

# AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024  
Number 3422, 42 pp., 20 figures, 1 table  
December 9, 2003

## A Possible Heptaxodontine and Other Caviidan Rodents from the Quaternary of Jamaica<sup>1</sup>

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### ABSTRACT

New World hystricognath rodents (parvorder Caviida) easily qualify as the most diversified members of the nonvolant Quaternary land mammal fauna of the West Indies. This paper describes three intriguing but problematic representatives of this group from Jamaican cave deposits. The first is the holotype (and still the only) specimen of *Alterodon major* from Wallingford Roadside Cave, a taxon that continues to generate controversy because specialists disagree as to its placement within Caviida. We reject the argument that it should be placed in Octodontidae and reaffirm the high probability that it is a clidomyine. The second fossil is a large proximal femur, apparently recovered from Sheep Pen locality near Windsor (Trelawney Parish) in the 1960s. Much larger than the femur of *Clidomys* (previously thought to be Jamaica's largest Quaternary mammal), in size and morphology the new fossil somewhat resembles femora of the eastern Caribbean heptaxodontine *Amblyrhiza*. Although firm allocation is not possible, the Sheep Pen femur is possibly that of a megafaunal caviidan. The third fossil described in this paper is the jaw of a previously unknown caviidan from a dated end-Pleistocene cave context in Portland Ridge (Jackson's Bay, Clarendon Parish). *Xaymaca fulvopulvis*, new genus and species, differs from all West Indian caviidan species presently known. The jaw is well preserved but retains only the incisor and premolar (the latter in a very worn state). The few features for which the new species can be usefully analyzed and compared to caviidan groups represented in the West Indian Cenozoic (capromyids, heteropomyines, heptaxodontines, and clidomyines) are largely indecisive from a systematic perspective. However, on balance the strongest indicators seem to lie with the "giant" heptaxodontines of the central and eastern Caribbean (the grouping composed of *Amblyrhiza*, *Elasmodontomys*, and possibly *Quemisia*), and despite its diminutive size *Xaymaca* is tentatively placed within that group. It is increasingly apparent that much still remains to be learned about the origin and history of the land mammal fauna of Jamaica.

<sup>1</sup> Contribution 6 to the series "Origin of the Antillean Land Mammal Fauna".

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## INTRODUCTION

In this paper we describe and attempt to interpret three “problematica” from the Quaternary of Jamaica. All three are more or less clearly caviidan,<sup>4</sup> but as they are incompletely or indifferently preserved and their morphology is strikingly unusual, they are bound to engender controversy. The first in the series—the holotype of *Alterodon major* (Anthony, 1920)—already has. Spencer (1987) has resurrected an earlier claim that *Alterodon* is an octodontid sensu stricto, a group not otherwise represented in the insular Neotropics. We show, with reference to some new character evidence, that Spencer’s (1987) alternative is much less likely than the one originally proposed by MacPhee et al. (1983), which is that *Alterodon* is a clidomyine. The second fossil is a remarkably large proximal femur—clearly that of a megafaunal mammal—which is insecurely documented as having been found at Sheep Pen, a locality near Windsor, Trelawney Parish (fig. 1). If the femur is indeed that of a rodent, it is safe to say that nothing like it has been found elsewhere on the island. The same can be said about the last member of the series, a diminutive jaw from a cave on the Portland Ridge near Jackson’s Bay (Clarendon Parish). These specimens and others adduced for comparison are depicted in figures 2–11.

Caviidans are the most diversified of the nonvolant mammal groups of the West Indies, whether this is measured by number of species, body size range, presumed ecological specializations, or any other appropriate index. Despite a certain amount of specialist interest in Antillean caviidans during the past century, many basic aspects of their evolutionary history remain obscure, in part be-

cause most islands have still not been adequately explored paleontologically (Morgan and Woods, 1986; Woods, 1989a, 1989b; MacPhee and Iturralde-Vinent, 1995; Iturralde-Vinent and MacPhee, 1999). This is of interest because the rodent fauna of the West Indies is now virtually defunct owing to modern-era extinctions: the few surviving lineages provide little in the way of clues to their former diversity (Woods, 1989a; MacPhee and Flemming, 1999).

The new species, described below, is represented by a dentally incomplete hemimandible (figs. 7–11). Determining its place on the caviidan cladogram has proven difficult, because in the absence of definitive evidence any one of several caviidan clades could represent its sister-group. This also applies to the Sheep Pen femur; *Alterodon* is less of a problem if our interpretation of its morphology is accepted. Although alternative placements are referenced as necessary, we concentrate on the likeliest taxonomic home for each fossil. Three groups—heteropsomyine echimyids (Antillean spiny rats), capromyids (hutias and coneys), and a probably paraphyletic group here informally named “Antillean platetooths” or \*heptaxodontids<sup>5</sup>—are central to most of our discussions, and therefore warrant a detailed introduction.

Heteropsomyine echimyids are usually placed within Octodontidae in recent classifications of extinct and extant caviidans (Woods, 1989a, 1993; McKenna and Bell, 1997). They are well characterized in the literature and require no special commentary except to note that, following Woods (1993), in this paper “heteropsomyines” will refer only to Antillean spiny rats (*Heteropsomys*, *Brotomys*, *Boromys*, *Puertoricomys*) and not to certain mainland echimyids with which they are sometimes arrayed (e.g., *Proechimys*, various Tertiary groups; see de Paula Couto, 1979; McKenna and Bell, 1997).

<sup>4</sup> Caviida (thus “caviidan”) includes the most recent common ancestor of Octodontoidea, Chinchilloidea, and Cavoidea, plus all of its descendants (Bryant and McKenna, 1995). Erethizontoidea, not part of the caviidan in-group according to McKenna and Bell (1997), is placed in the more inclusive grouping Hystricognathi (all the foregoing plus Bathyergidae, Thryonomyidae, Hystricidae, Petromuridae, and several wholly extinct higher level taxa). For other views founded on molecular phylogenies, see Nedbal et al. (1994) and Houchon and Douzery (2001). The informal term “New World hystricognaths” is used here to refer to all post-Tertiary hystricognaths, living and extinct, from this hemisphere.

<sup>5</sup> Asterisk implies that this family-level group is not alleged to be monophyletic (contrast with use of Heptaxodontinae). McKenna and Bell (1997) included *Amblyrhiza*, *Elasmodontomys*, *Clidomys*, and the Patagonian L. Miocene forms *Tetrastylomys* and *Pentastylomys* in this family. The two last-named (and very poorly known) taxa have also been considered dinomyids (Mones, 1981). The conflict essentially disappears if dinomyids and heptaxodontines are sister taxa (see text), although we do not formally endorse this proposal here.

TABLE 1  
Late Quaternary Endemic Nonvolant Land  
Mammals of Jamaica

Platyrrhini <sup>a</sup>
Ceboidea
Pitheciinae: Xenotrichini
<i>Xenothrix mcgregori</i> Williams & Koopman 1952
Rodentia
Myodonta: Muroidea
Muridae: Sigmodontinae
<i>Oryzomys antillarum</i> Thomas 1898
Hystriognathi: Caviida
Capromyidae: Capromyinae
<i>Geocapromys brownii</i> <sup>b</sup> (Fischer 1830)
Family incertae sedis: Clidomyinae <sup>c</sup>
<i>Clidomys osborni</i> Anthony 1920
<i>C. parvus</i> Anthony 1920
<i>Alterodon major</i> Anthony 1920
Family incertae sedis ?Heptaxodontinae <sup>d</sup>
<i>Xaymaca fulvopulvis</i> , n. gen. et sp.

<sup>a</sup>Regarding the unconfirmed existence of a second platyrrhine in Jamaican Quaternary, see footnote 6 in main body of text.

<sup>b</sup>Extant; all other species in this list are extinct.

<sup>c</sup>Although distinguished here, *A. major* is most likely a synonym of *C. osborni*. *Speoxnus cundalli* and *Spirodontomys jamaicensis*, also named by Anthony (1920), were synonymized with *C. osborni* and *C. parvus*, respectively, by MacPhee (1984). Morgan and Wilkins (2003) have recently discussed sinking *C. parvus* within *C. osborni*; if this is done, *Clidomys* becomes a monotypic taxon encompassing rather substantial individual variation, a feature also characteristic of *Amblyrhiza* (Biknevicius et al., 1993).

<sup>d</sup>The nominotypical taxon for this subfamily is *Heptaxodontomys bidens* (Anthony, 1917). The type of *H. bidens* is in fact the juvenile of *Elasmodontomys obliquus* (Anthony, 1916), as shown first by Stehlin and Schaub (1951) and later by Ray (1964) in greater detail. However, as Ray (1964) also noted, sinking *Heptaxodon* does not affect the nomenclatural act by which Anthony (1917) created the family-group name (subfamily in this case) Heptaxodontinae. According to art. 40.1 of the ICZN (2000, 4th ed.), a family-group name is not to be replaced merely because the name of its type genus is the junior synonym of the name of another genus.

Thus restricted, Antillean spiny rats are a morphologically homogeneous and clearly monophyletic group, and for comparative purposes here it will be sufficient to limit most observations to the Cuban genus *Boromys*.

Capromyidae is an endemic Antillean family with no accepted mainland representatives of any geological age, although echimyids and capromyids are clearly related as octodontoids and are frequently considered

to be each other's closest extant relative (Woods, 1982; but see Woods, 1993; Woods et al., 2001; Nedbal et al., 1994). Jamaica's only extant caviidan, the coney (*Geocapromys brownii*), is a member of this group. So are two other species that will be mentioned in the text, *Isolobodon portoricensis* and *Rhizoplagiodontia lemkei* from the central Caribbean. Their higher level systematics present no issues in need of comment here.

Antillean platetooths are a different matter. In the past, a diverse array of extinct rodents, including several mainland South American taxa with multilamellar teeth, have been brigaded under the family name \*Heptaxodontidae without much concern as to whether the resulting collocation was demonstrably monophyletic (for commentary see Woods, 1989a, 1993; Woods et al., 2001; Pascual et al., 1990). Not infrequently, in the caviidan systematic literature this group is simply ignored as uncharacterized and perhaps uncharacterizable (e.g., Vucetich et al. [1999], who reviewed the origin times of all mainland caviidan families *except* \*Heptaxodontidae). The named species of West Indian \*heptaxodontids as traditionally understood and their known distributions are: *Elasmodontomys obliquus* (Puerto Rico); *Amblyrhiza inundata* (Anguilla/St. Martin); *Quemisia gravis* (Hispaniola); and *Clidomys osborni*, *C. parvus*, and the doubtfully distinct *Alterodon major* (all from Jamaica) (see Ray, 1964; MacPhee, 1984; MacPhee et al., 1989; Woods, 1989a; McFarlane et al., 1998; Morgan and Wilkins, 2003; see also figs. 2–4 and table 1). In a few cases lower level relationships are reasonably clear. Thus *Amblyrhiza inundata* and *Elasmodontomys obliquus* share derived features of tooth and skeletal construction (Woods, 1989a; Flemming and MacPhee, 1996) and may therefore be considered a monophyletic group for which the subfamily name Heptaxodontinae is valid and appropriate, as noted by Ray (1964) (see also table 1). Similarly, species of *Clidomys* (and *Alterodon*, if different) are obviously closely related to each other and may be considered to constitute a second subfamily, Clidomyinae (Woods, 1989a, 1993). *Quemisia* has always been a problem: this very poorly known taxon, originally and still frequently considered to be a heptaxodontine (Miller,

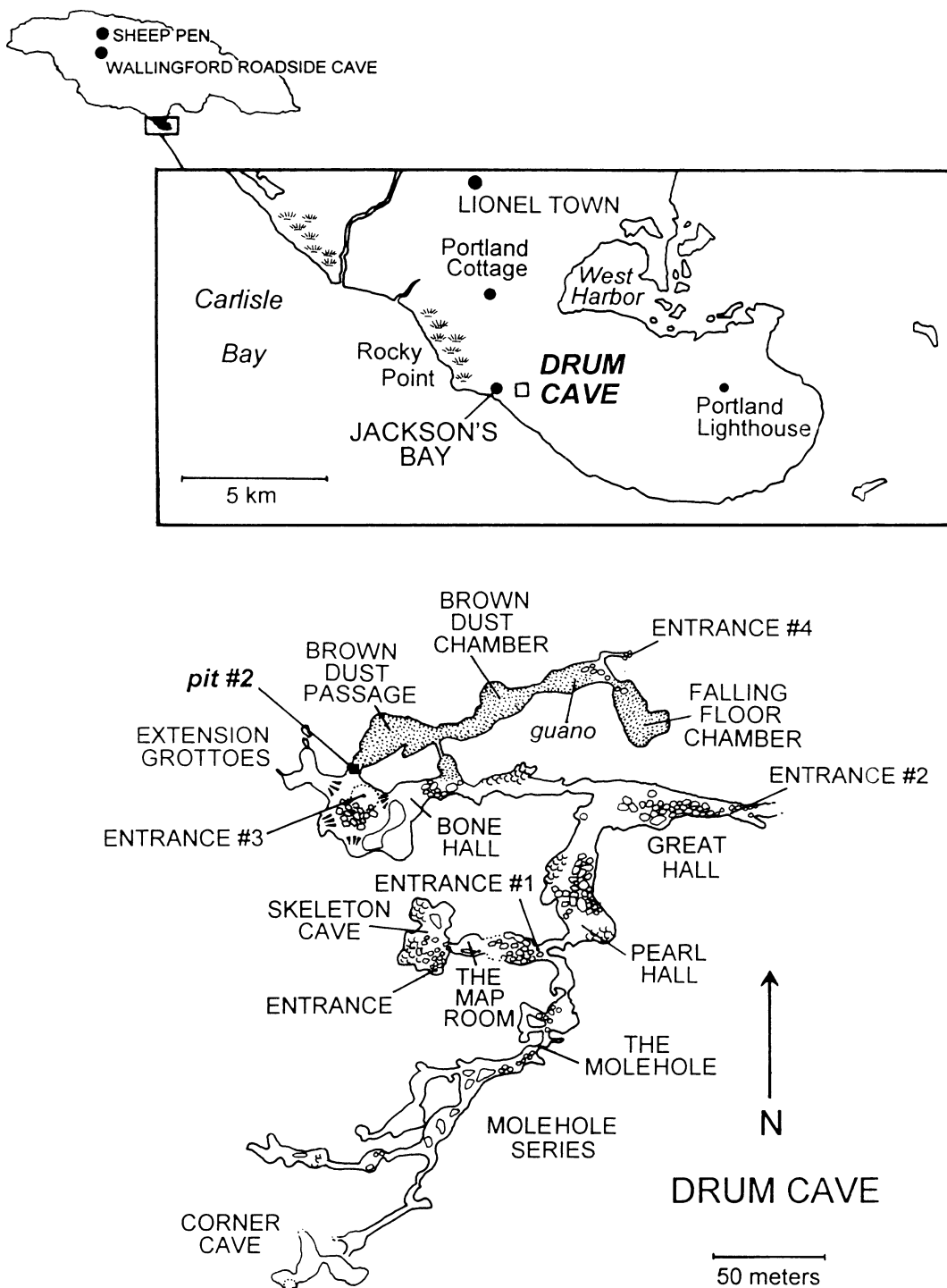


Fig. 1. Localities of specimens described in text: Wallingford Roadside Cave (holotype of *Alterodon major*), Sheep Pen (caviidan proximal femur), and Drum Cave (holotype of *Xaymaca fulvopulvis*). MacPhee (1984) provided detailed descriptions of Wallingford Roadside Cave and Sheep Pen. Survey map of Drum Cave (after Fincham, 1997) shows location of pit #2 in Brown Dust Passage, where type jaw of *Xaymaca* was recovered.

1929; Woods, 1989a; McFarlane et al., 2000), has also been identified as a possible capromyid (Ray, 1965). Woods (1982) contemplated the possibility that heptaxodontines are derived capromyids (thereby solving the problem of *Quemisia* indirectly), but ultimately rejected this notion in favor of the traditional view (see also Woods, 1989a, 1993). How heptaxodontines, clidomyines, and *Quemisia* are related *inter se* remains unresolved.

Lack of resolution regarding the affinities of Antillean platetooths extends to their higher level relationships (cf. Kraglievich, 1926; Simpson, 1945; Wood and Patterson, 1959; Patterson and Wood, 1982; Woods, 1989a, 1993; McKenna and Bell, 1997). In the most recent chapter of this debate, Pascual et al. (1990) have argued that the clidomyines of Jamaica are actually more closely related to mainland eumegamyine dinomyids than they are to *Amblyrhiza* and *Elasmodontomys* of the eastern Caribbean. But according to recent higher-level classifications, of which McKenna and Bell's (1997) is a pertinent example, eumegamyines are best considered cavioids, while heptaxodontines are (still) regarded as octodontoids. The biogeographical consequence of this conclusion is important: if the two major groups of Antillean platetooths occupy different limbs of the caviidan cladogram, then there had to have been a minimum of two invasions of the West Indies by progenitors which (?convergently) possessed platelike molars. This last point is intriguing, because the new species described elsewhere in this paper exhibits some notable similarities to heptaxodontines, yet it comes from the only island known to have supported clidomyines.

#### ABBREVIATIONS

##### ANATOMICAL

dp4	deciduous mandibular premolar (used only when tooth is known to be replaced)
I/i1	maxillary/mandibular incisor
M/m1, 2, 3	maxillary/mandibular molar 1, 2, 3
P/p4	maxillary/mandibular premolar

##### INSTITUTIONAL

AAHS	Anguilla Archaeological and Historical Society
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AMNHM	Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History
AMNHP	Division of Paleontology (Vertebrate Paleontology), American Museum of Natural History
BP	radiocarbon years before "present" (i.e., radiocarbon datum, AD 1950)
FLMNH	Florida Museum of Natural History, Gainesville
SEM	scanning electron microscopy/micrograph
UF	Systematic collections of Florida Museum of Natural History, University of Florida, Gainesville
USNM	United States National Museum of Natural History, Washington DC

#### PRELIMINARY CONSIDERATIONS

For convenience, odontological, histological, and histogenetic terms used in subsequent sections of this paper are briefly discussed and defined here. Several of these terms have meanings that are well understood in mammalian adult anatomy, but for the particular purposes of this paper an ontogenetic perspective on their definition and application is needed. Tooth-forming tissues are mineralized dense connective tissues; they therefore closely resemble one another in structure, histochemistry, and development (Fawcett, 1986; Hancox, 1972; Swindler, 2002). Definitions concentrate on diagnostic features of each tissue type that can be easily identified by microscopy or in photomicrographs. They are not meant to be exhaustive and in any case are limited to conditions encountered in the caviidans used in this study.

#### TOOTH ROOTS, SECONDARY DENTINE, AND THE SIGNIFICANCE OF APICAL HYPERTROPHY

In the dictionary definition, "tooth root" is the imbedded or basal portion of a tooth containing the pulp chamber and its feeder canals. Also by definition, at least in *Homo*, the root lies apical to a defined cervix and is normally composed of dentine only (no enamel), with a minor external wrapping of cementum. But in many other mammals the imbedded portions of teeth are differently organized, which requires that a somewhat different vocabulary be used to describe them. Our analyses of root categories are derived



from those adopted by Mones (1982), although we explicitly concentrate on ontogeny and histology of dental tissues rather than on general appearances in the adult.

Teeth develop in relation to primitive epithelial sheets possessing the competency to form new dental tissues (Fawcett, 1986). Dental tissues, like bone tissues, do not grow interstitially. In species with brachyodont cheekteeth (e.g., *Homo*), these sheets are programmed to shut down relatively early. Thus at a certain stage of development, ameloblasts on the inner enamel epithelium at a given locus will cease to differentiate, thereby fixing the position of the cervix, and no new enamel will be formed thereafter except pathologically. Odontoblasts typically continue to differentiate and produce primary dentine in an aboral direction after eruption, thus "completing" the root, but eventually production of new odontoblasts rapidly declines. Thereafter, only minor maintenance activities take place. For example, root canals may be narrowed by the deposition of secondary dentine, and cementum will be elaborated adjacent to the periodontal membrane to ensure that teeth remain tightly seated. But from an ontogenetic standpoint, a human tooth is essentially at the end of its developmental pathway shortly after it erupts and its roots close, except, of course, for the effects of attrition and, in the case of milk teeth, replacement.

This sequence should be contrasted with that found in mammals possessing hypsodont teeth. Hypsodont teeth are sometime described as "ever-growing" because dental epithelia remain competent to differentiate the same tissue types in the same proportions throughout the individual's lifespan. Typically although not universally, no matter what the rate of wear, a hypsodont tooth will retain more or less the same tooth pattern (q.v.) throughout ontogeny (e.g., *Equus*). This is understandable because pattern is determined by the unaltered original three-dimensional arrangement of epithelial sheets. Another feature of hypsodont teeth is that the apical end generally remains widely open, which also makes sense because this is the growing end of the tooth where new tissues are elaborated. If the growing end becomes contorted or loses competency, tooth pattern will ob-

viously change as well. This is exactly what happens in hypselodonty (q.v.), in which teeth cease to differentiate new tissues at the same rate and in the same proportion.

Although hypsodonty may be the most efficient way to produce ever-growing cheekteeth, under certain conditions both brachyodont and hypselodont teeth may add new material to apical ends, well after the completion of early ontogeny and root closure. We name this process apical hypertrophy (q.v.), as it involves the apical deposition of secondary dentine at a rate well above any conceivable maintenance level and (at least in the cases of interest here) has the notable effect of increasing useful tooth life. This process has not been well understood in the paleontological literature, often being confused with the hyperdevelopment of cementum, a process which is at most incidental in apical hypertrophy. Although material is added to the tooth, apical hypertrophy does not normally result in tooth elongation: just as in hypsodonty, new growth at the root end is offset by attrition at the crown end. In both instances, the physiological goal is to dynamically preserve a nearly constant tooth length.

Preservation of tooth length is important for another, functional reason: socketed teeth, especially ones subjected to heavy chewing forces, need to be securely fastened to alveolar walls by means of Sharpey's fibers developed in the periodontal membrane to prevent drift, uneven wear, or evulsion (Fawcett, 1986). Apical hypertrophy ensures that teeth do not become too short before the end of a normal lifespan, because the ever-diminishing crown end is perched on a growing stub of secondary dentine. From these considerations it is predictable that apical secondary dentine will progressively form more and more of a tooth's shaft as an animal possessing this adaptation grows older. Eventually, if the crown end becomes completely consumed, apical dentine will appear at the occlusal surface. These precise expectations are met with in several of the Antillean rodent groups discussed in this paper.

#### TERMS AND DEFINITIONS

**Apical end** (also root or aboral end) is the growing end of a tooth, which may be open

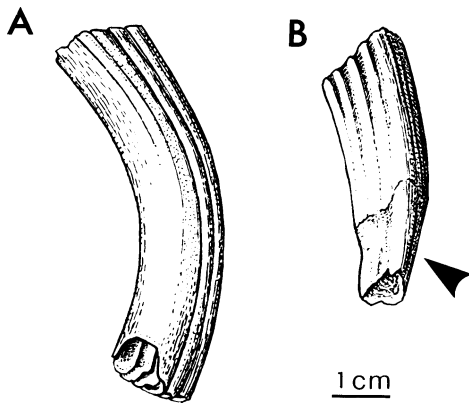


Fig. 2. Cheektooth morphology in Puerto Rican heptaxodontine *Elasmodontomys obliquus* (after Anthony, 1918); despite orientation, both specimens are maxillary molars. In **A**, from a young animal, root is open and apical hypertrophy has not begun. In **B**, from an aged animal, attrition has substantially reduced original tooth length. However, attritional loss is partly compensated by apical hypertrophy at root end, so crown appears to be perched on stub of secondary dentine (arrow).

or closed. Open roots represent the ontogenetically prior condition for all loci, inasmuch as the root sheath of the developing tooth is in broad contact with the capillary bed of the dental papilla, the surface cells of which are induced to form odontoblasts (Warwick and Williams, 1973: 1227–1235). We specifically define an “open” root as one still capable of continuing longitudinal growth through odontoblast differentiation and matrix mineralization. A “closed” root is one in which such differentiation has terminated or slowed to insignificance. Closure does not affect neurovascular bundles, which must remain functional to feed the pulp.

**Apical hypertrophy** (also root hypertrophy; incorrectly, “cement extension” of some authors) refers to significant posteruptive deposition of secondary dentine (q.v.) at the apical end of brachyodont or hypselodont cheekteeth, evidently a physiological response to increase useful tooth life (e.g., fig. 2). In the species examined, secondary dentine is morphologically continuous with primary dentine at the root end and may be difficult to separate from it histologically.

**Brachyodonty** is the condition of pos-

sessing teeth that are “low-crowned and provided with well-developed roots” (Peyer, 1968: 191), with “abrasion or any damage being of permanent character” (Mones, 1982: 110). Brachyodont teeth typically exhibit a definite enamelodentine or cementodentine junction (crown and root discrete). Typically, roots close at a relatively early ontogenetic stage, although apical hypertrophy (q.v.) may still occur (see text).

**Cementum** is “a layer of modified bone covering the dentin of the root and neck of a tooth” (Basmajian et al., 1976: 250). **Secondary cementum** is by definition cementum which forms on root surfaces after eruption. Diagnostically, it contains cementocytes (maintenance cells equivalent to osteoblasts, characterized by possession of long cellular processes). **Primary cementum** is typically noncellular and may lack lacunae, haversian systems, and lamellae. For this reason it may be difficult to distinguish from secondary dentine, but dentinal tubules should never be present in true cementum. Most descriptions of cementum are based on conditions in primates, which are not representative of mammals generally. In caviidans cementum is frequently a component of the tooth pattern (q.v.) and therefore appears in the crown and on occlusal surfaces (cf. “root cementum” vs. “crown cementum” [Peyer, 1968: 214]).

**Dentine** “resembles bone in structure and chemical composition” (Fawcett, 1986: 602), but differs at the gross histological level in various ways. **Primary dentine** is laid down during primordial tooth development. It differs diagnostically from bone and cementum in that its matrix is punctuated by swarms of relatively parallel, evenly spaced dentinal tubules (giving the dentine a radially striated appearance in longitudinal ground section). The tubules are the conduits for cytoplasmic processes of odontoblasts (Tomes’ fibers) whose cell bodies are stationed near the enamelodentine junction. **Secondary dentine** (also “irregular” dentine) is “formed after tooth eruption as a result of irritation from caries, abrasion, injury, or simply due to age” (Basmajian et al., 1976: 373). From the experimental literature it is clear that (unlike ameloblasts) lineages of odontoblast cells remain permanently competent. Dean (1993) found deposition rates of

3 and 4  $\mu\text{m}$  per day in permanent teeth of *Macaca*, suggesting a consistent rate of dentine formation. This, however, is a maintenance-level activity and should be distinguished from apical hypertrophy (q.v.), a specialized condition. In general, in secondary dentine the tubules depart from straight lines, are less numerous per unit area, and are distributed unevenly compared to primary dentine, although contrasts with primary dentine are often not very marked. In human teeth it has been observed that areas of irregular dentine may lack tubules altogether, implying that they consist solely of fibrillar calcified matrix (see Sicher, 1971). Also in humans, a resting line or sudden re-orientation of tubule direction may differentiate secondary from primary dentine. The degree to which this occurs in nonhumans has not been documented.

**Enamel** “is made up of oriented rods each of which consists of a stack of rodlets encased in an organic prism sheath” (Basmajian et al., 1976: 456). “Enamel formation is initiated along the dentinoenamel junction between the ameloblasts (enamel-forming cells) and odontoblasts (dentine-forming cells) when the latter commence to secrete predentine, which, in turn, almost immediately stimulates the ameloblasts to secrete the enamel matrix” (Swindler, 2002: 14).

**Enamelodentine junction** is the developmental resting line of enamel formation on the exterior of a tooth. “During the late bell stage, the sheet of cells comprising the inner enamel epithelium folds in a genetically determined way to take up the definitive outline of the future enamel-dentine junction. . . . [T]his folding process determines the ultimate shape of the tooth” (Warwick and Williams, 1973: 1230). Junction usually found on brachyodont teeth only.

**Hypselodonty** is the condition of possessing high-crowned, but not ever-growing, cheekteeth (also protohypodonty of Mones [1982]). The essential contrast between this condition and hypodonty (q.v.) lies not with crown height but with ontogenetic programming. Modern *Equus* is classed as possessing hypodont teeth, but, occasionally, in very old animals the root ends of the teeth finally close (Sisson and Grossman, 1938; see also Peyer, 1968: 194). This suggests that hyp-

sodonty and hypselodonty merely represent different positions on a developmental gradient. In any given species with high-crowned cheekteeth, if root closure is so delayed relative to average lifespan that it does not normally occur, the descriptive result will be hypodonty. Alternatively, if closure is accelerated relative to lifespan, the teeth will be classed as hypselodont. At the histogenetic level, hypselodonty occurs because tissues lose their competencies. Such teeth may continue to grow longitudinally via apical hypertrophy (q.v.), but the result is no longer the original tooth pattern but something else.

In Antillean heptaxodontines, pulp cavities are relatively large and open in young animals. Later in ontogeny, pulp cavities progressively narrow, owing to deposition of secondary dentine, until only tortuous channels remain (root canals for neurovascular bundles).

**Hypodonty** is the condition of possessing high-crowned cheekteeth that are truly ever-growing (i.e., tissue competency does not terminate, so tooth pattern is continually generated in much the same way for the life of the animal) (also euhypodonty of Mones [1982]). Although in old animals root closure of descriptively hypodont tooth is certainly possible, apical hypertrophy would not be expected to occur.

**Tooth pattern** refers to the specific arrangement (folds) of a tooth's primordial tissues (cementum, enamel, primary dentine), as seen at the initiation of wear (i.e., immediately after eruption). The pattern, however, is laid down early in histogenesis. The production of tooth pattern may be said to terminate with loss of epithelial competency (see above).

#### STATUS OF *ALTERODON MAJOR*

The dubious notion that Jamaica supported an endemic octodontid during the late Quaternary may be traced to Anthony's (1920) exceedingly brief description of the holotype of *Alterodon major*, a species based on a single, apparently hypodont cheektooth (AMNHP 17638) from Wallingford Roadside Cave (Manchester Parish) in central Jamaica (figs. 3, 4; see MacPhee [1984] for description and dating of faunule). In light of



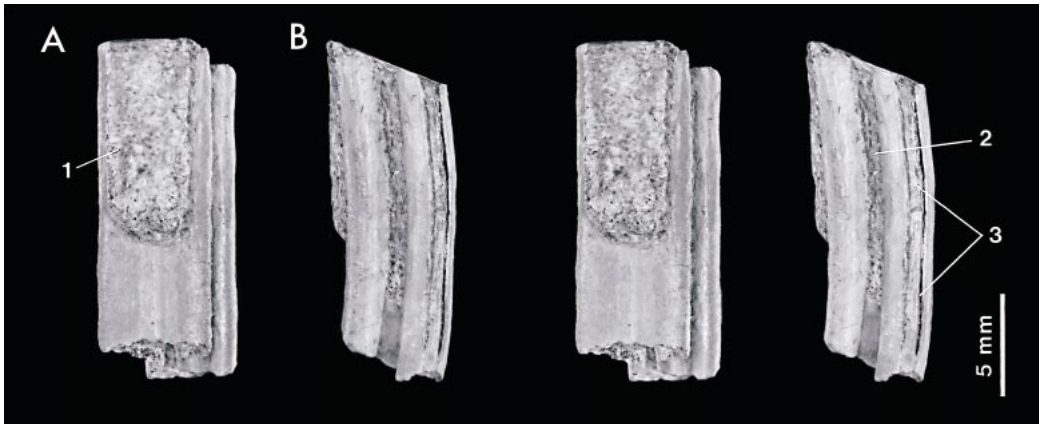


Fig. 3. *Alterodon major* AMNHP 17638 (holotype), stereopairs: (A) ?distal and (B) ?mesial aspects. We argue (see text) that this tooth is broken; in the intact state it would have closely resembled cheek-teeth of *Clidomys* in being composed of separate or conjoined lamellae connected by interlamellar plaques of cementum (indicated by dense stippling in fig. 4). Spencer (1987) argued instead that the plaque identified as **feature 1** in A is all that is left of a thick layer of cementum that originally enveloped the entire tooth (thus making the specimen, in his view, much more octodontid-like). **Feature 2** is a plaque that does not continue to the lateral surface because it fills a space formed by conjoined lamellae, but this is not unusual in *Clidomys* cheekteeth (cf. fig. 4C, E, I, J). **Feature 3** is a developmental interruption in enamel formation, also occasionally encountered in *Clidomys* (fig. 4B) and thus adding to the sense of similarity. For tooth pattern see figure 4E.

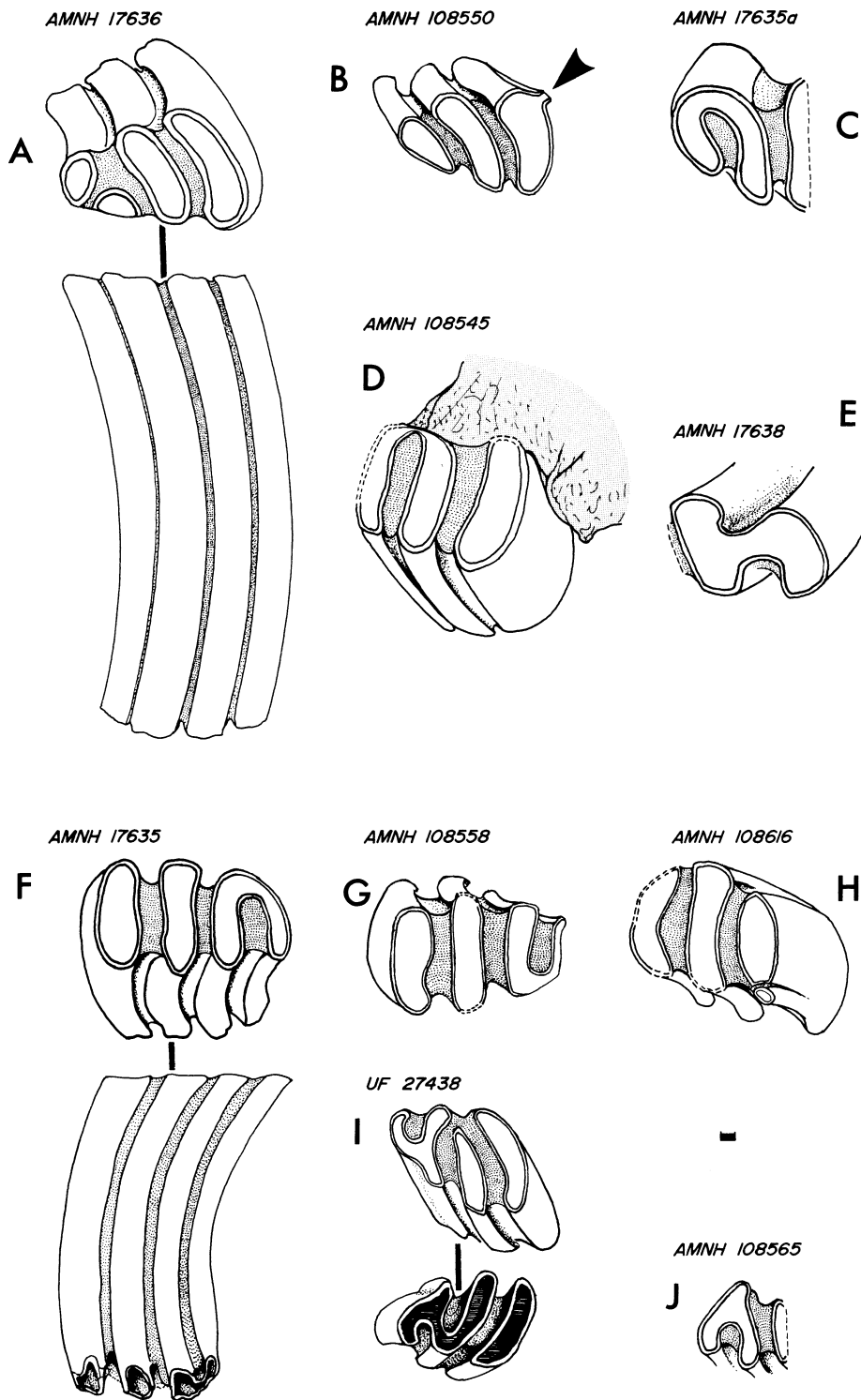
the new fossils described elsewhere in this paper, it is appropriate to briefly reconsider the status of *Alterodon*, with special reference to Spencer's (1987) arguments in favor of an octodontid affiliation for this genus.

Anthony (1920) was impressed by the fact that the holotype of *Alterodon* bore, in his view, a certain resemblance to the cheekteeth of Octodontidae, which are characteristically bilobate or dumbbell-shaped in cross-section. However, Anthony's remarks amount to no more than the mere recognition of vague similarity: in his only other published remarks on the matter, Anthony (1926: 206) simply noted that *Alterodon* may have unspecified "affinities to Octodontidae?".

Reference to Octodontidae was enough to get *Alterodon* into the biogeographical literature as an insular member of that family (e.g., Darlington, 1957), but not enough to get anyone interested in re-examining the holotype in print until MacPhee et al. (1983) did so. These authors concluded that Anthony's interpretation was fundamentally flawed, because the holotype tooth of *Alterodon* is incomplete: AMNHP 17638 as preserved (fig. 3) has a fracture surface on the

cementum lining its apparent distal aspect, which in our view is secure evidence that the tooth originally possessed at least one more lamella. This would make it unlike any accepted octodontid but suggestively like *Clidomys*, abundant remains of which occur in Wallingford Roadside Cave (MacPhee, 1984). However, as the partial tooth pattern of the *Alterodon* holotype did not precisely match that of any teeth assigned to *Clidomys* (cf. fig. 4), MacPhee et al. (1983) concluded that *Alterodon* might represent a different but closely related species of clidomyine. In a subsequent revision, MacPhee (1984) reconsidered this point and placed *Alterodon major* in synonymy with *C. osborni*, arguing that despite its shape the former was just another dental variant of the latter.

Spencer (1987) disagreed with each of these actions, arguing that MacPhee et al. (1983) misinterpreted the amount of damage to the *Alterodon* holotype. Far from being extensively damaged, he argued, the tooth has lost nothing but the greater part of a thick outer covering of cementum. That is, it is nearly complete as preserved, and therefore cannot have been multilamellar. Spencer



(1987: 108–109) went on to note that thick cementum sheathing is characteristic of the cheekteeth of the capromyid *Isolobodon* and “many octodontids”, and that therefore “*Alterodon major* could as easily be a capromyid like *Isolobodon*” or “a remnant octodontid as maintained by Anthony.”

Although there have been several new *Clidomys* discoveries in the past few years (e.g., McFarlane et al., 1998; Morgan and Wilkins, 2003), investigators have not turned up any more teeth with an *Alterodon*-like morphology. Spencer’s (1987) argument must therefore be analyzed on the basis of the existing fossil evidence. While it is true that cementum sheaths covering the cheekteeth of extant octodontids and their unquestioned relatives vary in thickness, none displays a substantial *local* thickening of the sort seen in the *Alterodon* holotype—situated exactly where the interlamellar plaque of cementum ought to be if the tooth belonged to a clidomyine, as MacPhee et al. (1983) originally contended. There is an additional aspect to this. On re-examining the few intact isolated cheekteeth of *Clidomys* in the AMNHP collection, we noticed that, disregarding the interlamellar plaques, the cementum covering is actually very thin or absent on all surfaces. Indeed, on most teeth in the collection cementum is not present *at all* on free surfaces, apparently because of overly vigorous preparation on Anthony’s part. Nevertheless, it is evident that the cementum covering on the *Alterodon* holotype could never have been of substantial, even thickness. On this analysis the type of *Alterodon* actually looks very much like other teeth in the *Clidomys* hypodigm, and we see no reason to infer that it once had a much thicker circumferential coating of cementum.

The other feature that Spencer (1987) em-

phasized is tooth pattern. Numerous examples of “unusual” occlusal-surface patterns in isolated cheekteeth from the *Clidomys* type site show that clidomyines were dentally variable (fig. 4A–J; MacPhee, 1984), a point which Morgan and Wilkins (2003) have additionally documented. To this we add the further observation that in *Clidomys* cheekteeth the enamel sheath of the mesialmost or distalmost lamella is occasionally interrupted or much thinner on one side than the other. In the holotype of *Alterodon* there are two interruptions that define a tiny splint of enamel (fig. 3B). One’s initial impression is that the interruptions are simply artifacts, but they lack fracture surfaces and can be traced continuously to the root end, where it is clear that they are developmental in origin. Such a minor, variable feature does not show beyond doubt that *Alterodon* is a clidomyine, but it is one more way in which its holotype fits within accepted variation in that group. How this variability ought to be reflected at lower taxonomic levels is possibly still an issue in need of resolution (see table 1), but at present there is no warrant to infer the presence of a family otherwise unrepresented in the Jamaican fossil record.

## THE SHEEP PEN PROXIMAL FEMUR

### PROVENANCE

One of the more unusual fossils to emerge from West Indian late Quaternary cave deposits is the large proximal femur (UF 27400) illustrated in figure 5A–C. Sadly, its history is not altogether clear. The Sheep Pen femur, as we shall refer to it here, was (apparently) collected in the mid-1960s and (we think) at least partly prepared under the direction of Thomas H. Patton, then a curator at the FLMNH. In 1981 MacPhee chanced

←

Fig. 4. Cheektooth morphology in Jamaican clidomyines (after MacPhee, 1984): (A–J) examples of variants in lamellar conformation. Specimen A, holotype of “*Spirodontomys jamaicensis*” (= *Clidomys parvus*); specimen E, holotype of *Alterodon major*; and specimen F, holotype of “*Speoxenus cundalli*” (= *C. osborni*). All other specimens assigned to *Clidomys* sp. Arrow in B points to developmental defect in enamel deposition, similar to that seen in *Alterodon* holotype (fig. 3B). Although no other teeth identical to the *Alterodon* holotype have been recovered, the existence of an appreciable amount of morphological variation in the existing hypodigm throws considerable doubt on the former’s distinctiveness. In this diagram only: AMNH = AMNHP. Scale = 1 mm.

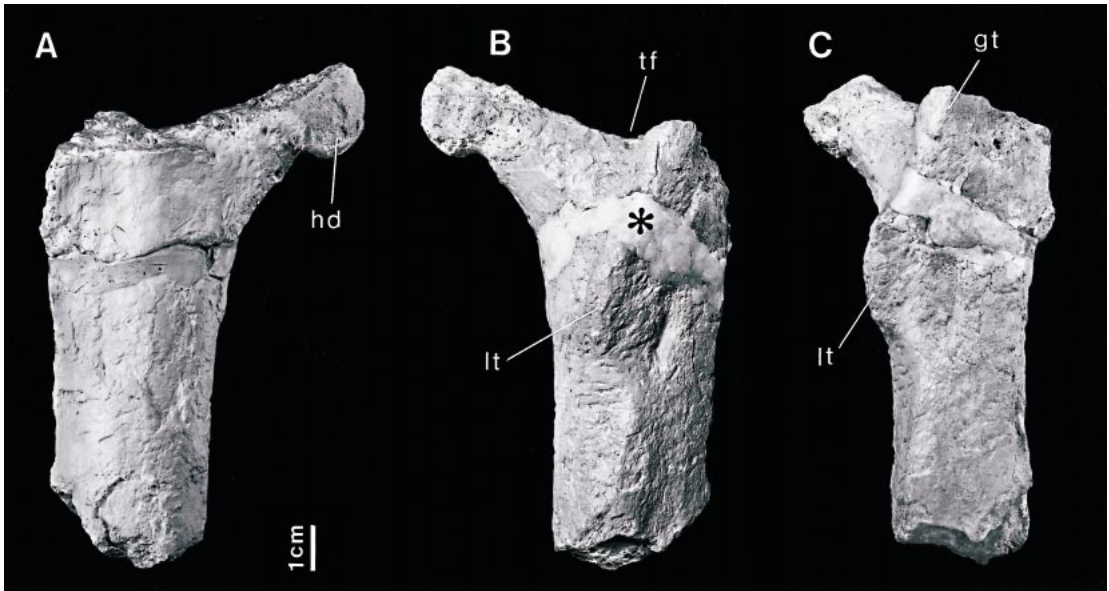


Fig. 5. Sheep Pen right proximal femur UF 27400, in (A) cranial (anterior), (B) caudal (posterior), and (C) lateral aspects, compared to similarly damaged right femur attributed to *Clidomys* AMNHP 108580 (D–F, same aspects). Although substantial parts of each specimen are missing, the contrast in size is obvious (note scales). Key: \*, modeling clay joining pieces of UF 27400; gt, greater trochanter; hd, head; lt, lesser trochanter; tf, trochanteric fossa.

upon the specimen, lying alone in a small box labelled “Sheep Pen” in the storage area of the FLMNH. The box was situated in the same area as several barrels of unsorted cave deposit collected by Patton during his several expeditions to Jamaica (1966, 1967, and 1970). Ordinarily, there would be no question about provenance, as, in addition to Jamaica, the Caymans are the only other West Indian islands in which Patton (e.g., Patton, 1966) is known to have collected (Gary S. Morgan, personal commun.). Unfortunately, the proximal femur was never accessioned by Patton, who left no records or preliminary descriptions of Sheep Pen material before leaving the museum (Charles A. Woods, personal commun.). This lack of documentation is important to mention, because the fossil does not closely resemble anything in the existing Jamaican record. If it is legitimately provenanced, Jamaica once possessed a truly megafaunal mammal, considerably larger than *Clidomys* in body size (fig. 5D–F).

Although the possibility must be considered, there is very little likelihood that the specimen represents the femur of a late Ce-

nozoic North American mammal which became incorporated accidentally into the West Indian collections at the FLMNH. Among alternatives that can be dismissed immediately are all domesticated mammals introduced by Europeans as well as Quaternary edentates (see below) and ungulates, although some large carnivores (e.g., bears) show weak resemblances to UF 27400 for such features as neck length. Among rodents having a North American range, the only possibility from the standpoint of size and morphology is the hydrochoerine *Nechoerus*—yet real correspondences are trivial even in the case of capybaras (cf. Biknevicius et al., 1993: fig. 3).

The locality known as Sheep Pen (see MacPhee, 1984) has also yielded several *Clidomys* teeth and a ?platyrrhine proximal femur (Ford and Morgan, 1988; Ford, 1990). Land snails occur throughout the section, establishing that the cave deposits exposed along the walls of this feature are exclusively terrestrial in origin. Goodfriend (1986) estimated the age of the snail fauna to be “probable Middle Pleistocene or older”, although

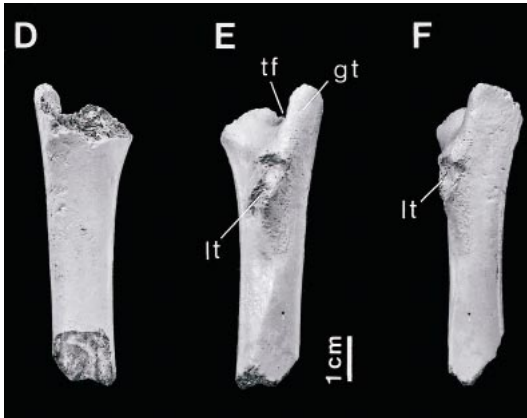


Fig. 5. *Continued.*

in our view it is doubtful that any part of the existing deposit predates the Quaternary. MacPhee and colleagues revisited the Sheep Pen locality in 1982 and 1994, but they were unsuccessful in finding additional megafaunal remains. Accordingly, as before, the evidence for the existence of a “giant” mammal in the Jamaican Quaternary continues to rest exclusively on the large femur described in following paragraphs.

#### DESCRIPTION AND EVALUATION

UF 27400 (fig. 5A–C) consists of most of the proximal end of a heavily mineralized right femur, found in two pieces in the collection. The neck, head, and greater trochanter comprise one piece and are truncated along the same plane, which may indicate that it broke off from the upper shaft (the second piece) while the bone was still encased in matrix. Although a small amount of material has been lost along the line of breakage, the pieces can be fitted together convincingly and doubtless come from a single individual. External surfaces of both pieces are scarred by chisel marks, seemingly caused by inexperienced preparation. Although measurements are not particularly illuminating in this case, the specimen’s maximum dimensions are approximately 125 mm (length)  $\times$  70 mm (proximal width). Approximately 50 mm of shaft is represented below the level of the lesser trochanter. Less than half of the head is preserved, and the greater trochanter is represented only by its basal portion. The light red, somewhat granular matrix remain-

ing in the medullary cavity resembles the kind of indurated fossiliferous deposit often found in Jamaican caves, but there is nothing about it that is diagnostic of Sheep Pen as such. On the other hand, it is relevant to note that indurated matrix of this sort is very rarely encountered in late Cenozoic Floridian localities (Gary S. Morgan, personal commun.), which reinforces our belief that this specimen has nothing to do with the mainland.

Only two groups—caviidans and the phyllophagan family Megalonychidae—are known to have had megafaunal representatives in the West Indies during the Quaternary. UF 27400 is not a megalonychid sloth because: (1) neck long and well differentiated from the rounded (not flattened) shaft; (2) head not appreciably angled; (3) trochanteric fossa present, probably deep; (4) lesser trochanter situated entirely on posterior aspect of shaft; and (5) intertrochanteric line strongly developed. In Antillean megalonychids, the neck is short and the head is sharply angled anterodorsally, the shaft is anteroposteriorly flattened, the trochanteric fossa is absent or barely indicated, the lesser trochanter is medially situated, and the intertrochanteric line is weakly indicated (cf. White and MacPhee, 2001). For completeness it may be mentioned that the femur does not resemble that of any known pinniped (and specifically not that of *Monachus tropicalis*, the extinct Caribbean monk seal). Insectivores and bats are out of the question.

Although certainty in allocation is not possible, the specimen exhibits a sufficient number of features in common with femora of large caviidans to allow the conjecture that the Sheep Pen femur belonged to a New World hystricognath. Figures 5D–F and 6A–E depict, respectively, femora of *Clidomys* and *Amblyrhiza*. These taxa constitute an admittedly narrow comparative set, but one adequate to make our point. The femoral fragment of *Clidomys* (AMNHP 108580) is unfortunately the most complete example of this element in the AMNHP collection, but it is obvious that even in the intact state it would have been far smaller than the Sheep Pen femur. By contrast, the latter is notably similar in size and morphology to specimens of *Amblyrhiza* (especially the “small” morph, AMNHP 11847; fig. 6A). Closer in



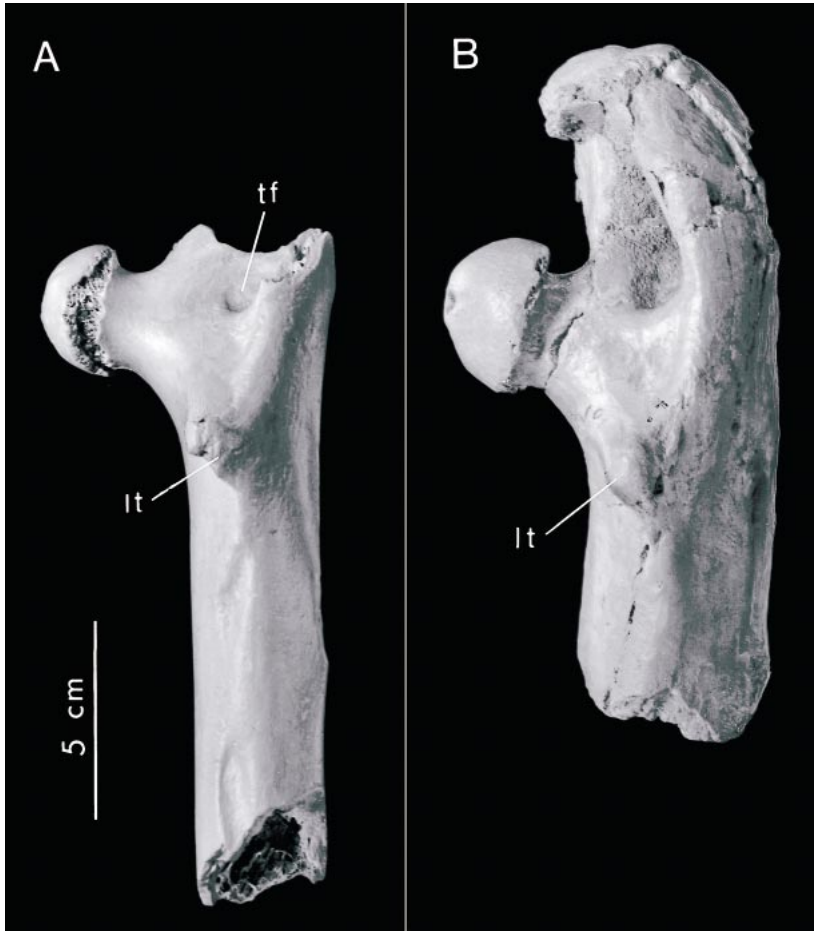
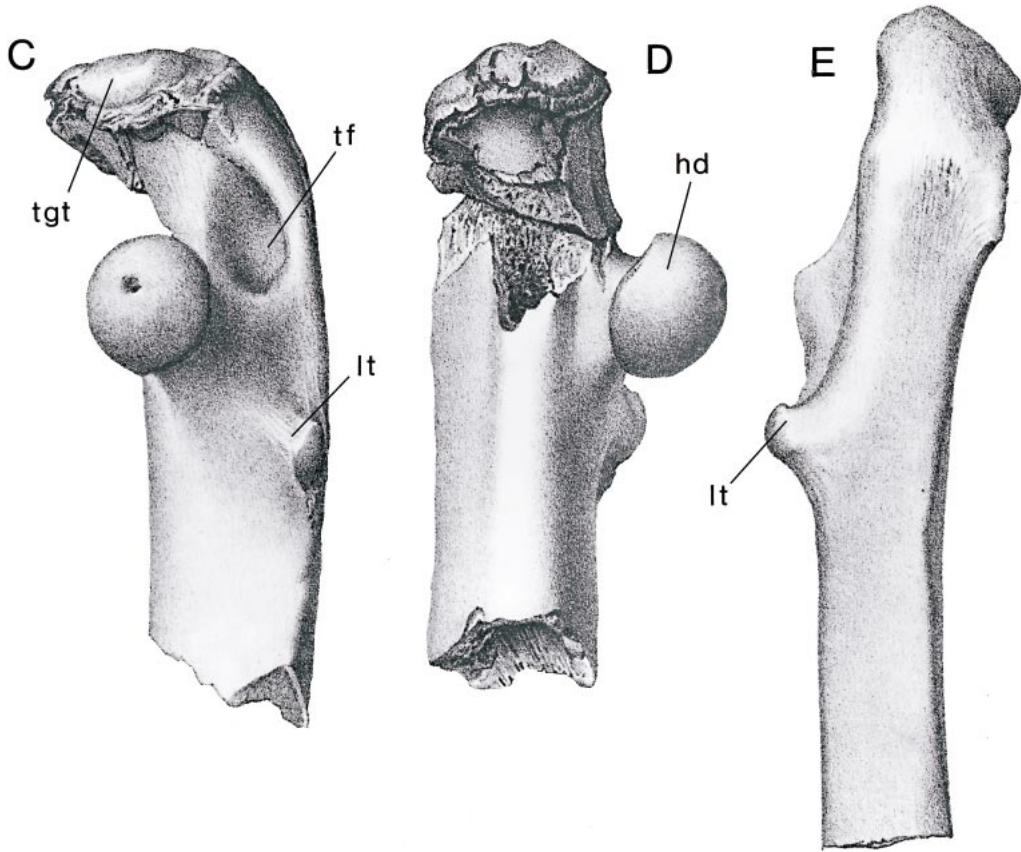


Fig. 6. Right proximal femora of heptaxodontine *Amblyrhiza inundata* (Anguilla/St. Martin): AMNHP 11847 (“small” morph) in (A) caudal aspect; AMNHP 11843/O (“large” morph) in (B) caudal, (C) caudomedial, and (D) craniolateral aspects; and AMNHP 11843/N (“large” morph) in (E) lateral aspect. (Photographs after Biknevicius et al., 1993; drawings after Cope, 1883.) Similarities in morphology suggest that Sheep Pen femur (fig. 5A–C) may belong to a megafaunal caviidan, although beyond general resemblance there is nothing that specifically indicates a relationship to *Amblyrhiza*. (For discussion of size variability in *Amblyrhiza*, see Biknevicius et al., 1993). Key: **hd**, head; **lt**, lesser trochanter; **tf**, trochanteric fossa; **tgt**, “towered” greater trochanter.

spection reveals minor differences in the size and angulation of the lesser trochanter and the depth and position of major muscle markings. It is a pity that possible diagnostic features, such as the degree of towering of the greater trochanter, cannot be evaluated for the Sheep Pen femur because of breakage. For the record, resemblances to femora of the other West Indian platetoths, *Elasmodontomys* (cf. Anthony, 1918: pl. 66, fig. 1) and *Quemisia* (cf. Ray, 1965: pl. 1), are not nearly so marked.

Given the strength of resemblances to *Amblyrhiza*, we wondered whether the Sheep Pen specimen might actually have come from Anguilla or St. Martin, but through some misadventure became incorporated into Patton’s West Indian collection. As already noted, nothing is certain about this specimen’s history. However, apart from the general morphological correspondences to the femur of *Amblyrhiza* already discussed, there is nothing else that makes Anguilla or St. Martin a likely bet. Indurated fossiliferous

Fig. 6. *Continued.*

matrix from caves on these islands tends to be a very distinctive brick red to light purple (McFarlane and MacPhee, 1989), without the granularity of the material adherent to the Sheep Pen femur. *Faute de mieux*, we tentatively accept UF 27400 as a Jamaican fossil rodent showing some provocative similarities to *Amblyrhiza*, without accepting that such similarities are necessarily indicative of close relationship.

Rodents of megafaunal size evolved a number of times during the late Cenozoic of South America. Some of the largest (e.g., *Telicomys*, *Eumegamys*, *Phoberomys*, *Tetrastylus*) had multilamellar teeth which have been favorably compared on occasion to those of Antillean \*heptaxodontids (e.g., Kraglievich, 1926; Wood and Patterson, 1959; Patterson and Wood, 1982; Pascual et al., 1990). However, little information is available on limb bones ascribed to one or

another of these mainland giants (some of which, it is necessary to add, have turned out to be meridiungulates rather than caviidans [Kraglievich, 1926, 1932]). Schaub (1935) published a description of a megafaunal rodent femur found in a ?Late Miocene context on the Savonetta River (Savaneta River on modern maps) in southern Trinidad. This femur, which is nearly complete, is 374 mm in maximum length and 128 mm in proximal breadth. It is thus even broader proximally than the largest known femur of *Amblyrhiza* (AMNHP 11843; proximal breadth, ~80 mm; fig. 6B–E). In addition to greater massiveness, the shaft of the Savonetta femur is notably bowed, unlike any of the Antillean heptaxodontines (including *Quemisia*), which have straight shafts (as do, however, many other nonmegafaunal caviidans, including *Clidomys*, *Dinomys*, and *Geocapromys*). No platetooths of any sort have been described

from Trinidad, although few vertebrate fossils from this island have been published (cf. Eshelman and Morgan, 1985).

The enormous femur ascribed to the Patagonian species *Phoberomys burmeisteri* (greatest length, 480 mm) by Kraglievich (1926) is also of interest. Again, there are similarities to both the Sheep Pen femur and that of *Amblyrhiza*. Although it is difficult to say to what degree such correspondences might be allometrically conditioned convergences, correlated with the relatively enormous body sizes of these animals, there are also profound dental similarities between *Amblyrhiza* and *Phoberomys* (especially the holotype of *P. bordasi*, AMNHP 22666; cf. Patterson, 1942; Pascual et al., 1990). This topic obviously requires revisitation, in detail.

In summary, from the comparisons we have been able to make we can point to nothing that exclusively connects the Sheep Pen femur with either heptaxodontines or clidomyines—except for the obvious but collateral matter that, on biogeographical grounds, these are the likeliest subfamilies to which it might belong. Since these groups are themselves of uncertain interrelationship, the proper solution is to assign the Sheep Pen femur to *Caviida incertae sedis*, pending further elucidation of its affinities.

## A NEW ?HEPTAXODONTINE RODENT FROM JAMAICA

### SYSTEMATIC PALEONTOLOGY

We name, diagnose, and classify the new species as follows:

MAGNORDER EPITHERIA MCKENNA 1975

ORDER RODENTIA BOWDICH 1821

INFRAORDER HYSTRICOGNATHI TULLBERG 1899

PARVORDER CAVIIDA BRYANT AND MCKENNA 1995

SUPERFAMILY OCTODONTOIDEA WATERHOUSE 1839

FAMILY: INCERTAE SEDIS

SUBFAMILY ?HEPTAXODONTINAE ANTHONY 1917

*Xaymaca*, new genus

TYPE SPECIES: *Xaymaca fulvopulvis* MacPhee and Flemming, new genus (figs. 7–11).

TYPE LOCALITY, ASSOCIATED FAUNA, AND DISTRIBUTION: As for type species.

ETYMOLOGY: *Xaymaca*, early Spanish variant spelling of Jamaica (Cundall, 1915), possibly ultimately from Arawak word meaning “land of springs”. Considered to be a feminine noun in the nominative singular.

DIAGNOSIS: As for type species.

### *Xaymaca fulvopulvis*, new species

HOLOTYPE AND ONLY REFERRED SPECIMEN: AMNHM 268011, a left hemimandible retaining the incisor (presumptive i1) and excessively worn p4 (figs. 7–11). Recovered (but not then identified) in January 1995 by the senior author with the assistance of Lisa DeNault, Don McFarlane, and Alan and Adam Fincham.

TYPE LOCALITY: Brown Dust Passage of Drum Cave, near Entrance #3 (fig. 1). Drum Cave, part of the “upper” sequence of the ~10 km Jackson’s Bay cave system (Fincham, 1997), is located on the south slope of Portland Ridge near Jackson’s Bay, in the southernmost part of Clarendon Parish, Jamaica. Entrance #3 is located at approximately 17°44′05″N, 77°13′15″W.

ASSOCIATED FAUNA AND DISTRIBUTION: A provisional vertebrate faunal list for late Quaternary levels in the Portland Ridge (Jackson’s Bay) caves has been assembled by McFarlane et al. (2002). The birds, which include some extinct forms, were identified and are now under study by Storrs Olson (Smithsonian Institution). Mammalian taxa recovered in Brown Dust Passage are either extant or survived until very recently (MacPhee and Horovitz, in press).

The most significant agent of small-mammal bone concentration in Jamaican cave deposits is the extant barn owl, *Tyto alba*. Since *Xaymaca* is evidently rare in such deposits, perhaps its size or behavior made it unlikely to be tracked by owls. *Quemisia gravis*, a relatively large species, is likewise known from very few specimens (McFarlane et al., 2000), although in Hispaniolan localities remains of other endemic rodents are encountered in great abundance (Woods, 1989b).

ETYMOLOGY: Species name (“of the brown dust”) is a manufactured Latin adjective in the nominative singular in agreement with

the genus name. Reference is to type locality, Brown Dust Passage of Drum Cave.

**DIAGNOSIS:** Hystricognathous, lower premolar cylindriform and apparently hypselodont, showing marked apical hypertrophy. Other cheekteeth probably also cylindriform and hypselodont. Inferred features of cheek-tooth root development closest (among Antillean caviidans) to heptaxodontines *Amblyrhiza* and *Elasmodontomys*. Attributes of cheektooth ontogeny, alveolar construction, incisor procumbency, and other minor features are consistent with tentative allocation to Heptaxodontinae (family incertae sedis).

The jaw is hystricognathous because its angular process is morphologically lateral to a parasagittal plane drawn through the incisor alveolar sheath (Landry, 1957). Cheektooth crown morphology not yet known. As may be seen plainly in figure 9 (bottom), the shape of the deeply striated p4 and the structure of the alveoli for m1–m3 in *Geocapromys brownii* immediately rule out referral to this taxon, the only extant hystricognath on the island and the only endemic of any age in the new species' body size range. Not an echimyid, because cheekteeth of all known species of Antillean spiny rats exhibit furcated roots, prominent cervix, and deep enamel infolds. Not a clidomyine, because all known clidomyines are far too large to be confused with the new taxon and in any case exhibit a substantially different tooth pattern.

**EXCAVATION RECORD AND DATING:** Detailed discussion of the stratigraphy, dating protocols, and chronology of the secondary deposits in Drum and associated caves is presented by McFarlane et al. (2002). The following remarks pertain to discovery of the *Xaymaca* holotype.

Pit 2, which yielded the holotype, was first opened in January 1995 and subsequently extended in July and September 1996. This relatively large amount of attention given to one site in one cave was warranted because the pit also yielded a well-preserved humerus of the extinct endemic monkey *Xenothrix mcgregori* and a number of jaws of the equally extinct endemic rice rat *Oryzomys antillarum*. The pit is located near Entrance #3, a major collapse feature (fig. 1). Excavations exposed ~1 m of deposits that have entered the cave through the collapse. A

loose surface layer of limestone fragments, cave earth, and modern owl pellet debris 20 cm thick is underlain by a discontinuous calcite layer (<2 cm). This calcite caps a distinctive and sharply delineated dark-brown layer of subfossil bat guano 34 cm thick, designated "Guano I", beneath which 6 cm of limestone fragments, clay, and huge concentrations of bone extend down to a second guano layer (3 cm thick) designated "Guano II". Beneath this, material extends to a solid calcite floor at 125 cm below surface, beyond which excavation did not continue.

The enormous quantity of lightly cemented small bones present in parts of Pit 2 formed a "bone cake" that had to be broken out and divided by hand. In this situation, dry screening was the only feasible method of recovering specimens. On the screen, representative samples of lizards, snakes, bats, and *Geocapromys* were collected by hand-picking, but much material was also simply bagged for later identification. The jaw which became the holotype specimen of *Xaymaca* was missed on the screen and was not recognized as distinctive until we sorted the material at the AMNH in New York.

Bone is present throughout the Brown Dust Passage section, but bone recovered from the Guano I and II horizons (including the *Xaymaca* holotype) is invariably and characteristically stained a deep brown color not seen in other layers. Thus, although it is known that AMNHM 268011 came from a ~12-cm interval between the bottom of Guano I and the bottom of the thin Guano II horizon, its stratigraphic position cannot be fixed more firmly. Fortunately, however, its temporal position can be fixed with considerable accuracy. Radiocarbon dating of the acid-insoluble organic component (crude chitin) of Guano I provided isotopically corrected dates of  $10,250 \pm 80$ ,  $11,050 \pm 70$ , and  $11,260 \pm 80$  BP in correct stratigraphic sequence; similarly, Guano II dated to  $11,980 \pm 80$  BP (see McFarlane et al., 2002). Thus although there is some uncertainty about the exact position of the holotype within Pit 2, its age can be fixed as lying between 10,090–11,420 BP (2 sigma error), or the terminal part of the late Pleistocene. Improved constraints on the "last occurrence" date for



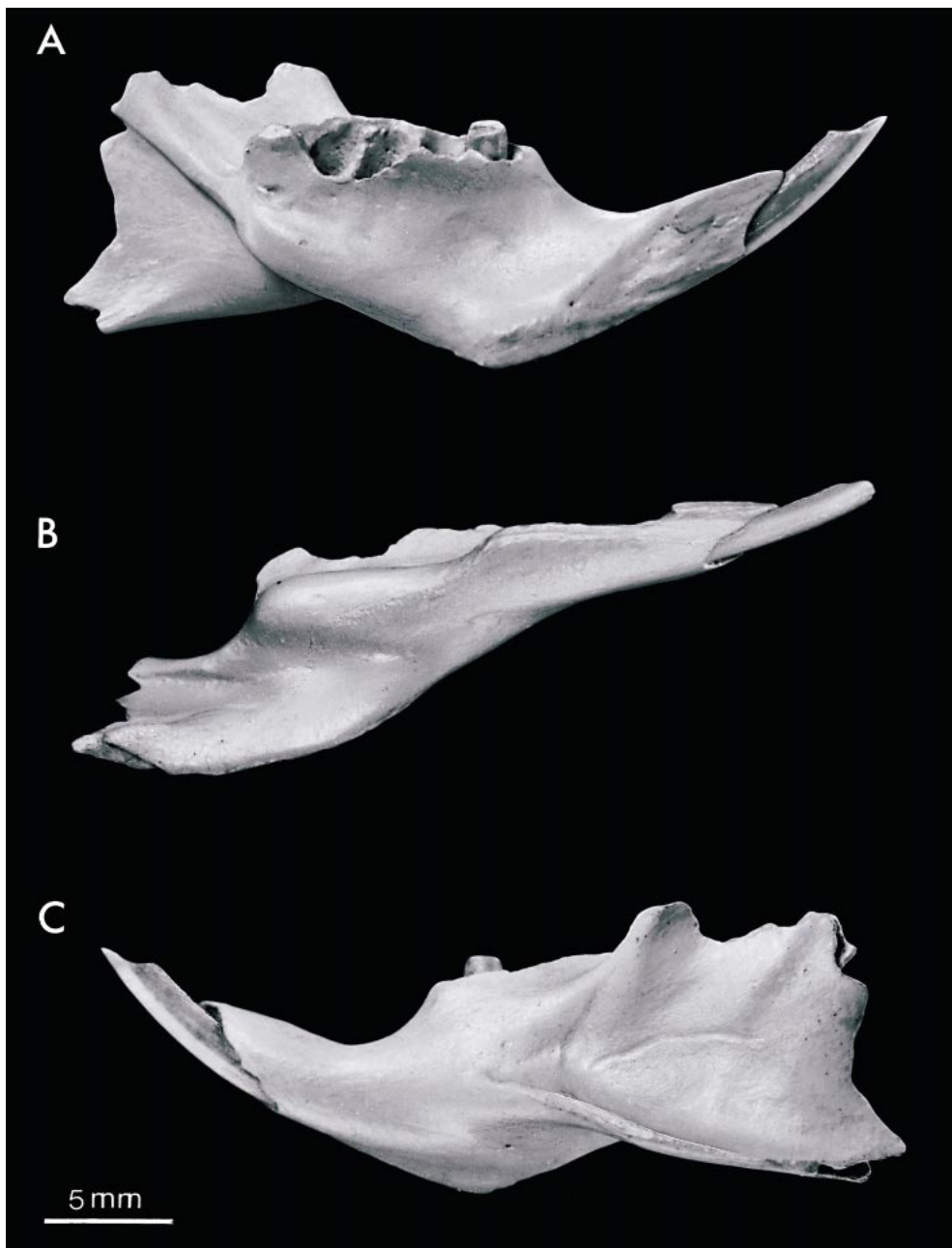
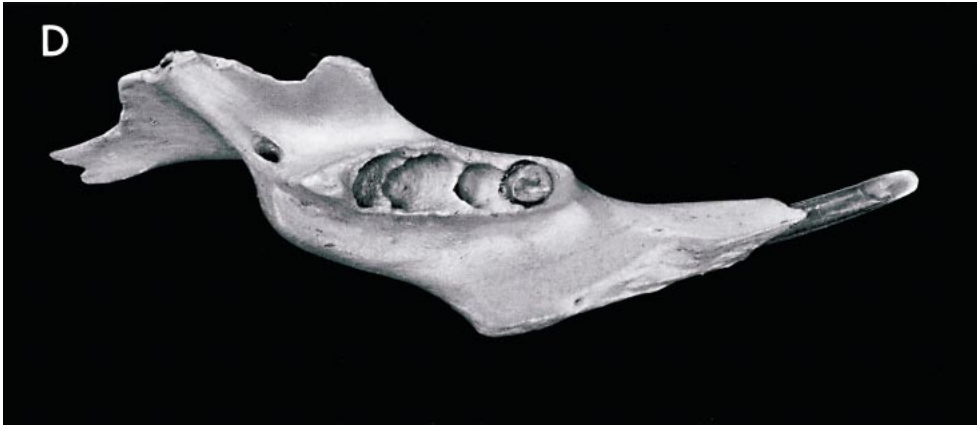


Fig. 7. Left hemimandible of *Xaymaca fulvopulvis* AMNHM 268011 (holotype), in (A) medial, (B) ventral, (C) lateral, and (D) occlusal aspects. In C, the groove winding across the fossa for the superficial masseter is an artifact of some sort, perhaps created by a feeding invertebrate. Notice in D that empty cheektooth alveoli are smooth-walled and sharply inclined; m2 alveolus is normal to axis of camera lens, and thus appears larger than the other molar alveoli (which it is not).



Fig. 7. *Continued.*

*Xaymaca* will have to await discovery of additional specimens.

We were unable to identify any other elements<sup>6</sup> relating to this species. Although *Xaymaca* is evidently an exceptionally rare fossil, it is improbable that it was so tied to local conditions in southern Jamaica that it never ventured into other parts of the island. In this regard it is worth noting that its jaw is similar in size to that of young specimens of *Geocapromys*, and for that reason may have been overlooked by other collectors in the past (including ourselves).

#### DESCRIPTION OF THE HOLOTYPE OF *XAYMACA FULVOPULVIS*

##### CORPUS AND RAMUS

The holotype jaw lacks part of the ascending ramus, much of the angular process, and all of the glenoid articulation (fig. 7). The i1 and remnant portion of p4, the only teeth still present, are described in detail in subsequent sections.

<sup>6</sup> Study of new postcranial finds of the monkey *Xenothrix mcgregori* (MacPhee and Horovitz, in press) establish that AMNHM 259905 and 259906 (right and left humeri) and 259908 (sacrum), originally listed by MacPhee and Fleagle (1991) as “not *Geocapromys brownii*”, do not belong to *Xenothrix* either. They must therefore represent some other taxon, possibly *Xaymaca fulvopulvis*. The same possibility may apply to the small mammalian femora from Coco Ree Cave (UF 40097) and Sheep Pen (UF 58350), interpreted as platyrrhine by Ford (1990) and Ford and Morgan (1986, 1988). Certainty on this point will only come with the discovery of associated remains.

Inclination of alveoli indicates that the cheekteeth of *Xaymaca* were emplaced at a progressively more acute angle from front to back. The m3 alveolus is the largest. All molar alveoli are smooth-walled with no internal divisions, indicating that the teeth occupying them must have been essentially cylindrical. This is an important clue, because it presumably means that the molars of *Xaymaca* lacked not only discrete roots but also deep, exposed longitudinal grooves (striae). Presence of deep striae, a common feature of many caviidan cheekteeth, can often be reliably inferred even when the teeth themselves are absent, because alveolar sidewalls have a distinctive fluted or scalloped appearance that matches the tooth's pattern of grooves (fig. 9, bottom). Cheektooth alveoli lacking internal divisions for discrete roots usually house hypsodont or hypselodont teeth and alveoli tend to be simple, tubular holes. *Amblyrhiza* and *Elasmodontomys* present excellent examples of this condition (figs. 13, 20). The tightly appressed lamellae which make up their cheekteeth leave no mark on alveolar sidewalls, because each tooth is wrapped in a continuous sheet of cementum which fills all potential striae. Clidomyine cheekteeth are quite different: although they too are composed of a series of plates (fig. 4A–J), interlamellar grooves are prominent and leave the expected decoration on alveolar walls (see MacPhee, 1984).

The hemimandible of *Xaymaca fulvopulvis* shows no signs of having been fused with its

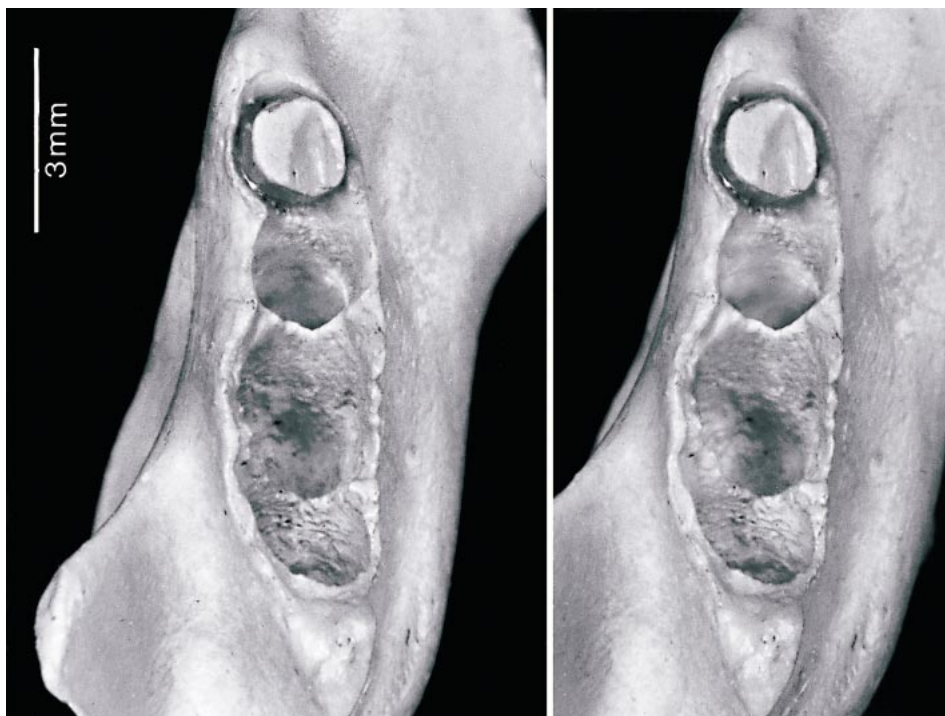


Fig. 8. Hemimandible of *Xaymaca fulvopulvis* AMNHM 268011 (holotype), stereopair of occlusal aspect, coated to emphasize surface textures (cf. fig. 9). Shallow groove crosscutting lingual moiety of p4's occlusal surface is evidently due to wear; it is not a fracture surface (see text).

partner at the mental symphysis (fig. 7A, B). Because the degree of wear on the premolar (see below) indicates that the jaw came from an aged individual, it seems reasonable to conclude that dentaries did not normally fuse in this species. In *Amblyrhiza*, by contrast, fusion is so complete that it is difficult to trace the mental suture in adult material (fig. 13B). A similar condition obtains in *Clidomys* (Morgan and Wilkins, 2003). In *Elasmodontomys* the mental suture fusion disappears dorsally but not ventrally, even in aged individuals (fig. 20B). Symphyseal fusion is always completely absent in capromyids and echimyids. It is also absent in the type jaw of *Quemisia* (cf. Ray, 1965), although this jaw is from a young animal (m3 unerupted).

The masseteric fossa is of moderate size and depth. Bone has been lost from the end of the coronoid process; its original size cannot be determined, although it may have been abbreviated rather than large and projecting as in *Elasmodontomys* (cf. Anthony, 1918) or capromyids (fig. 12A). No mental

foramen can be identified on the sidewall of the horizontal ramus. The root of the angular process is still present, although its tip is lost. Its form suggests that the process was flattened on its ventral surface and extended caudally as a narrow spike, as in many caviidans.

The alveolar process distal to the m3 alveolus forms a discrete, prowlike buttress which runs backward to the area of the missing condyle, as in many caviidans (including *Clidomys*, *Amblyrhiza*, *Quemisia*, and *Boromys*). The upwardly directed mandibular foramen is located deep within a shallow fossa distal to the m3 alveolus, as in *Amblyrhiza* (but not in *Elasmodontomys*, in which the mandibular foramen is located farther away and faces lingually).

#### DENTITION

**INCISOR:** The incisor is relatively procumbent in *Xaymaca*, and the diastema between p4 and i1 is long in proportion to total length

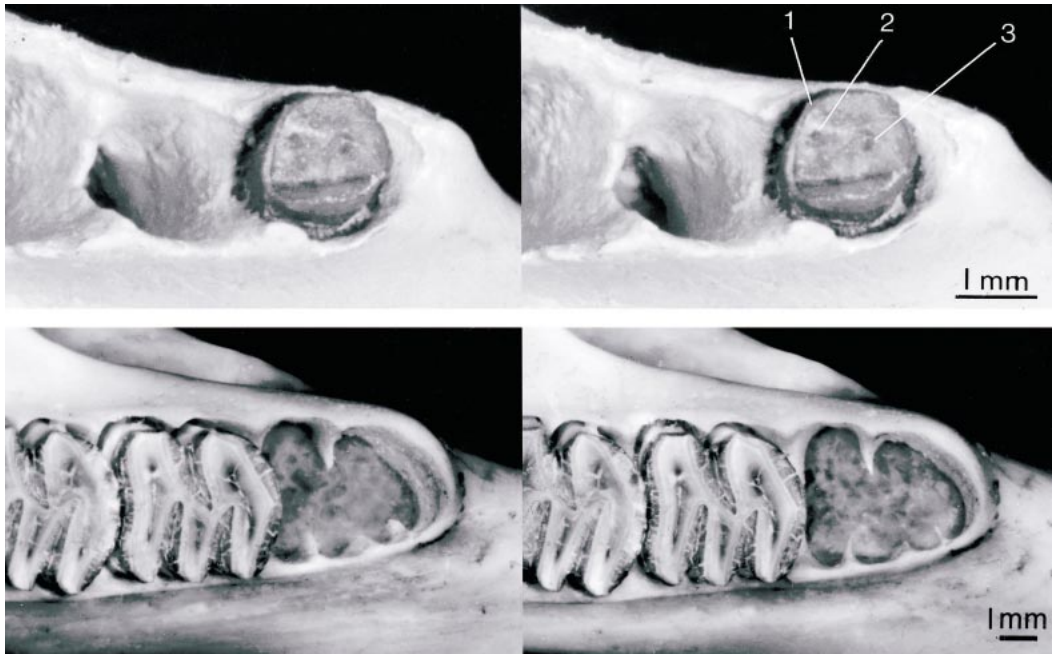


Fig. 9. *Xaymaca fulvopulvis* AMNHM 268011 (holotype, **top**) compared to jaw of Jamaican capromyid *Geocapromys brownii* AMNHM 45156 (**bottom**), stereopairs of occlusal aspect of left mandible, photographed in ordinary light (note difference in 1 mm scales). The worn p4 of the *Xaymaca* holotype is uncoated in this figure (cf. fig. 8), revealing small-scale features. Note sharp boundary (**feature 1**) between dark dentinal core of tooth and thin, light outer layer of cementum that encircles it (closeup of this boundary can be seen in fig. 16B). **Features 2** and **3** are possibly sections of the pulp chamber, seen through translucent dentine on the p4 trituration surface (cf. fig. 16D). *Geocapromys brownii* conspicuously differs from *Xaymaca* in alveolar orientation and internal ornamentation of tooth sockets (cf. empty p4 alveolus). *Geocapromys* and the endemic sigmodontine *Oryzomys antillarum* are the only other rodents represented in Pleistocene levels at Drum Cave.

(fig. 7A, C). Plateteeths (figs. 13, 20) resemble, and *Geocapromys* and *Boromys* (fig. 12A, B) differ from, *Xaymaca* in these respects (although not markedly so in either case). As in all caviidans, enamel is limited to the external aspect of the tooth. In *Xaymaca* the root of the incisor extends distal to the m3 alveolus, as in *Amblyrhiza*; the incisor of *Elasmodontomys* and *Clidomys* is somewhat shorter, and that of *Quemisia* is much shorter (Ray, 1965). In *Boromys* the incisor extends much farther posteriorly, into the substance of the coronoid process, where it produces a distinctive bump on the lateral aspect of the ascending ramus (fig. 12B).

The tip of the incisor was exposed to 3% hydrochloric acid for 15 seconds in order to visualize Hunter-Schreger banding (HSB) and the organization of the interprismatic

matrix (IPM) by SEM (fig. 10). As is typical for rodents, the incisor enamel of *Xaymaca* is two-layered, with HSB internal to the radially organized outer layer (Martin, 1992). The HSB is organized multiseriably, as in all caviidans (Martin, 1997). In a few areas, truncated sheets of IPM could be identified between prisms, but the angle of the photographed area was not favorable to determining IPM direction. According to Martin (1992), the pattern of incisor enamel microstructure in *Amblyrhiza* is like that of cavioids rather than octodontoids. This conflicts with the placement of this genus preferred by some authors (e.g., McKenna and Bell, 1997). Perhaps octodontoids are more variable than expected (cf. variation in other groups of rodents documented by Martin [1997]). Conditions in *Elasmodontomys* and

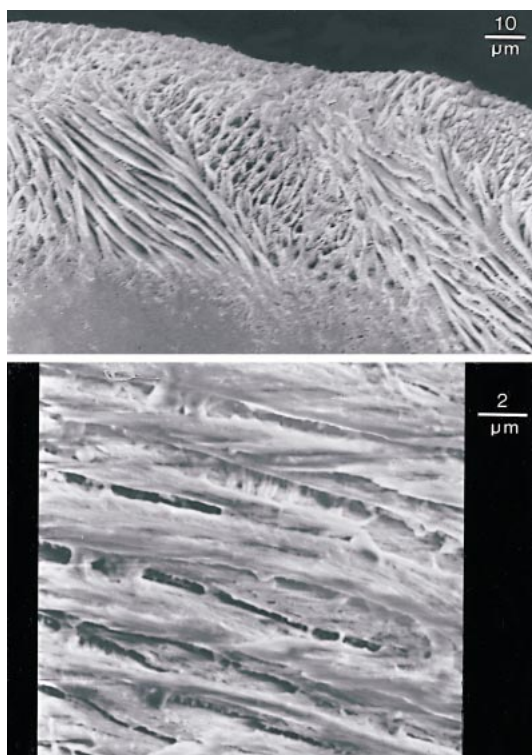


Fig. 10. Incisor tip (**top**) of *Xaymaca fulvopulvis* AMNHM 268011 (holotype) after brief exposure to 3% hydrochloric acid, showing in close-up (**bottom**) strong expression of multiserial Hunter-Schreger bands.

*Quemisia*, which might throw some light on the question of within-group variation, were not investigated by Martin (1992, 1997).

**PREMOLAR:** The p4 may be described as a small (diameter, 1.2 mm), nearly featureless post (figs. 8, 9, 11). The only detectable gross attribute of the tooth is the deep notch that crosscuts the lingual side of the otherwise flat trituration surface. The notch cannot be due to postmortem fracturing, as its surface exhibits microwear scratches like those found elsewhere on the occlusal surface. No developing successor tooth can be visualized radiographically (fig. 11), although whether premolar replacement occurred cannot be settled without a proper ontogenetic series. This is of some relevance because *Amblyrhiza*, *Elasmodontomys*, and *Quemisia* all replace dp4, while Quaternary echimyids and capromyids do not. It has been traditionally assumed that because the Deseadan taxon

*Sallamys* was certainly diphyodont, suppression of dp4 replacement may not have been fixed in spiny rats until late in the Cenozoic [Ray, 1964, 1965; Patterson and Wood, 1982]). Obviously, this character history is meaningful only if *Sallamys* is part of a monophyletic Echimyidae, a matter that has yet to be settled via a modern phylogenetic analysis.

The p4 of *Xaymaca* displays several unusual histological features that we have not previously encountered in any rodent, living or extinct. SEM of the trituration surface revealed numerous, regularly disposed tubules in all areas favorable for viewing. This is diagnostic evidence that this surface is composed of primary dentine (see Preliminary Considerations; fig. 16C, D). SEM also revealed the existence of a thin outer layer composed of material having a coarse, bone-like texture (fig. 16B), easily identified as cementum. We originally assumed that vestiges of crown enamel were represented in the three features indicated in figure 9 (top). Feature 1 is a discontinuous, quasicircumferential band which is visible under a raking ordinary light source. Under SEM (fig. 16B), however, it resolves as a thin ( $<10\ \mu\text{m}$ ) belt of material that is clearly continuous with local cementum in places. Its apparent distinctness under visible light seems to be an artifact, perhaps caused by postmortem separation of cementum and dentine at their interface. Features 2 and 3 (fig. 9, top) are two small lakelike areas in the middle of the tooth. Under SEM, these apparent lakes cannot be morphologically or histologically differentiated from the dentine that otherwise makes up all of the trituration surface (fig. 16D). This may be because the features lie deep to the surface and are thus visible through the somewhat translucent dentine under ordinary light. They may be the margins of the pulp chamber, or they may be fracture artifacts, but they are not enamel. In short, enamel does not exist anywhere on the tooth, at least as now preserved (cf. easily recognized enamel rods in sectioned molar of *Isolobodon*, fig. 19A, B).

Radiography (fig. 11) reveals additional features of interest. In radiographs, the root forms a continuous structure. Although at first glance it appears that the structure di-





Fig. 11. Radiograph of *Xaymaca fulvopulvis* AMNHM 268011 (holotype). The socketed part of p4 is essentially cylindrical, without discrete roots (opaque areas are sidewalls, not divisions; see text).

vides apically into two discrete rootlets, in fact only a single, cylindrical root is present. In radiographs of teeth with discrete roots (e.g., *Boromys*), the roots are bounded by sharp internal and external borders, due to radiopacity differences between bone and dentine or the latter and the pulp chamber (cf. fig. 14A–C). In the case of AMNHM 268011, internal “borders” are diffuse, indicating that apparent separation into “roots” is an artifact. Also, the tooth’s interior is evidently less mineralized (less radiopaque) than the periphery, which adds to the illusion of apical division. Finally, there is no sign of a neurovascular canal in either “root”. As already noted, the pulp chamber of the p4 probably lies centrally, just beneath the present trituration surface. However, although a sharp difference in radiopacity may be seen in the upper part of the tooth (fig. 11), a definite chamber cannot be discriminated.

To confirm the radiographic observations, a small amount of bone was removed from the lingual side of the p4 alveolus after photography was completed. As expected, it was found that the tooth does not furcate deeper within its alveolus: its core is solid and seems to consist of dentine only. Extraction of the tooth to determine whether the dentine is primary or secondary was rejected because of the possibility of inducing irreparable damage.

Interpreting these findings is challenging. The vague resemblance of the p4 to a phyllophagan molariform is no more than that,

and, in any case, even the most “rodentiform” of the Antillean sloths (e.g., Cuban *Megalocnus rodens*; Matthew and de Paula Couto, 1959) show no detailed convergences on caviidans for features like hystriognath. Total absence of cheektooth enamel throughout ontogeny would be unprecedented in a normal rodent, so there must be another explanation. The only plausible alternatives involve the assumption that the tooth as preserved is highly incomplete because the enamel-bearing portion broke away or wore off through use. The notch and microwear scratches noted above render implausible the argument that the enamel dissolved away while the tooth’s owner was lodged in some predator’s gut tube.

Breakage implies that a large crown was originally present, but because of some accident suffered during the individual’s life it fractured completely away from the dentine core. In this scenario the individual would have managed to survive for a time because the tooth core was hard enough to serve as a makeshift. There are two features of the p4 which make the breakage explanation improbable. First, there is no indication of tissue loss from the periphery of the tooth, which as noted is sheathed in an apparently intact band of cementum. Although in a lamellar tooth a cementum layer could certainly intervene between enamel and dentine, the fact that the free surface of the cementum is undisrupted militates against this possibility in *Xaymaca*. Secondly, there is a small but definite interproximal wear facet on the distal



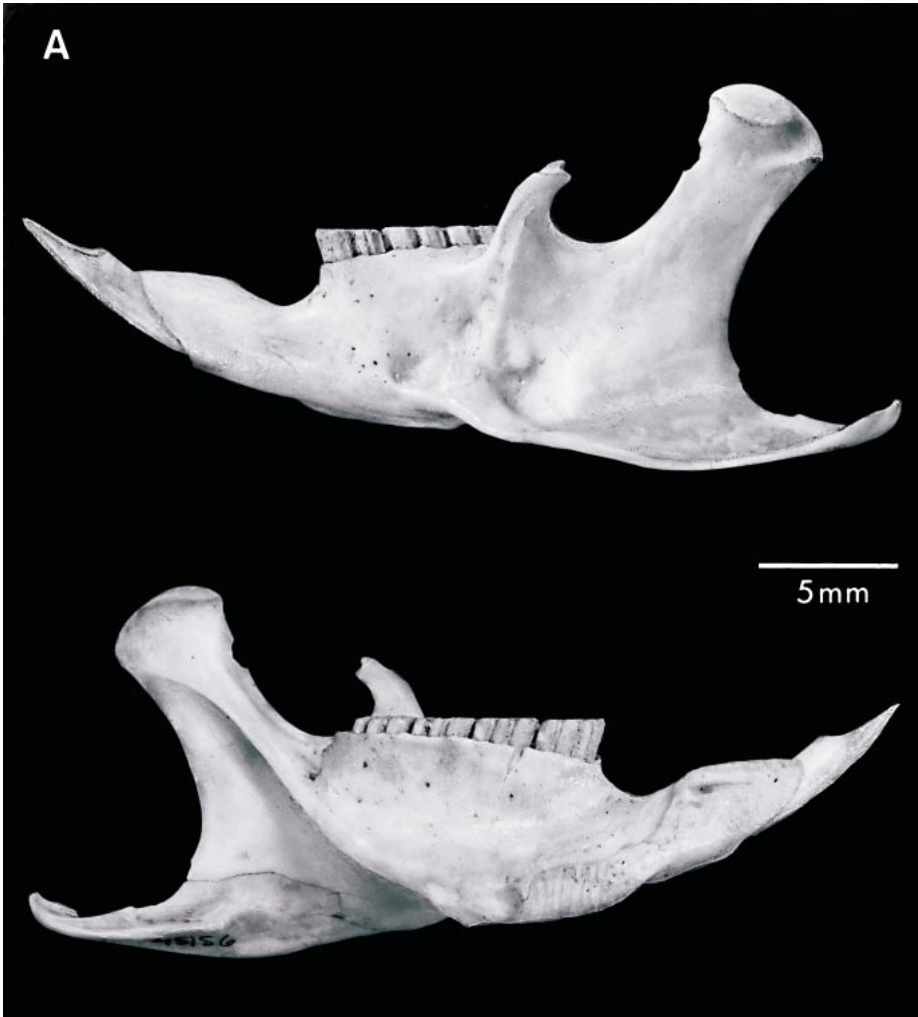


Fig. 12. Left hemimandibles of (A) Jamaican capromyid *Geocapromys brownii* AMNHM 45146 and (B, opposite page) Cuban heteropsomyine *Boromys torrei* AMNHP 140813, lateral (top) and medial (bottom) aspects. See text for comparisons to holotype of *Xaymaca fulvopulvis*.

edge of the trituration surface, below the notch (not illustrated). Such a facet could only be produced by the leading edge of the now-lost m1 wearing against the p4 as preserved—leaving no room for an interposed thickness of enamel. We suspect that extreme wear and apical hypertrophy constitute a better explanation, a point best made by a series of comparisons to relevant caviidan groups.

#### COMPARISONS

We made comparisons to ascertain whether there is any relevant caviidan taxon in

which extreme cheektooth wear might produce a result similar to that seen in the *Xaymaca* holotype, that is, a peglike, columnar tooth composed largely of dentine, with no remaining surface relief or crown enamel. For example, stripping the enamel and cementum away from the dentine core of a cheektooth of the sigmodontine murid *Oryzomys* would not produce a tooth like that of *Xaymaca* in either size or shape.

Although reference is made below to root closure, for many taxa the situation is ambiguous because authors either do not report

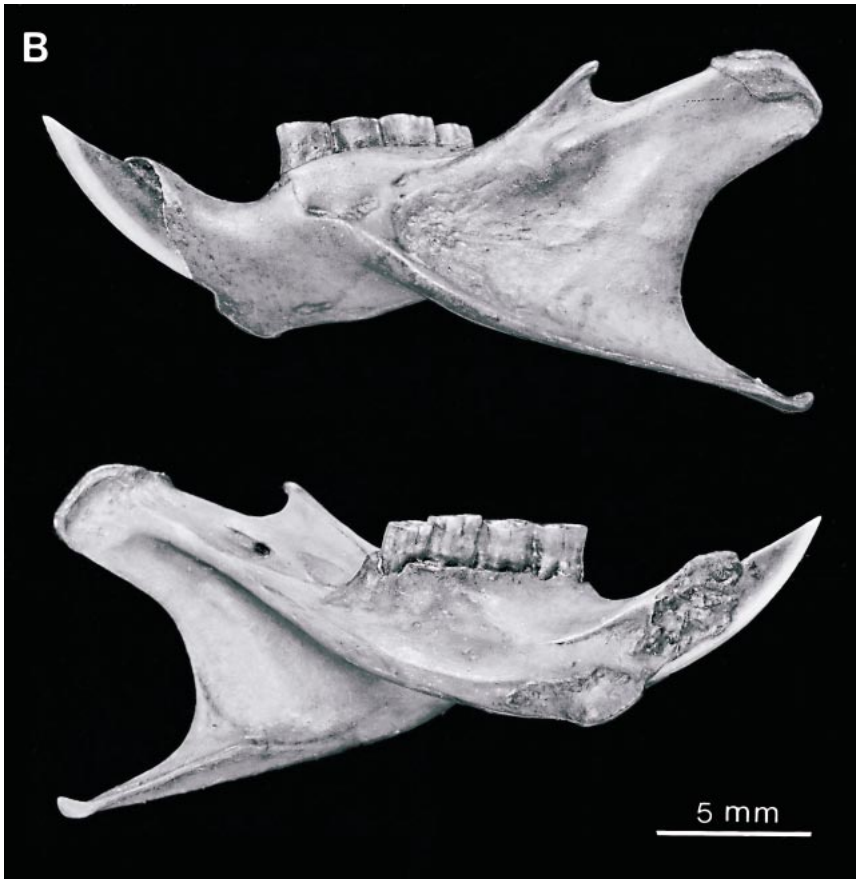


Fig. 12. *Continued.*

on the condition of the root(s) or they use terminology inconsistently (Mones, 1982). Given sufficient time, evolutionary gain or loss of the completely rooted (or completely open) condition is probably easily achieved, judging from family-level taxa that show both conditions (e.g., *Dinomyidae* sensu Fields, 1957). However, because we are dealing here with a Quaternary taxon we will concentrate on comparisons to extant groups in making a logical first cut.

Taxa in which the p4 has large, divergent roots housed in separate sockets can be immediately discounted, because the p4 of *Xaymaca* is a simple, apically widened column in an undivided alveolus. On this basis, we reject extant *Dasyproctidae* (including *Myoprocta* and *Agouti*) and *Myocastor*, whose oblong p4s possess two powerfully built roots at all ontogenetic stages. This conclu-

sion applies to noncaviidan *Erethizontidae* as well. Also discountable are taxa with hypodont teeth in which infoldings of enamel typically run the complete length of each cheektooth (hydrochoerids, chinchillids, dinomyids, capromyids, caviids). Octodontids, abrocomids, and ctenomyids differ in detail but all are quite distinct from *Xaymaca*. *Ctenomys* is of some interest because its cheekteeth are extremely simple, essentially consisting of an enamel sheath enclosing a dentine core. (Within the alveolus the enamel is covered by cementum as usual.) To this slim extent tuco-tucos may be said to resemble *Xaymaca*, but on inspection it is obvious that no wear regime, no matter how extensive, would result in total disappearance of the enamel layer in a ctenomyid. In any case, inasmuch as *Xaymaca* lacks any features indicative of fossorial life, a relationship with

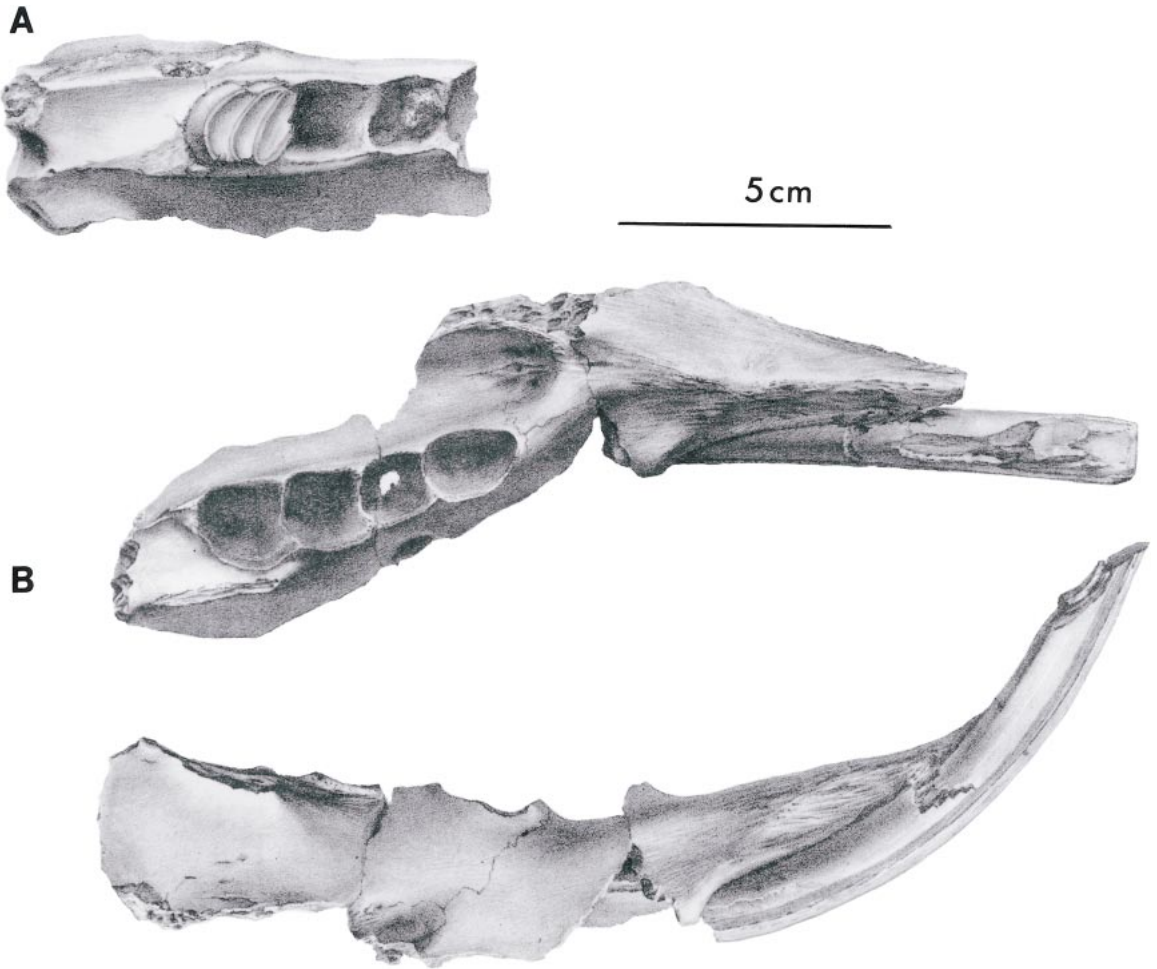


Fig. 13. Jaw and tooth structure of *Amblyrhiza inundata* (after Cope, 1883), illustrating (A) AMNHP 11836, lamelliform m3 in situ, and (B) AMNHP 11839, the most complete jaw in AMNHP collection. Although *Amblyrhiza* was larger than *Xaymaca* by two orders of magnitude, general shape, orientation, and lack of ornamentation of cylindriciform alveoli are similar (cf. fig. 9). One conspicuous difference is complete fusion of hemimandibles at mental symphysis in *Amblyrhiza*.

tuco-tucos, with their massively built jaws, seems most unlikely. The same reasoning applies to Old World hystricognaths such as bathyergids. For example, in the sand rat *Heliophobius* all cheekteeth are quasicylindrical and p4 is much smaller than the molars. However, in *Heliophobius* as in all other examined mole-rats (*Heterocephalus*, *Cryptomys*), enamel is thick and continuous deep into the root portion of each cheektooth.

Our nonexhaustive survey of mainland South American fossil taxa does not present anything that strongly corresponds to conditions in *Xaymaca*, although of course some

mainland groups (e.g., Late Miocene cardiomyine dinomyids) possessed relatively simple premolars. (The same point applies to Asian fossil hystricognaths whose cylindrical teeth wear to simple pegs, e.g., *Tsaganomys* [Bryant and McKenna, 1995]). Obviously, most discussions of dental features, and hence phylogenetic characterizations, of extinct South American hystricognaths focus on details of crown morphology (Vucetich et al., 1999), but this source of information is not available for *Xaymaca*. Rather than engage in a series of essentially nugatory comparisons, we propose instead to focus on the

two groups of extinct Antillean rodents that we think can shed the most light on dental ontogeny of *Xaymaca*—heteropsomyine echimyids and heptaxodontines.

#### DENTAL ONTOGENY IN ANTILLEAN HETEROPSOMYINES

To make comparisons of interest, we studied p4 wear in a large sample of jaws of *Boromys torrei* collected by Anthony (1919) in cave deposits near Daiquiri, Cuba. Judging from fossil remains, this species was somewhat smaller than *Xaymaca* in body size. Like other Antillean heteropsomyines, *Boromys* had relatively small, low-crowned cheekteeth (figs. 14, 15). As Miller (1916: 7) said of its close relative *Brotomys*, this taxon is “remarkable [among caviidans] for its combination of robust skull with weak teeth.”

In *B. torrei*, all cheekteeth have a distinct cervix, and roots are composed of dentine only with an external covering of cementum. In the specific case of the premolar (a non-replacing locus in Antillean heteropsomyines), two roots are typically present, occupying separate sockets within the large alveolus that holds the body of the tooth. Crowns of unworn p4s exhibit four striae—two major (buccal, lingual) and two minor (mesiolingual, distolingual). Major striae extend almost to the cervix; minor striae are much shorter. The enamel-lined infolds of the striae project deeply into the dentine forming the center of the tooth. Miller (1916) briefly considered wear in this taxon, but only in relation to features that (in his view) distinguished Cuban *Boromys* from Hispaniolan *Brotomys*. We found that as wear proceeded in *Boromys*, the enamel on the infold became progressively isolated from enamel on the sidewall of the tooth, eventually forming small, detached enamel rings or lakes (fossettids). Fossetid formation provides a basis for grading p4 wear stages:

*Stage 1: Early wear* (figs. 14A, D; 15A): Crown at maximum height and roots open at apical end. In later stages, roots progressively close. Occlusal surface assumes distinctive appearance as soon as wear is initiated: major striae are so deeply infolded that they effectively divide crown into mesial and distal

moieties, joined by narrow neck. Mesiolingual and distolingual infolds progressively lose connection with their striae, becoming isolated as fossettids.

*Stage 2: Moderate wear* (figs. 14B, E; 15B): Mesiolingual and distolingual fossettids become progressively smaller due to wear; buccal and lingual fossettids appear. For a short time all four fossettids may be present, in the form of enamel lakes surrounded by dentine. Roots close apically, begin to hypertrophy; apical production of secondary dentine pushes crown upward, thereby exposing cervix above alveolar border (cf. arrows, fig. 14D, E).

*Stage 3. Advanced wear* (figs. 14C, F; 15C): Cervix of tooth well above alveolar border. Hypertrophied roots have become wider and columnar, but remain separate (fusion does not take place). Buccal and lingual fossettids, already shallow at beginning of stage, eventually disappear. Premolar becomes a dentine peg.

In the oldest animal we were able to identify using wear criteria (figs. 14C, F; 15C), the p4 crown had completely disappeared (no enamel remaining) and wear was attacking the dentine root. However, tooth height (apex to trituration surface) was virtually the same as in stage 1 animals, indicating that throughout tooth ontogeny material is added to the root end at roughly the same rate at which it is removed from the trituration surface. Given the strong dental similarity of *Boromys* to *Heteropsomys* and *Brotomys*, it is reasonable to suppose that excessive attrition could lead to the same result in these taxa, although we were not able to find any good examples in the AMNHP collections. Unfortunately, the premolar is not preserved in the holotype (and only) jaw of *Puertoricomys* (cf. Woods, 1989a).

The *Xaymaca* holotype compares very well to the most advanced wear stage of *Boromys*—most particularly in the reduction of p4 to a dentine peg—but there is one obvious difference. In *Boromys*, divided, closed roots are retained into the most advanced stage, whereas in the *Xaymaca* holotype the root end appears to have been permanently unclosed and there is no sign of a divided root structure. Divided roots seem to be an old pattern among echimyids, inasmuch as De-

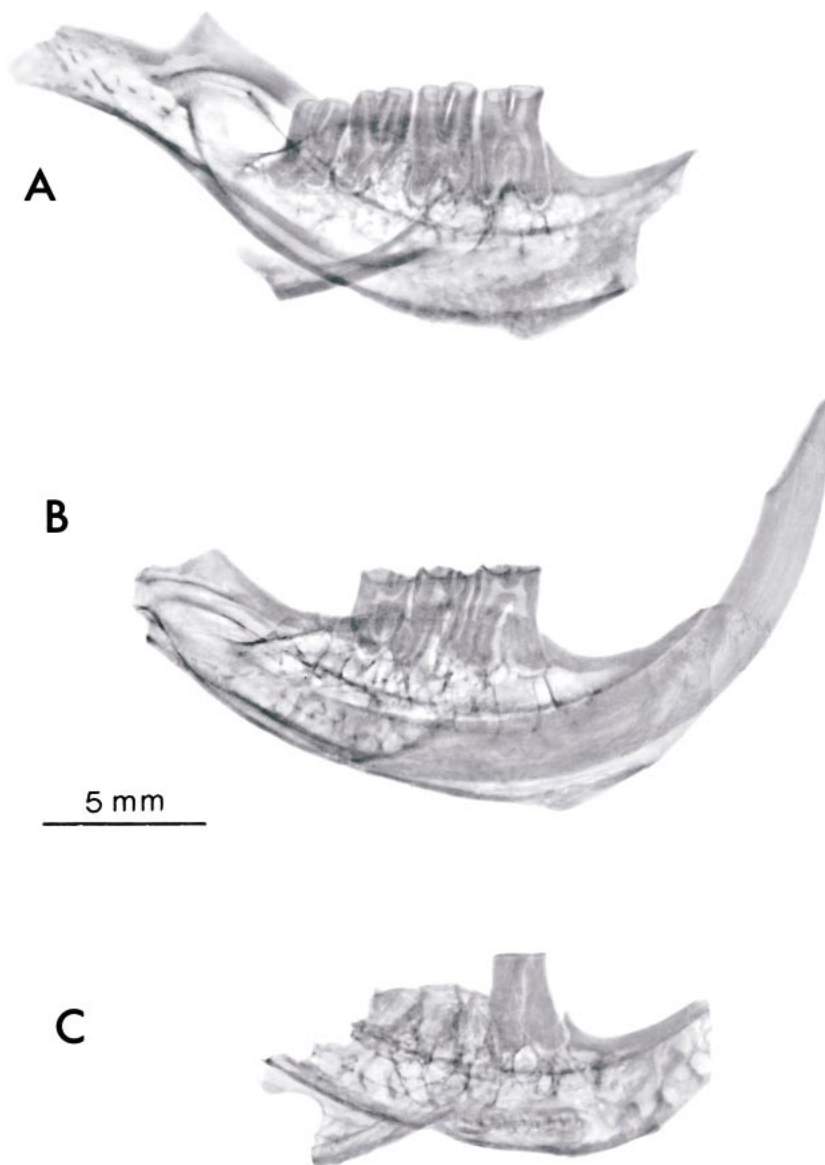


Fig. 14. Left hemimandibles of three individuals of Cuban heteropsomyine *Boromys torrei* as seen in radiographs (A–C) and ordinary-light photographs (D–F, **opposite page**) in medial aspect. Specimens illustrate cheektooth wear stages discussed in text: (A, D) AMNHP 140812 representing stage 1, slight wear; (B, E) AMNHP 140811 representing stage 2, moderate wear; (C, F) AMNHP 140810 representing stage 3, advanced wear (see also fig. 15). (Ascending ramus of specimen depicted in C and F was lost during set-up for radiography). Arrows in D and E show migration of relative position of cervix as teeth wear down; in F, enamelodentine junction has been consumed by attrition and root material is exposed at occlusal surface. In radiographs of the oldest stage (C), the thickened roots overlap and thus appear solid, but the line of separation can still be seen in the photograph (F).



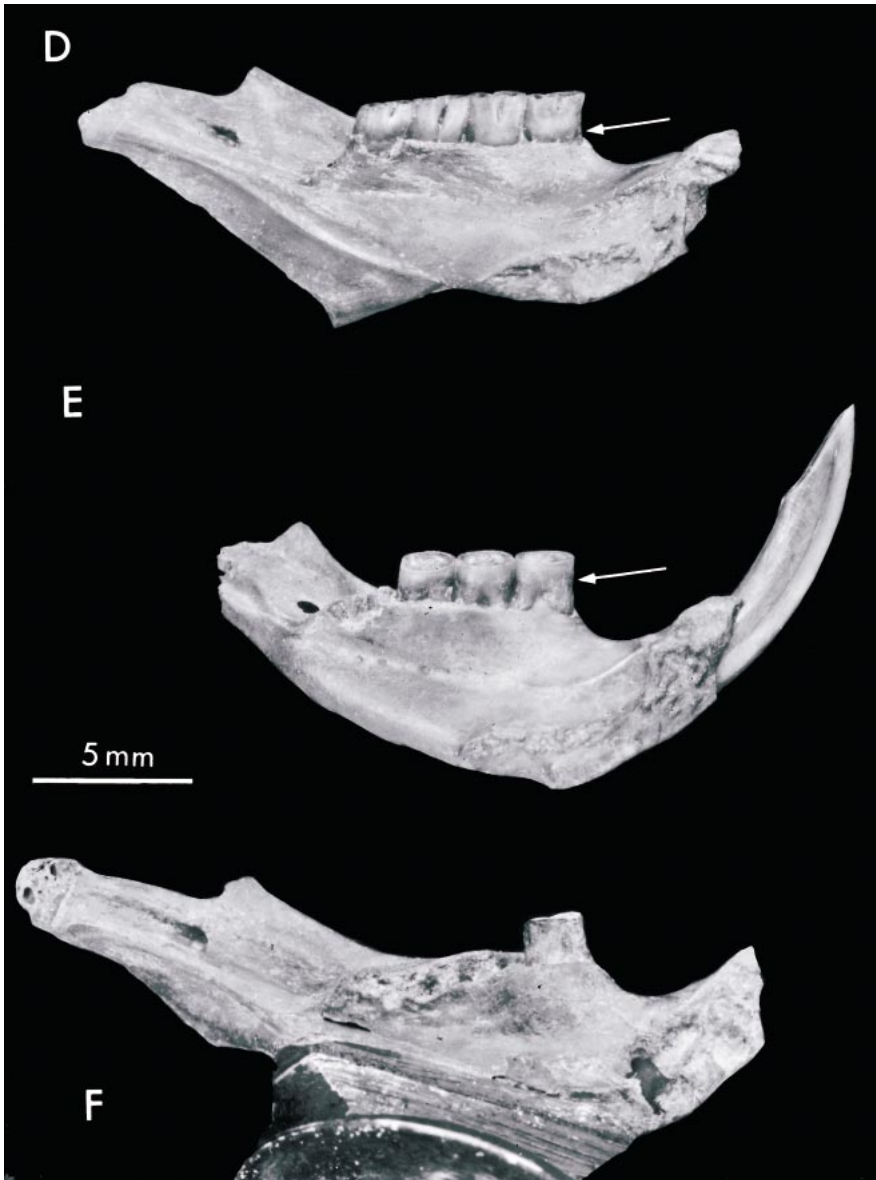


Fig. 14. *Continued.*

seadan *Sallamys* evidently possessed strong roots housed in separate sockets (Patterson and Wood, 1982). Nevertheless, strictly in terms of premolar shape, *Xaymaca* is more like small heteropsomyine echimyids than any other phylogenetic grouping of New World hystricognaths so far considered.

While it would be a simple matter to take this observation at face value and end this discussion by tentatively placing *Xaymaca* in

or near Heteropsomyinae, another set of parallels occurs in Heptaxodontinae. These are of interest because they not only concern shape but also developmental features connected with apical hypertrophy.

#### DENTAL ONTOGENY IN HEPTAXODONTINAE

**PREVIOUS OBSERVATIONS:** Using traditional criteria (see Preliminary Considerations),

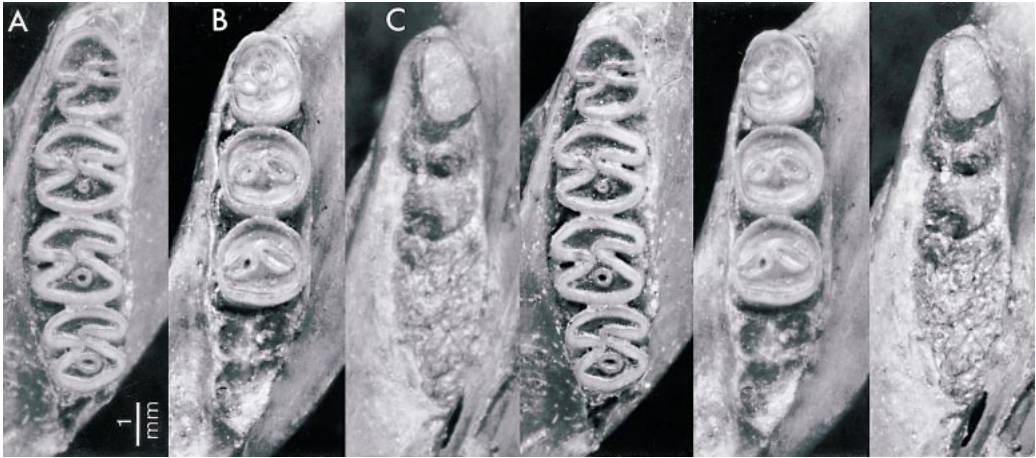


Fig. 15. Occlusal aspect (stereopairs) of same specimens of *Boromys torrei* shown in figure 14, illustrating cheektooth wear stages 1–3 (A–C). See text for description and evaluation. *Boromys* was probably similar to *Xaymaca* in body size, but cheekteeth differ radically (e.g., in spiny rats, cheekteeth exhibit furcated roots, prominent cervix, and deep enamel infolds).

heptaxodontine cheekteeth can be classed as hypselodont because the apical ends of cheekteeth tended to close in maturity (cf. Cope, 1883; Anthony, 1918). However, examination of a large series of *Elasmodontomys* jaws reveals that teeth do not become conspicuously lower-crowned in older animals. Part of the reason for this is that alveoli evidently grew shallower through ontogeny as crown ends were attritionally consumed. But another reason is that the apical ends of the cheekteeth continued to form dentine after root closure, so that the crown portion was, in effect, extruded by the continually growing stub of dentine at its base.

We emphasize this last point because previous commentators (Cope, 1883; Anthony, 1918; Ray, 1964) have assumed that the material formed at the base of mature heptaxodontine cheekteeth was cementum rather than dentine, a notion that is still repeated in the recent literature (e.g., Woods, 1989b). The histological evidence that necessitates a different conclusion is presented in the next section, but first it is useful to examine why previous authors reached erroneous conclusions. In this regard Anthony's (1918) observations on certain unusual features of late dental ontogeny and senescence in *Elasmodontomys obliquus* are particularly significant (see also Ray, 1964: 116). (In the following quotation, "cement" in the original

passage has been replaced by "secondary dentine" in brackets.) Anthony (1918: 383) stated that, in recently erupted teeth of this species,

... the laminae extend the full length of the tooth and the base is open, appearing as a cylindrical shell of enamel around a bundle of parallel plates. Later as the crown wears the tooth pushes up from the base to keep a constant height above the alveolar border and [secondary dentine] is deposited about the base. At the immediate base there is a slight constriction in the enveloping enamel and when [secondary dentine] is added the base is still further constricted. ... [Furthermore, the] alveolus closes and shortens with the wear of the enamel and in advanced age the [secondary dentine] reaches the plane of wear. At this stage the crown has a homogeneous structure with perhaps a hole down the center [for the neurovascular bundle], and the teeth are weak and brittle. ... In very old animals the crown surface is much reduced when the [secondary dentine] enters the wear plane.

Teeth of a skull (fig. 20A) from Anthony's excavations at Toraño Cave display precisely this set of wear-related features. In this specimen, the worn left P4 lacks all sign of the lamellar organization characteristic of *Elasmodontomys* cheekteeth (cf. same specimen's intact M3). Although the tooth's surface is unfortunately shattered, it is obvious that it is no more than a rounded peg and that whatever tooth pattern was originally present has been completely erased by wear. (The hole in the center of the tooth is the lumen of the pulp chamber.) Nevertheless, the tooth pro-

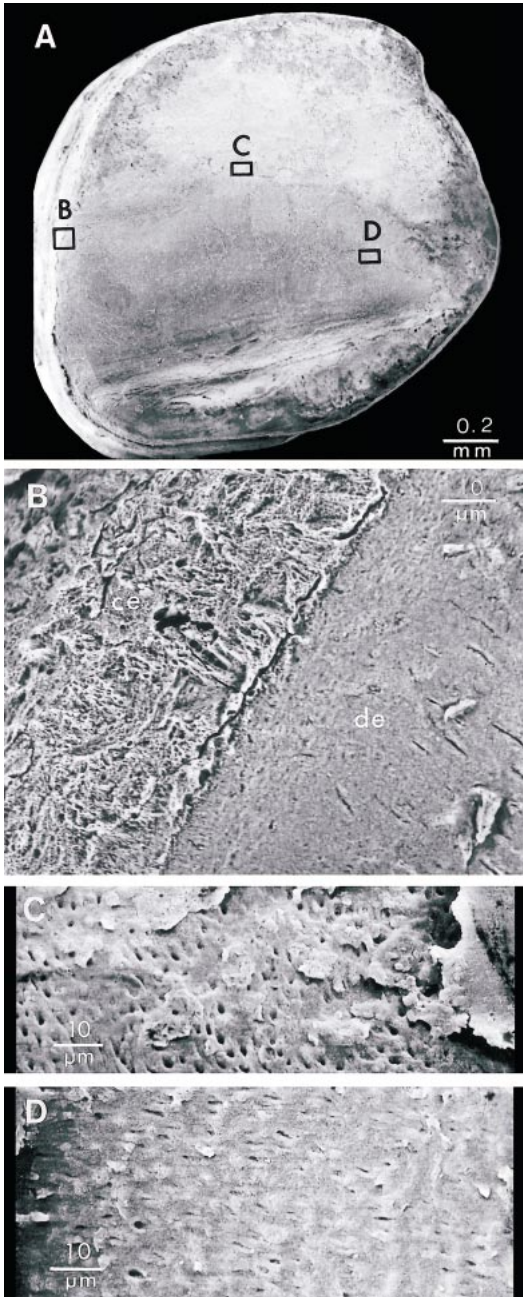


Fig. 16. SEM micrographs of p4 of *Xaymaca fulvopulvis* AMNHM 268011 (holotype), illustrating small-scale features and other details. (A) Occlusal surface; areas B, C, and D are shown at higher magnification in rest of figure (boxes show location and approximate sizes of area depicted). (B) Thin cementum (ce) band on periphery of tooth and dentine (de) matrix perforated by numerous tubules for odontoblast projections. (C) and (D) Organization

jects well beyond the alveolar border and must have been in functional occlusion with its antagonist at the time of the animal's death. Similar conditions obtain in a right p4 (also unfortunately shattered) in a lower jaw from the same site (fig. 20B). These structures are clearly roots, but what is their composition? Evidently, it did not occur to Anthony (1918) that highly friable cementum would be quite unsuitable for extending tooth life in mammals that occasionally live long enough to wear out the crown portions of their teeth. Obviously, finding cementum on the outside of a tooth root is not evidence that the entire root is formed from this material.

Although material of *Amblyrhiza* is more limited, the same observations that Anthony (1918) made on tooth wear in *Elasmodontomys* apply in equal measure to its larger relative. The degree of wear on the cheek-tooth illustrated in figure 20C is literally fantastic: the tooth, a ?P4, consists almost entirely of apical dentine except for a thin wedge of discontinuous crescents of enamel on the distal margin—all that is left of the original crown. This interpretation is corroborated by the fact that microwear scratches occur on the noncrown portion of the flattened surface evident in lateral view (fig. 20D), which must therefore be the occlusal surface. The holes next to the enamel area are exposed pulp cavity. The oddly contorted root end bears witness to the extraordinary amount of remodeling that must have gone on during the individual's life to keep this tooth in a functional position.

**HISTOLOGICAL OBSERVATIONS:** To gain some new insight into the ontogeny and histology of root hypertrophy, we embedded cheekteeth of *Amblyrhiza*, *Elasmodontomys*, and (for comparative purposes) *Isolobodon* in resin and cut them with a standard mineralogical saw (figs. 17–19). Both longitu-

←

of dental tubules in dentine at different locations on trituration surface. Area D overlaps position of feature 3 in figure 9; all that is visible in SEM is dentine (see text). Detritus on surface could not be removed without polishing and therefore destroying trituration surface.



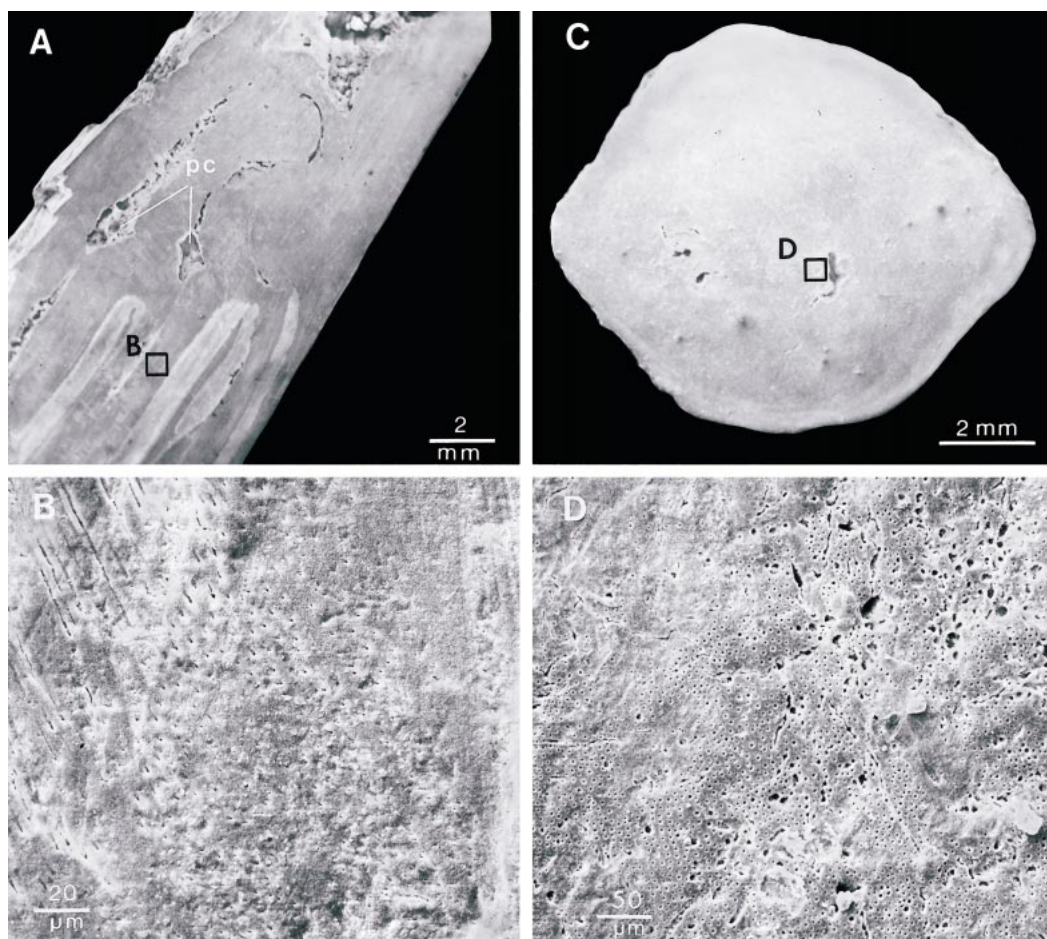


Fig. 17. Isolated molars of Antillean heptaxodontine *Amblyrhiza inundata* from Pitchapple Cave, Anguilla, SEMs at low and high magnification. (A) AAHS 91253a, longitudinal section at low magnification, showing distribution of enamel, dentine and cementum (root end faces top of page; **pc**, pulp chamber). (B) Closeup of boxed area in A, showing appearance of dentine in crown. (C) AAHS 91253b, transverse section through root end at low magnification, showing pulp chamber (to right of box). (D) Closeup of boxed area in C, showing characteristic appearance of dentine matrix in this region. In both specimens, the root end is nearly as long as the crown, indicating that they came from aged animals. In early ontogeny each pulp chamber would have been broadly open beneath the apical ends of the enamel folds. With continuing elaboration of dentine, the chambers became constricted and progressively elongated. Since root canals must be preserved to transmit neurovascular bundles, canals mark the previous extent and line of apical movement of pulp chamber. In *Amblyrhiza*, both primary and secondary dentine have an irregular appearance, with (in addition to characteristic tubules) many small vacuities that presumably housed cell bodies. There is no histologically sharp dividing line between the crown and root areas.

dinal and cross sections were collected; sections were then polished and photographed by SEM to facilitate comparison. Interpretation was based on the same tissue-specific criteria used to evaluate the p4 of *Xaymaca*.

In longitudinal section under low magni-

fication, the molar of *Amblyrhiza* (fig. 17A) presents two morphological areas. One may be regarded as the crown portion, as it consists of complexly folded sheets of enamel, primary dentine and cementum which together comprise the individual lamellae



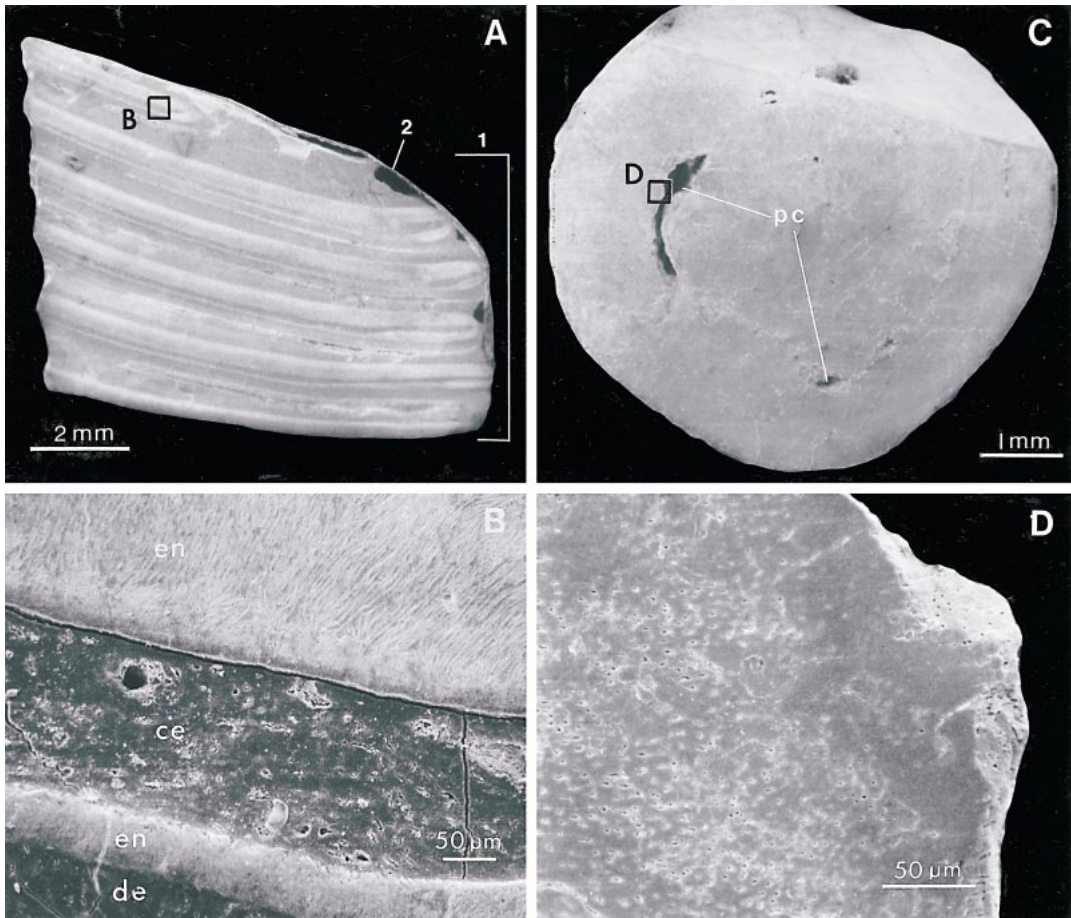


Fig. 18. Isolated p4 (AMNHP 140817) of Antillean heptaxodontine *Elasmodontomys obliquus* from Toraño Cave, near Utuado, Puerto Rico, SEMs at low and higher magnification. While this specimen was being cut, the apical end broke off, apparently along an undetected developmental boundary (**feature 1** in A). The boundary as seen on the crown end is in contact with the tape (**feature 2**) used to position the specimen for SEM. (A) Longitudinal section through crown end at low magnification, showing distribution of enamel, dentine and cementum (occlusal surface faces left). (B) Closeup of boxed area in A, showing characteristic histological differences between cementum (**ce**), enamel (**en**), and dentine (**de**). (C) Transverse section through apical end at low magnification; **pc**, pulp chamber. (D) Closeup of boxed area in C, showing secondary dentine on wall of pulp chamber. Secondary dentine is less irregular in this taxon than in *Amblyrhiza* (fig. 17).

forming the tooth pattern. The other part would ordinarily be regarded as the root: it is more uniform in appearance (only dentine present) and is penetrated by neurovascular canals. At the selected magnification there is no visible transition between the two. However, in the specimen of *Elasmodontomys*, the tooth pattern of which is similarly organized, the equivalent of the root portion broke off cleanly during preparation (fig.

18A, feature 1). This strongly suggests that there is a real developmental border between the two areas in both taxa, as may be seen also in the organization of the dentine. In the crown portion of each heptaxodontine specimen, the primary dentine has a well organized appearance: tubules stand out very clearly, in contrast to the prismatically organized enamel and the lacuna-filled cementum (figs. 17B, 18B). In the root portion,

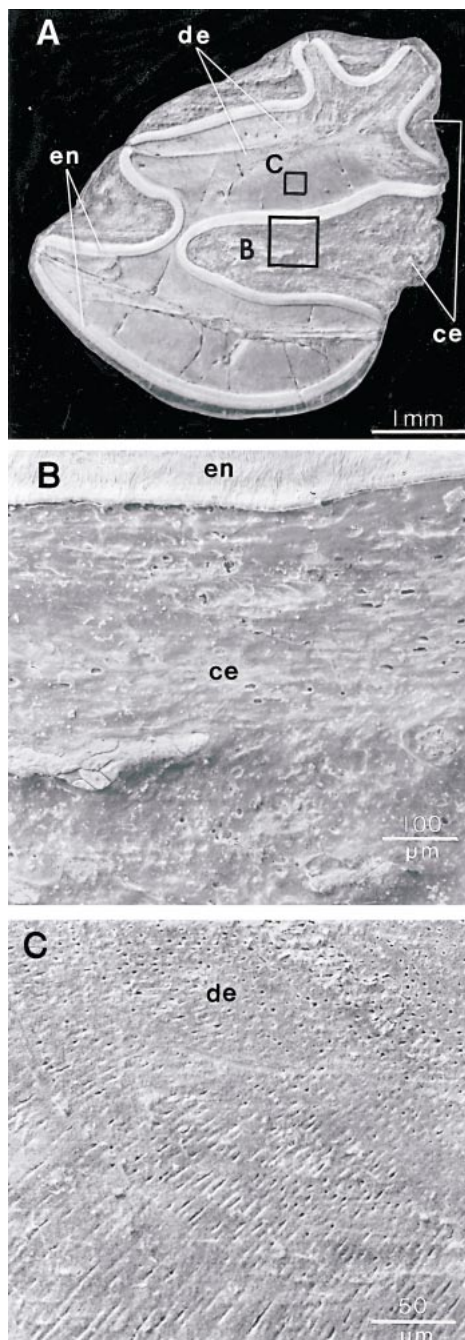


Fig. 19. Isolated p4 (AMNHP 140816) of capromyid *Isolobodon portoricensis* from Salt River Bay, St. Croix (?Amerindian site), SEMs at low and high magnification. (A) Transverse section at low magnification, showing distribution of enamel (en), dentine (de), and cementum (ce). (B) Closeup of large boxed area in A, showing cementum and enamel. (C) Closeup of small boxed

however, tubules are more patchily distributed and less organized (figs. 17C, D; 18C, D), a difference which is consistent with the dentine being of secondary origin—that is, as the result of apical hypertrophy. Although the hypertrophied area appears to be continuous and massive in the *Elasmodontomys* specimen (partly due to the obliquity of the plane of sectioning), apical ends of mature heptaxodontine teeth are usually hollowed out, apparently because dentine is deposited faster peripherally than centrally (fig. 2B).

We did not section projecting root stubs on the skull and jaw specimens of *Elasmodontomys* showing advanced wear because extraction would cause further damage. Nevertheless, in view of our other findings it is reasonable to assume that the tooth remnants in question are composed of dentine only, with a thin outer covering of cementum. Conditions in aged *Quemisia* are not known. The type and only published jaw of *Quemisia* (USNM 367229) is from a young animal in which m3 is not fully erupted (Miller, 1929). Not unexpectedly, the apical end of m2 (fortuitously exposed by breakage in this specimen) reveals no evidence of apical hypertrophy.

These conditions should be contrasted with those found in *Isolobodon*, which may be regarded as broadly representative of Capromyidae. In the illustrated specimen (fig. 19), the three main tissue types are easily distinguished by reference to diagnostic features. Each hypsodont cheektooth of *Isolobodon* consists of a continuous, curtainlike sheet of infolded enamel sheathing a core of primary dentine. Although the enamel is folded longitudinally in a complex fashion, the tooth as a whole has a suboval outline because cementum fills the outside gaps between infolds. From the standpoint of wear, all *Isolobodon* cheekteeth look much like the one illustrated: tooth pattern is preserved throughout life, and there is never evidence of apical hypertrophy. Judging from fossils only, the same description would apply

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area in A, showing dentine with tubules. *Isolobodon* is distinctive among capromyids for thickness of cementum sheathing cheekteeth.

equally well to clidomyines. Their cheek-teeth evidently grew continuously, elaborating the same tissue types in the same organizational pattern (with occasional deviations due to misdevelopment, as in any natural population; MacPhee, 1984).

**LIFESPAN AND WEAR:** One other observation on *Elasmodontomys* teeth is worth briefly noting. According to Anthony (1926), in some of the *Elasmodontomys* specimens which he collected the last molar was not yet fully erupted, even though all of the other teeth were significantly worn. Anthony (1926: 109) regarded this as unusual for a caviidan, especially a species "with unrooted molars, for the last molar to be so long in reaching a functional stage." Although relevant paleontological examples of the same phenomenon are in fact not hard to find (e.g., Kraglievich, 1926), the important point is that delayed eruption may be reasonably regarded as *prima facie* evidence of a relatively long lifespan, even if the span cannot be directly estimated. In addition to *Elasmodontomys*, delayed eruption might have occurred in *Amblyrhiza*, but very few complete jaws of this taxon have been recovered and no examples of a staggered eruption sequence have been reported. As already noted, the type of *Quemisia* also displays an unerupted m3 (Miller, 1929). Although there is no information relevant to estimating longevity in *Xaymaca fulvopulvis*, average lifespan need not have been short merely because the species was comparatively small. (For example, *Geocapromys* individuals have lived up to 17 years in captivity [Woods, 1982].)

**SUMMARY:** Although at the physiological level there might be several pathways for developing apical hypertrophy of cheektooth roots, the most plausible biological explanation for this phenomenon is that it represents an adaptation for prolonging the useful life of nonhypsodont teeth subjected to sustained wear. In this context "sustained" may mean either prolonged wear (over the course of a long lifespan) or intensive wear (due to a particular diet). *Elasmodontomys* may be an example of both factors at work, as there is some evidence for delayed m3 eruption as well as a high rate of tooth-surface consumption. In the case of *Boromys* there is no evidence one way or the other. To the extent

that we have been able to reconstruct dental ontogeny correctly in the various taxa discussed in preceding sections, we may conservatively conclude that apical hypertrophy can occur in taxa with closed roots as well as ones with open roots, whether teeth are brachyodont with a distinct enamelodentine junction or hypselodont and lamelliform without such junction. Whether apical hypertrophy has any far-reaching systematic importance remains to be seen, but it is obviously relevant to understand the ontogenetic basis for this previously misunderstood character.

#### CONCLUSION: RELATIONSHIPS OF *XAYMACA FULVOPULVIS*

It remains to provide a credible systematic seating-place for *Xaymaca*. This will have to be based on the type jaw only: despite much effort (see Excavation Record and Dating), we have not recovered any other material referable to this taxon. As if that were not offputting enough, caviidan groups are renowned for their tendency to display thoroughgoing convergences in dental characters (Woods, 1989a). We shall limit consideration to major taxa of caviidans represented in the Antillean Cenozoic, recognizing as we do so that the true affinities of *Xaymaca* may nevertheless lie elsewhere.

#### THE CASE FOR CAPROMYIDAE

There is little to be said in support of a possible capromyid connection for *Xaymaca*. All capromyids exhibit deeply striated cheek-teeth whose conformation is reflected in the channelled appearance of bony alveolar walls. By contrast, because alveolar walls are smooth in the *Xaymaca* holotype, longitudinal striae had to have been very shallow or absent. The p4 of *Xaymaca*, although only partly preserved, is nothing like the p4 of *Geocapromys* or its relatives, nor is the relative size or orientation of the new fossil's molar alveoli.

All known capromyids appear to possess ever-growing cheekteeth, with the exception of *Rhizoplagiodontia lemkei* from the Quaternary of Hispaniola in which roots are closed in aged individuals (Woods, 1989b). Woods (1989b: 66) noted that "[o]ld individ-



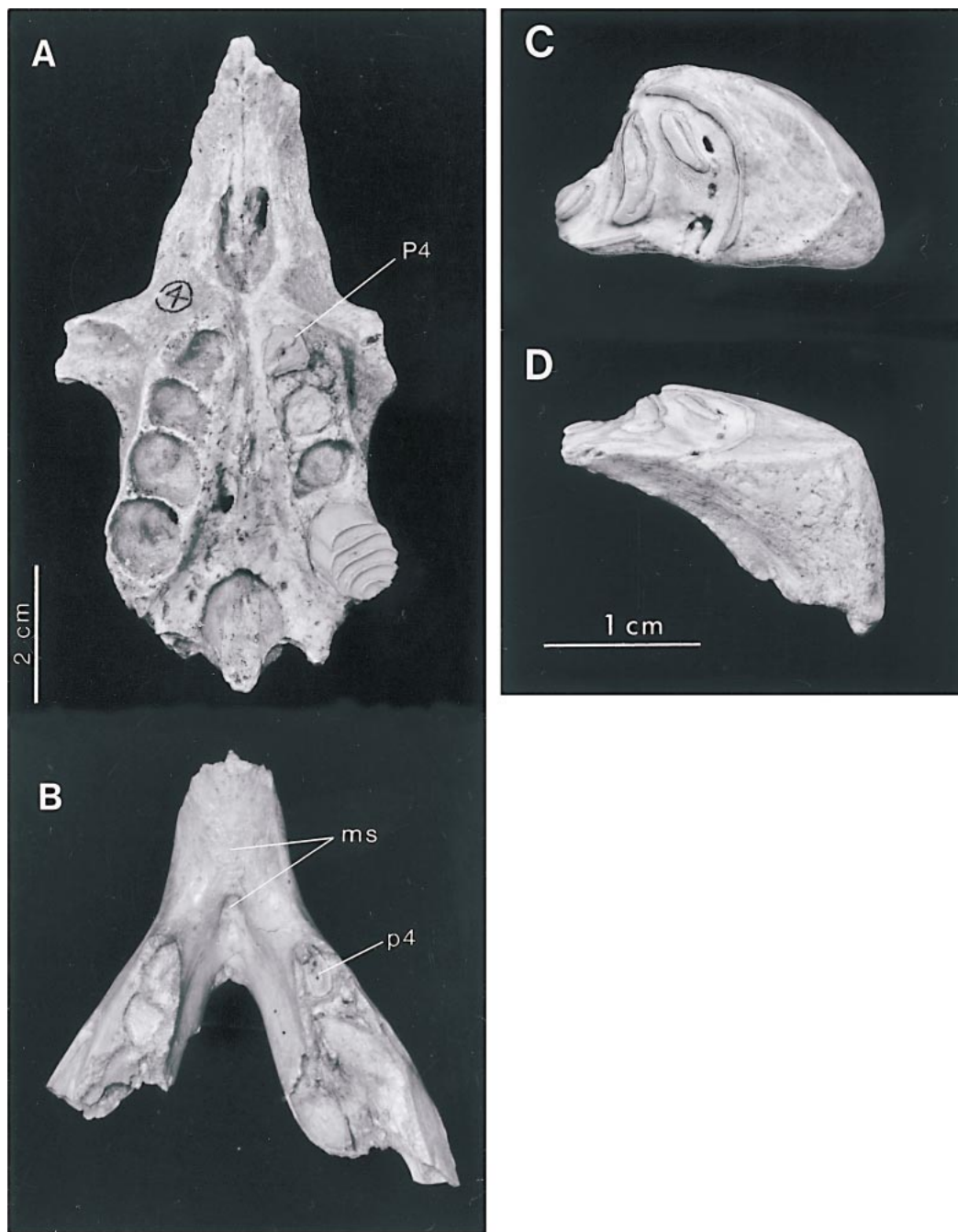


Fig. 20. Effects of extreme wear on heptaxodontine dentitions. (A) Ventral aspect of palate (AMNHP 140818) of aged individual of *Elasmodontomys obliquus* from Toraño Cave, Puerto Rico, showing broken right P4-M2 with root ends still in their sockets (M3 still intact). Anthony (1918) thought that the P4s of this animal were still functional at the time of death, although this is now difficult to corroborate because the occlusal surface of the remaining P4 is shattered. In any case, what is left of the tooth still projects well above the alveolar border and appears to consist entirely of dentinal tissue (no enamel). (B) Occlusal view of jaw (AMNHP 140819) of *E. obliquus* from same locality, showing worn p4 root exposed in its alveolus (other teeth lost). Note complete closure of mental suture (ms).



uals have molar teeth with elongated roots and shallow alveolar spaces filled with cement", but he does not indicate whether tooth pattern is ever lost or cheektooth roots become exposed at the trituration surface. In any case, in view of the results presented in this paper, the inference that this material is "cement" needs to be checked histologically.

#### THE CASE FOR CLIDOMYINAE

On the basis of the available evidence, a clidomyine affiliation for *Xaymaca* appears to be no more likely than a connection with Capromyidae. Bearing in mind what was said earlier about hypsodonty and hypselodonty being on a gradient of expression, the fact that clidomyine teeth were ever-growing does not by itself deny a relationship between *Xaymaca* and *Clidomys*, but it certainly does not support it. Nor do any of other features that can be examined empirically (premolar shape, alveolar conformation, histological constitution). Thus, whatever *Xaymaca* may be, there is no persuasive evidence that it was a member of either of the two recognized caviidan groups currently known from the Jamaican Cenozoic. In short, even if its affinities are difficult to ascertain, *Xaymaca* must represent a third and heretofore unknown caviidan colonizer of this island.

#### THE CASE FOR ECHIMYIDAE

During the Quaternary, endemic species of heteropsomyines lived on each of the Greater Antilles—with the egregious exception of Jamaica. Could *Xaymaca* be the "missing" Jamaican echimyid? Not with any degree of likelihood. Echimyids—or at least the post-Deseadan members of this uncertainly monophyletic family (Patton and Reig, 1989)—differ widely among themselves, but all bear distinct crowns with well-marked enamel junctions, fail to replace dp4, and develop two or more roots at each cheektooth locus.

Of these features, only the last can be directly examined in the *Xaymaca* holotype, and it is absent. Negative arguments are weak arguments, but at this stage of knowledge there is nothing that tips the scale decisively in favor of an echimyid ancestry for the new Jamaican species. In particular, the difference in late-stage root morphology is important: although the roots of aged *Boromys* clearly thicken and elongate relative to the crown, they remain discrete and do not resemble in aspect the single, cylindriciform root of *Xaymaca*. This also appears to be true of *Heteropsomys*, *Boromys*, and (probably) *Puertoricomys*. To our knowledge, hypsodonty/hypselodonty has not been reported for any mainland echimyid (*sensu stricto*).

#### THE CASE FOR HEPTAXODONTINAE

The case for allocating *Xaymaca* to Heptaxodontinae is admittedly not strong: it reduces to the fact that none of the available evidence positively bars this attribution, and none of it favors any other. For example, several details of jaw shape are consistent with heptaxodontine placement, but are by themselves hardly decisive. Somewhat more impressively, it appears that apical hypertrophy—clearly a normal ontogenetic process in Antillean heptaxodontines—occurred in *Xaymaca* in apparently the same way. Another, albeit functionally conditioned, similarity to *Elasmodontomys* (and probably *Amblyrhiza*) is that *Xaymaca* individuals must have occasionally lived long enough for (secondary) dentine in the hypertrophied root to wear through to the occlusal surface.

Among the points that might be raised against an affiliation of *Xaymaca* with heptaxodontines is the fact that *Elasmodontomys* and *Amblyrhiza* were large-bodied (exceptionally so in the case of *Amblyrhiza*; Bknevicus et al., 1993). However, there are far too many examples of gigantism (and of nanism, for that matter) in the records of diverse mammalian lineages—especially those

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(C) Occlusal view of excessively worn ?P4 (AMNHP 140814) of *Amblyrhiza inundata* from Pitchapple Cave, Anguilla. More than half of the functional occlusal surface is contributed by the hypertrophied root. (D) Same specimen as C in lateral aspect. Mesial side of tooth faces right.

that spread to islands—to place much emphasis on size as a gatekeeper in deriving phylogenetic relationships. Antillean heptaxodontines and large-bodied platetooths from southern South America (e.g., *Phoberomys*) may or may not be closely related, but they presumably derived from ancestors of much smaller body size. *Xaymaca* may simply preserve primitive proportions.

For completeness it should be noted that there is no evidence that *Xaymaca* is particularly close to *Quemisia*, another taxon that has proven hard to place (Ray, 1965). The teeth of *Quemisia* can be described as somewhat capromyidlike, as Ray (1964) concluded when critically evaluating the hypothesis that *Quemisia* was a \*heptaxodontid. As noted in the Introduction, at one time Woods (1982) came close to endorsing the notion that *Quemisia* was a capromyid, but this was less of a solution than it seemed because he regarded all Antillean \*heptaxodontids as derived capromyids at that time. None of this uncertainty about *Quemisia*, of course, makes a case for its connection with *Xaymaca*.

Although we acknowledge the pertinency of the questions raised by Pascual et al. (1990) concerning Antillean \*heptaxodontid paraphyly, until a cladistic study of the group is conducted it is premature to conclude where heptaxodontines should be positioned. At one time or another, taxa identified as \*heptaxodontids have been placed in each of the caviidan superfamilies (cf. Anthony, 1918; Kraglievich, 1926; Simpson, 1945; Ray, 1964; Woods, 1989a; McKenna and Bell, 1997), or even left out of this framework altogether as incertae sedis (Patterson and Wood, 1982). They have been associated more or less intimately with a broad swath of families (e.g., Neoepiblemidae, Dinomyidae, Capromyidae), often on the basis of little more than a common (and surely multiply convergent) tendency to develop large to gigantic body sizes and multilamellar cheek-teeth. With so little to go on, it is unsurprising that a small legion of taxa from the Miocene and Pliocene of South America have been successively thrust into—and out of—\*Heptaxodontidae, all of which has added to the confusion as to what a \*heptaxodontid really is. In short, the identity of the more

inclusive group containing Heptaxodontinae and its sister group is an open question, one which we do not attempt to solve here.

For the interim, *Xaymaca* is placed in Heptaxodontinae on a provisional basis, pending more information about the former and a detailed revision of the latter. If heptaxodontines and clidomyines turn out not to be very closely related, then an interesting biogeographical question arises. The mammalian fauna of Jamaica has always stood compositionally somewhat apart from that of the other Greater Antilles, especially in lacking otherwise widespread taxa such as sloths and insectivores (Morgan and Woods, 1986; Domning et al., 1997). However, the faunal distinctiveness of Jamaica during the late Cenozoic would be reduced if either *Xaymaca* or the Sheep Pen proximal femur turn out to be heptaxodontine in affiliation. (The effect would be the same in the less likely event that *Xaymaca* is an echimyid.) Whatever its final disposition, *Xaymaca fulvopulvis* is undoubtedly new and represents a taxon not previously documented for Jamaica (table 1). Its late discovery underlines how little we know about even the recent biotic past of this island.

#### ACKNOWLEDGMENTS

We are extremely grateful to friends, colleagues, and spelunkers who helped with our various projects in Jamaica over the years. These include Lisa DeNault, Steven Donovan, Adam Fincham, Alan Fincham, Ray Kielor, Judy Lemuir, Greg Mayer, and Don McFarlane. We also thank the Jackson's Bay Gun Club for permission to stay on their property and to Gun Club personnel Izzy and Makka for taking care of the camp. For drafting and mounting illustrations, we thank Patricia J. Wynne (fig. 1) and Lorraine Meeker (all other figures), who were assisted in various ways by Chester Tarka, Ruth O'Leary, Peling Fong-Melville, Angela Klaus, and Radford Arrindell (all current or former AMNH personnel). John H. Wahlert provided instruction on how to prepare rodent incisors for SEM, and Jim Webster (AMNH) permitted us to use his mineralogical equipment. Permission to work in Jamaica was granted by the Natural Resource Conserva-

tion Department, Ministry of Mining, Government of Jamaica. Permission to undertake destructive sampling of specimens was granted by Dick Tedford (AMNHP) and Nik Douglas (AAHS). Gary S. Morgan (New Mexico Museum of Natural History) provided very useful information on collections made by the FLMNH in the West Indies; he is not responsible for our use of it. Malcolm McKenna (AMNHP and University of Wyoming) read an earlier draft of this paper and made helpful suggestions concerning its improvement, for which we are grateful. We are also grateful to Gary Morgan (New Mexico Museum of Natural History) and an anonymous reviewer who commented on the version submitted for publication. Field investigations were partly supported by grants from the Adler Fund (to MacPhee) and the National Geographic Society (to Don McFarlane, Claremont-McKenna College).

## REFERENCES

- Anthony, H.E. 1916. Preliminary report of fossil mammals from Porto Rico, with descriptions of a new genus of ground sloth and two new genera of hystricomorph rodents. *Annals of the New York Academy of Sciences* 27: 193–203.
- Anthony, H.E. 1917. New fossil rodents from Porto Rico, with additional notes on *Elasmodontomys obliquus* Anthony and *Heteropsomys insulans* Anthony. *Bulletin of the American Museum of Natural History* 2: 329–435.
- Anthony, H.E. 1918. The indigenous land mammals of Porto Rico, living and extinct. *Memoirs of the American Museum of Natural History*, new series 2: 331–435.
- Anthony, H.E. 1919. Mammals collected in eastern Cuba in 1917, with descriptions of two new species. *Bulletin of the American Museum of Natural History* 40: 625–643.
- Anthony, H.E. 1920. New mammals from Jamaica. *Bulletin of the American Museum of Natural History* 42: 469–475.
- Anthony, H.E. 1926. Mammals of Porto Rico, living and extinct—Rodentia and Edentata. *Scientific Survey of Porto Rico and the Virgin Islands* 9(2): 97–241. New York: New York Academy of Sciences.
- Basmajian, J.V., et al. (editors). 1976. *Steadman's medical dictionary*. Baltimore, MD: Williams & Wilkins.
- Biknevicius, A.R., D.A. McFarlane, and R.D.E. MacPhee. 1993. Body size in *Amblyrhiza undata* (Heptaxodontidae, Caviomorpha), an extinct megafaunal rodent from the Anguilla Bank, West Indies: estimates and implications. *American Museum Novitates* 3079: 1–25.
- Bryant, J.D., and M.C. McKenna. 1995. Cranial anatomy and phylogenetic position of *Tsaganomys altaicus* (Mammalia: Rodentia) from the Hsanda Gol Formation (Oligocene), Mongolia. *American Museum Novitates* 3156: 1–42.
- Cope, E.D. 1883. On the contents of a bone cave in the island of Anguilla (West Indies). *Smithsonian Contributions to Knowledge* 25: 1–30.
- Cundall, F. 1915. *Historic Jamaica*. London: West India Committee.
- Darlington, P.J. 1957. *Zoogeography: the geographical distribution of animals*. New York: Wiley & Sons.
- Dean, M.C. 1993. Daily rates of dentine formation in macaque tooth roots. *International Journal of Osteoarchaeology* 3: 199–206.
- de Paula Couto, C. 1979. *Tratado de paleomastozoologia*. Rio de Janeiro: Academia Brasileira de Ciências.
- Domning, D.P., R.J. Emry, R.W. Portell, S.K. Donovan, and K.S. Schindler. 1997. Oldest West Indian land mammal: rhinocerotoid ungulate from the Eocene of Jamaica. *Journal of Vertebrate Paleontology* 17: 638–641.
- Eshelman, R.E., and G.S. Morgan. 1985. Tobagan Recent mammals, fossil vertebrates, and their zoogeographical implications. *National Geographic Society Research Reports* 21: 137–143.
- Fawcett, D. 1986. *A textbook of histology*. Philadelphia: W.B. Saunders.
- Fields, R.W. 1957. Hystricomorph rodents from the late Miocene of Colombia, South America. *University of California Publications in Geological Science* 32: 273–404.
- Fincham, A.G. 1997. *Jamaica underground: the caves, sinkholes and underground rivers of the island*, 2nd ed. Kingston, Jamaica: University of the West Indies Press.
- Flemming, C., and R.D.E. MacPhee. 1996. Caribbean giants: relationships of Antillean heptaxodontids (Caviomorpha, Rodentia). *Journal of Vertebrate Paleontology* 16(suppl.): 34A.
- Ford, S.M. 1990. Platyrrhine evolution in the West Indies. *Journal of Human Evolution* 19: 237–254.
- Ford, S.M., and G.S. Morgan. 1986. A new ceboid femur from the late Pleistocene of Jamaica. *Journal of Vertebrate Paleontology* 6: 281–289.
- Ford, S.M., and G.S. Morgan. 1988. Earliest primate fossil from the West Indies. *American Journal of Physical Anthropology* 75: 209.
- Goodfriend, G.A. 1986. Pleistocene land snails from Sheep Pen Cave in the Cockpit Country of Jamaica. *Proceedings of the 8th International*

- Malacological Congress, Budapest, 1983: 87–90.
- Hancox, N.M. 1972. *Biology of bone*. Cambridge: Cambridge University Press.
- Houchon, D., and E.J.P. Douzery. 2001. From the Old World to the New World: a molecular chronicle of the phylogeny and biogeography of hystricognath rodents. *Molecular Phylogenetics and Evolution* 20: 238–251.
- Iturralde-Vinent, M.A., and R.D.E. MacPhee. 1999. Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History* 238: 1–95.
- Kraglievich, L. 1926. Los grandes roedores terciarios de la Argentina y sus relaciones con ciertos géneros pleistocenos de las Antillas. *Anales del Museo Nacional de Historia Natural "Bernardino Rivadavia"* 34: 121–135.
- Kraglievich, L. 1932. Diagnósis de nuevos géneros y especies de roedores cávidos y eumegámidos fósiles de la Argentina: rectificación genérica de algunas especies conocidas y adiciones al conocimiento de otras. *Anales de la Sociedad Científica Argentina* 114: 155–181, 211–237.
- Landry, S.C. 1957. The interrelationships of the New and Old World hystricomorph rodents. *University of California Publications in Zoology* 56: 1–118.
- MacPhee, R.D.E. 1984. Quaternary mammal localities and heptaxodontid rodents of Jamaica. *American Museum Novitates* 2803: 1–34.
- MacPhee, R.D.E., and J.G. Fleagle. 1991. Postcranial remains of *Xenothrix mcgregori* (Primates, Xenotrichidae) and other late Quaternary mammals from Long Mile Cave, Jamaica. *Bulletin of the American Museum of Natural History* 206: 287–321.
- MacPhee, R.D.E., and C. Flemming. 1999. *Requiem aeternum*: the last five hundred years of mammalian species extinctions. In R.D.E. MacPhee (editor), *Extinctions in near time: causes, contexts, and consequences*: 333–372. New York: Kluwer Academic/Plenum.
- MacPhee, R.D.E., and I. Horovitz. In press. New craniodental remains of the Quaternary Jamaican monkey *Xenothrix mcgregori* (Xenotrichini, Pitheciinae, Platyrrhini) and the *Aotus* hypothesis. *American Museum Novitates*.
- MacPhee, R.D.E., and M.A. Iturralde-Vinent. 1995. Origin of the Greater Antillean land mammal fauna, 1: New Tertiary fossils from Cuba and Puerto Rico. *American Museum Novitates* 3141: 1–31.
- MacPhee, R.D.E., C.A. Woods, and G.S. Morgan. 1983. The Pleistocene rodent *Alterodon major* and the mammalian biogeography of Jamaica. *Palaeontology* 26: 831–837.
- MacPhee, R.D.E., D.C. Ford, and D.A. McFarlane. 1989. Pre-Wisconsinan land mammals from Jamaica and models of late Quaternary extinction in the Greater Antilles. *Quaternary Research* 31: 94–106.
- Martin, T. 1992. Schmelzmikrostruktur in den Inzisiven alt- und neuweltlicher hystricognather Nagetiere. *Palaeovertebrata, Mémoire extraordinaire*, 1992: 1–168.
- Martin, T. 1997. Incisor enamel microstructure and systematics in rodents. In W. von Koenigswald and P. M. Sander (editors), *Tooth enamel microstructure*: 163–175. Rotterdam: Balkema.
- Matthew, W.D., and C. de Paula Couto. 1959. The Cuban edentates. *Bulletin of the American Museum of Natural History* 117: 1–56.
- McFarlane, D.A., and R.D.E. MacPhee. 1989. *Amblyrhiza* and the Quaternary bone caves of Anguilla, British West Indies. *Cave Science* 16: 31–34.
- McFarlane, D.A., J. Lundberg, C. Flemming, R.D.E. MacPhee, and S.-E. Lauritzen. 1998. A second pre-Wisconsinan locality for the extinct Jamaican rodent *Clidomys* (Rodentia: Heptaxodontidae). *Caribbean Journal of Science* 34: 315–317.
- McFarlane, D.A., A. Vale, K. Christenson, J. Lundberg, G. Atilles, and S.-E. Lauritzen. 2000. New specimens of late Quaternary extinct mammals from caves in Sánchez Ramírez Province, Dominican Republic. *Caribbean Journal of Science* 36: 163–166.
- McFarlane, D.A., J. Lundberg, and A.G. Fincham. 2002. A late Quaternary paleoecological record from caves of southern Jamaica, West Indies. *Journal of Cave and Karst Studies* 64(2): 118–126.
- McKenna, M.C., and S.K. Bell. 1997. *Classification of mammals above the species level*. New York: Columbia University Press.
- Miller, G.S. 1916. Bones of mammals from Indian sites in Cuba and Santo Domingo. *Smithsonian Miscellaneous Collections* 66(12): 1–10.
- Miller, G.S. 1929. A second collection of mammals from caves near St. Michel, Haiti. *Smithsonian Miscellaneous Collections* 81(9): 1–30.
- Mones, A. 1981. Sinopsis sistemática preliminar de la familia Dinomyidae (Mammalia: Rodentia, Caviomorpha). *Anais II Congresso Latino-Americano Paleontología*, Porto Alegre, Abril 1981: 605–619.
- Mones, A. 1982. An equivocal nomenclature: what means hypsodonty? *Paläontologische Zeitschrift* 56: 107–111.
- Morgan, G.S., and L. Wilkins. 2003. The extinct rodent *Clidomys* (Mammalia: Rodentia: Hep-



- taxodontidae) from a Pleistocene cave deposit in Jamaica. *Caribbean Journal of Science* 39: 34–41.
- Morgan, G.S., and C.A. Woods. 1986. Extinction and the zoogeography of West Indian land mammals. *Biological Journal of the Linnean Society* 28: 167–203.
- Nedbal, M.A., M.W. Allard, and R.L. Honeycutt. 1994. Molecular systematics of hystricognath rodents: evidence from the mitochondrial 12S rRNA gene. *Molecular Phylogenetic and Evolution* 3: 206–220.
- Pascual, R., M.G. Vucetich, and G.J. Scillato-Yané. 1990. Extinct and Recent South American and Caribbean edentates and rodents: outstanding examples of isolation. In A. Azzaroli (editor), *Biogeographical aspects of insularity*. *Atti Convegni Lincei* 87: 627–640.
- Patterson, B. 1942. Two Tertiary mammals from northern South America. *American Museum Novitates* 1173: 1–7.
- Patterson, B., and A.E. Wood. 1982. Rodents from the Deseadan Oligocene of Bolivia and the relationships of the Caviomorpha. *Bulletin of the Museum of Comparative Zoology* 149: 371–543.
- Patton, T.H. 1966. Occurrence of fossil vertebrates on Cayman Brac, B.W.I. *Caribbean Journal of Science* 6: 181.
- Patton, J.L., and O. Reig. 1989. Genetic differentiation among echimoid rodents, with emphasis on spiny rats, genus *Proechimys*. In K.H. Redford and J.F. Eisenberg (editors), *Advances in Neotropical mammalogy*: 75–96. Gainesville, FL: Sandhill Crane Press.
- Peyer, B. 1968. *Comparative odontology* [transl. R. Zangerl]. Chicago: University of Chicago Press.
- Ray, C.E. 1964. The taxonomic status of *Heptaxodon* and dental ontogeny in *Elasmodontomys* and *Amblyrhiza* (Rodentia: Caviomorpha). *Bulletin of the Museum of Comparative Zoology* 131: 107–127.
- Ray, C.E. 1965. The relationships of *Quemisia gravis* (Rodentia: ?Heptaxodontidae). *Smithsonian Miscellaneous Collections* 149(3): 1–12.
- Sánchez-Villagra, M. R., O. Aquilera, and I. Horowitz. 2003. The anatomy of the world's largest extinct rodent. *Science* 301: 1708–1710.
- Schaub, S. 1935. Säugetierfunde aus Venezuela und Trinidad. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft* 55: 1–20.
- Sicher, H. (editor). 1971. *Orban's oral histology and embryology*, 6th ed. St. Louis, MO: C.V. Mosby.
- Simpson, G.G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* 85: 1–350.
- Sisson, S., and J.D. Grossman. 1938. *The anatomy of the domestic animals*, 3rd ed. Philadelphia: W. B. Saunders.
- Spencer, L. 1987. Fossil Abracomidae and Octodontidae (Rodentia: Hystricina), a phylogenetic analysis. Ph.D. dissertation, Loma Linda University, California.
- Stehlin, H. and S. Schaub. 1951. Die Trigonodontie der simplicidentaten Nager. *Schweizerische Paläontologische Abhandlungen* 67: 1–385.
- Swindler, D.R. 2002. *Primate dentition: an introduction to the teeth of non-human primates*. Cambridge: Cambridge University Press.
- Vucetich, M.G., D.H. Verzi, and J.-L. Hartenberger. 1999. Review and analysis of the radiation of the South American Hystricognathi (Mammalia, Rodentia). *Comptes Rendus de l'Académie des Sciences de Paris, Science de la Terre et des Planètes* 329: 763–769.
- Warwick, R., and P.L. Williams (editors). 1973. *Gray's anatomy* (35th British ed.). Philadelphia: W. B. Saunders.
- White, J.L., and R.D.E. MacPhee. 2001. The sloths of the West Indies: a systematic and phylogenetic review. In C.A. Woods and F.E. Sergile (editors), *Biogeography of the West Indies: patterns and perspectives*: 201–236. Boca Raton, LA: CRC Press.
- Wood, A.E., and B. Patterson. 1959. The rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. *Bulletin of the Museum of Comparative Zoology* 120: 279–428.
- Woods, C.A. 1982. The history of classification of South American hystricognath rodents: reflections on the far away and long ago. In M.A. Mares and H.H. Genoways (editors), *Mammalian biology in South America*: 377–392. Pittsburgh: University of Pittsburgh, Pymatuning Laboratory of Ecology.
- Woods, C.A. 1989a. The biogeography of West Indian rodents. In C.A. Woods (editor), *Biogeography of the West Indies: past, present, and future*: 741–798. Gainesville, FL: Sandhill Crane Press.
- Woods, C.A. 1989b. A new capromyid rodent from Haiti: the origin, evolution, and extinction of West Indian rodents and their bearing on the origin of New World hystricognaths. In C.C. Black and M.R. Dawson (editors), *Papers on fossil rodents in honor of Albert Elmer Wood*: 58–89. Los Angeles: Natural History Museum of Los Angeles County.
- Woods, C.A. 1993. Suborder Hystricognathi. In D.E. Wilson and D.M. Reeder (editors), *Mammal species of the world, a taxonomic and geo-*

graphic reference: 771–806. Washington, D.C.: Smithsonian Institution Press.  
Woods, C.A., R. Borroto Paéz, and C.W. Kilpatrick. 2001. Insular patterns and radiations of

West Indian rodents. *In* C.A. Woods and F.E. Sergile (editors), *Biogeography of the West Indies: patterns and perspectives*: 335–354. Boca Raton, LA: CRC Press.

*Note added in proof.* The article by Sánchez-Villagra et al. (2003) on the body mass and skeletal anatomy of Late Miocene *Phoberomys pattersoni* appeared after this paper was already in press. Although the Sheep Pen femur does not especially resemble that of this gigantic rodent, it is of great interest that the latter lived in northwestern South America, which provided the southern terminus of the Oligocene GAARlandia landspan (Iturralde-Vinent and MacPhee, 1999). Unfortunately, fossiliferous deposits of the correct age (30–35 Ma) for testing the GAARlandia hypothesis have not yet been identified in this region (Marcelo Sánchez-Villagra, personal commun.).

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