

Short Note

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The taxonomic status of *Copemyodon ecuadorensis* (Rodentia, Cricetidae), a supposedly extinct muroid from the Ecuadorean Quaternary

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Abstract: *Copemyodon ecuadorensis* was described as a non-sigmodontine extinct cricetid from two rich fossiliferous localities in northern Ecuador. It was hypothesized as being related to both the fossil genus *Copemys* and the living *Peromyscus* and, as such, is an example of an independent “copemyine-neotomine” attempt to colonize South America. Here, we re-study the holotype of *C. ecuadorensis* concluding that it cannot be separated from *Reithrodontomys* (Cricetidae, Neotominae) at a generic level. *Copemyodon* constitutes a junior synonym of *Reithrodontomys*. There are recent populations of *Reithrodontomys* in Ecuador and most likely it comprises several species. In this context, seems convenient to retain *ecuadorensis* as a species of *Reithrodontomys* until an appropriate revision of this genus is performed, although we identify morphological similarities between *Reithrodontomys ecuadorensis* and the nominal form *Reithrodontomys soederstroemi*.

Keywords: *Copemys*; Ecuador; neotominae; *Reithrodontomys*.

Muroid rodents are currently represented in South America by three sub-families, with sigmodontines being the dominant group (Patton et al. 2015). Concordantly, the

fossil record of cricetids in the subcontinent, although very poor compared with its recent diversity, is almost exclusively composed by members belonging to the subfamily (Pardiñas et al. 2002). As an exception, a form unearthed from Quaternary deposits in northern Ecuador, the genus *Copemyodon* Fejfar et al. 1996, was attributed to the Neotominae (Fejfar et al. 1996). Represented by a single species, *Copemyodon ecuadorensis* Fejfar 1996, this small cricetid was interpreted as morphologically close to the fossil genus *Copemys* Wood 1936, but also to the living one *Peromyscus* Gloger 1841 (Fejfar et al. 1993, 1996). In this systematic scenario and taking into account its isolated occurrence within a dense assemblage of fossil sigmodontines, *Copemyodon* was hypothesized as an example of an independent “copemyine-neotomine” attempt to colonize South America (Fejfar et al. 1996).

Despite its putative importance, *Copemyodon* was almost not discussed again after its original description. Probably coined too late to be listed by McKenna and Bell (1997), the genus was virtually ignored by all subsequent treatments (e.g. Patton et al. 2015), only briefly mentioned as linked to the fossil record of *Peromyscus* (cf. Musser and Carleton 2005) and in a few reviews about the evolutionary history of the group (e.g. Pardiñas et al. 2002, Zijlstra et al. 2014). As an example of the destiny of a plethora of fossil forms in a universe, currently dominated by molecular systematics, characteristic of the recent record of sigmodontine rodents, two decades later *Copemyodon* integrates a large number of enigmatic taxa.

In their analysis, Fejfar et al. (1996) posited an erroneous biogeographical scenario when they described *Copemyodon*; these authors stated “... the copemyine-peromyscine group, previously considered to be restricted to Northern and Central America, and which presence in South America has never before been reported” (Fejfar et al. 1996:138). Certainly the “copemyine-peromyscine group” is a heterodox construction; even in the 1990s because it combines stem cricetids, mostly represented by *Copemys* with a large array of crown members now subsumed within the Neotominae (Carleton and Musser

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1984). Beyond this, according to the authoritative view of Patton (2015:58–59), “The Sigmodontinae comprise the vast majority of cricetid rodents in South America, representing a large radiation. Only single species of *Reithrodontomys* and of *Isthmomys* of the otherwise highly diverse and mostly Northern or Middle American Neotominae... and of *Tylomys* of the lesser diverse Middle American Tylomyinae... extend into South America. Neotomine and tylomyine taxa are limited to western Colombia and adjacent Ecuador”. In brief, Fejfar et al. (1993, 1996) overlooked the occurrence of the neotomine genus *Reithrodontomys* Giglioli 1874 in Ecuador, formerly recognized by most authors since Thomas (1898), described *Reithrodontomys soederstroemi* with type locality in Quito.

When described by Fejfar et al. (1996:139), the holotype of *Copemyodon ecuadorensis* was referred as “Holotype: lower left jaw with m1–3, temporarily stored at the Department of Earth Sciences of the University of Florence”. Now, this material is correctly labeled as holotype under the number MECN 129, in the paleontological collections of the Museo Ecuatoriano de Ciencias Naturales (Quito, Ecuador). The correspondence of MECN 129 with the material figured by Fejfar et al. (1996: figures 2 and 3) is beyond doubt. In addition, several upper and lower tooththrows, cranial fragments and isolated molars originally referred by Fejfar et al. 1996 to *Copemyodon* are also available for study in MECN collections (see Appendix 1).

The holotype of *Copemyodon ecuadorensis* is a left dentary with m1–3 (molar nomenclature used here follows Reig 1977) and the horizontal ramus well preserved although both the angular and coronoid processes are broken and the incisor is missing. According to the degree of wear of the molars, it belongs to a moderately adult individual (Figure 1). It was recovered at La Calera (0°30′04.74″N, 77°51′47.33″W, 2710 m) in a profile described near Cantón Bolívar in the province of Carchi, northern Ecuador. The holotype of *C. ecuadorensis*, as well as abundant additional material referred for this taxon, include a late Holocene small mammal assemblage representing several sigmodontine rodents, lagomorphs, and soricomorphs (see Fejfar et al. 1993). A single specimen also attributed to *Copemyodon* was recovered at Quebrada Cuesaca (0°31′04.17″N, 77°53′13.53″W, 2640 m), a late Pleistocene-Holocene assemblage recovered very near to La Calera (see Fejfar et al. 1993, 1996).

Fejfar et al. (1996:139) described *Copemyodon* as a “medium sized cricetid” with lower brachydont molars displaying main cusps in alternate pattern and having bisected anteroconid, a “drop-like” mesostylid and an “ectolophid or ectostylid regularly joining the anterior side of hypolophid”. The upper molars were highlighted

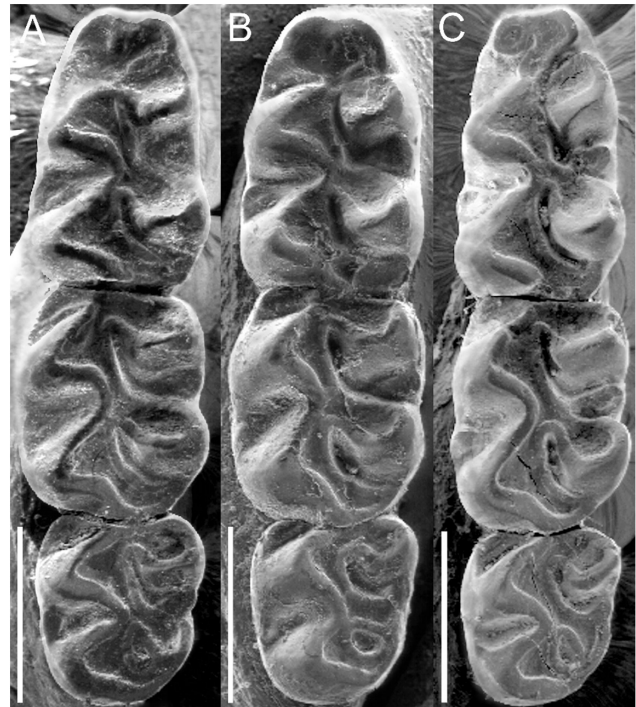


Figure 1: Comparison among the left m1–3 in occlusal view of the neotomines *Copemyodon ecuadorensis* (A=MECN 129, holotype; La Calera, Bolívar, Carchi, Ecuador; Holocene), *Reithrodontomys mexicanus soederstroemi* (B=MECN 1135; Quebrada Pistud, Carchi, Ecuador; Recent) and *Reithrodontomys mexicanus milleri* (C=MEPN 6416; Pinantura, Antisana, Pichincha, Ecuador; Recent). Scale = 1 mm.

by “labially shifted, asymmetric and wide anterocone” and large mesoloph. All these dental traits were considered as “very unique and primitive”. Probably guided by the incorrect presumption that the authors had at the unique South American neotomine, Fejfar et al. (1993, 1996) focused the comparisons to the widespread living genus of the subfamily, *Peromyscus*. They also compared the fossil Ecuadorean material to the Nearctic but extinct form, *Copemys*. These comparisons overlooked a basic rule in any taxonomic approach to first check the living assemblage at the local and regional scales to look for potential candidates for comparison. When such is done, *Copemyodon* is indistinguishable from *Reithrodontomys* and *Copemyodon ecuadorensis* is very close to the forms contained in the *Reithrodontomys mexicanus* species group (reviewed by Arellano 2015; figure 1). Beyond the general agreement that we found between the morphology of the material referred to *Copemyodon* and several recent specimens of *R. mexicanus* species group from Ecuador (see Appendix 1), additional confirmation of our taxonomic hypothesis is derived from the incisor morphology. *Reithrodontomys*, as a genus, is diagnosed by the presence of a well-developed

Table 1: Dental measurements (in mm) of *Copemyodon ecuadorensis* (MECN 129, holotype; left lower jaw from La Calera, Bolívar, Ecuador; Holocene) and the living neotomine *Reithrodontomys mexicanus* (Ecuadorian specimens).

	<i>C. ecuadorensis</i>	<i>R. m. eremicus</i>	<i>R. m. soedertroemi</i> (n=8)	<i>R. m. milleri</i> (n=9)
m1, length	1.62	1.50	1.45 ± 0.06	1.27 ± 0.06
m1, width	1.14	0.96	0.92 ± 0.03	0.81 ± 0.04
m2, length	1.20	1.11	1.09 ± 0.04	0.89 ± 0.13
m2, width	1.05	1.00	0.95 ± 0.02	0.87 ± 0.06
m3, length	1.11	1.00	1.07 ± 0.05	0.80 ± 0.07
m3, width	0.89	0.88	0.82 ± 0.03	0.74 ± 0.07
m1–3 alveolar length	3.70	3.76	3.62 ± 0.06	3.32 ± 0.21

groove, slightly displaced to the labial side, which cross the anterior face of each upper incisor (cf. Hooper 1952). These grooves resemble those of the sigmodontine rodent genus *Reithrodon* Waterhouse 1837 and are the basis of the generic epithet applied for this neotomine. In the context of the small size of the known species of *Reithrodontomys*, one of the smallest cricetids, the presence of grooved incisors is diagnostic (Hooper 1952). We searched the numerous isolated incisors recovered from La Calera and detected suitable examples that can be confidently attributed to *Reithrodontomys* (Supplemental Figure 1).

The holotype of *Copemyodon ecuadorensis* shares with the species comprised in the *Reithrodontomys mexicanus* species group several morphological traits (Figure 1, Supplemental Figure 1), including a gracile and slender dentary with a moderately marked masseteric crest, an inconspicuous capsular projection, small brachydont molars, main cusps arranged in alternate pairs, murids anteriorly-posteriorly aligned, procingulum of m1 composed by two conulids, mesostylids and ectostylids present in both m1–2 and a posteroflexid reduced to an enamel ring in the m3. Dental measurements are also in accordance and support the identity between both taxa (Table 1).

Summarizing, Fejfar et al. (1993, 1996) were correct in their assertion that a neotomine representative was present in the Quaternary deposits of northern Ecuador. However, they failed to connect their findings with the single living genus of this subfamily that reaches this country, *Reithrodontomys*. *Copemyodon* constitutes a junior subjective synonym of *Reithrodontomys* (*Aporodon*). The current taxonomic scenario for this genus in Ecuador (Arellano 2015) embraces a single species, *Reithrodontomys mexicanus* (Saussure 1860) containing at least three recognized subspecies, *Reithrodontomys mexicanus eremicus* (Hershkovitz 1941), *Reithrodontomys mexicanus milleri* (Allen 1912) and *Reithrodontomys mexicanus soedertroemi* (Thomas 1898). However, Moreno and Román (2013) highlighted relevant craniodental differences among these mentioned forms that suggest that each could be ranked as a species

(see also the genetic and morphometric data analyzed by Chávez 2012). For the present, we retain *ecuadorensis* as a species under the new name combination *Reithrodontomys ecuadorensis* (Fejfar et al. 1996). This name is therefore available in the context of a much needed revision of South American populations of this genus (see also Gardner and Carleton 2009). *Reithrodontomys ecuadorensis* differs metrically from *R. m. milleri* (see Table 1). Dental similarities, such as the well-developed paraflexus shared between *R. ecuadorensis* and *R. m. soedertroemi*, while in *R. m. eremicus* this structure is shorter (see Moreno and Román 2013), support their putative conspecificity (Figure 1).

As *Copemyodon* is a junior synonym of *Reithrodontomys*, the fossil records of La Calera and Quebrada Cuesaca are eloquent to indicate that the latter genus has, at least, Late Pleistocene and Holocene occurrences in Ecuador. Apparently, those from Quebrada Cuesaca (Late Pleistocene) are the oldest record for the subfamily in South America. Neotomines, as well as other major groups of rodents that today are primarily Nearctic in distribution such as Heteromyidae and Geomyidae, probably had an important local evolutionary history. However, to date, in absence of paleontological evidences, it is mostly a speculative matter (see, e.g. the discussion about the history of heteromyids in Alexander and Riddle 2005).

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Appendix

Appendix 1: Specimens studied in this contribution belong to the collections of Museo Ecuatoriano de Ciencias Naturales (MECN; Quito, Ecuador) and Instituto de Ciencias Biológicas de la Escuela Politécnica Nacional (MEPN; Quito, Ecuador).

Copemyodon ecuadorensis. MECN 129 (holotype), incomplete left lower jaw; MECN 128, 2 M1; MECN 130, 8 M1, right premaxillary, left maxillary tooth-row and 6 M1; MECN 132, 7 M1; MECN 133, 5 m1; MECN 134, 6 M1 and 13 m1; La Calera, Bolívar, Carchi, Ecuador; Holocene.

Reithrodontomys mexicanus soederstroemi. MECN 1138, 1139, 1140, Quebrada de Cuesaca, Bolívar, Carchi, Ecuador; MECN 1132, 1133, 1135, 1136, 1137, Quebrada de Pistud, Bolívar, Carchi, Ecuador.

Reithrodontomys mexicanus milleri. MEPN 6415, 6416, 6417, 6418, 6419, Pinantura, Antisana, Quito, Pichincha, Ecuador; MEPN 6891, 6902, 11624, 11625, Papallacta, Oyacachi, Napo, Ecuador.

Reithrodontomys mexicanus eremicus. MEPN 11790, El Cabuyal, Pablo Arenas, Imbabura, Ecuador.

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