

28 Divisaderan: Land Mammal Age or local fauna?

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Abstract

The mammalian fauna from the Divisadero Largo Formation type locality (Mendoza, Argentina) was originally characterized by the coexistence of taxa with generalized morphology along with some of much more modern aspect. This unique composition led to the proposition that the assemblage represented a Divisaderan South American Land Mammal Age (SALMA). The notoungulates *Etheotherium carettei* (Hegetotheriidae) and “*Trachytherus? mendocensis*” (Mesotheriidae) are the two species with most derived characteristics, comparable to closely related taxa in Deseadan and even post-Deseadan faunas. Based on arguments presented here, these two species probably do not come from the Divisadero Largo Formation but rather from the overlying Mariño Formation, and the systematic position of many other elements of this fauna are reinterpreted. This revision leads to a new proposition that the Divisaderan should not be considered a SALMA, but a local fauna with taxa that are much older than previously considered. The antiquity of the Divisadero Largo fauna is best established with reference to the sequence at Gran Barranca, and provides an example of the significance of this sequence for correlation.

Resumen

La fauna exhumada en la localidad tipo de la Formación Divisadero Largo (Mendoza, Argentina) se caracterizó por la coexistencia de taxa de características generalizadas junto a otros de aspecto mucho más moderno. Esto permitió sustentar la “Edad Mamífero” Divisaderense, la cual está representada exclusivamente por esta fauna. Los notoungulados *Etheotherium carettei* (Hegetotheriidae) y “*Trachytherus? mendocensis*” (Mesotheriidae) son las dos especies de características más derivadas, comparables a las presentes en especies deseadenses y aún postdeseadenses. En este trabajo se certifica que estas dos especies no provendrían de niveles de la Formación Divisadero Largo sino de la suprayacente Formación Mariño y se reinterpreta la posición sistemática de muchos otros integrantes de esta fauna. Esto permite establecer que la “Edad Mamífero” Divisaderense carece de identidad y que no debería ser considerada como tal, sino como una Fauna Local. Por otro lado, el análisis de los taxa que

conforman la fauna Divisaderense sugiere considerarla como mucho más antigua de lo que, hasta el momento, se consideraba. La antigüedad de la fauna de Divisadero Largo se hace con referencia a la secuencia de Gran Barranca, un ejemplo de la utilidad de la secuencia para fines de corelacion.

Introduction

The “magic slate” was a very popular toy in the seventies; it consisted of a small board with a dark waxed cardboard background overlaid by a clear celluloid sheet. A pointed stylus was used to draw or write, and the strokes could be immediately erased by lifting the celluloid sheet. As early as 1924 Sigmund Freud expressed his interest in this toy which provided him a metaphor for the way memory works. Freud observed that while lines were immediately erased, more intense strokes remained impressed in the dark background for ever.

Since its discovery, the fauna from the Divisadero Largo Formation in Mendoza Province has been controversial, not only with respect to the taxonomic identity and mixed evolutionary stage of its components, but also its age, correlation, and validity as a land mammal age. However, like a “magic slate,” careful scrutiny reveals a few indelible strokes that further clarify its relationships.

When referring to the fossil mammals in this fauna, Simpson *et al.* (1962, p. 290), stated that “most and perhaps all of these mammals do not seem to belong in or near lineages known from rich earlier and later faunas” and added later that they “do not know of any such markedly aberrant mammalian fauna from any other continent.”

The fauna from the Divisadero Largo Formation was the basis for the Divisaderan South American Land Mammal Age (SALMA) and defined by Pascual *et al.* (1965) as an assortment of taxa, some with generalized features comparable to Casamayoran and Mustersan taxa along with others with much more modern aspect comparable to Deseadan and post-Deseadan taxa. It was precisely this peculiar concurrence of archaic and advanced taxa that prompted Pascual *et al.* (1965) to propose that this fauna could correspond to a different SALMA that could partially bridge the gap between the Mustersan and Deseadan Ages. Within this context the Divisaderan SALMA was assigned to the late Eocene.

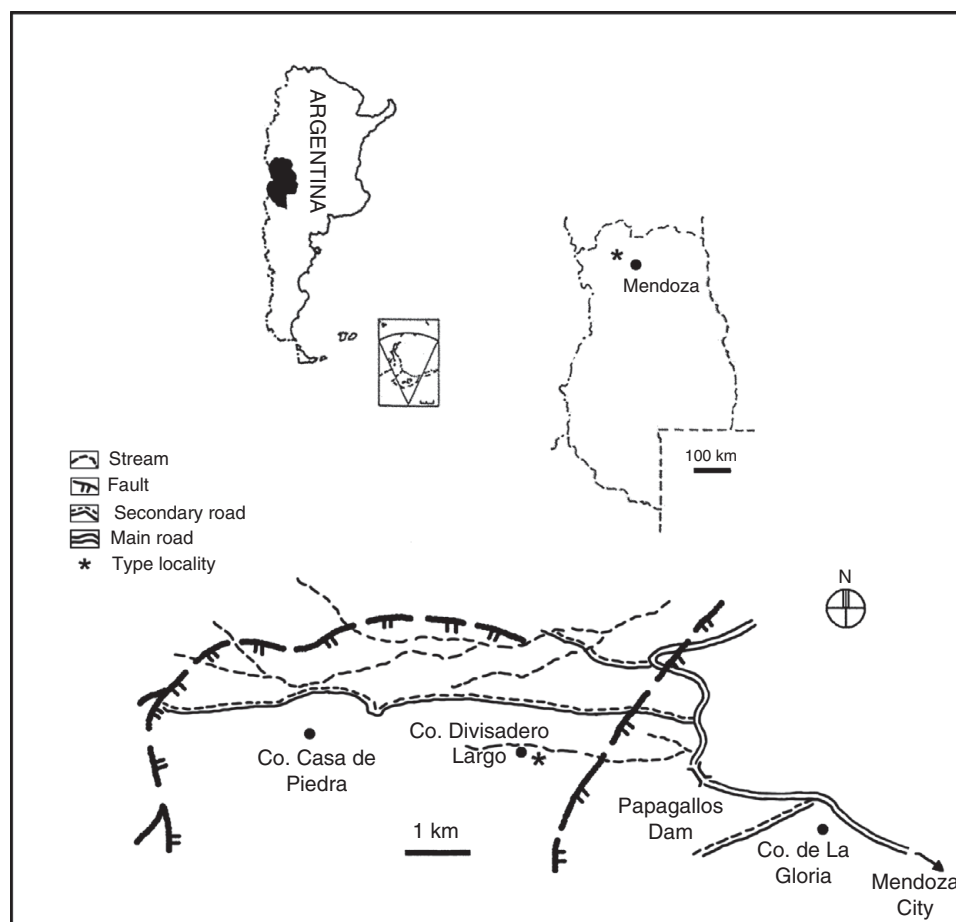


Fig. 28.1. Location map.

The type locality for the Divisadero Largo Formation is located 8 km west of the city of Mendoza in western Argentina (Fig. 28.1), an area where mainly Triassic continental sequences are overlaid by Tertiary synorogenic sediments (Simpson *et al.* 1962) that are in turn overlaid by Quaternary alluvium (Fig. 28.2) in erosive discordance.

The Divisadero Largo Formation of Chiotti (1946) comprises three members distinguished by informal designations “Conglomerado rojo,” “Zona con anhidrita,” and “Arcillas abigarradas” by petroleum geologists of Yacimientos Petrolíferos Fiscales. As currently understood, the Divisadero Largo Formation comprises only the two upper units of Chiotti, whereas the lower member (i.e. “Conglomerado rojo”) was named the Papagallos Formation by Simpson *et al.* (1962). Thus, the lower boundary of Divisadero Largo Formation is the contact with the Papagallos Formation of possibly early Tertiary age and the upper boundary is the contact with the overlying Mariño Formation (= “Serie de las Areniscas Entrecruzadas” or “Inestratificadas” *sensu* Chiotti). At this locality, the Divisadero Largo Formation is an elongate NNE–SSW-trending

band approximately 2.2 km long and between 160 and 250 m thick, that extends from the height of Divisadero Largo to the vicinity of Papagallos. During field work at the type locality, Simpson *et al.* (1962) prospected two fossiliferous exposures, one on the east side of Cerro Divisadero Largo and the other in the cut bank of Arroyo Papagallos.

The Divisadero Largo fauna is comprised entirely of endemic taxa, a fact that has hindered comparisons with other South American faunas. The fact that no comparable faunal assemblage has ever been found in the essentially complete and fossil-rich stratigraphic sequence of Gran Barranca has always been very remarkable.

The temporal hiatus between the Mustersan and Deseadan ages in older biostratigraphic schemes was among the longest of the Cenozoic, and the recognition by Pascual *et al.* (1965, p. 175) of a Divisaderan age was an attempt to fill this gap. However, far from completing the record, the insertion of a Divisaderan age only served to emphasize further the fact that this succession of faunas was apparently still missing crucial pieces. Thus, for many years the

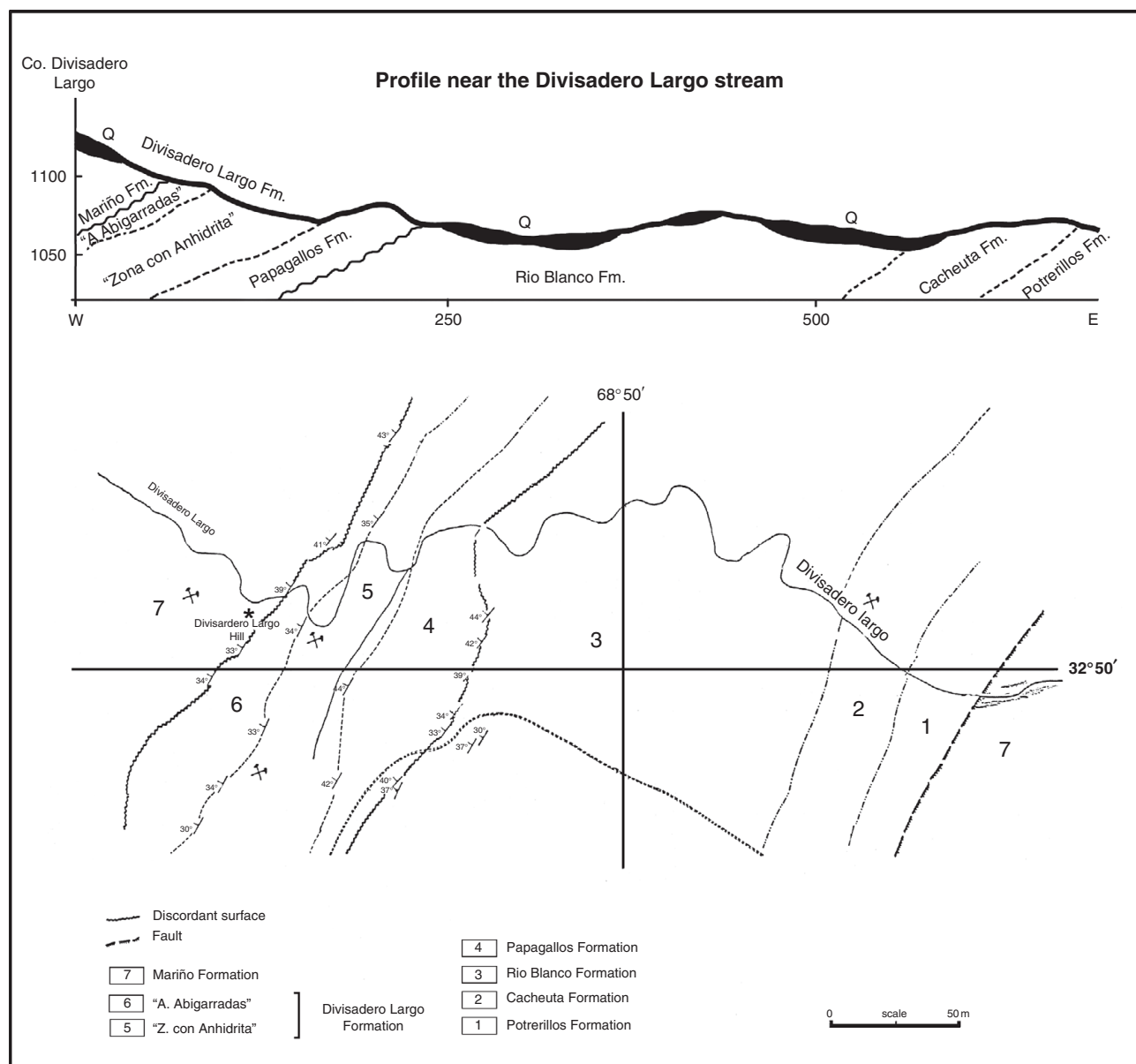


Fig. 28.2. Profile and geologic map of Divisadero Largo-Papagallos area, Mendoza Province.

standard scheme included two well-supported ages (i.e. Mustersan and Deseadan) and an intermediate but poorly understood Divisaderan age, comprising a mixture of taxa that had unclear relationships with both previous and later faunas.

During the last decade, many faunal associations have been discovered that could be referred to the post-Mustersan to pre-Deseadan interval by their intermediate composition. One is the fauna from Tinguiririca in central Chile that was the basis for the Tinguirirican age (Flynn *et al.* 2003). Afterwards, some Patagonian local faunas (e.g. Lomas Blancas, Cañadón Blanco, La Cancha in Gran Barranca,

and Rinconada de los López) were found to be referable to the Tinguirirican age (Reguero *et al.* 2004). Remarkably, in spite of the fact that these assemblages were referred to this temporal interval, none was comparable with the Divisaderan fauna. Even a comparison of "stage of evolution" of their taxa did not suggest correlations between the Divisaderan and other faunas.

In addition, it seemed very striking that in such a complete sequence as the one in Gran Barranca, no fauna comparable to the Divisaderan assemblage had been discovered. Thus, Divisadero Largo fauna retained its enigmatic character as recognized by Simpson *et al.* (1962).

A review of attempts to correlate the Divisadero Largo fauna with other faunal associations reveals two clearly differing opinions: those who found a close relationship with Deseadan associations and those who considered the fauna to have closer affinities with older SALMAs (e.g. Mustersan).

Doubtless the papers by Simpson and his collaborators were the most significant contributions in the first group. The close relationship between Divisadero Largo and Deseadan faunas was supported by four phylogenetic relationships: (1) the species *Phoradiadius divortiensis* is a probable Proterotheriidae; (2) the species *Adiantoides leali* is an Adiantidae; (3) the mesotheriid "*Trachytherus? mendocensis*" is related to species of *Trachytherus* recorded at Deseadan levels in Patagonia; and (4) that *Ethegotherium carettei* displays a suite of derived characters comparable to Deseadan taxa. The species mentioned in items 3 and 4 are precisely those distinguished by Marshall *et al.* (1986, p. 946) as representing "taxonomic ties" with Deseadan associations.

Other researchers adopted to the position that the Divisadero Largo fauna had a closer relationship with older associations. Ortiz Jaureguizar (1986, 1988), applying techniques of multivariate analysis, recognized an "Infraceozoic Faunistic Episode" comprising the Itaboraian, Riochican, Casamayoran, Mustersan, and Divisaderan Ages, and a "Pre-Patagonian Faunal Cycle" to comprise the last three of these ages. This criterion was followed by Pascual and Ortiz Jaureguizar (1990) and Pascual *et al.* (1996). In addition, Bond (1991), when presenting a critique of MacFadden *et al.*'s (1985, p. 243) proposal that the lowermost levels of Salla "is either pre-Deseadan (? Divisaderan) or earliest Deseadan in age", marshaled lines of evidence to suggest that the Divisaderan fauna is older than Deseadan.

For almost 20 years, then, as other South American Paleogene faunas became better known, the endemism of the fauna from Divisadero Largo came to be viewed as a peculiar and isolated ecological enclave with no clear relationships. The discovery of mammals in lower Tertiary sediments in northwestern Argentina (e.g. Mealla and Lumbraera Formations: Pascual *et al.* 1981), in levels referred to the Eocene–Oligocene boundary in Chile (i.e. Tinguirirican age: Flynn *et al.* 2003) and the reinterpretation of several Patagonian faunas that are partly equivalent to the Tinguiririca fauna, along with a revised assessment of the temporal gap that was originally recognized by the Ameghino brothers (i.e. "Astraponotéen le plus supérieur": Bond *et al.* 1996), now provide insights into the affinities of some of the lineages occurring in this peculiar fauna.

The Divisaderan fauna

The lower and middle Divisadero Largo Formation has yielded a vertebrate fauna composed essentially of mammals and a few reptiles (i.e. turtles, crocodiles, and boas).

Minoprio (1947) mentioned the existence of a turtle shell, which he illustrated but did not describe. In their list of Cenozoic fossil vertebrates of Mendoza, Pascual and de la Fuente (1993) referred these remains to indeterminate pleurodiran turtles. The Order Crocodylia is represented by the species *Ilchunaia parca* Rusconi (1946b) on the basis of mandibular and cranial remains assigned to the Family Crocodylidae. Later, Langston (1956) tentatively assigned this species to the Sebecosuchia and Gasparini (1972) referred it with some doubt to the Sebecidae. The assignation of the original material, along with other remains found later, to Sebecosuchia is based on the high long rostrum and laterally compressed teeth with serrated edges (Gasparini 1972). *Cunampaia simplex*, described by Rusconi (1946b, 1946c) based on remains of fore and hindlimbs, was thought to be the only fossil bird in this formation, but it has recently been recognized as a crocodile by Agnolín and Pais (2006). Simpson *et al.* (1962) briefly commented on the existence of ophidian remains from the Divisadero Largo Formation but did not provide a description. Albino (1989) describes this material (vertebrae with bodies that are short, broad, high, and robust) and refers them to Family Boidae. The subfamilial assignation of this material remains doubtful; some are possibly Erycinae, others Boinae, and two fragments are indeterminate.

Mammals comprise more than 95% of the remains collected from this unit, and remarkably, almost all of them can be referred to South American native ungulates. Two marsupial species were recognized: *Groeberia minoprioi* Patterson 1952 and *Groeberia pattersoni* Simpson 1970. *Groeberia* is characterized by an unusual combination of characters (e.g., gliriform upper and lower incisors, with enamel restricted to the labial face, small canines, forward-directed orbits, a very deep mandibular ramus with a vertical symphysis. Family Groeberiidae (Patterson 1952) and Order Groeberida (Pascual *et al.* 1994) were created. Flynn and Wyss (1999) based in part on more recently described *Klohnia charrieri*, a groeberid from Tinguiririca with more derived traits than *Groeberia*, refer this family to the Argyrolagoidea (Ameghino 1904) which includes *Groeberia minoprioi*, *G. pattersoni*, *Klohnia charrieri*, and *Patagonia peregrina* Pascual and Carlini (1987), the last based on material from the Colhuehuapian at Gaiman in Patagonia.

Carlos Rusconi, the former director of the Museo de Historia Natural (now Museo de Ciencias Naturales y Antropológicas "J.C. Moyano") in Mendoza, mentioned the existence of osteoderms of "desipodinos terciarios" (*sic* Rusconi 1946a) in the Divisadero Largo Formation and in that same year (Rusconi 1946c) referred these alleged scutes to "un dasipodino del tamaño de los eutatus, pero de figura confusa." Unfortunately, none of these were illustrated by Rusconi and they are currently lost. Given that

| Simpson <i>et al.</i> 1962 | In this chapter |
|--|---|
| <p>ORDER MARSUPIALIA Family Groeberiidae <i>Groeberia minoprioi</i> Patterson 1952.</p> | <p>MARSUPIALIA Order Groeberida Family Groeberiidae <i>Groeberia minoprioi</i> Patterson 1952. <i>Groeberia pattersoni</i> Simpson 1970.</p> |
| <p>ORDER LITOPTERNA Family Adiantidae <i>Adiantoides leali</i> Simpson and Minoprio, 1949.</p> | <p>ORDER LITOPTERNA Family Sparnotheriodontidae <i>Phoradiadius divortiensis</i> Simpson <i>et al.</i> 1962.</p> |
| <p>Family Proterotheriidae? <i>Phoradiadius divortiensis</i> Simpson <i>et al.</i> 1962.</p> | |
| <p>ORDER NOTOUNGULATA Family Oldfieldthomasiidae? <i>Brachystephanus postremus</i> Simpson <i>et al.</i> 1962. <i>Xenostephanus chiottii</i> Simpson <i>et al.</i> 1962. <i>Allalmeia atalaensis</i> Rusconi 1946.</p> | <p>ORDER NOTOPTERNA Family Indaleciidae <i>Adiantoides leali</i> Simpson and Minoprio 1949.</p> |
| <p>Family Hegetotheriidae <i>Ethegotherium carettei</i> (Minoprio 1947).</p> | <p>ORDER NOTOUNGULATA Unnamed family <i>Brachystephanus postremus</i> Simpson <i>et al.</i> 1962. <i>Xenostephanus chiottii</i> Simpson <i>et al.</i> 1962. <i>Allalmeia atalaensis</i> Rusconi 1946.</p> |
| <p>Family Mesotheriidae <i>Trachytherus? mendocensis</i> Simpson and Minoprio 1949.</p> | <p>Family Henricosborniidae? <i>Acamana ambiguus</i> Simpson <i>et al.</i> 1962.</p> |
| <p>ORDER AND FAMILY INDET. <i>Acamana ambiguus</i> Simpson <i>et al.</i> 1962.</p> | <p>ORDER ASTRAPOTHERIA Trigonostylopidae Gen et sp. indet. López 2006.</p> |

Fig. 28.3. Comparison between taxa recognized by Simpson *et al.* (1962) and those presented in this chapter.

no armadillo scutes have ever been collected by any of the numerous later expeditions, it is possible that this material could have been chelonian plates. The lack of any record of dasypodids or any other xenarthran at Divisadero Largo is especially noteworthy because the order is very diverse and material is common in both older and younger faunal associations. Their absence at Divisadero Largo could be due to paleoenvironmental factors (Lopez 2008).

The marked dominance of native ungulates in the Divisadero Largo Formation (Orders Notoungulata, Litopterna, Notopterna, and Astrapotheria) is striking. Although Notoungulata are the most abundant and diverse, their occurrence is restricted to two families. Simpson *et al.* (1962) reported the families Hegetotheriidae and Mesotheriidae (each represented by a single species) but referred the most abundant taxa (*Brachystephanus*, *Xenostephanus* and *Allalmeia*) with doubt to the Family Oldfieldthomasiidae (Fig. 28.3). Bond (1981) recognized that on dental and cranial characters, these genera should be grouped with *Colbertia* (from the Itaboraian of Brazil and Eocene of northwestern Argentina) and *Maxschlosseria* (from the Patagonian Vacan) rather than with the remaining Oldfieldthomasiidae. Later, López and Bond (2003) recognized a new family as yet unnamed for these five taxa. This new

family unites taxa that differ from Oldfieldthomasiidae by the possession of:

- (1) skull with shorter rostrum, proportionally larger bullae, marked sagittal and cranial ridges, and more anteriorly implanted zygomatic arch;
- (2) teeth typically brachydont (whereas the molars of the Oldfieldthomasiidae have proportionally higher crowns);
- (3) I1 not enlarged; P1 very small and not elongated mesiodistally; P2 and P3 with transverse-oriented major axis, simple premolar crowns with one lingual cusp and one labial cusp developed into a short ectoloph without metacone; P4 without hypocone;
- (4) M1–2 with protocone and hypocone independent from each other or only basally united, ectoloph normally lacking mesostyle or with a very rudimentary one, and small and ephemeral antero- and posteroexternal fossettes; M3 normally without hypocone, when present very small and bunoid (e.g. *Allalmeia*) and with a very rudimentary mesostyle only in *Colbertia lumbrense*; and
- (5) p1 small, p2 very simple, and p3–4 not molarized.

Most of these features are relatively primitive with respect to other Oldfieldthomasiidae, yet derived with respect to Henricosborniidae (Lopez 2008).

On the basis of a relatively complete skull and mandible preserved in two rock fragments, Minoprio (1947) described *Prohegetotherium carettei* and later Simpson *et al.* (1962) recognizing differences at the generic level, established the new combination *Ethegotherium carettei*. This species is known only by its type material and its very high-crowned teeth were one crucial element used to refer the Divisadero Largo fauna to a Deseadan (Simpson and Minoprio 1950) or “approximately early Deseadan or latest pre-Deseadan” age (Simpson *et al.* 1962, p. 290). Although *E. carettei* is clearly a more modern species compared with the other notoungulates from Divisadero Largo, its stratigraphic provenance was never doubted. Recently, López and Manassero (2008), based on a petrographic study of formation sediments, demonstrated that it comes from younger levels of the overlying Mariño Formation, rather than from the Divisadero Largo Formation.

A similar situation concerns the other species of this fauna with derived characteristics. The description of the mesotheriid “*Trachytherus? mendocensis*” Simpson and Minoprio 1949 was based on isolated teeth from a single individual, of which the premolars (P2–3), one M1, and fragments of M2, all from the right side, are the most complete elements. These teeth, along with many other materials from the Museo de Ciencias Naturales y Antropológicas “J. C. Moyano,” are regrettably lost and no illustrations were ever published except for a simple sketch. Simpson *et al.* (1962) added to the hypodigm one isolated right M, collected by Olivo Chiotti in 1945 and deposited in the Museo de La Plata (MLP 45-VII-10–2). All these teeth are high-crowned and, although their roots are not preserved, they can be considered protohypsodont, a remarkable characteristic in the general context of the Divisadero Largo fauna. Recently, Cerdeño *et al.* (2005, 2008) reported finding an indeterminate mesotheriid from the basal levels of the Mariño Formation, 100 m above the levels bearing the Divisadero Largo fauna. As this specimen is indistinguishable from the M3 referred to “*Trachytherus? mendocensis*” (the only material currently preserved), the originally supposed stratigraphic provenance of the species is brought into question. Cerdeño (2008) noted the close phylogenetic relationship of this new material with *Altitypothierium chucalensis* (Croft *et al.* 2004), a mesotherine from the early Miocene Chucal Formation in Chile.

The enigmatic species *Acamana ambiguus* Simpson *et al.* 1962 was originally of uncertain ordinal and familial affinity. When created, the peculiar combination of small I1–2, enlarged I3, reduced C, and diastema was unknown in any other South American mammal. The subsequent description of *Simpsonotus* (Pascual *et al.* 1979), an henricosborniid from the Mealla Formation, allowed Bond and Vucetich (1983) to establish possible phylogenetic

relationships with *Acamana* although the type and only known material of *A. ambiguus* has been lost.

Divisadero Largo Litopterna are represented by *Phoradiadius divortiensis* (Simpson *et al.* 1962), originally referred to the Proterotheriidae. Later Soria (1980b) demonstrated its close relationship with *Sparnotheriodon epsilonoides* (Soria 1980a) and *Victorlemoinea emarginata* (Ameghino 1901), and referred these taxa to Sparnotheriodontidae. New undescribed material confirms the close phylogenetic relationship between *P. divortiensis* with species of *Victorlemoinea*, especially *V. labyrinthica* Ameghino 1901. Although the systematic position of the Sparnotheriodontidae is debated, López (1999) argued for litoptern affinity on the basis of dental characteristics.

The species *Adiantoides leali* Simpson and Minoprio 1949 was originally described as an adiantid litoptern, but the discovery of *Indalecia grandensis* Bond and Vucetich 1983 revealed affinities between the two species and justifies the establishment of the family Indaleciidae (Soria 1984). Indalecids, Amilnedwardsiidae, and Notonychopidae comprise the Order Notopterna (Soria 1989a, 1989b).

Based on fragmentary but diagnostic material, López (2006) established the first record of the Order Astrapotheria in the Divisadero Largo fauna. The material consists of a mandibular symphysis (MLP 87-II-20–74) preserving part of the crown of the left i1, the right i2 and canine, as well as the alveoli of the right i1 and i3. The roots of i2, i3, and canine can be seen on the left side. The hemimandibles are completely fused and bear evident mental foramina on both sides near the midline. The implantation of the canines and the morphology of the preserved canine crowns and incisors indicate affinities with trigonostyloid astrapotheres, in particular to *Trigonostylops* sp., a taxon characteristic of the Patagonian Casamayoran SALMA (López 2006).

Is the Divisaderan a South American Land Mammal Age?

As the two species with derived characteristics (i.e. “*Trachytherus? mendocensis*” and *Ethegotherium carettei*) do not come from the same stratigraphic level as the rest of the Divisadero Largo fauna, the mixture of primitive and modern taxa used to argue in support a different SALMA for the post-Mustersan and pre-Deseadan allocation collapses.

After excluding the elements with advanced characteristics, the age of the Divisaderan fauna still needs to be established. On the basis of its composition, the Divisadero Largo faunal assemblage shows closer affinity with Casamayoran age faunas than with faunas from the Mustersan.

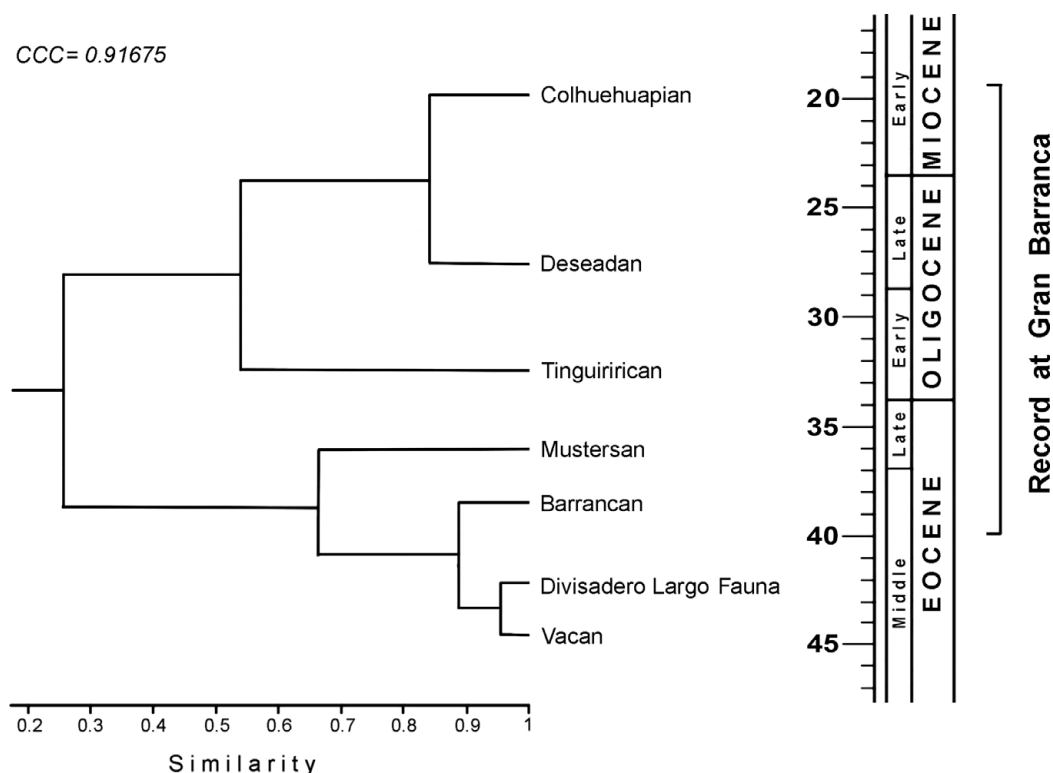


Fig. 28.4. Cluster analysis using mammal assemblages as operational units and families as characters.

The two species of *Groeberia* are not indicative of a particular age but support a correlation with faunas older than Tinguirirican.

The Sparnotheriodontidae *Phoradiadius divortiensis* is at an “evolutionary stage” comparable to *Victorlemoinea labyrinthica* Ameghino 1901 from western Río Chico, of Vacan age (Simpson 1967). The Family Sparnotheriodontidae is recorded in sediments referable to Itaboraian, Riochican, and Casamayoran in Argentina and Brazil, and from levels assignable to Eocene in the Antarctic Peninsula.

The Indalecidae of the Divisadero Largo fauna are represented by *Adiantoides leali*, which is morphologically very similar except for its larger size to *Adiantoides magnus* Cifelli and Soria 1983 from Cañadón Vaca. Bond and Vucetich (1983) in the description of the species *Indalecia grandensis* from the Lumbrera Formation of Casamayoran age (Pascual *et al.* 1981) recognized its close relationship with *A. leali*.

Brachystephanus, *Xenostephanus*, and *Allalmeia* have been referred to a new unnamed family by López and Bond (2003) comprising the species of *Colbertia* from the Brazilian Itaboraian and the Lumbrera Formation in northwestern Argentina and another species from Cañadón Vaca (López 2008). The characteristics of this new family are clearly primitive with respect to those of oldfielthomasiids.

The Family Henricosborniidae characterize both Riochican and Casamayoran faunas. If the referral of *Acamana*

ambiguus to this family is confirmed, it would represent an additional element suggesting a much older age for the Divisadero Largo fauna. Likewise the astrapothere *Trigonostylops* is characteristic of the Casamayoran levels in Patagonia.

Mammals are not the only elements available for comparison. Sebecids and boas are prominent elements in Casamayoran associations and are not found in Mustersan faunas.

A multivariate cluster analysis was performed using different mammal assemblages as operational units and families as characters. The mammal-bearing units include various levels recorded in Gran Barranca (i.e. Barrancan, Mustersan, Tinguirirican, Deseadan, and Colhuehuapian) and the Vacan subage. Because the Divisadero Largo Fauna includes endemic genera, families were the hierarchical category used in the analysis.

On a data matrix of 43 taxa and 7 faunas (Appendix 28.1), cluster analysis was performed in NTSYS 2.0 software (Rohlf 1977) using the Jaccard coefficient. The Cophenetic Correlation Coefficient is elevated (CCC = 0.91675).

The cluster analysis shows two principal groups. The branch including the Divisadero Largo fauna is arranged as follows: (((Vacan subage + Divisadero Largo Fauna) Barrancan subage) Mustersan). The second branch

is formed by the Tinguirirican plus the Deseadan and Colhuehuapian SALMAs (Fig. 28.4).

Based on G.G. Simpson's field notes, Cifelli (1985) recognized two subages for the Casamayoran, an older Vacan and a younger Barrancan. Remarkably, although these subages are well supported, they are seldom used in practice and the term Casamayoran is often still used. As mentioned above, the endemic nature of the taxa in the Divisadero Largo fauna hinders comparisons, and consequently any referral to either Vacan or Barrancan subage implies a degree of uncertainty. Nevertheless, the absence of a directly comparable fauna in the rich and complete stratigraphic sequence at Gran Barranca might be attributed to a still older age for the Divisadero Largo local fauna,

possibly corresponding to either the Vacan subage or the temporal hiatus between the Vacan and the Barrancan. Levels of such age have not been recorded at Gran Barranca nor elsewhere in Patagonia.

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Appendix 28.1 Data matrix of families and mammal assemblages

| | Div. Largo | | | | | | |
|-------------------------|------------|-------|-----------|-----------|--------------|----------|--------------|
| | Vacan | Fauna | Barrancan | Mustersan | Tiguirirican | Deseadan | Colhuehupian |
| BONAPARTHERIIDAE | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| BORHYAENIDAE | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| DIDELPHIDAE | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| GROEBERIIDAE | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| POLYDOLOPIDAE | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| PREPIDOLOPIDAE | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| DASYPODIDAE | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| GLYPTODONTIDAE | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| MEGATHERIIDAE | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| OROPHODONTIDAE | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| PALAEOPELTIDAE | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| DIDOLODONTIDAE | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| INDALECIIDAE | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| SPARNOTH ERIODONTIDAE | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| ADIANTHIDAE | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| MACHRAUCHENIIDAE | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| PROTOTHERIIDAE | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| ARCHAEOHYRACIDAE | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| ARCHAEOPITHECIDAE | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| HEGETOTHERIIDAE | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| HENRICOSBORNIIDAE | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| HOMALODOTHERIIDAE | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| INTERATHERIIDAE-NOTOPIT | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| INTERATHERIIDAE-INTERAT | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| ISOTEMNIDAE | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| LEONTINIDAE | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| MESOTHERIIDAE | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| NOTOHIPPIDAE | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| NOTOSTYLOPIDAE | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| OLDFIELDTHOMASIIDAE | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| UNNAMED FAMILY | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| TOXODONTIDAE | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| ASTRAPOTHERIIDAE | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| TRIGONOSTYLOPIDAE | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| PYROTHERIIDAE | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| CEBIDAE | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| CEPHALOMYIDAE | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| DASYPROCTIDAE | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| DINOMYIDAE | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| ECHIMYIDAE | 0 | 0 | 0 | 0 | 0 | 1 | 1 |

(cont.)

| | Div. Largo | | | | | | |
|----------------|------------|-------|-----------|-----------|--------------|----------|---------------|
| | Vacan | Fauna | Barrancan | Mustersan | Tiguirirican | Deseadan | Colhuehuapian |
| EOCARDIDAE | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| ERETHIZONTIDAE | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| OCTODONTIDAE | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| CHINCHILLEDIAE | 0 | 0 | 0 | 0 | 1 | 1 | 1 |

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