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New insights into the identities of the elasmobranch fauna of Sri Lanka

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Abstract

Identities of elasmobranchs from Sri Lanka encountered during collections conducted in an intensive nine-day survey of fish markets and landing sites at 11 localities in the North Western, Northern, and Eastern Provinces in March of 2018 were assessed. In total, 111 specimens representing 34 elasmobranch species were examined. Sequence data for the NADH2 gene were generated for all specimens. Independent Neighbor-Joining analyses, which included data for related taxa, were conducted for 25 subgroups of elasmobranchs to help confirm specific identifications. Five of the 34 species encountered are likely new to science. These consist of one species each of the batoid genera *Brevitrygon*, *Narcine*, and *Torpedo*, and the selachian genera *Centrophorus*, and *Chiloscyllium*. The specific identities of 12 species previously known to occur in Sri Lanka are updated to conform to current taxonomy; four of these (*Gymnura* cf. *poecilura* 2, *Carcharhinus* cf. *limbatus*, *Echinorhinus* sp. 1, and *Iago* cf. *omanensis* 1) represent what appear to be undescribed species reported previously from other localities. Three species (*Maculabatis arabica*, *Acroteriobatus variegatus*, and *Centroscymnus owstonii*) are reported from Sri Lanka for the first time; the latter species also represents the first documented record of this genus and family for the island nation. One of the two specimens on which the recent description of the new species of *Planonasus indicus* was based was also collected as part of this survey. Although some of the species confirmed to occur in Sri Lanka have also been found in India, others were previously known only from the Persian Gulf, Gulf of Oman, or localities in Southeast Asia. The high amount of novelty discovered as a result of a survey of such short duration emphasizes the importance of more intensive survey efforts in this region now that the civil unrest that precluded such work for nearly three decades has come to an end.

Key words: Elasmobranchii, Batoidea, Selachii, sharks, rays, biodiversity, new species, new records, Indian Ocean

Introduction

The Sri Lankan elasmobranch fauna is known from a series of checklists, guides, and keys to the elasmobranchs of Sri Lanka that have been published for just over a century (e.g., Day, 1889; Misra 1947, 1948; Mendis 1954; Munro 1955; De Silva 1977, 1984–1985, 2006, 2015; De Bruin *et al.* 1995; Morón *et al.* 1998), augmented by fisheries reports (Amarasooriya & Dayaratne 1994; Joseph 1999) and studies of individual or narrow groups of taxa (e.g., Goonewardena 1971; De Silva 1978, 1993, 2013a, b, 2014; Weerakkody & Fernando 2000; Fernando *et al.* 2015; Ebert *et al.* 2017). These have both substantially expanded the number of elasmobranch species reported from this island nation and served to lay the foundation for updating species names to reflect global changes in elasmobranch nomenclature and taxonomy at both generic and specific levels. This fauna has been overlooked in the context of the most recent advances in elasmobranch taxonomy brought about by the application of a combination of molecular and morphological data to help inform elasmobranch identifications globally. With the

advent of this combination of methods, many elasmobranch taxa once considered to represent single, broadly distributed species have been discovered to represent complexes of multiple, more locally distributed species (e.g., White *et al.* 2010; Naylor *et al.* 2012a; Last & White 2013; Borsa *et al.* 2016; Last *et al.* 2016c). Given that Sri Lanka is home to many of the genera now known to include such species complexes, the elasmobranch fauna of this country has yet to be placed in the revised global context.

The civil unrest that ended in 2009 did much to hamper advancements in the understanding of Sri Lankan elasmobranchs for nearly three decades. Gratifyingly, the peace that followed has enabled unprecedented access not only to previously untapped fishing grounds, but also to fish markets and landing sites for surveys in the north and east of this island nation. Blue Resources Trust (BRT) began intensively documenting elasmobranch landings at multiple landing sites in Sri Lanka in August of 2017. In March of 2018, informed by this previous work, a collaborative project was initiated between researchers of BRT, the University of Kansas, the University of Connecticut, and the Pacific Shark Research Center/Moss Landing Marine Laboratories, aimed at conducting a more formal exploratory survey of the elasmobranchs of the region. This paper provides preliminary identifications for elasmobranch species encountered over the course of a nine-day expedition carried out in March of 2018, based on a combination of morphological and molecular data. Data were also included for six frozen specimens collected between 2015 and 2018 that included two species not encountered during the present survey. Given the extremely short duration of the expedition, this paper is not intended to be an exhaustive treatment of the elasmobranch fauna of Sri Lanka. However, it does serve to place the elements of the Sri Lankan fauna encountered over that time into a global context by updating the taxonomy and identifying potential novelty to help inform future work.

Documentation of the elasmobranch species diversity for this region will contribute to the current data void that exists for the northern Indian Ocean. Coupled with consistent data collection at landing sites, this will help to better inform prudent fisheries management practices and improve conservation measures.

Materials and methods

Specimen collection. Collections were conducted between March 8th and 16th of 2018 at fish markets from artisanal and commercial fisheries throughout much of the coast of Sri Lanka. The localities sampled are numbered in Figure 1. In the chronological order of sampling, these localities were: (1) Puttalam, North Western Province (08°01'47.84"N, 79°49'42.86"E); (2) Baththalangunduwa Island, North Western Province (08°29'53.00"N, 79°46'52.00"E); (3) Palkanththura, Gulf of Mannar, North Western Province (08°28'34.36"N, 79°51'45.80"E); (4) Pukulam landing site, North Western Province (08°33'35.00"N, 79°55'11.00"E); (5) Vankalai, Northern Province (08°53'39"N, 79°55'42"E); (6) Gurunagar market, Jaffna, Northern Province (09°39'14.48"N, 80°0'49.35"E); (7) Erinchamman Kovilady market, Point Pedro, Northern Province (09°49'53.06"N, 80°13'29.48"E); (8) Supparamadam market, Point Pedro, Northern Province (09°49'48.39"N, 80°13'47.23"E); (9) Kottadi market, Point Pedro, Northern Province, (09°49'41.94"N, 80°14'23.94"E); (10) Munai market, Point Pedro, Northern Province (09°49'42.11"N, 80°14'40.22"E); (11) Mutur landing site, Mutur, Eastern Province (08°27'48.96"N, 81°15'56.88"E); (12) Valaichchenai Fisheries Harbour, Valaichchenai, Eastern Province (07°55'38.48"N, 81°31'47.75"E); (13) main landing site Valaichchenai, Eastern Province (07°55'31.75"N, 81°31'33.80"E). Six additional frozen specimens collected from previous fieldwork were included. Three of these were from locality (12), two were from (14) the Peliyagoda fish market, Western Province, Colombo (06°58'11.00"N, 79°53'17.00"E), and one was from (15) the Negombo fish market, Negombo, Western Province (07°12'12.00"N, 79°49'45.00"E).

Specimens were assigned a unique combination of collection code and collection number (SL-1, SL-2, etc.). All specimens were photographed using an Olympus Tough TG-5 camera and sex and basic measurements were recorded. These data can be accessed in the Global Cestode Database (elasmobranchs.tapewormdb.uconn.edu; Caira *et al.* 2018) by entering “SL” in the Collection Code field and the host specimen number of interest in the Collection Number field. Complete specimens were opened with a mid-ventral incision extending from the pectoral to the pelvic girdle and a small sample of liver tissue was removed and placed in 95% ethanol. In the cases of fresh specimens, the spiral intestine was also removed, opened with a mid-ventral longitudinal incision, and preserved either in 95% ethanol or 10% formalin (buffered in sea-water) for future cestode work. In the cases of partial specimens or some of the previously frozen specimens, a small sample of muscle tissue was removed and placed in 95% ethanol. Only specimens from Sri Lanka for which molecular data were successfully generated are

treated here. Also included were two samples each from commercially sold bags of Rone and Arunalu dried, salted shark—the goal being to identify the species being sold commercially in dried form. In each case, the cube of tissue was rinsed multiple times in distilled water and then a small sample was removed from the center of each cube of tissue and transferred to 95% ethanol.

In addition to the specimens from Sri Lanka, for comparative purposes, sequence data for the protein-coding gene NADH dehydrogenase subunit 2 (NADH2) were generated for a reference specimen of each of the following four species collected previously by JNC and KJ, and collaborators from elsewhere: *Pateobatis bleekeri* (Blyth) (IN-2; India; MK335256), *Brevitrygon imbricata* (Bloch & Schneider) (IN-15; India; MK335257), *Maculabatis arabica* Manjaji-Matsumoto & Last (MM-602; Gulf of Oman; MK335258), and *Chiloscyllium arabicum* Gubanov (MM-903; Gulf of Oman; MK335259). Taxonomy generally follows Naylor *et al.* (2012a); however, the taxonomy of the batoids has been updated following Last *et al.* (2016a, b).

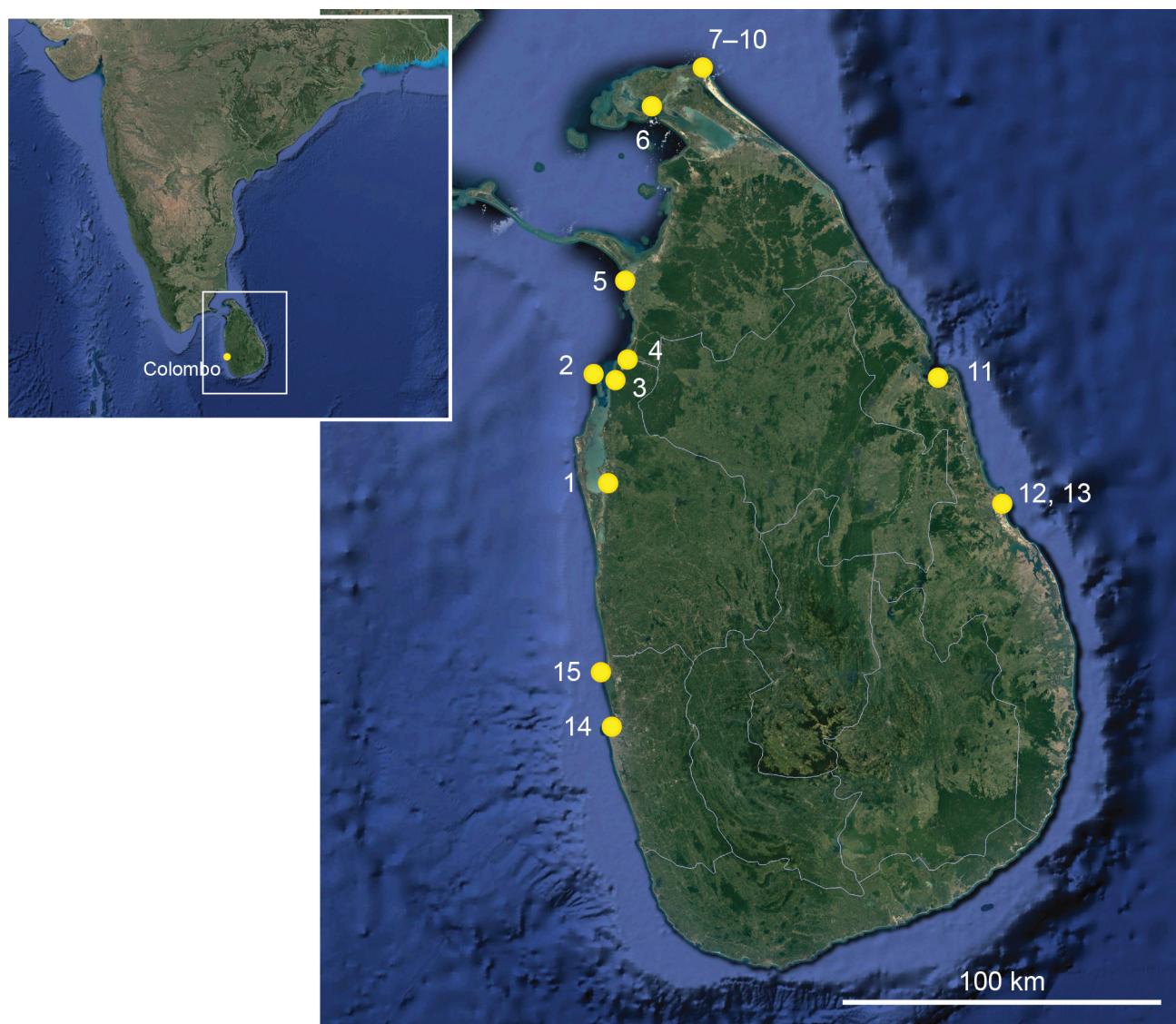


FIGURE 1. Map indicating collecting localities. *North Western Province*: Puttalam (1); Baththalangunduwa Island (2); Palkanththura (3); Pukulam landing site (4). *Northern Province*: Vankalai (5); Gurunagar market (6), Jaffna; near Erinachamman Kovilady market, Supparamadam market, Kottadi market, and Munai market (7–10), Point Pedro. *Eastern Province*: Mutur landing site (11), Mutur; Valaichchenai Fisheries Harbour and main landing site Valaichchenai (12, 13), Valaichchenai. *Western Province*: Peliyagoda fish market (14), Colombo; Negombo fish market (15), Negombo. Map source: Google Earth (Data SIO, NOAA, U.S. Navy, NGA, GEBCO; Image Landsat/Copernicus); copyright 2018 Google.

Sequence generation. DNA was extracted using DNeasy Blood & Tissue Kits (QIAGEN), following the kit protocol, and was quantified using a NanoDrop 2000 micro-volume spectrophotometer (Thermo Scientific,

Waltham, Massachusetts). Extracted DNA samples were diluted to a concentration of 50 ng/ μ L. Polymerase chain reaction (PCR) was used to amplify the mitochondrial gene NADH2. PCR reactions were carried out using 50 ng of DNA template, GoTaq Green 2X Master Mix (Promega Corporation, Madison, Wisconsin) at 1X final concentration, and 0.25 μ M (final concentration) of each of the forward and reverse primers, brought to a total volume of 10 μ L with molecular grade water. The following primers were used in different combinations for both the PCR amplification and cycle sequencing: ILEM (5'-AAGGAGCAGTTGATAGAT-3') and ASNM (5'-AACGCTTAGCTGTTAATTAA-3') (Naylor *et al.* 2005); and ILEM_SeqF (5'-AAGCTTTGGGCCATACC-3') and ASNM_SeqR (5'-AAGCTTGAGGCTTTGGT-3').

Amplification of the NADH2 gene was done using an S1000 thermal cycler (Bio-Rad Laboratories, Inc., Philadelphia, PA) with a touchdown cycling protocol as follows: an initial denaturation at 96°C for 4 min, followed by 12 cycles of denaturation at 96°C for 30 sec, annealing starting at 60°C (with a decrease of 1°C at each cycle) for 30 sec, and extension at 72°C for 1 min; then 30 additional cycles of 96°C for 30 sec, 48°C for 30 sec, and 72°C for 1 min; and a final extension at 72°C for 2 min.

Removal of PCR primers and excess dNTPs was done by adding 2U of Exonuclease I (20U/ μ L) (New England Biolabs, Ipswich, Massachusetts) and 0.4U of FastAP Alkaline Phosphatase (Thermo Scientific) (1U/ μ L) mixed with 1 μ L of water (molecular grade) to 8 μ L of each PCR product. The PCR and enzyme mix was then incubated at 37°C for 30 min followed by an enzyme deactivation step at 80°C for 20 min. Cleaned PCR products were then used as templates for cycle sequencing. The cycle sequencing PCR mix consisted of the following reagents in a final volume of 8.5 μ L: 1.75 μ L cleaned PCR product, 0.38 μ M of either a forward or reverse primer, 5X Sequencing Buffer (Applied Biosystems, Waltham, Massachusetts) at 1X final concentration, and 0.25 μ L BigDye Terminator v3.1 mix (Applied Biosystems). The thermal cycling protocol closely followed that of Platt *et al.* (2007) and consisted of a 3-step protocol: an initial denaturation for 3 min at 96°C; followed by 15 cycles of denaturation for 10 sec at 96°C, annealing for 5 sec at 50°C and extension for 1 min and 15 sec at 60°C; then an additional 10 cycles of denaturation for 10 sec at 96°C; annealing for 5 sec at 50°C and extension for 1 min and 30 seconds at 60°C; then a final 10 cycles of denaturation for 10 sec at 96°C, annealing for 5 sec at 50°C and extension for 2 min and 30 sec at 60°C. Cycle sequencing products were then cleaned by passing through columns containing 650 μ L hydrated Sephadex G-50 Fine beads (6.2 g Sephadex per 100 mL deionized water) (Sigma-Aldrich, St. Louis, Missouri). Electrophoretic separation was carried out on an ABI 3130xl genetic analyzer with a 50 cm capillary array (Applied Biosystems). Contigs were assembled and sequences were edited manually using Geneious 10.1.3 (Biomatters Ltd., Auckland, New Zealand).

Molecular analysis. NADH2 sequence data were successfully generated for 111 specimens from Sri Lanka; these included two samples each from a bag of Rone and a bag of Arunalu dried shark meat. NADH2 sequence data for all but the four dried samples have been deposited in GenBank (MK335260–MK335366); data deposited included the stop codon. Data were also successfully generated for the four reference specimens from India and the Gulf of Oman. Sequences were assembled in Geneious (v. 10.1.3) and aligned using the Geneious Alignment algorithm. Sequences were trimmed to a length of the protein-coding region (1,044 bp or 1,041 bp for *Galeocerdo*); the stop codon was excluded from the analyses. Sequence data for 77 of the 111 specimens were complete. The amount of missing data for the remaining 34 specimens ranged from 1–354 bp, with a mean of 58 bp and a median of 20 bp. Neighbor-Joining analyses were conducted using PAUP* v. 4. b10 (Swofford 2003) in Geneious using the uncorrected p-distance model. Separate analyses were run for each of the 25 subgroups of elasmobranchs represented by our collections. In each case, the analysis also included NADH2 sequence data for reference specimens of relevant species available in GenBank, drawing primarily from Naylor *et al.* (2012a, b), but augmented by individual sequences from Straub *et al.* (2013), Chang *et al.* (2016), Gaitán-Espitia *et al.* (2016), and Muktha *et al.* (2018) obtained from GenBank to expand species representation as much as possible. It is unfortunate that sequence data for additional relevant taxa from a number of previous molecular analyses (e.g., Henderson *et al.* 2016; Last *et al.* 2016a, d; White *et al.* 2016) have not been deposited in GenBank. GenBank numbers for all specimens are provided in the trees. Also included in the taxon labels in the trees, in parentheses, are the collection code and collection number for specimens collected by JNC and KJ, and collaborators, followed by a GN number in the case of sequences from Naylor *et al.* (2012a). Specimens from Sri Lanka for which sequence data were generated as part of this study are indicated in bold. We emphasize that Neighbor-Joining analysis was used as a way to identify our Sri Lankan material based on their similarity to samples of verified identity. This provides molecular confirmation of our initial species identifications based on morphology. However, we caution that the resulting clustering diagrams (i.e., Neighbor-Joining trees) are not appropriate for assessing phylogenetic relationships for multiple reasons, including our use of uncorrected p-distances and the fact that

greater sequence similarity between species does not always reflect a closer relationship. Formal assessment of phylogenetic relationships using model-based methods will be done in the future in the context of a greater number of genes and a much more inclusive set of elasmobranch taxa.

Morphological analysis. Given our goal was solely to provide a preliminary assessment of a subset of the elasmobranch diversity found in Sri Lankan waters, we limited our morphological comparisons with taxa from other regions to (1) published descriptions, (2) images of elasmobranch specimens collected by JNC and KJ from around the world, and (3) images of elasmobranch specimens from elsewhere in Sri Lanka and adjacent regions from previous collections by DAE and other collaborators, rather than examination of comparative specimens. The literature examined to aid in specific identifications is given in each species treatment. Morphological details are presented only in instances in which questions surrounding the identity of a species may exist. A series of images of an exemplar of most species encountered is presented so as to help ground the molecular identities provided. However, in anticipation of future descriptive work, which would require the study of specimens, reference specimens of a subset of the species encountered have been deposited in the Blue Resources Trust (BRT) Ichthyology Collection, Kalkudah, Eastern Province, Sri Lanka. Accession numbers for these specimens are given in the species treatments; stars on the trees indicate these specimens. Additional museum abbreviations: CSIRO, Australian National Fish Collection, Hobart, Tasmania, Australia.

Results

In total, 34 species of elasmobranchs were identified. Reference specimens for 18 of these have been deposited in the BRT Ichthyology Collection. Each of the species encountered is treated separately below, beginning with the batoids, alphabetically by order, family, and genus. In each case, the specimens examined and their collecting localities are summarized. The identity of each species is assessed in the context of current global taxonomy. The nomenclature is revised accordingly. Previous reports, or potential reports, of each species are also addressed. Images (Figs. 2–19) have also been included in most cases.

Batoidea

Myliobatiformes

Aetobatidae

Aetobatus ocellatus (Kuhl)

(Figs. 2A, 6A, B)

The eight specimens of *Aetobatus* Blainville from Sri Lanka were collected from landing sites in Palkanththura (SL-2) and Pukulam (SL-7) in the North Western Province and from fish markets in Kottadi (SL-26, SL-27, SL-62), Munai (SL-41), and Vankalai (SL-68, SL-69) in the Northern Province. All eight specimens exhibited the general color pattern that distinguishes *Aetobatus ocellatus* from its four described congeners in that the dorsal disc surface bears small white, round spots that do not extend onto the head. Some variation was seen across specimens—in the cases of SL-41, SL-62, and SL-69; the white spots were essentially restricted to the posterior margins of the disc and the pelvic fins. The tree resulting from Neighbor-Joining analysis of NADH2 data, which included representation of all four described species and the potentially undescribed species referred to as *Aetobatus* cf. *ocellatus* 1 and *Aetobatus* cf. *ocellatus* 2 by Naylor *et al.* (2012a), generally supports this identification in that all eight specimens clustered most closely with our reference specimen of *A. ocellatus* from Malaysian Borneo (BO-296; JQ519092). However, within that cluster, two subclusters were apparent. Specimens SL-26 and SL-41 were identical in sequence, differing from the reference specimen of *A. ocellatus* by 6 bp. The six specimens in the second subcluster (SL-2, SL-7, SL-27, SL-62, SL-68, and SL-69), which differed from one another by 0–1 bp, differed from those in the first subcluster by 8–13 bp. However, these subclusters did not correspond to the color pattern differences seen. Investigation of additional specimens of *Aetobatus* from Sri Lanka is recommended and a comprehensive review of the white-spotted eagle rays in the Indo-West Pacific is sorely needed.

This species has been referred to as *Aetobatus narinari* (Euphrasen) in all prior reports from Sri Lanka (see De Silva 1978, 2006, 2015; De Bruin *et al.* 1995; Morn *et al.* 1998). However this name is now reserved for the Atlantic member of this genus (see White *et al.* 2010).

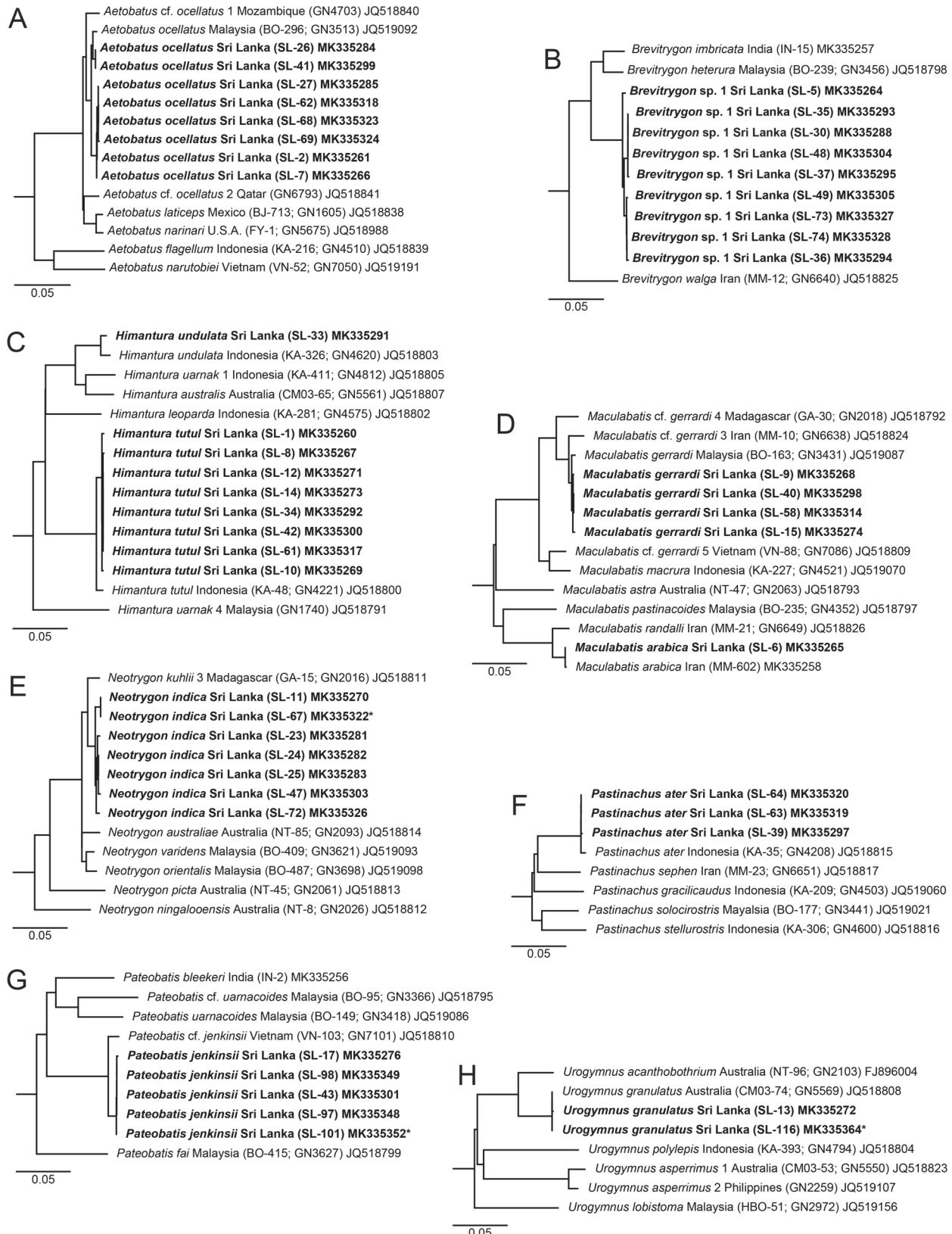


FIGURE 2. Neighbor-Joining trees of p-distances based on 1,044 bp of aligned NADH2 sequence data for individual batoid genera or groups of genera. Taxon names are followed by country, host specimen number (in parentheses), and GenBank number. Outgroup taxa used in each analysis were omitted from the individual trees. Scale bar values indicate substitutions per site. Specimens deposited in the Blue Resources Trust Ichthyology Collection are indicated by stars (see text for details). **A.** *Aetobatus* (Aetobatidae). **B.** *Brevitrygon* (Dasyatidae). **C.** *Himantura* (Dasyatidae). **D.** *Maculabatis* (Dasyatidae). **E.** *Neotrygon* (Dasyatidae). **F.** *Pastinachus* (Dasyatidae). **G.** *Pateobatis* (Dasyatidae). **H.** *Urogymnus* (Dasyatidae).

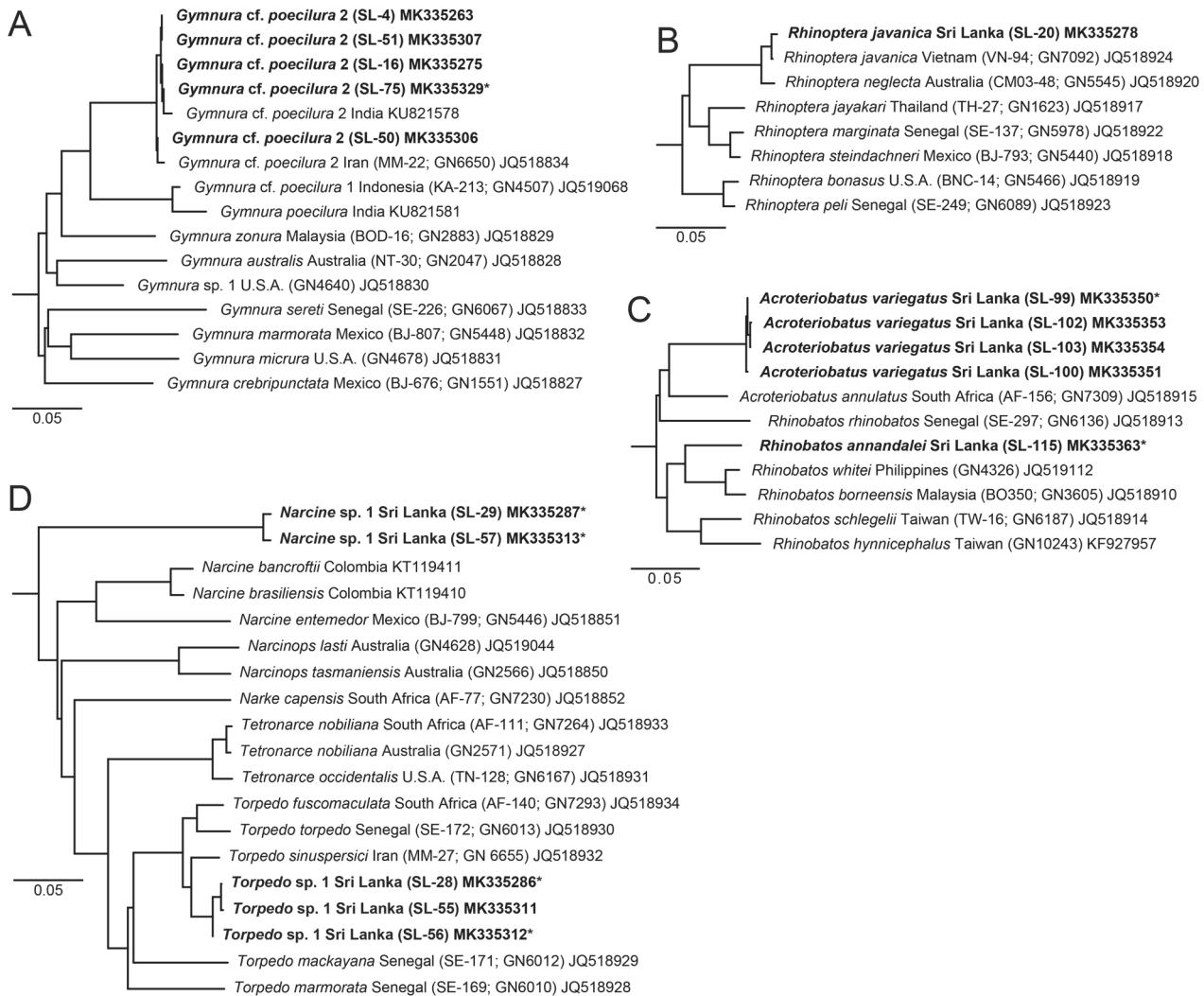


FIGURE 3. Neighbor-Joining trees of p-distances based on 1,044 bp of aligned NADH2 sequence data for individual batoid genera or groups of genera. Taxon names are followed by country, host specimen number (in parentheses), and GenBank number. Outgroup taxa used in each analysis were omitted from the individual trees. Scale bar values indicate substitutions per site. Specimens deposited in the Blue Resources Trust Ichthyology Collection are indicated by stars (see text for details). **A.** *Gymnura* (Gymnuridae). **B.** *Rhinoptera* (Rhinopteridae). **C.** *Acroteriobatus* and *Rhinobatos* (Rhinobatidae). **D.** Torpediniformes.

Dasyatidae

Brevitrygon sp. 1

(Figs. 2B, 6C, D)

Specimens of a species of *Brevitrygon* Last, Naylor & Manjaji-Matsumoto were examined from the Palkanththura market (SL-5) in the North Western Province, from the Munai (SL-30, SL-35, SL-36, SL-37) and Erinchamman Kovilady (SL-48, SL-49) markets in Point Pedro in the Northern Province, and from Mutur (SL-73, SL-74) in the Eastern Province. In the tree resulting from the Neighbor-Joining analysis, these nine specimens clustered together away from our reference specimens of *Brevitrygon heterura* (Bleeker) (BO-239; JQ518798) from Malaysian Borneo, of *B. imbricata* (IN-15; MK335257) from India, and of *Brevitrygon walga* (Müller & Henle) (MM-12; JQ518825) from the Gulf of Oman. The specimens from Sri Lanka differed from one another by 0–8 bp. They were

highly divergent from the three reference species, differing from the *B. heterura* specimen by 62–67 bp, from the *B. imbricata* specimen by 62–67 bp, and from the *B. walga* specimen by 97–102 bp. Morphologically, the specimens from Sri Lanka differ from all of their congeners except *Brevitrygon javaensis* (Last & White), which unfortunately was not included in our molecular analysis, in bearing few to no enlarged thorns on the base of the tail. However, the Sri Lankan specimens differ conspicuously from *B. javaensis* in their possession of a narrow, rather than broad, denticle band (see Last & White 2013). As a consequence, it seems likely that the form from Sri Lanka represents a new species and has been referred to here with the provisional name *Brevitrygon* sp. 1.

This may be the species from Sri Lanka referred to as *Himantura imbricata* (Bloch & Schneider) by previous authors (e.g., De Bruin *et al.* 1995; Morón *et al.* 1998; De Silva 2006).

***Himantura tutul* Borsa, Durand, Shen, Arlyza, Solihin & Berrebi**

(Figs. 2C, 7A–C)

Eight specimens consistent in coloration with the *Himantura uarnak* (Gmelin) species complex were examined. These came from Palkanththura (SL-1), Pukulam (SL-8, SL-10), Baththalangunduwa Island (SL-12), and Puttalam (SL-14) landing sites in the North Western Province, and the Munai (SL-34, SL-42) and Kottadi (SL-61) markets in Point Pedro in the Northern Province. The dorsal surface of the disc of all four immature specimens (SL-1, SL-12, SL-34, and SL-61) had regular brown spots on a yellow or pale brown background. However, somewhat marked color pattern differences were seen among the four adult specimens. In two cases (SL-8 and SL-10), the dorsal surface of the disc is yellow to gray and bears numerous small spots that are essentially ocelli. In two other cases (SL-14 and SL-42), the dorsal surface of the disc is yellow and bears numerous, small, brown, irregular, elongate spots. However, the eight specimens differed from one another by only 0–4 bp and are thus likely conspecific. In terms of the identity of the Sri Lankan material, in the tree resulting from the Neighbor-Joining analysis, which included reference sequences of all five described members of the genus as well as the two undescribed species recognized by Naylor *et al.* (2012a) as *Himantura uarnak* 1 and *Himantura uarnak* 4, the specimens from Sri Lanka grouped most closely with the reference sequence of *H. tutul* (KA-48; JQ518800; formerly *H. uarnak* 3 of Naylor *et al.* 2012a) from Indonesian Borneo. Although the specimens from Sri Lanka differed from this specimen by 10–14 bp, the color pattern variation seen in our specimens from Sri Lanka is consistent with that seen in *H. tutul* by Borsa *et al.* (2013) and Borsa (2017a). We have assigned this name to these specimens at this time based on the following lines of evidence. (1) Our reference specimen (provisionally assigned the name *H. uarnak* 3 by Naylor *et al.* 2012a) from Indonesia Borneo (i.e., KA-48) was also included in the molecular analyses of NADH2 sequence data by Last *et al.* (2016a) who determined it to be conspecific with the three specimens from Tanzania (identified as *H. uarnak*) included in their analyses. (2) Results of unpublished analyses that included NADH2 sequence data for a specimen of *H. uarnak* we collected from its type locality in the Red Sea place this specimen as sister taxon to *H. leoparda* Manjaji-Matsumoto & Last, well away from our reference specimen of *H. uarnak* 3, suggesting that the name *H. uarnak* is not the appropriate name for the latter taxon. (3) Given point 1 above and the fact that the type locality of *H. tutul* is Tanzania, the latter name is the most appropriate to be applied to specimens provisionally identified as *H. uarnak* 3. (4) Given the specimens from Sri Lanka cluster with our reference specimen of *H. uarnak* 3, these specimens should also be referred to as *H. tutul* at this time. However, conspecificity of these forms remains provisional until a substantially greater amount of morphological work can be conducted, especially given the extensive color pattern variation seen across the *H. uarnak* species complex (e.g., Borsa *et al.* 2013, 2017a; Manjaji-Matsumoto & Last 2016).

This is likely the species generally referred to as *H. uarnak* in Sri Lanka (see De Bruin *et al.* 1995; Morón *et al.* 1998; De Silva 2006). In addition, although no specimens or references were cited, Borsa *et al.* (2013) listed the Laccadive Sea as part of the distribution of *H. tutul* suggesting they have evidence that this species occurs at least off the west coast of Sri Lanka.

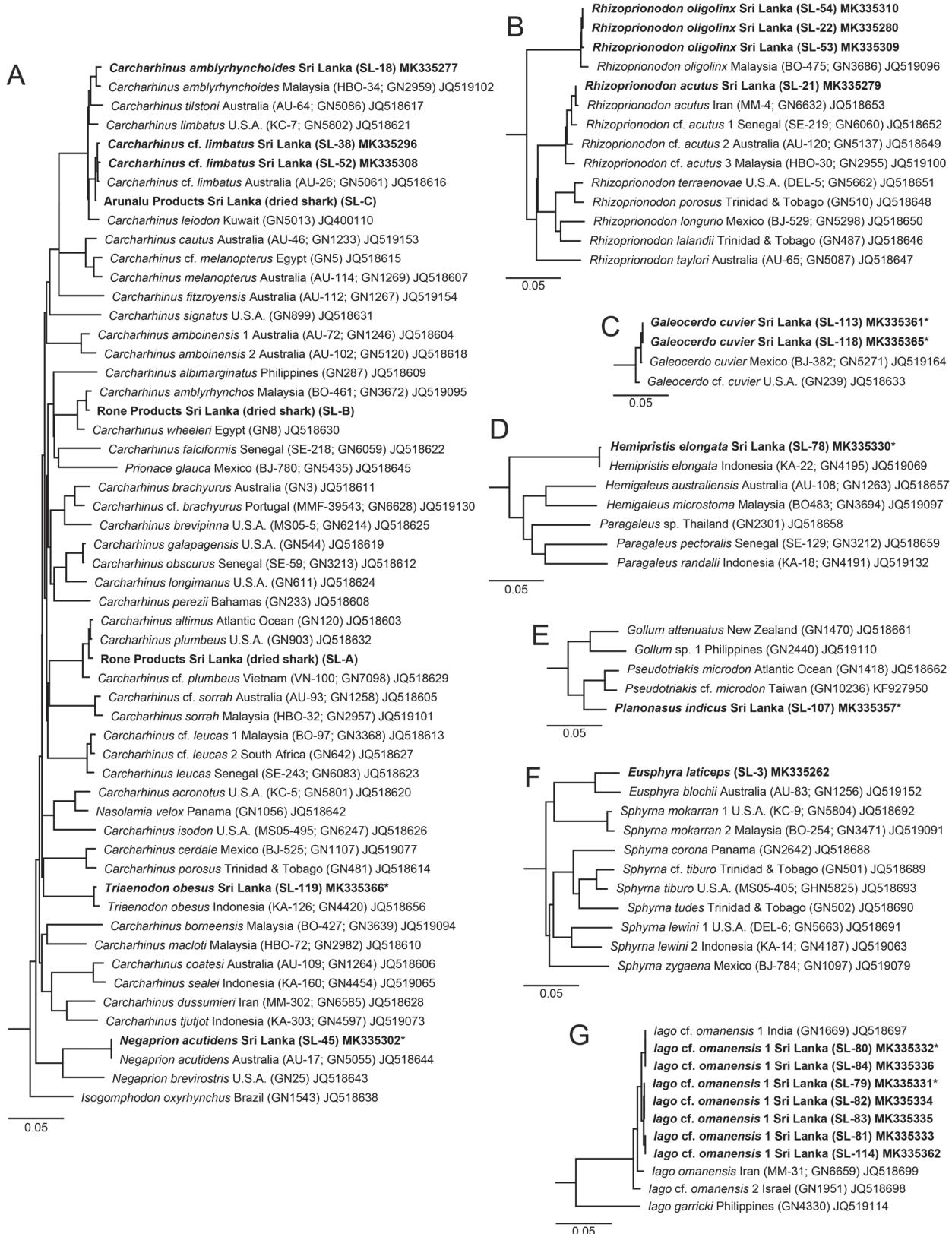


FIGURE 4. Neighbor-Joining trees of p-distances based on 1,044 bp of aligned NADH2 sequence data for individual selachian genera or groups of genera. Taxon names are followed by country, host specimen number (in parentheses), and GenBank number. Outgroup taxa used in each analysis were omitted from the individual trees. Scale bar values indicate substitutions per site. Specimens deposited in the Blue Resources Trust Ichthyology Collection are indicated by stars (see text for details). **A.** *Carcharhinus* and close relatives (Carcharhinidae). **B.** *Rhizoprionodon* (Carcharhinidae). **C.** *Galeoceridae*. **D.** *Hemigaleidae*. **E.** *Pseudotriakidae*. **F.** *Sphyrnidae*. **G.** *Iago* (Triakidae).

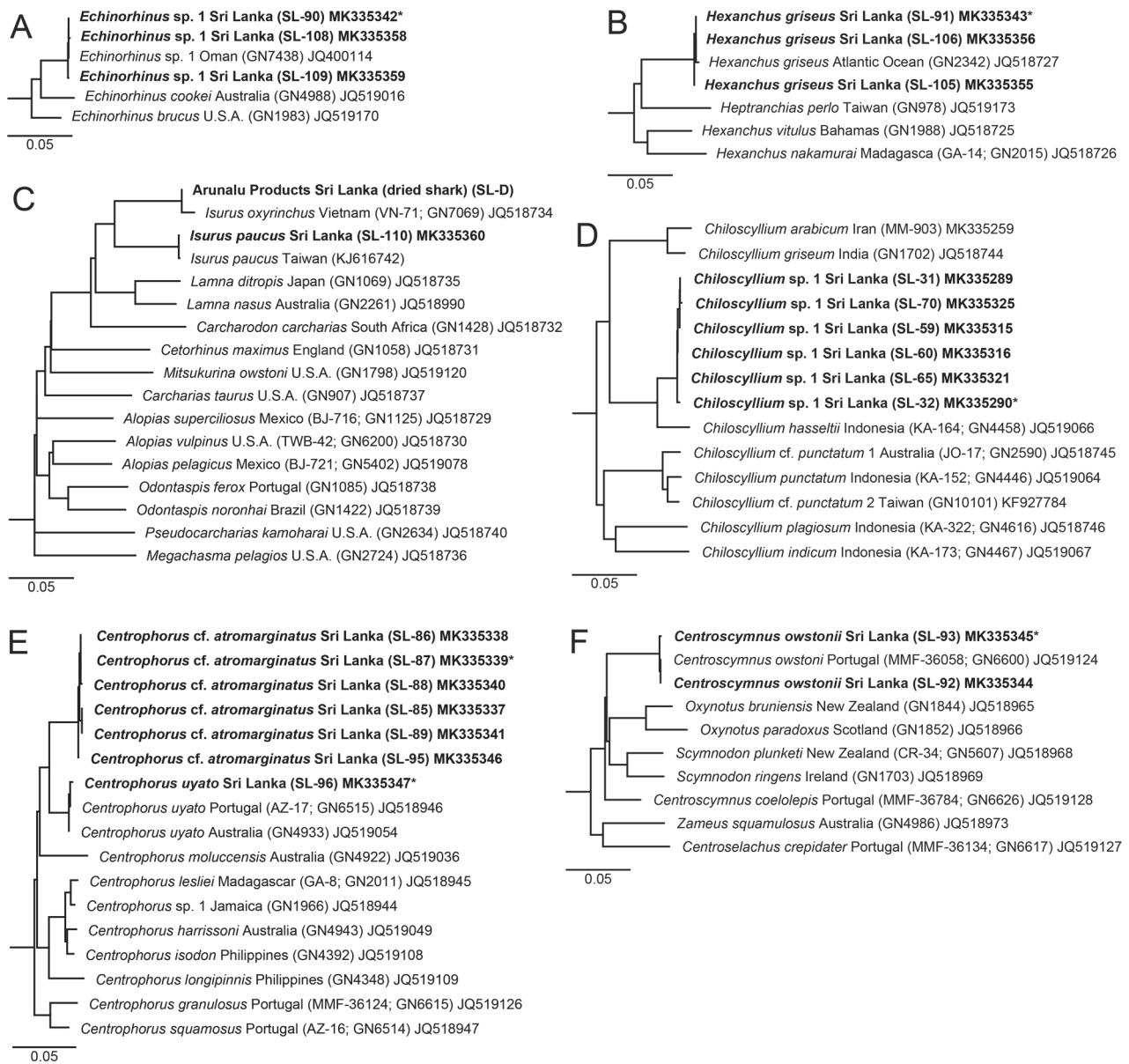


FIGURE 5. Neighbor-Joining trees of p-distances based on 1,044 bp of aligned NADH2 sequence data for individual selachian genera or groups of genera. Taxon names are followed by country, host specimen number (in parentheses), and GenBank number. Outgroup taxa used in each analysis were omitted from the individual trees. Scale bar values indicate substitutions per site. Specimens deposited in the Blue Resources Trust Ichthyology Collection are indicated by stars (see text for details). **A.** *Echinorhinidae*. **B.** *Hexanchidae*. **C.** *Lamniformes*. **D.** *Chiloscyllium* (Hemiscylliidae). **E.** *Centrophorus* (Centrophoridae). **F.** *Somniidae/Oxynotidae* (*Somniosus* omitted).

Himantura undulata (Bleeker)

(Figs. 2C, 7D)

A single, immature specimen of what appears to be *Himantura undulata* (SL-33) was examined at the Munai market in Point Pedro in the Northern Province. Its color pattern was similar to that of the immature specimen from Indonesian Borneo used as the reference specimen of *H. undulata* (KA-326; JQ518803) in the analysis. The dorsal surfaces of both specimens bear large, irregular brown spots, some of which are fused into bands, surrounded by narrow yellow margins. In the tree resulting from Neighbor-Joining analysis of NADH2 sequence data, which included representation of all four valid species of *Himantura*, this specimen grouped most closely with the specimen of *H. undulata*. It did, however, differ from that specimen by 14 bp. At this point, at least provisionally,

we have identified the specimen from Sri Lanka as *H. undulata*. Additional work, especially on adult specimens, is required to confirm this identification.

This species is not among the dasyatids included in some of the major checklists (e.g., De Bruin *et al.* 1995; De Silva 2006) of the country. It was, however, included in the report of Morón *et al.* (1998) in which this name is used.

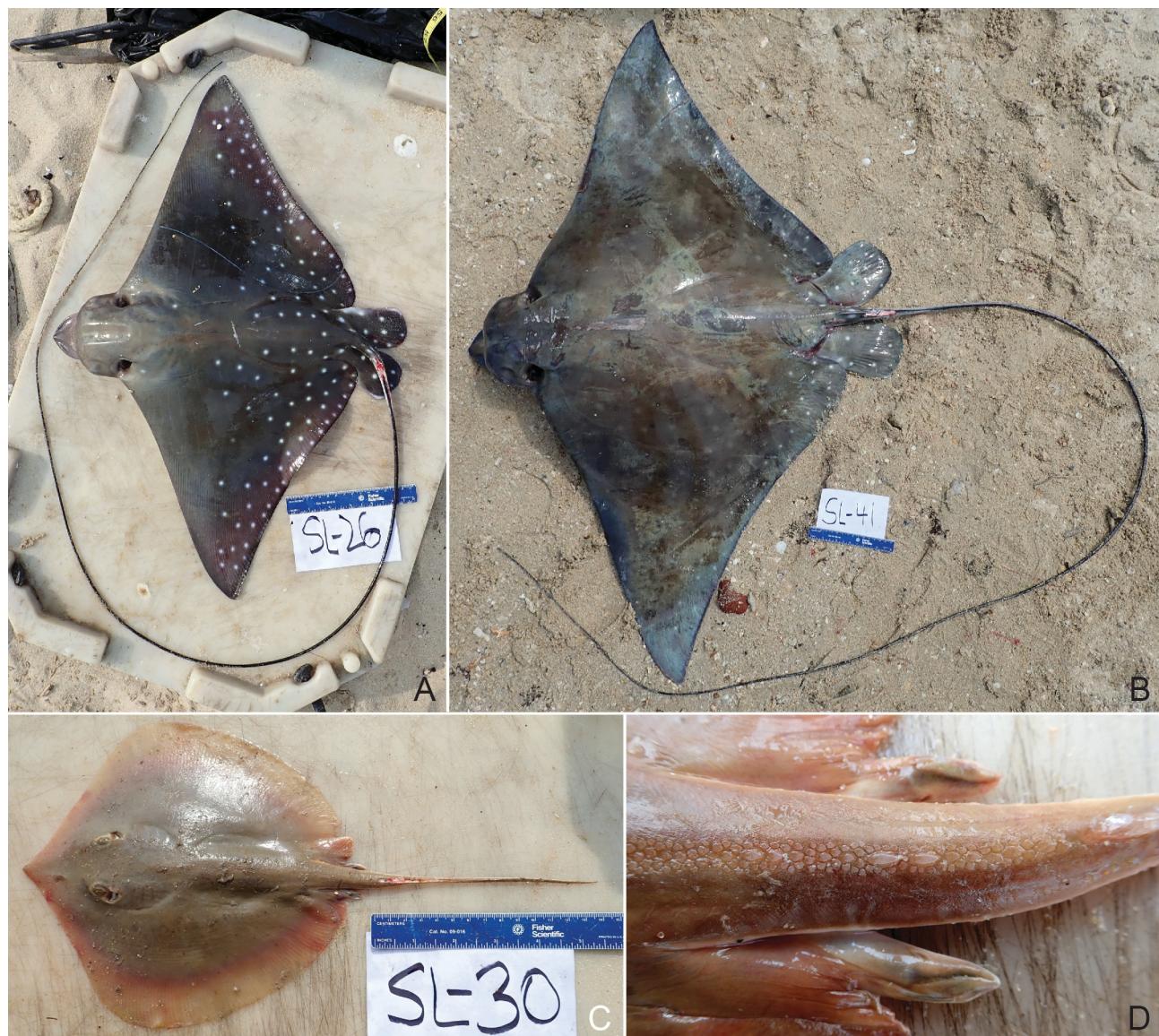


FIGURE 6. *Aetobatus ocellatus* (Aetobatidae) (A–B) and *Brevitrygon* sp. 1 (Dasyatidae) (C–D). **A.** Dorsal surface of immature male (SL-26). **B.** Dorsal surface of mature female (SL-41). **C.** Dorsal surface of maturing male. **D.** Thorns and denticles on base of tail of mature male (dorsal surface; SL-36).

Maculabatis arabica Manjaji-Matsumoto & Last (Figs. 2D, 8C–E)

An immature specimen (SL-6) from the Pukulam landing site in the North Western Province was difficult to identify to species based on morphology alone. The rhombic disc and sparse white spots on the lateral margins of the tail immediately anterior to, adjacent to, and immediately posterior to the spine suggested it was a member of the genus *Maculabatis* Last, Naylor & Manjaji-Matsumoto. In the tree resulting from the Neighbor-Joining analysis, this specimen clustered with our reference specimen of *Maculabatis arabica* (MM-602; MK335258) from the Gulf of Oman. It differed from this specimen by only 1 bp, and is likely an immature individual of the species.

Of note is that our specimen was somewhat inconsistent with the description of immatures of *M. arabica* presented by Manjaji-Matsumoto & Last (2016). Whereas they described the tail of immatures of *M. arabica* less than 33 cm in disc width (DW) to bear conspicuous white bands on the upper half of the tail behind the caudal sting, the tail of the specimen from Sri Lanka (DW of 17.6 cm) had inconspicuous white spots that were restricted to the region of the tail anterior and posterior to the tail spine. Examination of additional immature and adult specimens from Sri Lanka is required to confirm this identification.

To our knowledge, this is the first report of this species from Sri Lanka.

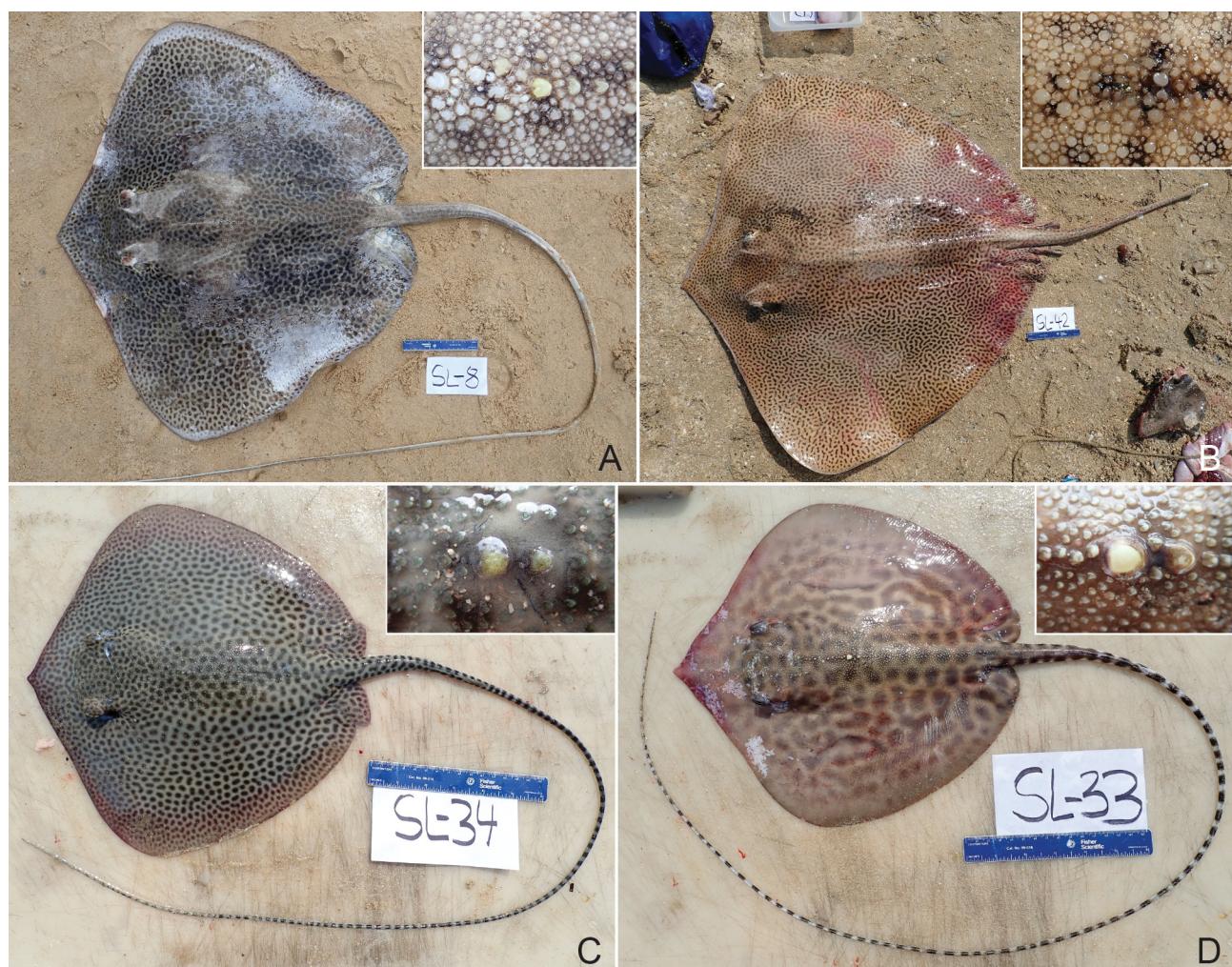


FIGURE 7. *Himantura tutul* (A–C) and *Himantura undulata* (D) (Dasyatidae). **A.** Dorsal surface of mature female (SL-8); inset showing scapular denticles. **B.** Dorsal surface of mature female (SL-42); inset showing scapular denticles. **C.** Dorsal surface of immature male (SL-34); inset showing scapular denticles. **D.** Dorsal surface of immature male (SL-33); inset showing scapular denticles.

Maculabatis gerrardi (Gray)

(Figs. 2D, 8A, B)

Four specimens morphologically consistent with *Maculabatis gerrardi* were examined. These came from landing sites in Pukulam (SL-9) and Puttalam (SL-15) in the North Western Province and fish markets in Munai (SL-40) and Kotaddi (SL-58) at Point Pedro in the Northern Province. Two (SL-9 and SL-58) were immatures and two (SL-40 and SL-15) were mature. The latter mature specimen had already been processed for sale and consisted solely of the right side of the disc. Both immature specimens were morphologically consistent with the immature specimen from Malaysian Borneo used as the reference specimen for *M. gerrardi* (BO-163; JQ519087) in our analysis; both specimens possessed a few white spots on the dorsal surface of the base of the tail grading into alternating black

and white bands throughout the length of the tail. Both of the mature specimens exhibited sparse, small white spots restricted to the posterior margin of the disc and pelvic fins, typical of adults of *M. gerrardi*. All four specimens from Sri Lanka grouped in a tight cluster with the reference specimen of *M. gerrardi*. They differed from one another by 0–3 bp and from the reference specimen by 5–6 bp.

This species has previously been referred to as *Himantura gerrardi* (Gray) (e.g., De Bruin *et al.* 1995; Morón *et al.* 1998; De Silva 2006). That name has been updated here to reflect current nomenclature (Last *et al.* 2016).



FIGURE 8. *Maculabatis gerrardi* (A–B) and *Maculabatis arabica* (C–E) (Dasyatidae). A. Dorsal surface of mature female (SL-40); inset showing scapular denticles. B. Dorsal surface of immature male (SL-58); inset showing scapular denticles. C. Dorsal surface of immature female (SL-6); inset showing scapular denticles. D. Oronasal region of immature female (SL-6). E. Tail base and anterior tail region of immature female (lateral view; SL-6).

Neotrygon indica Pavan-Kumar, Kumar & Borsa (Figs. 2E, 9A, B)

In total, seven specimens of *Neotrygon* Castelnau were examined. These came from a landing site in Pukulam (SL-11) in the North Western Province, fish markets in Kottadi (SL-23, SL-24, and SL-25), Erinchamman Kovilady (SL-47), and Vankalai (SL-67) in the Northern Province, and the landing site in Mutur (SL-72) in the Eastern Province. These specimens formed a tight cluster in the tree resulting from the Neighbor-Joining analysis. They differed from one another by 0–10 bp. They clustered most closely with our reference specimen of the species referred to as *Neotrygon kuhlii* 3 by Naylor *et al.* (2012a). However, they differed from that specimen by 20–25 bp, suggesting that the Sri Lankan specimens may represent a distinct species. Although NADH2 data are not available

for the recently described *Neotrygon indica*, the specimens from Sri Lanka are morphologically consistent with the description of that species of Pavan-Kumar *et al.* (2018). Further supporting these findings is the fact that two of our specimens were landed at fish markets or landing sites adjacent to the Gulf of Mannar—the body of water in which the type locality of *N. indica* is also found (i.e., the Inico Nagar, Tuticorin fish landing centre [9.12°N, 79.46°E] in India; Pavan-Kumar *et al.* 2018). A voucher specimen of this species was deposited in the BRT Ichthyology Collection (SL-67; BRT-I 0016).

This is likely the species referred to as *Dasyatis kuhlii* (Müller & Henle) in Sri Lanka (De Bruin *et al.* 1995; Morón *et al.* 1998; De Silva 2006)—a taxon now assigned to the genus *Neotrygon* (see Last & White 2008) and known to belong to a species complex that includes several new regionally distributed species (Borsa *et al.* 2016, 2018; Last *et al.* 2016c; Borsa 2017b; Pavan-Kumar *et al.* 2018). This is the first formal report of *N. indica* from Sri Lanka.



FIGURE 9. *Neotrygon indica* (A–B) and *Pastinachus ater* (C–E) (Dasyatidae). A. Dorsal surface of mature male (SL-72). B. Dorsal surface of female (SL-24). C. Dorsal surface of mature male (SL-39). D. Scapular denticles of mature male (SL-39). E. Oronasal region of mature male (SL-39).

***Pastinachus ater* (Macleay)**

(Figs. 2F, 9C–E)

All three specimens of this species examined were collected from fish markets in Point Pedro in the Northern Province, one from the Munai market (SL-39) and two from the Kottadi market (SL-63 and SL-64). These specimens were morphologically consistent with *Pastinachus ater*. This identification was supported by the tree resulting from the Neighbor-Joining analysis, which included representation of all five members of this genus. The Sri Lankan specimens formed a tight cluster with our reference specimen of *P. ater* (KA-35; JQ518815) from Indonesian Borneo. These specimens differed from one another by 0–1 bp, and from the reference specimen of *P. ater* by 4–5 bp. They differed from the reference specimen of *P. sephen* (MM-23; JQ518817) from the Gulf of Oman by 70–79 bp.

Specimens of this taxon in Sri Lanka have previously been referred to as *Pastinachus sephen* (Forsskål) (see De Bruin *et al.* 1995; Morón *et al.* 1998; De Silva 2006). The latter species is now considered to occur only from the Red Sea to Pakistan (Last *et al.* 2016). This is the first formal report of *P. ater* from Sri Lanka.

***Pateobatis jenkinsii* (Annandale)**

(Figs. 2G, 10A, B)

Five specimens of a species of *Pateobatis* Last, Naylor & Manjaji-Matsumoto were collected from fish markets in Puttalam (SL-17) in the North Western Province, and Munai (SL-43) at Point Pedro in the Northern Province, and a landing site in Mutur (SL-97, SL-98, and SL-101) in the Eastern Province. However, our molecular analysis, which included representation of four of the five described members of the genus as well as the undescribed taxon referred to as *Pateobatis* cf. *uarnacoides* by Naylor *et al.* (2012a), raised issues regarding the identity of *Pateobatis jenkinsii* across its current distribution as defined by Last *et al.* (2016b). The five specimens from Sri Lanka differed from one another by 0–1 bp. They grouped most closely with our reference specimen of *P. jenkinsii* (VN-103; JQ518810) from Vietnam but differed from that specimen by 18–19 bp. An immature specimen from Mutur has been deposited in the BRT Ichthyology Collection (SL-101; BRT-I 0028). Given the type locality of *P. jenkinsii* is the Ganjam coast of Orissa State, India (Eschmeyer *et al.* 2018), we consider the form in Sri Lanka to be *P. jenkinsii*. Thus, it seems appropriate to refer to the specimen from Vietnam as *P. cf. jenkinsii* until such time as the conspecificity of specimens from across the current distribution of *P. jenkinsii* (see Last *et al.* 2016b) can be investigated in more detail.

Morón *et al.* (1998; pg. 152) reported three forms of this taxon as *Himantura jenkinsii* (Annandale), *H. jenkinsii* A?, and *H. jenkinsii* B?, for specimens of different sizes, all from Beruwela in the Western Province. Clearly, the identity of specimens referred to as this, or related, species in Sri Lanka requires further study.

***Urogymnus granulatus* (Macleay)**

(Figs. 2H, 10D–H)

The left portion of the disc of a specimen (SL-13) found in a fish market in Puttalam in the North Western Province was preliminarily identifiable as *Urogymnus granulatus* based on the coloration of the dorsal surface of the disc which was yellowish brown with small white spots; it also had several irregular rows of enlarged, thorn-like denticles more or less restricted to the midline of the body. While this denticle pattern is inconsistent with that described for this species by Last *et al.* (2016a, b), it is consistent with that reported in the redescription of *U. granulatus* by Ishihara *et al.* (1993). This identification was supported by our molecular analysis in which this specimen was found to differ from our reference specimen of *U. granulatus* (CM03-74; JQ518808) from Australia by only a single bp. Our molecular work also confirmed the identity of a specimen, which has been deposited in the BRT Ichthyology Collection (SL-116; BRT-I 0030), collected from the Valaichchenai Fisheries Harbor in the Eastern Province earlier in the year, as *U. granulatus*. This immature specimen was identical to the reference specimen from Australia and differed from SL-13 by 1 bp.



FIGURE 10. *Pateobatis jenkinsii* (A–C) and *Urogymnus granulatus* (D–H) (Dasyatidae). A. Dorsal surface of mature female (SL-98). B. Wedge-shaped thorns and denticles on base of tail of mature female (SL-43). C. Dorsal surface of immature male (SL-101; BRT-I 0028). D. Dorsal surface of portion of disc of large specimen (partial; SL-13). E. Thorns and denticles on base of tail of mature specimen (SL-13). F. Ventral surface of portion of disc of large specimen (partial; SL-13). G. Dorsal surface of immature female (SL-116; BRT-I 0030). H. Scapular denticles of immature female (SL-116; BRT-I 0030).

This is the first report of *U. granulatus* from Sri Lanka. This may be the species referred to previously in Sri Lanka as *Urogymnus africanus* (Bloch & Schneider) by De Silva (1978) or possibly as *Urogymnus asperrimus* (Bloch & Schneider) (see De Bruin *et al.* 1995; Morón *et al.* 1998; De Silva 2006). Last *et al.* (2016b) suggested that both *U. granulatus* and *U. asperrimus* co-occur in Sri Lanka, and a specimen consistent with *U. asperrimus* collected since our survey confirms this. However, whether the form of this species in Sri Lanka is *Urogymnus asperrimus* 1 or *Urogymnus asperrimus* 2 (*sensu* Naylor *et al.* 2012a) remains to be determined.

Gymnuridae

Gymnura cf. poecilura 2

(Figs. 3A, 11A–D)

In total, five specimens of *Gymnura* van Hasselt were examined. These came from fish markets in Palkanththura (SL-4) and Puttalam (SL-16) in the North Western Province, from Jaffna (SL-50, SL-51) in the Northern Province, and from the Mutur landing site (SL-75) in the Eastern Province. The latter specimen was deposited in the BRT Ichthyology Collection (BRT-I 0017). All five specimens lacked a dorsal fin. However, some morphological variation was seen across the five specimens. A tiny spine was present on the tails of three (SL-16, SL-50, and SL-75) specimens. The tails of all five specimens were cross-banded, but the number of bands varied from 9–11. In some specimens—mainly small specimens of less than 32 cm DW—a single black dot was present between the bands (Fig. 11D); in other specimens—mainly larger specimens greater than 63 cm DW—a dark spot surrounded by four smaller dark spots was present between each band and the dark band had a central white spot (Fig. 11B). However, the five specimens from Sri Lanka differed from one another in NADH2 sequence by only 0–7 bp. In the tree resulting from the Neighbor-Joining analysis, which included sequence data for seven of the 12 described as well as the three undescribed members of the genus recognized by Naylor *et al.* (2012a) (*i.e.*, *Gymnura* sp. 1, *Gymnura* cf. *poecilura* 1, and *Gymnura* cf. *poecilura* 2), all five specimens from Sri Lanka grouped in a tight cluster with our reference specimen of *G. cf. poecilura* 2 (MM-22; JQ518834) from the Gulf of Oman. The Sri Lankan specimens differed from this specimen by 3–5 bp, suggesting they are likely conspecific.

To expand taxon representation to include *Gymnura* from India, data for a specimen of *Gymnura poecilura* (Shaw) (KU821581) from its type locality in Visakhapatnam on the eastern coast of India (see Eschmeyer *et al.* 2018), and a specimen identified as *G. cf. poecilura* (KU821578) from Mumbai on the western coast of India, were obtained from GenBank. These sequences, which are only 677 and 644 bp in length, respectively, were generated by Muktha *et al.* (2018) to help inform a redescription of *G. poecilura* in which a neotype was designated. In total, Muktha *et al.* (2018) presented NADH2 data for five specimens of *G. poecilura* from Visakhapatnam, which differed from one another by 0–7 bp, but unfortunately they failed to indicate which, if any, of these specimens was the neotype. In the tree resulting from our Neighbor-Joining analysis, the specimen of *G. poecilura* from India grouped well away from the specimens from Sri Lanka, supporting the identity of the Sri Lankan specimens as a taxon other than *G. poecilura*. Moreover, the specimen identified as *G. cf. poecilura* from India by Muktha *et al.* (2018) clustered with the specimens from Sri Lanka, suggesting that *G. cf. poecilura* 2 occurs in both countries. The Sri Lankan specimens differed by 3–4 bp across the 644 bp available for this specimen.

This species is typically referred to in Sri Lanka as *G. poecilura* (*e.g.*, De Silva 1978, 2006; De Bruin *et al.* 1995; Morón *et al.* 1998). However, it is more accurately referred to as *G. cf. poecilura* 2 in recognition of the fact that the Sri Lankan form appears to represent this undescribed species. As noted above, *G. poecilura* appears to represent a complex of genetically diverse, yet morphologically similar butterfly rays (Naylor *et al.* 2012a). Examination of additional specimens from throughout its current nominal distribution (Last *et al.*, 2016) is required to fully resolve the taxonomy of this group.

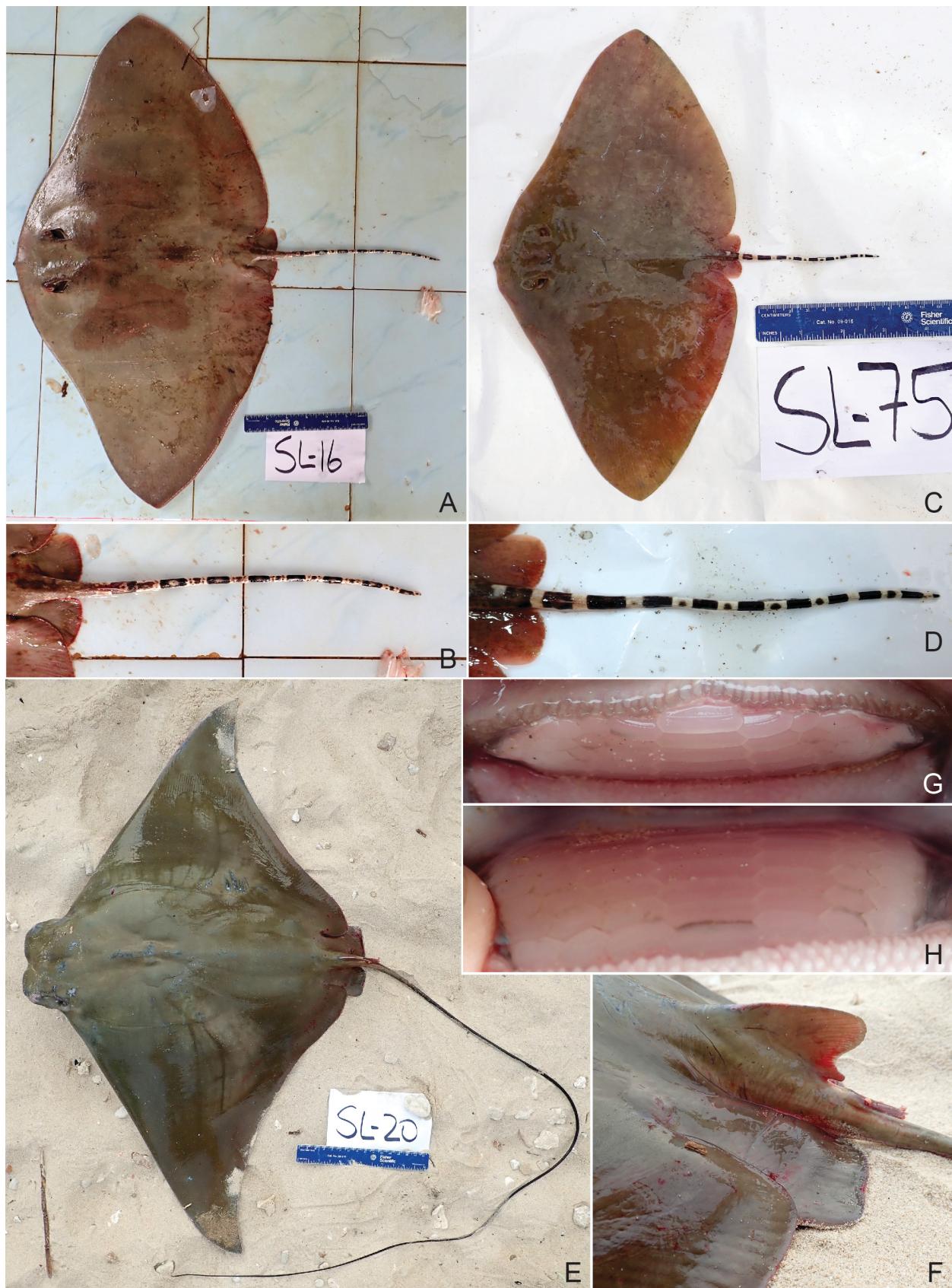


FIGURE 11. *Gymnura* cf. *poecilura* 2 (Gymnuridae) (A–D) and *Rhinoptera javanica* (Rhinopteridae) (E–H). **A.** Dorsal surface of female (SL-16). **B.** Tail of female (SL-16). **C.** Dorsal surface of immature male (SL-75; BRT-I 0017). **D.** Tail of immature male (SL-75; BRT-I 0017). **E.** Dorsal surface of immature male (SL-20). **F.** Dorsal fin and base of tail (lateral view; SL-20). **G.** Tooth plates (7) of upper jaw (SL-20). **H.** Tooth plates (7) of lower jaw (SL-20).

Rhinopteridae

Rhinoptera javanica Müller & Henle

(Figs. 3B, 11E–H)

The single specimen (SL-20) of cownose ray examined was landed at the Erinchamman Kovilady market in Point Pedro in the Northern Province. Seven of 10 species in this genus were included in our molecular analysis, with this specimen clustering most closely with our reference specimen of *Rhinoptera javanica* (VN-94; JQ518924) from Vietnam, but differing from the latter specimen by 5 bp. The specimen from Sri Lanka was morphologically consistent with *R. javanica* in its possession of a long tail and seven rows of teeth in both the upper and lower jaws, the middle three rows of which are much broader than the lateral rows.

This name is in current use for this species in Sri Lanka (see De Bruin *et al.* 1995; Morón *et al.* 1998; De Silva 2006).



FIGURE 12. *Acroteriobatus variegatus* (A, B) and *Rhinobatos annandalei* (C, D) (Rhinobatidae). A. Dorsal surface of immature male (SL-99; BRT-I 0027). B. Ventral snout and oronasal region of immature male (SL-99; BRT-I 0027). C. Dorsal surface of female (SL-115; BRT-I 0003). D. Ventral snout and oronasal region of female (SL-115; BRT-I 0003). E. Dorsal surface of immature male (SL-28). F. Oronasal region of immature male (SL-28).

Rhinopristiformes

Rhinobatidae

Acroteriobatus variegatus (Nair & Lal Mohan)

(Figs. 3C, 12A,B)

Four specimens (SL-99, SL-100, SL-102, and SL-103) of a relatively small guitarfish were collected at the landing site in Mutur in the Eastern Province. These specimens exhibited anterior nasal flaps that extended well into the internarial space, placing them in the genus *Acroteriobatus* Giltay (see Ebert 2014a; Last *et al.* 2016b). Their color pattern, in combination with their possession of small thorns near the orbits and spiracles as well as a conspicuous mid-dorsal row of small thorns, fits the description of *A. variegatus* (see Nair & Lal Mohan 1973), which was

originally reported from the Gulf of Mannar, India. As NADH2 data for a specimen of this species of confirmed identity are not available, we were unable to confirm this identification using molecular data. However, NADH2 sequence data were generated for all four specimens and they were included in our Neighbor-Joining analysis. These specimens differed from one another by 1–5 bp; in comparison, these specimens differed from our reference specimen of *Acroteriobatus annulatus* (Müller & Henle) (AF-156; JQ518915) from South Africa, the only other member of this genus included in the analysis, by 100–106 bp. An immature male of this species was deposited in the BRT Ichthyology Collection (SL-99; BRT-I 0027).

The distribution of this species in the map presented by Ebert (2014a) includes the northwestern coast of Sri Lanka. However, to our knowledge, this is the first formal report of this species from the country.

***Rhinobatos annandalei* Norman**

(Figs. 3C, 12C, D)

A muscle sample was taken from a frozen specimen of *Rhinobatos* Linck (SL-115) collected in 2015 from the Peliyagoda fish market in Colombo in the Western Province. This specimen has now been formally deposited in the BRT Ichthyology Collection (BRT-I 0003). Morphologically, this appears to be a specimen of *Rhinobatos annandalei*. It bears a symmetrical pattern of small, white spots on its dorsal surface and it exhibits broad grayish brown patches on the ventral surface of the disc and possibly also the tail, although the color of the latter is obscured as a result of freezing. NADH2 data for a reference specimen of confirmed identity was unavailable. However, this specimen differed from the five of its congeners included in the Neighbor-Joining analysis by 83–137 bp.

This name is in current use for this species in Sri Lanka (see De Silva 1978, 2006; De Bruin *et al.* 1995; Morón *et al.* 1998).

Torpediniformes

Narcinidae

***Narcine* sp. 1**

(Figs. 3D, 13A, B)

Two specimens of a species of *Narcine* Henle, one each from Point Pedro's Munai (SL-29) and Kottadi (SL-57) markets in the Northern Province, were examined. Both have been deposited in the BRT Ichthyology Collection (SL-29, BRT-I 0010; SL-57, BRT-I 0015). Both specimens were conspicuous in their possession of a dorsal surface bearing numerous, large (i.e., larger than eye-size) brown, mostly circular to oval spots on a paler brown background. Only two (i.e., *Narcine baliensis* Carvalho & White and *Narcine lingula* Richardson) of the 15 species of *Narcine* recognized by Last *et al.* (2016b) exhibit a dorsal surface with similar large brown spots. However, the specimens from Sri Lanka appear to differ morphologically from both species. They differ from *N. lingula* in bearing a disc that is heart-shaped and widest at a point posterior to, rather than at, the mid-disc, and a caudal fin with a dark, rather than plain, posterior margin. They most closely resemble *N. baliensis*, known only from eastern Indonesia. However, the disc is heart-shaped rather than broadly oval and, rather than plain, the lower caudal lobe bears brown pigmentation. As a consequence, it seems likely that these specimens represent an undescribed member of the genus, which we have referred to as *Narcine* sp. 1. The specimens from Sri Lanka differed from one another by 11 bp. The results of the Neighbor-Joining analysis contribute little to help inform the identity of these species because it included data for only three other species of *Narcine*. Nonetheless, the Sri Lankan specimens differ from their three congeners by 266–302 bp.

Previous reports of elasmobranchs from Sri Lanka include only *Narcine timlei* (Bloch & Schneider) (e.g., De Bruin *et al.* 1994; Morón *et al.* 1998; De Silva 2006), which bears a dorsal surface without elaborate markings, and *Narcine brunnea* Annandale (e.g., De Bruin *et al.* 1994; De Silva 2006), which is now considered a junior synonym of the former species. However, it is interesting to note that both sources refer to *N. timlei* as the spotted electric ray

and the illustration of *N. timlei* presented by De Bruin *et al.* (1994) is of an electric ray with small dark spots on its dorsal surface that is unlikely to be conspecific with *N. timlei*. Given the spots illustrated are small, rather than large, it seems likely that these authors were dealing with a member of the genus other than *Narcine* sp. 1.



FIGURE 13. *Narcine* sp. 1 (A, B) and *Torpedo* sp. 1 (C, D). A. Dorsal surface of maturing male (SL-29; BRT-I 0010). B. Oronasal region of maturing male (SL-29; BRT-I 0010). C. Dorsal surface of immature male (SL-28; BRT-I 0009); inset showing left eye, and spiracle with knobs and papillae. D. Oronasal region of immature male (SL-28; BRT-I 0009).

Torpedinidae

Torpedo sp. 1

(Figs. 3D, 13C, D)

Three specimens of a species of *Torpedo* Duméril were examined from Point Pedro's Munai (SL-28) and Kottadi (SL-55, SL-56) markets in the Northern Province. Two of these specimens have been deposited in the BRT Ichthyology Collection (SL-28, BRT-I 0009; SL-56, BRT-I 0014). This species bears a conspicuous pale reticulated pattern, apparently formed by fused spots, on a dark brown dorsal surface and thus most closely resemble *Torpedo sinuspersici* von Olfers as characterized by de Carvalho *et al.* (2002). However, the number of pale spots composing the reticulations, and thus the size of the reticulations, is smaller than seen in *T. sinuspersici*. These three specimens differed from one another by 2–5 bp. In the tree resulting from our Neighbor-Joining analysis

these specimens grouped most closely with *T. sinuspersici*; however, they differed from our reference specimen of the latter species (MM-27; JQ518932) by 32–42 bp. Of the five members of the genus not included in our analysis, only *T. panthera* von Olfers bears reticulations on its dorsal surface. But, the white markings on the dorsal surface of the disc of the latter species are not clustered (Last *et al.* 2016b). Our specimens differed from our reference specimen of *Torpedo marmorata* (SE-169; JQ518928) from Senegal by 110–148 bp. It seems likely that the Sri Lankan specimens represent an undescribed species of *Torpedo*, which we have referred to here as *Torpedo* sp. 1.

This may be the species referred to as *Torpedo marmorata* Risso by Morón *et al.* (1998).

Selachii

Carcharhiniformes

Carcharhinidae

Carcharhinus amblyrhynchoides (Whitley)

(Figs. 4A, 14A–D)

One specimen morphologically consistent with *Carcharhinus amblyrhynchoides* (SL-18) was examined near the main Erinchamman Kovilady market in Point Pedro in the Northern Province. It differed in NADH2 sequence from our reference specimen of this species from Malaysian Borneo (HBO-34; JQ519102) by 8 bp.

This name is in current use for this species in Sri Lanka (see De Silva 1984–1985, 2006, 2015; De Bruin *et al.* 1995; Morón *et al.* 1998).

Carcharhinus cf. limbatus

(Figs. 4A, 14E–H)

Two specimens of blacktip sharks were examined, one each from Point Pedro's Munai (SL-38) and Kottadi (SL-52) markets in the Northern Province. Following Naylor *et al.* (2012a), we refer to this species as *Carcharhinus cf. limbatus* in recognition of the fact that, despite their overall morphological similarity, the Indian and Pacific Ocean-dwelling form is molecularly distinct from the Atlantic-dwelling form of *Carcharhinus limbatus* (Müller & Henle). The two specimens from Sri Lanka differed from one another by 4 bp and from our reference sequence of *C. cf. limbatus* from Australia (AU-26; JQ518616) by 3 bp.

This species is routinely referred to in Sri Lanka as *C. limbatus* (e.g., De Silva 1977, 1984–1985, 2006, 2015; De Bruin *et al.* 1995; Joseph 1999). Use of the *C. cf. limbatus* designation for the form in Sri Lanka would serve as a reminder of the distinct nature of this form relative to the Atlantic form.

Negaprion acutidens (Rüppell)

(Fig. 4A)

The bisected head of a large shark (SL-45) was found in a cooler in the Munai market at Point Pedro in the Northern Province. The owners graciously pieced it back together for us to photograph and also allowed us to remove several muscle tissue samples and both the upper and lower jaws. Portions of the upper and lower jaws have been deposited in the BRT Ichthyology Collection (BRT-I 0013). The specimen was identical in NADH2 sequence to our reference specimen of *Negaprion acutidens* collected from Australia (AU-17; JQ518644). The teeth of the upper and lower jaws are also consistent with those of this species.

This name is in current use for this species in Sri Lanka (see De Silva 1984–1985, 2006, 2015; De Bruin *et al.* 1995; Morón *et al.* 1998). It appears there may be some confusion with the Atlantic member of this genus, *Negaprion brevirostris* (Poey), which has also been reported on occasion (e.g., Joseph 1999).

***Rhizoprionodon acutus* (Rüppell)**

(Figs. 4B, 14I–J)

The existence of undescribed diversity in the *Rhizoprionodon acutus* species complex complicates identification of the single specimen (SL-21) of this complex we encountered in the Erinchamman Kovilady market in Point Pedro in the Northern Province. Based on the molecular and morphological data presented by Caira & Jensen (2015), the specimen from Sri Lanka is most similar to *R. acutus* from the Gulf of Oman, rather than to any of the numbered designations (i.e., *Rhizoprionodon* cf. *acutus* 1, *Rhizoprionodon* cf. *acutus* 2, and *Rhizoprionodon* cf. *acutus* 3) for the three undescribed members of this species complex recognized by Naylor *et al.* (2012a). In the tree resulting from our Neighbor-Joining analysis, which included all seven described members of the genus and all three undescribed member of the *R. acutus* complex, the specimen from Sri Lanka grouped most closely with the reference specimen of *R. acutus* (MM-4; JQ518653) from the Gulf of Oman, differing from this specimen by only 1 bp. In contrast, it differed from our reference specimen of *R. cf. acutus* 1 from Senegal (SE-219; JQ518652) by 10 bp, from our reference specimen of *R. cf. acutus* 2 from Australia (AU-120; JQ518649) by 13 bp, and from our reference specimen of *R. cf. acutus* 3 from Malaysian Borneo (HBO-30; JQ519100) by 18 bp.

This name is in current use for this species in Sri Lanka (e.g., De Silva 1984–1985, 2006, 2015; De Bruin *et al.* 1995; Joseph 1999).

***Rhizoprionodon oligolinx* Springer**

(Figs. 4B, 14K–L)

Three specimens that were morphologically consistent with *Rhizoprionodon oligolinx* were examined from the Supparamadam (SL-22) and Kottadi (SL-53, SL-54) markets in Point Pedro in the Northern Province. In the tree resulting from the Neighbor-Joining analysis, they grouped most closely with our reference specimen of *R. oligolinx* (BO-475; JQ519096) collected from Malaysian Borneo. They differed from one another by 0–3 bp and from the reference specimen by 8–9 bp.

This name is in current use for this species in Sri Lanka (e.g., De Silva 1984–1985, 2006, 2015; De Bruin *et al.* 1995; Morón *et al.* 1998).

***Triaenodon obesus* (Rüppell)**

(Fig. 4A)

A tissue sample was taken from a frozen specimen of *Triaenodon obesus* (SL-119) that had been collected earlier in 2018 from the Negombo fish market in Negombo in the Western Province. This specimen has now been deposited in the BRT Ichthyology Collection (BRT-I 0031). This specimen is morphologically consistent with *T. obesus*. It clustered most closely with our reference specimen of this species (KA-126; JQ518656) from Indonesian Borneo included in the Neighbor-Joining analysis. It differed from this specimen in NADH2 sequence by 7 bp.

This is the name currently applied to this species in Sri Lanka (e.g., De Silva 1977, 1984–1985, 2006, 2015; De Bruin *et al.* 1995; Joseph 1999).

Galeoceridae***Galeocerdo cuvier* (Péron & Lesueur)**

(Fig. 4C)

A tissue sample was taken from each of two frozen immature specimens of *Galeocerdo cuvier* (SL-113 and SL-118) collected in 2017 from the Valaichchenai fisheries harbor in the Eastern Province. These specimens have now been deposited in the BRT Ichthyology Collection (SL-113, BRT-I 0004; SL-118, BRT-I 0005). These specimens were identical in NADH2 sequence and grouped most closely with our reference specimen of this species (BJ-382;

JQ519164) from the Gulf of California in the tree resulting from the Neighbor-Joining analysis; they differed from the latter specimen by 2 bp.

This is the name currently applied to this species in Sri Lanka (e.g., De Silva 1984–1985, 2006, 2015; De Bruin *et al.* 1995; Morón *et al.* 1998; Joseph 1999).



FIGURE 14. *Carcharhinus amblyrhynoides* (A–D) and *C. cf. limbatus* (E–H) (Carcharhinidae), and *Rhizoprionodon acutus* (I–J) and *Rhizoprionodon oligolinx* (K–L). A. Lateral view of female (SL-18). B. Ventral view of head of female (SL-18). C. Teeth of upper jaw of female (SL-18). D. Teeth of lower jaw of female (SL-18). E. Lateral view of immature female (SL-52). F. Ventral view of head of immature female (SL-52). G. Teeth of upper jaw of immature female (SL-52). H. Teeth of lower jaw of immature female (SL-52). I. Lateral view of mature female (SL-21). J. Ventral view of head of mature female (SL-21). K. Lateral view of maturing male (SL-22). L. Ventral view of head of mature male (SL-23).

Hemigaleidae

Hemipristis elongata (Klunzinger)

(Figs. 4D, 15A–D)

One specimen (SL-78) of *Hemipristis elongata* was collected from the deep-sea longline fishery in Mutur, Trincomalee Harbor in the Eastern Province. That specimen was morphologically consistent with *H. elongata*. It clustered most closely with our reference specimen (KA-22; JQ519069) of this species collected from Indonesian,

Borneo in the tree resulting from the Neighbor-Joining analysis, and differed from the latter specimen by only a single bp. This specimen has been deposited in the BRT Ichthyology Collection (BRT-I 0018).

This is the name currently applied to this species in Sri Lanka (e.g., De Silva 1984–1985, 2006, 2015; De Bruin *et al.* 1995; Morón *et al.* 1998; Joseph 1999).



FIGURE 15. *Hemipristis elongata* (Hemigaleidae) (A–D) and *Planonatasus indicus* (Pseudotriakidae) (E–H). **A.** Lateral view of immature male (SL-78; BRT-I 0018). **B.** Falcate pectoral fins of immature male (ventral view; SL-78; BRT-I 0018). **C.** Ventral view of head of immature male (SL-78). **D.** Teeth of upper jaw of immature male (SL-78; BRT-I 0018). **E.** Lateral view of mature female (SL-107; BRT-I 0029). **F.** Ventral view of head of mature female (SL-107; BRT-I 0029). **G.** Teeth of upper and lower jaw of mature female (SL-107; BRT-I 0029). **H.** Denticles on left side below dorsal fin of mature female (SL-107; BRT-I 0029).

Pseudotriakidae

Planonasus indicus Ebert, Akhilesh & Weigmann

(Figs. 4E, 15E–H)

Following up on an earlier report of what appeared to be a specimen of the poorly known *Planonasus* Weigmann, Stehmann & Thiel from Trincomalee Outer Harbor by Ebert *et al.* (2017), one of the fisheries we targeted was the deep-sea longline fishery in Mutur, Trincomalee Harbor in the Eastern Province. We were fortunate that on the second of the two days we spent at that location, fishers returned with dead bycatch retained for us. Fishing at 350 fathoms, their catch that day included a specimen (SL-107) of *Planonasus* allowing us to confirm the novelty of this, only the second known member of the genus. The species was recently described as *Planonasus indicus* (see Ebert *et al.* 2018). The original description was based on a holotype from India and our specimen from Sri Lanka; the latter has been designated a paratype and deposited in the BRT Ichthyology Collection (BRT-I 0029).

Ebert *et al.* (2017) originally reported this species from Sri Lanka as *Planonasus parini* Weigmann, Stehmann & Thiel.

Sphyrnidae

Eusphyra laticeps (Cantor)

(Figs. 4F, 16A–C)

One of the most intriguing specimens (SL-3) examined in Sri Lanka was caught in the Gulf of Mannar and landed at Palkanththura in the North Western Province. The distinctive narrow blades of its wing-shaped head seemed to unambiguously confirm its identity as *Eusphyra blochii* (Cuvier). However, it was found to differ from our reference specimen of *E. blochii* (AU-83; JQ519152) from Australia by 46 bp. This substantial difference in NADH2 sequence suggests that the form from Sri Lanka may represent a second species of winghead shark. Although generally considered a synonym of *E. blochii*, *Eusphyra laticeps* is a candidate name for the Sri Lankan form. This species was described by Cantor (1837), as *Zygaena laticeps* Cantor, from the Bay of Bengal and, based on Cantor's description, clearly exhibits the extremely expanded head that is diagnostic of *E. blochii*—a feature also seen in the specimen from Sri Lanka. The potential existence of two species with this characteristic head raises an interesting question regarding the identity of *E. blochii* for which the type locality is unknown (Gilbert, 1967), but which is currently considered to be distributed throughout the Indo-West Pacific (Compagno, 1984). Clearly examination of additional specimens and comparison with specimens from other localities in the Indo-West Pacific is in order.

It seems likely that this is the taxon in Sri Lanka referred to as *Sphyra blochii* Cuvier by Goonewardene (1971) and De Silva (1977) and as *E. blochii* by De Silva (1984–1985, 2006, 2015), De Bruin *et al.* (1995), Morón *et al.* (1998), and Joseph 1999.

Triakidae

Iago cf. omanensis 1

(Figs. 4G, 16D–G)

The existence of undescribed diversity in the *Iago omanensis* (Norman) species complex from elsewhere across the globe (see Naylor *et al.* 2012a) complicates identification of the specimens of this genus examined in Sri Lanka, six of which (SL-79, SL-80, SL-81, SL-82, SL-83, and SL-84) were collected at the Mutur landing site in the Eastern Province in 2018, and one of which (SL-114) was collected at the Peliyagoda Fish Market in Colombo, in the Western Province. Based on morphology, we initially thought we had encountered two different species of *Iago*. In one case (i.e., SL-80; Fig. 16F), the second dorsal fin was only slightly larger than the anal fin, and the anal fin origin was located slightly anterior to the middle of the second dorsal fin with the anal fin posterior rear tip extending posterior to that of the second dorsal fin; this specimen has been deposited in the BRT Ichthyology

Collection (BRT-I 0020). In contrast, in the other six specimens (SL-79 [Fig. 16D], SL-81, SL-82, SL-83, SL-84, and SL-114), the second dorsal fin was conspicuously larger than the anal fin and the anal fin origin was only slightly posterior to the origin of the second dorsal fin with the posterior rear tip of the second dorsal fin extending to approximately the same level as that of the anal fin; a female specimen of this form was deposited in the BRT Ichthyology Collection (SL-79; BRT-I 0019). However, this distinction was not supported by our molecular data. In the tree resulting from the Neighbor-Joining analysis of NADH2 data, all seven specimens from Sri Lanka formed a tight cluster with the reference specimen of the undescribed species from India given the designation *Iago* cf. *omanensis* 1 (JQ518697) by Naylor *et al.* (2012a). Two subclusters were evident within this cluster. The three specimens in the first subcluster, which included the reference specimen from India, were identical in sequence; the five specimens in the second subcluster differed from one another by 0–2 bp. Although the subclusters differed from one another by 6–7 bp, the first subcluster included specimens of both morphological forms.

In terms of existing names for *I. cf. omanensis* 1, we gave some consideration to whether *Iago mangalorensis* (Cubelio, Remya & Kurup), originally described as *Mustelus mangalorensis* Cubelio, Remya & Kurup from a specimen in a fish collection in India, collected from Mangalore on the west coast of India, was appropriate. However, based on Cubelio *et al.*'s (2011) original description, the extremely pointed snout, among other features, is inconsistent with the specimens from Sri Lanka. The other potential candidate is the taxon referred to by Compagno *et al.* (2005) as *Iago* sp. A occurring off the northwestern coast of Sri Lanka. However, the low dorsal fins and small pectoral fins of this taxon are inconsistent with those of our specimens from Sri Lanka. We would note that there appears to be some confusion in the literature regarding the identities of *I. mangalorensis* and *I. sp. A*, given that the illustrations and description of the former species in Ebert *et al.* (2013) is actually of the latter taxon as defined by Compagno *et al.* (2005).

This may be the species reported previously from Sri Lanka by Morón *et al.* (1998) as *Iago omanensis*. However, species of *Mustelus* Linck have commonly also been reported (e.g., De Silva 1984–1985, 2006, 2015; De Bruin *et al.* 1995; Joseph 1999) and thus generic verification of reports of triakid sharks more broadly from the region should be a future priority.

Echinorhiniformes

Echinorhinidae

Echinorhinus sp. 1

(Figs. 5A, 17A–D)

Three bramble shark specimens (SL-90, SL-108, and SL-109) were examined at the landing site of the deep-sea longline fishery in Mutur in the Eastern Province. The upper and lower jaws of SL-90 have been deposited in the BRT Ichthyology Collection (BRT-I 0022). The morphology of these specimens is consistent with that of *Echinorhinus brucus* (Bonnaterre), especially in their possession of large, irregularly scattered thorn-like denticles and characteristic teeth with a single main laterally-directed cusp and one to two cusplets. However, our molecular work calls this identification into question. The specimens formed a tight cluster in the tree resulting from Neighbor-Joining analysis of NADH2 data with the reference specimen (JQ400114) of an undescribed species, referred to by Naylor *et al.* (2012b) as *Echinorhinus* sp. 1, from the Gulf of Oman. These four specimens differed from one another by 0–2 bp. In contrast, the specimens from Sri Lanka differed from our reference specimen of *E. brucus* (JQ519170) from the Gulf of Mexico by 52–53 bp. What is even more interesting is that, despite their possession of conspicuous, large, thorn-like denticles as seen in *E. brucus*, the specimens from Sri Lanka clustered more closely with the reference specimen of *Echinorhinus cookei* Pietschmann (JQ519016)—a species known to lack enlarged thorns—but differed from this specimen by 48–50 bp. Although more detailed morphological work remains to be done, our results suggest that the bramble shark in Sri Lanka may represent an undescribed species that also appears to occur in the Gulf of Oman.

It seems likely this is the taxon currently referred to as *E. brucus* in Sri Lanka (e.g., De Silva 1984–1985, 2006, 2015; De Bruin *et al.* 1995; Morón *et al.* 1998; Joseph 1999).



FIGURE 16. *Eusphyra laticeps* (Sphyrnidae) (A–C) and *Iago* cf. *omanensis* 1 (Triakidae) (D–G). **A.** Lateral view of mature male (SL-3). **B.** Dorsal view of head of mature male (SL-3). **C.** Ventral view of head of mature male (SL-3). **D.** Lateral view of female (SL-79; BRT-I 0019). **E.** Ventral view of head of female (SL-79; BRT-I 0019). **F.** Lateral view of mature male (SL-80; BRT-I 0020). **G.** Ventral view of head of mature male (SL-80; BRT-I 0020).

Hexanchiformes

Hexanchidae

***Hexanchus griseus* (Bonnaterre)**

(Figs. 5B, 17E–H)

All three specimens (SL-91, SL-105, and SL-106) of *Hexanchus griseus* examined were seen at the landing site of the deep-sea longline fishery in Mutur in the Eastern Province. The upper and lower jaws of SL-91 have been deposited in the BRT Ichthyology Collection (BRT-I 0023). These specimens are morphologically consistent with *H. griseus*. All three specimens formed a tight cluster with our reference specimen of *H. griseus* (JQ518727) from the Caribbean Sea in the tree resulting from the Neighbor-Joining analysis. They were identical in sequence to each other and differed from the reference specimen by 2 bp.

This is the name currently applied to this species in Sri Lanka (e.g., De Silva 2006, 2015; Morón *et al.* 1998; Joseph 1999).

Lamniformes

Lamnidae

***Isurus paucus* Guitart**

(Fig. 5C)

One small specimen (SL-110) of *Isurus paucus* was examined at the Valaichchenai Fisheries Harbor landing site in the Eastern Province. It is morphologically fully consistent with *I. paucus*. It differs from the reference specimen (KJ616742.1) of this species from Taiwan included in our analysis by 1 bp.

This name is in current use for this species in Sri Lanka (e.g., De Silva 1984–1985, 2006, 2015; Morón *et al.* 1998; Joseph 1999).

Orectolobiformes

Hemiscylliidae

***Chiloscyllium* sp. 1**

(Figs. 5D, 17I–K)

Six specimens of an interesting species of *Chiloscyllium* Müller & Henle were examined from the Munai (SL-31) and Kottadi (SL-32, SL-59, SL-60) markets at Point Pedro, and Vankalai (SL-65, SL-70) in the Northern Province. Immature specimens of this species exhibited brown bands and saddles that persisted, but were less conspicuous, in adults. Morphologically, among its congeners, these specimens most closely resemble *Chiloscyllium arabicum*, particularly in fin shape and position. Our molecular analysis included six of the eight described and both undescribed members of the genus (i.e., *Chiloscyllium* cf. *punctatum* 1 of Naylor *et al.* [2012a] from Australia and *Chiloscyllium* cf. *punctatum* 2 from Taiwan of Straub *et al.* [2013]). Because of the resemblance to *C. arabicum*, we included newly generated NADH2 data for a reference specimen (MM-903; MK335259) of the latter species from the Gulf of Oman. In the tree resulting from the Neighbor-Joining analysis, the specimens from Sri Lanka formed a distinct cluster, differing from one another by 1–4 bp. They grouped most closely with our reference specimen of *Chiloscyllium hasselti* Bleeker (KA-164; JQ519066) from Indonesian Borneo. However, they differed from this specimen by 37–43 bp. They were even more divergent from *C. arabicum* and *Chiloscyllium griseum* Müller & Henle, differing from the reference specimen of the former species by 109–124 bp and from that of the latter species by 100–115 bp. With respect to the two known species not included in our molecular analysis, the specimens from Sri Lanka conspicuously differ from both. They lack the blue-white spots characteristic of *Chiloscyllium caeruleopunctatum* Pellegrin (see Compagno 1984) and the diagnostic dark fin webs of *Chiloscyllium burmensis* (see Dinkerkus & DeFino 1983). It could be argued that these specimens raise a question regarding the validity of *Chiloscyllium confusum* Dinkerkus & DeFino—a species originally described from India

by Dingerkus & DeFino (1983), but synonymized with *C. arabicum* (see Randall 1995). However, Dingerkus & DeFino (1983; pg. 11) differentiated *C. confusum* from all of its congeners, including *C. arabicum*, on the basis of the fact that "This is the only species of *Chiloscyllium* in which the immature body color is uniform, and identical with that of the adult", yet all of our specimens (immature and adults) exhibit a clear pattern of brown bands and saddles. Furthermore, unlike *C. confusum* our Sri Lankan specimens exhibit a first dorsal fin base that is longer, rather than shorter, than the second dorsal fin base. It thus seems apparent that our specimens represent an undescribed species. We have provisionally referred to them here as *Chiloscyllium* sp. 1. An immature male of this species was deposited in the BRT Ichthyology Collection (SL-32; BRT-I 0011).



FIGURE 17. *Echinorhinus* sp. 1 (Echinorhinidae) (A–D), *Hexanchus griseus* (Hexanchidae) (E–H), and *Chiloscyllium* sp. 1 (Hemiscylliidae) (I–K). **A.** Lateral view of female (SL-108). **B.** Ventral view of head of female (SL-108). **C.** Teeth of upper jaw of female (SL-108). **D.** Teeth of lower jaw of female (SL-108). **E.** Lateral view of immature male (SL-106). **F.** Ventral view of head of female (SL-91). **G.** Teeth of upper jaw of female (SL-91). **H.** Teeth of lower jaw of female (SL-91). **I.** Lateral view of mature male. **J.** Ventral view of head of mature male (SL-59). **K.** Dorsal view of head and trunk of mature male (SL-59).

It seems likely that this is the species that has been previously reported as *C. griseum* from Sri Lanka (e.g., De Silva 1984–1985, 2006, 2015; De Bruin *et al.* 1995; Morón *et al.* 1998; Joseph 1999). If so, the presence of *C. griseum* in Sri Lanka remains to be confirmed.

Squaliformes

Centrophoridae

Centrophorus cf. atromarginatus

(Figs. 5E, 18A–C)

Six specimens (SL-85, SL-86, SL-87, SL-88, SL-89, and SL-95) of the short-snout group of *Centrophorus* Müller & Henle species were examined from the deep-sea longline landing site in Mutur in the Eastern Province. Although definitive identification of many species of *Centrophorus* remains problematic (e.g., see Verissimio *et al.* 2014; White *et al.* 2017), these specimens do not conform to the description of any of the 12 valid species in the genus. A female specimen of this species has been deposited in the BRT Ichthyology Collection (SL-87; BRT-I 0021). In the tree resulting from the Neighbor-Joining analysis, these six specimens grouped in a tight cluster, differing from one another by 0–4 bp in NADH2 sequence. We have preliminary identified these specimens as *Centrophorus* cf. *atromarginatus*. The specimens most closely resemble *Centrophorus atromarginatus* Garman but appear to differ from this species in that the black coloration on the dorsal fins is not restricted to the posterior margins but covers the dorsal half of both fins. In addition, the pectoral fins lack black posterior margins, as does the upper lobe of the caudal fin. Examination of the holotype and voucher specimens of *C. atromarginatus* from throughout its current known distribution from Japan to the Gulf of Aden reveals some morphological variation, suggesting it may constitute a species complex (DAE, unpubl data). Unfortunately, NADH2 data for a confirmed reference specimen of *C. atromarginatus* were unavailable. Further comparison of regional specimens and generation of NADH2 data for specimens of *C. atromarginatus* from its type locality in Japan (see Eschmeyer *et al.* 2018) would be useful to confirm this lack of conspecificity. We have employed this name in recognition of the fact that these specimens may represent additional novelty in the genus.

Three species of *Centrophorus* have been reported from Sri Lanka: *Centrophorus moluccensis* Bleeker (e.g., Joseph, 1999; tentatively Ebert, 2013; De Silva, 2015), *Centrophorus squamosus* (Bonnaterre) (e.g., Morón *et al.* 1998; Weerakkody & Fernando 2000; De Silva 2006, 2015), and *Centrophorus uyato* Rafinesque (e.g., tentatively Morón *et al.* 1998; Joseph, 1999). This is one of the candidates for the species referred to in one or more of these reports, but in the absence of detailed images, this is difficult to assess.

Centrophorus uyato

(Figs. 5E, 18D–F)

A single specimen (SL-96) of a second species of *Centrophorus* was also collected at the deep-sea longline landing site in Mutur in the Eastern Province. This specimen, which has been deposited in the BRT Ichthyology Collection (BRT-I 0026), is morphologically consistent with photographs of a specimen of *Centrophorus uyato* from Norway presented by Wienerroither *et al.* (2015) in a paper synonymizing the latter species with *Centrophorus zeehaani* White, Ebert & Compagno from Australia. In our molecular analysis, the specimen from Sri Lanka was identical in NADH2 sequence to both a paratype of *C. zeehaani* (CSIRO H 6628-03; JQ519054) and a specimen (JQ518946) referred to as *C. cf. zeehaani* by Naylor *et al.* (2012a) from Portugal that Wienerroither *et al.* (2015) also considered to represent *C. uyato*. The specimen of *C. uyato* from Sri Lanka grouped most closely with the cluster of specimens of *Centrophorus* cf. *atromarginatus* in the tree resulting from the Neighbor-Joining analysis, but differed from these specimens by 31–32 bp.

This is another candidate for the reports of species of *Centrophorus* from Sri Lanka included in our treatment of *Centrophorus* cf. *atromarginatus*.



FIGURE 18. *Centrophorus* cf. *atromarginatus* (A–C) and *Centrophorus uyato* (D–F) (Centrophoridae). A. Lateral view of female (SL-87; BRT-I 0021). B. Ventral view of head of female (SL-87; BRT-I 0021). C. Denticles on left side below dorsal fin of female (SL-87; BRT-I 0014). D. Lateral view of female (SL-96; BRT-I 0026). E. Ventral view of head of female (SL-96; BRT-I 0026). F. Denticles on left side below dorsal fin of female (SL-96; BRT-I 0026).

Somniosidae

Centroscymnus owstonii Garman

(Figs. 5F, 19A–C)

Two specimens (SL-92 and SL-93) of *Centroscymnus* Barboza du Bocage & de Brito Capello were also collected from the deep-sea longline landing site in Mutur in the Eastern Province. Morphologically these specimens are consistent with *Centroscymnus owstonii* following Weigmann *et al.* (2016). In the tree resulting from our Neighbor-Joining analysis of NADH2 data, these specimens grouped most closely with our reference specimen of *C. owstonii* from Portugal. The two specimens from Sri Lanka differ from each other by 2 bp; one is identical to the reference specimen. A mature male has been deposited in the BRT Ichthyology Collection (SL-93; BRT-I 0024).

To our knowledge, this is the first documented report of this family, genus, and species from Sri Lanka. It is also the first record of this genus from the northern Indian Ocean.



FIGURE 19. *Centroscymnus owstonii* (Somniosidae). **A.** Lateral view of mature male (SL-93; BRT-I 0024). **B.** Ventral view of mature male (SL-93; BRT-I 0024). **C.** Teeth of upper and lower jaw of mature male (SL-93; BRT-I 0024).

Dried shark tissues

NADH2 sequence data were generated for four samples of dried shark product, two haphazardly taken from a bag of dried shark meat sold commercially by Arunalu and two from a bag of dried shark meat sold by Rone. The four samples were of four different species of sharks. One Arunalu sample (SL-C) clustered most closely with *C. cf. limbatus* (Fig. 4A), differing by 3–4 bp from the two Sri Lankan specimens. The second Arunalu sample (SL-D) grouped most closely with *Isurus oxyrinchus* Rafinesque (Fig. 5C), differing by 6 bp from the reference specimen from Vietnam. One Rone sample (SL-B) grouped most closely with *Carcharhinus amblyrhynchos* (Bleeker) (Fig. 4A), differing from our reference specimen from Malaysian Borneo by 7 bp. Because of the high degree of

NADH2 sequence similarity between *Carcharhinus altimus* (Springer) and *Carcharhinus plumbeus* (Nardo) a definitive specific identification for the second Rone sample (SL-A) is not possible. That sample grouped with our reference specimens of both species from the Atlantic Ocean (Fig. 4A), differing from the former by 6 bp and the latter by 7 bp.

Discussion

This preliminary survey has helped to inform our understanding of the identity, nomenclature, and distribution of the majority of the elasmobranch species examined. The most unexpected result of our brief survey was the remarkable degree of novelty discovered in Sri Lankan waters. In total, five species are likely new to science. These are the batoids *Brevitrygon* sp. 1, *Narcine* sp. 1, and *Torpedo* sp. 1, and the selachians *Centrophorus* cf. *atromarginatus*, and *Chiloscyllium* sp. 1, in addition to the recently described *Planonasus indicus*. The identities of 12 species previously known to occur in Sri Lanka are updated to conform to current taxonomy (i.e., *Aetobatus ocellatus*, *Eusphyra laticeps*, *Himantura tutul*, *Maculabatis gerrardi*, *Neotrygon indica*, *Pastinichus ater*, *Urogymnus granulatus*, *Centrophorus uyato*, *Gymnura* cf. *poecilura* 2, *Carcharhinus* cf. *limbatus*, *Iago* cf. *omanensis* 1, and *Echinorhinus* sp. 1). The latter four likely represent undescribed species reported previously from other localities by Naylor *et al.* (2012a). This is the first report of three additional known species (i.e., *Acroteriobatus variegatus*, *Maculabatis arabica*, and *Centroscymnus owstonii*) from the country; *C. owstonii* also represents both the first documented report of this family and genus from the northern Indian Ocean.

Current estimates of the elasmobranch diversity of Sri Lanka are generally somewhere between 110 and 120 species (de Bruin *et al.* 1995; De Silva 2006, 2015; Last *et al.* 2016b; Ebert *et al.* 2017). We examined only 34 species over only nine days in the field. Moreover, we spent no more than two days at any single locality. We sampled from no eastern localities in the Northern Province and from only two neighboring localities in the entire Eastern Province. No samples were collected from the Southern Province. Finally, with the exception of a few frozen specimens collected prior to our formal survey, we spent no time in Negombo, which arguably is the largest elasmobranch landing site in the country, or Peliyagoda, which is the largest fish market in the country. Despite these limitations, the new species and new records from the country underscore the need and value of future survey work employing a blend of morphological and molecular data.

Our study also revealed some unexpected geographic similarities between elements of the elasmobranch fauna of Sri Lanka and those of other regions. Despite the country's location on the southeastern tip of the Indian subcontinent—only 50 km from India—a number of the species we encountered in the waters of Sri Lanka have not been reported from India. Furthermore, they are known from geographic localities that are relatively distant from Sri Lanka. For example, the butterfly ray *Gymnura* cf. *poecilura* 2 was previously known only from the Gulf of Oman and the Persian Gulf (Naylor *et al.*, 2012a); *Echinorhinus* sp. 1 was previously reported from the Gulf of Oman (Naylor *et al.*, 2012b); *Carcharhinus* cf. *limbatus* was previously reported by Naylor *et al.* (2012a) from Australia, Borneo, Gulf of California, Hawaii, India, Madagascar, Philippines, Sierra Leone, South Africa, Taiwan, and Vietnam. In addition, the houndshark *Iago* cf. *omanensis* 1, previously known only from India, also appears to occur in Sri Lanka.

One of the primary motivations for this survey arose from an interest in investigating the cestode fauna of the elasmobranchs of Sri Lanka. This was largely because much of the early foundational work on the taxonomy of elasmobranch cestodes globally was motivated by an interest in the adverse effects cestodes were having on the Pearl Oyster Fisheries in the Gulf of Mannar (e.g., Shipley & Hornell 1904, 1905, 1906; Herman & Hornell 1906; Southwell 1911, 1912, 1924, 1925, 1927, 1929, 1930). In order for the cestode fauna of the elasmobranchs of Sri Lanka to be placed into a meaningful global context, it was first necessary to update the taxonomy of the elasmobranchs of Sri Lanka to conform to current global standards. As a result of this survey, we are now poised to explore the identities and affinities of the cestodes that parasitize the 34 species of elasmobranchs examined here. Additional survey work is required before our cestode work can be expanded to include additional host species in the country.

Sequence data generated for two samples each from both the Rone and Arunalu dried shark meat products proved to be interesting. Given all four samples sequenced, which were haphazardly selected from among the more than 20 pieces of shark tissue in each bag of shark meat, were determined to represent different species, it seems likely that sequence data generated for additional portions of shark tissue may reveal yet additional diversity.

Finally, it is worth noting that, given five new species to science have likely been discovered in Sri Lanka through this brief study, and that with additional time and effort further species may be discovered, there is an urgent need to ensure that a greater focus on national elasmobranch management is undertaken. This is essential given the large-scale target and bycatch, artisanal, and commercial fisheries affecting these species. Severe population declines for many commercially harvested elasmobranchs have already been recorded in Sri Lanka (SL-NPOA-Sharks 2013; Davidson *et al.* 2016). It is highly likely that many of these novel species will be threatened by these same fisheries if no appropriate management measures are introduced.

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