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A new Adianthid Litoptern (Mammalia) from the Miocene of Chile

Un nuevo Litopterno de la Familia Adianthidae (Mammalia) del Mioceno de Chile

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ABSTRACT

A new species of *Adianthus* is described from the Río Cisnes (type locality of the Friasian age), Miocene of Chile. The species is represented by unusually complete remains, including the first postcranial elements known for a member of the family Adianthidae. In its skeletal anatomy, *Adianthus godoyi,* new species generally resembles lightly-built Santacrucian proterotheriids. The new species is unique among litopterns in having the proximal tibia and fibula solidly fused. Like Santacrucian proterotheres, *Adianthus godoyi* was probably cursorially adapted; the narrowness of the anterior dental arcade suggest that it was a selective-feeding herbivore, and perhaps consumed mixed vegetation in an open habitat. *Adianthus godoyi* appears to be closely related and to an as yet unidentified species from the early Santacrucian (*Notohippus* fauna) of Argentina and to *Adianthus bucatus,* from the Santacrucian of that country, which otherwise represents the latest known occurrence of the family Adianthidae. The occurrence of *Adianthus godoyi* in the type fauna of the Friasian thus suggests either that the family was more long-lived than had been previously appreciated, or that the type Friasian local fauna is more similar to those of Santacrucian age than their placement in different land-mammal ages would suggest.

Key words: *Adianthus*, Chile, Friasian, Galera Formation, Mammalia.

RESUMEN

Se describe una nueva especie del género *Adianthus*, de Río Cisnes (localidad tipo de la edad Friasense), Mioceno de Chile. La especies está representada por restos excepcionalmente completos, incluyendo los primeros elementos postcraneanos del esqueleto que se conocen para un miembro de la familia Adianthidae. En cuanto a la morfología del esqueleto, *Adianthus godoyi*, nueva especie, es similar a los Proterotheriidae pequeños del Santacrucense. La nueva especie es única entre los Litopterna en la fusión sólida de la parte proximal de la tibia y la fíbula. *Adianthus godoyi*, como los Proterotheriidae santacrucenses, estaba probablemente adaptado para locomoción cursorial. La estrechez de la arcada dental sugiere que la especie, probablemente fue un herbívoro selectivo, posiblemente consumiendo una vegetación mixta en un ambiente abierto o llano. *Adianthus godoyi* parece estar muy relacionado a una especie todavía no identificada del Santacrucense temprano (Notohippidense) de la República Argentina, y a *Adianthus bucatus*, del Santacrucense, que además de la nueva especie, representan la última aparición de la familia Adianthidae. La presencia de *Adianthus godoyi* en la fauna tipo del Friasense sugiere que la familia Adianthidae fue más longeva que anteriormente supuesto, o que la fauna tipo del Friasense es más similar a la fauna del Santacrucense de lo sugerido por su ubicación en una edad mamífero diferente.

Palabras claves: *Adianthus,* Chile, Formación Galera, Friasense, Mammalia.

INTRODUCTION

Adianthid litopterns are among the poorest known of indigenous South America mammals, being represented by relatively scarce isolated teeth and dentulous jaw fragments. Adianthidae probably share a most recent common ancestry with Macraucheniidae (Cifelli 1983a). The earliest adianthid appears to be *Proectocion*, from the Casamayoran of Chubut Province, Argentina (Cifelli 1983a). Two other early Tertiary genera, *Adiantoides* (Casamayoran to Divisaderan) and *Indalecia* (Casamayoran) are generally placed in the family (Simpson *et al.,* 1962, Bond & Vucetich 1983), but are here considered to represent another group, perhaps the Sparnotheriodontidae (Soria 1980) or Indaleciidae (Bond and Vucetich 1983, Soria 1989), that is hypothesized to have converged on Adianthidae in some dental features (see also Cifelli & Soria 1983, Cifelli 1985, Soria 1989). The greatest diversityof Adianthidae is known from the Deseadan, where four species, representing three genera (*Proadiantus, Tricoelodus*, and *Thada-*

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nius) are present. One monotypic genus is known from each of the succeeding land-mammal ages, the Colhuehuapian (*Proheptaconus*) and Santacrucian (*Adianthus*), the last-named genus representing the latest hitherto known record of the family.

A new species of *Adianthus*, described herein from the Río Cisnes local fauna, Chile, is of interest in that it is represented by a complete jaw and by postcranial materials, neither of which have been previously reported for any member of the family. The occurrence of *Adianthus* in the type local fauna for the Friasian Land-mammal Ae implies either a temporal range extension for the family or a closer affinity of the Río Cisnes local fauna with the Santacrucian than previously recognized.

Abbreviations used in the text: Duke-MNHN, specimen collected by joint Duke MNHN expedition and deposited in the Museo National de Historia Natural, Santiago, Chile; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina.

SYSTEMATIC PALEONTOLOGY

Family Adianthidae Ameghino, 1891
Genus *Adianthus* Ameghino, 1891
Adianthus godoyi, new species

Type specimen-Duke-MNHN CH89-109, lower jaw and partial skeleton including mandibular symphysis and left ramus, with right I_{1-3}, C, and P_1, and left I_{1-3}, C, P_{1-4}, and M_{1-3}; distal part of humeral shaft, one lumbar vertebra, both innominates, proximal right femur, distal left femur, left tibia/fibula lacking the distal end of the fibula, and several fragments.

Hypodigm. –The type only.

Horizon and locality. –Duke-MNHN locality 15, Galera Formation, XI Region, Chile.

Etymology. –For Alejandro Godoy, who coordinated Duke-MNHN field activities, in recognition of his contributions to the research program and his companionship in the field.

Diagnosis. Species closely similar to, but slightly larger than *A. bucatus*. Lower premolars broader and of more robust construction than in that species.

Description. Wear on the lower dentition of Duke-MNHN 89-109 (Fig. 1) is more advanced than on the type of *Adianthus bucatus*, MACN A-1812, the only other lower dentition surely referable to a species of *Adianthus*. The incisors and canines, which are worn flat, project anteriorly and are arranged in a tight U-shaped arcade at the front of the jaw. I_1 is strongly compressed mesiodistally; I_2 is less compressed, and I_3 is oval in occlusal view. Faint grooves are present at the posterolabial borders of I_3 and the canine, as described for *Adianthus bucatus* (Cifelli & Soria 1983). P_1, also worn flat, is broader than the corresponding tooth of *A. bucatus* and, perhaps, was higher crowned as well,

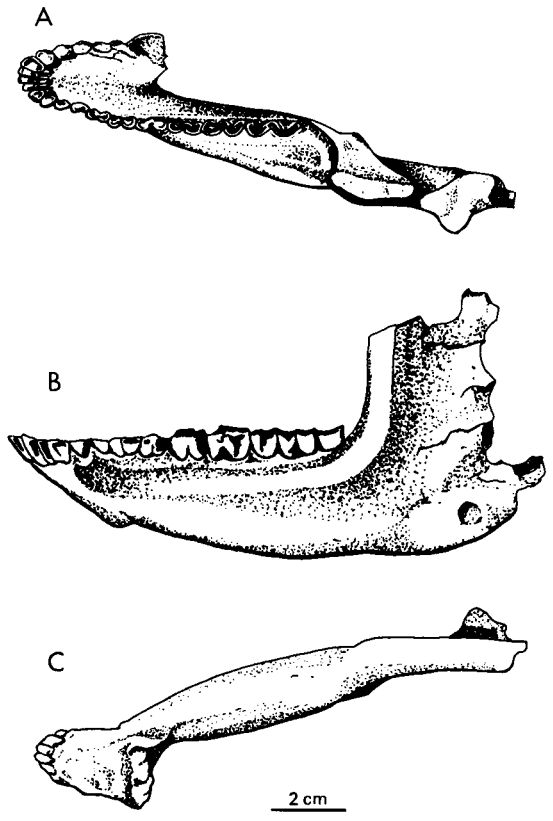

Fig. 1: Adianthus godoyi, new species. Right mandibular ramus (Duke-MNHN CH89-109, type) in oclusal (A), lateral (B), and inferior (C) views.

Adianthus godoyi, nueva especie. Rama de la mandíbula derecha (Duke-MNHN CH89-109, tipo), en vistas oclusal (A), labial (B) y ventral (C).

although this is difficult to determine owing to differences in relative wear. The succeeding premolars, P_{2-4}, are similar to those of *A. bucatus* except for being broader and having a more robust appearance. The lower molars are bicrescentic and lack secondary coronal complications such as fossettids or entolophids; the coronal pattern is nearly obliterated from M_1, while M_3 is just coming into wear. The molars increase in length from first to third; M_2 is the broadest tooth of the series. With wear, M_3 would increase in length because its distal edge slopes posteriorly. Dental measurements are given in Table 1.

The mandibular symphysis is solidly fused. The symphyseal region is laterally compressed, and the incisors and canines project anteriorly in spoutlike fashion. A shallow labial fossa is present beneath P_{1-2}, and a small foramen is located beneath M_1, about midway from the dental to the inferior margin of the mandible. The horizontal ramus deepens markedly beneath M_1. The ascending ramus rises normally with respect to the horizontal ramus. The coronoid process is not preserved, but the mandibular condyle is located well above the tooth row. The borders of the masseteric fossa are not clearly delimited, nor are other muscle scars well marked. The angle projects well posterior to the ascending ramus, but appears to have had a gently rounded profile rather than a sharp hook. The angle is slightly deflected medially.

The humerus deserves no more than passing comment because so little of it is preserved. What remains of the distal end

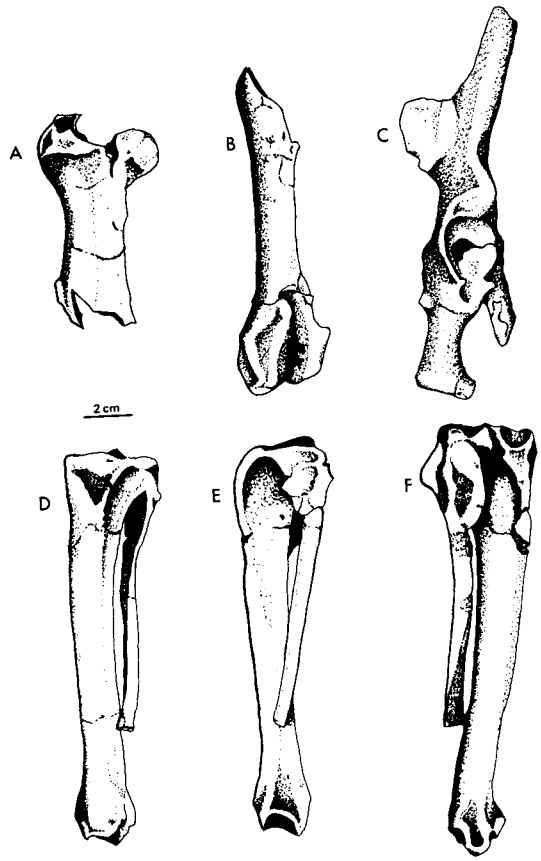

Fig. 2: Adianthus godoyi, new species (Duke-MNHN CH89-109, type). A, proximal right femur in anterior view; B, distal left femur in anterior view; C, right innominate in lateral view; D-F, left tibia and fibula in anterior (D), lateral (E), and posterior (F) views.

Adianthus godoyi, nueva especie (Duke-MNHN CH89-109, tipo). A, porción proximal del fémur derecho, vista anterior; B, porción distal del fémur izquierdo, vista anterior; C, pelvis derecha en vista lateral; D-F, tibia y fíbula izquierdas en vistas anterior (D), lateral (E) y posterior (F).

TABLE 1

Dental Measurements (mm) of *Adianthus godoyi*, new species (Duke-MNHN CH89-109).

Medidas (mm) de los dientes de *Adianthus godoyi*, nueva especie (Duke-MNHN CH89-109).

P_1	L	4.2	M_1	L	8.6
P_1	W	3.1	M_1	W	5.2
P_2	L	6.3	M_2	L	11.1
P_2	W	3.6	M_2	W	5.4
P_3	L	6.3	M_3	L	12.9
P_3	W	4.1	M_3	W	5.2
P_4	L	7.8			
P_4	W	4.5			

indicates that the olecranon fossa was fenestrate, as is common among cursorial mammals such as Santacrucian proterotheres. Both innominates are nearly complete, although neither preserves the tip of the ilium or the medial part of the ischium. The pelvis (Fig. 2) generally resembles that of Santacrucian proterotheres, figured by Scott (1910). The base of the ilium is more slender than in *Theosodon*. The ilium flares ventrolaterally to a slender tip, much as in *Thoatherium*; the dorsomedial (sacral) part of the ilium is not so strongly projecting dorsally nor so extensively developed as in *Theosodon*. A well-marked protuberance and a keel, indicating the origin of the rectus femoris muscle, is present near the anterior border of the acetabulum. A well-marked knob, perhaps marking the attachment of the anterior gemellus muscle, is present on the dorsolateral margin of the ischium, just posterior to the acetabulum; this protuberance is not present, or at least achieves lesser development, in *Theosodon*.

Neither femur is complete, but the morphology of the entire element is represented (Fig. 2). The head is more or less spherical. The greater trochanter is robust and is generally similar to that of "*Proterotherium*" or *Theosodon* (although the rugosity for insertion of the deep gluteal muscle is less extensive than in the latter genus), lacking the tall, dominating appearance of *Thoatherium* or *Prothoatherium* (Cifelli & Guerrero 1989). The lesser trochanter is unremarkable in size or form. The third trochanter, where the gluteus maximus inserted, is located about one-half the distance from femur head to condyles. It is knoblike but, compared to *Theosodon*, is modest in development. A slight ridge on the lateral surface of the distal femur shaft marks the origin of the vastus lateralis muscle, and a small eminence at the base of the medial condyle indicates the origin for the medial head of the gastrocnemius, but the element is otherwise devoid of muscle scars or rugosities. The distal femur is not as anteroposteriorly expanded as in either *Theosodon* or Santacrucian proterotheres.

The left tibia (Fig. 2), which is complete, is slightly shorter (128 mm) than the estimated length of the femur (151 mm). It is proportionately longer and less robust than the corresponding element in *Theosodon*, being more comparable to Santacrucian proterotheres in these respects. No groove for the patellar tendon is present on the cnemial crest. A prominent crest, indicating the insertion of the semimembranosus muscle, is present at the posteromedian border of the proximal tibia. Laterally, the proximal part of the fibula is solidly fused to the tibia, a condition unknown in any other litoptern. A strong protuberance, for attachment of the peroneus longus muscle, is present at the anterior margin of the proximal fibula. The distal fibula is lacking, but it was not fused to the tibia. The distal tibia is deeply grooved for the trochlea of the astragalar body, as in all litopterns (Cifelli 1983b). A prominent beak is present posteriorly and the medial malleolus is lacking, features also shared by all other litopterns.

DISCUSSION

The genus *Adianthus* was founded by Ameghino (1891) for the species *A. bucatus* (the spelling of which was later emended, variably and in all cases invalidly, by Ameghino and others), based on an upper cheek tooth. He later (1894) referred to the species a partial mandible, MACN A-1812. The original specimen of the species, evidently lost during Ameghino's lifetime (there is no evidence of any researcher having studied it since 1891), apparently belonged to a caviomorph rodent. Following a suggestion by Simpson *et al.* (1962), Soria (1981) suggested that MACN A-1812 might be taken as a neotype of the species. This was adopted by Cifelli & Soria (1983), and a proposal for designation of neotype under the plenary powers (Cifelli & Soria 1984, 1985) was approved by the International Commission on Zoological Nomenclature. Ameghino (1903-4) added a Colhuehuapian species, based on a left M^3, to the genus. This species was removed to *Proheptaconus*, as *P. patagonicus* by Soria (1981), who de-

monstrated it to be synonymous with *P. trelewensis* Bordas, 1936, which was based on a badly preserved skull with part of the upper dentition. An undetermined genus and species of Adianthidae, represented by a mandible with M_{1-2}, is known from an early Santacrucian (*Notohippus*) faunule in Santa Cruz Province, Argentina (Cifelli & Soria 1983). This specimen (MLP 68-I-17-192) may represent the lower dentition of *P. patagonicus*, but it cannot be compared directly with that species because of non-comparable representation. The generic status of *Proheptaconus* is thus, by implication, uncertain. Of the known species of Adianthidae, *Adianthus godoyi* appears most closely related to *A. bucatus* and the undetermined genus and species (possibly representing the lower dentition of *Proheptaconus patagonicus*). Deseadan taxa (species of *Thadanius, Proadiantus,* and *Tricoelodus*) share presumably derived morphology (such as the anterior placement and labial attachment of the lower molar entoconid resulting, in advanced species, in the development of an entolophid) not seen in Colhuehuapian and later species. *Adianthus bucatus, A. godoyi,* and the species represented by MLP 68-I-17-192 are derived with respect to the Deseadan taxa in having much higher crowned cheek teeth and completely bicrescentic lower molars lacking distinct talonid cusps (entoconid, hypoconulid, hypoconid).

The latest hitherto known record of Adianthidae is that of *Adianthus bucatus*, from Corriguen Aike (see Marshall 1976), Santa Cruz Formation, of Santacrucian age. *Adianthus godoyi* derives from the Río Cisnes at the type locality for the Friasian Land-mammal Age (Marshall *et al.*, 1983), thus implying a range extension for the family, greater temporal equivalence between the Rio Cisnes local fauna and "typical" Santacrucian faunas than previously recognized, or both. Unfortunately, the status and biochronologic relationships of the Friasian Land-mammal Age itself are rather uncertain. Assemblages supposed to represent local faunas of this age are represented by relatively small collections; stratigraphic relationships of these assemblages and systematics of the mammals themselves remain to be properly evaluated. As summarized by Simpson (1940, p. 666), "Virtually no stratigraphic data have been published, or apparently preserved with the collections, and the little that is known includes the statement... that the fossils from the most important locality, Rio Frias, were found at several different levels and are not all of the same age". In his initial notice on fossil vertebrates from the Rio Cisnes area, Roth (1908) described three different faunal levels, corresponding to localities identified by their relative elevation above sea level. It is probable, although not demonstrated, that the type of *Adianthus godoyi* is from approximately the same level as Roth's intermediate faunal zone. However, Roth later (1920, 1925) revised the identifications upon which he had based these zones, so that their status and circumscription is in question.

Remains of *Adianthus godoyi* are suggestive (although not indicative) of paleobiology of the species and, by implication, the paleobiology of other pygmy litopterns, for which little is known other than the cheek teeth. The muzzle appears to have been extremely narrow relative to jaw breadth at the cheek tooth battery. Relative oral dimensions have been shown to be important factors in resource partitioning among living ungulates (Owen-Smith 1985, 1989). Based on a comprehensive survey of living ungulates, Janis & Ehrhardt (1988) found relative muzzle width to vary predictably with dietary preference, selective feeders having narrower muzzles. Among the selective feeders, narrowest muzzle width was found among mixed feeders in open habitat, which select grass and low level dicotyledenous material, and among high level browsers, which eat leaves from branches. Quantitative comparison of fossil with recent data is not possible in the present case. However, the small body size of *Adianthus godoyi*, coupled with its extremely narrow muzzle, suggests that it was a selective feeder, possibly feeding on mixed vegetation in an open habitat.

The postcranial skeleton of *Adianthus godoyi*, although incompletely known, is

similar to that of other small-bodied Miocene Litopterna. The presence of a fenestrate olecranon fossa on the humerus, of hind limb proportions similar to those of Santacrucian proterotheres, and of a specialized articulation of the distal tibia with the astragalus, are suggestive of some degree of cursorial adaptation for the species. The significance of the proximally fused tibia and fibula is unclear, but this feature is often associated with cursorial or saltatorial locomotion in recent mammals (Howell 1965). In the postcranial skeleton, *Adianthus godoyi* is generally more comparable to three-toed Santacrucian proterotheres, such as *Diadiaphorus*, than to the presumably more closely related (and contemporaneous) macraucheniid *Theosodon*. However, these similarities, such as the relative robusticity of the femur and the relative development of sacroiliac contact, are presumably size-related rather than indicative of relationship: *Theosodon* is much larger than either *Adianthus godoyi* or Santacrucian Proterotheriidae.

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