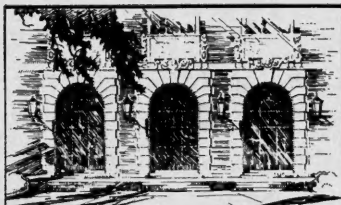


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No. 2

**AN ADIANTHINE LITOPTERN FROM THE
DESEADO FORMATION OF PATAGONIA**

BY BRYAN PATTERSON
ASSISTANT CURATOR OF PALEONTOLOGY

RESULTS OF THE MARSHALL FIELD PALEONTOLOGICAL EXPEDITIONS
TO ARGENTINA AND BOLIVIA, 1922-27

Among the Deseado vertebrates collected by the First Marshall Field Expedition is a specimen of an adianthine consisting of the greater part of the upper dentition. This individual and the holotype of *Proheptaconus trelewense* Bordas¹ give a fairly good idea of the upper cheek teeth of the *Adianthus* phylum, knowledge of which was until recently limited to a single upper molar each of the Santa Cruzean *Adianthus buccatus*² and of the Colhuehuapian *A. patagonicus*. The group, represented by perhaps a dozen specimens, is the least known of the order Litopterna, and its affinities have been somewhat uncertain. The new specimen is of importance in that it sheds some light on the problem of relationships.

I wish to express my sincere thanks to Professor Alejandro F. Bordas of the Museo Argentino de Ciencias Naturales for his kindness in sending me drawings of *Proheptaconus trelewense*. The drawings in this paper are the work of Mr. Frank Gulizia.

Order **Litopterna**
Family **Machraucheniiidae**
Subfamily **Adianthinae**
Proadiantus Ameghino 1897

F.M. No. P14698, found by Mr. George F. Sternberg in the Deseado formation at Cabeza Blanca, Chubut, and consisting of

¹ Originally placed in the Protheroheriidae (Bordas, 1936, pp. 111-112), but later transferred to the Adianthinae (1939, p. 417).

² So spelled in the type description; in certain subsequent papers changed to *Adiantus buccatus*.

LC(?), P^{2-3} , M^{1-3} and RP^3-M^2 , is referred to this genus. Since the specimen differs from both *Proheptaconus* and *Adianthus* and is similar in size to described species of *Proadiantus*, the only known Deseado adianthine, the determination may be considered as reasonably secure. No specific assignment is possible, however. Three species have been named by Ameghino on portions of the mandible—*P. excavatus* (1897, pp. 455–456, fig. 42), *P. pungidens* (1901, p. 372; 1906, p. 345, fig. 178) and *P. gibbus* (1901, p. 372). The first two are said to be about equal in size and the third larger, but practically no comparative data are given.¹ P14698 agrees fairly well in dimensions with *P. pungidens* and *P. excavatus*.

Description.—The anterior tooth appears to be either a canine or a first premolar. In its present state of wear the crown is low and rather long antero-posteriorly. It consists of a main cusp and a posterior prolongation, between which there is a shallow groove on the external face. A slight depression is present in the anterior portion of the internal surface, and posterior to this is an abraded area indicating the former presence of a median spur from the principal cusp. The single root is long with a moderate inward curvature. When partially worn, the canine and P^1 of such macrauchenines as *Cramauchenia* and *Theosodon* are broadly comparable to this tooth, but there is no evidence that the crown in *Proadiantus* was as high and as acute when newly erupted. P^1 of the Santa Cruz protheroids is more complicated.²

The second and third premolars are structurally identical. The ectoloph is exceedingly sinuous with a prominent parastyle, a small metastyle and strong swellings in the region of the paracone and metacone. The metacone swelling extends outward to a very considerable extent. The grooves between these prominences are of varying depth, that between the paracone and metacone being the deepest and largest, and that between the metacone and metastyle the shallowest and smallest. On the grinding surface there is a large, elongate anterior fossa which is partially divided by a transverse ridge. All other features of this surface have been obliterated by wear. The sides and inner face of each tooth describe a broad U. P^{2-3} in the earlier Macraucheniinae lack any indication of paracone and metacone swellings and have a more triangular outline. Never-

¹ For example, *P. pungidens* is stated to differ from *P. excavatus* in the structure of M^3 , yet all that has been published about the latter species concerns a ramus fragment bearing P^3-4 .

² The small tooth (C or I^3) present in the Deseado *Deuterotherium distichum* (Simpson, 1932, p. 2, fig. 1) may have been similar but it is too worn for adequate comparison.

theless, in the structure of these teeth, *Proadiantus* resembles the macrauchenines much more closely than it does the proterotherids. The contour of the grinding surface—convex anteriorly, concave posteriorly—is the same in *Proadiantus*, *Cramauchenia*, and *Theosodon*. The anterior fossa of *Proadiantus* with its dividing transverse ridge is exactly matched in P^3 of a specimen of *Cramauchenia* (F.M. No. P13301). P^4 is more quadrangular in outline

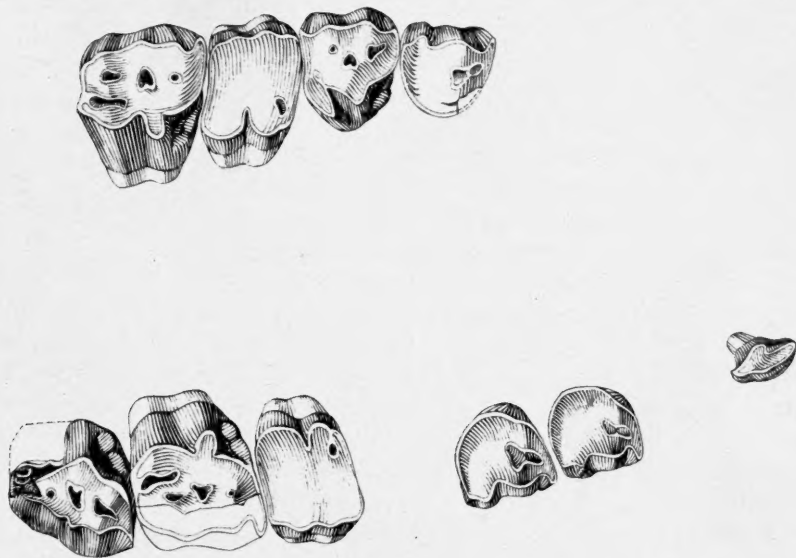


FIG. 6. *Proadiantus* sp., F.M. No. P14698. Crown view of right P^3 - M^2 , left C^7 , P^{2-3} , M^{1-2} . $\times 2/1$.

than P^{2-3} and has a more regular ectoloph due to the nearly equal prominence of the paracone and metacone; unlike conditions in the Macraucheninae, there is no indication of a mesostyle. The division of the anterior fossa, foreshadowed on the preceding teeth of the series, into antero-external and median external fossettes is complete. Small vestiges of postero-external and -internal fossettes indicate that, as on the molars, the posterior fossa was divided. The protocone is prominent but small, and forms a noticeable angle with the protoloph. As in *Proheptaconus*, a hypocone appears to be present, one of the few points of contrast to the macrauchenines and of agreement with the proterotherids. The antero-internal corner of the tooth is occupied by a low, crenulated cingulum which does not extend on to the anterior side.

The first molar is heavily worn; the few structural details that are still visible indicate that it was similar to the other teeth of the series. M^{2-3} are structurally alike and closely comparable in size. The ectoloph bears parastyle and mesostyle, paracone and metacone swellings, but no definite metastyle. The protocone is small and narrow and tends to be somewhat constricted near its base. The hypocone is much the larger of the two internal cusps, is separated from the protocone by a deep, narrow cleft and is considerably expanded antero-posteriorly. As shown on M^2 , it remains for some time separate from the protocone-metacone crest; the same is true of the holotype of *Adianthus patagonicus* (Ameghino, 1904a, p. 92, fig. 98). The bicuspidate antero-internal cingulum is very stout but does not extend farther than half way along the anterior face of the tooth. The large fossa enclosed by the rather high posterior cingulum is partially filled by cuspules. Some of these have coalesced with each other and with the ectoloph and protocone-metacone crest to isolate a small postero-external fossette,¹ and others have coalesced with the hypocone. Five fossettes are thus present on the crown, the antero- and median external, the antero-internal and the postero-external and -internal. Not all of these were present in the grinding surface at the same time, however; the antero-external fossette was evidently worn away before abrasion reached the antero-internal, as in the Pliocene and Pleistocene macrauchenines. As revealed by the much worn M^1 , the antero-internal is the most persistent. The internal roots are strongly inclined inward and, in common with those of the Macrauchiinae and in contrast to those of the Protheroheriidae, are united.

MEASUREMENTS

	C?	P ²	P ³	P ⁴	M ¹	M ²	M ³
A.-p. diam.*	5.4	6.1	6.4	7.3	6.5†	9.2	9.1
Tr. diam.*	3.0	5.8	6.3	8.0	9.6	10.3	9.4

*Maximum.

†Length considerably reduced by wear.

Discussion.—Before reviewing the taxonomic position of the Adianthinae, the dental characters of the three better known genera² of the group may be contrasted in so far as this is now possible. These three forms are *Adianthus* of the Santa Cruz and Colhué-

¹ This is a typically notoungulate character which I have not seen in the other litoptern groups.

² The very inadequately known *Pseudadianthus* of the Casamayor (Ameghino 1901, pp. 372-373) is the only other genus that has been described.

Huapí,¹ *Proheptaconus* of the Trelew² and *Proadiantus* of the Deseado.¹

Adiantus.—Molars higher crowned than those of *Proadiantus*, without mesostyle, hypocone not elongate antero-posteriorly.³

Proheptaconus.—M² without mesostyle and with metastyle,⁴ hypocone moderately elongate, postero-internal fossette on M¹⁻² divided into two parts (possibly on M² also but this is uncertain due to breakage).

Proadiantus.—Molars relatively low crowned, mesostyle present on M¹⁻², no clearly defined metastyle, hypocone elongate, postero-internal fossette undivided, internal roots united.

The lower dentition of *Proheptaconus* is unknown. Ameghino mentioned no differences between the lower dentitions of *Adiantus* and *Proadiantus*, but from an examination of his figures (1897, p. 455, fig. 41; 1906, p. 345, fig. 178), and of specimens⁵ in the Tournouër

¹ Ameghino's lists of the Colhué-Huapí and of the "notohippidéene" faunas (1906, pp. 474, 476) include *Proadiantus* as a member of both and do not include *Adiantus*. I am sure that this is a *lapsus* because earlier papers mention *Adiantus buccatus* as occurring in the "notohippidéene" and do not record any generic transfer of the Colhué-Huapí *A. patagonicus*.

² The Trelew and the Colhué-Huapí (*Colpodon* beds) are formations of the same latest Oligocene or earliest Miocene age. Kraglievich's (1930, pp. 157, 161) use of Trelewense to cover both and his transfer of Colhuehuapiense to the "notostylopense inferior" of Ameghino (a part of what is now known as the Casamayor), an arrangement still followed by some authors, is confusing. It is also doubly unnecessary; first, because C. Ameghino's use of Colhuehuapiense for the "Colpodon beds" has priority, and second, because the supposed divisions "Notostylopense superior" and "inferior" have no faunal basis (Simpson, 1933, pp. 5, 9). To extend Colhuehuapiense *sensu* Kraglievich to include the Paleocene Río Chico formation (roughly equivalent to Ameghino's "notostylopense basal"), as has been done, is quite unwarranted. Kraglievich explicitly stated that his Colhuehuapiense was intended for Ameghino's "notostylopense inferior" and made no mention of the "notostylopense basal." The Casamayor and the Río Chico faunas are thoroughly distinct, and to bracket the latter with a hypothetical fraction of the former is to run counter to the known facts.

³ These characters are taken from the well-figured *A. patagonicus* (Ameghino, 1904a, pp. 92-93, figs. 98, 100). The type of *A. buccatus* (M¹ or M²) has, according to Ameghino (1891, pp. 134-135, fig. 31), an almost straight ectoloph, a deep cleft between the protocone and hypocone extending into the grinding surface for a considerable distance, divided internal roots and but three fossettes on the crown. One of these is the antero-internal, but, from an examination of the inadequate figure, it is impossible to homologize the remaining two with the fossettes of the other described specimens.

⁴ Probably true of M¹ and M² also, but the ectolophs of these teeth are broken on the type and only specimen.

⁵ A ramus fragment with M_{T-3} and alveoli from the Colhué-Huapí, and a ramus fragment with M_{T-3} from the Deseado. The latter is probably either *P. pungidens* or *P. excavatus*. The former may well be *A. patagonicus*; it is certainly too large to be referred to the small *Proheptaconus trelewense*. My thanks are due to the American Association of Museums for the award of a Carnegie Grant-in-Aid which made it possible for me to examine the Patagonian fossil mammals in the Muséum National d'Histoire Naturelle, Paris.

collection it is evident that the lower cheek teeth, as well as the upper, are noticeably higher crowned in *Adiantus*. The presence of entoconids on M_{1-3} of the Deseado genus is an additional distinction between the two genera.

Ameghino consistently maintained that the *Adiantus* group should be placed in a family distinct from, but related to, the Macraucheniidae.¹ He admitted the close resemblance to the macrauchenids in dental structure but believed that separation was justified by the following characters: in upper molars—absence of

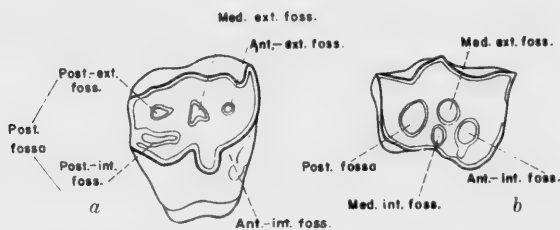


FIG. 7. Crown views of right M_2 . a, *Proadiantus* sp., F.M. No. P14698. $\times 2/1$. b, *Promacrauchenia antiqua* Ameghino, F.M. No. P14448. $\times 1/2$.

mesostyles, presence of postero-external fossettes, greater separation of protocones and hypocones and absence of median internal fossettes² (1904a, pp. 92-93; 1904b, pp. 56-57); in lower molars—absence of entoconids (1894, p. 283). Scott (1910, p. 2) was not greatly impressed by these distinctions (relatively slight in any case) and preferred to unite the Adianthidae with the Macraucheniidae, a course in which he was followed by Simpson (1934, pp. 8-9). The newer evidence upholds this action, for in the sum of their characters both *Proadiantus* and *Proheptaconus* are considerably closer to the macrauchenids than to the proterotherids. Furthermore, *Proadiantus* possesses two of the characters upon the absence of which Ameghino relied in erecting the Adianthidae. P14698 has a mesostyle on each of the upper molars, and a figured specimen of *Proadiantus pungidens* (Ameghino, 1906, fig. 178 o, i, p. 345) has a large independent entoconid on M_3 and smaller entoconids on M_{1-3} that are not yet completely united with the talonid crescents. The speci-

¹ In the index to his work on ungulate upper molars (1904a, p. 513) he placed the family in the Hyracoidea, but this was either a *lapsus* or an opinion that was quickly changed, for shortly thereafter he again listed them following the Macraucheniidae (1906, faunal lists on pp. 467-473).

² He also thought that the parastyle was non-homologous in the two groups, a view for which I can see no evidence.

men in the Tournouër collection is similar to this individual although with somewhat larger entoconids on M_{1-3} .¹

Adianthus and its relatives cannot be separated familiarly from the Macraucheniidae but they are nevertheless a line apart from the typical members of that family. In addition to possessing certain structural peculiarities in the upper premolars and upper and lower molars (see above, under description), the *Adianthus* phylum is decidedly precocious in molar evolution. The development of a flat, grinding surface with enclosed enamel fossettes evidently began early and had progressed so far by Oligocene time that *Proadiantus* is almost comparable in this respect to the Pliocene *Promacrauchenia* (see fig. 7). Taxonomic segregation of the phylum seems warranted, and Bordas' recent division of the family into Macraucheniinae and Adianthinae (1939, pp. 416-417) is in accord with the available evidence.

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¹ It is probable that Ameghino made his statement concerning absence of entoconids without knowledge of M_{3} in *Adianthus bucatas*, for his subsequent figure (1897, fig. 41, p. 455) of the specimen that he described shows this tooth in outline only.

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