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Research Article

Squalus longispinis, a new species of spurdog (Elasmobranchii: Squalidae) from La Réunion, southwestern Indian Ocean

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Abstract

A new species of spurdog, *Squalus longispinis* n. sp., from La Réunion is described on the basis of a single specimen collected with a longline at 1,000 m depth; another specimen was observed but not collected in the same area at 900 m depth. The new species is diagnosed by the following characters: snout short, preorbital length 8.2% of total length (TL), prenarial length in inner nostril-narial furrow space 0.86; body very high, abdomen height 16.4% of TL, head height in trunk height 0.5; dorsal fin beginning on a vertical above posterior lobes of pectoral fin; second dorsal fin positioned in the middle between anal fin and caudal fin; first and second dorsal-fin spines long, first dorsal-fin spine 5.8% of TL, second-dorsal fin spine 5.3% of TL; flank denticles tricuspid; monospondylous vertebrae 37, precaudal vertebrae 86, caudal vertebrae 26, total vertebrae 112; upper caudal-fin lobe broad; caudal fin distally with a narrow, light grey margin. The new species is compared with other species in the genus. A key to the species of *Squalus* of the Indian Ocean is presented.

Keywords: Spurdogs, new species; Mascarenes, geographical distribution, identification key
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Introduction

The dogsharks or spurdogs of the family Squalidae comprise a group of elasmobranchs that have been known since the Cretaceous (Cappetta, 2012); they are now living in cold temperate through tropical waters of the world oceans, benthopelagic, on continental and insular shelves and slopes, from shallow waters to more than 1,000 m depth. Currently, a total of 40 species in 2 genera (*Cirrhigaleus* Tanaka 1912 and *Squalus* Linnaeus 1758) are known in the family (Fricke et al., 2022a). In addition, there were four extinct genera: †*Centrophoroides* Davis 1887, †*Centrosqualus* Signeux 1950, †*Megasqualus* Herman 1982, and †*Protosqualus* Cappetta 1977 (Cappetta, 2012). The family is characterized by having both dorsal fins with spines and spines not grooved; teeth on lower jaw not much larger than those on upper jaw; upper precaudal pit

usually present; and a caudal peduncle with a pair of lateral keels (Nelson et al., 2016).

The genus *Squalus* was originally described by Linnaeus (1758: 233), based on *Squalus acanthias* Linnaeus 1758 (type by subsequent designation of Gill 1862: 369). *Acanthias* Leach 1818 (Leach, 1818: 62) is a junior synonym, based on the same type species. Bigelow & Schroeder (1948: 452) redefined the genus as having the following combination of characters: well developed dorsal spines without lateral grooves ... ; a labial furrow on each jaw and a voluminous pit at corner of mouth; upper and lower teeth alike, with 1 cusp, deeply notched outwardly, and so oblique that their inner margins form a nearly continuous cutting edge; ... nostrils far from mouth, without barbels; ... caudal without subterminal notch, its lower anterior corner expanded as a definite lobe, but much shorter than the upper lobe and much smaller in area; luminous organs lacking. The genus currently includes 37 valid species (Table 1). In addition, 14 fossil species are known in the genus (Cappetta, 2012; Pollerspöck et al., 2021): *S. abaticus* Andreae 1892 from the Oligocene of eastern France, *S. almeidae* Antunes & Jonet 1970 from the Miocene of Portugal and southern France, *S. argentinensis* (Bogan et al., 2016) from the Maastrichian (Cretaceous) of Argentina, *S. balingsloevensis* Siverson 1993 from the Maastrichian (Cretaceous) of Sweden and North Dakota (U.S.A.), *S. balsvikensis* Siverson 1993 from the Maastrichian (Cretaceous) of Sweden, *S. chiconis* (Jordan 1907) from the Maastrichian (Cretaceous) of California (U.S.A.), *S. crenatidens* Arambourg 1952 from the Paleocene of Morocco, *S. gabrielsoni* Siverson 1993 from the Maastrichian (Cretaceous) of Denmark and Sweden, *S. huntensis* Case & Cappetta 1997 from the Maastrichian (Cretaceous) of North Carolina and Texas (U.S.A.), *S. minor* (Daimeries 1888) from the Paleocene of Belgium and the Eocene of England (U.K.), *S. nicholsae* Cappetta, Morrison & Adnet 2019 from the Campanian (Cretaceous) of British Columbia (Canada), *S. serriculus* Jordan & Hannibal 1923 from the Miocene of California (U.S.A.), *S. vondermarcki* Müller & Schöllmann 1989 from the Cretaceous of Germany, Angola and Canada, *S. worlandensis* (Case 1987) from the Campanian (Cretaceous) of Alberta (Canada) and Wyoming (U.S.A.).

The recent species of *Squalus* may be arranged in three species groups (Compagno et al., 2005; Ebert et al., 2010; Viana et al., 2016): A *Squalus-acanthias* group (with the following combination of characters: 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); B *Squalus-mitsukurii* group (with the following combination of characters: 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; usually 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); C *Squalus-megalops* group (with the following combination of characters: 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 usually smaller than inner nostril-labial furrow space; pectoral fins with pointed free rear tips and strongly concave posterior margin; often unicuspid dermal denticles). Group A includes the two species *Squalus acanthias* and *S. suckleyi*; group B comprises a total of 19 species, *S. bahiensis, S. bassi, S. blainville, S. boretzi, S. chloroculus, S. clarkae, S. crassispinus, S. edmundsi, S. grahami, S. griffini, S. hawaiiensis, S. japonicus, S. lobularis, S. melanurus, S. mitsukurii, S. montalbani, S. nasutus, S. quasimodo,* and *S. shiraii*; group C includes 16 species, *S. acutipinnis, S. albicaudus, S. albifrons, S. altipinnis, S. brevirostris, S. bucephalus, S. cubensis, S. formosus, S. hemipinnis, S. lalannei, S. mahia, S. margaretsmithae, S. megalops, S. notocaudatus, S. probatovi,* and *S. raoulensis*.

A group of short-snouted and high-bodied species in the genus *Squalus* includes *S. acutipinnis* Regan 1908 (Regan 1908: 248, pl. 37) from the southwestern Indian Ocean; *S. crassispinus* Last, Edmunds & Yearsley 2007 (Last et al., 2007e: 11, figs. 1-4) from Australia and Papua New Guinea; *S. lalannei* Baranes 2003 (Baranes 2003: 42, figs. 6-7, 8A, 9A, 10-12) from the Seychelles; *S. megalops* (Macleay 1881) (Macleay 1881: 367 as *Acanthias megalops*) from the Atlantic and Indo-West Pacific; *S. quasimodo* Viana, Carvalho & Gomes 2016 (Viana et al., 2016: 58, figs. 35-40) from the western Atlantic; *S. shiraii* Viana & Carvalho 2020 (Viana & Carvalho 2020: 277, figs. 1, 3A-B, 7A-B) from the Okinawa Trough, northwestern Pacific.

This group represents high-bodied species of both the *Squalus-megalops* group and the *Squalus-mitsukurii* group (Viana et al., 2016).

In the course of a study of deep-water fishes of La Réunion (Objectif 1000), a previously undescribed species of *Squalus* was discovered. The new species is described in the present paper.

Table 1. Valid species in genus *Squalus* Linnaeus 1758 and their occurrence in the Indian Ocean. Species groups: A) *Squalus-acanthias* group; B) *Squalus-mitsukurii* group; C) *Squalus-megalops* group.

Species	Indian Ocean	Group
Squalus acanthias Linnaeus 1758	+	A
Squalus acutipinnis Regan 1908	+	C
Squalus albicaudus Viana, Carvalho & Gomes 2016		C
Squalus albifrons Last, White & Stevens 2007		C
Squalus altipinnis Last, White & Stevens 2007	+	C
Squalus bahiensis Viana, Carvalho & Gomes 2016		B
Squalus bassi Viana, Carvalho & Ebert 2017	+	B
Squalus blainville (Risso 1827)	+	B
Squalus boretzi Dolganov 2019		B
Squalus brevirostris Tanaka 1917		C
Squalus bucephalus Last, Séret & Pogonoski 2007		C
Squalus chloroculus Last, White & Motomura 2007		B
Squalus clarkae Pfleger, Grubbs, Cotton & Daly-Engel 2018		B
Squalus crassispinus Last, Edmunds & Yearsley 2007	+	B
Squalus cubensis Howell Rivero 1936		C
Squalus edmundsi White, Last & Stevens 2007	+	B
Squalus formosus White & Iglésias 2011		C
Squalus grahami White, Last & Stevens 2007		B
Squalus griffini Phillipps 1931		B
Squalus hawaiiensis Daly-Engel, Koch, Anderson, Cotton & Grubbs 2018		B
Squalus hemipinnis White, Last & Yearsley 2007	+	C
Squalus japonicus Ishikawa 1908		B
Squalus lalannei Baranes 2003	+	B
Squalus lobularis Viana, Carvalho & Gomes 2016		B
Squalus mahia Viana, Lisher & Carvalho 2017	+	C
Squalus margaretsmithae Viana, Lisher & Carvalho 2017	+	C
Squalus megalops (Macleay 1881)	+	C
Squalus melanurus Fourmanoir 1979		B
Squalus mitsukurii Jordan & Snyder 1903	+	B
Squalus montalbani Whitley 1931	+	B
Squalus nasutus Last, Marshall & White 2007	+	B
Squalus notocaudatus Last, White & Stevens 2007		C
Squalus probatovi Myagkov & Kondyurin 1986	+	C
Squalus quasimodo Viana, Carvalho & Gomes 2016		B
Squalus raoulensis Duffy & Last 2007		C
Squalus shiraii Viana & Carvalho 2020		B
Squalus suckleyi (Girard 1855)		A

Materials and Methods

The type material of the new species is deposited in the following collections: Muséum d'Histoire Naturelle, Saint-Denis, Réunion, France (MNHRUN); Staatliches Museum für Naturkunde in Stuttgart, Germany (SMNS). Abbreviations of museum collections (see below) follow Fricke and Eschmeyer (2022a).

Methods follow Last et al. (2007e) and Viana et al. (2017a). The total length is abbreviated TL, the head length HL

Generic classification and nomenclature follows Fricke et al. (2022b); higher classification follows Nelson et al. (2016) and Laan et al. (2014). Reference and journal citations follow Fricke and Eschmeyer (2022b). The map was composed using QGIS 3.6. The key to species to western Indian Ocean *Squalus* is updated, based on the key presented by Ebert (2022).

Results

Systematics

The present paper follows the classifications provided by Nelson (2016) and Laan et al. (2014):

Superclass Gnathostomata
Infraclass Elasmobranchii
Division Selachii
Order Squaliformes Linnaeus 1758
Family Squalidae Blainville 1816
Genus *Squalus* Linnaeus 1758

Squalus longispinis new species (Figs. 1-5)

Common name: La Réunion longspine spurdog

Holotype*:* MNHNRUN uncat. (2022.E.4.1), 730 mm TL, southwestern Indian Ocean, La Réunion, France, 18.4 km west-northwest of Cap de La Houssaye, 20°57'48.564"S 55°04'26.652"E, bottom longline, 1,000 m depth, Patrick Durville, Cruise OBJECTIF 1000, St. 16, 7 Oct. 2022. SMNS 27700, skin sample of holotype from upper right flank, data see holotype.

Figure 1. *Squalus longispinis* n. sp., MHNRUN uncat. (2022.E.4.1), holotype, 730.0 mm TL, southwestern Indian Ocean, La Réunion, France, 18.4 km west-northwest of Cap de La Houssaye, 1,000 m depth. Lateral view.

Figure 2. *Squalus longispinis* n. sp., MHNRUN uncat. (2022.E.4.1), holotype, 730.0 mm TL, southwestern Indian Ocean, La Réunion, France, 18.4 km west-northwest of Cap de La Houssaye, 1,000 m depth. Dorsal view.

Figure 3. *Squalus longispinis* n. sp., MHNRUN uncat. (2022.E.4.1), holotype, 730.0 mm TL, southwestern Indian Ocean, La Réunion, France, 18.4 km west-northwest of Cap de La Houssaye, 1,000 m depth. Head, ventral view.

Figure 4. *Squalus longispinis* n. sp., MHNRUN uncat. (2022.E.4.1), holotype, 730.0 mm TL, southwestern Indian Ocean, La Réunion, France, 18.4 km west-northwest of Cap de La Houssaye, 1,000 m depth. Upper jaw.

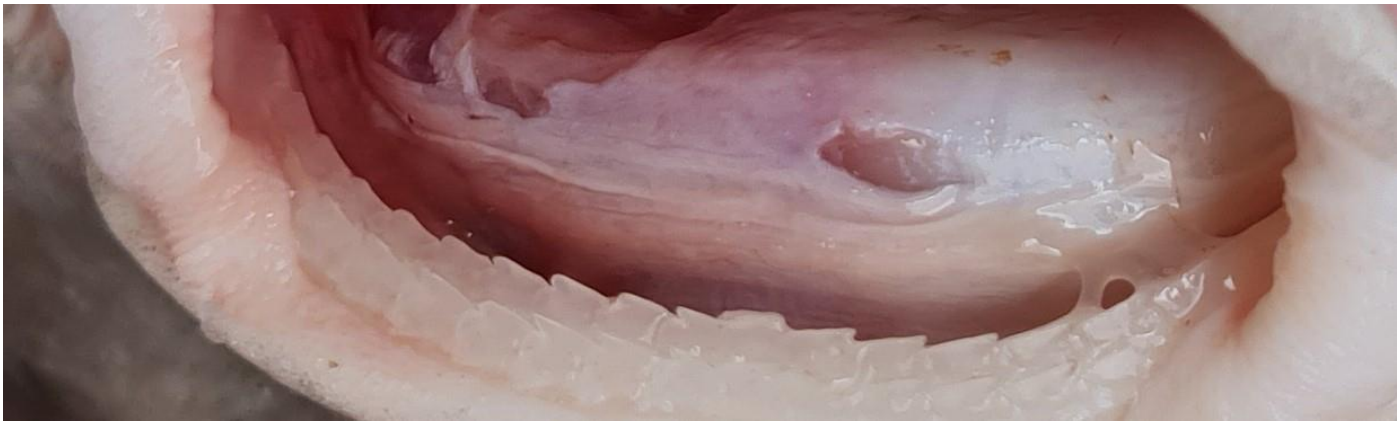

Figure 5. *Squalus longispinis* n. sp., MHNRUN uncat. (2022.E.4.1), holotype, 730.0 mm TL, southwestern Indian Ocean, La Réunion, France, 18.4 km west-northwest of Cap de La Houssaye, 1,000 m depth. Lower jaw.

Diagnosis: A species of *Squalus* distinguished from other members of the genus by the following combination of characters: snout short, preorbital length 8.2% of total length (TL), prenarial length in inner nostril-narial furrow space 0.86; body very high, abdomen height 16.4% of TL, head height in trunk height 0.5; dorsal fin beginning on a vertical above posterior lobes of pectoral fin; second dorsal

fin positioned in the middle between anal fin and caudal fin; first and second dorsal-fin spines long, first dorsal-fin spine 5.8% of TL, second-dorsal fin spine 5.3% of TL; flank denticles tricuspid; monospondylous vertebrae 37, precaudal vertebrae 86, caudal vertebrae 26, total vertebrae 112; upper caudal-fin lobe broad; caudal fin distally with a narrow, light grey margin.

Description: Measurements and proportions are summarized in Table 2. Body fusiform and robust, arched dorsally from posterior margin of eyes to origin of first dorsal fin (Fig. 1); body with greatest width at abdomen (head width 0.85 times trunk width and 0.96 times abdomen width) (Fig. 2) and deepest at trunk (head height 0.5 times trunk height and 0.6 times abdomen height). Head relatively small, its length 11.0% TL, corresponding to 1.05 times length of dorsal caudal margin. Snout obtuse and elongate (Fig. 1), its preorbital length 3.7% TL; anterior margin of nostrils bilobed; prenarial length 0.4 times pre-oral length and 0.9 times the distance from nostrils to upper labial furrow; internarial space 1.2 times eye length. Eyes oval with anterior margin concave and posterior margin notched; eyes large, their length 2.15 times greater than their height. Prespiracular length 0.46 times prepectoral length and 2.7 times larger than preorbital length. Spiracles crescent and relatively large, their length 0.8 times eye length. Prebranchial length 1.6 times greater than prespiracular length. Gill slits vertical, somewhat convex and tall with height of fifth gill slit 1.4 times height of first gill slit.

Preoral length 0.85 times greater than mouth width. Mouth arched and narrow, its width 1.2 times prenarial length and 2.0 times internarial space; upper labial furrow elongate, its length 2.6% TL with thin fold; lower labial furrow larger than upper one, lacking the fold. Teeth similar in both jaws, upper teeth slightly smaller than lower teeth (Figs. 4-5); 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 11–11 rows and 11–10 rows on lower jaw. Lateral and lower sides of head with numerous sensory pores.

Pre-dorsal(1) length 35.7% TL, corresponding to 1.65 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. 1); first dorsal-fin apex markedly rounded and free rear tip pointed; first dorsal fin elongate, its length 1.5 times greater than its height; first dorsal-fin base length corresponding to 1.7 times preorbital length and 0.9 times first dorsal-fin height; first dorsal fin oblique and moderately low, its height 2.0 times pre-orbital length and 1.6 times length of first dorsal-fin inner margin. First dorsal-fin spine thick, its base width 0.8% TL and long, its length 5.8% TL, not reaching apex of first dorsal fin; length of first dorsal-fin spine 0.8 times first dorsal-fin height. First dorsal fin 1.6 times greater in length than second dorsal fin.

Interdorsal space 1.4 times prepectoral length and 3.1 times greater than dorsal-caudal space. Pre-dorsal (2) length 3.2 times greater than prepectoral length and 3.5 times greater than length of dorsal caudal margin. Origin of second dorsal fin located one pelvic-fin length behind vertical traced at pelvic-fin free rear tips. Second dorsal fin raked with anterior margin convex and posterior margin falcate (Fig. 1); second dorsal-fin apex rounded and lobe-like and free rear tip pointed; second dorsal fin small, its length 1.55 times greater than its height; second dorsal-fin base length corresponding to 0-8 times second dorsal-fin height and 0.4 times dorsal caudal space; second dorsal fin oblique and low, its height 1.1 times second dorsal-fin inner margin length. Second dorsal-fin spine heavy and elongate, its length 1.2 times height of second dorsal fin, reaching beyond apex of second dorsal fin; second dorsal-fin spine 0.9 times in length of first dorsal spine. Pectoral fins elongate (anterior margin length 16.9% TL) and wide (posterior margin length 11.8% TL); pectoral-fin anterior and inner margins convex; pectoral-fin posterior margin concave; pectoral-fin free rear tips rounded and apex slightly pointed (Fig. 1); pectoral-fin anterior margin 1.6 times greater in length than pectoral-fin inner margin and 1.4 times larger than length of pectoral-fin posterior margin; pectoral-fin posterior margin transcending trunk height when adpressed on body, its length 0.6 times trunk height.

Pectoral-pelvic distance 1.15 times pelvic-caudal space. Pelvic fins subtriangular and narrow with anterior and posterior margins straight; pelvic-fin free rear tips rounded in female; pelvic fins small, their length 7.4% TL; pelvic fins placed at midline between dorsal fins.

Table 2. Measurements and proportions (expressed as percentages of total length) of the holotype of *Squalus longispinis* n. sp., MHNRUN uncat. (2022.E.4.1).

	Measurement (mm)	% of total length
Total length	730.0	--
Precaudal length	597.7	81.9
Predorsal(2) length	505.2	69.2
Predorsal(1) length	256.9	35.7
Prevent length	404.4	55.4
Prepelvic length	392.5	53.8
Prepectoral length	155.7	21.3
Head length	151.3	11.0
Prebranchial length	111.9	15.3
Prespiracular length	72.0	9.9
Preorbital length	59.9	8.2
Prenarial length	33.5	4.6
Preoral length	81.1	11.1
Inner nostril-narial furrow space	39.0	5.3
Mouth width	67.4	9.2
Labial furrow length	20.0	2.7
Internarial space	46.8	6.4
Interorbital space	65.1	8.9
Eye length	38.2	5.2
Eye height	17.8	2.4
Spiracle length	14.5	2.0
First gill-slit height	15.8	2.2
Fifth gill-slit height	22.4	3.1
Interdorsal space	220.3	30.2
Dorsal-caudal space	71.5	9.8
Pectoral-pelvic space	188.7	25.8
Pelvic-caudal space	163.6	22.4
First dorsal length	79.9	10.9
First dorsal anterior margin length	63.6	8.7
First dorsal base length	45.8	6.3
First dorsal height	53.4	7.3
First dorsal inner margin length	34.3	4.7
First dorsal posterior margin length	69.7	9.5
First dorsal spine length	42.0	5.8
First dorsal spine width	5.6	0.8
Second dorsal length	50.9	7.0
Second dorsal anterior-margin length	35.9	4.9
Second dorsal-base length	27.0	3.7
Second dorsal height	32.8	4.5
Second dorsal inner-margin length	30.3	4.2
Second dorsal posterior-margin length	34.1	4.7
Second dorsal-spine length	38.2	5.2
Second dorsal-spine base width	5.6	0.8
Pectoral anterior-margin length	123.6	16.9
Pectoral inner-margin length	79.1	10.8
Pectoral-base length	30.0	4.1
Pectoral posterior-margin length	86.2	11.8
Pelvic-fin length	53.9	7.4
Pelvic inner-margin length	15.5	2.1
Dorsal caudal-margin length	144.5	19.8
Pre-ventral caudal-margin length	76.8	10.5
Caudal-fork width	61.0	8.4
Head width at nostrils	74.0	10.1
Head width at mouth	101.4	13.9
Head width	104.2	14.3
Trunk width	122.2	16.7
Abdomen width	108.1	14.8
Head height	69.9	9.6
Trunk height	139.9	19.2
Abdomen height	119.5	16.4

Upper and lower precaudal pits weak; caudal keel relatively long, longer than first dorsal-fin base, lateral on caudal penduncle. Caudal fin rather rectangular at upper caudal lobe with dorsal caudal

margin straight, upper postventral caudal margin convex; lower postventral caudal margin nearly straight; preventral caudal margin markedly convex; dorsal and ventral caudal tips rounded; length of dorsal caudal margin 1.0 times head length and 1·9 times greater than length of preventral caudal margin; preventral caudal margin relatively long, its length 5.0 times length of pelvic-fin inner margin; caudal fork discontinuous, markedly concave but narrow, its width 8.4% TL.

Dermal denticles. (Figs. 6-7) Dermal denticles closely-set, tricuspid and rhomboid, weakly imbricate and broad at crown, their length almost equal to their width; cusps posteriorly rounded and elongate; lateral cusps forming posterior concavity with median cusp on each side; median ridge large and thick with anterior furrow wide but shallow; anterior margin of median ridge weakly arrow-shaped; lateral ridges markedly thin, slightly curved, their length about three-fourtsh of length of median ridge.

Vertebral counts. Monospondylous vertebrae 37; precaudal vertebrae 86; caudal vertebrae 25; total vertebrae 111.

Colour in life: (Figs. 8-9) Head and body dorsally brownish grey, ventrally white. Iris bright turquoise. Fins brownish grey. Outer margin of posterior part of dorsal fins and pectoral fin whitish; caudal fin with a narrow distal light grey margin.

Colour in preservative: (Figs. 1-3) Similar to fresh colouration, but the lower parts of the body are more greyish than white, and the iris fades to dark grey.

Distribution: This species is only known from the holotype collected, and another specimen observed, at La Réunion (Mascarenes, southwestern Indian Ocean), at a depth of 900-1,000 m (Fig. 10).

Etymology: The new species is named after its long dorsal spines; it stems from the Latoin longus (long) and spinis (spines). It is the masculine form of an adjective.

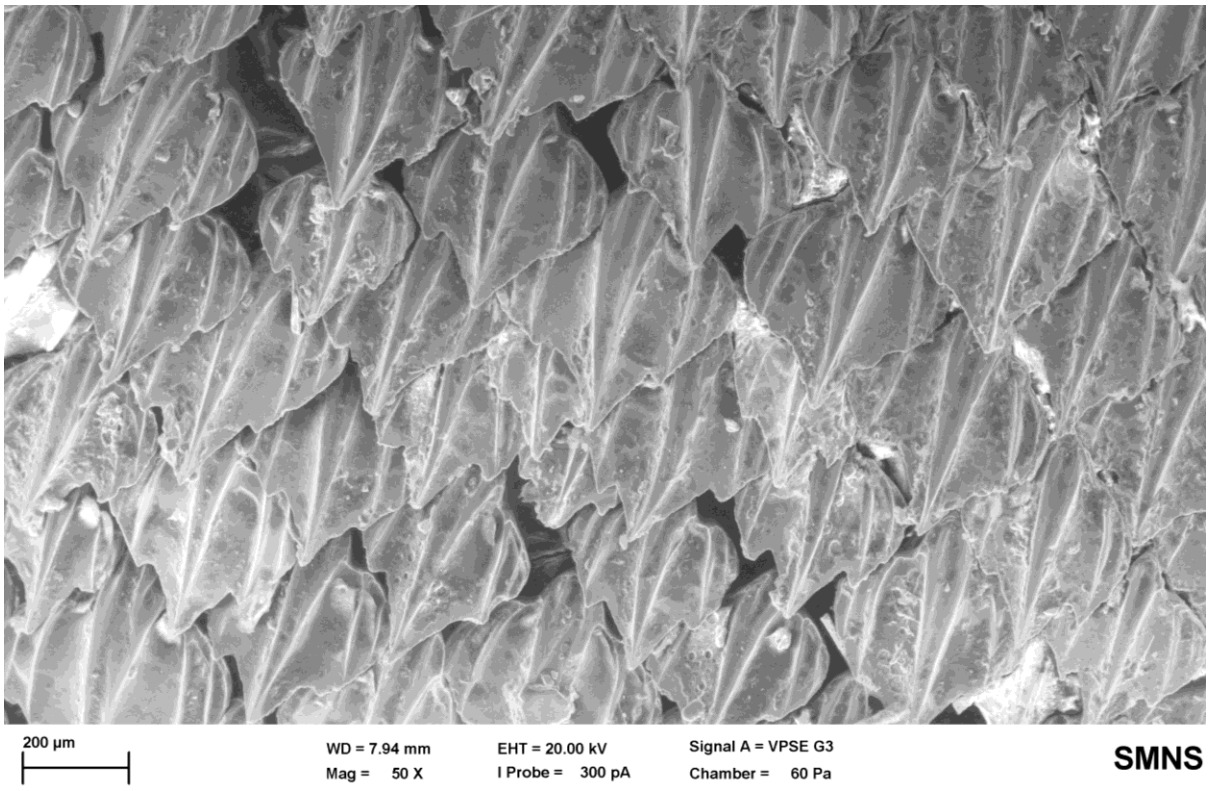

Figure 6. *Squalus longispinis* n. sp., SMNS 27700, holotype, 730.0 mm TL, southwestern Indian Ocean, La Réunion, France, 18.4 km west-northwest of Cap de La Houssaye, 1,000 m depth. Flank dermal denticles. SEM image taken by Cristina Gasco Martin.

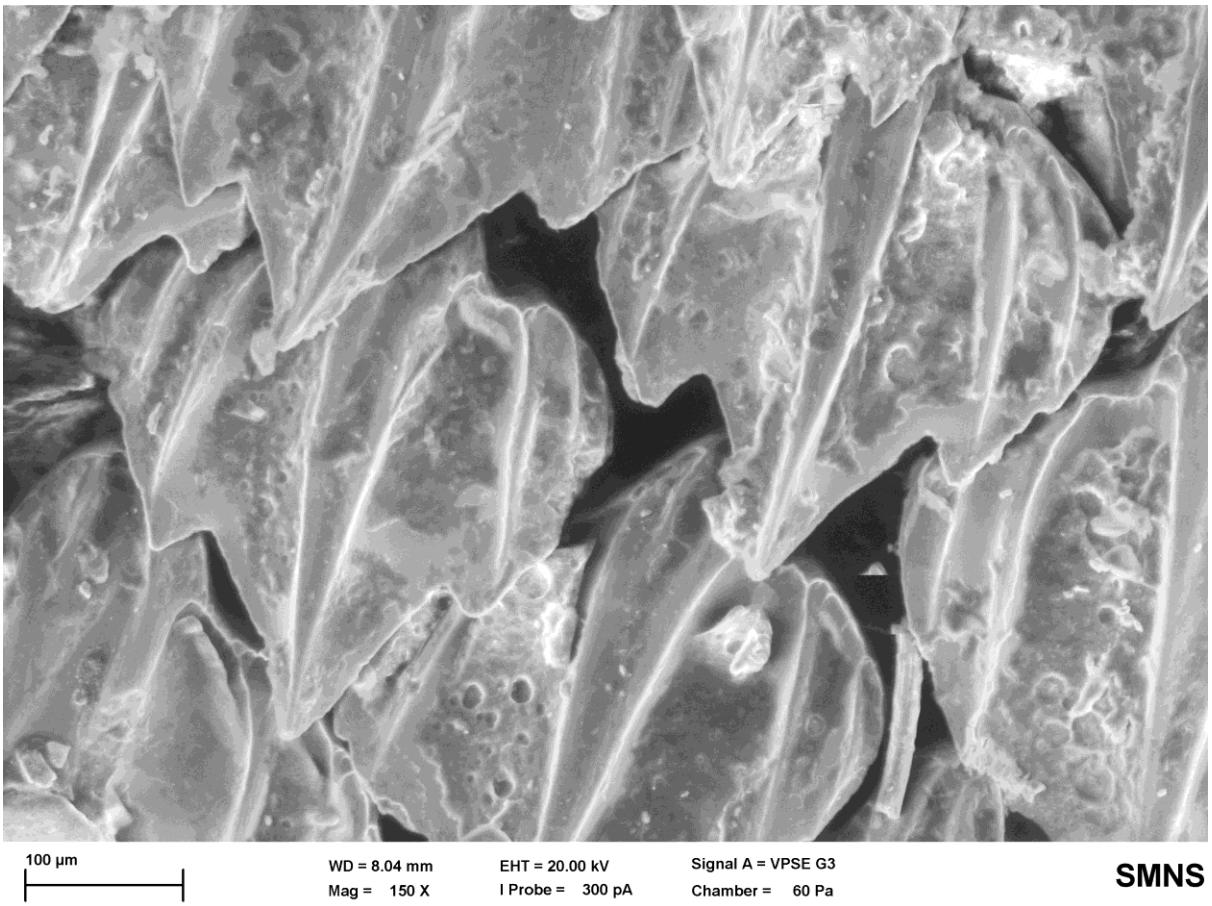

Figure 7. *Squalus longispinis* n. sp., SMNS 27700, holotype, 730.0 mm TL, southwestern Indian Ocean, La Réunion, France, 18.4 km west-northwest of Cap de La Houssaye, 1,000 m depth. Flank dermal denticles in detail. SEM image taken by Cristina Gasco Martin.

Figure 8. *Squalus longispinis* n. sp., MHNRUN uncat. (2022.E.4.1), holotype, 730.0 mm TL, southwestern Indian Ocean, La Réunion, France, 18.4 km west-northwest of Cap de La Houssaye, 1,000 m depth. Fresh colouration, lateral view.

Figure 9. *Squalus longispinis* n. sp., MHNRUN uncat. (2022.E.4.1), holotype, 730.0 mm TL, southwestern Indian Ocean, La Réunion, France, 18.4 km west-northwest of Cap de La Houssaye, 1,000 m depth. Fresh colouration, detail of head.

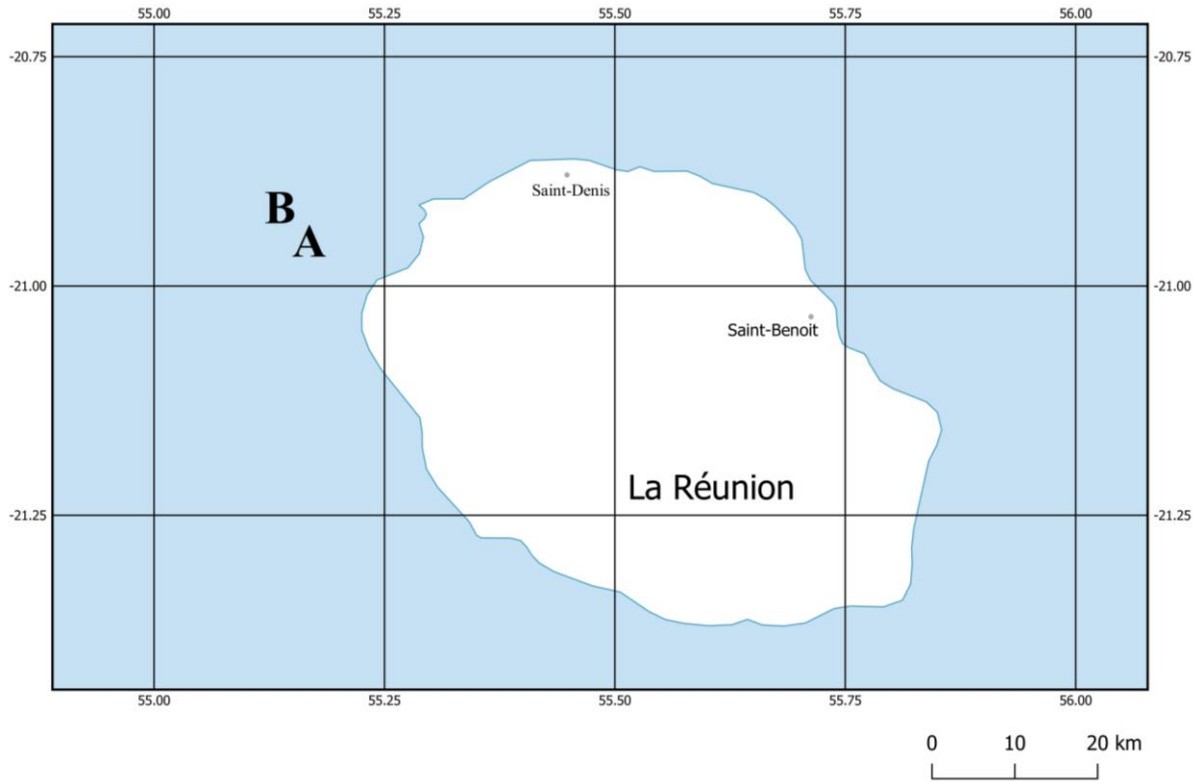

Figure 10. Distribution of *Squalus longispinis* n. sp. in La Réunion, southwestern Indian Ocean. **A.** Holotype, MNHRUN uncat. (2022.E.4.1), **B.** Second female specimen observed on video.

Comparisons: Within This new short-snouted spurdog species from La Réunion that is distinguished from all other species by an unusually high body abdomen height 16.4% of TL (vs. 6.4-14.8% in the other species), head height in trunk height 0.5 (vs. 0.76-1.23 in the other species); it differs from other short-snouted and high-bodied species of the genus, including *S. acutipinnis, S. crassispinus, S. lalannei, S. megalops, S. quasimodo* and *S. shiraii* (Table 3), in its 86 precaudal vertebrae (vs. 81-84 in *S. acutipinnis*, 67-69 in *S. lalannei*, 79-83 in *S. megalops*, 91-94 in *S. shiraii)*, 26 caudal vertebrae (vs. 29 in *S. quasimodo* and *S. shiraii*), 112 total vertebrae (vs. 93-95 in *S. lalannei*, 116-121 in *S. quasimodo*, 120-123 in *S. shiraii*), 27 monospondylous vertebrae (vs. 39-42 in *S. crassispinus*, 39-41 in *S. megalops*, 45-46 in *S. quasimodo*, 44-48 in *S. shiraii*), upper tooth rows 11 (vs. 12-14 in *S. acutipinnis*, 13 in *S. crassispinus*, 12-13 in *S. megalops*, 14 in *S. quasimodo*, 13-14 in *S. shiraii*), flank denticles tricuspid (vs. unicuspid in *S. acutipinnis, S. crassispinus, S. megalops, S. shiraii*), prenarial length in inner nostril-narial furrow space 0.86 (vs. 1.00-1.04 in *S. crassispinus*, 1.02-1.12 in *S. quasimodo*, 1.12-1.26 in *S. shiraii*), preorbital length 8.2% of TL (vs. 6.9-7.3% in *S. crassispinus*, 9.0-9.2% in *S. lalannei*, 8.8-10.7% in *S. megalops*, 9.5-10.2% in *S. quasimodo*), mouth width in prenarial length 2.01 (vs. 2.12-2.36 in *S. crassispinus*, 1.43 in *S. lalannei*, 2.58-3.40 in *S. megalops*, 1.59-1.62 in *S. quasimodo*, 1.32-1.33 in *S. shiraii*), length of first in dorsal-fin spine 5.8% of SL (vs. 1.9-4.9% in *S. acutipinnis*, 4.6 in *S. lalannei*, 1.8-3.6 in *S. megalops*, 3.3-4.3 in *S. quasimodo* and *S. shiraii*), width of base of first-dorsal fin spine 0.8% of TL (vs. 1.2-1.3% in *S. crassispinus*), height of first dorsal fin in length of its inner margin 1.56 (vs. 1.00-1.33 in *S. megalops*, 1.14-1.25 in *S. quasimodo*, 1.63-1.68 in *S. shiraii*), length of second dorsal-fin spine 5.2% of TL (vs. 3.5% in *S. lalannei*, 3.9-4.4% in *S. quasimodo*), length of first dorsal-fin spine in length of second dorsal-fin spine 1.09 (vs. 0.47-1.02 in *S. acutipinnis*, 1.31 in *S. lalannei*, 0.47-0.69 in *S. megalops*, 0.85-0.98 in *S. quasimodo*, 0.71-0.85 in *S. shiraii*), second dorsal-fin height in length of its inner margin 1.08 (vs. 0.71-1.04 in *S. megalops*, 1.40-1.78 in *S. shiraii*), length of anterior margin of pectoral fin in its inner margin length 1.56 (vs. 1.92-2.19 in *S. crassispinus*, 2.22 in *S. lalannei*, 1.83-1.86 in *S. shiraii*), upper caudal-fin lobe broad (vs. slender in *S. megalops, S. shiraii*), caudal fin distally with a narrow light grey margin (vs. distally white in *S. crassispinus*, *S. megalops*, *S. shiraii*; distally dark in *S. lalannei*, *S. quasimodo*).

Table 3. Comparison of the short-snouted and high-bodied species of the genus *Squalus*. Differences to *S. longispinis* n. sp. are printed in **bold face**. Species group: B *Squalus-mitsukurii* group; C *Squalus-megalops* group.

	S. longispinis **n.sp.**	*S. acutipinnis*	*S. crassispinus*	*S. lalannei*	*S. megalops*	*S. quasimodo*	*S. shiraii*
Precaudal vertebrae	86	**81-84**	82-86	**67-69**	**79-83**	87-92	**91-94**
Caudal vertebrae	26	25-29	24-27	26-27	26-30	**29**	**29**
Total vertebrae	112	**107-111**	107-112	**93-95**	**107-111**	**116-121**	**120-123**
Monospondylous vertebrae	37	37-42	**39-42**	?	**39-41**	**45-46**	**44-48**
Upper tooth rows (right)	11	**12-14**	14	**12-13**	**13-14**	**14**	**13-14**
Upper tooth rows (left)	11	11-14	13	**12-13**	**12-13**	**14**	**13-14**
Lower tooth rows (right)	11	10-12	12	11-12	11-12	11	11
Lower tooth rows (left)	10	10-13	11	11-12	10-12	11	11-12
Upper tooth series	3	2-3	?	3	2	2	2
Lower tooth series	2	2-3	?	2	2	2	2-3
Flank denticles	tricuspid	**unicuspid**	**unicuspid**	tricuspid	**unicuspid**	tricuspid	**unicuspid**
Prenarial length in inner nostril-narial furrow space	0.86	0.73-0.96	**1.00-1.04**	0.78-1.09	0.79-1.01	**1.02-1.12**	**1.12-1.26**
Preorbital length	8.2	8.4-9.2	**6.9-7.3**	**9.0-9.2**	**8.8-10.7**	**9.5-10.2**	**7**.4-8.1
Mouth width in prenarial length	2.01	1.54-2.14	**2.12-2.36**	**1.43**	**2.58-3.40**	**1.59-1.62**	**1.32-1.33**
Abdomen height (% of TL)	16.4	**7.3-11.9**	**8.9.13.0**	**12.4-13.3**	**9.0-13.8**	**8.2-12.8**	**8.6-13.4**
Trunk height (% of TL)	19.2	**9.6-12.2**	**10.1-13.1**	**11.6-12.5**	**10.0-12.8**	**8.5-12.3**	**8.8-12.2**
Head height in trunk height	0.50	**0.89-1.08**	**0.84-0.97**	**0.79-0.90**	**0.89-0.99**	**0.85-1.05**	**0.91-1.00**
Predorsal(2) length in P1 anterior margin length	4.09	3.45-4.95	3.67-4.21	4.64-4.72	4.06-4.97	3.88-3.98	4.12-4.40
D1 spine length (% TL)	5.8	**1.9-4.9**	2.3-5.9	**4.6**	**1.8-3.6**	**3.3-4.3**	**3.3-4.3**
Base of D1 spine width (% TL)	0.8	0.6-0.9	**1.2-1.3**	1.0	0.6-0.8	0.7-1.0	0.9
D1 height in inner margin length	1.56	1.36-1.67	1.32-1.70	1.52	**1.00-1.33**	**1.14-1.25**	**1.63-1.68**
D2 spine length (% TL)	5.2	3.8-5.1	4.5-6.5	**3.5**	3.8-5.2	**3.9-4.4**	4.3-5.3
D1 spine length in D2 spine length	1.09	**0.47-1.02**	0.50-1.18	**1.31**	**0.47-0.69**	**0.85-0.98**	**0.71-0.85**
D2 height in inner margin length	1.08	1.10-1.52	1.08-1.30	2.08	**0.71-1.04**	0.89-1.08	**1.40-1.78**
P1 anterior margin in inner margin length	1.56	1.43-2.18	**1.92-2.19**	**2.22**	1.41-1.88	1.46-1.91	**1.83-1.86**
Upper C lobe	broad	broad	broad	broad	**slender**	broad	**slender**
C colouration (preserved)	distally narrow light grey	distally pale	**distally mostly white**	**distally dark**	**distally mostly white**	**distally dark**	**distally broadly white**
Species group	C	C	B	C	C	B	B
Source	Present study	Viana & Carvalho (2016)	Last et al. (2007a); Viana et al. (2017b)	Baranes (2003)	Viana & Carvalho (2016)	Viana et al. (2016)	Viana & Carvalho (2016)
Distribution	La Réunion	Southwestern Indian Ocean	Australia and Papua New Guinea	Seychelles	Australia	Western Atlantic	Okinawa Trough; Emperor Seamount
Depth range (m)	900-1,000	1-732	187-262	1,000	30-750	**?**	310-390

The new species is distinguished from other species of the *Squalus-megalops* group in the Indian Ocean, including *S. altipinnis, S. hemipinnis, S. mahia, S. margaretsmithae* and *S. probatovi* (Table 4), by its 86 precaudal vertebrae (vs. 88-93 in *S. altipinnis*, 72-76 in *S. hemipinnis*, 80-84 in *S. mahia*), 26 caudal vertebrae (vs. 28-31 in *S. probatovi*), 112 total vertebrae (vs. 114-120 in *S. altipinnis*, 96-100 in *S. hemipinnis*, 118-124 in *S. probatovi*), 37 monospondylous vertebrae (vs. 42-45 in *S. altipinnis*, 45-48 in *S. probatovi*), flank denticles tricuspid (vs. unicuspid in *S. mahia* and *S. margaretsmithae*), length of first dorsal-fin spine 5.8% of TL (vs. 4.9-5.3% in *S. altipinnis*, 4.1-5.5% in *S. hemipinnis*, 5.2-5.1% in *S. mahia*, 3.0-5.4% in *S. margaretsmithae*, 3.6-5.4% in *S. probatovi*), height of first dorsal fin in length of its inner margin 1.56 (vs. 1.34-1.46 in *S. altipinnis*, 1.34-1.43 in *S. hemipinnis*, 1.24-1.45 in *S. mahia*, 1.34-1.48 in *S. margaretsmithae*), length of second dorsal-fin spine 5.2% of TL (vs. 4.7-4.8% in *S. altipinnis*), preorbital length 8.2% of TL (vs. 6.8% in *S. altipinnis*, 6.4-6.7% in *S. hemipinnis*, 9.5-11.1% in *S. mahia*), mouth width in prenarial length 2.01 (vs. 1.67-1.68 in *S. altipinnis*, 1.75-1.77 in *S. hemipinnis*, 1.68-1.76 in *S. mahia*, 1.33-1.92 in *S. probatovi*), predorsal(2) length in length of anterior pectoral-fin margin 4.09 (vs. 4.33-4.34 in *S. altipinnis*, 3.43-3.69 in *S. margaretsmithae*, 3.68-3.85 in *S. probatovi*), length of first dorsal-fin spine in length of second dorsal-fin spine 1.09 (vs. 0.83-0.98 in *S. mahia*, 0.71-0.88 in *S. margaretsmithae*, 0.68-0.95 in *S. probatovi*), height of second dorsal fin in length of its inner margin 1.08 (vs. 1.20-1.38 in *S. mahia*), length of anterior pectoral-fin margin in length of its inner margin 1.56 (vs. 1.96-2.14 in *S. altipinnis*, 1.94-2.04 in *S. hemipinnis*, 1.69-1.73 in *S. margaretsmithae)*, upper caudal-fin lobe broad (vs. slender in *S. margaretsmithae*), caudal fin distally with a narrow light grey margin (vs. distally white in *S. altipinnis*, *S. mahia*, *S. probatovi*; distally dark in *S. margaretsmithae*).

Table 4. Comparison of *Squalus longispinis* n. sp. with additional species of the *Squalus-megalops* group in genus *Squalus* in the Indian Ocean. Differences to *S. longispinis* n. sp. are printed in **bold face**.

	S. longispinis **n.sp.**	*S. altipinnis*	*S. hemipinnis*	*S. mahia*	*S. margaretsmithae*	*S. probatovi*
Precaudal vertebrae	86	**88-93**	**72-76**	**80-84**	80-85	87-96
Caudal vertebrae	26	25-29	22-26	27-29	27-30	**28-31**
Total vertebrae	112	**114-120**	**96-100**	107-112	107-115	**118-124**
Monospondylous vertebrae	37	**42-45**	35-38	39-42	38-43	**45-48**
Upper tooth series	3	**2**	2	2-3	2-3	2-3
Lower tooth series	2	2	2-3	2-3	1-2	2-3
Flank denticles	tricuspid	tricuspid	unicuspid to tricuspid	**unicuspid**	**unicuspid**	tricuspid
Prenarial length in inner nostril-narial furrow space	0.86	0.94-0.96	0.81-0.83	0.64-0.94	0.89-0.94	0.83-1.22
Abdomen height (% of TL)	16.4	**9.0-10.6**	**9.1-11.8**	**8.8-12.6**	**6.7-12.6**	**8.8-12.1**
Trunk height (% of TL)	19.2	**9.3-9.4**	**9.0-10.6**	**10.1-12.4**	**7.7-11.9**	**9.8-12.9**
Head height in trunk height	0.50	**0.97-1.04**	**0.94-0.96**	**0.85-0.97**	**0.80-1.12**	**0.76-1.01**
D1 spine length (% TL)	5.8	**4.9-5.3**	**4.1-5.5**	**4.2-5.1**	**3.0-5.4**	**3.6-5.4**
Base of D1 spine width (% TL)	0.8	**1.1**	0.7-0.9	0.8-1.5	0.6-1.0	0.7-1.1
D1 height in inner margin length	1.56	**1.34-1.46**	**1.37-1.43**	1.24-1.45	**1.34-1.48**	1.49-1.52
D2 spine length (% TL)	5.2	**4.7-4.8**	3.7-5.5	4.3-6.1	4.2-6.3	4.4-8.0
Preorbital length	8.2	**6.8**	6.4-6.7	**9.5-11.1**	8.2-9.6	6.6-9.4
Mouth width in prenarial length	2.01	**1.67-1.68**	**1.75-1.77**	**1.68-1.76**	1.90-2.00	**1.33-1.92**
Predorsal(2) length in P1 anterior Predorsal(2) length in P1 anterior	4.09	**4.33-4.34**	3.85-4.50	4.02-4.60	**3.43-3.69**	**3.63-3.85**
D1 spine length in D2 spine length	1.09	1.04-1.10	0.85-1.24	**0.83-0.98**	**0.71-0.88**	**0.68-0.95**
D2 height in inner margin length	1.08	1.05-1.09	0.85-0.93	**1.20-1.38**	0.96-1.23	1.10-1.32
P1 anterior margin in inner margin length	1.56	**1.96-2.14**	**1.94-2.04**	1.41-1.62	**1.69-1.73**	1.60-1.99
Upper C lobe	broad	broad	broad	broad	**slender**	broad
C colouration (preserved)	distally narrow light grey margin	**distally broad white margin**	distally narrow light grey margin	**broad white margin**	**distally dark**	**distal white margin**
Source	Present study	Last et al. (2007f); Viana et al. (2017b)	White et al. (2007a)	Viana et al. (2017b)	Viana et al. (2017b)	Viana & Carvalho (2018a)
Distribution	La Réunion	NW Australia to Philippines	Indonesia	South Africa to So cotra, Madagascar	E Atlantic, South Africa	E Atlantic, SW Indian Ocean
Depth range (m)	900-1,000	300	below 100	202-500	55-460	56-503

Squalus longispinis n. sp. differs from other species of the *Squalus-megalops* group outside the Indian Ocean, including *S. albicaudus, S. albifrons, S. brevirostris, S. bucephalus, S. cubensis, S. formosus, S. notocaudatus* and *S. raoulensis* (Table 5), in its 86 precaudal vertebrae (vs. 89-93 in *S. albifrons*, 80-84 in *S. brevirostris*, 94-95 in *S. formosus*, 94-97 in *S. notocaudatus*), caudal vertebrae 26 (vs. 28-30 in *S. formosus*, 29-30 in *S. notocaudatus*), total vertebrae 112 (vs. 116-122 in *S. albifrons*, 123-124 in *S. formosus*, 123-127 in *S. notocaudatus*), monospondylous vertebrae 37 (vs. 39-41 in *S. albicaudus*, 44-46 in *S. albifrons*, 39-40 in *S. brevirostris*, 45 in *S. bucephalus*, 39-43 in *S. cubensis*, 45-46 in *S. formosus*, 47-49 in *S. notocaudatus*, 41-43 in *S. raoulensis*), flank denticles tricuspid (vs. unicuspid in *S. albicaudus, S. brevirostris, S. cubensis, S. raoulensis*), preorbital length 8.2% of TL (vs. 9.2-11.2% in *S. albicaudus*, 6.7-7.0% in *S. albifrons*, 9.2-10.5%

in *S. bucephalus*, 8.7-11.8% in *S. cubensis*, 7.0-7.4% in *S. formosus*, 6.4-7.0% in *S. notocaudatus*, 7.1-7.3% in *S. raoulensis*), mouth width in prenarial length 2.01 (vs. 1.52-1.60 in *S. albicaudus*, 1.70-1.93 in *S. albifrons*, 1.85-1.86 in *S. brevirostris*, 1.62-1.81 in *S. bucephalus*, 1.67-1.95 in *S. cubensis*, 1.59-1.91 in *S. formosus*, 1.60-1.70 in *S. notocaudatus*, 1.74-1.80 in *S. raoulensis*), predorsal(2) length in length of anterior pectoral-fin margin 4.09 (vs. 4.47-4.90 in *S. albicaudus*, 3.64-3.93 in *S. notocaudatus*), length of first dorsal-fin spine 5.8% of TL (vs. 3.4-5.1% in *S. albicaudus*, 3.1-4.2% in *S. brevirostris*, 2.6-3.5% in *S. bucephalus*, 2.1-4.9% in *S. cubensis*, 3.6-4.5% in *S. notocaudatus*, 2.6-4.0 in *S. raoulensis*), first dorsal-fin height in length of its inner margin 1.56 (vs. 1.31-1.41 in *S. albicaudus*, 1.44-1.48 in *S. albifrons*, 1.28-1.30 in *S. brevirostris*, 1.22-1.43 in *S. cubensis*, 1.14-1.34 in *S. raoulensis*), length of second dorsal-fin spine 5.2% of TL (vs. 3.8-4.6 in *S. bucephalus*, 4.7-4.9 in *S. raoulensis*), length of first dorsal-fin spine in length of second dorsal-fin spine 1.09 (vs. 0.68-0.82 in *S. albicaudus*, 0.65-0.66 in *S. brevirostris*, 0.68-0.76 in *S. bucephalus*, 0.50-0.78 in *S. cubensis*, 0.62-1.02 in *S. formosus*, 0.80-0.86 in *S. notocaudatus*, 0.57-0.82 in *S. raoulensis*), second dorsal-fin height in length of its inner margin 1.08 (vs. 1.16-1.21 in *S. brevirostris*, 0.86-0.92 in *S. raoulensis*), length of anterior pectoral-fin margin in length of its inner margin 1.56 (vs. 1.97-2.22 in *S. albifrons*, 1.40 in *S. brevirostris*, 1.91-1.93 in *S. bucephalus*), upper caudal-fin lobe broad (vs. slender in *S. albicaudus*, *S. albifrons*, *S. bucephalus*, *S. formosus*, *S. notocaudatus*, *S. raoulensis*), and caudal-fin with a narrow distal light grey margin (vs. distally white in *S. albicaudus*, *S. albifrons*, *S. brevirostris*, *S. cubensis*, *S. formosus*, *S. notocaudatus*, *S. raoulensis*; a white upper lobe in *S. bucephalus*).

Table 5. Comparison of *Squalus longispinis* n. sp. with additional species of the *Squalus-megalops* group in genus *Squalus* outside the Indian Ocean. Differences to *S. longispinis* n. sp. are printed in **bold face**.

	S. longispinis **n.sp.**	*S. albicaudus*	*S. albifrons*	*S. brevirostris*	*S. bucephalus*	*S. cubensis*	*S. formosus*	*S. notocaudatus*	*S. raoulensis*
Precaudal vertebrae	86	81-89	**89-93**	**80-84**	86-89	83-92	**94-95**	**94-97**	84-85
Caudal vertebrae	26	27-29	26-31	24-27	27-30	26-31	**28-30**	**29-30**	27-28
Total vertebrae	112	110-116	**116-122**	106-112	113-118	111-118	**123-124**	**123-127**	112-113
Monospondylous vertebrae	37	**39-41**	**44-46**	**39-40**	**45**	**39-43**	**45-46**	**47-49**	**41-43**
Upper tooth series	3	3	?	?	**1-2**	**2**	?	**2**	**2**
Lower tooth series	2	2	?	?	1-2	2	?	2	2
Flank denticles	tricuspid	**unicuspid**	weakly tricuspid	**unicuspid**	unicuspid+multicuspid	**unicuspid**	tricuspid	tricuspid	**unicuspid**
Prenarial length in inner nostril-narial furrow space	0.86	0.91-1.00	0.94-1.00	0.80-0.81	0.98-1.04	0.78-1.13	0.86-1.07	0.96-1.02	0.85-0.89
Abdomen height (% of TL)	16.4	**9.6-13.2**	**10.4-12.6**	**9.0-13.2**	**11.3-12.6**	**7.3-12.1**	**11.4-12.6**	**8.6-11.1**	**9.6-10.5**
Trunk height (% of TL)	19.2	**10.0-12.7**	**10.8-12.3**	**9.4-13.1**	**11.5-13.1**	**7.9-13.5**	**10.7-13.0**	**9.2-10. 2**	**10.0-10.8**
Head height in trunk height	0.50	**0.89-1.03**	**0.92-0.96**	**0.91-0.99**	**0.86-1.04**	**0.87-1.16**	**0.84-0.92**	**0.93-0.98**	**0.91-0.96**
Preorbital length	8.2	**9.2-11.2**	**6.7-7.0**	8.4-10.0	**9.2-10.5**	**8.7-11.8**	**7.0-7.4**	**6.4-7.0**	**7.1-7.3**
Mouth width in prenarial length	2.01	**1.52-1.60**	**1.70-1.93**	**1.85-1.86**	**1.62-1.81**	**1.67-1.95**	**1.59-1.91**	**1.60-1.70**	**1.74-1.80**
Predorsal(2) length in P1 anterior Predorsal(2) length in P1 anterior	4.09	**4.47-4.90**	3.86-4.13	4.06-4.46	3.65-4.11	4.04-5.21	4.00-4.50	**3.64-3.93**	3.63-4.01
D1 spine length (% TL)	5.8	**3.4-5.1**	**4.4-5.4**	**3.1-4.2**	**2.6-3.5**	**2.1-4.9**	3.4-6.2	**3.6-4.5**	**2.6-4.0**
Base of D1 spine width (% TL)	0.8	0.6-0.9	0.9-1.0	0.5-0.7	0.8	0.6-1.1	0.9-1.1	0.7-1.0	0.6-0.7
D1 height in inner margin length	1.56	**1.31-1.41**	**1.44-1.48**	**1.28-1.30**	1.39-1.50	**1.22-1.43**	1.25-1.57	1.46-1.66	**1.14-1.34**
D2 spine length (% TL)	5.2	3.4-5.1	3.8-5.2	4.7-6.5	**3.8-4.6**	4.2-6.5	5.5-6.3	4.2-5.6	**4.7-4.9**
D1 spine length in D2 spine length	1.09	**0.68-0.82**	0.98-1.16	**0.65-0.66**	**0.68-0.76**	**0.50-0.78**	**0.62-1.02**	**0.80-0.86**	**0.57-0.82**
D2 height in inner margin length	1.08	1.08-1.20	0.98-1.05	**1.16-1.21**	0.84-1.00	1.00-1.25	1.11-1.25	1.02-1.13	**0.86-0.92**
P1 anterior margin in inner margin length	1.56	1.37-1.54	**1.97-2.22**	**1.40**	**1.91-1.93**	1.32-3.14	1.42-2.05	1.42-2.25	1.68-1.86
Upper C lobe	broad	**slender**	**slender**	broad	**slender**	broad	**slender**	**slender**	**slender**
C colouration (preserved)	distally narrow light grey margin	**distally with broad white margin**	**distally with narrow white margin**	**distally uniformly white**	**distally white upper lobe**	**distally with white margin**	**broad white margin**	**distally with white margin**	**distally with broad white margin**
Source	Present study	Viana et al. (2016)	Last et al. (2007f)	Tanaka 1917; Viana et al. (2017)	Last et al. (2007c)	Howell Rivero (1936); Viana et al. (2016)	White & Iglésias (2011); Viana & Carvalho (2020)	Last et al. (2007f)	Duffy & Last (2007a)
Distribution	La Réunion	SW Atlantic: Brazil	SW Pacific E Australia	NW Pacific: China, Philippines to Japan	SW Pacific: Norfolk Ridge	W Atlantic	NW Pacific: Taiwan to Japan	SW Pacific: E Australia	SW Pacific: Kermadec Rid.
Depth range (m)	900-1,000	195-334	131-450	130	405-880	60-400	?	282-402	320

As we observed a considerable overlap in the defining characters between the *Squalus-megalops* group and the *Squalus-mitsukurii* group, we are also comparing the new species in detail with species

of the latter group. The new species is distinguished from other species of the *Squalus-mitsukurii* group in the Indian Ocean, including *S. bassi, S. blainville, S. edmundsi, S. mitsukurii, S. montalbani* and *S. nasutus* (Table 6), by its 86 precaudal vertebrae (vs. 80-81 in *S. nasutus*), 26 caudal vertebrae (vs. 28-33 in *S. bassi*, 29-31 in *S. mitsukurii*), 112 total vertebrae (vs. 115-120 in *S. bassi*, 116-117 in *S. mitsukurii*, 103-109 in *S. nasutus*), 37 monospondylous vertebrae (vs. 43-48 in *S. bassi*, 40-45 in *S. blainville*, 43-45 in *S. edmundsi*, 45-46 in *S. mitsukurii*, 41-47 in *S. montalbani*), prenarial length in inner nostril-narial furrow space 0.86 (vs. 1.14-1.74 in *S. bassi*, 1.21-1.24 in *S. edmundsi*, 1.05-1.30 in *S. mitsukurii*, 1.26-1.49 in *S. nasutus*), preoral length 11.1% of TL (vs. 7.6-10.3% in *S. mitsukurii*, 9.7-10.6% in *S. montalbani*), mouth width in prenarial length 2.01 (vs. 1.48-1.61 in *S. bassi*, 1.26-1.39 in *S. edmundsi*, 1.54-1.83 in *S. mitsukurii*, 1.41-1.78 in *S. montalbani*, 0.83-1.07 in *S. nasutus*), predorsal(2) length in length of anterior pectoral-fin margin 4.09 (vs. 3.51-3.97 in *S. bassi*, 4.17-4.36 in *S. edmundsi*, 4.77-5.66 in *S. nasutus*), length of first dorsal-fin spine 5.8% of TL (vs. 2.5-4.8% in *S. bassi*, 1.6-5.4% in *S. blainville*, 3.1-4.6% in *S. mitsukurii*, 2.1-4.0% in *S. montalbani*, 2.2-3.8% in *S. nasutus*), width of first dorsal-fin spine base 0.8% of TL (vs. 1.0-1.2% in *S. edmundsi*), first dorsal-fin height in length of its inner margin 1.08 (vs. 1.21-1.53 in *S. bassi*, 1.46-1.58 in *S. mitsukurii*, 0.71-0.85 in *S. montalbani*), length of anterior pectoral-fin margin in length of its inner margin 1.56 (vs. 1.64-1.72 in *S. bassi*, 2.12-2.23 in *S. edmundsi*, 1.73-2.17 in *S. nasutus*), upper caudal-fin lobe broad (vs. slender in *S. blainville*), and caudal-fin with a narrow distal light grey margin (vs. distally white in *S. bassi*, *S. edmundsi*, *S. nasutus*; distally dark in *S. blainville*, *S. mitsukurii*, *S. montalbani*).

Table 6. Comparison of *Squalus longispinis* n. sp. with additional species of the *Squalus-mitsukurii* group in genus *Squalus* from the Indian Ocean. Differences to *S. longispinis* n. sp. are printed in **bold face**.

	S. longispinis **n.sp.**	*S. bassi*	*S. blainville*	*S. edmundsi*	*S. mitsukurii*	*S. montalbani*	*S. nasutus*
Precaudal vertebrae	86	86-89	80-92	86-91	86-87	79-85	**78-81**
Caudal vertebrae	26	**28-33**	26-33	26-29	**29-31**	26-34	23-28
Total vertebrae	112	**115-120**	107-121	113-120	**116-117**	105-118	**103-109**
Monospondylous vertebrae	37	**43-48**	**40-45**	**43-45**	**45-46**	**41-47**	36-39
Upper tooth series	3	1-3	**2**	**2**	?	?	3
Lower tooth series	2	2	2	2-3	?	?	2
Flank denticles	tricuspid	tricuspid	tricuspid	tricuspid	tricuspid	tricuspid	tricuspid
Prenarial length in inner nostril-narial furrow space	0.86	**1.15-1.74**	0.58-1.02	**1.21-1.24**	**1.05-1.30**	0.87-1.08	**1.26-1.49**
Abdomen height (% of TL)	16.4	**8.0-14.8**	**6.5-11.5**	**9.9-11.5**	**7.7-12.4**	**9.3-13.0**	**7.8-12.2**
Trunk height (% of TL)	19.2	**8.9-13.6**	**7.4-13.3**	**9.2-10.7**	**10.3-12.7**	**8.9-13.4**	**9.2-11.4**
Head height in trunk height	0.50	**0.88-0.96**	**0.87-1.15**	**0.90-0.94**	**1.00-1.23**	**0.76-1.01**	**0.84-0.93**
Preorbital length	8.2	7.6-9.1	5.9-8.4	7.9-8.1	6.9-10.7	6.7-8.1	8.3-10.1
Preoral length	11.1	9.0-11.8	7.7-11.8	10.3-10.8	**7.6-10.3**	**8.7-10.6**	11.1-12.7
Mouth width in prenarial length	2.01	**1.48-1.61**	1.58-2.39	**1.26-1.39**	**1.54-1.83**	**1.41-1.78**	**0.83-1.07**
Predorsal(2) length in P1 anterior Predorsal(2) length in P1 anterior	4.09	**3.51-3.97**	3.56-5.07	**4.17-4.36**	3.70-4.20	4.05-4.62	**4.77-5.66**
D1 spine length (% TL)	5.8	**2.5-4.8**	**1.6-5.4**	4.8-5.7	**3.1-4.6**	**2.1-4.0**	**2.2-3.8**
Base of D1 spine width (% TL)	0.8	0.5-1.0	0.5-1.2	**1.0-1.2**	0.7-1.0	0.5-0.7	0.7-1.0
D1 height in inner margin length	1.56	1.21-1.53	1.15-1.50	**1.40-1.43**	1.46-1.58	**0.98-1.16**	**1.05-1.38**
D2 spine length (% TL)	5.2	3.2-5.5	2.2-7.1	5.0-5.5	3.4-5.3	**2.0-3.9**	**3.2-4.7**
D1 spine length in D2 spine length	1.09	**0.76-0.87**	**0.47-0.96**	0.96-1.03	**0.87-0.93**	0.58-1.10	0.62-1.19
D2 height in inner margin length	1.08	**1.21-1.53**	0.86-1.38	1.02-1.07	**1.46-1.58**	**0.71-0.85**	0.69-1.09
P1 anterior margin in inner margin length	1.56	**1.64-1.72**	1.50-1.80	**2.13-2.23**	1.60-1.78	1.53-1.88	**1.73-2.17**
Upper C lobe	broad	broad	**slender**	broad	broad	broad	broad
C colouration (preserved)	distally narrow light grey margin	**distally with white margin**	**distally black**	**distally with white margin**	**distally dark**	**distally dark**	**distally with white margin**
Source	Present study	Viana et al. (2017a)	Viana et al. (2016)	White et al. (2007b)	Viana et al. (2017a)	Last et al. (2007d)	Last et al. (2007b)
Distribution	La Réunion	SE Atlantic, SW Indian Ocean	E Atlantic, SW Indian Ocean	Western Australia, *E* Indonesia	E Atlantic, Indo West Pacific	E Indian Ocean, W Pacific	Western Australia, Indonesia, Philippines
Depth range (m)	900-1,000	142-387	16-780	312-850	29-600	415-670	305-850

Squalus longispinis n. sp. differs from other species of the *Squalus-mitsukurii* group outside the Indian Ocean, including *S. bahiensis, S. boretzi, S. choroculus, S. clarkae, S. grahami, S. griffini, S. hawaiiensis, S. japonicus, S. lobularis* and *S. melanurus* (Table 7), in its 26 caudal vertebrae (vs. 28-30 *in S. bahiensis*, 28-32 in *S. boretzi*), 112 total vertebrae (vs. 115-117 in *S. bahiensis*, 114-120 in *S. melanurus*), 37 monospondylous vertebrae (vs. 43-45 in *S. bahiensis*, 41-45 in *S. boretzi* and *S. hawaiiensis*, 43-46 in *S. chloroculus* and *S. lobularis*, 44-45 in *S. clarkae*, 45-47 in *S. griffini*, 40-45 in *S. japonicus*, 41 in *S. melanurus*), preorbital length 8.2% of TL (vs. 7.3-7.9% in *S. bahiensis*, 5.5-6.6% in *S. boretzi*, 7.0-7.3% in *S. clarkae*, 7.4-7.8% in *S. hawaiiensis*, 7.8-8.8% in *S. japonicus*, 7.0-7.9% in *S. lobularis*), preoral length 11.1% of SL (vs. 9.9-10.5% in *S. bahianus*, 7.8-9.2% in *S. boretzi*, 9.5-10.1% in *S. chloroculus*, 9.6-10.4% in *S. hawaiiensis*, 8.6-9.9% in *S. lobularis*, 12.6-14.3% in *S. melanurus*), mouth width in prenarial length 2.01 (vs. 1.44-1.51 in *S. bahiensis*,

1.41-1.81 in *S. boretzi*, 1.45-1.72 in *S. chloroculus*, 1.36-1.53 in *S. clarkae*, 1.21-1.25 in *S. grahami*, 1.12-1.29 in *S. griffini*, 1.35-1.59 in *S. hawaiiensis*, 1.16-1.29 in *S. japonicus*, 1.37-1.56 in *S. lobularis*, 0.75-0.93 in *S. melanurus*), predorsal(2) length in length of anterior pectoral-fin margin 4.09 (vs. 4.34-4.40 in *S. bahiensis*, 2.34-2.87 in *S. boretzi*, 4.25-6.08 in *S. clarkae*, 4.41-5.81 in *S. japonicus*, 4.17-4.46 in *S. melanurus*), first dorsal-fin spine length 5.8% of TL (vs. less than 5.2% on the other species), dorsal-fin height in length of its inner margin 1.56 (vs. 1.03-1.21 on *S. bahiensis*, 1.11-1.16 in *S. chloroculus*, 1.05-1.15 in *S. clarkae*, 1.19-1.24 in *S. grahami*, 1.29-1.36 in *S. griffini*, 1.25-1.44 in *S. hawaiiensis*, 1.64-1.78 in *S. melanurus*), second dorsal-fin spine length 5.2% of TL (vs. 3.7-4.3 in *S. bahiensis*, 5.5-5.6 in *S. boretzi*, 2.5-4.0 in *S. chloroculus*, 4.4-4.9 in *S. clarkae*), first dorsal-fin spine length in second dorsal-fin spine length 1.09 (vs. 0.68-0.78 in *S. bahiensis*, 0.67-0.68 in *S. boretzi*, 0.85-0.92 in *S. chloroculus*, 0.69-0.96 in *S. clarkae*, 0.78-0.89 in *S. grahami*, 0.61-0.75 in *S. griffini*, 0.58-0.87 in *S. japonicus*, 0.65-0.76 in *S. lobularis*, 0.51-0.78 in *S. melanurus*), second dorsal-fin height in its inner margin length 1.08 (vs. 0.75-1.00 in *S. bahiensis*, 0.78-0.89 in *S. chloroculus*, 0.79-0.86 in *S. clarkae*, 0.87-1.00 in *S. grahami*, 1.47-1.67 in *S. melanurus*), pectoral-fin anterior margin length in its inner-margin length 1.56 (vs. 1.96-1.97 in *S. chloroculus*, 1.92-1.98 in *S. grahami*, 2.09-2.48 in *S. griffini*, 1.88-2.42 in *S. hawaiiensis*, 1.74-1.93 in *S. melanurus*), upper caudal-fin lobe broad (vs. slender in *S. chloroculus, S. grahami, S. griffini, S. hawaiiensis, S. japonicus, S. melanurus*), and caudal-fin with a narrow distal light grey margin (vs. distally white in *S. bahiensis*, *S. boretzi*, *S. japonicus*; distally with white-black margin in *S.chloroculus*; distally dark in *S. clarkae*; ventral lobe black in *S. melanurus*).

Table 7. Comparison of *Squalus longispinis* n. sp. with additional species of the *Squalus-mitsukurii* group in genus *Squalus outside* the Indian Ocean. Differences to *S. longispinis* n. sp. are printed in **bold face**.

	S. longispinis **n.sp.**	*S. bahiensis*	*S. boretzi*	*S. chloroculus*	*S. clarkae*	*S. grahami*	*S. griffini*	*S. hawaiiensis*	*S. japonicus*	*S. lobularis*	*S. melanurus*
Precaudal vertebrae	86	87	82-87	84-86	87-90	80-87	86-91	85-89	82-91	80-89	85-94
Caudal vertebrae	26	**28-30**	**28-32**	27-29	24-27	26-32	27-30	27	28	23-33	26-29
Total vertebrae	112	**115-117**	111-116	111-115	111-114	105-116	113-121	112-116	110-119	110-120	**114-120**
Monospondylous vertebrae	37	**43-45**	**41-45**	**43-46**	**44-45**	37-42	**45-47**	**41-45**	**40-45**	**43-46**	**41**
Upper tooth series	3	2-3	?	**1-2**	3	**2**	?	?	?	**2**	2-3
Lower tooth series	2	2	?	2-3	2	2	?	?	?	2	1-3
Flank denticles	tricuspid	tricuspid	tricuspid	tricuspid	tricuspid	weakly tricuspid	tricuspid	tricuspid	weakly tricuspid	tricuspid	tricuspid
Prenarial length in inner nostril-narial furrow space	0.86	**1.04-1.17**	**1.11-1.47**	**1.06-1.08**	**1.07-1.17**	**1.19-1.27**	**1.07-1.22**	**1.11-1.15**	0.90-1.12	**1.20-1.25**	**1.42-1.54**
Preorbital length	16.4	**9.6-10.5**	**9.6-10.1**	**10.1-13.5**	**9.6-12.8**	**10.1-12.6**	**6.9-14.7**	**8.6-14.2**	**8.1-9.6**	**6.4-13.5**	**8.8-13.7**
Mouth width in prenarial length	19.2	**9.1-9.8**	**11.1-11.6**	**10.4-13.8**	**9.4-11.5**	**9.8-11.5**	**8.6-13.9**	**8.8-12.4**	**8.2-9.5**	**6.4-12.5**	**9.2-13.3**
Abdomen height (% of TL)	0.50	**0.95-1.05**	**0.79-0.85**	**0.83-0.97**	**0.85-0.99**	**0.90-0.94**	**0.79-0.94**	**0.86-0.95**	**0.75-0.98**	**0.85-1.17**	**0.82-0.96**
Trunk height (% of TL)	8.2	**7.3-7.9**	**5.5-6.6**	7.5-8.1	**7.0-7.3**	8.3-9.0	7.4-8.8	**7.4-7.8**	**7.8-8.8**	**7.0-7.9**	9.6-10.9
Head height in trunk height	11.1	**9.9-10.5**	**7.8-9.2**	**9.5-10.1**	**8.7-9.5**	10.5-11.3	8.8.-11.4	**9.6-10.4**	10.2-11.4	**8.6-9.9**	**12.6-14.3**
Predorsal(2) length in P1 anterior margin length	2.01	**1.44-1.51**	**1.41-1.81**	**1.45-1.72**	**1.36-1.53**	**1.21-1.25**	**1.12-1.29**	**1.35-1.59**	**1.16-1.28**	**1.37-1.56**	**0.75-0.93**
D1 spine length (% TL)	4.09	**4.24-4.40**	**2.34-2.87**	3.75-4.43	**4.28-5.08**	4.09- 4.13	3.83-4.65	4.11-5.12	**4.41-5.81**	3.73-4.35	**4.17-4.46**
Base of D1 spine width (% TL)	5.8	**2.8-3.0**	**3.7-3.8**	**2.3-3.4**	**3.4-4.4**	**3.1-4.2**	**1.9-4.0**	**3.6-4.6**	**3.0-4.7**	**2.2-4.0**	**2.9-5.1**
D1 height in inner margin length	0.8	0.6-0.8	0.8-1.0	0.6-0.8	0.5-0.9	0.6-0.8	0.6-0.9	0.7-1.0	0.6-1.0	0.6-0.9	0.7-1.0
D2 spine length (% TL)	1.56	**1.03-1.21**	1.42-1.48	**1.11-1.16**	**1.05-1.15**	**1.19-1.24**	**1.29-1.36**	**1.25-1.44**	**1.08-1.31**	1.14-1.97	**1.64-1.78**
D1 spine length in D2 spine length	5.2	**3.7-4.3**	**5.5-5.6**	**2.5-4.0**	**4.4-4.9**	3.5-5.4	3.1-5.3	4.1-5.0	5.2-5.9	3.4-5.3	4.9-6.5
D2 height in inner margin length	1.09	**0.68-0.78**	**0.67-0.68**	**0.85-0.92**	**0.69-0.96**	**0.78-0.89**	**0.61-0.75**	0.76-1.12	**0.58-0.87**	**.65-0.76**	**0.51-0.78**
P1 anterior margin in inner margin length	1.08	**0.75-1.00**	0.90-1.16	**0.78-0.89**	**0.79-0.86**	**0.87-1.00**	1.10-1.12	0.87-1.00	0.85-1.05	0.92-1.32	**1.47-1.67**
Upper C lobe	1.56	1.63-1.76	1.31-1.67	**1.96-1.97**	1.52-2.00	**1.92-1.98**	**2.09-2.48**	**1.88-2.42**	1.48-2.11	1.50-1.56	**1.74-1.93**
C colouration (preserved)	broad distally narrow light grey margin	broad **distally white**	**slender distally with white margin**	broad **distally with white-black margin**	**slender distally dark**	slender distally w/ grey margin	slender distally w/ grey margin	slender distally w/ grey margin	**slender distally w/ white margin**	broad distally w/ grey margin	**slender ventral lobe black**
Species group											
Source	Present study	Viana et al. (2016)	Dolganov (2019)	Last et al. (2007d)	Pfleger et al. (2018)	White et al. (2007b	Duffy & Last (2007b)	Daly-Engel et al. (2018)	Chen et al. (1979)	Viana et al. (2016)	Viana & Carvalho (2018b)
Distribution	La Réunion	SW Atlantic: Brazil -	N Pacific: Emperor Seam.	SW Pacific: SE Australia	NW Atlantic, Gulf of Mexico, Caribbean Sea	SW Pacific E Australia:	SW Pacific: New Zealand	Central Pacific Hawaiian Is.	NW Pacific Taiwan to Japan	SW Atlantic: S Brazil to N Argentina	SW Pacific: New Caledonia to Norfolk Is
Depth range (m)	900-1,000	599	100-525	400-1,370	242-613	148-504	37-543	305-360	150-300	?	34-480

Key to species of the genus *Squalus* of the Indian Ocean

1a. First dorsal fin posteriorly set, with origin behind or sometimes over pectoral-fin free rear tips; origin of 1st dorsal-fin spine well behind pectoral-fin free rear tips; medial barbel on anterior nasal flaps minute or absent; flanks usually with white spots; [circumglobal] ..... *Squalus acanthias*

1b. First dorsal-fin origin usually in front of pectoral-fin free rear tips; origin of 1st dorsal-fin spine usually over pectoral-fin inner margins and ahead of pectoral-fin free rear tips (but varying from just behind to well ahead of tips); medial barbel on anterior nasal flaps well-developed; no white spots on flanks 2

2a. Distance from snout tip to inner edge of nostril shorter than distance from inner edge of nostril to front of upper lip furrow 3

2b. Distance from snout tip to inner edge of nostril longer than distance from inner edge of nostril to front of upper lip furrow 13

3a. Abdomen height more than 15% TL; trunk height more than 18% TL; [southwestern Indian Ocean: La Réunion] ..... *Squalus longispinis* **n. sp.**

3b. Abdomen height less than 14% TL; trunk height less than 14% TL 4

4a. Caudal fin distally dark 5

4b. Caudal fin with a distal light margin 8

5a. Second-dorsal fin height in inner margin length more than 1.8; [western Indian Ocean: Seychelles] ..... *Squalus lalannei*

5b. Second-dorsal fin height in inner margin length less than 1.6 6

6a. Second-dorsal fin height in inner margin length more than 0.9 7

6b. Second-dorsal fin height in inner margin length less than 0.86; [eastern Indian Ocean, western Pacific] ..... *Squalus montalbani*

7a. Flank dermal denticles unicuspid; second-dorsal fin height in inner margin length 0.96-1.23; [eastern Atlantic to South Africa] ..... *Squalus margaretsmithae*

7a. Flank dermal denticles tricuspid; second-dorsal fin height in inner margin length 1.21-1.53; [eastern Atlantic, southwestern Indian Ocean] ..... *Squalus blainville*

8a. Second-dorsal fin height in inner margin length less than 1.05 9

8b. Second-dorsal fin height in inner margin length more than 1.04 10

9a. Dorsal-fin height in inner margin length 1.37-1.43; first dorsal-fin spine length in second dorsal-fin spine length 0.85-1.24; [Indonesia] ..... *Squalus hemipinnis*

9b. Dorsal-fin height in inner margin length 1.00-1.33; first dorsal-fin spine length in second dorsal-fin spine length 0.47-0.69; [circumglobal] ..... *Squalus megalops*

10a. First dorsal-fin spine length in second dorsal-fin spine length more than 1.03; [eastern Indian Ocean, western Pacific] ..... *Squalus altipinnis*

10b. First dorsal-fin spine length in second dorsal-fin spine length less than 1.03 11

11a. Flank dermal denticles unicuspid; precaudal vertebrae less than 85 12

11b. Flank dermal denticles tricuspid; precaudal vertebrae more than 86; [eastern Atlantic, southwestern Indian Ocean] ..... *Squalus probatovi*

12a. Preorbital length 8.4-9.2 in TL; [southeastern Atlantic, southwestern Indian Ocean] ..... *Squalus acutipinnis*

12b. Preorbital length 9.5-11.1 in TL; [western Indian Ocean] ..... *Squalus mahia*

13a. Mouth width in prenarial length more than 2.5; [circumglobal] ..... *Squalus megalops*

13b. Mouth width in prenarial length less than 2.4 14

14a. Mouth width in prenarial length less than 1.1; [eastern Indian Ocean, western Pacific] ..... *Squalus nasutus*

14b. Mouth width in prenarial length more than 1.1 15

15a. Caudal fin distally dark 16

15b. Caudal fin with a distal light margin 19

16a. Pectoral-fin anterior margin length in inner margin length more than 2.0; [western Indian Ocean: Seychelles] ..... *Squalus lalannei*

16b. Pectoral-fin anterior margin length in inner margin length less than 2.0 17

17a. Second dorsal-fin height in inner margin length more than 1.45; [eastern Atlantic, Indo-West Pacific] ..... *Squalus mitsukurii*

17b. Second dorsal-fin height in inner margin length less than 1.40 18

18a. First dorsal-fin height in inner margin length more than 1.14; [eastern Atlantic; southwestern Indian Ocean] ..... *Squalus blainville*
18b. First dorsal-fin height in inner margin length less than 1.17; [eastern Indian Ocean, western Pacific] ..... *Squalus montalbani*
19a. Mouth width in prenarial length more than 2.0; [Australia and Papua New Guinea] ..... *Squalus crassispinus*
19b. Mouth width in prenarial length less than 1.7 20
20a. Predorsal (2) length in length of anterior pectoral-fin margin more than 4.1; [Western Australia, eastern Indonesia] ..... *Squalus edmundsi*
20b. Predorsal (2) length in length of anterior pectoral-fin margin less than 4.0 21
21a. Mouth width in prenarial length more than 1.45; [southeastern Atlantic, southwestern Indian Ocean] ..... *Squalus bassi*
21b. Mouth width in prenarial length less than 1.35; [eastern Atlantic, southwestern Indian Ocean] ..... *Squalus probatovi*

Discussion

The snort-snouted Réunion spurdog *S. longispinis* n. sp. is the second species known to occur around the Mascarenes. The other species, *Squalus acutipinnis* Regan 1908, was originally described from Mauritius, and later reported from La Réunion as *Acanthias vulgaris* (non Risso 1827) by Guichenot (1863: C31), and as *S. megalops* (non Macleay, 1882) by Fricke (1999: 27) and Fricke et al. (2009: 11), based on a specimen collected off Saint-Gilles-les-Bains. While that species is known from shallower water of 1-732 m depth, it was a surprising finding to procure another, endemic species from 900-1,000 m depth. This depth range is near the lower limits for the genus *Squalus*; only four other species are known to occur below 850 m: *S. acanthias*, circumglobal (1-1,460 m), *S. chloroculus* from southeastern Australia (400-1,370 m depth), *S. lalannei* from the Seychelles (1,000 m), and *S. suckleyi* from the North Pacific (15-1,244 m).

Besides the holotype from 1,000 m depth, another, female specimen of *Squalus longispinis* n. sp. was observed on an underwater video, also taken off Saint-Paul, La Réunion, 20°56'52.044''S 55°03'58.716''E, at 900 m depth (Fig. 11), on 28 Sept. 2022. This shark was quite active, trying to feed on some fish meat bait.

The new species has an unusually high body and long dorsal-fin spines; it is here arranged in a short-snouted and high-bodied group of species also including *S. acutipinnis*, *S. crassispinus, S. lalannei, S. megalops, S. quasimodo, S. shiraii.* These species are distributed in the western Atlantic (*S. quasimodo*) and in the Indo-West Pacific (Fig. 12). The distinction between the classical *Squalus mitsukurii*-group and *Squalus-megalops* group seems weakly defined, as considerable overlap is observed in the distinguishing characters (snout length, dermal denticle shape, pectoral-fin shape). The species in this short-snouted and high-bodied group would have been classified in both the *Squalus mitsukurii*-group (*S. crassispinus*, *S. quasimodo, S. shiraii*) and the *Squalus-megalops* group (*S. acutipinnis*, *S. lalannei*, *S. longispinis* n. sp., *S. megalops*). For good measure, we have compared the new species in detail with the species in both groups.

The two Mascarene species are both in the same species group, and obviously closely related to each other, although they well distinguishable by several morphological characters. Especially the dermal denticles are strikingly different; in the new species they are closely-set and rhomboid (vs. sparse and cross-shaped in *S. acutipinnis*), tricuspid (vs. unicuspid), lateral ridges well developed and long (vs. lacking). It might be hypothesised that both stemmed from a common ancestral population, that was subsequently separated with an isolate at the Mascarenes (possibly during glacial periods), so that two distinct species were formed (*S. acutipinnis, S. longispinis* n. sp.). When the widespread species (*S. acutipinnis*) later expanded its distribution range again to the Mascarenes, some ecological separation between the two species occurred, and the former isolate (*S. longispinis* n. sp.) moved deeper, below the range of the invading, widespread species.

On the x-ray photograph of the holotype, six large eggs are distinguishable. This is comparable to the litter of *S. acutipinnis*, which amounts to 1-6 (usually 2-3) (Ebert, 2022). The gestation period in that species would be two years, and embryos are born at 23-28 cm TL.

The research program Objectif 1000 provided an interesting insight into a previously unknown deep-water fauna. The finding of this new shark species proves that it is worth to further investigate

the deep water ichthyofauna (below 500 m depth) in this region. The present study was limited by the application of bottom longline fishing and traps only; these methods favour predators, but the majority of the deep-water fish fauna remains still unknown. Future studies should attempt to use bottom trawl nets, dredges, and pelagic nets, to get a more complete picture of the fish diversity at these depths.

Figure 11. *Squalus longispinis* n. sp., second specimen observed on underwater video, southwestern Indian Ocean, La Réunion, France, west-northwest of Cap de La Houssaye, 900 m depth.

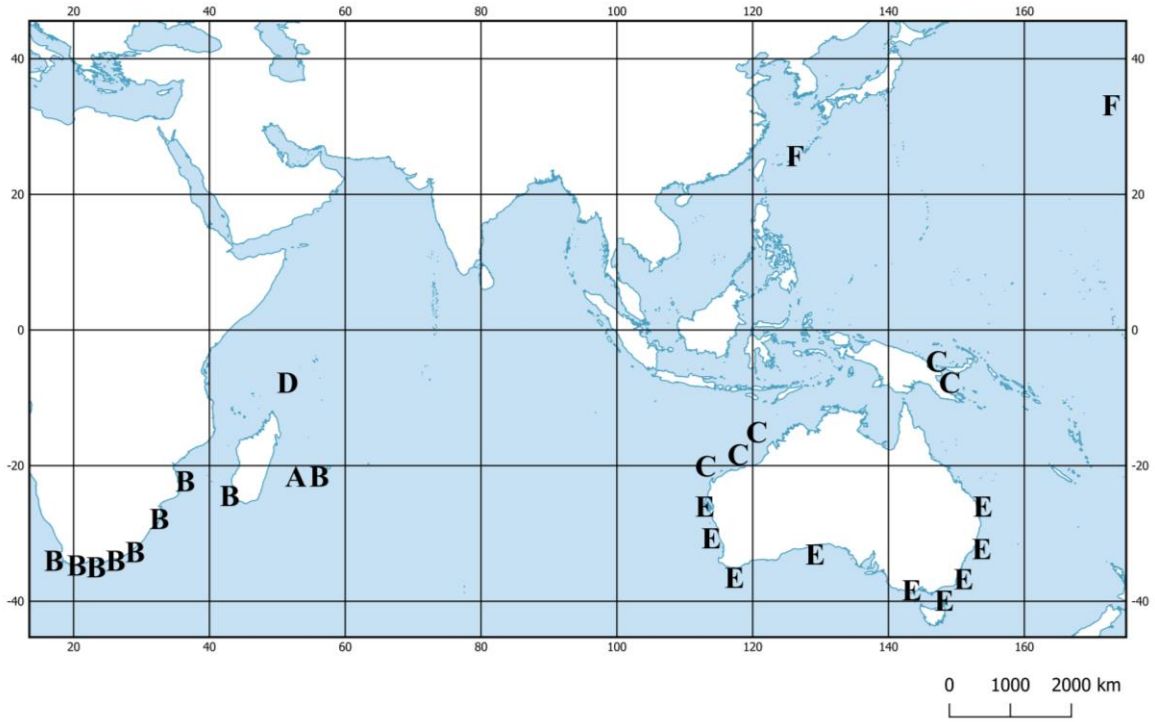

Figure 12. Distribution of short-snouted and high-bodied of the genus *Squalus* in the Indo-West Pacific. **A.** *Squalus longispinis* n. sp., **B.** *S. acutipinnis*, **C.** *S. crassispinus*, **D.** *S. lalannei*, **E.** *S. megalops* (sensu strictu), **F.** *S. shiraii*.

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