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GOGOLIA FILEWOODI, A NEW GENUS AND SPECIES OF SHARK FROM NEW GUINEA (CARCHARHINIFORMES: TRIAKIDAE), WITH A REDEFINITION OF THE FAMILY TRIAKIDAE AND A KEY TO TRIAKID GENERA

By

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INTRODUCTION

On the night of July 18–19, 1970, Mr. Komet Kisokau handlined a peculiar small shark in Astrolabe Bay, off the Gogol River near Madang, New Guinea. Mr. Kisokau and Mr. R. T. Gibson (Fisheries Officer, Madang, and a former shark fisherman) recognized the unusual nature of the specimen and sent it to Mr. L. W. Filewood (Biologist-In-Charge of the Department of Agriculture, Stock and Fisheries, Konedobu, Papau-New Guinea), who is currently studying the elasmobranchs of the New Guinean region. Mr. Filewood discovered that the specimen represented a new genus and species of triakid and intended to describe it in collaboration with the present writer. Unfortunately Mr. Filewood was unable to participate in this task and generously relinquished both it and the specimen to me.

Gogolia Compagno, new genus

TYPE SPECIES. *Gogolia filewoodi* Compagno, new species.

DERIVATION OF NAME. *Gogolia* (considered feminine), from the Gogol River of Northern New Guinea.

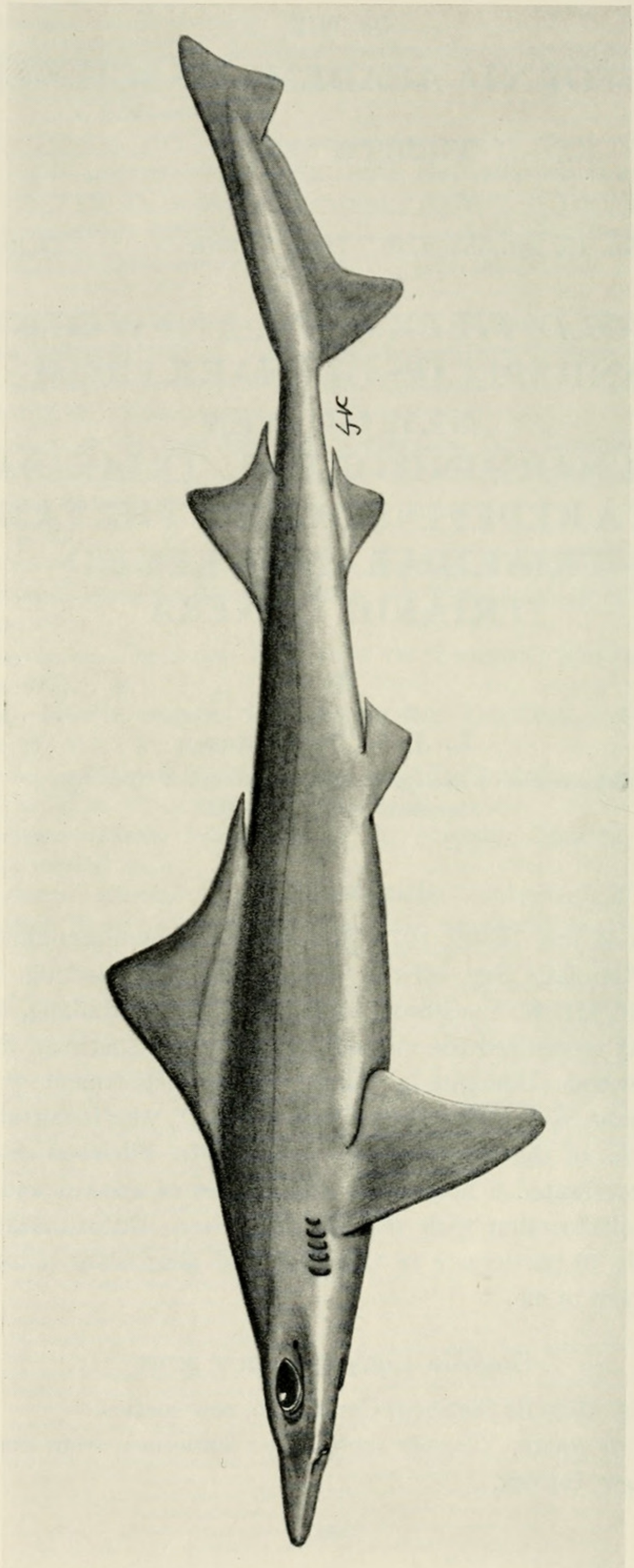
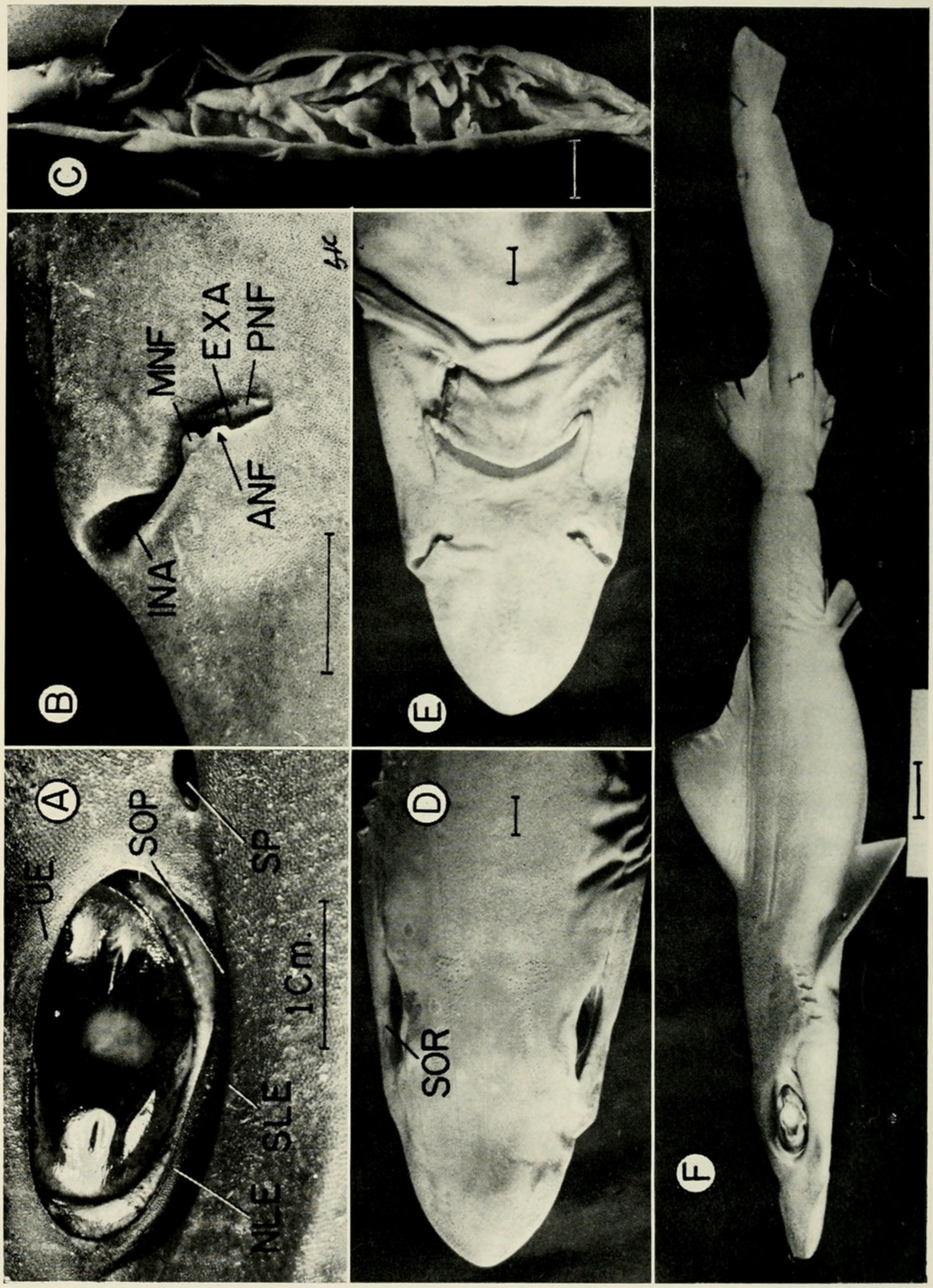


Figure 1. *Gogolia filewoodi* Compagno, new genus and species. Lateral view of holotype, 739 mm. adult female, Australian Museum no. I. 16858–001.

GENERIC DEFINITION. (Terminology follows Compagno, 1970; Compagno and Springer, 1971; and Compagno, 1973a.). Triakid sharks with a moderately long head, length from snout tip to level of 5th gill openings about 1.4–1.5 times the distance between the dorsal fin bases and about 22–24 percent of total length. Head and snout acutely wedge-shaped and blunt-tipped in lateral view (figs. 1, 2F). Outline of snout bell-shaped in dorsoventral view (fig. 2D–E) and parabolic in front of nostrils. Snout very long, preoral length (distance from snout tip to upper symphysis) about 1.6–1.7 times mouth width and 2.1–2.2 in head length. Subocular ridges very strong and prominently visible in dorsal view of head (fig. 2D: SOR) and blocking off view of eyes ventrally (fig. 2E). Eyes very large, elliptical, and about twice as long as high. Nictitating lower eyelid external and having a diagonal edge (fig. 2A: NLE). Subocular pouch shallow and entirely covered with denticles. Gill openings very small, width of 3rd about 2.2–5.2 in eye length. Anterior nasal flaps very low and virtually vestigial (fig. 2B: ANF), not barbel-like or greatly expanded. Posterior ends of anterior nasal flaps well forward of mouth (fig. 2E). No nasoral grooves. Nasal cavities communicating to the exterior only by narrow incurrent and excurrent apertures (fig. 2B: INA and EXA), not exposed ventrally. Internarial width about 2.0 times nostril widths. Nostrils about 2.5 times farther from the snout tip than from the mouth. Mouth arcuate in shape (fig. 2E). Mouth very short, its length from level of upper symphysis to level of mouth corners 2.5–3.0 in width of mouth between corners. Lower jaw very flat, with its sides hardly protruding or not showing below ventral surface of head in lateral view (figs. 1, 2F). Upper labial furrows extending anteriorly to level of upper symphysis.

Tooth-row counts 40–41/35 (2). 2–3/2–4 series of teeth functional. Premedial edges of most teeth convex and undifferentiated, but in adult the medials and some upper anteroposteriors have premedial cusplets or strong serrations (figs. 3C–D, 4A). Primary cusps very strong on all teeth except for the last lower posteriors (fig. 4B: teeth nos. 14–15). Postlateral edges of crowns strongly notched in all cusped teeth, these differentiated basally into postlateral cusplets or blades. Roots of teeth relatively low (fig. 3C–H: RT). Teeth strongly compressed, sharp-edged, and blade-like, but not molariform. Teeth not enlarged at symphysis to form a knob and not extending onto edges and ventral surface of lower jaw. Tooth-row groups poorly differentiated and including medials (fig. 4: M) and anteroposteriors (fig. 4A, teeth nos. 1–20; and fig. 4B, teeth nos. 1–15) in both jaws. Medials have erect or semioblique cusps and relatively higher and narrower crowns than the lower, broader, oblique-cusped anteroposteriors. Dignathic heterodonty strong in anteroposteriors near symphysis, but much weaker near the ends of the dental bands. In an adult these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parasymphysial anteroposteriors have premedial cusplets or serrations, narrow cusps, prominent transverse ridges or striations, and more postlateral cusplets in the upper jaw, while lower teeth have no premedial cusplets and very few postlateral ones, broader cusps, and no ridges (compare fig. 3C–E with F–H).

Interdorsal ridge present in adult and absent in fetus. Caudal peduncle short, its length from second dorsal insertion to upper caudal origin about 4/5 of second dorsal base. Lateral trunk denticles from dorsum below first dorsal fin with teardrop-shaped crowns that are considerably longer than wide and have rudimentary lateral cusps or none (fig. 3A–B).

Longest distal radials of pectoral fin skeleton about 1.6 times as long as longest proximal radials (fig. 5A–B: DRA and PRA). Anterior margins of pelvic fins about 2/5 as long as pectoral anterior margins.

First dorsal origin far anterior, varying from over pectoral insertions to about over pectoral midbases. Free rear tip of first dorsal slightly posterior to pelvic origins. First dorsal base extremely long (figs. 1, 2F), its length almost equal to length of dorsal caudal margin, 2.3–3.2 times the first dorsal height, and 1.3–1.4 times the distance between dorsal bases. Second dorsal much smaller than first, its height about 2/3 of first dorsal height and its base length less than half of first dorsal base. Anal fin smaller than second dorsal, its height 0.5–0.6 of second dorsal height and its base 0.5–0.7 of second dorsal base. Anal insertion slightly anterior to second dorsal insertion by a distance about 0.1–0.2 of second dorsal base.

Caudal fin with a short but strong ventral caudal lobe in adult but a weak one in a fetus (figs. 1, 2F). Postventral caudal margin shallowly indented but not deeply notched. Length of terminal caudal sector from subterminal notch to tip of caudal about 3.1–3.8 in length of dorsal caudal margin.

Cranium with a long rostrum, with the length of the medial rostral cartilage from its base to the anterior edge of the rostral node about 1.4–1.9 in nasobasal length (distance from the base of the medial rostral cartilage to the posteroventral edge of the occipital centrum, here used as an independent variable for cranial proportions). Bases of lateral rostral cartilages connected by a ridge (fig. 6A, C: RRF) to the edge of the anterior fontanelle. Nasal capsules trans-

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FIGURE 2. *Gogolia filewoodi.* A–E, photographs from 739 mm. holotype. A, left eye in lateral view. B, left nostril in ventral view. C, valvular intestine cut longitudinally to show spiral valve. D, head, dorsal view. E, head, ventral view. F, photograph in lateral view of 224 mm. fetus, CAS–27588. All scale lines equal 1 centimeter. Abbreviations: ANF, anterior nasal flap; EXA, excurrent aperture; INA, incurrent aperture; MNF, mesonarial flap; NLE, nictitating lower eyelid; PNF, posterior nasal flap; SLE, secondary lower eyelid; SOP, subocular pouch; SOR, subocular ridge; SP, spiracle; UE, upper eyelid.

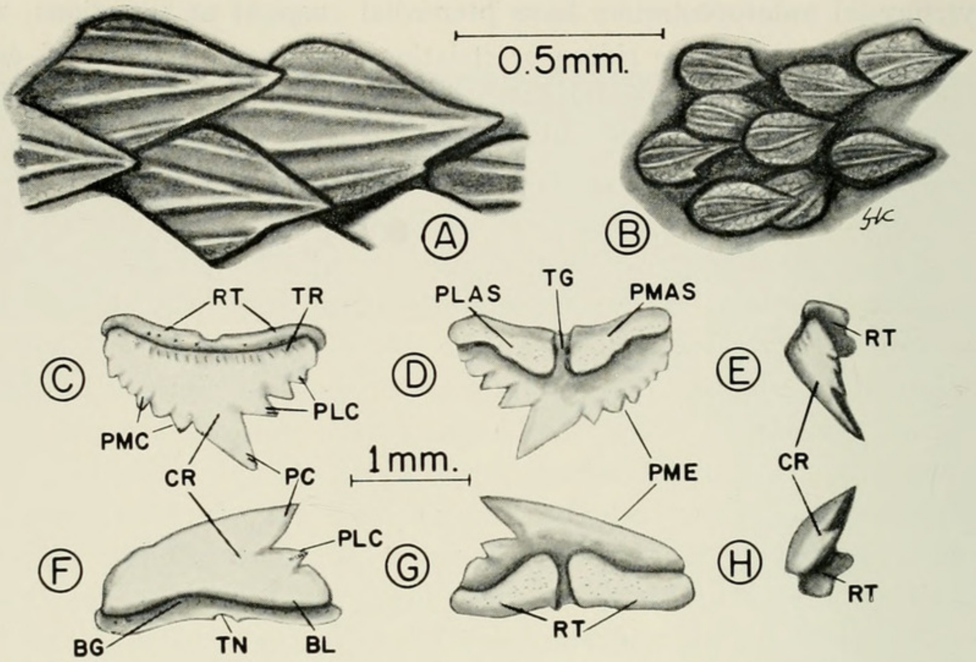

FIGURE 3. *Gogolia filewoodi.* A, crowns of lateral trunk denticles from dorsum below first dorsal fin, 739 mm. holotype. B, same from 224 mm. fetus. C–E, teeth from 739 mm. holotype. Labial (C), lingual (D), and lateral (E) views of tooth from 4th upper anteroposterior row (numbered from symphysis). Labial (F), lingual (G), and lateral (H) views of tooth from 4th lower anteroposterior row. Abbreviations: BG, basal groove; BL, basal ledge; CR, crown; PC, primary cusp; PLAS, postlateral attachment surface of root; PLC, postlateral cusplets; PMAS, premedial attachment surface of root; PMC, premedial cusplets; PME, premedial edge; RT, root; TG, transverse groove; TN, transverse notch; TR, transverse ridges.

versely elongated and anteriorly flattened, not circular (fig. 6: NC). Nasal fontanelles delimited anteriorly from nasal apertures (fig. 6B: NA and NF). Nasal openings of orbitonasal canals inside nasal capsules and well behind posterior edges of nasal fontanelles. Thickened ridges or ectethmoid condyles (fig. 6B–C: ECN) present on nasal capsules and articulating with the orbital processes of the palatoquadrates (fig. 7B–C). A depression or subethmoid fossa (fig. 6B: SEF) present on the ventral surface of the cranium between the ectethmoid condyles. Basal plate very narrow across orbital notches (fig. 6B: NP), its transverse width there about 3.0 in nasobasal length. Two pairs of arterial foramina present on basal plate, one for the internal carotid arteries and one for the stapedial or orbital arteries (fig. 6B: FC and FS). Least width across supraorbital crests (transverse to the long axis of the cranium) about 2.4 in nasobasal length. Postorbital processes short and shallowly notched distally (fig. 6: PT). Suborbital shelves narrow and not laterally expanded, ear-shaped, fenestrate, or notched. Greatest width across suborbital shelves (perpendicular to the long axis of cranium) about 1.7 in nasobasal length.

Total vertebral counts 180 (2). No stutter zone of alternating long and short centra in vertebral column. Thoracic vertebral centra with strong diagonal calcified lamellae (fig. 5D–E: DCL).

Other characteristics of *Gogolia* those of the family Triakidae and of the single species (see below).

Familial Classification of *Gogolia*

Gogolia is a genus that, with *Hemitriakis* and *Iago*, stands midway between the families Carcharhinidae and Triakidae (or their equivalents) as defined by Garman (1913), White (1936, 1937), Bigelow and Schroeder (1948), and Garrick and Schultz (1963). According to these workers, triakids have several functional series of small, molariform or blade-like and multicuspidate teeth and 'nictitating folds,' whereas carcharhinids have not more than 1 or 2 series of small to large, blade-like teeth and 'nictitating membranes.' The failure of these characters to distinguish the two families is discussed elsewhere (Compagno, 1970). *Gogolia* itself has a 'nictitating fold' but has small, blade-like teeth in 2–4 functional series.

Previously I resolved the problem of triakid-carcharhinid intergradation by the unsatisfactory expedient of merging the two families (Compagno, 1970). Subsequent work on a revision of carcharhinoid genera indicated that a group of genera partially corresponding to the family Triakidae of White (1937) could be separated from the Carcharhinidae.

Part of the difficulty in separating the families Carcharhinidae and Triakidae of White (1937) and Bigelow and Schroeder (1948) was that each of the two families contained genera closer to the type genus of the other family than to its own type genus. Thus *Triaenodon* has many external, cranial, pectoral fin skeleton, and cephalic myological characters that ally it closely with typical carcharhinids such as *Carcharhinus*, but the strong cusplets on its teeth led many workers to place *Triaenodon* incorrectly in the Triakidae. *Galeorhinus* has often been placed in the Carcharhinidae but it similarly has many characters that indicate close affinities with the Triakidae. Also, *Galeorhinus* is linked with the genera *Triakis* and *Mustelus* by a group of roughly intermediate forms (*Gogolia, Hypogaleus, Iago, Furgaleus,* and *Hemitriakis*).

The reinstated family Triakidae includes the genera *Mustelus* Linck, 1790; *Galeorhinus* Blainville, 1816; *Triakis* Müller and Henle, 1838a; *Scylliogaleus* Boulenger, 1902; *Hemitriakis* Herre, 1923; *Furgaleus* Whitley, 1951; *Hypogaleus* J. L. B. Smith, 1957a; *Iago* Compagno and Springer, 1971; *Allomycter* Guitart, 1972; and *Gogolia*. *Triaenodon* Müller and Henle, 1837 is transferred to the Carcharhinidae (see also Gohar and Mazhar, 1964, and Kato, Springer, and Wagner, 1967, for discussion of the familial position of *Triaenodon*). The "scyliorhiniform triakoids" (Compagno, 1970) have often been placed in the family Triakidae or its equivalents and included in the genus *Triakis*. However, these genera, including *Proscyllium* Hilgendorf, 1904, *Eridacnis* H. M. Smith, 1913, *Ctenacis* Compagno, 1973a, and *Gollum* Compagno, 1973a, are sufficiently distinct from triakids to require a separate family, Proscylliidae (elevation of subfamily Proscylliinae Fowler, 1941). *Leptocharias* A. Smith, *in* Müller and Henle, 1838a is difficult to place but probably is best placed in its own family, Leptochariidae (elevation of tribe Leptochariana Gray, 1851) owing to its morphological distinctness from other carcharhinoids. *Leptocharias* has often been grouped with the triakids in proximity to *Triaenodon*, but these two genera are not closely related.

The Triakidae can be defined as follows:

Family Triakidae Gray, 1851, new rank

Subfamily Musteli Bonaparte, 1838, p. 199 (Family Squalidae. Type genus: *Mustelus* Cuvier, 1817, equals *Mustelus* Linck, 1790.). Preoccupied in Mammalia by families Mustelini Fischer, 1817 and Mustelidae Swainson, 1835 (Type genus: *Mustela* Linnaeus, 1758); references for mammalian families in Simpson (1945).

Family Galei Müller and Henle, 1839, p. 57 (Type genus: *Galeus* Cuvier, 1817, a junior synonym of *Galeorhinus* Blainville, 1816; not *Galeus* Rafinesque, 1809.).

Family Scylliodontes Müller and Henle, 1839, p. 63 (Not based on a type genus.).

Tribe Triakiana Gray, 1851, p. 39 (Family Squalidae. Type genus: *Triakis* Müller and Henle, 1838a.). The family Triakidae was independently proposed by White (1936a, 1936b, 1937).

Family Galeorhinoidae Gill, 1862b, p. 393 (Type genus: *Galeorhinus* Blainville, 1816.).

Family Scylliogaleidae Whitley, 1940, p. 68 (Type genus: *Scylliogaleus* Boulenger, 1902.). The family Scylliogaleidae was independently proposed by Smith (1957b).

Family Emissolidae Whitley, 1940, p. 68 (Type genus: *Emissola* Jarocki, 1822, probably a junior synonym of *Mustelus* Linck, 1790.).

Family Eugaleidae Gurr, 1962, p. 428 (Type genus: *Eugaleus* "Rafinesque, 1810", equals Gill, 1864, *not* Rafinesque, 1809–1810; a junior synonym of *Galeorhinus* Blainville, 1816.).

Carcharhinoid sharks with the head not expanded laterally into a wing-like blade. Eyes high on sides of head, with their ventral edges above the nostrils. Eye length 1.5–2.5 or more times eye height. Nictitating lower eyelid variably external, transitional, or internal (Compagno, 1970). Small to moderately large spiracles present, with their greatest widths about 3–10 in eye length. Labial furrows long and present on both jaws. Labial cartilages well developed.

Tooth-row groups poorly differentiated or absent, with medials often present but no symphysials, anteriors, or well defined posteriors. Posterior teeth not comb-like. Gynandric heterodonty absent or poorly developed as far as is known (data not available for *Scylliogaleus*, *Gogolia*, and *Allomycter*). Tooth-row counts 18–94/27–94. Teeth with strong basal ledges and grooves.

Precaudal pits absent. Pectoral fin skeleton with its radials projecting half of pectoral anterior margin length or less into fin (fig. 5A). Distal pectoral radials with parallel edges and truncate or distally rounded tips. Longest distal radials 1–2 times as long as longest proximal radials.

First dorsal fin with distinct apex and separate anterior and posterior margins, not arcuate-edged and keel-like. First dorsal base anterior to pelvic bases. Length of first dorsal base usually much shorter than dorsal caudal margin, but subequal to it in *Gogolia*. No undulations in dorsal caudal margin.

Neurocranium with bases of lateral rostral cartilages well separated. Nasal capsules not greatly depressed or transversely expanded (fig. 6). Large nasal fontanelles present and broadly continuous anteriorly with the nasal apertures (fig. 6B: NA and NF). Nasal openings of orbitonasal canals inside the nasal cavities, located at the posterior edges of the nasal fontanelles or behind them. Ectethmoid condyles, when present, without foramina for the anterior facial veins (ectethmoid foramina). Internasal septum a high, compressed plate. Arterial foramina on the basal plate usually include two pairs of stapedial and internal carotid foramina (fig. 6B: FS and FC), but *Furgaleus* has a single pair of common foramina apparently formed by the merging of the stapedials and internal carotids on each side. Parietal fossa single. Supraorbital crest present (fig. 6: SC).

Wedge-like intermedialia strongly developed in vertebral centra of adults and subadults (fig. 5E) but often absent or poorly developed in fetuses or newborn specimens (fig. 5D).

Valvular intestine with a spiral valve of 5–11 turns. Levator palatoquadrati muscles small, with their origins not expanded anterior to the postorbital processes (fig. 7C: MLP).

Triakidae is distinguished from the families Scyliorhinidae, Pseudotriakidae, and Sphyrnidae of Bigelow and Schroeder (1948) by many characters that need not be detailed here. The Proscylliidae as delimited above differ from the Triakidae in having rudimentary nictitating lower eyelids; very short labial furrows (sometimes absent in *Eridacnis*); comb-like posterior teeth; transverse grooves absent from teeth; distal pectoral radials much shorter than the proximal radials; and wedge-like intermedialia absent from the vertebral centra. The Leptochariidae differ from the Triakidae in having teeth without transverse grooves; strongly developed gynandric heterodonty; nasal openings of the orbitonasal canals not in the nasal cavities but posterior to them and penetrating the suborbital shelves; no supraorbital crest; and 14–16 turns in the spiral intestinal valve.

The family Carcharhinidae is restricted to the "advanced carcharhinids" of Compagno (1970) and includes *Carcharhinus* Blainville, 1816; *Scoliodon* Müller and Henle, 1837; *Galeocerdo* Müller and Henle, 1837; *Triaenodon* Müller and Henle, 1837; *Loxodon* Müller and Henle, 1838a; *Hypoprion* Müller and Henle, 1839; *Prionace* Cantor, 1849; *Aprionodon* Gill, 1862a; *Isogomphodon*

Gill, 1862b; *Lamiopsis* Gill, 1862b; *Rhizoprionodon* Whitley, 1929; and *Negaprion* Whitley, 1940. The "intermediate carcharhinids" of Compagno (1970) are sufficiently distinct from the Carcharhinidae to rate a family, Hemigaleidae (family Hemigalei or Hemigaleus of Hasse, 1879), that includes the genera *Hemipristis* Agassiz, 1843; *Hemigaleus* Bleeker, 1852 (including *Negogaleus* Whitley, 1931); *Dirrhizodon* Klunzinger, 1871 (including *Heterogaleus* Gohar and Mazhar, 1964); *Chaenogaleus* Gill, 1862b; and *Paragaleus* Budker, 1935. *Dirrhizodon* is usually synonymized with the fossil *Hemipristis* but is separable by differences in tooth histology (Compagno, 1973b).

The Carcharhinidae and Hemigaleidae differ from the Triakidae in having stronger monognathic heterodonty; precaudal pits present; pectoral fin skeleton extending into the distal parts of the fins; distal pectoral radials with pointed tips and tapering edges; longest distal radials over 3 times the length of the longest proximal radials; lateral undulations present in the dorsal caudal margin (irregular in *Scoliodon* and in some specimens of *Triaenodon*); nasal fontanelles either separated from the nasal apertures by a cartilaginous bridge (hemigaleids, *Galeocerdo* and *Loxodon*) or absent; no supraorbital crest; and levator palatoquadrati muscles greatly expanded anteriorly, with their origins extending in front of the postorbital processes and onto the sides and dorsal surface of the cranial roof (Moss, 1972, and unpublished data). The Hemigaleidae additionally differ from the Triakidae in having two pairs of foramina for the lateral aortae and efferent hyoidian arteries on the basal plate. Carcharhinids differ from triakids also in having weak or no basal ledges on their teeth; ectethmoid foramina present on the ectethmoid condyles; and scroll intestinal valves.

Comparison with other genera

Gogolia is separable from all other triakids by its unusually high ratio of preoral length to mouth width (this is below 1.5 in other genera); very short mouth (approached in this only by *Furgaleus*); very small gill openings; heterodonty pattern in adult (fig. 4); extreme anterior position of its first dorsal origin (*Iago* is similar in this but other genera have the first dorsal origin posterior to the pectoral insertions); very long and low first dorsal fin (other genera have the first dorsal base ⅔ of the dorsal caudal margin or less and the fin height over half of the base length); and high total vertebral counts (*Triakis acutipinna* has 175–176 centra, but other triakids usually have fewer than 160).

Gogolia is distinguished from other triakids in a key to the genera of Triakidae provided below. In this key the genera *Galeorhinus*, *Hypogaleus*, and *Hemitriakis* are restricted to the species listed in Compagno (1970). *Triakis* comprises the species placed in it by Compagno (1973a): *T. scyllium* Müller and Henle, 1839, including *Hemigaleus pingi* Evermann and Shaw, 1927; *T. megaloptera* (A. Smith, 1849), including *Mustelus nigropunctatus* J. L. B.

Smith, 1952; *T. semifasciata* Girard, 1854, including *Mustelus felis* Ayres, 1854; *T. maculata* Kner and Steindachner, 1866, including *Mustelus nigromaculatus* Evermann and Radcliffe, 1917; and *T. acutipinna* Kato, 1968. The poorly known genus *Allomycter* is tentatively placed in the Triakidae and included in the key. *Allomycter* (with a single species, *A. dissutus*) was described from photographs of a unique specimen of shark from Cuba, but this specimen was lost before its describer could examine it (Guitart, 1972).

FAMILY TRIAKIDAE. KEY TO GENERA

1a. Nostrils with broad nasoral grooves. Anterior nasal flaps very large, meeting each other at midline of snout and overlapping mouth posteriorly........ *Scylliogaleus* Boulenger, 1902.

1b. Nostrils without nasoral grooves. Anterior nasal flaps small to absent, when present separated from each other and not reaching mouth .... 2.

2a. Preoral length 1.6–1.7 times mouth width. First dorsal fin with its base length almost equal to length of dorsal caudal margin and 2.3–3.2 times the first dorsal height .... *Gogolia* Compagno, new genus.

2b. Preoral length less than 1.5 times mouth width. First dorsal with its base length ⅔ or less of the dorsal caudal margin length and about 1.2–1.7 times the first dorsal height .. 3.

3a. Anterior nasal flaps absent. Nasal cavities widely open to the exterior .... *Allomycter* Guitart, 1972.

3b. Anterior nasal flaps present. Nasal cavities not widely open to the exterior but communicating with it through restricted incurrent and excurrent apertures .... 4.

4a. Teeth markedly unlike in upper and lower jaws. Anterior nasal flaps formed into slender barbels .... *Furgaleus* Whitley, 1951.

4b. Teeth not markedly unlike in upper and lower jaws. Anterior nasal flaps not barbel-like .... 5.

5a. Origin of first dorsal far forward, over pectoral bases .... *Iago* Compagno and Springer, 1971.

5b. Origin of first dorsal farther back, over inner margins of pectorals or posterior to them .... 6.

6a. Second dorsal fin about as large as anal fin, with its height ⅖ or less of first dorsal height and its base about half as long as first dorsal base. Terminal sector of caudal about half as long as dorsal caudal margin .... *Galeorhinus* Blainville, 1816.

6b. Second dorsal fin noticeably larger than anal fin, its height ½ to virtually equal to first dorsal height and its base ⅔ to about equal to second dorsal base. Terminal sector of caudal about ⅓ as long as dorsal caudal margin .... 7.

7a. Nostrils narrow and far apart, internarial space about 2.5–3.0 times nostril width. Teeth formed into compressed cutting blades. Medials present at symphysis of both jaws .... 8.

7b. Nostrils wider and closer together, internarial space about 1.0–2.0 times nostril width. Teeth molariform to semibladelike, not greatly compressed. No differentiated medials at symphysis .... 9.

8a. Eyes fusiform in shape and over 2 times as long as high. Mouth broadly arched. Second dorsal over ⅔ of height of first dorsal. Ventral caudal lobe very short .... *Hemitriakis* Herre, 1923.

8b. Eyes pear-shaped and less than twice as long as high. Mouth triangular. Second dorsal about half as high as first dorsal. Ventral caudal lobe very long .... *Hypogaleus* J. L. B. Smith, 1957.

9a. Snout bluntly rounded in dorsoventral view, thick and blunt in lateral view. Mouth arcuate in shape, lower jaw with convex edges. Teeth of lower jaw hardly overlapping or not extending onto its ventral surface, not enlarged at symphysis or forming a knob .... *Triakis* Müller and Henle, 1838.

9b. Snout bluntly parabolic to subtriangular in dorsoventral view, bluntly to narrowly pointed in lateral view. Mouth subtriangular or triangular in shape, lower jaw with straight or nearly straight edges. Teeth of lower jaw prominently overlapping onto its ventral surface, more or less enlarged at symphysis to form a knob resembling those of rays of the genus *Rhynchobatus* .... *Mustelus* Linck, 1790.

Gogolia is closest to *Galeorhinus*, *Hypogaleus*, and *Hemitriakis* within the Triakidae and is intermediate in some characters between *Hemitriakis* and the other genera. Thus *Gogolia* resembles *Hemitriakis* in having strong subocular ridges, external nictitating lower eyelids, shallow subocular pouches, and poorly developed lateral cusps on the trunk denticles, but agrees with *Galeorhinus* and *Hypogaleus* in eye shape, greatly reduced anterior nasal flaps and protruding mesonarial flaps, and size disparity between first and second dorsal fins. The premedial cusplets on the upper parasymphysial teeth of *Gogolia* recall similar cusplets on upper and lower anteroposteriors of the Eocene fossil "*Galeus recticonus*" (as described and illustrated by Leriche, 1905). However, the teeth of "*G. recticonus*" have heavier cusps, larger and more regular premedial cusplets, less compressed crowns and roots, and stronger transverse notches than in those of *Gogolia*. Living *Galeorhinus* species also have a few irregular premedial cusplets on anteroposteriors closest to the symphysis, but these are less prominent than the premedial cusplets of *Gogolia* and "*G. recticonus*."

Gogolia filewoodi Compagno, new species.

Holotype. A pregnant adult female, 739 mm. total length, with 2 fetuses (1 retained by Mr. L. W. Filewood), Australian Museum (Sydney) no. I. 16858–001. The remaining fetus, a 224 mm. male, is cataloged as CAS–27588.

Type locality. Astrolabe Bay, Northern New Guinea, about 1 mile north of the Gogol River mouth at 40 fathoms depth; about 5° 18′ S. Latitude and 145° 50′ E. Longitude.

Species name. Named for Mr. L. W. Filewood in recognition of his work on the poorly known elasmobranch fauna of New Guinea.

Measurements and proportions. These are given as percentages of total length for the adult female holotype and the male fetus (table 1).

Description (based on the adult female and fetal male). Head broad, width at spiracles about half head length. Head moderately depressed and trape-

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Figure 4. *Gogolia filewoodi*. Set of detached teeth from left jaw half of 739 mm. holotype in labial view, with anteroposterior teeth numbered sequentially from medial row at symphysis (M) to last row at end of dental band. A, upper teeth. B, lower teeth.

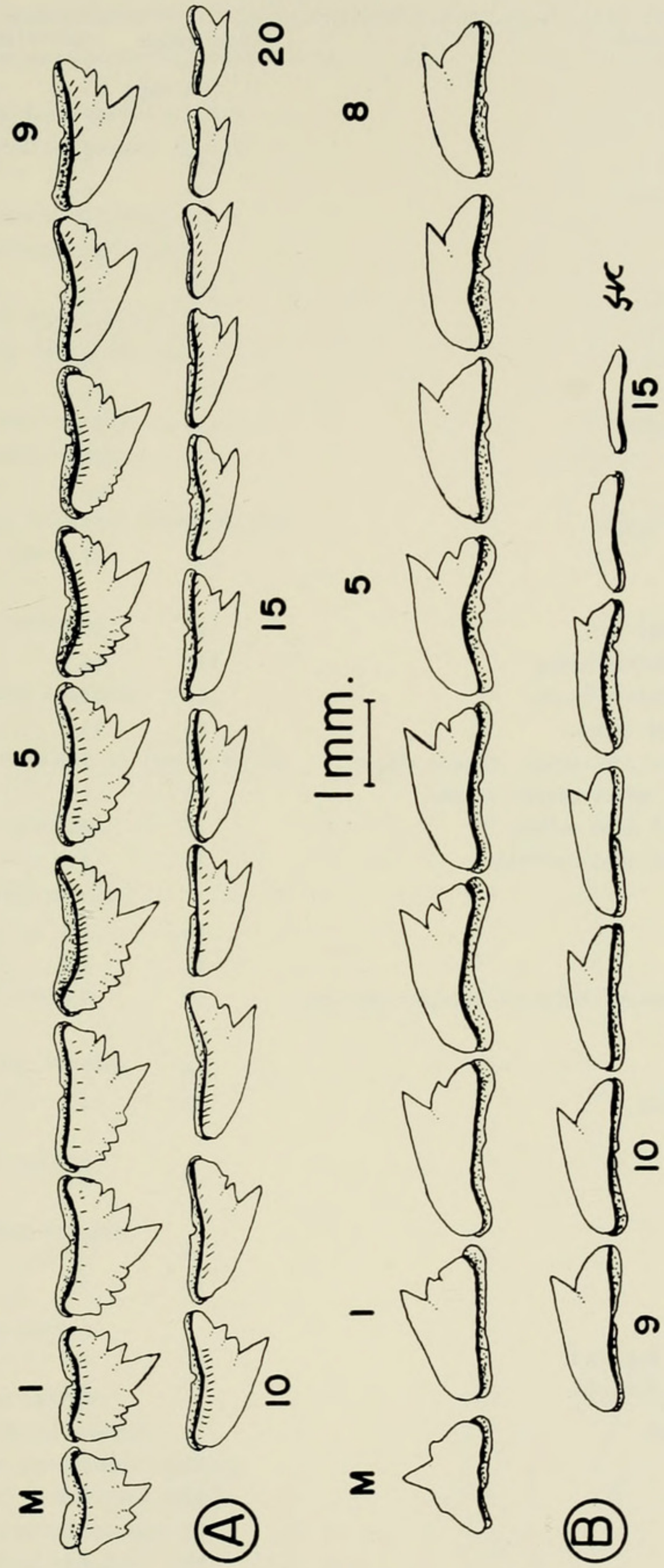
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TABLE 1. *Measurements of two specimens of* Gogolia filewoodi.

Measurement	Adult female	%	Male fetus	%
Total length:	739 mm.	—	224 mm.	—
Tip of snout to:				
Nostrils.	45	6.1	15	6.7
Upper symphysis.	72	9.8	25	11.2
Eyes.	57	7.7	20	8.9
Spiracles.	94	12.7	33	14.7
1st gill openings.	133	18.0	46	20.6
5th gill openings.	158	21.5	53	23.7
Pectoral origins.	152	20.1	51	22.8
1st dorsal origin.	173	23.4	62	27.7
2nd dorsal origin.	434	57.7	138	61.6
Pelvic origins.	336	45.5	106	47.3
Anal origin.	445	60.2	140	62.5
Upper caudal origin.	560	75.8	172	76.8
Vent.	353	47.8	106	47.4
Distance between:				
Vent and caudal tip.	386	52.2	118	52.6
1st and 2nd dorsal bases.	119	16.1	35	15.6
Pectoral and pelvic bases.	162	21.9	44	19.7
Pelvic and anal bases.	81	11.0	28	12.5
2nd dorsal base and upper caudal origin.	58	7.9	14	6.3
Anal base and lower caudal origin.	58	7.9	14	6.3
2nd dorsal and anal origins.	17	2.3	3	1.3
2nd dorsal and anal insertions.	11	1.5	2	0.9
Eyes:				
Length.	26	3.5	13	5.8
Height.	13	1.8	6	2.7
Transverse distance between anterior corners.	52	7.0	20	8.9
Nostrils:				
Width.	16	2.2	6	2.7
Internarial space.	33	4.5	12	5.6
Spiracles:				
Diameter.	4	0.5	2	0.9
Mouth:				
Length.	14	1.9	6	2.7
Width.	42	5.7	15	6.7
Labial furrows:				
Length upper furrows.	17	2.3	6	2.7
Length lower furrows.	9	1.2	3	1.3
Gill opening widths:				
1st.	11	1.5	3	1.3
2nd.	12	1.6	3	1.3
3rd.	12	1.6	2.5	1.1
4th.	10	1.4	2	0.9
5th.	8	1.1	1.5	0.7

Table 1. *Continued.*

Measurement	Adult female	%	Male fetus	%
Head:				
Width at anterior corners of eyes.	66	8.9	25	11.2
Height at anterior corners of eyes.	35	4.7	11	4.9
Trunk:				
Width at pectoral insertions.	68	9.2	18	8.0
Height at pectoral insertions.	78	10.6	20	8.9
Caudal peduncle:				
Width at 2nd dorsal insertion.	24	3.2	6	2.7
Height at 2nd dorsal insertion.	26	3.5	7	3.1
Pectoral fins:				
Length anterior margins.	118	16.0	31	13.8
Length posterior margins.	84	11.4	18	8.0
Length bases.	44	6.0	13	5.8
Distance from origin to free rear tip.	81	11.0	24	10.7
Length inner margins.	45	6.1	14	6.3
Claspers:				
Length outer margins.	—	—	3	1.3
Pelvic fins:				
Length anterior margins.	46	6.2	13	5.8
Length bases.	43	5.8	10	4.5
Distance from origin to free rear tip.	59	8.0	17	6.7
Height.	33	4.5	7	3.1
Length inner margins.	30	4.1	8	3.6
1st dorsal fin:				
Length anterior margin.	121	16.4	32	14.3
Length base.	157	21.3	49	21.9
Height.	67	9.1	15	6.7
Length inner margin.	32	4.3	8	3.6
2nd dorsal fin:				
Length anterior margin.	76	10.3	22	9.8
Length base.	72	9.7	20	8.9
Height.	46	6.2	11	4.9
Length inner margin.	23	3.1	6	2.7
Anal fin:				
Length anterior margin.	51	6.9	13	5.8
Length base.	50	6.8	10	4.5
Height.	27	3.7	6	2.7
Length inner margin.	19	2.6	6	2.7
Caudal fin:				
Length dorsal margin.	167	22.6	51	20.9
Length preventral margin.	57	7.7	18	8.0
Length lower postventral margin.	21	2.8	5	2.2
Length upper postventral margin.	77	10.4	21	9.4
Length subterminal margin.	32	4.3	11	4.9
Length terminal margin.	58	7.9	10	4.5
Length terminal sector.	64	8.7	16	7.2

zoidal in transverse section at eyes. Outline of head in lateral view slightly convex ventrally and undulated dorsally, with a slight concavity in front of eyes and a convexity above them (figs. 1, 2F). Head outline with prominent notches just anterior to nostrils when viewed dorsoventrally (fig. 2D–E). Dorsal surface of suborbital ridges with depressions over the nostrils and in front of eyes. Eyes dorsolaterally situated on head, without eye notches. Ends of nictitating lower eyelid attached to upper eyelid (fig. 2A). Secondary lower eyelid sharp-edged and extending below the entire length of the eye. Kinetics and morphology of the nictitating lower eyelids, secondary lower eyelids, subocular pouches, and levator nictitans muscles (see below) indicate that *Gogolia* may not be able to completely close its eyes with its nictitating lower eyelids. Spiracles large, oval, and about $\frac{1}{7}$ as long as eyes. Spiracles positioned posterior to eyes by about their own lengths and about opposite the nictitating lower eyelids. No papillose gill rakers on gill arches. Small lobes or mesonarial flaps (fig. 2B: MNF) present on the bases of the anterior nasal flaps above their tips and protruding from the nasal apertures (as in *Galeorhinus*). Low posterior nasal flaps present (fig. 2B: PNF). Mouth width about $\frac{3}{5}$ of width of head at mouth corners. No large buccal papillae in mouth. Upper labial furrows about twice as long as lower ones, with their anterior ends slightly in front of eye pupils.

Teeth showing strong gradient monognathic heterodonty in anteroposterior teeth of both jaws of adult. Teeth become proportionately longer, lower, smaller, and more oblique-cusped towards the ends of the dental bands (fig. 4). Postlateral cusplets are reduced and replaced by postlateral blades in this direction in both jaws, while premedial cusplets are replaced by undifferentiated premedial edges in the upper jaw. Ontogenic heterodonty apparently similar to that of *Hemitriakis* (Compagno, 1970), with the fetus lacking cusplets and having postlateral blades only on all of its anteroposterior teeth. Teeth not forming a pavement and hardly protruding when mouth is closed.

Body moderately slender, with trunk high and subtriangular in section at first dorsal base in adult but lower in fetus. Caudal peduncle short and nearly oval in section, not greatly compressed and without lateral dermal keels. No predorsal or postdorsal ridges present. Lateral trunk denticles with strong medial cusps and a pair of medial ridges in fetus and adult, but with lateral ridges also present in adult (fig. 3A–B). Denticle crowns have reticulated depressions on their dorsal surfaces, much as in *Iago* (Compagno and Springer, 1971, fig. 6) and many other carcharhinoids.

Pectoral fins broad and subangular, with slightly convex anterior margins, narrowly rounded apices, slightly concave posterior margins, and broadly rounded free rear tips and inner margins. Pectorals slightly smaller than first dorsal. Origins of pectorals about under 3rd gill openings. Apex of pectoral posterior to its free rear tip when fin is elevated and appressed to body.

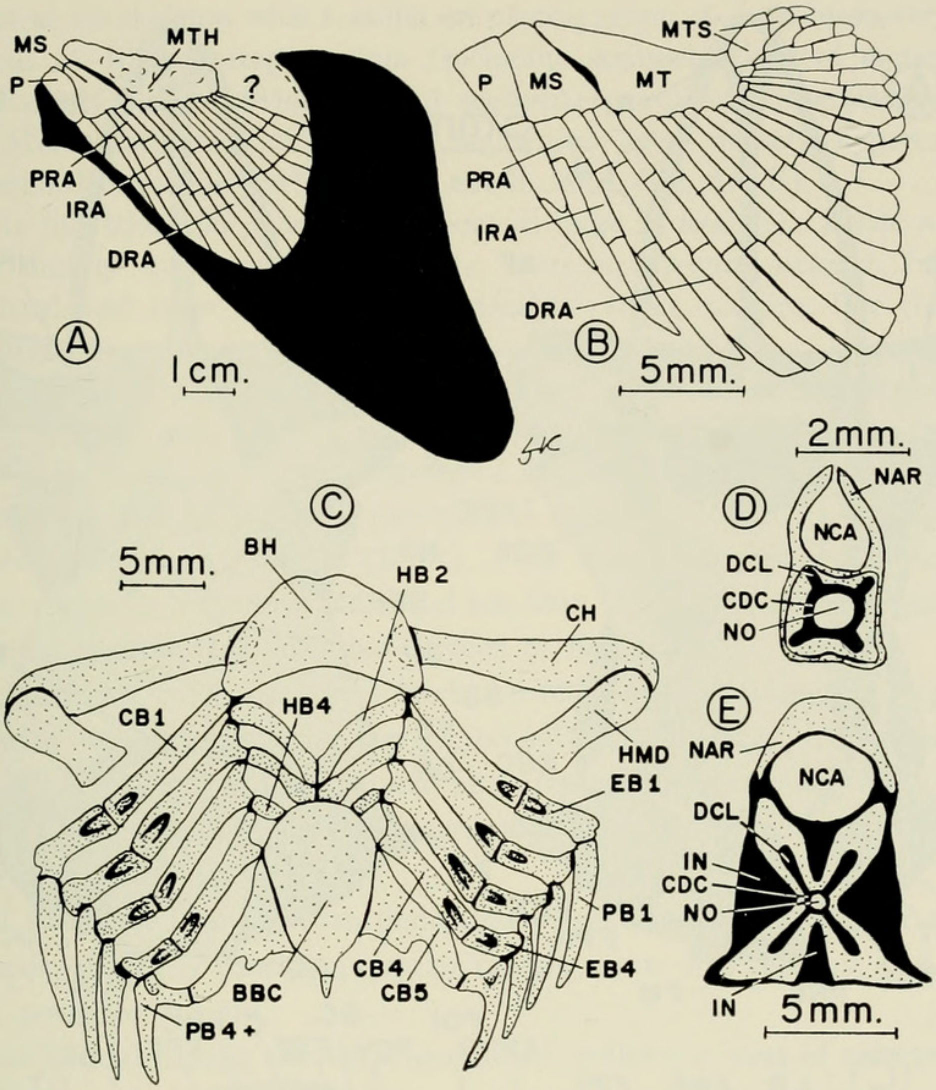

Figure 5. *Gogolia filewoodi.* A, pectoral fin skeleton of 739 mm. holotype, traced from radiograph (details of the axial segments of the metapterygium could not be distinguished), with outline of pectoral fin indicated in black. B, dissection of pectoral fin skeleton from 224 mm. fetus. C, hyobranchial skeleton (excluding hyobranchial rays and extravisceral cartilages) from 224 mm. fetus. D–E, transverse sections of MP vertebral centra from below first dorsal fin base, with sections cut through the apices of the calcified double cones of each centrum; calcified structures are in heavy black and cartilage stippled. D, centrum from 224 mm. fetus. E, centrum from 739 mm. holotype. Abbreviations: BBC, basibranchial copula; BH, basihyoid; CB 1–5, 1st to 5th ceratobranchials; CDC, calcified double cone; CH, ceratohyal; DCL, diagonal calcified lamella; DRA, distal radial segments; EB 1–4, 1st to 4th epibranchials; HB 2–4, 2nd to 4th hypobranchials (1st absent); HMD, hyomandibula; IN, intermedialia; IRA, intermediate radial segments; MS, mesopterygium; MT, basal segment of metapterygium (lightly calcified in fetus); MTH, basal segment of metapterygium (heavily hypercalcified and irregular in shape in adult); MTS, distal segments of metapterygium (metapterygial axis); NAR, neural arch; NCA, neural canal; NO, notochordal canal; P, propterygium; PB 1–4 +, 1st to 4th pharyngobranchials (4th one probably a compound element); PRA, proximal radial segments.

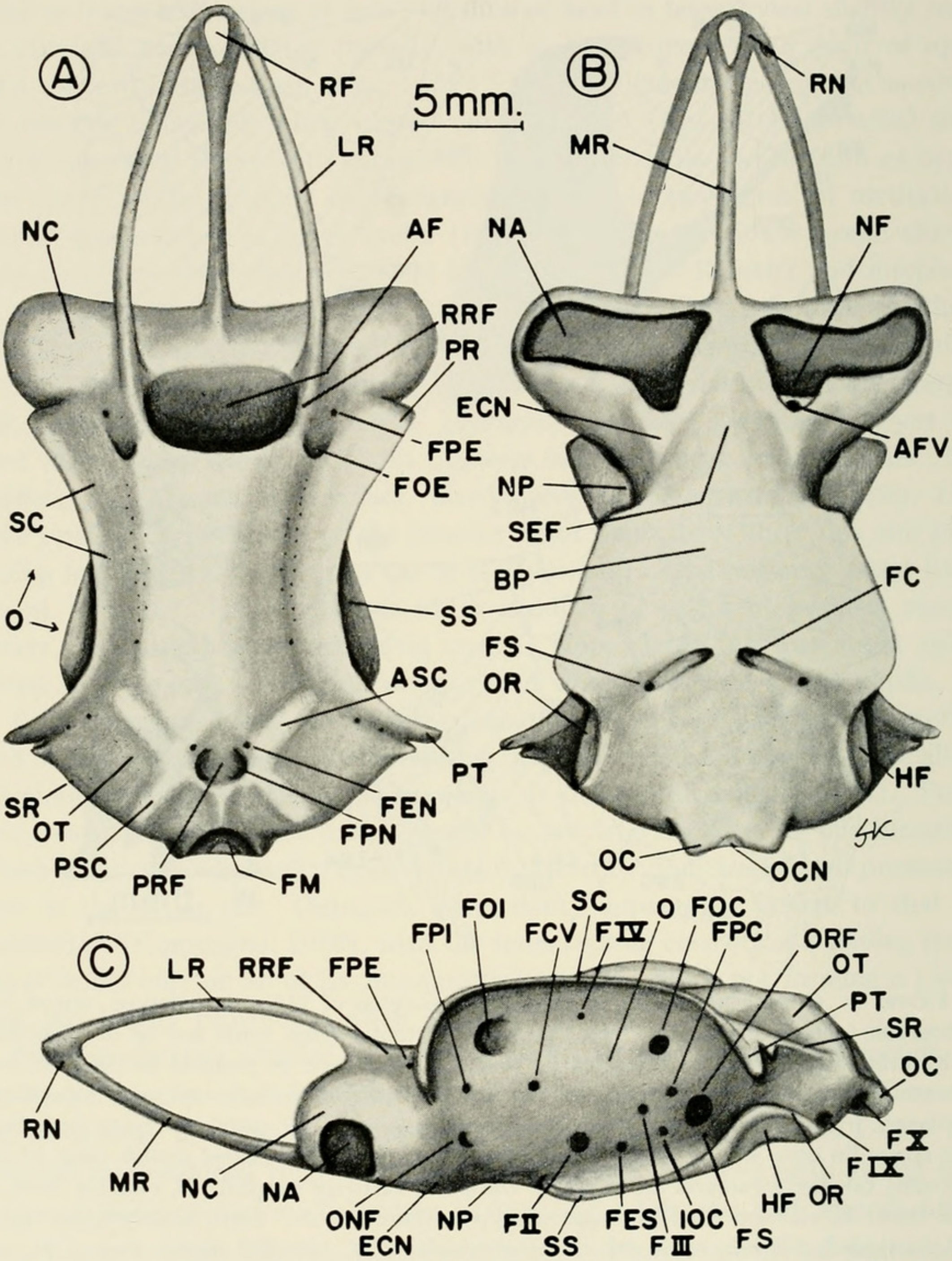

FIGURE 6. *Gogolia filewoodi*. Neurocranium dissected from 224 mm. fetus, in dorsal (A), ventral (B), and lateral (C) views. Abbreviations: AF, anterior fontanelle; AFV, position of anterior facial vein in nasal fontanelle; ASC, anterior semicircular canal; BP, basal plate; ECN, ectethmoid condyle; F II, optic nerve foramen; F III, oculomotor nerve foramen; F IV, trochlear nerve foramen; F IX, glossopharyngeal nerve foramen; F X, vagus nerve foramen; FC, foramen for internal carotid artery; FCV, foramen for anterior cerebral vein; FEN, foramen for endolymphatic duct; FES, foramen for efferent spiracular artery; FM, foramen magnum; FOC, orbitocerebral foramen for superficial ophthalmic nerve; FOE and FOI, preorbital and orbital foramina for supraorbital canal through supraorbital crest,

Pectoral fin skeleton with 1 radial on propterygium, 4–5 on mesopterygium, and about 15–16 on metapterygium (including segmented axis of metapterygium). Radials mainly divided into 3 segments: proximal, intermediate, and distal. Metapterygium (exclusive of segmented axis) densely hypercalcified and irregularly expanded in adult but not in fetus (fig. 5A–B).

Pelvic fins triangular, short, and about as large as anal fin. Pelvic anterior margins slightly convex, apices subacute, posterior margins straight, free rear tips pointed, and inner margins nearly straight. Inner margins, free rear tips, and posterior margins of pelvics forming a broad triangle.

First dorsal broadly triangular, with convex to undulated anterior margin, narrowly rounded apex, concave posterior margin, acute and attenuate free rear tip, and concave inner margin. Midpoint of first dorsal base varying from about equidistant between pectoral and pelvic bases (fetus) to about 1.6 times farther from pelvic bases than pectorals (adult). First dorsal insertion slightly anterior to pelvic origins by a distance somewhat less than the lengths of the pelvic bases. First dorsal insertion far posterior to apex of first dorsal.

Second dorsal much narrower-based and more acutely triangular than first dorsal, with undulating anterior margin, broadly rounded apex, moderately concave posterior margin, acutely pointed and attenuate free rear tip, and concave inner margin. Second dorsal origin anterior to anal origin by a distance less than ¼ of second dorsal base length.

Anal fin a low triangle, with undulated to slightly convex anterior margin, round apex, shallowly concave posterior margin, acute free rear tip, and nearly straight posterior margin.

Dorsal caudal margin convex to undulated, without a crest of enlarged denticles. Preventral margin slightly convex, tip of ventral lobe narrowly rounded, upper and lower postventral margins and subterminal margin nearly straight, and terminal margin slightly concave. Subterminal margin about 0.6–1.1 times

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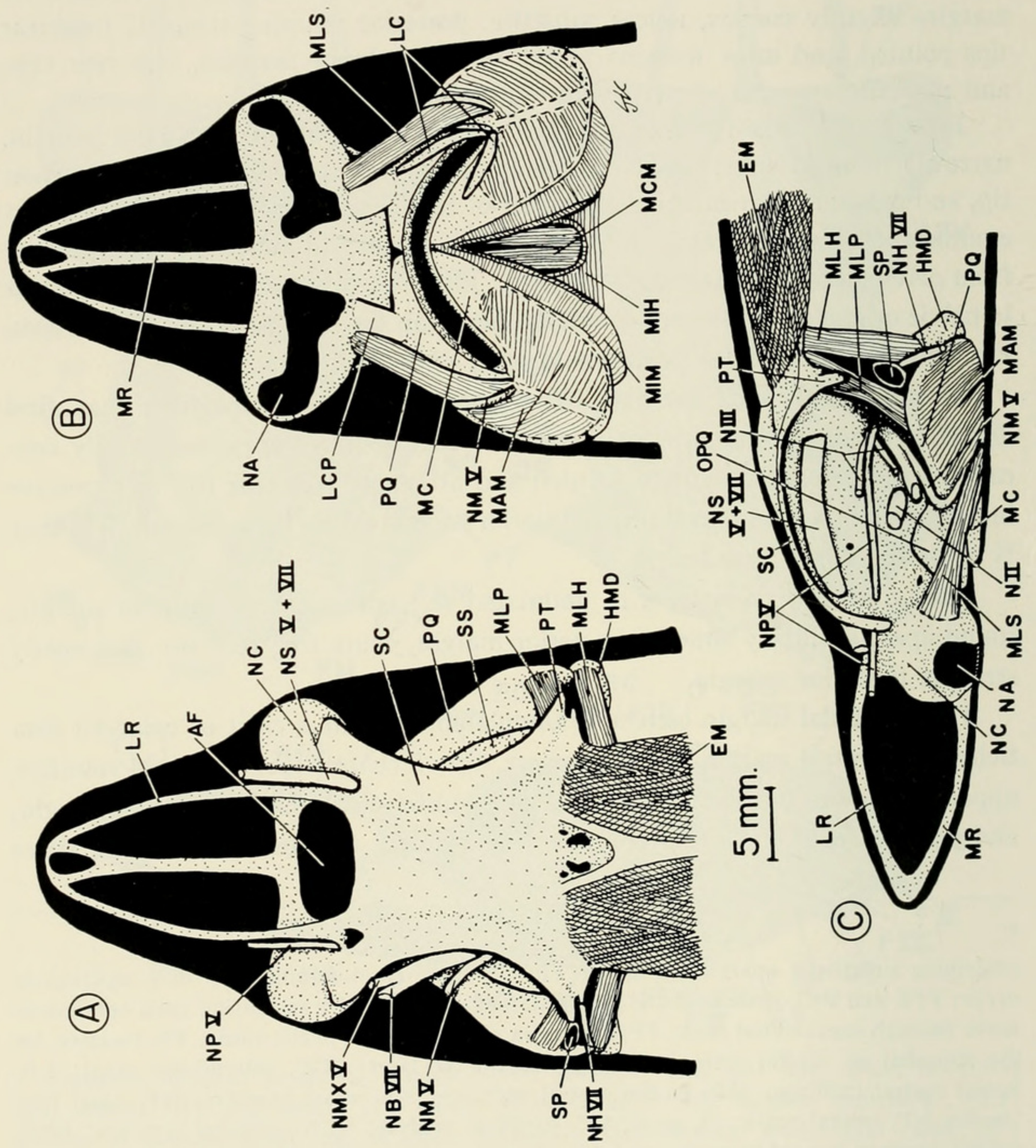
containing superficial ophthalmic nerve; FPC, orbitocerebral foramen for deep ophthalmic nerve; FPE and FPI, preorbital and orbital foramina for canal transmitting deep ophthalmic nerve through supraorbital crest; FPN, fenestra for the perilymphatic canal; FS, foramen for the stapedial or orbital artery; HF, hyomandibular facet; IOC, interorbital canal; LR, lateral rostral cartilage; MR, medial rostral cartilage; NA, nasal aperture; NF, nasal fontanelle; NP, orbital notch; O, orbit; OC, occipital condyle; OCN, occipital centrum; ONF, orbital foramen for orbitonasal canal (nasal foramen or ectethmoid chamber for the canal is inside nasal capsule); OR, opisthotic ridge; ORF, orbital fissure; OT, otic capsule; PR, preorbital process; PRF, parietal fossa; PSC, posterior semicircular canal; PT, postorbital process; RF, rostral fenestra; RN, rostral node; RRF, ridge between base of lateral rostral cartilage and edge of anterior fontanelle; SC, supraorbital crest; SEF, subethmoid fossa; SR, sphenopterotic ridge; SS, suborbital shelf.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terminal margin, relatively shorter in adult than fetus. Vertebral axis of caudal noticeably raised.

Total vertebral counts 180 (2). Counts of monospondylous precaudal (MP) centra 27.2 percent, counts of diplospondylous precaudal (DP) centra 35.0–36.7 percent, and counts of diplospondylous caudal (DC) centra 35.0–36.7 percent of total counts. Ratios of DP/MP counts 1.3–1.4, DC/MP counts 1.3–1.4, A ratios (length of penultimate MP centrum/length of first DP centrum × 100) 150–160, and B ratios (length/width of penultimate MP centrum × 100) 67–68 (methods of counting and ratios follow Springer and Garrick, 1964, and Compagno, 1970). Transition between MP and DP centra over region of pelvic fin bases. Last few MP centra before MP–DP transition not greatly enlarged.

Vertebral calcification patterns studied from transverse sections of MP centra below first dorsal base (terminology from Ridewood, 1921). Diagonal calcified lamellae very long in adult but short in fetus. Dorsal, ventral, and lateral intermedialia are present in the adult but not in the fetus (fig. 5D–E). Notochordal canal very small at apices of calcified double cones in adult (unlike adults of *Iago*) but large in fetus.

Neurocranium was dissected in the fetus (fig. 6) and studied by stereoradiographs in the adult. Cranial terminology is modified from Gegenbaur (1872), Allis (1923), Holmgren (1941), Gilbert (1967), and Compagno (1973a and b). The cranium of *G. filewoodi* is most similar to those of *Hemitriakis*, *Galeorhinus*, and *Hypogaleus*, and less like those of other triakids (the neurocranium was dissected and examined by the writer from all triakid genera except *Allomycter*). Rostral cartilages slender and not hypercalcified in adult, fused at their tips to form a fenestrate rostral node. Nasal capsules slightly wider than long, greatest transverse width across them 1.1–1.3 in nasobasal length. Anterior fontanelle horizontally oval, with its width about 3.4–3.7 in nasobasal length.

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FIGURE 7. *Gogolia filewoodi*. Head of 224 mm. fetus in dorsal (A), ventral (B), and lateral (C) views, dissected to show relation of neurocranium to jaws, jaw and hyoid muscles, and cranial nerve roots. Head outline in black. Abbreviations: AF, anterior fontanelle; EM, epibranchial myomeres; HMD, hyomandibula (distal end); LC, labial cartilages; LCP, cushioning ligament between ectethmoid condyle and orbital process of palatoquadrate; LR, lateral rostral cartilage; MAM, adductor mandibulae muscle; MC, Meckel's cartilage; MCM, coracomandibular muscle; MIH, interhyoid muscle; MIM, intermandibular muscle; MLH, levator hyomandibuli muscle; MLP, levator palatoquadrati muscle; MLS, levator labii superioris or preorbitalis muscle; MR, medial rostral cartilage; N II, optic nerve; N III, oculomotor nerve; NA, nasal aperture; NB VII, buccal ramus of facial nerve; NC, nasal capsule; NH VII, hyomandibular ramus of facial nerve; NM V, mandibular ramus of trigeminal nerve; NMX V, maxillary ramus of trigeminal nerve; NP V, deep ophthalmic ramus of trigeminal nerve; NS V + VII, supraorbital trunk or superficial ophthalmic ramus of trigeminal and facial nerves; OPQ, orbital process of palatoquadrate; PQ, palatoquadrate; PT, postorbital process; SC, supraorbital crest; SP, spiracle; SS, suborbital shelf.

Dorsal lip of fontanelle not anteriorly flared and without an epiphysial foramen. Cranial roof broadly arched between orbits. Orbital notches very prominent (fig. 6B: NP). No keels on basal plate. Internal carotid foramina closer to each other than to the stapedial foramina. Edge of supraorbital crests arcuate in dorsal view. Orbit oval in lateral view, with contents indicated in fig. 6C. No ledges between nasal capsules and suborbital shelves. Otic capsules not greatly expanded or inflated, their lengths about 3.3 in nasobasal length and the greatest transverse width across them about 1.9 in nasobasal length. Hyomandibular facets small and horizontally elongate. Occipital condyles short, with a single occipital centrum between them (fig. 6B–C: OC and OCN).

The hyobranchial skeleton was studied in the fetus by dissecting it out, staining it with methylene blue by Van Wijhe's method (Gray, 1954), and clearing it with the tricresyl phosphate-tributyl phosphate clearing solution of Groat (1941). It resembles comparable structures in other carcharhinoids examined (*Leptocharias* and *Scoliodon*) but has an unusually large and broad basihyoid and basibranchial copula (fig. 5C: BH and BBC). The hyomandibulae are short and moderately stout, the ceratohyals long and stout, and 3 pairs of hypobranchials (apparently nos. 2–4) are present.

Jaws and musculature associated with them are relatively weak (terminology for muscles follows Lightoller, 1939). Palatoquadrates and Meckel's cartilages flat and weak, with low orbital processes on palatoquadrates. The orbital processes articulate with the ectethmoid condyles on the nasal capsules and are attached to them by cushioning ligaments (fig. 7B–C: LCP and OPQ). Levator labii superioris or preorbitalis muscles small and single-headed, their origins on the sides of the nasal capsules lateral to the ectethmoid condyles and their insertions on the adductor mandibulae muscles near the mouth angles. Levator palatoquadrati muscles very slender, originating at the bases of the postorbital processes and inserting on the posterodorsolateral ends of the palatoquadrates. Levator hyomandibuli muscles very slender, originating on the sides of the otic capsules below the sphenopterotic ridges and inserting on the dorsolateral ends of the hyomandibulae. Levator nictitans short and poorly differentiated (not shown in fig. 7). Coracomandibular (fig. 7B: MCM), coracohyoid, and coracobranchial muscles very large, but branchial constrictors could not be found in the specimen examined.

Stomach divided into a moderately large fundus and a long, slender pylorus. The fundus extends posteriorly about half the length of the pleuroperitoneal cavity then reverses direction as the pylorus nearly to the base of the liver, where it connects with the valvular intestine. The intestine (fig. 2C) has 7 turns in its spiral valve. The rectum has a bulbous rectal gland attached to it by a stalk. Liver moderately large, irregularly bilobate, and extending posteriorly over ¾ of the length of the pleuroperitoneal cavity. Liver not obscuring other viscera entirely in ventral view. Spleen elongate and not nodular, with an irregularly thickened part opposite the end of the fundus and a slender anterior part extending along the pylorus. Pancreas small, located at junction of spiral intestine and pylorus. Ovary present on right side only, with follicles up to 6 mm. in diameter present. Both oviducts are developed, each having a moderately large nidimental gland.

Development ovoviviparous. The 2 fetuses (probably full-term or nearly so) were carried one to an oviduct and lacked placental connections to the mother.

Color of adult dark gray tinged with brown on dorsum, fins, and underside of head, light gray or gray-cream on abdomen and flanks. Dorsal fin edges dusky or blackish and posterior margin of pectorals light. Fetus is gray-brown above, lighter below, and dusky finned.

Summary

Gogolia filewoodi, new genus and species, is described from two specimens of triakid shark from northern New Guinea. The genus differs from other triakids in having an unusually high ratio of preoral length to mouth width, very short mouth, small gill openings, extremely long first dorsal base, and high vertebral counts. The family Triakidae is resurrected, redefined, and limited to the genera *Mustelus, Galeorhinus, Triakis, Scylliogaleus, Hemitriakis, Furgaleus, Hypogaleus, Iago, Allomycter*, and *Gogolia*. The family Carcharhinidae is confined to the genera *Carcharhinus, Scoliodon, Galeocerdo, Triaenodon, Loxodon, Hypoprion, Prionace, Aprionodon, Isogomphodon, Lamiopsis, Rhizoprionodon*, and *Negaprion*. *Hemipristis, Hemigaleus, Dirrhizodon, Chaenogaleus*, and *Paragaleus* are referred to the family Hemigaleidae, *Leptocharias* tentatively to its own family, Leptochariidae, and the 'scyliorhiniform triakoid' genera *Proscyllium, Eridacnis, Ctenacis*, and *Gollum* to the family Proscylliidae.

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