A PRELIMINARY ASSESSMENT OF THE MAMMALIAN FAUNA FROM THE PLIOCENE-PLEISTOCENE EL BREAL DE OROCUAL LOCALITY, MONAGAS STATE, VENEZUELA

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ABSTRACT--Preliminary collections from a new asphalt seep deposit in northeastern Venezuela produced a diverse vertebrate faunal assemblage of latest Pliocene or early Pleistocene age. This unique taxonomic assemblage includes 24 mammalian taxa described herein. Seven taxa represent new records for Venezuela (including *Pachyarmatherium* cf. *P. leiseyi*, *Hoplophorus* sp., Erethizontidae, *Hippidion* sp., and *Platygonus* sp.), and two of these represent the first definitive records for South America (a new tapir similar to *Tapirus webbi* and a homotheriine cat). The fauna represents the first diverse biota of Pliocene-early Pleistocene age from northern South America and fills an important geographical gap in our knowledge of faunal dynamics associated with the Great American Biotic Interchange.

INTRODUCTION

The paleontological potential of tar seeps and other asphalt-impregnated deposits became widely recognized following the remarkable and abundant discoveries made in the early 1900s at Rancho La Brea in Los Angeles, California (Stock, 1930). Although several additional important localities surfaced in the 20th century, including the Talara deposits in Peru (e.g., Hoffstetter, 1952; Churcher, 1959, 1965, 1966; Lemon and Churcher, 1961; Campbell, 1979), Las Breas de San Felipe in Cuba (e.g., Iturralde-Vinent et al., 2000), and Pitch Lake in Trinidad (Wing, 1962), Rancho La Brea has long held title as the greatest discovery among the world's fossiliferous tar seeps, and is the standard against which other deposits may be evaluated. In the last decade, new discoveries in Venezuela revealed important additional tar seep deposits that are similar to Rancho La Brea in their spatial extent, fossil preservation, diversity of species, and potential for scientific yield. The best documented of these is Mene de Inciarte, situated near the foothills of the Sierra de Perijá Mountains west of Lago de Maracaibo in Zulia State, western Venezuela (e.g., Czaplewski et al., 2005; Rincón, 2006a, b; Rincón R. et al., 2006; Prevosti and Rincón, 2007; Rincón et al., 2008). We here provide a preliminary description of the mammalian fauna from El Breal de Orocual, a recently discovered site situated approximately 20 km northeast of the city of Maturín in Monagas State in northeastern Venezuela (Fig. 1), and we assess its significance and potential.

MATERIALS, METHODS, AND GEOLOGIC SETTING

Fossiliferous deposits at Orocual were discovered in July, 2006, when Petróleos de Venezuela S. A. (Venezuelan petroleum company, PDVSA) field crews were excavating a trench for an oil conduit pipeline. A portion of the trench along the edge of a hillside cut through an extensive bone-bed preserved in an asphalt-impregnated sedimentary sequence associated with a now-inactive tar seep. The bone bed exposed along the walls of the trench extends for a length of approximately 15 m, with a depth of greater
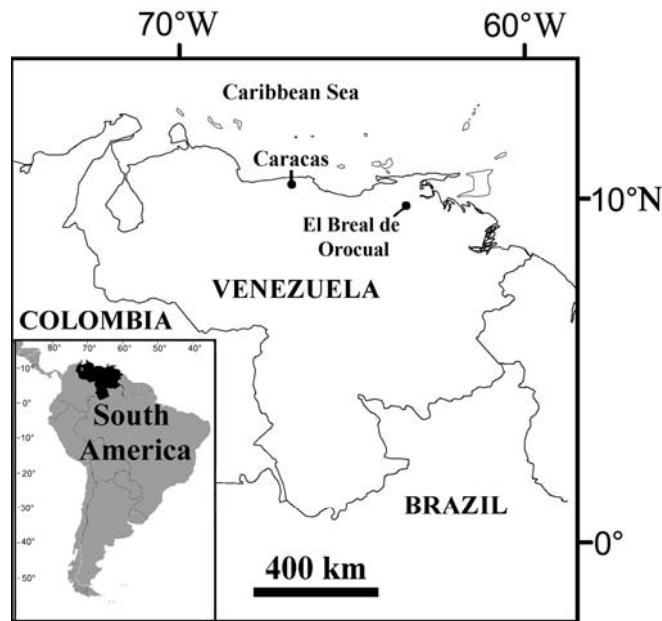
Figure 1. Map showing the location of El Breal de Orocual in Venezuela.

than 2 m (the depth of the trench at the time it was cut). The lateral extent of the bone bed and of the entire deposit is not known, but in September, 2006, one of us (AR) visited the site and estimated that the total extent of fossiliferous sediments on the hill could exceed 18,000 m^2 in extent.

The exposed portion of the deposit at Orocual revealed an extreme concentration of fossil bones, terrestrial mollusks, and plant material. In many places along the trench wall, the deposit appears to be a bone-supported matrix. The paleontological significance of the deposit was apparent, construction efforts ceased, and the conduit pipeline was relocated beyond the apparent extent of fossiliferous deposits. A preliminary assessment of potential significance was filed and permission was granted by the Instituto del Patrimonio Cultural to salvage materials exposed in the trench wall and in the back dirt from the excavation. Salvage activities began in October, 2006, and continued sporadically through April, 2007. The only collections made from the site so far consist of material from the back-dirt of the trench, and selective removal of important and threatened specimens from the bone bed exposed in the trench wall.

The deposit appears to be emplaced within the Mesa Formation, the age of which is assumed to be Pleistocene based on its stratigraphic position with respect to the Pliocene Las Piedras Formation (González de Juana, et al., 1980:713). No obvious stratigraphy is evident within the vertebrate-bearing deposits exposed in the wall of the trench. The bones and sediments were clearly impregnated with asphalt at some time in the past, but no fluid asphalt is present in the deposit today. Solidified asphalt blocks are exposed in cross section in the wall of the trench in several places. These blocks are surrounded by a weathered corona of badly degraded wood, and appear to represent hollow cavities within logs or branches that were filled with asphalt that could not escape when the rest of the deposit was drained. No articulated skeletons were recovered or recognized during salvage operations, but individual skeletons of at least some the larger mammals (e.g., *Eremotherium*) may still be associated in the deposit. Evaluation of these associations must await excavation of the deposit.

Specimens reported here were revealed by the trench-cutting machinery, and were exposed for variable lengths of time to intense sunlight and rainfall. Extensive excavation was not attempted, and collections were made with minimal disruption of the deposit. Specimens were exposed with brushes or small excavation tools, impregnated with Butvar in the field, and in some cases enclosed in plaster jackets for transportation to the laboratory. Specimens were cleaned in the laboratory, reconstructed if damaged, stabilized, and numbered individually. All specimens reported here are housed at the Instituto Venezolano de Investigaciones Científicas (IVIC) in Caracas, and are cataloged and curated under the locality

designation OR for Orocual. Individual specimen numbers are listed below, but the OR designation is provided only at the beginning of each Referred Material section.

The recovered material reveals a diverse biota including as-yet unidentified plants, mollusks, frogs, lizards, snakes, turtles, birds, and the assemblage of 24 mammal taxa reported herein. It is clear that many additional taxa will be discovered at the site.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order DIDELPHIMORPHIA Hill, 1872
Family DIDELPHIDAE Gray, 1821
Genus *DIDELPHIS* Linnaeus, 1758
DIDELPHIS sp.
(Fig. 2A, B)

Referred Material--Edentulous right dentary, with alveoli for c1, p1 to m4, OR-252; right dentary ramus with p2 to m4, and the alveoli for c1 to p2, the coronoid and angular processes are broken and missing, but the anterior part of the masseteric fossa and submasseteric crest are preserved, 1327.

Description--Molars with trigonid longer than wide; talonid shorter than trigonid; m4 longer than m3; molars with metaconid slightly higher than paraconid; protoconid in molars larger and higher than metaconid; paraconid well-separated from protoconid by sharp cleft; molars with anterior cingulum highly developed and increasing in prominence from m1 to m4; talonid of m4 triangular in shape and narrower than trigonid; m1 to m3 with trigonid and talonid similar in breadth, talonid square in shape, and entoconid and hypoconid subequal in size and height; hypoconulid on m4 larger than entoconid, m1 to m3 badly worn (so hypoconid and entoconid cannot be seen); small (almost imperceptible) cuspule present on anterior part of paraconid; p3 conical with very small anterorbasal cuspule; weak posterolingual and posterolabial cingulum; posterobasal cuspule converges and merges with descending crest of posterior face of protoconid; posterolingual and posterolabial cinguli and posterobasal cuspule talonid-like; p2 and p1 have double-rooted alveoli (Fig. 2A); masseteric fossa deep; posterior mental foramen below connection of p3 and m1; mental foramen below p1 (Fig. 2B); OR-252 more robust with larger alveoli than OR-1327, suggesting individuals of different ontogenetic ages; no diastema between canine and first premolar or between the first and second premolars; alveoli for first premolar in both specimens oblique with respect to mandibular ramus. Measurements (in mm) of the dental elements on OR-1327 are: tooth row length p2-m4= 27.6; p2L=5.6, p2W= 2.4; p3L= 4.9, p3W= 2.5; p4L=5.3, p4W=2.9; m1L= 5.7, m1W= 3.0; m2L= 6.6 , m2W=2.9.

Remarks--The Didelphinae (sensu Hershkovitz, 1992) include the extant *Chironectes*, *Didelphis*,

Figure 2. Right dentary of *Didelphis* sp. (OR-1327) in **A**, occlusal; and **B**, lingual view.

Lutreolina, and *Philander*, and the extinct genera *Hyperdidelphis* and *Thylophorops* (Reig et al., 1987). More recent taxonomic arrangements of this group (Gardner, 2005) exist, but we restrict our discussion to the morphological characters that were used previously by Hershkovitz (1992) and thus follow his taxonomic arrangement.

Using morphological features in the mandible allows separation of *Didelphis* from the other Didelphinae (Reig et al., 1987). In *Chironectes* the trigonid of the molars is as wide as it is long, but in the other Didelphinae the molar trigonid is longer than wide. The talonid on m4 in *Chironectes*, *Didelphis*, and *Philander* is the same size and shape as that on m3; but in *Hyperdidelphis*, *Thylophorops*, and *Lutreolina*, the m4 talonid is reduced and narrower than that on m3.

The metaconid on molars is subequal to or slightly reduced relative to the paraconid in *Hyperdidelphis*, *Didelphis*, and *Philander*; but in *Lutreolina* and *Thylophorops* the metaconid is noticeably reduced. In *Didelphis*, *Philander*, and *Chironectes* the molar protoconid is moderately larger and higher than the paraconid; but in *Hyperdidelphis*, *Lutreolina*, and *Thylophorops* the protoconid is much higher than the paraconid. *Didelphis* is the only didelphine with a highly developed anterior cingulum; *Metachirus* has the same condition, but the molar trigonid is as wide as it is long.

Order XENARTHRA (Cope 1889)
Suborder PHYLLOPHAGA Owen 1842
Infraorder TARDIGRADA Latham and Davies in Forster 1795
Superfamily MEGATHEROIDEA Gray 1821
Family MEGATHERIIDAE (Gray 1821)
Subfamily MEGATHERIINAE Gill 1872
Genus *EREMOTHERIUM* Spillman 1948
EREMOTHERIUM sp.
(Fig. 3A)

Referred Material--Left astragalus, OR-1330.

Description--The dorsal one third of the navicular facet on the astragalus projects above the level of the discoid facet; odontoid process well-developed, located dorsomedially, and in 90° orientation relative to discoid facet; ectal and sustentacular facets separated by deep and wide sulcus tali; distance between discoid and ectal facets greater in dorsolateral view; fibular facet subtriangular in shape.

Remarks--The distance between the ectal and discoid facets is considered a reliable generic character (De Iuliis, 1996). In *Eremotherium* and primitive Megatheriinae (*Megathericulus patagonicus* and *Pyramiodontherium bergi*) the discoid and ectal facets are widely separated, but in *Megatherium* they closely approach one another or are in contact (De Iuliis, 1996).

In *Pyramiodontherium bergi* and *M. patagonicus* the dorsomedial half of the navicular facet projects above the level of the discoid facet. By contrast, in *Megatherium americanum* the dorsomedial part of the navicular facet is at the same level as the discoid facet. At the other extreme, in *Eremotherium laurillardi* and *Megatherium urbinai* the dorsal third of the navicular facet projects above the level of the discoid facet. The navicular facet in *Megatherium tarijense* displays an intermediate position between *M. americanum* and *M. urbinai* (Pujos and Salas, 2004).

The Orocual material shows relatively large separation between the discoid and ectal facet in the astragalus, supporting referral of the specimen to *Eremotherium*.

Family MEGALONYCHIDAE Gervais, 1855
MEGALONYCHIDAE gen. et sp. indet.
(Fig. 3B)

Referred Material--Two molariform teeth, OR-1372, 1374.

Description--The molariform teeth are wider than long, sub-trapezoid to triangular in shape, with rounded corners; each has two transversely oriented low lophs, one mesial and one distal, both separated by an excavated fossa within the vasodentine, but converging to apex of triangle.

Remarks--Megalonychidae molariform teeth are sub-trapezoid to triangular in cross section, with the mesial and distal lophs of the occlusal surface converging towards the apex of the triangle (McDonald

et al., 2000), whereas megatheriid molariform teeth are square in shape, with two transverse and parallel crests separated by a deep V-shaped valley (Saint-André and De Iuliis, 2001; Cartelle and De Iuliis, 2006), and mylodontid molariform teeth are oval, elliptical, or lobulate (Cattoi, 1966; Paula Couto, 1979). The Orocual material displays all the features of Megalonychidae, but generic allocation is not possible on the basis of material recovered so far.

Suborder CINGULATA Illiger, 1811
Superfamily DASYPODOIDEA Gray, 1821
Family DASYPODIDAE Gray, 1821
Subfamily DASYPODINAE Gray, 1821
Genus *PROPRAOPUS* Ameghino, 1881
PROPRAOPUS SULCATUS (Lund, 1842)
(Fig. 3C)

Referred Material--94 Buckler osteoderms: OR-19-21, 24-25, 217-221, 223, 225-235, 237-239, 241-249, 391-421, 855, 861, 868-872, 877, 907, 1016-1027, 1227-1234; seven caudal osteoderms: 22, 27, 69, 222, 236, 240, 850; 16 imbricating osteoderms: 26, 224, 388-390, 1028-1035, 1224-1226.

Description--Buckler osteoderms are hexagonal, isometric, and ornamented with central figure more or less circular in shape, and peripheral figures smaller than central figure; all peripheral figures separated from central figure by sulcus that completely encircles central figure; anterior peripheral figures small and two or three in number; posterior peripheral figures smaller than anterior peripheral figures or absent; three to four hair pits within the sulcus between central and peripheral figures; buckler osteoderms twice the size of those in fossil and extant *Dasypus*, with low anterior part and raised posterior portion.

The imbricating osteoderms are elongated, with two divergent sulci forming a subtriangular inverted figure 'V' in shape, the base of which covers almost the entire posterior border where a few hair pits are located. The tail rings are composed of two rows of osteoderms, pentagonal in shape, and shorter than the imbricating osteoderms.

Remarks--*Propraopus* Ameghino 1881 appears to be a valid genus; diagnostic characters include osteoderms that are twice the size of those in *Dasypus*, a carapace with seven movable bands, and osteoderms with three or four peripheral figures that are separated from the central figure by a deeper and wider sulcus than that in *Dasypus*. The hair pits in *Propraopus* sit in the central sulcus between the central figure and the peripheral figures; in *Dasypus* the hair pits are found at the intersection of the central groove with the radial groove. The central figure is circular in shape, unlike that in *Dasypus*, which is always elliptical (Ameghino, 1881; Winge, 1915; Paula Couto, 1979; Carlini et al., 1997).

Propraopus includes four nominal species, all based on osteoderm morphology. *Propraopus punctatus* (Lund, 1838) and *P. sulcatus* (Lund, 1842) are reported from the Pleistocene of northeastern Brazil; *P. magnus* (Wolf, 1875) from Pleistocene deposits in Ecuador; and *P. grandis* (Ameghino, 1881) from the Pleistocene of Argentina and Bolivia. *Propraopus magnus* was considered a *nomen nudum* by Hoffstetter (1952), who noted its similar morphology and size to *P. grandis* and *P. sulcatus*. He also noted that Wolf's (1875) description of *P. magnus* was not sufficient to discriminate between that species and *P. sulcatus* or *P. grandis*. *Propraopus magnus* and *P. grandis* were both later considered to be synonyms of *P. sulcatus* (Paula Couto, 1979). We recognize two valid species of *Propraopus*, *P. sulcatus* and *P. punctatus*.

Propraopus sulcatus was described from Brazil (Lund, 1842). It is similar in size to *P. punctatus*, but is distinguished by having deeper radial and central grooves and fewer hair pits than *P. punctatus*. The osteoderm size, the number and distribution of hair pits, and the sculpture all support referral of the El Breal de Orocual material to *Propraopus sulcatus*.

Superfamily GLYPTODONTOIDEA Simpson 1931
Family GLYPTODONTIDAE Gray 1869
Subfamily GLYPTATELINAE Castellanos, 1932
Genus *PACHYARMATHERIUM* Downing and White, 1995
PACHYARMATHERIUM SP. CF. *P. LEISEYI* Downing and White, 1995

(Fig. 3D)

Referral Material--184 buckler osteoderms: OR-1-18, 87-178, 422-454, 799, 803, 807, 831, 846, 851, 866-867, 873-876, 942, 956, 1058-1060, 1235-1258.

Description--Osteoderms hexagonal and extremely thick for size, with hexagonal central figure displaced toward posterior edge, and separated from three to six smaller peripheral figures by well defined groove (sulcus) around central figure; peripheral figures well developed, separated from each other by radial sulci, but not found along posterior margin; all are wider, but less deep than in *P. leiseyi*; peripheral figures flat, and central figure less conical than in *P. leiseyi*; hair follicle pits or foramina large
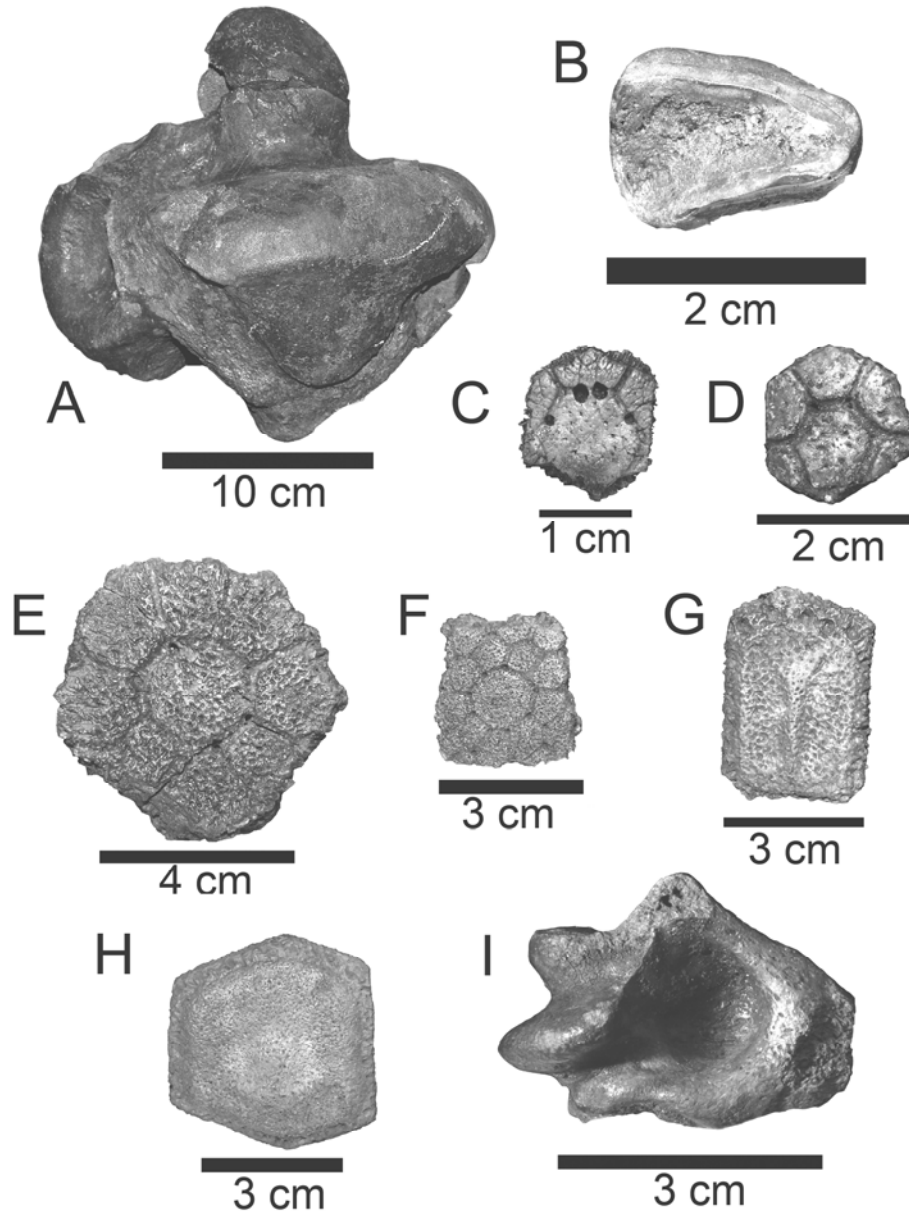

Figure 3. Xenarthra from Orocual. **A**, *Eremotherium* sp. fibular view of left astragalus (OR-1330); **B**, Occlusal view of Megalonychidae molariform (OR-1374); **C**, Buckler osteoderm of *Propraopus sulcatus* (OR-246); **D**, Buckler osteoderm of *Pachyarmatherium leiseyi* (OR-132); **E**, Buckler osteoderm of *Glyptodon* sp. (OR-1038): **F**, Buckler osteoderm of *Hoplophorus* sp. (OR-1002); **G**, Buckler osteoderm of *Holmesina occidentalis* (OR-050); **H**, Buckler osteoderm of *Pampatherium humboldtii* (OR-600); **I**, distal part of third metacarpal of *Myrmecophaga* sp. (OR-1012).

and few (0-3 in number) and located in intersections of the sulcus around central figure and in radial grooves; exterior surface rough and more sculptured and pitted than in *P. leiseyi*.

Remarks--The Glyptatelinae Castellanos, 1932, ranges from the late Eocene through early Pleistocene of North and South America (Vizcaíno et al., 2003), and is the oldest and most primitive glyptodont group according to McKenna and Bell (1997). It probably includes the genera *Glyptatelus* Ameghino 1897, *Clypeotherium* Scillato-Yané 1977, *Neoglyptatelus* Carlini, Vizcaíno and Scillato-Yané 1997, and *Pachyarmatherium* Downing and White 1995 (Vizcaíno, et al., 2003).

Glyptatelus was described on the basis of osteoderms and an (apparently) associated glyptodont-like lower jaw, resulting in its referral to the Glyptodontidae (Ameghino, 1897). Subsequent authors followed that precedent, and placed additional genera within Glyptatelinae. A nearly complete carapace and skeleton of *Pachyarmatherium leiseyi* was described by Downing and White (1995), who noted that the skull fragments associated with that specimen included an edentulous lower jaw with an articulation on the same level with the dorsal border of the horizontal ramus, a derived feature not found in the Glyptodontidae. They considered *P. leiseyi* to represent a dasypodoid of uncertain affinity. Monophyly of Gylptatellinae is not established and the phylogenetic affinities of glyptateline taxa are clearly uncertain. We follow McKenna and Bell (1997) in placing *Pachyarmatherium* within Glyptodontidae, but acknowledge that our decision is somewhat arbitrary.

The central figures of the osteoderms in *Glyptatelus tatusinus* and *G. fractus* are circular or subcircular in shape, with the dorsal surface of the central and peripheral figures strongly convex and smooth. In *Clypeotherium magnum* the central figure is polygonal, the central and peripheral figures are convex, and the dorsal surface is smooth; also the central and radial sulci are shallow and narrow. *Clypeotherium* is the largest genus in Glyptatelinae with the mean area of the central figure measuring up to 1085 mm^2. This combination of features is not present in the Orocual specimens.

The osteoderm morphology of *Pachyarmatherium* differs from that of *Neoglyptatelus*. *Pachyarmatherium* has a strongly convex central figure that forms a conical point displaced toward the back, and the peripheral figures are convex and separated by deep and narrow sulci. In *Neoglyptatelus originalis* and *N. sincelejanus* Villarroel and Clavijo, 2005, the central figure is only slightly convex and does not form a conical point, the peripheral figures are flatter than in *Pachyarmatherium*, and the peripheral and central sulci are shallower than those of *Pachyarmatherium*. Specimens from Orocual are morphologically similar to those of *Pachyarmatherium leiseyi* in having an extreme thickness relative to their size and in their dorsal surface architecture. However, the slight morphological differences between the Orocual specimens and the type material of *P. leiseyi* reduce our confidence in species identification. Although certainly allied with *P. leiseyi*, the Orocual material may represent a distinct species.

The first record of *Pachyarmatherium* in South America, based on the material from El Breal de Orocual, was reported as *P. leiseyi* by Rincón et al. (2007). Additional records of *Pachyarmatherium* were reported from the Lujanian of Uruguay and Southern Brazil (Bostelmann et al., 2008) and from the Late Pleistocene of Brazil (Porpino et al., 2008). Another interesting record of *P. leiseyi* was reported from the Pleistocene of Costa Rica (Laurito Mora et al., 2005). These records and the type material from Florida provide an interesting biogeographic pattern for this genus from the Pliocene through late Pleistocene deposits of Florida, through Central America, and much of South America.

Genus *GLYPTODON* Owen, 1839
GLYPTODON sp.
(Fig. 3E)

Referred Material--54 buckler osteoderms, OR-28-31, 461-473, 475-480, 794, 798, 801, 810, 814, 818, 821, 897-898, 999, 1036-1048, 1268-1275.

Description--Osteoderms generally thick and hexagonal or pentagonal in shape; dorsal surfaces covered with typical rosette sculpturing pattern, with central figure larger than peripheral figures; single row of six or seven peripheral figures and no indication of intercalations of a second row; central figure elevated above plane of peripheral figures and separated by relatively deep groove; central figure slightly concave in central part, forming a marked depression.

Remarks--Osteoderms of *Glyptodon* are larger and thicker than those of *Pachyarmatherium*, with a sub-circular or polygonal central figure that is separated by a well-marked sulcus from the peripheral figures, which are usually of smaller diameter than the central figure. This combination of characters, which agrees closely with those given by Ameghino (1889), forms the basis of our identification of the El Breal de Orocual glyptodont as *Glyptodon*.

Numerous species of *Glyptodon* Owen, 1839 are described. Only nine species were recognized by Castellanos (1954), but 28 species names were listed by Mones (1986), many of which he considered either *nomina nuda*, or for which the type specimens are now lost (thus *nomina dubia*). Consequently, few of these are considered valid. *Glyptodon clavipes*, *G. reticulatus*, and *G. elongatus* are recognized from the late Pleistocene (Lujanian SALMA), and *G. munizi* and *G. perforatus* from the early to middle Pleistocene (Scillato-Yané et al., 1995; Soibelzon et al., 2006).

The North American genus *Glyptotherium* Osborn, 1903, has osteoderms with a rosette pattern essentially identical to that of *Glyptodon*. The central figure is usually equal in size or somewhat larger than peripherals for interior scutes, with increasing importance of the central figure in the scutes nearer the margins of the carapace. There is only a single row of peripheral figures, varying from seven to 13 in number, surrounding the central figure. The peripheral figures are usually confined to one scute, although they occasionally overlap across sutural contacts (Gillette and Ray, 1981).

Glyptodon and *Glyptotherium* not only share osteoderm morphology, but also skull and postcranial features (see discussions by Ameghino, 1889; Cattoi, 1966; Gillette and Ray, 1981). Recent suggestions that these genera are clearly differentiable and that they can be distinguished by features of the skull and mandible, carapacial osteoderms, and the caudal shield (Carlini et al., 2008), must be tested through a rigorous phylogenetic and taxonomic analysis that documents and incorporates patterns of individual, ontogenetic, sexual, and other forms of variation within both nominal taxa. We suspect that the taxa could be synonymous.

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Subfamily HOPLOPHORINAE Weber, 1928
Genus *HOPLOPHORUS* Lund, 1839a
HOPLOPHORUS sp.
(Fig. 3F)

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Referred Material--69 Buckler osteoderms, OR-455-460, 957-998, 1000-1005, 1049-1055, 1260-1267.

Description--Osteoderms of *Hoplophorus* are thick for their size, but thinner than those of *Glyptodon*; central figure circular to subcircular, surrounded by two rows of polygonal peripheral figures smaller than central figure; central and peripheral sulci shallow and narrow, with follicular pits present; central and peripheral figures flat and rise to same level, with dorsal surfaces generally smooth to weakly sculptured.

Remarks--Glyptodontine osteoderms have a single row of peripheral figures, but hoplophorines have two rows. The Orocual specimens display a double row of peripheral figures, and their morphology is consistent with referral to *Hoplophorus*. These specimens document the only record of *Hoplophorus* in Venezuela.

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Family PAMPATHERIIDAE Edmund 1987
Subfamily PAMPATHERIINAE Paula Couto 1954
Genus *HOLMESINA* Simpson 1930
HOLMESINA OCCIDENTALIS (Hofftetter, 1952)
(Fig. 3G)

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Referred Material--30 buckler osteoderms, OR-49-57, 484, 498, 499,633-638, 825, 849, 1061-1065, 1277-1281.

Description--The submarginal band of each osteoderm is a sharply raised ridge above the low marginal band. The central portion of the osteoderm includes a prominent central ridge surrounded by a broad and shallowly excavated sulcus. The submarginal band gently descends into the sulcus. The marginal band is continuous around most of the osteoderm, but may become indistinct posteriorly, and

may merge somewhat with the central ridge. The sulcus in the central portion of the osteoderm is broad, but posteriorly it is not always clear where the sulcus ends and the submarginal band begins. Numerous follicular pits are present; they are shallow and elongate, and positioned along the marginal band. The average thickness of the Orocual specimens is 9 mm (observed range 6.8 to 11.8 mm), and the mean area (*sensu* Edmund, 1996) is 1041 mm (observed range 551.4 to1659.0 mm).

Remarks--The osteoderms of pampatheriids are thinner than those of other Glyptodontoidea, but thicker and larger in area than in the Dasypodoidea. Each pampatheriid osteoderm also has a rough, sutured margin. The anterior part of the dorsal surface is distinguished by an area of follicular pits and these may be continuous around the margin of the osteoderm, usually along the narrow, depressed, rugose marginal band. The central figure is often ridge or crest-shaped, but varies in morphology and height (Edmund, 1996).

Although somewhat subtle, the ornamentation of the osteoderms in *Holmesina* is more pronounced than in the *Vassallia-Plaina-Pampatherium* group (Edmund, 1987). The two genera of pampatheriids with osteoderms most closely resembling those from Orocual are *Pampatherium* and *Holmesina*, and they can be distinguished based on features of their osteoderms (Scillato-Yané et al., 2005). One of the most diagnostic features for distinguishing between these genera is the presence of a raised keel-like central figure in *Holmesina*, absent (or nearly so) in *Pampatherium* (broad, flat, low, and elongated when present). The dorsal surface of the osteoderms of *Holmesina* is strongly ornamented by deep pits, but the dorsal surface of those in *Pampatherium* is weakly ornamented. Osteoderms of *Holmesina* are thicker than those of *Pampatherium*. The diagnostic presence of a raised keel-like central figure and the thickness of the osteoderms allow us to assign these specimens to *Holmesina occidentalis*, but we note that the osteoderms from Orocual have a mean area below the averages reported by Edmund (1996) for *H. occidentalis* from Talara, Peru (1806 mm), and Santa Elena, Ecuador (1933 mm).

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Genus *PAMPATHERIUM* Ameghino, 1875
PAMPATHERIUM HUMBOLDTII (Lund, 1839b)
(Fig. 3H)

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Referred Material--347 buckler osteoderms, OR-32-48, 179-216, 481-483, 485-497, 500-629, 745-746, 748, 802, 804, 806, 811-813, 816, 819, 823, 832, 841-843, 845, 853-854, 857-858, 878-885, 887-896, 899, 1066-1126, 1259, 1283-1326; six imbricating osteoderms, 630-632, 809, 822, 1282.

Description--In general these osteoderms are poorly ornamented dorsally. Measurements of a sample of 50 buckler osteoderms from Orocual were taken, and the average thickness was 7.97 mm (observed range 5.9 to 10.5 mm); the mean area was about 1469 mm^2 (observed range 2830.2 to 917.4 mm^2). The central figure is broad, elongate, low, and flat, and is isolated from the submarginal band. The central figure often is not perceptible and sometimes is tapered posteriorly. The sulcus around the central figure is shallow and continuous posteriorly. The submarginal band is narrow, slightly elevated and although it often completely surrounds the sulcus, it occasionally is absent anteriorly. The marginal band is wide and continuous around the osteoderm, but is narrow posteriorly. The anterior part of the marginal band is wide, but the posterior part is narrow or absent.

The imbricating osteoderms are thin and poorly ornamented dorsally. The central figure is low, broad, and at the same height as the submarginal band.

Remarks--Two genera and seven species of Pleistocene Pampatheriidae were recognized by Paula Couto (1954). These are *Pampatherium humboldtii* (Lund, 1839b) from Brazil, *Pampatherium typum* Ameghino, 1875 from Argentina, *Pampatherium mexicanum* Edmund, 1996 from Mexico, *Holmesina majus* (Lund, 1842) from Brazil, *Holmesina septentrionalis* (Leidy, 1889) from the United States, *Holmesina paulacoutoi* (Cartelle and Bohórquez, 1985) from Brazil, and *Holmesina occidentalis* (Hoffstetter, 1952) from Peru, Ecuador, Colombia, and Venezuela. Distinguishing generic characters were listed above (under *Holmesina*).

The Orocual specimens have a narrow, slightly elevated and shallow submarginal band; it is approximately 0.8-1 mm deep, and continues posteriorly as in *P. humboldtii*. The central figure of the osteoderms from Orocual is broad, elongated, low, and flat, and in some specimens almost imperceptible.

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It does not rise posteriorly; it is isolated from the submarginal band, and it often tapers posteriorly. These characters justify assignment of these Orocual osteoderms to *Pampatherium humboldtii*.

Suborder VERMILINGUA Illiger, 1811
Family MYRMECOPHAGIDAE Gray, 1825
Genus *MYRMECOPHAGA* Linnaeus, 1758
cf. *MYRMECOPHAGA* sp.
(Fig. 3I)

Referred Material--Distal fragment of third metacarpal, OR-1012.

Description--Deep, broad concavity on anterodorsal part; distal carina strong dorsoventrally; tuberosity of exterior tendon well developed.

Remarks--The Orocual material is more robust than *Tamandua* and *Neotamandua*, and is similar to *Myrmecophaga* (Hirschfeld, 1976; Shaw and McDonald, 1987). The morphology of the distal third metacarpal in *Tamandua*, *Neotamandua,* and *Myrmecophaga* is similar, but in *Myrmecophaga* the distal end of the shaft is more displaced medially than it is in *Tamandua* or *Neotamandua* (Hirschfeld, 1976; Shaw and McDonald, 1987). Only tentative identification of this myrmecophagid is possible.

Order RODENTIA Bowdich, 1821
Suborder HYSTRICOGNATHI Tullberg, 1899
Superfamily CAVIOIDEA Kraglievich, 1930
Family HYDROCHAERIDAE Gray, 1825
Subfamily PROTOHYDROCHOERINAE Kraglievich, 1930
cf. CHAPALMATHERIUM Ameghino, 1908
(Fig. 4A)

Referred Material--Fragment of the left dentary with the dp4, OR-1333.

Description--Hypsodont-elasmodont fourth lower premolar; anterior secondary prism (pr.s.a.), first prism (pr.I), and second prism (pr.II) connected lingually; secondary posterior internal flexid (h.s.i.p.) included on lingual side of pr.I, mesial to fundamental external flexid (h.f.e.); h.s.i.p. achieves a depth of penetration similar to that of secondary anterior internal flexid (h.s.i.a.); h.f.e. and secondary external flexid deep, essentially transverse, and straight; fourth internal flexid (h.4i.) similar in depth to primary internal flexid (h.p.i.); fifth internal flexid (h.5i.) absent; h.p.i. up to 50% of total width.

Remarks--The p4 in Protohydrochoerinae have a deep h.s.i.p. on the lingual side of the first prism. The h.f.e. is transversely directed and deeper than in Hydrochoerinae, in which it is obliquely directed (Bondesio, 1975; Pascual, 1966). In Hydrochoerinae h.s.i.a is similar in depth to h.s.i.p, and h.s.i.p. is excluded from pr.I (Pascual, 1966). In Cardiatheriinae, specifically in *Cardiatherium*, the h.s.i.p is included in pr.I, with a depth of penetration that extends labially beyond the level of lingual penetration by the h.f.e. (Pascual, 1966).

The number and depth of penetration of flexids in hydrochoerid teeth vary ontogenetically, but the relative positions of these structures appears to be stable through ontogeny. The patterns of ontogenetic variation historically led to various taxonomic designations being assigned to specimens that merely represented ontogenetic variants (Vucetich et al., 2005).

The single Hydrochoeridae specimen from Orocual represents a juvenile, so our identification is tentative. The position of the secondary posterior internal flexid on the lingual side of the first prism, and the fact that it penetrates labially beyond the level of lingual penetration by the h.f.e., suggest that the specimen could belong to either Protohydrochoerinae or Cardiatheriinae, but is inconsistent with referral to Hydrochoerinae. In Cardiatheriinae, specifically in *Cardiatherium*, the h.s.e. is strongly directed anteriorly, except in the younger stages, where the h.4i. is not developed (it appears only in late stages of ontogeny; Deschamps et al., 2007). On the Orocual specimen, the h.s.e. is oriented anterolingually, suggesting it is not a member of Cardiatheriinae.

The fossil record of Protohydrochoerinae is represented by *Protohydrochoerus* and *Chapalmatherium*. In the p4 of *Protohydrochoerus* the h.4i. and h.s.i.p are deeper than they are in the p4 of *Chapalmatherium*. These characters suggest an affinity of the Orocual material with the genus

Chapalmatherium, but because ontogenetic transformations within Protohydrochoeridae are unknown, we provide only tentative referral.

Family ERETHIZONTIDAE Bonaparte, 1845
ERETHIZONTIDAE gen. et sp. indet.
(Fig. 4B, C, D)

Referred Material--Associated right and left M1, and left(?) M2, OR-1334.

Description--Brachyodont and pentalophodont low-crowned teeth, longer than wide, thick enamel and long roots, slight unilateral hypsodonty, convex walls, mesoflexid extended across three quarters of occlusal surface; two medial roots thick, three lateral roots thin; anteroloph fused with protoloph labially, forming anterofossette; mesolophule fused with posteroloph labially, forming metafossette; metaloph shaped like small spur and almost fused with the posteroloph in P4.

Remarks--Diagnostic features of Erethizontidae (*Stereiomys*, *Erethizon*, and *Coendou*) were reported by Scott (1905) to include low-crowned teeth covered with thick enamel, long roots, and a masticating surface with deep valleys. *Paradoxomys cancrivorus* was suggested to be a member of Erethizontidae because it has brachyodont molars with convex walls, and the mesoflexid extends across three quarters of the width of the occlusal surface (Vucetich and Candela, 2001). Although their description pertained to lower teeth only, those conditions are observed in the upper molars in most extant and extinct Erethizontidae. The cheek teeth of erethizontids are markedly brachyodont, medium to large sized, and with thick enamel layers. That combination of features is not necessarily apomorphic for porcupines, but it is clearly characteristic of the group.

The Orocual teeth are referred to Erethizontidae because they are characterized by all of the features recognized for that family, but no specific assignation is possible because most diagnostic features are derived from skull. The Orocual specimens appear to represent the first fossil record of Erethizontidae in Venezuela.

Family ECHIMYIDAE Gray, 1825
Subfamily EUMYSOPINAE Rusconi, 1935
Genus *PROECHIMYS* Allen, 1899
PROECHIMYS sp.
(Fig. 4E)

Referred Material--m3, OR-1335; skull fragment with associated right P4 to M2, and left P4 to M3, 1356.

Description--Generally mesodont and tetralophodont teeth. Third lower molar with two counter folds (mesoflexid and metaflexid); mesoflexid open lingually and fused with hypoflexid, separating posterolophid and hypoconid; mesoflexid and anteroflexid almost closed lingually; mesolophid small and spur-like, and not connected to mesostylid; anterior part of anterolophid slightly curved; upper cheek teeth (OR-1356) with three counter folds; molariform P4; M1, M2, and M3 with labial fold closed, forming anterofossette, mesofossette, and parafossette; hypoflexus deep and close to parafossette.

Remarks--Mesodont teeth with two or four isolated folds permit referral to the Eumysopinae (Ellerman, 1940; Patton, 1987; Vucetich et al., 1993). Heteropsomyinae have protohypsodont teeth with three folds (Anthony, 1918).

Eumysopinae (sensu Woods, 1993) includes the extant genera *Proechimys*, *Hoplomys*, *Euryzygomatomys*, *Clyomys*, *Carterodon*, *Thrichomys*, *Mesomys*, and *Lonchothrix* (Nowak, 1999); extinct taxa include *Pampamys*, *Eumysops*, *Chasichimys*, and *Reigechimys*, all of which are from late Miocene to early Pliocene deposits (Nasif, 1998). *Carterodon*, *Hoplomys*, *Mesomys*, and *Lonchothrix* have brachyodont and pentalophodont teeth; *Eumysops*, *Euryzygomatomys*, *Clyomys*, *Thrichomys*, *Pampamys*, *Chasichimys*, and *Reigechimys* have simple trilophodont to bilophodont teeth (Verzi et al., 1995). *Carterodon* was included in Eumysopinae by Woods (1993), but now is considered incertae sedis and could belong to another subfamily (Vucetich and Verzi, 1991; Verzi et al., 1995). *Proechimys* has a tetralophodont or simplified trilophodont pattern (Patton, 1987). For those reasons the Orocual material is referred to *Proechimys*.
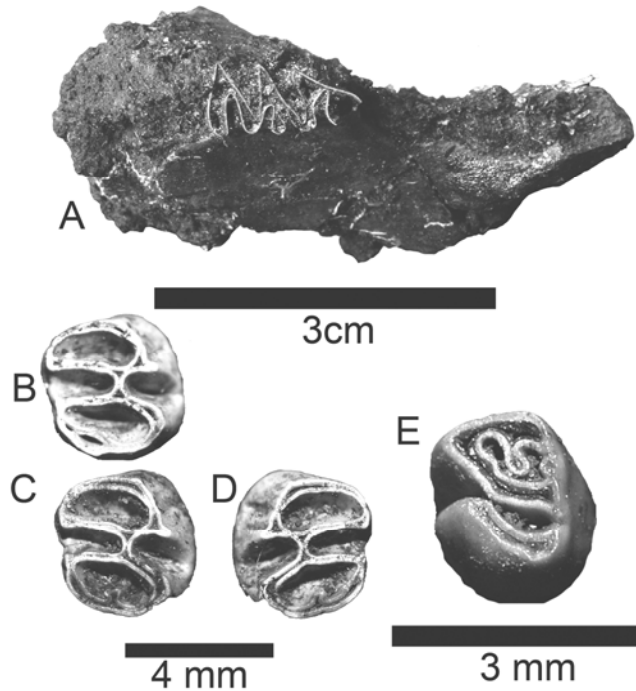
Figure 4. Rodentia from Orocual. **A**, Fragment of the left mandible with the fourth premolar of cf. *Chapalmatherium* sp. (OR-1333); **B**, Erethizontidae gen. et sp. indet. right P4 (OR-1334); **C**, right M1; **D**, left M1; **E**, m3 of *Proechymis* sp. (OR-1335).

Order CARNIVORA BOWDICH, 1821
Family CANIDAE FISCHER, 1817
Subfamily CANINAE FISCHER, 1817
cf. *PROTOCYON*
(Fig. 5A)

Referred Material--Right dentary with i3-m2, and incomplete left dentary with i1-3, c1, p2-m3, OR-1332; right m1, 791; fragment of right dentary with m2, 1336; left m1, 1338; right m1, 1337; right M1, 242; left p2?, 789; fragment of right maxilla with P3, 713; left metacarpal V, 261.

Description--Labial cingulum of M1 reduced; hypocone low but conspicuous, and contacts mesial cingulum; metacone much smaller than paracone on M1, with small paraconule and metaconule; angular process of mandible deep, with wide scars for inferior and superior branches of medial pterygoid muscle; well developed subangular lobule and strong horizontal ramus; except for p4, premolars lack accessory cusps; principal cusps of teeth acute; m1 with small metaconid, wrinkled enamel, small crest-like hypoconulid, and entoconid reduced to a crest; in OR-791, adjacent to the hypoconid, entoconid crest elevated as a cone but still more crest-like than in typical entoconid; m2 with reduced mesiolabial cingulum; entoconid reduced to a cingulum and metaconid smaller than protoconid. Measurements (in mm) of the dental elements on the OR-1332 right dentary: tooth row length c1-m2= 105.5; c1L= 12.7, c1W=8.9; p1L=5.8, p1W= 4.3; p2L=11.8, p2W=5.4; p3L= 12.1, p3W= 5.4; p4L= 15.9, p4W= 7.0; m1L= 26.6, m1W= 11.2; m2L= 10.1, m2W= 7.3.

Remarks--The size and most of the characters of these specimens are consistent with referral to *Protocyon*, as it was redefined by Prevosti (2006), and they also permit separation from other large canids. *Theriodictis*, *Canis dirus*, and "*Canis*" *gezi* are larger, and have a well-developed and conical entoconid on m1. In *Canis* the m1 metaconid is larger. An entoconid reduced to a crest on m1 is present in some specimens of *Protocyon tarijensis*, but the metaconid is absent in all known individuals of the genus (see Prevosti, 2006). In *Theriodictis platensis* (and other species like *Cuon alpinus*), the presence of the metaconid on m1 is variable (see Berta, 1988; Prevosti, 2006). These specimens were preliminarily identified as *Canis* by Rincón et al. (2007), but the pattern of the premolars (presence of acute principal
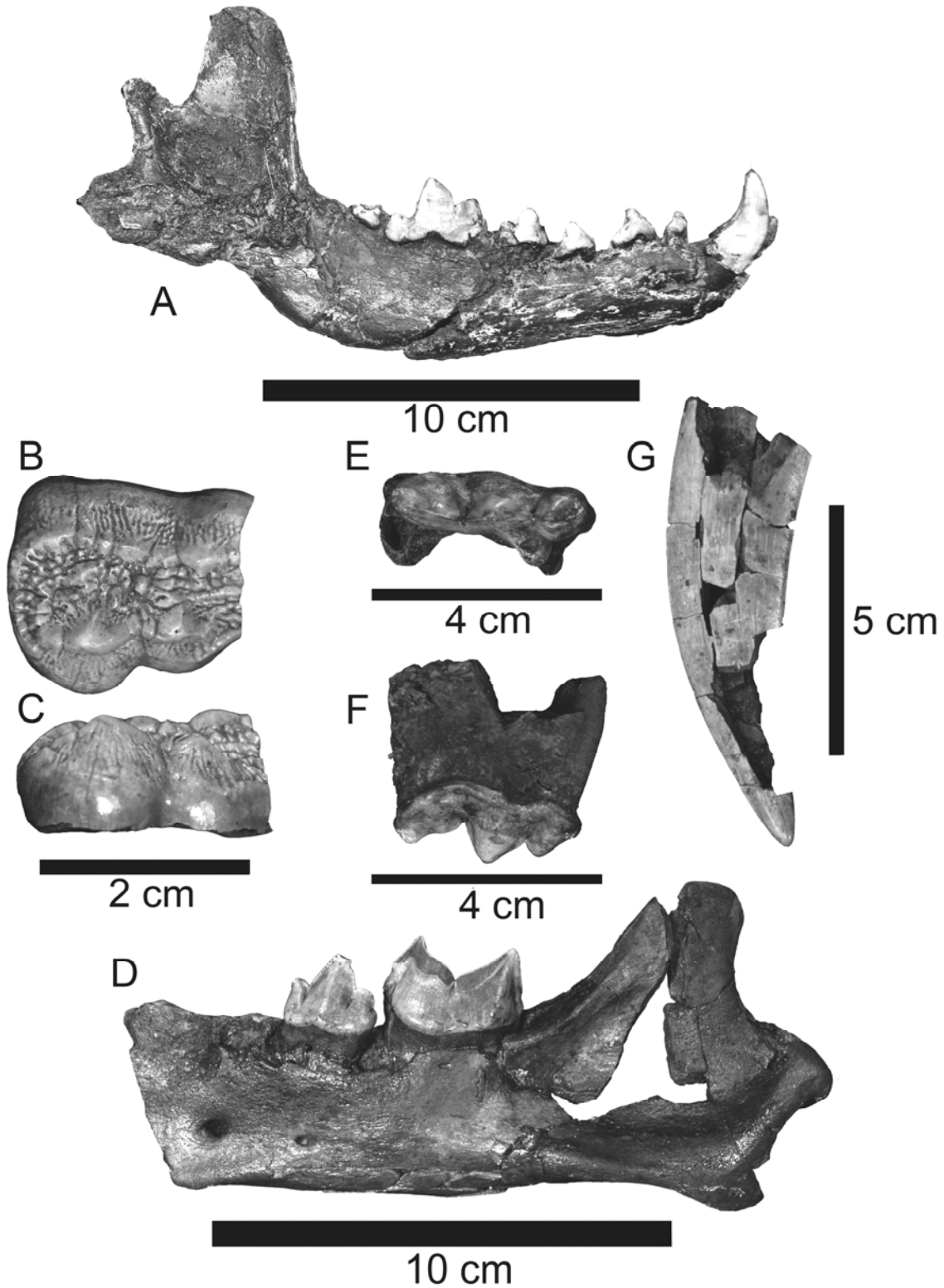
Figure 5. Carnivora from Orocual. **A**, cf. *Protocyon* right dentary with i3-m2 (OR-1332); **B**, *Arctotherium* cf. *A. wingei*, anterior fragment of left M2 (OR-1339), occlusal view; **C**, labial view of same; **D**, Homotheriini, left dentary (OR-259), labial view; **E**, *Smilodon* sp., right P4 (OR-1343), occlusal view; **F**, labial view of same; **G**, upper crown of left canine (OR-1342), lingual view.

cusps) agrees with *Protocyon* and differentiates the Orocual specimens from other large canids (e.g., *Canis*, *Cuon*, *Lycaon*). The combination of characters of the m1 from Orocual could correspond to a new species of *Protocyon*, because it appears to be unique, but available material is insufficient to justify a new species description.

Family URSIDAE Gray, 1825
Subfamily TREMARCTINAE Merriam and Stock, 1925
ARCTOTHERIUM cf. A. WINGEI
(Fig. 5B, C)

Referred Material--Anterior fragment of left M2, OR-1339.

Description—Tooth small and apparently relatively wide (width at the mesial portion, 20.5 mm) with straight labial and mesial borders; biconvex lingual border with convexities formed by protocone and hypocone (Fig. 5B); cusps low, some subdivided (Fig. 5C); large paracone and metacone labially; protocone and hypocone form continuous crest, but separated by shallow groove.

Remarks--The morphology and size of this specimen agrees with the description of *Arctotherium wingei* by Soibelzon and Rincón (2007), but its fragmentary nature precludes definitive identification. M2 is smaller than in other species of *Arctotherium* and larger than in *Tremarctos*. This species is reported from late Pleistocene sites in Brazil, Bolivia, and Venezuela (see Soibelzon and Rincón, 2007).

Suborder FELIFORMIA Kretzoi, 1945
Superfamily FELOIDEA Simpson, 1931
Family FELIDAE Gray, 1821
Subfamily MACHAIRODONTINAE Gill, 1872
Tribe HOMOTHERIINI (Fabrini, 1890)
(Fig. 5D)

Referred Material--Two left dentaries, OR-259, 330; two dentary fragments, 710-711; upper incisor, 1346; four upper canines, 712, 1342, 1349-1350; two upper canine fragments, 258, 1219; I3, 256; left P3, 1344; right P3, 1347; right P4, 1343; P4, 255; left P4 fragments, 1345; lower incisor, 785; four lower canines, 254, 1166, 1220-1221; p4, 257; teeth fragments, 767; left humerus, 1351.

Description--Teeth coarsely serrated, upper canine shorter than in Smilodontini; lower incisors strongly procumbent with tall and acute principal cusps, and strong distal accessory basal cusps; P4 long and extremely compressed in lateral dimension, with extremely reduced protocone, and finely serrated margins; p4 with short distal cingulum and strong mesial accessory cusp; as in upper carnassial, m1 elongated and laminated, with strong mesial and distal vertical crests on paraconid and protoconid, respectively; mandible has deep ramus, reduced coronoid process, ventrally directed angular process, and shallow masseteric fossa; alveolus for single-rooted p3 present but small. Measurements (in mm) of the dental elements of OR-259 are: tooth row length p3-m1=67.7; p4L=21.1, p4W= 10.3; m1L= 30.9, m1W= 13.6.

Remarks--The hypertrophied upper canines with strong serrations, the elongated carnassials , and a mandible with a strongly fused symphysis are diagnostic of a large homotheriine cat (Meade, 1961; Rawn-Schatzinger, 1992; Martin, 1998). The mandibular morphology shows a unique suite of characters and cannot be unambiguously referred to any known homotheriine. The shallow masseteric fossa is elsewhere thought to be characteristic of *Xenosmylus*, but the presence of a p3 suggests affinity with *Homotherium*.

The southernmost definitive records of homotheriine cats are in the southern United States. A fragmentary dentary from Uruguay may represent a homotheriine (Mones and Reinderknecht, 2004), but the Orocual material definitively documents the presence of this lineage in northern South America.

Tribe SMILODONTINI Kurtén, 1963
Genus *SMILODON* Lund 1842
SMILODON sp.
(Fig. 5E, F, G)

Referred Material--Upper incisor, OR-1346; fractured left upper crown of canine, 1342; left P3, 1344; right P3, 1347; right P4, 1343; left P4 fragments, 1345.

Description--P4 is elongated and transversally narrowed, with a large metastyle and parastyle (Fig. 5E), and a small ectoparastyle (Fig. 5F); protocone present but small and low. As in other sabertooth cats, the canine is much hypertrophied, long, and transversally narrowed (Fig. 5G); the crown is curved distally and shows tiny serrations on its margins (as opposed to coarse serrations in homotheriines). Measurements (in mm) of the dental elements of OR-1342, C1L= 27.4, C1W=14.7; OR-1344, P3L= 17.8, P3W= 7.8; OR-1343, P4L=33.3, P4W= 14.4.

Remarks--The morphology and size of these teeth match the diagnosis of *Smilodon*, but they lack diagnostic characters to allow specific determination (Berta, 1985, 1987; Kurtén and Werdelin, 1990).

Order PERISSODACTYLA Owen, 1848
Family EQUIDAE Gray, 1821
Subfamily EQUINAE Gray, 1821
Tribe EQUINI Gray, 1921
Subtribe PLIOHIPPINA Prado and Alberdi, 1996
Genus *HIPPIDION* Owen, 1869
HIPPIDION sp.
(Fig. 6A, B, C, D)

Referred Material--One right upper molar, M1-2, OR-761; unworn right lower m1-2, 732; right third metacarpal, 1328; distal part of a possible third metacarpal, 796.

Description--We follow the nomenclature of Eisenmann et al. (1988) and Evander (2004), and the systematics of Alberdi and Prado (1993) and Prado and Alberdi (1996). The upper right molar (OR-761) is from a young adult, with a thin parastyle and mesostyle, an enlarged oval protocone with a marked pli caballin, and an oval enlarged hypocone with a marked hypoconal groove (Fig. 6B, C). The tooth is covered by a thick layer of cementum and is curved lingually. The upper molar is intermediate in size with respect to other *Hippidion* from South America.

The lower right molar (m1-2, OR-732) is probably from a juvenile, as the tooth is not yet fully erupted and the pattern of the occlusal surface is only partially formed (i.e., the metaconid-metastylid, linguaflexid, hypoflexid, preflexid, and postflexid are in juvenile condition; only the protoconid and hypoconid are well rounded; Fig. 6D). The tooth is covered by a thick layer of cementum. The lower molar is large relative to other *Hippidion* from South America.

The right third metacarpal (OR-1328) is massive and relatively short, characteristic of the genus *Hippidion*, and it has the articulation facet for the fourth metacarpal (Fig. 6A).

Remarks--We compared the Orocual material with a database of metacarpals from South America (developed by MTA). A discriminate analysis placed this specimen in a zone of overlap between *H. principale* and *H. devillei*. The morphology of the upper and lower teeth is characteristic of *Hippidion*, but this morphology is not diagnostic to a particular species. With large enough samples, species can be differentiated by size; but current sample sizes are too small to permit species identification. The upper molar is too small to be *H. principale*, but the lower molar is too big to be referred to *H. devillei*. These specimens represent the first record of *Hippidion* from Venezuela.

Family TAPIRIDAE Burnett, 1830
Genus *TAPIRUS* Brünnich, 1771
TAPIRUS new species
(Fig. 6E, F)

Referred Material--Maxilla fragment with P4 to M3, OR-1367; dentary fragment with c1 to m3, 1369; dentary fragment with m2 and m3, 1367; M3, 276; lower incisor, 274.

Description--Check teeth brachyodont and bunolophodont, and relatively high-crowned; P4 and M1 with strong anterior and posterior cingulum; posterior cingulum weaker in M2 and M3; parastyle strongly developed (Fig. 6E); infraorbital foramen dorsal to fourth upper premolar and mental foramen slightly anterior to second lower premolar (Fig. 6F). Measurements (in mm) of the dental elements of OR-

1369 are tooth row length c1-m3= 216.9; diastema length c1-p2= 67.8; c1L= 13.3, c1W= 11.4; p2L= 21.4, p2W= 13.6; p3L= 18.3, p3W= 19.1; p4L= 21.1, p4W= 17.7; m1L= 21.0, m1W= 16.1; m2L= 24.8, m2W=17.7; m3L= 26.2, m3W= 18.3.

Remarks--Only *Tapirus johnsoni* and *T. webbi* are known to have the infraorbital foramen dorsal to the fourth upper premolar. The parastyle is only moderately developed in *Tapirus johnsoni*, but is strongly developed in *T. webbi*, as it is in the Orocual material. The mental foramen in *T. webbi* is located directly ventral to the p2, whereas in *T. johnsoni* it is more anteriorly positioned (Hulbert, 2005). The material available from Orocual presents a combination of features consistent with referral to *Tapirus webbi*, but additional material and more detailed comparisons are required before definitive species allocation can be made. These specimens appear to represent a new species of *Tapirus*, but one with close morphological affinity to *T. webbi*.
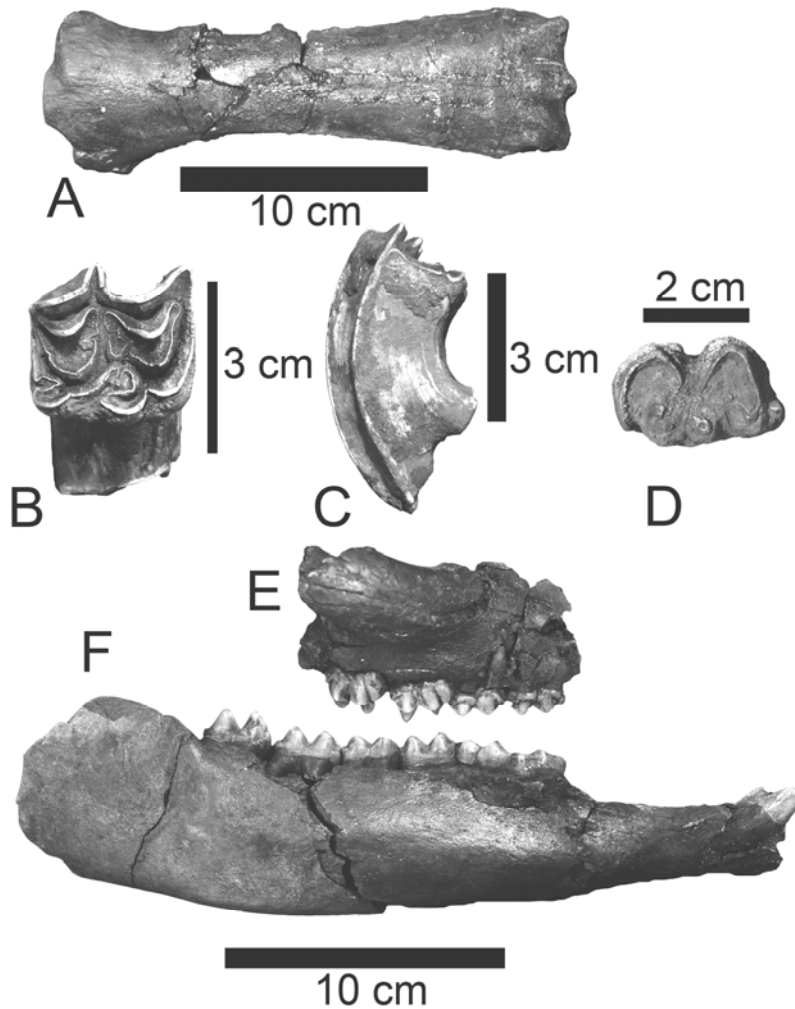

Figure 6. Perissodactyla from Orocual. **A**, *Hippidion* sp., anterior view of right third metacarpal (OR-1328); **B**, *Hippidion* sp., right M1 or M2 (OR-761), occlusal view; **C**, same, lateral view; **D**, *Hippidion* sp., possible juvenile right m1 or m2 (OR-732); **E**, *Tapirus* n. sp., maxilla fragment with P4 to M3 (OR-1367); **F**, *Tapirus* n. sp., dentary with c1 to m3 (OR-1369).

Order ARTIODACTYLA Owen 1848
Family TAYASSUIDAE Palmes 1821
Subfamily TAYASSUINAE Hay 1902
Genus *PLATYGONUS* Le Conte 1848
PLATYGONUS sp.

(Fig. 7A)

Referred Material--Partial skull with maxillary tooth rows, OR-1354; right skull fragment with P2 to M3, 1355; dentary fragment with deciduous tooth, 777; broken left dentary with m2 and m3, 1353; four P2, 281, 283, 291, 1364; P3, 290; three P4, 282, 778, 1129; M1, 1217; two M2, 280, 331; three M3, 779, 1009, 1363; lower canine, 1210; five p2, 284, 332, 334, 783, 1357; seven p3, 287, 1008, 1127, 1128, 1358, 1360, 1365; three p4, 1211, 1359, 1361.

Description--Lower canine large, tusk-like, and triangular in cross-section; lower premolars nonmolariform with single pair of well-developed cusps; anterior cingulum small and posterior cingulum well-developed; p4 larger than p3; p3 larger than p2; lower molars longer than wide, bilophodont, with high cusps; m1 and m2 tetracuspidate with protoconid and paraconid connected to form anterior transverse crest (loph) separated from posterior crest formed by metaconid and hypoconid; m3 is pentacuspidate with no accessory cuspule between hypoconulid and posterior crest; upper and lower molars with well-developed anterior, posterior, and labial cingulae; upper premolars nonmolariform, bicuspidate, with well-developed anterior and posterior cingulum; P2 triangular; P3 and P4 wider than long; upper molars tetracuspidate; protocone and paracone united by crest, but separated from posterior crest (connecting the metacone and hypocone) by deep valley; M1 and M2 quadrangular in shape; M3 with anterior crest wider than posterior. Measurements (in mm) of the dental elements of OR-1355, tooth row length p2-m3= 81.6; p2L=11.6, p2W= 11.3; p3L= 11.8, p3W= 13.4; p4L=11.7, p4W=14.1; m1L=14.7, m1W= 13.9; m2L=16.5 m2W= 16.3; m3L= 18.6, m3W= 16.4.

Remarks--Referral to Tayassuidae is based on brachyodont and bunodont, or bunolophodont, molars, the triangular cross-section and vertical orientation of the canines, and by the occlusion of the posterior side of the lower canine with the anterior surface of the upper (Ortega Hinojosa, 1966; Hulbert et al., 2001).

Tayassuids are represented by *Platygonus* and *Mylohyus* in the late Pliocene and Pleistocene of North America (Hulbert et al., 2001). The South American fossil record includes *Platygonus* (late Pliocene to early Pleistocene), *Selenogonus* (Pliocene-Pleistocene), *Catagonus* (early-middle Pleistocene to Holocene), and *Tayassu* (late Pleistocene to Holocene; Menégaz and Ortiz Jaureguizar, 1995).

Referral to *Platygonus* is supported by the nonmolariform premolars, bunolophodont molars, third lower molar with five cusps, and no cuspules among the principal cusps. The Orocual material represents the first record of this genus in Venezuela.

TAYASSU sp.
(Fig. 7B)

Referred Material--Left m3, OR-294.

Description—Low-crowned, five-cusped, bunodont, and brachyodont tooth, with many small extra cuspules. Measurements in mm of m3 L=24.1, and W= 13.7.

Remarks--*Platygonus* and *Catagonus* have high crowned teeth. *Mylohyus* and *Tayassu* have lower-crowned teeth; *Mylohyus* is more bunodont than *Tayassu* (Wetzel, 1977). *Catagonus*, *Platygonus*, and *Tayassu* have five cusps on m3, *Mylohyus* has six. *Catagonus*, *Tayassu*, and *Mylohyus* have many accessory cuspules among the principal cusps. *Selenogonus* is known only from a posterior dentary fragment and an associated posterior portion of a broken m3 (Stirton, 1946), and its validity is uncertain. The features preserved on the Orocual specimen support referral to the genus *Tayassu*, but no further identification can be supported based on the material available.

Order ARTIODACTYLA Owen, 1848
Family CAMELIDAE Gray, 1821
Subfamily CAMELINAE Gray, 1821
Tribe LAMINI Webb, 1965
Genus *PALAEOLAMA* Gervais, 1869
PALAEOLAMA sp.
(Fig. 7C, D)

Referred Material--Left dentary fragment with m1 to m3, OR-1340; right dentary fragment with m2 to m3, 1341; left P4, 762; left M2, 272; deciduous lower premolar, 065; p3, 763; deciduous lower molar, 066, 273. Measurements (in mm) of dentary, OR-1340: tooth row length m1-m3= 79.1; m1L= 21.8, m1W=14.5; m2L=24.1, m2W= 14.1; m3L=31.7, m3W= 15.6.

Description--M2 brachyodont and selenodont, with mesial lobe larger than distal; mesostyle larger than parastyle; parastyle larger than metastyle; metastyle smallest labial style; hypostyle and entostyle absent; protostyle small; trigon and talon fossa shallow and V-shaped; protocone and hypocone V-shaped in occlusal view (Fig. 7C); lower molars (OR-1340 and OR-1341) relatively less hypsodont than in *Hemiauchenia* (maximum crown height on the second lobe of m3 is 21.2 mm; Fig. 7D); molars with thin cementum; protoconid and hypoconid V-shaped in occlusal view; parastylid, metastylid, and endostylid small; protostylid small and almost imperceptible; mesostylid absent; m3 with third distal lobe formed by hypoconulid, without a fossid.

Remarks--Although Viret (1961) noted that *Lama* possesses a well-marked parastyle, mesostyle, and metastyle on m2 and m3, Hoffstetter (1952) indicated that these are absent or reduced from m2 and
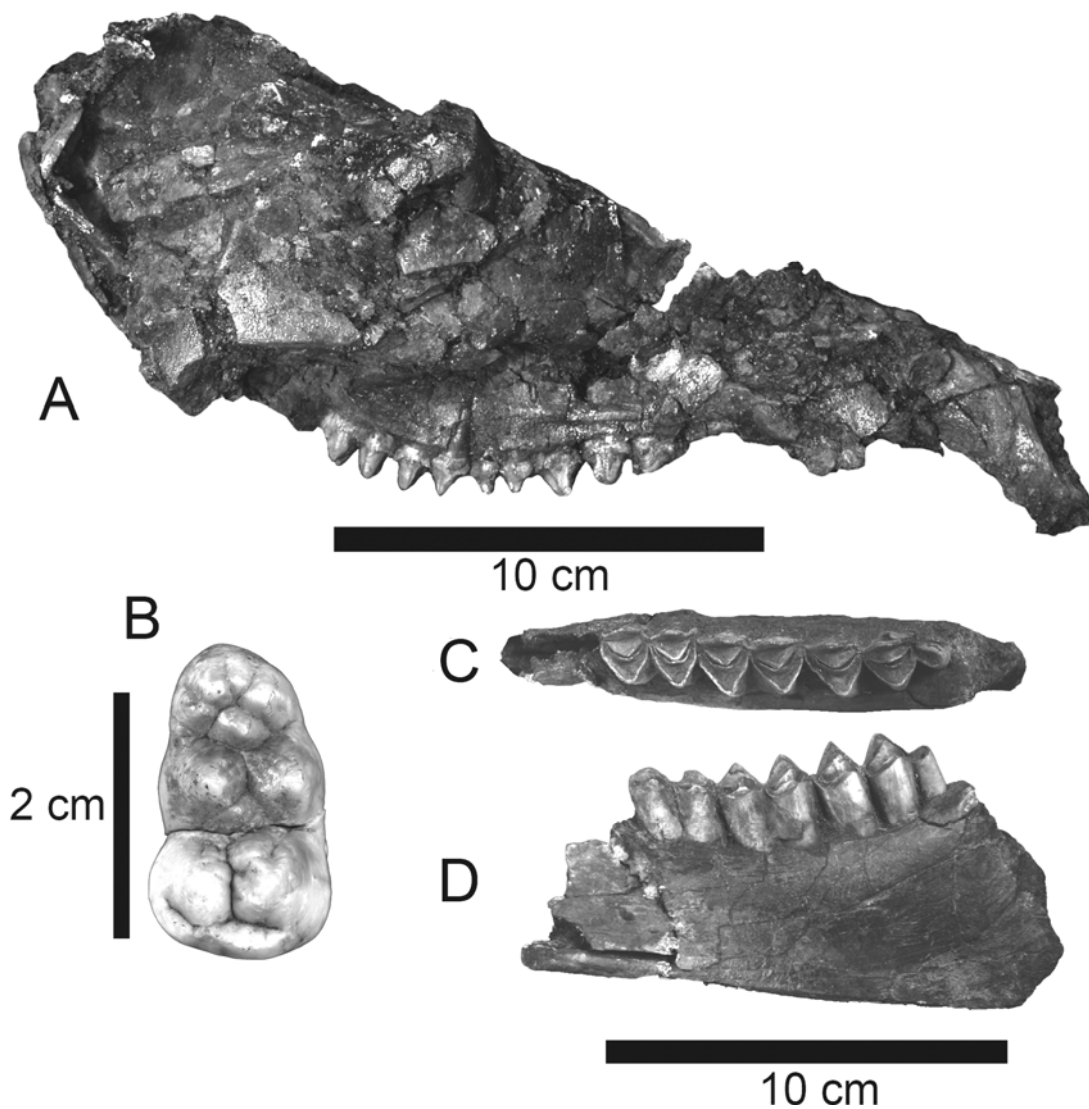

Figure 7. Artiodactyla from Orocual. **A**, *Platygonus* sp., partial skull with p2 to m3 (OR-1355); **B**, *Tayassu* sp., left m3 (OR-294), occlusal view; **C**, *Palaeolama* sp., left dentary with m1 to m3 (OR-1340), occlusal view; **D**, labial view of same.

m3 in some *Palaeolama* species. Because the Orocual specimens have a reduced parastyle, mesostyle, and metastyle, they do not belong to *Lama*.

Palaeolama and *Hemiauchenia* can be distinguished on the basis of some dental features (Webb and Stehli, 1995; Scherer et al., 2007). The lower molars of Plio-Pleistocene *Palaeolama* are less hypsodont than those of *Hemiauchenia* (Webb and Stehli, 1995). The maximum crown height measured on the second lobe of m3 seldom exceeds 25 mm in *Palaeolama mirifica*, whereas in *Hemiauchenia seymourensis* it often exceeds 35 mm (Webb and Stehli, 1995). Only thin cementum is developed in *Palaeolama*, whereas *Hemiauchenia* cheek teeth have thick cementum (Webb and Stehli, 1995). In *Hemiauchenia*, the protoconid and hypoconid (labial lophids) form a U-shape and the protostylid and parastylid are pronounced; in *Palaeolama* the labial lophids are V-shaped and the protostylid and parastylid are almost imperceptible (Scherer et al., 2007). We assign the El Breal de Orocual material to *Palaeolama* based on the lower crowned cheek teeth having reduced parastylids and protostylids and the V-shaped labial lophids.

Order NOTOUNGULATA Roth, 1903
Suborder TOXODONTIA Owen, 1858
Family TOXODONTIDAE Gervais, 1847
Subfamily HAPLODONTHERIINAE Kraglievich, 1934
Genus *MIXOTOXODON* Van Frank, 1957
MIXOTOXODON LARENSIS Van Frank, 1957
(Fig. 8)

Referred Material--Isolated m2, OR-1375; tooth fragment, OR-773; lower molar fragment, 815; incisor fragment, 908.

Description--The m2 paraconid is not anteriorly projected and lacks meta-entoconid fold; metaconid smaller than m1 metaconid and covered by lingual enamel band; ento-hypoconid fold reflected 85° anteromedially; hypoconid buccolingually broad, approximately same size as trigonid; anterior facet of trigonid convex; lingual enamel band extends from metaconid to anterolingual side of hypoconid, without totally covering it; buccal enamel fold deeper; buccal enamel band covers entire buccal surface of tooth, and includes anterior portion of the protoconid and posterior part of hypoconulid; hypoconid projects lingually; buccal enamel longer than lingual enamel.

Remarks--The m2 of *Mixotoxodo*n normally lacks a meta-entoconid fold, but sometimes this structure is weakly developed (Van Frank, 1957; Saint-Andre, 1999). A recent survey by AR of the known m2 specimens of *Mixotoxodon* revealed interesting patterns of variation in expression of the meta-entoconid fold (= anterior fold of Madden, 1990, and Nasif et al., 2000). It is weakly developed in *Mixotoxodon larensis crusafonti* from Colombia (Porta, 1959), absent in the specimens from Costa Rica (Laurito, 1993), and absent in the new material from Orocual. The meta-entoconid and ento-hypoconid folds in *Toxodon* are well developed in m1 and m2 (Pascual, 1957). The morphological and metric variation of this character in *Mixotoxodon* could be interpreted as individual, ontogenetic, and/or wear-related variation. A phylogenetic analysis of the Haplodontherinae is lacking, but *Mixotoxodon* is currently considered monotypic.

Order PROBOSCIDEA Illiger, 1811
PROBOSCIDEA indet.

Referred Material--Anterior tooth fragment, with anterior cingulum of molar, OR-306.

Description--Fragmented tooth; heavy, crenulated enamel, preserving only a strongly developed anterior cingulum oblique toward mesial side.

Remarks--During the Pleistocene proboscideans were represented in South America by *Cuvieronius hyodon*, *Stegomastodon platensis*, and *Stegomastodon waringi* (Prado et al., 2003). Although the dental morphology of South American proboscideans is complex, Prado et al. (2003) and Alberdi et al. (2002; 2004) noted that some tooth fragments can be identifiable. Unfortunately, our material is too fragmentary for any reliable identification.

Figure 8. *Mixotoxodon larensis*, m2 (OR-1375).

DISCUSSION

A minimum of 24 mammalian taxa were recovered from preliminary salvage excavations at El Breal de Orocual. The relatively small assemblage of specimens collected so far represents a minuscule fraction of the total amount of material preserved there, and additional taxa were discovered during all phases of the salvage operation (including three taxa on the last day). The scientific potential of the site is truly incredible, and even our preliminary discoveries yield important new data bearing on the taxonomic composition and paleobiogeography of South American mammals.

Chronological Control

It is clear that the overarching question of chronological control for the Orocual biota must be addressed before this deposit can be fully appreciated. External age control for the biota itself is not yet available. The age assessment of "Pleistocene" for the Mesa Formation was based on stratigraphic relationships with superpositionally lower sequences suggested to be Pliocene (González de Juana et al., 1980; Zinck and Urriola, 1970). The Mesa Formation, or parts of it, may be Pliocene in age, but adequate data do not currently exist to resolve its age with any certainty (Código Geológico de Venezuela, 2007). Thermoluminescence ages were obtained for the Mesa Formation at Maripe, State of Anzoategui; two of these suggest that the formation dates to between 0.5 and 1 Ma, whereas two others suggest an age in excess of 2 Ma (Carbón et al., 1992).

Some measure of chronological control based on the mammalian fauna itself is possible, and we venture some preliminary assessments here. These efforts, however, are hampered by a number of factors. The most immediate complication is that the limited samples currently available represent, in many cases, poorly preserved or non-diagnostic elements that prevent confident species-level assignation. It is anticipated that this practical complication can be overcome with the recovery of additional material when full excavation is authorized to proceed.

At least three of the mammalian taxa from Orocual provide some suggestion of an age for the deposit, but none are definitive. The hydrochoerid *Chapalmatherium* is elsewhere known from Pliocene deposits (Vucetich and Verzi, 1995), but our material can be only tentatively assigned to that taxon. A similar problem concerns the tapir. The material identified here probably represents a new species of tapir, but one that is closely related to the North American *Tapirus webbi*, known from the late Miocene. Because the material is unique, no specific chronological significance can yet be assigned, but the morphological similarity with *T. webbi* is at least suggestive of antiquity greater than late Pleistocene. The type material of *Pachyarmatherium leiseyi* was collected from the Bermont Formation, which dates to between 1.5 and 1.1 Ma, with the faunal-bearing sediments dated to approximately 1.3 Ma (Morgan and Hulbert, 1995). It also is known from the Lujanian of Uruguay and Brazil, Irvingtonian-equivalent sediments from Costa Rica, and the late Pleistocene of Brazil. *Pachyarmatherium* is a presumed immigrant into the United States; its presence in the southeastern U.S. near the Pliocene-Pleistocene boundary suggests at face value a similar age for the Orocual material, but a younger age for the Venezuelan material is certainly possible given the age range known within South and Central American.

In southern South American faunas, both *Propraopus* and *Glyptodon* make their earliest appearance, and *Platygonus* makes its last appearance in the *Mesotherium cristatum* biozone. That biozone forms the biostratigraphic basis of the Ensenadan mammal age, spanning the latest Pliocene through middle Pleistocene (Cione and Tonni, 2005).

The stratigraphic provenience of the Orocual biota, the preliminary taxonomic identifications of its mammalian component, and the known or inferred ages of the constituent taxa (or their morphologically close kin) elsewhere in South America and the southeastern United States all converge on a consistent approximate age assessment. That conservative assessment suggests that the El Breal de Orocual deposit dates to somewhere between the latest Pliocene and the middle Pleistocene.

Faunal Provinciality and the Great American Biotic Interchange

A diverse vertebrate assemblage of late Pliocene or early Pleistocene age in northern South America is a remarkable and exciting discovery in itself, but the Orocual biota yields additional insights into aspects of faunal dynamics associated with the Great American Biotic Interchange (GABI). There is a general paucity of sites of this age from the northern part of South America (Ochsenius, 1980), and there are no diverse biotas from that time interval known from north of the Amazon Basin. The extensive and well-known deposits from Argentina and Bolivia have long formed the basis for much of what we think we know about the GABI (e.g., Marshall, 1985; Webb, 1985, 1991; Cione and Tonni, 1999).

A renewed interest over the last decade in the GABI is yielding important new perspectives on nearly every aspect of that famous biogeographic and paleoecologic phenomenon. One of the major deficiencies in the material record of the GABI is the minimal biotic record from tropical latitudes (Webb, 1991). Documentation of Central American vertebrate faunas and their stratigraphic and temporal contexts has expanded significantly in recent years (e.g., Carranza Castañeda and Miller, 2004; Flynn et al., 2005; Carranza-Castañeda and Lindsay, 2006), and occurs in parallel with renewed efforts to place the southern South American faunas into a reliable stratigraphic and chronologic framework (e.g., Campbell et al., 2001; Cione and Tonni, 2001, 2005). Much work remains, but an emerging consensus is that biostratigraphic correlations and biochronological interpretations must be established, tested, and implemented initially in limited or localized geographic areas (see Cione and Tonni, 1995). The reality of biotic provincialism in Pliocene and Pleistocene biotas is now clearly recognized in Central and North America (Bell et al., 2004; Woodburne et al., 2006). For the moment, Orocual stands alone in representing northernmost South American biotas during the Great American Biotic Interchange, in turn providing important documentation that the mammalian fauna in this region was distinctive. The records of *Pachyarmatherium*, *Hoplophorus*, Erethizontidae, *Hippidion*, and *Platygonus* are new occurrences for Venezuela, and the homotheriine cat and apparently new species of tapir represent the first definitive occurrences anywhere on the South American continent. Our preliminary analysis suggests that the Orocual biota will contribute significantly to the renewed research cycle centered on understanding faunal and floral dynamics of the American Biotic Interchange. This rich, well-preserved biota provides an important first step in filling a major gap in our understanding of the Pliocene-Pleistocene vertebrate history of the Western Hemisphere.

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