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Evolution

Superfamily Gondwanatherioidea: A previously unrecognized radiation of multituberculate mammals in South America

(Cretaceous/Paleocene/Argentina/Multituberculata/Edentata)

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ABSTRACT **Multituberculates were the longest-lived order of the Class Mammalia and, during the Mesozoic and early Cenozoic, were among the most diverse and abundant representatives of the class. However, until the recent discovery of two Cretaceous teeth, one from South America and one from Africa, they were known only from northern continents. Additional material of the South American form *Frugliotherium* has confirmed its multituberculate affinities and indicates that it may be a derived member of the Suborder Plagiaulacoidea. New specimens provide evidence that two other South American forms, *Gondwanatherium* and *Sudamerica*, are also multituberculates and that they are closely related to *Frugliotherium*. *Gondwanatherium* and *Sudamerica*, each possessing highly specialized hypsodont molars, were previously thought to be the earliest known representatives of the Edentata, to be involved in the origin of edentates, or to represent a previously unknown higher taxon of mammals. However, there are detailed similarities in gross dental morphology, enamel microstructure, and inferred direction of jaw movement among *Frugliotherium*, *Gondwanatherium*, and *Sudamerica*. All three genera are here regarded as representatives of a highly derived, endemic radiation of South American multituberculates and are allocated to the superfamily Gondwanatherioidea. Multituberculates were therefore more common elements of Late Cretaceous and early Paleocene mammalian faunas of South America than previously recognized.**

Sudamerica, from the early Paleocene Salamanca Formation of Argentina, was originally known from a single, hypsodont, rodent-like, molariform tooth. The genus was considered a xenarthran edentate and placed in its own family, the Sudamericidae (1, 2). Prior to discovery of *Sudamerica*, the earliest known remains of edentates (armadillos, anteaters, and sloths; plus pangolins according to some authors) from South America (or anywhere) were from the late Paleocene (Riochican) of Argentina (3, 4). *Gondwanatherium*, from the Late Cretaceous Los Alamitos Formation of Argentina, was initially based on only isolated, hypsodont, rodent-like molariform teeth (5). Bonaparte (5, 6) believed *Gondwanatherium* to be most closely related to *Sudamerica* but, based on the different pattern of enamel ridges on the molariform teeth of the two genera, he erected a new, monotypic family, Gondwanatheriidae, to receive *Gondwanatherium*. Mones (7) united the Gondwanatheriidae and Sudamericidae in a new order, Gondwanatheria, which he placed in the Cohort Edentata, Superorder ?Xenarthra. Bonaparte,§ on the basis of recently discovered teeth of *Sudamerica* showing various stages of wear, recognized the close similarities of *Sudamerica* and *Gondwanatherium*. Bonaparte§ therefore rejected the Gondwanatheriidae and considered the Sudamericidae, which has taxonomic priority, to include both genera.

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Most workers regard edentates as the most primitive known placental mammals (see refs. 9 and 10 and references therein). However, assuming that *Sudamerica* and *Gondwanatherium* were involved in the ancestry of Edentata, Bonaparte (11) postulated that, since the molars of these two genera are nontribosphenic, edentates may be relicts of an endemic radiation that evolved in isolation prior to the differentiation of placentals from some primitive therian stock. Nonetheless, several workers (12–15) have since observed important differences between the teeth of *Gondwanatherium* and/or *Sudamerica* and those of Edentata, primarily in that hypsodonty is achieved via root elongation in edentates but via crown elongation in gondwanatherioids. Therefore, reservations have been expressed concerning allocation of *Gondwanatherium* and/or *Sudamerica* to, or phylogenetically near, the Edentata; however, no other, more appropriate sister taxon has been identified and substantiated. Van Valen (ref. 13, p. 44) opined that "*Gondwanatherium* could . . . easily be a hypsodont derivative of the early Cretaceous monotreme *Steropodon* . . . or even of something like *Frugliotherium*." Jenkins (ref. 12, p. 7), on the other hand, concluded that "*Gondwanatherium* is unequivocal evidence of a Mesozoic mammalian radiation beyond the bounds of previously recognized major taxonomic categories."

First described on the basis of an isolated brachydont M_2 (lower second molar), *Frugliotherium windhauseni* was placed in a new family, the Frugliotheriidae, and provisionally assigned to the Multituberculata—the first record of the order from any southern continent (16). Additional specimens of *F. windhauseni*, including M_1 and M^1 and tentatively referred upper and lower incisors and premolars, confirm its multituberculate affinities (11, 17). As in other multituberculates, *Frugliotherium* possesses: (*i*) molars each with more than one longitudinal row of multiple cusps; (*ii*) palinal (posterior) direction of dentary motion during power stroke of grinding cycle; (*iii*) anterior upper premolars with conical cusps, each with radiating ridges; and (*iv*) lower premolars with apical serrations from which arcuate buccal and lingual ridges descend. Furthermore, Krause *et al.* (17) and Krause (18) recently concluded that *Vucetichia gracilis*, also from the Upper Cretaceous Los Alamitos Formation and originally assigned to the Gondwanatheriidae (11), is a junior synonym of *F. windhauseni*.

Gross Morphology of the Molars

Although *Frugliotherium*, *Gondwanatherium*, and *Sudamerica* are each known from only isolated teeth, they all appear to be represented by M_1s and M_2s (as identified in

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§Bonaparte, J. F., Joint Meeting of the Argentine Mammal Society and the American Society of Mammalogists, June 17–20, 1990, Buenos Aires, pp. 39–40 (abstr.).

Fergliotherium [17]). Particularly striking similarities exist among the M_1s at certain stages of wear; in all three taxa the crown pattern consists of three similarly shaped transverse ridges (anterior, middle, posterior) separated by two prominent furrows (anterior, posterior) (Fig. 1). The anterior ridge is V-shaped in *Fergliotherium* and *Gondwanatherium*. As inferred from an unworn specimen recently assigned to *Fergliotherium* (18), the apex of the V is directed lingually, and the limbs of the V join two cusps in the buccal row to a single cusp in the lingual row. The anterior limb of the V is more curved in *Gondwanatherium* than in *Fergliotherium*, to the extent that the ends of the limbs almost touch each other buccally; in *Sudamerica* the two limbs are joined buccally to form a D-shaped ridge (at least in the stage of wear represented by Museo Argentino de Ciencias Naturales specimen number CH 1483). The transverse furrow following the anterior ridge in all three taxa is oriented obliquely (anterolingual–posterobuccal) and opens onto the sides of the crown, creating indentations, both lingually and buccally, into the occlusal outline. These indentations are most prominent in *Sudamerica*. The middle ridge in all three taxa is constricted at approximately mid-width; the constriction is created primarily by an anterior indentation from the anterior furrow. The posterior furrow, between the middle and posterior ridges, is less obliquely oriented than the anterior furrow. The posterior ridge is C-shaped owing primarily to a prominent indentation from the posterior furrow. The size of the indentation becomes progressively larger in the sequence *Fergliotherium* → *Gondwanatherium* → *Sudamerica* (at least as indicated by the stages of wear represented in the available specimens).

The M_2s of *Fergliotherium*, *Gondwanatherium*, and *Sudamerica* are similar in that the crown is wider anteriorly than posteriorly and the occlusal surface consists of two essentially D-shaped, reciprocally arranged ridges separated by a deep transverse furrow. The straight side of the anterior D-shaped ridge is positioned posteriorly, whereas that of the posterior D-shaped ridge is positioned anteriorly. The centers of each D are fossae; in *Fergliotherium* the fossa surrounded by the anterior ridge has an additional small, obliquely directed enamel bridge. The anterior and posterior D-shaped ridges are connected, or nearly connected (presumably depending upon the amount of wear), on the buccal side in all three forms. Unlike the condition in *Fergliotherium*, the posterior D-shaped ridges in *Gondwanatherium* and *Sudamerica* are not completely closed; this too may be a function of wear.

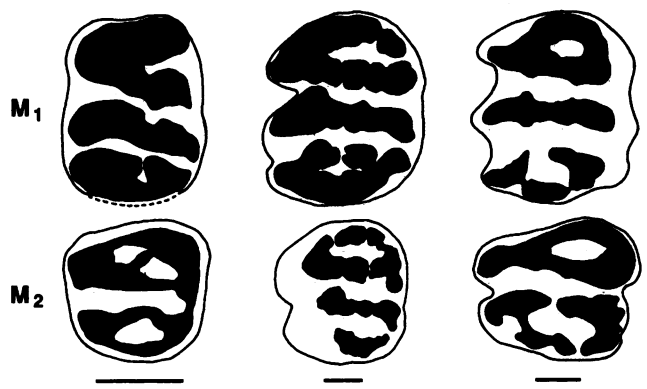

FIG. 1. Comparison of occlusal morphology of molariform teeth tentatively identified as M_1s and M_2s of *Fergliotherium windhauseni* (*Left*) [right M_1: Museo Argentino de Ciencias Naturales (MACN) specimen number RN 174, holotype of junior synonym *Vucetichia gracilis*; right M_2: MACN-RN 20, holotype of *F. windhauseni*], *Gondwanatherium patagonicum* (*Center*) [left M_1 (reversed): MACN-RN 22, holotype; left M_2 (reversed): MACN-RN 24], and *Sudamerica ameghinoi* (*Right*) (right M_1: MACN-CH 1483; right M_2: MACN-CH 1484). Anterior surface is to the top, buccal to the right. White areas indicate unworn enamel and, if present, cementum; black areas represent worn enamel and, if present, exposed dentine. (Bars = 1 mm.)

In our view, the basic similarities in ridge and furrow morphology on M_1 and M_2 of the three taxa are the result of close phyletic affinity and not of convergence. In addition to minor differences in ridge and furrow morphology, the molars of *Gondwanatherium* and *Sudamerica* differ from those of *Fergliotherium* in being hypsodont and considerably larger. Also, unlike the condition in *Fergliotherium* (but presumably related to the hypsodonty), the elongate crown and roots of M_2 in *Gondwanatherium* and *Sudamerica* are oblique to the occlusal plane. The molars of *Sudamerica* are more derived than those of *Gondwanatherium* in at least two features: (*i*) the furrows on the sides of the crown extend further cervically, all the way to the base of the tooth; and (*ii*) the cementum is not restricted to the root area but extends cuspally to cover the sides as well as all of the occlusal surface (except those parts of the enamel and dentine in occlusal contact).

Gross Morphology of the Incisors

Included in the collection of specimens from the Los Alamitos Formation are several fragments of upper and lower incisors with distinctly limited bands of enamel that can be tentatively assigned to *Gondwanatherium* and *Fergliotherium* (17) (Fig. 2). Among Mesozoic mammals, no known group other than multituberculates has a restricted band of enamel on the incisors. Similar incisors have not yet been found in deposits yielding molars of *Sudamerica*. Although different in size, lower incisors (presumably I_1) of both *Fergliotherium* and *Gondwanatherium* are strongly compressed laterally, with a flat side medially and a convex side laterally. Enamel is limited to the ventral aspect but ascends farther dorsally on the lateral side than on the medial side. The upper incisors (presumably I^2) of both genera, by contrast, exhibit stronger curvatures in side view, are much less laterally compressed in cross section, and have a less acute angle formed between the apical wear facet and the anterior margin of the crown.

Enamel Microstructure

The enamel microstructure of *Fergliotherium* (sampled in anterior upper premolar, M_1, and M_2), *Gondwanatherium* (sampled in lower incisor and molar), and *Sudamerica* (sampled in molar) is very similar in that each exhibits small (<5 μm in diameter), circular prisms (15, 17). In all three the

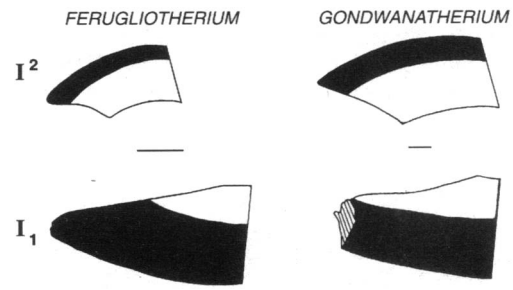

FIG. 2. Comparison of incisor morphology of *Fergliotherium windhauseni* (*Left*) [left? I^2: Museo Argentino de Ciencias Naturales (MACN) specimen number RN 702C; left I_1: MACN-RN 701A] and *Gondwanatherium patagonicum* (*Right*) [left I^2: MACN-RN 970; right I_1 (reversed): MACN-RN 254] in lateral view. Anterior surface is to the left. White areas represent dentine, black areas represent enamel, and the hatched area indicates breakage. (Bars = 1 mm.)

prisms exhibit some alignment into rows, tubules are present, and there is no evidence of decussation. The enamel of *Sudamerica* appears to differ somewhat from that of *Gondwanatherium* and *Fergliotherium* in that small areas also contain some arc-shaped prisms, but like the circular prisms, these are small, not large as in taeniolabidoids and at least one primitive ptilodontoid (*Cimolodon*). Krause and Carlson (19) argued that, within Late Cretaceous and Paleogene multituberculates, small, circular prisms, which are present only in derived ptilodontoids and the taeniolabidoid *Neoliotomus* [and perhaps *Liotomus* (20)], are derived relative to large, arc-shaped prisms. If this assessment is correct, then it would appear that gondwanatherioids developed this condition independently.

Inferred Direction of Jaw Movement

The dentary of *Fergliotherium* moved palinally (posteriorly) during the power stroke of the grinding cycle (17), an assessment based on three lines of evidence: (*i*) the anteroposterior orientation of wear striations on molars, (*ii*) the reciprocal pattern of cusp margins in upper and lower molars (concave cutting edges positioned posteriorly on lower molars and anteriorly on upper molars), and (*iii*) the identification of leading and trailing enamel edges on the periphery of dentine islands on molars. Krause (21) argued that this pattern of jaw movement is characteristic of multituberculates and is unique among mammals.

Anteroposterior wear striations are also evident on the molars of *Gondwanatherium* (5) and *Sudamerica*. Confirmation that these striations are anteroposterior in orientation rather than mediolateral comes from independent evidence concerning orientation of the teeth in the jaw. This evidence consists of interdental wear facets, which are particularly well developed on the molars of *Gondwanatherium*, as well as an edentulous jaw fragment provisionally assigned to the genus (11). The highly derived nature of enamel ridges and furrows on the molars of *Gondwanatherium* and *Sudamerica* and the general absence of discrete cusps preclude a comparison of the shape of cusp margins with those in *Fergliotherium*. However, the pattern of wear in the well-exposed dentine islands on the molars of *Gondwanatherium*, and *Sudamerica* in particular, allows determination of directionality of jaw movement (i.e., whether anteriorly or posteriorly along the longitudinal axis indicated by the wear striations). The degree of wear in dentine islands of herbivorous mammals is asymmetrical with respect to the direction of jaw movement in that dentine is most deeply eroded near the trailing edge of enamel (22–24). Thus, if the M_1s and M_2s of *Gondwanatherium* and *Sudamerica* are correctly identified to both position and taxon, the trailing edges would be expected to be situated anterior to the dentine islands, as in *Fergliotherium*. This pattern of wear is indeed evident in the teeth of *Gondwanatherium* but is best exhibited in those of *Sudamerica* (Fig. 3). Based on this evidence, the dentary in these forms is inferred to have moved palinally during the power stroke of the grinding cycle, as it did in *Fergliotherium* and other multituberculates.

Relationships

The similarities in gross molar and incisor morphology, enamel microstructure, and inferred direction of jaw movement are independent lines of evidence that indicate similarity through common ancestry among *Fergliotherium*, *Gondwanatherium*, and *Sudamerica*. Multituberculates alone have developed this suite of similarities (17). Krause *et al.* (17) concluded that, among known multituberculates, *Fergliotherium* is probably most closely related to an undescribed plagiaulacoid from the Upper Jurassic Morrison

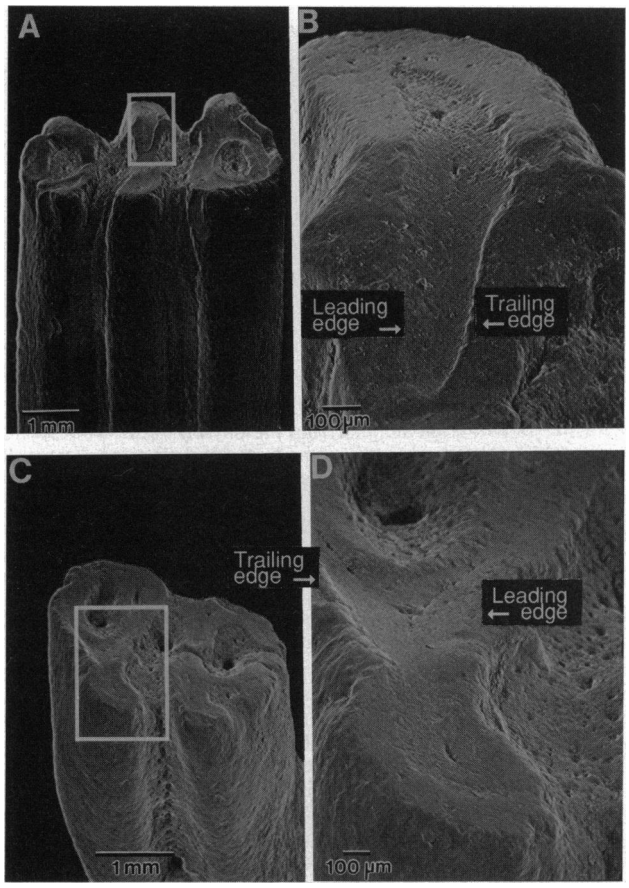

FIG. 3. Scanning electron micrographs of the right M_1 (*A* and *B*) [occlusolingual view with the anterior surface to the right, Museo Argentino de Ciencias Naturales (MACN) specimen number CH 1483; *B* is an enlargement of the white rectangular outline in *A*] and the right M_2 (*C* and *D*) (occlusobuccal view with the anterior surface to the left, MACN-CH 1484; *D* is an enlargement of the white rectangular outline in *C*) of *Sudamerica ameghinoi* to show the position of leading and trailing edges of enamel on the periphery of dentine islands.

Formation (25); therefore, he tentatively referred the genus to the Suborder Plagiaulacoidea. As detailed above, *Gondwanatherium* is more derived than *Fergliotherium* in several features. If *Fergliotherium* is a multituberculate (11, 17) and *Gondwanatherium* is derived from a *Fergliotherium*-like morphology, then *Gondwanatherium* must also be a multituberculate. Similarly, if, as has been suggested or argued previously (5, 7, 11, 12, 15) and in this paper as well, *Sudamerica* is the derived sister genus of *Gondwanatherium*, then *Sudamerica* must also be a multituberculate. This hypothesis of phylogenetic relationships is summarized in Fig. 4.

It appears that gondwanatherioids evolved some adaptations (e.g., enlarged, procumbent incisors with a restricted band of enamel) convergently with other mammalian groups and even with Late Cretaceous and Paleogene multituberculates known from Laurasia. In other respects, however, the gondwanatherioids are uniquely derived among known multituberculates, as evidenced by the prominent ridges and furrows on the molars and the tendency to develop hypsodonty. Furthermore, it should be noted that gondwanatherioids are not closely related to the multituberculate represented by a single tooth (M_2) from the Early Cretaceous of Morocco (26), which has been assigned to the more primitive Suborder Paulchoffatoidea (see also refs. 27 and 28).

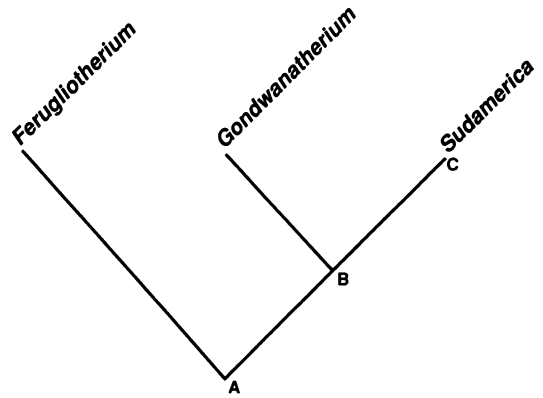

FIG. 4. Cladogram summarizing the phylogenetic hypothesis of relationships presented in this paper. Derived character states defining each of the lettered nodes in the cladogram are as follows: A, derived character states uniting *Ferugliotherium* (and "*Vucetichia*"), *Gondwanatherium*, and *Sudamerica*: (*i*) prominent transverse ridges and furrows on molar crowns, (*ii*) both upper and lower incisors enlarged and procumbent with a restricted band of enamel (unknown in *Sudamerica* and convergent upon condition in Taeniolabidoidea), and (*iii*) presence of small circular prisms in enamel (convergent upon condition in derived ptilodontoids, *Neoliotomus*, and *Liotomus*); B, derived character states uniting *Gondwanatherium* and *Sudamerica*: (*i*) large size, (*ii*) hypsodont molars, (*iii*) prominent furrows on the sides of molars, (*iv*) cementum present on at least the roots of molariform teeth, and (*v*) M_2s with longitudinally sloping occlusal plane; C, derived character states of *Sudamerica*: (*i*) furrows on sides of molars extending far toward the midline of tooth and cervically to the base of the crown, (*ii*) cementum present on the sides of the crown and in furrows and fossae on the occlusal surface, and (*iii*) tendency for more connections between the enamel ridges on molars, particularly along the midline.

Our reassessment of the phyletic interrelationships of *Ferugliotherium*, *Gondwanatherium*, and *Sudamerica* and of their relationship as a group to other mammals necessitates a revision of the classification, including erection of the new superfamily Gondwanatherioidea and emendation of previous diagnoses of higher taxa as follows.

Subclass Allotheria; Order Multituberculata; Suborder ?Plagiaulacoidea

Superfamily Gondwanatherioidea Mones, 1987 (new rank). *Included families.* Ferugliotheriidae Bonaparte, 1986, and Sudamericidae Scillato-Yane and Pascual, 1984.

Distribution. Late Cretaceous (Alamitian) and early Paleocene of Argentina.

Diagnosis. Differs from all other Multituberculata in possessing prominent transverse ridges and furrows on molars. Differs from Haramiyoidea in possessing approximately equal height of cusps on molars. Differs from Haramiyoidea, Paulchoffatoidea, most Plagiaulacoidea, and Ptilodontoidea in possessing unicuspid central incisors with strongly restricted enamel. Differs from Haramiyoidea, Paulchoffatoidea, and Plagiaulacoidea in possessing a large M_1 relative to M_2 and a well-developed lingual row of cusps on M^1. Differs from Haramiyoidea and Paulchoffatoidea in possessing prismatic enamel and from primitive Ptilodontoidea and all Taeniolabidoidea except *Neoliotomus* (and perhaps *Liotomus*) in possessing small, circular enamel prisms.

Family Ferugliotheriidae Bonaparte, 1986. *Included genera. Ferugliotherium* Bonaparte, 1986 (="*Vucetichia*" Bonaparte, 1990).

Distribution. Late Cretaceous (Alamitian) of Argentina.

Revised diagnosis. Differs from Sudamericidae in possessing small, brachydont molars supported by transverse pairs of fission roots (on at least M_1).

Family Sudamericidae Scillato-Yane and Pascual, 1984. *Included genera. Gondwanatherium* Bonaparte, 1986, and *Sudamerica* Scillato-Yane and Pascual, 1984.

Distribution. Late Cretaceous (Alamitian) and early Paleocene of Argentina.

Revised diagnosis. Differs from Ferugliotheriidae in being much larger and in possessing large, hypsodont molars, each supported by a massive root covered with cement. Coronal pattern of ridges and furrows on molars is generally more complex than in Ferugliotheriidae.

Summary and Conclusions

The superfamily Gondwanatherioidea (new rank), including two families, the Ferugliotheriidae (*Ferugliotherium*) and Sudamericidae (*Gondwanatherium* and *Sudamerica*), is here considered to be a highly derived group of multituberculates. Gondwanatherioids are tentatively assigned to the Suborder Plagiaulacoidea, an allocation that extends the temporal range of the suborder into the Late Cretaceous and Paleocene. Plagiaulacoids are elsewhere restricted to the Late Jurassic and Early Cretaceous of Europe, the Late Jurassic of North America, and the Early Cretaceous of Asia (27, 28). The reallocation of *Gondwanatherium* and *Sudamerica*, previously considered to have affinities with Edentata (1, 2, 5–7, 11, 29), to the Multituberculata removes any known pre-late-Paleocene record of edentates or near-edentates. The origin of Edentata remains enigmatic (30).

As indicated by the highly derived nature of their dental anatomy relative to that of previously known multituberculates, gondwanatherioids appear to have evolved in isolation for some considerable time. The known assemblage of mammals from the Upper Cretaceous (Campanian) Los Alamitos Formation, in addition to *Ferugliotherium* (including *Vucetichia*) and *Gondwanatherium*, includes a new genus of triconodont and five new families and nine new genera of symmetrodonts and eupantotheres recently described by Bonaparte (11, 31, 32)—further testimony to a high degree of endemicity.

Bonaparte and Kielan-Jaworowska (11, 31, 33) have elsewhere argued that isolation of Gondwanan terrestrial vertebrates from those of Laurasia began before the end of the Jurassic. Separation of South America from North America and Africa appears to have been initiated in Middle Jurassic to Early Cretaceous time (34–37). However, whether gondwanatherioids were restricted to Gondwana as a whole, the South American continent, or just to the Patagonian region cannot be confidently determined without the discovery of more Middle Jurassic–Late Cretaceous mammals from southern continents. Nonetheless, current knowledge concerning the distribution of gondwanatherioids does not refute the hypothesis that the group, along with others (see refs. 38 and 39 and references therein), may have been restricted to Patagonia. In particular, it is interesting to note that *Sudamerica* is apparently absent from the only well-sampled early Paleocene mammalian fauna from South America, the Tiupampa assemblage of Bolivia (40). *Sudamerica* is the only known Paleocene descendant from the Los Alamitos assemblage; triconodonts, symmetrodonts, or eupantotheres have yet to be found in post-Campanian horizons of South America. In this regard, a parallel can be found in North America where triconodonts, symmetrodonts, and eupantotheres have been discovered in Upper Cretaceous horizons (8, 41, 42) but only multituberculates are known from younger levels.

It is premature to conclude that multituberculates comprised a substantial component of Late Cretaceous and/or Paleocene mammalian faunas in South America, in large part because faunas of these ages are, in general, not yet well known on the continent. This is largely owing to a paucity of

mammal-bearing localities, but even in the case of the Los Alamitos assemblage, many specimens of non-gondwanatherioid taxa remain to be described. Nonetheless, the inclusion of *Gondwanatherium* and *Sudamerica* in the Multituberculata and the identification of more specimens of *Ferugliotherium* (17, 18), *Gondwanatherium* (17), and *Sudamerica* (8) indicate that multituberculates were certainly more diverse and more abundant in the Late Cretaceous and early Paleocene of South America than previously recognized.

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