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PALAEO

Miocene fish faunas from the northwestern Amazonia basin (Colombia, Peru, Brazil) with evidence of marine incursions

Kenneth A. Monsch*

Paleontological working-room, Royal University of Groningen, Kerklaan 30, P.O. Box 14, 9750 AA Haren, The Netherlands

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Abstract

New evidence indicates marine influences during the Miocene in the northwestern Amazonia basin. This is the first major survey of the ichthyofauna from this area in the Miocene. Fossil fish remains from taxa such as the Dasyatoidea, Myliobatoidea, Characiformes, Siluriformes and Sciaenidae are found. Conspicuous finds were two pharyngeal teeth of *Stephanodus minimus*, a species that so far had only ever been found in Late Cretaceous sediments. The fish remains of freshwater, brackish and marine taxa are deposited together throughout the area. This is thought to be related to marine influences during the Miocene. These finds agree with earlier studies that suggest episodic marine influences, which most likely lasted up to the Late Miocene, and disagree with studies that suggest a connection between the Atlantic and the Caribbean Sea over the South American continent. The ichthyofaunas also indicate a warm climate, as well as shallow and possibly torrential waters. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Miocene; Amazonia; Pisces; taxonomy; marine transgressions; palaeoecology

1. Introduction

The Miocene history of the northwestern Amazon has been as fascinating as complex. Recent data published were mainly of a sedimentological and/or palynological nature and provided a framework for palaeogeographical reconstructions (Horn, 1993, 1994a,b, 1996; Horn et al., 1995; Räsänen et al., 1995; Marshall and Lundberg, 1996). Additional palaeoenvironmental information can be gained from the presence of molluscs and fishes. There has not

yet been a major review on these fishes. Recently, substantial information by Nuttall (1990) and Wesselingh (1993) on molluscs has been provided, although molluscs have been a subject of study since the last century (e.g. Gabb, 1869; Etheridge, 1879). The Miocene Solimões/Pebas Formation is very rich in fish remains. I have studied these considering the palaeoenvironmental study of this area. The studied samples were collected between 1989 and 1991 at various localities in the northwestern Amazon. They contained pollen, which were studied by Horn (1994b), molluscs and foraminifera (Horn, 1994b), as well as remains of tortoises, crocodiles, birds, vertebrae of tetrapods (reptiles and/or amphibians) and remains of bony fishes, sharks and rays.

I made an inventory of the Miocene ichthyofauna

* Present address: University of Bristol, Department of Earth Sciences, Wills Memorial Building, Queens Road, Bristol BS8 1RJ, UK. Fax: +44-117-9253385; E-mail: kenny.monsch@bristol.ac.uk

and interpreted it in a palaeoecological way. Moreover, this study contributes to the knowledge of the evolutionary history of fishes in northern South America.

2. Depositional environment

The area encompasses parts of the following basins which supply sedimentary infill: the Solimões Basin (Brazil), the Amazonas Basin (Colombia and Peru) and the Pastaza–Marañón Basin (Peru). These basins expand up to the area where the boundaries of Colombia, Brazil and Peru meet (see Fig. 1).

The sediments of the study area can be described as one great formation, which has different names depending on the country where these are found. In Brazil, it is called the Solimões Formation (Moraes Rego, 1930; Hoon, 1993), the Pebas Formation in Peru (Gabb, 1869) and in Colombia (Khobzi et al., 1980; Hoon, 1994b). The Formation consists of clay, silt, sandy clay and sand and fossil-rich layers, with remnants of vertebrates, molluscs, ostracodes and plants (Hoon, 1993).

The environment must have been humid and warm, indicated by mangroves as a typical coastal vegetation, mainly palms and grasses on the alluvial plain, which is followed by a tropical forest further inland. Furthermore, due to episodic marine incursions, the palaeoenvironmental history is divided in alternating stages where either the coastal plain or alluvial plain conditions dominated (Hoon, 1993).

3. Materials and methods

3.1. Material (including localities)

The material was collected during expeditions taking place between 1988 and 1991. The samples contained bony material, scales, teeth and otoliths. Some sediment samples, collected in Los Chorros, still had to be processed to separate the fish material in them.

All material was collected from the Neogene Solimões/Pebas Formation (see Fig. 1). The La Tagua beds and the Sta. Teresa section of the Pebas Formation are of Early Miocene to early Middle

Miocene age; the Iquitos, Indiana and Pevas sections (Peru) are of Middle Miocene age and the Sta. Sofia, Mocagua and Los Chorros sections (Colombia), the rest of the Peruvian samples and all Brazilian samples are of Middle to Late Miocene age, according to results of pollen studies by Hoon (1994b), or the mollusc fauna (see Tables 1 and 2). These periods do not overlap. These localities are clarified in Figs. 1–3.

3.2. Methods

The material collected by Wesselingh consists of residues of sieving of sediment samples weighing between 0.5 and 1 kg. The material collected by Hoon at La Tagua consists of residues of sediment samples weighing about 500 g. Other material collected by her consists of residues of sieving of samples of about 100 g. I separated recognisable bones in all the samples above. When I started the study, there was some unprocessed material, namely samples 23–26 (Table 1). These are residues of sediment of a few kilograms. Some of the bigger elements within these samples have been hand-picked. This material needed to be sieved further and the fish remains within to be identified.

4. Results

4.1. Identification of the material

The sample numbers indicated are the same as figured in Tables 1 and 2.

Superclass PISCES
Class CHONDRICHTHYES
Chondrichthyes indet.

Systematics of the chondrichthyans are according to Cappetta (1987).

One item: a typical chondrichthyan spine, belonging to fin of which the original place on the body is unclear; chondrichthyan spines which may be either fin spines or frontal spines of rays: bilaterally ornamented with blunt thorns. Bases and apices of spines missing.

Samples: fin spine: 13, fin/rostral spines: 20 and 24.

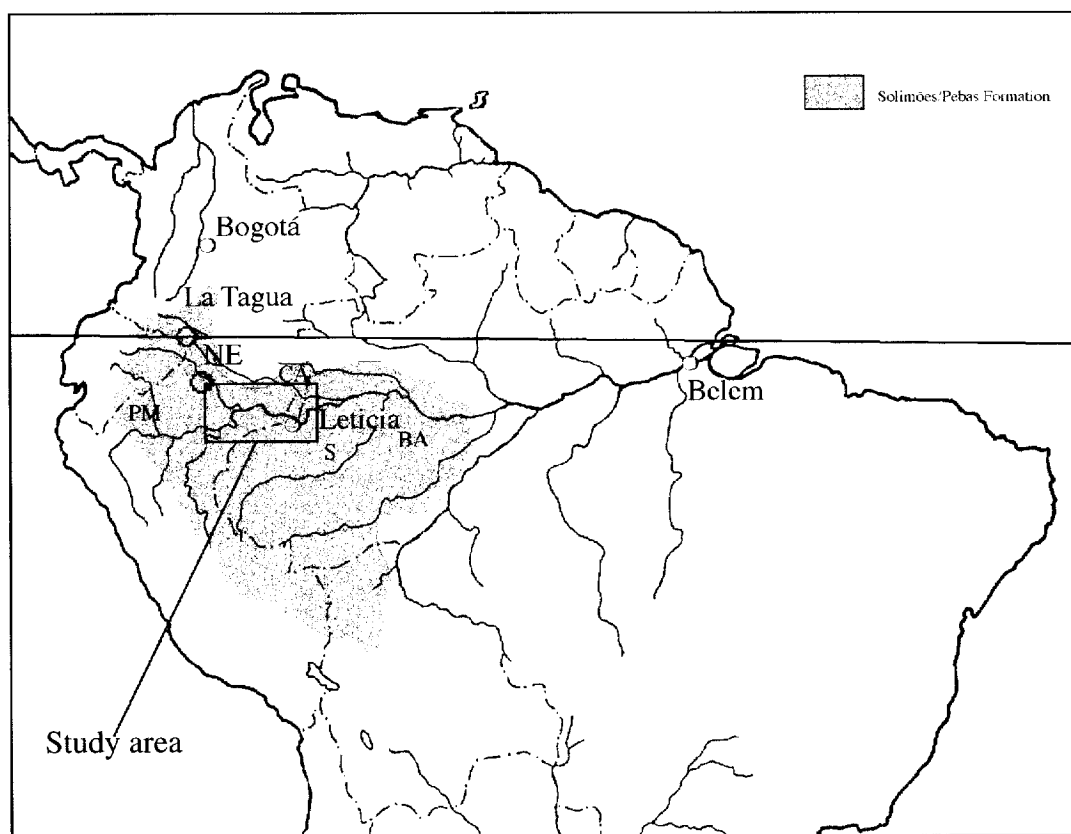


Fig. 1. Overview of study area, Solimões/Pebas Formation and the basins involved in this study. Outline of formation based on Hoon (1994b). BA = Brazilian Amazonas; CA = Colombian Amazonas; PM = Pastaza–Marañón; S = Solimões; NE = Nuevo Esperanza.

Subclass ELASMOBRANCHII

Cohort EUSELACHII

Euselachii indet.

One typically shark-like tooth, lacking root, but very flattened labio-lingually (typical for a shark's tooth), with serrated cutting edge.

Sample: 11.

Family CARCHARHINIDAE

Genus *Carcharhinus* Blainville 1816

Carcharhinus sp. (Plate I, 4)

One jaw tooth with a relatively low, triangular crown and large root. Crown unicuspid, cusp bent slightly laterally, cutting edge serrated. Root consisting of one piece, with bilobed appearance. Tooth (including root) approximately 3 mm high. *Carcharhinus*-teeth

can also be upright and less serrated (Longbottom, 1979; J.G. Lundberg, pers. commun., 1996).

Sample: 11.

Superorder BATOMORPHII

Batomorphii indet.

One rostral spine, bilaterally toothed, broadening in rostral direction, with a blunt, rounded apex and clearly striated; one tooth of the holaulacorhize stage (sensu Cappetta, 1987: holaulacorhize = with a bilobed root) with a flat, plate-shaped crown.

Samples: Spine: 28; Tooth: 1.

Table 1
Coding of Colombian samples used, stored in INGEOMINAS,
Bogotá, Colombia

No.	Location	Era	Collector
1	Buenos Aires	LM ^a	Wesselingh
2	Buenos Aires	LM	Wesselingh
3	Los Chorros	LM	Wesselingh
4	Los Chorros	LM	Wesselingh
5	Los Chorros	LM	Wesselingh
6	Los Chorros	LM	Wesselingh
7	Los Chorros	LM	Wesselingh
8	Los Chorros	LM	Wesselingh
9	Los Chorros	LM	Wesselingh
10	Los Chorros	LM	Wesselingh
11	Los Chorros	LM	Wesselingh
12	Los Chorros	LM	Wesselingh
13	Los Chorros	LM	Wesselingh
14	Los Chorros	LM	Wesselingh
15	Los Chorros	LM	Wesselingh
16	Los Chorros	LM	Wesselingh
17	Los Chorros	LM	Wesselingh
18	Los Chorros	LM	Wesselingh
19	Los Chorros	LM	Wesselingh
20	Los Chorros	LM	Wesselingh
21	Los Chorros	LM	Hoon
22	Los Chorros	LM	Hoon
23	Los Chorros	LM	Hoon
24	Los Chorros	LM	Hoon
25	Los Chorros	LM	Hoon
26	Los Chorros	LM	Hoon
27	Macedonia	LM	Wesselingh
28	Mocagua	LM	Wesselingh
29	Mocagua	LM	Wesselingh
30	Mocagua	LM	Wesselingh
31	Mocagua	LM	Hoon
32	Mocagua	LM	Hoon
33	Puerto Nariño	LM	Wesselingh
34	Puerto Nariño	LM	Wesselingh
35	Puerto Nariño	LM	Wesselingh
36	Puerto Nariño	LM	Wesselingh
37	Puerto Nariño	LM	Hoon
38	Quebrada confluyente del Pamate	LM	Wesselingh
39	Salado del Pamate	LM	Wesselingh
40	San Martin	LM	Wesselingh
41	Santa Sofia	LM	Wesselingh
42	Santa Sofia	LM	Wesselingh
43	Santa Sofia	LM	Wesselingh
44	Santa Sofia	LM	Wesselingh
45	La Tagua	EM ^b	Hoon
46	La Tagua	EM	Hoon
47	Villareal	LM	Wesselingh
48	Villareal	LM	Wesselingh
49	Zaragoza	LM	Wesselingh
50	unknown	?	Hoon

^a Middle to Late Miocene.

^b Early Miocene.

Table 2
Coding of non-Colombian samples used

No.	Location	Country	Era	Collector
51	Atalaya do Norte	Brazil ^a	LM ^b	Hoon
52	Benjamin Constant	Brazil	LM	Hoon
53	Benjamin Constant	Brazil	LM	Hoon
54	Barrio Florido	Peru ^c	EM ^d	Hoon
55	Barrio Florido	Peru	EM	Hoon
56	Barrio Florido	Peru	EM	Hoon
57	Chimboté	Peru	LM	Hoon
58	Indiana	Peru	EM	Hoon
59	Indiana	Peru	EM	Hoon
60	Indiana	Peru	EM	Hoon
61	Iquitos, Pto. G.A. ^e	Peru	EM	Hoon
62	Iquitos, Pto. G.A.	Peru	EM	Hoon
63	Mishana	Peru	MM ^f	Hoon
64	Nuevo Horizonte	Peru	LM	Hoon
65	Puerto Almendras	Peru	MM	Hoon
66	Pevas	Peru	MM	Hoon
67	Pevas	Peru	MM	Hoon
68	Rio Napo, Nuevo Esperanza	Peru	EM	M. Räsänen
69	Santa Julia (Pevas)	Peru	MM	Hoon
70	Santa Julia (Pevas)	Peru	MM	Hoon
71	Santa Julia (Pevas)	Peru	MM	Hoon
72	Santa Julia (Pevas)	Peru	MM	Hoon
73	Santa Julia (Pevas)	Peru	MM	Hoon
74	Santa Julia (Pevas)	Peru	MM	Hoon
75	Santa Julia (Pevas)	Peru	MM	Hoon
76	Santa Julia (Pevas)	Peru	MM	Hoon
77	Santa Julia (Pevas)	Peru	MM	Hoon
78	Santa Teresa	Peru	EM	Hoon
79	Santa Teresa	Peru	EM	Hoon
80	Santa Teresa	Peru	EM	Hoon
81	Santa Teresa	Peru	EM	Hoon
82	Santa Teresa	Peru	EM	Hoon

^a Brazilian samples are stored in DNPM-Departamento Paleontologica, Rio de Janeiro, Brazil.

^b Middle to Late Miocene.

^c Peruvian samples are stored in INGEMMET, Lima, Peru.

^d Early to early Middle Miocene.

^e Iquitos, Puerto Ganso-Azul.

^f Middle Miocene.

Order RAJIFORMES

Family PRISTIDAE

Genus cf. *Pristis* Linck 1790

cf. *Pristis* sp. (Plate I, 5)

Jaw teeth, resembling description and figure of *Pristis* in Cappetta (1987, pp. 158–160, fig. 137O–Q), with lateral expansions that lie more at the lingual face of teeth. These expansions could be regarded

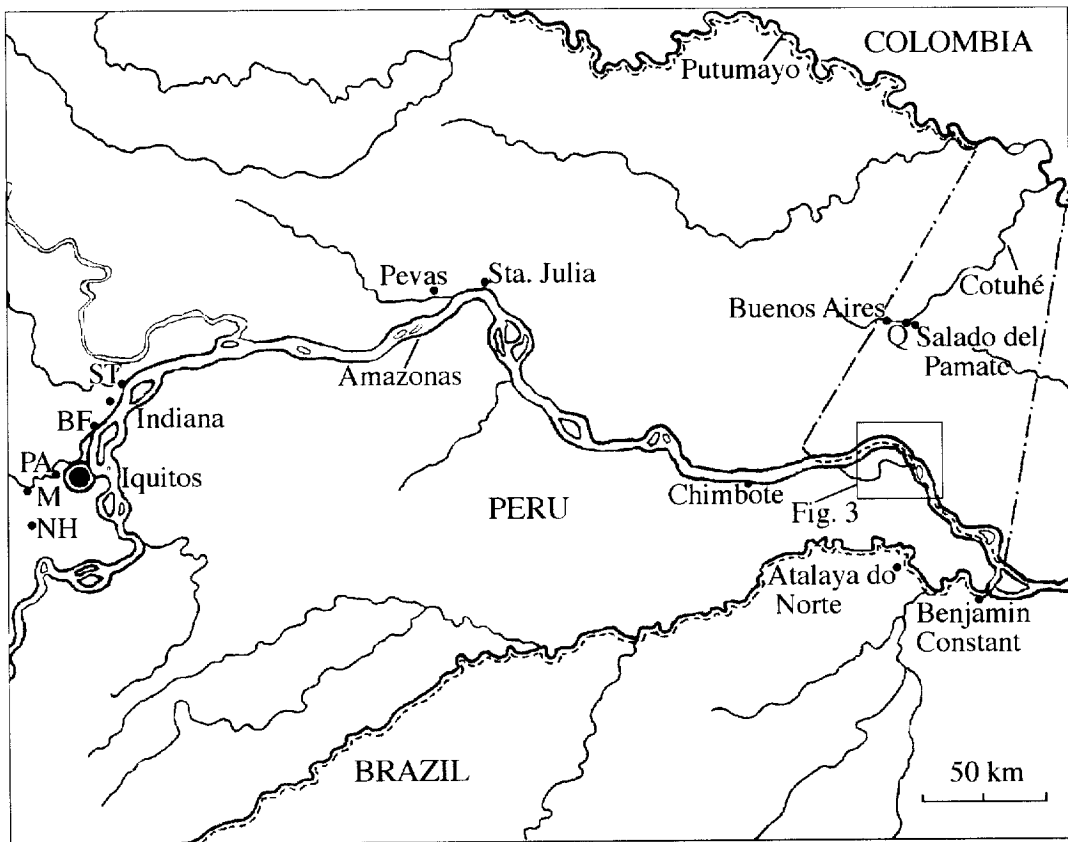


Fig. 2. Detail of study area I. BF = Barrio Florido; In = Indiana; M = Mishana; NH = Nuevo Horizonte; PA = Puerto Almendras; Q = Quebrada; ST = Santa Teresa.

as lateral uvulas, which *Pristis* is not supposed to possess (Cappetta, 1987). Another aspect in which these teeth differ from Cappetta's descriptions is the width of the groove of the root: much smaller in the studied specimens.

Samples: 4, 11–13, 20.

Order MYLIOBATIFORMES
Superfamily DASYATOIDEA
Dasyatoidea indet. (Plate I, 6)

Numerous dermal denticles: small cones, diameter $\pm 1\text{--}3$ mm, with basal expansions that give them a star-like shape. Belonging to either Dasyatidae (marine stingrays) or Potamotrygonidae (freshwater stingrays), or both. I find it impossible to make a distinction between the two based on these denticles alone. These two families are similar in many

respects (see also Lundberg, 1997) which even convinced Nelson (1994) to lump them in one family, the Dasyatidae.

Samples: 4, 12, 13, 19, 31, 33, 46, 65, 71 and 74.

Family cf. DASYATIDAE

Genus cf. *Dasyatis* Rafinesque 1810

cf. *Dasyatis* sp. (Plate II, 7a: ♀, b: ♂)

Jaw teeth. On the basis of Cappetta (1987), first diagnosed as *Dasyatis*, but as Lundberg (1997) pointed out, *Dasyatis* and potamotrygonid teeth strongly resemble each other and it is hazardous to make the distinction. These teeth: small, up to 6 mm wide, often with globular crown. Labial and lingual face separated by an often sharp transverse crest. Convex or flat labial face of crown apically rounded (♀), or triangular and overhanging the lingual face (♂).

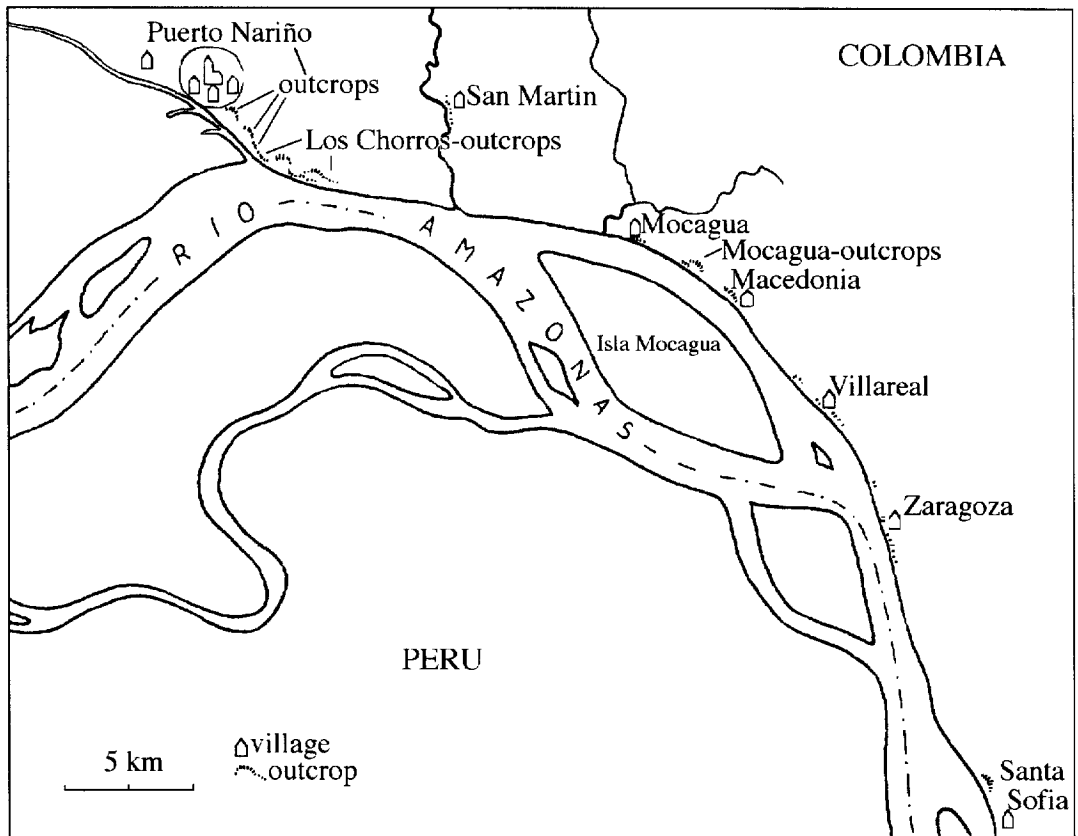


Fig. 3. Detail of study area II.

Labial face sometimes with ellipse-shaped to round depression, smooth or with a tuberculated ornamentation. Lingual face always concave, less developed than labial face, sometimes with central uvula, never lateral uvulas. Lingual face also with vertical crest, originating in the transverse crest. Root bilobed, one or more central foramina but no latero-lingual ones.
Samples: 1, 2, 4, 6, 11–13, 17, 27, 29, 31, 33, 37, 39, 42, 44, 45, 50, 53, 54, 58, 64 and 65.

Superfamily MYLIOBATOIDEA
 Myliobatoidea indet.

Myliobatis Cuvier 1817 and *Rhinoptera* Cuvier 1829 with polyaulacorhize teeth (root like a caterpillar track) are recognisable by their more or less hexagonal lateral teeth. Subsequently, *Myliobatis* and *Rhinoptera* can be identified by the ratios of transverse and anterior–posterior dimensions, which

differ between the genera (Gillette, 1984). Hence, in case of a complete tooth, these two genera can be identified. In all other cases, the polyaulacorhize teeth were identified as ‘*Myliobatoidea* sp.’.
Samples: 1, 6, 14, 48, 54 and 69.

Order MYLIOBATIDAE
 Genus *Myliobatis* Cuvier 1817
Myliobatis sp. (Plate II, 8)

Hexagonal jaw teeth of polyaulacorhize stage, differing from closely related *Rhinoptera* by the ratios of dimensions only. For interior lateral teeth of *Myliobatis*, transverse diameter at least four times greater than the anterior–posterior diameter, while in *Rhinoptera* transverse diameter not more than three times as great as anterior–posterior diameter (Gillette, 1984).
Samples: 2, 7, 12, 33, 56 and 71.

PLATE I

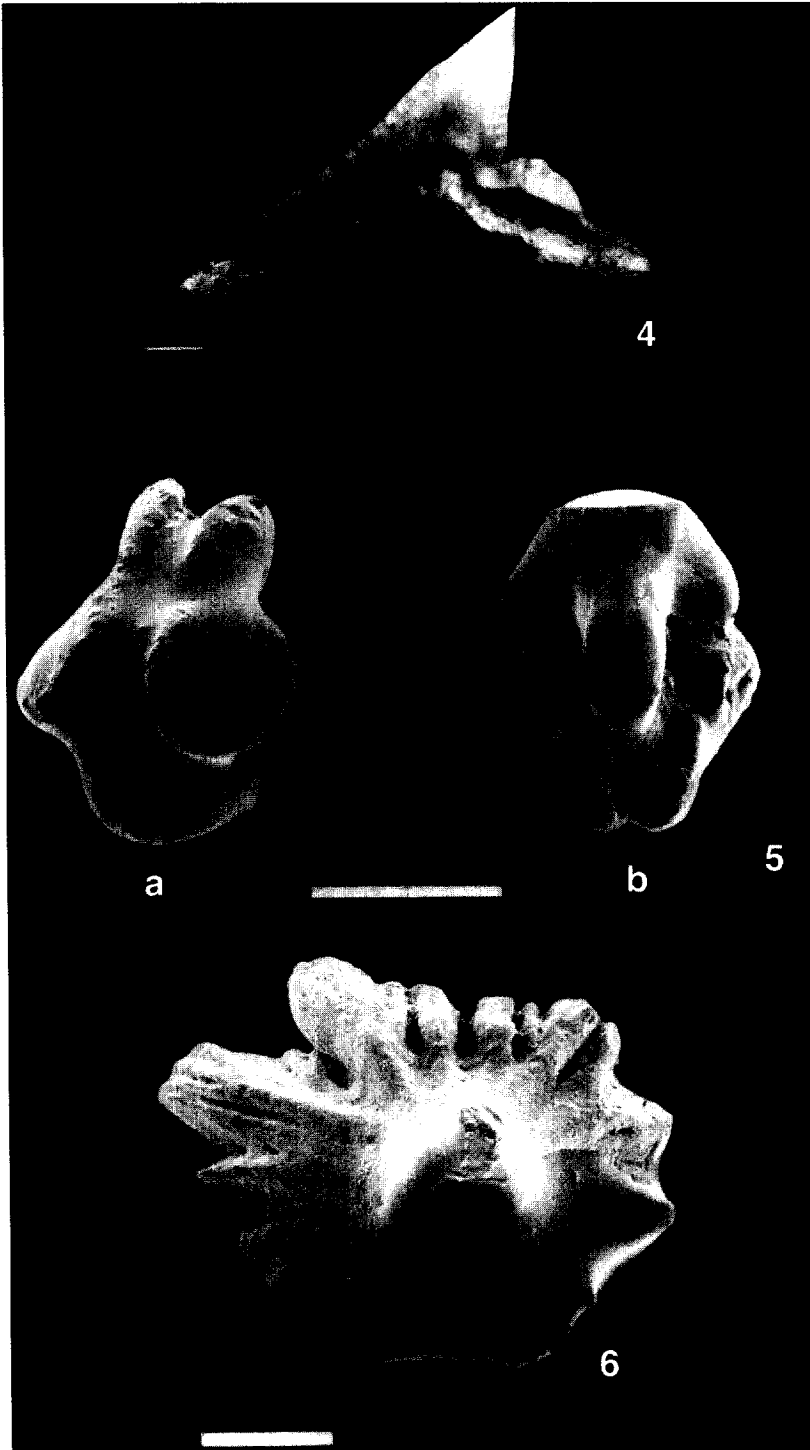
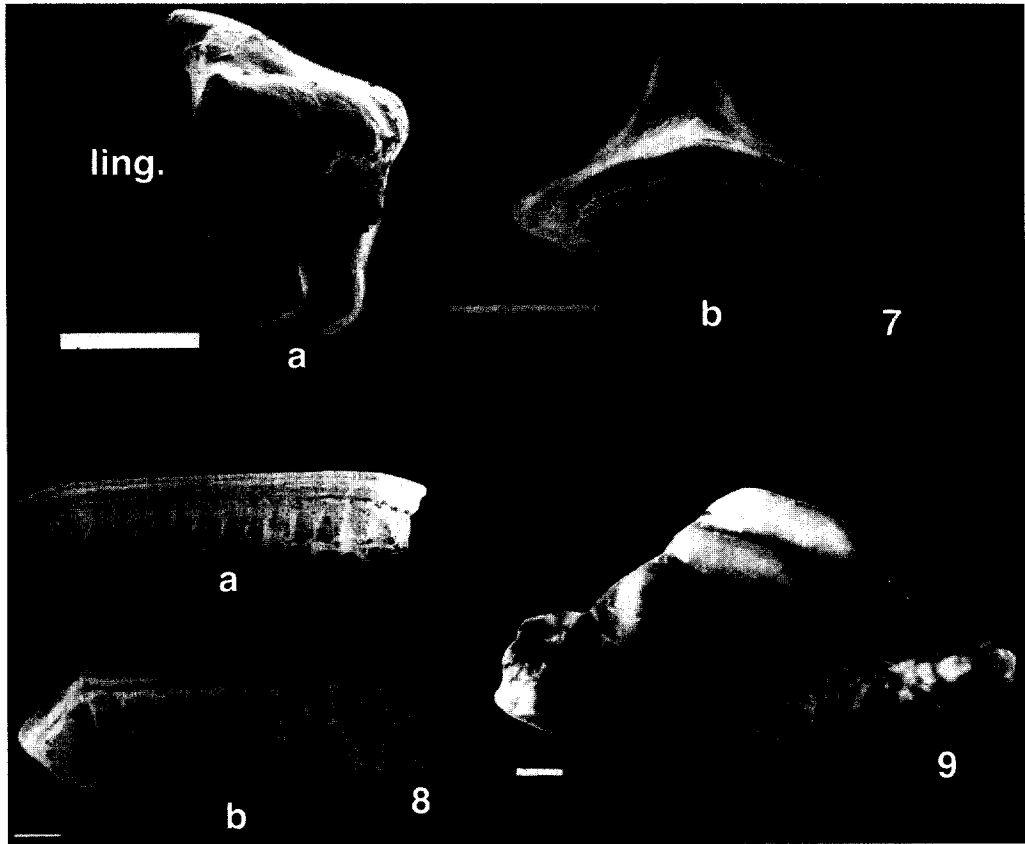


PLATE II



7. Jaw tooth (cf. *Dasyatis* sp.). a: profile. Scale bar: 0.84 mm; b: basi-lingual view. Scale bar: 0.81 mm.
 8. Jaw tooth (*Myliobatis* sp.). a: basal view, b: occlusal view. Scale bar: 0.53 mm.
 9. Jaw fragments (*Tetraodontiformes* indet.). Scale bar: 0.4 mm.

Order rhinopteridae

Genus *Rhinoptera* Cuvier 1829*Rhinoptera* sp.

Hexagonal jaw teeth of polyaulacorhize stage, resembling those of *Myliobatis* very closely, but differing from these about their dimensions (see descrip-

tion of *Myliobatis* sp.).

Samples: 5, 14, 33, 34 and 70.

Class OSTEICHTHYES

Osteichthyes indet.

Vertebrae, tooth-bearing elements such as dentaries and premaxillaries, skull-parts, teeth, scales (probably teleost), radiiform bones that are probably branchiostegial rays and/or ribs and indeterminate otoliths, which are probably of teleost origin, as are nearly all identifiable otolith-based fossil fishes (Nolf, 1985).

Samples: from localities throughout the whole study area.

PLATE I

4. Jaw tooth (*Carcharhinus* sp.). Scale bar: 0.4 mm.
 5. Jaw tooth (cf. *Pristis* sp.). a: basal view; b: occlusal view. Scale bar: 0.82 mm.
 6. Dermal denticle (*Potamotrygonidae/Dasyatidae* indet.). Scale bar: 0.83 mm.

Superorder TELEOSTEI

Order TETRAODONTIFORMES

Tetraodontiformes indet. (Plate II, 9)

Two jaw fragments. Recognisable by their partially sponge-like outer surface and their slightly basin-like shape, on the inner surface, one row of broad teeth. Previously mentioned by Hoorn (1994b) as a Chimaeridae, a previous but faulty diagnosis of these specimens. The identity as Tetraodontiformes was revealed through comparisons with material in the British Museum (Natural History), London.

Sample: 53.

Family EOTRIGONODONTIDAE

Genus *Stephanodus*

Stephanodus minimus Gayet 1991

Stephanodus minimus Gayet, 1991, pp. 482–483, fig. 29.

Two pharyngeal teeth, very typically shaped (Gayet, 1991, fig. 29). The most conspicuous feature of these teeth is their almost absolute flatness, produced by lateral flattening. Other characteristics are: round posterior processes which produce hook-shaped apical extremity. Both teeth very small (less than 2 mm). *Stephanodus* has so far only been found in marine sediments of Late Cretaceous age (Gayet, 1991).

Samples: 23 and 25.

Order CHARACIFORMES

Characiformes indet. (Plate III, 10)

Identified as characiform teeth by their blackened tips, but these conical, striated, reasonably curved teeth do not fit in with characid or anostomid morphology and are identified as Characiformes indet. Jaw teeth of Characidae and jaw and pharyngeal teeth of Anostomidae are easily recognised because of their peculiar morphology (see below).

Samples: 4, 6, 7, 13, 15, 16, 38, 53, 55, 78, 69 and 71.

Family ERYTHRINIDAE

Genus *Hoplias*

Hoplias sp. (Plate III, 11)

Jaw teeth with wide range of morphologies: characterised by lateral cutting edges, a conicoid shape

(although sometimes seemingly flat at first sight) sometimes curved, sometimes upright and then triangular in labial and lingual view, always with striated base.

Samples: 4, 6, 7, 9, 10, 12, 13, 15, 16, 18, 23, 25, 26, 29, 31, 32, 38, 46, 50, 53, 58, 75 and 76.

Genus cf. *Hoplias*

cf. *Hoplias* sp.

Jaw teeth resembling *Hoplias* teeth but showing some differences, making it difficult to identify them with certainty as *Hoplias*: these are either clearly longer, shorter or rounder than most of the *Hoplias* teeth, but other characteristics such as the lateral cutting edge and striated surface make them possibly *Hoplias*.

Localities: 26, 31 and 51.

Family ANOSTOMIDAE

Anostomidae indet. (Plate III, 12)

Pharyngeal teeth: basally barrel-shaped, two apices, the distal, large one the best distinguishable. Distal apex hook-shaped, pointing in rostral direction. Frontal apex much smaller, often hard to distinguish, blunt and upright. Apical sides clearly blackened. Morphology of pharyngeal teeth of closely related Chilodontidae identical, but tips not blackened. Only Characidae and Anostomidae have black-tipped teeth (Roberts, 1975).

Samples: 4, 7, 13, 24, 25, 31, 46 and 53.

Genus *Leporinus*

Leporinus sp.

Two small oral teeth with conspicuous morphology: long, cylindrical crown, suddenly broadened and flattened apically (cf. Roberts, 1975, fig. 4).

Samples: 13 and 46.

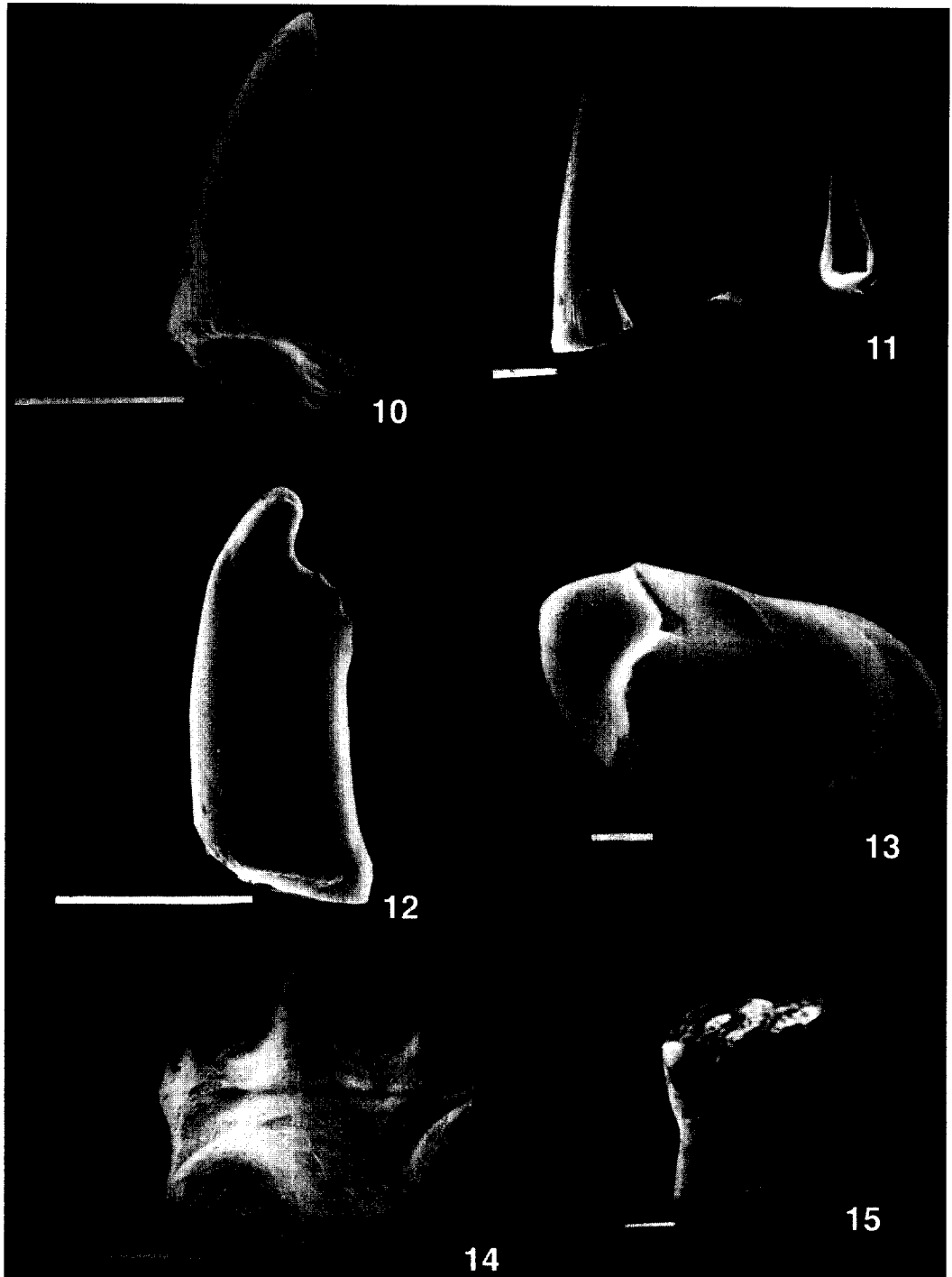
Family cf. CHILODONTIDAE

cf. Chilodontidae indet.

Pharyngeal teeth, similarly shaped as anostomid pharyngeal teeth. Identified as cf. Chilodontidae, as they do not have blackened tips, but possibly darkening is poorly visible due to darkening of the teeth as a whole as a result of their age.

Samples: 4, 13, 26 and 71.

PLATE III



Family cf. SERRASALMIDAE

cf. Serrasalmidae indet. (Plate III, 13)

Jaw teeth, resembling teeth of Serrasalmidae (subfamily Myleinae), as described by Gayet (1991, fig. 15) but of far greater size. Teeth figured by Gayet are 1–2 mm wide, whereas these approximately 5 mm wide. Crown small and broad, triangular in labial and lingual view, with a sharp edge. In basal view, crown invisible, because root, visible as hollow cup, is too broad.

Samples: 11, 15 and 23.

Family CHARACIDAE

Subfamily TETRAGONOPTERINAE

Tetragonopterinae indet. (Plate III, 14)

Jaw teeth, superficially resembling sharks' teeth, but having rounder outline and higher root, higher than the crown itself. Crown uni- or tricuspid, middle cusp clearly larger than lateral ones, slightly striated basally, with a lateral cutting edge.

Samples: 4, 6, 7, 13, 26, 49 and 53.

Order CYPRINIFORMES

Family INCERTAE SEDIS

Genus cf. *Molinichthys*cf. *Molinichthys inopinatus* Gayet, 1982 (Plate III, 15)*Molinichthys inopinatus* Gayet, 1982, pp. 405–407.

One tooth: barrel-shaped, bent-over crown with relatively large diameter and wrinkled, flat apex, root more slender and longer than crown, the whole resembling a mammalian tooth. Since *M. inopinatus* is the only living and fossil Cyprinoid in South America (Gayet, 1991) this tooth is tentatively assigned to that species, but a description of teeth of this species was not available.

Sample: 65.

PLATE III.

10. Tooth (Characiformes indet.). Scale bar: 0.82 mm.
11. Jaw teeth (*Hoplias* sp.). Scale bar: 0.83 mm.
12. Pharyngeal tooth (Anostomidae indet.). Scale bar: 0.82 mm.
13. Jaw tooth (cf. Serrasalmidae indet.). Scale bar: 0.85 mm.
14. Jaw tooth (Tetragonopterinae). Scale bar: 0.81 mm.
15. Jaw tooth (cf. *Molinichthys inopinatus*). Scale bar: 0.55 mm.

Order SILURIFORMES¹

Siluriformes indet. (Plate IV, 16)

Numerous pectoral and dorsal fin spines, clearly of siluroid origin. Pectoral spines recognisable by their rounded or oval outline, striated surface and often ornamented with tubercles or thorns on the inner and/or outer surface. Often only bases of these spines found. Dorsal fin spines much more slender than pectoral spines (e.g. Plate IV, 16a, a callichthyin) not rounded or oval: distally often hollow. Base more gradually broadened than in pectoral spines, symmetrical and looks much different. Pectoral spine's base abruptly broadened and asymmetrical (Plate IV, 16b). Base of dorsal spines only broadened laterally, whereas base of the pectoral spine also broadened rostrally and distally. Basal foramen in dorsal spine often relatively bigger than in pectoral spines.

Samples: Dorsal fin spines: 2, 7, 8, 10–12, 15, 20, 23–26, 30, 53, 59, 65, 68, 71 and 78. Pectoral fin spines: 1, 2, 11, 23–26, 30, 41, 47–49, 53, 60, 64, 68 and 79–82.

Suborder LORICARIOIDEI

Loricarioidei indet. (Plate IV, 17)

Odontodes sensu Isbrücker and Nijssen (1992), occurring only in this suborder (Isbrücker and Nijssen, l.c.), identifiable from other teeth by their extremely slender appearance in combination with a relatively large length.

Localities: 1, 19, 25, 33 and 53.

Family CALLICHTHYIDAE

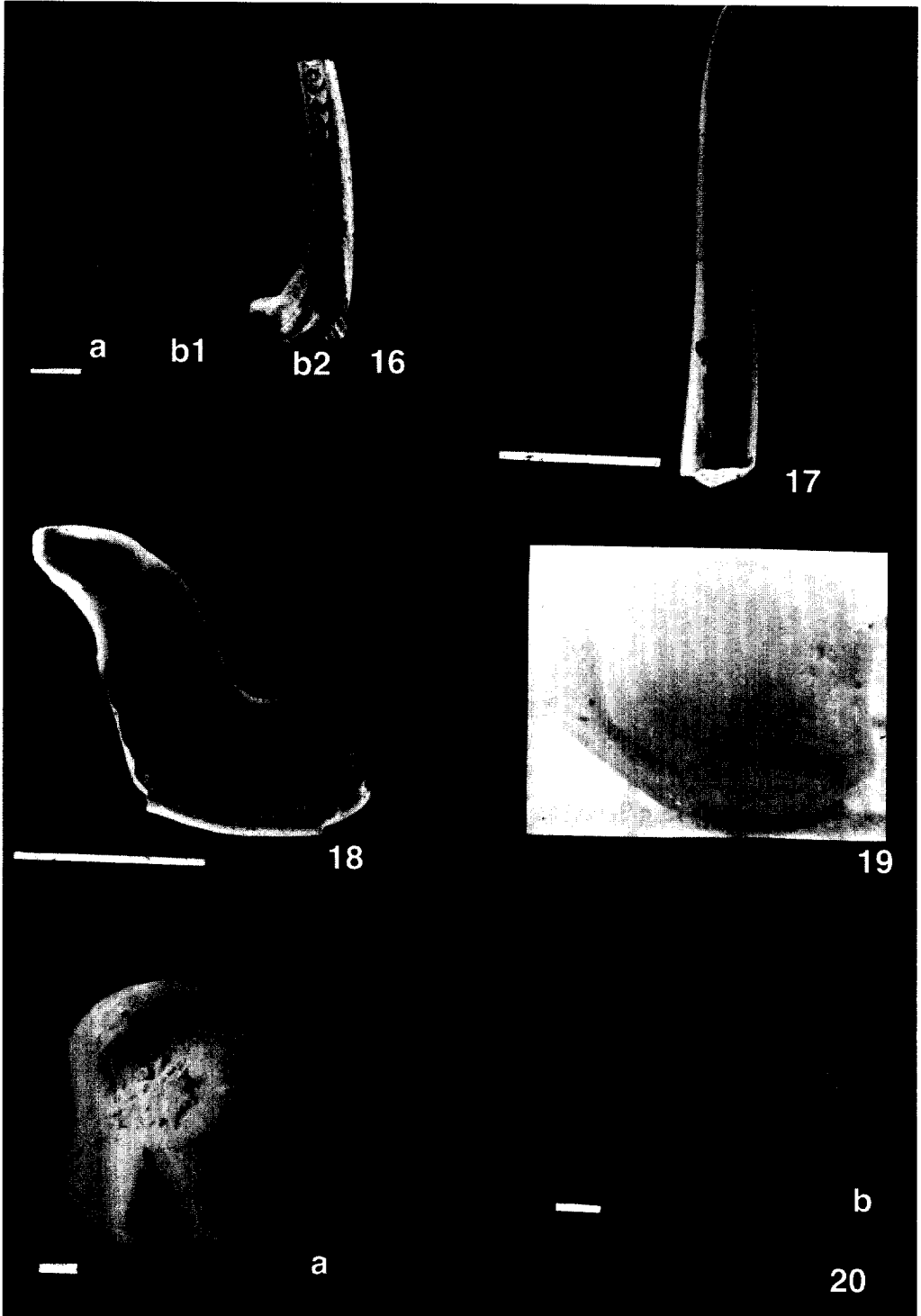
Subfamily CALLICHTHYINAE

Callichthyinae indet. (Plate IV, 16b)

Pectoral spines, recognisable from their oval and relatively flat outline, striated surface and frontal surface with numerous small tubercles (not visible on Plate IV, 16b). Ventral side ornamented with one row of, sometimes slightly curved sharp thorns, bigger towards the apex. Morphology of pectoral spines the same as in Corydorinae but with a difference in size: spines of Callichthyinae are clearly bigger: the maximum diameter in Corydorinae no

¹ Fig. 16a resembles percoid's median fin spine (J.G. Lundberg, pers. commun., 1996).

PLATE IV



more than approximately 1.5 mm, while 2.5–5 mm in Callichthyinae.

Samples: 23–26 and 68.

Subfamily CORYDORINAE

Corydorinae indet.

Pectoral spines. Morphology described together with that of pectoral spines of Callichthyinae.

Samples: 14 and 23–27.

Family LORICARIIDAE

Loricariidae indet. (see Plate IV, 18)

Curved, often apically bifurcated jaw teeth.

Samples: 3, 6, 7, 9, 11–13, 16, 17, 19, 20, 31, 35, 36, 38, 39, 53, 57, 64, 71, 74 and 79.

Family ARIIDAE

Ariidae indet. (Plate IV, 19).

One otolith, typical for utricular otoliths in ariids: relatively big, consisting of sponge-like material at the internal face, compact external face, without cristae. One other otolith compact on both sides, but has the typical ariid's otolith shape (Plate IV, 19).

Samples: 2 and 71.

Genus *Arius* Cuvier and Valenciennes 1840

Arius cf. *gigas*

Arius sp., Nolf, 1976, pp. 716–717, pl. II, figs. 12–17.

Arius gigas (pectoral spine), Gayet and Van Neer, 1990, pp. 241–251.

Arius cf. *gigas*, own interpretation on the basis of otolith size and species epitheton, this paper.

One otolith, typical of *Arius* (see description of *Arius* sp., below), but significantly bigger (rostral–caudal diameter clearly more than 1 cm) all other *Arius*

otoliths studied. The size of this otolith leads to my supposition that it might be of *A. gigas* (mentioned in Gayet and Van Neer, 1990).

Sample: 4.

Arius sp. (Plate IV, 20)

Pectoral spines and otoliths. Pectoral spines conspicuously flattened dorso-ventrally and more or less regularly striated, external face more than internal face. Internal face with small thorns for the distal two-thirds, relatively small internal fossa and large 'superio-internal bony part' ('partie osseuse supéro-interne', sensu Gayet and Van Neer, 1990, fig. 1). External face with regularly spaced tubercles over the whole length. Otoliths typical ariid: sponge-like at the internal side, compact at the external side and without cristae. *Arius* otoliths round, biconvex but not very bulging, with irregular surfaces and a little less long than 1 cm.

Samples: Otoliths: 13, 32, 72 and 77; Pectoral spines: 48, 53 and 81.

Genus cf. *Arius* Cuvier and Valenciennes 1840

cf. *Arius* sp.

One pectoral spine, bearing all the characteristics of *Arius* spines (see description), but relatively small and lacking the characteristic base (broken off).

Sample: 53.

Order PERCIFORMES

Family SCIAENIDAE

Sciaenidae indet.

Otoliths that are typically sciaenid-like: relatively big ostium ('head of the tadpole'), enclosed by cristae at the internal side of the otolith and a long cauda ('tail') of which rostral part parallel to dorsal border of otolith and caudal part curving in ventrad [example: Plate V, 21 (*Ctenosciaena* sp.)]. Unfortunately these otoliths cannot be identified further due to wear.

Samples: 22, 30, 31, 48, 63 and 70.

Genus *Ctenosciaena* Fowler and Bean 1923

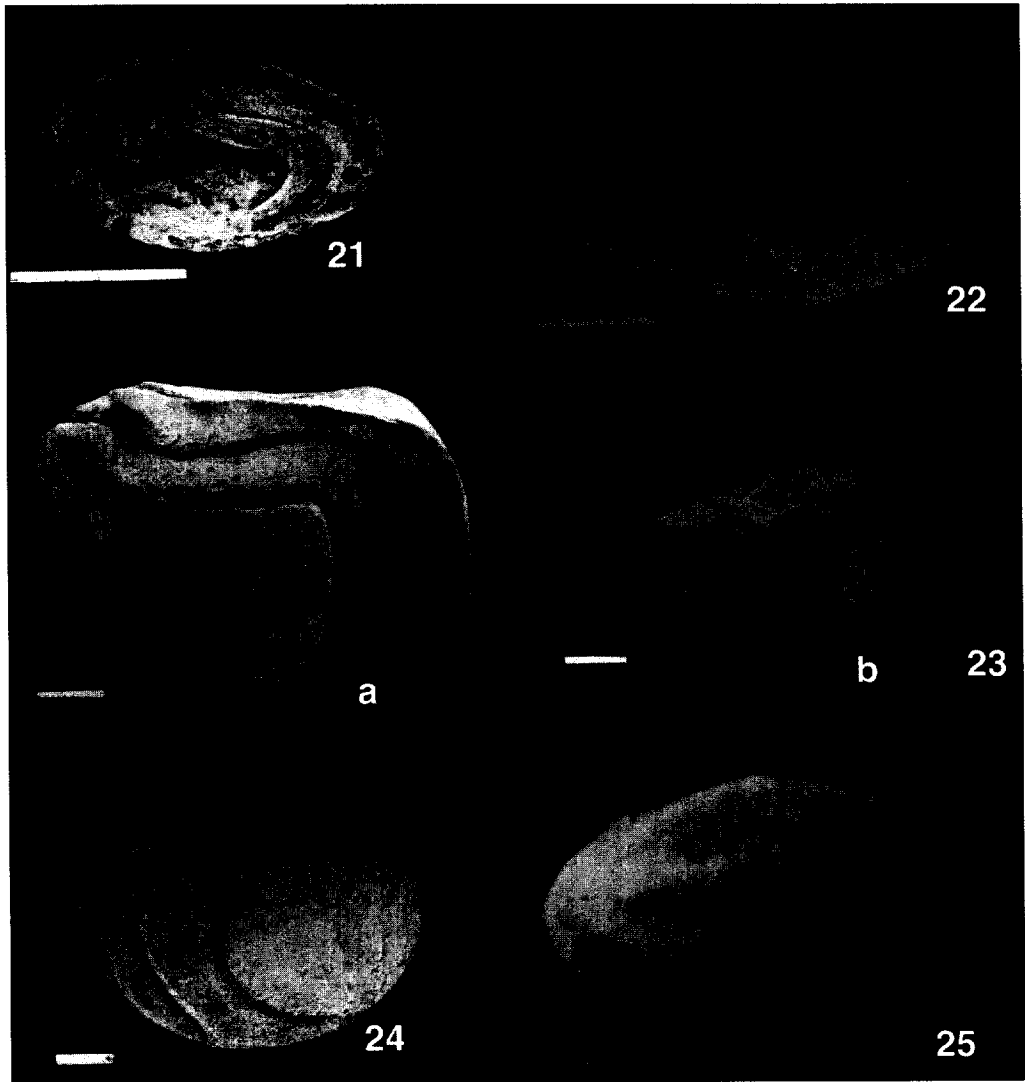
Ctenosciaena cf. *peruviana* Chirichigno 1975

Ctenosciaena peruviana Chirichigno, 1975, p. 1.

PLATE IV

16. Siluroid spines. a: dorsal spine (Callichthyinae indet.), b: pectoral spines (Siluriformes indet.). Scale bar: 0.86 mm.
17. Odontode (Loricarioidei indet.). Scale bar: 0.83 mm.
18. Jaw tooth (Loricariidae indet.). Scale bar: 0.83 mm.
19. Otolith (Ariidae indet.). Sides of squares: 1 mm.
20. Otolith (*Arius* sp.). a: internal view. Scale bar: 0.55 mm. b: external view. Scale bar: 0.83 mm.

PLATE V



21. Otolith (*Ctenosciaena* sp.). Scale bar: 0.83 mm.
 22. Otolith (*Larimus* sp.). Scale bar: 0.85 mm.
 23. Otolith (*Plagioscion* sp.). a: internal view. b: profile. Scale bars: 0.83 mm.
 24. Otolith (*Umbrina* sp.). Scale bar: 0.83 mm.
 25. Otolith (*Dactyloscopidae* indet.). Scale bar: 0.22 mm.

Identifications on the basis of pers. comm. with D. Nolf (1994), Royal Belgian Institute for Natural Sciences

Otoliths, resembling very closely otoliths of *Ctenosciaena* sp. (see description, this paper). These specimens, of which D. Nolf identified a few as *C.*

cf. peruviana, are characterised by a short cauda, which is only slightly bent in ventral direction.
Samples: 6, 11, 13, 21, 63 and 85.

Ctenosciaena sp. (Plate IV, 21)

Otoliths with square-like shaped, not very large os-

tium. Rostral part of cauda running parallel to dorsal margin of otolith, caudal part bending ventrad. *C. cf. peruviana* Otoliths resembling the otolith in Plate V, 21, only the cauda is clearly shorter.

Samples: 33, 54, 59 and 61.

Genus *Larimus* Cuvier 1830

Larimus sp. (Plate V, 22)

Otoliths with ostia which are relatively flattened dorso-ventrally and have sharp angles in the lower cristae, which curve dorsad rostrally. Distal part of cauda makes angle of 90° with rostral part. Distal part points in rostro-ventral direction.

Samples: 44, 45 and 69.

Genus *Pachypops* Gill 1861

Pachypops fourcroi (Lacépède 1802)

Perca fourcroi Lacépède, 1802, p. 289, fig. 242.

Corvina biloba Cuvier, 1830, in Cuvier and Valenciennes, 1828–1849, p. 112.

Pachypops camposi Fowler, 1954, p. 252, fig. 843.

P. cevegei Cervignon, 1982, p. 237, figs. 17–18.

Otoliths resembling the figure of this species in Nolf (1976, pl. 8, fig. 3) and also resembling otoliths of *Larimus* sp. The differences: *Pachypops* otoliths with a longer cauda, without an angle of 90° as in *Larimus*, but with a rather rounded contour and with a less sharp angle in the crista ostiale inferior (the lower part of the crista around the ostium).

Samples: 37, 45 and 58.

Genus *Plagioscion* Gill 1861

Plagioscion sp. (Plate V, 23)

Small to large otoliths with a typical morphology. Ostium very large, crista ostiale inferior runs like an almost straight line to the rostro-ventral margin of the otolith (Plate V, 23a). Cauda long, runs along the dorsal, caudal and almost the whole ventral margin of otolith, almost reaching ostium. Large otoliths characterised by a conspicuously bulging ventral side. If viewed upside-down from the lateral side, they resemble empty tortoise shells (Plate V, 23b). Smaller otoliths from this genus without such a conspicuous ventral side, and relatively smaller ostium.

Samples: 11–13, 15, 21, 27, 62 and 65.

Genus *Umbrina* Cuvier 1817

Umbrina sp. (Plate V, 24)

Otoliths with relatively big ostia and caudas. Ostium oval or square with strongly rounded corners and crista ostiale inferior bulging in caudal direction. Cauda situated closely to margin of otolith and bending in rostrad ventrally, thus almost reaching the ostium.

Samples: 11, 12, 17, 31, 32, 41, 52, 59, 60, 62, 64–68, 71 and 72.

'Genus *Sciaenidarium*' Nolf 1976

'Genus *Sciaenidarium*' *sasakii* (Schwarzahns 1993)

'Genus *Sciaenidarium*' sp., Nolf, 1976, pp. 734–735, pl. IX, figs. 1 and 2.

Xenotolithus sasakii Schwarzahns, 1993, pp. 230–231, figs. 203–206.

One otolith of a fossil species, shaped like an apple seed with the point at caudal side of otolith and very conspicuously shaped colliculum ('tadpole'): ostium very small, shaped like a pear, cauda making a sharp angle with the ostium and pointing in ventro-caudal direction. In Nolf (1976, pl. 9, figs. 1 and 2) two otoliths of this 'genus' are figured. Ostia of the otoliths in those figures are slightly differently shaped than the one examined and have a cauda running slightly upwards before making an angle in ventral direction. According to Nolf (1985) describing a genus on the basis of otoliths only (until now the only remains known of this 'genus') is undesirable. I share this point of view.

Sample: 32.

Family cf. DACTYLOSCOPIDAE

cf. *Dactyloscopidae* indet. (Plate V, 25)

One small otolith (± 2 mm broad) and conspicuously oval, with blunt endings. The internal side has in the middle a bilobed, short, shallow groove, with upright margins. Nelson (1994) mentions this family as marine (rarely brackish), occurring in tropical America amongst others in the Pacific.

Sample: 64.

Table 3

Distribution of cartilaginous fishes in the Pebas Formation throughout the Miocene

Early Miocene–early Middle Miocene	Middle Miocene	Middle–Late Miocene
Chondrichthyes indet.	Chondrichthyes indet.	Chondrichthyes indet. Euselachii indet. CARCHARHINDAE <i>Carcharhinus</i> sp. BATOMORPHII Batomorphii indet. RAJIFORMES cf. <i>Pristis</i> sp. MYLIOBATIFORMES Myliobatoidea indet.
MYLIOBATIFORMES Myliobatoidea indet. Dasyatidae/Potamotrygonidae cf. <i>Dasyatis</i> sp. <i>Myliobatis</i> sp.	MYLIOBATIFORMES Dasyatidae/Potamotrygonidae cf. <i>Dasyatis</i> sp. <i>Myliobatis</i> sp.	Dasyatidae/Potamotrygonidae cf. <i>Dasyatis</i> sp. <i>Myliobatis</i> sp. <i>Rhinoptera</i> sp.

5. Discussion

The results indicate that not all taxa occur in the area throughout the whole of the Miocene (see Tables 3 and 4). When taxa are equivocally lacking in the Middle Miocene period, like the Callichthyidae, this is probably due to the small sample size from this period. In the Middle Miocene (from ± 14 Ma onwards) a global cooling took place (Kennett, 1982). In the composition of the fish faunas there is little to reflect that event. The fact that Callichthyidae, Tetraodontiformes and Myliobatoidea do not or rarely occur before the Middle Miocene could indicate that the climate in the Amazon region, being less warm than before (as in the whole world) favoured the invasion of these taxa. The rest of the Miocene fauna does not seem affected by the global cooling.

(Peripheral) freshwater, marine and brackish water taxa were found together in many of the studied samples. Most Siluriformes must be regarded as freshwater fishes. Loricariidae have a very low salinity tolerance (Isbrücker and Nijssen, 1992). The only marine South American siluriform family are the Ariidae (Nelson, 1994). Also marine are the ray genera *Dasyatis* (Dahl, 1971), *Myliobatis* (Cappetta, 1987) and *Rhinoptera* (Gillette, 1984). The Dasyatidae may enter estuaries just like the Pristidae, which may even occur in lakes (Cappetta, 1987). Potamotrygonidae (river stingrays) are probably amongst the dermal denticles here identified as 'Dasyatoidea indet.'. Most sharks are regarded

as marine fishes. Two shark teeth were found, one of which belongs to *Carcharhinus*. Gillette (1984) described *Carcharhinus* in a marine ichthyofauna. *Stephanodus* was only known from marine sediments from the Late Cretaceous, but the order it belongs to (Tetraodontiformes) has members that can enter rivers (Gayet, 1991). Two jaw fragments of further unidentified tetraodontiforms have been found. Sciaenidae are essentially marine, inhabiting coastal regions. Many species can enter brackish waters and in South America there are species which are strictly fresh water dwellers (Bauchot, 1992). According to Gillette (1984) they are common inshore fishes. The Characiformes and *Molinichthys inopinatus* are considered freshwater dwellers (Roberts, 1975; Gayet, 1991). Fossil Characiformes were adapted to both brackish and marine water (Gayet, 1991). The presence of all these (peripheral) marine taxa indicates that during the Miocene there were marine incursions in an area that is nowadays fluvial. However, this mix of freshwater, brackish water and marine fossils could also be explained by the following scenarios: remnants of brackish and marine taxa could have been transported inland, or freshwater elements of the fauna could have been brought to littoral marine deposits by rivers. The first scenario can be rejected because of the quantity of specimens from marine and brackish waters, which is convincing evidence for a partially salty environment. The second scenario could have occurred in either the case of episodic marine incursions, or in the case of a

Table 4
Distribution of bony fishes in the Pebas Formation throughout the Miocene

Early Miocene–early Middle Miocene	Middle Miocene	Middle–Late Miocene
CHARACIFORMES	CHARACIFORMES	CHARACIFORMES
Characiformes indet.	Characiformes indet.	Characiformes indet.
<i>Hoplias</i> sp.	<i>Hoplias</i> sp.	<i>Hoplias</i> sp.
Anostomidae indet.		cf. <i>Hoplias</i> sp.
<i>Leporinus</i> sp.		Anostomidae indet.
	cf. Chilodontidae indet.	<i>Leporinus</i> sp.
		cf. Chilodontidae indet.
		cf. Serrasalmidae indet.
		Tetraodonterinae indet.
	CYPRINIFORMES	
	cf. <i>Molinichthys inopinatus</i>	
SILURIFORMES	SILURIFORMES	SILURIFORMES
Callichthyinae indet.		Callichthyinae indet.
		Corydorinae indet.
Siluriformes indet.	Siluriformes indet.	Siluriformes indet.
		Loricariidae indet.
Loricariidae indet.	Loricariidae indet.	Loricariidae indet.
	Ariidae indet.	Ariidae indet.
<i>Arius</i> sp.	<i>Arius</i> sp.	<i>Arius</i> sp.
		<i>Arius</i> cf. <i>gigas</i>
		cf. <i>Arius</i> sp.
PERCIFORMES	PERCIFORMES	PERCIFORMES
		cf. Dactyloscopidae indet.
	Sciaenidae indet.	Sciaenidae indet.
<i>Ctenosciaena</i> sp.	<i>Ctenosciaena</i> cf. <i>peruviana</i>	<i>Ctenosciaena</i> cf. <i>peruviana</i>
<i>Larimus</i> sp.	<i>Larimus</i> sp.	<i>Ctenosciaena</i> sp.
<i>Pachypops fourcroi</i>	<i>Pachypops fourcroi</i>	<i>Larimus</i> sp.
	<i>Plagioscion</i> sp.	<i>Pachypops fourcroi</i>
<i>Umbrina</i> sp.	<i>Umbrina</i> sp.	<i>Plagioscion</i> sp.
		<i>Umbrina</i> sp.
		'genus <i>Sciaenidarium</i> ' <i>sasakii</i>
		TETRAODONTIFORMES
		Tetraodontiformes indet.
		<i>Stephanodus minimus</i>

marine influence that was so far-reaching that the area was actually inundated. However, as discussed below, I also reject this scenario.

Marine influence in this area was first suggested by Von Ihering (1927), who postulated a marine connection between the Caribbean, at Venezuela, and the Southern Atlantic at Argentina (near Uruguay) during the Cretaceous. Räsänen et al. (1995) suggest, on the basis of a very small dataset, that this connection has existed in the Miocene as well. They also state that marine transgressions existed during the Late Miocene. This is well contradicted by studies by Hoorn (1993, 1994b); Hoorn et al. (1995) and Nuttall (1990), which implicate merely episodic

marine influences but no real long-lasting transgressions. Hoorn (1996) states that in the late Miocene there were no marine incursions, as there were during the Early and Middle Miocene. This is supported by Vonhof et al. (1998) by means of isotopic and molluscan studies of the area. I agree that there is a more than reasonable amount of (peripheral) marine fishes in the sediments dated from the Middle to Late Miocene. A great deal of them could originate solely from the geologically accepted period of the Middle Miocene. It could very well be that there were marginal marine influences in the Late Miocene but I do not believe it was as far-reaching as Räsänen et al. suggest. Also contradicting the conclusions of

Räsänen et al. (1995) is the fact that the area from which this new set of samples originate is well in the area which they suggested as being marine. The ratio of saltwater, brackish water and marine fossils does not support the supposition of this area having been marine, with some transport into the area of fresh-water fossils. The theory of Marshall and Lundberg (1996) — a tectonic cause for marine incursions in the Late Miocene — is probably not more than an explanation of how episodic marine influence could have existed despite the then relatively low sea level.

The fish taxa discussed in this paper are probably a fraction of the Miocene species in this area. Nowadays, the Amazon region contains a very rich ichthyofauna with a large number of species (Roberts, 1972). Yet, some comparisons between recent and Miocene faunas can be made. The biggest difference between the extant and the Miocene faunas is the occurrence of the chondrichthyans. An example: Myliobatoidea that occur in Pebas samples are not known from these faunas nowadays (Géry, 1969). Géry does not mention *Carcharhinus* in Recent faunas, but Dahl (1971) reported that *Carcharhinus leucas* (Muller and Henle 1841) sometimes enters rivers far upstream in Colombia. Although they do occasionally enter rivers, sharks are still essentially marine, and cannot be called typically Amazonian. The study material contained only two shark teeth, one of them *Carcharhinus*, suggesting that they were not very frequent during the Miocene either and marine influences were not at all far reaching.

6. Conclusions

The results present a first inventory of Miocene fish faunas from the northwestern Amazon basin. At the same time, additional data for palaeoenvironmental and palaeogeographical models are provided, which support the model of riverine/lacustrine deposits inferred by marine incursions. Not all taxa seem to have occurred in this region throughout the entire Miocene.

Between the ichthyofaunas of samples from different ages there are no far-reaching differences (Tables 3 and 4). The biggest difference between the extant and the Miocene faunas is the occurrence of the chondrichthyans in the Miocene. Nowadays,

the only occurring chondrichthyans are Dasyatoids, sharks of the genera *Carcharias* Cuvier 1816 and *Carcharhinus*. Dasyatoids are peripheral fresh-water dwellers. Sharks like *Carcharias* occasionally enter rivers but still depend on sea for reproduction and are not considered typically Amazonian (Géry, 1984). Myliobatoidea do nowadays not occur in these areas. Osteichthyan taxa such as Cypriniformes, Tetragonopterinae, Erythrinidae, Anostomidae, Aridae, Callichthyidae, Loricariidae, Tetraodontiformes and Perciformes such as Sciaenidae, which occur in recent South American faunas, were also present during the Miocene. Sciaenidae and Tetraodontiformes only occur peripherally in fresh water. There are few tetraodontoid specimens (*Stephanodus minimus* and jaws from unidentified tetraodontiforms) within the material, but numerous sciaenid otoliths.

Freshwater fish remains are found together with brackish water and salt water fish remains. The occurrence of salt and brackish water fishes in the same area, which is nowadays riverine and inland indicates again the occurrence of marine influence in this area. The Miocene fauna is typically Amazonian: fish taxa and crocodiles indicate the area must have had a warm climate during the Miocene, as it has now. This agrees with palynological data (Hoorn, 1993).

During the deposition of the Pebas Formation the area was covered by relatively shallow water, for many abundant taxa such as Pristidae, cf. Dasyatidae and Myliobatidae are inhabitants of shallow marine waters (Cappetta, 1987). Many Sciaenidae are known to spawn in shallow brackish waters (Gillette, 1984). This also shows that the marine influence was indeed only marginal and not as extreme as Räsänen suggested. The presence of Loricariidae indicates torrents and cataracts (Géry, 1969).

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