

THE MESOZOIC AND PALEOCENE VERTEBRATES OF BOLIVIA AND THEIR STRATIGRAPHIC CONTEXT : A REVIEW

MIREILLE GAYET*, LARRY G. MARSHALL** & THIERRY SEMPERE***

*URA 11 du CNRS, Centre des Sciences de la Terre, Lyon I, 27-43 boulevard du 11 novembre, 69622 Villeurbanne, France

** Institute of Human Origins, 2453 Ridge Road, Berkeley, California 94709, USA

***Convenio YPF-B-Orstom (UR 1H), Santa Cruz de la Sierra, Bolivia.

Present address: Centre de Géologie Générale et Minière,
Ecole des Mines, 35 rue Saint-Honoré, 77305 Fontainebleau, France

INTRODUCTION

Bolivia has a rich and diverse record of fossil vertebrates for the Mesozoic and early Cenozoic. The majority of the 56 known fossil localities for this time interval occur in the southern Altiplano and in the southern part of the Cordillera Oriental (Figs. 1-4).

In this paper we review the middle Triassic through Paleocene fossil vertebrate record of Bolivia in its stratigraphic and paleoenvironmental context and attempt to correlate these rocks and faunas with those in adjacent Argentina, Brazil, Chile and Peru. As documented below, the highlights of the Bolivian vertebrate record include: the taxonomically richest and best studied faunas of late Cretaceous age (from the marine and continental El Molino Formation) and the spectacularly rich and only well known land mammal fauna of early, but not earliest, Paleocene age (from the Santa Lucía Formation at Tiupampa) in all of South America. We show that many of the late Cretaceous taxa (especially selachians) are of chronostratigraphic value within the Andean basin. The problem of the K/T boundary in the Andean basin of Bolivia is critically evaluated and based on this study is believed to occur within the upper part of the middle member of the El Molino Formation.

The following abbreviations are used: km, kilometers; m, meters; Ma, megannum or millions of years ago, a point in time; Myr, millions of years, a duration of time.

STRATIGRAPHY

The "Mesozoic" stratigraphy of Bolivia comprises two distinct time intervals (Sempere, 1990): the first spans the middle Triassic - most of Jurassic, and the second latest Jurassic-Paleocene (Fig. 1).

The fluvio-eolian middle Triassic-Jurassic sedimentary rocks were deposited in what is now the eastern half of the Andean domain, the Subandean belt and a large part of the Bolivian lowlands (Oller & Sempere, 1990); their lithologies and depositional environments show similarities with coeval rocks in the Paraná basin of southern

Brazil, eastern Paraguay, northern Uruguay and northeastern Argentina. In contrast, the latest Jurassic-Paleocene depositional area was mainly restricted to the Andean domain and belonged to the back-arc basin of the Pacific margin (Sempere *et al.*, 1988), although some late Cretaceous-Paleocene units are also known in parts of the northern and central Subandean belt (Figs. 1, 2).

The "Condo event" that separates these two intervals can be interpreted as the capture of the Bolivian Andean domain, which until then had belonged to the cratonic area, by the Pacific back-arc. This event, accompanied by numerous synsedimentary tectonic manifestations (Sempere, in press), correlates with the Kimmeridgian age Araucan event in westcentral Argentina and adjacent Chile (Sempere *et al.*, 1988).

A. MIDDLE TRIASSIC TO MIDDLE JURASSIC (Serere supersequence)

The rich Phanerozoic record of Bolivia was traditionally thought to lack Jurassic deposits. However, recent studies have shown that certain stratigraphic units from the Subandean belt and from the Andean domain should be correlated and assigned a middle Triassic and Jurassic age (Fig. 1) (Oller & Sempere, 1990; Sempere, 1990). The Serere supersequence consists of these units, and includes the Entre Ríos Basalt, Ipagunzú, Tapeçun, Castellón, Ichon and Yantata formations, as well as the partly equivalent Beu, Tiquina, Sayari and Ravelo formations (Fig. 1). The Tacurú Group of the central and southern Subandean belt is distinct from the Serere supersequence because it includes the latest Cretaceous Cajones Formation but not the Ipagunzú Formation (Sempere, 1990). In general, sedimentary continuity characterizes the Serere supersequence (Oller & Sempere, 1990). As will be documented below, its deposits to date are sparsely fossiliferous.

The Castellón Formation is probably of late Triassic-early Jurassic age (Sempere & Oller, 1987; Oller & Sempere, 1990), although it has been tentatively assigned to the early Cretaceous based on four new species of ostracods (Pinto & Sanguinetti, 1987). It is correlated

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with the Piramboia Formation of Brazil and the lower part of the Tacuarembó Formation of Uruguay (Sempere & Oller, 1987).

The lower boundary of the Serere supersequence is a diachronous unconformity except in the southern Subandean belt where, the oldest and elsewhere unknown Ipaguazú Formation overlies the late Permian-early Triassic Vitiacua Formation with only a slight, non-erosional, lithologic discontinuity (Sempere *et al.*, 1990, 1992). In other areas of the basin, younger units of the Serere supersequence unconformably overlie Permian or older strata, reflecting onlapping deposition on an altered, eroded and/or deformed substratum. The upper boundary of the Serere supersequence is the surface that marks the "Condo event" (see above). This unconformity shows different characteristics which relate to its location and position in the latest Jurassic-Paleocene basin.

In summary, the middle Triassic-Jurassic geologic evolution of Bolivia involves: 1) an initial rifting process with deposition of red beds in narrow troughs, locally with gypsum and halite (middle to late Triassic); 2) termination of rifting and onlapping fluvio-eolian sedimentation (late Triassic to earliest Jurassic?); and 3) extensive erg development (early and middle Jurassic?) (Oller & Sempere, 1990).

B. LATEST JURASSIC TO PALEOCENE (Puca supersequence)

Classic works on the Bolivian "Cretaceous" Puca Group are by Lohmann & Branisa (1962), Russo & Rodrigo (1965), Kriz & Cherroni (1966), Lohmann (1970), Reyes (1972) and Cherroni (1977).

The "Cretaceous" sequence stratigraphy of Bolivia and Peru is currently being re-evaluated and synthesized (Jaillard & Sempere, 1989; Sempere, in press). The Puca supersequence (Sempere, 1990) is bound below by the k0 discontinuity (*i.e.*, the Kimmeridgian Araucan-"Condo" event at about 144 Ma; Cowie & Bassett, 1989), and above by the k5 discontinuity which records the functional onset of western Bolivia as a continental external foreland basin of the paleo-Andes (Sempere *et al.*, 1989). The age of k5 is close to the Paleocene-Eocene boundary (53 Ma; Cowie & Bassett, 1989) and could be as young as 50-51 Ma (Sempere, 1990; Marshall & Sempere, 1991).

In this paper we divide the Puca supersequence into three megasequences. The Puca A megasequence includes the partly equivalent Condo, Kosmina, La Puerta s.s., Sucre and Tarapaya formations (Fig. 1), and consists of azoic non-marine deposits; the marine Miraflores Formation constitutes the Puca B megasequence; and the Puca C megasequence includes the Aroifilla, Chaunaca, El Molino, Santa Lucía and Impora formations, and their stratigraphic and temporal equivalents (Fig. 1). Unlike the Puca A, the Puca B and C have yielded many marine (Puca B and C) and/or continental (Puca C) fossils.

The marine Miraflores Formation consists of fossiliferous limestones and minor mudstones, up to 28 m in total thickness; it is of Cenomanian and Turonian age (Jaillard & Sempere, in press). Within the Puca supersequence, the Miraflores Formation is the only unit of undisputed marine origin because it contains ammonites and echinoids (Branisa, 1968; Reyes, 1972). It is separated from the overlying Aroifilla Formation by an erosional discontinuity which is

accompanied by synsedimentary tensional tectonic and magmatic manifestations (Sempere *et al.*, 1988; Sempere, in press) and is termed the "Vilcapujio event" in Bolivia (Chávez, 1987) or k3 in the central Andes (Jaillard & Sempere, unpublished). Thus, the Miraflores Formation stands as a specific "hinge" unit in the Bolivian latest Jurassic-Paleocene stratigraphic sequence.

Mainly red mudstones with minor sandstones and evaporites (gypsum, anhydrite, halite) were deposited between discontinuities k3 and k4 in fluvial and lacustrine environments [Aroifilla Formation and most of Chaunaca Formation (Sempere, in press); the stratigraphically equivalent Torotoro Formation consists mainly of red sandstones of fluvial origin]. Two greenish levels, which consist of very fine sandy, green to black marls, black to grey laminated limestones and yellow dolomites, occur in the Chaunaca Formation. The former is more conspicuous, traditionally marks the base of the unit, and is termed the "basal limestone" of the Chaunaca Formation. This 30 m-thick sub-unit commonly yields abundant bivalves (*Mytilidae*, *Brachidontes* sp.) which have been interpreted to indicate an intertidal environment (Branisa *et al.*, 1966). However, a restricted marine origin for the "basal limestone" is now questioned (G. Camoin, personal communication). Identical *Brachidontes* sp. are recorded from a limestone level in the Lomas Negras Formation of northern Chile (Marinovic & Lahsen, 1984). The "basal limestone" of the Chaunaca Formation yielded a palynological assemblage of Santonian to earliest Campanian age (Pérez, 1987), and may be partly equivalent to the Santonian age shallow-marine limestones known from the Querque and Omoye formations of southern Peru (Jaillard & Sempere, 1989). The Aroifilla and Chaunaca formations are equivalent, respectively, to the lower and middle Vilquechico Formation of southeast Peru (Jaillard *et al.*, in press) (Fig. 1). The upper greenish level of the Chaunaca Formation is equivalent to the uppermost green level of the middle Vilquechico (Jaillard *et al.*, in press; Sempere, in press), which has yielded the selachian *Schizorhiza stromeri*. Thus, its age is not older than middle Campanian (Jaillard *et al.*, in press).

The El Molino, Santa Lucía and Impora formations occur between discontinuities k4 and k5 in Bolivia (Fig. 1). The El Molino Formation is equivalent to the Lecho, Yacoraite, Tunal and Olmedo formations of northwestern Argentina (Fig. 1); to the Areniscas de Azúcar, Vivian and Cachiayacu formations of Subandean Peru (Sempere *et al.*, 1987; Jaillard & Sempere, 1989); to the upper Vilquechico Formation of the Peruvian Altiplano (Jaillard *et al.*, in press) (Fig. 1); and to the Estratos de Quebrada Blanca de Poquis, and possibly parts of the Lomas Negras, Pajonales and Tonel formations in northern Chile (Gardeweg & Ramírez, 1985; Salfity *et al.*, 1985; Muñoz *et al.*, 1989; Charrier & Reutter, 1990).

The basal sandstones of the El Molino Formation are partly equivalent to the Lecho and Vivian formations. The thickness of these sandstones in Bolivia is highly variable and usually decreases basinwards. Several lines of evidence suggest that these sandstones and other associated sedimentary rocks are of latest Campanian age (Jaillard & Sempere, 1989). The lowest part of the El Molino Formation records a major marine transgression of apparent latest Campanian and/or early Maastrichtian age; coeval transgressions are known in many parts of South America and the world (Haq *et al.*, 1987).

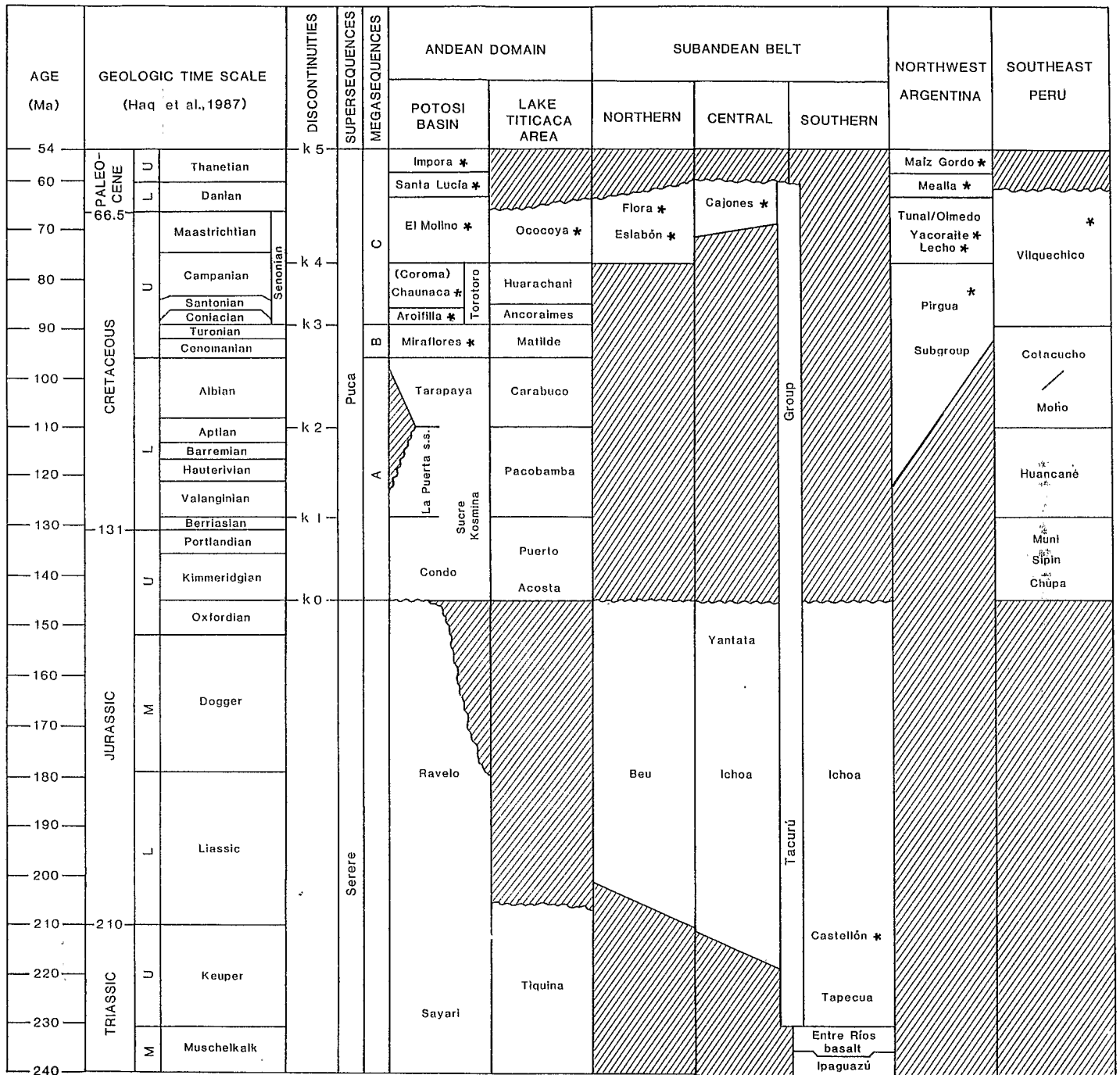


Figure 1. Chronostratigraphic chart showing vertebrate-bearing formations (*) of middle Triassic-Paleocene age in Bolivia, and in adjacent Argentina and Peru.

Based on recognition of large-scale transgressive-regressive sequences, the El Molino Formation is divided into lower, middle and upper members which are of stratigraphic value (Jaillard *et al.*, in press; Jaillard & Sempere, unpublished; Sempere, in press). Common sedimentary facies in the El Molino Formation include: mudstones and marls (green to black or purplish, reddish); grey to light brown limestones (micritic to bioclastic and/or oolitic); stromatolitic boundstones referred to as *Pucalithus* by Steinmann (1923) and Ahlfeld & Branisa (1960); fine to medium-grained sandstones, usually calcareous and light-colored; some yellow dolomites, often with algal laminations; very rare evaporites (gypsum and halite casts); and a few white altered tuffs of porcelain aspect. Mudstones, marls and thin limestones largely predominate in the basin; sandstones, dolomites and evaporites are more common along its borders; and tuff levels are thicker and more frequent in the west, *i.e.* in the direction of the active volcanic sources located in present-day Chile and Peru. In the basinal localities, lime turbidites are common and where fossiliferous the paleontological materials were deposited a substantial distance from their life environment.

Concordant paleocurrent data indicate that the basin deepened toward the northwest in Bolivia (Sempere *et al.*, 1987; Sempere, in press), and probably connected with a marine basin in the Peruvian Subandean region. Ammonites are reported 2 m below the top of the Cachiycu Formation in the Huallaga area (7°S) of northern Peru (Vargas, 1988). In Bolivia, several fish groups, which reputedly indicate a marine environment (see below), are known from the lower and basal middle El Molino. Dinoflagellate cysts are present in at least some levels of the formation in Bolivia and in stratigraphic equivalents in northwestern Argentina (Industry, unpublished; J. Oller, personal communication). Ammonite embryos have been reported from the lower El Molino (Sempere *et al.*, 1987), but their identification needs confirmation. Foraminifera (Miliolidae, Discorbidae) are present in many levels and facies (G. Tronchetti, in Camoin *et al.*, 1991), but no detailed study has yet been made of their taxonomy or paleoenvironmental implications. Molluscs are reported from various localities (*e.g.* at El Molino; Pilsbry, 1939), although the systematics of these taxa is out-dated and the relevance of described species has yet to be established. Echinoids are apparently lacking and the proportion of brackish water ostracods is locally high (J. F. Babinot, in Camoin *et al.*, 1991).

A petrographic study of the Yacoraite Formation of northwestern Argentina led Marquillas (1985) to interpret its depositional environment as a restricted carbonate basin. An oligohaline lacustrine environment has also been proposed (Camoin *et al.*, 1991). However, paleontological data do suggest that communication of the basin with an open marine realm was frequent during deposition of the El Molino Formation, but that the basin itself was never openly marine, at least in Bolivia and Argentina (Gayet *et al.*, 1992; Sempere, in press). For reasons discussed below, we believe that most of the El Molino Formation was deposited principally in a restricted marine environment which connected with a more typically open marine realm located northwest of Bolivia (see also Sempere, in press).

The overlying Santa Lucía and Impora formations were deposited in fluvial to lacustrine environments. No marine fossils or facies are known from these units which consist principally of red to purplish siliciclastic sedimentary rocks. Gypsum and "gypsified" anhydrite (J.

M. Rouchy, personal communication), are abundant in the upper part of the Santa Lucía Formation near Potosí. Some green marls and light-colored limestones occur in the Impora Formation of southern Bolivia.

The Santa Lucía and Impora formations are, respectively, stratigraphically equivalent to the Paleocene age Mealla and Maíz Gordo formations of northwestern Argentina (Marocco *et al.*, 1987) (Fig. 1). The Mealla Formation can be correlated with the Tiupampian (early Paleocene) Land Mammal Age based on its equivalence with the Santa Lucía Formation (see below) and the Maíz Gordo Formation with the Riochican (late Paleocene) Land Mammal Age based on palynology (Volkheimer *et al.*, 1984) and stratigraphic position (Pascual *et al.*, 1981).

VERTEBRATE FAUNAS AND LOCALITIES IN BOLIVIA

A. TACURU GROUP

Ahlfeld & Branisa (1960) reported remains of large bones, possibly of dinosaurs, from the Tacurú Group in the Serranía de Mandeyapeca, southeastern Bolivia. In this area the Tacurú Group includes rocks of middle Triassic and Jurassic age, namely the Tapeuca, Castellón and Ichon formations (Fig. 1).

B. CASTELLON FORMATION

Scales and bones of semionotiform fishes were found in the late Triassic-early Jurassic age Castellón Formation on the western flank of the Charagua anticline in the Quebrada de Charagua, 7 km west of the town of Charagua (Wenz, in Goñi & Hoffstetter, 1964). Nothing definite can be said of these bones, although a study of the scales with Scanning Electron Microscopy (Gayet & Meunier, 1986) and of their transverse sections permits reference to the family Semionotidae, probably *Lepidotes* sp. (Gayet, 1991).

C. MIRAFLORES FORMATION

The Miraflores Formation is a marine limestone unit which, based on knowledge of ammonites, bivalves, gastropods and echinoids, was regarded as middle to late Cenomanian in age (Branisa *et al.*, 1966; Jaillard & Sempere, 1989), although detailed sequence stratigraphy now suggests that the entire rock unit spans Cenomanian and Turonian time (Jaillard & Sempere, in press). Near the locality of Macha, 90 km north-northwest of Potosí, L. Branisa found minute pharyngeal teeth which are tentatively assigned to cf. Cyprinodontiformes or Pycnodontiformes (Gayet, 1991).

D. AROIFILLA FORMATION

The continental Aroifilla Formation overlies the marine Cenomanian-Turonian age Miraflores Formation and underlies the Santonian-late Campanian age Chaunaca Formation; it is therefore considered Coniacian and possibly early Santonian in age (Fig. 1). A series of four footprints of a large quadrupedal dinosaur were discovered by the Brigada 10 of YPFB at Calerías, 4 m below the "basal limestone" of the Chaunaca Formation. The footprints were imprinted in soft sediment and are otherwise indeterminate.

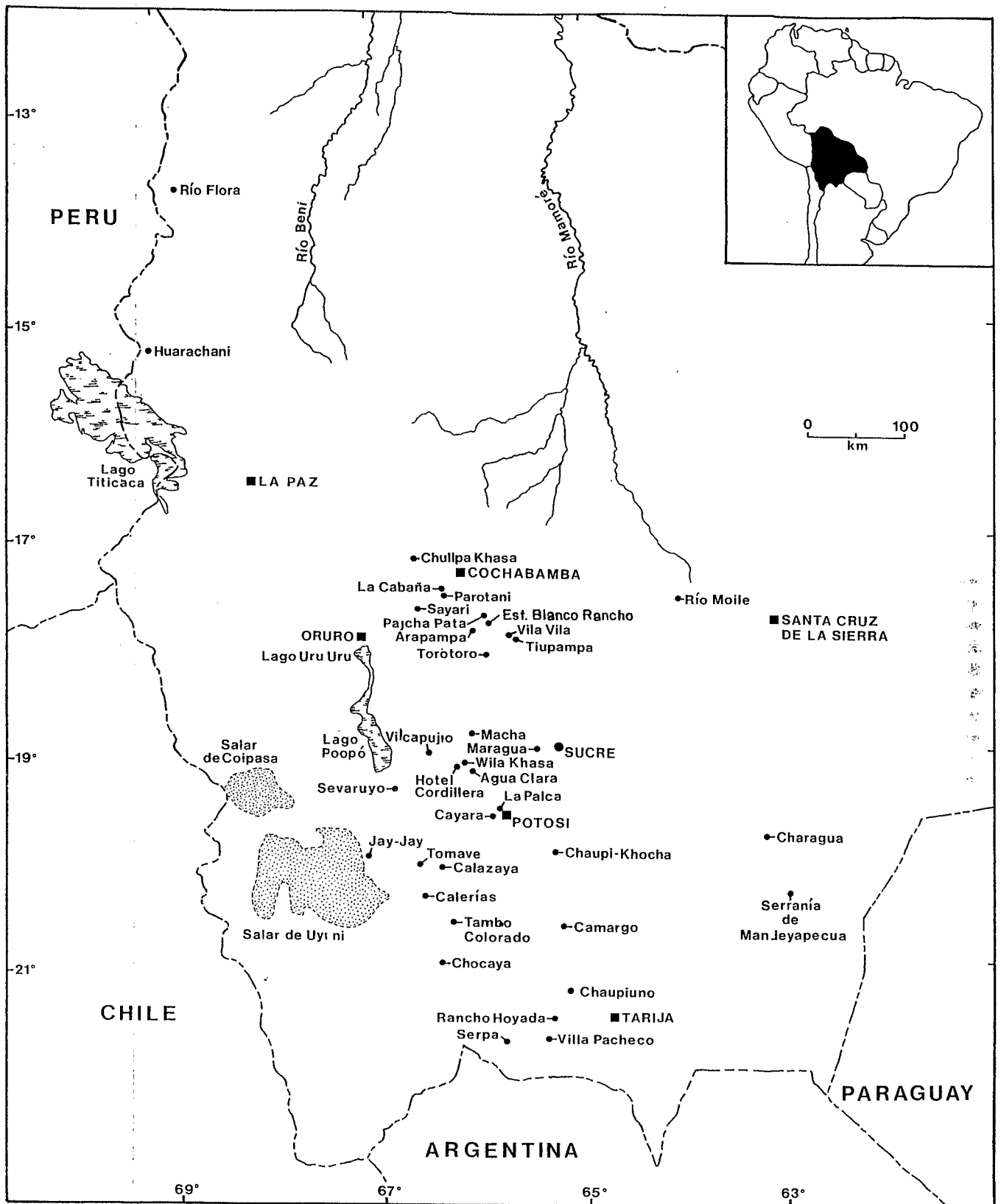


Figure 2. Map of Bolivia showing vertebrate localities of middle Triassic-Paleocene age.

E. CHAUNACA FORMATION

The Santonian-middle Campanian age Chaunaca Formation has yielded microfossils (estheries, ostracods, charophytes) and bivalves (Mytilidae, *Brachidontes* sp.) (Branisa *et al.*, 1966). At La Palca, about 8 km northwest of Potosí, a tooth of an indeterminate pycnodontiform fish (Pycnodontidae) was discovered in a red, very fine-grained sandstone level (Gayet, 1991). At Agua Clara, about km 95 on the Potosí-Challapata-Oruro road, Branisa reportedly found a hypocoracoid of the clupeiform fish *Gasteroclupea branisai*, although this needs confirmation (Branisa *et al.*, 1964).

F. EL MOLINO FORMATION

All three members of the El Molino Formation have yielded diverse vertebrate faunas which were long interpreted to indicate a late Campanian-Maastrichtian age for this entire rock unit (Cappetta 1975, 1990; Muizon *et al.*, 1983; Muizon, *et al.*, 1984a; Marshall *et al.*, 1985; Gayet, 1986a, 1988a; Carrasco *et al.*, 1989). However, Paleocene palynological assemblages are reported from the Tunal Formation of northwestern Argentina (Quattrochio *et al.*, 1986) which is a stratigraphic equivalent of the upper El Molino Formation, and secure Cretaceous age taxa are recognized only in the lower member and basal middle member of the El Molino (see below). Van Valen (1988) has argued that at least some, if not all, of the faunas of the El Molino Formation are of early, but not earliest, Paleocene age. His arguments relied in large part on the belief by Muizon *et al.* (1983) and others, that the Tiupampa vertebrates all come from the El Molino Formation. However, recent stratigraphic studies conclusively demonstrate that the mammal-bearing level at Tiupampa belongs to the Santa Lucía Formation (Sempere and Marshall, in press). For reasons documented below, the El Molino Formation as herein defined encompasses latest Campanian-early Paleocene time (Fig. 1).

1. Agua Clara-Potosí Region

At La Palca, about 8 km northwest of Potosí, a partial crocodile jaw identified as *Dolichochoamps minima* (Dolichochoampsidae) by Buffetaut (1987) was collected from the upper El Molino. This genus and species were named by Gasparini & Buffetaut (1980) on the basis of specimens collected from the upper part of the late Cretaceous-early Paleocene age Yacoraite Formation in Salta Province, northwest Argentina. Remains of Siluriformes (Ariidae, *Rhineastes* sp.) were recovered from the upper El Molino at the same La Palca locality (Gayet, 1991).

From the lower El Molino, about 67 m above the base of the formation along the road to Cayara, about 15 km west-northwest of Potosí, disarticulated Clupeiformes (*Gasteroclupea branisai*) were recovered from a black shale. At Cayara in the same lower member, but from a different level, has come a rich selachian fauna, including Sclerorhynchidae (*Pucapristis branisi*, *Ischyrrhiza hartenbergeri*, *Schizorhiza* aff. *stromeri*), Dasyatidae (*Dasyatis molinoensis*, *Dasyatis schaefferi*), and Rhombodontidae (*Pucabatis hoffstetteri*) (Cappetta, 1991). The type locality of the clupeiform fish *Gasteroclupea branisai* Signeux (in Branisa *et al.*, 1964) is in the lower member at Cerro Muyurina south of Hacienda Cayara.

Other poorly preserved and indeterminate teleosts were recovered in association with *Gasteroclupea* in the same grey-green shales (Wenz, 1969). From the upper El Molino, at the same locality, are several calcareous and hard sandstone levels with siluriform (Ariidae) fishes, turtles and crocodiles.

From Agua Clara, about 60 km northwest of Potosí, numerous marine and/or freshwater taxa were recovered from levels belonging to the lower El Molino. Just below the uppermost stromatolite level at this locality (Ahlfeld & Branisa, 1960) is a calcareous conglomerate of limited extension with a rich assemblage of marine and freshwater fishes including: selachians (Cappetta, 1991) (Dasyatidae, *Dasyatis* nov. sp. 1; Sclerorhynchidae, *Ischyrrhiza hartenbergeri*, *Schizorhiza* aff. *stromeri*; Rhombodontidae, *Pucabatis* nov. sp.); "holosteans" (Gayet, 1982a, 1987a, 1991) (Pycnodontiformes, Pycnodontidae indet.; Semionotiformes, Semionotidae, nov. gen.; Ginglymodi, Lepisosteidae, *Lepisosteus* sp.); teleosts (Branisa *et al.*, 1964; Gayet, 1982b, 1982c, 1991; Gayet & Meunier, 1983); Clupeiformes, Clupeidae, *Gasteroclupea branisai*; Osteoglossiformes, Osteoglossidae, *incertae sedis*; "Salmoniformes", Enchodontidae, *Enchodus* sp., family *incertae sedis* 1, *?Apateodus* sp., family *incertae sedis* 2, gen. and sp. indet.; Cypriniformes, family *incertae sedis*, *Molinichthys inopinatus*; Characiformes, Erythrinidae, cf. *Hoplias*, Characidae, Tetragonopterinae; Siluriformes, Ariidae, *Rhineastes* sp.; cf. Cyprinodontiformes; Tetraodontiformes, Eotrigonodontidae, *Stephanodus minimus*; and teleosts indet.

Just above the same uppermost stromatolite level are two levels of green marls with *Gasteroclupea branisai* and smooth-shelled ostracods. The recovery of a complete fish specimen testifies to the absence of postmortem movement. About 1 m above the same stromatolite level are two calcareous beds with tiny fish bones mostly concentrated in a 2 mm-thick layer on the top of each bed, in which remains of Clupeiformes (Clupeidae, *Gasteroclupea branisai*), Cypriniformes (family *incertae sedis*, *Molinichthys inopinatus* Gayet, 1982b), Siluriformes (Ariidae, *Rhineastes* sp.) and Tetraodontiformes (Eotrigonodontidae, *Stephanodus minimus*; Gayet, 1991) were recovered.

Further along the "quebrada" are several calcareous levels in the lower El Molino with Siluriformes, and green shales with Clupeiformes (*Gasteroclupea branisai*) generally associated with ostracods and sometimes fragments of indeterminate plants.

Following the road to Challapata are three additional localities. The first is near Wila Khasa in a curve of the road at about km 100, northwest of Potosí, which corresponds to the basal sequence of the lower El Molino. Between the last two stromatolite horizons is a restricted level with a few small complete cf. cyprinodontiform fishes (Gayet, 1986a, 1991).

A little further, on the left side of the road 600 m south of the village of Wila Khasa, is the locality Hotel Cordillera (Gayet, 1982a, 1982c) where, in a grey limestone bed of the basal middle El Molino were found a few reptiles (crocodiles, indeterminate vertebrae) and fishes. Selachians are represented by *Pucapristis branisi*, *Ischyrrhiza hartenbergeri*, *Schizorhiza* aff. *stromeri*, *Dasyatis branisai* and *D. schaefferi* (Cappetta, 1991). The teleosts and holosteans are identical to those of the lower El Molino at Agua Clara (see above), while some teeth of Characiformes (Serrasalminidae, Myleinae) are also represented. Nearly all bones found in this level belong to a

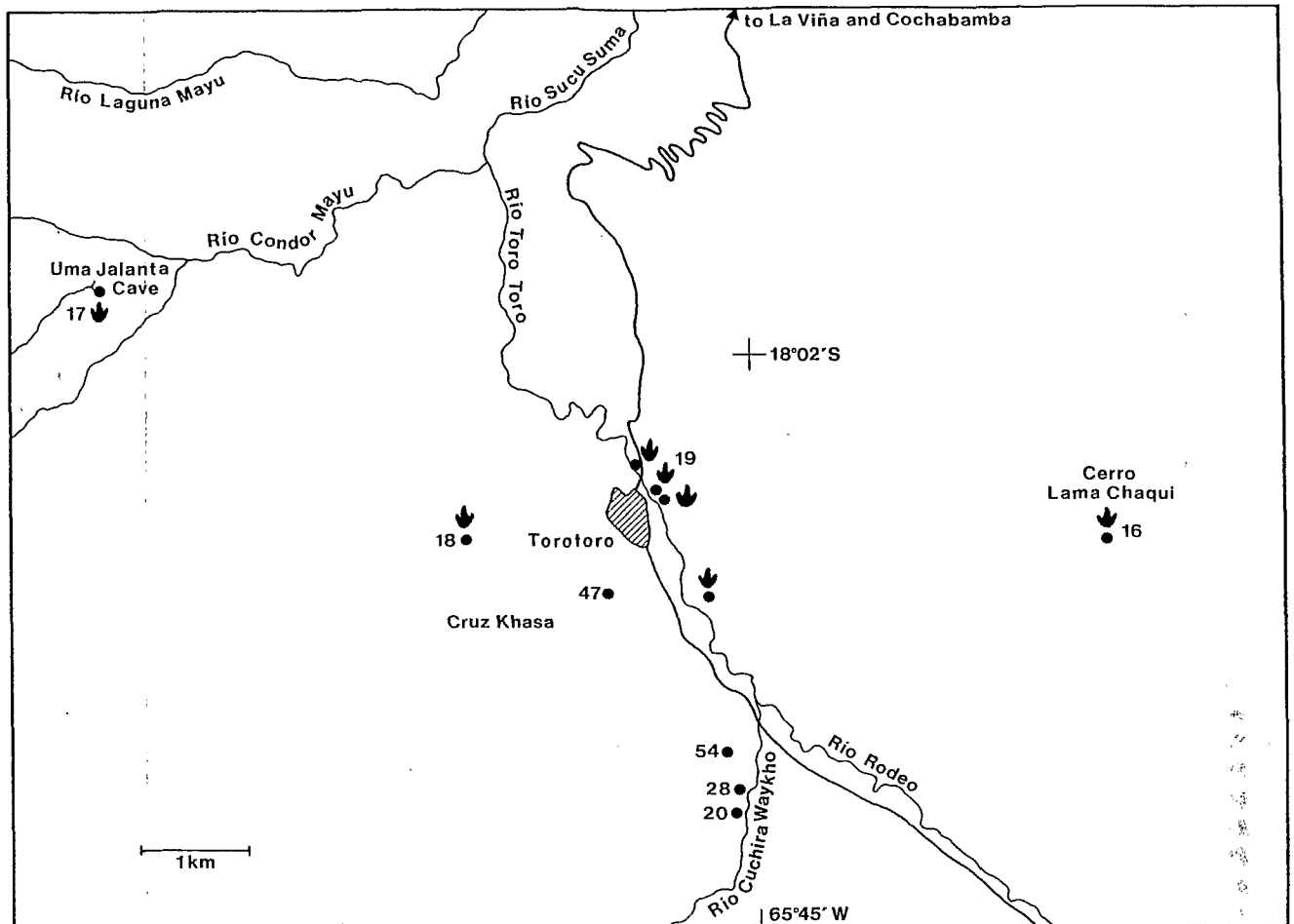


Figure 3. Detailed map of the Torotoro area (for location, see Fig. 2) showing vertebrate localities in the El Molino and Santa Lucía formations. The numbers correspond to those in Table 1. Based on Carta Nacional, Bolivia, Torotoro Quadrangle, Hoja 6439 IV, serie H731, 1/50,000, 1968 edition, Instituto Geográfico Militar, La Paz VIII-68; and San Vicente Quadrangle, Hoja 6439 I, serie H731, 1/50,000, 1968 edition, Instituto Geográfico Militar, La Paz III-68.

siluriform (Ariidae, *Rhineastes* sp.) of very large size (more than 2 m in total length). Vertebrae of *Lepisosteus* sp. found in association with the Siluriformes are also larger (more than 3 cm-long) than those of Agua Clara (about 1 cm-long). As in some levels at Agua Clara, the presence of selachians, pycnodontiforms, tetraodontiforms and "salmoniforms" (*Enchodus* sp., ?*Apateodus* sp.) testifies to some communication to a sea (Gayet, 1991; Gayet *et al.*, 1992).

Ten meters below the calcareous level just described, a restricted conglomeratic unit was recently found with remains of Siluriformes (Ariidae) and Teleostean indet. A little farther, at the crossing of the Quebrada Saytu Jokhu with the road, are grey-green mudstones of the upper El Molino with remains of Clupeiformes (*Gasteroclupea branisai*) and ostracods (Gayet, personal observation).

At Vilcapujio (=Wila Apacheta), at about km 140 northwest of Potosí on the Potosí-Challapata-Oruro road, is a bone bed probably belonging to the basal middle El Molino which yielded fishes

(Pycnodontiformes; Characiformes, Serrasalminae, Myleinae; Siluriformes, Ariidae, *Rhineastes* sp.) and reptiles (turtles and crocodiles). In the vicinity have also been found several levels with holostean Ginglymodi (Lepisosteidae), teleostean Clupeiformes (Clupeidae, *Gasteroclupea branisai*), Characiformes (Serrasalminae, Myleinae), Siluriformes (Ariidae, *Rhineastes* sp.), and/or reptiles (crocodiles, turtles).

At Sevaruyo, south of Lake Poopó, about 120 km west-northwest of Potosí, are reported two levels with remains of *Gasteroclupea* sp. (Branisa *et al.*, 1964). The first level apparently belongs to the lower El Molino. Because of the large (double) size of the hypocoracoids found in the second level relative to *Gasteroclupea*'s holotype, Branisa *et al.* (1964) questioned the age of this level. However, hypocoracoids of very large size have also been found at Agua Clara where a transitional series exists that includes all sizes recorded at other localities.

2. Uyuni Region

At the localities of Jay-Jay, Calazaya and Tomave, respectively north-northwest, east and northeast of Uyuni, were found remains of Siluriformes (Ariidae, *Rhineastes* sp.; Tomave only) and Clupeiformes (*Gasteroclupea branisai*) by the Brigada 10 of YPFB (specimens in CTP, Santa Cruz). At Tambo Colorado, southeast of Uyuni, was found a selachian (*Pucapristis* sp.) associated with gastropods (*Melania potosiensis*; specimens in CTP, Santa Cruz). With the exception of Calazaya which is upper El Molino, the stratigraphic position of fossils at the other localities have not yet been established.

3. Southern Region

In the Río Angosto, 9 km south-southwest of Chocaya, holostean Ginglymodi (Lepisosteidae, *Lepisosteus* sp.), Semionotiformes (Semionotidae, nov. gen.), teleostean Clupeiformes (Clupeidae, *Gasteroclupea branisai*) and Siluriformes (Ariidae, *Rhineastes* sp.) were recovered from the lower El Molino.

In Quebrada Taxisca, 1 km west of Rancho Hoyada along the Río San Juan del Oro, 29 km north-northeast of Tojo, were recovered remains of holostean Pycnodontiformes (Pycnodontidae, indet.), Ginglymodi (Lepisosteidae, *Lepisosteus* sp.), teleostean Osteoglossiformes (Osteoglossidae, indet.), Siluriformes (Ariidae, *Rhineastes* sp.) and Tetraodontiformes (Eotrigonodontidae, *Stephanodus minimus*) (Gayet, 1991) from the lower El Molino. The same Pycnodontidae, Osteoglossidae, Ariidae and Eotrigonodontidae, plus two new selachians (*Dasyatis* nov. sp. 2 et 3; Cappetta, 1991) and a crocodile tooth were recovered from the basal middle El Molino at the same locality.

Fish remains, including *Pucapristis branisi*, have also been found by J. Blanco (YPFB, Brigada 10) near Serpa about 35 km south of Tupiza, and dinosaur trackways were observed by Leonardi (1981) near Camargo, 100 km north of Rancho Hoyada.

4. Cochabamba Region

At Torotoro, about 95 km south-southeast of Cochabamba, several fossil levels are known (Fig. 3). From the middle part of the lower El Molino some 3 km south-southeast of Torotoro, Cappetta (1975) described numerous selachians [Sclerorhynchidae, *Pucapristis branisi*, *Ischyrliza hartenbergeri*; Dasyatidae, *Dasyatis branisai*, *D. molinoensis*, *D. schaefferi*; Rhombodontidae, *Pucabatis hoffstetteri* (Cappetta, 1987)] and Broin (1991) recorded turtles (Podocnemididae, *?Roxochelys* sp.).

In a higher level in the same member, on the northeast side of Torotoro, numerous dinosaur trackways were found that have been called the "pista de danzas" (Fig. 3). At least five types of dinosaurs are represented, including sauropods, theropods and ornithopods (Branisa, 1968; Leonardi, 1981); one trackway named *Ligabueichnium bolivianum* represents an ankylosaur or ceratopsian (Leonardi, 1984).

Near the base of the lower El Molino at Uma Jalanta, close to the cave entrance, about 5 km west-northwest of Torotoro, occur some small tridactyle (Coelurosauria?) footprints and isolated bones of turtles (*?Roxochelys* sp.). At Cerro Llama Chaqui, about 4.3 km east

of Torotoro, occur several sets of trackways of a small theropod dinosaur (Coelurosauria?). The same type of trackway occurs near the top of the lower El Molino on the path to Uma Jalanta, about 2 km west of Torotoro.

From the transgressive base of the middle El Molino in the Río Cuchira Waykho, 3 km south-southeast of Torotoro, a long rostrum of a "salmohiform" (family indet. 2, gen. and sp. indet.; Gayet 1991) is assigned to the marine Cretaceous suborder Ichthyotringoidei (*sensu* Goody, 1969).

From an undetermined member at Cruz Khasa, on the west side of the cemetery south of Torotoro, remains of *Pucapristis* sp., crocodiles and turtles (*?Roxochelys* sp.) have been recovered (R. Céspedes, personal communication; specimens in Museo de Historia Natural, Cochabamba).

At Tiupampa, located about 95 km southeast of Cochabamba, two fossil levels are known (Fig. 4). The lowest, near Hera Mokho, is about 90 m above the base of the Cretaceous section from a calcareous sandstone horizon of the middle El Molino (see Marshall *et al.*, 1985, Fig. 4); vertebrates are represented only by a selachian (Dasyatidae, *Dasyatis schaefferi*) and an indeterminate crocodile (Marshall *et al.*, 1985). There are also abundant gastropods (Melanidae, *Melania potosiensis*) which unfortunately are not useful for age resolution (Ahlfeld & Branisa, 1960). Higher in the section, along the Río Pucarani, is an upper El Molino bone bed with Siluriformes (Ariidae, *Rhineastes* sp.), indeterminate turtles and crocodiles.

At Vila Vila (=Villa Viscarra), about 90 km southeast of Cochabamba and 6 km northwest from Tiupampa, a fossil level in the lower El Molino about 100 m above the base of the Cretaceous section (see Marshall *et al.*, 1985, Fig. 4) has yielded some of the same selachians recorded by Cappetta (1975) from the lower El Molino at Torotoro (*Pucapristis branisi*, *Ischyrliza hartenbergeri*, *Pucabatis hoffstetteri*); numerous actinopterygian fishes: holostean Pycnodontiformes (Pycnodontidae, indet.), Semionotiformes (Semionotidae, nov. gen.); teleostean Characiformes (Serrasalminae, Myleinae), Siluriformes (Ariidae, *Rhineastes* sp., Andinichthyidae indet.), cf. Cyprinodontiformes; Brachiopterygii (=Cladistia), Polypteriformes (Polypteridae, *Dajetella sudamericana*; Gayet & Meunier, 1991a, b, c); Dipnoi (Lepidosirenidae, *Lepidosiren* cf. *paradoxa*; Schultze, 1991a); a turtle (Podocnemididae, *?Roxochelys* cf. *vilavilensis*; Broin, 1991), and two indeterminate crocodiles (Marshall *et al.*, 1985).

Two new localities were discovered during the 1989 field season, Estancia Blanco Rancho and Pajcha Pata, midway along the Cliza-Anzaldo road, about 40 km southeast of Cochabamba. At Pajcha Pata (lower El Molino) were recovered remains of selachians (*Pucabatis hoffstetteri*, *Pucapristis branisi*), "holostean" Pycnodontiformes (Pycnodontidae, *Coelodus toncoensis*; Lepisosteidae, *Lepisosteus* sp.; ganoid holostean scales), Clupeiformes (*Gasteroclupea branisai*), Siluriformes (Ariidae, *Rhineastes* sp.; Andinichthyidae, indet.), cf. Cyprinodontiformes, numerous bones belonging to as yet unidentified small teleosteans, lungfish teeth (Lepidosirenidae, *Lepidosiren* cf. *L. paradoxa*), amphibian Anura, one vertebra which could be an atypical Urodela, two other vertebrae which have the morphology of a Urodela but are procoelic (the vertebrae of Urodela are always opisto- or amphicoelic), probably a snake, a tooth of a small theropod

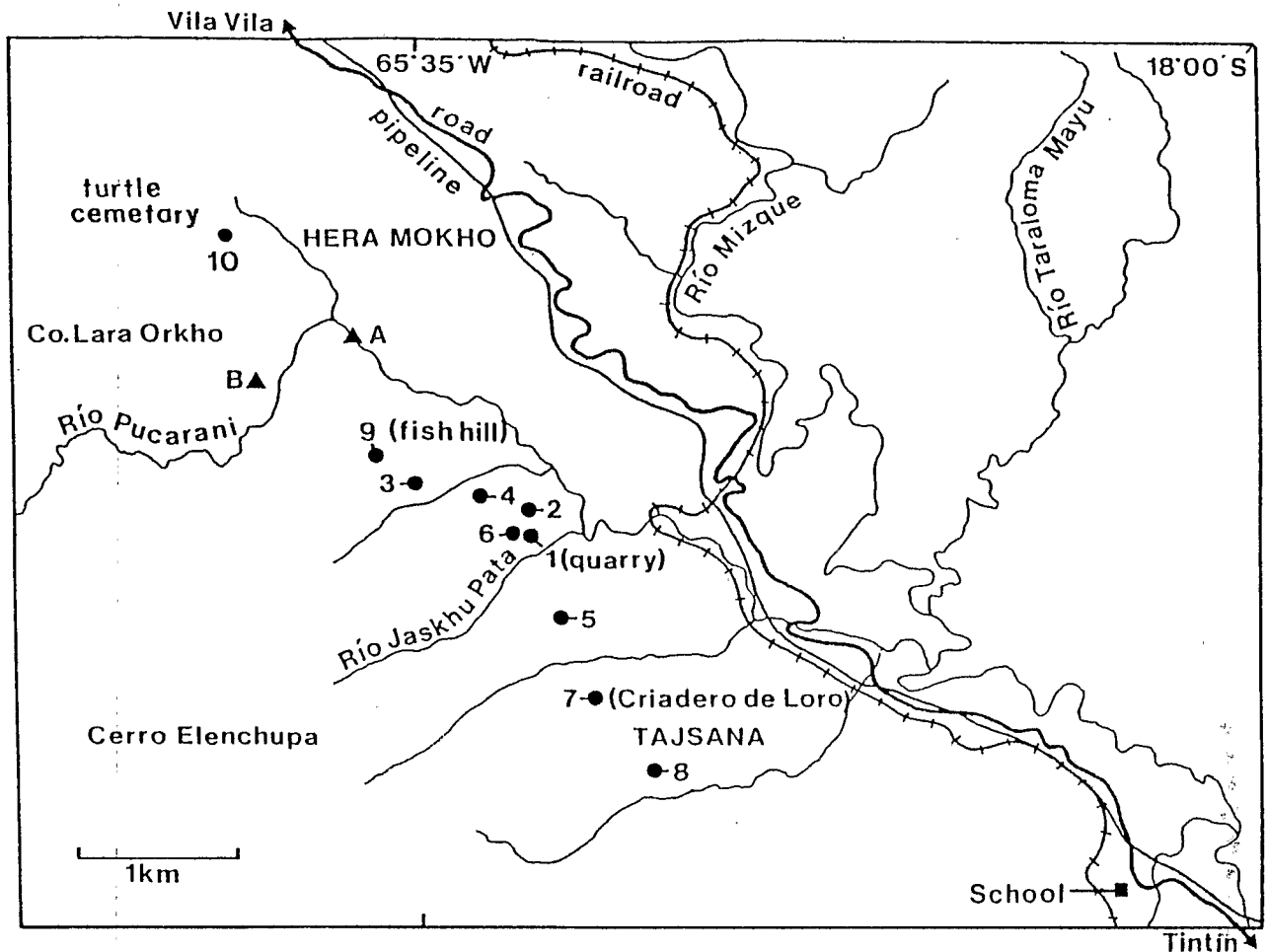


Figure 4. Detailed map of the Tiupampa area (for location, see Fig. 2) showing localities (1-9) from the principal vertebrate level of the Santa Lucía Formation, and localities in the middle (A) and upper (B) El Molino Formation. Tiupampa is the local name used by Quechua Indians for the area shown on the map. Based on Carta Nacional, Bolivia, San Vicente Quadrangle (see caption to Fig. 3).

(Coelurosauria; Marshall, 1989b), indeterminate turtles, various crocodiles and indeterminate trackways. At Blanco Rancho (upper El Molino) were found Clupeiformes (*Gasteroclupea branisai*), Siluriformes (Ariidae, *Rhineastés* sp.), cf. Cyprinodontiformes, turtles and numerous ostracods.

Trackways of small bipedal dinosaurs (Coelurosauria?) are recorded from Arapampa at Cerrito de Llamachaqui, Department of Potosí (Leonardi, 1981).

Fragments of large bones, possibly of dinosaurs, and "dientes de tipo cónico simple" were observed in a level with gastropods in the El Molino Formation near La Cabaña, north of Parotani and west of the Río Rocha about 35 km southwest of Cochabamba (Ahlfeld & Branisa, 1960).

Leonardi (1981: 935) reports a series of six poorly preserved footprints of a bipedal dinosaur in the Santa Lucía Formation along the Cochabamba-La Paz road near Parotani in the Suticollo Syncline,

southeast of Cochabamba. These are apparently the same footprints described by Marshall & Molina (1990) from the lower El Molino Formation 4 km south-southeast of Santivañez and 10 km east of Parotani. The best preserved footprints appear referable to an ornithopod, probably of the family Hadrosauridae, while others may represent a small theropod, possibly a coelurosaur.

From Sayari at km 87 on the road from Cochabamba to Oruro, R. Céspedes recovered remains of a selachian (*Pucapristis branisi*), a siluriform (Ariidae, *Rhineastes* sp.) and an indeterminate turtle from the lower El Molino (specimens in the Museo de Historia Natural, Cochabamba).

Chullpa Khasa, 6 km southwest of Morochata, has yielded a fish mandible (Osteoglossiformes, Osteoglossidae, Phareodontinae) and remains of reptiles (turtles, crocodiles) from an undetermined El Molino member.

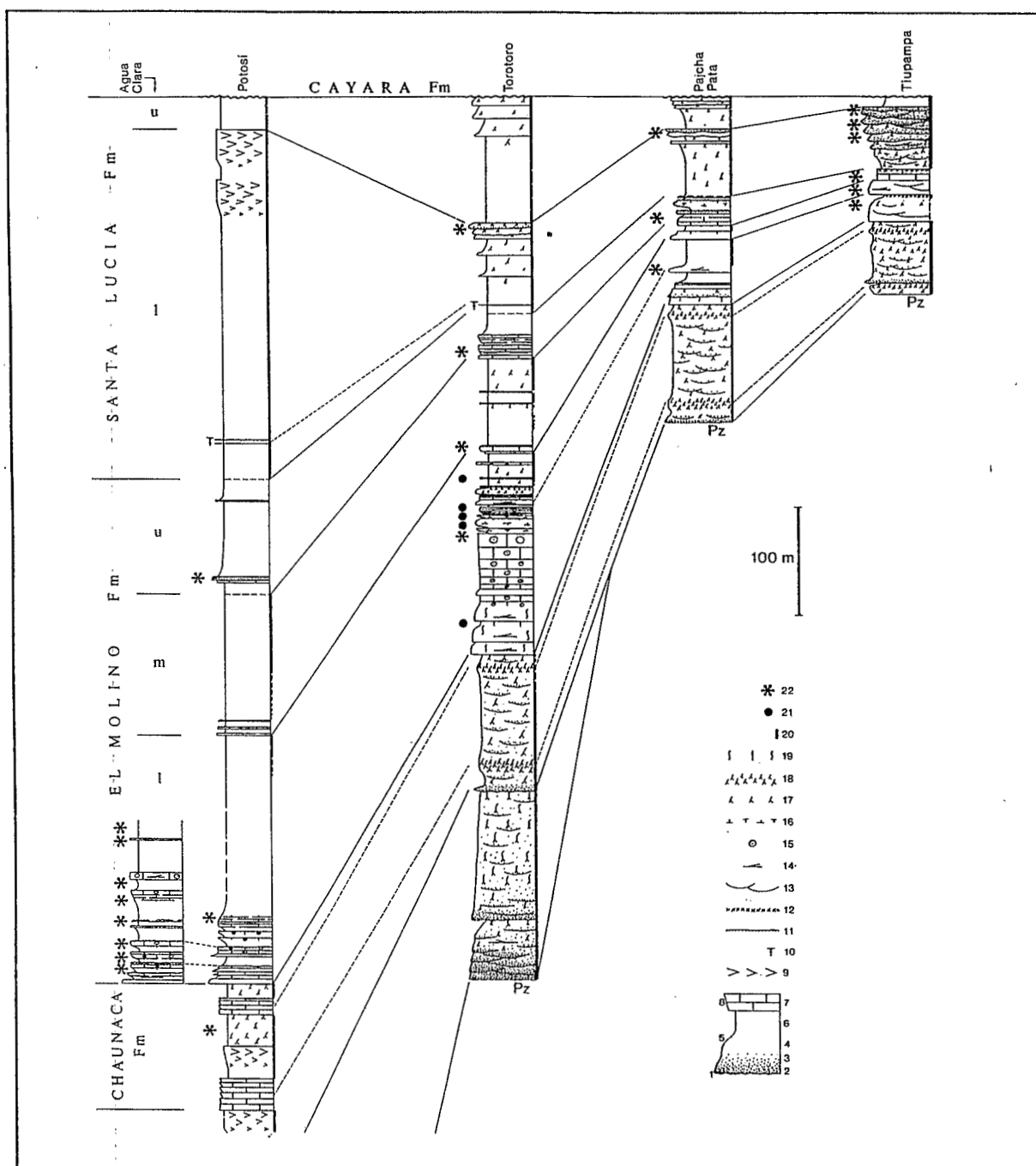


Figure 5. Stratigraphic sections of late Cretaceous-Paleocene rock units at Tiupampa, Pajcha Pata (+ Estancia Blanco Rancho), Torotoro (+ Caranota), Potosí (road to La Palca and Cayara) and, in part, Agua Clara, showing location of main fossiliferous levels. Undecompressed thicknesses. The base of the unconformable Cayara Formation is held horizontal. Fm, Formation; l, lower; m, middle; u, upper; Pz, Paleozoic. 1, erosional surface; 2, conglomerates; 3, conglomeratic sandstones; 4, sandstones; 5, fining and/or thinning-upward; 6, siltstones and mudstones; 7, carbonates (mostly limestones); 8, coarsening and/or thickening-upward; 9, gypsum; 10, tuffite bed; 11, stromatolitic level; 12, dissolution breccia; 13, channels; 14, cross-bedding; 15, ooids; 16, calcareous cement; 17, rooting; 18, coalescent rhizolith-rich levels; 19, bioturbation; 20, red color predominant; 21, dinosaur trackways; 22, vertebrate-bearing levels. All sections measured by T. Sempere, except parts of Torotoro-Caranota and Potosí (respectively by the Brigadas 10 and 9 of YPF) and of Pajcha Pata and Agua Clara (by G. Camoin and J. M. Rouchy); all were checked by the authors.

5. Huarina fold-thrust belt

A vertebrate fauna described originally as of possible Paleocene age was reported from the northern flank of the Huarachani syncline, just north of the pueblo Huarachani along the Bolivia-Peru border north of Lake Titicaca (Argollo *et al.*, 1987). The fauna includes a fish (Osteoglossomorpha, Osteoglossidae, Phareodontinae; Gayet, 1987b, 1991) and a crocodile vertebra (Mesosuchia, Dyrosauridae, gen. and sp. indet.). However, these fossils come from the middle member of the El Molino Formation (called Ococoya Formation in this area; Fig. 1), and are therefore of late Cretaceous age (Martinez, 1980: 183; Gayet, 1987b; Mourier *et al.*, 1986, 1988: 171; see below).

6. Northern Subandean belt

About 60-70 m above the base of the late Cretaceous age Eslabón Formation (=Flora Formation s.l. of Perry, 1963), from levels that can be correlated to the lower El Molino, along the Río Flora, 315 km north-northwest of La Paz, were collected remains of *Pucapristis* sp. (=Onchopristis), *Gasteroclupea branisai* and charophytes (including *Peckichara compressa*) (Perry, 1963; Dávila & Ponce de León, 1971). In the same area, *Gasteroclupea branisai* was recovered from the overlying Flora Formation s.s., an equivalent of the upper El Molino (Vernet & Botello, 1975).

7. Central Subandean belt

Sanjinés-Saucedo (1982) and López (1983) reported remains of *Gasteroclupea branisai* from the Cajones Formation (partly or totally equivalent to the El Molino Formation; Fig. 1) in the Moile Syncline along the Río Moile about 95 km west-northwest of Santa Cruz. The level in which the fossils were found probably represents the upper El Molino.

G. SANTA LUCIA FORMATION

The richest vertebrate fauna, in terms of both number and quality of specimens, is from Tiupampa about 95 km southeast of Cochabamba (Figs. 2, 4). Two fossil levels at Tiupampa belong to the basal middle and upper El Molino (see above). A third fossil level is located about 130 m above the base of the Cretaceous section (see Marshall *et al.*, 1985, Fig. 4). Sempere & Marshall (in press) demonstrate that this main fossil level, which represents the type fauna of the Tiupampian Land Mammal Age (Marshall, 1989a) belongs to the Santa Lucía Formation (see Figure 5). The following vertebrate taxa are recorded:

a) Fishes (Gayet, 1988b, 1990, 1991; Gayet & Meunier, 1991a, 1991b, 1992; Schultze, 1991a): teleostean Clupeiformes (Clupeidae, *Gasteroclupeinae*, *Gasteroclupea branisai*), Osteoglossiformes (Osteoglossidae, Phareodontinae, *Phareodusichthys tavernei*; Osteoglossinae, *incertae sedis*) (Hiodontidae *sensu* Muizon *et al.*, 1983 is a confusion with Osteoglossinae; Gayet, 1991), Characiformes (Characidae, Tetragnopterinae, indet., cf. Rhoadsiinae; Serrasalminae, Serrasalminae, Myleinae; Erythrinidae, *Hoplias* nov. sp.), Siluriformes (Ariidae, *Rhineastes* sp.; Andinichthyidae, *Andinichthys bolivianensis*; families *incertae sedis*

1 and 2, *Hoffstetterichthys pucai* and *Incaichthys suarezi*), Perciformes (Centropomidae), Polypteriformes (Polypteridae, *Dajetella sudamericana*) and Dipnoi (Ceratodontidae, *Ceratodus* sp. and ceratodont n. g., n. sp.; Lepidosirenidae, *Lepidosiren* cf. *paradoxa*).

b) Amphibians (Rage, 1986, 1991a): Anura (Leptodactylidae); Gymnophiona (family indet.).

c) Turtles (Broin, 1988, 1991): Podocnemididae, *Roxochelys* cf. *vilavilensis*.

d) Lizards (Rage, 1991b): Lacertilia, ?Iguanidae and family indet.

e) Snakes (Rage, 1991b): Aniliidae n. g.; Boidae, two species indet.; ?Madtsoiidae; Tropidophiidae.

f) Crocodiles (Buffetaut, 1991; Buffetaut & Marshall, 1991): Mesosuchia, Sebecidae, *Sebecus querejazus*; Dyrosauridae, *Sokotosuchus* aff. *ianwilsoni*.

g) Mammals (Muizon *et al.*, 1983; Muizon, *et al.*, 1984a, b; Marshall *et al.*, 1983a, 1985, 1989; Muizon & Marshall, 1985, 1987a, b, c, d, 1988, 1991, in press; Marshall, 1992; Marshall & Muizon, 1988, 1992): Deltatheroidea (family indet., *Jaskhadelphys minutus*), Peradectia (Peradectidae, Peradectinae, *Peradectes austrinum*; Caroloameghiniinae, *Roberthoffstetteria nationalgeographica*), Microbiotheria (Microbiotheriidae, *Khasia cordillerensis*), Didelphimorphia (Didelphidae, Didelphinae, *Pucadelphys andinus*, *Incadelphys antiquus*, *Mizquedelphys pilpinensis*; Eobrasiliinae, *Tiulordia floresi*), Sparassodonta (Hathliacynidae, *Allqokirus australis*), Paucituberculata (Kollpaniidae, *Kollpania tiupampina*), order and family indet. (*Andinodelphys cochabambensis*), Leptictida (Palaeoryctidae?, cf. *Cimolestes* sp.), Pantodonta (Pantolambidae, *Alcidedorbignya inopinata*), Condylarthra (Hyopsodontidae, Mioclaeninae, *Tiulaenus minutus*, *Molinodus suarezi*, *Pucanodus gagnieri*, *Andinodus boliviensis*), and Notoungulata (cf. Henricosborniidae or Oldfieldthomasiidae, gen. et sp. indet.).

Criadero de Loro, a new locality about 1.2 km south-southeast of the quarry at Tiupampa and from the same horizon (Fig. 4, locality 7), was discovered in 1989. The taxa seem to be the same as those from the quarry and adjacent localities (Fig. 4, localities 1-6, 9) and include, Siluriformes (Ariidae, *Rhineastes* sp.), Perciformes (Centropomidae), Polypteriformes (Polypteridae, *Dajetella sudamericana*), numerous large lungfish teeth (including Ceratodontidae and Lepidosirenidae), snakes (Boidae sp. indet.), turtles (?*Roxochelys vilavilensis*), crocodiles and a pantodont (*Alcidedorbignya inopinata*).

At Vila Vila, from an upper level located about 160 m above the base of the Cretaceous section (see Marshall *et al.*, 1985, Fig. 4), have come a turtle (Podocnemididae, ?*Roxochelys vilavilensis*; Broin, 1971) and a crocodile (Sebecosuchia, Sebecidae, *Sebecus querejazus*; Buffetaut & Marshall, 1991).

At the two newly discovered localities of Estancia Blanco Rancho and Pajcha Pata, south of Cliza (Fig. 2), are bone beds of the lower and/or upper members of the El Molino described above, which are overlain by red sandstones of the Santa Lucía Formation similar to those at Tiupampa (Montaño, 1968). A brief survey of Blanco Rancho resulted in the recovery of numerous teleostean fishes (Osteoglossiformes, Osteoglossidae; Siluriformes, Ariidae, *Rhineastes* sp., Andinichthyidae, indeterminate teleosts), amphibians, crocodiles (Dyrosauridae, complete skulls), turtles

TABLE 1. VERTEBRATE FOSSIL LOCALITIES OF MESOZOIC AND PALEOCENE AGE IN BOLIVIA ARRANGED BY STRATIGRAPHIC OCCURRENCE.

TACURU GROUP

1. Serranía de Mandeyapeca

CASTELLON FORMATION

2. Quebrada de Charagua

MIRAFLORES FORMATION

3. Macha

AROIFILLA FORMATION

4. Calerías (dinosaur footprints)

CHAUNACA FORMATION

5. Agua Clara
6. La Palca

EL MOLINO FORMATION

LOWER MEMBER

7. Agua Clara
8. Cayara (Cerro Muyurina)
9. Chocaya (Río Angosto)
10. Hotel Cordillera near Wila Khasa; Quebrada Saytu Jokhu with *Gasteroclupea*
11. La Palca (black shale level with *Gasteroclupea*, and below stromatolites)
12. Pajcha Pata
13. Rancho Hoyada (Quebrada Taxisca)
14. Sayari (km 87)
15. Sevaruyo
16. Torotoro (Cerro Llama Chaqui, dinosaur footprints)
17. Torotoro (Uma Jalanta cave, dinosaur footprints)
18. Torotoro (Uma Jalanta road, dinosaur footprints)
19. Torotoro ("pista de danzas", dinosaur footprints)
20. Torotoro (selachian level)
21. Vila Vila (*Pucapristis* level)
22. Wila Khasa (km 100)
23. Río Flora
24. Parotani (=Santivañez) (dinosaur footprints)

MIDDLE MEMBER

25. Hotel Cordillera (near Wila Khasa)
26. Huarachani
27. Rancho Hoyada (Quebrada Taxisca)
28. Tiupampa (Hera Mokho)
29. Torotoro (Río Cuchira Waykho)
30. Vilcapujio (Wila Apacheta)

UPPER MEMBER

31. Calazaya
32. Cayara (Cerro Muyurina)
33. La Palca (*Dolichochampsia minima* level)
34. Pajcha Pata
35. Estancia Blanco Rancho
36. Río Flora
37. Río Moile
38. Tiupampa (Río Pucarani)

INDETERMINATE MEMBER

39. Arapampa (dinosaur footprints)
40. Camargo (dinosaur footprints)
41. Chullpa Khasa
42. Jay-Jay
43. Serpa
44. Tambo Colorado
45. Tomave
46. Torotoro (Cruz Khasa)

SANTA LUCIA FORMATION

47. Chaupi Khocha
48. Maragua
49. Pajcha Pata
50. Estancia Blanco Rancho
51. Tiupampa (quarry and associated localities)
52. Tiupampa (Criadero de Loro)
53. Torotoro
54. Vila Vila

IMPORA FORMATION

55. Chaupiuno
56. Villa Pacheco

TABLE 2. SYSTEMATIC LIST OF VERTEBRATES FROM THE MESOZOIC AND PALEOCENE OF BOLIVIA WITH AUTHORSHIP.

CLASS SELACHII

Order Rajiformes

Suborder Sclerorhynchoidei

Family Sclerorhynchidae

Pucapristis branisi Schaeffer, 1963*Ischyrhiza hartenbergeri* Cappetta, 1975*Schizorhiza aff. stromeri* Cappetta, 1975

* Order Myliobatiformes

Family Dasyatidae

Dasyatis branisai Cappetta, 1975*Dasytis molinoensis* Cappetta, 1975*Dasytis schaefferi* Cappetta, 1975*Dasytis* nov. sp. 1*Dasytis* nov. sp. 2*Dasytis* nov. sp. 3

Family Rhombodontidae

Pucabatis hoffstetteri Cappetta, 1975*Pucabatis* nov. sp.

CLASS OSTEICHTHYI

Subclass Actinopterygii

Superorder "Holostei"

Order Pycnodontiformes

Family Pycnodontidae

Coelodus toncoensis Benedetto & Sanchez, 1972

Pycnodontidae indet.

Order Semionotiformes

Family Semionotidae

Lepidotes sp.

nov. gen.

Order Ginglymodi

Family Lepisosteidae

Lepisosteus sp.

Superorder Teleostei

Order Clupeiformes

Family Clupeidae

Gasteroclupea branisai Signeux in Branisa *et al.*, 1964

Order Osteoglossiformes

Family Osteoglossidae

Subfamily Phareodontinae

Phaerodusichthys tavernei Gayet, 1991

Subfamily Osteoglossinae

nov. gen.

Order "Salmoniformes"

Family Enchodontidae

Enchodus sp.

Suborder ichthyotringoidei

Family incertae sedis 1

? *Apateodus* sp.

- Family incertae sedis 2
 - gen. and sp. *indet.*
- Order Cypriniformes
 - Family incertae sedis
 - Molnichthys inopinatus* Gayet, 1982c
- Order Characiformes
 - Family Erythrinidae
 - Hoplias* nov. sp.
 - cf. *Hoplias*
 - Family Serrasalminidae
 - Subfamily Myleinae
 - gen. and sp. *indet.*
 - cf. Subfamily Serrasalminae
 - gen. and sp. *indet.*
 - Family Characidae
 - Subfamily Tetragonopterinae
 - gen. and sp. *indet.*
 - cf. Subfamily Rhoadsiinae
 - gen. and sp. *indet.*
- Order Siluriformes
 - Family Ariidae
 - Rhineastes*
 - Superfamily Andinichthyoidea
 - Family *indet.*
 - nov. gen.
 - Family Andinichthyidae
 - Andinichthys bolivianensis* Gayet, 1988b
 - Family incertae sedis 1
 - Inaichthys suarezi* Gayet, 1990b
 - Family incertae sedis 2
 - Hoffstetterichthys pucai* Gayet, 1990b
 - at least five gen. and sp. nov.
- Superorder Atherinomorpha
 - cf. Order Cyprinodontiformes
 - gen. and sp. *indet.*
- Superorder Acanthopterygii
 - Order Perciformes
 - Suborder Percoidei
 - Family Centropomidae
 - gen. and sp. *indet.*
 - Order Tetraodontiformes
 - Family Eotrigonodontidae
 - Stephanodus minimus* Gayet, 1991
- Subclass Sarcopterygii
 - Order Dipnoi
 - Family Ceratodontidae
 - Ceratodus* sp.
 - gen. and sp. *indet.*
 - Family Lepidosirenidae
 - Lepidosiren* cf. *paradoxa*
- CLASS CLADISTIA (= BRACHIOPTERYGII)
 - Order Polypteriformes
 - Family Polypteridae
 - Dajetella sudamericana* Gayet & Meunier, 1991

CLASS AMPHIBIA

Order Anura

Family Leptodactylidae

gen. and sp. *indet.*

Order Gymnophiona

Family *indet.*

gen. and sp. *indet.*

Order Urodela

Family *indet.*

gen. and sp. *indet.*

CLASS REPTILIA

Order Chelonia

Family Podocnemididae

? *Roxochelys vilavilensis* Broin, 1971

? *Roxochelys cf. vilavilensis*

Order Squamata

Suborder Lacertilia

Family ?Iguanidae

gen. and sp. *indet.*

Family *indet.*

gen. and sp. *indet.*

Suborder Ophidia

Family Aniliidae

gen. and sp. *indet.*

Family Boidae

gen. and sp. 1 *indet.*

gen. and sp. 2 *indet.*

Family ?Madtsoiidae

gen. and sp. *indet.*

Family Tropidopheidae

gen. and sp. *indet.*

Order Crocodilia

Suborder Mesosuchia

Family Sebecidae

Sebecus querejazus Buffetaut & Marshall, 1991

Family Dyrosauridae

Sokotosukus aff. ianwilsoni Halstead, 1975

Suborder Eusuchia

Family Dolichochampsidae

Dolichochampsia minima Gasparini & Buffetaut, 1980

Order Saurischia

Suborder Theropoda

Infraorder Coelurosauria

gen. and sp. *indet.*

Suborder Sauropodomorpha

Infraorder Sauropoda

gen. and sp. *indet.*

Order Ornithischia

Suborder Ornithopoda

gen. and sp. *indet.*

Suborder Ankylosauria or Ceratopsia

Ligabueichnium bolivianum Leonardi, 1984

Order *indet.*

gen. and sp. *indet.*

CLASS MAMMALIA

Infraclass Metatheria

Order Deltatheroidea

Family *indet.*

Jaskhadelphys minutus Marshall & Muizon, 1988

Order Peradectia

Family Peradectidae

Subfamily Peradectinae

Peradectes austrinum (Sigé, 1971)

Subfamily Caroloameghiniinae

Roberthoffstetteria nationalgeographica Marshall *et al.*, 1983

Order Microbiotheria

Family Microbiotheriidae

Khasia cordillerensis Marshall & Muizon, 1988

†Order Didelphimorphia

Family Didelphidae

Subfamily Didelphinae

Pucadelphys andinus Marshall & Muizon, 1988

Incadelphys antiquus Marshall & Muizon, 1988

Mizquedelphys pilpinensis Marshall & Muizon, 1988

Subfamily Eobrasiliinae

Tiulordia floresi Marshall & Muizon, 1988

Order Sparassodonta

Family Hathliacynidae

Allqokirus australis Marshall & Muizon, 1988

Order Polydolopoidea

Family Polydolopidae

Epidolops sp.

Order Paucituberculata

Family Kollpaniidae

Kollpania tiupampina Marshall & Muizon, 1988

Order *indet.*

Family *indet.*

Andinodelphys cochabambensis Marshall & Muizon, 1988

Infraclass Eutheria

Order Leptictida

Family Palaeoryctidae?

cf. *Cimolestes* sp.

Order Pantodonta

Family Pantolambdidae

Alcidedorbignya inopinata Muizon & Marshall, 1987a

Order Condylarthra

Family Hyopsodontidae

Subfamily Mioclaeninae

Tiuclaenus minutus Muizon & Marshall, 1987b

Molinodus suarezi Muizon & Marshall, 1987c

Andinodus boliviensis Muizon & Marshall, 1987c

Pucanodus gagnieri Muizon & Marshall, 1991

Order Notoungulata

Family cf. Henricosborniidae or Oldfieldthomasiidae

gen. and sp. *indet.*

TABLE 3 . SYSTEMATIC LIST OF VERTEBRATES FROM THE MESOZOIC AND PALEOCENE OF BOLIVIA WITH INDICATION OF LOCALITIES AND STRATIGRAPHIC OCCURRENCE BASED ON INFORMATION IN TABLE 1 AND TEXT. Abbreviations: Ca, Castellón Formation; Mi, Miraflores Formation; Ar, Aroifilla Formation; Ch, Chaunaca Formation.

TAXA	Ca Fm	Mi Fm	Ar Fm	Ch Fm	El Molino Formation			Santa Lucía Fm	Impora Fm
					lower member	middle mb	upper member		
Class Selachii									
Order Rajiformes									
Suborder Sclerorhynchoidei									
Family Sclerorhynchidae									
<i>Pucapristis branisi</i>					11, 12, 14, 20, 21	23, 25			
<i>Ischyrhiza hartenbergeri</i>					7, 11, 20, 21	25			
<i>Schizorhiza aff. stromeri</i>					7, 11	25			
Order Myliobatiformes									
Family Dasyatidae									
<i>Dasyatis branisai</i>					20	25			
<i>Dasyatis molinoensis</i>					11, 20				
<i>Dasyatis schaefferi</i>					11, 20	25, 28			
<i>Dasyatis</i> nov. sp. 1					7				
<i>Dasyatis</i> nov. sp. 2						27			
<i>Dasyatis</i> nov. sp. 3						27			
Family Rhombodontidae									
<i>Pucabatis hoffstetteri</i>					11, 20, 21				
<i>Pucabatis</i> nov. sp.					7				
Class Osteichthyes									
Subclass Actinopterygii									
Infraclass "Holostei"									
Order Pycnodontiformes									
Family Pycnodontidae									
<i>Coelodus toncoensis</i>					12				
gen. and sp. indet.		3?		6	7, 12, 13, 21	25, 27, 30			
Order Semionotiformes									
Family Semionotidae									
<i>Lepidotes</i> sp.	2								
gen. and sp. nov.					7, 9, 21		25		
Order Ginglymodi									
Family Lepisosteidae									
<i>Lepisosteus</i> sp.					7, 9, 13		25, 27		
Infraclass Teleostei									
Order Clupeiformes									
Family Clupeidae									
<i>Gasteroclupea branisai</i>				5?	7, 8, 9, 10, 11, 12, 15	25	32, 35, 36, 37	51	

TAXA	Ca Fm	Mi Fm	Ar Fm	Ch Fm	El Molino Formation			Santa Lucía Fm	Impora Fm
					lower member	middle mb	upper member		
Order Osteoglossiformes					7, 13	25, 27		49, 51, 52	
Family Osteoglossidae									
Subfamily Phareodontinae								51	
<i>Phareodusichthys tavernei</i>						26			
Subfamily Osteoglossinae								51	
gen. and sp. nov.									
Order "Salmoniformes"									
Family Enchodontidae					7	25			
<i>Enchodus</i> sp.									
Suborder Ichthyotringoidei									
Family incertae sedis 1					7	25			
? <i>Apateodus</i> sp.									
Family incertae sedis 2									
gen. and sp. indet.						29			
Order Cypriniformes									
Family incertae sedis					7	25			
<i>Molinichthys inopinatus</i>									
Order Characiformes									
Family Erythrinidae								51	
<i>Hoplias</i> nov. sp.					7	25		51	
cf. <i>Hoplias</i>									
Family Serrasalminae									
Subfamily Myleinae					21	25, 30		51	
gen. and sp. indet.									
cf. Subfamily Serrasalminae								51	56
gen. and sp. indet.									
Family Characidae									
Subfamily Tetragonopterinae					7	25		51	
gen. and sp. indet.									
cf. Subfamily Rhoadsiinae								51	
gen. and sp. indet.									
Order Siluriformes									
Family Ariidae					7, 9, 12, 13, 14, 21	25, 27, 30	33, 35, 38	47-52	56
<i>Rhineastes</i> sp.									
Superfamily Andinichthyoidea									
Family indet.								51	
gen. nov.									
Family Andinichthyidae								51	
<i>Andinichthys bolivianensis</i>					12		34, 35	49, 51, 52	
<i>Andinichthys</i> sp.									
Family incertae sedis								51	
<i>Incaichthys suarezi</i>								51	
<i>Hoffstetterichthys pucai</i>									

TAXA	Ca Fm	Mi Fm	Ar Fm	Ch Fm	El Molino Formation			Santa Lucía Fm	Impora Fm
					lower member	middle mb	upper member		
Superorder Atherinomorpha cf. Order Cyprinodontiformes gen. and sp. <i>indet.</i>		3?			7, 12, 22	25	35		
Superorder Acanthopterygii Order Perciformes Suborder Percoidae Family Centropomidae gen. and sp. <i>indet.</i>								50, 51, 52	
Order Tetraodontiformes Family Eotrigonodontidae <i>Stephanodus minimus</i>					7, 13	25, 27			
Subclass Sarcopterygii Order Dipnoi Family Ceratodontidae <i>Ceratodus</i> sp.								53, 54	
Family Lepidosirenidae <i>Lepidosiren</i> cf. <i>paradoxa</i>					12, 21			51, 52	
Class Cladistia (= Brachiopterygii) Order Polypteriformes Family Polypteridae <i>Dajetella sudamericana</i>					21				
Class Amphibia Order Anura Family Leptodactylidae gen. and sp. <i>indet.</i>								51	
Order Gymnophiona Family <i>indet.</i> gen. and sp. <i>indet.</i>								51	
Order Urodela Family <i>indet.</i> gen. and sp. <i>indet.</i>					12				
Class Reptilia Order Chelonia Family Podocnemididae ? <i>Roxochetys vilavilensis</i> ? <i>Roxochetys</i> cf. <i>vilavilensis</i>					14	30	33, 35, 38	48, 49, 50 51-54	55, 56
Order Squamata Suborder Lacertilia Family ?Iguanidae gen. and sp. <i>indet.</i>						20, 21			
Family <i>indet.</i> gen. and sp. <i>indet.</i>								51	
Suborder Ophidia Family Aniliidae gen. and sp. <i>indet.</i>								51	
								51	

TAXA	Ca Fm	Mi Fm	Ar Fm	Ch Fm	El Molino Formation			Santa Lucía Fm	Impora Fm
					lower member	middle mb	upper member		
Family Boidae								51	
gen. and sp. <i>indet.</i> 1								51	
gen. and sp. <i>indet.</i> 2									
Family ?Matsoiidae								51	
gen. and sp. <i>indet.</i>									
Family Tropidopheidae								51	
gen. and sp. <i>indet.</i>									
Order Crocodilia					12, 21	25, 27, 28, 30	33, 38	48-50, 54	
Suborder Mesosuchia									
Family Sebecidae								51	
<i>Sebecus querejazus</i>								54	
Family Dyrosauridae						26		51	
<i>Sokotosaurus aff. ianwilsoni</i>								51	
Suborder Eusuchia									
Family Dolichochampsidae									
<i>Dolichochampsia minima</i>							33		
Order Saurischia									
Suborder Theropoda					19				
Infraorder Coelurosauria									
gen. and sp. <i>indet.</i>					12, 16, 17, 18				
Suborder Sauropodomorpha									
Infraorder Sauropoda									
gen. and sp. <i>indet.</i>					19				
Order Ornithischia									
Suborder Ornithopoda									
gen. and sp. <i>indet.</i>					19, 24				
Suborder Ankylosauria or Ceratopsia									
<i>Ligabueichnium bolivianum</i>					19				
Order Indet.									
gen. and sp. <i>indet.</i>			4						
Class Mammalia									
Infraclass Metatheria									
Order Deltatheroidea									
Family <i>indet.</i>									
<i>Jaskhadelphys minutus</i>								51	
Order Peradectia									
Family Peradectidae									
Subfamily Peradectinae									
<i>Peradectes austrinum</i>								51	
Subfamily Caroloameghiniinae									
<i>Roberthoffstetteria nationalgeographica</i>								51	

TAXA	Ca Fm	Mi Fm	Ar Fm	Ch Fm	El Molino Formation			Santa Lucía Fm	Impora Fm
					lower member	middle mb	upper member		
Order Microbiotheria									
Family Microbiotheriidae								51	
<i>Khasia cordillerensis</i>									
Order Didelphimorphia								50	
Family Didelphidae									
Subfamily Didelphinae								51	
<i>Pucadelphys andinus</i>								51	
<i>Incadelphys antiquus</i>								51	
<i>Mizquedelphys pilpinensis</i>								51	
Subfamily Eobrasiliinae								51	
<i>Tiulordia floresi</i>									
Order Sparassodonta									
Family Hathliacynidae								51	
<i>Allqokirus australis</i>									
Order Polydolopoidea									
Family Polydolopidae								50	
<i>Epidolops sp.</i>									
Order Paucituberculata									
Family Kollpaniidae								51	
<i>Kollpania tiupampina</i>									
Order indet.									
Family indet.								51	
<i>Andinodelphys cochabambensis</i>									
Infraclass Eutheria									
Order Leptictida									
Family Palaeoryctidae?								51	
cf. <i>Cimolestes sp.</i>									
Order Pantodonta									
Family Pantolambdidae								51, 52	
<i>Alcidedorbignya inopinata</i>									
Order Condylarthra									
Family Hyopsodontidae								51	
Subfamily Mioclaeninae								51	
<i>Tiuclaenus minutus</i>								51	
<i>Molinodus suarezi</i>								51	
<i>Andinodus boliviensis</i>								51	
<i>Pucanodus gagnieri</i>									
Order Notoungulata									
Family cf. Henricosborniidae or Oldfieldthomasiidae gen. and sp. indet.								51	

(*?Roxochelys vilavilensis*, complete shells), and mammals (Didelphimorphia, Didelphidae, indet.; Polydolopidea, Polydolopidae, *Epidolops* sp.). Indeterminate turtles and crocodiles were observed at Pajcha Pata.

About 3 km south of Torotoro, remains of lungfish (Ceratodontidae, *Ceratodus* sp.; Lepidosirenidae, *Lepidosiren* cf. *paradoxa*), turtles (*?Roxochelys* cf. *vilavilensis*), crocodiles and an indeterminate mammal were collected from a sequence of fine to medium grained red sands of the Santa Lucía Formation (Marshall *et al.*, 1985; Broin 1991; Schultze, 1991a) (Fig. 3).

At Maragua (18 km west of Sucre) and Chaupi Khocha (11 km west-northwest of San Lucas) were collected remains of siluriform fishes (Ariidae), turtles and crocodiles by M. Gayet and L. G. Marshall in September 1989.

H. IMPORA FORMATION

Fossil vertebrates of possible late Paleocene age were recovered from two localities of the Impora Formation in the Camargo Syncline, southern Bolivia. One is on the north side of Villa Pacheco near the Río San Juan del Oro, about 14 km north of Tojo, which has yielded remains of siluriform fishes. Just north of this locality remains of crocodiles and turtles were collected. The other locality is at Chaupiuno, about 60 km northwest of Tarija, where indeterminate fish remains were found.

IMPORTANT LATE CRETACEOUS-PALEOCENE VERTEBRATE FAUNAS FROM ELSEWHERE IN SOUTH AMERICA

A. ANDEAN BASIN

In northwestern Argentina, a sauropod (Titanosauridae, *Laplatasaurus* sp.) and a theropod (family *incertae sedis*, *Unquillosaurus ceibalii*) are known from the Los Blanquitos Formation (a temporal equivalent of the Chaunaca and/or Aroifilla formations) in the upper part of the Pirgua Subgroup (Powell, 1979) (Fig. 1). Frogs (Eoxenopidae, *Eoxenopoides saltensis*) are known from the Las Curtiembres Formation, which transitionally underlies the Los Blanquitos Formation (Parodi-Bustos, 1962).

From the Lecho Formation (a basal lower El Molino equivalent; Fig. 1) are reported sauropods (Titanosauridae, *Saltasaurus loricatus*), Coelurosauria (Noosauridae, *Noasaurus leali*) and theropods (Carnosauria indet. and Avisauridae, *Avisaurus archibaldi*) (Bonaparte *et al.*, 1977; Bonaparte & Powell, 1980; Brett-Surman & Paul, 1985; Bonaparte, 1986). The Yacoraite Formation (another El Molino equivalent; Fig. 1) has yielded a crocodile (Dolichochampsidae, *Dolichochampsia minima*; Gasparini & Buffetaut, 1980) which was collected in association with a pycnodont (*Coelodus toncoensis*; Benedetto & Sanchez, 1972), a clupeid (*Gasteroelupea branisai*) and turritellid gastropods (see Gasparini & Buffetaut, 1980; Cione *et al.*, 1985: 296). Other taxa reported from various localities and levels of the Yacoraite Formation include a selachian (*Pucapristis branisi*) and a siluriform (indet.) (Cione *et al.*, 1985; Powell, 1979: 202); the tooth of an indeterminate theropod (Powell, 1979: 203); and trackways of carnosaurs (*Saltitichnus mentoor*), ornithopods (Hadrosauridae?,

Hadrosaurichnus australis, *Taponichnus donottoi*, *Telosichnus saltensis*), indeterminate reptiles, and birds (*Yacoraiteichnus avis*) (Alonso, 1980; Alonso & Marquillas, 1986).

The Mealla Formation (a Santa Lucía equivalent; Fig. 1) has yielded remains of teleostean fishes (indet.), turtles (indet.) and two notoungulate mammals (Henricosborniidae, *Simpsonotus praecursor*, *S. major*; Pascual *et al.*, 1978), whereas the Maíz Gordo Formation (an Impora Formation equivalent; Fig. 1) has yielded specimens of teleostean fishes (Callichthyidae, *Corydoras revelatus*; Poeciliidae, indet.), pleurodire turtles (*"Podocnemis" argentinensis*; Cattoi & Freiberg, 1958) and possibly a notoungulate mammal (Henricosborniidae, *Simpsonotus* sp.) (Pascual *et al.*, 1981).

In northern Chile, the following vertebrates are reported from Senonian age rock units: a selachian (*Pucapristis branisi*) from the Tonel Formation (=lower part of Purilactis Formation *s.l.*) (fide Cione *et al.*, 1985) and dinosaurs (sauropods indet.) from the Estratos de Quebrada Blanca de Poquis (an El Molino equivalent) and the base of the Pajonales Formation (Salinas *et al.*, 1991a, b).

In Peru, vertebrates from the Vilquechico Formation at its type locality near Vilquechico, include *Pucapristis branisi* and *Gasteroelupea branisai* (Dávila & Ponce de León, 1971; Cione *et al.*, 1985: 297). A more detailed faunal list is provided by Jaillard *et al.* (in press). From the base of their middle Vilquechico Formation (a Chaunaca Formation equivalent) they report three fish (*Ptychotrygon* sp., rhinobatid?, actinopterygian). Their upper Vilquechico Formation is divided into three sequences which are equivalent, respectively, to the lower, middle and upper El Molino members in Bolivia. From the lower sequence they report an actinopterygian fish and name two dinosaur trackways (Coelurosauria, Ornithomimidae, *Ornithomimipus jaillardi*; Ornithopoda, Hadrosauridae, *Hadrosaurichnus titicacaensis*); from the base of the middle sequence are two fish (*Pucapristis branisi* and an actinopterygian); and from the upper sequence are two fish (*Dasyatis* sp. and an actinopterygian) and numerous charophytes.

At Laguna Umayo, from what was called the Vilquechico Formation and is now called the Umayo Formation (Laubacher & Marocco, 1990; Jaillard *et al.*, in press) are reported charophytes, actinopterygian fishes (Characiformes, Erythrinidae, *Hoplias* sp., Serrasalminae, Myleinae, indet., Characidae, Tetragonopterinae, indet.; Siluriformes *incertae sedis*; Perciformes, family indet.), lungfish (Ceratodontidae, *Ceratodus* sp., Lepidosirenidae, *Lepidosiren* cf. *paradoxa*), frogs (Leptodactylidae indet.), snakes (Aniliidae), turtles (Podocnemididae, *?Roxochelys* cf. *vilavilensis*), crocodiles (indet.), egg shell fragments reportedly of dinosaurs, marsupials (Peradectidae, *Peradectes austrinum*; Didelphidae?; Pardiomyidae or Microbiotheriidae), and two placentals (Condylarthra, Didolodontidae, undescribed; Notoungulata, Perutheriidae, *Perutherium altiplanense*) (Grambast *et al.*, 1967; Sigé, 1968, 1971, 1972; Bonaparte & Powell, 1980; Rage, 1981; Marshall *et al.*, 1983b, 1985; Kerourio & Sigé, 1984; Marshall & Muizon, 1988; Schultze, 1991a; Gayet, personal observation).

B. SOUTHERN ARGENTINA AND SOUTHERN BRAZIL

There are four important vertebrate faunas outside the Andean basin that warrant special consideration: they are from the Los Alamitos Formation in Patagonia (late Cretaceous), the Adamantina

and Marília formations in the Paraná basin (late Cretaceous), the Banco Negro Inferior in Patagonia (middle Paleocene?), and the fissure fillings in the limestones of São José de Itaboraí near Rio de Janeiro (middle Paleocene?).

1. Late Cretaceous

From the Los Alamitos Formation at Estancia Los Alamitos in Río Negro Province, southern Argentina, numerous vertebrate fossils were found in this mainly brackish-lacustrine rock unit which was tentatively assigned a late Campanian-early Maastrichtian age (Bonaparte *et al.*, 1987). The taxa include: selachians (Batoidei, *indet.*), holosteans (Semionotidae, *Lepidotes* sp.; Lepisosteidae, cf. *Atractosteus* sp.), teleosteans (Siluriformes, cf. Diplomystidae, cf. Ariidae; Perciformes, Percoidei, *indet.*), Neopterygii *indet.* (*Lepidotes* or Sparidae), Dipnoi (Ptychoceratodontidae, *Ceratodus iheringi*), amphibians (Pipidae, cf. *Xenopus* sp.; Leptodactylidae, *indet.*), turtles (Meiolaniidae, cf. *Niolamia*; Chelidae, *indet.*), snakes (Boidae, Madtsoniinae, *Alamitophis argentinus*, *Patagoniophis parvus*, *Rionegrophis madtsoioides*), dinosaurs (Titanosauridae, *Aelosaurus rionegrinus*?; Hadrosauridae, *Kritosaurus australis*), and mammals including Symmetrodonta (Bondesiidae, *Bondesius ferox*; fam. *indet.*, *Casamiquelia rionegrina*; ?Spalacotheriidae, *Brandonia intermedia*; Barbereniidae, *Barberenia araujoae*, *Quirogatherium major*), Dryolestidae (Dryolestidae, *Groebertherium stipanicici*, *G. novaci*, *Leonardus cuspidatus*; Mesungulidae, *Mesungulatum housayi*; Reigitheriidae, *Reigitherium bunodonta*), Triconodonta (Triconodontidae, *Austrotriconodon mckennai*), Multituberculata (Ferugliotheriidae, *Ferugliotherium windhauseni*) and two Gondwanatheria (Gondwanatheriidae, *Gondwanatherium patagonicum*, *Vucetichia gracilis*) (Albino, 1987; Baez, 1987; Bonaparte & Soria, 1983, 1985; Bonaparte, 1986a, b, c, 1987, 1990; Bonaparte & Pascual, 1987; Bonaparte & Rougier, 1987; Broin, 1987; Cione, 1987; Mones, 1987; Powell, 1987). In northern Patagonia, some levels of the Los Alamitos Formation are probably associated with a marine transgression from the west (Andreis, 1987). The Los Alamitos Formation is overlain by the transgressive marine Roca Formation of Maastrichtian-Danian age (Bonaparte, 1990) which probably correlates with the coeval and transgressive lower El Molino Formation of Bolivia. Because of their characteristics and stratigraphic positions, we thus propose temporal correlation of the Los Alamitos Formation with the Chaunaca Formation. Hence, the Los Alamitos Formation is likely to be of Campanian age.

The vertebrate faunas from the Adamantina and Marília formations (Upper Bauru Group) in the northern part of the Paraná basin, southcentral Brazil, include fishes (Lepisosteiformes, Lepisosteidae, *Lepisosteus cominatoi*; Osteoglossiformes, Osteoglossidae; Characiformes; Siluriformes, cf. Doradidae; Perciformes, ?Percichthyidae), lungfish (Dipnoi, Neoceratodontidae, *Neoceratodus* sp.), frogs (Leptodactylidae, *Baurubatrachus pricei*), turtles (Podocnemididae, *Roxochelys harrisi*, cf. *R. elegans*, aff. *Podocnemis brasiliensis*), lizards (Iguanidae?, *Pristiguana brasiliensis*), snakes (*indet.*), crocodiles (Baurusuchidae, *Baurusuchus pachecoi*; Peirosauridae, *Peirosaurus torminni*; Goniopholidae, ?*Goniopholis paulistanus*; Trematosuchidae, *Itasuchus jesuinoi*; family *indet.*, *Brasileosaurus pachecoi*, *Sphagesaurus huenei*), dinosaurs (Carnosauria, Abelisauridae,

family *indet.*; Coelurosauria, family nov. 1, nov. 2; Sauropoda, Titanosauridae, ?*Antarctosaurus brasiliensis*, *Titanosaurus* cf. *australis*; Ornithischia), and mammals (Placentalia, *indet.*) (Gayet & Brito, 1989; Bertini *et al.*, in press). Both formations are of continental, mostly fluvial, origin and are thought to be Senonian in age.

2. Middle Paleocene?

A local fauna is known from the Banco Negro Inferior in the base of the Río Chico Formation about 1 km southwest of Punta Peligro (40 km north-northeast of Comodoro Rivadavia along the Atlantic coast) and another at Las Flores, 60 m above the Banco Negro Inferior in the base of the Gran Barranca south of Lago Colhué-Huapí. Both local faunas are in the San Jorge basin, Chubut Province, southern Argentina and were discovered in January 1979 during a National Geographic Society sponsored research program under the direction of one of the authors (Marshall *et al.*, 1981). The fossils from Punta Peligro include turtles (Chelidae, at least four taxa; Broin, 1988), crocodiles (Sebecosuchia?; Crocodylidae, *Necrosuchus ionensis* Simpson, 1937; Alligatoridae, *Eocaiman* sp., *Allognatosuchus*? sp.), a possible edentate or multituberculata (Sudamericidae, *Sudamerica ameghinoi* Scillato Yané & Pascual, 1985), condylarths (Arctocyoniidae and/or Mioclaenidae) and several indeterminate bone fragments (Marshall *et al.*, 1981, n16; Pascual & Ortiz-Jaureguizar, 1991). Those from Las Flores include the polydolopoid marsupial *Epidolops* sp. (Pascual & Bond, 1981), and other taxa which show affinities with Itaboraian faunas in Brazil (Pascual & Ortiz-Jaureguizar, 1991). Many additional fossils of marsupials and ungulates from Las Flores were collected by L. G. Marshall and colleagues in 1979, and numerous unpublished specimens from both Punta Peligro and Las Flores are now available (Van Valen, 1988). The Banco Negro Inferior is predominantly a black bentonitic mudstone (Andreis *et al.*, 1975). The Salamanca/Río Chico contact records a noteworthy marine regression which, according to associated geochronologic age constraints (Marshall *et al.*, 1981), probably corresponds to the major regression identified by Haq *et al.* (1987) in the early Thanetian (about 58.0-58.5 Ma).

The Itaboraí fauna comes from fissure fillings in the early Paleocene (?) age São José de Itaboraí Formation located about 25 km east of Niterói, state of Rio de Janeiro, Brazil. Taxonomic lists of this exceptionally diverse fauna are provided by Paula Couto (1970), Palma & Brito (1976) and Marshall *et al.* (1983). The vertebrates were recovered from numerous karst cavities in a lower limestone unit and predate an upper limestone unit (Brito *et al.*, 1972). For most specimens, their association among themselves and/or with specific cavities was never recorded. Although some mammals appear referable to what has been interpreted as middle Paleocene time (*i.e.* the Itaboraian Land Mammal age; *sensu* Marshall, 1985), others appear more progressive and may represent faunas of late Paleocene and possibly early Eocene age (*i.e.* the Riochican and Casamayoran Land Mammal Ages, respectively; see Soria, 1987; Van Valen, 1988; A. Cione, personal communication). In the following discussion, we regard this fauna as middle Paleocene, but caution that it may include taxa that accumulated between middle Paleocene and early Eocene time.

Although a hydrothermal origin has been classically favored for the São José de Itaboraí lacustrine limestones (Francisco & Cunha,

1978), water level in the tectonic near-shore lake where the limestones were deposited might have been controlled by the level of the nearby Atlantic Ocean through adjustment of marine and continental phreatic levels. In such a case, the lacustrine episode evidenced by the lower Itaboraf limestones would have been coeval with a marine highstand. Since middle (and later?, see above) Paleocene mammals are known from the infilling of the karstic cavities that formed after lake dessication, it would be possible to correlate this highstand period with the one in the late Danian, and the subsequent dessication with the early Thanetian regression which is also recorded near the Salamanca/Río Chico contact in southern Argentina (see above). A subsequent highstand period would have resulted in the deposition of the upper limestones of São José de Itaboraf.

DISCUSSION

A. BIOSTRATIGRAPHY

The Mesozoic and Paleocene age vertebrate fossil localities in Bolivia (Fig. 2) are arranged in Table 1 according to their stratigraphic context. A systematic list of all the known fossil vertebrates is given in Tables 2, and in Table 3 with indication of locality and stratigraphic occurrence.

In this section we review the known occurrence of the taxa listed in Tables 2 and 3 in order to identify their chronostratigraphic ranges and hence potential usefulness for calibrating the Bolivian rock sequence. Of particular interest is the apparent position of the Cretaceous/Paleocene (K/T) boundary, within the El Molino Formation (see below).

1. Selachians

In Bolivia, selachians were recovered from the lower and basal middle members of the El Molino Formation. Rhombodontidae are present only in the lower member, whereas Sclerorhynchidae and Dasyatidae are present in both. Sclerorhynchidae range from Albian to Maastrichtian (Cappetta, 1990). *Schizorhiza* is known only in Maastrichtian age rocks from numerous localities around the world (Texas, Morocco, Middle-East, Niger, Nigeria and Zaire), while *Ischyrhiza* ranges from the Turonian to Maastrichtian in North America and Niger (Cappetta, 1987, 1990, 1991). *Pucapristis* (Sclerorhynchidae), *Pucabatis* (Rhombodontidae) and the three named species of *Dasyatis* (*D. molinoensis*, *D. schaefferi*, *D. branisai*) (Dasyatidae) are currently endemic to the Andean basin where they are proving exceptionally useful in intra-basin correlation (Cappetta, 1990). *Pucapristis branisi* is also known from a level below another which yielded dinosaurs in the lower part of the Yacoraite Formation in northwest Argentina (Powell, 1979). *Dasyatis* is known in the Cenomanian of Texas, and from Maastrichtian to Recent world-wide.

2. Pycnodontiformes

Pycnodontiformes (Pycnodontidae) were collected in Bolivia from the Chaunaca Formation and the lower and basal middle members of the El Molino. *Coelodus* was reported from the lower Cretaceous of Brazil (Santos, 1963; Wenz, 1989), Colombia (Porta, 1970) and

Chile (Schultze, 1981), and existed until the middle Eocene in marine deposits around the world (Blot, 1987). Cione (1977) tentatively referred specimens discussed by Wenz (1969) from Bolivia to *Coelodus toncoensis* which was erected by Benedetto & Sánchez (1972) upon material from the Yacoraite Formation of northwest Argentina. Gayet (1991) cautions that the species identity of some Bolivian pycnodontids has still to be verified, while others from the lower and basal middle El Molino Formation can be referred with confidence to *Coelodus toncoensis* which was apparently endemic to the Andean basin.

3. Semionotiformes

In Bolivia, *Lepidotes* sp. was collected securely from the late Triassic-early Jurassic. Elsewhere in South America, *Lepidotes* is reported from the Tithonian (=Portlandian) of Neuquén Province, Argentina (Aramayo, 1981), the Aptian-Albian of Brazil (Agassiz, 1841; Roxo & Löfgren, 1936; Woodward, 1895, 1908) and a possible record from the late Campanian-early Maastrichtian age Los Alamitos Formation in Argentina (Cione, 1987). Elsewhere in the world, *Lepidotes* is recorded from the Rhetian of Germany to Cretaceous/Paleocene of India (Gayet *et al.*, 1984).

Pillow-shape scales which represent a new genus of the family Semionotidae are known only in the lower and basal middle members of the El Molino Formation in Bolivia (Gayet & Meunier, personal observation) and in the Yacoraite Formation in Argentina (A. L. Cione, pers. com.).

4. Ginglymodi

In Bolivia, *Lepisosteus* sp. is reported from the lower and basal middle El Molino. The earliest Lepisosteidae are reported from the early Cretaceous of Niger (Arambourg & Joleaud, 1943) and Congo (Casier, 1943). Younger fossils, including *Lepisosteus*, are known from the late Cretaceous of India (Jain & Sahni, 1983; Gayet *et al.*, 1984) and from the Cenozoic of Europe, India and North America (Wiley, 1976). In South America, Lepisosteidae are known in Argentina from the late Campanian-early Maastrichtian age Los Alamitos Formation (cf. *Atractosteus* sp.; Cione, 1987) and from the El Abra Formation of uncertain age (A. L. Cione, pers. com.) (*Lepisosteus*; M. G., pers. obs.); *Lepisosteus* is known from the late Cretaceous Adamantina and Marília formations of the Upper Bauru Group in Brazil (Santos, 1984; Gayet & Brito, 1989; Brito & Gayet, in press), and the late Cretaceous of Colombia (Gayet, 1991). *Lepisosteus* exists to Recent in southeastern USA and in Central America.

5. Clupeiformes

Gasteroclupea branisai is apparently endemic to the Andean basin where in Bolivia it is reported from the Chaunaca (possibly), Cajones, all three members of the El Molino, and the Santa Lucía formations; in Argentina it is known only from the Yacoraite Formation (Cione *et al.*, 1985) and has never been found in overlying Paleocene formations. The oldest known Clupeidae are from the Neocomian of northern Kyushu, Japan (*Diplomystus primotinus*, *D. kokuraensis*) (Uyeno, 1979).

6. Osteoglossiformes

In Bolivia, the subfamilies Osteoglossinae and Phareodontinae of the family Osteoglossidae are recorded from the El Molino and Santa Lucía formations (see Table 3). The earliest record for Osteoglossiformes in South America is from the Aptian age Areado Formation in Brazil (Santos, 1985) where the taxon is referred to the family Arapaemidae (Laelichthyinae) which has African affinities. Phareodontinae were reported from the Paleocene and Eocene of Africa (Cappetta, 1972) and Europe (Woodward, 1901; Taverne, 1978), Paleocene of southeast Asia (Sanders, 1934), late Paleocene of Turkmenia (Danil'chenko, 1968), Paleocene of Australia (Taverne, 1975; Gayet, 1991), and middle Eocene of North America. Thus, the Phareodontinae record from the El Molino is the earliest known to date.

Squamules (parts of scales) of Osteoglossidae (Phareodontinae and Osteoglossinae) were reported in the Maastrichtian of Niger, Cretaceous/Paleocene of India and Paleocene of Pakistan (Gayet & Meunier, 1983). Osteoglossinae were reported from the Paleocene of Sumatra (Sanders, 1934), and range to Recent in South America, Asia, Africa and Australia.

7. "Salmoniformes"

In Bolivia, Enchodontidae (*Enchodus* sp.) and Ichthyotringoidei (family indet. and ?*Apateodus* sp.) were collected from the lower and basal middle El Molino. *Enchodus* is known only from marine Maastrichtian age rocks in Congo (Dartevelle & Casier, 1949), Morocco (Arambourg, 1952), Brazil (Rebouças & Santos, 1956), Europe (Goody, 1968), North America (Goody, 1969), Lebanon (Goody, 1969) and Israel (Chalifa, 1989) to note only the most important in both preservation and quantity.

Apateodus is a member of the suborder Ichthyotringoidei which ranges from early Cretaceous (?Albian) to Maastrichtian (Goody, 1969).

8. Cypriniformes

The cypriniform (*Molinichthys inopinatus*; Gayet, 1982b) from the lower and basal middle El Molino represents the only record, fossil or extant, of this order in South America. Elsewhere in the world, this group is first known from the Eocene of North America (Grande *et al.*, 1982). Gayet (1986b, c) described *Ramallichthys* from the marine Cenomanian in Israel which may be considered an ancestral, if not true, cypriniform.

9. Characiformes

In Bolivia, this order is represented by the families Erythrinidae, Serrasalminidae (including Serrasalminae and Myleinae) and Characidae (including Tetragonopterinae and Rhoadsiinae). All these groups have been found in the Santa Lucía Formation, while members of the Erythrinidae, Myleinae and Tetragonopterinae were also found in the lower and basal middle El Molino Formation.

The oldest previous known Erythrinidae (*Hoplias*) are reported from the Miocene of Ecuador (Roberts, 1975); Serrasalminidae (Myleinae) from the Maastrichtian? Umayo Formation at Laguna

Umayo in Perú (Gayet, 1991), Miocene Loyola Formation of Ecuador (Roberts, 1975) and Miocene of Colombia (Lundberg *et al.*, 1986); Characidae (Tetragonopterinae) from the Umayo Formation at Laguna Umayo in Peru (Gayet, 1991), Miocene of Ecuador (Roberts, 1975) and early Miocene of Taubaté in Brazil (Schaeffer, 1947); Characidae (indet.) from the Paleocene of Morocco (Cappetta *et al.*, 1978); Serrasalminidae (Serrasalminae) and Characidae (Rhoadsiinae) had not yet been found as fossils. The oldest known record of characiforms outside of South America is *Salminops ibericus* from the marine late Cenomanian of Portugal (Gayet, 1985a). Characiforms range to Recent in Africa and in South America. One recent genus colonized Central America.

10. Siluriformes

In Bolivia, this order is represented by members of the families Ariidae and Andinichthyidae from both the El Molino and Santa Lucía formations, and at least by two families *incertae sedis* from the Santa Lucía Formation at Tiupampa (Gayet, 1991).

The other known siluriforms elsewhere in South America are represented by cf. Diplomystidae and cf. Ariidae in the Campanian age Los Alamitos Formation in Argentina (Cione, 1987); Siluriformes indet. from the Maastrichtian age Coli Toro (Cione & Laffite, 1980) and Yacoraita formations (Cione *et al.*, 1985) in Argentina; cf. Doradidae from the late Cretaceous age Adamantina and Marília formations in the Upper Bauru Group, Brazil (Gayet & Brito, 1989; Brito & Gayet, in press); and Ariidae from the Maastrichtian? age Umayo Formation at Laguna Umayo in Peru (Gayet, 1991).

The only records for Cretaceous age Siluriformes outside of South America are a single tooth referred to *Arius* sp. from the latest Cretaceous of Central India (Jain & Sahni, 1983) and doubtful otoliths from the late Cretaceous of North America (Frizzell, 1965; Fitch, 1975).

Siluriformes are known in the Paleocene of Argentina, [*Arius?* and *Bachmania* in Patagonia (Dolgopol de Saez, 1941), and *Propygidium* (Bocchino, 1964) and *Corydoras* (which in Recent times is restricted to freshwater in South America) from the Maíz Gordo Formation (Bardack, 1961)], Africa (in Congo; Dartevelle & Casier, 1949; Casier, 1960), Europe (Belgium; Leriche, 1902), Indonesia (Sanders, 1934); and in the Eocene of North America (Lundberg, 1975; Grande, 1987; Grande & Lundberg, 1988), Europe (Woodward, 1901; Casier, 1946), Africa (Peyer, 1928) and India (Sahni & Misra, 1975). Ariidae range to Recent.

11. Cyprinodontiformes

In Bolivia, pharyngeal teeth from the Miraflores Formation are tentatively referred to indeterminate cyprinodontiforms. In the lower member of the El Molino Formation are known several very primitive cf. Cyprinodontiformes (Gayet, 1991). The earliest previous record of this group was from the Oligocene of France (Gaudant, 1988), and it ranges to Recent world-wide.

12. Perciformes

In Bolivia, perciforms of the family Centropomidae are known

from the Santa Lucía Formation (Gayet, 1991). Indeterminate specimens of this order are reported in South America from the Campanian age Los Alamitos Formation of Argentina (Cione, 1987), the Maastrichtian age Marília Formation of Brazil (Gayet & Brito, 1989), and the Umayo Formation at Laguna Umayo in Peru (Gayet, 1991). The earliest Centropomidae were previously recorded from the middle Eocene of Italy (Sorbini, 1970), and they range to Recent world-wide.

13. Tetraodontiformes

In Bolivia, *Stephanodus* (Eotrigonodontidae) is recorded from the lower and basal middle El Molino Formation. Eotrigonodontidae was reported from marine beds in the ?Albian-Aptian of Morocco (Tabaste, 1964), Cenomanian of Egypt (Weiler, 1935), late Cretaceous of Nigeria (White, 1934), Congo (Dartevelle & Casier, 1949), Niger (Tabaste, 1963; Cappetta, 1972), Morocco (Arambourg, 1952), Israel (Raab, 1963), Upper Cretaceous of India (Jain & Sahni, 1983) and Tertiary levels of Europe (Leriche, 1906; Casier, 1946), Angola (Dartevelle & Casier, 1959) and Egypt (Peyer, 1928). Eotrigonodontidae range from ?Albian-Aptian to middle Eocene, whereas *Stephanodus* was reported only from the Cretaceous (same references).

14. Polypteriformes

Dajetella sudamericana (Gayet & Meunier, 1991a, b, 1992) from the lower El Molino and Santa Lucía formations is the only record for Polypteriformes outside of Africa, where members of this order are known from the Senonian of In Becetem in Niger (Gayet *et al.*, 1988), Miocene of Tunisia and Kenya (Greenwood, 1951, 1973), and Pleistocene of Ethiopia (Arambourg, 1948). They range to Recent in Africa where they occur in freshwater.

15. Lungfish

In Bolivia, Ceratodontidae (*Ceratodus* sp. and ceratodont n. sp.) and Lepidosirenidae (*Lepidosiren* cf. *paradoxa*) tooth plates occur together in the early Paleocene of Tiupampa. In South America, the first ceratodonts occur in the Upper Cretaceous of Patagonia (Ameghino, 1906; Pascual & Bondesio, 1976; Cione, 1987) and were also described from the Lower Cretaceous of northern Brazil (Cunha & Ferreira, 1980). Ceratodonts were distributed world-wide in the Mesozoic, still occurring during the Cretaceous in Africa, Madagascar, Australia, North and South America, whereas the Neoceratodontidae which occur in the early Cretaceous of Australia persist there until today (Schultze, 1991a).

Lepidosirenidae are reported from the Maastrichtian El Molino Formation at Vila Vila and the Paleocene Santa Lucía Formation at Torotoro. Fossils are recorded from the Maastrichtian? at Laguna Umayo in Peru (Sigé, 1968), Eocene of Argentina (Fernandez *et al.*, 1973; Fernandez, 1976) and Miocene of Brazil (Santos, 1987) and Colombia (Bondesio & Pascual, 1977). Lepidosirenids occur today in the Amazonian and Paraguayan regions of South America.

16. Amphibians

In Bolivia, indeterminate Leptodactylidae are known only from the Santa Lucía Formation at Tiupampa. Elsewhere in South America indeterminate Leptodactylidae are recorded from the Campanian age Los Alamitos Formation in Argentina (Baez, 1987), and, questionably, from the Umayo Formation at Laguna Umayo in Peru (Sigé, 1968). A probable Leptodactylidae, *Baurubatrachus pricei* has been recorded in the Maastrichtian age Marília Formation in Brazil (Báez, 1985; Báez & Perí, 1989; Bertini *et al.*, in press). The oldest known Leptodactylidae are from the Marília Formation and the family extends to the Recent (Báez, 1987).

The oldest known Gymnophiona are represented by two vertebrae from the Santa Lucía Formation at Tiupampa (Rage, 1986, 1991b). Previously this group was known from the middle Paleocene (at Itaboraí) to the Recent.

Vertebrae of urodels are known from the lower El Molino Formation at Pajcha Pata. This is the earliest record of this group in the world (Rage, pers. com.).

17. Turtles

Roxochelys was based on specimens collected from the Campanian age Adamantina Formation of the Upper Bauru Group in Brazil (Broin, 1991; Bertini *et al.*, in press). *?Roxochelys vilavilensis* Broin, (1971), from the Santa Lucía Formation is probably referable to a genus distinct from *Roxochelys* (Broin, 1991). The species *vilavilensis* is definitely known only from the Santa Lucía Formation in Bolivia and possibly from the Maastrichtian? Umayo Formation at Laguna Umayo in adjacent Peru (see above), while very fragmentary material from the lower El Molino of Bolivia is referred to *?Roxochelys* cf. *vilavilensis*. This species was apparently endemic to the Andean basin.

18. Lizards

An unidentified member of what appears to be the family Iguanidae is recorded from the Santa Lucía Formation at Tiupampa (Rage, 1991b). A possible iguanid (*Pristiguana brasiliensis*; Estes & Price, 1973) is known from the Maastrichtian age Marília Formation of the Upper Bauru Group in Brazil, while the earliest uncontested members of this family are from the middle Paleocene of Brazil (Estes, 1983) and North America (Sullivan, 1982).

19. Snakes

The four families of snakes listed below are known only from the Santa Lucía Formation at Tiupampa in Bolivia.

In South America, Aniliidae are first reported from the Umayo Formation at Laguna Umayo in Peru (Rage, 1981) and middle Paleocene at Itaboraí in Brazil (Rage, 1987).

The earliest Boidae are from the Maastrichtian of North America (Estes & Báez, 1985), Europe (Rage, 1987) and India (Jain & Sahni, 1983), while in South America, previous to this work, they were first reported in the middle Paleocene in Brazil (Rage, 1987) and early Eocene of Argentina (Albino, 1986).

Madtsoiidae are first known in the Santonian/Campanian of Madagascar (Rage, 1984; Bonaparte, 1986) and Campanian age Los Alamitos Formation in Argentina (Albino, 1986, 1987). In fact, the oldest Madtsoiidae is probably from Niger (early Senonian) (Rage, 1984).

Previous to this work, Tropidopneidae were first reported from the middle Paleocene in Brazil (Rage, 1987), middle Eocene in North America (Holman, 1979), and Eocene-early Oligocene in Europe (Rage, 1984).

20. Crocodiles

Three families are known in Bolivia: Dyrosauridae (basal middle El Molino and Santa Lucía formations), Dolichochampsidae (upper El Molino Formation) and Sebecidae (Santa Lucía Formation).

Dyrosauridae are known from late Maastrichtian to late Eocene rocks around the world (Buffetaut, 1982). In South America, dyrosaurids are known from what appears to be the Maastrichtian in Brazil (Cope, 1886; Buffetaut, 1978), and a possible dyrosaurid is known from the Maastrichtian in Argentina (Gasparini, pers. com.). *Sokotosuchus ianwilsoni* (Halstead, 1975) is from the late Maastrichtian Dukamaje Formation in Nigeria.

Dolichochampsidae (*Dolichochampsia minima*) is known elsewhere only from the upper part of the Yacoraite Formation in northwest Argentina and the upper El Molino Formation in Bolivia (see above). The family was apparently endemic to the Andean basin.

Sebecidae were previously known from the middle Paleocene-middle Miocene (Buffetaut, 1982; Gasparini, 1984); they were endemic to South America. *Sebecus querejazus* from the Santa Lucía Formation is the earliest known member of the family (Buffetaut & Marshall, 1991).

21. Dinosaurs

Dinosaur trackways are known from four localities in the lower El Molino near Torotoro and at Santivañez near Parotani, and from two localities (Arapampa, Camargo) in an indeterminate El Molino member. The only dinosaur fossils in Bolivia are a tooth of a Coelurosauria (Marshall, 1989b) from the lower El Molino at Pajcha Pata, and undescribed bones from two localities of the Cajones Formation near Santa Cruz (R. Suárez, pers. com.).

Although a detailed study of the trackways has yet to be undertaken, it appears that at least four suborders (Theropoda, Sauropoda, Ornithopoda and Ankylosauria or Ceratopsia) are represented within the lower El Molino at Torotoro. This demonstrates that dinosaurs were taxonomically diverse in lower El Molino time.

For chronostratigraphic purposes we follow the general consensus that dinosaurs became extinct at the end of Cretaceous time and that there is no compelling evidence (*contra* Van Valen, 1988) to substantiate that they may have continued into the early Paleocene. Recent work by Lofgren *et al.* (1990), for example, negates a Paleocene age for dinosaurs from the upper Hell Creek Formation in Montana. Our position is concordant with the biostratigraphic data in the Andean basin summarized above and below.

22. Mammals

Mammals are known only from the Santa Lucía Formation in Bolivia. *Peradectes austrinum* was based on a specimen collected from the Umayo Formation at Laguna Umayo in Peru (Sigé, 1971, 1972; Crochet, 1980) and a second specimen from the Santa Lucía Formation at Tiupampa in Bolivia was later referred to this species (Marshall & Muizon, 1988). The earliest known *Peradectes* is from the base of the early Paleocene in North America (Van Valen, 1988: 29) and is common thereafter in early Tertiary age rocks in North America and Europe (Crochet, 1980).

Roberthoffstetteria is most closely related to *Procaroloameghinia* from the middle Paleocene of Brazil (Marshall *et al.*, 1983a), although other more primitive members of the subfamily Caroloameghiniinae are known from the Maastrichtian in North America (Marshall *et al.*, 1989). The genera and species of Microbiotheriidae, Didelphidae, Hathliacynidae and Kollpaniidae are known only from the Santa Lucía Formation at Tiupampa, and they all represent the earliest known members of these families in South America (Marshall & Muizon, 1988; Marshall *et al.*, 1989).

Cf. *Cimolestes* sp. is the only known member of the order Leptictida in South America. *Cimolestes* is recorded from the Maastrichtian and early Paleocene in North America (Marshall & Muizon, 1988).

The pantodont *Alcidedorbignya* is the only known member of this order in South America. Pantodonts are first known in the middle Paleocene of North America where *Pantolambda bathmodon* represents a potential descendant of *Alcidedorbignya* (Marshall & Muizon, 1988). Among the New World pantodonts, *Alcidedorbignya* is the earliest and most primitive member yet known.

The mioclaenine Hyopsodontidae are the only representatives of this family in South America. In North America, members of this group are first recorded in the early Paleocene (Marshall & Muizon, 1988; Van Valen, 1988).

The earliest known notoungulates are represented by *Perutherium altiplanense* (Perutheriidae) from the Umayo Formation at Laguna Umayo in Peru (Marshall *et al.*, 1983b), *Simpsonotus* (Henricosborniidae) from the Mealla Formation in northwest Argentina (Pascual *et al.*, 1979), and cf. Henricosborniidae or Oldfieldthomasiidae from the Santa Lucía Formation at Tiupampa in Bolivia (Marshall & Muizon, 1988).

B. THE CRETACEOUS/PALEOCENE (K/T) BOUNDARY IN THE ANDEAN BASIN

Based on the above discussion of chronostratigraphic ranges, the taxa can be grouped into five categories (see Table 3):

1. Those which presently are known only from the El Molino Formation and its stratigraphic equivalents in the Andean basin. These are currently regarded as "endemics" which are potentially useful for intra-basin correlation although their usefulness in calibrating these rocks with the geologic time scale has yet to be firmly established. Included are *Pucapristis* (Sclerorhynchidae), *Pucabatis* (Rhombodontidae), the three species of *Dasyatis* (Dasyatidae), *Coelodus toncoensis* (Pycnodontidae), and *Dolichochampsia* (Dolichochampsidae).

2. Taxa from the El Molino and Santa Lucía formations (and their stratigraphic equivalents) which are "endemics" in the Andean basin. Included are *Gasteroclupea branisai* (Clupeidae), *Andinichthys bolivianensis* (Andinichthyidae), *Andinichthyidae*, *Hoffstetterichthys pucari*, *Incaichthys suarezi* (families *incertae sedis*) and *Roxochelys vilavilensis* (Podocnemididae).

3. Taxa known only from the lower and basal middle El Molino Formation which are currently regarded as late Cretaceous "guide fossils" based on their records elsewhere in the world. Included are *Schizorhiza* and *Ischyrhiza* (Sclerorhynchidae), apparently *Lepidotes* (Semionotidae) which has only one dubious record in the Cretaceous/Paleocene of India, *Enchodus* (Enchodontidae), *?Apateodus* (family indet.), Ichthyotringoidei (gen. and sp. indet.), *Stephanodus* (Eotrigonodontidae) and dinosaurs.

4. Taxa which occur in the El Molino and/or Santa Lucía formations and, which based on records from elsewhere in the world, transgressed the K/T boundary and are of dubious or no value in defining this boundary. These include *Lepisosteus* (Lepisosteidae), Osteoglossidae, Cypriniformes, Characiformes, Siluriformes, Cyprinodontiformes, Perciformes, Polypteriformes, Dipnoi, Leptodactylidae, Podocnemididae, Lacertilia, Boidae, Matsoiidae, Dyrosauridae, and Leptictida.

5. Taxa recorded only in the Santa Lucía Formation which are the earliest or only records for these groups in South America. They do not occur in association with diagnostic Cretaceous taxa and therefore are regarded as Paleocene. Included are Ceratodontidae n. gen. and sp., Gymnophiona, Aniliidae, Tropidopneustidae, Sebectidae, Peradectidae, Caroloameghiniidae, Microbiotheriidae, Didelphidae, Hathiacyridae, Kollpaniidae, Pantodontia, Hyopsodontidae and Notoungulata.

As demonstrated by group 3 (above), apparent late Cretaceous taxa occur only in the lower and basal middle members of the El Molino Formation. It therefore appears that the K/T boundary occurs above the basal middle member, while the upper El Molino member may be regarded as early Paleocene based on palynological study of a stratigraphic equivalent in northwestern Argentina (Quattrocchio *et al.*, 1986) and on the absence of diagnostic Cretaceous taxa. We therefore suggest that the K/T boundary lies somewhere in the upper part of the middle member of the El Molino Formation. In addition, the Santa Lucía Formation, which also lacks diagnostic Cretaceous taxa and conformably overlies the early Paleocene upper member of the El Molino Formation, may be regarded as early, but no earliest, Paleocene in age.

C. PALEOENVIRONMENT

Fishes

Fishes have been divided into four main categories (Myers, 1938) based on their tolerance to fresh or salt water: 1) primary freshwater fishes found only in fresh water; 2) secondary freshwater fishes, found normally in fresh water, but capable of entering and surviving in marine water; 3) peripheral freshwater fishes, diadromous, which

migrate between fresh water and marine; and 4) marine fishes.

The definition of these four categories is based on living fishes and is not always evident with fossil forms (see below). For this reason, the identification of paleoenvironment based only on one or a few taxa is generally of dubious value.

1. Primary freshwater fishes

a. Semionotidae

The fossil Semionotidae are generally considered as primary freshwater fishes. A new genus is reported in Bolivia in the lower and basal middle members of the El Molino Formation. Except for the questionable Cretaceous/Paleocene record from India (Gayet *et al.*, 1984), Semionotidae are not known to survive beyond the Cretaceous/Paleocene boundary. Their absence at Tiupampa is probably related to the Paleocene age of the Santa Lucía Formation.

The new genus from Agua Clara and Hotel Cordillera, known only by scales and referred to the Semionotidae, seems endemic to Bolivia and northern Argentina where it is recorded in both marine and fresh water environments.

b. Osteoglossidae

Living Osteoglossidae are restricted to freshwater environments in tropical South America, Africa and Asia. Some fossil remains were reported from fresh water (Green River basin, Wyoming, Grande 1984; Sumatra, Sanders, 1934; Australia, Taverne, 1979), some from brackish water (middle Cretaceous of Zaire; Taverne, 1976) and some from marine environments (Paleocene of Zaire; Darteville & Casier, 1959; Turkmenistan, Danil'chenko, 1968; Niger, Cappetta, 1972; Gayet & Meunier, 1983; Eocene of Italy, Taverne, 1979; England, Woodward, 1901; Morocco, Arambourg, 1952; and Denmark, Bonde, 1966). In well known marine Cretaceous levels (Lebanon, Israel, Morocco, Italy, Portugal and Yugoslavia) where the ichthyofauna is abundant, no fossils of this order are represented. Consequently, Osteoglossiformes are considered as primary freshwater fishes following Nelson (1969) and Gayet (1987b). In Bolivia, Osteoglossinae were reported in all members of the El Molino and in the Santa Lucía formations, whereas Phareodontinae were reported in the Santa Lucía Formation only (Tiupampa). In the El Molino Formation, they occur in association with marine fishes.

c. Cyprinodontiformes

Nothing can be said about the paleoenvironment of the cf. Cyprinodontiformes in Bolivia, because this group is too poorly known.

d. Polypteridae

Living Polypteridae are African freshwater fishes as are all fossils of this group known from Senonian to Pleistocene. In Bolivia they were reported at Tiupampa (Santa Lucía Formation) and occur in association with marine fishes at Vila Vila (lower El Molino Formation).

e. Lungfishes

Ceratodonts are generally associated with fresh water environments by extrapolation based on occurrence of extant forms. Nevertheless, ceratodonts occur in undoubtedly marine deposits in Zaire (Casier, 1961), Niger and Algeria (Martin, 1984), Mali (Tabaste, 1963), Egypt (Schaal, 1984) and Kansas (Schultze, 1981). According to these different authors, these faunas may be interpreted as death assemblages of marine, brackish and fresh water forms or that they were tolerant of a wide range of salinity.

Lepidosirenids are restricted to fresh water environments.

2. Secondary freshwater fishes

a. Lepisosteidae

Most of the living Lepisosteidae are found in fresh water, but one species may tolerate brackish or even marine conditions and is found along the coast of the Gulf of Mexico (Suttkus, 1963). Because of their thick scales covered with ganoine which are more resistant than any other parts of the fish, the fossil Lepisosteidae are often reported on scales only, which may be transported far from their biotope without damage. In Bolivia, Lepisosteidae are always found in association with marine fishes including selachians, pycnodonts and eotrigonodonts in the lower and basal middle members of the El Molino Formation, but they are always disassociated, indicating postmortem movement. In the only locality where no true marine fishes were found (i.e. Tiupampa), Lepisosteidae are absent but this absence may be the consequence of age (Paleocene) and not of environment. Lepisosteidae had a nearly world-wide distribution during Cretaceous and early Tertiary times. Subsequently, they disappeared from all the continents except North America where they are now restricted to the southeastern part of the USA and Central America.

b. Clupeidae

Gasteroclupea branisai is a Clupeiformes endemic to the Andean basin. Clupeiformes are generally marine fishes with the exception of some South American living genera (*Ramnogaster*, *Pristigaster*; Géry, 1969; Cione & Pereira, 1985). In the middle Eocene of the Green River Formation (Wyoming, USA), *Knightia* and *Diplomystus* which are known to be marine, are reported in strictly fresh water environments (Grande, 1982a, b). *Gasteroclupea branisai* is reported at Tiupampa (Santa Lucía Formation) where no marine fishes are found, and in some levels of the El Molino Formation (at Agua Clara) in association with marine fishes. In some green marl levels at Agua Clara, *Gasteroclupea* is found in association only with brackish-water ostracods. Consequently, *Gasteroclupea* may be considered, with some confidence, as a secondary freshwater clupeid.

c. Centropomidae

The family Centropomidae, as defined by Greenwood (1976), is composed of marine and fresh water genera. *Lates*, to which the Bolivian genus may be compared, is known to include marine and

fresh water species. This family includes the genus *Centropomus* from the coastal waters of the New World, a species which enters Brazilian rivers (Berra, 1981). Centropomidae are present at Tiupampa and Criadero de Loro in Bolivia.

d. Cypriniformes

Cypriniformes are living freshwater fishes and fossil remains attest, as far as is known, to a similar environment. Only *Ramallichthys* from Ein Jabrud (Israel) which may be considered as an ancestral Cypriniformes (but is not a true Cypriniformes) is marine. Cypriniformes are reported in the lower and basal middle members of the El Molino Formation in association with marine fishes.

e. Characiformes

Living Characiformes are freshwater fishes (only a few exceptions enter brackish waters) while some fossils were apparently adapted to brackish water (Cappetta *et al.*, 1972; Gaudant, 1980). The oldest true Characiformes, *Salminops* (Gayet, 1985), was marine (Gayet, 1981). In Bolivia, Characiformes are reported in the lower and basal middle members of the El Molino Formation (Serrasalminae, Myleinae; Characidae, Tetragonopterinae), in the Santa Lucía Formation at Tiupampa (Serrasalminae, Myleinae and Serrasalminae; Characidae, Tetragonopterinae and cf. Rhoadsiinae) and in the Eocene age Cayara Formation (Serrasalminae, Myleinae). In the El Molino Formation they occur in the same levels as marine fishes.

f. Siluriformes

Most Siluriformes occur in fresh water. However, the Plotosidae are an advanced marine family which today occur around Australia and the Ariidae live along the coast or enter estuaries and coastal rivers. Tertiary Siluriformes were reported in fresh water areas and/or in brackish water (see Gayet, 1991). In Bolivia, Andinichthyoidea (3 families) are known in the Santa Lucía Formation at Tiupampa and Blanco Rancho (the ichthyofauna of the later locality is not yet well enough known to provide paleoenvironmental interpretation); they are not reported at Agua Clara or Hotel Cordillera where marine fishes are present and may be considered as freshwater forms. Ariidae are reported everywhere in both formations with or without marine fishes. They are present at Tiupampa, but are few in number. At Hotel Cordillera they are very numerous and occur in association with a few marine taxa.

3. Marine fishes

a. Selachians

Selachians are considered as marine fishes. Nevertheless, one family of American batoids (Potamotrygonidae) lives exclusively in fresh waters. One pristid fish and a shark can also enter rivers or

lakes, but it is important to note that these elasmobranch fishes are marine species which temporarily enter fresh water. According to Cappetta (1991), it is highly probable that the rocks containing selachians in Bolivia were deposited in marine environments.

b. Pycnodontiformes

Pycnodonts, a purely fossil group, are considered to have been marine fishes (Cione & Pereira, 1985). They were flat and high fishes that apparently swam slowly along the coast and were linked to the substratum for their alimentation. Some could probably enter waters of lesser salinity. Wenz (1989) noted that the Brazilian lower Cretaceous pycnodontid *Iemanja* may have lived in fresh water. Traquair (1910) thought that pycnodonts found at Bernissart (Belgium) with the reptile *Iguanodon* were living in fresh water without any connection with the sea. Nevertheless, these examples are sporadic and pycnodonts are typically found in more or less open marine environments in rocks of Jurassic and Cretaceous age (Hakel and Hajula in Lebanon; Ein Jabrud in Israel; Jebel Tselfat in Morocco; etc.). In Bolivia, pycnodonts were reported in the Chaunaca Formation (only one tooth of no paleoenvironmental significance) and in the lower and basal middle El Molino.

c. "Salmoniformes"

"Salmoniformes" are a paraphyletic group present in all kinds of environments (Berra, 1981). Nevertheless, Enchodontidae (*Enchodus*) and Ichthyotringoidei (including ?*Apateodus*) are known only in marine rocks (Goody, 1969). In Bolivia, "Salmoniformes" were reported in the lower and basal middle members of the El Molino Formation.

d. Tetraodontiformes

One living family of the order Tetraodontiformes, the Tetraodontidae with about 90 species, has a few fresh water representatives in South America, Africa and India (Berra, 1981). However, Eotrigonodontidae is a fossil family so far known only in marine deposits. *Stephanodus* has only been found in late Cretaceous marine sediments. In Bolivia, the eotetragonopterid *Stephanodus* has been reported in the first two members of the El Molino Formation.

In conclusion, we note that at Tiupampa and Criadero de Loro (Santa Lucía Formation, Paleocene), no true marine fishes (selachians, pycnodonts, Salmoniformes and Eotrigonodontidae) have been reported. All of the primary freshwater fishes reported in Bolivia, with the exception of Semionotidae (*Lepidotes*) which do not cross the Cretaceous/Paleocene boundary, are present at these localities. Although some Osteoglossidae may occur in marine waters (i.e. *Brychaetus*), the subfamily Phareodontinae is known thus far only in fresh water levels. Tiupampa is the only Bolivian locality where nearly complete skulls (Osteoglossiformes, Siluriformes and Characiformes) were found. In all other localities bones are always separated, attesting to postmortem movement. Thus, based solely on the ichthyofauna, we can confidently conclude that the Tiupampa and Criadero de Loro fossiliferous sediments were deposited in a fresh water environment.

More difficult is the interpretation of the ichthyofauna from the El Molino Formation. In nearly all the localities, marine and fresh water fishes occur in association and, as noted above, bones, teeth and scales are never found articulated. It is probable that the calcareous fossiliferous levels of the lower member of the El Molino Formation at Agua Clara were deposited in or near the sea (lagoon or coast). Other levels at the same locality (e.g. some green marls) were probably deposited farther from the sea (perhaps without any connexion with it). *Gasteroclupea*, which has been found articulated in these levels, has also been reported at Tiupampa and is possibly a freshwater genus. Nevertheless, this does not dismiss the possibility of a brackish water habit for this genus.

Camoin *et al.* (1991) concluded that the El Molino rocks were deposited in a continental environment, while Gayet *et al.* (1992) and Sempere (in press) noted that marine fish taxa occur in these sedimentary rocks and discuss their depositional environment.

Higher vertebrates

Crocodyles of the family Dyrosauridae generally occur in shallow marine near-shore deposits, but can exist in fresh water as well (Buffetaut, 1982). The amphibians, lizards, snakes, turtles, other families of crocodiles and mammals all indicate terrestrial and/or fresh water paleoenvironments.

D. PALEOBIOGEOGRAPHY

Numerous vertebrate groups in the late Cretaceous and Paleocene of South America are also recorded in North America, and these faunal "links" were used by paleontologists to postulate that a trans-Caribbean land bridge existed during part or all of this time interval (see Gayet *et al.*, in press; Marshall & Sempere, in press and references therein). These conclusions have recently been corroborated by geodynamic data (see Pindell *et al.*, 1988; Stephan *et al.*, 1990). It now appears that the Caribbean plate began its east-northeastward migration in Campanian time. The now submerged Greater Antilles and the Aves Ridge formed a subaerial volcanic arc established on the northeastern edge of the Caribbean plate during the late Cretaceous and early Paleocene. It is likely that this arc was the land bridge that provided the pathway for dispersal of continental (and fresh water) vertebrates. However, the land bridge provided by the Aves Ridge was apparently strongly dependent on the magmatic and tectonic activity of this arc, and on sea level changes. Magmatic-tectonic quiescence and/or marine high-stand periods would have promoted relative subsidence of part of the isthmus below sea level. In view of the probable fragility of the Aves Ridge connection, faunal interchange is likely to have occurred in several "pulses" beginning in the Campanian until the land bridge finally disappeared in late Paleocene time as is suggested by paleontological data. This "pulse-hypothesis" would have permitted opportunities for endemic evolution of first-wave immigrants and for subsequent dispersal during a later "pulse". For this reason, the direction of dispersal of most groups is not certain (Marshall & Sempere, in press).

Some vertebrate groups which participated in this interchange(s) include dinosaurs (Avisauridae, Ceratopsidae, Hadrosauridae, Titanosauridae), snakes (Anilioidea, Boidea), possibly lizards (Teiidae) and shore-dwelling turtles (Bothremydidae) (Gayet *et al.*,

in press; Marshall & Sempere, in press and references therein). Among fishes are the Lepisosteidae (*Lepisosteus*), Osteoglossidae (Phareodontinae) and possibly Cypriniformes and Ariidae (Gayet *et al.*, in press).

Multiple taxonomic similarities among mammals (10 examples) "link" late Cretaceous and/or Paleocene faunas in North America with early and middle Paleocene (Tiupampian and Itaboraian, respectively) faunas in South America. Among marsupials, *Peradectes* is known in Tiupampian faunas of Bolivia and Peru, and is present in early Paleocene faunas of North America; caroloameghiniids (*Glasbius*) are present in the late Cretaceous of North America and Tiupampian (*Roberthoffstetteria*) of South America; Didelphidae are present in the early Eocene of North America and Tiupampian of South America; and Pedomyidae (late Cretaceous of North America) are a sister-group of Microbiotheriidae (first recorded in the Tiupampian of South America). Among placentals, a Leptictida (*cf. Cimolestes*) is known from Tiupampa while *Cimolestes* occurs in the late Cretaceous and early Paleocene of North America; Pantodonta (*Alcidedorbignya*) at Tiupampa are first known in the middle Paleocene in North America; mioclaenine hyopsodontid Condylarthra at Tiupampa are first recorded in early Paleocene faunas of North America; Xenarthra (Dasypodidae) first appear in Itaboraian faunas in South America and in the late Paleocene in North America; and Dinocerata which first appear in the late Paleocene of North America are regarded as a sister-group of Xenungulata which occur in the Itaboraian of South America (Marshall & Muizon, 1988; Marshall & Sempere, in press; Gayet *et al.*, in press and references therein).

Although latest Cretaceous and Paleocene interchanges are well documented, it is of interest to note that several terrestrial groups of vertebrates which were often rather widely distributed either in the Laurasian realm or on Gondwanian continents in the late Cretaceous and Paleocene, never crossed the Caribbean nor Tethyan areas. Acipenserid, polyodontid and goniorhynchoid fishes, as well as palaeobatrachid frogs, baenid turtles, and anguimorph lizards inhabited North America during the Cretaceous; hiodontid and esocid fishes were present on that continent during the Paleocene. None of these northern groups reached South America. Conversely, polypterid and characiforms, as well as pipid frogs and arapemyid turtles of Gondwanian origin, known in the Cretaceous of South America, did not reach North America. The above listed vertebrates rank among the most significant ones that did not take part in the late Cretaceous and Paleocene interchange(s). Other groups could be added to this list but, for the time being, they cannot be considered to be very conclusive because their distribution is still inadequately known.

The failure of various groups to cross the Caribbean area would apparently favour the hypothesis of a discontinuous terrestrial route or even an island hopping hypothesis. But the ascertained dispersals of large-size animals as Titanosauridae and of freshwater fishes (Lepisosteidae, Phareodontinae, and perhaps Ariidae) are inconsistent with such possibilities as they require a continuous land (fluvial for the fishes) route. These failures could result from climatic, faunal interactions (niches occupied by ecologically vicarious autochthonous forms) or shortness of duration of the unbroken nature of the land route.

CONCLUSIONS

This paper is the first attempt to provide a detailed overview of the Mesozoic and Paleocene vertebrate faunas of Bolivia within their stratigraphic context. Much of the information presented here is new, and includes data obtained as a result of an intense paleontological program started in 1981 (M. G., L. G. M and others) and of geologic studies initiated in 1984 (T. S. and others). Most of the fossils are still being described and it will be many years before monographic publications can be completed. In addition, magnetostratigraphic and isotopic (Ar/Ar, K-Ar) studies of the El Molino and Santa Lucía formations and isotopic oxygen and strontium analyses on fishes are in progress, and completion of this geochronologic program will hopefully permit secure calibration of these rock units with the geologic time scale. Synthetic overviews for the biostratigraphy of Argentinian, Chilean and Peruvian rocks in the Andean basin are now urgently needed to permit refined correlation with those in Bolivia.

Despite the fact that this is by necessity only a "progress report", many advances in knowledge have been made on the Bolivian Mesozoic-Paleocene sequence during the last few years, and in this study we have been able to clarify some debated issues. The most important of these is the apparent, although still ill-defined, location of the K/T boundary and its position relative to the mammal-bearing level at Tiupampa. Within the El Molino Formation, undoubted late Cretaceous taxa occur only in the lower and basal middle members. It therefore appears that the K/T boundary lies somewhere in the upper part of the middle member, while the upper member may be regarded as earliest Paleocene based on the absence of diagnostic Cretaceous taxa and on the palynological studies of a stratigraphic equivalent in northwestern Argentina. The El Molino thus appears to range from latest Campanian to earliest Paleocene, while the disconformably overlying Santa Lucía Formation appears to be early, but not earliest, Paleocene. Thus, *contra* Van Valen (1988), the El Molino dinosaurs were all late Cretaceous (apparently early Maastrichtian), while the land mammals from the Santa Lucía Formation at Tiupampa were Paleocene.

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