



The Sandy Zebra Shark: A New Color Morph of the Zebra Shark *Stegostoma tigrinum*, with a Redescription of the Species and a Revision of Its Nomenclature

Authors: Dahl, Rikke Beckmann, Sigsgaard, Eva Egelyng, Mwangi, Gorret, Thomsen, Philip Francis, Jørgensen, René Dalsgaard, et al.

Source: Copeia, 107(3) : 524-541

Published By: The American Society of Ichthyologists and Herpetologists

URL: <https://doi.org/10.1643/CG-18-115>

The Sandy Zebra Shark: A New Color Morph of the Zebra Shark *Stegostoma tigrinum*, with a Redescription of the Species and a Revision of Its Nomenclature

Rikke Beckmann Dahl^{1,2,3,4}, Eva Egelyng Sigsgaard⁵, Gorret Mwangi⁶, Philip Francis Thomsen⁵, René Dalsgaard Jørgensen⁶, Felipe de Oliveira Torquato¹, Lars Olsen⁷, and Peter Rask Møller¹

The Zebra Shark, in recent years known as *Stegostoma fasciatum* (Hermann, 1783), is well known for its dramatic ontogenetic change of color pattern, from striped (“zebra”) juveniles to spotted (“leopard”) adults. Nevertheless, many aspects of the species’ biology, ecology, and morphology are still unknown or inadequately described, and its nomenclature is contentious. This study introduces a hitherto undescribed color morph of the Zebra Shark and provides an updated diagnosis and redescription of the species. Firstly, we establish that the Zebra Shark remains a single species based on genetic data from mitochondrial COI and ND4 markers. Secondly, through morphological analyses, we conclude that there are two morphs of the species, the known, zebra striped morph and a new, sandy colored morph. Both morphs were studied morphometrically to expose any ontogenetic changes, such as a decrease in the relative length of the tail with increasing total length (TL). The external coloration pattern clearly differentiates the two morphs, and both morphs can be further divided into three stages based on color pattern and size: juveniles (255–562 mm TL), transitionals (562–1395 mm TL), and adults (>1300 mm TL). The transitional sandy morph is dorsally covered by a swirly pattern of thin, dark brown bands edged with freckle-like brown spots. The adults are a uniform sandy beige, partially covered with brown freckles. A mature male of the zebra morph displayed a yet unknown feature of the claspers: a small, triangular spike extruding from the dorsal terminal of the clasper glands. Finally, we reviewed the nomenclature of the species and suggest that the original name *Stegostoma tigrinum* Forster, 1781 should be used as the senior synonym for the species.

THE carpet sharks (Orectolobiformes) comprise a diverse group of elasmobranchs originating in the early Jurassic period approximately 200 million years ago (Srdic et al., 2016). The ca. 45 species vary notably in habitat choice, size, and coloration (Schmeyer et al., 2019). The popular name, carpet sharks, is derived from the species having a marbled or mottled appearance reminiscent of carpet designs, which is thought to serve mainly for camouflage purposes. The detailed biology of the distinct coloration patterns is still poorly studied for most species, but mimicry (Dudgeon and White, 2012) and cryptic coloration (shading or bottom camouflage) have been suggested (Cut-hill et al., 2005; Garla et al., 2015).

The Zebra Shark is one of the most iconic species of carpet sharks and is known to undergo dramatic change of color from a “zebra” pattern in the juvenile, through the transitional stage, to a “leopard” pattern in the adult stage. Until now, these three stages are only roughly distinguished by color and pattern. Because of the difference in appearance between juveniles and adults, until 1823 the two stages were believed to be two different species (van Hasselt, 1823).

Historically, Artedi (1738) was the first to describe the Zebra Shark under the name of *Squalus* spp., but the first official description was presented by Seba (1759) under the name of *Squalus varius*. Until 1939, the Zebra Shark had been

described under 15 different scientific names, and it was not until after Compagno (1984) that *Stegostoma fasciatum* was widely accepted as the official scientific name for the species. The Zebra Shark has its common name from Shaw (1804), who named the shark *Squalus zebra*, referring to the banded pattern of black and white displayed by juveniles. This study presents a revised synonymy of the species and suggests a name change from *Stegostoma fasciatum* (Hermann, 1783) to *Stegostoma tigrinum* Forster, 1781. This is, in our opinion, the only valid name for this species, as Forster (1781) was the first to properly, binominally name the Zebra Shark and included type specimens for the description.

Today, the phylogenetic position of *S. tigrinum* is in the monotypic family Stegostomatidae proposed by Applegate (1972) and later accepted by Compagno (1973, 2001). Recent authorities, however, disagree with this and suggest that *S. tigrinum* is grouped with the Shorttail Nurse Shark *Pseudoginglymostoma brevicaudatum* (Nelson et al., 2016) based on Naylor et al. (2012a). It has also been presented as a sister group to the Whale Shark *Rhincodon typus* (Dingerkus, 1986; Chen et al., 2016), as a sister group to a clade consisting of Nurse Sharks *Ginglymostoma* spp. and the Whale Shark (Goto, 2001), and as a sister group to a clade including the Whale Shark and the Shorttail Nurse Shark (Naylor et al., 2012b).

¹ Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark; Email: (RBD) rikke.beckmann.dahl@gmail.com; (FOT) felipe.torquato@snm.ku.dk; and (PRM) pdrmloller@snm.ku.dk. Send reprint requests to RBD.

² Department of Life Science, National Taiwan Normal University, Taipei, Taiwan 11677.

³ Biodiversity Program, Taiwan International Graduate Program, Academia Sinica, Taipei, Taiwan 11529.

⁴ Biodiversity Research Center, Academia Sinica, Taipei, Taiwan 11529.

⁵ Department of Bioscience, University of Aarhus, Ny Munkegade 116, Building 1540, 8000 Aarhus C, Denmark; Email: (EES) eva.sigsgaard@bios.au.dk; and (PFT) pftthomsen@bios.au.dk.

⁶ Kenya Tropical Sealife Ltd, P.O. Box 10570-80101, Bamburi, Kenya; Email: (GM) gorret@kenyatropicalsealife.com; and (RDJ) rene@kenyatropicalsealife.com.

⁷ Danish National Aquarium (Den Blå Planet) Jacob Fortlingsvej 1, 2770 Kastrup, Denmark; Email: iso@denblaaplanet.dk.

Submitted: 1 September 2018. Accepted: 25 May 2019. Associate Editor: M. T. Craig.

© 2019 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/CG-18-115 Published online: 25 September 2019

Today, *S. tigrinum* is a well-known species due to its wide distribution across the Indian and Western Pacific oceans and to its ability to thrive in captivity. Recent studies have contributed to the biological knowledge of the species, including its demography (Dudgeon et al., 2008), group seasonality (Dudgeon et al., 2013), population genetics (Dudgeon et al., 2006, 2017; Dudgeon and Ovenden, 2015), and reproduction (Kunze and Simmons, 2004), including parthenogenetic reproduction (Robinson et al., 2011; Dudgeon et al., 2017). Still, numerous basic morphological characters and their ontogenetic variation are not described in detail.

Therefore, the present study thoroughly redescribes *S. tigrinum* and, for the first time, describes a beige color morph of the species: the Sandy Zebra Shark. Uniformly colored Zebra Sharks have previously been observed off the coast of NW Australia (William T. White and Christine Dudgeon, pers. comm.), but it remains to be confirmed whether these are in fact similar to the color morph here described from off the coast of East Africa. Also, Nakaya (1973) described a uniformly colored Zebra Shark specimen that he referred to as an albino. The color of the iris, however, was described as blackish brown, inconsistent with the lack of pigmentation in true albinos where the color of the iris is usually pink. Thus, it is a possibility that the specimen described by Nakaya (1973) is the first encountered sandy morph. The name was chosen based on the colors of the morph and the fact that this is, so far, the only known difference between the two morphs. The well-known zebra striped/leopard spotted color morph will be referred to as the 'zebra morph.' Whether the beige color morph represents a new species was evaluated by DNA barcoding using the COI (cytochrome c oxidase subunit 1) and ND4 (mitochondrial NADH dehydrogenase subunit 4) markers. Furthermore, a full morphological study of *S. tigrinum* was conducted by encompassing morphometric and meristic measurements, including coloration, oral teeth, and dermal denticles. Lastly, we detailed the description of the reproductive organ of mature males revealing a hitherto unknown spike on the clasper gland.

MATERIALS AND METHODS

Molecular work.—Total genomic DNA was extracted from tissue samples (fin clips) from four different sandy color morph specimens (ZMUC P6268, ZMUC P2395374–75, ZMUC P2395470) and two zebra morph specimens (ZMUC P2395372–73). All six individuals were sequenced for a part of the ND4 gene, and three specimens of the sandy color morph were also sequenced for the COI gene. The DNA was extracted with the DNeasy® Blood and Tissue Kit (Qiagen) following the instructions of the manufacturer. The ND4 gene was amplified through polymerase chain reaction (PCR) using the primers ND4_new (5'-CATCTCTGACTCC CAAAAGCACATGTAGAAGC-3') and H12293-LEU (5'-TTGCACCAAGAGTTTTTGGTTCCTAAGACC-3'). The ND4_new primer is a modified version of the ND4 primer designed by Arévalo et al. (1994). Reactions were conducted in a total volume of 25 µl, consisting of 1 µl DNA, 2.5 µl GeneAmp™ 10X PCR buffer I (Applied Biosystems), 18.4 µl ddH₂O, 1 µl of each primer (10 mM), 0.1 µl AmpliTaq® polymerase, and 1 µl dNTPs (2.5 mM). PCRs were conducted with the initial denaturation step at 95°C for 5 min, followed by 30 cycles of 95°C for 15 sec, 56°C for 30 sec, and 72°C for 1 min, and a final extension at 72°C for 7 min. The sequences

of the sandy color morph were compared to those of the zebra color morph in Geneious v. 10.2.3 (Biomatters Ltd.). The COI gene was PCR amplified using primers (FishF1/FishR1) from Ward et al. (2005). Reactions were conducted in a total volume of 25 µl, consisting of 1 µl DNA, 10 µl TaqMan Environmental Master Mix 2, 12 µl ddH₂O, and 1 µl of each primer. PCRs were conducted with the initial denaturation step at 95°C for 10 min, followed by 45 cycles of 94°C for 30 sec, 54°C for 30 sec, and 72°C for 1 min, and a final extension at 72°C for 7 min. The sequences were searched against the GenBank nucleotide database using BLAST.

Morphology.—A total of 58 individuals were used in the morphological analyses. All morphological features and their associated terminology are summarized in Figure 1 and Table 1. Samples of dermal denticles were always taken from the lateral flank above the right pectoral fin in a non-ridge skin area and a ridge area. Oral teeth were extracted from the left anterior region of the upper and lower jaws of five specimens, using a scalpel. All samples were cleansed with distilled water and a 4 mm brush. Teeth and denticles were mounted on stubs, sputter coated with palladium in argon for 110 seconds, and then examined in a JEOL scanning electron microscope (SEM) at the Natural History Museum of Denmark. Presentation of data was done with the CorelDRAW X3 version 13 and CorelPhotoPaint X3 version 13.

A total of six specimens were radiographed for the examination of fin-ray structures and for vertebral counts. Body weight was measured with a hand-held weigh net for live specimens ($n = 33$) and a weighing scale for dead specimens ($n = 2$). The intestinal type, number of valvular turns, and female sexual maturity were examined by dissection ($n = 2$).

Fifty-two morphometric features were compared and tested for statistically significant differences among juveniles ($n = 14$ specimens, none live), transitionals ($n = 33$, 32 live), and adults ($n = 5$, none live) of the zebra morph; between transitionals ($n = 4$, all live) and adults ($n = 2$, 1 live) of the sandy morph; and between the two morphs. The latter comparison was done with all individuals of the same morph treated as a single group. A t-test was used to test differences in morphometric features between two groups (e.g., juveniles and adults; sandy and zebra morph), and comparisons among all three stages were done using a one-way ANOVA test. The latter was followed by a Tukey pairwise comparison test to test all possible pairs of means.

Stegostoma Müller and Henle, 1837

Squalus Seba, 1759; Forster, 1781; Hermann, 1783; Bloch, 1784; Broussonet, 1784; Bonnaterre, 1788; Gmelin, 1789; Pennant, 1791; Shaw, 1804; Bleeker, 1852; Gronow, 1854.
Scyllia van Hasselt, 1823.
Scyllium Rüppel, 1837.
Stegostoma Müller and Henle, 1837; Blyth, 1847; Günther, 1870; Garman, 1913; Whitley, 1939; Bass et al., 1975; Dingerkus, 1986; Compagno, 2001; Goto, 2001; Weigmann, 2016.
Stegostonea Regan, 1929: 293, possible error for *Stegostoma* Müller and Henle, 1837.
Stegastoma Herre, 1934: 10, possible error for *Stegostoma* Müller and Henle, 1837.
Stegastoma Last and Stevens, 1994: 138 apparent error for *Stegostoma* Müller and Henle, 1837.

Table 1. Morphometric measurements (% of TL) and meristic characters of *S. tigrinum*. Both morphs are represented. See Figure 1 for illustration of specific morphometrics.

		Zebra color morph		Sandy color morph		Total	
		Low–High (Avg)	<i>n</i>	Low–High (Avg)	<i>n</i>	Low–High (Avg)	<i>n</i>
1	Total length (TL, mm)	255–2050 (732.0)	52	586–1535 (1007.7)	6	225–2050 (760.5)	58
	Weight (kg)	0.4–40.0 (2.2)	31	0.6–13.2 (5.3)	5	0.4–40.0 (2.6)	36
Morphometric characters (%TL)							
2	Precaudal-fin length	41.4–58.7 (51.7)	50	50.0–55.2 (52.3)	6	41.4–58.7 (51.8)	56
3	Caudal-fin length	41.0–54.2 (47.7)	52	45.9–51.4 (49.4)	6	41.0–54.2 (48.6)	58
4	Precaudal tail	—	—	19.9–21.9 (20.9)	2	19.9–21.9 (20.9)	2
5	Snout to vent length	28.7–38.0 (32.6)	50	29.5–32.6 (30.9)	6	28.7–38.0 (32.4)	56
6	Prepelvic-fin length	26.5–33.9 (29.7)	50	28.4–31.2 (29.4)	6	26.5–33.9 (29.6)	56
7	Vent to caudal-fin tip	64.3–72.2 (68.5)	49	69.2–73.0 (70.3)	6	64.3–73.0 (68.7)	55
8	Vent to anal-fin origin	2.3–12.5 (9.5)	46	8.0–10.7 (9.3)	6	2.3–12.5 (9.5)	52
9	Prepectoral-fin length	8.3–20.1 (13.5)	52	12.4–14.0 (13.0)	6	8.3–20.1 (13.4)	58
10	Prebranchial length	9.1–16.9 (11.8)	51	10.4–11.8 (11.3)	6	9.1–16.9 (11.8)	57
11	Preorbital length	4.8–12.0 (7.2)	51	6.5–7.4 (7.0)	6	4.8–12.0 (7.2)	57
12	Preoral length	1.8–6.2 (3.7)	51	3.2–4.5 (3.8)	6	1.8–6.2 (4.0)	57
13	Prespiracular length	6.8–11.8 (8.6)	51	4.2–8.7 (7.5)	6	4.2–11.8 (8.5)	57
14	Pre-first dorsal-fin length	12.6–32.1 (19.3)	50	12.4–22.9 (18.0)	6	12.4–32.1 (19.2)	56
15	Snout to ridge length	6.2–12.1 (8.8)	49	7.5–8.9 (8.2)	5	6.2–12.1 (8.7)	54
16	Head width	9.2–14.8 (10.7)	51	9.8–10.7 (10.2)	6	9.2–14.8 (10.7)	57
17	Head depth	5.7–12.5 (7.3)	50	5.8–8.6 (7.1)	6	5.7–12.5 (7.3)	56
18	Intergill length	3.4–7.3 (4.2)	52	3.6–4.3 (4.0)	6	3.4–7.3 (4.2)	58
19	First gill slit height	1.1–2.5 (1.8)	52	1.4–1.9 (1.6)	6	1.1–2.5 (1.8)	58
20	Fifth gill slit height	1.0–2.4 (1.8)	51	1.5–1.8 (1.7)	6	1.0–2.4 (1.8)	57
21	Eye length	0.9–2.1 (1.4)	51	1.0–1.6 (1.3)	6	0.9–2.1 (1.4)	57
22	Eye height	0.4–1.5 (0.8)	48	0.4–0.9 (0.7)	6	0.4–1.5 (0.8)	54
23	Spiracle height	0.5–1.5 (0.9)	49	0.8–1.2 (1.0)	6	0.5–1.5 (1.0)	55
24	Spiracle length	0.4–1.7 (0.7)	49	0.6–0.8 (0.6)	6	0.4–1.7 (0.7)	55
25	Chin width	2.3–3.6 (2.9)	48	2.3–3.0 (2.7)	6	2.3–3.6 (2.9)	54
26	Nasal flap width	3.3–5.9 (4.2)	49	2.9–4.7 (3.8)	6	2.9–5.9 (4.1)	55
27	Lower labial furrow length	0.9–1.7 (1.2)	50	0.8–1.3 (1.1)	6	0.8–1.7 (1.2)	56
28	Upper labial furrow length	0.8–3.1 (1.6)	50	1.0–1.9 (1.5)	6	0.8–3.1 (1.6)	56
29	Barbel length	0.6–2.2 (1.5)	48	1.1–2.8 (1.6)	6	0.6–2.8 (1.7)	54
30	Mouth width	2.9–6.8 (5.0)	51	3.9–5.5 (4.6)	6	2.9–6.8 (4.9)	57
31	Bony interorbital width	3.9–6.2 (5.3)	11	—	—	3.9–6.2 (5.3)	11
32	Fleshy interorbital width	5.7–15.5 (10.2)	48	9.6–10.2 (10.0)	6	5.7–15.5 (10.2)	54
33	Preanal-fin body depth	4.4–9.8 (5.9)	48	5.4–7.6 (6.4)	6	4.4–9.8 (5.9)	54
34	Max caudal-fin height	5.9–9.0 (7.8)	49	6.9–8.8 (7.9)	5	5.9–9.0 (7.8)	54
35	Interdorsal distance	2.4–6.3 (4.9)	49	3.7–6.7 (4.7)	6	2.4–6.7 (4.0)	55
36	Clasper length inner	0.7–8.7 (3.6)	26	3.7–7.0 (4.9)	4	0.7–8.7 (3.7)	30
37	Clasper length outer	0.8–6.5 (2.0)	26	0.8–3.0 (1.6)	4	0.8–6.5 (1.9)	30
38	Pectoral-fin inner margin	3.6–14.4 (4.8)	50	4.1–5.1 (4.6)	6	3.6–14.4 (4.8)	56
39	Pectoral-fin anterior margin	10.4–19.1 (14.0)	52	11.9–15.9 (14.2)	6	10.4–19.1 (14.0)	58
40	Pectoral-fin base to tip	7.8–15.7 (12.0)	49	11.8–14.8 (13.1)	6	7.8–15.7 (12.1)	55
41	Pelvic-fin length inner	2.5–7.0 (5.7)	49	3.3–7.0 (5.0)	5	2.5–7.0 (5.7)	54
42	Pelvic-fin length outer	4.5–11.0 (7.1)	50	5.3–8.5 (7.0)	6	4.5–11.0 (7.1)	56
43	Pelvic-fin width	2.6–5.9 (4.2)	49	4.2–6.7 (5.1)	5	2.6–6.7 (4.3)	54
44	First dorsal-fin base	7.1–17.7 (13.3)	50	12.6–18.1 (14.9)	6	7.1–18.1 (13.5)	56
45	First dorsal-fin height	2.0–5.9 (3.7)	52	3.9–4.7 (4.2)	6	2.0–5.9 (3.7)	58
46	First dorsal-fin inner margin	2.1–4.7 (2.8)	49	2.2–3.6 (3.0)	6	2.1–4.7 (2.8)	55
47	Second dorsal-fin base	2.1–14.4 (7.7)	50	5.2–8.3 (6.7)	6	2.1–14.4 (7.6)	56
48	Second dorsal-fin height	1.3–3.4 (2.1)	52	2.1–2.6 (2.3)	6	1.3–3.4 (2.1)	58
49	Second dorsal-fin inner margin	0.2–8.7 (2.4)	49	2.0–3.3 (2.7)	6	0.2–8.7 (2.5)	55
50	Anal-fin base	5.7–13.3 (8.6)	47	6.3–9.8 (8.4)	6	5.7–13.3 (8.6)	53
51	Anal-fin height	1.7–4.9 (2.9)	51	2.2–3.7 (3.1)	6	1.7–4.9 (2.9)	57
52	Anal-fin inner margin	0.6–2.6 (1.7)	49	1.2–2.4 (1.7)	6	0.6–2.6 (1.7)	55

Table 1. Continued.

	Zebra color morph		Sandy color morph		Total	
	Low–High (Avg)	<i>n</i>	Low–High (Avg)	<i>n</i>	Low–High (Avg)	<i>n</i>
Meristic characters						
Tooth rows (upper jaw)	27–30 (28.5)	4	13–28 (20.5)	2	13–30 (25.8)	6
Tooth rows (lower jaw)	22–30 (25.5)	4	25–26 (25.5)	2	22–30 (25.5)	6
Tooth series (upper jaw)	7–18 (13)	3	11–27 (19)	2	7–27 (15.4)	5
Tooth series (lower jaw)	8–16 (12.7)	3	13 (13)	1	8–16 (12.8)	4
Vertebrae count	220–262 (231.3)	4	222–230 (226)	2	222–262 (231)	6
Monospondylous precaudal count	46–47 (46.8)	4	46–48 (47)	2	46–48 (46.8)	6
Diplospondylous precaudal count	40–49 (44)	4	45–47 (46)	2	40–49 (44.7)	6
Diplospondylous caudal count	126–175 (140.5)	4	131–144 (137.5)	2	126–175 (139.5)	6
Precaudal count	89–96 (90.8)	4	91–95 (93)	2	89–96 (91.5)	6
Valvular turns	—	—	18–20 (19)	2	18–20 (19)	2

barbed shark) and La gallonné (the braided one), the latter name was incorrectly interpreted in Kottelat (2013).

Squalus tigrinus Gmelin, 1789: p. 1493. Cites Bloch (1784), Gronovius (1754), Gronovius (1763: p. 33, no. 147), Seba (1759), Hermann (1783), and Broussonet (1784).

Squalus longicaudus Gmelin, 1789: p. 1496. No description other than a few words from Gronovius (1754), Gronovius (1763), and Seba (1759). In the same publication on p. 1493, he described the species as *Squalus tigrinus*, suggesting that he wanted to rename it to *S. longicaudus*.

Squalus tigrinus Pennant, 1791: p. 55 and 92, pl. 16 (XVI). Pennant cited Gmelin (1789), Bloch (1784), Gronovius (1754), Seba (1759), Hermann (1783), and Forster (1781). According to Kottelat (2013), the description was based on syntypes mentioned by Seba (1759). But the schematic drawing of a specimen is from Forster (1781).

Squalus zebra Shaw, 1804: p. 352, pl. 148. First entry of the common name “Zebra Shark” in the literature. Figure is from Bloch (1784). Shaw cites Seba (1759), Gmelin (1789), and Bloch (1784).

Scyllia quinquecornautum van Hasselt, 1823: p. 315 (see Alfred, 1961: p. 81 for English translation). Based on specimens found by Kuhl and van Hasselt in Java, Indonesia, measuring >8 feet (2400 mm) with reference to Seba (1759). Van Hasselt was aware that *S. tigrinum*, which had previously only been portrayed in the juvenile stage, was in fact the same species as the >2400 mm specimens he had described. Van Hasselt placed this species in the order Chondropterygiens in the family Cyclostomes and the genus *Scyllia* (based on Cuvier’s *Scyllium*, 1816 and today accepted as *Scyliorhinus* Blainville, 1816).

Scyllium heptagonum Rüppel, 1837: p. 61, pl. 17 fig. 1. Description was based on a single specimen from the Red Sea, Didda (Jeddah), Saudi Arabia; Holotype: SMF 3152. Kottelat (2013) mentioned that Klauswitz (1960: p. 290) designated lectotypes from Rüppel’s types, but this information is inaccurate as Rüppel explicitly based his description on a single specimen. The specimen is 1060 mm TL, and the figure reveals a mix of transitional and adult patterning.

Stegostoma carinatum Blyth, 1847: p. 725, pl. 25, fig. 1. Based on an adult specimen caught in India (holotype possibly preserved at the Zoological Survey of India). Blyth (1847) described the shark as a new, second species of the genus *Stegostoma*. He portrayed the specimen in pl. 25, fig. 1 as the adult stage with details of the enlarged dermal denticles on the dorsal ridge.

Stegostoma fasciatum Bleeker, 1852: p. 23. Based on a single female of 425” caught off Saramang in 1846. Bleeker was aware that Blyth (1847) already described this species, as he included Blyth’s name *S. carinatum* in a synonymy. He noted the developmental stage of each specimen (juvenile/ adolescence), which indicates that Bleeker was aware of the ontogenetic pattern difference.

Squalus pantherinus Kuhl and van Hasselt, mentioned by Bleeker (1852) in synonymy.

Squalus cirrosus Gronow, in Gray, 1854: p. 6. Described the species with references to Gronovius (1763), which is based on Gronovius (1754) and Seba (1759). Description is brief and Gray (1854) suggested *S. cirrosus* as a new name for the species.

Stegostoma tigrinum Günther, 1870: p. 409. Provided a synonymy briefly describing the skin colors observed in the species and mentioning specimens preserved in collections at the time.

Stegostoma varium Garman, 1913: p. 59. Based on two specimens of 300 mm TL (juvenile) and 1500 mm TL (adult), with details on the juvenile and adult patterns and their individual variation (based on other literature). Includes a synonymy. Location: East Indies to Africa. Syntypes are MCZ 55-S (1 specimen, Philippines: Manila), 33437 (1 specimen, Mauritius), and 1 uncat. specimen (Eschmeyer et al., 2019).

Stegostoma tigrinum naucum Whitley, 1939: p. 229, fig. 2. Mentioned that type specimens from the Indian Ocean are banded, while other types are spotted. Never suggested that the two morphs belong to a single species. Suggested that a spotted example from Hawkesbury River, New South Wales, Australia, was a new subspecies *naucum*, based on morphometric differences, such as a longer distance between the anal fin and subcaudal lobes, fin proportions, larger spots and thicker nasal cirri. Holotype: AMS I.4174 (Paxton et al., 1989).

Diagnosis

Stegostoma tigrinum is characterized by a long caudal fin (49.9–54.2% TL) and five dorsolateral ridges along the body, visible even in hatchlings. Spiracles bean shaped, large (length 0.4–1.7% TL); eyes small (length 0.9–2.1% TL); barbels two, short (0.6–2.8% TL); gill slits five, but fourth and fifth partly fused so only four noticeable from a distance; pectoral fins large (anterior margin length 10.4–19.1% TL), broad and rounded; first dorsal fin originates far posteriorly above pelvic fins. Two color morphs, with a three-stage

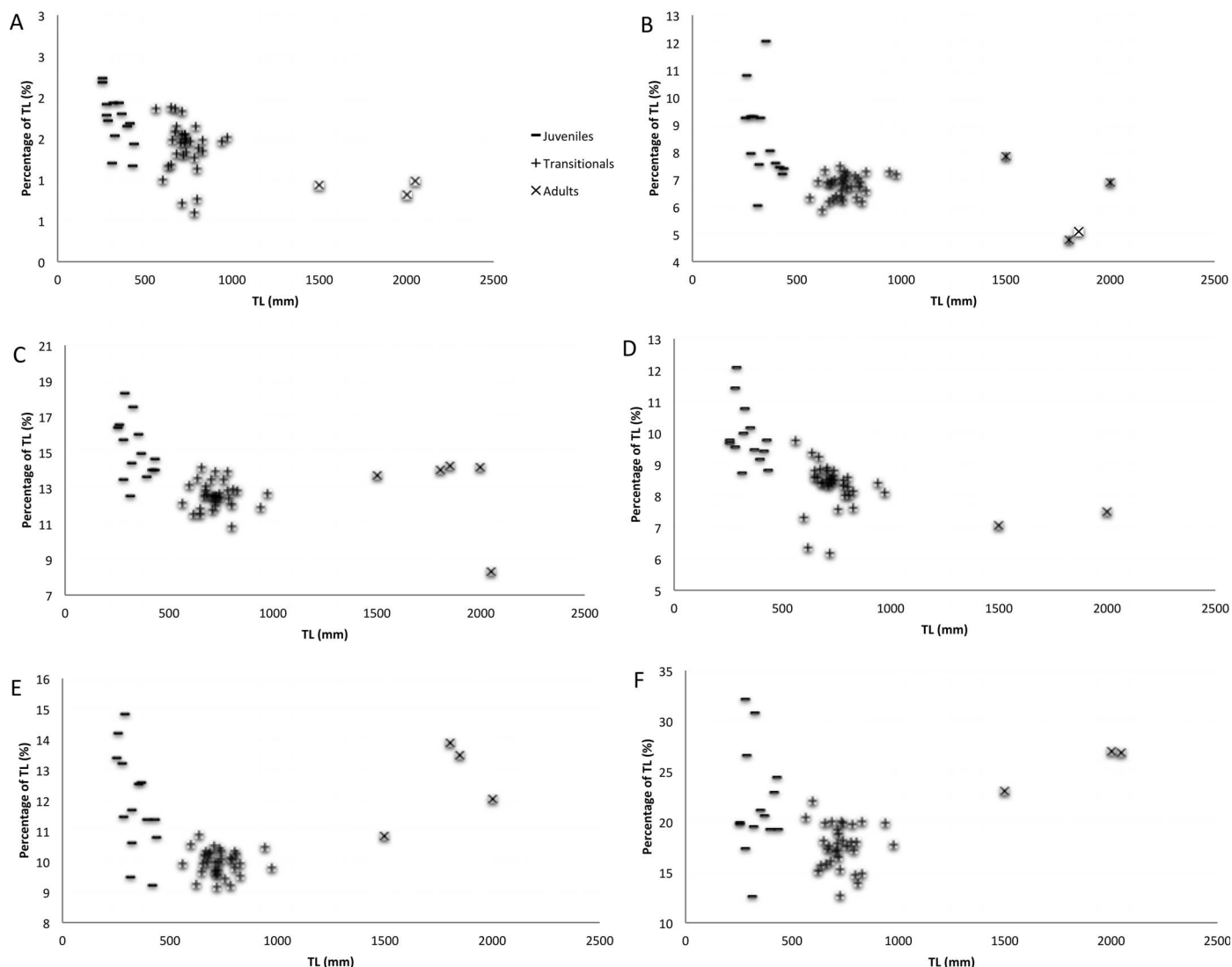


Fig. 2. Six plots of morphometric characters of the zebra morph of *S. trigrinum* measured in % of TL. (A) Barbel length: decreases with growth of individual shark ($P = 0.0002$). (B) Preorbital length: longer in zebra juveniles ($P = 0.0001$). (C) Prepectoral-fin length: longer in zebra juveniles ($P = 0.0002$). (D) Pre-ridge length: longer in zebra juveniles ($P = 0.0001$). (E) Head width: shorter in zebra transitionals ($P = 0.001$). (F) Pre-first dorsal-fin length: shorter in zebra transitionals ($P = 0.001$). '—' Juveniles, '+' transitionals, 'x' adults.

ontogenetic color and pattern change. Zebra morph: juveniles with dark brown background and cream colored bands (zebra-like); transitionals light brown with dark bands, broken up by dots; adults beige to yellow with spotted pattern (can be leopard-like). Sandy color morph: transitionals light beige background with swirly pattern of narrow, darker brown bands with tiny spots breaking up the pattern; adults uniformly sandy beige with tiny dark brown freckles. Maximum length 2050 mm TL, hatchlings approx. 250 mm TL; pectoral-fin rays of semi-plesodic structure, reaching approx. 66–88% of pectoral fin. Total vertebrae 207–262, monospondylous precaudal vertebrae 43–49, diplospondylous precaudal vertebrae 38–50, diplospondylous caudal vertebrae 120–175, precaudal vertebrae 81–101. Tooth rows upper jaw: 13–30, lower jaw: 22–30, and series count, upper jaw: 7–27, lower jaw: 8–16. Ring-type intestine with 18–20 valvular turns.

Description

Body long and slender. Caudal fin approximately half TL. Head truncate and rounded with an almost straight,

subterminal mouth; mouth corners framed with an upper and a lower labial furrow, lower furrows intervened by chin (a trilobate lower lip); nasal flap covers teeth and originates from two large nostrils, each with a small barbel; long and strongly developed nasoral grooves below nasal flap; teeth tricuspid and homodont; eyes small and oval, positioned laterally on head prior to a large bean-shaped spiracle; no nictitating eyelid and no subocular pockets, but eye can be almost closed by muscle contraction if disturbed. Four gill slits visible externally, as the fourth and fifth slit share the same opening; no filter screens internally. Pectoral fins originate below second gill slit and are large and rounded; pectoral-fin web semi-plesodic, so that fin radials extend further distally in the fin web than in the aplesodic type; mesopterygium and metapterygium are separated, and according to Compagno (2001), the propterygium is small and separated from the latter ones; first dorsal-fin origin at level of post spiracle, but a strong dorsal ridge obscures exact origin; ridges are made of enlarged and strengthened dermal denticles; two additional ridges on each lateral flank, all ridges clearly visible from neonate stage, upper lateral ridge

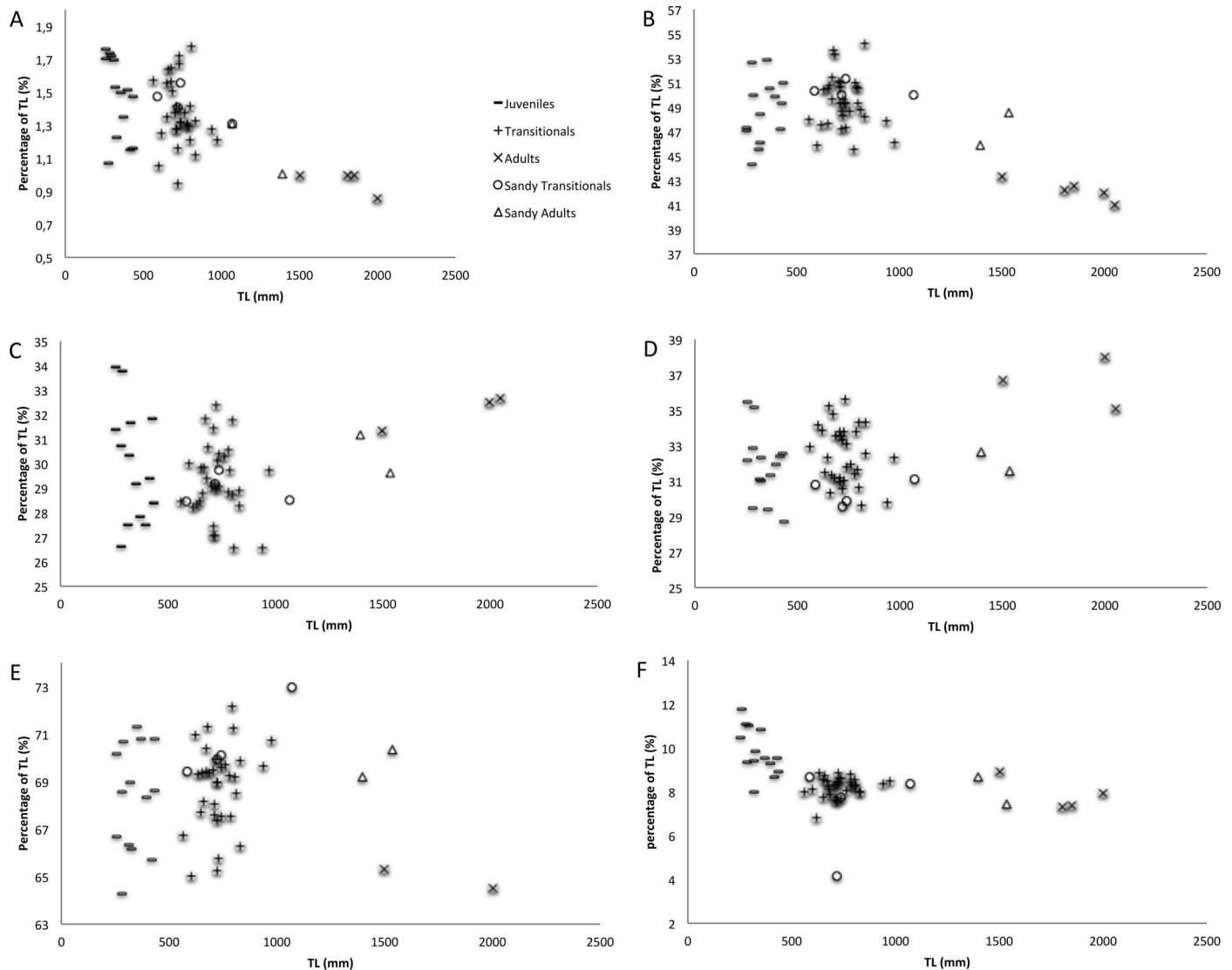


Fig. 3. Six plots of morphometric characters of the zebra and the sandy morphs of *S. tigrinum* measured in % of TL. (A) Eye length: smaller in adults of both morphs (zebra $P = 0.002$, sandy $P = 0.005$). (B) Caudal-fin length: shorter in adults of both morphs (zebra $P = 0.0001$, sandy $P = 0.027$). (C) Prepelvic-fin length: longer in adults of both morphs (zebra $P = 0.02$, sandy $P = 0.092$). (D) Snout to vent length: longer in adults of both morphs (zebra $P = 0.0003$, sandy $P = 0.049$), and longer in zebra morph as a group ($P = 0.055$). (E) Vent to caudal-fin tip: longer in zebra morph adults ($P = 0.024$), and for the sandy morph as a group ($P = 0.055$). (F) Prespiracular length: larger in zebra morph as a group ($P = 0.017$). '—' Zebra juveniles, '+' zebra transitionals, 'x' zebra adults, 'o' sandy transitionals, 'Δ' sandy adults.

originates above mid pectoral fin and ends below second dorsal fin, where the lower lateral ridge originates after pectoral fin and ends at caudal-fin origin, first dorsal fin triangular in shape with rounded edges, immediately followed by an elevation of the dorsal skin which turns into the second dorsal fin, the latter half the size of the first but proportions are similar; pelvic fins positioned below first dorsal fin but end further caudally; pelvic fins are smaller than first dorsal fin but larger than second dorsal fin; anal-fin origin below mid second dorsal fin and ends at caudal-fin origin; anal fin larger than second dorsal fin; caudal peduncle smooth with no keel or precaudal pits; caudal fin long, broad and distally narrowed in a strong, single terminal lobe with a subterminal notch; consists of a dorsal lobe only. Mature males express an outer clasper size of minimum 6.9% of TL and an inner size of 12.5% of TL. Vertebral count highly variable but no indication of differences between the two morphs (Table 1); total vertebrae 207–262, monospondylous precaudal count 43–49, diplospondylous precaudal count

38–50, diplospondylous caudal count 120–175, precaudal count 81–101. Valvular intestine is of ring type and turns range from 18–20. For more details on head cartilage (cranium, jaws) and jaw muscles, see Compagno (2001) and Goto (2001).

Genetics

A comparison of the ND4 and COI sequences between the sandy morph (own sequences) and the zebra morph (own and GenBank sequences) revealed a 99.49–100% and 99.69–100% identity, respectively. Thus, the genetic results indicate that the two color morphs represent the same species. Nucleotide sequences for the COI and ND4 genes can be found in GenBank under accession numbers MK495838–MK495846.

Morphometrics

Ontogenetic changes within both morphs.—Barbel length of the zebra color morph is significantly different among all

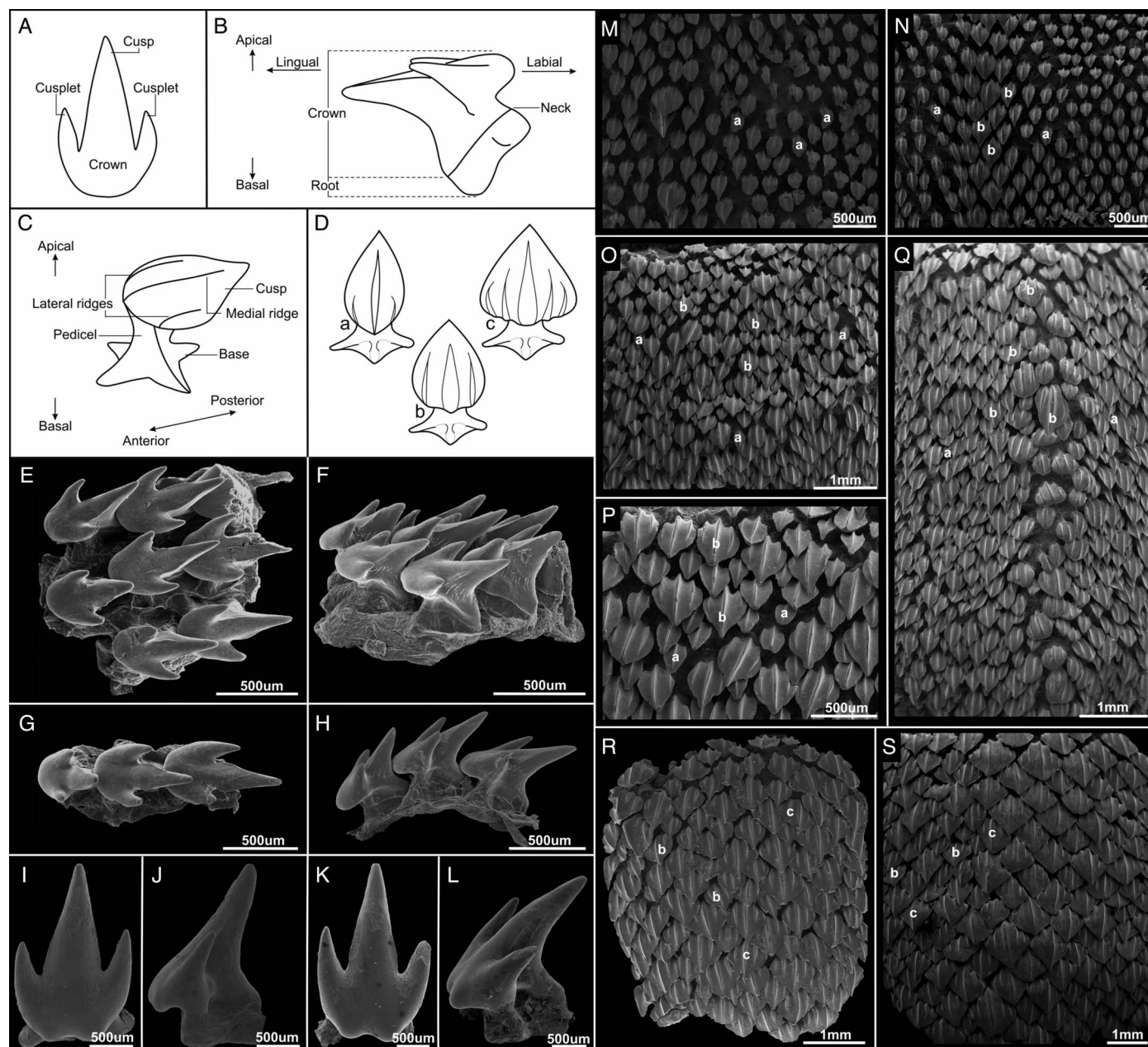


Fig. 4. Oral teeth and dermal denticles of *S. tigrinum*: schematic presentation and nomenclature of oral teeth (A–B) and the three types of dermal denticles, type *a*, *b*, and *c* (C–D). Oral teeth from a juvenile specimen (ZMUC P2394733, 325 mm TL) from upper (E–F) and lower jaw (G–H); oral teeth from an adult (ZMUC P6268, 1395 mm TL) upper (I–J) and lower (K–L) jaw; dermal denticles from a juvenile specimen (ZMUC P2394733, 325 mm TL) from a non-ridge area (M) and a ridge area (N); a transitional specimen (ZMUC P2395470, 630 mm TL) non-ridge (O–P) and ridge (Q); and of an adult specimen (ZMUC P6268, 1395 mm TL) non-ridge (R) and ridge (S).

three stages. There is a negative allometric change in barbel size, meaning that the barbels become proportionally shorter with increased body size ($P = 0.0002$, Fig. 2A). Juveniles of the zebra color morph have the longest preorbital length ($P = 0.0001$, Fig. 2B), the longest prepectoral-fin length ($P = 0.0002$, Fig. 2C), and the longest pre-ridge length ($P = 0.0001$, Fig. 2D), compared with transitionals and adults. This implies that the heads of juveniles have longer dimensions and become shorter and more compact with age. For the zebra color morph, the head width ($P = 0.001$, Fig. 2E) and the pre-first dorsal-fin length ($P = 0.001$, Fig. 2F) are significantly shorter in the transitional stage. Adults of both morphs have significantly smaller eye length than transitionals and juveniles ($P = 0.002$ zebra morph and $P = 0.005$ sandy

morph, Fig. 3A). Adults of both morphs have a significantly shorter caudal-fin length than both transitionals and juveniles ($P = 0.0001$ zebra morph and $P = 0.027$ sandy morph, Fig. 3B). There is a tendency that adults of both morphs have a longer prepelvic-fin length ($P = 0.20$ zebra morph and $P = 0.092$ sandy morph, Fig. 3C) and a longer snout to vent length ($P = 0.0003$ zebra morph and $P = 0.049$ sandy morph, Fig. 3D) than transitionals and juveniles. Adults of the zebra morph have a longer distance from vent to caudal-fin tip than transitionals and juveniles ($P = 0.024$, Fig. 3E).

Differences between the two morphs.—No diagnostic differences between the two morphs were found, though the

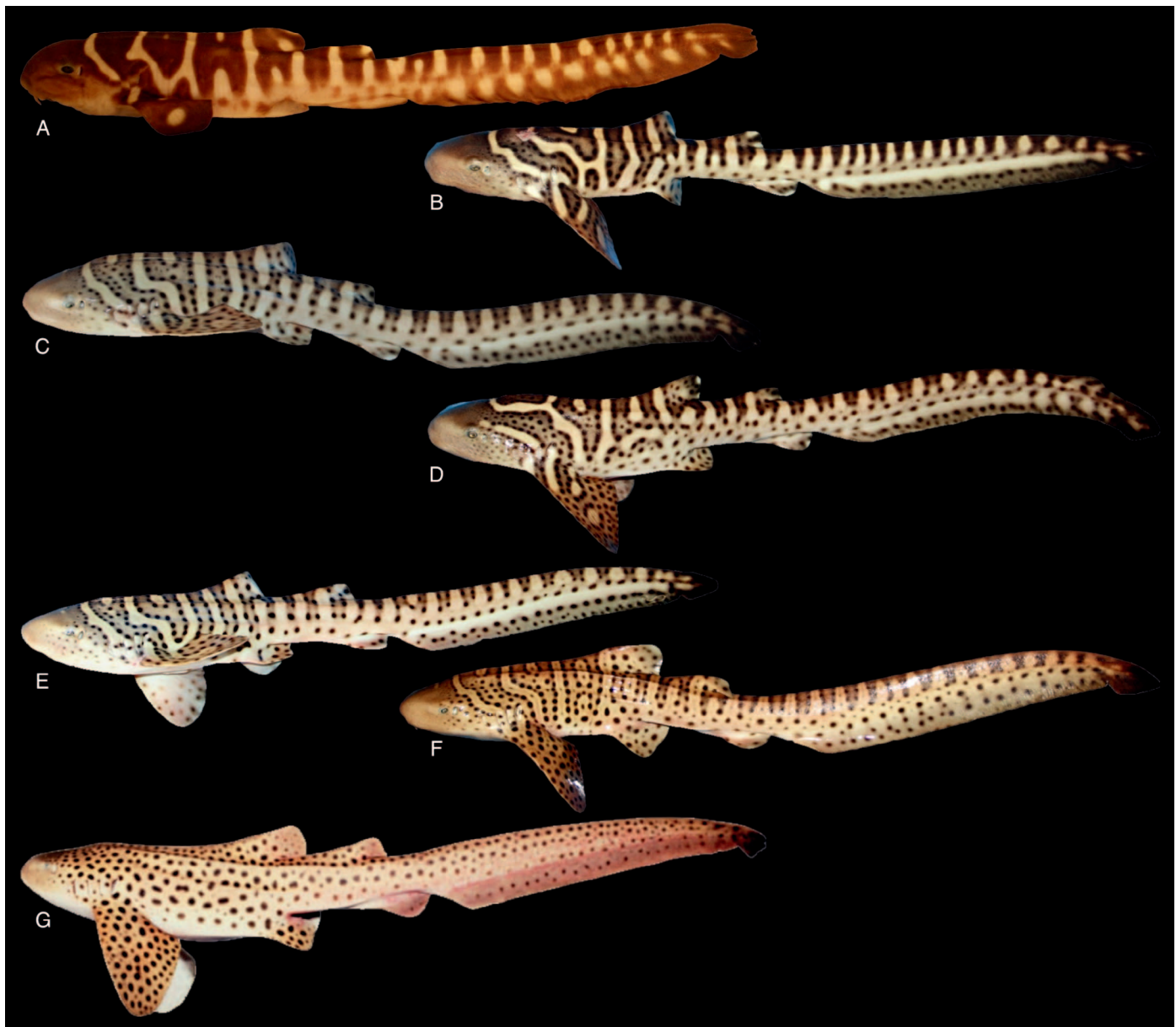


Fig. 5. The three ontogenetic stages of the external morphology of the zebra morph of *S. tigrinum*: juvenile (A), transitional (B–F), and adult (G).

sample size of the sandy morph was below the ideal size and the results should be interpreted as tendencies. A few characters appear to be different when comparing average values; for instance, the sandy morph displayed a longer distance from vent to caudal-fin tip than the zebra morph ($P = 0.055$, Fig. 3E), while the zebra morph displayed a larger snout to vent ($P = 0.055$, Fig. 3D) and prespiracular length ($P = 0.017$, Fig. 3F). These differences, however, are in all likelihood a result of the ontogenetic variation in those characters and the different average TL in the two groups.

Oral teeth

No differences in the oral teeth were found between the two color morphs. *Stegostoma tigrinum* has homodont teeth with no apparent sexual dimorphism. Each tooth has a strong, elongated medial cusp and two smaller lateral cusplets (Fig. 4A, B, E–L). The cusplets are rounded, whereas

the cusp has blade-like edges. The tooth sheets reveal that the teeth are positioned closer to each other in the series than in the rows (Fig. 4E–H). The oral dentition expresses individual variation, where the curvature of the cusps can be either concave or convex (Fig. 4J, L). The tooth root is mildly bilobed with small lateral and a large labial/centered nutrient groove.

Dermal denticles

Elevated lateral ridges along the flanks of *S. tigrinum* consist of denticles that appear thicker, broader, and more densely positioned in ridge areas compared to non-ridge areas. There appear to be no differences between the zebra and the sandy color morph in the dermal denticles (Fig. 4).

Three types of dermal denticles are present, identified by the number of scutes and the width of the dorsal denticle cusp (Fig. 4C). The first type, *a*, is a simple droplet-shaped

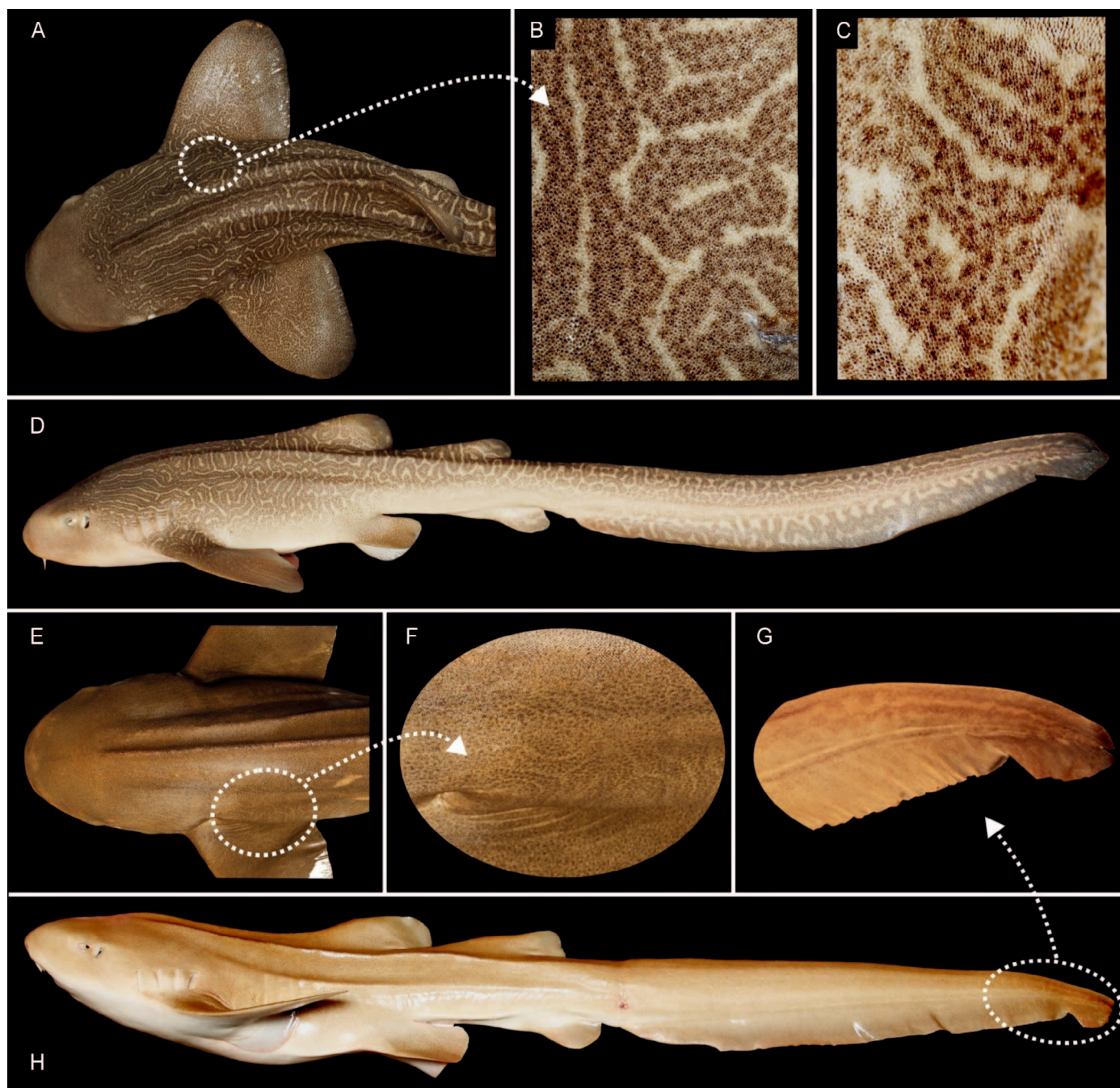


Fig. 6. The sandy morph of *S. tigrinum*: transitional (A–D) and adult (E–H). Close up of the skin pattern on the right lateral flank of a transitional specimen (B–C) and of remnants of the transitional pattern on flank and caudal-fin tip of adults (F–G).

denticle, with a single medial scute on the dorsal cusp. The second type, *b*, has a broader cusp with one medial and two lateral scutes protruding from the surface. The medial scute can vary in thickness by being either broad and flat or high and narrow. The third type, *c*, has an even broader dorsal cusp than type *b*, with one medial scute and two lateral scutes on each side. Type *c* denticles appear to be thicker, and thus stronger, than type *a* and type *b* (see Fig. 4C for a schematic overview of the denticle types), and the width of the root increases with the width of the crown.

The ridges consist of more type *b* and *c* denticles compared with the non-ridge areas. Non-ridge areas consist mainly of type *a* and *b* denticles, but all examined specimens also expressed intermittent pairs of enlarged denticles in the non-ridge area of type *b* and *c* (Fig. 4M). These were found in a

straight line between the two lateral ridges always with one denticle overlapping the other.

The denticles change with the growth of the individual shark, ranging from type *a* to type *b* in a non-ridge area, and from type *b* to type *c* in a ridge area. In juveniles, the non-ridge area is mainly made up of type *a* denticles (Fig. 4M), while the ridge area is of type *b* (Fig. 4N). As the transitional stage is long, and the animal grows extensively in this period, the denticle composition was different between a small (630 mm TL, ZMUC P2395470) and a large transitional specimen (885 mm TL, ZMB 5258), the latter being more reminiscent of an adult in the denticle composition. The smallest specimen exhibited type *a* and type *b* denticles in the non-ridge area (Fig. 4O) and type *b* denticles in the ridge area (Fig. 4P, Q).



Fig. 7. Specimens of *S. tigrinum* from Kenya in the transitional stage, shown from smallest to largest body size (no. 1–24) in dorsal and lateral view. No. 1–6: 565–670 mm TL, no. 7–12: 675–710 mm TL, no. 13–18: 740–800 mm TL, and no. 19–24: 802–975 mm TL.

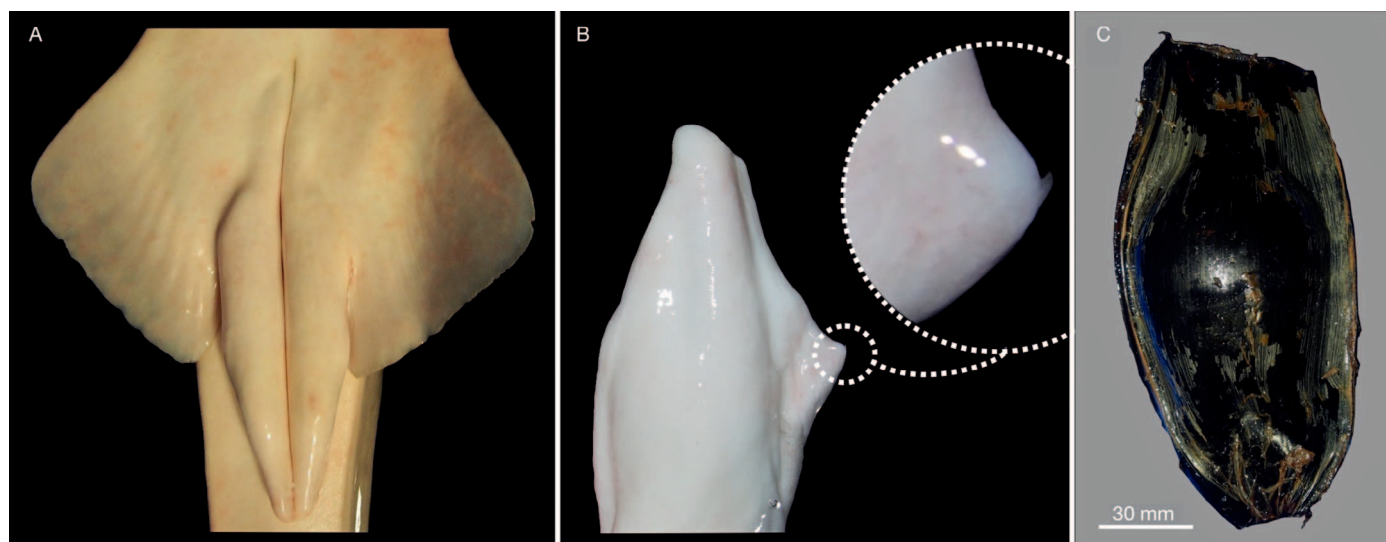


Fig. 8. Claspers of a mature, male *S. tigrinum*, DBP4, 1935 mm TL (A) with close up of the short, triangular spike extruding from the dorsal terminal of the clasper gland (B) and an unfertilized egg from a female, DBP2/3 (C).

For the adults, the non-ridge denticles were of type *b* and *c* (Fig. 4R), and the ridge area was mainly of type *c* with only sporadic occurrences of type *b* (Fig. 4S).

Coloration

Zebra morph of *Stegostoma tigrinum*.—The juvenile coloration consists of a dark brown background on the dorsal side and lateral flanks, with 18–25 cream white to yellowish bands stretching from flank to flank, only interrupted by large round or elongated dots of the same color (Fig. 5A). The bands show clear individual variation, but there are still some repeated features seen on most of the specimens: the third anterior-most band branches distally into two branches on each flank; the first or the second anterior-most band continues onto the pectoral fin; one or two large round dots or short bands and two elongated dots or short bands are seen on each pectoral fin; the upper dorsal lobe has short- to

dot-like bands repeated to the tip of the fin. Correspondingly, the lower dorsal lobe displays round or elongated dots in either a horizontal or vertical direction; there are one or two round dots on the first dorsal fin and a single dot on the second dorsal fin. The ventral side is cream colored from snout to lower caudal-fin origin.

The breaking up of the juvenile pattern marks the transitional stage (Figs. 5B–F, 7). Only some of the Kenyan specimens have the third anterior-most band distally split in two (Fig. 7: no. 3, 4, 5, 6, 13, 15, 16, 19, 21). The most noticeable repeated features are those of the pectoral fins: two elongated, slightly curved dots/short bands are positioned anteriorly, stretching from the lateral flank toward the anterior margin of the pectoral fin; and a single dot in the middle of the distal-most half of the fin. In the transitional stage, small dots appear around the edges of the cream colored bands on the whole body of the shark, along with dots on the dark background of the pectoral fins, the lower lateral flanks, and the dorsal lobe of the caudal fin. The dark brown color becomes lighter and is much more variable between transitionals than between juveniles. In some individuals, the small dots also cover the dark areas between the bands prior to the first dorsal fin. The snout is always pale without dots. Over time, the bands disappear and merge to a uniform background color and the dots spread out evenly over the body (Fig. 5F). Toward the end of the transitional stage, the largest specimen in this study (975 mm TL) had pectoral fins completely covered by dots (Fig. 7: no. 24), and the remnants of the two short bands and the single dot were very vague.

The adult coloration is a uniform sandy beige to yellowish background, with a spotted pattern spreading out from above the eyes to the caudal-fin tip (Fig. 5G). The spots can vary greatly in shape, size, and frequency, from small dots to larger leopard-like shapes. The two dried adults examined in this study had visible but faint coloration due to the state of preservation. Both these adults had medium sized dots covering the body in a spacious pattern. The remaining four adult specimens (DBP1–4) displayed dark brown, uniformly shaped dots, though one of the females (DBP2) expressed a cream colored ring around each dot.

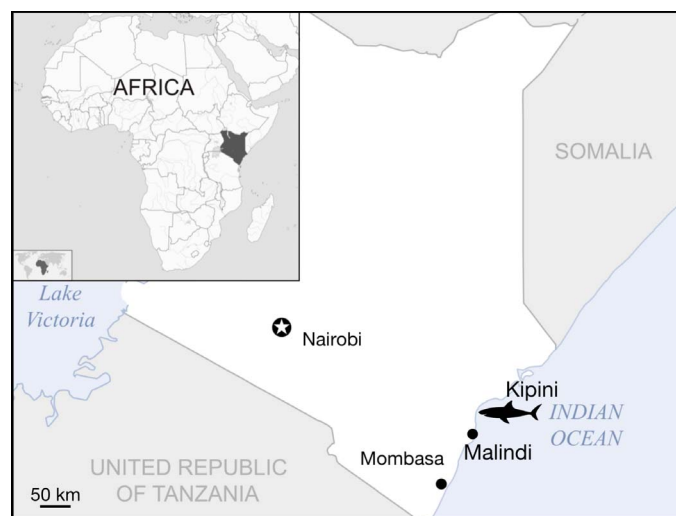


Fig. 9. Point map of catch location for the sandy morph of *S. tigrinum* (shark icon), marking 10 km north of Malindi, off the coast of Kipini, Kenya, Africa. Map is modified and based on UN Office for the Coordination of Humanitarian Affairs (OCHA) map.

Sandy morph of *Stegostoma tigrinum*.—The juvenile coloration of the sandy color morph is currently not described. The long-term observations of ZMUC P2395374 (transitional) and ZMUC P2395374 (adult) in this study reveal the pattern ontogeny from transitional to adult (Fig. 6A–H). The transitional coloration is a light brown/beige background with a darker brown pattern. The pattern is comprised of many narrow, twisted bands in swirly formations (Fig. 6A–D). The pattern begins dorsally above the eyes and covers the shark dorsolaterally, leaving the lower lateral flanks and the ventral side cream white and covered with tiny dots. Despite pattern differences compared to the zebra color morph, there are similarities in how the pattern transforms to the next stage. In the sandy color morph, the pattern also breaks up into dots, though the dots are tiny and freckle-like. These freckles are found on the edge of every curved and twisted band along the body, on pectoral fins spreading inward from all margins, along the lower lateral flanks from below the spiracle to lower caudal-fin origin, including the pelvic fins. When the freckles break the bands, a thin line of cream color appears within the bands. Along the lower dorsal lobe on the caudal fin, the freckles have also broken the pattern and been replaced by the same cream color. Over time, as seen in the long-term observations, the cream/light beige color replaces the pattern from the ventral to the dorsal side, and the bands expand in width with the overall growth of the animal. Observations of the specimen ZMUC P2395374 (1070 mm TL) revealed almost fully dotted pectoral fins with scarcely any pattern left. The anal fin was never seen with dots.

Of the two adult specimens, one was a dark brown female (ZMUC P6268, Fig. 6E, F) and the other a light brown male (ZMUC P2395375, Fig. 6G, H), both with dark brown freckles covering the dorsolateral body. On both adults, it was possible to see remnants of the transitional pattern above the pectoral fins (Fig. 6F) and on the tip of the caudal fin (Fig. 6G). Over time, the adults express fewer freckles, though the freckles still cover most of the body except the ventral side, the anal fin, and the head close to the snout.

Size and sexual maturity

The specimens examined in the present study measured between 185–2000 mm TL. Embryos were identified by the presence of a yolk sac and included two specimens of 185–195 mm TL. Juveniles were identified by the lack of a yolk sac and by the black and white striped pattern, and measured 255–562 mm TL. The transitional specimens were identified by the appearance of dots in the coloration pattern and measured between 600–1535 mm TL. Mature male individuals were recognized by the clasper length exceeding the length of the pelvic fins and by the state of calcification of the claspers, and measured 1935–2000 mm TL. The long-term observations of the larger male sandy color morph (ZMUC P2395375) showed considerable growth of the claspers from first to last observation, though the animal was still not fully mature at the time of the last observation. A live, mature male of the zebra color morph (DBP4) of 1935 mm TL had claspers well exceeding the pelvic fins, almost reaching the anal-fin origin, with internal calcification (Fig. 8A). Outer clasper length measured 135 mm and inner length 243 mm, which corresponds to 6.9% and 12.5% of TL, respectively. Each clasper of this male also carried a short, triangular spike extruding from the dorsal terminal of the clasper gland (Fig. 8B). The live, immature male of the sandy color morph (ZMUC P2395374) had a TL of 1270 mm. Outer

clasper length measured 21 mm and inner clasper length was 69 mm, which corresponds to 1.7% and 5.4% of TL. An immature specimen (ZMB 5258) of 885 mm TL had an outer clasper length of 107 mm and an inner length of 532 mm, corresponding to 1.2% and 3.9% of TL, respectively. These examples show an incremental increase in clasper length as a percentage of TL with animal growth. The female sandy color morph of 1395 mm TL (ZMUC P6268) was dissected to establish the state of maturity, which showed that the ovarian follicles were small and equal in size, and the uterus width measured 25 mm, indicating an immature female.

Eggs

Over the last 3.5 years, approximately 10–20 eggs per year have been found in a tank with mature female *S. tigrinum* of the zebra morph at The National Aquarium of Denmark. It has not been established whether one or both of the females have laid eggs, as egg-laying has not been observed directly. In this period, the contents of all the eggs were emptied by other species within the tank; however, two eggs have yielded two juveniles in April and May of 2019. The eggs are large, dark green, and taper off bluntly at each end. No hair-like structures extrude from the corners. The eggs measure 175 mm in length and 93 mm in width at the broadest point (Fig. 8C). The lack of hair-like structures is inconsistent with previous descriptions of Zebra Shark eggs and could be a result of unfavorable conditions for the ovulating females.

Distribution

The sandy color morph of *S. tigrinum* has in the present study been documented from a single location, off the coast of Kenya, ca. 10 km north of Malindi (Fig. 9). Six specimens of this morph were caught in June 2016 (rainy season) at a depth of 12 m, on a sandy substrate. A seventh specimen was caught in May 2017, 15 km north of Malindi on sandy bottom, also at 12 m depth.

Etymology

The name *Stegostoma tigrinum* is made up of the Greek *stego* meaning cover, and *stoma* meaning mouth, and can thus be translated to ‘covered mouth’ (Froese and Pauly, 2018). The epithet *tigrinum* refers to the juveniles’ banded pattern.

DISCUSSION

The nomenclature of the Zebra Shark has a long and complicated history, and no real consensus has yet been reached. Although *Stegostoma fasciatum* has been the most commonly used name in the last decades, other names are used as well (Compagno, 1984; Goto, 2001). Kottelat (2013) mentions that *Stegostoma tigrinum* Forster, 1781 should have priority under code article 23.9.1, which states that if a name has been used after 1899, it cannot be suppressed. *Stegostoma tigrinum* has been used at least 21 times from 1903 (Kishinouye and Zashi, 1903) to 2016 (Feldheim et al., 2016). Nevertheless, *Stegostoma fasciatum* Hermann, 1783 has been accepted as the scientific name for the Zebra Shark by Compagno (1984) and most authors since, even though this description is based on Seba (1759) and not on an actual specimen. Fowler (1941) presented a full synonymy of the species. However, he mistakenly states that the description of *Squalus tigrinus* by Forster, 1781 is from 1795, and that

Gmelin thus precedes Forster by applying this name in 1789. Post 1899, references to the name *S. fasciatum* were not made until the 1940s, with one mention by Barnard (1948). Subsequently, until the beginning of the 1990s, relatively few studies referred to the Zebra Shark as *S. fasciatum* (Smith, 1955; Murty, 1969; Nakaya, 1973; Paepke and Schmidt, 1988; Balasubramanian et al., 1993); however, the use of the name increased drastically thereafter. The conclusion by Compagno (1984) that *S. fasciatum* should be the accepted name was biased by an incomplete synonymy, as the work of Forster (1781) was not included (perhaps due to the incorrect synonymy by Fowler, 1941). Compagno (1984) correctly states that *Stegostoma varium* Seba, 1759 cannot be accepted as a valid name due to an inconsistent use of uninomial, binomial, and polynomial nomenclature in Seba's work. We argue that the correct species name should be *Stegostoma tigrinum* Forster, 1781 and not *Stegostoma fasciatum* Hermann, 1783, and we encourage future studies to use this name as the scientific name for the Zebra Shark. Likewise, the International Commission on Zoological Nomenclature should rule on the official scientific name for this species.

Our results indicate that the two color morphs of *S. tigrinum* are genetically similar and do not exhibit morphological differences except for the external color patterning. However, we also compared the ND4 sequences for the sandy and zebra morphs from Kenya with those of zebra morphs from other populations (Dudgeon et al., 2009), to establish possible variations between geographically separated populations. Here, we found that the sandy and zebra morph from Kenya only showed 100% identity with the zebra morph from a population in Mozambique (FL183482.1), but only 99.49–99.87% identity with the remaining populations from Western Australia, Northern Territory (Australia), Queensland (Australia), Java (Indonesia), and Japan. Thus, we conclude that the two morphs represent the same species but that the Kenyan Zebra Shark population differs slightly from other geographically separated Zebra Sharks.

We found that during the growth of *S. tigrinum*, the most pronounced ontogenetic change in body proportions is the elongation of the body and the shortening of the caudal fin, as measured relative to body size. The long, slender caudal fin in juveniles could possibly also be related to the theory of mimicry, which proposes that juveniles mimic the shape of a banded sea snake (Dudgeon and White, 2012). Adult Zebra Sharks from Australasian waters have seasonal migrations (Dudgeon et al., 2013), and it is thus possible that the shortened, more compact, and powerful caudal fin in adults compared to the juveniles is an adaptation to migration. Furthermore, an elongation of the body length from juvenile to adult is common in elasmobranchs in order to create room for reproductive organs (Conrath, 2005). For juveniles, there were three head-related morphometric measurements (pre-orbital length, prepectoral-fin length, and pre-ridge length) that suggested a longer head than both transitionals and adults. This has also been observed in the Gulper Shark *Centrophorus granulosus* and the Leopard Shark *Triakis semifasciata*, and appears to be a common ontogenetic change relating to a shift in prey size and feeding mechanisms (Lowry et al., 2007; White et al., 2013). The barbels and the eyes of the shark, both of which are used for locating food, become relatively smaller with increasing size of the animal. It is possible that these features are more important for juveniles than adults in the search for prey, especially as juveniles are extremely dependent on fast initial growth to survive to adulthood.

The present results concerning the dermal denticles of the Zebra Shark largely confirm what has been observed in other sharks. Garrick (1960) suggested that simple denticles of young sharks are replaced by more advanced denticles during growth. Generally, he mentioned that the ontogenetic changes include addition of cusps or scutes based on the Prickly Dogfish *Oxynotus bruniensis* (Oxynotidae) and the Plunket Shark *Centroscyrmus plunketi* (Somniosidae). The change in morphology occurs when an older generation of denticles is replaced with a new, more developed one, induced by a certain developmental step, i.e., time-associated (Steenstrup, 1861). This replacement mechanism results in denticles of different morphs being present simultaneously in the same skin area. Hertwig (1874) described the shift as new denticles emerging in between the existing generation of denticles. The current study found evidence of a similar development, where denticles of *S. tigrinum* were found to change from type *a* to type *c* in non-ridge areas and from type *b* to type *c* in ridge areas in the transition from juvenile to adult (Fig. 4M–S). There is, however, great variation in dermal denticles between groups and species of sharks, and Ferrón and Botella (2017) found five different categories of denticle-use defined by lifestyle. The denticles of *S. tigrinum* are morphologically most comparable with the category described as 'generalized usage.' Garrick (1960) states that dermal denticles cannot be used to differentiate species with certainty, unless all ontogenetic changes are known for the species in question. However, it seems that the denticles of a single species generally have a basic morphology; cusps or scutes can be added, and the denticles can become broader, but their morphology does not change entirely.

In contrast to the great ontogenetic variation in the dermal denticulation, the oral teeth showed no such changes except for growing in size from the juvenile to the adult stage. This study found no differences in oral teeth between the two morphs.

For *S. tigrinum*, the only character that definitively separates the two morphs is the coloration, and this single character is not enough to diagnose the sandy color morph as a new species. More or less stable color morphs are well known in teleosts, but are rare among elasmobranchs. Often the taxonomy of the involved species is puzzling and it can be difficult to judge whether the color morphs represent species, a continuum of variation, or fixed morphs. In the Smoothhound Shark genus *Mustelus* (Carcharhiniformes), for example, white dorsal spots were long used as a 'safe' species-specific character, but the apparently diagnostic white spots of, e.g., *M. asterias* turned out to be very variable and even absent in some individuals (Heemstra, 1973; Farrell et al., 2009). Also, the common skate *Dipturus batis* (Rajiformes) had been defined as a species complex for 90 years until Iglésias et al. (2009) found that this complex was in fact two separate species, *D. cf. flossada* and *D. cf. intermedia*. This species complex endured for so long despite differences between the two skates in eye and body color, and also in the projection of 'thorns' on the tail, the inter-dorsal distance, and the adult dentition (Heessen et al., 2015). These two examples sum up some of the difficulties of defining new species even when morphological characters strongly suggest so. Interestingly, the reversed case is seen for the Bamboo Shark genus *Hemiscyllium* (Orectolobiformes), where the species identification is primarily distinguished by coloration and patterns (Allen et al., 2016). An example that relates more to the case in the present study is of the White-spotted Wedgefish *Rhynchobatus australiae*. This species exhibits at

least three distinctly different color variations of yellow-brown, dark brown, and gray observed in immature and mature adults (Giles et al., 2016).

The puzzling question of how the color variation emerged in the Zebra Shark is not easily answered with the present data. None of the sandy color morphs were observed in their natural habitat, and we only know that they were caught on a sandy substrate. The suggestion that the juvenile zebra morph mimics the pattern of venomous brown banded sea snakes (Elapidae) to avoid predation (Dudgeon and White, 2012) cannot be applied for the sandy color morph. Here, the swirly pattern and the sandy colors fit the theory of camouflage better, especially camouflaging on a sandy substrate. Thus, several scenarios for the evolution of the sandy zebra morph can be proposed: (1) it has evolved due to a mutation in a color-coding gene, (2) it can be explained by epigenetics, or (3) by sexual selection. Epigenetics study the organismal change of a phenotypic trait caused by environmental factors, which is inherited to the next generation (Hu and Barrett, 2017). Such phenotypic changes are caused by alterations in the gene expression, and in this case a change in the pattern and coloration of the Zebra Shark. Sexual selection is the promotion of specific phenotypic traits chosen by a mate with a corresponding preference for the trait. This is seen most frequently in cichlid fish that display extreme phenotypic diversity and fast speciation through genetic predisposition, mate preferences, and environmental variation (Maan and Sefc, 2013).

The presence of several individuals of the sandy color morph off the coast of Kenya in 2017 and 2018, including both males and females of different sizes, shows that it represents an independent morph of *S. tigrinum*. Future studies could elaborate on the genetic differences between these two morphs, e.g., by including sequencing of additional genes and samples from other regions where uniformly colored Zebra Sharks have also been reported. However, since the special curly pattern of the sandy transitionals are so far only reported from Kenya, it is likely that the uniformly colored specimens from NW Australia (William T. White and Christine Dudgeon, pers. comm.) and Japan (Nakaya, 1973) have a different origin. It is imperative that the sharks are also studied in their natural habitat to understand the nature of the co-existence of two morphs.

MATERIAL EXAMINED

Institutional abbreviations follow Sabaj (2016), with the addition of DBP (Den Blå Planet, Danish National Aquarium).

Zebra morph of *Stegostoma tigrinum*: ZMB 4449 (holotype) Bloch, 1784, female alcohol, 370 mm TL, Indian Ocean; DBP1, male live, Jakarta, Indonesia; DBP2, female live, Jakarta, Indonesia; DBP3, female live, Jakarta, Indonesia; DBP4, male live, 1935 mm TL, Jakarta, Indonesia; MNHN no label, female alcohol, 195 mm TL, unknown location; MNHN no label, female dry, 720 mm TL, unknown location; MNHN-IC-0000-1002, male alcohol, 435 mm TL, 11°58'58.8"N, 79°49'58.8"E, India; MNHN-IC-1988-0700, female dry, 620 mm TL, 11°58'58.8"N, 79°49'58.8"E, India; MNHN-IC-2002-1146, female alcohol, 255 mm TL, 12°30'0"N, 112°30'0"E, New Caledonia; MNHN-IC-2002-1146, female alcohol, 370 mm TL, 12°30'0"N, 112°30'0"E, New Caledonia; MNHN-IC-A-4297, male alcohol, 283 mm TL, 2°13'58.8"N, 102°13'58.8"E, Malaysia; MNHN-IC-A-7769, male alcohol,

320 mm TL, 11°58'58.8"N, 79°49'58.8"E, India; MNHN-IC-A-7770, female alcohol, 258 mm TL, 11°58'58.8"N, 79°49'58.8"E, India; MNHN-IC-A-7804, male alcohol, 352 mm TL, Madagascar; MNHN-IC-A-7805, male alcohol, 395 mm TL, 13°4'58.8"N, 80°28'1.2"E, India; MNHN-IC-A-7806, female alcohol, 185 mm TL, 17°30'0"S, 167°30'0"E, New Caledonia; MNHN-IC-A-8901, female dry, 315 mm TL, 11°58'58.8"N, 79°49'58.8"E, India; MNHN-IC-A-8901, female dry, 600 mm TL, 11°58'58.8"N, 79°49'58.8"E, India; MNHN-IC-A-9467, female dry, 418 mm TL, 11°58'58.5"N, 79°49'58.8"E, India; MNHN-IC-A-9640, male dry, 2000 mm TL, 11°58'58.8"N, 79°49'58.8"E, India; MNHN-IC-A-9647, female dry, 1500 mm TL, 20°0'0"N, 39°0'0"E, Egypt; ZMB 5256, male alcohol, 885 mm TL, Malacca, Malaysia; ZMUC P2394717, male alcohol, 290 mm TL, Kerteh, Trengganu, Malaya; ZMUC P2394732, female alcohol, 430 mm TL, East India; ZMUC P2394733, male alcohol, 325 mm TL, Indian Ocean; ZMUC P2394734, male alcohol, 280 mm TL, unknown location; ZMUC P2395356, dry, unknown location.

The following specimens share the locality off Kipini, Kenya, ca. 2°33'44.9"S, 40°32'06.1"E: ZMUC P2394968, female live, 730 mm TL; ZMUC P2394974, male live, 740 mm TL; ZMUC P2394975, male live, 830 mm TL; ZMUC P2394976, male live, 685 mm TL; ZMUC P2394977, female live, 785 mm TL; ZMUC P2394978, male live, 562 mm TL; ZMUC P2394979, male live, 653 mm TL; ZMUC P2394980, male live, 710 mm TL; ZMUC P2394981, male live, 675 mm TL; ZMUC P2394982, male live, 715 mm TL; ZMUC P2394983, female live, 830 mm TL; ZMUC P2394984, female live, 670 mm TL; ZMUC P2394985, female live, 975 mm TL; ZMUC P2394987, female live, 802 mm TL; ZMUC P2394989, female live, 680 mm TL; ZMUC P2394990, male live, 705 mm TL; ZMUC P2394991, male live, 660 mm TL; ZMUC P2394992, male live, 940 mm TL; ZMUC P2394993, male live, 760 mm TL; ZMUC P2394994, female live, 740 mm TL; ZMUC P2394995, male live, 720 mm TL; ZMUC P2394996, male live, 780 mm TL; ZMUC P2394997, male live, 710 mm TL; ZMUC P2394998, male live, 725 mm TL; ZMUC P2394999, female live, 635 mm TL; ZMUC P2395000, female live, 810 mm TL; ZMUC P2395001, male live, 725 mm TL; ZMUC P2395002, female live, 800 mm TL; ZMUC P2395003, female live, 650 mm TL; ZMUC P2395004, female live, 790 mm TL; ZMUC P2395372, sex unknown, live; ZMUC P2395373, sex unknown, live.

Sandy morph of *Stegostoma tigrinum*: The following specimens share the locality off Kipini, Kenya, ca. 2°33'44.9"S, 40°32'06.1"E: ZMUC P6268, female alcohol, 1395 mm TL; ZMUC P2394986, female live, 720 mm TL; ZMUC P2394988, male live, 740 mm TL; ZMUC P2395374, male live, 1070 mm TL; ZMUC P2395375, male live, 1535 mm TL; ZMUC P2395470, female alcohol, 630 mm TL.

ACKNOWLEDGMENTS

All authors would like to thank Kasper Jørgensen (DBP) for lending his invaluable skills and sharing his expertise on Zebra Sharks in captivity; all zookeepers at DBP for collaboration and expert care of live specimens used in the study; and Dr. Agnes Dettai (collection curator) and Zora (correspondent) at the Natural History Museum of Paris (MNHN), Peter Barch (curator) and Edda Aßel (collection manager) of the Natural History Museum of Berlin (ZMB) for

help with accessioning of museum specimens. RBD acknowledges travel grants from Bøje Benzons Støttefond and would like to thank Mads Burchardt Mundt for help with statistical analyses and Niklas Dreyer (NHMD) for help with SEM and expert advice throughout the project. All authors would like to thank Anders Illum, NHMD, for help with SEM, Tammes Menne, NHMD, for help with radiography, Marcus Anders Krag, NHMD, for advice and assistance, Thomas Pape, NHMD, for help with nomenclature, and Henrik Carl, NHMD, for advice and help with photos and translation.

LITERATURE CITED

- Alfred, E. R. 1961. The Javanese fishes described by Kuhl and van Hasselt. Bulletin of the National Museum of Singapore 30:80–88.
- Allen, G. R., M. V. Erdmann, W. T. White, Fahmi, and C. L. Dudgeon. 2016. Review of the Bamboo Shark genus *Hemiscyllium* (Orectolobiformes: Hemiscyllidae). Journal of the Ocean Science Foundation 23:51–97.
- Applegate, S. 1972. A revision of the higher taxa of orectoloboids. Journal of the Marine Biological Association of India 14:743–751.
- Arévalo, E., S. K. Davis, and J. W. Sites, Jr. 1994. Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae) in central Mexico. Systematic Biology 43:387–418.
- Artemi, P. 1738. Ichthyologia sive opera omnia de piscibus scilicet: Bibliotheca ichthyologica. Philosophia ichthyologica. Genera piscium. Synonymia specierum. Descriptiones specierum. Omnia in hoc genere perfectiora quam antea ulla posthuma vindicavit, recognovit, coaptavit et edidit Carolus Linnaeus, volume 5, chapter In quibus systema totum ichthyologiae proponitur cum classibus, ordinibus, generum characteribus, specierum differentiis, observationibus plurimis redactis speciebus 242 ad genera 52, page 68. Wishoff.
- Balasubramanian, T. S., S. Rajapackiyam, H. Mohamed Kasim, and K. M. S. Ameer Hamsa. 1993. On the egg-cases of Zebra Shark *Stegostoma fasciatum* caught off Tuticorin Gulf of Mannar. Marine Fisheries Information Service CMFRI 121:11.
- Barnard, K. H. 1948. XVIII.—New records and descriptions of new species of parasitic Copepoda from South Africa. Journal of Natural History 1:242–254.
- Bass, A. J., J. D. D'Aubrey, and N. Kistnasamy. 1975. Sharks of the east coast of Southern Africa. IV. The families Odontaspidae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhiniodontidae. The Oceanographic Research Institute, Republic of South Africa.
- Blainville, H. de 1816. Prodrome d'une nouvelle distribution systématique du règne animal. Bulletin des Sciences, par la Société Philomathique de Paris v. 8:105–112.
- Bleeker, P. 1852. Bijdrage tot de kennis der Plagiostomen van den indischen archipel. Verhandelingen van het Bataviaasch Genootschap van Kunsten en Wetenschappen 24(12):1–92, 4 pls.
- Bloch, M. E. 1784. Naturgeschichte der ausländischen Fische. Erster Theil, Berlin.
- Bloch, M. E. 1787. Ichthyologie ou histoire naturelle, générale et particulière des poissons. Quatrième partie. De La Garde, Berlin, Didot, Paris and White, London.
- Blyth, E. 1847. Zoological department—Mr. Blyth's report. Journal of the Asiatic Society of Bengal 16(7):725–727.
- Bonnaterre, J. P. 1788. Tableau encyclopédique et méthodique des trois règnes de la nature. Ichthyologie. Chez Panckouke, Paris.
- Broussonet, P. M. A. 1784. Mémoire sur les différentes espèces de chiens de mer. Histoire de l'Académie Royale des Sciences, Paris, 1780 [1784]:641–680.
- Chen, H., X. Chen, W. Ai, and J. Wang. 2016. Complete mitochondrial genome and the phylogenetic position of the Zebra Shark (*Stegostoma fasciatum*). Mitochondrial DNA Part B 1:105–106.
- Compagno, L. J. V. 1973. Interrelationships of living elasmobranchs. Zoological Journal of the Linnean Society 53:15–61.
- Compagno, L. J. V. 1984. FAO Species Catalogue. Vol. 4. Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species Known to Date. Part 1. Hexanchiformes to Lamniformes. FAO Fisheries Synopsis No. 125, Vol. 4, Part 1. FAO, Rome.
- Compagno, L. J. V. 2001. Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species Known to Date. Vol. 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO Species Catalogue for Fishery Purposes No. 1, Vol. 2. FAO, Rome.
- Conrath, C. L. 2005. Reproductive biology, p. 119. In: Management Techniques for Elasmobranch Fisheries. J. A. Musick and R. Bonfil (eds.). FAO, Rome.
- Cuthill, I. C., M. Stevens, J. Sheppard, T. Maddocks, C. A. Párraga, and T. S. Troscianko. 2005. Disruptive coloration and background pattern matching. Nature 434:72–74.
- Cuvier, G. 1816. Le Règne Animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Les reptiles, les poissons, les mollusques et les annélides. Edition 1. 2 (i-xviii): 1-532, Pls. 9-10, in v. 4.
- Dingerkus, G. 1986. Interrelationships of orectolobiform sharks (Chondrichthyes: Selachii), p. 227–245. In: Proceedings of the Second International Conference on Indo-Pacific Fishes, Tokyo.
- Dudgeon, C. L., D. Broderick, and J. R. Ovenden. 2009. IUCN classification zones concord with, but underestimate, the population genetic structure of the zebra shark *Stegostoma fasciatum* in the Indo-West Pacific. Molecular Ecology 18:248–261.
- Dudgeon, C. L., L. Coulton, R. Bone, J. R. Ovenden, and S. Thomas. 2017. Switch from sexual to parthenogenetic reproduction in a Zebra Shark. Nature Scientific Reports 7: 40537.
- Dudgeon, C. L., K. Feldheim, M. Schick, and J. R. Ovenden. 2006. Polymorphic microsatellite loci for the Zebra Shark *Stegostoma fasciatum*. Molecular Ecology Notes 6:1086–1088.
- Dudgeon, C. L., J. M. Lanyon, and J. M. Semmens. 2013. Seasonality and site fidelity of the Zebra Shark, *Stegostoma fasciatum*, in southeast Queensland, Australia. Animal Behaviour 85:471–481.
- Dudgeon, C. L., M. J. Noad, and J. M. Lanyon. 2008. Abundance and demography of a seasonal aggregation of Zebra Sharks *Stegostoma fasciatum*. Marine Ecology Progress Series 368:269–281.
- Dudgeon, C. L., and J. R. Ovenden. 2015. The relationship between abundance and genetic effective population size in elasmobranchs: an example from the globally threatened Zebra Shark *Stegostoma fasciatum* within its protected range. Conservation Genetics 16:1443–1454.

- Dudgeon, C. L., and W. T. White.** 2012. First record of potential batesian mimicry in an elasmobranch: juvenile Zebra Shark mimic banded sea snake? *Marine and Freshwater Research* 63:545–551.
- Eschmeyer, W. N., R. Fricke, and R. van der Laan (Eds.).** 2019. Catalog of Fishes: Genera, Species, References. <http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>. Electronic version accessed 3 January 2019.
- Farrell, E. D., M. W. Clarke, and S. Mariani.** 2009. A simple genetic identification method for Northeast Atlantic Smoothhound Sharks (*Mustelus* spp.). *ICES Journal of Marine Science* 66:561–565.
- Feldheim, K. A., A. Clews, A. Henningsen, L. Todorov, C. McDermott, M. Meyers, J. Bradley, A. Pulver, E. Anderson, and A. Marshall.** 2016. Multiple births by a captive Swellshark *Cephaloscyllium ventriosum* via facultative parthenogenesis. *Journal of Fish Biology* 90:1047–1053.
- Ferrón, H. G., and H. Botella.** 2017. Squamation and ecology of thelodonts. *PLoS ONE* 12:e0172781.
- Forster, J. R.** 1781. Indische Zoologie oder systematische Beschreibungen seltener und unbekannter Thiere aus Indien, mit 15 illuminirten Kupfertafeln erläutert. Nebst einer kurzen vorläufigen Abhandlung über den Umfang von Indien und die Beschaffenheit des Klima, des Bodens und des Meeres daselbst, und einem Anhang, darin ein kurzes Verzeichniss der Thiere in Indien mitgetheilt wird/ *Zoologia indica selecta* [...]. Praemittitur de finibus et indole aeris, soli, marisque indici brevis lucubratio. Sequitur ad calcem brevis enumeratio animalium Indiae. Gebauer, Halle.
- Fowler, H. W.** 1941. Contributions to the biology of the Philippine archipelago and adjacent regions. *Bulletin of the United States National Museum* 13(100):1–879.
- Froese, R., and D. Pauly (Eds.).** 2018. FishBase. World Wide Web electronic publication. <http://www.fishbase.org> (accessed 2018).
- Garla, R. C., D. Garrone-Neto, and O. B. F. Gadig.** 2015. Defensive strategies of neonate Nurse Sharks, *Ginglymostoma cirratum*, in an oceanic archipelago of the Western Central Atlantic. *Acta Ethologica* 18:167–171.
- Garman, S. W.** 1913. The Plagiostomia (sharks, skates, and rays). *Memoirs of the Museum of Comparative Zoology at Harvard College* 36:1–515.
- Garrick, J. A. F.** 1960. Studies on New Zealand Elasmobranchii. Part XI.—Squaloids of the genera *Deania*, *Etmopterus*, *Oxynotus* and *Dalatias* in New Zealand waters. *Transactions of the Royal Society of New Zealand* 88:489–517.
- Giles, J. L., C. Riginos, G. J. P. Naylor, Dharmadi, and J. R. Ovenden.** 2016. Genetic and phenotypic diversity in the Wedgefish *Rhynchobatus australiae*, a threatened ray of high value in the shark fin trade. *Marine Ecology Progress Series* 548:165–180.
- Gmelin, J. F.** 1789. Caroli a Linné systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Beer, Lipsiae, vol. 1, pars 3:1033–2224.
- Goto, T.** 2001. Comparative anatomy, phylogeny and cladistic classification of the order Orectolobiformes (chondrichthyes, elasmobranchii). *Memorandum of the Graduate School of Fisheries Science Hokkaido University* 48:1–100.
- Gray, J. E.** 1854. Catalogue of fish collected and described by Laurence Theodore Gronow, now in the British Museum. British Museum, London.
- Gronovius, L. T.** 1754. Museum ichthyologicum, sistens piscium indigenorum & quorundam exoticorum, qui in museo Laurentii Theodori Gronovii, J. U. D. adservantur, descriptiones, ordine systematico. Accedunt nonnullorum exoticorum piscium icones, aeri incisae. Haak, Lugduni Batavorum, Leiden.
- Gronovius, L. T.** 1763. Zoophylacii Gronoviani fasciculus primus exhibens animalia quadrupeda, amphibia atque pisces, quae in museo suo adservat, rite examinavit, systematice disposuit, descripsit atque iconibus illustravit Laurentii Theodori Gronovius. Published by author, Lugduni Batavorum, Leiden.
- Günther, A. C. L. G.** 1870. Catalogue of the fishes in the British Museum: Catalogue of the Phytostomi containing the families Gymnotidae, Symbranchidae, Murænidae, Pegasidae and of the Lophobranchii, Plectognathi, Dipnoi, Ganoidei, Chondropterygii, Cyclostomata, Leptocardii, in the British Museum. Volume 8. British Museum, London.
- Heemstra, P. C.** 1973. A revision of the shark genus *Mustelus* (Squaliformes Charcharhinidae). Unpubl. Ph.D. diss., University of Miami, Miami, Florida.
- Heessen, H. J. L., N. Daan, and J. R. Ellis (Eds.).** 2015. Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea: Based on International Research-Vessel Surveys. Wageningen Academic Publishers.
- Hermann, J.** 1783. Tabula affinitatum animalium olim academico specimine edita, nunc uberiore commentario illustrata com annotationibus ad historiam naturalem animalium augendam facientibus. J. G. Treuttel, Argentorati.
- Hertwig, J.** 1874. Ueber bau und entwicklung der placoschuppen und der zahne der selachier. *Jenaische Zeitschrift für Naturwissenschaft* 8:331–404.
- Hu, J., and R. D. H. Barrett.** 2017. Epigenetics in natural animal populations. *Journal of Evolutionary Biology* 30:1612–1632.
- Iglésias, S. P., L. Toulhoat, and D. Y. Sello.** 2009. Taxonomic confusion and market mislabeling of threatened skates: important consequences for their conservation status. *Marine and Freshwater Ecosystems* 20:319–333.
- Kishinouye, K., and D. Zashi.** 1903. On yasurizame (*Rhinodon pentalineatus*) and torafuzame (*Stegostoma tigrinum*). *Zoological Magazine*.
- Kottelat, M.** 2013. The fishes of the inland waters of Southeast Asia: a catalogue and core bibliography of the fishes known to occur in freshwater, mangroves and estuaries. *The Raffles Bulletin of Zoology, Supplement* No. 27:1–663.
- Kunze, K., and L. Simmons.** 2004. Notes on reproduction of the Zebra Shark, *Stegostoma fasciatum*, in a captive environment, p. 493–497. In: *Elasmobranch Husbandry Manual: Captive Care of Sharks, Rays, and Their Relatives*. M. F. L. Smith (ed.). Ohio Biological Survey, Columbus, Ohio.
- Lowry, D., P. J. Motta, and R. E. Hueter.** 2007. The ontogeny of feeding behavior and cranial morphology in the Leopard Shark *Triakis semifasciata* (Girard 1854): a longitudinal perspective. *Journal of Experimental Marine Biology and Ecology* 341:153–167.
- Maan, M. E., and K. M. Sefc.** 2013. Color variation in cichlid fish: developmental mechanisms, selective pressures and evolutionary consequences. *Seminars in Cell and Developmental Biology* 24:516–528.

- Murty, V. S.** 1969. Catalogue of fishes (excluding from the Laccadives) in the reference collection of the Central Marine Fisheries Research Institute. Bulletin of the Central Marine Fisheries Research Institute 10.
- Nakaya, K.** 1973. An albino Zebra Shark *Stegostoma fasciatum* from the Indian Ocean, with comments on albinism in elasmobranchs. Japanese Journal of Ichthyology 20:120–122.
- Naylor, G. J. P., J. N. Caira, K. Jensen, K. A. M. Rosana, N. Straube, and C. Lakner.** 2012b. Elasmobranch phylogeny: a mitochondrial estimate based on 595 species, p. 31–56. *In: The Biology of Sharks and Their Relatives*. Second edition. J. C. Carrier, J. A. Musick, and M. R. Heithaus (eds.). CRC Press, Taylor & Francis Group, Boca Raton, Florida.
- Naylor, G. J. P., J. N. Caira, K. Jensen, K. A. M. Rosana, W. T. White, and P. R. Last.** 2012a. A DNA sequence-based approach to the identification of shark and ray species and its implications for global elasmobranch diversity and parasitology. Bulletin of American Museum of Natural History 367:1–262.
- Nelson, J. S., T. C. Grande, and M. V. H. Wilson.** 2016. Fishes of the World. Fifth edition. John Wiley and Sons, Hoboken, New Jersey.
- Paepke, H. J., and K. Schmidt.** 1988. Kritischer Katalog der Typen der Fische Sammlung des Zoologischen Museums Berlin. Teil 2: Agnatha, Chondrichthyes. Mitteilungen aus dem Zoologischen Museum in Berlin 64:155–189.
- Paxton, J. R., D. F. Hoese, G. R. Allen, and J. E. Hanley.** 1989. Pisces: Petromyzontidae to Carangidae. Zoological Catalogue of Australia vol. 7. CSIRO Publishing, Australia.
- Pennant, T.** 1791. Indian Zoology. Second edition. Faulder, London.
- Robinson, D. P., W. Baverstock, A. Al-Jaru, K. Hyland, and K. A. Khazanehdari.** 2011. Annually recurring parthenogenesis in a Zebra Shark *Stegostoma fasciatum*. Journal of Fish Biology 79:1376–1382.
- Rüppel, E.** 1837. Fische des Rothen Meeres, p. 53–80. *In: Neue Wirbelthiere zu der Fauna von Abyssinien gehörig*. Siegmund Schmerber, Frankfurt am Main, Germany.
- Sabaj, M. H.** 2016. Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. Version 6.5 (16 August 2016). Electronically accessible at <http://www.asih.org/>, American Society of Ichthyologists and Herpetologists, Washington, D.C.
- Seba, A.** 1759. Locupletissimi rerum naturalium thesauri accurata descriptio et iconibus artificiosissimis expressio per universam physices historiam. Volume 3. H. K. Arksteus, Amstelaedami.
- Shaw, G.** 1804. A general zoology or systematic natural history [...] with plates from the first authorities and most select specimens. Vol. V. Part II. Pisces. Kearsley, London.
- Smith, J. L. B.** 1955. The fishes of Aldabra. Part 1. Journal of Natural History 8(88):304–312.
- Srdic, A., C. J. Duffin, and D. M. Martill.** 2016. First occurrence of the orectolobiform shark *Akaimia* in the Oxford Clay Formation (Jurassic, Callovian) of England. Proceedings of the Geologists' Association 127:506–513.
- Steenstrup, J. J. S.** 1861. Om Forskiellen mellem Beenfiskenes og Bruskfiskenes Skiældannelse. Forhandlinger ved de Skandinaviske Naturforskeres. Kjöbenhavn 8:688–689.
- van Hasselt, J. C.** 1823. Uittreksel uit een' brief van Dr. J. C. van Hasselt, aan den Heer C. J. Temminck. Algemeene Konsten Letter-Bode.
- Ward, R. D., T. S. Zemlak, B. H. Innes, P. R. Last, and P. D. N. Hebert.** 2005. DNA barcoding Australia's fish species. Philosophical Transactions of the Royal Society B 360: 1847–1857.
- Weigmann, S.** 2016. Annotated checklist of the living sharks, batoids and chimaeras (Chondrichthyes) of the world, with a focus on biogeographical diversity. Journal of Fish Biology 88:837–1037.
- White, W. T., D. A. Ebert, G. J. P. Naylor, H-C. Ho, P. Clerkin, A. Verissimo, and C. F. Cotton.** 2013. Revision of the genus *Centrophorus* (Squaliformes: Centrophoridae): Part 1—Redescription of *Centrophorus granulosus* (Bloch & Schneider), a senior synonym of *C. acus* Garman and *C. niaukang* Teng. Zootaxa 3752:035–072.
- Whitley, G. P.** 1939. The fishes of Australia, Part 1. The sharks, rays and devilfish, and other primitive fishes of Australia and New Zealand. Royal Zoological Society of the New South Wales, Sydney.