Aspistor verumquadriscutis, a new fossil species of sea catfishes (Siluriformes; Ariidae) from the upper Miocene of Venezuela

Orangel Aguilera · Alexander P. Marceniuk

Abstract The Late Miocene Urumaco Formation, Northwestern Venezuela, one of the most fossiliferous units in the Neogene of tropical America, represents a shallow, marginal marine to deltaic wetland and fluvial system. A new extinct species of sea catfishes is described from the Urumaco Formation. *Aspistor verumquadriscutis* n. sp. is placed in the genera *Aspistor* based on five synapomorphies shared with modern congeners: epioccipital dorsally exposed, parieto-supraoccipital posterior margin convex, nuchal plates forming a large butterfly-shaped or moon-shaped structure, anterior margin of nuchal plate slightly concave, and nuchal plate overlapping parieto-supraoccipital. The new fossil species is distinguished from its modern congeners by having a shorter parieto-supraoccipital process, and a larger and longer nuchal plate, nuchal plate length 0.9–1.0 in parieto-supraoccipital process length (vs. 1.1–1.7 in *A. luniscutis*), and nuchal-plate width at medial area 0.9–1.0 in parieto-supraoccipital process length (vs. 1.1–1.5 in *A. luniscutis*); nuchal plate granulose over its entire surface (vs. with half lateral surface smooth in *A. quadriscutis*), nuchal plate subquadrangular shaped, almost as long as wide (vs. nuchal plate subtrapezoidal or butterfly shaped, anterior portion always narrower than the posterior portion in *A. quadriscutis*), and lateral margin of the nuchal plate straight (vs. with a constriction at the medial portion in *A. quadriscutis*).

Keywords Ariidae · Urumaco Formation · Neogene · Palaeontology

Abbreviations
UNEFM PR	Universidad Nacional Experimental Francisco de Miranda, Venezuela
USNM	National Museum of Natural History, Smithsonian Institution, USA
MZUSP	Museu de Zoologia da Universidade de São Paulo, Brazil

Introduction

Sea catfishes of the family Ariidae are a well-diagnosed monophyletic group of primarily marine fishes. Most ariid species occur in tropical and temperate areas around the world in coastal waters, estuaries, and the lower portions of rivers, with some species found exclusively in either marine or freshwaters (Marceniuk and Menezes 2007; Betancur-R. 2009; Marceniuk et al. in press). In past decade, systematic and taxonomic knowledge of modern Neotropical Ariidae has been advanced with the descriptions of new species and revisions of nominal species (Betancur and Acero 2005, 2006; Marceniuk 2005a, 2007a, b; Acero and Betancur-R. 2006; Betancur and Willink 2007; Marceniuk and Betancur-R. 2008; Marceniuk et al. 2009, 2012), and with hypotheses on phylogenetic relationships and redefinitions of genera based on shared derived features (Betancur-R. 2009; Marceniuk et al. in press).

O. Aguilera (✉)
Museu Paraense Emilio Goeldi, Coordenação de Ciências da Terra e Ecologia, CCTE, Av. Perimetral, 1901, Terra Firme, Belém, PA 66077-830, Brazil
e-mail: orangel.aguilera@gmail.com

A. P. Marceniuk
Universidade Federal do Pará, Instituto de Estudos Costeiros, Campus de Bragança, Alameda Leandro Ribeiro, Bragança, PA 68600-000, Brazil
e-mail: a_marceniuk@hotmail.com

The Ariidae comprises 30 living genera and 138 species (Marceniuk and Menezes 2007), including 16 fossil species described from Africa (six), the Americas (three), Asia (one), and Europe (six) ranging in age from the Lower Eocene to the Pliocene (Ferraris 2007). Most of them are based on the pectoral spine morphology. Gayet and Meunier (2003) provide a worldwide overview of the geographic and geochronologic distributions of fossil Ariidae. In South America an additional early to middle Miocene ariid species was recently described from Argentina by Bogan and Agnolin (2011). In tropical South America the fossil occurrence of Amphi-American Neogene sea catfishes Ariidae was treated at length by Aguilera and Rodrigues de Aguilera (2004), with modern species reported in the fossil record (Miocene to Pleistocene) based on skulls and/or otoliths (Aguilera and Rodrigues de Aguilera 2004; Aguilera 2010; Lundberg 1975, 1998; Nolf 1976; Nolf and Aguilera 1998). In the Caribbean region fossil ariids are common and diverse in the Venezuelan subprovince (Aguilera et al. 2011).

The Late Miocene Urumaco Formation is one of the most fossiliferous units in the Neogene of tropical South America (see Sánchez-Villagra et al. 2010, for a review of the vertebrates). Located in the Urumaco trough, northwestern Venezuela, the generalized stratigraphic section from the Urumaco region shows alternating palaeo-environments through a sequence of six formations, characterized by a shallow and marginal marine to wetlands deltaic plain and fluvial system (Quiroz and Jaramillo 2010). The lithology of the Urumaco Formation was treated in the Léxico Estratigráfico de Venezuela (1997) and Quiroz and Jaramillo (2010). In this paper, three fossil ariid specimens, represented by fragmentary skull, dorsal fin, Weberian apparatus, and anterior vertebrae, are described as *Aspistor verumquadriscutis* n. sp. from the Urumaco Formation in the Upper Miocene of Venezuela. Characteristics of the nuchal plate and in the parieto-supraoccipital process morphology allow diagnosis of the specimens as conspecific representatives of the genus *Aspistor*.

Materials and methods

The specimens were collected during several expeditions to the Urumaco Formation (Fig. 1) between 1995 and 2010 by OA and Julio Reyes (Universidad Francisco de Miranda), Rodolfo Sánchez (Alcaldía del Municipio Urumaco), and Marcelo Sánchez-Villagra (University of Zurich) under the scope of the Urumaco and Venezuela Vertebrate Palaeontology Project (see Sánchez-Villagra et al. 2010). The fossils are the posterior portions of three-dimensional, articulated skull. Preservation ranges from

nearly perfect to strongly abraded. The matrix materials surrounding the specimens vary from fine, loose sand that was removed with brushes, to iron-stained claystone requiring softening with water and manual cleaning with dental tools. The stratigraphic section from the Urumaco Formation was provided by Luis Quiróz and Carlos Jaramillo (Smithsonian Tropical Research Institute), and adapted to the present paper.

The names of bones are those used by Mo (1991) with the following exceptions: "parieto-supraoccipital" instead of "supraoccipital" (Arratia and Gayet 1995). The term "nuchal plate" refers to the fusion of the anterior and the medial nuchal plates (Royero 1987). Parieto-supraoccipital process length was measured as specified in Marceniuk (2007b) and nuchal plate length and nuchal plate width at medial area as specified in Betancur-R et al. (2008).

Comparative material examined. *Aspistor quadriscutis*: UNEFM PR 068, 1 skeleton, off coast of Paria Gulf in the Orinoco Delta, Venezuela; UNEFM PR 019, 1, off coast of Paria Gulf in the Orinoco Delta, Venezuela; USNM 236084, 2, off coast of Venezuela; USNM 66287, 2, Guyana; USNM 215967, 2, off coast of Amapá, Brazil; USNM 215965, 2, off coast of Amapá, Brazil; USNM 207411, 2, off coast of Amapá, Brazil; USNM 213652, 2, off coast of Amapá, Brazil; USNM 213664, 2, off coast of Pará, Brazil; USNM 286508, 2, off coast of Pará, Brazil; MZUSP 48521, 1, Jubim, baía de Marajó, Pará, Brazil; MZUSP 48525, 2, Jubim, baía de Marajó, Pará, Brazil; MZUSP 71709, 3, fish market of Vigia, Pará, Brazil; MZUSP 104092, 1, fish market of São Luis, Maranhão, Brazil. *Aspistor luniscutis*: USNM 167851, 1, fish market of Georgetown; MZUSP 24476, 1, Morro Branco, Ceará, Brazil; MZUSP 104094, 1, fish market of Maragogi, Alagoas, Brazil; MZUSP 22600, 1, Aracajú, Sergipe, Brazil; MZUSP 22601, 1, Aracajú, Sergipe, Brazil; MZUSP 52841, 1, Pirambú, Sergipe, Brazil; MZUSP 23795, 2, fish market of Salvador, Bahia, Brazil; MZUSP 72616, 2, between Manguinhos and Cabo Frio, Rio de Janeiro, Brazil; MZUSP 23642, 1, Cabo de São Tome, Rio de Janeiro, Brazil; MZUSP 28299, 1, Guarda river, Itaguaí, Rio de Janeiro, Brazil; USNM 41496, 1, off coast of Rio de Janeiro state, Brazil; MZUSP 22209, 1, between Rio de Janeiro and São Paulo states, Brazil; MZUSP 72638, 1, between Rio de Janeiro and São Paulo states, Brazil; MZUSP 72624, 1, between Rio de Janeiro and São Paulo states, Brazil; MZUSP 104093, 1, fish market of Ubatuba, São Paulo, Brazil; MZUSP 2292, 1, rio Juqueriquere, Caraguatatuba, São Paulo, Brazil; MZUSP 99712, 1, Pouca Farinha, Guarujá, São Paulo, Brazil; MZUSP 2293, 1, Santos, São Paulo, Brazil; MZUSP 22219, 1, Santos, São Paulo, Brazil; MZUSP 51690, 1, off coast of São Paulo state, Brazil.

Fig. 1 *Top*: view of "Corralito" locality. *Bottom*: map showing locations where fossil ariids were collected in the Upper Miocene Urumaco Formation, Venezuela
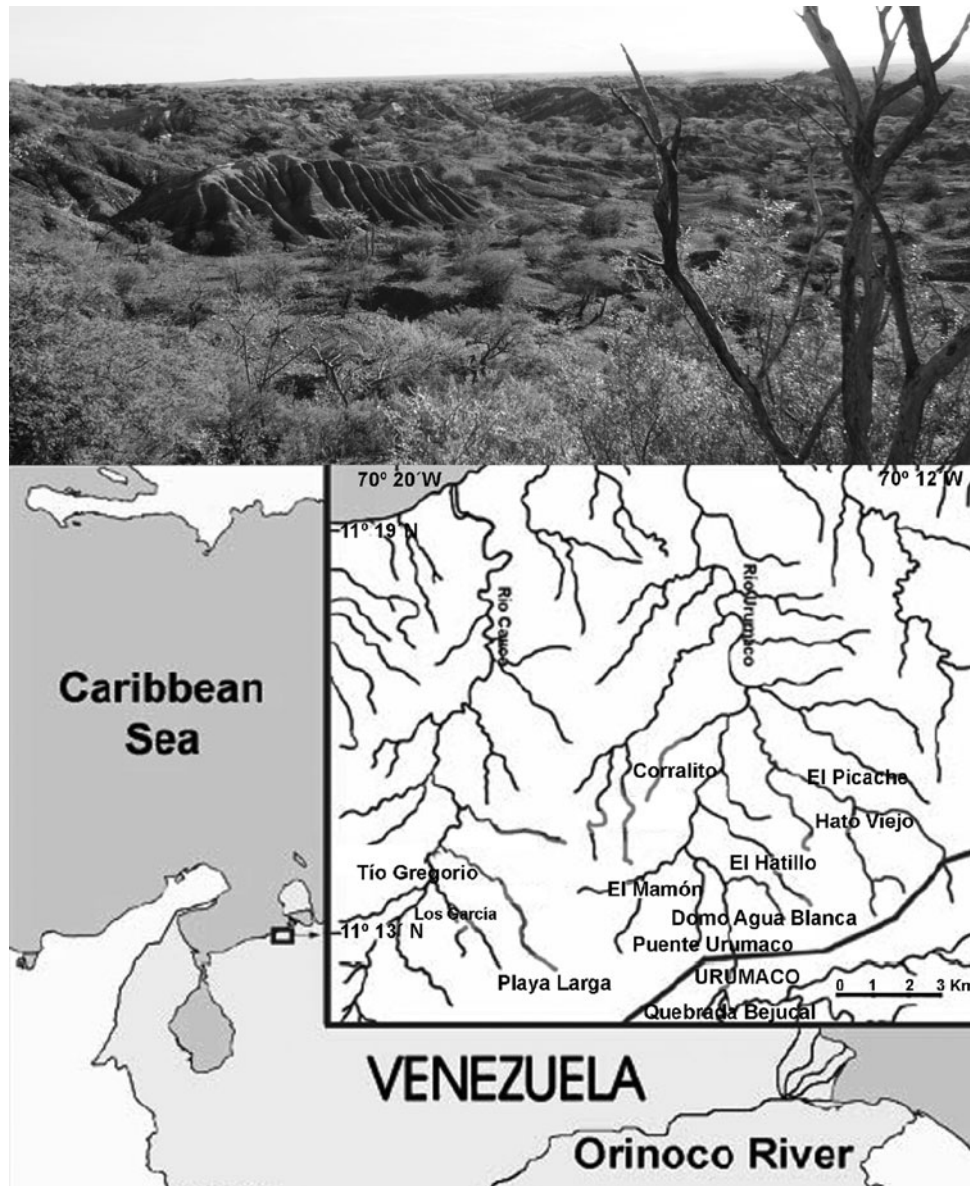
Systematic Palaeontology

Siluriformes *sensu* Berg 1940
Ariidae Bleeker 1862
Aspistor Jordan and Evermann 1898
Aspistor verumquadriscutis, new species
Figs. 3, 4, 5

"*Arius*" *quadriscutis* Valenciennes 1840. Aguilera and Rodrigues de Aguilera 2004 (skull figure and descriptive osteology).

Aspistor quadriscutis Valenciennes, 1840. Aguilera 2010 (skull figure with descriptive osteology and otolith); Aguilera and Lunddberg 2010 (listed).

Holotype. UNEFM-PF-3222, most of posterior part of a neurocranium, preserved length 56.2 mm (specimen described by Aguilera, 2010) from the Tio Gregorio locality (11°14′26.8″N, 70°18′41.2″W) in the Upper Member of the Urumaco Formation (Upper Miocene), Falcón State, Venezuela.

Paratypes. All localities in Falcón State, northwestern Venezuela. UNEFM-PF-0154, most of posterior part of a neurocranium, preserved length 55 mm (specimen described by Aguilera and Rodrigues de Aguilera 2004) from Corralito locality (11°15′06″N, 70°15′56″W), Upper Member of the Urumaco Formation (Upper Miocene). UNEFM-PF-0395, most of posterior part of a neurocranium, preserved length 47 mm, from El Mamón locality (11°14′06″N, 70°16′00″W), Upper Member of the Urumaco Formation (Upper Miocene).

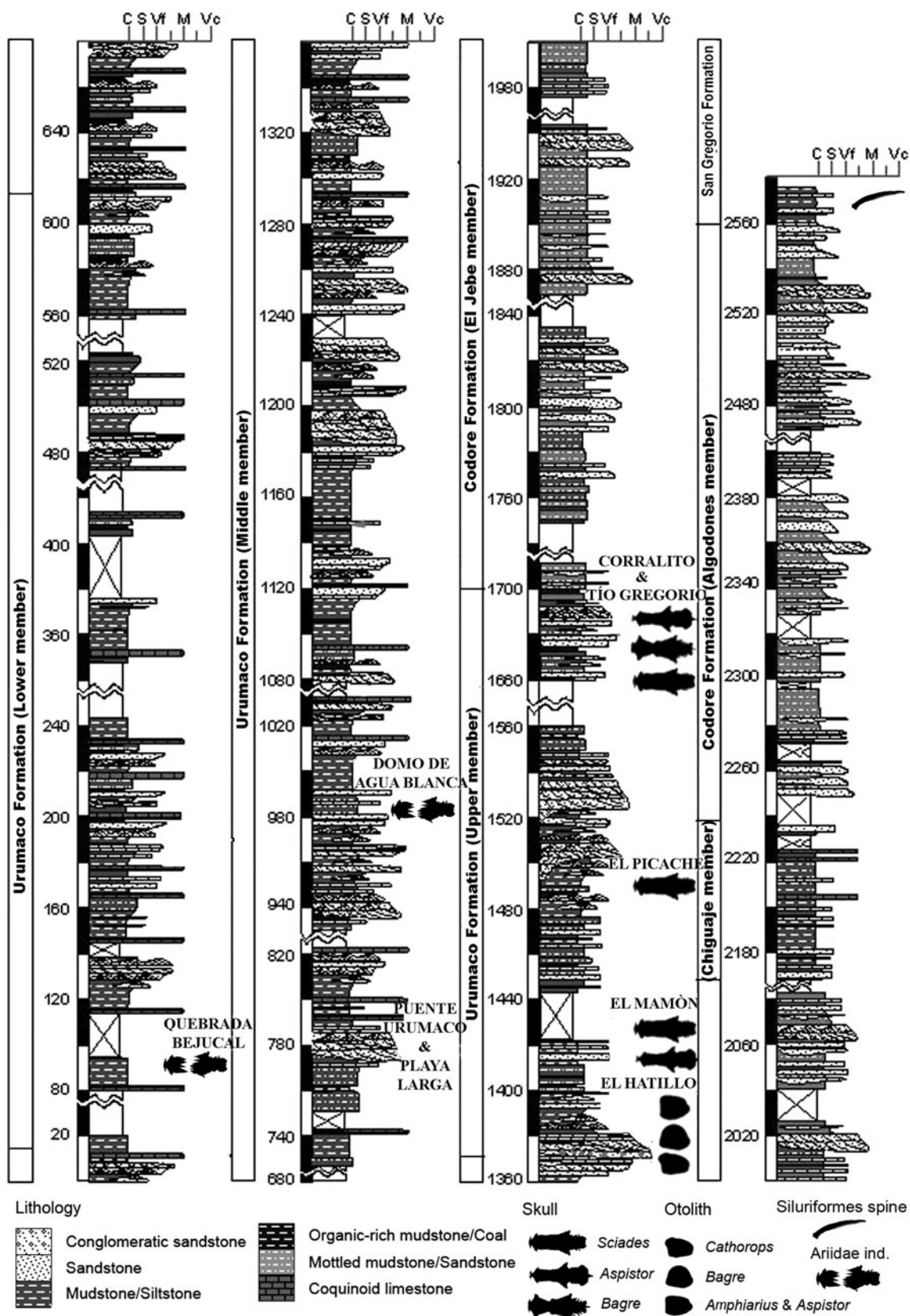**Locality and geological age.** *Aspistor verumquadriscutis* n. sp. is only known from the Upper Miocene Urumaco

Fig. 2 Stratigraphic section of the Urumaco Formation, Northwestern Venezuela (modified from Quiroz and Jaramillo 2010). *C* clay, *S* silt, *Vf* very fine sand, *M* medium sand, *Vc* very coarse sand
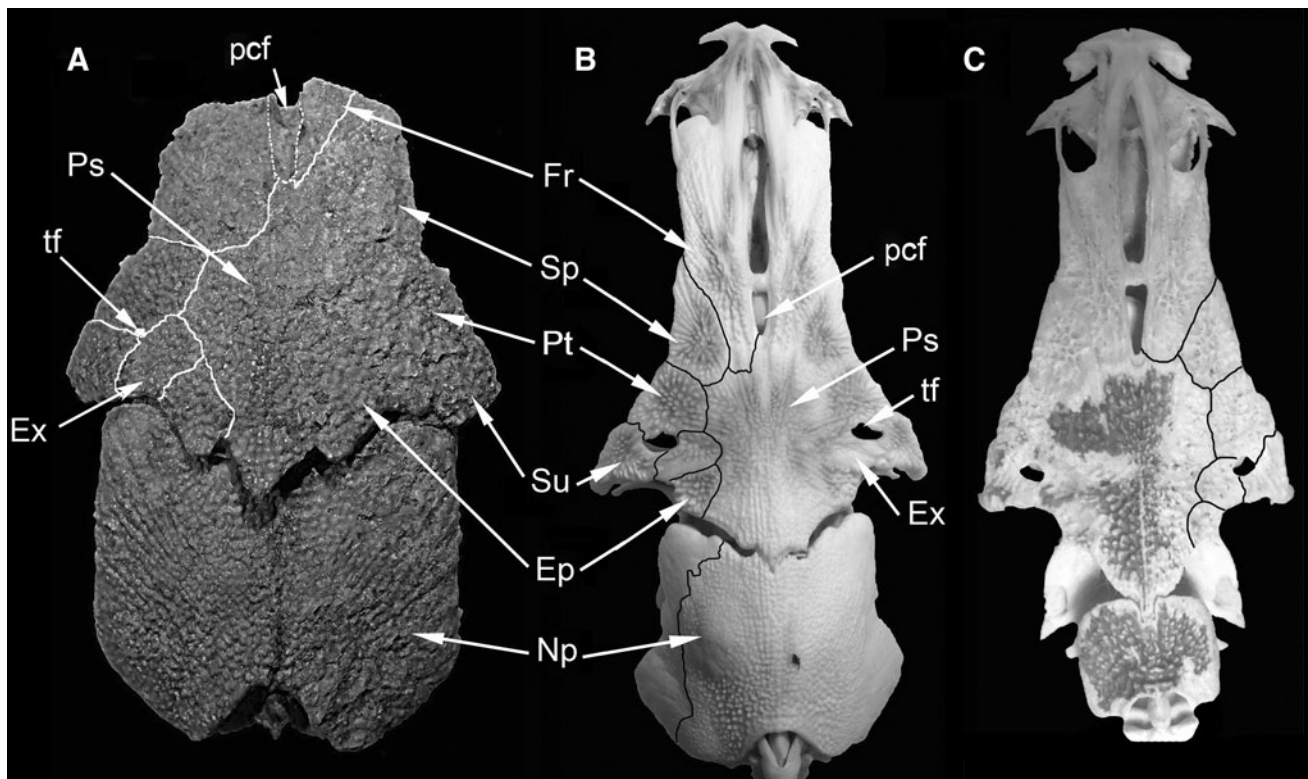
Fig. 3 *Dorsal* view of broken neurocrania, posterior portion, and dorsal fin. **a** Holotype of *Aspistor verumquadriscutis*, UNEFM-PF-3222, preserved length 56.2 mm; **b** *Dorsal view* of complete neurocranium and dorsal fin from Recent *A. quadriscutis*, UNEFM PR 068; **c** *Dorsal view* of complete neurocranium and dorsal fin of Recent *A. luniscutis*, MZUSP 51690. *Ep* Epioccipital, *Ex* Extrascapular, *Fr* Frontals, *Np* Nuchal plate, *pcf* posterior cranial fontanel, *Ps* Parieto-supraoccipital, *Pt* Pterotic, *Sp* Sphenotic, *Su* Supracleithrum, *tf* temporal fossa. *Solid line*: observed sutures, *dashed line*: inferred sutures

Formation (Figs. 1, 2), occurring in the shale and mudstone sediments from El Mamón, El Picache, Corralito, and Tío Gregorio localities, Urumaco Municipality, Falcón state, Venezuela.

Etymology. The names *quadriscutis* and *luniscutis* of the modern species refer to the nuchal plate shape. It represents the main diagnostic character used to distinguish *Aspistor* species (Marceniuk 2005b). The name *verumquadriscutis* refers to real quadrangular or subquadrangular shape of the nuchal plate, in contrast to *A. quadriscutis* [as *A. parkeri* (Traill 1832) sensu Marceniuk and Ferraris 2003; Marceniuk 2005b; Marceniuk and Menezes 2007, see Betancur-R et al. 2008], which presents a nuchal plate of subtrapezoidal or butterfly shape. The other modern species, *A. luniscutis*, have a nuchal plate with the form of a full moon or rounded shield.

Diagnosis. (Figs. 3, 4, 5). *Aspistor verumquadriscutis* n. sp. is distinguished from its modern congeners as follows: from *A. luniscutis* by having a shorter parieto-supraoccipital process, and larger and longer nuchal plate, nuchal plate length 0.9–1.0 in parieto-supraoccipital process length (vs. 1.1–1.7), and nuchal plate width at medial area

0.9–1.0 in parieto-supraoccipital process length (vs. 1.1–1.5); from *A. quadriscutis* by possessing nuchal plate granulose in the entire surface (vs. with half lateral surface smooth, Fig. 3), nuchal plate subquadrangular shaped, almost as long as wide (vs. nuchal plate subtrapezoidal or butterfly shaped, anterior portion always narrower than the posterior portion, Fig. 3), and lateral margin of the nuchal plate straight (vs. with a constriction at the medial portion, Fig. 3).

Description

Neurocranium. (Figs. 3, 4, 5). Bones of the cephalic shield have a granular texture. The posterior cranial fontanel is relatively wide and long, and bounded laterally by the frontals, and posteriorly by the parieto-supraoccipital. The condition of the epiphyseal bar is indeterminate, and the medial groove of the cranium is indistinct. The frontal is in contact posteriorly with the parieto-supraoccipital and postero-laterally with the sphenotic. The sphenotic is flat and dorsally it articulates with the frontal, parieto-supraoccipital and pterotic. The sphenotic is ventrally sutured to the pterotic, prootic, pterosphenoid, and it carries the
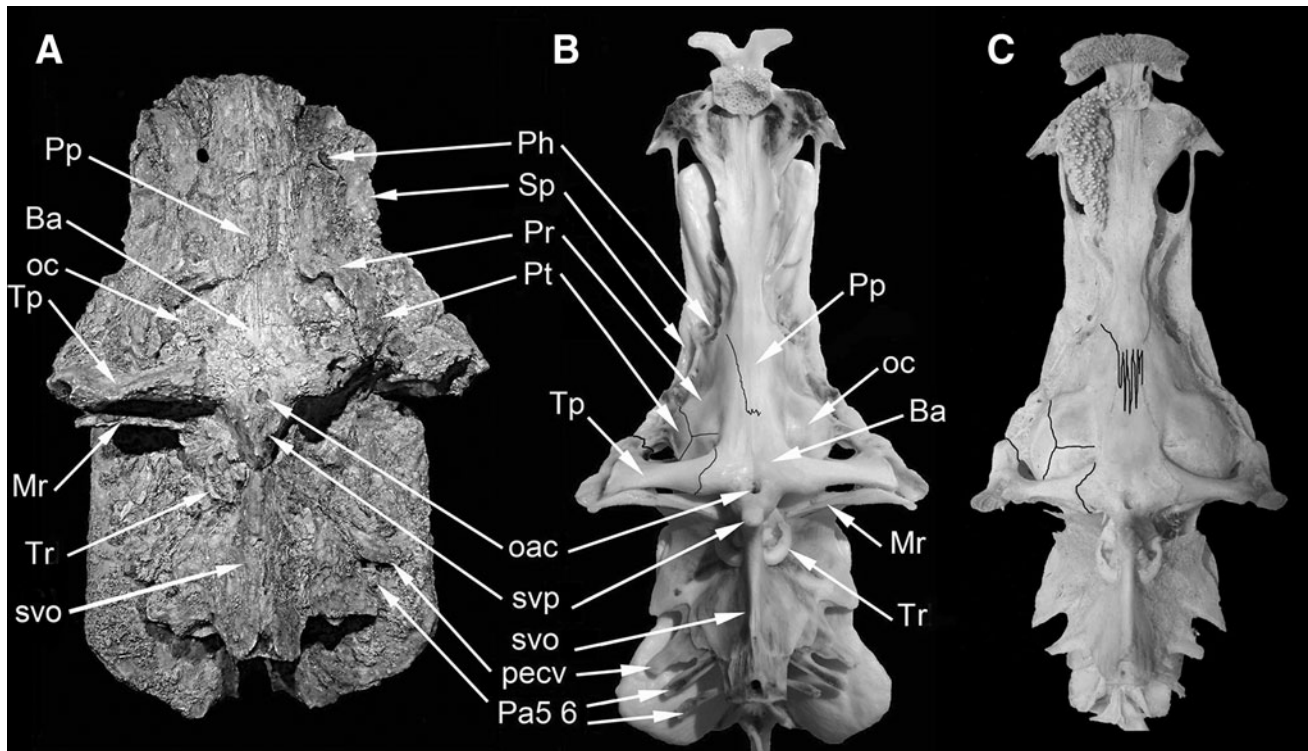
Fig. 4 *Ventral view* of broken neurocrania, posterior portion, Weberian apparatus and anterior axial skeleton. **a** Holotype of *Aspistor verumquadriscutis*, UNEFM-PF-3222, preserved length 56.2 mm; **b** *Ventral view* of complete neurocrania, Weberian apparatus and anterior axial skeleton from Recent *A. quadriscutis*, UNEFM PR 068; **c** *Ventral view* of complete neurocrania, Weberian apparatus and anterior axial skeleton from Recent *A. luniscutis*, MZUSP 51690. *Ba* Basioccipital, *Mr* Müllerian ramus, *oac* opening of the aortic canal, *oc* otic capsule, *Pa5 6* parapophyses of the fifth and sixth vertebrae, *Pecv* posterior expansion of the complex vertebra, *Ph* Pterosphenoid, *Pp* Paresphenoid, *Pr* Prootic, *Pt* Pterotic, *Sp* Sphenotic, *Svo* Superficial ventral ossification of the Weberian apparatus, *Svp* Subvertebral process, *Tp* Transcapular process, *Tr* Tripus

projecting socket of the sphenotic-hyomandibular joint. The pterotic is posterior to the sphenotic and has a subrectangular shape, laterally delimiting the skull; in ventral view the pterotic bone is the most lateral element of the otic capsule. The extrascapular has an oval to subquadrangular shape, is about as long as wide, and viewed from the dorsal plane, it is located on the posterodorsal region of the neurocranium, and it is sutured to the parieto-supraoccipital, pterotic, epioccipital, and the supracleithrum. The temporal fossa is wide, and delimited by the supracleithrum, pterotic and the extrascapular. In the fossil specimens the temporal fossa are partially obliterated by the sediment. The epioccipital is dorsally exposed, and bordering the posterior process of the parieto-supraoccipital, its laminated posterior process is not visible in the fossils. The parieto-supraoccipital is the largest bone of the upper skull roof, and it is sutured with the frontal, sphenotic, pterotic, extrascapular, epioccipital, and the exoccipital; its posterior process is wider at the base than the posterior portion, its lateral margins are abruptly convergent, and the posterior margin contacts the nuchal plate through a convex–concave articulation. The upper branch of the supracleithrum is flat, of subtriangular shape and is

lateroposteriorly articulated to the cephalic shield; its inferior limb, or transcapular process, is cylindrical to columnar in shape; it is relatively short and thick, and forms a right angle relative to the body axis. The space between the transcapular process and the otic capsule is moderately large. The pterosphenoid forms the ventrolateral wall of the cranial cavity, and the otic capsule. The prootic has lateral and posterior portion convex at its suture with the exoccipital and the pterotic; its concavity is less pronounced at its articulation with the basioccipital and the paresphenoid. The otic capsules are well differentiated and very large, and limited by the prootic, pterotic, and exoccipital; the suture between the prootic and the pterotic lacks the anterior angular process. The poorly preserved exoccipital subsequently limited the auditory capsule. The basioccipital is dagger-shaped, the bone is short and anteriorly wide, and is intertwined with the parasphenoid; it is posteriorly joined with the first vertebra by a jagged suture, forming the distinct and long subvertebral process. The foramen of the aortic canal still open towards the anterior direction and its localized in front of the subvertebral process. The basioccipital has a distinct short lateral process and its posterior portion is extending further laterally
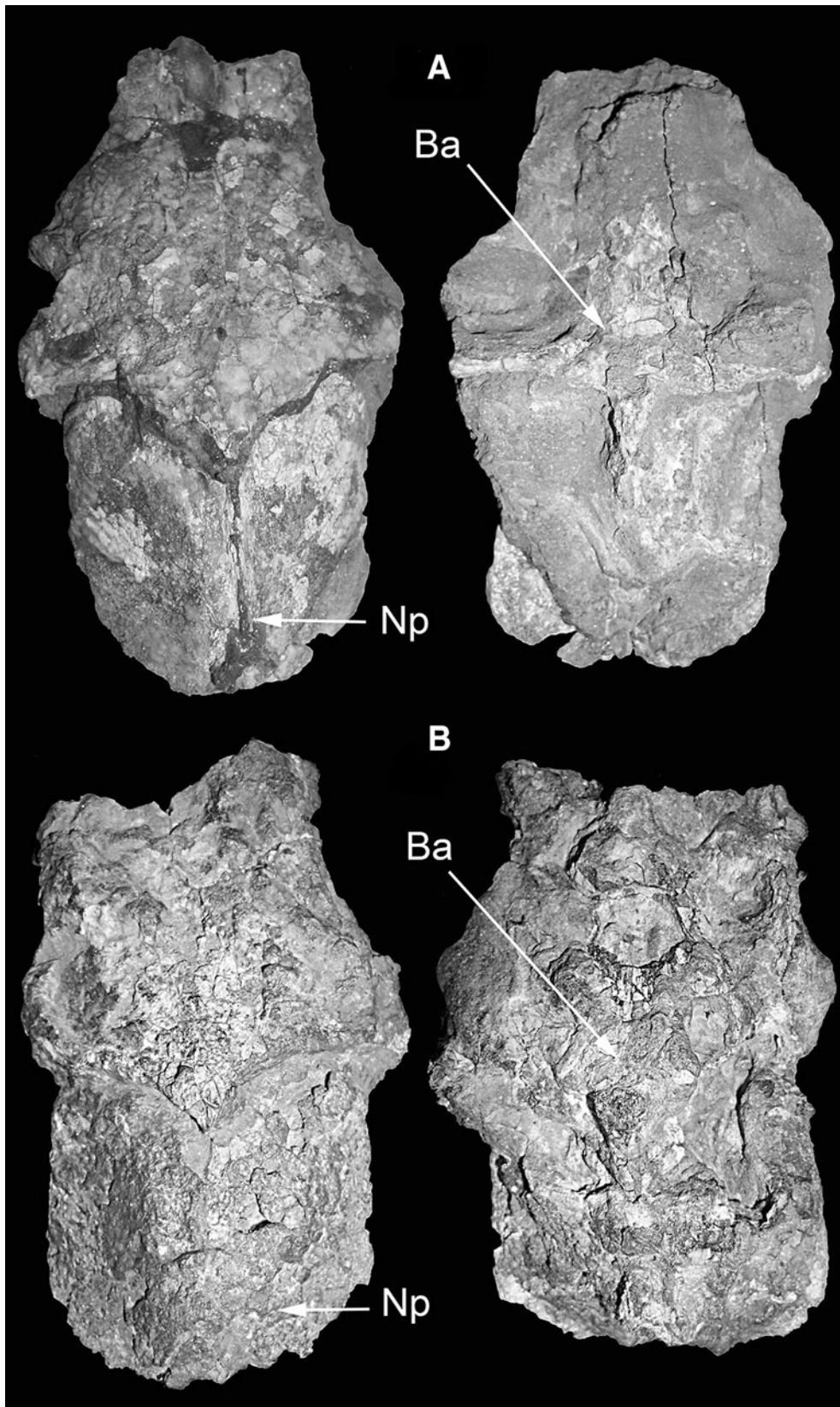
Fig. 5 *Dorsal view* of broken neurocrania, *posterior portion*, and dorsal fin (*left*) and *ventral view* of broken neurocrania, *posterior* portion, Weberian apparatus and *anterior* axial skeleton (*right*), from paratypes of *Aspistor verumquadriscutis*. **a** UNEFM-PF-0154, preserve length 55 mm, **b** UNEFM-PF-0395, preserved length 47 mm. *Ba* Basioccipital, *Np* Nuchal plate

than anteriorly. The joint for articulation with the transcapular process is small and columnar. The posterior process of the exoccipital is absent, and not supporting the Müllerian ramus.

Weberian apparatus and anterior axial skeleton. The parapophysis of complex vertebrae and the 5° vertebra have no superficial ossification. The complex vertebrae are composed by mostly three fused vertebrae (inferred), which is closed by the ventral superficial ossification, and together with the ventral Weberian apparatus reinforces the anterior portion of the axial skeleton. Individual vertebrae and its sutures cannot be recognized by the fusion; its ossified ventral surface covers the entire aortic canal. The superficial ossification forms a carina fitting precisely in the groove located at the dorso-medial depression of the swimbladder. In cross section the structure looks like an inverted triangle in which the aorta is located on the inferior vertex and the cardinal veins on the superior angles. The parapophyses of the fifth and sixth vertebrae are projected latero-posteriorly and fused proximally to the centra. The parapophysis of the fifth vertebra are larger than the sixth, and is firmly sutured to the posterior expansion of the complex vertebra. The transformator process of the tripus is slender.

Dorsal fin. The anterior and the middle nuchal plates are fused, forming a subquadrangular shield-like structure. They are ornamented with granular bone across the entire dorsal surface. The anterior margin of the nuchal plate is slightly concave, overlaying posterior portion of the parieto-supraoccipital process.

Discussion

Systematics. The genus *Aspistor* is monophyletic and endemic to eastern South America, with two living species inhabiting estuarine and brackish waters (Marceniuk and Menezes 2007; Marceniuk et al. in press). The new species is placed in the genus *Aspistor* based on five synapomorphies, two of them unique, shared with modern species (Marceniuk et al. in press): epioccipital dorsally exposed (convergent in *Amphiarius rugispinis*, *Carlarius*, *Plicofollis*, excluded *P. platystomus* and *P. tenuispinis*, *Cinetodus* and *Pachyula*); parieto-supraoccipital posterior margin convex (convergent in *Sciades proops*); anterior and median nuchal plates forming a large butterfly-shaped or moon-shaped plate; anterior margin of nuchal plate slightly concave; nuchal plate overlapping parieto-supraoccipital (convergent in *Notarius troschelii*, *Sciades parkeri* and *S. proops*). *Aspistor verumquadriscutis* can be additionally distinguished from fossil and modern representatives of Neotropical ariid genera by following supplementary morphological characters: bones forming cephalic shield granulated (vs. smooth or grooved in *Bagre* and

Galeichthys, Marceniuk and Menezes 2007, Figs 1 and 15); posterior cranial fontanel present (vs. absent in *Sciades*, Marceniuk and Menezes 2007, Fig. 90); posterior cranial fontanel relatively wide (vs. reduced to a small opening in *Bagre*, *Cathorops,* excluding *C. dasycephalus*, *Galeichthys*, and *Genidens*, Marceniuk and Menezes 2007, Figs. 1, 15 and 32, or narrow in *Cathorops dasycephalus*, *Notarius*, *Occidentarius*, and *Potamarius*, Marceniuk and Menezes 2007, Fig. 87); osseous medial groove of cranium absent (vs. present in *Bagre*, *Cathorops*, *Galeichthys*, *Genidens*, *Notarius planiceps*, *Occidentarius*, and *Potamarius*, Marceniuk and Menezes 2007, Figs. 1, 15, 32 and 87); parieto-supraoccipital process at base distinctly wider than posterior portion (vs. almost as narrow as posterior portion in *Galeichthys*, Marceniuk and Menezes 2007, Fig. 1 and base conspicuously narrower than posterior portion in *Notarius grandicassis*); opening of the aortic canal at base of the subvertebral process distinct (vs. indistinct in *Galeichthys*); opening of the aortic canal at base of subvertebral process and anteroventrally oriented (vs. slightly anterior of subvertebral process and ventrally oriented in *Bagre*, *Genidens*, *Occidentarius*, *Potamarius*, and *Sciades*, or within base of subvertebral process and anteriorly oriented in *Cathorops*, Marceniuk and Menezes 2007, Fig. 31); subvertebral process conspicuous (vs. indistinct or weakly developed in *Occidentarius*, and *Sciades*); transcapular process cylindrical to columnar (vs. depressed in *Cathorops*); transcapular process forming a right angle in relation to body axis (vs. forming an acute angle in *Bagre*, *Genidens*, *Occidentarius*, *Potamarius*, and *Sciades*); space between transcapular process and otic capsule moderately large (vs. very large *Occidentarius* and *Sciades* or absent in *Amphiarius* and *Cathorops*); superficial ventral ossification of the Weberian apparatus entirely covering the aortic canal (vs. not or only partially covering the aortic canal in *Galeichthys* and *Bagre*); superficial ventral ossification keeled (vs. arched in *Cathorops*). The conspecificity of the three fossil specimens treated herein is supported by the unique morphology of the parieto-supraoccipital process and nuchal plate that characterizes *Aspistor verumquadriscutis*.

Palaeoenvironment and occurrences of ariids fossils. The stratigraphic section of Late Miocene Urumaco Fomation includes three members (lower, middle and upper) comprising 2,560 m of sedimentary sequence containing ariid remains, especially associated with the prodelta, delta front, and delta plain palaeoenvironment (Fig. 2). Unidentified ariids from the prodelta facies in the lower member come from coquinoid limestone, containing a mixed assemblage of vertebrates marine (e.g. grouper skull) and freshwater fishes (e.g. serrasalmine or "pacu" tooth), fluvial/lacustrine crocodiles (e.g. caiman teeth and skull remains), semi-aquatic snakes (e.g. boids vertebrae),

terrestrial rodents (e.g. capybara tooth), and broken shells resulting from strong storm littoral surge and torrential drainage flooding in coastal zone. The transitional change to delta front in the lower member has ariid fossils at the top in mudstone associated with a low-energy shallow palaeoenvironment. The delta plain facies in the middle and upper members contains the highest known ariid diversity in tropical South America (Aguilera and Rodrigues de Aguilera 2004), and the long-term occurrence of *Aspitor verumquadriscutis* can be used as a fossil guidance in the assemblage context for the late Miocene, delta plain, Venezuelan subprovince, and Proto-Caribbean fauna.

This particular palaeoenvironment and faunal assemblage predate the isolation of the Urumaco trench in the Falcón basin from main continental drainage in North-western South America (Johnson et al. 2009) and the isolation from main inter-oceanic Pacific-Atlantic corridor (Aguilera et al. 2011). Following the Panamanian land bridge emplacement, local estuarine conditions disappeared and the Proto-Caribbean ariid species (Venezuelan subprovince) from the Urumaco Formation became extinct. During the Plio-Pleistocene the recent Caribbean ariids species assemblage developed.

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