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MAMMALS FROM THE EARLY CENOZOIC OF CHUBUT, ARGENTINA

George Gaylord Simpson

ABSTRACT. *Angelocabrerus daptus*, new genus and species (Mammalia, Marsupialia, Borhyaenidae), *Coelostyodon florentinoameghinoi*, new genus and species (Mammalia, Notoungulata, ?Isotemnidae) and *Coelostyodon caroloameghinoi*, new species, are described from the Casamayor formation, probably early Eocene. Knowledge of upper premolars of *Didolodus* (Mammalia, Condylarthra, Didolodontidae) is increased and the status of *Acoelodus* (Mammalia, Notoungulata, Acoelodidae) is discussed. The latter genus and the family based on it are essentially indeterminate, and previous usage of the names is unjustified.

INTRODUCTION

A visit to Mar del Plata, Provincia de Buenos Aires, Argentina, early in 1970 enabled me for the second time to examine parts of the important collections of fossil mammals in the Museo Municipal de Ciencias Naturales of that municipality. In collections from the Casamayoran Stage of Chubut, three specimens were found to be of particular interest and to make especially important contributions to knowledge. The Director of the Museo, Sr. Galileo J. Scaglia, very kindly permitted me to study those specimens and to publish descriptions and discussions of them, presented herewith. I am again and increasingly indebted to Sr. Scaglia and to the whole staff of the Museo for their courtesy and cooperation. The accompanying illustrations were prepared by RaVae Marsh.

In the following, MMP precedes catalogue numbers of the Museo Municipal de Ciencias Naturales de Mar del Plata and MACN those of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires.

While carrying out the research for this paper I was employed jointly by the Museum of Comparative Zoology and the University of Arizona.

Order Marsupialia Illiger
Family Borhyaenidae Ameghino
Angelocabrerus, new genus

Etymology. For the late Angel Cabrera, a great mammalogist, who, among many other things, wrote an important study of borhyaenids. This kind of nomenclature is Ameghinian and is consonant with the related *Arminiheringia*. I have ventured to give the compound an appropriately masculine ending.

Type-species. *Angelocabrerus daptus*, new species, *infra*.

Known distribution. Casamayoran, Argentine Patagonia.

Diagnosis. Specialized borhyaenines. Canines with closed, rapidly tapering roots; short, heavy, fully enameled crowns. P_3 one-cusped, heavy, with small distinct talonid. M_{1-4} essentially two-cusped, with paraconid anterior and only slightly lingual to the larger protoconid. No trace of metaconid. Talonids unbasined, reduced to very slight, simple ledges. Protoconids and paraconids truncated with wear on M_{1-3} , becoming sharp points on M_4 with protoconid a high slender needle.

Discussion. As far as known, the dentition is similar to that of the much later (Santacrucian) *Borhyaena* and by the same token is also similar to the contemporary Casamayoran *Arminiheringia*. The talonid reduction seems to have gone even further in *Angelocabrerus* than in the other genera. The lower canine is unlike that of *Arminiheringia*, with a shorter closed root and more fully enameled crown. The way in which M_4 wears, quite distinctive from either *Arminiheringia* or *Borhyaena*, would seem to imply different occlusion and hence different structure in the unknown upper teeth, M_{3-4} , with which M_4 occluded. This wear is much as in *Plesiofelis*, considered by Cabrera (1927: 274-278) Deseadan in age and synonymous with *Pharsophorus* but almost certainly Mustersan and probably distinct from *Pharsophorus*. However, in *Plesiofelis* the molar talonids are considerably less reduced than in *Angelocabrerus*.

In *Arminiheringia auceta*, the only adequately known species of its genus, there is a rapid increase in size of the molars posteriorly, M_4 being about twice as large as M_1 . The figures (somehow omitted in Simpson, 1948) are here given in Table 1. It is there shown that the increase is much less in *Angelocabrerus daptus*, with M_4 only about half again as large as M_1 . The increase

is even less in *Borhyaena*. As far as the evidence goes, *Angelocabrerus* could be ancestral to *Borhyaena*, and in that case the rate of evolution in known parts must have been extremely slow. Knowledge of the present genus is too incomplete, however, to warrant a firm conclusion.

As in *Arminiheringia* and *Borhyaena* but to even more marked degree, P_3 is a large and heavy tooth. It here approximates M_3 in dimensions. It has a single main cusp, with a long anterior and short, nearly vertical posterior slope. There is a minute cuspule at the anterior base. There is a distinct but small, shelflike talonid with a single cuspule. This is absent in *Borhyaena* and also in the only known specimen of *Arminiheringia* that might show it, but the latter is so worn that a small talonid could have been present originally. Except for the points already mentioned, the lower molars are like *Arminiheringia* and *Borhyaena* in structure.

Angelocabrerus daptus, new species.

Etymology. Greek *daptus*, eater, gnawer, from the inferred carnivorous, possibly ossifragous habits of the animals.

Holotype. MMP 967M, part of right mandibular ramus with M_{2-4} , left P_3 , M_1 , and M_2 probably of the same individual, two lower canines somewhat broken, and small caniniform tooth and tip of another doubtfully associated.

Hypodigm. Holotype only.

Horizon and locality. Casamayoran, south of Lago Colhué-Huapí, Chubut, Argentina. The specimen was a surface find high in the beds, and derivation from an overlying formation is possible but quite improbable.

Diagnosis. Only known species of the genus as diagnosed above.

Discussion. The loose left M_2 has somewhat darker enamel and is slightly less worn than the right M_2 in the mandibular fragment. Its color and wear are more consonant with those of the loose teeth identified as left P_3 and M_1 . However, there can be little serious doubt that those and the two loose lower canines do in fact belong to the same individual as the mandibular fragment. All were found together, they are congruent in size and structure, and they add up to a unique specimen of a group extremely rare in these beds. The two slender caniniform teeth are dubious and I do question whether they belong to the same animal.

The diagnosis and discussion of the genus and the illustrations make further description unnecessary.

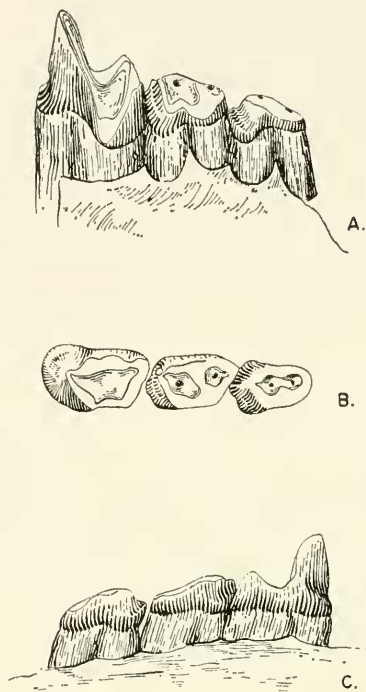


Figure 1. *Angelocabrerus daptis*, new genus and species. Holotype, MMP 967M. Right M_{2-4} . A, buccal view. B, occlusal view. C, lingual view. $\times 1$.

Order Condylarthra Cope
 Family Didolodontidae Scott
Didolodus sp. indet.

Specimen. MMP 696M, fragment of right maxilla with P²⁻⁴.

Horizon and locality. Casamayoran of Cañadón Vaca, tributary to the left (northwest) bank of the Río Chico, Chubut, Argentina.

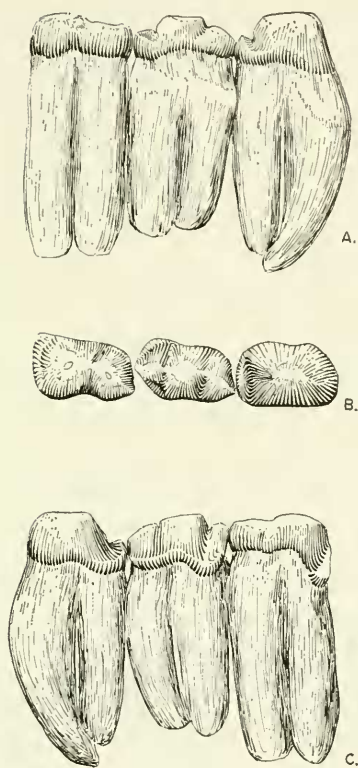


Figure 2. *Angelocabrerus daptus*, new genus and species. Holotype, MMP 967M. Left $P_3 - M_2$. A, lingual view. B, occlusal view. C, buccal view. $\times 1$.



Figure 3. *Angelocabrerus daptus*, new genus and species. Holotype, MMP 967M. Lower canine. $\times 1$.

Discussion. This specimen is interesting because it shows the coronal structure of P^{2-4} of *Didolodus* in relatively little worn condition and because the proportions of these teeth are distinctive.

Comparison is mainly with MACN 10690, holotype of *Didolodus multicuspis* Ameghino, the only other specimen of *Didolodus* known to me that includes P^{2-4} . It is figured in Simpson, 1948, text figures 25 and 26 and plate 10, figures 1 and 2. MACN 10738 includes P^2 , which has not been figured but was included in my description of *D. multicuspis* (Simpson, 1948: 101). AMNH 2847 is a P^3 referred to *D. minor* by me (Simpson, 1948: 103) but not separately described or figured.

As shown in Table 2, P^2 and P^4 are each shorter than in the holotype by 7 per cent, which does not in itself suggest specific distinction, and P^3 has almost the same length in the two specimens. However, all three teeth are more notably narrower in MMP 696M, by 16 per cent, 20 per cent, and 19 per cent for P^2 , P^3 , and P^4 respectively. A result is that all three teeth are longer relative to their widths in MMP 696M. This is especially notice-

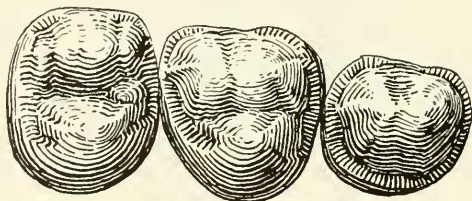


Figure 4. *Didolodus* sp. MMP 696M. Right P^{2-4} , occlusal view. $\times 3$.

able in P^3 , which is distinctly transverse in MACN 10690 but equidimensional in MMP 696M. P^3 of AMNH 28471, referred to *D. minor*, is even more transverse than in the holotype of *D. multicuspis*. Its width slightly exceeds that of P^3 in MMP 696M, although its length is decidedly (25 per cent) shorter. The individual represented by MMP 696M was probably closer to *D. multicuspis* in over-all size, but the differences in some dimensions and in proportions make reference doubtful either to that species or to *D. minor*. At the same time, they do not warrant definition of a new species, which in any case should preferably not be based on upper premolars, for which there is so little comparative material.

Specimens of known origin referable to *D. multicuspis* without much doubt are all from south of Lago Colhué-Huapí, and those similarly referable to *D. minor* are from Cañadón Vaca. MMP 696M is from Cañadón Vaca but probably does not belong to *D. minor*. Specimens and field data for *Didolodus* are still far from sufficient for identification of populations within the genus and for determination of their distribution.

P² of MMP 696M, unlike the less well-preserved specimens previously known, is seen to have two distinct external cusps, conate above the tips but still separated by grooves. These are at least descriptively paracone and metacone, and the metacone is only slightly lower and smaller than the paracone. The tooth is completely surrounded by a cingulum, but this is feeble on the middle of the labial face. The lingual slope from paracone plus metacone to the labial cingulum is slightly uneven, but is without really distinct cusps. P³ and P⁴ also have distinct paracone and metacone but, unusually, the metacone is lower and smaller relative to the paracone progressively from P² to P⁴. P³ and P⁴ have well-developed protocones, and the cingula do not cross their lingual faces. A distinct cingular cusp or style is present on each tooth anterior and slightly labial to the paracone and there is a similar but smaller and less distinct cuspule posterior to the metacone. Each tooth has a distinct protoconule but no metaconule. There is no hypocone. It is also unusual that P⁴ is distinctly shorter than P³, although wider.

The structure of P² in this specimen seems to be rather different from that in the holotype of *D. multicuspis* and more molariform. Except for dimensions and proportions, apparent differences in structure of P³⁻⁴ are possibly due only to the more worn condition of the holotype of *D. multicuspis*.

Although far from identical, there is considerable resemblance between P²⁻⁴ of MMP 696M and the homologous teeth of North American *Phenacodus*. A fairly close ancestral relationship is confirmed to that extent. However, considerable independent evolution is also suggested. For example, P²⁻³, especially, of MMP 696M, are more distinctly molariform than their homologues in *Phenacodus*.

Order Notoungulata Roth
 Family Isotemnidae Ameghino
Coelostylodon, new genus

Etymology. Greek *koilos*, hollow, *stylos*, pillar, *odon*, tooth. The name is meant to recall former reference to *Acoelodus* and resemblance to *Pleurostylodon*. It is also consonant with much Ameghinian nomenclature.

Type-species. *Coelostylodon florentinoameghinoi*, new species, *infra*.

Known distribution. Casamayoran, Argentine Patagonia.

Diagnosis. Primitive notoungulates with complete, nearly closed dentition. Upper canine small and fully incisiform. Cheek teeth brachydont, P²-M³ soon wearing so that crown presents a single fossa, without complex folds or anterior opening. M¹⁻³ with flattened, slightly bifid lingual faces. M¹⁻³ with slight parastyle and paracone folds and very feeble metacone swelling on ectoloph, no mesostyle. M³ subtriangular, with short but distinct metaloph, longer than M¹ or M² and almost as long as broad.

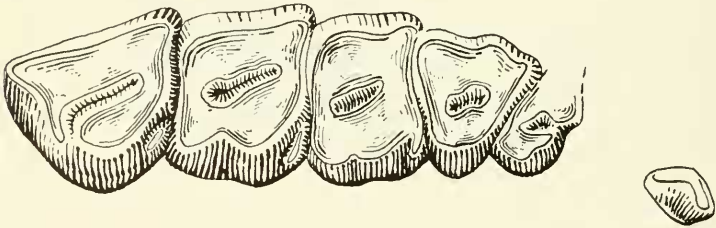


Figure 5. *Coelostylodon florentinoameghinoi*, new genus and species. Holotype, MMP 1723M. Right C and P³ - M³. $\times 1\frac{1}{2}$.

Discussion. This genus is essentially that called *Acoelodus* by Ameghino (1901: 467) and discussed by me (Simpson, 1967: 57) under that name, but that application of the name can no longer be sustained. The type-species of *Acoelodus* is *A. oppositus* Ameghino, 1897 (p. 454). The holotype of that species is MACN 10770, a fragment of a left mandibular ramus with much worn P₂₋₃ and part of P₄. That specimen is essentially indeterminate. In 1901 Ameghino referred to the species a poorly preserved skull, MACN 10753, and redefined the genus essentially on the basis of

that specimen. Desiring to validate as much as possible of Ameghino's nomenclature, I accepted the reference and redefinition, taking MACN 10753 as essentially a neotype in Ameghino's usage and designating it as such (Simpson, 1967: 58). However, that action is invalid under the present code of nomenclature (Stoll *et al.*, 1964, Article 75) because in fact the holotype, MACN 10770, has not been lost or destroyed.

If now there were a reasonable probability that the referred skull and the holotype belong to the same genus and species, the type designation would have no practical importance and one could continue to use the name *Acoelodus* for the genus and *A. oppositus* for the species represented by the referred skull. In fact, however, as I already mentioned in previous discussion (1967), there is no good evidence that the two specimens are of the same genus and species, and there is some contrary evidence. The contrary evidence is weightier than I previously indicated. If the comparative sizes of P₂₋₃ and P²⁻³ in *Acoelodus* were approximately as in *Pleurostylodon*, a reasonable assumption, then P²⁻³ of the skull MACN 10753 are some 22 to 44 per cent larger in various dimensions than would be expected from the holotype of *Acoelodus oppositus* and are also different in relative sizes and proportions. It is thus highly improbable that the two specimens are conspecific, and if they are not conspecific, there is no reason to consider them congeneric.

The genus represented by the holotype of *Acoelodus oppositus* is indeterminate, a notoungulate *incertae sedis* as far as my knowledge and judgment go. The genus represented by MACN 10753 is determinate and is distinct from any other for which there is comparable material known to me. This conclusion is reinforced by discovery of another specimen, MMP 723M, that can be referred to the same genus as MACN 10753 but is specifically distinct. In order to avoid possible further confusion with *Acoelodus*, the species represented by MMP 723M is made type-species for the new generic name.

In order to avoid still another confusion, it must be noted that none of Ameghino's figures labeled "*Acoelodus oppositus*" in several of his publications are conspecific or congeneric either with the holotype of that species or with MACN 10753 (for details and discussion see Simpson, 1967: 58-59).

Ameghino considered *Acoelodus* as closely related to *Oldfieldthomasia* and so placed the latter in his family Acoelodidae, but

that was based on specimens dubiously or incorrectly referred to *Acoelodus*, including at least one that in fact belongs in *Oldfieldthomasia*. Since the holotype of the type-species of *Acoelodus* is not identifiable as to family, the name Acoelodidae has no established significance. For that reason, I named a family Oldfieldthomasiidae for *Oldfieldthomasia* and its probable relatives (Simpson, 1945: 126). In revision of the Casamayoran fauna, I put MACN 10753, under the incorrect reference name *Acoelodus oppositus*, in the Oldfieldthomasiidae. The genus *Coelostylodon*, to which that specimen is now referred as holotype of *C. caroloameghinoi*, is of uncertain family position. It differs from all adequately characterized previously named genera of both the Oldfieldthomasiidae and the Isotemnidae, but has resemblances to both families. Present reference to the Isotemnidae is very tentative. The upper molar structure is most nearly similar to that of *Pleurostylodon*, an isotemnid, among adequately known genera, but *Coelostylodon* differs from *Pleurostylodon* and other isotemnids in its small, incisiform canine and various other details. The canine is more like that of *Oldfieldthomasia*, but the molars are quite different.

Coelostylodon florentinoameghinoi, new species

Etymology. For Florentino Ameghino, famed describer of most of the Casamayoran fauna. Combination of given and family names is a nomenclatural device that he often used.

Holotype. MMP 723M, nearly complete but badly crushed skull.

Hypodigm. The holotype only.

Horizon and locality. Lowest Casamayoran beds in the baranca south of Lago Colhué-Huapí, Chubut.

Diagnosis. Significantly larger than *C. caroloameghinoi* (see Table 3). Posterolabial angle of M^3 less projecting.

Discussion. The teeth are deeply worn in both of the holotypes now referred to this genus. As preserved, there is no marked, discernible difference in structure of the cheek teeth. MMP 723M clearly has the small canine considered characteristic of the genus. P^{1-2} are almost completely fragmented, but seem to have been quite small, perhaps more so, relatively, than in MACN 10753. The posterolabial corner of M^3 does not project so distinctly as in MACN 10753.

The skull is too badly crushed to make out much significant detail. It seems to have been a primitive, unspecialized notoungulate skull generally similar to that of *Pleurostylodon*.

Coelostylodon caroloameghinoi, new species.

Acoelodus oppositus, in error, Ameghino, 1901: 365; Simpson, 1967: 58 and plate 11, fig. 1.

Etymology. For Carlos Ameghino, who discovered the Casamayoran fauna and found the holotype of this species.

Holotype. MACN 10753, poorly preserved anterior part of skull.

Hypodigm. The holotype only.

Horizon and locality. Casamayoran, barranca south of Lago Colhué-Huapi.

Diagnosis. Significantly smaller than *C. florentinoameghinoi* (see Table 3). Posterolabial angle of M^3 sharply produced posteriorly (or distally).

Discussion. In 1901 and thereafter Ameghino based his concept of *Acoelodus oppositus* mainly on this specimen, but he did not figure it, and none of the specimens figured by him as *Acoelodus oppositus* belong to the present genus or species. The holotype is adequately figured in my previous memoir, as cited above.

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TABLE 1

Measurements in millimeters of teeth of *Angelocabrerus* and allied borhyaenids.

	<i>Angelocabrerus</i>		<i>Arminiheringia</i>		<i>Borhyaena</i>
	<i>daptes</i>	<i>auceta</i>	<i>contigua</i>	<i>tuberculata</i>	
	Holotype, MMP 967M	Holotype	Holotype	Princeton 15701†	
	Right	Left	MACN 10970*	MACN 10319	
P ₃	Length Width	12.4 7.4	11½ 7½	10.7	14.3 6.5
M ₁	Length Width	9.8 6.3	9½ 7	7.8	12 6
M ₂	Length Width	10.5 7.2	12 7½	—	12 7
M ₃	Length Width	12.8 7.9	15 10	—	13 7½
M ₄	Length Width	14.4 10.4	21 12½	—	16 9

*Measurements taken by me to the nearest half millimeter, the condition of the specimen suggesting that the apparent accuracy of measurements to a tenth of a millimeter would be spurious.

†Measurements from Sinclair (1906). It appears that Sinclair measured P₃ to tenths but M₁₋₄ to half millimeters.

TABLE 2

Measurements in millimeters of upper premolars of *Didolodus*.

		<i>D. multicuspis</i> MACN 10690	<i>D. minor</i> AMNH 28471	<i>D. sp.</i> MMP 696M
P ²	Length	7.6	—	7.1
	Width	7.4	—	6.2
	L/W	1.03	—	1.15
P ³	Length	7.5	5.7	7.6
	Width	9.5	7.8	7.6
	L/W	.79	.58	1.00
P ⁴	Length	7.0	—	6.5
	Width	10.0	—	8.1
	L/W	.70	—	.80

TABLE 3

Comparative measurements in millimeters of dentitions of holotypes of *Coelostylodon florentinoameghinoi* and *C. caroloameghinoi*.

		<i>C. florentinoameghinoi</i> MMP 723M	<i>C. caroloameghinoi</i> MACN 10753
P ⁴	Length	9.9	7.5
	Width	12.5	9.9
M ¹	Length	Ca.10	8.0
	Width	15.4	11.5
M ²	Length	12.6	8.5
	Width	17.0	11.8
M ³	Length	15.1	10.0
	Width	15.4	10.7