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FOSSIL MAMMALS FROM THE BEGINNING OF THE CENOZOIC IN BRAZIL

MARSUPIALIA: DIDELPHIDAE

By Carlos de Paula Couto¹

INTRODUCTION

Marsupials of the family Didelphidae are poorly represented in the lower Tertiary fauna of Patagonia, as are the Caenolestidae and the Caroloameghiniidae. The Polydolopidae and, to a lesser degree, the Borhyaenidae are relatively common in the Patagonian Paleocene (Río Chican) and Eocene (Casamayoran). Didelphid remains are scarcely known from the Casamayor formation. The Caenolestidae were probably represented during Eocene times by their more primitive forms.

In the Mustersan stage (upper Eocene) the Borhyaenidae were numerous, but the Polydolopidae and Caroloameghiniidae were possibly extinct, since they are not found in the strata of that time and in any later strata. The Didelphidae were certainly present in the Mustersan, although no evidence of their remains has yet been found, while the existence of the Caenolestidae in that time is doubtful.

Until now, the only surely identifiable South American didelphine prior to the Oligocene (Colhué-Huapí) was the Casamayoran Coöna Simpson, 1938, a small form, slightly larger than the Recent Marmosa. According to Simpson (1938), Coöna more closely resembles the Cretaceous Pediomyinae and the Tertiary Didelphinae, both of North America, than it does the Microbiotheriinae, the only subfamily of the Didelphidae otherwise known from Patagonia from the Eocene to the Miocene.

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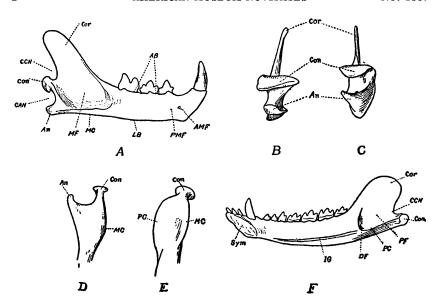


Fig. 1. Diagram to illustrate common descriptive terms applied to the mammalian mandible. A. Felis, external view. B. Felis, posterior view. C. Bettongia, posterior view. D. Bettongia, inferior view of posterior part of mandible. E. Djadochtatherium, inferior view of posterior part of mandible. F. Priacodon, internal view. All right rami, not to scale. Abbreviations: AB, alveolar border; AMF, anterior mental foramen: An, angle or angular process; CAN, condylo-angular or subcondylar notch; CCN, condylo-coronoid or supracondylar notch; Con, condyle; Cor, coronoid process; DF, dental foramen; IG, internal groove; LB, lower border; MC, masseteric crest; MF, masseteric fossa; PC, pterygoid crest; PF, pterygoid fossa; PMF, posterior mental foramen; Sym, symphysis. (After Simpson.)

Simpson admits three possibilities with regard to *Coona*: (1) that this genus may be ancestral to the microbiotheres, which would have become a well-differentiated subfamily only in middle Tertiary times; (2) that it may be ancestral to the Didelphinae, and that this subfamily of opossums evolved only in South America, or in both South and North America (not much is known about them in the middle Tertiary faunas, which are very limited as to facies and geographical distribution); or (3) that it may be only another branch of the didelphoid stock, perhaps pediomyine, that, reaching South America some time before the Eocene, represents a minor extinct phylum, ancestral neither to the Microbiotheriinae nor to the modern Didelphinae.

As is shown in this paper, the variety of South American didelphids was great in the very early Cenozoic days, which is especially remarkable since all of our material comes from a single small basin. There were already, at the beginning of the Tertiary, as many or perhaps even more forms of didelphids than are found in South America today.

Some authors, as McGrew (1937, p. 451), have advanced the theory that the South American Recent didelphids are descended from upper Tertiary North American forms, which would have reached South America by the end of the Tertiary, when the Panamanian land bridge was reëstablished. This idea is based on the complete lack, until recently, of paleontological evidence for the presence of didelphines in South America before the Pliocene and on the sudden appearance of the group in Araucanian times (lower Pliocene) in Argentina. The absence of fossil specimens of didelphids in the middle and upper Tertiary of North America does not necessarily imply that they did not exist there during the Miocene and Pliocene, because their arboreal mode of life would have lessened their changes of becoming fossilized.

The presence of a typical non-microbiotheriine didelphid (*Coöna* Simpson) in the lower Eocene (Casamayoran) of Patagonia and of the numerous forms here described in the Paleocene of the State of Rio de Janeiro, Brazil, makes it clear that the group is undoubtedly very old in South America, and that the Recent South American didelphids may be considered the descendants of these ancient forms. This does not preclude, however, an earlier, perhaps Cretaceous, North American origin for the group.

The fossil didelphids of São José de Itaborai, although positively didelphine in character, are undoubtedly more primitive than the later representatives of the group, rather resembling the Pediomyinae of the North American Cretaceous and constituting, as it were, a transition between these earliest of the known didelphids and the Recent forms. The $P_3^{\rm a}$ of the Itaboraian didelphids, e.g., are the largest teeth of the premolar series, in agreement with those of the Pediomyinae and in contrast with those of the modern forms, in which the $P_2^{\rm a}$ are the largest premolars.

All the material here described was collected in a marl which fills channels and underground caves in a limestone quarry at São José de Itaborai, some miles northeast of Niteroi, the capital of the State of Rio de Janeiro, and on approximately the same latitude as the city of Rio de Janeiro. This quarry is under the manage-

ment of the Companhia Nacional de Cimento (Portland) Mauá, which has given generous cooperation in this work.

A note about the geology of this deposit was given by the author in an earlier paper (1949, pp. 6–10).

The present paper is a preliminary report for description of the new forms of the family Didelphidae. The final report, which will include detailed descriptions of all the fossil mammals from São José de Itaborai, will be published by the Museu Nacional, Rio de Janeiro, in collaboration with the Divisão de Geologia e Mineralogia do Departamento Nacional da Produção Mineral. Completion of the final report will take considerable time, and for this reason I have decided to present a series of preliminary notes reporting on the results of my investigations of the different groups involved.

The following abbreviations are used to designate the collections of which mention is made in the text:

A.M.N.H., the American Museum of Natural History

D.G.M., Divisão de Geologia e Mineralogia do Departamento Nacional da Produção Mineral (formerly Serviço Geologico do Brasil)

M.A.C.N., Museo Argentino de Cicencias Naturales "Bernardino Rivadavia," Buenos Aires

M.N.R.J., Museu Nacional do Rio de Janeiro

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The Companhia Nacional de Cimento (Portland) Mauá, Rio de Janeiro, besides granting me permission to collect fossils in the limestone quarry at São José de Itaborai, frequently gave me help in transportation of equipment and the material collected.

The John Simon Guggenheim Memorial Foundation renewed the Fellowship granted me last year, to enable me to complete the study of the fossil mammals from São José de Itaborai, in direct comparison with the important lower Eocene collection from Patagonia in the American Museum of Natural History.

The American Museum of Natural History kindly gave me every facility needed for carrying on my work on these collections satisfactorily. I am especially grateful to the Department of Geology and Paleontology, to the Department of Mammals, and to the General Library for all the help I have received from them.

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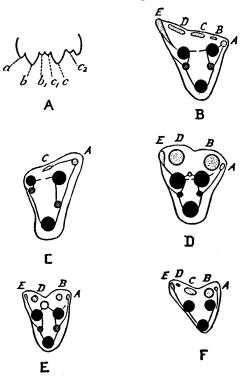


FIG. 2. Didelphid upper molars. A. Bensley's stylar designations, not used here. B. *Pediomys*, showing five primitive stylar cusps and their designations. as suggested by Simpson and adopted here. C. Last upper molar of *Pediomys*. D. *Ectoconodon*. E. *Alphadon*. F. *Didelphis*. (After Simpson.)

for literature and for fossil and Recent specimens for comparative study with the Paleocene specimens from Brazil.

To all of them I extend my most sincere thanks.

ORDER MARSUPIALIA ILLIGER, 1811 FAMILY **DIDELPHIDAE** GRAY, 1821 SUBFAMILY **DIDELPHINAE** SIMPSON, 1927 **PROTODIDELPHIS,** NEW GENUS

Genotype: Protodidelphis vanzolinii, new species.

DIAGNOSIS: P² (roots) larger than P¹ but slightly smaller than P³. P³ almost as long as M¹, strong, with only one central main cusp. M^{1-3} increasing in size backward, M^4 slightly smaller than M^3 . Metacone enlarged in M^{1-3} , larger than the protocone and paracone, but in M4 a little lower than the paracone. Stylar cusps B and D as large as, or larger than, the paracone and metacone in M¹⁻⁴, which also have a small stylar cusp A.¹ M¹⁻³ with a stylar cusp E, absent in M4. M1 and M4 with distinct anterior cingulum, from the base of stylar cusp A to the base of the protocone. One pair of anterior palatine foramina, apparently rather distinct. Posterior palatine foramina probably present and relatively large. Preorbital foramen above the middle P2. Lower canine (alveolus) large. P₃ strong, larger than P₂, as large as M₁, with relatively large talonid on the postero-internal angle. Talonid slightly smaller than trigonid on M₁₋₄. Trigonid relatively low. Protoconid and entoconid distinctly larger than the remaining cusps. Paraconid and metaconid subequal, the hypoconid the lowest cusp. Hypoconulid very small and situated next to the middle of the posterior border of the entoconid. Anterior mental foramen under and between P₁₋₂; two other smaller foramina under P_3 and M_1 .

DISCUSSION: *Protodidelphis* is undoubtedly a typical didelphid. It is one of the most ancient known South American representatives of the Didelphinae.

Among the Recent forms, *Didelphis* shows the closest affinities with this Paleocene form, and they may be placed in the same phyletic line. *Paradidelphis* Ameghino, 1904, known from a right mandibular ramus bearing all the premolars and molars, and *Cladodidelphis* Ameghino, 1904, known from the right anterior part of a skull, both from the Montehermosan (Pliocene) of Argentina, although of the same size as *Protodidelphis*, differ markedly from it in structure.

Protodidelphis vanzolinii, new species²

Figure 3

HOLOTYPE: D.G.M. No. 271-M. Facial and palatal portion of a skull (somewhat incomplete), with partial alveolus of C,

¹ One vestigial stylar cusp C may be seen in M.N.R.J. No. 1426-V.

² In honor of Dr. Paulo Emílio Vanzolini.

roots of P¹⁻², with P³-M¹, alveoli of M²⁻³, and M⁴ present. Collector, Júlio da Silva Carvalho, 1949.

PARATYPE: D.G.M. No. 250-M. Right mandibular ramus, almost complete, with partial alveolus of C, roots of P_{1-2} , with P_3 - M_1 , roots of M_2 , and with M_{3-4} present. Same collector, 1949.

REFERRED SPECIMENS: D.G.M. No. 319-M, left mandibular ramus, with alveolus of last I and C, P_{1-3} present, alveoli of M_{1-4} ; No. 303-M, fragment of right maxilla, with M^{1-4} present. A.M.-N.H. No. 49857, right mandibular ramus, almost complete, with alveolus of C, with P_1 -M₁, roots of M_{2-3} , anterior root and tal-



Fig. 3. Protodidelphis vanzolinii, new genus, new species. Paratype, D.G.M. No. 250-M, right P_3 - M_1 , and M_3 , internal view. \times 3.

onid of M_4 present. All collected by Júlio da Silva Carvalho, 1949. M.N.R.J. No. 1371-V, left M_1 or M_2 , rootless; No. 1426-V, left $M^{1(?)}$; No. 1427-V, right M^3 . A.M.N.H. No. 49803, right $M_{2(?)}$; No. 49858, portion of left mandibular ramus with P_2 – M_2 present. All collected by Carlos de Paula Couto, 1948.

DIAGNOSIS: The only known species of the genus.

Measurements: Holotype, D.G.M. No. 271-M: P^{1-3} , 11.3 mm.; M^{1-4} , 19.2 mm.; ratio M^{1-4}/P^{1-3} , approximately 1.7. Paratype, D.G.M. No. 250-M: P_{1-3} , 13.9 mm.; M_{1-4} , 21 mm. Average ratio M_{1-4}/P_{1-3} (three specimens), approximately 1.4.

REMARKS: This species approaches in size the Recent *Didelphis marsupialis aurita*. The paratype was not found associated with the holotype but seems to belong to the same species.

DIDELPHOPSIS, NEW GENUS

Genotype: Didelphopsis cabrerai, new species.

DIAGNOSIS: P^2 (roots) well developed. P^3 (alveolus) much larger than P^{1-2} and the molars. Upper molars with protocone, paracone, and metacone normally developed. Metaconule vesti-

gial. No paraconule discernible. External cingulum wide, with distinct stylar cusps A, B, C, D, and E; styles B, C, and D apparently predominating. M4 anteroposteriorly compressed, as wide as M³, approximately oval in posterior outline, stylar cusps B, C, D, and E absent. Trigon still distinct, protocone and paracone predominating. Paracone situated internal to the longitudinal axis of the tooth; metacone minute. Parastylar spur bent forward against the stylar cusp D of M3. In M1-4 a short anterior basal cingulum, extending from style A to approximately the base of the paracone. Pre-orbital foramen above the middle of P³. Paroccipital process well developed, conical, pointed, situated on the same sagittal plane as the tips of the occipital condyles, well behind the precondyloid foramen. Lower incisors (root of I_4) probably similar to those of *Didelphis*. relatively enormous, heavy, bulky, the largest of the cheek teeth, with a large conical principal cusp, preceded by a small cusp; a small basal talonid, facing backward. Lower molars with high trigonid. Protoconid, paraconid, and metaconid well developed. the protoconid the largest, the paraconid the smallest. Talonid low, approximately as broad and long as the trigonid, with all the cusps well developed, the hypoconid the largest, the hypoconulid situated close to the entoconid and directed backward. M₄ with laterally compressed talonid, which is much narrower than the trigonid. Lower jaw, as far as known, similar to that of the modern didelphids. Symphysis reaches the middle of P2. Anterior mental foramen under the diastema between P_{1-2} . Another small, elongated foramen below the middle of M₁.

DISCUSSION: Didelphopsis is a typical member of the Didelphinae, very similar to Protodidelphis and consequently to Didelphis. It is clearly distinct from Protodidelphis (see table 1). Its affinities with Paradidelphis and Cladodidelphis, from the Argentinian Pliocene, are only on the subfamily level.

The unusual development of the bulky P₃, the largest of the premolars, recalls the Pediomyinae, from the North American Cretaceous, e.g., *Eodelphis cutleri*. All other characters are, however, clearly didelphine.

Didelphopsis cabrerai, new species¹

HOLOTYPE: M.N.R.J. No. 1429-V. Left maxilla, almost complete, with part of the alveolus of C, the roots of P^{1-2} , alveolus

¹ In honor of Dr. Ángel Cabrera.

of P³, and with M¹-⁴ present. Collected by Júlio da Silva Carvalho, 1949.

PARATYPES: D.G.M. No. 243-M, right mandibular ramus, incomplete, with roots of I₄ and C, and with P₁-M₄ complete, collected by Júlio da Silva Carvalho, 1949. M.N.R.J. No. 1345-V, right M₄, collected by Carlos de Paula Couto, 1948.

REFERRED SPECIMENS: M.N.R.J. No. 1346-V, left lower molar, probably M_3 ; No. 1347-V, left M_4 ; both collected by Carlos de Paula Couto, 1948.

DIAGNOSIS: The sole known species of the genus.

Measurements: Holotype, M.N.R.J. No. 1429-V: P^{1-3} , 15 mm.; M^{1-4} , 17 mm.; ratio M^{1-4}/P^{1-3} , approximately 1.1. Paratype, D.G.M. No. 243-M: P_{1-3} , 14.6 mm.; M_{1-4} , 17 mm.; ratio M_{1-4}/P_{1-3} , approximately 1.2.

REMARKS: The referred specimens are approximately one-fifth larger than the types, from which they differ otherwise in the complete absence of the outer basal cingulum of the lower molars. These differences may possibly be individual.

ISCHYRODIDELPHIS, NEW GENUS

GENOTYPE: Ischyrodidelphis castellanosi, new species.

DIAGNOSIS: Large size. P3 strong, laterally compressed, larger than P_{1-2} and M_{1-2} , with high, mesial, sharp-pointed cusp, which has a vestigial cusp on its anterior border, and with very short, basal talonid, turned slightly outward. M1 compressed laterally, less molariform than the posterior molars, with trigonid medianly high and narrow, and low talonid, slightly wider than the trigonid. Protoconid predominant, paraconid a little smaller, and slightly internal to the middle line, and a vestigial or small metaconid pressed against the protoconid. Hypoconid well developed, entoconid smaller, and hypoconulid minute, near the entoconid. M₂ appreciably larger than and structurally similar to M₁, but with trigonid high and as wide as talonid, paraconid more internal, and metaconid well developed, although lower and weaker than protoconid. Talonid low, well basined. conid, entoconid, and hypoconulid well developed, the first M₃₋₄ probably like M₂, but progressively larger. Mandible strong and high. Anterior mental foramen below P₁; a smaller, posterior one under P₃.

DISCUSSION: *Ischyrodidelphis* is clearly a member of the Didelphinae. Its closest affinities seem to be with the largest Recent

species of the genus Didelphis. Its size was about the same as or perhaps larger than that of the latter. P_3 is the most developed of its premolars, as in the Cretaceous Pediomyinae, but different from the Recent Didelphidae, in which P_2 is the largest. M_1 is relatively weaker and less molariform, more similar to the premolars than in Didelphis. The antero-external cingulum of its lower molars is much weaker than in this Recent genus, denoting perhaps a relatively smaller development of the metacone of its upper molars. In its general features, however, Ischyrodidelphis looks very much like Didelphis.

TABLE 1
PRINCIPAL DIFFERENCES BETWEEN Protodidelphis, Didelphopsis, AND
Ischyrodidelphis, New Genera

Protodidelphis	Didelphopsis	Ischyrodidel p his	
P³ almost as long as M¹	P³ about 1.5 longer than M¹		
M ⁴ subtriangular, slightly smaller than M ³ , with stylar cusps A, B, D pres- ent. Metacone slightly smaller than paracone	M ⁴ subovate, much shorter than M ³ , without stylar cusps B, C, D, E. Metacone minute, much smaller than paracone		
Paracone and metacone on M ¹⁻⁴ almost contiguous to and almost as large as, or slightly larger than, stylar cusps B and D	Paracone and metacone on M ¹⁻⁴ well separated from and much larger than stylar cusps		
Pre-orbital foramen above the middle of P ²	Pre-orbital foramen above the middle of P ³		
P_3 as long as M_1 , shorter than M_2 , M_3 , or M_4	P ₃ bulky, much the longest of the cheek teeth	P ₃ almost laminate, longer than P ₁ , P ₂ , M ₁ , or M ₂ but smaller than M ₃ or M ₄	
Trigonid of lower molars relatively low	Trigonid of lower molars high	Trigonid of M_1 moderately high and very compressed laterally. High on M_{2-4}	
Talonid slightly wider than trigonid	Talonid low, almost as wide as trigonid on M_{1-3} , narrower than trigonid on M_4	Talonid wider than trigo- nid on M ₁ ; as wide as trigonid on M ₂ and probably on M ₃	
Anterior mental foramen under and between P_{1-2} ; two other smaller foram- ina under P_3 and M_1 , respectively	Anterior mental foramen under and between P_{1-2} ; another smaller one under M_1	Anterior mental foramer under P ₁ ; posterior smaller one under P ₃	

Protodidelphis, Didelphopsis, and Ischyrodidelphis were represented by large species, the species of the other contemporary genera being of medium or small size. The differences between these three Paleocene (Itaboraian) genera are summarized in table 1.

Ischyrodidelphis castellanosi, new species¹

HOLOTYPE: M.N.R.J. No. 1351-V. Median fragment of right mandibular ramus, with P_3 , M_{1-2} , and trigonid of M_3 present. Collected by Carlos de Paula Couto, 1949.

PARATYPES: M.N.R.J. Nos. 1352-V, 1353-V, two right M_2 ; 1354-V, left M_2 ; and 1425-V, right P_3 . Same collector, 1948–1949.

DIAGNOSIS: The sole known species of the genus.

Measurements: Holotype, M.N.R.J. No. 1351-V: P_2 -M₄, 31 mm.; P_{1-3} , approximately 14 mm.; M_{1-4} , 20.5 mm.; ratio LM_{1-4}/LP_{1-3} , approximately 1.5.

GUGGENHEIMIA, NEW GENUS²

Genotype: Guggenheimia brasiliensis, new species.

DIAGNOSIS: Primitive didelphine aspect. Mandible strong, with relatively short symphyseal region. Teeth (C-M₄) in continuous and closed series. C (root) strong. P₁ very small, obliquely placed. P_{2-3} relatively small, as high as, or slightly higher than, the molars, with strong anteromedian cusp and posterointernal talonid with vestigial cusp. Talonid of P₂ much lower than that of P_3 . P_3 the largest of the premolars, more molariform than P_{1-2} , with a small cusp in front of and on the middle height of the main cusp. M_{1-4} increasing in size from M_1 to M_3 , M_4 being smaller than M₂₋₃. Trigonid relatively low, protoconid and metaconid the most prominent cusps, paraconid very low, metaconid approximately on the same transverse line with protoconid. Talonid ample, broader than trigonid, of medium height, with well-developed, subequal hypoconid and entoconid. Hypoconulid almost absent on M_{1-3} ; small and close to the entoconid on M_4 . M_{1-4} with anterior basal cingula from the base of the paraconid to the external angle of the teeth.

¹ In honor of Dr. Alfredo Castellanos.

² In honor of the John Simon Guggenheim Memorial Foundation.

REMARKS: Guggenheimia is a didelphine of rather more primitive aspect than the modern members of the subfamily. Its teeth indicate closer relationship to the more omnivorous forms of the group.

Guggenheimia brasiliensis, new species

HOLOTYPE: D.G.M. No. 297-M. Incomplete left mandibular ramus, with root of C, and with P_1 - M_4 present. Collected by Júlio da Silva Carvalho, 1949.

DIAGNOSIS: The only known species of the genus.

Measurements: P_{1-3} , 6 mm.; M_{1-4} , 10.5 mm.; ratio $LM_{1-4}/-LP_{1-3}$, 1.80.

SCHAEFFERIA, NEW GENUS1

Genotype: Schaefferia fluminensis, new species.

DIAGNOSIS: Mandible strong, relatively more elongate than that of Guggenheimia. Symphysis narrow. I_1 and I_3 (alveoli) in normal position; I_2 above and between them. C (alveolus) very strong. P_{1-3} large, P_{2-3} much higher than the molars. P_3 the largest. P_1 obliquely placed, against the canine, and separated from P_2 by short diastema. An even shorter diastema between P_{2-3} . P_3-M_4 in continuous, closed series. M_{1-4} similar to those of Guggenheimia, but moderately high trigonid, metaconid slightly posterior, and talonid with well-developed hypoconulid; anterior basal cingulum as in Guggenheimia. M_{2-3} almost of the same size. M_4 shorter and narrower.

DISCUSSION: Schaefferia closely resembles Guggenheimia, but it has a relatively much more elongate lower premolar series, its P_{1-3} being much larger than those of Guggenheimia and separated by small diastemata instead of being in closed series. The lower molars of Schaefferia are also somewhat larger than those of Guggenheimia and differ structurally in having the metaconid slightly posterior to the paraconid, and in the well-developed hypoconulid, the hypoconulid of Guggenheimia being vestigial on M_{1-3} and very small on M_4 .

Among the Recent forms, *Philander* seems to be the genus that most closely approaches these two extinct genera in dental and mandibular morphology.

¹ In honor of Dr. Bobb Schaeffer.

Schaefferia fluminensis, new species

Figure 4

HOLOTYPE: M.N.R.J. No. 1350-V. Portion of left mandibular ramus, with alveoli of I_{1-3} and C, roots of P_1 , with P_{2-3} , alveolus of M_1 , roots of M_2 , and with M_{3-4} present. Collected by Carlos de Paula Couto, 1948.

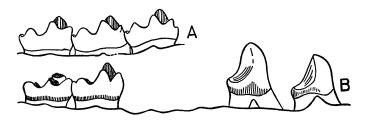


Fig. 4. Schaefferia fluminensis, new genus, new species. A. Paratype, D.G.M. No. 314-M, left M_{2-4} , internal view. B. Holotype, M.N.R.J. No. 1350-V, left P_{2-3} and M_{3-4} , internal view. \times 6.

Paratypes: D.G.M. No. 314-M, incomplete left mandibular ramus, with alveoli of I_{1-3} , C, P_{1-3} , M_1 , and with M_{2-4} present; No. 315-M, fragment of left mandibular ramus, with alveoli of C, P_1 - M_2 , and with M_3 and anterior alveolus of M_4 present. Both collected by Júlio da Silva Carvalho, 1949.

DIAGNOSIS: The only species of the genus.

Measurements: Holotype, M.N.R.J. No. 1350-V: P_{1-3} , 10 mm.; M_{1-4} , 12.8 mm. Paratype, D.G.M. No. 314-M: P_{1-3} , 8.5 mm.; M_{1-4} , 12.8 mm. Paratype, D.G.M. No. 315-M: P_{1-3} , approximately 9 mm.; M_{1-4} , approximately 12.8 mm. Ratio LM_{1-4}/LP_{1-3} , approximately 1.28–1.50.

DERORHYNCHUS, NEW GENUS

GENOTYPE: Derorhynchus singularis, new species.

DIAGNOSIS: Ante-molar region of the mandible unusually elongate and low. I_{1-2} (roots) well developed and procumbent, laterally compressed and probably very elongate. I_{3-4} apparently absent or I_3 very small and lateral to I_2 . Lower C (alveolus) relatively very large, somewhat procumbent, close to the incisors. P_3 larger than M_1 . M_1 (probably) and M_{2-4} with moderately elevated trigonid. Talonid wider than trigonid on M_2 , as wide as, or slightly narrower than, trigonid on M_3 , laterally compressed

and markedly narrower than trigonid on M_4 . Paraconid higher than metaconid, especially on M_4 . Metaconid intermediate in size between paraconid and protoconid. Hypoconulid very small, internal, immediately posterior to entoconid, lower than entoconid on M_2 and M_3 (and probably on M_1), only slightly lower than entoconid on M_4 . Entoconid slightly higher than hypoconid. Diastemata between C and P_1 , P_1 and P_2 , and sometimes between P_2 and P_3 .

Description and Discussion: In spite of its peculiar longirostrine shape, Derorhynchus recalls, in its other characters, the smaller forms of Recent didelphines. The molars are very similar to those of certain Recent forms; they differ, for example, from those of Marmosa only in very small structural details. But this Paleocene genus is markedly dissimilar from all other known didelphids in the unusual elongation of its mandible in front of P_3 .

The lower jaw as a whole is slender and elongate. Its dental border is low anterior to P₃, but reaches the normal height under P₃-M₄. Its lower border is evenly arched throughout the complete length of the horizontal ramus. The symphysis is long, low, and ends under the middle of P2. The anterior mental foramen is placed under and between C and P₁; another foramen is present beneath and between P_3 and M_1 . The roots of I_{1-2} indicate that these teeth were well developed and procumbent, laterally compressed, and probably very elongate, recalling in all their aspects the I₁ of Caenolestes. There is no discernible sign of I₃, but a small pit outside the middle height of I₂ may perhaps be considered as a part of the alveolus of a small I₃. I₄ was almost certainly absent. The lower C (alveolus) was very strong, placed immediately behind the incisors, somewhat procumbent, but probably with its tip turned upward. P₁₋₃ (roots) were tworooted and well developed, increasing progressively in size. P₃ was about three-fifths longer than M_1 . P_{1-2} , although well developed, were placed on a level much lower than that of the molars, the level of P₃ being intermediate. P₁₋₂ probably did not occlude with the upper teeth. M_1 is represented only by its roots. is the longest and widest, M4 being the shortest and narrowest. M₃ is slightly larger than M₁. The protoconid and hypoconid are distinctly V-shaped. The characteristic didelphid oblique

¹ There is no diastema between P₂ and P₃ in the paratype A.M.N.H. No. 49826.

anterior and posterior cingula are present on all the lower molars, except M₄ on which the posterior cingulum is absent.

Derorhynchus recalls the Recent Caenolestidae in specialization. It was almost certainly an insectivorous didelphid, rather than omnivorous, as are the didelphids in general. From this point

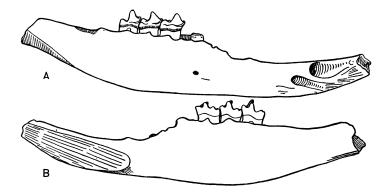


FIG. 5. Derorhynchus singularis, new genus, new species. Holotype, M.N.R.J. No. 1348-V, incomplete right mandibular ramus. A. External view, showing alveolus of C, mental foramen, and M_{2-4} . B. Internal view. \times 3.

of view, it is convergent with the caenolestids, which is especially interesting since, as far as known, the South American continent has not had true Insectivora throughout its entire history, aside from the dubious lower Miocene *Necrolestes* Ameghino, from the Patagonian Santacrucian.

It seems that insectivorous didelphids, with the Caenolestoidea in general, played the role of the placental Insectivora in the ecology of the South American Tertiary, as is the case today with the Recent Caenolestidae. Similarly, during Tertiary times, the borhyaenid marsupials took the place of the placental Carnivora in South America which reached the South American Continent much later.

Derorhynchus singularis, new species

Figure 5

Holotype: M.N.R.J. No. 1348-V. Incomplete right mandibular ramus, with roots of I_{1-2} , possible alveolus of I_3 , alveolus of C, roots of P_1 – M_1 , and with M_{2-4} present. Collected by Carlos de Paula Couto, 1948.

PARATYPE: A.M.N.H. No. 49826. Fragment of right mandibular ramus with M_{2-4} present. Same collector, 1948.

DIAGNOSIS: The only known species of the genus.

MEASUREMENTS: Holotype, M.N.R.J. No. 1348-V: P_{1-3} , 7.2 mm.; M_{1-4} , 7 mm.; ratio LM_{1-4}/LP_{1-3} , approximately 0.97. Height of the mandible under M_3 , 5 mm.; under P_1 , 2.8 mm.

GAYLORDIA, NEW GENUS¹

Genotype: Gaylordia macrocynodonta, new species.

DIAGNOSIS: Small and primitive didelphid. Jaws relatively short. Teeth in continuous closed series. Upper C very elongate, slightly curved, flattened, and sharp pointed. P_{1-2}^{1-2} very small, with a main central cusp, laterally compressed. $P_3^{\bar{3}}$ bulky, relatively enormous, much longer and higher than P₁₋₂ and than M_{1-4}^{1-4} , with thick mesial main cusp and minute, postero-internal basal cusp. M¹⁻² triangular in outline, M² wider than M¹ and than M³. M³ less triangular, abruptly narrowed, with welldeveloped and anteriorly salient protoconule. Lower jaw low but relatively strong. Lower C (alveolus) apparently large, but probably smaller than upper C. P₁ much smaller than P₂, obliquely implanted, compressed between C and P2. M1-3 progressively larger; M_4 as long as M_3 , longer than M_{1-2} , laterally compressed, narrower than M_{1-3} . Trigonid much higher than talonid, and anteroposteriorly compressed; protoconid slightly higher than metaconid, on M_{1-4} , paraconid the smallest. Talonid very low and somewhat reduced, anteroposteriorly compressed, much shorter and slightly narrower than trigonid on M_{1-3} ; much shorter and much narrower than trigonid on M₄: entoconid as high as hypoconid on M_{1-3} , higher than hypoconid on M_4 ; hypoconid immediately posterior to protoconid and pressed against it on M₁₋₃, mesial and more reduced on M₄; hypoconulid low, very salient posteriorly and nearest to entoconid on M_{1-3} ; minute and intermediate between hypoconid and entoconid on M₄.

DISCUSSION: The skull has an extensive maxillo-frontal connection and consequent naso-lacrimal separation, a feature found in the Dasyuridae but which is not uncommon among the Didelphidae, in which there is normally a trend to a maxillo-lacrimal-naso-frontal contact at a common point, situated just above the lacrimal and approximately on the vertical line corresponding to

¹ In honor of Dr. George Gaylord Simpson.

the lacrimal foramen. The character of this portion of the skull in the holotype of *Gaylordia macrocynodonta*, new species, is similar to that observed on the skull of a Recent didelphid, *Monodelphis brevicaudatus*, from Venezuela (A.M.N.H. No. 144-834), and is repeated with variations in *Metachirus*, *Marmosa*, *Philander*, and probably in other Recent genera.

It would appear, then, that *Gaylordia* should be classified among the Didelphidae-Didelphinae, in spite of the rather peculiar and primitive aspect of the teeth. It was probably an insectivorous rather than an omnivorous didelphid.

Gaylordia macrocynodonta, new species

Figure 6

HOLOTYPE: D.G.M. No. 329-M. Anterior part of a skull, with right C, P^{2-3} , M^{1-3} , and left M^{1-2} present, and with the roots of the right P^1 , and the antero-external root of the right M^4 , and the roots of left C, P^{1-3} , and M^3 present. Mesial fragment of left mandibular ramus, with P_2 and M_1 , and the roots of P_{1-2} , and M_{2-3} present. Collector: Júlio da Silva Carvalho, 1949.

REFERRED SPECIMENS: M.N.R.J. No. 1366-V, median fragment of left lower jaw with M_1 and alveoli of P_{2-3} , M_{2-4} present. A.M.N.H. No. 49801, median portion of right lower jaw with P_2 – M_2 and alveolus of M_3 present. M.N.R.J. Nos. 1357-V and 1358-V, respectively, left and right mandibular ramus with left P_3 and M_3 , and right P_3 present. D.G.M. No. 186-M, left mandibular ramus with P_3 – M_1 present. Collectors: Carlos de Paula Couto, 1948 (M.N.R.J. and A.M.N.H. specimens), and Júlio da Silva Carvalho, 1949 (D.G.M. specimen).

DIAGNOSIS: The only known species of the genus.

Measurements: Holotype, D.G.M. No. 329-M: P^{1-3} , 6 mm.; M^{1-3} , 5 mm.; M^{1-4} , approximately 7 mm.; ratio LM^{1-4}/LP^{1-3} , approximately 1.16; P_{1-3} , 5.8 mm.; M_{1-3} , 5.3 mm. Paratype, M.N.R.J. No. 1355-V: P_{1-3} , 5 mm.; M_{1-4} , 7 mm.; ratio LM_{1-4}/LP_{1-3} , 1.40.

Gaylordia macrocynodonta probably was about the size of the Recent Monodelphis brevicaudatus.

DESCRIPTION: The only part of the skull preserved is the facial region, with both sides present. The skull is broken anterior to the canines and immediately behind the lacrimals. The specimen was submitted to lateral compression and as a result is somewhat deformed.

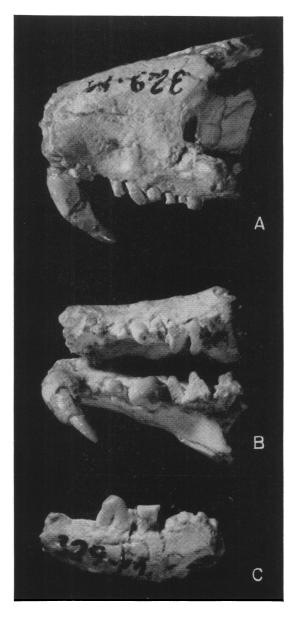


FIG. 6. Gaylordia macrocynodonta, new genus, new species. Holotype, D.G.M. No. 329-M. A, B. Anterior part of skull, left side view (A) and palatal view (B). C. Mesial fragment of left mandibular ramus, external view. Approximately \times 4.

The nasals are elongate. Their external borders are parallel from the anterior end to a point almost above the infraorbital foramen, become progressively wider posteriorly to the maxillofrontal suture, and narrower again back to the sagittal line of the skull, approximately at the level of the anterior border of the orbit. They are not in contact with the lacrimals, from which they are widely separated by the maxillae and frontals. The latter (maxillae and frontals) are in contact, as happens quite frequently in the dasyurids and less frequently among the didelphids. A very different condition is observed in the borhyaenids, in which the much larger posterolateral expansion of the nasals, combined with the relatively larger anterior extension of the lacrimals, produces a wide union between these two bones, and completely separates the maxillae from the frontals.

As the skull is broken along its sagittal line and the right nasal is fractured and reduced to its external half, it is impossible to observe the internasal suture, except in a very small posterior extension, near the frontals, where it can be seen that the suture was still open, i.e., not ossified.

The frontals are reduced to small anterior fragments. They were not yet coössified, a part of the suture being visible immediately behind the nasals. Their line of suture with the maxillae, lacrimals, and sphenorbitals is similar, in the preserved parts, with what is seen in the Recent didelphids, as, for example, in a skull of *Monodelphis brevicaudatus* from Venezuela (A.M.N.H. No. 144834).

The infraorbital foramen is large.

The left lacrimal is much better preserved than the right one. Its facial extension is a little smaller than in the Recent didelphids, on the part immediately anterior to the lacrimal foramen; its intraorbital extension is also slightly shorter than in the Recent didelphids. The lacrimal foramen is large, its longer diameter being the vertical; it is facial, placed immediately behind the maxillo-lacrimal suture and slightly before the anterior orbital border.

The maxillae do not present any important peculiar feature. The relations with the other facial bones are the same as those commonly observed in the Recent didelphids. As the anterior parts of the maxillae are lacking, it is impossible to know their relations with the premaxillae. But the reciprocal relations of these

bones were probably identical to the conditions observed in the Recent didelphids.

The palatal extension of the maxillae appears to have been as wide as in the Recent didelphids, but the palatine was apparently less extended anteriorly. The posterior palatine foramen seems to have been situated at the side of M^4 .

The upper incisors are not preserved. The upper right canine is almost complete, though fractured in several places. It is relatively very large, laterally compressed, gently curved, sharp-pointed, and looks like a "sabre tooth."

P¹ (roots) is normally oriented. P², slightly larger, ovate in outline, is slightly worn; the wear surface occupies the posterior face of the tooth, rising in inclined plane from the tip of the main cusp to the vestigial talon. P³ is enormous, bulky; its anterior root is inclined forward and is slightly thicker than the posterior one. Shallow external groove, between the two roots, divides the external face of the tooth into two distinct lobes, the posterior one being larger. This tooth is inclined against M¹. It is a little worn, as is P².

The upper molars are very worn. Because of this it is not possible to distinguish the structural elements of the crown. Only the right M³, partially broken, shows faint structural details. M^2 is the largest. M^{1-2} are similar in outline to those of the Recent didelphids. They are triangular. Their crowns are completely smoothed by wear. Apparently they were structurally similar to those of the Recent didelphids, with protocone, paracone, metacone, and external cingulum, as well as the stylar cusps, normally developed. M^3 is different from M^{1-2} in outline. Its protocone is much less expanded inward and slightly less developed anteroposteriorly; the paracone is salient on the anterointernal face of the tooth. The metastylar region is more reduced than that of M^{1-2} ; a small stylar cusp (D, E?) is present there. The parastylar region is partially broken but has normal develop-The width of the tooth is approximately equivalent to the length, making it different from M^{1-2} , which are much wider than long. M4 is lacking.

Only the middle portion of the holotype mandibular ramus (D.G.M. No. 329-M) is preserved, with P_3 - M_1 present, the latter being very worn. The referred specimen A.M.N.H. No. 49801, a median portion of a right mandibular ramus, with P_2 - M_2 present but very worn, is not in much better condition.

The description of the mandible and lower teeth is therefore based on the paratype M.N.R.J. No. 1355-V, an almost complete right lower jaw, with P_2 - M_4 present and well preserved. The anterior part of the horizontal ramus is broken immediately before the alveolus of P_1 ; the region behind M_4 is only partially preserved.

The mandible is relatively short and low. The lower border is slightly curved and more or less parallel with the dental border. A small mental foramen is present under the anterior part of P_2 , equidistant from the dental and lower borders; another foramen is seen under M_1 . The anterior part of the base of the articular ramus is external to M_4 . The masseteric fossa is normally developed and prolonged forward to a point under the anterior part of M_4 .

The lower incisors are not preserved. The lower canine (posterior part of alveolus) was, it seems, normally developed.

 P_1 (alveolus) was very small, two-rooted, pressed between the canine and P_2 , and oriented obliquely from outside inward, the anterior root being placed external to the posterior part of the canine, and the posterior root internal to the anterior part of P_2 . P_2 is slightly larger than P_1 , two-rooted, with a main cusp and vestigial talonid. P_3 is relatively enormous and bulky, much larger than P_2 and than M_{1-4} . It has a strong main cusp and a relatively well-developed talonid which bears, on the posterior end, a small, anteroposteriorly compressed cusp which is connected with the main mesial cusp by a weak, rising crest, on the internal side of the crown.

 M_{1-4} have strong oblique anterior cingula. M_{1-3} are progressively larger, M_4 being a little longer than M_1 , as long as M_2 , and slightly shorter than M_3 . The trigonid is much higher than the talonid, and anteroposteriorly compressed; the protoconid is dominant, V-shaped inward, slightly posterior to the metaconid (on M_{1-3}) or in line with the metaconid (on M_4); the paraconid is low, anteroposteriorly compressed; the metaconid is higher than the paraconid and conical. The talonid is singularly short, anteroposteriorly compressed, and very low; it is slightly narrower than the trigonid on M_{1-3} , but about half as wide as the trigonid on M_4 . The hypoconid is as high as, or slightly higher than, the entoconid on M_{1-3} , lower than the entoconid, and almost mesial on M_4 , pressed against the base of the protoconid. The entoconid is well developed and conical, not pressed against the

base of the metaconid but much closer to it than is usual in the didelphids. The hypoconulid is well developed and salient, almost internal, closer to the entoconid, on M_{1-3} , or weak and equidistant from entoconid and hypoconid, and as high as the latter, on M_4 .

The specimens M.N.R.J. No. 1357-V, incomplete left right mandibular ramus with P_3 and M_3 present, M.N.R.J. No. 1358-V, partial right mandibular ramus with P_3 present, and D.G.M. No. 186-M, almost complete left mandibular ramus with P_3 -M₁ present, are referred to this species with some doubt.

In the specimen M.N.R.J. No. 1357-V, the lower molars are slightly larger, with talonid a little more expanded posteriorly and a slightly wider basin. The hypoconulid is less salient, connected with the hypoconid by a low crest, and the anterior oblique cingulum is stronger.

The specimen M.N.R.J. No. 1358-V is broken just before P_1 , also lacks the angular region, the articular condyle, and the coronoid process. The posterior part of the alveolus of the canine, the posterior alveolus of P_1 , and the alveoli of P_2 and M_{1-4} are preserved. The posterior opening of the dental canal is placed approximately in the same position as in the Recent didelphines of equal size, as, for instance, *Monodelphis brevicaudatus*. The pterygoid crest is similar to that of these latter forms, and this was probably the case with the angular process. The mental foramen (vestiges) is under the anterior part of P_1 ; another foramen is placed beneath the anterior part of M_1 .

The specimen D.G.M. No. 186-M is an almost complete left lower jaw, with P_3 - M_1 , the posterior part of the alveolus of the canine, the alveoli of P_1 and M_{2-4} , and the anterior alveolus and the posterior root of P_2 present. It is somewhat larger than the above-mentioned specimens, but morphologically similar. It is broken immediately before P_1 and lacks the upper and the posterior part of the coronoid process and the posterior portion of the angular process. The articular condyle is low, its level being slightly higher than that of the tip of P_3 . The mandibular symphysis extends posteriorly to beneath the anterior part of P_3 .

The small differences presented by these specimens appear to be merely individual variations of Gaylordia macrocynodonta.

MIRANDAIA, NEW GENUS¹

GENOTYPE: Mirandaia ribeiroi, new species.

¹ In memory of Alípio de Miranda Ribeiro.

DIAGNOSIS: Small primitive didelphids. P_1 – M_4 in continuous closed series. P_3 trenchant, as large as M_1 . M_{1-4} with trigonid low; paraconid low, directed forward; metaconid intermediate in size between protoconid and paraconid. Talonid markedly wider than, and as long as, trigonid on M_{1-3} ; as wide as, or slightly narrower than, trigonid on M_4 ; entoconid slightly higher than hypoconid; hypoconulid small, internal to the midline, and close to entoconid. M_{1-3} progressively larger; M_4 narrower and shorter than M_{2-3} , as long as M_1 .

Mirandaia ribeiroi, new species¹

HOLOTYPE: M.N.R.J. No. 1359-V. Median fragment of right mandibular ramus with P_{2-3} , M_{1-2} , alveoli of P_1 , M_3 , and anterior alveolus of M_4 present. Collector: Carlos de Paula Couto, 1948.

PARATYPES: D.G.M. No. 361-M and A.M.N.H. No. 49859. Two partial right mandibular rami with M₂₋₄ and alveolus of M₁ present. Collector: Júlio da Silva Carvalho, 1949.

REFERRED SPECIMENS: M.N.R.J. No. 1362-V, median fragment of right lower jaw with M₂₋₃, alveolus of M₁, and anterior root of M₄ present. A.M.N.H. No. 49802, median portion of right lower jaw with M₂, anterior root and talonid of M₁, and roots of M₃ present. M.N.R.J. No. 1363-V, part of right lower jaw with M₂ and talonid and anterior root of M₁ present; No. 1364-V, right M₃. D.G.M. No. 360-M, posterior part of right mandibular ramus with M₂₋₄, and alveolus of M₁ present; No. 362-M, posterior fragment of right lower jaw with M₂₋₃, talonid of P₃, roots of M₁ and M₄ present. Collectors: Carlos de Paula Couto, 1948–1949 (M.N.R.J. and A.M.N.H. specimens) and Júlio da Silva Carvalho, 1949 (D.G.M. specimens).

DIAGNOSIS: The only known species of the genus.

Measurements: Holotype, M.N.R.J. No. 1359-V: P_{1-3} , 5.8 mm.; M_{1-4} , 10.3 mm.; ratio LM_{1-4}/LP_{1-3} , approximately 1.77.

DESCRIPTION: P_{2-3} are about the same height, but P_2 is shorter and slightly narrower. Both are cutting teeth, with a main sharp-pointed cusp and very small talonid, from which a weak crest rises to the tip of the main cusp. M_{1-4} have oblique anterior cingula, the posterior cingulum being absent or very weak on M_{1-3} , absent on M_4 .

¹ In memory of Alípio de Miranda Ribeiro.

The anterior mental foramen is not discernible in any of the specimens. The holotype (M.N.R.J. No. 1359-V) has a foramen under the posterior part of P_3 , equidistant from the mandibular borders. The specimen A.M.N.H. No. 49859 has a foramen beneath and between P_3 and M_1 . The specimen D.G.M. No. 360-M has two posterior foramina, one under the posterior part of M_1 , the other beneath the posterior part of M_2 . The specimen D.G.M. No. 362-M bears a foramen under and between M_1 and M_2 .

MONODELPHOPSIS, NEW GENUS

GENOTYPE: Monodelphopsis travassosi, new species.

DIAGNOSIS: Very small didelphids. P_2 larger than P_3 but shorter than M_1 and higher than P_3 – M_1 . M_1 with trigonid moderately elevated, slightly compressed, longer than and as wide as, or slightly narrower than, talonid. Paraconid low, slightly higher



Fig. 7. Monodelphopsis travassosi, new genus, new species. Holotype, M.N.R.J. No. 1365-V, fragment of left lower jaw with P_2 - M_1 , internal view. \times 3.

than entoconid, almost mesial, with sharp anterior edge; metaconid as high as, or a little higher than, paraconid. Talonid low, fully basined; hypoconulid strong, dominant; entoconid relatively weak, apparently as high as hypoconid; hypoconulid relatively well developed, almost internal, immediately posterior to and connected with entoconid by a low crest.

DISCUSSION: Monodelphopsis is less primitive in aspect than the genera described above. It is more similar to the modern didelphids in dental structure and in the relative size of P_{2-3} . It looks very like the Recent Monodelphis in several ways. In the fact that P_2 is the largest tooth of the lower premolar series this genus resembles the Recent didelphids and differs markedly

from the other Itaboraian genera, in which P_3 is the largest of the series or is at least as large as P_2 . The lower canine seems to have been about as large as in the Recent *Monodelphis*, judging by the remaining part of its alveolus.

Monodelphopsis travassosi, new species¹

Figure 7

HOLOTYPE: M.N.R.J. No. 1365-V. Fragment of left lower jaw with P_2 - M_1 , part of the anterior alveolus and posterior root of P_1 , and partial alveolus of C present. Collector: Carlos de Paula Couto, 1948.

DIAGNOSIS: The only known species of the genus.

Measurements: P_{1-3} , approximately 4.8 mm.; length of M_1 , 2 mm. This species would have been equivalent in size to *Monodel-phis brevicaudatus*.

DIDELPHIDAE INDET.

Among the Paleocene remains from São José de Itaborai there are two very small posterior fragments of right lower jaws, each with M₄ present: M.N.R.J. Nos. 1367-V and 1368-V.

 M_4 is so similar to that of the Recent species of Marmosa, and the fragments themselves look so like the corresponding part of the mandible of Marmosa, that it seems preferable to consider them provisionally as belonging to an undetermined form of the family Didelphidae rather than to give them new generic and specific names, at least until more complete and elucidative specimens are found.

It is hard to imagine that any Recent genus, such as *Marmosa*, even one with very primitive features, could have survived from the Paleocene times, as this long a period of generic survival is not known in any mammalian genera, living or extinct.

The specimen M.N.R.J. No. 1367-V, especially, looks like the corresponding part of *Marmosa elegans*.

As in the M_4 of this Recent species, the trigonid is moderately elevated, and the talonid is narrower and shorter than the trigonid. The arrangement of the cusps of the trigonid, as well as their relative sizes, is exactly the same as in *Marmosa elegans*. The hypoconid and entoconid are very small and about the same size

¹ In honor of Drs. Lauro and Haroldo Travassos.

TABLE 2

MEASUREMENTS (IN MILLIMETERS) OF FOSSIL SPECIMENS FROM SÃO JOSÉ DE ITABORAI AND THE CORRESPONDING PARTS OF Marmosa elegans and Marmosa murina roraimae

	Length of M ₄	Width of M₄	Depth of Mandible under M ₃	Depth of Mandible under M ₄
M.N.R.J. No. 1367-V	1.2	0.9	2.5	2.2
M.N.R.J. No. 1368-V	2.0	1.1	2.6	2.5
Marmosa elegans, A.M.N.H. No. 22334	1.6	1.0	2.0	1.9
Marmosa murina roraimae, A.M.N.H. No. 75704	2.0	1.0	3.0	3.0

(almost indistinguishable in worn teeth), and the hypoconulid is vestigial.

The posterior opening of the dental canal is situated exactly in the same place as in *Marmosa elegans*, and the position and strength of the masseteric fossa are also the same.

Possibly these specimens indicate the presence of a distinct species of a *Marmosa*-like genus in the South American Paleocene, but there is not yet enough evidence to permit establishment of a diagnosis for this probable new form.

The measurements of the specimens M.N.R.J. Nos. 1367-V and 1368-V, in comparison with specimens of *Marmosa elegans* and *Marmosa murina roraimae*, are given in table 2.

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