A highly derived docodont from the Patagonian Late Cretaceous: evolutionary implications for Gondwanan mammals

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ABSTRACT

Reigitherium bunodontum (Mammalia, Docodonta, Reigitheriidae), from the Late Cretaceous (Campanian-Maastrichtian) La Colonia Formation (Patagonia, Argentina), is the first known docodont mammal from the southern hemisphere. Even though its lower dentition resembles more closely the North American Late Jurassic *Docodon* than other Eurasian docodonts (e.g., intermolar basins formed by the adjacent halves of molars, and vertical crenulations [or ribs and furrows]), it radically differs from Laurasian docodonts in that the crowns of the lower cheekteeth are transversely enlarged: several lingual cingular cusps are incorporated to the masticatory surface. The evolution of the reigitheriid lower molar pattern from the morganucodontid one seems to have involved three main modifications, resulting in a step-like process: 1) expansion of the lingual cingulum; 2) elevation of the lingual cingular cusps,

becoming interconnected to each other by a crest high as or higher than the labial one, and enlargement of the masticatory surface by the close connection of both lingual and buccal crests; 3) aggregation of labial pillar-shaped cusps. *Reigitherium bunodontum* adds support to the hypothesis that Gondwanan land mammals evolved as vicariants of the Laurasian ones, and that in mammals the universal trend to increase the masticatory surface of the cheekteeth was also accomplished without passing through the reversed triangle stage that led to the tribosphenic pattern.

RÉSUMÉ
Un docodonte très dérivé du Crétacé supérieur de la Patagonie : implications évolutives pour des mammifères gondwaniens.
Reigitherium bunodontum (Mammalia, Docodonta, Reigitheriidae) du Crétacé supérieur (Campanien-Maastrichtien) de la Formation La Colonia (Patagonie, Argentine) est le premier mammifère docodonte de l'hémisphère Sud. Sa dentition inférieure ressemble plus à celle de *Docodon* du Jurassique supérieur d'Amérique du Nord qu'à celle d'autres docodontes d'Eurasie (e.g., bassins intermolaires formés par des moitiés de molaires adjacentes et dentellées verticales [ou bords et raies]). Il diffère des docodontes de Laurasie, en général, par les couronnes de ses dents molariformes qui sont transversalement élargies : plusieurs cuspides à bourrelet lingual sont incorporées à la surface masticatoire. L'évolution du patron des molaires inférieures des Reigitheriidae à partir de celui des morganucodontides semble avoir subi trois modifications principales, résultats d'un processus graduel : 1) expansion du bourrelet lingual ; 2) élévation des cuspides du bourrelet lingual liées l'une à l'autre par une crête haute ou plus haute que la crête labiale et agrandissement de la surface masticatoire en raison de l'étroite connexion des deux crêtes, linguale et buccale ; 3) agrégation des cuspides labiales sous forme de pilier. *Reigitherium bunodontum* conforte l'hypothèse que les mammifères terrestres gondwaniens sont les taxons vicariants des taxons de Laurasie. De plus, chez les mammifères la tendance générale à l'augmentation de la surface masticatoire des dents molariformes s'est réalisée sans passer par l'état des triangles renversés, qui conduisit au patron tribosphénique.

INTRODUCTION

During February-March and November-December 1996, joint Argentinian expeditions of the Museo de La Plata, the Museo Paleontológico "Egidio Feruglio" (Trelew), and the Dirección Nacional del Servicio Geológico (Buenos Aires) to the southern slopes of the North Patagonian Massif ("Comarca Norpatagónica" or "Meseta de Somuncura"), in North-Central Chubut Province (Argentina), permitted us to recover the first land mammal remains, and other vertebrates, invertebrates, and plants, from the Late Cretaceous La Colonia Formation (see below). This constitutes the second unquestionable Late Cretaceous mammal-bearing locality in Patagonia. The first one, farther north in Patagonia, was discovered and its mammals studied by Bonaparte (1996, and references therein).

In this paper, we analyse the regional stratigraphical context and the paleobiogeographical framework of this new Late Cretaceous fossiliferous locality, and describe one of the non-tribosphenic taxa that shed light on the unique Gondwanan land mammal history, and the K-T transition in Gondwanan mammal communities (Pascual & Ortiz-Jaureguizar 1991, 1992; Pascual 1996, 1998; Vizcaíno *et al.* 1998). This non-tribosphenic mammal taxon supports our hypothesis that Gondwanan land mammals evolved as vicariants of the Laurasian ones (Pascual *et al.* 1993, 1999). Another probable example of a vicariant group relationship between a Gondwanan (Gondwanatheria) and a Laurasian (Multituberculata) counterpart has been recently provided by Krause *et al.* (1997). Although not specifically treated as such, gondwanatherians were regarded as dubious Allotherians, and implicitly as the vicariant sister-group of the Laurasian multituberculates.

In a paper in preparation, we are offering a preliminary report of all the paleontological evidence recovered from the La Colonia Formation, including new evidence on the peculiar mammalian evolution of the basal Gondwanan Prototribosphenida toward the complex therian radiation (see Rougier *et al.* 1992; Rougier 1993; Wible *et al.* 1995).

ABBREVIATIONS
MEF   Museo Paleontológico "Egidio Feruglio", Trelew (Chubut Province, Argentina);
MACN-RN Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires;
SALMA   South American Land Mammal Age;
pm   premolars;
m   molars (based on the relative shape of the preserved cheekteeth on the new specimen of *Reigitherium*, we tentatively homologize their loci with those recognized for *Docodon*, i.e., pm4, m1, and m2);
L   length;
W   width.

For the cusp terminology used in this paper, see Figure 4 and Jenkins (1969). All measurements are in mm.

THE GONDWANAN RECORD OF MAMMALS: A GENERAL OVERVIEW

More than 40 years ago, Patterson wrote: "Had the adaptive shift from the pantothere to the tribosphenic stage not taken place in the Theria, it is conceivable that a docodont radiation might have occurred, in which case mammalian history would have been a very different affair" (Patterson 1956: 64). Actually, the docodont radiation did occur in Gondwana, but as part of a general radiation affecting all the non-tribosphenic and pre-tribosphenic mammals, characterizing a distinct episode in mammalian evolution which we recognized as the Gondwanan stage (Pascual 1996; Vizcaíno *et al.* 1998: fig. 4). Docodonts became extinct by the Late Jurassic in Laurasia (see, e.g., Kron 1979); in contrast, a highly derived taxon of the Gondwanan docodont radiation, which is described in this paper, was still living in the present Patagonian region by the end of the Cretaceous. Thus, Patterson's vision became a prediction, illustrating how the radiation of docodonts could have been realized all over the world.

With respect to the tribosphenic mammals, it is pertinent to remember another prediction. Based on the global fossil record combined with a paleogeographical framework, Lillegraven (1974: 279) envisioned as "…highly possible that yet other therian adaptations may have been developing independently on the African and South American continents through the Cretaceous". A "placental-like" petrosal bone (under study by G. W. Rougier) also found in La Colonia Formation, and a new dentary having tribosphenic-like molars and apparently an eutherian formula, quite recently described by Rich *et al.* (1997) from Lower Cretaceous beds of southeastern Australia (*Ausktribosphenos nyktos* Rich *et al.*, 1997), supports the therian adaptations envisioned by Lillegraven as developing independently in South America through the Cretaceous. Actually, based on the mandibular characters, Kielan-Jaworowska, Cifelli & Luo (1998: 267) suggest that *Ausktribosphenos nyktos* represents a relict of a more ancient radiation, possibly originating from "…extremely primitive mammals – early
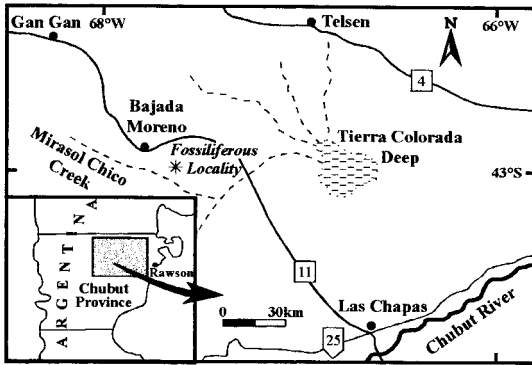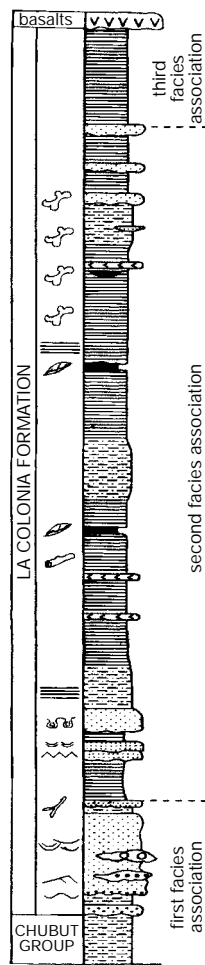
symmetrodonts – rather than placentals", known from a well established fossil record on the Gondwana continent. To us, the Madagascan early Late Jurassic holotherian *Ambondro mahabo* Flynn *et al.*, 1999 is another example of an eastern Gondwanan origin of tribosphenidans on the southern continents, as implied by the authors (Flynn *et al.* 1999). Although the record of Mesozoic mammals on southern continents is extremely poor relative to that in the north, the scarce South American and Australian Cretaceous record is enough to suggest that it was both extraordinarily extensive in the range of the morphologies, and intensive in the processes that led to that diversification (see Bonaparte 1996, and literature therein). The extant Gondwanan Ornithorhynchidae (monotremes) are a good example: they appear to represent the first known shift of a mammal to an aquatic mode of life, which succeeded at least from the early Paleocene (the Patagonian *Monotrematum sudamericanum* Pascual *et al.*, 1992; see also Pascual *et al.* 1992b; Flannery *et al.* 1995). If the large dental canal of both *Steropodon galmani* Archer *et al.*, 1985, and *Kollikodon ritchiei* Flannery *et al.*, 1995 is indicative of the existence of sensitive rhynaria and electrosensory organs (Flannery *et al.* 1995), related with an aquatic mode of life, that ecological shift was much older (Early Cretaceous). Other examples could be an Early Cretaceous triconodont from North America (Slaughter 1969) and two triconodont mammals from the Early Cretaceous of Morocco, described by Sigogneau-Russell (1995). In any case, aquatic environments were probably already conquered by non-tribosphenic mammals during the later part of the Mesozoic.

GEOLOGICAL SETTING, AGE AND CORRELATION

The La Colonia Formation was named by Pesce (1979) for a relatively homogeneous series of upward fining sediments. This author identified a clear depositional sequence exposed over wide areas of the southern slopes of the North

Patagonian Massif ("Comarca Norpatagónica") in North-Central Chubut Province. The area we are prospecting is situated along the eastern slopes of the La Colonia range, between El Buitre Chico and El Buitre hills, approximately between 42°55'S-43°02'S and 67°28'W-67°41'W (Fig. 1). Here, the La Colonia Formation is separated by a regional angular unconformity of less than five degrees from the subjacent red beds (sandstones and conglomerates) of the Cerro Barcino Formation (Chubut Group), of Cenomanian age (Codignoto *et al.* 1979). Above, an erosional unconformity separates this formation from the continental whitish pyroclastic Paleogene Sarmiento Group. Within this region, the thickness of this formation varies between 210 and 240 m (Ardolino & González 1996), but it decreases from southwest to northeast, in such a way that farther northeast, around Telsen, it is only 17 m thick (Ardolino & Delpino 1987). Along the eastern slopes of the La Colonia range, we recognize three main vertical and lateral facies associations, broadly representing continental to marginal marine depositional settings (Fig. 1).

The first and lowest facies association is composed of a single facies, and is a coarse-grained sandy-conglomeratic and crossed-bedded granule conglomeratic deposit. It reaches a maximum thickness of 16 m, shaping prominent re-entrants in the clifts along local valleys, as along Arroyo Mirasol Chico. This facies is attributed to a non-marine setting, drained by a channeled fluvial system featuring moderate to low sinuosity implanted on the sandy substratum of the Cerro Barcino Formation. The overall lithology, its yellowish brown color, and the remarkable grain-size change at the boundary, contrast with the Cerro Barcino Formation, and reveal that deposition was interrupted by a modification of the paleoenvironmental conditions. This distinctive facies was segregated by some authors (e.g., Pesce 1979; Lapido & Page 1979; Lapido 1981; Page 1987) as a discrete lithostratigraphic unit, named the Puntudo Chico Formation. To us, this is the basal component of the same depositional sequence known as La Colonia Formation.

The second facies association crops out approximately in the middle part of the sequence, and is composed of three facies: laminated mudstones, pelite-fine sandstones, and banded silstones and claystones. Laminated mudstones are yellowish brown in color, sometimes interstratified with psammitic nodules. Pelites are mostly claystones and siltstones, greenish-brown to grayish-brown in color, and featuring parallel lamination and lenticular stratification. Usually, it is interstratified not only with reddish fine-grained sandstones but also with black pelites and gypsum; the sandstone beds are tabular or lenticular, with planar and trough cross-bedding, most of them about 0.30 m thick, and occassionally up to 1 m thick, bearing frequent but fragmentary remains of fresh water fish. The black pelites are about 0.10 m thick, occasionally reaching a thickness of 0.60 m, bearing frequent plant remains. The most common evaporitic component is gypsum, which is light brown in color. It is arranged in tabular beds internally featuring cone-in-cone structures and dessication cracks. Finally, the banded siltstones and claystones are yellowish brown in color. The banding is well displayed by its interstratification features. Internally, the beds show parallel lamination or lenticular stratification. This second facies association is interpreted as having been deposited in an estuary, tidal flat or coastal plain environment, influenced both by occasional high fresh water streamflow from the continent and tidal currents from the sea. This environment occurred under a seasonal climate (Ardolino & Delpino 1987; Ardolino *et al.* 1995), alternating periods of humidity and aridity. The humid periods are represented by some laminated pelites with intense bioturbation, frequent remains of either aquatic animals (e.g., fresh-water fish, such as ceratodontid dipnoans, turtles, crocodiles and marine plesiosaurs) or land plants and tetrapods (lizards, snakes, dinosaurs and mammals). The arid periods are represented by saline mudflats with dessication cracks, evaporitic deposits and some red beds. The only macrofossils recorded in these sediments are dental plates of a ceratodontid dipnoan fish (*Ceratodus* sp.). This second facies

association is the thicker and most representative of the La Colonia Formation, on which present day erosion produces a peculiar landscape of badlands, with a relatively deep (up to 1 m in thickness) and soft weathered cover. The mammal remains described in this paper, as well as most of the remaining vertebrates so far collected, including the peculiar carnosaur dinosaur *Carnotaurus sastrei* Bonaparte, 1985 (se also Bonaparte *et al.* 1990), come from this second facies association (Fig. 1).

The third facies association represents the upper section of the sequence. Like the first one, it is composed by only one facies, so called laminated pelites. This is a distinct set of yellow, yellowish brown or greenish brown laminated silty claystones, without sandy beds. It contains fragments of shells, and rare complete shells of bivalves, predominantly ostreids, some of them still preserved in living position. This facies is interpreted as the same transitional paleoenvironment as the preceding, but corresponding to the upper part of an intertidal flat.

Based on the regional stratigraphic setting, Pesce (1979) assigned the La Colonia Formation to the post-Danian Paleocene. Former pollen studies by Pothe de Baldis (1976) also led Lapido & Page (1979) to tentatively assign this formation to the Paleocene *s.l.* Ardolino & Delpino (1987) established that this formation lies on top of the Cenomanian Cerro Barcino Formation, and is overlain by the Danian (?) Salamanca Formation. These authors mentioned Campanian-Maastrichtian foraminifers and ostracods found in the upper third of the sequence. These data, as well as the stratigraphical relationships of the whole formation, led them to tentatively regard the lower and middle part as representing the Coniacian-Santonian span ("Senonian" pre-Campanian). In turn, while reporting a new horned carnosaur dinosaur (*Carnotaurus sastrei*) recovered from the second facies association of this formation, Bonaparte (1985) assigned it to the Albian, in the belief that they were part of the Albian Gorro Frigio Formation (Chubut Group). Later on, Bonaparte *et al.* (1990) still maintained that the dinosaur-bearing beds pertain to the Gorro Frigio Formation, although this time admitting that it could be Aptian or Cenomanian in age. The ostreid *Ambigostrea clarae* (Ihering, 1907) has been recorded from the upper beds of the third facies association. This species is well represented in the Late Maastrichtian levels of either one of the Northpatagonian sedimentary groups known as Roca "Formation", and Malargüe Group (see below) in the Neuquén Basin. Within the latter, this species appears associated with *Amphidonte mendozana* (Ihering, 1907), *Austrotrigonia pampeana* Leanza & Casadío, 1982, *Pacitrigonia sobrali* Leanza & Casadío, 1980, *Pterotrigonia (Rinetrigonia) windhauseniana* (Wilkens, 1921), *Roudairia pampaensis* Leanza & Hünicken, 1982, *Panopea inferior* Wilkens, 1921, *Baculites* sp., and *Eubaculites argentinicus* Weaver, 1931. *Ambigostrea clarae* is confined to the CC25 and CC26 nannozones (Perch-Nielsen 1985) of the Late Maastrichtian (S. Casadío, pers. comm.). As radioisotopic dates are not yet available, attempts to correlate the whole La Colonia Formation to the stages used for the Late Cretaceous of Europe presently depend on the microfossils (mostly on planktonic foraminifera) that are in study. In turn, considering that the Salamanca Formation ranges widely southward of the Northpatagonian Massif (Legarreta & Uliana 1994), that the Roca Formation ranges widely northward of it (Bertels 1969a, 1969b, 1970), and that both represent the Campanian-Paleocene span, it is quite probable that the uppermost part of the La Colonia Formation could represent the earliest part of the Paleocene. On the other hand, the lower part of the La Colonia Formation could be older than Campanian if the subjacent Gorro Frigio Formation is Cenomanian in age (Codignoto *et al.* 1979). In short, the La Colonia Formation was deposited, at least, during the Campanian-Maastrichtian span, beginning probably sometimes earlier than the Campanian and extending sometimes later than the Maastrichtian.

THE PATAGONIAN LATEST CRETACEOUS-DANIAN PALEOGEOGRAPHICAL AND PALEOBIOGEOGRAPHICAL SETTING

During latest Cretaceous and early Paleocene times southern South America withstood the first and most widespread epeiric Atlantic flooding episode, known as "Mar de Káwas" or "transgresión de Schiller" by Casamiquela (1978), that transformed this region into a great archipelago (see Legarreta *et al.* 1989: fig. 1; Pascual *et al.* 1996: figs 9; 11). To Legarreta & Uliana (*in* Bond *et al.* 1995: 49), the land mass had similarities with the modern Java-Flores Sea physiography. This (these) transgression(s) extended as a seaway northwestward of southern South America, biogeographically acting similarly to the North American Western Interior Sea (Lillegraven & Ostresh 1990), in this case separating a northeastern South American region from a southwestern one (Pascual *et al.* 1996: fig. 11).

Within the southern slopes of the La Colonia range, the La Colonia Formation represents the older part of that/those first Atlantic flooding event/s (Maastrichtian-Danian), and as such it is correlated to the older units of the stratigraphical sequences found in central and northern Patagonia, and up to the northern limits of the Neuquén Basin (Casamiquela 1978: fig. 1; Legarreta *et al.* 1989). The different components of these sequences are known as distinct lithostratigraphic units. Among others, and from south to north, these units are Mata Amarilla Formation (Ameghino's "Shehuenense"), Salamanca Formation (or Group = "Salamanquense" auct., i.e., "Glauconítico" + "Fragmentosa" + "Banco Verde" + "Banco Negro"), Lefipán Formation + Paso del Sapo Formation, Coli-Toro Formation, Roca Formation ("Rocanense" auct.), Jagüel Formation, Allen Formation, Malargüe Group (Loncoche Formation + Pircala Formation + Coihueco Formation), Pedro Luro Formation, Las Chilcas Formation, and Mariano Boedo Formation. Throughout northern Patagonia, southwestern La Pampa Province, and southern Mendoza Province, the lacustrine or near-shore fresh-water deposits of this sequence were distinguished by Wichmann (e.g., 1927) as "Facies Lacustre Senoniana de los Estratos con Dinosaurios", which correlates with the middle part of the La Colonia Formation, or part of it.

As Lillegraven (1974: 277-278) stated, "[g]reater restriction of circumglobal currents during the Late Cretaceous at the region of today's Central America, and at various times and points along the European and Asiatic Tethys, would help explain the progressive increase in worldwide climatic zonations observed through the Cretaceous...", and "...opportunities (during the last part) for intercontinental exchange increased, especially between North America and Asia and possibly between North and South America". The possibilities of inter-American exchange were supported by Donnelly's (1985) geotectonic studies within the Carribbean region, and empirically demonstrated by the record of fossil land vertebrates (Bonaparte 1996, and literature therein), and probably also by land mammals (Marshall *et al.* 1997). To Donnelly, at about 85 my ago, the movement of South America relative to North America changes to northward, supplanting a formerly tensional environment by a compressional one. Consequently, compressive features surround the Caribbean sea: subduction and island-arc or continental-margin magmatism in Costa Rica, the Greater Antilles, and northern South America. These second-order phenomena appear to have created circumstantial links between the Americas, permitting the interchange of some land vertebrates. Actually, the Hadrosauridae dinosaurs are among the first and more successful colonizers. By that time they had colonized up to the southern tip of the South American continent (Casamiquela 1964, 1978; Bonaparte *et al.* 1984; Bonaparte 1986, 1996; Bonaparte & Rougier 1987). Although still without any record, it is quite probable that the first tribosphenid (*sensu* McKenna 1975) land mammals arrived by that time, or shortly afterwards, from North America, and probably following the same path as the hadrosaurian dinosaurs. Marsupials, and probably also placentals (cf. Godthelp *et al.* 1992, with

Woodburne & Case 1996), initiated by then the population of the Australian sector of Gondwana. Unfortunately, the South American mammal record representing the latest Cretaceous-earliest Paleocene span is a blank. And it is more unfortunate because through this span there had to occur the most significative turnover in mammal communities, from those almost exclusively composed by non-tribosphenic and pre-tribosphenic mammals (Gondwana Stage) to those composed almost exclusively by the Laurasian immigrant tribosphenids (marsupials and placentals) (Pascual 1998). Two more stages (South American Stage and Neotropical Stage) characterized the new era that followed the extinction of the Gondwanan non-tribosphenic/pre-tribosphenic stocks, and the immigration of the Laurasian tribosphenids (Pascual & Ortiz Jaureguizar 1991, 1992; Pascual 1996, 1997; Vizcaíno *et al.* 1998). The record of land mammals in South America during the Cretaceous-Cenozoic span suggests that all those events of mammalian evolution were causally related to the geographical steps that affected the South American continent: at the beginning, as part of Gondwana (Gondwanan Stage), later on as a relatively isolated continent (Souh American Stage), to finish, as present and for the first time, firmly connected to Laurasia by mean of the North American continent (Neotropical Stage) (see Pascual 1997; Vizcaíno *et al.* 1998).

SYSTEMATIC

Class MAMMALIA Limnaeus, 1758
Order [†]DOCODONTA Kretzoi, 1946
Family [†]REIGITHERIIDAE Bonaparte, 1990
Genus *Reigitherium* Bonaparte, 1990

Reigitherium bunodontum Bonaparte, 1990

Reigitherium bunodonta Bonaparte, 1990. As the generic name is in neutrum the specific name should also be in neutrum, and should be *bunodontum*.

HOLOTYPE. — MACN-RN 175, a left lower m3?

HYPODIGM. — The holotype and MEF 606, fragment of a left dentary with pm4-m2.

DISTRIBUTION. — The holotype comes from the middle section of Los Alamitos Formation, Río Negro Province (northern Patagonia), Argentina; its age is Campanian-Maastrichtian (Alamitan SALMA). Specimen MEF 606 comes from the second facies association of La Colonia Formation (see above), on the southern slopes of the North Patagonian Massif ("Comarca Nordpatagónica" or "Meseta de Somuncura"), North-Central Chubut Province, Patagonia, Argentina. Campanian to Late Maastrichtian age (Alamitan SALMA).

MEASUREMENTS. — L pm4-m2: 6.44; L pm4: 2.47; W pm4: 1.73; L m1: 1.98; W m1: 2.23; L m2: 1.81; W m2: 2.89; height of ramus below m1: 4.13; width of ramus below m1: 2.64.

DIAGNOSIS. — (The holotype and MEF 606 are the only known specimens of the family; thus, the following diagnosis is valid for the species, genus and family). *Reigitherium bunodontum* differs from the other docodont species, in that the crowns of the lower cheekteeth are laterally enlarged because the lingual cingular cusps became incorporated to a notably expanded, discrete masticatory surface. The lower last premolar is, at least, three-rooted. From pm4 to at least m2 the shape changes progressively from rectangular, with the longer diameter antero-posteriorly oriented (pm4 and m1), to almost subquadrate, but being, at the base of the crown, wider transversely than antero-posteriorly (m2), particularly because new basic buccal cusps are added. The dentary is stronger, without a postdentary groove, at least absent below m1 and m2.

REMARKS

Up to now, the holotype was the only known specimen. Because of its unusually wide crown, it was logically regarded by Bonaparte (1990) as a left upper molar. The new specimen of *R. bunodontum* here studied (MEF 606) clearly corresponds with the molar pattern shown by the holotype; but, otherwise, it demonstrates that the holotype is actually a lower, not an upper molar (see Figs 2D, E; 4C; 5E). The precise molar locus of the holotype is unknown; it is somewhat smaller and more quadrate in occlusal view than the m1-2 of the MEF 606 specimen, suggesting that it was posteriorly implanted in the molar row. If the holotype represents the immediately posterior locus to m2, and considering that its posterior face shows a flat surface indicating a contact area with one more molar, we have to admit that, at least, there were four molars.

DESCRIPTION

Dentary

The only known dentary is the portion between pm4-m2 preserved in the specimen MEF 606. Compared to those of the species of *Docodon* Marsh, 1881, the horizontal ramus is stronger. Its labial face is slightly convex, and shows a small dental foramen at middle height below the posterior root of pm4. The lingual face is not straight but shows two planes divided by a rim, the upper one slightly concave, and the lower one flat. There are no traces of a postdentary groove.

Dentition

As seen from above, the lower last premolar and the two first molars preserved in the new specimen of *Reigitherium bunodontum* (MEF 606) are quadrangular in shape, with rounded corners. From pm4 to m2 the shape changes progressively from rectangular, with the longer diameter antero-posteriorly oriented (pm4 and m1), to almost subquadrate, but being, at the base of the crown, transversally longer than antero-posteriorly (m2). The pm4 has an elongate main cusp, from which descends an anterior cutting crest, as in *Docodon,* but even more trenchant. From the main cusp descends a posteriorly wider face, which in MEF 606 is strongly worn, forming an almost flat, backward and downward inclined facet, triangular in outline, whose base forms the transverse bottom of a half-basin (Fig. 4C); this bottom becomes a talonid-like heel, apparently built upon a distal cingulum. The flat posterior wear facet, succeeded by the anterior half-basin of the m1, apparently initiates the V-shaped (in profile) intermolar basins formed by the adjacent halves of molars that distinguish the lower molar dentition of this species (Figs 2B; 4B). The posterior slope of the basin, which is on the anterior part of the corresponding tooth, is steeper. On the posterolingual slope of the main cusp, it remains part of an accessory cusp, which was partially erased by the wearing action that built up the posterior facet; this wear also affected the posterolingual end of the crown (Figs 2B; 4B). There also exists an anterolingual cingulum, larger and separated from a posterolingual one; these are the cingula that give a rectangular shape to the crown, in spite of the trenchant anterior crest (Fig. 4C). There are two large roots, well separated, and, quite peculiarly, there is also a much smaller intermedial one, almost central, and only visible in lingual view (Figs 2B; 4B); the smaller and central root represents one of the more unusual features of this specimen, not only because of its reduced size, but because it occurs well-labial to the lingual surface of the tooth; this peculiar position is similar to those intermedial extra-roots present in the Miocene Australian ornithorhynchid Obdurodon insignis Woodburne & Tedford, 1975, apparently also present in the living *Ornithorhynchus anatinus* (Woodburne & Tedford 1975). However, occassional triply-rooted of pm3, as well as permanent triply- to multiply-rooted upper molars, also occur in *Haldanodon exspectatus* Kühne & Krusat, 1972, from the Upper Jurassic of Guimarota, Portugal (Lillegraven & Krusat 1991). As in the molars, the crown is characteristically inflated, and quite set off from the roots and the dentary, particularly the labial face, which appears as a balcony (Fig. 2C, D). Unusally, there are two labial wear facets affecting the expanded crown, respectively, over each of the two roots (Figs 2A; 4A).

Both m1 and m2 show a similar pattern, the first being simpler, and rectangular. These molars are composed of a lingual sector and a labial one, separated by a shallow longitudinal sulcus, which extends on both anterior and posterior descending faces (Figs 2E; 4C; 5E); although worn, each portion ends in a main central cusp, connected to each other by a tenuous crest, from which the anterior and the posterior crenullated sloping faces descend. The labial portion of the m1 is longer than the lingual one, ending anteriorly in a secodont crest. On the contrary, the m2 has both labial and lingual portions equally long. Quite peculiarly, both m1 and m2 have two additional lower labial cusps, which are pillar-shaped and, respectively, terminal to the labial extension of an anterior cingulum and a posterior one (Figs 2A, D; 4A, C).
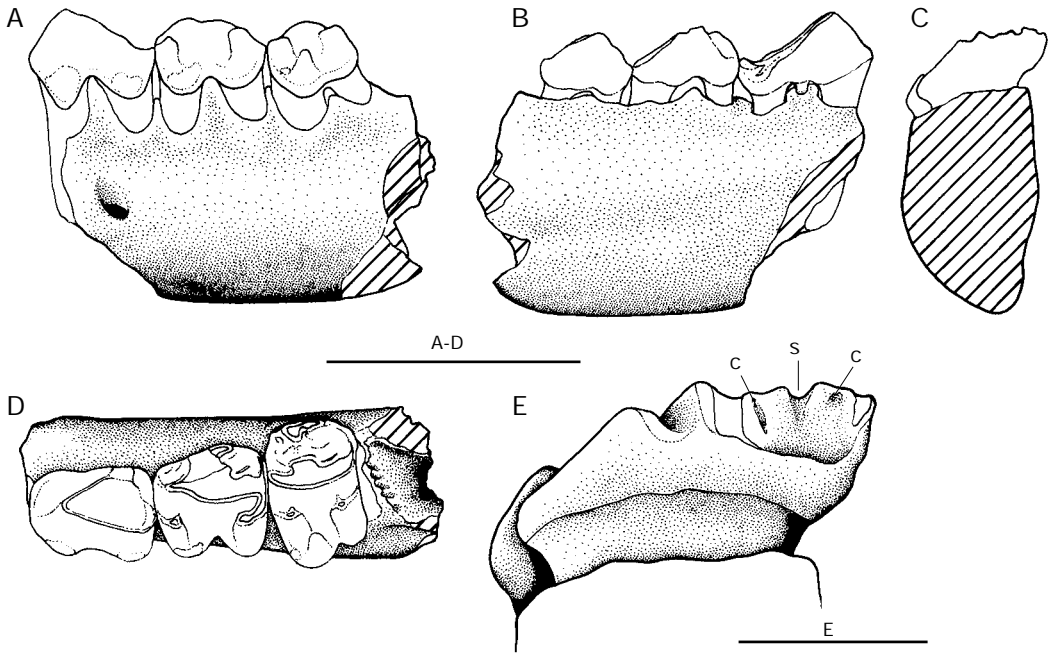
Fig. 2.— *Reigitherium bunodontum* Bonaparte, 1996, specimen MEF 606; **A**, **B**, fragment of left dentary with pm4-m2; **A**, external view; **B**, internal view; **C**, posterior view of the dentary section behind the m2; **D**, occlusal view of pm4-m2; **E**, posterior view of m2. Abbreviations: **c**, crenulations; **s**, sculus. Scale bars: 1 mm.

But, distinctively, the m2 has a third, intermediate and likewise pillar-shaped cusp, that also is terminal to an even lower tenuous anterior cingulum (Fig. 4C). In consequence, the crown base of the m2 is peculiarly inflated and expanded (exadaenodontic), in such a way that the whole tooth becomes wider than long, appearing also as a "balcony" on the labial side. Wear has affected the crown of both molars, erasing what apparently were prominent parallel labial and lingual ridges, with a higher medial cusp on each, and separated all along by a shallow furrow (Fig. 5E). The wearing action has been more intensive on the labial crest, which became lower and developed a deeper facet that exposes the dentine all along its extent; the dentine is also exposed on the lingual crest, but is restricted to what was the apex of the higher lingual cusp (Figs 2D; 4C). The descending anterior and posterior faces have also been worn in such a manner that the crenulations became smoothed, but without reaching the dentine. The additional lower labial cusps on both molars show cuspidate wear facets, incipient on the intermediate cusp of the m2 (Fig. 4C). As seen from above, the crown of both molars descend "en échelon" from the lingual to the labial sector, forming a step-like pattern (Figs 2E; 5E). In turn, as seen laterally, the wear has affected the normal intermolar basins, becoming V-shaped, and giving a saw-like profile to the molariform series (Figs 2B; 4B), similar to what is seen in Docodon. That is, the anterior half-basin of one molar joins with the posterior half-basin of the preceding molar to form a large intermolar basin, whose bottom becomes a talonid-like heel on the terminal end of each tooth, apparently built up on a distal cingulum. As on the pm4, both molars show wear facets on the labial faces, affecting the outward additional pillar-shaped cusps, although without exposing the dentine.

Occlusion

The adjacent halves of lower molars form intermolar basins (embrasures) on which, like in *Docodon,* had to occlude with a wedge-shaped

facet of an upper molar (unknown). The more advanced wear of the posterior facet is compatible with an upward and forward movement into centric occlusion, as proposed by Jenkins (1969) for *Docodon*. As noted by Butler (1997), docodonts were the only Jurassic mammals, apart from allotherians, in which the molars functioned by opposition. If, like in *Docodon* (see Jenkins 1969: fig. 9), *Reigitherium* has distinct wear facets on the posterior faces of the posterior cusps, wearing (thegosis) has transformed the entire posterior face into a flat facet. In such a manner, the shearing function against an upper facet (unknown) became much more effective than in *Docodon*. The development of these broad wear facets anticipated, although following a different pattern, a character that was distinctively developed in therian mammals (Crompton 1971). This feature, and the anterior crest of the last lower premolar, followed by the relatively crested anterior portion of m1, seems to indicate that shearing was the most important function in *Reigitherium*. However, the second type of occlusion proposed by Gingerich (1973) for *Docodon* also may have been active in *Reigitherium*. Actually, the incipient wear facet shown on the anterior face of the two first molars, appears to be made by an upward and backward movement into centric occlusion. The function of this movement was probably to puncture and separate large pieces of food, as interpreted by Gingerich (1973) for *Docodon*. Likewise, it could explain the puncturing action between the labial pointed pillar-shaped cusps of m1 and m2, as indicated by their horizontal wear facets (Figs 2D; 4C). It is evident that the shearing function between linear blades initiated in *Docodon* was enhanced in *Reigitherium* by the enlargement of the occlusal surfaces of the molars, and its transformation, by thegosis, into flat blade-like facets. It is also logical that the opposite action of the upper and lower blade-like facets produced a combined action of shearing and grinding, or crushing (*sensu* Butler 1997). A grinding or crushing action is attested to by the talonid-like heel apparently built up by the opposite action of an upper transverse crest at the end of the closing stroke. This grinding action might also been supplemented by the labial accessory cusps, which show relatively horizontal wear facets affecting their summits. Although no upper molar of this species have been recovered, the distribution of wear facets indicates as highly probable that, like in *Docodon,* the lingual half of each upper molar was also offset, even reaching a more advanced stage. The cuspidal wear facets affecting the additional lingual pillar-shaped cusps and, particularly, the unique wear facets affecting the base of the labial faces of all the molariform teeth, can only be explained by the bypassing action of an outcropping lingual extension of the upper molars. Although the "typical" docodontid interlocking of upper and lower transverse crests is compatible with a predominantly orthal movement, the more advanced mesio-distal wear facet on the buccal side of the lower molars might be produced by a relatively more prominent paraconecusp "c" during some antero-posterior movement.

DISCUSSION

Reigitherium bunodontum was previously considered to be a dryolestoid by Bonaparte (1990). However, we conclude that it represents a quite derived docodont. It shares with the North American Jurassic genus *Docodon* several derived dental features, e.g., lower intermolar basins formed by the adjacent halves of molars, and vertical crenulations (or ribs and furrows) on the molar crowns (see Simpson 1929; Patterson 1956; Jenkins 1969; Gingerich 1973; Kron 1979). Additionally, the presence of the triply-rooted pm4 supports the docodont affinities of *Reigitherium*. With the exception of monotremes, docodonts are the only mammalian group that have multiply-roots for the postcanines (at least in the uppers; see Lillegraven & Krusat 1991; Kermack *et al.* 1987; Luo 1994). In turn, the wear facets affecting the base of the labial faces of all the known lower molariform teeth (pm4-m1) appear as an autapomorphic feature, quite probably produced by a docodont-like outcropping lingual extension of upper molars. These dental features, and the resulting occlusal pattern, are not present in the other Laurasian (European and Asiatic)

Fig. 3. — *Reigitherium bunodontum* Bonaparte, 1996, specimen MEF 606; SEM stereopairs in occlusal view. Scale bar: 1 mm.

genera of the Docodonta, neither in any of the known non-therian mammals. On the one hand, the so derived dental autapomorphies indicate that *Reigitherium* is a highly derived docodont. On the other hand, they suggest that *Docodon* and *Reigitherium* may represent the derived sister-group of all other Docodonta. The closer affinities between North American (*Docodon*) and South American (*Reigitherium*) docodonts appear to be related to the closer geographical relation of both continents while part of Pangaea. In turn, the unique dental autapomorphies of *Reigitherium* imply a radical departure from the *Docodon* molar pattern. Taking into account the post-Jurassic geographic (and biogeographic) history of North and South American continents, we interpret these differences as one more example of vicariant evolution of both lineages.

Based on molar evidence, *Docodon* was considered not to have had a therian (i.e. Simpson's [1945] Theria) ancestry. According to Patterson (1956), as a non-therian mammal the docodontid cusp-on-line type of tooth did not pass through a reverse triangle stage in molar evolution. Crompton & Jenkins (1968), considering that both docodonts and therians derived from a common ancestor with a basically tricuspid dentition, suggested that more than one cusp on each upper and lower molar may be homologous. On this basis, they rejected cusp homologies and function previously proposed by Patterson (1956), Butler (1961) and Vandebroek (1961).
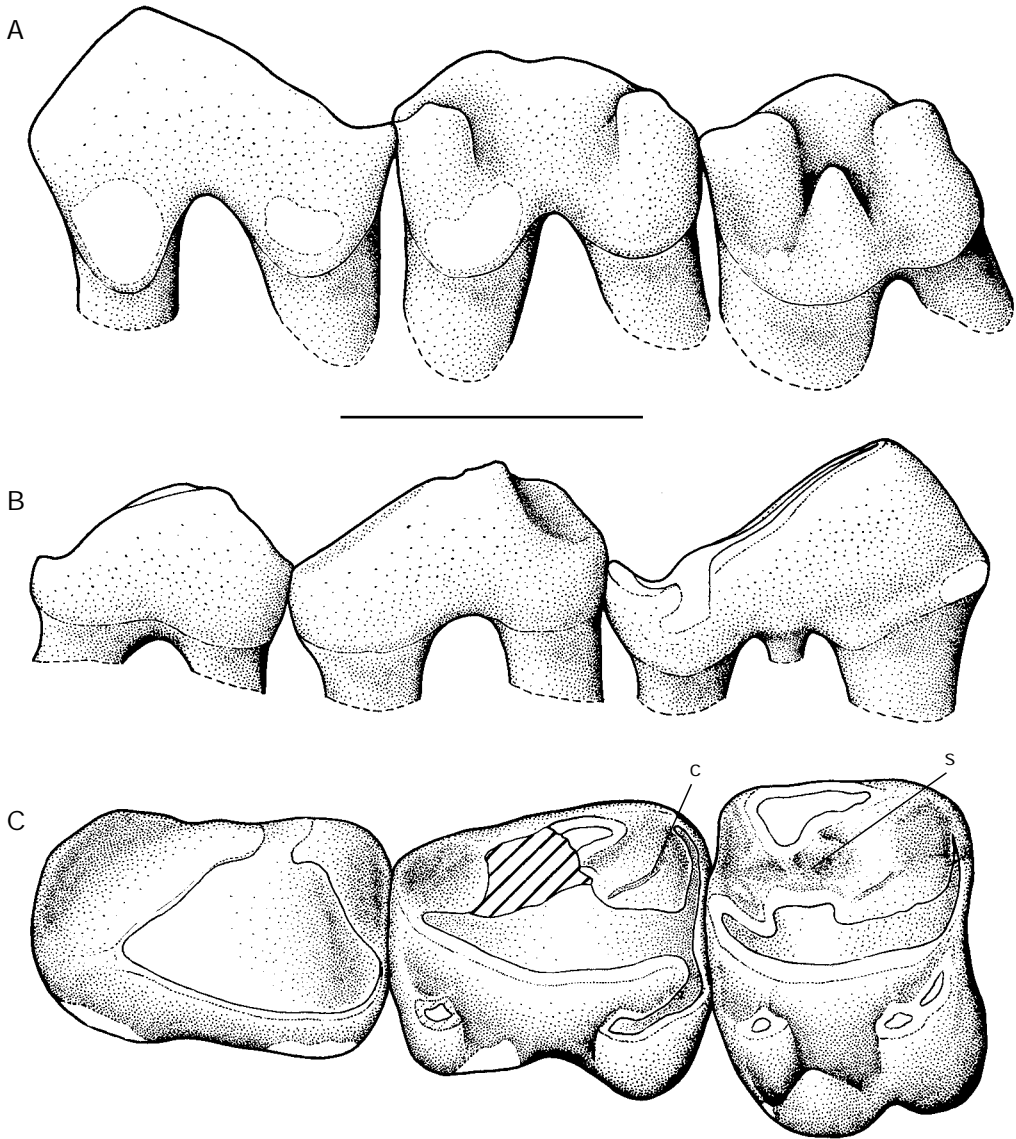
FIG. 4.— Left pm4-m2 series of specimen MEF 606 of *Reigitherium bunodontum* Bonaparte, 1990; **A**, external view; **B**, internal view; **C**, occlusal view. Abbreviations: **c**, crenulations; **s**, sculus. Scale bar: 2 mm.

Accordingly, they admitted that a molar pattern like that of *Morganucodon* Kühne, 1949 may have been the common ancestor of both docodonts and therians (Crompton & Jenkins 1968; Jenkins 1969). Even if this molar pattern appears to have been ancestral to the *Docodon* pattern, the cranio-mandibular comparison between the mor-ganucodontids and the Late Jurassic European *Haldanodon* – the best known among Docodonta – led Lillegraven & Krusat (1991) to consi-der the latter (and presumably docodonts in general) as a cladistically earlier stage of synapsid evolution than are the morganucodontids. Therefore, to them, docodonts "…assume a

cladistically basal position in the phylogenesis of mammals" (p. 122). Notwithstanding a rexamination of the craniodental characteristics of *Haldanodon* has shown that they are more derived at least by comparison to *Sinoconodon* Patterson & Olson, 1961 (Luo 1994). This is also ssupported by an independent study (Rougier *et al.* 1996) which again placed *Haldanodon* higher than morganucodontids in the mammalian phylogenetic tree. With respect to this aspect, see also Wible & Hopson (1993) and Wible *et al.* (1995). Already Kermack *et al.* (1987) had proposed that the docodont dentition could have evolved from some kind of therian-like teeth such as *Shuotherium*. On the same position, Butler (1997) admitted as possible that the origin of docodontid molar teeth passed through a triangular arrangement of cusps. This conclusion was suggested by the species of *Woutersia (W. mirabilis* Sigogneau-Russell, 1983 and *W. butleri* Sigogneau-Russell & Hahn, 1995) from the Rhaetic of France (Sigogneau-Russell 1983; Sigogneau-Russell & Hahn 1995), considered by these authors as a symmetrodont that was convergent with docodonts. The upper molars of these species have a lingual cusp, developed from the cingulum, that can be compared with the docodont "protocone" (cusp "X" of Krusat 1980), and a cusp B (homologized to the stylocone by Butler) that is diverted buccally. This triangular arrangement of cusps, to Butler resembling that in *Kuehneotherium*, is considered to be a synapomorphy shared with later therian mammals. If so, he said, the docodontid should be transferred to the Theria (Holotheria of Hopson 1994, diagnosed by having a reverse triangular pattern; see McKenna & Bell 1997: 43) as a sister-group of the Kuehneotheriidae. Consequently, docodonts could have been more closely related to therian mammals (i.e. Holotheria) than previously thought. More recently, Sigogneau-Russell & Godefroit (1997) studied new isolated teeth from the same Rhaetic Saint-Nicolas-de-Port quarry, and recognized them as representing a new genus and species (*Delsatia rhupotopi* Sigogneau-Russell & Godefroit, 1997), closely allied to the species of

Woutersia, although formally assigned to an uncertain family of the Docodonta, but recognizing that it combines characters of symmetrodonts and of docodonts. On this basis, they stated that the order Docodonta "...could be closer to Theria than to Eotheria", although cautiously pointing out that the evidence only got from teeth preclude hasty conclusions.

If both Butler's and Sigogneau-Russell & Godefroit's observations and suggestions were correctly founded, *Reigitherium* – as a docodont – could represent one more clade of mammals sharing advanced features with the most primitive therians. Additional studies of the cranial features (Luo 1994; Rougier *et al.* 1996) also support the higher placement of docodonts in the mammalian phylogenetic tree. Be that as it may, the morphological pattern of the lower molars of *Reigitherium* appears as derived relative to the general condition of *Docodon*, having two longitudinally parallel cusp rows of different heights, separated all along by a shallow sulcus, without any evidence that it passed through a triangular arrangement of cusps as that recognized in *Woutersia* spp., and *Delsatia rhupotopi* (Figs 2E; 3).

To Jenkins (1969), the evolution of the "*Docodon* molar type" from the "*Eozostrodon* (i.e. *Morganucodon*) cusp-on-line type" involved two basic modifications: 1) lingual expansion of both upper and lower molar crowns; 2) loss of one primary cusp on each lower and upper molar. The first modification is quite relevant since *Reigitherium* appears to represent a step further than previously known docodonts, and apparently succeeded according to the following scenario (Fig. 5). The lingual expansion of lower molar crowns, already initiated in *Docodon* (Fig. 5C), and the elevation of the cingular cusps to become very prominent features, was increased. In such a manner, in *Reigitherium* the lingual cingular cusps became as high or higher than the buccal ones, and connected each other to form a ridge parallel to the labial one (Fig. 5D-E). Thus, the evolution of reigitheriid lower molars may be envisaged as a further increase of the area of opposition, by expansion
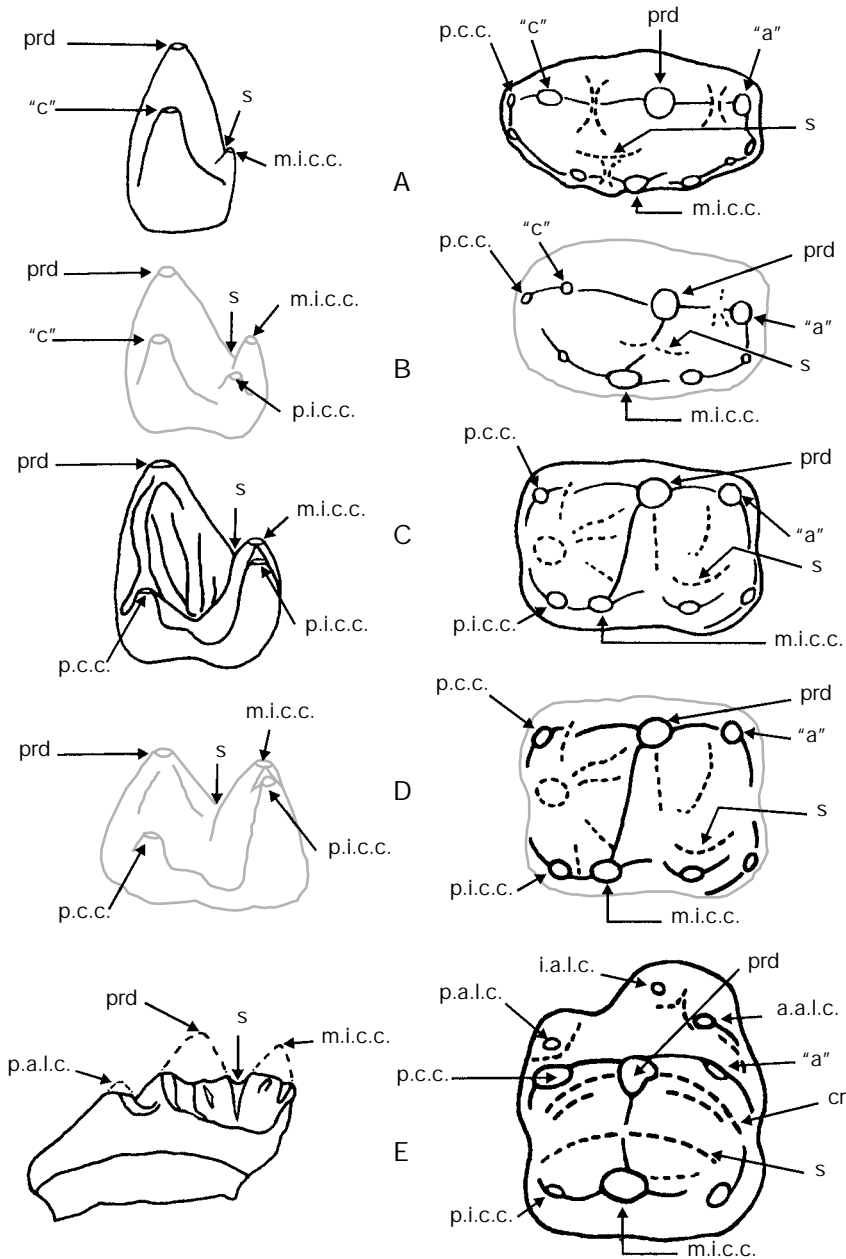
Fig. 5. — Molar evolution and cusp homologies in lower right molars of morganucodontids, docodontids, and reigitheriids. Posterior (left) and occlusal (right) views (anterior to the left; lingual below); **A**, *Morganucodon*; **B**, hypothetical Early or Middle Jurassic docodont; **C**, *Docodon* from the Late Jurassic Morrison Formation; **D**, hypothetical Late Jurassic or Early Cretaceous reigitheriid; **E**, *Reigitherium bunodontum* from the Campanian-?Maastrichtian La Colonia Formation, Patagonia. In the occlusal views (right), anterior is to the right, and lingual face is toward the bottom of the page. Abbreviations: "**a**", cusp a; **a.a.l.c.**, anterior additional lower cusp; "**c**", cusp c; **cr**, crenelation; **i.a.l.c.**, intermedium additional lower cusp; **m.i.c.c.**, main internal cingulum cusp; **p.c.c.**, posterior cingulum cusp; **p.i.c.c.**, postero-internal cingulum cusp; **p.a.l.c.**, posterior additional lower cusp; **prd**, protoconid; **s**, sulcus. Cusps nomenclature follows Jenkins (1969), except a.a.l.c., i.a.l.c. and p.a.l.c., that are new cusps and only known in *Reigitherium bonodontum*. Drawings are not to scale.

of the lingual sector. According to the hypothesis and nomenclature used by Jenkins (1969: fig. 1; see also Fig. 5), the labial ridge was formed by a crest running anteriorly and posteriorly from the higher protoconid (prd), respectively connecting it to "a", and to the posterior cingulum cusp (p.c.c.). The additional lingual ridge was formed by a crest connecting the now higher main internal cingulum cusp (m.i.c.c.) – as high or higher than the protoconid – with the postero-internal cingulum cusp (p.i.c.c.); otherwise, this ridge is shorter than the labial one since it is restricted to the posterior portion of the crown. Finally, both labial and lingual ridges became fused, although still separated by a shallow furrow or sulcus, which appears to be a remnant of the deeper one that in *Docodon* separates the additional lingual cusps from the original labial ones (cf. Fig. 5E with 5C). This process transformed the somewhat modified tricuspid cusp-on-line molar type, Jenkins' (1969) "eozostrodontid (i.e. morganucodontid) molar pattern", into a "docodontid molar pattern", to finally become a quadrangular molar, a "reigitheriid molar pattern".

Thus, accepting Crompton & Jenkins' (1968) hypothesis that a molar pattern like that of *Morganucodon* was in the ancestry of docodonts, and our hypothesis that docodontids and reigitheriids had a common ancestor, the evolution of the reigitheriid lower molar pattern from the murganucodontid molar pattern involved three main modifications (Fig. 5C-E), apparently succeeded "*en échelon*", resulting in a step-like pattern: 1) expansion of lingual cingulum and relative elevation of its cusps ("docodontid molar pattern"; Fig. 5C); 2) increased elevation of the lingual cingular cusps, becoming interconnected to each other by a crest as high or higher than the labial one, in turn connected to the latter to shape a discrete enlarged masticatory surface, that slopes anteriorly and posteriorly from the central transverse prd-m.i.c.c.' ridge, like a gable roof ("hypothetical pre-reigitheriid pattern"; Fig. 5D); 3) aggregation of labial pillar-shaped cusps, ranging from two – an anterior and a posterior one (m1) –, to three by the aggregation of an inter-medial one, somewhat lower (m2) ("reigitheriid molar pattern"; Fig. 5E).

The fact that such major morphological differences exist in the lower molars between *Docodon* and *Reigitherium* is not, in itself, surprising. Most of the duration of the Cretaceous Period separates the useable fossil records of the two genera. Some 70 my probably are involved, which would have allowed plenty of opportunities for divergent specializations as those existing between *Docodon* and *Reigitherium*, particularly considering that they were developed on Gondwana, under a quite distinct scenario.

Reigitherium bunodontum is one more eloquent example that in mammals the universal trend to increase the masticatory surface of the cheekteeth was also accomplished without passing through the reversed triangle stage that led to the tribosphenic pattern. Furthermore, *Reigitherium bunodontum* is an example of a group (Docodonta) that became extinct in one continent (Laurasia), in a time (late Jurassic) and under specific ecological circunstances, but that survived and evolved throughout most of the Cretaceous in a segregated continent (Gondwana), under distinct ecological circumstances, giving origin to a distinct and more advanced family (Reigitheriidae), to finally become extinct before the beginning of the Cenozoic.

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