

## MOLAR POLYMORPHISM AND VARIATION IN TOOTH NUMBER IN A SEMI-AQUATIC RODENT, *Neusticomys oyapocki* (SIGMODONTINAE, ICHTHYOMYINI).

François Catzefflis<sup>1</sup>, Benoit de Thoisy<sup>2</sup>,  
Maria Nazareth Ferreira da Silva<sup>3</sup> and Claudia Regina da Silva<sup>4</sup>

<sup>1</sup> Institut des Sciences de l'Evolution, CNRS UMR-5554, Université Montpellier-2, F-34095 Montpellier, France.

[Correspondence: François Catzefflis <[francois.catzefflis@univ-montp2.fr](mailto:francois.catzefflis@univ-montp2.fr)>]

<sup>2</sup> Laboratoire des Interactions Virus-Hôtes, Institut Pasteur de la Guyane, 23 Avenue Pasteur, BP 6010, 97306 Cayenne cedex, French Guiana & association Kwata, 16 avenue Pasteur, 97300 Cayenne, French Guiana

<sup>3</sup> Coleção de Mamíferos, Instituto Nacional de Pesquisas da Amazonia (INPA), Av. André Araújo, n° 2936, Bairro Petrópolis, CEP 69067-375 Manaus, AM, Brazil

<sup>4</sup> Laboratório de Mamíferos, Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá, Rodovia JK, Km 10, s/n, bairro Fazendinha, CEP 68912-250, Macapá, Amapá, Brazil

**ABSTRACT.** Newly collected specimens of the rare semi-aquatic mouse *Neusticomys oyapocki* (Rodentia: Sigmodontinae: Ichthyomyini) exhibit individual variation in tooth number. Whereas this Guianan ichthyomyine had previously been described as having only two molars per jaw quadrant, our study examines 31 specimens, of which 12 exhibit from one to four additional third molars. Specimens with at least one third molar come from 6 localities spanning Suriname, French Guiana, and the Brazilian states of Amapá and Pará. Third molars reported in this species are tiny (on average 0.55 mm crown length), about half the size of second molars. We show that *N. oyapocki* has between 8 and 12 molars, which represents extensive variation in the number of teeth. This kind of dental variation is rare in muroid rodents, as only a few such cases have been reported from some carnivorous water rats and moss mice from New Guinea.

**RESUMO.** Polimorfismo molar e variação no número de dentes em um roedor semi-aquático, *Neusticomys oyapocki* (Sigmodontinae, Ichthyomyini). Espécimes recém coletados do raro roedor semi-aquático *Neusticomys oyapocki* (Rodentia: Sigmodontinae: Ichthyomyini) exibem variação individual no número de dentes. Considerando que esse ichthyomyineo das Guianas foi descrito como tendo apenas dois molares por quadrante mandibular, o nosso estudo examina 31 espécimes dos quais 12 apresentam de um a quatro terceiros molares adicionais. Espécimes com pelo menos um terceiro molar são provenientes de 6 localidades que abrangem Suriname, Guiana Francesa, e os estados brasileiros do Amapá e Pará. Os terceiros molares relatados para essa espécie são dentes muito pequenos (comprimento médio da coroa 0.55 mm), cerca da metade do tamanho dos segundos molares. Mostramos que *N. oyapocki* tem entre 8 e 12 molares, o que é uma variação extensa no número de dentes. Esse tipo de variação dentária encontrada no Ichthyomyineo das Guianas é rara em roedores murídeos, já que apenas alguns casos similares foram relatados para alguns ratos de água carnívoros e ratos-musgos da Nova Guiné.

**Key words:** Dental polymorphism. Guianan Shield. Third molar.

**Palavras-chave:** Escudo das Guianas. Polimorfismo dentário. Terceiro molar.

## INTRODUCTION

Individual variation in tooth number can be experimentally induced and/or observed in laboratory mice and rats and imply different genetic mechanisms that have been reviewed by Cai et al. (2007), Caton and Tucker (2009), and Cobourne and Sharpe (2010). In humans, supernumerary teeth—which form in addition to the normal complement—are relatively common, occurring as an isolated finding in up to 3% of the population (Cobourne and Sharpe, 2010). Nevertheless, variation in tooth number in natural populations of cricetid rodents is seldom observed (Hooper, 1955; Libardi and Percequillo, 2014). Here we report a first case of widespread dental polymorphism in a free-ranging species of a Neotropical water mouse (Ichthyomyini Vorontsov, 1959).

Ichthyomyiines are New World cricetid rodents of the subfamily Sigmodontinae Wagner, 1843, which are ecologically and morphologically distinctive (Voss, 1988, 2015). There are two allopatric taxa of Ichthyomyini in the Guianan region (NE Amazonia), namely *Neusticomys venezuelae* (Anthony, 1929) in Venezuela and Guyana, and *N. oyapocki* (Dubost and Petter, 1978) in the south-eastern part of the Guianas, Amapá, and eastern Pará.

When the small (ca. 50 grams) semi-aquatic rodent *N. oyapocki* was first described by Dubost and Petter (1978), its diagnosis included the absence of upper and lower third molars, as well as the small size of its remaining cheek-teeth. At that time, *N. oyapocki* was the fourth known species of that ichthyomyine genus, and all specimens of the other taxa (*N. monticolus*, *N. venezuelae*, and *N. peruviansis*) had three molars in each quadrant of the jaw (Voss, 1988).

Subsequently, nine additional specimens of *N. oyapocki* were discovered (Voss et al., 2001; Nunes, 2002; Leite et al., 2007; Miranda et al., 2012) in French Guiana and in Brazilian states of Amapá and Pará, all having only two molars on each quadrant. With one exception, all known specimens of three recently described congeners also have three molars in each jaw quadrant: *N. mussoi* (Ochoa and Soriano, 1991) from the Andes of Venezuela, *N. ferreirai* from the Brazilian state of Mato

Grosso (Percequillo et al., 2005), and *N. vossi* from the eastern slope of the Ecuadorian Andes (Hanson et al., 2015). The exception is a paratype of *N. ferreirai* (MZUSP-32093), in which the lower right toothrow has only two molars (Percequillo et al., 2005).

We have been able to examine 26 additional specimens of *N. oyapocki* from Suriname, French Guiana, Amapá and Pará, among which we found considerable variation in numbers of molars, which we describe here.

## MATERIALS AND METHODS

We examined museum specimens, received descriptions and photographs for a total of 37 specimens of *Neusticomys oyapocki*, which are listed in the **Appendices 1 and 2**. The age of specimens (Tooth Wear Class—TWC—as defined in Voss, 1988) was roughly divided into juveniles (TWC1, open sphenoccipital suture, immature pelage), subadults (TWC2, closed—but not fused—sphenoccipital suture, immature pelage), and adults (TWC3 to TWC6, closed to fused sphenoccipital suture, adult pelage).

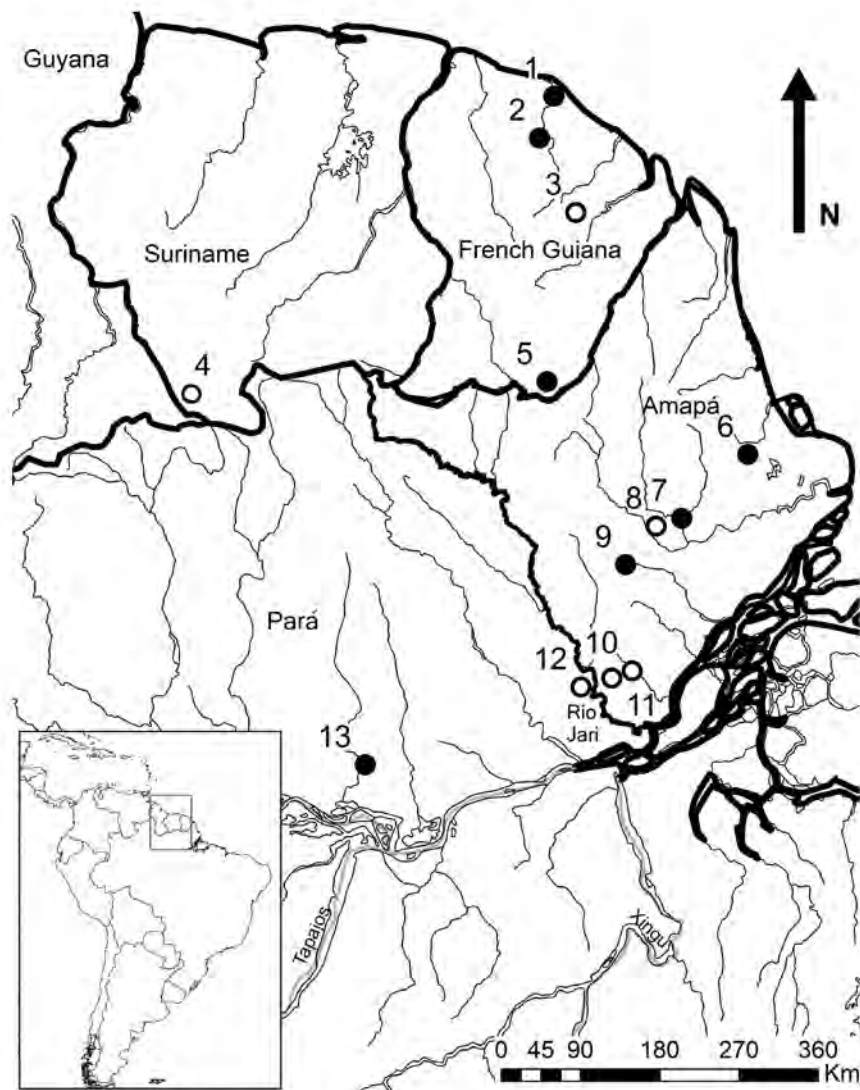
Standard external measurements (Head and Body Length; Tail Length; Hind Foot Length—with claws—; Ear Length) were those recorded by the collectors. We took two additional external measurements of well-preserved specimens: length of the mystacial vibrissae, and length of the terminal tuft of long hairs on the tail.

Cranial and dental measurements were taken as described by Voss (1988: 269-271) and Voss et al. (2001: 73-75). We paid careful attention to the crown-length measurements of upper and lower molars, in order to compare *Neusticomys* values with homologous variables in other similar-sized taxa.

For comparing dental lengths of *N. oyapocki* with those of other similar-sized rodents, we selected vouchered animals (list of specimens available from senior author ) collected in French Guiana for one scansorial (*Hylaeamys megacephalus*), one terrestrial (*Zygodontomys brevicauda*), and two arboreal (*Oecomys auyantepui* and *Rhipidomys nitela*) cricetid rodents. Statistical tests were performed using the software package PAleontological STatistics (Hammer et al., 2011).

## RESULTS

Our sample of *Neusticomys oyapocki* (N=37) includes 11 females, 25 males, and one specimen of unknown sex. **Fig. 1** indicates the 13



**Fig. 1:** Map of part of the Guianan Shield with 13 localities from where specimens of *Neusticomys oyapocki* have been examined. Open circles (localities 3, 4, 8, 10, 11 & 12) for locations where the presence of animals with at least one third molar has been evidenced. Closed black circles for localities with animals characterized by only two molars, as per the holotype of *N. oyapocki*.

localities from which these were collected in Amapá (6 localities, 18 individuals), Pará (2 localities, 12 specimens), French Guiana (4 localities, 6 specimens), and Suriname (1 locality, 1 specimen). Only 31 individuals (of which 10 females and 20 males, and one sex unknown) are represented by craniodental material, and these serve as the basis of our

comparisons; classified by age, these include 1 juvenile, 10 subadults, and 20 adults.

Statistical comparisons suggest that there is no sexual dimorphism in external measurements of *N. oyapocki* (Table 1), nor is any sexual dimorphism apparent for tested craniodental measurements (Table 2). Therefore, we treat all specimens as if there

**Table 1**

External measurements (in mm; weight in g) for *Neusticomys oyapocki*. Mann-Whitney non-parametric tests for comparing sexes. Abbreviations: HBL= Head and Body Length; TL= Tail Length; HF=Hind Foot length (with claws); Ea= Ear length; MV= Mystacial Vibrissae; TT= Tail Tuft; We= Weight; U (MW)= U-value for Mann-Whitney test.

<b>Females</b>	<b>HBL</b>	<b>TL</b>	<b>HF</b>	<b>Ea</b>	<b>MV</b>	<b>TT</b>	<b>We</b>
Mean	121.1	81.5	24.0	10.6	37.1	6.1	53.3
Min	96.0	66.0	20.0	6.0	32.0	4.0	21.0
Max	140.0	110.0	27.0	14.0	42.0	8.0	100.0
N	11	11	7	7	8	7	10
<b>Males</b>	<b>HBL</b>	<b>TL</b>	<b>HF</b>	<b>Ea</b>	<b>MV</b>	<b>TT</b>	<b>We</b>
Mean	115.4	80.4	24.9	10.9	37.2	4.2	41.8
Min	89.0	71.0	22.5	9.0	30.0	2.0	16.0
Max	151.0	91.0	27.0	12.0	47.0	8.0	69.0
N	14	14	14	14	11	9	14
U (MW)	57.0	75.5	32.5	46.5	42.0	11.0	53.5
p=	0.285	0.946	0.230	0.851	0.888	0.032	0.348

**Table 2**

Skull measurements (in mm) for *Neusticomys oyapocki*. Mann-Whitney non-parametric tests for comparing sexes. Abbreviations: CIL= Condylus-Incisor Length; ZB= Zygomatic Breadth; LN =Length of Nasals; LIB=Least Interorbital Breadth; LIF=Length of the Incisive Foramina; LD=Length of Diastema; BOC =Breadth of the Occipital Condyles; M1M2: crown length between first and second upper molars. U (MW)=U-value for Mann-Whitney test.

<b>Females</b>	<b>CIL</b>	<b>ZB</b>	<b>LN</b>	<b>LIB</b>	<b>LIF</b>	<b>LD</b>	<b>BOC</b>	<b>M1M2</b>
Mean	27.46	13.98	10.60	5.12	4.61	7.66	7.27	2.90
Min	24.00	12.10	9.00	4.52	4.10	6.60	6.50	2.70
Max	32.80	16.80	13.00	5.45	5.30	9.60	7.92	3.05
N	10	10	7	10	10	10	8	10
<b>Males</b>	<b>CIL</b>	<b>ZB</b>	<b>LN</b>	<b>LIB</b>	<b>LIF</b>	<b>LD</b>	<b>BOC</b>	<b>M1M2</b>
Mean	26.99	14.01	10.30	5.19	4.72	7.55	7.11	2.89
Min	22.00	12.00	8.85	4.80	3.90	5.80	6.83	2.74
Max	29.50	15.80	11.60	5.54	5.42	8.70	7.47	3.07
N	20	20	16	20	20	20	15	20
U (MW)	89.5	98	54	88	83	97	42.5	92.5
p=	0.6598	0.9474	0.9201	0.6125	0.4677	0.9123	0.2721	0.7568

were no sexual dimorphism in size, which seems to apply to all ichthyomyine taxa (Voss, 1988).

Of the 31 specimens with available dentitions, 19 (61%) have 2 molars on each jaw quadrant (8 molars total). Of the 12 remaining skulls, we encountered noteworthy variation in tooth number: 6 specimens have 2 upper molars on each side but 3 lower molars on at least 1 hemi-mandible (9 to 10 molars total), 2 specimens have 3 upper molars on one or both sides but 2 lower molars on each lower jaw (9 to 10 molars total), and 2 individuals have 3 molars in each jaw quadrant (12 molars total).

When present (Fig. 2), third molars are more often seen on lower jaws (in 10 individuals) than on upper jaws (6 individuals). The third molars are as frequent on the left (15 cases) as on the right (13 cases) sides.

The dental polymorphism can be assessed from several individuals that were collected from just two locations. These locations are from along the Rio Jari: 9 animals from the left bank at Laranjal do Jari (state of Amapa), near Cachoeira Santo Antônio (locality 12 on Fig. 1); and 8 animals from the right bank at Almeirim (state of Para), again near Cachoeira Santo Antônio (locality 11 on Fig. 1). As detailed on Table 3, dental polymorphism affects both upper and lower jaws in Laranjal do Jari, whereas it seems restricted to the lower jaws for Almeirim.

The third molars observed on *N. oyapocki* are tiny teeth (Fig. 2), half the size of the adjacent second molar (Table 4). Upper and lower third molars represent less than 19 and 21 percent, respectively, of the total crown length for first and second molars. Whereas M3 is a simple peglike tooth, m3 is slightly more complex, consisting of a reduced protoconid/metaconid pair.

The first and second molar teeth of *N. oyapocki* are also small by comparison with those of other similar-sized sigmodontine rodents. The relative size of molars (RSM) can be expressed by the ratio between condylo-incisive length (CIL) and crown length of the first and second upper molars (M1M2); RSM is 0.10 in *N.*

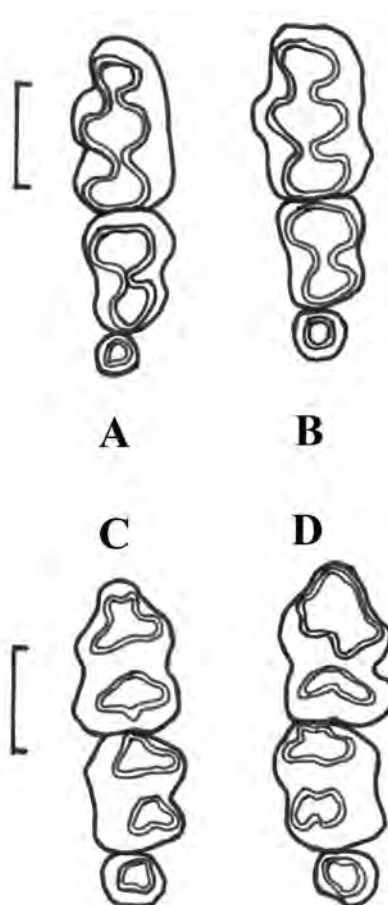


Fig. 2: Upper (A, B) and lower (C, D) dental rows in *Neusticomys oyapocki* specimens with three molars. A=INPA-5245; B=IEPA-3714; C=INPA-5154; D=ISEM-V-1647. The vertical bar is a 1 mm scale.

Table 3

Polymorphism in the numbers of molars in two opposite localities along the Rio Jari: Laranjal (left bank: Amapa side) and Almeirim (right bank: Para side). Molars are organized as upper left/upper right; lower left/lower right. One animal from Almeirim has its mandibles missing and is coded as ? / ? . Laranjal and Almeirim are localities 12 and 11, respectively, onto Fig. 1.

Molars	Laranjal	Almeirim
2 / 2 ; 2 / 2	4	4
2 / 2 ; 3 / 3	1	3
3 / 3 ; 2 / 2	1	0
3 / 3 ; 3 / 3	1	0
2 / 2 ; ? / ?	0	1

**Table 4**

Dental measurements (crown length, in mm) for upper (M) and lower (m) molars in *N. oyapocki*. Abbreviations: SD=Standard-Deviation; N=sample size.

	M1	M2	M3	m1	m2	m3
Mean	1.84	1.05	0.55	1.55	1.19	0.56
Min	1.69	0.92	0.46	1.37	1.02	0.51
Max	2.02	1.16	0.62	1.81	1.31	0.60
SD	0.08	0.07	0.07	0.11	0.06	0.03
N	25	25	5	24	24	9

*oyapocki* but ranges from 0.12 to 0.13 in *H. megacephalus*, *O. auyantepui*, *Z. brevicauda*, and *R. nitela* (Table 5). By contrast, the upper incisor (measured by the depth of incisor—DI of Voss, 1988) appears stronger

in *N. oyapocki* than in other similar sized species (Table 5). The ratio DI/M1M2 is 0.57 in *N. oyapocki* whereas it ranges from 0.41 (*H. megacephalus*) to 0.48 (*R. nitela*) in the four taxa under comparison.

**Table 5**

Selected measurements (in mm; weight in g) in *Neusticomys oyapocki* and in four similar-sized (average weight from 39 to 57 g) species of Guianan Sigmodontinae. Abbreviations: M1M2=crown length of upper first and second molars; DI=depth of upper incisor; CIL=condylo-incisive length. SD=standard-deviation; N=sample size

		M1M2	DI	CIL	Weight
<i>Neusticomys oyapocki</i>	mean	2.88	1.65	27.6	49.6
	SD	0.09	0.18	2.1	21.7
	min	2.7	1.4	23.7	24.0
	max	3.1	2.1	32.8	100.0
	N	25	25	25	15
<i>Hylaeamys megacephalus</i>	mean	3.45	1.40	26.8	45.3
	SD	0.14	0.13	1.5	10.0
	min	3.1	1.1	22.7	24.5
	max	3.8	1.6	29.1	80.0
	N	59	42	58	43
<i>Oecomys auyantepui</i>	mean	3.18	1.49	25.0	38.7
	SD	0.09	0.17	1.8	8.9
	min	3.0	1.2	21.3	24.0
	max	3.4	1.9	28.5	62.0
	N	63	62	63	37
<i>Rhipidomys nitela</i>	mean	3.34	1.60	27.6	53.1
	SD	0.11	0.16	1.7	12.9
	min	3.0	1.2	23.8	35.0
	max	3.6	1.9	31.3	85.0
	N	41	41	41	31
<i>Zygodontomys brevicauda</i>	mean	3.34	1.51	27.3	57.2
	SD	0.13	0.13	1.8	16.0
	min	3.1	1.2	22.9	26.0
	max	3.7	1.8	30.7	92.0
	N	60	59	59	38



## DISCUSSION

Male and female specimens of *N. oyapocki* overlap broadly in all external and craniodental dimensions, conforming to the general lack of sexual dimorphism previously reported for other ichthyomyines by Voss (1988). Consequently, we combined males and females of subadult and adult specimens in order to get more robust values of metric variables for characterizing the external and skull variability in this hitherto poorly known taxon.

Polymorphism in numbers of molars is extensive, with total numbers of molars ranging from 8 to 12; that variation occurs among specimens of *N. oyapocki* from several localities ranging from Suriname and French Guiana to the Brazilian states of Amapá and Pará. Thus, this phenomenon—which was not known previously in this species due to the scarcity of biological materials—appears to be rather widespread (see open circles in **Fig. 1**). Otherwise, dental polymorphism appears extremely rare in cricetid rodents, with one recent case of two individuals (out of 1763 examined specimens) with a supernumerary tooth in the sigmodontine *Necromys lasiurus* (Libardi and Percequillo, 2014). Because most ichthyomyines and all other cricetids normally have three upper and three lower molars, absence of third molars is probably a derived character state that has not yet been fixed in *N. oyapocki*.

The lengths of first and second molars are moderately variable in our sample of 31 *N. oyapocki*, with coefficients of variation ranging from 4.1 (for M1) to 7.3 (for m1), values at least twice as much as the corresponding statistics previously reported for the Central American ichthyomyine, *Rheomys thomasi* (Voss, 1988: **Table 1**). Nevertheless, the combined lengths of first and second molars are somewhat less variable, with coefficients of 3.3 for M1M2 and 4.7 for m1m2. Interestingly, the presence (or absence) of the third molar does not influence the crown length of the first and second molars. Unpaired Mann-Whitney tests indicate that the combined length of upper M1M2 or lower m1m2 does not vary with or without the presence of a third molar

(U (MW) = 58, and  $p = 0.7256$ ; U (MW) = 71, and  $p = 0.9774$ , for upper and lower jaws, respectively). Also, it appears that the presence of the third molar is not related to the size of the animal in *N. oyapocki*, as both F and t tests provide no statistical support for a size difference neither in Condylar-Incisor Length (6 skulls with 3 upper molars versus 25 skulls with 2 molars) nor in Mandibular Length (9 skulls with 3 lower molars versus 15 skulls with 2 molars).

In ichthyomyine rodents, the upper and lower third molars (M3/m3) are always small (or absent: this paper), and third molars have variable root morphologies (Voss, 2015). The third molars reported here for several specimens of *N. oyapocki* have a similar morphology as those of other species of *Neusticomys* (Voss, 1988: 339-347): M3 is very small, without a posterior track of metacone/hypocone; m3 is also very small, with or without a small posterior conule (see Fig. 39 in Voss, 1988).

The overwhelming majority of muroid rodents worldwide have three molars in each jaw. The few exceptions include some species and genera of carnivorous water rats and moss mice from New Guinea that have either no molar at all (*Paucidentomys*: Esselstyn et al., 2012) or only one or two molars per quadrant: *Rhynchomys*, *Pseudohydromys*, *Neohydromys*, *Microhydromys*, and *Paraleptomys* (Musser and Carleton, 2005; Balet et al., 2007; Musser et al., 2008; Esselstyn et al., 2012). In their revision of New Guinean moss mice, Helgen and Helgen (2009) have shown that there are differences in numbers of molars according to the species within the animalivorous genus *Pseudohydromys*: among the 12 recognized species of this Sahulian moss mouse, 5 have maxillary and mandibular tooththrows consisting of just 1 small molar each, and 7 species have two molars per quadrant. Furthermore, in the species *Pseudohydromys ellermanni* (Laurie and Hill, 1954), Helgen and Helgen (2009) have reported polymorphism in the number of molars which is probably similar to the one we describe for *Neusticomys oyapocki*: all 26 known specimens of *P. ellermanni* have 1 molar per quadrant except 2 individuals which retain an

additional small upper second molar. Another example of variation in number of molars is found in the scansorial rat *Leptomys arfakensis* Musser, Helgen & Lunde, 2008, in which the holotype has only 2 molars per jaw whereas the single paratype has a third extremely tiny molar (Musser et al., 2008); this is a rare exception, because four other species of *Leptomys*, each known by several dozen specimens, all have three molars per quadrant.

Tooth number, together with tooth size, cusp size and cusp number, are the four major factors of tooth patterning (Cai et al., 2007). As has been reported, the number of teeth is regulated by mesenchymal cell number (Cai et al., 2007), and tooth number as well as cusp number can be modelled as a reaction diffusion mechanism (Cho et al., 2007). Despite the enormous taxonomic and ecomorphological diversity of living rodents (especially Muroidea), we note that meristic variability in the molar row is more extensive in *N. oyapocki* than in any other known rodent species. Genomic and developmental studies of *N. oyapocki* could potentially offer key insights into the genetic control of molar development (Catón and Tucker, 2009; Jheon et al., 2013), as well as on the concerted effect of genetic and environmental factors on tooth development (Line, 2003).

## ACKNOWLEDGEMENTS

Burton Lim shared unpublished data for a specimen of *Neusticomys oyapocki* from Suriname. We are grateful to Rob Voss and to Tom Lee who offered extensive corrections to our text. We appreciate the generous hospitality of the Mastozoología team and the technical help of Jessica Souza dos Reis when studying specimens at the IEPA collection of Macapá. Our understanding of molar polymorphism in rodents benefitted from fruitful discussions with our colleague Helder Gomes Rodrigues. This research belongs to the project "Guyamazon II: Biodiversidade e zoogeografia de pequenos mamíferos no escudo das Guianas" which was funded by Ambassade de France in Brazil, IRD/AIRD (France), the French Guianan Region, CIRAD, FAPEAM, FAPEMA, and FAPEAP. Publication costs of that paper were covered by INDIGEN project of Benoit de Thoisy, through a FEDER/ERDF grant, funded by European Union, Collectivité Territoriale de Guyane, and DEAL Guyane.

## LITERATURE CITED

- BALETE DS, EA RICKART, RG ROSELL-AMBAL, SA JANSA and LR HEANEY. 2007. Descriptions of two new species of *Rhynchomys* Thomas (Rodentia: Muridae: Murinae) from Luzon Island, Philippines. *Journal of Mammalogy* 88:287-301.
- CAI J, S-W CHO, J-Y KIM, M-J LEE, Y-G CHA, and H-S JUNG. 2007. Patterning the size and number of tooth and its cusps. *Developmental Biology* 304:499-507.
- CATON J and AS TUCKER. 2009. Current knowledge of tooth development: patterning and mineralization of the murine dentition. *Journal of Anatomy* 214:502-515.
- CHO SW, J CAI and HS JUNG. 2007. Patterning of tooth in rodents. *European Cells and Materials* 14:82.
- COBOURNE MT and PT SHARPE. 2010. Making up the numbers: The molecular control of mammalian dental formula. *Seminars in Cell & Developmental Biology* 21:314-324.
- DUBOST G and F PETTER. 1978. Une espèce nouvelle de "rat-pêcheur" de Guyane française: *Daptomys oyapocki* sp. nov. (Rongeurs, Cricetidae). *Mammalia* 42:435-439.
- ESSELSTYN JA, AS ACHMADI and KC ROWE. 2012. Evolutionary novelty in a rat with no molars. *Biology Letters* 8:990-993.
- HAMMER Ø, DAT HARPER and PD RYAN. 2011. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4:1-9.
- HANSON JD, G D'ELIA, SB AYERS, SB COX, SF BURNEO and TE LEE. 2015. A new species of fish-eating rat, genus *Neusticomys* (Sigmodontinae), from Ecuador. *Zoological Studies* 54:1-11.
- HELGEN KM and LE HELGEN. 2009. Biodiversity and Biogeography of the Moss-mice of New Guinea: a taxonomic revision of *Pseudohydromys* (Muridae: Murinae). *Bulletin of the American Museum of Natural History* 331:230-313.
- JHEON AH, K SEIDEL, B BIEHS and OD KLEIN. 2013. From molecules to mastication: the development and evolution of teeth. *Wiley Interdisciplinary Review Developmental Biology* 2:165-183.
- LEITE RDN, MN DA SILVA and TA GARDNER. 2007. New records of *Neusticomys oyapocki* (Rodentia, Sigmodontinae) from a human-dominated forest landscape in northeastern Brazilian Amazonia. *Mastozoología Neotropical* 14:257-261.
- LIBARDI GS and AR PERCEQUILLO. 2014. Supernumerary teeth in *Necromys lasiurus* (Rodentia, Cricetidae): The first record in Sigmodontinae. *Mastozoología Neotropical* 21:219-229.
- LINE SR. 2003. Variation of tooth number in mammalian dentition: connecting genetics, development, and evolution. *Evolution & Development* 5:295-304.
- MIRANDA CL, RV ROSSI, TBF SEMEDO and TA FLORES. 2012. New records and geographic distribution extension of *Neusticomys ferreirai* and *N. oyapocki*



- (Rodentia, Sigmodontinae). *Mammalian Biology* 76:335-339.
- MUSSER GG and MD CARLETON. 2005. Superfamily Muroidea, Pp. 894-1531 in: *Mammal species of the world. A taxonomic and geographic reference* (DE Wilson and DM Reeder, eds.). Johns Hopkins University Press, Baltimore.
- MUSSER GG, KM HELGEN and DP LUNDE. 2008. Systematic review of New Guinea *Leptomys* (Muridae, Murinae) with descriptions of two new species. *American Museum Novitates* 3624:1-60.
- NUNES A. 2002. First record of *Neusticomys oyapocki* (Muridae: Sigmodontinae) from the Brazilian Amazon. *Mammalia* 66:445-447.
- OCHOA J and P SORIANO. 1991. A new species of water rat, genus *Neusticomys* Anthony, from the Andes of Venezuela. *Journal of Mammalogy* 72:97-103.
- PERCEQUILLO AR, AP CARMIGNOTTO and MJ SILVA. 2005. A new species of *Neusticomys* (Ichthyomyini, Sigmodontinae) from central Brazilian Amazonia. *Journal of Mammalogy* 86:873-880.
- ROWE KC, AS ACHMADI and JA ESSELSTYN. 2016. Repeated evolution of carnivory among Indo-Australian rodents. *Evolution* 70:653-695.
- VOSS RS. 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. *Bulletin of the American Museum of Natural History* 188:259-493.
- VOSS RS. 2015. Tribe Ichthyomyini Vorontsov, 1959, Pp. 279-290 in: *Mammals of South America, Volume 2. Rodents* (JL Patton, UFJ Pardinás and G D'Elia, eds.). The University of Chicago Press, Chicago.
- VOSS RS, DP LUNDE and NB SIMMONS. 2001. The mammals of Paracou, French Guiana: A Neotropical lowland rainforest fauna. Part 2: Nonvolant species. *Bulletin of the American Museum of Natural History* 263:1-236.

## APPENDIX 1

### Specimens of *Neusticomys oyapocki* examined

Specimens of *Neusticomys oyapocki* examined or mentioned are organized by country and locality according to the map of **Fig. 1**.

Abbreviations for Institutions: AMNH = American Museum of Natural History (New York); IEPA = Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá (Macapá); INPA = Instituto Nacional de Pesquisas da Amazonia (Manaus); ISEM = Institut des Sciences de l'Évolution de Montpellier (Montpellier); MHNG = Museum d'Histoire Naturelle de Genève (Geneva); MNHN = Museum National d'Histoire Naturelle (Paris); MPEG = Museu Paraense Emílio Goeldi (Belem); ROM = Royal Ontario Museum (Toronto).

BRAZIL: Amapá State: MPEG-34251: Amapá District: Fazenda Itapoa (locality 6); INPA-5243 to 5245: Área da Mineração Itajobi: approx. 15 km East from Serra do Navio (locality 8); IEPA-3269: Laranjal do Jari - próximo à BR 156 (locality 10); IEPA-1512, -1516, -2047, -2722, -2723, -2731, -3268, -3750: Laranjal do Jari: left bank of Rio Jari (locality 12); IEPA-3703, -3714: Mazagão: right bank of Rio Vila Nova (locality 9); IEPA-3258, 3536: Porto Grande, right bank of Rio Araguari (locality 7). Pará State: IEPA-1515, -1517, -1520, -1527, -1541, -1765, -2460, -2732, INPA-5141, -5151, -5154: Almeirim, right bank of Rio Jari (locality 11); MPEG-39999: Obidos municipality: Curua River (locality 13).

FRENCH GUIANA: MNHN-1977-775, ISEM-V-2832: Camopi: Trois Sauts (locality 5); ISEM-V-1647: Régina: Nouragues field station (locality 3); MNHN-1995-3234: Saint-Élie: Saint-Eugène along Courcibo River (locality 2); AMNH-267597, MNHN-1995-992: Sinnamary: Paracou (locality 1).

SURINAME: ROM-120588: Sipaliwini: Kutari River Camp (locality 4)

## APPENDIX 2

### List of specimens for comparisons with four other similar-sized Sigmodontinae.

#### Abbreviations for institutions as for Appendix 1.

##### *Hylaeamys megacephalus* (Fischer, 1814)

ISEM: V-1137, V-1693, V-2116, V-2137, V-2680;

MHNG: 1880.025, 1880.032, 1880.034, 1880.035, 1880.036, 1885.001, 1885.002, 1885.003, 1885.004, 1885.005, 1885.007, 1885.064, 1889.100, 1890.002, 1890.003, 1954.053, 1960.010, 1962.074, 1962.088, 1962.095, 1963.017, 1963.036, 1970.008, 1970.015, 1970.017, 1970.019, 1970.022, 1972.030, 1972.031, 1972.032, 1972.033, 1972.034, 1974.069, 1978.046, 1978.061, 1979.064, 1979.068, 1983.096, 1990.013, 1990.042, 1999.003, 1999.004, 1999.005, 1999.006, 1999.007, 1999.008, 1999.049;

MNHN: 1902-44, 1986-288, 1986-317, 1986-319, 2001-2229, 2001-2232, 2007-47;

##### *Oecomys auyantepui* Tate, 1939

IEPA: 3176, 3177, 3182, 3190;

ISEM: V-2126, V-2127;

MHNG: 1894.029, 1962.075, 1962.081, 1963.033, 1969.038, 1969.094, 1970.009, 1972.025, 1974.034, 1975.039, 1975.047, 1975.050, 1975.081, 1979.060, 1979.061, 1979.066, 1979.070, 1979.078, 1979.084, 1979.088, 1990.028, 1990.034, 1999.026, 1999.027, 1999.028, 1999.029, 1999.030, 1999.034, 1999.040, 1999.044;

MNHN: 1983-394, 1983-395, 1983-401, 1994-124, 1995-1027, 1995-3235, 1998-1844, 1999-140, 1999-141, 1999-142, 1999-143, 1999-144, 1999-145, 2003-50, 2004-324, 2007-40, 2007-41, 2007-42, 2007-43; ROM: 114022, 114121, 114314, 114331, 114338, 114342, 114357, 114358

##### *Rhipidomys nitela* Thomas, 1901

ISEM: V-0905, V-0914;

MHNG: 1886.054, 1890.013, 1890.014, 1894.016, 1962.094, 1969.090, 1969.093, 1969.096, 1969.100, 1972.064, 1972.065, 1972.066, 1974.050, 1975.048, 1975.073, 1975.080, 1975.085, 1975.088, 1979.071; MNHN: 2000-220, 2001-2063, 2001-2194, 2001-2195, 2001-2200, 2001-2201, 2001-2202, 2001-2203, 2001-2204, 2001-2206, 2001-2207, 2001-2208, 2001-2211, 2001-2212, 2003-42, 2003-43, 2007-55, 2007-56, 2007-57;

ROM: 114147;

##### *Zygodontomys brevicauda* (J.A. Allen & Chapman, 1893)

ISEM: V-0980, V-0984;

MHNG: 1885.012, 1885.013, 1885.014, 1885.015, 1885.016, 1885.017, 1885.018, 1886.055, 1886.056, 1886.057, 1889.083, 1974.054, 1975.015, 1975.084, 1984.045, 1984.055, 1990.027, 1990.051, 1990.052, 1990.055, 1990.057, 1990.058, 1990.059, 1990.061, 1990.062, 1990.063, 1990.064, 1990.065, 1990.066, 1990.067, 1990.068, 1990.069, 1991.029, 1991.030, 1991.031, 1991.032, 1996.016;

MNHN: 1986-917, 1986-921, 1986-924, 1986-926, 1986-929, 1986-930, 1986-936, 1986-937, 1986-938, 1986-945, 1986-946, 1986-947, 1986-948, 1986-949, 1986-950, 2000-1109, 2000-1111, 2000-1112, 2000-1113, 2001-2234, 2003-774