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from the Huayquerian (Pliocene)  
of Argentina





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## ABSTRACT

Late Tertiary beds in and around the Santa María Valley of the Province of Catamarca, Argentina, were long known by the invalid name "Araucanense" or derivatives therefrom. They can now be designated as a sequence of formations, from top to bottom: Corral Quemado, Andalgalá, Chiquimil A, and Chiquimil B. The Corral Quemado and Andalgalá formations are of Huayquerian (Pliocene, perhaps middle Pliocene) age. The age or ages of the Chiquimil are not adequately established. Didelphidae known from the Huayquerian of the Corral Quemado and Andalgalá are identified and a number of speci-

mens described: *Didelphis pattersoni*, *Lutreolina* cf. *crassicaudata*, and ?*Sparassocynus* species innominata. Those three very different genera represent the reappearance in the known record of varied South American didelphids after a long gap from the Riochican (nominal late Paleocene) during which only a few also quite different microbiotheres are known. The inferences are not only that sampling of small fossil mammals is inadequate in South America but also that much, perhaps most, of didelphid evolution was occurring outside the regions of known fossil fields.

## INTRODUCTION AND ACKNOWLEDGMENTS

In our study of the peculiar extinct Argentine didelphid *Sparassocynus*, Reig and Simpson (1972, p. 517-518) mentioned a specimen representing a member or relative of that genus from the Huayquerian of Catamarca. The specimen had been collected for, and catalogued in, the Field (formerly Chicago) Museum of Natural History, but it was not at that institution at the time of our study and could not be located. It has now been found and will be returned to the Field Museum on the completion of the present study. Its inclusion here is by kind permission of William D. Turnbull, who has also lent the Simroe Foundation three other Field Museum specimens of Huayquerian didelphids for this study. A specimen of similar provenience in the Peirano Collection of the Instituto Lillo, Tucumán, has been lent by courtesy of José F. Bonaparte. Both Turnbull and Bonaparte have also provided other data. For comparisons numerous specimens of later age (Chapadmalalan), especially but not exclusively of *Sparassocynus*, have been lent by Galileo Scaglia from the Museo Municipal de Ciencias Naturales de Mar del Plata.

This study was begun in Tucumán, where expenses were paid by the Instituto Lillo. It was completed at the Simroe Foundation, Tucson, Arizona. Travel, study at the Simroe Foundation, and preparation of the manuscript were at no public expense. Publication by the American Museum of Natural History is appreciated.

The illustrations are by Louis L. Jacobs, and

the manuscript was typed by Kathie Chadderdon.

The following abbreviations are used for institutions:

FMNH, Field Museum of Natural History, Chicago.

IL, Instituto Miguel Lillo, Tucumán.

MACN, Museo Nacional de Ciencias Naturales, Buenos Aires.

MMP, Museo Municipal de Ciencias Naturales de Mar del Plata.

All measurements are in millimeters.

## PROVENIENCE OF SPECIMENS

The specimens here discussed all come from a thick series of late Tertiary beds in the valley of the Río Santa María in the Province of Catamarca in northwestern Argentina. Study of stratigraphy and usage of nomenclature here have had a long and confusing history. That cannot be followed in detail in this study, but enough must be said to try to clear up the recorded origins of the specimens under consideration.

Doering (1882) early applied the name "Araucano" on the primary basis of Tertiary beds in southern Argentina, primarily in Río Negro, Patagonia, but with extension to rocks of supposedly similar age elsewhere in Argentina. In times when lithostratigraphic, chronostratigraphic, and geochronologic classifications were not distinguished, Doering's "Araucano" was

applied also to rocks and faunas, including those in Catamarca, believed to be synchronous. Most of the literature on the Santa María Valley has applied such terms as "Araucanense," "Araucanéen," "Araucanian," "Estratos araucanos," etc. to varying parts of the rock sequence and faunal succession there, for example the classic studies: Ameghino (1906), Rovereto (1914), L. Kraglievich (1934), Riggs and Patterson (1939), and Peirano (1956).

In fact the rocks and faunas so called in the Santa María Valley are later in age than those typical for Doering's original "Araucano," and in any case "Araucano," the name of an Indian tribe and not a geographic name, is not acceptable in modern geological nomenclature. I (Simpson, 1940) proposed "Huayquerian" as a time and time-rock (age and stage) designation for the "Araucanense" of Riggs and Patterson (1939), deriving the name from the Huayquería Formation (rock unit) in the Province of Mendoza, named by Carles (1911). That usage has since been generally adopted, for example in the semi-official work by Pascual et al. (1966).

The rocks of the Huayquerian stage in the Santa María Valley of Catamarca, are distinct from the Huayquería Formation of Mendoza. Frenguelli (1930, 1937) applied the name "Santamariano" to lower beds in Catamarca, not relevant to the present study, but called the upper beds "Araucanian." Riggs and Patterson (1939) reproduced two summary and combined graphic sections made by Rudolf Stahlecker, who accompanied Riggs on his expedition to Catamarca 1926-1927, one section in the vicinity of Chiquimil in the Department of Santa María and one near Puerta del Corral Quemado in the Department of Belén. The sketch map, in Peirano (1956, fig. 1), shows Chiquimil, but Peirano's text (p. 80) indicates that the name had been changed to Entre Ríos. Riggs and Patterson gave no map and referred for stratigraphic details to a manuscript by Stahlecker "to appear in Geol. Ser. Field Mus. Nat. Hist." The manuscript was not published and attempts to locate a copy of it have been unsuccessful.

On the basis of Stahlecker's now unavailable work, Riggs and Patterson divided Frenguelli's "Araucanian" into four lithostratigraphic units:

Corral Quemado (new in Riggs and Patterson, 1939)

Araucanense (a restriction of the classic but invalid name)

Chiquimil A (new in 1939)

Chiquimil B (new in 1939)

In a detailed stratigraphic study Peirano (1956) rejected the subdivisions and nomenclature of Riggs and Patterson and retrogressively called all the beds here in question "Araucanense," which he believed to be a single, conformable unit in the Santa María Valley. He did, however, indicate an "Araucanense superior," approximately the Corral Quemado of Riggs and Patterson, and an "Araucanense inferior," approximately their Araucanense and Chiquimil A, perhaps also including Chiquimil B.

In the meantime Rassmuss (1919) in a brief report of remarks had proposed that a name probably intended as "Andalgala" be applied to all the so-called Araucanense of Catamarca, including rather less than Peirano's "Araucanense" and distinctly more than that of Riggs and Patterson. J. Kraglievich (1952, plate opposite p. 30) took this for "Andalhualá," which he correlated with the Huayquería of Mendoza and confined to the restricted "Araucanense" of Riggs and Patterson, giving the Catamarca section as:

Corral Quemado

Andalhualá

Chiquimil

In a correlated work published simultaneously in the same journal, Reig (1952, p. 123) evidently intended the same usage but specified a "formación de Andalgala." There is some added confusion because there is, or was, both an Andalgala (also sometimes spelled Andagalá) Department of Belén, and an Andalhualá Department of Santa María near Chiquimil, in Catamarca. Andalgala is a more likely type locality, and that name is here retained for the formation (or member) in question.<sup>1</sup>

<sup>1</sup>The label of L. Kraglievich's type of *Microtragulus catamarcensis* has the name "Andalhualá," either as a locality or as a subdivision of the "Araucanense," and I took that to be a stratigraphic type locality (Simpson, 1970, pp. 8-9), following J. Kraglievich (1952). I now do not know what the label means, but there is no doubt that the age of the specimen is Huayquerian.



The rock names tentatively now in use should, I believe, be:

Corral Quemado

Andalgalá

Chiquimil A

Chiquimil B

The "Araucanian" collections from this region, on which the basic studies of Ameghino, Rovereto, L. Kraglievich, and others depended, have no reliable data as to levels and probably represent a mixture from all those units and possibly even some still younger or older. The Field Museum collections have adequate data, and Patterson, in Riggs and Patterson (1939), gave preliminary and summary faunal lists, fairly rich for the Corral Quemado and what is now called the Andalgalá, but very poor for either part of the Chiquimil. A complete description of that collection has not been published. Peirano made a less extensive collection from at least approximately the same beds, also with data adequate in themselves but not readily equated with the Field Museum data. That collection, now in the Instituto Lillo, Tucumán, has not been studied.

The extremely inadequate fossil evidence for the Chiquimil does not suffice to separate Chiquimil A from the Andalgalá or the Huayquerian Stage and suggests, but is entirely inadequate to demonstrate, that Chiquimil B might belong to the earlier Chasicuan Stage.

The Corral Quemado is stratigraphically higher than the Andalgalá and hence at least somewhat later. The available faunal lists are not identical, but do not demonstrate significant difference in geological age and may reflect merely the fortunes of collecting or, as Patterson suggested, some change in ecology. Both formations and their faunas, therefore the specimens included in the present paper, are considered Huayquerian in age. No relevant radiometric or geomagnetic dates are yet available, and despite the fact that a North American family (Procyonidae) first appears in the Huayquerian, the fauna is so unlike that of any other region that paleontological correlation is virtually useless. There is now a strong consensus that the age of the Huayquerian in general terms is Pliocene. More precise placing in the European or world scale is hardly justified at present, but Argentine paleontologists tend to

place it tentatively in the middle Pliocene (e.g., Pascual et al., 1966).

## SYSTEMATICS

DIDELPHIDAE GRAY, 1821

DIDELPHINAE GRAY, 1821<sup>1</sup>

*DIDELPHIS* LINNAEUS, 1758

*Didelphis pattersoni* (Reig, 1952)

*Didelphis inexpectata* Ameghino, Patterson in Riggs and Patterson, 1939, p. 148.

*Paradidelphys pattersoni* Reig, 1952, p. 123, figs. 3, 4, 5C.

**Holotype.** FMNH P14455, partial right dentary with C-M<sub>4</sub> all incomplete, and fragments of left dentary with part of crown of M<sub>2</sub> and roots of M<sub>3-4</sub>. Andalgalá Formation, level XVII of Stahlecker in Riggs and Patterson (1939, fig. 1), Chiquimil, Santa María Valley, Catamarca.

**Hypodigm.** The type and: FMNH P14519, partial left dentary with C, P<sub>1-2</sub>, dm<sub>3</sub>, M<sub>1-3</sub>. (The dm<sub>3</sub> has become detached and somewhat damaged but all teeth are well shown in sequence by an available, accurate plastic cast.) Corral Quemado Formation, level 20-21 of Stahlecker in Riggs and Patterson (1939, fig. 1), Corral Quemado, Department of Belén, Catamarca.

FMNH P14458, partial right dentary with P<sub>1-3</sub>M<sub>1</sub> and M<sub>3-4</sub>, all badly worn and broken, almost featureless, but almost certainly of this species. Andalgalá Formation, level XX of Stahlecker in Riggs and Patterson (1939, fig. 1), Chiquimil, Santa María Valley, Catamarca.

IL 3317, fragment of right dentary with posterior root of M<sub>2</sub>, bases of M<sub>2-3</sub>, and well-preserved crown of M<sub>4</sub>. Peirano Collection. Field number 632 and designation of level "OII (S.M.)F."—not clearly located in Peirano (1956).

<sup>1</sup>The latest version of the International Code of Zoological Nomenclature forces the falsification of history and confusion of bibliography by prescribing that the author of a family-group name and its date derive from first publication of any family-group name, regardless of its form or whether it was based on a valid generic name, used to include a genus in that family-group taxon. Gray did not spell, define, or use a subfamily name Didelphinae in 1821 or later.

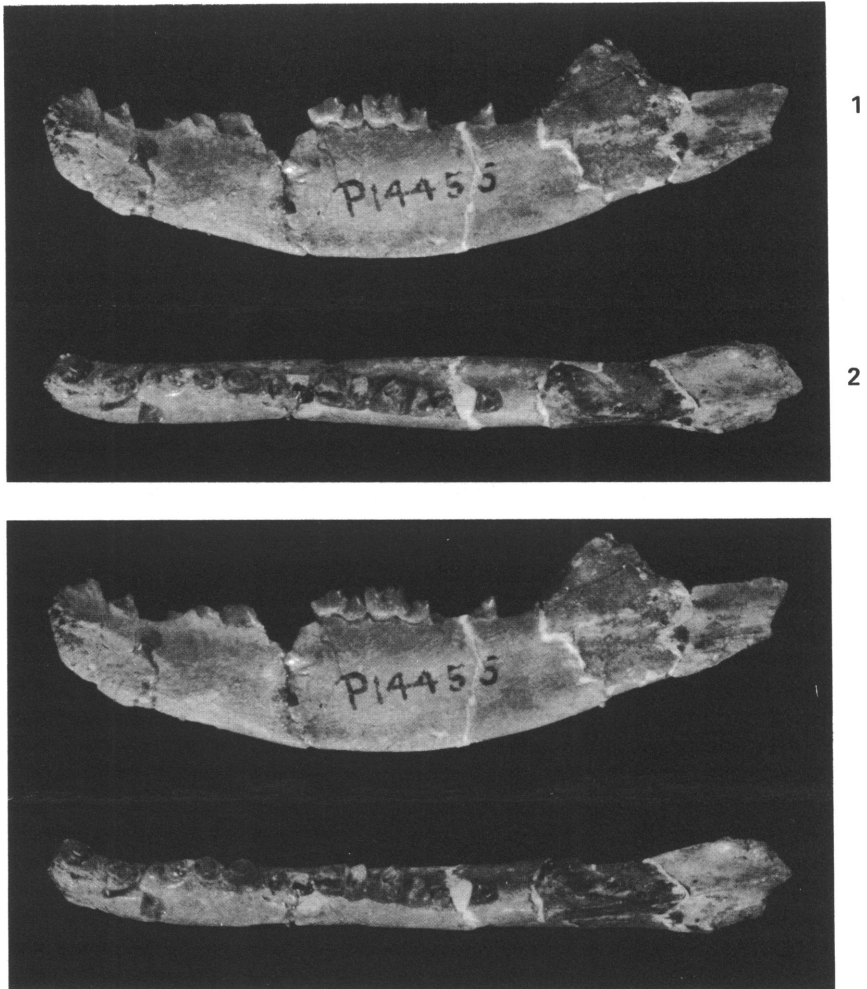


FIG. 1. *Didelphis pattersoni* (Reig, 1952), FMNH P14455, stereo pair of lingual view.  $\times 2$ .

FIG. 2. *Didelphis pattersoni* (Reig, 1952), FMNH P14455, same as figure 1 holotype, partial right dentary with incomplete C-M<sub>4</sub>, stereo pair of dorsal view.  $\times 2$ .

Locality (after Peirano) South-southeast of Chiquimil (Entre Ríos, eastern side of the Santa María Valley, Department of Santa María, Catamarca.

(The original hypodigm of Reig, 1952, did not include the last two specimens and did include MACN 8199, a fragment of left dentary with severely worn M<sub>3</sub> and M<sub>4</sub>, from the "Araucanense" of Catamarca, not seen by me.)

*Distribution.* Huayquerian of Catamarca.

*Diagnosis.* (Translated from the Spanish of Reig, 1952): "*Paradidelphys* of small size, smaller than *P. biforata*. M<sub>1</sub>-M<sub>4</sub>=17.5 mm. Talonid less short in comparison with the trigonid than in *P. inexpectata*. On M<sub>3</sub> the talonid is much narrower than the trigonid, while on M<sub>2</sub> both are of the same width. Metaconid strong, higher than the paraconid. Hypoconid strong and higher than the entoconid. Hypoconulid well developed. Talonid of M<sub>4</sub> three-cusped and less reduced than in *P.*



*inexpectata*.  $P_2$  much larger than  $P_3$ . Mandible strong, robust, and thick. Horizontal ramus relatively lower in the type species *P. inexpectata*. Masseteric fossa deep and coronoid crest strong. Symphysis short and high."

*New Diagnosis.* Not markedly different from *Didelphis azarae* or *marsupialis* in structure of known parts, but talonids relatively narrower, talonid of  $M_3$  more reduced and with hypoconulid not quite so lingual, trigonids of  $M_{2-3}$  when unworn somewhat higher and more piercing; smaller than those Recent species. Also smaller than "*Paradidelphys*" *inexpectata*, with relatively smaller molar talonids, that of  $M_4$  more (not less) reduced in length. For measurements see table 1.

*Discussion.* The right dentary of the holotype has suffered some damage since it was described and figured by Reig. It is broken in two pieces and  $P_3$  and  $M_1$ , shown by Reig's artist as essentially complete and in the jaw (Reig, 1952, figs.

3, 5C) are loose and broken. In table 1 I have given new measurements as far as available. They agree well enough with Reig's (1952, table 1) except that I believe that his figures for the maximum widths of  $M_2$  and  $M_3$  are significantly too low. My figures for those measurements are reasonably close to those scaled by Reig's artist (Reig, 1952, fig. 5C), so that the figures in Reig's table are probably misprinted. All available measurements of *Didelphis pattersoni* are significantly smaller than those of "*Paradidelphys*" *inexpectata* or most other species which *D. pattersoni* otherwise resembles.

Most of the morphological features noted in the original author's diagnosis occur equally in *Didelphis* and some other didelphids so that although they are correct for the most part they are not clearly diagnostic even at the generic level. In the new diagnosis I have selected such few characters as seem to be distinctive from

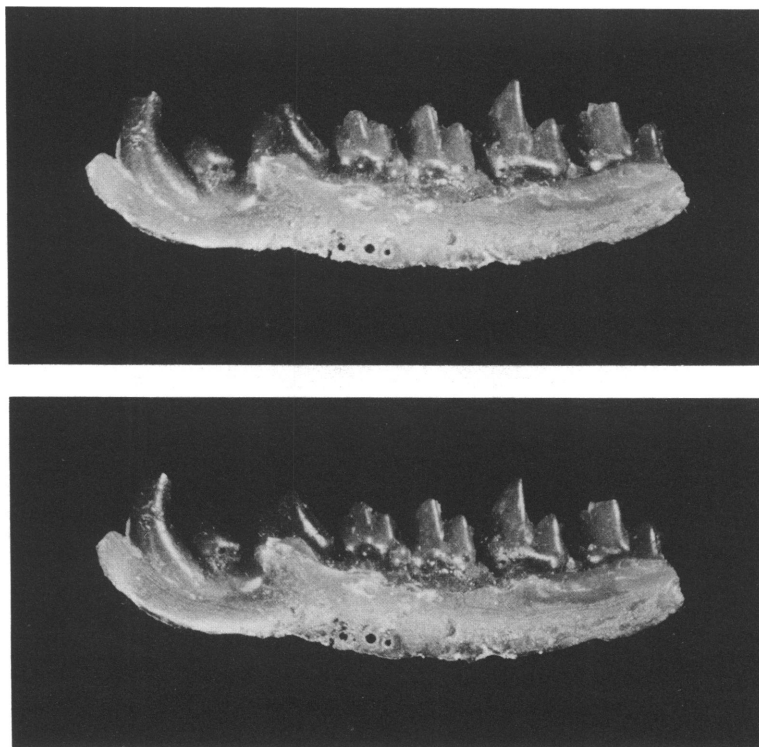


FIG. 3. *Didelphis pattersoni* (Reig, 1952), FMNH P14519, plastic cast made before specimen was damaged, partial left dentary with  $C_1P_{1-2}dm_3M_{1-3}$ , stereo pair of buccal view.  $\times 2$ .

other species currently referred to *Didelphis* and from "*Paradidelphys*" *inexpectata*. The only serious discrepancy is that Reig considered the talonid of  $M_4$  less reduced ("menos reducido") than that of "*P.*" *inexpectata*. That seems to be either an artifact or a difference of usage. As shown, I believe almost correctly, by Reig's artist (Reig, 1952, figs. 5B, C) the talonid of  $M_4$  in *D. pattersoni* is relatively about as wide as in "*P.*" *inexpectata* but is decidedly shorter, both absolutely and relative to the size of the trigonid of  $M_4$  or of the dentition as a whole. The specimen itself has been mended here with insertion of plaster between the trigonid and talonid of  $M_4$ . Reig's artist evidently corrected this, but without correction it makes the talonid appear excessively long. IL 3317, which may reasonably be referred to this species, has  $M_4$  perfectly preserved and seems to settle the matter; it has the talonid of  $M_4$  almost exactly as in Reig's figure and in apparent contradiction of his written diagnosis.

The generic placing of this species is probable but not certain. I have elsewhere (Simpson, 1972, pp. 6-10, 25-29) expressed and documented the conclusion that Chapadmalalan species previously referred to the typically Montehermosan genus *Paradidelphys* are better placed in *Didelphis*. Although it is distinct from the Chapadmalalan species, I believe that the same is true of *pattersoni*. Some recent species generally considered on totality of characters as generically distinct from *Didelphis* differ little in the cheek dentition, so that it can hardly be excluded that more complete knowledge of *pattersoni* would also suggest or warrant generic separation. Even so, however, as *pattersoni* is about equally distinct from the type-species of *Paradidelphys*, *P. inexpectata*, there is no reason to expect that removal from *Didelphis* would indicate return to *Paradidelphys*. In these circumstances, reference of *pattersoni* to *Didelphis* seems to me the most reasonable interim solution, at least.

On the basis of published data, the distinction

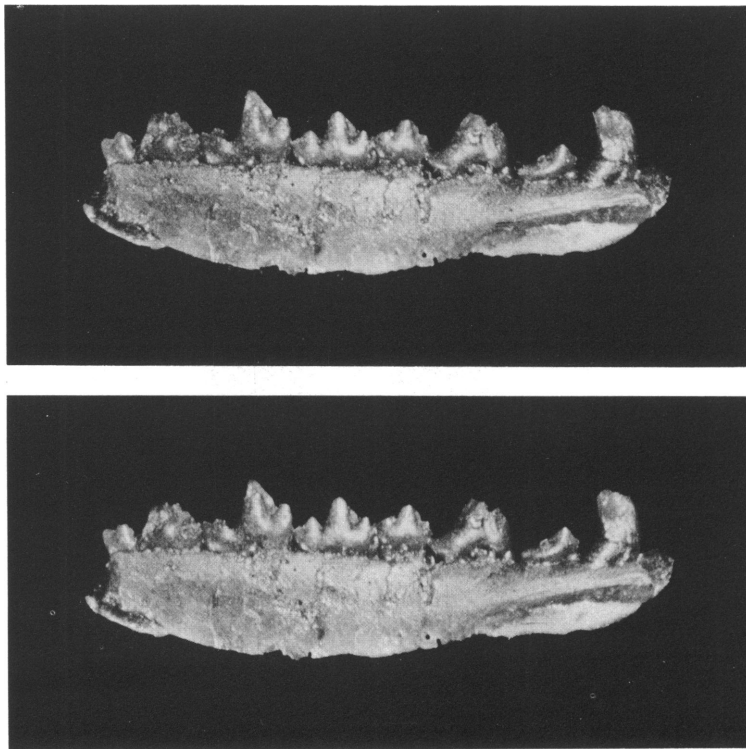


FIG. 4. *Didelphis pattersoni* (Reig, 1952), FMNH P14519, same as figure 3, stereo pair of lingual view.  $\times 2$ .



TABLE 1  
COMPARATIVE MEASUREMENTS (IN MILLIMETERS) OF LOWER CHEEK TEETH  
OF *DIDELPHIS PATTERSONI* AND "*PARADIDELPHYS*" *INEXPECTATA*

	<i>D. pattersoni</i>				<i>P. inexpectata</i> Type, MACN 1615 after Reig (1952)
	<i>D. pattersoni</i> Type, FMNH P14455	MACN 8199 after Reig (1952)	FMNH P14519	IL 3317	
<i>P</i> <sub>1</sub>					
Length	—	2.8	2.9	—	3.2
Width	—	1.7	1.7	—	1.9
<i>P</i> <sub>2</sub>					
Length	4.1	4.1	4.2	—	4.7
Width	—	2.0	1.9	—	2.5
<i>P</i> <sub>3</sub>					
Length	3.5	—	—	—	3.8
Width	1.9	—	—	—	2.2
<i>M</i> <sub>1</sub>					
Length	—	3.6	3.8	—	4.2
Width	—	2.4	2.7	—	2.9
<i>M</i> <sub>2</sub>					
Length	4.4	4.4	4.5	4.6	5.0
Width	2.9	2.8	2.8	ca. 3.0	3.3
<i>M</i> <sub>3</sub>					
Length	4.9	5.0	4.8	ca. 4.5	5.9
Width	3.2	2.8	2.9	ca. 3.5	3.4
<i>M</i> <sub>4</sub>					
Length	—	—	—	5.2	6.9
Width	—	—	—	3.4	3.6

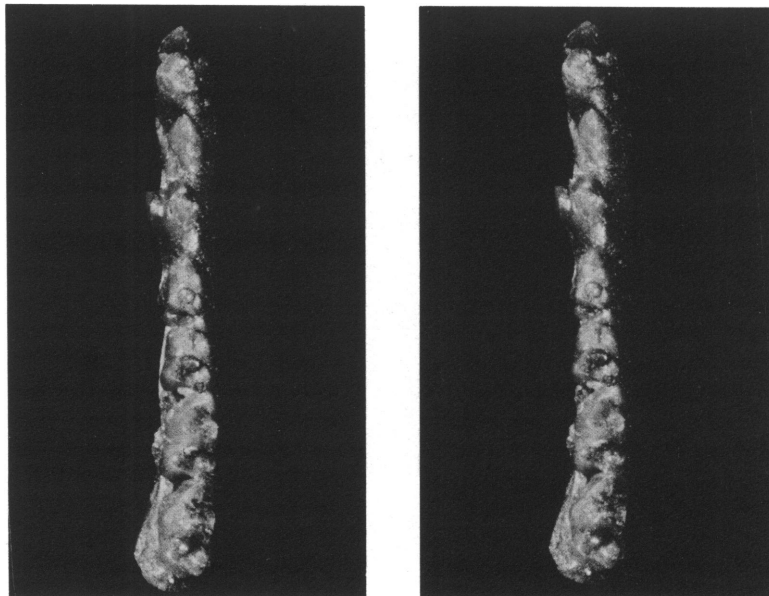


FIG. 5. *Didelphis pattersoni* (Reig, 1952), FMNH P14519, same as figures 3, 4, stereo pair of dorsal view.  $\times 2$ .

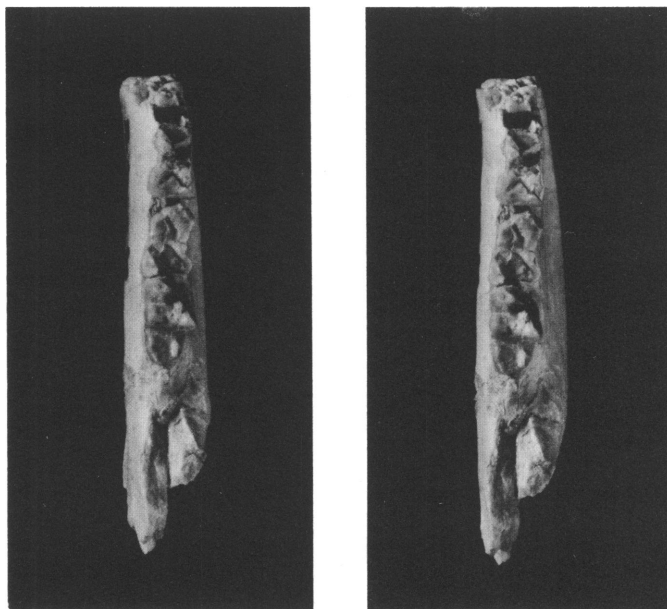


FIG. 6. *Didelphis pattersoni* (Reig, 1952), IL 3317, fragment of right dentary with posterior root of  $M_2$ , bases of  $M_{2-3}$ , and well-preserved  $M_4$ , stereo pair of dorsal view.  $\times 2.2$ .

of *Paradidelphys* from *Didelphis* seems to me somewhat questionable. However, I have not studied the holotype (MACN, Colección Ameghino 1615) of the type-species (*Paradidelphys inexpectata*) or other Montehermosan species and therefore do not now undertake the formal systematics of that supposed genus.

#### LUTREOLINA THOMAS, 1910

##### *Lutreolina* cf. *crassicaudata* (Desmarest, 1804)

The presence of this didelphid in the Huayquerian of Catamarca was noted by Patterson in Riggs and Patterson (1939, p. 148) as follows:

"*Lutreolina*—Discovery of a good specimen of this genus, one of the most specialized living didelphines, in the Corral Quemado (level 20) was most unexpected. The species is very similar to the living *L. crassicaudata*." The reference to level is again to Stahlecker's summary sections in Riggs and Patterson (1939, fig. 1). I have not restudied the specimen, the presence and identification of which is adequately established on Patterson's authority.

The presence in the Huayquerian of this specialized didelphid so close to a living species becomes somewhat less striking now that it is known that similar specimens occur in the Montehermosan (age and stage next younger than the Huayquerian), where they were first named "*Didelphys tracheia*" by Rovereto (1914) but later shown to be uncertainly separable from *Lutreolina crassicaudata* by Reig (1952, 1958). Virtually identical specimens also occur again in the next younger age-stage, the Chapadmalalan (Reig, 1958; Simpson, 1972). In this connection, a footnote in a prior publication (Simpson, 1972, p. 12) contains a misprint and is open to possible misunderstanding. I noted that Riggs and Patterson (1939, there misprinted as 1934) had considered *Didelphys tracheia* a synonym of *Didelphis inexpectata* but that this synonymy is impossible. That is correct, but when Riggs and Patterson wrote, it was not realized that *tracheia* belongs in *Lutreolina* and is doubtfully separable from *L. crassicaudata*. Riggs and Patterson of course did not intend to synonymize *Lutreolina* with *Didelphis*.



## SPARASSOCYNINAE REIG, 1958

## SPARASSOCYNUS MERCERAT, 1898

For references and diagnoses of the subfamily and generic taxa see Reig and Simpson (1972, pp. 513-514).

*Sparassocynus* species innominata

**Previous References.** This is presumably the form mentioned by Patterson (in Riggs and Patterson, 1939, p. 148) as "An extinct genus with very large alisphenoid bullae," and is surely that mentioned by Reig (1958, p. 279-280) as "A representative of *Sparassocynus* almost certainly of a distinct, much smaller species," and by Reig and Simpson (1972, p. 517-518) as "Cf. *Sparassocynus* sp. indet."

**Specimen.** FMNH 15225, cranium (lacking face), with bullae broken away and bone of anterior part flaked away from endocast.

**Provenience.** Catalogued as follows: "Marsupial cranium, orig. acc. # [field number] 260a; Chiquimil, Santa María, Catamarca, Argentina; Araucanense, Early Mid Pliocene, Level XX, 2nd Marshall Field Exped. 1927. Coll. R.C. Thorne."

The formation is now known as Andalgalá. The horizon XX is shown after Stahlecker in Riggs and Patterson (1939, p. 145, fig. 1). The age is Huayquerian, perhaps early Huayquerian.

**Description.** This handsome little cranium is characteristically didelphid or indeed didelphine in all preserved characters but one. In these same characters it agrees with *Sparassocynus*, the few nondidelphine parts of the adequately known species of the latter (*S. derivatus*), except for the ear region, not being present on this partially preserved specimen. The one strikingly nondidelphine character of the present specimen is the large epitympanic sinus, as in *Sparassocynus*. As in the latter also, this is lined with a thin lamina of a bone, probably an extension of the alisphenoid, suturally separate from the external bones surrounding it laterally and dorsally. Although large, this sinus is relatively somewhat smaller than in *S. derivatus*. It is a reasonable presumption that this specimen also has a complete osseous bulla, as in *S. derivatus*, that has been destroyed on the specimen as now preserved. In what was probably a reference to this specimen, as noted above, Patterson did speak of "very large alisphenoid bullae," which may indicate

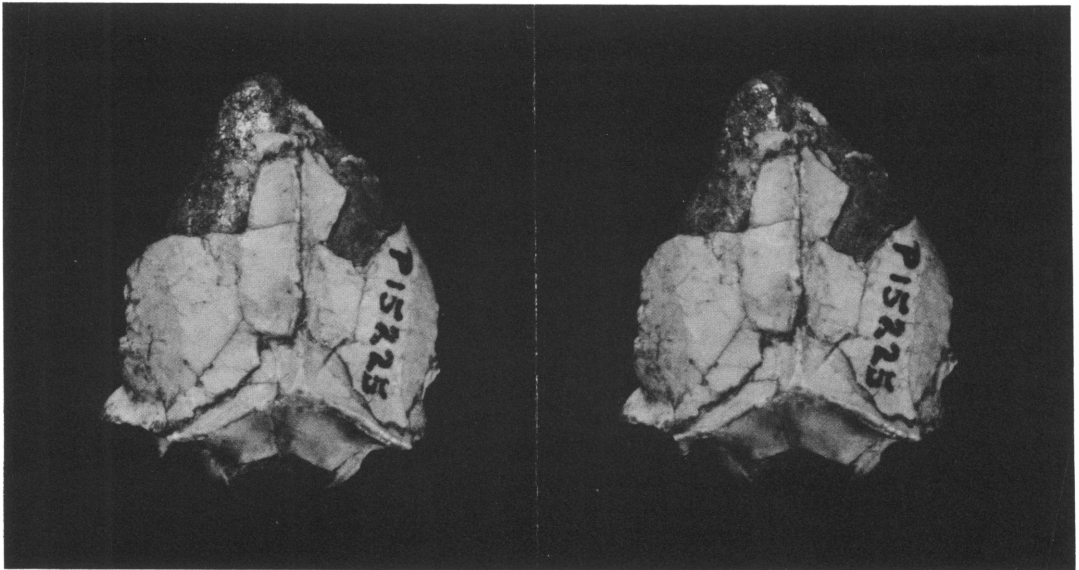


FIG. 7. *Sparassocynus* species innominata, FMNH 15225, partial cranium, stereo pair of dorsal view. Ca.  $\times 2.4$ .

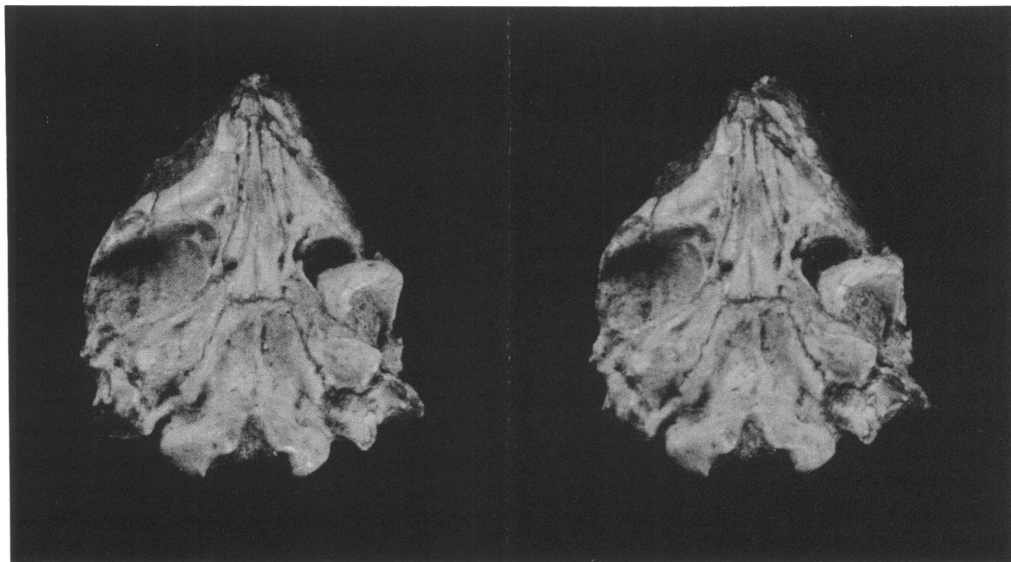


FIG. 8. *Sparassocynus* species innominata, FMNH 15225, same as figure 7, stereo pair of ventral view. *Ca.*  $\times 2.4$ .

that these were still present when he saw the specimen (approximately 35 years ago and before it disappeared from the Field Museum) or, more likely, that he considered the epitympanic

sinus a part or an indication of the bulla, a legitimate but not customary usage. On the left side of this specimen a part, at least, of the tympanic bone is preserved. It has the form of a half cylin-

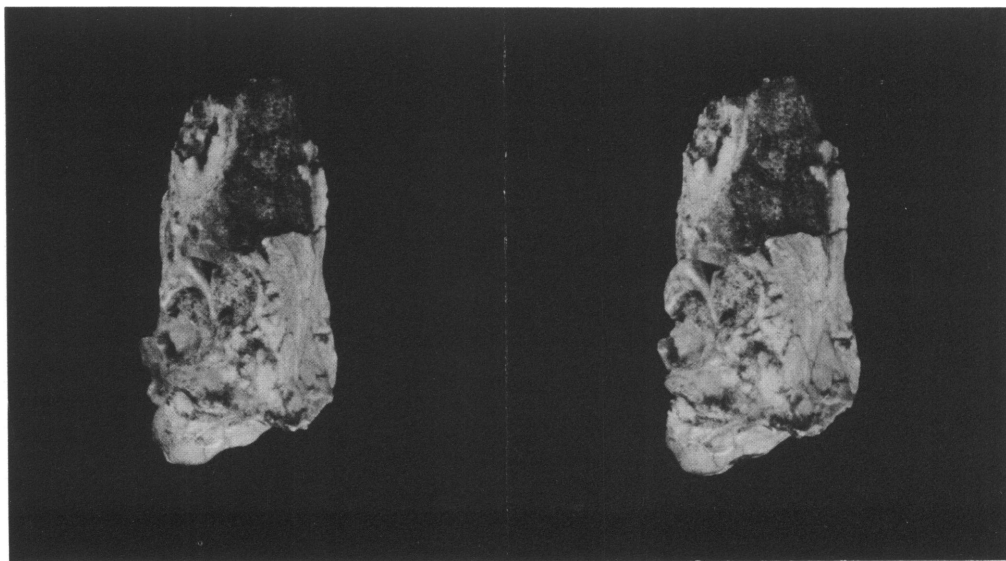


FIG. 9. *Sparassocynus* species innominata, FMNH 15225, same as figures 7, 8, stereo pair of left lateral view. *Ca.*  $\times 2.4$ .

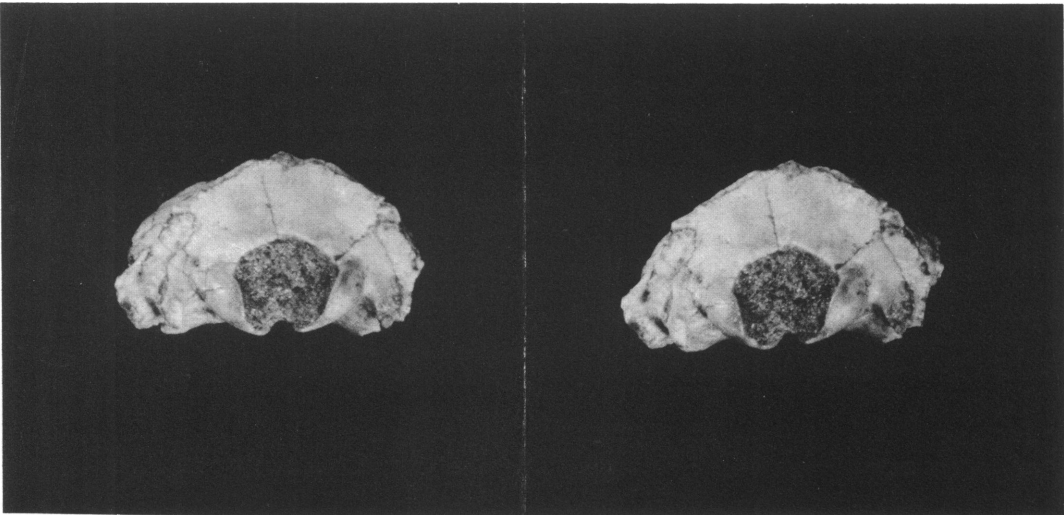


FIG. 10. *Sparassocynus* species innominata, FMNH 15225, same as figures 7-9, stereo pair of occipital view. Ca.  $\times 2.4$ .

der, crescentic or semilunar in transverse section, and seems to be relatively larger than in *S. derivatus* than is usual in didelphines.

*Classification.* *Sparassocynus* is the only known didelphid genus with similar epitympanic sinuses, and no character in this specimen warrants distinction from that genus. No didelphid other than *Sparassocynus* named from other parts, such as the dentition, is at all likely to be congeneric with this specimen. Reference to *Sparassocynus* is therefore justified, even though

it is provisional, and discovery of further material might demand generic separation. This specimen is much smaller than the only defined species of *Sparassocynus*, *S. bahiai* and *S. derivatus*, about two-thirds their size in available dimensions (see table 2). It differs also in other minor details, such as the perhaps primitively smaller size of the epitympanic cavity. It clearly represents an unnamed species, not an indeterminate one because its specific distinction and some of its specific characters are determined. Nevertheless it is not

TABLE 2  
CRANIAL MEASUREMENTS (IN MILLIMETERS) OF SPARASSOCYNUS

	<i>S. species innominata</i> FMNH P15225	<i>S. derivatus</i> MMP 967M      MMP 1725	
Width across occipital condyles	9.0	12.5	12.9
Width across inferolateral processes of petrosal	13.0	19.7	ca. 20
Oblique height of occiput	11.3	16.4	15.6
Height of top of epitympanic sinus above ventral level of basisphenoid	5.7	11.8	—
Approximate length from top of occiput to postorbital constriction	18	25	25



here named, because the postfacial cranium does not provide adequate comparison with fossil didelphid specimens that are most likely to be found in the future. It is therefore simply designated as a *species innominata*, with the hope that the few zoologists who attach their names to other students' *innominatae* will refrain in this case.

## DISCUSSION AND SUMMARY

The short but significant list of known Huayquerian didelphids, all from the Province of Catamarca, Argentina, is thus as follows:

### Didelphidae

#### Didelphinae

*Didelphis pattersoni*

*Lutreolina* cf. *crassicaudata*

#### Sparassocyninae

*Sparassocynus* species *innominata*

These are the earliest known occurrences for all three genera. The first known appearance of the Didelphinae depends on definitions, but it is now usually held that the subfamily was already present in the Late Cretaceous in both South and North America at least. This is the earliest known occurrence of Sparassocyninae. *Didelphis* and *Lutreolina* are still widespread in South America, the former now also in North America. In Argentina both are common as fossils in the Montehermosan and Chapadmalalan after their appearance in the Huayquerian. *Didelphis pattersoni*, probably, but not certainly, became extinct without issue after the Huayquerian. *Lutreolina* cf. *crassicaudata* may well be specifically inseparable from the Recent species or, if separable, may nevertheless be the direct ancestor of the latter. *Sparassocynus* survived into the Uquian, now usually considered early Pleistocene, but the genus and its subfamily are unknown thereafter and evidently became extinct without issue sometime during the Pleistocene. It is possible, but because of the abrupt difference in size, improbable, that *Sparassocynus* species *innominata* of the Huayquerian was ancestral to *S. bahiai* of the Montehermosan or hence to *S. derivatus* of the Chapadmalalan.

Into the 1930s all the known pre-Huayquerian didelphids belonged to the subfamily (or morphological type) Microbiotheriinae, and all known from the Huayquerian to the present

were believed to belong to the Didelphinae, while some Cretaceous and all known post-Cretaceous North American didelphids were evidently Didelphinae. It was therefore logical to adopt the hypothesis that the Microbiotheriinae were an early South American branch that became extinct in the Miocene, that the Didelphinae were of North American origin, and that they replaced the Microbiotheriinae by waif immigration at or shortly after the time of extinction of the latter, as suggested at that time by Patterson (1937, and in Riggs and Patterson, 1939). That view has, however, been made untenable by late discoveries, as noted especially by Patterson and Pascual (1968). An extraordinary variety of didelphids, some, at least, didelphine, have been found in the late Paleocene of Brazil; at least one didelphine occurs in the (conventional) Eocene of Patagonia; several living South American didelphids are structurally microbiotheriine; there is a didelphine from probable late Cretaceous beds in Peru; there are no didelphids in the now enormous collections of small mammals from the Pliocene of North America.

The most reasonable hypothesis now is therefore that didelphids early spread (in one direction or the other) between North and South America; that most lines of a Cretaceous radiation in North America soon became extinct and only a limited few didelphines survived into the Miocene and then in turn became extinct; that a marked radiation occurred into the early Cenozoic in South America and that subsequent didelphid evolution there also was multilinear and included didelphines; and finally that didelphines returned to North America from South America over the Colombian-Panamanian land bridge in the Pleistocene.

It thus appears that the sudden appearance in the known record of three very different genera of didelphids in the Huayquerian of Argentina represents not an invasion but the discovery of some results of long anterior radiating evolution of didelphids in South America. Failure of known possible ancestors of any of these three genera to appear in the known record between the Riochican (conventionally taken as late Paleocene) and the Huayquerian could have either of two causes, or most likely a combination of both: collecting from intervening stages has simply been inadequate to include fair sam-

ples of didelphids; or most didelphid evolution (perhaps all except for a few microbiotheres) was going on in parts of the continent where relevant fossil deposits have not been discovered or do not exist.

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