

A new species of water mouse, of the genus *Chibchanomys* (Rodentia, Muridae, Sigmodontinae) from Ecuador

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SYNOPSIS. A new species of the rodent genus *Chibchanomys* is described from Ecuador on the basis of external and cranial morphology. A phylogenetic analysis is used to assess the relationship of the new species to other ichthyomyine taxa.

INTRODUCTION

The New World rodents currently placed in the large and complex subfamily Sigmodontinae (*sensu* Carleton & Musser, 1984) include a morphologically and ecologically distinctive group of semi-aquatic South American genera (Voss, 1988), for which it is convenient here to use the name ichthyomyines. In a monograph of ichthyomyine rodents, Voss (1988) included five genera: *Ichthyomys* Thomas, 1893 (four species), *Anotomys* Thomas, 1906a (monotypic), *Rheomys* Thomas, 1906b (four species), *Neusticomys* Anthony, 1921 (four species) and a new genus, *Chibchanomys* Voss, 1988 for an enigmatic species of uncertain generic affinity. *Chibchanomys trichotis* (Thomas, 1897) was originally placed in *Ichthyomys* but was subsequently assigned to *Rheomys* (see Tate, 1932; Cabrera, 1961), then to *Anotomys* (see Handley, 1976). Subsequent to the revision by Voss, an additional ichthyomyine species, *Neusticomys mussoi* Ochoa & Soriano, 1991, has been described.

During the course of several zoological surveys of Las Cajas Plateau, Ecuador from 1981 to 1987, five specimens of an undescribed species of ichthyomyine rodent were captured. Observations were made on two of these animals, which subsequently escaped, while three specimens were donated to The Natural History Museum. Another specimen was filmed for the 1992 BBC National Geographic wildlife film 'Avenue of the Volcanoes' (Jim and Theresa Clare, personal communication). On the basis of external and craniodental characters the study specimens agree most closely with the generic diagnosis of *Chibchanomys* but are also sufficiently similar in some features to *Neusticomys* to warrant a phylogenetic analysis.

MATERIALS AND METHODS

The description of the new species is based on conventional morphological characteristics and the terminology used follows Voss (1988). Specimens were measured using dial calipers, with all measurements provided in millimetres. The skeletal elements remaining in the skins were observed by means of X-rays.

A parsimony analysis (PAUP Version 3.0) was carried out to determine the position of the new species relative to other ichthyomyines. Details of the eighteen characters used, listed below, are given more fully in Voss (1988 pages 440–442); the

hypothesised primitive state, using the criteria defined by Voss, is scored as '0'.

1. Pelage: glossy (0); dull (1).
2. Ventral pelage countershaded: absent (0); present (1).
3. Tail: unicolored (0); bicolored (1).
4. Philtrum: present (0); absent (1).
5. Pinnae: large, visible above fur (0); small, concealed in fur (1).
6. Superciliary vibrissae: present (0); absent (1).
7. Plantar pads of manus: hypothenar pad separate, not fused with third interdigital pad (0); hypothenar and third interdigital pads fused (1); hypothenar and thenar pads fused respectively with adjacent third and first interdigital pads (2).
8. Fringing hairs on pes: weakly developed (0); well developed (1).
9. Lower third molar: entoconid-hypoconid cusp pair distinct (0); m3 peglike, entoconid-hypoconid cusp pair absent or reduced to a small conule (1).
10. Nasal bones: long, produced anteriorly beyond premaxillae (0); short, truncated behind premaxillae (1).
11. Supraorbital foramina: on the lateral surface of the frontals, within orbital fossae (0); on the dorsal surface of the frontals between the orbital fossae (1).
12. Carotid arterial supply (see Voss, 1988 page 296): pattern 1 (0); pattern 2 (1); pattern 3 (2).
13. Orbicular apophysis of maleus: present (0); absent (1).
14. Metatarsal configuration: $III \geq IV > II \gg V > I$ (0); $IV > III > II, V > I$ (1).
15. Omohyoid muscle: present (0); absent (1).
16. Gastric glandular epithelium: present (0); restricted (1).
17. Gall bladder: present (0); absent (1).
18. Bacular cartilage: tridigitate, medial digit lacking a calcified centre (0); single digit (1); tridigitate, medial digit grossly swollen with calcified core (2).

The character states for the new species were assessed by PJ but the character state assessments for the other taxa were taken directly from Voss (1988 Table 45, page 441). Characters of the visceral and reproductive systems (characters 15–18 above) were unobservable in the new taxon because of the lack of whole bodies. In an initial analysis, all character states were unordered; in a second analysis, multistate characters were ordered (as by Voss): $0 \rightarrow 1 \rightarrow 2$ for characters 7, 12 but also for character 18. For character 18, the order recommended by Voss (1988) was $0 \rightarrow 1; 0 \rightarrow 2$, a sequence not readily handled by the analysis and affecting only one generic group

(*Rheomys*); Voss (personal communication) recommended an alternative ordering of this character (1 → 0 → 2) so in a third analysis, characters 7 and 12 were ordered as above and character 18 by this alternative.

ABBREVIATIONS USED IN THE TEXT

BMNH – The Natural History Museum [formerly British Museum (Natural History)]

M1, M2, M3 respectively first, second and third upper molars
m1, m2, m3 respectively first, second and third lower molars

ABBREVIATIONS USED FOR TAXA IN THE PAUP ANALYSIS:

Ale	<i>Anotomys leander</i> Thomas, 1906a
Ctr	<i>Chibchanomys trichotis</i> (Thomas, 1897)
Cor	<i>Chibchanomys</i> undescribed species
Ihy	<i>Ichthyomys hydrobates</i> (Winge, 1891)
Ipi	<i>Ichthyomys pittieri</i> (Handley & Mondolfi, 1963)
Itw	<i>Ichthyomys tweedii</i> Anthony, 1921
Nmo	<i>Neusticomys monticolus</i> Anthony, 1921
Nve	<i>Neusticomys venezuelae</i> (Anthony, 1929)
Rme	<i>Rheomys mexicanus</i> Goodwin, 1959
Rha	<i>Rheomys raptor</i> Goldman, 1912
Rtt	<i>Rheomys thomasi</i> Dickey, 1928
Run	<i>Rheomys underwoodi</i> Thomas, 1906b

RESULTS

Chibchanomys orcesi, sp. nov.

HOLOTYPE. BMNH 82.816, adult male, skin and skull; collectors' number 148; collected 22 August 1981 by members of the Oxford Expedition to Las Cajas from Lake Luspa, Las Cajas, Provincia Azuay, Ecuador, 02°50'S 79°30'W, altitude 3700m.

PARATYPES. BMNH 82.815, adult male, skin and skull; collectors' number 146, other details as for the holotype. BMNH 84.349, adult male, skin and skull; collectors' number 78; collected 7 August 1983 by members of the Combined Universities Expedition to Ecuador 1983, from Lake Llaviucu, Zorracucho Valley, Las Cajas, Provincia Azuay, Ecuador, 02°51'S 79°01'W, altitude 3100m.

DIAGNOSIS

An ichthyomyine species belonging to the genus *Chibchanomys* in the following combination of features. Dorsal pelage dull; small pinnae concealed in pelage of head; tail longer than head and body; manus with five separate plantar pads; hindfoot broad with well developed fringing hairs; supraorbital foramina open laterally within orbits; carotid circulation pattern 1.

Differing from *Chibchanomys trichotis* in the following characters. Rhinarium light brown; philtrum present; nasals medium in length, barely projecting anterior to premaxillae; orbicular apophysis of maleus present; upper incisors slightly inclined medially; M3 and m3 reduced in size; anteromedian flexid absent or barely indicated on anteroconid of m1; metatarsals III ≥ IV > II >> V > I.

DESCRIPTION

Tail subequal to or slightly longer than head and body (see Table 1

Table 1 External and cranial measurements of *Chibchanomys trichotis* and *C. orcesi*. Dimensions given as mean, plus or minus standard deviation, followed by range, with sample size in parentheses.

	<i>C. trichotis</i> Venezuela	<i>C. trichotis</i> Colombia	<i>C. trichotis</i> Peru	<i>C. orcesi</i> Ecuador
Head and body length	113.5 ± 5.50 105–120 (4)	125 (1)	102 (1)	105 ± 1.63 103–107 (3)
Tail length	126.8 ± 7.36 115–133 (4)	131 (1)	123 (1)	113.3 ± 6.18 108–122 (3)
Hindfoot length	31.8 ± 1.09 30–33 (4)	30, 33 (2)	31 (1)	22 ± 2.16 19–24 (3)
Ear length	7.5 ± 1.5 6–10 (4)	8 (1)	6 (1)	11.5 ± 1.87 9.5–14 (3)
Weight (in grams)	–	–	–	37 ± 2.83 35–41 (3)
Ratio of tail length to head and body length	1.12 ± 0.02 1.10–1.15 (4)	1.05 (1)	1.21 (1)	1.08 ± 0.06 1.02–1.16(3)
Ratio of tail length to condylo-incisive length	4.9 ± 0.12 4.7–5.0 (4)	5.1 (1)	5.2 (1)	4.3, 4.7 (2)
Ratio of hindfoot length to head and body length	0.28 ± 0.00 0.28–0.29 (4)	0.26 (1)	0.30 (1)	0.21 ± 0.02 0.18–0.23 (3)
Condyloincisive length	25.7 ± 1.01 24.3–26.9 (4)	25.9 (1)	23.8 (1)	23.0, 24.6 (2)
Diastema Length	6.3 ± 0.54 5.7–7.0 (3)	–	5.7 (1)	5.3 ± 0.29 5.0–5.7 (3)
Length of upper molars	4.4 ± 0.08 4.3–4.5 (3)	4.4 (1)	4.2 (1)	4.2 ± 0.05 4.1–4.2 (3)
Incisive foramina length	5.0 ± 0.27 4.6–5.3 (4)	5.1 (1)	4.5 (1)	4.5 ± 0.09 4.4–4.6 (3)
Breadth of incisor tips	1.2 ± 0.11 1.0–1.3 (4)	c1.2, 1.3 (2)	1.0 (1)	1.4 ± 0.05 1.4–1.5 (3)
Breadth of incisive foramina	1.9 ± 0.15 1.7–2.1 (4)	2.4 (1)	1.9 (1)	2.1 ± 0.09 2.0–2.2 (3)
Breadth of palatal bridge	3.1 ± 0.29 2.7–3.4 (3)	–	2.6 (1)	2.2 ± 0.08 2.1–2.3 (3)
Nasal length	9.0 ± 0.41 8.5–9.5 (3)	8.1 (1)	8.5 (1)	9.3 ± 0.29 8.9–9.6 (3)
Nasal breadth	3.0 ± 0.05 2.9–3.0 (4)	3.0 (1)	2.8 (1)	3.2 ± 0.05 3.1–3.2 (3)
Interorbital breadth	4.7 ± 0.13 4.5–4.8 (4)	4.9 (1)	4.3 (1)	4.6 ± 0.08 4.5–4.7 (3)
Zygomatic breadth	13.4 ± 0.66 12.3–14.1 (4)	c13.9 (1)	11.7 (1)	c12.8 (1)
Braincase breadth	13.4 ± 0.27 13.0–13.7 (4)	13.8 (1)	12.4 (1)	1.9, 12.0 (2)
Ratio of inter-orbital breadth to braincase breadth	0.35 ± 0.02 0.33–0.37 (4)	0.36 (1)	0.35 (1)	0.38, 0.39 (2)
Breadth of zygomatic plate	1.1 ± 0.05 1.0–1.1 (4)	1.0, 1.2 (2)	1.0 (1)	1.1 ± 0 1.1 (3)
Breadth of first upper molar	1.6 ± 0.05 1.5–1.6 (3)	1.5 (1)	1.4 (1)	1.3 ± 0.05 1.3–1.4 (3)
Height of upper incisor	4.6 ± 0.33 4.1–5.0 (4)	5.3 (1)	3.9 (1)	4.3–4.5 (3) 4.4 ± 0.08
Depth of upper incisor	1.3 ± 0.12 1.1–1.4 (4)	1.2 (1)	1.0 (1)	1.2–1.3 (3) 1.3 ± 0.05
Breadth across occipital condyles	7.4 ± 0.18 7.2–7.6 (4)	7.6 (1)	7.8 (1)	6.6, 6.7 (2)



Fig. 1 Live specimen of *Chibchanomys orcesi*.



Fig. 2 Skull of *Chibchanomys orcesi* (BMNH 1982.816) from left to right in dorsal, ventral and lateral view.

for measurements). Pelage soft, dense and woolly, dark brownish grey dorsally, light grey ventrally; tail greyish brown, densely haired, grey brown and brown hairs predominate proximally, with a proportional increase of buff and cream hairs distally, extending beyond tip in a short pencil. Distal portion of muzzle light grey in young adults, cream in older individuals (age based on degree of dental wear); rhinarium light brown in dry specimens; philtrum present; conspicuous silvery-grey mystacial vibrissae present. Pinnae small, concealed by pelage; region of more-or-less conspicuous light grey hairs ventro-lateral to pinnae. Manus with three interdigital and two carpal pads. Well developed fringe of stiff hairs on margin of metatarsus and digits of pes; claw of fifth digit extends beyond first interphalangeal joint of fourth digit; claw of first digit reaches midway along first phalange of second digit. See Fig. 1 for external features visible in a photograph of a live specimen.

Skull (see Fig. 2) with moderately long nasals, overlapping nasal orifice to conceal incisors in dorsal view but barely projecting beyond premaxillae; rostrum short and narrow, naso-lacrymal capsules evident in dorsal view; interorbital region moderately narrow relative to braincase breadth (0.38, 0.39 ($n = 2$)); frontals slightly inflated, braincase moderately broad and long; posterior border of incisive foramina between anterior roots of M1s, palatal foramina lie between posterior roots of M1s; bullae slightly inflated; orbicular apophysis of maleus present. Carotid circulation pattern 1, based on osteological features (see Voss, 1988: 298).

Upper incisors moderately narrow, anterior enamel surface pale buff, slightly inclined medially. No anteroloph on M1; small posteroloph on M2; M3 small, protocone and paracone evident in unworn dentition, posterior conule absent. Anteroconid of m1 simple or with slight indication of anteromedian flexid; no anterolophid on m2; small posterolophids on m1 and m2, small mesolophids present or absent; m3 small, with small posterior basally positioned conulid.

Metatarsal proportions: third metatarsal slightly longer than fourth, fourth longer than second; all three far longer than first and fifth; fifth longer than first. Configuration: $III \geq IV > II \gg V > I$.

ETYMOLOGY

This species is named in honour of Professor Gustavo Orcés, a pioneer of Ecuadorian mammalogy. He was of great help to AB with fieldwork organisation in Ecuador, and his kindness and knowledge were a source of inspiration.

DISTRIBUTION AND ECOLOGY

Known only from Las Cajas Plateau, Ecuador, where specimens have been recorded from three localities: Lake Luspa, Lake Llaviucu, Zorracucho Valley and Lake Torreadora. All specimens were trapped in close proximity to fast-flowing streams at altitudes ranging from 3100m to 4000m, in high-altitude moorland vegetation (paramo) (see Barnett, 1992). For more precise details of the habitat at each site and notes on diet see Barnett (1997).

COMPARISON WITH *C. TRICHOTIS*

The new species is similar in external appearance to *C. trichotis*, except that the pelage is paler and slightly harsher, and the rhinarium is light brown in dry specimens of *C. orcesi*, black in *C. trichotis*. A philtrum is present in *C. orcesi* but absent in *C. trichotis*. *Chibchanomys orcesi* is smaller in external size and averages smaller in cranial size than all known specimens of *C. trichotis*, with the exception of the single specimen from Peru (see below for comments on the status of this specimen). Both species of *Chibchanomys* are similar in external proportions, except that the hindfoot is proportionately shorter in *C. orcesi* (see Table 1). The metatarsal

configuration differs in the two species: $IV > III > II = V > I$ in *C. trichotis*; $III \geq IV > II \gg V > I$ in *C. orcesi*. The two species differ in the following cranial features: while the nasals of both species are of comparable length, those of *C. orcesi* are slightly broader and barely project anterior to the premaxillae, unlike those of *C. trichotis*, which project anteriorly and conceal the incisors and nasal orifice in dorsal view. In lateral view, the globose braincase of *C. trichotis* rises abruptly in the frontal region, unlike the narrower and less inflated braincase of *C. orcesi*; the braincase is slightly broader and the breadth across occipital condyles is greater in *C. trichotis* (see Table 1). The orbicular apophysis of the maleus is present in *C. orcesi* but absent in *C. trichotis*. The upper incisors of *C. orcesi* are less delicate and slightly broader than those of *C. trichotis* (see Table 1), the anterior enamel surface of *C. trichotis* is cream coloured and not medially inclined unlike *C. orcesi*. The third upper molar is smaller relative to M1 and M2, and m3 is smaller relative to m1 and m2 in *C. orcesi* than in *C. trichotis*. The anteromedian flexid is absent or barely indicated on the anteroconid of m1 in *C. orcesi* but present in *C. trichotis*, dividing the anteroconid into small but distinct lingual and labial conulids. The posterior conulid of m3 is positioned more basally in *C. orcesi* than in *C. trichotis* (when present).

According to Voss (1988) the young specimen that he identified as *C. trichotis* from Peru differs from the northern specimens of *C. trichotis* in several features: the braincase is much less inflated, the occipital condyles are slightly broader, the bullae are somewhat smaller and an indistinct philtrum is indicated; features that resemble those of the new species. Voss mentioned that these differences might indicate that southern populations of *Chibchanomys* are phenotypically distinctive from their northern counterparts. Unfortunately it has not proved possible to examine the Peruvian specimen, although information on it was kindly provided by Mark Hafner (personal communication). It is possible that the Ecuadorian and Peruvian specimens are conspecific but additional material and more extensive comparisons are required to elucidate the status of the latter specimen.

COMPARISON WITH OTHER ICHTHYOMINE GENERA

Chibchanomys is readily distinguished from *Anotomys*, *Ichthyomys* and *Rheomys* (see Voss, 1988). *Chibchanomys* and *Neusticomys* differ from other ichthyomyines in showing carotid arterial circulation pattern 1 and in the distribution of the glandular epithelium around the stomach. *Chibchanomys* differs from *Neusticomys* in having small pinnae concealed in the pelage (pinnae obvious in *Neusticomys*); ventral countershading present (absent in *Neusticomys*); tail longer than head and body (tail shorter than head and body in *Neusticomys*); the hindfoot is broader with longer digits and the fringing hairs are well developed (narrower with shorter digits and less developed fringing hairs in *Neusticomys*). The new species does however share several features with *Neusticomys* which are not exhibited by *C. trichotis*, such as the similar metatarsal configuration and presence of a philtrum, while the orbicular apophysis of the maleus is also present in some species of *Neusticomys*.

RESULTS OF THE PHYLOGENETIC ANALYSIS

There is evidence in support of the ichthyomyines as a monophyletic group of the subfamily Sigmodontinae (*sensu* Carleton & Musser, 1984) (see Voss, 1988). In contrast, evidence in support of the monophyly of the Sigmodontinae is lacking and a tribal level classification of this subfamily, while convenient in many respects, is unsatisfactory from a phylogenetic point of view, making difficult the choice of satisfactory outgroups for phylogenetic analyses (see Voss, 1988: 436–438, 1991: 33–37; Carleton & Musser, 1989: 53–55; Voss & Carleton, 1993: 21–22). The necessity of making such a

Table 2. Matrix showing character state distributions among 12 ichthyomyine species (for details see text and Voss, 1988). The character state assessments for all taxa other than *C. orcesi* were taken directly from Voss (1988 Table 45, page 441). Character states for the new species were assessed by PJ except for those of the visceral and reproductive systems (characters 15–18) which were unobservable in the new taxon, so scored as ‘?’.

Taxa	Characters																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Ale	1	1	0	1	1	0	1	1	1	0	0	1	0	1	1	1	0	1
Ctr	1	1	0	1	1	1	0	1	1	0	0	0	1	1	0	0	0	0
Cor	1	1	0	0	1	1	0	1	1	0	0	0	0	0	?	?	?	?
Ihy	0	1	0	0	0	1	0	1	0	1	1	2	0	1	0	1	1	0
Ipi	0	1	0	0	0	1	0	1	0	1	1	2	0	1	0	1	1	0
Itw	0	1	0	0	0	1	0	1	0	1	1	2	0	1	0	1	1	0
Nmo	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Nve	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0
Rme	0	1	1	1	1	2	1	1	0	0	2	0	1	1	1	1	0	2
Rha	0	1	0	0	0	1	1	1	0	0	0	2	0	1	0	1	0	2
Rtt	0	1	0	0	0	1	1	1	0	0	0	2	0	1	0	1	0	2
Run	0	1	1	1	1	2	1	0	0	0	2	0	1	0	1	0	2	2

choice has been avoided in the current study, since it is aimed at determining the level of affinity of the new taxon to other ichthyomyines, rather than seeking to add any new dimension to the phylogenetic status of the ichthyomyines as a group. Instead an hypothetical outgroup was constructed in which all character states were assessed as primitive, which was used to root the trees.

Using branch and bound algorithms, a search was made of the character data summarised in Table 2. In the analysis in which all character states were unordered, the length of the shortest tree was equal to 32 character state transformations and six trees were retained. In each of the other analyses (with the multistate characters 7 and 12 ordered, and character 18 varyingly ordered) the length of the shortest tree was equal to 33 character state transformations but

only three trees were retained. The variation in treatment of character 18, was not considered to be particularly important in this study, since character state 2 is exhibited only by taxa of the genus *Rheomys*. In both of the latter analyses *C. orcesi* and *C. trichotis* are non-monophyletic in all three trees and also in the semistrict consensus of these trees (see Fig. 3). The only evidence of a monophyletic generic grouping shown in the semistrict consensus tree is for *Ichthyomys*, and this tree is similar in most respects to the most parsimonious hypothesis of ichthyomyine relationships shown by Voss (1988: Fig.88).

DISCUSSION

There is obvious conflict in that the results of the phylogenetic analysis do not support the generic classification currently in use. The morphological data is sufficiently persuasive to conclude that, on the available material, the new taxon is correctly attributed to the genus *Chibchanomys* as currently construed.

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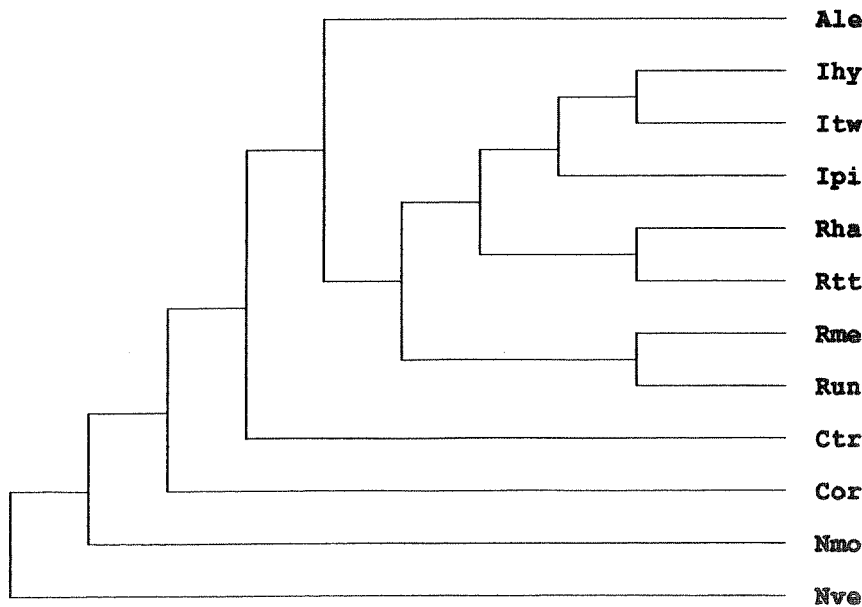


Fig. 3 Semistrict consensus tree showing hypothetical phylogenetic relationship of *Chibchanomys orcesi* to other taxa of ichthyomyine rodents. Consistency Index 0.636, Retention Index 0.786.

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