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Review of the Indian Ocean spikefish genus *Mephisto* (Tetraodontiformes: Triacanthodidae)

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Abstract

We redescribe the triacanthodid spikefish *Mephisto fraserbrunneri* Tyler 1966 based upon eight specimens (five newly reported herein) and the first color photographs of freshly collected specimens; these data are compared with that of the single specimen of the recently described *M. albomaculosus* Matsuura, Psomadakis, and Mya Than Tun 2018. Both species are found in the Indian Ocean, with *M. fraserbrunneri* known from the Arabian Sea off the east coast of Africa to the eastern Bay of Bengal, and *M. albomaculosus* confirmed only from the type locality in the Andaman Sea (a color photograph of an individual *M.* cf. *albomaculosus* from the Bay of Bengal that was not retained is also presented). We describe and diagnose the genus *Mephisto* and provide a key to the two species based upon all available specimens. We also provide a distribution map for both species and summarize literature records. Using micro-CT data, we show that *Mephisto fraserbrunneri* replaces teeth intraosseously, which suggests this tooth replacement pattern is plesiomorphic for Tetraodontiformes.

Key words: *Mephisto fraserbrunneri*; *Mephisto albomaculosus*; Andaman Sea; Bay of Bengal; morphometrics; intraosseous tooth replacement; CT scanning

Introduction

Mephisto fraserbrunneri Tyler 1966 was described based upon a single specimen from the Andaman Sea, Bay of Bengal, off the southern tip of Myanmar, Indian Ocean. A second specimen of *M. fraserbrunneri* was reported and described in comparison with the holotype by Tyler (1968) from the western Arabian Sea off Somalia, about 3000 miles (4800 km) west of the type locality. In the 1980s, two additional specimens of *M. fraserbrunneri* were collected by research vessels, both from off the coast of Somalia. One of these specimens was collected by the Russian R/V *Rift* on Error Seamount during an expedition arranged by N. V. Parin to study seamounts in the northwestern Indian Ocean. Parin recognized the importance of having collected a triacanthodid from a seamount, and he gave a thorough description of the specimen in a paper by Shcherbachev *et al.* (1986); Gorelova *et al.* (1993) also described this specimen. In both papers, the specimen was identified as *Mephisto* sp.; its specific identification was

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not confirmed because it had more spinules on the scales than had the previous two, smaller specimens described by Tyler (1968). Parin generously donated the specimen to the Smithsonian Institution for study (USNM 350153) in 1999; however, we only recently became aware of the literature that described this specimen (I. B. Shakhovskoy, pers. comm., 2019).

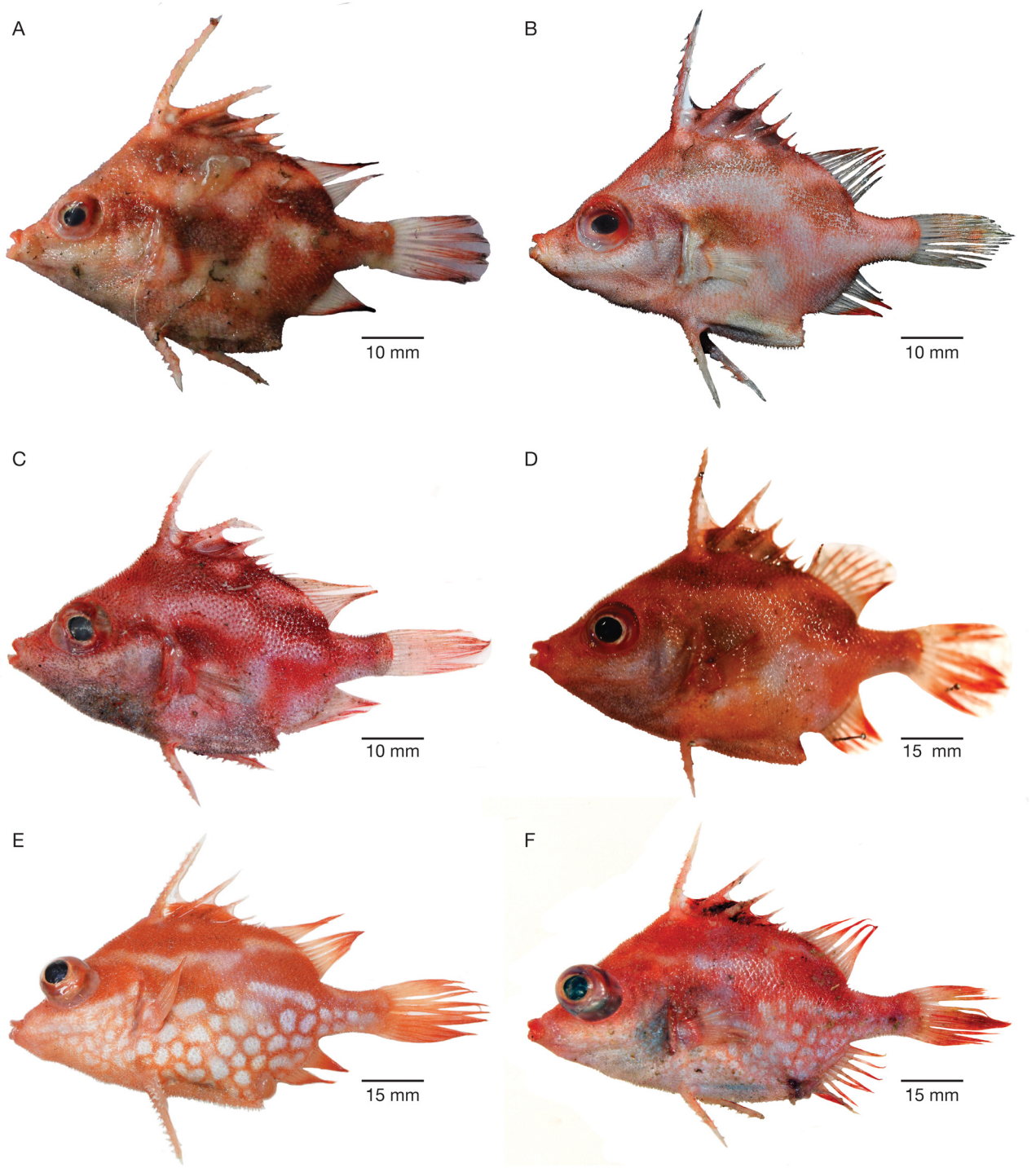

FIGURE 1. Color photographs of *Mephisto.* See Table 1 for collection localities. **A.** *Mephisto fraserbrunneri,* University of Kerala DABFUK/FI/301, 64.5 mm SL. Photograph by A. Biju Kumar. **B.** *Mephisto fraserbrunneri,* University of Kerala DABFUK/FI/303, 64.2 mm SL. Photograph by A. Biju Kumar. **C.** *Mephisto* cf. *fraserbrunneri,* specimen not retained, est. 54 mm SL. Photograph by Oddgeir Alvheim. **D.** *Mephisto* cf. *fraserbrunneri,* specimen not retained, est. 89 mm SL. Photograph by Tom Williams. **E.** *Mephisto albomaculosus,* holotype, NSMT-P 132271, 94.4 mm SL. Photograph by Oddgeir Alvheim, from Matsuura *et al.* (2018), photograph reprinted with permission from the Ichthyological Society of Japan. **F.** *Mephisto* cf. *albomaculosus,* specimen not retained, est. 94 mm SL. Photograph by Oddgeir Alvheim, from Matsuura *et al.* (2018), photograph reprinted with permission from the Ichthyological Society of Japan.

One of us (ABK), aboard the commercial trawler *Jerusalem* working off Kerala on the southwest coast of India, collected four specimens of *Mephisto fraserbrunneri* in 2018 and 2019. Color photographs were taken of the specimens while they were fresh on the deck of the trawler. These photographs are the first color images of this species (Fig. 1A, B).

Mephisto albomaculosus Matsuura, Psomadakis, and Mya Than Tun 2018 was described based upon a specimen that was collected in 2015 by the Norwegian R/V *Dr. Fridtjof Nansen* in the Andaman Sea off the southern tip of Myanmar, approximately 55 km from the type locality of *M. fraserbrunneri*. This species has a distinctive color pattern in comparison with that of *M. fraserbrunneri.* The original description of *M. albomaculosus* (Matsuura *et al.*, 2018) provided several additional morphological features that distinguish it from the two specimens of *M. fraserbrunneri* reported by Tyler (1968). Also collected by the R/V *Dr. Fridtjof Nansen* were individuals of *Mephisto* spp. that were photographed but not retained (e.g., Fig. 1C, D, F).

Based upon newly available specimens and information, we provide the following: (1) a revised diagnosis of the genus, including documenting its placement in the triacanthodid subfamily Triacanthodinae; (2) a redescription of *Mephisto fraserbrunneri* based upon the eight specimens now in natural history collections; (3) updated diagnostic characters for the two included species, *M. fraserbrunneri* and *M. albomaculosus*; (4) a key to the two species of *Mephisto*; and (5) a distribution map for both species. We also provide new meristic and morphometric data for *M. fraserbrunneri,* the first color photographs of it, new data on tooth replacement*,* and comments on the physical oceanographic environment it inhabits.

Methods

We studied eight specimens of *Mephisto fraserbrunneri* (Table 1) from ANSP, DABFUK, USNM, and ZMH; these include the holotype and all specimens of *M. fraserbrunneri* deposited in collections (Table 1). Measurements and counts were made as in Tyler (1968); scales studied for spinulation were sampled from the mid-lateral surface of the body just dorsal to the adpressed pectoral fin (Tyler, 1968: 7). Institutional abbreviations follow Sabaj (2019). We compare our data to that published by Matsuura *et al.* (2018) for *M. albomaculosus* and to that by Tyler (1968) for all of the other genera of triacanthodids. We also studied several photographs of individuals taken on board the R/V *Dr. Fridtjof Nansen* of *Mephisto* spp. that were collected but not retained (Fig. 1C, D, F; Table 1). For bathymetric plots (Fig. 2), we superimposed *Mephisto* spp. catch locations (depth, latitude, longitude) over a three-dimensional surface created from Smith and Sandwell (1997) seafloor topography, version 18.1. We estimated temperature and salinity values from World Ocean Atlas 2018 1/4º Climatology, objectively analyzed mean fields for in-situ sea water temperature and salinity (1955–2017; Locarnini *et al.*, 2018, Zweng *et al.*, 2018) using ocean_data_tools (Ferris, 2019). Values were linearly interpolated with respect to depth for each catch location. *Mephisto fraserbrunneri* ZMH 5629 was CT scanned at Cornell University in the Biotechnology Resource Center Multiscale Imaging Facility. We used the Xradia Versa XRM-500 nano-CT scanner to prepare data sets of 10–50 μm voxels and made 3D volume reconstructions using OsiriX™ (version 5.8.5, 64-bit edition) DICOM imaging software (Rosset *et al.*, 2004) on Apple Macintosh computers.

TABLE 1. Size, locality, and depth of collection for specimens and photographs of *Mephisto* spp.

Specimen number and preparation	Size (mm SL)	Locality	Date collected	Depth collected (m)	Collector, vessel, and station number
Specimens of *Mephisto fraserbrunneri*					
DABFUK/FI/304 Not formalin fixed, EtOH preserved	48.6	Lakshadweep Sea, off Kerala, southwest coast of India; 8°37'15.90"N; 76°9'54.44"E	21 Mar 2019	~ 300–350	A. Biju Kumar on F/V *Jerusalem*
ANSP 103314 Holotype Formalin fixed, EtOH preserved	52.2	Bay of Bengal, Andaman Sea, off southern tip of Myanmar; 10°39'N, 97°06'E	24 Mar 1963	290	J. C. Tyler on R/V *Anton Bruun*, Sta. 22B

Continued on the next page

TABLE 1. (continued)

Specimen number and preparation	Size (mm SL)	Locality	Date collected	Depth collected (m)	Collector, vessel, and station number
DABFUK/FI/303 Not formalin fixed, EtOH preserved	64.2	Lakshadweep Sea, off Kerala, southwest coast of India; 8°37'15.90"N; 76°9'54.44"E	21 Mar 2019	~ 300–350	A. Biju Kumar on F/V *Jerusalem*
DABFUK/FI/301 Formalin fixed, EtOH preserved	64.5	Lakshadweep Sea, off Kerala, southwest coast of India; 8°14'28.89"N; 76°4'53.19"E	27 Jan 2018	~ 300–350	A. Biju Kumar on F/V *Jerusalem*
ZMH 5629 (=BAH IOES-201) Formalin fixed, EtOH preserved	66.0	Arabian Sea, off tip of Somalia; 11°34–38'N, 52°52–54'E	20 Dec 1964	176–336	R/V *Meteor,* Sta. 102
USNM 306629 Formalin fixed, EtOH preserved	68.8	Indian Ocean, near coast of Somalia; 9°09'N, 50°56'E	14 Feb 1987	344–370	R/V *Beinta,* Cruise 19, Haul 25
DABFUK/FI/302 Not formalin fixed, EtOH preserved	102.7	Lakshadweep Sea, off Kerala, southwest coast of India; 8°37'15.90"N; 76°9'54.44"E	21 Mar 2019	~ 300–350	A. Biju Kumar on F/V *Jerusalem*
USNM 350153 Formalin fixed, EtOH preserved, subsequently cleared and stained	105.8	Arabian Sea, Error Seamount, Carlsberg Ridge, off Somalia; 10°45'N, 56°08'E	9 May 1983	415	N. V. Parin on R/V *Rift,* Cruise 2, Sta. 28; specimen received as a gift to J. C. Tyler from N. V. Parin in 1999; subsequently poorly cleared and stained by unknown person
Photographs of *Mephisto* cf. *fraserbrunneri*					
Fish in Figure 1C; specimen not retained	Est. 54	Off Myanmar; 14°40.38'N; 93°45.78'E	22 Nov 2013	85–88	R/V *Dr. Fridtjof Nansen* Myanmar survey, Sta. 50; photograph by O. Alvheim
Fish in Figure 1D; specimen not retained	Est. 89	Off Sri Lanka; Sta. 7: 10°2.67'N; 80°49.58'E Sta. 8: 9°56.25'N; 80°40.31'E	Sta. 7 and 8: 27 Jun 2018	Sta. 7: 436–446 Sta. 8: 85–86	R/V *Dr. Fridtjof Nansen* Sri Lanka survey, unknown if from Sta. 7 or Sta. 8; data for both included because depths different; photograph by T. Williams
Specimen of *Mephisto albomaculosus*					
NSMT-P 132271 Holotype	94.4	Andaman Sea, Indian Ocean, off Tanintharyi coast, Myanmar; 10°21.85'N, 96°44.83'E	28 May 2015	376–379	R/V *Dr. Fridtjof Nansen* Myanmar survey, Sta. 170; photograph by O. Alvheim
Photograph of *Mephisto* cf. *albomaculosus*					
Fish in Figure 1F; specimen not retained	Est. 94	Indian Ocean, off Myanmar; 14°23.33'N, 93°23.83'E	22 Nov 2013	74–75	R/V *Dr. Fridtjof Nansen* Myanmar survey, Sta. 47; photograph by O. Alvheim

Results

Mephisto Tyler 1966

Mephisto Tyler 1966a: 1–5 (original description; type species *Mephisto fraserbrunneri* Tyler 1966; etymology: genus named for the devil Mephisto, second only to Satan in the Faustian legend of Mephistopheles, in allusion to the reddish exterior, blackish interior (peritoneum), and the retrose-barbed dorsal-fin spines being the equivalent of horns in the type species).

Species. The genus *Mephisto* contains two species: *Mephisto fraserbrunneri* Tyler 1966 and *Mephisto albomaculosus* Matsuura, Psomadakis, and Mya Than Tun 2018.

Subfamilial placement. The two subfamilies of Triacanthodidae are diagnosed primarily by features in two different regions of the skeleton: the posterior process of the pelvis and the posterodorsal region of the skull. The width, shape, and structure of the posterior process of the pelvis (Fig. 3A, B) is visible externally; the shape of the supraoccipital and its relationship to the epioccipitals is only visible internally (Fig. 3C, D; see Tyler, 1968: 62; 1980: 56).

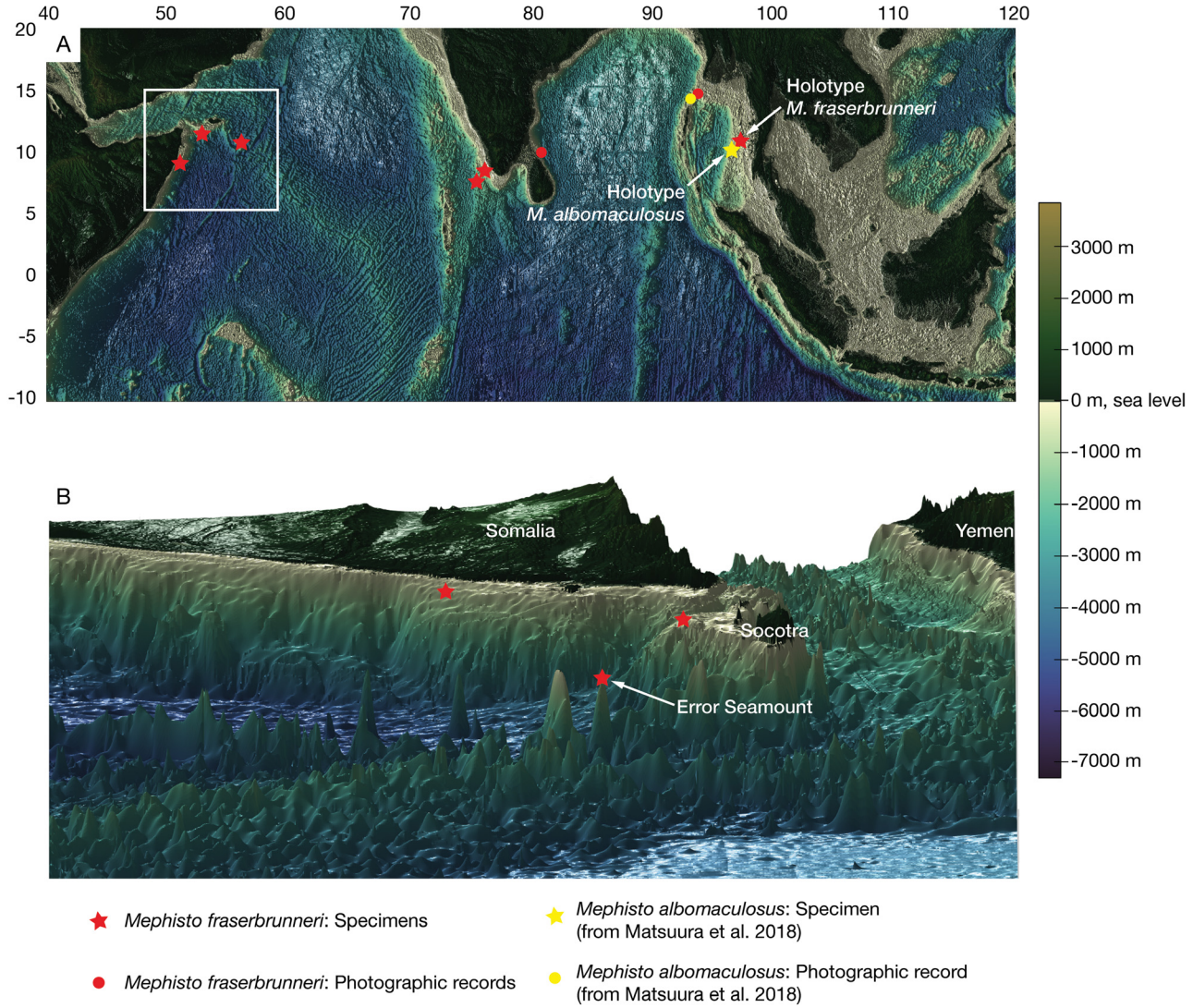

FIGURE 2. Distribution and habitat of *Mephisto*. **A.** All known records of *Mephisto,* including holotypes of *M. fraserbrunneri* and *M. albomaculosus,* non-type specimens of *M. fraserbrunneri,* and photographic records of specimens that were not retained. **B.** Detail of region in white box in part A highlighting collection localities on continental shelf off Somalia and Socotra, and Error Seamount (part of the Carlsberg Ridge). Bathymetric data from Smith and Sandwell (1997).

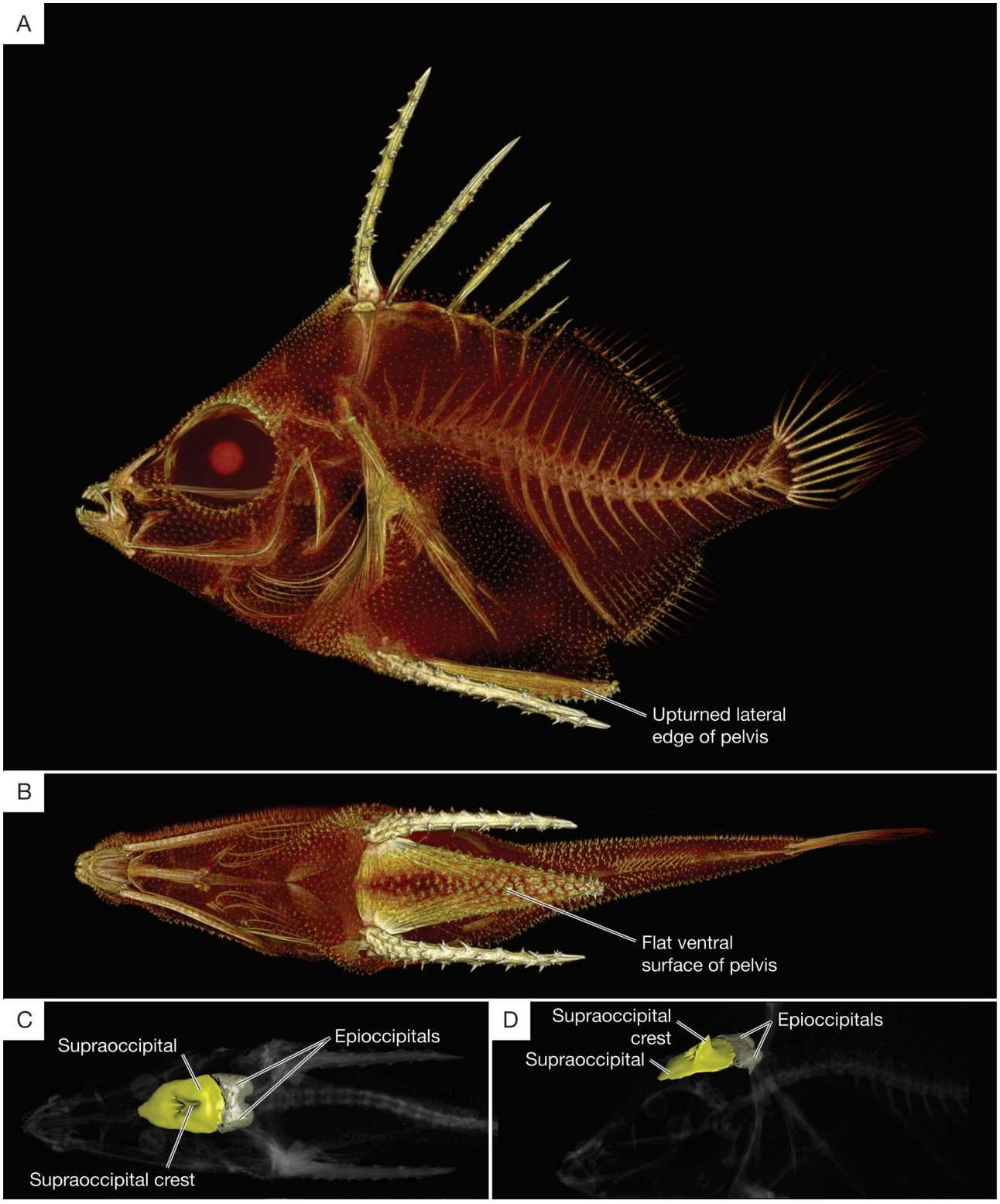

FIGURE 3. Micro-CT scan of *Mephisto fraserbrunneri,* ZMH 5629, 66.0 mm SL, showing subfamilial characters. **A.** Lateral view, highlighting extent of pelvis. **B.** Ventral view showing flat, scale-covered pelvis that tapers to a point posteriorly, much wider anteriorly between the pelvic spines than posteriorly. **C.** Dorsal view of the rear of the skull showing the flattened supraoccipital (yellow) and its low crest, with the supraoccipital not separating the epioccipitals (gray) on the dorsal surface of the skull. **D.** Oblique view of the rear of the skull highlighting the median, narrow, supraoccipital crest located in the middle of the supraoccipital.

The Hollardiinae (*Hollardia, Parahollardia,* western Atlantic, except one species in Pacific Oceania) have a shaft-like posterior process of the pelvis that is relatively rounded in ventral view and is not much wider between the bases of the pelvic spines than at the blunt posterior end, and they have a dome-like supraoccipital that separates the contralateral epioccipitals posteriorly on the dorsal surface of the skull. The Triacanthodinae (all other extant genera, Indo-Pacific except one species in western Atlantic) have a basin-like posterior process of the pelvis that is flat ventrally, with slightly dorsally upturned lateral edges, and is wider anteriorly between the pelvic spines than posteriorly where it tapers to an end (see Tyler, 1968 for illustrations of the posterior process of the pelvis in all genera of triacanthodids), and they have a flattened supraoccipital with a median crest that does not separate the epioccipitals posteriorly on the dorsal surface of the skull. The only fossil triacanthodids are two taxa from the Oligocene of the Polish Carpathian Mountains, the hollardiin *Prohollardia* and the triacanthodin *Carpathospinus*. The two triacanthodid subfamilies diverged no less than 29 to 24 MYA (see Tyler *et al.*, 1993).

TABLE 2. Meristic data from eight examined specimens of *Mephisto fraserbrunneri*. Dashes indicate data that could not be obtained because of specimen damage or specimen having been cleared and stained prior to this study.

	DABFUK/ FI/304	ANSP 103314	DABFUK/ FI/303	DABFUK/ FI/301	ZMH 5629	USNM 306629	DABFUK/ FI/302	USNM 350153
Character		**Holotype**						
Standard Length (mm)	48.6	52.2	64.2	64.5	66.0	68.8	102.7	105.8
Dorsal-fin rays	VI + 16	VI + 16	VI + —	VI + 16	VI + 16	VI + 16	VI + 15	VI + 16
Anal-fin rays	14	14	—	14	14	14	13	14
Pectoral-fin rays (Left, Right)	14, 15	14, 14	—	14, 14	14, 14	14, 14	13, 13	13, 13
Pelvic-fin rays (Left, Right)	1, 1	1, 1	1, 1	1, 1	1, 1	1, 1	1, 1	1, 1
Olfactory lamellae	—	10	—	10	9	10	—	—
Gill rakers	—	19	—	17	19	16	17	18
Lamellae in pseudobranch	—	18	—	17	19	17	20	19
Outer teeth in upper jaw	24	17	21	23	18	20	24	20
Inner teeth in upper jaw	0	0	0	0	0	0	0	0
Outer teeth in lower jaw	27	19	27	27	22	25	27	23
Inner teeth in lower jaw	0	0	0	0*	0	0	0	0

* 1 tooth offset from main series of teeth.

Mephisto fraserbrunneri has the diagnostic characters of the Triacanthodinae (Fig. 3). *Mephisto albomaculosus* has the pelvic characters of triacanthodins, but the shape of its supraoccipital and its articulation with the epioccipitals is not known; presumably it is typical of triacanthodins.

Diagnosis. The genus *Mephisto* is distinguished from all other triacanthodids by a long gill opening (13.5–17.6% SL; Table 3), with its lower edge reaching slightly below the lower edge of the lobe of the pectoral-fin base (Fig. 4A; see Tyler, 1968: figs. 137, 150, 164, 173 for comparisons of length of gill opening across ontogeny for all genera).

Description. (1) Pelvis thin and basin-like, its ventral surface flat but with slightly upturned edges; width between the pelvic-fin spines moderate to somewhat narrowed (diagnostically different between the two species, with *M. fraserbrunneri* 10.6–12.1% SL and *M. albomaculosus* 7.8% SL); pelvic width into the pelvic length 2.6–4.0 times (likewise diagnostically different between the two species, with *M. fraserbrunneri* 2.6–3.2 times and *M. albomaculosus* 4.0 times). (2) Deep bodied (45.8–54.2% SL). (3) Short snouted (12.4–14.5% SL). (4) Long postorbital length (11.6–13.2% SL). (5) Six dorsal-fin spines decreasing gradually in length from the first to the short last

spine, all visible externally (Table 2). (6) Origin of the anal fin distinctly posterior to the origin of the soft dorsal fin. (7) Mouth terminal, with a moderate number of conical teeth (17–25 in upper jaw and 19–27 in lower jaw; Table 2; Matsuura *et al.*, 2018) in a single series with no teeth internal to them (one specimen of *M. fraserbrunneri* has one lower jaw tooth slightly offset posteriorly from the main row, but we do not interpret this as an internal tooth *sensu* Tyler, 1968:58). (8) Few olfactory lamellae (9–11; Table 2; Matsuura *et al.*, 2018). (9) Moderate number of gill rakers (15–19; Table 2; Matsuura *et al.*, 2018). (10) Pseudobranch with a moderate number of lamellae (16–20; Table 2; Matsuura *et al.*, 2018), the lower edge of the base of the pseudobranch level with the upper edge of the lobe of the pectoral-fin base (Table 4; Matsuura *et al.*, 2018). (11) Few spinules per scale, consisting of one large central spinule and smaller spinules dorsal and ventral to it that increase in number and branching during ontogeny; only a single spinule present in scales of smallest known specimens (DABFUK/FI/304, 48.6 mm SL and ANSP 103314, 52.2 mm SL; Table 4); some spinules are branched in large specimens (e.g., Fig. 5; USNM 350153, 105.8 mm SL, DABFUK/FI/302, 102.7 mm SL, and NSMT-P 132271, 94.4 mm SL; Table 4; Matsuura *et al.*, 2018). (12) Retrose barbs on dorsal- and pelvic-fin spines (Fig. 3). (13) Pelvic fin with only one soft ray. (14) Small patch of isolated spinulose scales on middle of upper surface of dorsal lip (Fig. 6).

Geographic and depth distribution and physical environment. Specimens and photographs of *Mephisto* are known from the Indian Ocean from off Somalia to Myanmar (Fig. 2), from 74 m to 446 m (Table 1). Preliminary analysis, based on World Ocean Atlas 2018, suggests that *Mephisto* occurs in waters of 10.2–25.3°C and salinity of 34.00–35.43 psu (Table 5); however, more specimens are needed to confirm this because both salinity and temperature ranges were expanded by photographic records of unretained specimens of *M. albomaculosus* and *M. fraserbrunneri*.

TABLE 3. Morphometric data from eight examined specimens of *Mephisto fraserbrunneri*. Dashes indicate data that could not be obtained because of specimen damage or specimen having been cleared and stained prior to this study. Asterisk indicates data taken from Sheherbachev *et al.* (1986).

Character	DABFUK/ FI/304	ANSP 103314 Holotype	DABFUK/ FI/303	DABFUK/ FI/301	ZMH 5629	USNM 306629	DABFUK/ FI/302	USNM 350153
Standard Length (SL) (mm)	48.6	52.2	64.2	64.5	66.0	68.8	102.7	105.8
Head length as % SL	42.8%	42.7%	40.8%	40.8%	40.5%	39.5%	38.3%	40.6%
Snout length as % SL	13.4%	12.4%	14.5%	13.8%	13.2%	12.5%	13.1%	14.2%
Eye diameter as % SL	16.5%	17.0%	16.8%	15.0%	15.2%	14.8%	14.6%	15.9%
Postorbital length as % SL	12.6%	13.0%	11.8%	13.2%	13.2%	12.6%	11.6%	12.6%
Interorbital width as % SL	8.2%	7.8%	7.2%	6.4%	7.1%	8.3%	7.2%	7.4%
Mouth width as % SL	8.8%	10.1%	8.0%	8.4%	8.0%	8.1%	8.1%	8.2%
Gill opening length as % SL	17.6%	14.1%	17.1%	16.3%	13.8%	14.5%	17.1%	13.5%*
Snout to spinous dorsal-fin origin distance as % SL	49.4%	46.1%	50.4%	47.2%	46.8%	48.1%	47.2%	46.8%
Body depth as % SL	54.1%	52.2%	51.7%	54.2%	53.2%	53.3%	50.5%	45.8%
First dorsal spine length as % SL	33.6%	30.8%	35.2%	34.4%	32.3%	34.5%	33.9%	—
Second dorsal spine length as % SL	28.8%	26.2%	31.6%	30.4%	27.6%	27.8%	30.3%	—

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TABLE 3. (continued)

Character	DABFUK/ FI/304	ANSP 103314 Holotype	DABFUK/ FI/303	DABFUK/ FI/301	ZMH 5629	USNM 306629	DABFUK/ FI/302	USNM 350153
Soft dorsal-fin base length as % SL	—	19.1%	—	18.0%	19.7%	19.0%	19.2%	18.2%
Soft dorsal-fin height as % SL	—	19.7%	—	17.1%	17.3%	16.4%	17.5%	—
Anal-fin base % SL	—	15.9%	—	15.3%	16.7%	14.5%	16.7%	14.9%
Anal-fin height as % SL	—	17.2%	—	15.8%	16.8%	16.6%	15.0%	—
Anal-fin base length into soft dorsal-fin base length	—	1.2×	—	1.2×	1.2×	1.3×	1.2×	1.2×
Caudal-fin length as % SL	—	31.8%	—	28.7%	28.8%	26.3%	24.1%	—
Caudal-peduncle depth as % SL	10.4%	10.5%	10.0%	11.3%	11.4%	11.6%	11.3%	10.6%
Caudal-peduncle length as % SL	—	17.4%	16.0%	20.1%	18.9%	16.4%	20.4%	19.6%
Pelvic-fin spine length as % SL	30.9%	30.8%	35.5%	34.1%	30.8%	31.2%	33.5%	25.4%
Pelvic-fin ray length as % SL	3.9%	3.4%	2.6%	2.9%	3.5%	2.5%	2.1%	2.6%
Pelvic width as % SL	12.1%	11.3%	11.2%	11.6%	11.7%	10.6%	11.1%	10.7%
Pelvic length as % SL	32.3%	32.1%	31.8%	34.9%	32.0%	34.3%	30.6%	29.0%
Pelvic width into pelvic length	2.6×	2.8×	2.8×	3.0×	2.7×	3.2×	2.8×	2.7×
Pectoral-fin length % SL	17.7%	20.1%	—	17.7%	17.4%	16.4%	16.0%	—
Uppermost pectoral-fin ray length as % SL	3.3%	4.4%	—	2.0%	2.1%	3.7%	est. 1.3%	2.6%

Mephisto fraserbrunneri **Tyler 1966**

Devil's Spikefish

Mephisto fraserbrunneri Tyler 1966a: 1–5 (original description; based upon a single specimen, holotype: ANSP 103314, type locality: eastern Bay of Bengal, Andaman Sea, off southern Myanmar, Indian Ocean, 10°39′N, 97°06′E, R/V *Anton Bruun,* Station 22B, 159 fathoms (= 290 m), 24 March 1963; etymology: species named in honor of A. Fraser-Brunner for his pioneering revisions of many families of plectognaths). Tyler, 1966b: 4 (considered to be a generalized triacanthodid). Tyler, 1968: 133–138 (description, proposed relationships, illustration of pelvis and scales, photograph of BAH IOES-201 (= ZMH 5629)). Tyler, 1980 (summary of proposed relationships as given in Tyler (1968)). Shcherbachev *et al.*, 1986: 208 (description of USNM 350153; specimen identified as *Mephisto* sp. because scales have several spinules that are bifurcate). Tyler, 1986: 887 (*Mephisto* included in key). Gorelova *et al.*, 1993: 225 (mesobenthic species, captured on Error Seamount; stomach contents of 105 mm SL specimen (now USNM 350153) contained chitin fragments and peropods of a gammarid). Manilo and Bogorodsky, 2003: S123

(listed only). Matsuura, 2015: 75, 76 (range includes Somalia, Arabian Sea, and Andaman Sea). Mullasseri *et al.*, 2017: 76–81 (comparison of seven specimens from Andaman Islands of putative *Paratriacanthodes retrospinis* with data from Tyler (1968) on *M. fraserbrunneri,* but critical diagnostic measurements, such as length of gill opening, not provided, and the single specimen illustrated (figs. 2, 3, both in color; fresh and after preservation of the same specimen) of putative *P. retrospinis* has the typical blotchy color pattern and long gill opening that is diagnostic of *M. fraserbrunneri* rather than the horizontally lined pattern and shorter gill opening typical of *P. retrospinis*; these specimens require re-examination for proper identification). Matsuura *et al.*, 2018: 30–33 (comparison of *M. fraserbrunneri* with *M. albomaculosus*).

Material. Known from the holotype ANSP 103314, seven additional specimens, and two separate photographic records of individuals that were not retained (Table 1).

Diagnosis. A species of *Mephisto* with red to pink coloration and lighter, almost white, areas and darker red blotches; the ventral part of the head and body beginning under the eye is light in coloration, but no white, rounded markings are present (Fig. 1A–D). Pelvic width 10.6–12.1% SL; pelvic width into pelvic length 2.6–3.2 times; gill rakers 16–19; pseudobranch lamellae 17–20.

Description. Data on meristics (Table 2), proportional measurements (Table 3), and additional characters (Table 4) are summarized for all eight specimens.

Coloration. *Mephisto fraserbrunneri* is red to pink with lighter, almost white, areas and darker red blotches (Fig. 1A–D). The darkest red regions are below the spinous dorsal fin, below the posterior part of the soft dorsal fin, and above the pectoral fin from behind the eye. The ventral part of the head, beginning under the eye, is light in coloration. The spinous dorsal fin is predominantly dark red, whereas the soft dorsal and anal fins are white proximal to the body and darker distally. In alcohol, the blotchy pattern remains, and the darkest red areas in life are brown (Fig. 4A). The peritoneum and branchial cavity are tan to blackish and speckled with darker spots (Table 4).

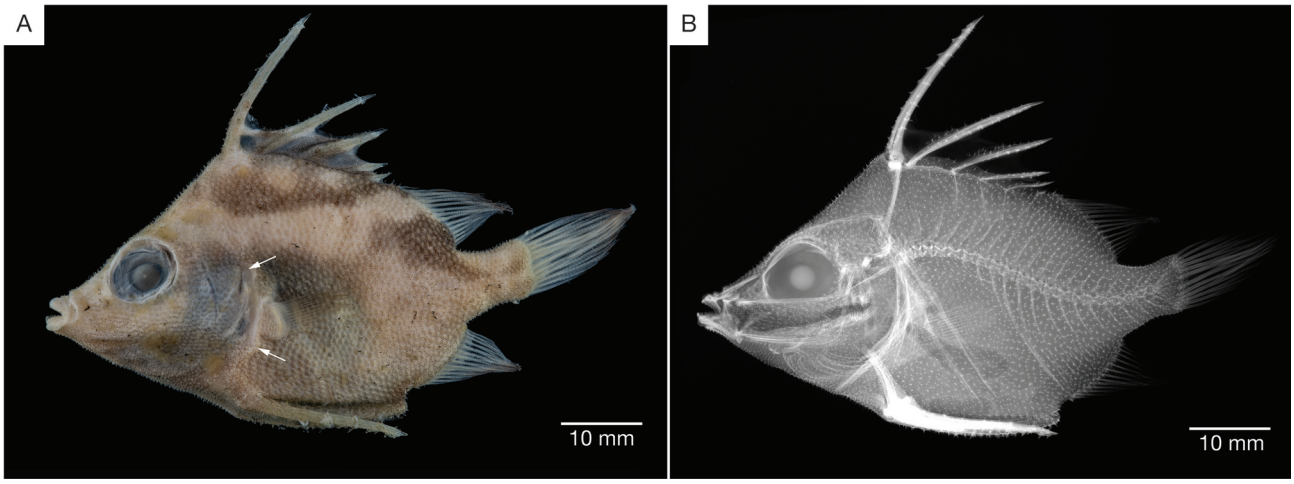

FIGURE 4. *Mephisto fraserbrunneri*, University of Kerala DABFUK/FI/301, 64.5 mm SL. **A.** Specimen in alcohol. White arrows indicate the length of the gill opening, which is the diagnostic character for *Mephisto*. **B.** Radiograph of same specimen. Images by Sandra Raredon.

Description of scales during ontogeny. The scales of *Mephisto fraserbrunneri* begin with a single spinule and increase in number of spinules during their ontogeny; the branching of spinules also increases with specimen length. Matsuura *et al.* (2018: fig 2) described the scales of *M. albomaculosus* as differing from those of *M. fraserbrunneri* because the scales of *M. albomaculosus* have a bifurcate spinule at the base of the central spinule (Fig. 5D). However, the new specimens reported herein increase the size range known for *M. fraserbrunneri,* and we now have more information on how the number of spinules and their branches change throughout ontogeny (Table 4). We confirm that large *M. fraserbrunneri* (DABFUK/FI/302, 102.7 mm SL and USNM 350153 105.8 mm SL) have up to six spinules per scale, with 1–3 branched spinules and the central and largest spinule having a bifurcate spinule at the base (Fig. 5). Thus, having a bifurcate spine on the central spinule is not diagnostic for *Mephisto* species. Shcherbachev *et al.* (1986) identified USNM 350153 as *Mephisto* sp. because at the time it was collected and examined only two small specimens of *Mephisto fraserbrunneri* were known, and each had scales with a single, unbranched spinule; we recognize the multiple spinule pattern present in the largest specimens as representing an advanced stage of ontogeny (Fig. 5A–C).

TABLE 4. Qualitative characters for the eight examined specimens of Mephisto fraserbrunneri. Dashes indicate data that could not be obtained because of specimen damage or specimen having been cleared and stained prior to this study. Asterisk indicates data taken from Shcherbachev et al. (1986).

Character	DABFUK/ FI/304	ANSP 103314 Holotype	DABFUK/FI/303	DABFUK/FI/301	ZMH 5629	USNM 306629	DABFUK/FI/302	USNM 350153
Standard Length (mm)	48.6	52.2	64.2	64.5	66.0	68.8	102.7	105.8
Number of upright spinules on scales	1 central, unbranched spinule; no bifurcate spinule at base	1 central, unbranched spinule; no bifurcate spinule at base	3 spinules; central spinule frequently with one branch; dorsal and ventral spinules unbranched	3 spinules; central spinule frequently with one branch; dorsal and ventral spinules unbranched	3 spinules; central, dorsal, and ventral spinules all unbranched	3 or 4 spinules; central, dorsal, and ventral spinules all unbranched	4–6 spinules; central spinule with birfucate spine at base; branching in 1 or 2 of dorsal and ventral spinules	4 or 5 spinules; central spinule with birfucate spine at base; branching in 1 or 2 of dorsal and ventral spinules
Gill opening extension	Well below pectoral-fin base	Slightly below pectoral-fin base	Well below pectoral-fin base	Slightly below pectoral-fin base	Slightly below pectoral-fin base	Slightly below pectoral-fin base	Well below pectoral-fin base	Level of lower margin of pectoral-fin base*
Pseudobranch extension	—	Upper origin of pectoral-fin base	—	Upper origin of pectoral-fin base	Upper origin of pectoral-fin base	Upper origin of pectoral-fin base	Upper origin of pectoral-fin base	Above upper origin of pectoral-fin base
Retrose barbs	Present on 1st dorsal and pelvic spine	Present on 1st dorsal and pelvic spine	Present on 1st dorsal and pelvic spine	Present on 1st dorsal and pelvic spine	Present on 1st dorsal and pelvic spine	Present on 1st dorsal and a few on pelvic spine	Present on 1st dorsal and pelvic spine	Dorsal spine broken, pelvic spine without retrose spines
Peritoneum color	Blackish	Dark tan with darker speckles	Blackish	Dark tan with dark speckles	Tan with darker brown speckles	Dark tan with darker speckles	Blackish	—
Brachial cavity color	Blackish	Dark tan	Blackish	Dark tan	Tan	Tan	Blackish	—
Sex based on gonads	?	Immature	Female (?)	Male	Female	Male (?)	Mature female	—

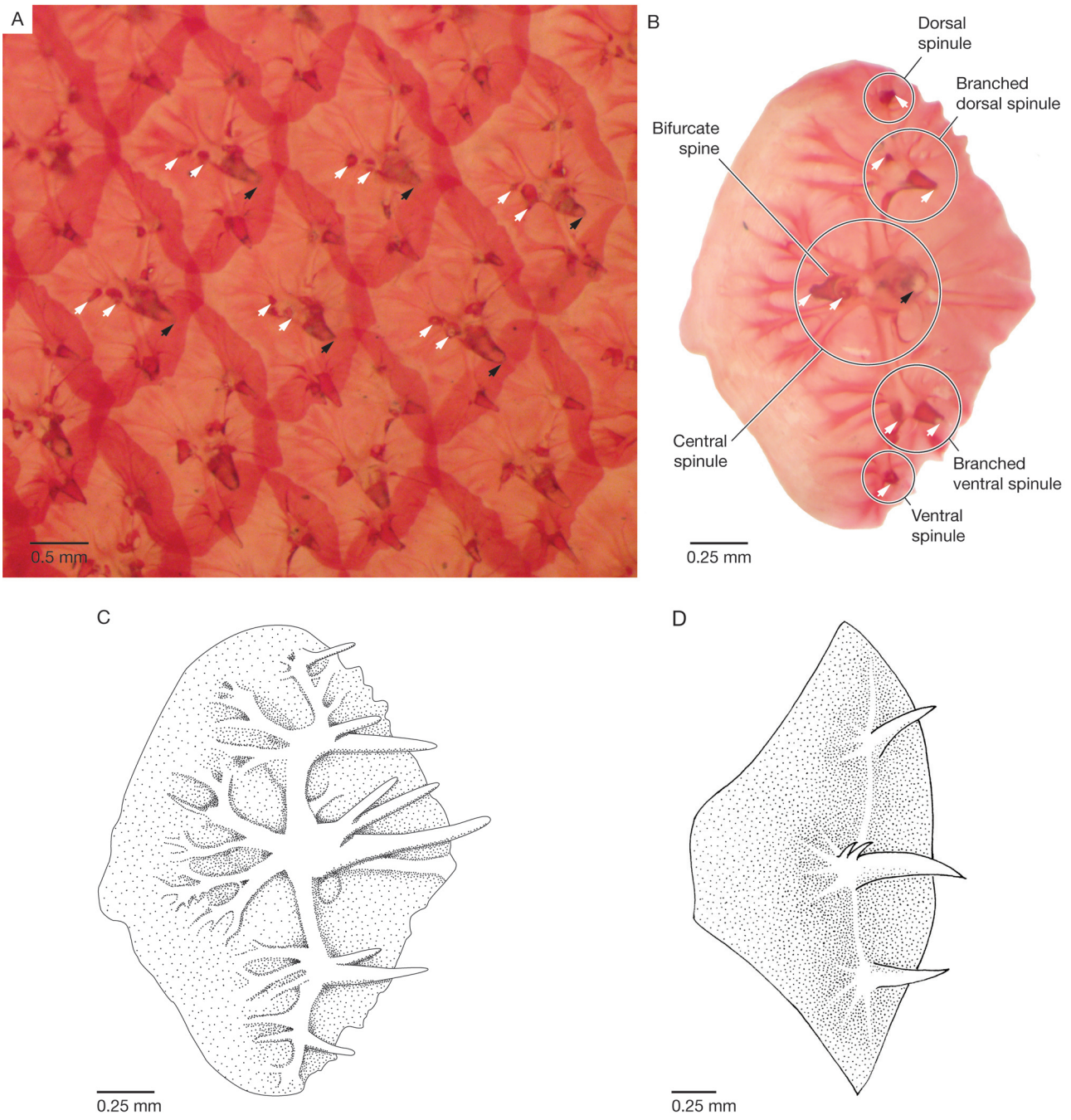

FIGURE 5. Mid-body scales of *Mephisto.* Anterior to left. **A–C** *Mephisto fraserbrunneri,* USNM 350153, 105.8 mm SL. **A.** Patch of scales. White arrows indicate tips of bifurcate spinules at base of central spinules; black arrows indicate tips of central spinules. **B.** Single scale showing five spinules, including a central spinule with a bifurcate spinule at its base and both branched and unbranched dorsal and ventral spinules. White arrows indicate tips of single or bifurcate spinules; black arrow indicates central spinule tip. **C.** Illustration of single scale from *M. fraserbrunneri* to show relative length of spinules when viewed obliquely and for comparison with images B and D. **D.** Illustration of a single scale of *M. albomaculosus,* NSMT-P 132271, 94.4 mm SL. Illustration from Matsuura *et al.* (2018), reprinted with permission from the Ichthyological Society of Japan. Note, scale has been reflected so image faces left. In large specimens of both *M. fraserbrunneri* and *M. albomaculosus* the central spinule has a bifurcate branch. Apparent differences in shape of scale plates in parts C and D is because the regions of overlap are not shown in part D.

Description of teeth and tooth replacement. *Mephisto* has relatively few stoutly conical teeth that are larger in the anterior part of the jaw and smaller posterolaterally on the premaxilla and dentary (Table 2; Fig. 6). Teeth are re-

placed intraosseously (Fig. 6). Teeth develop underneath functional teeth and erupt on the labial side of the jaw. There is no obvious pattern of replacement; several teeth in the jaws of various specimens were in the process of replacement. For example, in the specimen shown in Figure 6, there are nine teeth in both the left and right premaxillae; two or three teeth are undergoing replacement (loci 3 and 7 in the left premaxilla; loci 1, 3, and 9 in the right premaxilla). On each side of the left and right dentary there are 11 teeth; two to four teeth are undergoing replacement (loci 2 and 10 on the left dentary and loci 1, 3, 7, and 9 on the right dentary). In the right dentary, locus 1 has an eroding tooth and an erupting replacement tooth beneath it.

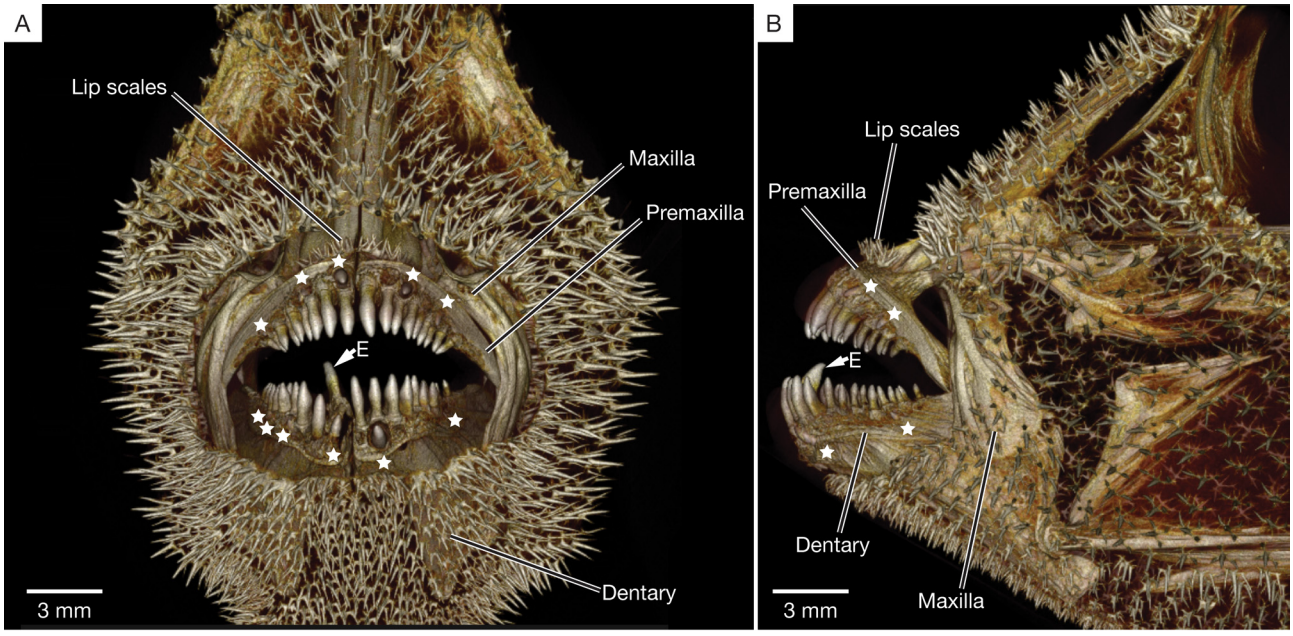

FIGURE 6. Micro-CT scan of jaws and dentition of *Mephisto fraserbrunneri,* ZMH 5629, 66.0 mm SL. Tooth loci with developing teeth are indicated with stars, and an eroding tooth is indicated with an E. **A.** Anterior view showing intraosseous tooth replacement in left and right premaxillae and dentaries. **B.** Lateral view of teeth developing intraosseously that are nearing eruption.

Diet. Three specimens of *Mephisto fraserbrunneri* had stomach contents: DABFUK/FI/304 contained primarily foraminiferans and secondarily pteropods. Both planktic (*Globorotalia menardii, Globigerinella siphonifera, Globigerinoides ruber, Neogloboquadrina dutertrei,* and *Trilobatus sacculifer*) and benthic (*Bolivina* and *Uvigerina*) foraminiferans were present (Brian Huber, pers. comm., 2020). Pteropod shells, as well as several scaphopods and an echinoderm spine, were also in the stomach. The shells of these organisms had sediment on them, and the foraminiferans did not appear to have been ingested alive. USNM 306629 had well-digested amphipods in its stomach. The largest specimen, USNM 350153, had chitin fragments and peropods of a gammarid in its stomach (Gorelova *et al.*, 1993), which were lost when it was cleared and stained. Based upon this data, we conclude that *M. fraserbrunneri* feeds on a diversity of small organisms found on or in bottom sediment.

Geographic and depth distribution. The holotype of *Mephisto fraserbrunneri* was collected in the Andaman Sea off Myanmar. Three of the eight known specimens of *M. fraserbrunneri* were collected off Somalia. The four most recently collected specimens of *M. fraserbrunneri* were caught off Kerala on the southwest coast of India in the Lakshadweep Sea (Fig. 2). All eight specimens of *M. fraserbrunneri* were caught in bottom trawls at depths of 176–415 m (Table 1).

Mephisto albomaculosus **Matsuura, Psomadakis, and Mya Than Tun 2018**

White Spotted Spikefish

Mephisto albomaculosus Matsuura, Psomadakis, and Mya Than Tun 2018: 30–33: (original description; described from a single specimen, holotype: NSMT-P 132271; type locality: eastern Bay of Bengal, Andaman Sea, off Tanin-

tharyi coast, southern Myanmar, Indian Ocean, 10°21.85′N, 96°44.83′E, R/V *Dr. Fridtjof Nansen* Station 170, 379 m, 28 May 2015; etymology: refers to the white markings on the head and body; comparison of *M. albomaculosus* with *M. fraserbrunneri*).

Material. Known only from the holotype (Matsuura *et al.*, 2018) and one photographed individual, presumed to be conspecific with the holotype, that was not retained (Fig. 1E, F).

Diagnosis. A species of *Mephisto* with prominent white, rounded (more-or-less circular to oval) markings that are up to as large as the pupil diameter and located on the lower half of the body (Fig. 1E, F). Pelvic width 7.8% in SL; pelvic width into pelvic length 4.0 times; gill rakers 15; pseudobranch lamellae 16 (Matsuura *et al.*, 2018).

Description. See Matsuura *et al.* (2018:31).

Geographic and depth distribution. The holotype of *Mephisto albomaculosus* is from the Andaman Sea off Myanmar at 376–379 m. The photograph of the referred specimen of *M.* cf. *albomaculosus* (specimen not retained) was collected in the Bay of Bengal at 74–75 m.

TABLE 5. Depth interpolated temperature and salinity from World Ocean Atlas 2018 1/4º Climatology (1955–2017) based on catch location. Dashes indicate data not available.

Specimen number or photographic record	Locality	Depth (m)	Temperature (ºC)	Salinity (psu)
ANSP 103314	10°39’N, 97°06’E	290	11.4	34.97
ZMH 5629	11°34–38’N, 52°52–54’E	176–336	–	–
USNM 350153	10°45’N, 56°08’E	415	12.1	35.43
USNM 306629	9°09’N, 50°56’E	344–370	–	–
DABFUK/FI/301	8°14’28.89”N; 76°4’53.19”E	~300–350	11.5–12.1	35.13–35.15
DABFUK/FI/302 304	8°37’15.90”N; 76°9’54.44”E	~300–350	11.5–12.1	35.12–35.15
Photograph of *M.* cf. *fraserbrunneri*, Figure 1C; specimen not retained	14°40.38’N; 93°45.78’E	85–88	–	–
Photograph of *M.* cf. *fraserbrunneri*, Figure 1D; specimen not retained, Sta. 7	10°2.67’N; 80°49.58’E	436–446	10.2–10.3	35.03
Photograph of *M.* cf. *fraserbrunneri*, Figure 1D; specimen not retained, Sta. 8 (same specimen as entry above, but station number equivocal)	9°56.25’N; 80°40.31’E	85–86	–	–
NSMT-P 132271	10°21.85’N, 96°44.83’E	376–379	10.6–10.7	34.99
Photograph of *M.* cf. *albomaculosus*, Figure 1F; specimen not retained	14°23.33’N, 93°23.83’E	74–75	25.2–25.3	34.00–34.02

Discussion

Comparison of species. *Mephisto fraserbrunneri* is distinguished from the only other species in the genus, *M. albomaculosus,* primarily by color pattern (Fig. 1; Matsuura *et al.*, 2018). The dorsal coloration of *M. fraserbrunneri* and *M. albomaculosus* is similar; however, *M. albomaculosus* has prominent white, rounded (more-or-less circular to oval) markings that are up to as large as the pupil diameter and located on the lower half of the body that are not present in *M. fraserbrunneri* (Fig. 1). In addition to color differences, Matsuura *et al.* (2018) described four other diagnostic characters based on their comparison of the holotype of *M. albomaculosus* with data from the two specimens of *M. fraserbrunneri* described in Tyler (1968). Based upon our examination of additional specimens of *M.*

fraserbrunneri, we determined three of these are valid. (1) The pelvic width is greater in *M. fraserbrunneri* (10.6–12.1% SL, pelvic width into pelvic length 2.6–3.2 times) compared with *M. albomaculosus* (width 7.8% SL, pelvic width into pelvic length 4.0 times). (2) There are more gill rakers in *M. fraserbrunneri* than in *M. albomaculosus*. Our redescription expands the range to 16–19 gill rakers in *M. fraserbrunneri* compared with the holotype of *M. albomaculosus,* which has 15 gill rakers. (3) There are more pseudobranch lamellae in *M. fraserbrunneri* than in *M. albomaculosus*. Our redescription also expands the range of pseudobranch lamellae in *M. fraserbrunneri* to 17–20, whereas the holotype of *M. albomaculosus* has 16 lamellae. A fourth diagnostic character proposed by Matsuura *et al.* (2018) concerned tooth counts. Our data indicate that tooth number is not reliable as a diagnostic feature because *M. fraserbrunneri* has 17–24 outer teeth in the upper jaw and 19–27 outer teeth in the lower jaw. The single specimen of *M. albomaculosus* has 25 outer teeth in both jaws. Finally, although not included in the diagnosis, Matsuura et at. (2018) also described differences in the branching pattern of the scales. With larger specimens now available for study, we show that *M. fraserbrunneri* also has bifurcate branching at the base of the central spinule (Fig. 5); thus, this character is not diagnostic between species.

Key to species of *Mephisto*

1. Red to pink with lighter, almost white, areas and with darker red blotches below spinous dorsal fin, below posterior part of soft dorsal fin, and above pectoral fin from behind eye; ventral part of head, beginning under eye, light in coloration. Spinous dorsal fin mostly dark red; soft dorsal and anal fins white proximal to body and darker at distal tips (see Fig. 1A–D). In alcohol, blotchy pattern remains and darkest red areas in life are brown (see Fig. 4A). Pelvic width 10.6–12.1% SL, pelvic width into pelvic length 2.6–3.2 times; 16–19 gill rakers; 17–20 pseudobranch lamellae… . . . . . *Mephisto fraserbrunneri*
2. Red with lighter, almost white, areas and with darker red blotches and prominent ventral, white, rounded (more-or-less circular to oblong) markings of up to as large as pupil diameter, to about half-way up body (see Fig. 1E, F). Pelvic width 7.8% SL, pelvic width into pelvic length 4.0 times; 15 gill rakers; 16 pseudobranch lamellae (measurements and counts based on holotype only) . . . . . *Mephisto albomaculosus*

***Distribution and life history of* Mephisto.** *Mephisto fraserbrunneri* and *M. albomaculosus* are only known from the Indian Ocean. The holotype of *M. fraserbrunneri* is from the Andaman Sea off Myanmar (10°39′N, 97°06′E) at 290 m; the holotype of *M. albomaculosus* also was collected off Myanmar (10°21.85′N, 96°44.83′E) at 379 m, which is only 55 km from the type locality of *M. fraserbrunneri.* Seven of the eight preserved specimens of *Mephisto fraserbrunneri* are from continental slope habitats (176–370 m) and regions characterized by steep escarpments along the continental margin (Fig. 2). The eighth specimen is from a similar depth (415 m) on Error Seamount, part of the Carlsberg Ridge, off the coast of Somalia (Fig. 2; Shcherbachev *et al.*, 1986; Gorelova *et al.*, 1993). Little is known about triacanthodid eggs and larvae (Aboussouan and Leis, 1984; Leis, pers. comm., 2019), and nothing is presently known regarding how larval *Mephisto* identify suitable habitats upon which to settle.

Tooth replacement. *Mephisto fraserbrunneri* has intraosseous tooth replacement like other species of Tetraodontiformes (Fig. 6; Bemis *et al.*, 2017). The Triacanthodidae and Triacanthidae are basal to the remaining extant lineages of Tetraodontiformes that includes the following: Ostraciidae and Aracanidae, with conical teeth similar to those of triacanthodids; Balistidae and Monocanthidae, with closely fitted, chisel-like teeth; and Triodontidae, Tetraodontidae, Diodontidae, and Molidae, with various forms of beaks and triturating surfaces (e.g., Tyler, 1980; Santini and Tyler, 2003; Arcila and Tyler, 2017). Our results for *M. fraserbrunneri* show that intraosseous replacement is the plesiomorphic condition for all Tetraodontiformes; this is interesting because in Lophiiformes, the hypothesized sister group (e.g., Arcila and Tyler, 2017), tooth replacement is extraosseous (Trapani, 2001).

Phylogenetic relationships. Tyler (1966a, 1968, 1980), based upon morphological data, proposed that *Mephisto* is most closely related to *Triacanthodes* and *Paratriacanthodes*. Recent molecular work suggests that *Triacanthodes* and *Paratriacanthodes* are not each other's closest genetic relatives based on six markers (Bemis *et al.*, 2019). No tissue samples for *M. albomaculosus* are currently available for molecular phylogenetic analysis, but tissue samples were collected from the specimens of *M. fraserbrunneri* off Kerala, and these will be included in a forthcoming analysis.

Acknowledgments

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