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## FOSSIL MAMMALS FROM THE BEGINNING OF THE CENOZOIC IN BRAZIL

### MARSUPIALIA: POLYDOLOPIDAE AND BORHYAENIDAE

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#### INTRODUCTION

The lower Tertiary fauna of Patagonia includes a great variety of marsupials. The families Didelphidae, Caenolestidae, and Caroloameghiniidae are poorly represented, while the Polydolopidae and, to a lesser extent, the Borhyaenidae are relatively common in the Patagonian Paleocene (Rio Chican: Polydolopidae and Borhyaenidae) and Eocene (Casamayoran: Polydolopidae, Borhyaenidae, Didelphidae, and possibly Caenolestidae). In the following stage, the Mustersan (upper Eocene), the Borhyaenidae are well represented, while according to our present knowledge, the Polydolopidae and Caroloameghiniidae disappear, and the Caenolestidae are doubtfully present. As Simpson (1948) points out, it is possible that the Polydolopidae and Caroloameghiniidae were really extinct by Mustersan times, since they are not found in any later strata. The Didelphidae, however, were certainly present in the Mustersan, although no evidence of their remains has yet been found.

Until recently, the only known identifiable South American didelphine prior to the Oligocene (Colhuehuapian) 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

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Microbiotheriinae, the only subfamily of the Didelphidae otherwise known from Patagonia from the Eocene to the Miocene.

*Eobrasilia* Simpson, 1947, from the Paleocene (Itaboraian) of São José de Itaboraí, Brazil, although classified among the Didelphidae, may be a borhyaenid. Its known characters do not permit a conclusion in either direction, and it therefore offers no solution to the problem of the origin and age of the South American didelphids, although it does cast light on the origin of the Borhyaenidae.

The recent discovery of remains of undoubted typical didelphids in São José de Itaboraí shows clearly that the group is very ancient in South America. It even justifies the supposition that their appearance on the continent dates back to the Cretaceous, since the fauna of Itaboraí, although resembling that of the Casamayoran, is certainly older (Paleocene). This is indicated by the primitive character of its components and confirmed by the presence of *Carodnia* Simpson, 1935, described from the Paleocene of Argentina.

Polydolopid remains are also frequent in the São José de Itaboraí site but, in contrast to the didelphids, the variety of forms is small, only one genus, with two species, being represented. This genus (*Epidolops*, new genus) is, in all aspects, more primitive than the genera from the Casamayoran of Patagonia, and gives a clearer idea of the relationships of this aberrant group.

The Borhyaenidae are poorly represented in the collections from São José de Itaboraí, in number both of species and individuals. The few known remains belong to two forms: one, to which almost all of the material is referred, belonging to the genus *Patene* Simpson, 1935, but smaller and more primitive than the genotype, *P. coluapiensis* Simpson, 1935, from the lower Eocene (Casamayoran) of Patagonia. Another species, represented by a very large lower molar, is doubtfully assigned to *Arminiheringia* Ameghino, 1902.

All of the material here described was collected in a limestone quarry at São José de Itaboraí, some miles northeast of Niterói, 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 management of the Companhia Nacional de Cimento Portland (Mauá), which has given generous cooperation in this work, and to which I am grateful for this help.

A note and a bibliography on the geology of this deposit were given by the author in an earlier paper (1949, pp. 6-10).

The present paper is a preliminary report, for the description of the new forms of the extinct families Polydolopidae and Borhyaenidae. It will be followed by another paper in which the new forms of Didelphidae from the same place will be described. The final report, which will include detailed descriptions of all the fossil remains from São José de Itaboraí, 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.

The following abbreviations are used to designate the collections to which reference 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, Rio de Janeiro (formerly Serviço Geológico do Brasil)

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

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I want to thank also the American Museum of Natural History, for the attentions and courtesy which I have invariably received from all its departments and for the publication of my papers.

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Thanks are also due to Mrs. Rachel Husband Nichols for help with manuscript and library references, and to Mr. William Fish, technician, who prepared the type mandible of *Epidolops ameghinoi*, new genus, new species. Mr. John Le Grand made the drawings of the type skull and mandible (top view) of the same species. Messrs. Hobart M. Van Deusen and George G. Goodwin, as well as Dr. George H. H. Tate, in the Department of Mammals, gave me great help in my search for material from

recent caenolestids and Australian marsupials, for comparative study with the extinct South American polydolopids. I am deeply indebted to all these friends and colleagues.

ORDER MARSUPIALIA ILLIGER, 1811

SUPERFAMILY CAENOLESTOIDEA OSBORN, 1910

FAMILY **POLYDOLOPIDAE** AMEGHINO, 1897

The polydolopids are, aside from the didelphids, the most representative element in the Paleocene fauna of São José de Itaborai, not in the number of forms but the number of specimens, all of which belong to two species of the same genus. An almost complete, although flattened skull, with premolars and molars present, and an associated complete mandible; with the dentition well preserved, were collected there, as well as several fragments of maxillae and mandibles, with and without teeth, and a large number of isolated teeth.

These are the most complete skull, mandible, and dentitions of marsupials of this family ever found, and from them we have reached a better understanding of the morphology, structure, and affinities of the Polydolopidae. Study of these specimens has especially broadened our knowledge of the dentition of the marsupials of this family.

Nothing has been known until now about the teeth anterior to  $P^3$ ; and knowledge of the teeth preceding  $P_2$  (until now considered as  $P_3$ ) and of the lower premolars and molars was incomplete, since the specimens collected in Patagonia are very fragmentary.

It is now known that the polydolopids had at least five teeth anterior to  $P^3$ :  $P^2$ , rudimentary and non-functional; the canine (C), well developed; and three or more incisors (I); while anterior to  $P_3$  (until now considered to be  $M_1$ ) they had at least four teeth:  $P_2$ , also rudimentary and non-functional, strong canine (C), and two or more incisors (I). A long diastema separates the canines from  $P_2^2$ . The lower diastema sometimes has a vestige of what might possibly have been  $P_1$ .

The enormous lower sectorial tooth is certainly  $P_3$ , not  $M_1$ , as was believed, since there are four molars behind it. The last of these ( $M_4$ ) is very small and disappearing, being still present in the polydolopids of São José de Itaborai but completely absent in the Patagonian polydolopids.

It is also clear that the upper molars of the polydolopids ( $M^{1-4}$ ) were primitively alike, more or less quadrangular in outline, with normal four-cusped crown. This differs from what is known of the Patagonian relatives, in which  $M^1$  is laterally compressed, blade-like, cutting, more similar to  $P^3$  than to the posterior molars in the type genus, *Polydolops*, or molariform, but multicuspitate in all the other genera.

Moreover, none of the Patagonian specimens examined in the American Museum of Natural History and in the Argentinian museums shows the smallest trace of the  $M_4$  which, as above mentioned, was still present, although diminutive and vanishing, in the Itaboraian polydolopids.

This circumstance, in addition to some other differential characters, indicates that the polydolopids of São José de Itaboraí are more primitive than their Patagonian relatives, whose ideal, ancestral, structural characters they seem to display.

With the more complete data now available, a better definition of the family Polydolopidae can now be given, modifying Simpson's (1948) definition.

#### FAMILY POLYDOLOPIDAE AMEGHINO, 1897

DEFINITION: Early Tertiary South American marsupials. Dental formula:

$$\frac{3}{2(3)} : \frac{1}{1} : \frac{2}{2(3)} : \frac{4}{4-3}$$

Upper incisors in continuous, longitudinal series. Lower incisors very elongated, thin, laterally compressed, procumbent, with chisel-like crown.  $I_1$  much more elongated than  $I_2$ . Lower C relatively strong, laterally compressed, procumbent, contiguous to  $I_2$ , a rather incisor-like, but sharp-pointed crown, with the tip turned upward.  $P_1$  absent or vestigial.  $P_2^2$  very small, sometimes vestigial or absent, separated from the C by a large diastema.  $P_3^3$  and, in the later forms,  $M^1$  laminar, trenchant, with serrate edges, no distinct trace of normal cuspidate structure.  $M_{1-4}$  multicuspitate, basined, enamel of crown finely wrinkled when unworn. Trigonid of  $M_1$  more or less elevated anteriorly to a shearing apex.  $M_{2-3}$  with one internal and one or two external cusps (in the latter case the posterior one stronger) in trigonid, poorly differentiated from talonid. Talonid of  $M_{1-4}$  with two principal cusps, one external, the other internal, with

small accessory cuspules.  $M_4$  very small, generally two-rooted, present only in the most primitive forms.  $M^{2-4}$  generally, in the later forms, with three imperfectly differentiated inner, and three or (especially on  $M^2$ ) more outer, cuspules, imperfectly differentiated. Skull with moderately elongated and wide rostrum. Nares terminal; nasals elongated, moderately wide, but posteriorly expanded outward and extending to a line passing the posterior border of the orbits. Frontals flat, wide anteriorly, with weak sagittal crest. Zygomatic arch strong, its base stout and opposite  $P^3-M^2$ . A pair of wide and elongated anterior palatal foramina, limited posteriorly at a line passing the canines; another small and rounded palatine foramen lateral to  $M^3$ . Mandible strong, relatively short. Deep masseteric fossa, anteriorly limited by strong crest on the anterior border of the high and wide coronoid process; masseteric crest well developed, wider posteriorly. Condyle strong, moderately elevated, a little above the dental level. Pterygoid fossa moderate. Angular process strong, horizontally directed inward, but with the posterior end well turned up. Symphyseal region thin, abruptly narrowed before  $P_2$ , and oriented obliquely up and forward.

DISCUSSION: Ameghino described a large number of genera in this family, which were reduced to three (*Polydolops*, *Amphidolops*, and *Eudolops*) by Simpson (1948), who had earlier proposed one more (*Seumadia* Simpson, 1935).

Simpson gave good diagnoses of these genera, which are repeated below, with modifications in the dental notations based on the new specimens.

#### POLYDOLOPS AMEGHINO, 1897

DIAGNOSIS:  $P_2$  present.  $P_3^3$  large, shearing, strongly denticulated. Molar crowns moderate in height, well basined, cuspules small but distinct, enamel somewhat wrinkled.  $M^1$  shearing, similar to  $P^3$  but much smaller than the latter.  $M^{2-3}$  and  $M_{1-2}$  moderate in size.  $M^4$  and  $M_3$  reduced, ovate.  $M^2$  with a few disconnected, conical, external cuspules.  $M_4$  absent.

#### AMPHIDOLOPS AMEGHINO, 1902

DIAGNOSIS: Shearing teeth ( $P_3^3$ ) very large. Molar crowns moderately high but basins and coronal relief as a whole shallow, cusps all small, tending to become very numerous and indistinct. Enamel strongly wrinkled.  $M^2$  with a continuous external row

of accessory cuspules, nearly or quite as prominent as the main row immediately internal to them.  $M_4$  absent.

#### EUDOLOPS AMEGHINO, 1897

DIAGNOSIS:  $P_2$  (and probably C and  $P_1$ ) absent. Shearing teeth ( $P_3^3$ ) relatively small, denticulation slight. Molar crowns low, with large distinct cusps and relatively few accessory cuspules.  $M^1$  shearing.  $M^{2-3}$  and  $M_{1-2}$  subequal.  $M^4$  and  $M_3$  enlarged. No external accessory cuspules on  $M^2$ .  $M_4$  absent.

#### SEUMADIA SIMPSON, 1935

DIAGNOSIS:  $M^4$  triangular, slightly wider than long, the corners somewhat elevated but without any distinct cusps. Crown very low, with a very shallow basin, with numerous irregular, anastomosing small grooves and ridges.  $M_4$  probably absent.

The specimens from São José de Itaboraí seem to belong to two species of a genus quite distinct from the four previously known genera, above defined.

#### EPIDOLOPS, NEW GENUS

GENOTYPE: *Epidolops ameghinoi*, new species.

DIAGNOSIS: Upper and lower incisors (I) numerous, probably  $\frac{3}{2}$ . Upper and lower C strong, one-rooted.  $P_2^2$  present, but small, non-functional, almost vestigial.  $P_3^3$  shearing, much larger than the molars, with cutting denticulated edge, oriented quite obliquely from outside inward. Molar crowns low, with moderate basins, small but distinct cusps, and slightly wrinkled enamel. Upper and lower molars approximately subequal, tetracuspitate.  $M^1$  perfectly molariform, with two small accessory cuspules intermediate between the four main cusps.  $M^2$  similar to  $M^1$ , without outer cuspules. Lower molars with vestigial cuspules.  $M_{1-2}^{1-2}$  moderate in size.  $M_3^3$  similar to the preceding molars, but considerably smaller and quadrangular in outline.  $M_4^4$  minute, one- or two-rooted. Skull and mandible as in the family.

#### *Epidolops ameghinoi*, new species<sup>1</sup>

HOLOTYPE: D.G.M. No. 321-M. Almost complete but much crushed and flattened skull, lacking the upper part of the brain

<sup>1</sup> In memory of the Ameghino brothers, Carlos and Florentino.

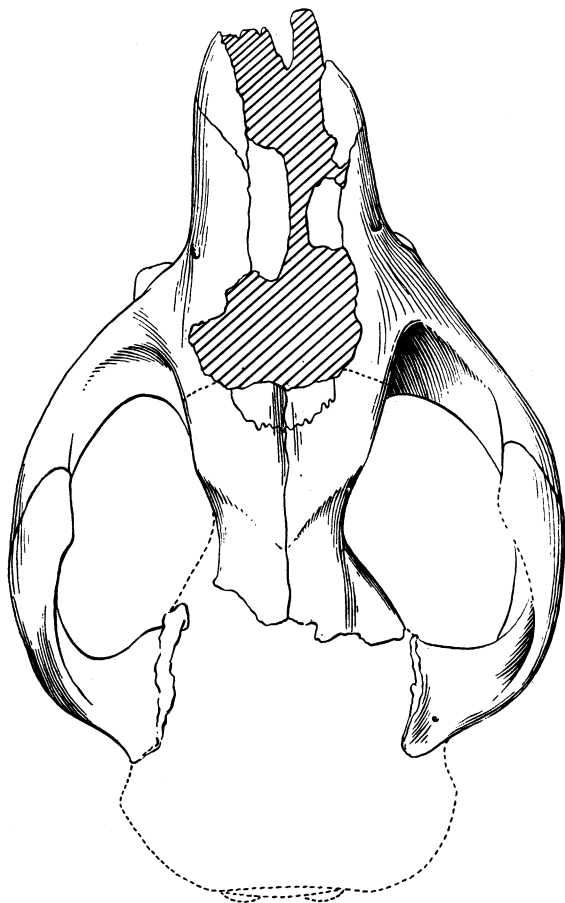


FIG. 1. *Epidolops ameghinoi*, new genus, new species. Type skull (D.G.M. No. 321-M), top view.  $\times 2$ .

case and the part posterior to the basisphenoid, as well as the anterior end of the premaxillae. Almost complete mandible, lacking the anterior end of the incisor border. Right  $I_{1-2}$ , left lower C,  $P_{2-3}^{2-3}$ ,  $M_{1-2}^{1-2}$ ,  $M_3$  from both sides present. Collector: Júlio da Silva Carvalho, 1949. (Cast A.M.N.H. No. 49851.)

REFERRED SPECIMENS: D.G.M. Nos. 170-M to 197-M, and 207-M to 209-M, fragmentary right and left lower jaws with and without teeth; and D.G.M. Nos. 198-M to 206-M, partial right and left maxillae with teeth; all collected by Júlio da Silva Carvalho, 1949. M.N.R.J. Nos. 1372-V to 1374-V, 1376-V to



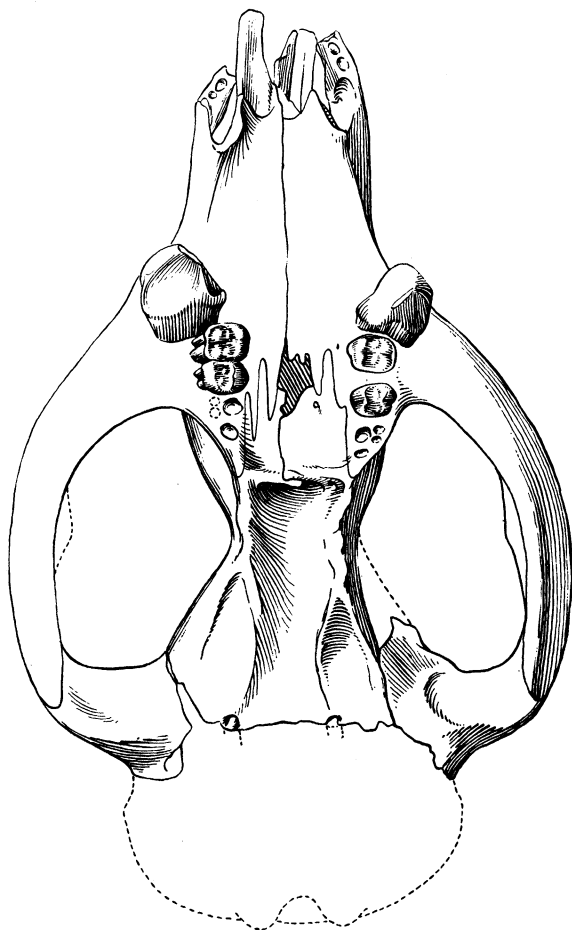


FIG. 2. *Epidolops ameghinoides*, new genus, new species. Type skull (D.G.M. No. 321-M), palatal view.  $\times 2$ .

1378-V, 1381-V to 1392-V, 1394-V and 1395-V, 1397-V to 1405-V, incomplete right and left lower jaws with and without teeth; 1407-V to 1416-V, portions of right and left maxillae with and without teeth; 1417-V to 1419-V, partial right  $P^3$ ; 1420-V, incomplete left  $P^3$ ; 1421-V, left  $M^2$ ; 1422-V, right  $M^1$ ; 1423-V, anterior part of left  $M^1$ ; and 1424-V, right  $I_{2.}$  A.M.N.H. Nos. 49806 to 49809, 49811 and 49813, fragmentary lower jaws with teeth. All collected by Carlos de Paula Couto, 1948-1949.

DIAGNOSIS: Moderate size.  $P^3$  enormous, much larger than the molars, with curved and denticulated edge; two strong,

antero-external crests limit a deep vertical groove, which runs from the apex to the base of the crown; two other similar but slightly weaker crests limit a shallow groove, which runs from the apex to the base of the crown, on the anterior border of the internal face of the tooth (these crests disappear progressively with wear).  $M^1$  with definite external basal cingulum. Mandible moderately strong and relatively low. Ratio  $LP_3/LM_1$ , 1.60–2.03.

DISCUSSION: There is great variation in size and proportions among the specimens referred to this species. The ratio  $LP_3/LM_1$ , for instance, varies between 1.60 and 1.82 in 48 specimens, and between 1.87 and 2.03 in nine specimens (these two groups having been separated according to size), the latter nine specimens being generally larger than the specimens of the first group.

These differences could, perhaps, be regarded as an indication of the existence of two subspecific groups if the specimens did not come from the same locality or if there were evidence that they came from different strata. Evidence on this point is lacking, however, at least for the present, since none of the fossils here considered were found in beds but were mixed into a marl filling channels and underground caves, as is pointed out above.

### ***Epidolops gracilis*, new species**

HOLOTYPE: D.G.M. No. 188-M. Fragment of right lower jaw with  $P_{2-3}$ ,  $M_{1-2}$  present. Collector: Júlio da Silva Carvalho, 1949.

PARATYPE: M.N.R.J. No. 1400-V. Partial left lower jaw with  $P_{2-3}$ ,  $M_{1-2}$  present. Collector: Carlos de Paula Couto, 1948.

REFERRED SPECIMENS: D.G.M. No. 191-M, part of left lower jaw with  $P_3$ ,  $M_1$  present; No. 198-M, portion of left maxilla with  $P^3$ ,  $M^{1-2}$  present; both collected by Júlio da Silva Carvalho, 1949. M.N.R.J. Nos. 1390-V and 1391-V, anterior parts, respectively, of right lower jaw with roots of  $P_2$  and with  $P_3$  present, and of left lower jaw with  $P_{2-3}$  present; No. 1412-V, part of right maxilla with  $P^3$ ,  $M^{1-2}$  present; No. 1404-V, fragment of left maxilla with  $P^3$  present; No. 1411-V, portion of right maxilla with  $P^3$  present; all collected by Carlos de Paula Couto, 1948–1949. A.M.N.H. Nos. 49809, 49810, 49812 to 49814, and 49860, lower jaw fragments with teeth; the first five specimens collected by Carlos de Paula Couto, 1948–1949; the last, by Júlio da Silva Carvalho.

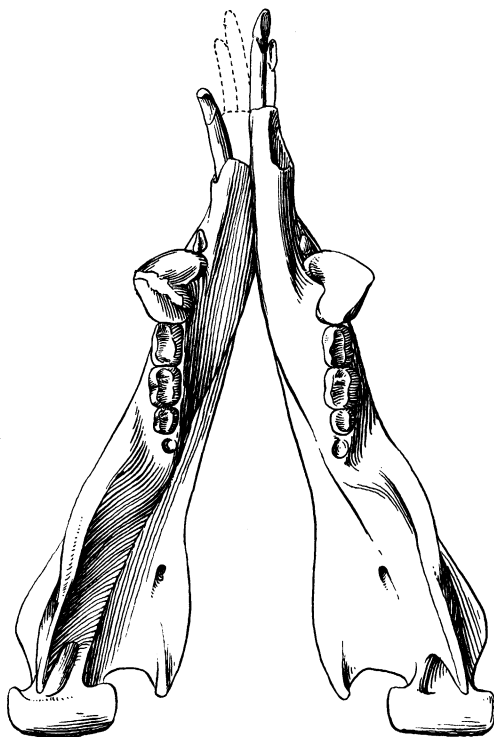


FIG. 3. *Epidolops ameghinoi*, new genus, new species. Type mandible (D.G.M. No. 321-M), top view.  $\times 2$ .

DIAGNOSIS: Smaller than *E. ameghinoi*.  $P_3^3$  much smaller and more compressed laterally than in the type species, with edge less curved and weakly denticulated; antero-external vertical groove of the crown weak; the antero-internal one very slight and reduced to its upper third part.  $M^1$  without external cingulum. Mandible thin. Ratio  $LP_3/LM_1$ , 1.34–1.53.

#### AFFINITIES OF THE POLYDOLOPIDAE

The origin and affinities of the Polydolopidae have been discussed by many authors, with quite divergent opinions.

According to Ameghino, they would be directly connected, on the one hand, with the Multituberculata, a very primitive group known mostly from the Jurassic and Cretaceous of the Northern Hemisphere (Eurasia and North America), from which they would originate, as well as with the marsupials classified in

the former group Diprotodontia (the South American Caenolestidae and the Australian Phalangeridae, Thylacoleonidae, Macropodidae, Phascolomidae, and Diprotodontidae), and, on the other hand, with the Rodentia, which would be descended from them.

The general tendency of other authors has been to classify the Polydolopidae among the Multituberculata, in accordance with Ameghino's view, although Gregory (1910) disagrees with this opinion, saying that their resemblances to Multituberculata and Rodentia would be merely the effects of convergence and that their most probable relationships would be with the marsupial family Caenolestidae.

Simpson (1928) also refuses to accept the relationships of the Polydolopidae to Multituberculata, saying:

1. "The horizontal ramus [of the mandible] in the Polydolopidae is fairly long and slender with alveolar and lower borders roughly parallel and quite unlike the Multituberculata in aspect [that of the Multituberculata being relatively short and thicker, with its alveolar and lower borders divergent].

2. "[In the Polydolopidae] there are two mental foramina, one beneath the middle of the premolar series or of the diastema and one beneath  $M_1$  or  $M_2$  [which is] the usual primitive marsupial arrangement and contrasts fundamentally with the single mental foramen just back of the incisor in the Multituberculata.

3. "According to Ameghino there is evidence that *Propoly-mastodon* [now considered by Simpson as a synonym of *Eudolops*] had two pairs of lower incisors, [whereas] even in the Jurassic no multituberculate has any vestige of more than one pair.

4. "The occurrence" [in the Polydolopidae] of two or more small apparently functionless premolars is another marked difference from any known Multituberculata [whose premolars are generally functional and well developed, especially the upper ones] and out of keeping with the whole evolutionary trend of the Multituberculata.

5. "The Polydolopidae. . . differ again fundamentally from any multituberculates [because they have three more or less molariform teeth behind the shearing tooth (until now called  $P^3$  and  $M_1$ , but here proved to be  $P_3^3$ )], for in the long line of plagiaulacoid multituberculate genera from the Jurassic into the Eocene none has more than two molariform teeth in either jaw.

6. "[In the Polydolopidae] the shearing tooth itself is unlike

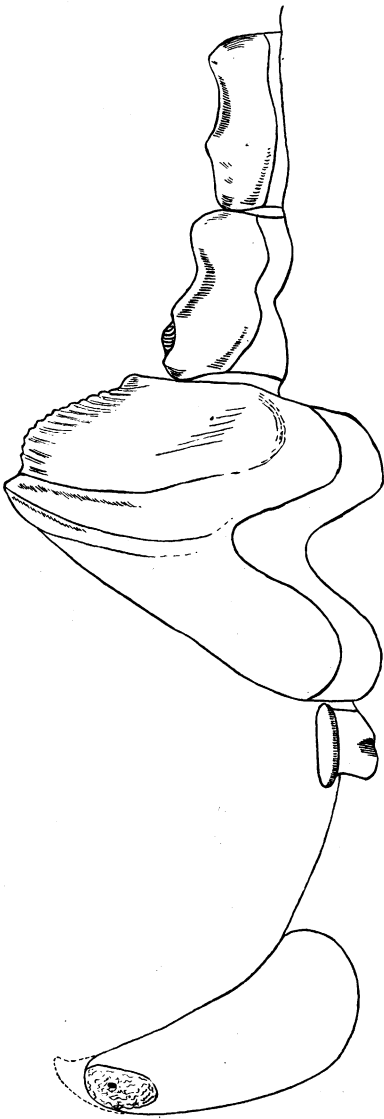


FIG. 4. *Epidolops ameghinoides*, new genus, new species. Incomplete left lower dentition, canine and P<sub>2</sub>-M<sub>2</sub>, external view (D.G.M. No. 178-M).  $\times 4$ .

that of the multituberculates in contour and structure [since its edge is coarsely notched (*Polydolops*) or finely serrate (*Eudolops*) or may be quite smooth (*Archaeodolops*, perhaps synonymous with *Polydolops*, according to Simpson, 1945), and its lateral surfaces are smooth, whereas in the Multituberculata (save Taeniolabidae) the same tooth has the lateral surfaces grooved or ridged as in the Abderitinae and many macropids].

7. "The resemblance [of the Polydolopidae] to the Multituberculata in lower molar structure is entirely superficial and lies only in the fact that they have a number of cusps roughly arranged in two rows, as have a host of other quite unrelated mammals. [The molars of the Polydolopidae are] multituberculate [solely] in the literal, etymological sense [but not in the taxonomic sense].

8. "Mammals which furnish an excellent morphological ancestry for the later marsupials (and placentals) are present in the middle Jurassic and are then quite as distinct from the Multituberculata as are the Cretaceous and Paleocene Theria."

Simpson's observations are exact and convincing. It seems to me that they cannot be contested.

On the basis of the more complete material that I have at my disposal, I can say, supporting Simpson's views, that:

1. The morphological conditions of the skull and mandible of the Polydolopidae are so similar to those of the most typical marsupials in all essential features that it seems to me impossible to have the smallest doubt as to their marsupial status; whereas the Multituberculata belong in a subclass (Allotheria) distinct from, and more primitive than, the Subclass Theria, which includes the Marsupialia, and are not related either to the latter or to the Rodentia, as was supposed by Ameghino. (The Multituberculata seem, in fact, to be unrelated to any of the later mammalian orders; most contemporary authors consider them a sterile side branch of the original mammalian stock.)

2. The polydolopids are now known to have at least three pairs of upper incisors and two pairs of lower ones, whereas the known Multituberculata have no more than  $\frac{3}{1}$  I, which indicates that they are more specialized than the polydolopids, although earlier in time. The Multituberculata, therefore, cannot be considered as ancestors of the polydolopids, since evolution is unlikely to have been reversed in this respect.

3. In the most primitive polydolopids, the upper and lower molariform teeth have four main cusps and no more than two

small intermediate cuspules (upper molars), being therefore simpler than the molariform teeth of the later genera of the same family and obviously not derived from the multicuspid molars, more complex and specialized, of the Multituberculata.

4. In the polydolopids, as in the Caenolestidae,  $I^1$  is probably the most developed, whereas in the Multituberculata  $I^2$  is the larger.

The following features of the skull and mandible of the Polydolopidae are, in fact, clearly marsupial: angular process of the mandible completely inflected inward and upward (absent in the true Multituberculata); the coronoid process of the mandible is large and high, reminiscent of that of the polyprotodonts and diprotodonts; the malar bone runs backward to the anterior border of the glenoid cavity (primitive feature common to the Multituberculata and to the Reptilia Cynodontia); palatal foramina present.

With regard to the Rodentia, it is absolutely sure that the Polydolopidae have nothing in common with these placental mammals, aside from the fact that they both are mammals.

What is the position of the Polydolopidae among the Marsupialia?

The authors who for good reasons do not accept the classification of them among the Multituberculata or their descent from them are generally in accord in classifying the Polydolopidae within the marsupial Diprotodontia or, more usually, the Caenolestoidae, comparing them with the Abderitinae, universally admitted to this group, and undoubtedly very similar to the Polydolopidae.

This is, for example, the opinion of Simpson (1928, 1948) who classifies the Polydolopidae within the Caenolestoidae for the following reasons:

1. The mandible of "*Polydolops*. . . clearly had an inflected angle thoroughly caenolestoid in character."

2. The enlarged incisors of the polydolopids are similar to those of the caenolestoids and agree thoroughly with the caenolestoid resemblances of the other known parts, though they "have no independent value as evidence of affinities, similar ones [enlarged incisors] having been acquired at least six times quite independently within the Class Mammalia."

3. The supposition that the polydolopids had more than one

pair of lower incisors accords, too, with the condition known in the caenolestoids which may have from one to four pairs.

4. The reduction of the ante-molar teeth in the polydolopids, though carried farther than in other caenolestoids, is produced in the same direction.

5. The lower shearing tooth of the polydolopids (until now supposed to be  $M_1$ , but now proved to be  $P_3$ ) is similar to that of the Palaeothentinae (= Epanorthinae) and Abderitinae, although more specialized than that of these two groups (and not homologous with it, as we have seen above).

6. The fact that the Palaeothentinae and Abderitinae, from the Oligocene and Miocene, are structurally more primitive than the Polydolopidae, which preceded them in the Paleocene and Eocene, is not a good reason for rejecting the hypothesis that the first two groups are close collaterals of the last group, but it makes impossible the supposition that the first two could be descendants of the last. The Palaeothentinae and Abderitinae, although more persistent in time, would have constituted two less specialized groups, arising, side by side with the more specialized, although older, Polydolopidae, from a common primitive stock; "similarly, the living caenolestids are more primitive than the majority of the known Miocene forms and represent a structural stage ancestral to the latter."

7. Caenolestinae more primitive than the living ones and possibly their ancestors do occur in the Miocene (*Halmarhiphus*, etc.), side by side with the more specialized groups of the same family (Palaeothentinae and Abderitinae). The absence of analogous annectant types in the Casamayor (lower Eocene) must be considered more apparent than real, since such forms obviously must have existed at that time. "The Casamayor represents only a fauna of rather limited area and of one facies, and even if present these small and rather rare mammals might easily fail to appear in collections."

8. "The true annectant forms must be pre-Casamayor and the only definable pre-Casamayor mammal yet known from South America is *Proteodidelphis*, known from a single specimen. Under such conditions negative evidence should be given no weight."

9. "Like the shearing teeth, the grinding teeth of the Polydolopidae are, except for relatively unimportant details, simply a further development of the abderitine type."



10. The polydolopids (*Polydolops*, *Amphidolops*, *Eudolops*, etc.) "are essentially unified with regard to lower molar structure and are clearly linked structurally with the Abderitinae and through them eventually with the primitive tuberculo-sectorial type."

According to Simpson, the interpretation of relationships of the Polydolopidae to the Caenolestidae on the basis of the upper molar series is much more difficult.

Comparing the  $M^1$ , typically molariform, of the Palaeothentinae (= Epanorthinae) with the highly modified  $M^1$  of the Casamayoran Polydolopidae, which "retains no trace of its probable ancestral condition," Simpson says that no annectant forms between these two types of structure are known, adding, "the abderitine series is not sufficiently well known to be of conclusive value, but it does not appear to be as nearly transitional structurally as in the case of the lower teeth.  $M^{2-4}$  also present difficulties." Although they are much more complicated than those of the Caenolestidae, Simpson admits that they "could be derived from the caenolestid ones by broadening and cusp proliferation, thoroughly in keeping with the apparent evolutionary trend of the group."

In regard to paragraph 1, it is possible to say now, on the basis of the more complete material found in Brazil, that the mandibular angle of the Polydolopidae is bent well inward, reminiscent of that of the Caenolestidae. But it seems to me that it is more similar to that of the Phalangeridae, since in the forms of this family (*Trichosurus*, *Dactylopsila*, etc.), the angular process is very wide and is directed almost horizontally inward, on a level with the lower border of the mandible, limiting wide pterygoid fossa, while in the Caenolestidae it is usually projected downward and a little inward, and its level is higher than that of the mandibular lower border. Moreover, the complete posterior region of the mandible is, in the Polydolopidae, much more similar, even almost identical, to that of the Phalangeridae, rather than to that of the Caenolestidae: it is strong, with a wide, high coronoid process, bending backward much more than that of the Caenolestidae, strong masseteric fossa, wide and large masseteric crest, very similar in form and position to that of the Phalangeridae, well developed, low condyle, etc.

As for the items in paragraphs 2 and 3, we note that the presence of more than one pair of lower incisors in the Polydolopidae

agrees with conditions observed in the Caenolestidae, which have from one to four pairs of lower incisors, but it may also suggest the condition observed in the Australian diprotodonts. Again, the fact that  $I_1$  is the most developed of the lower incisors suggests the beginning of the diprotodont specialization, which has

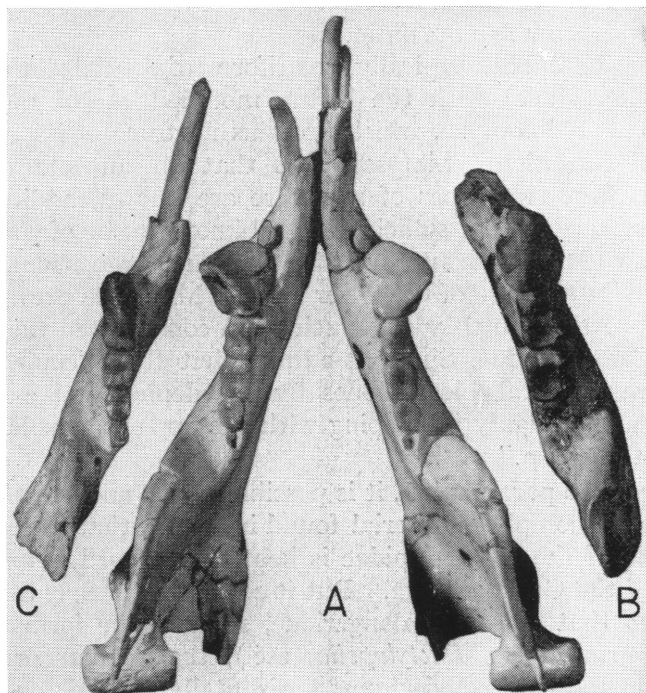


FIG. 5. Mandibles and lower dentitions of caenolestoids, for comparison (top view). A. *Epidolops ameghinoi*, new genus, new species, type mandible with right  $I_{1-2}$ ,  $P_2-M_3$ , and left C,  $P_2-M_3$  (D.G.M. No. 321-M). B. *Polydolops thomasi thomasi* (Ameghino), right lower jaw with  $P_3-M_2$  (A.M.N.H. No. 28444), Casamayor beds (lower Eocene), Cañadon Vaca, Patagonia. C. *Abderites crispus* Ameghino, left lower jaw with  $I_1$ ,  $P_3$  (not seen),  $M_{1-4}$  (A.M.N.H. No. 29663), Colpodon beds (upper Oligocene), Colhué-Huapí, Argentina. All  $\times 1.5$ .

acquired its greatest development in the Recent diprotodonts, but this condition is also similar to that of  $I_1$  of the caenolestids, which is much more developed than the posterior incisors. We must not forget, also, the fact that the polydolopids had three or four pairs of upper incisors, a condition which is also observed in both caenolestids and the diprotodonts. We have as yet not

enough elements to know the relative development of the upper incisors of the polydolopids, since they are completely absent in the skull found in Brazil, the incisors being represented only by their alveoli. They cannot therefore be compared with the upper incisors of the two other groups here considered.

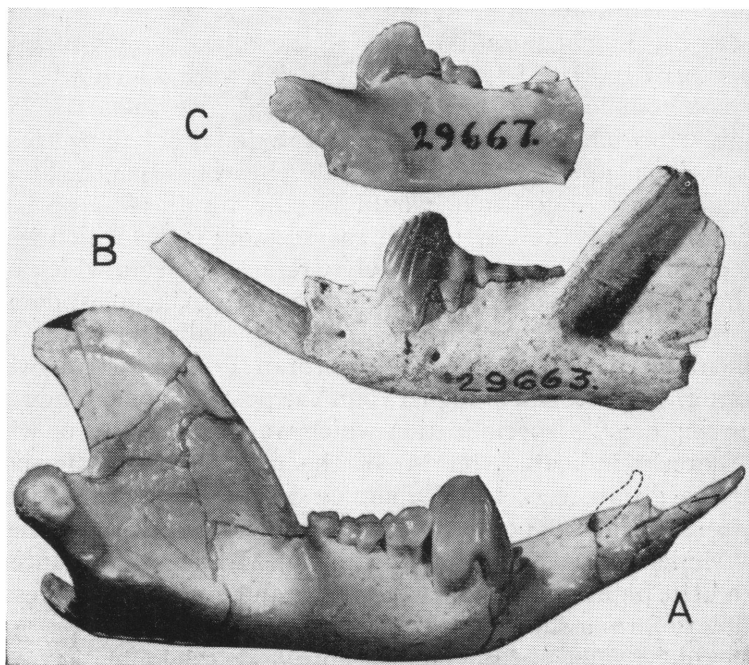


FIG. 6. Mandibles and lower dentitions of caenolestoids, for comparison (external side view). A. *Epidolops ameghinoi*, new genus, new species, type mandible, right ramus with  $I_{1-2}$  and  $P_2-M_3$  (D.G.M. No. 321-M). B. *Abderites crispus* Ameghino, left lower jaw with  $I_1$ ,  $P_3$ ,  $M_{1-4}$  (A.M.N.H. No. 29663), Colpodon beds (upper Oligocene), Colhué-Huapi, Argentina. C. *Abderites crispus* Ameghino, right lower jaw with  $M_{1-2}$  (A.M.N.H. No. 29667), same locality as B. All  $\times 1.5$ .

With regard to paragraph 4 it is now possible to say that the reduction in number of the ante-molar teeth in the polydolopids is produced in the same way as in the caenolestids in general, although with more gradation. But (except for the lower canine, which is absent in all the diprotodonts [Tate, 1948, p. 243], but present and well developed in the polydolopids) this can also be said of the diprotodonts. The  $P_3$  of the polydolopids (which

hitherto was considered  $M_1$ , because of the imperfection of the paleontological record) looks in general like the homologous tooth of the more specialized diprotodonts, although relatively much larger. Besides being the most developed tooth of the cheek teeth series, the  $P_3$  of the polydolopids is, as is that of the more specialized diprotodonts, modified to the sectorial type and is structurally much more like that of the diprotodonts than like the sectorial tooth ( $M_1$ ) of the caenolestids, with which otherwise it is not homologous. From this point of view then, the Polydolopidae are more similar to the diprotodonts (Phalangerioidea) than to the caenolestids. The laminate, shearing  $M_1$  of the Palaeothentinae and Abderitinae would be the result of a posterior specialization of the  $M_1$  of the caenolestoid forms which would have constituted the stock, possibly Cretaceous, from which both the Polydolopidae, on the one hand, and the Caenolestidae, on the other, might have arisen. This specialization was still incipient on the  $M_1$  of the Casamayoran Polydolopidae, where the anterior lobe is much higher than the posterior one, tending to a shearing crest, a specialization which was not present, or which was scarcely indicated, on  $M_1$  of the more primitive forms of the same group, e.g., the Itaboraian polydolopids. Otherwise, still from the above point of view, the Phalangeridae, especially, show similarity with the Polydolopidae,  $M_1$  having the anterior lobe a little higher than the posterior one and laterally compressed, tending to form a shearing crest.

The upper molars of the more primitive polydolopids, as *Epidolops*, new genus, were much more similar to those of the caenolestids than were those of the Casamayoran Polydolopidae.

In *Epidolops*, as is shown above, the upper molars are virtually tetracuspoid, even  $M^1$ , as are those of the caenolestids (Palaeothentinae, etc.), while the molars of the Casamayoran polydolopids (*Polydolops*, *Eudolops*, *Amphidolops*, at least) are much more complicated than those of caenolestids and also than those of the more primitive members of the same family, as the Itaboraian polydolopids, which show, also from this point of view, the ideal ancestral condition for the group to which they belong.

*Epidolops*, new genus, represents therefore the ideal intermediate structural stage between the Palaeothentinae or, better still, between the Caenolestidae, and the later Polydolopidae. The Polydolopidae and Caenolestidae (Palaeothentinae, Abderitinae, and Caenolestinae) would be collateral groups emerging

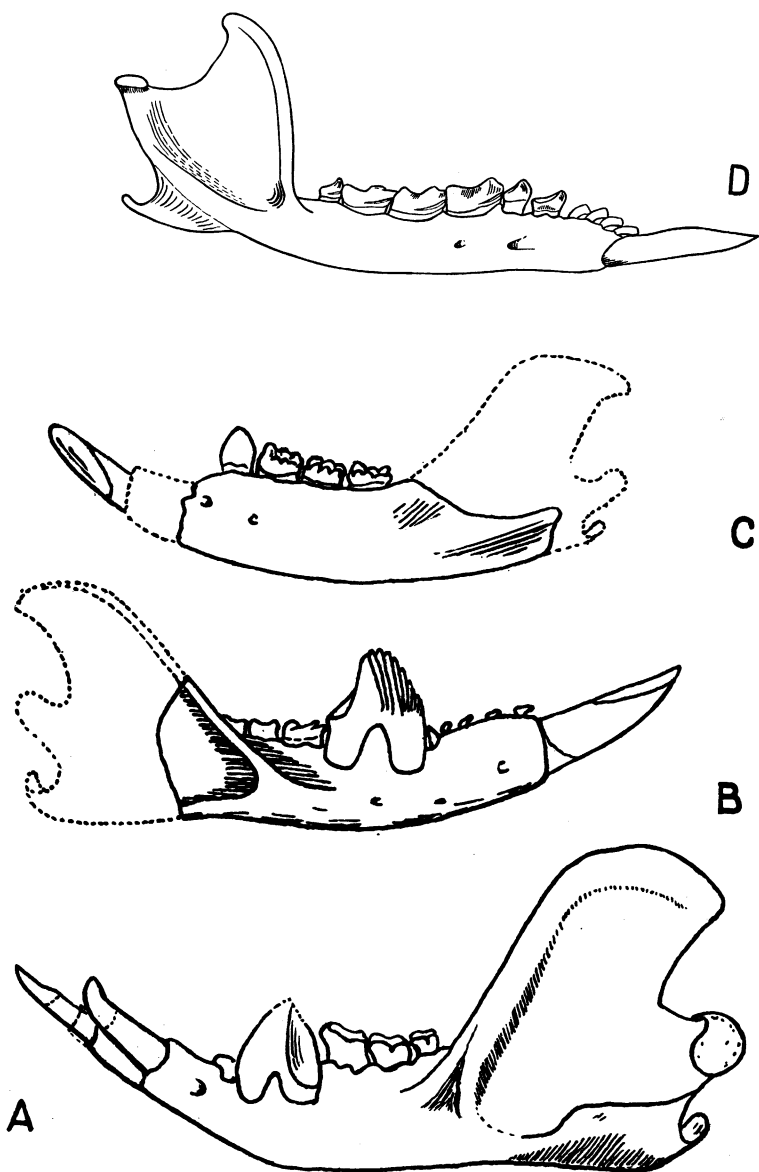


FIG. 7. Mandibles of caenolestoids, for comparison. A. *Epidolops ameghinoi*, new genus, new species, left side view. Approximately  $\times 2$ . B. *Abderites meridionalis* Ameghino, new restoration of right ramus of lower jaw (continuous lines redrawn after Ameghino), Santa Cruz formation (lower Miocene), Patagonia. Approximately  $\times 2$ . C. *Eudolops carolo-ameghinoi* (Ameghino), new restoration of left lower jaw (parts in continuous lines after Ameghino, from Simpson), Casamayor beds (lower Eocene), Patagonia.  $\times 1$ . D. *Caenolestes* sp., right ramus of lower jaw with complete dentition, Recent, Ecuador.  $\times 4$ .

from a common ancestral caenolestoid stock just before the beginning of Cenozoic time. The Polydolopidae having become specialized more rapidly, became extinct first, during the Eocene, whereas the Abderitinae and Palaeothentinae, more conservative in development, persisted until the Miocene. The Caenolestinae, which survived to the Recent, are still more conservative, having structural features more primitive than those of the Miocene Palaeothentinae and Abderitinae. They cannot be considered descendants of these Miocene groups, but form part of a collateral line. The Palaeothentinae and Abderitinae, on the other hand, may be considered to be descendants of the most primitive, pre-Miocene Caenolestinae.

As we have seen above, there are undeniable morphological similarities between the Polydolopidae and even between the Caenolestoidea, in general, and the Australian diprotodonts (Phalangeridae especially).

Are these resemblances the result of convergence, or do they indicate an actual close relationship between these South American and Australian marsupial groups?

In his discussion concerning the relationships of the Caenolestidae, Sinclair (1905, p. 81), after admitting that the two groups referred to above (Caenolestoidea, and Diprotodontia or Phalangerioidea) could have descended from a common ancestral stock, concluded (1906, p. 443) that the similarities between them may be considered as resulting from convergence and that "at present the arguments in favor of the alternatives expressed are about equally balanced."

Scott (1937, pp. 723-724), discussing the relations of the Australian and South American marsupials in general, states that "to maintain that the Australian genera, on the one hand, and the South American genera, on the other, were independently derived from didelphid ancestors, involves such a degree of convergence as has never been admitted for any other group and for which there is no warrant."

But in general it seems that most contemporary authors prefer the hypothesis of convergence to that of a close relationship between the South American and the Australian marsupials, which is adopted by a few authors. Simpson, for example, is frankly favorable to the hypothesis of convergence.

The literature on this subject is almost as voluminous as it is

controversial. As the matter is apart from the true objectives of this paper, I prefer not to discuss it further here.

It seems to me that the solution of this controversy depends upon a better knowledge of the paleontological records both of the Australian and the South American Tertiary, especially the lower Tertiary, and perhaps the uppermost Cretaceous of both these continents.

SUPERFAMILY BORHYAENOIDEA SIMPSON, 1930

FAMILY **BORHYAENIDAE** AMEGHINO, 1894

SUBFAMILY **BORHYAENINAE** CABRERA, 1927

**PATENE** SIMPSON, 1935

GENOTYPE: *Patene coluapiensis* Simpson, 1935.

DIAGNOSIS: Borhyaenids of medium to small size in the known species, with molars of primitive pattern. Protocone large on all molars. Paracone present and well separated from the metacone on  $M^{1-3}$ , slightly smaller than metacone, both these cusps more external on  $M^{1-2}$  and median on  $M^3$ . Increasingly large metastylar spur on  $M^{1-3}$ , that of  $M^3$  projecting strongly posteriorly as well as externally.  $M^{1-3}$  with distinct vestigial protoconules and metaconules.  $M^4$  with strong parastylar spur, paracone median, metacone represented by a basal cuspule, this tooth still retaining distinct molar-like character.

**Patene coluapiensis** Simpson, 1935

HOLOTYPE: A.M.N.H. No. 28448. Part of right maxilla with  $M^{1-4}$  present. Collector: C. S. Williams.

HORIZON AND LOCALITY: Casamayor formation, south of Lago Colhué-Huapí, Chubut, Argentina.

DIAGNOSIS: Distinct conical stylar cusps immediately external to, and separate from, the paracone on  $M^{1-2}$ .  $M^4$  as wide as  $M^3$ , parastylar spur slightly internal to that of the preceding molars.  $M^{1-4}$ , 24.5 mm.

**Patene simpsoni**, new species<sup>1</sup>

HOLOTYPE: M.N.R.J. No. 1331-V. Incomplete right maxilla with  $P^3$  and  $M^{1-4}$  present. Collector: Júlio da Silva Carvalho, 1949.

<sup>1</sup> In honor of Dr. George Gaylord Simpson.

PARATYPES: D.G.M. No. 324-M, fragment of right lower jaw with alveolus of  $P_2$  and roots of  $P_3$ , anterior root of  $M_1$ , talonid and anterior root of  $M_2$ , with  $M_3$ , and with roots of  $M_4$  present, collected by Júlio da Silva Carvalho, 1949. M.N.R.J. Nos. 1332-V, right  $M^4$ , and 1335-V, right  $M^1$  or  $M^2$ , the latter incomplete; both collected by Carlos de Paula Couto, 1949.

REFERRED SPECIMENS: M.N.R.J. Nos. 1336-V to 1343-V, and 1428-V, eight left lower molars, and one right lower molar, reduced to the trigonid; all collected by Carlos de Paula Couto, 1949. D.G.M. No. 331-M, part of left maxilla, with the alveoli of  $M^{1-3}$  and incomplete alveoli of  $P^3$  and  $M^4$ ; collected by Júlio da Silva Carvalho, 1949.

DIAGNOSIS: Approximately one-fourth smaller than *P. coluapiensis*. Large infraorbital foramen from above the anterior part of  $M^1$  to above the middle part of  $P^3$ .  $P^3$  with one simple and well-developed main cusp, the tip of which is higher than the crown of  $M^{1-2}$ . A vestigial cusp on the posterior end of the base of the main cusp. Short and low talonid, from which an external cingulum, progressively narrower forward, runs anteriorly to the vertical passing the posterior end of the tip of the main cusp.  $M^{1-4}$  very similar to those of *P. coluapiensis*. Distinct stylar cusps immediately external to, and separate from, the paracone on  $M^{1-3}$ , well developed on  $M^{1-2}$ , minute on  $M^3$ . A series of very small stylar cusps on the external border of parastylar spur of  $M^{3-4}$ .  $M^{1-4}$  with strong anterior basal cingulum from the base of paraconule to that of the antero-external angular stylar cusp. Less strong basal cingulum from the metaconule to the base of metacone on  $M^3$ .  $M^4$  wider than  $M^3$ , with parastylar spur projected forward and outward, and much more prominent externally than that of  $M^3$ , paracone much more developed than metacone.  $M^{3-4}$  presenting, when unworn, a well-developed crest running down from the tip of paracone to the anterior end of the parastylar spur. Lower molar two-rooted, with very high and well-developed trigonid and low, narrower, and shorter talonid. Protoconid, paraconid, and metaconid ( $M_3$ ) conical disposed in a triangle, almost as in the Didelphidae, the protoconid much higher and stronger than the well-developed paraconid and metaconid, the metaconid slightly smaller than the paraconid. Talonid ( $M_2$ ) basined, with distinct and almost equally well-developed hypoconid, entoconid, and hypoconulid, the last equidistant from the first two. Measure-



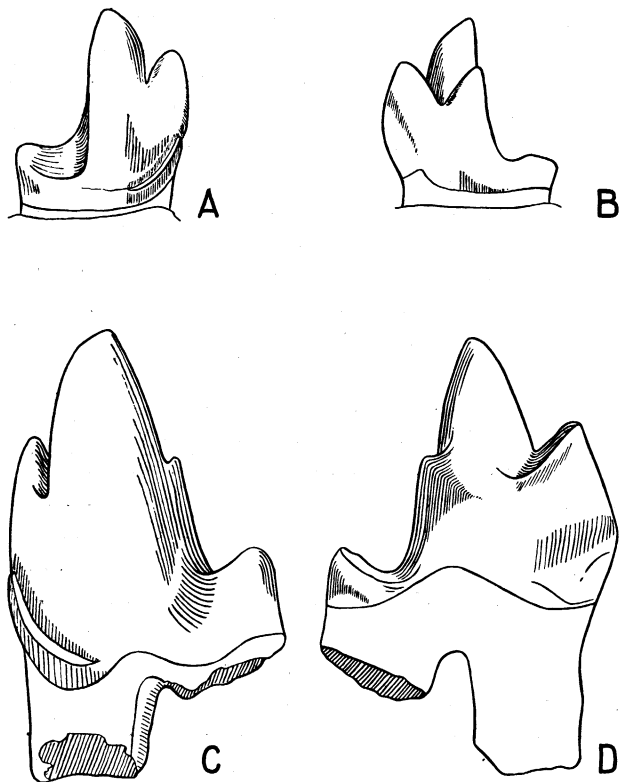


FIG. 8. Lower molars from borhyaenids. A, B. Right  $M_3$  of *Patene simpsoni*, new species, paratype (D.G.M. No. 324-M). A. External side. B. Internal side. C, D. Lower left molar of ?*Arminiheringia* sp. (M.N.R.J. No. 1344-V). C. External side. D. Internal side. All  $\times 2$ .

ments: holotype (M.N.R.J. No. 1331-V),  $P^3-M^4$ , 23.3 mm.;  $M^{1-4}$ , 18.2 mm.; paratype (D.G.M. No. 324-M),  $P_2-M_4$ , 26.7 mm. Height of the mandible under  $M_1$ , 11.1 mm.

#### ? ARMINIHERINGIA AMEGHINO, 1902

Among the specimens collected in São José de Itaboraí is a large lower left molar (M.N.R.J. No. 1344-V), which undoubtedly came from a borhyaenid.

The trigonid is well developed, with very high, sharp-pointed, and subtrihedral protoconid, much smaller paraconid, and minute, almost vestigial metaconid, the latter compressed against the

base of the postero-internal edge of the protoconid. The talonid is very low and small, almost a half narrower than the trigonid, with minute posteromesial cusp (hypoconulid?) and vestigial basin. A basal cingulum runs down, with strong declivity, from the middle part of the base of the paraconid to the antero-internal angle of the base of the protoconid. A styler, basal cusp must have been present, in vestigial form, immediately before the base of the paraconid, where there is a fracture mark.

This tooth is essentially similar, in all its features, to A.M.N.H. No. 28433, a right lower molar from the *Notostylops*-beds, Colhué-Huapí, Patagonia, which has more or less the same size, and is doubtfully classified as *Arminiheringia* Ameghino, 1902, a genus characteristic of these lower Eocene beds.

It seems possible that this tooth, judging by its size and appearance, came from a species of the genus *Arminiheringia*, probably different from the known species, but not yet sufficiently characterized to be surely distinguished from the described species.

Measurements of the lower molar tooth: length, 8.9 mm.; width of the trigonid, 4.7 mm.; width of the talonid, 3.2 mm.

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