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 Dahl¹,²,³,⁴, 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), transitional (562–1395 mm TL), and adults (>1300 mm TL). The transitional sandy morph is dorsally covered by a swirl 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 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), transitional (562–1395 mm TL), and adults (>1300 mm TL). The transitional sandy morph is dorsally covered by a swirl 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.
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 (1.050 bp) and COI (1.150 bp) gene sequences were amplified by PCR using the primers ND4_new (5’–CATCCTGACTCCCAAAGCGACATGTAAGCC–3’) and H12293-LEU (5’–TTGCAACCAAGGTTTGTGTTCTAAGACC–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 1 (Applied Biosystems), 18.4 μl ddH2O, 1 μl of each primer (10 mM), 0.1 μl AmpliTaq Gold 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 Genious v. 10.2.3 (Biomatters Ltd.). The COI gene was PCR amplified using primers (F31F1/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), transitional (n = 33, 32 live), and adults (n = 5, none live) of the zebra morph; between transitional (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.

**Stegostoma Regan, 1929: 293, possible error for Stegostoma Müller and Henle, 1837.**

**Stegostoma Herre, 1934: 10, possible error for Stegostoma Müller and Henle, 1837.**

**Stegostoma Last and Stevens, 1994: 138 apparent error for Stegostoma Müller and Henle, 1837.**
**Type species.** — *Squalus fasciatus* Bloch and Schneider, 1801, by original designation, equals *Squalus fasciatus* Hermann, 1783.

**Number of recognized species.** — 1.

### Stegostoma tigrinum
Zebra Shark
Figures 1–9, Table 1

The following is a revised synonymy based on Kottelat (2013).

*Squalus varius* Seba, 1759: p. 105, pl. 34, fig. 1. Claimed by Compagno (1984, 2001) to be unavailable, as binominal nomenclature was not used consistently. Description was based on two juvenile individuals, one of which measured 406 mm TL. No type locality or specimens, except for an illustration.

*Squalus tigrinus* Forster, 1781: p. 24, pl. 13, fig. 2. Description and schematic presentation was based on Seba's (1759) specimens.


*Squalus fasciatus* Bloch, 1784: p. 19, pl. 113. Bloch (1784) discovered the fifth gill slit and based his thorough description on two specimens (one measures >300 mm TL) from Tranquebar, India (Tharangambadi). Kottelat (2013) mentions three specimens: ZMB 4449 (holotype), ZMB 7833, and ZMB 22610. According to Paepke and Schmidt (1988), Bloch (1784) had 15 specimens in his collection. Bloch (1787) published another description of the species with additions to table CXIII presented in Bloch (1784) showing the anterior ventral part of a female next to the original figure.

*Squalus tigrinus* Broussonet, 1784: 659. Based on Gronovius, 1754: p. 62, no. 136; Seba (1759) and Forster (1781). Type locality: “mer des Indes” (Indian Ocean), China: “rivère de Canton” (Canton River).

*Squalus tygrinus* Bonnaterre, 1788: p. 8 pl. 8, fig. 23. Description based on Bloch (1787) p. 17; Forster (1781) and Broussonet (1784). Considered a misspelling from Forster (1781) and Broussonet (1784). Bonnaterre (1788) also referred to the species as *S. varius* based on Seba (1759). Drawing of specimen is from Bloch (1784): p. 19. No types known.

*Squalus fasciatus* Bonnaterre, 1788: p. 8. Description based on Broussonet (1784). Locality: South Africa, Cape of Good Hope: BMNH. Bonnaterre (1788) already described the species under *S. tygrinus*, but believed that *S. fasciatus* was a different species. He also used two different common names for the two descriptions; Le requin barbu (the...

---

**Fig. 1.** Schematic presentation of the morphology of *S. tigrinum*, including 52 morphometric measurements performed in the present study. Each number refers to a specific measurement further elaborated in Table 1.
Table 1. Morphometric measurements (% of TL) and meristic characters of *S. tigrinum*. Both morphs are represented. See Figure 1 for illustration of specific morphometrics.

<table>
<thead>
<tr>
<th>Zebra color morph</th>
<th>Sandy color morph</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Low–High (Avg)</td>
<td>n</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total length (TL, mm)</td>
<td>255–2050 (732.0)</td>
<td>52</td>
</tr>
<tr>
<td>Weight (kg)</td>
<td>0.4–40.0 (2.2)</td>
<td>31</td>
</tr>
<tr>
<td>Morphometric characters (%TL)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 Precaudal-fin length</td>
<td>41.4–58.7 (51.7)</td>
<td>50</td>
</tr>
<tr>
<td>3 Caudal-fin length</td>
<td>41.0–54.2 (47.7)</td>
<td>52</td>
</tr>
<tr>
<td>4 Precaudal tail</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>5 Snout to vent length</td>
<td>28.7–30.0 (32.6)</td>
<td>50</td>
</tr>
<tr>
<td>6 Prefacial-fin length</td>
<td>26.5–33.9 (29.7)</td>
<td>50</td>
</tr>
<tr>
<td>7 Vent to caudal-fin tip</td>
<td>64.3–72.2 (68.5)</td>
<td>49</td>
</tr>
<tr>
<td>8 Vent to anal-fin origin</td>
<td>2.3–12.5 (9.5)</td>
<td>46</td>
</tr>
<tr>
<td>9 Prepectoral-fin length</td>
<td>8.3–20.1 (13.5)</td>
<td>52</td>
</tr>
<tr>
<td>10 Prebranchial length</td>
<td>9.1–16.9 (11.8)</td>
<td>51</td>
</tr>
<tr>
<td>11 Preorbital length</td>
<td>4.8–12.0 (7.2)</td>
<td>51</td>
</tr>
<tr>
<td>12 Preoral length</td>
<td>1.8–6.2 (3.7)</td>
<td>51</td>
</tr>
<tr>
<td>13 Prespiracular length</td>
<td>6.8–11.8 (8.6)</td>
<td>51</td>
</tr>
<tr>
<td>14 Pre-first dorsal-fin length</td>
<td>12.6–32.1 (19.3)</td>
<td>50</td>
</tr>
<tr>
<td>15 Snout to ridge length</td>
<td>6.2–12.1 (8.8)</td>
<td>49</td>
</tr>
<tr>
<td>16 Head width</td>
<td>5.7–12.5 (7.3)</td>
<td>51</td>
</tr>
<tr>
<td>17 Head depth</td>
<td>3.4–7.3 (4.2)</td>
<td>52</td>
</tr>
<tr>
<td>18 Intergill length</td>
<td>0.9–2.1 (1.4)</td>
<td>51</td>
</tr>
<tr>
<td>19 First gill slit height</td>
<td>0.4–1.5 (0.8)</td>
<td>48</td>
</tr>
<tr>
<td>20 Fifth gill slit height</td>
<td>0.5–1.5 (0.9)</td>
<td>49</td>
</tr>
<tr>
<td>21 Eye length</td>
<td>0.1–0.6 (0.3)</td>
<td>51</td>
</tr>
<tr>
<td>22 Eye height</td>
<td>0.1–0.6 (0.3)</td>
<td>51</td>
</tr>
<tr>
<td>23 Spiracle height</td>
<td>0.5–1.5 (0.9)</td>
<td>49</td>
</tr>
<tr>
<td>24 Spiracle length</td>
<td>0.1–0.6 (0.3)</td>
<td>49</td>
</tr>
<tr>
<td>25 Chin width</td>
<td>2.3–3.6 (2.9)</td>
<td>48</td>
</tr>
<tr>
<td>26 Nasal flap width</td>
<td>3.3–5.9 (4.2)</td>
<td>49</td>
</tr>
<tr>
<td>27 Lower labial furrow length</td>
<td>0.9–1.7 (1.2)</td>
<td>50</td>
</tr>
<tr>
<td>28 Upper labial furrow length</td>
<td>0.8–3.1 (1.6)</td>
<td>50</td>
</tr>
<tr>
<td>29 Barbel length</td>
<td>0.6–2.2 (1.5)</td>
<td>48</td>
</tr>
<tr>
<td>30 Mouth width</td>
<td>2.9–6.8 (5.0)</td>
<td>51</td>
</tr>
<tr>
<td>31 Bony interorbital width</td>
<td>3.9–6.2 (5.3)</td>
<td>11</td>
</tr>
<tr>
<td>32 Fleshy interorbital width</td>
<td>5.7–15.5 (10.2)</td>
<td>48</td>
</tr>
<tr>
<td>33 Preanal-fin body depth</td>
<td>4.4–9.8 (5.9)</td>
<td>48</td>
</tr>
<tr>
<td>34 Max caudal-fin height</td>
<td>5.9–9.0 (7.8)</td>
<td>49</td>
</tr>
<tr>
<td>35 Interdorsal distance</td>
<td>2.4–6.3 (4.9)</td>
<td>49</td>
</tr>
<tr>
<td>36 Clasper length inner</td>
<td>0.7–8.7 (3.6)</td>
<td>26</td>
</tr>
<tr>
<td>37 Clasper length outer</td>
<td>0.8–6.5 (2.0)</td>
<td>26</td>
</tr>
<tr>
<td>38 Pectoral-fin inner margin</td>
<td>3.6–14.4 (4.8)</td>
<td>50</td>
</tr>
<tr>
<td>39 Pectoral-fin anterior margin</td>
<td>3.6–14.4 (4.8)</td>
<td>50</td>
</tr>
<tr>
<td>40 Pectoral-fin base to tip</td>
<td>7.8–15.7 (12.0)</td>
<td>49</td>
</tr>
<tr>
<td>41 Pelvic-fin length inner</td>
<td>2.5–7.0 (5.7)</td>
<td>49</td>
</tr>
<tr>
<td>42 Pelvic-fin length outer</td>
<td>4.5–11.0 (7.1)</td>
<td>50</td>
</tr>
<tr>
<td>43 Pelvic-fin width</td>
<td>2.6–5.9 (4.2)</td>
<td>49</td>
</tr>
<tr>
<td>44 First dorsal-fin base</td>
<td>7.1–17.7 (13.3)</td>
<td>50</td>
</tr>
<tr>
<td>45 First dorsal-fin height</td>
<td>2.0–5.9 (3.7)</td>
<td>52</td>
</tr>
<tr>
<td>46 First dorsal-fin inner margin</td>
<td>2.1–4.7 (2.8)</td>
<td>49</td>
</tr>
<tr>
<td>47 Second dorsal-fin base</td>
<td>2.1–14.4 (7.7)</td>
<td>50</td>
</tr>
<tr>
<td>48 Second dorsal-fin height</td>
<td>1.3–3.4 (2.1)</td>
<td>52</td>
</tr>
<tr>
<td>49 Second dorsal-fin inner margin</td>
<td>0.2–8.7 (2.4)</td>
<td>49</td>
</tr>
<tr>
<td>50 Anal-fin base</td>
<td>5.7–13.3 (8.6)</td>
<td>47</td>
</tr>
<tr>
<td>51 Anal-fin height</td>
<td>1.7–4.9 (2.9)</td>
<td>51</td>
</tr>
<tr>
<td>52 Anal-fin inner margin</td>
<td>0.6–2.6 (1.7)</td>
<td>49</td>
</tr>
</tbody>
</table>
Table 1. Continued.

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

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 quinquecornuta** 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. tigrinus*, 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 Chondropterygii in the family Cyclostomes and the genus *Scyllia* (based on Cuvier’s *Scyllium*, 1816 and today accepted as *Scyllorhinus* 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 Klausewitz (2013) mentioned that type specimens from the Indian Ocean are not included in Kottelat (2013).

**Scyliorhinus** genus Chondropterygiens in the family Cyclostomes and the 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.

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

**Stegostoma 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. Synotypes are MCZ 55-5 (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

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 apleosodic type; mesopterygium and metaopterygium are separated, and according to Compagno (2001), the proppterygium 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. 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.
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
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 ($P = 0.0001$, Fig. 2E) and the pre-first dorsal-fin length ($P = 0.0001$, Fig. 2F) are significantly shorter in the transitional stage. Adults of both morphs have significantly smaller eye length than transitionals and juveniles ($P = 0.0002$ zebra morph and $P = 0.0005$ sandy morph, Fig. 3A). Adults of both morphs have a significantly shorter caudal-fin length than both transitionals and juveniles ($P = 0.0003$ zebra morph and $P = 0.049$ sandy morph, Fig. 3B). Adults of both morphs 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
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...
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 dentine 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 dentine 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 dentine 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 dentine 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. 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).
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.
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.
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 swirlly 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 Squalleus 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; Faepke 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 variun 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 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 batti (Rajiformes) had been defined as a species complex for 90 years until Iglesias 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 altercations 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 transitional 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 Aquari- um).

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, 283 mm TL, 11°58′58.8″N, 102°13′58.8″E, Malaysia; MNHN-IC-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; ZUMC P2394732, female alcohol, 430 mm TL, East India; ZMUC P2394733, male alcohol, 325 mm TL, Indian Ocean; ZUMC P2394734, male alcohol, 280 mm TL, unknown location; ZUMC P2395365, 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 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.

**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 Dettaï (collection curator) and Zora (correspondent) at the Natural History Museum of Paris (MNHN), Peter Barch (curator) and Edda Åijel (collection manager) of the Natural History Museum of Berlin (ZMB) for...
help with accessioning of museum specimens. RBD acknowledges travel grants from Boje Benzons Støttetond 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


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.


Herrmann, J. 1783. Tabula affinitatum animalium olim academico specimen edita, nunc ubiorei commentario illustrata com annotationibus ad historam naturalem animalium augendam facientibus. J. G. Treuttel, Argentorati.


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.


