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Review of the moray eels (Anguilliformes: Muraenidae) of the Red Sea, with description of a new species

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Table of Contents

Abstract

Thirty-eight species of moray eels (Muraenidae) from the Red Sea are reported in an updated review. A species account is provided for each species, along with a full synonymy of all nominal species described from the Red Sea. One species is new to science, *G. pharaonis*, and two species are new for the Red Sea, *Gymnothorax phasmatodes* (Smith) and *Scuticaria tigrina* (Lesson). *Gymnothorax pharaonis* **n. sp.** is a common species that has long been misidentified as *G. undulatus* (Lacepède), although it more closely resembles *G. margaritophorus* Bleeker, to which it is closely related phylogenetically. It is characterized by the following combination of characters: total vertebrae 123–128; body slender, depth at anus 17–28 in TL; maxillary teeth biserial, dentary and vomerine teeth in a single row; color brown with irregular dendritic pale markings, not interconnected or chain-like, with oblique, conspicuous, parallel streaks posteriorly in dorsal

fin. The new record of the distinctive whitish *G. phasmatodes* is based on an underwater photograph taken at Jeddah, Saudi Arabia. The new record of *Scuticaria tigrina* is based on a specimen collected from Jeddah, Saudi Arabia, and underwater photographs taken from the northern part of the Red Sea. Based on an integrative taxonomical approach by a combination of morphological and phylogenetic analyses and re-examination of holotype specimens, *Gymnothorax cinerascens* (Rüppell) is resurrected as a valid species, and it is shown that previous records of *G. hepaticus* (Rüppell), with which it has previously been synonymized, should refer to *G. cinerascens*. The true *G. hepaticus* is redescribed based on examination of the holotype and additional specimens collected during the course of this study. The two species are distinguished by the color of the jaws, the position of the median intermaxillary teeth, and a slight difference in the preanal length. They are also clearly distinct genetically. The Red Sea record of *Gymnothorax atolli* (Pietschmann) is based on an error, possibly a misidentification of *G. griseus* (Lacepède). A key to the species of Red Sea moray eels and a phylogenetic tree of presently known lineages of Indo-Pacific moray eels are provided including recently collected Red Sea specimens.

Key words: Muraeninae, Uropterygiinae, systematic, phylogenetic analysis, Egypt, Saudi Arabia

Introduction

The Moray Eel family Muraenidae currently contains 16 genera with about 210 species. The family is divided into two subfamilies, the Snakemorays (Uropterygiinae), which have the dorsal and anal fins restricted to the end of the tail, and the remaining species (Muraeninae), with the origin of dorsal fin close to head and origin of anal fin just behind anus, the latter with the largest genus *Gymnothorax* Bloch with 135 recognized species. Members of both subfamilies occur in the Red Sea, where they were first reported by Rüppell (1830), who treated six species of morays in the genus *Muraena*. Only three of these are now considered valid, *M. flavimarginata*, *M. hepatica*, and *M. cinerascens*. Later, Rüppell (1838) described a new species *Uropterygius concolor*.

Klunzinger (1871) recognized 13 species of morays; two of them were described as new, *Muraena hemprichii* (synonym of *Enchelycore schismatorhynchus* (Bleeker 1853)) and *M. corallina* (synonym of *Gymnothorax buroensis* (Bleeker 1864)). Several other publications (e.g. Tortonese 1937, 1955; Ben-Tuvia & Steinitz 1952; Fowler & Steinitz 1956; Smith 1962) were published since Klunzinger (1871) and discussed in detail by Randall & Golani (1995). Dor (1984) compiled a checklist based on all available information to that date. Two rare species were recorded from moderately deep waters of the Gulf of Aqaba, *Gymnothorax elegans* Bliss 1883 by Ajiad & El-Absy (1986) and *Strophidon sathete* (Hamilton 1822) (as *Thyrsoidea macrura* (Bleeker)) by Ajiad (1987). The occurrence of the rare species *Gymnothorax johnsoni* (Smith 1962) was mentioned by McCosker *et al*. (1993). The first record of *Gymnothorax favagineus* Bloch & Schneider 1801 is based on an underwater photograph taken by Randall (1994) from Yemen.

Randall & Golani (1995) summarized all known data, with corrections of errors given in previous publications, and reviewed the Red Sea morays, recognizing 32 species. Eleven of these were new records and one was described as a new species, *Uropterygius genie*. Since their publication, several new species have been described, and some changes have been made. A single specimen from Nuweiba, assigned by Randall & Golani (1995) to *Gymnothorax punctatofasciatus* Bleeker, in fact represents *G. randalli* Smith & Böhlke 1997. McCosker & Smith (1997) described two new, similar species of *Uropterygius*, characterized by the unusual form of the teeth in the jaws (wedge-shaped instead of conical, and uniserial instead of biserial or multiserial on the maxilla); one is *U. golanii* from the northern Red Sea. Böhlke (2000) described *Gymnothorax pseudoherrei* from specimens collected from the Red Sea to the western Pacific and showed that Red Sea and Arabian Gulf records of *G. herrei* Beebe & Tee-Van were based on misidentification of this species. Böhlke & Smith (2002) concluded that the holotype of *Muraena hemprichii* is not conspecific with *Gymnothorax hepaticus* (Rüppell 1830), as treated by Randall & Golani (1995), but is a synonym of *Enchelycore schismatorhynchus*. The species is known in the Red Sea only from this record. Later, *Gymnothorax baranesi* Smith, Brokovich & Einbinder 2008 was described from three specimens collected from deep water (about 200 m) from the Gulf of Aqaba. Debelius (1998) reproduced a photograph of *G. thyrsoideus* (Richardson) (as *Siderea thyrsoidea*) from Hurghada, but the record is a locality error; the species is known from the Maldives east to French Polynesia. Golani & Bogorodsky (2010) cited all mentioned publications and listed 35 species in their checklist.

Böhlke & McCosker (2001: 85) reported *Gymnothorax atolli* (Pietschmann) from the Red Sea based on a single record, but this has come into question. D. Golani (pers. comm.) informs us that the specimen, HUJ 15133, is actu-

ally *Gymnothorax griseus*, not *G. atolli*, and that the latter species does not occur in the Red Sea. McCosker (pers. comm.) does not recall seeing this specimen and has no records of it himself. In light of this confusion and in the absence of confirming evidence of this western Pacific species, we are removing *G. atolli* from the list of Red Sea morays.

During surveys of a project on the biodiversity of Saudi Arabian Red Sea coastal waters, many specimens of morays provisionally identified as *G. undulatus* (Lacepède 1803) *sensu* Randall & Golani (1995) were collected. Close examination of museum material and phylogenetic analysis revealed that these are not related to *G. undulatus* but are very similar to *G. margaritophorus* Bleeker 1864, from which they can be distinguished by vertebral count, coloration, and details of morphology, and supported by low divergence in phylogenetic analysis. They are described herein as a new species, *G. pharaonis*, which appears to be nearly endemic to the Red Sea (one specimen is known from Socotra).

Many underwater photographs taken by Hagen Schmidt and colleagues from Jeddah were available for the study, among them a photograph of the distinctive moray *Gymnothorax phasmatodes* (Smith 1962), previously not recorded from the Red Sea. *Scuticaria tigrina* (Lesson 1828) is broadly distributed in the Indo-Pacific region including tropical eastern Pacific but still was unknown from the Red Sea despite careful searching of museum collections. About a dozen underwater photographs taken at several localities in Egypt recently became available to us as well as the first voucher specimen collected by the second author from a steep slope at Jeddah in 2013. It represents the first record for the Red Sea of this distinctive moray.

The aim of the present study is to update known data on Red Sea morays with description of a new species, two new records, and redescription of *G. cinerascens* and *G. hepaticus*, bringing the number of species in the region to 38. A species account for each species is included, and a key for distinguishing the Red Sea morays is provided. Furthermore, we establish genetic barcodes for Red Sea moray species by sequencing the barcoding portion of the mitochondrial cytochrome oxidase subunit I (COI) gene for specimens collected during this study, and we use available sequence data of moray lineages from the Indo-Pacific region in order to reveal affinities at the intra- and interspecific level in a phylogenetic framework.

Materials and methods

Specimens from the following institutions have been examined: Bernice P. Bishop Museum, Honolulu (BPBM); Hebrew University of Jerusalem (HUJ); King Abdulaziz University Marine Museum, Jeddah (KAUMM); Senckenberg or Senckenberg Research Institute and Natural History Museum Frankfurt (SMF); Tel-Aviv University (TAU), and Smithsonian Institution National Museum of Natural History, Washington (USNM). The KAU number given in square brackets in the list of material refers to the field number of the specimen (and the corresponding tissue sample). Other institutional abbreviations are as in Fricke & Eschmeyer (2019). Material recorded from the Red Sea includes the specimens examined by us and those listed by Randall & Golani (1995). Species descriptions are given alphabetically within each subfamily.

The length of morays is given as a total length (TL), measured from the tip of the snout to the posterior end of the caudal fin. The length can be determined only approximately for many preserved specimens due to their distorted condition after preservation; they are straightened as much as possible along a meter stick or rule. Body depth is measured at the anus excluding the dorsal and anal fins. Head length is measured from the tip of the snout to the anterior edge of the gill opening. Snout length is measured from the tip of the snout to the anterior edge of the orbit (the clear area covering the eye). Eye diameter is the greatest horizontal diameter of the orbit. The distance between the third median intermaxillary tooth and the eye is measured from the middle of the tooth base to the anterior margin of the orbit; the distance between the same tooth and the tip of the snout is likewise measured from the middle of the tooth base. Predorsal length is measured from the tip of the snout to the origin of the dorsal fin. Preanal length in Muraeninae is measured from the tip of the snout to the origin of the anal fin; for the Uropterygiinae, which have a greatly reduced anal fin, it is measured from the snout tip to the anus. The length of the upper jaw is measured from the tip of the snout to the rictus (the posterior corner of the mouth where the upper and lower jaws meet). Predorsal vertebrae are those up to and including the one directly below the dorsal-fin origin; preanal vertebrae are those up to and including the one directly above the anal-fin origin; for the Uropterygiinae, a pre-anus count is also given. Abbreviations for pores are as follows: IO = infraorbital, LL = lateral-line, POM = preoperculomandibular, SO = supraorbital.

Presented morphometric data are given as ratio to TL (preanal, predorsal, and head) or head length (snout, eye, and upper jaw). All measurements are rounded to the nearest 0.5 mm. Terminology of cephalic sensory systems is provided in Fig. 1. Some specimens were stained in 2% solution of Cyanine Blue in distilled water (Saruwatari *et al*. 1997) for positive confirmation of data on pores. The tooth pattern in the upper jaw is shown in Fig. 2. The teeth in the lower jaw (dentary) are in one row, but sometimes one or two larger teeth anteriorly are displaced slightly inside the main row. Vertebral counts include the hypural. Lateral-line pores are limited to one or two in the branchial area at the anterior end of the canal; these are usually referred to as branchial pores. Meristic and morphometric data presented here are taken from our own work and from selected references, primarily Randall & Golani (1995) and Böhlke & Randall (2000).

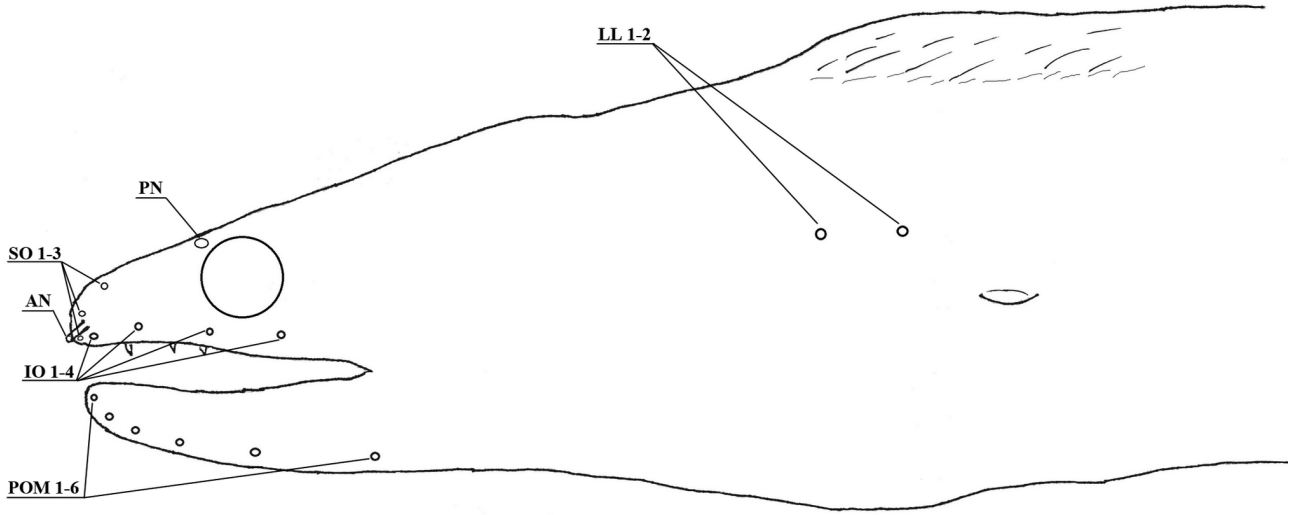


FIGURE 1. Cephalic sensory system of a moray (*Gymnothorax* spp.). **AN**—anterior nostril; **PN**—posterior nostril. Pores: **IO**—infraorbital; **LL**—branchial; **POM**—preoperculo-mandibular; **SO**—supraorbital. Drawing by D.G. Smith.

Except for the original description, synonymies include only references to the Red Sea.

Tissue samples of freshly collected specimens were stored in 96% EtOH and kept refrigerated or at –25°C until extraction of DNA with a DNeasy tissue kit (Qiagen, Hilden, Germany) or according to the protocol developed by the Canadian Centre for DNA Barcoding (Ivanova *et al*. 2006). Amplification of the barcoding portion of the mitochondrial cytochrome oxidase subunit 1 (COI) gene was carried out either with a combination of M13-tailed oligonucleotide primers (primer set COI-3 from Ivanova *et al*. (2007) or COI-Fish-F/COI-Fish-R from Kochzius *et al*. (2010)). Amplicons were Sanger sequenced from both ends with primers M13F (-21) and M13R (-27) (Messing 1983) and contigs were assembled in Geneious Pro 5.4.4 (Biomatters, Auckland, New Zealand). Sequences have been deposited to GenBank (accession numbers MN243489–MN243533, see Supplementary Table 1 for details). Sequences were aligned with all COI sequences of the family Muraenidae that could be retrieved from the following publicly accessible data collections: GenBank (https://www.ncbi.nlm.nih.gov/genbank/), Barcode of Life Data Systems, BOLDSYSTEMS (http://boldsystems.org/), and French Polynesia Fish Barcoding Database CRIOBE (http://fishbardb.criobe.pf/). Taxonomic identifications of specimens that were not collected in this study correspond to the original identifications retrieved with the sequences unless vouchers or images of vouchers or other information have been used for re-assignment of specimens to other taxa herein (re-assignments are indicated in the resulting phylogeny, see Fig. 48 and the corresponding Supplementary Table 1 with information on voucher specimens and sequences).

From this alignment, all species that do not occur in the Indo-Pacific region were excluded. The alignment was then strongly reduced to include only one or a few sequences of Indo-Pacific species that do not occur in the Red Sea. For Red Sea species, sequences were also much reduced, but a number of sequences from different localities was maintained in the alignment so that in the resulting collection of sequences the observed level of interspecific genetic variability was well represented across the distribution range of a species. The best-fitting model of nucleotide substitution (TIM1+G+I) was selected according to the Akaike Information Criterion with jModelTest 0.1.1 (Guindon & Gascuel 2003; Posada 2008) and a maximum likelihood phylogeny was inferred under this model with PhyML 3.0 (Guindon & Gascuel 2003; Guindon *et al*. 2010). Reliability of the branching pattern of the resulting

phylogeny was estimated by 100 bootstrapped replicates. Phylogenetic analyses were carried out via the software package Geneious Pro 5.4.4 and a respective plug-in for PhyML (developed by V. Lefort, J. Heled, S. Guindon and the Geneious team).

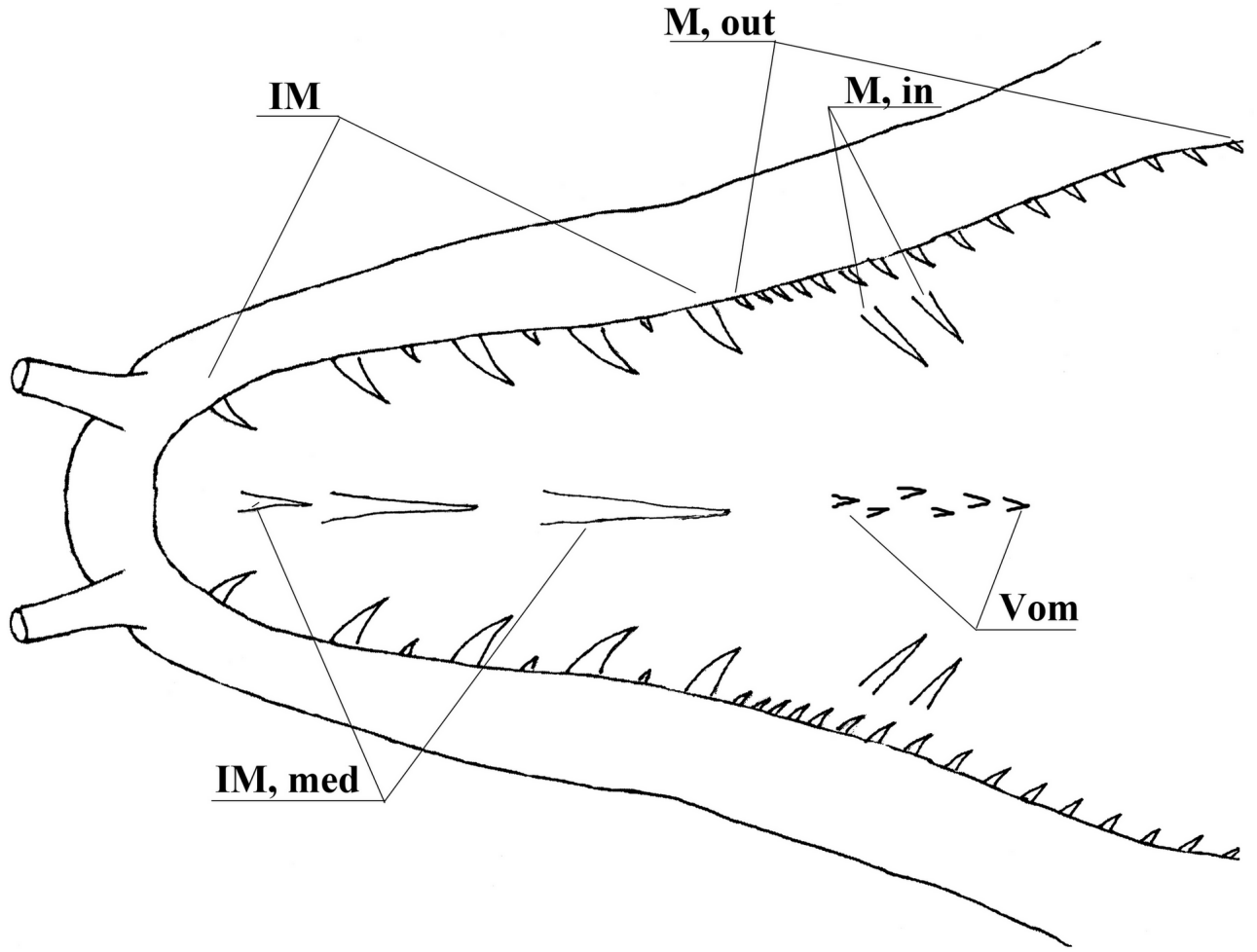


FIGURE 2. Diagram of dentition, upper jaw. **IM**-intermaxillary teeth; **M**-maxillary teeth; **Vom**-vomerine teeth. Drawing by D.G. Smith.

Results

Key to the species of the Red Sea morays.

1a. Dorsal and anal fins not confined to posterior end of body, origin of anal fin immediately behind anus . . . 2 (MURAENINAE)
1b. Dorsal and anal fins confined to posterior end of body, origin of anal fin well behind anus. . . . . 31 (UROPTERYGIINAE)
2a. Anus well behind mid-length, preanal length 1.4–1.5 in TL; dorsal-fin origin behind gill opening; color dark brown to orange-brown, with numerous narrow pale yellowish or white bars on head and body; teeth molariform . . . . . ***Gymnomuraena zebra***
2b. Anus near mid-length, preanal length 1.8–2.9 in TL; dorsal-fin origin before or above gill opening; teeth and color variable 3
3a. Teeth in jaws stout, some molariform, none long and needle-like; vomerine teeth molariform in 2–6 rows . . . . . 4 **(*Echidna*)**
3b. Teeth in jaws moderate to slender, pointed, not molariform, some long and needle-like; vomerine teeth sharp to bluntly pointed 5
4a. Head length 8.1–11 in TL; maxillary teeth uniserial; vomerine teeth in 2 rows; color in adults light gray or white, finely flecked with black, with two longitudinal rows of snowflake-like black blotches containing yellow spots . . . . . ***E. nebulosa***
4b. Head length 6.8–7.8 in TL; maxillary teeth biserial; vomerine teeth in 5–6 rows in adults; head and body with alternating broad dark brown and narrow white bars, obscure with growth . . . . . ***E. polyzona***
5a. Body slender, depth at anus 37–63 in TL; vertebrae 183–212; eye small, closer to tip of snout than to rictus; grayish brown, paler ventrally, the fins darker . . . . . .***Strophidon sathete***
5b. Body moderately elongate to moderate, depth at anus 11–37 in TL; vertebrae 106–167; eye moderate, over middle of upper jaw; color variable 6

6a. Jaws strongly arched, meeting only at their tips, long fangs exposed when mouth closed; color plain brown . . . . . 7 (***Enchelycore***)

6b. Jaws usually not arched, closing completely and teeth not exposed when mouth is closed; if jaws arched, conspicuous markings present on body. 8

7a. Preanal length 2.3–2.6 in TL; predorsal length 6.0–8.3 in TL; vomerine teeth biserial, becoming uniserial posteriorly; tip of anterior nostril not flared, posterior nostril before eye; margin of median fins yellow . . . . . ***E. bayeri***

7b. Preanal length 2.0–2.2 in TL; predorsal length 9.5–11 in TL; vomerine teeth uniserial; tip of anterior nostril flared and funnel-like, posterior nostril over eye; margin of median fins white. . . . . ***E. schismatorhynchus***

8a. Posterior nostril long and tubular, its length almost half eye diameter; head anteriorly dark brown, the posterior half and anterior trunk mottled with whitish flecks with three longitudinal rows of large whitish blotches posteriorly . . . . . ***Muraena helena***

8b. Posterior nostril not tubular, at most with a low rim much less than half eye diameter; color not as described above. . . . . 9 (***Gymnothorax***)

9a. Dorsal-fin origin above gill opening; vomerine teeth biserial, diverging anteriorly in large specimens; color highly variable, usually light tan or gray, usually finely speckled with small dark spots, often grouped to form irregular blotches . . . . ***G. pictus***

9b. Dorsal-fin origin before gill opening; vomerine teeth in 1 or 2 rows; color not as described above. 10

10a. Intermaxillary teeth in 5 longitudinal rows, a median row and 2 lateral rows on each side; body mottled with pale and dark brown or pale grayish brown with about five longitudinal rows of small black spots superimposed anteriorly and with pale flecks posteriorly . . . . . ***G. buroensis***

10b. Intermaxillary teeth in 3 longitudinal rows, a median row and 1 lateral row on each side; color not as described above 11

11a. Color uniform or mainly uniform. 12

11b. Color pattern barred, spotted, mottled or with irregular markings. 18

12a. Ground color pale yellowish to whitish gray 13

12b. Ground color brown to dark brown 14

13a. Body moderately stout, depth at anus 15–26 in TL; maxillary teeth biserial, vomerine teeth biserial anteriorly; color pale yellowish or whitish gray, densely covered with irregular darker markings; head pores not in pale spots; sensory papillae on head and anterior body black, forming conspicuous lines; fins with inconspicuous light blue edge. . . . . ***G. griseus***

13b. Body slender, depth at anus 31–37 in TL; maxillary and vomerine teeth uniserial; color uniform light tan or gray; head pores in pale spots; sensory papillae not black; fins with a conspicuous light blue edge (white in preservative) . . . . . ***G. phasmatodes***

14a. Predorsal length 11–13 in TL, body elongate, depth at anus 25–34 in TL; vertebrae 143–152; teeth finely serrate on posterior edge; color light brown to tan, often white ventrally, head pores in white spots, fins with narrow pale edge . . . . . ***G. angusticauda***

14b. Predorsal length 6.6–12 in TL, body not elongate, depth at anus 15–25 in TL; vertebrae 111–138; teeth smooth (except *G. pindae*); color mainly uniform, head pores not in white spots 15

15a. Maxillary teeth biserial, rows equal in length, those in outer row obtusely pointed; dentary teeth blade-like, in one row, except for several larger conical inner teeth anteriorly on each side; color brown, posterior one-fourth of body and fins yellow in smaller specimens, yellow color gradually disappears with growth . . . . . ***G. pseudoherrei***

15b. Maxillary teeth uniserial or biserial, when biserial inner row shorter than outer, teeth conical or triangular in form; dentary teeth conical, triangular or retrorse; color not as described above 16

16a. Teeth triangular, the large anterior ones in both jaws serrate; vertebrae 118–123; ground color uniform dark brown, with fine reticular pattern on body; tail and fins blackish posteriorly. . . . . ***G. pindae***

16b. Teeth slender, conical, smooth; vertebrae 128–138; ground color uniform brown 17

17a. Preanal length usually 2.0 in TL; preanal vertebrae 58–61; vomerine teeth uniserial or slightly irregular; third median intermaxillary tooth distant from eye; third IO pore under or slightly ahead of anterior margin of eye; color uniform brown except lower jaw and ventral part of branchial area pale (pale yellow in life); head pores unmarked . . . . . ***G. hepaticus***

17b. Preanal length usually 2.1 in TL; preanal vertebrae 55–57; vomerine teeth biserial in adults; third median intermaxillary tooth close to eye; third IO pore slightly behind anterior margin of eye; color uniform brown, lower jaw and ventral part of branchial area not pale; head pores with dark rim . . . . . ***G. cinerascens***

18a. Body with dark bars or bar-like markings 19

18b. Body with spots or irregular markings. 21

19a. Teeth smooth; light grayish brown with about 15–20 dark brown bars about as wide as pale interspaces, without superimposed markings; top of head yellow in life. . . . . ***G. rueppelliae***

19b. Teeth serrate; bars with superimposed small spots or irregular markings 20

20a. Preanal length 2.2–2.4 in TL; trunk with two rows of moderately large irregular brown spots superimposed with small spots on dorsal half and another row midventrally forming short bars posteriorly; markings on branchial region a series of simple spots . . . . . ***G. randalli***

20b. Preanal length 2.0–2.2 in TL; body with 16-20 dark brown bars on ventral two-thirds of body, obscured dorsally by irregular, small spots, forming reticular pattern, dorsal and anal fins with short black bars; markings on branchial region forming horizontal lines . . . . . ***G. reticularis***

21a. Body with irregular markings. 22

21b. Body with discrete pale or dark spots. 25

22a. Body yellow, densely mottled with dark brown, snout dark brown; a black blotch over gill opening; fins with a yellow or pale green margin posteriorly. . . . . ***G. flavimarginatus***

22b. Color with variable irregular pattern, margin of fins not yellow; no black blotch on gill opening 23

23a. Body grayish with irregular dark markings, the lighter background often forming reticulations; head greenish-yellow in life .

. . . . . ***G. undulatus***

23b. Body brown with pale dendritic markings, never forming a reticulation; head not yellow 24

24a. Preanal length 2.2–2.4 in TL; vertebrae 123–128; pale markings irregular, those on tail forming oblique streaks dorsally . . . . . ***G. pharaonis* n. sp.**

24b. Preanal length 2.0–2.1 in TL; vertebrae 137–142; pale markings as rosettes anteriorly, more discrete spots on tail, not drawn out into oblique bars dorsally . . . . . ***G. baranesi***

25a. Body with dark spots on light background 26

25b. Body with light spots on dark background 27

26a. Body with small to moderate-size spots, not overlapping, sometimes forming larger blotches; gill opening in a black blotch . . . . . ***G. javanicus***

26b. Head and body with moderate to large polygonal black spots separated by narrow white interspaces; gill opening not in a black blotch . . . . . ***G. favagineus***

27a. Predorsal length 11–14 in TL; head and trunk with close-set pale spots as large as eye, becoming vertically elongate and bar-like posteriorly; gill opening in a black blotch . . . . . ***G. elegans***

27b. Predorsal length 6.6–11.0 in TL; spots somewhat uniformly round, not bar-like posteriorly; no black blotch on gill opening 28

28a. Body covered with white or bluish white spots, increasing in size posteriorly and becoming black-edged; gill opening and inside of mouth yellow in life . . . . . ***G. nudivomer***

28b. Body of adults with small round or irregular spots; gill opening and inside of mouth not yellow 29

29a. Preanal length 1.8–2.0 in TL; teeth serrate; vomerine teeth biserial or staggered; space between spots greater than spot diameter . . . . . ***G. moluccensis***

29b. Preanal length 2.1–2.4 in TL; teeth smooth; vomerine teeth uniserial; space between spots usually subequal to spot diameter 30

30a. Vertebrae 138–144; spots smaller, those on tail and dorsal fin posteriorly close-set, round . . . . . ***G. punctatus***

30b. Vertebrae 131–140; spots larger, those on tail and dorsal fin posteriorly not close-set, those in dorsal fin elongate ***G. johnsoni***

31a. Anus well behind midlength, preanal length 1.5–1.6 in TL; head and body with large brown spots . . . . . ***Scuticaria tigrina***

31b. Anus near or before midlength, preanal length 2.0–2.4 in TL; color uniform or with irregular markings (except spotted *U. polyspilus*) . . . . . 32 **(*Uropterygius*)**

32a. Ground color tan to white, with rounded dark brown spots . . . . . ***U. polyspilus***

32b. Head and body without spots 33

33a. Teeth in upper jaw uniserial, wedge-shaped; vertebrae 145–148; color uniform brown . . . . . ***U. golanii***

33b. Teeth in upper jaw conical, in more than one row; vertebrae 110–140; color variable 34

34a. Teeth in upper jaw in 4 rows, at least anteriorly; color uniform brown . . . . . ***U. genie***

34b. Teeth in upper jaw in 2–3 rows; color variable 35

35a. Teeth in upper jaw in 3 rows; 0–1 branchial pore; vertebrae 135–140; color tan with large, dendritic, vertically aligned dark brown markings . . . . . ***U. nagoensis***

35b. Teeth in upper jaw in 2 rows; 1 branchial pore; vertebrae 103–124; color variable 36

36a. Pre-anal fin vertebrae 109–118; color usually uniform brown, sometimes with irregular, indistinct pale markings; head pores in white spots . . . . . ***U. concolor***

36b. Pre-anal fin vertebrae 92–111; body with reticular or dendritic pattern; head pores not white 37

37a. Head large, the length 6.3–8.3 in TL; color dark with complexly dendritic lighter blotches, not forming reticulations; gill opening below mid-side . . . . . ***U. macrocephalus***

37b. Head moderate, the length 8.1–9.9 in TL; color light brown or gray with irregular dark brown lines on upper head and body, partly interconnected to form a fine reticulation; gill opening at mid-side . . . . . ***U. micropterus***

SUBFAMILY MURAENINAE

Diagnosis. Dorsal and anal fins not confined to posterior end of body; anal fin begins immediately behind anus. Most species with 2 branchial pores, some with 1 and a few with more than 2.

Echidna nebulosa (Ahl 1789)—Snowflake Moray

(Figure 3)

Muraena nebulosa Ahl 1789: 7, pl. 1 (right fig.) (East Indies). No types known to exist, although Fricke (1999: 42) designated the illustrated specimen as the lectotype.—Klunzinger 1871: 21; Borsieri 1904: 218.

Muraena ophis Forsskål, 1775: xiv. *Nomen nudum*.

Muraena ophis Rüppell 1830: 116, pl. 29 (fig. 2) (Red Sea). Holotype (unique): SMF 19. Objectively invalid, preoccupied by *Muraena ophis* Linnaeus 1758.

Echidna nebulosa: Marshall 1952: 223; Tortonese 1968: 9; Dor 1984: 26; Goren & Dor 1994: 6; Randall & Golani 1995: 851; Khalaf & Disi 1997: 39; Khalaf 2004: 35; Golani & Bogorodsky 2010: 9; Golani & Fricke 2018: 19.

Red Sea material. ***Red Sea***: SMF 19 (1, 547, holotype of *Muraena ophis*). ***Israel***: HUJ 5239 (1, 547), Eilat; HUJ 5241 (1, 536), Eilat; HUJ 15020 (2, 410–476), Gulf of Aqaba, El Arkana. ***Egypt***: USNM 166911 (2, 408–518), Ghardaqa (Hurghada); USNM 312130 (1, 601), channel at Ras Muhammad.

Comparative material. ***Mauritius***: USNM 342096 (1, 352); USNM 345794 (1, 220). ***Taiwan***: USNM 312122 (1, 156). ***Hawaii***: USNM 126552 (3, 91–360). ***Panama***: USNM 312135 (1, 267).

Description. In TL: preanal length 1.9–2.1, predorsal length 8.9–12, head length 8.1–11, body depth at anus 18–26. In head length: snout length 5.6–7.0, eye diameter 9.3–13, upper-jaw length 2.6–3.7. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 4–6, preanal 54–58, total 119–125.

Body moderately stout, generally deeper with growth; anus near midlength; dorsal fin begins slightly anterior to gill opening; anal fin begins immediately behind anus. Head moderate in length, snout relatively short and deep. Eye moderately small, closer to rictus than to snout tip.

Teeth stout, triangular to molariform. Intermaxillary with ca 5–6 peripheral teeth on each side, triangular to bluntly pointed, slightly retrorse, with finely serrate posterior margins in larger individuals; 0–3 median teeth bluntly pointed. Maxillary teeth uniserial, ca 6–10 on each side, bluntly pointed. Dentary teeth somewhat variable, uniserial or biserial with an outer row of small nodular teeth and an anterior inner row of 2–3 larger, stout, bluntly conical teeth; posterior to this point a single series of teeth, which in some cases appear to be a continuation of the inner series, in other cases a continuation of the outer series; in largest specimen examined, teeth become multiserial and molariform posteriorly. Vomerine teeth biserial, large and molariform, ca 6–10 on each side.

Color: light gray, white or pale brown (darker with growth), finely flecked with black, with two longitudinal rows of large, complex snowflake-like black blotches (those of ventral row are vertically elongate), containing one or more yellow spots and irregular dark edges; anterior tip of snout and lower jaw varying from white to gray; iris and anterior nostrils yellow.

Distribution and habitat. Widely distributed across the entire Indo-Pacific, from the east coast of Africa and the Red Sea to Central America. Common inhabitant of coral reefs, typically found on reef flats, sometimes in seagrass areas, usually from depth less than 3 m, but reported from the depth of 48 m; feeding largely on crustaceans, usually crabs.

Remarks. Fricke (1999) designated the specimen in the original illustration reproduced in Ahl (1789) as the lectotype and noted that Ahl published his dissertation of 1798 in 1801. Fricke (1999: 41) dated the original description of *Muraena nebulosa* to 1801, but that is apparently incorrect as there is a 1789 publication that differs from the 1801 reference. Smith (2012) gave the type locality as East Indies and mentioned Fricke's designation of the lectotype as the illustrated specimen, which no longer exists. *Muraena ophis* Forsskål, 1775 was published in the synonymy of *E. nebulosa*, but without any comment or description; it is a *nomen nudum*, hence an unavailable name.

This species shows little morphological variation over its vast range. The three specimens from the Red Sea have slightly fewer vertebrae (119–122, N = 5) than those from elsewhere (122–125, N = 7), but the sample size is too small to draw any firm conclusions.

The three specimens from the Red Sea (Israel), the Western Pacific (Philippines) and the South Pacific (Society Islands) formed one joint monophyletic lineage in the phylogenetic analysis without apparent genetic divergence of the Red Sea specimen from e.g. the specimen from the Philippines (TZAIC707-06, see Fig. 48). A study on the genetic differentiation within *E. nebulosa* across the Indo-Pacific showed no marked intra-specific genetic variation in mitochondrial haplotypes (Reece *et al*. 2011). One COI sequence of a specimen that was originally identified as *Echidna nebulosa* in Reece *et al*. (2010) (HQ122453) was part of a clade composed of specimens of *Gymnothorax pictus* (Ahl). The reason remains unclear, and examination of the voucher specimen and/or re-sequencing of the COI gene would be required to solve the issue; however, we preliminarily re-assigned the sequence/specimen to *G. pictus* and suggest either a sequence mix-up or a misidentification as the cause for the unexpected placement of the sequence. *Echidna nebulosa* formed a well-supported clade with three other species, i.e. *G. pictus*, *G. pseudothyrsoideus* (Bleeker) and *Echidna xanthospilos* (Bleeker). Other species of *Echidna* also formed part of well-supported clades in other parts of the phylogeny leading to a polyphyletic genus *Echidna*.

FIGURE 3. *Echidna nebulosa*. **A**: Dahab, Egypt; **B**: Dahab, Egypt. Photos by S.V. Bogorodsky.

Echidna polyzona (Richardson 1845)—Barred Moray
(Figure 4)

Muraena polyzona Richardson 1845: 112, pl. 55 (figs. 11–14) (No locality). Lectotype, BMNH 1977.4.22.3, designated by Böhlke & Randall 2000: 220.—Klunzinger 1871: 617.
Echidna polyzona: Marshall 1952: 223; Goren & Dor 1994: 7; Randall & Golani 1995: 851; Khalaf 2004: 35; Golani & Bogorodsky 2010: 9; Golani & Fricke 2018: 20.

Red Sea material. ***Israel***: BPBM 35748 (1, 173), Eilat; HUJ 5243 (1, 435), Eilat. ***Egypt***: HUJ 15093 (3, 110–128), Nabq; USNM 312209 (2, 66.5–143), Marsa Muqabila. ***Eritrea***: USNM 312158 (1, 364).

Comparative material. ***Mauritius***: USNM 342100 (3, 94–ca 290). ***Solomon Is***.: USNM 385375 (3, 57–185).

Vanuatu: USNM 362155. ***French Polynesia***, Tahiti: USNM 66087 (1, 242); USNM 312154 (1, 182). ***Hawaii***: USNM 89537 (1, 193); USNM 109332 (2, 75–272).

Description. In TL: preanal length 2.1–2.2, predorsal length 8.1–9.1, head 6.8–7.8, body depth at anus 13–22. In head length: snout length 5.6–7.0, eye diameter 6.6–10, upper-jaw length 2.7–3.4. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 4–6, preanal 50–52, total 119–125.

Body moderately stout; anus near midlength; dorsal fin begins slightly anterior to gill opening; anal fin begins immediately behind anus. Head moderate in length, snout relatively short and deep. Eye moderately small, closer to rictus than to snout tip. Rim of posterior nostril slightly raised, edge fimbriated.

Teeth stout, bluntly pointed to molariform, somewhat variable in number and arrangement, generally more numerous in larger specimens. Intermaxillary with a peripheral series of ca. 4–7 on each side; sometimes an intermediate series of 2–3 on each side; 1–3 median teeth. Maxillary teeth biserial; 3–7 larger teeth in inner row, 4–12 smaller teeth in outer row. Dentary teeth biserial, those in inner row larger, ca. 11–13 in adults, fewer in juveniles; ca. 12–20 in outer row. Vomerine teeth large, molariform, in an elliptical, multiserial patch, narrowest at anterior and posterior ends, biserial in smaller specimens, up to 5–6 teeth across in larger ones.

Color: variable, changing considerably with growth. Typical pattern ca. 25 contrasting alternating broad dark brown and narrow white bars on head and body and extending onto dorsal fin; bars best developed in smaller adults, white bars becoming progressively more obscure with growth; body becoming mottled with brown overall and the bars less distinct, visible only on tail with further growth. Corner of mouth dark; anterior nostrils brownish yellow.

Maximum size about 600 mm.

Distribution and habitat. Found across the Indo-West Pacific from the Indian Ocean to Hawaiian Islands and French Polynesia. Occurs in shallow water, common on coral reefs, sometimes found on reef flats; observed from depths of 3–15 m.

Remarks. This species shows little morphological variation over its range. Three Red Sea specimens have slightly fewer vertebrae (117–122) than 14 specimens from elsewhere (119–125). Similar slight differences occur in predorsal vertebrae (4–5 *vs*. 5–7) and preanal vertebrae (49 *vs*. 50–52).

The species superficially resembles *Gymnothorax rueppelliae*, but the dentition is very different. In addition, the snout is longer in *G. rueppelliae*, and the bars on the head do not extend onto the lower jaw.

FIGURE 4. *Echidna polyzona*, Dahab, Egypt. Photo by S.V. Bogorodsky.

The variation in color pattern and dentition over the life cycle of this species has resulted in 11 synonyms, seven of them from the Hawaiian Islands alone.

In the COI-based phylogeny, *E. polyzona* was very close to *E. leucotaenia* Schultz with no strong genetic divergence between them, which is in agreement with the multigene analysis in Reece *et al*. (2010), from which COI sequences of both species were used herein as no specimens of this species were collected during the present study. As in the aforementioned multigene analysis, no close allies of these two species could be identified from the phylogenetic tree (see Fig. 48).

Enchelycore bayeri (Schultz 1953)—Bayer's Moray

(Figure 5)

Gymnothorax bayeri Schultz in Schultz *et al*. 1953: 124, figs. 23f, 26 (Lagoon coral head at Kieschiechi I., Rongelap Atoll, Marshall Is., western Pacific, 20 ft [6.1 m]), holotype USNM 141608.
Enchelycore bayeri: Randall & Golani 1995: 852; Golani & Bogorodsky 2010: 9; Golani & Fricke 2018: 20.

Red Sea material. ***Egypt***: HUJ 5845 (1, 525), Ras Muhammad; HUJ 15051 (1, 550), Gulf of Aqaba; USNM 312200 (5, 163–700), Strait of Jubal. ***Sudan***: USNM 397541(1, 172), Shaab Suedi. ***Saudi Arabia***: BPBM 30642 (2, 238–344), Jeddah; KAUMM 391 [KAU12-1058] (1, 305), Al Lith; SMF 35805 [KAU13-679] (1, 197), Jeddah, Obhur.

Comparative material. Taiwan: USNM 312203 (1, 288). ***Philippines***: USNM 293364 (1, 250); USNM 293365 (1, 493); USNM 293370 (1, 447); USNM 293423 (1, 260). ***Indonesia***: USNM 312201 (1, 515). ***Fiji***: USNM 242079 (1, 231). ***Marshall Is.***: USNM 141608 (1, 393, holotype). ***French Polynesia***, Moorea: MNHN 2008-0451 (1, 157); MNHN 2008-0452 (1, 99); USNM 392231 (1, 95).

Description. In TL: preanal length 2.3–2.6, predorsal length 6.0–8.3, head length 7.0–7.7, body depth at anus 20–34. In head length: snout length 4.5–5.1, eye diameter 10–20, upper-jaw length 2.3–2.7. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 9–11, preanal 50–53, total 146–152.

Head and body moderately elongate; anus slightly before midlength; dorsal fin low, its origin above gill opening. Jaws very slender, strongly arched, mouth not closing completely, leaving a prominent elliptical gap between jaw tips and rictus. Eye well developed, at about midpoint of upper jaw. Anterior nostril tubular, small, not reaching edge of lip when depressed; posterior nostril elliptical with raised rim, located anterior to eye except in very small specimens.

Teeth long, smooth, and sharply pointed. Intermaxillary with a peripheral series of about four large canines on each side separated by much smaller teeth, the latter forming a row slightly outside the large teeth; 3 median teeth. Maxillary teeth biserial, with about four large inner teeth and ca. 25–30 smaller outer teeth, some of these larger than others. Dentary teeth biserial anteriorly, uniserial posteriorly; inner teeth much larger, converging on outer row at about midpoint of jaw; outer teeth smaller, more numerous, somewhat variable in size. Vomerine teeth biserial, short and bluntly pointed, becoming uniserial posteriorly.

Color: uniform brown, fins with greenish yellow or yellow edge. Throat in an indistinct dark violet blotch. Head pores narrowly dark edged.

Maximum size about 600–700 mm.

Distribution and habitat. Across the Indo-West Pacific from the Indian Ocean and the Red Sea to French Polynesia; absent from Hawaiian Islands. Primarily on coral reefs in relatively shallow water, known from depth of 3–38 m. Very secretive and may be seen occasionally on reefs with rich coral growth.

Remarks. This is a very distinctive eel, with its narrow, highly arched jaws and the posterior nostril located distinctly before the eye. It shows little variation over its range. Six Red Sea specimens have 146–151 vertebrae, the holotype from the Marshall Islands has 148, and three specimens from Moorea in the Society Islands have 149–152. Randall & Golani (1995) reported the first Red Sea record from several localities. According to the COI-based phylogeny there is no marked evolutionary divergence among specimens of this species from the Red Sea to the South Pacific. Interestingly, there was no obvious close association with other species of the genus included in the phylogeny. *Enchelycore schismatorhynchus* as well as *E. ramosa* (Griffin) and *E. pardalis* (Temminck & Schlegel) were also associated with different clades of moray species (mostly from the genus *Gymnothorax*).

FIGURE 5. *Enchelycore bayeri*. **A**: alive, ~ 600 mm TL, Lahami Bay, southern Egypt; **B**: SMF 35805 [KAU13-679], 197 mm TL, fresh specimen, Obhur, Jeddah, Saudi Arabia. Photos by S.V. Bogorodsky.

***Enchelycore schismatorhynchus* (Bleeker 1853)—Funnel-nostril Moray**
(Figure 6)

Muraena schismatorhynchus Bleeker 1853: 301 (Benkulen [Bengkulu], Sumatra, Indonesia). Holotype (unique), BMNH 1867.11.28.248.
Muraena hemprichii Klunzinger 1871: 613 (Al-Quseir [Kosseir], Egypt, Red Sea). Holotype (unique), ZMB 4048.
Enchelycore schismatorhynchus: Golani & Bogorodsky 2010: 9; Golani & Fricke 2018: 20.

Red Sea material. ***Egypt***: ZMB 4048 (1, 585, holotype of *Muraena hemprichii*), El Quseir.

Comparative material. ***Cargados Carajos Shoals***: USNM 312172 (1, 633); USNM 312174 (2, 380–514). ***Mauritius***: USNM 342103 (1, 314). ***Taiwan*****:** BPBM 23335 (1, 502). ***Philippines*****:** USNM 343388 (2, 112–199); USNM 379229 (1, 207). ***Indonesia***: BMNH 1867.11.28.248 (1, 764, holotype); BMNH 1867.11.28.348 (1, 466, holotype of *Muraena congeroides* Bleeker); RMNH 3776 (1, 426, holotype of *Eurymycterus crudelis* Kaup); USNM 312173 (2, 203–545). ***Wallis I.***: USNM 374952 (1, 340). ***Samoa***: USNM 51717 (1, 586, holotype of *Rhinamuraena* [sic] *eritima* Jordan & Seale. ***French Polynesia***, Austral Is.: USNM 423355 (1, 178); USNM 423413 [AUST-100] (1, 178).

Description. In TL: preanal length 2.0–2.2, predorsal length 9.5–11, head length 6.9–8.3, body depth at anus 17–29. In head length: snout length 4.9–5.7, eye diameter 9.5–12, upper-jaw length 2.2–2.6. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 4–6, preanal 61–65, total 137–146.

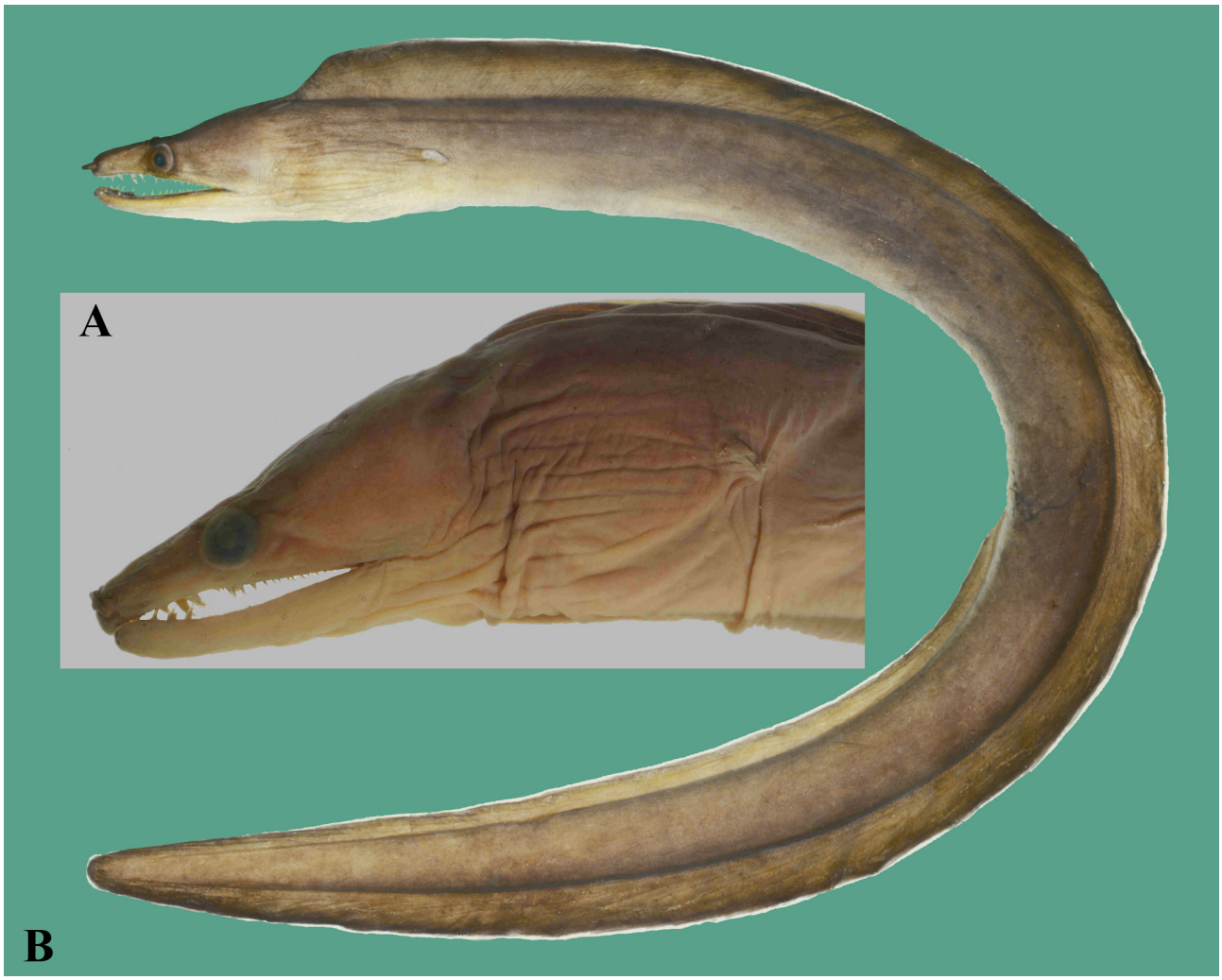


FIGURE 6. *Enchelycore schismatorhynchus*. **A**: USNM 312174, 514 mm TL, preserved, Cargados Carajos Shoals; **B**: BPBM 23335, 502 mm TL, fresh specimen, Taiwan. Photos by D.G. Smith (A), J.E. Randall (B).

Body moderately elongate; anus at or slightly before midlength; dorsal fin moderately tall, begins anterior to gill opening; anal fin begins immediately behind anus. Jaws slender, arched, not completely closing, leaving an el-

liptical gap between jaw tips and rictus, this gap generally more strongly developed in larger specimens. Eye well developed, at about midpoint of upper jaw. Gill opening small, broadly tubular, midlateral in position. Anterior nostril relatively long, reaching slightly beyond edge of upper lip when depressed, distal end distinctly flared and slightly funnel-shaped; posterior nostril rounded, located above anterior margin of eye.

Teeth slender, conical, sharply pointed. Intermaxillary with a peripheral series of about 4–5 large teeth on each side, with several much smaller teeth in between; 3 median teeth, increasing in size from back to front. Maxilla with 3–6 enlarged inner teeth anteriorly, and about 16–26 much smaller outer teeth. Dentary with 4–5 large inner teeth anteriorly, and about 27–45 smaller outer teeth. Vomerine teeth uniserial, about 5–11, moderate in size and somewhat stouter than other teeth.

Color: uniform medium brown, paler ventrally on head and trunk; fins with a conspicuous white edge; tip of anterior nostril dark brown.

Maximum size at least 764 mm.

Distribution and habitat. Widely distributed from the Indian Ocean, where it is known from the Red Sea, Mauritius, and Chagos Archipelago, to French Polynesia; absent from Hawaiian Islands. In shallow water, commonly found on coral reefs at depths of 3–35 m; very secretive.

Remarks. The only record of this species from the Red Sea is the holotype of *Muraena hemprichii*. Randall & Golani (1995) listed it as a synonym of *G. hepaticus* in their introduction but did not include it in the species account of the latter. Böhlke & Smith (2002: 114) determined that it is conspecific with *Enchelycore schismatorhynchus*, thus becoming its junior synonym. It has 137 vertebrae; specimens examined from elsewhere have 137–146. There is no clear pattern of geographic variation. The species was also not collected during this study. *Enchelycore schismatorhynchus* (the barcode sequence comes from a voucher specimen collected from the Austral Islands that was originally identified by the first author of this study) formed part of a well-supported clade with species assigned to *Gymnothorax* including the Red Sea species *G. hepaticus*.

Gymnomuraena zebra (Shaw 1797)—Zebra Moray

(Figure 7)

Gymnothorax zebra Shaw in Shaw & Nodder 1797: 4 unnum. pp., pl. 322 (Sumatra, Indonesia [erroneously given originally as American seas]). Holotype (unique), BMNH 1977.4.22.4.
Muraena zebra: Klunzinger, 1871: 620.
Echidna zebra: Fowler 1945: 119; Clark *et al*. 1968: 21; Dor 1984: 27; Goren & Dor 1994: 7; Khalaf & Disi 1997: 39.
Gymnomuraena zebra: Khalaf 2004: 37; Randall & Golani 1995: 853; Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 20.

Red Sea material. ***Egypt***: HUJ 15143 (1, 495), Ras Muhammad. ***Eritrea***: USNM 312170 (2, 545–547), Isola Delemme.

Comparative material. ***Chagos Archipelago***: USNM 306603 (1, 362); USNM 312169 (1, 370). ***Indonesia***, Sumatra: BMNH 1977.4.22.4 (1, 732, holotype). ***Hawaii***: USNM 108807 (1, 499); USNM 402389 (1, 663). ***Panama***: USNM 318328 (1, 386); USNM 361595 (1, 165).

Description. In TL: preanal length 1.4–1.5, head length 8.3–11, body depth at anus 16–22. In head length: snout length 5.4–7.4, eye diameter 10–12, upper-jaw length 2.5–3.3. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 13–17, preanal 82–86, total 127–134.

Body moderately stout; anus well behind mid-length; tail blunt; dorsal fin begins slightly behind gill opening; anal fin begins immediately behind anus, fins largely concealed externally by thick skin. Head relatively deep, snout short. Eye well developed, over middle of upper jaw. Gill opening small, low on side. Anterior nostril tubular, relatively short; posterior nostril in a short tube, above anterior part of eye.

Teeth large, blunt, molariform. Intermaxillary teeth in an oval patch, about 4–5 teeth across, outer teeth smaller than inner. Maxillary teeth small, in a short row, one to two series. Dentary teeth biserial, with a few small teeth anteriorly forming a third row, anterior teeth in main series somewhat larger anteriorly. Vomerine teeth large and prominent, in an elliptical patch, narrowing to a single tooth posteriorly, two teeth anteriorly, confluent with intermaxillary teeth.

Color: dark brown to orange-brown, with numerous narrow pale yellowish or white bars on head and body; number of bars varying from about 25 in small individuals to about 100 in large adults, some bars interrupted in adults; anterior nostril pale.

Commonly grows to about 1 m in length, occasionally to 1.5 m.

Distribution and habitat. Across the entire Indo-Pacific, from the Indian Ocean including Red Sea to Hawaiian Islands, Marquesas Islands, and Central America. Occurs in shallow water and on coral reefs at depths of 1–50 m; feeds mainly on crabs, also on molluscs and sea urchins; rarely seen in the open.

Remarks. This species has sometimes been placed in *Echidna* because of its blunt, molariform teeth, but it is distinguished by the posterior position of the anus, well behind mid-length. There is a slight difference in the number of vertebrae between the Red Sea (127–130, N = 2) and elsewhere (129–134, N = 6). Genetic samples were not available from the Red Sea, and, as in the multigene phylogeny by Reece *et al.* (2010), the species does not show a close affiliation with other species of Muraeninae in the COI-based phylogeny (Fig. 48). A study on the genetic differentiation within *G. zebra* across the Indo-Pacific showed no marked intra-specific genetic variation in mitochondrial haplotypes (Reece *et al*. 2011).

FIGURE 7. *Gymnomuraena zebra*, Dahab, Egypt. Photo by A. Ryanskiy.

Gymnothorax angusticauda (Weber & de Beaufort 1916)—Shorttail Moray

(Figure 8)

Muraena (*Priodonophis*) *angusticauda* Weber & de Beaufort 1916: 389, fig. 388 (Near Supiori, Schouten Is., Papua New Guinea). Holotype (unique), ZMA 102162.

Gymnothorax angusticauda: Randall & Golani 1995: 854, Pl. 1a; Golani & Bogorodsky 2010: 10; Bogorodsky *et al*. 2014: 411; Golani & Fricke 2018: 20.

Red Sea material. ***Egypt***: BPBM 19844 (2, 458–503), Nuweiba. ***Saudi Arabia***: SMF 34962 [KAU12-731] (1, 383), Jizan.

Comparative material. ***Taiwan***: USNM 438183 (1, 486); USNM 438650 (1, 547); USNM 439078 (1, 513). ***Philippines***: USNM 408880 (1, 560). ***Papua New Guinea***: ZMA 102.062 (1, 474, holotype).

Description. In TL: preanal length 1.9–2.2, predorsal length 11–13, head length 8.0–9.8, body depth at anus 25–34. In head length: snout length 5.3–7.1, eye diameter 8.8–11, upper-jaw length 2.8–3.5. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 4, preanal 58–70, total 143–152.

Body moderately elongate; anus near mid-length; dorsal fin begins slightly before gill opening; tail relatively slender. Head and jaws moderate, jaws closing completely. Eye well developed, at about midpoint of upper jaw. Gill opening nearly horizontal, midlateral. Anterior nostril tubular, reaches edge of lip when depressed; posterior nostril oval, with a slightly raised rim, over anterior part of eye.

Teeth conical to narrowly triangular, finely serrate on posterior edge. Upper jaw with about 5 or 6 peripheral intermaxillary teeth, narrowly triangular, retrorse; 0–3 median teeth, conical. Maxillary teeth uniserial, about 7–14, similar in shape to intermaxillary teeth. Dentary teeth uniserial, similar in shape to those in upper jaw, with about 7–19 teeth on each side. Vomer with about 3–6 teeth in a single row.

Color: medium to light brown or tan, snout and lower jaw darker, abdomen sometimes white; head pores in conspicuous white spots, nostrils white; fins with narrow pale edge; iris yellow.

Of the ten known specimens, the largest is 560 mm.

Distribution and habitat. Known from the Red Sea, Taiwan, the Philippines, Indonesia (Bali and Sulawesi), and Papua New Guinea. The two larger specimens from the Red Sea were collected in less than 0.5 m from the fringing reef at Nuweiba. The smaller specimen was captured in a trawl at about 30 m from the southern Saudi Arabia, off Jizan, from a sandy area close to the island. Information on depth and habitat is not available for the Philippine and Indonesian specimens. Fricke (2015) reported an additional specimen collected from a depth of 15 m from Madang, Papua New Guinea.

Remarks. The smallest trawled Red Sea specimen differs from all the other specimens in having the anus slightly behind midlength rather than slightly before. It also has more total vertebrae (152 *vs*. 143–148) and distinctly more preanal vertebrae (70 *vs*. 58–60). The other two Red Sea specimens do not differ in these characters from the western Pacific specimens. With the limited material available and without genetic information from other parts of the distribution area, we cannot assess the significance of these distinctions. In the COI-based phylogeny, the species is most closely related to *Gymnothorax albimarginatus* (Temminck & Schlegel) and an unidentified *Gymnothorax* species (*Gymnothorax* sp. 4, BOLD voucher of SBF244-11 collected from Madagascar), with which it forms a well-supported clade.

FIGURE 8. *Gymnothorax angusticauda*, SMF 34962 [KAU12-731], 383 mm TL, fresh specimen, Jizan, Saudi Arabia. Photo by S.V. Bogorodsky.

***Gymnothorax baranesi* Smith, Brokovich & Einbinder 2008—Barane's Moray**
(Figure 9)

Gymnothorax baranesi Smith, Brokovich & Einbinder 2008: 63, figs. 1–4 (Off Eilat, Israel). Holotype, HUJ 18976.—Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 20.
Gymnothorax sp.: Khalaf & Disi 1997: 40.

Red Sea material. ***Israel***: HUJ 18976 (1, 857, holotype), Eilat; HUJ 18975 (1, 762, paratype), Eilat; USNM 388603 (1, 828, paratype), Eilat.

Description. In TL: preanal length 2.0–2.1, predorsal length 7.9–8.1, head length 6.6–7.5, body depth at anus 14–19. In head length: snout length 4.8–5.7, eye diameter 11–13, upper -jaw length 2.5–2.6. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 6–7, preanal 52–55, total 137–142.

Body moderate, anus near midlength; dorsal fin begins before gill opening. Head and jaws moderate, jaws not closing completely. Eye moderate in size, over middle of upper jaw. Gill opening midlateral. Anterior nostril tubular, short, not reaching edge of lip when depressed; posterior nostril elliptical, without raised rim, over anterior part of eye.

Teeth sharp, conical to triangular, smooth. Intermaxillary with a peripheral series of 5–7 teeth on each side and 1–3 long, slender, median teeth. Maxillary teeth biserial or uniserial, the inner row with two long depressible teeth and the outer row with 14–17 smaller, triangular, retrorse teeth, continuous with peripheral intermaxillary teeth. Dentary teeth uniserial, larger anteriorly, conical to triangular. Vomer with 3–12 small teeth, in a single staggered row.

FIGURE 9. *Gymnothorax baranesi*, HUJ 18975, 762 mm TL, fresh specimen, Eilat, Israel. Photo by E. Brokovich.

Color: brown, covered with moderate-size pale spots in approximately three rows, largest around midbody, the spots rosette-like anteriorly, irregularly rounded near end of tail; spots much smaller on head, inconspicuous or absent on snout and lower jaw; spots extending onto fins; tubular anterior nostril dark brown or black; gill opening darker than surrounding area; a narrow dark blotch at angle of jaw.

Maximum size at least 800–900 mm.

Distribution and habitat. Apparently endemic to the Red Sea, in relatively deep water, approximately 200 m, all known records from the Gulf of Aqaba.

Remarks. This species resembles *Gymnothorax pharaonis* n. sp. (see below) in its color pattern, but in the latter species the markings on the tail are more irregular in shape and tend to be drawn out into oblique streaks dorsally and ventrally. In addition, *G. pharaonis* has fewer vertebrae (122–128 *vs*. 137–142) and lives in shallower water. The teeth in *G. baranesi* are sexually dimorphic, the males having larger and fewer teeth and lacking the inner maxillary teeth. *Gymnothorax baranesi* was not collected during the present study and no COI sequence information was available for this species, so it could not be included in the phylogenetic analysis carried out in this study.

Gymnothorax buroensis (Bleeker 1857)—Latticetail Moray

(Figure 10)

Muraena buroensis Bleeker 1857: 79 (Kajeli, Buru I., Molucca Is., Indonesia). Holotype (unique), RMNH 7197.
Muraena corallina Klunzinger 1871: 614 (Al-Quseir [Kosseir], Egypt, Red Sea). No types known.
Gymnothorax meleagris (non Shaw): Marshall 1952: 223.
Gymnothorax corallinus: Tortonese 1955: 51; Goren & Dor 1994: 7.
Lycodontis corallinus: Dor 1984: 27.
Lycodontis buroensis: Dor 1984: 431.
Gymnothorax buroensis: Goren & Dor 1994: 7; Randall & Golani 1995: 854; Khalaf 2004: 35; Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 20.

Red Sea material. ***Israel***: BPBM 18248 (2, 195–247), Eilat; HUJ 15092 (4, 132–205), Eilat. ***Egypt***: BMNH 1951.1.16.67-72 (6, 104–171), Sanafir Island; BPBM 20849 (1, 338), Marsa el Mukabeila; HUJ 7174 (1, 348), El Himeira; HUJ 10686 (2, 330–345), Nuweiba; HUJ 15088 (5, 170–265), El Kura; USNM 312283 (1, 205), Ras Burqa; USNM 312299 (7, 156–224), Egypt, Strait of Jubal; USNM 312308 (5, 99–220), Marsa el Mukabeila; USNM 312310 (4, 86–295), between Marset Mahash El Ala and Marset Abu Samra; USNM 312317 (5, 103–279), El Himeira. ***Saudi Arabia***: KAUMM 392 [KAU13-545] (1, 227), Al Wajh; KAUMM 393 [KAU14-813] (1, 142), Al Lith; KAUMM 416 [KAU11-528] (1, 135), Al Wajh; SMF 35806 [KAUST 11-481] (1, 164), An-Nuwayshiziyah; SMF 35805 [KAU14-808] (1, 203), Al Lith; SMF 35829 [KAU11-21] (1, 173), Al Lith; SMF 33619 (1, 253), Jeddah; USNM 147427 (1, 211), 5 km north of Jeddah. ***Yemen***: USNM 397543 (1, 98), Hanish Island.

Comparative material. ***Agalega I.***: USNM 312319 (7, 142–265). ***Indonesia***: RMNH 7197 (1, 208, holotype); USNM 312264 (3, 170–253). ***Australia***: USNM 312276 (1, 222). ***Tonga***: USNM 334259 (4, 214–253), USNM 338836 (2, 172–230). ***French Polynesia***, Moorea: MNHN 2008-0235 (1, 190); MNHN 2008-0236 (1, 138); MNHN 2008 -0321 (1, 181); MNHN 2008-0322 (1,182); MNHN 2008-0434 (1, 245); MNHN 2008-0435 (1, 231); MNHN 2008-0436 (1, 275); USNM 390971 (2, 129–166); USNM 391228 (1, 133). ***French Polynesia***, Marquesas: USNM 409086 [MARQ-086] (1, 256). ***Clipperton I.***: USNM 352344 (3, 128–273).

Description. In TL: preanal length 2.0–2.3, predorsal length 6.9–10, head length 6.4–8.3, body depth at anus 11–21. In head length: snout length 5.2–8.7, eye diameter 6.3–11, upper-jaw length 2.0–3.3. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 4–6, preanal 43–51, total 106–115.

Body stout, anus usually before midlength, dorsal-fin origin before gill opening. Head and jaws moderate, jaws closing completely. Eye moderate, over middle of upper jaw. Gill opening mid-lateral. Anterior nostril in a short to moderate tube; posterior nostril oval, above anterior margin of eye, without a raised rim except in large specimens.

Teeth conical, sharp, smooth. Intermaxillary teeth in five rows across: a peripheral series of small teeth, an intermediate series of 3–4 larger teeth on each side, and a median series of 2–3 depressible teeth. Maxillary teeth biserial, those of outer row smaller and more numerous, the inner teeth larger and fewer; outer row slightly longer than inner. Dentary teeth in one row except for one or two larger teeth anteriorly slightly inside the main row. Vomerine teeth small, uniserial.

Color: ground color variable, pale grayish brown to brown, body gradually becoming darker posteriorly; body mottled with pale and dark brown but no spots, or with about five longitudinal rows of small black spots superimposed anteriorly, posterior half of body with pale flecks; head uniformly grayish brown anteriorly, usually uniform darker brown or occasionally mottled with pale brown posteriorly; fins yellow-edged posteriorly; anterior nostril dark brown.

FIGURE 10. *Gymnothorax buroensis*. **A**: SMF 33619, 253 mm TL, fresh specimen, Jeddah, Saudi Arabia; **B**: KAUMM 392 [KAU13-545], 227 mm TL, alive, Al Wajh, Saudi Arabia; **C**: alive, Dahab, Egypt. Photos by S.V. Bogorodsky.

A small species, perhaps not exceeding 400 mm.

Distribution and habitat. Throughout the Indo-Pacific from the Red Sea to Central America, perhaps absent from Hawaiian Islands. Primarily in shallow water, although recorded to 25 m (Böhlke & Randall, 2000: 230). Common on coral reefs, where it lives cryptically. The range of this species is largely complementary to that of the related species *Gymnothorax eurostus* (Abbott), an antitropical species that occurs mainly north and south of about 16° latitude. The latter species does not occur in the northern Indian Ocean.

Remarks. There is a marked modal difference in the number of vertebrae between specimens from the Red Sea and elsewhere. Twenty-five Red Sea specimens had 106–111 total vertebrae, whereas 30 specimens from the Indian Ocean to Central America (Agalega Island, Indonesia, Australia, Tonga, Moorea, and Clipperton Island) had 110–115. The comparable numbers for preanal vertebrae are 43–47 *vs*. 45–51. *Muraena corallina* Klunzinger would be available if the Red Sea population were recognized as a species, although we refrain from taking such action at this time, as there is no difference in genetics, and there are no other morphological distinctions. The COI gene does not differentiate any of the populations of this species, either inside or outside the Red Sea. From the present phylogeny it becomes apparent that *Gymnothorax buroensis* is closely related to *G. meleagris* (Shaw) and *G. eurostus* (Abbott). The latter name is assigned (by the respective sequence authors) to two distinct genetic lineages that most likely represent similar but separate species. We cannot at present contribute to solving the question if one of these lineages is correctly identified and what name (if any) would apply to the other species.

Gymnothorax cinerascens (Rüppell 1830)—Plain Moray

(Figures 11, 12, 19, 20)

Muraena cinerascens Rüppell 1830: 120 (Mohila, Red Sea). Holotype (unique), SMF 3486.
Gymnothorax hepatica: Bamber 1915: 478 (part?).
Gymnothorax hepaticus (non Rüppell): Clark *et al*. 1968: 21(part?); Goren & Dor 1994: 7 (part?); Randall & Golani 1995: 859, fig. 3; Golani & Bogorodsky 2010: 10 (part?) ; Golani & Fricke 2018: 21 (part ?).
Lycodontis hepaticus: Dor 1984: 28 (part?).
Gymnothorax monochrous (non Bleeker): Khalaf 2004: 36 (part?).

Red Sea material. ***Red Sea***: SMF 3486 (1, 475, holotype); SMF185 (2 of 3, 176–253). ***Egypt***: USNM 166913 (1, 445), Ghardaqa (Hurghada). ***Sudan***: BPBM 20758 (3, 225–385), Suakin Archipelago. ***Saudi Arabia***: KAUMM 395 [KAU12-290] (1, 603), Farasan Archipelago; KAUMM 396 [KAU13-643] (1, 376), Al Khoreybah; KAUMM 397 (KAU13-116) (1, 755), Al Wajh bank; SMF 185 (2 of originally 3, 178–253), Al Muwaylih; SMF 35808 [KAU12-016] (1, 675), Farasan Archipelago; SMF 35809 [KAU12-247] (1, 234), Farasan Archipelago; SMF 35810 [KAU12-416] (1, 890), Farasan Archipelago; SMF 35828 [KAU12-1085] (1, 191), Jeddah, Obhur; SMF 35875 [KAU17-157] (1, 569), Dumsuk I., 6–10 m. ***Eritrea***, Dahlak Archipelago: USNM 312570 (1, 496), Difnein Island; USNM 312571 (4, 309–450), Sciumma Island; USNM 446881 (16, 221–592), Delemmi; USNM 312569 (3, 301–795), Melita Bay.

Diagnosis. Moderate-size moray, moderate in length and depth, tail relatively slender, head behind eye slightly elevated. Preanal length 2.0–2.2 in TL. Third intermaxillary tooth close to vertical at anterior margin of eye. Vomerine teeth biserial in adults. Head and body plain brown without markings; margin of dorsal and anal fins yellowish to yellow at tip of tail. Vertebrae 5–6 / 55–57 / 128–135.

Description. In TL: preanal length 2.0–2.2, predorsal length 7.5–10.4, head length 6.2–8.1, body depth at anus 15–23. In head length: snout length 5.3–6.6, eye diameter 8.6–13.8, upper-jaw length 2.2–3.6. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 5–6, preanal 55–57, total 128–135.

Body moderately elongate; anus at or slightly before midlength; dorsal-fin origin before gill opening; height of dorsal fin about one-third body depth. Jaws slender, of equal length, may be slightly hooked. Eye moderate, over middle of upper jaw. Anterior nostril tubular; posterior nostril with a raised rim, above anterior margin of eye. Third infraorbital pore slightly behind level of anterior margin of eye.

Teeth smooth, slender and pointed or blade-like. Intermaxillary teeth long and slender, in a single peripheral series, 3–6 on each side sometimes with a few much smaller teeth between; three slender, depressible median teeth; third intermaxillary tooth close to vertical through anterior margin of eye, ratio between distance from third intermaxillary tooth to tip of snout and distance from same tooth to anterior margin of eye 3.2–12.6. Maxilla with

about 10–18 triangular teeth in a single row in large adults, smaller specimens with 1–3 larger inner teeth anteriorly. Dentary with 1–4 larger inner teeth and about 12–22 smaller outer teeth. Vomerine teeth biserial in adults, uniserial in young.

Color: body and fins dark brown, fins with yellow margin at tip of tail, yellowish or yellow more obscure with growth. Throat grooves darker brown. Head pores with a narrow dark margin. Iris in life reddish brown. Some smaller specimens light grayish brown with scattered dark markings.

FIGURE 11. *Gymnothorax cinerascens*. **A**: Dumsuk I., Farasan Archipelago, Saudi Arabia; **B**: KAUMM 397 [KAU13-116], 755 mm TL, Al Wajh bank, Saudi Arabia. Photos by S.V. Bogorodsky.

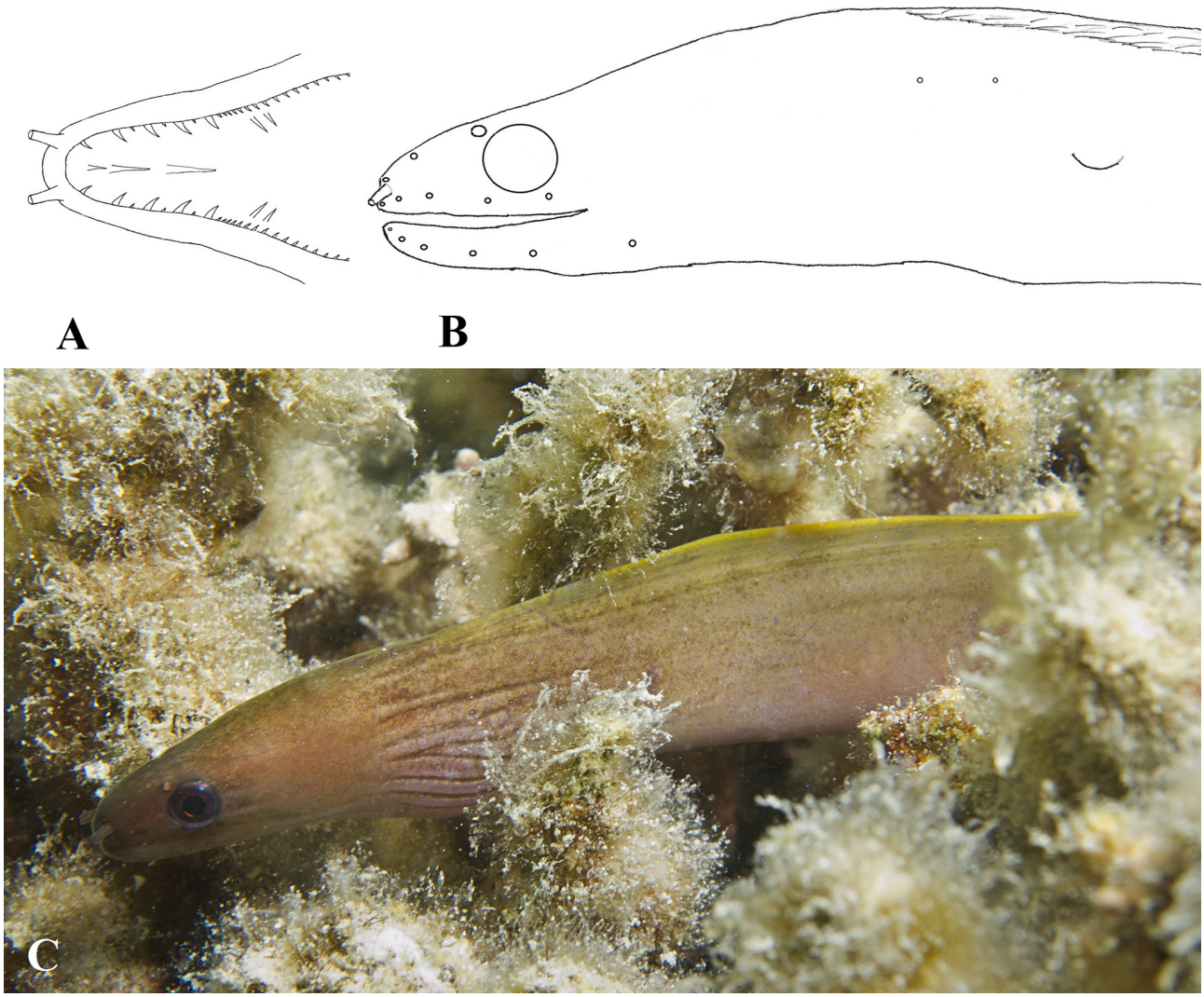


FIGURE 12. *Gymnothorax cinerascens*, SMF 35828 [KAU12-1085], 191 mm TL, Obhur, Jeddah, Saudi Arabia. **A**: drawing of upper jaw; **B**: drawing of head close-up; **C**: alive. Drawings by D.G. Smith, photo by S.V. Bogorodsky.

Maximum size at least 890 mm.

Distribution and habitat. Known with certainty only from the Red Sea, where it occurs primarily in turbid, silty water, on dead reefs, and in sheltered areas at depths of 1–20 m. More common in the southern part of the Red Sea than in the north.

Remarks. This species has long been considered a synonym of *Muraena hepatica* Rüppell, but our studies indicate that it is distinct, based on both morphological and genetic characters. The holotype of *M. cinerascens* actually belongs to the species most commonly reported as *Gymnothorax hepaticus*. The true *G. hepaticus* has been redefined; see the account of that species for a more detailed explanation of the differences between the two species. Two of the specimens, SMF 35828 and SMF 35875 differ somewhat in their color pattern from the others (Fig. 12). In preservative, they are medium brownish gray with scattered black markings. In life, SMF 35828 is pale brown speckled with dark brown, with edge of fins pale yellow. The live colors of SMF 35875 were not recorded, but it belongs to the same COI lineage as the other specimens of *G. cinerascens* (see Fig. 48), and we treat it here as an aberrant color pattern of that species. SMF 35828 was not tissue-sampled, but it agrees in most other characters, and we are placing it in this species. The specimens in SMF 185 were originally labeled as syntypes of *Muraena cinerascens*, but Böhlke & Smith (2002) showed that they are not. They were listed by Rüppell (1852) as *Muraena cinerascens* var. *umbrina* but without a description or a reference to a description, leaving the name as a *nomen nudum*, hence unavailable. SMF 185 contains three specimens; two of them are *G. cinerascens* and one is *G. hepaticus* (now SMF 35879).

For the phylogenetic analysis, no sequences of *G. hepaticus* from other regions could be identified. The four

sequences from the Red Sea showed very little variation and the next closely related species are *G. fimbriatus* (Bennett) and an undescribed species of *Gymnothorax* with collection locality Red Sea (Israel, *Gymnothorax* sp. 5), with which *G. hepaticus* was placed on a joint branch with moderately high bootstrap support.

Previous records of *Gymnothorax hepaticus* in the Red Sea undoubtedly include *G. cinerascens*. These specimens would have to be re-examined to determine their true identity. We can confirm that BPBM 20758 belongs to *G. cinerascens* because Randall & Golani (1995, Fig. 3) included a photograph of one of the specimens. It appears to be more common than the true *G. hepaticus*. It is uncertain whether it occurs outside the Red Sea.

Gymnothorax cinerascens has rarely been mentioned in the literature. Klunzinger (1871: 615) included it (as *Muraena cinerascens*) as a synonym of *Muraena undulata*, although he suggested that it might be a separate species. However, he described it as having broad crossbands ("*Körper mit breiten Querbändern"*), and it is obviously not Rüppell's species.

Gymnothorax elegans Bliss 1883—Elegant Moray

(Figure 13)

Muraena flavimarginata Kaup 1856: 67 (Réunion I.). Syntypes, MNHN A-8811 (1, dry), A-8812 (1, dry). Preoccupied by *Muraena flavimarginata* Rüppell 1830.

Gymnothorax elegans Bliss 1883: 60 (Mauritius). Holotype (unique), MCZ 5954.—Goren & Dor 1994: 7; Randall & Golani 1995: 857; Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 21.

Lycodontis elegans: Ajiad & El-Absy 1986: 297.

Red Sea material. ***Jordan***: Marine Science Station Aqaba 150–151 (2, 440–510).

Comparative material. ***Mauritius***: MCZ 5954 (1, 622, holotype); MCZ 5946 (1, 550, holotype of *Gymnothorax albomaculatus* Bliss). ***Maldives***: BPBM 34735 (1, 495). ***Hawaii***: USNM 50617 (1, 540, holotype of *Gymnothorax goldsboroughi* Jordan & Evermann).

Description. In TL: preanal length 2.1–2.4, predorsal length 11–14, head length 7.5–9.9, body depth at anus 18–30. In head length: snout length 4.5–6.9, eye diameter 9.0–12.0, upper-jaw length 2.2–2.8. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 2–5, preanal 52–57, total 141–146.

Body moderately elongate; anus before midlength; dorsal-fin origin before gill opening. Jaws moderate, of equal length or lower jaw slightly protruding. Eye moderate, over middle of upper jaw. Anterior nostril tubular, reaching edge of lip when depressed; posterior nostril in a low tube, over or just in front of anterior edge of eye.

Teeth in jaws uniserial, triangular, finely serrate; a single median intermaxillary tooth. Vomerine teeth small, in a single row.

Color: a complex pattern of pale spots on a dark brown background, continued onto head and dorsal fin. Anteriorly, spots smaller and more closely set, with the pale background often reduced to a narrow reticulation; in the middle of body spots as large as or slightly larger than eye; posteriorly, spots larger and farther apart, becoming aligned dorsoventrally, eventually forming irregular pale bars. Anal fin dark at base with a white edge, dorsal fin with a narrow white edge posteriorly. A dark spot around gill opening. Sometimes a dark stripe midventrally on throat and anterior trunk.

Maximum size at least 800 mm.

Distribution and habitat. Across the Indo-Pacific from the western Indian Ocean and Red Sea to Hawaiian Islands and French Polynesia, at about 90–400 m depth. Red Sea records from the Gulf of Aqaba only, where it was first reported on the basis of two specimens collected by hook and line at a depth of 180 m (Ajiad & El-Absy 1986).

Remarks. This species is known in the Red Sea from the two specimens cited above and another specimen photographed from a submarine at a depth of 350–400 m, also in the Gulf of Aqaba (Randall & Golani, 1995: 857). We did not examine the specimens and do not know the number of vertebrae. Böhlke & Randall (2000: 233) gave a range of 138–150 total vertebrae for this species, which seems excessive for one species, but they did not break down the counts geographically. The counts given above (141–146) are of specimens from Mauritius and Hawaii, and there seems little difference between those two widely separated localities. This species is not commonly collected, undoubtedly due to its deep-water habitat and probably cryptic habits. Nevertheless, we were able to include the species in the present phylogeny, although we did not obtain specimens and tissue samples from the Red Sea

during the past surveys carried out in the frame of the project on biodiversity of the Red Sea. The two specimens, for which COI sequence data are included here, come from the southwestern Indian Ocean (South Africa) and the South Pacific (Society Islands). Despite this large geographic distance, the sequences showed no strong divergence, hinting at a rather low level of differentiation across the distribution range.

FIGURE 13. *Gymnothorax elegans*, BPBM 34735, 495 mm TL, fresh specimen, Maldives. Photo by J.E. Randall.

Gymnothorax favagineus Bloch & Schneider 1801—Honeycomb Moray

(Figure 14)

Gymnothorax favagineus Bloch & Schneider 1801: 525, pl. 105 (Tranquebar, India). Holotype (unique), ZMB 7782 (stuffed).—Randall 1994: 260; Randall & Golani 1995: 858; Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 21.

Red Sea material. None.

Comparative material. ***Taiwan***: USNM 312734 (1, 303); USNM 312736 (2, 182–278). ***Australia***: USNM 176690 (2, ca 600–614); USNM 312733 (1, 304); USNM 312735 (1, 290).

Description. In TL: preanal length 2.0–2.2, predorsal length 9.4–11, head length 7.6–8.8, body depth at anus 19–24. In head length: snout length 5.1–6.7, eye diameter 9.4–11, upper-jaw length 2.5–3.0. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 5–6, preanal 61–64, total 139–148.

Body moderately elongate, anus slightly before midlength, dorsal-fin origin before gill opening. Jaws moderate, of equal length. Eye moderate, over middle of upper jaw. Anterior nostril tubular; posterior nostril in a low tube, over or just in front of anterior edge of eye.

Teeth smooth, conical to narrowly triangular; intermaxillary teeth in a single peripheral series of about 4 on each side, 2 or 3 median teeth. Maxillary teeth biserial, 2–3 larger inner teeth and about 11–15 smaller outer teeth. Dentary with 2 or 3 large teeth anteriorly followed by about 11–14 smaller teeth, the larger teeth sometimes distinctly medial to smaller teeth. Vomerine teeth uniserial in young, biserial in adults.

Color: body and head white covered with numerous, polygonal, black spots separated by narrow interspaces often forming a honeycomb-like pattern. Spots larger and more widely separated in young.

Maximum size at least 2 m.

Distribution and habitat. Widely distributed in the Indo-West Pacific from the southern Red Sea south to South Africa, east to Australia and Papua New Guinea. Occurs on coral and rocky reefs from depths of 1–50 m; feeds on fishes and octopuses.

Remarks. The record from the Red Sea is based on a photograph taken at Hanish Island off Yemen (Randall 1994). The three specimens examined from Taiwan have fewer vertebrae (139–141) than the four specimens from Australia (146–148). This species has been confused with other dark-spotted species such as *Gymnothorax isingteena* (Richardson) and *G. melanospilus* (Bleeker). The species was not collected during the present study, and no tissue samples or COI sequence data for *G. favagineus* specimens from the Red Sea are available at present. The one sequence of *Gymnothorax favagineus* included in the phylogenetic analysis (Fig. 48) and other near identical sequences from the southwestern Indian Ocean that are deposited in BOLD (not included in the present analysis) do not differ markedly from sequences from specimens collected in distant parts of the distribution area of the species (e.g. Taiwan, Indonesia and Western Australia) indicating low levels of intra-specific genetic differentiation (not shown in the present phylogeny, Fig. 48). The closest phylogenetic relationship, although only weakly supported by bootstrapped analyses, is with *Gymnothorax formosus* Bleeker (represented by a specimen from the Society Islands in the present analysis, see Fig. 48).

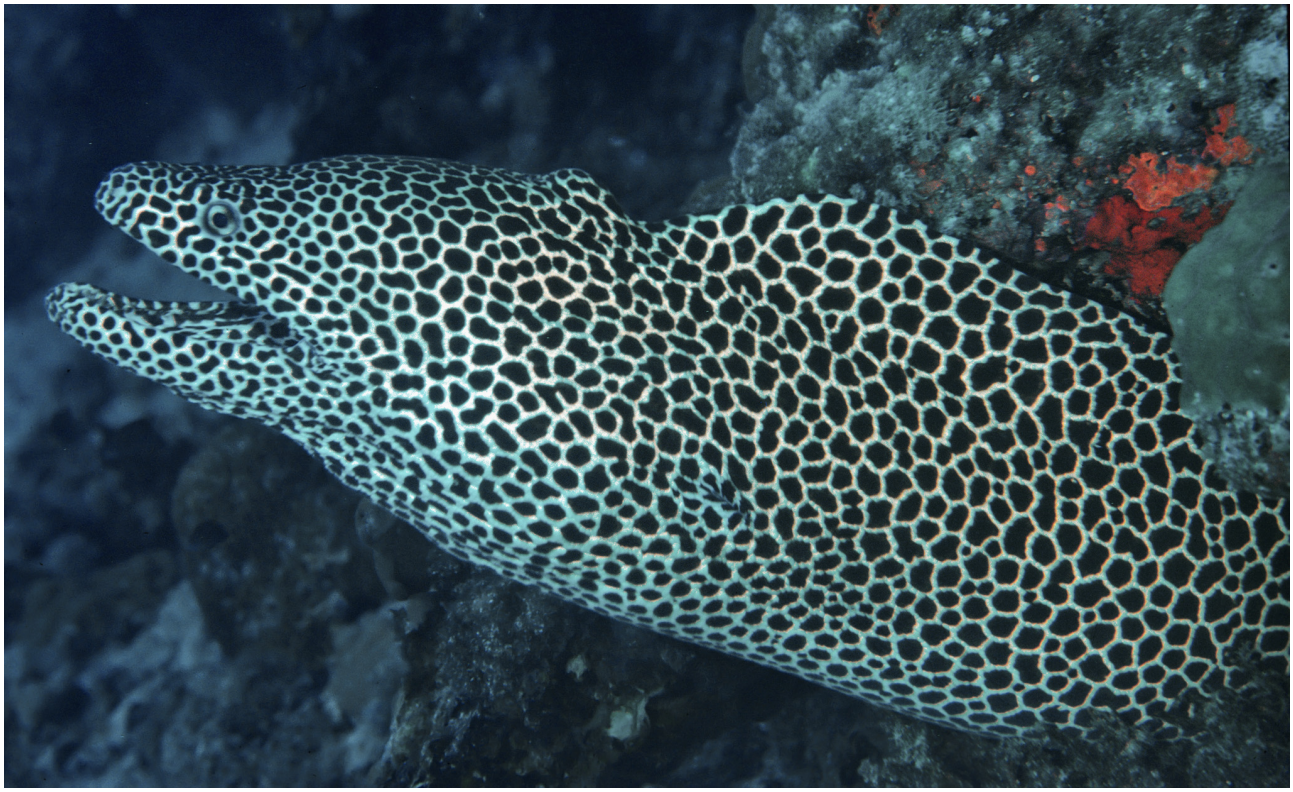


FIGURE 14. *Gymnothorax favagineus*, Seven Brothers, Djibouti. Photo by J.E. Randall.

Gymnothorax flavimarginatus (Rüppell 1830)—Yellowmargin Moray
(Figure 15)

Muraena flavimarginata Rüppell 1830: 119, pl. 30 (fig. 3) (Red Sea). Holotype (unique), SMF 765.—Klunzinger 1871: 615.
Gymnothorax flavimarginatus: Marshall 1952: 223; Tortonese 1955: 51; Goren & Dor 1994: 7; Randall & Golani 1995: 858; Debelius 1998: 13; Khalaf 2004: 35; Lieske & Myers 2004: 36; Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 21.
Lycodontis flavimarginatus: Roux-Estève 1956: 62 (as *flavomarginatus*); Dor 1984: 27.

Red Sea material. ***Red Sea***: SMF 765 (1, 550, holotype). ***Sudan***: BPBM 19734 (1, 195), one mile north of Port Su-

dan. ***Saudi Arabia***: SMF 35172 [KAU13-583] (1, 317), Duba; USNM 147422 (2, 233–554), 2 km north of Jeddah; USNM 147429 (3, 254–307), 5 km north of Jeddah. ***Eritrea***: USNM 312430 (7, 150–286), Difnein Island; USNM 312453 (3, 261–412), Difnein Island.

Comparative material. ***Mauritius***: MNHN B-2468 (1, 450, lectotype of *Muraena mauritiana* Kaup); MNHN A-3738 (1, 300, paralectotype of *Muraena mauritiana* Kaup). MCZ 6146 (1, 215, holotype of *Gymnothorax viridipinnis* Bliss). ***Taiwan*:** USNM 312225 (2, 74–82). ***Indonesia***: BMNH 1867.11.28.253 (1, 464, holotype of *Muraena batuensis* Bleeker). ***Micronesia***: USNM 323385 (1, 75). ***Fiji***: USNM 312700 (2, 75–84); USNM 410229 (1, 128). ***Tonga***: USNM 334796 (1, 103). ***Hawaii***: USNM 50619 (1, 590, holotype of *Gymnothorax thalassopterus* Jenkins).

Description. In TL: preanal length 2.0–2.3, predorsal length 8.3–11, head length 7.5–11, body depth at anus 14–27. In head length: snout length 4.8–6.5, eye diameter 6.9–12, upper-jaw length 2.1–2.7. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 4–6, preanal 54–58, total 130–139.

Body moderately elongate; anus usually slightly before midlength; dorsal-fin origin before gill opening. Jaws moderate, of equal length. Eye moderate, over middle of upper jaw. Anterior nostril tubular; posterior nostril with a raised rim, above and behind anterior margin of eye.

Teeth smooth, slender, conical to triangular. Intermaxillary teeth in a single peripheral series, usually 2 median teeth. Maxillary teeth biserial, inner teeth fewer and larger. Dentary teeth biserial anteriorly, with 2–4 large inner teeth, uniserial posteriorly. Vomerine teeth uniserial.

Color: yellowish, densely and finely mottled with dark brown spots sometimes in gravel-like pattern, often to the extent that little of the pale yellowish ground color remains; small specimens with spots larger and more widely spaced; snout, front of lower jaw, and anterior nostril purplish brown; a black blotch over gill opening; fins dark basally with a conspicuous greenish yellow or yellow margin posteriorly.

Maximum size at least 1.2 m.

Distribution and habitat. Widely distributed across the Indo-Pacific, from the Red Sea and east coast of Africa east to the Hawaiian Islands and French Polynesia, and islands off Central America. Occurs on coral and rocky reefs from depths of 0.5–150 m, usually 5–30 m.

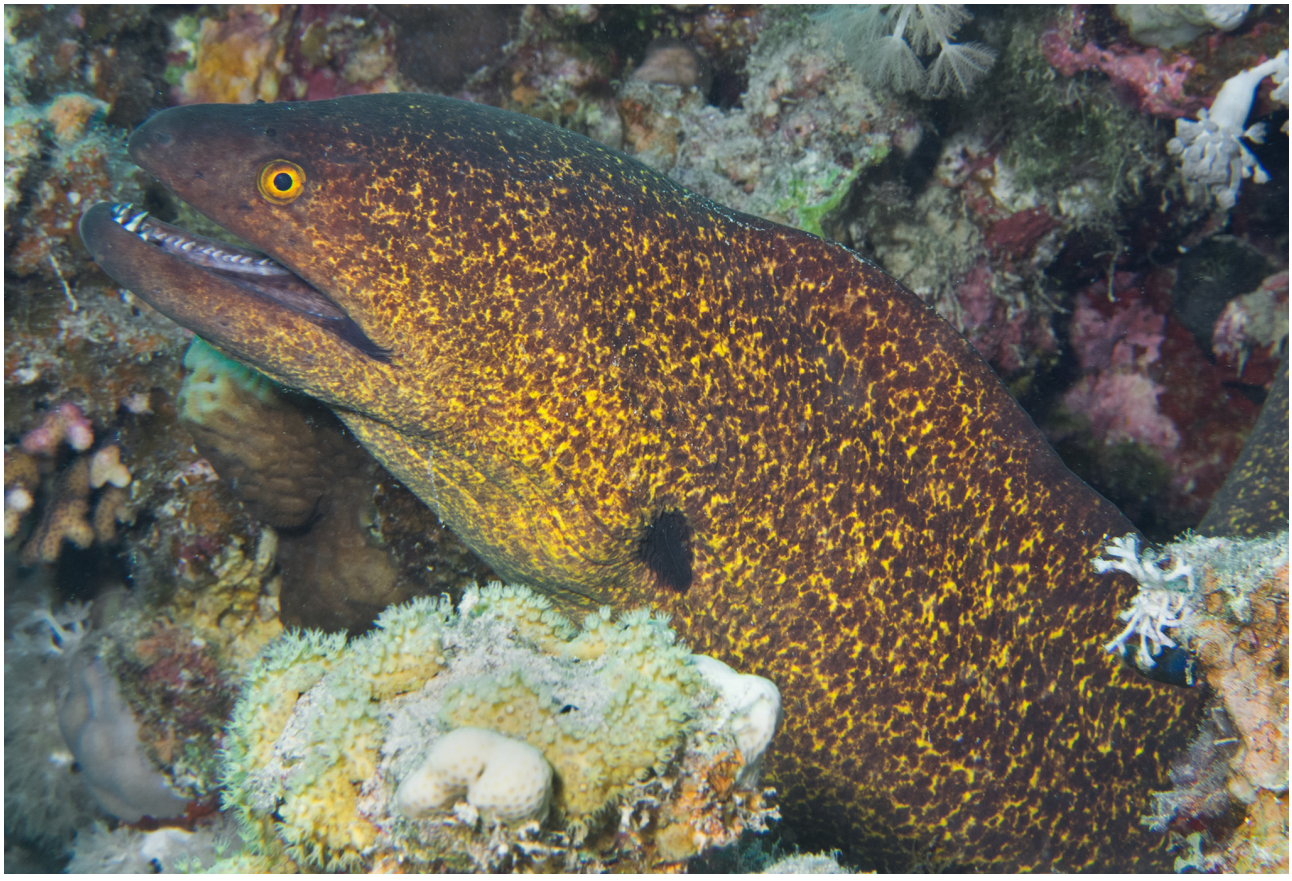


FIGURE 15. *Gymnothorax flavimarginatus*, Dahab, Egypt. Photo by S.V. Bogorodsky.

Remarks. There is little difference in the vertebral counts between specimens from the Red Sea (130–134) and those from elsewhere (131–139). The second author once observed this species at Ras Muhammad in a feeding association with the jackfish *Caranx melampygus*, in which the latter fed on prey driven from hiding places by the eel. The phylogeny (Fig. 48) shows that *G. flavimarginatus* is closest related to *G. javanicus*, although bootstrap support for this relationship is only moderately high in the present phylogeny based on partial mitochondrial COI. High support for the close phylogenetic relation of these two species, however, was shown in a multigene phylogeny by Reece *et al.* (2010).

Gymnothorax griseus (Lacepède 1803)—Gray Moray

(Figure 16)

Muraenophis grisea Lacepède (ex Commerson) 1803: 629, 642, pl. 19 (fig. 3) (locality uncertain). No types known.
Muraena geometrica Rüppell 1830: 118, pl. 30 (fig. 1) (Massawa, Eritrea, Red Sea). Holotype (unique), SMF 130.—Klunzinger 1871: 617; Borsieri 1904: 219.
Muraena bilineata Rüppell 1838: 84 (Jidda [Jeddah], Saudi Arabia, Red Sea). Holotype, SMF 911.
Gymnothorax geometricus: Marshall 1952: 223.
Echidna geometrica: Tortonese 1955: 52; Roux-Estève 1956: 62.
Siderea geometrica: Clark *et al*. 1968: 21.
Echidna grisea: Tortonese 1968: 9; Tortonese 1983: 106.
Siderea grisea: Dor 1984: 29; Goren & Dor 1994: 7; Randall & Golani 1995: 870; Khalaf & Disi 1997: 40; Debelius 1998: 15.
Gymnothorax griseus: Khalaf 2004: 35; Lieske & Myers 2004: 38; Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 21.

Red Sea material. ***Egypt***: BPBM 18133 (2, 378–388), Marsa el Mukabeila; HUJ 15062 (7, 252–404), Gulf of Aqaba, El Arkana; HUJ 15164 (3, 503–645), Nuweiba; USNM 312476 (1, 320), El Himeira; USNM 312478 (2, 362–373), Gulf of Suez, El Tur. ***Saudi Arabia***: KAUMM 394 [KAU12-248] (1, 197), Farasan Archipelago; SMF 911 (1, 510, holotype of *Muraena bilineata*), Jeddah; SMF 7186 (1, 198, paratype of *Muraena bilineata*), Jeddah; SMF 35250 (1, 336), Al Khoreybah; SMF 35807 [KAU12-438] (1, 358), Farasan Archipelago. ***Eritrea***: SMF 130 (1, 213, holotype of *Muraena geometrica*), Massawa; USNM 312472 (2, 219–362), Massawa; USNM 312473 (1, 174), Melita Bay.

Comparative material. ***Mozambique***: SAIAB 106 (1, 368, holotype of *Siderea schonlandi* Smith). ***Mauritius***: USNM 267367 (2, 180–275); USNM 312486 (2, 248–265); USNM 312487 (3, 116–138). ***Aldabra***: USNM 312467 (2, 93–233). ***Agalega I***.: USNM 312488 (1, 258).

Description. In TL: preanal length 2.2–2.6, predorsal length 9.7–14.0, head length 7.7–11., body depth at anus 15–26. In head length: snout length 5.8–7.1, eye diameter 9.5–13, upper-jaw length 2.8–3.7. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 3–5, preanal 49–54, total 128–140.

Body moderately elongate; anus slightly before midlength; dorsal fin high, its origin before gill opening. Jaws moderate, of equal length. Eye moderate, over middle of upper jaw. Anterior nostril short and tubular; posterior nostril with a raised rim, above anterior margin of eye.

Teeth short and stout, not sharply pointed, smooth. Intermaxillary teeth in a single peripheral series, one or two median teeth. Maxillary teeth biserial, teeth of inner row larger. Dentary teeth biserial anteriorly, uniserial posteriorly. Vomerine teeth small, conical, biserial anteriorly.

Color: body pale yellowish or whitish gray densely mottled with irregular darker markings forming an obscure honeycomb pattern. Head and anterior nostril lavender-gray, the pores outlined in black. Rows of sensory papillae on head and anterior body marked by small dark spots forming conspicuous lines; one row on snout forming an inverted "U" shape, then continuing posteriorly along side of upper lip; transverse row of slightly larger black spots on nape; spots continuing along lateral line behind head for a varying distance, disappear in large individuals. Iris white.

Maximum size about 650 mm.

Distribution and habitat. Found in the western Indian Ocean from Oman to South Africa and east to the Chagos Archipelago; common in shallow water where it can be seen foraging for food among corals and rocks; reported in depth range of 1–30 m.

Remarks. One of the most common Red Sea morays, sometimes seen in groups of up to five individuals. Closely related to *Gymnothorax thyrsoideus* (Richardson), which occurs in similar habitats in the eastern Indian Ocean and Pacific. The phylogenetic analysis of the mitochondrial COI barcoding gene does not show reciprocal monophyly for specimens of *G. griseus* and *G. thyrsoideus* (Richardson), indicating a very recent divergence of these very similar species. *Gymnothorax griseus* has sometimes been placed in the genus *Siderea*, but the type species of that genus is *Muraena picta* Ahl, 1789, which has more acute, uniserial teeth. The dentition of *Gymnothorax griseus* and *G. thyrsoideus* approaches that of *Echidna*. In the phylogenetic analysis, two species of *Echidna* (*E. unicolor* Schultz and *E. delicatula* Kaup) are within a well-supported clade with *G. griseus*, *G. thyrsoideus* and *G. pseudoherrei*, and *E. delicatula* is the next closely related species to *G. griseus* and *G. thyrsoideus* (see Fig. 48), questioning the validity of the currently applied generic concepts.

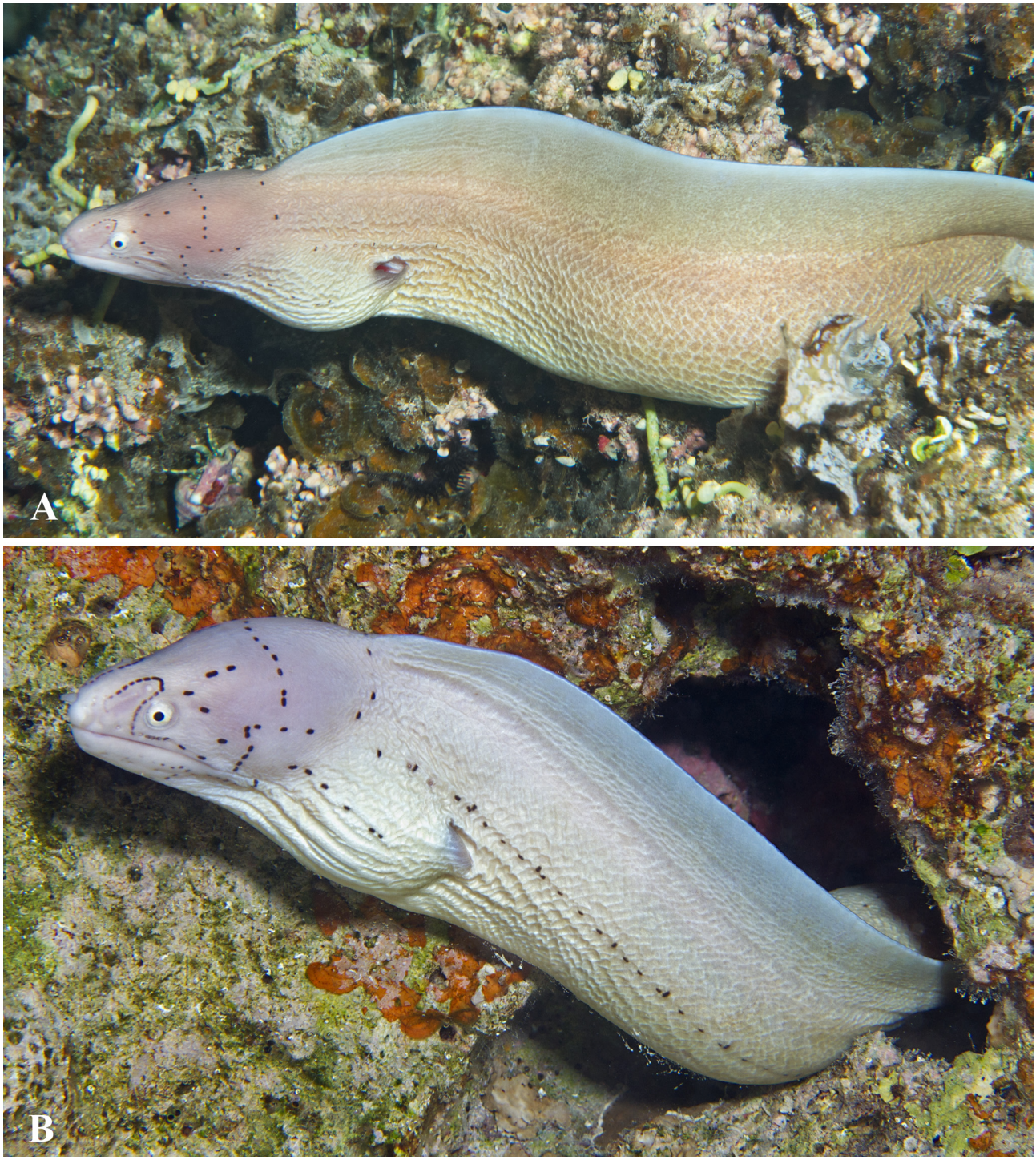


FIGURE 16. *Gymnothorax griseus*. **A**: Dahab, Egypt; **B**: Sharm el Moya, Egypt. Photos by S.V. Bogorodsky.

Specimens from the Red Sea have fewer vertebrae than those from elsewhere (128–134 *vs*. 132–140 respectively), but in its mitochondrial COI sequences the one included Red Sea specimen does not differ much from either *G. griseus* outside the Red Sea or from the closely related *G. thyrsoideus*. The synonymy follows Dor (1984).

There is some uncertainty about the type locality of this species. Randall & Golani (1995: 870) stated "probably Mascarenes," as it was based on Philibert Commerson's manuscript and Commerson spent some time in Mauritius after leaving Bougainville's expedition. However, that expedition was circumglobal and visited many locations before arriving at Mauritius. In his very brief description of *Muraenophis grisea*, Lacepède stated that "La grise aime les mêmes eaux que l'étoilée et la colubrine" (The gray [*Muraenophis grisea*] likes the same waters as the étoilée and the colubrine [two other species]), but the habitat for those was given as New Britain and Amboina, both far outside the range of *Gymnothorax griseus*. The illustration given with the description is somewhat ambiguous and could also be interpreted as *Gymnothorax thyrsoideus*, which does occur in the stated localities. At some point, it might be necessary to select a neotype, but we leave that for another study.

Gymnothorax hepaticus (Rüppell 1830)—Yellow-jaw Moray

(Figures 17–20)

Muraena hepatica Rüppell 1830: 120 (Red Sea). Holotype (unique), SMF 3554.
Gymnothorax hepatica: Bamber 1915: 478 (part?).
Gymnothorax hepaticus: Clark *et al*. 1968: 21(part?); Goren & Dor 1994: 7 (part?); Randall & Golani 1995: 858 (part?); Golani & Bogorodsky 2010: 10 (part?); Golani & Fricke 2018: 21 (part ?).
Lycodontis hepaticus: Dor 1984: 28 (part?).
Gymnothorax monochrous (non Bleeker): Debelius 1998: 14; Khalaf 2004: 36 (part?).

Red Sea material. ***Red Sea***: SMF 3554 (1, 535, holotype), no further data; SMF 35879 (1, 260; out of SMF 185). ***Saudi Arabia***: SMF 35811 [KAU14-302] (1, 490), Red Sea, Saudi Arabia, off Jizan, sand bottom, 16°54' N 42°28' E, 15–17 m, 01 Nov. 2014, T.J. Alpermann, S.V. Bogorodsky, A.O. Mal & M. Gabr; SMF 35876 [KAU17-139] (1, 240), Red Sea, Saudi Arabia, Farasan Archipelago, Dumsuk Island, reef slope with mix of rocks and corals, 16°33'N 42°04'E, 12–14 m, 07 Feb. 2017, T.J. Alpermann & S.V. Bogorodsky; KAUMM 452 [KAU17-156] (1, 468), the same locality; USNM 444253 [KAU17-155] (1, 345), same locality; SMF 35879 [ex SMF185] (1 of originally 3 in SMF 185, 260), Al Muwaylih. ***Eritrea***: USNM 312567 (2, 175–178), Massawa; USNM 312568 (4, 114–195), Dahlak Archipelago, Delemmi.

Diagnosis. Medium-sized moray, moderate in length and depth, tail relatively slender, head behind eye distinctly elevated. Preanal length 1.9–2.1 in TL. Third intermaxillary tooth somewhat distant from vertical at anterior margin of eye. Upper head and body plain brown without markings; lower jaw and ventral part of branchial area pale yellow in life; margin of dorsal and anal fins pale grey to yellowish at tip of tail. Vertebrae 4–6 / 58–61 / 128–132.

Description. In TL: preanal length 1.9–2.1, predorsal length 9.0–11, head length 7.1–7.8, body depth at gill opening 13–23, depth at anus 15–23. In head length: snout length 5.0–5.9, eye diameter 9.0–11, upper-jaw length 2.5–3.0. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 4–6, preanal 58–61, total 128–132.

Body moderately elongate, anus near midlength, tail relatively slender; dorsal-fin-origin before gill opening, anal fin beginning immediately behind anus. Head with a distinctly raised profile behind eyes; jaws and snout moderately slender and slightly arched, a slight gap visible when mouth closed, upper and lower jaws nearly equal in length. Eye moderate, over middle of upper jaw. Gill opening small, slightly elongate, on side of head slightly below lateral midline. Anterior nostril tubular, relatively short, not reaching edge of lip when depressed. Posterior nostril oval, with a slightly raised rim, above eye, its anterior margin about level with anterior margin of eye. Third infraorbital pore at or slightly ahead of anterior margin of eye.

Teeth smooth, slender and pointed or blade-like. Intermaxillary teeth in one peripheral series of 4–6 on each side, increasing in size from anterior to posterior, and a median series of three sharp, depressible teeth, increasing in size from anterior to posterior. Third intermaxillary tooth somewhat distant from vertical through anterior margin of eye, ratio between distance from third intermaxillary tooth to tip of snout and distance from same tooth to anterior margin of eye 1.8–3.0. Maxillary teeth uniserial or biserial; inner row with 0–3 larger teeth anteriorly; outer teeth smaller, about 9–16. Dentary teeth uniserial, the largest in front, decreasing in size posteriorly; 12–21 full-sized teeth with 1–3 much smaller teeth anteriorly between large teeth. Vomerine teeth inconspicuous, uniserial or slightly irregular.

Color: brown without markings on body, lower jaw and ventral part of branchial area pale yellow in life, throat grooves slightly darker. Head pores without dark margin. Fins dark with an inconspicuous pale edge posteriorly.

Size. The specimens range in size from 114 to 535 mm TL. They are all immature.

FIGURE 17. *Gymnothorax hepaticus*, SMF 35811 [KAU14-302], 490 mm TL, Jizan, Saudi Arabia. **A**: entire moray; **B**: head close-up. Photos by S.V. Bogorodsky.

Distribution and habitat. The known specimens were all collected from the southern Red Sea. It seems less common than *Gymnothorax cinerascens*, but the two species have not been distinguished previously, and the actual abundance and distribution are still uncertain. Most specimens were collected in coral-reef areas with mix of rocks and corals from depths of 12–17 m; one specimen was trawled from soft substrata.

FIGURE 18. *Gymnothorax hepaticus*, USNM 444253 [KAU17-155], 345 mm TL, Dumsuk I., Farasan Archipelago, Saudi Arabia. **A**: entire moray; **B**: head close-up. Photos by S.V. Bogorodsky.

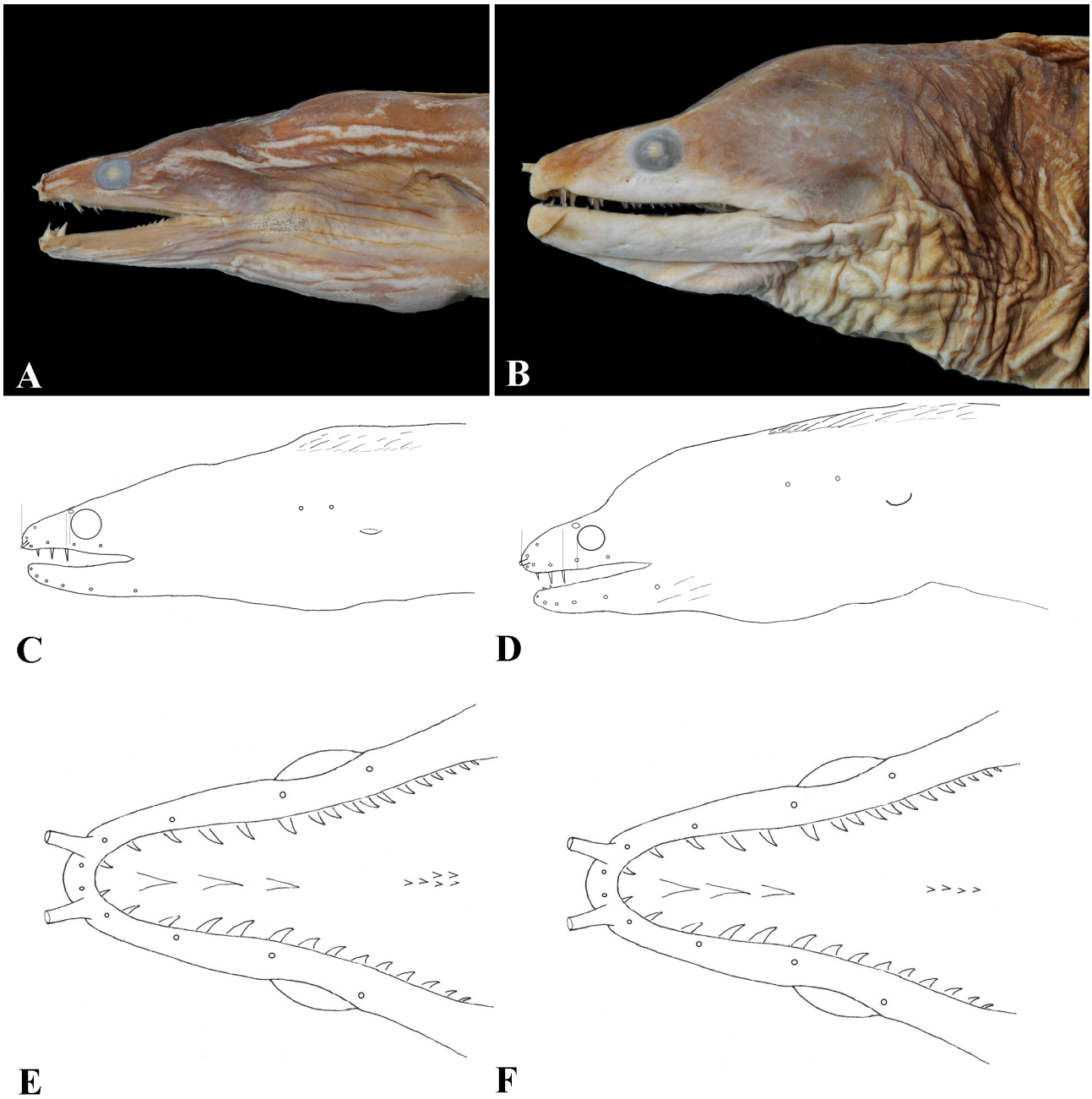


FIGURE 19. *Gymnothorax cinerascens* (A, C, E) and *G. hepaticus* (B, D, F). **A**: SMF 3486, 475 mm TL, holotype, Red Sea; **B**: SMF 3554, 535 mm TL, holotype, Red Sea; **C** & **D**: drawing of the head showing cephalic sensory system and position of third intermaxillary tooth and IO pore; **E** & **F**: drawing of the dentition on the upper jaw. Photos by S. Traenkner (**A** & **B**), drawings by D.G. Smith.

Remarks. As noted, this species has long been confused with *Gymnothorax cinerascens*, and both species have likely been reported as *G. hepaticus*. The original descriptions are brief and largely devoid of distinguishing characters. The two species are similar in general appearance but can be distinguished by several characters. The preanal length is slightly greater in *G. hepaticus* (1.9–2.1, mean 2.0 in TL) than in *G. cinerascens* (2.0–2.2, mean 2.1 in TL) (Fig. 20A); this is reflected in the number of preanal vertebrae, 58–61 *vs.* 55–57 respectively. *Gymnothorax hepaticus* is somewhat lighter in overall color, and the lower jaw and ventral part of the branchial area are yellowish in life, pale in preserved specimens. *Gymnothorax cinerascens* is usually uniformly dark brown, including all of the head and lower jaw; some specimens are light gray-brown with scattered small dark patches, but none have the yellow lower jaw. The head pores have dark rims in *G. cinerascens*, whereas in *G. hepaticus* they are unmarked. The median intermaxillary teeth are distinctly closer to the eye in *G. cinerascens* than in *G. hepaticus*. In *G. cinerascens*,

the distance from the third median intermaxillary tooth to the anterior margin of the eye is contained 3.2–12.6 times in the distance from the same tooth to the tip of the snout, compared to 1.8–3.0 times in *G. hepaticus* (Fig. 20B). The vomerine teeth in *G. cinerascens* are more numerous and distinctly biserial in adults, whereas in *G. hepaticus* they are fewer and uniserial or at most slightly irregular. The third infraorbital pore is located behind the anterior margin of the eye in *G. cinerascens*, whereas in *G. hepaticus* it is under or slightly ahead of that point. There are also a couple of differences in shape between the two species. The dorsal profile of the head relatively straighter in *G. cinerascens*, only slightly elevated behind the eye. In *G. hepaticus*, there is a more distinct hump behind the eye, although this is more obvious in larger specimens. *Gymnothorax hepaticus* has a more slender tail than *G. cinerascens*, a character that becomes apparent when they are examined side by side.

The two species are genetically distinct, and this is what brought them to our attention. We had originally treated this as a new species, but a re-examination of the holotypes showed that they correspond to Rüppell's two species. The four COI sequences from the Red Sea specimens collected during the present study showed no substantial variation and formed a clade that was closely affiliated with a specimen from New South Wales, Australia, identified as *G. monochrous* (Bleeker), another uniformly colored species. Among four other species that were grouped with *G. hepaticus* and *G. monochrous* in a larger clade that received moderately high support were *Enchelycore schismatorhynchus* and an unidentified species from South Africa (*Gymnothorax* sp. 3) and two distinct lineages, both identified as *G. reevesi* (Richardson) by the respective sequence authors. It is unknown whether either *G. cinerascens* or *G. hepaticus* occurs outside the Red Sea. The plain brown *Gymnothorax* are confusing and need to be studied in more detail to sort them out.

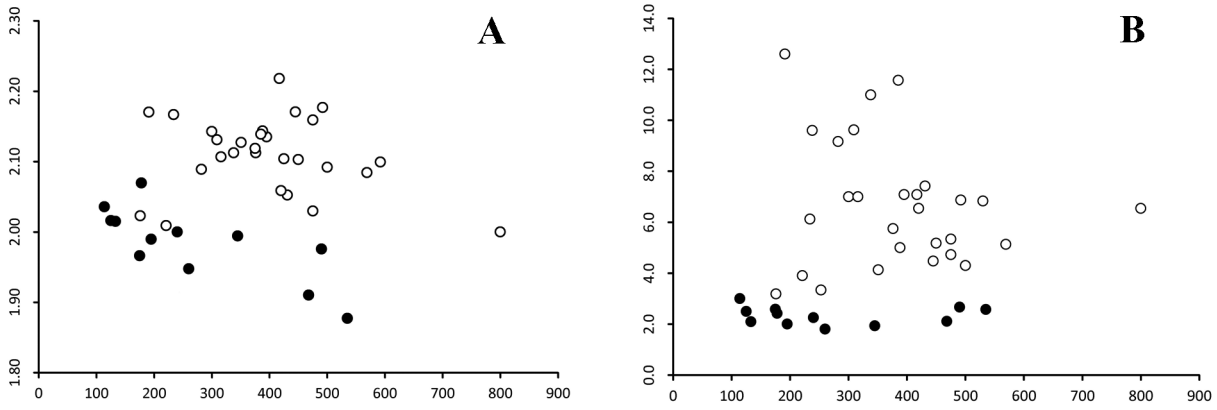


FIGURE 20. Relationship of two characters to TL. **A**: preanal distance to TL; **B**: ratio between distances "third intermaxillary tooth-tip of snout" and "third intermaxillary tooth-vertical at anterior margin of eye" to TL. Open circle- *G. cinerascens*, solid circle- *G. hepaticus*. Drawing by T.J. Alpermann.

Gymnothorax javanicus (Bleeker 1859)—Giant Moray

(Figure 21)

Muraena javanica Bleeker 1859: 347 (Patjitan, Java, Indonesia). Holotype (unique), BMNH 1867.11.28.214.—Klunzinger, 1871: 616.

Lycodontis javanicus: Dor 1984: 28.

Gymnothorax javanicus: Goren & Dor 1994: 7; Randall & Golani 1995: 861; Debelius 1998: 11, 12; Khalaf 2004: 36; Lieske & Myers 2004: 36; Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 21.

Red Sea material. ***Sudan***: BPBM 17901 (1, 156), Suakin Archipelago; SMF 7464 (1, 550), Sanganeb Atoll. ***Saudi Arabia***: KAUMM 398 [KAU13-206] (1, 680), Al Wajh; SMF 35386 [KAU13-355] (1, 230), Al Wajh; SMF 35812 [KAU12-1087] (1, 211), Al Lith; SMF 35813 [KAU13-202] (1, 610), Al Wajh; USNM 147424 (4, 312–605), Jeddah; USNM 147426 (1, 281), Jeddah. ***Eritrea***: USNM 312505 (1, 718), Massawa.

Comparative material. ***Indonesia***: BMNH 1867.11.28.214 (1, 718, holotype). ***French Polynesia***, Manua'e (Scilly) Atoll: USNM 435186 [SCIL-297] (1, 242). Gambier Is. USNM 438468 [GAM-646] (1, image only, specimen not retained).

Description. In TL: preanal length 2.0–2.2, predorsal length 7.9–10, head length 6.6–8.1, body depth at anus

16–24. In head length: snout length 5.6–6.5, eye diameter 9.3–13, upper-jaw length 2.5–2.9. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 5–7, preanal 60–61, total 137–141.

Body moderate to robust, the depth increasing with growth; anus at or slightly before midlength; dorsal-fin origin before gill opening. Jaws moderate, of equal length. Eye moderate, over middle of upper jaw. Anterior nostril tubular; posterior nostril with a raised rim, above or slightly behind anterior margin of eye.

Teeth smooth, slender and pointed or blade-like. Intermaxillary teeth in a single peripheral series, 4–5 on each side sometimes with a few much smaller teeth between; 2–3 median teeth. Maxillary teeth uniserial except in small specimens, which may have 1–3 larger inner teeth anteriorly, and about 13–15 smaller teeth in outer row. Dentary with 2–3 larger inner teeth anteriorly and about 10–20 smaller outer teeth. Vomerine teeth biserial anteriorly.

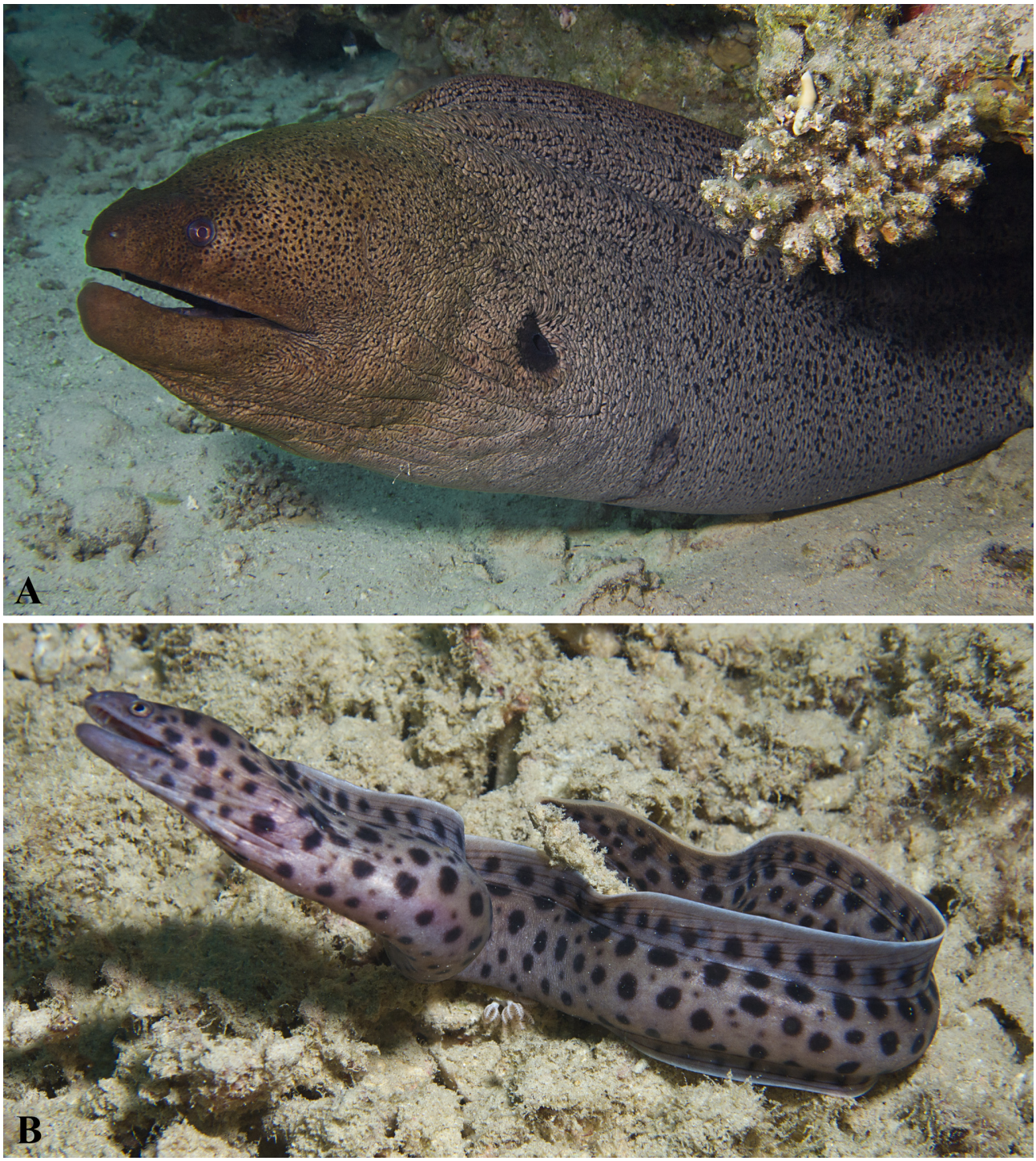


FIGURE 21. *Gymnothorax javanicus*. **A**: adult, Sharm el Moya, Egypt; **B**: SMF 35812 [KAU12-1087], juvenile, 211 mm TL, Al Lith, Saudi Arabia. Photos by S.V. Bogorodsky.

Color: body and fins brown, with small, darker brown or black markings consisting of subquadrate to irregular spots (those dorsally are larger), sometimes with a pale center, in approximately three irregular rows. Head usually darker than body. Small specimens have a lighter background color with broadly spaced, obvious, round spots, most of them larger than eye. Large specimens tend to be darker overall with smaller spots. Gill opening in a conspicuous dark spot. Iris brown.

Maximum size 2 m or greater.

Distribution and habitat. Widely distributed throughout the Indo-Pacific region from the Red Sea and east coast of Africa east to the Hawaiian Islands, Line Islands, and Pitcairn Islands, also reported from Costa Rica and Panama in the eastern Pacific. Common on coral reefs and rocky substrata, at depths of 0–46 m.

Remarks. This is the largest of all moray species in terms of weight. Adults can reach more than 2 m in length and weigh as much as 70 kg. Due to their large size and piscivorous habits, they can be a serious source of ciguatera poisoning and should not be eaten. Little geographic variation is evident from the morphology of the species. However, in the phylogenetic analysis two weakly diverging subclades were evident with comparatively little divergence within the two subclades (Fig. 48). However, the clades did not represent biogeographic subgroupings, as sequences from the Southern Pacific were present in both subclades. The sequence of a specimen from the Red Sea (SMF 35386) collected in the present study formed part of a subclade, in which another Indian Ocean sequence (from Madagascar) was included. This preliminary observation certainly is interesting and as more data become available, it would be worthwhile investigating the nature of the apparent genetic divergence among specimens of *G. javanicus* observed in this study. Concerning close affiliations at the species level, *G. javanicus* was included in one clade with *G. flavimarginatus* that received moderately high support from bootstrapped analyses in the present phylogeny.

Gymnothorax johnsoni (Smith 1962)—Johnson's Moray

(Figure 22)

Lycodontis johnsoni Smith 1962: 438, pl. 56 (figs. C–D) (Algoa Bay, South Africa, 40 fm [82 m]). Holotype, SAIAB 104.
Gymnothorax johnsoni: McCosker *et al*. 1993: 165; Baranes & Golani 1993: 302; Randall & Golani 1995: 861; Khalaf & Disi 1997: 39; Khalaf 2004: 36; Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 22.

Red Sea material. ***Israel***: BPBM 35744 (1, 650), Eilat; BPBM 18240 (1, 166), Gulf of Aqaba, Coral Island; HUJ 10432 (1, 310), Eilat; HUJ 17016 (1, 540), Eilat; HUJ 17017 (2, 810–865), Eilat. ***Egypt***: BPBM 18167 (1, 236), Dahab.

Comparative material. ***South Africa***: SAIAB 104 (1, 545, holotype). ***Mozambique***: SAIAB 5019 (1, 273, paratype). ***Somalia***: USNM 301970 (2, 235–413). ***Mauritius***: USNM 342128 (1, 105).

Description. In TL: preanal length 2.1–2.4, predorsal length 6.6–9.9, head length 6.6–8.1, body depth at anus 16–24. In head length: snout length 4.6–5.6, eye diameter 7.4–12, upper-jaw length 2.1–2.8. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 5, preanal 50–55, total 131–140.

Body moderately elongate, anus slightly before midlength, dorsal-fin origin before gill opening. Jaws slender, of equal length. Eye moderate, over middle of upper jaw. Anterior nostril tubular, rather long, reaching lip when depressed; posterior nostril elliptical, without a raised rim, above anterior margin of eye.

Teeth smooth, slender and pointed or blade-like. Intermaxillary teeth long and slender, in a single peripheral series, 3–6 on each side; 3 slender, depressible median teeth. Maxillary teeth uniserial except in small specimens, which may have 1–4 larger, inner teeth anteriorly; about 9–14 smaller outer teeth. Dentary with 3 larger inner teeth anteriorly on each side and about 15–20 smaller teeth in one row. Vomerine teeth uniserial.

Color: smaller individuals brown with medium-sized round pale spots, covering body and commencing on posterior part of head, larger and more widely spaced posteriorly; spots extending onto fins, those on posterior fourth of dorsal fin are elongate. Spots on body become more closely spaced and irregular with growth. Corner of mouth and throat grooves dark. Edge of orbit narrowly dark brown.

Maximum size at least 880 mm.

Distribution and habitat. Recorded from the east coast of Africa from Algoa Bay, Madagascar and Mascarene Islands to Kenya, Somalia and the Red Sea. Typically living in deep waters, the deepest record from 400 m off Eilat (Randall & Golani 1995). The holotype and paratype were collected from about 75 m; Baranes & Golani (1993)

reported three specimens from depths of 150–200 m, one of them (HUJ 14147) is largest known for species (880 mm TL). The shallowest records reported by Randall & Golani (1995) were from depths of 15 and 49 m, and the Mauritian specimen was collected at 11–13 m. All known records from the Red Sea are from the Gulf of Aqaba. McCosker *et al*. (1993) published the first record from the Red Sea.

Remarks. The specimen from Mauritius has distinctly fewer vertebrae than those from the African coast and the Red Sea (50 *vs*. 53–55 preanal, 131 *vs*. 137–140 total, respectively). It is also the smallest of the specimens examined, but no other obvious differences are evident. Böhlke & Smith (2002) noted that the overall appearance and the description of *Muraena stellifer* Richardson could suggest that it may be the senior synonym of *G. johnsoni* but may also be a junior synonym of *G. punctatus*, which also has white spots and a similar vertebral count. Later, Smith (2012) placed *M. stellifer* as *incertae sedis* because the holotype is in poor condition and cannot be identified. May be easily confused with the similar *G. punctatus* (see below). In the field surveys that were carried out during the present study, no specimens of *G. johnsoni* were collected. The two specimens for which COI data were available come from the Red Sea (Israel) and the southwestern Indian Ocean (South Africa). The latter sequence comes from a larva (BOLD entry DSLAG1244-11) that was originally assigned to *G. prionodon* Ogilby, but which was re-assigned here to *G. johnsoni* based on its genetic indistinctness (in COI) from the specimen from Israel. The fine-scale pattern of divergence among *G. johnsoni* and its closest relatives is not well resolved, but the species forms part of highly supported clade with a number of other species, including the new Red Sea species *Gymnothorax pharaonis* described in this study and the recently redescribed species *G. mucifer* Snyder (Huang *et al.* 2019).

FIGURE 22. *Gymnothorax johnsoni*, BPBM 35744, 650 mm TL, fresh specimen, Eilat, Israel. Photo by J.E. Randall.

Gymnothorax moluccensis (Bleeker 1864)—Molucca Moray
(Figure 23)

Priodonophis moluccensis Bleeker 1864: 48 (Ambon I., Molucca Is., Indonesia). Holotype (unique), BMNH 1867.11.28.227.
Gymnothorax moluccensis: Randall & Golani 1995: 863; Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 22.

Red Sea material. ***Yemen***: USNM 312236 (1, 241).

Comparative material. ***Indonesia***: BMNH 1867.11.28.227 (1, 399 [387], holotype). ***New Caledonia***: USNM 323536 (2, 140–163). ***Coral Sea, Chesterfield Bank***: BPBM 33592 (2, 277–366); ANSP 171494 (1, 347). ***Australia***: ANSP 144425 (1, 357).

Description. In TL: preanal length 1.8–2.0, predorsal length 6.7–9.0, head length 7.4–8.5, body depth at anus 18–32. In head length: snout length 5.6–6.9, eye diameter 10–14, upper-jaw length 2.8–3.0. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 6–8, preanal 58–63, total 130–135.

Body moderate; anus slightly behind midlength; dorsal-fin origin slightly before or slightly behind gill opening. Jaws moderate, of equal length. Eye moderate, over middle of upper jaw. Anterior nostril tubular; posterior nostril elliptical, with a slightly raised rim, above anterior margin of eye.

Teeth serrate, moderately stout, conical to compressed and blade-like. Intermaxillary teeth in a single peripheral series, 4–7 on each side; 1–2 median teeth. Maxillary teeth uniserial in larger specimens, biserial in smaller ones, which have 5 larger, inner teeth anteriorly; about 11–16 outer teeth. Dentary with 2–3 larger inner teeth anteriorly and about 11–16 smaller outer teeth. Vomerine teeth biserial.

Color: head and body medium brown, body and fins densely covered with very small pale spots, interspace between spots greater than spot diameter. Anterior nostril brown.

FIGURE 23. *Gymnothorax moluccensis*, BPBM 33592, 366 mm TL, fresh specimen, Chesterfield Bank, Coral Sea. Photo by J.E. Randall.

Maximum size at least 387 mm (holotype).

Distribution and habitat. This is a rare species known from only about a dozen specimens including the holotype. It was described from Indonesia (Moluccas Islands and East Timor) and has since been collected in the Coral Sea, off New Caledonia, Australia (Queensland) and in the Red Sea.

Remarks. The Red Sea specimen has slightly more predorsal (8) and fewer preanal (58) and total (130) vertebrae than those from the Pacific (6–7, 60–63, 131–138, respectively), but the difference is slight, and the sample size is small. The holotype is a faded mottled brown color, but all the others are brown with small pale spots. No specimens of *G. moluccensis* were collected during the field surveys of the present study, but two sequences were available from specimens collected in Western Australia. The phylogeny (Fig. 48) shows that the species is closest related to a species identified as *G. neglectus* Tanaka. The two species are placed in a well-supported clade with another species that could not be assigned to any described species of the genus by the first author (*Gymnothorax* sp. from Marquesas Islands).

Gymnothorax nudivomer (Günther 1867)—Yellowmouth Moray
(Figure 24)

Muraena nudivomer Günther in Playfair & Günther 1867: 127, pl. 18 (Zanzibar). Lectotype, BMNH 1867.3.9.48, designated by Günther 1870: 104.
Lycodontis cf. *nudivomer*: Ben Tuvia & Steinitz 1952: 4.
Gymnothorax nudivomer: Fowler & Steinitz 1956: 271; Goren & Dor 1994: 7; Randall & Golani 1995: 864; Khalaf & Disi 1997: 40; Lieske & Myers 2004: 34; Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 22.
Lycodontis nudivomer: Smith 1962: 438.

Red Sea material. ***Israel***: BPBM 18286 (1, 560), Eilat; HUJ 15178 (8, 202–562), Eilat; HUJ 15182 (2, 460–675), Eilat; SMF 4523 (2, 600–715), Eilat. ***Egypt***: BPBM 13891 (1, 442), Taba; HUJ 17023 (1, 676), Ras Burka; USNM 191670 (1, 312); USNM 312753 (1, 480), El Himeira.

Comparative material. ***Mauritius***: MCZ 5912 (1, 768, holotype of *Gymnothorax insignis* Seale). ***Hawaii***: USNM 50869 (1, 860, holotype of *Gymnothorax xanthostomus* Snyder).

Description. In TL: preanal length 2.0–2.3, predorsal length 9.4–11, head length 7.4–8.5, body depth at anus 15–19. In head length: snout length 5.1–5.8, eye diameter 9.0–14, upper-jaw length 2.6–3.1. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 3–4, preanal 52–53, total 126–139.

Body moderate; anus slightly behind midlength; dorsal-fin origin well before gill opening. Jaws moderately short, of equal length or lower jaw slightly protruding. Eye moderate, over middle of upper jaw. Anterior nostril tubular, short; posterior nostril elliptical, with a slightly raised rim, above anterior margin of eye.

Teeth uniserial, serrate, moderately stout and pointed, most compressed and blade-like. Intermaxillary teeth in a single peripheral series, 6–7 on each side, increasing in size posteriorly; 1–2 median teeth. Maxillary teeth uniserial, about 7–11. Dentary with 14–21 teeth, largest ones anteriorly. Vomerine teeth small, in a single short series, not obvious, apparently absent in large adults.

Color: head and body light to medium brown becoming darker posteriorly, covered with ocellated white or bluish white spots, increasing in size posteriorly. Gill opening yellow within a large black blotch. White spots on dorsal and anal fins sometimes joined to form a continuous white margin. Inside of mouth yellow in life. Eye pale with black bar.

Maximum size about 1 m.

Distribution and habitat. Widely distributed in the Indo-Pacific from East Africa and the Red Sea to Hawaiian Islands and French Polynesia, primarily at depths of 30–271 m, occasionally shallower. Usually seen with its open distinctive yellow mouth.

Remarks. There appears to be some geographic variation in the number of vertebrae. Four specimens from Hawaiian Islands have 137–139, two specimens from Mauritius and the Comoros have 132–133, and four specimens from the Red Sea have 134–135 (Randall & Golani 1995, plus our own observations). Castle & McCosker (1986: 171) reported 126–129, without giving the locality but presumably from the East African coast. Specimens from the Red Sea apparently have fewer and smaller white spots on the body posteriorly (Randall 1983). Randall & Golani (1995) reported that this species is commonly seen at depths of 15 m or less in the northern Red Sea; the second author confirms this. Still, no specimens of *G. nudivomer* were collected during the field surveys of the present study, but one sequence was available from a specimen collected in the southwestern Indian Ocean (South Africa). *Gymnothorax elegans* is the next closely related species according to the present phylogeny (Fig. 48).

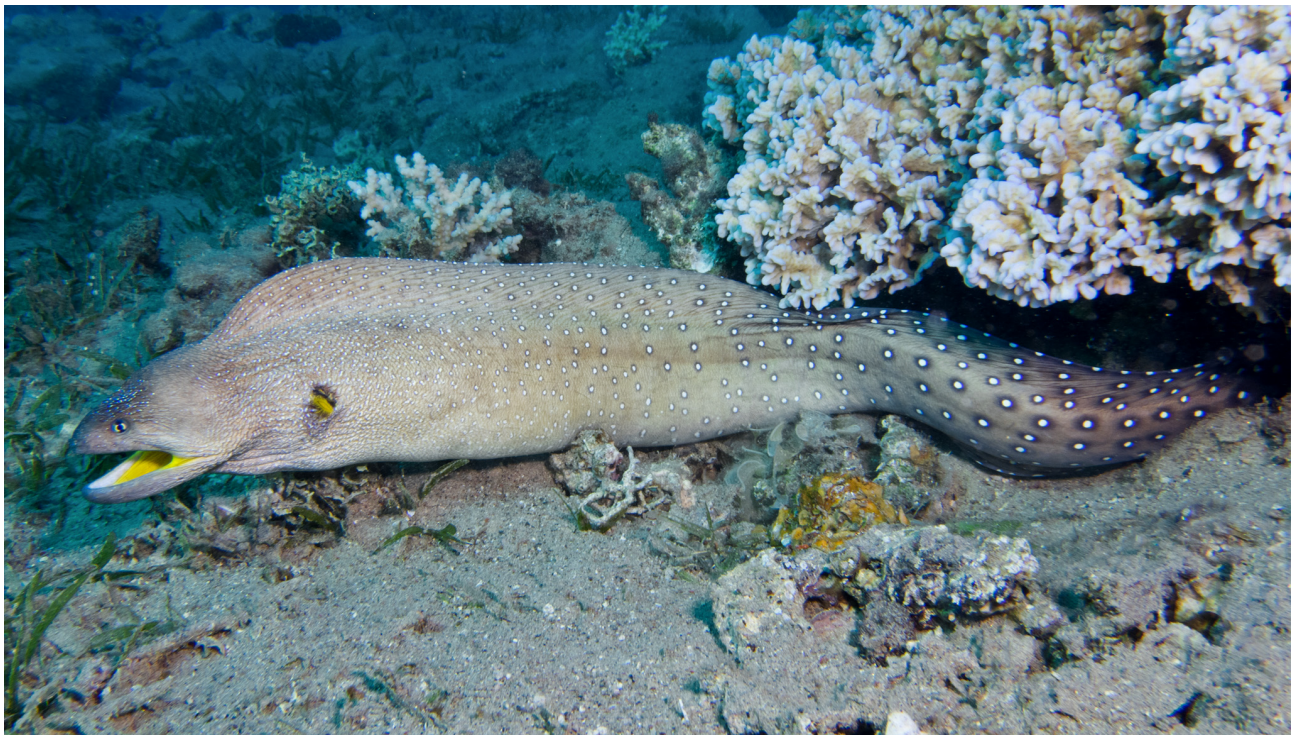


FIGURE 24. *Gymnothorax nudivomer*, Dahab, Egypt. Photo by S.V. Bogorodsky.

Gymnothorax pharaonis n. sp.—Pharaoh's Moray
(Figures 25–29)

?*Muraena undulata*: Klunzinger 1871: 615 (Quseir, Egypt).
?*Gymnothorax meleagris* (non Shaw & Nodder): Fowler & Steinitz 1956: 270 (Eilat).
Gymnothorax undulatus (non Lacepède): Randall & Golani 1995 (in part, Pl. 1F, Fig. 6).

Holotype. SMF 35814 [KAU13-614] (322), Red Sea, Saudi Arabia, Al Khoraybah, Yabua Island, isolated coral block on slope, 27°47'24.66" N, 35°07'48.00" E , 14–16 m, 23 Jun. 2013, S.V. Bogorodsky.

Paratypes. ***Israel***: BPBM 31848 (1, 475), Gulf of Aqaba, Eilat, North Beach, mooring, 7 m, 11 Nov. 1986, J.E. Randall. ***Egypt***: BPBM 18265 (2, 270–284), S end of Sinai Peninsula, Sharm-el-Moya, reef, 15 m, 21 Sep 1974, J.E. Randall and A. Levy; BPBM 19805 (1, 331), Ras Muhammad, S tip of Sinai Peninsula, reef front in 4–6 m, 26 Oct. 1975, J.E. Randall *et al*.; BPBM 20825 (1, 277), Gulf of Aqaba, 7 km S of Nuweiba, A. Ben-Tuvia, 3 Aug. 1976; USNM 262775 (1, 305 mm TL), NW coast Gulf of Aqaba, Bay at El Himeira, 0–18 m, 16 July 1969, V.G. Springer *et al*.; USNM 312604 (6, 133–380), Gulf of Aqaba, Bay Between Marsa Mokrakh and El Himeira, NW Coast, 0–3 m, 15 July 1969, V.G. Springer *et al*.; USNM 312605 (4, 187–228), NW Gulf of Aqaba, Ras Burqa, 9–15 m, 21 July 1969, V.G. Springer *et al*.; USNM 312609 (3, 303–419), Strait of Jubal S end of Sinai Peninsula at Ras Muhammad, 0–9 m, 26 Sep 1969, V.G. Springer *et al*.; USNM 405385 (4, 233–260), NW coast of Gulf of Aqaba, reef near road at Marsa Muqabila, 0–2 m, 29 July 1969, V.G. Springer *et al*.; USNM 410185 (7, 123–227), same data as USNM 312604; USNM 410188 (4, 223–299), same data as USNM 262775; USNM 410628 (1, 310), Gulf of Aqaba, Dahab, Lighthouse, 18 m, 25 Nov. 2011, S.V. Bogorodsky. ***Sudan***: BPBM 19733 (1, 156), 1 mile N of Port Sudan, reef flat in 0.5–1.0 m, 9 Oct 1975, J.E. Randall. ***Saudi Arabia***: KAUMM 400 [KAU12-1059] (1, 225), Al Lith, 8 Mar. 2012, T.J. Alpermann & S.V. Bogorodsky; KAUMM 401 [KAU13-286] (1, 145), 50 km south of Al Wajh, fringing reef of seaward reef, 8–12 m, 13 Jun. 2013; KAUMM 402 [KAU13-615] (1, 224), same data as holotype; SMF 33617 (1, 49), Al Wajh, Rykhah Is, 10 Apr. 2011, S.V. Bogorodsky; SMF 33618 (1, 78), Al Lith, 30 Mar. 2011, T.J. Alpermann & S.V. Bogorodsky; SMF 35815 [KAU12-1028] (1, 182), Al Lith, 9 m, 7 Mar. 2012, T.J. Alpermann & S.V. Bogorodsky; SMF 35816 [KAU12-1060] (1, 208), Al Lith, 8 Mar. 2012, T.J. Alpermann & S.V. Bogorodsky.

Non-type material (detailed counts and measurements not taken). KAUMM 403 [KAU14-818] (1, 125), Al

Lith, 6–8 m, 16 Nov 2014, T.J. Alpermann & S.V. Bogorodsky; KAUMM 404 [KAU14-1011] (1, 246), Al Lith, 8–10 m, 19 Nov 2014, T.J. Alpermann & S.V. Bogorodsky; SMF 35817 [KAU14-928] (1, 213), Al Lith, 6–9 m, 18 Nov. 2014, T.J. Alpermann & S.V. Bogorodsky; USNM 312606 (4, 62–140), Egypt, NW Coast, Gulf of Aqaba, about 1 Mile North of Ras Burqa, 21 July 1969; USNM 312607 (12, 49–160), Egypt, just N of Ras Burqa, Gulf of Aqaba, NW Coast, 23 July 1969, V. G. Springer *et al*.; USNM 313223 (9, 64–96), Egypt, Gulf of Aqaba, Bay at El Himeira, 8 Sept. 1969, V. G. Springer *et al*.; USNM 410183 (28, 50–192), same data as USNM 262775; USNM 410184 (14, 56–265), same data as USNM 312604; USNM 410186 (17, 77–280), same data as USNM 312609; USNM 410187 (28, 75–225), same data as USNM 405385; USNM 410189 (1, 227), same data as USNM 262775 (cleared and stained).

Comparative material. *Gymnothorax margaritophorus* Bleeker. ***Indonesia***: BMNH 1867.11.28.268 (1, 207, holotype). ***Samoa***: USNM 51713 (1, 253, holotype of *Gymnothorax talofa* Jordan & Starks). ***French Polynesia***, Moorea: MNHN 2008-0437 (1, 72); MNHN 2008-0438 (1, 72); MNHN 2008-0439 (1, 63); MNHN 2008-0442 (1, 290); MNHN 2008-0443 (1, 290); MNHN 2008-0444 (1, 219); MNHN 2008-0446 (1, 57). Gambier Is.: USNM 401788 [GAM-412] (1, 457). Manua'e (Scilly) I.: USNM 435145 [SCIL-256] (1, 168).

Diagnosis. Small to medium-size moray with slender head and jaws. Teeth sharp, slender, and smooth; intermaxillary teeth in one peripheral and one medial series; maxillary teeth in two rows, an outer row of 14–20 small teeth, and an inner row of 0–6 large, depressible teeth; dentary teeth in one row, with two large fixed teeth at anterior end, followed by a single row of 15–20 small teeth, and one large, depressible tooth just behind the large anterior teeth. Color brown with irregular dendritic pale markings, not interconnected or chain-like; oblique, conspicuous, parallel streaks present in dorsal fin (on tail). Total vertebrae 123–128.

Description (data for the holotype first, for paratypes in parentheses). In TL: preanal length 2.3 (2.2–2.4), predorsal length 9.0 (7.7–10), head length 7.8 (7.0–8.4), body depth at gill opening 19 (15–28), depth at anus 23 (17–28). In head length: snout length 5.2 (4.9–7.1), eye diameter 8.7 (7.6–11), upper-jaw length 2.3 (2.3–3.1). Predorsal vertebrae 8 (5–8), preanal vertebrae 48 (47–50), total vertebrae 125 (123–128).

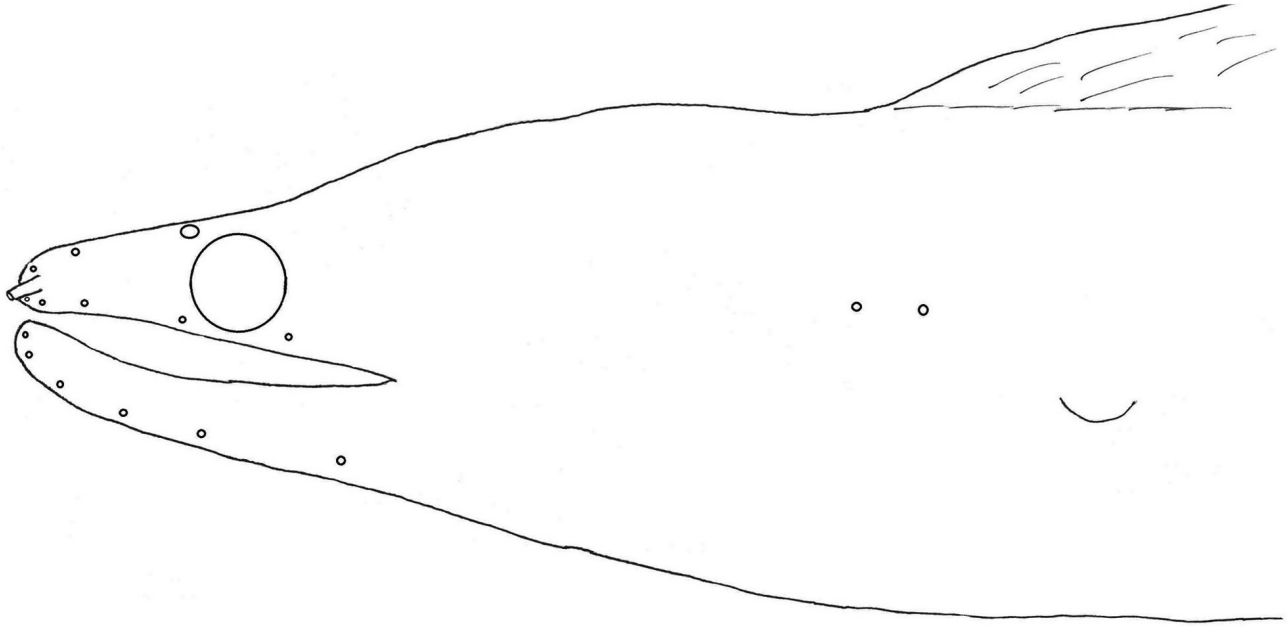


FIGURE 25. *Gymnothorax pharaonis* **n. sp.**, drawing of the head showing cephalic sensory system. Drawing by D.G. Smith.

A small to medium-sized moray eel, moderately elongate, with the anus slightly anterior to midlength. Dorsal and anal fins continuous with caudal fin, anal fin beginning immediately behind anus, dorsal fin beginning anterior to gill opening. Jaws and snout moderately slender, edges usually straight, concealing teeth when closed, but sometimes slightly arched in larger specimens; upper and lower jaws nearly equal in length. Gill opening small and pore-like, on side of head slightly below lateral midline. Anterior nostril tubular, relatively long, reaching slightly beyond edge of lip when depressed. Posterior nostril a broadly oval opening, without a conspicuous raised rim, above anterior part of eye, at a point where a horizontal line drawn from dorsal edge of eye would meet a vertical line drawn from anterior edge of eye.

Lateral line with two small, inconspicuous pores at anterior end of canal, approximately under dorsal-fin origin; second pore closer to first pore than to gill opening (Fig. 25). Preoperculo-mandibular canal with six pores, all of them along lower jaw: the first and smallest located at the anterior tip of jaw, the second below and behind that, the remaining four pores extending in a line posteriorly to a point slightly anterior to rictus. Infraorbital canal with four pores: the first slightly below and behind base of anterior nostril, the second about a third of the way to eye, the third just anterior to eye, and the fourth under posterior margin of eye. Supraorbital series with three pores: the first and smallest at tip of snout just above edge of lip, the second slightly above anterior edge of base of anterior nostril, the third on top of snout directly above second infraorbital pore. No pores in supratemporal canal.

Teeth slender, sharp, and smooth, without any serrations (Fig. 26). Intermaxillary teeth large, conical, sharply pointed; peripheral series with about 8–14 teeth, the anteriormost teeth smallest, increasing in size posteriorly; two or three median teeth, long, extremely sharp and depressible. Maxillary teeth in one or two rows: the inner row with 0–6 long, sharp, widely separated, depressible teeth at anterior end, the outer row with about 13–20 much smaller, fixed, triangular, recurved teeth, smallest at anterior end of row, increasing in size posteriorly to a point approximately under eye, then decreasing in size again posteriorly. Lower jaw with two large, fixed teeth at anterior end, followed by approximately 15–25 much smaller, triangular, recurved teeth; directly behind the two large anterior teeth is an even larger, depressible tooth just inside the row of smaller teeth. Approximately 3–9 very small vomerine teeth, in a single row, partly hidden in the folds of skin in roof of mouth.

Color: in adults, ground color medium to dark brown with irregular, dendritic, pale markings, variable in size and form (Figs. 27 & 28). The most common form is short, broadly linear, vermicular lines or spots, sometimes expanded into snowflake-like blotches, but not interconnected or reticulated. On tail, the spots often line up to form oblique streaks extending onto dorsal fin. Markings sometimes become smaller and more closely spaced anteriorly. Fins with a narrow white edge, but this often not conspicuous. Grooves on throat as dark streaks. An inconspicuous pale stripe usually present on dorsal midline of snout. Corner of mouth dark. Posterior nostril and pores usually edged in dark brown. Juveniles uniform brown with lower jaw and throat pale (Fig. 29).

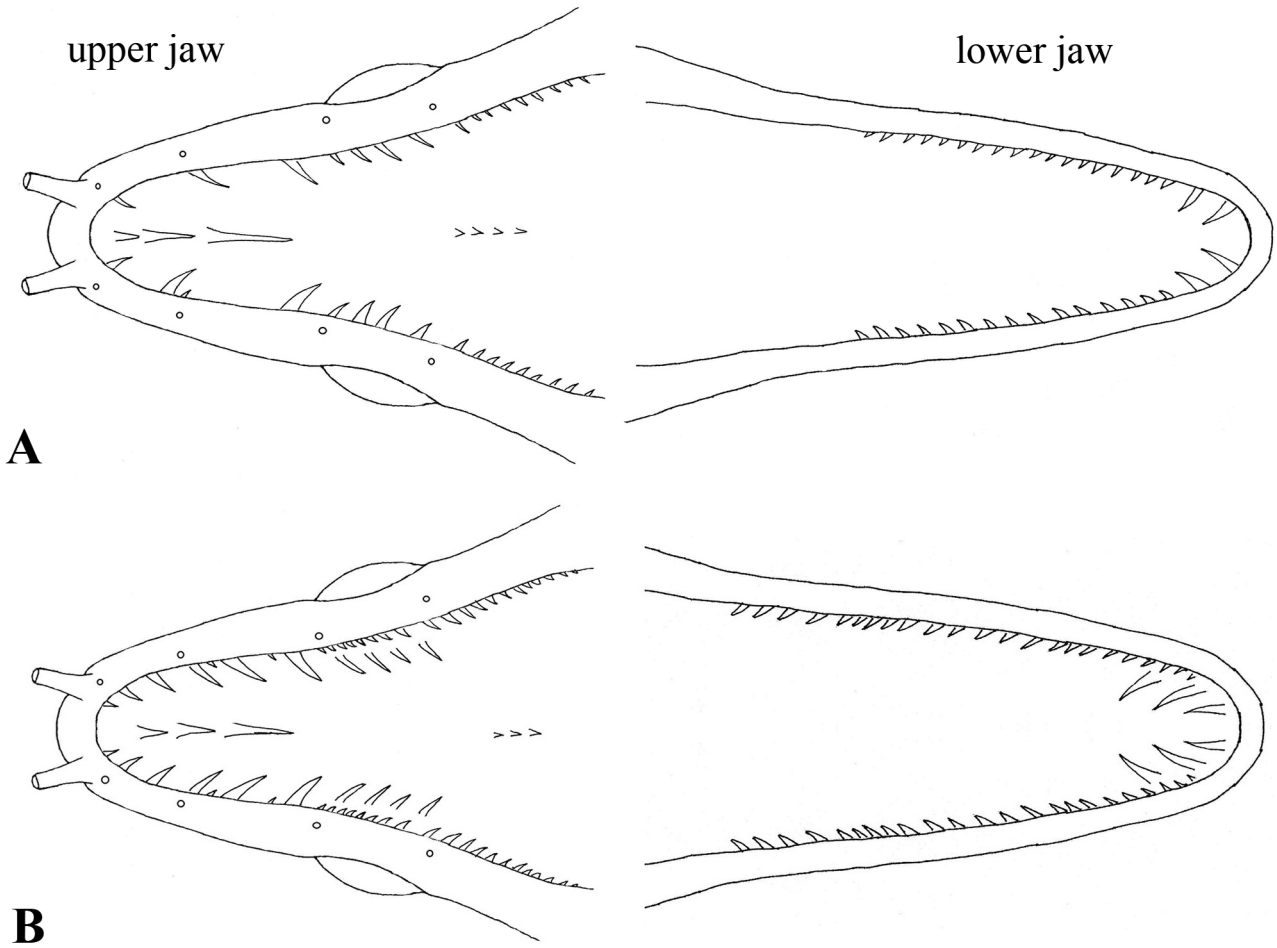


FIGURE 26. *Gymnothorax pharaonis* **n. sp.**, drawing of the dentition. **A**: male; **B**: female. Drawing by D.G. Smith.

Size and development. This is a relatively small species, the largest specimen examined was 475 mm TL, but only one other specimen was greater than 400 mm and only three over 300 mm. Females with large eggs were found in specimens as small as 223 mm. Males appear to mature at larger sizes than females; two that were clearly males were among the largest specimens examined, 299 and 419 mm. Females were measured at 380, 325, and 305 mm. There is some evidence of sexual dimorphism in dentition. The two males mentioned above lack the inner maxillary teeth; they also have fewer dentary teeth (14 *vs*. 18–26 in females).

Small juveniles of this species are uniform brown with a conspicuous white lower jaw (Fig. 29A). At about 50 mm, pale spots begin to develop behind the head. As the eel grows, the spots progress posteriorly and become larger and more conspicuous, eventually assuming the dendritic pattern characteristic of adults (Fig. 29B). With growth, the pale lower jaw becomes less distinct.

Variation. The specimens collected and examined were all brown with pale markings. The relative extent of pale and dark areas varies considerably among individuals, however. In most cases, the dark areas are more extensive, giving the fish a brown appearance, but occasionally the pale areas prevail. In such cases, the eel may appear pale with brown markings. In most specimens, the pale and dark markings are relatively large, but in others the markings are smaller and more scattered, giving a vermiculated appearance. In some specimens, the markings are larger posteriorly and smaller anteriorly. In larger specimens, the jaws can become arched, leaving the teeth visible when the mouth is closed. This approaches the condition seen in *Enchelycore*, but the dentition of *Enchelycore* is quite different (Smith *et al*. 2008: 68).

Distribution and habitat. Known from the Red Sea, where it is common in shallow water, but also collected by the second author from Socotra Island outside the Gulf of Aden (Zajonz *et al*. 2019, listed as *G*. cf *chilospilus* Bleeker 1864). Typical habitats are crevices and shelters of fringing seaward reefs, observed from depths of 2–30 m. May be seen out of shelter at night only.

FIGURE 27. *Gymnothorax pharaonis* **n. sp.**, SMF 35814 [KAU13-614], holotype, 322 mm TL, Yabua I., Al Khoraybah, Saudi Arabia. Photo by S.V. Bogorodsky.

FIGURE 28. *Gymnothorax pharaonis* **n. sp. A**: KAUMM 400 [KAU12-1059], paratype, 225 mm TL, Al Lith, Saudi Arabia; **B**: Ras Abu Galum, Egypt. Photos by S.V. Bogorodsky.

Etymology. Named for the pharaohs, the rulers of ancient Egypt, whose realm included the Red Sea. Referring also to the regal appearance of this handsomely marked fish.

Remarks. This species has been confused with *Gymnothorax undulatus*. Like *G. pharaonis*, *G. undulatus* has pale markings on a dark background, but in *G. undulatus* the markings are generally interconnected in a reticulated or chain-like pattern, whereas in *G. pharaonis* the markings are separate. At larger sizes, *G. undulatus* has a distinct yellowish-green color on the head in life, which is never found in *G. pharaonis*. *Gymnothorax undulatus* is a much larger species, growing to well over 1 m in length. Mature *G. pharaonis* can be found at lengths less than 300 mm, a size at which *G. undulatus* is still immature. The two species also differ in the number of vertebrae, 122–128 in

G. pharaonis vs. 126–138 in *G. undulatus*. *Gymnothorax pharaonis* also resembles *G. baranesi*, but in that species the pale markings on the body are more like snowflakes or rosettes. On the tail, the markings on *G. baranesi* are in the form of discrete spots rather than the oblique streaks found in *G. pharaonis*. In addition, *G. baranesi* has more vertebrae, 137–142. *Gymnothorax pharaonis* most closely resembles and is closest genetically (Fig. 48) to *G. margaritophorus* Bleeker, which is widely distributed in the Indo-Pacific but does not occur in the Red Sea. The latter is also a small species, brown with pale markings and a pale stripe on the top of the snout. It has horizontal dark streaks behind the eye, however, which are lacking in *G. pharaonis*, and it has more vertebrae (127–134). Pale individuals (e. g. from Dahab, Fig. 28B) may be confused with *G. chilospilus* Bleeker, but the latter species almost always has a distinctive pale spot at the corner of the lower jaw, which is lacking or not obvious in *G. pharaonis*. As in *G. griseus* and *G. thyrsoideus*, no reciprocal monophyly has yet evolved in the species pair *G. pharaonis* and *G. margaritophorus*. The closest relative to this pair of sibling species cannot be identified with high confidence from the present phylogeny, however, it is evident that the two species form part of a highly supported group of taxa to which another Red Sea species belongs, *G. johnsoni* (Fig. 48).

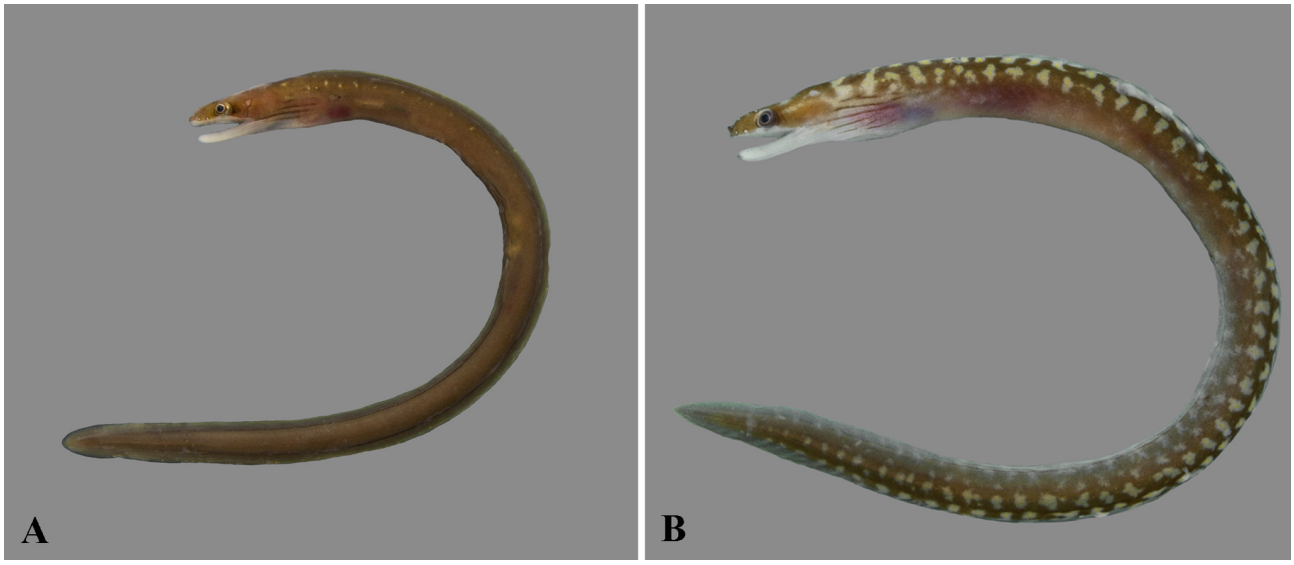


FIGURE 29. *Gymnothorax pharaonis* **n. sp.**, juveniles. A: SMF 33617, 49 mm TL, Al Wajh, Rykhah Is, Saudi Arabia; B: SMF 33618, 78 mm TL, Al Lith, Saudi Arabia. Photos by S.V. Bogorodsky.

Gymnothorax phasmatodes (Smith 1962)—Phantom Moray
(Figure 30)

Lycodontis phasmatodes Smith 1962: 436, pl. 53 (figs B, C & I) (Inhaca I., Mozambique). Holotype, SAIAB 108.
Red Sea material. None.

Comparative material. ***Mozambique***: SAIAB 108 (holotype, 447). ***Mauritius***: USNM 342265 (1, 245). ***Indonesia***: USNM 210916 (2, 255–350). ***Philippines***: USNM 378712 (1, 317). ***Fiji***: USNM 245633 (1, 335).

Description. In TL: preanal length 1.9–2.0, predorsal length 13–14, head length 10–11, body depth at anus 31–37. In head length: snout length 5.1–6.7, eye diameter 7.6–12, upper-jaw length 2.9–3.6. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 5–6, preanal 72–80, total 164–167.

Body elongate; anus at or slightly behind midlength; dorsal-fin origin before gill opening. Jaws moderate, of equal length or lower jaw slightly protruding. Eye moderate, over middle of upper jaw. Anterior nostril tubular; posterior nostril elliptical, without a noticeably raised rim, above anterior margin of eye.

Teeth uniserial, smooth, conical to slightly triangular. Intermaxillary teeth in a single peripheral series, 3–6 on each side; 3 median teeth, slender and depressible. Maxillary teeth uniserial, about 5–10. Dentary with 9–14 teeth, largest ones anteriorly. Vomerine teeth small, in a single short series, 2–9.

Color: head and body light tan or gray, head slightly darker, head pores in pale spots. Fins with a conspicuous light blue edge in life, becoming white in preservative. Iris white; anterior nostril pale.

Maximum size about 500 mm.

Distribution and habitat. From the east coast of Africa, the Red Sea, and the islands of the western Indian Ocean to the Philippines, Indonesia, and at least as far east as Fiji; the closest record to the Red Sea is from the Arabian Gulf, Jana Island (Randall 1995). In shallow water on sand and rocky bottom, reported from depth less than 2 m from reef flat to depth of 34 m.

Remarks. The first record for the Red Sea is from a photograph taken at Jeddah, reproduced in Fig. 25. There seems to be little geographical variation; two specimens from the western Indian Ocean have 164–166 vertebrae, two from the Philippines and Indonesia have 164–165, and one from Fiji has 167. No other differences are apparent. Unfortunately, this species could not be included in the present phylogeny (Fig. 48) as no specimens were collected during field survey carried out in this study nor were any COI sequence data available.

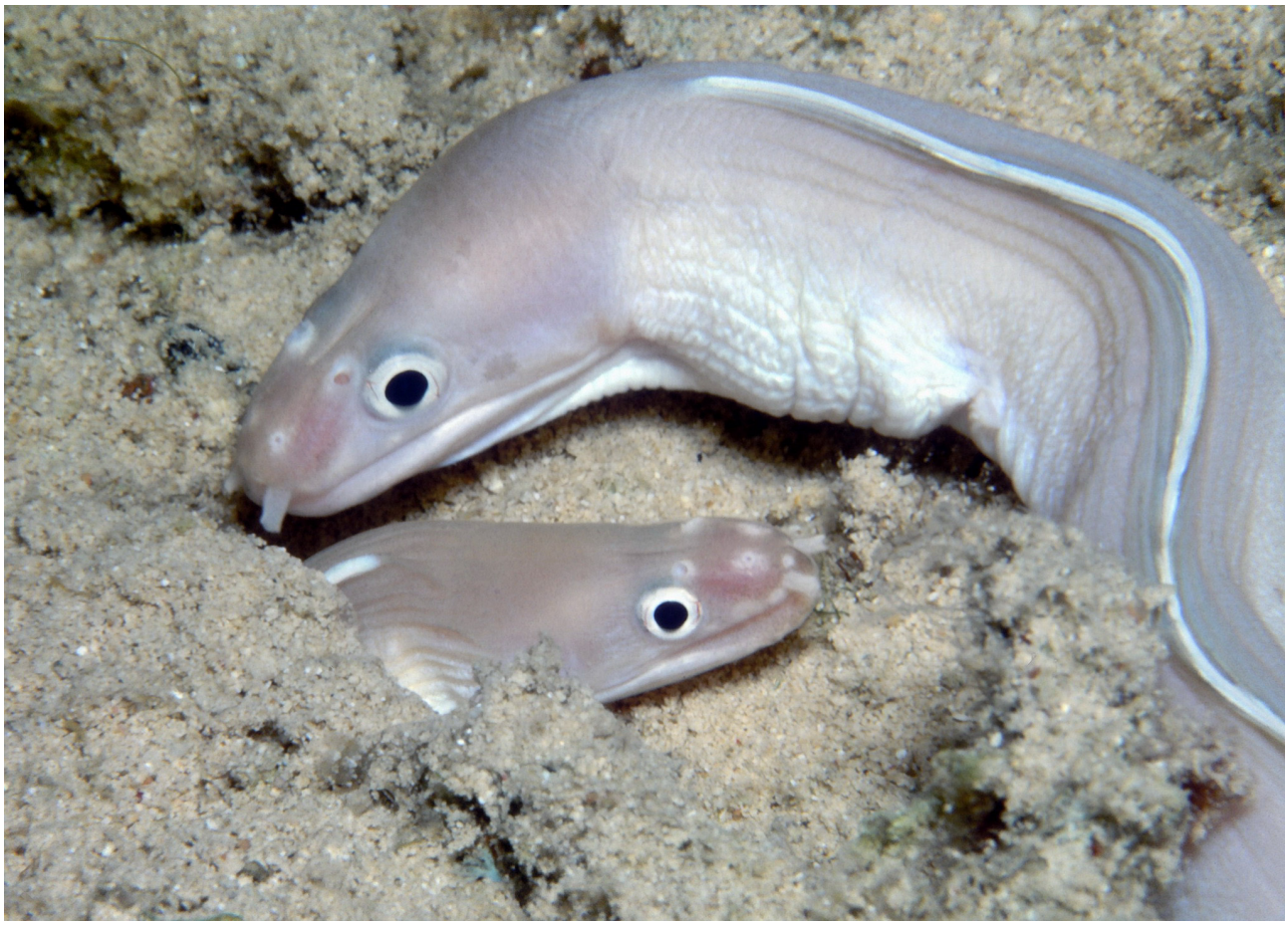


FIGURE 30. *Gymnothorax phasmatodes*, Obhur, Jeddah, Saudi Arabia. Photo by K. Metcalfe.

Gymnothorax pictus (Ahl 1789)—Peppered Moray

(Figure 31)

Muraena picta Ahl 1789: 8, pl. 2 (right fig.) (East Indies). No types known.
Siderea picta: Dor 1984: 30; Goren & Dor 1994: 7; Randall & Golani 1995: 870.
Gymnothorax pictus: Tortonese 1937: 166; Tortonese 1983: 106; Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 22.

Red Sea material. ***Red Sea***: USNM 47605 (1, 494); USNM 47606 (2, 287–300); USNM 47607 (2, 293–347); USNM 47608 (2, 298–335); USNM 47609 (2, 243–250). ***Israel***: HUJ 11428 (1, 410), Eilat.

Comparative material. ***Aldabra***: USNM 264173 (1, 124); USNM 289752 (1, 130); USNM 312707 (2, 150–201). ***Chagos Archipelago***: USNM 312706 (2, 425–430). ***Indonesia***: BMNH.1846.2.16.111 (1, 454, holotype of *Muraena lita* Richardson); BMNH 1867.11.28.286 (1, 518, holotype of *Muraena pfeifferi* Bleeker); BMNH 1867.11.28.332 (1, 110, holotype of *Muraena polyophthalmus* Bleeker). ***Australia***: MNHN B.2466 (1, 195, holotype of *Muraena elegantissima* Kaup); BMNH 1846.9.11.16 (1, 640, holotype of *Muraena siderea* Richardson).

Mariana Is.: MNHN B.3142 (1, 630, holotype of *Muraena variegata* Quoy & Gaimard). ***Hawaii***: USNM 50618 (1, 240, holotype of *Gymnothorax hilonis* Jordan & Evermann). ***Galapagos Is.***: AMNH 255216 (1, 858+, holotype of *Muraena thomsoni* Borodin). ***Locality unknown***: MNHN B.3142 (1, 252, holotype of *Muraena pantherina* Lacepède).

Description. In TL: preanal length 1.8–2.2, predorsal length 6.6–8.8, head length 6.8–8.3, body depth at anus 13–29. In head length: snout length 5.3–7.5, eye diameter 8.6–16, upper-jaw length 2.6–3.7. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 6–10, preanal 53–62, total 113–135.

Body moderate; anus near midlength; dorsal-fin origin above gill opening. Jaws moderate, of equal length. Eye moderate, over middle of upper jaw. Anterior nostril tubular, short; posterior nostril above anterior margin of eye.

Teeth smooth, moderate in length and pointed. Intermaxillary teeth in a single peripheral series, 6–7 on each side, conical, increasing in size posteriorly; 1–3 median teeth. Maxillary teeth usually uniserial, about 9–13, smaller specimens sometimes with a few larger inner teeth anteriorly. Dentary with 1–4 larger inner teeth anteriorly, about 13–20 smaller outer teeth. Vomerine teeth biserial, diverging anteriorly in large specimens.

Color: variable, usually light tan or gray, usually finely speckled with small dark spots, often grouped to form irregular blotches, sometimes with pale centers, sometimes with irregular edges forming a snowflake-like pattern. Some specimens, like the one described as *Gymnothorax hilonis* from the Hawaiian Islands, are dark with large spots and narrow interspaces. Iris yellowish white with irregular black circle at margin.

Maximum size about 1.2 m.

Distribution and habitat. Widely distributed in the Indo-Pacific from East Africa to Central America, mainly in shallow water on reef flats and rocky shores to at least 20 m deep. It seems uncommon in the Red Sea, having been collected only on a few occasions. Randall & Golani (1995: 871) listed one specimen. The USNM specimens were collected many years ago. More recent expeditions have failed to collect it, although it has been photographed.

FIGURE 31. *Gymnothorax pictus*, Gulf of Oman, Oman. Photo by A. Nikolaev.

Remarks. It has not been noted previously, but specimens from the Red Sea have much lower vertebral counts than those from elsewhere. Nine specimens from the Red Sea have 53–56 preanal and 113–117 total vertebrae. The 13 specimens examined from Aldabra to Hawaiian Islands have 56–60 preanal and 128–135 total vertebrae. Böhlke & Randall (2000: 247) reported similar numbers for 37 specimens, although they did not give the collection localities. Insufficient attention has been paid to geographic variation in moray eels, so we do not know what recurring patterns might be found in this group. We have no genetic samples from the Red Sea, and no COI sequence data

from Red Sea specimens of the species were available from other sources. Hence, we cannot contribute to answering the question, if the observed morphological differentiation within the species is accompanied by genetic divergence in geographically separated populations of the species. In the present phylogeny, *Gymnothorax pictus* is placed with high support in a joint clade with specimens from several other species that were identified as *Echidna nebulosa*, *E. xanthospilos* and *G. pseudothyrsoideus* by the respective sequence authors (Fig. 48).

Gymnothorax pictus often has been classified in the genus *Siderea*, whose type species is *Muraena siderea* Richardson, a junior synonym of the former, together with *S. grisea* and others. Böhlke & Randall (2000), however, placed *Siderea* in synonymy with *Gymnothorax* due to the lack of distinguishing characters.

Gymnothorax pindae Smith 1962—Pinda Moray
(Figure 32)

Gymnothorax pindae Smith 1962: 430, pl. 55 (fig. D) (Pinda, Mozambique). Holotype (unique), SAIAB 105.—Randall & Golani 1995: 865; Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 22.

Red Sea material. ***Red Sea***: USNM 191669 (1, 251). ***Egypt***: USNM 312698 (4, 145–210), El Himeira, Gulf of Aqaba. ***Saudi Arabia***: KAUMM 405 [KAU12-1088] (1, 127), Al Lith; KAUMM 406 [KAU13-489] (1, 222), Al Wajh; KAUMM 407 [KAU13-596] (1, 104), Duba; KAUMM 408 (KAU14-993), (1, 162), Al Lith; KAUMM 414 [KAU13-692] (1, 103), Jeddah, Obhur; SMF 35169 (1, 340), Duba; SMF 35398 [KAU13-352] (1, 323), Al Wajh; SMF 35818 [KAU12-1027] (1, 210), Al Lith; SMF 35819 [KAU13-447] (1, 304), Al Wajh; SMF 35820 [KAU13-595] (1, 198), Duba; SMF 35827 [KAU13-693] (1, 252), Jeddah, Obhur.

Comparative material. ***Mauritius***: USNM 312725 (1, 99). ***Philippines***: USNM 315563 (1, 144). ***Vanuatu***: USNM 363336 (2, 50–146); USNM 363689 (1, 258). ***French Polynesia***, Mururoa: USNM 408155 (1, 153). Manua'e (Scilly) I.: USNM 435224 [SCIL-335] (1, 114). ***Hawaii***: BPBM 37447 (1, 285).

Description. In TL: preanal length 2.2–2.5, predorsal length 6.6–11, head length 6.5–8.3, body depth at anus 15–24. In head length: snout length 4.1–6.8, eye diameter 6.8–11, upper-jaw length 2.2–3.2. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 5–6 (1 specimen with 10), preanal 42–44, total 118–123.

Body moderately stout; anus before midlength; dorsal-fin origin before gill opening. Dorsal and anal fins high, dorsal fin height up to half body depth. Snout relatively short and tapering, jaws of equal length. Eye moderate, over middle of upper jaw. Anterior nostril long and tubular, reaching edge of lip when depressed; posterior nostril above anterior margin of eye.

Intermaxillary teeth in a single peripheral series, 6–7 on each side, triangular, increasing in size posteriorly; 1–3 median teeth, long, conical. Maxillary teeth uniserial in larger specimens, biserial in smaller specimens, which have a few large inner teeth anteriorly. Dentary with 1–3 larger inner teeth anteriorly, an outer row of smaller teeth, decreasing in size posteriorly. Larger teeth anteriorly in jaws serrate. Vomerine teeth uniserial or slightly staggered, small and inconspicuous.

Color: medium to dark brown, becoming nearly black posteriorly on tail and fins, with an indistinct marbled pattern of lighter brown separated by obscure darker interspaces on body and basally in the dorsal fin; often obscure horizontal lines on branchial area and anterior body. Anterior nostril dark brown. Iris yellow, margin of eye darker brown, wider posteriorly.

Maximum size about 400 mm.

Distribution and habitat. Throughout the Indo-Pacific from the Red Sea and east coast of Africa to the Society Islands and Hawaiian Islands. Usually found in shallow lagoon reefs and from fringing reefs in depth range 2–43 m.

Remarks. This species has been confused in the past with other plain brown morays. Schultz (1953: 113) misidentified it as *Gymnothorax moluccensis* and *G. monochrous* (see Randall & McCosker 1975: 17–18). Randall & Golani (1995: 865) reported vertebral counts of 130–135 for three specimens from Midway, but these specimens (presumably SIO 68-498 as reported by Randall & McCosker 1975: 17) are most probably *Gymnothorax atolli* (Pietschmann), a species that was not recognized until later. Böhlke & Randall (2000: 249) reported the range of vertebral counts as 110–124, but we have examined specimens from all corners of the Indo-Pacific and found no confirmed counts lower than 118. We suspect that the figure of 110 is either an error or based on a damaged specimen. There appears to be a considerable high level of intraspecific genetic variation. Two of the Red Sea specimens

FIGURE 32. *Gymnothorax pindae*. **A**: SMF 35818 [KAU12-1027], 210 mm TL, fresh specimen, Al Lith, Saudi Arabia; **B**: SMF 35819 [KAU13-447], 304 mm TL, alive, Al Wajh, Saudi Arabia. Photos by S.V. Bogorodsky.

collected in this study (KAUMM 414 and SMF 34818) fall apart from the others on the COI phylogeny (Fig. 48). The majority of sequences derived from Red Sea specimens, however, fall into a subclade with specimens from the South Pacific (New Caledonia and Society Islands). The divergence between the two genetic subgroups is as prominent as that among sub-groups in *G. javanicus* (see above), but as in that case, we can find no morphological characters that separate them, and we cannot explain the significance of the observed genetic divergence. No closely related species can be identified from the present phylogeny for *G. pindae* (Fig. 48).

Gymnothorax pseudoherrei Böhlke 2000—Dwarf Brown Moray
(Figure 33)

Gymnothorax pseudoherrei Böhlke 2000: 408, figs. 2F, 3D, 7 (W side of Solino [Selinog] I., Zamboanga Del Norte, Mindanao, Philippines, 8°51'24"N, 123°24'36"E, 0–4.6 m). Holotype, USNM 357430.—Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 22.
Gymnothorax herrei (non Beebe & Tee Van): Randall & Golani 1995: 860.

Red Sea material. ***Saudi Arabia***: KAUMM 409 [KAU12-1082] (1, 112), Al Lith; KAUMM 410 [KAU14-869] (1, 116), Al Lith; SMF 33616 (1, 107), Al Lith; SMF 35822 [KAU12-1083] (1, 171), Al Lith; SMF 35877 [KAU17-245] (1, 127), Farasan Archipelago, Abkar Island. ***Eritrea***: HUJ 15113 (2, 185-193), Dahlak Archipelago, Romia Island; USNM 312234 (8, 116–204), Sheikh el Abu; USNM 312247 (1, 150), Melita Bay. ***Yemen***: USNM 397542 (1, 171), Hanish Island.

Comparative material. ***Arabian Gulf***: BPBM 33328 (1, 291); BPBM 33356 (3, 208–256). ***Gulf of Oman***: BPBM 21473 (1, 208). ***Sri Lanka***: USNM 357433 (3, 116–155, paratypes). ***Philippines***: USNM 357430 (1, 147, holotype), Mindanao; USNM 357432 (2, 114–121, paratypes), Palawan. ***Indonesia***: USNM 210269 (1, 148); USNM 274957 (1, 103). ***Papua New Guinea***: USNM 357431 (2, 126–156, paratypes).

Description. In TL: preanal length 2.0–2.4, predorsal length 8.1–12, head length 7.2–9.5, body depth at anus 16–25. In head length: snout length 5.7–6.9, eye diameter 7.9–11, upper-jaw length 2.7–3.4. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 5–8, preanal 42–50, total 111–120.

Body somewhat elongate in smaller specimens, becoming moderately stout with growth; anus slightly before midlength; dorsal-fin origin before gill opening. Snout relatively short and tapering, jaws of equal length. Eye moderate, over middle of upper jaw. Anterior nostril tubular; posterior nostril above anterior part of eye.

Teeth smooth, relatively short, stout and pointed. Intermaxillary teeth in a single peripheral series, 6–8 on each side, conical, increasing in size posteriorly; 1–2 median stout teeth. Maxillary teeth biserial, about 7–14 larger inner teeth and 19–21 smaller outer teeth, those in outer row obtusely pointed. Dentary with 1–4 larger inner conical teeth anteriorly and about 17–25 smaller blade-like outer teeth. Vomerine teeth stout, blunt, uniserial or staggered, about 7–13.

Color: medium to dark brown with an irregular network of indistinct small, darker markings, head paler than body, lower part of head lighter, sometimes with dark lines along throat grooves, one continuing into angle of mouth. Posterior one-fourth of body and fins yellow in smaller specimens, yellow color gradually disappears with growth. Iris white with black outer ring. Body frequently covered with a gray or greenish mucus.

Maximum size about 300 mm.

Distribution and habitat. Northwestern Indian Ocean and western Pacific, from the Red Sea and Arabian Gulf to the Solomon Islands, in shallow water, generally less than 10 m depth. It has not been collected from the coast of Africa or the islands of the western Indian Ocean west and south of the Maldives. A cryptic species living inside coastal reefs, never seen alive.

Remarks. Specimens from the northwestern Indian Ocean (Red Sea, Arabian Gulf, and Gulf of Oman) apparently grow larger than those from elsewhere. Out of more than 100 specimens reported by Böhlke (2000) from east of the Maldives, the largest was 182 mm (ANSP 144601 from Queensland, Australia). The largest of only 12 specimens reported from the northwestern Indian Ocean, by contrast, was 291 mm (BPBM 33328, from the Arabian Gulf). Several other specimens from this area exceeded 200 mm. There is a slight difference in the number of vertebrae between these two groups. Nineteen specimens from the Red Sea, Arabian Gulf, and Gulf of Oman had 113–120 total vertebrae; nine specimens from Sri Lanka, Indonesia, the Philippines, and Papua New Guinea had 111–116. The Red Sea and Arabian Gulf specimens also have dark throat grooves, which are not evident in those

from the Pacific. We have no genetic data from outside the Red Sea. This species was confused in the past with the superficially similar *Gymnothorax herrei* Beebe & Tee-Van, from which it differs by having two branchial pores instead of one, the origin of the dorsal fin more anterior, and lacking an intermediate row of small intermaxillary teeth. In the present COI phylogeny (Fig. 48) two specimens are included that have been collected during the course of this study. As no COI sequence data from other specimens are available, we cannot infer the level of intraspecific genetic divergence. *Gymnothorax pseudoherrei* forms part of a well supported clade with a number of other taxa, such as *G. griseus* and *G. thyrsoideus*, but also *Echidna unicolor* and *E. delicatula* (Fig. 48).

FIGURE 33. *Gymnothorax pseudoherrei*, SMF 35822 [KAU12-1083], 171 mm TL, fresh specimen, Al Lith, Saudi Arabia. Photo by S.V. Bogorodsky.

Gymnothorax punctatus Bloch & Schneider 1801—Spotted Moray
(Figure 34)

Gymnothorax punctatus Bloch & Schneider 1801: 526 (Tranquebar, India). Syntypes, ZMB 6141 (1, ca. 710, stuffed), 3989 (1, 210).—Fowler & Steinitz 1956: 269; Dor 1984: 28; Goren & Dor 1994: 7; Randall & Golani 1995: 866; Lieske & Myers 2004: 37; Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 22.
Lycodontis cf. *undulatus*: Ben Tuvia & Steinitz 1952: 4.

Red Sea material. ***Israel***: BPBM 35745 (1, 775), Eilat; HUJ 4708 (1, 760), Eilat; HUJ 4989 (1, 780); HUJ 4992 (1, 783), Eilat. ***Egypt***: USNM 312701 (1, 704), Gulf of Aqaba, El Himeira; USNM 316922 (3, 220–673), Gulf of Aqaba, El Himeira.

Comparative material. ***India***: ZMB 3989 (1, 201 mm, syntype); ZMB 6141 (1, ca. 710, syntype).

Description. In TL: preanal length 2.2–2.4, predorsal length 8.4–9.5, head length 6.5–7.7, body depth at anus 13–24. In head length: snout length 4.5–6.0, eye diameter 8.1–13, upper-jaw length 2.3–3.1. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 5–7, preanal 55–56, total 138–144.

FIGURE 34. *Gymnothorax punctatus*. **A**: BPBM 35745, 775 mm TL, fresh specimen, Eilat, Israel; **B**: alive, Hurghada, Egypt. Photos by J.E. Randall (A), S. Kahlbrock (B).

Body moderately elongate; anus before midlength; dorsal-fin origin before gill opening. Snout somewhat elongate, jaws of equal length. Eye moderate, over middle of upper jaw. Anterior nostril tubular; posterior nostril above anterior part of eye.

Teeth smooth, slender and pointed. Intermaxillary teeth in a single peripheral series, about 4–6 on each side,

conical, increasing in size posteriorly; 3 median teeth. Maxillary teeth biserial in smaller specimens, with 2–3 larger inner teeth anteriorly, outer series of 12–19 smaller teeth. Dentary teeth with 2–3 larger inner teeth anteriorly, 18–20 smaller outer teeth. Vomerine teeth small, uniserial, about 7–11.

Color: reddish brown, covered with small pale spots on body and dorsal part of head and snout, the spots smaller and more numerous anteriorly. Spots in smaller specimens round, in 3–4 rows on tail, extending onto dorsal fin but not anal fin. In larger specimens, spots more numerous and irregular in shape.

Maximum size about 800 mm.

Distribution and habitat. Our specimens all came from the Red Sea; the syntypes were collected at Tranquebar, on the southeastern coast of India. A rare species, the few other specimens known in museum collections came from Pakistan and Sri Lanka. The usual habitat is coastal rocky and coral reefs from depths of 3–20 m.

Remarks. It is not certain that our specimens belong to the same species described by Bloch & Schneider (1801), and it is not completely clear whether the two syntypes represent the same species. The larger syntype, ZMB 6141, ca. 710 mm, is covered with round, ocellated spots, somewhat larger and more regular than those in our large specimens. The smaller syntype, ZMB 3989, 201 mm, has much larger spots, at least as large as the eye, distinctly larger than those on our small specimens. The larger syntype is stuffed and mounted, and a vertebral count is not available. The smaller syntype was examined by E. B. Böhlke, who recorded an approximate count of 134, which is lower than those of our specimens. Our specimens resemble *Gymnothorax johnsoni*, but the spots are smaller at all sizes, and there are more vertebrae (138–144 *vs*. 131–140). The white-spotted *Gymnothorax* species are confusing and further study is needed to sort them out, using both genetic and morphological characters. No Red Sea specimen for sequencing of the mitochondrial COI barcoding gene was collected during this study. The only specimen with available sequence data under the name *G. punctatus* in BOLD comes from the southeast coast of India. This specimen forms part of a highly supported clade with *G. undulatus*. However, as in other cases where we do not add our own data, we solely rely here on the species identification by the sequence authors.

Gymnothorax randalli Smith & Böhlke 1997—Randall's Moray

(Figure 35)

Gymnothorax punctatofasciatus (non Bleeker): Randall & Golani, 1995: 865.

Gymnothorax randalli Smith & Böhlke 1997: 185, figs. 1, 2, 8 (Sorongjunkong, Lombok, Indonesia). Holotype, BPBM 30138.—Golani & Bogorodsky 2010: 10; Bogorodsky *et al*. 2014: 411; Golani & Fricke 2018: 22.

Red Sea material. ***Egypt***: HUJ 9410 (1, 365), Nuweiba, May 1976. ***Saudi Arabia***: SMF 34963 [KAU12-732] (1, 396), Jizan, 20–25 m, 1 Mar 2012.

Comparative material. ***Indonesia***: BPBM 30138 (1, 324, holotype); ANSP 175205 (1, 268, paratype); USNM 343860 (1, 317, paratype).

Description. In TL: preanal length 2.2–2.4, predorsal length 8.9–11, head length 7.8–8.6, body depth at anus 21–29. In head length: snout length 5.7–7.6, eye diameter 7.5–10, upper-jaw length 2.8–3.3. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 5–9, preanal 48–52, total 124–130.

Body moderately elongate; anus before midlength; dorsal-fin origin before gill opening. Snout moderately short, jaws of equal length. Eye moderate, over middle of upper jaw. Anterior nostril tubular; posterior nostril above anterior part of eye.

Teeth conical to triangular, pointed, finely serrate on posterior edge. Intermaxillary teeth in a single peripheral series, 6 on each side; 0–3 median teeth. Maxillary teeth uniserial or biserial, 0–3 inner and 12–20 outer. Dentary teeth uniserial or biserial, with 0–5 larger inner teeth anteriorly, 16–24 smaller outer teeth. Vomerine teeth small, uniserial or biserial, about 6–12.

Color: body pale yellowish with two longitudinal rows of 35–39 irregular dark brown spots, most notably larger than orbit and in vertical alignment with spot of other row; a third row of irregular dark brown spots midventrally, these merging with spot above to form short bars on posterior two-thirds of tail; pale interspaces between large spots with numerous small dark brown spots of variable size, except ventrally. Head with numerous dark brown spots of variable size, a few dorsally on posterior half of head larger than orbit. Iris white. Anterior nostril pale.

Maximum size at least 396 mm.

Distribution and habitat. A rare species known from only five specimens from southern Indonesia and the

Red Sea. Smith & Böhlke (1997: 186) pointed out that the specimen from Madras, India illustrated by Day (1878, pl. 169, fig. 4) as *Muraena punctatofasciata* appears to be *Gymnothorax randalli*, indicating that the species probably occurs continuously across the northern Indian Ocean to Indonesia. Probably living in open areas on silty sand substrata. The specimen from Saudi Arabia off Jizan was trawled from at a depth of 20–25 m in open area. One individual was photographed in sand area covered with seagrasses at depth of about 15 m at Nuweiba, Egypt (Sonja Ooms, pers. comm.).

Remarks. The two Red Sea specimens differ slightly in predorsal (5–7), preanal (48–49), and total (124–126) vertebrae from the Indonesian ones (7–9, 50–52, 127–130, respectively). SMF 34963 has a short row of distinctly biserial teeth on the vomer. The vomerine teeth of the other specimens are uniserial. We have no genetic data from outside the Red Sea. The sequence of the Red Sea specimen of *G. randalli* is part of a highly supported clade with *G. minor* (Temminck & Schlegel), *G.* cf. *minor* and *G. mccoskeri* Smith & Böhlke, the latter being phylogenetically closest to *G. randalli* (Fig. 48).

FIGURE 35. *Gymnothorax randalli*, SMF 34963 [KAU12-732], 396 mm TL, fresh specimen, Jizan, Saudi Arabia. Photo by S.V. Bogorodsky.

Gymnothorax reticularis Bloch 1795—Reticulate Moray
(Figure 36)

Gymnothorax reticularis Bloch 1795: 85, pl. 416 (Coromandel coast, India). Holotype (unique), ZMB 3986.—Randall & Golani 1995: 867; Golani & Bogorodsky 2010: 10; Bogorodsky *et al*. 2014: 411; Golani & Fricke 2018: 23.
Muraena reticulata: Rüppell 1830: 117.

Red Sea material. ***Israel***: HUJ 14667 (1, 240), Eilat. ***Saudi Arabia***: KAUMM 415 [KAU14-155] (1, 400), Jizan, 60–65 m, 01 Nov 2014; SMF 34964 [KAU12-733] (1, 350), Jizan, 55–60 m, 29 Feb 2012.

Comparative material. ***Mozambique***: SAIAB 5052 (1, 346). ***Pakistan***: USNM 427632 (1, 297). ***India***: ZMB 3986 (1, 302, holotype), Coromandel (Tranquebar); ANSP 127987 (3, 207–256); USNM 343723 (1, 200). ***Myanmar***: USNM 438261 (1, 271).

Description. In TL: preanal length 2.0–2.2, predorsal length 7.1–11, head length 6.5–8.2, body depth at anus 19–29. In head length: snout length 5.2–7.8, eye diameter 8.1–13, upper-jaw length 2.9–3.5. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 5–7, preanal 48–53, total 115–126.

Body moderately elongate; anus at or slightly before midlength; dorsal-fin origin before gill opening. Snout moderately short, jaws of equal length. Eye moderate, over middle of upper jaw. Anterior nostril tubular; posterior nostril above anterior part of eye.

Teeth uniserial, conical to triangular, pointed, serrate. Intermaxillary teeth in a single peripheral series, 3–6 on each side; no median teeth. Maxillary teeth uniserial, 3–11. Dentary teeth uniserial except 1 specimen with 2 inner teeth on one side, 7–15. Vomerine teeth small and inconspicuous, uniserial but biserial in 1 specimen, about 6–12.

Color: body pale gray with yellowish hue dorsally, with 16–20 dark brown bars on ventral two-thirds of body, narrower than pale interspace, obscured dorsally by numerous, irregular, small spots, some forming a reticular pattern. Dorsal and anal fins alternating with black and white or pale gray, spots on body extending onto white interspaces basally in fins. Head pale gray with dark brown spots of variable size that are longitudinally elongate posteriorly.

Maximum size about 460 mm (specimen from the Mediterranean Sea).

Distribution and habitat. Known from India, Pakistan, Mozambique, and the Red Sea. Both Red Sea specimens trawled off Jizan from soft substrata, from a depth of 50–65 m. Reported also from the eastern Mediterranean Sea by Stern & Goren (2013).

FIGURE 36. *Gymnothorax reticularis*, SMF 34964 [KAU12-733], 350 mm TL, fresh specimen, Jizan, Saudi Arabia. Photo by S.V. Bogorodsky.

Remarks. This species was long confused with *Gymnothorax minor*. The true *Gymnothorax reticularis* is restricted to the Indian Ocean; records from the Pacific refer to *G. minor* (Smith & Böhlke 1997). Specimens from the Red Sea have more preanal (51–53) and total (123–126) vertebrae than those from elsewhere (48–50 and 115–122). The Mozambique specimen is intermediate with 122 vertebrae *vs*. ca 115–120 in those from India and Pakistan. Also in the Red Sea specimens, the bars are less distinct dorsally, where they tend to be lost in the general spotting. We have no genetic data from outside the Red Sea. Smith & Böhlke (1997: 187) reported that the specimen described by J.L.B. Smith (1962: 429) from Mozambique could not be located. However, the first author found it during his visit to South Africa in 2001 and took the relevant counts and measurements. Li *et al*. (2018) demonstrated that previous records of specimens identified as *G. reticularis* in the western Pacific are based on misidentification of *G. minor*. No COI sequences were available for *G. reticularis* from outside the Red Sea. Sequences of the mitochondrial COI from two Red Sea specimens that were collected during the present study were included in the multi-sequence alignment. In the resulting phylogenetic tree (Fig. 48), *G. reticularis* did not show a close phylogenetic affiliation with any other clade of moray eels included in the analysis.

Gymnothorax rueppelliae (McClelland 1844)—Yellowhead Moray
(Figure 37)

Dalophis rueppelliae McClelland 1844: 213 (Red Sea). Lectotype, SMF 151, designated by Böhlke 1982: 44.
Muraena umbrofasciata Rüppell 1852: 33 (Red Sea). Syntypes, SMF 151 (1), SMF 2870 (1, skeleton, lost), SMF 7346 (1, missing).
Muraena interrupta Kaup 1856: 67, pl. 10 (fig. 51) (Clot Bay, Red Sea). Holotype (unique), MNHN B-2470.
Muraena Rüppellii: Klunzinger 1871: 615.
Lycodontis rueppelli: Dor 1984: 29.
Gymnothorax rueppelli: Goren & Dor 1994: 7.
Gymnothorax rueppelliae: Randall & Golani 1995: 867; Debelius 1998: 12; Khalaf 2004: 37; Lieske & Myers 2004: 38; Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 23.

Red Sea material. ***Red Sea***: SMF 151 (1, 390, lectotype); SMF 7346 (1, 245, paralectotype of *Dalophis rueppelliae*); MNHN B.2470 (1, 440, holotype of *Muraena interrupta* Kaup). ***Israel***: HUJ 15145 (1, 500), Eilat; HUJ 15161 (1, 165), Eilat. ***Egypt***: BPBM 35737 (2, 191–265), Gulf of Aqaba, Nabq; HUJ 4859 (2, 161–230), Ras Muhammad; HUJ 4959 (1, 88); HUJ 15090 (2, 82–86), Gulf of Aqaba, El Arkana; HUJ 15117 (11, 245–420); HUJ 15121 (1, 192), Gulf of Aqaba, El Arkana; HUJ 15137 (cited by Randall & Golani, 1995, number of specimens and lengths not given), Nabq; USNM 312676 (5, 173–385), Strait of Jubal. ***Saudi Arabia***: USNM 147431 (1, 391), 5 km north of Jeddah.

Comparative material. ***Mauritius***: MCZ 6147 (1, 180, holotype of *Gymnothorax signifer* Bliss). ***Indonesia***: BMNH 1867.11.28.282 (1, 457, holotype of *Muraena petelli* Bleeker); RMNH 7187 (1, 235). ***Hawaii***: USNM 50682 (1, 504, holotype of *Gymnothorax leucacme* Jenkins); USNM 50870 (1, 102, holotype of *Gymnothorax waialuae* Snyder). ***French Polynesia***, Moorea: MNHN 2008-0317 (1, 136). ***Galapagos Is.* (?)**: USNM 20385 (1, ca 235, holotype of *Siderea chlevastes* Jordan and Gilbert).

Description. In TL: preanal length 2.1–2.3, predorsal length 8.5–10, head length 7.6–8.3, body depth at anus 14–22. In head length: snout length 5.1–5.9, eye diameter 8.3–9.9, upper-jaw length 2.3–2.7. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 4–5, preanal 50–55, total 124–135.

Body moderately elongate, anus slightly before midlength, dorsal-fin origin before gill opening. Jaws moderate, equal length. Eye moderate, over middle of upper jaw. Anterior nostril tubular, reaching edge of lip when depressed; posterior nostril elliptical with a raised rim, above anterior margin of eye.

Teeth smooth, slender, acute. Intermaxillary teeth in one peripheral series, about 6 on each side, and three median teeth. Maxillary teeth biserial, about 1–3 larger inner teeth, 11–15 smaller outer teeth. Dentary with 2–3 larger inner teeth anteriorly, 18–25 outer teeth. Vomerine teeth small, uniserial.

Color: light grayish brown with 16–22 dark brown bars about as wide as pale interspaces on head, body, and fins, those on head and trunk not reaching ventral margin (dark bars may be obscure on large adults); top of head yellow; abdomen and margin of dorsal fin between dark bars white; top of head yellow; a dark brown spot at corner of mouth; anterior nostrils blackish.

Maximum size about 800 mm.

Distribution and habitat. Widespread from the western Indian Ocean east to the Hawaiian Islands and French Polynesia. Occurs on coral reefs and rocky substrata at depths of 1–55 m, often observed on reef flats at night.

Remarks. Randall & Golani (1995) reported a marked difference in number of vertebrae between eight specimens from the Red Sea (124–128) and 10 specimens from Mauritius and Oceania (130–134). Our own data support this: three specimens from the Red Sea have 126–127 vertebrae whereas four specimens from the Pacific have 131–135 vertebrae. We have no genetic data from the Red Sea, and therefore cannot add information from this side towards the existence of a potential population divergence. The two specimens included in the COI based phylogeny (Fig. 48), did not associate closely to any other lineage. In the multigene phylogeny by Reece *et al*. (2010), however, the species was part of a well-supported clade including among other species *G. undulatus* (originally identified as *G. polyuranodon* (Bleeker) in Reece *et al*. 2010) and *G. fimbriatus*, two species that are associated with *G. rueppelliae* in the present analysis as well, although this grouping did not receive support from bootstrapped analyses. Two other COI sequences were found for specimens identified as *G. rueppelliae* (i.e., ANGBF9290-12 from China and FOAN927-11from Queensland, Australia), but due to their phylogenetic placement these two specimens were re-assigned to *Gymnothorax minor* and *Gymnothorax* sp., respectively (Fig. 48).

FIGURE 37. *Gymnothorax rueppelliae*, Dahab, Egypt. Photo by S.V. Bogorodsky.

Gymnothorax undulatus (Lacepède 1803)—Undulated Moray
(Figure 38)

Muraenophis undulata Lacepède (ex Commerson) 1803: 629, 642, pl. 19 (fig. 2) (No locality). Holotype (unique), whereabouts unknown.
?*Muraena undulata*: Klunzinger 1871: 615 (Quseir, Egypt).
?*Gymnothorax meleagris* (non Shaw & Nodder): Fowler & Steinitz 1956: 270 (Eilat).
Gymnothorax undulatus: Randall & Golani 1995: 868 (in part: Pl. 2F); Debelius 1998: 13; Lieske & Myers 2004: 36; Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 23.

Red Sea material. ***Red Sea***: USNM 47604 (1, 490). ***Egypt***: USNM 312603 (1, 674), Gulf of Aqaba, Marsa Muqabila. ***Saudi Arabia***: USNM 147430 (1, 500), Gubat Ashra. ***Eritrea***: USNM 312608 (1, 357), Dahlak Archipelago, Delemmi.

Comparative material. ***Arabian Gulf***: BPBM 29469 (1, 693); BPBM 33383 (1, 760); BPBM 33384 (2, 432–533). ***Mauritius***: BPBM 20132 (1, 207). ***Chagos Archipelago***: USNM 312615 (5, 263–407). ***Madagascar***: MNHN B.2426 (1, 400); MNHN B.2432 (1, 317); MNHN B.2728 (1, 434); MNHN 1965-338 (1, 206); MNHN 1991-0402 (3, 498–595). ***Mozambique***: SAIAB 60389 (1, 223). ***South Africa***: SAIAB 60166 (9, 80–360); USNM 312712 (1, 570); USNM 330982 (1, 454). ***Wallis I.***: USNM 371033 (1, 141).

Description. In TL: preanal length 2.1–2.4, predorsal length 7.8–11, head length 6.6–8.2, body depth at anus 12–21. In head length: snout length 4.6–6.4, eye diameter 6.4–12, upper-jaw length 2.2–2.9. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: predorsal 3–6, preanal 50–58, total 126–136.

Body moderately elongate; anus before midlength; dorsal-fin origin before gill opening. Snout moderate, jaws of equal length. Eye moderate, over middle of upper jaw. Anterior nostril tubular; posterior nostril above anterior part of eye.

FIGURE 38. *Gymnothorax undulatus*. **A**: Dahab, Egypt; **B**: Dahab, Egypt. Photos by S.V. Bogorodsky.

Teeth conical, pointed, smooth. Intermaxillary teeth in a single peripheral series, 2–6 on each side; 2–4 median teeth, usually 3. Maxillary teeth uniserial or biserial, with 1–2 larger inner teeth anteriorly, about 9–18 smaller outer teeth. Dentary teeth biserial, with 2–4 larger inner teeth anteriorly, 16–20 smaller outer teeth. Vomerine teeth uniserial but biserial in 1 specimen, about 4–7.

Color: variable over range. In Red Sea, small individuals with body and fins dark gray to black with narrow pale markings arranged in a reticular pattern. Larger individuals more grayish, pattern becoming more irregular and obscure. Top of head olive-green to yellow-green, densely spotted with small irregular dark brown spots posteriorly; snout and lower jaw yellow-green to light grey-brown without spots; corner of mouth with a white spot. Outside Red Sea most commonly dark brown to black, with narrow pale markings usually interconnected to form a reticulation; the pattern generally more obscure in larger specimens. One specimen (BPBM 33383, 760 mm, from Jana Island, Arabian Gulf), apparently of this species, dull whitish with small, irregular black spots.

Maximum size about 1.5 m.

Distribution and habitat. Widely distributed in the Indo-Pacific from the Red Sea and East Africa eastward to the islands off Central America. Mainly in shallow water, common on coral reefs, reported from depths of 1–110 m.

Remarks. As pointed out above, this species was confused with *Gymnothorax pharaonis* **n. sp.** described here. *Gymnothorax undulatus* is highly variable over its range, and further study may show that it represents a complex of species. Specimens examined from the Red Sea and Arabian Gulf have fewer vertebrae (126–129) than those from Mauritius and Chagos Archipelago (130–134) and South Africa (134–136). The specimen from Wallis Island has 131. The South African specimens differ further in coloration, showing a densely spotted, gravel-like pattern rather than reticulations (see Pl. 57E in Smith 1962).

Randall & Golani (1995: 868) listed Klunzinger's (1871) record of *Muraena undulata* and Fowler & Steinitz's record of *Gymnothorax meleagris* in their synonymy of *Gymnothorax undulatus*, but as they confused *G. undulatus* with *G. pharaonis*, these may refer to the latter species instead. No Red Sea specimen was collected during this study and no sequences of the mitochondrial COI barcoding gene were available for other Red Sea specimens of *G. undulatus*. We therefore included COI sequences of each of two closely related clades for which COI sequences could be retrieved from various databases. One clade was largely restricted to the Indian Ocean and the other to the Pacific Ocean. However, as the type locality of the species is not documented, the whereabouts of the holotype is unknown, and we did (with the exception of one South Pacific specimen) examine only Red Sea and Indian Ocean material herein, we refrain from guessing which of the two clades might represent *Gymnothorax undulatus* and if the other clade represents another species. Hence, both clades are under the name *G. undulatus* in the presented phylogeny (Fig. 48), where they form part of a highly supported clade with *G. punctatus*.

Muraena helena Linnaeus 1758—Mediterranean Moray

(Figure 39)

Muraena helena Linnaeus 1758: 244 (Europe; America). Syntypes, ZMUU Linn. Coll. 57 (1, only surviving specimen).—Randall & Golani 1995: 869; Golani & Bogorodsky 2010: 10; Golani & Fricke 2018: 23.

Red Sea material. ***Egypt***: HUJ 9048 (2, 650–880), Nuweiba; HUJ 9012 (1, 545), Nuweiba.

Comparative material. ***Mediterranean Sea***: HUJ 15173 (2, 310–412), Cyprus; HUJ 16192 (1, 520), Israel.

Description. In TL: preanal length 2.1–2.2, predorsal length 9.7–10, head length 8.2–8.7, body depth at anus 15. In head length: snout length 4.6–5.2, eye diameter 9.3–12, upper-jaw length 2.3–2.6. Pores: LL 2, SO 3, IO 4, POM 6. Vertebrae: total 144–145 (137–146 for 15 specimens reported by E. B. Böhlke, as stated by Randall & Golani 1995).

Body moderate; anus slightly before midlength; dorsal-fin origin before gill opening. Snout moderate, jaws of equal length. Eye moderate, over middle of upper jaw. Anterior nostril tubular; posterior nostril long and tubular, its length almost half eye diameter, above anterior margin of eye.

Teeth uniserial, conical to triangular, pointed, smooth. Intermaxillary teeth in a single peripheral series; 2–3 median teeth. Vomerine teeth sharply conical.

Color: anterior half of head dark brown, the posterior half and anterior trunk mottled with whitish flecks and short irregular lines; posterior trunk and tail with three longitudinal rows of large whitish blotches, each with a clus-

tering of very dark brown spots and white dots. Posterior margin of fins with a series of small hemispherical whitish spots. Edge of gill opening blackish.

Maximum size to 1.3 m.

Distribution and habitat. Eastern Atlantic from the British Isles to Senegal, including the Mediterranean and the islands. An immigrant to the northern Red Sea via the Suez Canal; three specimens collected from Nuweiba, Gulf of Aqaba.

Remarks. The genus *Muraena* is characterized by the long posterior nostril, a feature it shares with *Enchelycore pardalis*, a species that does not occur in the Red Sea. The Red Sea specimens do not differ in any meaningful way from those in the Atlantic, and they undoubtedly represent migrants that entered the Red Sea through the Suez Canal. The COI sequence of a specimen from the Mediterranean included in the phylogenetic analysis showed that the morphological similarity between *Muraena helena* and *Enchelycore pardalis* is accompanied by a relatively close phylogenetic affiliation of these two species in that they formed a moderately well supported joint clade (Fig. 48).

FIGURE 39. *Muraena helena*, Bodrum, Turkey. Photo by S.V. Bogorodsky.

Strophidon sathete (Hamilton 1822)—Longtail Moray
(Figure 40)

Muraenophis sathete Hamilton 1822: 17, 363 (Ganges estuaries near Calcutta, India). No types known.
Thyrsoidea macrura (Bleeker): Ajiad 1987: 102 (Gulf of Aqaba).
Strophidon sathete: Randall & Golani 1995: 871; Golani & Bogorodsky 2010: 11; Golani & Fricke 2018: 23.

Red Sea material. None examined, based on report by Ajiad (1987).

Comparative material. ***Mozambique***: USNM 312253 (1, 1041). ***Pakistan***: USNM 199673 (1, 182); USNM 427620 (1, 1197). ***India***: MNHN 2134 (1, 1460, holotype of *Thyrsoidea longissima* Kaup). ***Indonesia***: BMNH 1867.11.28.212 (1, 2265, holotype of *Muraena macrura* Bleeker); RMNH 7206 (1, 2425). ***Philippines***: USNM 84213 (1, 1021); USNM 135176 (1, 590); USNM 136598 (1, 1510). ***Taiwan***: USNM 312252 (1, 486). ***Japan***: USNM 75945 (1, 824); USNM 160610 (1, 1118). ***Fiji***: USNM 259863 (1, 130).

Description. In TL: preanal length 2.2–2.9, predorsal length 11–17, head length 8.1–13, body depth at anus 37–63. In head length: snout length 6.8–12, eye diameter 13–29, upper-jaw length 2.7–3.7. Pores: LL 1–8, SO 2–3, IO 3–4, POM 6. Vertebrae: predorsal 7–14, preanal 71–84, total 183–212.

Body very elongate; anus well before midlength; dorsal-fin origin before gill opening. Snout long, jaws of equal length. Eye small, closer to tip of snout than to rictus. Anterior nostril tubular; posterior above and slightly behind anterior margin of eye. Usually three infraorbital pores; 1–8 branchial pores.

Teeth pointed, smooth. Intermaxillary teeth in a single peripheral series, about 4–9 on each side; 1–4 median teeth. Maxillary and dentary teeth biserial anteriorly and uniserial posteriorly, the inner teeth larger and fewer than outer. Vomerine teeth uniserial, about 8–17.

Color: grayish brown, paler ventrally, the fins darker.

Reported to reach 375 cm.

Distribution and habitat. Indo-West Pacific from East Africa and the Red Sea to New Caledonia and Fiji. Occurs on mud bottom in burrows in lagoons and estuaries; nocturnal. The Red Sea record is based on two specimens reported by Ajiad (1987) taken by hook and line in 50 m at Nuweiba, Gulf of Aqaba.

Remarks. This is the longest of all moray eels, reaching nearly 4 m, but very slender. The forward placement of the eye is distinctive, as is the usual presence of three rather than four infraorbital pores and up to eight branchial pores. The wide range of vertebral counts and recent DNA evidence indicate that more than one species are included under this name. It has frequently been referred to in the literature as *Thyrsoidea macrura*. No COI sequence data from Red Sea specimens was available for this species, but the phylogeny (Fig. 48) includes sequences from specimens from other localities. In our search for sequences representative for this species, we found that there are two closely related clades with reciprocally exclusive distributions (as of the sequences found in BOLD). One clade only contained specimens from China and Taiwan, whereas the other included specimens from a wider area, encompassing Australia, Indonesia, Philippines, India and South Africa (not all localities were included in the present analysis, see Fig. 48). With its type locality in India, we suggest that the latter clade represents the species described as *Strophidon sathete*, but without further analysis we refrain from any firm conclusions and we provisionally keep both clades under that name. *Strophidon sathete* formed a highly supported clade with two other congeneric species (i.e. *S. dorsalis* (Seale) and *Strophidon* sp.).

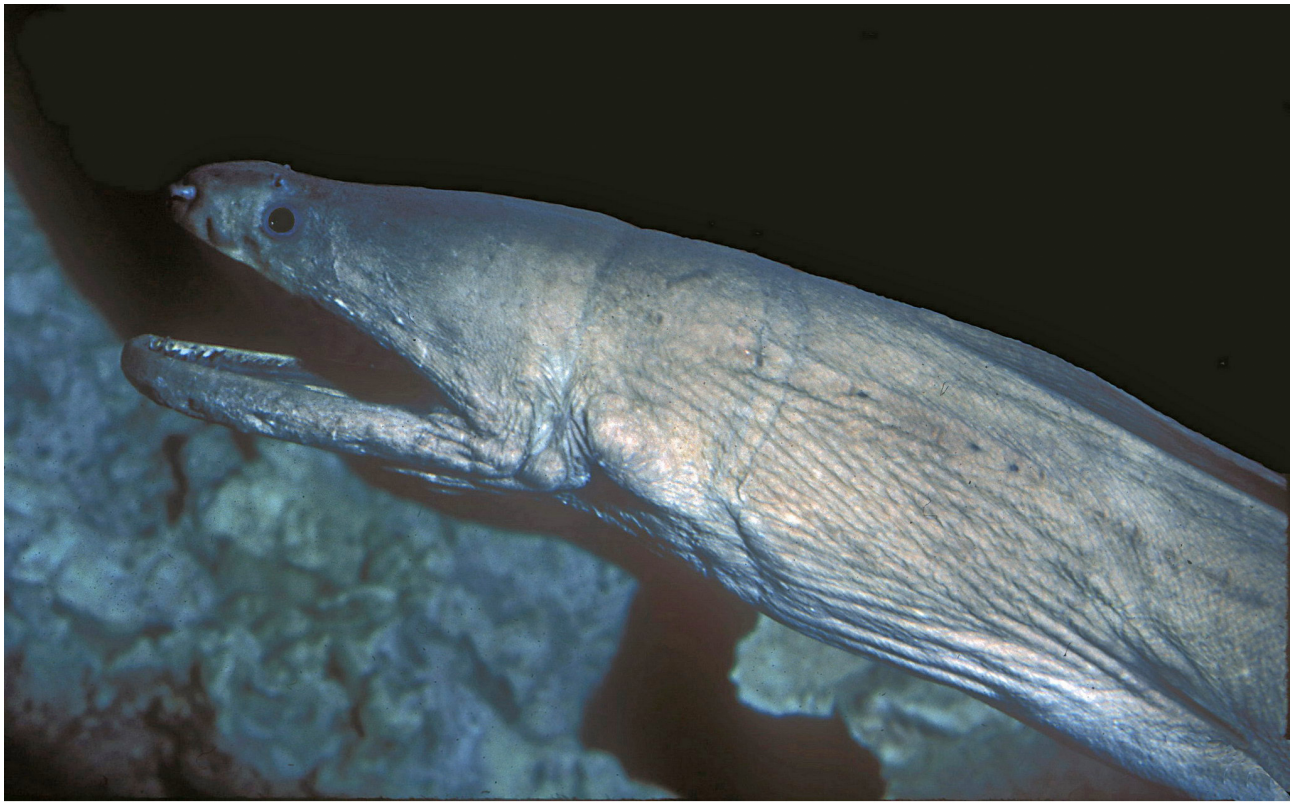


FIGURE 40. *Strophidon sathete*, Maumere Bay, Indonesia. Photo by J.E. Randall.

SUBFAMILY UROPTERYGIINAE

Diagnosis. Dorsal and anal fins confined to posterior end of body; anal fin begins well behind anus. Usually 1 branchial pore, sometimes 2 or none.

Scuticaria tigrina (Lesson 1828)—Tiger Snakemoray
(Figure 41)

Ichthyophis tigrinus Lesson 1828: 399 (Bora Bora, Society Is.). Lectotype, MNHN B-2454, designated by Böhlke & McCosker 1997: 174.

Red Sea material. ***Saudi Arabia***: SMF 35823 [KAU13-680] (1, 553), Jeddah, Obhur, steep slope with many corals and caves, 14–16 m, S.V. Bogorodsky, 01 July 2013.

Comparative material. ***Chagos Archipelago***: USNM 312867 (1, 451). ***Samoa***: USNM 52273 (1, 814), Apia. ***Wallis I.***: USNM 370488 (1, 527). ***French Polynesia***, Bora Bora: MNHN B.2454 (1, 605, lectotype). Huahine: USNM 312866 (1, 405). ***Hawaii***: USNM 52764 (1, 845).

Description. Data for the Red Sea specimen given in parentheses. In TL: preanal length 1.5–1.6 (1.5), head length 11–15 (13), body depth at anus 26–45 (36). In head length: snout length 5.2–7.9 (6.0), eye diameter 12–18 (15), upper-jaw length 2.8–3.4 (3.1). Pores: LL 1, SO 3, IO 4, POM 6. Vertebrae: predorsal 152–166 (152), pre-anus 100–104 (100), pre-anal fin 156–167 (156), total 161–174 (161).

Body moderate, robust, nearly cylindrical; anus well behind midlength, at about two-thirds TL. Snout moderate, jaws about equal length. Eye moderate, over middle of upper jaw. Anterior nostril tubular; posterior nostril a low tube, above anterior margin of eye.

Teeth biserial, conical, smooth. Intermaxillary teeth in five rows across, about 4–9 peripheral, 4–5 intermediate, 2–4 median. Maxilla with an outer series of 6–15 small teeth and an inner series of 6–9 larger, depressible teeth; the inner series extends only about half as far back as the outer series. Dentary with 6–8 large inner teeth and 13–22 smaller outer teeth. Vomerine teeth uniserial.

Color: head posterior to corner of mouth and body pale yellowish to light brown, with well-separated, irregularly round, dark brown spots of variable size. Head anterior to corner of mouth with many small dark brown spots.

Maximum size about 1.4 m.

Distribution and habitat. Widely distributed across the Indo-Pacific from the Red Sea and South Africa to the Hawaiian Islands and Society Islands, also reported from islands off Mexico and Central America, but not common anywhere. May be seen night or day on coral reefs at depths of 7–25 m, in the Red Sea observed under water from the Gulf of Aqaba (Dahab), Marsa Alam, and Saudi Arabia (vicinity of Jeddah and at Al Lith).

Remarks. This is the first record of the species from the Red Sea, based on the collected specimen and underwater photographs. The examined specimen was collected at 14–16 m on a steep reef slope with numerous caves. It superficially resembles *Uropterygius polyspilus* but is easily distinguished by the more posterior anus. The Red Sea specimen has slightly fewer predorsal (152 *vs*. 157–166), preanal-fin (156 *vs*. 159–167) and total (161 *vs*. 165–174) vertebrae than those from elsewhere. The phylogenetic tree (Fig. 48) shows a slight difference between the Red Sea specimen and two from Hawaii and Taiwan, reinforcing the difference in vertebral counts. Formerly, the species was placed in the genus *Uropterygius*, but it was reclassified in the genus *Scuticaria* by Böhlke & McCosker (1997) in their review of the genus. The present phylogeny, although deeper phylogenetic splits in general did not receive high bootstrap support, is in accordance with the multi-gene phylogeny in Reece *et al*. (2010) that places *Scuticaria* within *Uropterygius* with high support, questioning the validity of the generic assignment in a phylogenetic context.

Uropterygius concolor Rüppell 1838—Unicolor Snakemoray
(Figure 42)

Uropterygius concolor Rüppell 1838: 83, pl. 20 (fig. 4) (Massawa, Eritrea, Red Sea). Lectotype, SMF 746, designated by Böhlke 1982: 40.—Goren & Dor 1994: 7; Randall & Golani 1995: 871; Golani & Bogorodsky 2010: 11; Golani & Fricke 2018: 23.

Gymnomuraena concolor: Klunzinger 1871: 620.

FIGURE 41. *Scuticaria tigrina*. **A**: alive, Dahab, Egypt; **B**: SMF 35823 [KAU13-680], 553 mm TL, fresh specimen, Obhur, Jeddah, Saudi Arabia. Photo by A. Ryanskiy (A), S.V. Bogorodsky (B).

Red Sea material. ***Egypt***: USNM 410630 (1, 89), Sharm el Sheikh, Sharm el Moya. ***Saudi Arabia***: KAUMM 411 [KAU12-1084] (1, 71), Farasan Archipelago; KAUMM 412 [KAU12-1086] (1, 189), Al Lith; KAUMM 413 [KAU12-1089] (1, 108), Al Lith; SMF 35824 [KAU12-309] (1, 176), Farasan Archipelago; SMF 35825 [KAU13-288] (1, 118), Al Wajh; SMF 35826 [KAU13-346] (1, 178), Al Wajh (marbled); SMF 33615 (1, 153), Al Lith (mar-

bled). ***Eritrea***: HUJ 4939 (1, 191), Dahlak Archipelago; HUJ 15127 (1, 146), Dahlak Archipelago; SMF 746 (1, 218, lectotype of *Uropterygius concolor*), Massawa; SMF 7422 (1, 188, paralectotype of *Uropterygius concolor*), Massawa; USNM 235348 (5, 151–195), Melita Bay; USNM 312832 (4, 131–187), Dahlak Archipelago, Delemmi; USNM 312833 (1, 144), Dahlak Archipelago, Harat Island; USNM 397544 (1, 145), Massawa.

Description. In TL: preanal length 2.1–2.5, head length 8.1–10, body depth at anus 20–34. In head length: snout length 5.9–9.3, eye diameter 9.1–13, upper-jaw length 2.4–3.6. Pores: LL 1, SO 3, IO 4, POM 6. Vertebrae: predorsal 107–115, pre-anus 47–50, pre-anal fin 109–118, total 117–124.

Body moderate; anus before midlength; gill opening at mid-side. Snout moderate, jaws about equal length. Eye moderate, over middle of upper jaw. Anterior nostril tubular; posterior nostril above anterior margin of eye.

Teeth biserial, conical, smooth, those of intermaxillary and maxillary continuous, the outer series small and numerous, the inner series longer and fewer; the inner maxillary row extends almost to posterior end of jaw. Two median intermaxillary teeth. Dentary teeth biserial, those of inner row larger than those of outer; the inner row extending a half to two-thirds the length of outer row. Vomerine teeth uniserial.

Color: medium brown, usually uniform, occasionally with irregular, indistinct pale markings. Head pores white. Conspicuous rows of small, white neuromasts on head and along lateral line. In life branchial cavity in a diffuse dark magenta blotch.

FIGURE 42. *Uropterygius concolor*. **A**: SMF 35825 [KAU13-288], 118 mm TL, alive, Al Wajh, Saudi Arabia; **B**: SMF 35826 [KAU13-346], 178 mm TL, alive, Al Wajh, Saudi Arabia. Photos by S.V. Bogorodsky.

Maximum size about 200–250 mm.

Distribution and habitat. Occurrence and distribution outside the Red Sea is uncertain. The name has been widely applied to small, brown *Uropterygius* in the Indo-Pacific, but it is not certain whether all of these represent the same species. Further studies are needed. Specimens were collected from fringing reefs of seaward reef from depths of 3–15 m.

Remarks. There are no obvious differences between the plain-colored and patterned specimens. They are identical in dentition, pore pattern, position of the gill opening, and number of vertebrae, and we presume that they are simply color phases of the same species. The phylogeny (Fig. 48) includes, next to Red Sea specimens collected in this study, specimens originally identified as *Uropterygius concolor* (here *Uropterygius* cf. *concolor*) from the southwestern Indian Ocean (South Africa), the southeastern Indian Ocean (Western Australia) and the South Pacific (Society Islands), which all form well divergent clades and presumably represent a number of different species. Closest of these clades to the Red Sea *Uropterygius concolor* (with type locality in Massawa, Eritrea) is *Uropterygius* cf. *concolor* from the Southwest Indian Ocean (South Africa), with which it is placed in a joint clade with moderately high bootstrap support.

Uropterygius genie Randall & Golani 1995—Genie's Snakemoray
(Figure 43A)

Uropterygius genie Randall & Golani 1995: 872, figs. 7–9 (Ras Muhammad, Sinai Peninsula, Red Sea). Holotype, HUJ 5863.—Golani & Bogorodsky 2010: 11; Golani & Fricke 2018: 23.

Red Sea material. ***Egypt***: HUJ 5863 (1, 178, holotype), Ras Muhammad; USNM 312814 (1, 118, paratype), bay at El Himeira.

Description. In TL: preanal length 2.2, head length 9.4–9.7, body depth at anus 23–24. In head length: snout length 7.9–8.5, eye diameter 8.8–9.6, upper-jaw length 2.7. Pores: LL 1, SO 3, IO 4, POM 6. Vertebrae: predorsal 102–105, pre-anus 52–54, pre-anal fin 111–114, total 121–122.

Body moderate; anus before midlength; gill opening above mid-side. Snout moderate, jaws about equal length. Eye moderate, closer to tip of snout than to rictus. Anterior nostril tubular; posterior nostril above anterior half of eye.

Teeth multiserial, conical, slender, and smooth, the inner teeth larger. Intermaxillary and maxillary teeth continuous, in about 4 rows. Median intermaxillary teeth 4. Dentary teeth in 4 series anteriorly, the inner teeth larger, becoming uniserial posteriorly. Vomerine teeth needle-like, 6 subequal teeth in a single row.

Color: uniform medium brown, fins yellowish brown, head pores and nostrils white, inside of mouth white.

Maximum size at least 178 mm.

Distribution and habitat. Known from the Red Sea, in shallow water. At present known from two specimens only, the holotype from Ras Mohammed at the southern end of the Sinai Peninsula and the paratype from the bay at El Himeira, Gulf of Aqaba. The paratype was collected from a coastal reef from a depth given as 0–18 m.

Remarks. Although this species is known only from the Red Sea, similar small, brown *Uropterygius* with multiserial teeth have recently been found at scattered locations in the Indian Ocean and South Pacific. Further study is needed to determine their relationship to each other and to *Uropterygius genie*. *Uroptergygius fuscoguttatus* Schultz and *U. supraforatus* (Regan) also have multiserial dentition, but they are larger and have distinctive color patterns. No tissue samples or COI sequences are available for analyzing the phylogenetic relationships of this species.

Uropterygius golanii McCosker & Smith 1997— Golani's Snakemoray
(Figure 43B)

Uropterygius golanii McCosker & Smith 1997: 1011, fig. 3 (Strait of Jubal, S end of Sinai Peninsula at Ras Muhammed, Egypt, Red Sea, 0–10 m). Holotype, USNM 312830.—Golani & Bogorodsky 2010: 11; Golani & Fricke 2018: 24.

Red Sea material. ***Israel***: HUJ 5266 (2, 426–453, paratypes), Eilat. ***Egypt***: USNM 312830 (1, 404, holotype), Strait of Jubal; USNM 312831 (1, 291, paratype), Gulf of Aqaba, bay between Marsa Mokrakh and El Himeira [erroneously cited as 31281 in McCosker & Smith 1997].

Description. In TL: preanal length 2.0–2.1, head length 11–13, body depth at anus 21–25. In head length: snout length 4.5–4.9, eye diameter 11–13, upper-jaw length 2.6–2.7. Pores: LL 1, SO 3, IO 4, POM 6. Vertebrae: predorsal 134–138, pre-anus 60–68, pre-anal fin 136–141, total 145–148.

Body moderate; anus before midlength; gill opening at mid-side. Snout moderate, jaws about equal length. Eye moderate, over middle of upper jaw. Anterior nostril tubular; posterior nostril in a short tube, above mid-eye.

Teeth conical or wedge-shaped, smooth. Intermaxillary teeth in five rows across: a peripheral series of small, wedge-shaped teeth, an intermediate series of 3 teeth on each side, and 3 median teeth. Maxillary teeth uniserial, small and wedge-shaped, continuous with peripheral intermaxillary teeth. Dentary teeth biserial, with 3 larger, conical inner teeth anteriorly and 13–22 smaller, wedge-shaped outer teeth. Vomerine teeth 3–5, uniserial or staggered.

Color: uniform brown, without markings.

Maximum size at least 453 mm.

Distribution and habitat. Found only in the Red Sea, known records from Eilat to southern tip of Ras Muhammad, in shallow water, less than 10 m deep.

Remarks. This species is apparently endemic to the Red Sea, but a closely related form, *U. xenodontus* McCosker & Smith, occurs in the central and western Pacific. The dentition of these two species and *U. inornatus* Gosline is atypical for *Uropterygius* and more closely resembles the pattern found in many species of *Gymnothorax*. It is uncommon, known so far only from the type series, and no tissue samples or COI sequences are available for analyzing the phylogenetic relationships of this species.

FIGURE 43. A: *Uropterygius genie*, HUJ 5863, preserved holotype, 178 mm TL, Ras Muhammad, Egypt. **B**: *Uropterygius golanii*, HUJ 5266, preserved paratype, 426 mm TL, Strait of Jubal, Egypt. Photos by D. Golani.

Uropterygius macrocephalus (Bleeker 1864)—Largehead Snakemoray

(Figure 44)

Gymnomuraena macrocephalus Bleeker 1864: 54 (Ambon I., Molucca Is., Indonesia). Holotype (unique), BMNH 1867.11.28.335.
Uropterygius makatei Gosline: Randall & Golani 1995: 874.
Uropterygius macrocephalus: Golani & Bogorodsky 2010: 11; Golani & Fricke 2018: 24.

Red Sea material. ***Egypt***: HUJ 9418 (1, 136), Gulf of Aqaba, Nabq.

Comparative material. ***Mauritius***: USNM 342094 (8, 102–299). ***Réunion***: MNHN B.3140 (1, 236). ***Indonesia***: BMNH 1867.11.28.335 (1, 185, holotype). ***Marshall Is.***: BPBM 29073 (1, 320). ***Fiji***: USNM 259858 (2, 160–135). ***French Polynesia***, Marquesas Is.: USNM 409356 [MARQ-356] (1, 158). Austral Is.: USNM 424083 (1, 227).

Description. In TL: preanal length 1.8–2.4, head length 6.3–8.3, body depth at anus 16–28. In head length: snout length 5.3–8.7, eye diameter 14–19, upper-jaw length 2.6–3.8. Pores: LL 1, SO 3, IO 4, POM 6. Vertebrae (Red Sea specimen in parentheses): predorsal 90–99 (97), pre-anus 41–44, pre-anal fin 92–99 (98), total 103–115 (108); the holotype has 103 vertebrae.

Body moderate; anus before midlength; gill opening below mid-side. Snout moderate, jaws about equal length. Eye rather small, over middle of upper jaw. Anterior nostril tubular; posterior nostril above anterior margin of eye.

Teeth biserial, conical, smooth. Intermaxillary teeth in five rows across, peripheral teeth small, intermediate and median teeth larger; 2–3 median teeth. Maxilla with an inner series of larger, depressible teeth and an outer series of smaller teeth, both series continuous with intermaxillary teeth, the combined inner series with 9–18 teeth, the outer with 27–40. Dentary with 8–16 large inner teeth and 29–49 smaller outer teeth. Vomerine teeth uniserial, long, conical, about 4–9.

Color: dark gray-brown, usually with several rows of complexly dendritic, light brown blotches; tip of tail pale yellowish; nostrils and head pores whitish.

Maximum size at least 429 mm.

Distribution and habitat. Throughout the Indo-Pacific from the Red Sea to the coast of Mexico and Central America; in shallow water, generally less than 15 m. Common in the Pacific, but rarely collected in the Indian Ocean.

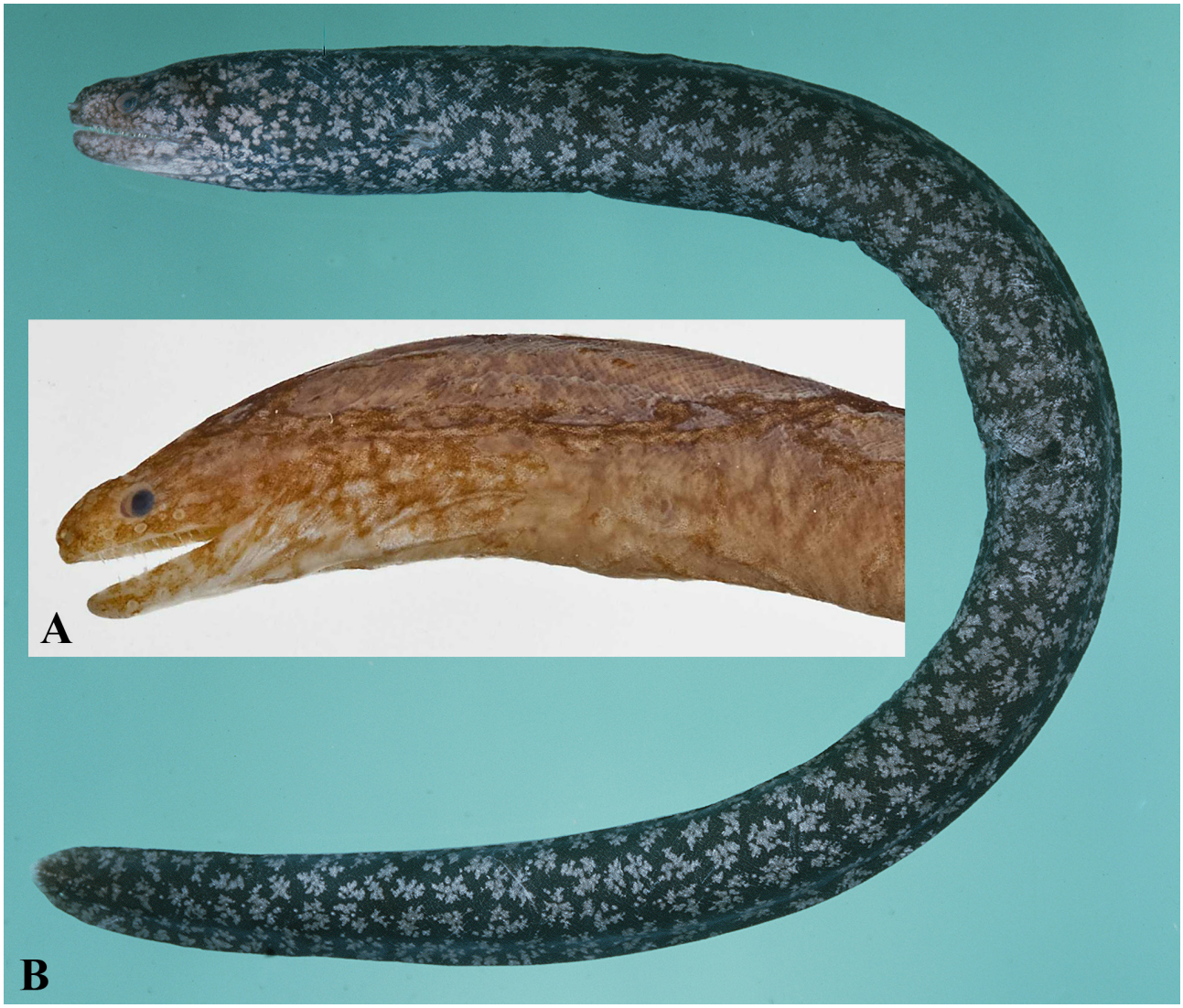


FIGURE 44. *Uropterygius macrocephalus*. **A**: HUJ 9418, 136 mm TL, preserved, Nabq, Egypt; **B**: BPBM 29073, 320 mm TL, fresh specimen, Enewetak Atoll, Marshall Islands. Photos by D. G. Smith (A), J.E. Randall (B).

Remarks. This species was reported by Randall & Golani (1995) as *Uropterygius makatei*, but the distinction of that species from *U. macrocephalus* is not clear, and recognizing it is perhaps premature. The species needs to be studied over its entire range to determine whether it is a single species or a complex. Its apparent rarity in the Indian Ocean compared to the Pacific is difficult to explain. The Mauritius specimens cited above were collected by rotenone at a shallow, rocky shore station and were among the last fishes to emerge. Perhaps they are particularly

resistant to rotenone and thus more difficult to collect. That does not explain their apparent abundance in the Pacific, however. The only other record from the Indian Ocean that we are aware of is a specimen reported by Quéro & Saldanha (1995) collected more than a century ago at Réunion (MNHN B.3140). The first author examined this specimen recently in Paris and confirmed its identification. In the COI-based phylogeny (Fig. 48), four close but well divergent clades from various localities have been identified as *U. macrocephalus*, and we are currently unable to decide, which (if any) of these represents the species.

Uropterygius micropterus (Bleeker 1852)—Shortfin Snakemoray
(Figure 45)

Muraena micropterus Bleeker 1852: 298 (Wahai, northern Ceram, Indonesia). Lectotype, BMNH 1867.11.28.326, designated by Böhlke & Smith 2002: 162.
Uropterygius micropterus: Randall & Golani 1995: 874; Golani & Bogorodsky 2010: 11; Golani & Fricke 2018: 24.

Red Sea material. ***Red Sea***: HUJ 17559 (1, 220), Gulf of Aqaba.

Comparative material. ***Indonesia***: BMNH 1867.11.28.326 (1, 232, holotype); USNM 312805 (1, 200). ***Philippines***: USNM 289910 (1, 214); USNM 318405 (1, 178). ***Taiwan***: USNM 312855 (1, 239). ***Mariana Is.***: ANSP 71585 (1, 188, holotype of *Uropterygius tinkhami* Fowler); ANSP 71586 (1, 74, paratype of *U. tinkhami*); USNM 123942 (1, 189); USNM 132839 (3, 130–164). ***Samoa***: USNM 52284 (2, 168–170).

Description. In TL: preanal length 2.0–2.3, head length 8.1–9.9, body depth at anus 17–27. In head length: snout length 6.4–8.6, eye diameter 11–18, upper-jaw length 2.7–3.7. Pores: LL 1, SO 3, IO 4, POM 6. Vertebrae: predorsal 102–110, pre-anus 49–53, pre-anal fin 104–111, total 113–121.

Body moderate; anus slightly before midlength. Head moderate, jaws equal. Gill opening at mid-side. Eye moderate, slightly closer to tip of snout than to rictus. Anterior nostril tubular; posterior nostril above anterior margin of eye.

Teeth slender, conical, smooth. Intermaxillary with a peripheral row of small teeth, an intermediate row of 2–3 larger teeth, and 3 large, depressible median teeth. Maxillary teeth in two rows, the outer row small and closely set, the inner row larger and fewer; the two rows continuous with intermaxillary teeth. Dentary teeth biserial, the outer teeth small and numerous, the inner teeth larger and fewer. About 12 vomerine teeth in single row.

FIGURE 45. *Uropterygius micropterus*, 320 mm TL, fresh specimen, Iriomote Is., Japan. Photo by K. Hatooka.

Color: light brown with irregular dark brown lines on upper two-thirds of head and body, partly interconnected to form a fine reticulum.

Maximum size about 250 mm.

Distribution and habitat. Indo-Pacific from the Red Sea south to South Africa (Durban), east to the Line Islands, Phoenix Islands, and Samoa Islands. Reported from rubble areas of intertidal reef flats, tide pools, and shallow reefs to a depth of 10 m.

Remarks. Randall & Golani (1995) reported the single record from the Red Sea based on a specimen from the Gulf of Aqaba. No obvious geographic variation is evident. Mitochondrial COI barcodes were retrieved for four specimens from BOLD (none of them from the Red Sea), and as they showed no substantial variation only one of them (FTWS419-09 from Taiwan) was included in the phylogeny (Fig. 48). Specimens in this clade, originally identified as *Strophidon sathete* (a species of the subfamily Muraeninae), were re-assigned herein as *Uropterygius micropterus* (see also Huang *et al*. 2019). The species forms part of a moderately well supported clade with lineages under the name *U. macrocephalus* (see remarks for *U. macrocephalus*).

Uropterygius nagoensis Hatooka 1984—Reticulate Snakemoray
(Figure 46)

Uropterygius nagoensis Hatooka 1984: 20, figs. 1–4 (Nago fish market, Okinawa I., Ryukyu Is.). Holotype (unique), FAKU 51431.—Randall & Golani 1995: 875; Golani & Bogorodsky 2010: 11; Golani & Fricke 2018: 24.

Red Sea material. ***Egypt***: USNM 312825 (1, 503), Sinai Peninsula, Ras Muhammad; USNM 440340 (1, 710), Sharm el Sheikh, Sharm el Moya. ***Sudan***: BPBM 20429 (2, 152–389), Port Sudan.

Comparative material. ***Indonesia***: USNM 312826 (1, 426). ***Fiji***: USNM 259853 (1, 396). ***Tonga***: USNM 338045 (1, 378).

Description. In TL: preanal length 2.0–2.2, head length 9.2–11, body depth at anus 19–23. In head length: snout length 6.1–7.1, eye diameter 12, upper-jaw length 2.5–2.7. Pores: LL 0–1, SO 3, IO 4, POM 6. Vertebrae: predorsal 115–116, pre-anus 61–65, preanal-fin 121–123, total 135–140.

Body moderate; anus slightly before midlength. Snout moderate, jaws about equal length. Eye relatively small, closer to tip of snout than to rictus. Gill opening at upper third of side. Anterior nostril tubular; posterior nostril above anterior margin of eye. Branchial pore present or absent.

Teeth slender, conical, smooth. Intermaxillary teeth in five rows across, peripheral teeth small, intermediate and median teeth larger; two median teeth. Maxillary teeth in 3–4 series anteriorly, biserial posteriorly, the outermost small and closely set, the innermost long and depressible. Dentary teeth in three irregular series anteriorly, uniserial posteriorly. Two or three vomerine teeth in a single row.

Color: tan with large, dendritic, vertically aligned dark brown markings interconnected to form a coarse reticular pattern; an irregular white band across interorbital space.

Maximum size about 800 mm.

Distribution and habitat. Known from widely scattered locations in the western and central Pacific and from the Red Sea; uncommon. In addition to the specimens recorded here, Randall & Golani (1995: 876) reported specimens from the Society and Solomon Islands. Other localities are Japan (type locality), Taiwan, Papua New Guinea, and Australia. In the Indian Ocean known only from the Red Sea. Red Sea records are from caves of fringing reefs at depths of 3–13 m.

Remarks. Randall & Golani (1995) reported the first Red Sea record based on two specimens from Sudan and one from Ras Muhammed, Sinai Peninsula. Two additional specimens were collected by the second author from Sharm el Moya, one of them (USNM 440340) is the one of the largest specimens known for the species, 710 mm TL. There is no significant morphological variation over its range; three specimens from the Red Sea have 136–139 vertebrae, and four specimens from the western Pacific have 135–140. Both Hatooka (1984) and Randall & Golani (1995) stated that there were no lateral-line pores anterior to the gill opening, but some specimens we examined clearly have one. The apparent absence of this moderately large species from elsewhere in the Indian Ocean is surprising. No tissue samples or COI sequences are available for analyzing the phylogenetic relationships of this species.

FIGURE 46. *Uropterygius nagoensis*, USNM 440340, 710 mm TL, fresh specimen, Sharm el Moya, Egypt. Photo by S.V. Bogorodsky.

Uropterygius polyspilus (Regan 1909)—Largespotted Snakemoray
(Figure 47)

Gymnomuraena polyspila Regan 1909: 438 (Tahiti, Society Is.). Holotype (unique), BMNH 1909.12.14.23.
Uropterygius polyspilus: Marshall 1952: 224; Dor 1984: 30; Goren & Dor 1994: 7; Randall & Golani 1995: 876; Golani & Bogorodsky 2010: 11; Golani & Fricke 2018: 24.

Red Sea material. ***Israel***: USNM 312859 (1, 495), Eilat.

Comparative material. ***Seychelles***: USNM 264162 (1, 410). ***Guam***: USNM 312858 (1, 542). ***Samoa***: USNM 115910 (2, 140–175). ***Johnston I.***: USNM 26823 (1, 441).

Description. In TL: preanal length 2.0–2.1, head length 10–11, body depth at anus 24–32. In head length: snout length 6.0–8.1, eye diameter 10–15, upper-jaw length 3.1–4.2. Pores: LL 1, SO 3, IO 4, POM 6. Vertebrae: predorsal 120–128, pre-anus 60–65, pre-anal fin 122–128, total 127–136.

Body moderate; anus near midlength. Snout moderate, jaws about equal length. Eye moderate, over middle of upper jaw. Gill opening at mid-side. Anterior and posterior nostrils tubular; posterior nostril tubular, above middle of eye.

Teeth slender, conical, smooth. Intermaxillary teeth in five rows across, peripheral teeth small, intermediate and median teeth larger; 3–4 median teeth. Maxillary teeth biserial; outer teeth small and closely spaced, continuous with peripheral intermaxillary teeth; inner teeth long and depressible, continuous with intermediate intermaxillary teeth, inner row extends about as far back as outer row. Dentary teeth biserial, the outer small and closely spaced, the inner larger and fewer. Vomerine teeth uniserial.

Color: tan to white, with rounded dark brown spots; spots on head smaller than those on body; nostrils white.

Maximum size at least 780 mm.

Distribution and habitat. Widespread but known from scattered localities; in the Indian Ocean including the Red Sea, Zanzibar, Comoro Islands, Seychelles, and Chagos Archipelago; in the western Pacific from Australia (Great Barrier Reef), Vietnam, the Philippines, Caroline Islands, Hawaiian Islands, Johnston Island, Samoa Islands, Line Islands, and Society Islands. Most records from reef flats but reported from coral reefs at depth of 18 m.

Remarks. The first Red Sea record is based on a specimen of 202 mm in length from Sanafir Island at the en-

trance to the Gulf of Aqaba (Marshall 1952). One individual was photographed by J.E. Randall off Jeddah, Saudi Arabia. May easily be confused in the field with *Scuticaria tigrina*, which has a similar color pattern, but it differs in having the anus at midlength of body, preanal length 2.0–2.1 in TL (*vs*. anus much closer to tail in *S. tigrina*, 1.3–1.6 in TL), fewer vertebrae (127–136 *vs*. 166–170), and having more scattered spots on body and a large spot on postorbital head between eye and gill opening below level of eye (*vs*. body with combination of large and small spots, and large spot on postorbital head between eye and gill opening at level of eye). No tissue samples or COI sequences are available for analyzing the phylogenetic relationships of this species.

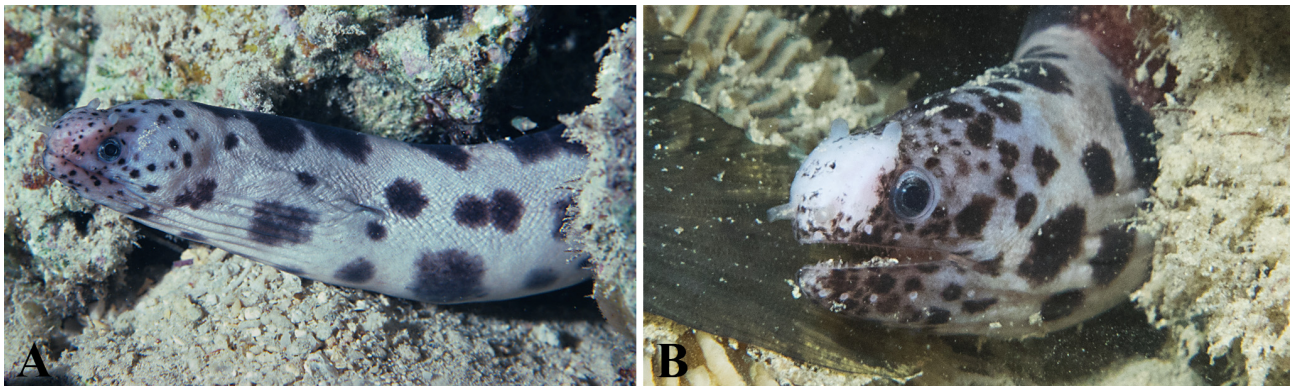
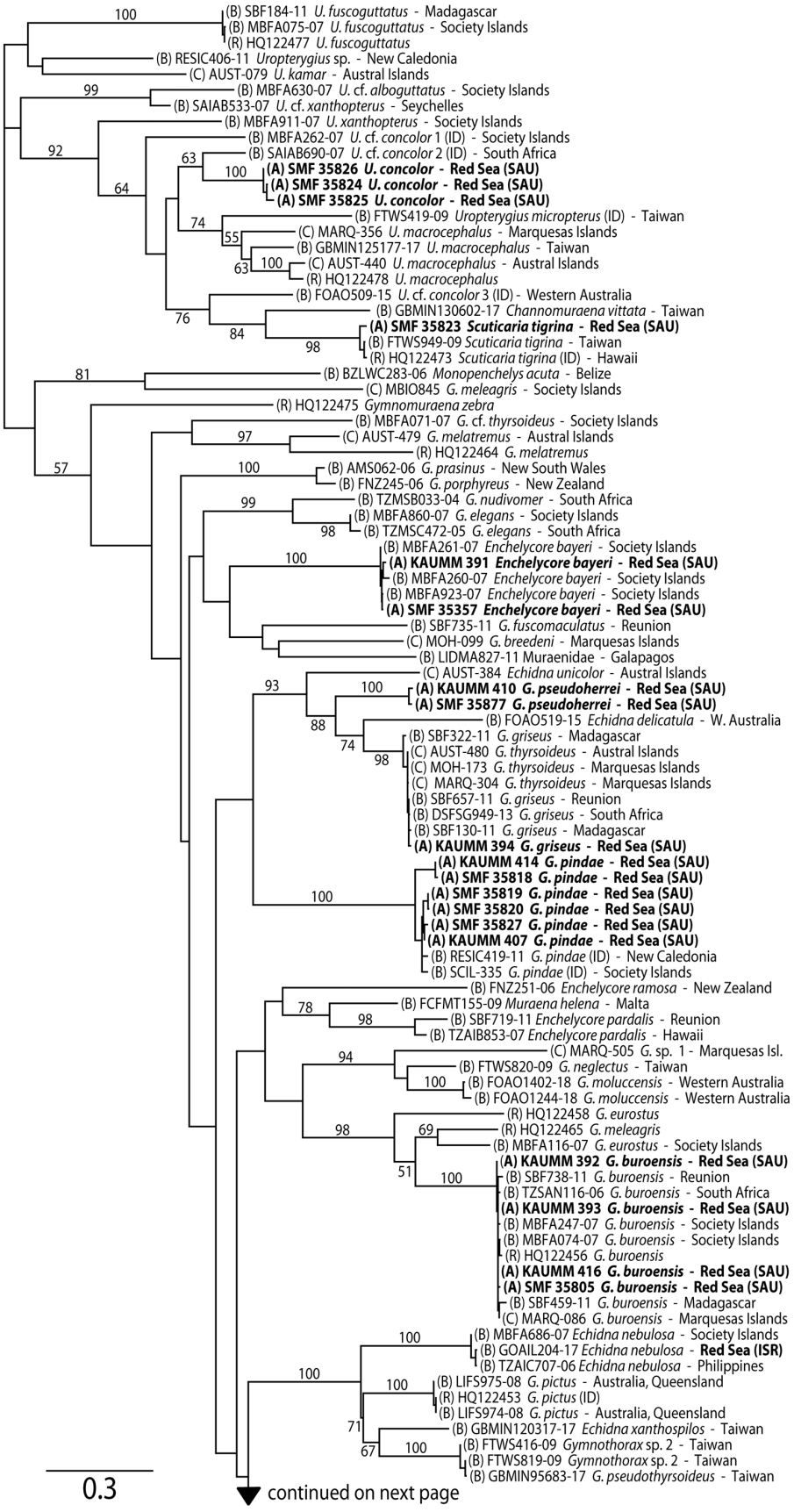


FIGURE 47. *Uropterygius polyspilus*. **A**: alive, Jeddah, Saudi Arabia; **B**: alive, Lahami Bay, southern Egypt. Photos by J.E. Randall (A), S.V. Bogorodsky (B).

Discussion

As currently defined, the family Muraenidae contains 16 genera. However, the monophyly of some of these genera, for example *Echidna*, *Enchelycore* and *Gymnothorax* is not supported by molecular evidence (see Fig. 48 and remarks on *Gymnothorax griseus*). *Echidna* is characterized by its blunt, molariform dentition, but this character is related to feeding habits and has apparently evolved more than once (Reece *et al*. 2010). *Enchelycore* is recognized on the basis of the sharp teeth and the strongly arched jaws that leave the teeth exposed when the mouth is closed. This character, too, has apparently evolved more than once, and the genus needs to be defined more precisely. *Gymnothorax* as it is currently recognized contains what is left after the other more distinctive genera have been removed. Much work remains to be done on the phylogenetic relationships within the Muraenidae. The COI-based approach used herein certainly is useful to show levels of deeper intraspecific variation and of divergence among closely related species, but as was expected, this relatively fast evolving protein coding sequence is not suited to show deeper phylogenetic divergence and consequently most of the early diverging branches of the tree did not receive substantial support in bootstrapped analyses. However, this was not the aim of the present study, which was (1) to establish barcodes for as many as possible moray species of the Red Sea, (2) to add information on the phylogeographic pattern of variation as inferred from COI barcodes and (3) to show close phylogenetic relations (if any exist) with other moray species/lineages. The first aim was achieved by establishing COI barcodes for seven Red Sea species, for which no data at all were available (including the new Red Sea species *G. pharaonis*). The second aim was met by jointly analyzing COI barcodes with sequence data from other regions of the distribution ranges of seven Red Sea moray species. Here, *Scuticaria tigrina*, *Gymnothorax javanicus* and *G. pindae* showed levels of genetic variation that might be interesting to look at in more detail as more samples from across the distribution ranges of the respective species become available (see remarks for the respective species). The third aim of the phylogenetic analysis could not be fully met as we acknowledge that the taxon sampling of morays must still be incomplete, although we researched all relevant public sources for sequence data that we were aware of. Also, as we limited our selection of sequences to Indo-Pacific moray species, no close relative of *Muraena helena*, a Red Sea immigrant species of Atlantic origin, was included. Nevertheless, the COI-based phylogeny presented here is to date the most comprehensive in terms of the number of included lineages of Indo-Pacific morays. This phylogeny might serve as a reference in future studies on the taxonomy and phylogenetic relationships of Indo-Pacific moray species.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(R) HQ122477 U. fuscoguttatus
(B) RESIC406-11 Uropterygius sp. - New Caledonia
(C) AUST-079 U. kamar - Austral Islands
(B) MBFA630-07 U. cf. alboguttatus - Society Islands
(B) SAIAB533-07 U. cf. xanthopterus - Seychelles
(B) MBFA911-07 U. xanthopterus - Society Islands
(B) MBFA262-07 U. cf. concolor 1 (ID) - Society Islands
(B) SAIAB690-07 U. cf. concolor 2 (ID) - South Africa
(A) SMF 35826 U. concolor - Red Sea (SAU)
(A) SMF 35824 U. concolor - Red Sea (SAU)
(A) SMF 35825 U. concolor - Red Sea (SAU)
(B) FTWS419-09 Uropterygius micropterus (ID) - Taiwan
(C) MARQ-356 U. macrocephalus - Marquesas Islands
(B) GBMIN125177-17 U. macrocephalus - Taiwan
(C) AUST-440 U. macrocephalus - Austral Islands
(R) HQ122478 U. macrocephalus
(B) FOAO509-15 U. cf. concolor 3 (ID) - Western Australia
(B) GBMIN130602-17 Channomuraena vittata - Taiwan
(A) SMF 35823 Scuticaria tigrina - Red Sea (SAU)
(B) FTWS949-09 Scuticaria tigrina - Taiwan
(R) HQ122473 Scuticaria tigrina (ID) - Hawaii
(B) BZLWC283-06 Monopenchelys acuta - Belize
(C) MBIO845 G. meleagris - Society Islands
(R) HQ122475 Gymnomuraena zebra
(B) MBFA071-07 G. cf. thyrsoideus - Society Islands
(C) AUST-479 G. melatremus - Austral Islands
(R) HQ122464 G. melatremus
(B) AMS062-06 G. prasinus - New South Wales
(B) FNZ245-06 G. porphyreus - New Zealand
(B) TZMSB033-04 G. nudivomer - South Africa
(B) MBFA860-07 G. elegans - Society Islands
(B) TZMSC472-05 G. elegans - South Africa
(B) MBFA261-07 Enchelycore bayeri - Society Islands
(A) KAUMM 391 Enchelycore bayeri - Red Sea (SAU)
(B) MBFA260-07 Enchelycore bayeri - Society Islands
(B) MBFA923-07 Enchelycore bayeri - Society Islands
(A) SMF 35357 Enchelycore bayeri - Red Sea (SAU)
(B) SBF735-11 G. fuscomaculatus - Reunion
(C) MOH-099 G. breedeni - Marquesas Islands
(B) LIDMA827-11 Muraenidae - Galapagos
(C) AUST-384 Echidna unicolor - Austral Islands
(A) KAUMM 410 G. pseudoherrei - Red Sea (SAU)
(A) SMF 35877 G. pseudoherrei - Red Sea (SAU)
(B) FOAO519-15 Echidna delicatula - W. Australia
(B) SBF322-11 G. griseus - Madagascar
(C) AUST-480 G. thyrsoideus - Austral Islands
(C) MOH-173 G. thyrsoideus - Marquesas Islands
(C) MARQ-304 G. thyrsoideus - Marquesas Islands
(B) SBF657-11 G. griseus - Reunion
(B) DSFSG949-13 G. griseus - South Africa
(B) SBF130-11 G. griseus - Madagascar
(A) KAUMM 394 G. griseus - Red Sea (SAU)
(A) KAUMM 414 G. pindae - Red Sea (SAU)
(A) SMF 35818 G. pindae - Red Sea (SAU)
(A) SMF 35819 G. pindae - Red Sea (SAU)
(A) SMF 35820 G. pindae - Red Sea (SAU)
(A) SMF 35827 G. pindae - Red Sea (SAU)
(A) KAUMM 407 G. pindae - Red Sea (SAU)
(B) RESIC419-11 G. pindae (ID) - New Caledonia
(B) SCIL-335 G. pindae (ID) - Society Islands
(B) FNZ251-06 Enchelycore ramosa - New Zealand
(B) FCFMT155-09 Muraena helena - Malta
(B) SBF719-11 Enchelycore pardalis - Reunion
(B) TZAIB853-07 Enchelycore pardalis - Hawaii
(C) MARQ-505 G. sp. 1 - Marquesas Isl.
(B) FTWS820-09 G. neglectus - Taiwan
(B) FOAO1402-18 G. moluccensis - Western Australia
(B) FOAO1244-18 G. moluccensis - Western Australia
(R) HQ122458 G. eurostus
(R) HQ122465 G. meleagris
(B) MBFA116-07 G. eurostus - Society Islands
(A) KAUMM 392 G. buroensis - Red Sea (SAU)
(B) SBF738-11 G. buroensis - Reunion
(B) TZSAN116-06 G. buroensis - South Africa
(A) KAUMM 393 G. buroensis - Red Sea (SAU)
(B) MBFA247-07 G. buroensis - Society Islands
(B) MBFA074-07 G. buroensis - Society Islands
(R) HQ122456 G. buroensis
(A) KAUMM 416 G. buroensis - Red Sea (SAU)
(A) SMF 35805 G. buroensis - Red Sea (SAU)
(B) SBF459-11 G. buroensis - Madagascar
(C) MARQ-086 G. buroensis - Marquesas Islands
(B) MBFA686-07 Echidna nebulosa - Society Islands
(B) GOAIL204-17 Echidna nebulosa - Red Sea (ISR)
(B) TZAIC707-06 Echidna nebulosa - Philippines
(B) LIFS975-08 G. pictus - Australia, Queensland
(R) HQ122453 G. pictus (ID)
(B) LIFS974-08 G. pictus - Australia, Queensland
(B) GBMIN120317-17 Echidna xanthospilos - Taiwan
(B) FTWS416-09 Gymnothorax sp. 2 - Taiwan
(B) FTWS819-09 Gymnothorax sp. 2 - Taiwan
(B) GBMIN95683-17 G. pseudothyrsoideus - Taiwan
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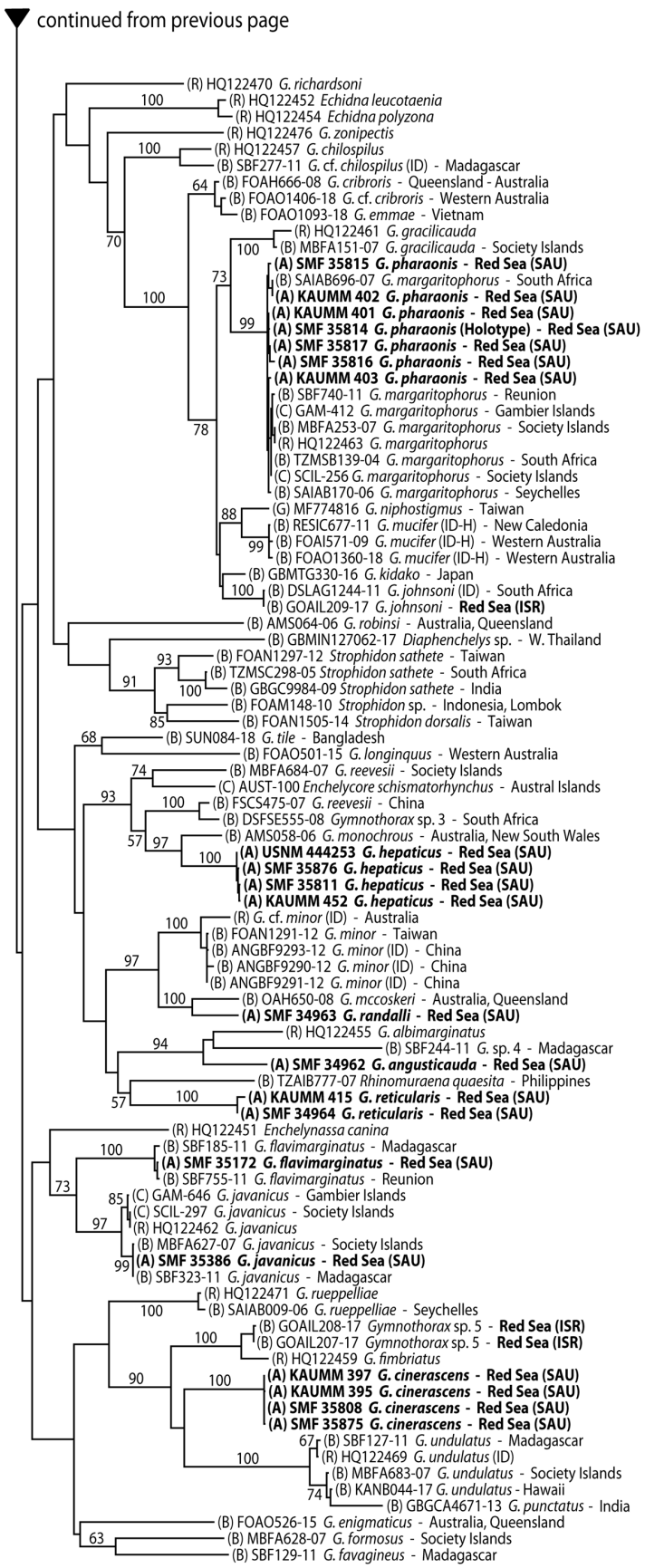
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(R) HQ122470 G. richardsoni
(R) HQ122452 Echidna leucotaenia
(R) HQ122454 Echidna polyzona
(R) HQ122476 G. zonipectis
(R) HQ122457 G. chilospilus
(B) SBF277-11 G. cf. chilospilus (ID) - Madagascar
(B) FOAH666-08 G. cribroris - Queensland - Australia
(B) FOAO1406-18 G. cf. cribroris - Western Australia
(B) FOAO1093-18 G. emmae - Vietnam
(R) HQ122461 G. gracilicauda
(B) MBFA151-07 G. gracilicauda - Society Islands
(A) SMF 35815 G. pharaonis - Red Sea (SAU)
(B) SAIAB696-07 G. margaritophorus - South Africa
(A) KAUMM 402 G. pharaonis - Red Sea (SAU)
(A) KAUMM 401 G. pharaonis - Red Sea (SAU)
(A) SMF 35814 G. pharaonis (Holotype) - Red Sea (SAU)
(A) SMF 35817 G. pharaonis - Red Sea (SAU)
(A) SMF 35816 G. pharaonis - Red Sea (SAU)
(A) KAUMM 403 G. pharaonis - Red Sea (SAU)
(B) SBF740-11 G. margaritophorus - Reunion
(C) GAM-412 G. margaritophorus - Gambier Islands
(B) MBFA253-07 G. margaritophorus - Society Islands
(R) HQ122463 G. margaritophorus
(B) TZMSB139-04 G. margaritophorus - South Africa
(C) SCIL-256 G. margaritophorus - Society Islands
(B) SAIAB170-06 G. margaritophorus - Seychelles
(G) MF774816 G. niphostigmus - Taiwan
(B) RESIC677-11 G. mucifer (ID-H) - New Caledonia
(B) FOAI571-09 G. mucifer (ID-H) - Western Australia
(B) FOAO1360-18 G. mucifer (ID-H) - Western Australia
(B) GBMTG330-16 G. kidako - Japan
(B) DSLAG1244-11 G. johnsoni (ID) - South Africa
(B) GOAIL209-17 G. johnsoni - Red Sea (ISR)
(B) AMS064-06 G. robinsi - Australia, Queensland
(B) GBMIN127062-17 Diaphenchelys sp. - W. Thailand
(B) FOAN1297-12 Strophidon sathete - Taiwan
(B) TZMSC298-05 Strophidon sathete - South Africa
(B) GBGC9984-09 Strophidon sathete - India
(B) FOAM148-10 Strophidon sp. - Indonesia, Lombok
(B) FOAN1505-14 Strophidon dorsalis - Taiwan
(B) SUN084-18 G. tile - Bangladesh
(B) FOAO501-15 G. longinquus - Western Australia
(B) MBFA684-07 G. reevesii - Society Islands
(C) AUST-100 Enchelycore schismatorhynchus - Austral Islands
(B) FSCS475-07 G. reevesii - China
(B) DSFSE555-08 Gymnothorax sp. 3 - South Africa
(B) AMS058-06 G. monochrous - Australia, New South Wales
(A) USNM 444253 G. hepaticus - Red Sea (SAU)
(A) SMF 35876 G. hepaticus - Red Sea (SAU)
(A) SMF 35811 G. hepaticus - Red Sea (SAU)
(A) KAUMM 452 G. hepaticus - Red Sea (SAU)
(R) G. cf. minor (ID) - Australia
(B) FOAN1291-12 G. minor - Taiwan
(B) ANGBF9293-12 G. minor (ID) - China
(B) ANGBF9290-12 G. minor (ID) - China
(B) ANGBF9291-12 G. minor (ID) - China
(B) OAH650-08 G. mccoskeri - Australia, Queensland
(A) SMF 34963 G. randalli - Red Sea (SAU)
(R) HQ122455 G. albimarginatus
(B) SBF244-11 G. sp. 4 - Madagascar
(A) SMF 34962 G. angusticauda - Red Sea (SAU)
(B) TZAIB777-07 Rhinomuraena quaesita - Philippines
(A) KAUMM 415 G. reticularis - Red Sea (SAU)
(A) SMF 34964 G. reticularis - Red Sea (SAU)
(R) HQ122451 Enchelynassa canina
(B) SBF185-11 G. flavimarginatus - Madagascar
(A) SMF 35172 G. flavimarginatus - Red Sea (SAU)
(B) SBF755-11 G. flavimarginatus - Reunion
(C) GAM-646 G. javanicus - Gambier Islands
(C) SCIL-297 G. javanicus - Society Islands
(R) HQ122462 G. javanicus
(B) MBFA627-07 G. javanicus - Society Islands
(A) SMF 35386 G. javanicus - Red Sea (SAU)
(B) SBF323-11 G. javanicus - Madagascar
(R) HQ122471 G. rueppelliae
(B) SAIAB009-06 G. rueppelliae - Seychelles
(B) GOAIL208-17 Gymnothorax sp. 5 - Red Sea (ISR)
(B) GOAIL207-17 Gymnothorax sp. 5 - Red Sea (ISR)
(R) HQ122459 G. fimbriatus
(A) KAUMM 397 G. cinerascens - Red Sea (SAU)
(A) KAUMM 395 G. cinerascens - Red Sea (SAU)
(A) SMF 35808 G. cinerascens - Red Sea (SAU)
(A) SMF 35875 G. cinerascens - Red Sea (SAU)
(B) SBF127-11 G. undulatus - Madagascar
(R) HQ122469 G. undulatus (ID)
(B) MBFA683-07 G. undulatus - Society Islands
(B) KANB044-17 G. undulatus - Hawaii
(B) GBGCA4671-13 G. punctatus - India
(B) FOAO526-15 G. enigmaticus - Australia, Queensland
(B) MBFA628-07 G. formosus - Society Islands
(B) SBF129-11 G. favagineus - Madagascar

FIGURE 48. Unrooted maximum likelihood phylogeny of Indo-Pacific moray eels (Muraenidae) based on partial mitochondrial COI. Branch support values were obtained by 100 bootstrapped replicates; only bootstrap values above 50 percent are shown. The scale bar represents average number of nucleotide substitutions. (A) = specimen sequenced in this study; (B) = sequence retrieved from BOLD; (C) sequence retrieved from CRIOBE; (G) = sequence retrieved from GenBank; (R) = sequence retrieved from Reece *et al.* (2010); (ID) = species ID re-assigned herein; (ID-H) = specimen re-assigned as of Huang *et al.* (2019); (SAU) = collected in Saudi Arabia; (ISR) = collected in Israel.

In this paper we recognize 38 species of moray eels in the Red Sea. Of these, only three appear to be endemic to the Red Sea and are found nowhere else: *Gymnothorax baranesi*, *Uropterygius genie*, and *U. golanii*. *Gymnothorax pharaonis* is also known from Socotra. Two others, *Gymnothorax cinerascens* and *G. hepaticus* may prove to be endemic when further information is available. Lips *et al*. (2016) produced underwater photograph of moray from the inner Gulf of Aden (Djibouti), identified them as *G. monochrous*, but details of jaws are not visible and an individual cannot be positively identify as *G. cinerascens* or *G. hepaticus*. One species, *Muraena helena*, is certainly a recent immigrant that entered the Red Sea through the Suez Canal. In comparison with the closest areas, the Red Sea has 38 species of morays, whereas only 17 species are known from Oman coastal waters (Randall 1995); furthermore, only one species of Uropterygiinae (*Scuticaria tigrina*) is reported therein. Richer in species of morays are the Maldives, where 47 species are presently known (Randall & Anderson 1993; C. Anderson, pers. comm.), and India where 46 species are reported (Mohapatra *et al*. 2018; Sumod *et al*. 2019).

The absence of the genus *Anarchias* (Uropterygiinae) from the Red Sea is noteworthy. This genus of small morays occurs all over the Indo-Pacific and on both sides of the Atlantic, but it has never been taken in the Red Sea. It is found largely on oceanic islands and open coasts, and its larvae are often found far from land. Perhaps the nearly landlocked Red Sea is not favorable to its life history and larval dispersal.

Morays are typical inhabitants of coral reef areas with rich growth of corals where they can hide. However, four of 38 Red Sea species were collected from open sand bottom by trawling: *G. angusticauda*, *G. randalli*, *G. reticularis*, and *G. hepaticus*. Among them, *G. reticularis* typically lives in open areas with soft substrata at depths of 30–65 m.

Of the remaining species, 10 differ to greater or lesser extents in the number of vertebrae between those in the Red Sea and those occurring elsewhere. They are *Echidna nebulosa*, *E. polyzona*, *Gymnomuraena zebra*, *Gymnothorax buroensis*, *G. griseus*, *G. pictus*, *G. randalli*, *G. reticularis*, *G. rueppelliae*, and *Scuticaria tigrina*. In nine of these, the Red Sea populations have fewer vertebrae than those from elsewhere. Only Red Sea specimens of *Gymnothorax reticularis* have more vertebrae. The two sister species *Uropterygius golanii* and *U. xenodontus* show the same pattern, as do *Gymnothorax pharaonis* and *G. margaritophorus*. The consistency of this ratio indicates some underlying cause. Perhaps it is related to the relatively high temperature and salinity characteristic of the Red Sea. Comparative genetic data are available for only four of these 11 species. *Scuticaria tigrina* shows a slight difference between Red Sea and elsewhere, but *Echidna nebulosa*, *Gymnothorax buroensis* and *G. griseus* do not.

Interestingly, the phylogenetic analysis of the mitochondrial COI barcoding gene does not show reciprocal monophyly for two species pairs, i.e. *G. griseus*/*G. thyrsoideus* and *G. pharaonis*/*G. margaritophorus* indicating a very recent divergence of these very similar species. According to commonly found mutation rates of the mitochondrial COI gene (see e.g. Lessios 2008), the timing of the onset of divergence of the two sibling species might be as recent as the last glacial maximum (LGM), about 20 to 15 thousand years ago (Siddall *et al*. 2003), when the Red Sea was more or less effectively separated from the Western Indian Ocean and gene flow was largely restricted between the Indian Ocean and the Pacific Ocean (see e.g. Klausewitz 1989 and Bowen *et al*. 2016). It seems most likely that speciation in these pairs of sibling species was triggered in allopatry by cessation of gene flow during sea level lows during the LGM, but from the current distribution ranges of the two species alone, it is not possible to conclude, which of the two barriers is more likely to have enabled the onset of the divergence of these two species. However, while *G. griseus* is also known from other regions of the western Indian Ocean, the presently known distribution range of *G. pharaonis* is restricted to the Red Sea (and Socotra), making it more likely that the species evolved as a Red Sea endemic with subsequent range extension to nearby areas.

Two specimens in the tree (Fig. 48), GOAIL207-17 and GOAIL208-17, form a separate clade distinct from all the others. Unfortunately, the specimens were not retained and cannot be examined (T. Gurevich, pers. comm.). They could represent an undescribed species or one of the known species that has not been barcoded.

Comparative material, extralimital species. *Echidna unicolor*, USNM 423417 (1, 213), French Polynesia,

Austral Is. *Gymnothorax breedeni*, USNM 397085 (1, 137), French Polynesia, Marquesas Is. *Gymnothorax melatremus*, USNM 424049 (1, 241), French Polynesia, Austral Is. *Gymnothorax thyrsoideus*, USNM 409304 (1, 490), French Polynesia, Marquesas Is.; USNM 424169 (1, 326), French Polynesia, Austral Is. *Gymnothorax* sp. 3, USNM 409505 (1, 197), French Polynesia, Marquesas Is. *Monopenchelys acuta*, USNM 416349 (1, 116), Caribbean Sea, Belize. *Uropterygius kamar*, USNM 423320 (1, 121), French Polynesia, Austral Is.

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APPENDIX TABLE 1. Voucher specimens of moray eels (and their collection localities) used in the phylogenetic analysis of the partial sequence (652 bp) of the *mitochondrial cytochrome oxidase subunit 1* (COI) gene. (ID) = specimen was re-assigned in this study; (ID-H) = specimen was re-assigned as of Huang *et al.* (2019); (B) = BOLD-ID; (C) = CRIOBE-ID; (G) = GenBank; (M) = museum voucher/tissue number; (R) = Sequence from GenBank from Reece *et al.* (2010), n/a = not available.

Taxon	BOLD-ID	GenBank	sample identifier	Museum ID	Locality
Muraeninae					
Diaphenchelys sp.	GBMIN127062-17	LC189004	(B) LC189004	PMBC:27945	Thailand, Phuket
Echidna delicatula	FOAO519-15	n/a	(B) BW-A12951	WAM P 34446-002	Western Australia
Echidna leucotaenia	UKFBBJ978-08	(R) KF929828	(R) KU7043	SAIAB 77824	Seychelles
Echidna nebulosa	GOAIL204-17	MF123860	(B) SMNHTAU P.15098	SMNHTAU P.15098	Israel (Red Sea)
Echidna nebulosa	MBFA686-07	JQ431696	(B) MBIO1169.4	MNHN-IC-2008-0898	Society Islands
Echidna nebulosa	TZAIC707-06	FJ583380	(B) HLC-11769	n/a	Philippines
Echidna polyzona	n/a	(R) HQ122454	(R) KU4026	CAS 217396	Fiji
Echidna unicolor	n/a	n/a	(C) AUST-384	USNM 423417	Austral Islands
Echidna xanthospilos	GBMIN120317-17	KU942777	(B) KU942777	ASIZP0806544	Taiwan
Enchelycore bayeri	MBFA260-07	JQ431705	(B) MBIO437	MNHN-IC-2008-0451	Society Islands
Enchelycore bayeri	MBFA261-07	JQ431704	(B) MBIO438	MNHN-IC-2008-0452	Society Islands
Enchelycore bayeri	MBFA923-07	JQ431703	(B) MBIO1602	MNHN-IC-2008-1076	Society Islands
Enchelycore bayeri	n/a	MN243527	(M) KAU12-1058	KAUMM 391	Saudi Arabia (Red Sea)
Enchelycore bayeri	n/a	MN243528	(M) KAU13-679	SMF 35357	Saudi Arabia (Red Sea)
Enchelycore pardalis	SBF719-11	JQ349949	(B) REU1873	REU1873	Reunion
Enchelycore pardalis	TZAIB853-07	FJ583395	(B) HLC-15183	n/a	Hawaii
Enchelycore ramosa	FNZ251-06	n/a	(B) P41273	n/a	New Zealand
Enchelycore schismatorhynchus	n/a	n/a	(C) AUST-100	USNM 423413	Austral Islands
Enchelynassa canina	n/a	(R) HQ122451	n/a	n/a	Fiji
Gymnomuraena zebra	n/a	(R) HQ122475	n/a	n/a	n/a
Gymnothorax albimarginatus	n/a	(R) HQ122455	n/a	n/a	n/a
Gymnothorax angusticauda	n/a	MN243533	(M) KAU12-731	SMF 34962	Saudi Arabia (Red Sea)

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APPENDIX 1. (Continued)

Taxon	BOLD-ID	GenBank	sample identifier	Museum ID	Locality
Gymnothorax breedeni	n/a	n/a	(C, M) MOH-099	USNM 397085	Marquesas
Gymnothorax buroensis	MBFA074-07	JQ431787	(B) MBIO132	MNHN-IC-2008-0236	Society Islands
Gymnothorax buroensis	MBFA247-07	JQ431791	(B) MBIO414	MNHN-IC-2008-0435	Society Islands
Gymnothorax buroensis	SBF459-11	JQ350017	(B) NBE1261	NBE1261	Madagascar
Gymnothorax buroensis	SBF738-11	JQ350021	(B) REU1938	REU1938	Reunion
Gymnothorax buroensis	TZSAN116-06	n/a	(B) DIA1-1	n/a	South Africa
Gymnothorax buroensis	n/a	n/a	(C) MARQ-086	USNM 409086	Marquesas Islands
Gymnothorax buroensis	n/a	(R) HQ122456	n/a	n/a	n/a
Gymnothorax buroensis	n/a	MN243525	(M) KAU13-545	KAUMM 392	Saudi Arabia (Red Sea)
Gymnothorax buroensis	n/a	MN243524	(M) KAU14-813	KAUMM 393	Saudi Arabia (Red Sea)
Gymnothorax buroensis	n/a	MN243523	(M) KAU11-528	KAUMM 416	Saudi Arabia (Red Sea)
Gymnothorax buroensis	n/a	MN243526	(M) KAU14-808	SMF 35805	Saudi Arabia (Red Sea)
Gymnothorax chilospilus	n/a	(R) HQ122457	n/a	n/a	n/a
Gymnothorax cf. *chilospilus* (ID)	SBF277-11	JQ350044	(B) NBE0606	NBE0606	Madagascar
Gymnothorax cinerascens	n/a	MN243503	(M) KAU17-157	SMF 35875	Saudi Arabia (Red Sea)
Gymnothorax cinerascens	n/a	MN243500	(M) KAU12-290	KAUMM 395	Saudi Arabia (Red Sea)
Gymnothorax cinerascens	n/a	MN243502	(M) KAU13-116	KAUMM 397	Saudi Arabia (Red Sea)
Gymnothorax cinerascens	n/a	MN243501	(M) KAU12-16	SMF 35808	Saudi Arabia (Red Sea)
Gymnothorax cribroris	FOAH666-08	n/a	(B) BW-A5577	n/a (CSIRO)	Australia, Queensland
Gymnothorax cf. *cribroris*	FOAO1406-18	n/a	(B) BW-A14660	CSIRO H 8307-06	Western Australia
Gymnothorax elegans	MBFA860-07	JQ431823	(B) MBIO1462.4	MNHN2008-1016	Society Islands
Gymnothorax elegans	TZMSC472-05	JF493575	(B) Smith41.8-2	n/a	South Africa
Gymnothorax emmae	FOAO1093-18	n/a	(B) BW-A14291	NMMB unreg	Vietnam
Gymnothorax enigmaticus	FOAO526-15	n/a	(B) BW-A12958	WAM P34470-002	Australia, Queensland
Gymnothorax eurostus	MBFA116-07	JQ431800	(B) MBIO196.4	MNHN 2008-285	Society Islands
Gymnothorax eurostus	n/a	(R) HQ122458	n/a	n/a	n/a
Gymnothorax favagineus	SBF129-11	JQ350025	(B) NBE0310	NBE0310	Madagascar

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APPENDIX 1. (Continued)

Taxon	BOLD-ID	GenBank	sample identifier	Museum ID	Locality
Gymnothorax fimbriatus	n/a	(R) HQ122459	n/a	n/a	n/a
Gymnothorax flavimarginatus	SBF185-11	JQ350026	(B) NBE0449	NBE0449	Madagascar
Gymnothorax flavimarginatus	SBF755-11	JQ250027	(B) REU2583	REU2583	Reunion
Gymnothorax flavimarginatus	n/a	MN243499	(M) KAU13-583	SMF 35172	Saudi Arabia (Red Sea)
Gymnothorax formosus	MBFA628-07	JQ431798	(B) MBIO1006.4	MNHN 2008-823	Society Islands
Gymnothorax fuscomaculatus	SBF735-11	JQ250030	(B) REU1934	REU1934	Reunion
Gymnothorax gracilicauda	MBFA151-07	JQ431803	(B) MBIO244.4	MNHN 2008-319	Society Islands
Gymnothorax gracilicauda	n/a	(R) HQ122461	n/a	n/a	n/a
Gymnothorax griseus	DSFSG949-13	KU176351	(B) ADC201341.13A	n/a	South Africa
Gymnothorax griseus	SBF130-11	JQ350034	(B) NBE0311	NBE0311	Madagascar
Gymnothorax griseus	SBF322-11	JQ350035	(B) NBE1026	NBE1026	Madagascar
Gymnothorax griseus	SBF657-11	JQ350033	(B) REU1674	REU1674	Reunion
Gymnothorax griseus	n/a	MN243522	(M) KAU12-248	KAUMM 394	Saudi Arabia (Red Sea)
Gymnothorax hepaticus	n/a	MN243507	(M) KAU17-156	KAUMM 452	Saudi Arabia (Red Sea)
Gymnothorax hepaticus	n/a	MN243506	(M) KAU14-302	SMF 35811	Saudi Arabia (Red Sea)
Gymnothorax hepaticus	n/a	MN243505	(M) KAU17-139	SMF 35876	Saudi Arabia (Red Sea)
Gymnothorax hepaticus	n/a	MN243504	(M) KAU17-155	USNM 444253	Saudi Arabia (Red Sea)
Gymnothorax javanicus	MBFA627-07	JQ431806	(B) MBIO1005.4	MNHN 2008-822	Society Islands
Gymnothorax javanicus	SBF323-11	JQ350038	(B) NBE1027	NBE1027	Madagascar
Gymnothorax javanicus	n/a	n/a	(C, M) GAM-646	USNM 438468	Gambier Islands
Gymnothorax javanicus	n/a	n/a	(C, M) SCIL-297	USNM 435186	Society Islands
Gymnothorax javanicus	n/a	(R) HQ122462	n/a	n/a	n/a
Gymnothorax javanicus	n/a	MN243498	(M) KAU13-355	SMF 35386	Saudi Arabia (Red Sea)
Gymnothorax johnsoni	DSLAG1244-11	n/a	(B) ADC11-0229	n/a	South Africa
Gymnothorax johnsoni	GOAIL209-17	MF123914	(B) SMNTAU P.15114	SMNTAU P.15114	Israel
Gymnothorax kidako	GBMTG330-16	NC004417	(B) NC 004417	n/a	Japan
Gymnothorax longinquus	FOAO501-15	n/a	(B) BW-A12933	WAM P33626-002	Western Australia
Gymnothorax margaritophorus	MBFA253-07	JQ431814	(B) MBIO424.4	MNHN 2008-442	Society Islands

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APPENDIX 1. (Continued)

Taxon	BOLD-ID	GenBank	sample identifier	Museum ID	Locality
Gymnothorax margaritophorus	SAIAB170-06	n/a	(B) SAIAB T187	SAIAB 78194	Seychelles
Gymnothorax margaritophorus	SAIAB696-07	n/a	(B) SAIAB T651	n/a	South Africa
Gymnothorax margaritophorus	SBF740-11	JQ350040	(B) REU1940	REU1940	Reunion
Gymnothorax margaritophorus	TZMSB139-04	JF493579	(B) ADC 41.15-1	n/a	South Africa
Gymnothorax margaritophorus	n/a	n/a	(C, M) GAM-412	USNM 401788	Gambier Islands
Gymnothorax margaritophorus	n/a	n/a	(C, M) SCIL-256	USNM 435145	Society Islands
Gymnothorax margaritophorus	n/a	(R) HQ122463	n/a	n/a	n/a
Gymnothorax mccoskeri	FOAH650-08	n/a	(B) BW-A5561	n/a	Australia Queensland
Gymnothorax melatremus	n/a	n/a	(C, M) AUST-479	USNM 424049	Austral Islands
Gymnothorax melatremus	n/a	(R) HQ122464	n/a	n/a	n/a
Gymnothorax meleagris	n/a	n/a	(C, M) MBIO845	MNHN 2008-0715	Society Islands
Gymnothorax meleagris	n/a	(R) HQ122465	n/a	n/a	n/a
Gymnothorax minor	ANGBF9290-12	HM461877	(B) HM461877	n/a	China
Gymnothorax minor	ANGBF9291-12	HM461873	(B) HM461873	n/a	China
Gymnothorax minor	ANGBF9293-12	HM461872	(B) HM461872	n/a	China
Gymnothorax minor	FOAN1291-12	n/a	(B) BW-A12084	CSIRO H7394-04	Taiwan
Gymnothorax cf. *minor* (ID)	n/a	(R) HQ122466	n/a	n/a	Australia
Gymnothorax moluccensis	FOAO1244-18	n/a	(B) BW-A14469	CSIRO H8221-03	Western Australia
Gymnothorax moluccensis	FOAO1402-18	n/a	(B) BW-A14656	CSIRO H8306-02	Western Australia
Gymnothorax monochrous	AMS058-06	n/a	(B) AMS I.41297-062	AMS I.41297-062	Australia, New South Wales
Gymnothorax mucifer (ID-H)	RESIC677-11	n/a	(B) MNHN PE796	MNHN 2010-1750	New Caledonia
Gymnothorax mucifer (ID-H)	FOAI571-09	HM422395	(B) BW-A6498	CSIRO H6465-01	Western Australia
Gymnothorax mucifer (ID-H)	FOAO1360-18	n/a	(B) BW-A14607	CSIRO H8275-01	Western Australia
Gymnothorax neglectus	FTWS820-09	n/a	(B) ASIZP0803273	ASIZP0803273	Taiwan
Gymnothorax niphostigmus	n/a	MF774816	(G) n/a	n/a	Taiwan
Gymnothorax nudivomer	TZMSB033-04	JF493583	(B) ADC 41.19-2	n/a	South Africa
Gymnothorax pharaonis	n/a	MN243490	(M) KAU13-286	KAUMM 401	Saudi Arabia (Red Sea)
Gymnothorax pharaonis	n/a	MN243496	(M) KAU13-615	KAUMM 402	Saudi Arabia (Red Sea)

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APPENDIX 1. (Continued)

Taxon	BOLD-ID	GenBank	sample identifier	Museum ID	Locality
Gymnothorax pharaonis	n/a	MN243494	(M) KAU14-818	KAUMM 403	Saudi Arabia (Red Sea)
Gymnothorax pharaonis	n/a	MN243489	(M) KAU13-614	SMF 35814	Saudi Arabia (Red Sea)
Gymnothorax pharaonis	n/a	MN243495	(M) KAU12-1028	SMF 35815	Saudi Arabia (Red Sea)
Gymnothorax pharaonis	n/a	MN243497	(M) KAU12-1060	SMF 35816	Saudi Arabia (Red Sea)
Gymnothorax pharaonis	n/a	MN243491	(M) KAU14-928	SMF 35817	Saudi Arabia (Red Sea)
Gymnothorax pictus	LIFS974-08	KP194043	(B) UG0782	n/a	Australia Queensland
Gymnothorax pictus	LIFS975-08	KP193971	(B) UG0783	n/a	Australia Queensland
Gymnothorax pictus (ID)	n/a	(R) HQ122453	n/a	n/a	n/a
Gymnothorax pindae	n/a	MN243513	(M) KAU13-596	KAUMM 407	Saudi Arabia (Red Sea)
Gymnothorax pindae	n/a	MN243518	(M) KAU13-692	KAUMM 414	Saudi Arabia (Red Sea)
Gymnothorax pindae	n/a	MN243519	(M) KAU12-1027	SMF 35818	Saudi Arabia (Red Sea)
Gymnothorax pindae	n/a	MN243515	(M) KAU13-447	SMF 35819	Saudi Arabia (Red Sea)
Gymnothorax pindae	n/a	MN243516	(M) KAU13-595	SMF 35820	Saudi Arabia (Red Sea)
Gymnothorax pindae	n/a	MN243511	(M) KAU13-693	SMF 35827	Saudi Arabia (Red Sea)
Gymnothorax pindae (ID)	RESIC419-11	n/a	(B) MNHN PE585	MNHN 2010-1492	New Caledonia
Gymnothorax pindae (ID)	n/a	n/a	(C, M) SCILL335-15	USNM 435224	Society Islands
Gymnothorax porphyreus	FNZ245-06	n/a	(B) P41275	n/a	New Zealand
Gymnothorax prasinus	AMS062-06	n/a	(B) AMS I.41084-036	AMS I.41084-036	Australia, New South Wales
Gymnothorax pseudoherrei	n/a	MN243521	(M) KAU17-245	SMF 35877	Saudi Arabia (Red Sea)
Gymnothorax pseudoherrei	n/a	MN243520	(M) KAU14-869	KAUMM 410	Saudi Arabia (Red Sea)
Gymnothorax pseudothyrsoideus	GBMIN95683-17	KU942764	(B) KU942764	n/a	Taiwan
Gymnothorax punctatus	GBGCA4671-13	KF297589	(B) KF297589	KF297589	India
Gymnothorax randalli	n/a	MN243510	(M) KAU12-732	SMF 34963	Saudi Arabia (Red Sea)
Gymnothorax reevesii	FSCS475-07	EU595145	(B) SCSIO- Z711135	ZC I07135	China, South China Sea
Gymnothorax reevesii	MBFA684-07	JQ431819	(B) MBIO 1163-.4	MNHN 2008-894	Society Islands
Gymnothorax reticularis	n/a	MN243508	(M) KAU14-155	KAUMM 415	Saudi Arabia (Red Sea)
Gymnothorax reticularis	n/a	MN243509	(M) KAU12-733	SMF 34964	Saudi Arabia (Red Sea)
Gymnothorax richardsoni	n/a	(R) HQ122470	n/a	n/a	n/a

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APPENDIX 1. (Continued)

Taxon	BOLD-ID	GenBank	sample identifier	Museum ID	Locality
Gymnothorax robinsi	AMS064-06	n/a	(B) AMS I.40666-060	AMS I.40666-060	Australia, Queensland
Gymnothorax rueppelliae	SAIAB009-06	n/a	(B) SAIAB T341	SAIAB 77822	Seychelles
Gymnothorax rueppelliae	n/a	(R) HQ122471	n/a	n/a	n/a
Gymnothorax thyrsoideus	n/a	n/a	(C, M) AUST-480	USNM 424169	Austral Islands
Gymnothorax thyrsoideus	n/a	n/a	(C, M) MARQ-304	USNM 409304	Marquesas Islands
Gymnothorax thyrsoideus	n/a	n/a	(C, M) MOH-173	USNM 410978	Marquesas Islands
Gymnothorax cf. *thyrsoideus*	MBFA071-07	JQ431827	(B) MBIO129.4	MNHN 2008-233	Society Islands
Gymnothorax tile	SUN084-18	n/a	(B) F1608sb-93	F1608sb-93	Bangladesh
Gymnothorax undulatus	KANB044-17	MG816692	AH9BM94	USNM 442319	Hawaii
Gymnothorax undulatus	MBFA683-07	JQ431828	(B) MBIO1161.4	MNHN 2008-893	Society Islands
Gymnothorax undulatus	SBF127-11	JQ350046	(B) NBE0307	NBE0307	Madagascar
Gymnothorax undulatus	n/a	(R) HQ122469	n/a	n/a	n/a
Gymnothorax zonipectis	n/a	(R) HQ122476	n/a	n/a	n/a
Gymnothorax sp. 1	n/a	n/a	(C, M) MARQ-505	USNM 409505	Marquesas Islands
Gymnothorax sp. 2	FTWS416-09	n/a	(B) ASIZP0803270	ASIZP0803270	Taiwan
Gymnothorax sp. 2	FTWS819-09	n/a	(B) ASIZP0803272	ASIZP0803272	Taiwan
Gymnothorax sp. 3	DSFSE555-08	JF493577	(B) ADC08 Smith41.11	n/a	South Africa
Gymnothorax sp. 4	SBF244-11	JQ350045	(B) NBE0539	NBE0539	Madagascar
Gymnothorax sp. 5	GOAIL207-17	MF123917	(B) RH1001	n/a	Israel
Gymnothorax sp. 5	GOAIL208-17	MF123918	(B) RH1302	n/a	Israel
Monopenchelys acuta	BZLWC283-06	JQ840939	(B, M) BZLW6283	USNM 416349	Belize
Muraena helena	FCFMT155-09	KJ709828	(B) MCFS07066	n/a	Malta
Muraenidae	LIDMA827-11	n/a	(B) gal490bm600	n/a	Galapagos
Rhinomuraena quaesita	TZAIB777-07	FJ584070	(B) HLC-15094	n/a	Philippines
Strophidon dorsalis	FOAN1505-14	n/a	(B) BW-A12299	CSIRO H7419-11	Taiwan
Strophidon sathete	FOAN1297-12	n/a	(B) BW-A12090	CSIRO H7397-11	Taiwan
Strophidon sathete	GBGC9984-09	FJ384683	(B) FJ384683	SV_8	India
Strophidon sathete	TZMSC298-05	JF494701	(B) Smith 41.28	n/a	South Africa
Strophidon sp.	FOAM148-10	n/a	(B) BW-A10111	LM563	Indonesia, Lombok

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APPENDIX 1. (Continued)

Taxon	BOLD-ID	GenBank	sample identifier	Museum ID	Locality
Uropterygiinae					
Channomuraena vittata	GBMIN130602-17	KU942768	(B) KU942768	n/a	Taiwan
Scuticaria tigrina	FTWS949-09	n/a	(B) ASIZP0803288	ASIZP0803288	Taiwan
Scuticaria tigrina	n/a	HQ122473	n/a	n/a	Hawaii
Scuticaria tigrina	n/a	MN243529	(M) KAU13-680	SMF 35823	Saudi Arabia (Red Sea)
Uropterygius cf. *alboguttatus*			(B) MBFA630-07		Society Islands
Uropterygius concolor	n/a	MN243531	(M) KAU12-309	SMF 35824	Saudi Arabia (Red Sea)
Uropterygius concolor	n/a	MN243532	(M) KAU13-288	SMF 35825	Saudi Arabia (Red Sea)
Uropterygius concolor	n/a	MN243530	(M) KAU13-346	SMF 35826	Saudi Arabia (Red Sea)
Uropterygius cf. *concolor* 1 (ID)	MBFA262-07	JQ431786	(B) MBIO440.4	MNHN 2008-453	Society Islands
Uropterygius cf. *concolor* 2 (ID)	SAIAB690-07	n/a	(B) SAIAB T644	n/a	South Africa
Uropterygius cf. *concolor* 3 (ID)	FOAO509-15	n/a	(B) BW-A12941	WAM unreg	Western Australia
Uropterygius fuscoguttatus	MBFA075-07	JQ432207	(B) MBIO134.4	MNHN 2008-237	Society Islands
Uropterygius fuscoguttatus	SBF184-11	JQ350411	(B) NBE0438	NBE0438	Madagascar
Uropterygius fuscoguttatus	n/a	(R) HQ122477	n/a	n/a	n/a
Uropterygius kamar	n/a	n/a	(C, M) AUST-079	USNM 423320	Austral Islands
Uropterygius macrocephalus	GBMIN125177-17	KU942740	(B) KU942740	n/a	Taiwan
Uropterygius macrocephalus	n/a	n/a	(C, M) AUST-440	USNM 424083	Austral Islands
Uropterygius macrocephalus	n/a	n/a	(C, M) MARQ-356	USNM 409356	Marquesas Islands
Uropterygius macrocephalus	n/a	(R) HQ122478	n/a	n/a	n/a
Uropterygius micropterus (ID)	FTWS419-09	n/a	(B) ASIZP0803277	ASIZP0803277	Taiwan
Uropterygius xanthopterus	MBFA911-07	JQ432213	(B) MBIO1569.4	MNHN 2008-1061	Society Islands
Uropterygius cf. *xanthopterus*	SAIAB533-07	n/a	(B) SAIAB T454	SAIAB 77814	Seychelles
Uropterygius sp.	RESIC406-11	n/a	(B) MNHN PE572	MNHN 2010-1479	New Caledonia