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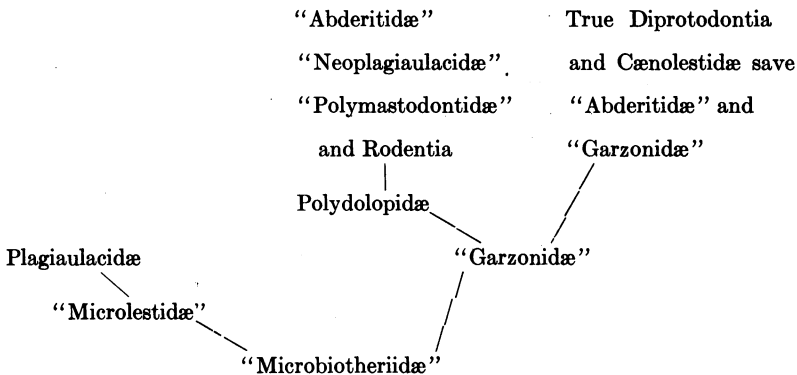
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AFFINITIES OF THE POLYDOLOPIDÆ

BY GEORGE GAYLORD SIMPSON

The family Polydolopidæ includes a number of South American genera, all described by Florentino Ameghino, which are commonly referred to the order Multituberculata. In attempting to unravel the history of this great order it is necessary to reach some definite opinion as to the relationships of these genera, and their importance is further enhanced by the extraordinary phylogenetic position assigned to them by Ameghino himself. His views are summed up in the following diagram:¹



According to this view the group Multituberculata of other authors is diphyletic, the true plagiaulacids being derived from the ?Eocene to Miocene microbiotheres (didelphids, somewhat aberrant) by way of the Triassic "microlestids" (microcleptids); and the Cretaceous and Paleocene multituberculates from the microbiotheres by way of the Miocene (possibly also Eocene and Oligocene) "garzoniids" (epanorthines) and Eocene polydolopids. Ameghino considered the polydolopids as related to three groups: Multituberculata, Cænolestoidea (and through them, the Australian Diprotodontia), and Rodentia.

¹Simplified from Ameghino 1903, p. 188 (see references at end of paper).

This highly original phylogeny, which transcends so many of the accepted lines of zoological classification and closely links three groups so unlike that modern classifications refer them to three separate subclasses, has had very little influence on scientific thought. Yet most later writers, while rejecting the collocation of groups which was the chief point of Ameghino's argument, have accepted his classification to the extent of retaining the Polydolopidæ where he put them, in the Order Multituberculata (Allotheria). They have copied his classification but passed over the abundant, and fundamentally sound, arguments of Ameghino that the polydolopids were really intimately related to the cæolestids. His phylogeny makes them descendants of one group of cæolestids—Epanorthinæ—and ancestors of another—Abderitinæ.

The only detailed objection to placing the Polydolopidæ in the Multituberculata is that of Gregory (1910, p. 211-4) who considers the resemblances to multituberculates (and rodents) as convergent and suggests tentatively that the polydolopids were highly modified cæolestoids. The whole problem is of such outstanding importance that as thorough a reconsideration, as the known facts will permit, is necessary.

The Patagonian forms referred to the Allotheria by Ameghino include fourteen genera, ranging in age from Eocene to Pliocene, according to the present accepted views, or Cretaceous to Oligocene according to Ameghino. Eight of these constituted the Polydolopidæ proper, all from the *Notostylops* Beds or Casa Mayor Formation. This deposit was placed by Ameghino in the Upper Cretaceous, but it is now unanimously referred to the Tertiary although opinions as to exact age vary from Paleocene to Upper Eocene. One of the most important arguments for placing it in the Paleocene has been the supposed presence of multituberculates, but this evidence is quite invalid. Exact correlation is impossible at present but the Casa Mayor is almost surely of true Eocene age and probably rather late Eocene.

The genera not referred to the Polydolopidæ were distributed in the "Promysopidæ" and in two families based on real multituberculates (not from South America). For convenient reference all of these genera are briefly listed as they were classified by Ameghino:

FAMILY POLYDOLOPIDÆ:

Polydolops. (Type *P. thomasi*; four other species). Genus based on an upper jaw, but several lowers later referred. Best known of all genera here considered. CASA MAYOR. Figs. 1D, 2C, 6B.

Eudolops. (Unique species, *E. tetragonus*). Based on a single upper molar. CASA MAYOR. Fig. 7A.

Pliodolops. (Unique species, *P. primulus*). Two associated upper molars. CASA MAYOR. Fig. 7B.

Amphidolops. (Type *A. serrula*; one other species). Two isolated lower molars referred to distinct species. CASA MAYOR. Fig. 1F.

Orthodolops. (Unique species, *O. sciurinus*). Based on a right ramus with P_3 - M_4 . CASA MAYOR. Fig. 1E.

Pseudolops. (Unique species, *P. princeps*). Based on various upper and lower teeth of uncertain association. CASA MAYOR. Figs. 1G, 7C.

Archæodolops. (Unique species, *A. clarulus*). Left ramus with P_2 - M_4 . CASA MAYOR. Fig. 3A.

Anadolops. (Unique species, *A. thylacoleoides*). Left ramus with M_2 - M_4 , so worn as to be uncharacteristic. M_4 erroneously stated to be absent.² CASA MAYOR. Fig. 3B.

FAMILY "NEOPLAGIAULACIDÆ" (including in addition to the following, all the smaller Cretaceous and Paleocene true multituberculates of Europe and North America):

Anissodolops. (Unique species, *A. serrifer*). M_2 - M_3 mentioned in description, only isolated M_3 figured. Generic distinction from *Polydolops* or *Pseudolops* not clear. CASA MAYOR. Fig. 5B.

Eomannodon (Unique species, *E. multituberculatus*). Single lower molar figured. PATAGONIAN (MIOCENE). Fig. 5C.

FAMILY "PROMYSOPIDÆ":

Promysops. (Type, *P. acuminatus*; one other species). Based on a fragment of lower jaw without any teeth. A lower molar later referred, but basis for reference uncertain. Second species based on an incisor from the *Astraponotus* Beds (Oligocene). CASA MAYOR. Fig. 5A.

Propolymastodon. (Type *P. carolo-ameghinoi*; one other species). Type a left ramus with all cheek teeth, and an isolated incisor. A second specimen with M_1 - M_3 referred to a distinct species. CASA MAYOR. Figs. 1H, 4.

FAMILY "POLYMASTODONTIDÆ" (including *Tæniolabis* of the North American Puerco in addition to the following):

Mannodon. (Unique species, *M. trisulcatus*). A single molar figured. SANTA CRUZ (MIOCENE). Fig. 5D.

Paradoxomys. (Unique species *P. patagonicus*). Based on an incisor. ENTRERIAN (PLIOCENE).

Ameghino's Polydolopidæ together with *Anissodolops* and *Propolymastodon*, which appear properly to belong to this family, will first be considered. As a group the various -*dolops* genera and *Propolymastodon* are characterized by the presence of an enlarged, procumbent incisor; reduction of the premolars; presence of a much enlarged, laterally compressed, trenchant lower cheek tooth (M_1); elevation and compression of the anterior part of the succeeding tooth (M_2), broad, low, basined

²Throughout this paper the tooth designations of Ameghino, who called all the cheek teeth molars and numbered them consecutively from one to seven, are translated into the more generally understood notation which assigns the ancestral formula $P_3^3 M_1^4$ to the Marsupialia.

M_{3-4} with multicuspidate rims; two trenchant upper cheek teeth (P^3 and M^1); and multicuspidate M^{2-4} .

One of the chief reasons for the rather general acceptance of the reference of the Polydolopidae to the Multituberculata is undoubtedly the very *Tæniolabis*-like aspect which Ameghino has given to the mandible of *Propolymastodon* in his widely copied restoration. One of the most striking characters of the true multituberculates is the absence

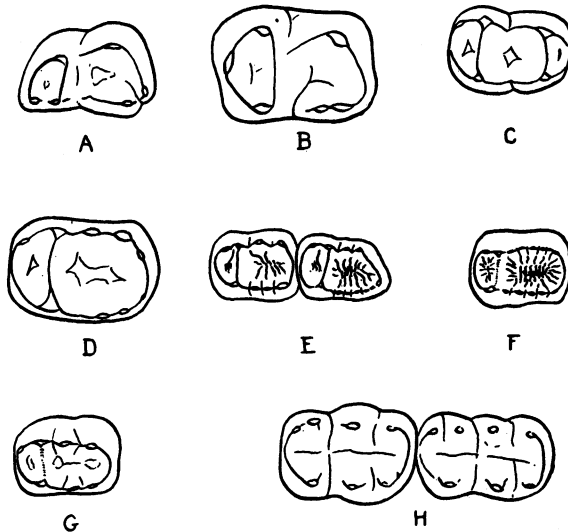


Fig. 1. Right lower molars of caenolestoids. A, *Halmarhiphus*, M_2 , $\times 5$. B, *Acedestis*, M_2 , $\times 5$. C, *Abderites*, M_2 , $\times 5$. D, *Polydolops*, M_2 , $\times 5$. E, *Orthodolops*, M_{3-4} , $\times 3$. F, *Amphidolops*, M_3 , $\times 3$. G, *Pseudolops*, M_3 , $\times 3$. H, *Propolymastodon*, M_{3-4} , $\times 3$. A-D are original, based on specimens in the Bavarian State Collection, Munich, and the American Museum of Natural History, New York. E-H are redrawn after Ameghino.

of an angular process, a continuous wide pterygoid crest taking its place. A similar condition is seen in the restoration of *Propolymastodon*, but an examination of all the published figures and descriptions shows that the known material may, indeed, permit such a restoration but certainly does not authorize nor necessitate it. The crucial parts are absent, and a few strokes of the pen, based on even better grounds than those of Ameghino, suffice totally to change the aspect of this jaw from multituberculate-like to caenolestoid-like (Fig. 4). Furthermore, *Polydolops*, an indispu-

tably close relative of *Propolymastodon*, clearly had an inflected angle thoroughly cænolestoid in character.

The horizontal ramus in the Polydolopidæ is fairly long and slender with alveolar and lower borders roughly parallel and quite unlike the Multituberculata in aspect. Furthermore, and more important, 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 . This is the usual primitive marsupial arrangement and contrasts fundamentally with the single mental foramen just back of the incisor in the Multituberculata.

It is, however, the lower teeth that must bear the chief burden of argument, as they are the best known and most characteristic. The enlarged incisors have no independent value as evidence of affinities, similar ones having been acquired at least six times quite independently within the Class Mammalia. They agree thoroughly however with the cænolestoid resemblances of the other known parts. According to Ameghino there is evidence that *Propolymastodon* had two pairs of lower incisors, which is of interest in view of the fact that even in the Jurassic no multituberculate has any vestige of more than one pair whereas the cænolestids may have from one to four. The reduction of the ante-molar teeth is carried farther than in other cænolestoids, but in the same direction. *Propolymastodon* appears to have lost the canine and all the premolars. *Polydolops* has one small premolar, while *Archæodolops* has at least two, and possibly more, which closely resemble those of the Abderitinæ. This occurrence of two or more small apparently functionless premolars is another marked difference from any known multituberculate and out of keeping with the whole evolutionary trend of the Multituberculata.

The shearing tooth itself is unlike that of the multituberculates in contour and structure. It may have a coarsely notched edge (*Polydolops*) or a finely serrate one (*Propolymastodon*) or may be quite smooth (*Archæodolops*). It does not have grooved or ridged lateral surfaces as in the Abderitinæ, Multituberculata (save Tæniolabidæ) and many macropids. This tooth is apparently homologous with the normal molariform M_1 of the Cænolestinæ (cf. *Cænolestes*, *Halmarhiphus*), as was first pointed out by Ameghino, and hence is not homologous with the shearing tooth in recent macropids, which is P_3 . The first step in modification is seen in the Epanorthinæ (Fig. 2A) in which the heel is normal and all the trigonid cusps are retained, but the trigonid is greatly elongated and compressed, forming a shearing edge. In the Abderitinæ, universally admitted to the cænolestoids, the anterior part of the tooth is more elevated, has lost its heritage of three cusps, and has become serrate; while the

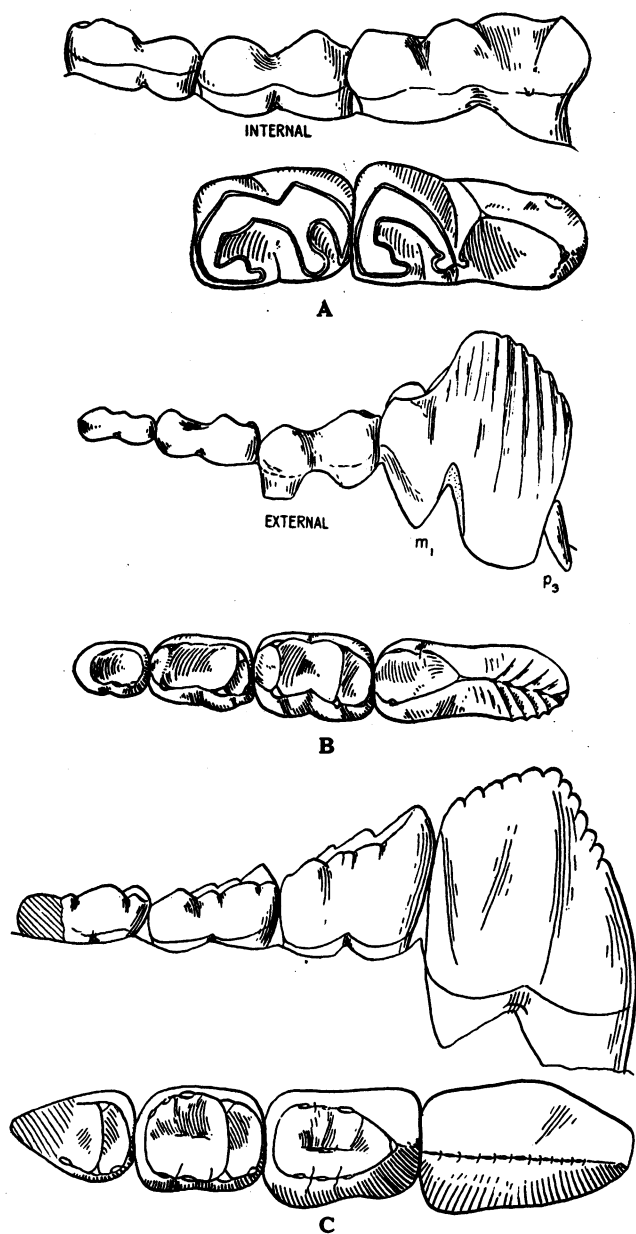


Fig. 2. A, *Acdestis*, left lower cheek teeth, crown and internal views. B, *Abderites*, right lower cheek teeth, crown and external views. C, *Polydolops*, right lower cheek teeth, crown and external views. All $\times 5$. A and B original, based on specimens in the Bavarian State Collection, Munich. C, redrawn after Ameghino with reference to original specimens in the Bavarian State Collection.

heel is retained and is still basined, but altered in character by the advancing specialization of the whole tooth (Fig. 2B). The polydolopids show the next structural stage in such a progressive shearing modification. In them M_1 has lost the basined heel and M_2 has an elevated trigonid which is beginning to be involved in the enlarging shearing apparatus (Fig. 2C).

This is not a natural phylogenetic sequence for, with the exception of the very inadequately known *Progarzonia*, all of the known undoubted Cænolestidæ are younger than the Polydolopidæ. Nevertheless it appears to be a legitimate example of the survival of slightly modified structural stages even after the extinction of the most specialized phylum of the



Fig. 3. A, *Archæodolops*, external view of left lower jaw, $\times 1.5$. B, *Anadolops*, external view of left M_{2-4} . $\times 1$. Both redrawn after Ameghino.

superfamily. Other examples may be found in almost any other group of mammals; it is, indeed, almost the general rule in the evolution of vertebrates that *more specialized phyla tend to become extinct before the less specialized ones of the same group*. Similarly, the living cænolestids are more primitive than the majority of the known Miocene forms and represent a structural stage ancestral to the latter. Forms more primitive than the living ones do occur in the Miocene (*Halmarhiphus* etc.) and the absence of analogous annectant types in the Casa Mayor may be felt seriously to weaken the argument. The difficulty is more apparent than real, however, for no forms which could be ancestral to the Santa Cruz ones appear in the Casa Mayor (again with the exception of the very little known *Progarzonia*) and this absence of mammals which obviously must have been present in South America at the time is quite as difficult to explain as the absence of the actual connecting types between the Polydolopidæ and the Cænolestidæ. The Casa Mayor 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. In fact, the true annectant forms must be pre-Casa Mayor and the only definable pre-Casa Mayor mammal yet known from South America is *Proteodidelphys*, known from a single specimen. Under such conditions

negative evidence should be given no weight. It is another case where the often lamented imperfection of the geological record forces one to have recourse to the methods of comparative anatomy, in this case especially to the comparative anatomy of the rich Miocene Santa Cruz fauna.

The first molar having been converted into a shearing tooth, three more or less molariform teeth remain. As throughout their whole known anatomy, the *Polydolopidæ* here differ again fundamentally from any multituberculates, 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.

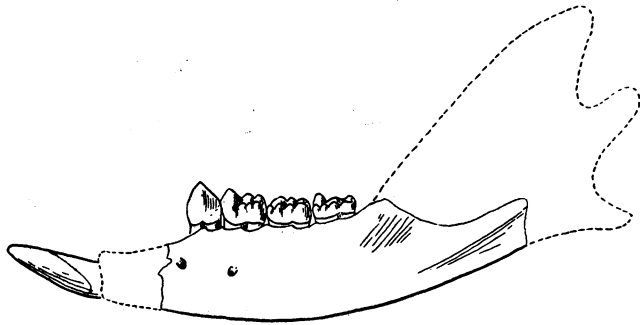


Fig. 4. *Propolymastodon carolo-ameghinoi*, new restoration of left lower jaw, $\times 1$. Parts in continuous lines redrawn after Ameghino.

M_3 is most suitable for comparison, M_2 being obviously modified by its participation in the shearing edge and M_4 frequently being somewhat degenerate. In M_3 of *Polydolops*, *Archæodolops*, and some of the less known genera the student of dental evolution would at once see traces of a tuberculo-sectorial ancestry were it not for the apparently anomalous condition of the trigonid. This has a single, higher *internal* cusp and two lower *external* cusps—the opposite of the tuberculo-sectorial type. The same structural series which appears to elucidate the mystery of the origin of the shearing tooth also explains this peculiar molar type, however (Fig. 1).

In *Halmarhiphus*, probably the most primitive of all known cænolestoids, the molars are typically tuberculo-sectorial and are, furthermore, almost exactly of the didelphid pattern. There is a normal tricuspid trigonid and a basined heel with three cusps, the hypoconulid being posterointernal and close to the entoconid, a character highly character-

istic of the Didelphiidæ and often seen in the less specialized marsupials of other families as a heritage character. With relatively slight variations the *Halmarhiphus* pattern is typical of the Cænolestinae, which have no true shearing teeth (Fig. 1A). In the Epanorthinae, with their beginning shearing adaptation, M_{2-4} are also beginning to specialize, the crowns being lower, broader, more adapted for crushing and grinding. The paraconid is no longer internal but *anterior* (Fig. 1B). In the Abderitinae, which, as has been shown, represent the next structural stage in modification for shearing, the molars are still more specialized in the same direction. The heel is very long and broadly basined, the trigonid relatively low, with the paraconid *external* (Fig. 1C). From this type to that of the

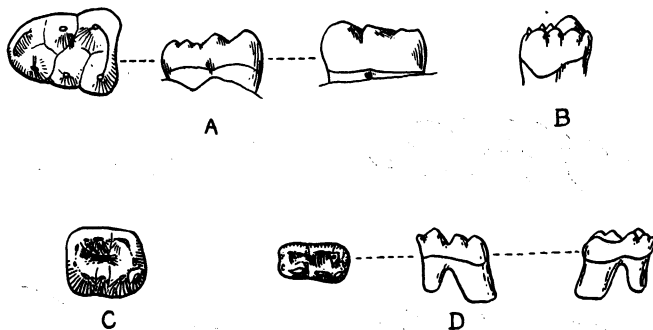


Fig. 5. A, *Promysops* (doubtfully referred), crown and side views of lower molar, $\times 3$. B, *Anissodolops*, external view of right M_3 , $\times 3$. C, *Eomannodon*, crown view of molar, $\times 7.5$. D, *Mannodon*, crown and side views of lower molar, $\times 3$. All redrawn after Ameghino.

less specialized polydolopids is a short and obvious step. Like the shearing teeth, the grinding teeth of the Polydolopidæ are, except for relatively unimportant details, simply a further development of the abderitine type. (Fig. 1D, 1G). The trigonid is absolutely identical in character. The heel is still more broadly basined and has additional cusps (in the less specialized forms only one more)—exactly the sort of change which has repeatedly occurred in other mammalian groups in correlation with similar specialization of food habits. Continuing the same sort of change, the transition to the other *-dolops* genera is slight. *Orthodolops* and *Amphidolops* (Fig. 1E, F) retain the abderitine trigonid, but the talonid rim becomes broken up into numerous small cuspules and the enamel of the basins is rugose. The *Propolymastodon* M_{2-4} are of almost the same

pattern as *Polydolops*, *Pseudolops*, and *Archæodolops*, with two external and one internal trigonid cusps and four chief talonid cusps, but judging from Ameghino's figures the distinction between trigonid and talonid tends to disappear. *Anissodolops* may be more on the order of *Orthodolops*, but the preservation is not sufficiently good for sound decision.

The polydolopids thus 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. The resemblance 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. These basined molars with distinct trigonid and talonid and cuspidate rims are as unlike the true multituberculate molars as is well possible.

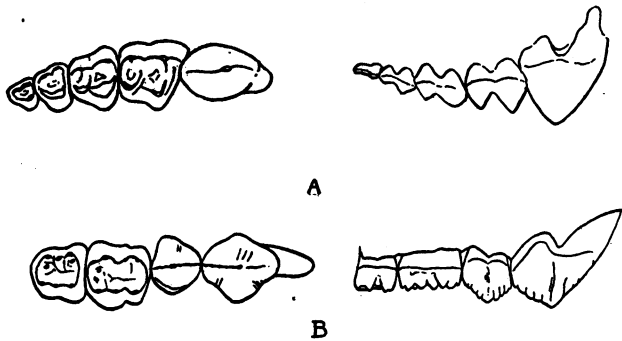


Fig. 6. A, *Epanorthus*, crown and external views of right upper cheek teeth, $\times 2$. B, *Polydolops*, crown and external views of right upper cheek teeth, $\times 2$. A, original, after specimens in the American Museum of Natural History. B, redrawn after Ameghino.

The upper molars are less well known, both in the Polydolopidae and in the Cænolestidae, and their interpretation is much more difficult. If, however, their relationship to the cænolestidae is less easily demonstrable, their differences from the Multituberculata are even more obvious.

There were two shearing teeth, both very like the main lower shearing tooth, with simple, ungrooved, compressed crowns, with or without a cuspidate edge, and with no heels or accessory cusp rows. Ameghino considered these teeth as P^3 and M^1 ("M³⁻⁴"), which must be correct although the whole series is not known in association. Unlike the

analogous lower tooth (M_2), M^1 retains no trace of its probable ancestral condition. Nothing save reasonable inference bridges the gap between the typical molariform epanorthine M^1 and the highly modified homologous tooth of the polydolopids. 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 very unlike the two multituberculate upper molars and could be derived from the cænolestid ones by broadening and cusp proliferation, thoroughly in keeping with the apparent evolutionary trend of the group.

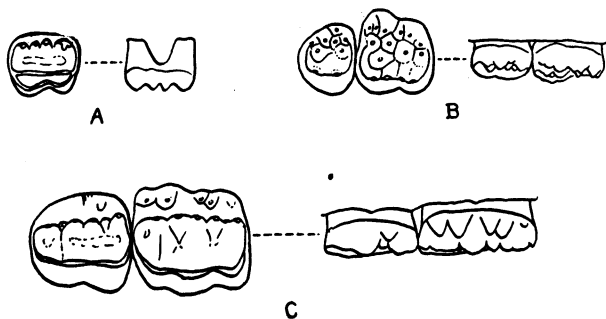


Fig. 7. A, *Eudolops*, upper molar, crown and external views, $\times 1.5$. B, *Pliodolops*, Crown and external views of right M_{3-4} , $\times 2$. C, *Pseudolops*, crown and external views of right M_{2-3} , $\times 3$. All redrawn after Ameghino.

The simplest type is seen in *Eudolops*, a single tooth of rather doubtful position in the series. It has two large internal cusps (as do the more advanced cænolestid upper molars) and an external crest, again as in the cænolestids, but with four cusps rather than the normal cænolestid two. *Polydolops* is more complicated, with three inner cusps and on M^2 five, on M^3 three outer cusps, while small secondary cuspules appear in the broad valley between inner and outer crests. In *Pseudolops* the inner crest again has three apices, the outer crests of M^2 and M^3 each having five, while accessory cuspules appear outside the outer crest along the base of the crown, four on M^2 and one on M^3 . The two teeth named *Pliodolops*, probably M^{3-4} , show the greatest specialization. The internal rim is much as before but with four and two apices, respectively, but the outer sides of the two teeth are occupied by numerous conical cuspules, about eleven on M^3 and seven on M^4 , very irregularly arranged. These teeth are "multituberculate" in the literal, etymological sense, but this

is far from an indication of relationship with the Order Multituberculata. "El gran parecido de las muelas superiores de este género con las de *Meniscoessus*" (Ameghino, 1903, p. 145) is non-existent. The two upper molars of *Meniscoessus* have strongly crescentic tubercles arranged in three absolutely parallel, straight longitudinal rows divided by deep V-shaped valleys. One cannot estimate relationships simply by counting cusps.

Turning to the six supposedly multituberculate South American genera referred to families other than the Polydolopidae, the inadequately known *Anissodolops* is clearly related to *Polydolops*. The even less well known, very minute *Eomannodon* (Fig. 5C) of the Miocene does not resemble the polydolopids at all closely, nor is it like any known multituberculate. Its relationships are altogether uncertain. *Promysops* (Fig. 5A) is apparently related to *Propolymastodon* and the latter has already been discussed. The Miocene *Mannodon* (Fig. 5D) has a modified tuberculo-sectorial lower molar and is of doubtful systematic position, although neither multituberculate nor polydolopid. It may possibly be an abderitine. *Paradoxomys* from the Pliocene is based on a single worn and broken incisor the reference of which to the same family as *Tæniolabis* ("*Polymastodon*") is, in view of its age and imperfections, no better than fantastic.

The only possible conclusion is that none of these genera nor any of the Polydolopidae are multituberculates and that members of the latter group are as yet quite unknown in South America. This does not necessarily mean that none ever lived there. They may have done so and, in view of current conceptions of later Mesozoic paleogeography, probably did. One would expect to find them only in deposits of Mesozoic or Paleocene age. It is now generally held that the Casa Mayor is post-Paleocene, and if so the only South American pre-Eocene mammal is *Proteodidelphys*.³ Further search of the *Proteodidelphys* Beds of the "areniscas abigarrados" may well reveal the presence of true multituberculates.

Granting that the Polydolopidae should be included in the Superfamily Cænolestoidea, it may yet appear that the view that the cænolestids were derived from the multituberculates by way of the polydolopids demands consideration. This is so nearly impossible that more than a brief discussion would not be profitable. It strongly opposes the known facts

³Aside from the wholly doubtful "*Archaeoplus*" and a supposed scute and caniniform tooth referred to the Edentata but possibly not even mammalian.

of morphology, evolutionary history, and geological distribution. It supposes typical grasping premolars, common to all truly primitive marsupials and placentals, to be derived from highly specialized shearing teeth. It supposes the appearance of three pairs of incisors, of the canines, and of two pairs of molars quite *de novo*. It supposes tritubercular upper and tuberculo-sectorial lower molars to be derived from the peculiar multituberculate type, suited only for a highly specialized type of jaw motion and musculature and adapted to a restricted diet. It overlooks the fact that skull and skeleton of multituberculates, now almost completely known, show them to be profoundly different from the contemporary early marsupials. It also overlooks the fact that 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. It forgets that the Jurassic, Cretaceous, Paleocene and Eocene multituberculates form a fairly compact series of genera of known evolutionary tendencies, in no way approaching the cæolestoids or any other known marsupials or placentals.

In concluding, the writer wishes to thank Dr. E. Stromer for his kindness in permitting and facilitating observations on the collection in his care at Munich which have been of great assistance in preparing the present paper.

CONCLUSIONS

1. None of the South American genera referred by Ameghino to the Multituberculata have anything whatever to do with that Order.

2. The family Polydolopidæ represents an early and specialized side branch of the group Cæolestoidea, more or less intimately allied to the true Cæolestidæ and like the latter ultimately derived from primitive Cretaceous polyprotodont marsupials similar to or belonging in the family Didelphiidæ in a broad sense.

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