Received 24 January 2017

Accepted 4 August 2017

Squalus bassi sp. nov., a new long-snouted spurdog (Chondrichthyes: Squaliformes: Squalidae) from the Agulhas Bank

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urn:lsid:zoobank.org:pub:7EC5FA29-7E27-4A71-A620-18FAA4CC2EE2

Running headline: *SQUALUS BASSI* SP. NOV. FROM THE AGULHAS BANK

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The long-snouted African spurdog *Squalus bassi* sp. nov. is described based on material collected from the outer shelf and upper continental slope off South Africa and Mozambique. *Squalus bassi* shares with *S. mitsukurii, S. montalbani, S. chloroculus, S. grahami*, *S. griffini, S. edmundsi*, *S. quasimodo* and *S. lobularis* a large snout with prenarial length greater than distance between nostrils and upper labial furrows, dermal denticles tricuspidate and rhomboid and elevated number of vertebrae. *Squalus bassi* can be distinguished from all its congeners by a combination of body and fin colouration, external morphometrics, vertebral counts and shape of dermal denticles. Similar long-snouted congeners from the Indo-Pacific region, including *S. montalbani*, *S. edmundsi* and *S. lalannei* are compared in detail with the new species. This new species has been misidentified as the Japanese *S. mitsukurii* and the Mediterranean *S. blainvillei* due to the lack of comparative morphological analyses. The validity of the nominal species *S. mitsukurii* in the south-eastern Atlantic Ocean and western Indian Ocean is also clarified herein, indicating it has a more restricted geographical distribution in the North Pacific Ocean.

Key words: dogfish; new species; south-eastern Atlantic Ocean; taxonomy; western Indian Ocean.

INTRODUCTION

Squalus L. 1758 comprises the second most diverse genus of sharks of the order Squaliformes (only behind *Etmopterus* Rafinesque 1810) with 30 valid species (Ebert *et al*., 2013; Viana *et al*., 2016). Four species are usually recognized off southern Africa ranging from Namibia to Mozambique (Bass *et al*., 1976, 1986; Compagno *et al*., 1991, 2005; Ebert, 2015; Ebert & Van Hees, 2015; Viana & Carvalho, 2016): Picked dogfish *Squalus acanthias* L. 1758; bluntnose spiny dogfish *S. acutipinnis* Regan 1908; Shortspine spurdog *S. mitsukurii* Jordan & Snyder 1903; Longnose spurdog *Squalus blainvillei* (Risso 1827). Validity of the latter two species, however, remains uncertain for this region. Additionally, two new short-snouted species, the Malagasy skinny spurdog *Squalus mahia* Viana, Lisher & Carvalho 2017 and the Smith's dogfish shark *Squalus magaretsmithae* Viana, Lisher & Carvalho 2017, were recently described from mostly southern African waters in Viana *et al*. (2017).

Squalus mitsukurii was originally described from Japan in the north-western Pacific Ocean, but it has records also in the tropical and temperate regions of the South Pacific, western Indian and Atlantic Oceans (Bass *et al*., 1986; Compagno, 2002, 2016; Ebert *et al*., 2013; Veríssimo *et al*., 2017; Weigmann, 2016). This species is characterized by having an elongate and rounded snout, short dorsal-fin spines, rounded pectoral-fin free rear tips, tricuspidate and rhomboid dermal denticles and caudal fin with a black upper caudal blotch and black caudal bar (Compagno, 1984; Last *et al*., 2007*a*; Viana *et al*., 2016). Other long-snouted species of the genus that occur in the Indo-Pacific and South Atlantic Oceans are (Ebert, 2013; Viana *et al*., 2016): Philippine spurdog *Squalus montalbani* Whitley 1931;

Seychelles spurdog *Squalus lalannei* Baranes 2003; greeneye spurdog *Squalus chloroculus* Last, White & Motomura 2007; Edmund's spurdog *Squalus edmundsi* White, Last & Stevens 2007; eastern longnose spurdog *Squalus grahami* White, Last & Stevens 2007; western longnose spurdog *Squalus nasutus* Last, Marshall & White 2007; Atlantic lobefin dogfish *Squalus lobularis* Viana, Carvalho & Gomes 2016; humpback western spurdog *Squalus quasimodo* Viana, Carvalho & Gomes 2016.

Difficulties in applying the correct nominal species to this *Squalus* form in southern Africa are frequently reported in the literature. Bass *et al*. (1976) recognized *S. blainvillei* in the western Indian Ocean but later Bass *et al*. (1986) re-identified it as *S. mitsukurii*, followed by Muñoz-Chápuli & Ramos (1989). Chen *et al*. (1979) stated that the long-snouted form from southern Africa is more similar morphologically to the Japanese *S. mitsukurii* than to the Mediterranean *S. blainvillei* regarding its low dorsal fins and short fin spines. Compagno (1984) corroborated the results of the latter authors. Myagkov & Kondyurin (1986) did not recognize *S. mitsukurii* in the eastern Atlantic Ocean and restricted the distribution of *S. blainvillei* to the north-eastern Atlantic Ocean. For other authors, the long-snouted *Squalus* from southern Africa is regarded as an undescribed species with a very similar morphology to *S. mitsukurii* (Compagno *et al*., 1991; Naylor *et al*., 2012; Pickering & Caira, 2012; Ebert & Van Hees, 2015; Veríssimo *et al*., 2017), although no comparative morphological supporting data were provided. Mitochondrial *nadh2* gene analysis supports that *Squalus cf. mitsukurii* collected in the western Indian Ocean is clearly separate from the north-western Pacific population and more closely related to *S. montalbani*, the Cuban dogfish *Squalus cubensis* Howell-Rivero 1936 and *S. lobularis* (Naylor *et al*., 2012). Ebert (2015) and Compagno

(2016) provisionally recognized *S. mitsukurii* and *S. blainvillei* off southern Africa as valid and distinct regarding height of dorsal fins, length of dorsal-fin spines and number of precaudal vertebrae. These authors also reinforced the need of a taxonomic re-evaluation of these species in order to properly apply their regional nomenclature. Veríssimo *et al*. (2017) corroborated that specimens from South Africa comprise a separate clade from the remaining forms of *S. mitsukurii* worldwide, especially those from the Atlantic Ocean, calling for an urgent clarification of their taxonomic status.

Succinct original descriptions, loss of type specimens and lack of broad comparative morphological analyses between regional representatives of *Squalus* have led the southern African form to be considered either a junior synonym of *S. blainvillei* or a valid species distinct from *S. mitsukurii* from Japan. In the present study, a new species of long-snouted species of *Squalus* is described based on material collected from South Africa and Mozambique. Comparative morphological analysis with similar long-snouted species and other regional representatives of the genus is provided. Furthermore, the taxonomic status of *S. mitsukurii* and its presence in southern African waters are discussed.

MATERIALS AND METHODS

Specimens examined were preserved in 70% ethanol. Nomenclature for external morphology and colouration follows Last *et al*. (2007*b*). Colouration is based on preserved specimens, unless otherwise noted. External measurements were obtained using digital callipers with a 0.1 mm precision or a metric tape for measurements greater than 150 mm. A

total of 62 external measurements were obtained for each specimen, following Last *et al*. (2007*b*) as provided in Viana *et al*. (2016) and are expressed as percentages of total length (% L_T). Meristic data for counting vertebrae were obtained through film or digital radiographs for holotype, 14 paratypes and three non-type specimens. Vertebral counts follow Springer & Garrick (1964). Tooth row count and terminology are according to Cappetta (1987) and Herman *et al*. (1989). Tooth samples from upper and lower jaws (three lateral teeth toward the first series) were taken and investigated using a stereoscopic microscope. Skin samples for analysis of dermal denticles measuring 1 x 1 cm were taken from below the first dorsal fin (right side) and analysed through a stereoscopic microscope or scanning electron microscope (SEM) at the Instituto de Biociências, Universidade de São Paulo (IBUSP) and Rhodes University (RU). Description of dermal denticles follows Deynat & Séret (1996).

All specimens were photographed in dorsal, ventral and lateral views using a digital camera, as well as specific body parts (*e.g*. fins, claspers). Photographs of teeth were taken using a digital camera attached to a Leica DFC295stereoscope microscope (www.leica.com). Map of geographical distribution was rendered using QGIS 2.14.2 Essen (QGIS Development Team, QGIS Geographic Information System, Open Source Geospatial Foundation Project; http://qgis.osgeo.org) and Google Earth (www.google.co.uk/intl/en_uk/earth/). In the description, single values are for holotype followed by range values for paratypes from which data were taken. Synonyms for species indicate authorship, date, page and figures when possible. The comparative material listed in the Appendix is only of species that are more similar to the new species described herein; for specimens of other species examined, see Viana *et al*. (2016, 2017). Types and other examined material are deposited in scientific

collections, whose institutional acronyms follow Sabaj (2016): AMNH, American Museum of Natural History, New York, NY; AMS, Australian Museum, Sydney; BMNH, Natural History Museum, London; CSIRO, Commonwealth Scientific & Industrial Research Organisation, Division of Marine & Atmospheric Research, Australian National Fish Collection (ANFC), Hobart; HUJ, Hebrew University of Jerusalem, Zoological Museum, Jerusalem; HUMZ, Hokkaido University Museum, Sapporo, and Fisheries Science Center, Hakodate; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; NMW, Naturhistorisches Museum, Wien [Vienna]; NSMT, National Museum of Nature and Science, Ueno Park, Tokyo; RMNH, Naturalis Biodiversity Center, Amsterdam; SAIAB, South African Institute for Aquatic Biodiversity, Grahamstown; SAM, South African Museum, Cape Town; SU, Stanford University, Palo Alto, CA; UERJ, Universidade do Estado do Rio de Janeiro, Instituto de Biologia Roberto Alcântara Gomes, Vila Isabel, Rio de Janeiro; USNM, National Museum of Natural History, Smithsonian Institution, Department of Vertebrate Zoology, Washington D.C.; ZMH, Zoological Museum Hamburg; ZUMT, University Museum, University of Tokyo, Tokyo.

Clasper morphological abbreviations are: ap, apopyle; cg, clasper groove; hp, hypopyle; p2, pelvic fin; rh, rhipidion.

RESULTS

SQUALUS BASSI SP. NOV.

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Figs 1–7 and Tables I–III

Long-snouted African spurdog (English); Langneus-penhaai (Afrikaans)

Squalus blainvillei. Bass *et al*., 1976 (in part): 15–16, 59 (description; Beira, Mozambique to Algoa Bay, South Africa); *S. blainville*. Chen *et al*., 1979: 39 (cited; South Africa); *Squalus mitsukurii*. Compagno, 1984 (in part): 121–122 (description; South Africa). Bass *et al*., 1986: 61–62 (cited; South Africa, Mozambique). Compagno *et al*., 1989: 22, (cited, illustrated; Namibia to Natal, South Africa, possibly Mozambique). Heemstra & Heemstra, 2004: 53 (cited; Namibia to Mozambique). Compagno *et al*., 2005 (in part): 67–68 (description; south-eastern Atlantic and western Indian Oceans). Ebert, 2013: 57, fig. 62 (cited; Indian Ocean). Ebert, 2015: 57–58 (cited; southern Africa). Compagno, 2016 (in part): 1157, 1163; fig. 4 (listed, description; south-eastern South Africa). Veríssimo *et al*., 2017: 1–15, figs. 1–2 (cited; South Africa).

Squalus cf. mitsukurii. Compagno *et al*., 1991 (in part): 44, 71, 72 (cited, listed; South Africa, Mozambique). Naylor *et al*., 2012: 57; fig. 42 (cited; South Africa). Pickering & Caira, 2012: 107–114 (cited; South Africa). Ebert, 2015: 57–58, figs. 57, 59 (cited; southern Africa). Ebert & Van Hees, 2015: 144 (cited; southern Africa)

Holotype.

SAM 33476, adult male, 683 mm L_T, near Agulhas Bank, Western Cape, South Africa, 36.21° S; 20.04° E; 201 meters depth. Collected on 11 June 1994 during South Coast Biomass Survey.

Paratypes

SAIAB 25923, adult male, 790 mm L_T, off west coast, South Africa, 32.10º S; 16.90º E; 281 m depth, collected on 20 January 1986 (unknown collector); SAIAB 25924, adult male, 730 mm L_T, off west coast, South Africa, 32.10º S; 16.90º E; 281 m depth, collected on 20 January 1986 (unknown collector); SAIAB 26419, juvenile female, 450 mm L_T, off west coast, South Africa, 30.60° S; 17.17° E; 142 m depth, collected on 15 July 1986 (unknown collector); SAIAB 26420, juvenile female, 485 mm L_T, off west coast, South Africa, 30.60° S; 17.17° E; 142 m depth, collected on 15 July 1986 (unknown collector); SAIAB 26421, juvenile male, 450 mm L_T, off west coast, South Africa, 30.60° S; 17.17° E; 142 m depth, collected on 15 July 1986 (unknown collector); SAIAB 53305, adult male, 750 mm L_T, off west coast, South Africa, 34.06º S; 17.49º E; 430 m depth, collected on 13 January 1986 (unknown collector); SAM 32611, adult male, 695 mm L_T, juvenile male, 285 mm L_T, off west coast, South Africa, 30.09º S; 16.69º E; 213 m depth, collected on 22 January 1990 by Sea Fisheries Research Institute; SAM 33150, adult female, 925 mm L_T, off west coast, South Africa, 35.26º S; 18.92º E; 232 m depth, collected on 7 January 1994 (unknown collector); SAM 33153, adult male, 750 mm L_T, off west coast, South Africa, 34.83º S; 18.40º E; 387 m depth, collected on 7 January 1994 (unknown collector); SAM 33154, two adult males, 730–740 mm L_T, off west coast, South Africa, 30.93º S; 16.61º E; 249 m depth, collected on 23 January 1994 (unknown collector); SAM 34004, adult male, 700 mm L_T, adult female, 740 mm L_T, off Saint Francis Bay, Eastern Cape, South Africa, 34.41º S; 25.91º E; 294 m depth, collected on 1 July 1994 (unknown collector); SAM 38042, juvenile male, 570 mm L_T, off

west coast, South Africa, 29.95° S; 15.11° E; 315 m depth, collected on 24 January 1990 during West Coast Hake Biomass Survey; SAM 38334, two juvenile males, 282–388 mm L_T, off Mozambique, 23.53° S; 35.85° E; unknown depth, collected on 20 June 1996 by L. J. V. Compagno; SAM 41904 (formerly SAM 33476), adult female, 750 mm L_T, near Agulhas Bank, Western Cape, South Africa, 36.21° S; 20.04° E; 201 meters depth, collected on 11 June 1994 during South Coast Biomass Survey.

Other material

SAIAB 21872, adult male, 507 mm L_T, off Jakkalsbaai, South Africa, 29.33° S; 14.96° E; SAIAB 25339, adult male, 515 mm L_T, off west coast, South Africa, 30.10° S; 14.76° E; SAIAB 25340, juvenile male, 440 mm L_T, off west coast, South Africa, 30.60° S; 15.41° E; SAIAB 25341, adult female, 680 mm L_T, off west coast, South Africa, 32.16° S; 16.86° E; SAIAB 25342, adult female, 621 mm L_T, off west coast, South Africa, 31.63° S; 16.34° E; SAIAB 26321, juvenile male, 425 mm L_T, off West coast, South Africa, 31.76° S; 16.46° E; SAIAB 26322, juvenile female, 450 mm L_T, off West coast, South Africa, 31.76° S; 16.46° E ; SAIAB 26418, juvenile female, 440 mm L_T, off west coast, South Africa, 30.66° S; 15.55° E; SAIAB 82057, juvenile male, 345 mm L_T, Mozambique, 23.53° S; 35.86° E; SAIAB 203801 (formerly SAIAB 186461), juvenile male, 392 mm L_T, off Durban, South Africa, 30.03° S; 31.30° E; SAIAB 188839, juvenile female, 223 mm L_T, Tugela Deep, Kwazulu-Natal, South Africa, 29.12° S, 31.75° E; SAM 33155, juvenile female, 400 mm L_T, adult male, 715 mm L_T, off west coast, South Africa, 29.83º S; 15.54º E; SAM 33197, adult male, 730 mm L_T, off west coast, South Africa, 30.39° S; 16.09° E; SAM 33283, juvenile

female, 390 mm L_T, off west coast, South Africa, 29.83° S; 15.54° E; SAM 36412, adult female, 745 mm L_T, off west coast, South Africa, 31.93º S; 16.38º E; SAM 38283, juvenile female, 416 mm L_T, off Tsitsikamma, Eastern Cape, South Africa, 34.78° S; 24.18° E; SAM 39883, adult female, 956 mm L_T, Kwazulu-Natal, South Africa; SAM 39885, adult female, 925 mm L_T, South Africa.

DIAGNOSIS.

A long-snouted spurdog species from southern Africa that is distinguished from other long-snouted species *S. montalbani*, *S. edmundsi*, *S. chloroculus*, *S. nasutus* and *S. grahami* by lacking the black caudal bar on postventral caudal margins *v*. evident in these species. It is distinct from the Japanese *S. mitsukurii* and the Mediterranean *S. blainvillei* by having body grey dorsally *v*. body dark grey to blackish dorsally in *S. mitsukurii* and body light reddish brown in *S. blainvillei*. Pelvic fins of *Squalus bassi* are located at the midline between the dorsal fins, while they are nearest second dorsal fin in *S. montalbani*, *S. chloroculus* and *S. edmundsi* and nearest to first dorsal fin in *S. blainvillei*. Origin of second dorsal fin is just posterior to the vertical line traced at pelvic-fin free rear tips in adults of *Squalus bassi v*. origin of second dorsal fin far behind the vertical line traced at pelvic-fin free rear tips in adults of *S. mitsukurii*, *S. blainvillei* and *S. lalannei*. *Squalus bassi* is distinct from *S. mitsukurii*, *S. montalbani* and *S. lalannei* by having a concave pectoral-fin posterior margin near its free rear tip *v*. pectoral-fin posterior margin straight in these three species.

Squalus bassi is distinct from *S. blainvillei* and *S. edmundsi* by head length, 22.4%–25.2% L_T *v*. 19.8%–22.3% L_T for *S. blainvillei* and 25.6% L_T for *S. edmundsi*. It can be further separated from *S. mitsukurii* by: shape of caudal fin, which exhibits a rectangular upper caudal lobe, caudal fork concave and dorsal and ventral caudal tips rounded *v*. subtriangular upper caudal lobe, caudal fork strongly raked and dorsal and ventral caudal tips conspicuously pointed in *S. mitsukurii* and more elongate eyes, their length 4.2%–6.2% L_T *v*. 3.5%–4.0% L_T in *S. mitsukurii*. *Squalus bassi* has more monospondylous and diplospondylous vertebrae than *S. blainvillei* (43–48, 69–75 for *S. bassi v*. 40–41, 67–68 for *S. blainvillei*). It has more precaudal vertebrae (86–89) than *S. blainvillei* (80–83), *S. montalbani* (84) and *S. lalannei* (67–69) and more total vertebrae (115–120) than *S. blainvillei* (107–109) and *S. lalannei* (93–95).

DESCRIPTION.

Measurements and meristic data are summarized in Tables I–III. Body fusiform and robust, arched dorsally from posterior margin of eyes to origin of first dorsal fin (Fig. 1); body with greatest width at head (head width 1.2, 1.0–1.3 times trunk width and 1.3, 1.2–1.7 times abdomen width) and deepest at trunk (head height 0.9, range 0.8–1.1 times trunk height and 0.9, range 0.8–1.2 times abdomen height). Head large, its length 22.4%, 22.4%–25.2% L_T, corresponding to 1.1 (range 1.0–1.3) times length of dorsal caudal margin. Snout obtuse and elongate (Fig. 1), its preorbital length 8.2%, range 7.6%–9.1% L_T; anterior margin of nostrils bilobed; prenarial length 0.5 (range 0.4–0.8) times pre-oral length and 1.2 (range 0.9–

1.7) times the distance from nostrils to upper labial furrow; internarial space 1.0 (range 0.8–1.1) times eye length. Eyes oval with anterior margin concave and posterior margin notched; eyes very large, their length 2.1 (range 2.1–3.7) times greater than their height. Prespiracular length 0.6 (range 0.5–0.7) times prepectoral length and 1.5 (range 1.6–1.8) times larger than preorbital length. Spiracles crescent and short, their length 0.3 (range 0.3–0.4) times eye length. Prebranchial length 1.5 (range 1.4–1.6) times greater than prespiracular length. Gill slits vertical, somewhat convex and tall with height of fifth gill slit 1.2 (range 0.9–1.3) times height of first gill slit.

Preoral length 1.3 (range 1.2–1.4) times greater than mouth width. Mouth arched and narrow, its width 1.5 (range 0.9–1.6) times prenarial length and 1.8 (range 1.6–1.9) times internarial space; upper labial furrow very elongate, its length 2.3% (range 2.1%–2.7%) L_T with thin fold; lower labial furrow larger than upper one, lacking the fold. Teeth similar in both jaws, upper teeth smaller than lower teeth (Fig. 2); teeth unicuspid with cusp thick, short and oblique; mesial cutting edge straight; mesial heel rounded on lower jaw and notched on upper jaw; distal heel notched; apron conspicuously short and slender. Upper jaw with three series of functional teeth and two series on lower jaw in holotype. Upper teeth in holotype in 13–13 rows (13–13 in paratypes) and 11–12 (10–10) rows on lower jaw (Table II).

Pre-first dorsal length 31.6% (range 28.4%–33.2%) L_T, corresponding to 1.4 (range 1.2–1.5) times greater than prepectoral length; origin of first dorsal fin prior to vertical traced at pectoral-fin free rear tips. First dorsal fin broad at fin web with anterior margin convex and posterior margin straight, although concave distally near its free rear tip (Fig. 3); first dorsal-fin apex markedly rounded and free rear tip pointed; first dorsal fin elongate, its length 1.8

(range 1.5–1.9) times greater than its height; first dorsal-fin base length corresponding to 0.9 (range 0.8–1.2) times preorbital length and 1.0 (range 0.8–1.1) times first dorsal-fin height; first dorsal fin oblique and moderately low, its height 0.9 (range 0.8–1.2) times pre-orbital length and 1.2 (range 0.8–1.8) times length of first dorsal-fin inner margin. First dorsal-fin spine thick, its base width 0.7% (range 0.5%–1.0%) L_T and small, its length 3.7% (range 2.5%–4.8%) L_T, not reaching apex of first dorsal fin; length of first dorsal-fin spine 0.5 (range 0.3–0.6) times first dorsal-fin height. First dorsal fin 1.0 (range 1.0–1.3) times greater in length than second dorsal fin.

Interdorsal space 1.1 (range 0.9–1.2) times prepectoral length and 2.3 (range 1.9–2.7) times greater than dorsal-caudal space. Pre-second dorsal length 2.7 (range 2.6–2.9) times greater than prepectoral length and 2.8 (range 2.7–3.3) times greater than length of dorsal caudal margin. Origin of second dorsal fin located just behind vertical traced at pelvic-fin free rear tips. Second dorsal fin raked with anterior margin convex and posterior margin falcate (Fig. 3); second dorsal-fin apex rounded and lobe-like and free rear tip pointed; second dorsal fin large, its length 2.3 (range 1.8–2.5) times greater than its height; second dorsal-fin base length corresponding to 1.3 (range 0.9–1.6) times second dorsal-fin height and 0.8 (range 0.6–0.9) times dorsal caudal space; second dorsal fin oblique and low, its height 1.1 (range 0.9–1.3) times second dorsal-fin inner margin length. Second dorsal-fin spine heavy and elongate, its length 0.8 (range 0.6–0.9) times height of second dorsal fin, not reaching apex of second dorsal fin; second dorsal-fin spine 1.3 (range 0.8–2.0) times greater in length than first dorsal spine.

Pectoral fins elongate (anterior margin length 15.4%, range 14.6%–18.2% L_T) and narrow (posterior margin length 10.2%, range 9.3%–12.6% L_T); pectoral-fin anterior and inner margins convex; pectoral-fin posterior margin straight, although somewhat concave near pectoral-fin free rear tip; pectoral-fin free rear tips rounded and apex broadly rounded (Fig. 1); pectoral-fin anterior margin 1.7 (range 1.3–1.9) times greater in length than pectoral-fin inner margin and 1.5 (range 1.3–1.6) times larger than length of pectoral-fin posterior margin; pectoral-fin posterior margin rarely transcending trunk height when adpressed on body, its length 0.9 (range 0.8–1.3) times trunk height. Pectoral-pelvic distance 0.8 (range 0.7–1.1) times pelvic-caudal space. Pelvic fins subtriangular and narrow with anterior and posterior margins straight; pelvic-fin free rear tips rounded in females and weakly pointed in males; pelvic fins moderately large, their length 11.7% (range 10.6%–13.0%) L_T; pelvic fins placed at midline between dorsal fins. Claspers elongate, their inner length 8.4% (range 2.6%–8.1%) L_T, corresponding to 1.3 (range 0.4–1.5) times length of pelvic-fin inner margin; clasper groove dorsal; apopyle broad, anterior in clasper groove; hypopyle very constricted, distal in clasper groove; rhipidion flap-like, very slender and elongate, posteriorly positioned on clasper (Fig. 4).

Upper and lower precaudal pits prominent; caudal keel short, lateral on caudal penduncle. Caudal fin rather rectangular at upper caudal lobe with dorsal caudal margin straight, upper postventral caudal margin almost straight, although convex distally near dorsal caudal tip [Fig. 5(a),(b)]; lower postventral caudal margin convex; preventral caudal margin markedly convex; dorsal and ventral caudal tips rounded; length of dorsal caudal margin 0.9 (range 0.8–1.0) times head length and 1.9 (range 1.6–1.9) times greater than length of

preventral caudal margin; preventral caudal margin short, its length 1.7 (range 1.7–2.8) times length of pelvic-fin inner margin; caudal fork discontinuous, markedly concave and very broad, its width 6.8% (range 6.6%–7.9%) L_T.

Dermal denticles

[Fig. 6(a),(b)].

Dermal denticles tricuspid and rhomboid, weakly imbricate and broad at crown, their length almost equal to their width; cusps posteriorly pointed and very elongate (conspicuously slender in juveniles); lateral cusps forming posterior concavity with median cusp on each side (more prominent in juveniles); median ridge large and thick with anterior furrow wide and profound (small and shallow in juveniles); anterior margin of median ridge weakly arrow-shaped (conspicuously narrow and concave in juveniles specimens); lateral ridges markedly thin, straight and short.

Colouration.

Body dark grey to brownish grey dorsally and pale ventrally and laterally from insertion of pelvic fins to caudal fin [Fig. 1(a)]. First dorsal fin mostly dark brown, but light brown distally at posterior margin; first dorsal-fin base whitish [Fig. 3(a)]. Second dorsal fin brown, slightly darker at tip, whitish at base [Fig. 3(b)]. First and second dorsal-fin spines brown, darker anteriorly and whitish at tip. Pectoral fins dark brown, somewhat white at posterior margin; ventral base of pectoral fin pale [Fig. 1(c)]. Pelvic fins brown dorsally and pale ventrally. Caudal fin dark brown, whitish over vertebral column; dorsal caudal margin

proximally white; postventral caudal margins white, except at caudal fork; dorsal and ventral caudal tips broadly white; black caudal stripe evident [Fig. 5(b)]. Juveniles differ from adults by having: body brown (light brown in neonates), although darker dorsally from insertion of first dorsal fin to caudal fin [Fig. 1(b)]. dorsal fins brown with their apices blackish; caudal fin brown (mostly white in neonates) with postventral caudal margin broadly white. Neonates and very young juveniles also have dorsal fins light brown and markedly black at apices; two black, rounded and large upper caudal fin blotches; lower caudal lobe mostly white with very elongate blackish basal marking [Fig. 5(a)].

VERTEBRAL COUNTS

Monospondylous vertebrae 45 in holotype, 43–47 in paratypes (mode 46); displospondylous vertebrae 75, 69–75 (mode 70); precaudal vertebrae 89, 86–89 (mode 87); total vertebrae 120, 115–120 (mode 116). For non-type specimens, it varies from 46–48 monospondylous vertebrae, 67–69 for diplospondylous vertebrae, 86–87 precaudal vertebrae and 115–118 total vertebrae (Table III).

GEOGRAPHICAL DISTRIBUTION

Squalus bassi occurs in the south-eastern Atlantic and western Indian Oceans from southwards along the Western Cape, South Africa and extending to Mozambique (Fig. 7).

ETYMOLOGY

The species is named after Alan John Bass, former shark specialist from the Oceanographic Research Institute in Durban, for his valuable contributions to the taxonomy of elasmobranch fishes from southern Africa.

ECOLOGICAL NOTES

Squalus bassi is abundant in the Western Cape waters of South Africa from north-west Cape Town to Cape Agulhas, mostly between 29°–32° S (Compagno *et al*., 1991). A few occurrences are observed in the Indian Ocean from St. Francis Bay in the Eastern Cape, South Africa, to the coast of Mozambique. This species possibly occurs northwest of the Orange River in Namibia, according to the F.R.S *Africana* survey data provided by Compagno *et al*. (1991), although this was not corroborated in the present study. It is often caught on the outer shelf or upper continental slope between 159–591 m depth with a mean depth of 300 m, representing the greatest depth for a species of *Squalus* from southern Africa according to Compagno *et al*. (1991).

Squalus bassi grow to a maximum total length of 1100 mm for females and 960 mm for males. Minimum size at maturity is *c.* 730 mm and 650 mm for females and males, respectively. Females have between 4–9 pups per litter. Size at birth is *c.* 210–300 mm, with the smallest free-swimming neonates measuring 230–235 mm L_T. The species is a voracious feeder on bony fishes, cephalopods and crustaceans (Ebert *et al*., 1992). Previous studies (Ebert *et al*., 1992) on ecological traits of this species may have included specimens from

other *Squalus* species from southern Africa in the analysis. Further studies are required for better understanding of patterns of phylogeography and migration as well as feeding and reproductive ecology. Additionally, these studies are valuable for comparisons with other *S. mitsukurii* forms that have been recognized elsewhere and may be distinct from both *S. bassi* and the Japanese *S. mitsukurii*.

COMPARATIVE MATERIAL EXAMINED

Squalus blainvillei

BMNH 1866.5.28.1, adult male, 480 mm L_T, France, Mediterranean Sea; BMNH 1963.5.14.19-22, juvenile male, 270 mm L_T, three juvenile females, 285–315 mm L_T, France, Mediterranean Sea; BMNH 2013.9.3.6, adult female, 540 mm L_T, Lisbon, Portugal; NMW 50125, adult male, 530 mm L_T, Palermo, Italy; NMW 83939, two juvenile males, 260–416 mm L_T, neonate female, 243 mm L_T, Dalmatia, Croatia; NMW 84901, juvenile female, 495 mm L_T, Trieste, Italy; NMW 85503, adult male, 560 mm L_T, Europe; RMNH.PISC. 4187, juvenile male, 352 mm L_T, Dalmatia, Croatia; RMNH.PISC. 34092, neonate male, 245 mm L_T, three neonate females, 230–252 mm L_T, Banyuls, France; ZMA 113.606, juvenile male, 385 mm L_T, Cádiz, Spain.

Squalus chloroculus

CSIRO H 2867-03 (paratype of *S. chloroculus*), adult male, 678 mm L_T, Great Australian Bight, Southern Australia; CSIRO H 4775-01 (holotype of *S. chloroculus*), adult

male, 752 mm L_T, off Portland, Victoria, Australia; CSIRO H 5941-01 (paratype of *S. chloroculus*), adult male, 760 mm L_T, West of Cape Sorell, Tasmania, Australia.

Squalus edmundsi

AMS I 31165-003, juvenile female, 468 mm L_T, juvenile male, 435 mm L_T, off Shark Bay, Western Australia; CSIRO H 2014-1, adult male, 595 mm L_T, North of Abrolhos Islands, Western Australia; CSIRO H 2264-3, adult male, 604 mm L_T, West of Geraldton, Western Australia; CSIRO H 2566-01 (holotype of *S. edmundsi*), adult male, 610 mm L_T, West of Bernier Island, Western Australia; CSIRO H 2599-01 (paratype of *S. edmundsi*), adult male, 581 mm L_T, west of Green Head, Western Australia; CSIRO H 2605-07 (paratype of *S. edmundsi*), juvenile female, 510 mm L_T, north-west of Rottnest Island, Western Australia; CSIRO H 2608-16 (paratype of *S. edmundsi*), adult female, 737 mm L_T, Rottenest Canyon, Western Australia; CSIRO H 2619-10, adult female, 665 mm L_T, west of Bunbury, Western Australia.

Squalus graham

CSIRO H 1311-3 (paratype of *S. grahami*), adult female, 652 mm L_T, east of Whitsunday Group, Queensland, Australia; CSIRO H 1347-1 (paratype of *S. grahami*), juvenile female, 371 mm L_T, east of Flinders Reef, Queensland, Australia; CSIRO H 4476-01 (holotype of *S. grahami*), adult male, 602 mm L_T, north-east of Batemans Bay, New South Wales; CSIRO H 4682-03 (paratype of *S. grahami*), adult female, 697 mm L_T, east of Broken Bay, New South Wales, Australia.

Squalus lalannei

HUJ 18445 (holotype of *S. lalannei*), adult female, 788 mm L_T, Alphonse Island, Seychelles.

Squalus lobularis

HUMZ 91806 (holotype of *S. lobularis*), juvenile female, 557 mm L_T, off Patagonia, Argentina; FURG 80.0609, adult male, 630 mm L_T, south of Mar del Plata, Argentina; MZUSP 37355, two juvenile female, 335–340 mm L_T; three juvenile male, 335–360 mm L_T, Uruguay; UERJ 1112, adult male, 635 mm L_T, Rio Grande do Sul, Brazil; ZMH 104558, adult male, 600 mm L_T, Argentina; ZMH 107897, adult male, 605 mm L_T, Argentina.

Squalus mitsukurii

SU 12793 (holotype of *S. mitsukurii*), adult female, 710 mm L_T, Honshu Island, Misaki, Japan; SU 12794 (paratype of *S. mitsukurii*), adult male, 770 mm L_T, locality same as SU 12793; SU 7748 (paratypes of *S. mitsukurii*), two neonate females, 240–243 mm L_T, neonate male, 247 mm L_T, same as SU 12793; AMNH 8822 (paratype of *S. mitsukurii*), neonate female, 248 mm L_T, same as SU 12793; HUMZ 33680, adult female, 760 mm L_T, East China Sea; HUMZ 89858, adult female, 705 mm L_T, off Hachijo-jima Island, Tokyo, Japan; HUMZ 102987, adult female, 970 mm L_T, central Pacific Ocean, near northern Mariana Islands; HUMZ 113587, adult female, 990 mm L_T, off Shirahama, Shimoda, Shizuoka Prefecture, Japan; NSMT-P 44097, juvenile female, 740 mm L_T, unknown locality, southern Japan;

NSMT-P 44381, adult male, 770 mm L_T, unknown locality, southern Japan; NSMT-P 72728, two juvenile females, 414–420 mm L_T, four adult females, 700–840 mm L_T, Japan; ZUMT 21114, neonate female, 190 mm L_T, Nagasaki.

Squalus montalbani

AMS I 45654-001, adult female, 840 mm L_T, Recorder Seamount, Queensland, Australia; CSIRO H 2564-25, juvenile male, 325 mm L_T, West of Bernier Island, Western Australia; CSIRO H 2566-04, juvenile male, 415 mm L_T, west of Bernier Island, Western Australia; CSIRO H 2606-02, juvenile female, 550 mm L_T, west of Rottnest Island, Western Australia; CSIRO H 2606-06, adult male, 575 mm L_T, west of Rottnest Island, Western Australia; CSIRO H 2609-07, adult male, 620 mm L_T, west of Rottnest Island, Western Australia; CSIRO H 4623-02, juvenile female, 482 mm L_T, east of Terrigal, New South Wales, Australia; MZUSP 121270 (formerly CSIRO uncatalogued), adult male, 713 mm L_T, east of Ballina, New South Wales, Australia; USNM 70256 (holotype of *S. philippinus* Smith & Radcliffe, 1912), juvenile male, 311 mm L_T, off Sombrero Island, west coast of Luzon Island, Philippines; WAM P 28111-002, neonate female, 202 mm L_T, Rowley Shoals, Western Australia.

Squalus nasutus

CSIRO H 1652-1 (paratype of *S. nasutus*), juvenile female, 316 mm L_T, north-west of Port Hedland, Western Australia; CSIRO H 2567-08 (paratype of *S. nasutus*), adult male, 467

mm L_T, west of Dorre Island, Western Australia; CSIRO H 2590-12 (holotype of *S. nasutus*), adult female, 503 mm L_T, west of Leander Point, Western Australia.

Squalus Quasimodo

MZUSP 118707 (holotype of *S. quasimodo*), adult female, 700 mm L_T, off the coast of Rio Grande do Sul, Brazil; UERJ 1741(paratype of *S. quasimodo*), adult female, 850 mm L_T, Brazil; UERJ 1819 (paratype of *S. quasimodo*), adult female, 740 mm L_T, Brazil; MCP 773 (paratype of *S. quasimodo*), juvenile female, 660 mm L_T, between coast of Rio Grande do Sul state, Brazil and Uruguay.

DISCUSSION

The long-snouted African spurdog *S. bassi* shares with *S. mitsukurii, S. montalbani, S. chloroculus, S. grahami*, *S. griffini, S. edmundsi*, *S. quasimodo* and *S. lobularis* (Fig. 8) an elongate snout with its prenarial length greater than distance between nostril and upper labial furrow and dermal denticles conspicuously tricuspidate and rhomboid. Except for *S. lalannei*, these species also share high number of vertebrae, although vertebral counts coincide among *S. bassi*, *S. mitsukurii*, *S. edmundsi*, *S. lobularis* and *S. quasimodo* (Table III). External measurements (Tables I and IV) overlap extensively as well (*e.g.* between *S. bassi*, *S. mitsukurii*, *S. lobularis* and *S. quasimodo*), even when only adult specimens are considered in the case of *S. bassi*, *S. mitsukurii* and *S. montalbani*. These results go against those of Viana *et al*. (2016, 2017) for separating *Squalus* spp. of similar morphology, as the above-listed

species, when considering stage of maturity for morphometric comparisons. *Squalus bassi* lacks a black caudal bar, a characteristic often addressed to species of the *S. mitsukurii* group. Due to this, we do not presently insert this species into a group or species complex of *Squalus*.

Squalus bassi is distinguished from these species by a combination of characters of external morphology along with meristics and morphometrics as provided in the diagnosis above, which is in agreement with Last *et al*. (2007*c*) for species described from the south-western Pacific Ocean and recent results of Viana & Carvalho (2016) and Viana *et al*. (2016, 2017) for those from the South Atlantic and western Indian Oceans. This species differs from similar congeners regarding body and caudal fin colouration, concavity of pectoral-fin posterior margin and location of second dorsal fin related to pelvic fins, highlighting the morphological complexity on providing exclusive diagnostic characters for *S. bassi*. Autapomorphic characters are unusual within *Squalus*, with few exceptions such as black marking on dorsal fins of *S. cubensis* in Howell-Rivero (1936) and whitish eyebrow of the eastern highfin spurdog *Squalus albifrons* Last, White & Stevens 2007 in Last *et al*. (2007*d*). Dorsal-fin spines width of the fatspine spurdog *Squalus crassispinus* Last, Edmunds & Yearsley 2007 in Last *et al.* (2007*e*) and head width of the bighead spurdog *Squalus bucephalus* Last, Sèret & Pogonoski 2007 in Last *et al*. (2007*f*) are current examples. Vertebral counts alone were noticed in Baranes (2003) for *S. lalannei* and White *et al*. (2007*b*) for the Indonesian shortsnout spurdog *Squalus hemipinnis* White, Last & Yearsley 2007 as diagnostic. Differences on number of vertebrae are observed for *S. bassi*, *S. lalannei* and *S. montalbani*.

Morphometric discrepancies are clearly noticed between *S. bassi* and *S. edmundsi*, regarding, respectively: prebranchial length (19.3%–21.3% *v*. 21.7% L_T); dorsal-caudal space (9.2%–11.8% *v*. 9.1% L_T); length of dorsal-fin spines (first dorsal-fin spine length 2.5%–4.8% L_T for *S. bassi v*. 5.5% L_T for *S. edmundsi*; second dorsal-fin spine length 3.2%–5.5% L_T for *S. bassi v*. 6.1 % L_T for *S. edmundsi*); length of pectoral fins (pectoral-fin inner margin length 8.5%–11.1% L_T for *S. bassi v*. 8.2 % L_T for *S. edmundsi*). *Squalus bassi* is also distinct from *S. edmundsi* by prone and smaller dorsal fins with length of first dorsal-fin posterior margin 7.2%–9.8% L_T *v*. upright and large dorsal fins, 10.0% L_T first dorsal-fin posterior margin for *S. edmundsi*. *Squalus bassi* is separated from *S. lobularis* by having body grey to brownish grey dorsally and clasper groove elongate *v*. body dark grey to blackish dorsally and clasper groove short in *S. lobularis* and from *S. quasimodo* by having body slightly arched dorsally and second dorsal fin low and oblique *v*. body markedly humped dorsally and second dorsal fin tall and upright in *S. lobularis*.

Investigations on the taxonomy of *Squalus* spp. demonstrated that *S. mitsukurii* might represent a species complex with different forms warranting recognition outside of Japan (Bigelow & Schroeder, 1957; Ward *et al*., 2005; Last *et al*., 2007*c*; Ebert *et al*., 2013; Veríssimo *et al*., 2017). *Squalus chloroculus*, *S. edmundsi* and *S. grahami* are examples of species previously identified as *S. mitsukurii* and described as new from the South Pacific Ocean and discovered to be distinct from *S. mitsukurii* through combined molecular and morphological data (Last *et al*., 2007*a*; Ward *et al*., 2007; White *et al*., 2007*a*). The resurrections of *S. montalbani* and the northern spiny dogfish *Squalus griffini* Phillipps 1931 from Philippine and New Zealand waters in Last *et al*. (2007*a*) and Duffy & Last (2007,

2015), respectively, are further examples. More recently, three new species of the genus in the south-western Atlantic Ocean were described as morphologically distinct from *S. mitsukurii* (Viana *et al*., 2016): *S. quasimodo*, *S. lobularis* and the north-eastern Brazilian dogfish *Squalus bahiensis* Viana, Carvalho & Gomes 2016. The results provided herein are in congruence with these recent findings and in agreement with Compagno *et al*. (1991), Naylor *et al*. (2012), Pickering & Caira (2012) and Veríssimo *et al*. (2017) who noticed the African form as a potentially new species separate from *S. mitsukurii* and with Veríssimo *et al*. (2017) that recognized genetic differentiation with south-western Atlantic Ocean species. Examination of photo vouchers of a specimen collected in the eastern coast of South Africa, AF-100 (JQ518980) [collection data available in Caira *et al*. (2016) at the Global Cestode Database], identified as *Squalus cf. mitsukurii* revealed to be conspecific with *S. bassi*. Naylor *et al*. (2012) and Veríssimo *et al*. (2017) included this specimen in their molecular investigation, which gives additional support in recognizing *S. bassi* as a valid and distinct species. Furthermore the results underline the hypothesis that *S. mitsukurii* is likely to be more restricted to the North Pacific Ocean rather than a cosmopolitan species as proposed in Viana *et al*. (2016) and Veríssimo *et al*. (2017). Other *Squalus* spp. that used to be recognized as of worldwide distribution have revealed to be more restricted to a particular region, including the shortnose spurdog *Squalus megalops* (Macleay 1881) (Last *et al*., 2007*c*; Naylor *et al*., 2012; Viana & Carvalho, 2016; Veríssimo *et al*., 2017; Viana *et al*. 2016, 2017) and *S. blainvillei* (Veríssimo *et al*. 2017; Viana *et al*. 2016, 2017). Joint efforts are imperative to corroborate this assumption and for clarifying the taxonomic status of *S. mitsukurii* by

comparative examination of topotypic specimens and remaining similar forms recognized elsewhere, including those from Gulf of Mexico, Uruguay and Hawaii.

Squalus blainvillei is another synonym often applied to *S. bassi* (Bass *et al*. 1976). The Mediterranean species is characterized by having a short snout, high dorsal fins, elongate dorsal-fin spines and low vertebral counts as also noticed in Viana *et al*. (2017), which are not congruent with the characteristics of *S. bassi*. Morphometrics reveal to be highly distinct between *S. bassi* and topotypic specimens of *S. blainvillei*. The former species is separated from the latter by larger pre-vent length 47.3%–52.4% *v*. 43.8%–46.9% L_T, more elongate snout, its prenarial length 5.0%–9.4% *v*. 3.9%–4.8% L_T, broader internarial space, its width 4.2%–4.9% *v*. 3.1%–4.1% L_T and dermal denticles tricuspid and rhomboid *v*. unicuspid and lanceolate. When compared with adults of *S. blainvillei*, morphometric differences include prepelvic length (43.9%–50.3% L_T for *S. bassi v*. 41.1%–43.7% L_T for *S. blainvillei*), prepectoral length (21.6%–24.1% L_T for *S. bassi v*. 19.0%–20.6% L_T for *S. blainvillei*), prebranchial length (19.3%–20.9% L_T for *S. bassi v*. 17.0%–18.4% L_T for *S. blainvillei*), prespiracular length (12.5%–13.3% L_T for *S. bassi v*. 11.2%–12.3% L_T for *S. blainvillei*), pre-orbital length (7.6%–8.4% L_T for *S. bassi v*. 6.3%–7.1% L_T for *S. blainvillei*), interdorsal space (23.3%–25.7% L_T for *S. bassi v*. 22.0%–22.7% L_T for *S. blainvillei*) and pectoral-pelvic distance (19.9%–25.1% L_T for *S. bassi v*. 17.9%–19.5% L_T for *S. blainvillei*). It is further easily separated from adults of *S. blainvillei* by having a shorter second dorsal-fin spine, its length 3.2%–4.9% L_T in adults (*v*. 6.3%–7.3% L_T for *S. blainvillei*). *Squalus blainvillei* may exhibit a more restricted geographical distribution (*i.e*. north-eastern Atlantic Ocean). These results highlight the confused morphological characterization of *S. blainvillei* as reported in

the literature in Chen *et al*. (1979) and Muñoz-Chápuli & Ramos (1986), in Veríssimo *et al*. (2017) through molecular comparative analysis among specimens from the eastern Atlantic Ocean and the Mediterranean Sea and Viana *et al*. (2017) using morphological evidence. This species is under morphological investigation and its taxonomic clarification requires scrutiny of other available nominal species [*e.g*. little gulper shark *Centrophorus uyato* (Rafinesque 1810); Angolan dogfish *S. probatovi* Myagkov & Kondyurin 1986] as they are possible synonyms. *Squalus probatovi* was described as distinct from *S. blainvillei* and distributed in the south-eastern Atlantic and western Indian Oceans. Subsequent authors considered *S. probatovi* as a *nomen dubium* (Muñoz-Chápuli & Ramos, 1989; Compagno *et al*., 1991) or synonym of either *S. acutipinnis* (Ebert & Van Hees, 2015) or *S. megalops* (Compagno *et al*., 1991; Weigmann, 2016), but this synonymy was refuted in Viana *et al*. (2017). *Squalus probatovi* is characterized by having a bluish grey body with prenarial length less than internarial space (Myagkov & Kondyurin, 1986), characters which clearly separate it from *S. bassi* that has a brownish grey body and prenarial length conspicuously greater than internarial space.

Species of *Squalus* in southern Africa are updated herein to include *S. acanthias*, *S. acutipinnis*, *S. bassi*, *Squalus cf. blainvillei*, *S. mahia* and *S. margaretsmithae*. *Squalus bassi* is clearly separated from *S. acanthias* by lacking white spots on dorsolateral body, by having bilobate nostrils and origin of first dorsal fin anterior to the vertical line traced at pectoral-fin free rear tips *v*. white dorsolateral spots, unilobate nostrils and origin of first dorsal fin behind vertical line traced at pectoral-fin free rear tips in *S. acanthias*. It is differentiated from *S. acutipinnis*, *S. mahia* and *S. margaretsmithae* by having a prenarial length greater than

distance from nostrils to upper labial furrows, tricuspidate dermal denticles and higher number of vertebrae (*v*. prenarial length smaller than distance from nostrils to upper labial furrows, unicuspid dermal denticles and lower number of vertebrae in *S. acutipinnis*, *S. mahia* and *S. margaretsmithae*). Species delineation in African waters through DNA barcode is so far limited to *S. bassi* and *S. acutipinnis* from which genetic fragments have been taken. Sampling efforts to include their regional congeners are imperative to elucidate the taxonomic complexity behind the genus *Squalus*.

The authors would like to thank O. Gon, R. Bills, P. Cowley, A. Whitfield and their staff (SAIAB), D. Clark, M. Bougaardt and A. Bosman (SAM), M. Stiassny and R. Schelly (AMNH), M. McGrouther (AMS), L. Rocha, D. Catania and J. Fong (CAS), P. R. Last, W. T. White, A. Graham and J. Pogonoski (CSIRO), R. Leslie (DAFF), T. Kawai (HUMZ), C. A. de Lucena, Z. M. de Lucena and R. Reis (MCP), K. Hartel and A. Williston (MCZ), J. Maclaine (NHM), A. Palandacic (NMW), M. Nakae (NSMT), A. Datovo and M. Gianeti (MZUSP), R. de Ruiter (RMNH), U. L. Gomes and H. Ricardo (UERJ), M. Bemvenuti and C. Vooren (UFRGS), J. Williams and S. Raredon (USNM), S. Morrison (WAM), R. Thiel and I. Eidus (ZMH) and K. Sakamoto (ZUMT) for their technical assistance with specimens

and museum facilities. Special thanks to N. Mazungula (SAIAB) for taking radiographs of type specimens and to J. N. Caira (UCONN) and K. Jensen (KU) for sending photo vouchers for examination.. The first author was supported by the Fundação de Amparo a Pesquisa do Estado de São Paulo (FAPESP) under grants 2011/18861-7, 2014/26503-1, Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) under grant 158773/2011-0 and by Geddes Collection Visiting Fellowship (2013) of the Australian Museum (Sydney). The second author was supported by a grant from CNPq (305271/2015-6). The third author was provided funding supported by NOAA/NMFS to the Pacific Shark Research Center, Moss Landing Marine Laboratories, David and Lucile Packard Foundation and the South African Institute for Aquatic Biodiversity.

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Manuscript Number	MS 17-045
All Authors	Sarah T. de F. L. Viana, PhD; Marcelo R. de Carvalho, PhD; David A Ebert, PhD
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Running head	SQUALUS BASSI SP. NOV. FROM THE AGULHAS BANK
Number of Color Figures	6
Number of B&W Figures	1
Number of Line Figures	1
Initial Date Submitted	24/01/2017
Accepted	08/04/2017
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