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Source: American Museum Novitates, 2000(3303) : 1-32

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/0003-0082(2000)3303<0001:NMSPXF>2.0.CO;2

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3303, 32 pp., 12 figures, 6 tables October 16, 2000

New Megalonychid Sloths (Phyllophaga, Xenarthra) from the Quaternary of Hispaniola

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ABSTRACT

As part of ongoing revisionary work on Antillean Megalonychidae, we document four new sloth species from Quaternary cave localities in Haiti and the Dominican Republic.* The new taxa and their tribal affiliations are as follows: *Megalocnus zile* (Megalocnini), *Acratocnus ye* (Acratocnini), and *Neocnus dousman* and *N. toupiti* (Cubanocnini). Significantly, each is closely related to species in genera long known from Cuba. This observation is of primary biogeographical importance because the most parsimonious explanation for the presence of parallel arrays of lower-level clades of sloths on opposite sides of the Windward Passage is vicariance, not a series of uncoordinated over-water dispersals. For a brief period in the late Paleogene, eastern Cuba, northern Hispaniola, Puerto Rico, and the Aves Rise formed a large positive structure (GAARlandia) that was evidently briefly continuous with northwestern South America. We infer that the later subdivision and subsidence of major portions of GAARlandia must have finely vicariated its biota (which included sloths at least as early as the Early Oligocene). On this argument, *Megalocnus*, *Acratocnus*, *Neocnus*, and *Parocnus* (= *Mesocnus*) must have already been in existence as independent clades at the time of origin of the Windward Passage (early Neogene), because cladistically diagnosable members of these taxa occur in Quaternary contexts in both Cuba and Hispaniola. This interpretation is consistent with several new lines of evidence concerning the paleontological and paleogeographical history of the Caribbean region.

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* Contribution 4 to series ‘‘Origin of the Greater Antillean Land Mammal Fauna.’’

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ISSN 0003-0082 / Price $3.70

INTRODUCTION

During the 1970s and 1980s, one of us (CAW) conducted a major effort to collect Quaternary faunal remains in caves and deep sinkholes in various parts of Haiti (République d'Haïti). The material recovered included an extensive array of extinct megalonychid sloths, including several nearly complete skeletons. It was immediately obvious on examination of these collections that species new to science were represented therein (Woods, 1989, 1990), but for a number of reasons systematic investigations begun by others on the sloths were never completed. White and MacPhee subsequently joined forces with Woods to begin the work afresh.

The present paper concentrates on naming several new species of Hispaniolan phyllophagans, together with basic information of the localities where sloth finds were made by Woods' expeditions. To provide a reasonably self-contained systematic context, we also provide preliminary phylogenetic definitions of some of the suprageneric groupings employed here. More detailed information on the phylogenetic relationships of Antillean sloths will be reported elsewhere (White and MacPhee, in press; White and MacPhee, in prep.).

Although fossil evidence for the presence of sloths in the Greater Antilles goes back at least 30 Ma (MacPhee and Iturralde-Vinent, 1994, 1995; Iturralde-Vinent and MacPhee, 1999), and although this group underwent significant radiation in the insular Neotropics, the systematic position of Antillean megalonychids remains obscure and understudied. The sloths of Cuba represent a partial exception to this statement, in that the alpha taxonomy of the Quaternary megalonychid fauna of this island may be said to have been at least adequately surveyed, thanks to the work of such able investigators as Leidy (1868), De La Torre (1910), Matthew (1919, 1931), Paula Couto (1967, 1979), Mayo (1969, 1978a, 1978b), Arredondo (1961, 1988), and Fischer (1971). However, many questions remain concerning species boundaries and relationships, and it has long been clear that Cuban sloths are in need of a thorough revision conducted along modern, cladistic lines. (For example, more than a dozen Cuban species are listed as valid by some authors, while others recognize only half this number.)

By contrast, much less is known about phyllophagan diversity on the other West Indian islands where they lived (Curaçao, Grenada, Puerto Rico, and Hispaniola and its satellites), and in most cases no new collections have been made in decades. Efforts to unravel the biogeographical and phylogenetic history of Antillean sloths on a regional basis are notably few (e.g., White, 1993a; White et al., 1996; Gaudin, 1995; MacPhee and Iturralde-Vinent, 1995), as are functional studies (White, 1993a, 1993b, 1993c, 1997). Indeed, it seems that most work has been conducted under the assumption that common-cause explanations are *not* possible because every island's biotic history is unique. Paula Couto (1967, p. 52, fn. 1), for example, stated that

> . . . I am now more inclined to think that each of the islands is characterized by the presence of unique genera, each representing an independent phylum, though probably remotely descendant from a common ancestral group or originating from closely related groups within the family Megalonychidae.

This assumption is refutable from both biological and geological points of view (Iturralde-Vinent and MacPhee, 1999). In fact, it is the very lack of uniqueness in certain higher-level patterns that provides a basis for assembling a biogeographical history of the Caribbean region that fully comports with tectonic and paleogeographical history.

Before deeper insights into the evolutionary history of Antillean sloths can be gained, it is critical to identify and fill some of the more egregious gaps in our knowledge. One such gap concerns megalonychid diversity in Haiti and Dominican Republic, the two countries that occupy Hispaniola. Although at 78,460 km^2 this island is more than two-thirds the size of Cuba (114,525 km^2), in the most recent revisionary work (Paula Couto, 1967) only two sloth species are recognized as valid for all of the Hispaniolan Quaternary—as compared to 6–14 species for Cuba, depending on author (cf. Varona, 1974; Arredondo, 1961, 1988). Although the Cuban megalonychids are surely oversplit, the seeming paucity of sloth species in Hispaniola is still peculiar, as noted by Morgan and Woods (1986). As might be expected, the explanation turns out to be limited reporting: except for a handful of specimens briefly described in the 1950s and 1960s (e.g., Hoffstetter, 1955; Hooijer and Ray, 1964; Paula Couto, 1967), no significant new collections of Hispaniolan sloths have been made and published since Miller's (1922, 1929, 1930) work in the 1920s. We rectify this situation here.

ACKNOWLEDGEMENTS

For assistance in the field, CAW wishes to thank Daniel and Tia Cordier, Ada Fowler, Margaret Langworthy, Deborah and Heather MacPherson, Roger Portell, Ellen Woods, Patricia Woods, Stott Woods, and Paul Paryski. JLW thanks Erika Simons for help with photography and translation of German texts. Specimen loans approved by our ever-helpful colleague S. David Webb (UF) were efficiently sent out by Marc Frank and Brian Beatty (also UF). All figures except fig. 1 (by Patricia Wynne) are the result of Lorraine Meeker's (AMNH) unequalled skills in specimen photography. Clare Flemming (AMNH) expertly helped with the preparation of the final draft. To everyone, our heartfelt thanks.

ABBREVIATIONS

AMNH	American Museum of Natural History
^{14}C	radiocarbon (dating method)
Fm	formation
Ma	millions of years (ago)
ML	mediolateral (measurement)
n	sample size
rcyrbp	radiocarbon years before "present" (AD 1950)
rev.	side reversed (in photographs)
UF	Department of Natural Sciences, Florida Museum of Natural History
†	extinct species (in tables)

PRELIMINARIES

SYSTEMATICS

In this paper our interest is restricted to "Antillean sloths," a phrase of convenience for making corporate reference to all of the phyllophagan taxa that once occurred on various land masses in the Caribbean Sea. In this instance, biogeographical and phylogenetic history appear to be fully coincident, in that all authorities agree that Antillean sloths are indisputably members of Megalonychidae, the most widely distributed of all sloth families (South, Central, and North America as well as several islands in the Caribbean Basin). Antillean sloths exhibit such defining features of Megalonychidae as: dental formula 5/4; premaxilla either absent or lacks teeth; molars quadrangular or elliptical; diastema long; first maxillary tooth usually caniniform; mandibular symphyseal region usually elongated; limbs relatively gracile and pentadactyl; calcaneal tuberosity mediolaterally expanded; and femoral third trochanter present (cf. Paula Couto, 1979; Muizon and McDonald, 1995; White and MacPhee, in press). However, disagreement is otherwise rife concerning names, content and interrelationships at lower hierarchical levels within the family (e.g., Engelmann, 1978, 1985; Mones, 1986; Arredondo, 1988; Pascual et al., 1990; White, 1993a, 1993c; Gaudin, 1995; McKenna and Bell, 1997). Our organization of major taxa with Antillean representation is similar to concepts developed by several other workers (e.g., Varona, 1974; Paula Couto, 1979; Mones, 1986), but differs substantially from McKenna and Bell's (1997) understanding of tribal and subtribal divisions within Megalonychidae. A cladistic reorganization of this family is sorely needed (Gaudin, 1995).

According to White and MacPhee (in press), based on phylogenetic evidence Antillean sloths should be distributed between two major clades, Choloepodinae and Megalocninae. Until recently, Choloepodinae (*nec* Choloepinae) was restricted to the extant two-toed sloth *Choloepus* and relegated to Bradypodidae. However, current taxonomic practice restricts Bradypodidae to the three-toed sloth *Bradypus* and places Choloepodinae in Megalonychidae (Scillato-Yané, 1980; Webb, 1985; Webb and Perrigo, 1985; Wetzel, 1985; White, 1993c; Gaudin, 1995; McKenna and Bell, 1997; White and MacPhee, in press; but see Engelmann, 1985).

Character evidence strongly supports the broadening of Choloepodinae to include several Antillean taxa (*Acratocnus*, *Neocnus*, and *Paulocnus* as relimited by White and

MacPhee [in press]). Diagnosis of this subfamily may be summarized as follows: cranium domed; first maxillary and mandibular tooth triangular in cross section; glenoid posterior shelf present and glenoid shelf mediolaterally wide; symphyseal spout present; rostrum flared; diastema long; plane of mandibular condyles located just dorsal to tooth row; coronoid superior to condyle; femoral head spherical and extends rostral to greater trochanter; fovea for ligamentum teres centric if present (i.e., located in middle of articular surface on femoral head) third trochanter of femur a distinct lateral crest; lesser trochanter conspicuous; tibial and fibular shafts bowed; tarsus alternate; astragalar neck long; fibular facet of astragalus concave; calcaneal tuberosity mediovolarly expanded; inferior scapular angle acute; deltoid and pectoral crests of humerus nonconfluent; ulna gracile and anteriorly bowed (after Anthony [1918] and Paula Couto [1967, 1979], with additional observations by present authors).

The concept of Megalocninae as defined by Kraglievich (1923) includes *Megalocnus* and *Parocnus* (= *Mesocnus*; for this synonymy, see White and MacPhee, in press), as well as several South American genera of Miocene age. It is important to emphasize that cladistic analysis reveals that Antillean megalocnines are closely related. In the past this conclusion was supported (e.g., Varona, 1974; Paula Couto, 1979; Mones, 1986; Pascual et al., 1990; McKenna and Bell, 1997) as often as it was denied (e.g., Simpson, 1945; Hoffstetter, 1955; Matthew and Paula Couto, 1959; Fischer, 1971), but the postcranial evidence appears to be decisively in its favor. Our diagnosis of Megalocninae is as follows: postorbital constriction absent; cranium long, of relatively uniform width, and flattened superiorly; jugal expanded; pterygoid inflation present; paroccipital process greatly enlarged and free-standing (Gaudin, 1995); lateral groove of pterygoid absent (Gaudin, 1995); pronounced airorrhynchy (posterior palate flexed ventrally); mandibular coronoid process not superior to condyle, and condyles well above tooth row; last maxillary molariform medially narrow; last mandibular molariform convex; femur with nonspherical head and anteroposteriorly deep distal end; fovea for ligamentum teres posterior and eccentric (i.e., located on periphery of articular surface on femoral head); rectus femoris tubercle prominent; shaft of tibia and fibula straight; tarsus serially arranged; calcaneal tuberosity symmetrical and thick with lateral foramen and lacking volar expansion; astragalar neck very short; astragalar articular surface distinctly divided; fibular facet of astragalus flat; deltoid and pectoral crests of humerus confluent; ulnar shaft straight; coronoid process of ulna extensive and shelflike.

LOCALITIES

Hispaniolan localities that have yielded holotypes or significant referred material are briefly described in appendix 1 (see fig. 1 for map locations). Woods (1989) should be consulted for detailed notes on past and present environmental conditions in Haiti relevant to the interpretation of the Quaternary fossil record.

Names of caves and sinkholes are mostly the local Haitian Creole toponyms for these places, although some names were developed by Woods' field parties. As a point of clarification, in Creole a large or easily entered horizontal cave is a *trou* [twoo]. The term *trou wòch* [twoo wohsh] is used to refer to caves, often quite small, located on limestone scarps. The word *trouing* [twooing], by contrast, refers to a vertical shaft or sinkhole. For the spelling of other Creole words, we have relied on the orthography in Theodore's (1995) dictionary. However, names presented as standard French-language spellings on recent maps of Haiti are retained as such here.

Most of the sloth-bearing localities are deep sinkholes; whatever fell into these holes did not get out. In several cases, essentially complete skeletons of single individuals were recognized as such in the field and collected as a unit. However, in many other cases associations were less clear, for any number of potential reasons. Accordingly, we have erred on the side of caution in assigning elements to single individuals. This affects designation of holotypes: only in cases in which associations are beyond doubt have we designated more than one skeletal element as part of a holotype. In all other cases,

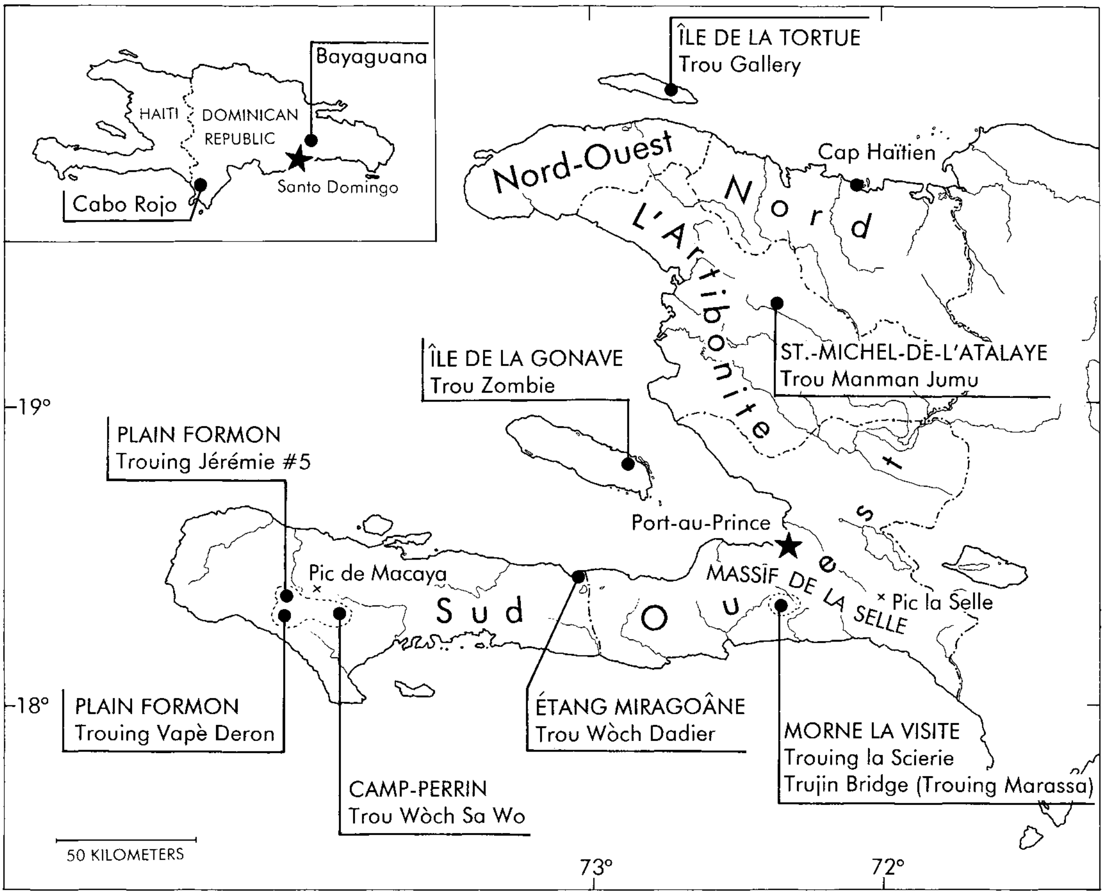

Fig. 1. Sketch map of Haiti and (as inset) island of Hispaniola, showing departmental boundaries, position of major localities or concentrations of localities, and other features mentioned in text. Dotted outlines indicate location of multi-site collecting areas in Plain Formon (western part of Presqu'île du Sud) and Morne La Visite (eastern part). For additional localities, see table 3 and appendix 1.

holotypes are single elements; other material of the same species from the same cave is listed with other referred specimens. This procedure may seem objectionable to neontologists used to collecting extant taxa, but the reason for proceeding in this manner ought to be obvious to any one who regularly deals with fossil remains. For reasons of economy of space, illustrations in this paper are restricted to holotypes and specimens that display important anatomical points. Associated material will be described and illustrated in more detail elsewhere.

It may be noted that there is no compelling reason to think that any of the sloth remains described here are earlier than Quaternary, as judged by faunal associations and the small number of available radiocarbon dates. When the sloths and other elements of the Antillean mammalian fauna died out is still highly conjectural, due to the lack of good radiocarbon dates for many taxa (MacPhee et al., 1999). However, it is certain that some and perhaps all Quaternary sloth extinctions occurred after the arrival of humans on the islands, beginning 5000–7000 years ago (Paula Couto, 1967; Burney et al., 1994; Flemming et al., 1998; MacPhee et al., 1999). Currently, the most recent radiometric date for sloth remains from Hispaniola is 3755 ± 175 rcyrbp, for taxonomically unallocated megalonychid bones from Trou Wòch Sa Wo (see appendix

1). It is believed that these and other ‘‘whole bone’’ ^{14}C dates reported in this paper are reliable within their stated margins of error, although redating of critical material by the accelerator mass-spectroscopy (AMS) technique would certainly be desirable (cf. MacPhee et al., 1999; Flemming and MacPhee, 1999).

MAGNORDER XENARTHRA COPE, 1889
ORDER PILOSA FLOWER, 1883
SUBORDER PHYLLOPHAGA OWEN, 1842
SUPERFAMILY MEGATHERIOIDEA GRAY, 1821
FAMILY MEGALONYCHIDAE GERVAIS, 1855
SUBFAMILY MEGALOCNINAE KRAGLIEVICH, 1923
TRIBE MEGALOCNINI KRAGLIEVICH, 1923

Megalocnus Leidy, 1868

Classically, *Megalocnus* is distinguished from all other phyllophagans by its specialized maxillary incisiform teeth (Matthew and Paula Couto, 1959). However, it also exhibits highly distinctive postcranial elements (White, 1993a; see also White and MacPhee, in press), exhibiting a number of hitherto unrecognized or underappreciated skeletal apomorphies. *Megalocnus* is also the only Antillean sloth taxon other than *Parocnus* that can be justifiably called megafaunal. (*M. rodens* was estimated by Paula Couto [1979] to have weighed ≥ 270 kg, but it would be useful to check this guess against results using cortical cross-sectional areas [Biknevicius et al., 1993] or other modern methods.) *Megalocnus rodens*, the first Antillean sloth to be identified as such (Leidy, 1868), is known from a large number of sites on the mainland of Cuba as well as Isla de Pinos (= I. de la Juventud) (Matthew and Paula Couto, 1959). A large number of species—and even subspecies—of Cuban *Megalocnus* have been named over the years; all are synonymized (as *M. rodens*) by White and MacPhee (in press), obviating the need for separate comparisons here.

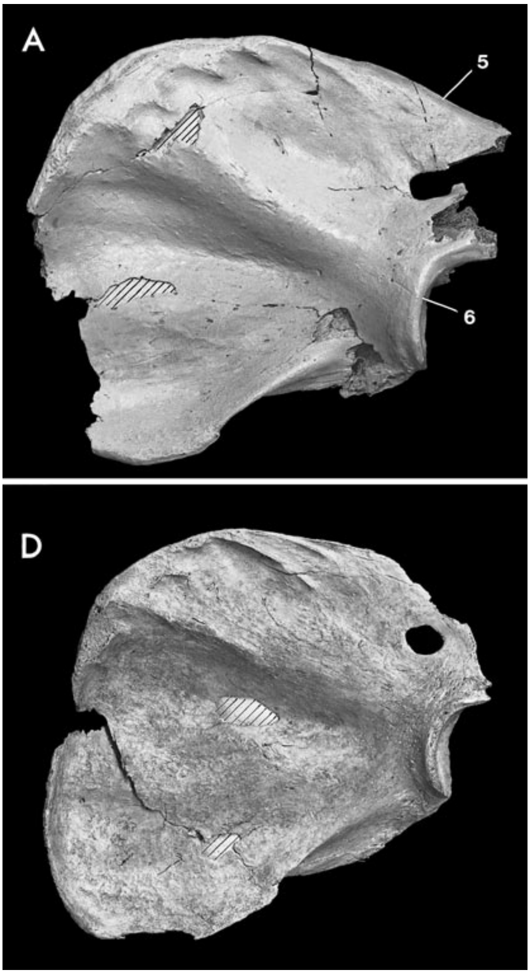

Fig. 2. *Megalocnus zile*, holotype left scapula (**A–C**; UF 169930) from Trou Gallery, Île de la Tortue, Département du Nord-Ouest, Haiti, compared to right scapula (rev.) of *Parocnus serus* (**D–F**; UF 169977) from Trujin Bridge, Morne la Visite, Département de l’Ouest: **A–C**, ventral, glenoid, and dorsal aspects of UF 169930; **D–F**, ventral, glenoid, and dorsal aspects of UF 169977. Compared to *P. serus*, in *M. zile* (1) fossa for teres

Diagnosis of Genus: Differs from *Parocnus* (=*Mesocnus*)[4] (the only valid genus with which it might be confused on the basis of size) in many details of cranial and postcranial construction, as follows: maxillary teeth pseudorodentiform or incisiform rather than caniniform (i.e., broad and anteroposteriorly compressed); femoral and humeral heads more convex; acetabular rim with large gap. In the case of the scapula (see fig. 2A–F), differences include: fossa for teres

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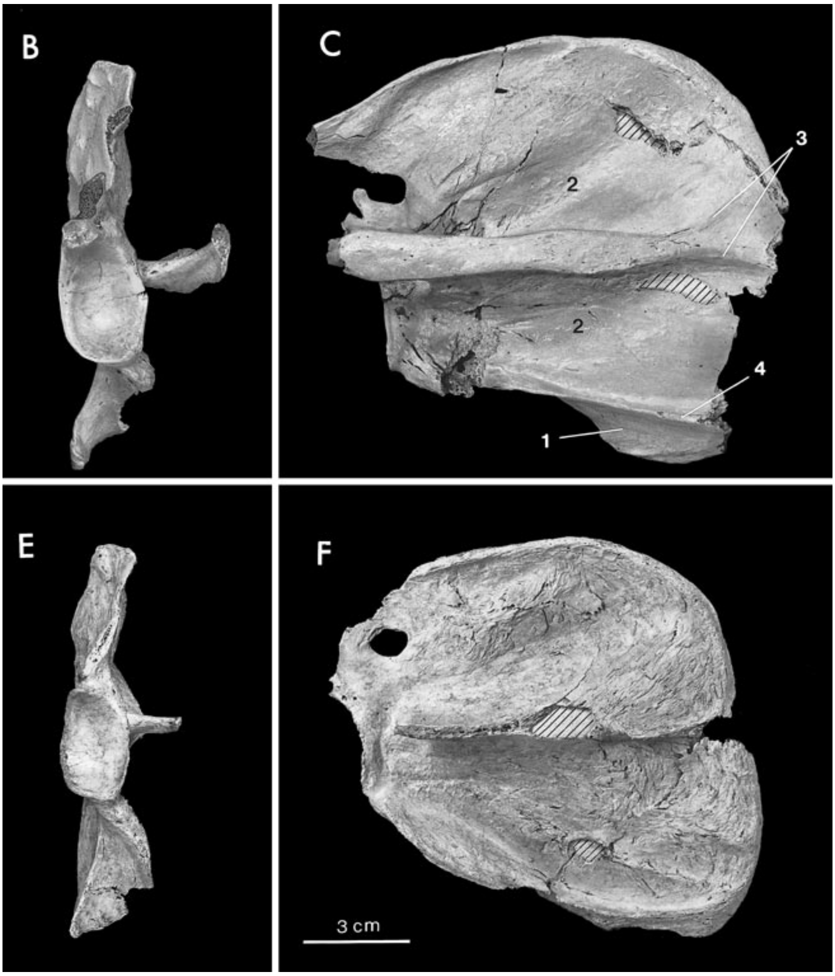
[4] Taxa conventionally grouped under *Mesocnus* and *Parocnus* are considered congeneric by White and MacPhee (in press); *Parocnus* (Miller, 1929) has priority over *Mesocnus* (latter not validly named until Matthew’s [1931] publication).



major is more developed; (2) post- and prescapular fossae are unequal (prescapular fossa much larger); (3) rostral and caudal borders of scapular spine are divergent (not parallel); (4) second scapular spine is more prominent at inferior angle; (5) anterior scapular border is smoothly curved (border damaged in UF 169977, but shape discernible in other specimens); and (6) glenoid fossa is more concave. Differs from *M. rodens* from Cuba in that fossa for teres major is much more capacious and expands abruptly beneath secondary scapular spine. These illustrations should be compared to the right scapula of *M. rodens* (AMNH 49968) depicted by Matthew and Paula Couto (1959: pl. 13). Although much reconstructed, the caudal border of AMNH 49968 is intact and shows only a comparatively small fossa for teres major (cf. *Parocnus*).

major much larger, expanded into a blade; pre- and postscapular (i.e., supra- and infraspinous) fossae unequal, with prescapular fossa being much the larger; rostral and caudal borders of scapular spine divergent (rather than parallel); second scapular spine more prominent; anterior scapular border smoothly curved (rather than sinusoidal); glenoid fossa strongly anteroposteriorly concave.

Megalocnus zile, new species

HOLOTYPE: Scapula (left side, UF 169930; fig. 2), found 20 March 1979 by C. A. Woods and party. No unambiguous association at type locality with other bones referred to same species.

TYPE LOCALITY AND AGE: Trou Gallery, Île de la Tortue, Département du Nord-Ouest, Haiti; late Quaternary (see appendix 1).

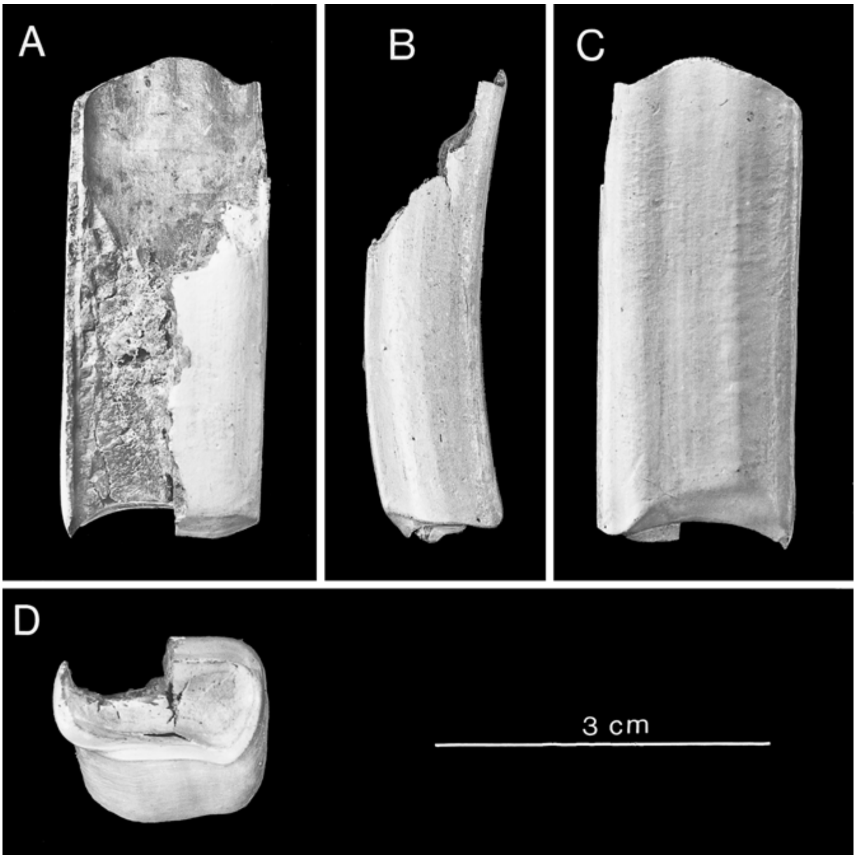


Fig. 3. *Megalocnus zile*, right maxillary molariform (UF 170492) from Trou Gallery, Île de la Tortue, Département du Nord-Ouest, Haiti: **A**, mesial; **B**, buccal; **C**, distal; and **D**, occlusal aspects. Dimensions: buccolingual, 18.7 mm; mesiodistal (measured across intact buccal moiety), 11.2 mm. These measurements are comparable to those reported for *M. rodens* by Fischer (1971: 670, table 26); the molariforms of *Parocnus brownii*, at least, are much smaller and show no overlap with either species of *Megalocnus* (Fischer, 1971: 664, table 6).

SYNONYMS: None (but see below).

REFERRED SPECIMENS: Several molariforms (UF 170490–170492; see fig. 3), acetabular fragment (UF 169931), femoral head (UF 169932), several patellae (UF 169924–169928), distal and proximal fibulae (UF 169929 and 169933), and partial scapula (UF 169934), all from Trou Gallery. Also included in the hypodigm is a fragmentary scapula from an unnamed locality near the town of Bayaguana, Prov. San Cristobal, Dominican Republic, from the Marcano collection (#318/325) and currently housed at UF (see appendix 1).

ETYMOLOGY: Haitian Creole noun (in apposition) meaning ‘‘island,’’ pronounced approximately [zee-leh]; reference is to species’ presence on Île de la Tortue as well as Hispaniolan mainland. Recommended common name: Hispaniolan megalocnus.

DISTRIBUTION: Haiti (including Île de la Tortue) and Dominican Republic.

DIAGNOSIS OF NEW SPECIES: With respect to known elements, agrees with features that define the genus as given above. The new species can be distinguished from *M. rodens* by reference to the fossa for teres major on the caudal border of the scapula, which is notably expanded beneath the secondary scapular spine (cf. fig. 2 and Matthew and Paula Couto, 1959: pl. 13). *Parocnus* contrasts with *M. zile* in the same regard, indi-

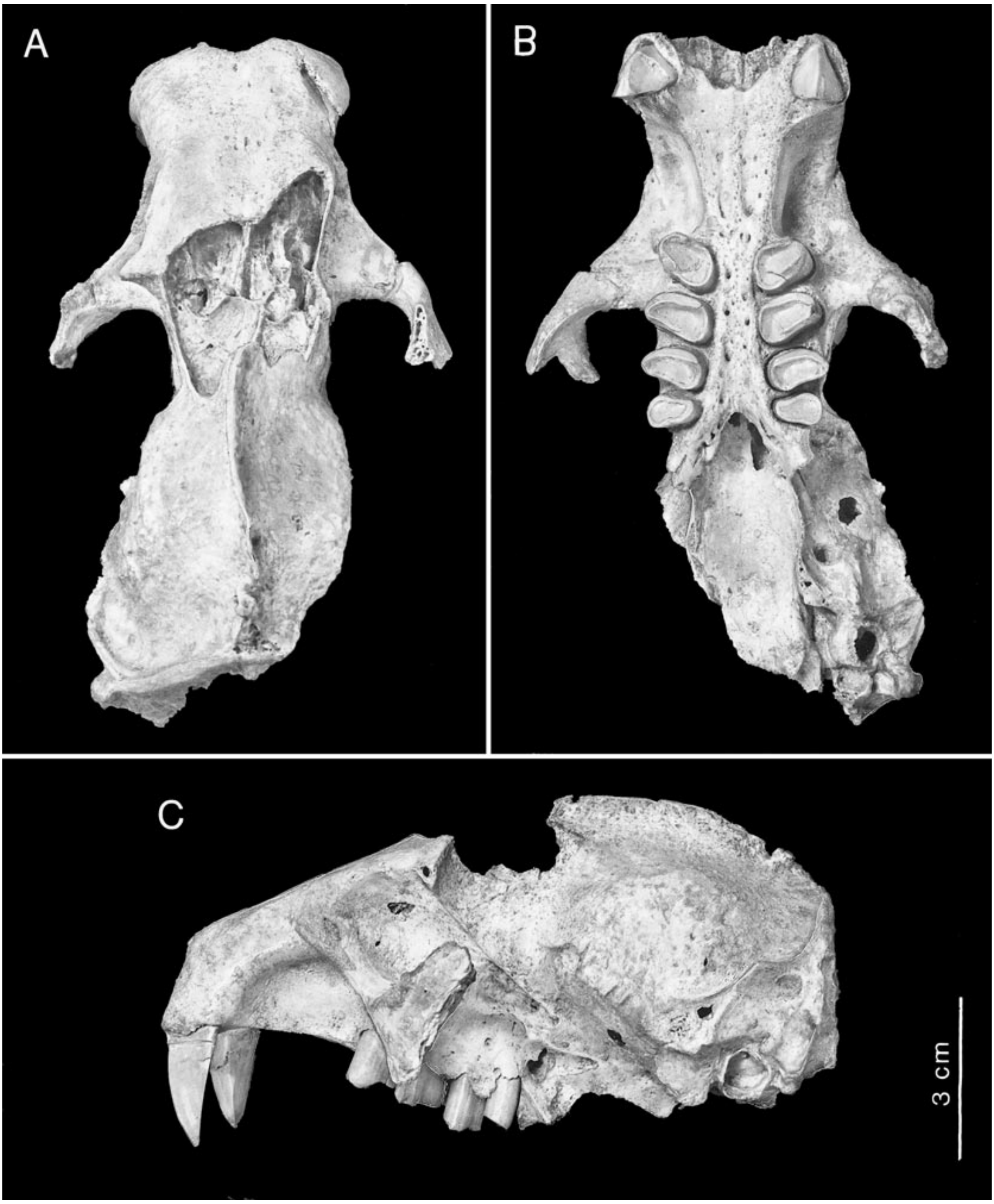


Fig. 4. *Acratocnus ye*, skull (UF 170533) of holotype individual from Trouing Vapè Deron, Plain Formon, Département du Sud, Haiti (rev.): **A**, dorsal; **B**, ventral; and **C**, lateral aspects. Note enormous size of frontal sinuses, which deeply impinge on anterior part of neurocranial roof. (Note scale; for relative size compared to other sloth species described here, see fig. 12.)

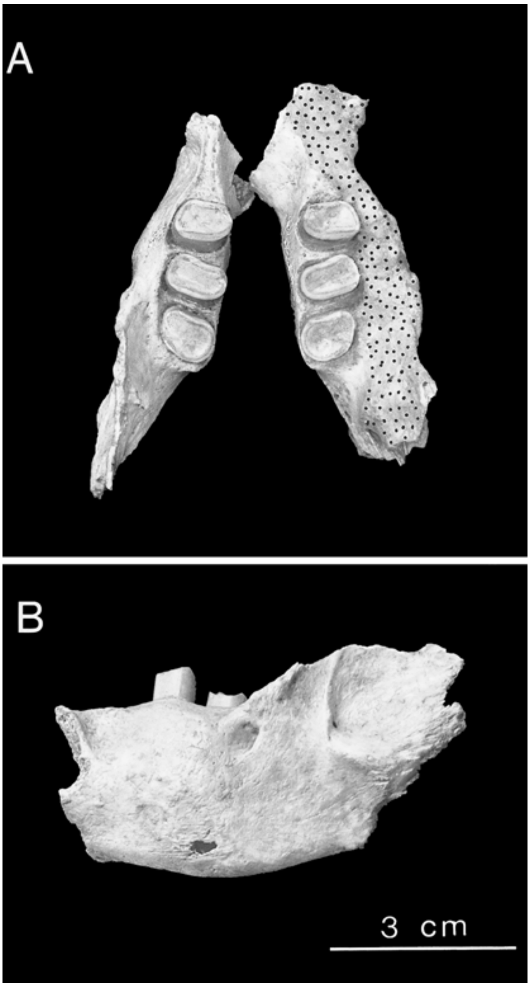


Fig. 5. *Acratocnus ye*, mandible from holotype individual (UF 170533) from Trouing Vapè Deron, Plain Formon, Département du Sud, Haiti (rev.): **A**, occlusal, and **B**, ''left'' lateral aspects. (Stippled area in A is calcite matrix that had not been removed at the time specimen was photographed.)

cating that an expanded teres major fossa is a derived feature within megalocnines. Also, the femoral head of *M. zile* is more spherical than that of *M. rodens*, nearly to the degree seen in the subfamily Choloepodinae.

DISCUSSION: The possibility that *Megalocnus* or a close relative lived in Hispaniola or one of its satellite islands has been raised repeatedly but inconclusively. Originally, Miller (1922) tentatively proposed that certain fragmentary postcranial remains from a cave near St.-Michel-de-l'Atalaye (Département de L'Artibonite) belonged to ''*Megalocuus*?'' [lapsus calami]), there being at this time no other place for their reception. Some years later he moved the St.-Michel material to a new genus, *Parocnus* (Miller, 1929). Hoffstetter (1955) challenged this maneuver, contending that Miller's sloth was indeed a member of *Megalocnus* and should therefore be designated *M. serus*. Most authors have recognized *Parocnus* and retained *serus* therein (e.g., Matthew and Paula Couto, 1959; Varona, 1974; White and MacPhee, in press; but see Hooijer and Ray, 1964, who retained *M. serus* without comment).

Although it has long been known that Cuban *Megalocnus* is distinctive in possessing incisiform maxillary front teeth, no similar teeth have as yet been found in Hispaniola. However, large molariforms, very like those of Cuban *Megalocnus*, have been recovered at Trou Gallery (fig. 3). It is possible that the highly specialized upper front teeth of *M. rodens* are autapomorphic, but this possibility cannot be evaluated in the absence of relevant remains of the Hispaniolan species. The postcranial material of *M. zile*, although limited, is distinctive of this genus and strongly corroborates the conclusion that *Megalocnus* was represented on both sides of the Windward Passage in the late Cenozoic. As far as we can ascertain, none of the material originally referred to *Megalocnus* sp. by Miller (1922, 1929) actually belongs to that taxon (i.e., all of it belongs to *Parocnus serus* as here delimited.)

Until sample sizes for this species are improved, we resist making any deeper inferences about the distribution of *Megalocnus zile* in Hispaniola. At least in comparison to *M. rodens* in Cuba, whose remains are frequently encountered in Quaternary localities (Matthew and Paula Couto, 1959), it seems that *M. zile* may have been relatively rare (or rarely preserved in the usual fossil locales). Whether it actually was or not can be determined only by additional discoveries and relevant analyses.

SUBFAMILY CHOLOEPODINAE GRAY, 1871

TRIBE ACRATOCNINI VARONA, 1974

Acratocnus Anthony, 1916

At one time or another, the name *Acratocnus* has been entered into the faunal lists of each of the three northern Greater Antilles (cf. Miller, 1929; Matthew and Paula Couto, 1959; Arredondo, 1961). Unfortunately, concepts and content of this taxon have differed greatly from author to author, making it quite uncertain whether, in fact, *Acratocnus* in any phylogenetically meaningful sense enjoyed the wide distribution claimed. Cladistic evaluation of the available character evidence, however, makes it abundantly clear that this taxon had a multi-island distribution with representatives in Puerto Rico, Cuba, and Hispaniola (White and MacPhee, in press). Additionally, in all probability *Paulocnus petrifactus* from Curaçao (Hooijer, 1962) is closely related to *Acratocnus* from the Greater Antilles, as is the unnamed sloth from Grenada described by MacPhee et al. (2000). In short, it is now evident that acratocnin sloths enjoyed a wide distribution in the West Indies—indeed, larger than that of any other Antillean land-mammal group except Capromyidae.

DIAGNOSIS OF GENUS: Cranium relatively tall and domed, with prominent postorbital constriction, sagittal crest, pronounced rostral mediolateral flare; symphyseal spout pointed and short; first maxillary tooth spike-shaped, trigonal, anteriorly projecting, and curved (i.e., caniniform); last maxillary molariform convex and narrowest lingually; first mandibular tooth straight, trigonal, and lacking posterointernal groove; last mandibular molariform convex lingually; femoral shaft cylindrical; tibial surface of astragalus parallel-sided, not divided, and posteriorly squared; fibular facet on astragalus deeply concave and funnel-shaped; radius with long, well-developed, abrupt pronator quadratus flange.

Acratocnus ye, new species

HOLOTYPE: Skull and mandible (UF 170533; fig. 4, 5) in unambiguous association (same individual), collected 26 January 1984 by C. A. Woods and party.

TYPE LOCALITY AND AGE: Trouing Vapè Deron, Plain Formon, Département du Sud, Haiti; late Quaternary (see appendix 1).

SYNONYMS: None.

REFERRED SPECIMENS: Hypodigm also includes several sets of associated postcranial elements from other localities (a sample of which are illustrated in fig. 6): left tibia (UF 75434), left scapula (UF 169985), and associated right femur (UF 76283), right and left fibulae (UF 75486, 75487), right astragalus and right and left calcanei (all numbered UF 170270), and right and left pelves (UF 170276), from Trujin Bridge, Morne la Visite; associated left humerus, ulna, radius (UF 169822) from Trouing Jérémie #3, Plain Formon. Other material: from Trujin Bridge, mandible (UF 76796), right tibia (UF 170271), right astragalus and left calcaneus (UF 170269), right humerus (UF 75528), right radius (UF 75579/80); from Trouing Jeremie #3, right fibula (UF 170453); from Trouing Bois Formon #1, Plain Formon, left ulna (UF 170089).

ETYMOLOGY: Haitian Creole noun (in apposition) meaning ‘‘yesterday,’’ pronounced approximately [yeh]; reference is to this species being part of Hispaniola's extinct fauna. Recommended common name: Yesterday's acratocnus.

DISTRIBUTION: Currently known only from Haiti, but presumed to have had a wider distribution in Hispaniola.

DIAGNOSIS OF NEW SPECIES: Agrees with *A. odontrigonus* (Puerto Rico) and *A. antillensis* (Cuba) in features that define the genus (see Anthony, 1918). Differs from these species in the following features: Skull markedly domed along sagittal crest in many individuals, forming a significant angle with rostrum; postorbital constriction not extreme; palatine foramina consistently prominent and abundant; symphyseal spout relatively short and pointed, laterally pinched and not smoothly conical, extremely ventrally pinched on either side of ventral keel, and projecting anteriorly at an angle significantly different from that of anterior border of mandible; rectus tubercle of pelvis very prominent and laterally projecting, creating a right angle in posterior view; acetabular rim nearly closed and pit (fossa) partly or completely filled in; femoral neck and head projecting anteriorly at an extreme angle; femoral head extremely large, globular, and afoveate; femoral shaft with great torsion and reduced third trochanter; tibial shaft with prominent anteromedial muscle scar; tibia with posterolaterally projecting proximal fibular articu-

Fig. 6. *Acratocnus ye*, representative postcranial elements: humerus (UF 75528), anterior (**A**) and posterior (**B**) aspects; femur (UF 76283), anterior (**C**) and distal (**D**) aspects; and calcaneus (UF 170269), dorsal (**E**) aspect (cf. especially *A. odontrigonus* postcranials, as figured by Anthony [1918]).

lation; distinct ridge separating cuboid and sustentacular facets of calcaneus; calcaneal tuberosity waisted and relatively symmetrical; humeral head extremely large; humeral trochlea mediolaterally flat with reduced distal flare; bridge over entepicondylar foramen bears distinct eminence; entepicondylar foramen slightly visible posteriorly; pectoral crest markedly projecting medially; forelimb greatly elongated (brachial indices of 0.97 and 0.96 on two associated skeletons, as compared to a mean of 0.90 for *A. odontrigonus* [White, 1993a]); ulnar shaft with prominent anterolateral ridge.

DISCUSSION: This species is very similar to *Acratocnus odontrigonus* in cranial, mandib-

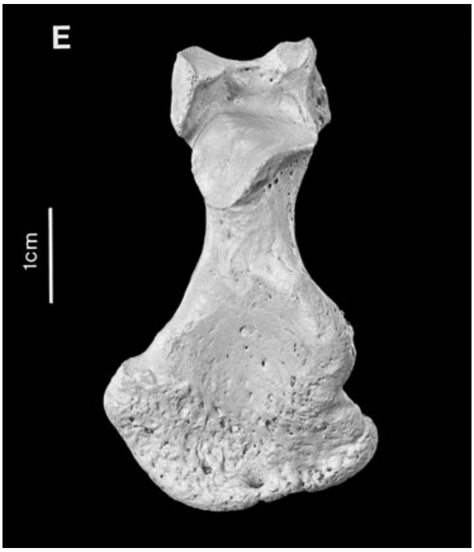


Fig. 6. Continued.

ular, femoral, humeral, ulnar, calcaneal, and pelvic features, and virtually identical in scapular, radial, tibial, fibular, and astragalar features. However, thanks to large sample sizes, we have been able to assess, both qualitatively and quantitatively, this species' normal range of individual variation for virtually all elements and thereby assess its differentiae from *A. odontrigonus* with some confidence.

As far as can be determined, published referrals to *Acratocnus* in the older literature seem in most cases to involve misallocations of specimens properly placed in a different taxon, *Neocnus* (see below), and are therefore not cladistically supportable. Although all choloepodines possess trenchant first maxillary teeth that are triangular in cross-section (see above), they can be distinguished by the diagnostic cranial and postcranial traits cited here.

TRIBE CUBANOCNINI VARONA, 1974[5]

Neocnus Arredondo, 1961

Neocnus is one of several Antillean sloth genera with a complicated systematic past, which witnessed taxa being multiply synonymized and specimens being reassigned with apparent abandon. Here it is sufficient to note that *Neocnus* as currently constituted by White and MacPhee (in press) is a relatively large but logically bounded genus, with two species in Cuba (*N. major*, *N.* [= *Microcnus*] *gliriformis*) and three in Hispaniola (*N.* [= *Synocnus*] *comes*[6], plus two new species diagnosed here). Ascertaining species limits in a group of highly variable but not necessarily well sampled taxa is challenging, and some of the *Neocnus* species listed here may require further systematic treatment. As a group, the outstanding features of neocnuses are their small body sizes and skeletal indications of great arboreal agility. Osteologically, it is of some interest that none of the Hispaniolan specimens was found with jugals attached; nor have any isolated jugals been recognized in the collections made thus far. Unlike other megalonychids, which exhibit a broad sutural attachment area for the jugal, *Neocnus* has an attachment area that is no more than a raised dimple or shallow pocket on the maxilla, suggesting that this element (and related masseteric musculature?) may have been highly reduced (see fig. 12).

DIAGNOSIS OF GENUS: Small body size; cranial flexion absent; postorbital constriction weak; mandibular caniniform grooved posterointernally; last mandibular molariform with deep lingual groove; femoral shaft anteroposteriorly flat and medially bowed with prong on anterior aspect (except for *N. toupiti*; see below); fibular facet of astragalus truncated and crescent-shaped; humerus short and slender but with prominent and squared supracondylar ridge; pronator quadratus flange confined distally.

Neocnus dousman, new species

HOLOTYPE: Skull (UF 76363; fig. 7) without clear associations, found 21–22 September 1983 by D. Cordier and party.

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[5] Although *Neocnus* (Arredondo, 1961) has priority over *Cubanocnus* (Kretzoi, 1968) at the genus level (operation of ICZN art. 40 [a][i]), Cubanocnini (Varona, 1974) was the first suprageneric nomen given to this group. It therefore has priority at the tribal level.

[6] Inclusion of *Synocnus* within *Neocnus* may seem controversial in that *Synocnus* is usually considered an ally of *Acratocnus*. However, this move is warranted because Paula Couto's (1967) hypodigm is mixed (includes elements that actually belong to *Parocnus*) and his taxon definition is therefore unworkable. Absent the *Parocnus* specimens, it is evident that the remaining hypodigm represents a species that is phylogenetically *Neocnus*, not *Acratocnus* (White and MacPhee, in press).

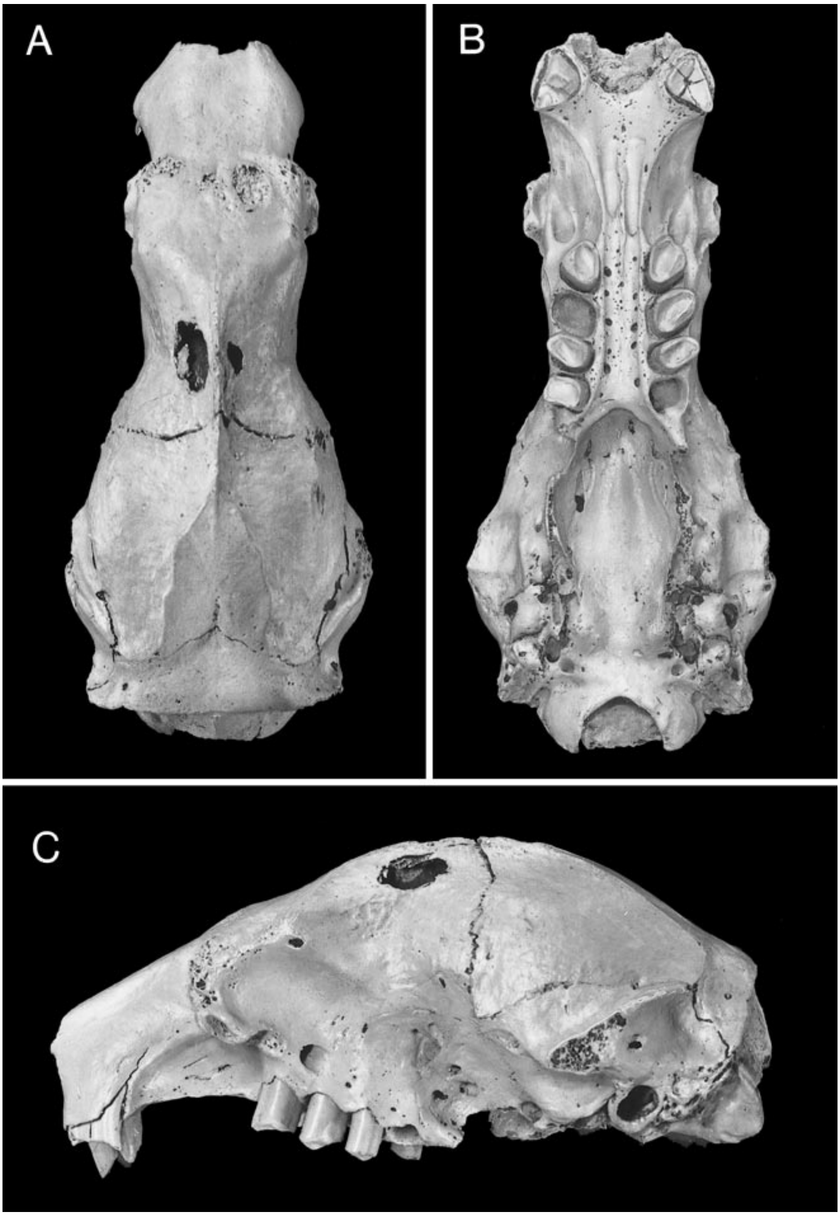

Fig. 7. *Neocnus dousman*, holotype skull (UF 76363) from Trouing de la Scierie, Morne la Visite, Département de l'Ouest, Haiti: **A**, dorsal; **B**, ventral; **C**, left lateral; **D**, right lateral; and **E**, occipital aspects. (Note scale; see also fig. 12.).

TYPE LOCALITY AND AGE: Trouing de la Scierie, Morne la Visite, Département del'Ouest, Haiti; late Quaternary (see appendix 1 for additional details).

SYNONYMS: None.

REFERRED SPECIMENS: Hypodigm also includes a mandible (UF 76370; see fig. 8) from the same locality and a number of postcranial elements from other localities (see fig. 11). From Trouing Deron #1, Plain Formon: right femur (UF 76204), right tibia (UF 170207), left humerus (UF 170105), left ulna (UF 170106), and right radius (UF 170107); from Trujin Bridge, Morne la Visite: right

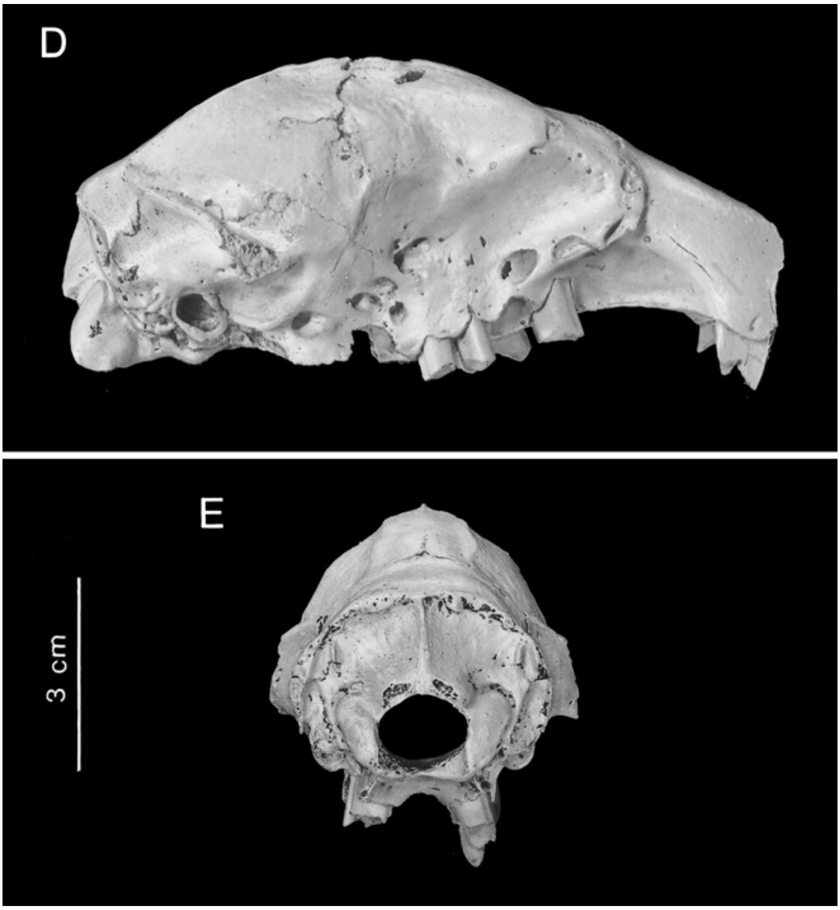

Fig. 7. Continued.

femur (UF 76270/285), left humerus (UF 75575), left ulna (UF 75634), right astragalus (UF 170240), and right tibia (UF 75469); from Trouing Jérémie #5, Plain Formon: right calcaneus (UF 170291); from Trou Diable, St.-Michel: right calcaneus (UF 170205).

ETYMOLOGY: Haitian Creole adjective meaning ‘‘slow,’’ pronounced approximately [doos-manh]; reference is to the classic behavioral characteristic of sloths. Recommended common name: Lesser neocnus.

DISTRIBUTION: Haiti and Dominican Republic.

DIAGNOSIS OF NEW SPECIES: With regard to known elements, agrees with features that define the genus. Differs from other *Neocnus* species in having sagittal crest consistently present; cranium flattened; lateral groove of pterygoid present; symphyseal spout long, narrow, and untapered (relative to *N. comes*); proximal fibular facet of tibia oval, robust, and posteriorly oriented; femoral shaft with slight anterior prong; quadriceps femoris tubercle (= tibial tuberosity) forming hook with groove; pronator quadratus flange forming abrupt lateral crest; bicipital tuberosity anteriorly placed.

DISCUSSION: See next entry.

Neocnus toupiti, new species

HOLOTYPE: This species is founded on a partial associated skeleton collected at the type locality on 3 June 1984 by D. Cordier and party. In addition to the skull (UF 156892), chosen for illustration here (fig. 9), the Jérémie #5 holotypic skeleton includes the following separately numbered elements

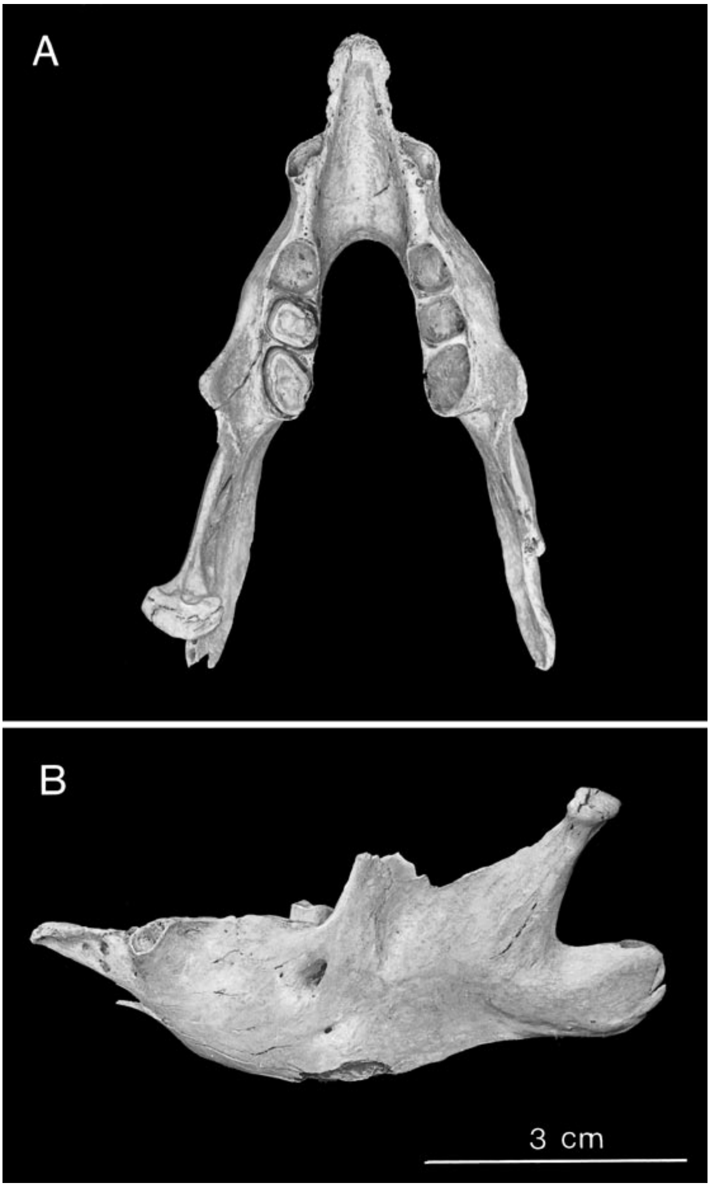

Fig. 8. *Neocnus dousman*, referred mandible (UF 76370), from Trouing de la Scierie, Morne la Visite, Département de l'Ouest, Haiti: **A**, occlusal, and **B**, lateral aspects. Specimen is from same site as holotype of this species, but is not known to belong to same individual.

(fig. 11): right humerus, right and left radii and ulnae (all numbered UF 170073); right and left femora (UF 76235, 76236); right and left tibia, and right calcaneus (all numbered UF 170281); and left scapula (UF 170072).

TYPE LOCALITY AND AGE: Trouing Jérémie #5, Plain Formon, Département du Sud, Haiti; late Quaternary (see appendix 1 for additional details).

SYNONYMS: None.

REFERRED SPECIMENS: Hypodigm also includes a referred skull (UF 156894) from Trou Wòch Dadier, Étang de Miragôane; mandible (UF 171296; fig. 10) from Trou Ni-

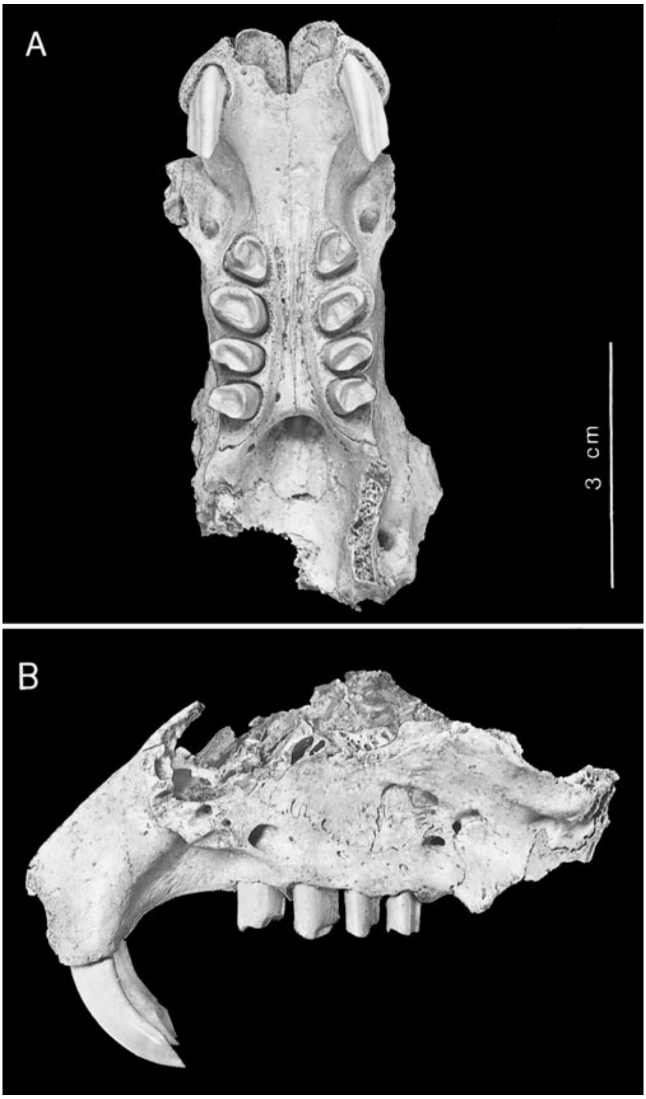

Fig. 9. *Neocnus toupiti*, skull (UF 156892) of holotypic partial skeleton from Trouing Jérémie #5, Plain Formon, Département du Sud, Haiti: **A**, ventral, and **B**, left lateral aspects. Upper caniniforms of this specimen were partially dislodged after death and have been cemented by $CaCO_3$ deposition into unnatural positions. (Note scale; see also fig. 12.)

colas, Morne la Visite; scapula (UF 170005) from Trujin Bridge, Morne la Visite; astragalus (UF 170286) from Trouing Jérémie #5; calcaneus (UF 170443) from Trouing Jérémie #3.

ETYMOLOGY: Haitian Creole adjective meaning ‘‘tiny,’’ pronounced approximately [too-pitee]; reference is to the very small body size of this species. Recommended common name: Least neocnus.

DISTRIBUTION: Haiti and Dominican Republic.

DIAGNOSIS OF NEW SPECIES: With respect to known elements, agrees with features that define the genus. Differs from other *Neocnus* species in having very small, extremely gracile skeleton; upper caniniform with very deep lingual groove; symphyseal spout long, narrow, and untapered (partly broken on holotype); femur lacking third trochanter; fem-

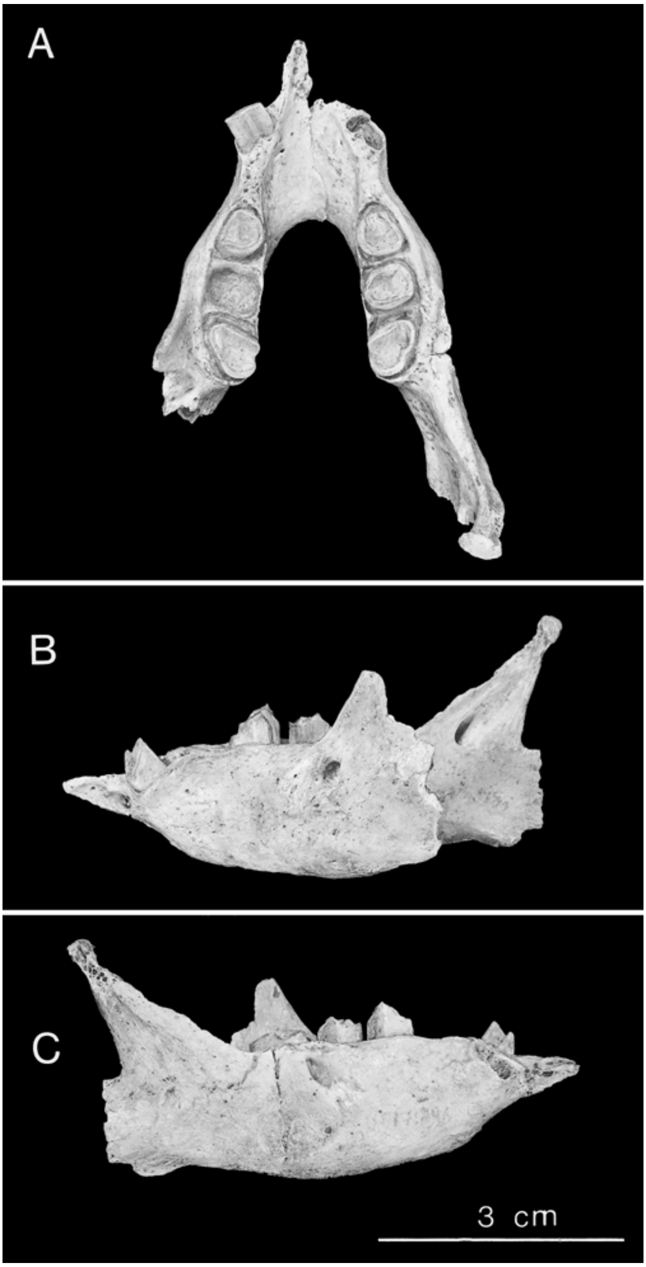

Fig. 10. *Neocnus toupiti*, referred mandible (UF 171296) from Trouing Nicolas, Morne la Visite, Département de l'Ouest, Haiti: **A**, occlusal; **B**, left lateral; and **C**, right lateral aspects. (Note scale; see also fig. 12.)

oral shaft cylindrical with reduced anterior prong; femoral head tiny; distal tibial articular surface very narrow and divided only at anterior edge; astragalus tiny with relatively long neck; ectal and sustentacular facets very close together; calcaneal tuberosity triangular and L-shaped (rather than J-shaped); ectal facet distinctly humped; most anterior aspect

TABLE 1

Morphometric Data Distinguishing *Neocnus dousman* and *Neocnus toupiti*: Comparisons of Means for Representative Measurements (in millimeters)

Measurement	*N. dousman* $\bar{x} \pm S$ (n)[a] (range)	*N. toupiti* $\bar{x} \pm S$ (n) (range)	*p* value[b]
Total length skull	110.3 ± 2.8 (2) (108.2–112.3)	97.0 ± 10.3 (3) (85.4–105.3)	—
Tooth length/diastema length	1.3 ± 0.1 (2) (1.2–1.4)	1.5 ± 0.1 (4) (1.5–1.6)	—
ML width, femoral head	19.7 ± 1.0 (13) (18.1–22.1)	17.4 ± 0.7 (8) (16.8–18.9)	<.001; ***
Maximum length, femur	115.3 ± 5.1 (8) (108.8–123.2)	106.9 ± 1.3 (4) (105.8–108.8)	.002; **
Maximum length, sigmoid notch	15.1 ± 0.4 (11) (14.5–16.1)	13.5 ± 0.7 (20) (11.4–14.4)	<.001; ***
Maximum length, tibia	90.1 ± 3.7 (13) (84.2–95.4)	84.5 ± 1.9 (5) (82.1–86.9)	<.01; **
Width, distal tibia articular surface	13.9 ± 0.7 (16) (12.6–15.0)	12.5 ± 0.8 (12) (11.4–13.9)	<.001; ***
Width, proximal astragalar articular surface	13.0 ± 1.0 (12) (11.7–14.3)	11.3 ± 0.6 (11) (10.5–12.3)	<.001; ***
Maximum distance across sustentacular and ectal facets of calcaneus	17.4 ± 0.8 (13) (15.7–18.8)	14.2 ± 0.8 (16) (13.1–15.8)	<.001; ***

[a] Mean ± standard deviation (sample size).

[b] Means were compared using two-tailed Students' t-tests after checking for homogeneity of variances; asterisks denote level of significance.

of glenoid fossa of scapula pointed; supracondylar ridge reduced; pronator quadratus flange gentle and reduced; ulnar shaft extremely laterally compressed; sigmoid notch of ulna unsegmented and shallow; proximal fibular facet of tibia round, reduced, and posteriorly oriented.

DISCUSSION: *Neocnus toupiti* is the smallest known Antillean sloth, being significantly smaller in linear dimensions and long-bone cortical cross-sectional thickness than either of the extant tree sloths, *Bradypus* and *Choloepus* (3–4 kg body mass; Silva and Downing, 1995). *Neocnus comes*, not otherwise discussed here, is larger and differs in a number of cranial and postcranial features; its inclusion within *Neocnus* is discussed elsewhere (see fn. 6; White and MacPhee, in press).

Species of Hispaniolan *Neocnus* can be distinguished from each other and from Cuban *Neocnus* by unique discrete traits as well as morphometric analyses (White, 1993a; White and MacPhee, in prep.). Whereas some discrete features are found in more than one *Neocnus* species, the sum total of all differentiae for each species serves to distinguish them from one another. Table 1 presents a sample of morphometric measurements that distinguish the two new species of *Neocnus* diagnosed here. The chosen measurements are all taken on elements that are also distinguished by discrete traits, to demonstrate that size is not the primary criterion for taxonomic assignment. Coefficients of variation (table 2) computed for some representative measurements also support the occurrence of two separate species; in most cases, coefficients of variation for each species alone fall within the normal range of mammalian variation, whereas coefficients of variation for the combined samples are higher than one would expect from a single species (Simpson et al., 1960).

TABLE 2
Morphometric Data Distinguishing *Neocnus dousman* and *Neocnus toupiti*: Coefficients of Variation[a] for Representative Measurements

Measurement	*N. dousman* V (n)	*N. toupiti* V (n)	Combined sample V (n)
ML width, femoral head	4.86 (13)	3.89 (8)	7.62 (21)
Maximum width across femoral trochanters	4.04 (10)	4.90 (6)	6.07 (16)
Maximum length, sigmoid notch	2.92 (11)	5.33 (20)	7.05 (31)
Maximum width, distal tibia	6.15 (15)	5.77 (11)	8.87 (26)
Length, ectal facet of calcaneus	7.95 (12)	6.5 (15)	12.26 (27)
Maximum length, astragalus	5.62 (12)	3.50 (11)	7.25 (23)
Maximum distance across sustentacular and ectal facets of calcaneus	4.76 (13)	5.48 (16)	11.43 (29)

[a] $V = 100s/\bar{x}$.

Further evidence for the distinctiveness of *Neocnus* species comes from articulating elements (fig. 11). For example, *N. toupiti* humeral heads are all too small for *N. dousman* glenoid fossae, and all *N. toupiti* glenoid fossae are too small for *N. dousman* humeral heads. The collection also revealed some immature bones of larger *Neocnus* species that are the same size as, or larger than, adult examples of smaller *Neocnus*

Fig. 11. Comparison of representative postcranials of two species of *Neocnus*: **A**, anterior aspect of femur of *N. dousman* (UF 76270), compared to **B**, that of *N. toupiti* (UF 76235); **C**, dorsal aspect of calcaneus of *N. dousman* (UF 170291), compared to **D**, that of *N. toupiti* UF 170443. See text for details.

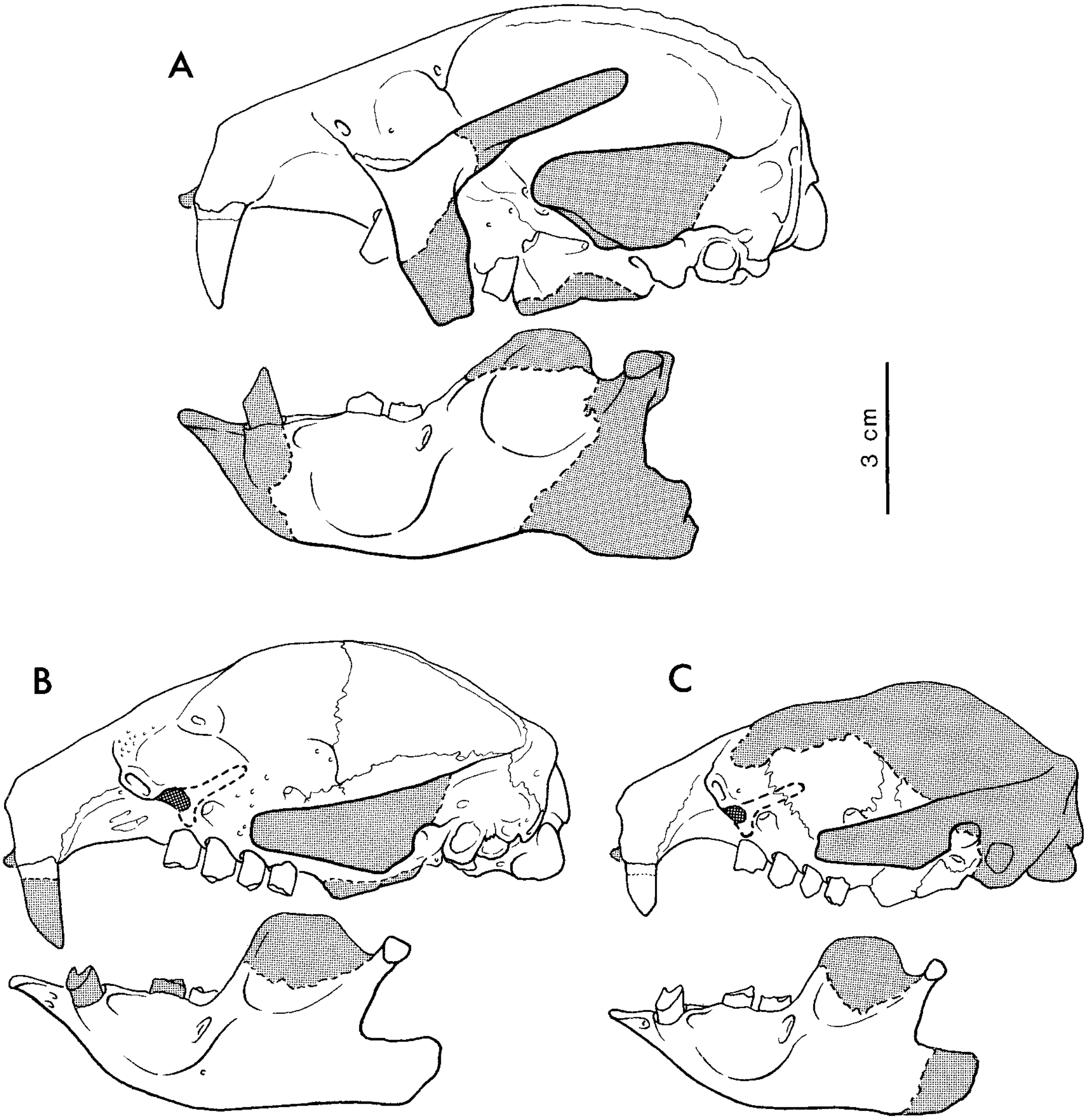

Fig. 12. Cranial reconstructions of *Acratocnus ye* (**A**), *Neocnus dousman* (**B**), and *N. toupiti* (**C**), based on holotype skulls and associated or referred jaws described in this paper, as well as other specimens in the UF collections. All drawn to same scale; areas not represented in illustrated holotypes are stippled. Jugals of *Neocnus dousman* and *N. toupiti* have not been identified in collections, and their shape as represented here is conjectural; tiny size of contact area for maxillojugal suture indicates substantial reduction. Position of dislocated upper caniniforms in *N. toupiti* holotype have been corrected (see fig. 9).

species. For example, UF 76292 is an immature femur that lacks epiphyses yet exhibits a third trochanter. On size alone it evidently belonged to either *N. dousman* or *N. comes*, yet it is the same size as fully adult femora of *N. toupiti*.

DISCUSSION

The immediate consequence of the systematic treatments presented here is that the phyllophagan fauna of Hispaniola rises from two species to six, a plausible figure given the size of the island and known level of diversity in neighboring Cuba (cf. Woods, 1990). The two small *Neocnus* species described here have evidently not been recovered heretofore, or at least never reported as being novel. In view of the small number of published investigations on Hispaniolan sloths, this is perhaps not surprising. Although it has been claimed previously that both *Megalocnus* and *Acratocnus* existed in Hispaniola, these claims were originally founded on material that does not, in fact, belong to these taxa. Fortunately, the new material from Haiti places beyond doubt the conclusion that species belonging to these genera were present in Hispaniola during the Quaternary.

Although Quaternary Antillean sloths must have divided their habitats in several different ways to avoid competition, it is difficult to recover relevant information on adaptation from cave faunules. However, functional and morphometric studies indicate the sloths ranged from large ground-dwellers (e.g., *Megalocnus zile*) to small arborealists (e.g., *Neocnus toupiti*) (White, 1993a). And they were evidently successful: with the exception of *M. zile* (so far known from very few sites), megalonychid species were well distributed across all of Haiti (and probably therefore all of Hispaniola).

Acratocnini, Cubanocnini, and Megalocnini are represented in the Quaternary of both Cuba and Hispaniola. This distribution, in which several distinct lineages are represented by different but closely related species on either side of a major barrier (in this case, the Windward Passage), might be explained in several ways (e.g., Hedges' [1996] view that virtually all Antillean land vertebrate distributions are the consequence of passive over-water transport). In the case of megalonychid sloths, the most parsimonious explanation of the evidence is that the lineages and their distribution in space antedated the appearance of the barrier. According to information summarized by Iturralde-Vinent and MacPhee (1999), the Windward Passage came into existence in the Oligocene and widened progressively in the Miocene as a consequence of sinistral strike-slip movements along major faults and deformations along the northern margin of the Caribbean plate. Before this, eastern Cuba and northern Hispaniola were continuous with each other, constituting the western end of a larger subaerial entity dubbed ‘‘GAARlandia.’’ Since there was at least one sloth—presumably a megalonychid—in eastern GAARlandia (future Puerto Rico) as early as the Early Oligocene (MacPhee and Iturralde-Vinent, 1995), it is conceivable that ancestors of all three of the major Antillean phyllophagan lineages entered (or evolved in) the Caribbean region at or near the end of the Eocene, during the brief interval in which GAARlandia is thought to have formed a landspan continuous with northwestern South America. Subsequently, subdivision of this landmass vicariated the existing biota (‘‘island-island’’ vicariance pattern of Iturralde-Vinent and MacPhee, 1999), resulting in the presence of essentially identical suites of sloth clades on the two sides of the Windward Passage.

If vicariance occurred in this manner, a logical corollary is that the Quaternary records of the islands have been shaped not only by immigration but also by extinction. This raises some interesting questions. For example, cubanocnin and megalocnin sloths have not been discovered in Puerto Rico, although the GAARlandia hypothesis specifies that this island was connected with Hispaniola earlier in the Cenozoic (Iturralde-Vinent and MacPhee, 1999). Is the apparent absence of other sloth lineages due to the fact that they were never present on the landmass that eventually became Puerto Rico, or is it because they were there but their fossils haven't yet been discovered? Only appropriate paleontological investigations will tell (MacPhee and Wyss, 1990).

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APPENDIX 1: REGISTRY OF LOCALITIES IN HISPANIOLA

This registry provides basic information on type localities and other sites discussed in the text. Most of the localities listed here were exacavated by C. A. Woods and colleagues in the 1970s and 1980s, although for completeness certain other sites are discussed as well (table 3). A more complete version of this registry, with information on additional sites not described here, is being prepared by the third author (see also Woods, 1989). Most of the quoted radiocarbon estimates are ‘‘whole bone’’ dates produced in the early 1980s; they have large standard errors and are not calibrated. However, they still have basic significance and, in any case, are the only ones available for most of the localities discussed.

Localities are grouped by civil division (*département* in the case of Haiti, *provincia* in the case of the Dominican Republic). Because of the large number of sites in the Presqu'île du Sud (Southwest Peninsula) of Haiti, localities in the Départements du Sud and de l'Ouest are further grouped by geographical area (Plain Formon, Étang de Miragôane, Pic de Macaya/Camp-Perrin, and Morne la Visite). No sites have been worked in Département du Nord, so the distribution of sloth species in the extreme northeast of Haiti remains undocumented.

Haiti

DÉPARTEMENT DU NORD-OUEST

ÎLE DE LA TORTUE

Île de la Tortue (28 × 8 km), lying 7.5 km N off the northwest coast of Haiti, appears to be of no great age: uplifted, wave-cut terraces in Plio-

TABLE 3

New Hispaniolan Vertebrate Localities

Locality information (elevation in m, if available)	Megalonychid species present[a]
HAITI	
NORD-OUEST	
Île de la Tortue	
Trou Gallery (40)	***Megalocnus zile***, *Parocnus serus*
L'ARTIBONITE	
St.-Michel-de-l'Atalaye	
Trou Manman Jumu	*P. serus, Acratocnus ye, Neocnus comes, N. dousman*
SUD	
Plain Formon	
Diran Zone	
Trouing Vapé Deron (1110)	***Acratocnus ye***, *N. comes*
Trouing Deron #1 (1000)	*A. ye, N. comes, N. dousman*
Trouing Deron #2 (995)	—
Eastern Zone	
Trouing Rat Niche (960)	—
Trouing Mesan Fort Diclaire (920)	—
Trouing Tilise Belle Jean (850)	—
Trouing Grande Fond (890)	—
Jérémie Zone	
Trouing Jérémie #1 (1210)	—
Trouing Jérémie #2 (1280)	—
Trouing Jérémie #3 (1235)	*A. ye, N. comes, N. dousman, N. toupiti*
Trouing Jérémie #4 (1200)	—
Trouing Jérémie #5 (1275)	***Neocnus toupiti***, *A. ye, N. comes, N. dousman, N. toupiti*
Trouing Jérémie #6 (1295)	—
Trouing Jérémie #7 (1270)	—
Trouing Jérémie #8 (1305)	—
Trouing Jérémie #9 (1290)	—
Trouing Jérémie #10 (1180)	—
Bois Formon Zone	
Trouing Titwe #2	*A. ye, N. comes*
Trouing Titwe #3	*N. comes*
Trou Sant	*A. ye, N. comes*
Trouing Bois Formon #1 (955)	*A. ye, N. dousman*
Trouing Bois Formon #2 (965)	—
Trouing Bois Formon #3 (965)	*N. comes*
Trouing Zambi	—
Trouing Ismays (970)	*N. comes*
Bois Cavalier Zone	
Trouing Dod (1000)	*N. toupiti*
Pic de Macaya/Camp-Perrin	
Trouing Lanj Genti #1 (1365)	—
Trou Wòch Sa Wo (250)	*P. serus, A. ye, N. comes, N. dousman, N. toupiti*
Trou Fon Pelon	*N. comes*
Étang de Miragôane	
Trou Wòch Dadier (160)	*P. serus, A. ye, N. comes, N. dousman, N. toupiti*

TABLE 3
(continued)

Locality information (elevation in m, if available)	Megalonychid species present[a]
OUEST	
Île de la Gonave	
Trou Zombie	*P. serus*
Morne La Visite	
Trouing la Scierie (1815)	***Neocnus dousman***, *P. serus, A. ye, N. comes, N. toupiti*
Trouing Pas Konnen (1980)	*N. comes*
Trouing à Kôté (1980)	—
Trouing Nicolas (1760)	*N. comes, N. toupiti,*
Trujin Bridge (1875)[b]	*P. serus, A. ye, N. comes, N. dousman, N. toupiti*
Trouing Jour Jour	*A. ye, N. comes, N. toupiti*
Trouing Jean Paul (1750)	—
Trouing Laura Lee (1825)	*A. ye, N. comes, N. toupiti*
Trouing Attié (1770)	*A. ye, N. comes, N. dousman*
Trouing Wanga Negress (1850)	—
Trouing de Vache (1820)	*N. comes*
Trouing Gros Basin Berac	*A. ye, N. comes, N. dousman*
DOMINICAN REPUBLIC	
SAN CRISTOBAL	
Bayaguana	*M. zile, P. serus, A. ye, N. comes*
PEDERNALES	
Cueva de las Abejas	*A. ye, N. comes, N. dousman*

[a] If type locality, status indicated by relevant species name in bold. Dash indicates that no megalonychids were recovered at site indicated.

[b] Also referred to as Trujin and Trouing Marassa (see appendix 1).

Pleistocene limestones form the bulk of the island, covering Cretaceous schists and Paleogene limestones outcropping along the island's south side (Lewis et al., 1990). Emergence is presumably related to the rapid (and still-continuing) uplift of the Cordillera Central of Hispaniola (Lewis et al., 1990).

Trou Gallery (20°03′05″N, 72°43′40″W)

This large cave is situated 4 km NNW of the community of Palmiste, close to the north shore of Île de la Tortue (breaking surf can be heard from the cave entrance). Cave located 19 March 1979 by M. Langworthy and excavated over an eight-day period.

The cave entrance is high and wide (~25 m × 25 m) and opens into a large, decorated interior chamber where paleontological work was conducted. Owing to the size of the opening, the cave is well lit. Substrate was dry, uncompacted, and shallow. Very few bats observed roosting in cave.

At and near the surface, remains of extinct *Isolobodon portoricensis* (Capromyidae) were especially common. In several pits, sloth bones were encountered at 12–15 cm (and in some cases deeper). Two units were discriminated:

Surface unit (0–10 cm): This unit is highly disturbed (charcoal fragments, human remains) and is not readily distinguishable from the next unit. The mammal fauna, presumably owl-derived, consisted of *Rattus rattus* and *Isolobodon portoricensis* in some abundance.

Deep unit (max. depth 55 cm): This unit is typical karst residuum, consisting of a fine red clay. Sloth remains were encountered at 25 cm below surface in several pits, with a notable concentration of bones at the 40-cm level where the team recovered the holotype scapula and several other elements of ***Megalocnus zile,*** new species. Remains of the now-extinct insectivore *Nesophontes*, often encountered in Hispaniolan cave deposits, were rarely found in this cave.

The faunal sample is of some antiquity: bone recovered from the 25 cm and 100 cm levels dated to 17,405 ± 900 and 21,170 ± 525 rcyrbp, respectively.

DÉPARTEMENT DE L'ARTIBONITE
St.-Michel-de-l'Atalaye

Trou Manman Jumu (19°23′30″N, 72°20′00″W)

This historically important area for Quaternary cave paleontology (cf. Miller, 1922, 1929) continues to yield significant fossil material, although relatively few completely untouched caves have been found in recent years. Trou Manman Jumu, located by the Woods party, produced sloth bones of several different species to a depth of 60 cm. Sloth bones from that depth yielded a ^{14}C date of 8,120 ± 216 rcyrbp.

DÉPARTEMENT DU SUD
Plain Formon

Plain Formon is a small, SE-tilting plateau situated near the western extremity of Presque'île du Sud, ranging in elevation from 850 m in the SE to 1400 m in the NW near Morne Cavalier. Most of the country rocks forming the plateau are massive limestones comprising the Macaya Fm (Late Cretaceous). This formation is underlain by the heterogeneous Demisseau Fm, a deep-water deposit consisting of basaltic volcanics, limestones, and siliceous sandstones. On Plain de Formon itself there is an extensive karst topography east and south of Morne Cavalier. Karst is also exposed along ridges at 1800–2000 m elevation E of Pic Formon (18°22′N, 74°02′W) and along the ridge between the latter and Pic de Macaya (18°24′N, 74°02′W). Haystack hills, doline collapses, and sinkholes abound. Of these features, the last is paleontologically the most important: deep, steep-sided sinkholes are perfect natural traps. During February–August, 1984, the third author and his colleagues investigated no fewer than 23 of them in a 3 km strip south of Pic de Macaya. Five sinkhole groups or zones were identified: Diran Zone, Eastern Zone, Jérémie Zone, Bois Formon Zone, and Bois Cavalier (table 3). Only the most significant sites are described here.

The richest sites were encountered east of the Jérémie area, in the upper part of Plain Formon (~1275 m elev.). In most of them no signs of human presence were encountered, nor any indication that they were visited by owls or other predators (i.e., no evidence of pellets). Typically, bones were found interspersed among breakdown piles in the center or in sediments ringing sinkhole floors. All such remains are presumed to have accumulated as a result of animals falling through the opening and dying outright or becoming permanently entrapped. In such a situation, articulated remains are to be expected; several of the Jérémie sinkholes have yielded essentially complete skeletons of a number of now-extinct mammals. In a few cases, the excavation party found associated skeletons of sloths and rodents in side chambers or pockets above the floor level of the sinkholes, indicating that animals had survived the initial fall and died later.

The present dominant plant community on Plain Formon is dry scrub forest (*rakbwa*), but earlier in the Quaternary the area was moister judging from the fossil mammal fauna. The fauna indicates that Plain Formon could have been associated with a montane area of relictual mesic habitat that was confined to this and other mesic montane sites in Haiti during relatively xeric times in the late Wisconsinan and early Holocene (see Woods, 1989).

Trouing Vapè Deron (Diran Zone; 18°19′N, 74°02′W)

This very wet (*vapè*, ‘‘humid’’) sinkhole, 8 m deep, is located in a patch of scrub forest 2 km E of Morne Cavalier and SE of a karst outcrop that divides the plain into two sections. The shaft, with a 5 m × 10 m opening, is 20 m wide at floor level. A huge pile of rocky debris lies at bottom. Located by D. Cordier and C. A. Woods 26 January 1984 and excavated the following day.

The material recovered from the sinkhole is limited but important. Strewn among the breakdown and remains of domestic animals was a partially associated sloth skeleton. In a side chamber, 8 m wide, two complete sloth skulls were recovered (including UF 170533, holotype skull and jaw of ***Acratocnus ye,*** new species). Also recovered was the skull and jaw of the extinct rodent *Plagiodontia ipnaeum*). No radiocarbon dates available.

Trouing Deron #1 (Diran Zone; 18°18′40″N, 74°01′40″W)

This locality, a deep shaft (20 m) 13 m wide, is situated 0.5 km SE of Trouing Vapè Deron and 2.5 km ESE of Morne Cavalier. Located 25 January 1984 by D. Cordier and C. Woods; explored and excavated next day by D. Cordier, T. Cordier, C. A. Woods, and A. Fowler.

The sinkhole floor is cluttered with small breakdown and detached speleothems. At surface were considerable numbers of *Plagiodontia* bones, a dog skeleton, and sloth remains (cranium and associated postcranials, isolated phalanges, and bones of an infant or juvenile). A shallow pit dug near the edge of the floor yielded remains of extinct *Nesophontes paramicrus* and *Hexolobodon phenax*. No radiocarbon dates available.

Trouing Jérémie #3 (Jérémie Zone; 18°20′05″N, 74°02′40″W)

Trouing Jérémie #3 is located 2.5 km W of Morne Cavalier in upper Plain Formon, in the forested foothills of Pic Formon ridge. This sinkhole is the last (most southeasterly) of the Jérémie series, and is located furthest from the edge of the Pic Formon foothills. Located and excavated 31 January 1984 by D. Cordier.

The sinkhole is 35 m deep; the main chamber is 30 m across, from which a small side chamber extends. The floor is littered with debris and many large fallen rocks. From this locality came an associated upper limb skeleton (UF 169822) referred to ***Acratocnus ye***, new species. No indication of owl roosts, past or present.

Trouing Jérémie #5 (Jérémie Zone; 18°20′30″N, 74°02′30″W)

This locality, situated on the upper edge of Plain Formon 2 km NW of Morne Cavalier, in the forested foothills of Pic Formon, was the most productive discovered by the field party in the entire Plain Formon area. Located 1 February 1984 by D. Cordier and subsequently worked by D. and T. Cordier 3 June, 8 June, and 4 July (last for mapping purposes only). Type locality of *Rhizoplagiodontia lemkei* (Woods, 1989) and ***Neocnus toupiti***, new species. This sinkhole has also yielded remains of the endemic monkey *Antillothrix bernensis* (C. Woods, unpubl. data).

The main shaft has an opening of 2.5 m and a depth of 16.5 m; width at base is 12 m. No indication of owl roosting sites, past or present. Very wet cave abounding in frogs, spiders, and land snails. Extensively excavated by field party, ~50 large bags of matrix removed for later picking.

The Camp-Perrin area to the east of Trouing Jérémie #5 is one of steep limestone cliffs and rolling hills at an elevation of 250 m. The current rainfall at Camp-Perrin is 2271 mm yr^{-1}, with over 5000 mm yr^{-1} falling in some areas of the Massif de la Hotte 5 km NW (Sedwitz and Canet, 1972). The natural forest cover in the area has been destroyed, but rainfall and evaporation data indicate that the original forest formation was very humid subtropical forest (Sedwitz and Canet, 1972).

The composition of the mammalian fauna of Trouing Jérémie #5 (table 4) was calculated based on an analysis of a large sample of bones collected in the top 5 cm of the deposit. The percentage of abundance was determined on the basis of the number of left mandibles (or femur, in case of *Antillothrix*). The most common mammal in the sample is *Plagiodontia aedium* (20.1%) followed by *Rattus rattus* (13.9%); *Rhizoplagiodontia lemkei* (12.3%); *Nesophontes paramicrus* and *N. hypomicrus* (combined, 11.5%); *Plagiodontia ipnaeum (= velozi)* (9.0%); *Brotomys voratus* (8.2%); *Hexolobodon phenax* (7.4%); several species of megalonychid ground sloths, including *Neocnus toupiti* (5.7%); *Solenodon paradoxus* and *S. marcanoi* (combined, 4.1%); *Isolobodon portoricensis* (4.1%) and *I. montanus* (1.6%); *Mus musculus* (0.8%); and *Antillothrix bernensis* (.08%). No remains of cats or mongoose were found.

TABLE 4

Faunal List: Trouing Jérémie #5

SURFACE AND ORGANIC UNIT (0–5 cm)

- *Rattus rattus*
- *Mus musculus*
- *Plagiodontia aedium*
- *Solenodon paradoxus*
- †megalonychids[a]
- †*Solenodon marcanoi*
- †*Hexolobodon phenax*
- †*Rhizoplagiodontia lemkei*
- †*Isolobodon portoricensis*
- †*Isolobodon montanus*
- †*Nesophontes paramicrus*
- †*Nesophontes hypomicrus*
- †*Brotomys voratus*
- †*Plagiodontia ipnaeum*

RED CLAY UNIT (5–25 cm)

- megalonychids[a]
- †*Rhizoplagiodontia lemkei*
- †*Antillothrix bernensis*[b]

[a] See table 3.

[b] Represented by a femur.

Pic de Macaya and Camp-Perrin

The area between Camp-Perrin, the western margin of the Plain Formon, and the high mountains to the north is the area of highest rainfall in Haiti (Sedwitz and Canet, 1972). This high precipitation is caused by local conditions and not by the direct influence of prevailing northeast trade winds blowing into the mountains. As a result, it is probable that the area was one of high rainfall during the period when other areas of southern Hispaniola were more xeric. It is likely, therefore, that the faunal assemblages, which include unusually large numbers of solenodons, small sloths adapted for tree-dwelling, and the endemic primate *Antillothrix bernensis*, were associated with a moist, well-forested habitat (cf. Plain Formon). Discovery of small aboreal sloths in the Massif de la Selle, Massif de la Hotte, and some areas on the Plain Formon indicates that these were refugial areas of mesic forest during times of reduced precipitation.

For some portion of the Neogene, the Presqu'île du Sud was an island, separated from central Hispaniola and the la Selle-Bahoruco block by a narrow seaway running through the peninsula along the line of Trouin Valley, which follows the Rivière Gauche between Jacmel and Carrefour Fauche near Grand Goave. Pleistocene uplifts (Maurrasse et al., 1982) united the peninsula with the mainland, producing the modern configuration. Until early to mid-Pleistocene times, the land vertebrates of the Massif de la Hotte to the west would have been separated from those of the la Selle-Bahoruco island to the east (which was itself separated from central Hispaniola until at least early Late Pliocene by the Cul-de-Sac seaway).

Trou Wòch Sa Wo (18°09′N, 73°53′W)

The location and fossil yield of this important rock shelter (''the hole in the rock that is up there''), also recorded as Caverne Sa Wo (MacPhee and Woods, 1982), is described in detail by Woods (1989). It is located 2 km SSW of Camp-Perrin. Sloth material encountered at 150 cm below surface produced a ^{14}C date of 3755 ± 175 rcyrbp, the youngest on record for West Indian megalonychids (MacPhee et al., 1999). The oldest dates on unspecified fauna from the cave were at or close to the Pleistocene/Holocene boundary.

Étang de Miragôane

Evidence that the Massif de la Hotte was separated from the Massif de la Selle by ecological factors in the past comes from pollen stratigraphy (Hodell et al., 1991). These data indicate that the environment in the Étang de Miragôane area was cool and dry between ca. 10,300 and 5370 rcyrbp. At that time xerophytic plant communities were widespread in southwestern Haiti and moist forest habitats would have been small and fragmented. During the middle Holocene (5370–2490 rcyrbp), Étang de Miragôane had high lake levels; pollen spectra indicate that the surrounding zone was a moist forest. During this time mesic forest zones would have expanded and xerophytic plant communities would have been reduced in size. This would have provided ideal conditions for the spread of forest dwelling mammals between la Hotte and la Selle (see Woods, 1989).

Trou Wòch Dadier (18°25′40″N, 73°08′30″W)

Woods (1989) previously referred to this cave as ''Kaven Dadier'' as well as ''Caverne Dadier Arawak,'' to indicate that it contained evidence of human activities in contradistinction to other caves nearby in which no such activities were evident. The current name is considered more appropriate; ''Dadier'' [dadjay] is the name of a local family.

The cave is located 6 km W of Étang Miragôane, on the E side of the old Reynolds Haitian Mines access road from the dock to the bauxite mine above the settlement of Paillant. The cave is 100 m from road, near a water tower.

Trou Wòch Dadier was located 9 January 1974 by C. A. Woods, and excavated at various times during the period 1 November 1977 and 3 January 1977 by C. A. Woods, E. Woods, S. Woods, P. Woods, H. MacPherson, and D. MacPherson. Additional excavation was undertaken 3–4 March 1983 by D. Cordier and M. Langworthy. The entrance is situated 2 m above groundlevel on a limestone outcrop (a true ''trou wòch'').

The main chamber is 3 m × 6 m in size and 2 m high, with a fire-blackened ceiling. The substrate is composed of dry soil and rocky debris. The cave was dug (11 pits) to bedrock. The deepest deposits, extending to a depth of 1.5 m in places, were found near the rear cave wall. At or very near the surface, the excavation party encountered remains of humans and introduced mammals, fish bones, crab and lobster fragments, and a few bones of extinct *Isolobodon portoricensis* and *Boromys voratus* (table 5). In pockets high up on the walls were accumulations of *Nesophontes* spp., doubtless brought in by barn owls (*Tyto alba*) or gray-faced owls (*T. glaucops*). Few living bats (all *Macrotus waterhousii*) were observed.

Bone concentrations varied greatly. Sloth remains were first encountered at the 25 cm level. The best fossil layer was encountered at ≥ 60 cm in several pits, in a red cave earth. Sloth remains were numerous at this depth; several extremely well preserved skulls were recovered, including UF 156894 referred to ***Neocnus toupiti***, new species. Sloth remains continued in some quantity to approximately the 80 cm level; deep to 100 cm, the party encountered a sandy layer with very few bones.

Samples of bones recovered from the 15 cm horizon date to 1600 ± 135 rcyrbp, suggesting that bones of extinct species from surficial layers could be as recent as the modern era. A second date, 19,960 ± 1100 rcyrbp, based on sloth bone encountered at 100 cm, provides a sandwich for material from this cave.

DÉPARTEMENT DE L'OUEST

Île de la Gonave

Trou Zombie (18°45′N, 72°52′W)

This site, located near Anse-á-Galets on the

TABLE 5

Faunal List: Trou Wòch Dadier

	Pit depth (in cm)				
Taxa	0–5	5–25	25–50	> 50	deep pockets (> 80)
Tyto glaucops	x				
Homo sapiens	x				
Felis catus (domestic)	x				
Macrotus waterhousii	x				
Rattus rattus	x				
Mus musculus	x				
Plagiodontia aedium	x				
†*Plagiodontia ipnaeum (=velozi)*		x	x		
†*Plagiodontia araeum*				x	x
†*Plagiodontia* sp.					x
†*Hexolobodon phenax*		x	x	x	
†*Brotomys voratus*	x	x			
†*Isolobodon portoricensis*	x	x		x	
†*Isolobodon montanus*		x			
†*Nesophontes zamicrus*[a]	x				
†*Nesophontes hypomicrus*[a]		x			
†*Nesophontes paramicrus*[a]		x	x		
†megalonychids[b]			x	x	x

[a] Recovered at surface in side pockets on cave walls (gray-faced owl roost sites).

[b] See table 3. Sloth remains began at 25 cm; particularly rich zone encountered in red earth at 60 cm, many nearly perfect sloth skulls.

northeast side of the island, has yielded only one sloth species, *Parocnus serus*. However, it is highly probable that other species existed on this island as well (cf. Île de la Tortue).

Morne la Visite

The pine-covered plateau spreading south and east of Morne la Visite (18°22′N,72°12′W) is similar in many ways to Plain Formon of the Massif de la Hotte. There are numerous karst outcrops, and the plateau has many sinkholes and caves. The area is a high plateau, mostly above 2000 m, and stretches 45 km from Pic la Selle (18°22′N, 71°59′W) in the east to an abrupt termination at Morne d'Enfer (18°22′N, 72°25′W) in the west. The plateau is at a higher elevation than Plain Formon, and there are no surrounding high peaks. La Visite receives less precipitation than Plain Formon, and, because it is higher, it is much cooler. Remains of sloths and large rodents are very common in the deep sinkholes of the plateau (see Woods, 1989).

While there is no direct evidence that glaciers existed in Hispaniola elsewhere than the highest elevations in the Cordillera Central, it is likely that ice and snow, and perhaps some glacier activity, were present in the Massif de la Selle during pleniglacial times. The highest elevation in Haiti is Pic la Selle (2674 m), in the Massif de la Selle. According to Schubert and Medina (1982), glaciers in the Cordillera Central (highest elev., 3087 m) descended to the 1800 m level in pleniglacial times.

Trouing la Scierie (18°20′N, 72°17′W)

This deep sinkhole is 500 m W of old sawmill (scierie [sea-ree]) on karst plain 4 km NW of Seguin, in the Massif de la Selle. Originally discovered by a French spelunking team in 1980; relocated by D. Cordier 10 August 1983. Excavated 4 workdays between 21 September 1983 and 9 May 1984.

Trouing la Scierie is deep and extensive. The opening, 8 m across, leads into a main shaft, 30 m deep. Two side shafts, unmeasured, drop steeply in opposite directions. Bones were found in the main shaft as well as the side shafts in pockets and on surface of rocks. In the main shaft, the party recovered sloth remains (including holotype of ***Neocnus dousman***, new species) as well as *Plagiodontia aedium*, *Solenodon paradoxus*, and *Hexolobodon phenax*. Only *Nesophontes paramicrus* and *Isolobodon portoricensis* were recovered from the side shafts; unlike most sinkholes visited, this was one was a gray-faced owl roost.

Trouing Nicolas (18°19′50″N, 72°17′20″W)

This small trouing, named after Nicolas Etienne, a locally prominent person, is situated in NE corner of a pasture near Rivière Blanche, 4.5 km NW of Seguin. To get to sinkhole, follow trail that cuts SW of main road, just W of Rivière Blanche. Discovered and excavated on 7 August 1983 by D. Cordier; excavated again 22 September 1983 by D. Cordier, C. A. Woods, P. Paryski.

Few species were recovered from this shallowly sedimented sinkhole. *Plagiodontia aedium*, *Plagiodontia* sp. (of large size), and sloth remains (including cranial fragments in association with postcranials) were recovered on the surface and between rocks.

Trujin (Trujin Bridge and Sinkhole, Trouing Marassa) (18°20′40″N,72°17′30″W)

This feature, which includes a cave as well as a sinkhole, is located N of Rivière Blanche, 1 km NW of old sawmill (see entry for Trouing la Scierie) and 5 km NW of Seguin.

The cave, described by Miller (1930), was discovered by Alexander Wetmore and Erik Ekman, who named it ‘‘Trujin’’ (possibly a corruption of *trou d'Inde* or *trou d'Indian*, India Cave or Indian Cave). Efforts were made to relocate the cave in 1983, but Wetmore's toponym was no longer known in the area. It was finally sorted out that the cave and sinkhole of Wetmore's description matched a feature now known locally as Trouing Marassa, investigated 29 March 1983 by D. Cordier and P. Paryski. Extensive excavations were conducted over a total of 10 days between March and September 1983.

The 1983 field party separately named the cave or upper chamber associated with the sinkhole ‘‘Trujin Bridge,’’ in reference to a large pine tree, felled by Wetmore in 1927, that crosses the opening and thus allows access to the chamber where most of the collecting was carried out.

The surface of the cave floor is rich in organic matter, and a wide variety of extinct and extant species were recovered (table 6). Sloths were recovered in a deeper layer of red cave earth, but not in the surface layer. This cave yielded a nearly complete postcranial skeleton of ***Acratocnus ye***, new species. The name Trujin is conserved here as the name of the whole complex because this was its original name and was published as such by Miller (1930).

TABLE 6
Faunal List: Trujin Bridge (Trouing Marassa)

SURFACE[a]	
	Rattus rattus
	Eptesicus fuscus
	Tadarida brasiliensis
	Plagiodontia aedium (= *P. hylaeum*)
	†*Nesophontes hypomicrus*
	†*Isolobodon portoricensis* (= *I. levir*)
	†*Brotomys voratus*
DEEP RED LAYER	
	†megalonychids[b]
	†*Plagiodontia araeum*

[a] Wetmore's surface collection (Miller, 1930), emended.

[b] See table 3.

Dominican Republic

PROVINCIA DE SAN CRISTOBAL

BAYAGUANA

Unfortunately the position of the locality (or localities) that produced the material of *Megalocnus zile* described in this paper is not known. Labels on or associated with the bones indicate that the site, which was prospected by E. Marcano about 1964, must be near the town of Bayaguana, San Cristobal Province, DR.

PROVINCIA DE PEDERNALES

CABO ROJO

Cueva de las Abejas

The exact location of this site is also lost, although it is known to lie about 8 km ESE of Cabo Rojo, 1.5 km N of road from Pedernales. This cave is included in this registry because remains from it have been referred to several of the new sloth species (see table 3).