

First record of a copemyine-peromyscine cricetid (Rodentia, Mammalia) in South America: hypotheses regarding its ancestry in the Palaearctic

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Abstract. Recent research in northern Ecuador (South America) has produced the first evidence of the occurrence of a copemyine-peromyscine cricetid in Late Pleistocene and Holocene deposits. Today, these forms occur only in North and Central America, and have never been reported, even in fossil faunas, in South America. This new copemyine-peromyscine form (*Copemyodon ecuadorensis* nov. gen et sp.) is very primitive, and resembles *Copemys* WOOD, 1936, rather than *Peromyscus* GLOGER, 1841. Few living species of *Peromyscus* (e. g., *P. truei* SHUFELDT, 1885, and *P. leucopus* RAFINESQUE, 1818) retain such archaic characters in the occlusal pattern of molars (FEJFAR et al. 1993). This record provides new evidence for the interpretation of faunal interchange between North and South America, and for the ancestry of copemyine-peromyscine cricetids in the Palaearctic. Some current hypotheses are discussed.

Key words: Rodents, Cricetidae, dental morphology, Ecuador, South America, late Pleistocene, Holocene.

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I. INTRODUCTION

A program of multidisciplinary scientific research in Ecuador has been carried out since 1987 by a staff of Italian and Ecuadorian students. In particular, efforts have been concentrated in the northernmost Interandean Depression (Bolívar area, Carchi Province) (Fig. 1). Two fossiliferous localities, Quebrada Cuesaca and La Calera, of Late Pleistocene and Holocene age, respectively, have been studied in detail (FICCARELLI et al. 1993a,b; FEJFAR et al. 1993). They have both yielded good fossil records, where small mammals, especially cricetids, dominate. The cricetid assemblage

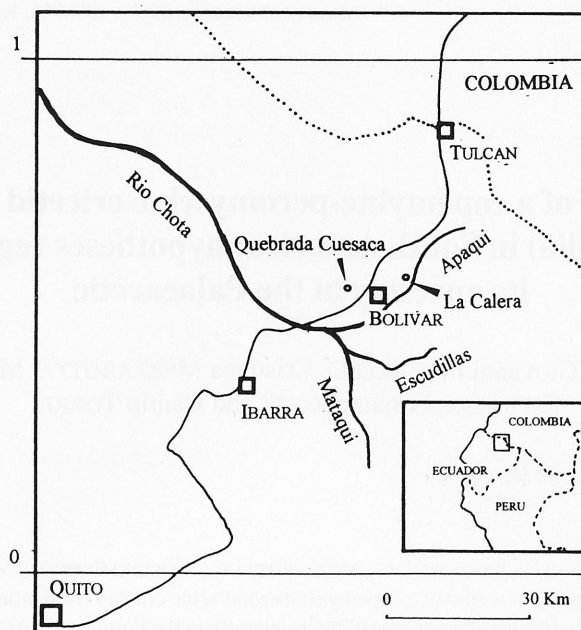


Fig. 1. Location of the fossiliferous sites in the Bolivar area, Carchi Province.

is represented by forms with a great variety of ecological adaptations. They mainly belong to the sigmodontine group, which includes typical Nearctic forms: the exception is a pastoral form, recognized as a member of the copemyine-peromyscine group, previously considered to be restricted to Northern and Central America, and whose presence in South America has never before been reported. This peculiar form, initially identified as cf. *Peromyscus* nov. sp. (FEJFAR et al. 1993), is here described as *Copemyodon ecuadorensis* nov. gen. et sp. It is present at both localities, being much more abundant in the Holocene site of La Calera. A description of the form and a dental analysis of selected specimens are presented in this paper: paleobiogeographical inferences on faunal interchange between North and South America and on patterns of adaptive radiations of the immigrant forms are revised and suggested.

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II. SYSTEMATIC PALAEONTOLOGY

Rodentia

Cricetidae ROCHEBRUNE, 1883

Cricetinae STEHLIN & SCHAUB, 1951

Copemyodon nov.gen.

Type species: *Copemyodon ecuadorensis* nov.gen. et sp. (monotypic).

D i a g n o s i s: *Copemyodon* nov.gen. from Late Pleistocene (late Lujanian land mammal age) and Holocene localities (Quebrada Cuesaca and La Calera, respectively; Bolivar area, Carchi Province, northern Ecuador) resembles *Copemys* WOOD, 1936 more than *Peromyscus* GLOGER, 1841 in the alignment of the main lingual and labial cusps of the molars. The cusps of the upper molars show only posterior connections, those of the lower molars have only anterior connections. The lower first molars are also characterized by the presence of a mesostylid instead of the absent mesolophid, while in the upper M1's a long and narrow mesoloph is attached to the anterior wall of the hypocone.

E t y m o l o g y: Named for the close affinity to the genus *Copemys* WOOD, 1936.

G e n e r a l r e m a r k s: Among cricetids recorded in Quebrada Cuesaca and La Calera, one form is very primitive, in many respects resembling Upper Miocene species of the genus *Copemys* WOOD, 1936, and the Pliocene to Recent genus *Peromyscus* GLOGER, 1841 (CLARK et al. 1964; LINDSAY 1972; SHOTWELL 1967; BASKIN 1978, 1986). No living species of *Peromyscus* displays such an archaic molar pattern.

D e n t a l c h a r a c t e r s: The dental morphology is very unique and primitive, with a pattern of alternation of the main cusps of the brachyodont molars. M1 inf.: anteroconid short and unequally double cusped, without spurs of anterolophulid; mesosinusid regularly closed by a transverse-oval ("drop like") mesostylid, never attached to the anterior wall of entoconid; mesolophid absent, and ectolophid or ectostylid regularly joining the anterior side of hypolophid. M1 sup.: rarely bilobed, wide, labially shifted (*Democricetodon*/*Copemys* like) anterocone; labial spur in the anterolophule; regular, long and independent mesoloph attached to the anterior wall of the hypocone; lingual sinus with small entostyle. Upper molars retain more primitive characters than lower ones. Both first upper and lower molars have one accessory root.

Copemyodon ecuadorensis nov.sp.

(Fig.2: 3-16, Fig.3)

H o l o t y p e: lower left jaw with m1-m3, temporarily stored at the Department of Earth Sciences of the University of Florence (Fig. 2: 4; Fig. 3: 4, 6).

T y p e l o c a l i t y: La Calera (Bolivar area, Carchi Province, northern Ecuador, South America).

D i a g n o s i s: Medium sized cricetid. Lower molars: short double cusped anteroconid without anterolophulid, presence of a "drop-like" mesostylid (not attached to the anterior wall of entoconid), instead of the absent mesolophid; ectolophid (ectostylid) on the anterior side of hypolophid. Upper molars: labially shifted, asymmetric and wide anterocone, straight labial outline, long mesoloph attached to the anterior mure of the hypocone in the first upper molars.

R e f e r r e d s p e c i m e n s: from Quebrada Cuesaca: one upper M1. From La Calera: 34 first lower molars; 49 first upper molars, 2 maxillaries with M1-M3, and 2 jaws with m1-m3. All specimens are temporarily stored at the Department of Earth Sciences of the University of Florence.

E t y m o l o g y: named for Ecuador, where the material has been found.

A g e: Late Lujanian land mammal age, Late Pleistocene (Quebrada Cuesaca) and Holocene (La Calera).

D e s c r i p t i o n: Lower molars (Fig. 2: 3, 4, 6-11, Fig. 3: 7-13); m1: symmetric and suboval occlusal outline, narrowing anteriorly. Features of anteroconid morphology: 1 – typically short and unequally double cusped, without spurs on the anterolophulid; 2 – anterior groove open or rarely closed; 3 – the larger lingual cusp joins the long anterior arm of the protoconid (anterolophulid), the labial cusp is isolated (Fig. 2: 6); 4 – the lingual cusp joins the medial part of

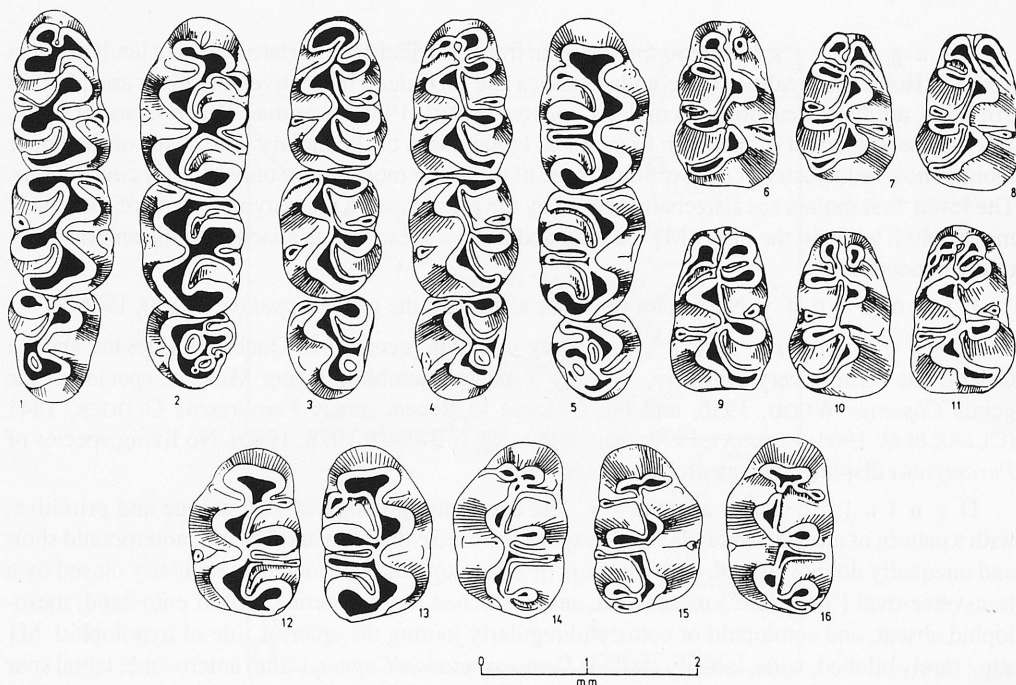


Fig. 2. 1-2: *Peromyscus leucopus* RAFINESQUE, 1818 (Muséum National d'Histoire Naturelle, Institut de Zoologie, Paris, 1950 no.107); 3-16: *Copemyodon ecuadorensis* nov. gen. et sp. from Quebrada Cuesaca, Late Pleistocene (12) and La Calera, Holocene (3-11, 13-16); 4: Type specimen: lower left jaw with m1-m3 (see Fig. 3: 4-6); right (1) and left (3, 4) m1-m3; right (5) and left (2) m1-m3; right (6-8, 10) and left (9, 11) m1; right (13, 15) and left (12, 14, 16) m1. Occlusal views.

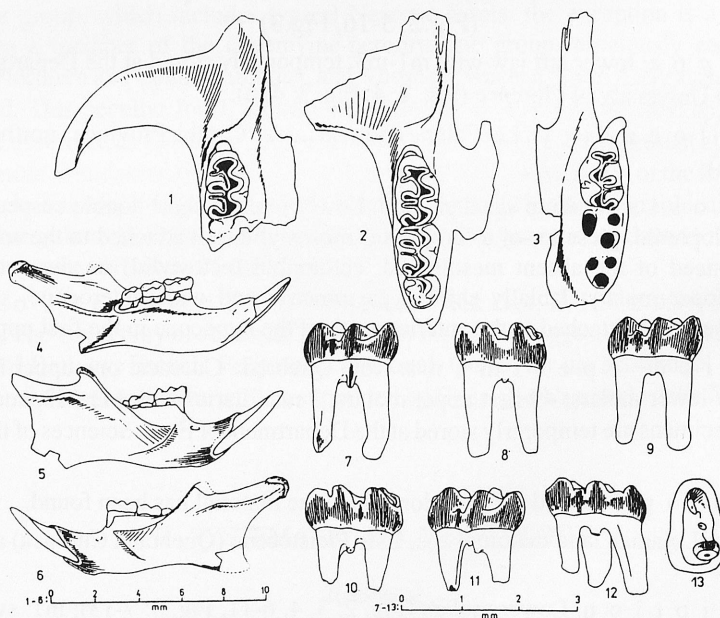


Fig. 3. *Copemyodon ecuadorensis* nov. gen. et sp. from La Calera, Holocene, 1-3: occlusal views of maxillaries: right with M1 (1); right with M1-M3 (2; see Fig.2: 5) and left with M1 (3); 4-6: left (type: 4, 6; see Fig.2: 4) and right (5) jaws; 7-11, 13: m1; 12 M1. - Buccal (7, 9, 11, 12), lingual (8, 10) and root (13) views.

metaconid; 5 – the anteroconid cusps are transversely connected; 6 – the labial cusp joins the union of the short metalophulid and protolophulid, the lingual cusp joins the anterolophulid; 7 – the lesser longitudinal labial anteroconid cusp points obliquely backward as a cingular crest. – Mesolophid absent, mesosinusid regularly closed by a transverse-oval ("drop-like") independent mesostylid, not attached to the mesial wall of the entoconid. A short and robust ectolophid (or ectostylid) regularly joins the anterior side of the hypolophid. m2: subrectangular occlusal outline, longer than wide, and narrowing anteriorly; the development of cusps and lophs is comparable to the first lower molars, with the lingual cusps positioned slightly anteriorly relative to the labial ones, and the metaconid and entoconid larger than the protoconid and hypoconid. The anterior arms of both lingual and labial cusps are slightly larger than the posterior ones. Mesolophid/mesosinusid and ectolophid/ectostylid similar to m1. m3: subtriangular occlusal outline, with the anterior margin wider and more flattened than the posterior, which is reduced and with a rounded corner; labial cusps positioned slightly posteriorly relative to the lingual ones. The anterior arms of the labial cusps are shorter than the posterior ones, with anterior and posterior arms of the metaconid similar in length. Wear often produces islet-like features, mainly positioned close to the lingual side of the tooth: the posterolophid closes such labial islets lingually and anteriorly (closed posterior valley of entoconid-hypoconid).

Upper molars (Fig. 2: 5, 12-16, Fig. 3: 1-3). M1: suboval occlusal outline, with anterocone shifted labially, producing the typical asymmetric shape and the straight labial outline. Morphology of the anterocone: 1 – wide, in unworn molars not or rarely weakly bilobed by a shallow mesial groove; 2 – the long transverse labial spur of the anterolophule joins to the posterior side of the labial part of the anterocone, or directly to the anterolophule. The paracone regularly joins the posterior arm of the protocone through protolophule II. The mesoloph is independent, regularly long and attached to the anterior mure of the hypocone. The hypocone has an oblique anterior arm that may be interrupted behind the paracone. A minute entostyle is generally present in the lingual sinus. The metacone joins obliquely to the posterior arm of the hypocone through metalophule II; the short labial posteroloph of unworn molars is fused with the large hypocone during wear (Fig. 2: 13). M2: subrectangular occlusal outline, narrowing anteriorly, with a flattened anterior corner and a slightly rounded posterior one. The paracone and metacone are offset in their alignment with the protocone and hypocone, respectively: the paracone joins the posterior arm of the protocone through a short protolophule II. The anterior and posterior arms of the hypocone are similar in length. A long mesoloph and a small entostyle are present in the lingual sinus as well as in the first upper molars, the latter being less evident. M3: rounded occlusal outline, with a flattened anterior margin and a rounded posterior one. No labial or lingual spurs are present; protolophule II and metalophule II are short, and often quite undistinguishable, mainly due to wear. A small and indistinct entostyle may be present in the lingual sinus of less worn specimens. Wear can disturb the morphology of the occlusal surface.

M e a s u r e m e n t s (Table I): Preliminary measurements of fossil teeth (first upper and lower molars only) from La Calera have been taken with the aid of a microscope reticule. All measurements are maximum dimensions regardless of wear (length L and width W). A comparison between the dimensions of the upper M1's of *Copemyodon* and of *Copemys pagei* (SHOTWELL, 1967) and *Copemys esmeraldensis* CLARK, DAWSON & WOOD, 1964 from the Barstow Formation, California, has been attempted (Fig. 4). The plot has resulted in the recognition of the sample of *Copemyodon* as intermediate between those of *Copemys pagei* (smaller size) and *Copemys esmeraldensis* (larger size). However, the scanty comparative material at our disposal suggests that we interpret the results with extreme caution. Comparable results have been obtained in a further comparison of the observed ranges and means for the lower m1's of other species of *Copemys* (*C. tenuis*, *C. russelli*, *C. longidens*, *C. barstowensis*) from the same locality. Measurements are taken from LINDSAY, 1972 (Table 12, pp. 79-80) (Fig. 5).

Table I

Measurements of the lower m1's of North American cricetids from LINDSAY, 1972 and *C. ecuadorensis* n. gen. et sp; L = length, W = width

Species (N)	Observed Range		Mean	
	L	W	L	W
<i>Copemyodon ecuadorensis</i> (13)	1.42-1.68	0.76-1.05	1.55	0.97
<i>Copemys pagei</i> (4)	1.35-1.49	1.05-1.10	1.42	1.075
<i>Copemys tenuis</i> (10)	1.55-1.75	1.03-1.11	1.63	1.07
<i>Copemys russelli</i> (6)	1.37-1.71	1.00-1.12	1.48	1.04
<i>Copemys longidens</i> (55)	1.55-1.90	1.00-1.30	1.72	1.15
<i>Copemys barstowensis</i> (8)	1.70-1.85	1.15-1.20	1.77	1.18
<i>Copemys esmeraldensis</i> (3)	1.90-1.95	1.23-1.30	1.92	1.26
<i>Bensonomys yazhi</i> (13)	1.20-1.37	0.75-0.90	1.28	0.84
<i>Bensonomys gidleyi</i> (7)	1.35-1.48	0.88-0.98	1.41	0.91
<i>Abelmoschomys simpsoni</i> (8)	1.40-1.45	0.90-1.00	1.48	0.95

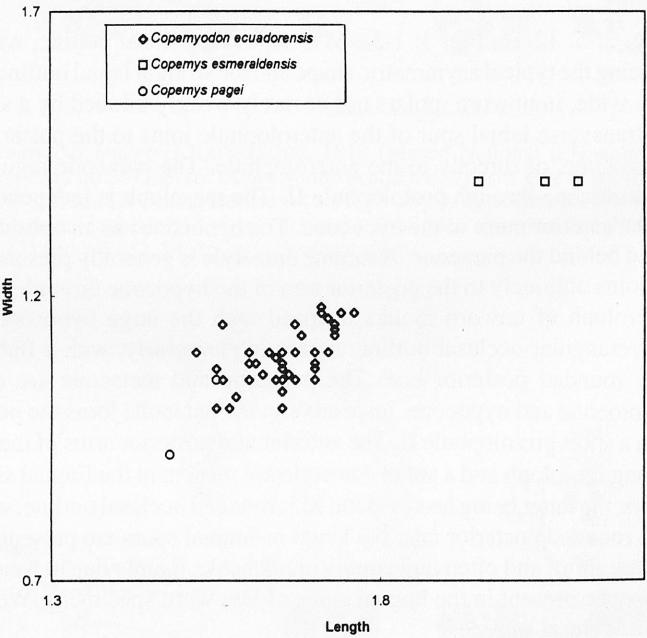


Fig. 4. Scatter diagram with length (L) plotted against width (W) of the first upper molars of *Copemyodon ecuadorensis* nov. gen. et sp., *Copemys pagei* and *Copemys esmeraldensis* from the Barstow Formation, California. Measurements of *C. pagei* and *C. esmeraldensis* are from LINDSAY, 1972. All measurements are in millimeters.

III. COMPARISON AND DISCUSSION

The sample of *Copemyodon ecuadorensis* is characterized by relatively small size, larger than that of *Copemys pagei*, and comparable to that of *Copemys tenuis*. *C. pagei* and *C. tenuis*, the smallest sized and most primitive forms recorded in the Barstow Formation, both show great morphological similarity to *Copemys* (*Democricetodon*) *minor* LARTET, 1851 from Miocene deposits of Europe. In particular, *Copemys pagei* is a little smaller than *Copemys* (*Democricetodon*)

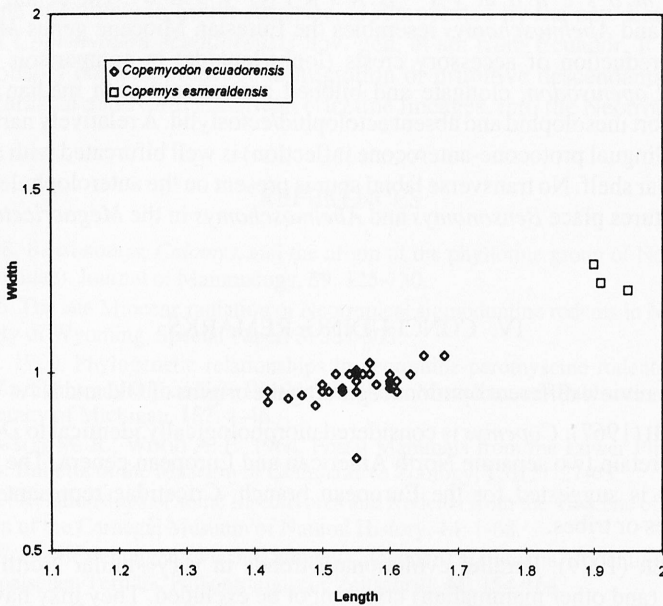


Fig. 5. Scatter diagram with length (L) plotted against width (W) of the first lower molars of *Copemyodon ecuadorensis* nov. gen. et sp. and *Copemys esmeraldensis* from the Barstow Formation, California. Measurements of *C. esmeraldensis* are from LINDSAY, 1972. All measurements are in millimeters.

minor, and could thus represent one of the earliest North American ancestral forms derived from Palearctic cricetids, as suggested by FAHLBUSCH (1967), and successively giving rise to most of the other species of *Copemys* reported from the Middle Miocene Barstow Formation. Among cricetids from this locality, LINDSAY (1972) also recognizes a lineage evolving from *Copemys pagei* to *Copemys esmeraldensis*, characterized by a marked increase in size and the retention of peculiar morphological features. Further, more detailed studies on larger samples of *Copemyodon* may suggest interesting inferences regarding its morphological evolution, and could clarify the intriguing aspects of the phylogenetic relationships of Old and New World cricetids.

C o m p a r i s o n w i t h C o p e m y s WOOD, 1936. Both *Copemyodon* and *Copemys* ("the earliest peromyscine") display similar alternation of buccal and lingual cusps. Advanced Early Pliocene species (e. g., *Copemys esmeraldensis* from the Esmeralda Formation of Nevada, U.S.A.) show broader bilobed anteroconid and accessory crests (mesoloph(id), ectolophid) similar to those in both *Peromyscus* and *Copemyodon*, and have been suggested as possibly being derived from *Copemys*. In a sense, in the *Copemys-Peromyscus* evolutionary line, *Copemyodon* represents a parallel to the Eurasiatic Miocene genera *Rotundomys* MEIN, 1966 and *Kowalskia* FAHLBUSCH, 1969.

C o m p a r i s o n w i t h P e r o m y s c u s GLOGER, 1841. In *Peromyscus*, the lower m1 is characterized by a mesostylid that is not independent, and attached to the mesial wall of the entoconid, while in the upper M1 a non-independent mesoloph is attached to the posterior wall of the paracone. Otherwise, *Copemyodon* and *Peromyscus* show a certain degree of resemblance, thus suggesting a close relationship and derivation from a common ancestor, *Copemys*.

C o m p a r i s o n w i t h *B e n s o n o m y s* G A Z I N, 1 9 4 2
a n d *A b e l m o s c h o m y s* B A S K I N, 1 9 8 6 . The dental morphology of
both *Bensonomys* and *Abelmoschomys* resembles the Eurasian Miocene genus *Megacricetodon*,
with pronounced reduction of accessory crests (lophs/lophids) in comparison with *Copemys*,
Peromyscus and *Copemyodon*, elongate and bilobed anteroconid with median anterolophulid
(anterior mure), short mesolophid and absent ectolophid/ectostylid. A relatively narrow anterocone
(with pronounced lingual protocone-anterocone inflection) is well bifurcated with a mesial groove
and anterior cingular shelf. No transverse labial spur is present on the anterolophule. The mesoloph
is short. These features place *Bensonomys* and *Abelmoschomys* in the *Megacricetodon* lineage.

IV. CONCLUDING REMARKS

We will briefly review different opinions regarding the origins of Old and New World cricetids.

1. V. FALBUSCH (1967): *Copemys* is considered morphologically identical to *Democricetodon*.
It is unjustified to retain two separate North American and European genera. The name *Copemys*
(*Democricetodon*) is suggested for the European branch. Cricetidae represent geographically
defined subfamilies or tribes.

2. B. ENGESSER (1979): Parallel evolutionary trends in very similar North American and
European cricetid (and other mammalian) taxa cannot be excluded. They may have been derived
from a common ancestor, probably of Asian origin, and later evolved along parallel pathways.

3. M. D. CARLETON (1980): Phenetic examination of muroids of North and South America
suggests the conclusion that North American neotomyine-peromyscines and South American
sigmodontines are closely related. Muroids with complex and simple penes represent a structural
continuum. Thus, close relationships between Old World muroids and South American cricetids
are not precluded.

4. B. H. SLAUGHTER & J. E. UBELAKER (1984): An origin of Neotropical cricetine rodents and
North American peromyscines from a common ancestor, *Copemys*, is considered. The *Copemys*-
Peromyscus branch is derived either from Nearctic eumyines (independent of the Old World
cricetodontines), or directly from Old World cricetodontine immigrants.

5. L. L. JACOBS & E. H. LINDSAY (1984): A separate non-copemyine origin for Neotropical
cricetine rodents is suggested. Their ancestor in North America is *Bensonomys* GAZIN, 1942 (with
variable supernumerary roots of M1) from the Late Hemphillian of Arizona, derived from the
separate Miocene lineage of *Megacricetodon* from Eurasia. *Bensonomys* (closely related to the
Recent Neotropical phyllotine genus *Calomys* WATERHOUSE, 1837) gave rise to the group of
sigmodontine cricetids that entered South America during the Great American Interchange.

6. J. A. BASKIN (1978, 1986): *Abelmoschomys simpsoni* BASKIN, 1986 (latest Clarendonian,
Florida) is the earliest record of the Neotropical sigmodontine branch that evolved and diversified
in North America. However, in contrast to our conclusions here, according to BASKIN *Bensonomys*
and *Abelmoschomys* are closely related to and derived from peromyscine cricetids.

On the basis of our preliminary comparisons with Old and New World cricetids, we consider
the new Copemyine-Peromyscine taxon of the Late Pleistocene and Holocene of Ecuador as a proof
of two distinct cricetid lines in the late Cenozoic of South America:

I. The Neotropical cricetine sigmodontines. We agree with JACOBS & LINDSAY (1984) that this
dominant and much more diversified branch is derived from the Eurasiatic Miocene genus
Megacricetodon; in our opinion the North American genera *Bensonomys* and *Abelmoschomys* both
represent descendants of *Megacricetodon*.

II. Another, much less diversified and until now unrecorded *Copemys-Peromyscus* branch (the simple-penis type cricetines) in South America, is represented by the new Late Pleistocene and Holocene taxon *Copemydon ecuadorensis* nov. gen. et sp. from Ecuador. It suggests an independent and probably contemporaneous immigration of primitive descendants of *Copemys-De-mocricetodon* Eurasian and North American cricetine lineages, into the Neotropical region.

REFERENCES

- BASKIN J. A. 1978. *Bensonomys*, *Calomys*, and the origin of the phyllotine group of Neotropical cricetines (Rodentia, Cricetidae). *Journal of Mammalogy*, **59**: 125-130.
- BASKIN J. A. 1986. The late Miocene radiation of Neotropical sigmodontine rodents in North America. *Con. Geol.*, University of Wyoming, Special Paper, **3**: 287-303.
- CARLETON M. D. 1980. Phylogenetic relationships in neotomine-peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within New World Cricetinae. *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, **157**: 1-46.
- CLARK J. B., DAWSON M. R., WOOD A. E. 1964. Fossil Mammals from the Lower Pliocene of Fish Lake Valley, Nevada. *Bulletin of the Museum of Comparative Zoology*, **131**(2): 27-63.
- ENGESSER B. 1979. Relationships of some Insectivores and Rodents from the Miocene of North America and Europe. *Bulletin of the Carnegie Museum of Natural History*, **14**: 1-68.
- FALBUSCH V. 1967. Die Beziehungen zwischen einigen Cricetiden (Mammalia, Rodentia) des nordamerikanischen und europäischen Tertiärs. *Paläontologische Zeitschrift*, **41**: 154-164.
- FEJFAR O., BLASETTI A., CALDERONI G., COLTORTI M., FICCARELLI G., MASINI F., ROOK L., TORRE D. 1993. New finds of cricetids (Mammalia, Rodentia) from the late Pleistocene-Holocene of Northern Ecuador. *Documenta, Laboratoire de Géologie, Lyon*, **125**: 151-167.
- FICCARELLI G., AZZAROLI A., BORSELLI V., COLTORTI M., DRAMIS F., FEJFAR O., HIRTZ A., SAGRI M., TORRE D. 1993a. Geomorphological and stratigraphical aspects of the Interandean depression in Northern Ecuador, South America. *Journal of South American Earth Sciences*, **6**(3): 145-150.
- FICCARELLI G., BORSELLI V., ESPINOSA M. M., TORRE D. 1993b. New *Haplo mastodon* finds from the Late Pleistocene of Northern Ecuador. *Geobios*, **26**(2): 231-240.
- HERSHKOWITZ P. 1962. Evolution of Neotropical Cricetine Rodents (Muridae). *Fieldiana, Zoology*, **46**: 1-524.
- JACOBS L. L., LINDSAY E. H. 1984. Holarctic radiation of Neogene muroid rodents and the origin of South American cricetids. *Journal of Vertebrate Paleontology*, **4**: 265-272.
- LINDSAY E. H. 1972. Small mammal fossils from the Barstow Formation, California. *University of California Publications in Geological Science*, **93**: 1-104.
- SHOTWELL J. A. 1967. *Peromyscus* of the Tertiary in Oregon. *Bulletin of the Museum of Natural History, University of Oregon*, **5**: 1-35.
- SLAUGHTER B. H., UBELAKER J. E. 1984. Relationships of South American cricetines to rodents of North America and the Old World. *Journal of Vertebrate Paleontology*, **4**: 255-263.

