Middle Maastrichtian vertebrates (fishes, amphibians, dinosaurs and other reptiles, mammals) from Pajcha Pata (Bolivia). Biostratigraphic, palaeoecologic and palaeobiogeographic implications

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Abstract

The Pajcha Pata fossil locality in south central Bolivia, in the upper part of the Lower Member of the El Molino Formation, is the first late Cretaceous fauna in South America which has yielded, in addition to some invertebrates and plants, all kinds of vertebrates except birds, but including dinosaurs and mammals. Its middle Maastrichtian age, indicated by geochronologic data, is consistent with the fauna, including the marine ichthyofauna. The vertebrate fossils reported here come from the main fossiliferous level which includes terrestrial, freshwater and marine taxa: vertebrates, Mammalia (both tribosphenic and non-tribosphenic therians), Theropoda (Coelurosauria and Sauropoda), Crocodylia, Squamata (Serpentes), Chelonia, Amphibia (Anura, Gymnophiona, Caudata) and fish (Dipnoi, Teleostei, Actinopteri, Cladistia, Chondrostei); invertebrates (Gastropoda, Bryozoa) and plants (charophytes). Amongst these taxa are the earliest records of some fish, Amphibia and tribosphenic Mammalia in South America and/or in the world. The fish concerned are: Polypteriformes (*Latinopollia suarezi*), Siluriformes of the family Andinichthyidae (*Andinichthys*) and two new families, Osteoglossiformes of the subfamily Heterotidinae (Osteoglossidae), Perciformes of the family Latidae, Dipnoi of the family Lepidosirenidae (*Lepidosiren* cf. *paradoxa*). The Amphibia concerned are: indeterminate Gymnophiona, Noterpetontidae (*Noterpeton bolivianum*). Pajcha Pata is the only known locality in South America with both non-tribosphenic and tribosphenic therian mammals. The depositional environment was probably estuarian or lagoonal as indicated by a mixed continental, freshwater, and marine fauna. Comparison of this local fauna with faunas of the same age at localities belonging to the same proximal part of the El Molino basin on one hand, and with others belonging to the distal part on the other hand, shows that the two continental areas seem to have their own endemic freshwater fish fauna (except the Characidae and the Lepisosteidae, known in all levels of Bolivia). However, these two areas have the same marine taxa. This implies some influence of the sea in the whole basin. Calculated temperatures of the marine waters range

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from 13 to 17° for a latitute of about 22°S, implying a southern Pacific upwelling. The El Molino Basin could have been also connected with the open sea through present-day Argentina and not only Venezuela as thought until now. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Maastrichtian; Bolivia; Vertebrates; Taxonomy; Palaeoecology; Palaeobiostratigraphy

1. Introduction

There currently exists a major dearth in knowledge of continental vertebrate evolution in South America for the middle and late Maastrichtian time. Taxonomically diverse local faunas are known only from the late Campanian-early Maastrichtian age Los Alamitos locality of Argentina (Bonaparte, 1987) and the early late Palaeocene age Tiupampa[51] locality of Bolivia, but these provide only intriguing glimpses into what may have been occurring during the intervening period [number following the Bolivian localities (e.g. Tiupampa[51]) is referring to those originally used by Gayet et al. (1991) and is useful in discussing levels of different age at the same locality (i.e. Tiupampa[28]: late Cretaceous; Tiupampa[51]: early late Paleocene) (see also Table 1)].

In this paper, we describe the vertebrate fauna from near the pueblo Pajcha Pata, about 40 km southeast of Cochabamba, in south central Bolivia (Fig. 1). The principal fossil locality (Pajcha Pata[12]), discovered by Marshall and Sempere in 1989, is located 1 km northeast of Pajcha Pata on the northern side of the Cliza–Anzaldo road. Several other fossiliferous levels of similar age in this area discovered by Gayet and Marshall in 1989 and by Gayet, Marshall and Meunier in 1994, 1997 have thus far yielded only fish; they are under preparation and study, and will be described in later publications. The only publications on the Pajcha Pata local fauna to date are the report of a coelurosaur tooth (Marshall, 1989), a preliminary faunal list (Gayet et al., 1991), description of a lungfish (Schultze, 1991), preliminary description of some fish (Gayet, 1991), and description of an enigmatic Caudata (Rage et al., 1993).

We describe herein, the first well-calibrated and taxonomically diverse continental and freshwater local fauna of middle Maastrichtian age in South America, i.e. the principal locality of the Pajcha Pata area, hereafter referred to as Pajcha Pata[12]. These fossils can be (and are) interpreted in a palaeoenvironmental context. Comparisons are

Table 1

Vertebrate fossil localities of Mesozoic and Paleocene age in Bolivia. Only the localities discussed in the text are listed. For more complete information, see Gayet et al. (1991, p. 404)

EL MOLINO FORMATION
(Maastrichtian–Danian)
Lower member (Maastrichtian)
7. Agua Clara
11. La Palca
12. Pajcha Pata
13. Rancho Hoyada (Quebrada Texisca)
16. Torotoro (Cerro Llama Chaqui)
17. Torotoro (Uma Jalanta cave)
18. Torotoro (Uma Jalanta road)
19. Torotoro ('pista de danzas')
20. Torotoro (Selacians)
21. Vila Vila

Middle member (late Maastrichtian–Danian)
24. Santivañez
25. Hotel Cordillera
26. Huarachani
28. Tiupampa (Hera Mokho)
30. Vilcapujio

Upper Member (latest Danian)
27. Rancho Hoyada (Quebrada Texisca)
35. Estancia Blanco Rancho
38. Tiupampa (Rio Pucarani)

Indeterminate member
39. Arapampa (dinosaur footprints)
40. Camargo (dinosaur footprints)

SANTA LUCIA FORMATION (early late Paleocene)
50. Estancia Blanco Rancho
51. Tiupampa (quarry and associated localities)
52. Criadero de Loro
53. Torotoro

IMPORA FORMATION (late Paleocene)
56. Villa Pacheco

made primarily with other late Cretaceous localities of the El Molino Formation in Bolivia, and with some early late Palaeocene ones from the Santa Lucía Formation, in which similar and diverse taxa occur.
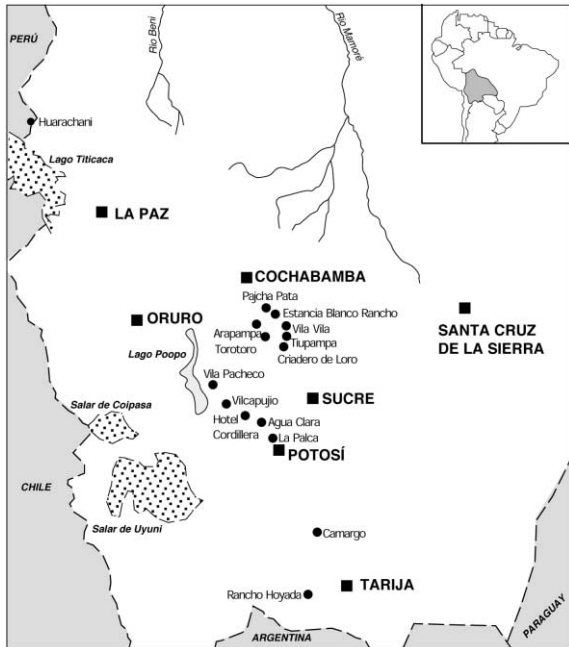
Fig. 1. Map of southern Bolivia showing the vertebrate localities of Maastrichtian to Paleocene noted in the text; for other Bolivian localities of the same age (see Gayet et al., 1993 fig. 2).

2. Stratigraphic context and age

The only study of the regional geology around Pajcha Pata is by Montaño (1968). A schematic stratigraphic section of the El Molino/Santa Lucía succession of this locality was published by Gayet et al. (1991). The fossils described in this paper occur about 30 m above the base of the El Molino Formation. This is in the base of the upper part of the Lower Member of the El Molino Formation (Gayet et al., 1993; Sempere et al., 1997) (Fig. 2). The fossiliferous unit is about 3-m thick, and consists of red to yellow, fine- to medium-grained sandstone.The bed represents a broad channel that can be followed for about 2 km to the northeast of Pajcha Pata.

Based on a detailed study of the magnetostratigraphy of the El Molino Formation at the La Palca stratotype section near Potosí, and applying sequence stratigraphic methods for correlating with the Pajcha Pata section, the fossil bed is ≈68.4 Ma (Sempere et al., 1997, following the time scale of Cande and Kent, 1992, 1995). The bed was deposited during a sharp and short regressive phase of the dominantly marine-influenced Lower El Molino at a time when deposition rates for the El Molino were highest. The channel sands derive from a large northeasterly draining river system (see Gayet et al., 1993).

3. Material and methods

The material was collected during two days (Marshall in 1989) and two weeks (Gayet and Meunier in 1994) of surface prospecting and three weeks of screen washing (Gayet, Meunier and Marshall in 1997). The samples contained bony material, teeth and scales. Sorting of the sediment was done in Lyon, Montpellier and Paris under binocular. The material collected at Pajcha Pata[12] and used in this paper belongs to the Museo de Historia Natural de Cochabamba, Cochabamba, Bolivia (MHNC); it is on loan to the UFR des Sciences de la Terre, Université Claude Bernard, Lyon I, Villeurbanne, France. Only the figured specimens are numbered.

4. Results (Tables 2 and 3)

4.1. Systematic palaeontology

The fossil remains found at Pajcha Pata[12] are mostly vertebrates. Nevertheless, a small number of invertebrates and plants have been recovered. They are generally very small and poorly preserved. There are gastropods (internal casts that seem identical to those found at Vila Vila[21] and Tiupampa[28]), and Bryozoa. The flora is composed of charophytes. Some fish taxa (Gasteroclupea, Atherinomorpha), already reported at Pajcha Pata (Gayet, 1991; Gayet et al., 1991) do not come from the main level but are from the area that includes this locality discussed in this paper. Consequently, they are not discussed in this present work.

The systematics follows 'The Fossil Record 2' according to Cappetta et al. (1993) (Chondrichthyes, pp. 591–609), Gardiner (Osteichthyes: basal Actinopterygians, pp. 611–619), Patterson (Osteichthyes: Teleostei, pp. 621–656) and Schultze (1993) (Osteichthyes: Sarcopterygii, pp. 657–663). Some taxa (i.e. Amphibia, Reptilia) are used even though they are acknowledged to be paraphyletic.
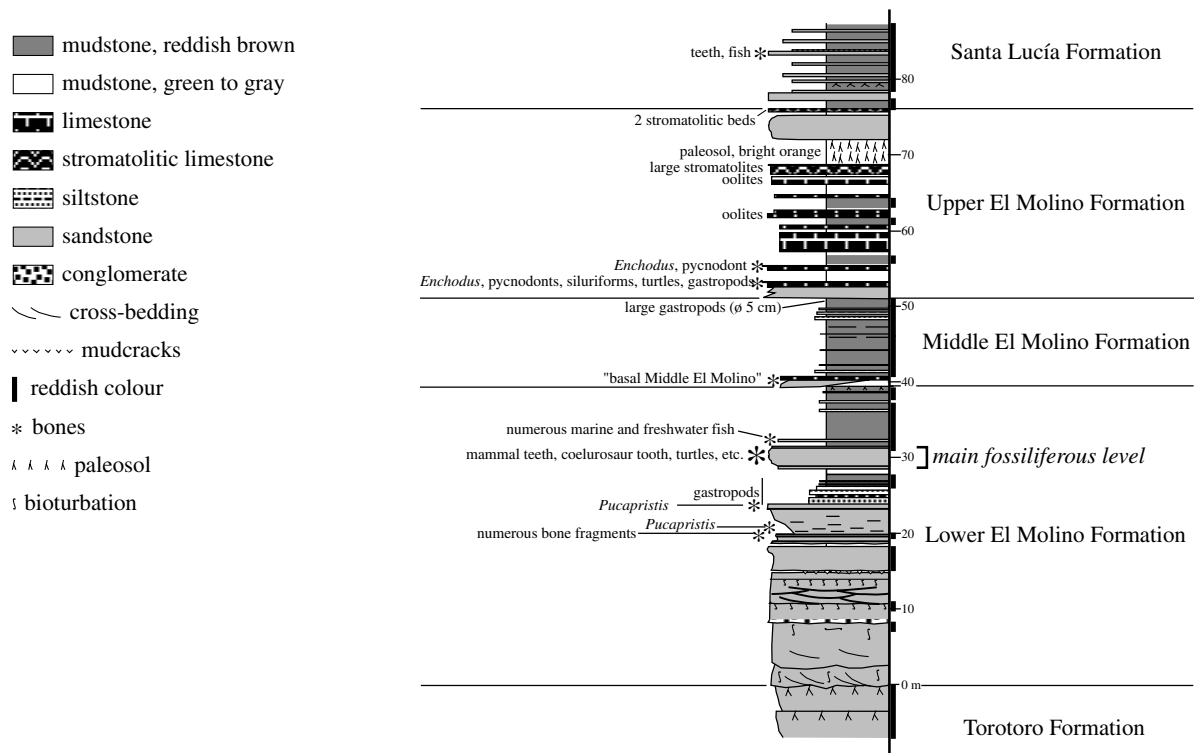
Fig. 2. Stratigraphic section of Pajcha Pata showing lithology, stratigraphic units and main fossil level.

Class: CHONDRICHTHYES
Order: RAJIFORMES
Family: SCLERORHYNCHIDAE
Genus *Pucapristis* Schaeffer, 1963
Pucapristis branisi Schaeffer, 1963
   Pajcha Pata[12] *material: 4 oral teeth; Vila Vila*[21] *material: 57 fragmentary rostral teeth.*
Oral teeth rather compressed mesio-distally with a well cuspidate crown showing a strong labial crest dividing above a prominent rounded apron (Fig. 3a); root high with a very convex basal face. All available rostral teeth broken (Fig. 3b); some of them reach a length of 6 cm.

Genus *Ischyrhiza* Leidy, 1856
Ischyrhiza hartenbergeri Cappetta, 1975
   Pajcha Pata[12] *material: 22 oral teeth, 10 fragmentary teeth; Vila Vila*[21] *material: three fragmentary rostral teeth.*
Oral teeth, on the whole, more transversally elongate than the teeth of *Pucapristis* except in the most anterior rows, cuspidate, with a strong undivided labial crest (Fig. 3c); root high with a flat basal surface; rostral teeth (Fig. 3d), small with a peduncle devoid of grooves and folds on the upper and lower surfaces; cusp rather thick, with some short anterior folds.

Order MYLIOBATIFORMES
Family DASYATIDAE
The three species cited below are currently attributed to the genus *Dasyatis*, but at least two of them (*D. branisai* and *D. molinoensis*) show enough peculiar dental morphology to be placed in new genera pending complete study of the material.

Genus *Dasyatis* Rafinesque, 1810
"Dasyatis" branisai Cappetta, 1975
   Pajcha Pata[12] *material: 4 oral teeth; Vila Vila*[21] *material: six oral teeth.*
Teeth of this species have a high and rounded crown showing a smooth transverse keel strongly convex in occlusal view (Fig. 3e); the crown can bear an occlusal

Table 2
List of fossil vertebrates from the Pajcha Pata[12] local fauna in the lower El Molino formation (Bolivia)

CHONDRICHTHYES
Order Rajiformes
  Family Sclerorhynchidae
    Pucapristis branisi
    Ischyrhiza hartenbergeri
Order Myliobatiformes
  Family Dasyatidae
    Dasyatis schaefferi
    '*Dasyatis*' *branisai*
    '*Dasyatis*' *molinoensis*
  Family Rhombodontidae
    Pucabatis hoffstetteri

OSTEICHTHYES
Infraclass Cladistia
  Family new
    Latinopollia suarezi
  Family Polypteridae
    Dagetella sudamericana
Infraclass Actinopteri
Division Ginglymodi
  Family Lepisosteidae
    Lepisoteus sp.
Division Halecostomi
  Family Semionotidae
    Lepidotyle enigmatica
  Order Pycnodontiformes
    Pycnodontiformes indet.
     Stephanodus minimus
    Family Pycnodontidae
     Coelodus toncoensis
     Coelodus sp.
Infraclass Teleostei
  Order Osteoglossiformes
    Family Osteoglossidae
     Subfamily Heterotidinae
      Heterotidinae indet.
     Subfamily Phareodontinae
      Phaerodusichthys taverni
Order Characiformes
  suborder Characoidei
    New genus
    Family Characidae
     Subfam. Serrasalminae
      Serrasalminae indet. 1
      ?Serrasalminae indet. 2
     Subfam. Tetragonopterinae
      Tetragonopterinae indet.
Order Siluriformes
  Family Andinichthyidae
    Andinichthys sp.
  Families indet.
    New genus 1 and 2

Table 2 (*continued*)

Doradoida
  New genus
  Order indet.
    New genus
  Order Aulopiformes
    Family Enchodotidae
     Enchodus sp.
  Order Perciformes
    Family Latidae
     New genus
    Family Percichthyidae
     cf. *Santosius* sp.
Subclass Sarcopterygii
  Order Dipnoi
    Family Ceratodontidae
     Ceratodus sp.
    Family Lepidosirenidae
     Lepidosiren cf. *paradoxa*

AMPHIBIA
Order Gymnophiona
  Family indet.
    Genus and species indet.
Order Caudata
  Suborder Urodela
    Family Noterpetontidae
     Noterpeton bolivianum
Order Salienta
  SuborderAnura
    Family indet.
     Genus and species indet.

REPTILIA
Order Chelonii
  Family Podocnemididae
    Gen. and sp. indet.
Order Squamata
  Suborder Serpentes
    Family ?Madtsoiidae
    New Genus
Order Crocodylia
  Crocodylia indet.
Order Saurischia
  Suborder Theropoda
    Infraorder Coelurosauria
     Family indet.
      Genus and species indet.
    Infraorder Sauropoda
     Family indet.
      Gen. and sp. indet.

MAMMALIA
    Gen. and sp. indet. 1
    Gen. and sp. indet. 2
    Gen. and sp. indet. 3

Table 3

Chronostratigraphic ranges of vertebrate taxa found at Pajcha Pata[12] (stippled column = Pajcha Pata[12]). Black lines represent the ranges of taxa before their discovery at Pajcha Pata[12]. Vertebrates, which are not biostratigraphically informative, are not listed. Ce = Cenomanian; Tu = Turonian; Co = Coniacian; Sa = Santonian; Ca = Campanian; Ma = Maastrichtian; Da = Danian; Th = Thanetian; E = Eocene, Ol = Oligocene; Mi = Miocene; Pli = Pliocene; Ple = Pleistocene; R = Recent. Subdivisions within the Maastrichtian (dotted lines) represent the Lower, Middle and Upper Members

Taxa known at Pajcha Pata	Upper Cretaceous					El Molino Fm	Cenozoic							R
	Ce	Tu	Co	Sa	Ca	Ma	Da	Th	Eo	Ol	Mi	Pli	Ple	
Pucapristis branisi														
Ischyrhiza hartenbergeri														
"Dasyatis" branisai														
"Dasyatis" molinoensis														
Dasyatis schaefferi														
Pucabatis hoffstetteri														
Latinopollia suarezi														
Dagetella sudamericana														
Lepisosteus sp.														
Lepidotyle enigmatica														
Coelodus toncoensis														
Stephanodus minimus														
Subfamily Heterotidinae														
Phaerodusichthys taverni														
Suborder Characoidei, nov. gen.														
Subfam. Serrasalminae														
Subfam. Tetragonopterinae														
Andinichthys sp.														
Arioida, nov. gen														
Enchodus sp.														
Family Latidae, nov. gen.														
cf. *Santosius* sp.														
Ceratodus sp.														
Lepidosiren cf. *paradoxa*														
Suborder Apoda														
Noterpeton bolivianum								?						
Suborder Anura														
Family ? Madtsoiidae														
Infraorder Coelurosauria														
Infraorder Sauropoda														

hollow in lateral teeth and eroded folds on the lingual surface; root high but rather narrow, mainly at the level of its basal surface; oblique lingually; main foramen in a labial position in the median groove. This species resembles *D. schaefferi* in its tooth morphology; but it differs from the latter in having a narrower and more lingually elongated root and a less regularly rounded crown, often with an occlusal hollow.
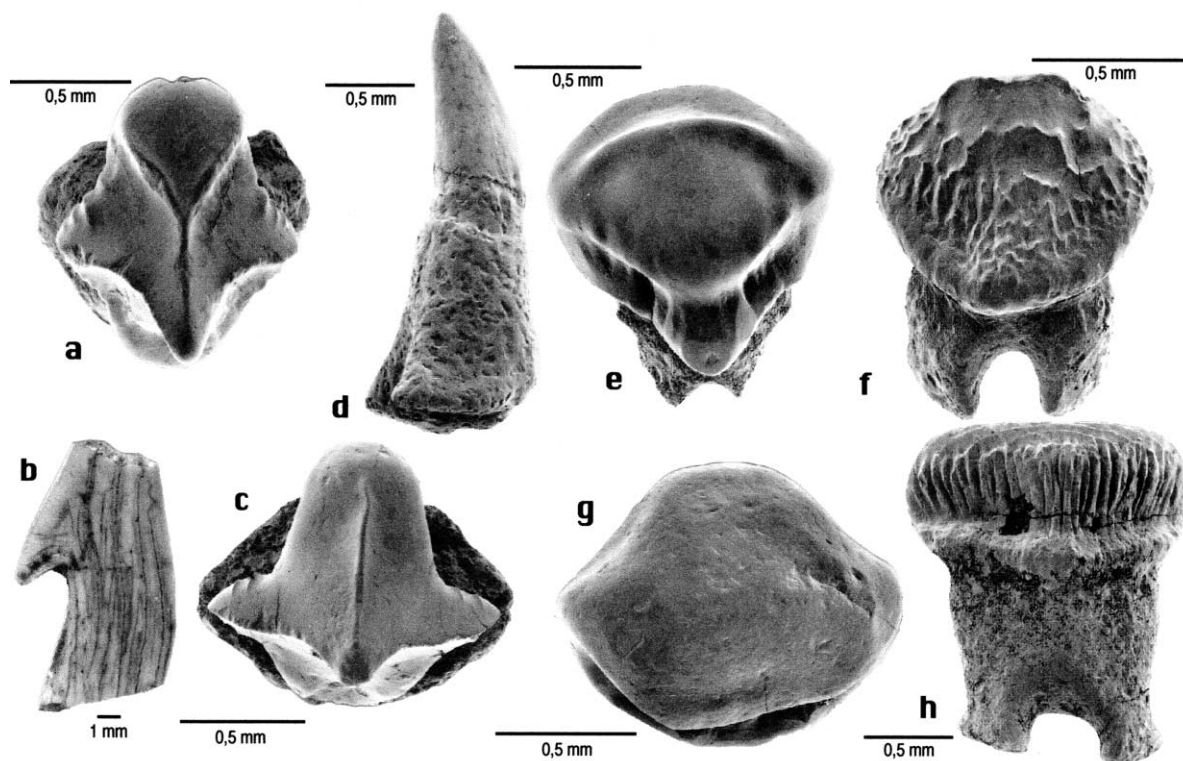
Fig. 3. Selachians: (a) *Pucapristis branisi* anterior tooth in oral view (MHNC 8545). (b) *Pucapristis branisi* rostral tooth in profile view (MHNC 8592). (c) *Ischyrhiza hartenbergeri* anterior tooth in oral view (MHNC 8546). (d) *Ischyrhiza hartenbergeri* rostral tooth in profile view (MHNC 8547). (e) *"Dasyatis" branisai*: lateral tooth in oral view (MHNC 8548). (f) *"Dasyatis" molinoensis*: lateral tooth in oral view (MHNC 8549). (g) *Dasyatis schaefferi:* lateral tooth in oral view (MHNC 8550). (h) *Pucabatis hoffstetteri*: tooth in posterior view (MHNC 8551).

"Dasyatis" molinoensis Cappetta, 1975
　Pajcha Pata[12] *material: three oral teeth; Vila Vila*[21] *material: two oral teeth.*

Very characteristic teeth, with a high crown bearing a cutting transverse keel and many irregular folds on the labial and lingual surfaces (Fig. 3f); root high and narrow mesio-distally. This species also occurs at Torotoro[20] and Vila Vila[21], but is always rare.

'Dasyatis' schaefferi Cappetta, 1975
　Pajcha Pata[12] *material: 8 oral teeth; Vila Vila*[21] *material: 5 oral teeth.*

High and rounded crown with hexagonal outline in occlusal view (Fig. 3g); no differentiated transverse keel and enamel always smooth; root not high, weakly developed lingually, with lobes showing a very flat basal surface. This species exhibits the most specialised crushing type of dentition among the dasyatid species occurring in Bolivia.

Family RHOMBODONTIDAE
Genus ***Pucabatis*** Cappetta, 1975
Pucabatis hoffstetteri Cappetta, 1975
　Pajcha Pata[12] *material: 74 oral teeth; Vila Vila*[21] *material: 157 oral teeth.*

Probably the most distinctive selachian species of Bolivia (Fig. 3h). Teeth high with a crown of rhombic outline in occlusal view; occlusal surface with a typical ornamentation made of herring-bone pattern folds, concave lingually in occlusal view; irregular, flexuous and more or less labio-lingually oriented folds above the labial and lingual angles of the crown; root very high; basal part of the lobes, short compared with the total root length, much narrower than the basal part of the root, just below the crown. The most striking

feature of this species is probably the completely labial position of the main foramen of the root. The teeth collected at Pajcha Pata[12] are smaller, on the whole, than at Vila Vila[21]; this could result from ecological causes or indicate a more juvenile population.

On the whole, selachians from the El Molino Formation in Bolivia contain a maximum of 11 species. Vila Vila[21], Torotoro[20] and Pajcha Pata[12] (basal upper part of the Lower Member of this formation), show the same faunal assemblage. They are easily distinguished from Agua Clara[7], which occurs in the lower part of the Lower Member and contains a new, more primitive species of *Pucabatis* and a new species of dasyatid (crown and root less high and less complex enamel ornamentation of the occlusal surface of the crown). Hotel Cordillera[25] (Middle Member) contains the same species except *"Dasyatis" molinoensis* and *D. schaefferi*, which are lacking. Rancho Hoyada[27] (Upper Member) contains a small assemblage of two dasyatids representing new species not occurring elsewhere. At Tiupampa[51], a strictly continental locality, no selachians have been found.

Practically all selachian species collected in Bolivia are endemic and are of only regional use in biochronology except the sclerorhynchid *Schizorhiza* aff. *stromeri*, which occurs only at Agua Clara[7] and Hotel Cordillera[25]. As sclerorhynchids are restricted to the Cretaceous, they are particularly important for biochronology; *Schizorhiza* is widespread in Maastrichtian deposits in North America (Dunkle, 1948), in Africa (Weiler, 1930; Arambourg, 1940; Arambourg, 1952; Dartevelle and Casier, 1943; Noubhani and Cappetta, 1997), in the Middle East (Signeux, 1959) and in Bolivia (Cappetta, 1991). It is possible that this genus, with a very derived rostral and oral dentition, occurs as early as the Campanian, in Bolivia and in Egypt, but this needs confirmation. The rhombodontid genus *Pucabatis* is endemic, and so is of biochronologic value only in the Andean basin. The Rhombodontidae, as far as known, are restricted to Maastrichtian deposits. The first dasyatids are known as early as the Cenomanian in North America (Meyer, 1974), but become abundant only in the Maastrichtian. In summary, despite the highly endemic character of the Bolivian elasmobranch faunas, their presence suggests a Cretaceous age.

OSTEICHTHYES
Subclass: ACTINOPTERYGII
Infraclass: CLADISTIA
Genus *Latinopollia* Meunier and Gayet, 1998
Latinopollia suarezi (Meunier and Gayet, 1996)
Family POLYPTERIDAE
Genus *Dagetella* Gayet and Meunier, 1992
Dagetella sudamericana Gayet and Meunier, 1992
    Pajcha Pata[12] and Vila Vila[21] material: isolated scales, neurocranial elements, spines of finlets, and vertebrae.

These remains can be assigned to cladistians because of the peculiar histology of the scales and morphology of the bones typical of this group (Gayet and Meunier, 1992; Meunier and Gayet, 1996; Bartsch and Gembella, 1992; Sire, 1989). Scales smooth on their upper surface without any ornamental ridges (Fig. 4a); some large (about 1 cm^2) and thick, others smaller and thinner, and with more numerous openings on their upper surface; histology typical of either *Dagetella* or *Latinopollia* (Meunier and Gayet, 1996); spines of finlets (the so-called pinnulae, Fig. 4b), and vertebrae typical of this group (Fig. 4c,d): neural arches fused together in a narrow and elongated tube along nearly the whole length of the centrum; cupule for insertion of the supraneural element either open, as in living forms, or closed. Large size of some vertebrae and morphological similarities with those found at Tiupampa[51] permit tentative assignment to *Latinopollia* (Fig. 4c); smaller ones probably belong to *Dagetella* (Fig. 4d). Vila Vila[21] has yielded numerous scales and fragments of neurocrania belonging to both genera, including a right extrascapular (holotype of *Dagetella sudamericana*; Gayet and Meunier, 1992). The other neurocranial bone fragments covered by thick ridges of ganoine, the cross sections of which are typical of Cladistia, cannot yet be identified.

The oldest known cladistians are from the Cenomanian of Africa (Stromer, 1936; Schaal, 1984; Sereno et al., 1996; Werner, 1993; Werner and Gayet, 1997; Dutheil, 1999a,b). Younger remains have been found from the Campano-Santonian of Niger, up to the Holocene of Mali (Gayet et al., 2001b). Recent cladistians are restricted to Africa. In South America, apart from Pajcha Pata[12] and Vila Vila[21], cladistians have been recovered at Tiupampa[51] and Criadero de
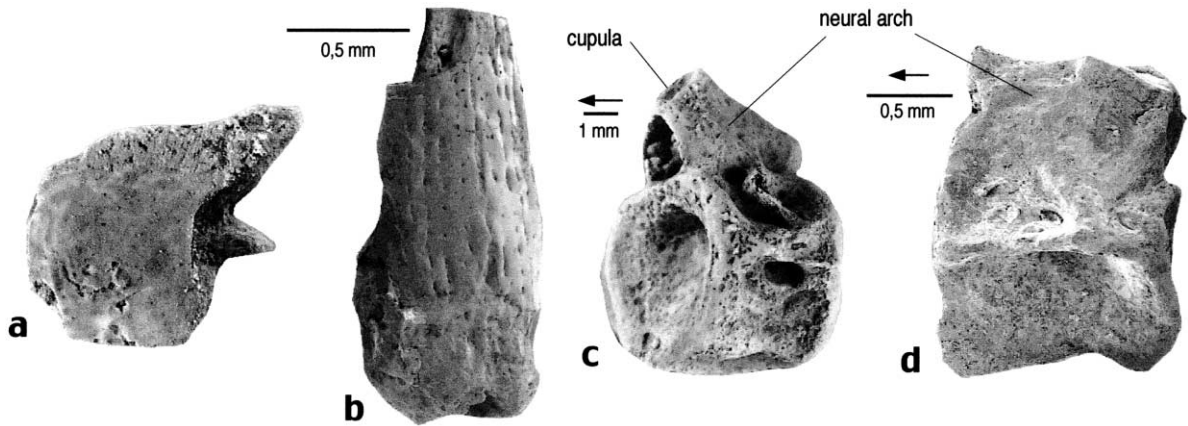
Fig. 4. Cladistia: (a) Scale of *Dagetella sudamericana* (MHNC 8552) in dorsal view. (b) Spine of finlet of *Dagetella sudamericana* (MHNC 8553) in antero-lateral view. (c) Vertebra of probably *Latinopollia* (MHNC 8554) in antero-lateral view. (d) Vertebra of probably *Dagetella* (MHNC 8555) in lateral view.

Loro[52]. In addition, scales of *Latinopollia* of late Cretaceous/early Palaeocene age, are known from Acre (western Brazil) (Meunier and Gayet, 1996). No cladistians have yet been discovered in the distal part of the Andean basin. In our present state of knowledge, the cladistian remains cannot give information about the age of the rocks in which they have been collected.

Infraclass: ACTINOPTERI
Division: GINGLYMODI
Family: LEPISOSTEIDAE
Genus: **Lepisosteus** Lacépède, 1803
Lepisosteus sp.
> *Pajcha Pata*[12] *material: isolated scales, 1 vertebra; Vila Vila*[21] *material: isolated scales, 2 vertebrae.*

Isolated ganoid scales are assigned to *Lepisosteus* because of the size of the tubercles and the spaces between them (Gayet and Meunier, 1986; 1993 which can be observed (with SEM) on the upper surface of the ganoine; Williamson canals; absence of dentine and odontod bases inserted in the ganoine layer; size of vertebrae (Fig. 5a) from 3 to 15 mm. Neurocranium remains are possibly of *Lepisosteus* (see below, *Lepidotyle*). *Lepisosteus* remains are numerous at Agua Clara[7], Hotel Cordillera[25] and Vila Vila[21]. The vertebrae discovered at Vila Vila[21] are very small (0.5 cm long) in comparison with those of Pajcha Pata[12] (1 cm long) or Hotel Cordillera[25] (4 cm long) (Gayet, 1991).

The earliest known lepisosteids are reported from the early Cretaceous of Africa (*Paralepidosteus*) (Arambourg and Joleaud, 1943; Casier, 1961) and Brasil (*Obaichthys*) (Wenz and Brito, 1992, 1996). Younger Lepisosteidae are known from the late Cretaceous of Africa and India (see Gayet and Meunier, 1993; Gottfried and Krause, 1998), to the Cenozoic of Europe, India and North America (see Wiley, 1976). Recent Lepisosteidae live in the southeastern USA and in Central America (Berra, 1981). *Lepisosteus* has been reported from the late Cretaceous Upper Baurú Group in Brazil (Santos, 1984; Gayet and Brito, 1989; Bertini et al., 1993), from the El Abra Formation (uncertain Cretaceous age) in Argentina (Gayet et al., 1991) and from Upper Cretaceous of Colombia (Gayet, 1991). *Atractosteus* is only reported in the Cenozoic of Europe and North America (Wiley, 1976; see Gayet and Meunier, 1993). Remains assigned to this genus from France (Buffetaut et al., 1996) and Argentina (Cione, 1987) are *Lepisosteus* (Gayet, unpublished data). The family Lepisosteidae was still present during Cenozoic time in Laurasia only; it seems to disappear in South America as in Africa by the end of the Cretaceous.

Division: HALECOSTOMI
Order: SEMIONOTIFORMES
Family: SEMIONOTIDAE
Genus: **Lepidotyle** Meunier and Gayet, 1992
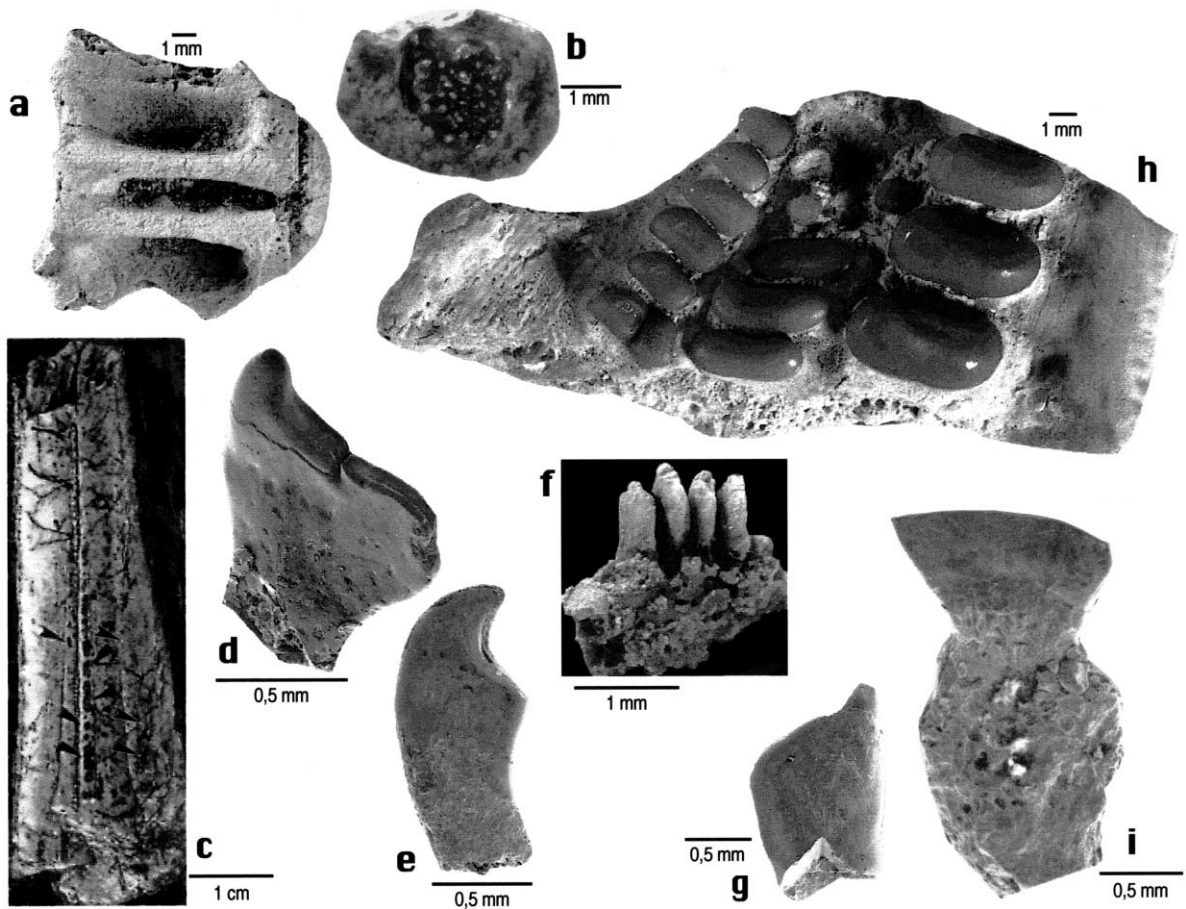*Lepidotyle enigmatica* Meunier and Gayet, 1992

Fig. 5. (a) Vertebra of *Lepisosteus* sp. (MHNC 8558) in lateral view. (b) Scale of *Lepidotyle enigmatica* (MHNC 8556) in dorsal view. (c) Rostrum of supposed *Lepidotyle enigmatica* (MHNC 8557) in dorsal view; arrows indicate ganoin patches. (d) Left splenial dentition of *Coelodus toncoensis* (MHNC 8559) in dorsal view. (e) Incisive tooth of pycnodont indet. (MHNC 8562) in anterior view (f) Series of pharyngeal teeth of pycnodont indet. (MHNC 8560) in antero-lateral view. (g) Separate pharyngeal tooth of pycnodont indet. (MHNC 8561) (h, i) Pharyngeal teeth of *Stephanodus* (MHNC 8563, MHNC 8564).

Pajcha Pata[12] material: scales, ?fragments of neurocranial bones, rostrum; *Vila Vila*[21] material: scales, ?fragments of neurocranial bones.

Peculiar ganoid quadrangular or rhomboidal-shaped scales: thick, globulous, without articular process, and with smooth or indented upper surface of ganoine, the thickness of which could be irregular (Fig. 5b); size from 1 to 8 mm; ganoid layer covering the entire surface of the scale or restricted to a crescent; scales characterised in section by the frequent presence of a remarkable remodelling of the ganoine that appears only in adult scales (Meunier and Gayet, 1992). A large, incomplete rostrum could belong to

Lepidotyle (Fig. 5c) because are the presence of large vacuums in transversal section, a remarkable remodelling of the bone, and small patches of ganoine included within the bone and covered with bony tissue; Williamson canals numerous and secondary bone lamellar; two large longitudinal bones in contact in the sagittal plan; several small, rounded patches of ganoine aligned on the median line. No tubercles are visible on the upper surface of the ganoine because of abrasion.

Semionotidae are known from the Triassic to the Maastrichtian (Patterson, 1993). Bolivian semionotids

are only represented by this endemic *Lepidotyle enigmatica* which is found in numerous localities belonging only to the Lower and basal Middle Members of the El Molino Formation (Agua Clara[7], Hotel Cordillera[25], Vila Vila[21]) and in the Yacoraite Formation, of Maastrichtian age, in Argentina (Arratia and Cione, 1996). *Lepidotyle* indicates, as far as known, a late Cretaceous age.

Order: PYCNODONTIFORMES
Pycnodontiformes indet.
Genus: **Stephanodus** Zittel, 1888
Stephanodus minimus Gayet, 1991
   Pajcha Pata[12] material: numerous pharyngeal and incisiform teeth; Vila Vila[21] material: some pharyngeal teeth.

There are some problems with the taxonomic attribution of small, flattened pharyngeal teeth (Fig. 5d,e) similar to those from Agua Clara[7] and Rancho Hoyada[13] named *Stephanodus minimus* and assigned to eotrigonodontids (Gayet, 1991). According to Patterson (1993) and Arratia and Cione (1996), who referred to Patterson in Estes and Sanchíz (1982), these teeth ought to be pharyngeal teeth of pycnodontids like those from Spain (Estes and Sanchíz, 1982) but these spanish teeth are bulbous, as those of Fig. 5f,g (Gayet, unpublished data) and differ from those markedly flattened from Bolivia. Kriwet (1999) described some flattened teeth from the early Cretaceous of Spain, similar to the Bolivian ones, that belong to the pycnodontid *Anomoedus*. In addition, *Stephanodus minimus* teeth have been recently discovered (but not figured) in the Miocene of the Amazon basin (Monsch, 1998), long after the supposed Eocene disappearance of the Pycnodontiformes (Gardiner, 1993). If this last report of *Stephanodus* is correct, it could indicate either that the pycnodonts lived more recently than previously thought, or that *Stephanodus minimus* is not a pycnodont. This implies that we must be very careful in the attribution of isolated pharyngeal teeth to pycnodonts or to tetraodontiforms (or to any fish with flattened pharyngeal teeth). We place *Stephanodus* in pycnodonts indet. pending discovery of more informative fossils.

Family: PYCNODONTIDAE
Genus: **Coelodus** Heckel, 1854
Coelodus toncoensis Benedetto and Sánchez, 1972
   Pajcha Pata[12] material: fragments of splenial bones, two vomerian bones, teeth; Vila Vila[21] material: small fragments of bones, teeth.

Numerous fragmented or complete splenial (Fig. 5h), vomerian bones and isolated molariform teeth; numerous isolated premaxillary or dentary incisiform teeth (Fig. 5i), often preserved with a fragment of bone; largest median row of vomerian bones with at least 7 (maybe 8) teeth and latero-internal row composed of at least 8 (maybe 9) teeth.

Coelodus indet.
   Pajcha Pata[12] material:1 fragment of splenial bone.

One fragment of splenial bone differs from *C. toncoensis* in the ratio length/width of the teeth and the ornamentation of their surface, and the similar size of the teeth of its two lateral rows. According to Benedetto and Sánchez (1972), *C. fimbriatus* and *C. inaequidens* are the only two species of *Coelodus* with similar size between the teeth of the two lateral rows, but their teeth are subtriangular to ovoid-shaped and not subrectangular as in our specimen. This fragment could belong to a new species of *Coelodus*. Because of the fragmentary nature of the remains, we prefer not to erect a new taxon pending further discoveries.

Pycnodontidae indet.
   Pajcha Pata[12] and Vila Vila[21] material: numerous teeth.

Some more or less bulbous teeth are reported here as pharyngeal teeth of pycnodonts indet. (Fig. 5f,g).

Pycnodontids are known from the Jurassic of Europe and disappear during the Eocene. In South America, pycnodontids have been reported from the early Cretaceous of Brazil, Chile, Colombia and Argentina (see Gayet, 1991). The genus *Coelodus* is known for the whole time range of the order. *C. toncoensis* is only known in the El Molino Formation (Bolivia) and in the Yacoraite Formation in Argentina (Benedetto and Sanchez, 1972) which are of the same age. Bolivia is the only area in South America where pycnodontiforms have been found in levels of late Cretaceous age (Agua Clara[7], Hotel Cordillera[25], Rancho Hoyada[13], Vila Vila[21], and Vilcapujio[30]). If we except the Miocene *Stephanodus* (Monsch, 1998) of which the attribution to pycnodontiforms is under debate, then the Bolivian fossils are until

now the youngest remains of this order in South America.

Infraclass: TELEOSTEI
Order: OSTEOGLOSSIFORMES

The phylogeny of the Osteoglossiformes is currently under debate (see Taverne, 1979; Li and Wilson, 1996; Bonde, 1996; Taverne, 1998; among others). According to the classification of Bonde (1996), two subfamilies are present at Pajcha Pata[12], the Heterotidinae and the Phareodontinae.

Subfamily: HETEROTIDINAE
Heterotidinae indet.

> Pajcha Pata[12] material: fragments of man-
> dibles, squamules.

Fragments of mandibles (Fig. 6a), strongly orna- mented with sinuous ridges, are assigned to Hetero- tidinae; bone slightly covers the base of the teeth but does not extend more than half of their height. Strongly ornamented dentaries with sinuous ridges cited as Osteoglossinae (Gayet, 1991, fig. 9a,b) prob- ably belong to this subfamily. Similar mandibles and premaxillaries from Tiupampa[51] are closer to *Arapaima* than to any other Osteoglossidae, including their closest relative *Heterotis* (Gayet and Meunier, 1998).

The squamules (polygonal parts of scales), totally flat on both sides, differ from those attributed to *Phaerodusichthys* found at Tiupampa. Upper (exter- nal) side ornamented with small tubercles and lower (internal) side, smooth. This contrasts to the concave squamules of *Phaerodusichthys* or other Osteoglossi- formes. Only the squamules of *Arapaima*, which have uniform mineralisation on the whole lower surface (Gayet and Meunier, 1983; Meunier 1984), are similar (not concave) to those described above.

Fossil heterotidins occur in South America only in the early late Palaeocene of Tiupampa[51] and Criadero de Loro[52] (Gayet and Meunier, 1998), the Miocene of La Venta in Colombia (Lundberg and Chernoff, 1992) and Brazil (Taverne, 1979). *Laeliichthys ancestralis* from the Aptian of the Areado Formation (Minas Gerais, Brazil) has been considered as a heterotidin Osteoglossidae (=Arapaimidae) by Santos (1985) and Taverne (1979, 1998). Nevertheless, study of a speci- men of *Laeliichthys* indicates that the scales of this genus are not reticulated like those of all other Osteo- glossoidei. Therefore, the referral of *Laeliichthys* to

the Heterotidinae is doubtful and the remains of Heterotidinae in Pajcha Pata[12] are consequently the oldest record of this family in the Mesozoic. Hetero- tidinae are known up to the Recent with some inter- vening in the Cenozoic (Patterson, 1993).

Subfamily PHAREODONTINAE
Genus *Phaerodusichthys* Gayet, 1991
Phaerodusichthys taverni Gayet, 1991

> Pajcha Pata[12] material: fragments of man-
> dibles, anterior part of a premaxilla.

Laterally compressed teeth closely spaced, and mandibular bone (Fig. 6b) without ornamentation; second to fourth teeth of the premaxilla very close together and smaller than the first (teeth absent on this specimen, only alveoli are visible); open ascend- ing process similar to those of phareodontins (Gayet, 1991; Gayet and Meunier, 1998). Some squamules, similar to those from Tiupampa[51], can also be assigned to this subfamily.

Phaerodontins are reported from the Palaeocene of Africa, Europe, Turkmenistan and Asia (see Taverne, 1979) to the middle Eocene of North America (Grande, 1984). *Phaerodusichthys taverni* is reported mainly from the early late Palaeocene of Tiupampa[51] and Criadero de Loro[52]. Until now, only one premax- illary has been reported from the Maastrichtian, at Huarachani[26] (Argollo et al., 1987; Gayet, 1991), and squamules from the late Cretaceous of Tiupampa[38]. Thus, the discovery of this subfamily at Pajcha Pata[12] does not contradict a Cretaceous age.

Order: CHARACIFORMES
Suborder: Characoidei
Family: indet.
Genus: **new**

> Pajcha Pata[12] material:fragment of mandible,
> isolated lower and/or upper jaws.

Fragment of mandible with two teeth (and space of a third one) belonging to the lateral border of the bone, plus one smaller acute tooth belonging to the inner (lingual) row of replacement teeth (Fig. 7a,b) set in a totally open trench; enlarged canines slightly curved and sharp-pointed with a crest on their mesial and distal borders. This fragment of mandible is similar to remains found at Tiupampa[51] and referred to cf. *Hoplias* (Gayet, 1991). This genus shares some char- acters with both the African *Hepsetus* and the characid *Acestrorhynchus*, and other features with the South
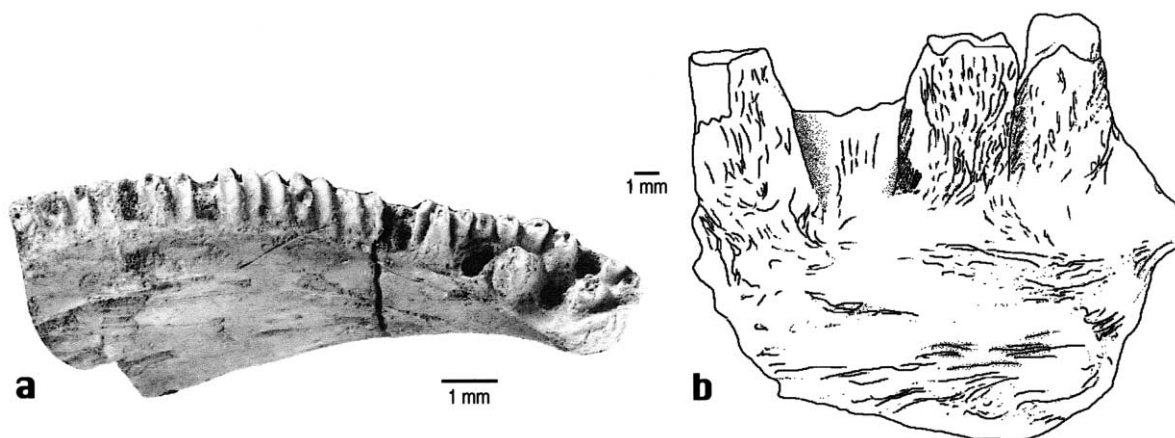
Fig. 6. Osteoglossiformes (a) Anterior part of a mandible of Heterotidinae indet. (MHNC 8565) in medial view. (b) Fragment of mandible of *Phaerodusichthys taverni* (MHNC 8566) in lateral view.

American Erythrinidae, but lacks the specialised characters of that later family. It will be described in another paper (Gayet et al., 2001a).

Characoid remains (close to erythrinids) are known in both the Maastrichtian (Agua Clara[7], Hotel Cordillera[25]) and the early late Palaeocene (Tiupampa[51] and Criadero de Loro[52]). Similar isolated teeth are present in the Maastrichtian of the Uberaba Formation in Brazil (Gayet and Brito, 1989) while Erythrinidae has been reported from the Miocene of Colombia (Lundberg, 1997; Monsch, 1998) and Ecuador (Roberts, 1975) based on isolated teeth, and the Mio-Pliocene of Acre in Brazil (Lundberg, 1997, 1998; Gayet et al. 2001) based on a jaw; nevertheless, the Ecuadorian and Colombian teeth seem similar to those of Bolivia.

Family: CHARACIDAE *sensu* Patterson, 1993
Subfamily SERRASALMINAE *sensu* Machado-Allison, 1985
Serrasalminae **indet. 1**
  Pajcha Pata[12] and Vila Vila[21] material: isolated teeth.
Teeth (Fig. 7c) smaller than and not so flat as those found at Vila Vila[21] or Tiupampa[51] (Gayet, 1991). Their shapes, different according to their position in the mouth, show a median sharp cusp with two small lateral ones. No accessory tubercles present lingually.

Serrasalminae **indet. 2**
  Pajcha Pata[12] material: some isolated teeth.
The teeth (Fig. 7d,e), circular shaped in dorsal view, show the same three lateral cusps; in addition, they have a series of accessory small cusps lingually. Depression between the two series of cusps always deep. Some teeth from Tiupampa[51] (Gayet, 1991, fig. 15a–c) show accessory cusps, few in number, but the depression is flat and oval shaped. The teeth from Pajcha Pata[12] seem closer to the alestid teeth of Africa and more so to the fossil alestids (=Characidae of the authors) from southern France (Cappetta et al., 1972) than to any South American families. Because of the possible palaeobiogeographical consequences resulting from the discovery of the African Alestidae in South America, we prefer to assign these teeth to Serrasalminae indet. pending more complete discoveries.

?Serrasalminae **indet. 3**
  Pajcha Pata[12] material: several isolated teeth.
Triangular shaped teeth with a posterior hook for interlocking them to each other (Fig. 7f) as in some Serrasalminae close to *Serrasalmus* or *Pygobrycon*. They differ from these genera in that the teeth are flatter and have straighter borders (M. Jégu, pers. comm.). If the role of this posterior hook is to lock the teeth to each other into functional position as in the piranhas, then a random replacement of them was probably physically impossible. According to Roberts (1967), such a simultaneous replacement of entire tooth rows that occurs only in the Characidae (but not all), is evidently more specialised than a random
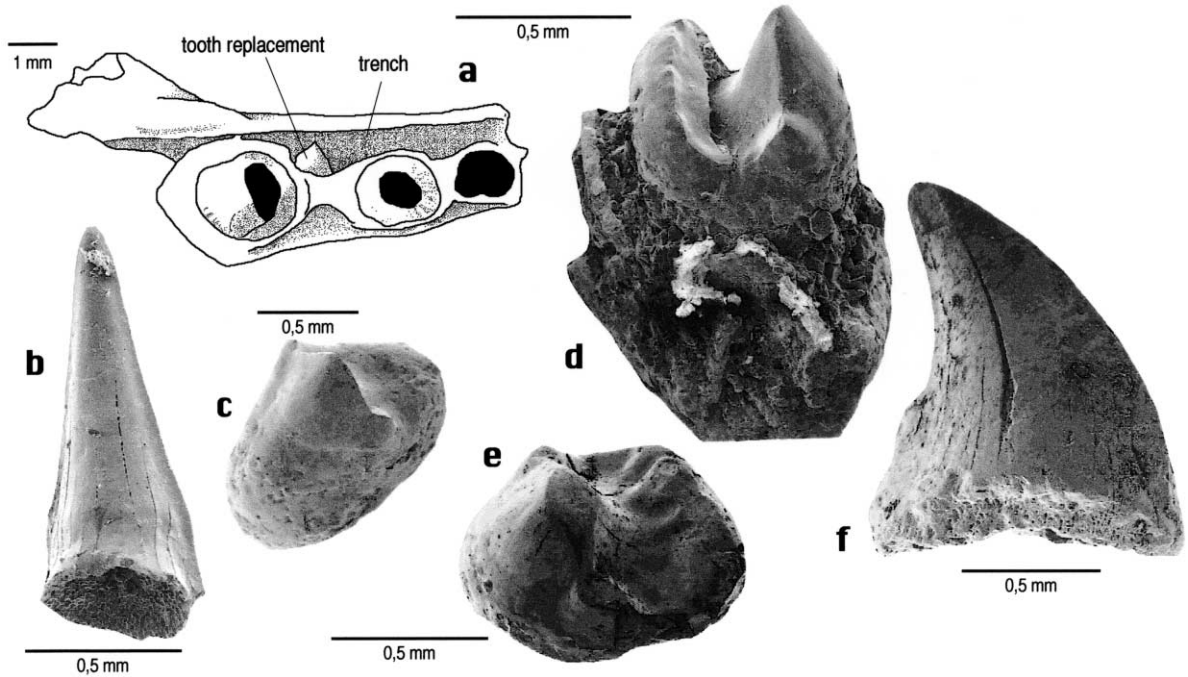
Fig. 7. Characiformes (a) Posterior part of a mandible of erythrinid-like (MHNC 8567) in dorsal view. (b) Separate tooth of characoid taxon (MHNC 8568) in medial view. (c) Premaxillary tooth of Serrasalminae indet. 1 (MHNC 8569) in upper-lateral view. (d, e) Isolated teeth of Serrasalminae indet. 2 (MHNC 8570, 8571) in upper-lateral views. (f) Isolated teeth of Serrasalminae indet. 3 (MHNC 8572) in lateral view.

replacement; it means that it was already achieved by the middle of the Maastrichtian.

The characid Serrasalminae appear to be the most common characiform fossils of Bolivia. They have been found in nearly all the localities from the Lower Member of the El Molino Formation (Agua Clara[7]) to the early late Palaeocene Impora Formation (Villa Pacheco[56]). They are known from the Miocene of the Loyola Formation in Ecuador (Roberts, 1975), of the Magdalena Basin in Colombia (Lundberg et al., 1986), of Acre in Brazil (Gayet, unpublished data), and Paraná in Argentina (Cione, 1986). Serrasalminae-like teeth are reported from the Miocene of the Pebas Formation in Colombia (Monsch, 1998).

Subfamily: TETRAGONOPTERINAE
Tetragonopterinae **indet.**

Pajcha Pata[12] *material: numerous isolated teeth.*

Very small teeth, as wide as high, and with three aligned cusps, could belong to lower or to upper jaws. Three cusps irregular in their development, the two lateral ones being smaller than the median cusp. No teeth with five cusps, like those found at Tiupampa[51] (Gayet, 1991), are known from Pajcha Pata[12].

Tetragonopterinae have been recorded from the Middle Member of the El Molino Formation (Hotel Cordillera[25]) to the Santa Lucía Formation at Tiupampa[51]. In South America, they have been also recorded from the Miocene of the Loyola Formation in Ecuador (Roberts, 1975) and of Pebas (Colombia) and Solimões (Brazil) formations (Monsch, 1998).

The oldest undisputed characiform remains are from the Cenomanian of Sudan (Werner, 1994). Characidae (indet.) have been recorded in Africa from the Palaeocene (Cappetta et al., 1978) to Recent (see Otero, 1997), and in Europe in the Lower Eocene of Italy (Cappetta et al., 1972), the Oligocene of France (Gaudant, 1980) and the Miocene of Portugal (Antunes et al., 1995). Alestin teeth are present in the Oligocene of Rumania (Gayet, unpublished data). In Bolivia, Characidae are present in all localities of the El Molino and Santa Lucía formations (Gayet, 1991; Gayet and Meunier, 1998). Thus, the

only biostratigraphic information given by the Characiformes is their presence in other undoubtedly Cretaceous localities such as Agua Clara[7] and Hotel Cordillera[25].

Order: SILURIFORMES
Family: ANDINICHTHYIDAE
Genus *Andinichthys* Gayet, 1988
Andinichthys
    Pajcha Pata[12] *and Vila Vila*[21] *material: more or less complete pectoral and dorsal spines.*

In order to securely identify the genera and most species of the siluroid remains from Pajcha Pata[12] and Vila Vila[21], an overview of the Bolivian siluriforms must be made. Some fragmentary remains of pectoral girdles, pectoral (Fig. 8a) and dorsal spines belong to the andinichthyids (Gayet, 1988) Until now, this family was only known at Tiupampa[51], Criadero de Loro[52] (Gayet, 1991) and Estancia Blancho Rancho[50] (unpublished data), i.e., localities of early late Palaeocene age, and in the Middle Member of the El Molino Formation at Tiupampa[28]. Their presence at Pajcha Pata[12] marks the earliest record of the genus *Andinichthys*.

ARIOIDA (Lundberg, 1993)
Genus **new**
    Pajcha Pata[12] *material: fragments of dermal cranium and of pectoral and dorsal spines; Vila Vila*[21] *material: fragments of pectoral and dorsal spines, 1 pharyngeal tooth plate.*

A few fragments of dermal cranium and fragments of pectoral and dorsal spines similar to those known from Agua Clara[7] and Hotel Cordillera[25], previously assigned to the ariid *Rhineastes* (Gayet, 1991). Spines ornamented with multiple rows of tubercles on their anterior edge (Fig. 8b,c); sides finely striated; head of pectoral spine of rectangular shape in posterior view, a character never observed in any other fossil or living siluriform spines. Recent discoveries at Hotel Cordillera[25] (Gayet and Meunier, 1998), indicate that this siluriform is not an Ariidae and could belong to the Arioida group as defined by Lundberg in 1993 (Gayet and Lundberg, in preparation).

In Bolivia, this new genus of Arioida is recorded from all three members of the El Molino Formation, but not from the Santa Lucía Formation at Tiupampa[51] [*vs* Gayet, 1991 reported; remains which are now referred to Pimelodidae (Gayet and Meunier, 1998)].

In Argentina, Upper Cretaceous fragments of spines with similar ornamentation are reported from the Coli Toro Formation (Cione and Laffitte, 1980) and from the late Campanian/early Maastrichtian Los Alamitos Formation (Cione, 1987), and attributed to Ariidae. New Argentinean discoveries other than spines will be necessary to confirm that the material is referable to Ariidae and not to Arioida. The presence at Pajcha Pata[12] of Arioida, otherwise only known in the Lower Member of the El Molino Formation, does not contradict a Cretaceous age of this local fauna.

Siluriformes indet.
    Pajcha Pata[12] *material: fragments of pectoral and dorsal spines.*

In addition to the Andinichthyidae and Doradoida, at least two kinds of spines (Fig. 8d–f) surely do not belong to either of the two families described above or to any Recent families. They are considered as Siluriformes indet. until more material is available.

Order indet.
    Pajcha Pata[12] *material: fragments of dorsal spines.*

Some median fragments of dorsal spines are placed with taxa for which the bones are cellular, and because of this they probably do not belong to perciforms. At first glance they look like spines of siluriforms, but the articular head is always lacking contrary to the majority of the known fossil siluriform spines. They show a perfect bilateral symmetry (Fig. 8g); denticulation, located on the posterior side of the spine, belongs to both hemispines. No known siluriform has dorsal spines with double posterior denticulation.

Order: AULOPIFORMES
Family: ENCHODONTIDAE
Genus: *Enchodus* Agassiz, 1835
Enchodus sp.
    Pajcha Pata[12] *material: some isolated teeth.*

Teeth striated at their base with acuminate cusp as that figured in Gayet (1991 fig. 11a).

Enchodus is known only from marine Maastrichtian rocks in Africa (Congo, Morocco), Middle East (Lebanon, Israel), Europe and North America (see Gayet et al., 1991). In South America it has been reported from Brazil (Rebouças and Santos, 1956) and, in the Lower and basal Middle Members of the El Molino Formation (Gayet, 1991; Gayet et al.,
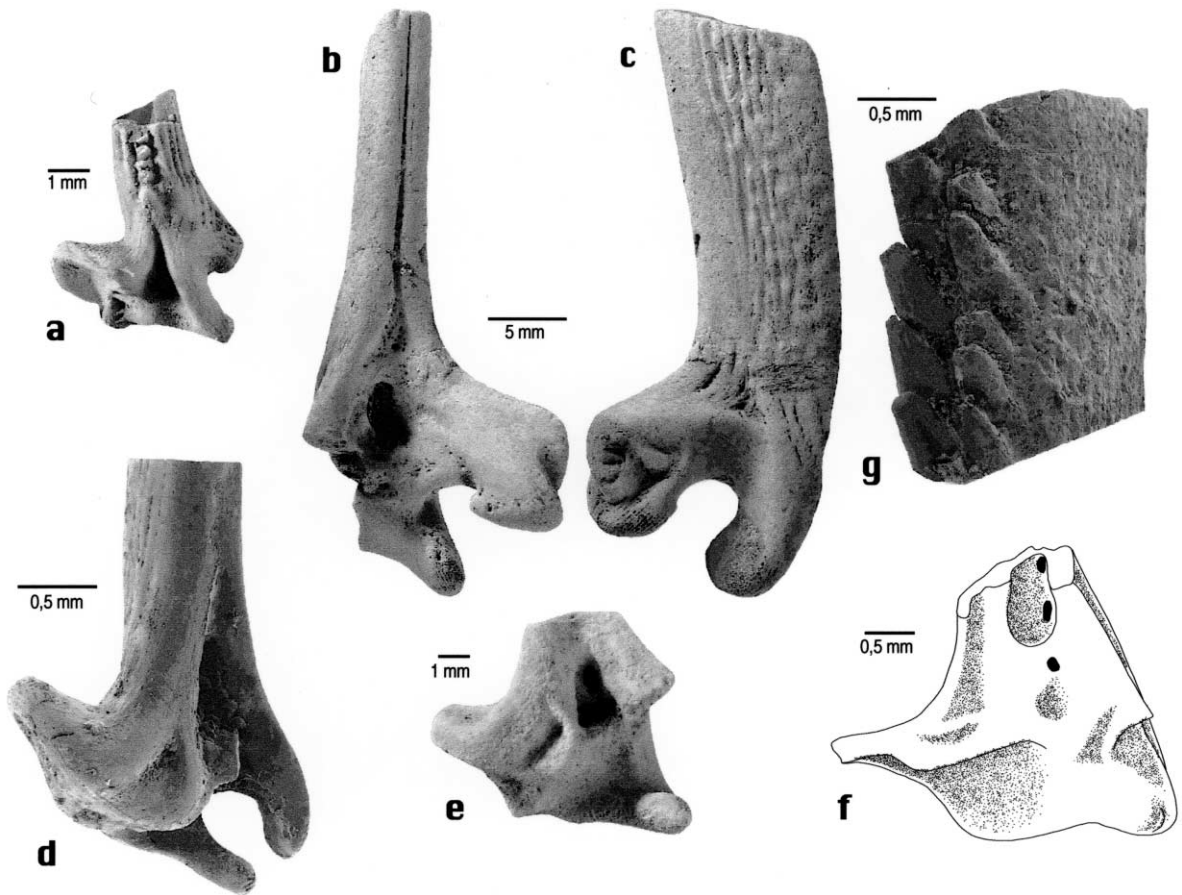
Fig. 8. Siluriformes (a) Left pectoral spine of Andinichthyidae indet. (MHNC 8574) in anterior view. (b, c) Right pectoral spine of Arioida (MHNC 8575) in anterior and lower views. (d) Articular part of a right pectoral spine of Siluriformes family indet. 1 (MHNC 8576) in posterior view. (e, f) Articular part of a right pectoral spine of Siluriformes family indet. 2 (MHNC 8577) in posterior view. (g) Fragment of possible dorsal spine of Osteichthyes order indet. (MHNC 8578) in postero-lateral view.

1991) in Bolivia. Thus, the presence of *Enchodus* at Pajcha Pata[12] is congruent with a late Cretaceous age.

Order: PERCIFORMES
Family: LATIDAE *sensu* Otero, 1997
Genus **new**
    Pajcha Pata[12] material: 2 fragments of mandible; several vertebra.
Two fragments of mandible (Fig. 9a) and vertebrae similar to those found at Tiupampa[51] and Criadero de Loro[52], and assigned at that time to a centropomid genus close to the African *Lates* (Gayet, 1991). Recent studies (Otero, 1997) keep *Centropomus* alone in the family Centropomidae and erect the

family Latidae in place of the subfamily Latinae. Comparison with the extant intertropical *Centropomus* shows that the Bolivian remains are different (Gayet and Meunier, 1998; Gayet, in preparation).

Latidae similar to those from Pajcha Pata[12] were reported from Estancia Blanco Rancho[50], Tiupampa[51] and Criadero de Loro[52] (all of Palaeocene age), and from Tiupampa[28] of Cretaceous age. They are very similar to the fossil and recent latids of Africa and not to Percichthyidae or Perciliidae known in South America (Arratia, 1982; Gayet and Meunier, 1998). This family was previously recorded, outside of South America, in the middle Eocene of Italy, France, Saudi Arabia and Turkey (see Otero, 1997). If the remains of
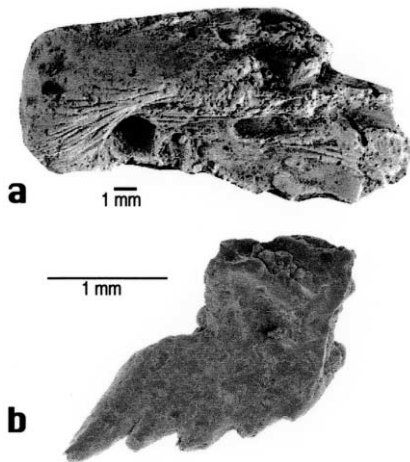
Fig. 9. (a) Anterior part of a mandibular fragment of Latidae (MHNC 8580) in lateral view. (b) Preopercular fragment of possible Percichthyidae *Santosius* sp. (MHNC 8581) in lateral view.

Fig. 10. Dipnoi *Ceratodus* sp. left pterygoid tooth plate (MHNC 8582).

indeterminate Perciformes recorded from the Campanian of Argentina (Cione, 1987), Maastrichtian of Brazil (Gayet and Brito, 1989) and from Laguna Umayo in Peru (Gayet, 1991) are not that of Latidae (material too incomplete for secure identification at that time), the remains from Pajcha Pata[12] would be the oldest known.

Family: PERCICHTHYIDAE
Genus *Santosius* Arratia, 1982
cf. *Santosius* sp.
    Pajcha Pata[12] material: 3 spiny parts of preoperculum.

Three spiny parts of preoperculum (Fig. 9b) are tentatively assigned to the percichthyid cf. *Santosius* because of the presence of isolated preoperculars and hyomandibulars of this genus known in other levels (with only fish) of the same locality.

Percichthyidae are known from the Lower and Upper Members of the El Molino Formation at La Palca[11] and at an unnumbered site near Potosí (Gayet and Meunier, 1998), from the Miocene of Argentina and Chile (Arratia, 1982), while the percichthyid *Santosius* is known from the same Bolivian localities and from the Miocene of southern Brazil (Schaeffer, 1947; Arratia, 1982). The discovery of this family at Pajcha Pata[12] does not provide new biostratigraphic information for this group.
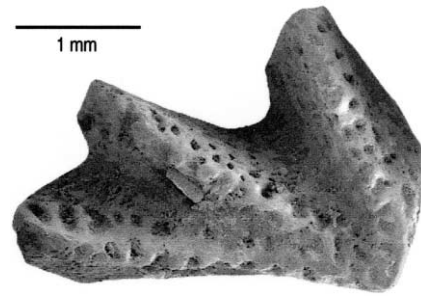
Subclass: SARCOPTERYGII
Order: DIPNOI
Family: CERATODONTIDAE
Genus: *Ceratodus* Agassiz, 1838
Ceratodus sp.
    Pajcha Pata[12] material: 3 tooth plates.

Three tooth plates, about 4–6 mm long (Fig. 10), have three ridges with deep indentations (separations between teeth 1–2 and 2–3 are similar in size). The pitted surface suggests a juvenile individual with very little or no abrasion.

Ceratodontids were distributed worldwide from the Mesozoic up to the Palaeocene (see Schultze, 1991). In South America, ceratodontids have been reported in the Cretaceous and Tertiary of Argentina and in Bolivia from the Santa Lucía Formation at Tiupampa[51] and at Torotoro[53]. Ceratodontids disappear in the Lower Tertiary; those of Tiupampa[51] and Torotoro[53] represent the youngest record of this family.

Family LEPIDOSIRENIDAE
Genus: *Lepidosiren* Fitzinger, 1837
Lepidosiren cf. *paradoxa* Fitzinger, 1837
    Pajcha Pata[12] material: 3 pterygoid, 1 prearticular tooth plates; Vila Vila[21] material: 1 pterygoid tooth plate.

All pterygoid and prearticular toothed plates are small. A left pterygoid tooth plate and a right prearticular with tooth plate of *Lepidosiren* cf. *L. paradoxa* were described by Schultze (1991). These specimens are not distinct from a large sample from Tiupampa[51], which in turn is not clearly distinguishable from those of the living species *Lepidosiren paradoxa*.
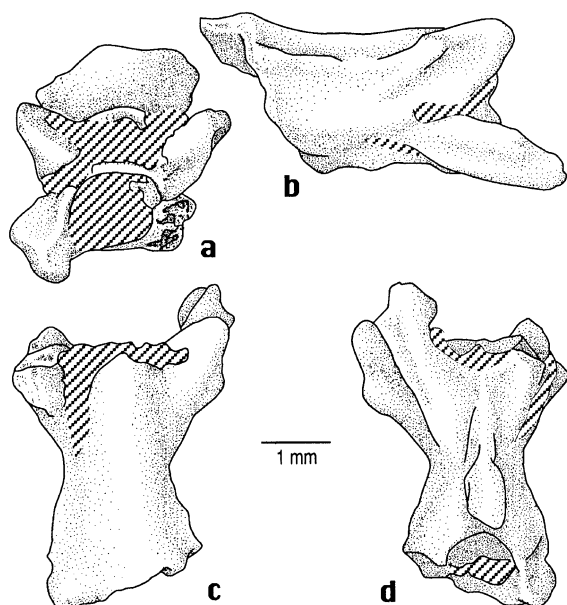
The family Lepidosirenidae is endemic to South

Fig. 11. Indeterminate gymnophionan genus (MHNC 8583). Trunk vertebra in: (a) frontal view, (b) right lateral view; (c) dorsal view, (d) ventral view.

America. The earliest previous record is from Laguna Umayo in southeastern Peru. These specimens are identified as *Lepidosiren* cf. *L. paradoxa* (Sigé, 1968). As summarised by Schultze (1991), Cenozoic fossils of *Lepidosiren* are also known from Argentina, Bolivia, Brazil and Colombia, and the only extant species, *Lepidosiren paradoxa,* occurs today in Brazil, Bolivia, Paraguay, and Argentina. Thus, the specimens of Pajcha Pata[12] represent the earliest known record of Lepidosirenidae and are not distinguishable from the living species *L. paradoxa.* The specimen of *Lepidosiren* cf. *L. paradoxa* reported at Vila Vila[21] (*Pucapristis* level) is not from the Santa Lucía Formation, but from the Lower El Molino Formation (vs Schultze, 1991)

Class: AMPHIBIA
Order: GYMNOPHIONA
Family, genus, species indet.
    Pajcha Pata[12] material: 7 vertebrae.
Vertebrae (Fig. 11) elongate, amphicoelous; centrum more or less hourglass-shaped with a deep sagittal keel; presence on either side of the cotyle of a typical process which projects anteriorly. These features secure referral to the group, but no attempt has been made at more precise assignment.

In South America, apodans were first reported from the late Paleocene of Itaboraí, Brazil (Estes and Wake, 1972); they are also known in the early late Paleocene of Tiupampa[51] (Rage, unpublished data). The fossils from Pajcha Pata[12] are the oldest apodans from South America. The oldest apodan comes from the Cenomanian of Africa (Werner, 1994; Evans et al., 1996), whereas, the oldest gymnophionan (*Eocaecilia*, a limbed form) was recovered from the early Jurassic of North America (Jenkins and Walsh, 1996). Apodans afford no biostratigraphic information; Pajcha Pata[12] vertebrae also represent the oldest known gymnophionan from South America.

Order: CAUDATA
Suborder: URODELA
Family: NOTERPETONTIDAE
Genus: ***Noterpeton*** Rage et al., 1993
Noterpeton bolivianum Rage et al., 1993
    Pajcha Pata[12] and Vila Vila[21] material: 46 and 16 vertebrae, respectively.
New remains of the very peculiar salamander *Noterpeton* with procoelous vertebrae (Fig. 12), have been discovered. There are of great interest regarding the phylogenetic relationships of the family Noterpetontidae presently under debate (Rage et al., 1993; Evans et al., 1996; Rage, 1997). Vila Vila[21] has provided additional vertebrae, which do not display differences with those from Pajcha Pata[12]. One of these vertebrae is complete and shows that the reconstruction of a vertebra (based on several fragments) in Rage et al. (1993 fig. 2) is accurate on the whole; however, it demonstrates that the transverse process has no dorsal lamina.

In South America, procoelous Caudata are represented by *Noterpeton bolivianum* known at Pajcha Pata[12] and Vila Vila[21] only. A fragment of vertebra from the early late Palaeocene of Estancia Blanco Rancho[50] appears to be morphologically consistent with that species, but this referral cannot be ascertained. Procoelous Caudata are also known in the Cenomanian of Sudan (Evans et al., 1996), Marocco (Rage, unpublished data), and in the Lower Senonian of Niger (Rage et al., 1993). These salamanders are still too poorly known and cannot be useful for chronostratigraphy.
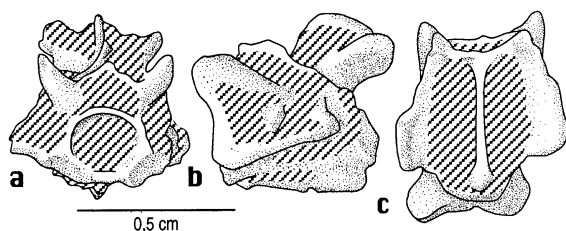
Fig. 12. Noterpetontid *Noterpeton bolivianum*(MHNC 8584). Trunk vertebra: (a) frontal view; (b) left lateral view; (c) ventral view.

Order: SALIENTA
Suborder: ANURA
Family, genus, species indet.
Pajcha Pata[12] material: 3 presacral vertebrae.
Neural arch of these presacral vertebrae broad, but not of the imbricate type (Fig. 13). Neural spine present. Prezygapophysial facets small and markedly slant above the horizontal. Procoelous centrum slightly depressed; in ventral view, clearly delimited by subparallel lateral borders. The overall morphology appears to be reminiscent of Bufonidae and Leptodactylidae.

The most common anurans from the Cretaceous and the early Cenozoic of South America are pipid frogs, but although the vertebrae from Pajcha Pata[12] cannot be securely assigned to a family, a referral to the Pipidae, whose vertebrae are opisthocoelous, may be ruled out. Fossils belonging to the Leptodactylidae and Bufonidae, the two families to which the fossils from Pajcha Pata[12] may belong, are presently known in South America. The Leptodactylidae, a probably paraphyletic assemblage, are first reported in South America from the late Cretaceous Baurú Group (Brazil) and the Campanian/Maastrichtian Los Alamitos Formation (Argentina) (Báez, 1991). Estes
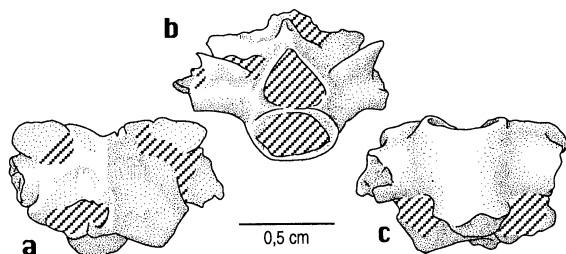
(1970) indicated that Bufonidae occur in the Palaeocene of Brazil (that is, implicitly, the late Palaeocene of Itboraí, sensu Marshall et al., 1997).

Class: REPTILIA
Order: CHELONII
Family: PODOCNEMIDIDAE
Genus and species indet.
Numerous fragments of turtle plates were observed in the field and some of them collected, but all were regarded as indeterminate podocnemidids.

Order: SQUAMATA
Suborder: SERPENTES
Family ?MADSempereOIIDAE
Madtsoiidae indet.
Genus **new**
Pajcha Pata[12] material: 2 incomplete trunk vertebrae.
Two incomplete trunk vertebrae (Fig. 14) apparently belong to the same species. Parazygantral foramina apparently present; such foramina characteristic of the Madtsoiidae. Whatever its correct family referral is, this snake represents a new genus.

Order: CROCODYLIA
Crocodylia indet.
Pajcha Pata[12] material: fragments of teeth.
These fragmentary teeth are the only evidence of presence of crocodiles at this locality.

Order: SAURISCHIA
Suborder: THEROPODA
Infraorder: COELUROSAURIA
Family, genus and species indet.
Pajcha Pata[12] material: 1 tooth; numerous tooth fragments.
A nearly complete isolated tooth (Fig. 15, Marshall, 1989) collected by surface prospecting, along with

Fig. 13. Indeterminate anuran genus (MHNC 8585) Presacral vertebra in: (a) dorsal view; (b) frontal view; (c) ventral view.
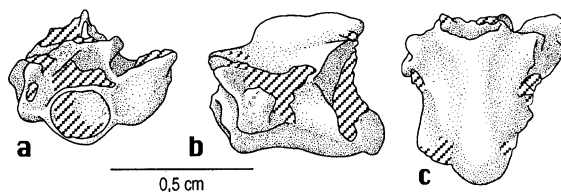

Fig. 14. -?Madtsoiidae indet. (MHNC 8586) Posterior trunk vertebra in: (a) frontal view; (b) left lateral view; (c) ventral view.

numerous tooth fragments collected during screen washing represent Coelurosauria, family, genus and species indet.

Infraorder: SAUROPODA

Family, genus and species indet.

Pajcha Pata[12] material: tooth fragments.

Numerous partial teeth and tooth fragments collected by screen washing represent the Infraorder Sauropoda. These specimens are identified as Sauropoda, family, genus and species indet.

Prior to the discovery of this locality, both groups, coelurosaurs and sauropods, were represented only by trackways in the Lower El Molino at Santivañez-Parotani[24] (Cochabamba Department), Cambari (Tarija department), Cal Orcko near Sucre (Chuquisaca Department), at four localities near Torotoro[16–20], and from an indeterminate El Molino Member at Arapampa[39] and Camargo[41] (Leonardi, 1981; Marshall and Molina, 1990; Gayet et al., 1991). The first bones of dinosaurs from Bolivia, including sauropods (Titanosauridae), have been recovered from two localities of the Cajones Formation (Maastrichtian) near Santa Cruz de la Sierra (Gutiérrez and Marshall, 1994).

Class: MAMMALIA

Mammals are represented at Pajcha Pata[12] by two complete and possibly one partial tooth. A detailed description with discussion of the affinities of these teeth is in preparation. For the purposes of this paper we deem it prudent to simply present SEM photographs of each tooth, general observations on tooth morphology, and to refer them as Mammalia indet.

Genus and sp. indet 1 (Fig. 16a,b).

Pajcha Pata[12] material: 1 upper right molar.

The protocone of this tooth is the largest cusp, the metacone is smaller, while the paracone is the smallest and is about half the size of the metacone. No trace of a centrocrista connects meta- and paracone. The protocone has large inflated base labially that extends across trigon to the base of meta- and paracone, and fills the central part of the trigon basin, isolating a small basin anteriorly and a larger basin posteriorly. There is only a hint of a stylar shelf labial to the meta- and paracone, but a distinct cuspule anterolabial to the paracone may represent a stylar cusp B (or A?).
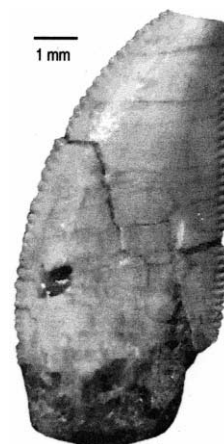

Fig. 15. Indeterminate coelurosaur tooth in lateral view (MHNC 3702). Photo O. León, Museo nacional de Historia natural, Santiago de Chile.

The ectoflexus is distinct but shallow. There is no trace of meta- or paraconules. The overall molar morphology is consistent with a tribosphenic mammal, while dryolestoid affinities are suggested.

Genus and sp. **indet. 2** (Fig. 16c,d).

Pajcha Pata[12] material: 1 upper right tooth.

A complete isolated upper right tooth, with three distinct roots, possibly represents a eutherian P4. The labial side is dominated by a massive cusp medially and a smaller cusp posterior to it. The two cusps are fused basely and have a common occlusal wear surface labially. The lingual side has a low small rounded basined cusp, presumably the protocone.

Genus and sp. **indet. 3** (Fig. 16e,f).

Pajcha Pata[12] material: fragment of an upper molar.

This specimen is tentatively regarded as a non-tribosphenid therian largely by exclusion from other groups as well as showing clear evidence of cusp structure. Because of the fragmentary nature of the specimen, orientation is not secure. As seen in Fig. 16e,f, the specimen has part of a large cusp with an occlusally worn surface; an elevated but lower worn surface area next to it; and a cingular area with a narrow ridge (adjacent to the worn surface) and a small cuspule adjacent to the large cusp.
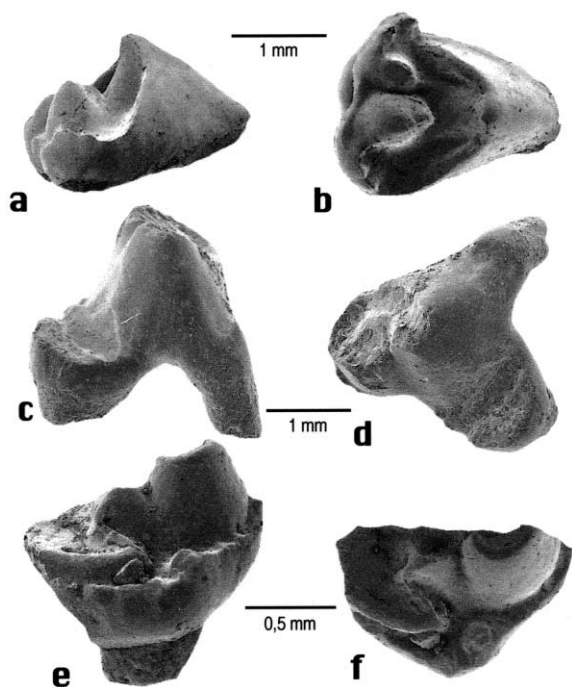
Fig. 16. Mammal teeth. (a, b) mammal indet. 1 (MHNC 8588) in: (a) anterior and (b) occlusal views. (c, d) mammal indet. 2 (MHNC 8589) in (c) posterior and (d) occlusal views. (e, f) mammal indet. 3 (MHNC 8590) in (e) lingual and (f) occlusal views.

4.2. Discussion with special reference to biostratigraphy

Concerning the late Cretaceous (middle Maastrichtian; Sempere et al., 1997) age of Pajcha Pata[12], palaeontological indications are as follows: some taxa known at Pajcha Pata[12] have a world-wide occurrence no later than Cretaceous (selachian *Ischyrhiza*; semionotids; dinosaurian sauropods and theropods), or are restricted to Maastrichtian deposits elsewhere in South America (*Pucabatis, Lepidotyle, Lepisosteus, Coelodus toncoensis*); some endemic taxa from these localities of the Lower Member of the El Molino Formation occur also in the Yacoraite Formation of Maastrichtian age in northwest Argentina (Cione and Pereira, 1985). On the whole, this fauna seems to provide evidence for a Maastrichtian age for the Pajcha Pata[12] locatity.

The geochronological data as presented by Sempere et al. (1997) seem, however, more secure and precise than the paleontological data. The El

Molino and Santa Lucía formations are each subdivided into three sequences of stratigraphic value, the ages of which are as follows: Lower El Molino, about 73–66.9 Ma; Middle El Molino, 66.9–60.8 Ma; Upper El Molino, 60.8–60.0 Ma; Lower and Middle Santa Lucía (=Mealla), 60.0–58.5 Ma; Upper Santa Lucía (=Impora = Maíz Gordo), 58.5–58.2 Ma (Sempere et al., 1997). According to these authors who follow the time scale of Cande and Kent (1992, 1995), and based on magnetostratigraphy and sequence stratigraphy of the El Molino and Santa Lucía formations, the regression marked by the El Molino/Santa Lucía contact is correlated with the Danian/Selandian boundary (60.0 Ma). Therefore the El Molino Formation spans the 73–60.0 Ma interval.

The bed which yielded continental vertebrates at Pajcha Pata[12] is about 30 m above the base of the El Molino Formation, i.e. in the upper part of the Lower Member (Sempere et al., 1997). It is correlated to a level ≈140 m above the base of the El Molino at La Palca[11] near Potosí and is thus ≈68.4 Ma. This bed is the lowest level in the El Molino Formation which has a diverse continental fauna (Jaillard et al., 1993; Sempere et al., 1997). Levels equivalent to this bed are to be found in the upper part of the middle formation of the Vilquechico Group in southern Peru (Sempere et al., 2000) and in the lower part of the Yacoraite Formation in Argentina (Sempere et al., 1997).

5. Depositional environment

The issue of the palaeoenvironment of the El Molino Formation has been addressed and debated in previous controversal papers (Cappetta, 1975, 1991; Gayet et al., 1991, 1992, 1993; Camoin et al., 1991, 1992, 1997; Gayet et al., 1992, 1993; Rouchy et al., 1993; Sempere et al., 1997). In Gayet et al.'s papers the palaeoenvironment of the fish was based on both comparison with living similar taxa and other palaeoenvironmental data such as those provided by microfauna (Foraminifera) and invertebrates (Bryozoa, Echinodermata, etc.). The hypothesis of marine influence (Gayet et al., 1992; Sempere et al., 1997) was strengthened by the fact that nowhere today is there a freshwater locality with so great a generic and specific diversity of marine taxa (Gayet et al.,

1993), and that the totality of the marine fish are present or absent from the different localities. Preliminary isotopic study (Dromart et al., 1999) indicates that at least some selachians and the pycnodontids of Pajcha Pata[12] are marine, while the lepisosteids are freshwater. The isotopic results of *Lepidotyle* do not permit assessment of the palaeoenvironment of this taxon (see below).

5.1. Data (Table 4)

5.1.1. Selachians

The selachian fauna is quite unusual in the fact that it completely lacks sharks; only batoids have been collected. This situation indicates, without doubt, very peculiar environmental conditions. Among the selachian assemblage, the sclerorhynchids remain the most indicative elements concerning the palaeoenvironmental conditions. As *Ischyrhiza* occurs in marine deposits, one can suppose that the same conditions prevailed in levels where this genus has been collected in Bolivia. Isotopic analyses of *Pucapristis* indicate a marine environment (Dromart et al., 1999). The marine dasyatids and Recent pristids (presumed to be the living ecological equivalent of Cretaceous sclerorhynchids) can enter fresh waters. So it can be concluded, on the basis of the selachians, that the environmental conditions at Pajcha Pata[12] were marine influenced, at least periodically, but may have been diluted by freshwater inflow from the continent.

5.1.2. Cladistia

Recent cladistians live only in fresh water in African rivers and lakes, with the exception of the Recent *Erpetoichthys*, which may have contact with the sea in estuaries (Gosse, 1990; Nelson, 1994). All the localities from Africa which have yielded fossil cladistians are considered to be continental (Broin et al., 1974; Schaal, 1984; Werner, 1994, Van Neer and Gayet, 1988). Tiupampa[51] has yielded only continental and/or true freshwater forms such as characid fish, anurans, gymnophionans, turtles, lizards, snakes, crocodiles and mammals (Muizon et al., 1983; Gayet et al., 1991). The cladistians of Tiupampa[51] are freshwater forms (Dromart et al., 1999), but isotopic analyses of the specimens from Pajcha Pata[12] are still in progress.

5.1.3. Ginglymodi

Most recent Lepisosteidae live in fresh waters, but one species (*L. osseus*) may tolerate brackish or even marine conditions (Suttkus, 1963). Nevertheless, no fossil Lepisosteidae has ever been proved to have lived in brackish or marine environments. The presence of *Lepisosteus* sp. in the marine Campano-Maastrichtian Niobrara Formation (Wiley and Stewart, 1977) is not proof that lepisosteid fish lived in marine waters of neritic platform (vs Gaudant, 1993). In fact, these lepisosteid remains were deposited in unusual conditions (as noted by the authors in their paper); contrary to all the other fish, with articulated skeletons, all the lepisosteid remains were dissociated and dispersed. Hence, coastal rivers probably transported these lepisosteids. In Bolivia, they can be found in association with marine taxa such as selachians, pycnodontids, etc. but the isotopic analyses indicate they are freshwater elements (Dromart et al., 1999). In addition, in the only localities of Bolivia where no truly marine fish were found (i.e. Estancia Blanco Rancho[50], Tiupampa[51], Criadero de Loro[52]), they are absent, but this absence may be the consequence of the age (early late Palaeocene; lepisosteids disappeared by the end of the Cretaceous in Africa) and not of the environment.

5.1.4. Semionotidae

In all the Bolivian localities, the semionotids are mixed with marine and freshwater taxa. The remodelling of the ganoine observed in the scales and in the rostrum indicates physiological modification linked to calcium, which can be related either to reproduction (with migration from a thalassic to a freshwater environment), or to an input of freshwater from the continent (Meunier and Gayet, 1992). Nevertheless, because *Lepidotyle* is the unique ganoid fish showing remodelling of the ganoine, the first hypothesis (reproduction) is favoured; an input of fresh water would have affected the other ganoid fish, the lepisosteids and the cladistians, as well. It is interesting to note that among all the fossils of Bolivia on which isotopic study has been made, only *Lepidotyle* shows a dubious result (Dromart et al., 1999).

5.1.5. Pycnodontiformes

Pycnodontids generally occurred in marine or

Table 4

Distribution of the vertebrate faunas from the Agua Clara[7] — Potosí and Tiupampa[51] basins with indication of their modern and/or known environment (M = marine; FW = freshwater; T = terrestrial). The numbers by the names of the localities are from Table 1

Taxa known at Pajcha Pata[12]	Prox. reg.	Dist. reg
Order Rajiformes		
Pucapristis branisi	M	M
Ischyrhiza hartenbergeri	M	M
Schizorhiza aff. *stromeri*	–	M
Order Myliobatiformes		
'Dasyatis' branisai	M/FW	M/FW
'Dasyatis' molinoensis	M/FW	–
Dasyatis schaefferi	M/FW	M/FW
Pucabatis hoffstetteri	M	–
Order Polypteriformes		
Latinopollia suarezi	FW	–
Dagetella sudamericana	FW	–
Order Lepisosteiformes		
Lepisosteus sp.	M–FW	M–FW
Order Semionotiformes		
Lepidotyle enigmatica	M–FW	M–FW
Order Pycnodontiformes		
Coelodus toncoensis	M	M
Stephanodus minimus	M	M
Order Clupeiforme		
Gasteroclupea branisai	–	M/FW?
Order Osteoglossiformes		
Heterotinae indet.	FW	–
Phaerodusichthys taverni	FW	–
Order Characiformes		
Characoidei, nov.gen.	FW	FW
Subfam. Serrasalminae	FW	FW
Subfam. Tetragonopterinae	FW	FW
Order Siluriformes		
Andinichthys sp.	FW	–
Doradoidae nov. gen.	M/FW?	M/FW?
Order Aulopiformes		
Enchodus sp.	M	M
Order Perciformes		
Latidae nov. gen.	FW?	–
cf. *Santosius* sp.	FW	FW
Order Dipnoi		
Lepidosiren cf. *L. paradoxa*	FW	–
Ceratodus sp.	FW	–
Order Gymnophiona		
Family indet.	T/FW?	–
Order Caudata		
Noterpeton bolivianum	FW	–
Order Salienta		
Anura indet.	T/FW?	–
Order Chelonia		
Podocnemididae	FW	–
Order Squamata		
? Madtsoiidae, nov. gen.	–	–

Table 4 (*continued*)

Taxa known at Pajcha Pata[12]	Prox. reg.	Dist. reg
Order Crocodilia		
Crocodilia indet.	T/FW	T/FW
Order Saurischia		
Coelurosauria indet.	T	–
Sauropoda indet.	T	–
Class Mammalia		
Gen. and sp. indet. 1	T	–
Gen. and sp. indet. 2	T	–
Gen. and sp. indet. 3	T	–

littoral coastal environments (Nurshall, 1996). Nevertheless, it seems that some of them, including *Coelodus*, may have entered water of less salinity (Wenz, 1989; Schaeffer and Patterson, 1984). Recently, Poyato-Ariza et al. (1998) have demonstrated on the basis of isotopic analysis that the pycnodonts of Las Hoyas (Cuenca, Spain) were true freshwater fish. In the El Molino Formation the pycnodonts, always found in association with several marine fish such as selachians and the aulopiform *Enchodus*, were considered as marine. When pycnodontids are absent, so are the other marine fish. Recent isotopic analysis (Dromart et al., 1999) confirms this assertion.

5.1.6. Osteoglossiformes

Extant Osteoglossiformes are restricted to fresh water of tropical South America, Africa and India (Berra, 1981). Fossil remains are reported from fresh, brackish and marine waters (see Gayet et al., 1991). According to Nelson (1969), who worked on living fish, and Gayet (1987), all marine Osteoglossiformes are of Palaeocene or younger age. Osteoglossiformes are considered as primary freshwater fish (see Bonde, 1996). In addition, *Phaerodusichthys* has only been found at Huarachani[26], Tiupampa[51] and Criadero de Loro[52], three localities of secure continental palaeoenvironment. Heterotidinae are only known in freshwater environments.

5.1.7. Characiformes

Extant Characiformes are freshwater fish with very few African exceptions, which can enter brackish waters. European Tertiary fossils may have lived in brackish waters (Cappetta et al., 1972; Gaudant,

1980). In the Cretaceous, the oldest true characiform from the Cenomanian of Sudan is a freshwater one (Werner, 1994), but those from Portugal were marine (Gayet, 1981). Nevertheless, these Portuguese taxa are not considered as Characiformes by some authors (see Patterson, 1993), but as Otophysan only. In Bolivia they occur in strict continental localities as Tiupampa[51] and Criadero de Loro[52], but they are mixed with marine fish in other sites of the Cretaceous part of the El Molino Formation. We can postulate that the Cretaceous Characiformes from Bolivia were true freshwater fish, but isotopic analyses are necessary to support this hypothesis.

5.1.8. Siluriformes

Andinichthyoidea are known in the Santa Lucía Formation in strictly continental areas (Estancia Blanco Rancho[50], Tiupampa[51], Criadero de Loro[52]). This superfamily is considered as a freshwater one.

Arioids comprises freshwater families (Doradoids + Mochockidae) and marine taxa (Ariidae and *Titanoglanis*) (Lundberg, 1993); they are reported in the El Molino Formation only in localities in which supposed marine taxa are present. Thus, nothing can be said about the palaeoenvironmental signal of the Bolivian taxa.

5.1.9. Aulopiformes

Enchodus is only known in marine sediments (Goody, 1969; Patterson, 1993).

5.1.10. Perciformes

The latids are composed of marine and freshwater taxa. In South America, this family includes the marine genus *Psammoperca*. The fossil latids of Bolivia are close to *Lates*, a freshwater form of Africa and marine from the Sea of Japan. Until now, Bolivian latids were only known at Tiupampa[51] and Criadero de Loro[52] and were consequently probably freshwater forms. The recent Percichthyidae are strictly freshwater fish.

5.1.11. Dipnoi

By extrapolation based on occurrence of other fossils and extant forms, Lepidosirenidae are restricted to fresh water environments. Ceratodontids may be even strictly freshwater forms or tolerant of a wide range of salinity (Schultze, 1991).

5.1.12. Amphibia

One of the major characteristics of the Amphibia is that they cannot live in marine water. *Noterpeton* was an elongate salamander, probably paedomorphic; like all elongate living Caudata, probably lived in freshwater. The gymnophionan and anuran, whose family identity is unknown, could have been either land or freshwater dwellers.

5.1.13. Reptiles and mammals

All indicate terrestrial or freshwater environments.

5.2. Discussion

The palaeoenvironment of the Pajcha Pata[12] fossil bed was undoubtedly continental as indicated by such vertebrates as coelurosaurs, snakes, amphibians and mammals, and by some fish supposed to be freshwater ones (cladistians, characiforms, andinichthyids, lepidosirenids). Anuran and gymnophionan amphibians could have been either freshwater or terrestrial, but the only Caudata (*Noterpeton*) was likely a freshwater dweller. Nevertheless, the presence of numerous fish of marine affinities (rajiforms, myliobatiforms, pycnodontiforms, aulopiforms, and probably the semionotid *Lepidotyle*) indicates nearby marine influence as already observed in other levels of the El Molino Formation (Gayet et al., 1992, 1993; Sempere et al., 1997). To try to explain this mixture of freshwater, brackish and marine elements, one may suppose that continental and freshwater taxa were transported and deposited in a margino-littoral environment by streams. A recent geochemical study (Dromart et al., 1999) confirms the palaeoenvironment of the fish as already noted by Gayet (1991) and Gayet et al. (1992, 1993). Study in progress could decide exactly which fish are from marine or fresh waters based on isotopic analyses. Calculated temperatures of the marine waters range from 13 to 17° for a latitute of about 22°S (Dromart et al., 1999). If so, the value of seawater temperature implies a southern Pacific upwelling (ibid.). The El Molino basin could well have been connected with open sea also through present-day Argentina (Ihering, 1927) as figured (but not discussed) by Gayet et al. (1993, fig. 12) and not only Venezuela (Fig. 17). In Argentina, the Yacoraite Formation also yielded an 'abnormal' freshwater, brackish or marine ichthyofauna (Cione
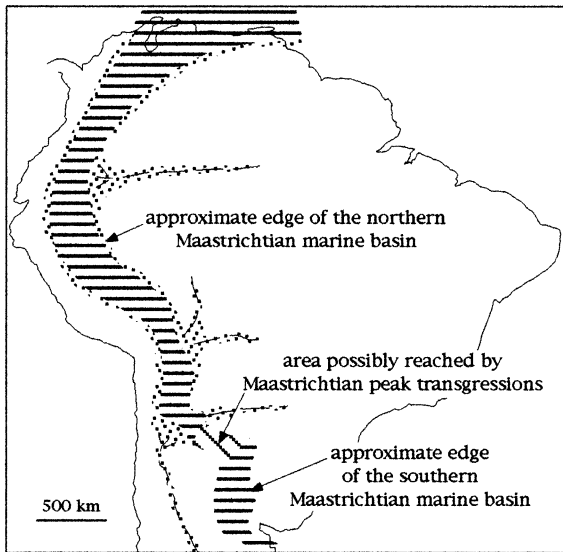
Fig. 17. Palaeogeographic sketch-map of northern South America for the Maastrichtian showing the position of the Bolivian region at the southern tip of an elongate marine to restricted-marine basin connected to the open sea in present-day Venezuela and at the northern tip of a shorter marine to restricted-marine basin connected to the open sea in present-day Argentina (modified after Gayet et al., 1993).

and Pereira, 1985) and Argentine geologists (see Zambrano, 1987) agree with sub-normal marine deposition in this region.

6. Comparison between the Cretaceous localities in the proximal and in the distal regions of the El Molino basin

The Cochabamba area is located in a proximal region of the El Molino basin which includes the late Cretaceous localities of Pajcha Pata[12], Vila Vila[21], Tiupampa[28] (Hera Mokho), Estancia Blanco Rancho[35] and Tiupampa[38] (Río Puracani), and the lower Upper Paleocene localities Estancia Blanco Rancho[50], Tiupampa[51] and Criadero de Loro[52]. The Potosí area is located in a distal region that includes the late Cretaceous localities of Agua Clara[7], La Palca[11], Hotel Cordillera[25] and Vilcapujio[30], which have yielded mostly fish. The fish taxa of Cretaceous age which are common to the two regions (i.e., present in the whole basin), are of marine origin (even if some

of them were able to enter rivers), like the selachians *Pucapristis*, *Ischyrhiza* and *Dasyatis*, the pycnodonts *Coelodus* and *Stephanodus*, and the salmoniform *Enchodus*, or of freshwater origin, but which could enter the sea, as the holostean *Lepidotyle*, and maybe the Arioida.

On the other hand, the primary freshwater fish of the proximal region partly differ from those of the distal area, except the characiforms and the lepisosteids, which are found in both regions. The clupeid *Gasteroclupea* is frequent in the whole Potosí region, in El Molino localities in southern Bolivia (as Rancho Hoyada[13]), and in the Maastrichtian Yacoraite Formation in Argentina, but has not yet been found at Pajcha Pata[12] (*contra* Gayet, 1991) or at Vila Vila[21], but it is known (one fragment) in the early late Palaeocene of Tiupampa[51]. The siluriforms Andinichthyidae, the cladistians and the Dipnoi occur in the Cretaceous localities of the Cochabamba region (Pajcha Pata[12], Vila Vila[21]) but are absent from the coeval distal localities of the Potosí region (Agua Clara[7], Hotel Cordillera[25]). These Maastrichtian freshwater fish found in an Upper Cretaceous level at Tiupampa[51] are still present in the early late Palaeocene at Tiupampa[52].

In summary, the following picture emerges: (1) the same marine fauna lived in the whole basin, (2) freshwater fish from the proximal and distal regions were different (in part), and (3) terrestrial tetrapods [amphibians, reptiles (except turtle and crocodiles), mammals], which include some freshwater forms, were obviously present only in the proximal region.

Although we cannot exclude that the absence of some fossils in a region results from a sampling bias, we suggest that there are sufficient data to support the view that the sampled faunas do reflect palaeogeography. The above-mentioned distribution of fossils in the basin is consistent with the hypothesis of the presence of freshwater in areas encroached by marine water at times of marine highstands and/or sufficient subsidence (Cappetta, 1975; Gayet et al., 1993; Sempere et al., 1997). Reduced freshwater areas of the proximal region (Tiupampa[51] — Pajcha Pata[12] — Vila Vila[21] in a part of the basin; Agua Clara[7] — Hotel Cordillera[25] in another part) have their own endemic freshwater ichthyofaunas, but they show common marine taxa, which demonstrates that marine influence reached these places.

7. Conclusion

In conclusion, the fauna of Pajcha Pata[12], located in the upper part of the Lower Member of the El Molino Formation, corroborates the middle Maastrichtian age ($\approx$68.4 Ma) deduced from the magnetostratigraphic and sequence stratigraphic study of the El Molino Formation. Therefore, Pajcha Pata[12] is the oldest late Cretaceous locality in South America which has yielded all kinds of vertebrates except birds. The fauna of Pajcha Pata[12] includes the oldest records in South America for several fish as the Heterotidinae and the Phareodontinae (Osteoglossiformes, Osteoglossidae), the Andinichthyidae and two other families (Siluriformes), the Latidae (Perciformes), and Amphibia (Gymnophiona, Caudata). It represents the only locality in Bolivia which has yielded Coelurosauria remains; until now this group was represented in that country only by trackways. Finally, undisputed Cretaceous mammals including tribosphenic and non-tribosphenic therians are unique for the Bolivian record.

The depositional environment was probably estuarian or lagoonal as indicated by a mixed fauna: continental taxa (?anurans, ?gymnophionans, reptiles, mammals), freshwater taxa (Caudata, ?anurans, ?gymnophionans, some fish) and numerous and diverse marine taxa (fish). Nevertheless, the ratio freshwater/marine taxa is unbalanced, with more numerous marine taxa (in number of specimens) than freshwater ones, and probably indicates a strong influence of the sea at that time in this place. The faunas from the proximal and the distal part of the El Molino basin seem different, but this assessment should be confirmed by new field research, screen-washing of more sediment, and exploration of the surroundings of Pajcha Pata[12]. Finally, isotopic analyses of all the fish taxa promise to provide further insights into the palaeoenvironment of the late Cretaceous and Paleocene in South America.

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