



NEW RODENTS (CRICETIDAE) FROM THE NEOGENE OF CURAÇAO AND BONAIRE, DUTCH ANTILLES

by JELLE S. ZIJLSTRA^{1,2*}, DONALD A. McFARLANE³, LARS W. VAN DEN HOEK OSTENDE² and JOYCE LUNDBERG⁴

¹914 Rich Avenue #3, Mountain View, CA 94040, USA; e-mail: jelle.zijlstra@gmail.com

²Department of Geology, Naturalis Biodiversity Center, PO Box 9517, Leiden, RA 2300, the Netherlands; e-mail: dmcfarla@jsd.claremont.edu

³W. M. Keck Center, The Claremont Colleges, 925 North Mills Avenue, Claremont, CA 91711-5916, USA; e-mail: lars.vandenhoekestende@ncbnaturalis.nl

⁴Department of Geography and Environmental Studies, Carleton University, Ottawa, ON K1S 5B6, Canada; e-mail: joyce_lundberg@carleton.ca

*Corresponding author

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Abstract: *Cordimus*, a new genus of cricetid rodent, is described from Neogene deposits on the islands of Curaçao and Bonaire, Dutch Antilles. The genus is characterized by strongly cuspidate molars, the presence of mesolophids in most upper molars and the absence of mesolophids in lower molars. Similarities with the early cricetid *Copemys* from the Miocene of North America coupled with apparent derived characters shared with the subfamily Sigmodontinae suggest that *Cordimus* may be close to the root of the sigmodontine lineage, a possibility that remains to be tested through explicit phylogenetic analysis. Three species are recognized on the basis of size and details of molar morphology. *Cordimus hooijeri* sp. nov. is

described from Bonaire on the basis of Holocene owl pellet material that consists of dentaries and postcranial material only. This species is presumed to be extinct, but focused surveys are needed to confirm this hypothesis. *Cordimus debuisonjei* sp. nov. and *Cordimus raton* sp. nov. are described from deposits on Tafelberg Santa Barbara in Curaçao. Although the age of these deposits is not known, they are most likely of late Pliocene or early Pleistocene age. Both are represented by numerous isolated molars and some osteological material.

Key words: biogeography, Holocene, insular rodents, Pleistocene, Sigmodontinae.

CRICETIDAE, including voles, lemmings, hamsters, deer mice, wood rats, rice rats, vesper mice and many other species, is the most diverse mammalian family of the Western Hemisphere and one of the most widely distributed (Wilson and Reeder 2005). Its most diverse subfamily is Sigmodontinae, a mainly South American group that since the beginning of the Great American Biotic Interchange has become a major component of the South American mammal fauna (Smith and Patton 1999). Sigmodontines, already recognizable as members of the extant tribes Akodontini and Phyllotini, first appear in the South American fossil record in the latest Miocene and Pliocene of Argentina (Pardiñas *et al.* 2002). The origin and historical biogeography of this subfamily has been the subject of much debate, as reviewed by Pardiñas *et al.* (2002). This debate has centred on the timing of origin of the subfamily (as early as the early Miocene or as late as the Pliocene), the number of sigmodontine lineages that originally entered South America (one or several) and the relationships of certain fossils from the Neogene of North America (*Bensonomys*, *Jacobsomys*, *Abelmoschomys* and *Symmetrodontomys*), which have been interpreted either

as close to specific extant sigmodontine tribes (e.g. Czaplewski 1987) or as distant relatives of sigmodontines (e.g. Steppan 1995). Molecular data (e.g. Steppan *et al.* 2004) indicate that the bulk of sigmodontine diversity results from a rapid radiation at the base of a clade that Steppan *et al.* (2004) called Oryzomyalia, which includes all sigmodontines that have been sampled genetically except for members of the tribes Sigmodontini and Ichthyomyini. Their molecular clock model suggests that the common ancestor of *Sigmodon* and Oryzomyalia lived about 12–13 Ma and that the radiation of Oryzomyalia took place 6–9 Ma. Steppan *et al.* (2004) suggested that the radiation of Oryzomyalia coincided with the arrival of an ancestral oryzomyalian in South America. South American representatives of Sigmodontini and Ichthyomyini, which are both diverse in North America, would have been the result of separate invasions, and North American oryzomyalians (mainly derived members of the oryzomyalian tribe Oryzomyini; Weksler 2006) would derive from a relatively recent invasion of North America from South America. Such a biogeographical scenario implies that alleged North American sigmodontines such as

Bensonomys are not closely related to extant sigmodontines and that basal sigmodontines would have occurred in or near northern South America during the Late Miocene.

During the Neogene, several lineages of cricetids, mainly oryzomyines, entered the islands of the West Indies by overwater dispersal, resulting in the evolution of various endemic subspecies, species and even genera, such as the oryzomyines *Megalomys*, *Agathaeromys* and *Pennatomys* (Musser and Carleton 2005; Turvey *et al.* 2010; Zijlstra *et al.* 2010). All endemic species are now extinct, but several insular populations of mainland species remain, such as *Oryzomys palustris* on the Florida Keys and *Calomys hummelincki* on Curaçao in the Dutch Antilles. The taxonomic status of many of the Caribbean fossil cricetids is still unsettled, as material is often limited and rigorous taxonomic studies are rare. Thus, many of the extinct cricetids of the Lesser Antilles remain unnamed, and species boundaries and generic allocations are unclear, which hampers biogeographical study.

The cricetid fauna of the islands of Aruba, Curaçao and Bonaire, which are part of the Kingdom of the Netherlands but located before the Venezuelan coast, has recently received some much-needed attention, which has resulted in the identification of new taxa and in new information on previously known taxa (Martino 2000; McFarlane and Debrot 2001; McFarlane and Lundberg 2002; Voss and Weksler 2009; Zijlstra *et al.* 2010). Still, many species known from fossil and subfossil material remain unidentified, and the affinities of those that have been named are mostly unclear. In this article, we describe material from Curaçao and Bonaire that includes three new species referable to a new genus with traits suggesting a basal position within Sigmodontinae.

MATERIALS AND METHODS

Lower and upper molars are referred to as m1, m2 and m3, and M1, M2 and M3, respectively. The following abbreviations are used for measurements: Lm1–3, length of mandibular toothrow; LM1–3, length of maxillary toothrow; Lm1, length of lower first molar; Wm1, width of lower first molar; LM1, length of upper first molar; WM1, width of upper first molar; and etcetera. Dental nomenclature follows Reig (1977) and Weksler (2006), and general anatomical nomenclature follows Carleton and Musser (1989) and Weksler (2006). Following Hershkovitz (1993), we use the term *distoflexid* to describe a notch located behind the hypoconid of the lower molars, usually without any posterior border, and lingual to the posterolophid. Cricetid taxonomy follows Musser and Carleton (2005). We use the revised definition of the

Pleistocene that places its base at 2.6 Ma (Gibbard *et al.* 2010).

All material described is housed in the collections of the Naturalis Biodiversity Center in Leiden, the Netherlands (collection numbers RGM 444351–444372, 592996–593193). The material was measured using a Leica Ortholux measuring microscope. Molar length was measured along the maximum length of the tooth, and width was measured perpendicularly to the length at the middle of the tooth (for M1–2 and m1–2, at the mesoloph(id); for M3, at the protocone–paracone pair; and for m3, at the protoconid–metaconid pair). Full descriptions are given for occlusal morphology and root number; descriptions of dentaries focus on characters used by Steppan (1995) and Weksler (2006). In descriptions, the number of specimens with particular traits is indicated for variable characters. Thus, ‘anterolabial cingulum present (4/6)’ indicates that the anterolabial cingulum is present in four of six specimens examined and absent in two. When a feature could be examined in a limited number of specimens only, this number is also indicated within brackets.

The Bonaire material was recovered by McFarlane and Lundberg from 10 to 20 cm depth in unconsolidated sediments in Cueba di Curado, a 10-m-deep open pit cave approximately 7 km north-west of Kralendijk, the capital of Bonaire. The material apparently comes from an owl pellet assemblage and is considered late Holocene in age based on its co-occurrence in the upper levels with *Rattus rattus*, which did not occur on Bonaire before the island was first visited by Europeans in 1499. Radiocarbon dating was precluded by the absence of suitable organic material in the specimens.

Material from Curaçao was excavated during the 1950s and 1960s by P.H. de Buissonjé and others. All material is from cave deposits in Tafelberg Santa Barbara, described in detail by De Buissonjé (1974). Material described here is from the base of the middle part of these deposits (localities C2-633 and C2-637) and from the lower part of the deposit, which is the type locality of the fossil sloth *Paulocnus petrifactus* Hooijer (1962); we refer to the latter site as the *Paulocnus* locality.

De Buissonjé (1974) tentatively correlated the upper part of these deposits with the Highest Terrace of Curaçao. This would imply for the deposits discussed here an age of over 2.3 Ma, because Stienstra (1983) suggested that the Highest Terrace was deposited during the interval 2.3 to 1.3 Ma. The upper part of the deposits contains bird bones only. The middle part consists of flowstones and cave pearls; the geology indicates that this deposit was formed under humid conditions (De Buissonjé 1974, p. 182). Capybaras (*Hydrochoerus* sp.) were found at the top of this part of the deposits. The rodents described were found near the base of the middle part of the

section. The lower part of the deposit contains the fossil sloth *Paulocnus* and various indeterminate vertebrate bones in addition to the rodent described here.

SYSTEMATIC ZOOLOGY

This published work and the nomenclatural acts it contains, have been registered in Zoobank: <http://www.zoobank.org/References/9DD8D93D-C5E9-45B3-8950-7100F88CBF3E>

Order RODENTIA Bowdich, 1821

Family CRICETIDAE Fischer, 1817

Subfamily SIGMODONTINAE Wagner, 1843

Genus CORDIMUS gen. nov

LSID. urn:lsid:zoobank.org:act:5FC3640C-9446-43B6-9837-9F5F3693BF0D

Type species. *Cordimus debuisonjei* sp. nov.

Referred species. *Cordimus hooijeri* sp. nov.; *Cordimus raton* sp. nov.

Derivation of name. The genus name combines the Latin words *cor* 'heart' and *mus* 'mouse' and refers to the island of Curaçao, where remains of two species of *Cordimus* have been found. The name 'Curaçao' may have been derived from a Spanish or Portuguese word meaning 'heart' (*corazón* or *coração*, respectively).

Diagnosis. A cricetid rodent distinguished by the following combination of characters: molars strongly cuspidate; cusps opposite in upper molars, slightly alternate in lower molars; anteroloph of M1 short or absent; paracone of M1 connected to anterior part of median mure; median mure of M1 connected to protocone; mesoloph present in most upper molars; paracone of M2 connected singly to protocone at middle of protocone; protoflexus of M2 present; posteroloph and hypoflexus present on M3, hypoflexus shallow to moderately deep; M3 relatively narrow; mesolophid absent in nearly all lower molars; m1 relatively long; anterolabial cingulum present on m1–3, but relatively weak on m2; anterolophid absent from m2 and m3; lower second molar with two roots; masseteric ridges conspicuous. Upper molar traits are unknown for *C. hooijeri*.

Comparisons. Among the extant cricetid fauna of South America, *Cordimus* resembles some oryzomyines and thomomyines in having bunodont, brachydont molars with a mesoloph on M1 and M2 and in the presence of a complex M3, with five ridges that reach the labial margin

of the tooth. However, it is distinct from most of those in having reduced mesolophs and a reduced anteroloph on M1 and lacking the mesolophid and anterolophid in all lower molars. The monotypic oryzomyine genera *Lundomys* and *Pseudoryzomys* are among the cricetids most similar to *Cordimus*, but *Cordimus* differs from *Pseudoryzomys* in lacking lingual accessory roots on m1 (present); having m2 two-rooted (three-rooted); M1 paraloph attached posterior to protocone (to anterior portion of protocone); mesoloph better developed on M1 and M2, often reaching labial margin, and present on M3 (poorly developed on M1 and M2, never reaching labial margin; absent on M3); anterior margin of coronoid process gently rising (steeply rising). It differs from *Lundomys* in lacking lingual accessory roots on m1 (present); mesoloph well developed on M1 and M2 and present on M3 (poorly developed on M1 and M2, absent on M3); paracone of M3 connected to protocone (to hypocone); mesolophids on lower molars almost always absent (small mesolophids present); posterolophid of m3 present (absent). The extant species *C. hummelincki* occurs on the islands of Curaçao and Aruba and is superficially similar to *C. hooijeri* in the lower dentition, but species of *Cordimus* differ from this animal in being larger; having m2 and m3 clearly longer than wide, $Lm2/Wm2 > 1.12$ and $Lm3/Wm3 > 1.18$ (m2 and m3 squarish, $Lm2/Wm2 < 1.01$ and $Lm3/Wm3 < 1.10$); m3 distoflexid present in unworn molars (absent); masseteric ridges conspicuous (faint); m2 with two roots (with three roots, *vide* Steppan 1995, table 4, and RGM 257828); mesoloph present in all upper molars (absent); M3 more complex, with a mesoloph (reduced, without a mesoloph).

Cordimus also displays some similarities to North American cricetids that are thought to be related to the extant sigmodontines, neotomines or both (reviewed in Lindsay 2008). *Cordimus* differs from the oldest modern North American cricetid, *Copemys* (as described by Lindsay 1972), in having a weak anterolabial cingulum on m2 (strong); paracone of M2 connected singly to protocone at middle of protocone (singly at median mure or doubly at median and anterior mures); more prominent cuspidation, with high, narrow crests; m1 relatively longer; M3 relatively narrower. *Bensonomys*, *Symmetrodontomys*, *Tregomys* and *Pseudomyiscus* all lack a distinct entoconid and mesolophid on m3 and generally have less distinct cusps (Hibbard 1950; Wilson 1968; Korth 1997). Furthermore, *Cordimus* has only one mental foramen (*Pseudomyiscus* has two; Korth 1997), and the superior and inferior masseteric ridges do not unite into a single ridge (the anterior masseteric crest or amc of Martin *et al.* 2002), as they do in *Bensonomys* and *Symmetrodontomys*.

Antecalomys lacks a mesolophid on m3 and a mesoloph on the upper molars (Korth 1998). *Cordimus* differs from

Jacobsomys in having a single protolophule on M2 (double), no strong mesolophid on m1 and a distinct mesolophid on m3 (Czaplewski 1987; Lindsay and Czaplewski 2011). *Postcopemys* has a more reduced M3 and lacks a distinct mesolophid on m3 (Lindsay and Czaplewski 2011). *Abelmoschomys* is known from a very small sample, and the third molars, which are generally diagnostic of *Cordimus*, are unknown (Baskin 1986). *Cordimus* differs from *Abelmoschomys* in having a broader anteroconid on m1 and generally lacking a mesolophid on m1. Fejfar *et al.* (1996) named a putative ‘copemyine-peromyscine’ from the Quaternary of Ecuador, *Copemydon ecuadorensis*. However, Zijlstra (unpubl. data) has found that this animal is undistinguishable from extant species of the *Reithrodontomys mexicanus* group, which still occur in Ecuador. Unlike *Cordimus*, *Reithrodontomys* lacks a mesoloph on M3 and mesolophid on m3.

Remarks. We assign material from three localities on Curaçao and one on Bonaire to this new genus. All three Curaçao localities are in the cave deposits on Tafelberg Santa Barbara, but two, C2-633 and C2-637, are in the middle part of the deposits and one, the *Paulocnus* locality, is in the lower part. The two localities from the middle part are presumably of about the same age and contain material that is morphologically and

metrically identical; they are considered together here. Comparison between the localities is hampered by differences in anatomical coverage: the Curaçao material consists of numerous isolated molars and a few severely damaged bones, while the Bonaire assemblage consists of numerous relatively complete dentaries, partly with molars *in situ*, and lacks upper molars. Differences in wear form an additional hurdle, because the molars from C2-633 and C2-637 are mostly unworn, but those from Bonaire are all in an advanced stage of wear. Thus, comparisons between the Bonaire and Curaçao material need to be confined to the lower molars and differences between the two samples arising from wear need to be carefully distinguished from taxonomically significant characters.

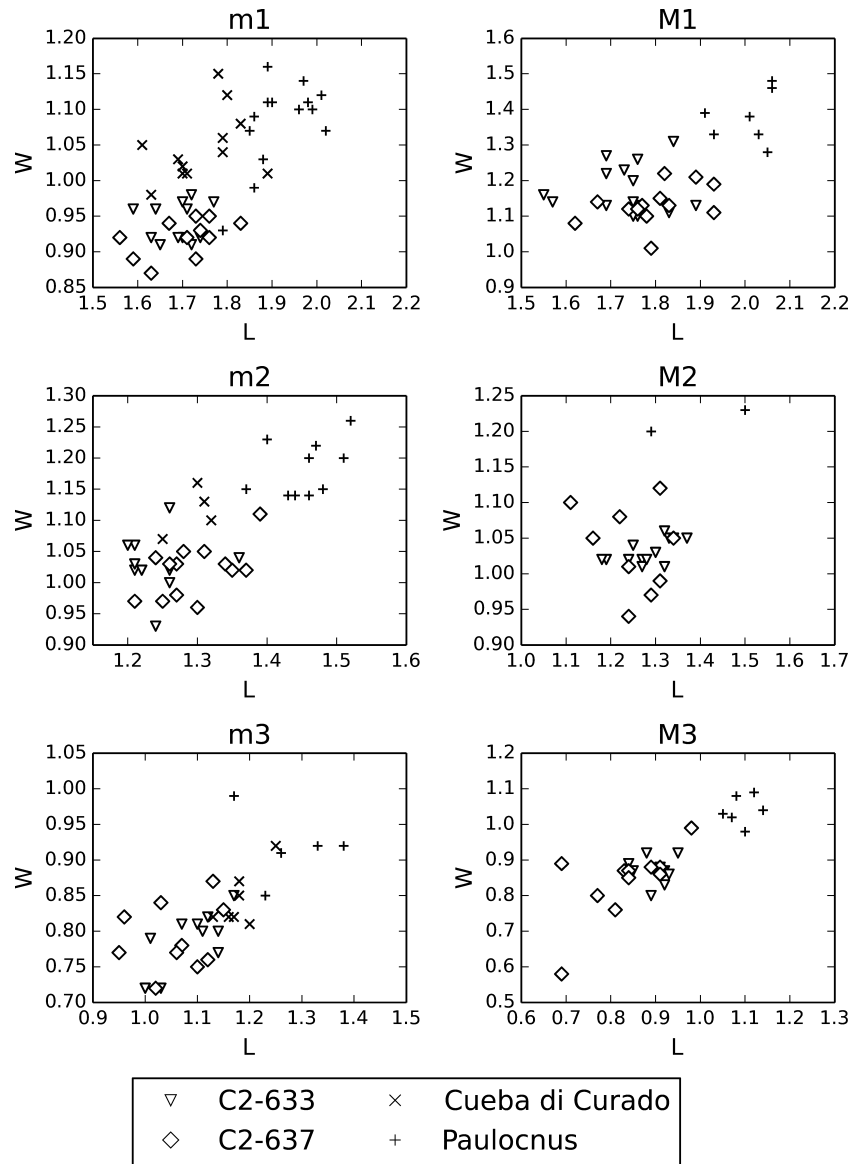
Metrically, the three groups appear to be slightly, but significantly different, with material from the *Paulocnus* locality consistently larger than that from C2-633 and C2-637, usually without overlap (Table 1; Fig. 1). The Bonaire material falls between these two extremes, but is characterized by unusually broad m1s and m2s. Most pairwise comparisons between measurements of fossils from Bonaire, the *Paulocnus* locality and C2-633/C2-637 reveal statistically significant differences (results not shown). Among the qualitative differences, we observed a subtle but consistent difference in the shape of m1: in

TABLE 1. Measurements of three species of *Cordimus* gen. nov.

Locality	M	n	Length	Width	Length/Width
CdC	m1	12	1.74 (1.61–1.89) ± 0.083	1.05 (0.98–1.15) ± 0.049	1.67 (1.53–1.87) ± 0.087
C2-633	m1	12	1.69 (1.59–1.77) ± 0.051	0.94 (0.91–0.98) ± 0.027	1.79 (1.66–1.89) ± 0.071
C2-637	m1	12	1.70 (1.56–1.83) ± 0.077	0.92 (0.87–0.95) ± 0.027	1.85 (1.70–1.95) ± 0.073
<i>Paulocnus</i>	m1	14/13	1.92 (1.79–2.02) ± 0.070	1.09 (0.93–1.19) ± 0.068	1.78 (1.63–1.93) ± 0.085
CdC	m2	4	1.30 (1.25–1.32) ± 0.031	1.12 (1.07–1.16) ± 0.039	1.16 (1.12–1.20) ± 0.033
C2-633	m2	11	1.24 (1.20–1.36) ± 0.045	1.03 (0.93–1.12) ± 0.046	1.21 (1.13–1.33) ± 0.069
C2-637	m2	14	1.29 (1.21–1.39) ± 0.054	1.02 (0.96–1.11) ± 0.040	1.27 (1.19–1.35) ± 0.053
<i>Paulocnus</i>	m2	10/9	1.45 (1.37–1.52) ± 0.046	1.19 (1.14–1.26) ± 0.044	1.23 (1.14–1.29) ± 0.049
CdC	m3	7	1.18 (1.13–1.25) ± 0.037	0.84 (0.81–0.92) ± 0.040	1.40 (1.36–1.48) ± 0.044
C2-633	m3	10	1.09 (1.00–1.17) ± 0.059	0.79 (0.72–0.85) ± 0.042	1.38 (1.28–1.48) ± 0.057
C2-637	m3	10	1.06 (0.95–1.15) ± 0.069	0.79 (0.72–0.87) ± 0.047	1.34 (1.17–1.47) ± 0.105
<i>Paulocnus</i>	m3	5	1.27 (1.17–1.38) ± 0.083	0.92 (0.85–0.99) ± 0.050	1.39 (1.18–1.50) ± 0.124
C2-633	M1	15	1.73 (1.55–1.89) ± 0.090	1.18 (1.10–1.31) ± 0.068	1.48 (1.33–1.67) ± 0.114
C2-637	M1	13	1.80 (1.62–1.93) ± .091	1.13 (1.01–1.22) ± 0.056	1.59 (1.47–1.77) ± 0.089
<i>Paulocnus</i>	M1	7	2.01 (1.91–2.06) ± 0.062	1.38 (1.28–1.48) ± 0.072	1.46 (1.37–1.60) ± 0.081
C2-633	M2	13	1.28 (1.18–1.37) ± 0.057	1.03 (1.01–1.06) ± 0.017	1.24 (1.16–1.31) ± 0.046
C2-637	M2	10	1.24 (1.11–1.34) ± 0.076	1.04 (0.94–1.12) ± 0.058	1.20 (1.01–1.33) ± .112
<i>Paulocnus</i>	M2	2	1.40 (1.29–1.50) ± 0.148	1.22 (1.20–1.23) ± 0.021	1.15 (1.08–1.22) ± 0.103
C2-633	M3	9	0.90 (0.84–0.95) ± 0.037	0.87 (0.80–0.92) ± 0.039	1.04 (0.94–1.11) ± 0.060
C2-637	M3	11	0.83 (0.69–0.98) ± 0.091	0.84 (0.58–0.99) ± 0.103	1.00 (0.76–1.19) ± 0.100
<i>Paulocnus</i>	M3	6	1.09 (1.05–1.14) ± 0.033	1.04 (0.98–1.09) ± 0.040	1.05 (1.00–1.12) ± 0.047

Location CdC represents *C. hooijeri*, locations C2-633 and C2-637 represent *C. debuisonjei*, and location *Paulocnus* represents *C. raton*. Measurements are in the form mean (minimum–maximum) ± standard deviation. *Abbreviations.* m, M, molar tooth position; n, number of teeth measured. When two values are given for n, the first is for length and the second for width.

FIG. 1. Scatterplots of measurements of molars of *Cordimus* spp.



Bonaire m1s, the labial and lingual margins of the molar (posterior to the anteroconid) are about parallel, and the molar is not noticeably narrower anteriorly than posteriorly, but in m1s from Curaçao, the labial and lingual margins are convergent anteriorly, so that the tooth is narrower anteriorly than posteriorly. This morphological difference may explain some of the differences in m1 width observed, because we measured the width over the middle of the molar.

Some differences in occlusal morphology between the Curaçao and Bonaire material were also observed, which may or may not be related to wear. The Curaçao material shows a posterolophid with a pronounced angle at the posterior margin between a portion parallel to the molar axis that connects the lophid to the hypocone and a per-

pendicular portion that extends lingually posterior to the entoconid. The distoflexid is strong. The angle in the posterolophid is much less sharp in the Bonaire material and the distoflexid is weak. In the m2, the distoflexid appears to be very weak at best in the Bonaire species, because it is absent in all specimens, possibly as the result of wear. In contrast, it is present in all molars from Curaçao. In the material from the *Paulocnus* site, the anteroconid on most m1s consists of two conules connected by a relatively narrow bridge; this morphology is not observed in the other material.

In view of the metrical and morphological differences, as well as the geographical and temporal separation, between the three groups of samples, we recognize three species, which are diagnosed and described below.

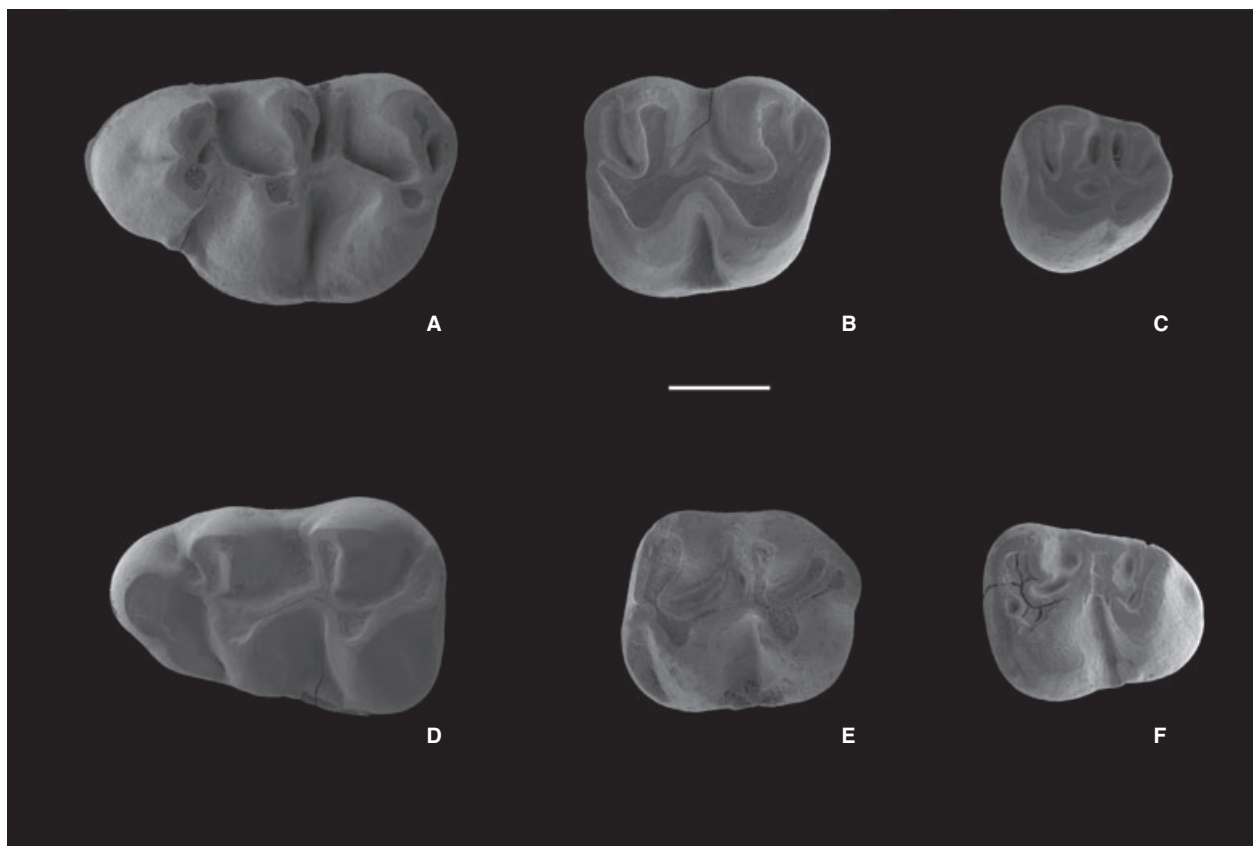


FIG. 2. *Cordimus debuissonjei* sp. nov. from Tafelberg Santa Barbara locality C2-633, Curaçao. A, M1 sin. RGM 593035. B, M2 dext. RGM 593012. C, M3 dext. RGM 593028. D, m1 dext. RGM 593035 (holotype). E, m2 sin. RGM 593051. F, m3 dext. RGM 593057. B, C, D and F are inverted images. Scale bar represents 1 mm.

Cordimus debuissonjei sp. nov.

Figure 2, Table 1

LSID. urn:lsid:zoobank.org:act:B80ABB13-A1D5-467C-A712-BFF9E8C569CB

1974 *Oryzomys* sp.; De Buissonjé, pp. 182, 183, 214, 218.

Derivation of name. The specific name honours Dr Paul Henri de Buissonjé, who unearthed the remains of this species and who has contributed greatly to the scientific study of the palaeontology and geology of Aruba, Curaçao and Bonaire.

Holotype. RGM 593035, isolated right m1 (length 1.69 mm and width 0.92 mm; Fig. 2D).

Paratypes. Fifteen M1s (RGM 592996–593010); 14 M2s (RGM 593011–593024); eight M3s (RGM 593025–593032); 10 m1s (RGM 593033–593034, 593036–593043); 11 m2s (RGM 593044–593054); 10 m3s (RGM 593055–593064); partial maxilla with M3 (RGM 593065); dentary with m1 (RGM 593066); five edentulous dentaries (RGM 593067–593071); two M fragments (RGM 593072–593073); all from the type locality.

Type locality. C2-633, base of middle part of Tafelberg Santa Barbara deposits, Curaçao.

Referred material. Thirteen M1s (RGM 593074–593086); 10 M2s (RGM 593087–593096); 12 M3s (RGM 593097–593108); 12 m1s (RGM 593109–593120); 14 m2s (RGM 593121–593134); 10 m3s (RGM 593135–593144); all from C2-637, base of middle part of Tafelberg Santa Barbara deposits, Curaçao.

Diagnosis. A species of *Cordimus* diagnosed by the following combination of traits: size small for the genus; m1 anteriorly convergent; m1 anteroconid not divided into anterolingual and anterolabial conules, or only superficially divided; m1 posterolophid with two portions which are nearly perpendicular one to another; m1 distoflexid strong; m2 distoflexid strong.

Description

Site C2-633 (type locality) M1 (n = 15). Prominent cuspidation, flexi broad, cusps opposite. Anterocone clearly displaced labially. Anterocone divided into anterolabial and anterolingual conules

by superficial notches at anterior and posterior margins (12) or division not apparent (3). Anterolabial cingulum absent (9) or descending from anterolabial conule, connected to paracone (6). Anterior mure connects anterolingual conule to protocone. Paracone connected to median mure slightly posterior to protocone. Paraloph attached to posterolabial corner of paracone. Median mure connects protocone to hypocone. Mesoloph short (7/14), long (6/14) or absent (1/14). Posteroloph descends from hypocone. Metacone connected to base of posteroloph or posterior hypocone, posteroflexus present. One large anterior and two large posterior roots present; accessory central rootlet present (6/7).

M2 ($n = 14$). Anteroloph present, partly parallel to axis of molar and with sharp angle at anterior margin, protoflexus well developed (8/13) or anteroloph not parallel to axis of molar, without sharp angle at anterior margin, protoflexus small (5/13). Paracone connected to middle of protocone, but not to end of anteroloph (10/13). Median mure connects protocone to hypocone. Mesoloph short (5/12), long (2/12) or absent (5/12). Posteroloph descends from hypocone. Metacone connected to base of posteroloph. One large lingual and two smaller labial roots.

M3 ($n = 9$). Anteroloph present. Paracone connected to base of anteroloph, but not to mesoloph (6). Median mure present at lingual margin, connects protocone to hypocone. Hypoflexus long and deep (2/8) or shallow and short (6/8). Mesoloph long. Posteroloph descends from hypocone. Metacone connected to end of posteroloph and to anterior hypocone (7) or to median mure (2). Two anterior roots and one posterior root (2/2).

m1 ($n = 12$). Prominent cuspidation, flexids broad, cusps slightly alternate, with lingual cusps anterior to labial ones, sides of molar anteriorly convergent, as seen primarily at labial side. Anteroconid not divided by anteromedian flexid or fossettid. Anterolabial cingulum present. Anterior murid connects anteroconid to protoconid. Metaconid connected to anterior murid (9/11) or to anterior side of protoconid (2/11). Median murid connects protoconid to hypoconid. Mesolophid absent. Entoconid connected to median murid slightly anterior to hypoconid. Posterolophid clearly separated from hypoconid, with distinct angle at posterior margin between nearly parallel part leading to hypoconid and nearly perpendicular part at posterior margin, distoflexid strong. Labial and lingual cingulum complete but low. Accessory labial root present (2/3 specimens with roots; 4/5 dentaries with exposed alveoli); one large anterior and one large posterior root.

m2 ($n = 12$). Prominent cuspidation, flexids broad, cusps slightly alternate. Anterolabial cingulum present. Metaconid and protoconid connected at anterior margin. Median murid connects protoconid to hypoconid. Mesolophid absent. Entoconid connected to median murid slightly anterior to hypoconid. Hypoflexid approximately perpendicular to axis of molar (3) or slanted backward (1). Posterolophid descends from hypoconid. Labial and lingual cingulum complete but low. One large anterior and one large posterior root (4/4).

m3 ($n = 10$). Prominent cuspidation, flexids broad, cusps slightly alternate. Anterolabial cingulum present. Anterolophid absent (9). Metaconid and protoconid connected at anterior margin. Median murid connects protoconid to hypoconid via entoconid. Mesolophid absent. Hypoflexid slanted slightly backward relative to axis of molar. Posterolophid descends from hypoconid. Lingual cingulum present. One large anterior, one large posterior root (2/2).

Dentary ($n = 5$). All preserved dentaries are severely damaged; consequently, the features of the posterior part of the dentary in particular could not be described. Mental foramen opens laterally. Masseteric ridges conspicuous, converge anteriorly as an open chevron and do not continue anterior to anterior m1 alveolus (4/4). Capsular process of lower incisor alveolus present (1/1). Anteroventral process weak (1/1). Coronoid process gently rising at anterior margin (1/1).

Site C2-637. In the description of the series from site C2-637, only traits that differ between sites C2-637 and C2-633 or that are variable in either series are included.

M1 ($n = 13$). Anterocone superficially divided (11) or undivided (2). Anterolabial cingulum descends from anterolabial conule, connected to paracone. Mesoloph long (7), short (5) or absent (1). One large anterior and two large posterior roots present; accessory central rootlet present (5/6).

M2 ($n = 10$). Anteroloph present, and partly parallel to axis of molar and with sharp angle at anterior margin, protoflexus well developed (9) or not parallel to axis of molar, without sharp angle at anterior margin, protoflexus small (1). Paracone connected to anterior protocone, but not additionally to end of anteroloph (8). Mesoloph long (4), short (4) or absent (2). Metacone connected to base of posteroloph (5) or to middle of hypocone (5).

M3 ($n = 12$). Hypoflexus shallow and short (8/11) or long and deep (3/11). Mesoloph connected accessorially to paracone by a central paralophule (5). Metacone connected to hypocone.

m1 ($n = 12$). Anteroconid not divided into conules (11) or with two small broadly connected conules (1). Anterior murid connects anteroconid to protoconid (9) or is absent (3). Metaconid connected to anterior murid (6) or anterior part of protoconid (5), or isolated (1). Mesolophid absent (10) or present (2). One large anterior and one large posterior root; accessory labial root absent (2/3).

m2 ($n = 14$). Mesolophid absent (12/13) or short mesolophid present (1/13).

m3 ($n = 10$). Metaconid and protoconid connected at anterior margin (8/9); posterior metaconid additionally connected to middle of protoconid (5). Anterior arm of entoconid at labial cingulum present.

Distribution and stratigraphical range

This species is known from two localities, coded C2-633 (type locality) and C2-637, at the base of the middle part of the cave deposits in Tafelberg Santa Barbara, Curaçao, Netherlands Antilles. The age of these deposits is unknown, but may be early Pleistocene or late Pliocene (see Materials and methods).

Cordimus raton sp. nov.

Figure 3, Table 1

LSID. urn:lsid:zoobank.org:act:DDF66878-FC89-489B-A93B-76F9F469F7AF

Derivation of name. The specific name is the Papiamentu word for 'mouse', *raton*. Papiamentu is the native language of the majority of the population of the ABC islands of Aruba, Bonaire and Curaçao.

Holotype. RGM 593170, isolated left m1 (length 1.88 mm and width 1.03 mm; Fig. 3D).

Paratypes. Eight M1s (RGM 593145–593152); two M2s (RGM 593153–593154); six M3s (RGM 593155–593160); 10 m1s (RGM 593161–593170); nine m2s (RGM 593171–593179); four m3s (RGM 593180–593183); edentulous maxilla (RGM 593184); two dentaries with m1 (RGM 593185–593186); two dentaries with m1–2 (RGM 593187, 593189); dentary with m1 and m3 (RGM 593188); four edentulous dentaries (RGM 593190–593193); all from the type locality.

Type locality and age. *Paulocnus* locality, lower part of the cave deposits of Tafelberg Santa Barbara, Curaçao. The age of this deposit is unknown, but is older than that of the overlying deposits yielding *C. debuissonjei* and may be late Pliocene.

Diagnosis. A species of *Cordimus* diagnosed by the following combination of traits: size largest in genus; m1 anteriorly convergent; m1 anteroconid divided into anterolingual and anterolabial conules connected by narrow bridge; m1 posterolophid with two portions which are nearly perpendicular one to another; m1 distoflexid strong; m2 distoflexid strong.

Description

M1 ($n = 7$). Prominent cuspidation, flexi broad, cusps opposite. Anterocone clearly displaced labially. Anterocone divided into anterolabial and anterolingual conules by superficial notches at anterior and posterior margins (5/6) or undivided (1/6). Anterolabial cingulum descends from anterolabial conule. Anterior mure connects anterolingual conule to protocone. Paracone connected to median mure slightly posterior to protocone. Paraloph attached to posterolabial corner of paracone. Median mure

connects protocone to hypocone. Mesoloph long (4/6) or short (2/6). Posteroloph descends from hypocone. Metacone and hypocone connected at posterior margin, posteroflexus not apparent (5) or metacone connected to base of posteroloph, posteroflexus present (2). One large anterior and two large posterior roots present; accessory central rootlet present (7/7).

M2 ($n = 2$). Anteroloph present, partly parallel to axis of molar and with sharp angle at anterior margin, protoflexus well developed. Paracone connected to middle of protocone. Median mure connects protocone to hypocone. Mesoloph present, long. Posteroloph descends from hypocone. Metacone connected to base of posteroloph and to hypocone. One large lingual and two smaller labial roots.

M3 ($n = 6$). Anteroloph present. Paracone connected to base of anteroloph and to mesoloph. Median mure present at lingual margin, connects protocone to hypocone. Hypoflexus moderately long and deep (1/5) or shallow (4/5). Mesoloph long. Posteroloph descends from hypocone. Metacone connected to end of posteroloph. Two anterior roots and one posterior root.

m1 ($n = 12$). Prominent cuspidation, flexids broad, cusps slightly alternate, with lingual cusps anterior to labial ones, sides of molar slightly anteriorly convergent, as seen primarily at labial side. Anteroconid divided into two conules, connected by a narrow bridge (10) or conules fused (1). Anterolabial cingulum present. Anterior murid connects anterolingual conule to protoconid. Metaconid connected to anterior murid (10) or to anterior part of protoconid (2). Median murid connects protoconid to hypoconid via entoconid. Mesolophid absent. Entoconid connected to median murid slightly anterior to hypoconid. Ectostylid present (1). Posterolophid distinct from hypoconid, with distinct angle at posterior margin between nearly parallel part leading to hypoconid and nearly perpendicular part at posterior margin, distoflexid strong. Labial and lingual cingulum present. Accessory labial root present (3/3); one large anterior and one large posterior root.

m2 ($n = 11$). Prominent cuspidation, flexids broad, cusps slightly alternate. Anterolabial cingulum present. Anterolophid absent (10). Metaconid and protoconid connected at anterior margin. Median murid connects protoconid to hypoconid via entoconid. Mesolophid absent. Entoconid connected to median murid slightly anterior to hypoconid. Posterolophid descends from hypoconid. Labial and lingual cingulum present. One large anterior and one large posterior root (8/8).

m3 ($n = 5$). Flexids broad, cusps slightly alternate. Anterolabial cingulum present, but poorly developed. Metaconid and protoconid connected at anterior margin. Median murid connects protoconid to hypoconid via entoconid. Hypoflexid deep. Mesolophid absent, entoconid reduced. Posterolophid descends from hypoconid, distoflexid present (4/5). Labial and lingual cingulum present. One large anterior and one large posterior root (3/3).

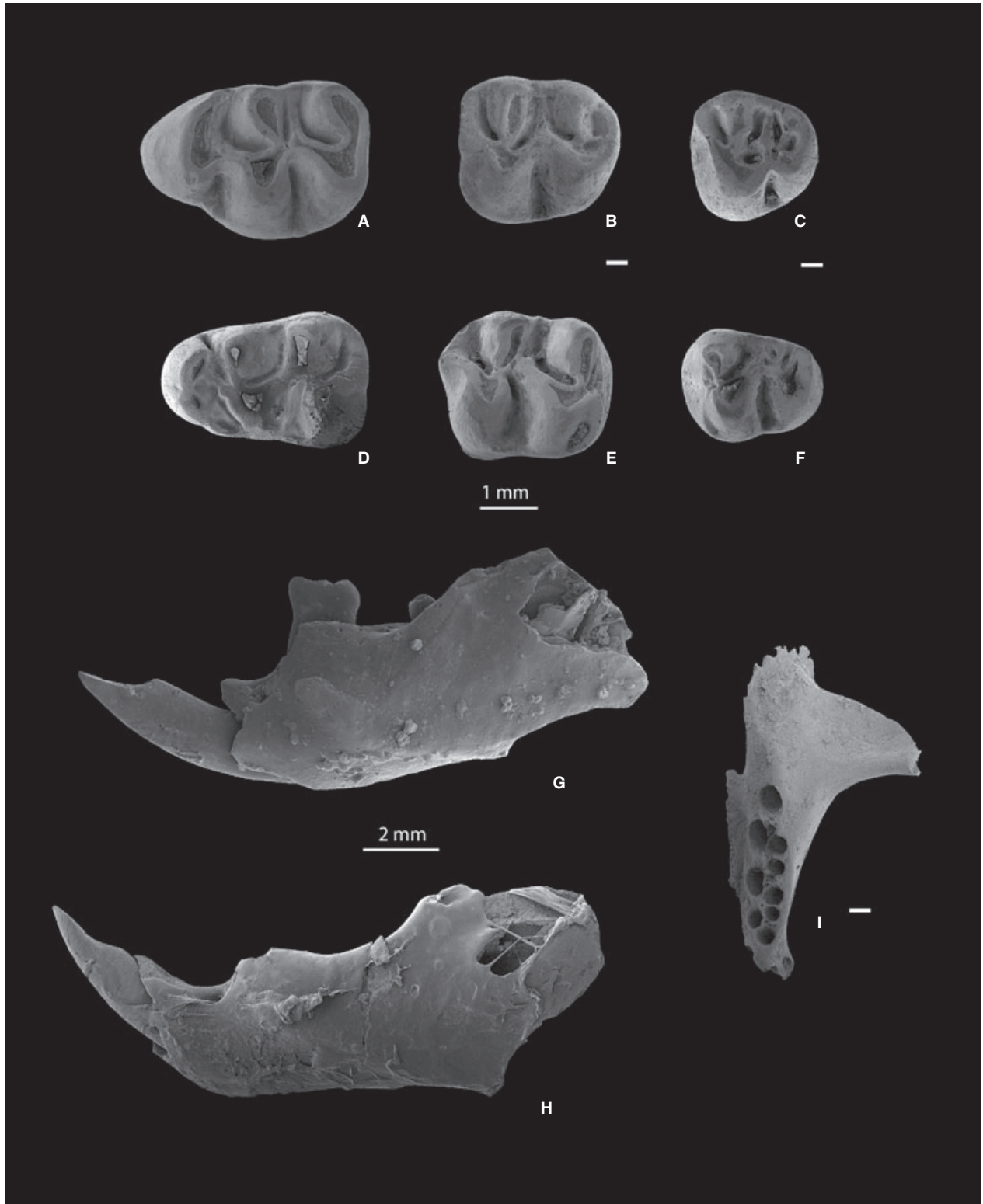


FIG. 3. *Cordimus raton* sp. nov. from Tafelberg Santa Barbara *Paulocnus* site, Curaçao. A, M1 sin. RGM 593149. B, M2 dext. RGM 593153. C, M3 dext. RGM 593157. D, m1 sin. RGM 593170 (holotype). E, m2 sin. RGM 593174. F, m3 sin. RGM 593182. G, mandible sin. with m1 and m3 RGM 593188. H, edentulous mandible sin. RGM 593190. I, edentulous maxillary dext. RGM 593184. B, C and I are inverted images. Upper scale bar (A–F) represents 1 mm and lower scale bar (G–I) represents 2 mm.

Maxilla ($n = 1$). Posterior margin of zygomatic plate about level with anterior M1 alveolus. Incisive foramen does not extend to anterior M1 alveolus. M1, M2 and M3 each with three alveoli.

Dentary ($n = 10$). Dentary robust. Mental foramen opens laterally (7/7). Masseteric ridges conspicuous, converge anteriorly as an open chevron and do not continue anterior to anterior m1 alveolus (5/5). Anteroventral process weak (1/1). Coronoid process gently rising at anterior margin (5/5). Superior notch shallow (2/2), inferior notch deep and rounded (1/1). Retromolar region forms a shallow groove (4/4). One large anterior and one large posterior alveolus present under m1, as well as one smaller median alveolus (2/2). One anterior and one posterior alveolus under m2 (5/5). One anterior and one posterior alveolus present under m3 (3/4) or two anterior alveoli, one lingual and one labial, and one posterior alveolus (1/4).

Cordimus hooijeri sp. nov.

Figure 4, Table 1

LSID. urn:lsid:zoobank.org:act:0F834ABA-3DDF-4914-BA02-BDF393E05F42

Derivation of name. Named after Dutch palaeontologist Dr D.A. Hooijer, who made several important contributions to the palaeontology of the Caribbean region.

Holotype. RGM 444360, nearly complete right dentary with m1–3 and i1 (Fig. 4A, B). Measurements are: Lm1 1.70 mm, Wm1 1.01 mm, Lm2 1.32 mm, Wm2 1.10 mm, Lm3 1.17 mm, Wm3 0.82 mm, Lm1–3 4.20 mm.

Paratypes. RGM 444351, left dentary with m1–3; RGM 444352, left dentary with m1–2; RGM 444353, left dentary with m1 and part of m2; RGM 444354, left dentary with m1; RGM 444355, left dentary with m1; RGM 444356, severely damaged left dentary with m1; RGM 444357, severely damaged left dentary with m1 and m3; RGM 444358, left dentary with m3; RGM 444359, left dentary with m3; RGM 444361, damaged right dentary with m1–2; RGM 444362, right dentary with m3; RGM 444363, isolated right m3; RGM 444364, nearly complete left dentary with m1; RGM 444365, left dentary with m1; RGM 444366, nearly complete left dentary with m1 and m3; RGM 444367, edentulous right dentary; RGM 444368, isolated i1; RGM 444369, 11 slightly damaged to nearly complete edentulous left dentaries, two with i1, and an isolated i1; RGM 444370, 17 slightly damaged to nearly complete edentulous right dentaries, three with i1; RGM 444371, nine isolated i1s; RGM 444372, eight femora and six tibiae; all from the type locality.

Type locality and age. Cueba di Curado, Bonaire; late Holocene (after 1499) in age. See Materials and methods section for details.

Diagnosis. A species of *Cordimus* diagnosed by the following combination of traits: size medium for genus; m1

not anteriorly convergent; m1 anteroconid not divided into conules; m1 posterolophid simple; m1 distoflexid weak; m2 distoflexid weak, disappearing rapidly with wear.

Description

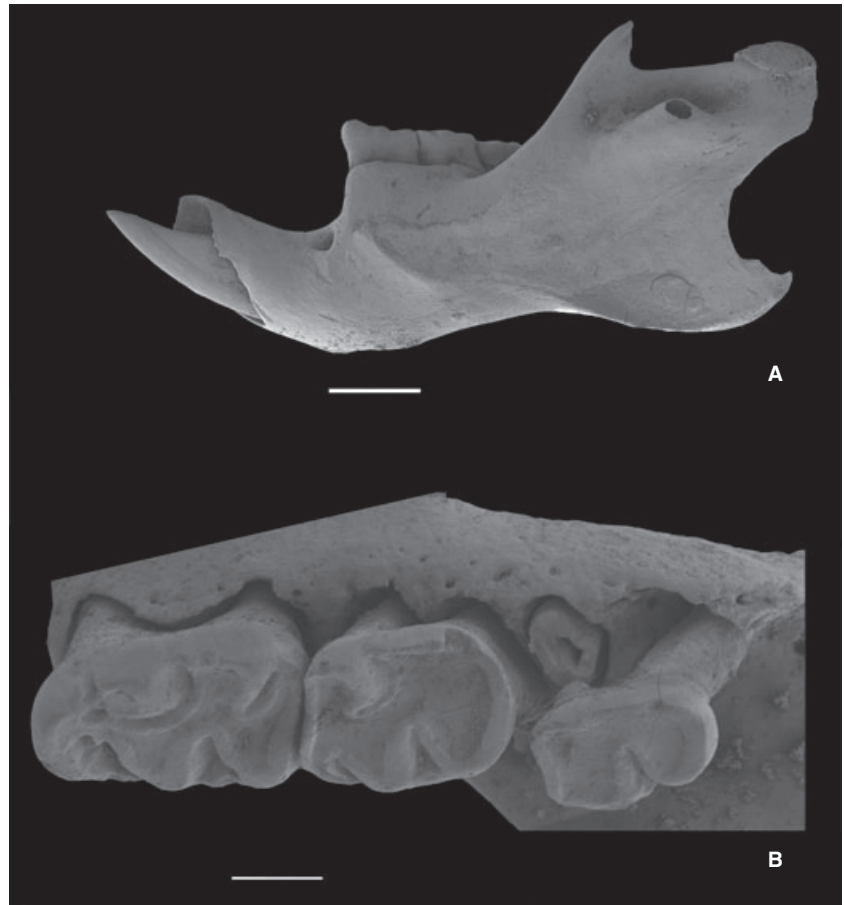
m1 ($n = 9$). Cusps slightly alternate, molar not tapering forward. Anteroconid large, centrally placed, not divided into conules. Anterolabial cingulum long, reaching close to protoconid. Anterior median murid connects lingual side of anteroconid to protoconid. Metaconid isolated (2/8), fused with anteroconid and protoconid by wear (3/8), broadly connected with anterior median murid (2/8) or narrowly so (1/8). Posterior median murid connects protoconid to labial extension of entoconid and then to hypoconid. Mesolophid absent, possibly due to wear. Entoconid and hypoconid may be fused due to wear (2). Anterior arm of entoconid at lingual margin present (6). Anterior arm of hypoconid at labial margin absent (5). Posterolophid a direct continuation of hypoconid, without distinct angle at posterior margin, distoflexid weak (6/8) or posterolophid distinct from hypoconid, with distinct angle at posterior margin between nearly parallel part leading to hypoconid and nearly perpendicular part at posterior margin, distoflexid strong (1/8) or distoflexid worn away, posterolophid fused with entoconid and hypoconid (1/8).

m2 ($n = 3$). Metaconid connected to protoconid at anterior margin (1/3) or broadly fused with protoconid because of wear (2/3). Anterolabial cingulum present anterior and anterolabial to protoconid. Median murid connects protoconid to entoconid–hypoconid. Mesolophid absent, possibly due to wear. Entoconid and hypoconid broadly fused, possibly due to wear.

m3 ($n = 5$). Entoflexid present between entoconid and metaconid, reaching anteriorly so that metaconid and protoconid are connected only at anterior margin (4), or protoconid and metaconid forming a single noncuspidate lamina (1). Median murid connects posterolingual corner of protoconid to entoconid (4) or connects protoconid–metaconid to entoconid–hypoconid at lingual margin (1). Mesolophid absent, possibly due to wear. Hypoflexid approximately perpendicular to axis of molar. Entoconid and hypoconid form a single noncuspidate lamina (3) or entoconid and hypoconid distinct from each other and distinct posterolophid and distoflexid present at posterior margin, connected to hypoconid (2). Entoconid with anterior arm at lingual margin (4).

Dentary. Dentary robust. Three alveoli for m1: one large anterior alveolus, a small median alveolus and a large posterior alveolus (19/25) or median alveolus absent (3/25) or two (2/25) or three median alveoli present (1/25). Two large alveoli for m2 (29) and m3 (25): one anterior, one posterior. Capsular process present, large (25). Coronoid process about as high as condyloid process (8), gently rising at anterior margin (26). Superior notch shallow (6), inferior notch rounded and deep (2), angular

FIG. 4. *Cordimus hooijeri* sp. nov. from Cueva di Curado, Bonaire. Mandible dext. with incisor and complete toothrow RGM 44360 (holotype). A, labial view; B, close-up of the molar row in occlusal view. A and B are inverted images.



process slightly shorter than condyloid process (2). Retromolar region forms a shallow groove (42). Superior and inferior masseteric ridges distinctive, converge ventral to front of anterior m1 alveolus and do not continue beyond that point as a single ridge (40). Mental foramen opens labially (38) or lingually (1) to diastema. Weak medioventral process present (4/9). Anteroventral process weak (18).

DISCUSSION

Phylogenetic relationships

Even with the larger pool of characters available from extant species, phylogenetic relationships between cricetids have long been controversial (Musser and Carleton 2005). Superficial resemblances in dental characters may often be misleading (Voss and Carleton 1993), and putative synapomorphies of sigmodontine rodents are mainly postcranial (Steppan 1995). Given these limitations, it is difficult to assess the relationships of a taxon known almost exclusively from dental remains, such as *Cordimus*. However, the close resemblance (noted above) between *Cordimus* and *Copemys* may provide clues about the relationships of the new genus. *Copemys* has traditionally been regarded as ancestral to

North American neotomines such as *Peromyscus* (Pardiñas *et al.* 2002) and is almost undistinguishable from the Eurasian genus *Democricetodon* (Lindsay 1995). These early and middle Miocene taxa occur at the right time and place to be considered as ancestors for the other members of Cricetidae, a clade recognized in molecular studies of extant taxa that consists of Cricetinae, Arvicolinae, Neotominae, Tylomyinae and Sigmodontinae (Jansa and Weksler 2004; Steppan *et al.* 2004). Further study is needed to determine the relationships between fossil taxa and extant clades diagnosed so far mainly by molecular characters, and our description of *Cordimus* provides one contribution to this interesting research area.

As noted in the Comparisons section above, *Cordimus* does differ from *Copemys* in a few details of occlusal morphology (single connection of paracone and protocone on M2 and weak anterolabial cingulum on m2) and molar proportions (longer m1 and narrower M3). The states seen in *Cordimus* are apparently derived characters that are also seen in extant sigmodontines. This combination of a close general resemblance to *Copemys* with derived characters shared with sigmodontines suggests that *Cordimus* may be close to the sigmodontine stem, an early offshoot of the *Copemys*-like stock that presumably

entered South America and radiated into the Sigmodontinae. The oldest known South American sigmodontine is *Auliscomys formosus* from the early Pliocene of Argentina, which is already recognizably phyllotine (Pardiñas *et al.* 2002). Cricetids have not been recovered from the Miocene or Pliocene of northern South America; faunas from this interval could shed light on the relationship between *Copemys* and *Cordimus*. The possible copemyine affinities of *Cordimus* may also be tested through a comprehensive phylogenetic study of early American cricetids.

Island biogeography

Ongoing investigations are uncovering a diverse indigenous rodent fauna on the ABC islands of Aruba, Bonaire and Curaçao. The Quaternary fauna of Aruba includes three species of pentalophodont oryzomyines (*Megalomys curazensis*, *Oligoryzomys* sp. and *Oryzomys gorgasi*), species of *Sigmodon* and *Zygodontomys* and *Calomys hummelincki* (De Buissonjé 1974; Musser and Carleton 2005; JSZ, unpubl. data). In addition to the extant *C. hummelincki*, several extinct oryzomyines are known from Curaçao, including ‘*Megalomys*’ *curazensis*, *O. gorgasi*, and *Dushimys larsi* (Zijlstra, 2012; JSZ, unpubl. data), as well as *C. debuissonjei* and *C. raton*. Previously, the known indigenous rodent fauna of Bonaire consisted of only two species of the endemic genus *Agathaeromys*, which probably went extinct no later than about 230 ka, and of one other species represented by a single dentary only (Zijlstra *et al.* 2010). Although Bonaire and Curaçao are only 70 and 80 km from the modern coastline of Venezuela, they are separated from the continental shelf by a major tectonic feature, the Bonaire basin, with a maximum water depth of 1344 m. The isolation of Bonaire and Curaçao from the mainland dates from at least the Miocene (Jackson and Robinson 1994). Thus, the ancestors of *Cordimus* must have reached the islands by overwater dispersal somewhere in the last few millions of years. The two Curaçao species are the oldest known rodents from the island and are presumably derived from an unknown, proto-sigmodontine mainland ancestor. They occur in consecutive strata, and in the absence of evidence to the contrary, we assume that they represent a single anagenetic lineage. However, they are apparently separated from their Bonaire congener, *C. hooijeri*, by a gap of as much as two million years. In the meantime, both Curaçao and Bonaire were occupied by unrelated oryzomyines, which are known from abundant fossil remains (McFarlane and Lundberg 2002; Zijlstra *et al.* 2010). Three explanations may be invoked for the temporally disjunct distribution of *Cordimus*: (1) the Curaçao and Bonaire species independently derived from an unknown mainland population of *Cordimus* that persisted throughout the Pleistocene; (2) Cur-

açao and Bonaire species are not in fact closely related and *Cordimus* is diphyletic; or (3) *Cordimus* survived at low frequencies or in conditions unfavourable to fossilization on either Curaçao or Bonaire throughout the Pleistocene. This last option receives circumstantial support from the find of a single dentary of a different rodent among the numerous remains of *A. donovani* from the site of Porto Spanjo, Bonaire (Zijlstra *et al.* 2010). Apparently, the island could in fact support more than one rodent. The monophyly of *Cordimus* may be tested by continued study of the existing hypodigm or by the discovery of new, more anatomically complete material, such as upper molars of *C. hooijeri*.

Insular rodents are often characterized by large size (Meiri *et al.* 2008), but this is not the case for *Cordimus* spp., which are comparable in size to North American *Copemys* (Lindsay 1972). There are some very large insular forms among the Quaternary cricetids of the Caribbean (e.g. some species of *Megalomys* and ‘*Ekbletomys hypenemus*’; Ray 1962), but also others that show no signs of insular gigantism (e.g. *Agathaeromys praeuniversitatis* and the Curaçao population of *Oryzomys gorgasi*; Voss and Weksler 2009; Zijlstra *et al.* 2010). On Curaçao, we document a lineage of insular rodents characterized by decreasing size; *Cordimus debuissonjei* is about 10 per cent smaller than *C. raton*.

Age and status

Of the three new species described herein, the age of only one (*C. hooijeri*) is known with any degree of certainty; the deposits in which it has been found are undoubtedly Holocene in age. It survived at least until about 1500, as indicated by its association with *R. rattus* in the same deposit. No live specimens are known, and it may well have become extinct during the last few centuries, but this needs to be confirmed by focused searches on Bonaire. While most of the Holocene cricetid rodents on Caribbean islands (e.g. *Pennatomys nivalis*, *Megalomys* spp., *Oligoryzomys victus*, *Oryzomys antillarum* and the Curaçao population of *O. gorgasi*) are now extinct (Musser and Carleton 2005; Voss and Weksler 2009; Turvey *et al.* 2010), the small mouse *Calomys hummelincki* still survives on the islands of Curaçao and Aruba (Musser and Carleton 2005). The extinction of Caribbean cricetids has been attributed to habitat degradation and the introduction of the mongoose *Herpestes javanicus*, among other factors (Ray 1962; Turvey *et al.* 2010); however, the mongoose was never introduced to Bonaire, and the original vegetation has not been affected as much as on some other islands. Nevertheless, introduced murines, goats, cats and other animals coupled with habitat degradation may have caused *C. hooijeri* to become extinct.

As discussed in the Materials and Methods section above, the age of the Curaçao species is unknown, but the most likely estimate would put their age at least in the early Pleistocene and possibly in the late Pliocene.

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