

***Glyphis fowlerae* sp. nov., a new species of river shark (Carcharhiniformes; Carcharhinidae) from northeastern Borneo**

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ABSTRACT.— A new river shark, *Glyphis fowlerae* sp. nov., is described from 14 type specimens from Malaysian Borneo, including 13 specimens collected in freshwater from the vicinity of Kampung Abai in the lower reaches of the Kinabatangan River, Sabah. *Glyphis fowlerae* differs from other members of the genus by a combination of vertebral counts, dentition, coloration and morphology, particularly in the comparative heights of the dorsal fins. A second, rarely collected species of *Glyphis* from Sarawak (Malaysian Borneo) is also compared (based on colour images) to the new species and its status discussed. One of the syntypes of *Glyphis gangeticus*, described from India, is designated as a lectotype for that species.

Key words: Carcharhinidae – *Glyphis fowlerae* – new species – Borneo – freshwater

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INTRODUCTION

The genus *Glyphis* was proposed by Agassiz (1843) for a living species of carcharhinid shark (Family Carcharhinidae), *Carcharias (Prionodon) glyphis*, which had been described by Müller & Henle (1839) from a single stuffed specimen without locality but with distinctive spear-shaped (hastate) lower anterior teeth, small eyes and a large second dorsal fin. A detailed account of the nomenclatural history of *Glyphis* can be found in Compagno (1979, 1988, 2003). Although considered by many authors to be a synonym of the genus *Carcharhinus* Blainville, 1816, Compagno (1984) revived *Glyphis* as a genus for *C. (P.) glyphis* and *C.(P.) gangeticus*, and noted that there were additional species represented by specimens from Borneo, New Guinea and Queensland, Australia (Prof. J.A.F. Garrick pers. comm., to senior author). The vernacular name ‘river sharks’ was proposed by Compagno (1984) for *Glyphis* species because the Ganges Shark (*G. gangeticus*) and other species occur in tropical rivers and associated deltas in the Indo–West Pacific.

Compagno *et al.* (2008) provided a detailed description of a new species of *Glyphis* from northern Australia and New Guinea, *G. garricki* Compagno, White & Last, 2008, which had previously been referred to as *G. sp. C* [*sensu* Compagno & Niem, 1998; Compagno *et al.*, 2005]. These authors also synonymised *G. sp. A* [*sensu* Last &

Stevens, 1994; *sensu* Compagno & Niem, 1998] with *G. glyphis* (Müller & Henle, 1839) and provided a detailed redescription of this species. Compagno *et al.* (2008) recognised 5 species of *Glyphis*: *G. garricki* Compagno, White & Last, 2008; *G. gangeticus* (Müller & Henle, 1839); *G. glyphis* (Müller & Henle, 1839); *G. siamensis* (Steindachner, 1896); and an undescribed species from Borneo, *G. sp. B* [*sensu* Compagno & Niem, 1998].

The presence of *Glyphis* in Borneo was first reported by Compagno (1984), based on a specimen in a museum in Vienna (NMW), was tentatively identified as *G. glyphis*, but differences in vertebral counts and the need for further work were noted. In 1996, the Darwin Elasmobranch Biodiversity Conservation and Management project in Sabah was established in collaboration with the Department of Fisheries Sabah, the IUCN Species Survival Commission’s Shark Specialist Group, WWF Malaysia and the Universiti Malaysia Sabah. During an elasmobranch survey of Sabah between January 1996 and July 1997, which included riverine and estuarine habitats, a number of *Glyphis* specimens were collected from the vicinity of Kampung Abai on the Kinabatangan River that were considered conspecific with the NMW specimen collected over a century ago (Manjaji, 2002a, b). Compagno & Niem (1998) provided a brief account of this species and provided the name Borneo River Shark *Glyphis* sp. B. In market surveys of greater Borneo funded by the National Science Foundation (NSF) over

the last decade, several additional specimens of *G. sp. B* were collected near the same locality on the Kinabatangan River. During the same surveys, two specimens of another species of *Glyphis* were collected from Mukah (Sarawak, Malaysian Borneo) that is not conspecific with *G. sp. B* and requires further investigation to determine its identity.

Yano *et al.* (2005) provided a description of the Kinabatangan River Shark, *Glyphis sp. B* (as *G. sp.*), based on one of the Darwin project specimens. Compagno *et al.* (2005) also provided an account of *G. sp. B* and a comparison of vertebral and tooth counts with other members of the genus. More recently, Fahmi & Adrim (2009) provided the first record of a species of *Glyphis* from Indonesian Borneo. This specimen, an adult male collected in 2005 from Sampit Bay in Central Kalimantan, was not retained due to its large size (1660 mm total length, TL). They noted its similarity and difference to *G. sp. B* in many morphological characters, but given the specimen was not retained, an accurate identification could not be made.

The present account provides a formal name and description of *Glyphis sp. B* based on a population from the Kinabatangan River, eastern Sabah. Comparisons with other members of this genus are also provided and a lectotype is designated for *Glyphis gangeticus*.

METHODS

Terminology for morphology follows Compagno (1973, 1979, 1988, 2001, 2003), Compagno & Springer (1971), Compagno *et al.* (2005) and Taylor *et al.* (1983). Measurement terminology is from Compagno (1984, 2001, 2003) who assigned names and abbreviations to measurements often indicated by descriptive phrases (example: snout to upper caudal origin = precaudal length = PRC). Dentional terms are modified from Compagno (1970, 1979, 1988, 2001, 2003). The major differences as used here are the substitution of the orientation terms 'distal' for 'postlateral', 'mesial' for 'premedial', 'labial' for 'outer' and 'lingual' for 'inner', more in conformity with current European terminology. Vertebral terminology, method of counting and vertebral ratios follow Springer & Garrick (1964) and Compagno (1970, 1979, 1988, 2003), including 'A' ratio (length of penultimate monospondylous precaudal centrum/length of first diplospondylous precaudal centrum x 100) and 'B' ratio (length/width of penultimate monospondylous precaudal centrum x 100).

The holotype and all 13 paratypes of *Glyphis fowlerae* were measured in full (Table 1). For comparison, the two *G. gangeticus* types and the holotype of *G. siamensis* were also measured (Table 1). Comparative measurements for *G. garricki* and *G. glyphis* from northern Australia are provided in Compagno *et al.* (2008). Meristics were taken

from radiographs of the holotype, 12 of the paratypes and one other specimen of *Glyphis fowlerae*, and from the paralectotype (MNHN 1141) of *G. gangeticus* and the holotype (NMW 61397) of *G. siamensis*. 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 (Table 2). Morphometric and meristic data for the holotype are followed in parentheses by the ranges of the paratypes in the descriptive section. Tooth row counts were taken *in situ*, from radiographs or from excised jaws. Teeth and denticles were examined after maceration with sodium hypochlorite (NaOCl).

Specimens, including types, are referred to by the following prefixes for their registration numbers: CSIRO, Australian National Fish Collection, Hobart, Australia; IPMB, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia; SMEC, Sabah Museum Elasmobranch Collection, Kota Kinabalu, Sabah, Malaysia; LWF, L.W. Filewood field numbers for specimens collected in Papua New Guinea; MNHN, Museum National d'Histoire Naturelle, Paris; NMW, Naturhistorisches Museum, Vienna; NTM, Museum and Art Gallery of the Northern Territory, Darwin, Australia; SAM, South African Museum, Cape Town, South Africa; QM, Queensland Museum, Brisbane, Australia; WAM, Western Australian Museum, Perth, Australia; ZMB, Zoologisches Museum, Humboldt Universitat, Berlin, Germany; ZSI, Zoological Survey of India, Calcutta, India. Field accession numbers for specimens collected on the NSF elasmobranch project (NSFEP) in Sarawak, Malaysian Borneo, which were photographed but retained specimens are missing, are prefixed with the letters BO (data and images for these specimens are available at <http://tapeworms.uconn.edu>).

FAMILY CARCHARHINIDAE Jordan & Evermann, 1896

Genus *Glyphis* Agassiz, 1843

Type species. *Carcharias (Prionodon) glyphis* Müller & Henle, 1839, by absolute tautonymy.

SPECIES.— *Glyphis* includes five nominal species: *G. fowlerae* sp. nov.; *G. garricki* Compagno, White & Last, 2008; *G. gangeticus* (Müller & Henle, 1839); *G. glyphis* (Müller & Henle, 1839); *G. siamensis* (Steindachner, 1896); and possibly another, undescribed species from Borneo, *G. sp.*. *Carcharias murrayi* Günther, 1883 (from the delta of the Indus River, Pakistan) is a possible synonym of *G. gangeticus* or a distinct species, but the unique holotype, a stuffed specimen in the collection of the British Museum of Natural History, is missing, presumably lost (O. Crimmen, J. Macclaine, pers. comm.).

***Glyphis fowlerae* sp. nov.**

Figs 1–4; Tables 1 and 2

Glyphis glyphis (Müller & Henle, 1839): Compagno, 1984: p 509, figs. Misidentification.*Glyphis* sp. B: Compagno & Niem, 1998: pp 1318, 1360, fig. 25; Compagno *et al.*, 2005: pp 309, 311, 312, figs, pl. 55.*Glyphis* sp.: Yano *et al.*, 2005: pp 248–250, pl. 160, 161.**Holotype.** IPMB 38.14.02, female 577 mm TL, Kampung Abai, Kinabatangan River, Sabah, Malaysia, 05°41'10.81" N 118°23'08.35" E, 30 Apr. 2003.**Paratypes.** 13 specimens: CSIRO H 5784–01, juvenile male 517 mm TL, Kampung Abai, Kinabatangan River, Sabah, Malaysia, Mar. 1999; IPMB 38.14.03, juvenile male 487 mm TL, collected with holotype; BMNH 1997.10.14.1, female 538 mm TL, SMEC 352, female 582 mm TL, SMEC 354, female 505 mm TL, SMEC 355, juvenile male 575 mm TL, SMEC 356, juvenile male 667 mm TL, SMEC 357, juvenile male 632 mm TL, SMEC 348 (currently housed in LJVC collection Cape Town), female 778 mm TL, SMEC 358 (currently housed in LJVC collection Cape Town), juvenile male 600 mm TL, SMEC 359 (currently housed in LJVC collection Cape Town), juvenile male 606 mm TL, SMEC 353 (location uncertain), female 566 mm TL Kampung Abai, Kinabatangan River, Sabah, Malaysia, 05°41'10.19" N 118°23'02.21" E, 1997; NMW 61401, female 627 mm TL, Borneo, no further locality data.**Other material.** 1 specimen: CSIRO H 7089–01, juvenile male 473 mm TL, Kampung Abai, Kinabatangan River, Sabah, Malaysia, 05°41' N, 118°23' E.**DIAGNOSIS.**— A species of *Glyphis* with the following combination of characters: snout short, broadly rounded in dorsoventral view; minimum distance from mouth to nostril 1.1–1.6 times nostril width; lips usually concealing teeth when mouth closed; lower teeth with erect, narrow, moderately hooked to straight cusps, with notched mesial and distal edges, and low mesial and distal shoulders or blades (except in posterior teeth); anteroposterior tooth row counts 13–15/13–15; total tooth row counts 28–31/29–32 or 60–63; interdorsal space 17.0–19.5% TL; anterior margin of pectoral fin slightly convex, pectoral length 11.6–13.4% TL; length of pelvic-fin anterior margin 6.3–7.7% TL, 36–40% of length of pectoral-fin anterior margin; pelvic-fin height 4.6–6.3% TL; first dorsal fin not falcate, with concave posterior margin, free rear tip just anterior to pelvic-fin origins, its length 16.9–19.1% TL; second dorsal-fin length 10.5–12.3% TL, anterior margin length 7.5–9.7% TL, its base length 7.4–9.3% TL and 1.4–1.9 times second dorsal-fin height, its height 4.7–6.0% TL and 58–68% of first dorsal height; anal-fin height 4.1–5.0% TL and 74–102% of second dorsal-fin height, its base 65–94% of second dorsal-fin base; caudal-fin subterminal margin weakly concave; total vertebral count 196–209; monospondylous precaudal count 60–67, 30–33% of

total count; diplospondylous precaudal count 43–52, 22–26% of total count; diplospondylous caudal count 82–96, 42–46% of total count; precaudal count 108–114, 54–58% of total count; boundary coloration (watermark) on head diffuse, extending through lower level of eye; in young, watermark well defined, diffuse along trunk, situated near lateral midline; dorsal, pectoral, pelvic and anal fins plain; ventral caudal-fin lobe, and postventral and dorsal margins, dusky to blackish.

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 1.10 (1.01–1.12) 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, very low, inconspicuous lateral ridge on each side at middle of the peduncle that extends anteriorly to the pelvic-fin midbases and posteriorly onto the caudal-fin base; height of caudal peduncle at second dorsal-fin insertion 1.03 (1.11–1.36) times its width, 1.58 (1.21–1.63) times in dorsal–caudal space. Precaudal pits present; upper pit a pronounced, subtriangular depression, not arcuate and crescentic; lower pit rudimentary, essentially a dimple at the lower caudal-fin origin.

Head length to fifth gill opening 0.84 (0.74–0.82) times in pectoral–pelvic space. Head broad and somewhat flattened, ellipsoidal-lenticular in shape in cross-section at eyes. Outline of head in lateral view undulated dorsally, nearly straight on snout, convex above eye, concave at nape and convex above gills and progressively elevated towards first dorsal fin; slightly convex ventrally along lower jaws and beneath gills. In dorsoventral view, head anteriorly rounded and U-shaped, with gill septa expanded outwards. Snout short, preoral snout length 0.80 (0.70–0.83) times mouth width; tip broadly rounded in dorsoventral view and with a slight angle at nostrils but not noticeably indented anterior to nostrils; snout narrowly rounded in lateral view, slightly convex above and below.

External eye opening of fleshy orbit without anterior or posterior notches, circular in shape, with height 1.01 (0.79–1.23) in eye length. Eyes small, length 19.79 (18.13–26.27) times in head length; situated lateral on head; subocular ridges absent. Nictitating lower eyelids internal, with deep subocular pouches and secondary lower eyelids fused to upper eyelids.

Spiracles absent. First three gill slits subequal in height, first opening usually much larger, fifth smallest; fifth slit about 0.85 (0.60–0.88) times height of third; height of third about 9.07 (6.95–8.93) in head length, 2.18 (2.03–3.58) times eye length. Margins of first four gill slits nearly straight, posterior margin irregular; fifth slightly

A



B



Figure 1. Juvenile female holotype of *Glyphis fowlerae* sp. nov. (IPMB 38.14.02, 577 mm TL, fresh): A. lateral view; B. anterior ventral view.

concave; upper edges of gill slits 2–4 most elevated; upper end of highest gill about level with upper edge of eye. Gill filaments not visible from outside. Gill-raker papillae absent from gill arches.

Nostrils with large, oval incurvent apertures; prominent triangular anterior nasal flaps with bluntly pointed tips, mesonarial flaps absent, small subcircular excurrent apertures, posterior nasal flaps vestigial or absent; well in front of mouth; width 4.04 (3.21–3.95) in internarial width, 0.70 (0.45–0.73) in eye length, 1.52 (1.31–1.86) in longest gill-opening.

Mouth broadly parabolic and large; width 2.67 (2.36–2.76) in head length; mouth length 1.71 (1.76–1.98) in mouth width. Lips usually 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, 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 1.08 (0.37–1.52) times as long as lowers, lowers concealed by overlapping upper lip; anterior ends of uppers far behind eyes. Labial cartilages appear to be absent.

Table 1. Proportional dimensions as percentages of total length for the holotype (IPMB 38.14.02) and ranges for the 13 paratypes of *Glyphis fowlerae* sp. nov. Measurements of the lectotype and paralectotype of *G. gangeticus* and the holotype of *G. siamensis* are also provided.

	<i>G. fowlerae</i> sp. nov.			<i>G. gangeticus</i>		<i>G. siamensis</i>
	Holotype	Paratypes (n=13)		Lect.	Paralect.	Holotype
		Min.	Max.	ZMB 4474	MNHN 1141	NMW 61397
TL	577	487	778	1850	556	630
PCL	74.8	73.5	75.8	75.8	73.6	73.0
PRN	4.8	4.8	5.3	3.6	4.6	3.8
POR	7.7	7.5	8.3	6.5	6.6	7.3
POB	8.3	8.3	10.5	7.0	7.7	7.8
PGI	21.3	20.4	22.1	17.3	19.5	19.7
HDL	25.7	24.5	26.0	24.1	24.6	24.3
PP1	24.3	21.6	24.1	21.1	22.2	23.0
PP2	51.5	48.7	50.5	49.8	48.0	50.0
SVL	53.9	52.0	53.6	54.3	50.9	–
PAL	61.0	59.1	62.1	64.6	59.4	–
PD1	28.6	28.0	30.5	28.9	28.8	28.6
PD2	61.4	58.5	62.0	61.6	60.8	61.4
IDS	18.3	17.0	19.5	20.4	19.0	19.2
DCS	6.9	6.4	7.1	7.0	6.3	6.8
PPS	21.5	18.9	21.0	21.7	18.8	–
PAS	5.9	4.7	5.9	9.0	5.8	–
ACS	5.7	5.0	6.1	6.4	5.7	–
EYL	1.3	0.9	1.4	0.8	1.3	0.7
EYH	1.3	1.0	1.4	0.8	1.4	–
INO	12.1	11.5	12.7	10.4	10.9	–
NOW	1.9	1.9	2.3	1.1	1.9	1.4
INW	7.5	7.0	7.7	8.8	6.7	7.3
ANF	0.6	0.3	0.8	0.0	0.6	0.5
MOL	5.6	4.9	5.7	3.8	6.2	5.9
MOW	9.6	9.4	10.7	10.3	9.3	9.5
ULA	0.4	0.3	0.6	0.0	0.6	0.5
LLA	0.4	0.2	0.9	0.0	0.5	–
GS1	2.9	2.9	3.8	3.6	3.5	2.7
GS2	2.9	2.9	3.8	3.6	3.7	–
GS3	2.8	2.9	3.6	3.5	3.7	–
GS4	2.7	2.5	3.4	3.4	3.2	–
GS5	2.4	2.0	2.9	–	3.5	–
HDH	11.0	11.8	17.8	–	11.5	–
HDW	12.8	12.3	17.2	–	11.5	11.9
TRH	11.1	12.2	14.9	11.9	10.8	13.0
TRW	11.9	11.0	15.3	–	9.4	–
CPH	4.4	4.2	5.7	4.0	4.3	4.0
CPW	4.2	3.1	4.7	–	2.3	–
P1L	12.0	11.6	13.4	11.4	11.5	–
P1A	17.1	16.7	20.0	20.0	19.9	18.3
P1B	7.1	6.9	8.5	7.3	6.9	–

Table 1. cont'd.

	<i>G. fowlerae</i> sp. nov.			<i>G. gangeticus</i>		<i>G. siamensis</i>
	Holotype	Paratypes (n=13)		Lect.	Paralect.	Holotype
		Min.	Max.	ZMB 4474	MNHN 1141	NMW 61397
P1H	15.0	12.1	17.9	18.6	16.9	–
P1I	4.8	4.1	6.1	4.4	6.3	–
P1P	14.0	12.8	15.0	18.4	17.2	–
P2L	8.9	8.8	10.3	7.8	8.9	7.0
P2A	6.3	6.3	7.7	5.6	7.3	–
P2B	5.9	5.5	6.8	6.2	5.8	–
P2H	6.3	4.6	6.3	4.5	6.1	–
P2I	3.0	2.6	3.7	2.4	3.3	–
P2P	6.6	5.9	7.7	6.0	6.6	–
CLO	–	1.6	2.2	6.4	1.4	–
CLI	–	4.0	4.7	8.6	4.5	–
CLB	–	0.7	0.8	1.2	0.5	–
D1L	18.2	16.9	19.1	15.5	17.0	17.3
D1A	13.2	11.7	14.6	13.2	14.4	–
D1B	14.2	12.6	14.7	12.4	12.0	12.4
D1H	7.8	7.6	10.2	8.6	9.9	–
D1I	4.5	3.8	4.8	2.9	5.0	4.3
D1P	10.2	9.4	12.9	11.0	10.7	–
D2L	10.5	11.0	12.3	11.9	10.6	10.6
D2A	7.5	8.0	9.7	7.0	7.8	–
D2B	7.4	7.8	9.3	7.7	7.1	6.7
D2H	5.1	4.7	6.0	4.3	4.6	–
D2I	3.5	2.9	4.0	2.7	3.4	3.3
D2P	6.2	5.6	7.5	6.5	6.4	–
ANL	10.2	8.7	11.5	7.6	10.0	–
ANA	8.4	7.4	9.3	5.8	8.8	–
ANB	7.0	5.8	7.9	5.2	6.9	–
ANH	4.7	4.1	5.0	3.6	4.4	–
ANI	3.4	3.0	3.7	2.2	3.4	–
ANP	5.3	4.3	5.3	4.3	5.0	–
CDM	25.5	24.7	26.5	24.3	27.1	27.0
CPV	10.8	11.0	12.3	11.1	11.6	–
CPL	4.7	4.4	5.5	6.2	5.9	–
CPU	14.3	12.8	14.7	13.5	13.4	–
CST	3.6	2.2	4.1	2.7	3.2	2.9
CTR	6.4	5.2	6.5	6.5	6.7	4.4
CTL	7.6	6.0	8.0	6.5	7.7	6.8
CFL	8.2	8.5	9.4	6.9	8.2	–
DPI	4.9	4.0	5.9	–	6.3	–
DPO	17.1	12.7	15.8	–	11.9	–
PDI	12.5	8.8	12.3	–	9.2	–
PDO	5.5	5.8	7.7	–	9.4	–
DAO	1.7	1.0	2.6	–	0.5	–
DAI	0.4	0.2	0.8	–	0.7	–



Figure 2. Lateral head view of juvenile female holotype of *Glyphis fowlerae* sp. nov. (IPMB 38.14.02, 577 mm TL, fresh).

Teeth relatively few, in 28–31/29–32 rows or 60–63 total rows (both jaws), 1–2/2–3 series functional (n=5); not arranged in diagonal files, no toothless spaces at symphysis; highly differentiated in upper and lower jaws and along jaws; tooth row groups include upper and lower medials (M), anteriorised lower symphysials (AS), and anteriors (A), laterals (L), and posteriors (P) in both jaws. Tooth formula (n=5): upper jaw 4–5(P) 9–10(L) 1(A) + 1(M) + 1(A) 9–10(L) 3–4(P); lower jaw 4–5(P) 7–8(L) 2(A) + 1(S) 1(M) 1(S) + 2(A) 7–8(L) 4–5(P); or upper jaw 14–15 + 1 + 13–15, lower jaw 13–15 + 3 + 13–15. Lower teeth erect, narrow, with moderately hooked to straight cusps; mesial and distal edges notched; mesial and distal shoulders or blades low (except in posterior teeth). Upper teeth broader, flatter, more triangular, more bladelike than lowers; usually with broader, erect to semi-oblique straight cusps (except posteriors), coarser serrations (except for most posteriors); mesial edges un-notched; roots slightly arched. Upper medial teeth relatively high-crowned, very small; with a broad, triangular hooked cusp; a few coarse serrations on each side. The single row of upper anteriors have erect straight broad triangular cusps and are over three times as high as the medials and smaller and somewhat narrower than the adjacent laterals; these are compressed, bladelike teeth with straight edges and coarse serrations. Upper laterals begin as erect triangular flat, coarsely serrated bladelike teeth with broader bases than the anteriors and nearly straight or slightly concave mesial and distal edges; the second lateral being the largest upper tooth; the laterals gradually decrease in size from the second, with the cusp becoming more oblique, the mesial edge more convex, and the distal edge more concave until at the 9th or 10th tooth they make a transition to the carinate posteriors. Upper posteriors are low-crowned keel-like teeth with cusps weak or absent, a broad convex edge, and with serrations absent from most rows.

Lower medials are moderately large, erect and hooked-

cusped, narrow symmetrical teeth with arched roots, finely serrated semihastate cusps, and crown feet developed as smooth shoulders without a blade and cutting edge. Lower symphysials larger and more robust than medials, and similar to adjacent anteriors except for being slightly smaller, with erect, moderately hooked, serrated non-hastate cusps, small mesial and distal blades, and deeply arched roots. Lower anteriors larger than symphysials but otherwise similar. Lower laterals with considerable variation along the dental band but with lower crowns, flatter cusps and relatively broader less arched roots than anteriors, large to small narrow-cusped teeth with shallowly notched mesial and distal edges and erect or semierect narrow, serrated cusps and blades. Lateral teeth decrease in size distally, with cusps becoming considerably lower and slightly more oblique. Lower posteriors similar to uppers, without cusps or cusplets and with convex broad edges, but smaller and lower-crowned than uppers. All teeth with transverse grooves and prominent centrolingual foramen on linguobasal attachment surface of roots. Tooth histological type orthodont, with a definite pulp cavity, crown formed of orthodentine and enameloid, and osteodentine confined to roots.

Lateral trunk denticles with flat, rhomboidal crowns about as wide as long, covered with faint reticulated depressions. Crown with 3 prominent longitudinal ridges that extend its entire length onto the cusps; medial cusp short but strong, shorter than the rest of crown; a pair of much shorter lateral cusps present. Denticle crowns widely spaced, not closely imbricated, with skin clearly visible between them. Denticle pedicels short and thick, but elevated crowns well above skin; denticle roots with 4 lobes.

Pectoral fins large, fairly narrow, weakly falcate; anterior margin moderately convex, apices narrowly rounded; posterior margin undulated, distal half convex, mesial half shallowly and broadly concave; free rear tip broadly rounded, inner margin moderately convex; base broad about 60% of fin length; length from origin to rear tip 1.43 (1.30–1.55) in anterior margin length; greater in area than first dorsal fin; origin varying from about under 2nd or 3rd gill slits; fin apex about opposite inner margin when fin is elevated and addressed to body.

Pelvic fins triangular and not falcate; length of anterior margins 0.37 (0.36–0.40) of pectoral-fin anterior margins; area slightly larger than that of anal fin; anterior margin nearly straight; apices rounded; posterior margin nearly straight to weakly convex distally; free rear tip bluntly rounded, inner margin nearly straight; posterior margin, rear tip and inner margin forming a broadly triangular apex. Claspers of adult males not examined; those of immature males small, undifferentiated.

First dorsal fin apically narrow (apically angular in CSIRO H 5784–01) and broadly triangular, not falcate; angle of apex about 80–90°; anterior margin shallowly

concave basally and distally slightly convex; apex narrowly rounded to subangular; posterior margin distally straight and basally shallowly concave; free rear tip bluntly pointed, inner margin slightly concave; origin about opposite pectoral-fin insertion, midpoint of base 3.5 (2.4–3.8) times closer to pectoral insertions than pelvic origins; free rear tip just anterior to pelvic-fin origins; posterior margin arcing posteroventrally from apex; insertion well behind level of dorsal-fin apex. First dorsal-fin base 1.28 (1.20–1.51) in interdorsal space, 1.79 (1.71–2.09) in dorsal caudal margin; height 1.82 (1.23–1.83) in base length; inner margin 1.74 (1.74–2.32) in height, 3.17 (2.63–3.84) in base length.

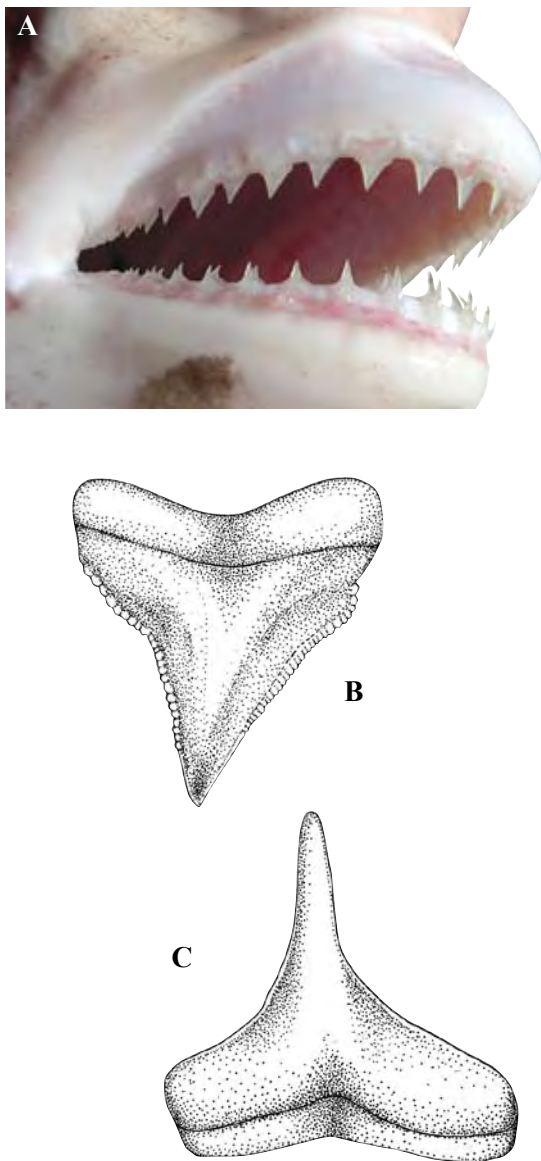


Figure 3. Teeth of the female holotype of *Glyphis fowlerae* sp. nov. (IPMB 38.14.02, 577 mm TL, fresh): A. jaw when fresh; B. upper mesial tooth; C. lower mesial tooth. Illustrations by Lindsay Marshall.



Figure 4. Flank denticles of *Glyphis fowlerae* sp. nov. (IPMB 38.14.02, holotype, juvenile female 577 mm TL).

Second dorsal fin apically narrow (moderately rounded in CSIRO H 5784–01), broadly triangular, very weakly falcate; height 0.65 (0.58–0.69) times first dorsal-fin height, base 0.52 (0.58–0.69) times first dorsal-fin base; anterior margin concave basally, becoming weakly convex distally; apex moderately rounded; posterior margin distally convex and then slightly concave; free rear tip acutely pointed, inner margin nearly straight; origin well behind pelvic-fin insertions and about opposite or slightly behind pelvic-fin free rear tips; rear tip about opposite anal-fin free rear tip, in front of upper caudal-fin origin by 0.53 (0.32–0.76) times its inner margin length; posterior margin curving posteroventrally from apex; insertion slightly behind fin apex. Second dorsal-fin base 0.93 (0.74–0.90) in dorsal–caudal space; height 1.45 (1.32–1.92) in base; inner margin 1.44 (1.32–1.68) in height, 2.09 (2.23–3.00) in base.

Anal fin apically narrow and falcate; height 0.93 (0.74–1.02) times second dorsal-fin height, base length 0.94 (0.65–0.93) times second dorsal-fin base; anterior margin concave basally and distally convex; apex bluntly pointed or narrowly rounded; posterior margin broadly notched at slightly more than a right angle; free rear tip acutely pointed, inner margin nearly straight to slightly concave; origin slightly behind second dorsal-fin origin; insertion opposite or slightly behind second dorsal-fin insertion, slightly in front of fin apex; free rear tip in front of lower caudal-fin origin by a distance about equal to its inner margin length; posterior margin slanting very slightly anterodorsally and then abruptly posterodorsally. Anal fin base expanded anteriorly as short preanal ridges, less than a quarter length of rest of base. Anal-fin base 0.81 (0.66–0.96) in anal–caudal space; height 1.47 (1.21–1.52) in base; inner margin 1.41 (1.21–1.52) in height, 2.08 (1.75–2.34) in base.

Caudal fin narrow-lobed and asymmetrical, with short

Table 2. Vertebral counts and ratios for the holotype (IPMB 38.14.02) and ranges for the 13 paratypes of *Glyphis fowlerae* sp. nov. Counts from the paralectotype of *G. gangeticus* and the holotype of *G. siamensis* are also provided.

	<i>G. fowlerae</i> sp. nov.		<i>G. gangeticus</i>	<i>G. siamensis</i>	
	Holotype	Paratypes (n=12)		Paralec.	Holotype
		Min	Max	MNHN 1141	NMW 61379
TL	577	487	778	556	630
Vertebrae:					
MP	65	60	67	50	66
DP	47	43	52	30	51
DC	91	82	96	89	92
PC	112	108	114	80	117
TC	203	196	209	169	209
%MP	32.0	30.0	33.2	29.6	31.6
%DP	23.2	21.8	26.0	17.8	24.4
%DC	44.8	41.8	45.9	52.7	44.0
%PC	55.2	54.1	58.2	47.3	56.0
DP/MP	0.72	0.66	0.87	0.60	0.77
DC/MP	1.40	1.28	1.48	1.78	1.39
A ratio	126.2	108.8	142.3	159.5	153.7
B ratio	71.2	48.8	72.5	100.0	74.6

terminal lobe and prominent, long, narrowly expanded, non-falcate ventral lobe; dorsal caudal margin proximally and distally convex, and slightly concave just anterior to subterminal notch, with prominent lateral undulations; pre-ventral margin moderately convex, tip of ventral caudal-fin lobe bluntly pointed or narrowly rounded; lower postventral margin convex; upper postventral margin nearly straight except for convex section at subterminal notch; notch between postventral margins deep, forming about a 90–120° angle; subterminal notch a narrow, deep slot; subterminal margin slightly concave, terminal margin slightly concave where not damaged, lobe formed by these margins angular, tip of tail bluntly pointed or narrowly rounded and angular. Length of dorsal caudal margin 2.94 (2.77–3.08) in precaudal length, pre-ventral caudal margin 2.35 (2.11–2.40) in dorsal caudal margin, terminal lobe from caudal tip to subterminal notch about 3.35 (3.27–4.11) in dorsal caudal margin, subterminal margin length 1.32 (1.28–2.49) in terminal margin.

Vertebral counts listed in Table 2. Counts of total vertebral centra (TC) 203 (196–209 in 12 paratypes), precaudal centra (PC) 112 (108–114), monospondylous precaudal (MP) centra 65 (60–67), diplospondylous precaudal (DP) centra 47 (43–52), diplospondylous caudal (DC) centra 91 (82–96); MP centra 32.0 (30.0–33.2)%, DP centra 23.2 (21.8–26.0)%, and DC centra 44.8 (41.8–45.9)% of TC centra. Ratios of DP/MP centra 0.72 (0.66–0.87), DC/MP centra 1.40 (1.28–1.48), 'A' ratio 126.2 (108.8–

142.3), 'B' ratio 71.2 (48.8–72.5). Transition between MP and DP centra about over pelvic-fin bases and just behind pelvic girdle. Last few MP centra before MP-DP transition not enlarged and not forming a 'stutter zone' of alternating long and short centra.

COLORATION.— When fresh and in preservative: Medium grey on dorsal surface of sides of head, trunk, and tail, shading to paler grey on the flanks, abruptly creamy white on lateral and ventral surfaces and lower base of caudal fin, eye pupil black. Demarcation of pale lower and dark upper surface (waterline) of head at level of nostrils and lower edge of eye, extending to about mid-height of gill openings; a more or less conspicuous narrow light ring around eyes; gill septa dark on their upper thirds but with their margins and lower surfaces whitish; flanks grey over pectoral-fin bases but shifting to whitish above pectoral-fin rear tips and over pelvic fins; a short, inconspicuous, and weakly defined light line extending from pelvic base onto mid-flank; precaudal tail grey above lateral line, much paler below it, bicolour extending onto caudal-fin base. Pectoral fins with a conspicuous rounded-angular dusky patch on dorsal surface of base, demarcated anteriorly at fin origin by abrupt white patch that extends to gills; dorsal pectoral fin web below and posterior to dark basal spot pale greyish, without light or dark markings; underside of pectoral whitish with pale dusky margin. Dorsal surfaces of pelvic fins with a dusky basal patch surrounded by

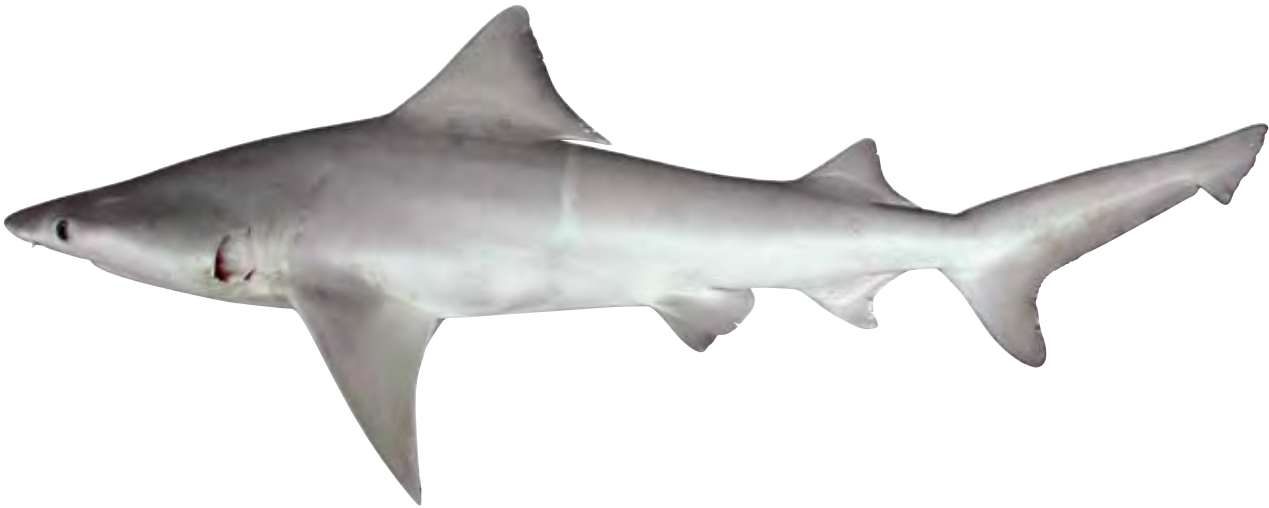


Figure 5. Lateral view of juvenile male *Glyphis* sp. (NSFEP BO471, 610 mm TL, fresh).

white, fin web whitish-grey, underside of fins and claspers white with light whitish grey web. First dorsal fin with a dusky grey base, conspicuous paler whitish-grey web with paler area on the free rear tip and a dusky margin; second dorsal fin with a similar highlighted fin web but with a broader dusky apex and posterior margin. Anal fin mostly whitish, sometimes with a dusky to blackish posterior web. Caudal fin medium grey with a white to pale greyish basal stripe that extends onto the hypaxial and epaxial fin web, pre-ventral margin white, ventral lobe and post-ventral margin dusky to blackish, terminal lobe dusky or blackish, dorsal margin dusky.

BIOLOGY.— Essentially unknown; development presumably by placental viviparity as suggested by the newborn young and by reference to other, related carcharhinids, but adults of either sex including pregnant females were not available for examination.

SIZE.— Type specimens range in length from 487–778 mm TL, but these are all immature individuals and maximum total length of this species is probably between 2000 and 3000 mm, by comparison with species of *Carcharhinus*. Specimens ranging in size from 487–582 mm TL possessed open umbilical scars indicating they were only recently born; specimens between 600 and 632 mm TL possessed closed umbilical scars; two specimens of 667 and 778 mm TL had no umbilical scars. Thus, size at birth in this species is likely to be about 490–580 mm TL.

DISTRIBUTION AND HABITAT.— All but one of the specimens were collected in the vicinity of Kampung Abai (05°41' N, 118°23' E), on the Kinabatangan River in eastern Sabah; the other specimen, deposited at the NMW in Vienna has no specific locality data within Borneo. The Kinabatangan River at this locality has

very low banks that slope gradually down to a flat and muddy bottom (Manjaji, 2002a). Although there is little information available on the hydrology of the area, the Lower Kinabatangan Segama Wetlands RAMSAR site (available at http://www.sabah.gov.my/sabc/downloads/RIS_LKSW_2008.pdf) provides the following hydrological characteristics for the streams of the Kulumba Wildlife Reserve where Kampung Abai is located: salinity 1.7–1.9, pH 6.4–7.5, temperature 25.5–29.9°C, conductivity 27.6–31.2 $\mu\text{S}/\text{cm}$, total suspended solids 126.8–214.5 mg/L, dissolved oxygen 4.6–5.9 mg/L. The most important features to take note of are the very low salinity (practically freshwater) and high suspended solids. Despite extensive sampling effort throughout Sabah, Sarawak and Kalimantan, this species has not been collected elsewhere.

ETYMOLOGY.— The epithet acknowledges the considerable efforts of Dr Sarah Fowler (Nature Bureau, UK) who has dedicated a lifetime of work towards the conservation of sharks, and who led the first major study on the elasmobranchs of Sabah in 1996 which culminated in the discovery of this species. Vernacular: Borneo River Shark

CONSERVATION.— Not evaluated by the IUCN *Red List of Threatened Species* but four other members of this genus are listed as either Critically Endangered or Endangered, and the issues facing those species are similar to those facing *G. fowlerae*, especially given its apparently very restricted range and human impacts on its habitat. The extent of logging and the increasing development of palm-oil plantations within the region also add to the threatening processes. Thus, *G. fowlerae* is likely to fall into one of the highly threatened categories and its conservation status urgently requires assessment.

DISCUSSION

Glyphis fowlerae is clearly separable from its congeners by a combination of morphology, meristics and coloration, and also on a molecular level (G. Naylor, unpubl. data). The key characters which distinguish species of *Glyphis* are comparative heights of the dorsal fins, vertebral counts and teeth morphology. *Glyphis gangeticus* has the greatest intraspecific difference in dorsal-fin heights (lowest second dorsal-fin height about 0.46 times first dorsal-fin height) compared to *G. fowlerae* (0.54–0.68) and *G. garricki* (0.58–0.66). In contrast, *G. glyphis* has a relatively taller second dorsal fin and as a result, the least difference in dorsal-fin heights of 0.67–0.84.

Glyphis fowlerae has a high number of vertebrae (total centra 196–209, monospondylous centra 60–67, $n=13$) compared to *G. garricki* (137–151 and 44–50, $n=14$) and *G. gangeticus* (169 and 50, $n=1$), but much less than *G. glyphis* (213–222 and 69–73, $n=8$). The counts for the single known specimen of *G. siamensis* (total centra 209, monospondylous centra 66) fall within the range of *G. fowlerae*, but they differ on a number of morphometric characters discussed later. *Glyphis fowlerae* has a higher tooth count (60–63, $n=5$) than *G. siamensis* (58, $n=1$), *G. glyphis* (53–58, $n=4$), but similar counts to *G. gangeticus* (62–71, $n=3$) and *G. garricki* (62–68, $n=15$).

Glyphis gangeticus was described by Müller & Henle in 1839 and in that description two syntypes were referred to: one dried specimen deposited in the Berlin Museum (ZMB 4474) and one in alcohol in the Paris Museum (MNHN 1141). Although their description is possibly based on both specimens, it is clear that the larger dried adult male specimen, ZMB 4474, was the one from which data was taken by Müller & Henle (1839), based on the



Figure 6. Lateral view of head of juvenile male *Glyphis* sp. (NSFEP BO470, 658 mm TL, fresh).

larger size of this specimen (1850 vs. 556 mm TL). The illustration provided in the description is also clearly of an adult male also referable to the ZMB specimen. We designate the dried specimen (ZMB 4474) as the lectotype of *Glyphis gangeticus* and the smaller specimen in alcohol (MNHN 1141) as a paralectotype. Although it is often difficult to obtain accurate measurements from dried specimens, the few comparable measurements obtained from the original description were very similar to those recorded for the dried specimen despite a substantial increase in total length, probably due to overstretching of the skin (1700 mm TL fresh vs. 1850 mm TL dry).

In addition to the differences provided above, *G. fowlerae* further differs from *G. gangeticus* (based on both types) in having a longer snout (prenarial length 4.8–5.3 vs. 3.6–4.6% TL, preoral length 7.5–8.3 vs. 6.5–6.6% TL, preorbital length 8.3–10.5 vs. 7.0–7.7% TL), a shorter pelvic midpoint to second dorsal-fin origin measurement (5.5–7.7 vs. 9.4% TL), a slightly stockier head, body and tail (interorbital width 11.5–12.7 vs. 10.4–10.9% TL, head width 12.3–17.2 vs. 11.5% TL, trunk width 11–15.3 vs. 9.4% TL, caudal peduncle width 3.1–4.7 vs. 2.3% TL), shorter pectoral-fin posterior margin (12.8–15.0 vs. 17.2–18.4% TL), and a slightly shorter lower postventral caudal margin (4.4–5.5 vs. 5.9–6.2% TL). The specimens of *G. gangeticus* examined also have some of the lower teeth visible when the mouth is closed, whereas in the new species, the lower teeth are all concealed by the lips when the mouth is closed.

Glyphis fowlerae can be distinguished from *G. glyphis* from northern Australia in having a longer snout (prenarial length 4.8–5.3 vs. 3.3–4.7% TL, preorbital length 8.3–10.5 vs. 6.3–7.5% TL) and nostrils further apart (internarial width 7.0–7.7 vs. 5.2–6.6% TL). It can also be distinguished from *G. garricki* from northern Australia in having a slightly shorter and lower caudal-fin lobe (preventral caudal margin 10.8–12.3 vs. 12.7–13.9% TL, lower postventral margin 4.4–5.5 vs. 5.7–7.9% TL), a slightly shorter caudal terminal lobe (terminal lobe length 5.2–6.5 vs. 6.7–7.4% TL), first dorsal fin slightly closer to pectoral insertions (DPI length 4.0–5.9 vs. 6.1–7.0% TL), a taller caudal peduncle (caudal peduncle height 4.2–5.7 vs. 3.6–4.0% TL), a smaller pectoral fin (anterior margin 16.7–20.0 vs. 19.6–22.4% TL, posterior margin 12.8–15.0 vs. 15.6–19.6% TL), and a lower pelvic fin (pelvic-fin height 4.6–6.3 vs. 6.9–8.1% TL).

Comparison of the new species with *G. siamensis* is restricted to the unique holotype. *Glyphis fowlerae* differs from this specimen in having a longer snout (prenarial length 4.8–5.3 vs. 3.8% TL, preorbital length 8.3–10.5 vs. 7.8% TL), wider nostrils (nostril width 1.9–2.3 vs. 1.4% TL), taller pelvic fins (pelvic-fin length 8.8–10.3 vs. 7.0% TL), and a longer second dorsal-fin base (7.4–9.3 vs. 6.7% TL).

Two specimens of *Glyphis* collected from Mukah in



Figure 7. Lateral view of adult male lectotype of *Glyphis gangeticus* (ZMB 4474, 1850 mm TL, dried).

Sarawak during recent National Science Foundation (NSF)-funded surveys are clearly distinguishable from *G. fowlerae*, based on several morphometric characters, and they also exhibit substantial DNA sequence divergence in the mitochondrial marker NADH2 (G. Naylor, pers. comm., Florida State University). This species has since been temporarily identified as *Glyphis* sp. (Compagno *et al.*, 2008). Unfortunately, on a recent trip to Kuching (Nov. 2009) to examine these specimens, they could not be located and we consider both specimens missing, possibly lost. Based on an image of a fresh specimen of *G.* sp. (Fig. 5), it differs from *G. fowlerae* in having larger eyes, a much taller first dorsal fin, a greater first dorsal-fin height vs. second dorsal-fin height ratio, a more concave second dorsal-fin posterior margin, the waterline extending through mid-level of eye (vs. below eye), possibly larger pectoral fins, and appears to be less stocky. The large (1660 mm TL) adult male *Glyphis* recorded from Sampit Bay (Central Kalimantan) by Fahmi & Adrim (2009) has a much taller first dorsal fin and a relatively low (compared to congeners) second dorsal fin. This species appears to be much closer to, and possibly an adult of, *G.* sp. recorded from Mukah, rather than being conspecific with *G. fowlerae*. Although the first dorsal fin is relatively taller than in the juvenile specimen of *G.* sp., this difference is probably due to ontogenetic change similar to that observed in *G. garricki* and *G. glyphis* from northern Australia where large specimens have much larger first dorsal and pectoral fins than juveniles. Based on relative dorsal-fin heights, *Glyphis* sp. is clearly distinct from *G. garricki*, *G. glyphis* and *G. fowlerae*, and is closer to *G. gangeticus* and *G. siamensis* from the northern Indian Ocean. Specimens of this species need to be accessed to determine whether it is conspecific with *G. gangeticus* or *G. siamensis*, or whether it is undescribed.

A publication by Roberts (2006b) suggested that the type locality of *G. gangeticus* is likely to be from ‘the lower Sundarbans south of Kulna, and relatively near to the sea, in what is now Bangladesh’; thus from brackish rather than freshwater as originally suggested. Roberts (2006b) also suggested that *G. siamensis* is a junior synonym of

G. gangeticus, but vertebral counts and tooth counts collected by the senior author do not support this argument and *G. siamensis* should provisionally be considered as a valid nominal species. Roberts (2006b) reported on numerous specimens of *G. gangeticus* collected (by the author) from marine habitats in the Bay of Bengal, off Bangladesh and Myanmar, suggesting a preference for marine rather than riverine habitats as previously thought. However, the validity of these findings must be brought into question based on the following error in this manuscript. Roberts (2006b, Figure 7) provided images of 3 fresh juvenile specimens of *G. gangeticus* (one deposited at MNHN in Paris and one at the AMS in Sydney, AMS I 43504–001), but they are clearly misidentifications of the Bull Shark, *Carcharhinus leucas* (Müller & Henle, 1839). This was confirmed by examination by one of us (WW) of images of the AMS specimen which are clearly *C. leucas*. Although some other images provided in Roberts (2006b) are of *Glyphis gangeticus*, these misidentifications of juvenile sharks raises concern over the validity of identifications by this author of a large collection of jaws as *G. gangeticus*. Thus, the findings of his paper need to be treated somewhat cautiously which is unfortunate, given the general lack of knowledge on this group of sharks.

Roberts (2006a) provided a note on a set of *Glyphis* jaws from Pulo Condor off the Vietnam coast (ZMB 14850) that he considered to be from *G. glyphis*, which would be a large range extension from the known range of northern Australia and Papua New Guinea. He also suggested that the dried holotype was probably collected from either the Ganges delta or off the Sundarbans (Bangladesh). Further investigation of *G. glyphis* is required to determine the extent of its range and to determine whether it may also occur in waters between these known localities, e.g. off Borneo or Indonesia.

Comparative material.

Carcharhinus leucas: AMS I 43504–001, female 863 mm TL, Sittway market, Rakhine district, Bay of Bengal, Myanmar, May 2004 (identified as

G. gangeticus in Roberts (2006b).

Glyphis gangeticus: ZMB 4474 (lectotype), adult male 1850 mm TL, according to Müller & Henle (1839) “Im Ganges, 60 Stunden oberhalb des Meers bei Houghly gefangen.” (In the Ganges, captured in the Hooghly River 60 leagues above the sea, if correct possibly near the city of Navadwip at ca. 23°24' N, 88°22' E) photos and measurements contributed by Dr. H. Paepke of the Humboldt Museum, Berlin; MNHN 1141 (paralectotype), juvenile male 556 mm TL, “Bengal”; ZSI 8067, newborn female 610 mm TL, Hooghly River, West Bengal, India. ZMB 4474 was considered as lost (Garrick, 1982, 1985, Compagno, 1984, 1988) but was later rediscovered (Paepke & Schmidt, 1988).

Glyphis garricki: CSIRO H 5262–01 (holotype), female 670 mm TL, East Alligator River, Kakadu National Park, Northern Territory, 12°07' S, 132°38' E, 09 Jun. 1999; CSIRO H 6173–01 (jaws), female 1770 mm TL, northeast of entrance to Cambridge Gulf, Western Australia, 14°42' S, 128°34' E, 22 Oct. 2003; CSIRO H 6635–01 (jaws), adult male ca. 1450 mm TL, South Alligator River, 3 km downstream from 12°39' S, 132°29' E, 11 m depth, 10 May 1996; LWF–E227, juvenile male 720 mm TL, LWF–E294, juvenile male 720 mm TL, New Guinea (specimens lost but radiographs, drawings and photos provided by Prof. J.A.F. Garrick); LWF–E217 (jaws, supplied by P. Kailola), adult male ca. 1500–1700 mm TL, LWF–E219 (jaws, supplied by J.A.F. Garrick), Port Romilly, New Guinea, 07°40' S, 144°50' E, 12 Mar. 1966; LWF–E473 (jaws, supplied by P. Kailola), 1020 mm TL, Baimuru, New Guinea, 07°33' S, 144°51' E, 28 Mar. 1974; SAM uncatalogued (previously WAM P 32600–001) (chondrocranium, jaws, pelvic fin skeleton, pectoral girdle), juvenile female 1350 mm TL, King Sound, Western Australia, ca. 17°13' S, 123°40' E, 09 Jun. 2003; WAM P 32598–001, juvenile male 906 mm TL, Doctors Creek, Derby, Western Australia, 17°13' S, 123°40' E, 07 Jun. 2003; WAM P 32599–001, female 957 mm TL, Doctors Creek, Derby, Western Australia, 17°13' S, 123°40' E, 06 Jun. 2003; WAM P 32600–001 (3 specimens), adult male 1418 mm TL, juvenile male 1191 mm TL, juvenile male 1022 mm TL, King Sound, Western Australia, ca. 17°13' S, 123°40' E, 09 Jun. 2003; WAM P 32597–001, (deformed) adolescent male 994 mm TL, Doctors Creek, Derby, Western Australia, 17°13' S, 123°40' E, 2002. Also, data on specimen not seen but reported by Taniuchi et al. (1991), juvenile female 1314 mm TL, 100 km up from the mouth of the Adelaide River, Northern Territory, Australia, 13°00' S, 131°15' E, 26 May 1989.

Glyphis glyphis: CSIRO H 5261–01, juvenile male 770 mm TL, East Alligator River, Kakadu National Park, Northern Territory, 12°12' S, 132°47' E, 1–3.5 m, 10 Jun. 1999; CSIRO H 5756–01, juvenile male 631 mm TL, Marrakai Creek, Adelaide River, Northern Territory, 12°41' S, 131°20' E, 28 Nov. 2001; NTM S 15097–001, juvenile male 792 mm TL, Brooks Creek, South Alligator River, Kakadu National Park, Northern Territory, 12°12' S, 132°24' E, 04 Jun. 1999; NTM S 15351–001, female

678 mm TL, Marrakai Creek, Adelaide River system, Northern Territory, 12°41' S, 131°20' E, 11 Sep 2001; NTM S 15508–001, female 595 mm TL, NTM S 15508–002, juvenile male 590 mm TL, Adelaide River system, Northern Territory, 12°37' S, 132°47' E, 16 Nov. 2002; NTM S 16217–001, adolescent male 1447 mm TL, Wenlock River, Cape York Peninsula, Queensland, 12°03' S, 141°55' E, 01 Feb. 2006; QM I 19719, juvenile male 745 mm TL, 17 km upstream from Bizant River mouth, Princess Charlotte Bay, Queensland, 14°33' S, 144°05' E, 23 Mar. 1982; QM I 36881, female 1095 mm TL, QM I 36882, juvenile male 705 mm TL, QM I 36883, juvenile male 867 mm TL, QM I 36884, juvenile male 723 mm TL, QM I 36885, 770 mm TL, Gloughs Landing, Wenlock River, Queensland, 12°45' S, 142°59' E, 28 Apr. 2005; LWF–E218 (jaws), juvenile female ca. 1600–1800 mm, Port Romilly, New Guinea, 07°40' S, 144°50' E, 12 Mar. 1966; LWF–E405B (jaws, supplied by P. Kailola), ca. 1700–1800 mm, Alligator Island, Fly River, New Guinea, 07°19' S, 141°11' E; ZMB 5265 (holotype), stuffed specimen, juvenile female 1023 mm TL, locality unknown but probably Indian Ocean (photos, morphometrics and radiographs of tail from Dr. H. Paepke).

Glyphis siamensis: NMW 61379 (holotype), juvenile male 630 mm TL, Irrawaddy River mouth, Rangoon, Myanmar, photos, radiographs and measurements contributed by Dr. Ernst Mikschi, Vienna Museum.

Glyphis sp.: NSFEP BO470, juvenile male 658 mm TL, NSFEP BO471, juvenile male 610 mm TL, Mukah, Sarawak, Malaysia, 02°53.52' N, 112°05.44' E, 29 Apr. 2004, specimens were not found during a trip to the IPPS location by one of the authors (WW) in November 2009.

Key to the nominal species of *Glyphis*

- 1 Second dorsal fin relatively low, about half height of first dorsal fin 2
 Second dorsal fin relatively large, more than half height of first dorsal fin 3
- 2 Total vertebral count 209; tooth row count 58 (from only known specimen).....
 *G. siamensis* (Myanmar)
 Total vertebral count 169 (from one specimen); tooth row count 62–71 *G. gangeticus* (India, Pakistan)
- 3 Total vertebral count more than 210, monospondylous count more than 68; total tooth row count less than 59; black blotch at ventral tip of pectoral fins
 *G. glyphis* (northern Australia, New Guinea)
 Total vertebral count less than 210, monospondylous count less than 67; total tooth row count more than 60; no black blotch at ventral tip of pectoral fins 4

- 4 Total vertebral count 196–209, monospondylous count 60–67; waterline (demarcation of dark upper and pale lower surfaces) at level of lower eye on head *G. fowlerae* (Sabah, Borneo)
- Total vertebral count 137–151, monospondylous count 44–50; waterline (demarcation of dark upper and pale lower surfaces) at a level greater than an eye diameter below lower level of eye *G. garricki* (northern Australia, New Guinea)

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