

BIOSTRATIGRAPHIC CONSIDERATIONS OF THE DIVISADERAN FAUNAL ASSEMBLAGE

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Since the 1930s, a rich vertebrate fauna has been collected in Cenozoic sediments of the Divisadero Largo Formation in the Divisadero Largo area, 8 km West of Mendoza city, Mendoza Province, Argentina (see Simpson et al., 1962 and references therein; Fig. 1). This faunal assemblage was mainly based on eight mammal species (Simpson et al., 1962), but also contained several reptiles (turtles, crocodiles, and boas) and a running bird, recently recognized as a crocodile (Agnolin and Pais, 2006). The peculiarity of this association led to the establishment of the Divisaderan Land Mammal Age (Pascual et al., 1965), corresponding to late Eocene, partially filling the gap between the Mustersan and Deseadan ages. The most outstanding feature of this faunal assemblage was the coexistence of primitive, generalized mammal taxa with two other species that presented advanced characters—such as hypsodonty—comparable to those observed in younger Deseadan (late Oligocene) and post-Deseadan taxa. These two taxa are the notoungulates ‘*Ethgetotherium carettei*’ (Minoprio, 1947) (Hegetotheriidae: Hegetotheriinae) and ‘*Trachytherus? mendocensis*’ Simpson and Minoprio, 1949 (Mesotheriidae: Trachytheriinae?). A third taxon, *Acamana ambiguus*, very incompletely known, was also used to tie the fauna to the Deseadan fauna of Salla, Bolivia (MacFadden et al., 1985; Marshall et al., 1986); this species was later related to the Henricosborniidae *Simpsonotus* from the Riochican age of northwestern Argentina (Bond and Vucetich, 1983). The discovery of mammal remains in the Mariño Formation (early Miocene) of Divisadero Largo (Cerdeño et al., 2006; Cerdeño and Vucetich, 2007) and the accuracy of the stratigraphic provenance of the ‘*E. carettei*’ remains (López and Manassero, 2006, 2008) lead us to state that these aforementioned taxa do not correspond to the Divisaderan levels. Therefore, doubts arose about the validity of the Divisaderan land mammal age as firstly characterized.

Taxonomic and Sedimentological Remarks

The recent discovery of a mesotheriine (Mesotheriidae) from the Miocene levels of the Mariño Formation has revealed the presence of mammals in this formation (Cerdeño et al., 2006), which overlies the Divisadero Largo Formation in the same area of the Natural Reserve of Divisadero Largo.

The M3 of this new material presents clear similarities with MLP 45-VII-10-2, the mesotheriid from the Divisadero Largo Formation referred to ‘*Trachytherus? mendocensis*’ by Simpson et al. (1962) and presently stored at the Museo de La Plata (MLP) (also figured in Cerdeño, 2007). This M3, originally included in Chiotti’s collection, has no detailed stratigraphic infor-

mation, although Minoprio (1947) stated that specimens given by Chiotti to Dr. Cabrera came from the same red-brown and chocolate sandstones as ‘*E. carettei*’ (see discussion below on its origin). Consequently, the M3 at least could correspond to the Mariño Formation and to the same taxon as the new described mesotheriine (Cerdeño, 2007).

The holotype of ‘*T. mendocensis*’ is a partial upper dental series with isolated right P2–P3, M1 and M2, and fragments of three other left teeth; it was described by Simpson and Minoprio (1949) and Simpson et al. (1962) but has been lost and no photograph was ever published, only the schematic drawing reproduced in Figure 2. Dimensions were only provided for M1, and some discrepancies have been detected in different papers concerning which parts of M2 were preserved. Compared to the Mariño Formation specimen, the figured P2–3 could actually correspond to P3–4, which would imply a probable absence of P2, a feature characteristic of Mesotheriinae instead of Trachytheriinae. The morphology of M1 (as seen in the original drawing) suggests referral to Trachytheriinae because mesotheriines usually have a more developed median lobe in M1. Nevertheless, among the three mesotheriines from the Chucal Formation in Chile (Croft et al., 2004), *Altityotherium chucalensis* shows a M1 with a less developed median lobe, intermediate between that of ‘*T. mendocensis*’ and other mesotheriines. The mesotheriine from the Mariño Formation has been identified as cf. *A. chucalensis* (EC, pers. observ.; Cerdeño, 2007) and its M1 fragment also has a short median lobe. Details on the precise locality

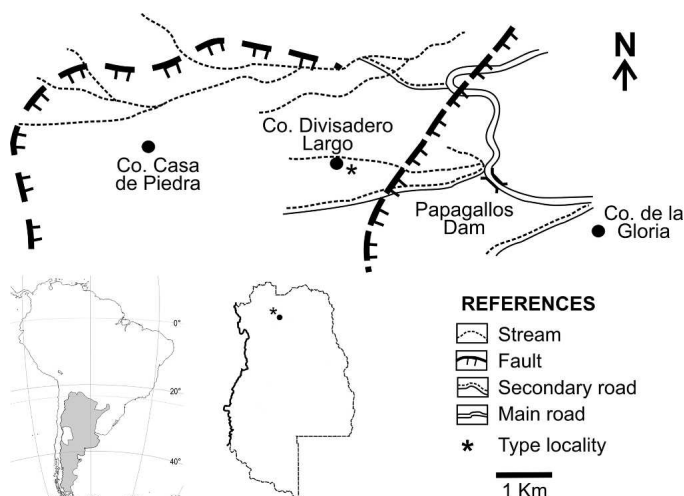


FIGURE 1. Geographic location of the Divisadero Largo area, Mendoza Province, Argentina.

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TABLE 1. Age implications of “Divisaderan” mammals.

Provenance	Taxon	Implied age	Comments
Mariño Fm.	Mesotheriine	Santacrucian	Similar to <i>Altitypotherium chucalensis</i>
	Hegetotheriid	Deseadan?	Related to <i>Prohegetotherium sculptum</i>
Divisadero Largo Fm.	<i>Groeberia</i> sp.	Pre-Tinguirirican	Two endemic species, more basal than Tinguirirican form.
	<i>Phoradiadus divortiensis</i>	Vacan subage	Related to <i>Sparnotheriodon</i> sp. and <i>Victorlemoinea emarginata</i>
	<i>Adiantoides leali</i>	Vacan subage	Related to <i>A. magnus</i> and <i>Indalecia grandensis</i>
	cf. <i>Trigonostylops</i>	Casamayoran s.l.	Related to <i>Trigonostylops wortmani</i>
	“Oldfieldthomasiidae”	?Vacan subage	Three endemic genera, probably represent a new family
	<i>Acamana ambiguus</i>	? Riochican or ? Casamayoran	Related to <i>Simpsonotus</i> from Mealla Fm.

where the holotype specimen was discovered are ambiguous. Simpson and Minoprio (1950) indicated the “pie del Cerro Divisadero Largo” (Divisadero Largo foothill), but the sediments closer to the foothill are Mariño Formation. Thus, this fact, together with the lack of a real knowledge of the type material, supports referral of all material to the Mesotheriinae.

In their description of ‘*Trachytherus mendocensis*,’ Simpson and Minoprio (1949) only compared it with Deseadan *T. spegazzinianus* Ameghino, assuming the previously assigned Deseadan age for the fauna of Divisadero Largo. In Simpson et al.’s (1962) later description of the additional M3, they doubted its generic position, referring it to *Trachytherus?* *mendocensis*. Reguero (1999) recently considered it as a possible new trachytheriine genus, but the noted differences with respect to *Trachytherus* are similarities with respect to mesotheriines. In a recent phylogenetic analysis of the Mesotheriidae (Reguero and Castro, 2004), *T.?* *mendocensis* appears as a basal mesotheriid and the Subfamily Trachytheriinae as a paraphyletic group. However, it must be taken into account that 27 of the 38 considered characters are missing for this species, and some others are incorrectly coded (e.g., character 7 is 1, not 0; character 16 is unknown and should be coded as ‘?’ instead of 1) or debatable (characters 9, 11, and 19); a new analysis probably would affect the position of this species, placing it closer to mesotheriines.

The hegetotheriid ‘*E. carettei*’ was first described as a new species of *Prohegetotherium* (Minoprio, 1947) and later assigned to a new genus, *Ethegotherium* (Simpson et al., 1962). Reguero (1999) considered it synonymous with *P. sculptum*, but López (2002) later revalidated the genus and species. More recently, it was compared with material from the Deseadan of Salla (Bolivia) and subsumed into *P. schiaffinoi*, known from Uruguay, Argentina and Bolivia (Reguero and Cerdeño, 2005). The most recent phylogenetic analysis performed by Reguero and Prevosti (submitted) shows that *P. schiaffinoi*, *P. sculptum*, and *Sallatherium altiplanensis* form the sister group to the clade of post-Deseadan hegetotheriids. No temporal differences are seen between *P. sculptum* and *P. schiaffinoi* from these results. ‘*E. carettei*’ is based on a nearly complete skull and mandible (Fig. 3) divided between two rock fragments, each presently stored in a different institution: the Museo Argentino de Ciencias Naturales, Buenos Aires, and the Museo Paleontológico of the Uni-

versity of Córdoba (see López, 2002, for details). Under the suspicion that ‘*E. carettei*’ could come from younger stratigraphic levels—supported by the finding of mammal remains in the Mariño Formation—a petrographic analysis was performed for the holotype sediment as well as for Divisadero Largo and Mariño formations samples (López and Manassero, 2006, 2008). The sediment containing the holotype of ‘*E. carettei*’ was found to share more similarities with the sediments of the Mariño Formation than the Divisadero Largo Formation. This species therefore does not likely correspond to the Divisadero Largo Formation and should not pertain to the Divisaderan Fauna.

‘*Trachytherus?* *mendocensis*’ and ‘*E. carettei*’ were considered for years as the oldest records of their respective families, Mesotheriidae and Hegetotheriidae (e.g., Flynn et al., 2003), but this is now invalidated due to their revised stratigraphic provenances. The systematic relationships with other mesotheriines and hegetotheriines, respectively, have to be re-examined to clarify the relative ages of both taxa. ‘*T.?* *mendocensis*’ is likely related to the Chucal mesotheriines, indicating an early Santacrucian age (EC, pers. observ.; Cerdeño, 2007), whereas ‘*E. carettei*’ is likely related to *P. schiaffinoi* from Salla and Corrientes, of Deseadan age (Reguero and Cerdeño, 2005). The latter observation is not compatible with the established early Miocene age for the Mariño Formation fossiliferous beds, however. A very careful revision of this taxon is necessary to resolve this discrepancy, but such an analysis is beyond the scope of this paper.

Another observation that should be taken into account regarding the provenance of these species is the fact that through years of collecting fossils from the Divisadero Largo Formation, particularly during the last 6 years, no other remains of these taxa have been discovered (we have preliminarily reviewed the new material). This supports the doubtful provenance of both holotypes and the probability that they correspond to the Mariño Formation, which still has been little explored.

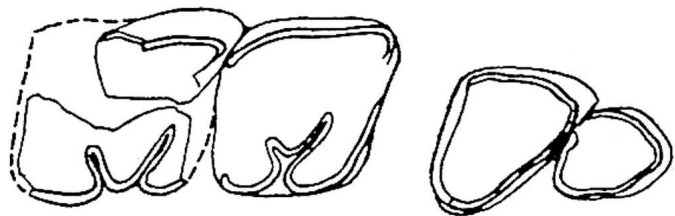


FIGURE 2. Schematic drawing of the holotype of “*Trachytherus mendocensis*” MHNM 2494 (presently MCNAM-PV 2494, now lost), after Simpson et al. (1962). The specimen was originally interpreted as P2-P3 and M1-M2 but is here reinterpreted as probably P3-P4-M1-M2.



FIGURE 3. Holotype of “*Ethegotherium carettei*” (MACN 16609). The other half of the specimen stored in the Córdoba University has been defined as cotype. Scale bar equals 3 cm.

In addition, taxonomic revisions of the Divisaderan taxa by one of us (GL, pers. observ.; López, 2008) and other authors have led to several systematic changes that separate this fauna from typical Deseadan assemblages, as already stated by Bond (1991). Several notoungulates originally considered as belonging to the Oldfieldthomasiidae are recognized as a new, still unnamed family (López and Bond, 2003) that includes older Paleogene genera. The enigmatic *A. ambiguus* is related to the Henricosborniidae *Simpsonotus* from the Paleocene Mealla Formation (Bond and Vucetich, 1983). *Phoradiadus divortiensis* (Simpson et al., 1962) has been shown to be a Sparnotheriidae, together with the Casamayoran taxa *Sparnotheriodon* and *Victorlemoinea* (Soria, 1980). *Adiantoides leali* Simpson and Minoprio, 1949, presents affinities with the early Eocene *Indalecia grandensis* Bond and Vucetich, 1983, both species belonging of the Family Indaleciidae within the Order Notopterna (Soria, 1989a, b). Most recently, López (2006) has also recognized an astrapothere in the Divisaderan assemblage (cf. *Trigonostylops*) that presents similarities with the Casamayoran *T. wortmanii*. The marsupial *Groeberia* is related to the Chilean genus *Klohnia* from Tinguiririca (early Oligocene) and the genus *Patagonia* from the early Miocene of Chubut (Pascual and Carlini, 1987; Flynn and Wyss, 1999), within the Family Groeberiidae (considered as Order Groeberiidae by Pascual et al., 1994). Even though *Groeberia minoprio* and *G. pattersoni* (exclusively from the Divisadero Largo Formation) do not indicate any accurate age considering the long temporal range of the family, they are the most basal taxa of this group, compatible with an age older than that of Tinguiririca (Flynn and Wyss, 1999). All these taxonomic changes support a much older age for the 'Divisaderan' fauna than previously thought. These differences are established with respect to Deseadan faunas, but also with respect to Mustersan faunas (late Eocene). It is interesting to note that the Divisaderan fauna most closely resembles Casamayoran assemblages.

Conclusions

Different taxonomic, stratigraphic, and sedimentological data strongly suggest that the Divisaderan faunal association is no longer valid as first defined and that it is a mixture of primitive and derived mammal taxa of different ages; the Divisaderan should therefore not be used as a land mammal age. The typical fauna from the Divisadero Largo Formation is much older than previously thought. The derived taxa, '*T. mendocensis*' and '*E. carettei*,' do not belong to the Divisaderan assemblage but come from the Mariño Formation; they are therefore not the oldest representatives of their respective families, Mesotheriidae and Hegetotheriidae, as previously considered.

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