

**J.L.B. SMITH INSTITUTE OF ICHTHYOLOGY**

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*SPECIAL PUBLICATION*

No. 37

***PARAGALEUS LEUCOLOMATUS*, A NEW SHARK  
FROM SOUTH AFRICA, WITH NOTES ON THE  
SYSTEMATICS OF HEMIGALEID SHARKS  
(CARCHARHINIFORMES: HEMIGALEIDAE).**

by

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Port Elizabeth Museum

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**ABSTRACT**

*Paragaleus leucolomatus* sp.n. is described from a pregnant female shark 957 mm total length collected off Kosi Bay, Natal, South Africa. This represents the first *Paragaleus* and the second hemigaleid species recorded from South African waters. *P. leucolomatus* differs from its congeners by its broad snout, long mouth, lower anterior teeth mostly erect-cusped and without distal cusplets, 180 total vertebrae, and coloration. The species has conspicuous white-edged fins, a black apical spot on its second dorsal, and dusky blotches on the underside of its snout. *P. leucolomatus* may be conspecific with a Madagascar *Paragaleus* erroneously assigned to the West African *P. pectoralis*. Diagnoses of the Family Hemigaleidae and the Genus *Paragaleus* are presented, as well as diagnostic keys to hemigaleids of the western Indian Ocean and to *Paragaleus* species.

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In a review of sharks from the west coast of Madagascar, Fourmanoir (1961) described and illustrated a 102 cm female hemigaleid shark from 7 m depth off Nosy-Iranza (Fig. 1) and also mentioned a second specimen from Nosy-Bé, that he assigned to the West African species *Paragaleus pectoralis* (Garman, 1906). Bass et al. (1975) mentioned Fourmanoir's sharks under "*Hemigaleus* sp. (incertae sedis)", and concluded that the Madagascar sharks agreed with *Paragaleus pectoralis* as illustrated in Garman (1913), except for dentitional differences. They noted that confirmation of the identity of this shark must await the collection of further specimens from the southwestern Indian Ocean.

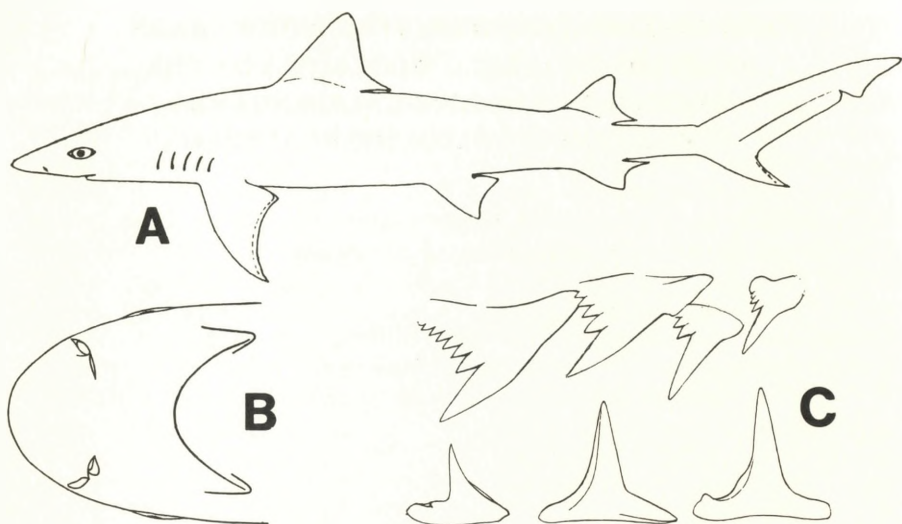


Figure 1. *Paragaleus* sp., 102 cm female from Madagascar, after Fourmanoir (1961, figs. 40-42). A, lateral view, B, underside of head, and C, teeth from right side of mouth.

In a revision of the Family Hemigaleidae, Compagno (1979) confirmed the placement of Fourmanoir's Madagascar shark in *Paragaleus* but noted that it was closest to *P. tengi* (Chen, 1963) in its mouth and snout shape and its dentition, and was definitely distinct both from *P. pectoralis* and an undescribed species of *Paragaleus* he had studied from the northwestern Indian Ocean. This species will be described elsewhere by the senior author. Compagno (1979) lacked material of the Madagascar *Paragaleus* and did not place it further.

Recently the junior author participated in a scientific cruise of the South African research vessel *Meiring Naude* in May 1984 off northern Natal. On May 18 the crew of the vessel caught a hemigaleid shark by handline approximately 1.5 km east and 2 km south of the mouth of Kosi Bay, Natal, in 20 m depth. The shark, a 957 mm pregnant female was obtained by the junior author and donated to the J.L.B. Smith Institute of Ichthyology. This represents the first South African record of a member of the genus *Paragaleus*, and the second species of the Family Hemigaleidae from South Africa. Previously Bass et al. (1975) recorded another hemigaleid, the snaggletooth shark *Hemipristis elongata* (Klunzinger, 1871), from Margate, Natal. The Kosi Bay *Paragaleus* agrees quite well with Fourmanoir's (1961) Madagascar *Paragaleus* in most details, although Madagascar specimens need to be examined to determine if the two are conspecific. In any case, the *Paragaleus* from Kosi Bay is clearly not referable to *P. pectoralis*, *P. tengi*, or to Compagno's (1979) undescribed northwestern Indian Ocean species, and apparently represents a new species, described below.

## TERMINOLOGY AND METHODS

Terminology for external structures and viscera follows Compagno (1973, 1979), Compagno & Springer (1971), and Taylor *et al.* (1983). Measurement terminology is from Compagno (1984) who assigned names and abbreviations to measurements often indicated by descriptive phrases (example: snout to upper caudal origin = precaudal length.). Dentitional terms are modified from Compagno (1970, 1979) according to a system developed by Dr. Bruce Welton of Chevron Oil Fields Research Company (Bakersfield, California) and the senior author. The major difference as used here is 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), 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). Terms for crania and head muscles and cranial measurements are from Compagno (1979) and Compagno & Garrick (1983).

Vertebrae, crania and pectoral fin skeletons were examined by radiography on the adult holotype, and one of the two fetuses was dissected to examine its neurocranium, head muscles and pectoral fin skeleton. Teeth and denticles were examined after maceration with sodium hypochlorite (NaClO).

### FAMILY HEMIGALEIDAE HASSE, 1879 WEASEL SHARKS

**DIAGNOSIS** (Following the plan of the definition of Carcharhinidae by Compagno & Garrick, 1983, and abridged from the definition of Hemigaleidae in Compagno, 1979): Carcharhiniform sharks with **HEAD** not formed into a winglike blade. **EYES** low on sides of head, subocular ridges absent or virtually so, with ventral edges of eyes reaching horizontal head rim. Eyes horizontally oval to nearly circular, often almond-shaped, and about 1.1-1.9 times as long as high. **NICTITATING LOWER EYELIDS** internal at all stages, with diagonal edges. Secondary lower eyelids strongly differentiated, continuous anteriorly and posteriorly with upper eyelid. Subocular pouches very deep, curving below eyeballs, and denticulate only on their inner faces. **SPIRACLES** small or minute and inconspicuous, with their greatest width 10-60 or more in eye length. No nasoral grooves. **ANTERIOR NASAL FLAPS** not barbel-like, expanded and narrowly triangular. Large **PAPILLAE** absent from buccal cavity, except on maxillary valve. **LABIAL FURROWS** well-developed and on both jaws. Labial cartilages moderately large.

**TEETH** well-differentiated in upper and lower jaws: upper teeth large, triangular, broad-cusped, compressed, blade-like, and with strong cusplets or coarse serrations; lower teeth smaller, narrow-cusped, not compressed, and with few or no cusplets or serrations. Teeth highly differentiated into row groups along jaws, with medials and symphysials in both jaws and variably differentiated anteriors, laterals, and posteriors. Teeth never in a pavement. Tooth rows relatively few, 25-36/28-43; functional tooth series 1-3/2-4.

Both upper and lower **PRECAUDAL PITS** present. **LATERAL TRUNK DENTICLES** have subcircular or subrhomboidal crowns, as wide as long or slightly wider than long and with 3-7 low ridges and short cusps.



**PECTORAL FIN SKELETON** plesiodic, with radials protruding about half to three-quarters or more of pectoral anterior margin length into fin. Distal pectoral radials pointed, tapering, and greatly elongated, with the longest over 3 times length of longest proximal radials.

**CLASPERS** without exorhynchia. Clasper siphons reaching at least to free rear tips of pectorals. Cover rhipidion large, hard-edged, and occupying distal third of clasper glans nearly to clasper tip. Rhipidion vestigial and apparently represented by a low, soft strip. Dorsal edges of clasper groove not fused between hypopyle and apopyle. Pseudosiphons and pseudoperae present and large.

Midpoint of **FIRST DORSAL FIN** base equidistant between pectoral and pelvic bases or slightly closer to the pectoral bases. First dorsal insertion well anterior to pelvic origins. First dorsal with distinct anterior margin, apex, and posterior margin, without a continuous arcuate edge. First dorsal height about 0.6-1.0 times its base length. **SECOND DORSAL FIN** somewhat larger than anal; height of **ANAL FIN** 0.6 to about equal to second dorsal height; anal base 0.6-0.9 of second dorsal base. Ventral lobe of **CAUDAL FIN** well-developed at all stages. Postventral caudal margin deeply notched. Dorsal caudal margin with strong undulations or ripples. Caudal axis at an angle to body axis.

**NEUROCRANIUM** with rostral cartilages always fused together at their distal tips, forming a basin-like or yoke-like rostral node. Nasal capsules spherical, oval or wedge-shaped, not greatly depressed, with nasal apertures confined to their anteroventral surfaces and separated from the mesoposterior nasal fontanelles by wide bridges of cartilage. Ectethmoid chambers separated from posterior edges of nasal fontanelles by broad ventral shelves. Nasal capsules with a pair of posteroventral ectethmoid condyles that articulate with the orbital processes of the palatoquadrates. Ectethmoid condyles without ectethmoid foramina. A deep subethmoidal fossa present between ectethmoid condyles on the ventral surface of the cranium. Pattern of arterial foramina on basal plate unique among carcharhinoids: a medial pair of foramina for the lateral aortae and a lateral pair for the efferent hyoidian arteries. No supraorbital crests connecting the separate preorbital and postorbital processes. Preorbital processes low and subquadrate; postorbital processes long and triangular.

**LEVATOR PALATOQUADRATI MUSCLES** of **JAWS** greatly expanded, with their origins extending into the orbits anterior to the postorbital processes, and their bodies extending diagonally posterolaterally to their insertions on the palatoquadrates. **VERTEBRAL CENTRA** with strong, solid, wedge-shaped intermedialia and diagonal calcified lamellae. Notochordal canal restricted or blocked at apices of calcified double cones in vertebral centra of adults and subadults. **VALVULAR INTESTINE** with a spiral valve having 4-6 turns. **REPRODUCTION** viviparous with a yolk-sac placenta of 'entire' type; umbilical cord with prominent appendiculae.

**DISCUSSION:** Compagno (1979) removed four closely related genera usually included in the family Carcharhinidae and placed them in the family Hemigaleidae: *Chaenogaleus* Gill, 1862, *Hemigaleus* Bleeker, 1852, *Hemipristis* Agassiz, 1843, and *Paragaleus* Budker, 1935. Compagno (1979) distinguished the Hemigaleidae as the primitive sister group of the Families Carcharhinidae and Sphyrnidae, differing from members of the latter families by their spiral (rather than scroll) intestinal valve, and by a number of cranial characters. The hemigaleids, with internal nictitating lower eyelids, precaudal pits and undulating dorsal caudal margin, resemble small carcharhinids, but externally are easily separable from all requiem sharks by the combination of long labial furrows, posterior eye notches present, small spiracles, narrow head and slender body, small, narrow, falcate or semifalcate pectoral fins, second dorsal fin about two-thirds height of first dorsal and with a short inner margin, and an anal fin smaller than the second dorsal.

All four genera and five of approximately seven species in this tropical Eastern Hemisphere family occur in the western Indian Ocean, but only two species are currently known from southern Africa. In view of the sketchy state of knowledge of the shark fauna of this area at present, the possibility exists that additional hemigaleid species will be found in southern African waters. Until a recent revision (Compagno, 1979) hemigaleids were poorly known and often confused with one another. Three northern Indian Ocean species were confused under *Hemigaleus balfouri* Day, 1878, although this is properly a synonym of *Chaenogaleus macrostoma* (Bleeker, 1862) (Compagno, 1979).

Recently other carcharhinoids have been found to occur far southwest of their previously known ranges in the northwestern Indian Ocean: *Mustelus mosis* Hemprich & Ehrenberg, 1899 (Triakidae), otherwise known from the Red Sea east to India and Sri Lanka, has been collected off Natal (P. C. Heemstra, *pers. comm.*, 1982); and both *Eridacnis radcliffei* Smith, 1913 (Proscylliidae), from the Gulf of Aden east to India and the western Pacific, and *Scoliodon laticaudus* Müller & Henle, 1839 (Carcharhinidae), from Pakistan east to India and the western Pacific, were recently collected off Tanzania (G. Bianchi, *pers. comm.*, 1983). In anticipation of additional hemigaleid records from southern Africa, a key to the western Indian Ocean species is provided below.

#### KEY TO SPECIES OF HEMIGALEIDAE FROM THE WESTERN INDIAN OCEAN

- 1a. Lower teeth near symphysis with large, long, strongly hooked cusps that prominently protrude from the mouth; gill openings long, 1.8-3.5 times eye length in adults .. 2
- 1b. Lower teeth near symphysis with small, short, straight or weakly hooked cusps that are concealed in the mouth or protrude slightly from it; gill openings short, longest 1.0-1.3 times eye length in adults ..... 3
- 2a. Snout bluntly rounded in dorsoventral view; lower jaw truncated at symphysis; no medial tooth rows, a toothless space between symphyseal teeth on both jaws; mesial edges of upper teeth and most lowers serrated or with a few cusplets in adults and subadults, smooth in young below 55 cm; fins strongly falcate, posterior margins of anal, second dorsal, pectorals, and pelvics deeply concave; total vertebrae 186-198 ..... *Hemipristis elongata* (Klunzinger, 1871)  
South Africa, Mozambique, Tanzania, Red Sea, Persian Gulf, Pakistan, India, Thailand, Vietnam, China, Australia, and Philippines.
- 2b. Snout obtusely wedge-shaped in dorsoventral view; lower jaw rounded at symphysis; space between symphyseal teeth filled by medial tooth rows; mesial edges of teeth not serrated; sometimes a few cusplets on lower teeth; fins not falcate or semifalcate, posterior margins of anal and second dorsal moderately concave, posterior margins of pelvics and pectorals straight or slightly concave; total vertebrae 131-139 ..... *Chaenogaleus macrostoma* (BLEEKER, 1862):  
Persian Gulf to Pakistan, India, Sri Lanka, Singapore, Thailand, Vietnam, China, Taiwan, Java, Celebes.

- 3a. Upper anterolateral teeth with short primary cusps; cusps of lower anterolateral teeth erect, with edges sloping gradually downwards towards roots, without notches separating them from crown feet; root lobes and crown feet deeply arched on lower anterolateral teeth, giving teeth an inverted Y shape; no cusplets on lower teeth; tooth row counts 25-34/37-54, 6-20 (usually over 10) more rows in lower jaw than in upper; pelvic, dorsal and caudal fins strongly falcate; 111-163 total vertebrae.....  
*Hemigaleus microstoma* Bleeker, 1852  
 Southern India and Sri Lanka, Singapore, Java, China, Taiwan, Philippines?; Australia. Possibly a species complex or series of allopatric subspecies, with western Indian Ocean and Australian specimens differing in vertebral counts and other particulars from the typical form (Stevens & Cuthbert, 1983; Compagno, 1979).
- 3b. Upper anterolateral teeth with elongated primary cusps; cusps of a few to almost all lower anterolateral teeth oblique, with edges delimited abruptly at crown feet anterolateral teeth oblique, with edges delimited abruptly at crown feet by distinct notches separating feet from cusps; root lobes and crown feet straight or nearly so on lower anterolaterals, giving teeth an inverted T shape; distal and sometimes mesial cusplets present on some lower anterolateral teeth; tooth row counts 26-30/27-33, with one less to 5 more rows in lower jaw than in upper; pelvic, dorsal and caudal fins not falcate or moderately so; 165-186 total vertebrae..... 4
- 4a. Snout narrower and usually obtusely pointed; most rows of lower anterolateral teeth with oblique cusps and distal cusplets; paired narrow black lines on underside of snout; fins not conspicuously white-edged ..... *Paragaleus* sp  
 Gulf of Oman and Persian Gulf to Pakistan, India and Sri Lanka.
- 4b. Snout broader and bluntly rounded; most lower anterolateral teeth with erect cusps and no cusplets, except distalmost 2 or 3 rows; underside of snout with dusky patches instead of black lines; fins with conspicuous white margins .....  
*Paragaleus leucomatus* sp.n.  
 Natal, South Africa; possibly Madagascar.

## GENUS *PARAGALEUS* BUDKER, 1935

*Paragaleus* Budker, 1935: 107 (Type-species: *Paragaleus gruveli* Budker, 1935 by monotypy; a junior synonym of *Hemigaleus pectoralis* Garman, 1906).

**DEFINITION:** Hemigaleid sharks with the SNOUT narrowly rounded to somewhat pointed in lateral view. MOUTH crescentic or parabolic, with its length 44-64% of width. LOWER JAW very shallow to moderately deep, its ventral edge visible in lateral view of head or not. GILL OPENINGS relatively short; third gill openings 2.6-3.1% of total length at all stages and about 1.1-1.3 times eye length in adults. Anterior ends of upper LABIAL FURROWS reaching level of posterior corners of eyes. Upper anterolateral TEETH with moderately long cusps that are noticeably longer than the distal cusplets. Lower anterolateral teeth slightly smaller than uppers. Cusps of lower anterolaterals short, stout, straight or slightly hooked, and differentiated from the crown foot by mesial and sometimes distal notches. Some or almost all cusps on lower anterolaterals oblique or semioblique. Distal and sometimes mesial cusplets



present on some lower anterolateral teeth. Lower anterolaterals protruding slightly from mouth when jaws are closed. Anterolateral teeth of lower jaw with straight, horizontal, ventral edges on root lobes and crown feet, giving teeth an inverted T shape. Lower teeth rows usually about equal in number to uppers, ranging from one row less to 5 rows more than uppers. Tooth row counts 26-30/27-33. PECTORAL FINS falcate or semifalcate, other fins not falcate or weakly so. Diplospondylous precaudal VERTEBRAE with or without a "stutter zone" of alternating long and short centra.

**SPECIES:** The definition and scope of the genus *Paragaleus* presented here follows Compagno (1979) and includes four species: *P. pectoralis* (Garman, 1906), *P. tengi* (Chen, 1963), the undescribed northwestern Indian Ocean species, and the new *P. leucolomatus*. The holotype of *P. pectoralis*, obtained from an aquarium and possibly collected off New England, was placed in *Hemigaleus* by Garman (1906, 1913), but Bigelow & Schroeder (1948) transferred it to *Paragaleus*. *Paragaleus gruvelli* from the Eastern Atlantic was separated from *P. pectoralis* by Budker (1935), but Krefft (1968) and Compagno (1979) synonymized the two. *Negogaleus longicaudatus*, described by Bessednov (1966) from the Gulf of Tonkin, appears to be a synonym of *Negogaleus tengi*, described by Chen (1963) from Taiwan and placed by Compagno (1979) in *Paragaleus*.

## PROVISIONAL KEY TO SPECIES OF *PARAGALEUS*

- 1a. 5 or more rows of lower anterolateral teeth with distal cusplets; lower anterior teeth mostly with oblique cusps ..... 2
- 1b. 2 or 3 rows of lower anterolateral teeth with distal cusplets; lower anterior teeth mostly with erect cusps ..... 3
- 2a. Mouth shorter, upper symphysis level or slightly anterior to anterior ends of upper labial furrows; prenarial snout short and rounded or obtusely wedge-shaped; total vertebrae 135-150 (n = 4); in life, sides with horizontal yellow stripes, not obvious in preserved specimens ..... *Paragaleus pectoralis*  
Cape Verde Islands and Mauritania to Angola, possibly north to Morocco, New England?
- 2b. Mouth longer, jaw symphyses extending well in front of upper labial furrows; prenarial snout long and obtusely wedge-shaped; total vertebrae 165-186 (n = 14); sides probably lacking yellow stripes .... *Paragaleus* sp.  
Northwestern Indian Ocean (Compagno, 1979).
- 3a. Total vertebrae 131-135 (n = 3); underside of snout without dusky markings; fins without conspicuous white margins ..... *Paragaleus tengi*  
Vietnam, southern China, Taiwan, Japan.
- 3b. Total vertebrae 180; underside of snout with dusky markings; fins with conspicuous white margins ..... *Paragaleus leucolomatus*, sp. n.

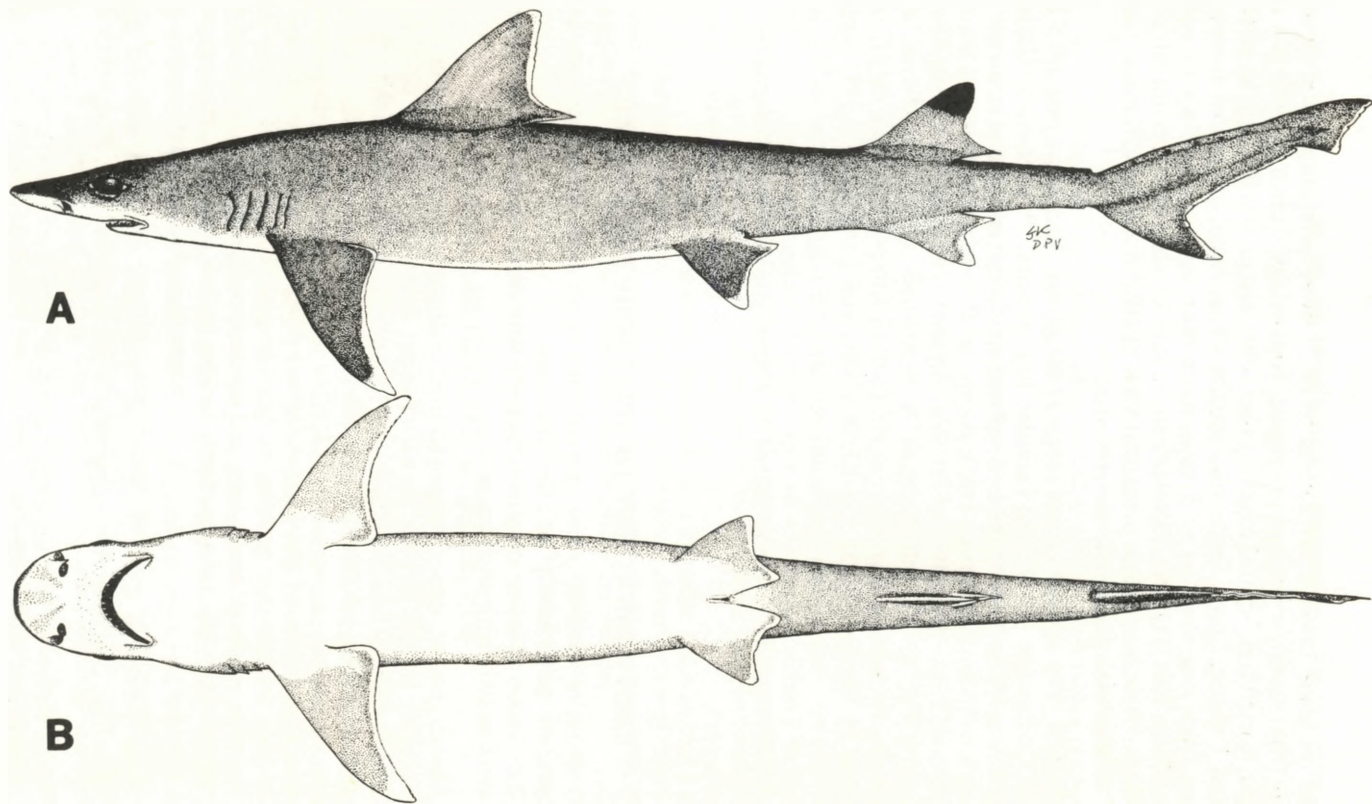


Figure 2. *Paragaleus leucolomatus*, sp. n., holotype, 957 mm pregnant female. A, lateral, B, ventral views.

***Paragaleus leucomatus*, sp. n.**

**WHITETIP WEASEL SHARK**

Figs. 2-8

**HOLOTYPE:** A pregnant female, 957 mm total length, 3.20 kg weight (including fetuses), J.L.B. Smith Institute of Ichthyology, RUSI 21175, south-east of the mouth of Kosi Bay, Natal, South Africa, 20 m depth, 18 May 1984.

**DIAGNOSIS:** A species of *Paragaleus* with a broadly rounded prenarial snout. Snout with a bluntly rounded tip in lateral view preoral snout about 1.1 times mouth width. Mouth long, jaw symphyses extending well anterior to upper labial furrows. Lower jaw relatively deep, prominently visible in lateral view. Longest gill openings about 1.1 times eye length in adult. Lower anterolateral teeth mostly erect-cusped and without distal cusplets, except for last two or three rows. Adult with pectoral fins strongly falcate, dorsals and anal fin with deeply concave posterior margins. Total vertebrae 180, 44 monospondylous precaudal centra, 53 diplospondylous precaudal centra, 83 diplospondylous caudal centra; caudal vertebrae fewer than precaudals; no "stutter zone" of alternating long and short centra in region of monodiplospondylous transition. Color: Broad dusky patches but no black lines on underside of prenarial snout; no horizontal yellow stripes on sides of body; conspicuous white tips and posterior edges on most fins; second dorsal with a black apical spot.

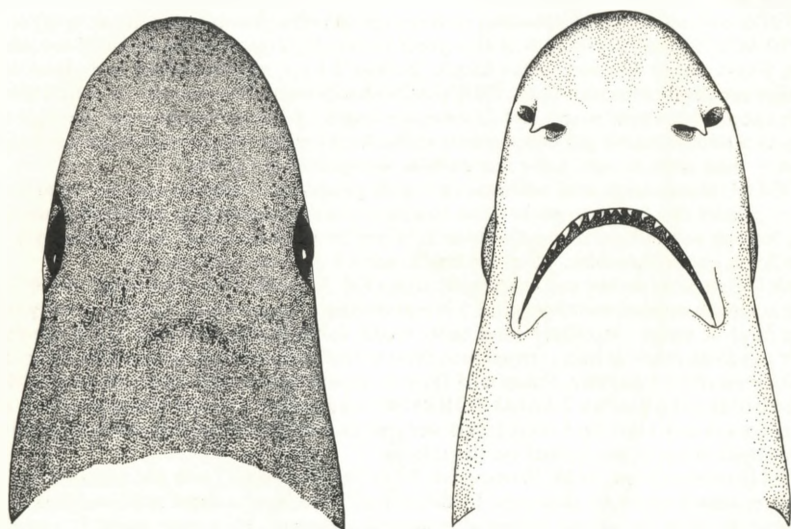


Figure 3. *P. leucomatus*, holotype, dorsal and ventral views of head.



**DESCRIPTION: PROPORTIONAL DIMENSIONS** as percentages of total length for the holotype: SNOUT TIP to various points: Precaudal length 78.0%; preorbital length 6.3; prenarial length 3.1; preoral length 6.5; prespiracular length 9.7; prebranchial length 14.5; head length to 5th gill openings 19.1; prepectoral length 17.6; prepelvic length 46.7; snout-vent length 48.6; preanal length 62.3; pre-1st dorsal length 27.6; pre-2nd dorsal length 61.8. **INTERSPACE** measurements: Interdorsal space 24.2; dorsal-caudal space 9.6; pectoral-pelvic space 24.6; pelvic-anal space 10.2; anal-caudal space 9.4. **EYE** length 2.6; eye height 1.4; interorbital space 6.6. **NOSTRIL** width 1.7; internarial space 3.6; anterior nasal flap length 0.8. **SPIRACLE** length 0.03; eye-spiracle space 0.9. **MOUTH** length: 2.8; mouth width 6.1. Upper **LABIAL FURROW** length 1.9; lower labial furrow length 1.1. **FIRST GILL OPENING (SLIT)** height 2.9; 2nd 2.9; 3rd 2.9; 4th 2.9; 5th 2.6. **HEAD** height 8.5; head width 10.2; trunk height 9.8; trunk width 8.9; caudal peduncle height 4.1; caudal peduncle width 3.8; girth 30.3. **PECTORAL** length 8.5; pectoral anterior margin 15.7; pectoral base 4.8; pectoral height 13.3; pectoral inner margin 3.6; pectoral posterior margin 11.2. **PELVIC** length 7.8; pelvic anterior margin 7.3; pelvic base 5.3; pelvic height 5.1; pelvic inner margin 2.7; pelvic posterior margin 4.5. **FIRST DORSAL** length 14.0; first dorsal anterior margin 14.1; first dorsal base 10.2; first dorsal height 8.2; first dorsal inner margin 3.7; first dorsal posterior margin 8.5. **SECOND DORSAL** length 10.6; second dorsal anterior margin 9.7; second dorsal base 7.6; second dorsal height 5.2; second dorsal inner margin 2.8; second dorsal posterior margin 5.4. **ANAL** length 8.4; anal anterior margin 7.4; anal base 5.6; anal height 3.9; anal inner margin 2.7; anal posterior margin 3.4. **Dorsal CAUDAL** margin 21.3; preventral caudal margin 10.2; lower postventral caudal margin 4.0; upper postventral caudal margin 10.4; subterminal caudal margin 3.0; terminal caudal margin 5.0; terminal caudal lobe 6.8; caudal fork 6.8.

**HEAD** length to 5th gill openings 1.3 times in pectoral-pelvic space. Head fairly narrow and flattened, roughly rectangular in shape in cross-section at eyes. Outline of head in lateral view undulated dorsally, flat above eyes but convex above gills, slightly convex ventrally along lower jaws and nearly flat beneath gills; in dorsoventral view head anteriorly rounded and posteriorly tapering along branchial region. Preoral **SNOUT** length 1.1 times mouth width. Snout tip broadly rounded in dorsoventral view (Fig. 3), not noticeably indented anterior to nostrils; snout narrowly rounded or bluntly pointed in lateral view, convex above and below.

External **EYE** opening or fleshy orbit with prominent posterior notch but no anterior ones; eyes large, length 7.3 times in head length. Eyes laterally situated on head, but with lower edges just reaching horizontal head rim in dorsal view, subocular ridges absent. **NICTITATING LOWER EYELIDS** internal, with deep subocular pouches and secondary lower eyelids fused to upper eyelids.

**SPIRACLES** unusually small for a hemigaleid and hardly larger than the ampullal and lateral line pores, length about 83 times in eye length, located 0.4 eye lengths behind and about opposite posterior eye notch. First four **GILL OPENINGS** equally wide, fifth about 0.9 of their width; width of third about 6.6 in head length and 1.1 times eye length. Edges of first three gill openings convex, first with a noticable lobe, gill filaments not visible from outside. Upper ends of gill openings about opposite lower edges of eyes. Gill-raker papillae absent from gill arches.

**NOSTRILS** with large oval incurrent apertures, prominent triangular anterior nasal flaps with acutely pointed tips, low mesonarial flaps, small oval excurrent apertures, and small posterior nasal flaps. Nostrils well in front of mouth, about 1.7 times farther from snout tip than from eyes. Nostril width 2.1 in internarial width, 1.6 in eye length, and 1.8 in longest gill-opening.

**MOUTH** broadly arched and moderately large (Fig. 3), width 3.2 in head length and 0.7 of head width at mouth corners; mouth length 2.2 in mouth width. Tongue large, flat and broadly rounded, filling floor of mouth. Maxillary valve fairly broad, width slightly less than 1/3 of eye diameter, highly papillose. No large buccal papillae on floor or roof of mouth behind maxillary valve, but with regular lines of tiny papillae. Palate and floor of mouth naked, with buccopharyngeal denticles confined to dorsal gill arches. **LABIAL FURROWS** long, uppers 1.6 times as long as lowers, anterior ends of uppers under last third of eye length and reaching about halfway from level of mouth corners to symphysis of upper jaw. Labial cartilages large.

**TEETH** relatively few, in 28/30 rows, 1-3/2-3 series functional. Teeth not arranged in diagonal files, no toothless spaces at symphysis. Teeth highly differentiated in upper and lower jaws and along jaws (Fig. 4), tooth row groups include alternates (A1), medials (M), symphyseals (S), anteriors (A), anterolaterals (AL), and posteriors (P). Tooth formula :

	P2	L9	A1	SI	A11	SI	A1	L9	P3		12--3--13
Left	-----	-----	-----	-----	-----	-----	-----	-----	-----	Right; or	-----
	P5	AL8	SI	MI	SI	AL8	P6				13--3--14

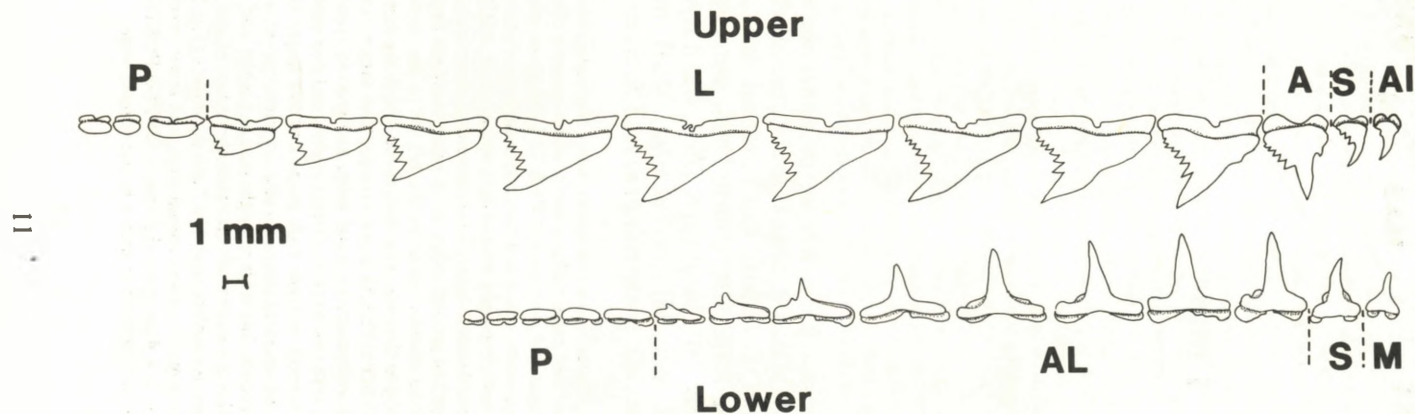


Figure 4. *Paragaleus leucomatus*, 957 mm holotype, set of detached teeth from right jaw half in labial view. Abbreviations: A, anterior, Al, alternate, AL, anterolateral, M, medial, P, posterior, and S, symphyseal tooth rows.



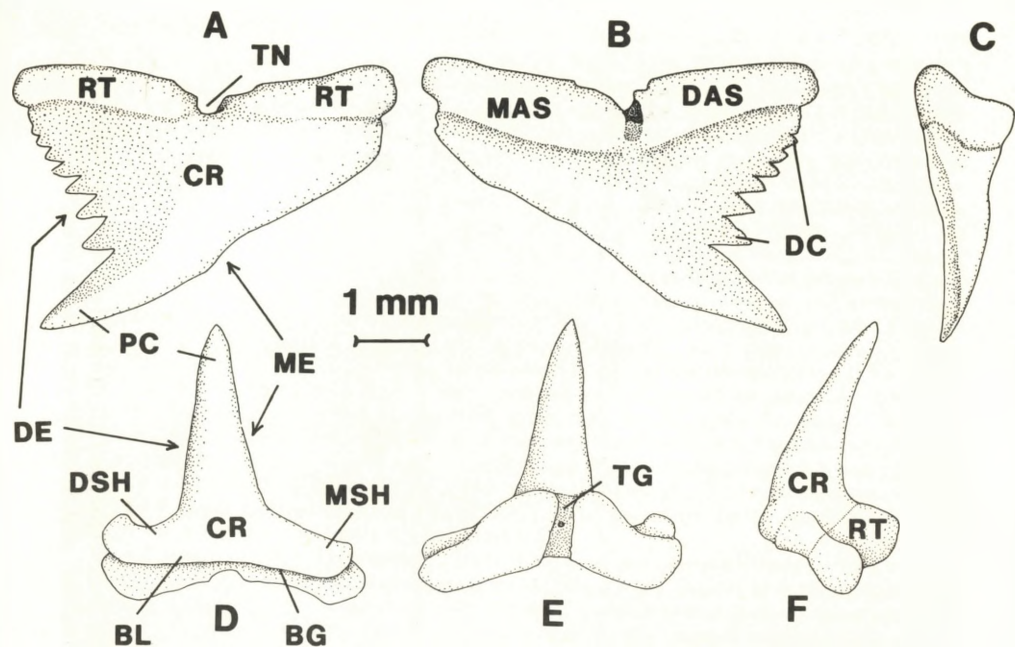


Figure 5. *P. leucolomatus*, 957 mm holotype, upper and lower teeth. A-C, 3rd upper lateral tooth in A, labial, B, lingual, and C, mesial views. D-F, 2nd lower lateral tooth in D, labial, E, lingual, and F, mesial views. Abbreviations: BG, basal groove, BL, basal ledge, CR, crown, DAS, distal attachment surface of root, DC, distal cusplets, DE, distal edge, DSH, distal shoulder, MAS, mesial attachment surface of root, ME, mesial edge, MSH, mesial shoulder, PC, primary cusp, RT, root, TG, transverse groove, TN, transverse notch.

UPPER TEETH broader, flatter, more triangular, more bladelike than lowers, and usually with well-developed distal cusplets and more oblique and broader cusps (except posteriors), unnotched mesial edges and no basal ledges and grooves; LOWER TEETH have cutting edges reduced in some anterolaterals, more erect, narrower cusps and notched mesial and distal edges (except posteriors), cusplets mostly absent, and well developed basal ledges and grooves. UPPER ALTERNATES very high, narrow cusped, narrow and small, spike-like asymmetrical teeth with one or two low cusplets on each side and a low basal ledge and groove; cusps are virtually erect and lingually hooked but their tips alternate in direction, pointing distally either to the left or to the right along the row; cusplets alternate in number according to the cusp direction, being two in the direction the cusp points and one opposite it. UPPER SYMPHYSEALS are broader and larger than alternates though still narrow, not blade-like, and asymmetrical; basal ledge and groove prominent, cusps long, nearly erect, and lingually hooked, with two to three distal cusplets and one mesial one. The single row of UPPER ANTERIORS have erect straight high cusps and are larger than the symphyseals and smaller and narrower than the adjacent laterals; these are compressed, somewhat blade-like teeth without basal ledges and grooves but with a single mesial cusplet and 5 prominent short distal cusplets. UPPER LATERALS are more blade-like than the anteriors and have an abruptly oblique, long, prominent cusp, no mesial cusplets, and 4 to 7 distal cusplets (Fig. 5); distally the laterals get smaller, thicker-cusped, with a more convex mesial edge, and fewer cusplets; from mesial to distal cusplets number 6, 7, 6, 6, 6, 5, 4, 4 on upper right teeth. UPPER POSTERIORS are low-crowned keel-like teeth without cusps or cusplets but with a broad convex edge.

LOWER MEDIALS are small, erect and straight-cusped, narrow symmetrical teeth with arched roots and crown feet and no cusplets. LOWER SYMPHYSEALS larger than medials and similar in shape, but with nearly transverse crown feet and higher cusps. LOWER ANTEROLATERALS with considerable variation along the dental band but not well differentiated, large narrow-cusped teeth with broad low crown feet and roots and strongly notched mesial and distal ledges (Fig. 5). The first row of anterolaterals is somewhat narrower footed than second through sixth and is apparently an incipient and weakly differentiated anterior. Anterolateral teeth decrease in size distally, with cusps becoming considerably lower and slightly more oblique; the first few rows have smooth mesial and distal shoulders but the distal shoulder becomes a blade with cutting edges on row 4, the proximal shoulder a blade also on row 5, and one or two low distal cusplets on teeth of rows 7 and 8. LOWER POSTERIORES similar to uppers, without cusps or cusplets and with convex broad edges, but smaller and lower-crowned than uppers and with prominent basal ledges and grooves. All TEETH with broad 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.

BODY elongate and slender, trunk vertically oval in section at first dorsal base, length of trunk from fifth gill openings to vent 1.5 times head length. A low interdorsal ridge on midline of back between dorsal fins, but without predorsal or postdorsal ridges; lateral ridges absent from body. Caudal peduncle slender, cylindrical-tapering and without lateral keels; height of caudal peduncle at 2nd dorsal insertion 1.1 times its width there and 2.4 times in dorsocaudal length. Upper and lower precaudal pits present, upper transverse and slightly crescentic.

LATERAL TRUNK DENTICLES with flat, oval crowns about as wide as long, covered with faint reticulated depressions. Crown with 3 prominent longitudinal ridges that extend the entire length of the crown onto the cusps, a short but strong medial cusp that is much shorter than the rest of the crown, and a pair of much shorter lateral cusps. Denticle crowns closely imbricated, not wide-spaced. Denticle pedicels short and thick, but elevating crowns well above skin; denticle roots with 4 lobes.

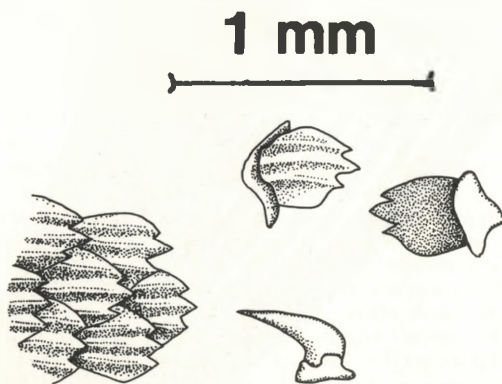


Figure 6. *P. leucolomatus*, 957 mm holotype, lateral trunk denticles from below first dorsal fin.

PECTORAL FINS narrow and falcate, with broadly convex anterior margins, acutely pointed apices, broadly concave posterior margins, broadly rounded free rear tips, convex inner margins, and narrow bases. Pectoral length from origin to rear tip 1.9 times in anterior margin length. Pectorals slightly smaller in area than first dorsal. Origins of pectorals about under interspace between third and fourth gill openings. Apex of pectoral posterior to its free rear tip when fin is elevated and appressed to body.

**PECTORAL FIN SKELETON** (Fig. 7) with radials extending about 0.6 of pectoral anterior margin length into fin. Radials mostly divided into three segments, longest distal segment 2.7 times length of its proximal segment. Pectoral skeleton tribasal, propterygium with a single radial, mesopterygium with 2 or 3 radials, and metapterygium with 9-11 radials on basal segment and 6-7 on metapterygial axis; total radial count 19-22. Propterygium short, narrow and distally elongated in the axis of its radial. Mesopterygium short, subquadrate, and elongated distally in the axes of its radials. Metapterygial basal segment triangular, elongated diagonal to the axes of its radials; metapterygial axis long, trisegmental, and with length about 2/3 of metapterygial basal segment.

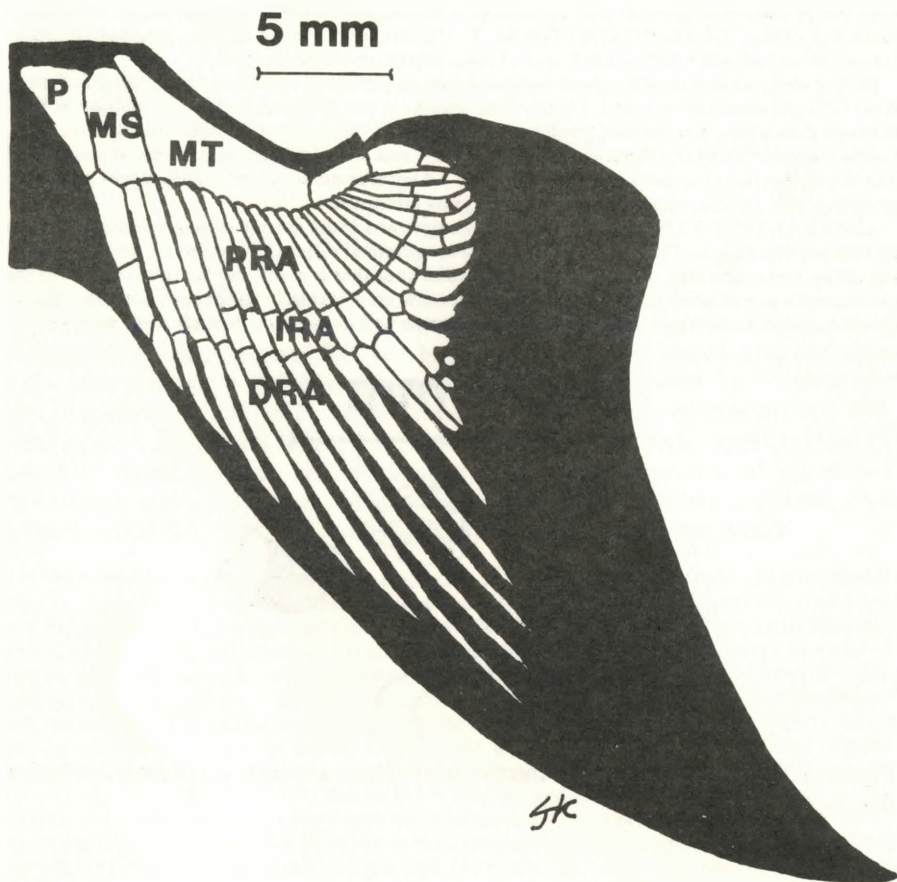


Figure 7. *P. leucolomatus*, 219 mm fetus from holotype, pectoral fin skeleton from right side in ventral view. Abbreviations: DRA, distal radials, IRA, intermediate radials, MS, mesopterygium, MT, metapterygium, P, propterygium, PRA, proximal radials.



**PELVIC FINS** triangular and semifalcate; length of anterior margins 0.47 of pectoral anterior margins; area slightly greater than anal fin. Pelvic anterior margins slightly convex, apices bluntly pointed, posterior margin broadly concave, free rear tips bluntly pointed, inner margins straight; inner margins, posterior margins, and rear tips forming a broad triangle.

**FIRST DORSAL FIN** high, apically narrow and semifalcate, with basally concave and distally convex anterior margin, narrowly rounded apex, broadly notched posterior margin, acutely pointed free rear tip, and nearly straight inner margin. First dorsal origin about opposite free rear tips of pectorals, midpoint of base 1.5 times closer to pectoral insertions than pelvic origins, and insertion and free rear tip well anterior to pelvic origins. Posterior margin slanting anteroventrally and abruptly posteriorly from apex, insertion slightly anterior to level of dorsal apex. Base 2.4 times in interdorsal space and 2.1 in dorsal caudal margin, height 1.5 times in base, and inner margin 1.9 times in height and 2.7 times in base.

**SECOND DORSAL FIN** high, apically narrow and semifalcate, height 0.6 times first dorsal height, base 0.8 times first dorsal base. Anterior margin concave basally and distally convex, apex narrowly rounded, posterior margin broadly notched, free rear tip acutely pointed, and inner margin slightly concave. Second dorsal origin well behind pelvic insertions by a space about equal to the pelvic bases and free rear tip extending slightly behind anal free rear tip but far in front of upper caudal origin. Posterior margin slanting anteroventrally and abruptly posteroventrally from apex, insertion slightly in front of dorsal apex. Base 1.3 times in dorsal-caudal space, height 1.5 times in base, and inner margin 1.9 times in height and 2.7 times in base.

**ANAL FIN** high, apically narrow, and semifalcate, height 0.7 times second dorsal height, base length 0.7 times second dorsal base. Anterior margin concave basally and distally convex, apex bluntly pointed, posterior margin broadly notched, free rear tip acutely pointed, and inner margin nearly straight. Anal base expanded anteriorly as short preanal ridges less than half length of rest of base, anal origin slightly behind second dorsal origin, anal insertion opposite second dorsal insertion, and free rear tip well in front of lower caudal origin. Anal posterior margin slanting anterodorsally and then abruptly posterodorsally, anal insertion in front of apex. Base 1.7 times in anal-caudal space, height 1.5 times in base, and inner margin 1.4 times in height and 2.1 times in base.

**CAUDAL FIN** narrow-lobed and asymmetrical, with short terminal lobe and prominent, falcate ventral lobe. Length of dorsal margin 3.6 times in precaudal length, preventral caudal margin 2.1 times in dorsal caudal margin, terminal lobe from caudal tip to subterminal notch about 3.1 in dorsal caudal margin, subterminal margin length 1.7 times in terminal margin. Dorsal caudal margin proximally and distally convex, and mesially concave, with prominent lateral undulations. Preventral margin broadly convex, tip of ventral caudal lobe pointed, lower and upper postventral margins nearly straight, notch between postventral margins forming nearly a 90 degree angle, subterminal notch a narrow, deep slot, subterminal and terminal margins slightly concave, lobe formed by these margins narrowly rounded, and tip of tail bluntly pointed.

Counts of total VERTEBRAL centra (TC) 180, monospondylous precaudal (MP) centra 44, diplospondylous precaudal (DP) centra 53, diplospondylous caudal (DC) centra 83; MP centra 24.4%, DP centra 29.4%, and DC centra 46.1% of TC centra. Ratios of DP/MP centra 1.205, DC/MP centra 1.886, 'A' ratio 182.3, 'B' ratio 104.6. Transition between MP and DP centra about over pelvic bases and just behind pelvic girdle. Last few MP centra before MP-DP transition moderately enlarged, not forming a 'stutter zone' of alternating long and short centra. Fetuses with vertebral column not sufficiently calcified to permit counts.

**NEUROCRANIUM** dissected from 219 mm female fetus; cranial MEASUREMENTS given as percentages of nasobasal length (23 mm) from base of medial rostral cartilage to occipital centrum: Length of medial rostral cartilage, 40.9%; width between bases of lateral rostral cartilages, 26.1; width across nasal capsules, 79.1; length of nasal capsule, 39.1; width of nasal capsule, 41.3; nasal aperture width, 19.6; width between nasal apertures, 32.6; length from rostral base to dorsal lip of anterior fontanelle, 43.5; anterior fontanelle height, 26.1; anterior fontanelle width, 30.4; cranial height, 50.0; basal plate width at orbital notches, 18.7; cranial roof width over orbital notches, 35.2; width across paired aortic foramina, 13.0; width across efferent hyoidian foramina, 29.6; width across preorbital processes, 68.2; preorbital process length, 8.7; orbit length, 54.8; orbit height, 37.4; width across postorbital processes, 80.4; postorbital process length, 22.6; width across suborbital shelves, 49.6; otic capsule length, 27.0; width across otic capsules, 51.3.

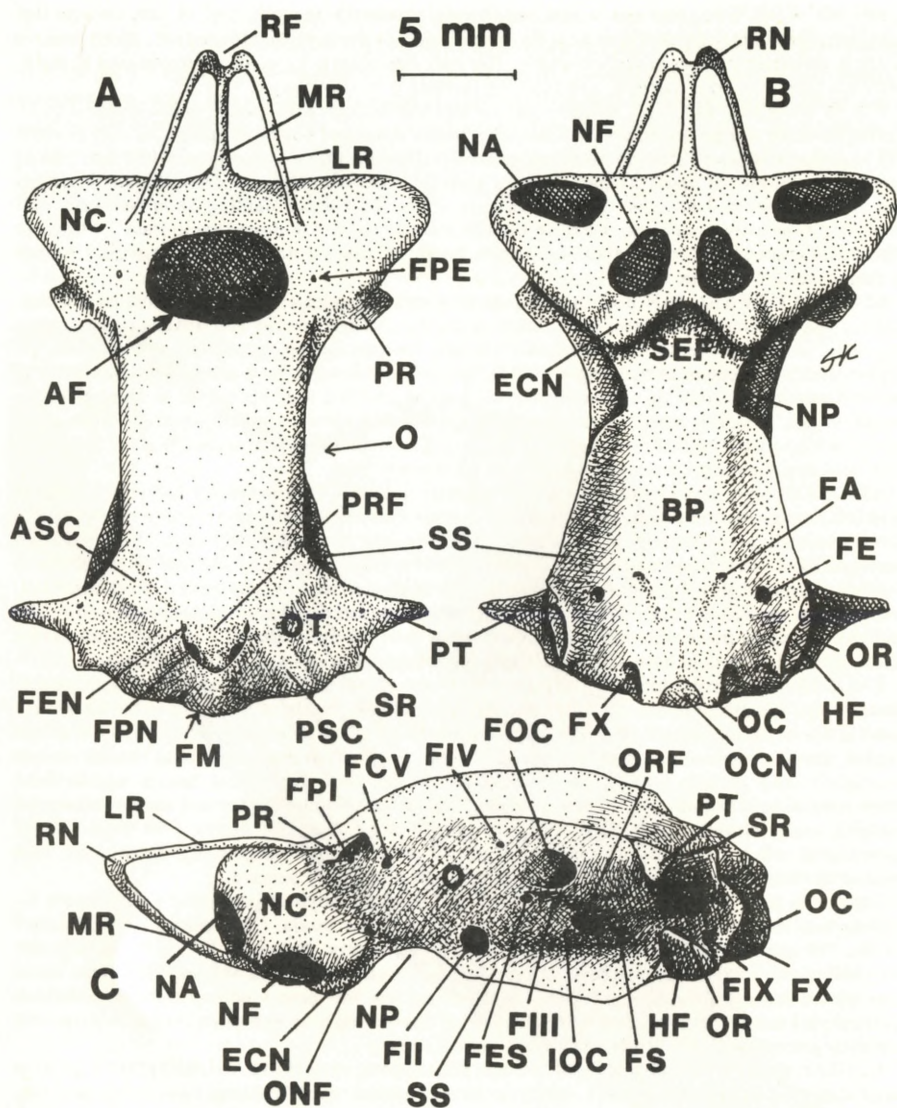


Figure 8. Neurocranium of *Paragaleus leucomatus*, 219 mm fetus from holotype, in A, dorsal, B, ventral, and C, lateral views. Abbreviations: AF, anterior fontanelle, ASC, anterior semicircular canal, BP, basal plate, ECN, ectethmoid condyle, FII, optic nerve foramen, FIII, oculomotor nerve foramen, FIV, trochlear nerve foramen, FIX, glossopharyngeal nerve foramen, FX, vagus nerve foramen, FA, foramen for paired lateral aorta, FCV, foramen for anterior



cerebral vein, FE, foramen for efferent hyoidean artery, FEN, foramen for endolymphatic duct, FES, foramen for efferent spiracular artery, FM, foramen magnum, FOC, foramen for superficial ophthalmic nerve, FPE and FPI, preorbital and orbital foramina for canal transmitting deep ophthalmic nerve through base of preorbital process, FPN, fenestra for the perilymphatic canal, FS, orbital 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, 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 (open anteriorly to form a yoke), RN, rostral node, SEF, subethmoid fossa, SR, sphenopterotic ridge, SS, suborbital shelf.

CRANIUM (Fig. 8) with slender, short ROSTRAL CARTILAGES, not hypercalcified in adult, fused at their tips to form a yoke-shaped rostral node. Length of medial rostral cartilage about 2.5 in nasobasal length, width across bases of lateral rostral cartilages about 1.6 in length of medial rostral cartilage. Bases of lateral rostral cartilages not connected to edges of anterior fontanelle by ridges. NASAL CAPSULES slightly wider than long, with nearly straight anterior edges and a rounded-wedge shape. Width of cranium across nasal capsules 1.3 in nasobasal length. NASAL APERTURES small and transversely oval, separated by a space 1.7 times their widths, NASAL FONTANELLES large and nearly oval. SUBETHMOID FOSSA narrow and V - shaped. ANTERIOR FONTANELLE nearly circular, slightly wider than long, with dorsal lip not flared and lacking an epiphysial notch or foramen. CRANIAL ROOF broadly arched between orbits. ORBITAL NOTCHES very prominent, without ledges connecting nasal capsules and suborbital shelves, transverse width across notches much less than width of cranial roof above them. No keels on BASAL PLATE. FORAMINA for PAIRED LATERAL AORTAE closer to EFFERENT HYOIDIAN FORAMINA than to each other. ORBITS nearly rectangular in lateral view, with contents indicated in Figure 8. SUBORBITAL SHELVES narrow and with anteriorly converging edges. OTIC CAPSULES not greatly expanded or inflated, with broad PTEROTIC PROCESSES. HYOMANDIBULAR FACETS small and diagonally wedge-shaped. OCCIPITAL CONDYLES short, with a single OCCIPITAL CENTRUM between them.

JAWS and associated MUSCLES weak. Palatoquadrates and Meckel's cartilages flat, with low orbital processes on the palatoquadrates articulating with the ectethmoid condyles through cushioning ethmopalatine ligaments. Preorbitalis muscles small and single-headed, originating on sides of nasal capsules lateral to ectethmoid condyles and inserting on the adductor mandibulae muscles near mouth angles. Levator palatoquadrati muscles slender, with origins expanded onto the cranial roof from beneath the postorbital processes, but occupying less than a third of the roof edge above the orbits. Levator nictitans long and well-differentiated. Levator hyomandibuli slender, originating on the sides of the otic capsules below the sphenopterotic ridges and inserting on the dorsolateral ends of the hyomandibulae.

STOMACH divided into a short fundus and a long, slender pylorus; the fundus extends posterior about 40% of length of pleuroperitoneal cavity and reverses direction as the pylorus almost to the base of the liver, where it connects to the valvular intestine. Valvular INTESTINE unusually long and narrow, extending nearly entire length of pleuroperitoneal cavity; intestinal VALVE of conicospiral type with 5 anteriorly elongated turns. Rectum with a moderately elongated, club-shaped rectal gland. LIVER strongly bilobate, with both lobes narrow and extending nearly the entire length of the body cavity, only partially obscuring other viscera. SPLEEN elongated and not nodular, with a slender part looping around the end of the fundus and a broader part extending along the

pylorus. PANCREAS small and ovoid, at junction of intestine and pylorus. OVARY present on right side only, with poorly differentiated ova. Both oviducts present, expanded into large uteri posteriorly, anteriorly with small nidamental glands.

**COLOR** when freshly thawed after two months in a freezer: dark gray on dorsal surface of head, trunk, and tail, shading to medium gray on the sides down to the pectoral and pelvic bases and underside of the prenarial snout and caudal peduncle; white on underside of head behind nostrils extending to abdomen in front of vent; no white lines or horizontal stripes on flanks. Underside of prenarial snout with a dusky medial blotch and a pair of lateral blotches, separated by narrow white areas, but without black lines. All fins mostly dark gray, including undersides of pectoral and pelvic fins, except for prominent white tips and posterior edges on first dorsal, pectoral, pelvic, and anal fins, a white tip on ventral caudal lobe and white edges on the postventral, subterminal and terminal caudal margins, and a large, abrupt black spot on upper half of second dorsal fin. Iris of eye dark gray-green, pupil not conspicuous. Fetuses differ from mother in coloration: first and second dorsals with black margins and tip, dorsal caudal margin and caudal tip also black.

**DEVELOPMENT** viviparous; holotype with one sub-term female fetus in each uterus. Lefthand fetus 215 mm long and 28 g weight; righthand fetus 219 mm long and 26 g weight. Fetuses with denticles not erupting and with first dentition not visible. Placenta of entire type, oval on an axis transverse to the umbilical cord and about 33 mm long by 15 mm wide, surrounded by shell membrane. Placenta attached to uterine wall in posteriormost fourth of uterus. Umbilical cord with minute, lobate, close-set appendiculae, cord 129 mm long on lefthand fetus.

**FOOD:** Stomach checked for food but found to be empty.

**SPECIES NAME:** Derived from the Greek words *leukos*, white, and *lomatos*, border, in allusion to the prominent white fin margins of this species.

**COMPARISON WITH OTHER SPECIES:** *Paragaleus leucolomatus* differs from other species of *Paragaleus* in its conspicuously marked fins, more deeply concave posterior margins on its dorsal and anal fins, and possibly more reduced spiracles that are hardly distinguishable from ampullal or lateral-line pores. *P. tengi* closely resembles *P. leucolomatus* in dentition, snout and mouth shape, but has 45-49 fewer vertebrae, possibly longer gill slits, less falcate pectorals, and less concave posterior margins on pelvic fins. *Paragaleus pectoralis* has a more acutely angular snout in lateral view, a shorter mouth with upper labial furrows about reaching the upper jaw symphysis, a flatter lower jaw, 5 or 6 distalmost rows of lower anterolateral teeth with oblique cusps and distal cusplets, 30-45 fewer vertebrae, and horizontal yellow lines on the sides of the body. The undescribed northwestern Indian Ocean *Paragaleus* mentioned by Compagno (1979) and to be named elsewhere by the senior author agrees with

*P. leucomatus* in its high vertebral counts (165-186 centra) but differs in its narrower, longer, more pointed snout, lower anterolateral teeth mostly with oblique or semioblique cusps and distal cusplets, less falcate fins, and in having a pair of black lines on the underside of its snout tip. Fourmanoir's (1961) Madagascar *Paragaleus* differs from the holotype of *P. leucomatus* in having more rhomboidal lateral trunk denticles with 5 or 6 ridges and keels rather than 3, possibly less falcate dorsal and anal fins, and possibly the absence of a black spot on the second dorsal, but in the absence of specimens from Madagascar and a series of *P. leucomatus*, the significance of these differences is uncertain.

**MATERIAL EXAMINED:** Abbreviations: AB, RV *Anton Bruun* field numbers, specimens at Tiburon Center for Environmental Studies, to be assigned to other institutions; GVF-HK, George Vanderbilt Foundation collection, Hong Kong material, in California Academy of Sciences. LACM, Los Angeles County Museum of Natural History; LJVC, writer's personal collection; MCZ, Museum of Comparative Zoology, Harvard; MNHN, Muséum National d'Histoire Naturelle, Paris; PCH, P. C. Heemstra field number, Sri Lanka, specimen at Tiburon Center for Environmental Studies, to be assigned to another institution; SU, Stanford University, Division of Systematic Biology, collection now housed in California Academy of Sciences; TRR, Tyson R. Roberts field number, Sri Lanka, specimen at Tiburon Center for Environmental Studies, to be assigned to another institution; UMMZ, University of Michigan Museum of Zoology; USNM, U.S. National Museum of Natural History.

*Paragaleus pectoralis*: MCZ-847, 651 mm immature female, from "Aquarial Gardens" (holotype of *Hemigaleus pectoralis* Garman, 1906); LACM-F-168, 860 mm adult male (jaws only), LJVC-0286, 885 mm adult male (skeletonized), USNM-196163, 336 mm fetal female, all from Gorée, Senegal; USNM-197626, 3 immature males, 493-540 mm, and 3 immature females, 490-553 mm, Nigeria; USNM-BBC-983, 2 fetal males, 220-224 mm, Point Guinea, Guinea. Tooth counts, vertebral counts, and measurements were contributed by Prof. J. A. F. Garrick for 3 additional specimens from Senegal: USNM-196158, 431 mm female, MNHN-36-32, 463 mm immature male (paratype of *Paragaleus gruveli* Budker, 1935), MNHN-38-28, 1380 mm pregnant female (jaws only; holotype of *Paragaleus gruveli* Budker, 1935).

*Paragaleus tengi*: GVF-HK-87, 881 mm adult male, about 100 mi. SW of Hong Kong, South China Sea; GVF-HK-83, 850 mm adult male, south of Hong Kong, South China Sea; UMMZ-177114, 784 mm adult male, East China Sea, from Nagasaki, Japan.

*Paragaleus* sp.: AB-4B-260A, 2 adult males, 685-695 mm, Ra's Musandam, Gulf of Oman; USNM-202652, 384 mm immature female, off Quilam, Kerala State, India; PCH-69-195, 811 mm pregnant female, Wadge Bank, off Cape Comorin, India; TRR-70-14, 715 mm adult male, Wadge Bank, off Cape Comorin, India; SU-67145, 615 mm maturing male, Visagapatam (Vishakhapatnam), India.

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