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The late Miocene *Phractocephalus* catfish (Siluriformes: Pimelodidae) from Urumaco, Venezuela: additional specimens and reinterpretation as a distinct species

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Based on additional specimens the fossil pimelodid catfish from the upper Miocene Urumaco Formation, Falcón State, Venezuela originally assigned to the extant species *Phractocephalus hemioliopterus* is described as a new, extinct species. †*Phractocephalus nassi* n. sp. is diagnosed by the following combination of characters: 1) posterior half of frontals and anterior half of supraoccipital with elongate, coarse ridges and sulci in addition to reticulating ridges and subcircular pits; 2) very broad and ornamented mesethmoid bone; 3) lateral ethmoid margin convex and eliminating orbital notch but not projecting far anteriorly over palatine condyle; 4) anterior cranial fontanelle closed or represented by a small pit; 5) supraoccipital process rounded laterally and posterolaterally, concave posteriorly and completely concealing Weberian complex in dorsal view; 6) opercle covered with reticulating ridges and pits; 7) cleithrum coarsely ornamented along ventral edge and bulging outward lateral to spine articulation; 8) pectoral spine mostly ornamented with coarse ridges and sulci. †*Phractocephalus nassi* is compared to modern *P. hemioliopterus* and an undescribed extinct species from the upper Miocene Solimões Formation, Acre, Brazil. New diagnostic characters of *Phractocephalus* are presented that apply to the modern and fossil species, including: 1) ornamentation of skull, pectoral girdle and fin spines comprising a coarse meshwork of reticulating ridges surrounding rounded pits plus some elongate ridges and sulci; 2) supraoccipital posterior process greatly expanded laterally and posteriorly behind occipital wall; 3) lateral ethmoid and sphenotic broadly sutured behind eye; 4) anterior cranial fontanelle reduced or completely closed and posterior cranial fontanelle closed; 5) vomerine tooth plate large, roughly pentagonal to triangular in form, and with fine teeth. Today *Phractocephalus* ranges widely throughout the lowland Orinoco, Amazon and Essequibo basins. However, the genus does not occur west or north of the Andes or Venezuelan coastal ranges. Recognizing the Urumaco *Phractocephalus* as a distinct species does not alter the obvious conclusion that this catfish marks a large river connection between the Caribbean coastal region and the Orinoco system during at least part of the Neogene. Other Urumaco fossils show this same biogeographic relationship.

É descrita uma nova espécie fóssil de bagre pimelodídeo proveniente da Formação Urumaco do Mioceno superior no estado Falcón, Venezuela. O exemplar fóssil foi originalmente atribuído a espécie recente *Phractocephalus hemioliopterus*. Porém, com base em exemplares fósseis adicionais provenientes da Formação Urumaco, essa espécie extinta é descrita como uma nova espécie. As características diagnósticas da nova espécie †*Phractocephalus nassi* são as seguintes: 1) a metade posterior do frontal e a metade anterior do supraocciptal apresentam uma ornamentação caracterizada por altos relevos e sulcos alongados, assim como reticulações e algumas depressões subcirculares; 2) o mesetmóide é muito largo e está ornamentado; 3) a margem do etmóide lateral é convexa, não apresenta o entalhe orbital e não se projeta anteriormente sobre o côndilo palatino; 4) a fontanela cranial anterior está fechada e forma uma pequena depressão; 5) a margem do processo supraoccipital é redonda lateral e posteriormente, e cobre completamente o complexo de Weber quando visto dorsalmente; 6) o opérculo está ornamentado com reticulações e depressões; 7) o cleitro encontra-se densamente ornamentado ao longo da margem ventral da área de articulação do espinho peitoral; 8) o espinho peitoral encontra-se ornamentado com estrias e sulcos. †*Phractocephalus nassi* é comparada com a espécie recente *P. hemioliopterus* e com outra especie fóssil da Formação Solimões do Mioceno

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superior do Acre no Brasil, a qual ainda não foi descrita. Apresentam-se novas características diagnósticas para o gênero que incluem as espécies recente e fóssil tais como: 1) a ornamentação do crânio, da cintura peitoral e dos espinhos apresenta-se como uma rede de altos relevos e sulcos alongados, assim como reticulações e algumas depressões subcirculares; 2) a sutura entre o etmóide lateral e o esfenótico é ampla e localiza-se por detrás da órbita; 3) a fontanela cranial anterior está reduzida ou fechada, a fontanela cranial posterior se fecha completamente; 4) a placa dental do vômer é grande, aproximadamente de forma pentagonal a triângular e encontra-se provida de pequenos dentes. Atualmente, *Phractocephalus* encontra-se amplamente distribuído nos rios de terras baixas e nas encostas do Orinoco, Amazonas e Essequibo. No entanto, não é encontrado ao norte e a oeste dos Andes e tão pouco ao longo da costa venezuelana. O reconhecimento do *Phractocephalus* de Urumaco como uma espécie diferente da espécie recente não altera as conclusões prévias de que esse bagre pimelodideo representa o testemunho da ampla conexão fluvial que existiu entre a região costeira do Caribe e a bacia do Orinoco no final do Neogeno. Outras espécies fósseis de Urumaco também demonstram esta relação biogeográfica.

Key words: †*Phractocephalus nassi*, fossils, Urumaco Formation, Paleo-Amazon-Orinoco.

Introduction

Lundberg *et al*. (1988) described a large catfish skull from the upper Miocene Urumaco Formation, Falcón State, Venezuela. Based on characteristics known at the time, the fossil was assigned to the extant species *Phractocephalus hemioliopterus* (Bloch & Schneider, 1801), family Pimelodidae. While the 1988 paper was in press a nearly complete and extraordinarily well preserved cranium came to light and briefly noted (Lundberg *et al*., op. cit., p. 138). Now we have had the opportunity to examine and assess the details of that specimen. In addition, several more Urumaco specimens of *Phractocephalus* Agassiz have been collected that contribute significant new information on this catfish. Comparisons of these additional fossils with modern specimens (Aguilera, 1994, and herein) show that the Urumaco *Phractocephalus* is taxonomically distinct from modern *P. hemioliopterus.*

Well-preserved fossils of *Phractocephalus* have also been reported in the upper Miocene Solimões Formation in Acre, Brazil (Latrubesse *et al*., 1997; Bocquentin-Villanueva, Jégu & Brito, 1997), and fragmentary material is preserved in the middle Miocene La Venta fauna of Colombia (Lundberg, 1997, 1998). The Acre fossil is being named and described by J. Bocquentin-Villanueva, M. Jégu and P. Brito. Those worker's and our comparisons of the Urumaco and Acre fossils reveal that the latter represents a second fossil species of *Phractocephalus.* Accordingly, in this paper we name and diagnose the Urumaco *Phractocephalus* as a new species.

Phractocephalus has been considered monotypic. Modern *P. hemioliopterus* has a wide distribution in the lowland, meandering rivers and lagoons of the Orinoco, Amazon and Essequibo basins. This species, known as the "cajaro" in Venezuela and Colombia and "pirarara" in Brazil, is one of the most distinctive and important food and ornamental fishes in South America (Fig. 1). Based on the strong overall similarity between modern *Phractocephalus* and available fossil specimens from Urumaco, Lundberg *et al*. (1988) hypothesized that *P. hemioliopterus* is a long-lived species with no detectable morphological change since the late Miocene. The additional specimens show that is not the case. The modern and fossil specimens are closely similar in most details, including many characters that are uniquely derived among catfishes, yet these are demonstrably distinct species. The revised taxonomic status of the Urumaco fossil *Phractocephalus* does not alter its biogeographic significance. This fossil catfish provides direct evidence for former biotic and riverine connections between the Orinoco watershed and the Caribbean coastal region of South America (Lundberg *et al*., 1988; 1998; Díaz de Gamero, 1996). Thus, the Urumaco and Acre fossils expand our knowledge of the diversity of *Phractocephalus* over time and space.

Material and Methods

The specimens were collected during several expeditions to the Urumaco Formation (Fig. 2) between 1972 and 2002 by MCZ (B. Patterson), UNEFM (O. Aguilera; J. Bocquetin-Villanueva; R. Sánchez), USB (O. Linares; E. Pannier), and ANSP (J. Lundberg). The fossils are three-dimensional articulated crania and post-cranial disarticulated and usually broken bones obtained individually from surface exposures in the field. Preservation ranges from nearly perfect to badly abraded or broken bones. Matrix materials surrounding Urumaco specimens vary from fine, loose sand that was removed with brushes, to iron-stained claystone requiring softening with water and manual cleaning with fine tipped dental tools. Some broken but clearly associated specimens were reconstructed.

Comparative materials. Fossil *Phractocephalus* sp. from the Solimões Formation in Acre, Brazil, deposited at UFAC. Also, skeletal preparations of modern *P. hemioliopterus* from the Orinoco [ANSP 179553 (1, ex DU F925A), UNEFM-PR-040, UNEFM-PR-041, MBUCV – uncat.] and Amazon [ANSP 179554 (2), ANSP 179559]. The modern skeletal specimens range in standard length from 265 - 900 mm. Measurement data of fossils emphasize overall specimen size and, as preservation allows, landmark-based linear dimensions for proportional (shape) comparisons among species (Table 1). Measurements were taken with vernier calipers and dividers, rounded to nearest mm.

Fig. 1. The living “cajaro” or “pirarara” *Phractocephalus hemioliopterus*, a specimen about 130 cm captured in the Orinoco river basin by an artisanal fisherman. Photo courtesy of K. Arnal (www.kikearnal.com).

Institutional abbreviations: ANSP Academy of Natural Sciences, Philadelphia, PA, USA; DU Duke University, USA; MBUCV Museo de Biología, Universidad Central de Venezuela, Caracas, Venezuela; MCN.USB Museo de Ciencias Naturales, Universidad Simón Bolívar, Caracas, Venezuela; MCZ Museum of Comparative Zoology, Cambridge, MA, USA; UFAC Universidade Federal do Acre, Rio Branco, Brazil; UNEFM Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela.

Osteological abbreviations: AD anterior dentations of pectoral spine, BOC Basioccipital, BL ossified Baudelot´s ligament, EXOC Exoccipital, FR Frontal, HYO Hyomandibula, LE Lateral ethmoid, ME Mesethmoid, ORB Orbit, ORS Orbitosphenoid, PAS Parasphenoid, PD posterior dentations of pectoral spine, EXT Extrascapular, POP Preopercle, PROT Prootic, PTO Pterotic, Q Quadrate, SPH Sphenotic, SCL Supracleithrum, SOP Supraoccipital, VTP Vomerine tooth plate, W Weberian complex.

Fig. 2. Locality map of the Urumaco area and fossiliferous sites.

Results

Order Siluriformes *sensu* Berg, 1940
Family Pimelodidae *sensu* Lundberg & Littmann, 2003
Genus *Phractocephalus* Spix & Agassiz, 1829

Type species. *Phractocephalus bicolor* Spix & Agassiz, 1829, by monotypy, a junior objective synonym of *Silurus hemioliopterus* Bloch & Schneider, 1801.

Diagnosis. *Phractocephalus* contains three species, one extant and two extinct. The following diagnosis of the genus emphasizes phylogenetically derived characters of the skeleton that are known to occur in all species.

1) Dermal bones of skull, pectoral girdle and fin spines extensively ornamented with a coarse meshwork of reticulating ridges surrounding rounded pits (Figs. 3a, 4a, 5a, g-i) plus some elongate ridges and sulci.

No other siluriforms known to us have a closely similar ridged and pitted style of ornamentation. Among other pimelodids, dermal bone ornamentation ranges from absent (smooth bone surfaces), to spongy or trabeculated, to fine or very coarsely striate ridges or tubercles.

2) Supraoccipital posterior process greatly expanded laterally and posteriorly behind occipital wall, extrascapulars and supracleithra (Figs. 3a, 4a). In association with this, the anterior nuchal plate is also much enlarged and similarly ornamented. These features were noted in the original description of *Phractocephalus* (Spix & Agassiz, 1829). The condition of the nuchal plate is directly known in modern *P. hemioliopterus* and the Acre fossil species. The anterior nuchal plate is inferred to have been present in the Urumaco species based on the shape and texture of articulation site along the posterior edge of the supraoccipital process (see Fig. 3).

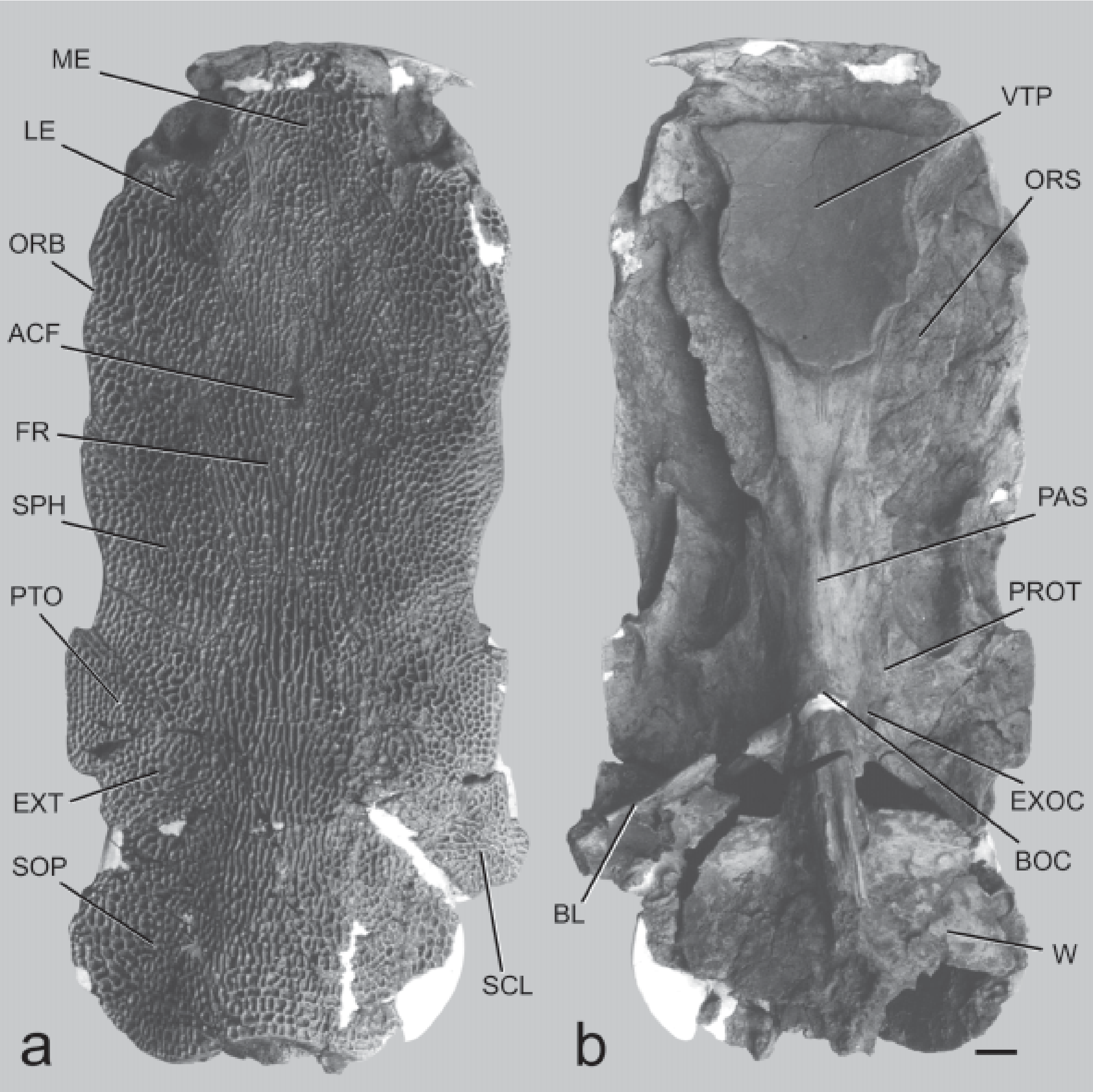

Fig. 3. Skull of †*Phractocephalus nassi* new species, holotype, MCN.USB OL-2142, from the upper Miocene Urumaco Formation, El Mamón, Venezuela; **a**, dorsal view and **b**, ventral view. Scale bar equal to 20 mm.

No other siluriforms known to us have a similarly enlarged or shaped supraoccipital posterior process, or similarly expanded anterior nuchal plate. In all other pimelodids the supraoccipital process is narrowly triangular and tapered posteriorly toward and usually contacting a relatively small, triangular anterior nuchal plate. The supraoccipital process and nuchal plate are much reduced in a few pimelodid species.

3) Lateral ethmoid and sphenotic broadly sutured behind level of eye, eliminating frontal bone from margin of skull roof and orbit (Figs. 3a, 4a).

All other pimelodids and most other catfishes have the lateral ethmoid and sphenotic well separated by the frontal that forms much of the skull roof edge including the dorsal margin of the orbit. Elsewhere among siluriforms the lateral ethmoid contacts the sphenotic in all Siluridae and some Loricariidae (Bornbusch, 1991).

4) Anterior cranial fontanelle reduced to a narrow slit or tiny foramen between frontal bones, or completely closed (Figs. 3a, 4a); posterior cranial fontanelle completely closed.

All catfishes, at least early in development, have large, open anterior and posterior cranial fontanelles on the dorsal midline of the skull roof. In most species both fontanelles become restricted to narrow slits or small foramina during growth, and may close completely. Siluriforms exhibit a wide variety of relative growth patterns of skull bones that reduce cranial fontanelle size. Among pimelodids near or complete closure of the posterior fontanelle is common. Reduction of the anterior fontanelle to a persistent slit and surrounding sulcus running from the mesethmoid and between the frontals is common.

5) Vomerine tooth plate massive in size, roughly pentagonal to triangular in form, and covered with very fine teeth (Figs. 3b, 4b).

The presence of vomerine teeth is a primitive feature of

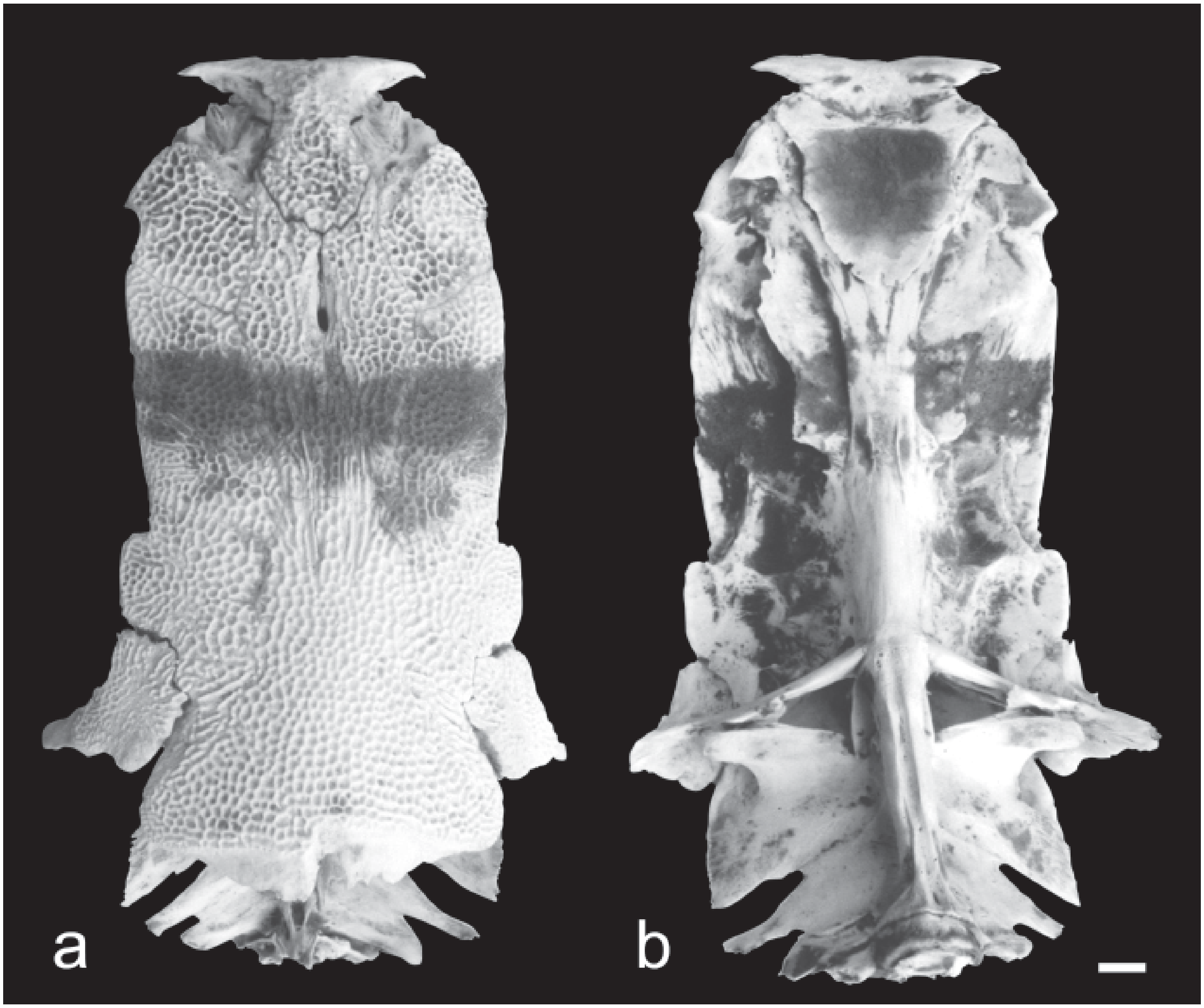

Fig. 4. Skull of the modern *Phractocephalus hemioliopterus*, UNEFM-PR-040, from the Orinoco river; **a**, dorsal view and **b**, ventral view. Scale bar equal to 20 mm.

siluriforms that is retained in many pimelodids, where either a pair of tooth patches or a median vomerine plate may be present. The size and shape of vomerine tooth patches varies greatly, but the oddly large size, distinctive shape and very fine teeth of *Phractocephalus* are unique.

Etymology. *Phractocephalus* from the Greek "phraktos" meaning fenced or walled in, plus *cephalus* reference to the unusual well-developed dermal bones of the skull and nape. Gender masculine.

†*Phractocephalus nassi*, new species

Figs. 3, 5a-b, 5e-h, 5k-l

Phractocephalus hemiliopterus (misspelling) Lundberg *et al*. 1988:131-138 (description, phylogeny, biogeography); Lundberg 1997:80 (listed).

Phractocephalus Lundberg & Chernoff. 1992:10 (listed).

Phractocephalus hemioliopterus Lundberg 1998:59-62 (phylogeny, biogeography).

Holotype. MCN.USB OL-2142, nearly complete, undistorted neurocranium plus most of the Weberian complex (broken into two pieces at the basioccipital). El Mamón oil field, 350 m north of oil well number 1, locality USB 56-FU, 11º 15´ N, 70º 13´ W, Urumaco Formation, middle member, Falcón State, northwestern Venezuela, O. Linares, E. Pannier & R. Sánchez, 1987.

Paratypes. All localities in Falcón State, northwestern Venezuela (Fig. 2). MCN.USB 72-85 PB, nearly complete neurocranium, margins partly chipped or eroded (specimen described by Lundberg *et al*., 1988). Locality USB 26-FU, 11º 15´ 00´´ N, 70º 13´ 00´´ W, Urumaco Formation, upper member.

UNEFM-PF-0365, three dimensional Weberian complex and supraoccipital. Tío Gregorio, locality UNEFM OA00-7, 11º, 14´ 31´´ N; 70º 18´ 40´´ W, Urumaco Formation, upper member, O. Aguilera & R. Sánchez, 2000.

UNEFM-PF-0158, cranium in two large and several small parts; slightly crushed and flattened, most margins chipped or broken. Anterior moiety includes mesethmoid, lateral ethmoids, frontals and sphenotics. Ventrally includes vomer and parasphenoid. Smaller posterior part includes supraoccipital (anterior part to frontal and partial supraoccipital process with all margins chipped). Associated bones including nearly complete right hyomandibula, right quadrate, left opercle and left cleithrum. El Hatillo, locality UNEFM OA94-7, 11º, 13´ 03´´ N; 70º 14´ 06´´ W, Urumaco Formation, middle member, O. Aguilera & R. Sánchez, 1994.

UNEFM-PF-0363, right side, articulated, cleithrum, coracoid and pectoral spine. El Mamón, locality UNEFM OA01-11, 1000m west of oil field, upper Miocene Urumaco Formation (middle member), Falcón State, northwestern Venezuela, O. Aguilera & J. Lundberg, 2001.

UNEFM-PF-0311, partial left pectoral spine shaft (base missing). Quebrada El Mamón, locality UNEFM OA94-8, 11º 14´ 27´´ N, 70º 16´ 00´´ W, Urumaco Formation, middle member, O. Aguilera & R. Sánchez, 1994.

Non-type specimens. UNEFM-PF-0366 skull fragment. Tío Gregorio, locality UNEFM OA00-7, 11º 14´ 31´´ N, 70º 18´ 40´´ W, Urumaco Formation, upper member, O. Aguilera & R. Sánchez, 2000.

UNEFM-PF-0364 supraoccipital fragment. El Mamón, 500 m west of oil field, locality UNEFM OA01-12, Urumaco Formation, middle member, O. Aguilera & R. Sánchez, 2001.

MCC-URU-2002-141, cranium in two large parts; slightly crushed and flattened, most margins chipped or broken. Anterior moiety includes mesethmoid, lateral ethmoids, frontals and sphenotics. Smaller posterior part includes supraoccipital (anterior part to frontal and partial supraoccipital process with all margins chipped). Tío Gregorio between Quebrada Tío Gregorio and Arcas fault, locality MCZ 141-72V, Urumaco Formation, upper member, B. Patterson, 1972.

UNEFM-PF-0159, nearly complete right cleithrum. Tío Gregorio, locality UNEFM OA00-7, 11º, 14´ 31´´ N; 70º 18´ 40´´ W, Urumaco Formation, upper member, O. Aguilera & R. Sánchez, 2000.

UNEFM-PF-0356, left side suspensorium, reassembled articulated bones including nearly complete hyomandibula, quadrate and part of metapterygoid. El Mamón, 1000 m northeast of oil field, locality UNEFM OA01-7, Urumaco Formation, middle member, O. Aguilera, J. Lundberg & R. Sánchez, 2001.

Locality, geological context and age. The sample area (Fig. 2) includes the following named localities: El Mamón, Tío Gregorio, Corralito and El Hatillo, all north of the town of Urumaco, Falcón State, northwestern Venezuela. The geological units from which the specimens were obtained are the middle and upper members of the Urumaco Formation of Venezuela. These units have been recently summarized in the Léxico estratigráfico de Venezuela (1997).

The middle member of the Urumaco Formation consists of claystone and sand. The gray claystone is microfossiliferous, and the brown claystone contains vertebrate remains such as reptiles, mammals, marine and freshwater fish, and also coprolites and wood (Díaz de Gamero & Linares, 1989). The limestone changes from conchiferous sandstones to consolidated coquina limestone. In the lower half of this middle member, an abundant and diverse marine mollusk fauna exists in a sandy matrix. This matrix also contains elasmobranch teeth and teleostean otoliths. The paleoenvironments are interpreted as inner sub-littoral and coastal lagoon environments with riverine and estuarine influence (Díaz de Gamero, 1996).

The upper member of the Urumaco Formation also comprises gray to brown often limey claystone with thin intercalated and locally conchiferous sandstones. The uppermost layer is referred to as the “capa de tortugas” because of its abundant remains of the turtle *Bairdemys* Gaffney & Wood. Several localities and levels have concentrations of vertebrate fossils. The vertebrate fauna includes marine, estuarine and freshwater fishes, terrestrial, freshwater and marine turtles and crocodilians, and terrestrial and aquatic/semiaquatic mammals (Sánchez-Villagra *et al*., 2003). The paleoenvironments were tropical near shore marine to low coastal savannas with freshwater rivers.

A Late Miocene age for the Urumaco Formation is indicated by foraminiferans, and the mammals suggest a South American land mammal age between Chasicoan and Huayquian **(**Díaz de Gamero & Linares, 1989), or approximately 9 Ma (Marshall & Sempere, 1993).

Diagnosis. 1) Ornamentation of posterior half of frontals and anterior half of supraoccipital with both reticulating ridges and pits, and equally coarse, elongate, nearly parallel ridges and sulci (Fig. 3a).

In modern *P. hemioliopterus* the corresponding central region of the skull roof is almost completely ornamented by reticulating ridges and pits, with few or no elongate, parallel ridges and sulci (Fig. 4a). In the Acre *Phractocephalus* the central region of the skull roof has many elongate ridges and sulci plus reticulating ridges and pits.

2) Mesethmoid bone very broad (Table 1); dorsal surface extensively ornamented; anterior edge scarcely emarginate to gently rounded (Fig. 3a).

The mesethmoid bone of *P. hemioliopterus* is relatively narrow-necked, less extensively ornamented only centrally and posteriorly, and its anterior edge is emarginate or shallowly concave (Fig. 4a). The mesethmoid bone of the Acre *Phractocephalus* is similar to that of †*P. nassi.*

3) Lateral ethmoid not excessively projecting anteriorly over palatine condyle; its lateral margin convex and eliminating orbital notch on margin of skull roof (Fig. 3a).

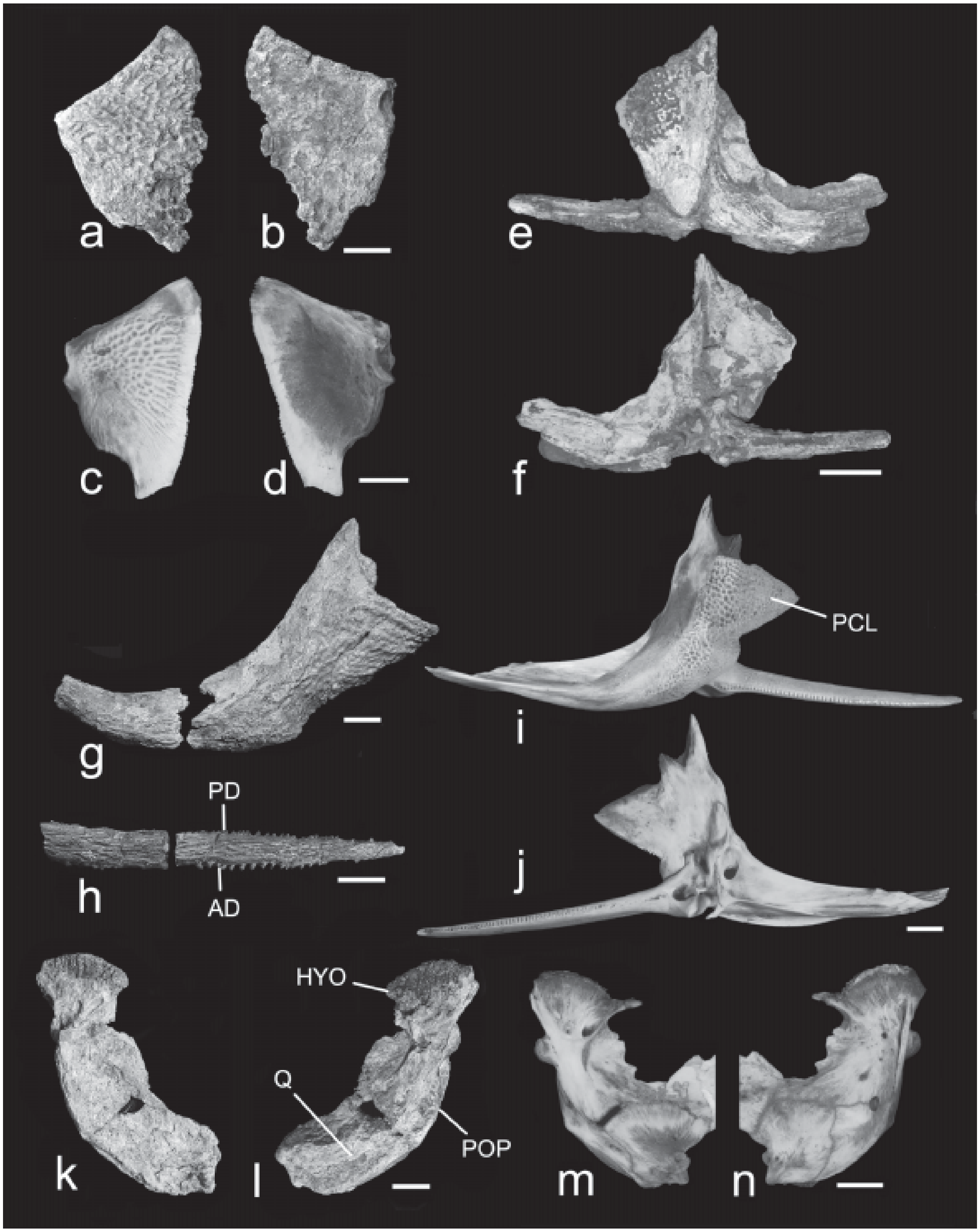

Fig. 5. Osteological features of †*Phractocephalus nassi* new species and the living *Phractocephalus hemioliopterus* ANSP 179559; **a**, **b**, left opercle of †*P. nassi*, paratype, UNEFM-PF-0158, Urumaco Formation (middle member), El Hatillo; **c**, **d**, left opercle of *P*. *hemioliopterus* ANSP 179559 from the Amazon river; **e**, **f**, right pectoral girdle of †*P. nassi* , paratype, UNEFM-PF-0363, Urumaco Formation (middle member), El Mamón; **g**, left broken cleithrum of †*P. nassi*, paratype, UNEFM-PF-0158, Urumaco Formation (upper member), Tío Gregorio; **h**, left pectoral spine of †*P. nassi*, paratype, UNEFM-PF-0311, Urumaco Formation (middle member), El Mamón; **i**, **j**, pectoral left girdle and spine of *P*. *hemioliopterus* ANSP 179559 from the Amazon river; **k**, **l**, right suspensorium of †*P. nassi*, UNEFM-PF-0158, Urumaco Formation (middle member), El Hatillo; **m**, **n**, left suspensorium of *P. hemioliopterus* ANSP 179559 from the Amazon river. Scale equal to 20 mm.

Table 1. Measurement data for †*Phractocephalus nassi*, holotype and paratype, and a sample of modern *P. hemioliopterus* from the Orinoco and Amazon basins. Measurements in mm are: Ventral skull length from mesethmoid tip to edge of attachment scar of ossified Baudelout's ligament; Dorsal skull length from mesethmoid tip to posterior edge of supraoccipital process; Minimum mesethmoid width across ventral surface behind cornua; Width of ornamented dorsal surface of mesethmoid; Width of skull at lateral ethmoid wings; Width of skull at orbits; Vomer width across anterior edge; Parasphenoid width below trigeminofacial foramina; Width of skull between medial edges of hyomandibular facets; Length of hyomandibular facet.

	Holotype MCN.USB OL-2142		Paratype MCN.USB 72-85 PB		Modern sample		
	Raw	Ratio to VSL	Raw	Ratio to VSL	Raw	Ratio to VSL	N
Ventral skull length	327		318		79-220		8
Dorsal skull length	485	1.48	442	1.39	112-312	1.39-1.48	7
Min mesethmoid width	113	0.35	77	0.24	22-57	0.24-0.28	7
Mesethmoid ornament	81	0.25	.	.	17-32	0.15-0.19	3
Width at lateral ethmoids	202	0.62	186	59	50-137	0.60-0.67	8
Width at interorbital	200	0.61	176	0.55	41-128	0.51-0.58	8
Vomer width	115	0.35	90	0.28	24-68	0.24-0.31	7
Parasphenoid width	64	0.20	56	0.18	15-46	0.17-0.23	7
Hyomandibula facet width	147	0.45	145	0.46	38-108	0.41-0.49	8
Hyomandibula facet length	54	0.17	60	0.19	16-40	0.18-0.21	8

The lateral ethmoid bone of *P. hemioliopterus* is also not excessively projecting anteriorly over the olfactory region or palatine condyle; but it is concave laterally, and has a well defined orbital sulcus on the margin of skull roof (Fig. 4a). In the Acre *Phractocephalus* the lateral ethmoid projects far anteriorly over the olfactory region and palatine condyle; it is convex laterally, eliminating the orbital sulcus on margin of skull roof.

4) Anterior cranial fontanelle absent or represented by a small pit in epiphyseal region between frontals (Fig. 3a).

Modern *P. hemioliopterus* have an open anterior cranial fontanelle within a prominent depression of epiphyseal region (Fig. 4a), whereas in the Acre *Phractocephalus* the fontanelle and depression of the epiphyseal region are lacking.

5) Supraoccipital process with rounded lateral and postero-lateral margins, posterior margin concave medially; supraoccipital process long, in dorsal view completely covering modified anterior vertebrae of Weberian complex (Fig. 3a).

In modern *P. hemioliopterus* the supraoccipital process is short, in dorsal view not completely covering modified vertebrae of Weberian complex; it has angular lateral and posterolateral margins, and its posterior margin is irregular to concave medially and bearing a deep unornamented extension below anterior nuchal plate (Fig. 4a). In the Acre *Phractocephalus* the supraoccipital process is long, completely covering the Weberian complex; its process has angular corners and straight lateral margins, and its posterior margin concave is slightly convex and lacks an unornamented extension below anterior nuchal plate.

6) Opercle almost completely covered with reticulating ridges and pits (Fig. 5a).

The opercle *P. hemioliopterus* is incompletely covered with reticulating ridges and pits (Fig. 5c). The opercle is thus far unknown in the Acre *Phractocephalus*.

7) Cleithrum with coarse ornamentation extending along ventral edge forming outward bulge or "shoulder" lateral to spine articulation; bulge of "shoulder" terminating posteriorly, in line with termination of articular socket of pectoral spine (Figs. 5e-g).

The cleithrum of *P. hemioliopterus* lacks coarse ornamentation along ventral edge of "shoulder," and the lateral bulge of "shoulder" terminates posterior to the level of articular socket of pectoral spine (Figs. 5i, j). No cleithrum of the Acre *Phractocephalus* has been found.

8) Pectoral spine ornamentation dominated by coarse subparallel ridges and sulci, and relatively few reticulating ridges and pits (Fig. 5h).

The pectoral spine ornamentation of *P. hemioliopterus* is dominated by reticulating ridges and pits (Fig. 5i). The pectoral spine of the Acre *Phractocephalus* is yet unknown.

Etymology. The Urumaco species of *Phractocephalus* is named for Dr. Pedro Nass in recognition of his contributions to the systematics and morphology of pimelodid catfishes of South America.

Description. See Lundberg *et al*. (1988) for description of neurocranium (MCN.USB 72-85 PB) and additional measurements. The following information is provided by the holotype and recently obtained specimens.

Neurocranium, dorsal aspect (Fig. 3a). Outline form of skull approximately rectangular, width across lateral ethmoids equal to width across sphenotics, and these widths slightly less than maximum width across pterotic wings; width across pterotics contained 2.25 times in (45% of) dorsal skull length from mesethmoid tip to posterior edge of supraoccipital process. Surface mostly flat but margins curved slightly downward and dorsal midline increasingly arched posteriorly. All bones ornamented with coarse reticulating ridges and circular pits and some longitudinally elongate ridges and grooves, except for olfactory capsules and extremities of mesethmoid cornua.

Mesethmoid broad, mushroom-shaped, anterior margin scarcely emarginate (entire in MCN.USB OL-2142), otherwise gently rounded; cornua stout, pointed, little recurved and reaching laterally to a parasagittal line projected before palatine condyle. Mesethmoid without traces of anterior cranial fontanelle. Lateral ethmoid projecting anteriorly into olfactory capsule region; orbital margin short, gently concave, antorbital process a slight curved bulge; contact with sphenotic a long, nearly straight suture running obliquely from skull roof margin behind orbit to frontal near anterior cranial fontanelle. Olfactory capsule floored by mesethmoid and lateral ethmoid. Nasal and infraorbitals unknown.

Frontal flat to slightly concave, confined to center of skull roof, laterally suturing to and excluded from skull-roof margin by lateral ethmoid and sphenotic. Anterior cranial fontanelle present as reduced circular foramen in a midline pit at transverse level of sphenotic-lateral ethmoid-frontal junction (fontanelle obsolete in MCN.USB OL-2142). Frontal ornamented mostly with reticulating ridges and circular pits, except near midline posterior to cranial fontanelle about 5 - 6 parallel longitudinally oriented ridges and grooves.

Sphenotic very large, twice the width of adjacent frontal, approaching a parallelogram in form, broadly sutured to lateral ethmoid, frontal, supraoccipital and pterotic; free lateral margin with a gently convex bulge but lacking prominent postorbital process. Pterotic with angular wing projecting from posterolateral corner; broadly contacting sphenotic, supraoccipital, extrascapula and supracleithrum, the last joint horizontally elongate suggesting limited mobility to dorsoventral axis.

Supraoccipital unusually large, flask-shaped; contacting frontals, sphenotics, extrascapulars, supracleithra and anterior nuchal plate (the last by inference from structure of posterior process and similarity to congeneric species). Expanded part of supraoccipital posterior process is posterior to occipital wall and articulations with upper shoulder girdle elements; process long, covering Weberian complex. Process with broadly rounded lateral and posterolateral margins, ornamented part posterior margin emarginate to truncate across midline, plus a projecting unornamented shelf that would form a lap joint with anterior nuchal plate. Ornamentation of supraoccipital mostly irregular but ridges and pits loosely arranged in 5 or 6 outer concentric rows. Dorsal surface flat behind frontals, then becoming convexly arched along midline to posterior margin, laterally sloping downward concavely to margins of posterior process; cross-sectional shape depressed "bell shaped."

Extrascapula an ovoid plate isolated from skull margin by surrounding pterotic, supracleithrum and supraoccipital. Supracleithrum preserved in holotype on right side where broken posterolaterally; expanded as roughly lozenge-shaped plate, ornamented as the skull roof; horizontally elongate, weak sutural joint with pterotic and extrascapula; arthrosis style with supraoccipital indeterminate.

Neurocranium, ventral aspect (Fig. 3b). Mesethmoid visible ventrally only as flattened, narrow band, anterior to vomerine tooth patch, to which premaxillae (not preserved) articulate; mesethmoid cornua not downwardly deflected. Vomer dominated by massive median tooth plate, approximately pentagonal form, surface concave upward and completely covered by minute pediculate tooth-attachment bases (no teeth preserved). Vomer expanded antrolaterally in front of tooth plate to suture with mesethmoid and lateral ethmoids; tapering posterior limb deeply sutured with parasphenoid.

Palatine condyle projecting prominently from lateral ethmoid, very long and in horizontal plane, convex anteriorly, nearly straight laterally, abruptly truncate posteriorly. Prominent, thin, horizontal "orbital shelf" arises on ventral surface of lateral ethmoid just posterior to palatine condyle and lateral to vomer. "Orbital shelf" continuing onto orbitosphenoid, parasphenoid and prootic to terminate ventral to trigeminofacial foramen; along lateral ethmoid and orbitosphenoid "orbital shelf" is the surface of origin for adductor arcus palatini muscle. Orbitosphenoid dominated by "orbital shelves," widest anteriorly, about 75% of skull width across lateral ethmoids, narrowing posteriorly to about 45% of skull width across sphenotics at level of hyomandibular facet. Foramina of orbitosphenoid deeply situated and indeterminate. Parasphenoid median stem broad, center of parasphenoid marked by medially converging pair of low ridges and elongate roughened surfaces (associated with contact of anterior branchial arches); parasphenoid weakly sutured to prootics, deeply sutured to basioccipital, indeterminate contact with pterosphenoid.

Anterior half of ventral surface of sphenotic planar and bare; posterior half of sphenotic sharply elevated laterally, forming anterior two-thirds of elongate, horizontal, trough-like hyomandibular facet that runs mediolaterally to sphenotic-pterotic suture near skull roof margin, then along edge of pterotic. Hyomandibular facet on pterotic followed at right-angles by another articular facet, short, flat-faced and ventrally buttressed, for posterodorsal corner of hyomandibula. Neither pterosphenoid nor prootic participate in hyomandibular facet or other articulation with hyomandibula.

Medioventrally adjacent to hyomandibular facet, sphenotic, pterotic and prootic together form roof of ovoid, shallow subotic fossa.

Prootic side wall flat dorsal to contact with parasphenoid; position of matrix-filled trigeminofacial foramen indicated by semicircular notch in anterior border of prootic and sharp edged terminus of "orbital shelf" ventral to foramen. Pterosphenoid largely obscured by matrix but no evidence that it is more extensive than in modern species where it is restricted as a small quadrangular element between the prootic, sphenotic and orbitosphenoid.

Basioccipital weakly sutured to exoccipital and prootic; vertebral-like joint with first centrum. Articulation site on basioccipital for ossified Baudelot's ligament elevated and rugose. Exoccipital weakly sutures with basioccipital, prootic, pterotic and epioccipital; contributing small dorsal process to cranial articulation with Baudelot's ligament; vagal foramen large, circular, ventrally directed, centered on a vertical through the anterior edge of basioccipital-Baudelot's ligament joint. Baudelot's ligament of supracleithrum ossified and heavy; round in section medially near contact with basioccipital and exoccipital. Exoccipital and epioccipital forming sharp posterolateral corner of braincase that vertically buttresses expanded cranial articulation of pterotic-supracleithrum. Anterolateral face of epioccipital concave and weakly sutured to pterotic. Posterior end of pterotic wing produced and expanded ventral to cranial articulation of supracleithrum. Ventral side of supraoccipital posterior process with strong median vertical keel.

Suspensorium (Fig. 5k, l). Hyomandibula broad and deep, sutured to preopercle via lateroposterior flange, and metapterygoid via wide anterior process; anteriorly sutured and posteriorly synconchondrally jointed to quadrate. Cranial articulation of hyomandibula including slender anterodorsal process abutting weak ridge on sphenotic in front of hyomandibular facet; long, gently rounded condyle articulating with hyomandibular facet of sphenotic and pterotic; plus short, vertically-truncate posterodorsal surface articulating with pterotic behind hyomandibular facet. Lateral face with low, oblique rise between anterior process and preopercular flange, marking attachment limit of inner bundles of adductor mandibulae muscle. Low crest on medioposterior edge ventral to pterotic articulation, otherwise no enlarged articulating processes or muscle origin crests dorsal to opercle condyle. Opercle condyle centered slightly above midpoint on posterior margin; condyle twice as deep as wide. Lateral foramen of facial canal centrally located on anterior surface of adductor muscle crest at level of opercle condyle; medial foramen of facial canal anteriorly located above adductor arcus palatini crest. Medial face with centrally located vertical and crescentic adductor arcus palatini scar more prominent than in modern *P. hemioliopterus* (Fig. 5m) but is shape and placement similar.

Preopercle sutured to quadrate in addition to hyomandibula; lateral face shallowly concave forming fossa for posterior sections of adductor mandibulae muscle; posterior margin raised in a gentle curve and likely with sensory canal but no discernable lateralis pores; no evidence of external foramen for symplectic canal, but medial foramen of symplectic canal present between quadrate and preopercle.

Quadrate lateral face mostly shallowly concave; anteroventral blade broadly sutured to metapterygoid; mandibular condyle broad and strongly bilobed flanking central saddle, medial lobe of condyle braced by vertical buttress.

Anterior vertebrae (Fig. 3b). First centrum articulated to basioccipital and deeply sutured to compound or Weberian complex centrum (2-4). Aortic groove open along midventral line, flanked by low parallel ridges along first and compound centra; broken before centrum of vertebra 5. Weberian complex lacking prominent mid-dorsal vertical lamina; neural arch-spine complex incompletely preserved but anteriorly projecting to contact supraoccipital and exoccipitals. Indistinct pieces of tripus and low os suspensorium remain in place; anterior limbs of transverse processes meet compound centrum at right angle, wide and thickened laterally, broadly contacting ventral articulation flange of supracleithrum; vertebra 5 indeterminate.

Pectoral girdle (Figs. 5 e, f, g). Dorsal articulating process of cleithrum bifid, anterior limb longest, and overall similar in size to postcleithral process; postcleithral process deep and nearly equilaterally triangular, coarsely ornamented especially along ventral and ventrolateral edges lateral to articulating fossa of pectoral spine. In ventral view outward bulge of cleithrum in transverse alignment with posterior limit of articulating fossa of pectoral spine. Mesocoracoid not preserved but elevated surface near dorsal edge of coracoid shows its articulation site. Coracoid keel strongly elevated proximally, extending about midway to pectoral symphysis; coracoid keel divides jointed horizontal limbs of cleithrum and coracoid into equal halves; two parallel ridges run toward midline horizontal limbs of coracoid.

Pectoral spine shaft (Figs. 5 e, f, h) depressed, in section more ovoid than quadrangular, mostly covered by coarse, elongate and anastomosing ridges and grooves (neither mesh-like nor finely-striate); anterior dentations erect, blunt, none strongly antrorse, relatively heavy and about half as numerous as posterior dentations; posterior dentations erect and irregularly spaced, some transversely widened but not exceptionally flattened, sharper and fewer than anterior dentations; anterior and posterior dentation rows without deep trenches and flanking ridges; no anterior distal serrations; spine tip bluntly pointed; spine base robust but details indeterminate.

Discussion

The pimelodid genus *Phractocephalus* has long been regarded as monotypic. The morphological variation among modern and well-preserved fossil skulls and some postcranial elements indicates that *Phractocephalus* comprises three species: *P. hemioliopterus*, †*P. nassi* and the unnamed Neogene Acre *Phractocephalus*. These species are differentiated by well-preserved characteristics of dermal bone ornamentation and enlargement of the casque-like skull roof and occipito-nuchal bony plating. The *Phractocephalus* from the middle Miocene, Colombian La Venta fauna is too incompletely known (partial mesethmoid and partial pectoral spine) to assess its species status. Despite this new understanding of greater taxic diversity, the species of *Phractocephalus* are closely similar in most details of their highly apomorphic cranial and pectoral-fin morphology. The Late Miocene †*P. nassi* and the Acre fossil give a minimum age of about 8 or 9 Ma for the origin of the distinctive osteology of *Phractocephalus* and at least some species diversification within this small clade.

A thorough analysis of phylogenetic relationships among the species must await a detailed description of the Acre species. However, both †*P. nassi* and Acre species have more hypertrophied skull and occipito-nuchal elements than modern *P. hemioliopterus*. The expanded dorsal armor plating can be interpreted as a synapomorphy uniting the two Miocene species. In this light the less extensive skull roof of modern *P. hemioliopterus* might be either a retained primitive condition within the genus (it is still a more derived condition than found in all other extant pimelodids), or a secondary reduction. Furthermore, in *P. hemioliopterus* the full reticulating ridge and pit style of dermal bone ornamentation is more derived than that of the fossils which retain more longitudinal ridges and groove ornament.

Despite its uncertain systematic placement within the genus, the La Venta *Phractocephalus* provides a minimum age of ca. 13.5 Ma for the genus and its sister group *Leiarius* Bleeker + *Perrunichthys* Schultz (Lundberg *et al*., 1988, 1991; Nass, 1991).

Today no *Phractocephalus* live west or north of the Andes or Venezuelan coastal ranges. The biogeographic significance of Late Miocene *Phractocephalus* from the northern Venezuelan Urumaco site was discussed by Lundberg *et al*. (1988) and subsequent authors (Aguilera, 1994; Lundberg, 1997, 1998; Sánchez-Villagra *et al*., 2003). Recognizing the Urumaco *Phractocephalus* as a distinct species does not alter the obvious conclusion that this catfish marks a former large freshwater connection between the Caribbean coastal region and the Orinoco system. Other Urumaco fossils show the same biogeographic relationship: mata-mata turtles (*Chelus* Dumeril), freshwater iniid dolphins, crocodilians (*Caiman* Spix), freshwater sciaenids (*Plagioscion* Gill), indeterminate doradids, loricariids, pimelodids and serrasalmine characins. The phylogenetic relationships of many modern endemic freshwater fish species or genera of the Maracaibo Basin also corroborate a former link to the Orinoco and more broadly with the Amazon and Magdalena system. Examples of these among the Pimelodidae are *Perrunichthys perruno* Schultz, sister to the Orinocoan-Guianan-Amazonian genus *Leiarius*; *Platysilurus malarmo* Schultz and *Cheirocerus abuelo* (Schultz), belonging to monophyletic genera with species in the Orinoco, Amazon and Guianas; and *Megalonema psammium* Schultz and *Sorubim cuspicaudatus* Littmann, Burr, & Nass (belonging to genera with species in the Orinoco, Amazon, Guianas, Magdalena and Paraná).

The foregoing biotic relationships correlate well with current models of Neogene landscape and drainage evolution in northern South America. Rod (1981), Lundberg *et al.* (1988), and Díaz de Gamero (1996) discussed evidence for a major outlet of a paleo-Orinoco system into the Caribbean from northwestern Venezuela. A mounting body of evidence has now been presented for a long persistent, large river system originating far south in western Amazonia that flowed north in the Andean foreland basin (Hoorn, 1993, 1994 a, b, c; Hoorn *et al*., 1995; Lundberg *et al*., 1998). This "Paleo-Amazon-Orinoco" river system would have contained a common freshwater fauna including fish species represented as fossils from Urumaco (Aguilera & Rodrigues de Aguilera, 2003; Sánchez-Villagra *et al*., 2003). At times marine and estuarine conditions extended southward into the Andean foreland basin from the Caribbean (Hoorn, 1994 a, b, c; Monsch, 1998) thus providing some opportunities for marine taxa to penetrate far into the South American continent (Lovejoy *et al*., 1998). Sometime in the Late Miocene, the rising mountain divides of the Eastern Andes and Coastal Cordilleras closed the Caribbean outlet of the "Paleo-Amazon-Orinoco" system. Concomitant or subsequent to the isolation of the coastal region of Urumaco and Falcón State much of the former freshwater biota disappeared.

Additional fossil pimelodid, doradid, loricariid and characiform fishes from the Urumaco fauna are now available for study and should provide more information on the intriguing biotic and landscape histories of northern South America.

The paleo-environments within the Urumaco Formation are a complex mixture of freshwater, estuarine and marine. Deposition occurred on a relative narrow coastal plain. There is no indication of major reworking of fossil remains. Fossils of the "cajaro" catfish (†*Phractocephalus nassi*) are often associated with remains of "sierra" catfishes (doradids), gavialids (*Ikanogavialis* Sill, *Gryposuchus* Gürich), crocodilians (*Purussaurus* Barbosa-Rodrigues, *Mourasuchus* Price), "arrau" turtles (*Bairdemys* Gaffney & Wood), sirenids (indeterminate dugongid) and "tonina" freshwater dolphin (indeterminate iniid). This entire fauna is relatively common in the freshwater facies from the Urumaco Formation, especially in the upper member. Present also in this assemblage are fossils of coastal fishes such as, sea catfish (*Arius* Valenciennes, *Bagre* Cloquet, *Sciadeops* Fowler) and sawfish (*Pristis* Linck) that often enter freshwaters.

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