Resurrection and redescription of the Borneo Broadfin Shark *Lamiopsis tephrodes* (Fowler, 1905) (Carcharhiniformes: Carcharhinidae)

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ABSTRACT.— The genus *Lamiopsis* was previously considered to be monotypic, represented by a single species *L. temminckii*. Recent molecular analyses from across the range of this genus has shown that two species should be recognised, one in the Indian Ocean centred around India and another in the Western Central Pacific centred around Borneo. *Lamiopsis tephrodes* (Fowler, 1905) was described from Borneo and is resurrected from being a junior synonym of *L. temminckii* to a valid species. A redescription of *L. tephrodes,* based largely on recently collected material is provided. This species differs from *L. temminckii* in dentition, some morphological characters and possibly size. It also exhibits substantial DNA sequence divergence in the mitochondrial marker ND2. A lectotype is also herein designated for *L. temminckii*. The conservation of these species needs to be reassessed, with both species likely to fall in one of the highly threatened IUCN Red List categories.

Key words: *Lamiopsis temminckii* – *Lamiopsis tephrodes* – Borneo – resurrection – redescription – threatened

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INTRODUCTION

The genus *Lamiopsis* was proposed by Gill (1862) for *Carcharias (Prionodon) temminckii* Müller & Henle, 1839 which was described from several specimens from Pondicherry in India. Prior to the 1970s, this genus was often synonomised with *Carcharhinus*, but was considered valid by Compagno (1970, 1979, 1984, 1988) and Garrick (1982). The genus *Lamiopsis* shares many of the key characteristics with the genus *Glyphis* Agassiz, 1843 which, in combination, distinguishes them from other carcharhinid genera, e.g. dentition, large second dorsal and pectoral fins, and longitudinal (rather than crescentic) precaudal pits. *Lamiopsis* differs from *Glyphis* in having a nearly straight anal-fin posterior margin, larger and more ventrolaterally situated eyes, longer snout and more posterior first dorsal fin (Compagno, 1988).

Lamiopsis tephrodes was described by Fowler (1905) as *Carcharhinus tephrodes* based on two specimens collected from off Baram in Sarawak (Borneo), a ~637 mm holotype and a ~372 mm paratype. Fowler (1905) did not define the characteristics that distinguish *L. tephrodes* from *L. temminckii*. Garrick & Schultz (1963) synonomised *L. tephrodes* with *L. temminckii*, and although Fowler (1930, 1941, 1968) retained *L. tephrodes*, examination of the types by Compagno (1979, 1988) revealed nothing to separate the species. Fowler (1941, 1968) synonomised *Carcharias sealei* Pietschmann, 1913 with *L. tephrodes,* and listed *C. borneensis* (Bleeker, 1858) as a doubtful synonym. However, *C. sealei* and *C. borneensis* are both considered valid *Carcharhinus* species and are not congeneric or conspecific with *L. tephrodes* (Compagno, 1979). Fowler's misidentification is possibly due to the paratype of *L. tephrodes* not being a *Lamiopsis* species, and hence not congeneric or conspecific with the holotype. Instead, the paratype of *L. tephrodes* represents an undescribed *Carcharhinus* species of the '*C. porosus*' group (Compagno, 1979, 1988), i.e. *Carcharhinus* sp. A [*sensu* Compagno *et al*., 2005].

The collection of fresh specimens of *Lamiopsis* during recent surveys throughout South-east Asia has allowed for more detailed taxonomic and molecular comparisons of this genus throughout its range. The present account reviews the nominal species of *Lamiopsis*, resurrects *L. tephrodes* as a valid taxon and provides a detailed redescription of this species. One of the syntypes of *L. temminckii* is also designated as a lectotype.

METHODS

Measurement terminology follows Compagno (1984, 1988, 2001) who assigned names and abbreviations to measurements often indicated by descriptive phrases (example: snout to upper caudal origin = precaudal length = PRC). Dentitional terms generally follow Compagno (1979, 1988, 2001). Vertebral terminology, method of counting and vertebral ratios follow Springer & Garrick (1964) and Compagno (1979, 1988, 2001).

A total of 11 *Lamiopsis tephrodes* were measured in full (Table 1). A subsample of measurements from the dried lectotype of *Lamiopsis temminckii* (BMNH 1851.8.16.11) was also taken. Morphometric ranges of the 11 measured specimens of *L. tephrodes* are provided in the descriptive section. Meristics were taken from radiographs of 4 specimens of *L. tephrodes* (CSIRO H 6662–01, CSIRO H 6137–07, CSIRO H 7083–01 and CSIRO H 7084–01). Counts were obtained separately for trunk (monospondylous), precaudal (monospondylous + diplospondylous to origin of upper lobe of caudal fin) and caudal (centra of the caudal fin) vertebrae. Tooth row counts were taken in situ or from excised jaws of 8 specimens of *L. tephrodes* and 7 specimens of *L. temminckii*.

Muscle tissue samples were taken from specimens collected in the field and stored in either 95% ethanol or DMSO until processed in the laboratory. Total DNA was extracted from the tissue samples using High Pure PCR Template Preparation Kit (Roche Diagnostics). Extracted total DNA was stored at -20° C. Sub-sets of the extracted template were diluted to 1/10 of original strength and stored for subsequent use in PCR reactions. Samples were PCR amplified using Hot Start Taq (Promega) using primers designed to target the complete coding sequence for NADH dehydrogenase subunit 2 (Naylor *et al*., 2005). These primers are designed to bind to the ASN and ILE tRNA regions flanking the NADH2 gene in the mitochondrial genome of elasmobranchs. PCR reactions were generally carried out in 25 µl tubes by adding 1–2 µl of DNA template containing 1 unit of Taq, PCR buffer, 2.5 mM of $MgCl^2$, 1.0 mM of DNTPs, and 1.0 mM of each primer. The reaction cocktail was denaturised at 94°C for 3 minutes, after which it was subjected to 35 cycles of 94°C /30s, 48°C /30s and 72°C /90s followed by an indefinite hold in the thermal cycler at 4°C.

A sample of the completed PCR reaction was run on 1% agarose gels, stained, visualised and photographed under UV light to assess the success of PCR amplification. Samples with successful amplification products were purified using purification plates (Millipore, MA) attached to a vacuum manifold. The purified PCR products were quantified and diluted to between 30–100 ng/µl and subsequently sent to SeqWright (Houston, TX) for sequencing. The software packages Phred and Phrap were used to read sequence traces, assign quality values, make base calls and produce output files for subsequent alignment. Sequences were translated to amino acids and aligned using the software package MUSCLE (Edgar, 2004). The aligned amino acid sequences were translated back, but in frame to their original nucleotide sequences to yield a nucleotide alignment.

The aligned nucleotide sequences were subjected to Phylogenetic analysis using PAUP* (v4.0b106). The data were subjected to Neighbour joining based on K2P Distance, Parsimony and Maximum Likelihood analysis using parameter optimised models that best fit the data. The topologies across all methods were consistent with each other.

Specimens are referred to by the following prefixes for their registration numbers: BMNH, British Museum of Natural History, London; CSIRO, Australian National Fish Collection, Hobart; IPPS, Institut Penyelidikan Perikanan Sarawak, Kuching, Malaysia; RMNH, Rikjsmuseum van Natuurlkjke Histoire, Leiden; PMH, Mark Harris personal collection. In the molecular trees, field codes (prefixed by BO, DF or KA) are provided for samples collected by Drs J. Caira and K. Jensen, and data and images for these specimens are available at http://tapeworms.uconn.edu.

FAMILY CARCHARHINIDAE Jordan & Evermann, 1896

Genus ***Lamiopsis*** Gill, 1862

Type species. *Carcharias (Prionodon) temminckii* Müller & Henle, 1839

SPECIES.— *Lamiopsis* includes two nominal species: *L. temminckii* (Müller & Henle, 1839); *L. tephrodes* (Fowler, 1905). *Carcharhinus microphthalmus*, described by Chu (1960), is likely to be a synonym of *L. tephrodes*.

Lamiopsis tephrodes (Fowler, 1905)

Figs 1–6, Table 1

Carcharhias (Prionodon) temminckii (non Müller & Henle): Martens, 1876: 409 (Makassar Strait).
Carcharhinus tephrodes Fowler, 1905: 455–458, fig. 1 (Type locality: Baram, Borneo).
Eulamia tephrodes: Fowler, 1930: 493 (Java).
Eulamia temminckii: Fowler, 1930: 493 (Java).
Carcharhinus microphthalmus Chu (Zhu), 1960: 84, figs 78, 79 (Type locality: Jia-bo, China).
Lamiopsis temmincki (in part, non Müller & Henle): Compagno, 1979: 542, 543 (Makassar Straits and Borneo).

Material examined. 17 specimens: CSIRO H 6137–07, juvenile male 600 mm TL (dorsal, pectoral and lower

caudal fins missing), Muara Baru fish landing site, Jakarta, Indonesia (caught from southern Kalimantan according to fisheries information), 31 Jan. 2003; CSIRO H 6662–02, juvenile male 408 mm TL, Muara Baru fish landing site, Jakarta, Indonesia (caught from southern Kalimantan according to fisheries information), 19 Apr. 2004; CSIRO H 7083–01, female 542 mm TL, Kota Baru, South Kalimantan, Indonesia, 03°14.45′ S, 116°13.24′ E, 28 Nov. 2006; CSIRO H 7084–01, female 570 mm TL (finless and cut along dorsal midline), Desa Bunyu, Pulau Bunyu, East Kalimantan, Indonesia, 03°27.31′ S, 117°50.34′ E, 22 Jul. 2008; IPPS 28404–11, female 706 mm TL, IPPS WWPLAL#7, juvenile male 789 mm TL, IPPS WWPLAL#8, female 806 mm TL, Mukah, Sarawak, Malaysia, 02°53.52′ N, 112°05.44′ E, 28 Apr. 2004; IPPS 08–18, adult male 1282 mm TL, IPPS 08–19, subadult male 1080 mm TL, Batang Lupar, Sarawak, Malaysia, 01°25′ N, 111°06′ E; 26 May 2008; IPPS BO259, juvenile male 710 mm TL, Mukah, Sarawak, Malaysia, 02°53.52′ N, 112°05.44′ E, 20 May 2003; IPPS HBO1, juvenile male 765 mm TL, Sarawak, Malaysia, 2002; RMNH 4292, female 493 mm TL, Borneo; RMNH 4293, juvenile female 450 mm TL, Borneo; PMH 293–1 (jaw only), female 1235 mm TL, PMH 293–2 (jaw only), female 1250 mm TL, PMH 293–3 (jaw only), male 1280 mm TL, Penang, Malaysia; PMH 293–4 (jaw only), unsexed ~1250–1300 mm TL, Phuket, Thailand.

DIAGNOSIS.— A species of *Lamiopsis* with the following combination of characters: a moderately long snout; similarly-sized dorsal fins; lips mostly concealing teeth when mouth is closed, except near symphysis; upper anterior teeth broadly triangular, serrated; lower anterior teeth long, narrow, erect, with non-hastate cusps which are either smooth or finely serrated; tooth row counts 33–40/34–40; interdorsal space 16.2–20.4% TL; pectoral-fin anterior margins weakly convex, its length 12.4–14.4% TL; pelvic fin anterior margins 7.4–9.3% TL and 48–53% of pectoral anterior margin; first dorsal fin relatively small, raked, subtriangular, with nearly straight to shallowly concave posterior margin its free rear tip just anterior to pelvic-fin origins, length 14.9–17.1% TL, height 5.6–8.1% TL; second dorsal fin large, subtriangular, almost as high as first dorsal fin, length 11.8–14.3% TL, height 4.8–7.3% TL and 83–93% of first dorsal-fin height; anal fin height 3.8–5.6% TL and 70–85% of second dorsal-fin height, base 78–98% of second dorsal-fin base; total vertebral centra 174–181, precaudal counts 98–100, monospondylous precaudal centra 50–51 and 28–29% of total centra, diplospondylous precaudal centra 48–49 and 27–28% of total centra, diplospondylous caudal counts 75–81 and 43–45% of total counts; demarcation of light and dark colour surfaces (waterline) on head strong, extending from lateral angle of snout to upper margin of eye, dark surface not visible in ventral view of head; fins lacking distinct black or white tips or markings.

DESCRIPTION.— Body stout, trunk subcircular and almost pear-shaped in section at first dorsal-fin base, length of trunk from fifth gill slits to vent 1.06–1.35 times head length. Predorsal, interdorsal and postdorsal ridges absent from midline of back, lateral ridges absent from body. Caudal peduncle stout, rounded-hexagonal in section at second dorsal-fin insertion, postdorsal and postventral spaces flattened and often with a shallow median groove anteriorly, lateral surfaces subangular and with a broad, low, inconspicuous lateral ridge on each side at middle of the peduncle that extends anteriorly to anal-fin origin and posteriorly onto the caudal-fin base; height of caudal peduncle at second dorsal-fin insertion 1.10–1.61 times its width, 1.29–1.64 times in dorsal–caudal space. Precaudal pits present; upper pit a shallow, subtriangular depression, not arcuate and crescentic; lower pit rudimentary or absent, essentially a dimple at the lower caudal-fin origin.

Head length to fifth gill opening 0.73–0.85 times in pectoral–pelvic space. Head broad, moderately long, flattened anteriorly, ellipsoidal-lenticular in shape in cross-section at eyes. Outline of head in lateral view undulated dorsally, nearly straight on snout, weakly convex above eye, moderately concave at nape and convex above gills, convex ventrally along lower jaws and beneath gills. In dorsoventral view, head narrowly parabolic, with gill septa expanded outwards. Snout moderately long, preoral snout length 0.73–0.89 times mouth width; tip moderately rounded in dorsoventral view and with a weak angle at nostrils but not noticeably indented anterior to nostrils; snout bluntly pointed in lateral view, weakly convex above and below.

External eye opening of fleshy orbit without anterior or posterior notches, circular in shape, with height 0.97–1.18 in eye length. Eyes very small, length 12.2–23.2 in head length; situated mostly laterally and at about level of head rim; subocular ridges absent. Nictitating lower eyelids internal, with deep subocular pouches and secondary lower eyelids fused to upper eyelids.

Spiracles absent. First three gill openings subequal in height, fourth and fifth increasingly smaller, fifth about 0.72–0.99 of height of third; height of third about 6.01–8.74 in head length and 1.39–3.58 times eye length. Margins of gill openings nearly straight, posterior margins irregular; first three openings upright, fourth and fifth sloping slightly posterodorsally from lower edges. Gill filaments not visible from outside. Upper end of highest gill opening just above level of upper edge of eye. Gill-raker papillae absent from gill arches.

Nostrils with very large oval incurrent apertures; prominent triangular anterior nasal flaps with narrowly pointed tips, mesonarial flaps absent, small suboval excurrent apertures, posterior nasal flaps absent; well in front of mouth; width 1.98–2.36 in internarial width, 0.55–0.93 in eye length, 1.33–1.91 in longest gill-opening.

Mouth broadly arched and large; margin of lower jaw

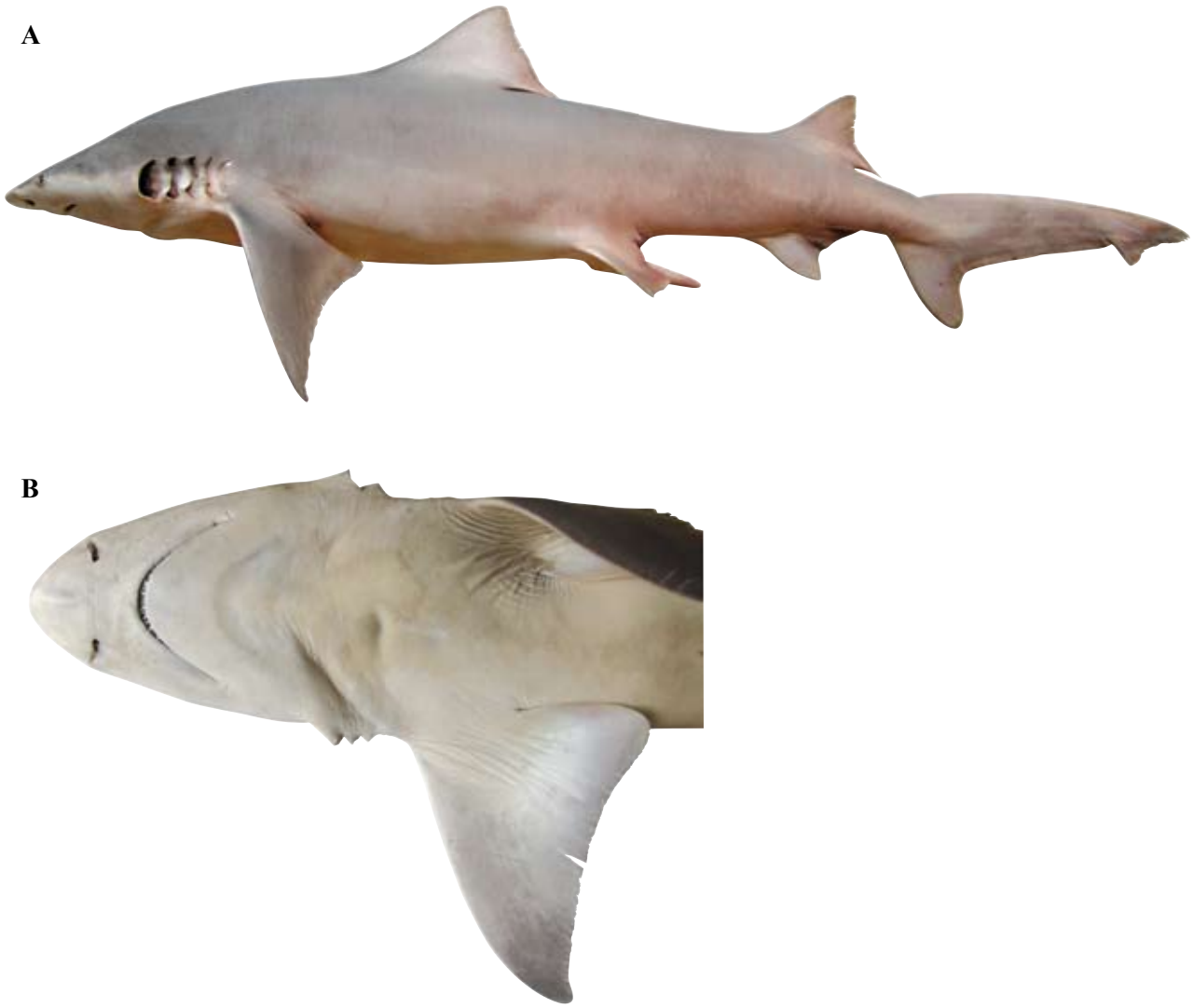

Figure 1. Adult male *Lamiopsis tephrodes* (IPPS 08–18, 1282 mm TL): A. lateral view (fresh); B. anterior ventral view (left pectoral not in view, preserved).

slightly less convex near symphysis; width 2.53–2.82 in head length; mouth length 1.67–1.91 in mouth width. Lips mostly concealing teeth when mouth is closed. Tongue large, flat and broadly rounded, filling floor of mouth. Maxillary valve narrow, width slightly less than eye diameter, strongly papillose. No large buccal papillae on floor or roof of mouth behind maxillary valve. Palate, floor of mouth and gill arches covered with buccopharyngeal denticles. Labial furrows short, uppers 0.69–1.15 times as long as lowers, lowers only barely concealed by overlapping upper lip; anterior ends of uppers far behind eyes by distance about 40% of mouth width.

Odontological meristics: 33–40/34–40 (n=8) with functional tooth series averaging 1–4/2–5, increasing in lower posteriors. Sexual dimorphism in dental morphology not evident; dignathic heterodonty strongly evident.

Monognathic heterodonty graduated but evident in upper jaw. Presence of 1–5 distinct, well developed medial teeth arranged asymmetrically and approximately one quarter height of medials in lower jaw. Upper teeth compressed, broadly triangular and not distinctly cordiform in shape; gradient serrations present, ascending from very fine at the apex of cusps to moderately coarse basally; distal and mesial shoulders somewhat pronounced on anterior teeth but less so in laterals, becoming more symmetrical with crown foot on mesial surface of posteriors and only slightly pronounced on distal surface; mesial root lobe noticeably shorter than distal root lobe in first two to three rows of anterior teeth, becoming more symmetrical laterally and subsequently reversing with posteriors having shorter distal lobes; contour of basal root edge on anterior teeth somewhat concave, becoming nearly straight-edged in laterally positioned teeth; cusps of first three to four rows of anterior teeth symmetrical with straight mesial and distal edges but mesial edges become more convex with lateral rows in series; distal

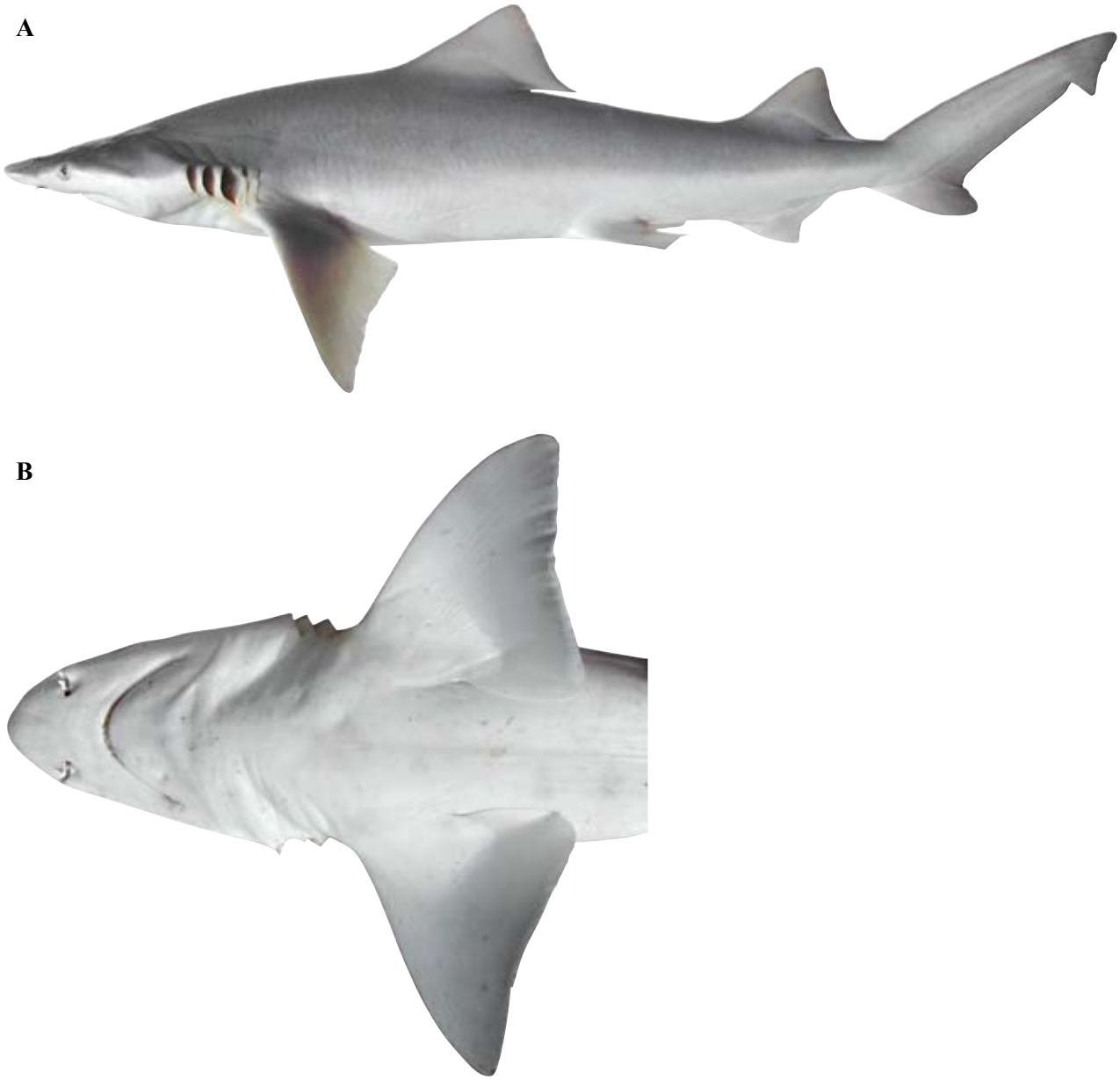

Figure 2. Female *Lamiopsis tephrodes* (not retained, 750 mm TL, Mukah, Sarawak, fresh): A. lateral view; B. anterior ventral view.

edges remain virtually straight except for posteriors; heterodonty more pronounced from lateral to posterior tooth positions; crown height and overall tooth size decrease abruptly in posteriors with the presence of approximately 3–5 rows of carinate molariforms; cusp retention at this level either weak or nonexistent.

Monognathic heterodonty graduated but evident in lower jaw. Presence of a single row of large, well developed, conical medial teeth not asymmetrically positioned; cusps of lower anteriors non-hastate with either smooth or extremely finely serrated cutting edge spanning entire length of cusp and reaching crown foot; cusps somewhat long and recurving lingually with apex slightly reflexed labially; basal ledges strongly pronounced on anterior teeth, becoming less protrusive laterally; roots of anterior teeth strongly arched, lobate and deeply concave with distal and mesial root lobes symmetrical and equal in size; cusps on lateral rows significantly shorter than anteriors, only slightly recurving lingually and with little or no reflexing of apex labially; cutting edges descend onto crown foot and distal shoulder; root lobes well developed and expanded laterally and are only weakly concave; heterodonty more pronounced from laterals to posteriors; crown height and overall tooth size decrease abruptly with the presence of 3 or more rows of semi-molariform teeth with blunt but variably developed cusps.

Lateral trunk denticles of adult male (IPPS 08–18) small, imbricate, transversely oval, with 5 short, stout cusps; crowns about 1.5 times wider than long, with 5

Table 1. Proportional dimensions as percentages of total length and ranges for 11 specimens of *Lamiopsis tephrodes*. The specimens are arranged in order of increasing size from left to right.

	CSIRO H 6662–02	RMNH 4293	RMNH 4292	CSIRO H 7083–01	CSIRO H 6137–07	IPPS 28404–11	IPPS HBO1	IPPS WWPLAL#7	IPPS WWPLAL#8	IPPS 08–19	IPPS 08–18	Min.	Max.
TOT	408	450	493	542	600	706	765	789	806	1080	1282	408	1282
PRC	75.7	76.4	75.9	75.5	74.5	75.4	75.2	74.8	74.3	75.2	75.5	74.3	76.4
PD2	61.0	61.8	60.3	61.1	59.8	59.9	60.7	59.6	60.5	59.5	61.1	59.5	61.8
PD1	32.3	33.1	33.3	33.1	32.0	32.0	31.9	33.2	32.6	31.9	31.4	31.4	33.3
HDL	24.4	24.9	25.4	24.2	23.9	24.0	23.0	23.2	23.9	22.9	21.9	21.9	25.4
PG1	20.5	20.4	20.8	20.2	19.1	20.0	19.0	19.3	19.7	18.6	18.0	18.0	20.8
POB	9.0	9.2	9.4	8.8	8.6	8.8	8.2	8.1	8.5	8.2	7.8	7.8	9.4
POB(horiz.)	7.1	7.5	7.9	6.8	7.2	7.0	7.0	7.0	7.3	6.3	6.6	6.3	7.9
POR	7.8	6.9	7.1	7.4	7.3	7.6	6.8	6.8	7.5	6.7	6.5	6.5	7.8
PRN	5.4	5.1	5.3	5.3	5.1	5.5	4.7	5.0	5.3	4.8	4.5	4.5	5.5
PRN(horiz.)	4.9	4.6	4.5	4.7	4.8	5.0	4.3	4.6	4.8	4.2	3.9	3.9	5.0
PP1	23.3	23.8	25.4	23.7	23.1	22.5	22.2	21.6	23.2	21.9	21.6	21.6	25.4
PP2	47.3	48.2	48.9	47.4	47.0	47.7	45.9	46.4	47.5	46.4	46.0	45.9	48.9
SVL	50.4	51.8	51.1	50.9	49.8	50.7	48.9	49.4	50.0	49.2	49.1	48.9	51.8
PAL	61.0	60.7	59.8	59.0	60.3	58.8	59.0	58.7	58.4	59.5	59.8	58.4	61.0
IDS	17.6	17.6	16.2	18.6	18.1	17.7	18.4	17.6	17.5	18.8	20.4	16.2	20.4
DCS	5.9	5.8	5.7	6.1	6.0	6.3	6.6	6.1	5.7	6.0	6.5	5.7	6.6
PPS	18.5	19.5	19.4	17.7	19.1	20.3	17.5	19.0	18.7	18.6	18.5	17.5	20.3
PAS	7.9	6.7	5.8	5.1	7.0	5.3	6.7	7.3	5.4	7.7	7.6	5.1	7.9
ACS	5.2	5.8	5.4	5.8	5.4	6.0	5.7	6.4	5.9	5.3	5.6	5.2	6.4
EYL	2.0	1.5	1.4	1.5	1.3	1.2	1.2	1.2	1.1	1.0	0.9	0.9	2.0
EYH	1.7	1.3	1.4	1.4	1.2	1.1	1.2	1.2	1.0	1.0	0.9	0.9	1.7
INO	10.3	10.0	10.9	10.3	10.0	9.6	9.5	9.5	9.7	9.0	9.0	9.0	10.9
NOW	2.2	2.0	1.9	2.0	2.1	2.0	1.9	1.9	1.9	1.8	1.6	1.6	2.2
INW	4.6	4.4	4.4	4.6	4.1	4.4	4.3	4.1	4.3	3.9	3.9	3.9	4.6
ANF	0.1	0.5	0.7	0.4	0.8	0.6	0.6	0.7	0.7	0.5	0.5	0.1	0.8
MOL	5.0	5.0	5.6	5.1	5.0	4.8	4.9	4.7	5.1	4.5	4.6	4.5	5.6
MOW	8.8	9.5	9.4	9.6	9.2	8.9	8.5	8.4	9.2	8.1	8.2	8.1	9.6
ULA	0.5	0.6	0.5	0.4	0.5	0.5	0.5	0.4	0.4	0.5	0.5	0.4	0.6
LLA	0.6	0.5	0.8	0.5	0.6	0.4	0.6	0.5	0.5	0.5	0.5	0.4	0.8
GS1	2.9	3.0	3.5	3.2	2.8	3.4	3.1	3.1	3.6	3.1	3.5	2.8	3.6
GS3	2.8	3.1	3.1	3.3	3.2	3.2	3.8	3.2	3.9	3.1	3.3	2.8	3.9
GS5	2.3	2.2	2.6	2.8	2.7	2.6	2.8	3.2	2.9	2.5	2.4	2.2	3.2
HDH	9.9	10.4	11.6	12.8	10.5	11.9	11.6	11.0	12.2	11.4	11.5	9.9	12.8
TRH	11.4	11.1	13.3	14.2	13.2	13.6	12.7	11.9	12.9	12.6	13.3	11.1	14.2
TAH	8.3	8.9	8.5	9.2	8.4	9.4	9.4	8.4	9.8	8.4	9.2	8.3	9.8
CPH	4.1	4.2	4.4	4.1	4.0	4.3	4.3	3.9	4.2	4.0	4.0	3.9	4.4
HDW	10.4	12.0	11.5	12.8	12.7	12.7	12.4	12.6	12.8	12.0	12.1	10.4	12.8
TRW	8.8	11.0	9.8	12.2	12.3	11.9	11.5	13.1	13.2	12.0	12.1	8.8	13.2
TAW	6.4	6.5	6.3	8.0	7.3	8.1	7.9	8.0	8.3	8.0	7.8	6.3	8.3
CPW	3.4	3.2	2.7	3.2	3.4	3.3	3.9	3.5	3.7	3.0	2.8	2.7	3.9
P1L	12.7	12.4	12.9	13.3	–	14.4	13.1	13.4	14.0	13.7	12.6	12.4	14.4
P1A	14.5	14.4	15.1	15.6	–	17.5	15.2	16.3	17.4	17.0	15.8	14.4	17.5
P1B	6.5	6.7	6.4	7.0	7.2	7.6	6.3	6.9	7.1	6.9	6.6	6.3	7.6

Table 1. cont'd.

	CSIRO H 6662–02	RMNH 4293	RMNH 4292	CSIRO H 7083–01	CSIRO H 6137–07	IPPS 28404–11	IPPS HBO1	IPPS WWPLAL#7	IPPS WWPLAL#8	IPPS 08–19	IPPS 08–18	Min.	Max.
P1H	12.7	13.1	15.6	14.2	–	15.1	13.8	15.1	16.2	16.2	15.4	12.7	16.2
P1I	7.0	6.7	8.0	7.2	–	8.0	6.9	6.7	7.3	7.3	6.6	6.6	8.0
P1P	11.3	11.0	13.9	13.6	–	15.5	12.8	14.3	16.6	15.8	14.9	11.0	16.6
P2L	10.0	9.5	10.3	10.5	10.7	11.7	10.6	11.2	11.5	10.5	10.2	9.5	11.7
P2A	7.7	7.6	7.9	7.7	8.3	8.8	7.4	8.6	9.3	8.3	7.7	7.4	9.3
P2B	6.3	6.1	5.0	5.7	6.6	6.6	5.8	6.7	6.8	6.0	6.2	5.0	6.8
P2H	5.4	5.7	6.6	7.7	5.6	7.7	7.1	8.3	8.7	7.9	7.2	5.4	8.7
P2I	4.2	4.5	5.2	4.8	4.6	5.2	4.7	4.8	4.8	4.9	5.2	4.2	5.2
P2P	6.4	6.3	7.0	8.0	8.1	8.5	7.8	8.6	9.2	7.4	7.8	6.3	9.2
CLO	–	–	–	–	–	–	–	–	–	7.3	6.6	6.6	7.3
CLI	–	–	–	–	–	–	–	–	–	11.0	10.6	10.6	11.0
CLB	–	–	–	–	–	–	–	–	–	1.5	1.5	1.5	1.5
D1L	16.0	14.9	15.0	15.7	–	17.1	16.5	15.3	16.8	15.9	15.9	14.9	17.1
D1A	12.0	11.4	11.9	12.4	–	13.3	12.6	12.2	13.6	13.0	13.3	11.4	13.6
D1B	11.4	11.0	10.6	11.3	10.7	11.7	12.1	10.2	11.7	11.3	11.2	10.2	12.1
D1H	5.8	5.6	7.4	7.0	–	7.3	7.0	7.4	8.1	7.4	6.7	5.6	8.1
D1I	4.6	4.1	4.5	4.7	–	5.4	4.4	5.5	5.3	4.8	4.8	4.1	5.5
D1P	6.9	7.4	8.3	8.4	–	9.0	8.4	8.2	8.8	8.9	8.1	6.9	9.0
D2L	12.8	11.8	14.0	12.9	13.7	14.3	13.5	13.3	13.9	12.8	12.2	11.8	14.3
D2A	9.9	10.0	12.0	10.1	10.6	11.2	10.7	10.5	10.9	9.9	9.7	9.7	12.0
D2B	9.0	9.1	10.2	8.9	9.7	9.8	9.7	9.3	9.4	9.0	9.0	8.9	10.2
D2H	4.9	4.8	6.5	6.0	6.7	6.5	6.0	6.4	7.3	6.1	6.2	4.8	7.3
D2I	3.8	2.9	4.2	4.1	4.0	4.6	3.8	4.3	4.4	3.8	3.4	2.9	4.6
D2P	6.2	6.1	7.6	7.6	8.2	8.0	7.2	7.2	8.6	7.9	7.3	6.1	8.6
ANL	11.0	11.1	12.1	12.6	12.0	12.8	11.5	12.8	12.5	10.9	10.7	10.7	12.8
ANA	7.8	8.4	9.2	8.7	9.2	9.6	8.5	9.7	9.9	8.2	8.1	7.8	9.9
ANB	7.1	7.9	8.7	8.7	8.0	8.3	7.7	8.1	8.4	7.5	7.6	7.1	8.7
ANH	4.0	3.8	4.6	4.8	5.2	5.1	4.3	5.4	5.6	4.8	4.4	3.8	5.6
ANI	3.6	3.3	3.8	4.1	4.1	4.6	3.9	4.6	4.2	4.0	3.5	3.3	4.6
ANP	6.5	5.9	6.0	6.0	6.9	5.8	6.0	6.6	6.7	5.5	6.0	5.5	6.9
CDM	24.2	23.8	24.5	24.6	25.2	24.8	24.7	25.0	25.6	25.4	24.5	23.8	25.6
CPV	11.1	10.3	11.3	10.7	–	11.3	10.0	11.2	11.4	10.5	10.7	10.0	11.4
CPL	2.9	2.6	3.3	3.4	–	3.8	3.9	3.8	4.0	4.3	4.4	2.6	4.4
CPU	11.7	12.2	12.5	12.2	–	13.1	11.6	12.5	12.3	12.9	13.6	11.6	13.6
CFW	6.3	6.3	7.6	6.7	–	7.2	6.9	7.3	7.3	6.9	6.7	6.3	7.6
CFL	9.6	8.9	9.5	9.6	–	9.5	8.5	9.4	9.5	8.2	8.1	8.1	9.6
CST	3.3	3.3	3.6	3.9	3.8	3.3	3.3	3.4	3.4	3.2	3.1	3.1	3.9
CTR	5.0	5.0	5.5	6.2	7.3	6.6	6.2	5.3	7.2	6.9	6.0	5.0	7.3
CTL	6.8	6.9	7.0	7.5	8.1	7.7	7.2	7.1	7.8	8.0	7.4	6.8	8.1
DAO	0.6	0.6	0.5	1.8	0.5	1.0	0.7	1.4	1.2	0.5	1.6	0.5	1.8
DAI	1.6	1.5	1.9	1.5	1.2	1.6	0.8	1.6	1.6	1.0	1.6	0.8	1.9
DPI	8.7	10.0	8.7	9.4	10.2	9.5	8.0	10.4	9.5	9.5	8.3	8.0	10.4
DPO	10.1	8.7	9.4	9.4	9.5	10.0	9.4	9.2	9.7	8.8	9.4	8.7	10.1
PDI	7.2	6.1	7.4	7.5	8.1	7.9	7.2	6.7	7.1	6.6	7.4	6.1	8.1
PDO	11.3	10.2	8.5	10.2	9.3	10.0	10.7	10.9	9.6	11.4	10.8	8.5	11.4

(occasionally 3) prominent longitudinal ridges (medial ridge much stronger and more pronounced) that extend entire length of crown onto cusps; medial cusp short but strong, much shorter than rest of crown, flanked by two pairs of slightly shorter lateral cusps, outer pair much shorter.

Pectoral fins large, broadly triangular, very weakly falcate; anterior margin weakly convex, apex narrowly rounded; posterior margin shallowly concave; free rear tip broadly rounded, inner margin convex; base broad 48–54% of fin length; length from origin to rear tip 1.20–1.34 times in anterior margin length; much more than twice area of first dorsal fin; origin about under third gill slit; fin apex about opposite free rear tip when fin is elevated and adpressed to body.

Pelvic fins broadly triangular and not falcate; length of anterior margin 0.58–0.71 of pectoral-fin anterior margin; area about 1.5 times that of anal fin; anterior margin nearly straight and slightly concave near base; apex moderately rounded to subangular; posterior margin nearly straight; free rear tip moderately rounded, inner margin nearly straight; posterior margin, rear tip and inner margin forming a broad triangle with an ~60° apex. Claspers of adult male (IPPS 08–18, 1282 mm TL) moderately short and stout, relatively broad, not tapering sharply distally, outer length 6.6–7.3% TL, base width 22.0–22.8% of outer length; clasper glans extending to about a third of clasper outer length.

First dorsal fin relatively small, low, raked, subtriangular, not falcate; angle of apex about ~90°; anterior margin nearly straight, slightly concave basally; apex angular; posterior margin nearly straight to very shallowly concave; free rear tip pointed, inner margin slightly concave; origin over posterior half of pectoral-fin inner margin, midpoint of base 0.87–1.17 times closer to pectoral insertions than pelvic origins; anterior margin sloping strongly posterodorsally from its base; free rear tip just anterior to over pelvic-fin origin; posterior margin arcing strongly posteroventrally from apex at an angle of ~45°; insertion just posterior to level of dorsal-fin apex. First dorsal fin base 1.49–1.81 in interdorsal space, 2.04–2.44 in dorsal caudal margin; height 1.38–1.97 in base; inner margin 1.26–1.64 in height, 1.85–2.74 in base.

Second dorsal fin large, apically narrow, subtriangular; almost as tall as first dorsal fin, height 0.83–0.93 times first dorsal-fin height, base 0.79–0.96 times first dorsal-fin base; anterior margin weakly concave basally, slightly convex distally; apex moderately rounded; posterior margin convex distally and basally concave; free rear tip acutely pointed, inner margin slightly concave; origin behind pelvic-fin free rear tips; rear tip slightly behind anal-fin free rear tip, in front of upper caudal-fin origin by 0.29–0.98 times its inner margin; posterior margin curving posteroventrally from apex; insertion slightly

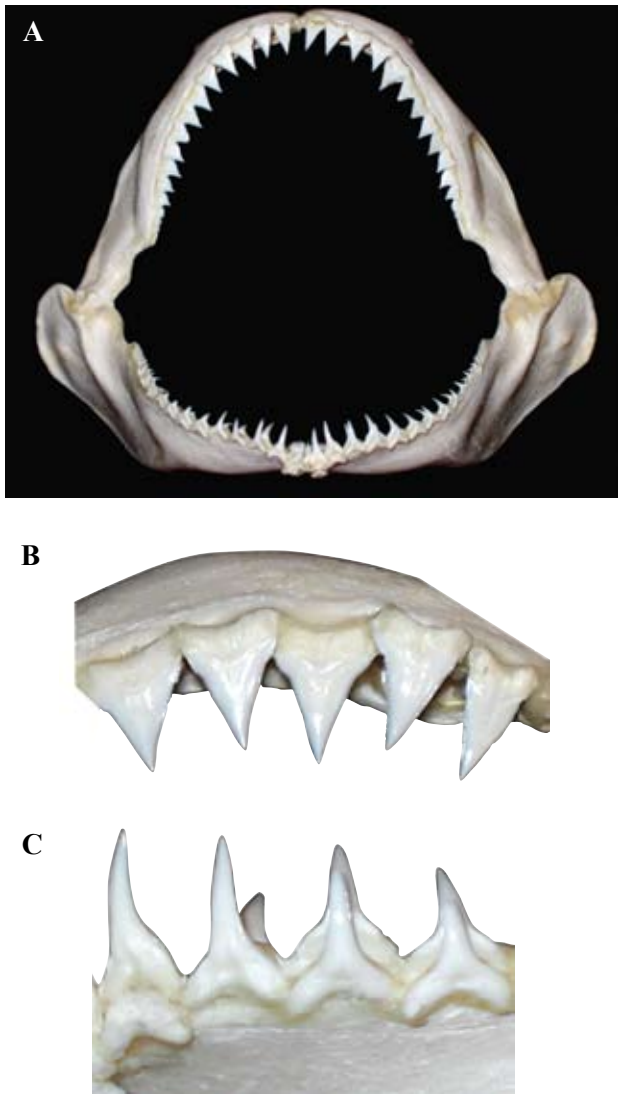

Figure 4. Jaw (A), upper anterior (B) and lower anterior (C) teeth of *Lamiopsis tephrodes* (PMH 293–3, male 1280 mm TL).

Figure 3. Upper precaudal pit of an adult male *Lamiopsis tephrodes* (IPPS 08–18, 1282 mm TL, fresh). Arrow indicates the shallow, longitudinal precaudal pit.

behind fin apex. Second dorsal-fin base 0.55–0.72 in dorsal–caudal space; height 1.30–1.88 in base; inner margin 0.55–0.78 in height, 2.12–3.08 in base.

Anal fin apically narrow and semi-falcate; height 0.70–0.85 times second dorsal-fin height, base length 0.78–0.98 times second dorsal-fin base; anterior margin indented basally and slightly convex distally; apex subangular; posterior margin notched at much greater than a right angle; free rear tip acutely pointed, inner margin nearly straight; origin almost opposite second dorsal-fin origin; insertion slightly anterior to second dorsal-fin insertion, slightly posterior to anal-fin apex; free rear tip in front of lower caudal-fin origin by about a third of its inner margin length; posterior margin slanting slightly posterodorsally and then abruptly posterodorsally. Anal-fin base expanded anteriorly as very short preanal ridges (obscure), less than a quarter length of rest of base. Anal-fin base 0.62–0.79 in anal–caudal space; height 1.49–2.10 in base; inner margin 0.74–0.90 in height, 1.77–2.41 in base.

Caudal fin narrow-lobed and asymmetrical, with short terminal lobe and prominent, long, narrowly expanded, weakly falcate ventral lobe; dorsal caudal margin proximally and distally convex, and slightly concave just anterior to subterminal notch, with prominent lateral undulations; preventral margin moderately convex, tip of ventral caudal-fin lobe subangular; lower postventral margin nearly straight; upper postventral margin nearly straight except for convex section at subterminal notch; notch between postventral margins deep; subterminal notch a narrow, deep slot; subterminal margin slightly concave to almost straight, terminal margin irregular and deeply concave, lobe formed by these margins angular, tip of tail narrowly rounded. Length of dorsal caudal margin 2.90–3.22 in precaudal length, preventral caudal margin 2.16–2.48 in dorsal caudal margin, terminal lobe from caudal tip to subterminal notch about 3.09–3.55 in dorsal caudal margin, subterminal margin length 1.49–2.15 in terminal margin.

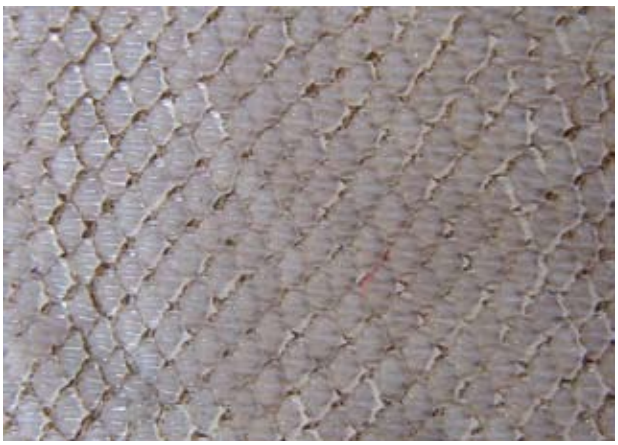

Figure 5. Cusps of the flank denticles of *Lamiopsis tephrodes* (IPPS 08–18, adult male 1282 mm TL, preserved).

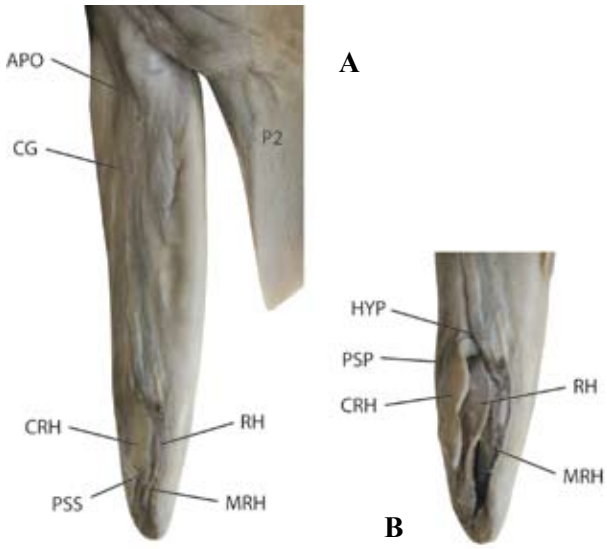

Figure 6. Clasper (left) of an adult male *Lamiopsis tephrodes* (IPPS 08–18, 1282 mm TL): A. glans not dilated; B. glans spread. APO, apopyle; CG, clasper groove; CRH, cover rhipidion; HYP, hypopyle; MRH, mesorhipidion; P2, pelvic fin; PSP, pseudopera; PSS, pseudosiphon; RH, rhipidion.

Counts of total vertebral centra (TC, n=4) 174–181, precaudal centra (PC) 98–100, monospondylous precaudal (MP) centra 50–51, diplospondylous precaudal (DP) centra 48–49, diplospondylous caudal (DC) centra 75–81; MP centra 27.9–28.7%, DP centra 26.8–28.2%, and DC centra 43.1–45.3% of TC centra. Ratios of DP/MP centra 0.96–0.98, DC/MP centra 1.50–1.62.

COLORATION.— When fresh: dorsal surface of head, trunk and tail slate-grey, graduating to white ventrally on midlateral surface. Demarcation of light and dark surfaces (waterline) of head strong, extending along lateral angle of the snout anteriorly to level of nostrils, then extending dorsoposteriorly towards upper margin of eye; from posterior eye extending from upper margin to midpoint of first gill opening, diffuse over mid-level of 3rd gill opening, elevated along upper ends of 4th and 5th openings (most of membranes of 4th and 5th openings whitish); a narrow dark area extending around ventral margin of eye, not visible ventrally; waterline irregular, jagged along abdomen to origin of pelvic fin; waterline directed posterodorsally above pelvic-fin base, diffuse, extending along tail mid-laterally; pale area continuing onto base of caudal fin, barely apparent as a pale marking along upper lobe to origin of the terminal lobe. Dorsal fins similar in colour. First dorsal fin bi-tonal, dark anterior margin with broad slate-grey posterior margin

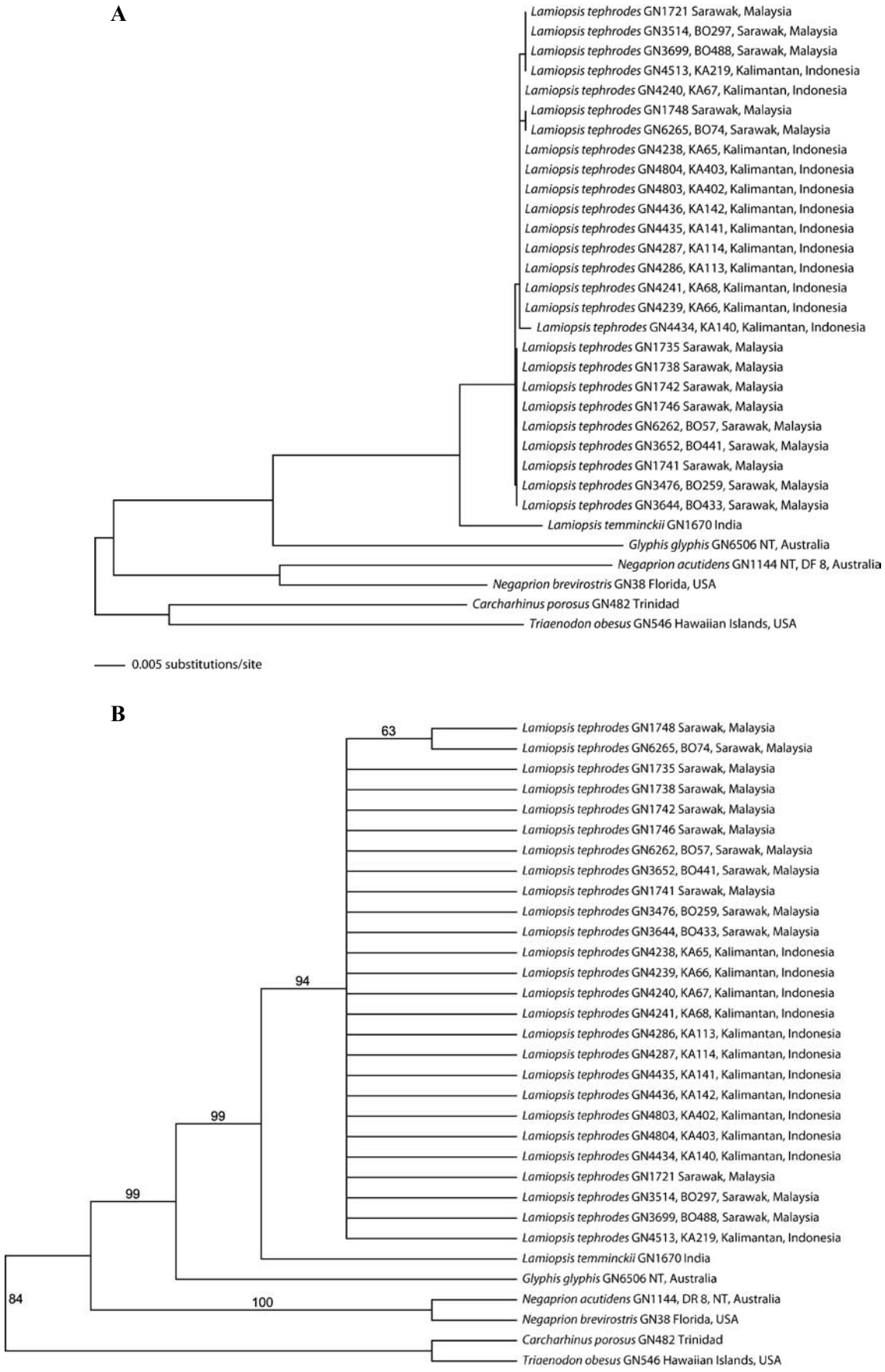

Figure 7. (A) Neighbour-Joining tree based on K2P distance, (B) Parsimony Bootstrap with 1000 replicates and (C) Maximum Likelihood tree using a GTR+I+Γ model (General Time Reversible + Invariant sites + gamma distributed rates). Model parameter values were optimized recursively for the Likelihood analysis as the search progressed.

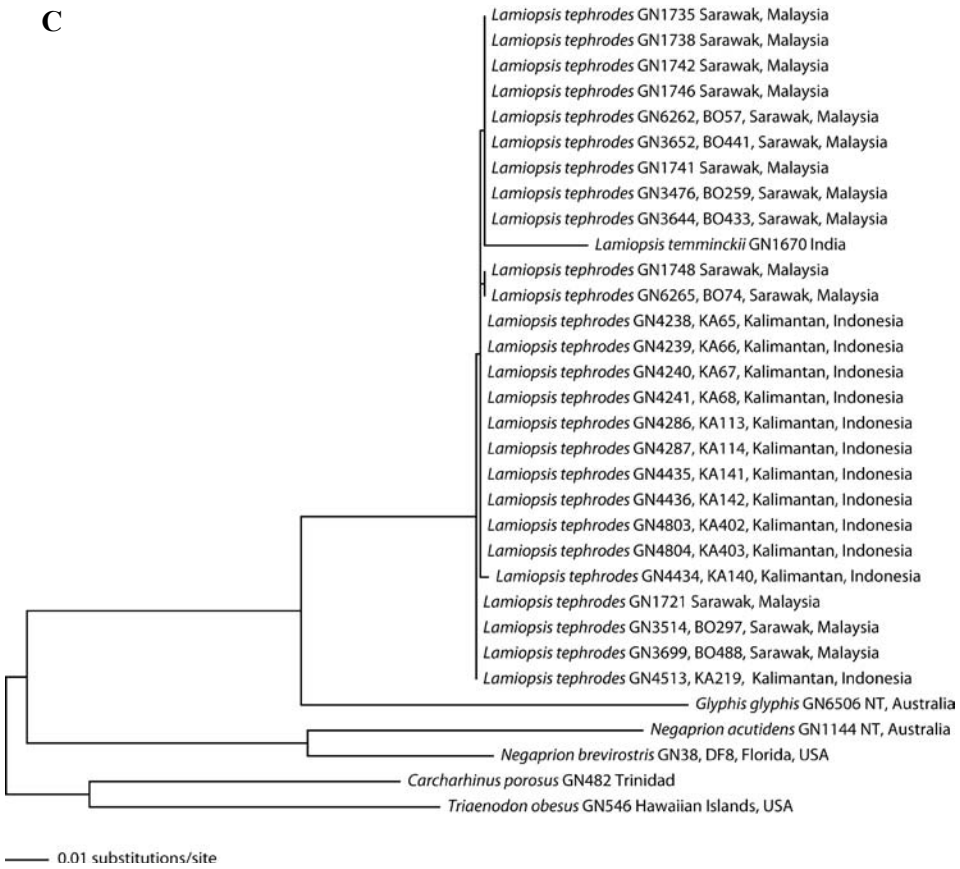

Figure 7. cont'd.

and fin base; central portion of fin for more than half its height pale off-whitish, patch extending posteriorly and converging towards fin insertion; inner margin whitish. Second dorsal fin with a posterior dark marginal band, similar in width to that of first dorsal fin; pale anterior margin distinctly smaller than that of first; inner margin whitish. Anal fin mostly pale, posterior half dusky. Caudal fin dusky, paler medially; anterior margin narrowly black-edged; terminal lobe with broad greyish marking (similar to those of dorsal fins); similar dark marking extending along postventral margin to ventral lobe apex. Pectoral fins not uniform on both surfaces; upper surface slate grey basally, grading rapidly to paler, almost whitish posterior and inner margin (more distinct in larger fixed specimens), basal third of anterior margin narrowly whitish; naked insertion with a blackish and white membrane; ventral surface uniformly white. Pelvic fins similar to pectoral fins except basal portion of fin whitish rather than dark; whitish ventrally (largest fixed specimens dusky distally). Claspers white (adult males with some dusky areas on dorsal surface of claspers). Eyes silvery yellow with a black pupil; nictitating membrane translucent.

SIZE.— Whole specimens examined ranged in length from 408–1282 mm TL. Three males of 408–789 mm TL were juveniles, one male of 1080 mm TL was a subadult (claspers almost fully calcified), and one male was fully mature at 1282 mm TL. The smallest specimen (408 mm TL) had an umbilical scar indicating that it is close to the size at birth. Additional specimens collected in Borneo, but not retained, included a mature female of 1450 mm TL and two subadult males of 1050 and 1060 mm TL. Maximum sizes for males and females is poorly defined as published information is combined with data for *L. temminckii* from Indian waters.

DISTRIBUTION.— Specimens examined in this study were mostly collected from off Borneo, with the three of the four jaws examined from Penang (Malaysia) and one from Phuket (Thailand). The two Indonesian specimens collected from Jakarta were from fishers operating off southern Kalimantan and should not be considered as from Java. The extent of occurrence of this species is poorly defined. Possibly also occurs off southern China and more widespread in the Indo–Malay Archipelago but validated records need to be obtained.

DISCUSSION

Although the holotype of *Lamiopsis tephrodes* was not examined, there is no doubt that the specimen described and illustrated by Fowler (1905) belongs to the genus *Lamiopsis*. As previously mentioned, the smaller paratype

Figure 8. Lateral view of lectotype of *Lamiopsis temminckii* (BMNH 1862.8.16.11, juvenile male 1057 mm TL).

described by Fowler (1905) is referrable to *Carcharhinus* sp. A [*sensu* Compagno *et al*., 2005] and not *Lamiopsis tephrodes*.

Following examination of the dried syntype of *L. temminckii* in the BMNH collection (BMNH 1862.8.16.11) and comparison with the measurements in the original description by Müller & Henle (1839), it is apparent that this is the specimen on which Müller & Henle based their description. Their illustration of the species lacks claspers so it may be of a different specimen or a composite. We herein designate the dried specimen BMNH 1851.8.16.11 as the lectotype for *L. temminckii*. A further syntype of *L. temminckii* listed as being deposited in the Paris museum (MNHN) was not found during a visit by the senior author (WW) in November 2009 and curatorial staff noted that there was no record of this specimen on their database. Another syntype of this species deposited at RMNH was also not encountered during the same trip. If these other syntypes are located and belong to *Lamiopsis*, these should be recognised as paralectotypes for this species.

Comparisons of the morphology of *Lamiopsis tephrodes* with *L. temminckii* was limited to the dried lectotype of the latter species (Fig. 8) and a number of measurements in the original Müller & Henle description (converted to mm using conversions of the German Fuss, Zoll and Linie measurements originally used). Only a subset of characters could be measured on the lectotype. Most of the morphometrics taken fell within, or close to, the ranges for the same character taken for *L. tephrodes*, but several characters differed markedly in the dried lectotype. The main differences between the dried lectotype of *L. temminckii* and the 11 specimens of *L. tephrodes* were: more posteriorly positioned dorsal fins (pre-first dorsal length 35.5 vs. 31.4–33.3% TL, pre-second dorsal length 66.3 vs. 59.5–61.8% TL), preanal length (66.5 vs. 58.4–61.0% TL), shorter dorsal fin bases (first dorsal-fin base 9.3 vs. 10.2–12.1% TL, second dorsal-fin base 7.7 vs. 8.9–10.2% TL), shorter caudal fin (dorsal caudal margin 21.4 vs. 23.8–25.6% TL). Although the differences listed

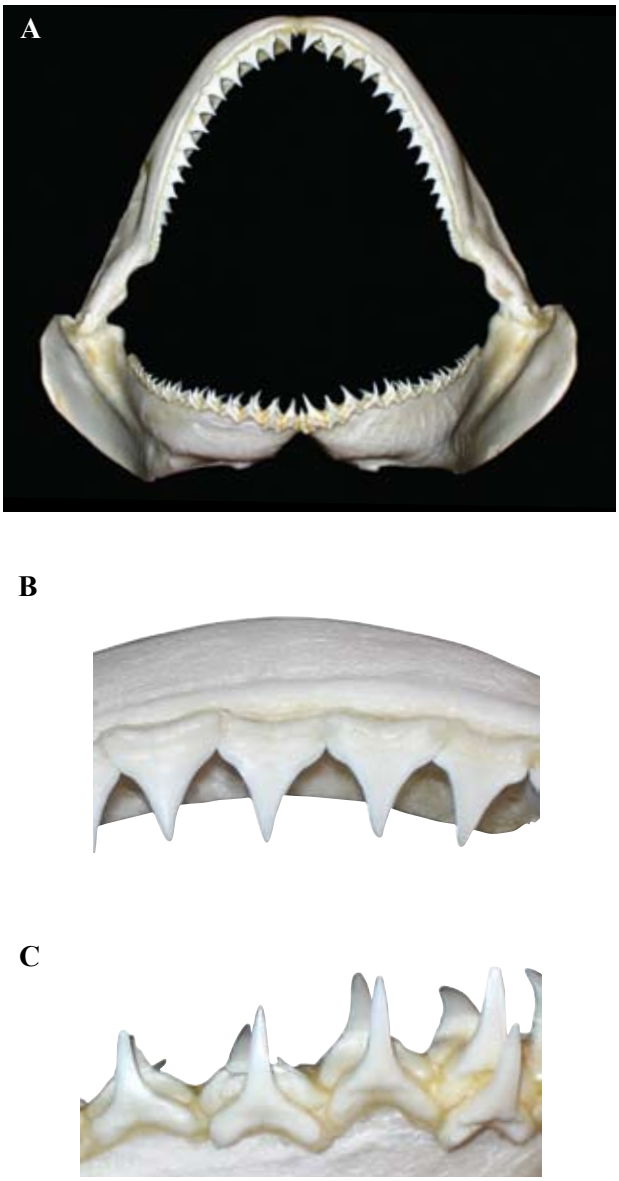

Figure 9. Jaw (A), upper anterior (B) and lower anterior (C) teeth of *Lamiopsis temminckii* (PMH 201–2, female 1475 mm TL).

Table 2. Differences between the dentition of *Lamiopsis tephrodes* and *Lamiopsis temminckii*.

Lamiopsis tephrodes	*Lamiopsis temminckii*
Upper teeth triangular in shape, both margins symmetrical. Distal and mesial shoulders mildly pronounced	Upper teeth more cordiform in shape, tapering just below basal ledge. Distal mesial shoulders very pronounced
Posterior molariform teeth in upper jaw relatively few. Generally 3–5 rows	Posterior molariform teeth in upper jaw more numerous in count. Generally 5–7 rows
Upper lateral and posterior teeth noticeably oblique with convex mesial margins	Upper lateral and posterior teeth relatively straight with mesial margins slightly angular but rarely convex
Serrations on upper teeth usually coarser basally on shoulders, descending to much finer serrations towards apex	Serrations more evenly distributed, and not noticeably coarser basally
Serrations generally coarse in upper teeth of adults	Serrations generally finer in upper teeth of adults
Lower teeth sometimes with very finely serrated cutting edges in adults	Lower teeth with entirely smooth cutting edge
Slightly fewer tooth rows, 33–40/34–40	Slightly more tooth rows, 42–44/40–43

above are significant, they could be due to the specimen of *L. temminckii* being a dried and stuffed specimen. For example, using approximate measurements from the illustration of *L. temminckii* in Müller & Henle, estimates of 33.8 and 62.3% TL are obtained for pre-first dorsal and pre-second dorsal lengths, respectively. Although these are still greater than the ranges for *L. tephrodes*, they are relatively similar. Furthermore, from the original description, the measurements of the dorsal-fin bases are shorter in *L. temminckii* compared to *L. tephrodes*, i.e. first dorsal-fin base 2.9 vs. 2.0–2.4 in dorsal caudal margin, second dorsal-fin base 4.0 vs. 2.4–2.8 in dorsal caudal margin.

All three of the molecular analyses (Fig. 7) show identical interrelationships between *Lamiopsis* and the outgroup taxa. All three analyses also indicate that *Lamiopsis tephrodes* is distinct from *Lamiopsis temminckii* at this locus. However, the parsimony and the neighbour-joining analyses of the data suggest that *L. temminckii* is the sister taxon to a monophyletic *L. tephrodes*. The Maximum Likelihood (ML) analysis, by contrast, suggests that *L. temminckii* arose and differentiated as a lineage from within *L. tephrodes*. Distinguishing between these two alternative scenarios must await collection and analysis of sequence data from nuclear markers. While the molecular data suggests that the Indian form *L. temminckii* is distinct from the South-east Asian form *L. tephrodes*, we caution that the inference is based on a single mitochondrial marker (ND2). The inference is thus the tree topology for that particular gene. Gene trees do not always correspond to the species trees that contain them. This is because gene tree lineages coalesce at rates that are affected by the mutation rate, the effective population size and the migration rate; parameters that often vary between genes. In order to deduce robust species trees from gene trees it is important to base inferences from a suite of independent genetic markers from both the nucleus and the mitochondrial genomes. This said, there is generally a reasonably close correspondence between broad patterns of diversification assessed by mitochondrial markers and species differentiation.

Additional, preserved or fresh material of *L. temminckii* is required to investigate whether these differences are accurate and to determine what other differences there may be. *Lamiopsis temminckii* possibly attains a larger size, or at least matures at a larger size than *L. tephrodes*. The lectotype of *L. temminckii* is a juvenile male of 1057 mm TL with very little development of the claspers, whilst a specimen of *L. tephrodes* at 1080 mm TL had well-developed, almost fully calcified claspers. More specimens are required to determine whether such size differences are real.

Certain diverse aspects of the dental morphology of this species as compared to *Lamiopsis temminckii* have been noted and are discussed here (see Figs 4 and 9). Although noticeable, these interspecific differences are only mildly consistent and may vary to some extent, particularly when taking into account the small number of positively identified specimens of *Lamiopsis tephrodes* for which the dental characters have been noted. The primary characters separating these two species are outlined in Table 2.

Lamiopsis temminckii is listed as Endangered in the IUCN *Red List of Threatened Animals* based on its distribution in heavily exploited regions and its apparent rarity (White *et al*., 2008). Given the resurrection of *Lamiopsis tephrodes* from Borneo, this assessment needs to be revised and a separate assessment established for

L. temminckii. The absence of this genus from Indonesian waters, other than off Kalimantan, during extensive surveys of fish landing sites over the last 10 years, indicates that localised depletions have likely occurred (White *et al*., 2006). Both species occur in shallow areas, often near large river outflows, in regions with heavy exploitation levels. Thus, both are likely to be of conservation concern and threatened in their respective regions.

Comparative material

Lamiopsis temminckii: 8 specimens: BMNH 1851.8.16.11 (lectotype, dried and stuffed), juvenile male 1057 mm TL, India; PMH 201–1 (jaw only), male 1440 mm TL, PMH 201–2 (jaw only), female 1475 mm TL, PMH 201–3 (jaw only), male 1490 mm TL, PMH 201–4 (jaw only), female 1517 mm TL, PMH 201–5 (jaw only), female 1530 mm TL, PMH 201–6 (jaw only), female 1563 mm TL, Baleshwar, India; PMH 201–7 (jaw only), unsexed ~1450–1500 mm TL, Chittagong, Bangladesh.

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