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Taxonomy, phylogeny, and diversity of the extinct Lesser Antillean rice rats (Sigmodontinae: Oryzomyini), with description of a new genus and species

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Rice rats (Sigmodontinae: Oryzomyini) are abundant in the Late Quaternary fossil record and in Holocene pre-Columbian archaeological middens across the Lesser Antilles. All of these rice rats are now extinct, and their regional diversity and systematics remain extremely poorly understood. We redescribe all of the region’s rice rat taxa known from adequate diagnostic material (Megalomys desmarestii, Megalomys luciae, and Oligoryzomys victus), and describe a new genus and species, Pennatomys nivalis gen. et sp. nov., from archaeological sites on St. Eustatius, St. Kitts, and Nevis, which formed a single larger island during Quaternary low sea-level stands. Cladistic analysis supports the inclusion of O. victus within Oligoryzomys, and identifies Megalomys as a sister group of the large-bodied genera Sigmodontomys or Sigmodontomys + Nectomys, suggesting that large body size in Megalomys represents phylectic gigantism rather than ‘island gigantism’. Megalomys and Pennatomys belong to an oryzomyine clade that has undergone remarkable radiation throughout the oceanic and continental-shelf islands of the Neotropical region, but these genera do not represent a monophyletic group within the Nectomys subclade, indicating multiple over-water colonization events of the Lesser Antillean island chain. Although Lesser Antillean rice rats were heavily exploited by prehistoric Amerindians, it is likely that most or all of these taxa survived until European arrival in the region.


INTRODUCTION

The Neotropical sigmodontine rodent tribe Oryzomyini (the rice rats) is one of the most species-rich New World mammal clades, with 28 extant genera and approximately 115 species currently recognized (Weksler, 2006; Weksler et al., 2006). Oryzomyines are also abundantly represented in the Late Quaternary fossil record and Holocene pre-Columbian archaeological sites throughout the main Lesser Antillean island chain (the Windward and Leeward Islands) (Steadman et al., 1984a; Pregill et al., 1994; Wing, 2001a, b; Newsom & Wing, 2004) (Fig. 1). Rice rats probably occurred on all of the Lesser Antillean islands from Grenada northwards to the Anegada Passage, and the lack of records from a few islands in this chain (notably Dominica) almost certainly represents a sampling artefact rather than a genuine
Figure 1. Map of the Windward and Leeward Islands of the Lesser Antilles, showing the distribution of extinct rice rats in Holocene archaeological sites (black stars) and Late Quaternary palaeontological sites (open circles), and islands from which rice rat species have been formally described. The modern-day sea level and 200 m isobath are both indicated, to show locations of shallow submarine banks that would have been exposed above water during Late Quaternary low sea-level stands, and which may have shared conspecific rice rat populations. Data from Pregill et al. (1994), Crock (2000), Newsom & Wing (2004), and LeFebvre (2007).
Barbuda.

limited Late Quaternary fossil material from *audreyae* Hopwood, 1926, was erected to describe species from the Leeward Islands, (Allen, 1942; IUCN, 2008). A fourth extinct rice rat little morphological or taxonomic investigation over (Fischer, 1829) and *desmarestii* ‘pilories’ from Martinique and St. Lucia, adequate diagnostic material are the giant rice rats or described rice rat species from the region known from extremely poorly understood. The only formally and regional species diversity and systematics remain 1999; Newsom & Wing, 2004; Kozuch & Wing, 2006), resources (e.g. Gullick, 1980; Jones, 1985; Nokkert, tence strategies and exploitation of biological by zooarchaeologists interested in Amerindian subsis- turvey, 2009), they have so far been studied mainly by zooarchaeologists interested in Amerindian subsistence strategies and exploitation of biological resources (e.g. Gullick, 1980; Jones, 1985; Nokkert, 1999; Newsom & Wing, 2004; Kozuch & Wing, 2006), and regional species diversity and systematics remain extremely poorly understood. The only formally described rice rat species from the region known from adequate diagnostic material are the giant rice rats or ‘pilories’ from Martinique and St. Lucia, *Megalomys desmarestii* (Fischer, 1829) and *Megalomys luciae* (Forsyth Major, 1901), and a pygmy rice rat from St. Vincent, *Oryzomys victus* Thomas, 1898, which is now usually placed in the mainland Neotropical genus *Oligoryzomys* (e.g. Tate, 1932b; Hershkovitz, 1969; Carleton & Musser, 1989; Musser & Carleton, 1993, 2005; MacPhee & Flemming, 1999). All three species were described from complete specimens collected during the 19th century (Fig. 2), and are thought to have become extinct by the start of the 20th century (Allen, 1942; IUCN, 2008). A fourth extinct rice rat species from the Leeward Islands, *Megalomys audreyae* Hopwood, 1926, was erected to describe limited Late Quaternary fossil material from Barbuda.

These four species have been the subject of very little morphological or taxonomic investigation over the past century, making wider systematic comparisons difficult (Friant et al., 1940; Friant, 1941; Steadman & Ray, 1982), and no new rice rat species have been described from the Windward or Leeward Islands for over 80 years, despite the abundant material available in archaeological and palaeontological collections. Different authors have proposed various hypothetical intra-island (Steadman et al., 1984b; Lippold, 1991) and inter-island (Woods, 1989; Alcover et al., 1998; Turvey, 2009) species groupings for the Lesser Antillean rice rat radiation, but these remain impossible to evaluate without a better understanding of the extensive collections of currently undescribed rice rat material. Because rice rats comprised an important component of Amerindian diets, species concepts for extinct rice rats are further confused by the substantial evidence for prehistoric translocation of a wide range of land mammals and other vertebrates between different Caribbean islands by Amerindians (Miller, 1929, 1930; Newsom & Wing, 2004; Diaz-Franco & Jiménez Vázquez, 2008; Olson & Maíz López, 2008). New taxonomic studies of West Indian rice rats urgently need to be carried out, not only to clarify the diversity, systematics, ecology, and evolution of this largely ‘forgotten’ group of mammals, but also to understand the dynamics and magnitude of late Holocene mammal extinctions at a global level.

Undescribed rice rat remains, typically referred to ‘Oryzomys’ or ‘Oryzomyini’ in the archaeological literature, have been recorded from late Holocene midden deposits on St. Eustatius, St. Kitts, and Nevis, three islands located close together on the shallow submerged St. Kitts Bank in the Inner Volcanic Arc of the Leeward Islands (Fig. 1). Branch (1907) first noted that bones of a small mammal were extremely plentiful in a midden on St. Kitts that was exposed by a road cut, and rice rat remains are also abundant on this island in the post-Saladoid Sugar Factory/Sugar Factory Pier (AD 700–1000), Bloody Point (AD 660–1115), and Cayon (dates unknown) archaeological sites (Hoffman, 1973; Wing, 1973; Wing & Scudder, 1980; Pregill et al., 1994; J.E. Robb, pers. comm.). They have also been reported on St. Eustatius from the Saladoid/post-Saladoid Golden Rock archaeological site (80 BC–AD 980) (van der Klift, 1992; Schinkel, 1992), and on Nevis from the Archaic-age site of Hichmans’ Shell Heap (790–520 BC), the Saladoid site of Hichmans (100 BC–AD 600), and the post-Saladoid sites of Indian Castle (AD 650–880), Sulphur Ghaut (AD 900–1200), and Coconut Walk (dates unknown) by Wing (2001a, b), Newsom & Wing (2004), and Kozuch & Wing (2006).

Large samples of zooarchaeological rice rat specimens from all three islands on the St. Kitts Bank, differing markedly in body size and craniodental morphology from *Megalomys*, were investigated, together...
with existing historical specimens and/or zooarchaeological or palaeontological material of all previously described extinct rice rat species from the Windward and Leeward Islands. This forms the basis for a redescription of the region’s known rice rat taxa, a description of a new genus and species of extinct Holocene rice rat from the St. Kitts Bank, and the cladistic analysis of these rice rats based on morphological character data to investigate their phylogenetic relationships within the Oryzomyini and trends in insular evolution across the group.

MATERIAL AND METHODS

MORPHOLOGICAL ANALYSIS

Dental terminology follows Reig (1987). Measurements were made using dial calipers, accurate to the nearest 0.1 mm. Repositories of described or cited specimens are: Mammalogy and Palaeontology collections, The Natural History Museum, London, UK (NHM); Environmental Archaeology Program, Florida Museum of Natural History, Gainesville, FL, USA (FLMNH-EAP). Examined material is listed under the systematic summary for each taxon.

CHARACTER SCORING AND PHYLOGENETIC ANALYSIS

West Indian rice rats were scored for the characters employed by Weksler (2006) in previous phylogenetic analyses of oryzomyines. Morphological characters were combined with the molecular data available for extant oryzomyines (Irbp nuclear gene sequence; see Weksler, 2003 and 2006 for details), and subjected to cladistic parsimony analyses. Changes in taxonomic scope and in certain morphological characters from that of Weksler (2006) were made as described elsewhere (Weksler et al., 2006; McCain et al., 2007; Voss & Weksler, 2009). All characters were equally weighted. The Irbp sequence characters were treated as unordered, but some morphological characters were ordered as described in Weksler (2006). Characters with intraspecific variation were treated using the ‘polymorphic’ coding of Wiens (1995; ‘composite’ coding of Weksler, 2006). Morphological characters, including state descriptions and illustrations, can be viewed at the Morphobank repository at http://morphobank.org.

We performed maximum parsimony phylogenetic analyses on the combined morphological and molecular matrix, and on the morphological matrix only. In the combined analyses, nine taxa (including all extinct taxa) lack the Irbp sequence data, resulting in many missing entries in the data matrix. This caused decreased nodal support values (see below), but we could not detect any other potential effect of extensive missing data, such as a lack of resolution arising from wild-card taxa. A nexus file of the morphological and molecular matrices is available in Appendix S1.

The heuristic search algorithm implemented by PAUP* 4.0b10 (Swofford, 2001) was used in all parsimony analyses. Each heuristic search employed 1000 replicates of random taxon addition with tree bisection–reconnection (TBR) branch swapping. Only clades with at least one unambiguous synapomorphy (i.e. present in both ACCTRAN and DELTRAN character reconstructions; Wilkinson, 1995) were retained (commands PSET COLLAPSE = MIN; FILTER BEST in PAUP*). Nodal support was inferred via jackknife resampling and Bremer support (BS) values. Jackknife values (Farris et al., 1996) for the parsimony analysis were calculated using 1000 pseudoreplicates, with heuristic searches employed within each replicate (ten random addition replicates, TBR branch swapping, with no more than 20 trees saved per replicate). Bremer support values (Bremer, 1988, 1994) were calculated with the help of TreeRot 3 (Sorenson & Franzosa, 2007) and PAUP*. Differences in tree length between the most-parsimonious unconstrained trees and trees constrained for alternative hypotheses of Megalomys relationships were tested using the Kishino–Hasegawa test (Kishino & Hasegawa, 1989).
61ters include: pes without well-developed natatory fringes and interdigital webs, and with interdigital pads large and fleshy; robust skull with interorbital region convergent anteriorly, with well-developed supraorbital crests and squared braincase; zygomatic plate lacks an anterodorsal spinous process; small incisive foramina, not extending posteriorly between M1 alveoli; large posterolateral palatal pits recessed in deep fossae; stapedial foramen and posterior opening of alisphenoid canal small, and squamosal–alisphenoid groove and sphenofrontal foramen absent. Well-developed capsular process of lower incisor alveolus; and superior and inferior masseteric ridges joined anteriorly as an open chevron. Molars are bunodont, with M1 anterocone divided by a shallow anteromedian flexus; accessory rootlets are present on M1 and m1; m2 and m3 have three roots.

**Description (based on M. desmarestii and M. luciae only):** Very large rats, as large or larger than any extant oryzomyines (Table 1). Dorsal pelage dark, blackish brown (almost black) (tan brown in one specimen in which the colour might have faded); ventral pelage abruptly paler in *M. desmarestii*, all white, except for a few darker guard hairs; in *M. luciae*, general ventral colour is dark, with plumbeous base, but there are distinct paler areas under the chin and throat and under the lower thorax, the two regions being separated by a streak of darker fur (Fig. 3). Soft fur, subauricular patches absent. Pinnae small, not reaching eye when laid forward. Mystacial and superciliary vibrissae not extending posteriorly beyond pinnae when laid back. Manual claws small and unkeeled. Hindfoot without well-developed natatory fringes and interdigital webs; tufts of ungual hairs at bases of claws on dII–dV vestigial or absent; plantar surface covered with distinct squamae distal to thenar pad; hypothenar pad absent or vestigial in *M. luciae*, present but reduced in *M. desmarestii*; interdigital pads large and fleshy, pads 1 and 4 contiguous with 2 and 3; claw of digit I (dI) extending just beyond first interphalangeal joint of dII; claw of dV extending to middle of second phalange of dIV (Fig. 4). Tail about same length as head and body, sparsely haired and covered with conspicuous epidermal scales; without tuft of long terminal hairs, and unicoloured (dark). Mammary complement unknown.

**Skull with stout rostrum flanked by moderate or deep zygomatic notches; interorbital region convergent anteriorly with well-developed supraorbital crests (symmetrically constricted in an older adult specimen of *M. desmarestii*); braincase squared, with**

Table 1. Measurement data for *Megalomys desmarestii*, *Megalomys luciae*, and *Oligoryzomys victus* (mm)

<table>
<thead>
<tr>
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<tbody>
<tr>
<td>Greatest skull length</td>
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<td>–</td>
<td>47.5</td>
<td>–</td>
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<tr>
<td>Condylar–incisive length</td>
<td>53.6</td>
<td>–</td>
<td>15.6</td>
<td>7.8</td>
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<tr>
<td>Breadth of occipital condyles</td>
<td>9.6</td>
<td>–</td>
<td>9.8</td>
<td>–</td>
</tr>
<tr>
<td>Length of diastema</td>
<td>17.8</td>
<td>16.9</td>
<td>15.6</td>
<td>7.8</td>
</tr>
<tr>
<td>Palatal bridge</td>
<td>14.0</td>
<td>12.8</td>
<td>13.0</td>
<td>6.2</td>
</tr>
<tr>
<td>Length of incisive foramen</td>
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<td>8.3</td>
<td>7.8</td>
<td>5.4</td>
</tr>
<tr>
<td>Breadth of incisive foramen</td>
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<td>3.1</td>
<td>2.7</td>
<td>2.1</td>
</tr>
<tr>
<td>Length of maxillary molars</td>
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<td>7.7</td>
<td>4.5</td>
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<td>Breadth of first maxillary molar</td>
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<td>2.6</td>
<td>2.5</td>
<td>1.4</td>
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<tr>
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<td>10.5</td>
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<td>–</td>
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<td>11.2</td>
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<td>Rostrum breadth</td>
<td>11.4</td>
<td>10.6</td>
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<td>6.1</td>
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<td>Least interorbital breadth</td>
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<td>9.7</td>
<td>9.4</td>
<td>5.1</td>
</tr>
<tr>
<td>Orbital length</td>
<td>17.4</td>
<td>17.5</td>
<td>15.6</td>
<td>11.0</td>
</tr>
<tr>
<td>Zygomatic breadth</td>
<td>30.6</td>
<td>–</td>
<td>26.9</td>
<td>16.7</td>
</tr>
<tr>
<td>Breadth of braincase</td>
<td>16.9</td>
<td>–</td>
<td>15.1</td>
<td>11.4</td>
</tr>
<tr>
<td>Breadth of zygomatic plate</td>
<td>7.8</td>
<td>6.1</td>
<td>6.1</td>
<td>3.9</td>
</tr>
<tr>
<td>Head–body length</td>
<td>257</td>
<td>312</td>
<td>261</td>
<td>94</td>
</tr>
<tr>
<td>Tail length</td>
<td>254</td>
<td>278</td>
<td>145*</td>
<td>121</td>
</tr>
<tr>
<td>Hindfoot length (with claw)</td>
<td>45</td>
<td>59</td>
<td>50</td>
<td>25</td>
</tr>
<tr>
<td>Length of internal side of ear</td>
<td>18</td>
<td>20</td>
<td>18</td>
<td>14</td>
</tr>
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</table>

*The tail of NHM 53.12.16.2 is incomplete.*
well-developed temporal crests; lambdoidal and nuchal crests well developed in older adults. Posterior margin of zygomatic plate dorsal to M1 alveolus; zygomatic plate lacks an anterodorsal spinous process. Jugal present and small (the maxillary and squamosal zygomatic processes overlap). Nasal bones with acutely angled posterior nasal margins; extending posteriorly behind lacrimals; lacrimals sutured mainly to maxillary. Posterior wall of the orbit with postorbital ridge (faint in *M. luciae*). Frontosquamosal suture anterior to frontoparietal suture. Parietals with broad lateral expansions. Incisive foramina small, not extending posteriorly between M1 alveoli, spindle-shaped. Bony palate between the molar rows is smooth or weakly sculpted. Posterolateral palatal pits large, complex, and recessed in deep fossae; mesopterygoid fossa penetrating anteriorly between maxillae; bony roof of mesopterygoid fossa completely ossified in an older adult specimen of *M. desmarestii*, perforated by small (slit-like) sphenopalatine vacuities in a younger specimen of *M. desmarestii* and in *M. luciae*. Alisphenoid strut absent (buccinator–masticatory foramen and accessory foramen ovale confluent). Alisphenoid canal with large anterior opening. Stapedial foramen and posterior opening of alisphenoid canal small; squamosal–alisphenoid groove and sphenofrontal foramen absent; secondary anastomosis of internal carotid crosses dorsal surface of pterygoid plate (= carotid circulatory pattern 3 of Voss, 1988). Posterior suspensory process of the squamosal absent. Postglenoid foramen small and dorsoventrally compressed, covered by tegmen.

**Figure 3.** Dorsal, lateral, and ventral views of *Megalomys* skins. Top, *Megalomys desmarestii* (NHM 55.12.24.201); bottom, *Megalomys luciae* (NHM 53.12.16.2). Scale bar: 5 cm.
tympani; subsquamosal fenestra vestigial or absent. Periotic exposed posteromedially, between ectotympanic and basioccipital, extending anteriorly to carotid canal; mastoid unfenestrated. Capsular process of lower incisor alveolus well developed in adult specimens (smaller in *M. luciae*); superior and inferior masseteric ridges joined anteriorly as open chevron below m1 (slightly anterior in *M. desmarestii*) (Fig. 5).

Upper incisors with smoothly rounded enamel bands. Maxillary tooth rows parallel. Molars bunodont and with labial flexi enclosed by a cingulum; labial and lingual flexi of M1 and M2 meet at midline, enamel overlaps. M1 anterocone divided into anterolabial and anterolingual conules by shallow anteromedian flexus; anteroloph well developed and fused with anterostyle on labial cingulum, separated from anterocone by persistent anteroflexus; protostyle absent; mesolophid present on all upper molars; paracone connected by enamel bridge to anterior or middle moiety of protocone; median mure connected to protocone. M2 protoflexid absent; mesoflexid present as single internal fossette; paracone without an accessory loph. M3 with posterolophid and developed hypoflexid (the latter remaining excavated with moderate to heavy wear) (Fig 6A, B). Accessory labial root of M1 present.

m1 anteroconid without an anteromedian flexid; anterolabial cingulum present on all lower molars; ectolophid absent on m1 and m2; anterolophid present on m2 and m3; mesolophid distinct on un worn m1 and m2; m2 hypoflexid short; posteroflexid present on m3 (Fig. 7A). Accessory lingual and labial roots of m1 present; m2 and m3 each with two small anterior roots and one large posterior root.

First rib with double articulation. Humerus without entepicondylar and supratrochlear foramina. Twelve ribs (false thirteenth rib present in older adult specimen). Fifth lumbar (seventeenth thoracicolumbar) vertebra with well-developed anapophysis. Hemal arch between second and third caudal vertebrae, with posterior spinous process.

Conditions of soft anatomy (stomach, liver, and male accessory reproductive glands) and glans penis characters are unknown.

Remarks: The complex early taxonomic history of *Megalomys* was described by Tate (1932a). Although historical museum specimens of *M. desmarestii* and *M. luciae* have permitted redescription of the genus and comparison of *Megalomys* with other extinct rice rats from the Windward and Leeward Islands, the status of other species that have been assigned to the genus requires further clarification through future research. The limited type material of *M. audreyae* (Fig. 7B) is difficult to evaluate, and the genus-level identity of this species remains unclear. Abundant fossil and zooarchaeological rice rat material is known from the Antigua–Barbuda Bank (Wing et al., 1968; Steadman et al., 1984a; Jones, 1985; Pregill et al., 1994; MacPhee & Flemming, 1999; Steadman & Hilgartner, 1999), and fossil material from Barbuda has been named ‘Ekbletomys hypenemus’ by Ray (1962); however, this taxon remains a nomen nudum because Ray’s work has never been formally published. Although further material apparently referable to *M. audreyae* has been reported and radiometrically dated by MacPhee & Flemming (1999), the identity of rice rats from the Antigua–Barbuda Bank cannot be determined in the absence of further investigation of this material, which is beyond the scope of the present study.

Two other large-bodied extinct insular cricetid rodents, *Megalomys curioi* Niethammer, 1964 from the Galápagos Islands and *Megalomys curazensis* Hooijer, 1959 from Curaçao, were also originally referred to the genus. *Megalomys curioi* has since been transferred to the new genus *Megaoryzomys* (Lenglet & Coppois, 1979) and reinterpreted as a thomaseomyine (Steadman & Ray, 1982). The southern Netherlands Antilles show little biogeographical affinity with the Windward and Leeward Islands, and have close faunal and floral similarities to mainland...
South America (Hooijer, 1959, 1966, 1967; Trejo-Torres & Ackerman, 2001; Vázquez-Miranda et al., 2007; Voss & Weksler, 2009), and it has been hypothesized that *M. curazensis* is derived from a different mainland oryzomyine ancestor (McFarlane & Lundberg, 2002). A redescription of *M. curazensis* will form the basis for a future study in this series, and it is not considered further herein.

**GENUS OLIGORYZOMYS BANGS, 1900**

(Type species *Oryzomys navus* Bangs, 1899; = *Hesperomys fulvescens* Saussure, 1860)

*Oligoryzomys victus* (Thomas, 1898)

**Holotype:** NHM 97.12.26.1 (skin and skull).

**Examined material:** Holotype only.

**Diagnosis:** *Oligoryzomys victus* can be diagnosed by its small size, absence of jugal, absence of cranial crests, presence of large stapedial foramen and posterior opening of alisphenoid, absence of squamosal–alisphenoid groove and sphenofrontal foramen, presence of large sphenopalatine vacuities, presence of divided anterocone on M1, presence of two mesofossetti on M2, and presence of ectolophid on m1. This diagnosis, however, is similar to that for South American species of *Oligoryzomys*, and differentiation between insular and continental species requires further study (see below).

**Description:** Very small rodent (Table 1) with brown/ochre dorsal coloration, greyish white ventral pelage, and soft fur without subauricular patches (Fig. 8).
Hindfeet without well-developed natatory fringes and interdigital webs, and with tufts of ungual hairs at bases of claws on dII–dV. Plantar surface densely covered with distinct squamae distal to thenar pad (smooth heel); hypothenar pad large, interdigital pads small and fleshy (pads 1 and 4 displaced proximally relative to 2 and 3). Claw of dI extends to first half of first phalange of dII; claw of dV extends to first interphalangeal joint of dIV. Tail longer than combined length of head and body, sparsely haired, and covered with more or less conspicuous epidermal scales; it lacks a long tuft of terminal hairs, and is weakly bicoloured (dark above, pale below). The mammae are inguinal, abdominal, postaxial, and pectoral, and number eight.

Skull with delicate rostrum flanked by moderate zygomatic notches; interorbital region symmetrically constricted (amphoral shape), with rounded, unbeaded supraorbital margins; braincase without temporal, lambdoidal, and nuchal crests. Zygomatic plate without anterodorsal spinous process, its posterior margin lying anterior to the M1 alveolus. Jugal absent (maxillary and squamosal processes in contact). Nasal bones with blunt posterior margins, not extending posteriorly beyond lacrimals, which are equally sutured to maxillary and frontal bones. Posterior wall of the orbit smooth, frontosquamosal suture colinear with the frontoparietal suture. Parietals without lateral process, interparietal strap shaped. Incisive foramina with posterior border anterior to molar alveoli, and with parallel lateral borders. Bony palate between molar rows smooth and long, mesopterygoid fossa not extending anteriorly between maxillae. Posterolateral palatal pits not recessed in fossae. Bony roof of mesopterygoid fossa perforated by very large sphenopalatine vacuities. The alisphenoid strut is absent (buccinator–masticatory foramen and accessory foramen ovale are confluent), and the alisphenoid canal has a large anterior opening. Stapedial foramen and posterior opening of the alisphenoid canal large, squamosal–alisphenoid groove and sphenofrontal foramen absent (= carotid circulatory pattern 2 of Voss, 1988). Posterior suspensory process of the squamosal absent, postglenoid foramen large and rounded, and subsquamosal fenestra patent but covered by translucent membrane. Periotic exposed posteromedially between the ectotympanic and the basioccipital, extending anteriorly to carotid canal. Mastoid perforated by conspicuous posterodorsal fenestra. In the mandible, the capsular process of the lower incisor alveolus is well developed, and the superior and inferior masseteric ridges converge anteriorly as an open chevron below m1 (Fig. 9).

The upper incisors have smoothly rounded enamel bands, and the maxillary tooth rows are parallel. The
molars are bunodont, with labial flexi enclosed by a cingulum, and longitudinal flexi not overlapping. M1 anterocone divided into anterolabial and anterolinguinal conules by deep anteromedian flexus; anteroloph well developed, separated from anterocone by persistent anteroflexus; protostyle absent; mesolophs present on all upper molars; paracone connected by enamel bridge to anterior moiety of protocone; median mure connected to protocone. M2 protoflexus absent; mesoflexus present as two internal fossetti; paracone without an accessory loph. M3 with posteroloph and large hypoflexus (Fig. 6C). m1 anteroconid without anteromedian flexid, but with anteromedian fossettid; anterolabial cingulum present on all lower molars; posterolophid present on m1, but absent on m2 and m3; ectolophid present on m1 and m2; mesolophid distinct on unworn m1 and m2; posteroflexid present on m3 (Fig. 7C).

Remarks: This species shares several characters with the other species of the genus *Oligoryzomys*, such as: small size; absence of jugal; smooth and amphoral supraorbital margins; absence of cranial crests; caudad-oriented foramen magnum; divided anterocone on M1; presence of posteroloph on M3; presence of large stapedial foramen and posterior opening of alisphenoid, and absence of squamosal–alisphenoid groove and sphenofrontal foramen (carotid circulation pattern 2 of Voss, 1988); and presence of large sphenopalatine vacuities. The last three characters are among the recovered synapomorphies for *Oligoryzomys* listed by Weksler (2006), and the present phylogenetic results (see below) provide the first cladistic corroboration of the placement of *O. victus* within that genus.

*Oligoryzomys victus* consistently differs from other studied species of *Oligoryzomys* in certain characters, such as the presence of two mesosossetti in M2, and presence of ectolophid on m1. However, the alpha taxonomy of the genus *Oligoryzomys* is among the most poorly known within the Sigmodontinae. Although a revision of the northern South American and Central American species (probable relatives of *O. victus*) is beyond the scope of this study, further morphological comparisons of *O. victus* with species of continental *Oligoryzomys* are still necessary to establish its status as a distinct species from mainland taxa. It is interesting to note that *O. victus* has apparently not been recorded from pre-Columbian archaeological sites on St. Vincent, in marked...
contrast to rice rat taxa on other Lesser Antillean islands. This raises the possibility that the species may represent a relatively recent human-assisted translocation to the Windward Islands from an unknown source population in mainland South America. However, it is important to note that *O. vicius* is substantially smaller in body size than other described Lesser Antillean rice rats, and so may not have been perceived as a valuable food item by pre-Columbian Amerindians. In addition, a few undescribed small-bodied rice rat specimens that may represent this species have been reported from Amerindian middens on the neighbouring islands of Carriacou and Grenada (Lippold, 1991; LeFebvre, 2007). Further investigation of archaeological sites in the southern Windward Islands, and detailed morphological studies of mainland *Oligoryzomys* species, are required to test these alternative hypotheses regarding the native distribution and status of *O. vicius*.

**Etymology:** From the Latin ‘*pennatus*’, winged or feathered, combined with ‘*mys*’, the standard suffix for mouse. In honour of Elizabeth S. Wing, to commemorate her extensive contributions to Caribbean zooarchaeology.

**Diagnosis:** Oryzomyine rodents with short and blunt nasals; dual articulation of lacrimal with maxillary and frontal; slightly convergent anterior interorbital region; subtle supraorbital crests; posterior margin of incisive foramen terminating immediately posterior to anterior margin of alveolus of M1; long bony palate (mesopterygoid fossa does not extend anteriorly between maxillary bones); well-developed capsular process in mandibular ramus; and single anterior masseteric crest. M1 with undivided anterocone and well-developed mesoloph, with anterior protocone–paracone crista; M2 without protoflexus, and mesoflexus with single internal fossette; M3 with developed mesoloph, but posteroloph absent or vestigial, and hypoflexus narrow and disappearing with moderate wear. m1 with enclosed anteromedian fossettids, but without anteromedian flexid; with small ectolophid

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**Figure 8.** Dorsal, lateral, and ventral views of *Oligoryzomys vicius* skin (NHM 97.12.26.1). Scale bar: 2 cm.

**GENUS PENNATOMYS GEN. NOV.**

*Type species:* *Pennatomys nivalis* gen. et sp. nov.
and ectostylid. Mesolophid and mesostylid present, connected to entoconid by lingual cingulum. All lower molars with anterolabial cingula. M1–M3 with three alveolar roots, m1 with four roots (including accessory), m2 with three roots, and m3 with two roots. Additional morphological information is provided under the species description below.

**Differences from other genera:** From the available material, *Pennatomys* does not seem to possess any remarkable anatomical feature that is not also shared with other oryzomyines. The combination of several traits, however, differentiates this taxon from all other oryzomyines. *Pennatomys* displays three synapomorphies for a ‘Nectomys’ subclade within clade D.

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*Figure 9.* Cranium and mandible of *Oligoryzomys victus* (NHM 97.12.26.1). Scale bar: 5 mm.
of the Oryzomyini (see Weksler, 2006): absence of protoflexus and presence of single mesofossette on M2 (Fig 10A, B), and single anterior masseteric crest (Fig. 10J). *Pennatomys* can be differentiated from all other members of the *Nectomys* subclade, including *Megalomys*, by a combination of the following characters: dual articulation of the lacrimal with the maxillary and frontal (other taxa have major articulation with the maxillary and frontal (other taxa have major articulation with the maxillary and frontal), absence of accessory root on M1 (labial accessory root present in other taxa), and absence of posteroloph (posteroloph present in other taxa). Additional character differentiation among the three described oryzomyine taxa from the Lesser Antilles (*Pennatomys*, *Megalomys*, and *O. victus*) is shown in Table 2.

**Pennatomys nivalis** gen. et sp. nov.

*Holotype:* NHM M 82452, right hemimandible with i1 and m1–3 (Fig. 10D).

*Type locality:* Hichmans (site GE-5 of Wilson, 2006), Saladoid-era Amerindian archaeological site, 100 BC–AD 600; test pit 14, spit 4/2, context 1363, sample BS 5402 (see Crosby, 2003 for specific site details); St. George, Gingerlands, Nevis, Federation of St. Kitts–Nevis.

*Paratypes:* Four hemimandibles (NHM M 82453, M 82454, M 82459, and M 82460) from test pit 14, spit 4/2, context 1363, sample BS 5402; one maxilla (NHM M 82455) from test pit 14, spit 4/1, context 1362, sample BS 5344; one maxilla (NHM M 82456), and one humerus and one femur (NHM M 82458), from test pit 14, spit 2/2, context 1362, sample BS 5319; paired frontals with associated left nasal (NHM M 82457) from test pit 14, spit 2/2, context 1362, sample DS 5322; one premaxilla with associated incisor (NHM M 82461) from test pit 14, spit 5, context 1363, sample BS 5407; all from Hichmans (Fig 10B, E).

![Figure 10.](image-url)
Examined specimens: In addition to the type series, additional dissociated craniodental and postcranial rice rat skeletal material was also examined from the archaeological sites of Sugar Factory Pier, St. Kitts (FLMNH-EAP 02510001-02510008; see Wing, 1973); and Golden Rock, St. Eustatius (FLMNH-EAP 05270001–05270005; see van der Klift, 1992).

Distribution: Known from late Holocene pre-Columbian zooarchaeological sites on the islands of St. Eustatius, St. Kitts, and Nevis.

Etymology: From the Latin ‘nivalis’, snowy. In reference to ‘Nuestra Señora de las Nieves’, ‘Our Lady of the Snows’, the early Spanish name for Nevis, apparently so-called because of misidentification of the clouds surrounding Mount Nevis.

Description: No complete or partial skulls known; cranial morphology based on dissociated elements (Fig. 10H–K). Nasals short, terminating anterior to or extending slightly further than the maxillary–frontal–lacral suture, and with blunt posterior margin. Premaxillaries extend posteriorly almost as far as nasals. Interorbital region slightly convergent anteriorly, with subtle supraorbital crests. Postorbital ridge apparently absent; frontosquamosal suture colinear with frontoparietal suture, dorsal facet of frontal not in contact with squamosal. Zygomatic plate broad, with anterodorsal margin smoothly rounded and conspicuously anterior to superior maxillary root of zygoma, and posterior margin situated slightly anterior to alveolus of M1. Posterior margin of incisive foramen terminates immediately posterior to anterior margin of alveolus of M1. Posterior margin of incisive foramen terminates immediately posterior to anterior margin of alveolus of M1. Bony palate long and relatively flat, with shallow lateral excavations; mesopterygoid fossa does not extend anteriorly between maxillary bones.

Capsular process of lower incisor alveolus present in the mandible, situated either ventral to the coronoid process or between the coronoid process and the condyle process. Superior and inferior masseteric ridges often conjoined anteriorly as single crest, which terminates ventral to anterior margin of m1. Upper incisors with smoothly rounded enamel bands. Maxillary tooth rows parallel. Molars bunodont and brachyodont, with labial flexi enclosed by a cingulum; labial and lingual flexi meet at midline.

Table 2. Condition of morphological characters for West Indian rice rat taxa

<table>
<thead>
<tr>
<th>Character trait</th>
<th>Pennatomys</th>
<th>Megalomys</th>
<th>Oligoryzomys</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size</td>
<td>Medium</td>
<td>Large</td>
<td>Small</td>
</tr>
<tr>
<td>Pedal plantar pads</td>
<td>Unknown</td>
<td>Hypothenar absent or vestigial, digitals large</td>
<td>Hypothenar present, digitals small</td>
</tr>
<tr>
<td>Lacrimal articulation</td>
<td>Equal maxillary and frontal</td>
<td>Primarily with maxillary</td>
<td>Equal maxillary and frontal</td>
</tr>
<tr>
<td>Supraorbital shape</td>
<td>Slightly convergent anteriorly with weak crest</td>
<td>Convergent anteriorly with well-developed crest</td>
<td>Squared, smooth margins</td>
</tr>
<tr>
<td>Posterior margin of zygomatic plate</td>
<td>Slightly anterior to M1 alveolus</td>
<td>Approximately even with M1 alveolus</td>
<td>Anterior to M1 alveolus</td>
</tr>
<tr>
<td>Carotid circulation pattern</td>
<td>Unknown</td>
<td>III*</td>
<td>II*</td>
</tr>
<tr>
<td>Anterior section of masseteric crests</td>
<td>Joined</td>
<td>Separated</td>
<td>Separated</td>
</tr>
<tr>
<td>Labial accessory root on M1</td>
<td>Absent</td>
<td>Present</td>
<td>Unknown†</td>
</tr>
<tr>
<td>Roots on m2</td>
<td>3</td>
<td>3</td>
<td>Unknown†</td>
</tr>
<tr>
<td>Roots on m3</td>
<td>2</td>
<td>3</td>
<td>Unknown†</td>
</tr>
<tr>
<td>Anteromedian flexus on M1</td>
<td>Absent</td>
<td>Present, shallow</td>
<td>Present, deep</td>
</tr>
<tr>
<td>Mesofossette on M2</td>
<td>Single</td>
<td>Single</td>
<td>Double</td>
</tr>
<tr>
<td>Posteroloph on M3</td>
<td>Absent</td>
<td>Present</td>
<td>Present</td>
</tr>
<tr>
<td>Anterolophid on m2 and m3</td>
<td>Present</td>
<td>Present</td>
<td>Absent</td>
</tr>
</tbody>
</table>

Megalomys characters are based on Megalomys luciae and Megalomys desmarestii only.

*Pattern II, stapedial foramen present, sphenofrontal foramen absent; pattern III, stapedial foramen and sphenofrontal foramen absent.

†Other species of Oligoryzomys do not have a labial accessory root on M1, and have only two roots on m2 and m3.
enamel overlaps. All upper molars with three roots (accessory labial root of M1 absent). M1 with two large roots and two central accessory roots, M2 with one large posterior and two smaller anterior roots, and M3 with one large anterior and one large posterior root (Fig 10A-G).

M1 anterocone undivided and well developed (equal in length and width to protocone–paracone). Internal fold of procingulum circular, medially situated, and eliminated by heavy wear in older specimens. Anteroloph reaching labial margin, separated from anterocone by short anteroflexus, which extends to internal fold and disappears with slight wear. Protostyle absent; protoflexus broad and deep, with large, gently squared apex. Paraflexus transversely oriented from labial wall, deflected posteriorly close to crown midline, and extends along entire length of paracone. Mesoloph well developed; mesoflexus short, transverse, with slightly expanded apex. Paracone connected by enamel bridge to anterior or middle moiety of protocone; median mure connected to protocone. Hypoflexus slightly deeper than protoflexus, with triangular apex. Metaflexus deep, crescentic, extending over halfway across crown, almost reaching posterior wall, and reaching hypoflexus. Posteroflexus small, obliquely anterolingual notch at posterior margin of metacone. Very small internal fossette situated between posteroflexus and posterolabial margin of metaflexus, sometimes discernible on worn teeth.

M2 protoflexus absent; mesoflexus present as single internal fossette; paracone without accessory loph. Paraflexus slightly posterolinguad, extending halfway across crown. Mesoflexus very reduced, defining small triangular mesoloph. Mesoflexus internal fossette usually slightly anterolingual and anteroposteriorly constricted medially. Hypoflexus very deep, sometimes with slightly rounded, expanded apex, and anteroposteriorly shorter than on M1. Metaflexus crescentic, deep and broad, extending well over halfway across crown. Posteroflexus very small and faint, apparently apically bifurcated.

M3 with developed mesoloph, but posteroloph absent (or vestigial; joined to metacone with little wear). Hypoflexus narrow and extremely small in specimens with little wear, disappearing with moderate to heavy wear. Paraflexus slightly posterolinguad, broad and deep on unworn teeth, becoming greatly reduced by wear; can form separate small internal fold adjacent to apex. Mesoflexus large, transverse; can become isolated as an island. Paracone transverse, anteroposteriorly short or triangular; almost isolated by paraflexus and mesoflexus. Metaflexus posterolinguad, anteriorly convex, extending 75% of the distance across crown, often reaching hypoflexus region; can coalesce distally with diminutive posteroflexus to develop bifurcated apex.

m1 with enclosed anteroflexid and anteromedian fossettids crowded together, each with an anterior extension close to the crown midline; coalescing into a single transverse fossettid with minor wear. Anterolabial cingulum present, fused with anterolabial surface of protoconid. Protostyle narrowly compressed labially, with apex bifurcated, and obliquely anterolingual, almost reaching anterior fossettids; can become isolated internal island with moderate wear. Hypoflexid transverse broad, deep, and open, extending halfway across crown. Small ectolophid and ectostylid present. Metaflexid small, narrow, anteroposteriorly elongated or obliquely anterolingual; becomes isolated island with slight wear, and absent with moderate wear. Metafossetid deep and open, coalesced with deep and curved mesoflexid with slight wear, to almost completely outline the metaconid. Mesolophid and mesostylid present, connected to entoconid by lingual cingulum. Small entoflexid only present on unworn teeth. Posteroflexid and posterofossetid coalesce with slight wear, and outline entoconid. Posterofossetid deep, slightly expanded anteriorly; apex deflected posteriorly. Posteroflexid relatively straight, obliquely anterolabial. Metaconid and entoconid subquadrate; protoconid and hypoconid subtriangular.

m2 with shallow protoflexid, occupying 30% of the crown width, and obliquely anterolingual at 45°; defines shelf-like anterolabial cingulum. Hypoflexid broad and deep, but without apical bifurcation. Metaflexid small, becoming transverse island in anterolingual corner of metaconid. Mesolophid present, joined to entoconid by lingual cingulum. Mesoflexid almost completely circumscribes metaconid, very broad and deep, extending over half of the crown width, and widening gradually away from lingual wall; apex coalesced with transversely elliptical first internal fold. Posteroflexid very deep, even with slight wear; extends to midline, becoming more transverse with wear. Entoflexid slightly obliquely posterolabial, with distinct short medial anterior extension, extends labially just beyond crown midline.

Anterolabial cingulum and protoflexid of m3 similar to condition in m2, but with protoflexid slightly more transverse and shallow. Hypoflexid prominent, occupying over half of the crown width, but anteroposteriorly shorter than in m2; gently curved, or with anterior margin curved and posterior margin straight and obliquely anterolabial at 45°. Metaflexid small, transverse island in anterolingual corner of metaconid; disappears with slight wear. Mesoflexid long, deep, occupying 70% of the crown width, and curving around metaconid, with slight bifurcation at medial apex. Entoconid very small and subtriangular. Entoflexid and posteroflexid distinct only on unworn teeth, otherwise coalesced. Entofolexid 50–60% of the crown

width, and 35–40% of the crown length; obliquely posterolabial at almost 45°; with anterior extension close to lingual margin. Posteroflexid small and transverse.

Remarks: Our description of a new genus for this taxon is based on the morphological distinctiveness of the new material, both in size (Tables 1, 3) and in qualitative craniodental characters (Table 2), and in the results of phylogenetic analyses. The corroboration of this hypothesis awaits the discovery of additional material that would allow for a more complete phylogenetic assessment.

Although preliminary analysis of zooarchaeological material from Hichmans suggested that two rice rat size morphs might be found at the site (Nokkert, 2002), more detailed morphological and morphometric investigation indicates that only a single rice rat taxon is present (Table 3). The slight variation in body size of some specimens (e.g. NHM M 82459; = ‘Megalomys’ of Nokkert, 2002) is associated with increased age and extreme tooth wear.

The islands of St. Eustatius, St. Kitts, and Nevis share a submerged bank that would have formed a single, larger island during low sea-level stands in Quaternary glacial periods (Pregill et al., 1994; Lambeck & Chappell, 2001). They can therefore be considered as a single biogeographic unit, with only episodic barriers to gene flow between different populations of a single species. No morphological qualitative character was observed to vary between the three island samples. However, minor but statistically significant differences in maxillary and mandibular tooth-row length (interpreted as an indirect measure of overall body size) were observed between different sampled island populations of *Pennatomys* from the St. Kitts Bank. The Nevis sample is significantly smaller in mandibular tooth-row length than the St. Kitts sample, and is significantly smaller in maxillary tooth-row length than both the St. Kitts and St. Eustatius samples (one-way ANOVA: maxillary tooth row length, $F = 11.14, P < 0.001$; mandibular tooth row length, $F = 5.18, P = 0.008$; Table 3). This pattern may reflect genuine biological differences between the three populations, possibly associated with the ‘island rule’ (terrestrial vertebrate body mass increases with increasing island area; Burness et al., 2001), as St. Kitts (174.2 km$^2$) is approximately twice the size of Nevis (92.5 km$^2$). However, this pattern is not straightforward, as St. Eustatius, the smallest of the three islands (21 km$^2$), contains rice rats that do not differ significantly in body size from the St. Kitts population by either tooth-row measurement. As all examined material was retrieved from archaeological middens, these observed size differences might also be explained by differential patterns of Amerindian exploitation of rice rats on different islands. This alternative hypothesis is supported by the observation that femora and humeri with completely fused epiphyses were common, and maxillary and mandibular dentition was moderately/severely worn in all rice rat specimens in the St. Kitts sample, whereas although some mature individuals were also present in samples from the other islands (see above), fused limb bones were rare or absent, and less than 50% of tooth rows exhibited strong wear in the St. Eustatius and Nevis samples, indicating that the St. Kitts sample consisted of older rice rat individuals. Longer-term temporal patterns of body size change in rice rat populations apparently driven by Amerindian overexploitation of larger individuals have also been identified on other neighbouring Lesser Antillean islands (Nokkert, 1999; see below). Because of these difficulties in interpreting minor body size differences in otherwise morphologically uniform rice rats from sites across the St. Kitts Bank, all three island populations are interpreted here as representing the same species.

Although *P. nivalis* gen. et sp. nov. is an abundant component of Saladoid and post-Saladoid archaeological sites on the St. Kitts Bank, there are no confirmed records of its survival in the European historical period. The Englishman George Percy, who stopped at Nevis around 1606, reported that his men went hunting on the island and ‘got great store of Conies’ (Wilson, 2006), but this record almost certainly refers to agoutis (*Dasyprocta*), which had been translocated across the Windward and Leeward Islands from

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**Table 3. Tooth row measurements of *Pennatomys nivalis* gen. et sp. nov. populations from Nevis, St. Eustatius, and St. Kitts (mm)**

<table>
<thead>
<tr>
<th></th>
<th>Nevis</th>
<th>St. Eustatius</th>
<th>St. Kitts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maxillary molar row (occlusal)</td>
<td>6.12 (5.6–6.4)</td>
<td>6.39 (6.1–6.7)</td>
<td>6.57 (6.4–6.7)</td>
</tr>
<tr>
<td>SD = 0.249, n = 14</td>
<td>SD = 0.188, n = 14</td>
<td>SD = 0.137, n = 6</td>
<td></td>
</tr>
<tr>
<td>Mandibular molar row (occlusal)</td>
<td>6.61 (5.9–7.1)</td>
<td>6.65 (6.4–6.9)</td>
<td>6.84 (6.4–7.4)</td>
</tr>
<tr>
<td>SD = 0.237, n = 41</td>
<td>SD = 0.141, n = 22</td>
<td>SD = 0.240, n = 13</td>
<td></td>
</tr>
</tbody>
</table>

Size range, standard deviation, and sample size given for each measurement.
mainland South America by Amerindians in earlier centuries (Newsom & Wing, 2004). Sir Henry Colt reported in 1631 that animals specifically identified as rats provided ‘good meat’ on St. Kitts (Harlow, 1925), and in 1720 the Reverend William Smith claimed that ‘in Nevis some people do eat Rats, wrapping them up in Banano-leaves to bake them as it were under warm Embers’ (Merrill, 1958). However, black rats \((\text{Rattus rattus})\) have also been eaten in many parts of the West Indies during recent history (Merrill, 1958; Higman, 2008), and these historical records may conceivably also refer to exotic murids rather than endemic rice rats. Intriguingly, there are several reports of unusual-looking rats occurring on Nevis into recent times, and being eaten by inhabitants of the island until at least the 1930s (J. Johnson, Nevis Historical and Conservation Society, pers. comm.).

**CLADISTIC ANALYSIS**

We scored \(M. \text{desmarestii}\) for 81 (83%), \(M. \text{luciae}\) for 71 (72%), \(O. \text{victus}\) for 73 (74%), and \(P. \text{nivalis}\) gen. et sp. nov. for 49 (50%) morphological characters. \(M. \text{desmarestii}\) and \(O. \text{victus}\) were scored for most external, cranial, skeletal, and dental characters, whereas \(M. \text{luciae}\) was scored only for dental and cranial characters, and \(P. \text{nivalis}\) gen. et sp. nov. was scored for dental, mandibular, and very few cranial characters. By comparison, other oryzomyines, previously scored in Weksler (2006), ranged in completeness from 32% (\(\text{Amphinectomys}\)) to 100% (two taxa).

Parsimony analysis of the concatenated matrix of morphological and molecular (\(\text{irbp}\)) data sets resulted in four trees (1245 steps; consistency index, CI = 0.37; retention index, RI = 0.64), the strict consensus of which recover the same overall phylogenetic structure of a previous analysis of the oryzomyine data set (Weksler, 2006) with the addition of the newly scored West Indian rice rat taxa. \(M. \text{desmarestii}\) is recovered as a sister group of the clade containing \(\text{Nectomys}\) and \(\text{Sigmodontomys}\), whereas \(O. \text{victus}\) is recovered as the most basal scored member of the genus \(\text{Oligoryzomys}\). \(\text{Pennatonomys}\) is recovered as a sister group of the clade containing \(\text{Amphinectomys}\), \(\text{Aegialomys}\), \(\text{Nesoryzomys}\), \(\text{Melanomys}\), and the \(\text{Megalomys}\) plus \(\text{Nectomys–Sigmodontomys}\) clade. Nodal support for most clades in the tree is low (as also recovered by Weksler, 2006), but is high for the \(M. \text{luciae–M. \text{desmarestii}}\) node (jackknife = 99%; BS = 6). The placement of \(O. \text{victus}\) as the most basal scored member of \(\text{Oligoryzomys}\) also received moderate support (jackknife = 62%; BS = 2), but nodes in the tree area of \(\text{Pennatonomys}\) are uniformly low. Trees constrained for inclusion of the new material in \(\text{Megalomys}\) are six steps longer, a difference that is again not significant in the Kishino–Hasegawa test.

**DISCUSSION**

**Phylogenetic results**

Previous proposals for relationships of \(\text{Megalomys}\) are rejected by our analyses. In the most comprehensive comparative study of West Indian rice rat material available to date, the unpublished thesis of Ray (1962), \(\text{Megalomys}\) was considered to be closely related to \(\text{Mindomys hammondi}\) (then assigned to \(\text{Oryzomys}\); see Weksler et al., 2006 for the current oryzomyine classification). In fact, Ray (1962) included \(\text{Mindomys hammondi}\) as a member of the subgenus \(\text{Megalomys}\) within \(\text{Oryzomys}\) (see also Herskovitz, 1970). However, this phylogenetic hypothesis is falsified by our analyses. \(\text{Mindomys}\) is never recovered within clade D (see also Weksler, 2006), where \(\text{Megalomys}\) is robustly placed. Trees containing \(\text{Mindomys}\) and \(\text{Megalomys}\) as sister taxa are nine steps longer than the most-parsimonious tree (the difference is not significant in Kishino–Hasegawa tests, but both taxa lack molecular data).

McFarlane & Lundberg (2002), in turn, rejected the close relationship between \(\text{Megalomys}\) and \(\text{Mindomys hammondi}\) on biogeographic grounds, and suggested that \(\text{Megalomys}\) was more closely related to an oryzomyine taxon inhabiting the Caribbean coast of South America. Our results also do not corroborate
this scenario, as *S. aphrastus*, the recovered sister taxon of *Megalomys*, is a species known from scattered Transandean localities in Ecuador, Panama, and Costa Rica (McCain et al., 2007). The phylogenetic position of *S. aphrastus* is controversial (Weksler, 2006; McCain et al., 2007), and the present hypothesis of *Megalomys* plus *S. aphrastus* needs corroboration from additional data. Nevertheless, the
recovered close relationship of Mealomys to Nectomys and related taxa (e.g. Sigmodontomys and Melanomys) has been suggested by several authors (e.g. Allen, 1912; Musser & Carleton, 2005).

The newly described genus Pennatomys is also recovered within clade D in our analyses, but interestingly Pennatomys and Mealomys are not recovered as sister groups within this clade. This suggests that the Lesser Antillean island chain was colonized by multiple over-water dispersal events by representatives of clade D. However, support for the phylogenetic position of Pennatomys within clade D is low, and a more detailed understanding of the morphological character state combinations displayed by other undescribed rice rat taxa from the Windward and Leeward Islands is required to investigate this phylogenetic hypothesis further.

Our analyses corroborate the inclusion of O. victus in the genus Oligoryzomys, as proposed by several researchers of oryzomyine systematics. Its basal position in the genus indicates its distinctiveness from the other scored species, but further alpha taxonomy studies are necessary to corroborate its status in relation to continental Oligoryzomys species from Venezuela and Panama (e.g. Oligoryzomys fulvescens).

**Evolution, Biogeography, and ecology**

Mealomys and Pennatomys belong to a clade of oryzomyines (clade D of Weskler, 2006) that has undergone a remarkable radiation throughout the oceanic and continental shelf islands of the Neotropical region, including taxa in the Galápagos (Aegialomys and Nesoryzomys; Patton & Hafner, 1983), Fernando de Noronha (Noronhomys; Carleton & Olson, 1999), Curacao (Oryzomys; McFarlane & Debrot, 2001; Voss & Weskler, 2009), Trinidad (Nectomys; Hershkovitz, 1944), and Jamaica (Oryzomys; Thomas, 1898; Musser & Carleton, 2005), as well as the Windward and Leeward Islands. Several taxa within clade D (e.g. Lundomys, Oryzomys, Holochilus, Nectomys, Pseudoryzomys, and Sigmodontomys) have markedly semi-aquatic adaptations, such as the development of natatory fringes and interdigital membranes, and are associated with marshes, rivers, or streams (Stein, 1988; Santori et al., 2008). This ecology may have predisposed members of the clade for over-water flotsam dispersal from mainland South America to the insular Caribbean, as they probably have an increased likelihood of becoming associated with rafts of vegetation that could get carried into ocean currents, notably the south-east–north-west surface current flow of the North Atlantic Gyre (see Hedges, 2006).

In contrast, West Indian rice rats do not appear to have been semi-aquatic. Minimal information is recorded in contemporary historical accounts about the ecology of now-extinct rice rat species (Allen, 1942), but some clues are provided by the foot morphology of Mealomys (Stein, 1988; Voss, 1988; Weskler, 2006). Mealomys possesses a distinctly different plantar morphology from closely related oryzomyines, and does not display well-developed natatory fringes or interdigital membranes, indicating that representatives of the genus were terrestrial rather than semi-aquatic. This may reflect the relative lack of large rivers and streams on islands in the Lesser Antilles. Instead, Mealomys possesses other morphological features, such as a long tail and well-developed large, fleshy digital pads, which are found in arboreal or semi-arboreal (scansorial) rodents (e.g. Oecomys among oryzomyines). Several other extinct medium- to large-bodied rodents from the insular Caribbean are also believed to have been arboreal or scansorial, on the basis of skeletal adaptations, and all of the surviving West Indian rodents show varying degrees of arboreality (Turvey et al., 2006).

Phylogenetic analysis of the extinct West Indian rice rats also provides new insights into the nature of body size evolution in these insular oryzomyines, and challenges previously held assumptions about the evolution of Mealomys. The body size of Mealomys is among the largest of all sigmodontines, and this genus has been interpreted by several authors as a classic example of autapomorphic gigantism or ‘island gigantism’ derived from a small-bodied ancestor (e.g. Steadman & Ray, 1982; McFarlane & Lundberg, 2002). The closest relatives of Mealomys, however, are also some of the largest living oryzomyines (Weskler, 2006). Sigmodontomys aphrastus, the sister taxon of Mealomys, is a medium-sized rodent (head–body length = 152 mm; McCain et al., 2007), but some specimens of Nectomys are recorded as having a head–body length of 254 mm (Weskler, 2006). This suggests that the alternative hypothesis of phyletic gigantism may also explain the large body size of Mealomys, and emphasizes that phylogenetic analyses are required before making assumptions about body size evolution in insular taxa.

**Timing and causation of the ‘forgotten’ rice rat mass extinction**

The only native Quaternary non-oryzomyine land mammal known from the Windward and Leeward Islands, the giant heptaxodontine rodent Amblyryhiza inundata, is believed to have died out as a result of catastrophic habitat loss associated with Late Pleistocene sea level changes, which reduced island area on the Anguilla Bank before humans colonized the West Indies (McFarlane et al., 1998). Conversely, the region’s rice rat fauna survived into the period of...
human colonization of the West Indies during the late Holocene. *Megalomys desmarestii*, *M. luciae*, *O. victus*, and possibly also the Nevis and St. Kitts populations of *P. nivalis* gen. et sp. nov. and the undescribed rice rat from Barbados are all known from historical-era records (Schomburgh, 1848; Feilden, 1890; Harlow, 1925; Allen, 1942; Merrill, 1958; Marsh, 1984, 1985; Lorvelec et al., 2007), and all other taxa are known from Amerindian midden deposits (Fig. 1; Table 4). The disappearance of the Lesser Antillean rice rats therefore constitutes part of the wider-scale series of land mammal extinctions across the West Indies that were driven by direct or indirect human impacts during the historical era and recent prehistory. However, the dynamics, drivers, and timing of these extinctions remain poorly understood (Pregill & Olson, 1981; Morgan & Woods, 1986; MacPhee et al., 1989; Turvey et al., 2007; MacPhee, 2009; Turvey, 2009).

Rice rats were heavily exploited by prehistoric Amerindians, and constituted a significant component of their dietary intake (Wing, 2001a, b; Newsom & Wing, 2004). Prehistoric human impacts on the region’s terrestrial environments escalated over time, with substantial population growth as evidenced by an increase in the number and size of archaeological sites occurring between AD 500 and AD 1000 (Keegan, 2000; Wilson, 1997, 2001; Newsom & Wing, 2004), and anthropogenic hunting pressures on rice rats and other species may also have increased during this period. Some Amerindian sites show decreases in rice rat abundance over time (e.g. Mill Creek, Antigua; Wing et al., 1968) or reductions in rice rat body size over time (e.g. Anse des Pères, St. Martin; Nokkert, 1999), supporting the hypothesis of prehistoric over-exploitation and early preferential removal of larger individuals (cf. Lomolino et al., 2001). However, other archaeological sites show variable fluctuations in rice rat abundance, which may reflect cultural or taphonomic biases rather than true ecological patterns, and rice rats typically persist into the youngest stratigraphical levels and even increase in abundance over time in several sites (Jones, 1985; Newsom & Wing, 2004). There is little evidence that Amerindian environmental impacts led to the prehistoric extinction of any West Indian rice rats, and radiocarbon dates available for archaeological horizons from different islands show that many taxa definitely survived until close to the time of first European arrival in the region around 500 years ago (Table 4).

West Indian terrestrial ecosystems have experienced a range of human impacts during the historical era, including extensive forest clearance and associated habitat degradation, and the introduction of a wide range of exotic species. Identifying the primary causative factors for most Lesser Antillean rice rat extinctions remains impossible in the absence of historical last-occurrence dates for most taxa, to indicate how long they persisted after European arrival. However, although these rice rats evolved in the presence of avian predators, notably a radiation of now-extinct large tytonid owls apparently specialized to feed on oryzomyine rodents (Steadman & Hilgartner, 1999), the lack of native mammalian predators or competitors throughout the region suggests that they would have been extremely vulnerable to the introduction of exotic mammals. The last known records for *M. desmarestii*, *M. luciae*, and *O. victus* all date from around the 1880s or 1890s (Table 4), and although several authors have suggested that *M. desmarestii* was wiped out by the eruption of Mount Pelée in 1902 (e.g. Allen, 1942; Balouet & Alibert, 1990; Flannery & Schouten, 2001), it is more likely that all of these extinction events on islands with long volcanic histories were instead primarily driven by the introduction of the Indian mongoose (*Herpestes javanicus*) to the islands between 1889 and 1900 (Horst et al., 2001). However, it should be noted that *M. desmarestii* was already considered to be rare by some contemporary observers as early as 1820 (Lorvelec et al., 2007). Most or all of the other Lesser Antillean rice rat extinctions may have been caused by the accidental introduction of black rats across the insular Caribbean shortly after European arrival. Although further data are required to clarify the ecological mechanism(s) by which black rats and other exotic *Rattus* species act as extinction drivers, they have been implicated in the disappearance of small mammals (including other insular rice rats) and many other taxa on island systems across the world through competition, predation, disease transmission, and habitat modification (Harris et al., 2006; Towns et al., 2006; Harris & Macdonald, 2007; Turvey et al., 2007; Harris, 2008; Drake & Hunt, 2008; Wyatt et al., 2008).

Although the taxonomy and species status of the Lesser Antillean rice rats remains extremely confused, the Windward and Leeward Islands alone have lost approximately 20 separate island populations of rice rats during the historical period, many of which may have represented distinct species. This dramatic level of extinction is equivalent in magnitude to the much more widely known historical-era loss of marsupials and rodents in Australia (MacPhee & Flemming, 1999; Johnson, 2006; Turvey, 2009), but comprises only a part of the much greater series of recent land mammal extinctions documented so far from the West Indies. This highlights the vulnerability of insular mammal species, not only ancient ‘relict’ lineages (Purvis et al., 2000; Isaac et al., 2007), but also more evolutionarily recent insular radiations, and emphasizes the need for further investigation.
Table 4. Last-occurrence dates for extinct rice rats from the Windward and Leeward Islands, based on historical records or calibrated radiometric dates from archaeological or palaeontological horizons containing rice rat material

<table>
<thead>
<tr>
<th>Species</th>
<th>Island</th>
<th>Historical record</th>
<th>Site</th>
<th>Calibrated radiometric date, 2σ</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Megalomys desmarestii</em></td>
<td>Martinique</td>
<td>c. 1897</td>
<td></td>
<td></td>
<td>Allen (1942)</td>
</tr>
<tr>
<td><em>Megalomys luciae</em></td>
<td>St. Lucia</td>
<td>pre-1881</td>
<td></td>
<td></td>
<td>Allen (1942)</td>
</tr>
<tr>
<td><em>Oligoryzomys victus</em></td>
<td>St. Vincent</td>
<td>1892</td>
<td></td>
<td></td>
<td>Allen (1942)</td>
</tr>
<tr>
<td>Undescribed taxon (?<em>Megalomys audreyae</em> or ‘<em>Ekbletomys hypenemus’)</em></td>
<td>St. Kitts</td>
<td>1631?</td>
<td>Bloody Point</td>
<td>AD 660–1115</td>
<td>J.E. Robb, pers. comm.</td>
</tr>
<tr>
<td>Undescribed taxon</td>
<td>Antigua</td>
<td></td>
<td>Indian Creek</td>
<td>AD 900–1100</td>
<td>Rouse &amp; Morse (1999)</td>
</tr>
<tr>
<td>Undescribed taxon</td>
<td>Barbados</td>
<td>1848?</td>
<td></td>
<td></td>
<td>Schomburgk (1848), Ray (1962), Feilden (1890), Marsh (1984, 1985)</td>
</tr>
<tr>
<td>Undescribed taxon (large morph)</td>
<td>Carriacou</td>
<td></td>
<td>Grand Bay</td>
<td>AD 390–1280</td>
<td>LeFebvre (2007); S.M. Fitzpatrick, pers. comm.</td>
</tr>
<tr>
<td>Undescribed taxon (small morph)</td>
<td>Grenada</td>
<td></td>
<td>Pearls</td>
<td>37 BC–AD 533</td>
<td>Havisier (1997)</td>
</tr>
<tr>
<td>Undescribed taxon</td>
<td>Guadeloupe</td>
<td></td>
<td>Morel</td>
<td>AD 21–881</td>
<td>Havisier (1997)</td>
</tr>
<tr>
<td>Undescribed taxon</td>
<td>La Desirade</td>
<td></td>
<td>Petite Rivièrè</td>
<td>AD 600–1400</td>
<td>de Wael (1996)</td>
</tr>
<tr>
<td>Undescribed taxon</td>
<td>Marie Galante</td>
<td></td>
<td>Taliseronde</td>
<td>AD 350–665</td>
<td>Havisier (1997)</td>
</tr>
<tr>
<td>Undescribed taxon (large morph)</td>
<td>Montserrat</td>
<td></td>
<td>Trants</td>
<td>774 BC–AD 622</td>
<td>Petersen (1996)</td>
</tr>
<tr>
<td>Undescribed taxon (small morph)</td>
<td>Montserrat</td>
<td></td>
<td>Trants</td>
<td>774 BC–AD 622</td>
<td>Petersen (1996)</td>
</tr>
<tr>
<td>Undescribed taxon</td>
<td>Saba</td>
<td></td>
<td>Kelbey’s Ridge II</td>
<td>AD 1290–1400</td>
<td>Hoogland (1996)</td>
</tr>
</tbody>
</table>

Calibrated dates were calculated from conventional ¹⁴C ages (years BP) for *Megalomys audreyae* and for undescribed taxa from Grenada, Guadeloupe, and Marie Galante using OxCal 4.0 (Bronk Ramsey, 1995, 2001). The calibrated date for *M. audreyae* is based on a direct radiocarbon date from subfossil rice rat material; all other radiometric last-occurrence dates are based on calibrated dates of stratigraphically associated material from archaeological sites.
and description of the region’s poorly known extinct mammal fauna.

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Nexus file of morphological and molecular matrices.

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