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Taxonomy and morphology of species of the genus *Squalus* Linnaeus, 1758 from the Southwestern Atlantic Ocean (Chondrichthyes: Squaliformes: Squalidae)

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Abstract

Squalus is a genus of reportedly cosmopolitan shark species that have a high taxonomic complexity due to difficulties in their morphological differentiation; many of its species need revision. Currently, there are 26 valid species of *Squalus*, which have been divided into three species-groups according to overall morphological similarity, the *S. acanthias*, *S. megalops*, and *S. mitsukurii* groups. Loss of type specimens, propagation of erroneous identifications in the literature, and difficulties in obtaining representative series for comparison are secondary challenges that have impeded a global taxonomic revision of the genus. This problem applies clearly to species from the Southwestern Atlantic Ocean, including species that occur off Brazil. Following a current global tendency, a regional taxonomic revision of *Squalus* was conducted in order to investigate which species are valid in the Southwestern Atlantic Ocean and provide diagnostic morphological characters that can be efficiently used for identifying species. Comparative detailed analysis of external (e.g. morphometrics, dentition, and color pattern) and skeletal morphology (primarily meristic data, neurocrania and claspers) of specimens of *Squalus* from the region revealed four new species that are herein described (*S. albicaudus* **sp. nov.**, *S. bahiensis* **sp. nov.**, *S. lobularis* **sp. nov.**, and *S. quasimodo* **sp. nov.**), as well as *S. acanthias*, which is redescribed from the region based on new material. Comparisons are offered based on examinations of congeneric species; this work is part of a global systematic revision of *Squalus*.

Key words: dogfishes, new species, systematics, anatomy, Brazil

Introduction

Species of the genus *Squalus* Linnaeus, 1758 have a complex taxonomic history. The correct identity of certain supposedly widespread species remains doubtful, a problem reinforced by the overlap of morphological characters among species in many geographical regions (Last *et al*., 2007). Thorough descriptive and regional taxonomic studies on species of *Squalus* have been conducted in the past half-century or so (e.g. Bigelow & Schroeder, 1948; Garrick, 1960; Bass *et al*., 1976; Last *et al*., 2007), which has placed the majority of the available nominal species of *Squalus* in synonymy and described new species based on greater sampling (in the case of Last *et al*., 2007). Morphological characters for separating species of *Squalus* are often limited to color, morphometric data and vertebral counts (e.g. Compagno *et al*., 2005; Last & Stevens, 2009), with very few skeletal components (e.g. neurocranium, clasper) employed as diagnostic features (e.g. Muñoz-Chápuli & Ramos, 1989; Marouani *et al*., 2012).

Squalus and a second squalid genus, *Cirrhigaleus* Tanaka, 1912, share many characteristics such as two dorsal fins each preceded by a spine, dorsal spines without lateral grooves, a caudal peduncle with distinct lateral keels, absence of subterminal notch on the caudal fin, and teeth similar in both jaws with only a single oblique cusp (Bigelow & Schroeder, 1957; Shirai, 1992). *Squalus* may be distinguished from the three species of *Cirrhigaleus* by having a short anterior nasal flap not elongated as barbels, and a distinct upper precaudal pit (Bass *et al*., 1976). Species of *Squalus* are distributed on continental shelves, insular slopes and submarine rifts of the Atlantic (including the Mediterranean Sea), Pacific and Indian Oceans. They also occur in boreal and cold temperate waters

close to the coast, as well as demersally in tropical waters far from the coast (Compagno, 1984; Compagno *et al*., 2005).

Currently, there are 26 valid species of *Squalus* (Last *et al*., 2007; Ebert *et al*., 2013): *Squalus acanthias* Linnaeus, 1758 (type-species); *S. acutipinnis* Regan, 1908; *S. albifrons* Last, White & Stevens, 2007; *S. altipinnis* Last, White & Stevens, 2007; *S. blainvillei* (Risso, 1826); *S. brevirostris* Tanaka, 1912; *S. bucephalus* Last, Séret & Pogonoski, 2007; *S. chloroculus* Last, White & Motomura, 2007; *S. crassispinus* Last, Edmunds & Yearsley, 2007; *S. cubensis* Howell-Rivero, 1936b; *S. edmundsi* White, Last & Stevens, 2007; *S. formosus* White & Iglésias, 2011; *S. grahami* White, Last & Stevens, 2007; *S. griffini* Phillipps, 1931; *S. hemipinnis* White, Last & Yearsley, 2007; *S. japonicus* Ishikawa, 1908; *S. lalannei* Baranes, 2013; *S. megalops* (Macleay, 1881); *S. melanurus* Fourmanoir & Rivaton, 1979; *S. mitsukurii* Jordan & Snyder *in* Jordan & Fowler (1903); *S. montalbani* Whitley, 1931; *S. nasutus* Last, Marshall & White, 2007; *S. notocaudatus* Last, White & Stevens, 2007; *S. rancureli* Fourmanoir & Rivaton, 1979; *S. raoulensis* Duffy & Last, 2007; and *S. suckleyi* (Girard, 1854).

Three groups of species are recognized in *Squalus*, which may or may not represent monophyletic groups, and the nomenclature for which is somewhat ambiguous in the literature. Bigelow & Schroeder (1948) were pioneers in defining them according to relative position of the pectoral fins, coloration and shape of the anterior nasal flap based on material from the Western Atlantic Ocean: *acanthias* group, *blainville*[sic]-*fernandinus* group, and the *brevirostris-cubensis* group. These authors later renamed these groups based on the oldest described representative for each: *S. acanthias*, *S. fernandinus*, and *S. megalops* groups (Bigelow & Schroeder, 1957). Garrick (1960) suggested a new nomenclature supported by the same characters previously proposed but with some modifications, recognizing *S. fernandinus* Molina, 1782 as a junior synonym of *S. acanthias*: *S. acanthias*, *S. blainville* [sic], and the *S. megalops/S. cubensis* groups. Cadenat & Blache (1981) also recognized three groups of species represented in an identification key: the *acanthias*, *blainvillei*, and *megalops* groups. Compagno *et al*. (2005) and subsequent authors (e.g. Ward *et al*., 2007; Ebert *et al*., 2010) recognized them as the *S. acanthias*, *S. mitsukurii*, and *S. megalops* groups. Each group of species of *Squalus* is characterized as follows:

***Squalus acanthias* group**: first dorsal spine located close or posterior to the inner margin of the pectoral fins; unilobed anterior nasal flap; origin of the pelvic fins at about midway in the distance between the two dorsal-fin origins; pectoral fins with rounded free rear tips and moderately concave posterior margin; unicuspid dermal denticles; presence of white spots dorsolaterally on trunk, which is more conspicuous in juveniles than in adults. It presently contains two species: *S. acanthias* and *S. suckleyi*.

***Squalus mitsukurii* group**: first dorsal-fin spine located anterior to the inner margin of the pectoral fins; bilobed anterior nasal flap; origin of the pelvic fins closer to the first dorsal-fin origin than to the second dorsal-fin origin; pectoral fins with rounded free rear tips and slightly straight posterior margin; tricuspid dermal denticles; prenarial length greater than inner nostril-labial furrow space; higher vertebral counts; presence of black caudal bar on posterior margin of caudal fin. *Squalus mitsukurii*, *S. blainvillei*, *S. japonicus*, *S. griffini*, *S. montalbani*, *S. melanurus*, *S. rancureli*, *S. chloroculus*, *S. edmundsi*, *S. grahami*, and *S. nasutus*, are included in this group.

***Squalus megalops* group**: very similar to the previous group in relation to the position of the first dorsal spine and pectoral fins, as well as in the shape of the anterior nasal flap. However, it may be distinguished by: short snout; prenarial length smaller than inner nostril-labial furrow space; pectoral fins with pointed free rear tips and strongly concave posterior margin; unicuspid dermal denticles. It includes seven species: *S. cubensis*, *S. acutipinnis*, *S. brevirostris*, *S. crassispinus*, *S. raoulensis*, *S. bucephalus*, and *S. megalops*, with the latter considered a species complex (e.g. Last *et al*., 2007). A new subgroup within this group was proposed by Last *et al*. (2007), the 'highfin *megalops*' subgroup, in which species are characterized by upright dorsal fins with greater height and strong dorsal spines, including *S. notocaudatus*, *S. altipinnis*, *S. formosus* and *S. albifrons*.

Taxonomic revisions of regional representatives of *Squalus* have been undertaken to elucidate the correct application of nominal species (e.g. Bigelow & Schroeder, 1948; Garrick, 1960; Ledoux, 1970; Bass *et al*., 1976; Chen *et al*., 1979; Kondyurin & Myagkov, 1984; Cervigón & Alcal, 1999; Compagno, 2002; Last & Stevens, 2009; Viana & Carvalho, in press), which are still unclear in a variety of regions, including the Southwestern Atlantic Ocean. Recent global accounts on the genus have usually recognized three valid species for the Southwestern Atlantic Ocean: *Squalus acanthias*, *S. mitsukurii*, and *S. cubensis* (Compagno *et al*., 2005; Ebert *et al*., 2013). *Squalus acanthias* is the species that is most correctly identified throughout this region, and identification of *Squalus* species is presently more reliable at the level of species-group due to difficulties in separating them morphologically. The lack of taxonomic revisions of the genus in this region is apparent as most descriptive

information comes from studies of adjacent areas. Few studies have been attempted, for example Menni *et al*. (1984) and Meneses & Paesch (2003) for Argentina and Uruguay, which recognized five species: *S. acanthias*, *S. blainvillei*, *S. cubensis*, *S. megalops*, and *S. mitsukurii*.

In Brazil, studies on the genus are limited to general occurrences and superficial aspects of its biology (e.g. Lessa *et al*., 1999; Haddad & Gadig, 2005; Hazin *et al*., 2006), in part due to difficulties in identification and to limited access to significant numbers of specimens of each species. Studies with a greater taxonomic relevance from the Southwestern Atlantic Ocean are Schreiner & Miranda Ribeiro (1903) and Miranda Ribeiro (1907, 1923). Figueiredo (1977) recognized *S. cubensis* as the only species occurring in waters off southeastern Brazil, and was followed by Sadowsky & Moreira (1981). Lucena & Lucena (1981) recognized three species for southern Brazil, while Figueiredo (1981) recognized no more than three groups of species. Marques (1994, 1999) morphologically characterized Brazilian specimens of the *megalops* group, and Gomes *et al*. (1997) indicated the presence of three groups of species with three separate species: *S. acanthias*, *Squalus* sp. of the *mitsukurii* group, and *Squalus* sp. of the *megalops* group. Gadig (2001) and Rosa & Gadig (2014) reported *S. acanthias*, *S. blainvillei*, *S. megalops*, *S. mitsukurii*, and *S. cubensis* in the Southwest Atlantic Ocean, although these studies merely listed species with no further data regarding their taxonomy. Soto (2001) listed *S. acanthias* for Southern Brazil, and *S. cubensis*, *Squalus* sp. A and *Squalus* sp. B as occurring from the northeast to the south of Brazil. The latter two species were referred to as *Squalus* sp. 1 and *Squalus* sp. 2 by Gadig & Gomes (2003), a clear indication of the difficulty in identifying species from Brazil. Nunan & Senna (2007) also reported the occurrence of *S. cubensis* from Salvador, Bahia to Rio de Janeiro.

With this lack of resolution in mind, the present study was undertaken to revise the taxonomy and provide a detailed comparative analysis of the external morphology and skeletal anatomy of the species of *Squalus* from the Southwestern Atlantic Ocean (herein after SWAO), including morphometric and meristic data, in order to better morphologically characterize and recognize valid species from this region.

Material and methods

Morphological data were obtained from specimens usually preserved in 70% ethanol. Nomenclature for external morphology, including color pattern, follows Last *et al*. (2007). The description of coloration is based on preserved specimens. Description of dermal denticles taken from below the first dorsal fin is according to Deynat & Séret (1996). Terminology for skeletal components such as neurocranium, pelvic fin and girdle follows Compagno (1988) and Shirai (1992), and Marinelli & Strenger (1959) for pectoral fin and girdle. Clasper terminology is from Jungersen (1899). Radiographs (digital and printed film) were obtained for meristic data, such as vertebral counts and tooth row counts. Vertebral counts are according to Springer & Garrick (1964). Tooth row counts and nomenclature for dentition follow Cappetta (1987, 2012) and Herman *et al*. (1989).

Analysis of dermal denticles was based on skin samples measuring 1 cm^2, taken from below the first dorsal fin (right side) and analyzed through a stereoscopic microscope or Scanning Electron Microscope (SEM) at the Instituto de Biociências, Universidade de São Paulo (IBUSP). Teeth samples from upper and lower jaws (three lateral teeth toward the first series) were taken and investigated using a stereoscopic microscope.

Measurements are expressed as percentages of total length (% TL). External measurements were taken using digital callipers with a 0.1 millimeter (mm) precision and/or a metric tape (for measurements greater than 150 mm). A total of 62 external measurements were obtained according to Last *et al*. (2007), and are listed in Appendix 1. Measurements of neurocrania were also taken (Fig. 1), modified from Muñoz-Chápuli & Ramos (1989) and Compagno (1988), and are expressed as percentages of neurocranial total length (% CL). These measurements are defined in Appendix 2.

All specimens were photographed digitally in dorsal, lateral and ventral views, as well as specific body parts (e.g. fins) and disarticulated skeletal structures. Photographs of teeth and dermal denticles of the specimens were taken using a high-resolution digital camera attached to stereoscope microscope Leica DFC295. QGIS 2.4 Chugiak (QGIS Development Team, QGIS Geographic Information System, Open Source Geospatial Foundation Project; http://qgis.osgeo.org) and Google Earth were used to produce the distribution maps.

Synonyms for species include authorship, date, pages and figures when possible. Single values in the descriptions are for holotype, while ranges represent values for paratypes from which data were taken (except when

otherwise mentioned). References included in species synonymies are usually restricted to occurrences in the Western Atlantic and original descriptions of nominal species.

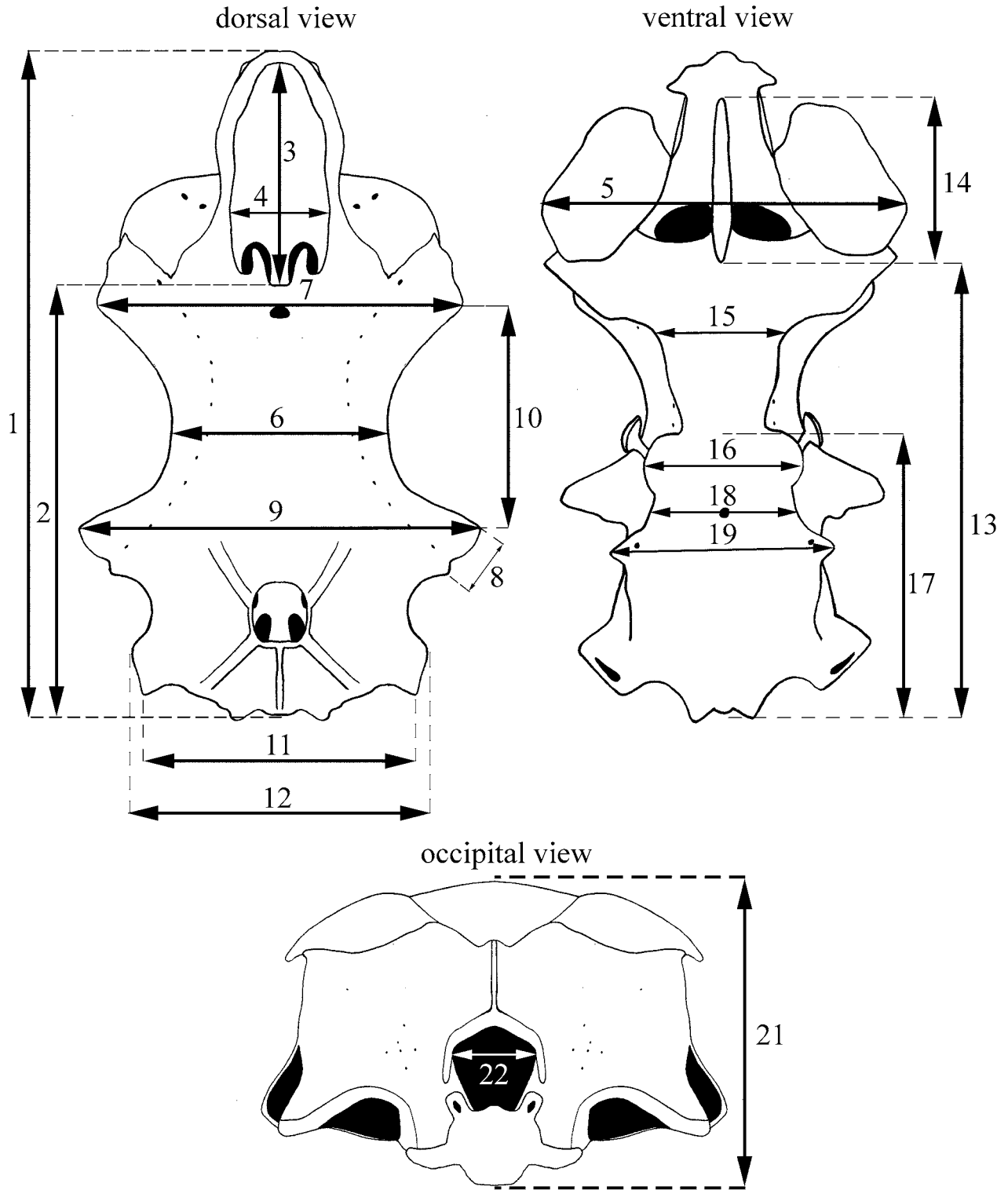

FIGURE 1. Cranial measurements for species of *Squalus*, modified from Muñoz-Chápuli & Ramos (1986) and Compagno (1988).

Institutional abbreviations. American Museum of Natural History, New York (AMNH); Australian Museum, Sydney (AMS); California Academy of Sciences, San Francisco (CAS); Florida Museum of Natural History, Florida (FLMNH); Fundação Universidade do Rio Grande, Rio Grande (UFRGS); Hokkaido University, Museum

of Zoology, Hakodate (HUMZ); Hospital Universitário Pedro Ernesto (HUPE); Laboratório de Ictiologia da Universidade Estadual de Feira de Santana, Feira de Santana (LIUEFS); Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCP); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro (MNRJ); Museu de Zoologia da Universidade Federal da Bahia, Salvador (MZUFBA); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP); Natural History Museum, London (NHM); Núcleo de Pesquisa e Estudos em Chondrichthyes, Santos (NUPEC); Projeto Tamar, Praia do Forte, Bahia (TAMAR); Universidade do Estado do Rio de Janeiro, Rio de Janeiro (UERJ); Universidade Federal da Paraíba, João Pessoa (UFPB); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); National Museum of Nature and Science, Tokyo (NSMT); Naturhistorisches Museum, Wien (NMW); Zoological Museum Hamburg, Hamburg (ZMH); Museum für Naturkunde, Berlin (ZMB).

Anatomical and regional abbreviations. **abv**: anterior pelvic basal; **ap**: apopyle; **ax**: axial cartilage; **ba**: basal angle; **bp**: basal plate; **bpt**, basipterygium; **btp**: basitrabecular process; **b1**: intermediate segment; **cg**: clasper groove; **co**: coracoid bar; **cp1**: first cartilaginous process; **cr**: cranial roof; **csa**: anterior semicircular canal; **csl**: lateral semicircular canal; **csp**: posterior semicircular canal; **dpf**: m. *depressor pectoralis* facet; **ec**: ethmoidal canal of ophthalmicus superficialis nerve; **eec**: ectethmoid chamber; **elf**: endolymphatic foramen; **ep**: epiphysial pit; **es**: eye-stalk; **fca**: foramen for carotid artery; **fd**: diazonal foramen; **feld**: endolymphatic fossa; **foa**: foramen for orbital artery; **fopp**: profundus canal for the ophthalmicus profundus nerve; **fops**: series of foramina for superficial ophthalmic branch of trigeminal nerve; **fvn**: foramen for ventral fin nerves; **gb**: glossopharyngeal base; **hmf**: hyomandibular facet; **hmVII**: foramen for hyomandibularis facialis; **hp**: hypopyle; **lag**: lateral auditory groove; **lpp**: lateral prepelvic process; **lra**: lateral rostral appendage; **ms**: mesopterygium; **mt**: metapterygium; **mtx**: metapterygial axis; **NEAO**: Northeastern Atlantic Ocean; **NEPO**: Northeastern Pacific Ocean; **ns**: nasal capsule; **NWAO**: Northwestern Atlantic Ocean; **oc**: otic capsule; **occ**: occipital condyle; **opp**: opisthotic process; **otc**: otic crest; **pcf**: precerebral fossa; **pecet:** ectethmoid process; **plf**: perilymphatic foramen; **poc**: preorbital canal of superficial ophthalmic nerve; **pop**: postorbital process; **potp**: prootic process; **pow**: preorbital wall; **ppe**: preorbital process; **psb**: efferent pseudobranchial artery foramen; **pub**: puboischiadic bar; **p1**: pectoral fin; **p2**: pelvic fin; **r**: rostrum; **mra**: median rostral appendage; **mrp**: median rostral prominence; **pr**: propterygium; **rd**: dorsal marginal cartilage; **rh**: rhipidion; **rk**: rostral keel; **rl**: radials; **rv**: ventral marginal cartilage; **sc**: scapula; **sec**: subethmoid chamber; **sep**: supraethmoidal process; **SEPO**: Southeastern Pacific Ocean; **ser**: subethmoidean ridge; **snf**: subnasal fenestra; **soc**: supraorbital crest; **sphr**: sphenopterotic ridge; **SWAO**: Southwestern Atlantic Ocean; **td**: dorsal terminal cartilage (claw); **td2**: dorsal terminal 2 cartilage; **tv**: ventral terminal cartilage; **t3**: accessory terminal cartilage (spur); **II**: optic foramen; **III**: oculomotor foramen; **IV**: trochlear foramen; **V, VII**: foramen prooticum; **VI**: abducens foramen; **IX**: foramen for glossopharyngeal nerve; : **β** beta cartilage; *****: segmented processes of coracoid bar.

Family Squalidae Blainville, 1816

Genus *Squalus* Linnaeus, 1758

Squalus Artedi, 1738: 504 (description); Linnaeus, 1758: 233 (original description; "Oceano Europaeo"); Molina, 1782: 188, 189 (listed; Chile); Rafinesque, 1810: 45 (listed; Sicily); Girard, 1855 (listed; Chile); Gill, 1862: 367–405 (in classification); Poey, 1868: 211, 213, 454 (listed; Cuba); Berg, 1895: 5, 6 (listed; Argentina and Uruguay); Jordan & Evermann, 1898: 53, fig. 24 (listed; North and Central America); Schreiner & Ribeiro, 1903: 79 (listed; Brazil); Jordan, 1907: 202 (cited); Miranda Ribeiro, 1907: 167, 168 (listed; Brazil); Regan, 1908: 39, 45, 48 (identification key, listed; global); Garman, 1913: 191 (description; global); Miranda Ribeiro, 1923 (listed; Brazil); Howell-Rivero, 1936: 45 (revision; Cuba); Fowler, 1936: 69–71 (description; Western Africa); Fowler, 1941: 129 (listed; Brazil); Bigelow & Schroeder, 1948: 451–480, figs 87–90 (revision; Northwestern Atlantic); Bigelow, Schroeder & Springer, 1953: 220–222 (cited; Western Atlantic); Bigelow & Schroeder, 1957: 26–37, figs 3, 4 (description); Ledoux, 1970, 65–69 (revision; Mediterranean Sea); Bass *et al*., 1976 (revision; Eastern South Africa); Figueiredo, 1977: 8 (listed; Southeastern Brazil); Cadenat & Blache, 1981: 46–52; figs 28–31 (revision; Mediterranean Sea, North Atlantic Ocean); Figueiredo, 1981: 17 (listed; Brazil); Lucena & Lucena, 1981: 2–4 (listed; Brazil); Compagno, 1984: 109–123 (revision; global); Kondyurin & Myagkov, 1984: 118–120, (revision; Western Atlantic); Menni *et al*., 1984: 62, 83, 84 (listed; Argentina and Uruguay); Myagkov & Kondyurin, 1986: 1–20 (revision; Atlantic); Muñoz-Chápuli & Ramos, 1989 (revision; Eastern Atlantic);

Gadig & Moreira, 1992: 112, 118 (cited; Brazil); Calderón, 1994 (cited; Brazil); Marques, 1994 (description; Brazil); Gomes *et al*., 1997: 93–98 (listed, description; Brazil); Cervigón & Alcal, 1999: 122 (revision; Venezuela); Compagno & Niem, 1999: 1229–1232 (revision; Western-Central Pacific); Lessa *et al*., 1999 (cited, listed; Brazil); Marques, 1999 (description; Brazil); Mazzoleni & Schwingel, 1999: 114 (listed; South Brazil); Gadig *et al*., 2000: 129 (cited; Cear, Brazil); Gadig, 2001: 54–59 (revision; Brazil); Soto, 2001: 94–96 (listed; Brazil); Compagno, 2002: 380–385 (revision; Western Central Atlantic); Nion *et al*., 2002: 4, 65 (listed; Uruguay); Haimovici *et al*., 2003 (cited; Brazil); Meneses & Paesch, 2003: 7, 8, 25 (listed; Uruguay, Argentina); Heemstra & Heemstra, 2004 (cited, Southern Africa): 49, 53–54; Soto & Mincarone, 2004: 73–82 (listed; Brazil); Compagno *et al*., 2005: 72 (description; global); Haddad & Gadig, 2005 (cited; Brazil); Lamilla & Bustamante, 2005: 9, 26 (cited; Chile); Hazin *et al*., 2006 (cited; Northeastern Brazil); Jablonski *et al*., 2006 (cited; Brazil); Nelson, 2006: 66 (listed; global); Last *et al*., 2007 (revision; Australia); Louro & Rossi-Wongtschowski, 2007 (cited; Brazil); Menni & Lucifora, 2007: 2, 3 (listed; Argentina, Uruguay); Pon & Gandini, 2007 (cited; Argentina); Carrier *et al*., 2010: 44, 127, 139 (cited); Gomes *et al*., 2010: 44, 45 (cited; Brazil); Menni *et al*., 2010 (cited; Southwestern Atlantic); Saéz *et al*., 2010: 623, 624 (identification key; Chile); Tomás *et al*., 2010 (cited; Brazil); Viana, 2011: 1–373 (description; Southwestern Atlantic); Eschmeyer & Fricke, 2015 (listed; global); Bornatowski & Abilhoa, 2012: 35 (cited; Brazil); Rosa & Gadig, 2014: 92, 97 (listed, cited; Brazil).

Acanthorhinus Blainville, 1816: 121 (original description, not illustrated); Fowler, 1936: 61 (cited); Bigelow & Schroeder, 1948: 452 (cited).

Spinax: Cuvier, 1817: 130 (cited); Cuvier, 1863: 320 (listed).

Acanthias Risso, 1826: 131 (original description, not illustrated; Mediterranean Sea); Müller & Henle, 1841: 83 (listed); Gill, 1861: 60 (listed; North and Central America; used *Squalus* for *Carcharhinus* in this work); Duméril, 1865: 435, 436 (description); Günther, 1866: 384, 396 (listed; Central America); Vaillant, 1888: 7 (cited; Argentina).

Type species: *Squalus acanthias* Linnaeus, 1758 by subsequent designation of Gill (1862: 405).

Diagnosis. *Squalus* is characterized by the following combination of characters: slender and fusiform body, arched dorsally at anterior region; lateral keels restricted to caudal peduncle; short snout, rounded or obtuse at the tip; anterior nasal flaps lobe-like, however without forming nasal barbels; presence of slender dorsal spines without lateral grooves prior to each dorsal fin, extending or not to the apex of corresponding fin; second dorsal fin considerably smaller and more raked than first dorsal fin; caudal peduncle with conspicuous upper and lower precaudal pits; asymmetric caudal fin without subterminal notch; dorsal caudal lobe considerably greater in length than ventral caudal lobe; teeth unicuspid, small, similar in both jaws with short, slightly oblique cusps; dermal denticles unicuspid or tricuspid.

Squalus is distinguished from *Cirrhigaleus* in having anterior nasal flaps with short secondary lobe without forming nasal barbels (*vs*. secondary lobe very elongated and forming nasal barbels extending to anterior margin of mouth), second dorsal fin smaller and lower than first dorsal fin (*vs*. dorsal fins of similar length and height with second dorsal fin as high and large as first dorsal fin), second dorsal-fin spine larger in length than first dorsal-fin spine (*vs*. second dorsal-fin spine equal in length to first dorsal-fin spine), and conspicuous upper and lower precaudal pits (*vs*. absence of lower precaudal pit). It is further differentiated from *Cirrhigaleus* by having narrow dermal denticles (*vs*. denticles conspicuously broad), and body fusiform and somewhat arched dorsally throughout all of its length (*vs*. body robust and markedly humped dorsally).

***Squalus acanthias* Linnaeus, 1758**

(Figs. 2–15, Tables 1–4)

Spotted spiny dogfish; Piked dogfish; Cação-bagre-espinhoso (Portuguese)

Squalus acanthias Linnaeus, 1758: 233 (original description, “Oceano Europaeo”); Rafinesque, 1810: 45 (listed; Sicily); Gill, 1862: 405 (cited; global); Poey, 1868: 213, 454 (cited; Cuba); Berg, 1895: 5, 6 (listed; Argentina, Uruguay); Jordan & Evermann, 1896: 54 (listed; North and Central America); Schreiner & Ribeiro, 1903: 79 (listed; Brazil); Regan, 1908: 45, 46 (identification key, listed; global); Garman, 1913: 192, plates 14 (figs. 1–4), 43 (figs. 9, 10), 59 (figs. 1, 2) (description; global); Fowler, 1936: 69–71, figs. 19, 20 (revision; Eastern Atlantic); Bigelow & Schroeder, 1948: 455–473, figs. 87 (A–D), 88 (revision; Northwestern Atlantic); Bigelow & Schroeder, 1953: 47–51, fig. 17 (description, cited; Western North Atlantic); Bigelow, Schroeder & Springer, 1953: 221 (cited; Western Atlantic); Bigelow & Schroeder, 1957: 30, fig. 3D (description; global); Garrick, 1960: 520, figs. 1 (A–C), 3 (G–M), 5 (revision; New Zealand); Bass *et al*., 1976: 13, 14, figs. 8 (F–G), 9 (revision; Eastern South Africa); Cadenat & Blache, 1981: 46–48; fig. 28 (A–E) (revision; Mediterranean Sea); Lucena & Lucena, 1981: 2, fig. 3 (listed; Brazil); Compagno, 1984: 109-113 (revision; global); Kondyurin &

Myagkov, 1984: 118–120, fig. 1A (revision; Western Atlantic); Menni *et al*., 1984: 62, 83, 84 (listed; Argentina, Uruguay); Myagkov & Kondyurin, 1986: 1–20, fig. 1 (A, E, F, H) (revision; Atlantic); López *et al*., 1996: 7, 8 (listed; Argentina); Cousseau & Perrotta, 1998: 34–35 (description; Argentina); Lessa *et al*., 1999: 26, 61, 150 (cited, listed; Brazil); Mazzoleni & Schwingel, 1999: 114 (listed; Itajaí, Brazil); Gadig, 2001: 29, 36, 54–57, fig. 27 (description; Brazil); Soto, 2001: 94, 95 (listed; Brazil); Compagno, 2002: 380, 381, 383 (revision; South Atlantic); Nion *et al*., 2002: 4 (listed; Uruguay); Haimovici *et al*., 2003: 38, 39 (cited; Brazil); Meneses & Paesch, 2003: 7, 25, 45 (cited; Argentina); Smith & Heemstra, 2003: 61, 62, fig. 5.24 (identification key; description; South Africa); Heemstra & Heemstra, 2004 (cited, Southern Africa): 54; Soto & Mincarone, 2004: 73, 74 (listed; Brazil); Lamilla & Bustamante, 2005: 9, 26 (cited; Chile); Nelson, 2006: 66 (listed; global); Menni & Lucifora, 2007: 3 (cited; Argentina, Uruguay); Pon & Gandini, 2007 (cited; Argentina); Carrier *et al*., 2010: 44, 127, 139 (cited); Gomes *et al*., 2010: 44, 45 (cited; Brazil); Menni *et al*., 2010 (cited; Southwestern Atlantic); Saéz *et al*., 2010: 623 (identification key; Chile); Viana, 2011: 28–56 (description; Southwestern Atlantic); Menezes, 2011: 4 (listed; Southern Brazil); Rosa & Gadig, 2014: 92 (listed; Brazil).

Squalus fernandinus Molina, 1782: 188, 189, 285 (original description, not illustrated; Chile); Regan, 1908: 45, 46 (cited; Chile); Bigelow, Schroeder & Springer, 1953: 220–222 (cited; Western Atlantic).

Acanthorhinus acanthias: Bigelow & Schroeder, 1948: 452 (in synonymy of *S. acanthias*).

Spinax acanthias: Cuvier, 1817: 130 (cited); Cuvier, 1863: 320 (listed); Bigelow & Schroeder, 1948: 452 (in synonymy of *S. acanthias*).

Acanthias vulgaris Risso, 1826: 13 (original description, not illustrated; Mediterranean, Sea); Müller & Henle, 1841: 83 (description); Duméril, 1865: 437 (description); Günther, 1866: 384, 396 (listed; Central America); Macleay, 1881: 366 (description; Australia); Vaillant, 1888: 5 (listed; Argentina).

Acanthias americanus Storer, 1846: 506 (original description; United States of America); Gill, 1861: 60 (listed; North America).

Spinax acantheus: Cuvier, 1863: 320 (cited).

Acanthias lebruni Vaillant, 1888: 5, 13, 14, plate 1, fig. 2 (original description; Chile).

Squalus lebruni: Berg, 1895: 6 (description; Argentina, Uruguay); Menni *et al*., 1984: 62, 84 (listed; Argentina, Uruguay).

Squalus blainvillei: Schreiner & Ribeiro, 1903: 79 (listed; Brazil); Miranda Ribeiro, 1907 (in part): 168 (description; Brazil).

Squalus barbouri Howell-Rivero, 1936: 47, 48 (original description, not illustrated; Cuba).

Squalus tasmaniensis Howell-Rivero, 1936 (original description, not illustrated; Tasmania); Last *et al.*, 2007: 109–113, figs. 1B, 2B (revision; Tasmania).

Flakeus tasmaniensis: Whitley, 1940: 139, fig. 150 (listed; Australia).

Koinga whitleyi: Whitley, 1940: 139, figs. 151, 152 (listed; Australia).

Koinga kirki: Whitley, 1940: 140, fig. 153 (listed; Australia).

Squalus kirki Phillipps, 1931 (original description, not illustrated; New Zealand).

Squalus sp. of *acanthias* group: Figueiredo, 1981: 17 (listed; Brazil); Gomes *et al*., 1997: 93 (description; Brazil); Marques, 1999 (cited; Brazil).

Syntype. NRM 85, juvenile female, 177 mm TL, unknown locality. Donation by King Gustav IV Adolf of Sweden. Other possible syntypes in Uppsala (refuted by Wheeler, 1991): UUZM 159, juvenile male, 346 mm TL; UUZM 160, neonate female, 380 mm TL. Type locality: “Oceano Europaeo”. Possibly from off Sweden, Finland or Norway.

Material examined (59 SWAO specimens). AMNH 4099, neonate male, 230 mm TL, between the mouth of the rivers Coyle and Gallegos, Santa Cruz, Argentina; BMNH 1936.8.26.17, adult male, 635 mm TL, near Strait of Magellan, Argentina, Southwestern Atlantic Ocean, 52.18°S, 68°W; BMNH 1999.5.4.4, juvenile male, 550 mm TL, Falkland Islands, Southwest Atlantic Ocean; BMNH 1999.5.4.13, juvenile female, 448 mm TL, Falkland Islands; BMNH 1999.5.4.15, adult female, 535 mm TL, Falkland Islands; BMNH 1999.5.4.16, juvenile male, 496 mm TL, Falkland Islands; HUMZ 30173, adult male, unknown TL, off Patagonia, Argentina, 47°S, 6516’W (dissected); HUMZ 30178, adult male, 693 mm TL, off Patagonia, Argentina, 47°S, 6516’W; HUMZ 30200, adult male, 655 mm TL, off Patagonia, Argentina, 47°S, 6516’W; HUMZ 30285, adult male, 720 mm TL, off Patagonia, 47°S, 6516’W; HUMZ 30291, adult male, 595 mm TL, off Patagonia, Argentina, 47°S, 6516’W; HUMZ 30303, juvenile female, 487 mm TL, off Patagonia, 47°S, 6516’W; HUMZ 30310, juvenile female, 520 mm TL, off Patagonia, Argentina, 47°S, 6516’W; HUMZ 30324, adult male, 760 mm TL, off Patagonia, 47°S, 6516’W; HUMZ 107285, juvenile female, 340 mm TL, off Argentina, 4659.5’S, 6516’W (dissected); MCT 7439, adult female, 587 mm TL, Tramandaí, Rio Grande do Sul, Brazil; MCZ 1435-S, neonate male, 175 mm TL; neonate male, 205 mm TL, Suriname; MNRJ 509, juvenile male, 403 mm TL, Rasa Island, Rio de Janeiro, Brazil; MNRJ 513, juvenile female, 440 mm TL, Rasa Island, Rio de Janeiro, Brazil; NMW 83924, neonate male, 215 mm TL, unspecified locality, Brazil; ZMH 104416, adult male, 725 mm TL; adult female, 755 mm TL, near Peninsula del Valdes, Argentina, 5948'W, 438'S; ZMH 104461, two juvenile females, 510, 557 mm TL; one adult female, 742 mm TL, near Peninsula del Valdes, Argentina, 608'W, 433'S; ZMH 104519, two adult females, 670, 745 mm TL,

near Cabo Blanco, Argentina, 6112'W, 478'S; ZMH 104951, adult male, 715 mm TL, near Santa Cruz, Argentina, 6340'W, 490'S; ZMH 104955, seven neonates males, 187–192 mm TL; five neonate females, 185–200 mm TL, near Santa Cruz, Argentina, 6546'W, 4750'S; ZMH 104968, six juvenile male, 226–233 mm TL; four juvenile female, 225–235 mm TL, near Cabo Blanco, Argentina, 6518'W, 470'S; ZMH 107911, four juvenile males, 213–225 mm TL; six juvenile females, 215–223 mm TL, near Santa Cruz, Argentina, 640'W, 460'S; ZMH 108038, adult male, 670 mm TL, near Cabo Blanco, Argentina, 650'W, 470'S; ZMH 115469, juvenile male, 322 mm TL, near Santa Cruz, Argentina, 6324'W, 4551'S.

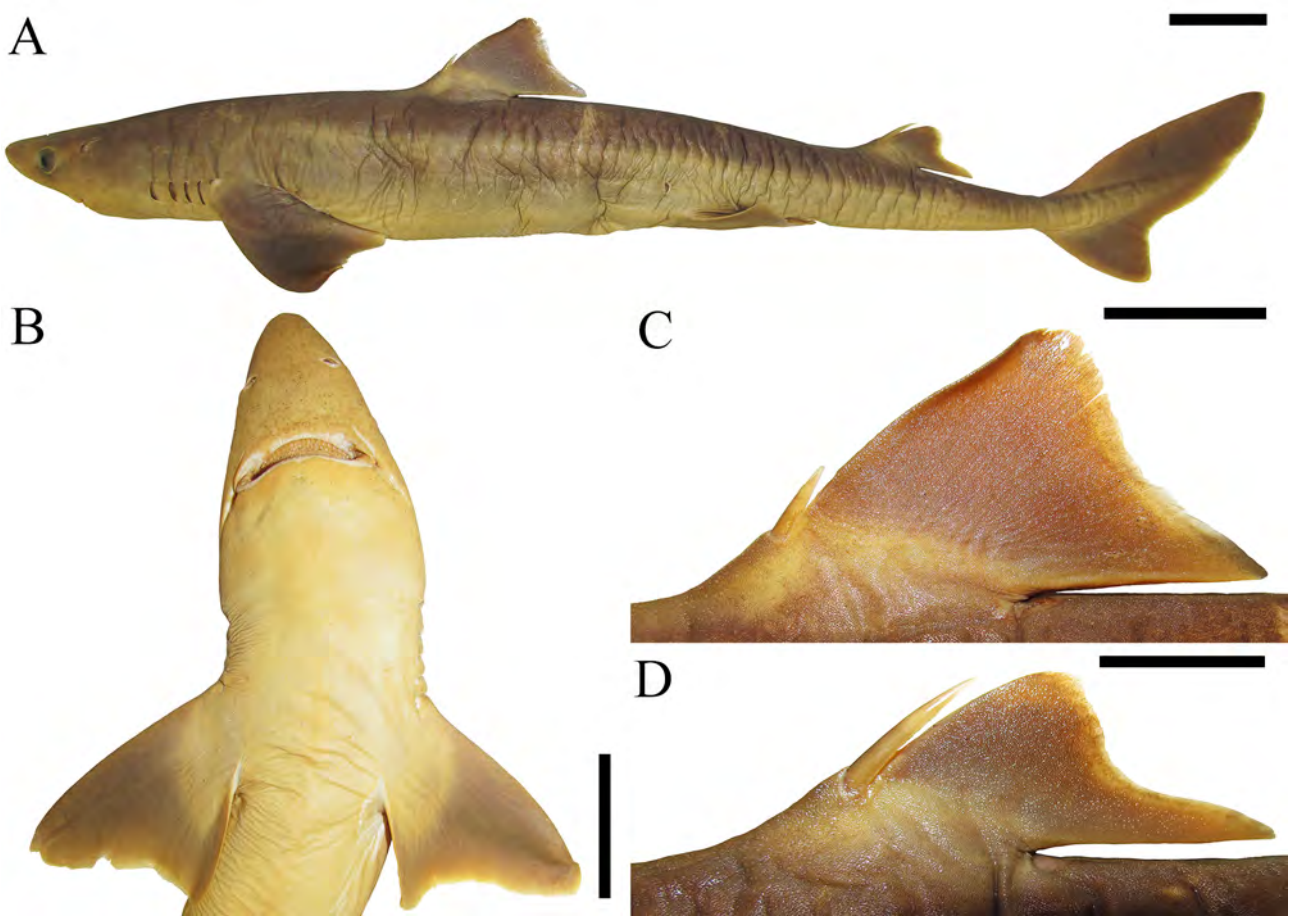

FIGURE 2. *Squalus acanthias* from the Southwestern Atlantic Ocean, ZMH 108038, adult male, 670 mm TL in (A) lateral and (B) ventral views (scale bar: 50 mm); (C) detail of first and (D) second dorsal fins (scale bar: 20 mm).

Diagnosis. *Squalus acanthias* from the Southwestern Atlantic Ocean is distinguished from all local congeners by the following unique characters: rounded white spots dorsolaterally on body; anterior margin of nostrils unilobate; origin of first dorsal-fin spine behind the free rear tips of the pectoral fins; first dorsal-fin spine length much lower than fin height (first dorsal-fin spine length 1.5%–2.8% TL *vs*. first dorsal-fin height 6.0%–8.1% TL); second dorsal-fin spine very elongated (1.9%–4.5% TL), taller than second dorsal-fin apex; interdorsal distance 1.8 (1.5–2.2) times greater than dorsal-caudal distance; pectoral-pelvic distance 1.0 (0.6–1.3) times pelvic-caudal distance; dermal denticles unicuspid; coracoid bar with segmented processes anterolaterally.

Description. **External morphology**. Measurements and counts are summarized in Tables 1–2 (in the description of *S. acanthias* below, single values represent the mean followed by the range for non-type specimens from which data were taken). Body fusiform and slender, slightly more arched anteriorly as of posterior margin of spiracle to level of pectoral fin insertion; head height 0.8–1.1 times trunk height, and 0.8–1.5 times abdomen height. Head flattened, small (its length 18.4%–23.3% TL) and broad, its width 1.2 (1.0–1.5) times trunk width and 1.4 (1.1–2.2) times abdomen width. Snout somewhat elongate (5.8%–8.1% TL), slightly obtuse in ventral view. Nasal apertures located laterally, small and slightly oblique; anterior margin of nostril unilobate or slightly bilobate in young specimens (Fig. 3); distance from snout tip to nostrils 1.0 (0.9–1.2) times distance from nostrils to upper labial furrow; prenarial length corresponding to half of preoral length; internarial distance 0.9 (0.6–1.4) times eye

length. Eyes oval with anterior margin rounded and posterior margin angular, not notched; length 2.0 (1.4–3.5) times eye height; eyes closer to snout tip than to first branchial arch. Prespiracular length 1.7 (1.5–2.0) times preorbital length and 0.6 (0.5–0.6) times pre-pectoral length. Spiracles crescent-shaped, located posterodorsally to eye, oblique in relation to longitudinal axis of body; diameter at least one-quarter eye length. Prebranchial length 1.5 (1.3–1.7) times prespiracular length. Gill slits concave, located in front of pectoral fins, tall with fifth gill slit 1.2 (0.7–1.7) greater in height than first gill slit.

TABLE 1. External measurements expressed as percentages of total length (% TL) of *Squalus acanthias* from the Southwestern Atlantic Ocean, and for holotypes of *Squalus barbouri* (MCZ 1463-S) and *Squalus tasmaniensis* (MCZ 146-S). TL expressed in mm. N: number of specimens; x: mean; SD: standard deviation.

Measurements	Holotypes		*Squalus acanthias*			
	S. barbouri	*S. tasmaniensis*				
	MCZ 1463-S	MCZ 146-S	N	Range	x	SD
TL (mm)	267.0	245.0	21	200.0–880.0	487.7	212.3
PCL	77.2	77.6	21	31.2–81.1	76.3	10.4
PD2	59.2	57.1	21	53.4–62.2	58.8	2.1
PD1	34.5	30.6	21	29.1–33.7	32.4	0.9
SVL	52.4	49.0	21	44.2–52.8	49.7	2.3
PP2	54.3	44.9	21	41.9–50.3	46.8	2.1
PP1	21.8	19.6	21	17.8–22.8	20.4	1.2
HDL	22.4	19.9	21	18.4–23.3	20.9	1.3
PG1	18.5	16.4	21	15.5–20.5	17.4	1.2
PSP	12.6	9.8	21	9.9–14.1	11.3	1.2
POB	7.0	5.4	21	5.8–8.1	6.9	0.6
PRN	5.1	3.3	21	3.8–5.1	4.5	0.4
POR	9.9	7.6	21	7.8–10.9	9.1	1.0
INLF	4.9	3.6	21	3.7–5.6	4.4	0.5
MOW	6.6	5.6	21	6.5–8.1	7.2	0.4
ULA	2.5	2.2	21	2.0–2.9	2.3	0.2
INW	2.8	3.2	21	2.8–4.8	3.4	0.4
INO	7.2	6.2	21	6.5–9.7	7.4	1.0
EYL	3.5	3.1	21	2.7–5.7	3.7	0.9
EYH	0.9	1.6	21	1.4–3.6	1.9	0.5
SPL	1.3	1.8	21	0.9–2.1	1.4	0.4
GS1	1.7	1.0	21	1.3–2.3	1.7	0.3
GS5	1.8	1.6	21	1.2–2.9	2.0	0.3
IDS	18.9	19.9	21	17.1–22.7	20.2	1.7
DCS	10.8	11.9	21	9.6–11.9	11.1	0.6
PPS	24.9	22.2	21	16.5–26.8	22.8	2.5
PCA	22.2	22.4	21	20.3–28.1	22.8	1.9
D1L	12.1	13.2	21	10.5–13.1	12.1	0.7
D1A	11.5	11.2	21	8.5–11.6	9.5	0.8
D1B	7.0	7.9	21	6.4–7.5	7.0	0.3
D1H	7.8	6.9	21	6.0–8.1	6.7	0.4
D1I	5.7	5.8	21	4.4–6.0	5.2	0.4

.....continued on the next page

TABLE 1. (Continued)

Measurements	Holotypes		*Squalus acanthias*			
	S. barbouri	*S. tasmaniensis*				
	MCZ 1463-S	MCZ 146-S	N	Range	x	SD
D1P	5.9	6.2	21	4.9–8.2	6.7	0.9
D1ES	2.7	2.4	21	1.5–2.8	2.1	0.3
D1BS	0.6	0.9	21	0.4–0.9	0.6	0.1
D2L	12.6	13.1	21	11.0–14.3	12.5	0.9
D2A	11.1	10.0	21	8.1–11.3	9.7	0.9
D2B	7.9	7.8	21	5.6–9.8	7.8	1.0
D2H	7.0	5.9	21	4.4–6.1	5.0	0.6
D2I	5.0	5.5	21	4.2–5.4	4.8	0.3
D2P	3.3	5.6	21	3.5–6.2	5.1	0.6
D2ES	4.3	4.4	21	1.9–4.5	3.5	0.6
D2BS	1.0	1.1	21	0.5–1.1	0.7	0.2
P1A	12.3	13.1	21	11.2–16.3	13.8	1.2
P1I	7.3	8.7	21	7.2–11.1	8.1	0.8
P1B	4.3	4.2	21	3.2–5.2	4.3	0.7
P1P	7.7	10.0	21	6.7–11.4	8.8	1.2
P2L	8.0	9.4	21	8.6–12.4	10.3	0.9
P2I	4.6	5.3	21	3.3–6.4	4.9	0.8
CDM	22.7	22.7	21	19.0–22.0	20.5	0.9
CPV	10.3	11.9	21	10.5–12.3	11.2	0.4
CFW	5.4	6.5	21	6.0–7.4	6.7	0.4
HANW	5.9	5.9	21	5.5–7.7	6.4	0.7
HAMW	7.3	8.6	21	8.7–11.9	9.7	0.8
HDW	7.8	8.7	21	8.3–12.6	10.6	0.9
TRW	7.2	6.4	21	6.6–11.2	8.8	1.2
ABW	4.1	3.2	21	4.7–11.1	7.6	1.5
HDH	6.5	6.2	21	6.7–10.0	8.5	0.9
TRH	6.4	6.9	21	6.8–11.1	9.2	1.2
ABH	4.9	4.7	21	5.8–11.6	8.6	1.5
CLO	–	–	21	1.1–5.8	3.5	2.0
CLI	–	–	21	2.2–8.7	5.3	2.6

FIGURE 3. Anterior margin of nostrils of *Squalus acanthias*. (A) HUMZ 30285, adult male, 720 mm TL; (B) HUMZ 104416, adult female, 755 mm TL; (C) BMNH 1999.5.4.13, juvenile female, 448 mm TL.

TABLE 2. Meristic data for *Squalus acanthias* . N: number of specimens.

Character	Southwestern Atlantic			Northwestern Atlantic			Mediterranean Sea			Southeastern Atlantic			Northwestern Pacific			Southeastern Pacific		
	N	Range	Mode	N	Range	Mode	N	Range	Mode	N	Range	Mode	N	Range	Mode	N	Range	Mode
precaudal vertebrae	7	75–81	75	3	80–85	–	3	80–81	80	3	75–78	–	2	71–72	–	2	77–77	77
caudal vertebrae	7	26–30	27	3	29–31	31	3	28–29	28	3	27–30	–	2	27–30	–	2	28–33	–
total vertebrae	7	101–109	101	3	111–116	111	3	108–110	108	3	104–107	–	2	99–101	–	2	105–110	–
monospondylous vertebrae	7	43–47	44	3	46–47	46	3	40–41	40	3	43–45	–	2	40–41	–	2	44–44	44
diplospondylous vertebrae	7	57–63	61	3	64–70	–	3	67–70	–	3	60–63	–	2	58–61	–	2	61–66	–
upper teeth rows (right)	16	13–15	14	6	12–14	13	4	10–14	–	8	9–14	13	4	12–14	14	2	12–14	–
upper teeth rows (left)	16	13–15	13	6	13–14	14	4	10–14	14	8	9–14	13	4	12–14	12	2	12–13	–
lower teeth rows (right)	16	10–12	12	6	11–14	11	4	10–13	–	8	7–12	11	4	10–11	10	2	13–13	13
lower teeth rows (left)	16	11–12	12	6	11–14	12	4	11–13	12	8	9–12	12	4	10–12	10	2	12–13	–
upper teeth series	16	1–3	2	6	2–3	2	4	2–2	2	8	2–2	2	4	1–3	3	2	2–2	2
lower teeth series	16	2–3	2	6	2–2	2	4	2–2	2	8	2–2	2	4	2–2	2	2	2–2	2
propterygium radials	5	1–1	1	3	1–2	1	3	1–1	1	2	1–1	1	–	–	–	1	1	–
mesopterygium radials	5	8–10	9	3	7–9	–	3	8–9	9	2	9–11	–	–	–	–	1	9	–
metapterygium radials	1	8	–	3	6–10	6	3	7–8	7	2	6–10	–	–	–	–	1	6	–
total pectoral radials	1	19	–	3	14–21	–	3	17–17	17	2	16–22	–	–	–	–	1	16	–
total pelvic radials	5	13–16	15	1	13	–	1	14	–	1	14	–	–	–	–	2	13–14	–

Mouth arched and evidently broad, its width 1.6 (1.4–1.9) times prenarial length and 2.1 (1.6–2.5) times internarial space; upper labial furrow slender and large, its length corresponding to 2.0%–2.9% TL; lower labial furrow inconspicuous. Teeth unicuspid, similar in both jaws, flattened labial-lingually and laterally overlapped; teeth broad, although short at crown; upper teeth smaller than lower teeth; cusp thick and elongate, oblique and directed laterally (cusp strongly vertical in most adult males); convex mesial cutting edge; both distal and mesial heels rounded; apron well elongated in both jaws; one intermediate tooth present at least in upper jaw, usually smaller than the following teeth, with cusp completely vertical, short apron, and both distal and mesial heels markedly rounded; two series of functional teeth in upper and lower jaws; teeth rows varying from 14–1–14 in upper jaw and 11–1–12 in lower jaw (Fig. 4).Origin of first dorsal fin posterior to free rear tips of pectoral fin; in young specimens, origin over free rear pectoral tips (pre-first dorsal length 29.1%–33.7% TL in neonates and juveniles); horizontal distance between origins of pectoral fin and first dorsal fin 1.8 (1.2–2.3) times preorbital length. First dorsal fin vertical and markedly wide at its fin web, relatively large (10.5%–13.1% TL) and low, its length 1.8 (1.5–2.1) times its height, its height and base length 1.0 (0.9–1.2) times preorbital length; anterior margin convex, posterior margin moderately concave near free rear tip; apex rounded, and free rear tips pointed; inner margin length 0.8 (0.6–0.9) times fin height. Origin of first dorsal-fin spine slightly posterior to free rear tips of pectoral fins. First dorsal-fin spine conspicuously slender and low, its length not greater than half dorsal-fin height, never reaching fin apex. Interdorsal distance 1.0 (0.8–1.3) times prepectoral length and 1.8 (1.5–2.2) times dorsal-caudal distance. Pre-second dorsal length 4.3 (3.7–5.2) times the anterior margin length of pectoral fin and 2.9 (2.6–3.2) times dorsal caudal lobe length. Second dorsal fin rather oblique and broad at its fin web, relatively large, its length 1.0 (0.9–1.2) times first dorsal-fin length, and 2.5 (1.9–3.0) times second dorsal-fin height; anterior margin convex and posterior margin falcate; apex rounded, and free rear tip pointed; inner margin elongate, its length 1.0 (0.8–1.1) times fin height. Second dorsal-fin spine slightly inclined, elongated (1.9%–4.5% TL) and reaching the fin apex (in some adult specimens, second spine exceeds the fin apex); slender and low, its length 0.7 (0.4–0.9) times second dorsal-fin height and 1.8 (1.3–2.5) times first dorsal-fin spine length; second dorsal-fin spine broader than first dorsal-fin spine, its base length 1.3 (1.0–1.5) times first dorsal-fin spine base length.

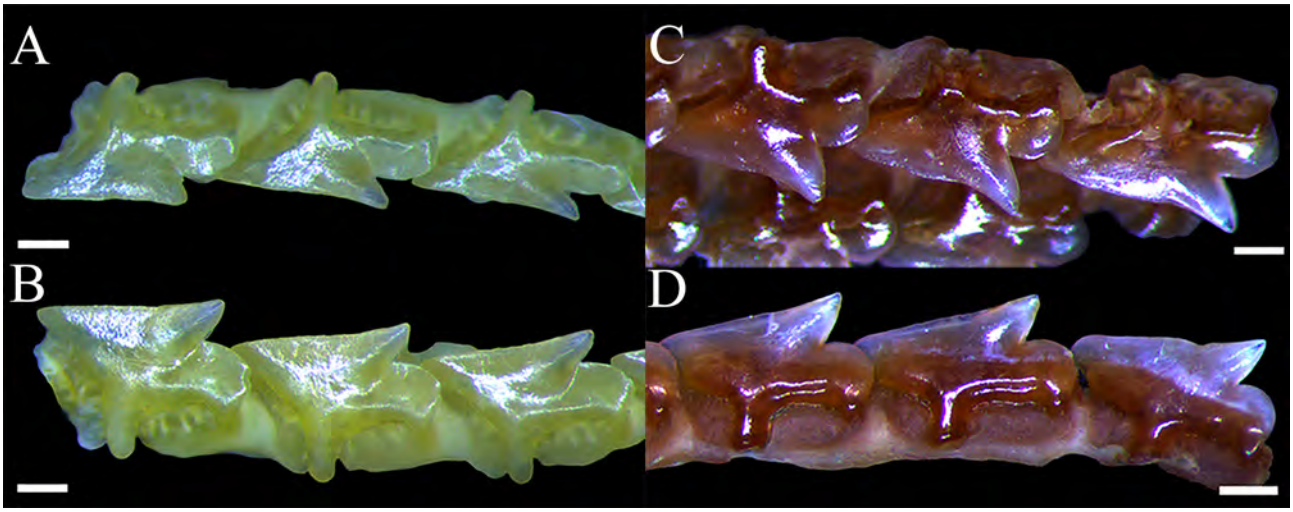

FIGURE 4. Upper (A, C) and lower (B, D) teeth of *Squalus acanthias* in labial view. (A, B) ZMH 104416, adult male, 725 mm TL; (B, D) HUMZ 30178, adult male, 693 mm TL. Scale bar: 1 mm.

Pre-pectoral length 0.6 (0.6–0.7) times pre-first dorsal length, 0.4 (0.4–0.5) times pre-vent length. Pectoral fins with both anterior and inner margins convex, and posterior margin straight; anterior margin length 1.6 (1.4–1.6) times posterior margin length, but its tip reaches same level of its apex; apex and free rear tips evidently rounded, but not lobe-like; pectoral fin base length varying from 3.2%–5.2% TL.

Pelvic fins narrow and elongate, their length 8.6%–12.4% TL anterior margin; slightly convex and posterior margin straight; apex and free rear tips rounded, the latter lobe-like; origin of pelvic fins 1.8 (1.5–2.0) times distance between origins of the two dorsal fins, nearest to second dorsal fin (in young specimens, nearest to first dorsal fin); pectoral-pelvic distance 1.0 (0.6–1.3) times pelvic-caudal distance, usually equal in adults. Clasper cylindrical, compressed dorsoventrally throughout its extension, greatly extended beyond free rear tips of pelvic

fin, its outer length 1.1%–5.8% TL; siphon large, located medioventrally from the anteriormost end of puboischiadic bar level of intermediate cartilage; clasper groove longitudinal and dorsomedially, sinuous and deep; apopyle broad, placed more anteriorly in clasper groove; hypopyle narrow, located posteriorly to rhipidion; rhipidion elongate, blade-like, located medially at distal end of clasper (Fig. 5).

Caudal peduncle with inconspicuous lateral keels, originating behind insertion of second dorsal fin; upper and lower precaudal pits marked. Caudal fin conspicuously rectangular on dorsal lobe with dorsal-caudal margin straight and upper postventral margin strongly convex; dorsal-caudal margin length 1.0 (0.9–1.1) times head length and 1.8 (1.7–2.0) times preventral margin length; caudal fork markedly concave and broad, its width corresponding to 6.0%–7.4% TL; lower postventral margin also convex; preventral caudal margin convex and large, its length 2.4 (1.7–3.5) times pelvic fin inner margin length.

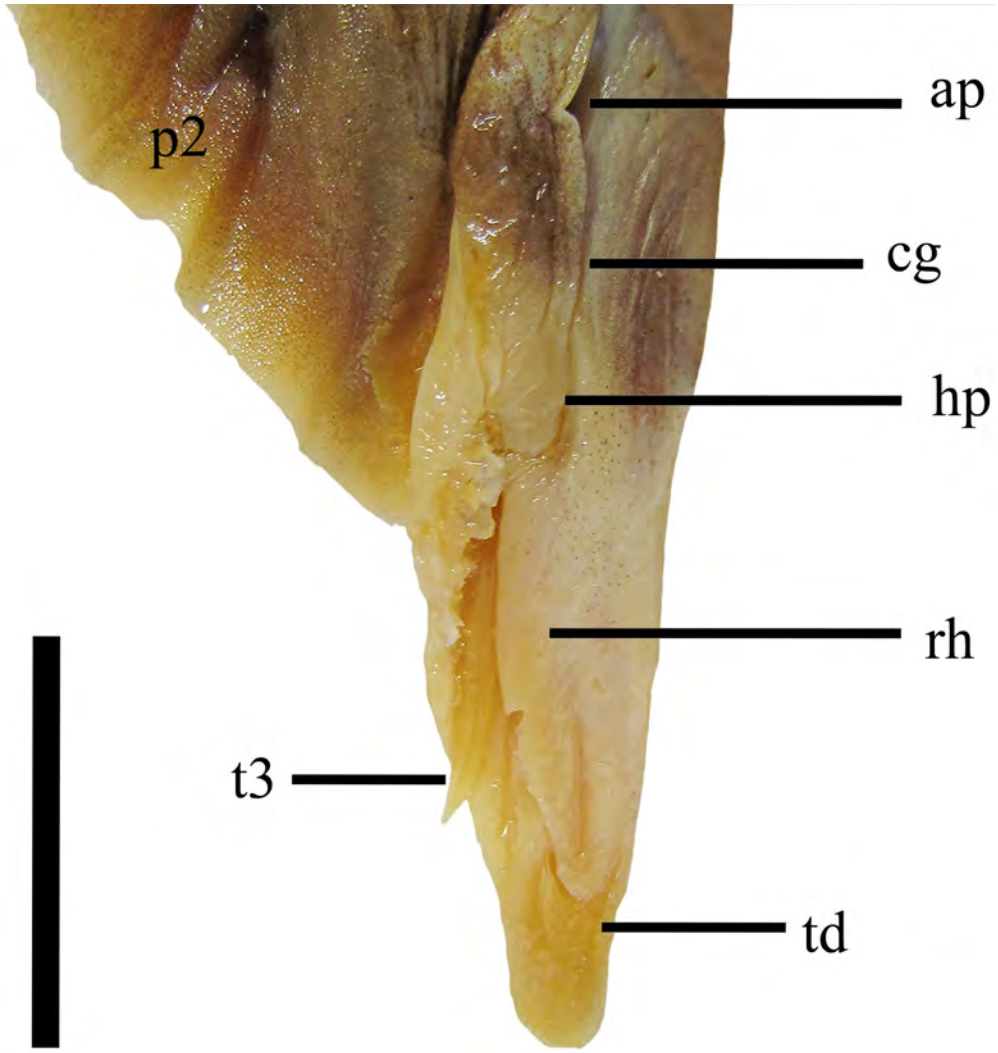

FIGURE 5. Left clasper of *Squalus acanthias* in dorsal view (ZMH 104951, adult male, 715 mm TL). Abbreviations: **ap**, apopyle; **cg**, clasper groove; **hp**, hypopyle; **p2**, pelvic fin; **rh**, rhipidion; **td**, dorsal terminal cartilage (claw); **t3**, accessory terminal cartilage (spur). Scale bar: 10 mm.

FIGURE 6. Variations of dorsolateral white spots on *Squalus acanthias*. (A) single and isolated (HUMZ 30285, adult male); (B) fused (HUMZ 30200, adult male); (C) double series (HUMZ 104955, neonate male). Scale bar: 50 mm.

Dermal denticles (Fig. 7). Denticles unicuspid, their length and width equivalent, relatively sparsely positioned, not imbricated; median ridge pronounced, elongate and narrow, projecting anteriorly beyond crown base; median cusp pointed posteriorly. In neonates, denticles smaller, markedly sparse and underdeveloped throughout body.

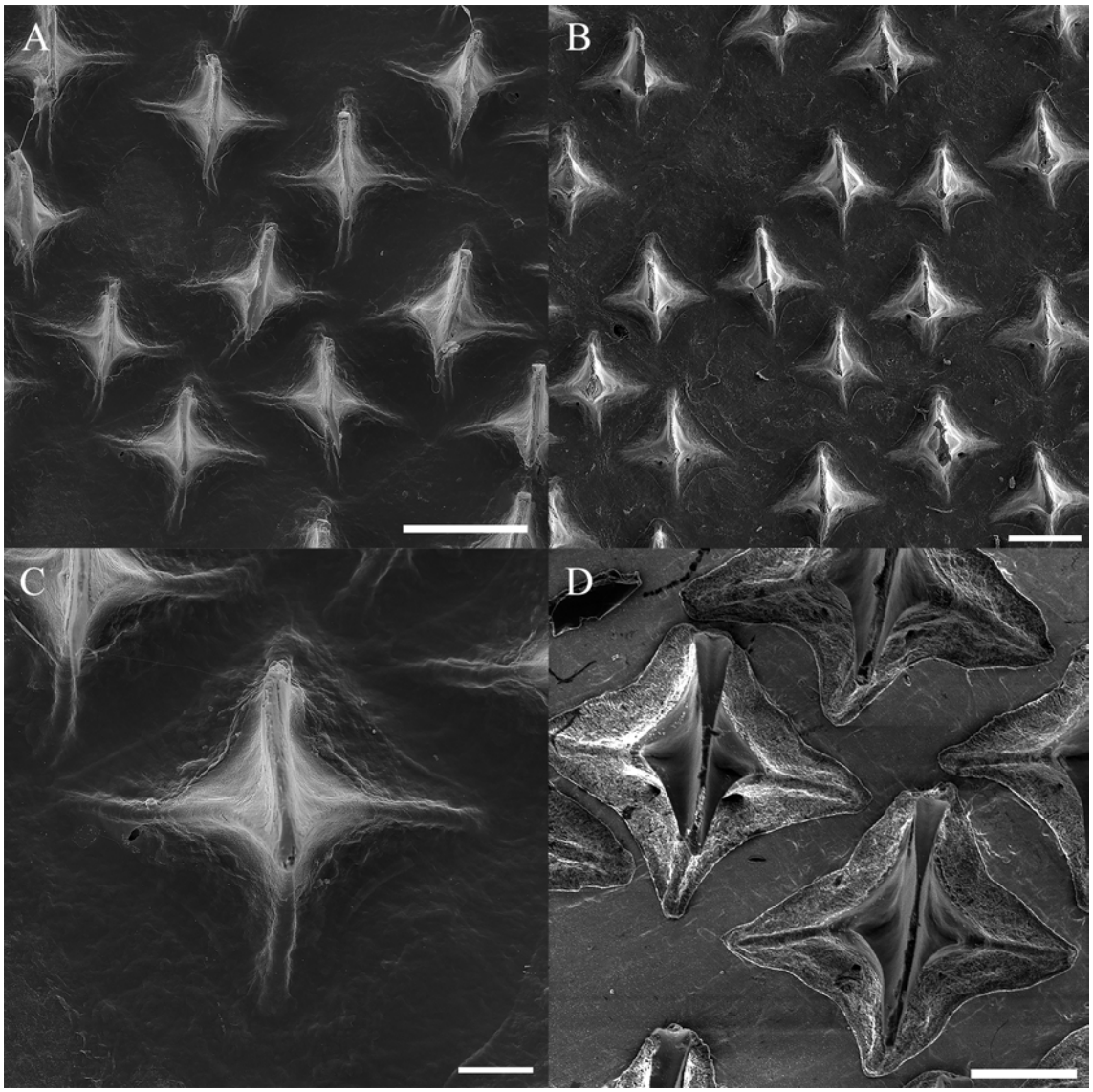

FIGURE 7. Dermal denticles of *Squalus acanthias*. (A, C) HUMZ 30200, adult male; (B) HUMZ 30303, juvenile female; (D) BMNH 1999.5.4.15, adult female. Scale bars: 200 ìm (A, B); 50 ìm (C); 100 ìm (D).

Coloration (Figs. 2, 6). Body dark gray dorsal and laterally, and light gray more posteriorly from the lower lateral half of the body just in front of the pectoral fin origin to the caudal fin; white ventrally; large and few paired white spots dorsolaterally, usually anterior to second dorsal fin. Both dorsal fins dark gray with apex slightly darker at tip than rest of fin, white at fin base and on free rear tips; dorsal-fin spines dark gray to brownish anteriorly and whitish at tips. Pectoral fins also dark gray dorsoventrally with both inner and posterior margins broadly whitish. Pelvic fins gray dorsally and ventrally, lighter ventrally, with anterior and posterior margins evidently white. Caudal fin gray, darker at posterior tip, slightly white at dorsal caudal margin, forming a white caudal bar; black caudal stripe strong and wide, dorsal to vertebral column on caudal fin; postventral caudal margins discreetly white; preventral caudal margin white, including at ventral tip (Fig. 2). In young specimens (between 200–330 mm TL), body usually light gray with numerous white spots, often fused (Fig. 6); dorsal fins markedly darker at tip; caudal fin conspicuously dark gray with broad white caudal bar at dorsal caudal margin; black upper caudal blotch near the terminal region from vertebral column to posterior caudal tip; preventral and postventral margins largely white.

TABLE 3. Cranial measurements of *Squalus acanthias, Squalus lobularis* sp. nov., and *Squalus albicaudus* sp. nov. expressed as percentage of neurocranial total length (% CL). CL expressed in mm. N: number of specimens; *x* : mean; SD: standard deviation.

	Measurements	***S. acanthias***				***Squalus lobularis***		***Squalus albicaudus***
		N	Range	*x*	SD	Paratype UERJ 1661	Non-type UERJ 1112	Paratype MNRJ 30184
1	Total length of neurocranium (CL) (mm)	3	48.4 – 92.7	73.6	22.8	90.2	80.9	70.4
2	Postcerebral length	3	57.8 – 64.7	62.3	3.9	58.3	65.0	58.5
3	Precerebral fossa length	3	36.0 – 42.3	38.6	3.3	40.6	36.1	40.1
4	Precerebral fossa width	3	11.5 – 16.9	14.7	2.8	13.6	15.6	14.9
5	Width across nasal capsules	3	44.0 – 48.7	46.7	2.4	52.3	57.8	52.8
6	Interorbital width	3	28.5 – 31.8	30.0	1.7	30.2	28.8	28.8
7	Width across preorbital processes	3	47.9 – 50.2	49.1	1.1	52.3	54.6	48.9
8	Postorbital process length	3	7.8 – 9.7	9.0	1.1	6.9	9.4	10.2
9	Width across postorbital processes	3	50.0 – 53.4	51.2	1.9	55.8	57.2	57.1
10	Distance between orbital processes	3	28.4 – 28.7	28.5	0.1	35.0	39.1	34.7
11	Distance across opistotic processes	3	32.6 – 35.5	34.5	1.7	37.9	39.3	36.5
12	Width across hyomandibular facets	3	36.8 – 44.1	40.9	3.8	43.5	51.3	41.5
13	Nasobasal length	3	62.8 – 67.4	64.8	2.3	64.5	63.7	64.9
14	Rostral keel length	3	21.9 – 26.1	24.2	2.1	20.8	30.0	25.0
15	Subethmoidean width	3	10.5 – 13.6	12.5	1.8	15.3	16.9	16.5
16	Basal angle width	3	16.8 – 19.0	18.3	1.3	18.1	19.0	16.1
17	Basal plate length	3	36.9 – 42.2	40.0	2.8	42.4	41.5	38.6
18	Basal plate width	3	17.8 – 20.7	19.4	1.5	19.8	20.8	17.9
19	Width across first cartilaginous processes	3	28.1 – 32.8	29.7	2.7	30.6	31.1	30.3
20	Width across second cartilaginous processes	–	–	–	–	–	–	–
21	Maximum sagital length	3	17.5 – 22.2	20.0	2.4	18.5	20.0	18.9
22	Foramen magnum width	3	7.2 – 10.7	8.6	1.9	8.8	8.4	9.2

Skeletal morphology. Measurements and counts are summarized in Tables 2–3.

Neurocranium (Fig. 8). Neurocranium greatest width at level of postorbital processes (50.0%–53.4% CL), narrower at interorbital region (28.5%–31.8% CL) and between the opisthotic processes in the otic region (32.6%–35.5% CL). Rostrum elongate (its length 36.0%–42.3% CL), slender proximal and distally, and wide medially, its width 11.5%–16.9% CL; lateral rostral cartilages cylindrical, somewhat depressed anteriorly; ventrally, two lateral rostral appendices thick and hook-like; median rostral prominence small; rostral keel conspicuous and well elongate, extending anterior to nasal capsules (its length 21.9%–26.1% CL). Prefrontal fontanelle rounded, located at base of rostrum and anterior to cerebrum. Nasal capsules oval and strongly oblique, very narrow, width across nasal capsules 44.0%–48.7% CL; small fissures evident ventrally on nasal capsules (not shown); anterior nasal margin with a unique cartilaginous lobe; subnasal fossa oval and large, located ventrally on each side of rostral keel.

Cranial roof strongly concave medially at interorbital region with a prominent lateral supraorbital crest; longitudinal sulcus deeper anteriorly, carrying the profundus canal for the ophtalmicus profundus and a series of foramina (8–9 foramina) of the superficial ophthalmic branches of trigeminal (V) and facial (VII) nerves; preorbital canal rounded and markedly large, placed anteriorly to a series of foramina; canal for the ophtalmicus profundus rounded, located anterior to the preorbital canal and beside the ethmoidal canal. Preorbital processes small, neurocranium broad between them (width 47.9%–50.2% CL). Postorbital processes prominent and triangular, not elongate (length 7.8%–9.7% CL). Distance between orbital processes 28.4%–28.7% CL.

Supraethmoidal processes in ethmoidal region prominent and triangular not elongate, and placed at dorsal base of prefrontal fontanelle; epiphyseal pit rounded and broad, posterior to supraethmoidal processes; ethmoidal canal rounded and narrow, placed at the base of each nasal capsule; ethmoidal chamber flattened, somewhat constricted ventrally with a triangular and prominent ectethmoid process on each side; conspicuous subethmoidal ridge, posterior to rostral keel, extending to subethmoidal region; subethmoidal region elongate and very narrow, its width 10.5%–13.6% CL.

Otic region deep anterodorsally between the otic capsules; otic capsules narrow and heptagonal on each side; dorsally, two conspicuous anterior and two posterior semicircular canals, the former placed almost in parallel to neurocranial longitudinal axis; endolymphatic fossa oval and large, with two anterior endolymphatic foramina, slightly oblique, and two posterior and vertical perilymphatic foramina; strong otic crest located posteriorly to endolymphatic fossa; prominent sphenopterotic ridge at sides of otic capsules; opisthotic process rather discreet at distal portion of sphenopterotic ridge; laterally, otic wall delimited by a prominent lateral semicircular canal below the sphenopterotic ridge, a shallow ventrally situated hyomandibular facet, and anteriorly by a deep lateral auditory groove; width across hyomandibular facets between 36.8%–44.1% CL.

Orbital region very narrow with concave preorbital wall, with orbitonasal canal at base; optic foramen (II) large, placed midventrally in interorbital wall; trochlear foramen (IV) small dorsoanterior to optic foramen (II); eye-stalk located more posteriorly in this region between the oculomotor foramen (III) and abducens foramen (VI), positioned, respectively, dorsally and ventrally to eye-stalk; a broad foramen prooticum for trigeminal (V) and facial (VII) nerves positioned in the posterior edge of the interorbital wall, just anterior to the postorbital process; the foramen prooticum also opens posteriorly for the hyomandibular branch of the facial nerve (VII) at the base of hyomandibular facet; transbasal canal small located ventroposterior to the anterior opening of the foramen prooticum.

Basal plate flattened and large (length 36.9%–42.2% CL), narrower anteriorly at basitrabecular process, broader posteriorly with its width between 17.8%–20.7% CL; basitrabecular processes conspicuous and bean-shaped, perpendicular to basal plate axis; basal angle width 16.8%–19.0% CL; two sinuous lateral prominences on each side at basitrabecular processes and the first cartilaginous process; a single cylindrical cartilaginous process on each side of the basal plate, width across processes 28.1%–32.8% CL; single foramen for carotid artery anteromedially located in basal plate; foramina for orbital artery with its ventral opening in the anterior base of the cartilaginous process and its lateral opening in the lateral otic wall.

Occipital region with two broad occipital condyles distally, and a wide foramen magnum between them, its width 7.2%–10.7% CL; vagus foramen (X) rounded, lateral to occipital condyles; thick and subtriangular glossopharyngeal base, although not very prominent, located more laterally in the occipital region, with an oval and broad foramen for glossopharyngeal nerve (IX).

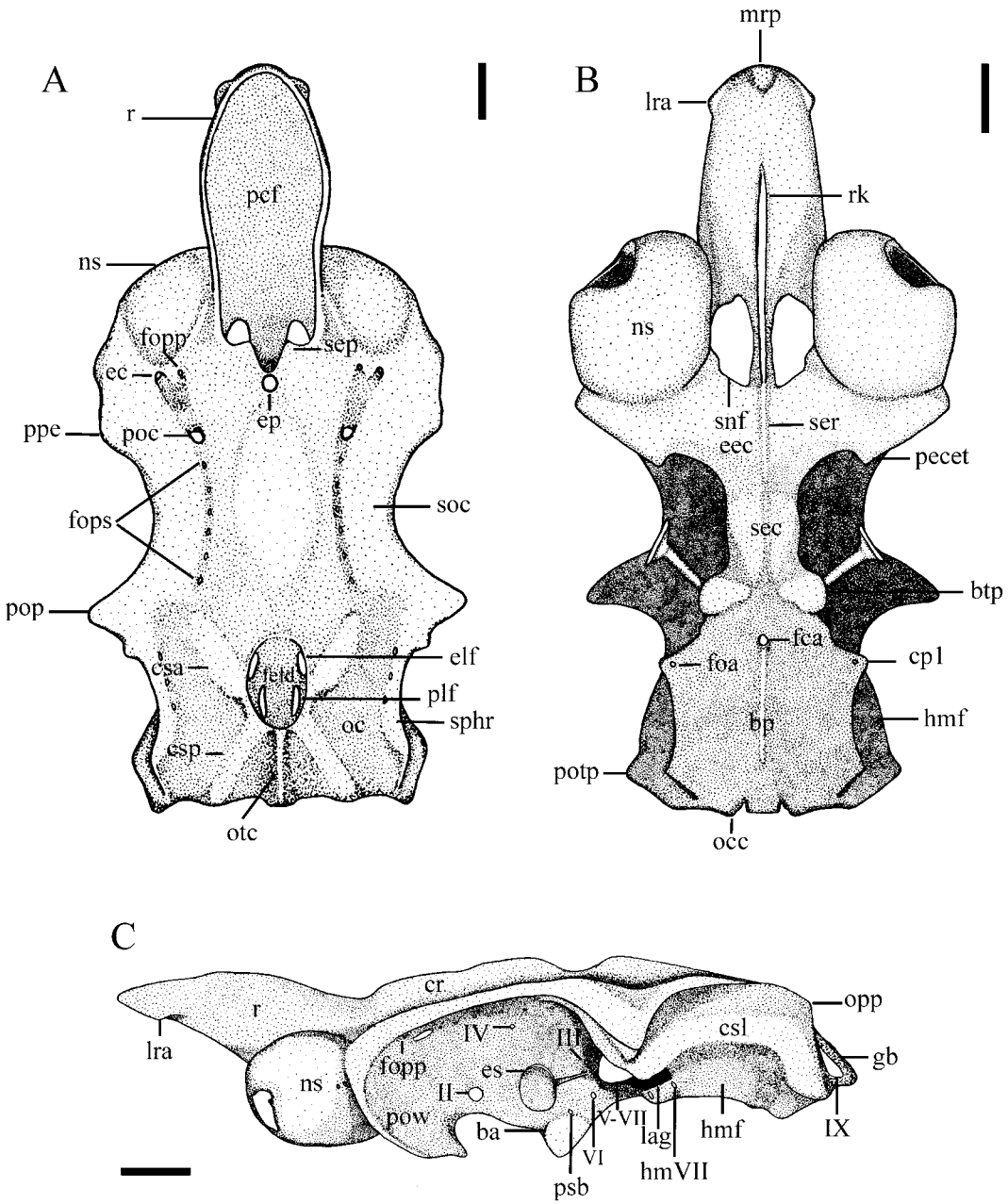

FIGURE 8. Neurocranium of *Squalus acanthias* (ZMH 104416, adult male). (A) dorsal view; (B) ventral view; (C) lateral view. Abbreviations: **ba**, basal angle; **bp**, basal plate; **btp**, basitrabecular process; **cp1**, first cartilaginous process; **cr**, cranial roof; **csa**, anterior semicircular canal; **csl**, lateral semicircular canal; **csp**, posterior semicircular canal; **ec**, ethmoidal canal; **eec**, ectethmoid chamber; **elf**, endolymphatic foramen; **ep**, epiphysial pit; **es**, eye-stalk; **fca**, foramen for carotid artery; **feld**, endolymphatic fossa; **foa**, foramen for orbital artery; **fopp,** profundus canal; **fops**, series of foramina for superficial ophthalmic branch of trigeminal and facial nerves; **gb**, glossopharyngeal base; **hmf**, hyomandibular facet; **hmVII**, foramen for hyomandibularis facialis; **lag**, lateral auditory groove; **lra**, lateral rostral appendage; **mrp**, median rostral prominence; **ns,** nasal capsule; **oc,** otic capsule; **occ,** occipital condyle; **opp**, opisthotic process; **otc,** otic crest; **pcf**, precerebral fossa; **pecet**, ectethmoid process; **plf**, perilymphatic foramen; **poc**, preorbital canal; **pop**, postorbital process; **potp**, prootic process; **pow**, preorbital wall; **ppe**, preorbital process; **psb,** efferent pseudobranchial artery foramen; **r,** rostrum; **rk,** rostral keel; **sec**, subethmoid chamber; **sep**, supraethmoidal process; **ser**, subethmoidean ridge; **snf**, subnasal fenestra; **soc**, supraorbital crest; **sphr**, sphenopterotic ridge; **II**, optic foramen ; **III**, oculomotor foramen; **IV**, trochlear foramen; **V, VII**, foramen prooticum; **VI**, abducens foramen; **IX**, foramen for glossopharyngeal nerve. Scale bars: 10 mm.

Pectoral fin and girdle (Figs. 9, 10). Coracoid bar unpaired, strongly concave dorsally, convex ventrally, flattened and slender at midline, and thick and cylindrical at dorsal tips; two conspicuous facets anteriorly, an anterior facet and the m. *depressor pectoralis* facet, located more laterally and bearing the diazonal foramen; a pair

of longitudinal segmented processes attached ventrally to the coracoid bar, comprised by 3–4 units of small barrel-shaped cartilages, evident laterally and dorsally to the m. *depressor pectoralis* facet; posteriorly, a pair of medioventral facets support the origin of the m. *parietalis pars hypaxonica*; a conspicuous caudal process present on each side of the hindmost part of this facet that, with the base of the articular process, supports the origin of m. *pterygii ventralis* muscle. Scapulae dorsal to, and continuous with, the coracoid bar, forming a U-shaped scapulocoracoid cartilage; articular process of scapulocoracoid with a single rounded condyle articulating with mesopterygium of pectoral fin; the m. *levator pectoralis* facet, located more distally to the articular process of pectoral girdle, supports the origin of m. *pterygii dorsalis*. Suprascapulae paired and triangular, cylindrical distally and somewhat flattened proximally, attaching dorsally to each side of scapulae, directed upward toward the vertebral column.

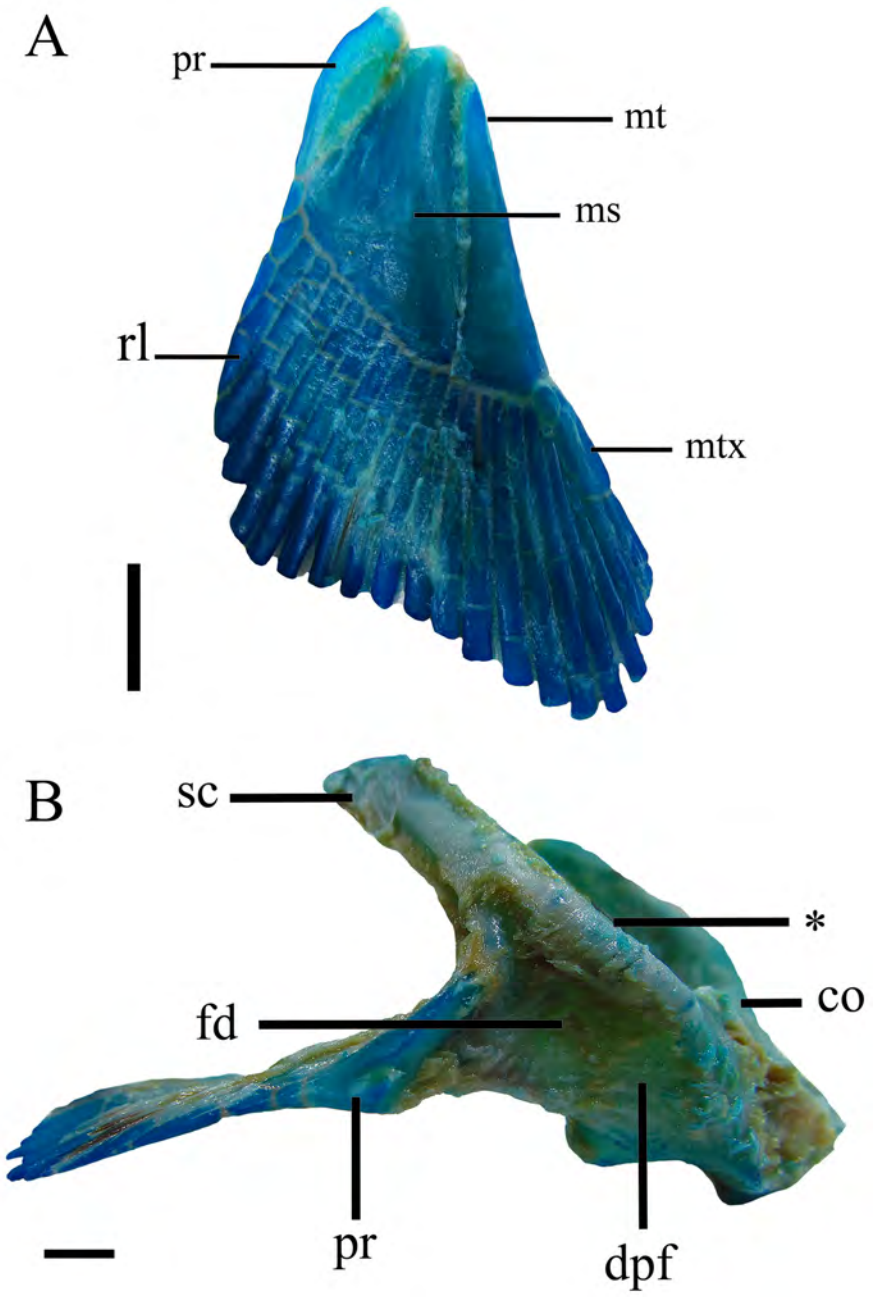

FIGURE 9. Pectoral fin (A) and girdle (B) of *Squalus acanthias* (HUMZ 30173, adult male). Abbreviations: **co**, coracoid bar; **dpf**, m. *depressor pectoralis* facet; **fd**, diazonal foramen; **ms**, mesopterygium; **mt**, metapterygium; **mtx**, metapterygial axis; **pr**, propterygium; **rl**, radials; **sc**, scapula; *, segmented processes of coracoid bar. Scale bar: 10 mm.

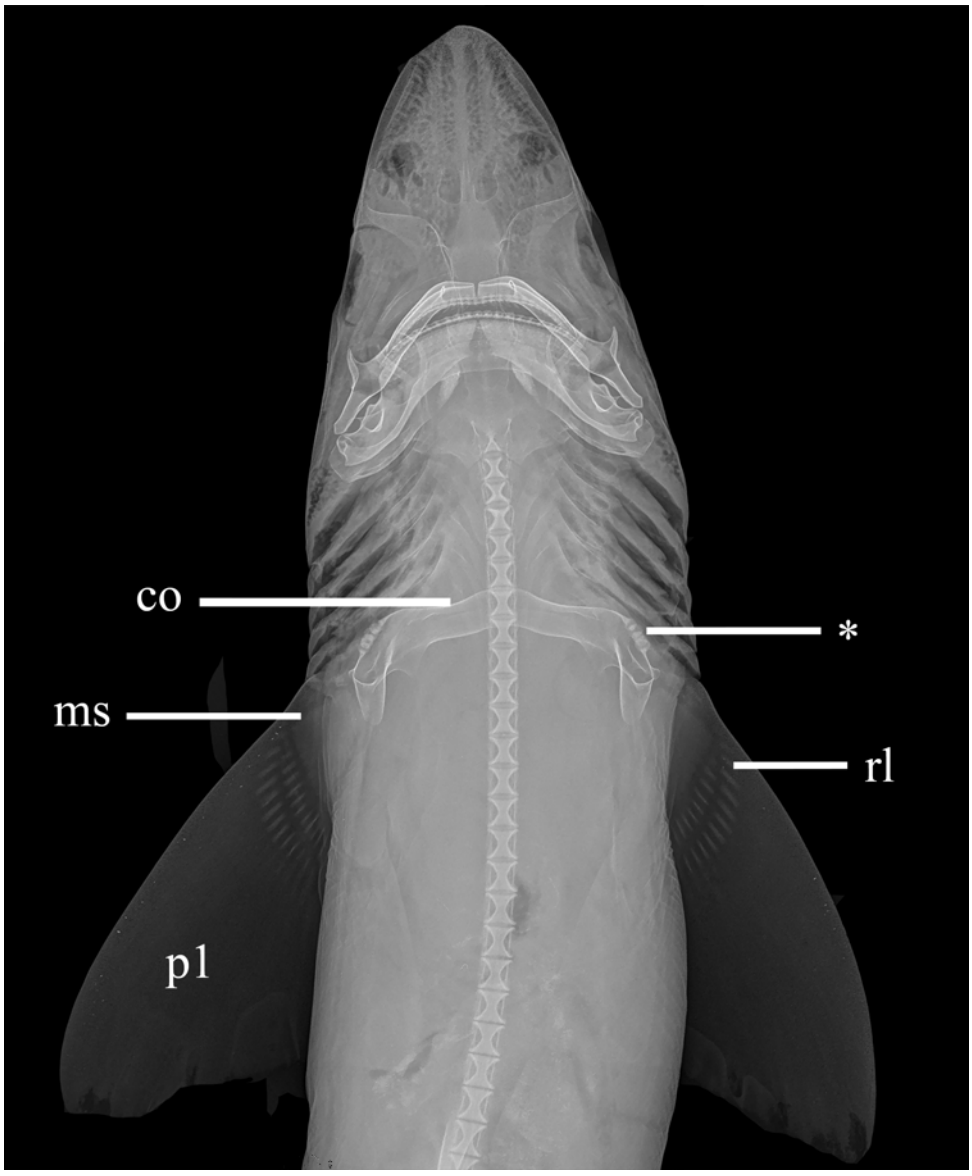

FIGURE 10. Radiograph of *Squalus acanthias* in ventral view (ZMH 104461, adult female) showing the pectoral girdle. Abbreviations: **co**, coracoid bar; **ms**, mesopterygium; **p1**, pectoral fin; **rl**, radials; *****, segmented processes of coracoid bar.

Pelvic fin and girdle (Fig. 11). Pelvic girdle with puboichiadic bar rectangular, short and slightly slender, with anterior margin somewhat straight and posterior margin convex; two conspicuous expansions posteriorly articulate puboischiadic bar to the basipterygium and to the anterior pelvic fin element; a single pelvic nerve foramen present at each side of pubosichiadic bar. Anterior pelvic fin basal element subrectangular and wide with three series of irregular and small radials; basipterygium elongate markedly slender, cylindrical and sinuous; pelvic radials thin and large, cylindrical, and segmented into proximal and distal elements, the former much larger; 14 total pelvic radials.

Claspers (Fig. 12). Intermediate element barrel-shaped, attaching pelvic fin basipterygium to axial cartilage; beta cartilage single, slender and cylindrical, located laterodorsally between intermediate element and axial cartilage; axial cartilage small, slender, conspicuously sinuous medioproximally; end-style elongate and thin, mediodistal to axial cartilage; dorsal marginal cartilage slim, located dorsolaterally to axial cartilage; dorsal terminal cartilage conspicuously elongate, not reaching distal end of clasper, hook-like, connected proximally to dorsal marginal cartilage and axial cartilage, and medially to end-style; dorsal terminal 2 cartilage leaf-like and flattened, also elongate, with concave lateral margin, attached medially to dorsal terminal cartilage, and proximally to dorsal marginal cartilage, externally supporting the rhipidion; ventral marginal cartilage slightly thick and broad, concave and grooved laterally at its inner side, emerging as a folded plate at insertion of accessory terminal

cartilage; ventral terminal cartilage also large, slender and spatula-like with rounded distal tip somewhat sinuous laterally, located at distal end of clasper, and attached proximally to ventral marginal cartilage and medially to end-style; accessory terminal 3 cartilage (or spur) markedly slim and elongate with an evident dorsal groove, distally pointed, with a rounded proximal edge, partially attached to ventral margin and ventral terminal cartilages.

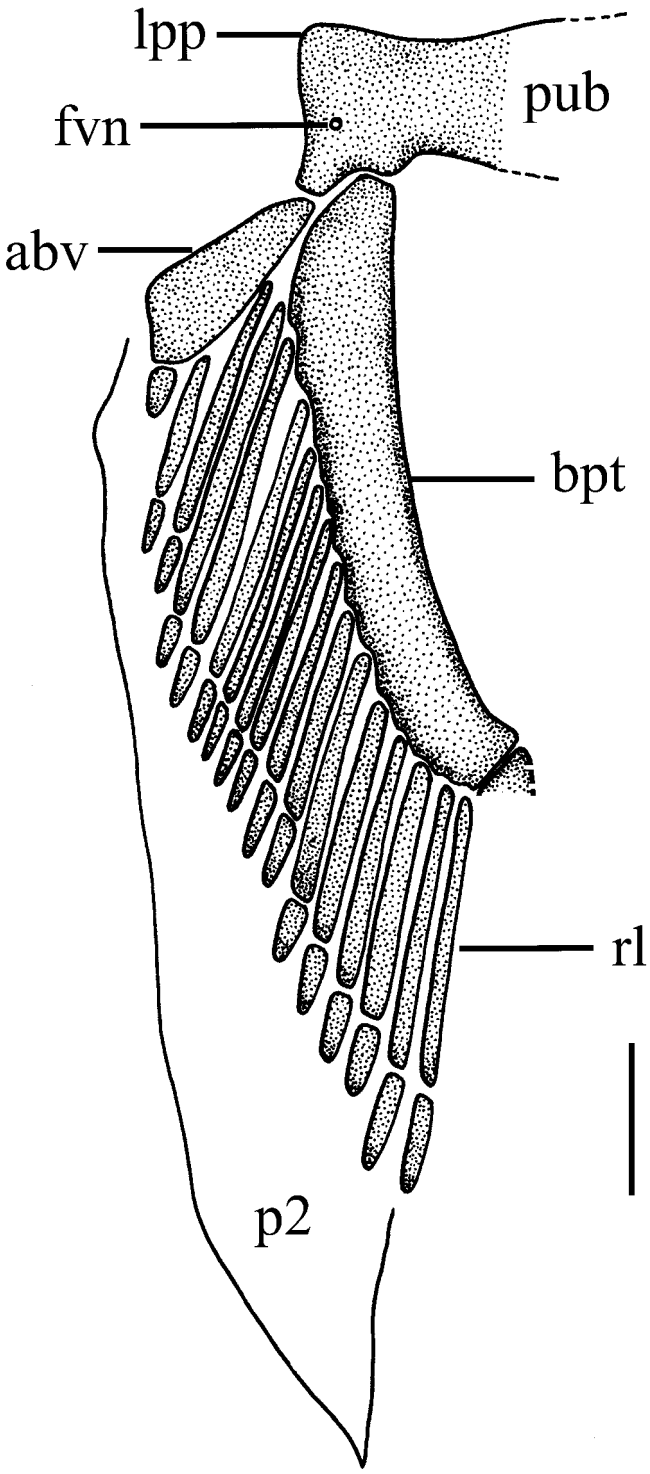

FIGURE 11. Right pelvic clasper of *Squalus acanthias* (ZMH 104416) in ventral view. Abbreviations: **abv**, anterior pelvic basal; **bpt**, basipterygium; **fvn**, foramen for ventral fin nerves; **lpp**, lateral prepelvic process; **pub**, puboischiadic bar; **p2,** pelvic fin; **rl**, radials. Scale bar: 10 mm.

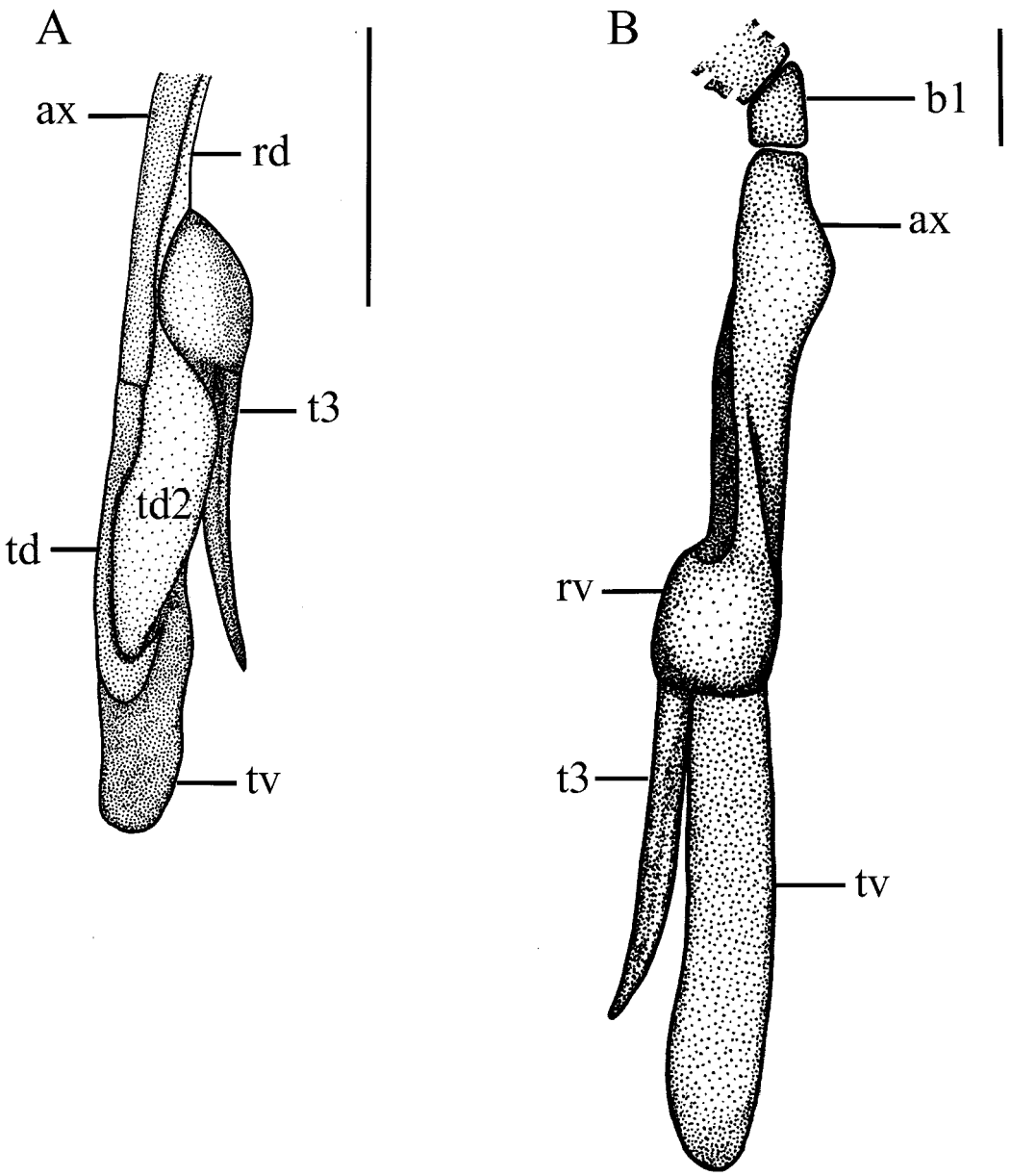

FIGURE 12. Clasper cartilages, right side, of *Squalus acanthias* (ZMH 104416, adult male). (A) detail of terminal cartilages in dorsal view; (B) ventral view. Abbreviations: **ax**, axial cartilage; **b1**, intermediate segment; **rd**, dorsal marginal cartilage; **rv**, ventral marginal cartilage; **td**, dorsal terminal cartilage (claw); **td2**, dorsal terminal 2 cartilage; **tv**, ventral terminal cartilage; **t3**, accessory terminal cartilage (spur). Scale bars: 10 mm.

Vertebral counts (Table 2). Monospondylous vertebrae with mode value 44 (43–47); diplospondylous vertebrae 61 (57–63); precaudal vertebrae 75 (75–81); total vertebrae 101 (101–109).

Geographical distribution (Fig. 13). In the SWAO, *S. acanthias* is more commonly found from southern Brazil off Tramandai, Rio Grande do Sul state to the southern coast of Argentina in Santa Cruz, Patagonia, as well as in the Falkland Islands. Few occurrences are observed in warmer equatorial waters from Suriname and southeastern Brazil (e.g. Rasa Island, Rio de Janeiro state). For its distribution elsewhere, see Ebert *et al*. (2013).

Etymology. The epithet *acanthias*, from the Greek αγκάθι, means spine.

Remarks. In the 10th edition of the *Systema Naturae*, Linnaeus (1758) defined this species through a combination of superficial characters that may be applied to any species of shark of the order Squaliformes, among them: absence of anal fin; presence of dorsal-fin spines, and slender body. The type locality is regarded as "Europaeo Ocean without further specifications. Type specimens were not designated in the original description. The lack of information in fish collections contributed to mystery of the whereabouts of the types, and there have

been speculations regarding possible syntypes in the fish collection of the Natural History Museum in Stockholm based on pre-Linnean and Linnean data in the literature (Fernholm & Wheeler, 1983; Wheeler, 1991). This situation may have contributed to confuse the identity of *S. acanthias*, as seen by the numerous misidentifications in the literature, and compounded by the fact that the species was not well characterized.

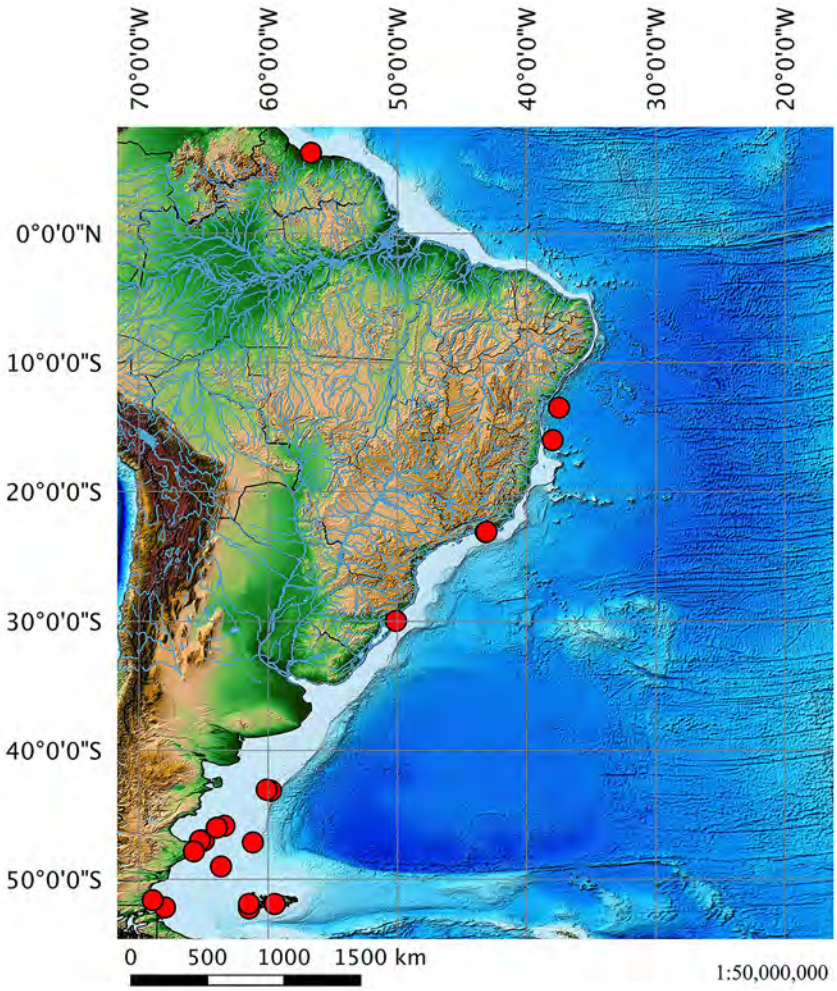

FIGURE 13. Map of the Southwestern Atlantic Ocean, showing the distribution of *Squalus acanthias* based on material examined.

This species also has a worldwide distribution and exhibits varying patterns of its biological functions such as reproduction and growth, distribution and abundance, and populational structure (Gallucci *et al*., 2009; Ebert *et al*., 2013). Thus, it is commonly considered a polytypic species or a complex of cryptic species or populations, supported by morphological and molecular data, which have allowed for the recognition of new species (Myagkov & Kondyurin, 1986; Veríssimo *et al*., 2010; White & Last, 2012).

The taxonomy of *S. acanthias* is not yet completely clarified due to the morphological and molecular variation between specimens from different localities worldwide (e.g. Bigelow & Schroeder, 1948, 1957; Springer & Garrick, 1964; Bass *et al*., 1976; Ward *et al.*, 2007). Our results corroborate these studies from a morphological standpoint, despite that external measurements mostly overlap between specimens of *S. acanthias* from SWAO and other localities, indicating that they appear to be conspecific (Table 4). Specimens of *S. acanthias* share the following characteristics (Table 2): anterior margin of the nostrils with a simple lobe, not bifurcated when adults; 14–1–14 teeth in the upper jaw and 12–1–12 in the lower jaw; first dorsal-fin spine located posterior to the free rear tips of the pectoral fins; unicuspid dermal denticles without lateral expansions; presence of white spots on dorsum.

Significant differences are noticed compared to specimens from the Southeastern Pacific Ocean (SEPO): smaller direct length for SWAO specimens such as precaudal length (31.2%–81.1% TL *vs*. 81.8%–82.1% TL), pre-first dorsal fin length (29.1%–33.7% TL *vs*. 34.0%–34.3% TL), pre-second dorsal fin length (53.4%–62.2% TL *vs*. 63.4%–64.8% TL) and interdorsal space (17.1%–22.7% TL *vs*. 24.5%–24.6% TL); greater first dorsal fin-spine

length in SWAO than in SEPO (1.5%–2.8% TL *vs*. 0.8%–1.3% TL); and pre-second dorsal fin length 2.6–3.2 times dorsal caudal margin length (vs. 3.3–4.0 times in SEPO). Two nominal species are often applied in the Southeastern Pacific Ocean, *S. fernandinus* Molina, 1782 from Juan Fernandez Island, Chile, and *S. lebruni* (Vaillant, 1888) from Tierra del Fuego, Argentina, which are both recognized as junior synonym of *S. acanthias* (e.g. Garrick, 1960; White *et al*., 2007). The former species, however, is also frequently treated as a junior synonym of *S. blainvillei* (e.g. Fowler, 1936; Compagno, 1984) due to the size of its dorsal spines (approximately 63.5 mm according to Molina, 1782). The presence of white spots refers undoubtedly to *S. acanthias* but the dorsal spine length represents a morphological regional peculiarity (Garrick, 1960). Few authors support *S. lebruni* as a valid species distinct from *S. acanthias* (e.g. Berg, 1895; Menni *et al*., 1984) based on the presence of upper central teeth with a vertical cusp and lateral expansions that provide a tricuspid shape, although this was not noticed in the present study. Specimens from the Southeastern Pacific Ocean are also distinct in external morphometrics, color pattern, and vertebral counts from specimens from the Northwestern Atlantic Ocean (NWAO), Northeastern Atlantic Ocean (NEAO), Northeastern Pacific Ocean (NEPO), and Mediterranean Sea, calling for further studies regarding the taxonomy of *S. acanthias* in the SEPO.

We noticed slight but possibly significant variations in external measurements among specimens of *S. acanthias* worldwide (Table 4): mouth width (7.4%–7.7% TL in NEAO; 7.3%–9.4% TL in NEPO; 7.0%–7.1% TL in SEPO); first dorsal fin-spine length (1.6%–3.1% TL in NWAO; 2.0%–4.6% TL in the Mediterranean Sea; 1.5%–2.2% TL in NEAO; 1.5%–2.5% TL in NEPO; 0.8%–1.3% TL in SEPO); pectoral-fin posterior margin length (10.5%–13.7% TL in Mediterranean Sea; 9.4%– 10.3% TL in NEAO; 5.5%–10.3% TL in NEPO); and dorsal caudal margin length (16.0%–19.5% TL in SEPO; 19.8%–22.2% TL in Mediterranean Sea; 19.9%–21.9% TL in NEAO; 20.4%–24.6% TL in NEPO). Specimens from NEPO and SEPO have pelvic fins located almost at mid-space between origins of the dorsal fins, while in the remaining specimens these fins are placed closer to the second dorsal fin. Small juvenile specimens have pelvic fins usually nearest the first dorsal fin, which is in agreement with the ontogenetic observations of Garrick (1960).

Variations in monospondylous, diplospondylous, precaudal, and total vertebrae (Table 2) are also present among specimens of *S. acanthias* from the Northwestern Atlantic, Southeastern Atlantic, Northwestern Pacific, Northeastern Pacific, and Southeastern Pacific oceans, in agreement with the previous results of Springer & Garrick (1964). These results, however, do not demonstrate consistent morphological variation for a North Pacific population separate from a second population that includes South Pacific and Atlantic specimens, as supported in a molecular analysis (Veríssimo *et al*., 2010) and in terms of data on general biology (e.g. Galucci *et al*., 2009).

Squalus suckleyi (Girard, 1854) from the Northwest Pacific Ocean has also been considered a junior synonym of *S. acanthias* (e.g. Bigelow & Schroeder, 1948, 1957; Compagno, 1984), but which has been recently resurrected as valid (Ebert *et al*., 2010). Molecular analysis (e.g. Ward *et al*., 2007; Veríssimo *et al*., 2010) strongly support its separation, despite the fact that mostly overlapping morphological characters were used to distinguish this species from *S. acanthias* (e.g. Jordan & Evermann, 1896; Regan, 1908; Garman, 1913; Ebert *et al*., 2010), such as a less obtuse snout, the position of the first dorsal-fin spine located right after the free rear tip of the pectoral fin, pelvic fins located slightly closer to the second dorsal fin than to the first dorsal fin, and a smaller number of total vertebrae. These differences, however, were not observed by us with exception of the position of the first dorsal spine in relation to the pectoral fin. Other morphological characters are still needed to better distinguish *S. suckleyi* from *S. acanthias*.

Many attempts (e.g. Rafinesque, 1810; Müller & Henle, 1841; Duméril, 1865) have been made to provide additional characters for *S. acanthias*. Garman (1913), however, was the first author to provide detailed distinctive characters and important information about its synonymy. He based his conclusions on a specimen from the Mediterranean Sea whose characteristics are similar to the specimens of *S. acanthias* examined by us from the SWAO. However, few variations exist between specimens of these two regions: shorter interdorsal space in specimens from SWAO (17.1%–22.7% TL *vs*. 22.9%–24.8% TL), and claspers more elongate in specimens from the Mediterranean Sea (clasper inner length 8.8%–9.9% TL *vs*. 2.2%–5.7% TL for SWAO).

Later, Bigelow & Schroeder (1948, 1957) provided some diagnostic characters of *S. acanthias* from the North Atlantic Ocean, which overlap with those of specimens from the Southwestern Atlantic Ocean. These authors further emphasized that sexual dimorphism may be present in this species, as the first dorsal-fin spine length is greater in males than in females, and the second dorsal-fin spine reaches the dorsal-fin apex only in males. Our results, however, do not support this dimorphism once all specimens have the first dorsal-fin spine always below half of the first dorsal-fin height, and the second dorsal-fin spine is always taller than the second dorsal-fin in both males and females.

TABLE 4. External measurements expressed as percentage of total length (% TL) of *Squalus acanthias* from diferent localities. N: number of specimens; *x* : mean; SD: standard deviation.

Measurements	Northwestern Atlantic				Central Western Atlantic		Mediterranean Sea				Northeastern Atlantic				Northeastern Pacific				Southeastern Pacific			
	N	Range	*x*	SD	N		N	Range	*x*	SD	N	Range	*x*	SD	N	Range	*x*	SD	N	Range	*x*	SD
TL (mm)	17	210.0 – 910.0	618.4	203.4	1	685.0	4	520.0 – 650.0	591.3	53.9	4	570.0 – 700.0	640.0	53.5	13	260.0 – 710.0	379.6	123.8	2	670.0 – 795.0	732.5	88.4
PCL	17	76.7 – 82.1	80.1	1.3	1	80.3	4	77.9 – 80.8	79.6	1.2	4	78.1 – 82.5	80.0	2.0	13	75.0 – 81.0	78.3	1.7	2	81.8 – 82.1	81.9	0.2
PD2	17	59.2 – 64.9	62.4	1.6	1	62.0	4	58.7 – 62.8	60.8	1.7	4	59.3 – 63.8	62.2	2.0	13	58.8 – 65.5	61.4	1.7	2	63.4 – 64.8	64.1	1.0
PD1	17	31.7 – 36.7	33.7	1.3	1	33.6	4	29.8 – 33.1	31.9	1.5	4	32.5 – 35.0	33.8	1.0	13	32.4 – 37.1	35.5	1.2	2	34.0 – 34.3	34.1	0.3
SVL	17	48.0 – 55.9	53.1	1.8	1	52.6	4	45.2 – 54.2	51.5	4.3	4	51.4 – 53.9	52.6	1.3	13	50.0 – 53.3	51.7	1.1	2	50.9 – 54.5	52.7	2.5
PP2	17	45.0 – 53.1	50.1	1.8	1	49.6	4	42.3 – 51.7	48.8	4.4	4	47.1 – 51.1	49.2	1.7	13	47.4 – 50.0	48.9	0.9	2	48.4 – 50.7	49.6	1.6
PP1	17	19.9 – 23.8	21.4	1.2	1	20.4	4	19.0 – 22.4	20.8	1.4	4	17.5 – 21.9	19.9	1.9	13	21.1 – 25.9	23.2	1.3	2	20.8 – 21.6	21.2	0.6
HDL	17	20.9 – 25.2	22.4	1.4	1	20.1	4	19.4 – 22.8	21.5	1.5	4	19.7 – 21.9	21.1	1.0	13	21.3 – 24.5	22.7	1.0	2	22.0 – 23.1	22.6	0.8
PG1	17	16.7 – 20.0	18.3	1.0	1	16.6	4	16.2 – 17.8	17.2	0.7	4	15.9 – 18.3	17.4	1.2	13	17.4 – 20.4	18.9	0.8	2	17.9 – 18.7	18.3	0.6
PSP	17	10.3 – 13.4	11.3	0.9	1	10.8	4	10.8 – 11.4	11.1	0.2	4	10.1 – 11.4	10.7	0.5	13	11.1 – 22.7	13.1	3.0	2	10.8 – 11.2	11.0	0.3
POB	17	5.8 – 8.2	6.9	0.7	1	6.2	4	6.1 – 7.0	6.5	0.4	4	5.5 – 6.9	6.4	0.6	13	6.7 – 8.7	7.5	0.5	2	6.4 – 7.2	6.8	0.6
PRN	17	3.9 – 5.2	4.6	0.4	1	3.8	4	3.9 – 4.9	4.3	0.4	4	3.9 – 4.9	4.4	0.4	13	4.4 – 6.0	5.1	0.5	2	3.9 – 4.5	4.2	0.4
POR	17	7.4 – 11.0	9.4	1.0	1	8.4	4	8.4 – 9.1	8.8	0.4	4	8.1 – 9.2	8.5	0.5	13	8.4 – 11.6	10.0	0.9	2	8.3 – 8.7	8.5	0.3
INLF	17	3.8 – 5.3	4.5	0.4	1	4.0	4	3.9 – 4.9	4.3	0.4	4	3.8 – 4.0	3.9	0.1	13	3.2 – 5.3	4.7	0.6	2	4.0 – 4.1	4.0	0.0
MOW	17	6.2 – 7.9	7.1	0.4	1	6.7	4	6.6 – 7.9	7.4	0.6	4	7.4 – 7.7	7.5	0.1	13	7.3 – 9.4	8.0	0.5	2	7.0 – 7.1	7.1	0.1
ULA	17	1.8 – 3.0	2.3	0.3	1	2.3	4	2.1 – 2.5	2.3	0.2	4	2.1 – 2.6	2.4	0.2	13	2.1 – 3.0	2.6	0.3	2	2.0 – 2.4	2.2	0.2
INW	17	3.0 – 3.7	3.4	0.2	1	3.1	4	2.8 – 3.6	3.3	0.4	4	3.0 – 3.8	3.4	0.4	13	3.2 – 4.6	4.0	0.4	2	3.1 – 3.5	3.3	0.3
INO	17	6.6 – 8.2	7.2	0.5	1	5.2	4	5.9 – 7.8	6.9	0.8	4	6.6 – 7.6	7.1	0.4	13	0.9 – 9.1	7.7	2.1	2	6.6 – 7.0	6.8	0.3
EYL	17	1.9 – 3.6	2.7	0.5	1	2.7	4	2.5 – 3.5	2.9	0.4	4	2.2 – 2.6	2.4	0.2	13	2.6 – 4.3	3.3	0.5	2	2.0 – 2.5	2.3	0.3
EYH	17	0.8 – 3.1	1.9	0.6	1	0.9	4	0.8 – 1.8	1.2	0.5	4	1.3 – 1.9	1.6	0.3	13	1.5 – 3.0	2.2	0.4	2	1.4 – 1.6	1.5	0.1
SPL	17	0.8 – 2.0	1.2	0.3	1	0.7	4	1.0 – 1.1	1.1	0.0	4	1.1 – 1.4	1.3	0.1	13	1.0 – 1.9	1.5	0.3	2	0.9 – 1.2	1.0	0.2
GS1	17	1.4 – 2.3	1.6	0.2	1	1.2	4	1.1 – 2.0	1.5	0.4	4	1.3 – 2.1	1.7	0.4	13	1.3 – 1.9	1.7	0.2	2	1.4 – 1.5	1.5	0.1
GS5	17	1.8 – 2.6	2.2	0.2	1	2.1	4	1.9 – 2.3	2.1	0.2	4	1.9 – 2.4	2.1	0.2	13	1.9 – 2.5	2.1	0.2	2	2.0 – 2.1	2.1	0.0
IDS	17	18.7 – 26.5	22.5	2.2	1	22.6	4	22.9 – 24.8	23.5	0.9	4	17.9 – 24.6	22.1	3.0	13	17.9 – 24.1	20.6	1.9	2	24.5 – 24.6	24.6	0.1
DCS	17	9.7 – 12.0	11.2	0.6	1	11.7	4	10.9 – 13.5	12.0	1.1	4	9.7 – 12.2	10.9	1.0	13	10.5 – 13.8	12.0	0.9	2	11.2 – 12.5	11.8	0.9
PPS	17	23.0 – 28.6	25.9	1.9	1	21.9	4	21.2 – 26.4	24.6	2.5	4	21.4 – 27.2	24.4	2.4	13	20.1 – 26.8	23.9	2.1	2	25.2 – 27.6	26.4	1.7
PCA	17	19.7 – 25.3	22.7	1.2	1	24.1	4	24.0 – 27.9	25.5	1.7	4	20.6 – 24.6	22.0	1.7	13	20.4 – 25.9	22.8	1.4	2	23.1 – 23.3	23.2	0.1
D1L	17	11.2 – 13.6	12.3	0.7	1	12.1	4	11.5 – 14.3	12.5	1.2	4	12.9 – 14.8	13.4	0.9	13	11.4 – 12.9	12.0	0.5	2	12.0 – 13.6	12.8	1.1
D1A	17	8.1 – 12.0	9.6	0.9	1	8.6	4	9.1 – 11.9	10.4	1.1	4	9.3 – 10.1	9.6	0.4	13	9.0 – 10.4	9.7	0.5	2	8.8 – 10.3	9.6	1.1
D1B	17	6.2 – 8.5	7.2	0.6	1	7.0	4	7.3 – 7.8	7.5	0.2	4	7.1 – 8.6	7.8	0.7	13	6.3 – 7.9	7.0	0.5	2	7.2 – 8.7	7.9	1.1
D1H	17	6.0 – 7.6	6.8	0.4	1	5.8	4	6.4 – 9.2	7.4	1.2	4	5.9 – 6.6	6.3	0.3	13	6.5 – 8.0	6.9	0.4	2	5.8 – 6.9	6.4	0.8
D1I	17	5.0 – 6.5	5.6	0.4	1	5.5	4	4.6 – 6.8	5.4	1.0	4	5.2 – 6.2	5.7	0.4	13	4.9 – 5.9	5.3	0.3	2	4.9 – 5.2	5.0	0.2
D1P	17	6.0 – 8.3	7.2	0.7	1	7.5	4	5.3 – 7.5	6.8	1.0	4	7.1 – 7.4	7.3	0.1	13	5.9 – 8.0	6.7	0.6	2	6.4 – 8.4	7.4	1.4
D1ES	15	1.6 – 3.1	2.0	0.4	1	1.6	4	2.0 – 4.6	2.7	1.2	4	1.5 – 2.2	1.9	0.3	13	1.5 – 2.5	2.0	0.2	2	0.8 – 1.3	1.1	0.3
D1BS	17	0.4 – 0.8	0.6	0.1	1	0.5	4	0.5 – 0.8	0.6	0.1	4	0.5 – 0.6	0.5	0.1	13	0.4 – 0.7	0.5	0.1	2	0.4 – 0.5	0.5	0.1
D2L	17	10.0 – 13.2	11.9	0.8	1	12.2	4	11.5 – 13.4	12.2	0.9	4	10.9 – 13.5	12.1	1.4	13	9.4 – 14.3	11.3	1.2	2	10.8 – 11.0	10.9	0.2
D2A	17	7.6 – 10.1	9.0	0.7	1	8.5	4	8.6 – 11.5	9.5	1.3	4	7.7 – 9.7	8.6	1.1	13	6.8 – 10.8	8.4	1.1	2	6.8 – 8.2	7.5	1.0
D2B	17	5.7 – 8.1	7.0	0.6	1	7.2	4	7.1 – 7.7	7.5	0.3	4	6.3 – 8.3	7.1	1.0	13	4.8 – 9.5	6.6	1.1	2	5.8 – 7.1	6.4	0.9
D2H	17	4.4 – 6.9	5.1	0.7	1	4.9	4	4.6 – 6.6	5.2	1.0	4	4.5 – 4.7	4.6	0.1	13	4.1 – 5.4	4.7	0.4	2	3.7 – 4.4	4.1	0.5
D2I	17	4.4 – 6.1	5.1	0.5	1	5.2	4	4.1 – 5.8	4.8	0.7	4	4.5 – 6.1	5.1	0.7	13	4.0 – 5.4	4.9	0.4	2	4.3 – 4.9	4.6	0.5
D2P	17	4.2 – 6.7	5.4	0.6	1	5.8	4	4.3 – 5.5	5.0	0.5	4	4.6 – 5.6	5.3	0.4	13	4.1 – 5.7	5.2	0.5	2	4.7 – 5.4	5.0	0.5
D2ES	16	2.5 – 4.1	3.4	0.5	1	3.4	4	3.1 – 6.0	4.0	1.4	3	2.5 – 3.4	3.0	0.4	13	3.1 – 4.6	3.6	0.4	2	1.5 – 2.9	2.2	1.0

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TABLE 4. (Continued)

Measurements	Northwestern Atlantic				Central Western Atlantic		Mediterranean Sea				Northeastern Atlantic				Northeastern Pacific				Southeastern Pacific			
	N	Range	*x*	SD	N		N	Range	*x*	SD	N	Range	*x*	SD	N	Range	*x*	SD	N	Range	*x*	SD
D2BS	17	0.6 – 1.3	0.8	0.2	1	0.7	4	0.7 – 1.0	0.8	0.1	4	0.6 – 0.7	0.6	0.1	13	0.6 – 3.8	1.0	0.8	2	0.6 – 0.7	0.6	0.1
P1A	17	10.9 – 17.6	14.6	1.7	1	14.2	4	14.2 – 17.3	15.7	1.4	4	14.3 – 15.9	15.0	0.7	13	11.0 – 15.0	13.1	1.1	2	14.1 – 15.3	14.7	0.8
P1I	17	7.3 – 9.0	8.2	0.5	1	8.3	4	7.6 – 10.2	8.9	1.3	4	7.6 – 8.9	8.3	0.6	13	7.3 – 10.2	8.3	0.7	2	8.0 – 8.4	8.2	0.2
P1B	17	4.1 – 5.5	4.9	0.4	1	4.5	4	2.8 – 5.8	4.5	1.4	4	4.4 – 5.1	4.7	0.3	13	3.7 – 5.2	4.4	0.5	2	4.5 – 5.4	4.9	0.6
P1P	17	6.6 – 11.9	9.7	1.6	1	10.6	4	10.5 – 13.7	11.5	1.5	4	9.4 – 10.3	9.9	0.4	13	5.5 – 10.3	8.6	1.5	2	10.8 – 10.8	10.8	0.0
P2L	17	9.2 – 12.3	10.7	1.1	1	11.1	4	10.0 – 11.8	11.1	0.8	4	10.6 – 12.8	11.5	1.0	13	9.6 – 11.1	10.3	0.6	2	10.6 – 11.4	11.0	0.6
P2I	17	3.9 – 6.7	5.2	0.8	1	6.3	4	4.4 – 7.0	5.9	1.2	4	4.1 – 7.4	5.5	1.4	13	4.0 – 6.9	5.2	0.7	2	5.1 – 5.5	5.3	0.3
CDM	17	11.3 – 22.0	20.3	2.4	1	21.6	4	19.8 – 22.2	20.7	1.0	4	19.9 – 21.9	20.9	1.1	13	20.4 – 24.6	21.6	1.1	2	16.0 – 19.5	17.8	2.5
CPV	17	5.6 – 22.0	11.4	3.1	1	10.6	4	9.7 – 11.7	10.7	1.1	4	10.1 – 12.7	11.2	1.1	13	10.1 – 12.9	11.3	0.7	2	10.4 – 11.3	10.8	0.6
CFW	17	6.1 – 7.5	6.8	0.4	1	6.9	4	4.9 – 7.5	6.4	1.1	4	6.7 – 8.2	7.6	0.7	13	6.0 – 7.4	6.7	0.4	2	6.6 – 7.1	6.9	0.4
HANW	17	4.9 – 6.6	5.8	0.5	1	4.9	4	4.9 – 6.6	5.7	0.7	4	5.3 – 6.2	5.9	0.4	13	5.8 – 7.8	6.8	0.6	2	4.9 – 5.7	5.3	0.6
HAMW	17	8.1 – 10.5	9.1	0.6	1	6.9	4	8.2 – 10.8	9.4	1.1	4	9.4 – 10.0	9.8	0.3	13	8.8 – 11.3	10.0	0.7	2	8.4 – 9.1	8.8	0.5
HDW	17	9.1 – 12.5	10.8	0.8	1	10.0	4	9.4 – 11.7	10.5	1.0	4	11.3 – 20.0	13.7	4.2	13	6.8 – 12.1	10.8	1.4	2	9.8 – 12.9	11.4	2.2
TRW	17	7.1 – 11.1	8.8	1.3	1	8.5	4	7.4 – 8.4	8.0	0.4	4	8.3 – 10.2	9.1	0.9	13	5.2 – 10.4	8.4	1.4	2	6.4 – 8.4	7.4	1.4
ABW	17	5.4 – 8.8	7.0	1.0	1	6.8	4	4.8 – 6.6	5.6	0.9	4	5.9 – 8.4	7.1	1.1	13	4.3 – 7.6	5.9	0.8	2	4.6 – 5.5	5.1	0.7
HDH	17	5.7 – 10.0	8.9	1.0	1	10.2	4	6.7 – 9.1	8.2	1.1	4	8.2 – 9.6	8.8	0.7	13	5.1 – 9.7	8.5	1.2	2	7.9 – 8.6	8.3	0.5
TRH	17	6.9 – 11.3	9.3	1.2	1	10.7	4	7.7 – 10.1	9.0	1.0	4	6.9 – 9.3	8.6	1.1	13	6.7 – 10.8	8.7	1.2	2	6.1 – 8.0	7.1	1.3
ABH	17	6.1 – 10.5	8.3	1.3	1	10.5	4	5.8 – 7.2	6.5	0.6	4	7.1 – 8.7	8.0	0.7	13	5.1 – 9.3	7.7	1.3	2	5.0 – 9.9	7.5	3.5
CLO	9	1.3 – 6.7	4.6	2.4	1	5.9	2	6.0 – 6.0	6.0	0.0	2	5.5 – 6.4	5.9	0.6	9	1.5 – 3.1	2.0	0.5	1	–	6.0	–
CLI	9	1.4 – 9.6	6.6	3.3	1	8.4	2	8.8 – 9.9	9.4	0.8	2	7.9 – 9.4	8.7	1.0	9	2.3 – 4.3	3.5	0.7	1	–	8.1	–

The dorsolateral white spots in *S. acanthias* usually are smaller and in greater quantity in neonates and young juveniles than in adults as they reduce with maturity, as supported by previous authors (e.g. Jordan & Evermann, 1896; Bigelow & Schroeder, 1948; Myagkov & Kondyurin, 1986). Bass *et al*. (1976) and Cadenat & Blache (1981) also demonstrated variation in dermal denticles with growth, although this was not observed by us once; even the largest specimens also had unicuspid dermal denticles without any lateral expansions.

Myagkov & Kondyurin (1986) recognized four subspecies of *S. acanthias* due its great apparent morphological variation: *S. acanthias acanthias* (sensu Lindberg & Legeza, 1956) from the North Atlantic, *S. acanthias* ssp. from the North Pacific, *S. acanthias ponticus* Myagkov & Kondyurin, 1986 from the Black Sea, and *S. acanthias africana* Myagkov & Kondyurin, 1986 from the Southeastern Atlantic Ocean. The first two subspecies had been differentiated anteriorly by Lindberg & Legeza (1956, 1959) by pectoral-fin length. According to these authors, pectoral length is greater in *S. acanthias suckleyi* than in *S. acanthias acanthias*, as was also reported by Regan (1908). Myagkov & Kondyurin (1986) present additional characters to separate them, concerning tooth formula and the number of total vertebrae, in which the latter is greater in specimens from the North Atlantic Ocean. However, these characters were based on neonates and used an unclear methodology that leaves doubt regarding its reliability. Myagkov & Kondyurin (1986) also provided the following features for *S. acanthias acanthias*: base length of pelvic fins 1.5 times greater than base length of the second dorsal fin; distance from snout tip to nostrils much greater than internarial distance; teeth varying from 14–14 on the upper jaw and 11–12 on the lower jaw; number of total vertebrae greater than 106. These characters, however, overlap with other species of *Squalus* described in their work.

We analyzed the holotypes of *Squalus tasmaniensis* Howell-Rivero, 1936 from Tasmania and *Squalus barbouri* Howell-Rivero, 1936 from Cuba. The characters used by Howell-Rivero (1936a) to distinguish these two species from congeners, such as small white spots on the dorsum and the position of the first dorsal-fin spine in relation to the pectoral fins, are problematic as they vary ontogenetically. Both holotypes correspond to juveniles (245 mm and 267 mm, respectively) very similar to typical young specimens of *S. acanthias* regarding external morphology and dermal denticles (Figs. 14, 15). Some body measurements (Table 1), however, are quite distinct, such as pre-first dorsal fin length, prepelvic length, second dorsal-fin height, and mouth width, although many of these variations are not relevant due to the lack of accuracy for the measurements of the holotypes that are in poor condition.

Squalus acanthias can be easily identified by the presence of white spots on the dorsum once no other congener has this particular color pattern (other than *S. suckleyi*), associated with the more posterior position of the first dorsal-fin spine in relation to the free rear tips of the pectoral fin, and the presence of a single simple lobe on the anterior margin of the nostrils, as corroborated by the present study and earlier studies, such as Meneses & Paesch (2003) for Mar del Plata, Argentina, Gomes *et al*. (1997) for Brazil, and Lamilla & Bustamante (2005) for Chile.

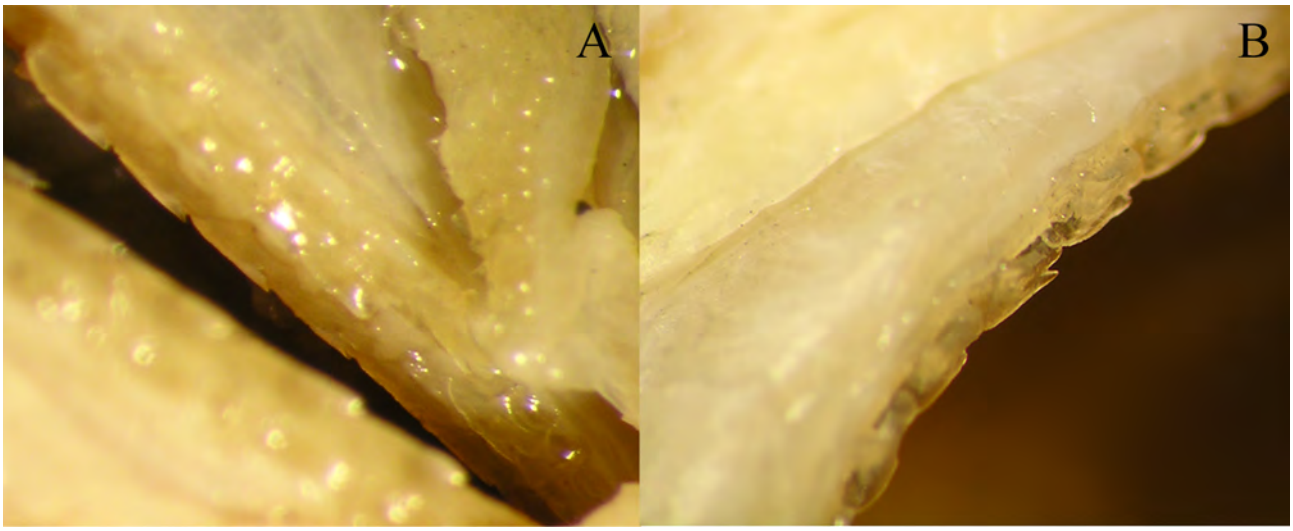

FIGURE 14. Teeth of holotypes of (A) *Squalus tasmaniensis* (MCZ 146-S, neonate female) and (B) *Squalus barbouri* (MCZ 1463-S, neonate female).

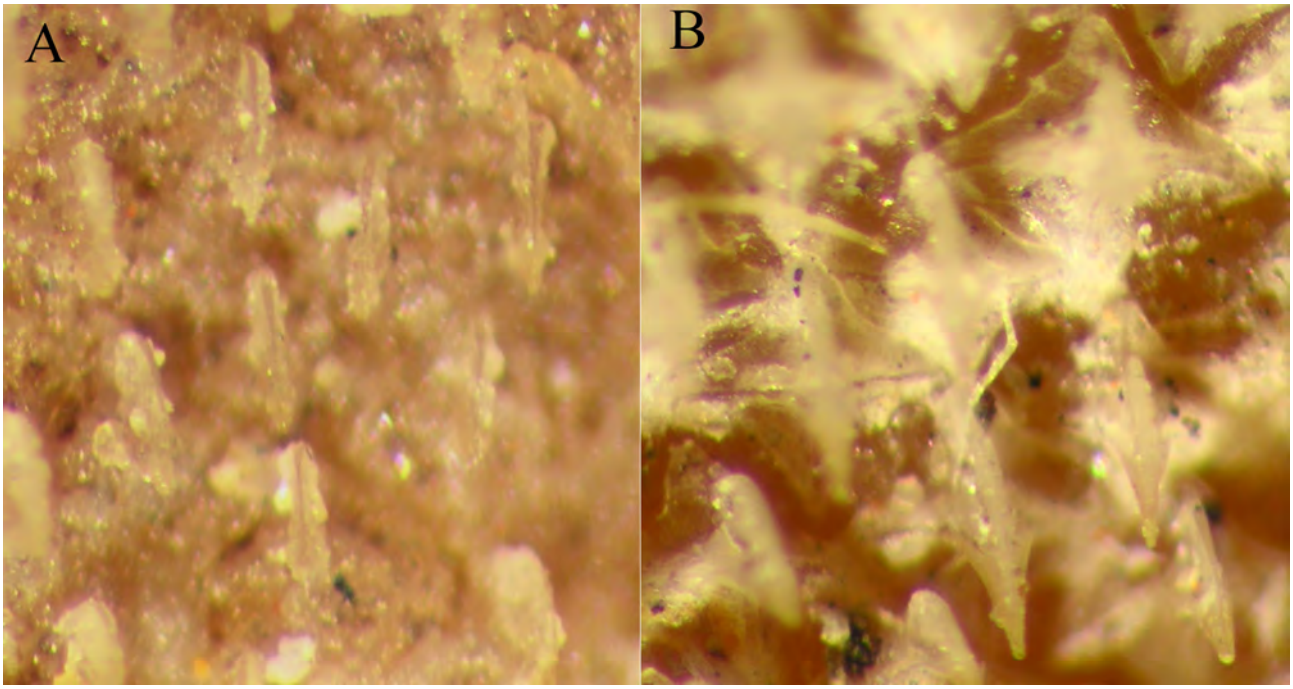

FIGURE 15. Dermal denticles of holotypes of (A) *Squalus tasmaniensis* (MCZ 146-S) and (B) *Squalus barbouri* (MCZ 1463-S) in ventral view.

Despite the morphological particularities observed in specimens of different geographical regions, it is still difficult to subdivide *S. acanthias* into different species based on morphology (including *S. suckleyi*); recognizing a complex of cryptic species with the tenuous data presently in hand may disrupt nomenclatural stability. Revising *S. acanthias* taxonomically on a global scale through a detailed morphological analysis (external and skeletal) and taking into account all of its regional variations is ongoing (Viana & Carvalho, in prep.).

Comparative material. *Squalus acanthias*: Northwestern Atlantic Ocean (151 specimens): AMNH 1, neonate female, 165 mm TL, neonate male, 153 mm TL, no data; AMNH 652, neonate female, 209 mm TL, New York, U.S.A.; AMNH 656, neonate female, 158 mm TL, New Jersey, U.S.A.; AMNH 3518, neonate female, 186 mm TL; three neonate males, 177–187 mm TL, Canada; AMNH 7175, juvenile female, 305 mm TL, New Jersey, U.S.A.; AMNH 8955, nine neonate females, 155–205 mm TL, three neonate males, 169–190 mm TL, Massachusetts, U.S.A.; AMNH 36980, neonate female, 207 mm TL, neonate male, 198 mm TL, Monhegan Island, Maine, U.S.A.; AMNH 40205, three neonate females, 242–254 mm TL, two neonate males, 252–253 mm TL, Rhode Island, U.S.A.; AMNH 40802, two neonate females, 190–207 mm TL, two neonate males, 189–190 mm TL, Woods Hole, Massachusetts, U.S.A.; AMNH 44117, adult male, 755 mm TL, Rhode Island, U.S.A.; AMNH 56194, neonate male, 226 mm TL, New York, U.S.A.; AMNH 65177, juvenile female, 445 mm TL, North Carolina, U.S.A.; AMNH 73637, neonate female, 163 mm TL, North Carolina, U.S.A.; AMNH 76046, two neonate females, 188–198 mm TL, South Carolina, U.S.A.; AMNH 216291, two neonate females, 93–118 mm TL, U.S.A.; AMNH 221591, four neonate male, 250–287 mm TL, New York, U.S.A.; AMNH 3517 (skeleton, no data), Weymouth, St. Mary Bay, Nova Scotia, Canada; AMNH 53052 (skeleton, no data), U.S.A.; AMNH 97553 (skeleton, no data), U.S.A.; AMNH 221706 (skeleton), adult female, 860 mm TL, Worcester County, Maryland, U.S.A.; AMNH 221711, neonate female, 139 mm TL, Worcester County, Maryland, U.S.A.; AMNH 225783 (skeleton, no data), North Carolina, U.S.A.; CAS 11226, neonate male, 200 mm TL, Massachusetts, U.S.A.; CAS 11227, neonate female, 166 mm TL, Massachusetts, U.S.A.; CAS 11228, neonate male, 185 mm TL, Massachusetts, U.S.A.; SU 3990, neonate male, 167 mm TL, Massachusetts, U.S.A.; MCZ 168-S, adult female, 910 mm TL, Grand Manan Island, New Brunswick, Canada; MCZ 172-S, 18 neonate females, 155–205 mm TL, Massachusetts Bay, U.S.A.; MCZ 454-S, adult male, 720 mm TL, Massachusetts Bay, U.S.A., 42.41°N, 70.88°W; MCZ 458-S, adult female, 820 mm TL, Waquoit, Massachusetts, U.S.A., 41.58°N, 70.52°W; MCZ 520-S, five neonate females, 180–215 mm TL, seven neonate males, 160–210 mm TL, Massachusetts Bay, U.S.A., 42.42°N, 70.90°W; MCZ 840-S, adult female, 675 mm TL, New Hampshire, U.S.A.; MCZ 851-S, adult female, 625 mm TL, Massachusetts Bay, U.S.A.,

42.37°N, 70.74°W; MCZ 872-S, adult female, 870 mm TL, Gloucester, Massachusetts, U.S.A., 42.61°N, 70.66°W; MCZ 1426-S, two neonate females, 190 mm TL, nine neonate males, 163–210 mm TL, Cape Ann, Massachusetts, U.S.A., 42.64°N, 70.64°W; MCZ 34406, neonate female, 280 mm TL, Rhode Island, U.S.A., 41°4´N, 70°46´W; MCZ 35862, adult female, 805 mm TL, Buzzard Bay, Massachusetts, U.S.A., 41.56°N, 70.74°W; MCZ 35863, adult female, 790 mm TL, Massachusetts, U.S.A., 41.56°N, 70.74°W; MCZ 35864, adult male, 695 mm TL, Buzzard Bay, Massachusetts, U.S.A., 41.56°N, 70.74°W; MCZ 39679, adult female, 720 mm TL, no data; MCZ 58675, 10 neonate females, 188–210 mm TL, seven neonate males, 180–210 mm TL, Buzzard Bay, Massachusetts, U.S.A., 41.70°N, 70.75°W; MCZ 99596, four neonate females, 178–210 mm TL, five neonate males, 180–215 mm TL, Massachusetts, U.S.A., 43°39´N, 69°58´W; MCZ 167209, juvenile female, 540 mm TL, adult female, 660 mm TL, New England, U.S.A.; MCZ 502-S, juvenile male, 470 mm TL, unknown locality (probably Europe); MCZ 861-S, adult female, 860 mm TL, unknown locality; MCZ 51312-S, neonate female, 265 mm TL, unknown locality; NRM 36067, adult female, 935 mm TL, Gulf of Maine, Nahant, Massachusetts, U.S.A., 4242'N, 709'W; UFPB 1480, neonate female, 222 mm TL, Virginia, U.S.A.; USNM 31965, adult male, 605 mm TL, British Columbia, Canada; USNM 72285, adult female, 670 mm TL, New River Rocks, North Carolina, U.S.A.; USNM 201930, adult female, 755 mm TL, two adult males, 683–690 mm TL, juvenile male, 565 mm TL, Cape Hatteras, North Carolina, U.S.A., 36°90'N, 74°65'W; USNM 201943, adult male, 670 mm TL, Cape Hatteras, Virginia, U.S.A., 36°90'N, 74°65'W; USNM 205051, adult female, 680 mm TL, adult male, 665 mm TL, Silver Bay, North Carolina, U.S.A., 35°50'N,75°45'W; USNM 205052, adult male, 615 mm TL, Virginia, U.S.A.; USNM 205056, adult male, 650 mm TL, Silver Bay, South Carolina, U.S.A., 32°80'N, 79°60'W; USNM 386056, juvenile female, 548 mm TL, subadult juvenile male, 600 mm TL, Massachusetts, U.S.A., 42°50'N, 68°56'W; ZMB 10237, adult female, 720 mm TL, Woods Hole, Massachusetts, U.S.A.; ZMH 101004, juvenile male, 555 mm TL, Newfoundland, Canada, 5924'W, 4740'N. Western Central Atlantic (17 specimens): MCZ 201-S, adult female, 880 mm TL, Minas Bay, Cuba, 21°30´N,77°38´W; MCZ 1463-S (holotype of *Squalus barbouri*), neonate female, 267 mm TL, Jaimanitas Beach, Cuba; USNM 116902, three neonate females, 143–225 mm TL, four neonate males, 143–223 mm TL, Tortugas, Florida, U.S.A.; USNM 201917, adult male, 685 mm TL, Silver Bay, Florida,U.S.A., 29°93'N, 81°23'W; USNM 205049, juvenile male, 452 mm TL, Silver Bay, Florida, U.S.A., 29°90'N, 80°18'W; USNM 205050, two juvenile females, 455–465 mm TL, Silver Bay, Florida, U.S.A., 29°97'N, 80°12'W; USNM 205053, juvenile male, 520 mm TL, Silver Bay, Florida, U.S.A., 29°97'N, 80°12'W; USNM 205054, adult female, 725 mm TL, Silver Bay, Georgia, U.S.A., 31°73'N, 79°63'W; USNM 205055, adult male, 615 mm TL, Silver Bay, Florida, U.S.A., 29°90'N, 80°18'W; USNM 205057, juvenile female, 470 mm TL, Silver Bay, Florida, U.S.A., 29°97'N, 80°12'W. Northeastern Atlantic Ocean (12 specimens): MCZ 85-S, adult male, 650 mm TL, Le Havre, English Channel, France; MCZ 408-S, juvenile male, 650 mm TL, Trieste, Italy; MCZ 466-S, juvenile male, 520 mm TL, Maritime Alps, Nice, France; MCZ 467-S, juvenile female, 590 mm TL, Maritime Alps, Nice, France; MCZ 468-S, adult female, 640 mm TL; two neonate males, 140–145 mm TL; neonate male, 145 mm TL, Le Havre, English Channel, France; MCZ 478-S, adult female, 720 mm TL, North Sea; MCZ 905-S, adult female, 780 mm TL, Bohustan, Sweden; MCZ 906-S, juvenile female, 375 mm TL, Venice, Italy; UERJ 182, adult female, 1000 mm TL, Gulf of Lion, Mediterranean Sea; UERJ 185, adult male, 710 mm TL, Gulf of Lion, Mediterranean Sea. Southeastern Atlantic Ocean (13 specimens): MCZ 346-S, adult male, 1010 mm TL, South Africa; SAIAB 21873, adult male, 675 mm TL, Cape Columbine, South Africa, 3259'S, 1736'E; SAIAB 25918, adult male, 700 mm TL, West coast of South Africa, 3148'S, 1727'E; SAIAB 26301, adult female, 670 mm TL, West coast of South Africa, 3270'S, 1720'E; SAM 32584, adult male, 705 mm TL, West coast of South Africa, 3108'S, 1651'E; SAM 33184 juvenile female, 527 mm TL, West coast of South Africa, 2991'S, 1617'E; UF 46768, juvenile male, 570 mm TL, southwestern region of Cape Town, South Africa; USNM 197692, adult female, 733 mm TL, west coast of Cape Town, South Africa; USNM 199655, adult female, 640 mm TL; adult male, 700 mm TL, Gabon; ZMB 21982, juvenile male, 555 mm TL, Southeastern Atlantic Ocean (no specific locality); ZMB 22989, juvenile male, 562 mm TL, Southeastern Atlantic Ocean (no specific locality); ZMH 151302, juvenile male, 520 mm TL, off Namibia. Northwestern Pacific Ocean (7 specimens): HUMZ 87733, juvenile male, 495 mm TL, off Shiretoko, Hokkaido, Japan (dissected); HUMZ 68927, adult female, 952 mm TL, Yamasedomari Fish Market, Hakodate, Hokkaido, Japan; HUMZ 107865, juvenile female, 465 mm TL, off Sekinai, Kumaishi, Hokkaido, Japan; HUMZ 123859, adult male, 815 mm TL, north Japan, 4400.1'N, 15500.1'E; MCZ 158057-S, juvenile male, 490 mm TL, Korea; NSMT-P 92640, adult female, 740 mm TL, Northern Japan, Japan; SU 23469, neonate female, 280 mm TL, Japan. Northeastern Pacific Ocean (58 specimens): CAS 11229, neonate male, 210 mm TL, Steinhart Aquarium,

San Francisco, California, U.S.A.; CAS 13038, neonate male, no data, Northeast California, U.S.A.; CAS 13127, neonate male, 380 mm TL, Roberts reef, Puget Sound, Washington, U.S.A.; CAS 19149, neonate male, 210 mm TL, San Francisco Bay, California, U.S.A.; CAS 21292, neonate male, 225 mm TL, San Francisco Bay, California, U.S.A.; CAS 21424, five neonate females, 235–290 mm TL, neonate male, 235 mm TL, two juvenile males, 300–375 mm TL, San Francisco Bay, California, U.S.A.; CAS 21444, neonate female, 180 mm TL, neonate male, 195 mm TL, San Francisco Bay, California, U.S.A.; CAS 21468, neonate female, 290 mm TL, neonate male, 185 mm TL, San Francisco Bay, California, U.S.A.; CAS 21767, juvenile female, 410 mm TL, San Francisco Bay, California, U.S.A.; CAS 21898, neonate female, 250 mm TL, neonate male, 260 mm TL, San Francisco Bay, California, U.S.A.; CAS 21971, seven neonate females, 250–285 mm TL, two juvenile females, 310–315 mm TL, four neonate males, 232–305 mm TL, three juvenile males, 310–330 mm TL, San Francisco Bay, California, U.S.A.; CAS 40863, juvenile male, 340 mm TL, California, U.S.A.; CAS 40865, neonate male, 220 mm TL, San Francisco, California, U.S.A.; CAS 40866, neonate female, 212 mm TL, San Francisco Bay, California, U.S.A.; CAS 40872, two neonate males, 245 mm TL, San Francisco Bay, California, U.S.A.; CAS 40873, two juvenile females, 340–355 mm TL, five juvenile males, 320–390 mm TL, Roberts reef, Puget Sound, Washington, U.S.A.; CAS 56093, four neonate females, 270–265 mm TL, neonate male, 260 mm TL, San Francisco Bay, California, U.S.A.; SU 13023, adult male, 710 mm TL, San Diego Bay, California, U.S.A.; SU 58376, juvenile male, 480 mm TL, Monterey Bay, California, U.S.A.; MCZ 167-S, two adult males, 770–810 mm TL, San Francisco, California, U.S.A.; MCZ 36466-S, juvenile male, 670 mm TL, La Jolla, California, U.S.A.. Southwestern Pacific (3 specimens): MCZ 146-S (holotype of *Squalus tasmaniensis*), neonate female, 245 mm TL, Hobart, Tasmania, Australia; USNM 176796, adult female, 780 mm TL, New Zealand; USNM 176800, adult male, 740 mm TL, New Zealand. Southeastern Pacific (3 specimens): MZUSP 37366, neonate female, 260 mm TL, Valdivia, Chile; SU 13381, adult male, 670 mm TL, Gregory Bay, Strait of Magallanes, Chile; USNM 208074, adult female, 795 mm TL, Chile, 39°70'S, 73°45'W.

***Squalus lobularis* sp. nov.**

(Figs. 16–24; Tables 3, 5–6)

Suggested common names: Atlantic lobefin dogfish; Cação-bagre-de-nadadeiras-lobadas (Portuguese).

Squalus cubensis (not Howell-Rivero): Figueiredo, 1977: 8, fig. 7 (description; Southern Brazil and Uruguay).
Squalus sp. of the *blainvillei* group: Figueiredo, 1981: 17 (listed; Brazil); Gomes *et al*., 1997: 94–95 (listed; Brazil); Marques, 1999 (description; Brazil).
Squalus mitsukurii (not Jordan & Snyder): Calderón, 1994: 1–43, fig. 5b (cited; Brazil); Lessa *et al*., 1999: 61, 150 (cited, listed; South Brazil); Lamilla & Bustamante, 2005: 9, 26 (listed; Chile); Compagno, 2002: 385 (description; Northeast Brazil and Argentina); Compagno *et al*., 2005: 77–78, plate 3 (cited; Southeast Brazil).
Squalus of the *blainvillei*/*mitsukurii* group: Gadig, 2001 (in part): 29, 36, 54–55, fig. 29 (cited; Brazil).
Squalus sp. B: Soto, 2001: 96 (listed; Brazil); Soto & Mincarone, 2004: 79–82 (listed; Brazil).
Squalus sp. 1: Gomes *et al*., 2010: 44, 45 (cited; Brazil).
Squalus sp.: Viana, 2011: 163–185, figs. 78–80, 83, 85, 87–92 (revision; Brazil, Argentina, Uruguay); Naylor *et al*., 2012: 57, 205, fig. 42 (molecular systematics; Western South Atlantic).

Holotype. HUMZ 91806, juvenile female, 557 mm TL, off Patagonia, Argentina, 3930'S, 5828'W. Unknown collector. Collecting date 16 January 1979.

Paratypes (9 specimens). HUMZ 30026, adult female, 725 mm TL, off Patagonia, Argentina, 4235'S, 6311'W; HUMZ 30032, adult female, 675 mm TL, off Patagonia, Argentina, 4235'S, 6311'W; HUMZ 91801, adult female, 650 mm TL, off Patagonia, Argentina, 3930'S, 5828'W; HUMZ 91804, juvenile female, 545 mm TL, off Patagonia, Argentina, 3930'S, 5828'W; HUMZ 91807, juvenile female, 605 mm TL, off Patagonia, Argentina, 3930'S, 5828'W; UERJ 1661, adult male, 640 mm TL, unknown locality (dissected), Southeast Brazil; UERJ 2024, juvenile female, 530 mm TL, off Espírito Santo, Brazil; UERJ 2025, adult female, 600 mm TL; same locality as UERJ 2024. UERJ 2026, adult female, 675 mm TL, same locality as UERJ 2024.

Non-type material (32 specimens). FURG 80.0607, juvenile female, 510 mm TL, off Rio Grande do Sul coast, Brazil, 3219'S, 5152'W; FURG 80.0609, adult male, 630 mm TL, South of Mar del Plata, Argentina, 38°S, 51°W; FURG 98.0031, two juvenile males, 380–450 mm TL, off Rio Grande do Sul coast, Brazil, 3219'S, 5152'W; MZUSP 37351, neonate female, 240 mm TL, juvenile male, 340 mm TL, Uruguay, 3550'S, 5306'W; MZUSP

37355, two juvenile female, 335–340 mm TL; three juvenile male, 335–360 mm TL, Uruguay, 3544'S, 5322'W; UERJ 1112, adult male, 635 mm TL, Rio Grande do Sul, Brazil (dissected); ZMH 104558, adult male, 600 mm TL, Argentina, 380'S, 5633'W; ZMH 104707, juvenile male, 247 mm TL, Argentina, 3649'S, 5437'W; ZMH 104945, neonate female, 235 mm TL, Argentina, 4216'S, 6153'W; ZMH 107897, adult male, 605 mm TL, Argentina, 400'S, 590'W.

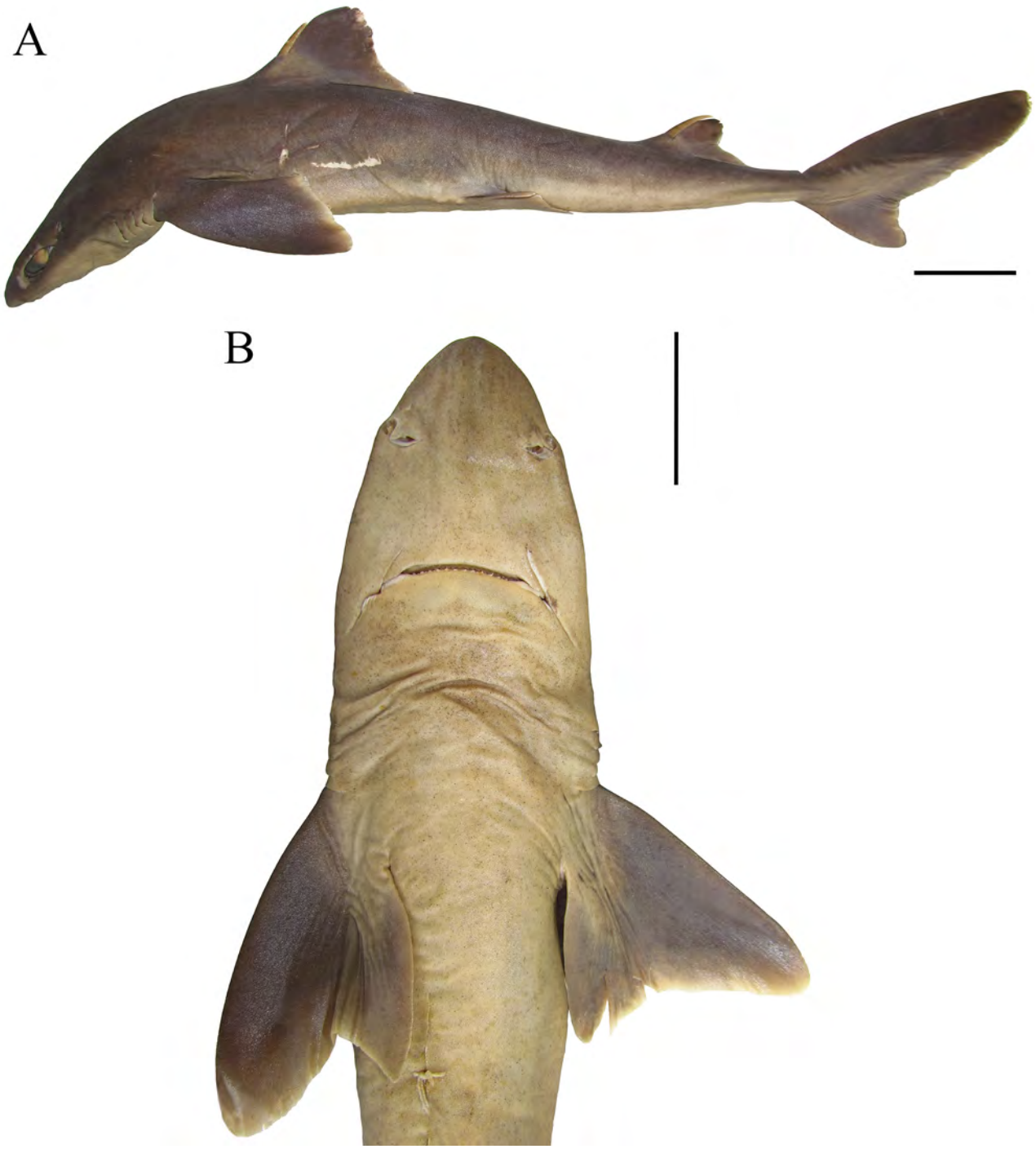

FIGURE 16. Holotype of *Squalus lobularis* **sp. nov.** (HUMZ 91806, juvenile female, 557 mm TL) in (A) lateral and (B) ventral views. Scale bar: 50 mm.

Diagnosis. A species of *Squalus* from SWAO that differs from its congeners by the combination of having markedly broad and lobe-like dorsal fins and short clasper groove, not reaching the rhipidion. *Squalus lobularis* **sp. nov.** is clearly distinct from *S. mitsukurii* from Japan, its morphologically closest congener, by having a slender

body (*vs*. highly robust body in *S. mitsukurii*), pectoral-fin posterior margin concave (*vs*. pectoral-fin posterior margin straight in *S. mitsukurii*), narrower interorbital space (8.8%, 6.8%–8.5% TL *vs*. 9.3%, 9.1%–9.8% TL in *S. mitsukurii*); and inner clasper length 1.4 times pelvic-fin inner margin length (*vs*. 0.7–1.1 times in *S. mitsukurii*). *Squalus lobularis* **sp. nov.** further differs from species of the *Squalus megalops* group by: snout relatively long *vs*. snout short; pectoral fins markedly broad *vs*. pectoral fins often very narrow; pectoral free rear tips rounded and lobe-like *vs*. pectoral free rear tips often triangular; dermal denticles tricuspidate *vs*. lanceolate. It further differs from all its congeners by having a much larger pectoral-inner margin length (10.5%, 9.2%–11.0% TL), except from *S. acanthias*.

Description. **External morphology**. Measurements and meristic data are summarized in Tables 5–6. Body fusiform, slender and depressed through, with head height 0.9 (0.8–1.3) times trunk height and 1.0 (0.8–1.2) times abdomen height; greatest width of body at head with head width 1.3 (1.0–1.3) times trunk width and 1.6 (1.2–1.7) times abdomen width. Head flattened dorsally and elongate, its length 22.7% (21.5%–24.3% TL); head broader at mouth than at nostrils (width at mouth 12.2%, 9.7%–12.2% TL *vs*. width at nostrils 7.5%, 6.3%–7.4% TL). Snout very large (preorbital length 7.9%, 7.0%–7.9% TL), obtuse and rounded at tip; anterior margin of nostrils strongly bilobate, positioned more laterally; prenarial length 1.2 (1.0–1.2) times distance from nostril to upper labial furrow; prenarial length 1.3 (1.1–1.4) times eye length; internarial space 1.1 (0.9–1.5) times eye length. Eyes oval, placed laterally closer to the snout tip than first gill slit, with anterior margin convex and posterior margin notched; eyes enlarged, their length 2.3 (1.7–2.9) times their height. Prespiracular length 1.6 (1.6–1.7) times preorbital length. Spiracles subtriangular and conspicuously broad, their length 1.2% (1.0%–1.6% TL), and corresponding to 0.3 (0.3–0.4) times eyes length. Prebranchial length 1.5 (1.5–1.7) times prespiracular length. Gill slits vertical and tall, with fifth gill slit 1.2 (1.0–1.6) times higher than first gill slit.

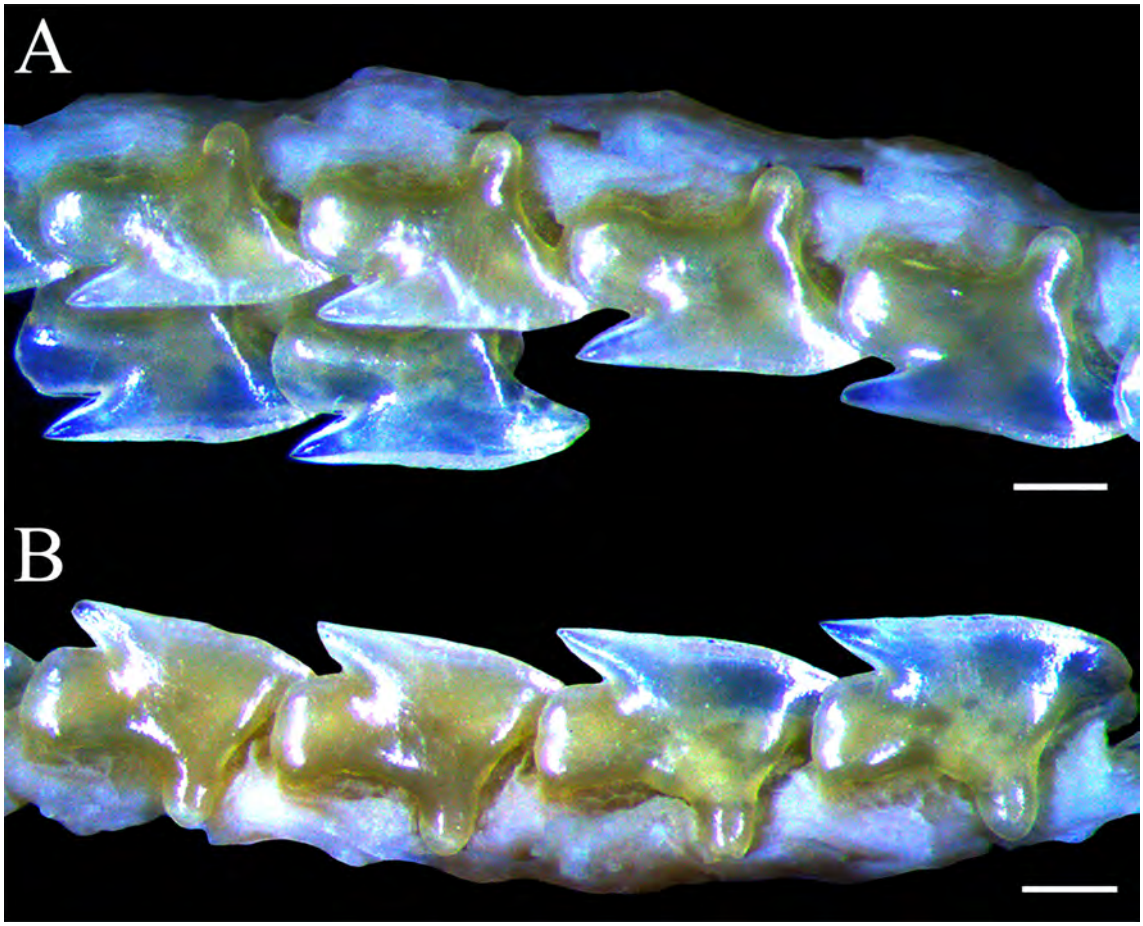

FIGURE 17. Upper (A) and lower (B) teeth of holotype of *Squalus lobularis* (HUMZ 91806, juvenile female, 557 mm TL) in labial view. Scale bar: 1 mm.

Preoral length 9.7% (8.6%–9.9% TL), corresponding to 1.3 (1.1–1.4) times mouth width. Mouth somewhat arched, markedly broad, its width 1.7 (1.5–2.0) times internarial width and 1.4 (1.4–1.7) prenarial length; upper labial furrow elongate, its length 2.4% (2.0%–2.6% TL), with a slender fold; lower labial furrow conspicuously deep and elongate, reaching laterally on head, without a fold. Unicuspid teeth, similar in both jaws, markedly broad at crown, flattened labial-lingually and alternating; upper teeth smaller and narrower than lower teeth; cusp thick and short, oblique and directed laterally; mesial cutting edge conspicuously convex; mesial heel pointed; distal heel markedly rounded; apron thick, although larger on lower teeth than upper teeth; two series of functional teeth in upper and lower jaws; tooth rows varying from 13–13 (13–13 paratypes) in upper jaw and 11–10 (12–11 paratypes) in lower jaw (Fig. 17).

Pre-first dorsal fin length 1.4 (1.3–1.5) times prepectoral length; distance from first dorsal fin origin to pectoral fin origin 1.2 (0.8–1.4) times preorbital length. Origin of first dorsal fin prior to pectoral free rear tips. First dorsal fin markedly broad at fin web, lobe-like, and elongate (its length 1.9, 1.6–2.0 times its height); first dorsal fin tall, its height 7.6%, 6.5%–8.1% TL, corresponding to 1.0 (0.9–1.1) times preorbital length and 1.1 (1.0–2.2) times its inner margin length; first dorsal-fin anterior margin evidently convex and elongate, its length 11.1% (10.3%–11.9% TL); its posterior margin almost straight, its length 9.6% (6.7%–9.2% TL) (Fig. 18); first dorsal-fin apex strongly rounded and its free rear tip triangular; inner margin large, its length 6.6% (3.3%–7.1% TL). First dorsal-fin spine somewhat broad at base (width at base 0.7%, 0.6%–0.9% TL) and short (its length 3.8%, 2.2%–4.0% TL), reaching half of fin height. First dorsal fin 1.1 (1.0–1.2) times larger than second dorsal fin. Interdorsal space short, its length 24.6% (21.9%–24.1% TL), and corresponding to 1.1 (1.0–1.2) times prepectoral length and 2.4 (2.1–2.3) times dorsal-caudal space. Second dorsal fin also broad at fin web, lobe-like, and low with its height 1.0 (0.6–1.4) times its inner margin length; anterior margin markedly convex and elongate (length 11.1%, 9.2%–11.6% TL); its posterior margin conspicuously falcate, its length 5.5% (4.1%–6.4% TL); second dorsal-fin apex rounded and free rear tip triangular; its inner margin very large, its length 5.8% (2.8%–6.1% TL). Second dorsal-fin spine slender and conspicuously elongate, reaching fin apex, its length 0.9 (0.7–1.4) times second dorsal-fin height and 1.4 (1.0–1.6) times larger than first dorsal-fin spine (Fig. 18).

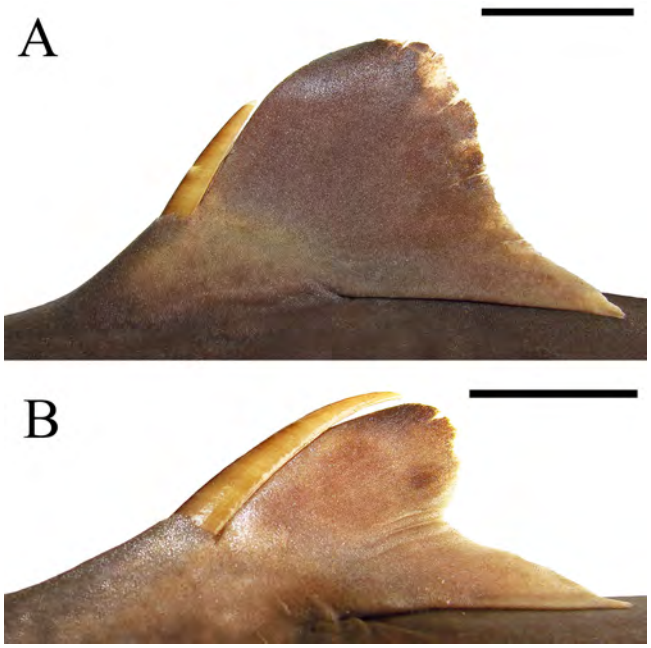

FIGURE 18. First dorsal fin (A) and second dorsal fin (B) of holotype of *Squalus lobularis* **sp. nov.** (HUMZ 91806, juvenile female, 557 mm TL). Scale bar: 20 mm.

Pre-pectoral length 0.7 (0.7–0.8 paratypes) times pre-first dorsal length and 0.4 (0.4–0.5 paratypes) times pre-vent length. Pectoral fin markedly broad posteriorly (posterior margin length 11.2%, 9.7%–11.7% TL) and elongate, its anterior margin length 16.0%, 13.8%–17.2% TL; anterior margin length 1.5 (1.5–1.8) times inner margin length; posterior margin length 0.9 (0.9–1.8) times trunk height; anterior and inner margins rather straight, posterior margin concave; apex strongly rounded and lobe-like; free rear tips also rounded and lobe-like reaching the horizontal line traced at pectoral fin apex.

TABLE 5. External measurements expressed as percentage of total length (% TL) for *Squalus lobularis* sp. nov. and for type specimens of *Squalus mitsukurii*. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	***Squalus lobularis* sp. nov.**					**Squalus mitsukurii**				
	Holotype	Paratypes				Holotype	Paratypes			
	HUMZ 91806	N	Range	*x*	SD	SU 12793	N	Range	*x*	SD
TL (mm)	557.0	8	530.0 – 725.0	637.5	59.3	710.0	5	240.0 – 770.0	349.6	235.0
PCL	78.5	8	78.3 – 80.5	79.5	0.8	77.5	5	76.9 – 78.6	77.6	0.7
PD2	61.0	8	60.0 – 64.1	61.3	1.4	61.0	5	58.4 – 60.5	59.7	0.9
PD1	31.1	8	29.8 – 31.1	30.4	0.5	32.4	5	30.2 – 31.3	30.8	0.4
SVL	47.0	8	46.9 – 51.9	49.5	1.8	50.0	5	47.3 – 48.9	48.1	0.6
PP2	44.9	8	44.6 – 48.9	46.6	1.5	47.9	5	45.3 – 47.6	46.3	1.0
PP1	22.0	8	20.5 – 23.4	21.8	0.9	24.6	5	22.1 – 24.7	22.9	1.1
HDL	22.7	8	21.5 – 24.3	22.2	0.9	24.2	5	22.7 – 24.4	23.3	0.7
PG1	19.2	8	17.7 – 20.3	18.8	0.9	20.4	5	19.9 – 20.9	20.3	0.4
PSP	12.6	8	11.5 – 12.7	12.1	0.4	12.8	5	12.7 – 21.5	14.9	3.7
POB	7.9	8	7.0 – 7.9	7.4	0.3	7.3	5	7.2 – 8.8	7.8	0.6
PRN	5.4	8	4.5 – 5.3	4.7	0.3	5.6	5	4.7 – 6.4	5.4	0.7
POR	9.7	8	8.6 – 9.9	9.4	0.4	10.3	5	8.9 – 11.5	10.2	0.9
INLF	4.5	8	3.6 – 4.4	4.1	0.3	4.3	5	4.4 – 5.3	4.7	0.4
MOW	7.4	8	7.0 – 8.1	7.6	0.3	8.6	5	7.6 – 8.1	7.8	0.2
ULA	2.4	8	2.0 – 2.6	2.4	0.2	2.5	5	2.1 – 2.7	2.5	0.2
INW	4.4	8	3.8 – 4.9	4.2	0.4	4.7	5	4.0 – 4.5	4.2	0.2
INO	8.8	8	6.8 – 8.5	8.0	0.6	9.3	5	9.1 – 9.8	9.5	0.3
EYL	4.1	8	3.1 – 4.4	3.9	0.5	3.6	5	3.1 – 4.6	3.8	0.5
EYH	1.8	8	1.4 – 2.3	1.7	0.3	0.9	5	1.2 – 2.5	1.7	0.5
SPL	1.2	8	1.0 – 1.6	1.4	0.2	1.3	5	1.3 – 1.5	1.4	0.1
GS1	1.9	8	1.4 – 1.9	1.7	0.2	1.7	5	1.7 – 2.3	2.0	0.2
GS5	2.2	8	1.9 – 2.4	2.1	0.2	2.3	5	1.8 – 2.7	2.3	0.3
IDS	24.6	8	21.9 – 24.1	23.3	0.9	21.1	5	21.9 – 24.7	23.1	1.1
DCS	10.1	8	10.4 – 11.5	10.7	0.4	10.6	5	8.1 – 11.9	10.4	1.5
PPS	18.9	8	20.3 – 24.4	22.2	1.4	21.8	5	18.2 – 23.4	20.1	2.1
PCA	26.0	8	24.8 – 28.1	26.0	1.1	23.7	5	23.0 – 26.2	24.7	1.3
D1L	14.4	8	11.8 – 14.1	13.2	0.7	13.6	5	11.8 – 14.5	13.5	1.3
D1A	11.1	8	10.3 – 11.9	11.2	0.6	12.0	5	10.2 – 13.2	12.0	1.3
D1B	7.5	8	7.1 – 8.4	7.8	0.5	8.2	5	5.3 – 8.8	7.4	1.5
D1H	7.6	8	6.5 – 8.1	7.3	0.5	9.8	5	7.0 – 9.8	8.0	1.2
D1I	6.6	8	3.3 – 7.1	5.7	1.2	6.2	5	6.1 – 6.5	6.3	0.1
D1P	9.6	8	6.7 – 9.2	8.0	0.9	9.3	5	7.0 – 10.6	8.7	1.3
D1ES	3.8	7	2.2 – 4.0	3.3	0.6	3.9	5	2.1 – 5.4	2.9	1.4
D1BS	0.7	8	0.6 – 0.9	0.8	0.1	1.0	5	0.5 – 1.0	0.7	0.2
D2L	13.7	8	11.3 – 13.0	12.3	0.7	12.3	5	11.6 – 12.6	12.0	0.4
D2A	11.1	8	9.2 – 11.6	10.0	0.8	10.2	5	9.9 – 11.6	10.5	0.7
D2B	8.2	8	6.8 – 9.2	7.5	0.8	7.2	5	6.2 – 7.1	6.6	0.4
D2H	6.0	8	3.7 – 5.6	4.7	0.8	6.8	5	4.8 – 7.9	6.0	1.2

.....continued on the next page

TABLE 5. (Continued)

Measurements	*Squalus lobularis* sp. nov.						Squalus mitsukurii					
	Holotype	Paratypes					Holotype	Paratypes				
	HUMZ 91806	N	Range		*x*	SD	SU 12793	N	Range		*x*	SD
D2I	5.8	8	2.8	– 6.1	4.8	1.1	5.3	5	4.9	– 5.9	5.6	0.4
D2P	5.5	8	4.1	– 6.4	5.4	0.9	6.3	5	4.5	– 6.3	5.6	0.8
D2ES	5.3	6	3.4	– 5.3	4.6	0.7	4.2	5	3.3	– 4.4	3.9	0.4
D2BS	0.8	8	0.7	– 1.0	0.9	0.1	0.9	5	0.8	– 1.1	0.9	0.1
P1A	16.0	8	13.8	– 17.2	15.9	1.1	15.2	5	12.3	– 16.7	13.5	1.8
P1I	10.5	8	9.2	– 11.0	9.8	0.7	9.5	5	8.1	– 9.2	8.7	0.5
P1B	4.6	8	4.3	– 5.4	4.7	0.3	5.3	5	3.5	– 5.8	4.5	0.9
P1P	11.2	8	9.7	– 11.7	10.9	0.6	11.7	5	9.5	– 12.1	10.6	1.2
P2L	10.4	8	9.9	– 11.6	10.5	0.5	11.5	5	8.4	– 12.6	10.0	1.6
P2I	5.4	8	4.2	– 5.7	4.9	0.5	6.3	5	3.1	– 7.9	5.3	1.8
CDM	21.7	8	19.7	– 22.0	20.7	0.9	24.4	5	21.2	– 23.4	22.1	0.8
CPV	11.8	8	10.6	– 12.2	11.6	0.5	12.1	5	11.5	– 12.4	12.0	0.4
CFW	6.9	8	6.3	– 7.4	7.0	0.4	7.0	5	6.4	– 7.7	7.2	0.5
HANW	7.5	8	6.3	– 7.4	6.9	0.4	7.3	5	6.9	– 7.7	7.4	0.3
HAMW	12.2	8	9.7	– 12.2	11.0	0.7	12.2	5	10.4	– 11.9	11.0	0.6
HDW	13.4	8	11.4	– 13.9	12.8	0.9	22.5	5	9.4	– 15.8	11.9	2.3
TRW	10.0	8	8.9	– 12.7	10.6	1.2	18.3	5	5.8	– 10.1	8.7	1.8
ABW	8.6	8	6.5	– 11.1	9.4	1.6	15.5	5	5.4	– 6.7	6.2	0.5
HDH	10.6	8	7.5	– 10.6	9.2	1.3	12.7	5	8.3	– 11.2	9.7	1.2
TRH	12.0	8	6.4	– 12.5	9.3	2.4	10.3	5	5.7	– 10.4	9.1	1.9
ABH	10.9	8	6.4	– 13.5	9.3	2.8	7.7	5	4.9	– 8.5	6.7	1.6
CLO	–	1	–		4.3	–	–	2	2.7	– 4.5	3.6	1.3
CLI	–	1	–		7.3	–	–	2	3.4	– 8.4	5.9	3.5

Pelvic fins somewhat wide with anterior margin slightly concave; inner and posterior margins straight; free rear tips and apex rounded, the former conspicuously lobe-like; pelvic fin length 10.4% (9.9%–11.6% TL); origin of pelvic fins 3.0 (2.9–3.2) times distance between origins of the two dorsal fins, nearer to first dorsal fin than to second dorsal fin (although closer to midline between the origins of two dorsal fins in paratypes); pectoral-pelvic space 0.7 (0.8–0.9) times pelvic-caudal space. Claspers in male paratype cylindrical, markedly thick and compressed dorsoventrally throughout, extending beyond free rear tips of pelvic fins, its outer length 4.3% TL; elongate and wide siphon, placed medioventrally from midline of basipterygium to origin of ventral marginal cartilage; clasper groove longitudinal, short (not reaching the rhipidion) and very constricted, dorsally located; apopyle narrow anteriorly in clasper groove; hypopyle also narrow, located posteriorly in clasper groove; rhipidion conspicuously large, blade-like and thin, positioned medially at distal end of clasper (Fig. 19).

Lateral keels well demarked on each side of caudal peduncle with their origin behind insertion of second dorsal fin; upper and lower precaudal furrows deep. Caudal fin subrectangular with dorsal caudal margin straight and large, its length 21.7% (19.7%–22.0% TL); dorsal caudal margin length 1.0 (0.8–1.0) times head length and 1.8 (1.7–2.0) times greater than preventral caudal margin length; posterior caudal tip rounded; both postventral caudal margins convex; upper caudal lobe narrow, its width at caudal fork 6.9% (6.3%–7.4% TL); caudal fork between lobes strongly concave; preventral caudal margin convex and elongate, its length 11.8% (10.6%–12.2% TL) and corresponding to 2.2 (2.0–2.7) times pelvic inner margin length; ventral caudal tip rounded (Fig. 20).

TABLE 6. Meristic data for type specimens of *Squalus lobularis* sp. nov. A: UERJ 2024; B: UERJ 2025; C: UERJ 2026; D: UERJ 1661; E: HUMZ 30032. Values for *S. mitsukurii* are also provided for comparisons.

Character	***Squalus lobularis***						***Squalus mitsukurii***			
	Holotype	Paratypes					Holotype	Paratype SU 12794	Non type USNM 62467	
		A	B	C	D	E				
precaudal vertebrae	88	89	89	87	88	80	–	–	1	87
caudal vertebrae	30	29	29	28	31	30	30	30	1	30
total vertebrae	118	118	118	115	119	110	–	–	1	117
monospondylous vertebrae	45	44	44	44	44	48	–	–	1	45
diplospondylous vertebrae	73	74	74	71	75	62	68	72	1	72
upper tooth rows (right)	13	13	13	13	14	14	13	11	1	14
upper tooth rows (left)	13	13	13	13	15	13	15	11	1	15
upper intermediate teeth	–	–	–	–	–	–	–	1	–	–
lower tooth rows (right)	11	11	12	12	12	11	12	13	1	13
lower tooth rows (left)	10	9	10	12	12	11	12	12	1	12
lower intermediate teeth	–	–	–	–	–	–	–	1	–	–
upper tooth series	2	2	2	2	2	2	2	2	1	2
lower tooth series	2	2	2	2	2	2	2	2	1	2
Propterygium radials	–	1	1	1	–	–	1	1	1	1
Mesopterygium radials	–	10	10	10	–	–	9	10	1	10
Metapterygium radials	–	–	–	–	–	–	8	6	1	6
Total pectoral radials	–	–	–	–	–	–	18	17	1	17
Total pelvic radials	–	–	–	–	15	–	15	17	1	14

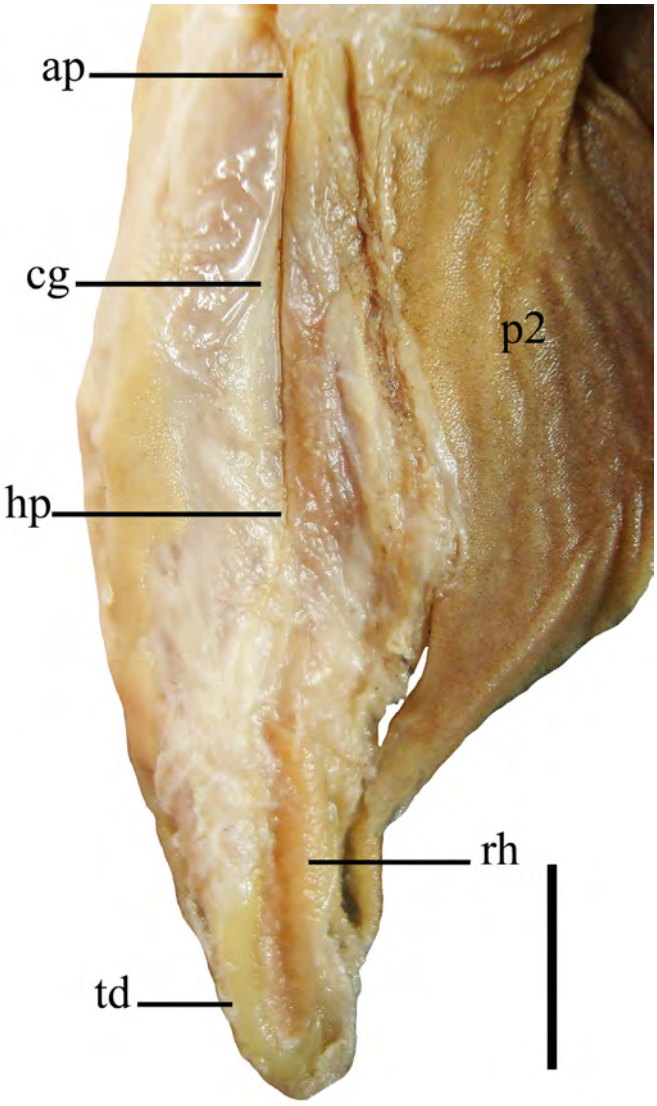

FIGURE 19. External morphology of clasper of male paratype of *Squalus lobularis* (UERJ 1661, adult male, 640 mm TL) in dorsal view. Abbreviations: **ap**, apopyle; **cg**, clasper groove; **hp**, hypopyle; **p2**, pelvic fin; **rh**, rhipidion; **td**, dorsal terminal cartilage (claw). Scale bar: 10 mm.

Dermal denticles (Fig. 21). Denticles tricuspid with cusps conspicuous and pointed; median projection anteriorly on crown prominent and rounded with small expansions posterolaterally on each side, and crown furrow medially; lateral cusps much shorter than median cusp; lateral ridges prominent and bifurcate, reaching tips of lateral cusps; median ridge conspicuous and tall with its origin far anteriorly at crown base and reaching the tip of median cusp distally; dermal denticles markedly broad at crown, although their length slightly greater than their width; dermal denticles imbricated and adjacent to each other. Dermal denticles also tricuspid in juveniles, although much smaller than in adults and not imbricated; their cusps markedly slender and pointed with lateral cusps forming a prominent concavity with a median cusp on each side.

Coloration (Figs. 16, 20). Body darkish gray dorsally and pale ventrally. Dorsal fins also dark gray, whitish at fin base; first dorsal fin slightly white at posterior margin and free rear tip, darker at apex and upper half of posterior margin; second dorsal fin also dark gray with posterior margin white and apex slightly blackish; dorsal spines gray, blackish anteriorly, white posteriorly and at tips. Pectoral fins dark gray dorsoventrally and pale under pectoral radials; pectoral-fin posterior margin markedly white; pectoral-fin apex broadly white; pectoral-fin inner margin light gray. Pelvic fins gray dorsally and light gray ventrally; both pelvic anterior and posterior margins white. Caudal fin also dark gray and whitish over vertebral column; dorsal caudal margin somewhat whitish, although not uniform; posterior caudal tip white; upper postventral caudal margin white, except for dark gray

caudal fork; lower postventral caudal margin also white; ventral caudal tip broadly white; preventral caudal margin slightly white; black caudal stripe conspicuous in dorsal lobe (Fig. 20). Juveniles with body much darker than adults.

FIGURE 20. Detail of caudal fin of holotype of *Squalus lobularis* **sp. nov.** (HUMZ 91806, juvenile female, 557 mm TL). Scale bar: 20 mm.

Skeletal morphology. Measurements and meristic data are summarized in Tables 3, 6.

Neurocranium (Fig. 22). Rostrum spoon-shaped, thick and elongate (precerebral fossa 40.6% CL), narrow anteriorly and broad posteriorly; lateral rostral cartilages somewhat cylindrical, although compressed more anteriorly; precerebral fossa markedly profound and broad, its width 13.6% CL; three conspicuous rostral appendices ventrally with median rostral appendix shorter than lateral appendices; prefrontal fontanelle rounded and narrow, placed dorsally and posterior to the precerebral fossa at the base of rostrum; rostral keel strongly prominent and elongate, its length 20.8% CL, reaching posterior margin of subnasal fenestra. Nasal capsules markedly rounded and broad (width across nasal capsules 55.2% CL); subnasal fossa vertical, large, placed ventrally on each side of rostral keel.

Cranial roof strongly concave medially and delimited by preorbital processes anteriorly, supraorbital crest laterally, and postorbital processes posteriorly; its greatest width at orbital processes (width across preorbital processes 52.3% CL; width across postorbital processes 55.8% CL), clearly narrow and concave in the interorbital space (interorbital width 30.2% CL); preorbital processes inconspicuous; postorbital processes triangular and small, its length 6.9% CL; supraorbital crest prominent laterally with a deep longitudinal sulcus located at its base, carrying a series of eight foramina for the superficial ophthalmic branches of trigeminal (V) and facial (VII) nerves; preorbital canal markedly broad and rounded, placed anteriorly to the series of foramina; profundus canal for ophthalmicus profundus nerve rounded, located anteriorly to the preorbital canal in the longitudinal sulcus; supraethmoidal processes conspicuous, cylindrical and elongate, placed mediodorsally at the base of the ethmoidal region; ethmoidal canal rounded and wide, although narrower than the preorbital canal, placed dorsoanteriorly at the lateral base of ethmoidal region; epiphyseal pit rounded and wide, located medially behind supraethmoidal processes; ectethmoid process prominent, slightly pointed posteriorly on each side; subethmoidean chamber small, broader anteriorly than posteriorly (its width 15.3% TL); subethmoidal ridge follows rostral keel ventrally in the subethmoidean region.

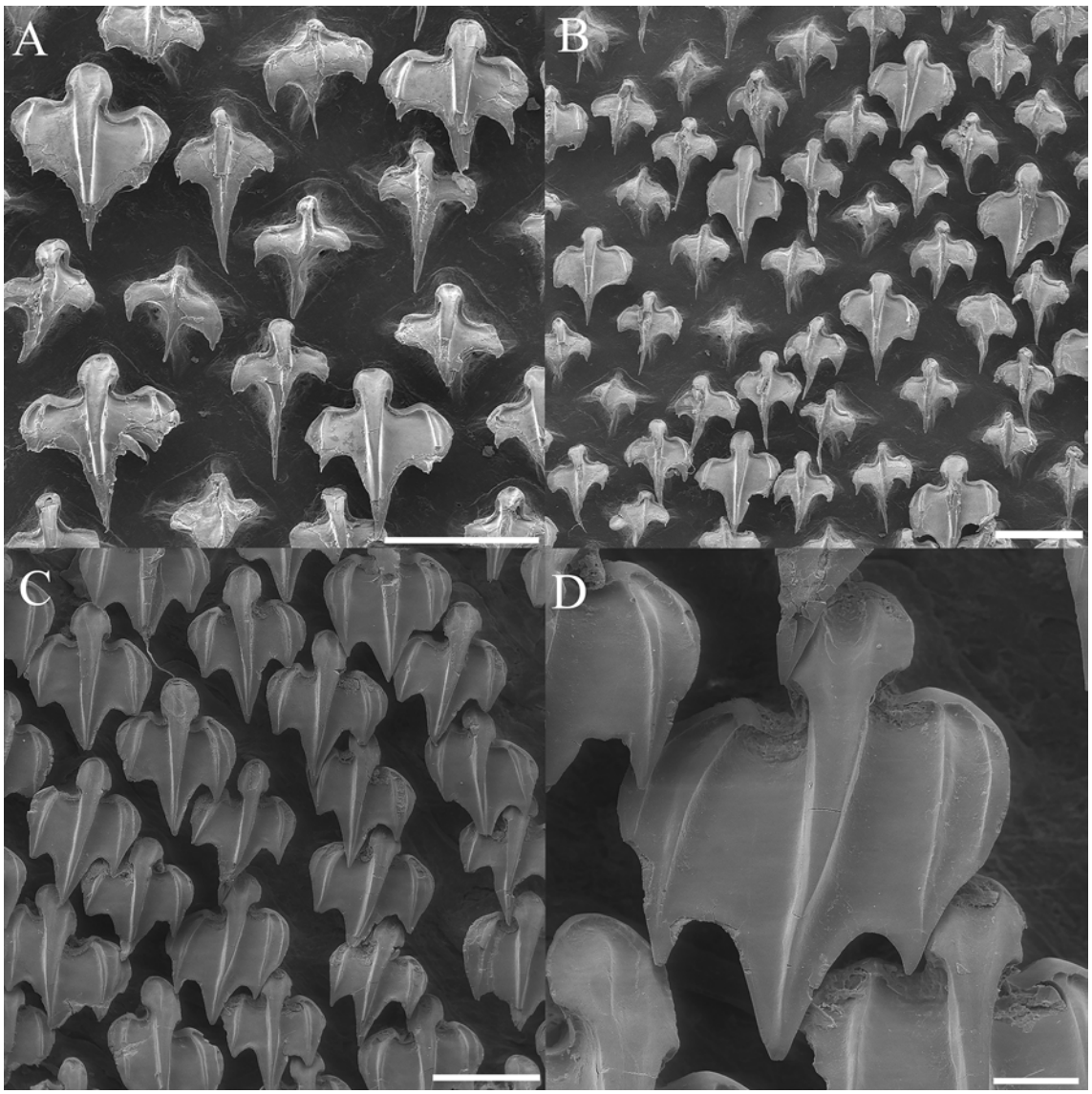

FIGURE 21. Dermal denticles of *Squalus lobularis*. (A, B) holotype (HUMZ 91806, juvenile female); (C, D) paratype (UERJ 1661, adult male). Scale bars: 200 ìm (A–C); 50 ìm (D).

Otic region comprised by two oval otic capsules on each side, separated by deep endolymphatic fossa; each otic capsule delimited by anterior semicircular canal anteriorly, posterior semicircular canal posteriorly, sphenopterotic ridge dorsolaterally, and lateral semicircular canal laterally which is dorsal to the hyomandibular facet; endolymphatic fossa rounded, placed medially in otic region, with two anterior endolymphatic foramina and two posterior perilymphatic foramina, with the later much broader than the former; otic crest prominent located medioposteriorly, running from posterior margin of the endolymphatic fossa to foramen magnum; opisthotic process conspicuous posteriorly in the otic capsule; lateral auditory groove shallow, placed afore the hyomandibular facet; hyomandibular facet profound and broad, located lateroventrally in otic region.

Interorbital wall wide and profound, delimited by preorbital wall anteriorly, otic capsule posteriorly, supraorbital crest dorsally and groove for orbital process ventrally; preorbital wall concave, with a single orbitonasal canal at its base; optic foramen (II) conspicuously broad, placed midventrally in interorbital wall near groove for orbital process; trochlear foramen (IV) tiny, located middorsally just below supraorbital crest; eye-stalk prominent, posteriorly in interorbital wall anterior to prooticum foramen (V, VII); oculomotor foramen (III) and abducens foramen (VI) somewhat wide, placed dorsal and ventrally to eye-stalk, respectively; prooticum foramen for the trigeminal (V) and facial (VII) nerves with markedly wide aperture, placed ventroposteriorly in interorbital wall, just anterior to postorbital process; two apertures for hyomandibular branch of the facial nerve (VII) opening more posteriorly at base of hyomandibular facet; transbasal canal for the pituitary vein clearly wide, placed ventral

to eye-stalk; foramen for efferent branch of pseudobranchial artery broad, located just anterior to transbasal canal. Occipital region with two triangular occipital condyles ventrally; glossopharyngeal bases strongly conspicuous, subtriangular and thick, located laterally and with a broad foramen for glossopharyngeal nerve (IX) at base; foramen for vagus nerve (X) rounded and wide, medial to foramen for glossopharyngeal nerve (IX), lateral to occipital condyles; foramen magnum broad, its width 8.8% CL.

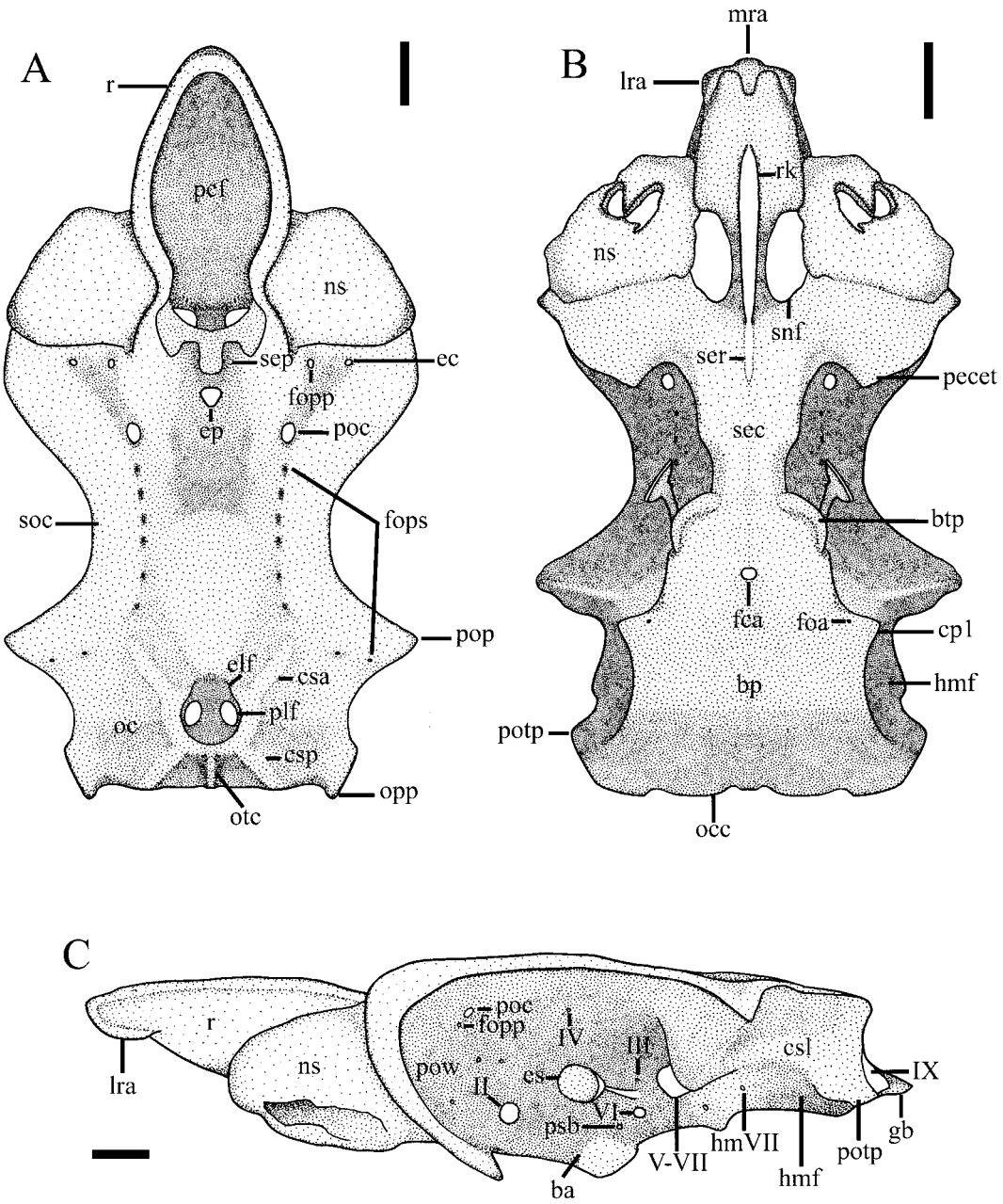

FIGURE 22. Neurocranium of paratype of *Squalus lobularis* (UERJ 1661, paratype) in (A) dorsal, (B) ventral and (C) lateral views. Abbreviations: **ba**, basal angle; **bp**, basal plate; **btp**, basitrabecular process; **cp1**, first cartilaginous process; **csa**, anterior semicircular canal; **csl**, lateral semicircular canal; **csp**, posterior semicircular canal; **ec**, ethmoidal canal; **elf**, endolymphatic foramen; **ep**, epiphysial pit; **es**, eye-stalk; **fca**, foramen for carotid artery; **foa**, foramen for orbital artery; **fopp**, profundus canal; **fops**, series of foramina for superficial ophthalmic branch of trigeminal and facial nerves; **gb**, glossopharyngeal base; **hmf**, hyomandibular facet; **hmVII**, foramen for hyomandibularis facialis; **lra**, lateral rostral appendage; **mra**, median rostral appendage; **ns**, nasal capsule; **oc**, otic capsule; **occ**, occipital condyle; **opp**, opisthotic process; **otc**, otic crest; **pcf**, precerebral fossa; **pecet**, ectethmoid process; **plf**, perilymphatic foramen; **poc**, preorbital canal; **pop**, postorbital process; **potp**, prootic process; **pow**, preorbital wall; **psb**, efferent pseudobranchial artery foramen; **r**, rostrum; **rk**, rostral keel; **sec**, subethmoid chamber; **sep**, supraethmoidal process; **ser,** subethmoidean ridge; **snf,** subnasal fenestra; **soc,** supraorbital crest; **II**, optic foramen; **III**, oculomotor foramen; **IV**, trochlear foramen; **V, VII,** foramen prooticum; **VI**, abducens foramen; **IX**, foramen for glossopharyngeal nerve.

Basal plate flattened and elongate, its length 42.4% CL, narrow anteriorly at basal angle (its width 18.1% CL) and wide posteriorly at prootic process (width across hyomandibular facets 43.5% CL); basitrabecular process conspicuous and bean-shaped; lateral sinuosity prominent between basitrabecular process and first cartilaginous process; first cartilaginous process conspicuous and triangular, with a single foramen for orbital artery at its base on each side of basal plate; single foramen for carotid artery anteromedially placed at level of lateral sinuosity.

Pelvic fin and girdle (Fig. 23). Puboischiadic bar transverse, rectangular, somewhat thick, especially at sides, biconvex medially and biconcave laterally; lateral prepelvic process rounded evident on each side of the puboischiadic bar; single foramen for pelvic nerve present lateroanteriorly in the puboischiadic bar; three prominent expansions lateroposteriorly on puboischiadic bar for pelvic fin articulation. Basipterygium vertical, elongate, concave medially and convex laterally; anterior pelvic basal small, its length not reaching one-third the basipterygium length, and subrectangular, with four tiny series of irregular radials; pelvic radials slender and elongate, segmented into proximal and distal elements, the former larger than the later; 15 total pelvic radials.

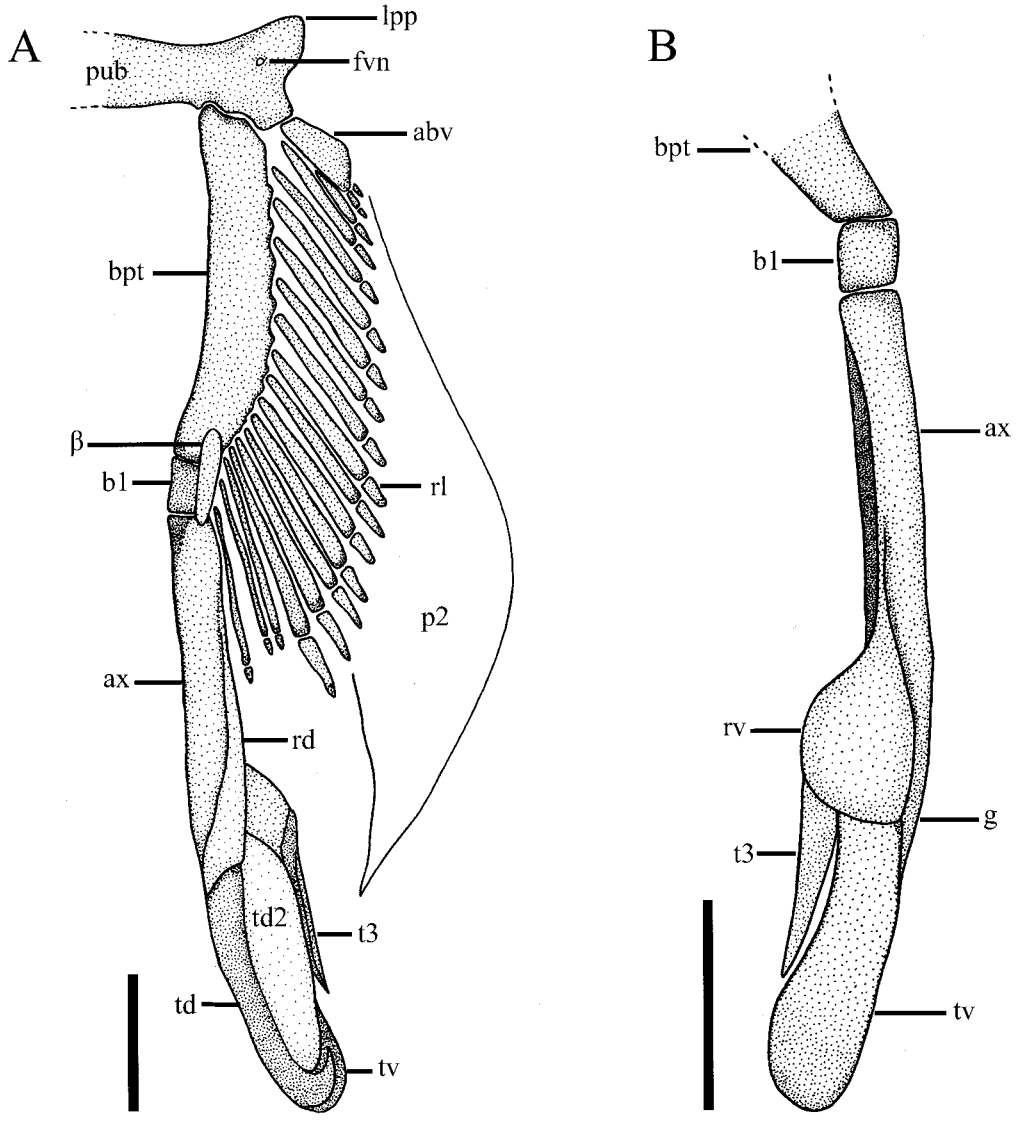

FIGURE 23. Pelvic fin and right clasper cartilages of (A) *Squalus lobularis* **sp. nov.** (UERJ 1661, paratype) in dorsal view; (B) detail of cartilages in ventral view. Abbreviations: **abv**, anterior pelvic basal; **ax**, axial cartilage; **bpt**, basipterygium; **b1**, intermediate segment; , beta cartilage; **fvn**, foramen for ventral fin nerves; **g**, end-style; **lpp**, lateral prepelvic process; **pub**, puboischiadic bar; **p2,** pelvic fin; **rl**, radials; **rd**, dorsal marginal cartilage; **rv**, ventral marginal cartilage; **td**, dorsal terminal cartilage (claw); **td2**, dorsal terminal 2 cartilage; **tv**, ventral terminal cartilage; **t3**, accessory terminal cartilage (spur). Scale bars: 10 mm.

Claspers (Fig. 23). Intermediate element barrel-shaped, connecting pelvic fin basipterygium to axial cartilage; single beta cartilage evident dorsally, thin and cylindrical, somewhat small, its length not reaching one-third the dorsal terminal cartilage (or claw) length, placed laterodorsally for attaching pelvic fin basipterygium to axial cartilage. Axial cartilage elongate and somewhat thick, slightly sinuous; dorsal marginal cartilage inconspicuous, slightly thicker distally, located laterally over axial cartilage; end-style slim and elongate, reaching more than one-half the length of dorsal terminal cartilage, medially at end of axial cartilage between dorsal marginal cartilage and dorsal terminal cartilage; dorsal terminal cartilage (or claw) clearly slender and elongate, its length more than two-thirds axial cartilage length, strongly hook-like with prominent concavity distally and pointed at its tip, connected proximally to dorsal marginal cartilage and axial cartilage, and medially to end-style; dorsal terminal 2 cartilage leaf-like and compressed, noticeably large, connected medially to dorsal terminal cartilage and proximally to dorsal marginal cartilage, supporting the rhipidion. Ventral marginal cartilage inconspicuous, thicker and broader posteriorly than anteriorly, placed distally under the axial cartilage as an evident folded plate laterally; accessory terminal 3 cartilage (or spur) markedly slender and elongate, thicker proximally and distally strongly pointed with single groove present medially, associated to folded plate of ventral marginal cartilage; ventral terminal cartilage conspicuously large, its length more than one-third the length of axial cartilage, spatula-like, rounded at its distal tip and sinuous laterally, placed at the distal end of clasper and connected proximally to ventral marginal cartilage and medially to end-style.

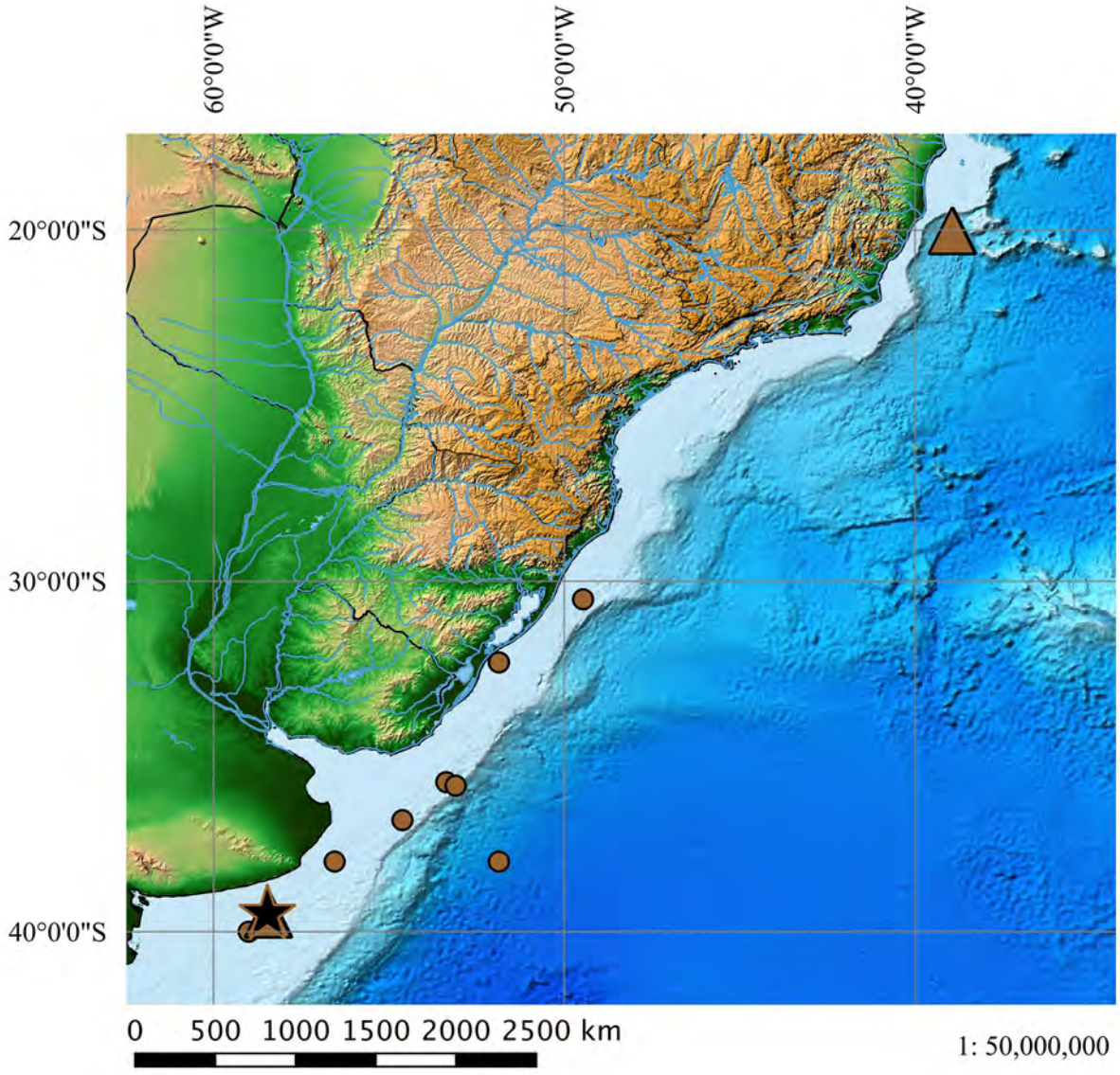

FIGURE 24. Map of geographical distribution of *Squalus lobularis* **sp. nov.** in the Southwestern Atlantic Ocean. Black star: location of holotype; brown triangle: location of paratypes; brown circle: location of non-type specimens.

Vertebral counts (Table 6). Monospondylous vertebrae 45 in holotype (44–48 in paratypes); precaudal vertebrae 88 (80–89); caudal vertebrae 30 (28–31); total vertebrae 118 (110–119).

Geographical distribution (Fig. 24). *Squalus lobularis* occurs from southern Brazil to Uruguay and Patagonia in Argentina, where it seems to be more common. Its occurrence in the coast of Espírito Santo, Brazil (C. Magenta, pers. comm.), is still doubtful due to lack of precise locality information.

Etymology. From the Latin *lobus*, in reference to its diagnostic broad and lobe-like dorsal and pectoral fins.

Remarks. *Squalus lobularis* has previously been misidentified in the SWAO as *S. mitsukurii* a valid species originally described from Japan (Fig. 25), or as a member of the *S. mitsukurii* group at least in the SWAO (e.g. Figueiredo, 1981; Lucifora *et al*., 1999; Marques, 1999; Gomes *et al*., 1997, 2010). Calderón (1994) recognized *S. mitsukurii* off the southern Brazilian coast based on morphological characters provided by Compagno (1984), specifically proportional measurements of the head, pectoral and dorsal-fin base lengths, and pelvic-fin length. These characters occur, however, in more than one species of *Squalus*, which may have led to the misidentification *S. mitsukurii* in this region (Fig. 25).

Squalus lobularis shares with *S. mitsukurii* a few morphological characters (Table 5): body moderately elongate; snout obtuse and markedly elongate (preorbital length 7.3%, 7.0%–7.4% TL for *S. lobularis vs*. 7.3%, 7.2%–8.8% TL for *S. mitsukurii*); nostrils closer to the mouth than to snout tip (prenarial length 1.0, 1.1–1.2 times inner nostril-labial length *vs*. 1.3, 1.1–1.4 times for *S. mitsukurii*); pectoral fins broad and smaller than head length; dermal denticles tricuspid; and presence of a dark caudal bar. However, this species can be distinguished from *S. mitsukurii* by the characters provided in its diagnosis above, most notably in having a slender body (*vs*. highly robust body in *S. mitsukurii*), and concave pectoral-fin posterior margin (*vs*. pectoral-fin posterior margin straight in *S. mitsukurii*). Despite overlapping, the distance from nostrils to upper labial furrow may be useful for separating them: 4.5%, 3.6%–4.4% TL for *S. lobularis vs*. 4.3%, 4.4%–5.3% TL for *S. mitsukurii*. *Squalus lobularis* also has a shorter prespiracular length (12.6% TL, 11.5%–12.7% TL *vs*. 12.8% TL, 12.7%–21.5% TL for *S. mitsukurii*).

Chen *et al*. (1979) provided vertebral counts for *S. mitsukurii* from Japan that are higher than those for *S. lobularis* despite of some overlapping, respectively: total vertebrae (118–127 *vs*. 118, 110–119). According to Last *et al*. (2007), members of *S. mitsukurii* group share a relatively great total length, presence of dark caudal bar, dorsal spines small, first dorsal fin short and falcate, tricuspidate dermal denticles, pectoral fin not falcate with rounded free rear tips, and high number of vertebrae. *Squalus lobularis* differs from members of this group by having dorsal spines robust and elongate (first dorsal-fin spine length 3.8% for holotype, 2.2%–4.0% TL for paratypes; second dorsal-fin spine length 5.3%, 3.4%–5.3% TL), as well as first dorsal fin conspicuously broad and lobe-like, not falcate.

A paratype of *S. mitsukurii* (SU 7184) was not taken into account in our morphometric comparisons because it corresponds to a specimen of *S. acanthias* clearly identified by the presence of white spots dorsally and first dorsal-fin spine located posterior to the pectoral fins, as previously noticed by Bigelow & Schroeder (1957) and Muñoz-Chápuli & Ramos (1989). This type specimen was illustrated in the original description of *S. mitsukurii* and posteriorly reproduced by Tanaka (1912), but it does not agree with the diagnosis of the Japanese species. Recently, investigations concerning the taxonomy and geographical distribution of *S. mitsukurii* (e.g. Last *et al*., 2007) have strongly demonstrated that it might be a complex of species rather than a single valid species (e.g. Bigelow & Schroeder, 1957; Chen *et al*., 1979; White & Iglésias, 2011).

Squalus lobularis is also distinguished from *S. edmundsi*, *S. grahami*, and *S. nasutus* when compared to data taken from original descriptions provided in Last *et al*. (2007), by a smaller snout (prenarial length 5.4%, 4.5%–5.3% TL for *S. lobularis*; 5.8%, 5.6%–5.8% TL for *S. edmundsi*; 5.6%, 5.7%–6.3% for *S. grahami*; and 7.3%, 6.4%–6.7% TL for *S. nasutus*). It also differs from *S. acanthias* from SWAO, *S. montalbani*, *S. nasutus*, *S. hemipinnis*, *S. crassispinus*, *S. megalops*, and *S. raoulensis* by greater total and precaudal vertebrae (Table 12). It also differs from *S. grahami*, *S. griffini*, *S. nasutus*, *S. hemipinnis*, *S. crassispinus*, *S. megalops*, *S. bucephalus*, *S. raoulensis*, and *S. notocaudatus* by number of monospondylous vertebrae (Table 12).

The recognition of *S. lobularis* as new species supports that the current acceptance of *S. mitsukurii* as a cosmopolitan species is probably erroneous, propagated when using the general descriptive literature (e.g. Compagno, 1984) for identifying species regionally. Further analysis of material identified as *S. mitsukurii* from other localities where it is reported to occur, such as in the Southeastern Atlantic and Western Indian Oceans, and Northeastern Pacific Ocean, is needed to check if this species is indeed widespread or more restricted (e.g. Compagno *et al*., 2005).

Comparative material. *Squalus mitsukurii* (8 specimens): SU 12793 (holotype of *Squalus mitsukurii*), adult female, 710 mm TL, Honshu Island, Misaki, Japan; SU 12794 (paratype of *S. mitsukurii*) adult male, 770 mm TL, same as SU 12793; SU 7184, paratype of *S. mitsukurii* (identified as *S. acanthias*), neonate male, 277 mm TL, same as SU 12793; SU 7748 (paratypes of *S. mitsukurii*), two neonate females, 240–243 mm TL, neonate male, 247 mm TL, same as SU 12793; AMNH 8822 (paratype of *S. mitsukurii*), neonate female, 248 mm TL, same as SU 12793; USNM 62467, Hawaii, U.S.A..

FIGURE 25. Holotype of *Squalus mitsukurii* (SU 12793, adult female, 710 mm TL) in lateral view.

***Squalus bahiensis* sp. nov.**

(Figs. 26–33; Tables 7–8)

Suggested common names: Northeastern Brazilian dogfish; Cação-bagre-da-Bahia (Portuguese).

Squalus fernandinus (not Molina): Fowler, 1936: 71 (description; South Atlantic); Bigelow & Schroeder, 1948: 480 (revision; Brazil).

Squalus cubensis (not Howell-Rivero): Kondyurin & Myagkov, 1984: 118–120, fig. 1B (revision; Western Atlantic); Nunan & Senna, 2007: 169, 170 (cited; Brazil).

Squalus blainvillei (not Risso): ?Lucena & Lucena, 1981: 2, 4, 5, fig. 3 (listed; Brazil); ?Menni *et al*., 1984: 84 (listed; Argentina, Uruguay); ?Canizarro *et al*., 1994: 113 (cited; Western Atlantic Ocean); ?Nion *et al*., 2002: 4 (listed; Uruguay); ?Meneses & Paesch, 2003: 8, 25 (cited; Argentina, Uruguay); ?Saéz *et al*., 2010: 623 (identification key; Chile); Viana, 2011 (in part): 57–91, figs. 18–34 (revision; Brazil).

Squalus mitsukurii (not Jordan & Snyder): Calderón, 1994: fig. 5B (cited; Brazil); ?Lessa *et al*., 1999: 61, 150 (cited, listed; Northeast Brazil); Compagno, 2002: 385 (description; Northeast Brazil); Jablonski *et al*., 2006: 177 (cited; Brazil); Louro & Rossi-Wongtschowski, 2007: 18, 27, 28, 30, 49 (cited; Brazil); ?Fischer *et al*., 2006: 495–501 (cited; Northeastern Brazil).

Squalus sp. of the *blainvillei* group: Gomes *et al*., 1997: 93–95, 109 (listed; Brazil); Marques, 1999 (cited; Brazil).

Squalus of the *blainvillei*/*mitsukurii* group: Gadig, 2001 (in part): 29, 36, 54, 55, 57, 58, fig. 29 (listed; Brazil).

Squalus sp. B: Soto, 2001: 96 (listed; Brazil); Soto & Mincarone, 2004: 79–82 (listed; Brazil).

Squalus sp. 1: Gomes *et al*., 2010: 44, 45 (cited; Brazil).

Holotype. MNRJ 30180, adult male, 590 mm TL, Bahia coast, Brazil, 1548'30"S, 3835'16"W, 599 m. Collected on 12 June 2000, Station 0510, Thalassa cruise, Revizee program.

Paratypes (2 specimens). MNRJ 30178, adult male, 615 mm TL, 599 m; MNRJ 30179, adult male, 690 mm TL, 599 m. Same locality as holotype.

Diagnosis. *Squalus bahiensis* **sp. nov.** is distinct from all species of the *S. megalops* group by having pectoral fins with free rear tips rounded (*vs*. free rear tips pointed), snout blunt and elongate (*vs*. snout rounded and short), and dermal denticles tricuspid and rhomboid (*vs*. dermal denticles unicuspid and lanceolate). *Squalus bahiensis* **sp. nov.** is distinct from *S. mitsukurii* by having a narrower interorbital space (8.2%, 7.9%–8.3% TL *vs*. 9.3%, 9.1%–9.8% TL in *S. mitsukurii*), and shorter lower caudal fin lobe (preventral caudal margin 11.4%, 10.9%–11.3% TL *vs*. 12.1%, 11.5%–12.4% TL). *Squalus bahiensis* **sp. nov.** can be easily distinguished from *S. blainvillei* from the Mediterranean Sea by having lower dorsal fins (first dorsal-fin height 6.9%, 7.0%–7.1% TL *vs*. 8.2%, 7.3%–8.7% TL in *S. blainvillei*; second dorsal-fin height 5.3%, 4.2%–4.4% TL *vs*. 7.2%, 6.6%–7.5% TL in *S. blainvillei*), and a shorter upper labial furrow (its length 2.3%, 2.2% TL *vs*. 2.5%, 2.4%–2.7% TL in *S. blainvillei*). *Squalus bahiensis* **sp. nov.** is distinct from *S. lobularis* by: caudal fin somewhat slender *vs*. upper caudal lobe rectangular in

S. lobularis; second dorsal-fin spine not reaching dorsal-fin apex *vs*. reaching dorsal-fin apex in *S. lobularis*; shorter pectoral-fin inner margin (its length 8.1%, 8.4%–8.9% TL *vs*. 10.5%, 9.2%–11.0% TL in *S. lobularis*); and clasper outer length greater (5.0%, 4.6%–5.1% TL *vs*. 4.3% TL in *S. lobularis*).

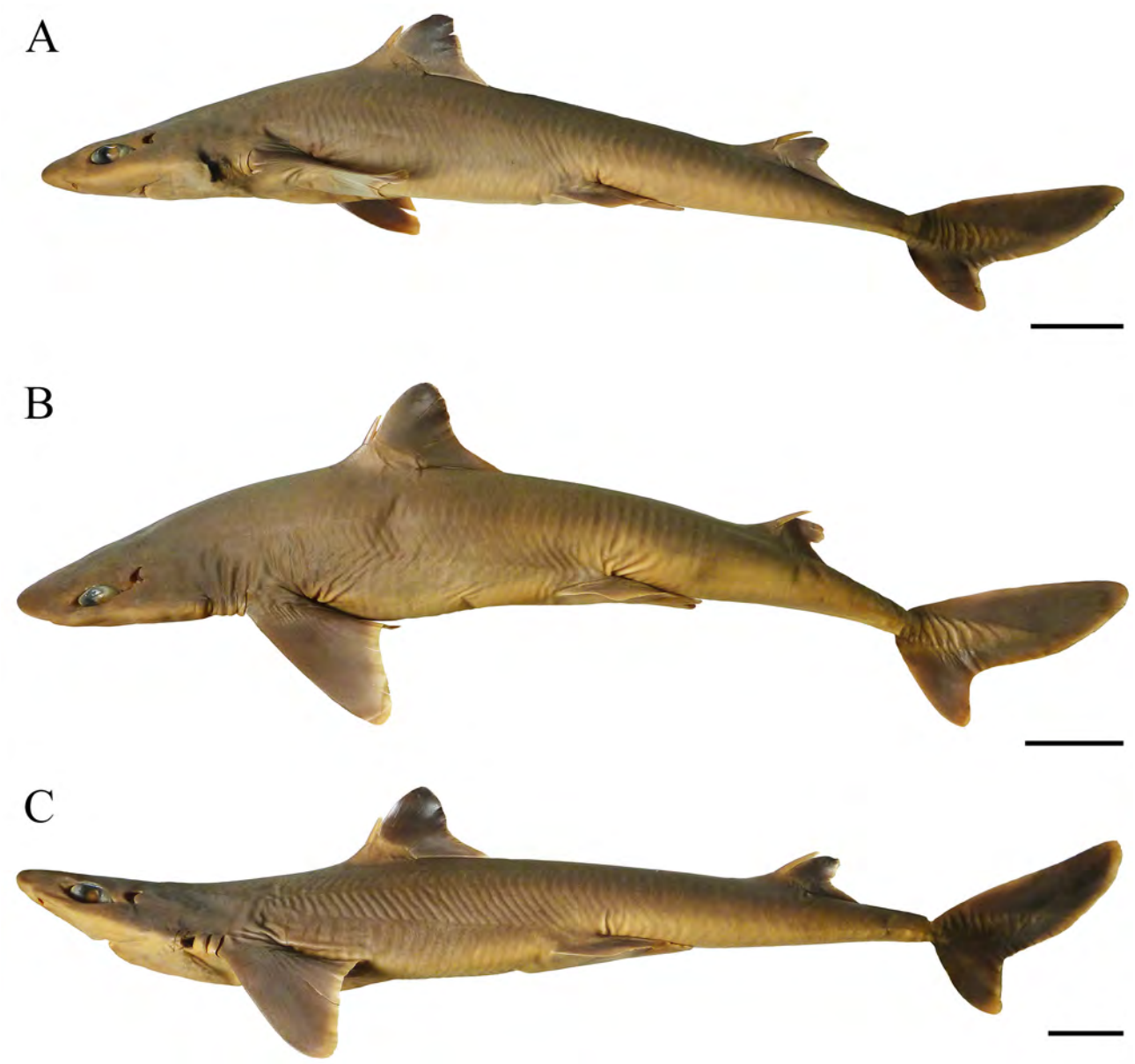

FIGURE 26. *Squalus bahiensis* **sp. nov.** in lateral view. (A) holotype (MNRJ 30180, adult male, 590 mm TL); (B) paratype (MNRJ 30178, adult male); (C) paratype (MNRJ 30179, adult male). Scale bars: 50 mm.

Description. External morphology. Measurements and meristic data are summarized in Tables 7–8. Body slender and fusiform, arched dorsally and somewhat flattened ventrally; its greatest depth at head and abdomen (head height 9.3%, 9.6%–10.0% TL; abdomen height 10.1%, 9.6%–10.5% TL) with head height corresponding to 0.9 (1.0–1.0) times trunk height and 0.9 (1.1–1.1) times abdomen height. Head rather elongate (length 21.4%, 22.8%–22.9% TL), narrower at nostrils (width 7.0%, 7.0%–7.1% TL), and much broader at gills (11.9%, 12.4%–12.6% TL). Snout markedly blunt and broad at tip (not obtuse) and elongate (preorbital length 7.3%, 7.4%–7.9% TL); anterior margin of nostrils bilobate, positioned laterally and nearer to the mouth than to snout tip (prenarial length 1.1, 1.0–1.2 times inner nostril-labial length); prenarial length 1.4 (1.4–1.4) times eye length; internarial space 1.2 (1.3–1.4) times eye length. Eyes oval and horizontal, placed nearer to snout tip than to gill slits; its anterior margin convex and posterior margin notched; eyes large, their length 2.0 (1.9–2.7) times its height. Prespiracular length 12.2% (12.2%–12.9% TL), corresponding to 0.6 (0.5–0.6) times prepectoral length. Spiracles

crescent-shaped, located more dorsally behind eyes; spiracle length 0.4 (0.3–0.5) times eye length. Prebranchial length 17.9% (18.4%–18.8% TL), corresponding to 1.5 (1.4–1.5) times prespiracular length. Gill slits vertical and low, fifth gill slit height 1.0 (1.1–1.2) times greater than first gill slit height; gill slits just anterior to pectoral fins.

FIGURE 27. Holotype of *Squalus bahiensis* **sp. nov.** in ventral view, MNRJ 30180, adult male. Scale bar: 40 mm.

Preoral length 9.9% (10.2%–10.5% TL), corresponding to at least 1.4 times mouth width. Mouth arched and somewhat broad, its width 1.7 (1.5–1.6) times internarial space and 1.4 (1.4–1.5) times prenarial length; upper labial furrow long, its length 2.3% (2.2%–2.2% TL) with a slender fold; lower labial furrow also elongate, although without a fold. Teeth unicuspid, similar in both jaws, broad and compressed labial-lingually at crown, imbricate laterally; upper teeth smaller and narrower than lower teeth; cusp small and heavy, markedly oblique and upturned, directed laterally; mesial cutting edge conspicuously convex; mesial heel notched; distal heel strongly rounded; apron thick; two series of functional teeth on upper jaws of holotype and three series in paratypes; two series of functional teeth in lower jaws; tooth rows varying from 13–14 (13–14 paratypes) in upper jaw and 11–12 (11–11 paratypes) in lower jaw (Fig. 28).

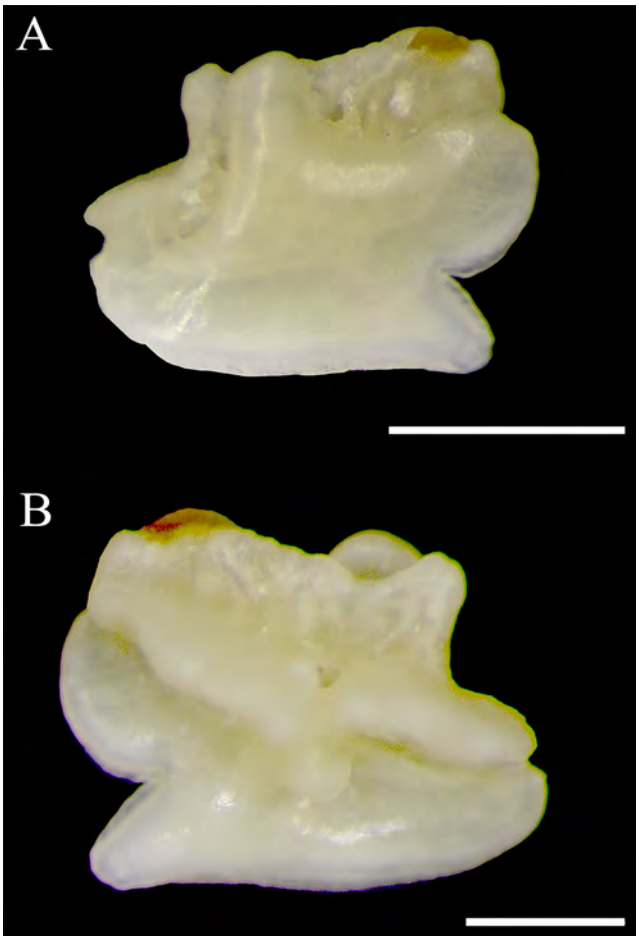

FIGURE 28. Upper tooth of paratype of *Squalus bahiensis* in (A) labial and (B) lingual views (MNRJ 30179, adult male). Scale bar: 2 mm.

Pre-first dorsal fin length 29.9% (29.7%–30.9% TL), corresponding to 1.4 (1.3–1.4) times prepectoral length. Origin of first dorsal fin preceding pectoral free rear tips. First dorsal fin wide at fin web and rather large (Fig. 29), its length 12.8% (13.8%–13.8% TL), corresponding to 1.8 (1.9–2.0) times its height; anterior margin convex and elongate, its length 10.5% (10.3%–10.6% TL); posterior margin markedly concave and large, its length 7.9% (9.2%–9.6% TL); first dorsal-fin apex strongly rounded and slender; first dorsal-fin free rear tip triangular; first dorsal-fin inner margin length 5.7% (6.4%–6.9% TL); first dorsal fin low, its height 6.9% (7.0%–7.1% TL) and corresponding to 1.2 (1.0–1.1) times its inner margin length, and 0.9 times preorbital length. First dorsal-fin spine slender and small, its length 2.8% (2.9%–3.0% TL) and corresponding to 0.4 times first dorsal-fin height, not reaching first dorsal-fin apex. First dorsal-fin length 1.1 times second dorsal-fin length. Interdorsal space 1.2 (1.1–1.2) times prepectoral length and 2.4 (2.0–2.4) times dorsal-caudal space. Pre-second dorsal fin length 2.8 times prepectoral length and 4.3 (4.2–4.4) times pectoral anterior margin length. Second dorsal fin slender, small, its length 11.6% (12.1%–12.6% TL) and 2.2 (2.8–2.9) times its height; anterior margin convex and short, its length 9.4% (9.3%–9.7% TL); posterior margin conspicuously concave and falcate, its length 5.0% (5.7%–5.7% TL); second dorsal-fin apex rounded and lobe-like; second dorsal-fin free rear tip triangular; second dorsal-fin inner margin somewhat elongate, its length 5.3% (5.6%–5.6% TL); second dorsal fin also low, its height 1.0 (0.8–0.8) times its inner margin length. Second dorsal-fin spine thin and short, its length 0.8 (0.8–1.0) times second dorsal-fin height and 1.5 (1.2–1.5) times greater than first dorsal-fin spine; second dorsal-fin spine not reaching second dorsal-fin apex (Fig. 29).

Prepectoral length 21.7% (22.0%–22.8% TL). Pectoral fins markedly narrow and small (anterior margin length 14.3%, 14.4%–14.5% TL); anterior margin 1.8 (1.6–1.7) times greater in length than inner margin length and 1.4 (1.3–1.4) times posterior margin length; pectoral-fin anterior margin straight and posterior margin convex; inner margin markedly concave, its length 8.1% (8.4%–8.9% TL); pectoral-fin apex rounded and lobe-like; pectoral-fin free rear tips also rounded and lobe-like, reaching the horizontal line traced from pectoral fin apex (Fig. 27).

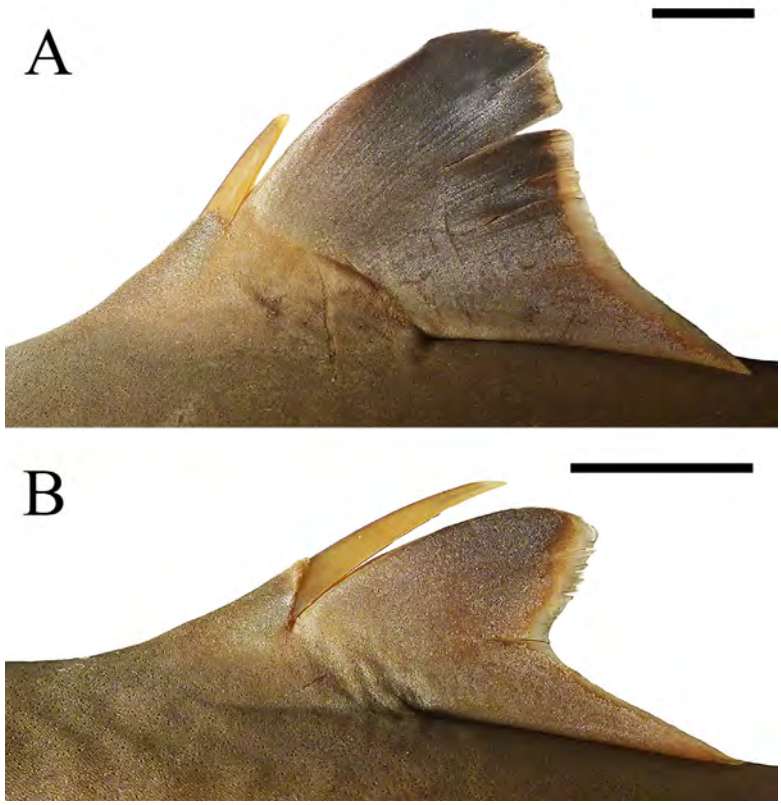

FIGURE 29. First dorsal fin (A) and second dorsal fin (B) of holotype of *Squalus bahiensis* **sp. nov.** (MNRJ 30180, adult male, 590 mm TL). Scale bars: 20 mm.

Prepelvic length 44.4% (45.5%–48.6% TL). Pectoral-pelvic space 0.7 (0.8–0.9) times pelvic-caudal space. Pelvic fins also narrow, its anterior and posterior margins straight; pelvic-fin free rear tips slightly pointed, triangular and elongate, its length 5.8% (5.1%–5.4% TL). Origin of pelvic fins 2.8 (2.9–3.0) times the distance between the origins of the two dorsal fins, closer to the first dorsal fin than to second dorsal fin in holotype (somewhat closer to midline between the origins of two dorsal fins in paratypes); pectoral-pelvic space short, its length 19.7% (19.5%–20.3% TL) and corresponding to 0.7 (0.7–0.8) times pelvic-caudal space. Claspers cylindrical and slender, compressed dorsoventrally; claspers large, extending far posterior to pelvic-fin free rear tips, its outer length among 5.0% (4.6%–5.1% TL); clasper inner margin 1.3 (1.3–1.4) times greater in length than pelvic-fin inner margin; clasper groove longitudinal and very elongate, positioned dorsally; apopyle very narrow, located anteriorly in clasper groove; hypopyle also narrow, located posteriorly in clasper groove; rhipidion markedly large, blade-like and slender, placed medially at distal end of clasper (Fig. 30).

Caudal peduncle with soft lateral caudal keels from opposite second dorsal-fin free rear tip to caudal fin origin; upper and lower caudal pits profound. Caudal fin with straight dorsal caudal margin, its length 21.9% (20.0%–21.4% TL) and corresponding to 1.0 (0.9 in paratypes) times head length and 1.9 (1.8–1.9) times preventral caudal margin length; upper postventral caudal margins strongly convex (Fig. 31); lower postventral caudal margin convex; posterior caudal tip rounded; preventral caudal margin straight and short, its length 2.0 times (2.1 in paratypes) pelvic-fin inner margin length; ventral caudal tip also rounded; caudal fin narrow at lobes and conspicuously concave at caudal fork, its width 6.7% (6.4%–7.1% TL).

Dermal denticles (Fig. 32). Description based on paratype MNRJ 30178. Denticles tricuspid and imbricate dermal denticles, very broad at crown, their length somewhat equal to their width; cusps triangular and wide with median cusp larger than lateral cusps; lateral cusps forming a right angle with median cusp; median anterior projection conspicuous and rounded with small posterolateral expansions on each side; median ridge conspicuous and bifurcate, forming a superficial furrow anteriorly, reaching the median cusp tip; two lateral ridges on each side of the denticle, thick and prominent, reaching the lateral cusp tips; lateralmost ridge often shorter than the medial ridge. In holotype, dermal denticles more slender and not imbricate; cusps very thin and cylindrical; lateral cusps forming a prominent concavity with the median cusp on each side.

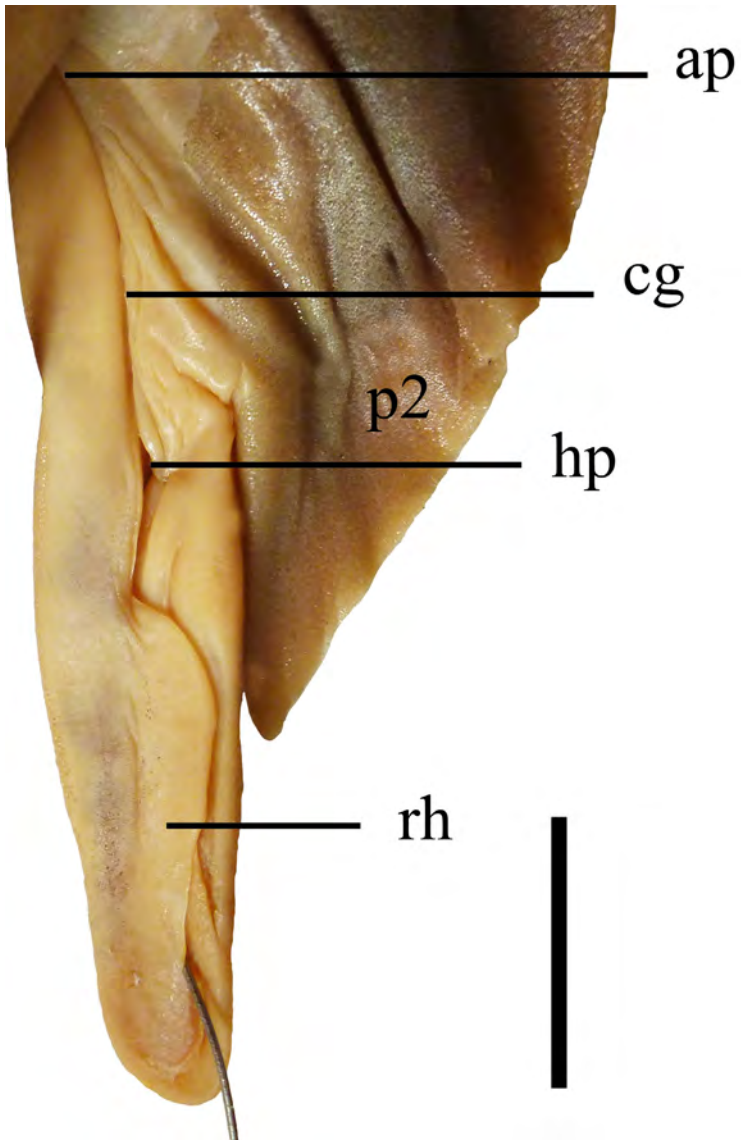

FIGURE 30. External morphology of clasper of male paratype of *Squalus bahiensis* (MNRJ 30180, adult male) in dorsal view. Abbreviations: **ap**, apopyle; **cg**, clasper groove; **hp**, hypopyle; **p2**, pelvic fin; **rh**, rhipidion. Scale bar: 10 mm.

Coloration (Fig. 26). Body gray dorsally, white ventrally and on its posterior half. First dorsal fin gray, darker at apex and whitish at base; anterior margin slightly white on first half; posterior margin white. Second dorsal fin also gray and darker at apex; posterior margin slightly white. First and second dorsal-fin spines white, slightly gray anteriorly. Pectoral fins gray dorsal and ventrally, whitish at ventral base; pectoral-fin posterior margin uniformly white. Pelvic fins light gray dorsally and ventrally; pelvic-fin posterior margin white. Caudal fin dark gray, whitish over vertebral column; dorsal caudal margin white; upper and lower postventral caudal margins whitish; posterior caudal tip broadly white; ventral caudal tip also white; preventral caudal margin somewhat whitish; caudal stripe small and gray.

Vertebral counts (Table 8). Monospondylous vertebrae 43 in holotype (43–45 in paratypes); precaudal vertebrae 87 (87); total vertebrae 117 (115–116).

Geographical distribution (Fig. 33). *Squalus bahiensis* is apparently endemic to the coast near Salvador, Bahia (Brazil).

Etymology. The epithet is in reference to the state of Bahia, northeastern Brazil, from where this species is described.

FIGURE 31. Detail of caudal fin of holotype of *Squalus bahiensis* **sp. nov.** (MNRJ 30180, adult male, 590 mm TL). Scale bar: 20 mm.

Remarks. *Squalus mitsukurii* and the Mediterranean species *S. blainvillei* (Risso, 1826) are often listed in the literature from the northern Brazilian coast to southern Argentina (e.g. Miranda Ribeiro, 1907; Compagno, 1984; Calderón, 1994; Compagno *et al*., 2005; Fischer *et al*., 2006; Viana, 2011). These two species were probably misidentified in these regions for sharing characters of species of the *S. mitsukurii* group, such as an elongate snout, tricuspidate dermal denticles, and low dorsal fins, which are also present in both *S. bahiensis* and *S. lobularis*. *Squalus bahiensis*, however, can be easily distinguished from all species of this group by the absence of a black caudal blotch in the caudal fin. *Squalus bahiensis* further differs from *S. lobularis* (its most similar congener) by a shorter first dorsal-fin anterior margin (its length in *S. bahiensis* 10.5%, 10.3%–10.6% TL *vs*. 11.1%, 10.3%–11.9% TL in *S. lobularis*), and greater interdorsal space (26.5%, 24.4%–26.8% TL *vs*. 24.6%, 21.9%–24.1% TL, respectively).

Squalus bahiensis can also be distinguished from the Japanese *S. mitsukurii* by a more elongate precaudal length (79.5%, 79.2%–81.2% TL *vs*. 77.5%, 76.9%–78.6% TL in *S. mitsukurii*), pre-second dorsal fin length (61.5%, 61.0%–63.8% TL *vs*. 61.0%, 58.4%–60.5% TL in *S. mitsukurii*), and first gill slit closer to snout tip in *S. bahiensis* than in *S. mitsukurii* (prebranchial length 17.9%, 18.4%–18.8% TL *vs*. 20.4%, 19.9%–20.0% TL in *S. mitsukurii*). *Squalus bahiensis* has a body depth almost equal from the head to abdomen (head height 0.9, 1.1–1.1 times trunk height, and 0.9, 1.0–1.0 times abdomen height) while *S. mitsukurii* has its greatest depth in the head (head height 1.2, 1.0–1.4 times trunk height and 1.6, 1.2–1.7 times abdomen height). It is also easily distinct from *S. montalbani* by having a more slender and deep body (vs. markedly robust body in *S. montalbani*), and a shorter ventral caudal lobe (its length 11.4%, 10.9%–11.3% TL *vs*. 11.5%–13.2% TL in *S. montalbani*).

TABLE 7. External measurements expressed as percentage of total length (% TL) for holotype and paratypes of *Squalus bahiensis* sp. nov. and *Squalus quasimodo* sp. nov. N: number of specimens; *x* : mean; SD: standard

Measurements	***Squalus bahiensis* sp. nov.**					***Squalus quasimodo* sp. nov.**				
	Holotype	Paratypes				Holotype	Paratypes			
	MNRJ 30180	N	Range	*x*	SD	MZUSP 118707	N	Range	*x*	SD
TL (mm)	585.0	2	615.0 – 690.0	652.5	53.0	700.0	3	660.0 – 830.0	745.0	85.0
PCL	79.5	2	79.2 – 81.2	80.2	1.4	82.9	3	78.5 – 80.1	79.4	0.8
PD2	61.5	2	61.0 – 63.8	62.4	2.0	63.6	3	60.1 – 62.3	61.5	1.2
PD1	29.9	2	29.7 – 30.9	30.3	0.8	32.9	3	28.4 – 31.8	30.3	1.7
SVL	47.0	2	47.2 – 50.7	48.9	2.5	49.7	3	47.0 – 50.6	48.4	1.9
PP2	44.4	2	45.5 – 48.6	47.0	2.1	49.3	3	44.7 – 48.0	46.2	1.6
PP1	21.7	2	22.0 – 22.8	22.4	0.6	23.7	3	21.8 – 22.6	22.2	0.4
HDL	21.4	2	22.8 – 22.9	22.8	0.1	24.7	3	22.2 – 23.0	22.6	0.4
PG1	17.9	2	18.4 – 18.8	18.6	0.3	20.7	3	17.4 – 19.2	18.5	1.0
PSP	12.2	2	12.2 – 12.9	12.6	0.5	12.8	3	11.5 – 12.6	12.2	0.6
POB	7.3	2	7.4 – 7.9	7.7	0.3	7.9	3	6.8 – 7.7	7.4	0.5
PRN	5.0	2	4.9 – 5.1	5.0	0.1	4.8	3	4.5 – 4.9	4.7	0.2
POR	9.9	2	10.2 – 10.5	10.3	0.2	10.2	3	9.5 – 10.0	9.7	0.3
INLF	4.6	2	4.2 – 4.9	4.6	0.5	4.7	3	4.0 – 4.7	4.5	0.4
MOW	7.2	2	7.2 – 7.7	7.5	0.3	7.8	3	7.3 – 7.8	7.5	0.2
ULA	2.3	2	2.2 – 2.2	2.2	0.0	2.6	3	2.2 – 2.5	2.4	0.1
INW	4.2	2	4.7 – 4.8	4.8	0.1	5.0	3	3.9 – 4.1	4.0	0.1
INO	8.2	2	7.9 – 8.3	8.1	0.3	8.8	3	7.7 – 8.0	7.9	0.2
EYL	3.6	2	3.5 – 3.8	3.6	0.2	3.5	3	3.1 – 4.9	4.2	0.9
EYH	1.8	2	1.4 – 1.9	1.6	0.3	1.3	3	1.0 – 2.1	1.5	0.5
SPL	1.3	2	1.3 – 1.6	1.5	0.2	1.3	3	1.1 – 1.4	1.3	0.1
GS1	1.7	2	1.6 – 2.0	1.8	0.3	2.0	3	1.7 – 2.0	1.8	0.2
GS5	1.8	2	1.9 – 2.2	2.0	0.2	2.3	3	2.0 – 2.2	2.1	0.1
IDS	26.5	2	24.4 – 26.8	25.6	1.7	26.4	3	24.0 – 25.8	24.9	0.9
DCS	11.2	2	11.0 – 12.2	11.6	0.8	12.1	3	10.7 – 11.4	11.1	0.4
PPS	19.7	2	19.5 – 20.3	19.9	0.5	22.1	3	20.0 – 22.9	21.6	1.5
PCA	27.4	2	25.2 – 27.8	26.5	1.9	27.1	3	25.3 – 26.2	25.6	0.5
D1L	12.8	2	13.8 – 13.8	13.8	0.0	13.7	3	13.3 – 14.3	13.7	0.5
D1A	10.5	2	10.3 – 10.6	10.4	0.3	11.2	3	10.8 – 11.4	11.1	0.3
D1B	7.5	2	7.2 – 7.3	7.3	0.0	8.2	3	7.7 – 8.5	8.2	0.4
D1H	6.9	2	7.0 – 7.1	7.1	0.0	6.4	3	6.9 – 7.6	7.2	0.3
D1I	5.7	2	6.4 – 6.9	6.7	0.3	5.6	3	5.6 – 6.1	5.9	0.3
D1P	7.9	2	9.2 – 9.6	9.4	0.3	9.4	3	7.7 – 8.4	8.1	0.3
D1ES	2.8	2	2.9 – 3.0	2.9	0.1	4.3	3	3.3 – 4.3	3.9	0.5
D1BS	0.6	2	0.8 – 0.8	0.8	0.0	0.9	3	0.7 – 1.0	0.8	0.2
D2L	11.6	2	12.1 – 12.6	12.4	0.4	12.0	3	11.1 – 12.5	12.0	0.8
D2A	9.4	2	9.3 – 9.7	9.5	0.3	9.7	3	8.1 – 10.6	9.6	1.3
D2B	6.2	2	6.6 – 6.8	6.7	0.2	7.5	3	6.7 – 8.0	7.3	0.6
D2H	5.3	2	4.2 – 4.4	4.3	0.1	4.0	3	4.7 – 5.3	5.0	0.3
D2I	5.3	2	5.6 – 5.6	5.6	0.0	4.5	3	4.6 – 4.9	4.7	0.2
D2P	5.0	2	5.7 – 5.7	5.7	0.0	5.7	3	5.1 – 5.4	5.2	0.2
D2ES	4.1	2	3.7 – 4.3	4.0	0.4	4.4	3	3.9 – 4.3	4.1	0.2
D2BS	0.8	2	0.7 – 0.9	0.8	0.1	1.0	3	0.8 – 0.9	0.8	0.1
P1A	14.3	2	14.4 – 14.5	14.5	0.1	15.9	3	15.5 – 16.0	15.9	0.3
P1I	8.1	2	8.4 – 8.9	8.7	0.4	10.9	3	8.1 – 8.8	8.5	0.4
P1B	4.8	2	4.2 – 4.5	4.4	0.2	4.6	3	4.4 – 5.2	4.8	0.4
P1P	9.8	2	10.5 – 11.3	10.9	0.5	12.3	3	10.2 – 12.5	11.2	1.2
P2L	10.5	2	10.3 – 10.5	10.4	0.1	11.3	3	9.9 – 11.2	10.6	0.6
P2I	5.8	2	5.1 – 5.4	5.2	0.2	4.8	3	4.3 – 5.3	4.7	0.5
CDM	21.9	2	20.0 – 21.4	20.7	1.0	19.7	3	20.2 – 21.3	20.6	0.6
CPV	11.4	2	10.9 – 11.3	11.1	0.3	10.9	3	11.5 – 12.2	11.8	0.4
CFW	6.7	2	6.4 – 7.1	6.7	0.5	7.2	3	6.6 – 7.1	6.9	0.3
HANW	7.0	2	7.0 – 7.1	7.1	0.1	7.6	3	6.4 – 7.2	6.7	0.4
HAMW	10.7	2	10.6 – 10.6	10.6	0.0	11.3	3	9.9 – 11.8	10.8	1.0
HDW	11.9	2	12.4 – 12.6	12.5	0.2	16.1	3	12.2 – 13.5	12.9	0.7
TRW	9.3	2	9.9 – 11.0	10.4	0.8	13.7	3	9.3 – 11.3	10.2	1.0
ABW	7.7	2	8.4 – 8.9	8.6	0.3	9.6	3	6.3 – 10.4	8.9	2.3
HDH	9.3	2	9.6 – 10.0	9.8	0.3	11.3	3	8.9 – 10.4	9.6	0.7
TRH	9.8	2	9.1 – 9.5	9.3	0.3	11.6	3	8.5 – 12.3	10.1	2.0
ABH	10.1	2	9.6 – 10.5	10.0	0.6	12.8	3	8.2 – 12.6	11.1	2.5
CLO	5.0	2	4.6 – 5.1	4.8	0.4	–	–	–	–	–
CLI	7.5	2	6.6 – 7.5	7.0	0.6	–	–	–	–	–

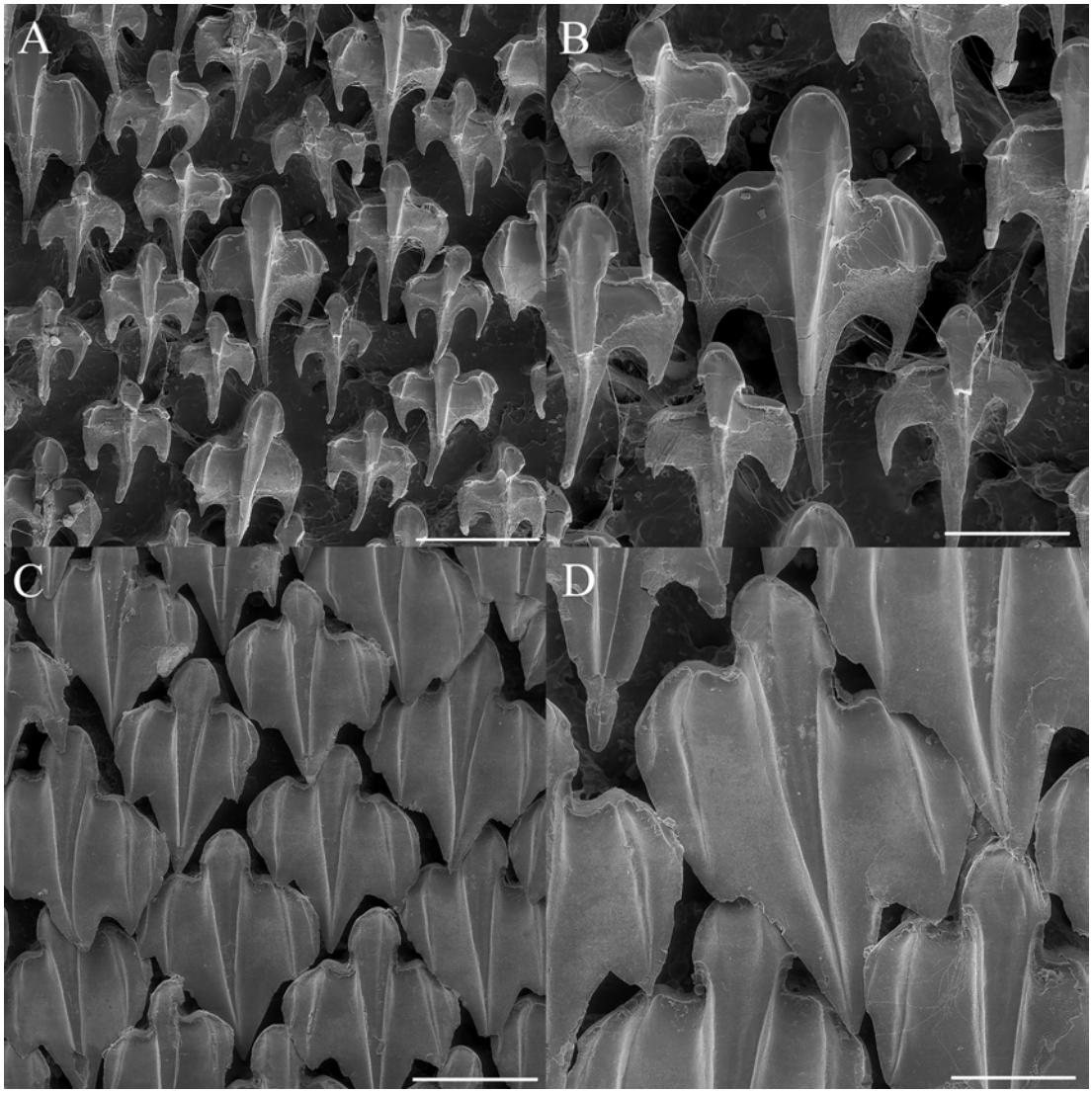

FIGURE 32. Dermal denticles of (A,B) holotype (MNRJ 30180) and (C, D) paratype (MNRJ 30178) of *Squalus bahiensis* sp. nov. Scale bars: 200 μm (A, C); 100 μm (B, D).

The longnose spurdog *S. blainvillei* (Fig. 34) was originally described from the temperate and tropical waters from the Eastern Atlantic Ocean and Mediterranean Sea (Risso, 1826). It is also known from the west coast of Africa, Gulf of Mexico, Caribbean Sea and, possibly, in the Pacific Ocean (Bigelow & Schroeder, 1948, 1957; Garrick, 1960; Bass *et al*., 1976, 1986; Muñoz-Chápuli & Ramos, 1989), and is believed to have wide geographical distribution throughout the Atlantic Ocean (both sides). Type specimens of *S. blainvillei* are unknown, and its original illustration does not refer to any specimens used by Risso (1826) that could suggest a possible type, which makes it difficult to comparatively analyze this species with congeners. However, our new species can be further distinguished from *S. blainvillei* from the Mediterranean Sea (Table 9) by having a wider internarial space (4.2%, 4.7%–4.8% TL *vs*. 3.8%, 3.5%–4.2% TL in *S. blainvillei*), preoral length 1.4 (1.4) times mouth width (*vs*. 1.2, 1.0–1.3 times in *S. blainvillei*), mouth width 1.4 (1.5) times prenarial length and 1.7 (1.5–1.6) times internarial space (*vs*. 1.9, 1.6–2.2 times, and 2.0, 1.9–2.2 times, respectively, for *S. blainvillei*). *Squalus bahiensis* also has a much larger snout than *S. blainvillei* (prenarial length 5.0%, 4.9%–5.1% TL *vs*. 4.1%, 3.3%–4.9% TL in *S. blainvillei*).

The distribution of *S. bahiensis* in other areas of the SWAO will be confirmed if misidentified previous reports of *S. mitsukurii* (e.g. Fischer *et al*., 2006) and *S. blainvillei* (e.g. Menni *et al*., 1984; Meneses & Paesch, 2003) turn out to be this species. The lack of morphological data and pictures in studies that list, cite or describe *S. blainvillei* have contributed to the doubtful occurrence of *S. bahiensis* in other areas.

TABLE 8. Meristic data for holotype and paratypes of *Squalus bahiensis* sp. nov. and *Squalus quasimodo* sp. nov. Range for specimens of *Squalus blainvillei* are also provided for comparisons. A: MNRJ 30178; B: MNRJ 30179; C: UERJ 1741; D: UERJ 1819. N: number of specimens.

Character	*Squalus bahiensis*			*Squalus quasimodo*			*Squalus blainvillei*										
	Holotype	Paratypes		Holotype	Paratypes		**Mediterranean Sea**			**Southeastern Atlantic**			**Northwestern Atlantic**			**Western Central Atlantic**	
		A	B		C	D	N	Range	Mode	N	Range	Mode	N	Range	Mode	N	
precaudal vertebrae	87	87	87	87	92	91	1	84	–	3	83–87	–	2	90–92	–	1	87
caudal vertebrae	30	29	27	29	29	29	1	27	–	3	31–33	31	2	29–31	–	1	30
total vertebrae	117	116	115	116	121	120	1	111	–	3	114–119	–	2	121	121	1	117
monospondylous vertebrae	43	45	43	45	46	46	1	43	–	3	41–44	44	2	44–45	–	1	45
diplospondylous vertebrae	74	71	72	71	75	74	1	68	–	3	73–75	–	2	76–76	76	1	72
upper tooth rows (right)	13	13	14	14	14	14	2	12–13	–	3	12–13	12	2	12–14	–	1	11
upper tooth rows (left)	14	13	15	14	14	14	2	13–13	13	3	12–13	13	2	11–13	–	1	11
lower tooth rows (right)	11	10	11	11	11	–	2	11–12	–	3	12–12	12	2	12–12	12	1	12
lower tooth rows (left)	12	11	11	11	11	11	2	11–11	11	3	12–12	12	2	11–13	–	1	11
upper tooth series	2	3	3	2	2	2	2	2–2	2	3	2–2	2	2	2–2	2	1	2
lower tooth series	2	2	2	2	2	2	2	2–2	2	3	2–2	2	2	2–2	2	1	2
Propterygium radials	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Mesopterygium radials	–	–	–	10	–	–	–	–	–	–	–	–	–	–	–	–	–
Metapterygium radials	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total pectoral radials	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total pelvic radials	–	–	–	16	–	–	–	–	–	–	–	–	–	–	–	–	–

TABLE 9. External measurements expressed as percentage of total length (% TL) for specimens of *Squalus blainvillei* . N: number of specimens; *x* : mean; SD: standard deviation.

Measurements	Mediterranean Sea				Eastern Atlantic Ocean				Western Central Atlantic				Northeastern Atlantic Sea			
	N	Range	*x*	SD	N	Range	*x*	SD	N	Range	*x*	SD	N	Range	*x*	SD
TL (mm)	3	215.0 – 635.0	423.3	210.0	9	221.0 – 780.0	438.1	216.3	8	340.0 – 665.0	532.3	93.9	18	213.0 – 832.0	513.0	160.6
PCL	3	79.1 – 81.0	79.8	1.0	9	76.7 – 81.4	78.4	1.4	8	77.9 – 80.0	78.9	0.6	18	77.5 – 82.3	79.6	1.2
PD2	3	61.4 – 62.8	62.0	0.7	9	57.5 – 64.1	60.3	2.0	8	59.4 – 62.4	61.0	1.0	18	58.7 – 64.4	61.6	1.6
PD1	3	29.1 – 31.6	30.6	1.3	9	29.1 – 33.3	31.3	1.3	8	28.8 – 32.4	30.8	1.2	18	29.4 – 32.2	30.8	0.8
SVL	3	45.7 – 50.2	48.6	2.6	9	45.3 – 50.0	47.7	1.7	8	29.4 – 50.0	45.3	6.6	18	30.6 – 53.3	45.9	6.0
PP2	3	42.5 – 46.5	45.1	2.2	9	41.8 – 47.5	45.0	1.7	8	27.5 – 46.5	42.7	6.2	18	28.1 – 51.1	42.4	6.8
PP1	3	20.5 – 23.7	21.8	1.7	9	22.2 – 25.9	23.5	1.2	8	21.4 – 24.8	23.1	1.4	18	10.5 – 24.0	20.9	3.0
HDL	3	21.5 – 24.5	22.9	1.5	9	22.6 – 26.0	24.2	1.0	8	22.3 – 25.4	23.5	1.0	18	20.7 – 24.3	22.2	1.2
PG1	3	17.9 – 20.5	19.1	1.3	9	18.9 – 21.5	20.5	0.9	8	18.9 – 19.9	19.6	0.4	18	17.4 – 20.0	18.7	0.9
PSP	3	11.0 – 13.5	12.2	1.3	9	11.7 – 14.2	13.0	0.8	8	12.0 – 13.2	12.6	0.4	18	10.1 – 13.3	12.1	0.7
POB	3	6.5 – 7.4	6.8	0.5	9	6.1 – 8.4	7.6	0.7	8	6.6 – 8.0	7.5	0.5	18	5.9 – 7.8	7.1	0.5
PRN	3	3.3 – 4.9	4.1	0.8	9	3.9 – 5.7	5.1	0.6	8	3.1 – 5.3	4.7	0.7	18	3.9 – 5.3	4.7	0.4
POR	3	7.7 – 10.3	9.2	1.4	9	9.1 – 11.8	9.9	0.8	8	9.5 – 11.4	10.1	0.6	18	8.5 – 10.9	9.7	0.6
INLF	3	4.0 – 4.8	4.5	0.4	9	4.4 – 9.5	5.4	1.6	8	4.5 – 5.2	4.8	0.2	18	4.0 – 5.3	4.6	0.3
MOW	3	7.3 – 8.1	7.8	0.4	9	7.5 – 9.0	8.4	0.5	8	7.4 – 9.0	7.9	0.5	18	6.8 – 8.4	7.4	0.4
ULA	3	2.4 – 2.7	2.5	0.2	9	2.3 – 2.8	2.6	0.2	8	1.9 – 2.7	2.3	0.2	18	2.0 – 2.6	2.4	0.2
INW	3	3.5 – 4.2	3.8	0.4	9	3.7 – 5.3	4.7	0.5	8	3.8 – 4.5	4.2	0.2	18	3.7 – 4.5	4.1	0.2
INO	3	7.9 – 8.9	8.3	0.5	9	4.9 – 10.4	8.6	1.6	8	7.9 – 8.7	8.4	0.3	18	7.6 – 9.3	8.3	0.5
EYL	3	3.3 – 4.7	3.9	0.7	9	3.5 – 5.3	4.2	0.7	8	3.6 – 4.2	3.9	0.2	18	3.0 – 5.3	3.8	0.6
EYH	3	1.7 – 2.4	2.0	0.4	9	1.5 – 2.3	2.0	0.3	8	1.3 – 2.1	1.6	0.3	18	1.2 – 1.9	1.5	0.2
SPL	3	1.2 – 1.9	1.5	0.4	9	1.6 – 2.4	2.0	0.3	8	1.2 – 1.6	1.5	0.1	18	1.0 – 1.6	1.3	0.1
GS1	3	1.8 – 2.0	1.9	0.1	9	2.0 – 2.5	2.2	0.2	8	1.3 – 1.8	1.6	0.1	18	1.3 – 2.2	1.7	0.2
GS5	3	2.2 – 2.5	2.4	0.2	9	2.1 – 2.6	2.4	0.2	8	1.9 – 2.5	2.1	0.2	18	1.7 – 2.5	2.0	0.2
IDS	3	25.0 – 26.8	25.6	1.0	9	20.9 – 26.5	23.3	2.1	8	22.1 – 27.1	24.9	1.5	18	23.2 – 27.5	25.5	1.3
DCS	3	9.6 – 11.7	10.9	1.1	9	10.0 – 11.3	10.6	0.4	8	10.5 – 11.8	11.3	0.5	18	10.1 – 12.9	11.6	0.8
PPS	3	18.9 – 22.0	20.8	1.7	9	15.2 – 22.5	18.7	2.3	8	17.0 – 21.5	19.2	1.3	18	16.3 – 25.9	20.8	2.4
PCA	3	23.9 – 27.9	25.9	2.0	9	24.3 – 27.9	25.8	1.2	8	25.3 – 27.7	26.5	1.0	18	24.1 – 29.1	27.2	1.3
D1L	3	13.6 – 15.2	14.3	0.8	9	13.5 – 16.3	14.8	0.9	8	11.6 – 15.2	13.2	1.2	18	11.8 – 14.0	12.5	0.6
D1A	3	11.5 – 12.6	12.1	0.5	9	10.5 – 14.3	12.9	1.3	8	9.0 – 13.4	10.7	1.5	18	7.4 – 12.7	10.0	1.1
D1B	3	8.0 – 8.6	8.2	0.3	9	7.8 – 9.0	8.6	0.4	8	5.8 – 8.8	7.4	1.0	18	6.4 – 8.5	7.1	0.5
D1H	3	7.3 – 8.7	8.2	0.8	9	7.7 – 10.2	9.1	0.8	8	6.6 – 9.9	7.6	1.4	18	6.0 – 9.9	7.6	0.9
D1I	3	5.8 – 6.5	6.2	0.4	9	5.4 – 7.3	6.5	0.6	8	5.3 – 6.7	6.2	0.4	18	5.2 – 6.6	5.6	0.4
D1P	3	7.6 – 9.9	8.8	1.2	9	5.7 – 9.6	8.4	1.3	8	7.0 – 10.2	8.1	1.0	18	6.0 – 9.3	7.6	0.8
D1ES	3	1.9 – 5.4	3.8	1.8	9	2.4 – 4.9	3.8	0.9	8	1.6 – 4.9	3.2	1.2	18	1.8 – 4.1	3.2	0.6
D1BS	3	0.7 – 1.1	0.9	0.2	9	0.7 – 1.1	0.9	0.1	8	0.6 – 1.2	0.8	0.2	18	0.5 – 1.1	0.8	0.1
D2L	3	11.6 – 13.1	12.4	0.8	9	11.8 – 13.8	12.7	0.8	8	10.9 – 13.4	12.4	0.9	18	10.5 – 13.3	11.8	0.8
D2A	3	10.0 – 10.8	10.5	0.4	9	9.3 – 11.8	10.8	0.9	8	8.4 – 11.6	10.0	1.2	18	8.1 – 11.1	9.5	0.9
D2B	3	6.5 – 8.0	7.1	0.8	9	6.7 – 8.4	7.5	0.5	8	6.1 – 8.3	7.4	0.7	18	5.5 – 8.0	6.8	0.7
D2H	3	6.6 – 7.5	7.2	0.5	9	4.4 – 7.3	6.2	0.8	8	4.5 – 7.6	5.6	1.0	18	4.4 – 7.7	5.8	0.8
D2I	3	5.2 – 5.8	5.5	0.3	9	5.1 – 6.0	5.4	0.3	8	4.5 – 5.7	5.2	0.4	18	4.5 – 5.6	5.1	0.3
D2P	3	4.4 – 5.6	4.9	0.6	9	4.1 – 6.2	5.2	0.6	8	4.3 – 5.3	4.8	0.3	18	4.1 – 5.6	5.0	0.4
D2ES	3	3.4 – 7.1	5.4	1.8	9	3.4 – 6.1	4.9	0.9	8	3.4 – 5.8	4.4	0.9	18	2.2 – 5.9	4.3	0.8
D2BS	3	0.9 – 1.0	0.9	0.1	9	0.8 – 5.1	1.4	1.4	8	0.7 – 1.0	0.8	0.1	18	0.7 – 4.7	1.0	0.9
P1A	3	12.1 – 15.2	14.1	1.7	9	12.4 – 18.0	15.0	1.9	8	12.6 – 17.8	14.6	2.0	18	12.0 – 15.4	13.5	1.0
P1I	3	7.5 – 9.6	8.9	1.2	9	8.2 – 10.3	9.2	0.7	8	8.4 – 9.9	9.1	0.6	18	7.4 – 10.1	8.6	0.6
P1B	3	4.3 – 5.3	4.8	0.5	9	4.0 – 5.5	4.9	0.5	8	3.9 – 5.6	4.8	0.5	18	4.1 – 5.4	4.6	0.4
P1P	3	9.9 – 12.0	10.7	1.2	9	8.6 – 13.9	11.0	1.9	8	8.7 – 14.7	10.7	2.0	18	8.8 – 12.3	10.1	0.9
P2L	3	4.4 – 11.9	9.2	4.1	9	9.5 – 12.8	11.1	1.2	8	9.4 – 11.5	10.8	0.7	18	5.0 – 11.0	9.9	1.4
P2I	3	4.7 – 5.5	5.0	0.4	9	4.8 – 7.5	5.8	0.9	8	5.0 – 6.6	5.6	0.7	18	3.8 – 10.4	5.4	1.4
CDM	3	20.8 – 22.8	21.8	1.0	9	20.5 – 23.1	22.2	0.8	8	20.8 – 21.8	21.3	0.3	18	19.7 – 22.2	20.8	0.7
CPV	3	11.1 – 12.1	11.7	0.5	9	11.3 – 13.1	12.1	0.5	8	10.6 – 12.7	11.7	0.7	18	10.4 – 12.8	11.4	0.7
CFW	3	6.6 – 8.9	7.4	1.3	9	6.0 – 8.4	7.2	0.6	8	6.3 – 11.3	7.8	1.6	18	6.0 – 7.5	6.5	0.4
HANW	3	6.6 – 8.8	7.4	1.2	9	7.1 – 9.0	7.9	0.6	8	6.3 – 7.5	7.0	0.4	18	6.1 – 9.2	7.2	0.8
HAMW	3	10.3 – 11.0	10.7	0.3	9	11.6 – 13.2	12.5	0.5	8	10.9 – 12.3	11.5	0.5	18	9.9 – 12.2	10.8	0.6
HDW	3	11.1 – 12.6	12.0	0.8	9	12.6 – 15.3	13.5	0.9	8	11.3 – 14.2	12.5	1.1	18	10.4 – 13.2	12.0	0.6
TRW	3	8.6 – 9.4	9.0	0.4	9	8.2 – 10.4	9.8	0.7	8	8.7 – 11.0	9.8	0.8	18	7.6 – 10.7	9.4	0.9
ABW	3	6.6 – 9.0	8.0	1.3	9	6.8 – 8.7	7.7	0.7	8	6.2 – 10.1	7.9	1.5	18	6.5 – 9.4	7.9	0.9
HDH	3	8.5 – 11.0	10.1	1.4	9	9.3 – 11.7	10.8	0.8	8	9.1 – 12.2	10.2	1.3	18	8.1 – 10.5	9.3	0.7
TRH	3	7.4 – 12.6	10.5	2.7	9	9.3 – 12.6	10.6	1.1	8	8.3 – 13.3	10.3	2.2	18	7.7 – 10.4	9.5	0.7
ABH	3	7.5 – 11.5	9.8	2.1	9	0.8 – 10.9	8.1	2.9	8	7.6 – 12.0	9.4	1.6	18	6.5 – 11.1	8.5	1.1
CLO	1	–	1.6	–	6	1.0 – 5.4	3.3	2.2	3	1.2 – 4.8	3.6	2.0	5	1.2 – 5.1	3.3	1.8
CLI	1	–	3.1	–	6	2.2 – 9.5	5.4	3.2	3	2.6 – 7.6	5.9	2.8	5	2.8 – 7.6	5.5	2.4

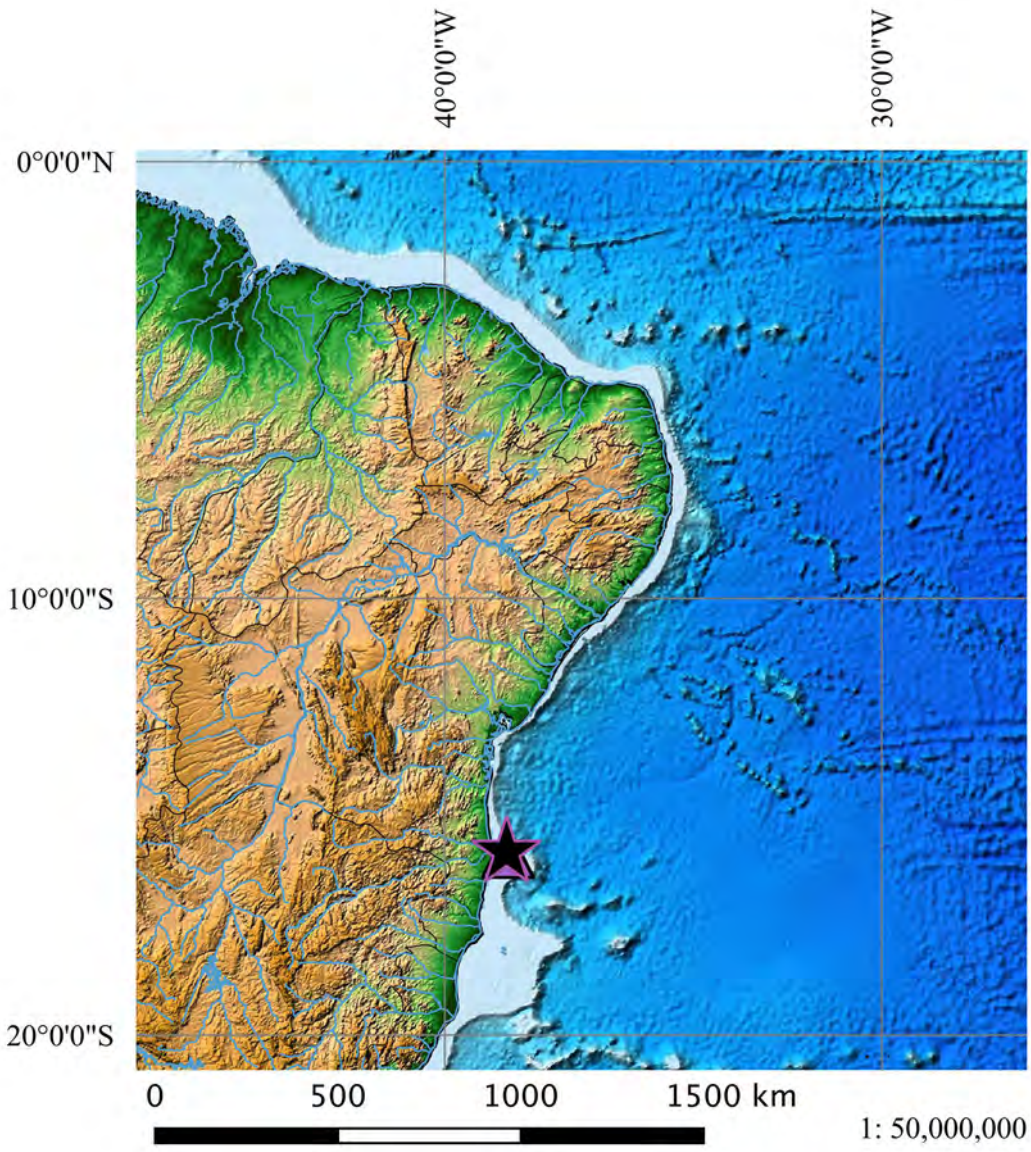

FIGURE 33. Map of the Southwestern Atlantic Ocean, showing the geographical distribution of *Squalus bahiensis* **sp. nov.** Black star: location of holotype; purple triangle: location of paratypes.

No morphological similarities, including morphometric and meristic data, were found between *S. bahiensis* and specimens of *S. blainvillei* from the Southeastern Atlantic, Western Central Atlantic and Northeastern Atlantic oceans (Table 9), indicating that the former species may not reach northward of the Southwestern Atlantic Ocean. Despite overlap in external measurements in *S. blainvillei* from different regions, a broad range of values are apparent that may indicate certain variability. Variations in vertebral counts are also noticed within this species that require further scrutiny, as pointed out by previous authors (e.g. Macleay, 1881 for Australia; Garrick, 1960 for New Zealand; Springer & Garrick, 1964; Chen *et al*., 1979 for Japan; Cadenat & Blache, 1981 for New Caledonia). A better morphological characterization of *S. blainvillei* and designation of a neotype are necessary in order to help distinguish it from congeners.

Comparative material. *Squalus mitsukurii*: same material examined for *Squalus lobularis*.

Squalus blainvillei: Northeastern Atlantic Ocean: (31 specimens). AMNH 1863, juvenile female, 420 mm TL, Naples, Italy; BMNH 1963.5.14.13-18, six juvenile males, 242–382 mm TL, France, Mediterranean Sea; MCZ 37064, juvenile male, 398 mm TL, Sargasso Sea; MCZ 37993, neonate male, 215 mm TL, Mediterranean Sea; MCZ 39818, neonate male, 235 mm TL, Sargasso Sea; MCZ 40716-S, neonate female, 221 mm TL, Senegal; UERJ 183, adult female, 770 mm TL, Gulf of Lion, Mediterranean Sea; UERJ 184, adult male, 600 mm TL, Gulf

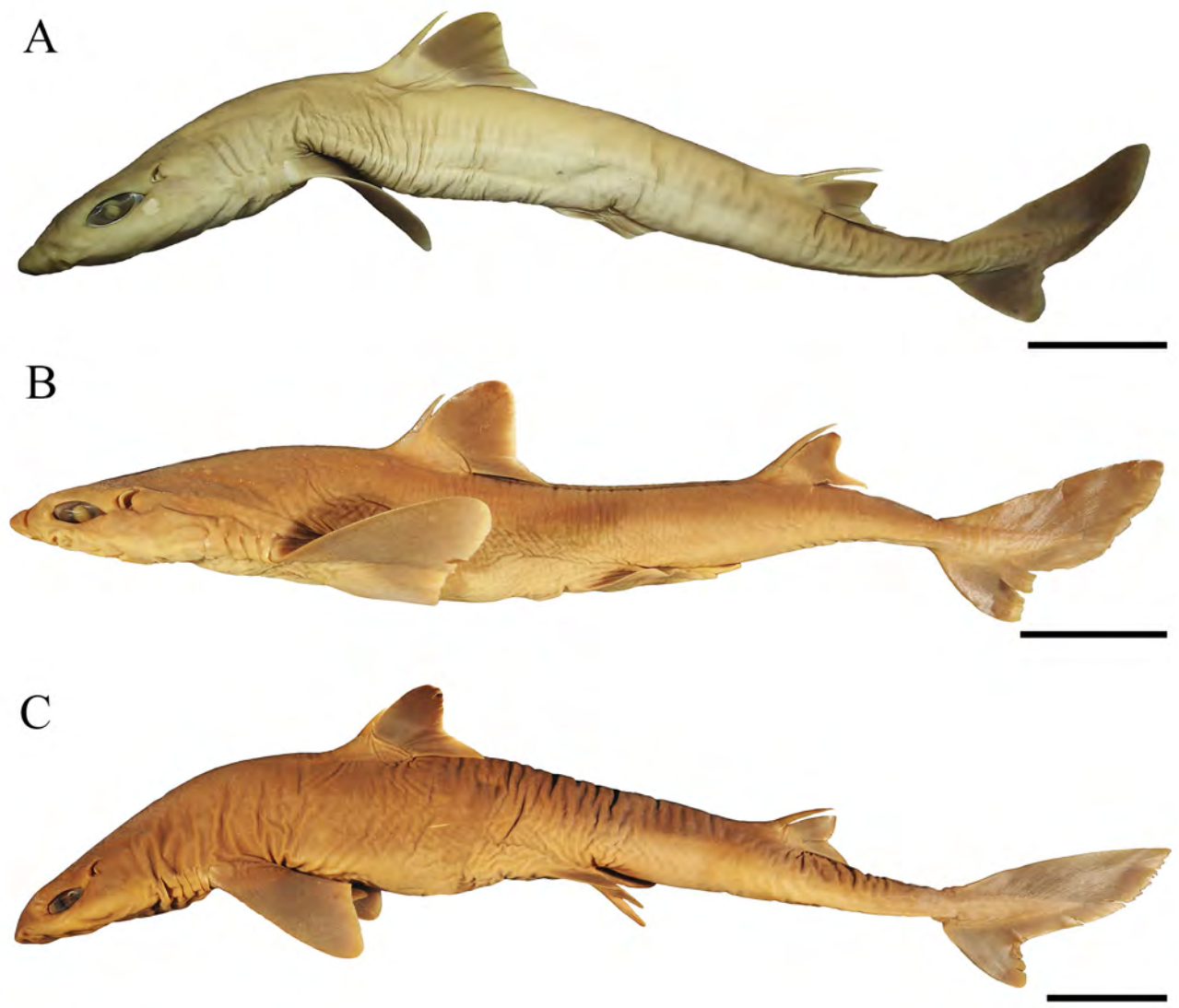

FIGURE 34. Specimens of *Squalus blainvillei*: (A) AMNH 1863; (B) UF 44560; (C) UF 213389. Scale bar: 50 mm.

of Lion, Mediterranean Sea; USNM 196153, neonate female, 218 mm TL; neonate male, 235 mm TL, Senegal; USNM 202938, neonate male, 287 mm TL, Serra Leone; USNM 203745, adult female, 635 mm TL, Gulf of Tunis; USNM 220516, six neonate females, 208–215 mm TL, seven neonate males, 205–235 mm TL, Sierra Leone; USNM 220515, neonate female, 262 mm TL, Liberia. Northwestern Atlantic Ocean: (44 specimens). AMNH 33451, juvenile female, 590 mm TL, adult female, 675 mm TL, Louisiana, U.S.A.; AMNH 97650, neonate female, 254 mm TL, Saint David Island, Bermuda; UF 213389, juvenile male, 500 mm TL, at 150 km northeast of Jacksonville Beach, Florida, U.S.A.; MCZ 39787, neonate female, 255 mm TL, Florida, U.S.A.; MCZ 39827, neonate female, 285 mm TL, Florida, U.S.A.; MCZ 39878, neonate female, 242 mm TL, two neonate males, 193–198 mm TL, South Carolina, U.S.A.; MCZ 39888, neonate female, 213 mm TL, North Carolina, U.S.A.; MCZ 39893, three neonate males, 183–205 mm TL, Florida, U.S.A.; MCZ 39902, neonate female, 183 mm TL, two neonate males, 188–223 mm TL, Florida, U.S.A.; MCZ 40116, three neonate males, 190–231 mm TL, Florida, U.S.A.; MCZ 40137, two neonate females, 170–213 mm TL, Florida, U.S.A.; MCZ 42457, juvenile female, 552 mm TL, Florida, U.S.A.; MCZ 42460, juvenile female, 462 mm TL, Florida, U.S.A.; MCZ 42483, adult female, 498 mm TL, Florida, U.S.A.; USNM 157748, juvenile female, 370 mm TL, Florida, U.S.A.; USNM 157864, juvenile female, 540 mm TL, juvenile male, 375 mm TL, Florida, U.S.A.; USNM 158478, neonate female, 295 mm TL, New Orleans, U.S.A.; USNM 160831, adult female, 625 mm TL, Florida, U.S.A.; USNM 187787, adult

female, 710 mm TL, Florida, U.S.A.; USNM 188025, juvenile female, 360 mm TL, North Carolina, U.S.A.; USNM 188082, juvenile female, 555 mm TL, two juvenile males, 535–580 mm TL, Florida, U.S.A.; USNM 203490, juvenile female, 528 mm TL, Florida, U.S.A.; USNM 203496, juvenile female, 468 mm TL, Florida, U.S.A.; USNM 203497, juvenile female, 455 mm TL, Florida, U.S.A.; USNM 203498, juvenile female, 487 mm TL, Florida, U.S.A.; USNM 206054, adult female, 832 mm TL, Florida, U.S.A.; USNM 206056, adult female, 640 mm TL, Austin, U.S.A.; USNM 220517, juvenile male, 370 mm TL, Florida, U.S.A.; USNM 220602, juvenile female, 415 mm TL, Florida, U.S.A.; USNM 220967, juvenile female, 555 mm TL, Florida, U.S.A.; USNM 220968, juvenile male, 575 mm TL, Florida, U.S.A.. Western Central Atlantic Ocean: (11 specimens). AMNH 33449, juvenile male, 545 mm TL, Nicaragua; AMNH 33450, juvenile female, 480 mm TL, Nicaragua; AMNH 33452, juvenile female, 540 mm TL, Leeward Islands; USNM 220514, neonate female, 197 mm TL, Windward Islands, Martinique; USNM 220966, adult male, 560 mm TL, juvenile male, 475 mm TL, Colombia; USNM 187718, juvenile female, 560 mm TL, Nicaragua; USNM 187719, juvenile female, 510 mm TL, between Jamaica and Honduras; USNM 187727, juvenile male, 340 mm TL, Panama; USNM 206055, adult female, 665 mm TL, Dominican Republic; USNM 206059, juvenile female, 533 mm TL, Leeward Islands. Eastern Central Atlantic Ocean: (3 specimens). AMNH 75328, two juvenile females, 545 –590mm TL, South of Puerto Rico, Spain. Southeastern Atlantic Ocean: (3 specimens). UF 44560, juvenile male, 395 mm TL, Northwest of Walvis Bay, Namibia; USNM 197691, adult female, 733 mm TL, adult male, 780 mm TL, South Africa. Indian Ocean: (1 specimen). USNM 205588, juvenile female, 435 mm TL, Mozambique. South Pacific Ocean: (1 specimen). SU 12159, adult female, 930 mm TL, New Zealand. Northwestern Pacific Ocean: (2 specimens). SU 26907, two neonate females, 170–175 mm TL, Philippines.

Squalus quasimodo **sp. nov.**

(Figs. 35–41; Tables 7–8)

Suggested common names: Humpback Western dogfish; cação-bagre-corcunda (Portuguese)

Squalus blainvillei (not Risso): Regan, 1908 (in part): 45, 47 (identification key, listed); Bigelow & Schroeder, 1948: 454, 455 (cited, identification key; Brazil); Lucena & Lucena, 1981: 2, 4, 5, fig. 3 (listed; Brazil); Compagno, 1984: 110, 115, 116 (revision; global); Menni *et al*., 1984: 84 (listed; Argentina, Uruguay); Muñoz-Chápuli, 1985: 397, 398, fig. 1 (cited); Muñoz-Chápuli & Ramos, 1989: 21, figs. 1, 2B, 3B (revision; Eastern Atlantic); Canizarro *et al*., 1994: 113 (cited); Nion *et al*., 2002: 4 (listed); Meneses & Paesch, 2003: 8, 25 (cited; Argentina, Uruguay); Compagno *et al*., 2005 (in part): 74, 75, pl. 3 (description; global); Lamilla & Bustamante, 2005: 9, 26 (listed; Chile); Saéz *et al*., 2010: 623 (identification key; Chile); Viana, 2011 (in part): 57–91, figs. 18–34 (revision; Brazil); Rosa & Gadig, 2014: 92 (listed; Brazil).

Squalus fernandinus (not Molina): Garman, 1913: 195 (description); Fowler, 1936: 71 (description; South Atlantic); Bigelow & Schroeder, 1948: 478–480 (revision; Northwestern Atlantic); Bigelow, Schroeder & Springer, 1953: 220–222 (cited; Western Atlantic); Bigelow & Schroeder, 1957: 32–36 (description); Menni *et al*., 1984: 62 (identification key; Argentina and Uruguay); Myagkov & Kondyurin, 1986: 13, 14 (revision; Atlantic).

Squalus lebruni: Myagkov & Kondyurin, 1986: 1–20, fig. 2 (revision; Atlantic).

Squalus mitsukurii (not Jordan & Snyder): Calderón, 1994: fig. 5B (cited; Brazil); Lessa *et al*., 1999: 61, 150 (cited, listed; South Brazil); Haimovici *et al*., 2003: 38, 39 (cited); Compagno *et al*., 2005: 77–78, pl. 3 (description; Southeast Brazil); Jablonski *et al*., 2006: 177 (cited); Louro & Rossi-Wongtschowski, 2007: 18, 27, 28, 30, 49 (cited); Menni & Lucifora, 2007: 3 (listed).

Squalus sp. of the *blainvillei* group: Gomes *et al*., 1997: 93–95, 109 (description; Brazil); Marques, 1999 (cited; Brazil).

Squalus of the *blainvillei*/*mitsukurii* group: Gadig, 2001 (in part): 29, 36, 54, 55, 57, 58, fig. 29 (listed; Brazil).

Squalus sp. B: Soto, 2001: 96 (listed; Brazil); Soto & Mincarone, 2004: 79–82 (listed; Brazil).

Squalus sp. 1: Gomes *et al*., 2010: 44, 45 (cited; Brazil).

Holotype. MZUSP 118707 (formerly, UERJ 1111), adult female, 700 mm TL, off the coast of Rio Grande do Sul, Brazil.

Paratypes (3 specimens). UERJ 1741, adult female, 850 mm TL, Revizee sta. 6089 (nearest station 6088, 89.8W, 33S), Brazil; UERJ 1819, adult female, 740 mm TL, Revizee sta. 6104 (nearest station 6102, 62W, 20.8S), Brazil; MCP 773, juvenile female, 660 mm TL, between coast of Rio Grande do Sul state, Brazil and Uruguay.

Diagnosis. A species of *Squalus* from the SWAO that can be distinguished from its congeners through a combination of characters: body conspicuously robust and humped dorsally; second dorsal fin upright and markedly tall (its height 4.0%, 4.7%–5.3% TL); first and second dorsal-fin spines elongate (first dorsal-fin spine

length 4.3%, 3.3%–4.3% TL; second dorsal-fin spine length 4.4%, 3.9%–4.3% TL), and broad at base (first spine base length 0.9%, 0.7%–1.0% TL; second spine base length 1.0%, 0.8%–0.9% TL); caudal fin with conspicuous rectangular dorsal lobe; and dermal denticles tricuspid, markedly imbricate and broad at crown. *Squalus quasimodo* **sp. nov.** differs from *S. bahiensis* by having a larger pectoral-fin anterior margin length (15.9%, 15.5%–16.0% TL *vs*. 14.3%, 14.4%–14.5% TL, respectively) and more elongate first dorsal-fin spine (length 4.3%, 3.3%–4.3% TL *vs*. 2.8%, 2.9%–3.0% TL). *Squalus quasimodo* **sp. nov.** has a larger first dorsal fin than *S. bahiensis* with a greater anterior margin length (11.2%, 10.8%–11.4% TL *vs*. 10.5%, 10.3%–10.6% TL, respectively) and fin base (length 8.2%, 7.7%–8.5% TL *vs*. 7.5%, 7.2%–7.3% TL, respectively). *Squalus quasimodo* **sp. nov.** is clearly distinct from *S. lobularis* by having a greater interdorsal distance (26.4%, 24.0%–25.8% TL *vs*. 22.3%, 21.9%–23.6% TL, respectively).

FIGURE 35. Holotype of *Squalus quasimodo* **sp. nov.** (MZUSP 118707, adult female, 700 mm TL) in lateral view. Scale bar: 50 mm.

Description. **External morphology**. Measurements and meristic data are summarized in Tables 7–8. Body markedly robust and humped dorsally, more slender from pelvic fins to caudal fin; body extremely deep from head to tail (head width 1.0, 0.8–1.0 times trunk height and 0.9, 0.7–1.2 times abdomen height), very wide at head (head width 1.2, 1.2–1.4 times greater than trunk width, and 1.7, 1.3–1.9 times greater than abdomen width). Head flattened dorsally from snout to spiracle and elongate, its length 24.7% (22.2%–23.0% TL), corresponding to 1.3 (1.0–1.1) times dorsal caudal margin length. Snout strongly pointed at tip and elongate (preorbital length 7.9%, 6.8%–7.7% TL); anterior margin of nostrils broad and bilobate, placed ventrolaterally in snout; prenarial length 1.0 (1.0–1.1) times distance from nostrils to upper labial furrow and 1.4 (1.0–1.4) times larger than eye length; width between nostrils narrow (length 5.0%, 3.9%–4.1% TL), corresponding to 1.4 (0.8–1.2) times eye length. Eyes oval with anterior margin convex and posteriorly notched, very large, its length 3.5%, 3.1%–4.9% TL and corresponding to 2.6 (2.2–3.3) times its height. Prespiracular length 12.8% (11.5%–12.6% TL), corresponding to 1.6 (1.6–1.7) times preorbital length. Spiracles crescent-shaped, located posterodorsally to eyes and very wide, their length 1.3% (1.1%–1.4% TL). Prebranchial length 20.7%, 17.4%–19.2% TL. Gill slits vertical, markedly tall (fifth gill slit height 1.1, 1.1–1.2 times first gill slit height), placed laterally just before pectoral fins.

Preoral length 1.3 (1.2–1.4) times mouth width. Mouth straight and strongly broad, its width 1.6 (1.8–2.0) times greater than internarial space; upper labial furrow elongate, its length 2.6% (2.2%–2.5% TL) with prominent fold; lower labial furrow also long, although not supporting a fold. Teeth unicuspid, similar in both jaws, alternate, compressed and wide labial-lingually at crown; lower teeth markedly larger and taller than upper teeth; cusp pointed, somewhat elongate and thick, oblique, directed laterally; mesial cutting edge conspicuously convex (straight on lower lateral teeth); mesial heel notched; distal heel rounded; apron short and heavy; two series of functional teeth in upper and lower jaw; tooth rows from 14–14 (14–14 paratypes) in upper jaw and 11–11 (11–11 paratypes) in lower jaw (Fig. 37).

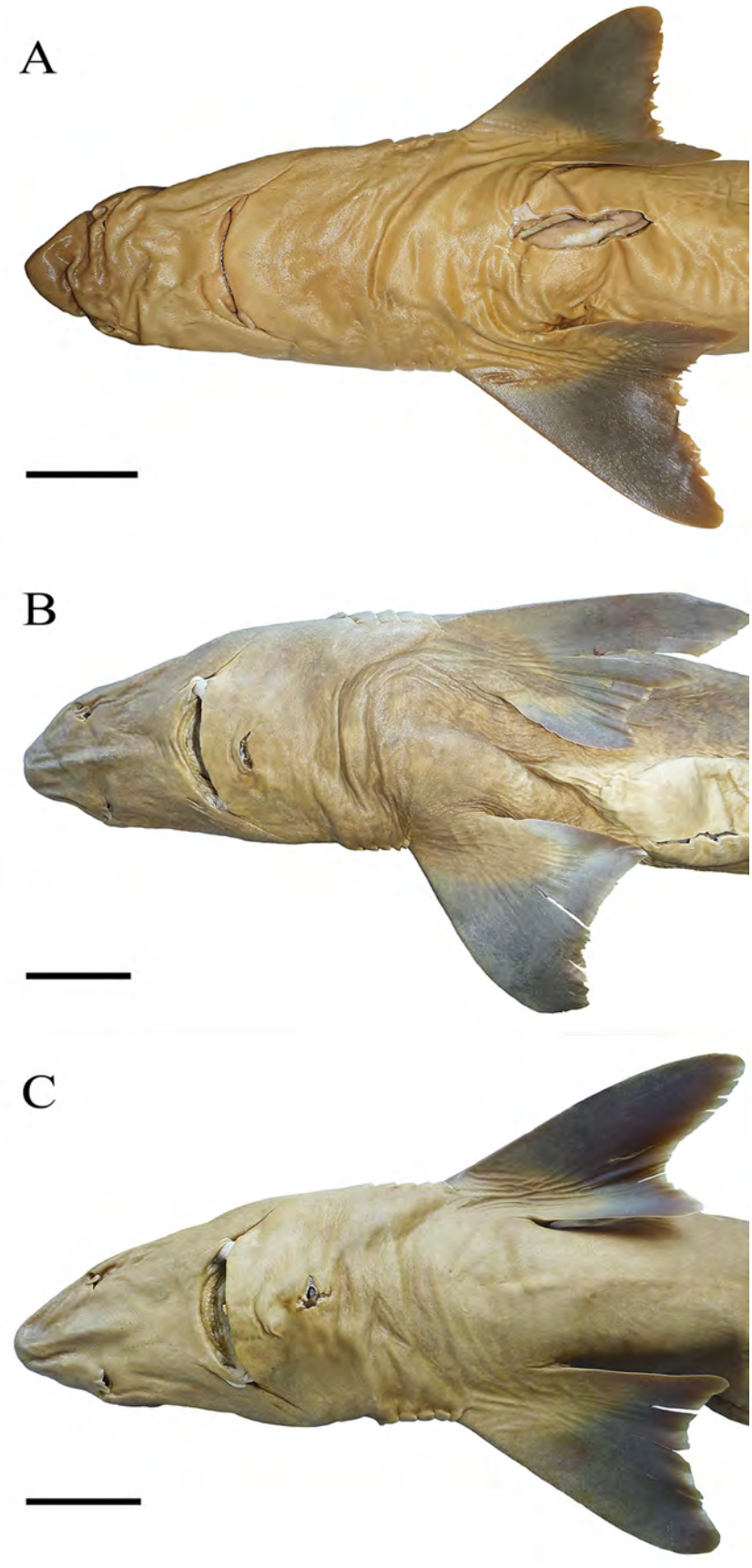

FIGURE 36. *Squalus quasimodo* **sp. nov.** in ventral view. (A) holotype (MZUSP 118707, adult female, 700 mm TL); (B) paratype (UERJ 1741, adult female, 850 mm TL); (C) paratype (UERJ 1819, adult female, 740 mm TL). Scale bar: 50 mm.

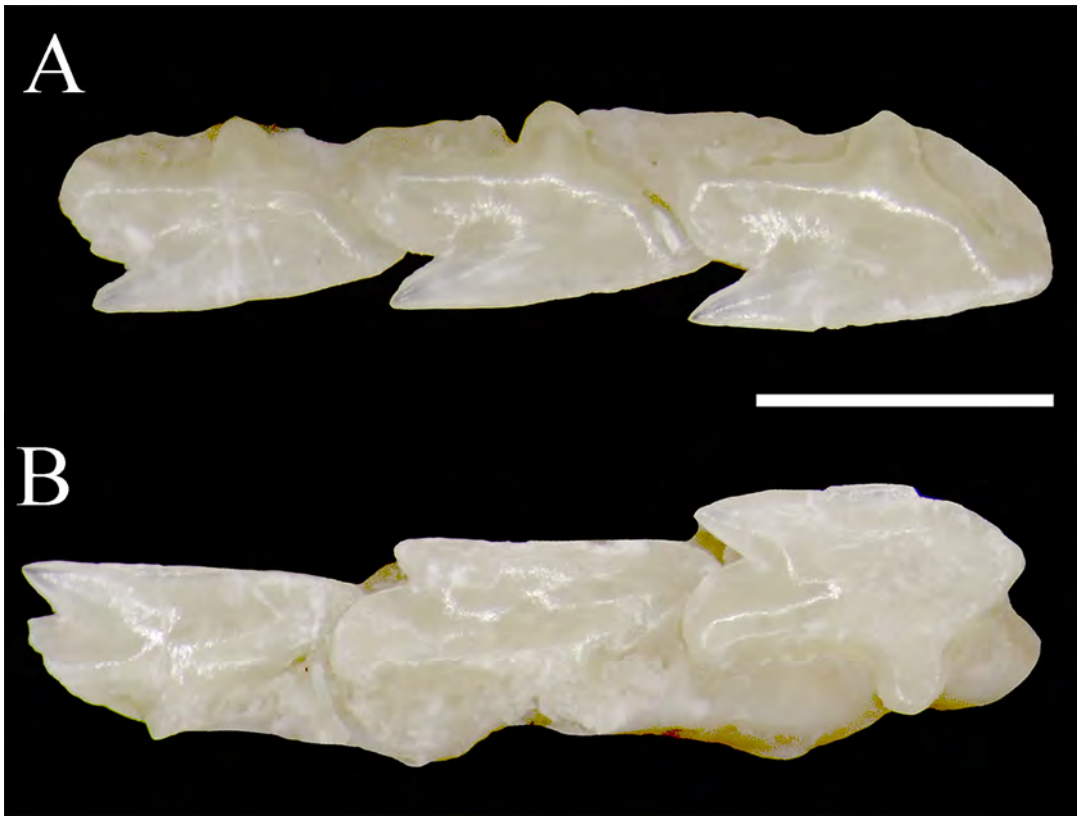

FIGURE 37. Upper (A) and lower (B) teeth of holotype of *Squalus quasimodo* **sp. nov.** (MZUSP 118707, adult female, 700 mm TL). Scale bar: 2 mm.

Pre-first dorsal fin length 32.9% (28.4%–31.8% TL), its origin well before the vertical line through pectoral free rear tips. First dorsal fin very large (length 2.2, 1.9–1.9 times greater than height), and upright, with anterior margin convex, posterior margin straight, although convex from its midline to more slender apex (Fig. 38); conspicuously rounded and slender at apex, free rear tip rounded; first dorsal-fin anterior margin length 11.2% (10.8%–11.4% TL); posterior margin length 9.4% (7.7%–8.4% TL); first dorsal fin markedly tall, its height 0.8 (0.9–1.0) times preorbital length and 1.1 (1.1–1.3) times its inner margin length. First dorsal-fin spine stout and large, its length 4.3% (3.3%–4.3% TL), corresponding to 0.7 (0.5–0.6) times first dorsal-fin height (not reaching fin apex). Interdorsal space 1.1 (1.1–1.2) times prepectoral length and 2.2 (2.1–2.3) times greater than dorsal-caudal space. Pre-second dorsal fin length 4.0 (3.9–3.9) times pectoral anterior margin length and 3.2 (2.8–3.1) times dorsal-caudal margin length. Second dorsal fin also upright with anterior margin convex, posterior margin straight but convex and falcate from midline to apex (Fig. 38); apex slightly rounded; free rear tip pointed; second dorsal fin large (its length 12.0%, 11.1%–12.5% TL) and tall, its height 4.0% (4.7%–5.3% TL), corresponding to 0.9 (1.0–1.1) times its inner margin length. Second dorsal-fin spine heavy and large, its length 4.4% (3.9%–4.3% TL), corresponding to 1.1 (0.8–0.9) times second dorsal-fin height (almost reaching fin apex); second dorsal-fin spine 1.0 (1.0–1.2) times greater than first dorsal-fin spine.

Pectoral fins with anterior margin straight, inner margin convex and posterior margin concave and fringed; apex and free rear tips rounded and lobe-like (Fig. 36); apex exceeding horizontal line through free rear tip (or reaching it in paratypes); pectoral fins conspicuously broad, its posterior margin length 12.3%, 10.2%–12.5% TL and corresponding to 1.1 (0.9–1.3) times trunk height; pectoral fin also very large, its anterior margin length 15.9% (15.5%–16.0% TL) or 1.5 (1.8–2.0) times greater than its inner margin length. Pectoral-pelvic space 0.8 (0.8–0.9) times pelvic-caudal space. Pelvic fins nearer to second dorsal fin than first dorsal fin, although it is nearest to first dorsal fin in young paratypes. Pelvic fins very broad and elongate, its length 11.3% (9.9%–11.2% TL); all margins straight, although posterior margin fringed; free rear tips markedly pointed.

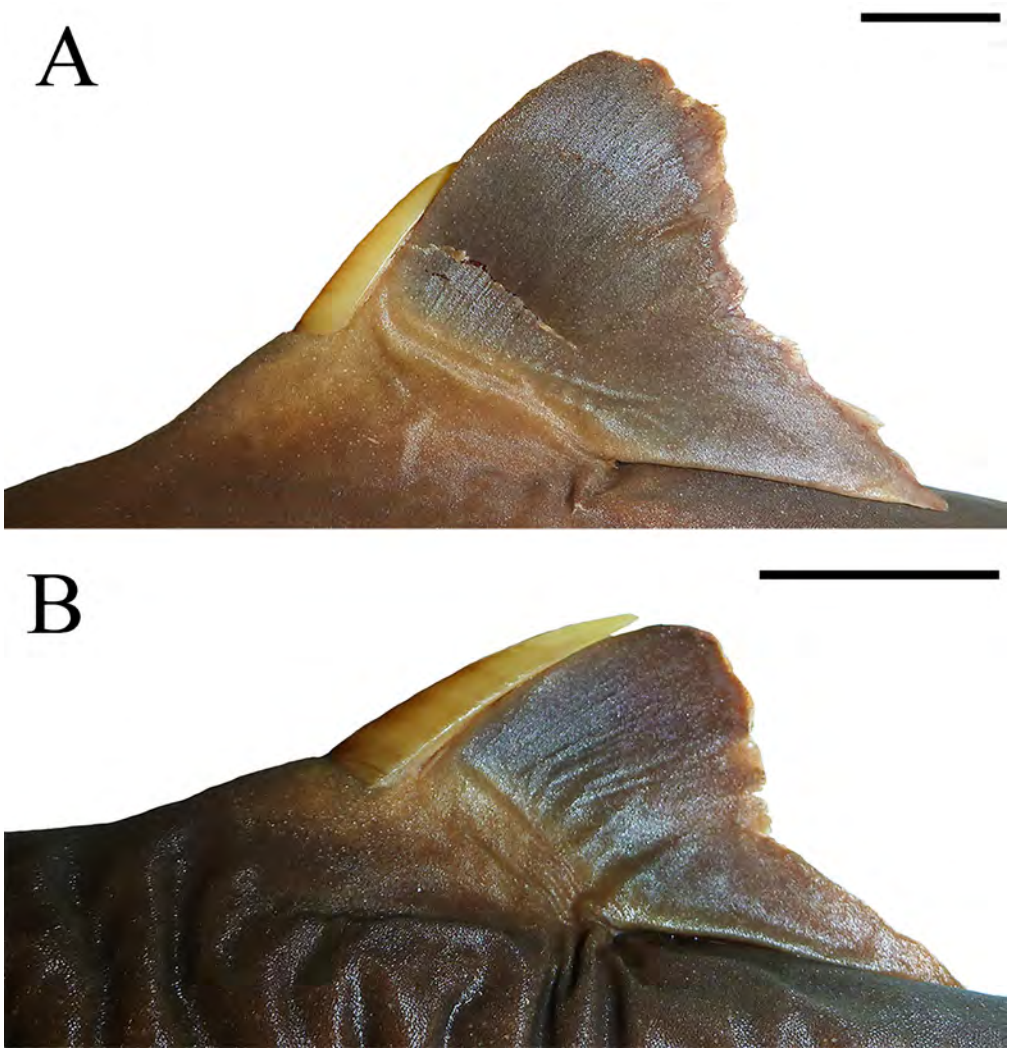

FIGURE 38. First dorsal fin (A) and second dorsal fin (B) of holotype of *Squalus quasimodo* **sp. nov.** (MZUSP 118707, adult female, 700 mm TL). Scale bar: 20 mm.

Caudal keels very strong, placed laterally in caudal peduncle from second dorsal fin insertion to upper precaudal pit; upper and lower precaudal pits profound. Caudal fin elongate, its dorsal caudal margin 19.7% (20.2%–21.3% TL), corresponding to 0.8 (0.9–1.0) times head length and 1.8 (1.7–1.8) times greater than preventral caudal margin length; upper caudal lobe conspicuously rectangular with dorsal caudal margin straight, upper postventral caudal margin convex, turning markedly convex at tip; posterior caudal tip slightly rounded (Fig. 39); preventral caudal margin convex, its length 2.3 (2.3–2.6) times larger than pelvic inner margin length; lower postventral caudal margin straight; ventral caudal tip rounded; caudal fin strongly broad at fin web, its caudal fork width 7.2% (6.6%–7.1% TL); caudal fork between lobes strongly notched.

Dermal denticles (Fig. 40). Denticles triscupid and markedly imbricate with pointed cusps, and lateral cusps much shorter than median cusp; denticles very broad at crown, their length greater than width; median projection prominent and rounded, located anteriorly at crown with small lateroposterior expansions on each side; two prominent lateral ridges on each side, reaching the lateral cusp; single median ridge conspicuous and elongate, bifurcated anteriorly, forming a profound groove in between.

Coloration (Figs. 35, 36). Body dark brown dorsally and pale ventrally. First and second dorsal fins also dark brown, whitish near each fin base and slightly blackish at apex; first and second dorsal-fin spines light brown, white at tip and dark brown anteriorly. Pectoral fins dark brown with posterior margin white, not uniform. Pelvic fins also brownish, lighter ventrally; pelvic posterior and inner margins white. Caudal fin dark brown, whitish near the vertebral column; dorsal caudal margin white; upper and lower post-ventral margins slightly white; faded black caudal stripe in preserved specimens.

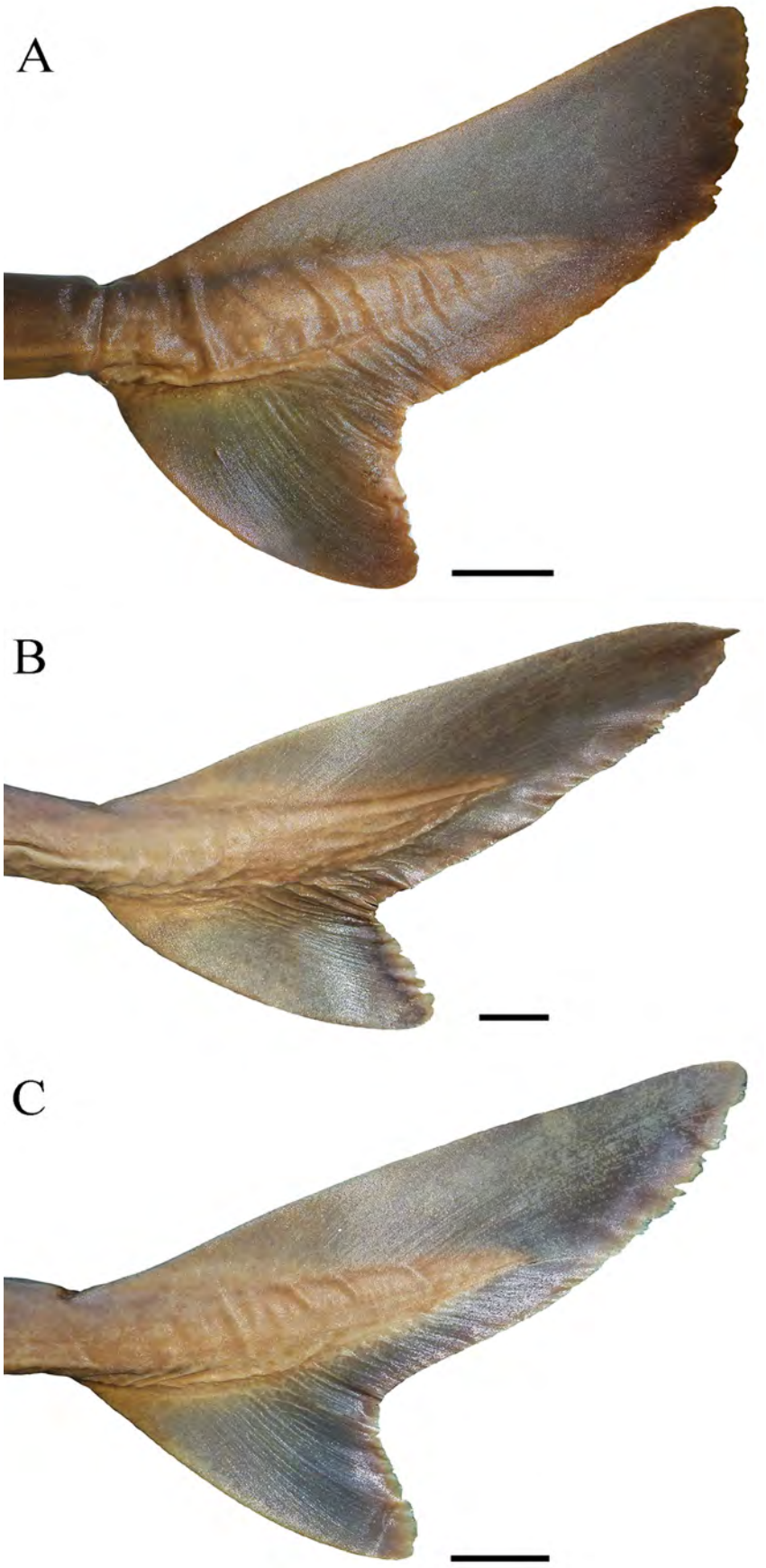

FIGURE 39. Caudal fin of *Squalus quasimodo* **sp. nov.** (A) holotype (MZUSP 118707, adult female); (B) paratype (UERJ 1741, adult female); (C) paratype (UERJ 1819, adult female). Scale bar: 20 mm.

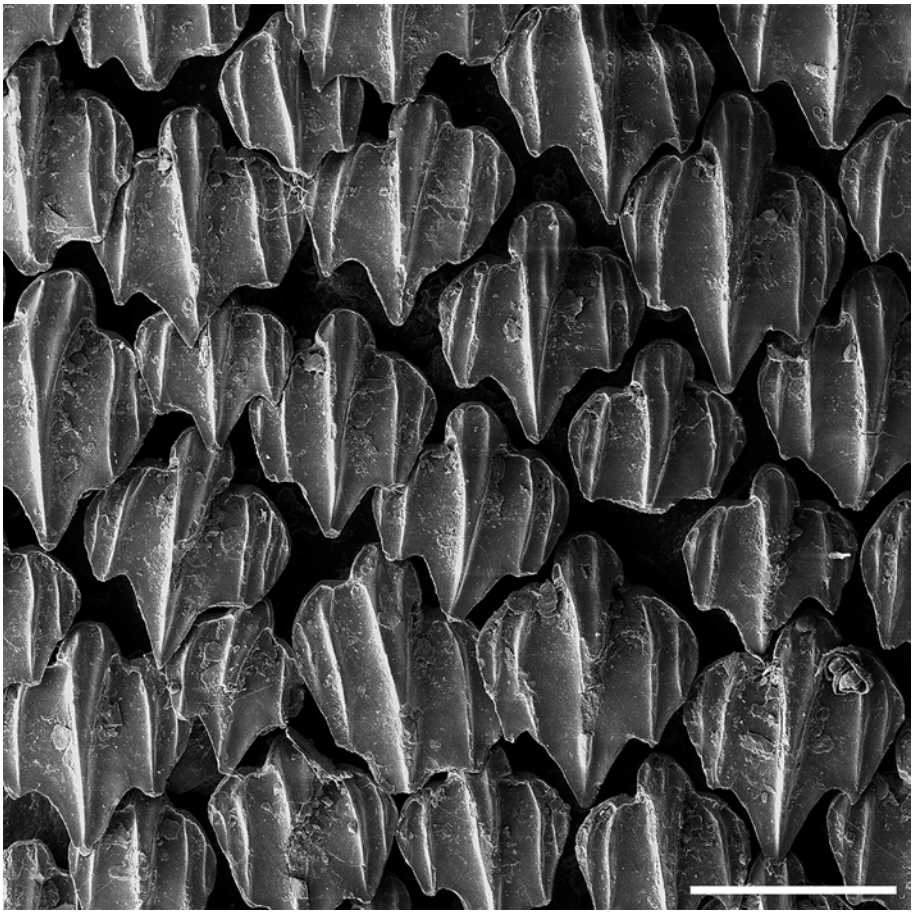

FIGURE 40. Dermal denticles of holotype of *Squalus quasimodo* **sp. nov.** (MZUSP 118707, adult female, 700 mm TL). Scale bar: 200 ìm.

Vertebral counts (Table 8). Monospondylous vertebrae 45 in holotype (46 in paratypes); diplospondylous vertebrae 71 (74–75); precaudal vertebrae 87 (91–92); caudal vertebrae 29 (29 paratypes); total vertebrae 116 (120–121).

Geographical distribution. *Squalus quasimodo* is so far known as an endemic species in southern Brazil (Fig. 41).

Etymology. Named for the hunchback of Notre-Dame from the 19th Century novel by Victor Hugo, in obvious reference to its most noticeable character.

Remarks. *Squalus fernandinus* Molina, 1782 was described from Juan Fernandez, Chile, but was reported to occur in the Atlantic (e.g. Miranda Ribeiro, 1907; Fowler, 1936, 1941; Bigelow & Schroeder, 1948, 1957). The taxonomic confusion regarding this species is due to its concise original description, lack of type specimens, and lack of illustration. Guichenot (1848) considered *S. fernandinus* as a senior synonym of *Squalus fernandezianus* described by him from Chilean waters, which is characterized by a brownish, robust body, first dorsal fin placed above the pectoral free rear tips, triangular dorsal fins, and pelvic fins located at the midline between the dorsal fins. Later, this species was often considered as either a junior synonym of *S. acanthias* or a senior synonym of *S. blainvillei* (e.g. Bigelow & Schroeder, 1948; Garman, 1960; Compagno, 1984). Since then, *S. blainvillei* has been identified in the Southwestern Atlantic Ocean while the taxonomic status of both *S. fernandezianus* and *S. fernandinus* remained uncertain. Our results clearly indicate no conspecificity between *S. quasimodo* and the original descriptions of *S. fernandezianus* and *S. fernandinus* that could suggest the validity of the Chilean species. An exhaustive investigation of these two nominal species from Chile is needed to elucidate their taxonomy in the South Pacific and South Atlantic oceans.

Squalus griffini is another species from the South Pacific Ocean, apparently endemic to the coast of New Zealand (Duffy & Last, 2007). *Squalus griffini* also has dorsal spots on the body that are also mentioned in the description of *S. fernandinus*, indicating that the latter species may also be a senior synonym of *S. griffini*. Its distribution in the opposite side of the Pacific Ocean is not yet reported (e.g. in Chile). *Squalus quasimodo* is very

similar morphologically to *S. griffini*, sharing characters such as tricuspid and imbricate dermal denticles that are strongly broad at crown, and absence of dark caudal bar, as well as overlapping in a variety of external measurements and vertebral counts (Table 12). *Squalus quasimodo* differs from *S. griffini* in lacking black spots dorsally on body (variable in *S. griffini*) and caudal fin with broad white posterior margin, and by having a more slender first dorsal fin. It is also distinct from *S. griffini* (data from Duffy & Last, 2007) by having a shorter prenarial length (4.8%, 4.5%–4.9% TL *vs*. 5.2%, 5.0%–5.9% TL in *S. griffini*), and more elongate pectoral-fin inner margin (length 10.9%, 8.1%–8.8% TL *vs*. 6.5%, 5.4%–7.7% TL in *S. griffini*).

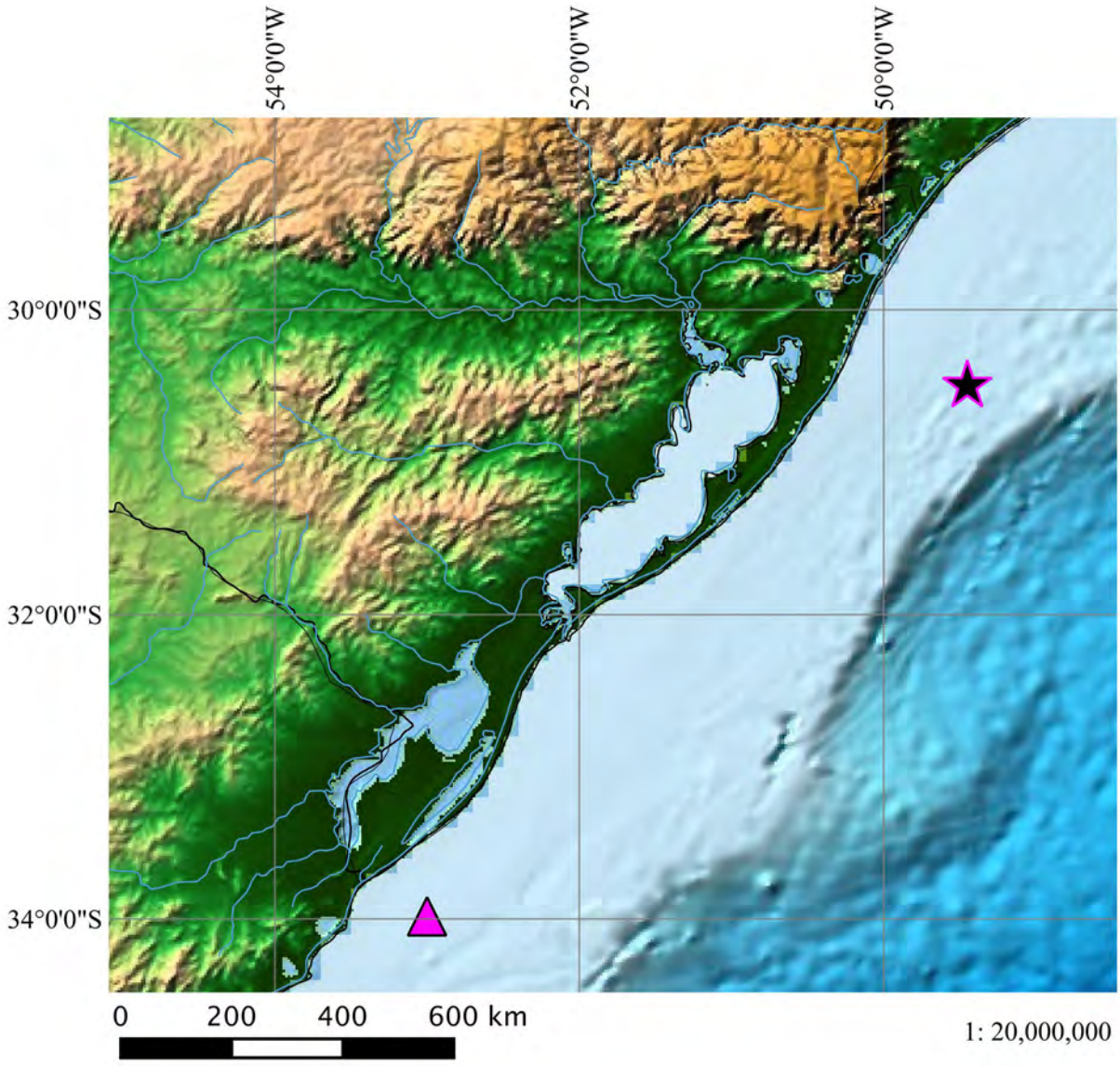

FIGURE 41. Map of the Southwestern Atlantic Ocean off southern Brazil, showing, showing the type locality of *Squalus quasimodo* **sp. nov.** Black star: location of holotype; reddish triangle: location of paratype.

Squalus quasimodo is also distinct from the Japanese *S. mitsukurii* (Table 5) by lacking a dark caudal bar, and having a narrower interorbital space (8.8%, 7.7%–8.0% TL *vs*. 9.3%, 9.1%–9.8% TL in *S. mitsukurii*). It differs from *S. blainvillei* of the Mediterranean Sea by its robust and markedly arched body (*vs*. slender and straight body) and triscuspid dermal denticles (*vs*. lanceolate denticles).

Squalus quasimodo is distinct from *S. lobularis* by having a shorter second dorsal-fin spine (length 4.4%, 3.9%–4.3% TL *vs*. 5.3%, 3.4%–5.3% TL in *S. lobularis*), and second dorsal-fin spine length 1.0 (1.0–1.2) times greater than first dorsal-fin spine length (*vs*. 1.4, 1.0–1.6 times in *S. lobularis*). *Squalus quasimodo* also has slightly

shorter prenarial and preoral lengths than *S. bahiensis* (prenarial length 4.8%, 4.5%–4.9% TL *vs*. 5.0%, 4.9%–5.1% TL in *S. bahiensis* and preoral length 10.2%, 9.5%–10.0% TL *vs*. 9.9%, 10.2%–10.5% TL in *S. bahiensis*).

Squalus quasimodo has a larger number of monospondylous vertebrae than *S. crassispinus*, *S. megalops*, *S. raoulensis*, *S. grahami*, *S. nasutus*, and *S. hemipinnis* based on data provided by Last *et al*. (2007) (Table 12): 45, 46 in *S. quasimodo vs*. 41, 39–42 in *S. crassispinus*, 37–40 in *S. megalops*, 41, 41–43 in *S. raoulensis*, 40, 38–42 in *S. grahami*, 39, 36–39 in *S. nasutus*, and 36, 35–38 in *S. hemipinnis*. It is also distinguished from *S. mitsukurii*, the Mediterranean *S. blainvillei*, and *S. chloroculus*, *S. montalbani*, and *S. notocaudatus* of Last *et al*. (2007) by total vertebrae (116, 120–121 in *S. quasimodo vs*. 112–113 in *S. mitsukurii* 111 in *S. blainvillei*, 114, 111–115 in *S. chloroculus*, 105–114 in *S. montalbani*, and 127, 123–125 in *S. notocaudatus*) (Table 12). It is distinct from *S. albifrons*, *S. altipinnis*, and *S. notocaudatus* (data from Last *et al*., 2007) by having a lower first dorsal fin, its height 4.0%, 4.7%–5.3% TL in *S. quasimodo vs*. 8.6%, 7.7%–8.9% TL in *S. albifrons*, 7.8%, 7.9% TL in *S. altipinnis*, and 8.2%, 8.3%–9.4% TL in *S. notocaudatus*).

Analysis of the claspers of *S. quasimodo* are needed to better characterize this species, as no adult males were found in the fish collections visited by the authors. More specimens are required for comparisons of skeletal anatomy, including neurocranium, with congeners.

Comparative material. *Squalus mitsukurii*: same material listed for *S. lobularis*. *Squalus blainvillei*: same material listed for *S. bahiensis*.

Squalus albicaudus **sp. nov.**

(Figs. 42–50; Tables 3, 10–11)

Suggested common names: Brazilian whitetail dogfish; Cação-bagre-de-cauda-branca (Portuguese).

Squalus megalops (not Macleay): Regan, 1908: 45, 47 (identification key, listed; global); Bigelow & Schroeder, 1948: 454 (cited); Bigelow & Schroeder, 1957: 29, 36, 37, figs. 3C, 4 (revision; Northwestern Atlantic); Bass *et al*., 1976: 11–13, 16–18, figs. 6B, 7B, 8 (C, D), 11, pl. 3 (revision; Eastern South Africa); Cadenat & Blache, 1981: 51, 52 (revision; Mediterranean Sea); Compagno, 1984: 118, 119 (revision; global); Muñoz-Chápuli, 1985: 397, 398, fig. 1 (cited); Muñoz-Chápuli & Ramos, 1989: 1–21, figs. 1, 2 (E, F), 3 (D, E) (revision; Eastern Atlantic); Calderón, 1994: 1–104, fig. 5A (cited); Nion *et al*., 2002: 4 (listed); Haimovici *et al*., 2003: 38, 39 (cited); Meneses & Paesch, 2003: 8, 25, 45 (cited); Bernades *et al*., 2005: 49, 70 (cited); Compagno *et al*., 2005: 74 (description; global); Hazin *et al*., 2006 (cited); Jablonski *et al*., 2006: 110, 177, 178 (cited); Louro & Rossi-Wongtschowski, 2007: 18, 27–30, 49, figs. 15, 16 (cited); Carrier *et al*., 2010: 44 (cited); Viana, 2011: 92–129, figs. 35–56 (revision; Brazil); Rosa & Gadig, 2014: 92 (listed; Brazil).

Squalus cubensis (not Howell-Rivero): Figueiredo, 1977 (in part): 8 (description; Southern Brazil); Lucena & Lucena, 1981: 4 (listed; Brazil); Myagkov & Kondyurin, 1986: 1–20, fig. 1 (A, E, F, H) (revision; Atlantic); Lessa *et al*., 1999: 14, 61, 150 (cited, listed; Northeast Brazil); Compagno, 2002: 384 (description; Northern and Southern Brazil, Argentina, Uruguay); Compagno *et al*., 2005: 75, pl. 3 (description; Southwest Atlantic Ocean); Last *et al*., 2007: 21–22, figs.10A, 11A (cited; Southeast Brazil); Nunan & Senna, 2007: 169, 170 (in part) (cited; Brazil); Viana, 2011 (in part): 130–162, figs. 57–77 (revision; Brazil).

Squalus sp. of the *megalops-acutipinnis-cubensis* group Cadenat & Blache, 1981: 51, 52, fig. 31 (F, G) (revision; Mediterranean Sea); Figueiredo, 1981: 17 (listed; Brazil).

Squalus sp. of the *megalops* group: Marques, 1994 (cited; Brazil); Gomes *et al*., 1997: 95, 98–109 (description; Brazil); Marques, 1999 (cited; Brazil).

Squalus sp.: Gomes *et al*., 1997: 98 (listed; Brazil); Tomás *et al*., 2010 (cited; Southeast Brazil).

Squalus of the *megalops/cubensis* group: Gadig, 2001: 29, 36, 54, 58–60 (listed; Brazil).

Squalus sp. A: Soto, 2001: 95, 96 (listed; Brazil); Soto & Mincarone, 2004: 74–79 (listed; Brazil).

Squalus sp. 2: Gomes *et al*. 2010: 44–46 (cited; Brazil).

Holotype. MNRJ 30188, adult male, 525 mm TL, north coast of Espírito Santo state, Brazil, 19°42'54"S, 39°25'57"W, 195 m. Collected on 30 June 2000, Station 0531, Thalassa cruise, Revizee program.

Paratypes (11 specimens). MNRJ 30173, adult female, 590 mm TL, south coast of Bahia state, between Itacaré and Ilhéus, Brazil, 14°28'58"S, 38°54'0"W, 278 m; MNRJ 30174, adult female, 580 mm TL, south coast of Bahia state, between Itacaré and Ilhéus, Brazil, 14°28'58"S,3 8°54'0"W, 278 m; MNRJ 30175, adult female, 560 mm TL, south coast of Bahia state, between Itacaré and Ilhéus, Brazil, 14°28'58"S, 38°54'0"W, 278 m; MNRJ 30176, adult female, 540 mm TL, south coast of Bahia state, between Itacaré and Ilhéus, Brazil, 14°28'58"S, 38°54'0"W, 278 m; MNRJ 30177, adult male, 450 mm TL, Morro de São Paulo, Bahia, Brazil, 13°21'51"S,

38°40'49"W, 421 m; MNRJ 30181, adult male, 482 mm TL, Canavieiras, Bahia, Brazil, 15°42'41"S, 38°37'18"W, 251 m; MNRJ 30183, juvenile female, 425 mm TL, Salvador, Bahia, Brazil, 13°8'54"S, 38°28'41"W, 334 m; MNRJ 30184, adult male, 480 mm TL, Salvador, Bahia, Brazil, 13°8'54"S, 38°28'41"W, 334 m; MNRJ 30185, adult male, 440 mm TL, Salvador, Bahia, Brazil, 13°8'54"S, 38°28'41"W, 334 m; MNRJ 30186, adult female, 590 mm TL, north coast of Espírito Santo state, Brazil, 19°42'54"S, 39°25'54"W, 202 m; MNRJ 30187, adult female, 610 mm TL, north coast of Espírito Santo state, Brazil, 19°42'54"S, 39°25'57"W, 195 m.

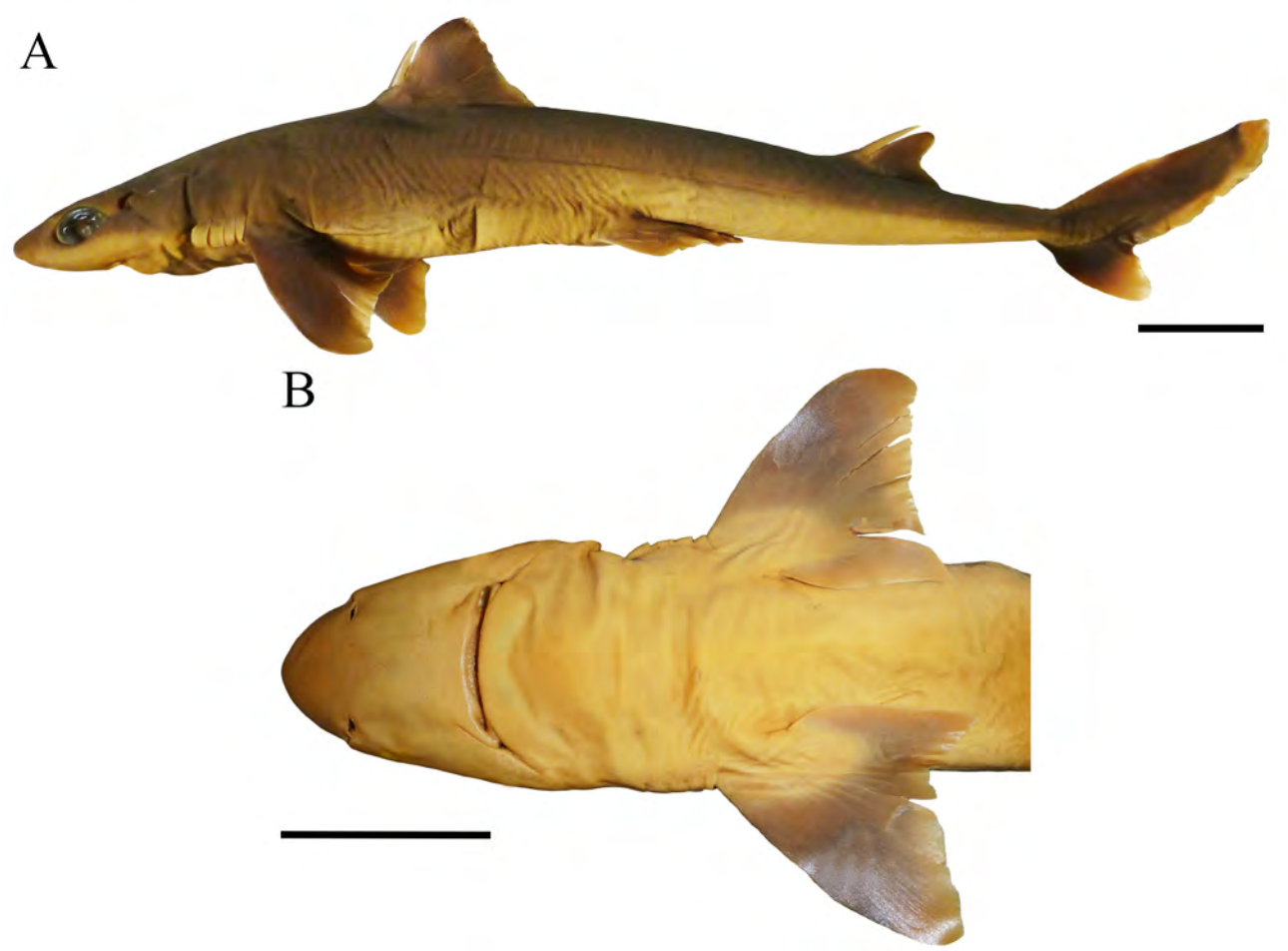

FIGURE 42. Holotype of *Squalus albicaudus* **sp. nov.** (MNRJ 30188, adult male, 525 mm TL) in (A) lateral and (B) ventral views. Scale bar: 50 mm.

Non-type material (9 specimens). MZUFBA uncatalogued, juvenile female, 420 mm TL, adult male, 502 mm TL, Praia do Forte, Mata de São João, Bahia, Brazil; NUPEC 96, adult male, 460 mm TL, South of Barra de Santos, São Paulo, Brazil; NUPEC 1354, neonate female, 285 mm TL, juvenile female, 355 mm TL, Ilha Vitória, São Paulo, Brazil; TAMAR 10.38, adult male, 490 mm TL, locality same as MZUFBA; TAMAR 10.39, juvenile female, 459 mm TL, locality same as MZUFBA; TAMAR 10.41, juvenile female, 445 mm TL, locality same as MZUFBA; TAMAR 10.42, juvenile female, 410 mm TL, locality same as MZUFBA.

Diagnosis. *Squalus albicaudus* **sp. nov.** can be distinguished from its congeners by the following combination of characters: caudal fin with a mostly white ventral caudal lobe, dorsal caudal margin white at midline, and postventral caudal margins broadly white; pectoral-fin posterior margin broadly white; first dorsal fin with anterior margin also conspicuously white on its anterior half. *Squalus albicaudus* **sp. nov.** differs from all species of the *S. mitsukurii* group by: snout short vs. snout large; pectoral-fin free rear tips pointed *vs*. pectoral-fin free rear tips rounded; dermal denticles lanceolate and unicuspid *vs*. dermal denticles rhomboid and tricuspid. *Squalus albicaudus* **sp. nov.** is clearly distinct from *S. cubensis* by: snout strongly pointed (*vs*. snout somewhat rounded); second dorsal-fin spine not reaching second dorsal-fin apex (*vs*. spine reaching second dorsal-fin apex); first dorsal fin with dark apex, but not as a black blotch (*vs*. conspicuous black blotch on both dorsal fins); pectoral fins with

posterior margin broadly white (*vs*. narrowly white). These two species also differ in external morphometrics such as: shorter first dorsal fin (anterior margin length 10.9%, 9.7%–11.2% TL *vs*. 11.6%, 11.6%–12.7% TL in *S. cubensis*); shorter second dorsal fin (anterior margin length 9.2%, 8.8%–10.8% TL *vs*. 12.3%, 11.2%–11.6% TL in *S. cubensis*; inner margin length 5.0%, 4.1%–5.2% TL *vs*. 5.6%, 5.5%–6.0% TL in *S. cubensis*); more slender second dorsal-fin spine (width at base 0.9%, 0.6%–0.9% TL *vs*. 1.0%, 1.0%–1.2% TL in *S. cubensis*); and clasper much more elongated in (inner margin length 7.1%, 6.9%–7.7% TL *vs*. 8.0%, 3.3%–3.8% TL in *S. cubensis*).

Description. External morphology. Measurements and counts are summarized in Tables 10–11. Body fusiform and thin throughout, slightly arched dorsally, equally deep from head to trunk (head height 1.0, 0.8–1.0 times trunk height and abdomen height), and broader at head than at trunk (head width 1.2, 1.0–1.4 times trunk height, and 1.4, 1.2–1.4 times abdomen height). Head very short and narrow (length 21.8%, 18.7%–24.7% TL; its greatest width at mouth (11.1%, 10.9%–12.0% TL). Snout pointed at tip, conspicuously short (length 7.1%, 6.8%–7.8% TL); anterior margin of nostrils bifurcate and wide, equally near snout tip and mouth; prenarial length 1.0, 0.8–1.0 times distance from nostrils to upper labial furrow, and 0.5, 0.4–0.5 times preoral length; internarial space 1.1, 0.8–1.0 times eye length. Eyes oval and markedly large (length 4.0%, 4.2%–5.3% TL, and 1.5, 1.8–2.1 times their height); anterior margin of eyes convex and posterior margin notched; interorbital space 8.4%, 8.2%–8.9% TL. Prespiracular length 12.5%, 11.7%–13.8% TL, and 0.5 (0.6–0.7) times prepectoral length and 1.7 (1.7–1.9) times preorbital length. Spiracles crescent-shaped and wide, their length 1.5% (1.3%–2.0% TL), and 0.4, 0.3–0.4 times eye length. Prebranchial length 1.5 (1.3–1.5) times prespiracular length. Gill slits vertical and low, with fifth gill slit 1.1 (1.0–1.4) higher than first gill slit.

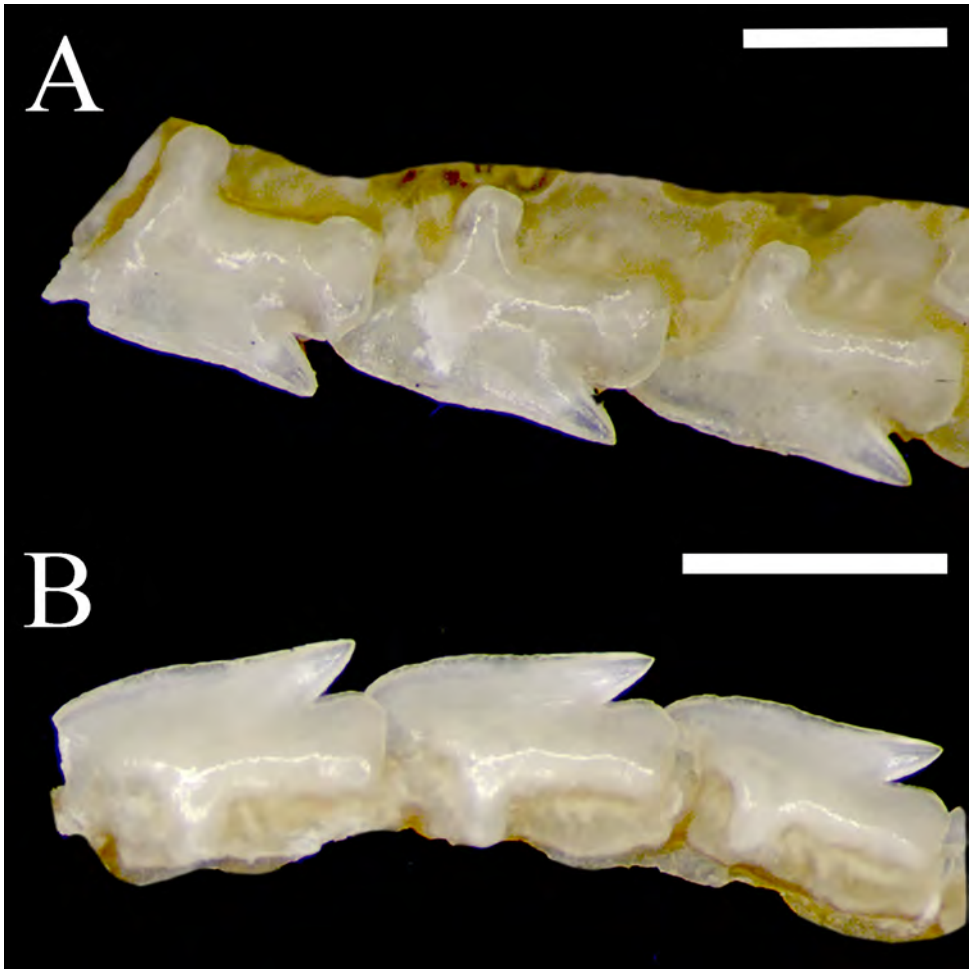

FIGURE 43. Upper (A) and lower (B) teeth of paratype of *Squalus albicaudus* (MNRJ 30184, adult male, 480 mm TL). Scale bars: 2 mm.

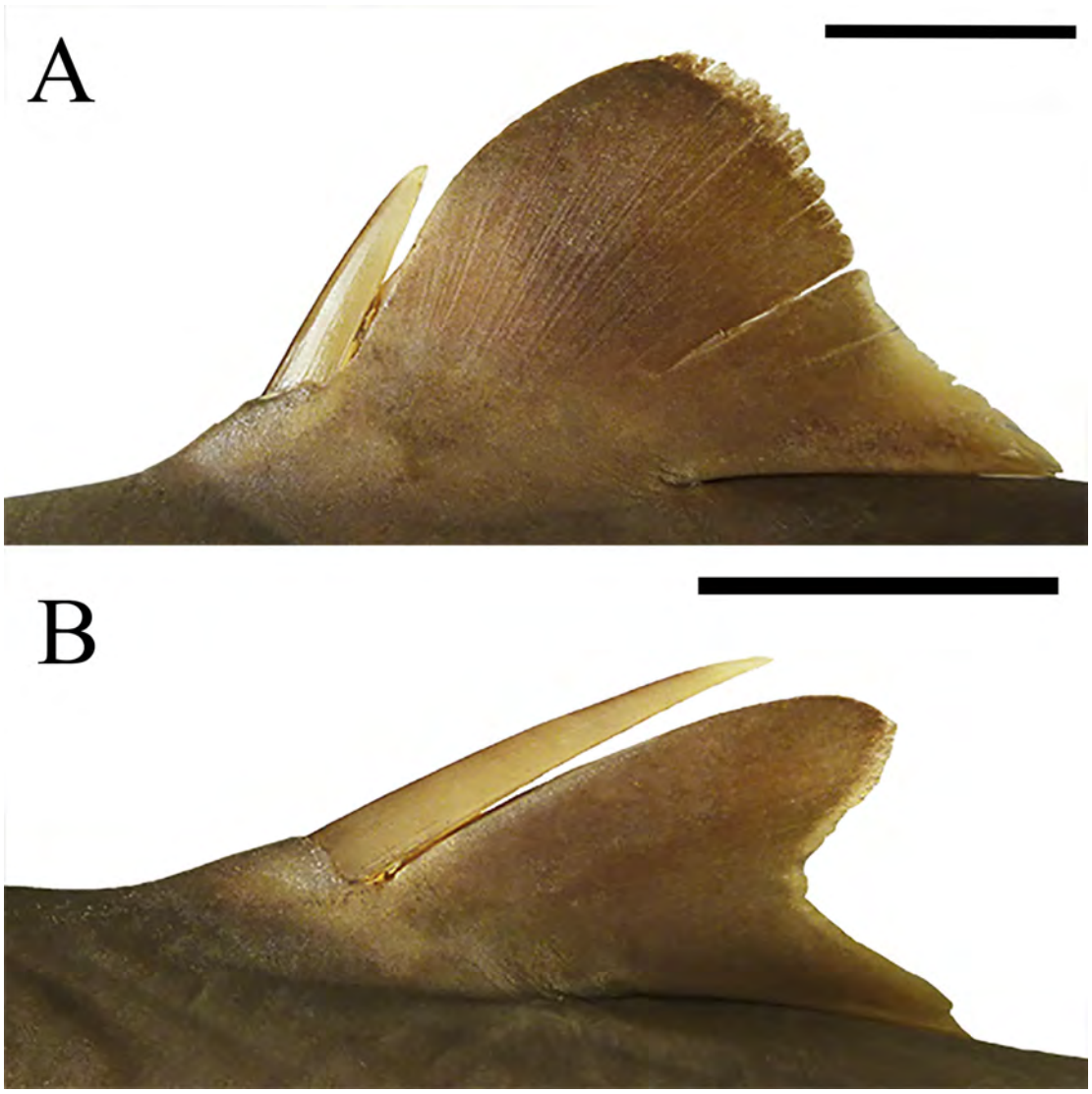

FIGURE 44. First dorsal fin (A) and second dorsal fin (B) of holotype of *Squalus albicaudus* **sp. nov.** (MNRJ 30188, adult male, 525 mm TL). Scale bar: 20 mm.

Preoral length 9.8%, 9.2%–11.2% TL and equal to 1.2, 1.3–1.5 times mouth width. Mouth arched and strongly broad, its width 1.5, 1.5–1.8 times prenarial length and 1.9, 1.9–2.0 times internarial space; upper labial furrow with thin fold, very large (length 2.3%, 2.1%–2.5% TL); lower labial furrow also large, although without a fold. Teeth unicuspid and similar in both jaws, wide and flattened labial-lingually at crown, imbricate laterally; upper teeth much smaller than lower teeth; cusp oblique, somewhat elongate and heavy, directed laterally; mesial heel slightly notched; distal heel rounded; mesial cutting edge somewhat straight; apron thick and rather elongate. Three series of teeth in upper jaw and two series of teeth in lower jaw in holotype (paratypes 2–3 series in both jaws); tooth rows ranging from 12–12 (13–14 paratypes) in upper jaw and 11–11 (11–12 paratypes) in lower jaw (Fig. 43). Pre-first dorsal fin length 1.1 (1.2–1.8) times prepectoral length. Origin of first dorsal fin anterior to pectoral free rear tips. First dorsal fin with anterior margin markedly convex and posterior margin straight, although concave anteriorly; first dorsal-fin apex rather rounded; first dorsal-fin free rear tip rounded (Fig. 44); first dorsal-fin inner margin very short, its length 5.6% (4.9%–6.1% TL); first dorsal fin short (length 1.7, 1.6–2.0 times its height) and low (height 7.9%, 6.8%–8.0% TL and 1.4, 1.2–1.6 times first dorsal-fin inner margin length, and 1.1, 0.9–1.1 times preorbital length). First dorsal-fin spine slender, thick (its base width 1.0%, 0.7%–1.1% TL) and elongate (its length 4.2%, 2.3%–4.1% TL), reaching one-half of first dorsal-fin height (0.3–0.5 times first dorsal-fin height in paratypes). First dorsal-fin length 1.3 (1.0–1.3) times larger than second dorsal-fin length. Interdorsal space 1.1 (1.0–1.3) times prepectoral length and 2.2 (1.7–2.6) times dorsal-caudal space. Pre-second dorsal length 2.8, 2.5–

3.1 times prepectoral length and 3.2, 2.8–3.3 times dorsal-caudal margin length. Second dorsal fin also short (length 2.0, 1.9–2.3 times its height) and somewhat tall (height 5.4%, 4.9%–6.2% TL, and 1.1, 0.9–1.3 times second dorsal-fin inner margin length); first dorsal-fin anterior margin convex and posterior margin markedly concave; first dorsal-fin apex rounded and pointed at free rear tip (Fig. 44); second dorsal-fin inner margin short, its length 5.0% (4.1%–5.2% TL). Second dorsal-fin spine conspicuously thin and large, almost reaching second dorsal-fin height, its length 5.1% (3.4%–5.0% TL), and 0.9 (0.7–0.9) times second dorsal-fin height, and 1.2 (1.0–1.8) times first dorsal-fin spine length.

Pectoral fins small but also broad with anterior margin length 13.4% (11.8%–14.4% TL), 1.2 (1.2–1.4) times posterior margin length, and 1.5 (1.3–1.5) times inner margin length; pectoral-fin posterior margin 10.7% (9.7%–11.8% TL); pectoral-fin anterior margin straight, inner margin convex and posterior margin concave; pectoral-fin apex rounded and lobe-like (Fig. 42); pectoral-fin free rear tips markedly pointed, extending beyond horizontal line at pectoral apex; posterior margin length 1.1 (0.8–1.0) times trunk height.

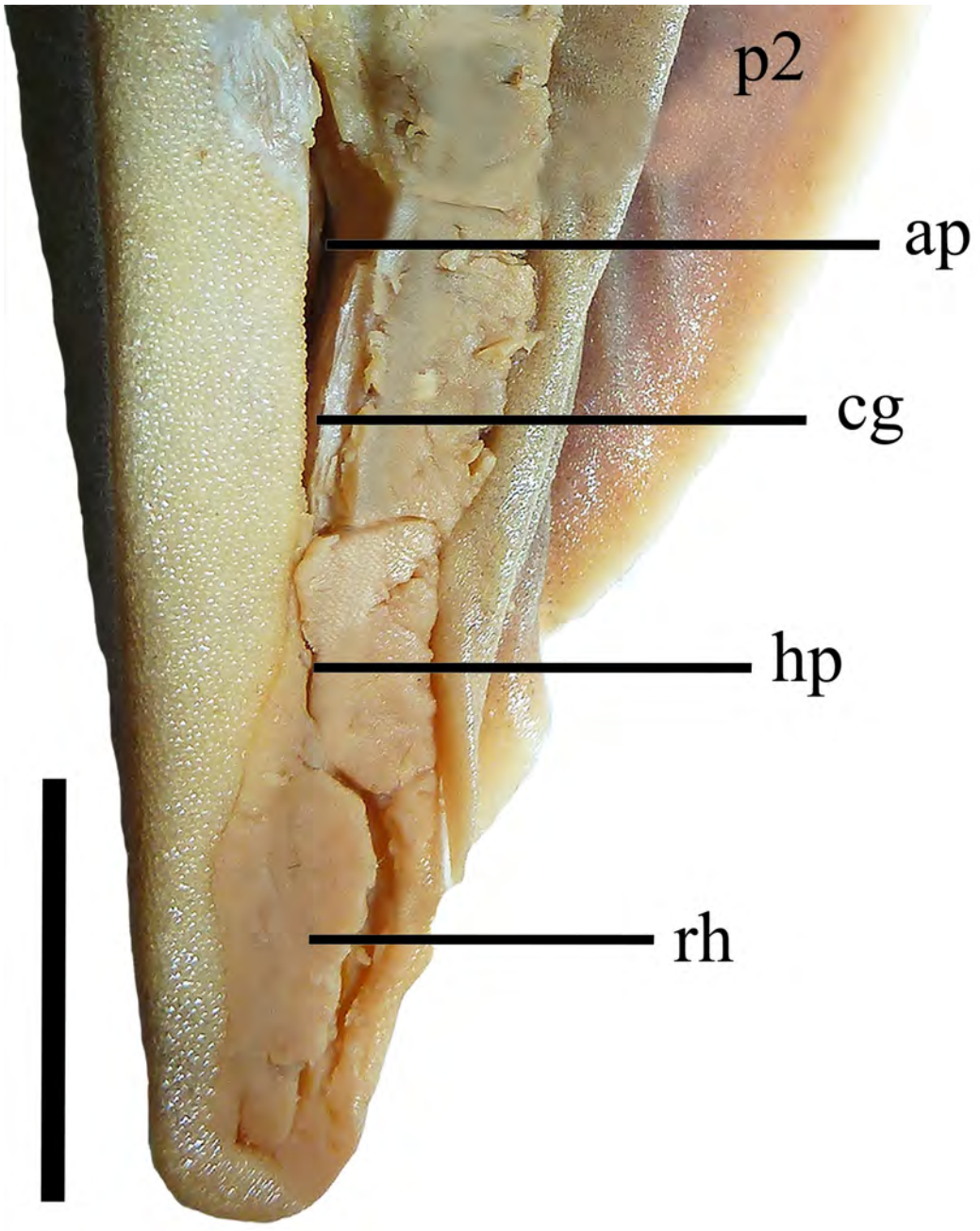

FIGURE 45. Dorsal view of clasper of paratype of *Squalus albicaudus* (MNRJ 30184, adult male, 480 mm TL). Abbreviations: **ap**, apopyle; **cg**, clasper groove; **hp**, hypopyle; **p2**, pelvic fin; **rh**, rhipidion. Scale bar: 10 mm.

Pectoral-pelvic space 0.7 (0.5–0.9) times pelvic-caudal space. Pelvic fins nearer first dorsal fin than second dorsal fin in holotype and young paratypes (or nearest second dorsal fin in adult paratypes). Pelvic-fin anterior margin convex and posterior margin straight; pelvic-fin apex rounded and narrow; pelvic-fin free rear tips rounded and lobe-like; pelvic fins elongate, their inner margin length 6.3% (4.2%–6.3% TL). Claspers cylindrical, thin, and flattened dorsoventrally; claspers short, slightly extending beyond pelvic-fin free rear tips, their inner length 7.1% (6.9%–7.7% TL) and 1.1 (1.2–1.4) times larger than pelvic-fin inner margin length; clasper groove longitudinal and small, located dorsally; apopyle narrow, placed in proximal end of clasper groove; hypopyle constricted at distal end of clasper groove; rhipidion narrow and short, blade-like and somewhat thick, positioned medially at distal end of clasper (Fig. 45).

Caudal peduncle slender with soft caudal keel on each side; upper and lower caudal furrows markedly deep. Caudal fin slender and short, its dorsal caudal margin length 19.8% (19.3%–21.2% TL), and 0.9 (0.8–1.1) times head length and 1.7 (1.7–1.9) times preventral caudal margin; dorsal caudal margin straight, post-ventral caudal margin (upper and lower) convex (Fig. 46); posterior tip pointed; caudal fork between lobes with conspicuous concavity and very narrow (width 6.5%, 6.2%–7.2% TL); ventral tip rounded; preventral caudal margin also convex and short, its length 11.4% (10.5%–11.9% TL) and 1.8 (1.7–2.6) times pelvic-fin inner margin length.

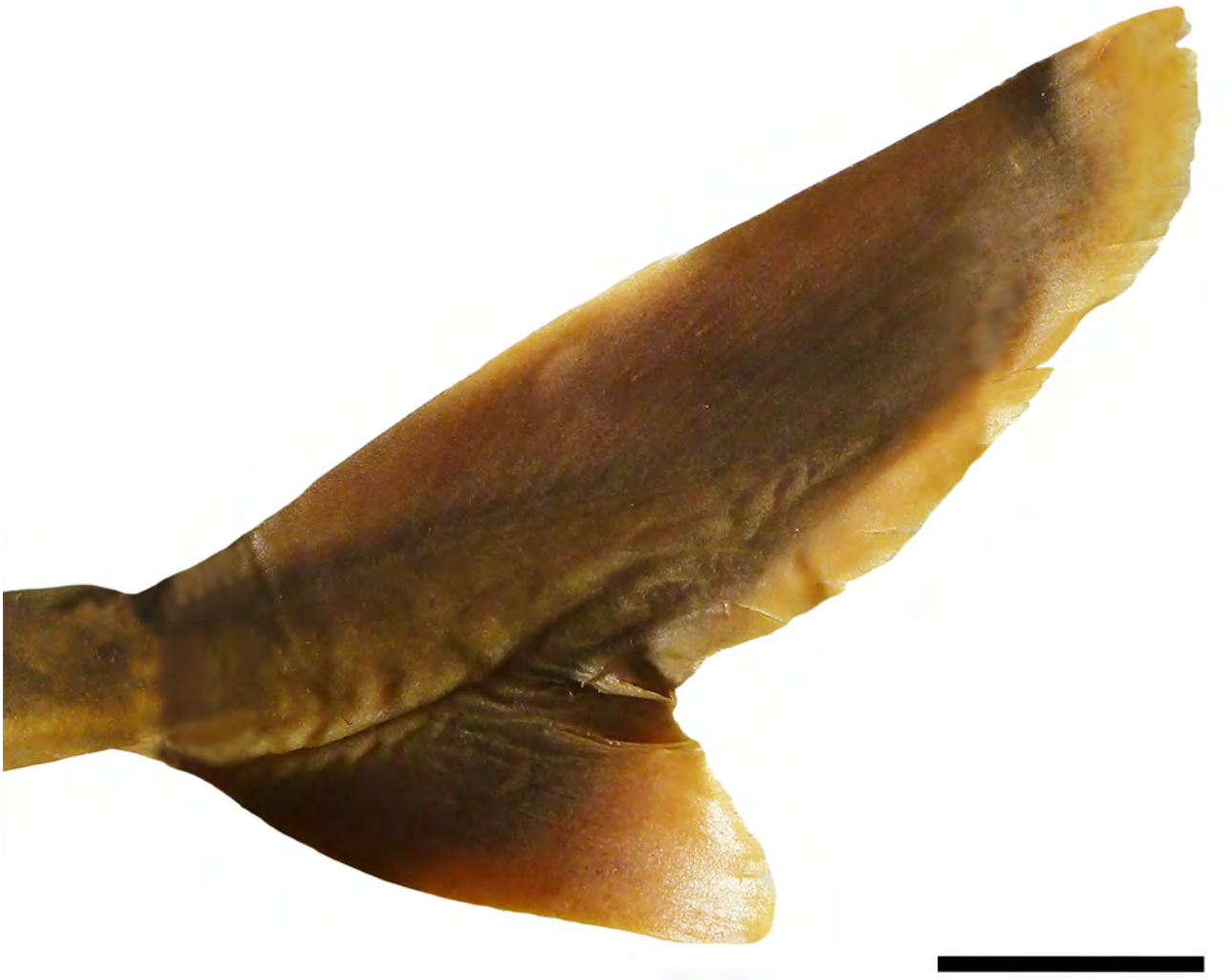

FIGURE 46. Caudal fin of holotype of *Squalus albicaudus* **sp. nov.** (MNRJ 30188, adult male, 525 mm TL). Scale bar: 20 mm.

Dermal denticles (Fig. 47). Denticles unicuspid, lanceolate and markedly slender, their length much greater than width; dermal denticles moderately asymmetrical and near each other but not imbricate; median and lateral ridges prominent, bifurcate anteriorly; crown conspicuously expanded anteriorly and rather expanded laterally; cusp rounded and elongate posteriorly.

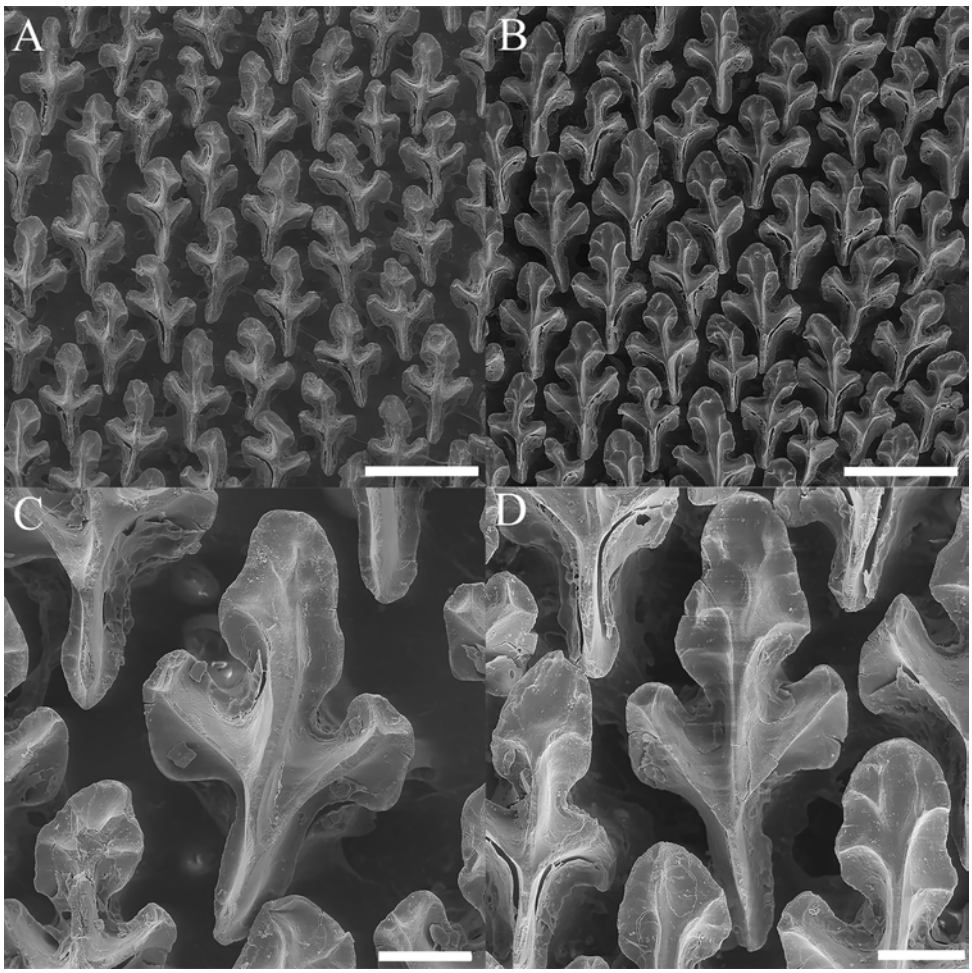

FIGURE 47. Dermal denticles of (A, C) holotype (MNRJ 30188) and (B, D) paratype (MNRJ 30186) of *Squalus albicaudus* **sp. nov.** Scale bars: 200 ìm (A, B); 50 ìm (C, D).

Coloration (Fig. 42). Body brownish gray dorsally and white ventrally, gray laterally from between the pectoral and pelvic fins, turning whitish at caudal fin origin. First dorsal fin brownish, darker at fin web to apex; anterior margin broadly white on anterior half and dark brown at apex; posterior margin slightly white on anterior half and brown at apex; first dorsal-fin spine gray, darker anteriorly, white laterally and attip. Second dorsal fin brown throughout (few paratypes with white apex); second dorsal-fin posterior margin white; second dorsal-fin spine also gray, darker anteriorly and white at tip. Pectoral fins brown dorsally and ventrally (except at base) with posterior and inner margins conspicuously white, including apex and free rear tips. Pelvic fins light brown dorsally and white ventrally; pelvic posterior margin broadly white. Caudal fin mostly dark brown with dorsal caudal margin markedly white at midline; upper caudal blotch dark gray distally at dorsal caudal margin; post-ventral caudal margins conspicuously white, except for light gray caudal fork (caudal bar); posterior caudal tip also broadly white; preventral caudal margin dark gray anteriorly; ventral caudal lobe conspicuously white, including ventral caudal tip; caudal stripe blackish, thick and short.

Skeletal morphology. Measurements and counts are summarized in Tables 3, 11.

Neurocranium (Fig. 48). Neurocranium greatest width at level of postorbital processes (width 57.1% CL) and narrower at interorbital region (28.8% CL) and between opisthotic processes in the otic region (36.5% CL). Rostrum spoon-like, comprised by precerebral fossa profound and short (its length 40.1% CL), narrower proximal and distally than at its median portion; lateral rostral cartilages slightly cylindrical, flattened laterally; two lateral rostral appendices anteroventrally, hook-like; rostral prominence small, placed medially at tip of rostrum; rostral keel conspicuous and elongate, its length 25.0% CL, slightly transcending anterior margin of nasal capsules; prefrontal fontanelle constricted and rounded, anterior to brain at rostrum base. Nasal capsules rounded and markedly wide (width across nasal capsules 52.8% CL), located lateral to rostrum; nasal apertures ventral; subnasal fossa oval and large, located at each side of rostral keel.

TABLE 10. External measurements expressed as percentage of total length (% TL) for *Squalus albicaudus* sp. nov. Values for *S. cubensis* are also provided for comparisons. N: number of specimens; *x* : mean; SD: standard deviation.

Measurements	***Squalus albicaudus* sp. nov.**						***Squalus cubensis***													
	Holotype	Paratypes					Holotype	Paratypes				Gulf of Mexico				Caribbean Sea				
		N	Range	*x*	SD			N	Range	*x*	SD	N	Range	*x*	SD	N	Range	*x*	SD	
TL (mm)	525.0	11	425.0 – 610.0	522.5	68.4		525.0	4	210.0 – 690.0	368.5	217.5	12	275.0 – 532.0	415.3	77.9	14	205.0 – 650.0	418.2	161.9	
PCL	81.5	11	78.1 – 82.5	80.0	1.3		79.0	4	74.1 – 79.7	76.9	2.4	12	77.5 – 81.6	79.3	1.3	14	76.6 – 81.5	79.4	1.4	
PD2	62.9	11	57.8 – 64.4	61.0	2.2		61.9	4	58.9 – 63.8	60.4	2.2	12	60.2 – 64.6	62.3	1.3	14	58.9 – 66.3	62.1	2.3	
PD1	25.1	11	27.1 – 39.9	29.7	3.5		30.5	4	28.9 – 31.0	30.0	0.9	12	30.3 – 43.4	33.2	3.5	14	29.4 – 34.4	31.1	1.4	
SVL	30.5	11	42.5 – 55.9	46.4	3.5		48.6	4	45.2 – 50.7	47.9	2.4	12	28.9 – 50.8	46.5	5.7	14	41.9 – 52.5	46.7	3.1	
PP2	27.6	11	39.3 – 54.2	43.7	3.9		45.7	4	42.9 – 47.8	45.7	2.2	12	43.1 – 48.9	45.2	1.7	14	40.7 – 50.8	44.2	3.1	
PP1	22.9	11	20.2 – 24.0	21.6	1.0		22.9	4	21.7 – 24.1	22.8	1.3	12	21.4 – 44.7	25.0	6.4	14	19.5 – 23.4	22.4	1.0	
HDL	21.8	11	18.7 – 24.7	21.7	1.4		23.6	4	22.8 – 24.6	23.7	0.8	12	20.4 – 25.9	23.0	1.4	14	19.9 – 24.0	22.9	1.0	
PG1	18.1	11	17.4 – 19.6	18.3	0.6		20.0	4	19.4 – 20.5	20.1	0.5	12	17.4 – 21.6	19.5	1.0	14	17.1 – 20.5	19.5	1.1	
PSP	12.5	11	11.7 – 13.8	12.7	0.6		13.0	4	12.6 – 14.2	13.8	0.8	12	11.7 – 14.1	13.1	0.6	14	10.7 – 14.8	13.1	1.0	
POB	7.1	11	6.8 – 7.8	7.5	0.3		7.3	4	7.5 – 8.1	7.7	0.3	12	6.4 – 8.1	7.3	0.5	14	6.8 – 8.2	7.5	0.4	
PRN	5.2	11	4.3 – 5.0	4.6	0.2		4.3	4	4.0 – 4.9	4.7	0.4	12	3.9 – 5.0	4.5	0.4	14	4.3 – 5.4	4.7	0.3	
POR	9.8	11	9.2 – 11.2	10.0	0.5		9.4	4	9.6 – 11.4	10.8	0.8	12	8.8 – 11.1	10.1	0.7	14	8.7 – 11.8	10.4	0.8	
INLF	5.2	11	4.6 – 5.5	5.1	0.3		5.2	4	5.1 – 6.0	5.7	0.4	12	4.7 – 5.8	5.3	0.3	14	3.8 – 5.9	5.2	0.5	
MOW	7.9	11	6.9 – 7.7	7.4	0.2		7.5	4	7.8 – 8.5	8.0	0.3	12	7.0 – 9.7	8.4	0.7	14	7.2 – 9.4	8.0	0.6	
ULA	2.3	11	2.1 – 2.5	2.3	0.1		2.4	4	2.1 – 2.9	2.6	0.3	12	2.2 – 4.3	2.7	0.6	14	2.3 – 2.8	2.5	0.2	
INW	4.3	11	3.6 – 4.3	4.0	0.2		3.6	4	2.7 – 4.4	3.6	0.7	12	3.9 – 4.5	4.2	0.2	14	3.6 – 4.8	4.3	0.3	
INO	8.4	11	8.2 – 8.9	8.5	0.2		8.5	4	8.5 – 10.1	9.3	0.7	12	7.5 – 9.7	9.0	0.6	14	7.8 – 11.1	9.0	0.8	
EYL	4.0	11	4.2 – 5.3	4.8	0.4		4.2	4	3.7 – 4.9	4.3	0.6	12	3.9 – 5.1	4.6	0.4	14	3.2 – 6.0	4.4	0.7	
EYH	2.6	11	2.2 – 2.8	2.4	0.2		1.8	4	1.3 – 2.9	2.1	0.6	12	1.6 – 2.9	2.3	0.4	14	1.0 – 2.7	2.0	0.4	
SPL	1.5	11	1.3 – 2.0	1.5	0.2		1.6	4	1.2 – 1.8	1.5	0.2	12	1.3 – 2.0	1.7	0.3	14	1.0 – 2.1	1.6	0.3	
GS1	2.2	11	1.9 – 2.3	2.1	0.2		1.4	4	1.5 – 1.9	1.7	0.2	12	1.2 – 2.2	1.7	0.3	14	1.2 – 2.4	1.8	0.3	
GS5	2.4	11	2.0 – 2.8	2.4	0.3		2.3	4	1.9 – 2.5	2.2	0.3	12	1.7 – 2.5	2.1	0.2	14	1.9 – 2.7	2.3	0.3	
IDS	25.9	11	22.8 – 27.5	25.0	1.2		23.8	4	22.2 – 26.1	23.6	1.7	12	22.4 – 28.4	25.1	1.8	14	20.0 – 27.7	24.1	2.4	
DCS	11.7	11	10.7 – 14.1	11.6	1.0		11.5	4	9.8 – 11.6	10.9	0.7	12	9.7 – 12.3	11.2	0.9	14	10.3 – 12.0	11.0	0.5	
PPS	19.0	11	15.4 – 25.4	18.8	2.6		19.0	4	17.9 – 23.6	20.6	2.6	12	14.6 – 22.9	19.2	2.7	14	14.9 – 22.7	17.7	2.5	
PCA	29.0	11	25.4 – 29.4	27.3	1.0		26.7	4	22.6 – 27.6	25.0	2.2	12	24.8 – 30.6	27.1	1.9	14	26.2 – 29.2	27.7	0.9	
D1L	13.6	11	12.4 – 14.5	13.1	0.6		14.7	4	12.5 – 14.6	13.8	0.9	12	12.0 – 13.7	13.0	0.5	14	12.6 – 14.5	13.6	0.6	
D1A	10.9	11	9.7 – 11.2	10.6	0.5		11.6	4	11.6 – 12.7	12.3	0.5	12	9.1 – 12.0	10.5	0.9	14	9.5 – 14.2	11.2	1.2	
D1B	8.2	11	7.0 – 8.7	7.6	0.5		8.8	4	6.9 – 8.9	8.3	1.0	12	6.7 – 7.9	7.4	0.4	14	6.9 – 9.3	7.8	0.6	
D1H	7.9	11	6.8 – 8.0	7.4	0.3		8.6	4	7.5 – 9.0	8.4	0.7	12	6.3 – 8.4	7.3	0.8	14	6.6 – 9.6	8.0	0.8	
D1I	5.6	11	4.9 – 6.1	5.5	0.3		6.1	4	5.8 – 6.9	6.3	0.5	12	5.1 – 6.8	6.1	0.6	14	5.4 – 6.7	5.9	0.4	
D1P	8.8	11	8.0 – 9.4	8.8	0.4		8.4	4	6.8 – 9.9	7.9	1.4	12	7.1 – 9.7	8.4	0.8	14	7.5 – 10.1	9.2	0.8	
D1ES	4.2	11	2.3 – 4.1	3.5	0.6		4.3	4	2.1 – 4.7	3.2	1.1	12	2.5 – 4.7	3.6	0.8	14	2.1 – 4.9	3.5	0.9	
D1BS	1.0	11	0.7 – 1.1	0.8	0.1		0.9	4	0.8 – 1.1	1.0	0.1	12	0.6 – 1.1	0.9	0.2	14	0.6 – 1.1	0.9	0.1	
D2L	10.9	11	10.4 – 12.6	11.4	0.7		13.1	4	11.6 – 12.4	12.1	0.3	12	10.6 – 12.8	11.6	0.6	14	11.0 – 12.7	12.0	0.5	
D2A	9.2	11	8.8 – 10.8	9.7	0.6		12.3	4	11.2 – 11.6	11.4	0.2	12	9.4 – 11.0	10.2	0.5	14	9.1 – 11.8	10.5	0.8	
D2B	6.3	11	5.7 – 7.2	6.5	0.5		7.6	4	6.6 – 6.9	6.7	0.1	12	5.5 – 7.9	6.6	0.7	14	5.9 – 7.7	6.7	0.6	
D2H	5.4	11	4.9 – 6.2	5.7	0.4		6.9	4	5.9 – 7.5	6.7	0.7	12	4.7 – 6.9	5.8	0.8	14	5.3 – 7.7	6.2	0.7	
D2I	5.0	11	4.1 – 5.2	4.9	0.3		5.6	4	5.5 – 6.0	5.8	0.3	12	4.7 – 6.1	5.3	0.4	14	4.8 – 6.4	5.5	0.5	
D2P	4.9	11	4.5 – 6.1	5.2	0.5		5.1	4	2.8 – 5.5	4.4	1.2	12	4.3 – 5.8	5.0	0.4	14	3.5 – 6.0	5.0	0.7	
D2ES	5.1	10	3.4 – 5.0	4.4	0.5		6.0	4	4.2 – 6.5	5.3	1.0	12	4.0 – 6.0	5.0	0.6	14	4.2 – 6.3	5.1	0.6	
D2BS	0.9	11	0.6 – 0.9	0.8	0.1		1.0	4	1.0 – 1.2	1.1	0.1	12	0.7 – 1.1	0.9	0.1	14	0.8 – 1.1	1.0	0.1	
P1A	13.4	11	11.8 – 14.4	13.6	0.7		15.2	4	13.3 – 15.8	14.2	1.2	12	13.2 – 14.7	13.9	0.5	14	11.3 – 15.1	13.6	1.2	
P1I	9.0	11	8.6 – 10.2	9.5	0.5		11.5	4	8.8 – 11.0	10.1	1.0	12	4.2 – 12.1	9.8	1.9	14	3.8 – 11.2	9.7	1.8	
P1B	4.0	11	3.7 – 4.7	4.2	0.3		3.9	4	4.0 – 4.4	4.2	0.2	12	3.7 – 9.8	4.7	1.6	14	3.5 – 10.4	4.9	1.6	
P1P	10.7	11	9.7 – 11.8	10.6	0.6		12.1	4	8.7 – 10.1	9.3	0.6	12	9.2 – 11.9	10.6	1.0	14	8.1 – 12.6	10.4	1.2	
P2L	12.1	11	9.9 – 12.2	10.9	0.7		13.0	4	9.4 – 11.5	10.7	1.0	12	10.0 – 12.3	11.1	0.8	14	10.0 – 12.9	11.2	0.9	
P2I	6.3	11	4.2 – 6.3	5.2	0.7		6.9	4	5.6 – 6.7	6.1	0.6	12	4.3 – 8.1	5.7	0.9	14	4.3 – 7.0	5.7	0.7	
CDM	19.8	11	19.3 – 21.2	20.1	0.8		21.6	4	20.8 – 23.8	22.0	1.4	12	20.1 – 22.9	21.3	0.9	14	19.5 – 22.9	21.5	1.0	
CPV	11.4	11	10.5 – 11.9	11.2	0.4		12.3	4	10.5 – 13.5	12.0	1.3	12	10.5 – 12.0	11.1	0.5	14	5.2 – 13.9	11.3	2.0	
CFW	6.5	11	6.2 – 7.2	6.7	0.2		6.8	4	6.6 – 7.0	6.8	0.2	12	6.3 – 7.4	6.8	0.3	14	5.5 – 7.7	6.7	0.6	
HANW	7.1	11	6.5 – 7.4	7.0	0.3		7.0	4	6.6 – 9.0	7.6	1.0	12	6.6 – 7.6	7.1	0.3	14	6.5 – 10.6	7.3	1.0	
HAMW	11.1	11	10.9 – 12.0	11.3	0.4		10.8	4	11.2 – 12.3	11.7	0.5	12	9.8 – 13.0	11.7	0.9	14	10.1 – 13.8	11.7	0.9	
HDW	11.9	11	10.9 – 12.9	12.1	0.5		12.5	4	10.8 – 13.5	12.2	1.2	12	10.8 – 13.5	12.3	0.8	14	10.2 – 15.0	12.4	1.3	
TRW	9.9	11	8.0 – 11.9	10.5	1.1		9.8	4	6.3 – 11.0	9.1	2.0	12	7.8 – 10.6	9.1	0.9	14	6.7 – 13.9	10.0	2.0	
ABW	8.2	11	8.0 – 10.9	9.5	0.9		6.3	4	5.5 – 8.8	7.5	1.4	12	6.2 – 9.5	7.5	0.9	14	6.3 – 11.8	8.3	1.4	
HDH	10.3	11	9.3 – 11.7	10.6	0.8		8.8	4	9.3 – 11.1	9.9	0.8	12	8.4 – 12.5	10.0	1.2	14	8.8 – 11.6	10.4	0.7	
TRH	10.0	11	10.5 – 12.7	11.8	0.7		8.0	4	8.0 – 12.7	10.6	2.3	12	7.9 – 13.5	10.1	1.4	14	8.8 – 12.6	10.5	0.9	
ABH	10.3	11	9.6 – 13.2	11.7	1.1		7.9	4	7.3 – 10.5	9.4	1.5	12	7.3 – 11.1	8.8	1.2	14	7.6 – 12.1	9.8	1.4	
CLO	4.1	4	4.0 – 4.8	4.4	0.4		4.4	2	1.2 – 1.5	1.4	0.2	8	1.3 – 4.8	3.6	1.3	7	1.3 – 5.9	3.4	1.8	
CLI	7.1	4	6.9 – 7.7	7.4	0.4		8.0	2	3.3 – 3.8	3.5	0.3	8	2.7 – 7.9	6.2	1.8	7	1.7 – 7.6	5.1	2.5	

TABLE 11. Meristic data for *Squalus albicaudus* sp. nov. Values for *S. cubensis* are also provided for comparisons.

Character	***Squalus albicaudus***				***Squalus cubensis***						
	Holotype	Paratypes			Holotype	Paratypes			Non-type specimens		
		N	Range	Mode		N	Range	Mode	N	Range	Mode
precaudal vertebrae	82	6	81 – 89	83	85	3	87 – 89	–	11	83 – 92	84
caudal vertebrae	28	10	26 – 29	27	30	3	27 – 29	–	11	26 – 31	29
total vertebrae	110	6	110 – 116	111	115	3	114 – 117	117	11	111 – 118	114
monospondylous vertebrae	39	10	40 – 41	40	43	3	41 – 44	–	11	39 – 43	41
diplospondylous vertebrae	71	6	69 – 75	71	72	3	70 – 76	–	11	70 – 75	71
upper tooth rows (right)	12	11	13 – 14	13	14	4	10 – 13	13	12	11 – 14	13
upper tooth rows (left)	12	10	13 – 14	14	14	4	11 – 13	13	11	12 – 14	13
lower tooth rows (right)	11	11	10 – 13	11	11	4	10 – 13	–	12	11 – 14	12
lower tooth rows (left)	11	10	11 – 13	12	12	4	10 – 12	10	12	11 – 14	13
upper tooth series	3	11	2 – 3	2	2	4	2 – 2	2	12	2 – 2	2
lower tooth series	2	11	2 – 3	2	2	4	2 – 2	2	12	2 – 2	2
propterygium radials	–	2	1 – 1	1	–	–	–	–	12	1 – 2	1
mesopterygium radials	–	2	9 – 9	9	–	–	–	–	12	8 – 10	9
metapterygium radials	–	2	8 – 8	8	–	–	–	–	12	6 – 8	7
total pectoral radials	–	2	18 – 18	18	–	–	–	–	12	16 – 20	18
total pelvic radials	–	5	12 – 13	12	–	–	–	–	9	12 – 15	13

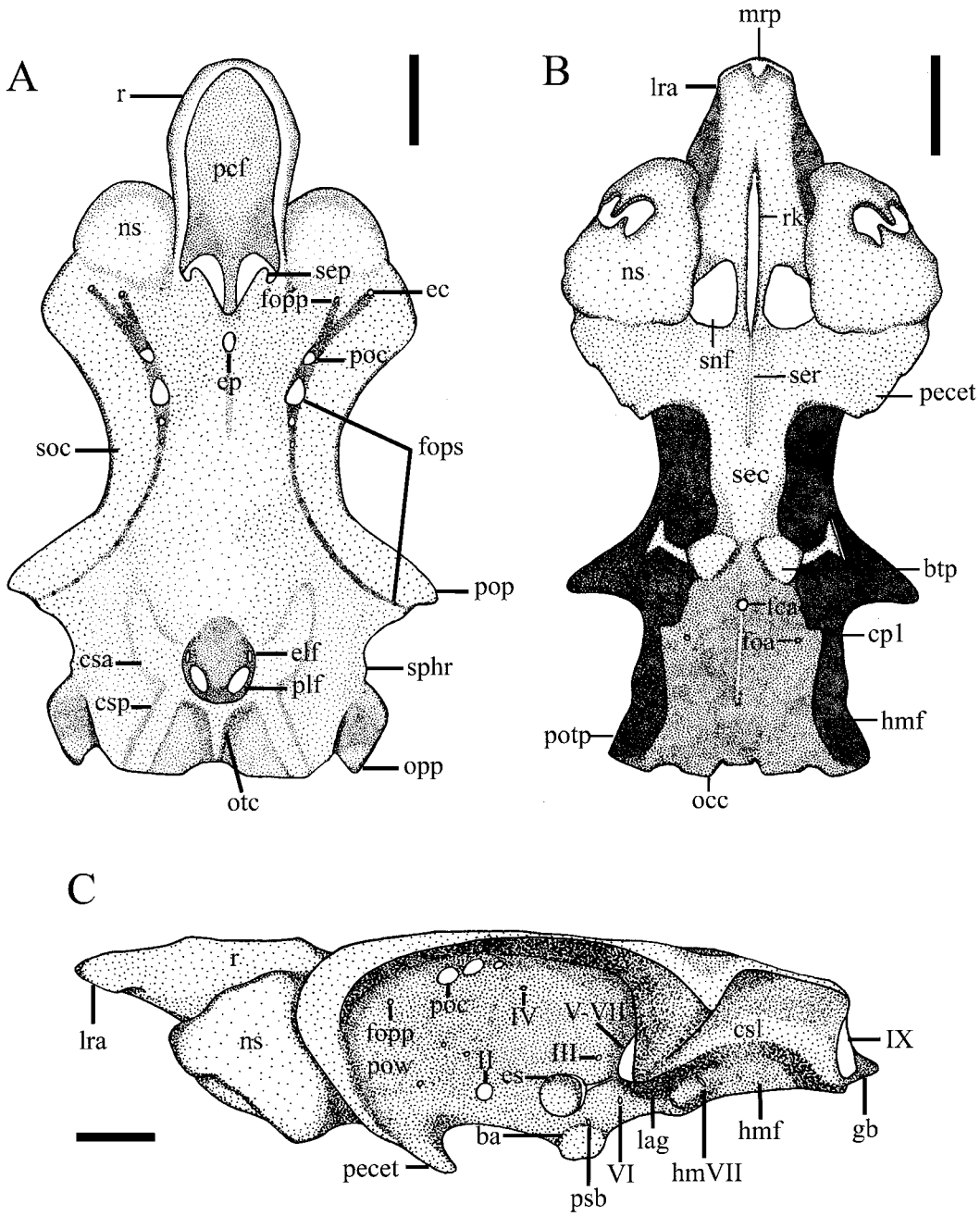

FIGURE 48. Neurocranium of paratype (MNRJ 30184) of *Squalus albicaudus* **sp. nov.** in (A) dorsal, (B) ventral, and (C) lateral views. Abbreviations: **ba**, basal angle; **btp**, basitrabecular process; **cp1**, first cartilaginous process; **csa**, anterior semicircular canal; **csl**, lateral semicircular canal; **csp**, posterior semicircular canal; **ec**, ethmoidal canal; **elf**, endolymphatic foramen; **ep**, epiphysial pit; **es**, eye-stalk; **fca**, foramen for carotid artery; **foa**, foramen for orbital artery; **fopp**, profundus canal; **fops**, series of foramina for superficial ophthalmic branch of trigeminal and facial nerves; **gb**, glossopharyngeal base; **hmf**, hyomandibular facet; **hmVII**, foramen for hyomandibularis facialis; **lag**, lateral auditory groove; **lra**, lateral rostral appendage; **mrp**, median rostral prominence; **ns,** nasal capsule; **occ**, occipital condyle; **opp**, opisthotic process; **otc**, otic crest; **pcf**, precerebral fossa; **pecet**, ectethmoid process; **plf,** perilymphatic foramen; **poc,** preorbital canal; **pop**, postorbital process; **potp**, prootic process; **pow**, preorbital wall; **psb**, efferent pseudobranchial artery foramen; **r**, rostrum; **rk**, rostral keel; **sec**, subethmoid chamber; **sep**, supraethmoidal process; **ser**, subethmoidean ridge; **snf**, subnasal fenestra; **soc**, supraorbital crest; **sphr**, sphenopterotic ridge; **II**, optic foramen; **III**, oculomotor foramen; **IV**, trochlear foramen; **V, VII**, foramen prooticum; **VI**, abducens foramen; **IX**, foramen for glossopharyngeal nerve. Scale bar: 10 mm.

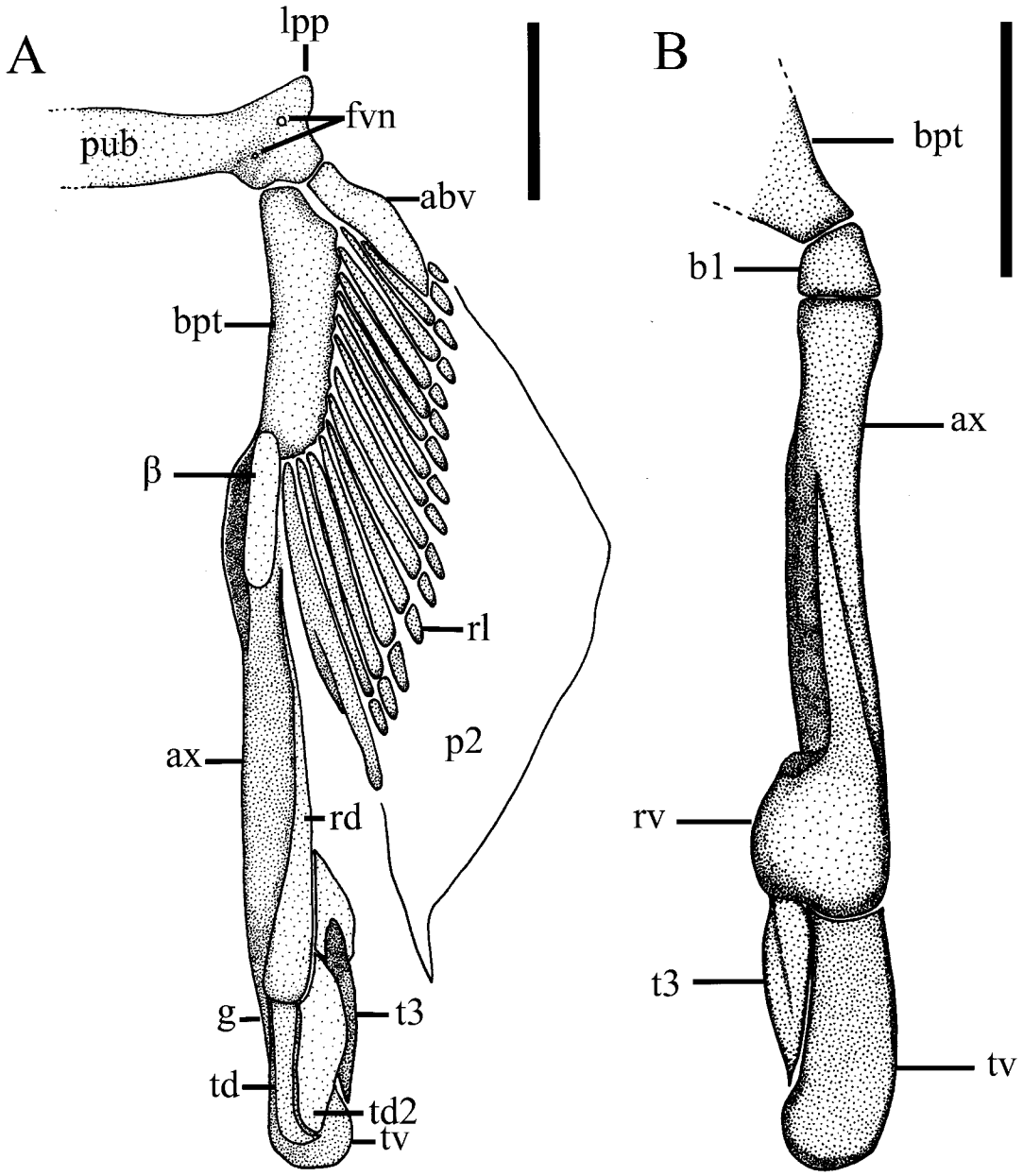

FIGURE 49. Pelvic fin and right clasper cartilages of *Squalus albicaudus* **sp. nov.** (MNRJ 30184, paratype) in (A) dorsal view; (B) detail of clasper in ventral view. Abbreviations: **abv**, anterior pelvic basal; **ax**, axial cartilage; **bpt**, basipterygium; **b1**, intermediate segment; , beta cartilage; **fvn**, foramen for ventral fin nerves; **g**, end-style; **lpp**, lateral prepelvic process; **pub**, puboischiadic bar; **p2,** pelvic fin; **rl**, radials; **rd**, dorsal marginal cartilage; **rv**, ventral marginal cartilage; **td**, dorsal terminal cartilage (claw); **td2**, dorsal terminal 2 cartilage; **tv**, ventral terminal cartilage; **t3**, accessory terminal cartilage (spur). Scale bars: 10 mm.

Cranial roof arched medially, strongly concave laterally at interorbital region, and elongate (postcerebral length 58.5% CL); supraorbital crest with deep longitudinal sulcus, with a series of 10 foramina for the superficial ophthalmic branch of the trigeminal (V) and facial (VII) nerves; preorbital canal markedly broad, located anterior to a series of foramina for superficial ophthalmic branches (V, VII); canal for the ophthalmicus profundus nerve also clearly wide, placed just anterior to preorbital canal for the ophthalmicus nerve; preorbital processes inconspicuous laterally (width across preorbital processes 48.5% CL); postorbital processes prominent, triangular and elongate (its length 10.2% CL).

Supraethmoidal processes conspicuous, cylindrical and paired, placed medioanteriorly in ethmoidal region; epiphyseal pit prominent and rounded, located posterior to supraethmoidal processes; ethmoideal region somewhat depressed ventrally with ectethmoid process wide, pointed and bifurcated distally; subethmoidean chamber

constricted until anterior to basal angle; subethmoidal ridge slender and very elongate, almost reaching the basitrabecular process of basal plate; two small ethmoidal canals, located far anteriorly in the cranial roof at base of each nasal capsule.

Otic region very narrow, comprised by a single and small otic capsule on each side; otic capsule delimited by anterior semicircular canal anteriorly, posterior semicircular canal posteriorly and sphenopterotic ridge laterally; lateral semicircular canal inconspicuous, located ventrally to sphenopterotic ridge; endolymphatic fossa rounded and shallow, placed between otic capsules; two small endolymphatic foramina, located anteriorly in fossa; two posterior perilymphatic foramina wide and rounded; otic crest slightly prominent mediodistally in the otic region; opisthotic processes somewhat pointed posterolaterally at each side of otic region (width across processes 36.5% CL); hyomandibular facet shallow, placed lateroventrally and below lateral semicircular canal; lateral auditory groove profound, positioned anterior to hyomandibular facet; prootic process thick and conspicuous, located posterior to hyomandibular facet (width across hyomandibular facets 41.5% CL).

Orbital region with preorbital wall concave; orbitonasal canal ventral at preorbital wall; interorbital wall deep and large with optic foramen (II) broad, placed midventrally; trochlear foramen (IV) small, placed dorsally near supraorbital crest; eye-stalk prominent, located more posteriorly in interorbital wall and anterior to prooticum foramen; oculomotor foramen (III) and abducens foramen (VI) small, placed, respectively, dorsally and ventrally to eye-stalk; foramen prooticum for the trigeminal (V) and facial (VII) nerves markedly broad, positioned ventroposteriorly in interorbital wall; foramen for efferent of pseudobranchial artery very small, positioned over basal angle; transbasal canal also small, located anteriorly to foramen prooticum.

Basal plate flattened and elongate (its length 38.6% CL), narrower anteriorly at basitrabecular processes (width across processes 16.1% CL) than posteriorly; basitrabecular process bean-shaped and prominent anteriorly; lateral prominence sinuous on each side of basal plate, posterior to basitrabecular processes; single cartilaginous process prominent laterally on each side, somewhat cylindrical (width across processes 30.3% CL); foramen for carotid artery rounded and small, located anteromedially in basal plate; foramen for orbital artery small, located at base of each cartilaginous process.

Occipital region with two triangular occipital condyles, placed ventrally; foramen magnum very wide (its width 9.2% CL); foramen for vagus nerve (X) narrow; glossopharyngeal base markedly thick and subtriangular, placed posterolaterally on each side of occipital region, with foramen for glossopharyngeal nerve (IX) strongly broad and oval.

Pelvic girdle and fin (Fig. 49). Puboischiadic bar transverse, short, slim, and thicker laterally, convex medially and concave more laterally at its anterior portion, posterior portion completely straight; lateral prepelvic process evident on each side, slightly rounded; two expansions lateroposteriorly articulating pubosichiadic bar to pelvic fin; two foramina at each side of puboischiadic bar. Basipterygium vertical, short and straight; anterior pelvic basal element subrectangular, elongate, its length corresponding to one-half length of basipterygium, and associated to three series of small irregular radials; pelvic radials elongate and slender, segmented into proximal and distal elements, the later shorter than the former; 13 total pelvic radials.

Claspers (Fig. 49). Intermediate segment barrel-shaped and short, placed between the pelvic fin basipterygium and axial cartilage; beta cartilage rod-like, cylindrical, and large, its length corresponding to more than one-third length of dorsal terminal cartilage, located dorsally for attaching pelvic fin basipterygium to axial cartilage. Axial cartilage slender and somewhat sinuous with a deep groove evident lateroventrally; end-style very short, not reaching half length of dorsal terminal cartilage (or claw), located medially at end of axial cartilage; dorsal marginal cartilage inconspicuous, laterally over the axial cartilage; dorsal terminal cartilage (or claw) short, its length corresponding to one-third the axial cartilage length, slightly concave and pointed distally, connected anteriorly to dorsal marginal cartilage; dorsal terminal 2 cartilage leaf-like, very soft and small, attached anteriorly to dorsal marginal cartilage and medially to dorsal terminal cartilage (or claw), externally supporting the rhipidion. Ventral marginal cartilage conspicuous and thick, bowl-shape, broader posteriorly than anteriorly, with a prominent folded plate laterally; ventral terminal cartilage spatula-like, small, its length less than one-half of axial cartilage length, attached proximally to ventral marginal cartilage and axial cartilage; accessory terminal 3 cartilage (or spur) thick and short, its length corresponding to one-half axial cartilage length, inserted into folded plate of ventral marginal cartilage, slightly distally pointed with two vertical grooves, one medially and the second ventrally.

Vertebral counts (Table 11). Monospondylous vertebrae 39 in holotype (40–41 in paratypes); precaudal vertebrae 82 (81–89); total vertebrae 110 (110–116).

Geographical distribution (Fig. 50). *Squalus albicaudus* occurs in warm tropical waters between the northeastern and southeastern Brazilian coast and is often registered between the states of Bahia and Espírito Santo. Its distribution to southern Brazil is unknown.

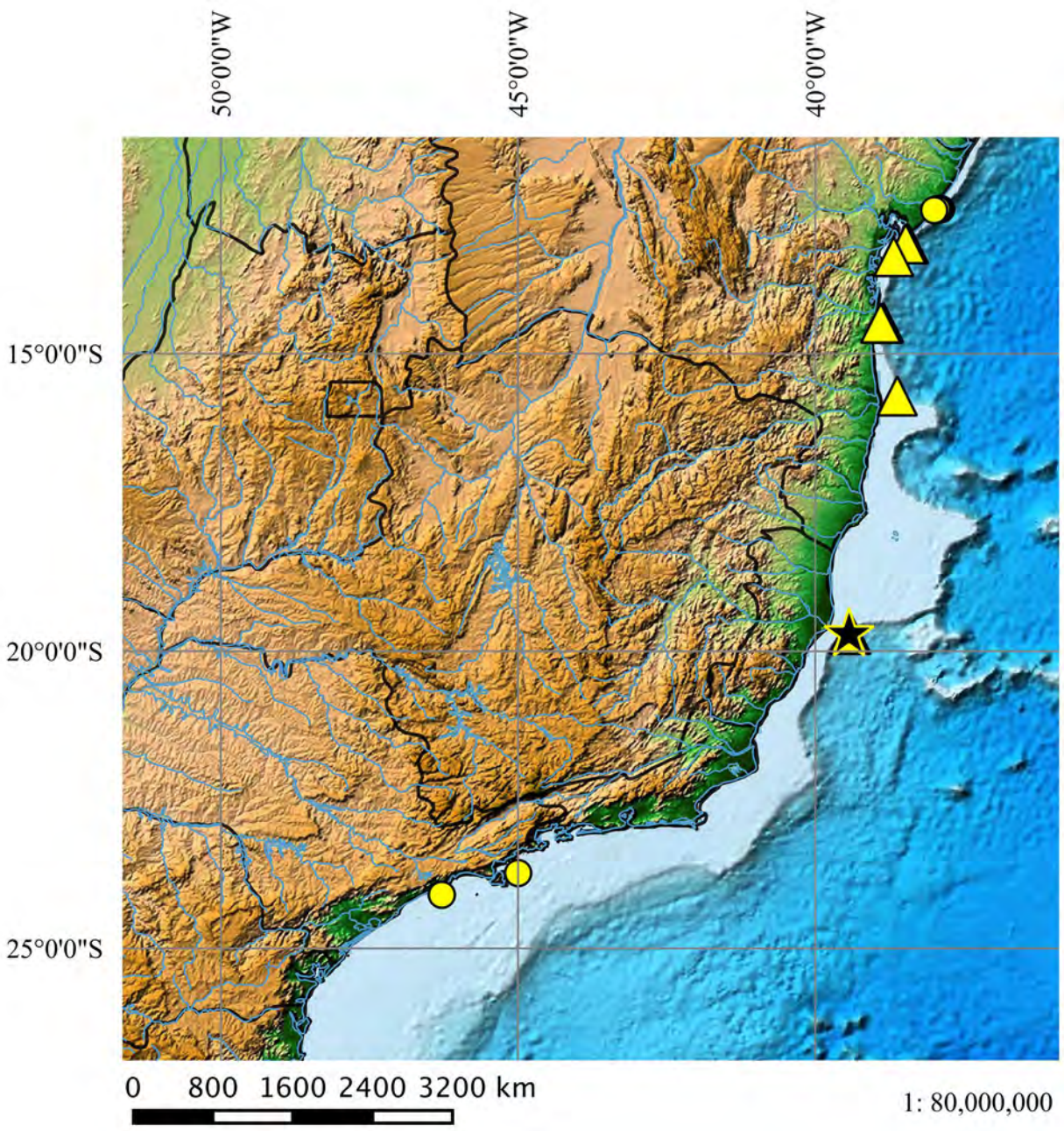

FIGURE 50. Map of geographical distribution of *Squalus albicaudus* **sp. nov.** in the Southwestern Atlantic Ocean. Black star: location of holotype; yellow triangle: location of paratypes; yellow circle: location of non-type specimens.

Etymology. From the Latin *albus*, white, and *cauda*, tail, in reference to the white ventral lobe of its caudal fin.

Remarks. *Squalus cubensis* is a valid species described originally from Havana, Cuba and occurs in the Caribbean Sea (Howell-Rivero, 1936b; Cervigón & Alcal, 1999; Compagno *et al*., 2005). *Squalus cubensis* is very similar to *S. albicaudus* in general morphology, sharing the following characters: dermal denticles unicuspid, slender and lanceolate, their length much greater than width; caudal fin with postventral margins conspicuously white; snout very short; and pectoral fins short but wide. One of the main characters employed to distinguish *S. cubensis* from its congeners has been the shape of the pectoral fins, with a strongly concave posterior margin and markedly pointed free rear tips (e.g. Bigelow & Schroeder, 1957; Garrick, 1960; Bass *et al*., 1976; Muñoz-Chápuli & Ramos, 1989). The same pattern of pectoral fins, however, is observed in other species, such as *S. brevirostris*, *S.*

blainvillei, *S. megalops* (including *S.* cf. *megalops* from South Africa), *S. crassispinus*, and *S. albicaudus*, indicating that it is not useful to differentiate *S. cubensis* from other species of the genus, including *S. albicaudus* from the SWAO. These characters have contributed to the taxonomic confusion regarding the occurrence of *S. cubensis* in the SWAO.

Bigelow & Schroeder (1948, 1957) pointed out that *S. cubensis* possibly occurs in South America based solely on the description of the pectoral fins of *S. blainvillei* by Miranda Ribeiro (1907, 1923) from Rio de Janeiro. Morphological characters provided by Miranda Ribeiro (1907, 1923), however, do not apply exclusively to a single species of *Squalus*, indicating that his observations were based on different species including *S. albicaudus* and *S. acanthias*. We verified this when we compared specimens studied by A. de Miranda Ribeiro in the MNRJ from Ilha Rasa (Rio de Janeiro, Brazil) collected by the vessel "Annie. Subsequent authors (e.g. Ledoux, 1970; Figueiredo, 1977; Sadowsky & Moreira, 1981; Myagkov & Kondyurin, 1986) also recognized the Cuban dogfish in southeastern Brazil. Figueiredo (1977) provided an illustration based probably on a juvenile male from Uruguay, but which does not represent *S. cubensis* or *S. albicaudus* due to differences in shape of the pectoral fins and coloration. Figueiredo (1981) also stated that two other species of *Squalus* may occur between Uruguay and southern Brazil in addition to *S. cubensis*. *Squalus albicaudus* has not yet been recorded in this area, however, indicating that Figueiredo (1981) was probably referring to another species of *Squalus* that has a more southern distribution. Large variation in vertebral counts reported in Sadowsky & Moreira (1981) and Myagkov & Kondyurin (1986) also support the current hypothesis that more than a single species of *Squalus* distinct from *S. cubensis* occurs in the Southwestern Atlantic Ocean, and that the Cuban species does not occur farther southward in the Atlantic Ocean.

Morphometric differences between *S. albicaudus* and the Cuban dogfish were not found, however, when non-type specimens of *S. cubensis* were taken into account (Table 10). No differences in vertebral counts were found between *S. albicaudus* and *S. cubensis* (see also Muñoz-Chápuli & Ramos, 1989) because *S. cubensis* always presents a broad range of values. However, *S. albicaudus* differs slightly from *S. cubensis* in caudal vertebrae (28, 26–29 vs. 29–30, respectively) as indicated by Springer & Garrick (1964). Specimens of *S. cubensis* exhibit great range of external measurements that together with vertebral count variations may indicate the existence of more than one morphological group, similar to *S. cubensis*, in the Western Central Atlantic Ocean and Caribbean Sea. Further investigation on the morphology of *S. cubensis* as well as molecular analyses are needed in order to better characterize this species.

According to Howell-Rivero (1936b), snout length and first dorsal-fin spine length are smaller in juveniles than in adults in *S. cubensis*, but no ontogenetic differences in external measurements were found in *S. albicaudus* by us, supporting its differentiation from *S. cubensis.* Ledoux (1970) considered *S. cubensis* to be an extreme subspecies of the Mediterranean *S. blainvillei* based on overlapping of external measurements. This author overlooked external morphological characters that distinguish these two species, characters typically used in the identification of *Squalus* species worldwide (e.g. Bass *et al*., 1976; Last *et al*., 2007), such as body coloration, length of dorsal spines, and shape of dermal denticles. Many authors (e.g. Bigelow & Schroeder, 1957) have reported overlap in external measurements among specimens of *S. cubensis*, *S. megalops* and *S. blainvillei* as well as in other characters (e.g. dermal denticles, teeth, coloration), impeding easy identification. The same difficulty is noticed for *S. albicaudus* and *S. cubensis*, although external morphology and morphometrics have significant taxonomic value in distinguishing them. Muñoz-Chápuli & Ramos (1981) mentioned that *S. cubensis* differs in clasper morphology from *S. megalops* from the Eastern Atlantic and Indo-Pacific oceans by possessing a less curved claw (dorsal terminal 2 cartilage) and a massive spur (accessory terminal cartilage). These differences are not apparent among species from the SWAO, although clasper morphology helps recognize groups of species within the genus.

Our current results support for the first time that *S. cubensis* does not occur further south in the Southwestern Atlantic Ocean. More material from north of northeastern Brazil is urgently needed to understand the northern limits of *S. albicaudus*, however. Additional comparisons with *S. cubensis* from the Caribbean Sea are welcome, but the characters provided above (see Diagnosis) allow for the distinction of *S. albicaudus* and *S. cubensis*. Despite the lack of the original coloration in the holotype of *S. cubensis*, it is possible to note a large black blotch at the apex of both dorsal fins. Juvenile specimens from the Western Central Atlantic and Caribbean Sea have large black blotches on the first dorsal fin and only adults have it on both dorsal fins. *Squalus albicaudus* has the apex of the first dorsal fin darker, but not as a black blotch as it is in *S. cubensis*, and has the second dorsal fin with a

whitish apex. In neonates and small juveniles of *S. albicaudus*, the black blotch is conspicuous on the first dorsal fin, located farther below on the fin web, while its apex is white, indicating an additional character for separating both species. We also noted that the pelvic fins are closer to the second dorsal fin in *S. albicaudus* but which changes ontogenetically, as previously pointed out by Sadowsky & Moreira (1981) for specimens *Squalus* from southeastern Brazil and *S. megalops* from Australia (Garrick, 1960). *Squalus cubensis* has pelvic fins closer to the midline between the origins of the two dorsal fins during all stages of maturity (as observed by Howell-Rivero, 1936b and Bigelow & Schroeder, 1948), which is distinct from *S. albicaudus* (as noticed by Figueiredo, 1981). However, this character is observed in different species of the genus in which intraspecific variation may also occur, suggesting it to be taxonomically unreliable.

Squalus albicaudus can be further distinguished from *S. megalops* (data for comparisons below from Last *et al*., 2007) by: 39 (41–44) monospondylous vertebrae (*vs*. 37–40 in *S. megalops*); 82 (81–89) precaudal vertebrae (*vs*. 78–84 in *S. megalops*); 110 (110–116) total vertebrae (*vs*. 102–110 in *S. megalops*) (Table 12). *Squalus albicaudus* is separate from *S. crassispinus* by having more slender dorsal-fin spines (first dorsal-fin spine width at base 1.0%, 0.7%–1.1% TL *vs*. 1.3%, 1.2%–1.3% TL in *S. crassispinus*; second dorsal-fin spine width at base 0.9%, 0.6%–0.9% TL *vs*. 1.5%, 1.3%–1.4% TL in *S. crassispinus*). It can be distinguished from *S. bucephalus* by having a narrower head (width at mouth 11.1%, 10.9%–12.0% TL *vs*. 13.0%, 12.1%–13.5% TL in *S. bucephalus*). *Squalus albicaudus* is distinct from *S. bucephalus* and *S. notocaudatus* by having a lower first dorsal fin (height 7.9%, 6.8%–8.0% TL *vs*. 8.5%, 8.1%–8.4% TL in *S. bucephalus* and 8.2%, 8.3%–9.4% TL in *S. notocaudatus*). *Squalus albicaudus* is distinct from *S. raoulensis* by having smaller pectoral fins (pectoral-fin anterior margin length 13.4%, 11.8%–14.4% TL *vs*. 15.3%, 15.0–16.9% TL in *S. raoulensis*). *Squalus albicaudus* differs from *S. albifrons* and *S. altipinnis* by its shorter first dorsal-fin spine (height 4.2%, 2.3%–4.1% TL *vs*. 4.8%, 4.4–5.4% TL in *S. albifrons* and 4.9%, 5.3% TL in *S. altipinnis*).

Comparative material. *Squalus cubensis* (84 specimens): Western North Atlantic, Gulf of Mexico and Caribbean Sea (76 specimens): AMNH 12306, juvenile female, 445 mm TL, Cuba; AMNH 33453, juvenile female, 490 mm TL, Yucatán, Mexico; AMNH 33454, adult male, 535 mm TL, Louisiana, U.S.A.; AMNH 33457, juvenile male, 375 mm TL, Mexico; AMNH 33458, juvenile female, 334 mm TL, Mexico; AMNH 33459, neonate male, 278 mm TL, Mexico; CAS 60863, adult male, 510 mm TL, Puerto Rico; CAS 61162, juvenile male, 400 mm TL, Puerto Rico; CAS 230367, two juvenile males, 395–415 mm TL, South of Pensacola, Florida, U.S.A.; MCZ 1458-S (holotype of *S. cubensis*), adult male, 531 mm TL, Havana, Cuba; MCZ 1459-S (paratype of *S. cubensis*), neonate male, 210 mm TL, Havana, Cuba; MCZ 1460-S (paratype of *S. cubensis*), neonate female, 297 mm TL, Havana, Cuba; MCZ 1461-S (paratype of *S. cubensis*), adult female, 690 mm TL, Havana, Cuba; MCZ 1462-S (paratype of *S. cubensis*), neonate male, 277 mm TL, Havana, Cuba; MCZ 37398, two juvenile females, 376–420 mm TL, Gulf of Mexico; MCZ 40138, adult male, 522 mm TL, Florida, U.S.A.; MCZ 40681, neonate female, 217 mm TL, Puerto Rico; UF 28449, juvenile female, 460 mm TL, Campeche Bank, Mexico; USNM 157843, neonate female, 205 mm TL, two neonate males, 210–215 mm TL, Alabama, U.S.A., 22º91’N, 79º45’W; USNM 157846, adult male, 495 mm TL, Cuba, 22º91'N, 79º26'W; USNM 157853, neonate female, 290 mm TL, Cuba, 22º91’N, 79º45’W; USNM 158589, juvenile female, 445 mm TL, Florida, U.S.A., 28º82’N, 85º75’W; USNM 160847, juvenile male, 410 mm TL, Gulf of Mexico; USNM 164247, adult female, 595 mm TL, Dominican Republic; USNM 187686, neonate male, 217 mm TL, Jamaica, 16º75’N, 81º45’W; USNM 187689, neonate female, 286 mm TL, Panama, 09º30'N, 80º36'W; USNM 187691, neonate male, 247 mm TL, Honduras, 16º63'N, 86º56'W; USNM 187700, juvenile female, 460 mm TL, Panama, 09º07'N, 81º42'W; USNM 187711, juvenile male, 405 mm TL, Nicaragua, 16º43'N, 81º58'W; USNM 187715, adult male, 460 mm TL, Nicaragua, 12º41’N, 82º25’W; USNM 187716, juvenile male, 403 mm TL, adult male, 510 mm TL, Nicaragua, 16º75’N, 81º45’W; USNM 187717, adult male, 510 mm TL, Nicaragua, 16º75’N, 81º45’W; USNM 187726, neonate male, 188 mm TL, Panama, 09º05'N, 81º37'W; USNM 187933, neonate female, 200 mm TL, neonate male, 192 mm TL; three juvenile males, 405–410 mm TL, Mississippi, U.S.A., 29º18’N, 88º10’W; USNM 187934, adult female, 532 mm TL, Cuba, 23º50'N, 79º45'W; USNM 187935, neonate male, 225 mm TL, neonate female, 306 mm TL, Cuba, 23º86'N, 79º38'W; USNM 187936, neonate female, 255 mm TL, Puerto Rico, 18º52’N, 66º83’W; USNM 187937, juvenile male, 425 mm TL, Cuba, 23º66’N, 79º30’W; USNM 188026, two neonate males, 210–260 mm TL, juvenile male, 422 mm TL, adult female, 400 mm TL, Cuba, 23º50'N, 79º45’W; USNM 188027, juvenile male, 400 mm TL, Cuba, 23º98'N, 79º28’W; USNM 188079, juvenile male, 415 mm TL, neonate female, 230 mm TL, Mississippi, U.S.A., 29º19’N, 88º19’W; USNM 188080, juvenile male, 400 mm TL, Mississippi, U.S.A., 29º21’N, 87º97’W; USNM

188081, two juvenile males, 410–430 mm TL, Mississippi, U.S.A., 29º18'N, 88º11'W; USNM 196544, adult male, 440 mm TL, Cuba, 22º98'N, 79º28'W; USNM 205325, adult male, 610 mm TL, adult female, 650 mm TL, Barbados; USNM 205587, two neonate males, 273–290 mm TL, juvenile male, 410 mm TL, Louisiana, U.S.A., 28º18'N, 90º13'W; USNM 206057, adult male, 540 mm TL, Saint Lucia Island, 13º68'N, 60º88'W; USNM 206058, adult female, 610 mm TL, Haiti, 20º72'N, 73º48'W; USNM 220519, neonate male, 215 mm TL, neonate female, 265 mm TL, Florida, U.S.A., 29º10'N, 88º43'W; USNM 220520, juvenile male, 383 mm TL, Texas, U.S.A., 26º52'N, 96º30'W; USNM 220521, neonate female, 275 mm TL, Texas, U.S.A., 26º50'N, 96º27'W; USNM 220522, juvenile male, 390 mm TL, juvenile male, 410 mm TL, Alabama, U.S.A., 29º17'N, 88º08'W; USNM 220584, neonate female, 235 mm TL, Colombia, 11º40'N, 73º78'W; USNM 220586, juvenile female, 395 mm TL, Texas, U.S.A., 27º80'N, 94º61'W; USNM 220587, juvenile male, 380 mm TL, Texas, U.S.A., 27º70'N, 94º43'W; USNM 220599, juvenile female, 400 mm TL, neonate male, 270 mm TL, two juvenile males, 355–450 mm TL, Texas, U.S.A., 27º43'N, 96º23'W; USNM 220600, neonate female, 267 mm TL, Mississippi, U.S.A., 28º98N, 88º80'W; USNM 220603, two juvenile males, 330–360 mm TL, juvenile female, 350 mm TL, Gulf of Maracaibo, Venezuela, 12º28'N, 72º51'W; USNM 220864, adult female, 460 mm TL, Louisiana, U.S.A., 27º87'N, 92º48'W. *Squalus megalops*: Southwestern Pacific Ocean (6 specimens): AMS I 16255-001 (holotype of *S. megalops*), adult female, 565 mm TL, Port Jackson, New South Wales, Australia; MCZ 38619-S, four juvenile female, 370–535 mm TL, New South Wales, Australia; MCZ 38620-S, juvenile female, 520 mm TL, Kangaroo Island, St. Stevens Bay, Australia. Southeastern Atlantic Ocean (2 specimens): SU 31545, neonate male, 280 mm TL, Table Bay, Cape of Good Hope, South Africa; UF 42102, adult male, 570 mm TL, Marrocos.

TABLE 12. Range of vertebral counts of species of *Squalus* taken from Last *et al*. (2007) for comparisons.

	Monospondylous vertebrae	Precaudal vertebrae	Caudal vertebrae	Total vertebrae
S. megalops	37–40	78–84	–	102–110
S. crassispinus	39–42	82–86	24–27	107–111
S. bucephalus	45	86–89	27–30	113–118
S. raoulensis	41–43	84–85	27–28	112–113
S. albifrons	44–46	89–93	26–31	116–122
S. altipinnis	42–44	88–92	26–28	114–120
S. notocaudatus	47–49	94–97	29–30	123–127
S. hemipinnis	35–38	72–76	22–26	96–100
S. montalbani	41–47	79–85	–	105–114
S. chloroculus	43–46	84–86	27–30	111–115
S. edmundsi	43–44	86–91	24–30	113–120
S. grahami	38–42	80–87	26–32	108–116
S. nasutus	36–39	78–83	23–28	103–109
S. griffini	45–47	86–91	26–30	113–121

Discussion

Our study incorporates a variety of morphological characters to separate *S. acanthias*, *S. lobularis*, *S. quasimodo*, *S. bahiensis*, and *S. albicaudus* from their congeners, especially external characters of the body including shape of dorsal, pectoral and caudal fins, as well as width and length of dermal denticles, and color pattern. The external morphology of species of *Squalus* was always thought to be problematic for distinguishing species due to overlap of various characters used to define them, which led authors to separate species into species-groups of similar external morphology (e.g. Bigelow & Schroeder, 1948; Garrick, 1960; Compagno *et al*., 2005). When the new species described in this study had overlapping external characters, coloration, morphometrics and vertebral counts were valuable for separating them in agreement with the findings of Last *et al*. (2007) for Australian species. First dorsal-fin height, first dorsal-fin spine length, pectoral-fin anterior margin length, dorsal-caudal space, and

interdorsal space are external measurements that proved diagnostic at species level in our study. It is important to note, however, that continuous morphometric ranges without any discontinuity are often observed when species are compared. *Squalus albifrons*, *S. altipinnis*, *S. chloroculus*, and *S. montalbani* are examples of species described in Last *et al*. (2007) in which external morphometric characters used in their diagnoses completely overlapped with congeners. However, continuous morphometric ranges serve as additional morphological information for species separation if ranges are elevated and have a minimum overlap between species. External proportions, such as prenarial length and distance from nostrils to upper labial furrow, as proposed by Bass *et al*. (1976) and followed by Chen *et al*. (1979), Compagno (1984), and Marouani *et al*. (2012), are not useful for differentiating species regionally or in a broader context, but they allow to identify species as part of a group of species with similar external morphology as a first approximation, as noticed by Gomes *et al*. (2010).

General shape of dermal denticles and pectoral fins, length of snout, and color pattern of caudal fin by themselves were not distinctive for species of *Squalus* nor for groups of species within the genus. These characters overlap among species from different morphological groups and are still known, however rarely, to be variable in conspecific specimens when different stages of maturity are compared. Last *et al*. (2007) noticed that *S. hemipinnis* from Indonesian waters share characters of two different groups of species, the *S. megalops* and *S. mitsukurii* groups, indicating that morphological overlapping can potentially occur among species-groups as well.

Squalus lobularis, *S. bahiensis*, and *S. albicaudus* share a concave pectoral-fin posterior margin, which should be exclusive to species of the *S. megalops* group as proposed by Bigelow & Schroeder (1948, 1957). *Squalus albicaudus* and *S. acanthias* share unicuspid dermal denticles, a character of the *S. megalops* group according to Bigelow & Schroeder (1948, 1957), even though the former species has lanceolate dermal denticles while the latter has bat-shaped denticles. Our findings disagree with Bigelow & Schroeder (1948, 1957) and Bass *et al*. (1976) who pointed out that *S. acanthias* has tricuspid dermal denticles. However, *S. acanthias* has a prenarial length equal or slightly greater than the inner nostril-labial furrow space, a character that should be restricted to species of the *S. mitsukurii* group as suggested by Bass *et al*. (1976). Thus, we prefer not to classify the new species of *Squalus* described here in any of the species-groups proposed. These new species can be identified by characters in combination but which are clearly diagnostic, although not autapomorphic. In this way we avoid compounding the current confusion regarding the identity and composition of species-groups of *Squalus*.

Muñoz-Chápuli & Ramos (1989) provided complementary characters of neurocranial morphology to distinguish *S. blainvillei* and *S. megalops* from the Eastern Atlantic Ocean and Mediterranean Sea, as the former species has a single prominent cartilaginous process in the basal plate while the latter species has two. All species of *Squalus* examined herein have only one cartilaginous process, in agreement with the observations of Muñoz-Chápuli & Ramos (1989) and Marouani *et al*. (2012) for *S. blainvillei*. Muñoz-Chápuli & Ramos (1989) also defined cranial measurements that are useful for separating species, representing the first such attempt within Squaliformes, which was followed by Marouani *et al*. (2012) and the present study, with some modifications (see Material and Methods). Our results indicate some variation in these measurements between species of *Squalus* from the Southwestern Atlantic Ocean; for instance, width across nasal capsules, width across preorbital and postorbital processes, length of postorbital process, distance between orbital processes, distance across opisthotic processes and hyomandibular facets, and subethmoidean width. A larger number of samples are required to evaluate more accurately variation in cranial measurements and whether they may be useful as diagnostic characters for species of the genus.

Muñoz-Chápuli & Ramos (1989) and Marouani *et al*. (2012) also noticed differences in clasper morphology between *S. acanthias*, *S. blainvillei*, *S. acutirostris*, *S. cubensis* and *S. megalops*, in which, according to them, the dorsal terminal (claw) and accessory terminal 3 (spur) cartilages vary in length and shape in mature males. *Squalus acanthias*, *S. lobularis* and *S. bahiensis* have a very elongate and slender spur, and a claw that is large and markedly concave and hook-like at the tip, while *S. albicaudus* has a very short and heavy spur, and a claw that is short and almost straight at the tip, as is shown by Muñoz-Chápuli & Ramos (1989) for *S. acanthias* and *S. blainvillei*, and for *S. acutirostris*, *S. cubensis* and *S. megalops*, respectively. Similarity in these terminal cartilages, however, support that clasper morphology is not useful for separating species of *Squalus* but only into species-groups with similar external morphology. A broader range of species is required for analyzing comparatively whether clasper morphology is species-specific.

The new species of *Squalus* described in this study indicate that the diversity of the genus in the Southwestern Atlantic Ocean is greater than was previously thought, supporting the assumptions of Figueiredo (1981), Gomes *et*

al. (1997), Gadig & Gomes (2003), and Rosa & Gadig (2014). There is a clear global tendency to increase the number of recognized species in the genus over the past decade or so, as seen for the Southwestern Pacific (e.g. Last *et al*., 2007), North Pacific (e.g. White & Iglésias, 2011), and Indian Oceans (e.g. Baranes, 2003), with recent systematic studies based on molecular analysis (e.g. Naylor *et al*., 2012) pointing out that some undescribed species may still occur in some regions. A worldwide investigation of the taxonomy of the family Squalidae based solely on morphological characters (Viana & Carvalho, in prep.) is being finalized in order to elucidate in detail the morphological and systematic complexity that still remains within *Squalus* and *Cirrhigaleus*.

Key to species of *Squalus* from the Southwestern Atlantic Ocean

1a. First dorsal spine placed well behind vertical line traced at adpressed pectoral free rear tips; white spots dorsally on body; unilobed anterior margin of nostrils; pectoral girdle with anterolateral segmented processes . . . . . *S. acanthias*.

1b. First dorsal spine placed over or before vertical line traced at adpressed pectoral rear tips; body uniformly colored dorsally; bilobed anterior margin of nostrils; pectoral girdle without any segmented processes . . . . . 2.

2a. Prenarial length smaller than distance between nostril and upper labial furrow; upper caudal lobe very narrow; pectoral fins very narrow with pectoral free rear tips pointed and angular; caudal fin mostly white; dermal denticles unicuspid and lanceolate; dorsal terminal cartilage (claw) short, thick and straight at tip; accessory terminal cartilage (spur) broad and small . . . . . *S. albicaudus*.

2b. Prenarial length greater than distance between nostril and upper labial furrow; upper caudal lobe broad and rectangular; pectoral fins broad with pectoral free rear tips rounded and lobe-like; caudal fin grayish; dermal denticles tricuspid and rhomboid; dorsal terminal cartilage (claw) very elongate, slender and hook-like at tip; accessory terminal cartilage (spur) thin and large . . . . . 3.

3a. Body robust and markedly humped dorsally; first dorsal fin conspicuously slender only from its midline to apex; second dorsal fin upright and markedly tall (height 4.0%–5.3% TL); dermal denticles markedly imbricate and broad at crown . . . . . *S. quasimodo*.

3b. Body very slender throughout, without a dorsal hump; first dorsal fin uniformly slender; second dorsal fin raked and low (height 3.7%–4.4% TL); dermal denticles not imbricate and very narrow. 4

4a. First and second dorsal fins very broad; caudal fin dark gray with dorsal caudal margin light gray and ventral caudal lobe uniformly dark gray; interdorsal space 21.9%–24.1% TL; dorsal caudal space 10.4%–10.9% TL; pectoral-caudal space 20.3%–24.4% TL in adults; pectoral inner margin 9.2%–10.6% TL . . . . . *S. lobularis*.

4b. First and second dorsal fins narrow; caudal fin light gray with dorsal caudal margin white and ventral caudal lobe mostly white; interdorsal space (24.4%–26.8% TL); dorsal-caudal space 11.0%–12.2% TL; pectoral-caudal space 19.5%–20.3% TL; pectoral inner margin 8.4%–8.9% TL . . . . . *S. bahiensis*.

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APPENDIX 1. Abbreviations and definitions for external measurements (following Last *et al*., 2007).

Total length (TL): greatest direct distance between snout tip and caudal-fin apex; Precaudal length (PCL): direct distance from snout tip to origin of upper caudal lobe; Pre-second dorsal length (PD2): direct distance from snout tip to second dorsal-fin origin; Pre-first dorsal length (PD1): direct distance from snout tip to first dorsal-fin origin; Pre-vent length (SVL): direct distance from snout tip to anterior end of cloaca; Prepelvic length (PP2): direct distance from snout tip to pelvic-fin origin (using finger to find origin); Prepectoral length (PP1): direct distance from snout tip to exposed base of pectoral fin; Head length (HDL): direct distance from snout tip to upper edge of the fifth gill slit; Prebranchial length (PG1): direct distance from snout tip to upper edge of the first gill slit; Prespiracular length (PSP): direct distance from snout tip to anterior margin of spiracle; Preorbital length (POB): direct distance from snout tip to fleshy, anterior margin of orbit; Prenarial length (PRN): direct distance from snout tip to anterior edge of outer nostril; Preoral length (POR): direct distance from snout tip to upper jaw (including teeth); Inner nostril-labial furrow length (INLF): shortest distance between nostrils and upper labial furrow; Mouth width (MOW): distance between apices of labial pleats (junction of labial furrows and postoral grooves); Labial furrow length (ULA): distance from apex of labial pleat to anterior edge of furrow; Internarial space (INW): shortest distance between the two nostrils; Interorbital space (INO): distance between soft interorbit in natural state (taken at mid-length of eye); Eye length (EYL): length of eye, not including eye socket; Eye height (EYH): height of eye; Spiracle length (SPL): maximum width of opening; First gill-slit height (GS1): vertical height of first gill slit (not following profile of gill); Fifth gill-slit height (GS5): vertical height of fifth gill slit (not following profile of gill); Interdorsal space (IDS): shortest distance between first dorsal-fin insertion and second dorsal-fin origin; Dorsal-caudal space (DCS): shortest distance between second dorsal-fin insertion and origin of upper caudal lobe; Pectoral-pelvic space (PPS): direct distance from pectoral-fin insertion to pelvic-fin origin (taken on ventral side); Pelvic-caudal space (PCA): direct distance from pelvic-fin insertion to origin of lower caudal lobe (taken on ventral side); First dorsal length (D1L): distance from first dorsal-fin origin (use thumbnail to find origin) to apex of free rear tip; First dorsal anterior margin (D1A): distance from first dorsal-fin origin (use thumbnail to find origin) to point of greatest curvature of apex of fin; First dorsal base length (D1B): distance from first dorsal-fin origin (use thumbnail to find origin) to first dorsal-fin insertion; First dorsal height (D1H): greatest vertical height from fin base to apex of fin; First dorsal inner margin length (D1I): distance from first dorsal-fin insertion to apex of free rear tip; First dorsal posterior margin length (D1P): distance from points of greatest curvature of the first dorsal-fin apex and apex of free rear tip; First dorsal spine length (D1ES): distance from junction of exposed portion of spine and soft part of dorsal fin to spine apex; First dorsal spine base width (D1BS): width of exposed spine at its junction with soft dorsal fin; Second dorsal length (D2L): distance from second dorsal-fin origin (use thumbnail to find origin) to apex of free rear tip; Second dorsal anterior margin (D2A): distance from second dorsal-fin origin (use thumbnail to find origin) to point of greatest curvature of apex of fin; Second dorsal base length (D2B): distance from second dorsal-fin origin (use thumbnail to find origin) to second dorsal-fin insertion; Second dorsal height (D2H): greatest vertical height from fin base to apex of fin; Second dorsal inner margin length (D2I): distance from second dorsal-fin insertion to apex of free rear tip; Second dorsal posterior margin length (D2P): distance from points of greatest curvature of the second dorsal-fin apex and apex of free rear tip; Second dorsal spine length (D2ES): distance from junction of exposed portion of spine and soft part of dorsal fin to spine apex; Second dorsal spine base width (D2BS): width of exposed spine at its junction with soft dorsal fin; Pectoral anterior margin length (P1A): distance from pectoral-fin origin to apex of fin (measured from ventral surface); Pectoral inner margin length (P1I): distance from pectoral-fin insertion to apex of free rear tip (measured from ventral surface); Pectoral base length (P1B): distance from pectoral-fin origin to pectoral-fin insertion (measured from ventral surface); Pectoral posterior margin length (P1P): distance between points of greatest curvature of pectoral-fin apex and free rear tip (measured from ventral surface); Pelvic length (P2L): distance from pelvic-fin origin (use finger to find origin) to point of greatest curvature of apex (measured from ventral surface); Pelvic inner margin length (P2I): distance from pelvic-fin insertion to apex of free rear tip (measured on ventral surface); Dorsal caudal margin length (CDM): distance from origin of upper caudal lobe to point of greatest curvature of apex of dorsal caudal lobe; Preventral caudal margin length (CPV): distance from origin of lower caudal lobe to point of greatest curvature of apex of ventral caudal lobe; Caudal fork width (CFW): perpendicular distance from greatest angle of caudal fork to dorsal caudal margin; Head width at nostrils (HANW): width of head at anterior margin of nostrils (use straight edge through anterior edge of nostrils); Head width at mouth (HAMW): width of head at level of anterior margin of mouth; Head width (HDW): width of head at fifth gill slit; Trunk width (TRW): width of body at pectoral-fin insertion; Abdomen width (ABW): width of body at first dorsal-fin insertion; Head height (HDH): vertical height of head at fifth gill slit; Trunk height (TRH): vertical height of body at pectoral-fin insertion; Abdomen height (ABH): vertical height of body at first dorsal-fin insertion; Clasper outer length (CLO): distance between lateral junction of pelvic-fin inner margin to apex of clasper; Clasper inner length (CLI): distance between connection of the clasper base dorsally with the tail to apex of clasper.

APPENDIX 2. Measurements taken on neurocrania (see Material and Methods; Fig. 1).

1. Total length of the neurocranium (% TL): distance from the occipital centrum to the anterior tip of the rostrum as measured along the longitudinal axis of the cranial roof; 2. Postcerebral length: distance from the occipital centrum to the hind end of the precerebral fossa (between supraoccipital processes when present); 3. Precerebral fossa length: distance from the hind end of the precerebral fossa between supraoccipital processes to the anterior tip of the rostrum; 4. Precerebral fossa width: the greatest width of the precerebral fossa measured from its inside edges; 5. Width across nasal capsules: the greatest distance across the sides of both nasal capsules transverse to the longitudinal axis of the neurocranium; 6. Interorbital width: distance between the supraorbital crests across the cranial roof; 7. Width across preorbital processes: transverse distance between the extreme distal tips of the preorbital processes; 8. Postorbital process length: distance between the distal tip of the postorbital process to the beginning of the sphenopterotic ridge; 9. Width across postorbital processes: transverse distance between the extreme distal tips of the postorbital processes; 10. Distance between orbital processes: distance from the tip of the preorbital process to the tip of the postorbital process; 11. Distance across opistotic processes: transverse distance across the opistotic processes measured dorsally; 12. Width across hyomandibular facets: transverse distance between the hyomandibular facets measured dorsally from the prootic process; 13. Nasobasal length: distance from the occipital centrum to the hind end of the rostral keel; 14. Rostral keel length: distance from the anterior to the posterior end of the rostral keel; 15. Subethmoidean width: transverse anterior distance across the subethmoidean region; 16. Basal angle width: transverse distance across basal angles; 17. Basal plate length: distance from the occipital centrum to the basal angle furrow; 18. Basal plate width: least transverse distance across the anterior sinuosity of the basal plate (posterior to the basal angle); 19. Width across first cartilaginous processes: transverse distance across the first cartilaginous processes of the basal plate; 20. Width across second cartilaginous processes (when present): transverse distance across the second cartilaginous processes of the basal plate; 21. Maximum sagittal height: vertical distance from the dorsal hind of the occipital crest to the basal plate; 22. Foramen magnum width: transverse distance across the foramen magnum.