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THE MIOCENE VERTEBRATES OF QUEBRADA HONDA, BOLIVIA

PART I. ASTRAPOTHERIA

by

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The central part of the Andean range was formed in three major orogenic events. Until the close of the Mesozoic, much of the Andes was at sea level. Beginning in the Cretaceous, a general emergence of land in southern Peru where formerly there had been a geosyncline marked the probable first expression of the Laramide Orogeny. Marine connections did remain, at least locally, east of the rising Cretaceous Andes in what was to become the eastern and central Andes of Bolivia. A period of quiescence then ensued during which the Andes stood at approximately 1000 m elevation (Jenks, 1956).

Recent discoveries of Tertiary faunas in structural basins have revised the timing of the second phase of uplift. A large Oligocene fauna at Salla, Bolivia, in the Cordillera Central (Hoffstetter, 1976) and the early Miocene fauna of Quebrada Honda in the Cordillera Oriental require the deformation of the Paleozoic strata much earlier than the middle to late Miocene date frequently given in the Andean literature for the rejuvenation of mountain building (Jenks, 1956; Ahlfeld, 1956, 1970) although such dates are con-

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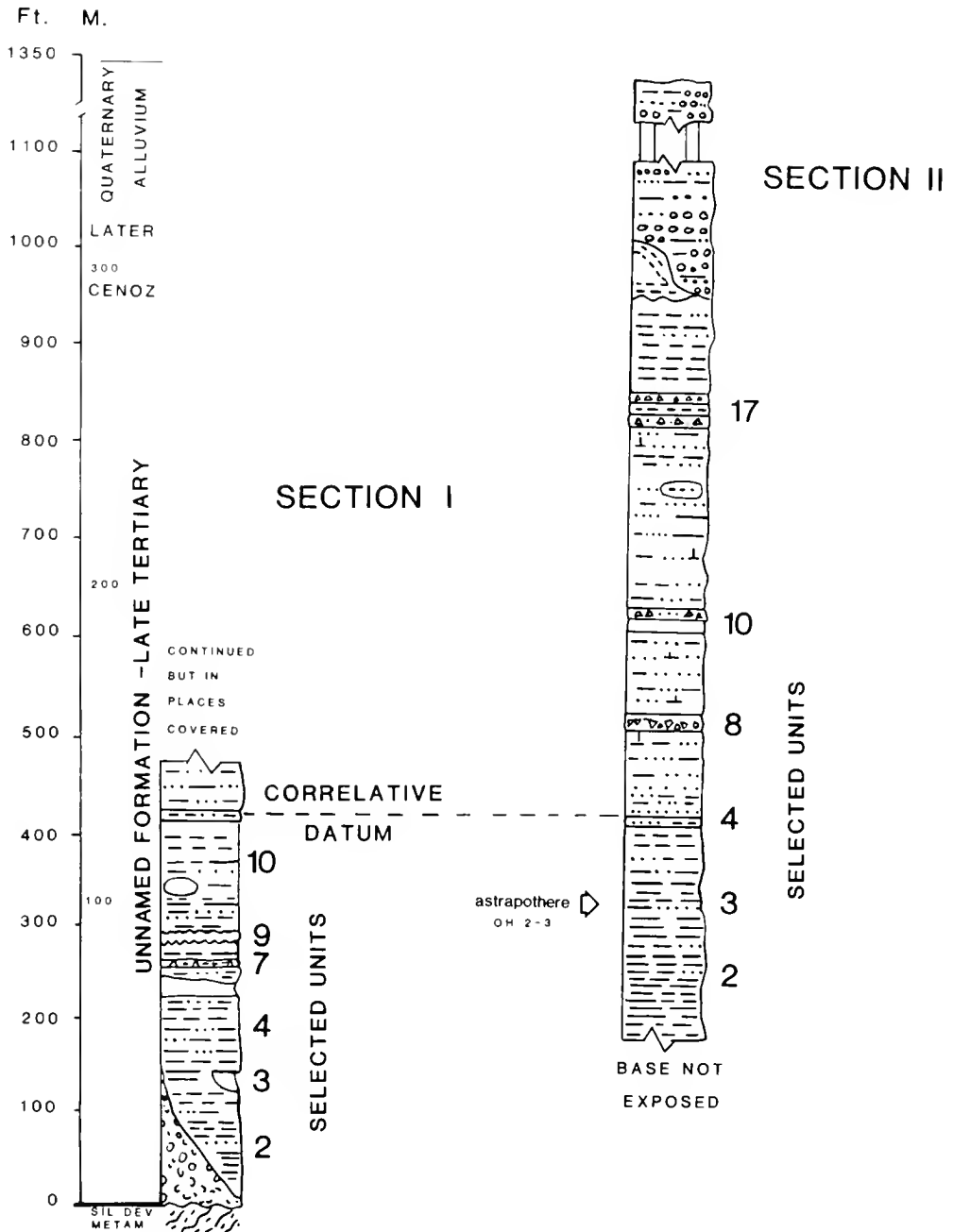


Fig. 1.—Geologic sections of Quebrada Honda, Bolivia. The stratigraphic level of the astrapothere skull, *?Xenastrapotherium*, at QH2-3 is indicated (modified from MacFadden and Wolff, 1981).

sistent with other interpretations (Charrier, 1973; Yrigoyen, 1979). This second phase of uplift was marked by intensive folding of the older strata, magmatic intrusion and volcanics. Enormous amounts of clastic sediments were deposited east and west of the orogenic belt at this time. Relative quiescence returned to the Andes in the late Miocene and brought about the development of a mature landscape (Jenks, 1956).

An extremely intense surge of movement at the close of the Tertiary formed the structure of the modern Andes with major thrust faulting and

vulcanism (Ahlfeld, 1956). A weak, later phase of the third orogeny occurred during the late Pleistocene and the present height of the Andes may not have been attained until the time of the last glaciation (Jenks, 1956).

In a large bowl-shaped structural valley in the Cordillera Oriental near the small village of Quebrada Honda, Bolivia, fossil-bearing deposits accumulated during the second orogenic episode. The sediments are primarily horizontal to subhorizontal tan clays and silts with a basal breccia conglomerate that developed during the first phase of slope wash deposition. An occasional band of coarse gravels indicates a channel deposit (Fig. 1). Several volcanic ash levels are present. Fossils were found throughout the 360 m section but the majority of fossils were taken from the lower and better exposed 100 m.

The Quebrada Honda locality was first visited by a paleontologist in 1976 and introduced to the scientific community shortly after (Hoffstetter, 1977). The fossils collected on the first visit were briefly discussed and the age of the fauna was tentatively given as Friasian (middle Miocene).

In August 1978, Dr. K. E. Campbell, Jr. (Los Angeles County Museum), Dr. R. G. Wolff (University of Florida), Dr. B. J. MacFadden (Florida State Museum), Ing. Oscar Siles (GeoBol), and I collected at Quebrada Honda and equivalent strata in the adjacent valley of the Rio Rosario. The site was re-visited in 1981 by Drs. Campbell, Wolff, MacFadden and Ing. Siles and Dr. A. Berta (San Diego State University). The specimen discussed in this paper was discovered in 1978.

This study of the Quebrada Honda Local Fauna utilizes a larger collection than was available to Hoffstetter and the conclusions differ from his in several aspects. Primarily, I differ in the age assessment of the local fauna (Frailey, in press). Rather than Friasian, the Quebrada Honda Local Fauna bears more affinities with the Santa Cruz Fauna of southern Argentina. As such, Quebrada Honda becomes the only major Santacrucian local fauna (early Miocene) that is found outside of southern Argentina.

The Santa Cruz Fauna was extensively studied in the monographic work edited and in large part authored by Scott (1903-1932). Much of this work remains valid, with major changes occurring only at the suprageneric taxonomic levels (for example, see Patterson and Pascual, 1968). One paper since 1932 (Bordas, 1941) has specifically addressed a faunule of the Santa Cruz Formation and little new material has been collected since 1904 (see review in Marshall, 1976). The Quebrada Honda Local Fauna therefore affords an opportunity to examine both the universality of the Santa Cruz Fauna in South America and the taxonomic status of Santacrucian faunal members.

The localities referred to in this paper are on file in the field notebooks of the Florida State Museum. The notation used refers to the geologic section and then stratigraphic level within that section. For example, QH2-3 refers to Quebrada Honda Geologic Section Number 2, the third definable level from the base of that level.

The Quebrada Honda fossils are housed at the Florida State Museum. All are catalogued into the FSM collection (acronym UF). Forty percent of the fossils and all the holotypes will be returned to the Republic of Bo-

livia at the conclusion of the study.

All measurements used in this paper are in millimeters; parentheses around a number indicate an approximate measurement. The abbreviation AMNH refers to the American Museum of Natural History, New York.

SYSTEMATICS

Order Astrapotheria Lydekker, 1894

Family Astrapotheriidae Ameghino, 1887

Subfamily Uruguaytheriinae Kraglievich, 1928

?*Xenastrapotherium* Kraglievich, 1928

Figs. 2, 3

Material. UF 26679, partial skull.

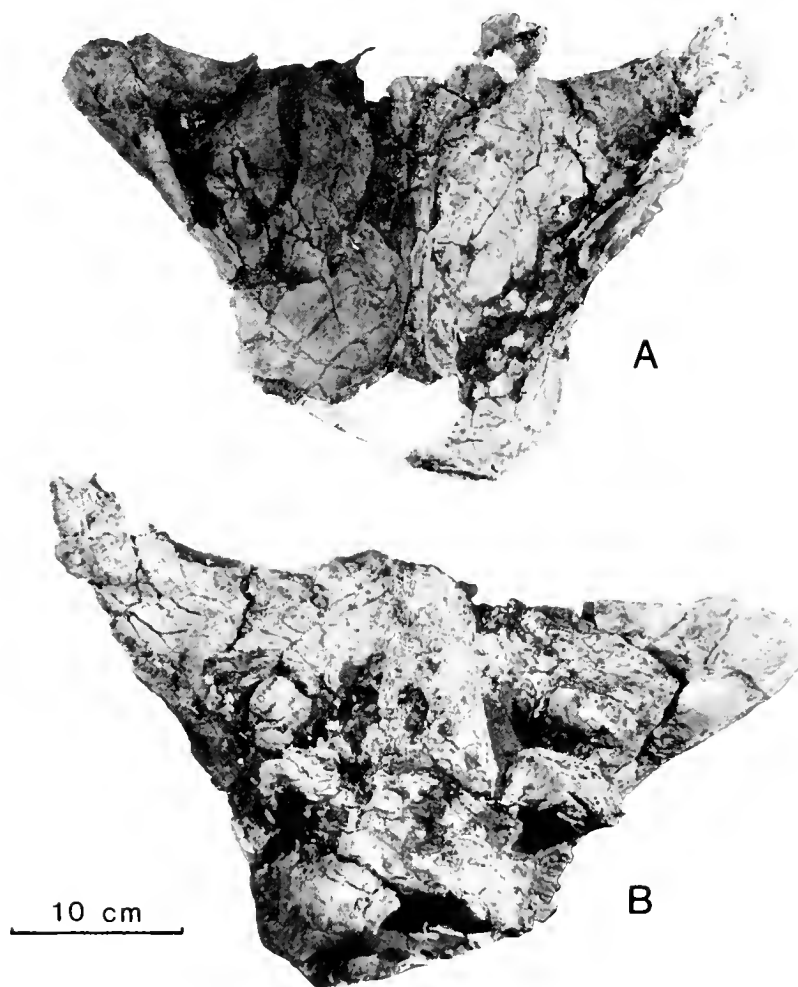


Fig. 2.—?*Xenastrapotherium* (UF 26679), partial skull. A. Dorsal view. B. Ventral view.

Locality. QH2-3.

Discussion. A large, advanced astrapothere is represented in the Quebrada Honda Local Fauna by a highly fragmented skull that consists of the cranium and pieces of the palate and upper teeth. The skull of only one genus of Astrapotheriidae is known in detail, *Astrapotherium* Burmeister, 1879 from the Santa Cruz Fauna of Argentina. The Quebrada Honda skull is approximately equal in size to the skull of *Astrapotherium magnum* (Owen), 1853 (see comparative measurements, Table 1) and similar in many respects. However, the preserved parts of the Quebrada Honda skull differ in two major features from that of *Astrapotherium*. The zygomatic arches are horizontal and flare widely, unlike the much narrower, dorsally curved zygomatic arches of *Astrapotherium*. The shape of the occiput, when viewed posteriorly, differs in that it is not constricted above the condyles but rather drops smoothly to meet the paroccipital processes. In these two features, the specimen from Quebrada Honda is more like *Trigonostylops* Ameghino, 1897 (as seen in *T. wortmani*, AMNH 28700). This is of taxonomic interest and is explored later in this discussion.

Hoffstetter (1977) stated that isolated upper and lower last molar teeth

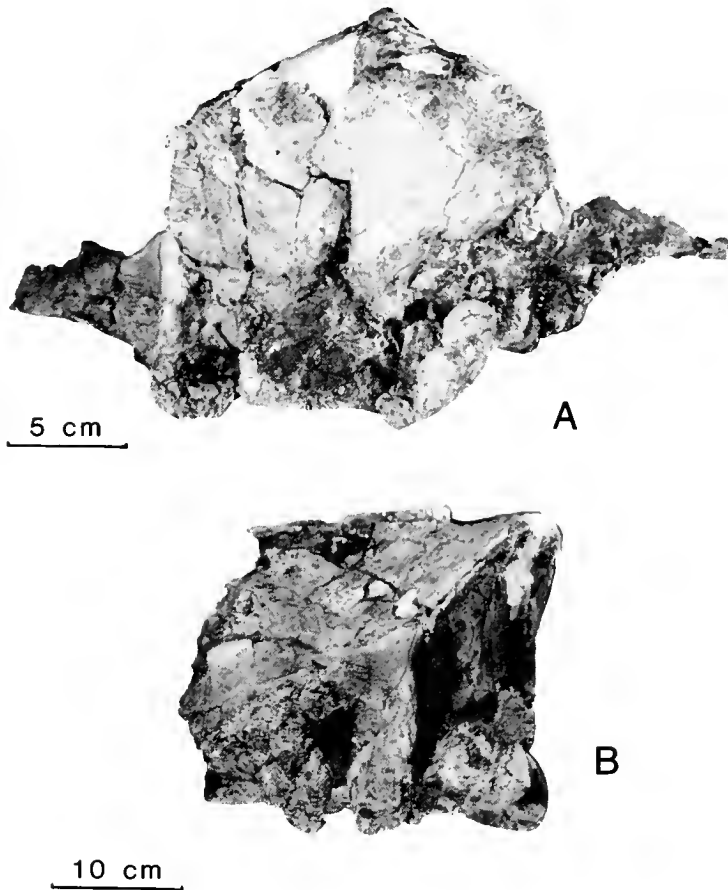


Fig. 3.—?*Xenastrapotherium* (UF 26679), partial skull. A. Occipital view. B. Left lateral view.

Table 1.—Comparative measurements between *Astrapotherium* and ?*Xenastrapotherium* from Quebrada Honda.

Measurement	<i>Astrapotherium</i> (AMNH 15261)	? <i>Xenastrapotherium</i> (UF 26679)
Occiput		
Height ¹	210 mm	146 mm
Width at base ¹	202 mm	165 mm
Width across condyles ¹	(125 mm)	(125 mm)
Width midway between foramen magnum and occipital crest ²	105 mm	186 mm
Zygomatic width ²	315 mm	(410 mm)

¹Measurements for *Astrapotherium* taken from Scott (1928).

²Measurements for *Astrapotherium* taken from illustrations in Scott (1928).

from Quebrada Honda were most similar to teeth of the *Uruguaytherium-Xenastrapotherium* group. Teeth of *Uruguaytherium* Kraglievich, 1927, all that is known of this Oligocene genus, are larger than *Xenastrapotherium*. On the basis of Hofstetter's (1977) opinion, this partial cranium is tentatively referred to *Xenastrapotherium* as the first skull material known of that genus.

Numerous well preserved crania of *Astrapotherium* from the Santa Cruz Fauna of Argentina exist and form the basis of comparisons between the Astrapotheria and other groups. These comparisons emphasize the unique morphology of the astrapotheres but have left their systematic position in doubt. *Astrapotherium* has a highly modified skull that may represent extreme modification in this group. In several features, the partial skull from Quebrada Honda is less specialized than that of *Astrapotherium* and more like that of *Trigonostylops*. *Trigonostylops* had originally been placed close to *Astrapotherium* in taxonomies (Ameghino, 1906, for example, although incorrectly placed in Amblypoda) but Simpson (1933, 1967), in comparing the skulls of *Trigonostylops* and *Astrapotherium*, saw little to unite these genera and ultimately separated them at the ordinal level as Trigonostylopoidea and Astrapotheria.

Simpson (1967) chose to abandon any special relationship between astrapotheres and trigonostylopoids despite numerous features in common (and which he listed, Simpson, 1933, and 1967, p. 211, reprinted here as Table 2). Simpson (1967) felt that the weight of evidence overwhelmingly favored separate lineages and listed 17 characters that supported this viewpoint (1933 and 1967, Table 73, p. 211, reprinted here as Table 3 with the characters numbered for discussion and the wording occasionally modified for discussion). The many differences that are so readily apparent between the skulls of *Trigonostylops* and *Astrapotherium* appear to derive from the great modification of the skull of *Astrapotherium*. The reduction of the anterior portion of the skull (presumably due to the acquisition of a trunk) in combination with the tremendous enlargement of the molars and the muscle attachment areas necessary to use them, and the massive frontal

doming and enlarged frontal sinuses have all served to emphasize the middle portion of the skull (Fig. 4). The anterior portion of the skull is reduced and the posterior portion of the skull is compressed.

Many of the differences which are due to the specialization of the skull and dentition of *Astrapotherium* become less striking when *Trigonostylops* is compared to a less specialized astrapothere such as *Scaglia* Simpson, 1957 or to the skull from Quebrada Honda. Several characters that are used by Simpson (1933, 1967) are functionally related and are better treated as part of a character suite. Thus several characters become one character and the weight of numbers that favors separation of these two groups is pared considerably. In no event is reversal of characters required in the change from the trigonostylopoid to the astrapothere condition.

My comments in regard to Simpson's comparison list (1933, 1967; see Table 3) with additional information gained from one partial skull from Quebrada Honda are as follows:

1. Multiple infraorbital foramina in *Trigonostylops* and not *Astrapotherium* is interesting but not exceptionally important. The number and placement of infraorbital foramina are highly variable within a species and between closely related species.

2. The prominence and cresting of the orbital rim is a distinctive feature of *Astrapotherium*. However, Simpson's Characters 2, 7, and 8 are actually only a single character that is related to the enlargement of the temporal crest in *Astrapotherium* due to the great lateral expansion and doming of the frontals (Fig. 4). The function of these crests is difficult to understand as they appear to restrict rather than expand the available attachment area for the temporal musculature at the same time that the molars have enlarged and assumed a greater grinding function. The positioning of these crests does not maintain the same approximate angle of action that is seen in *Trigonostylops*. *Scaglia*, in any event, does not have such extraordinary crests nor does the Quebrada Honda specimen.

3. Agree.

4. Agree.

5. Essentially agree. Perhaps "incompletely divided" is more correct for

Table 2.—Similarities between *Astrapotherium* and *Trigonostylops* (from Simpson, 1967:211).

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1. Domed frontals with large sinuses (skull wider at frontals than at parietals).
 2. Possible homologue of the ethmoid foramen in the orbit between the lacrimal foramen and posterior end of the infraorbital series.
 3. Similar arrangement of foramina in and around the orbitosphenoid.
 4. Alisphenoid unpierced externally.
 5. Foramen rotundum confluent with foramen lacerum anterius.
 6. Foramen ovale nearly, or quite, confluent externally with the foramen lacerum medium.
 7. The epitympanic (?) recess communicates with a small sinus in or near the zygomatic root of the squamosal, anterior to the ear region.
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Table 3.— Differences between *Astrapotherium* and *Trigonostylops* (modified from Simpson, 1967).

<i>Astrapotherium</i>	<i>Trigonostylops</i>
1. Infraorbital foramen single, just anterior to orbit, beneath rim.	1. Infraorbital foramen multiple, far from orbit.
2. Orbital rim prominent, crested.	2. Orbital rim low and rounded.
3. Lacrimal foramen, apparently also whole lacrimal, intraorbital.	3. Lacrimal foramen and lacrimal on orbital rim.
4. Palate normal.	4. Peculiar median, bilaterally alate process on palatines.
5. Choanae tubular, undivided.	5. Choanae completely divided by bony median partition.
6. Interorbital foramen entirely in palatine, posterior to maxilla.	6. Interorbital foramen at junction of palatine, orbitosphenoid, and maxilla.
7. Sagittal crest very short.	7. Crest very long.
8. Great overhanging temporal crests.	8. Crests virtually absent
9. Strong posttympanic process of squamosal, closely applied to paroccipital process.	9. Process very short, almost absent, far removed from paroccipital process.
10. Postglenoid and paroccipital processes strong, converging distally, enclosing a very deep, narrow auditory notch.	10. Processes weak, enclosing a broad, shallow, open auditory notch.

Astrapotherium.

6. Agree.

7. The sagittal crest of the Quebrada Honda skull is far longer than that of *Astrapotherium* and intermediate in length between *Astrapotherium* and *Trigonostylops*. This, again, as Character 2, is due to the short posterior portion of the skull and the great frontal doming in *Astrapotherium* (Fig. 4).

8. Great overhanging temporal crests, associated with frontal doming, are absent in the Quebrada Honda *astrapotherium*, hence more similar to *Trigonostylops* than to *Astrapotherium*.

9. Agree.

10. The auditory notch is deep in the Quebrada Honda skull but less narrow than in *Astrapotherium* as the posterior portion of the skull is less compressed than in *Astrapotherium*.

11. The occiput of the Quebrada Honda skull is not deeply constricted on both sides and thus more like *Trigonostylops* (Figs. 3A, 5).

12. Both *Trigonostylops* and *Astrapotherium* exhibit a lateral extension of the occipital-squamosal contact that envelops the mastoid. In *Trigonostylops*, the mastoid is readily visible in occipital view. In *Astrapotherium*, the contact is complete and the mastoid is not visible in occipital view. The Quebrada Honda skull exhibits a somewhat intermediate condition in that the sutural contact is complete or nearly so with a small depression

Table 3.— (cont.)

<i>Astrapotherium</i>	<i>Trigonostylops</i>
11. Occiput deeply emarginate on both sides.	11. Occiput not distinctly emarginate.
12. No occipital exposure of mastoid.	12. Good exposure of mastoid.
13. Basisphenoid-presphenoid exposures very short.	13. Exposures very long.
14. Condylar foramen large, separate at posterointernal end of paroccipital process.	14. Foramen small, opening into a large pit shared with posterior lacerate foramen, internal and some distance from paroccipital process.
15. Whole ventral aspect of auditory region exposed only in roof of a small, deep, constricted pit.	15. Region well exposed ventrally, periotic nearly on level with surrounding external elements.
16. Tympanic evidently small and loosely attached, not found with specimen.	16. Tympanic sutured, large, but not inflated.
17. Hyoid attachment crowded into a groove at junction of posttympanic and paroccipital processes	17. Attachment at posterior end of tympanic, far from processes.

located in the position where the mastoid is visible in *Trigonostylops*. The extensive occipital-squamosal contact appears to be a good apomorphic character for the advanced astrapotheres.

13. Agree; this is also related to shortening of the skull of *Astrapotherium* as discussed in Character 10.

14. Agree.

15. Agree; as in Characters 10 and 13 this too is a factor of face shortening.

16. Character 16 is only another part of Character 15, i.e., a large versus a small tympanic area.

17. Agree; Characters 12, 13–17 certainly are highly correlated features related to compression in this part of the skull.

The shape of the zygomatic arches is much different between *Trigonostylops* and *Astrapotherium* although Simpson did not use this in his list of characters. The zygomatic arches curve dorsally and lie close to the skull in *Astrapotherium*. In *Trigonostylops*, and in the Quebrada Honda skull, the more primitive condition is present in that the arches are relatively horizontal (Fig. 5).

As Simpson (1967) noted, there are certainly differences between the *Trigonostylopoidea* and the *Astrapotheria*. There are, at the same time, a number of characters which unite these two groups and which cause me to emphasize a closer relationship than that chosen by Simpson, i.e., an independent origin from the poorly defined and assuredly composite primitive group, *Condylarthra*. In view of the reexamination of characters

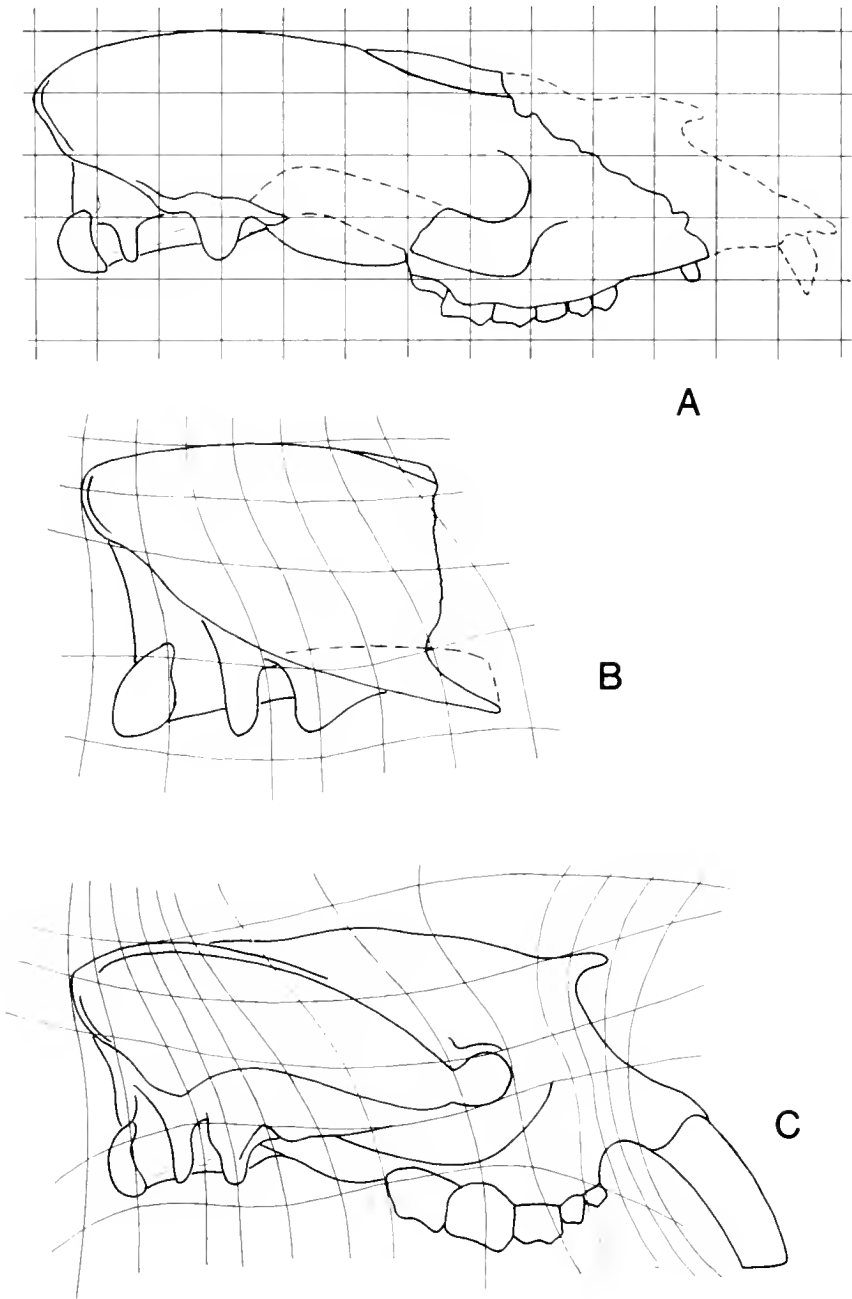


Fig. 4.—Deformed grid comparison of the skulls. A. *Trigonostylops* (AMNH 28700, from Simpson, 1933). B. ?*Xenastropotherium* (UF 26679). C. *Astrapotherium* (AMNH 15261, from Scott, 1928).

permitted by the discovery of the Quebrada Honda skull, placement of these two groups as families, Trigonostylopidae and Astrapotheriidae, within the Order Astrapotheria is sufficient to demonstrate their distinctness.

As so little is known of skeletal elements in this order, most genera of Astrapotheria are defined on dental features. Having reestablished a close relationship between the Trigonostylopidae and the Astrapotheriidae as a result of the discovery of the partial skull described in this paper, one may

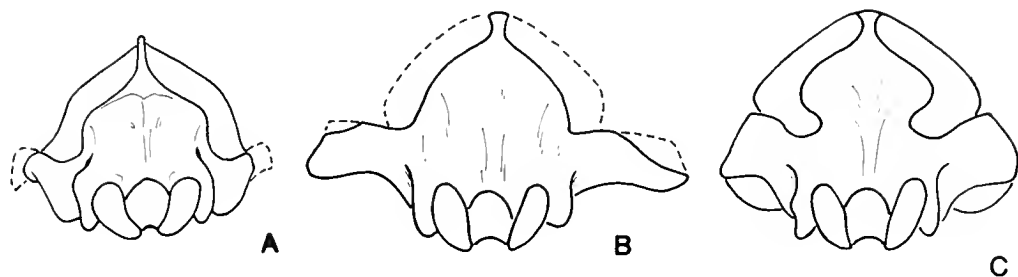


Fig. 5.—Occipital regions. A. *Trigonostylops* (AMNH 28700). B. ?*Xenastrapotherium* (UF 26679). C. *Astrapotherium* (AMNH 15261, from Scott, 1928).

examine the inferred development of dental features in the genera of these two families (Table 4). In so doing, the systematic placement of the genera of this order is hypothesized and presented here in a cladistic framework (Fig. 6). *Xenastrapotherium* and *Uruguaytherium* are not included on this cladogram but this group is included in the discussion that follows.

The progression of dental features in the Astrapotheria follows that of many Tertiary ungulates. Initially, the teeth are low-crowned and bunolophodont with clear evidence of an earlier tritubercular pattern. In later astrapotheres, the molars become fully quadrangular, higher-crowned (never fully hypsodont), and lophodont. There is increased emphasis on the rear portion of the tooth rows demonstrated by the reduction in size and loss of premolars and the enlargement of the molars.

Kraglievich (1928) suggested that the *Xenastrapotherium-Uruguaytherium* group (his Uruguaytheriinae) together with *Astrapotherium* might have originated from *Parastrapotherium* Ameghino, 1895. The Uruguaytheriinae would be a sister-group of *Astrapotherium* in a cladistic expression of this relationship. The skull from Quebrada Honda does not refute this proposal but indicates that the extreme cranial modifications of *Astrapotherium* were not present in *Parastrapotherium* and were not typical of all later-occurring astrapotheres. The Uruguaytheriinae may well represent a separate, and in many respects less modified, astrapotherine lineage in the Miocene.

Astrapotheria have in the past been linked to the Notoungulata (=Toxodonta of Scott, 1912 and later). Loomis (1914) took an extreme position and placed the Astrapotheria as a suborder of the Notoungulata. The notoungulates are well-defined by a number of characters that are not shared with the astrapotheres such as the unusual two-chambered inner ear, flat lower incisors, and the position of the posterior end of the zygomatic arch near the dorsal margin of the skull. However, that notoungulates are more closely related to astrapotheres than to any other known group is amply demonstrated in several characters which are listed in Table 4.

The Trigonostylopidae and the Astrapotheriidae are closely related sister groups that could form a direct ancestral-descendent phyletic relationship (Fig. 6). This agrees with their known temporal occurrences in which the Trigonostylopidae are the earlier occurring group, Riochican and Casa-

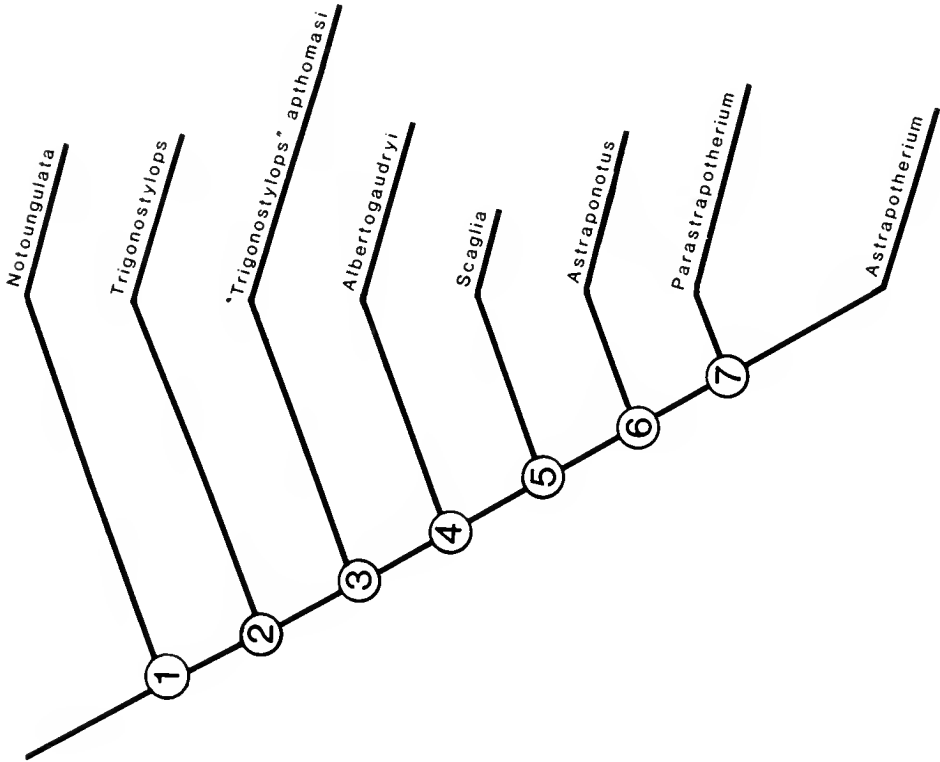


Fig. 6.—Cladistic relationships of Notoungulata and selected genera of Astrapotheria. See Table 4 for characters at nodes.

mayoran, with a Casamayoran to Friasian distribution for the Astrapotheridae.

Astrapotheres are a rare element in the Quebrada Honda Local Fauna and in fact were not included in the latest discussion of the site (Takai et al., 1984). It is interesting to speculate whether the better-known Santacrucian genus, *Astrapotherium*, might have occurred here also or whether certain environmental differences between the Miocene plains of Argentina and this mountain valley were reflected in the resident astrapotheres. The discovery of this specimen, however, adds more to the knowledge of the order than to the faunal assemblage of Quebrada Honda and indicates that the astrapotheres experienced a more complex evolutionary history than is frequently attributed to them.

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Table 4.—Nodes (numbers) and characters used in the phylogenetic tree of the Astrapotheria shown in Figure 6.

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1. Flat ectoloph in which the mesostyle has migrated well forward. Short snout and long cranial proportions of the skull in which the orbit sits well forward (as far as M^1). Bi-crescentic lower molars in which the talonid pillar, when present, sits close to and unites with the anterior part of the second crescent. (As opposed to litopterns in which the retention of the entoconid looks like a talonid pillar. The union is with the posterior end of the posterior crescent as it should be for an entoconid.)
 2. Astrapotheria (See Discussion and Table 2).
 3. Greater bi-crescent pattern, entoconid reduced (no talonid pillar), metaloph separates from protocone, cleft starts to form.
 4. Larger size, talonid pillar present, P_4 molariform, greater hypsodonty, hypocone more prominent.
 5. Astrapotheriidae: hypocone more prominent, metaloph almost complete (still a saddle between metacone and hypocone).
 6. Larger, more hypsodont, small crista present on ectoloph.
 7. Very large molars, very reduced premolars, face and cranial region shortened (middle region of skull emphasized).
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LITERATURE CITED

- Ahlfeld, F. 1956. Bolivia. *In*: W. F. Jenks (ed.). Handbook of South American Geology. Geological Society of America 65:167–186.
- Ahlfeld, F. 1970. Zur Tektonik des Andinen Bolivien. *Geologische Rundschau* 59:1124–1140.
- Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en las terranos Eocenos de la Patagonia austral y depositados en el Museo La Plata. *Boletín de Museo de La Plata* 1:1–26.
- Ameghino, F. 1906. Les formations sédimentaires du crétacé supérieur et du Tertiaire de Patagonie avec un parallèle entre leurs faunes mammalogiques et celles de l'ancien continent. *Anales del Museo Nacional de Buenos Aires* XV (3,VIII):1–568.
- Bordas, A. F. 1941. Restos fósiles de Rincón del Buque (Santa Cruz). *Physis* 19:55–61.
- Charrier, R. 1973. Interruptions of spreading and the compressive tectonic phases of the meridional Andes. *Earth Planetary Science Letters*

20:242-249.

- Frailey, C. D. (In press). The Miocene vertebrates of Quebrada Honda, Bolivia. Part II. Edentata. Occasional Papers Museum Natural History, Univ. Kansas.
- Hoffstetter, R. 1976. Rongeurs caviomorphes de l'Oligocène de Bolivie. I. Introduction au Déséadien de Bolivie. *Paleovertebrata* 7(3):1-14.
- Hoffstetter, R. 1977. Un gisement de mammifères Miocènes à Quebrada Honda (Sud Bolivien). *Comptes-Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris*. D:1517-1520.
- Jenks, W. F. 1956. Peru. *In*: W. F. Jenks (ed.). *Handbook of South American Geology*. Geological Society of America 65:215-247.
- Kraglievich, L. 1928. Sobre el supuesto *Astrapotherium Christi* Stehlin, descubierto en Venezuela, (*Xenastrapotherium* n. gen.) y sus relaciones con *Astrapotherium magnum* y *Uruguaytherium* Beaulieui. Buenos Aires, La Editorial Franco. pp. 1-16. (reprinted in Lucas Kraglievich, *Obras de Geología y Paleontología*, La Plata 2:173-187).
- Loomis, F. B. 1914. *The Deseado Formation of Patagonia*. Rumford Press, Concord, NH. 232 pp.
- Lydekker, R. 1894. Contributions to a knowledge of the fossil vertebrates of Argentina. 3. A study of extinct Argentine ungulates. La Plata, Universidad Nacional, Museo de La Plata, Anales, Sección Paleontológica 2:1-91.
- MacFadden, B. J. and R. G. Wolff. 1981. Geological Investigations of Late Cenozoic vertebrate-bearing deposits in southern Bolivia. II. Congreso Latino-Americano Paleontología, Anais, Porto Alegre. pp. 765-778.
- Marshall, L. G. 1976. Fossil localities for Santacruzian (early Miocene) mammals, Santa Cruz Province, southern Patagonia, Argentina. *Journal of Paleontology* 50(6):1129-1142.
- Patterson, B. and R. Pascual. 1968. New echimyid rodents from the Oligocene of Patagonia, and a synopsis of the family. *Breviora*, 301:1-14.
- Scott, W. B. (ed.). 1903-1932. *Mammalia of the Santa Cruz beds. Reports of the Princeton University Expeditions to Patagonia, 1896-1899*. Princeton University, Princeton, New Jersey.
- Scott, W. B. 1912. Toxodonta. *In*: W. B. Scott (ed.). *Mammalia of the Santa Cruz beds. Reports of the Princeton University Expeditions to Patagonia, 1896-1899* 6(2):111-238, pl. 12-28.
- Scott, W. B. 1928. Astrapotheria. *In*: W. B. Scott (ed.). *Mammalia of the Santa Cruz beds. Reports of the Princeton University Expeditions to Patagonia, 1896-1899* 6(4):v-viii, 301-359, 36 pl.
- Simpson, G. G. 1933. Structure and affinities of *Trigonostylops*. *American Museum Novitates* 608:1-28.
- Simpson, G. G. 1934. Provisional classification of extinct South American hoofed mammals. *American Museum Novitates* 750:1-21.
- Simpson, G. G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* 137:1-259.

- Simpson, G. G. 1967. The beginning of the age of mammals in South America. Part 2. Systematics: Notoungulata, concluded (Typotheria, Hegetotheria, Toxodonta, Notoungulata *incertae sedis*); Astrapotheria; Trigonostylopoidea; Pyrotheria; Xenungulata; Mammalia *incertae sedis*. Bulletin of the American Museum of Natural History, 137:1-260, 46 pls.
- Takai, F., T. Mizuno, A. Yoshida, H. Kondo, B. Arozqueta P., and A. Lema C. 1984. On fossil mammals from the Tarija Department, Southern Bolivia. The Research Institute of Evolutionary Biology, Publication 4:63 pp.
- Yrigoyen, M. R. 1979. Cordillera Principal. Segundo Simposio de Geología Regional Argentina, Córdoba, Argentina, I:651-694.

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