65	—
A. panamaensis	UF 254125	RP4	7.78	8.37	—
A. panamaensis	UF 254117	RM1	12.58	11.18	—
A. panamaensis	UF 254125	RM1	10.02	11.96	—
A. panamaensis	UF 254116	LM2	13.28	13.75	—
A. panamaensis	UF 254125	RM2	14.26	15.11	—
A. panamaensis	UF 254115	LM3	13.50	14.04	—
A. panamaensis	UF 245602	LM3	14.71	15.64	—
A. panamaensis	UF 244204	RM3	14.24	14.80	—
A. panamaensis	UF 257197	RM3	14.33	14.67	—
A. panamaensis	UF 254125	RM3	13.87	15.19	—
A. panamaensis	UF 246857	RM3	15.95	17.81	—
A. panamaensis	UF 246802	Li3	5.16	3.14	—
A. panamaensis	UF 254129	Li1	4.95	2.83	—
A. panamaensis	UF 254129	Li2	5.35	3.06	—
A. panamaensis	UF 254129	Li3	5.53	3.00	—
A. panamaensis	UF 254129	Ri1	4.60	2.84	—
A. panamaensis	UF 254129	Ri2	5.37	2.96	—
A. panamaensis	UF 236939	Lc1	5.26	3.80	—
A. panamaensis	UF 236939	Rc1	5.16	3.90	—
A. panamaensis	UF 246802	Rc1	5.68	3.81	—
A. panamaensis	UF 254129	Rc1	5.30	3.68	—
A. panamaensis	UF 254129	Rc1	5.22	3.86	—
A. panamaensis	UF 259884	Lc1	8.87	6.20	—
A. panamaensis	UF 236939	Rp1	5.86	3.52	—
A. panamaensis	UF 246802	Rp1	6.79	4.06	—
A. panamaensis	UF 246802	Lp1	7.04	3.97	—
A. panamaensis	UF 254124	Lp2	10.33	4.42	—
A. panamaensis	UF 254129	Lp2	10.20	4.42	—
A. panamaensis	UF 246802	Rp2	11.57	4.56	—
A. panamaensis	UF 236939	Rp2	9.88	4.61	—
A. panamaensis	UF 236939	Rp3	10.34	4.50	—
A. panamaensis	UF 246802	Rp3	11.55	4.43	—
A. panamaensis	UF 254124	Rp3	10.43	4.31	—
A. panamaensis	UF 254129	Lp3	10.16	4.53	—
A. panamaensis	UF 254127	Lp3	12.20	5.09	—
A. panamaensis	UF 246803	Lp3	9.48	4.02	—
A. panamaensis	UF 254124	Lp3	10.43	4.31	—
A. panamaensis	UF 244316	Lp3	9.69	4.43	—
A. panamaensis	UF 244288	Lp3	10.13	4.66	—
A. panamaensis	UF 254124	Lp4	9.41	5.62	—
A. panamaensis	UF 254129	Lp4	9.69	5.62	—
A. panamaensis	UF 254120	Lp4	9.75	5.08	—
A. panamaensis	UF 254118	Lp4	9.63	5.42	—
A. panamaensis	UF 246802	Rp4	10.11	5.28	—
A. panamaensis	UF 236939	Rm1	9.96	7.73	—
A. panamaensis	UF 246802	Rm1	9.97	8.06	—
A. panamaensis	UF 254124	Lm2	13.22	9.58	—
A. panamaensis	UF 236939	Rm2	13.42	9.81	—
A. panamaensis	UF 246802	Rm2	15.16	10.21	—
A. panamaensis	UF 254121	Lm2?	13.60	9.42	—
A. panamaensis	UF 254124	Lm3	17.96	9.74	5.61
A. panamaensis	UF 254123	Lm3	18.04	9.32	5.46
A. panamaensis	UF 257198	Lm3	17.97	9.66	6.36
A. panamaensis	UF 254122	Lm1	10.90	7.04	—
A. panamaensis	UF 236939	Rm3	19.83	9.51	6.03
A. panamaensis	UF 254114	Lm3	PARTIAL	—	—
A. panamaensis	UF 257196	Rm3	19.11	9.98	6.97

APPENDIX 2. Description of dental characters used in the phylogenetic analysis. All characters are treated as unordered. **Abbreviation**: **APL**, anterior-posterior length.

(1) p2–p3 diastema: absent (0); shorter than p3 length (1); longer than p3 length (2).
(2) Intercolumnar pillar between protoconid-hypoconid on lower molars: absent (0); conical and basal (1); more apical and strong (2).
(3) p1–p2 diastema: shorter than m2 APL (0); subequal to m2 APL (1); longer than m2 APL (2).
(4) Hypoconulid on m3: single (0); bilobed with basal invagination (1); bilobed with apical invagination (2).
(5) p4 posterior lobe: subequal or narrower than anterior(0); wider (1).
(6) Lingual notch between entoconid and metaconid on lower molars: present (0); absent (1).
(7) Protocone bifurcated posteriorly on upper molars: present (0); absent (1).
(8) c1 morphology: incisiform (0); caniniform (1).
(9) Ratio between lower premolar APL and molar APL: >0.7 (0); $0.6 < \text{ratio} < 0.7$ (1); <0.6 (2).
(10) Lake opening on p4: lingualy opened (0); posteriorly opened (1).
(11) Symphysis: ending beneath p2 (0); ending beneath p1 (1).
(12) p4 length: subequal to p3 (0); longer than p3 (1); shorter than p3 (2).

APPENDIX 3. Character-taxon matrix used in phylogenetic analyses of Floridatragulinae. See Appendix 2 for character descriptions.

	1	11
	1234567890	12
F. nanus	?2?2?0????	??
F. dolichanthereus	2221101111	12
F. texanus	22?2101?11	?2
A. wilsoni	0122101121	?1
A. panamaensis	0111001111	12
A. minuta	0111101111	11
Poebrotherium franki	1????100??	00
Poebrotherium sp.	0000011000	01
Eotylopus reedi	00000000?0	01
Camelidae indet. (Buda L. F.)	?1?1000?01	?2