PALEOCENE DINOSAURS

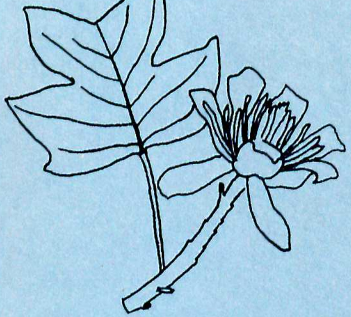
OR

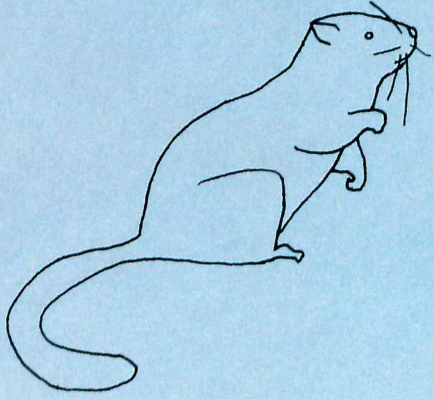
CRETACEOUS UNGULATES

IN

SOUTH AMERICA

Leigh M. Van Valen





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Paleocene Dinosaurs or Cretaceous Ungulates in South America?[1]

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Abstract: This is an inclusive paper, with discussions of various ancillary topics which are relevant to its main conclusion. This conclusion is that the mammal-bearing parts of the El Molino and Vilquechico Formations are Paleocene, and not earliest Paleocene, rather than Cretaceous. Therefore it is possible that dinosaurs extend one to three million years into the Paleocene in South America; ungulates, as well as all other placentals and marsupials, are unknown there before the Paleocene. I examine all available evidence in detail.

If dinosaurs did survive well into the Paleocene, for which I review evidence from other regions also, their extinction was not a direct result of the terminal Cretaceous environmental crisis. The marsupial extinction at that time remains severe. There is evidence for appreciable biotic interchange between South and North America in the Paleocene, and for skepticism that larger areas for evolution produce better competitors.

Two other South American dinosaur-bearing rock units, the Balbuena Subgroup of Argentina and the Bauru Group of Brazil, may also be Paleocene at least in part, on poorer evidence. I return the Itaborai Fauna of Brazil to a later Paleocene (Riochican) age. I comment on correlation of some other South American formations and of some other faunas on various continents, on the theory of correlation by phylogenies, and on charophytes and snails.

The mammalian orders Dinocerata and Pyrotheria (including Xenungulata) both probably originated from the North American arctocyonid condylarth Deuterogonodon, more or less separately. The Phenacolophidae and thereby the Tethytheria may also have done so. The Pantodonta probably originated from the new arctocyonid subfamily Deltatheriinae; Wangliidae and Wanglia in the Pantodonta are also new. I transfer the Bemalambdidae from the Pantodonta to the insectivoran superfamily Palaeoryctoidea. With more doubt I transfer the Arctostylopidae from the Notoungulata to the Astrapotheria; arctostylopids and notoungulates were probably derived separately from primitive astrapotheres. I propose the superorder Ameghinida for this group and the term "rectodont" for upper molars with a straight centrocrista. I comment on the evolution of the Edentata, condylarth phylogeny, the African genus Garatherium, astrapothere occurrences, the major classification of mammals, canned phylogenies, and the remarkable mammals now known from the real Cretaceous of South America.

Introduction

In two correlative formations in the Altiplano and eastern cordillera of Bolivia and southeast Peru, dinosaurs appear to occur together with primitive ungulates, or in beds which are said to correlate with the ungulate-bearing strata. The only other place in the world where this situation has been found is in Montana and nearby areas (Sloan and Van Valen, 1965; Archibald, 1982; Johnston and Fox, 1984; the Cretaceous ungulate described from Argentina by Bonaparte and Soria [1985] proved to be a pantothere, as noted in an erratum slip inserted in the same issue of the journal.) However, in the North American faunas, the ungulates consist of the most primitive species known and their immediate descendants, while in South America the ungulates are more derived. The South American formations have been dated as late Cretaceous (if occasionally with reservations, as by Pascual [1986] and as by Bonaparte and Pascual [1987]) by everyone since 1940 or so except Van Valen and Sloan (1977 and later, without detailed discussion.) I here examine all the available evidence and conclude that the basis for a Cretaceous age is weak and that the formations are very probably Paleocene. This conclusion affects the nature of the Cretaceous/Paleogene extinction, ungulate phylogeny, biogeographical history, and, in a minor way, the timing of part of the Andean uplift.

The formations are the Vilquechico of southeast Peru and the El Molino of western Bolivia. (These names are the ones in current use; because of geographic variation in lithology one or both may be subdivided in the future.) These continental to marginal-marine deposits are at least approximately correlative with each other and both were deposited in the Aimara Basin of Ricardi (1987), which extends into northwest Argentina. (This is the Andean Basin of Reyes [1972] and Bonaparte and Powell [1980], part of the Andean Basin of most authors, and the Subandean Basin of Malumián, Nullo, and Ramos [1983]. The latter name is normally applied to a quite separate basin to the east.) The two formational names refer to the same, originally continuous, unit in different countries (and in different later-formed structural basins), as discussed by Russo and Rodrigo Gainza (1965) and Reyes (1972). Several sub-basins occur (Reyes, 1972).

There are a number of localities where fossils have been found in discontinuous surface exposures, and fossils occur at different levels even at single localities. However, because there seems to be no good evidence for any significant age heterogeneity within these formations, I will treat the formations and localities as a single unit (except with respect to dinosaur extinction), while recognizing that this may prove incorrect. Mammals, including an ungulate, and have nevertheless been found at the same locality as eggshells identified as dinosaurian (Kerourio and Sigé, 1984). One would expect some dinosaur teeth, at least, even in size-sorted deposits, but none have been reported in the prolific Tiupampa Local Fauna. This lack suggests that the beds there may have been deposited after dinosaur extinction there, but even if this is true most or all of the non-dinosaurian species found elsewhere in the El Molino occur also at Tiupampa, so any age difference is presumably small. Dinosaur remains in the Vilquechico and El Molino have been limited to eggshells and tracks.

Figure 1 shows relevant stratigraphic sequences. I should say explicitly that I have tried not to accept any stage in any current or prior argument without adequate evidence. This applies to identifications of fossils as well as to other aspects, but in many cases an author makes identifications without giving justification. This can cause problems (cf. discussion of the charophyte Platychara) and I have given less weight to

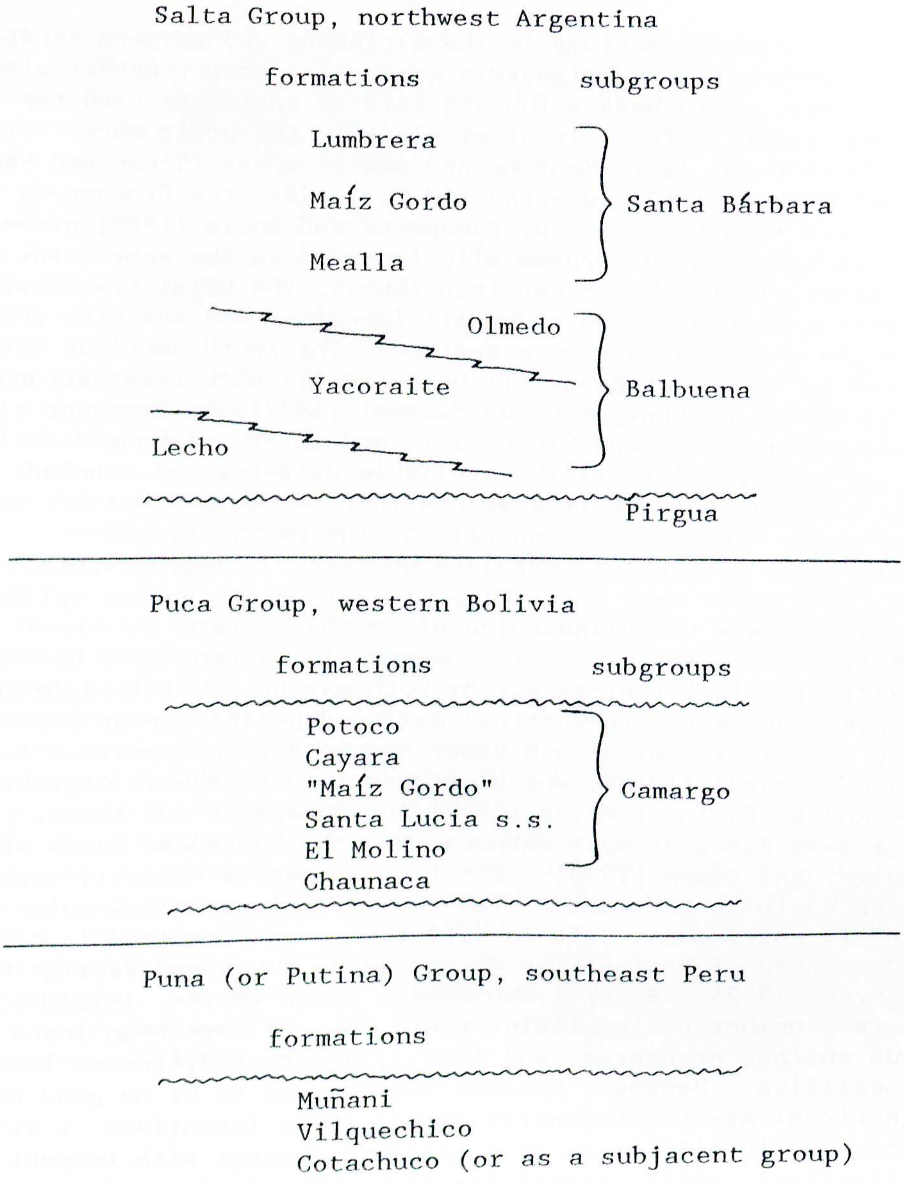

Figure 1. Stratigraphic sequences.

such evidence, especially from nonspecialists. (But even specialists can be misled by inadequate material, and they too can make unsupported assertions.) Indices of taxonomic and stratigraphic names appear at the end.

Yacoraite Formation

Before considering the direct evidence it is prudent to evaluate the Yacoraite Formation of the Salta Basin in Argentina, and some other matters. The Yacoraite was deposited at the south end of the Aimara Basin, is about as well known as the El Molino and Vilquechico, and is correlated with them (or sometimes with their lower part only). Dinosaurs but no mammals have been found in it. I do not know whether anyone has specifically searched for mammals here; they are unlikely to be found otherwise.

The basis for correlation with the northern formations is partly biotic and partly physical. The Yacoraite resembles especially the El Molino lithologically; both contain abundant carbonates and the stromatolite Pucalithus (Russo and Rodrigo Gainza, 1965). Pucalithus, however, also occurs above the Yacoraite in each of the formations of the Santa Bárbara Subgroup (Moreno, 1970; Russo, Ferello, and Chebli, 1979). Again, the Yacoraite appears to be the southern part of the same depositional unit, and like the northern formations it is continental to marginal marine. In each case the beds above and below are freshwater. The widespread, if now sporadic, geographical recurrence of the El Molino in Bolivia, including the south of the country, makes it likely that the Yacoraite is merely its continuation across the border and in southern sub-basins. The biotic evidence can be evaluated by comparing the taxa discussed for the El Molino and the Yacoraite; it supports the physical evidence.

The Yacoraite is part of the Balbuena Subgroup of the Salta Group. The Lecho and Olmedo Formations, below and above the Yacoraite respectively, are the other formations in the Balbuena; the Yacoraite interdigitates with each (Russo, Ferello, and Chebli, 1979), although Marquillas, Boso, and Salfity (1984) note that the boundary with the Lecho is well-defined. Each can be regarded as partly a facies of the others (Salfity and Marquillas, 1981). The Pirgua Subgroup apparently underlies the Balbuena with a regional disconformity (Lencinas and Salfity, 1973; Bonaparte et al., 1977; but see Salfity and Marquillas, 1981). Bonaparte et al. (1977) summarize three radiometric dates near the top of the Las Curtiembres Formation, the second formation from the top of the Pirgua Subgroup, as 75, 76, and 77 Ma.

The Santa Bárbara Subgroup overlies the Balbuena conformably (Salfity and Marquillas, 1981; Schwab, 1984), and in fact has been said to grade continuously into it (Pascual and Odreman, 1973). Its lowest formation, the Mealla, has produced specimens of a notoungulate near its base (Pascual, Vucetich, and Fernandez, 1979). This notoungulate, Simpsonotus, is primitive in some but not all respects (see also Cifelli, 1985) and suggests an age in the last half of the Paleocene.

Palynomorphs have been isolated from the basal part of the Olmedo Formation, but the evidence seems not to have been published and so cannot be evaluated. Bianucci, Acevedo, and Cerdan (1981) and Giudici and Gascon (1982) believe that the palynomorphs indicate a Paleocene age.

Musacchio (1972) and de Stach and Angelozzi (1984) have reported several charophytes from the Yacoraite: Porochara ovalis, P. gildemeisteri costata (see discussion for El Molino), Platychara compressa, Tectochara spp., and Amblyochara sp. As discussed for the El Molino, all these are neutral with respect to Maestrichtian vs. Danian age except Tectochara, which has been stated to come only from the Cenozoic (Feist and Grambast-Fessard, 1982), although Karczewska and Ziembieńska-Tworzydło (1970) had named some Cretaceous species.

Several benthic foraminiferans from the Yacoraite are not yet particularly useful. De Stach and Angelozzi (1984) report Miliolinella sp., which ranges from the Aptian to the present. Méndez and Vivers (1973) report forms "similar to" Discorbis aff. cretacea and three Coniacian-Santonian species of Valvulineria. Loeblich and Tappan (1964) record Discorbis as Eocene-Recent but note that it has usually been misidentified; they give Valvulineria as Albian-Recent. There were also three other forms, "evolutionary advanced" with respect to their Turonian or older presumed relatives of the genera Orostella, Lingulogavelinella, and Bilingulogavelinella. Malumián and Báez (1976) note the age anomaly for beds whose earliest reasonable age is Maestrichtian; it would help to have these forms restudied.

Mingramm et al. (1979) and Cortelezzi et al. (1973) record the snail genera Melania, Katosira (as Catosira) and Zygopleura (as Zigopleura) from the Yacoraite. W. Wenz (1938-1944) has the range of Melania as ?Paleocene to Recent, of Katosira as ?Permian, late Triassic to middle Jurassic, and of Zygopleura (including Katosira as a subgenus) as late Silurian to late Jurassic. At least Melania, however, is commonly used as a form genus. Termier and Termier (1952), Vostokova (1960), and Ovechkin and Pchelintsev (1960) give ranges included in those of Wenz except for Melania, which Ovechkin and Pchelintsev list as late Cretaceous to Recent.

Three ostracodes described from the Yacoraite by de Stach and Angelozzi (1984) have not been found elsewhere. One was Eucandona? cf. E.? huantraiconensis, the latter species coming from the Maestrichtian Huantraico (or Loncoche: Digregorio and Uliana, 1980) Formation in the Neuquen Basin in central Argentina. Another was Cypridopsis sp., compared with two species from the Maestrichtian and Danian. The third was Ilyocypris cf. I. wichmanni, the latter species having been described from late in the Senonian of the Neuquén Basin (Musacchio, 1973). Méndez and Viviers (1973) listed two other Yacoraite genera, Cytherura and ?Cytherella. All five genera are extant and standard sources (Benson et al., 1961; Van Morkhoven, 1962-1963) give ranges which in some cases do not even include the ages of the later-described species referred to here.

There are four fishes known from the Yacoraite (Leanza, 1969; Benedetto and Sanchez, 1971, 1972; Powell, 1979; Cione and Pereira, 1985; Cione et al., 1985): Pucapristis branisi, Coelodus toncoensis, Gasteroclupea branisai, and Siluriformes indet. These all occur, or may occur, in the El Molino and are discussed with that formation.

Benedetto and Sanchez (1971) listed a lizard, Dicarlesia incognita, from the Yacoraite. According to Estes (1983) this is not a lizard but probably a fish; the figure is poor and the type is lost, so it cannot affect the names of later-described fishes. The crocodilian Dolichochampsa minima de Gasparini and Buffetaut (1980), from the Yacoraite, is the only known member of its family.

There are also several sauropod and theropod dinosaurs from the Lecho and Yacoraite (Bonaparte et al., 1977; Powell, 1979; Bonaparte and Powell, 1980; Brett-Surman and Paul, 1985), and Alonso (1980) has reported hadrosaur tracks. Most of the material is either generically indeterminate or belongs to endemic genera, but Avisaurus also occurs in a locality (Archibald, 1982) only 20 m below the top of the Hell Creek Formation in Montana; the formational boundary is slightly above the base of the Paleocene (Sloan et al., 1986). This is the only other known occurrence of the genus and family and it represents the same or a similar species as the one from the Lecho (Brett-Surman and Paul, 1985). Bonaparte (1986b) regards Avisaurus as an enantiornithal bird, but this of course does not affect its use in correlation. Other enantiornithal birds also occur in the Lecho (Bonaparte and Powell, 1980; Walker, 1981, Bonaparte, 1986b), but apart from the Hell Creek Formation the group is known elsewhere only from the Australian Albian (R.E. Molnar, unpublished, *fide* Bonaparte 1986b).

I concur with Salfity and Marquillas (1981) that it is not clear where in the Salta Group the Cretaceous/Paleogene boundary lies. In particular, the age of part or all of the Balbuena Subgroup could at least as well be Danian as Maestrichtian. Groeber (1939) had considered the Yacoraite to be

Danian, but his evidence was weak, and Cione and Pereira (1985) noted in passing that the Yacoraite may be Paleocene.

Bauru Group

This sequence of rocks occurs in southern Brazil, extending a bit into Paraguay. It has a large area of outcrop but is only sparsely fossiliferous; its age is somewhat relevant to that of the El Molino and Vilquechico. It has recently been divided into several formations (Soares et al., 1980; Soares, 1981). Fossils are apparently restricted to the upper part of the Adamantina Formation, the lower part of the Marília Formation, and the partly intervening Uberaba Formation (Soares, 1981; Suguio and Barcelos, 1983). All three formations intertongue with each other; the Marília is the highest.

Correlation has been based mostly on fossils, for which Suguio and Barcelos (1983) provide a useful list, taken from a paper by Mezzalira which I have not seen. Estes and Price (1973), Estes and Báez (1985), and Báez (1985) have added other forms. As a first approximation the biota from the Bauru (the name lacks an accent in Portuguese) can be treated as a single unit because of its restricted distribution. In addition Soares and Landim (1975) say that some of the sediments of the Uberaba were provided by volcanos to the northeast, which are dated by unspecified means (they give no reference and later papers cite only this one) as 85 to 55 Ma. A charophyte is referred to the genus _Praechara_, which otherwise is of Triassic age (Grambast, 1961; Feist and Grambast-Fessard, 1982). This seems more likely to be a misidentification than an enormous range extension; in either case it does not help in correlation. (I omit discussion of several Bauru taxa which are obviously unhelpful.)

Paleolimnadiopsis, a conchostracan, has a range from the Carboniferous to the Cretaceous (Tasch, 1969). Two clams, _Anodontites_ (with three species) and _Monocondylaea_, are noted as "Tertiary-Recent" by Haas (1969). He cites a third, _Diplodon_, as "Cretaceous-Recent", and does not mention the three other Bauru genera, _Florencia_, _Sancticarolis_, and _Itaimbeia_. Possibly the latter genera are endemic. Three snails have been found in the Bauru: "_Physis_", _Viviparus_, and _Hydrobia_. If "_Physis_" is an error for _Physa_, all three are extant genera with records at least as old as the early Cretaceous (W. Wenz, 1938-1944; Zilch, 1959-1960).

There are two records of fishes in the Bauru, _Lepidotes_ and _Lepisosteus_. The former is known from the late Triassic to intertrappan beds near (on either side of) the Cretaceous/Paleocene boundary (Gayet, Rage, and Rana, 1986). _Lepisosteus_ ranges from the late Cretaceous to the present (Wiley, 1976).

A leptodactylid frog also occurs in the El Molino; closer identifications are unavailable. The earliest record of this extant family is in the approximately late Campanian Los Alamitos Formation of Patagonia (Báez, 1985; Bonaparte, 1986b). Two pelomedusid turtles occur in the Bauru, _Podocnemis_ and _Roxochelys_. The latter is endemic except for possible occurrences in the El Molino, Vilquechico, and Hanchipacha, while _Podocnemis_ may also occur in the El Molino but is otherwise late Eocene to the present (Młynarski, 1978). However, de Broin (in Estes and Báez, 1985) regards the Bauru species as generically indeterminate. _Pristiguana_ is the earliest iguanid lizard, endemic to the Bauru (Estes and Price, 1973). The earliest record of the family elsewhere is from the El Molino, and otherwise from the last half of the Paleocene (Estes, 1983).

There are several crocodilians, which prove to be less useful than would appear from the faunal list. Of the two placed in the Notosuchidae, Bonaparte (1978) says that *Brasileosaurus* is based on unidentifiable material and that *Sphagesaurus* should probably have a family of its own. The Goniopholidae fare even worse. Buffetaut (1982), who seems not to mention the two preceding genera, denies that there is adequate evidence even for the presence of the Goniopholidae in South America. The references to *Machimosaurus* and *Goniopholis* are apparently based on isolated teeth, which Buffetaut says are not characteristic. The third genus, *Itasuchus*, is endemic and probably belongs to some other, unspecified, family (Buffetaut, 1982). *Baurusuchus* is endemic; its family, Baurusuchidae, extends from the Cretaceous to the middle Eocene (Buffetaut, 1982). Another endemic genus, *Peirosaurus*, belongs to the Uruguaysuchidae, known from two other genera (Aptian-Senonian). *Peirosaurus* is on a different lineage from the Senonian genus (Buffetaut, 1982).

And, finally, dinosaurs occur in the Bauru. Two are sauropods, *Titanosaurus* cf. *T. australis* and *Antarctosaurus brasiliensis*. Bonaparte (1978) refers to the former only as cf. *Titanosaurus* sp. and notes that *A. brasiliensis* is also based on poor material. Both genera occur in the Senonian of Argentina. The two theropod records, for *Thecodontosaurus* and *Ceratosaurus*, are not even as good as those for the sauropods. *Thecodontosaurus* occurs in the late Triassic and earliest Jurassic, while *Ceratosaurus* is a late Jurassic genus (Glut, 1982; Norman, 1985). Dinosaur genera are not long-lived, and I strongly suspect that both records are based on misidentification of scrappy material. Bonaparte and Powell (1982) regard the carnosaurs as indeterminate.

I conclude that the universally accepted Cretaceous age for the fossiliferous part of the Bauru is possible but not well supported. If there are rocks suitable for bulk processing for charophyte oogonia or mammal teeth a better estimate may possibly be made than from the rare finds of macrofossils.

Itaboraí Fauna

The well-known but incompletely described vertebrate fauna known as Itaboraí actually occurs about 12 km south of Itaboraí, Brazil (and 25 km east of Rio de Janeiro) at the village of São José. The latest papers on the fauna are by Cifelli (1983a, b), who refers to earlier work.

A small lake initially formed in Precambrian rocks, in a basin about 1.4 km long and at least 0.4 km wide, close to São José. This lake filled with about 100 m of limestone, especially travertine, marl, and calcirudite. This limestone has been called the Itaboraí Formation by Baptista, Braun, and Campos (1984), and it seems best to follow their authority even though the name was first used off-handedly in a broad review (Oliveira et al., 1956) and has apparently never been really defined. Fonseca et al. (1979) called it the calcário de São José, but the latter name is in use already for two other formations in Brazil. The basin is, however, usually called the Itaboraí Basin (e.g., Petri and Fulfaro, 1983), although Fonseca et al. (1978, 1979) called it the São José Basin.

At some time (see below) the limestone was subjected to karstic erosion; internal solution channels and cavities were formed, but apparently none have been found with a connection to the top of the limestone. Clastic deposits filled these openings; the resulting rocks seem to be nameless. Fossils of all classes of tetrapods occur in these fillings and constitute the Itaboraí Fauna. There will be, probably, some perpetual awkwardness because the Itaboraí Fauna comes from a different rock unit from the

Itaboraí Formation. The limestone has been quarried for cement (in fact if it is not now quarried out it soon will be), and operations of the quarry have uncovered the fissures from time to time.

A fault at the south end of the current basin was reactivated some time after the deposition of the limestone. The rock to the north of it was downthrust and partly preserved; any lake deposits to its south have been eroded away.

Different views exist as to the relative timing of the fissure formation. In addition to the vertebrate fauna of the fissures, the limestone itself contains 15 to 20 species of gastropods, an ostracode, and angiosperm foliage and seeds. No fishes have been reported; the demonstrated hydrothermal activity may be relevant. Near the boundary fault, elements of this biota occasionally occur in fissures with the Itaboraí Fauna. It seems likely that they are redeposited in some way, but this is uncertain.

Paula Couto (1952a) also reported that some vertebrates were found in limestone, but no more detail is available. The usual view (e.g., Paula Couto, 1958; Fonseca et al., 1979) is that the non-vertebrate biota, which may be called the São José Biota, occurs in the rock which was partly removed by the fissures, and that it is therefore older than the fissures and the Itaboraí Fauna. However, Brito, Franke, and Campos (1972) and Palma and Brito (1974) claimed that the São José Biota occurs only in limestone deposited above the fissures and not cut by them, and so it would be later. This view marches with the apparent lack of extension of the fissures to the top of the total limestone; the tetrapods must have gotten in somehow. It is also more concordant with the mid-Cenozoic age suggested by the São José Biota itself, on which see Palma and Brito (1974). (However, a re-initiation of similar limestone deposition after a lapse of millions of years may be unlikely.) The cases of co-occurence of the two biotas would then be explained by the hydrothermal fluid from the fault dissolving the later limestone, with subsequent precipitation in the cavity. Francisco and Cunha (1978) mention the paper of Palma and Brito (1974) in another context but do not discuss the difference from their view, which is the usual one. This is odd, because they give the most detailed account of the physical stratigraphy and yet do not make an explicit statement on whether the São José Biota occurs in rocks cut by the fissures. The matter should be easily resolvable if any relevant rocks are left.

Most specimens from the Itaboraí Fauna lack precise data, but differences in preservation, co-occurrence, and collection time permit some segregation of specimens and give strong evidence for heterogeneity among fissures with respect to the species present (Cifelli, 1983a). It does not seem likely that there is significant age heterogeneity among different fissures, although this has not been treated explicitly.

In some of the secondary (?tertiary) literature the fillings are not distinguished from the limestone, and this confounding has caused some confusion as to the age of the fauna in the fillings. Francisco and Cunha (1978) regarded the limestone as about early Paleocene, presumably because of the angiosperms, the mammaliferous fissures cutting it, and the probable relation between deposition and karstic erosion here; the Itaboraí Fauna itself has thereby been put recursively into the early Paleocene by others. The English summary of the paper by Francisco and Cunha (1978) contains a consistent mistranslation, interchanging "early" and "late"; this has also caused some confusion.

The mammals of the Itaboraí Fauna permit its approximate correlation with the standard sequence in Patagonia. The overall composition of the faunas differs appreciably, presumably because of environmental differences such as the 23° difference in latitude, but this is of course irrelevant for correlation.

Despite recent revisions which have shown that some apparent resemblances are less close, several genera from the Itaboraí are found in Patagonia. The primitive borhyaenid marsupial Patene has a species at Itaboraí, P. simpsoni, apparently ancestral to one of the same genus in the Casamayor (Marshall, 1981). However, P. simpsoni also occurs in the Lumbrera Formation in the Salta Basin (Goin et al., 1986); this formation is at the top of the Santa Bárbara Subgroup and is regarded of Casamayoran age (Pascual, Bond, and Vucetich, 1981), although it may be late Ríochican. Another borhyaenid, Nemolestes, has been questionably reported from both the Itaboraí and the lower Río Chico, but the type species, from the Casamayor, is known merely from two trigonids and is nearly indeterminate (Marshall, 1978). The caenolestoid marsupial Epidolops apparently also occurs in the lower Río Chico (Pascual and Bond, 1981), as do diverse undescribed didelphoid marsupials like those in the Itaboraí (Pascual and Bond, 1986).

The "lower Río Chico" in the preceding sentence is a stratum variously called the Banco Negro Inferior, the Yacimiento Las Flores, and the top of the Hansen Member of the Salamanca Formation (or in the Río Chico Formation, where the bed is usually placed). It is well below the other fossiliferous parts of the Río Chico Formation, and it may eventually prove worthwhile to separate it as a separate land-mammal age (R. Pascual, personal communication). Whether its similarity in some ways to some of the Itaboraí fillings represents ecological similarity or temporal equivalence remains to be determined; in any case a regional age name would seem better derived from it because of the potential heterogeneity at Itaboraí. As far as I know only the name Hansen, of the two based on place names, has been defined in a publication (Andreis, Mazzoni, and Spalletti, 1975), and this rock unit includes much more than the bed itself.

Four dermal scutes of an armadillo from the Itaboraí were placed in the otherwise Casamayor genus Prostegotherium by Scillato Yané (1976). A didolodont or primitive litoptern, Asmithwoodwardia (Simpson, 1948; Paula Couto, 1952a; Cifelli, 1983a,b) occurs in the Itaboraí and in at least the Casamayor in Patagonia; the Itaboraí species is more primitive as far as known. The only known member of the Xenungulata, Carodnia (Paula Couto, 1952a, 1978a; Simpson, 1967; Cifelli, 1983a; see a later section), comes from the Itaboraí and the lower Río Chico. Different species are represented, with each being apparently more derived than the other in some ways. The primitive notoungulate Othnielmarshia, known from the Casamayor (Simpson, 1948), has been reported from the Itaboraí (Paula Couto, 1979; Marshall, Hoffstetter, and Pascual, 1983), but Cifelli (1983a) appears to agree with Paula Couto's original (1978c) naming of the Itaboraí species as a new genus, Camargomendesia. I have no opinion on this matter from the available figures, but the Itaboraí species is apparently ancestral to the Casamayor one. A tooth from the upper Río Chico figured by Simpson (1948) as cf. Othnielmarshia sp., but noted as probably generically different, is a trigonostylopid, cf. Shecenia (R.L. Cifelli, personal communication). It has an angulate pre- and postmetacristid, but so do some trigonostylopid M_3s (Simpson, 1967, Plate 44, Figure 2). Another primitive notoungulate, Colbertia, occurs in the Itaboraí and has an apparently descendant species in the approximately Casamayoran Lumbrera Formation (Bond, 1981).

Finally, the primitive astropothere Tetragonostylops from the Itaboraí (Paula Couto, 1952a, 1963) appears to have both more and less derived characters than the Casamayoran Trigonostylops and Albertogaudrya, on which see Simpson (1935, 1967), Carbajal et al. (1977), and Soria and Bond (1984), although Soria (1983) sees nothing more derived than Albertogaudrya. (Perhaps he is right for astrapotheres, although the more transverse molars of Albertogaudrya would usually be regarded as primitive.) The Astrapotherium-like flaring temporal crests of Tetragonostylops may also be mentioned. Tetragonostylops seems to be more derived than the ?middle Río Chico Shecenia (which is too poorly known to be of use here; see Simpson, 1967), and less derived than, but probably congeneric with, the Casamayor molar referred to by Simpson (1967) as ?Trigonostylopidae, genus and species indeterminate. Soria (1983) extended the range of Tetragonostylops to the Casamayor, even with an Itaboraí-like species, and I provisionally recognize a second species from the specimen which Simpson figured. Eoastrapostylops Soria and Powell (1982; see also Soria, 1984) unfortunately comes from a formation for which it itself provides the best age estimate.

The Itaboraí Fauna is thus rather clearly earlier than the Casamayor, but probably not much earlier. It can therefore be equated in age with the Rio Chico, sensu lato. Age differences within the Río Chico, and the correlation of the Itaboraí with one part or another, are not well established. (I therefore do not accept Marshall's [1985] reinstatement of an Itaboraían Land-Mammal Age. He considered only Epidolops and Carodnia in correlation, which give a biased inference. Pascual et al. [1985] implicitly agreed with my view, and Soria [1987] has recently come to the same conclusion on mostly the same evidence. However, Pascual [personal communication]] thinks that part of the Itaboraí can be correlated with the Banco Negro Inferior of Patagonia, a stratum well below the mammal-bearing parts of the Río Chico s.s. and now yielding many unpublished fossils.)

In principle it could also be possible to correlate the Itaboraí with faunas outside South America. It seems more likely than not (Rose, 1979; Cifelli, 1983a; Novacek, 1986) that the Xenarthra are derived from the Palaeanodonta, for which early members are known only from North America. These first occur (so far) in the late Tiffanian, with a poorly known genus not obviously more derived in any respect than any of the Xenarthra (Rose, 1978). The direction of dispersal, if it did occur, is unknown; fuzzy arguments can be made for each direction.

Ernanodon (Ding, 1979, 1987; Radinsky and Ting, 1984) is a late Paleocene genus from China which is xenarthran-like in some ways (and even partly convergent on sloths) but more primitive than any known xenarthran in others. It may perhaps best be regarded as an offshoot of the transition between primitive palaeanodonts and primitive xenarthrans, but if there is a real relationship with sloths this implies a longer ancestry than is likely to be available from palaeanodonts and also much convergence within the Xenarthra. The few edentates known from the Paleocene of South America (Simpson, 1948, Scillato Yané, 1976, Cifelli, 1983a; as noted in a later section I exclude Sudamerica from the Edentata) are all good xenarthrans or seem to be such and none of them can be specially related to Ernanodon.

Despite demurrals by various authors, presumably inspired by its anomalous geographical location, the poorly known genus Chungchienia (late early Eocene of China; Chow, 1963) morphologically resembles sloths and nothing else. However, it retains enamel as a vertical band on a hypsodont tooth and is therefore unlikely to be an edentate (see later discussion of Sudamerica), if in fact the enamel-like tissue really is enamel (it has apparently not been examined histologically). Chungchienia is quite incompatible with taeniodonts (Chow, 1963; Schoch, 1986) and tillodonts, the usually proposed alternatives. I suppose we will have to consider it for now convergent on sloths; its only reasonable ancestor is the rather different Ernanodon.

I discuss the relationships of Carodnia in the next section, concluding that it probably came from about the North American genus Deuterogonodon, of Torrejonian age. This may have happened independent of the origin of the Dinocerata from the same genus; Carodnia and Prodinoceras each have derived features the other lacks and do not share much that Deuterogonodon does not also have, in known parts. As the immediate ancestor of Deuterogonodon itself is Puercan, the branching was probably in Torrejonian time. If this somewhat extended argument is correct, Carodonia would probably have lived at a time equivalent to the Tiffanian.

The most convincing evidence on intercontinental relationships involves the didelphoid (and indeed, the other) marsupials (Paula Couto, 1952b, d, 1961, 1962, 1970a) and supposed notoungulates. The remarkably diverse marsupials are uniformly more derived than known North American genera from the late Cretaceous and Paleocene, but this is not very helpful in correlation. (Similarly, the didolodontid condylarths have apparent ancestors in the North American early Paleocene, as discussed below in relation to the El Molino, but they and their own descendants are diverse and in some cases quite derived in the Itaboraí.)

Even the notoungulate evidence is disputed (Cifelli, 1983b, 1985). The Arctostylopidae are a notoungulate-like family (although probably convergent from basal astrapotheres) first known from the late Tiffanian and approximate equivalent of North America and Asia. They cannot be derived from known notoungulates, even from the species which produced the upper molar from the El Molino, except (implausibly) for what little is known of Perutherium, whether or not the latter is a notoungulate (see a later section). They are therefore not useful in correlating the Itaboraí. Thus these comparisons with North America, while necessary, do not make the age of the Itaboraí more precise.

Asiostylops Zheng (1979), from the late Paleocene of Jiang-xi (Kiangsi) Province, China, is indeed remarkably primitive for a notoungulate. If it is related to more typical arctostylopids (and even to Petrolemur Tong, 1979), as seems quite likely in the former case, then most of the notoungulate-like features of the more derived arctostylopids evolved in parallel with those of notoungulates. Arctostylopid ancestry would then seem to lie with primitive astropotheres, like Tetragonostylops, Eoastrapostylops, and Trigonostylops but not as derived in the astrapothere direction. [Cifelli, Schaff, and McKenna (1987) have even doubted any South American affinity for arctostylopids.]

The same is true for the Notoungulata proper; my usage of Astrapotheria includes their common ancestor. Derived resemblances of notoungulates with primitive astropotheres are obvious anough from the teeth (Frailey [1987] gives a partial list), supported by derived resemblances between the astragali of Tetragonostylops and the notoungulate Colbertia as shown by the figures and descriptions of Cifelli (1983a). As compared with Protungulatum or Oxyclaenus rather than with the somewhat derived genus Arctocyon, the astragali of Colbertia and Tetragonostylops share a medial projection on the body, a small head, a large groove extending posteromedially from the superior astragalar foramen, and a more medial extension of the ectal facet. These derived tarsal features differ overall from those of the Litopterna and even the Didolodontidae. Astrapotheres, including Trigonostylops, have a moderately large epitympanic sinus, although it is oriented different from that characteristic of notoungulates. (Cifelli [1985] could not confirm the reported absence of an epitympanic sinus in the primitive notoungulate Simpsonotus; he says [personal communication] that G.G. Simpson agreed in 1982.) As reviewed by Simpson

(1967), various previous workers have suggested a special relationship between astrapotheres and notoungulates on weaker evidence. I also did so in 1978. I have not found a reasonably convincing ancestor for *Tetragonostylops*, *Eoastrapostylops*, and *Trigonostylops*, although an arctocyonid like *Loxolophus* is entirely plausible.

So that the astrapothere-notoungulate group may be referred to more concisely, I propose a new superorder for them:

Ameghinida, new superorder.

Included orders: Astrapotheria and Notoungulata.

Etymology: for Carlos and Florentino Ameghino.

The Río Chico Formation of Patagonia overlies the marine Salamanca Formation conformably (e.g., Marshall, 1985) or disconformably (e.g., Marshall, Hoffstetter, and Pascual, 1983). Marshall et al. (1981) report potassium-argon dates of 64.0 ± 0.8 and 62.8 ± 0.8 for a basalt underlying the Salamanca, and Marshall (1982b) gives one of 62.5 ± 5 for the base of the Río Chico. Bertels (1975a) dated the Salamanca as late Danian, and this statement has become conventional (and may indeed be correct, especially from the radiometric dates just given), but her evidence does not support so precise only a correlation. It was based on the presence of the planktonic foraminiferan *Globorotalia compressa* (and *Globoconusa daubjergensis*). Blow (1979), however, said that both species (and forms commonly referred to them) occur from the early Danian to the early Thanetian. It is therefore just possible that the Salamanca is correlative with the Roca Formation in the next basin to the north, which is also imprecisely dated, although Bertels (1975b) made them the types of different local stages.

Marshall et al. (1981) also gave magnetostratigraphic results for the Río Chico. In order to interpret such data, though, it is necessary to have a prior approximate correlation. One way is by the age of the top of the Danian. Unfortunately this is not yet well known, there having been problems both in the definition of the boundary and in interpolating the few radiometric age determinations which are relevant to it (none are very close to it and some are imprecise or biased). Recent estimates include the following: 61.5 Ma (Hardenbol and Berggren, 1978, modified for the revised ^{40}K decay constant), 60.2 Ma (Harland et al., 1982), 59 Ma (Curry and Odin, 1982), 63.6 Ma (Palmer, 1983), 61 or 62 Ma (Salvador, 1975), and 62.4 Ma (Berggren, Kent, and Flynn, 1985). Sometimes no real radiometric-age data are used between the Cretaceous and the middle Eocene, for reasons best known to the authors. Despite all this, the most reasonable magnetostratigraphic age for the Río Chico is most of chrons 25-26, as Marshall et al. (1981) proposed; the reversed part of chron 26 is the longest of the four segments, as it would be under the hypothesis of constant average sedimentation. Chrons 25 and 26 represent about the last half of the Paleocene and, with revised determinations for North America (Rapp, MacFadden, and Schiebout, 1983; Butler and Lindsay, 1985) the Ríochican is then equivalent to the Tiffanian (and perhaps part of the Clarkforkian) there, as Sloan (1987) has already noted. In North American usage, the Ríochican is late Paleocene. Less ambiguously but more fuzzily, one can say that it is "later" Paleocene. In each case, so is the Itaborai, on present evidence.

Dinocerata and Phylogenies

Carodnia, from the Itaboraí and Río Chico, is commonly and I think correctly related both to the (other) Pyrotheria and to the Dinocerata (uintatheres) (e.g., Simpson, 1935; Schoch and Lucas, 1985), although

Cifelli (1985) retains doubts as, to a lesser extent, do I. However, Schoch and Lucas (and Tong and Lucas, 1982, and Lucas, 1986) derive this joint clade from near *Pseudictops*, of all things. *Pseudictops* is an anagaloid insectivoran apparently not far from the origin of lagomorphs (Van Valen, 1964, and later work by others). It belongs to a group characterized by unilateral hypsodonty of the cheek teeth, a single wear surface of the trigonid and talonid of adjacent teeth, a lagomorph-like tarsus, and other extremely non-uintathere-like features. I regard its resemblances to uintatheres as convergent; the differences noted occur in a wider group than do the similarities. In constructing phylogenies one should consider all possibly relevant groups and apparent adaptive complexes, not characters and genera in isolation.

In 1978 I suggested, without giving the evidence, that the Dinocerata arose from the arctocyonid *Deuterogonodon*. I document that suggestion here. *Deuterogonodon* (on which see Figure 2 and Simpson, 1937, 1959; Van Valen, 1978; and probably Gazin, 1941, with a somewhat inaccurate drawing labeled "*Protogonodon? sp.*") is poorly known and there is at least one undescribed species, but the genus seems to have originated from a moderately primitive species of *Loxolophus*. Its (derived) differences from *Loxolophus* are the following:

larger size
horizontal ramus of mandible relatively deep
P^3 protocone lobe larger, with definite protocone
P$^{3-4}$ paracone more compressed transversely
P^4 protocone taller
P^4 almost as broad and long as M^1
P^4 postprotocrista pronounced, with a metaconule in *D. noletil* and the undescribed species
M^u cusps somewhat taller
conules larger and metaconule distinctly distal to metacone, especially on M$^{2-3}$ of *D. noletil*
trigon basin deeper
a definite hypocone present, usually with a crest to the metaconule
M^3 hypocone as large as that of M$^{1-2}$
distolingual region of M^3 expanded distally
M^3 usually nearly as large as M^2
P$_4$ metaconid considerably larger
P$_4$ metaconid hardly more distal than protoconid
P$_4$ relatively shorter and broader (except for *L. pentacus*, which is a different lineage)
P$_4$ protoconid relatively lower
lower molar paraconid usually almost as far lingual as metaconid (also sometimes in *L. hyattianus*)
M$_1$ paraconid unusually low
M$_{1-2}$ talonid somewhat shorter (as *Baioconodon*, the ancestor of *Loxolophus*)
entocristid usually reduced
hypoconid somewhat enlarged
cristid obliqua usually more transverse (oblique)
hypoconid definitely more proximal than entoconid
M$_3$ hypoconid relatively isolated

Every one of these differences is shared by *Prodinoceras*, which is the ancestral uintathere (Schoch and Lucas, 1985), except that the compression of the P$^{3-4}$ paracone is unclear in the molarized premolars and the conule size (and perhaps position) is indeterminate because the conules have become

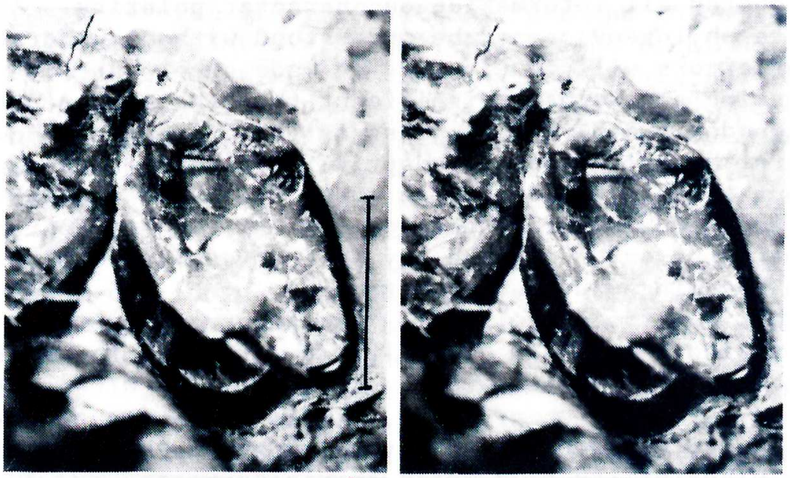

Figure 2. Deuterogonodon noletil, worn left M^3, American Museum of Natural History 95897, Torrejon, Chico Spring, San Juan Basin, New Mexico. Occlusal (stereo). Line is 5 mm.

incorporated into strong lophs. In some cases, of course, Prodinoceras has continued trends beyond their state in Deuterogonodon. In addition, Prodinoceras shares various other derived states with Deuterogonodon which are also shared by Loxolophus or by ancestors of Loxolophus.

Not all the characters are developmentally or functionally independent; counting derived character states in common is a poor way to estimate phyletic affinity, for this reason and others. (There are obviously other causes of unequal probabilities of change of characters, and characters themselves can often be split or lumped.) Therefore canned programs to estimate your phylogenies for you, while perhaps useful to provide initial guesses, should be viewed very skeptically for characters of the gross phenotype. Molecular data lack some but not all of these problems, although they have their own, such as paralogy and lack of a time dimension.

Carodnia (on which see Paula Couto, 1952a, 1978a, and Simpson, 1968) also shares most of these states. Of the ones listed, the following differences or inapplicabilities occur: the paracone of P^{3-4} is probably not compressed transversely, P^4 lacks a metaconule (as do some Deuterogonodon), M^{1-2} lack a hypocone, the paraconid seems to be absent from the lower molars, the entocristid is not as reduced at least on M_3, the cristid obliqua is absent, and the hypoconid is not clearly more proximal than the entoconid. Some of these differences would be expected from its bilophodont molars.

I have not found non-dental characters useful here, although I have not exhausted all possibilities. There are three problems. Few arctocyonids have definitely associated skeletal material, and the family is diverse. Character polarity is often less clearcut than for teeth. And when these problems are resolvable, primitive arctocyonids are very primitive placentals.

It is noteworthy that primitive arctocyonids have the primitive state for every one of the non-dental characters (and some of the dental ones) used by Novacek (1986) and Novacek and Wyss (1986) to define the Ungulata. Therefore even more parallel evolution occurred here than they recognized. The situation for some of the characters used by Shoshani (1986) is unclear for primitive arctocyonids, but his analysis will need to be redone because he deliberately ignored all information on character polarity. As a general statement, ungulate phylogeny cannot be understood without understanding condylarths; major errors will continue to be made otherwise.

It is interesting and perhaps significant that the most uintathere-like teeth of Deuterogonodon are M^3 and M_3, just as for Carodnia. The relatively sharp premolars are the only apparent adaptive distinction of Deuterogonodon, but this is the primitive state in whatever ancestry, and the species (and individuals) of Deuterogonodon vary in its degree. The lack of a small metacone on P^4 is probably a loss (earlier) which would have to be regained in becoming a uintathere, though.

Deuterogonodon is Torrejonian, while the Dinocerata are first known from the late Tiffanian. There is probably adequate time for a direct descent, although this is of course quite unproven. The Dinocerata may have originated in Asia, although the probable relationship with the Pyrotheria and the position of Deuterogonodon at or very close to the morphological fork suggests the plausibility of a North American origin.

Most of the differences of Deuterogonodon from Loxolophus in the above list are also shared with the Phenacolophidae, on which see McKenna and Manning (1977), Zhang (1978), and possibly Zhang (1979). Phenacolophus also has a mesostyle like that of some Deuterogonodon. If these shared derived resemblances indicate phyletic affinity, then the predominantly African Tethytheria may also have their eventual origin in North America. Possibly Deuterogonodon evolved into the Pyrotheria in South America, the Dinocerata in North America, and the Phenacolophidae and Tethytheria in Asia. Moreover, the resemblances long noted between the Pyrotheria and the Proboscidea may then not be entirely convergent. However, the evidence for a special relationship of the Hyracoidea with the Perissodactyla (Fisher, 1986, and others) and also to the (other) Tethytheria (contra Lucas, 1986), is inconsistent with this scenario (see Van Valen, 1978, for perissodactyl origin). At least one of the three reasonable direct or indirect affinities of hyracoids (Hyracoidea-Perissodactyla, Hyracoidea-Tethytheria, Tethytheria-Deuterogonodon) must be wrong.

Physical Evidence

I now consider individually the various fossil taxa and other kinds of evidence which have been used in the past 20 years or so for correlation of the Vilquechico and El Molino themselves, together with a few others which give some information.

In the Toquepala Formation, in the western cordillera of Peru, three radiometric dates ranging from about 60 to 70 Ma have been reported (Martínez, 1980), the difference between the old and revised decay constants being unimportant here. Unfortunately the Toquepala is a volcanic formation, apparently extruded from the contemporaneous coastal batholith during the formation of the latter (Bellon and Lefèvre, 1976), although it also has some conglomerates (Dalmayrac, Laubacher, and Marocco, 1980), and it cannot be correlated with rocks in the El Molino sequence except by inference as to times of deposition of the latter. No other possibly relevant radiometric dates seem to have been reported.

L.G. Marshall (personal communication) has said that paleomagnetic inference on the dating of the El Molino can probably be made, but this has not yet been reported. (There are difficulties with field work in this area; an unusual one recently was the capture of an expedition by the local villagers, who for a while held the members for ransom from the Bolivian bureaucracy, under threat of death.)

There are several other formations, perhaps not all mutually distinct, which have been correlated with the Vilquechico or El Molino on poor to moderate evidence. Most are continental red beds. They are all less well known and, because their own age is determined by this correlation or by fossils which are used in the correlation, or the correlation itself depends on independent estimates of age, I will not discuss them further. Examples are the Hanchipacha Formation in the western Altiplano (Audebaud, Laubacher, and Marocco, 1976) and the Flora Formation (Perry 1963; Dávila and Ponce de León, 1971; Martínez, 1980), the Izozog and Cajones Formations (Martínez, 1980; Sanjines-Saucedo, 1982), the Tacurú Formation (Ahlfeld and Braniša, 1960), the Vivian Formation (Marocco, 1978), the Arenisca de Azúcar and the Sol Formation (Koch and Blissenbach, 1960), the Cachiyacu Formation (Gutiérrez, 1975), the Huchpayacu Formation (Pardo and Zuñiga, 1976), the Tena Formation (Tschopp, 1953), and the lower part of the Palcazu Formation (Rivera, 1961) all of the Subandean Basin. The ages given in recent work for some of these formations have ranged as late as Oligocene (e.g., Seminario and Guizado, 1976, for the Sol), without good evidence.

According to Dalmayrac, Laubacher, and Marocco (1980, p. 341) the red beds are dated in part by marine incursions. However, the two references they give (Jenks [1951] and Mabire [1961]) present no evidence on which reasonably close dating can be based. The El Molino/Vilquechico incursion is relevant to the dating of red beds in their own sequence.

Regional tectonic relationships are another criterion that has been used, although a detailed argument is never given. There are two sorts of problems here. One is that the tectonic framework itself is dated by the formations under review and their putative correlatives. (The dating of subjacent or superjacent rocks is not better, for Senonian to Eocene formations.) There is thus a strict circularity here, not an opportunity for reciprocal illumination. The other problem is that marine transgressions and regressions need not be either synchronous or determined by eustatic changes. There are several transgressions from the Senonian to the Eocene; which one is represented locally must be inferred from other criteria. And in a tectonically active time and region the diastrophism itself is the major determinant of local transgressions and regressions. (Jeletzky [1971] has discussed this matter with respect to the Canadian interior for about the same time.) Although the interval around the Cretaceous/Paleogene boundary did not contain one of the major pulses of the Andean orogeny, there was epeirogeny in Peru and Bolivia, as Audebaud and Debelmas (1971), Mégard (1978), Portugal and Gordon (1975), and others have noted. This was also a time of batholith emplacement, volcanism, and perhaps extensional tectonism there (Mégard, 1978; Martínez, 1980), although Marocco et al. (1987) have given evidence for some compression and speculate that this was continuous after the Cretaceous.

The Vilquechico Formation is part of the Puna (or Putina, when the latter is segregated) Group and the El Molino is part of the Puca Group. (Branisa [1968] proposed the name Pilcomayo to replace Puca, because the latter is non-geographical [it means redbeds in Quechua] but no one seems to have followed him in this.) Both "groups", presumably a single group with different names, consist predominantly of continental redbeds, of which deposition started well into the Cretaceous.

According to Portugal (1974), the Vilquechico Formation grades into the Cotachuco Formation below and the Muñani Formation above. In fact, in their initial description Grambast et al. (1967) noted that the Laguna Umayo Biota could be from, or correlate with, the Muñani. Audebaud, Laubacher, and

Marocco (1976) correlate the Cotachuco with Cenomanian or earlier rocks, apparently by lithology, and the Muñani with Eocene on the basis of unspecified charophytes. Even if these correlations are correct there are presumably unrecognized hiatuses; the Vilquechico is only a few hundred meters of redbeds and freshwater carbonates.

Similarly, the El Molino lies apparently conformably on the Chaunaca Formation in the center of the basin, with some evidence of hiatus marginally (Lohman and Braniša, 1962; Russo and Rodrigo Gainza, 1965). Unfortunately the Chaunaca, and underlying beds above an angular unconformity, are inadequately dated. A radiometric date of 82.5 Ma for a basalt at the unconformity has been mentioned by Reyes (1972), and Braniša et al. (1966) report the pelecypod Brachidontes n. sp. from the Chaunaca. Brachidontes ranges from the Jurassic to the present (Soot-Ryen, 1969), although Braniša et al. note some resemblance of the Chaunaca species to two from the Cenomanian of Texas. The rocks comformably lying above the El Molino were formerly placed in the Santa Lucia Formation, but Marocco et al. (1987) have divided them into at least four formations, which they associate with the El Molino in the Camargo Subgroup (Figure 1). The three oldest of these formations above the El Molino are the (restricted) Santa Lucia, the Maíz Gordo, and the Cayara. [The Maíz Gordo is a formation in the Santa Bárbara Subgroup in the Salta Basin, Argentina, not far from the region in southern Bolivia studied by Marocco et al. (1987), and it was hypothetically extended to their region. The Camargo and Cayara appear to be new names but are not so designated and are inadequately defined.] The upper part of the Maíz Gordo is about late Paleocene in Argentina (Volkheimer, Quattrocchio, and Salfity, 1984) by palynomorphs, while the restricted Santa Lucia has given up a notoungulate tooth provisionally referred to Camargomendesia (Sigé et al., 1984; Marshall et al., 1985), a genus otherwise known only from the late Paleocene of the Itaboraí fillings.

The danger of correlations from general tectonic features is sharpened here; the "Cretaceous-Tertiary unconformity" of Newell (1949) and Russo and Rodrigo Gainza (1965) occurs above the Muñani Formation and the Camargo Subgroup respectively. No fossils were then known from these units.

Charophytes

Charophytes have been relied on as showing a pre-Danian age for the Vilquechico and El Molino, but this conclusion does not resist inspection. The following species have been reported: Amblyochara peruviana, Porochara gildemeisteri, P. ovalis, and Platychara compressa (Peck and Reker, 1947; Grambast et al., 1967; Braniša, Grambast, and Hoffstetter, 1969). A. peruviana is not known from more reliably dated beds elsewhere, but the genus Amblyochara occurs from the Albian well into the Paleocene in Europe (Feist, 1979).

Porochara gildemeisteri occurs into the middle part of the Palcazu Formation in northeast Peru, which Rivera (1961) dated as post-Danian Paleocene on unstated grounds. She regarded the formation itself as Cenozoic apparently because it conformably overlies the Cachiyacu Formation, which she stated to be Maestrichtian. (Kummel [1948] provisionally dated the Cachiyacu as late Cretaceous on the basis of ostracodes and snails, but the identifications given do not support this above a Paleocene age. Koch and Blissenbach [1960] reported four genera of benthic foraminiferans from nearby beds which Gutiérrez [1975] and Seminario and Guizado [1976] regard as the same as, or equivalent to, the Cachiyacu, but the shortest range of any is Cretaceous plus Cenozoic.) However, such superposition of course does not preclude the Palcazu from having been deposited at least partly in the same stage as the Cachiyacu.

Koch and Blissenbach (1960), who described P. gildemeisteri, also described a later variant of it, P. g. costata. (Gutiérrez [1975] reported both forms occurring together in the Huchpayacu Formation; P. g. costata and a new variant, P. g. solensis, occurred with P. g. costata in the lower part of the overlying Sol Formation. Whether these forms represent discrete morphs, different species, or continuous variation is unclear, although the third alternative seems unlikely from the descriptions. However, the variants are not subspecies because they occur together.) The figures of Grambast et al. (1967), of specimens from the Vilquechico, fit P. g. costata. The same form occurs in the Yacoraite Formation in Argentina (figures of de Stach and Angelozzi [1984] and of Uliana and Musacchio [1979]).

From the Huchpayacu, Gutiérrez (1975) and Seminario and Guizado (1976) have reported Amblyochara rolli, Sphaerochara spp., Nitellopsis cylindrata cylindrata, N. c. minuta, Gyrogona orientensis, Saportanella spp., Tolypella biacuta, and "Chara" spp. Feist (1979) gives the range of the extant genus Sphaerochara as beginning with the middle Danian, but according to Feist and Grambast-Fessard (1982) it begins in the early Cretaceous. Nitellopsis is unknown before the Paleocene (Feist and Grambast-Fessard, 1982) but Saportanella has been reported only from the Campanian and Maestrichtian (Feist, 1979). Gyrogona, on the other hand, has a known range of early Eocene to middle Oligocene (Feist and Grambast-Fessard, 1982). The other genera range throughout the Maestrichtian and Paleocene, at least, although Chara s.s. is not known before the middle Eocene. These ranges vaguely suggest a Paleocene age for the Huchpayacu. Kummel (1948) also reported a snail, Mitriculus incarnum, which he said that Pilsbry regarded as Eocene. Parodiz (1969) does not mention either this genus or species. Pilsbry (1944) described an endemic new genus and species Mitriculis incarum, but could not even place it in a family, so his dating was a guess. There is no genus Mitriculus.

P. gildemeisteri also occurs in the Mariano Boedo Formation in central Argentina (Musacchio, 1981), together with Peckichara sp., Pseudolatochara sp., and Amblyochara peruviana. No other fossils are known from this formation, which has been of uncertain age (Russo, Ferello and Chebli, 1979). Pseudolatochara and Peckichara each range from the late Cretaceous into the Eocene (Feist and Grambast-Fessard, 1982), but the species of Peckichara resembles P. cf. varians meridionalis from the El Carrizo Formation of Patagonia. The El Carrizo overlies the Danian Roca Formation (Musacchio and Moroni, 1983), while P. varians or very similar forms occur from the Danian to the Sparnacian of Europe (Grambast, 1957; Feist, 1979; Massieux, Tambareau, and Villatte, 1981).

Porochara ovalis is apparently unknown elsewhere than the Vilquechico and the Yacoraite, and in fact the species name is based on an indeterminate type (Peck and Reker, 1947), so it seems odd that the name is used. Porochara ranges from the Triassic into the Danian (Feist and Grambast-Fessard, 1982; Feist, 1979).

Platychara is in a confused state and I cannot resolve the situation. Peck and Forester (1979) said, after comparing samples from various Maestrichtran and Paleocene formations of North and South America, that they could find no adequate way to separate P. compressa and P. perlata. They did not give data by which this conclusion could be evaluated, but they did note that the species (or group of species) is quite variable among formations. Later, de Stach and Angelozzi (1984) have given three criteria for separation, with data for four samples. Unfortunately the distinctions do not hold even for one of their own samples, that from the El Carrizo Formation. Here the values for two criteria are more like P. compressa and the third is more like P. perlata. As both "species" are found in the Yacoraite Formation, although from different samples, unidirectional evolution is unlikely. The patterns of variation within samples, among environments, over space, and through time may well provide an evolutionarily interesting picture when this common genus is adequately studied, but for now Platychara is not helpful in close correlation. (A third supposed species from rocks of interest here, P. cruciana, is no longer recognized [Musacchio and Moroni, 1983; de Stach and Angelozzi, 1984.]) The genus itself ranges from the Campanian into the Montian (Feist, 1979) or even later (Riveline, 1986), while P. compressa or a similar species occurs even in Europe and India (Feist, 1986; G.V.R. Prasad, 1986; Prasad, Sahni, and Gupta, 1986).

Perry (1963) records another charophyte, Peckichara compresa (sic), from the Flora Formation. This formation also has two of the fish species which occur in the El Molino. However, as noted above, the range of Peckichara does not help in detailed correlation, and I have not been able to trace the species further unless it is a lapsus for Platychara compressa, which is the type species of Platychara.

There seems to be no detailed phylogeny available for any relevant group of charophytes, so their use in correlation here must be strictly on presence-absence data. Such data do not distinguish clearly between a Maestrichtian and Danian age; if anything the latter is suggested. All three relevant genera occur in both stages, and no species is restricted elsewhere to the Maestrichtran.

Stromatolite

Pucalithus is a stromatolite described from the El Molino and Yacoraite and claimed by Braniša, Hoffstetter, and Signeux (1964) to be useful in long-distance correlation. It is, however, clearly a facies indicator and has been reported from each of the formations of the Santa Bárbara Subgroup in Argentina (Moreno, 1970; Russo, Ferello, and Chebli, 1979), of Paleocene and perhaps early Eocene age.

Mollusks

Several mollusks from the El Molino have been described by Fritzsche (1924) and Pilsbry (1939), with others being listed by Braniša, Hoffstetter, and Signeux (1964). Parodiz (1969) revised the classification of some of these; see also Keen and Casey (1969).

Braniša, Hoffstetter, and Signeux (1964) regarded the collections which formed the basis for earlier work as of unclear stratigraphic position and probably heterogeneous. This is apparently correct for the collection which Fritzsche described, for echinoids occur in the Miraflores, of Cenomanian age (Braniša, 1968) and not in the El Molino, and his data do not distinguish the echinoids stratigraphically from snails known to occur in the El Molino. However, Pilsbry stated that the mollusks he described came from "a hard crystalline limestone of dark gray color," so his fauna is presumably all from the El Molino.

The El Molino snails are then the following: ?Doryssa andicola, Biomphalaria molino (usually given as molinoi), Gyrodes sp., ?Valvata humilis, Gyraulus sp., Pachychilus (Glyptomelania) bicarinata (a secondary homonym, not renamed), Pyrgulifera sp., and Zygopleura sp. There are also at least two clams: Corbicula dormitator and Pisidium sp. The species are not known elsewhere and infrageneric phylogenies are unavailable.

Pisidium ranges from the late Cretaceous to the present (Keen, 1969), but no subgenera are recorded from South America except for the El Molino occurrences, while Corbicula extends from the early Cretaceous to the present. The only subgenus of Corbicula known from South America, Cyanocyclas (= Neocorbicula, used as a genus by Parodiz), is recorded as "?Eocene, Pliocene-Recent" (Keen and Casey, 1969). The Treatise on Invertebrate Paleontology has not yet published the relevant volume for snails, but the ranges have been given elsewhere as follows: Doryssa, extant only (W. Wenz, 1938-1944); Biomphalaria, Pliocene-present (Zilch 1959-1960); Gyrodes, Permian (Termier and Termier, 1952), early Cretaceous-Eocene (W. Wenz, 1938-1944), Turonian-Maestrichtian (Korobkov, 1960); Valvata, Jurassic-present (W. Wenz, 1938-1944); Gyraulus, Jurassic-present (Zilch, 1959-1960); Pachychilus (Glyptomelania), late Cretaceous-present (W. Wenz, 1938-1944); Pyrgulifera, Cenomanian-Eocene (W. Wenz, 1938-1944); Zygopleura, Carboniferous-Triassic (Termier and Termier, 1952), Ordovician-early Jurassic (W. Wenz, 1938-1944). Paradiz (1969) transferred to Doryssa the several forms described as Zygopleura from the Puca Group, which includes the El Molino. This record (and other forms from Argentina described as Zygopleura and referred by Parodiz to Potamides) was presumably taken as Triassic by earlier compilers, this age having been given by the original describer. Following Parodiz, who was unaware of the paper by Branisa, Hoffstetter, and Signeux (1964), the occurrence of Zygopleura in the El Molino must be regarded as dubious until evidence is given.

The mollusks are therefore neutral in correlation, overall, on information now available. Pilsbry (1939) had, with little evidence, suggested from the mollusks about an Oligocene age. Parodiz (1969) combined records from several geographically and stratigraphically distinct units and regarded the assemblage as Danian on poor and old evidence, all non-molluscan. This provided the basis for his proposal of a Danian immigration of nonmarine mollusks to South America, a conclusion which is nevertheless supported qualitatively by my final correlation below.

Fishes

Fishes have, like charophytes, been strongly relied on for correlation; upon analysis they prove more useful. The recorded ichthyofauna is given in Table 1.

Three additional families are reported from the El Molino or Vilquechico Formations in the chart of de Muizon et al. (1984) but not in other papers. These are: Aspidorhynchidae (otherwise known from middle Jurassic to late Paleocene: Bryant, 1987), Cyprinodontidae (middle Eocene to present), and Eotrigonodontidae (Cenomanian to middle Eocene). These formation records may be erroneous, but their validity does not appreciably affect the correlation.

Two genera of the Chondrichthyes, Pucapristis and Pucabatis, are endemic and are useless for correlation because their immediate phylogenies are unknown, although Pucapristis branisi does occur in the Yacoraite and the Flora (Dávila and Ponce de León, 1971). Pucabatis is closest to Myledaphus, of late Cretaceous to early Eocene age (Estes, 1964), and to Rhombodus, of the late Cretaceous (Cappetta, 1975). The Ganopristidae (on the name see Estes, 1964) occur from the Albian to the Maestrichtian or Danian (Cappetta, 1974, 1987). Ischyrhiza is known from the Turonian to the

Table 1. Fishes reported from the El Molino and Vilquechico Formations. The references are to reports from these formations, usually not to the first description.

- Chondrichthyes
  - Rajiformes (= Batoidea)
    - Ganopristidae (= Sclerorhynchidae)
      - *Pucapristis branisi*: Schaeffer, 1963; Cappetta, 1975
      - *Ischyrhiza hartenbergeri*: Cappetta, 1975
      - *Schizorhiza* sp.: Braniša, Hoffstetter, and Signeux, 1964
    - Dasyatidae
      - *Dasyatis branisai*: Cappetta, 1975
      - *D. molinoensis*: Cappetta, 1975
      - *D. schaefferi*: Cappetta, 1975
    - Myliobatidae
      - *Pucabatis hoffstetteri*: Cappetta, 1975
- Osteichthyes
  - Dipnoi
    - Ceratodontidae: Marshall et al., 1985
    - Lepidosirenidae
      - *Lepidosiren* cf. *L. paradoxa*: de Muizon et al., 1983
  - Actinopterygii
    - Holostei
      - Semionotiformes
        - Semionotidae
          - *Lepidotes* sp.: Gayet, 1982b; Gayet, Rage, and Rana, 1986
        - Lepisosteidae
          - cf. *Lepisosteus*: Marshall et al., 1985
      - Pycnodontiformes
        - Pycnodontidae: de Muizon et al., 1983
        - Gyrodontidae or Sparidae
          - *Coelodus* cf. *C. toncoensis*: Cione, 1979
    - Teleostei
      - Osteoglossiformes
        - Osteoglossidae
          - cf. *Phareodus* sp.: de Muizon et al., 1983
        - Hiodontidae
          - cf. *Eohiodon* sp.: de Muizon et al., 1983
      - Clupeiformes
        - Clupeidae
          - *Gasteroclupea branisai*: Braniša, Hoffstetter, and Signeux, 1964
      - Cypriniformes
        - Cyprinidae
          - *Molinichthys inopinatus*: Gayet, 1982c
      - Characiformes
        - Serrasalmidae
          - cf. *Miletes* sp.: de Muizon et al., 1983
        - Erythinidae
          - cf. *Hoplias* sp.: de Muizon et al., 1983
        - Characidae
          - cf. *Rhoadsia* sp. (not "*Rhodsia*"): de Muizon et al., 1983
          - cf. *Triportheus* sp.: Gayet, 1982a
      - Siluriformes
        - cf. Ictaluridae, new genus: Marshall et al., 1985

Table 1 (continued)

Ariidae
  cf. Rhineastes sp. (not Rhineaster): de Muizon et al., 1983
Salmoniformes
  Enchodontidae
    Enchodus oliveirai: de Muizon et al., 1983
Perciformes
  Percichthyidae: de Muizon et al., 1983

* * *

Maestrichtian (and the Danian if, as now seems likely, the Harbicht Hill fauna of Montana is Danian [Sloan and Rigby, 1986]: see Estes [1964] for the occurrence), and perhaps even the Montian: see Slaughter and Steiner (1968), who recognized the possibility of redeposition but had two kinds of evidence opposing this. Schizorhiza is also a problem. Most of its occurrences are in the Maestrichtian, but it has also been reported in the Danian of Tunisia and Algeria (Arambourg, 1941). Arambourg and Signeux (1952) seemed to record one or both of these faunas as Maestrichtian, however. Schaeffer (1963) and others have accepted Danian occurrence but Cappetta (1975, 1987) has not. I have been unable to trace the disputed faunas adequately to resolve the question. The Ganopristidae now extends into the Thanetian (Herman, 1972). Dasyatis, on the other hand, is primarily a Cenozoic form genus (Ward, 1979), with only one Cretaceous species known. This species is quite different from those found in the El Molino, and one of the latter is close to a Montian species (Cappetta, 1980).

The lungfish Lepidosiren parodoxa is extant, but toothplates found throughout the Cenozoic have not been distinguished from it except for a form from the Miocene of Colombia (Bondesio and Pascual, 1977). The earliest record of the genus elsewhere is late Paleocene or early Eocene, in the Lumbrera Formation of northwest Argentina (Fernandez, Bondesio and Pascual, 1973). The Ceratodontidae occur from the early Triassic to the present (Romer, 1966).

Lepidotes was thought to represent a range extension in the opposite direction until it was discovered in an intertrappan bed of India (Gayet, Rage, and Rana, 1986) and the Bauru Group of Brazil (Suguio and Barcellos, 1983). It also occurs in the Campanian-Maestrichtian Los Alamitos Formation of Argentina (Bonaparte et al., 1985). The species resembles L. mawsoni from the Albian of Brazil but is more derived (Gayet, 1982b; Gayet, Rage, and Rana, 1986). The Deccan Traps may have begun eruption in the very late Maestrichtian (Courtillot et al., 1986, 1987); in any case the several intertrappan beds are near the Cretaceous/Paleogene boundary (see discussion in a later section). Lepisosteus occurs from the late Cretaceous to the present (Wiley, 1976).

Whether the fossils referred to the Pycnodontidae and to Coelodus are distinct from each other is unclear. There seems to be no paper which mentions both. The Pycnodontidae are known from the late Triassic to the late Eocene (Gayet, Rage, and Rana, 1986), while Coelodus occurs from the late Jurassic to the middle Eocene (Menon and Prasad, 1958; K.N. Prasad and Rao, 1958; Benedetto and Sanchez, 1972; Cappetta, 1972; Khare, 1976). C. toncoensis was first described from the Yacoraite Formation in Argentina and is endemic to the Aimara Basin.

Phareodus has been known only from the middle Eocene, from several formations in North America and Australia (Grande, 1984), but it is now also reported from an intertrappan bed in India (G.V.R. Prasad, Sahni, and Gupta, 1986). The El Molino is also about the oldest record for its family, the Osteoglossidae, which is extant (Grande, 1984, contra de Muizon et al., 1984). Eohiodon is still known elsewhere only from the middle Eocene of North America (Grande, 1979), which again is the oldest record for its extant family, the Hiodontidae (Grande, 1979, contra Marshall et al., 1985).

Gasteroclupea, a more or less endemic genus (the species occurs also in the Yacoraite Formation [Cione et al. 1985], the Flora Formation [Dávila and Ponce de León, 1971], and the Cajones Formation [Sanjines-Saucedo, 1982]), is the most primitive known clupeid as well as perhaps the earliest (Branisa, Hoffstetter, and Signeux, 1964). [Grande (1985) puts Gasteroclupea into a separate ?superfamily "Pristigasteroidea", but this seems to be merely an excessive result of his following the cladistic dogma that even natural paraphyletic taxa should be dismembered.] The earliest clupeids elsewhere are probably two species described as Horaclupea from an intertrappan bed in India; Knightia vetusta comes from the middle Paleocene of North America (Grande, 1985).

Molinichys is also the most primitive known genus of its family, the Cyprinidae (Gayet, 1982c). It is another endemic. The earliest previous record for this family, and indeed for the order Cypriniformes, is Blicca, an extant genus with its first occurrence in the very late Paleocene (King, 1981) of Europe (White, 1931).

The Characiformes are also unknown before the Cenozoic, and all three families and four genera involved are extant. The Serrasalmidae had been unknown before the Miocene (Marshall et al., 1985), Hoplias and the Erythinidae before the middle Miocene of Ecuador (Roberts, 1975), and the Characidae before the Montian or probably Thanetian of Morocco (Cappetta et al., 1978.) [Cappetta et al. say that their chondrichthyan fauna indicates an early Paleocene age, but this is clearly a lapsus, given their own evidence.] There are several Cretaceous records of the Characidae, but these are based on scales and are unreliable (Gayet, 1982a). Grigorescu et al. (1985) report the family, from unspecified evidence, in probably Maestrichtian beds of Romania. The Characidae is the basal family of its order, but the El Molino genera are not primitive within the family (Gayet, 1982c), so it must have had some previous evolution, however rapid or slow.

The Siluriformes have almost no pre-Cenozoic records. The earliest is in the Los Alamitos Formation of Argentina (Bonaparte et al., 1985; Cione et al., 1985), at about the Campanian/Maestrichtian boundary (Bonaparte and Soria, 1985). The only other good Cretaceous record is also from Argentina, in the Maestrichtian Coli-Toro Formation (Cione and Lafitte, 1980). Both records are from spines.

The Ictaluridae is an otherwise North American family, known from the late Paleocene to the present (de Muizon et al., 1984). The Ariidae have the Cretaceous records just mentioned for their order. Rhinastes was described from the middle Eocene of North America (Cope, 1872) and is extant (Romer, 1966). De Muizon et al. (1983) and Marshall et al. (1985) think that the Ariidae must have originated before the Aptian to permit intercontinental dispersal of these nearshore fishes. However, the difficulty seems less than for terrestrial animals, for which there is good evidence of late Cretaceous and Paleocene dispersal to and from South America (Parodiz, 1969; Van Valen and Sloan, 1977; Rage, 1978; Bonaparte, 1984): in fact de Muizon et al. (1983) accept this dispersal for terrestrial animals.

Enchodus is known from the Albian to the Danian (Gayet et al., 1986), while E. oliveirai occurs in Maestrichtian deposits of Morocco, Congo, and Brazil (Rebouças and Santos, 1956). The identification of the species in the El Molino, from isolated teeth, was said to be based on the lack of ornamentation on the teeth, although this is not the only distinguishing feature of teeth of E. oliveirai. I therefore provisionally question the specific identification until a full study is reported.

The earliest known member of the Percoidea, the basal suborder of the Perciformes, is a serranid from the Danian of Sweden (Marshall et al., 1985), while the Percichthyidae themselves are known from the early Eocene to the present (de Muizon et al., 1984).

Thus the fishes suggest a Paleocene, probably Danian, age overall. The evidence is not as clearcut as one would like, because most of it is negative (absence of a group before or after some particular time), and such evidence has a tendency to be chipped away as knowledge increases. But it is the best we can do now.

Reptiles

The dinosaurs themselves have provided the major reptilian evidence on the age of the El Molino and Vilquechico. There appear to be at least five species represented by tracks (de Muizon et al., 1983), with theropods and sauropods but apparently no ornithischians. Eggshell fragments also occur (Sigé, 1968; Kerourio and Sigé, 1984), but there are no definite records of dinosaur bones or teeth. Because various reports of Paleocene dinosaurs through the years have each eventually proved to be incorrect, there has been a strong presupposition that any rocks with unredeposited dinosaurs must be Mesozoic. In fact Branišа (1968) said that the dinosaur tracks "automatically" showed that the El Molino was Mesozoic.

Conventional wisdom is often correct, but it seems not to be so in this case. In a later section I discuss recent evidence for Paleocene dinosaurs elsewhere. Some of the evidence seems conclusive if the observations themselves are correct. Therefore dinosaurs can have no privileged position with respect to correlation. Unfortunately the nature of the fossils in the Vilquechico and El Molino precludes precise identification with skeletal remains elsewhere, and it is the latter which are particularly informative with respect to correlation. Although the predominantly Mesozoic occurrence of dinosaurs does remain relevant, one cannot implicitly divide the length of their total duration by the length of their Mesozoic duration to find a probability that a dinosaur fauna is Mesozoic. The realistic alternatives here are merely Maestrichtian and Danian.

Eggshells of some dinosaurs seem to be indistinguishable from those of birds, and Hirsch and Packard (1987) have stated that the only way to identify fossil eggshells is by the occurrence of an embryo inside or by associated bones. Thus the Vilquechico fragments would, by this reasoning, be unidentifiable, and this conclusion indeed has been made in conversation. However, the Vilquechico eggshells do not have the birdlike structure, so (because eggshells of other reptile groups also differ) a dinosaurian origin can be accepted provisionally. J.F. Bonaparte (personal communication) notes that the Peru eggshells are about 1 mm. thick and that the eggs were relatively small, while the many eggshells from dinosaurs in various strata in Patagonia are 3 to 5 mm. thick and about 16 cm. long. These points need to be evaluated by workers on eggshells, but the unbirdlike internal structure remains a key argument.

A large pelomedusid turtle, ?Roxochelys vilavilensis, was described from the El Molino by de Broin (1971). Price (1953) originally described the genus from a specimen in the Bauru Group of southern Brazil, where there may also be a second species (de Broin, 1971). The genus is not known elsewhere except possibly in the El Molino, Vilquechico, and the perhaps equivalent Hanchipacha, where ?R. vilavilensis may also occur (Bonaparte and Powell, 1980; Marshall et al. [1985] give only ?Roxochelys sp.) As noted in an earlier section, the Bauru Group is conventionally dated as late Cretaceous but this correlation seems insecure. A second pelomedusid also occurs in the El Molino, ?Podocnemis cf. P. brasiliensis (de Muizon et al., 1983), the latter species being known only from the Bauru. Podocnemis elsewhere ranges from the late Eocene to the present (Młynarski, 1976), but, as noted in an earlier section, de Broin (in Estes and Báez, 1985) regards the Bauru species as indeterminate generically.

There is also a terrestrial sebecosuchian crocodile of the family Baurusuchidae, Cynodontosuchus cf. C. rothi (Marshall et al., 1985). This is only the second specimen of the genus, C. rothi having been described from the Pichi Picun Leufu Formation (de Gasparini, 1972) of the Neuquén Basin, Argentina. This formation is of about Hauterivian age (Digregorio and Uliana, 1980) or early late Cretaceous (Bonaparte, 1978). Apparently study of the El Molino specimen, as with most of the fauna from this formation, is still incomplete. Another El Molino crocodile belongs to the Dyrosauridae, a family known from the Maestrichtian to the late Eocene (Buffetaut, 1982).

A primitive snake, Coniophis sp., of the Aniliidae, occurs in the El Molino (de Muizon et al., 1983) and from the Maestrichtran (or Campanian) to the late Eocene in North America and Europe (Rage, 1981, 1984). There are also three unidentified species of boids in the El Molino (de Muizen et al., 1983); the only good Cretaceous genus of this extant family is Madtsoia, on which see Rage (1981, 1984).

De Muizon et al. (1983) report an iguanid lizard and a leptodactylid frog (yes, not a reptile), neither more precisely specified, from the El Molino. The earliest known iguanid is the primitive genus Pristiguana (Estes and Price, 1973; Estes, 1983; Estes and Báez, 1985) from the Bauru, while the earliest known leptodactylids are from the Campanian-Maestrichtian Los Alamitos Formation of Patagonia and from the Bauru (Báez, 1985; Bonaparte, 1986b).

So, on the whole, the reptiles suggest a Cretaceous, probably Maestrichtian, age.

Marsupials

Of the several marsupials described from the Vilquechico and El Molino, much the best known is Roberthoffstetteria nationalgeographica Marshall, de Muizon, and Sigé (1983a), for which most of the dentition is available. It belongs to the South American Paleogene family (or subfamily) Caroloamegheniidae and is rather close to Procaroloameghinia Marshall (1982) from the Itaboraí. Although Roberthoffstetteria is overall probably somewhat the more primitive, to the extent that comparable parts are known, its weaker cristid obliqua and more bulbous cusps are more derived than in Procaroloameghinia. There are thus two lineages; Procaroloameghinia is apparently the direct ancestor of the other known genus in the family, Caroloameghinia, from the early Eocene. The immediate ancestry of the lineages is unknown.

Different isolated molars from the El Molino resemble two other Itaboraí genera, Gaylordia and Sternbergia (de Muizon, Marshall, and Sigé, 1984); perhaps they will prove referable to these genera when all the species concerned are better known (cf. Case and Woodburne, 1986).

Three incomplete isolated molars from the Vilquechico were described by

Sigé (1968, 1971, 1973) as Alphadon austrinum. Crochet (1978, 1979a, 1980) transferred this species to Peradectes; I agree, but the original reference was reasonable at the time. Both genera are otherwise North American; Peradectes extends into Europe (Crochet, 1979b), which was then part of North America rather than of Asia. The earliest and most primitive known species of Peradectes is P. cf. P. pusillus (Archibald, 1982), which occurs at the base of the Tullock Formation in Montana, less than 5 m above the Cretaceous/Paleogene boundary. Peradectes was also reported from the Harbicht Hill Fauna in Montana (Van Valen and Sloan, 1965), but this record remains to be documented and is in any case almost equivalent in age to Archibald's (Sloan and Rigby, 1986). P. cf. P. pusillus is more primitive than P. austrinum by the criteria of Crochet (1980, p. 55) and could, in the poor state of present knowledge, even be directly ancestral to it. P. austrinum also seems, from the available figures, to be more carnivorously adapted.

Other isolated marsupial teeth represent a few other taxa, not closely identifiable. One partial lower molar may represent a pediomyine (Sigé, 1973), a group known otherwise from the late Cretaceous of North America, extending to near the boundary with the Paleocene (Sloan and Van Valen, 1965; Archibald, 1982). De Muizon et al. (1984) note with considerable doubt (contra Case and Woodburne, 1986) the possibility of a pediomyine in the El Molino. A pediomyine also occurs in the Itaboraí (fide Marshall, in Case and Woodburne, 1986). A fragment of an upper molar from the Vilquechico may represent the earliest occurrence of the extant tribe (or subfamily) Didelphini (Crochet, 1979a), which may also occur in the Itaboraí and which is derivable from Peradectes. For a different classification see Reig, Kirsch, and Marshall (1985).

The marsupials thus suggest a Danian age.

Garatherium, a monospecific genus from the early Eocene of Algeria (Crochet, 1984), was described as a didelphid marsupial. One specimen is known, an upper molar. Molars of many didelphids resemble those of some placentals, and it may well be that Garatherum is a tupaiid. Crochet noted that it is aberrant for a didelphid; it seems to fit as well to tupaiid morphology. I have compared the drawings of the specimen with teeth of all recent genera and most species of tupaiids. It most resembles Dendrogale, the latter differing as follows: stylocone much lower, parastylar lobe smaller, protocone lobe longer proximodistally, conules nearly absent, small postcingulum present, and a wide and deep vally between the centrocristae, subdividing the mesostyle (stylar cusp C). All these are derived relative to the state in Garatherium and all but the first are variable among tupaiids, although not in most cases reaching as primitive a state as in Garatherium. Most tupaiids even have a stylar cups D, as Garatherium does. Particularly if Adapisoriculus should prove to be a tupaiid (Van Valen, 1965), Garatherium is also a plausible candidate. The main counterargument is the very large stylocone, which may have been reduced well before the origination of the family. This suggests the possibility of Garatherium being a dilambdodont palaeoryctid. (I propose the term rectodont for teeth whose centrocrista is straight, or nearly so, in occlusal view, to avoid common circumlocutions.) Simons and Bown (1984) found resemblance to Remiculus, a probably mixodectid, but they did not give details and I see no real indication of affinity, although their alternative suggestion of the Chiroptera may have more merit. More of the animal than one tooth would help.

Correlation by Phylogenies

The method of correlation I use here was unfamiliar to some readers, perhaps because cladists normally ignore ancestors, so I discuss it generally.

The first step is to estimate the phylogeny of the relevant taxa as closely as possible, by the usual methods. If one taxon is indistinguishable (on available evidence) from the ancestor of another, the simplest conclusion is that it is indeed that ancestor. (To say otherwise is to assume a difference for which there is no evidence.) One then arranges the taxa chronologically, if this has not already been done. The chronology may require that one or more divergence points be placed earlier, if an ancestral taxon is not recorded earlier than its descendant. This merely extends the range of the ancestral taxon in a realistic way; the ancestral taxon is of course paraphyletic, like any real ancestor. There are two sorts of flexible constraints on earlier divergence times: the time of the next known ancestral taxon, and the degree of divergence from the inferred ancestral phenotype of the least divergent known taxon of those under consideration. More accuracy is given the better the phylogeny is known, the more relevant taxa constrain it, and the faster its evolution was proceeding.

If taxon B in region B is derivable from taxon A in region A, but not from any known descendant of taxon A, then the earliest known or inferable time of the existence of taxon A gives a lower bound on the time of taxon B. Otherwise unwarranted homoplasy must be assumed. If dispersal is in both directions an upper bound for the horizon of taxon B can be derived in a similar way. An upper bound can also be inferred from the last likely occurrence (known or unknown) of A, but this is often less accurate.

Placentals

There are several placental mammals now known from the Vilquechico and El Molino, in a long-hoped-for discovery. Like the marsupials, they include relatives of both South American and Holarctic taxa. The absence of edentates to date is striking, although only four scutes and two astragali have been reported from the much larger fauna of the Itaboraí (Scillato Yané, 1976; Cifelli, 1983a) and none from the lower Río Chico (Marshall, Hoffstetter, and Pascual, 1983; see later section for Sudamericia).

On the whole the most primitive named form is Molinodus suarezi de Muizon and Marshall (1987b). I agree with their placement of it in the condylarth family Mioclaenidae, which is otherwise known only from Holarctica and which has an origin from the Arctocyonidae separate from that of the Hyopsodontidae (Van Valen, 1978). In this family the two most primitive genera are Bubogonia Johnston and Fox (1984) and Promioclaenus. In 1978 I added the first two early Paleocene species to the latter genus, and Middleton (1983) added a third. (Cifelli [1983b] believes that one of these species, P. vanderhoofi, should revert to a monotypic genus, but the only distinction he gave, an inflated P_4 without a distinct metaconid, is virtually duplicated by the undisputed later species P. acolylus, which commonly has a minute metaconid on P_4. I will elsewhere give reasons for disagreeing with others, although not all, of the modifications which he and others have made to my preliminary and summary paper of 1978.)

Early species of Promioclaenus occur in both levels of the Puerco Fauna of New Mexico (Van Valen, 1978), in the correlative Gas Tank Fauna of Utah (Robison, 1986; his P. acolytus record is based on an M_3, which does not clearly distinguish P. acolytus, a variable Torrejonian species, from the Puercan P. wilsoni), and in the correlative West Bijou Creek—1 Fauna of Colorado (Middleton, 1983, unless Litaletes gazini Robison, 1986, is conspecific). Each of these faunas is middle Puercan in age. Bubogonia is known from the lower level of the Puerco (Van Valen 1978, and below) and from Ravenscrag W-1 of Saskatchewan (Johnston and Fox, 1984). The latter fauna is early or probably middle Puercan. The report of Protoselene from the late Puercan Wagonroad Fauna of Utah (Robison, 1986, abstract) appears mistaken because it is not mentioned in the body of the paper. Protoselene is otherwise Torrejonian.

Bubogonia and Promioclaenus are both easily derivable from Protungulatum; perhaps the intermediate common ancestor would still fit in Promioclaenus. Bubogonia then gives rise to the middle Paleocene genus Protoselene. I agree with Johnston and Fox's tentative referral of the only early Paleocene species placed in Protoselene, P. bombadili, to Bubogonia, and take this opportunity to make that species better known (Figures 3 and 4). Figure 5 shows a Puercan species of Promioclaenus.

Molinodus appears to be a member of the Bubogonia—Protoselene clade. After the exclusion of the putative M^1 (YPFB PAL 6117) from Molinodus, as discussed below, only M_{1-3} and $M^{?2}$ are known. Molinodus shares the following derived character states with that lineage: metaconid distinctly distal to protoconid, hypoconid more proximal than entoconid, hypoconid relatively tall, hypoconulid near entoconid, incipient entoconulid present, paraconid appressed against the proximal to proximolabial surface of metaconid, $M^{?2}$ relatively quadrate, conules large and far apart, paracingulum and metacingulum barely interrupt lingual cingula, lingual cingula nearly continuous lingually, protocristae meeting at distinctly obtuse angle, giving protocone an elongate appearance. Known members of Bubogonia and Protoselene, although not all of Promioclaenus, are more derived than Molinodus in that M_1 is as long as M_2, the lateral walls of the lower molars are slightly less vertical, and the talonid is somewhat longer. In addition, by analogy with Tiuclaenus the P_4 of Molinodus was probably taller than that of Bubogonia and Protoselene but not taller than that of Promioclaenus. Shared primitive states which are transformed in many other condylarths include small size, a relatively large M_3, M_2 as the widest lower molar, M_2 trigonid wider than talonid, cusps relatively acute and conical for a condylarth, lower molars relatively narrow, metaconid not taller than protoconid, hypoconid appreciably larger than entoconid, paracristid arcuate, no hypocone, and strong labial cingulum on upper molar.

Protungulatum is known from four apparently Cretaceous localities as well as from several in the early Paleocene. The Cretaceous specimens, all referred at least provisionally to the primitive species P. donnae, come from Bug Creek Anthills in Montana (Sloan and Van Valen, 1965), Black Butte in Wyoming (Breithaupt, 1982), and Frenchman-1 and Long Fall in Saskatchewan (Johnston, 1980; Johnston and Fox, 1984). These all seem to be very late Maestrichtian in age and have been used to define the terminal Cretaceous Bugcreekian Land-Mammal Age (Sloan, 1987). More than the absence of Protungulatum (or other condylarths) from known earlier rocks, the very rapid diversification and adaptive evolution of condylarths which it initiated (Van Valen, 1978; Archibald, 1983; Sloan, 1987) strongly suggests that Protungulatum itself originated near that time.

The divergence of the Molinodus lineage can therefore be dated rather closely, namely in the Mantuan or early Puercan Land-Mammal Ages, say the first million years of the Cenozoic (Sloan, 1987). This time of divergence is not definitively established, but any other would involve an appreciable

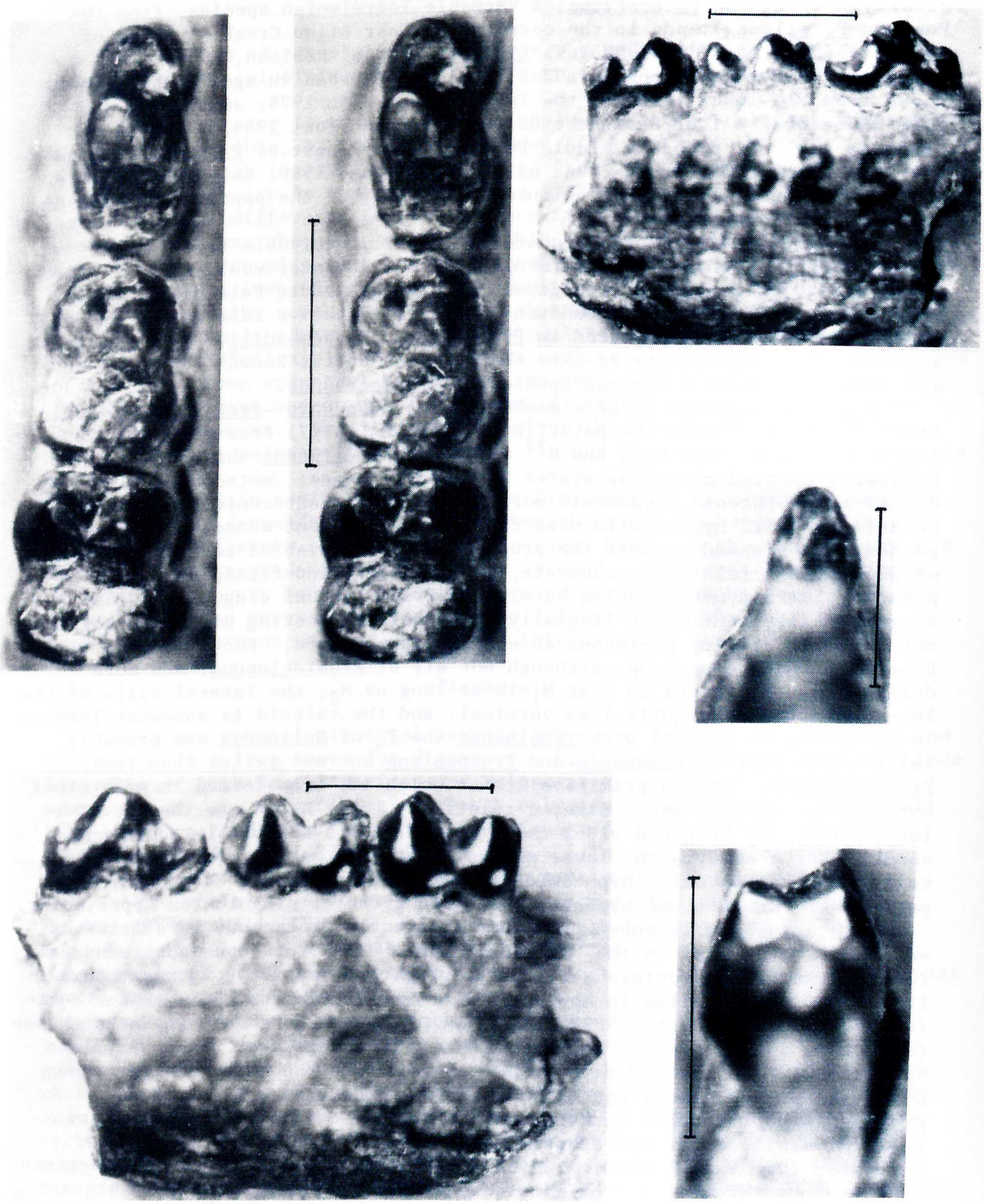

Figure 3. Bubogonia bombadili, left P_4-M_2, University of California Museum of Paleontology 36625, San Juan Basin, New Mexico. Occlusal (stereo), lingual, labial, distal P_4, distal M_2 trigonid. Lines are 5 mm.

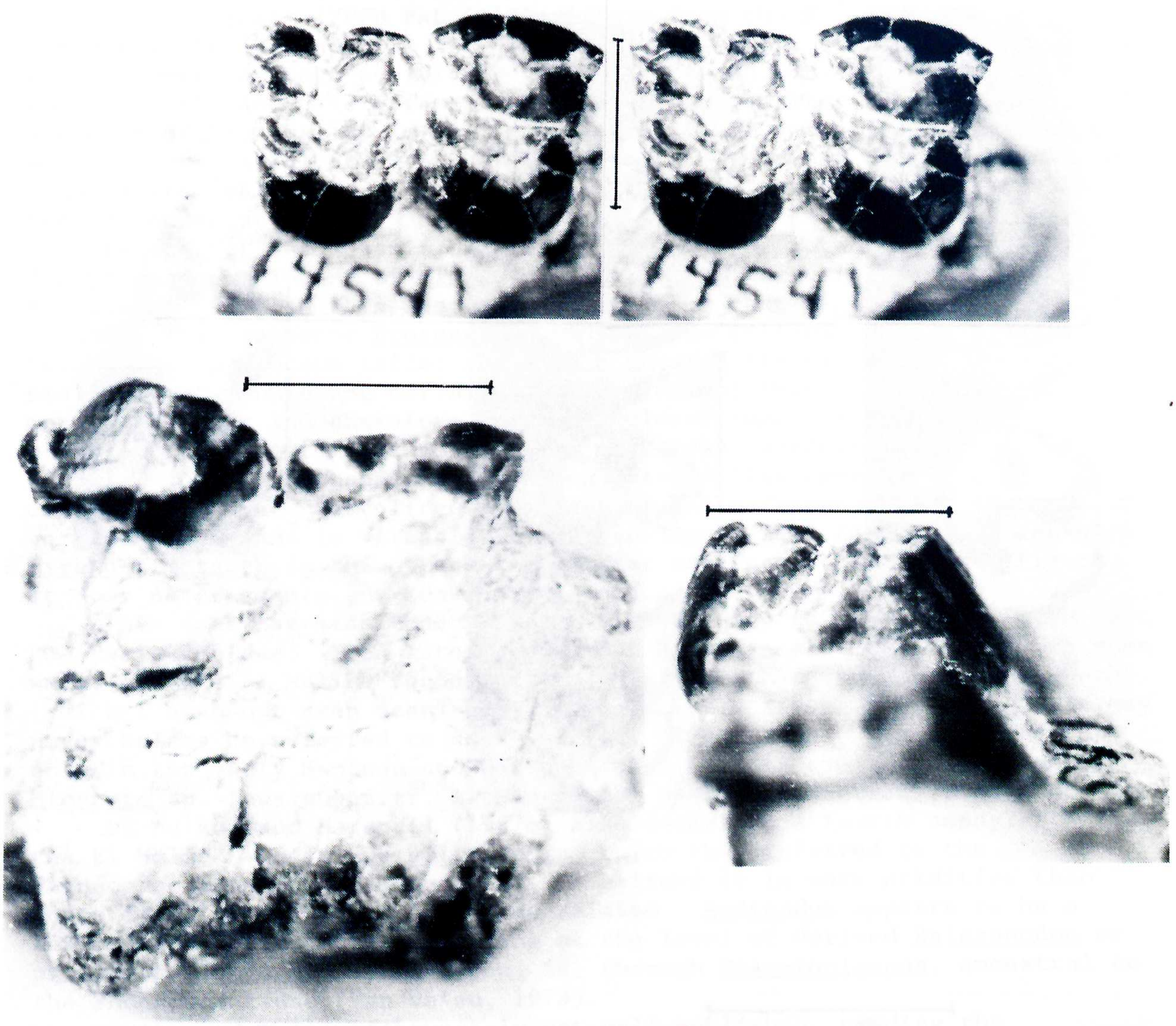

Figure 4. Bubogonia bombadili, right P^4-M^1, Yale Peabody Museum 14541, upper level of Puerco, 2 miles east of Ojo Alamo, San Juan Basin, New Mexico. Occlusal (stereo), labial, distal P^4. Lines are 5 mm.

amount of homoplasy (or upward range extension) which is unnecessary under the preferred hypothesis.

Tiuclaenus minutus de Muizon and Marshall (1987c), another mioclaenid from the El Molino, is derivable from Molinodus, i.e. an ancestor would be referable to Molinodus. Tiuclaenus shows about the same derived differences in the molars as Molinodus but has gone further. The lower premolars and canine are known here and are very like those of Bubogonia and Promioclaenus. (The P_3 and P_4 of Protungulatum and primitive Promioclaenus do have a moderately strong basal paraconid.) As far as I can tell from the figure the P_4 of Tiuclaenus is like that of Bubogonia except for being taller and having the paraconid proximal (rather than proximolingual) to the protoconid, primitive states retained in Promioclaenus. The figure of the more proximal teeth does not show differences from Promioclaenus; these teeth are unknown for Bubogonia.

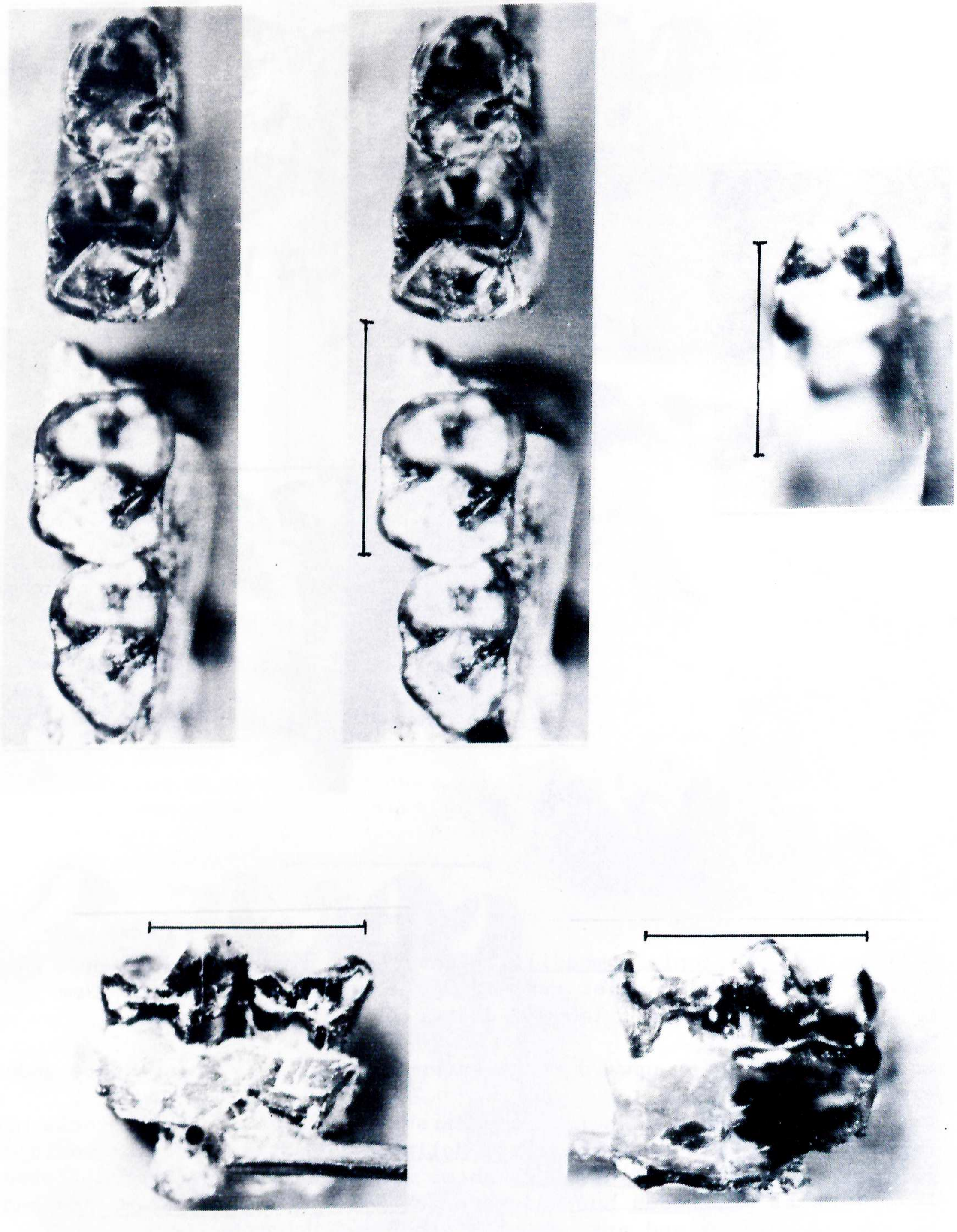

Figure 5. *Promioclaenus wilsoni*, left M_{1-2} (American Museum of Natural History 59904) and left M_{2-3} (American Museum of Natural History 59788), both from lower level of Puerco, Bitonitsoseh Arroyo, San Juan Basin, New Mexico. Occlusal (stereo), lingual, labial, distal M_2 trigonid of 59788. Lines are 5 mm.

The tooth which de Muizon and Marshall (1987b) regarded as M^1 of Molinodus suarezi (YPFB PAL 6117) differs from the $M^{?2}$ referred, I believe correctly, to that species in several ways which are unlikely to result from a difference in tooth position: the paracone and metacone are close together, the tooth is triangular rather than quadrate, the lingual cingula are appreciably smaller in both width and lingual extension, the protocone apex is more labial (the lingual slope of the protocone is wider), and the conules are smaller and bud off the protocristae rather than interrupting the protocristae.

Except for the absence of a hypocone these differences suggest the Periptychidae. The M^2 of Mimatuta morgoth Van Valen (1978; see also Archibald [1982] on this species) differs from that of its structural and probably real ancestor Protungulatum donnae as follows: tooth more triangular, protocone taller and with a greater lingual slope, conules smaller, metaconule not definitely more proximal than metacone, paracone and metacone larger and therefore appearing closer together, no tendency for the postcingulum to extend lingual to the protocone, average smaller lingual cingula, and the protocone not leaning forward (its apex is lingual to the centrocrista notch, not lingual to part of the paracone). The presence of a very weak hypocone is variable in each species. YPFB PAL 6117 agrees with Mimatuta morgoth in these respects insofar as I can tell from the figure. It does not resemble any known mioclaenid.

This does not mean that YPFB PAL 6117 belongs to Mimatuta or even to the Periptychidae. Even later species of Mimatuta are more derived in some ways, and the El Molino tooth differs in a few other ways. And one tooth (which I have not even seen) is inadequate for a strong conclusion. It may nevertheless be referred to as $M^{?2}$ of cf. Mimatuta sp. M. morgoth occurs only in the early Mantuan and was part of a rapidly evolving genus. Cf. Mimatuta sp. thus supports, although more weakly, a Mantuan divergence time.

De Muizon and Marshall (1987c) also described a fourth condylarth from the El Molino, Andinodus boliviensis, which they referred to the Phenacodontidae or Didolodontidae. I believe it is more primitive than these families, although it may be related. Andinodus appears to be a loxolophine arctocyonid, diverging at the level of derived Baioconodon or primitive Loxolophus. Loxolophus is, through Desmatoclaenus, ancestral to the Phenacodontidae (Van Valen, 1978).

Baioconodon is unfortunately not well published, pending the publication of the thesis of Middleton (1983). I follow him in including Ragnarok in Baioconodon, however. Loxolophus differs from Baioconodon in M_2, the only tooth known for Andinodus, mainly in greater bunodonty and a more expanded talonid. However, the talonid is narrower than the trigonid even in the Torrejonian species Loxolophus criswelli (Rigby, 1980).

Except for the bulbous distal extension of the metaconid, the description of Andinodus would also apply to several species of Baioconodon and Loxolophus. Even the metaconid enlargement is present, apparently convergently, in the larger species Loxolophus kimbetovius (Matthew, 1937), from the lower level of the Puerco, and to some extent in Baioconodon cf. B. denverensis of Johnston and Fox (1984), from Ravenscrag W-1. It is even possible that A. boliviensis will prove referable to Loxolophus when it is better known; they are not really separable at the generic level on the basis of the single known tooth.

The Baioconodon—Loxolophus transition was late Mantuan or perhaps early Puercan, and Baioconodon first appears in the very early Mantuan in a form not far from Protungulatum. The inferred divergence time is again in agreement, although here too only one tooth is involved.

Our understanding of the Didolodontidae has been improved by much of the revisionary work of Cifelli (1983a, b). His genus *Paulacoutoia*, although not the generally more primitive *Asmithwoodwardia*, is more primitive than any of the El Molino genera in having the hypoconulid central, rather than near the entoconid, and in having the protocristae meet at an acute angle. These could be reversals but do on their face oppose derivation of the Didolodontidae, and therefore the Litopterna, from known South American forms. None of the El Molino genera are clearly specially related to the Didolodontidae in a collateral way either.

Cifelli (1983b) may be correct that the Didolodontidae originated from the Mioclaenidae. However, the most derived genus without its own divergent features is *Promioclaenus*, not *Litaletes*, which is particularly characterized by an enlargement of the M^2 protocone and M_2 talonid basin (Van Valen, 1978). This suggests the possibility of a derivation from the *Molinodus* clade earlier than *Molinodus*, although the well-developed canine of the Sparnotheriodontidae (Soria, 1980) and others argues rather for an arctocyonid ancestry. The loxolophine arctocyonid *Desmatoclaenus* is at least as good a possibility (Van Valen, 1978) and indeed is partly convergent on *Promioclaenus*. It is, however, larger. It was derived from *Loxolophus* and is first known from the lower level of the New Mexico Puerco and correlative localities in Colorado.

Perutherium altiplanense Thaler (in Grambast et al., 1967; see also Sigé, 1973) is the only placental described from the Vilquechico. It is represented only by the talonid of M_1 and the trigonid of M_2; the small fragment of an upper molar which Sigé (1973) referred to it is uncharacteristic and could easily belong to an undiscovered member of the poorly known fauna.

The affinities of *Perutherium* are not entirely clear, but Marshall, de Muizon, and Sigé (1983) proposed that it is a primitive notoungulate. They may well be correct. Even more similar than the genera they used for comparison are the notoungulates *Simpsonotus* (Pascual, Vucetich, and Fernandez, 1979), *Colbertia* (Paula Couto, 1952c, 1978b), and *Maxschlosseria* (Simpson, 1967), in each of which the metacristid is angular like that of *Perutherium*. Nevertheless, the tooth of *Perutherium* is rather condylarth-like; it even retains a relatively large paraconid, not much reduced as implied by Marshall, de Muizon and Sigé (1983); as shown by a good cast, the paraconid is in front of the metastylid and is connected to the protoconid by an unusually strong, continuous paracristid. (The premetacristid is occasionally identified as a paraconid in notoungulates; both occur here. Cifelli [1985] says that Marshall, de Muizon, and Sigé misidentified the trigonid cusps of *Perutherium*, without specifying how, but in this respect I agree with them.)

If *Perutherium* really is a notoungulate its primitive nature suggests that the derived resemblances of notoungulates to most other South American ungulate orders are convergent. *Perutherium* has nothing particular in common (except geography) with didolodontids or the El Molino condylarths, although with some effort it could be derived from a pre-*Molinodus* stage. My 1978 suggestion of origin from the primitive periptychid *Mimatuta* is more plausible from the tooth itself, and the presence of cf. *Mimatuta* sp. in the El Molino lends some credence to this, but the upper molars of notoungulates are derived in a sufficiently different way from those of periptychids, even *Mimatuta*, that an origin of notoungulates from periptychids cannot be taken seriously. Nevertheless, *Perutherium* shares all the derived differences on M_{1-2} of *Mimatuta* from *Protungulatum donnae*: cusps more to the center of the tooth (lateral walls less vertical), trigonid relatively lower, paraconid usually slightly more lingual, and hypoconulid closer to entoconid. M. makpialutae Van Valen (1978) has a moderate postmetacristid on M_2, although there is no metastylid. The evidence on positive affinities is not strong, but because the much more primitive Protungulatum is the only known Cretaceous ungulate a Paleocene age is supported.

One definite but rather primitive notoungulate tooth comes from the El Molino, a partial upper molar which is not further identifiable (de Muizon, Marshall, and Sigé, 1984). It is too large to be referable to Perutherium altiplanense but like that species, and for the same reason, suggests a Paleocene age. In fact the resemblance to late Paleocene and early Eocene notoungulates is close, as the authors note. I discussed notoungulate affinities in an earlier section.

The last reasonably well-known placental from the El Molino is Alcidedorbignya inopinata de Muizon and Marshall (1987a). It belongs to the Pantodonta, an order otherwise unknown in the Southern Hemisphere, and it can be regarded as the most primitive member of the order, as de Muizon and Marshall note.

The origin of pantodonts is controversial, because of different interpretations of several animals which are either primitive pantodonts or else strongly convergent on pantodonts. Three groups are involved, and it seems likely that two are convergent because their apparent ancestries lie with three other orders or suborders. A resolution of this matter is beyond the scope of this paper; indeed, I do not even have access to all the relevant evidence. However, some comments are desirable because of their bearing on the time of divergence of Alcidedorbignya.

Cyriacotherium comes from the late Paleocene of North America and is placed in a family of its own (Rose and Krause, 1982). I agree with Lucas (1982) that it is probably a derivative of mixodectid insectivorans convergent on pantodonts; in fact I had suggested this to one of the authors while they were studying the material. The major difference from pantodonts is the shape of the ectoloph of the upper premolars: like that of the molars, it is W-shaped, not V-shaped as in pantodont premolars. However, it is probably not impossible developmentally for such a transition to occur, in one direction or the other (cf. the pantodont DP^4, including that of Coryphodon: Simons, 1960). I formally place it in the superfamily Mixodectoidea.

The Bemalambdidae (Bemalambda, Hypsilolambda, and Harpyodus) are from the Chinese Paleocene (Zhou et al., 1977; Qiu and Li, 1977; Wang and Ding, 1979; Li and Ting, 1983). They are unpantodont-like in having very transverse upper cheek teeth with a connate to semi-connate paracone and metacone and a very broad stylar shelf without a mesostyle. These features are characteristic of the Palaeoryctidae (Van Valen, 1966), and the Bemalambdidae have been regarded since their discovery as derived from this family. I agree, although the "Geolabididae" (Lillegraven, McKenna, and Krishtalka, 1981) may also be relevant. They have some other derived non-pantodont features, as Zhou et al. (1977) discussed, which are not palaeoryctid-like and which presumably evolved with the Bemalambdidae. As a result of the analysis below, I transfer the Bemalambdidae to the superfamily Palaeoryctoidea in the Insectivora.

The type species of Harpyodus is H. euros Qiu and Li (1977), although this may not have been the intention of the group of Chinese paleontologists, and Lucas (1982) has perhaps been misled. H. euros has all the palaeoryctid-like features while the referred species, H. decorus Wang (1979), has only the lack of a mesostyle and a moderately broad stylar shelf. Qiu and Li (1977), Wang (1979), and Lucas (1982) have given good photographs of the type specimens of these species. (The legend of Qiu and Li's plate has the figure numbered 4 rather than 3.) I do not believe that these species are congeneric or even confamilial; by my preferred interpretation (below) they are even convergent from unrelated orders. I therefore propose a new genus for H. decorus:

Wanglia, new genus.

Type species: Harpyodus decorus Wang (1979).

Etymology: For Wang Ban-yue and Li Chuan-kuei, in appreciation of their work on Paleogene mammals (including bemalambdids) of China. The double patronym follows the precedent of Ideker and Yan (1980) for Yantanglestes, which is a good mesonychid and is not related to the Didymoconidae, contra Gingerich (1981) and Wang (1976). The gender is feminine. In pronunciation the second syllable of "Wanglia" is stressed at least equally with the first.

Diagnosis: Upper molars only moderately transverse, rectodont, and without a mesostyle. Paracone distinctly separated from metacone and its apex more lingual on M^{1-2}, conules moderately well developed at least on M^1, postcingulum strong, protocristae meet on protocone at acute angle, ectoflexus pronounced on P^4-M^2, protocone lingual to paracone, not to centrocrista notch, so the trigon seems tilted forward lingually rather than backward as in bemalambdids. On P^{3-4} the trigon also is forward lingually, and the metacrista is appreciably longer than the paracrista; the ectoloph is broadly arcuate on P^3, not V-shaped.

Wanglia is morphologically closest to Alcidedorbignya, of known genera, and neither fall naturally into existing families. I therefore propose a natural, horizontal, probably paraphyletic, family for them:

Wangliidae, new family.

Included genera: Wanglia, new genus, and Alcidedorbignya de Muizon and Marshall (1987).

Diagnosis: Probably including the basal pantodonts. The upper molars are rectodont and moderately transverse and they lack a mesostyle. The conules are moderately well developed on the upper molars, which also have a pronounced postcingulum and ectoflexus and a moderate stylar shelf. On P^4 the protocone apex is proximal to the paracone apex, with the metacrista longer than the paracrista.

Wanglia decora comes from the late Paleocene of Jiang-xi (Kiangsi) Province, China (Li and Ting, 1983). That it is later than Pantolambda is of course not good evidence against its approximate ancestry (as a genus) to Pantolambda.

The third relevant group is Deltatherium, which is (or has been) known from a moderate amount of the skeleton as well as the complete dentition (Matthew, 1937). The main species is D. fundaminis from the Torrejon (middle Paleocene) of New Mexico; in 1978 I added a small late Paleocene species, D. durini.

Deltatherium is unquestionably an arctocyonid condylarth. It has occasionally been referred to the Pantodonta, and I suspect that its clade did give rise to the pantodonts, but this seems nearly incompatible with inclusion of the very differently constructed Bemalambdidae in the Pantodonta as basal or early-divergent members. The Bemalambdidae would have to re-acquire primitive features which are difficult to reconcile adaptively with the occlusion of other pantodonts but which would be reasonable as an incompletely adapted intermediate (or terminal clade) from palaeoryctids. The bemalambdids come from Chinese formations which are difficult to correlate with those elsewhere because of their largely endemic fauna (Li and Ting, 1983), but the presence of true mesonychids (descendants of *Eoconodon*), *Obtususdon* Xu (1977; a probable descendant of *Anisonchus*), *Yuodon* Zhou (Chow) et al. (1973; see Zhou et al. [1977]; a probable descendant of *Bubogonia*), and *Palasiodon* Zhou (Chow) et al. (1973; see Zhou et al. [1977]; a probable descendant of *Litaletes*) rather strongly suggests an age equivalent to Torrejonian, early Tiffanian, or just possibly late Puercan of North America. Sloan (1987) comes to a somewhat similar conclusion.

Deltatherium fundaminis is a rather variable species even for a condylarth. The dentition figured by Matthew (1937), and apparently used by most people as a standard for interpretation, is near one extreme of the variation. Most specimens are in the American Museum; Figure 6 shows a more typically arctocyonid specimen, near another exteme. Nevertheless, I now think that *Deltatherium* is distinct enough adaptively from other arctocyonids to warrant a separate subfamily:

Deltatheriinae, new subfamily.

Included genera: *Deltatherium* Cope (1881) and probably *Lantianius* Chow (1964). *Lantianius* comes from the late Eocene or early Oligocene of Shaanxi (Shensi) Province, China. *Andrewsarchus* (= *Paratriisodon*), on which see Van Valen (1975, p. 90) for affinity, is an approximate Asian contemporary with a similarly long absence of a record from direct or collateral ancestors in the North American early and middle Paleocene. Chow (1964) and Gingerich (1976) have given other interpretations of the affinity of *Lantianius*.

Diagnosis: Arctocyonids with tooth crests unusually well developed for condylarths, cusps relatively tall and acute, embrasure shear emphasized as shown by wear facets, P$_4$ semimolariform.

In Table 2 I give differences in the dentition of *Deltatherium* from its ancestor *Oxyprimus*, together with information on whether wangliid and the more primitive of the non-wangliid pantodonts share the derived states with *Deltatherium*. Despite some considerable comparison I have been able to find only one non-dental difference of *Deltatherium* from primitive arctocyonids (part of the dentition is all that is known for *Oxyprimus*) which is clearly both derived and not related to the larger body size or enlarged upper canine of *D. fundaminis*. This is the more anterior position of the orbit, related to a reduction of the snout. The anterior border of the orbit, in external view, is above the P^4-M^1 border in *Deltatherium* but above the M$^{1-2}$ border in the most primitive condylarths, including undescribed skulls of *Baioconodon* and *Maiorana*. *Pantolambda* and other primitive pantodonts resemble *Deltatherium* in this. Szalay (1977) noted that the feet of *Pantolambda* are very arctocyonid-like, while those Palaeoryctidae for which foot bones can reasonably be identified are more derived. Although this does not in itself support an arctocyonid ancestry for pantodonts, unless Szalay's character polarities were wrong, it argues against a palaeoryctid ancestry (but see below). Zhou et al. (1977) gave photographs of three astragali referred to *Bemalambda*. They differ from each other in ways which at least in part reflect incomplete preservation, but while primitive they are not clearly either specifically arctocyonid-like or palaeoryctid-like insofar as I can reconstruct them. Because of the dental resemblances of the Carnivora and Hyaenodonta to the Paleoryctidae (Van Valen, 1966, 1969) and the opposite apparent directions of evolution in the tarsus (Szalay, 1977), I suspect that the Palaeoryctidae as now constituted will prove to be variable in their tarsus.

Although the characters in Table 2 are not all independent of each other, either developmentally or functionally, I think it is clear that there is a good case for pantodonts having originated from a deltatheriine a

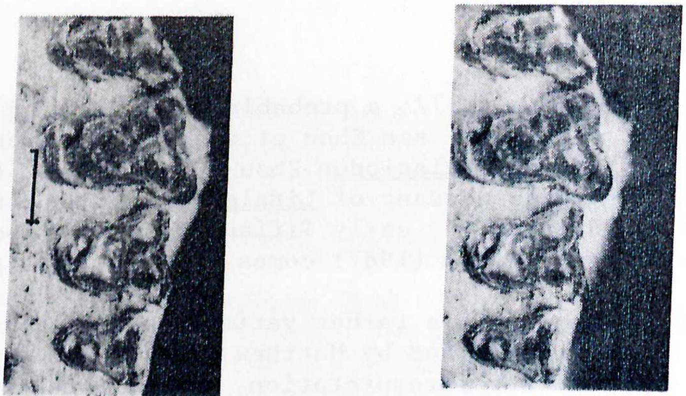

Figure 6. Deltatherium fundaminis, right P^4-M^3, American Museum of Natural History 16611, Torrejon, San Juan Basin, New Mexico, Occlusal (stereo).

bit more primitive than Deltatherium. (And the earliest known Deltatherium occurs with Pantolambda: Lucas and O'Neill, 1981). If so, then the divergence time is again constrained to the Mantuan and Puercan.

One final placental has been found in the El Molino, represented by most of a P_4 (de Muizon, Marshall, and Sige, 1984.) As they note, this tooth resembles the P_4 of Gypsonictops, from the late Campanian and Maestrichtian of North America, but it also resembles the P_4 of, e.g., some species or specimens of Centetodon (Lillegraven, McKenna, and Krishtalka, 1981), known from the late Paleogene of North America but probably of an older lineage. The tooth presumably does belong to the Insectivora, providing their first record in South America except for the small recent penetration of Cryptotis, but its closer affinities are dubious and it is therefore unhelpful in correlation.

A didolodontid condylarth has been said (Kerourio and Sige, 1984, p. 140, footnote) to occur in the Vilquechico locality, but no details are yet available. Didolodontid ancestry, not yet sure in detail (see earlier discussion), is in the Paleocene condylarth radiation.

To summarize the divergence intervals suggested, with high to moderate probability, by the placentals:

Molinodus (with Tiuclaenus): Mantuan or early Puercan
cf. Mimatuta: Mantuan
Andinodus: late Mantuan or perhaps early Puercan
Perutherium: Paleocene
Notoungulata: Paleocene
Alcidedorbignya: Mantuan or probably Puercan.

The agreement is striking, and the evidence itself is better than for any other group. I conclude that the age of the mammal-bearing parts of the El Molino and probably the Vilquechico is later than that of the Mantuan and is most likely equivalent to the late Puercan or early Torrejonian. The latter conclusion allows for some time for the evolution of the South American endemics to occur and does not require several million years of morphological quasi-stasis in the rapid early radiation of notoungulates.

Other Reports of Paleocene Dinosaurs

There thus may well be dinosaurs in the Paleocene of South America, as predicted (Van Valen and Sloan, 1977). However, reports of Paleocene dinosaurs have shown a uniform tendency for their subjects to return home to the Cretaceous after a few years. This is in itself grounds for skepticism. For instance, a possibly Danian dinosaur occurence from Argentina (Casamiquela, 1964) noted in that paper has later proved to come from the normally Maestrichtian Coli-Toro Formation (Casamiquela, 1980; Bertels, 1969), although the original weak evidence for a Danian age at the discovery

Table 2. Derived differences in the dentition of *Deltatherium* from that of *Oxyprimus*. In the left columns the Wangliidae and other rather primitive Pantodonta are compared with the states for *Deltatherium*. Y: agree, or even more derived. N: not agree. V: variable. ?: unknown. —: not applicable.

Wangliidae	Others	*Deltatherium*
Y	Y	Crests stronger.
Y	Y	Cusps somewhat more acute.
?	Y	Embrasure shear emphasized.
?	N	P^1_1 lost in most specimens (at least P_1 present in Univ. Kansas 7792 and 7795).
?	?*	Paraconid of P_{2-3} reduced.
?	Y	P_2 lower.
?	Y	P_3 protoconid expanded proximodistally into paracristid
?	Y	P_3 a little wider.
?	Y	P_3 with small metaconid
Y	Y	P_4 metaconid enlarged.
?	V	Entocristid of P_{3-4} reduced to a cingulum, so the talonid lacks a basin (entocristid sometimes absent P_3 *Oxyprimus*)
?	Y	P_4 lowered, no taller than molars.
Y	Y	P_4 paraconid partly incorporated into paracristid
**	**	M entocristid much reduced, so that talonid basin empties lingually.
Y	Y	M paraconid higher.
N	Y	M paracristid with only a weak arc in occlusal view, not a distinct angle.
Y	V	M hypoconulid taller and more distal.
N	V	M relatively somewhat narrower in most specimens.
Y	Y	Lateral walls of molar trigonid more vertical.
?	N	Upper canine elongated, with serrations on distal surface.
Y	Y	P^{2-3} more transverse.
Y	Y	P^{3-4} protocone larger.
N	Y	P^3 protocone usually directly lingual to paracone.
?	Y	P^4 paracone lower, intermediate between P^3 and molars.
Y	Y	P^4 preprotocrista accentuated.
V	V	P^4 postprotocrista lost.
Y	Y	P^4 paracrista and metacrista stronger.
V	Y	P^4 metacrista incorporates metastyle.
N	N	P^4 without labial shelf in metastylar area.
Y	Y	M^u cusps and crests taller.
Y	Y	M^u less transverse, especially lingual of paracone and metacone.
V	Y	M conules smaller (not much reduced *D. durini*).
Y	Y	M protocone apex closer to paracone and metacone.
Y	—	M centrocrista valley not as deep.
Y	Y	M ectoflexus usually deeper.
Y	Y	M metacrista accentuated.
Y	Y	M stylar shelf wider.

*: The paraconid of P_4 of *Deltatherium* is a neomorph; both it and the proximobasal cusp occur in some individuals. The molarized P_{2-3} trigonid of normal pantodonts probably reflects the extension of the neomorph more proximally in the tooth row.

**: Reduced, but primitively less so than in *Deltatherium*.

* * *

locality is not refuted.

Another Argentine case also looks unlikely. Brett-Surman (1979) described the new hadrosaur genus <u>Secernosaurus</u> from the "San Jorgé Formation, Río Chico, Patagonia, Argentina." This formational (actually San Jorge) name is an old one. [There are in fact two other Argentine formations with the name San Jorge, both Paleozoic (Anonymous, 1979-80).] The unit was later split into the Roca and Salamanca Formations, which were originally deposited in different basins; the one here is the Salamanca, which (like the Roca in most places, but see Bonaparte and Soria, 1985) is normally dated as Danian by planktonic foraminiferans (e.g. Bertels, 1975b). Bonaparte (1978) gave the horizon of the specimen as the base of the Salamanca, very late Cretaceous. The specimen is P13413 in the Field Museum. Its label reads, "San Jorge Formation, Late Cretaceous, Chubut, Argentina, 2 miles east of Río Chico". The catalogue card is the same except for "2 miles east of head of Río Chico". According to Anonymous (1967), the Río Chico has its head in wetlands by the southeast corner of Lago Colhué Huapí, 68.54° W, 45.63° S. The unrecopied version of the field book, by John Bernard Abbott for 1922-23, gives for the specimen (field number 618, November 9, 1923), "Dinosaur beds, Chico river 2 mi. East of head. Vert., pelvis, and limb bones. 5 plastered pieces."

Because the Río Chico Formation, which overlies the Salamanca, used to be called the "upper dinosaur beds" and similar names despite the absence of any dinosaurs known to be from it, the information is ambiguous. (The Chubut Group underlies the Salamanca and does contain dinosaurs.) How the specimen became attributed to the San Jorge or Salamanca, which is marine, is unclear, although such a provenance is not impossible. And finally, Marshall et al. (1981) said that the species (presumably the type specimen) came from a dinosaur-bearing level in the Bajo Borreal Formation 50 to 55 m below the basalt underlying the Salamanca Formation. This seems entirely plausible, even likely, but it also seems unwarranted by real evidence.

However, in Europe the situation seems to be different. Only a popular paper (Erben, 1983) and an abstract (Erben et al., 1984) are yet available, but the Cretaceous/Paleogene boundary in the regions of Marseille and the Pyrenees has been identified (see also Babintot et al., 1985, and Masriera and Ullastre, 1985). Five zones of dinosaur eggshells occur above this boundary, if indeed the same boundary is being used. Erben (1983) estimates the duration of Paleocene dinosaurs here as 2 Ma after the boundary, but the rest of us must await details of the evidence.

In India, Rao and Yadagiri (1981), Sahni, Rana, and Prasad (1984), and others have found dinosaur remains in intertrappan beds. These fossils are usually used (e.g., Rao and Yadagiri, 1981; Courtillot et al., 1986b) to date the beds as Cretaceous, as most other fossils (including the five charophytes reported in recent work: Bhatia and Mannikeri, 1976; G.V.R. Prasad, 1986) are ambivalent. A diverse flora (Prakash, 1969) is supposed to indicate an Eocene age. Radiometric dates (Courtillot et al., 1986a, 1987; Baksi, 1987; Wensink, 1987) are consistent with the main basalt flows being from chron 31N to 30N, from chron 30N to 29N, or from 29N to 28N. The Cretaceous/Paleogene boundary is after the first range, in the middle of the second, and earlier than the third. The early Paleocene was about the time India overrode the Réunion hot spot (Venkatakrishnan and Decker, 1986). However there may be appreciable diachroneity in flows from different areas (e.g., Sahni, 1986a). In the eastern (and probably oldest, if diachronous) area Govindan (1982) found very late Maestrichtian planktonic foraminiferans in an intertrappan bed. Benthonic foraminiferans nearby have been interpreted as Eocene (e.g., Bhalla and Khan, 1969), but this age seems too late except possibly for a minor tail of the extrusions. Thus the dinosaurs may satisfy the prediction of Van Valen and Sloan (1977) that dinosaurs would survive well into the Paleocene in India, but the evidence is not good. The geographical basis for the prediction itself may be wrong; the biota between and just below the Deccan Traps does not now seem to be endemic to India (see Sahni, 1986b, for review). Mathur (1987) has just reviewed other evidence supporting dinosaur survival into the Paleocene in India.

Sloan (1987) reports a bone from a mammal larger than any known in the Cretaceous, from a horizon below dinosaur eggshells in Hunan, China. Dinosaur-bearing beds also seem to conformably underlie rocks in that region bearing a mammalian fauna which he (as I do above) correlate with the North American Torrejonian. Both these arguments for dinosaur survival well into the Paleocene of China are obviously provisional.

In North America, there is somewhat inconclusive evidence for early Paleocene dinosaurs in the San Juan Basin, New Mexico. Fassett, Lucas, and O'Neill (1987) discuss several occurrences from the (upper, restricted, or Kimbeto Member of the) Ojo Alamo Sandstone. This sandstone is palynologically dated as Paleocene by them and by others (e.g., Newman, 1987), although their quoted report from Tschudy as "upper lower or lower middle Paleocene" is based on a species which Newman found earlier in the Paleocene, and anyway a classic locality for early Paleocene mammals overlies the Ojo Alamo in the place sampled. The sample is 2 km to the east of one of the dinosaur localities, but despite the absence of an evident intervening unconformity the normal local complexities of fluvial sandstones make it possible that the palynomorphs are later and thus above a temporal boundary. However, all palynological samples from this sandstone are Paleocene (Newman, 1987), so it does seem likely that the several dinosaur specimens found there (including a large limb bone) are also Paleocene. No dinosaur remains have been found as late as the middle Puercan mammal localities of the San Juan Basin, which have been assiduously collected for a century by various methods.

Stone and Langston (1975) reported apparently Paleocene pollen in and around a partial sauropod dinosaur skeleton, presumably <u>Alamosaurus</u>, from the Javelina (or Tornillo) Formation of Texas. The palynology has not been pubished in detail, and a recent thesis on the paleontology of this formation (Standhardt, 1986) does not even mention the report. The Paleocene age must for now be regarded as questionable.

In Montana there is good evidence for dinosaur persistence, for a short time only, into the Paleocene (Sloan et al., 1986; Sloan and Rigby, 1986; Rigby et al., 1987; Rigby, 1987). One channel with dinosaurs (J.K. Rigby, Jr., personal communication) does not even extend as far down as the putative iridium anomaly (which is so small here that it may be diagenetically caused, although it fits everyone's outlook and so has not been much questioned). Ordinary Cretaceous mammals do not occur with the dinosaurs, as would be expected on any hypothesis of reworking. Low abrasion is possible for transported material (Argast et al., 1987) but does not affect the evidence (Rigby et al., 1987; Rigby, 1987). Details of these and other arguments have not yet all been published, but the only real question is the exact position of the erathem boundary in the unlikely event that the iridium anomaly, which coincides with the usual palynological change, is not the standard one.

Biogeography

Two mammalian orders, the Marsupicarnivora (and therefore the Marsupialia as a whole) and the Edentata, are often thought to have originated in the Cretaceous of South America. Until recently this could easily have been an artifact of collecting techniques, but the Los Alamitos Formation of northern Patagonia (Bonaparte et al., 1985), of late Campanian or early Maestrichtian age, has now yielded a fauna of small mammals (Bonaparte and Soria, 1985; Bonaparte, 1986a, b, c; Bonaparte and Pascual, 1987; Bonaparte and Rougier, 1987). This is in a region where both orders are relatively abundant later, but neither has been found in the Los Alamitos.

In Laurasia (Holarctica), we see in the Cretaceous a variable dominance of the Multituberculata and Tribosphenida with rare persistence of Triconodonta and Pantotheria. (I use the name Tribosphenida McKenna, 1975, for the subclass consisting of the Marsupialia, Placentalia, and Trituberculata [infraclass for the order Aegialodontia and any other non-marsupial and non-placental tribosphenids]. Tribosphenida is the same as Eutheria of Gill, 1872, but the latter name is more commonly used as a synonym of Placentalia and is really too ambiguous to perpetuate.)

However, in the Los Alamitos there are no tribosphenids at all. Instead there are _Ferugliotherium_, a very aberrant ?multituberculate; _Austrotriconodon_, a triconodontid; an undescribed symmetrodont; _Groebertherium_, a dryolestid; _Mesungulatum_, which establishes the second known family of the Dryolesta and is somewhat convergent on condylarths in the form of the upper molars; and _Gondwanatherium_, discussed below. _Vincelestes_, representing a new family of peramurid-like Amphitheria, occurs in the ?Hauterivian La Amarga Formation and corroborates the general taxonomic similarity of this Gondwanatherian Fauna to the late Jurassic mammal fauna of Laurasia.

Gondwanatherium was compared most favorably by its author with some derived members of the Xenarthra, but I see no special resemblance beyond the bare fact of hypsodonty and its correlates. _Gondwanatherium_ could, for instance, easily be a hypsodont derivative of the early Cretaceous monotreme _Steropodon_ (on which see Archer et al., 1985, and Kielan-Jaworowska, Crompton, and Jenkins, 1987) or even of something like _Ferugliotherium_. Following Bonaparte (1986a), Mones (1987) has formally grouped _Gondwanatherium_ with the superficially more sloth-like late Paleocene genus _Sudamerica_ into a new order Gondwanatheria, still doubtfully associated with the Xenarthra, which he (like Scillato-Yané and Pascual [1985], for _Sudamerica_) regards as a superorder by cladistic oversplitting. I do agree that the two genera probably belong to the same order. Bonaparte (1986a, b and in Bonaparte and Pascual, 1987) seems to regard the Edentata as not even belonging to the Placentalia, with a separate origin from pantotheres. While primitive, edentates are good placentals in many ways (cf. Marshall, 1979).

I do not know what _Sudamerica_ is (it is known from one tooth), but it has no resemblances to the Xenarthra which are not very probably convergent. Its resemblances are not to the most primitive xenarthrans. Like _Gondwanatherium_ it even retains a thick layer of enamel on its teeth. The Xenarthra lost their enamel early, probably from a myrmecophagous habit, and much of the later skull and dental evolution of the group has been functionally compensatory for this loss in animals which would have been better served if their ancestors had kept at least the ability to develop enamel. Loss of thick enamel by an already very hypsodont animal would seem severely inadaptive; enamel reduces the tooth height that is necessary (Van

Valen, 1960) and also provides abrasive ridges.

The hypsodonty of Sudamerica is mostly or entirely produced by elongation of the cusps, as shown by the internal enamel rings ("lakes"), which are even filled with cement. Xenarthran hypsodonty, on the contrary, is mostly or entirely produced by elongation of the root. The thin enamel retained on a young specimen (epiphyses unfused) of the Eocene armadillo Utaetus (Simpson, 1932) does not extend below the lowest current level of wear, so much the largest part of the tooth produced during life was produced below the base of the enamel. Ernanodon may indicate a phyletically earlier stage, if it really is a primitive xenarthran, as it seems to be (Ding, 1987). It retains more enamel and its teeth are not yet evergrowing. In the deciduous teeth of Dasypus enamel is also deposited on the upper surface (Martin, 1916), but as these teeth are not hypsodont this restricted deposition is not good evidence on the kind of hypsodonty in the permanent teeth, although it is suggestive.

As the hypsodonty of Utaetus is presumably homologous to that of other xenarthrans, hypsodonty seems to have evolved by different paths in Sudamerica and the Xenarthra. This lack of homology indicates that Sudamerica is convergent on the Xenarthra in its hypsodonty.

In Gondwanatherium, however, there are no internal enamel rings or cement. The persistent pulp is a condition more derived than that of Sudamerica. (Evergrowing teeth are commonly called rootless, but this term is obviously inappropriate for root hypselodonty and defines away the possibility that enamel came to be deposited on parts of the tooth homologous to former roots, now fused.) The hypsodonty of Gondwanatherium is about half by elongation of cusps and about half by elongation of the crown below the cusps. Possibly some of the elongation in Sudamerica is also of crown below the cusps, but this cannot yet be shown. It is nevertheless plausible that Sudamerica and Gondwanatherium are collateral relatives, even though they are probably correctly placed in different families.

Mourier et al. (1986) have described a fragment of an upper tooth, probably of a primitive therian, from the basal part of red beds which overlie, apparently conformably, early Santonian marine rocks in northern Peru. Future work in this area (and, of course, elsewhere) may possibly modify some of my conclusions, which necessarily reflect only what we know now.

Indeed, Cretaceous marsupials are not definitely known outside of North America, where they have an abundant record (Clemens, 1979; Fox, 1980; Slaughter, 1981; Cifelli and Eaton, 1987). The recent tentative report from Europe (Antunes et al., 1986) does not affect this because Europe was then part of eastern North America (or vice versa) rather than of Asia. In most parts of the world there are no suitable faunas known, but their absence from central Asia seems real. The record of marsupial evolution in the Cretaceous of North America is now enough to show that this was either a main area of their early evolution or it frequently received immigrants from an area which was. South America seems to have been too far away to serve as such a source (Stehli and Webb, 1985), although coastal Asia is not really excluded. The apparent derivation of South American Cenozoic marsupials from forms like earlier North American ones, noted in an earlier section, implies that any indigenous marsupial evolution was either restricted to the Maestrichtian after an immigration then or became extinct. The latter is unlikely because of the early Gondwanatherian Fauna, and there is no evidence for either. In either case there is now no support for a South American origin of the diverse Cenozoic marsupials of South America. Thus the recent evidence confirms a standard view (e.g., Simpson, 1950;

Clemens, 1968). The ancestors of the Australian marsupial radiation came from part of the South American radiation (Szalay, 1982) and therefore also arrived in the Cenozoic.

If palaeanodonts gave rise to the Xenarthra, as I suspect occurred, then the same statement can be made, a bit more weakly, for the Xenarthra. Otherwise a South American origin of the Xenarthra would still be somewhat defensible because of the absence of early records elsewhere. Although the absence of any reported xenarthran from the Los Alamitos, the El Molino, or the Vilquechico is relevant, recall that they would probably not yet have been found if they were in the same proportion to other mammals as in the Itaboraí.

On its face, present evidence suggests that marsupials and placentals first arrived in South America in the Paleocene, as immigrants from North America. Do the remarkable Los Alamitos mammals indicate a whole earlier radiation in dinosaur-infested communities, which the immigrants extinguished? As Bonaparte (1986b) notes, the similarities of other Cretaceous tetrapods among the regions of disintegrating Gondwanaland suggest that the Gondwanatherian Fauna of mammals may prove to be more widespread on the southern continents.

It is now widely agreed, at least among paleontologists, that there was some filtered interchange between South and North America in the late Cretaceous. Rage (1981, 1986), Bonaparte (1984a, b, 1986b), and Estes and Báez (1985) give recent reviews which differ in a few details. Geophysical reconstructions will have to allow for this occurrence. The heterodox view of Donnelly (1985) is the most easily accommodated, but that obviously does not show its correctness. No microplate accretion to South America seems to have occurred during the late Cretaceous and Cenozoic (Dalziel and Forsythe, 1985).

It is interesting that the late Cretaceous interchange seems to have involved no mammals. Later mammals have been reasonable adept at filtered dispersal; did each biota prevent the establishment of mammals from the other?

During the Paleocene, however, the prevailing view is that the continents were too far isolated from each other for more than very rare interchange. We see, though, that the current evidence is that such dispersal was no more difficult than in the Cretaceous. The following events occurred or are reasonably likely:

several charophytes (direction unknown; some interchange possible in the very late Cretaceous)
several nonmarine mollusks (Parodiz, 1969. I discuss this in an earlier section; dispersal is likely but the data need re-evalution), N → S
Peradectes, N → S
Glasbiinae (possibly very late Maestrictian; see Pascual [1983, including addendum] for the South American record and relationships), N → S
Pediomyinae (also possibly Maestrichtian), N → S
an insectivoran (also possibly Maestrichtian), N → S
probably Palaeanodonta to produce Xenarthra, N → S
perhaps basal xenarthran to produce *Ernanodon*, S → N (or combined with the preceding, for one N → S)
deltatheriine or basal wangliid to produce *Alcidedorbignya*, N → S
perhaps *Alcidedorbignya* to produce *Wanglia* and more derived Pantodonta, S → N
probably *Loxolophus*-like arctocyonid to produce *Andinodus*, N → S
perhaps *Desmatoclaenus* to produce Didolodontidae, N → S
Bubogonia-like mioclaenid to produce *Molinodus* and *Tiuclaenus*, N → S
probably *Mimatuta*, N → S

perhaps primitive astrapothere to produce Arctostylopidae, S→N

These could not all have been synchronous, as discussed for each in other sections. The evidence does not require any dispersal in the last half of the Paleocene, although the last event on the list may have occurred then.

Most of the dipersal was from north to south. This seems to march with the received view that evolution in isolated areas tends to produce inferior competitors, a view which receives part of its popular support from neglect of the strongly selective late-Pleistocene extinctions in relation to migrants of South and North American origin. We see here an interesting apparent counterexample. The Pantodonta and Insectivora arrived in South America but became extinct very shortly thereafter, as apparently did either mioclaenids or arctocyonids. They diversified in Holarctica in company with the evolving biotas there. That the counterexample may only be apparent, and the trend itself only seeming to support the theory, comes from noting that North America was as isolated from Asia as from South America, and that even with Europe, part of the same continent, faunal resemblance at the generic level was less than it is today with the Atlantic and Siberia between. So there may not have been much, if any, effectively greater area and environmental diversity in North America. North America could communicate with three other continents or quasi-continents and South America with only one (or two, if Australia-Antarctica was relevant), and this may help to save the theory, but most mammalian evolution in the Paleocene of North America seems to have been autochthonous.

And, anyway, the theory may be based on a statistical artifact. There are more initially endemic species and other taxa on mainlands than on islands; this itself gives the prediction, ceteris paribus, that successful invaders will usually come from mainlands. They do not always do so; a major radiation in the Drosophilidae probably started on an ancestral group of Hawaiian islands before reaching any mainland (Throckmorton, 1967). Whether the probability of this happening differs between mainland and island taxa seems not to have been investigated.

I mentioned in the introduction that the revised correlation affects ungulate phylogeny. What it really does is preclude serious and awkward revisions, with a great increase in parallel evolution, which would be necessary if the relevant parts of the Vilquechico and El Molino were indeed Cretaceous. The same is true, to a lesser extent, for marsupial phylogeny.

Extinction

That dinosaurs may have survived one to three million years into the Paleocene is itself of some interest. That they may have done so longer in South America than in North America would confirm a prediction of Van Valen and Sloan (1977). Whether this prediction has a correct factual basis is another question; it involves the initial cause of the Cretaceous/Paleogene extinction, a matter which is beyond the scope of this paper (although I hope to return to it soon elsewhere).

Nevertheless, if dinosaurs did survive well into the rapid basal-Cenozoic radiation of mammals (in South America, of marsupials as well as placentals), this would imply that their final extinction was unlikely to be a direct result of the terminal Cretaceous environmental shock and its physical aftermath. It remains plausible that their final extinction was from competition (sensu lato, including perhaps some egg-eating) by mammals. Van Valen and Sloan (1977) discuss why this apparently unrealistic mechanism should be considered seriously.

The revised correlation also affects the pattern of marsupial extinction. There is no longer a large Cretaceous marsupial fauna known in South America, which gradually diversifies into the Paleocene and beyond, as Case and Woodburne (1986) especially have proposed. The available evidence is still that marsupials became nearly as extinct as the dinosaurs (Van Valen and Sloan, 1977), although it now seems likely that two additional lineages (the Glasbiinae [Pascual, 1983] and a pediomyine) survived to the south of present North American records. Marsupial diversity in the late Paleocene Riochican is not greater than ungulate diversity there or in the North American Tiffanian, and this diversity is easily compatible with derivation from known possible ancestors by rapid evolution like that characteristic of the first half of the Paleocene in North America.

Addendum

A paper just published (Marshall and de Muizon, 1988) provides some additional information. The authors give further evidence, not conclusive, for correlation of the mammal-bearing Tiupampa locality (El Molino Formation) with both the Laguna Umayo locality (Vilquechico Formation) and rocks below dinosaur tracks in the El Molino. A second species of insectivoran may be represented by several lower molars from the El Molino, and the paper gives better (and more) figures for the El Molino condylarths and pantodont. Nine new genera and species of primitive marsupials are described from the El Molino. Of these it is not clear that Incadelphys and Mizquedelphys are distinct from each other generically; evaluation of the generic distinctness of these and most of the others from their close relatives in the Itaborai must await the appearance (or arrival) of Marshall's revision of the latter, although Allqokirus is clearly distinct from its apparent descendant Patene, on which see Marshall (1981).

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