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Systematics of the Adianthidae (Litopterna, Mammalia)

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ABSTRACT

The genera and species of previously known Adianthidae are revised, with descriptions of original and more recently collected specimens. *Proectocion,* usually placed in the Didolodontidae, is in known morphology an appropriate primitive morphotype for the family. *Adiantoides* and the recently described *Indalecia* are placed in the subfamily Indaleciinae, which includes somewhat aberrant Eocene ?adianthids. *Tricoelodus,* usually considered of doubtful validity and affinities, is the best known genus and is represented by a new species from the Deseadan of Bolivia in addition to the type. *Tricoelodus, Proadiantus,* and *Thadanius* (a new monotypic genus from the Deseadan of Bolivia) form a monophyletic subgroup of Adianthidae, *Thadanius* being the most primitive; *Adianthus* may be most closely related to *Proheptaconus.*

RESUMEN

Géneros y especies previamente conocidos de Adianthidae son revisados agregando descripciones de espécimens ineditos. *Proectocion,* comunmente ubicado en los Didolodontidae, se considera como un ejemplo del posible antecesor estructural de los Adianthidae. *Adiantoides* e *Indalecia,* este último recientemente descripto por Bond y Vucetich, son colocados en una nueva subfamilia, Indaleciinae, de acuerdo con los citados autores. La misma incluye ¿adiantidos? eocenos algo aberrantes, no relacionados con las formas posteriores, las que se incluyen en otra subfamilia: Adianthinae. *Tricoelodus* usualmente considerado de validez y afinidades dudosas, es ahora el género mejor conocido y representado, con una nueva especie deseadense de Bolivia. *Tricoelodus, Proadiantus,* y *Thadanius* un nuevo género monotaxico de Bolivia, también deseadense, integran un subgrupo monofilético dentro de ésta subfamilia, de los cuales el último es el más primitivo; *Adianthus* parece más estrechamente relacionado a *Proheptaconus.*

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INTRODUCTION

The pygmy litopterns, family Adianthidae, are among the poorest known of the many native South American ungulate groups. Fossil remains of adianthids are extremely rare, probably reflecting an originally limited abundance, and most available material is fragmentary and frequently represents noncomparable parts of the various described forms. The family was founded, and most of the included species described, by the great Argentine paleontologist Florentino Ameghino around the turn of the century. Ameghino recognized the essential unity of the constituent families of the Litopterna and the similarity of adianthids to macraucheniids, but generally placed them in the Perissodactyla. Florentino Ameghino's adianthid material was collected by his brother, Carlos, in Chubut and Santa Cruz provinces during his many trips to Patagonia. The Santacrucian localities have been reviewed recently by Marshall (1976) and accounts of Deseadan localities are given by Chaffee (1952), Patterson and Marshall (1978), and Patterson and Wood (1982). An important additional specimen of Deseadan age from one of the Ameghinos' most important localities, Cabeza Blanca, was collected by the Marshall Field Expeditions of the Field Museum of Natural History in the 1920s (Patterson, 1940). Bordas (1936, 1939) added *Proheptaconus* to the family on the basis of an incomplete skull with natural endocast and some broken teeth collected in the Colhuehuapian beds of the Trelew-Gaiman region, Chubut. The peculiar *Adiantoides,* described by Simpson and Minoprio (1949) and Simpson, Minoprio, and Patterson et al. (1962) was the next addition to the Adianthidae. The Divisadero Largo Formation, from which it came, has produced a curious fauna of generally primitive aspect, with some forms related to species from the Lumbrera Formation (early Eocene of northwestern Argentina) and others to Casamayoran and Deseadan species from Patagonia, perhaps indicating that it is a latitudinal ecologic variant with respect to the South American land mammal faunas established from Patagonian sequences. This fauna has prompted the erection of a new, ?late Eocene, South American Land Mammal Age, the Divisaderan (Pascual et al., 1965). Hoffstetter (1968, 1976) listed the Patagonian genus *Proadiantus* among the Deseadan fauna of the La Salla-Luribay Basin, Bolivia. Soria (1981a) has reviewed the Colhuehuapian material pertaining to the family, and Quiroga (1981) described the natural endocast of the holotype of *Proheptaconus trelewense* Bordas, 1936. Most recently, Bond and Vucetich (in press) have described as new *Indalecia grandensis* from the Lumbrera Formation (early Eocene) of Salta Province, northwestern Argentina. These authors proposed a new subfamily of the Adianthidae, Indaleciinae, to include *Indalecia* and *Adiantoides.* This arrangement is followed here, although as detailed below the familial and even ordinal placement of the Indaleciinae is unclear.

The Adianthidae received only cursory accounts by Loomis (1914) and Scott (1910), and with the exception of brief additions and descriptions have been virtually ignored since Ameghino's time, with no detailed or first hand treatment of the new type specimens. In the present paper the species of the Adianthidae are revised, diagnosed, and described with attention focused on new materials or those not having received recent treatment.

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Abbreviations

AMNH, American Museum of Natural History, New York, NY
FMNH, Field Museum of Natural History, Chicago, IL
MACN, Museo Argentino de Ciencas Naturales "Bernardino Rivadavia," Buenos Aires, Argentina
MHNM, Museo de Historia Natural de Mendoza, Mendoza, Argentina
MLP, Museo de La Plata, La Plata, Argentina
MNHM, Musée National d'Histoire Naturelle, Paris, France
PU, Princeton University, Princeton, NJ
PVL, Laboratorio de Paleontología Vertebrados, Instituto "Miguel Lillo," San Miguel de Tucumán, Tucumán, República Argentina

SYSTEMATIC PALEONTOLOGY

ORDER LITOPTERNA AMEGHINO, 1889
FAMILY ADIANTHIDAE AMEGHINO, 1891

Adianthidae Ameghino, 1891, p. 143; Loomis, 1914, p. 51; Simpson, Minoprio, and Patterson, 1962, p. 245; Soria, 1981a, p. 23. Adiantidae Ameghino, 1894[3], p. 283. Adiantinae Bordas, 1939, p. 417 (as a subfamily of Macraucheniidae). Adianthinae Patterson, 1940, p. 13; Simpson and Minoprio, 1949, p. 6 (as a subfamily of Macraucheniidae).

TYPE: *Adianthus* Ameghino, 1891.

RANGE: Casamayoran to Santacrucian, South America.

INCLUDED SUBFAMILIES: Adianthinae Ameghino, 1891; Indaleciinae Bond and Vucetich (in press).

DIAGNOSIS: Small but dentally advanced litopterns (molars lophate; upper molars primitively with crescentic para- and metacones, columnar parastyle, weak or absent mesostyle; P^4 molarized; P_4 with lophate talonid; lower molars bicrescentic or nearly so, with cristid obliqua attaching to the metaconid). P^3–M^3, where known, with fossettes. Three primary upper molar fossettes present, formed by hypertrophied conule cristae; additional fossettes developing in later forms behind the protostylar cingulum and in front of the posthypocone cingulum, the latter fossettes becoming subdivided.

Ameghino, 1891, established the Adianthidae as a monotypic family based on *Adianthus bucatus* (invalidly emended in later publications to "*Adiantus buccatus*") from the Santacrucian, and subsequently (1894) defined the family and included with it the Notohippidae, "Mesorhinidae" (at that time based essentially on *Theosodon,* a cramaucheniine macraucheniid), and Proterotheriidae in the Litopterna, regarded in turn as a suborder of Perissodactyla (Ameghino indicated that *Adianthus* compared most closely with *Macrauchenia* but inexplicably omitted the Macraucheniidae from this account). The Deseadan genera *Proadiantus* and *Tricoelodus* were described by Ameghino in 1897; the former was referred to the Adianthidae and the latter to the "Mesorhinidae." Ameghino followed this arrangement in 1898, in which he recognized the Litopterna as a separate and distinct order, including in it the Adianthidae, "Mesorhinidae," Macraucheniidae, Proterotheriidae, and Notohippidae. Two new Deseadan species of *Proadiantus* and a new Casamayoran genus, *Pseudadiantus,* were subsequently added (Ameghino, 1901), followed by a new, Colhuehuapian species of *Adianthus, Adianthus patagonicus* (Ameghino, 1903–1904). In 1904 and also in his great treatise of 1906, Ameghino abandoned the Litopterna as a concept and simply referred the families Adianthidae, Macraucheniidae, and Proterotheriidae to the Perissodactyla; the Notohippidae were correctly removed to a position near the other toxodonts in this (his last) classification.

In Scott's revision (1910) of the Santa Cruz litopterns, he placed *Adianthus* in the Macraucheniidae; Loomis, 1914, followed Ameghino and maintained the Deseadan

[3] This is the date universally cited, although the volume is dated 1892. From internal evidence it cannot have been issued before 1893 at the earliest.

genera *Tricoelodus* and *Proadiantus* in the Adianthidae. Neither of these works were based on restudy of the materials involved. Bordas described a new genus, *Proheptaconus,* from the Colhuehuapian, at first (1936) placing it in the Proterotheriidae but later (1939) removing it to the Adianthinae, considered by him a subfamily of the Macraucheniidae. In this later opinion he was followed by Patterson (1940), who described an upper dentition from from the Deseadan as *Proadiantus,* and by Simpson and Minoprio (1949), who named as new a genus from the Divisaderan, *Adiantoides.* These authors noted also that *Pseudadiantus* is synonymous with a genus of notopithecine interatheriids, as later demonstrated by Simpson, 1967. The group was returned to familial status by Simpson, Minoprio, and Patterson, 1962. Soria, 1981, synonymized the Colhuehuapian species *Adianthus patagonicus* and *Proheptaconus trelewense,* recognizing the latter as a nonetheless valid genus. *Indalecia grandensis,* a newly described species from the Casamayoran of northwestern Argentina, appears to be closely related to *Adiantoides* and forms the basis for division of the family into two subfamilies, Adianthinae and Indaleciinae (Bond and Vucetich, in press).

Proectocion (including *Oxybunotherium*), now considered a didolodontid condylarth, should probably be grouped near the Adianthidae (Cifelli, in press a). New species are herein recorded from the Deseadan and Casamayoran, and a new genus from the Deseadan. As thus recognized, the Adianthidae comprise seven genera, ranging from the Casamayoran to Santacrucian. They are nowhere in the record a very abundant or taxonomically diverse group. Morphological comparisons presented elsewhere (Cifelli, in press) and as summarized in the above diagnosis support the long-held belief that the Adianthidae are closely related to the Macraucheniidae, although Quiroga (1981) has argued that the brain of *Proheptaconus* strongly resembles a pattern common to proterotheriids but not macraucheniids.

SUBFAMILY ADIANTHINAE AMEGHINO, 1891

Adianthinae Bond and Vucetich, in press (first usage in the present sense).

TYPE: *Adianthus* Ameghino, 1891.

RANGE: Deseadan to Santacrucian, South America.

INCLUDED GENERA: The type, and *Proheptaconus* Bordas, 1936; *Proadiantus* Ameghino, 1897; *Tricoelodus* Ameghino, 1897; and *Thadanius,* new genus.

DIAGNOSIS: Lower incisors and canines, where known, with a secondary posterior cutting surface and forming a continuous morphological series with the cheek teeth. Cheek teeth moderate to high crowned. M_{1-3} with distinct talonid cusps and/or entolophid in earlier forms; M_3 hypoconulid projecting as a third lobe. P^4 molarized, with five fossettes, metacone, and small hypocone. P^4–M^3 protocone to metacone crest present; parastyle moderately to strongly developed, mesostyle small or lacking. Upper molars with six fossettes, central fossette closed lingually; M^3 hypocone present.

This subfamily includes typical adianthids. The characters cited above, particularly the style of P^4 molarization and the cusp connections on the upper molars, clearly distinguish the Adianthinae as a monophyletic unit, exclusive of the Indaleciinae. Although primitive in a number of respects, the Indaleciinae bear several progressive features which indicate their relationship to adianthines to be remote, as shown by Bond and Vucetich (in press), and perhaps non-exclusive.

ADIANTHUS AMEGHINO, 1891

Adianthus: Ameghino, 1891, p. 134; Scott, 1910, p. 154.

Adiantus Ameghino, 1894, p. 283.

TYPE: *Adianthus bucatus* Ameghino, 1891.

DISTRIBUTION: Santacrucian, Patagonia.

DIAGNOSIS: Cheek teeth high crowned. I_2–C with three lingually directed crests coalescing to form two transient enclosed basins. P_{1-3} broadly bilophate, with crescents shallow and subequal; P_4 fully molariform. Anterolingual cingular crest lacking on P_4 and the molars; paralophid extending to lingual side of tooth on lower molars, not terminating in a median position as in *Proadiantus*; hypoconulid and entoconid not differentiated from talonid crescent, entolophid absent.

Ameghino, 1891, established this genus, type of the family, on an enigmatic cheek

tooth of uncertain provenience which possibly derived from the *Notohippus* beds, as noted below in connection with *Proadiantus*. Later he described (1894) and figured (1897) a hemimandible as pertaining to the type species, and in 1903–1904 described a new species from the Colhuehuapian, *A. patagonicus*. In these and later publications, he emended the generic name to "*Adiantus*," an emendation not generally followed by subsequent workers (e.g., Palmer, 1904; Scott, 1910; Patterson, 1940; Simpson, Minoprio, and Patterson, 1962). Simpson, Minoprio, and Patterson, 1962, observed that the type and only specimen of the Colhuehuapian species, *A. patagonicus*, is conspecific with *Proheptaconus trelewense* Bordas, 1936, but noted that the latter is a valid genus, being distinct from the type of *Adianthus, A. bucatus*. This suggestion was adopted by Soria (1981), who indicated further that Ameghino's referred specimen of the type species might be taken as neotype (as done by Scott, 1910, perhaps in ignorance of the original type). This course, followed here for reasons given below, introduces the problem of noncomparability of types. *Proheptaconus* is based on upper teeth and *Adianthus* now on lowers, and their validity as genera distinct from each other may not be evaluated. A fragmentary mandible in the collections of the Museo de La Plata, from a *Notohippus* horizon, differs from *Adianthus bucatus* and may pertain to *Proheptaconus* (although the possibility remains that it represents a third and otherwise as yet unknown late adianthid).

Adianthus bucatus Ameghino, 1891
Figures 1A, B

Adianthus bucatus Ameghino, 1891, p. 134.
Adiantus bucatus Ameghino, 1894, p. 283.
Adianthus buccatus Ameghino, 1906, p. 504
Adianthus buccatus Scott, 1910, p. 154.

NEOTYPE: MACN A1812, right hemimandible with I_2–M_2.

HYPODIGM: The type only.

HORIZON AND LOCALITY: Lower Santa Cruz beds (*fide* Ameghino, 1893), Corriguen Aike, Provincia de Santa Cruz, Argentina.

DIAGNOSIS: Sole known species of the genus.

Ameghino's original description (1891) of this species was based on a cheek tooth which he identified as an upper right molar. The specimen was lost or mislaid, apparently during Ameghino's lifetime, since he made no further reference to it, and it has not been found in the Ameghino Collection. No comparable materials have since come to light. The tooth was evidently complete, since Ameghino noted that the surrounding enamel was uninterrupted, but its structure is baffling and entirely unlike that of any described litoptern or, for that matter, South American ungulate. A deep reentrant is present ?lingually, so that the tooth is partially bilobate; ?labially, two transversely aligned oval fossettes are present. This specimen appears not to be litoptern or even ungulate, but instead probably belongs to a caviomorph rodent, perhaps a somewhat atypical dasyproctid or erethozontid. The name *Adianthus* is therefore not strictly valid for a genus of pygmy litopterns, nor by implication for a family of that order. Since the specimen has apparently been lost, the referred specimen described by Ameghino (1894) is here taken as neotype, in lieu of introducing the confusion which would inevitably be generated by proposing a new generic name for *Adianthus*, in use for nearly 100 years.[4]

Ameghino (1897, fig. 41) figured MACN A1812 in lateral view and identified the teeth present as I_1–M_2. The external surface of the mandible has been plastered anteriorly, but with one exception all the teeth appear to belong in the jaw. This exception is the first tooth, for which no portion of the surrounding alveolus remains. The tooth is broken, and the crown cannot belong to the root because they differ markedly in transverse dimension. The crown, simple, chisel-like, and lacking enamel on its medial and lingual faces, is very unlike the following teeth, which form a graded series as Ameghino correctly observed. I_2, the first tooth in the series actually belonging to this specimen, is broken at its tip. It bears two wear surfaces, medial and distal, the latter being partially overlapped

[4] A proposal for designation of this specimen as neotype, under the plenary power, has been made to the International Commission on Zoological Nomenclature.

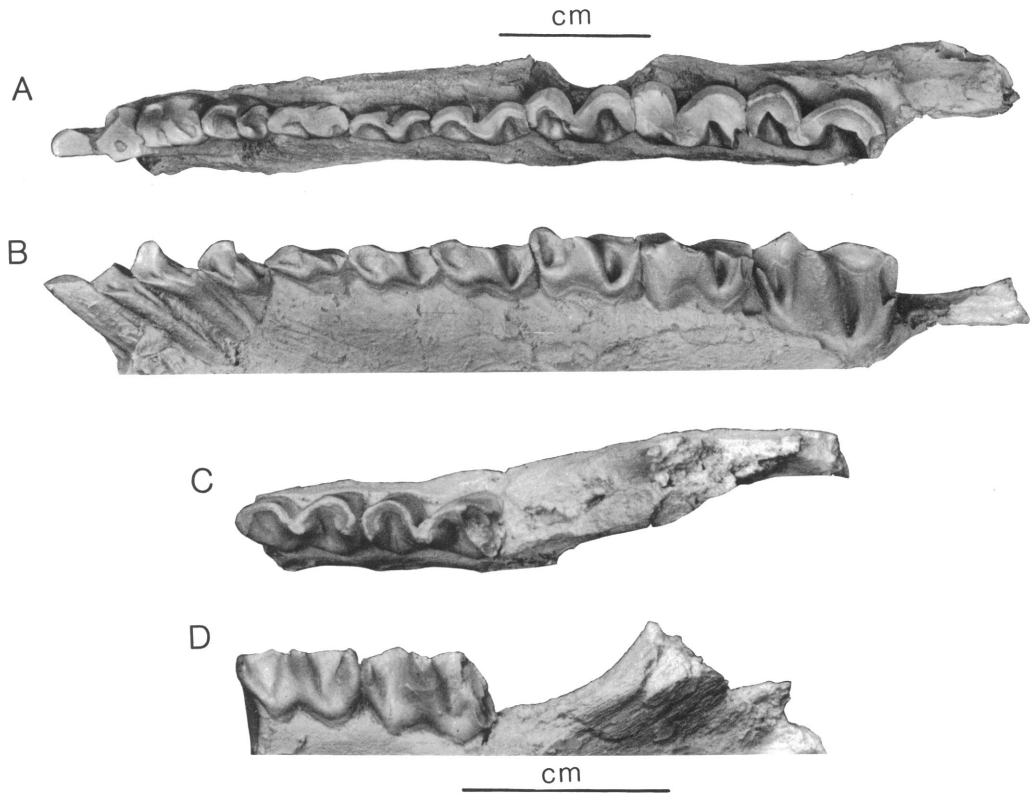

FIG. 1. *Adianthus bucatus* (MACN A1812, neotype). A, B, right I_2–M_2. (I_1 does not belong to this specimen.) C, D, Adianthinae, genus and species undetermined (MLP 68-I-17-192). A, C, occlusal view; B, D, lingual view. (Photographed from casts; lower parts of mandibular rami are deliberately omitted.)

by I_3 because I_2 is incorrectly positioned in the jaw as reconstructed. The medial I_2 wear surface bears a small enamel lake. I_3, larger than I_2, has an anterolabial apex from which three ridges extend lingually and posterolingually, enclosing two small basins. The canine, less worn than I_3, shows this complex crown arrangement to be analogous with that of the premolars and molars which follow, the two anterior crests forming the trigonid crescent and the posterior crescent forming a small, curved talonid loph. P_{1-3} are progressively enlarged and more molariform in appearance. P_1, heavily worn, is anteroposteriorly elongate with very open and subequal trigonid and talonid crests; P_{2-3} have, successively, deeper labial notches separating trigonid from talonid and deeper, more concave basins lingually. P_4 is fully molariform, with the trigonid crescent more compressed anteroposteriorly than in the preceding teeth. As with the molars, the anterolingual cingular crest seen in *Tricoelodus* and *Proadiantus* is lacking. M_{1-2}, progressively larger than P_4, are bicrescentic, with the trigonid not curved as tightly as in the Deseadan forms and with the talonid completely lacking entolophid and differentiation of cusps.

Measurements (in millimeters) are given in table 1.

PROHEPTACONUS BORDAS, 1936

Proheptaconus Bordas, 1936, p. 111; 1939, p. 417; Soria, 1981a, p. 24; Quiroga, 1981, p. 67.

TYPE: *Adianthus patagonicus* Ameghino, 1904.

DISTRIBUTION: Colhuehuapian, Patagonia.

DIAGNOSIS: Upper molars high crowned with strong parastyle and moderately devel-

oped metastyle; ectoloph concave labially with weak paracone and metacone folds, mesostyle lacking. Protostylar and posthypocone cingula high, enclosing deep fossettes; division of posterior fossette in a relatively lingual position.

Ameghino (1903–1904) described the species "*Adiantus*" *patagonicus* on the basis of an isolated M^3 from a Colhuehuapian horizon at the Gran Barranca; as noted in connection with *Proadiantus,* he probably later (1906) considered the species as belonging to that genus, since *Proadiantus* is listed in the Colhuehuapian fauna and this was the sole adianthid specimen of that age known to him. *Proheptaconus trelewense* was originally considered by its describer to be a proterotheriid (Bordas, 1936), but later correctly referred to the Adianthidae, placed in the Macraucheniidae as a subfamily (Bordas, 1939). Following a suggestion by Simpson, Minoprio, and Patterson, 1962, Soria (1981) synonymized "*Adiantus*" *patagonicus* Ameghino, 1904, with *Proheptaconus trelewense* Bordas, 1936, maintaining the latter genus as distinct from the type of *Adianthus, A. bucatus.* As mentioned above, the two forms are based on non-comparable types.

Proheptaconus patagonicus (Ameghino, 1904)

Figure 2

Adianthus patagonicus Ameghino, 1903–1904, vol. 18, p. 56.
Proheptaconus trelewense Bordas, 1936, p. 111.
Proheptaconus trelewensis Bordas, 1939, p. 418.
Proheptaconus patagonicus Soria, 1981a, p. 25; Quiroga, 1981, p. 67.

TYPE: MACN A52-218, isolated left M^3.

TYPE OF *Proheptaconus trelewense*: MACN 11453, poorly preserved skull with endocast and with broken left P^4–M^1 and right M^1 and M^3; right M^2 complete.

HYPODIGM: The types, as specified above.

HORIZON AND LOCALITIES: Colhuehuapian; Gran Barranca and left barranca opposite Gaiman; Provincia del Chubut, Argentina.

DIAGNOSIS: Sole known species of the genus.

This species was described by Soria (1981) and its major characters are given in the generic diagnosis. Although distinct from and more advanced than *Tricoelodus* in several features, the construction of the upper molar crowns, with six fossettes, is essentially the same in the two genera and distinguishes them from other forms for which the upper dentition is known. More complete comparisons are deferred to the discussion.

TABLE 1
Measurements (in Millimeters) of *Adianthus bucatus* and Adianthinae, Indeterminate

		Adianthus bucatus MACN A1812	Adianthinae, indet. MLP 68-I-17-192
P_1	L	5.3	–
	W	2.5	–
P_2	L	5.4	–
	W	2.6	–
P_3	L	6.7	–
	W	2.8	–
P_4	L	7.2	–
	W	3.8	–
M_1	L	7.5	6.6
	W	4.3	3.3
M_2	L	9.2	–
	W	4.4	3.5

The genoholotype M^3 (MACN A52-218) is 6.2 mm. in length and 7.8 mm. in width; no reliable figures may be given for the broken teeth of MACN 11453.

ADIANTHINAE, GENUS AND SPECIES UNDETERMINED

Figures 1C, D

MLP 68-I-17-192 is a portion of a right mandibular ramus bearing two cheek teeth, with a third in eruption, collected from a lower Santacrucian (*Notohippus*) level at Cerro Centinela, Provincia de Santa Cruz, Argentina, by R. Pascual and O. Odreman Rivas. These teeth, M_{1-2} (the latter broken) are smaller than, and differ from, those of MACN A1812, the neotype of *Adianthus bucatus.* They are of appropriate size for the earlier, Colhuehuapian species, *Proheptaconus patagonicus,* but cannot be compared directly with it. Reference to *Proheptaconus* is suggested, mainly by negative evidence, but since none of the materials in question are from the same localities or of the same age, this

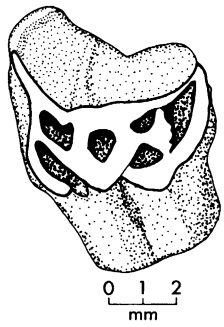

FIG. 2. *Proheptaconus patagonicus* (MACN A52-218, type). Left M^3 in occlusal view.

specimen cannot be placed more precisely than subfamily.

M_{1-2} are high crowned and fully bicrescentic, with subequal trigonid and talonid. The trigonid crescent of M_1, unlike M_2 which in this respect is similar to *Adianthus bucatus,* is narrower transversely than that of the talonid and less curved or anteroposteriorly compressed, so that the trigonid basin is broadly open lingually. The metaconid is distinct and gives origin to the cristid obliqua, the trigonid being less fully connected to it at its apex. The talonid crescent terminates in a posterolingually placed prominence, perhaps the remnant of an entoconid; there is no entolophid nor further differentiation of cusps.

Measurements (in millimeters) are given in table 1.

PROADIANTUS AMEGHINO, 1897

Proadiantus Ameghino, 1897, p. 455; 1901, p. 372; 1906, p. 345.
Proadianthus Loomis, 1914, p. 51.

TYPE: *Proadiantus excavatus* Ameghino, 1897.

DISTRIBUTION: Deseadan, Patagonia.

DIAGNOSIS: Small adianthid with moderately high crowned teeth. I_2–C_1 with secondary, posterior shearing surface, but lacking the coronal complications of *Adianthus.* P_4 with trigonid crescent very open lingually, anterolingual cingular crest lacking, and entoconid variably present and developed transversely. Hypoconulid of M_{1-2} slightly projecting and defined by labial and lingual sulci, the latter not forming a well-developed basin as in *Tricoelodus*: M_3 talonid enlarged, with strongly projecting hypoconulid developed as a third lobe and with basin formed between its lingual supporting crest and the entolophid, which is transverse and not oblique as in *Tricoelodus.*

Ameghino described two species of this genus in addition to the genotype; of these; *Proadiantus pungidens* is synonymous with *P. excavatus* and *P. gibbus* is of uncertain validity and affinities but is probably not adianthid. With the removal of the upper dentition described under this generic heading by Patterson, 1940, to *Tricoelodus,* only the lower dentition of *Proadiantus* is known; fortunately, however, the available specimens form a nearly complete series of lower teeth. The known characters of *Proadiantus* ally it closely with *Tricoelodus,* with which it is virtually identical except for size and the minor structural details noted in the diagnosis.

Originally described from the Deseadan (Ameghino, 1897, 1901), Ameghino later reported *Proadiantus* from beds of Colhuehuapian and early Santacrucian age (Colpodonéenne and Notohippidéenne, respectively, of his usage; 1906, pp. 474, 476). The only known adianthid specimen of Colhuehuapian age in the Ameghino collection is the M^3 described originally (Ameghino, 1903–1904) as "*Adiantus*" *patagonicus,* and it is probably this which he later referred to as *Proadiantus,* although no mention of species is given. The reference of *Proadiantus* to the *Notohippus* fauna is uncertain. Ameghino's original *Notohippus* faunal list (1903) includes *Adianthus bucatus,* of which two specimens were known to him. The original specimen, an isolated cheek tooth, was described in 1891 (before Ameghino had differentiated the *Notohippus* fauna) and probably lost soon thereafter. Carlos Ameghino's only collection from the type locality of the Notohippidense, Karaiken, was made in 1889–1890, and it is thus possible that this specimen was among those collected there, although there is no written indication that this is the case. The other specimen referred to *A. bucatus* is the mandible MACN A1812, which bears a label in Ameghino's hand indicating that it had been collected in 1892–1893 at Corriguen Kaik (=Corriguen

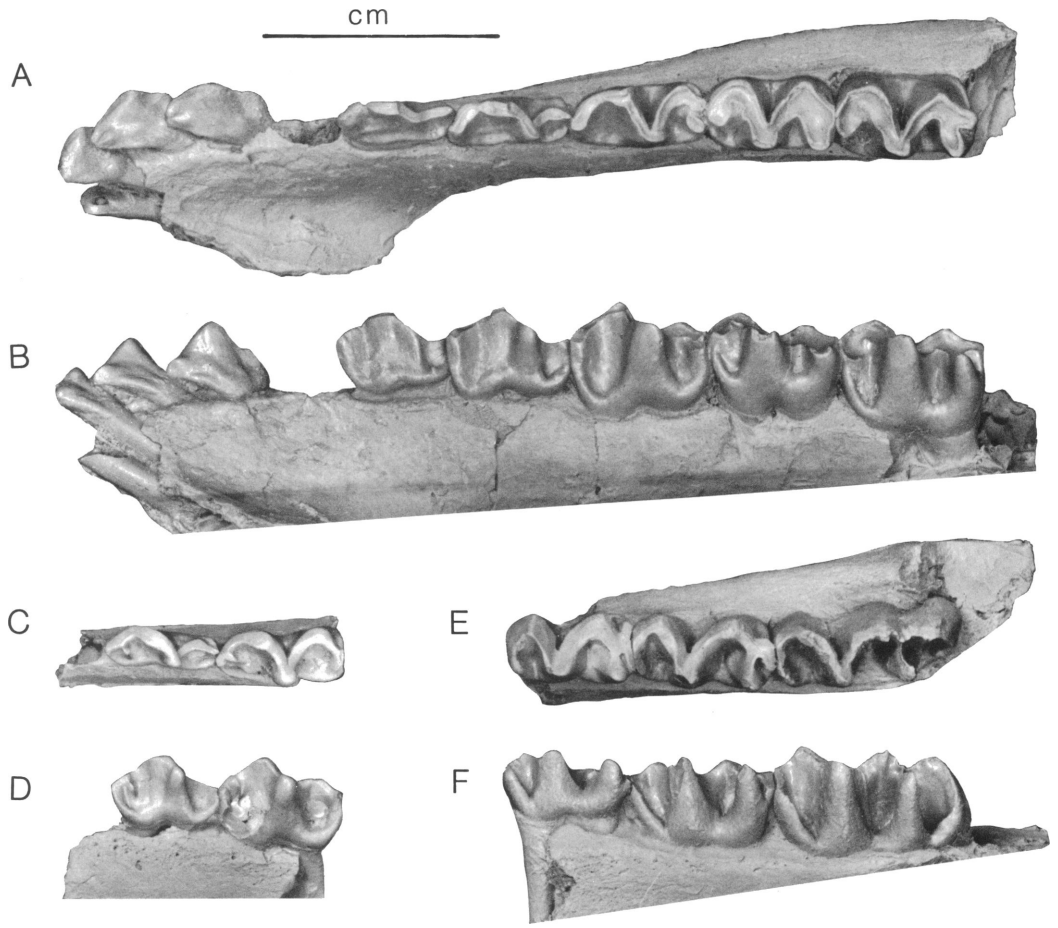

FIG. 3. *Proadiantus excavatus*. A, B, right I_2–C, P_2–M_2 (MACN A52-214). C, D, right P_{3-4_c} (MACN A52-213, type). E, F, right M_{1-3} (MACN A52-215). A, A, E, occlusal view; B, D, F, lingual view. (Photographed from casts; lower portions of mandibular rami are deliberately omitted.)

Aike), a rich and typical Santacrucian coastal locality. Undoubted *Proadiantus* specimens are all in the Ameghino Collection and are all apparently from a single Deseadan locality.

Proadiantus excavatus Ameghino, 1897
Figures 3A–F

Proadiantus excavatus Ameghino, 1897, p. 455.
Proadianthus excavatus Loomis, 1914, p. 51.
Proadiantus pungidens Ameghino, 1901, p. 372; 1906, p. 345.

TYPE: MACN A52-213, fragment of right mandible with P_{3-4}.

LECTOTYPE OF *Proadiantus pungidens*: MACN A52-214, right hemimandible with root of I_1 and with I_2–C and P_2–M_2 complete.

HYPODIGM: The types, as specified above, and MACN A52-217, fragment of right mandible with worn P_4–M_1; MACN A52-215, fragment of right mandible with M_{1-3}.

HORIZON AND LOCALITY: Deseadan, ?Cabeza Blanca,[5] Provincia del Chubut, Argentina.

DIAGNOSIS: Sole known species of the genus.

[5] Several of the specimen labels in Ameghino's hand specify "Río Chico, yac. Pyroth.," which accords with the fossil preservation as that of Cabeza Blanca (Patterson, 1952).

TABLE 2
Measurements (in Millimeters) of Cheek Teeth of *Proadiantus excavatus*[a]

		MACN A52-213	MACN A52-214	MACN A52-215	MACN A52-217
P_2	L	–	4.8	–	–
	W	–	2.0	–	–
P_3	L	4.7	5.1	–	–
	W	1.9	2.3	–	–
P_4	L	5.5	5.6	–	5.6
	W	2.5	2.8	–	2.8
M_1	L	–	5.5	5.5	5.4
	W	–	3.2	3.0	3.3
M_2	L	–	6.0	6.0	–
	W	–	3.4	3.3	–
M_3	L	–	–	8.0	–
	W	–	–	3.1	–

[a] In these and other measured specimens, interstitial wear has in certain cases reduced the length of some teeth (especially M1), so that they are shorter than when newly erupted.

There can be no doubt as to the type of *Proadiantus excavatus,* since Ameghino's original (1897) description and accompanying illustration fit only MACN A52-213. The description of *P. pungidens* (1901) mainly concerns M_3, present only in MACN A52-215, but mentions P_{3-4}, present not in that specimen but in MACN A52-214. It seems very likely that both were before him when he named the species, and the more complete specimen may be taken as lectotype. Ameghino distinguished *P. pungidens* from the genotype, *P. excavatus,* by the shallower mandibular ramus and rudimentary P_3 talonid lobe of the former species, neither of which appear to be appreciable differences.

The wear surface of I_2 is flat and chisel-like, very slightly expanded medially (anteriorly), and a slightly scalloped distal (posterior) edge; these features are progressively enhanced in I_3–C, in which two attritional surfaces are presented (the crown and posterior margin), both obliquely oriented with respect to the direction of orthal jaw movement. I_2–C are thus simpler than but similar to and form a graded series with the following anterior premolars. P_2 has two shearing ridges, of which the anterior is slightly notched and concave lingually. The posterior shearing ridge descends posterolingually to an eminence in the lingual wall of the tooth, a serial analog of the metaconid, and continues posteriorly as a short, nearly straight talonid crest. P_3 has a more distinctly molariform trigonid, with the paraconid and metaconid both differentiated and more lingually placed. The talonid crest is simple, descending labially from the metaconid and continuing posteriad for a short distance. P_4 is larger than P_3 and more completely bicrescentic. As with the molars, the metaconid is represented by a tall, salient column, and a deep labial groove separates trigonid from talonid. The latter is crescentic but terminates in a median position at the posterior margin of the tooth, not extending lingually. On P_4 of MACN A52-214, an obliquely expanded entoconid is developed, a structural variation lacking in MACN A52-213. The trigonid of the molars is more compressed anteroposteriorly than in P_4, so that the trigonid basin is less open lingually. The anterolingual cingular crest, well shown in *Tricoelodus bicuspidatus,* is weak and variably absent. The talonid is fully crescentic and larger than the trigonid. On M_{1-2} the hypoconulid projects slightly and supports weak labial and lingual cingula, the latter variably forming a small and very transient basin, enclosed anteriorly by the entoconid, which attaches to the talonid crescent just anterior to the hypoconulid. As in *Tricoelodus,* the talonid of M_3 is greatly enlarged, with a strongly projecting hypoconulid forming a third lobe. The lingual supporting hypoconulid crest attaches to the base of the entoconid, which is transversely expanded into an entolophid, thus enclosing the third M_3 basin described by Ameghino.

Measurements (in millimeters) are given in table 2.

Proadiantus gibbus Ameghino, 1901, *nomen vanum*

Proadiantus gibbus Ameghino, 1901, p. 372.

TYPE: MACN A52–216, right lateral incisor or canine and, of another individual, portion of a left mandibular symphysis with three tooth sockets.

HYPODIGM: The type only.

HORIZON AND LOCALITY: Deseadan, Pro-

vincia del Chubut (more specific locality data unknown).

DIAGNOSIS: Both specimens are, at present, indeterminate as to genus or family.

Ameghino's description distinguishes this species from *Proadiantus* "*pungidens*" by the greater size, roundness, and robustness of the mandible, and indicates the tooth (which does not correspond to the jaw) to be an upper incisor. Both specimens lack any identifiable adianthid feature, and the status of the species is extremely dubious.

TRICOELODUS AMEGHINO, 1897

Tricoelodus Ameghino, 1897, p. 454; Loomis, 1914, p. 51.
Proadiantus Patterson, 1940, p. 13.

TYPE: *Tricoelodus bicuspidatus* Ameghino, 1897.

DISTRIBUTION: Deseadan, South America.

DIAGNOSIS: Cheek teeth moderately high crowned. Upper molar and premolar ectolophs sinuous, not bowed anteroposteriorly; P^4–M^3 with weak mesostyles. P^4 with the metacone (lacking in P^3) in a triangular arrangement with the protocone and paracone and with five fossettes; molars with six fossettes. M_{1-2} with hypoconulid projecting slightly and with supporting crests on its lingual and labial flanks, the former strong and enclosing a small basin; M_3 with elongate hypoconulid and large auxiliary talonid basin and with entoconid anteriorly placed, partially enclosing the anterior talonid basin lingually and giving the entolophid an oblique rather than transverse orientation.

Ameghino originally (1897, 1898) included *Tricoelodus* in his "Mesorhinidae," in his usage a family of primitive macraucheniids such as *Protheosodon* (now believed to be a didolodontid or proterotheriid) and *Coniopternium,* but later removed it to the Adianthidae (1906, p. 472). This placement was adopted by Loomis (1914), but the genus has in later works been dismissed as inadequately known and probably not pertaining to the family (Simpson and Minoprio, 1949; Simpson, Minoprio, and Patterson, 1962) or ignored entirely (Scott, 1937; Patterson, 1940; Simpson, 1945; Soria, 1981a). It is thus somewhat of an irony that, with the referrals proposed herein, *Tricoelodus* is now the best represented genus in the family. Patterson (1940) referred the upper dentition FMNH P14698 to *Proadiantus* sp. because it differs from both *Proheptaconus* and *Adianthus,* and in the belief that it is similar in size to described species of *Proadiantus* and that this genus is (or was, as of 1940) the only described Deseadan pygmy litoptern. FMNH P14698 does differ from *Proheptaconus* and from the figure given by Ameghino, 1891, of *Adianthus bucatus,* but neither of these suppositions is correct. The upper dentition in question is far too large to correspond to *Proadiantus,* but is of appropriate size for *Tricoelodus bicuspidatus,* known by several specimens from the same locality (Cabeza Blanca). The association of these upper teeth to *Tricoelodus,* as proposed here, is not susceptible to direct proof, but seems very probable on the basis of distribution and relative size; both are surely adianthid and there is no other known Deseadan form to which the upper dentition might pertain. A new species, differing only slightly from the type, *T. bicuspidatus,* in size and several morphological details, is described from the La Salla-Luribay Basin, Bolivia.

Tricoelodus bicuspidatus Ameghino, 1897
Figures 4, 5A–D

Tricoelodus bicuspidatus Ameghino, 1897, p. 454; Loomis, 1914, p. 51.
Proadiantus sp. Patterson, 1940, p. 13.

TYPE: MACN A52-203, fragment of right mandible with P_4–M_2.

HYPODIGM: The type, and MACN A52-615, left mandibular fragment with badly broken M_3; FMNH P14698, associated right P^3–M^2 and left ?C, P^{2-3}, and M^{1-3}, FMNH P14696, associated right M_{2-3}; MLP 61-IV-11-65, associated maxillary fragments with right P^4–M^3 and left P^{2-4} and M^{2-3}.

HORIZON AND LOCALITIES: Deseadan; Cabeza Blanca and El Pajarito, Provincia del Chubut, Argentina.

DIAGNOSIS: The larger and higher crowned of the two species now referred to the genus. Labial attachment of M_3 entolophid somewhat anterior to hypoconulid; accessory upper and lower molar conules lacking.

The type specimen is of uncertain pro-

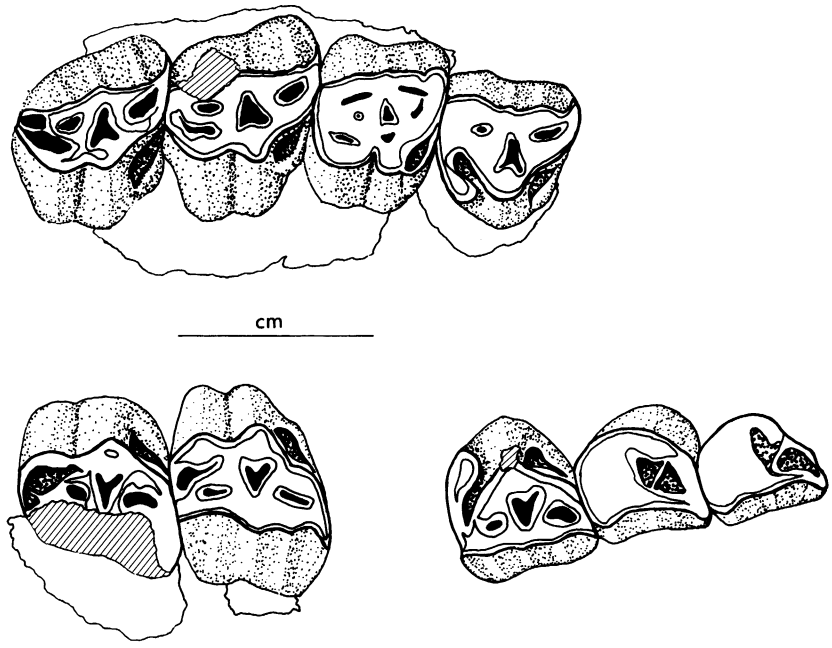

FIG. 4. *Tricoelodus bicuspidatus* (MLP 61-IV-11-65). Right P^4–M^3 and left P^{2-4}, M^{2-3} in occlusal view.

venience, but its preservation indicates that, as with the Field Museum specimens, it probably derived from Cabeza Blanca. As noted by Simpson and Minoprio (1949), Ameghino's description (1897) of this genus and species mentions four lower premolars but that of the specimen indicates only three teeth to be present. These are referred to in the text as P_{2-4} (M_{2-4} of Ameghino's terminology) but as P_3–M_1 ("M_{3-5}") in the accompanying figure; relative wear (greatest on the middle tooth of the series) and comparison with *Proadiantus excavatus* indicate them instead to be P_4–M_2. The puzzlement of students in the past regarding this genus and species may be due partly to the fact that Ameghino's figure, although fairly accurate, is somewhat stylized and confusing. The lower molars of *Tricoelodus* are, in fact, extremely similar to those of the much smaller *Proadiantus,* nearly to the point of generic synonymy.

The lower cheek teeth are moderately high crowned. As in *Proadiantus excavatus,* P_4 (subequal in size with M_1) is fully molariform except that the trigonid crescent is somewhat more open lingually and the hypoconulid is not as projecting or as well defined as in the molars. An anterolingual cingular crest curves posteriorly to partially enclose a pillar which is, topographically at least, the paraconid. The talonid crescent takes origin anteriorly at the metaconid, as in all advanced litopterns (Cifelli, in press), and terminates in a posteromedian position as a slight prominence (hypoconulid), defined, as in the molars, by a small sulcus on the labial side of the tooth. A crest descends anterolingually from the hypoconulid, partially enclosing the talonid basin; no entoconid is present. The trigonid of the molars is more constricted anteroposteriorly, so that the anterolingual cingular crest descends to nearly close off the trigonid basin lingually. The molars increase in size from first to third (as in *Proadiantus*), an unusual feature in litopterns; the hypoconulid is progressively better differentiated and more projecting. The labial hypoconulid sulcus is strongly marked on M_{1-2} and a strong crest extends anterolingually from that cusp to the base of the entoconid. A small hollow is formed between this crest and the entoconid to hypoconulid crest and the lower molars thus bear three basins, hence Ameghino's aptly chosen generic name. This feature is

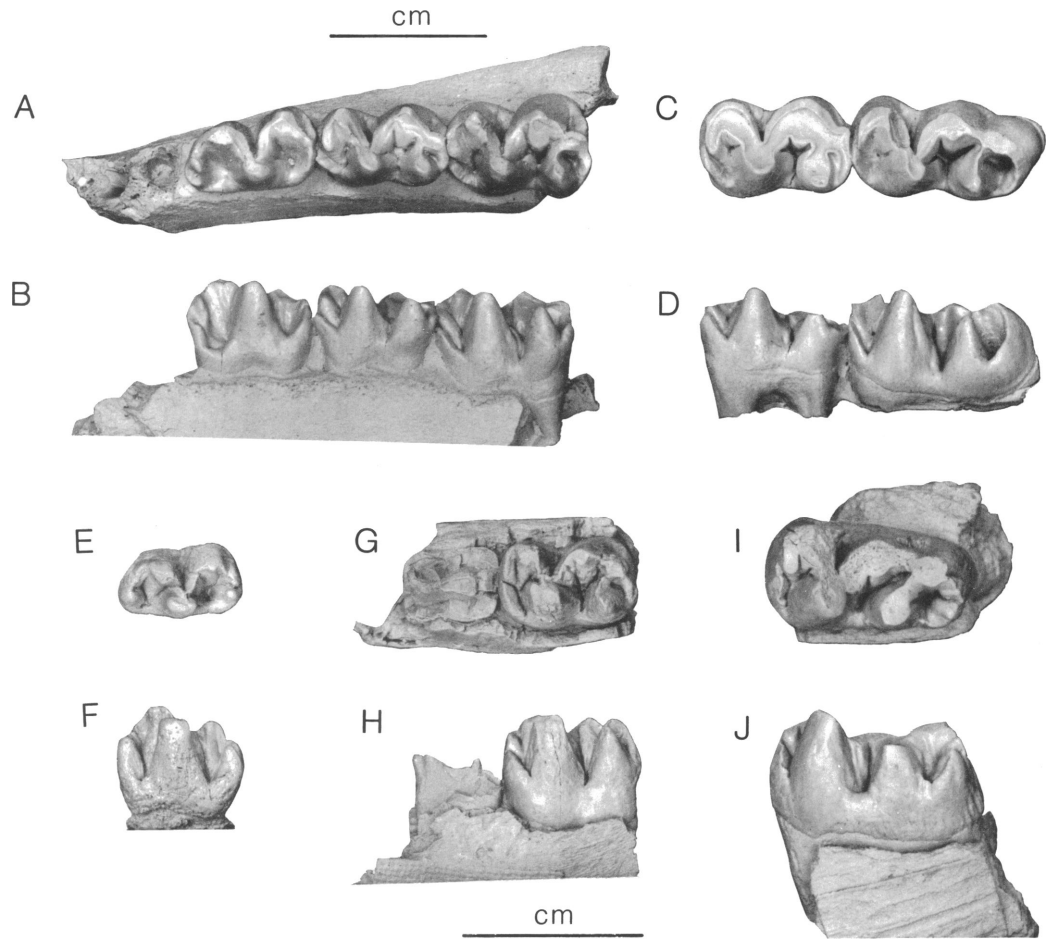

FIG. 5. *Tricoelodus bicuspidatus* (A–D) and *T. boliviensis* (E–J). A, B, right P_4–M_2 (MACN A52-203, type). C, D, right M_{2-3} (FMNH P14696). E, F, left P_4 (PU 23518, type [reversed]). G, H, left M_2 (PU 23518, type [reversed]). I, J, right M_3 (PU 23519). A, C, E, G, I, occlusal view; B, D, F, H, J, lingual view. (Photographed from casts; lower portions of mandibular rami are deliberately omitted.)

most prominent on M_3, in which the hypoconulid is strongly expanded and the labial attachment of the entoconid-hypoconulid crest is shifted somewhat anteriorly, thereby forming an entolophid.

The upper dentition of *Tricoelodus bicuspidatus* was well described by Patterson, 1940, but a new specimen (MLP 61-IV-11-65), much less worn than FMNH P14698, allows confirmation, additions, and emendations to be made. P^{2-3} are very similar, differing only in size. The lingual side of the tooth is broadly curved; the crown bears an anterior fossette and a wide and slightly basined posterior grinding area. The fossette in both P^2 and P^3 is subdivided by an obliquely oriented crest which appears to be a serial analog if not homolog of the crest on P^4 and the molars which separates the "anterolingual" and "median" fossettes; that is, a hypertrophied postprotoconule crista. The ectoloph is marked by a median bulge, the paracone, which is transversely aligned with the protocone; the anterobuccal and posterobuccal angles of the tooth are expanded into parastyle and metastyle, respectively. The metastyle is large and was indicated by Patterson, 1940, to include both metacone and metastyle; there is no sign of this differentiation, however, and a true metacone of this form

and in this position seems highly unlikely. It thus appears that the metacone was absent on teeth anterior to P^4, as in macraucheniids. P^4 is more fully molariform. The paracone and metacone are equally developed and, as in the molars, form an equilaterally triangular arrangement with the protocone. The ectoloph is marked also by small parastylar and metastylar spurs and a faint mesostyle. (Because it was obliterated early in wear, the mesostyle is not seen in Patterson's specimen.) The trigon crests and especially the postprotoconule and premetaconule cristae are hypertrophied, so that fossettes are formed.[6] The pre- and postprotoconule and metaconule cristae isolate fossettes lingual to the paracone and metacone, respectively, and separate them from a median fossette ("median external") which is formed at the buccal base of the protocone. A low protostylar cingulum, just anterior to the protocone, would enclose a small fossette in advanced wear, as in the molars. Similarly, the postcingulum encloses a fossette and terminates lingually in a swelling which is, descriptively, a rudimentary hypocone, a feature lacking in macraucheniids as Patterson (1940) observed. The molars are subequal or increase slightly in size from first to third. The ectoloph is marked by strong paracone and metacone ridges and small parastylar, metastylar, and mesostylar folds, the last faint and disappearing early in wear, as in P^4. The hypocone is large, fully incorporated into the crown surface on all three molars, and well separated from the protocone by a deep lingual notch extending to the base of the crown. The hypocone does not join the protocone directly as in proterotheres, but is instead joined to the protocone-metacone crest, more closely similar to macraucheniids but not so labial as in the latter. Together with the posthypocone cingulum, which sweeps posteriorly and labially, this forms a large, crescentic posterior fossette ("posterointernal"). As best seen in the least worn complete tooth available, right M^3 of MLP 61-IV-11-65, this fossette is subdivided by a transverse ridge connecting the protocone-metacone crest with the posthypocone cingulum, so that two fossettes are formed, the labial being very transient.[7] The upper molar crowns of *Tricoelodus bicuspidatus* thus actually have six fossettes, not five, although not all are present and functional at a given wear stage.

Measurements (in millimeters) are given in table 3.

Tricoelodus boliviensis, new species

Figures 5E–J

TYPE: PU 23518, fragment of left lower jaw with roots of dM_4, unerupted P_4 in the crypt, roots of M_1, and complete M_2.

HYPODIGM: The type, and PU 23520, fragment of left lower jaw with M_3; PU 23522, fragment of left lower jaw with M_2 and with M_3 in eruption; PU 23521, fragment of right lower jaw with badly broken P_{3-4}; PU 23519, right M_3; MNHM SAL 263 (cast, MACN 18704), worn right $?dM_{3\ or\ 4}$; MNHN SAL 268 (cast, MACN 18705), worn left $M^{?3}$; MNHN SAL 264 (cast, MACN 18707), right M_{2-3}; MNHN SAL 265 (cast, MACN 18700), left M_3; MNHN SAL 256 (cast, MACN 18702), left $M_{1\ or\ 2}$; MNHN SAL 257 (cast, MACN 18701), left $M_{1\ or\ 2}$; MNHN SAL 251 (cast, MACN 18703), left $M^{1\ or\ 2}$; MNHN SAL 248 (cast, MACN 18706), fragment of left mandible with M_2.

HORIZON AND LOCALITY: Deseadan; La Salla-Luribay Basin, Provincia Loaza, Departamento La Paz, Bolivia.

DIAGNOSIS: The smaller of the two species now assigned to this genus. Labial hypocon-

[6] The molar fossettes of adianthids are generally referred to in accordance with topographic position in the tooth, e.g., "anteroexternal," "posteroexternal," etc. Such terminology can be confusing or subject to misunderstanding because of the presence of additional, as yet unnamed fossettes (there are two "posteroexternal" fossettes in *Tricoelodus*) and because homology remains to be established when comparison is made to other groups specifically, the Macraucheniidae. While certain of these terms are employed here, reference is made also to the homologies of the crests which border the fossettes rather than strictly to the holes themselves.

[7] Patterson, 1940, p. 16, refers to this as the posteroexternal fossette, which is inconsistent with his own and general usage. As shown by his figure 7, the posteroexternal fossette (present through much more advanced wear stages) is actually that formed by the metacone and pre- and postmetaconule cristae, the labial division of the posterior fossette having already been obliterated.

TABLE 3
Measurements (in Millimeters) of Cheek Teeth of *Tricoelodus* Species[a]

	P^2		P^3		P^4			
	L	W	L	W	L	W		
Tricoelodus bicuspidatus								
FMNH P14698	6.1	5.8	6.5	6.5	7.3	7.7		
MLP 61-IV-11-65	6.2	5.1	6.6	6.6	6.9	8.0		
	M^1		M^2		M^3			
	L	W	L	W	L	W		
FMNH P14698	6.6	8.7	8.6	9.1	9.3	—		
MLP 61-IV-11-65	7.1	8.9	8.7	9.6	8.7	9.7		
	P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W
MACN A52-203	7.6	5.0	7.9	5.1	8.9	6.3	—	—
FMNH P14696	—	—	—	—	8.5	5.7	10.6	5.5
Tricoelodus boliviensis								
PU 23518	7.1	4.0	—	—	8.1	5.2		
PU 23520	—	—	—	—	—	—	9.8	5.3
PU 23519	—	—	—	—	—	—	9.6	5.3
PU 23522	—	—	—	—	7.7	4.9		
	Isolated Teeth							
	L	W						
MACN 18702	8.0	4.7						
MACN 18701	7.3	4.9						
MACN 18703	7.3	8.3						
MACN 18706	7.8	4.9						

[a] Where contralateral measurements of the same specimen differ, the figure given is an average of the two.

ulid cleft lacking on P_4 and probably M_1, faint on M_2; lower molar anterolingual cingular crest weak lingually and lacking anteriorly. Upper molars with small accessory cuspules at the anterolingual base of the hypocone, overlapping the protocone-hypocone sulcus, and at the base of the ectoloph, between the paracone and metacone folds.

Etymology: Alluding to the known geographic range of the species.

The principle characters of *Tricoelodus boliviensis* are given in the diagnosis; the species is otherwise so similar in known morphology to *T. bicuspidatus* that complete description is unnecessary. Hoffstetter (1968, 1976) listed *Proadiantus* sp. as a member of the La Salla fauna; it is uncertain as to whether he was referring to this species or the smaller one described below, neither of which pertains to that genus.

Measurements (in millimeters) are given in Table 3.

THADANIUS, NEW GENUS

Type: *Thadanius hoffstetteri*, new species.

Distribution: Deseadan, Bolivia.

Diagnosis: Small, moderately high crowned adianthid. Anterior lower molar cingula lacking, lingual portion weak; hypoconulid joined to its apex with hypoconulid but not expanded and forming a third lobe on M_3 as in *Tricoelodus* and *Proadiantus*. Entoconid not joining apex of hypoconulid but instead connected to hypoconulid-entoconid crest, so that a rudimentary entolophid is variably present, most notably on M_3; no third lower molar basin is formed.

Etymology: Anagram of *Adianthus*, the poorly known but type genus of the family.

This genus is most comparable in size to *Proadiantus*, but the features cited above distinguish it sharply from that genus and from *Tricoelodus*; in known morphology, however, *Thadanius* presents a suitable ancestral

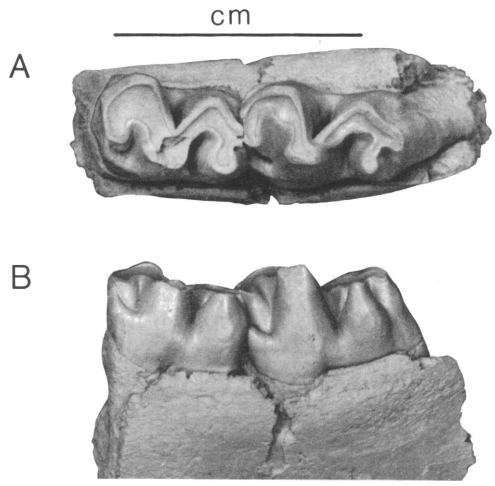

FIG. 6. *Thadanius hoffstetteri* (PU 23514, type). Right M_{2-3} in (A) occlusal and (B) lingual views. (Photographed from a cast; lower portion of mandibular ramus is deliberately omitted.)

morphotype for both these forms, and is in turn more advanced than *Proectocion* and differently specialized from *Adiantoides* or *Adianthus*.

Thadanius hoffstetteri, new species
Figures 6A, B

TYPE: PU 23514, fragment of right mandible with M_{2-3}.

HYPODIGM: The type, and PU 23517, isolated left M_3; PU 23515, fragment of right lower jaw with M_2; PU 23516, fragment of left lower jaw with broken M_1 and with M_2 complete; MNHN SAL 261 (cast, MACN 18710), worn left M_{2-3}; MNHN SAL 260 (cast, MACN 18711), broken right M_2; MNHN SAL 246 (cast, MACN 18708), fragment of left mandible with M_{2-3}; MNHN SAL 247 (cast, MACN 18709), fragment of right mandible with broken M_2 and complete M_3.

HORIZON AND LOCALITY: Deseadan; La Salla-Luribay Basin, Provincia Loaza, Departamento La Paz, Bolivia.

DIAGNOSIS: Sole known species of the genus.

ETYMOLOGY: For Professor Robert Hoffstetter, in recognition of his contributions to knowledge of fossil vertebrates from the Andean countries of South America.

TABLE 4
Measurements (in Millimeters) of Cheek Teeth of *Thadanius hoffstetteri*

	M_2		M_3	
	L	W	L	W
PU 23514	5.7	3.8	7.2	3.7
PU 23517	—	—	7.1	4.1
PU 23515	5.9	4.0	—	—
PU 23516	6.4	3.6	—	—
MACN 18708	5.0	3.6	7.5	3.5
MACN 18709	—	—	6.9	3.7

The upper and anterior lower cheek teeth of this species are not known, but the lower molars indicate it to be distinct from all other described adianthid genera. The paralophid is strongly curved and flanked lingually at its base by a weak cingular crest which, as in *Tricoelodus*, extends posteroinferiorly to partially close the trigonid basin. The metaconid is columnar, anteroposteriorly developed, and slightly bifid in unworn teeth, indicating partial separation of the attachment of trigonid and talonid crescents. The hypoconulid and hypoconid are distinct in the earliest wear stages, but are united nearly to their apices and soon become joined and indistinct. The hypoconulid projects slightly from the posterior margin of M_{1-2} and is indicated by a faint groove on the labial wall of the tooth. A deeper lingual furrow more clearly separates the hypoconulid from the entoconid, with which it is nearly aligned transversely and attached by a crest to its anterior margin, somewhat below the apex of that cusp. The talonid of M_3 is more elongate anteroposteriorly and the entoconid placed more anteriorly with respect to the hypoconulid, so that the groove between the two cusps is more marked; the entoconid is developed transversely into a weak and variable entolophid.

Measurements (in millimeters) are given in table 4.

SUBFAMILY INDALECIINAE BOND AND VUCETICH, 1982

Indaleciinae Bond and Vucetich (in press).

TYPE: *Indalecia* Bond and Vucetich, 1982.

RANGE: Casamayoran to Divisaderan, Argentina.

INCLUDED GENERA: The type, and *Adiantoides* Simpson and Minoprio, 1949.

DIAGNOSIS: Incisors, canines, and P1 small, subequal, and simple; cheek teeth brachyodont. P^{2-4} subtriangular to subquadrangular and forming a progressively molarized series; metacone and hypocone lacking and metastyle weak but parastyle salient. Upper molars with strong parastyle and slender paracone and metacone folds; mesostyle lacking. Hypocone, lacking on M^3, connected to metaconule by a transverse crest. Protocone to metacone crest lacking; central fossettes open lingually. Entolophid lacking on the lower molars; entoconid connected to hypoconulid by a continuous lingual extension of the talonid crescent.

This subfamily is based essentially on the newly described *Indalecia grandensis,* known by unusually good materials from the ?early Eocene of northwestern Argentina. Bond and Vucetich (in press) demonstrated that *Indalecia* is closely related to *Adiantoides* Simpson and Minoprio, 1949 (from the ?late Eocene Divisadero Largo Formation) and that together these genera represent a distinct, early radiation of ?Adianthidae distantly related to known Deseadan or later forms.

In a number of features, such as the small, simple anterior dentition, brachyodont cheek teeth, and lack of an upper molar mesostyle, M^3 hypocone, posterior upper premolar metacone, and lower molar entolophid, the Indaleciinae are undoubtedly primitive with respect to the Adianthinae. However, the precocious molarization of the anterior premolars, strong upper premolar-molar parastyle, upper molar crown pattern (loss of connection between protocone and metacone, transverse crest connecting metaconule and metacone) and fully crescentic lower molar talonid loph, are specializations which differ strikingly from those of other members of the family. This, together with the plesiomorphic features noted above, casts some uncertainty as to the familial and even subordinal placement of the Indaleciinae. Nonetheless, the characteristic presence of fossettes formed by hypertrophied conule cristae in the posterior upper cheek teeth is a diagnostic specialization of the Adianthidae alone among South American mammals. The structural "hiatus" between the two included subfamilies is great but not appreciably greater than those of most other South American ungulate groups including early as well as post-Eocene taxa.

The uniting of the lower molar talonid cusps and the well-developed parastylar prominence of the upper molars in the Indaleciinae may be features derived in common with *Proheptaconus* and/or *Adianthus,* as those genera are here understood, but the cheek teeth are otherwise very differently specialized and the Eocene forms lack several advanced characters shared by these genera with Oligocene Adianthinae. The Indaleciinae also bear certain resemblances (strong upper molar parastyle, bicrescentic lower molars) to a new mammal from the Río Loro Formation (?middle or late Paleocene), Provincia de Tucumán, briefly described by Soria (1981b). It differs, nonetheless, in other features of the upper molars and the upper and lower premolars. Detailed comparisons are postponed, pending completion of work in progress by Miguel F. Soria.

INDALECIA BOND AND VUCETICH, 1982

Indalecia Bond and Vucetich (in press).

TYPE: *Indalecia grandensis* Bond and Vucetich, 1982.

DISTRIBUTION: Casamayoran, northwestern Argentina.

DIAGNOSIS (after Bond and Vucetich, in press): Diastemata lacking between I3–C1 and C1–P1. Upper premolars more ovate and M^{1-2} broader, more quadrangular than in *Adiantoides*; M^3 triangular. Lower premolars more molarized than in *Adiantoides,* with broader, longer talonids and fuller development of the talonid crescents; metaconid present on P_2. Lower molars with paraconid placed more lingually than in *Adiantoides* and connected to metaconid by a low crest. Lower molar talonids relatively broader; hypoconulid and entoconid better differentiated, at least on M_2; M_3 talonid relatively longer than in *Adiantoides.*

Indalecia grandensis Bond and Vucetich, 1982

Figure 7

Indalecia grandensis Bond and Vucetich (in press).

TYPE: PVL 4186, crushed but nearly complete skull, with roots of I^{1-2} and right and

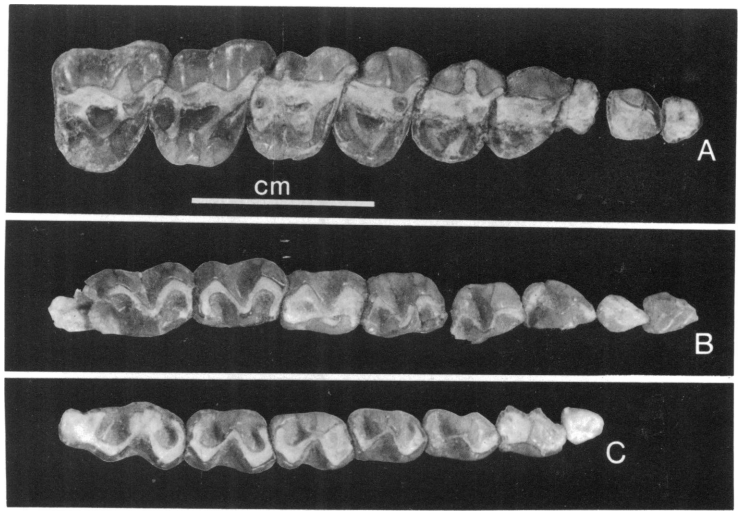

FIG. 7. *Indalecia grandensis* (PVL 4186, type). Right upper (A) and lower (B, C) dentitions. (Photograph by M. Bond and M. G. Vucetich.)

left I^3–M^3 complete; associated mandible with complete right C_1–M_3 and left I_3–M_3.

HYPODIGM: The type, and PVL 6S-12, fragment of right lower jaw with M_3 complete.

HORIZON AND LOCALITY: Casamayoran; beneath Faja Verde Inferior of the Lumbrera Formation, Estancia Pampa Grande, Provincia de Salta, Argentina.

DIAGNOSIS: Sole known species of the genus.

A Casamayoran age for *Indalecia grandensis* is indicated by its associated mammal fauna, which is most comparable to those of Casamayoran localities in Patagonia (Pascual, Bond, and Vucetich, 1981). The principal features of this species are given in the generic diagnosis; full description and measurements are given by Bond and Vucetich (in press), and repetition here is unnecessary.

ADIANTOIDES SIMPSON AND MINOPRIO, 1949

Adiantoides Simpson, and Minoprio, 1949, p. 6; Simpson, Minoprio, and Patterson, 1962, p. 246.

TYPE: *Adiantoides leali.*

DISTRIBUTION: Casamayoran to Divisaderan, Argentina.

DIAGNOSIS: Adianthid generally similar in dental morphology to *Indalecia,* but slight diastemata separate I3–P1, and the upper and lower premolars are less molarized. P^3 paracone fold not strongly developed and upper molars more transverse than in that genus; P_2 metaconid lacking, P_{3-4} talonids short. Paralophid of lower molars terminating in a median position; lower molar talonids transversely narrow, with cusps almost fully incorporated into the talonid loph, M_3 talonid relatively short.

The type species, *Adiantoides leali,* from the Divisadero Largo Formation near Mendoza, Argentina, has been fully described by Simpson and Minoprio, 1949, and Simpson, Minoprio, and Patterson, 1962, and repetition here is unnecessary. A new species from the Casamayoran is herein described on the basis of a lower jaw fragment. Simpson and Minoprio (1949) found *Adiantoides* to compare most closely with *Adianthus,* mainly in features of the upper dentition (poorly known in *Adiantoides*). With a revised concept of *Adianthus* (that adopted in large part here), Simpson, Minoprio, and Patterson (1962) later specified that resemblance of *Adiantoides* is to *A. bucatus* and not to "*A.*" *patagonicus,* a synonym of *Proheptaconus trelewense.* As Simpson, Minoprio, and Patterson pointed out, however, the original type upper molar of *Adianthus bucatus* is irrelevant to the entire group of ungulates under consideration, so that resemblance between

it and *Adiantoides* may be disregarded; resemblances in the lower molars are probably convergent, as detailed above.

Adiantoides leali Simpson and Minoprio, 1949

Adiantoides leali Simpson and Minoprio, 1949, p. 6; Simpson, Minoprio, and Patterson, 1962, p. 246.

TYPE: MHNM 3004 P.V., skull, lacking the occipital region, and associated jaws.

HYPODIGM: The type only.

HORIZON AND LOCALITY: Divisaderan (Pascual et al., 1965); Divisadero Largo Formation at its type locality, 8 km. W of Mendoza, Argentina.

DIAGNOSIS: The smaller of the two species currently assigned to this genus. M_2 entoconid indistinct from talonid crescent.

Measurements (in millimeters) and figures are given by Simpson and Minoprio, 1949.

Adiantoides magnus, new species

Figures 8A, B

TYPE: AMNH 28888, fragment of left mandible with M_{2-3}.

HYPODIGM: The type only.

HORIZON AND LOCALITY: Casamayoran; Cañadón Vaca, Provincia del Chubut, Argentina. Collected by the Scarritt Expeditions to Patagonia, 1930–1931.

DIAGNOSIS: The larger of the two species now referred to the genus; entoconid of M_2 distinct from talonid crescent.

ETYMOLOGY: Alluding to its large size.

The structure of the lower molars, with the trigonid notably wider than the talonid and with the recurved pattern of the talonid crescent of M_3, allies this species particularly with *Adiantoides leali* and with no other known form. Detailed comparison with the type species is not possible with the materials at hand, and it is conceivable that *A. magnus* might warrant generic status when better known.

The presence of the closest relative of *Adiantoides leali* in the Casamayoran heightens the primitive aspect of the Divisaderan fauna. Bond and Vucetich (1982) discussed the faunal relationships of the Divisadero Largo species and concluded that overall resemblance is closer to faunas from northwestern Argentina (Lumbrera and Mealla formations) than to those of the Patagonian Eocene and Oligocene. The possibility that *Acamana* (Divisadero Largo Formation) is a henricosborniid closely related to *Simpsonotus* (Mealla Formation) supports this hypothesis (Pascual, Vucetich, and Fernandez, 1978). Nonetheless, a number of contradictions are evident, and these would seem to preclude defining early Tertiary faunal provinces, at least at the present state of knowledge. Trachytheriinae, Hegetotheriinae, and the "*Victorlemoinea* group" (Soria, 1980) are common to Patagonian and the Divisadero Largo faunas; ?*Albertogaudrya carahuaensis* (Carbajal et al., 1977) of the Lumbrera Formation appears to be most closely related to *A. unica* from the Casamayoran of Patagonia; similar primitive astrapotheres are not known from the Divisadero Largo. ?Oldfieldthomasiids of the "*Colbertia* group" (Bond, 1981) are common to the Divisadero Largo and northwestern faunas, but *Maxschlosseria* of Patagonia is surely closely allied.

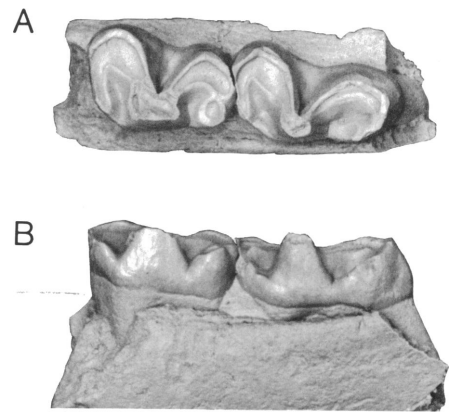

FIG. 8. *Adiantoides magnus* (AMNH 28888, type [reversed]). Left M_{2-3}. (Photographed from a cast; lower portion of mandibular ramus deliberately omitted.)

The teeth of AMNH 28888 are worn but the paralophid would have terminated in a median position, not extending completely to the lingual side. The trigonid is transversely expanded with respect to the talonid; the metaconid is easily the highest cusp of the

TABLE 5
Measurements (in Millimeters) of Cheek Teeth of *Adiantoides magnus*

M_2		M_3	
L	W	L	W
8.3	5.8	9.8	5.3

tooth. On M_2, the entoconid is seen as a separate cusp, fusing with the talonid crescent only late in wear; it is barely or not distinct on M_3 and extends anteriorly as a crest partially closing the talonid basin.

Measurements (in millimeters) are given in table 5.

DISCUSSION

As the name implies, Ameghino (e.g., 1904) considered *Proectocion* as ancestral to *Ectocion,* a North American phenacodontid; he placed both in the "Hyracotheriidae." Simpson (1948) referred *Proectocion* to the Didolodontidae, making detailed comparisons with *Didolodus. Oxybunotherium* was considered by Pascual (1965) to be an advanced condylarthran probably ancestral to the Mustersan *Polymorphis* group, generally believed to be primitive proterotheres. As argued elsewhere (Cifelli, in press), *Oxybunotherium* Pascual, 1965 is probably based on lower teeth of *Proectocion* Ameghino, 1904 and is therefore a junior synonym of that genus. The type specimen of *Oxybunotherium praecursor* was collected in an upper Casamayoran bed at Laguna de la Bombilla, central Chubut, but a referred specimen (AMNH 28769) is known from a horizon of similar age at the Gran Barranca, southern Chubut, where Carlos Ameghino collected the two known specimens of *Proectocion.* There are no other known forms to which teeth of *Proectocion* or *Oxybunotherium* might pertain, and they are of appropriate size, morphology, geographic, and probably temporal distribution for each other. No additional material has been collected, and since further evaluation of species may not be made at present, *Proectocion* has been omitted from the systematics section of the present paper.

The structure of P^4 in *Proectocion* is completely unlike that of known didolodonts, and allies the genus with advanced litopterns, or lopholipternans (Cifelli, in press). The paracone and metacone are widely spaced, and a small mesostyle is present. M^3 bears a hypocone, different in structure from that of didolodontids, which is found in macraucheniids and adianthids but not proterotheriids. The upper molar crown pattern is also unlike that of proterotheres, and more closely resembles macraucheniods, in which the hypocone attaches anteriorly to the protocone-metacone crest instead of joining the protocone directly at its apex. As Pascual (1965) noted, the attachment of the lower molar cristid obliqua to the metacone is an advanced litoptern character not found in didolodonts. The truncated, ventrally directed paralophid and the columnar aspect of the lower molar cusps, particularly the metaconid, are features characteristic of *Polymorphis* (which we consider to be related to macraucheniids, as did Ameghino, 1904) and other primitive macraucheniods. Fossettes are not developed in the upper cheek teeth of *Proectocion,* but the interconnecting cusp crests, particularly the conule cristae, are very strongly developed. The talonid of M_3 is elongate, with a salient, projecting hypoconulid. These features are suggestive of the Adianthidae.

Adianthids, together with macraucheniids and proterotheriids, form a cohesive and probably monophyletic group of dentally advanced litopterns; among these, the Adianthidae and Macraucheniidae appear to be most closely related, as Ameghino clearly recognized (Cifelli, in press). On the other hand, Quiroga (1981) has shown that the endocast of *Proheptaconus* is similar to that of proterotheres, not macraucheniids; since character polarities were not defined, however, it is difficult to say whether these resemblances are primitive or derived features.

The relative primitiveness of the Indaleciinae introduces several contradictions to this arrangement. Specifically, *Indalecia* lacks the hypocone of M^3 seen in *Proectocion,* Macraucheniidae, and Adianthinae; even basic lopholipternan features such as a P^4 metacone and a P^4–M^3 mesostyle are absent. The origin of the Indaleciinae, indeed of the family Adianthidae (if the indaleciines pertain to it), consequently is paradoxical and obscure. Be-

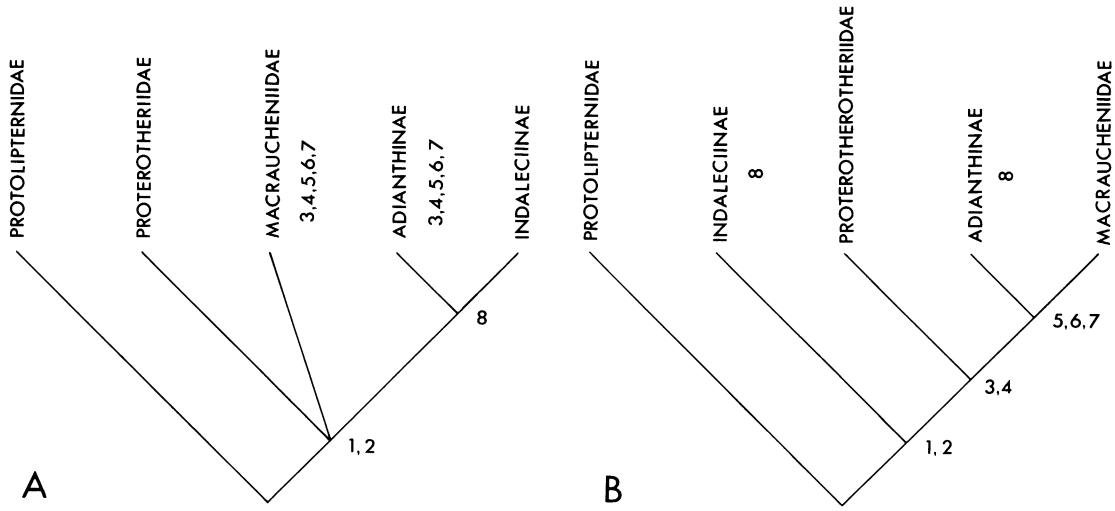

FIG. 9. Alternative hypotheses of indaleciine-adianthine relationships with respect to other Litopterna. Numbers refer to derived character states: 1, cristid obliqua of lower molars attaches anteriorly at base of metaconid; 2, molars lophate (upper molars with an ectoloph, lowers becoming bicrescentic); 3, mesostyle present on P^4–M^3; 4, P^4 with strong metacone, in a triangular arrangement with paracone and protocone; 5, hypocone present on M^3; 6, lower molar metaconid columnar; 7, hypocone of upper molars crescentic, with prehypocone crista connecting to protocone-metacone crest; 8, three primary upper molar fossettes present, formed by hypertrophied conule cristae. Numbers beneath family-group names refer to features developed convergently or loss (i.e., reversal) of these characters in the respective sister taxon. A, the Indaleciinae and Adianthinae as an exclusive, monophyletic unit (characters 3 and 4 are present also in the Proterotheriidae, not under consideration here); B, separate origins for the two subfamilies.

cause of the combination of indaleciine plesiomorphies and unique derived features with respect to adianthines and advanced litopterns in general, one of us (R.L.C.) would tentatively advocate their removal from the Adianthidae. The lower dentition of *Indalecia* greatly resembles that of an aberrant ungulate from the Casamayoran of Patagonia, *Sparnotheriodon* (Soria, 1980b), particularly in the precocious molarization of the anterior premolars. *Indalecia* lacks the strongly differentiated canine of *Sparnotheriodon,* however, and the affinities of that mammal are uncertain in the extreme. Possibly the Indaleciinae represents a lineage derived from a primitive didolodont-like form, which independently acquired certain advanced litoptern characters and some special similarities to adianthines. Evidence for this is mainly negative, however, and it seems best to retain the Indaleciinae in the Adianthidae for the present, pending further discoveries (particularly the tarsus; see Cifelli, 1983). These two alternative hypotheses for indaleciine origins and their implications are given in figure 9.

An hypothesis of relationships among the Adianthidae is given in figure 10. Because of their almost fully bunodont cheek teeth, lack of fossettes enclosed by the posthypocone and protostylar cingula on the upper molars, feeble development of the hypocone cingulum on P^4, and other features noted above, *Indalecia* and *Adiantoides* would appear to be the most primitive known members of the family. Simpson and Minoprio (1949) postulated *Adiantoides* to be related to *Adianthus* (including the Colhuehuapian species now placed in *Proheptaconus*), forming a subgroup of the family distinct from *Proadiantus* and *Proheptaconus*; later, with the realization that the Colhuehuapian forms are conspecific and probably a genus distinct from *Adianthus,* Simpson, Minoprio, and Patterson (1962) implied this exclusive relationship to include only *Adiantoides* and the type (Santacrucian)

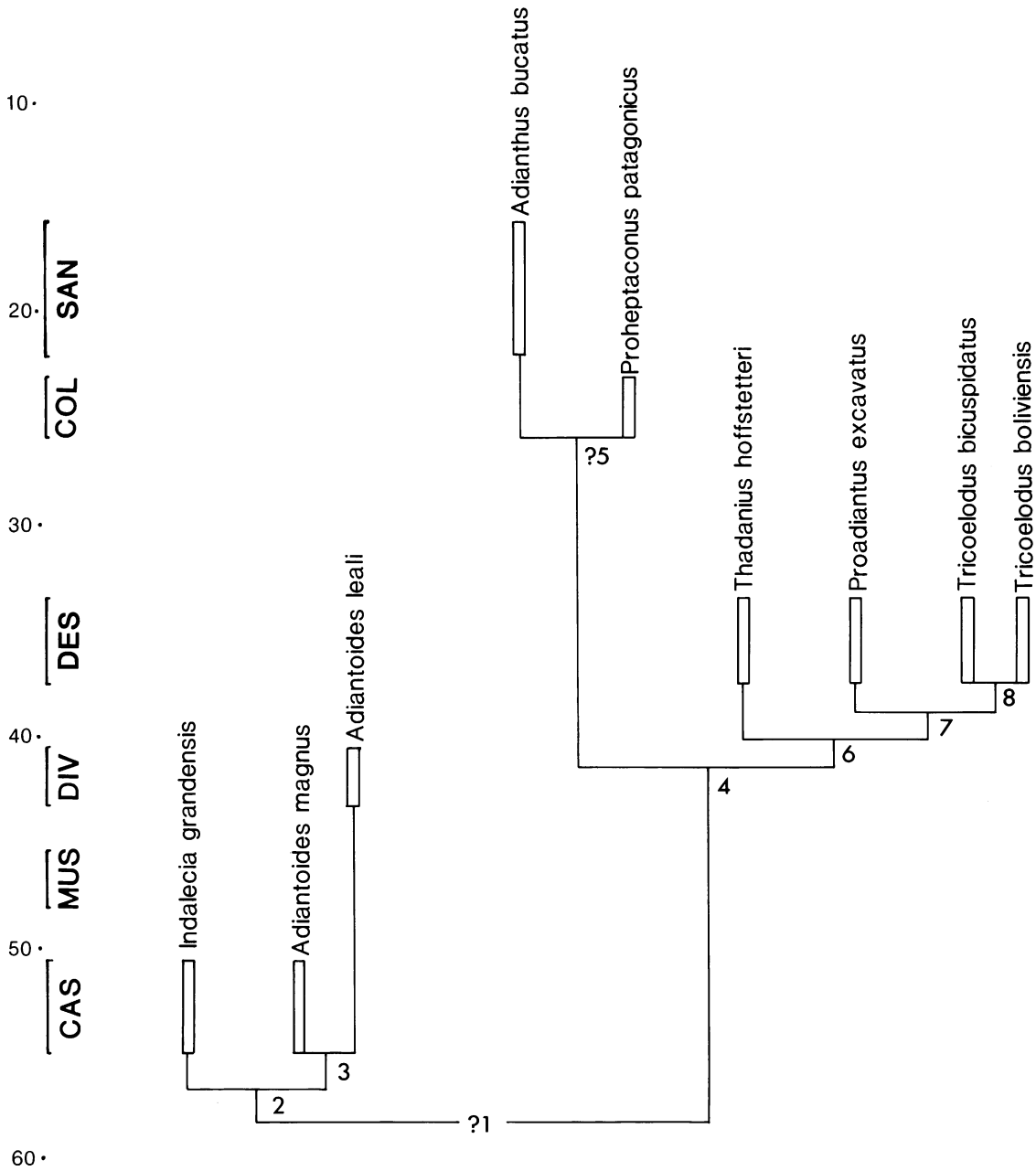

FIG. 10. Biostratigraphic distribution and hypothesized relationships of known species of Adianthidae. Vertical scale, left, adapted from Marshall et al. (1977), represents millions of years before present. *Abbreviations:* CAS, Casamayoran; MUS, Mustersan; DIV, Divisaderan; DES, Deseadan; COL, Colhuehuapian; SAN, Santacrucian. Derived characters at nodes (see text for detailed discussion): ?1; hypertrophied conule cristae form fossettes on upper molars and posterior premolars (see text and fig. 9 for discussion of alternative hypotheses of adianthine-indaleciine relationships with respect to other Litopterna). 2; strong upper molar-posterior premolar parastyle (also seen in *Proheptaconus*), loss of connection between protocone and metacone on upper molars, with metaconule developed into a transverse loph; lower molar talonid loph fully crescentic. 3; paralophid of lower molars terminating in a

species of *Adianthus, A. bucatus.* The basis for this hypothesis evidently lay in large part in comparison of the upper molars, poorly known in *Adiantoides* and, with the removal of the type specimen from the concept of *Adianthus* as detailed above, not now known for the Santacrucian form. The completion of the talonid crescent on the lower molars, with incorporation of the entoconid, is a specialization common to the two genera, to *Indalecia,* and perhaps also to *Proheptaconus* (if the mandible described above as Adianthinae, indet., pertains to that genus); *Proheptaconus* also resembles *Adiantoides* and *Indalecia* in the projecting parastyle of the upper molars. In view of the several derived features shared by these later adianthids with *Tricoelodus* and allies, however, the most plausible hypothesis at present seems to be that *Adiantoides* and *Indalecia* represent a lineage which differentiated early, acquiring some autapomorphous features and some convergent on later forms; all other adianthids being a monophyletic group. This is supported by the fact that the Indaleciinae are uniquely derived among the Litopterna in certain respects, such as the development of a metaloph-like crest in the upper molars vaguely reminiscent of the pattern seen in notoungulates.

Among the Adianthinae, *Tricoelodus, Proadiantus,* and perhaps the poorly known new genus *Thadanius* (all Deseadan in age) form a natural cluster. Upper molars are represented only in *Tricoelodus,* but the lower molars are basically similar in that the entoconid achieves a more anterior attachment to the labial margin of the talonid, so that a deep sulcus separates it from the hypoconulid and it becomes an entolophid. This development is only partially shown in *Thadanius,* the most primitive member of the group; in *Proadiantus* and *Tricoelodus* a third basin is formed lingually on the talonid of M_3, between the lingual supporting flank of the hypoconulid and the entolophid. Basins are also present, in incipient form, on M_{1-2} of these genera. *Proheptaconus* is more advanced than *Tricoelodus* in several features of the upper molars, such as increased crown height and the bowed ectoloph, with mesostyle lacking and parastyle projecting. If the mandible from the early Santacrucian (*Notohippus* fauna), described above, pertains to *Proheptaconus,* then that genus would appear to be specially allied to *Adianthus* rather than to the *Tricoelodus* group. In contrast to the condition in *Thadanius, Proadiantus,* and *Tricoelodus,* the entoconid is shifted posteriorly and its connection to the hypoconulid strengthened, so that it is indistinct and completely merged into the talonid crescent.

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median position; lower molar talonid narrowed with respect to the trigonid, M_3 talonid relatively short anteroposteriorly. 4; lower incisors and canines with a secondary, posterior cutting surface, forming a graded series with cheek teeth; cheek teeth moderately high crowned; lower molars primitively with distinct talonid cusps and/or an entolophid, M_3 hypoconulid projecting as a third lobe; P^4 with five well-developed fossettes, upper molars with six fossettes (additional characters, numbers 3–7 of fig. D, pertain to this node also if the Adianthinae and Indaleciinae share an exclusive common ancestor). ?5 (assuming that mandible MLP 68-I-17-192 pertains to *Proheptaconus*); cheek teeth high crowned; lower molars completely bicrescentic, with hypoconulid of M_{1-2} merged into talonid crescent. 6; entoconid of lower molars achieves an anterior attachment to labial margin of talonid. 7; lower molar entolophid well developed, with accessory talonid basins small on M_{1-2} and large on M_3. 8; increased size; M_{1-2} accessory talonid basin larger and better defined, M_3 entolophid oblique.

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