

**Abstract.**—Osteological differences confirm the validity of two species of *Grammatorcynus*, *G. bicarinatus* (Quoy and Gaimard 1825) and the long-recognized *G. bilineatus* (Rüppell 1836). In addition to having fewer gill rakers (12–15 vs. 18–24), a smaller eye (3.1–4.6% vs. 4.0–6.0% FL), small black spots on the lower sides of the body, and reaching a larger size (110 cm FL vs. 60 cm), *G. bicarinatus* differs from *G. bilineatus* in having a shorter neurocranium, shorter parasphenoid flanges, lower posterior edge of maxillary shank, shorter quadrate process, narrower first postcleithrum, wider ethmoid, wider vomer, wider lachrymal, longer teeth, wider palatine tooth patch, wider opercle, and a thin posttemporal shelf between the anterior processes. All but one of the 16 osteological differences previously found between *Grammatorcynus bilineatus* and *Scomberomorus* and *Acanthocybium* are confirmed with the inclusion of *G. bicarinatus* in the genus. *Grammatorcynus bilineatus* is widespread in tropical and subtropical waters of the Indo-West Pacific from the Red Sea to Tokelau Islands in Oceania. The range of *G. bicarinatus* is restricted to the western and eastern coasts of Australia and southern Papua New Guinea.

# Morphology, systematics, and biology of the double-lined mackerels (*Grammatorcynus*, Scombridae)

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Until recently, most authors considered the genus *Grammatorcynus* to be monotypic (Fraser-Brunner 1950, Silas 1963, Zharov 1967, Collette 1979). Electrophoretic work (Lewis 1981, Shaklee 1983) indicated there were two species of double-lined mackerels in Australia. This was confirmed by Collette (1983) who showed there are two species: the double-lined mackerel or scad *G. bilineatus*, (Rüppell 1836), widespread in the Indo-West Pacific, with more gill rakers (18–24), a larger eye (4.0–6.0% FL), and a smaller maximum size (60 cm FL); and the shark mackerel *G. bicarinatus* (Quoy and Gaimard 1825), restricted to the waters of northern Australia and southern New Guinea, with fewer gill rakers (12–15), a smaller eye (3.1–4.6% FL), and a larger maximum size (110 cm FL). All morphological information concerning *Grammatorcynus* in Collette (1979) and Collette and Russo (1985b) was based solely on *G. bilineatus*.

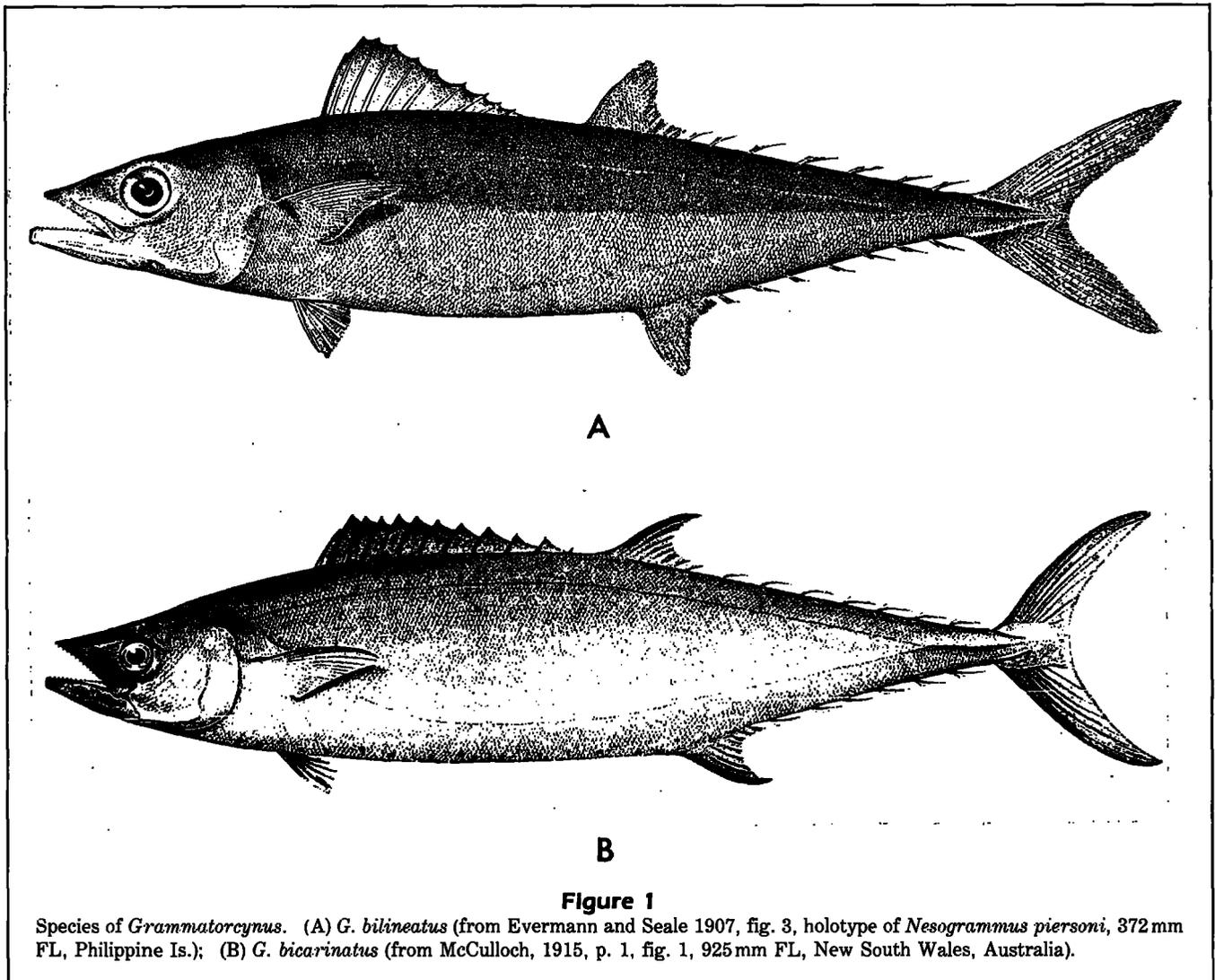
The purposes of this paper are to describe osteological differences between the two species of *Grammatorcynus*, redefine the genus and both species, and summarize the literature on both species. The paper is divided into two parts. Part 1, Comparative Morphology, contains

descriptions and illustrations of morphometry, meristic characters, soft anatomy, and osteology of the two species of *Grammatorcynus*; comparisons are made with *Scomberomorus* and *Acanthocybium* where appropriate. Part 2, Systematics and Biology, contains a generic description and accounts of both species, including synonymy, types of nominal species, diagnoses (based on characters from the first section), size, biology, interest to fisheries, geographic distribution, and material examined.

## Methods and materials

Methods are those used by Collette and Russo (1985b) in a revision of *Scomberomorus*, and by Collette and Chao (1975) in a revision of the bonitos (Sardini).

Material of *Grammatorcynus* is listed at the end of each species account; 80 specimens of *G. bilineatus* and 11 *G. bicarinatus*. Abbreviations of institutions housing the material follow Leviton et al. (1985). Comparative material of *Scomberomorus* and *Acanthocybium* was listed in the species accounts in Collette and Russo (1985b).



## Part 1: Comparative morphology

Morphological characters useful for distinguishing between species of *Grammatorcynus* and for evaluating phylogenetic relationships of the genus are divided into six categories: lateral line, color pattern, morphometry, meristic characters, soft anatomy, and osteology.

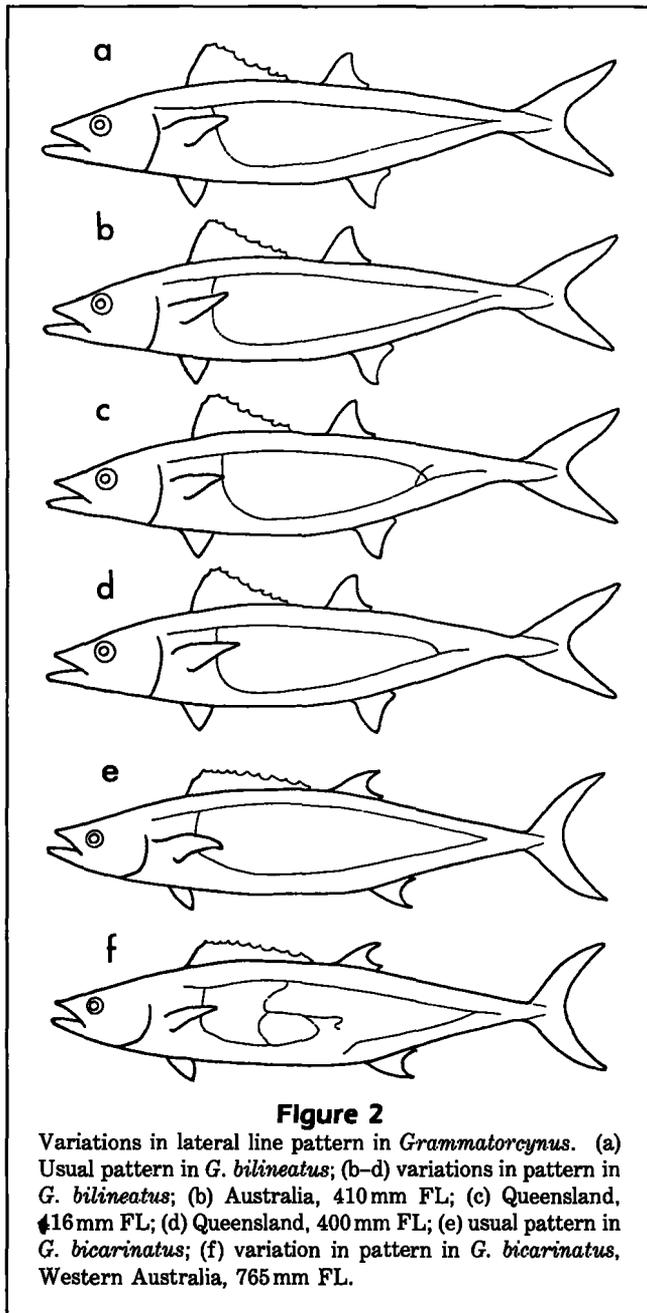
### Lateral line

The genus *Grammatorcynus* differs from all other genera of Scombridae in having two lateral lines, hence their common name, double-lined mackerels. The dorsal-most lateral line is slightly convex, originates near the dorsal portion of the opercle, and continues posteriorly until it converges with the second lateral line, just anterior to the median caudal keel. The sec-

ond lateral line originates from the first at a point below the first four spines of the dorsal fin. It starts ventrally, running under, or just posterior to, the pectoral fin, and abruptly turns into a concave line that continues posteriorly until meeting the dorsal lateral line (Fig. 1). The function of this additional lateral line is unknown. The characteristic two lateral lines are discernible in specimens as small as 56.9 mm SL (Nishikawa 1979:133). Anomalies in the pattern of the lateral lines are occasionally found, but none appear to be species specific (Fig. 2; Silas 1963:fig. 3).

### Color pattern

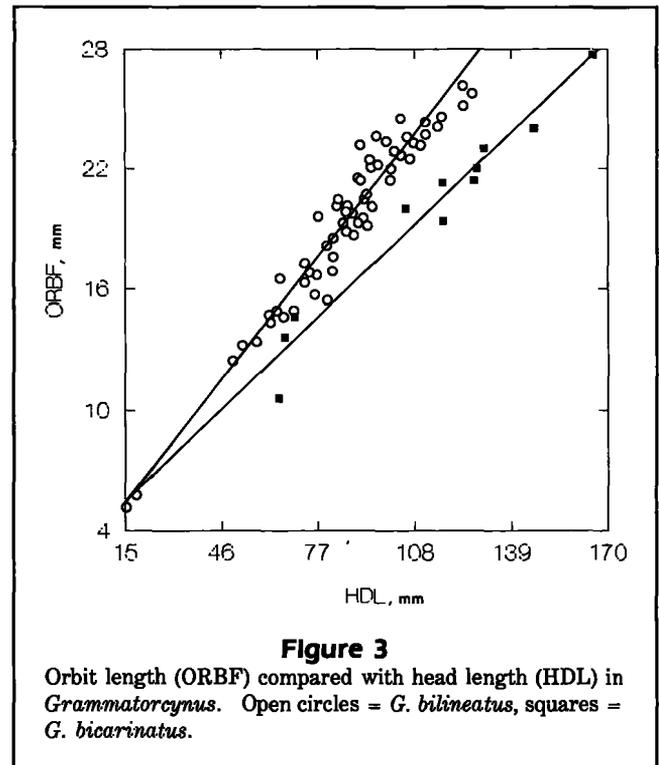
Dark spots are usually found on the ventral portion of *G. bicarinatus* (Fig. 1B). The spots are smaller than the pupil, originate near the ventral border of the oper-



culum, and continue posteriorly to the anal fin. They are found below the ventral lateral line on both sides of the fish. No spots were present in the two smallest specimens examined (AMS IB.5207-8, 306-315 mm FL). Spots are never present in *G. bilineatus* (Fig. 1A).

### Morphometric characters

In addition to fork length, 26 measurements were routinely made on all specimens. Several morphometric characters separate the two species. A summary table



shows the range and mean of all the characters as thousandths of fork length, and eight of the characters as thousandths of head length (Table 1). Scatter diagrams, with regression lines, show two of the best morphometric characters: *G. bicarinatus* has a smaller orbit (Fig. 3), and a longer first dorsal fin base (Fig. 4).

### Meristic characters

Numbers of fin rays (first dorsal spines, second dorsal rays, dorsal finlets, anal rays, anal finlets, and pectoral rays), gill rakers, and teeth on the upper and lower jaws are systematically valuable in *Grammatorcynus*. They are discussed in the relevant osteological sections of the paper.

### Soft anatomy

**Viscera** Emphasis was placed on the appearance of the viscera in ventral view, after removal of an oval segment of the belly wall. Previous descriptions of the viscera of *Grammatorcynus* include Kishinouye (1923), Silas (1963), and Collette and Russo (1985b).

The anterior end of the liver abuts the transverse septum anteriorly in the body cavity. The liver has three lobes. The right and left lobe are longer than the middle lobe, with the right lobe being longest (Fig. 5c-d). The liver is similar in shape in *Scomberomorus*,

**Table 1**  
Morphometric comparison of *Grammatorcynus bilineatus* and *G. bicarinatus*.

Character	<i>G. bicarinatus</i>					<i>G. bilineatus</i>				
	N	Min	Max	Mean	SD	N	Min	Max	Mean	SD
<b>Fork length (thousandths)</b>	10	306	325	551	186	64	226	575	408	77
Snout-A	7	596	626	613	10	61	581	641	606	13
Snout-2D	7	536	558	549	8	61	528	619	547	14
Snout-1D	9	267	301	280	11	64	276	322	295	9
Snout-P2	9	234	272	253	13	63	236	306	258	12
Snout-P1	9	197	230	216	10	63	199	245	226	9
P1-P2	10	91	255	115	49	62	90	135	101	7
Head length	10	191	223	207	9	64	197	236	218	7
Max. body depth	8	177	210	192	13	57	164	234	196	14
Max. body width	8	105	129	115	8	56	91	136	114	9
P1 length	10	118	137	127	5	63	106	142	126	8
P2 length	10	65	81	74	5	63	70	87	77	3
P2 insertion-vent	7	313	345	332	12	62	262	354	328	14
P2 tip-vent	9	238	281	260	15	61	228	275	251	10
Base 1D	9	253	272	264	6	63	207	261	235	11
Height 2D	6	97	111	103	5	54	82	116	98	7
Base 2D	10	76	102	90	8	62	68	118	102	9
Height A	10	94	116	104	8	49	67	114	94	9
Base A	9	66	91	80	8	63	73	105	87	7
Snout (fleshy)	10	77	88	81	4	64	58	90	80	5
Snout (bony)	10	64	76	70	4	64	60	80	72	5
Maxilla length	10	91	110	102	6	63	89	108	98	5
Postorbital	10	87	98	92	3	62	78	98	91	3
Orbit (fleshy)	10	31	46	37	5	64	40	60	49	4
Orbit (bony)	10	48	69	59	8	64	53	88	68	6
Interorbital	9	59	71	64	4	62	56	74	62	3
2D-caudal	9	412	475	454	27	60	427	496	470	13
<b>Head length (thousandths)</b>	11	64	165	112	33	64	50	126	89	17
Snout (fleshy)	11	379	410	393	8	64	248	397	366	21
Snout (bony)	11	313	356	340	16	64	281	357	329	16
Maxilla length	11	475	510	495	12	63	420	480	448	15
Postorbital	11	412	471	446	17	62	350	450	419	15
Orbit (fleshy)	11	164	211	179	16	64	191	257	226	14
Orbit (bony)	11	238	319	282	25	64	252	381	313	24
Interorbit	10	274	322	308	13	62	253	327	283	13

but in *Acanthocybium* the right and left lobes are about the same size. Two efferent vessels lead directly from the anterior surface of the liver into the sinus venosus.

The stomach is sometimes visible in ventral view, partially covered by the liver and caecal mass, but often completely hidden. Stomach contents included crustaceans and small fishes.

The pyloric portion of the intestine arises from the anterior end of the stomach, where the main branches of the pyloric caeca join the intestine. The caeca branch and form a dense dendritic conglomeration, the caecal mass. The intestine continues posteriorly as a simple straight tube to the anus. A straight intestine is also found in *Acanthocybium* (Fig. 5b) and *S. nipponius*, but all other species of *Scomberomorus* have folds (2 or 4) in the intestine (Fig. 5a).

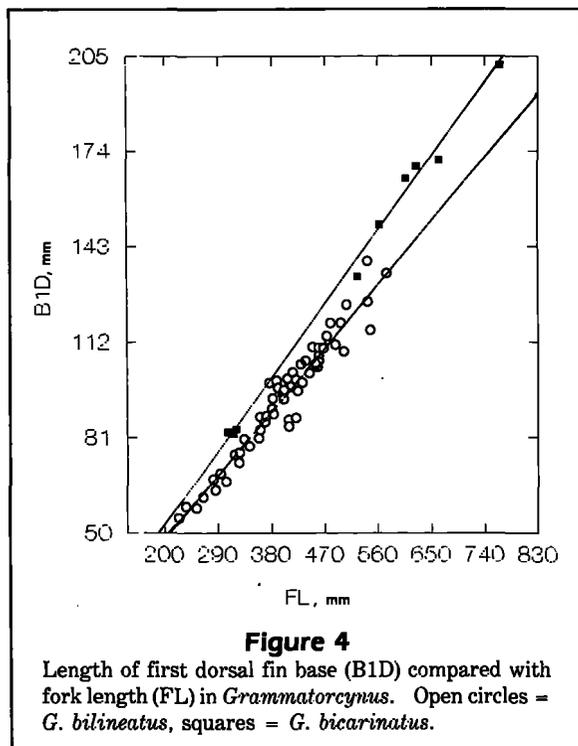
## Osteology

The osteological description is divided into five sections: skull, axial skeleton, dorsal and anal fins, pectoral girdle, and pelvic girdle. Osteological terminology and organization generally follow that of Collette and Russo (1985b).

**Skull** Description of the skull is presented in two sections: neurocranium (Figs. 6–9) and branchiocranium.

**Neurocranium** Following a general description of the neurocranium, the four major regions are discussed: ethmoid, orbital, otic, and basicranial.

**General characteristics** In dorsal view (Fig. 6), the neurocranium of *Grammatorcynus* is more or less triangular in shape, narrow at its anterior margin,



widening posteriorly. It is intermediate in shape between the elongate neurocranium of *Acanthocybium*, *Scomber*, and *Rastrelliger*, and the shorter, wider neurocranium of *Thunnus*. The posterodorsal surface is marked by a median ridge (supraoccipital crest), with two parallel ridges on either side. These five thin ridges of bone form six grooves, three on each side: dilator (very shallow), temporal (quite deep), and supratemporal (most easily seen in lateral view) (Allis 1903:49).

The median ridge originates just posterior to the thin, oval pineal foramen located between the posterior, median edges of the frontal bones. This ridge becomes larger posteriorly, and forms the supraoccipital crest. Internal or temporal ridges originate at the posterior portion of the frontals (midlevel of the orbit), continuing posteriorly to the epiotic. External or pterotic ridges also originate near the posterior margin of the frontals, continuing posteriorly to the pterotic.

Neurocrania of the two species of *Grammatorcynus* differ in size, relative to fork length. Length of the neurocranium, measured from the anterior tip of the vomer to the posterior margin of the basioccipital, is slightly longer in *G. bilineatus* (14–16% FL) than in *G. bicarinatus* (13% FL).

**Ethmoid region** This region is composed of the ethmoid, lateral ethmoid, and vomer. The nasal bone lies lateral to the ethmoid and lateral ethmoid, and, therefore, is included here.

**Ethmoid** The ethmoid (dermethmoid) has a smooth flat dorsal surface that is partially overlapped by the frontals. It connects ventrally to the vomer, posteriorly to the lateral ethmoids, and anterolaterally to the nasals. Its anterior border is nearly straight, with an anteromedian projection, unlike the relatively smooth, concave border in *Scomberomorus* and *Acanthocybium*. The ethmoid is clearly visible in dorsal view (Fig. 6), and is wider, relative to the length of the neurocranium, in *G. bicarinatus* (width 25–28% of length) than in *G. bilineatus* (19–21%).

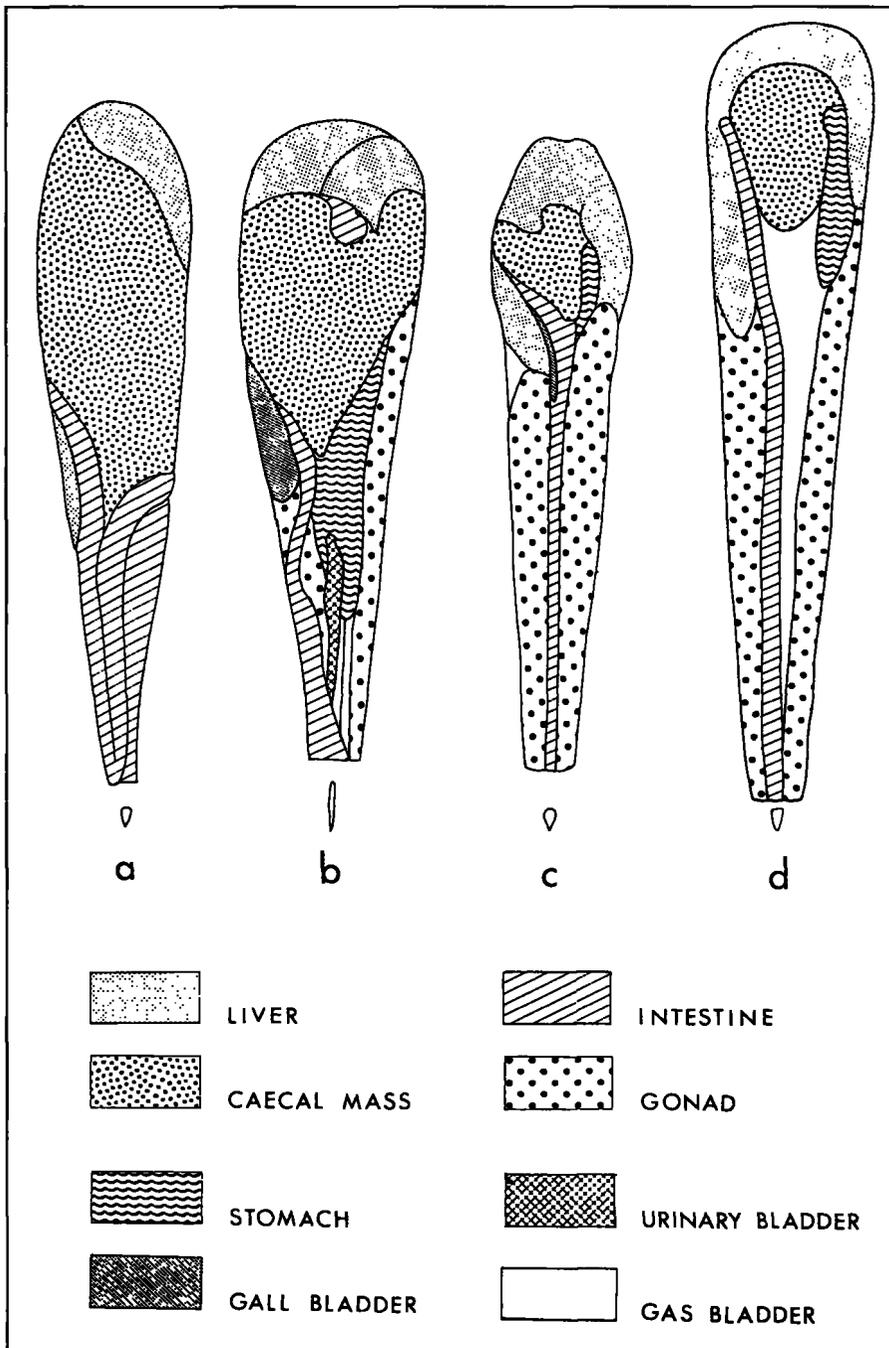
**Lateral ethmoid** The lateral ethmoids (parethmoids) are massive, paired bones that extend downward from the middle region of the frontals and form the anterior margin of the orbit and the posterior and mesial walls of the nasal cavity. The ventral surface of the lateral ethmoid bears an articulating surface for the palatine, and the posterolateral process serves as an articulation surface for the lachrymal. The lateral expansion of the bone is greater in *G. bicarinatus* (45–50% of neurocranium length) than in *G. bilineatus* (39–42%) (Fig. 8).

**Vomer** The anterior process of the vomer bears a circular or oval patch of fine teeth on its ventral surface. Its pointed posterior end is firmly ankylosed dorsally with the parasphenoid. The anterior process is wider in *G. bicarinatus* (16–18% of neurocranium length) than in *G. bilineatus* (13–15%) (Fig. 8).

**Nasal** The nasal bones are flat, elongate bones that articulate with the lateral edge of the frontals. They project out beyond the ethmoid and, from a dorsal view, reach about as far anteriorly as the vomer. There is no such projection of the nasal bones in *Scomberomorus* or *Acanthocybium*. Length divided by width is 2.8–3.4 in *Grammatorcynus*, which is intermediate between the ranges of *Scomberomorus* (2.0–3.1) and *Acanthocybium* (3.1–4.2). The anterior end of the bone forms a short, slightly angled arm. No differences were found between the nasals of the two species of *Grammatorcynus*.

**Orbital region** The orbit (Fig. 7) is surrounded by the posterior wall of the lateral ethmoid, the ventral side of the frontal, the pterosphenoid, sphenotic, prootic, suborbital, and lachrymal bones. The left and right orbits are partially separated by the basisphenoid. The sclerotic bones enclose the eyeballs.

The orbit of *G. bilineatus* is larger than that of *G. bicarinatus* (Fig. 7), reflecting the difference in orbit length (Fig. 3). The maximum height of the orbit measured from the parasphenoid to the pterosphenoid is 24–25% of neurocranium length in *G. bilineatus* vs. 16–17% in *G. bicarinatus*. Orbit length in *G. bilineatus* is 51–54% of neurocranium length vs. 47–49% in *G. bicarinatus*.

**Figure 5**

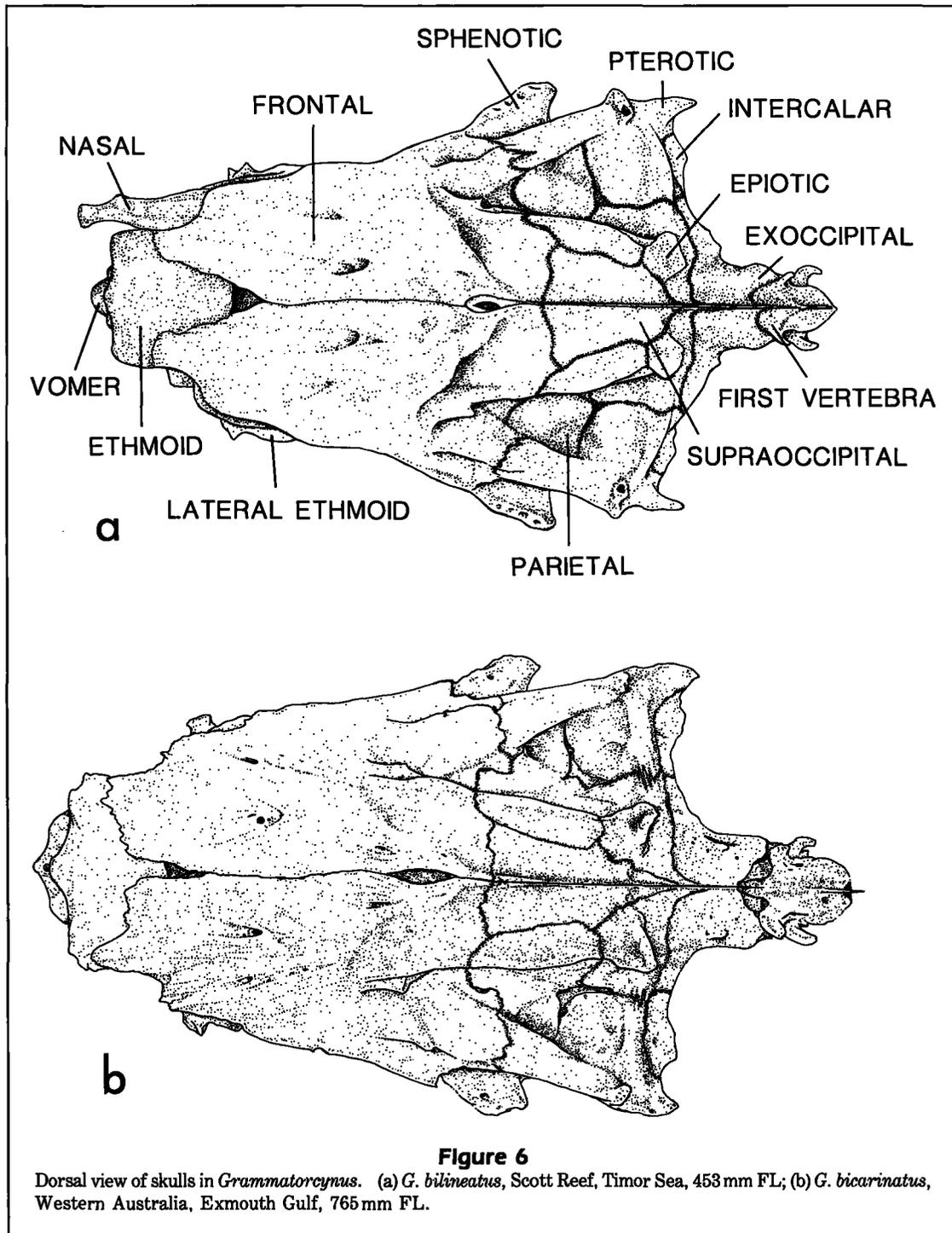
Ventral view of viscera. (a) *Scomberomorus maculatus*, Georgia, 290 mm FL; (b) *Acanthocybium solandri*, Campeche Banks, Mexico, 1280 mm FL; (c) *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL; (d) *G. bicarinatus*, Australia.

**Frontal** The paired frontals form the largest portion of the dorsal surface of the neurocranium. A small, elongate oval pineal opening is present between the posterior ends of the frontals. A larger and more irregular foramen is present in *Acanthocybium*, but *Scomberomorus* lacks this opening (Collette and Russo 1985b:figs. 11-12).

In *Scomberomorus* and *Acanthocybium*, the frontals form a median ridge that increases in height posteriorly

and joins the supraoccipital crest. *Grammatorcynus* lacks this ridge and the supraoccipital crest begins posterior to the pineal opening, giving the top of the skull a much flatter appearance than in the other two genera.

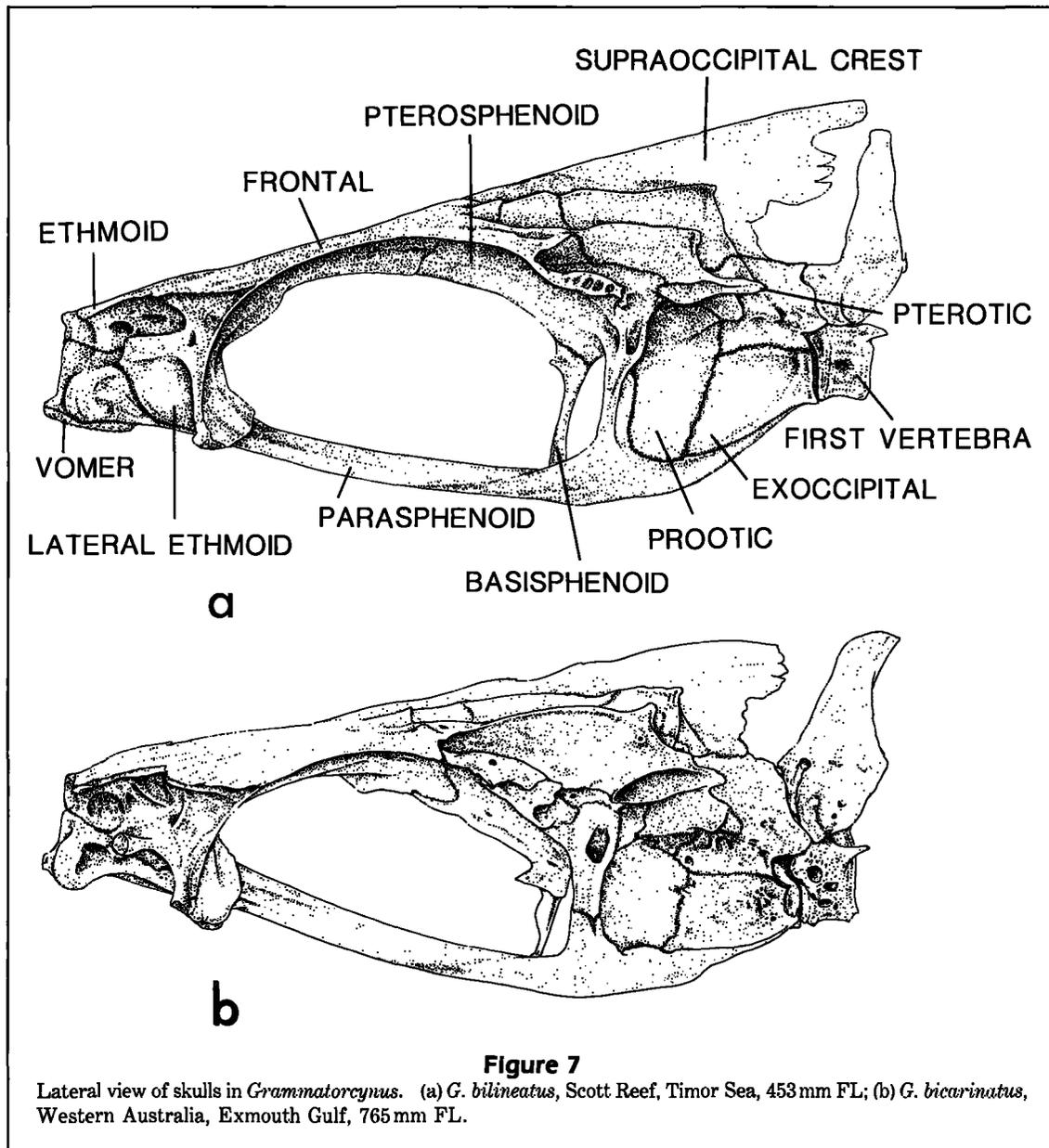
In ventral view (Fig. 8), the left and right frontals articulate with the pterosphenioids at the anterior end of a median opening into the brain cavity. The ridge around the anterior end of this space forms a point and



extends almost to the ethmoid in *G. bilineatus*. The ridge curves around the anterior end of the space and ends distinctly more posteriorly in *G. bicarinatus*. This difference cannot be seen in the ventral view of the skulls (Fig. 8) because the median part of the opening is obscured by the parasphenoid, so a separate outline

figure has been made (Fig. 9).

**Pterosphenoid** The pterosphenoids (alisphenoids) form the posterodorsal margin of the orbit. They serve as the base for the median basisphenoid, and abut the prootics posteriorly and the frontals and sphenotics laterally.



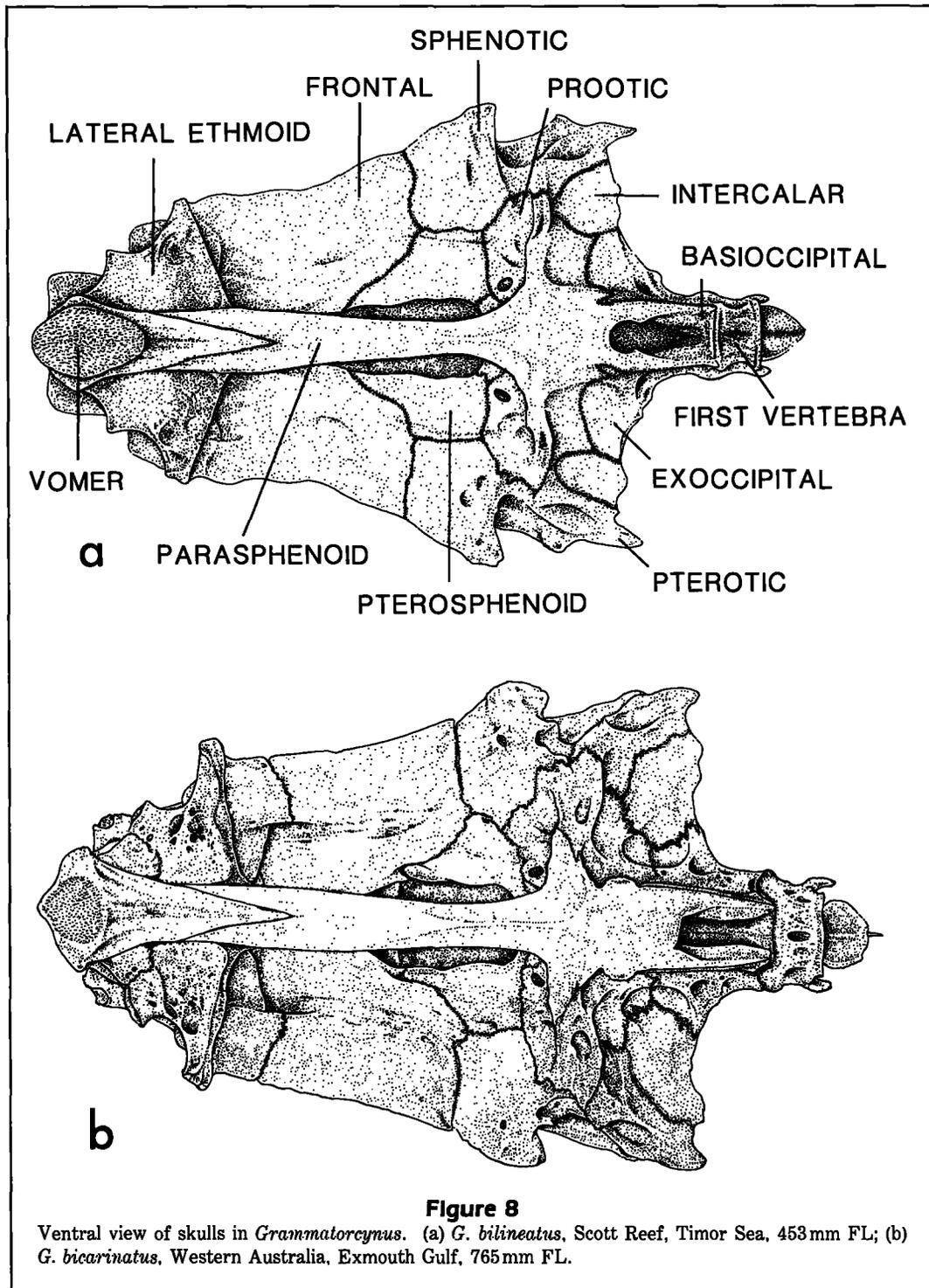
**Sclerotic** The sclerotic bones consist of two thickened, semicircular segments connected by cartilage on the inner surface and by corneal membranes on the outside. The sclerotic bones of *Grammatorcynus* are relatively larger and thinner compared with *Scomberomorus* and *Acanthocybium*.

**Basisphenoid** The basisphenoid is a small, median, Y-shaped bone that connects the prootics and pterosphenoids dorsally with the parasphenoid ventrally (Fig. 7). The dorsal compressed vertical base bears a slight anterior process, but no posterior process. This is similar to the condition in *Scomberomorus*, but the anterior process is much shorter in *Grammatorcynus*.

The basisphenoid is longer in *G. bilineatus* since the height of the orbit is greater in this species compared with *G. bicarinatus*.

**Infraorbitals** The bones of the infraorbital series (Fig. 10) enclose the infraorbital branch of the lateral sensory canal system. The canal enters the infraorbital series at what is usually considered the last element (dermosphenotic), and continues around the orbit, terminating on the first infraorbital (lachrymal).

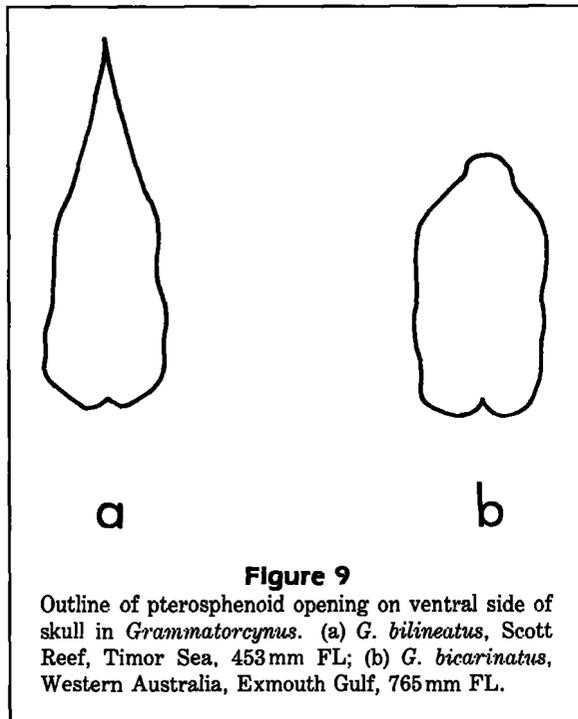
The lachrymal, the first and largest element, is elongate with a mesially-directed articular process just anterior to the middle of the bone. It covers part of the maxilla, and articulates with the lateral ethmoid



dorsally by the articular process. The process is larger in *G. bicarinatus*, making the lachrymal wider (30–35% of total bone length) than in *G. bilineatus* (27–30%). The anterior portion has a small notch in it, much more indistinct than the forked anterior region in *Scomberomorus* (Fig. 10a). The posterior region is distinct-

ly forked, with the ventral arm being wider and longer than the dorsal arm.

The second infraorbital connects to the forked posterior region of the lachrymal. It is a small, elongate bone. The third infraorbital is an elongate, tubular bone that connects to the posterior portion of the second



**Figure 9**

Outline of pterosphenoid opening on ventral side of skull in *Grammatocygnus*. (a) *G. bilineatus*, Scott Reef, Timor Sea, 453 mm FL; (b) *G. bicarinatus*, Western Australia, Exmouth Gulf, 765 mm FL.

infraorbital. It has a large, mesial, shelflike extension (subocular shelf of Smith and Bailey 1962). The fourth through penultimate elements total 13 in a specimen of *G. bilineatus* (Fig. 10c), are small, and are easily lost with cheek scales during dissection. No special effort was made to compare these bones in the two species.

**Otic region** This region encloses the otic chamber inside the skull, and is formed by the parietal, epiotic, supraoccipital, prootic, pterotic, sphenotic, and intercalar (opisthotic) bones.

**Parietals** The parietals articulate with the frontals anteriorly, the supraoccipital mesially, the pterotics laterally, sphenotics ventrally, and epiotics posteriorly. There is a short inner lateral crest on the parietals and epiotics, but this crest does not originate on the frontals as it does in *Scomberomorus* and *Acanthocybium*.

**Epiotics** The epiotics are irregular bones bounded by the parietals anteriorly, the supraoccipital mesially, the exoccipitals posteriorly, and the pterotics laterally. The medial process of the posttemporal bone attaches to a distinct roughened process on the posterior corner of the epiotic. *Scomberomorus* has a roughened area at the posterior end of the fronto-epiotic crest rather than a distinct process.

**Supraoccipital** The supraoccipital forms the dorsomedian portion of the posterior end of the neurocranium. It bears a well-developed crest that continues forward onto the parietals but stops at the pineal

opening instead of extending all the way forward onto the frontals as in *Scomberomorus*. The supraoccipital consists of a thin crest on a roughly hexagonal base. The crest extends down over the exoccipitals along the median line where the dorsal walls of the exoccipitals suture with each other. It extends posteriorly over the first vertebral centrum (Fig. 7).

**Prootics** In ventral view (Fig. 8), the prootics connect with all the bones in the posterior part of the neurocranium. Each prootic is bordered ventrally by the parasphenoid; posteriorly by the basioccipital, exoccipital, and intercalar; laterally by the pterotic and sphenotic; and anteriorly by the parasphenoid and basisphenoid. The prootics are irregular in shape and meet each other along the ventromedian line of the brain case to form the posterior portion of the myodome.

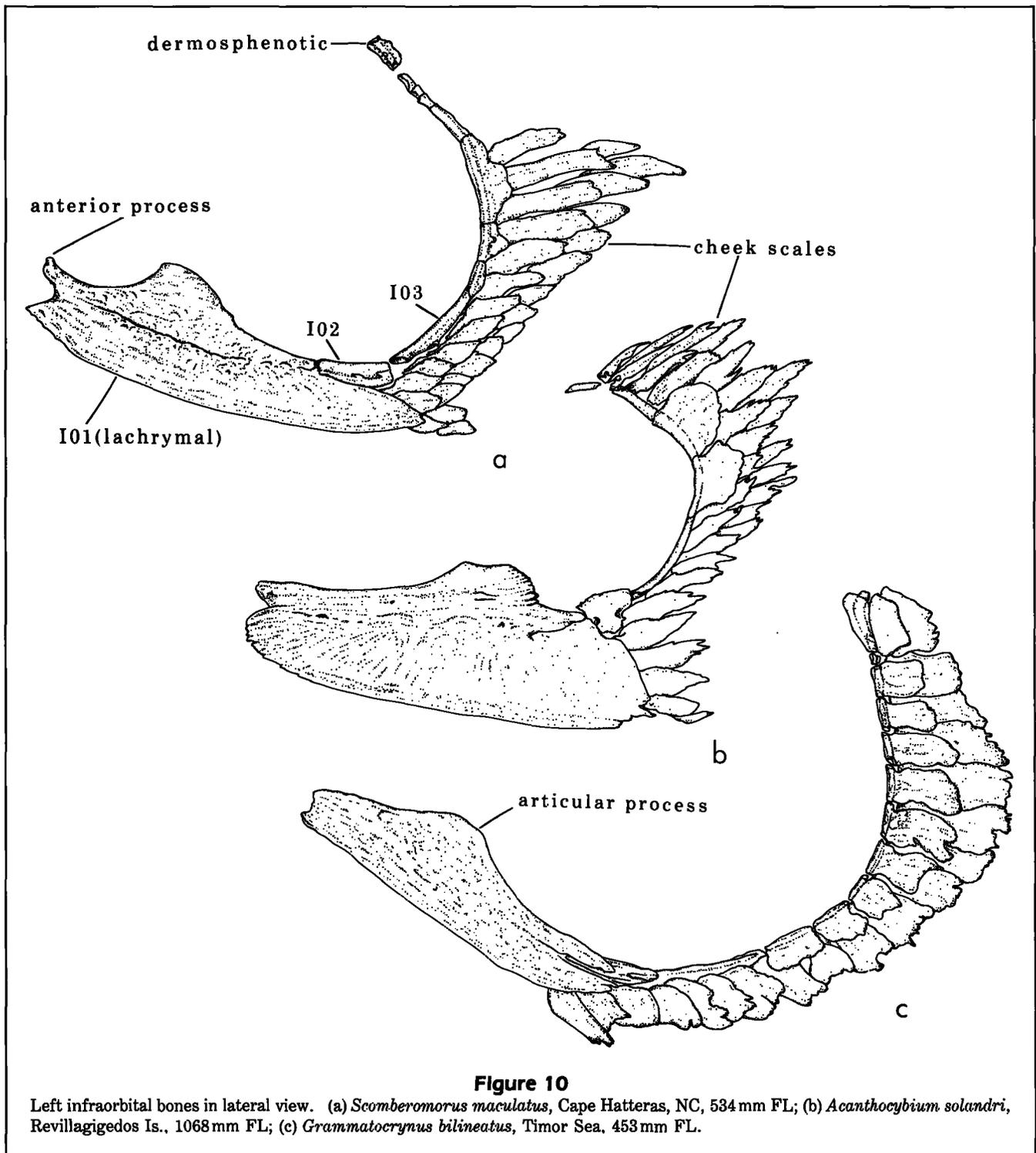
**Pterotics** The pterotics form the lateral posterior corners of the neurocranium. Each pterotic is produced posteriorly to form a spine. A pterotic ridge continues anteriorly onto the parietal, but does not extend onto the posterior part of the frontal as it does in *Scomberomorus*. In ventral view (Fig. 8), the pterotics articulate with the sphenotics anteriorly and the prootics and intercalars medially.

**Sphenotics** The sphenotics form the most posterior dorsolateral part of the roof of the orbit. They continue the outer lateral shelf from the frontals, and articulate with the pterosphenoid medially and the prootic and pterotic posteriorly. A fossa at the juncture of the sphenotic and pterotic receives the anterior condyle of the hyomandibula. In dorsal or ventral view, the distance between the tips of the two sphenotics is the widest portion of the cranium, 60–67% the length of the neurocranium in *Grammatocygnus*.

**Intercalars** The intercalars (opisthotics) are flat bones that form part of the posterior border of the neurocranium interposed between the pterotics and exoccipitals. The anterior portion on the dorsal surface is concealed by the overlapping pterotic, thus exposing the bone on the dorsal surface less than on the ventral surface (compare in Figures 6 and 8). Each intercalar has a roughened area on its dorsal surface to receive the lateral arm of the posttemporal. There is no posterior projection from the intercalars in *Grammatocygnus* or *Acanthocybium* as there is in eight species of *Scomberomorus*, such as *S. commerson* and *S. concolor* (Collette and Russo 1985b:figs. 11a and 12b).

**Basicranial region** This region consists of the parasphenoid, basioccipital, and exoccipital bones, and forms the posteroventral base of the skull.

**Parasphenoid** The parasphenoid is a long, cross-shaped bone. It articulates with the vomer anteriorly and forms the ventral axis of the skull. It also



forms the ventral border of the orbits and connects with the lateral ethmoids, basisphenoid, prootics, and basioccipital bones dorsally. The lateral wings of the parasphenoid extend dorsolaterally along the ventral ridge of the prootic bones on either side, and have

pointed ends which form part of the anteroventral wall of the posterior myodome. Posteriorly, the parasphenoid bifurcates into two lateral flanges that attach dorsally to the corresponding posteroventral flanges of the basioccipital bone, and surround the posterior

opening of the posterior myodome. These flanges are longer in *G. bilineatus* (18–21% of neurocranium length) than in *G. bicarinatus* (14%), making the posterior opening of the posterior myodome larger in *G. bilineatus* (Fig. 8). A ventrally projecting median keel is present in the area anterior to the origin of the lateral flanges. In ventral view, the parasphenoid narrows posteriorly until near the region of the median keel, where it widens slightly before the lateral wings. The anterior portion and the region just anterior to the lateral wings are about equal in width. In *Grammatorcynus*, the shaft of the parasphenoid is narrower than that of *Scomberomorus* and *Acanthocybium*. In *G. bilineatus*, the contour of the parasphenoid is concave, making the orbit larger than in *G. bicarinatus*, in which the parasphenoid is flat (Fig. 7).

**Basioccipital** The basioccipital has lateral flanges on either side of the skull and forms the roof and lateral walls of the posterior myodome. The lateral flanges expand ventrally to meet the flat posterior flanges of the parasphenoid. Anteriorly, the basioccipital is attached to the prootics and dorsally with the exoccipitals. The first vertebral centrum attaches to the posterior surface of the basioccipital.

**Exoccipital** The exoccipitals connect the skull with the first vertebra dorsally. The exoccipital articulates with the epiotic and supraoccipital bones anterodorsally, the intercalars laterally, and with the other exoccipital posterodorsally. In ventral view, the exoccipital articulates with the prootic anteriorly, basioccipital ventromedially, and intercalar laterally. In posterior view, the foramen magnum is framed by the exoccipitals.

**Branchiocranium** The branchiocranium is divided into five sections: mandibular arch, palatine arch, hyoid arch, opercular apparatus, and branchial apparatus.

**Mandibular arch** The mandibular arch is composed of the upper jaw (premaxilla, maxilla, and supramaxilla) and the lower jaw (dentary, angular, and retroarticular). Teeth are borne on the premaxilla and dentary, and the number of teeth on these bones differs between species.

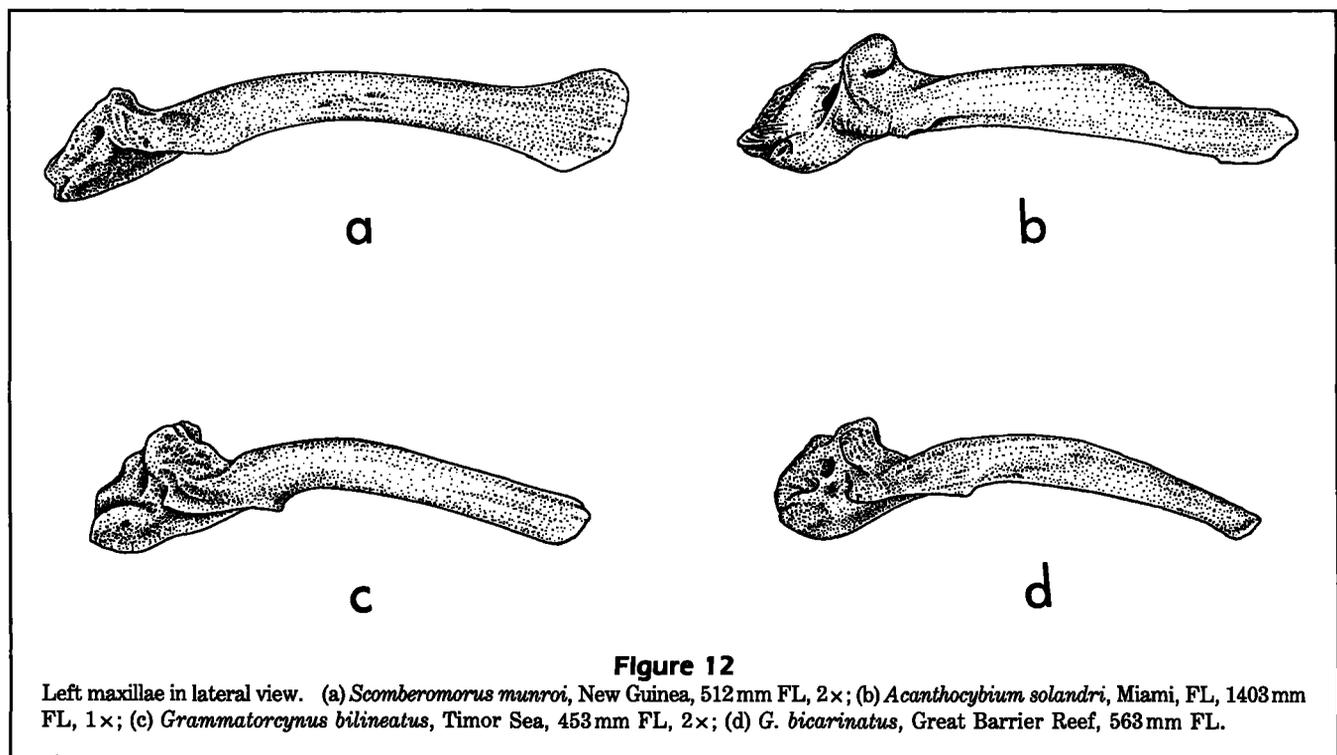
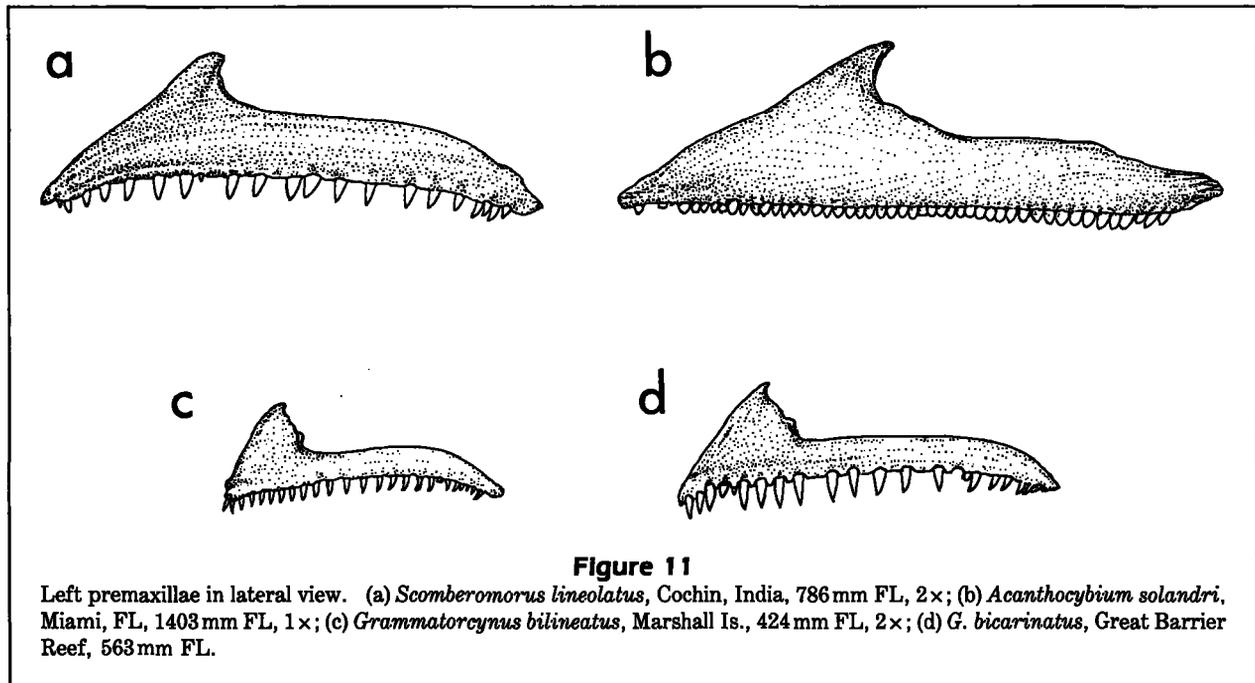
**Dentition** Long, thin, slightly laterally compressed teeth are present in a single row in the upper and lower jaws of *Grammatorcynus*. *Scomberomorus* has large, triangular, laterally compressed teeth similar to those of *Acanthocybium*, which

are blunter and more tightly compressed. The length of the jaw teeth differs between the species: *G. bicarinatus* has longer teeth than *G. bilineatus* (maximum length 6% vs. 4% dentary length). The number of jaw teeth in *Grammatorcynus* also varies. Teeth are often broken or lost, so the range in mean tooth count may not reflect accurately the actual number of teeth. However, the maximum number of teeth is useful. *Grammatorcynus bicarinatus* has a lower maximum tooth count on its upper jaw than *G. bilineatus* (25 vs. 37), and the same is true of the lower jaw, (23 vs. 32; Table 2). The maximum number of jaw teeth present in *Scomberomorus* is slightly higher than *G. bilineatus* (39, range 5–39 in the upper jaw; and 37, range 4–37 in the lower jaw). Collette and Russo (1985b) noted that in *Scomberomorus*, the species with the fewest teeth has the fewest gill rakers and the species with the most teeth has the most gill rakers. There is a similar correlation in *Grammatorcynus*: *G. bilineatus* also has more gill rakers (18–24 vs. 12–15 in *G. bicarinatus*).

**Premaxilla** The premaxilla (Fig. 11) is a long, curved bone with an arrowhead-shaped anterior end that extends dorsally and posteriorly as an ascending process. The posterior shank of the premaxilla is elongate and bears a row of 14–37 long, thin teeth on its ventral margin. There are two articular facets for the overlying maxilla at the junction of the posterior margin of the ascending process with the shank portion. Ascending processes of both premaxillae are closely approximated to each other mesially and fit into the median groove of the ethmoid bone. The ascending process forms an angle of 55–67° with the shank: *G. bilineatus* has a slightly larger angle (60–67°, Fig. 11c) than *G. bicarinatus* (55–58°, Fig. 11d). *Grammatorcynus* has a larger angle than any species of *Scomberomorus* except *S. guttatus* (60–61°). The ascending process is 33–40% of the total length of the premax-

**Table 2**  
Number of teeth in upper and lower jaws of *Grammatorcynus*.

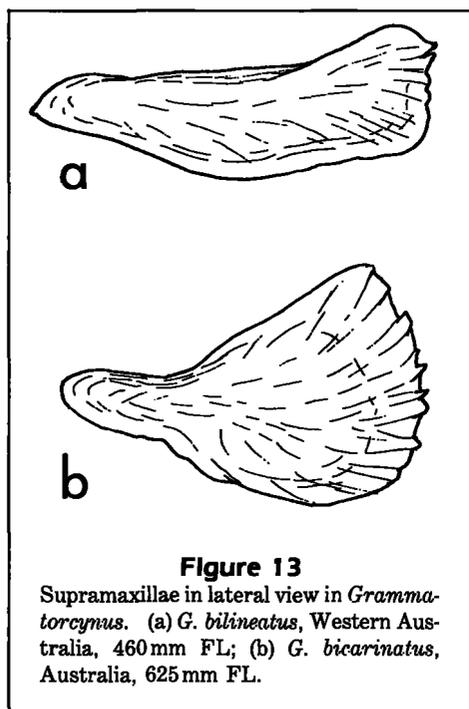
Species	Side	Min	Max	$\bar{x}$	Overall $\bar{x}$	<i>N</i>
<b>Upper jaw</b>						
<i>G. bilineatus</i>	L	14	37	23.5	24.0	39
	R	14	36	24.5		
<i>G. bicarinatus</i>	L	14	25	20.5	20.7	8
	R	17	24	20.9		
<b>Lower jaw</b>						
<i>G. bilineatus</i>	L	12	32	18.6	18.8	36
	R	14	30	19.1		
<i>G. bicarinatus</i>	L	16	20	17.5	17.5	7
	R	15	23	17.6		



illa. This is a small percentage relative to *Acanthocybium* (50%, Fig. 11b). *Scomberomorus* is intermediate (31–48%, Fig. 11a).

**Maxilla** The maxilla (Fig. 12) is a long, curved bone surmounting the premaxilla dorsolaterally by

means of an anterior head and ventral sulcus. The head consists of a thick, massive inner condyle and a small lateral process. The inner condyle possesses a prominent knob at its dorsolateral aspect that fits into the articular surface of the vomer, and an anterior, deep



**Figure 13**

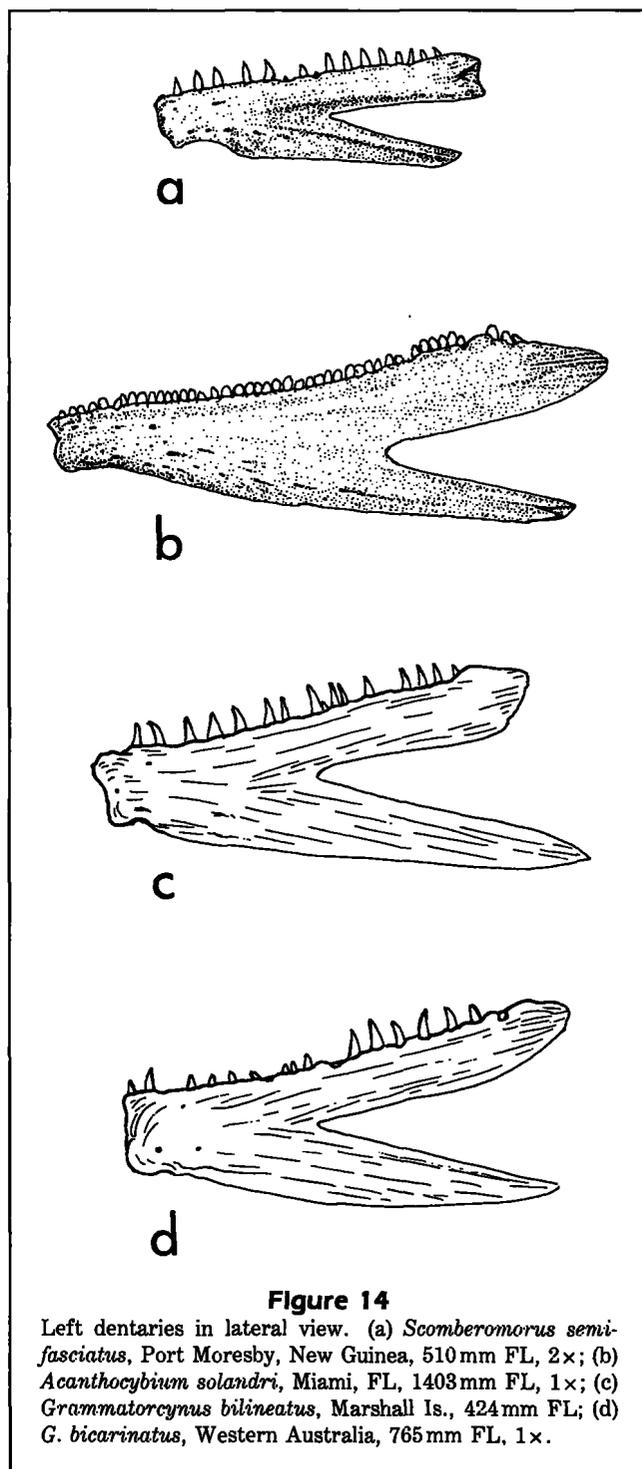
Supramaxillae in lateral view in *Grammatocynus*. (a) *G. bilineatus*, Western Australia, 460 mm FL; (b) *G. bicarinatus*, Australia, 625 mm FL.

concavity facing the inner wall of the premaxilla. Immediately posterior to the head is a shallow depression that receives the anterior articulating process of the palatine. The shank of the maxilla is narrow and somewhat flattened. It remains at a relatively constant height along its entire length, unlike the shank of *Scomberomorus* (Fig. 12a) in which the posterior end of the shank expands into a flat plate. The posterior end is distinctly thinner than the middle of the shank in *Acanthocybium* (Fig. 12b).

The head of the maxilla is longer (25–29% of total maxilla length) in *Grammatocynus* than in any species of *Scomberomorus* (18–25%) but shorter than in *Acanthocybium* (33%, Fig. 12b).

The height of the posterior end of the shank, relative to the total length of the maxilla, is less in *G. bicarinatus* (6–8%, Fig. 12d) than in *G. bilineatus* (8–11%, Fig. 12c). *Grammatocynus bilineatus* is similar to those species of *Scomberomorus* that have the least well-developed (lowest) posterior expansions: *S. multi-radiatus* (8–9%) and *S. sinensis* (9–11%). Other species of *Scomberomorus*, such as *S. munroi* (Fig. 12a), have larger posterior expansions (11–15%).

**Supramaxilla** The supramaxilla (Fig. 13) covers the posterior end of the maxilla. It is a small, flat bone that is expanded posterodorsally. The expansion is much more pronounced in *G. bicarinatus* (59–76% of bone length, Fig. 13b) than in *G. bilineatus* (35–42%, Fig. 13a).



**Figure 14**

Left dentaries in lateral view. (a) *Scomberomorus semifasciatus*, Port Moresby, New Guinea, 510 mm FL, 2×; (b) *Acanthocybium solandri*, Miami, FL, 1403 mm FL, 1×; (c) *Grammatocynus bilineatus*, Marshall Is., 424 mm FL; (d) *G. bicarinatus*, Western Australia, 765 mm FL, 1×.

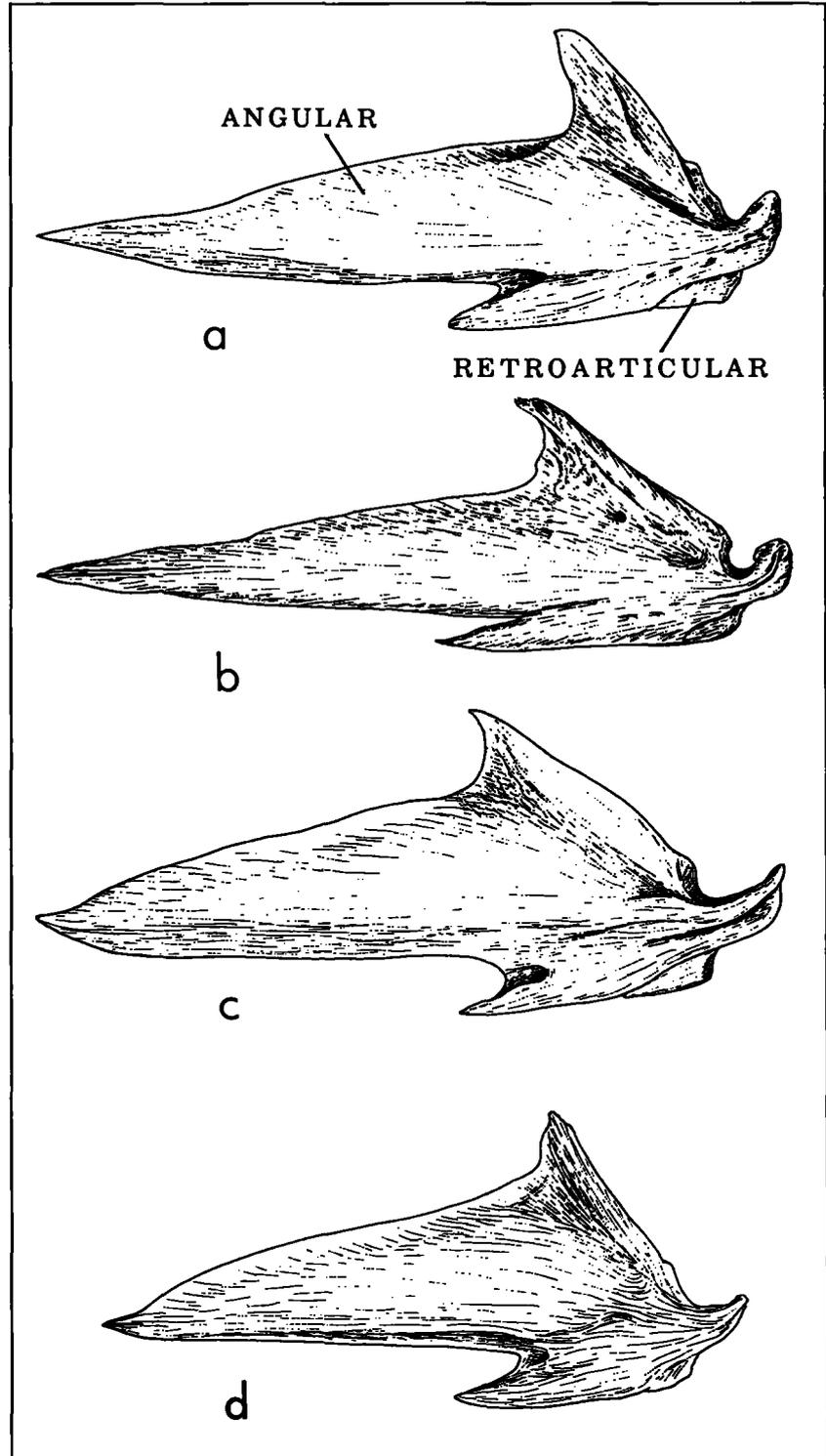
**Dentary** The dentary (Fig. 14) is laterally flattened and bears a single row of 12–32 long, thin teeth on the dorsal margin. Posteriorly, the dentary has two arms of the same relative width (the ventral arm may be slightly narrower), unlike *Scomberomorus* (Fig. 14a) and *Acanthocybium* (Fig. 14b) where the ventral arm

**Figure 15**

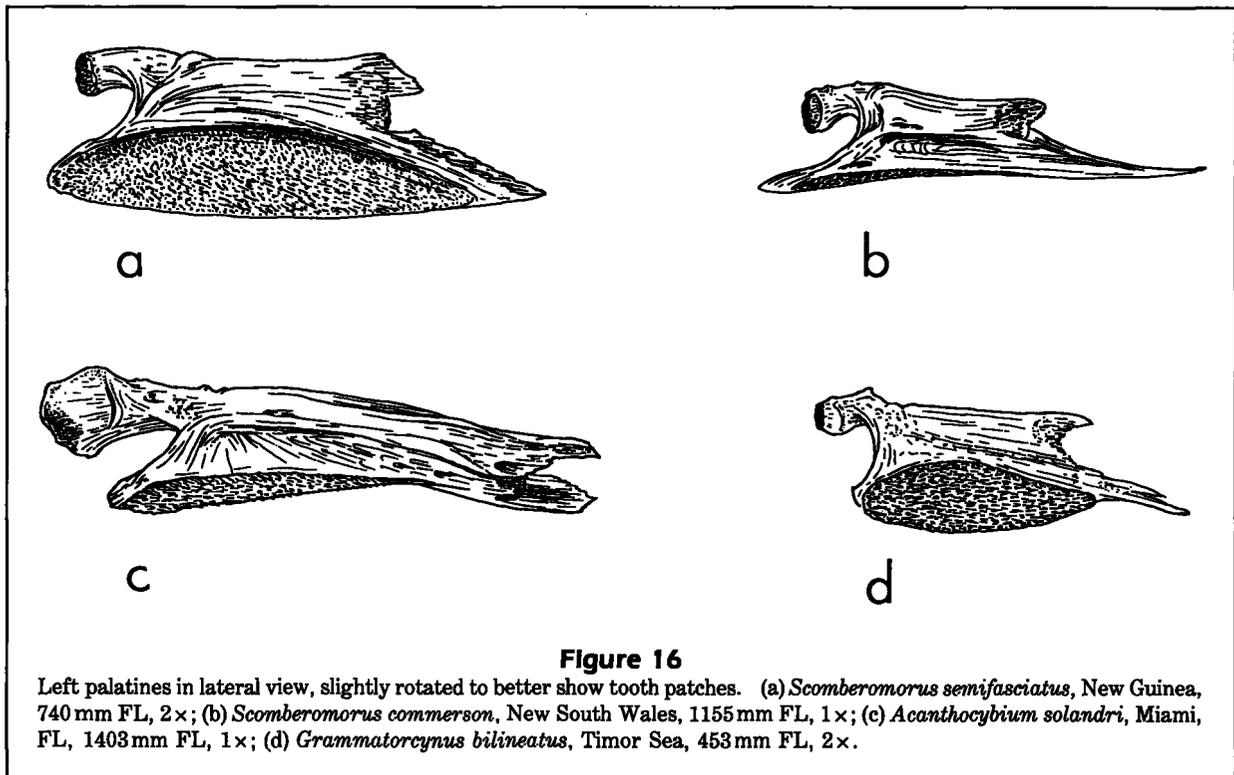
Left angulars and retroarticulars in lateral view. (a) *Scomberomorus semifasciatus*, Port Moresby, New Guinea, 510 mm FL, 3.5×; (b) *Acanthocybium solandri*, Miami, FL, 1403 mm FL, 1×; (c) *Grammatorcynus bilineatus*, Papua New Guinea, 382 mm FL, 4.5×; (d) *G. bicarinatus*, Western Australia, 765 mm FL, 2×.

is much narrower than the dorsal arm. The length of the dentary from its anterior margin to the tip of the ventral arm is 97–109% of the length of the dorsal arm. The ventral arm is longer in *G. bilineatus* (104–109% of dorsal arm length, Fig. 14c) than in *G. bicarinatus* (97–98%, Fig. 14d). The ventral arm is longer in *Grammatorcynus* than it is in *Scomberomorus* (86–97%) and *Acanthocybium* (91–96%). Species of *Grammatorcynus* and *Scomberomorus* have a notch on the anteroventral margin of the dentary that is absent in *Acanthocybium*. *Acanthocybium* has a prominent notch on the anterior margin of the dentary that is indistinct or absent in *Grammatorcynus* and *Scomberomorus*.

**Angular** (Fig. 15) The triangular anterior end of the angular (frequently called articular) fits into the dentary anteriorly. The posterior end of the angular bears three large processes: the dorsal process, directed forward and upward; the ventral process, directed forward; and the posterior process, directed backward and upward. The posterior process is hooked and carries a transverse articular facet for the quadrate. The length from the tip of the posterior process to the tip of the dorsal process is 40–47% of the total length of the bone. The length from the tip of the posterior process to the tip of the ventral process is slightly longer, 44–52% of bone length. The depth of the angular, measured from the tip of the dorsal process to the tip of the ventral process, is 36–48% of the total length, with the depth of *G. bicarinatus* being greater (44–48%, Fig. 15d) than that of *G. bilineatus* (36–41%, Fig. 15c). The ventral process is approximately as long or longer than the dorsal process in *Grammatorcynus*. In *G. bilineatus*, the



ventral process is 84–105% of the length of the dorsal process, and in *G. bicarinatus* the ventral process is longer than the dorsal process (153–200%). Only *Acanthocybium* (99–148%, Fig. 15b), *S. commerson* (99–162%), and *S. queenslandicus* (115–136%) also have a



ventral process as long or longer than the dorsal process. All other species of *Scomberomorus* (Fig. 15a) have ventral processes that are relatively shorter.

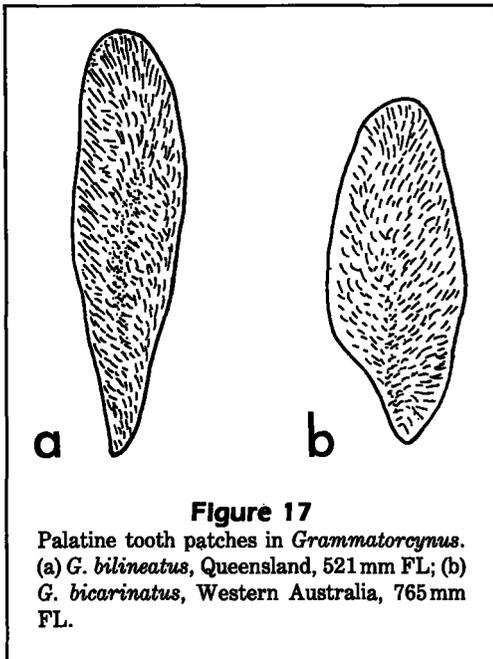
**Retroarticular** (Fig. 15) The retroarticular bone (frequently called the angular) is rhomboid and attached firmly, but not fused, to the posteroventral margin of the angular. No differences were found between the retroarticulars of the species of *Grammatorcynus*.

**Palatine arch** The palatine arch consists of four pairs of bones in the roof of the mouth: palatine, ectopterygoid, entopterygoid, and metapterygoid.

**Palatine** The palatine is forked both posteriorly and anterolaterally (Fig. 16). The dorsal branch of the anterolateral fork is hooked, and its anterior end articulates with a facet on the maxilla, immediately ventral to the nasal. The ventral branch appears almost indistinct in comparison with the longer ventral branch of *Acanthocybium* (Fig. 16c) and the even longer ventral branch of *Scomberomorus* (Fig. 16a-b). In *Scomberomorus*, the ventral branch is longer than the dorsal branch, which is not true of *Grammatorcynus* or *Acanthocybium*. The distance from the anterior end of the ventral branch to the end of the external branch divided by the distance from the tip of the dorsal hook to the end of the external branch is 118–125% in *Grammatorcynus*, 112–121% in *Acanthocybium*, and only

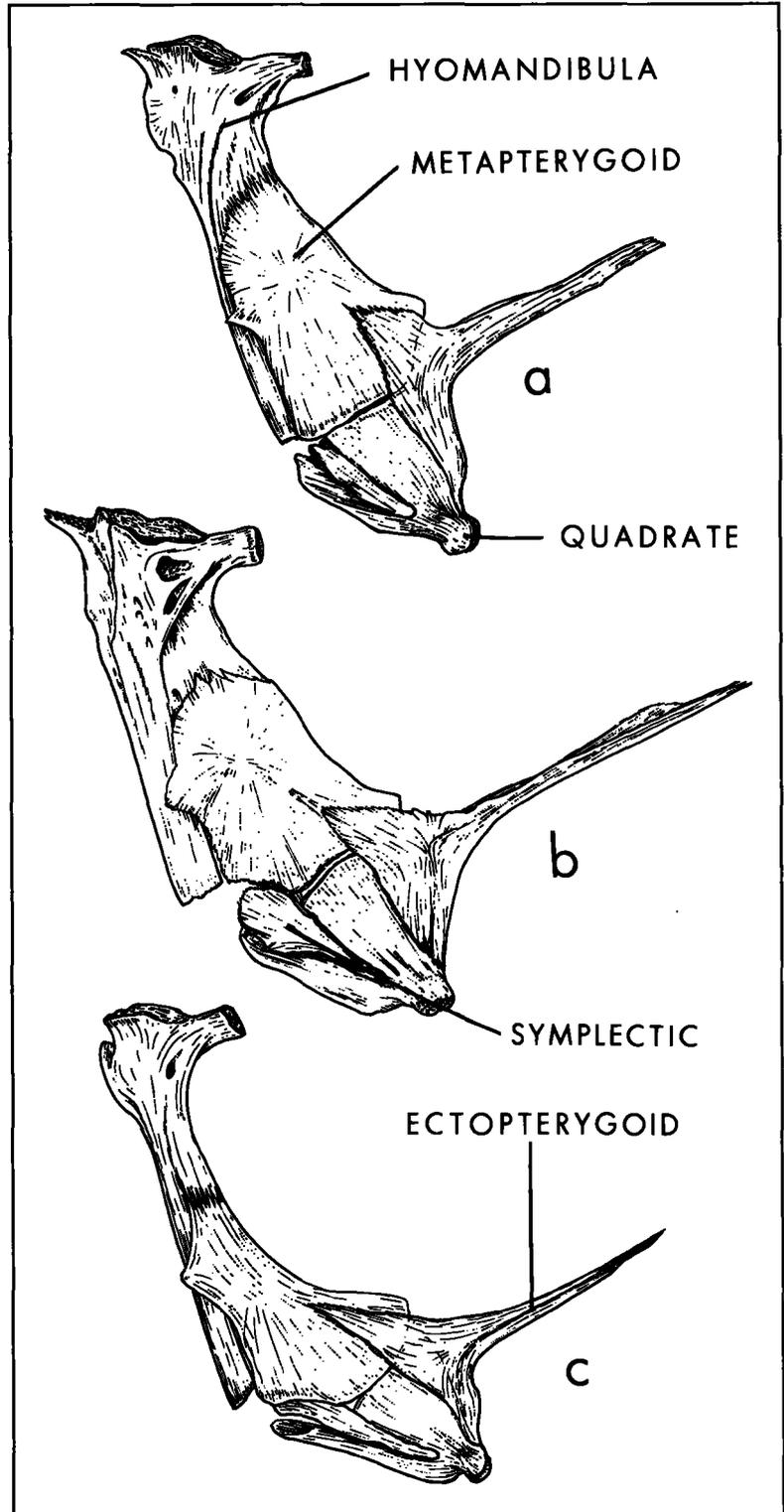
87–107% in *Scomberomorus*. The distance from the tip of the dorsal hook to the tip of the inner branch divided by the distance to the tip of the outer branch is 71–75% in *Grammatorcynus*, 54–84% in *Scomberomorus*, and 97–99% in *Acanthocybium*. Hence, *Acanthocybium* differs from both *Grammatorcynus* and *Scomberomorus* in that its posteriorly directed inner branch is almost as long as the outer branch. The tooth patch is short and wide in *Grammatorcynus* (Fig. 16d), more so in *G. bicarinatus* (width 38–42% of length, Fig. 17b) than in *G. bilineatus* (width 26–32% of length, Fig. 17a), long and narrow in *Acanthocybium*, and between the two extremes in *Scomberomorus*. The teeth are fine in all three genera, but are a little larger in *Grammatorcynus* and *Acanthocybium* than in most species of *Scomberomorus*.

**Ectopterygoid** The ectopterygoid is a T-shaped bone with the top of the T forming its posterior end. It joins with the entopterygoid dorsolaterally, the palatine laterally and anteriorly, and the quadrate and metapterygoid posteriorly (Fig. 18). Dividing the dorsal distance (from the anterior end of the bone to the tip of the dorsal arm) by the ventral distance (from the anterior end to the tip of the ventral process) results in a number that is greater than 100% in *Grammatorcynus* (107–116%, Fig. 18c) and *Acanthocybium* (103–109%, Fig. 18b), but only 85–100% in *Scombero-*



**Figure 17**

Palatine tooth patches in *Grammatorcynus*. (a) *G. bilineatus*, Queensland, 521 mm FL; (b) *G. bicarinatus*, Western Australia, 765 mm FL.



**Figure 18 (right)**

Left suspensoria in mesial view. (a) *Scomberomorus semifasciatus*, New Guinea, 510 mm FL, 2.5x; (b) *Acanthocybium solandri*, Revillagigedos Is., 1068 mm FL, 1.5x; (c) *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL, 2x.

*morus* (Fig. 18a). The shank is longer in *Acanthocybium* than in the other two genera. The posterior edge of the ectopterygoid (from the tip of the dorsal process to the tip of the ventral process) relative to the ventral distance is long, 63–72% in *Grammatorcynus*, and relatively shorter in *Acanthocybium* (41–47%) and *Scomberomorus* (43–63%).

**Entopterygoid** The entopterygoid is elongate and oval in shape (width 35–41% of length, Collette and Russo 1985b: fig. 28). The outer margin of the entopterygoid is the thickest part of the bone and attaches to the inner margin of the ectopterygoid. The entopterygoid also connects with the palatine anteriorly and the metapterygoid posterolaterally. The mesial and posterior borders are free from contact with other bony elements. The dorsal surface is roughly convex. The dorsal surface is similarly convex in *Acanthocybium*, but the dorsal surface in *Scomberomorus* is concave. The ventral sur-

face is convex in all three genera, and it forms the major part of the buccal roof. *Scomberomorus* contains species that have both narrower (*S. commerson*, width

23–28% of length) and wider (*S. maculatus* width 41–42% of length) entopterygoids. The entopterygoid of *Acanthocybium* (30–35%) is slightly narrower than that of *Grammatorcynus* (35–41%).

**Metapterygoid** The metapterygoid is a flat, quadrangular or somewhat triangular bone (Fig. 18). The posterodorsal margin of this bone is deeply grooved to receive the hyomandibula. The dorsal portion is strongly ankylosed to the lamellar region of the hyomandibula. The ventroposterior margin abuts the lowermost portion of the symplectic process of the hyomandibula, but does not touch the hyomandibula. There is a relatively long slit between the two bones through which the hyoidean artery passes (Allis 1903). The ventral border is divided into two portions: the horizontal portion in contact with the quadrate and the anterior oblique portion ankylosed to the ectopterygoid. On the mesial surface, the metapterygoid has a triangular-shaped area that forms an interdigitating articulation with the upper arm of the ectopterygoid. The posteroventral margin of the metapterygoid articulates with the dorsal end of the symplectic in *Grammatorcynus* (Fig. 18c) and *Acanthocybium* (Fig. 18b), but does not do so in most species of *Scomberomorus* (Fig. 18a). The posterior, horizontal part of the ventral border is shorter than the anterior oblique part in *Grammatorcynus* (anterior part 132–181% of posterior part) and *Acanthocybium* (188–218%); however, in *Scomberomorus* the posterior part is longer than the anterior part (anterior part 39–86% of posterior part).

**Hyoid arch** The hyoid arch is composed of the hyomandibula, symplectic, quadrate, hyoid complex (hypohyals, ceratohyal, epihyal, interhyal, and the seven branchiostegal rays), and two median unpaired bones, the glossohyal and urohyal.

**Hyomandibula** The hyomandibula is an inverted L-shaped bone (Fig. 18) connecting the mandibular suspensorium and opercular bones to the neurocranium. Dorsally, there are three prominent condyles. The long dorsal condyle forms the base of the L and fits into the fossa at the junction of the pterotic and sphenotic bones. The anterior condyle articulates with the ventral fossa of the pterotic, and the lateral process is attached to the inside of the opercle. Anterolaterally, the hyomandibula is drawn out into a lamellar region that joins the metapterygoid. Posterolaterally, it has a long articulation with the preopercle. Ventrally, the hyomandibula has a long symplectic process; at the posterodorsal corner there is a small, sometimes almost indistinct spine. A strong vertical ridge extends from the ventral margin to just below the dorsal border, where it then curves anteriorly to confluence with the anterior condyle. The areas lying anterior and posterior to this ridge are grooved for articulation with the metapterygoid and preopercle,

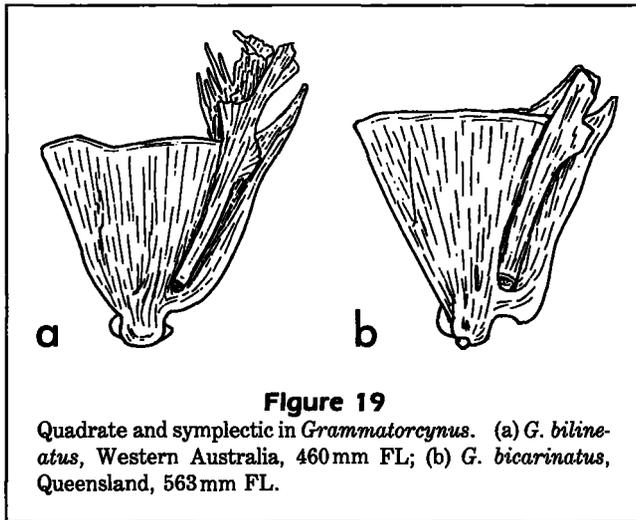
respectively; in situ, only the ridge and a portion of the upper broader surface are visible exteriorly. The upper surface of the symplectic is connected to the ventral border of the hyomandibula by way of a cartilage, best developed in *Acanthocybium*. There is one deep fossa on the inner surface of the hyomandibula in *Grammatorcynus* (Fig. 18c) and *Scomberomorus* (Fig. 18a); there are two such fossae in *Acanthocybium* (Fig. 18b).

The posterodorsal spine, which is quite small in *Grammatorcynus* and in most species of *Scomberomorus*, is best developed in *Acanthocybium*, *S. commerson* (Devaraj 1977), and *S. queenslandicus*. The maximum width (tip of anterior condyle to outer margin of posterior condyle) of the hyomandibula is least relative to the total length (ventral tip to dorsal margin of dorsal condyle) in *Grammatorcynus* (width 34–39% of length) and *S. multiradiatus* (36–39%). The hyomandibula is widest, relative to length in *S. sinensis* (45–52%). *Acanthocybium* and the other species of *Scomberomorus* fall between these two extremes (39–47%).

**Symplectic** The symplectic is a small bone that fits into a groove on the inner surface of the quadrate (Fig. 18). In *Grammatorcynus* the symplectic is slightly wider than it is in *Scomberomorus*; however, the groove into which the symplectic fits is narrower in *Grammatorcynus* than in *Scomberomorus*, so that the symplectic nearly fills the groove in *Grammatorcynus* and does not fill the groove in *Scomberomorus* (Fig. 18a). The symplectic is greatly expanded at its dorsal end in *Acanthocybium* (Fig. 18b). The symplectics in *Grammatorcynus* and *Acanthocybium* extend well beyond the dorsal margin and even beyond the dorsal end of the posterior process of the quadrate to make contact with the metapterygoids, making them much longer than the symplectics in most species of *Scomberomorus*. The symplectic of *G. bilineatus* (Fig. 19a) is longer than that of *G. bicarinatus* (Fig. 19b).

**Quadrate** The lower jaw is suspended from the cranium by means of the articulating facet of the ventral surface of the triangular quadrate (Fig. 18). The broad dorsal margin of the quadrate abuts the ventral border of the metapterygoid. There is a strong process on the posterior margin of the quadrate that is attached along the lower anterior arm of the preopercle. This process is quite long in *G. bilineatus* (its length measured from the ventral facet to the tip of the process is 134–145% of the distance from the ventral facet to the dorsal margin; Fig. 19a) and *Acanthocybium*, but shorter in *G. bicarinatus* (122–125%, Fig. 19b) and most species of *Scomberomorus*.

**Hyoid complex** This complex includes the two hypohyals (basihyal of Mago Leccia 1958), ceratohyal, epihyal, and interhyal bones, and the seven branchiostegal rays (Collette and Russo 1985b:fig. 29). The



**Figure 19**

Quadrated and symplectic in *Grammatorcynus*. (a) *G. bilineatus*, Western Australia, 460 mm FL; (b) *G. bicarinatus*, Queensland, 563 mm FL.

hypohyals, ceratohyal, and epihyal are closely associated and form a functional unit.

**Hypohyals** The hypohyals comprise separate dorsal and ventral elements joined longitudinally. In lateral view, the ventral hypohyal is clearly larger than the dorsal hypohyal in *Grammatorcynus*, but in *Scomberomorus* not quite as large relative to *Grammatorcynus*. In *Acanthocybium* the ventral hypohyal is three times larger than the dorsal hypohyal. Laterally, the suture that runs between the dorsal and ventral hypohyals curves ventrally at various angles in *Grammatorcynus* and *Scomberomorus*, but runs almost horizontally in *Acanthocybium*. Mesially, a pointed lateral process at the anterodorsal end of the dorsal hypohyal forms a symphysis with the glossohyal, urohyal, basi-branchial, and the process of the hypohyal from the opposite side in *Grammatorcynus* and *Scomberomorus*. *Acanthocybium* also has a pointed lateral process, but it appears to be further posterior due to also having an anterior pointed end to the hypohyals at the junction of the dorsal and ventral hypohyals. In addition, *Acanthocybium* has a prominent anterolateral process on the ventral hypohyal. The groove for the hyoidean artery runs along the outer surface of the epihyal, ceratohyal, and ventral portion of the dorsal hypohyal. In *Grammatorcynus* the groove in the dorsal hypohyal is relatively short, extending anteriorly 11–39% of the length of the dorsal hypohyal before becoming a covered tunnel leading to the inner side of the dorsal hypohyal. In *Scomberomorus* the groove extends 32–53% before becoming a tunnel to the inner side, and in *Acanthocybium* the groove extends 29–47% before becoming a foramen leading to the inner side. The opening on the inner side appears as a small to moderate pit, usually located in the ventral portion of

the dorsal hypohyal in *Grammatorcynus* and *Scomberomorus*.

**Ceratohyal** The ceratohyal is a long flat bone, broadest at the posterior end, and with an anteroventral projection that articulates with the posteroventral notch of the ventral hypohyal. It is the largest bone of the hyoid complex. Posteriorly, the middle part of the ceratohyal interlocks with the epihyal by means of odontoid processes issuing from both elements (ceratohyal-epihyal suture of McAllister 1968), while the upper and lower portions are joined by cartilage. Four acinaciform branchiostegal rays are attached to the respective articular surfaces along the concave middle portion of the ventral margin in *Grammatorcynus* and *Acanthocybium*. In *Scomberomorus* the fifth branchiostegal ray is also usually attached to the ceratohyal (most posterior part) or on the space between the ceratohyal and epihyal, not on the anterior part of the epihyal. In *Grammatorcynus* and *Acanthocybium* the fifth branchiostegal ray is on the anterior part of the epihyal. The hyoidean groove runs the length of the ceratohyal on its lateral surface. The groove is so deep in 10 species of *Scomberomorus* (*brasiliensis*, *commerson*, *concolor*, *multiradiatus*, *munroi*, *niphonius*, *queenslandicus*, *semifasciatus*, *sierra*, and *tritor*) that it forms a thin slit through the bone, the ceratohyal window or “beryciform” foramen. This slit is rare in *Grammatorcynus* and *Acanthocybium*, and is either rare or occasional in the other eight species of *Scomberomorus*. The dorsal margin of the ceratohyal is usually concave, but sometimes flat in *Grammatorcynus*. It is deeply concave in *Acanthocybium*, and varies from concave to convex in *Scomberomorus*.

**Epihyal** The epihyal is a triangular bone that interlocks anteriorly with the ceratohyal and has a posterior process that articulates with the interhyal. Three branchiostegal rays articulate with the epihyal in *Grammatorcynus* and *Acanthocybium*. Only two branchiostegal rays are found on the ventral portion of the epihyal in *Scomberomorus*. In *Grammatorcynus* the depth of the epihyal is 66–80% of the length from the smooth anterior margin of the bone to the tip of the posterior process. Epihyal depth is narrowest in *Acanthocybium* (58–62%), and in *Scomberomorus* it varies from 68% in *S. commerson* and *S. cavalla* to 98% in *S. koreanus*, with intermediate values for the other species.

**Interhyal** The interhyal is a small flattened bone that is attached to the epihyal dorsal to the posterior process. It is directed obliquely upward and links the hyoid complex to the hyomandibula and symplectic. No differences in interhyals were noted.

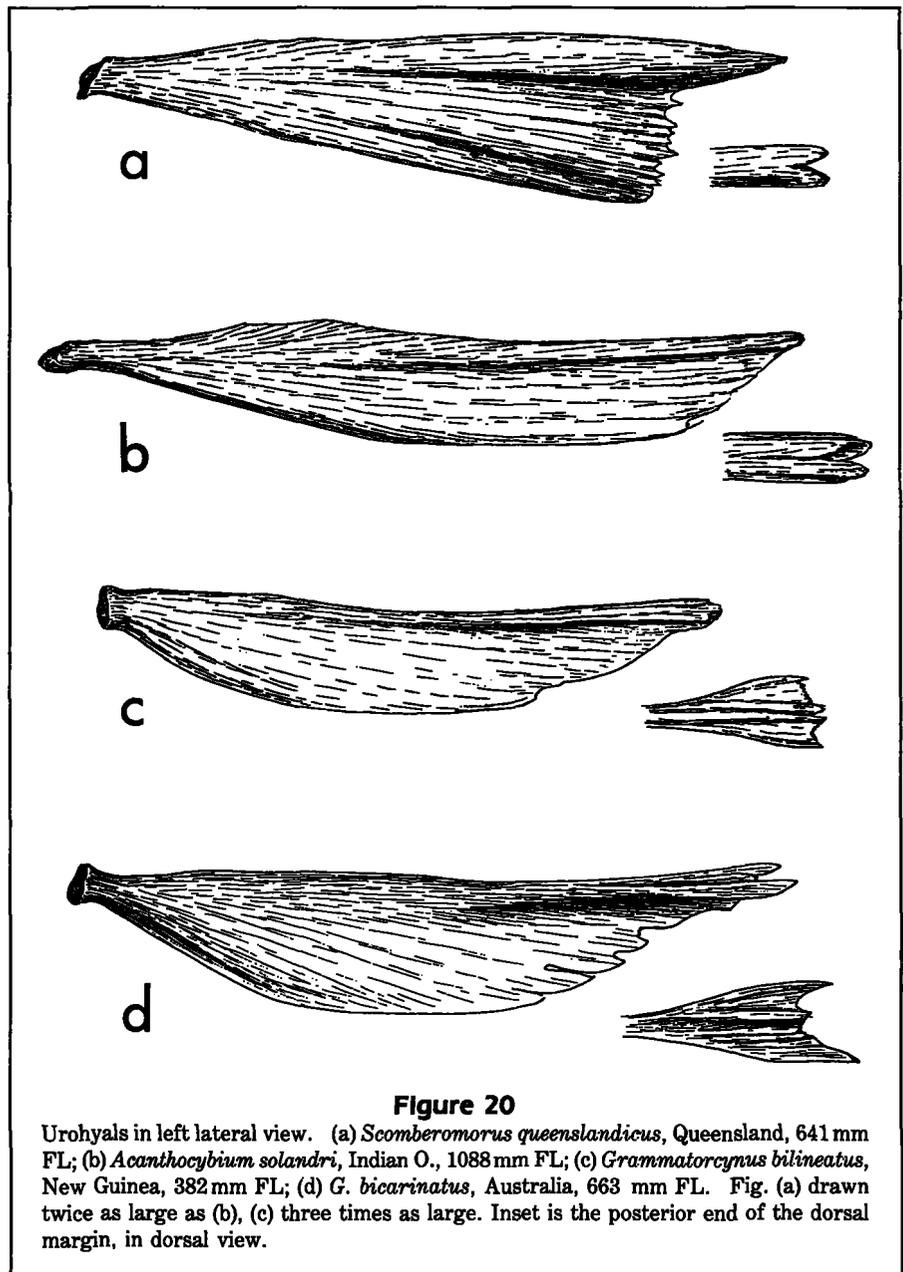
**Glossohyal** The glossohyal (basihyal) is a median bone that supports the tongue and overlies the

first basibranchial bone at the anterior end of the branchial arch. In *Grammatorcynus* there is a quadrangular to oval tooth plate fused to and covering the dorsal surface of the glossohyal (Collette and Russo 1985b:fig. 30). No tooth plate is present in *Acanthocybium* or *Scomberomorus*. The glossohyal of *Grammatorcynus* is slightly wider (width 47–55% of length) than the roughly rod-shaped or conical-shaped glossohyal of *Scomberomorus* (35–54%) and the flattened spatulate glossohyal of *Acanthocybium* (42%).

**Urohyal** The urohyal is a compressed, median, unpaired bone (Fig. 20). The anterior end of this element lies between, and is connected with, the hypohyals of the left and right sides. The most prominent difference in the urohyal of *Grammatorcynus* is that in dorsal view, the posterior end of the dorsal margin is tripartite (Fig. 20c–d) instead of forked, as it is in *Scomberomorus* and *Acanthocybium* (Fig. 20a–b). The dorsal and anterior portions of the ventral margins are thickened in *Grammatorcynus*. The anterior end has an articulation head; the posterior end is deepest in *Scomberomorus*, and much less deep in *Grammatorcynus* due to the convex shape of the ventral margin. The maximum depth of the urohyal in *Grammatorcynus* is 15–20% of the length of the dorsal margin. The maximum depth in *Acanthocybium* is not as great as this (13–15%), and in *Scomberomorus* it is greater (16–24%). In *Grammatorcynus* the ventral margin of the urohyal is relatively short, only 68–71% of the length of the dorsal margin, compared with 80–91% in *Acanthocybium* and *Scomberomorus*.

**Opercular apparatus** Four wide, flat bones (opercle, preopercle, subopercle, and interopercle) fit together to form the gill cover.

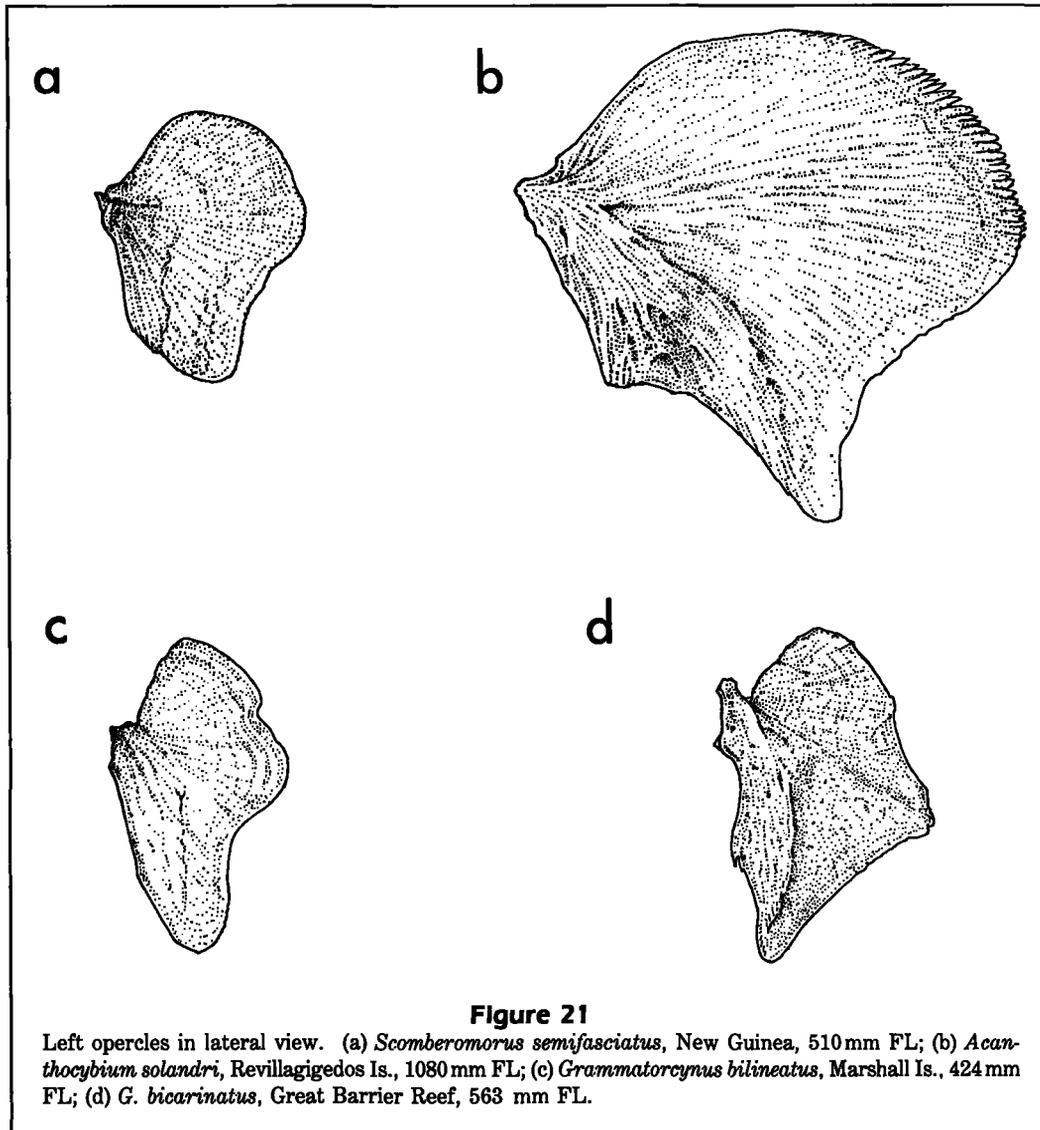
**Opercle** The opercle (Fig. 21) is overlapped laterally on its anterior margin by the posterior half of the preopercle. The narrow, elongate, articular facet



**Figure 20**

Urohyals in left lateral view. (a) *Scomberomorus queenslandicus*, Queensland, 641 mm FL; (b) *Acanthocybium solandri*, Indian O., 1088 mm FL; (c) *Grammatorcynus bilineatus*, New Guinea, 382 mm FL; (d) *G. bicarinatus*, Australia, 663 mm FL. Fig. (a) drawn twice as large as (b), (c) three times as large. Inset is the posterior end of the dorsal margin, in dorsal view.

for the opercular process of the hyomandibula is located on the medial surface of the anterodorsal corner of the opercle. *Grammatorcynus* and most species of *Scomberomorus* have a weak process at the posterodorsal corner. This process is absent in *Acanthocybium*. In *Grammatorcynus* the width of the opercle is 63–79% of the total length of the bone; *G. bicarinatus* has a wider opercle (width 72–79% of length, Fig. 21d) than *G. bilineatus* (63–72%, Fig. 21c). Both species of *Grammatorcynus* have narrow opercles compared with the extremely wide opercles found in *Acanthocybium* (Fig. 21b).



**Preopercle** The preopercle is a large, crescent-shaped flat bone, broadest at the lower posterior angle (Collette and Russo 1985b:fig. 33). The anterior portion of the bone is thickened into a bony ridge. A series of 5–7 pores along the lower margin of the ridge represents the preoperculo-mandibular canal of the lateral line system which continues onto the dentary. On the mesial side, the bony ridge possesses a groove for attachment to the hyomandibula and the quadrate. There is a shelf mesial to the anteroventral end of the preopercle in *Acanthocybium* that is absent in *Grammatorcynus* and *Scomberomorus*. The canals leading to the preopercular pores are visible through the bone in *G. bilineatus* and all species of *Scomberomorus*, but these canals could not be seen in the specimens of *G. bicarinatus* and *Acanthocybium* due to the thickness

of the bone. The posterior margin of the preopercle is distinctly concave in *Grammatorcynus* and most species of *Scomberomorus*. However, it is only slightly concave or flat in *Acanthocybium* and *S. commerson*. In *Grammatorcynus* the distance from the anterior margin of the bony ridge to the posterior end of the lower lobe is 64–75% of the height of the preopercle measured from the ventral margin to the dorsal tip of the bone. In *Scomberomorus* the lower lobe is 69–80% of the height of the preopercle. The anterodorsal margin terminates in a pore similar to the preoperculo-mandibular lateral-line canal pore at the anteroventral margin of the bone.

**Subopercle** The subopercle is a flat, roughly triangular bone with a prominent anterior projection (Collette and Russo 1985b:fig. 34). Two ridges

converge posteriorly from the anterior projection on the lateral side of the bone. The upper ridge articulates with the lower posterior projection of the opercle, and the lower ridge connects to the posterodorsal margin of the interopercle. The dorsal ridge is much more prominent than the ventral ridge and extends over the main part of the subopercle as a discrete shelf. The weaker ventral ridge is more difficult to detect in most specimens of *Grammatorcynus*. The angle between the anterior projection and the anterior margin of the subopercle is acute in *Grammatorcynus* and *S. multiradiatus*; however, in *Acanthocybium* and the other species of *Scomberomorus* the angle is close to 90°. The length of the anterior projection in *Grammatorcynus* varies from 23 to 33% of the length of the anterior margin dorsal to the projection. The projection is slightly longer (28–33%) in *G. bicarinatus* than in *G. bilineatus* (23–28%). The projection is longest in *Acanthocybium* (36–45%) and shortest in *S. commerson* (20–25%), with the rest of the species of *Scomberomorus* having projections between 21 and 43%.

**Interopercle** The interopercle is roughly oval in shape, narrow at the anterior margin and widening posteriorly, with a crest on the superior margin (Collette and Russo 1985b:fig. 35). There is a well-developed facet on the mesial side to receive the articular process of the interhyal. The maximum depth of the interopercle relative to the length of the bone is 35–43% in *Grammatorcynus*. The maximum depth of the interopercle is a little greater in *Acanthocybium* (40–49%), and much greater in the species of *Scomberomorus* (45–61%). Often there is a well-formed notch anterior to the crest on the sloping anterior margin in *Grammatorcynus* and *Scomberomorus*, which is not as well developed in *Acanthocybium*. The posterior margin is rounded in *Grammatorcynus* and *Scomberomorus* but divided into two by a notch in *Acanthocybium*.

**Branchial apparatus** The branchial apparatus is composed of five pairs of gill arches, gill filaments, gill rakers, pharyngeal tooth patches, and supporting bones. The general arrangement in *Grammatorcynus* is similar to that found in other scombrids such as the Sardini (Collette and Chao 1975), *Thunnus* (Iwai and Nakamura 1964:22, fig. 1; de Sylva 1955:21, fig. 40), *Scomberomorus* (Mago Leccia 1958:327, pl. 12; Collette and Russo 1985b:fig. 36), and *Rastrelliger* (Gnanamuttu 1971:14, fig. 6). Most branchial bones bear patches of tiny teeth.

**Basibranchials** The three basibranchials form an anteroposterior chain. The first and second are about the same size, and considerably shorter than the third. The first is covered dorsally by the glossohyal.

In lateral view, the first basibranchial is narrowest in the middle. In *Grammatorcynus* and *Acantho-*

*cybium* it is elongate. In *Scomberomorus* it is short with a wide base where it joins with the second basibranchial. The second basibranchial has a prominent notch in the ventral margin and a distinct groove laterally that extends from the anteroventral margin to the mid-dorsal region of the bone. This groove accepts the anterior end of the first hypobranchial. The third basibranchial has an expanded anterior end at its junction with the second basibranchial, and then tapers posteriorly. A prominent groove is present anteriorly that accepts the medial anterior end of the second hypobranchial. A section of cartilage extends posteriorly to articulate with the fourth and fifth ceratobranchials.

**Hypobranchial** Three hypobranchials are present. The first is interposed between the second basibranchial and the first ceratobranchial. The second is about the same size as the first, fits into a groove on the third basibranchial, and extends to the second ceratobranchial. The third hypobranchial is smaller than the first or second, fits snugly against the posterolateral margin of the third basibranchial, and its posterior end articulates with the third ceratobranchial.

**Ceratobranchials** The five ceratobranchials are the longest bones in the branchial arches. They have a deep groove ventrally for the branchial arteries and veins. The ceratobranchials support most of the gill filaments and gill rakers. The first three are morphologically similar and articulate with the posterior ends of their respective hypobranchials. The fourth is more irregular and attaches to a cartilage posterior to the third basibranchial. The fifth ceratobranchial is also attached to the cartilage, has a dermal tooth plate fused to its dorsal surface, and the complex is termed the lower pharyngeal bone. It is covered with small conical teeth that are directed slightly posteriad.

**Epibranchials** The posterolateral end of each of the four epibranchials is attached to the ends of the first four ceratobranchials. Each epibranchial bears a groove posterodorsally for the branchial arteries and veins. The first epibranchial is the longest and bears two processes mesially. The anterior process articulates with the first pharyngobranchial, and the posterior process attaches with the interarcual cartilage. The second epibranchial is similar to the first, but slightly shorter. The anterior end has two processes, an anterior process that attaches to the second pharyngobranchial and a posterior process that is coupled with the third pharyngobranchial by way of an elongate cartilage. This process is relatively elongate in *Grammatorcynus*, but shorter in *Acanthocybium* and *Scomberomorus*. The third epibranchial is the shortest in the series. Laterally, it is attached with the third ceratobranchial; mesially, it is attached with the third pharyngobranchial. An elongate posterodorsal process

is present. This process joins with the fourth epibranchial, which is larger than the third and is interposed between the fourth ceratobranchial and pharyngobranchial. It is a curved bone with the angle formed by the lateral and medial arms being much more acute in *Grammatorcynus* than in *Acanthocybium* and *Scomberomorus*. A dorsal process arises from the middle of the bone and attaches to the third epibranchial.

**Pharyngobranchials** There are four pharyngobranchials attached basally to the epibranchial of their respective gill arch. The first is long and slender, articulates dorsally with the prootic, and is frequently called the suspensory pharyngeal (Iwai and Nakamura 1964). The elongate second pharyngobranchial bears a patch of teeth. The third is the largest element in the series; it has a broad patch of teeth on its ventral surface, a broad posterior end, and tapers to a narrow anterior end. In *Grammatorcynus* and *Acanthocybium* the third pharyngobranchial is shorter than in *Scomberomorus*. The fourth pharyngobranchial also bears a ventral tooth plate, has a rounded posterior end, and has an elongate strut (pharyngobranchial stay) mesially which overlaps the third pharyngobranchial. This stay is much shorter in *Grammatorcynus* and *Acanthocybium* than in *Scomberomorus*.

**Gill rakers** The hypobranchial, ceratobranchial, and epibranchial of the first gill arch support a series of slender, rigid gill rakers. The longest gill raker is at or near the junction of the upper and lower arches, between the ceratobranchial and epibranchial. Magnusson and Heitz (1971) have clearly shown that there is a correlation between numbers of gill rakers, gap between gill rakers, and size of food items in a number of species of Scombridae.

The number of gill rakers is easily countable and is an especially useful taxonomic character in differentiating between the two species of *Grammatorcynus*: *G. bilineatus* has more gill rakers (18–24) than *G. bicarinatus* (12–15) (Table 3). *Acanthocybium* differs from all other genera of Scombridae in completely lacking gill rakers. Three species of *Scomberomorus* have greatly reduced numbers of gill rakers: *S. multiradiatus* (1–4 gill rakers), *S. commerson* (1–8), and *S. queenslandicus* (3–9). *Scomberomorus concolor*

stands out in having the most gill rakers (21–27). Other species of *Scomberomorus* fall between these extremes. There is a correlation between number of gill rakers and number of jaw teeth in *Grammatorcynus* and *Scomberomorus*. Species with the fewest gill rakers, *G. bicarinatus* and *S. multiradiatus*, also have the fewest jaw teeth, and species with the most gill rakers, *G. bilineatus* and *S. concolor*, have the most teeth.

**Axial skeleton** This section is divided into four parts: vertebral number, vertebral column, ribs and intermuscular bones, and caudal complex.

**Vertebral number** Vertebrae may be divided into precaudal (abdominal) and caudal. The first caudal vertebra is defined as the first vertebra that bears a notably elongate haemal spine and lacks pleural ribs. Vertebral counts include the urostyle which bears the hypural plate. *Grammatorcynus* has 31 vertebrae, which is less than *Scomberomorus* (41–56 vertebrae), which in turn is less than *Acanthocybium* (62–64). The same situation also applies to precaudal and caudal vertebrae. Both species of *Grammatorcynus* have 12 precaudal and 19 caudal (except for one specimen of *G. bicarinatus* with 11 plus 20 caudal). *Scomberomorus* has 16–23 precaudal and 20–36 caudal, and *Acanthocybium* has 31–33 precaudal and 31–33 caudal. The presence of only 31 vertebrae in *Grammatorcynus* is a primitive condition agreeing with *Scomber* and *Rastrelliger*, the most primitive members of the Scombrinae. The increased number of vertebrae in *Acanthocybium* is clearly a specialization.

**Vertebral column** The neural arches and spines are stout and compressed on the first to the fourth vertebra (especially the first 3) in *Grammatorcynus*. They extend farther back, to the fifth or sixth vertebrae, in most species of *Scomberomorus*, and extend farthest, to the seventh vertebra, in *Acanthocybium* and *S. commerson*. Posteriorly, toward the caudal peduncular vertebrae and caudal complex, the neural spines bend abruptly backward and cover most of the neural groove; caudally they merge into the caudal complex as in *Thunnus* (Kishinouye 1923, Gibbs and Collette 1967) and the bonitos (Collette and Chao 1975).

**Table 3**  
Number of gill rakers on first arch in *Grammatorcynus*.

	12	13	14	15	16	17	18	19	20	21	22	23	24	N	$\bar{x}$
<i>G. bilineatus</i>							1	10	15	30	10	5	1	72	20.8
<i>G. bicarinatus</i>	1	—	7	3										11	14.1

The neural prezygapophyses on the first vertebra are modified to articulate with the exoccipital where the vertebral axis is firmly articulated with the skull. Neural postzygapophyses arise posterodorsally from the centrum and overlap prezygapophyses posteriorly. The postzygapophyses progressively merge into the neural spine in the peduncular region to disappear by the last 5–6 vertebrae. The basic structure and elements of the neural arches and neurapophyses are similar to those of other scombrids (Kishinouye 1923, Conrad 1938, Mago Leccia 1958, Nakamura 1965, Gibbs and Collette 1967, Collette and Chao 1975, Potthoff 1975, Collette and Russo 1985b).

Variable characters are found on the haemal arches and haemapophyses. Laterally directed parapophyses, arising from the middle of the centrum, appear on the 4th–6th vertebrae where the intermuscular bones and pleural ribs are encountered (see section on Ribs and Intermuscular Bones). The parapophyses become broader and longer posteriorly and gradually shift to the anteroventral portion of the centra. In lateral view, the first ventrally visible parapophyses are found on the 6th–7th vertebra in *Grammatorcynus*, the 7th–9th in *Scomberomorus* (usually the 8th), and on the 14th–15th in *Acanthocybium*.

Posteriorly, the distal ends of the paired parapophyses meet, forming the first closed haemal arch. The first closed haemal arch is on the 8th vertebra in *Grammatorcynus*, 10th–16th vertebra in *Scomberomorus*, and 25th–28th vertebra in *Acanthocybium*. This location is correlated with the total number of vertebrae. The haemal spines become elongate and point posteriorly until they abruptly become more elongate on the first caudal vertebra. The paired pleural ribs (see section on Ribs and Intermuscular Bones) attach to the distal ends of the parapophyses and arches and extend posteriorly to the last precaudal vertebra. The haemal arches and spines bend posteriorly at the caudal peduncle and then merge into the caudal complex symmetrically with the neural arches and spines on the caudal vertebrae.

Haemapophyses include pre- and postzygapophyses, but their relative positions are different from those of the neurapophyses, and they do not overlap. The first haemal postzygapophyses arise posteroventrally from the 6th–7th centrum in *Grammatorcynus*, the 6th–8th in *Scomberomorus*, and the 9th–10th in *Acanthocybium*. They reach their maximum length at about the junction of the precaudal and caudal vertebrae. The haemal postzygapophyses fuse with the haemal spine or disappear in the caudal peduncle region. The haemal prezygapophyses arise from the anterior base of the haemal arches on the 8th–11th vertebra in *Grammatorcynus*, the 10th–22nd in *Scomberomorus*, and the 23rd–25th in *Acanthocybium*.

Struts between the haemal arch and the centrum form the inferior foramina. Foramina are present from the 17th–19th to the 25th–28th vertebra in *Grammatorcynus*, the 21st–33rd to the 35th–52nd in *Scomberomorus*, and the 49th–51st to the 56th–57th in *Acanthocybium*.

**Ribs and Intermuscular bones** Pleural ribs are present from the second or third vertebra posterior to the 12th–31st vertebra in the three genera. Intermuscular bones start on the back of the skull or the first vertebra and extend to the 10th–30th vertebra.

Correlated with its low number of vertebrae, *Grammatorcynus* has the fewest pleural ribs (10 pairs). *Acanthocybium* has the most pleural ribs (30 pairs) in agreement with its many vertebrae. Species of *Scomberomorus* are intermediate in number of vertebrae and also in number of pleural ribs (15–21). The first pleural rib articulates with the centrum of the third vertebra in *Grammatorcynus* and most species of *Scomberomorus*, and articulates with the centrum of the second vertebra in *Acanthocybium*, as noted by Devaraj (1977:44), and in at least one specimen each of *S. commerson*, *S. maculatus*, and *S. sinensis*. Pleural ribs usually extend posteriorly to about the last precaudal vertebra: 12 in *Grammatorcynus*, 17–23 in *Scomberomorus*, and 31 in *Acanthocybium*.

Intermuscular bones start on the first vertebra in *Grammatorcynus*, *Acanthocybium*, and some species of *Scomberomorus*. In some specimens of at least 13 species of *Scomberomorus*, the first intermuscular bone is attached to the exoccipital on the skull, and in *S. concolor*, *S. koreanus* (also noted by Devaraj 1977), and *S. sierra*, it appears to be the usual condition. *Grammatorcynus* has 19–21 pairs of intermuscular bones, many more than *Acanthocybium* (only 10 pairs, which seems odd given its high number of vertebrae and pleural ribs), but fewer than most species of *Scomberomorus* (20–30 pairs).

**Caudal complex** Three preural centra support the caudal fin in *Grammatorcynus*. In *Scomberomorus* four or five preural centra support the caudal fin, and in *Acanthocybium* there are five. The urostyle represents a fusion of preural centrum 1 and the ural centrum (Potthoff 1975). The urostyle is fused with the triangular hypural plate posteriorly and articulates with the uroneural dorsally. In *Grammatorcynus* there is very little compression of the preural centra. Preural centrum 4 is not shortened at all, preural centrum 3 is shortened slightly, and preural centrum 2 is shortened slightly more (Collette and Russo 1985b:fig. 39). In *Acanthocybium* and *Scomberomorus*, preural centra 2–4 are compressed more than any of the preural centra in *Grammatorcynus*, but still not as much as the centra in the bonitos and tunas (Collette and Chao

1975, Gibbs and Collette 1967). In *Grammatorcynus* the posterior-most neural and haemal spine bend away from the vertebral axis and parallel the dorsal and ventral edges of the hypural plate. In *Acanthocybium* and *Scomberomorus*, three posterior neural and haemal spines bend away from the vertebral axis more abruptly than in *Grammatorcynus*.

The triangular hypural plate is composed of 5 fused hypural bones (Potthoff 1975). In some specimens of *Grammatorcynus* (*G. bilineatus* 453 and 521 mm FL, and *G. bicarinatus* 563 mm FL) the dorsalmost (hypural 5) is partially fused with the dorsal part of the hypural plate (hypurals 3–4). However, in smaller specimens (382–424 mm FL) such fusion was absent, as is the case in *Scomberomorus* and *Acanthocybium*. There is a primitive hypural notch present on the middle of the posterior margin of the hypural plate. This notch is a remnant of the fusion of the dorsal part of the hypural plate with the ventral part (hypurals 1–2). The notch is absent in the more advanced bonitos and tunas (Collette and Chao 1975).

The parhypural is separate from the ventral hypural plate in *Grammatorcynus* and *Scomberomorus* but is fused with it in *Acanthocybium*. This fusion was also noted by Conrad (1938), Fierstine and Walters (1968), and Devaraj (1977). The two haemal arches preceding the parhypural are autogenous in the three genera, although Devaraj (1977) stated that they were fused with their centra in *Acanthocybium*.

The parhypural has a strongly-hooked process, the parhypurapophysis (or hypurapophysis), at its proximal end. The parhypurapophysis slopes slightly upwards similarly in *Grammatorcynus* and *Scomberomorus*. In *Acanthocybium* it has a right angle and then a level projection.

There are two epurals as in other scombrids (Potthoff 1975). In shape and size, the anterior epural (1) resembles the neural spine of adjacent preural centrum 3. The smaller, posterior epural (2) is a free splint located between the anterior epural and the uroneural and fifth hypural, which are joined together.

**Dorsal and anal fins** *Grammatorcynus* usually has 12 dorsal spines, rarely 11 or 13 (Table 4), fewer than either *Scomberomorus* (12–22) or *Acanthocybium* (23–27). Dorsal spine counts are roughly correlated with vertebral number: *Grammatorcynus* has the fewest precaudal, caudal, and total vertebrae, and the fewest dorsal spines, while *Acanthocybium* has the most precaudal and total vertebrae, and the most dorsal spines.

**Table 4**  
Number of dorsal spines, second dorsal fin rays, and dorsal finlets in *Grammatorcynus*.

	Spines			Rays			Finlets		
	11	12	13	10	11	12	6	7	8
<i>G. bilineatus</i>	4	65	1	10	55	4	61	9	
<i>G. bicarinatus</i>		10		10			1	9	1

**Table 5**  
Number of anal fin rays and finlets in *Grammatorcynus*.

	Rays			Finlets		
	11	12	13	5	6	7
<i>G. bilineatus</i>	12	42	17	1	61	8
<i>G. bicarinatus</i>	5	3	1		3	7

The range in number of second dorsal fin rays is 10–25 in the three genera. *Grammatorcynus* has 10–12 rays, 10 in *G. bicarinatus* and usually 11 in *G. bilineatus* (Table 4). There are usually more second dorsal rays in *Acanthocybium* (11–16) and *Scomberomorus* (15–25).

Dorsal finlets number 6–11 in the three genera. *Grammatorcynus* has 6–8, usually 7 in *G. bicarinatus*, and usually 6 in *G. bilineatus* (Table 4). *Acanthocybium* has 7–10, and *Scomberomorus* has 6–11. The total number of second dorsal elements is the same in both species of *Grammatorcynus*,  $11+6=17$  in *G. bilineatus*,  $10+7=17$  in *G. bicarinatus*.

Anal fin rays show a similar trend to that of dorsal fin rays. The range in the three genera is 11–29. *Grammatorcynus* has 11–13 (Table 5), similar to *Acanthocybium* (11–14), but much fewer than *Scomberomorus* (15–29).

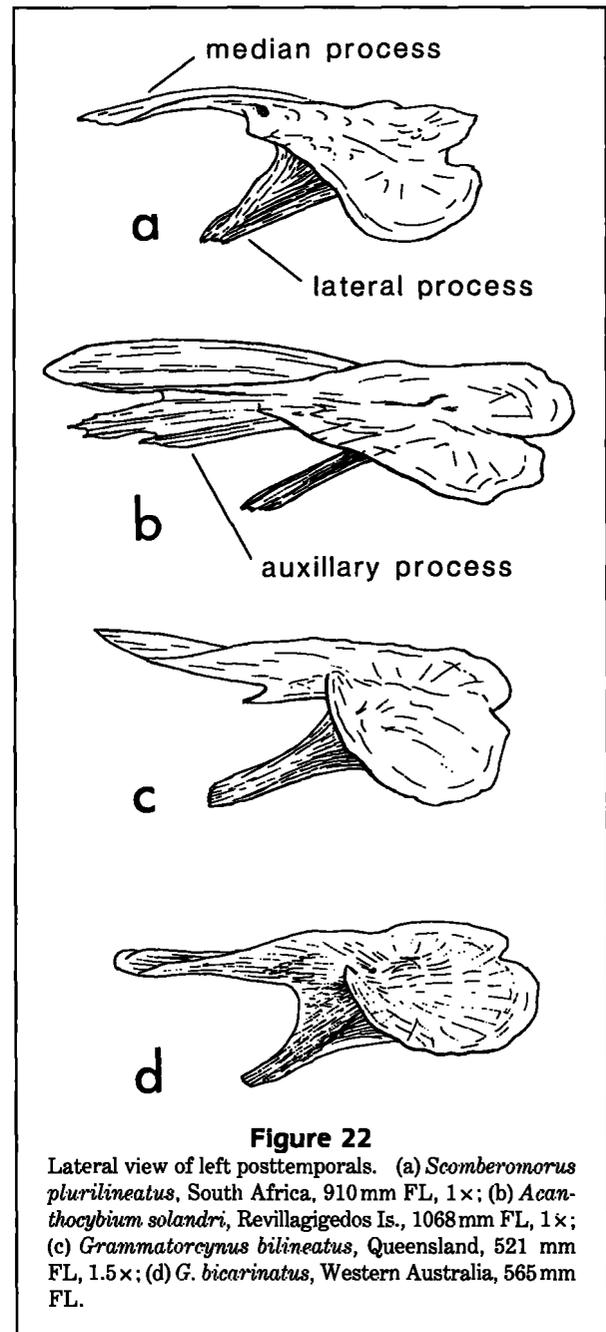
Anal finlets range in number from 5 to 12 in the three genera. *Grammatorcynus* has 5–7, usually 6 in *G. bilineatus*, and usually 7 in *G. bicarinatus* (Table 5), generally fewer than *Acanthocybium* (7–10) or *Scomberomorus* (5–12). Again, the total number of anal elements is the same in both species,  $12+6=18$  in *G. bilineatus*,  $11+7=18$  in *G. bicarinatus*.

**Pectoral girdle** The pectoral girdle consists of the girdle itself (cleithrum, coracoid, and scapula), the radials to which the pectoral fin rays attach, and a chain of bones that connect the girdle to the rear of the skull (posttemporal, supracleithrum, supratemporal, and two postcleithra).

**Posttemporal** The posttemporal (Fig. 22) is a flat elliptical bone with two sturdy anterior processes that attach the pectoral girdle to the neurocranium. The median (dorsal) process articulates with the dorsal surface of the epiotic. The lateral (ventral) process is shorter, round in cross section, and its hollow anterior end articulates with the dorsal protuberance of the intercalar. There is a thin shelf visible between these two processes in *G. bicarinatus* (Fig. 22d) and *Scomberomorus* (Fig. 22a), but this shelf is hidden behind the flat, posterior portion of the bone in *G. bilineatus* (Fig. 22c) and *Acanthocybium* (Fig. 22b). A variably-sized notch is present at the middle of the posterior edge of the flat body of the bone. *Grammatorcynus* usually has a distinct, variably-sized anteriorly directed spine on the ventral margin of the median process about one-third of the distance from the body of the bone to the anterior tip of the process. In *Acanthocybium*, there is a separate process extending anteriorly from the ventral wall of the median process. This auxillary process (Kishinouye 1923) is as long or almost as long as the median process itself. It ends in a series of several pointed processes. (Both Conrad 1938 and Devaraj 1977 referred to the auxillary process as the median process.) The lengths of the median and lateral processes vary among the species under discussion. The lengths were measured from the midpoint of the shelf that connects the two processes, to the end of the processes. Both the median and lateral processes are longer, relative to the length of the entire bone, in *G. bilineatus* where the shelf is hidden posteriorly (median process is 53–60% length of entire bone, and lateral process is 35–40%) than in *G. bicarinatus* where the shelf is not hidden, and is found more near the midpoint of the bone (median process is 49% and lateral process is 30%). In *Acanthocybium* (shelf hidden) the median process is 56–65% the length of the entire bone, and the lateral process is 27–37%. In *Scomberomorus* (shelf evident) the median process is 36–51% and the lateral process is 15–36%.

Another useful taxonomic character is the presence (if present, shape is important) or absence of a spine or process at the base of the lateral process on the inner surface of the posttemporal. It is present as a wide flap in *Grammatorcynus* (Fig. 22c, d), a blunt process in *Acanthocybium* (Fig. 20b), and as a shelf with a point in *S. commerson*, *S. munroi*, *S. nipponius*, *S. plurilineatus* (Fig. 22a), and sometimes in *S. sinensis*. It is absent or small and inconspicuous in the other 13 species of *Scomberomorus*.

**Supracleithrum** The supracleithrum is an ovate bone, overlapped dorsolaterally by the posttemporal and overlapping the anterior part of the dorsal wing-like extension of the cleithrum. The anterior border of the bone on the mesial side is thickened into a ridge.



**Figure 22**

Lateral view of left posttemporals. (a) *Scomberomorus plurilineatus*, South Africa, 910 mm FL, 1×; (b) *Acanthocybium solandri*, Revillagigedos Is., 1068 mm FL, 1×; (c) *Grammatorcynus bilineatus*, Queensland, 521 mm FL, 1.5×; (d) *G. bicarinatus*, Western Australia, 565 mm FL.

Dorsally there is a small handle-shaped process that curves into the posterior margin to end in a notch at the posterodorsal aspect. Both the anterior and posterior borders are extended so that they form humps in *Grammatorcynus* (Collette and Russo 1985b:fig. 41). A branch of the lateralis system extends from the posterior notch of the posttemporal onto the supracleithrum. This short canal lies ventral to the dorsal process of the supracleithrum and extends to the posterior edge of the bone.

The maximum width of the supracleithrum varies from 43 to 75% of the total length of the bone in the three genera. It is widest in *Grammatorcynus*, width 72–82% (89% in one 475 mm FL specimen of *bilineatus*) of length (due to the extensions of anterior and posterior borders). *Scomberomorus* varies in width from 43% in *S. multiradiatus* to 62% in *S. nipponius*. There is no evidence that size is a factor in the size of the supracleithrum in *Grammatorcynus* as was noted by Collette and Russo (1985b) for *Scomberomorus*.

The dorsal process is prominent in *Grammatorcynus*, *S. cavalla*, *S. commerson*, *S. lineolatus*, and especially in *Acanthocybium*. In other species of *Scomberomorus*, it is either small or less sharply set off from the main body of the supracleithrum.

**Supratemporal** The supratemporal is a thin flat bone having three distinct arms and lying just underneath the skin where its lateral arm articulates with a dorsal articular surface on the pterotic. The anterior-most arm is the longest, while the ventrally directed arm is the shortest. The arm directed posteriorly is intermediate in length. The anterior margin is deeply concave, and the greatly convex posterior margin slightly overlaps the dorsal arm of the posttemporal.

The supratemporal bears a prominent lateral line canal that extends out almost to the tips of all three arms (Collette and Russo 1985b:fig. 42). In these three genera, the canal along the anterior margin of the bone is the longest, and the canal along the lateral side is next longest. In *Grammatorcynus*, the first canal is not branched like it is in most species of *Scomberomorus*, and the second canal is relatively longer.

**Cleithrum** The main body of the cleithrum is crescent-shaped with an anterodorsal spine and a posteriorly projecting plate at the upper end (Collette and Russo 1985b:fig. 43). The angle between the spine and the plate is much smaller in *Grammatorcynus* and *Scomberomorus* than in *Acanthocybium*. In *Grammatorcynus*, the spine does not extend as far dorsally as the plate. In *Acanthocybium* and most species of *Scomberomorus*, the spine extends about equally as far dorsally as the plate, and in *S. sinensis* the spine extends well beyond the dorsal margin of the plate. In *Grammatorcynus* and most species of *Scomberomorus*, the plate narrows posteriorly. The posterior plate is longer and of uniform width in *Acanthocybium*.

The lower part of the cleithrum is large and folded back upon itself as two walls: one lateral and the other mesial, which meet at their anterior margins and run parallel to each other. The mesial wall of the cleithrum forms a large triangular slit with the coracoid. In *Grammatorcynus* and *Scomberomorus*, the lateral wall of the cleithrum is narrow enough to allow part of the slit to be visible in a lateral view. This slit is hidden

in lateral view in the species of *Scomberomorus* because of the great width of the lateral wall of the cleithrum (Devaraj 1977:46, Collette and Russo 1985b:figs. 43a–b).

**Coracoid** The coracoid is elongate and more or less triangular in shape. It connects with the scapula along its dorsal edge and with the mesial shelf of the cleithrum anterodorsally and anteroventrally. The coracoid is relatively wider in *Grammatorcynus* and *Scomberomorus* than in *Acanthocybium*.

**Scapula** The anterior margin of the scapula connects to the mesial shelf of the cleithrum. This attachment extends to the posterior projecting plate anterodorsally. The scapula is attached to the coracoid posteriorly and with the first two radials posterodorsally. The posterodorsal margin of the scapula is drawn out into a facet that accepts the most anterior ray of the pectoral fin. The scapula is pierced by a large, usually round, foramen near the lateral margin with the inner shelf of the cleithrum. A prominent suture leads to the dorsal and ventral margin of the scapula from the foramen. The suture is intermediate in size in *Grammatorcynus* relative to the large sutures present in *Acanthocybium*, *S. brasiliensis*, and *S. regalis*, and the small suture in *S. koreanus*.

**Radials** The four radials differ in size and shape and attach directly to the thickened posterior edges of the scapula and coracoid. The size of the radials increases posteroventrally. Small foramina are located between the 2nd and 3rd and the 3rd and 4th radials counting posteriorly. In *Grammatorcynus* the first two radials, and sometimes a small portion of the third, attach to the scapula; the second two, sometimes only one and a large portion of the second, attach to the coracoid. In *Acanthocybium* and *Scomberomorus* the upper one-third of the third radial, along with the first two radials, always attaches to the scapula, and the ventral two-thirds of the third radial plus the fourth radial attach to the coracoid. A much larger foramen is present between the largest (fourth) radial and the coracoid. Posteriorly, this foramen is framed by a posterior process of the upper part of the fourth radial meeting an anterior process from the posterior margin of the coracoid. This process is only slightly developed in *Grammatorcynus*. The foramen is about equal in size to, or larger than the scapular foramen in *Grammatorcynus* and *Scomberomorus*, whereas in *Acanthocybium* the scapular foramen is much larger.

**Pectoral fin rays** The first (uppermost and largest) pectoral fin ray articulates directly with a posterior process of the scapula. The other rays attach to the radials. The number of pectoral rays varies from 19 to 26 in the three genera. *Grammatorcynus* has 21–26

pectoral fin rays, similar to *Acanthocybium* (22–26). *Scomberomorus* shows greater variation (19–26) in this character and in most species averages less than either *Grammatorcynus* or *Acanthocybium*. There is a slight difference in number of pectoral fin rays between the species of *Grammatorcynus*: *G. bilineatus* has a range of 22–26, mode 25,  $\bar{x}$  24.4; *G. bicarinatus* 21–24, mode 24,  $\bar{x}$  23.2 (Table 6).

**First postcleithrum** The posterior projecting plate of the cleithrum has its posterior end attached to the first postcleithrum which connects ventrally to the second postcleithrum. The lamellar first postcleithrum has a narrower upper end and a wider, rounded lower margin (Fig. 23). The upper end is concave in *Grammatorcynus* (Fig. 23c–d) and pointed in both *Scomberomorus* (Fig. 23a) and *Acanthocybium* (Fig. 23b). The width of the postcleithrum varies from 46 to 62% of the length of the bone in *Grammatorcynus*. It is narrower in *G. bicarinatus* (width 46–52% of length, Fig. 23d) than in *G. bilineatus* (55–62%, Fig. 23c). In *Acanthocybium* (47–48%, Fig. 23b) the width is similar to that of *G. bicarinatus*. Species of *Scomberomorus* (Fig. 23a) have narrower postcleithra (24–41%) than the other two genera.

**Second postcleithrum** The second postcleithrum is broad and lamellar at the upper part with a short pointed ascending process and a long styliform descending process. *Grammatorcynus* (Fig. 24d) differs strikingly from *Acanthocybium* (Fig. 24c) and *Scomberomorus* (Fig. 24a–b) in having a distinct process extending anteriorly from the broad lamellar portion of the bone. The long descending process is so thin in most specimens that an accurate measurement of its length is nearly impossible because some portion of it usually breaks off. No differences were detected in this bone between the two species of *Grammatorcynus*.

**Pelvic girdle** The pelvic fin rays (I, 5) attach directly to the paired basipterygia that make up the pelvic girdle. The bones are united along the midline and are imbedded in the ventral abdominal wall, free from contact with other bones. Each basipterygium is composed of three main parts: a wide anterodorsal plate, a thin, flat anterior process, and a strong posterior process.

To compare the pelvic girdles, the lengths of the three parts were measured from their bases to their tips. *Grammatorcynus* has the longest anterior process (46–51% of the length of the anterodorsal plate, Fig. 25d), *Acanthocybium* has the next longest (35–47%, Fig. 25c), and *Scomberomorus* the shortest (15–52%, Fig. 25a–b). *Grammatorcynus* (29–33%, Fig. 25d) and *Acanthocybium* (30–39%, Fig. 25c) have shorter posterior processes than the species of *Scomberomorus*

	21	22	23	24	25	26	N	$\bar{x}$
<i>G. bilineatus</i>		1	11	19	27	4	62	24.4
<i>G. bicarinatus</i>	1	2	2	6			11	23.2

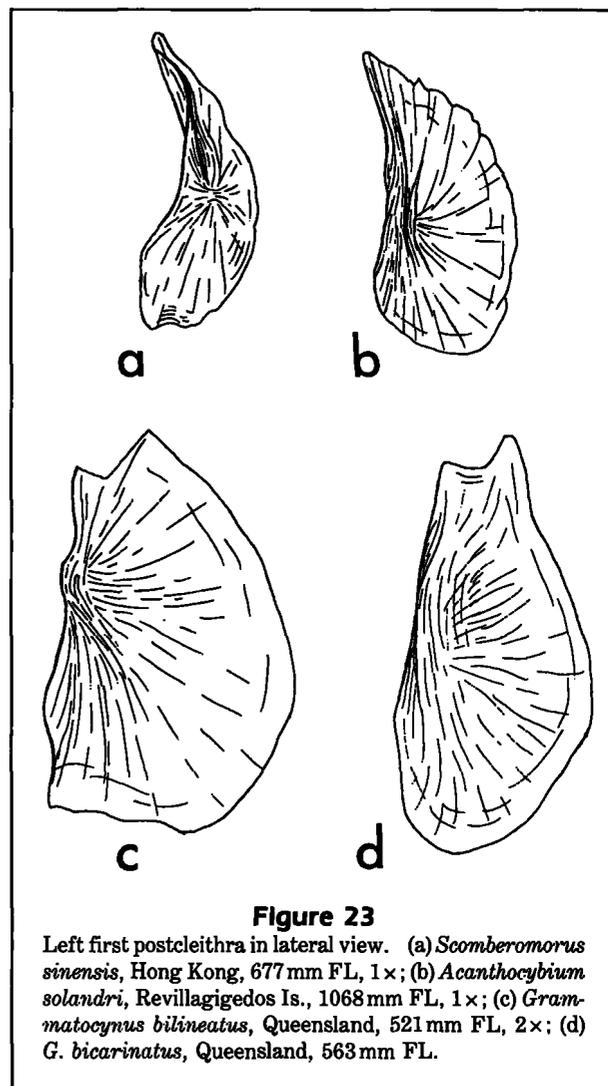
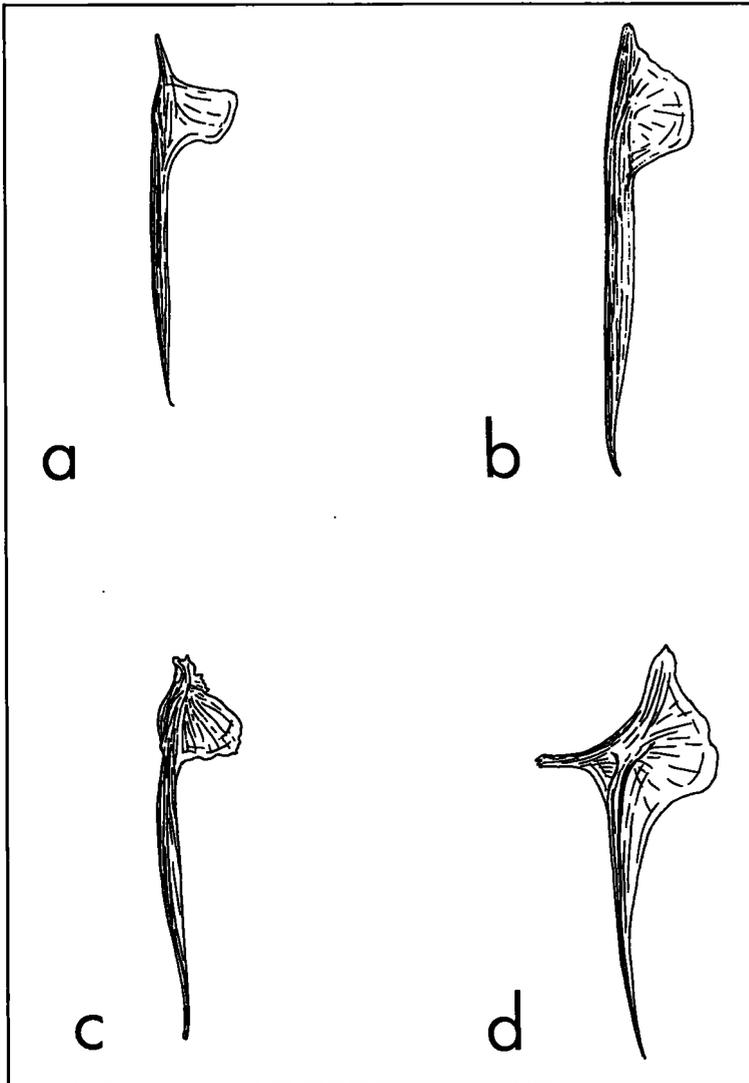


Figure 23

Left first postcleithra in lateral view. (a) *Scomberomorus sinensis*, Hong Kong, 677 mm FL, 1×; (b) *Acanthocybium solandri*, Revillagigedo Is., 1068 mm FL, 1×; (c) *Grammatorcynus bilineatus*, Queensland, 521 mm FL, 2×; (d) *G. bicarinatus*, Queensland, 563 mm FL.

(20–90%, Fig. 25a–b).

*Grammatorcynus*, some individuals of *Acanthocybium*, and several species of *Scomberomorus* have longer anterior than posterior processes. The lengths of the anterior process as a percentage of the posterior process are: *Grammatorcynus* (154–158%), *Acanthocybium* (91–156%), and *Scomberomorus* species (42–121%).



**Figure 24**

Left second postcleithra in lateral view. (a) *Scomberomorus queenslandicus*, Great Barrier Reef, 641 mm FL, 1×; (b) *S. koreanus*, Indonesia, 480 mm FL, 1.5×; (c) *Acanthocybium solandri*, Revillagigedos Is., 1068 mm FL, 1×; (d) *Grammatorcynus bilineatus*, Queensland, 382 mm FL, 2×.

*Grammatorcynus* differs from most other scombrids in having a single fleshy interpelvic process. *Auxis* and *Gymnosarda* also have a single interpelvic process; very large in the former, moderate-sized in the latter.

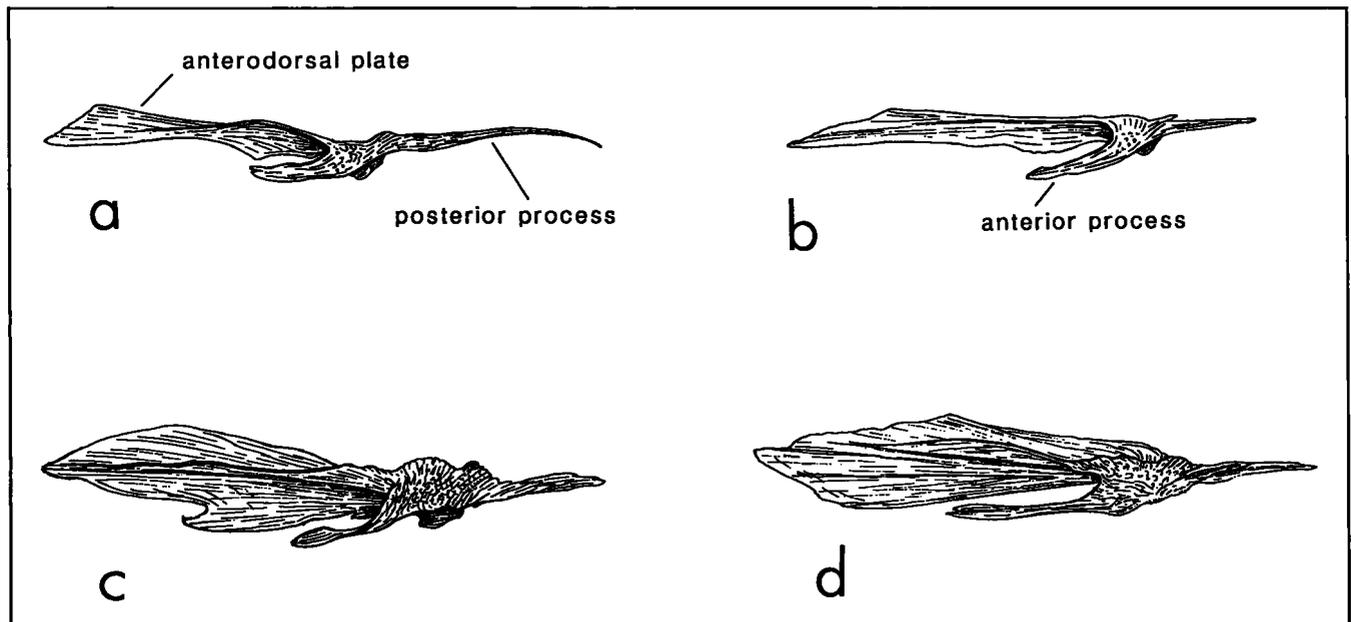
**Part 2: Systematics and biology**

***Grammatorcynus* Gill 1862**

*Grammatorcynus* Gill 1862: 125 (original description; type-species *Thynnus bilineatus* Rüppell 1836 by original designation).  
*Nesogrammus* Evermann and Seale 1907: 61 (original description; type-species *Nesogrammus piersoni* Evermann and Seale 1907 by original designation, = *Grammatorcynus bilineatus*).

**Figure 25 (below)**

Right basiptyrgia of the pelvic girdle in mesial view. (a) *Scomberomorus regalis*, Miami, FL, 469 mm FL, 1.5×; (b) *S. lineolatus*, Palk Strait, India, 428 mm FL, 2×; (c) *Acanthocybium solandri*, Miami, FL, 1403 mm FL, 1×; (d) *Grammatorcynus bilineatus*, Queensland, 521 mm FL, 1.5×.



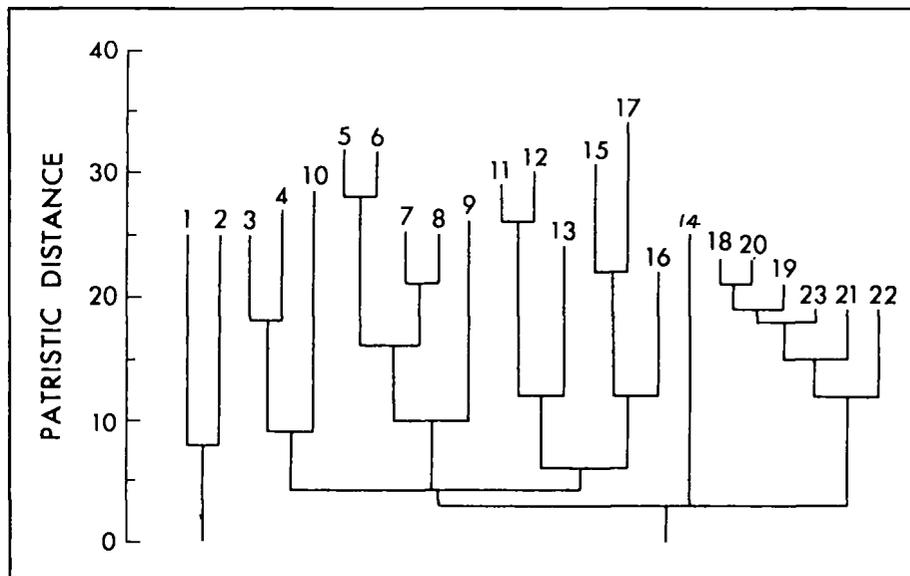
**Diagnosis** *Grammatorcynus* differs from all other scombrid genera in having a second ventral lateral line, and it differs from all other scombrids and billfishes in lacking a triangular bony stay on the fourth pharyngeal toothplate (Johnson 1986). Like the Scombrini, it has a low number of vertebrae (31) and the caudal fin rays are supported by only the last three vertebrae. Like the Scomberomorini, it has a well-developed median keel on the caudal peduncle, but it lacks the bony support for the keel that is present in bonitos and higher tunas. *Grammatorcynus* differs from *Scomberomorus* in having a pineal window, a single interpelvic process, and large scales.

Collette and Russo (1985b: 612) reported that *Grammatorcynus bilineatus* differed from *Scomberomorus* and *Acanthocybium* in 16 osteological characters. *Grammatorcynus bicarinatus* also differs in 15 of those 16 characters: (1) supracleithrum wide, 72–89% of length (narrow, 42–62% in *Scomberomorus* and *Acanthocybium*); (2) pores absent along dorsal branch of supratermporal (present); (3) nasal bones protrude far beyond ethmoid region (do not protrude far beyond); (4) posterior end of urohyal tripartite (forked); (5) glossohyal with large tooth patch fused to dorsal surface of bone (no fused tooth patch); (6) hyomandibula narrow, 34–39% of length (wide, 39–52%); (7) angle of lateral and medial arms of fourth epibranchial more acute (less acute); (8) anterior process of second epibranchial elongate (shorter); (9) three vertebrae support caudal fin rays (four or five vertebrae); (10) distinct anterior process on second postcleithrum (no such process); (11) anterior end of first postcleithrum notched (pointed); (12) first two pectoral radials attach

to scapula (upper one-third of third radial also attaches to scapula); (13) jaw teeth conical (compressed and triangular); (14) shaft of parasphenoid narrow and concave or flat (wider and convex); and (16) posterior edge of ectopterygoid long, 63–72% of ventral distance (short, 41–63%). Unlike *G. bilineatus*, *G. bicarinatus* resembles *Scomberomorus* and *Acanthocybium* in having the upper margin of the dentary longer than the lower margin (15).

**Relationships** Larval characters of *Grammatorcynus bilineatus* (as described by Wade 1951 from eight specimens 8.5–17.5 mm FL) were used by Okiyama and Ueyanagi (1977, 1978) and Ueyanagi and Okiyama (1979) to construct an “index of primitiveness” that divided the Scombrinae into four groups: mackerels, *Grammatorcynus*, tunas, and Spanish mackerels and bonitos. Nishikawa (1979) expanded the description of larvae based on 62 specimens, 4.75–56.9 mm SL, from Papua New Guinea. Nishikawa (1979) and Jenkins (1989) noted that *Grammatorcynus* larvae have preopercular spines characteristic of higher scombrids but absent in *Scomber* and *Rastrelliger*.

Lewis (1981) examined Australian scombrids electrophoretically and found that the two *Grammatorcynus* species showed fixed differences at 6 (23%) of 26 loci (GPD, ADA, ADH, GDA, PK<sub>2</sub>, and PGM<sub>1</sub>). Fixed differences were also observed at several other loci not used in his study, namely AD<sub>2</sub> and XO. He analyzed the electrophoretic data phenetically and cladistically. The two most parsimonious Wagner networks involved 308 steps. The species of *Grammatorcynus* were always paired and well-separated from



**Figure 26**

One of two equally parsimonious Wagner networks for 23 Australian species of Scombridae expressed in dendrogram form (from Lewis 1981: fig. 6.4). (1) *Scomber australasicus*, (2) *Rastrelliger kanagurta*, (3) *Grammatorcynus bicarinatus*, (4) *G. bilineatus*, (5) *Scomberomorus commerson*, (6) *S. queenslandicus*, (7) *S. multiradiatus*, (8) *S. semifasciatus*, (9) *S. munroi*, (10) *Acanthocybium solandri*, (11) *Sarda australis*, (12) *S. orientalis*, (13) *Cybiosarda elegans*, (14) *Gymnosarda unicolor*, (15) *Aucis* sp., (16) *Euthynnus affinis*, (17) *Katsuwonus pelamis*, (18) *Thunnus albacares*, (19) *T. tonggol*, (20) *T. obesus*, (21) *T. alalunga*, (22) *T. maccoyii*, (23) *T. thynnus orientalis*.

other Scomberomorini (Fig. 26). They were most often linked with *Acanthocybium* and then with species of *Scomberomorus*.

Based on both adult and larval morphological characters and Lewis' electrophoretic data, *Grammatorcynus* is clearly more advanced than the mackerels (Scombrini) and less advanced than the higher scombrids. Collette et al. (1984:fig. 312) placed it between *Gasterochisma* and the Scombrini on the one hand, and the more advanced Scomberomorini, Sardini, and Thunnini on the other hand. Collette and Russo (1985a, b) used *Grammatorcynus* as the primary outgroup in assessing relationships of the species of *Scomberomorus*. In his reappraisal of scombroid relationships, Johnson (1986: fig. 1 and p. 38–39) placed *Grammatorcynus* in its own tribe, Grammatorcynini, above the Scombrini, as the sister group of higher scombroids, which included the Sardini (including the Thunnini), Scomberomorini, Acanthocybiini, and billfishes.

***Grammatorcynus bilineatus* (Rüppell, 1836)**  
**Double-lined or scad mackerel**

*Thynnus bilineatus* Rüppell 1836:39–40 (original description, Red Sea), pl. 12, fig. 2. Günther 1860: 366–367 (description). Klunzinger 1871:443 (Red Sea). Meyer 1885:270 (Celebes).

*Grammatorcynus bilineatus*. Gill 1862:125 (*T. bilineatus* type species of new genus). Kishinouye 1923: 413–415 (description, anatomy; Ryukyu and Marshall Is.), fig. 10 (skeleton); pl. 16, fig. 8 (transverse section of vertebrae; pl. 34, fig. 62 (drawing). Hardenberg 1935:137–138 (description; W Java Sea). Okada 1938:170 (E. Indies, Red Sea; nijiyō saba). Morice 1953:36–40 (anatomy; after Kishinouye 1923). Schultz 1960:411–412 (description; Bikini, Marshall Is.). Kuronuma 1961:16 (listed, Vietnam). Lewis 1968:51 (Eniwetok, Marshall Is., infested with parasitic copepod *Caligus asymmetricus*). Collette 1983: 715–716 (distinguished from *G. bicarinatus*), fig. 1A. Collette and Nauen 1983:39–40 (description, range, fig.). Collette et al. 1984:608 (fig. 326, larva after Nishikawa 1979), 618 (larvae). McPherson 1984 (color pattern in Queensland, fig.). Masuda et al. 1984: 224–225 (description); color pl. 220A. Collette and Russo 1985a:141–144 (outgroup for *Scomberomorus*). Collette and Russo 1985b (anatomy, osteology, figures, comparisons with *Scomberomorus*). Allen and Russell 1986:101 (Scott Reef, NW Australia). Grant 1987:362–363 (scad mackerel; Queensland; color photo 769). Allen and Swainston 1988: 144 (Dampier Archipelago northwards, NW Australia), 145 (color painting 966). Bauchot et al. 1989: 657 (large brain, encephalization index of 226).

Zug et al. 1989:14 (Rotuma I.). Randall et al. 1990:443 (description, range), color plate VIII-14 (painting).

*Nesogrammus piersoni* Evermann and Seale 1907 (original description; Bulan, Sorsogon Province, Luzon, Philippine Is.); pl. 1, fig. 3.

*Grammatorcynus bicarinatus* not of Quoy and Gaimard 1825. Herre 1931:33 (Balabac and Jolo, Philippine Is.). Fraser-Brunner 1950:156 (synonymy), fig. 25. Umali 1950:9 (Zamboanga and Jolo, Philippine Is.). Warfel 1950:18 (Philippine Is.), fig. 13 (drawing of fish, gill arch, and liver). Wade 1951:456–458 (8 larvae, 8.5–17.5 mm; Philippine Is.), fig. 2 (8.5 mm specimen), fig. 3 (17.5 mm specimen). de Beaufort 1951:215–216 (description, synonymy), fig. 36. Herre 1953:248 (synonymy). Dung and Royce 1953: 168–169, table 97 (morphometric data on 17 specimens 408–580 mm FL, western Marshall Is.). Matsu- bara 1955:519 (2 lateral lines; range), fig. 222B. Munro 1958b:262–263 (New Guinea region records; CSIRO C492, New Hanover, examined). Jones et al. 1960:136 (Ross I., Port Blair, Andaman Is.). Collette and Gibbs 1963a:25 (monotypic genus). Collette and Gibbs 1963b:27 (description), pl. 7. Jones and Silas 1963:1781 (synonymy, Indian Ocean references, range). Silas 1963:811–833 (description, synonymy, synopsis of biological data). Kamohara 1964:34 (Miyako-jima, Ryukyu Is.). Jones and Kumaran 1964:364–365, figs. 70–71 (larvae, after Wade 1951). Jones and Silas 1964a:16, 18 (description, synonymy, range), pl. 4, fig. (449 mm female from Port Blair, Andaman Is.). Jones and Silas 1964b:258 (in key; Andaman Is.). Gorbunova 1965: 55 (references to Wade 1951 and Silas 1963). Tongy- yai 1966:6 (in key), 17 (pl. 1, outline fig. of specimen from Phuket I.). Kamohara 1967:43 (description). Munro 1967:197–198 (description of *G. bicarinatus*; New Guinea specimens are *G. bilineatus*). Ben- Tuvia 1968:35 (Entedibir Is., Red Sea), fig. 3g. Ben-Yami 1968:40 (schools probably occur in region of Sahlak Archipelago, southern Red Sea). Jones 1968:998 (occur in catches in Andaman area). Jones 1969:26 (Laccadive Archipelago, India). Tongyai 1970:558 (Thai common names; Indian Ocean coast of Thailand). Tongyai 1971:3–5 (description, Thai common names, Thai distribution). Shiino 1972:70 (common names). Richards and Klawe 1972:72 (references to larvae). Gushiken 1973:49 (color photograph of 60 cm specimen from Okinawa). Helf- man and Randall 1973:151 (Palau; common names mokorokor and biturturch). Magnuson 1973:350 (correlation of size, pectoral fin length, and presence of swim bladder). Lewis et al. 1974:83, 87 (Bismarck Archipelago, Papua New Guinea). Springer et al. 1974:40 (Indonesia). Romimohtairo et al. 1974:35

(Gamber Bay, Gag I., Indonesia). Gorbunova 1974:26 (fig. 2, after Wade 1951). Orsi 1974:174 (listed, Vietnam). Masuda et al. 1975:256 (color photograph F), 79 (description; Okinawa southward). Cressey 1975: 216 (parasitic copepod *Shiinoa oclusa* from nasal cavity of a specimen from N. Celebes). Kailola 1975:235 (5 collections from Papua New Guinea). Uyeno and Fujii 1975:14 (table 1, comparison of caudal complex with other scombrids). Fourmanoir and Laboute 1976:183 (description; New Caledonia), color photograph. Shiino 1976:229 (common names). Anonymous 1977:15 (table 4, Bagaman I., Louisiade Archipelago, Papua New Guinea). Klawe 1977:2 (table 1, range). Collette 1979:29 (characters, range). Céng and Yāng 1979:472-473 (description; Sisha Is., South China Sea), fig. 335. Yamakawa 1979:43 (Miyako-jima, Ryukyu Is., after Kamohara 1964). Joseph et al. 1979:38 (range, figure). Nishikawa 1979:125-140 (early development; 62 postlarval and juvenile specimens, mostly from Papua New Guinea). Shirai 1980:64 (description, Ryukyu Is.), color photograph. Cressey and Cressey 1980:46 (parasitic copepod fauna: *Shiinoa oclusa* and *Caligus asymmetricus*). Rau and Rau 1980: 512-513 (description, Philippine Is.). Jones and Kumaran 1981:581-582 (description; Laccadive Archipelago), fig. 494. Wang 1981:161 (listed; S. China Sea). Johannes 1981:156-157 (biology, Palau). Lewis 1981:13 (species B, scad; maximum size 60 cm FL, 3 kg), photograph. Kyushin et al. 1982:249 (description, common name nijō-saba), color photograph (specimen from Milne Bay, New Guinea). Cressey et al. 1983:238 (systematic position of genus), 264 (parasitic copepod fauna; 4 species of *Caligus* added). Lewis et al. 1983:7 (table 2, 203 specimens, 380-630 mm FL; Fiji). Wass 1984:31 (Fiji; common name "namuauli"). Masuda et al. 1984:224-225 (description, Japan), pl. 220A. Gillett 1987:20 (caught by Satawal tuna fishermen, central Caroline Is.). Nishikawa and Rimmer 1987:5 (larval description; fig. 5, larva, postlarva, and juvenile from Nishikawa 1979). Dyer et al. 1989:65 (monogenean *Caballerocotyla* sp. from Okinawa specimen). Rivaton et al. 1989:67 (listed, New Caledonia).

*Grammatorcynnus* (sic) *bicarlinatus* not of Quoy and Gaimard 1825. Roux-Estève and Fourmanoir 1955:201 (Abulat I., Red Sea).

*Grommatorcynnus* (sic) *bicarlinatus* not of Quoy and Gaimard 1825. Zhang 1981:302 (description of 3 larvae, Sisha Is., South China Sea; fig. 1, 6.4 mm larva).

*Grammatorcynnus* (sic) *bilineatus*. Myers 1988:168 (listed, Mariana Is.). Myers 1989:254 (description; range), underwater photo 134A, 280 (listed; Caroline, Mariana, and Marshall Is.).

**Diagnosis** *Grammatorcynnus bilineatus* has more gill rakers (18-24 vs. 12-15), a larger eye (4.1-6.0% vs. 3.1-4.6% FL), lacks black spots on the lower sides of its body, and does not reach as large a size (max. 600 mm FL) as *G. bicarinatus*.

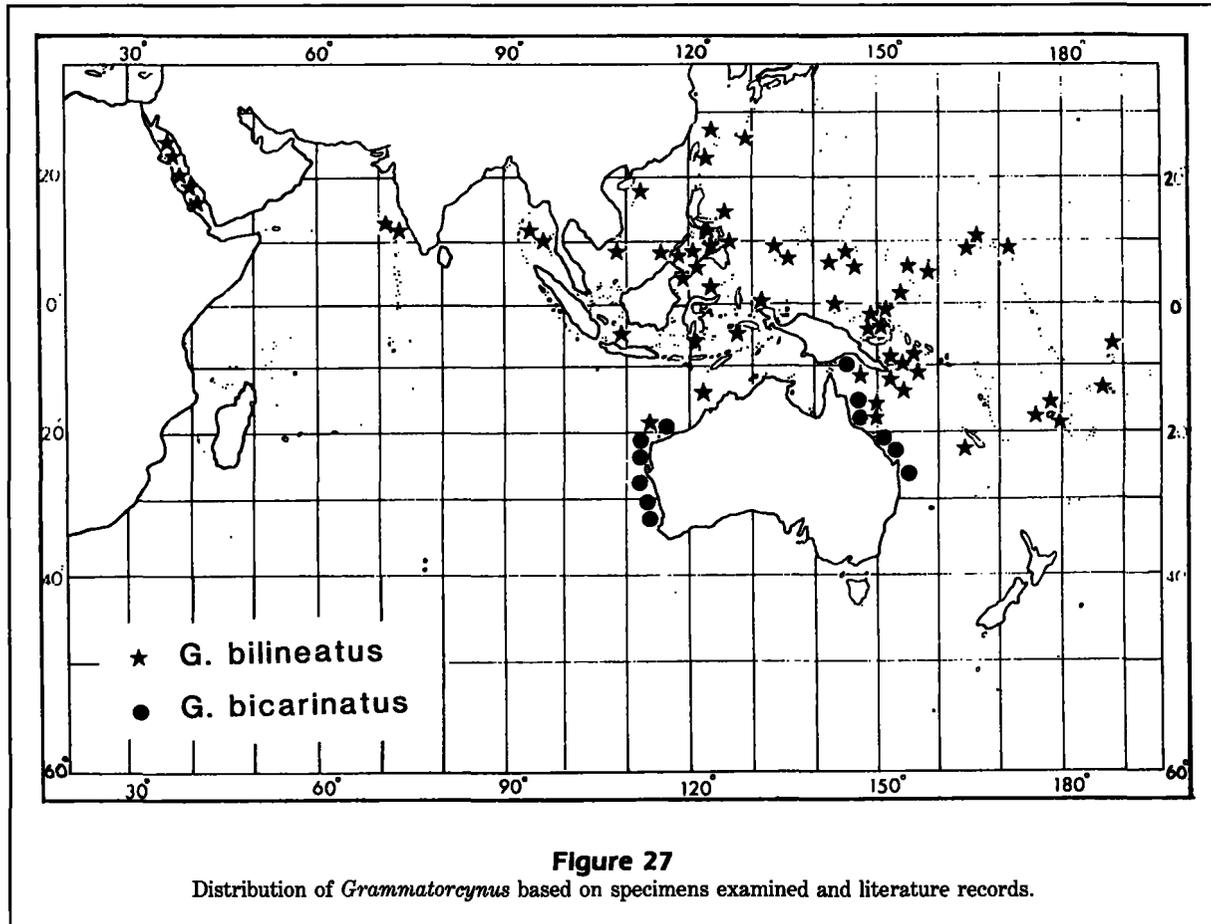
**Description** Dorsal spines 11-13, usually 12; rays 10-12, usually 11; finlets 6, rarely 7 (Table 4). Anal fin with one spine, 11-13, usually 12 rays; 6 finlets, rarely 5 or 7 (Table 5). Pectoral fin rays 22-26, usually 24 or 25 (Table 6). Gill rakers on first arch 18-24, usually 21,  $\bar{x}$  20.8 (Table 3). Upper jaw teeth 14-37,  $\bar{x}$  23.5 (left), 24.5 (right) (Table 2); lower jaw teeth 12-32,  $\bar{x}$  18.6 (left), 19.1 (right) (Table 2). Morphometric data summarized in Table 1.

*Grammatorcynnus bilineatus* has a longer neurocranium (14-16% FL vs. 13%), longer parasphenoid flanges (18-21% of neurocranium length vs. 14%), higher maximum number of teeth on the upper (37 vs. 25) and lower (32 vs. 23) jaws, higher posterior expansion of the maxilla (8-11% of maxilla length vs. 6-8%), longer quadrate process (134-145% of quadrate length vs. 122-125%), wider first postcleithrum (55-62% of length vs. 46-52%), narrower ethmoid (19-21% of length vs. 25-28%), narrower vomer (13-15% of length vs. 16-18%), narrower lachrymal (27-30% of length vs. 30-35%), shorter teeth (up to 4% of dentary length vs. up to 6%), narrower palatine tooth patch (26-32% of length vs. 38-42%), narrower opercle (63-72% of length vs. 72-79%), and the shelf between the post-temporal processes is hidden behind the flat posterior portion of the bone.

**Color** In life, the back is bright pale green, the upper sides and belly silvery, and there are no black spots on the belly as there are in *G. bicarinatus* (Grant 1987: 363). Underwater, it is reported to display a distinctive white patch on the caudal peduncle (McPherson 1984). There are color photographs of fresh specimens from Japan (Masuda et al. 1975:256, Shirai 1980:64), New Caledonia (Fourmanoir and Laboute 1976:183), South China Sea (Kyushin et al. 1982:249), and Australia (Grant 1987: fig. 769). An underwater photograph has been published from Micronesia (Myers 1989: photo 134A). There is a color painting in Randall et al. 1990 (pl. VIII-14).

**Size** Maximum size is about 63 cm FL, 3.3 kg weight (Lewis et al. 1983). Maturity seems to be attained at about 40-43 cm FL (Silas 1963, Johannes 1981, Lewis et al. 1983).

**Biology** The best summary of biological information on *G. bilineatus* is Silas (1963). It is an epipelagic species found mostly in shallow reef waters where it



forms large schools. The spawning season in Fiji extends from October through March (Lewis et al. 1983). Larvae and juveniles have been illustrated from the Philippines (Wade 1951), Papua New Guinea (Nishikawa 1979), and the South China Sea (Zhang 1981). Food includes adult and juveniles of crustaceans and fishes, particularly clupeoids such as *Sardinella* and *Thrissocles*, but also includes other fishes such as *Sphyræna* and *Balistes* (Silas 1963:831).

**Parasites** Six species of parasitic copepods have been reported from *G. bilineatus* (Cressey and Cressey 1980, Cressey et al. 1983): Shiinoidae: *Shiinoa oclusa* Kabata; Caligidae: *Caligus asymmetricus* Kabata, *C. regalis* Leigh-Sharpe, *C. bonito* Wilson, *C. pelamydis* Krøyer, and *C. productus* Dana. The monogenean *Caballerocotyla* sp. was found on an Okinawan specimen (Dyer et al. 1989).

**Interest to fisheries** Double-lined mackerel are taken incidentally with hand lines off Port Blair, Andaman Islands (Silas 1963). It is common in the offshore zones

of Fiji but is only occasionally seen in Fiji markets (Lewis et al. 1983). The flesh is reported to be mild and pleasantly flavored but it is necessary to remove the kidney tissue before cooking to avoid the ammonia smell. This characteristic has given rise to one of the Palauan names for the species, biturchurch, which means urine (Johannes 1981:187). It is valued for marlin bait in Queensland (McPherson 1984).

**Range** Widespread near coral reefs in the tropical and subtropical Indo-West Pacific (Fig. 27). Based on literature, specimens examined, and photographs, known from the Red Sea, Andaman Sea, East Indies, Philippines, South China Sea, Ryukyu Islands, New Guinea (New Britain, New Ireland, New Hanover, and the Louisiade Archipelago), Australia (northern Western Australia, from Dampier Archipelago north and Queensland), Solomon Islands, New Caledonia, Caroline Islands, Marshall Islands, Fiji, Tonga, and Tokelau Islands (photograph from Fakaofu Atoll received from Robert Gillett, Regional Fishery Support Programme, Suva, Fiji, Aug. 1985).

**Table 7**  
Morphometric comparison of *Grammatocygnus bilineatus* from the Red Sea and the western Pacific Ocean.

Character	Red Sea					Western Pacific Ocean				
	N	Min	Max	Mean	SD	N	Min	Max	Mean	SD
<b>Fork length (thousandths)</b>	15	264	432	364	53	44	226	575	430	72
Snout-A	15	592	628	615	11	41	581	641	603	12
Snout-2D	15	534	557	547	7	41	528	619	548	16
Snout-1D	15	287	306	296	7	44	276	322	295	10
Snout-P2	15	249	271	261	7	43	236	306	257	12
Snout-P1	15	220	244	230	7	43	199	245	224	9
P1-P2	15	94	135	105	9	43	90	111	100	5
Head length	15	213	234	220	6	44	197	236	218	8
Max. body depth	13	182	213	201	8	40	164	234	193	15
Max. body width	12	97	122	111	8	40	91	136	115	9
P1 length	14	110	142	122	9	44	106	142	128	7
P2 length	14	74	81	77	2	44	70	87	76	4
P2 insertion-vent	14	312	352	333	12	43	262	354	326	15
P2 tip-vent	13	242	275	256	11	43	228	273	249	9
Base 1D	15	207	246	230	10	43	211	261	236	10
Height 2D	12	88	109	98	6	37	88	116	99	7
Base 2D	14	88	114	102	8	43	79	118	102	8
Height A	11	84	102	93	7	34	82	114	96	7
Base A	14	74	89	84	4	44	73	101	88	7
Snout (fleshy)	15	77	86	81	3	44	58	90	79	5
Snout (bony)	15	71	78	74	3	44	60	80	71	5
Maxilla length	15	95	108	101	4	43	89	107	97	5
Postorbital	15	89	98	93	2	43	78	98	91	4
Orbit (fleshy)	15	44	57	49	4	44	40	60	49	4
Orbit (bony)	15	60	75	68	5	44	53	88	68	7
Interorbital	15	58	67	62	3	43	56	74	62	3
2D-caudal	15	458	475	468	5	41	427	496	471	16
<b>Head length (thousandths)</b>	15	62	94	80	11	44	50	126	94	16
Snout (fleshy)	15	340	384	369	11	44	248	397	365	22
Snout (bony)	15	313	351	336	11	44	281	357	326	18
Maxilla length	15	443	469	459	8	43	420	480	443	14
Postorbital	15	397	433	420	12	43	350	450	419	16
Orbit (fleshy)	15	206	253	222	13	44	191	257	226	15
Orbit (bony)	15	283	336	307	15	44	252	381	313	27
Interorbit	15	268	298	283	9	43	253	327	284	14

**Geographic variation** The wide range of *G. bilineatus* plus the gaps in distribution due to its preference for coral reef habitats lead to the possibility that some populations differ morphologically from others. However, comparison of frequency distributions by geographic areas of meristic characters summarized in Tables 2-6 showed general uniformity in the range and modes of these characters. The Red Sea population is the most isolated from the rest, but it showed no meristic differentiation. Comparisons of ranges and means of morphometric data showed few differences between the Red Sea and Pacific populations (Table 7).

**Dissections** 11 (382-521 mm FL). USNM 270386 (410), Australia, diss. 1-28-69. USNM 270390 (453), Scott Reef, J. McCosker 73-8, diss. 4-1-76. USNM 270387 (424),

Marshall Is., J. E. Randall, diss. 4-29-76. USNM 270384 (382), Kavieng, New Guinea, diss. 10-12-76. USNM 270385 (389), Cairns, Qld., G. McPherson, diss. 3-30-81. USNM 270389 (521), Port Douglas, Qld., diss. 3-31-81. USNM 270388 (416), Cairns, Qld., G. McPherson, diss. 1-5-83. USNM 270383 (475), Scott Reef, J. McCosker 72-18, diss. 1-10-83. USNM 270382 (399), Cairns, Qld., G. McPherson, diss. 1-11-83. USNM 270391 (400), Port Douglas, Qld., diss. 1-13-83. USNM 316130 (460), Scott Reef, J. McCosker 73-8, diss. 7-18-89.

**Material examined** 80 specimens (23.5-575 mm FL) from 58 collections.

**Red Sea** 16 (264-440) from 10 collections. SMF 2755 (1, 287); Massua; E. Rüppell; holotype of *Thynnus bilineatus*; stuffed. NMW uncat. (5, 362-432); Jambo; 1895-96; I.R.M. Expd. 62c. NMW uncat. (1, 424); Hassani; 1895-96; I.R.M.

Exped. 62b. NMW uncat. (1, 360); Djeddah; 1895-96; I.R.M. Exped. 62. NMW uncat. (2, 264-320); Rothes Meer; 1879-80; Klunzinger. NMW 16825 (2, 304-382); Rothes Meer; Klunzinger. MNHN 52-28 (1, 422); Mer Rouge; "Calypso". USNM 266928 (1, 327); near Entedebir; March 1962; ISRSE 4144. HUI E62/4399 (1, 368); S Red Sea; March-April 1962; Israel; S Red Sea Exped. BPBM 28388 (1, 440); Saudi Arabia, Jeddah market; 11 May 1982; J.E. Randall.

**Andaman Sea** 4 (235-294) from 2 collections. MFLB uncat. (2, 282-294); Thailand, Phuket Province; 23 Feb. 1966. MFLB uncat. (2, 235-237); Thailand, Phuket Province; 27 Jan. 1970.

**East Indies** 4 (108-413) from 4 collections. BMNH 1872. 4.6.25(1, 413); N. Celebes; Meyer. AMNH 17583 (1, 108) Celebes. USNM 213564 (1, 395); Indonesia, Ambon fish market; V.G. Springer; 19 March 1974. USNM 213565 (1, 360); Indonesia, Buton I., Teluk Buton; V.G. Springer and M.F. Gomon; VGS 74-26; 28 March 1974.

**Philippine Islands** 5 (275-390) from 5 collections. USNM 55899 (1, 372); Luzon, Sorsogon Province, Bulan; C.J. Pierson; holotype of *Nesogrammus piersoni*. USNM 195044 (1, 343); Cebu market; 6 April 1908; Albatross. CAS SU 13575 (1, 275); Balabac I.; A.W.C.T. Herre; 1929. CAS SU 13687 (1, 342); Jolo; A.W.C.T. Herre; 1931. CAS SU 40469 (1, 390); Gulf of Leyte, Leyte; R.F. Annereaux; 12 Sept. 1945.

**Okinawa** ZUMT 16738 (1, 378); Okinawa. ZUMT 52381 (1, ca. 500); Okinawa, Ishigaki I.; 4 June 1966.

**New Guinea** 10 (23.5-410) from 6 collections. CSIRO C.492 (1, 226); New Hanover, Drei Inseln Harbor, Kulinava R. USNM 270384, 316162 (2, 363-382); New Ireland, Kavieng; 20 March 1976. DASF 4247 (1, 23.5); New Britain; Borgen Bay; 13 April 1972. DASF 4248 (1, 37.9); New Britain; Tavanatangir; 11 Oct. 1972. DASF 4250 (2, 54.3-65.5); New Britain; Dikarua I.; Cape Lambert; 28 Nov. 1972. USNM 320095 (3, 385-410); Hermit Is., E side Jalun I.; 2 Nov. 1978.

**Australia** 9 (389-521) from 4 collections. USNM 270383 (1, 475); Western Australia, Scott Reef; J.E. McCosker 72-18. USNM 270390, 316130 (2, 453-460); Western Australia, Scott Reef, 14°05'S, 121°50'E; J.E. McCosker 73-8. USNM 270382, 270385, 270388, 316161 (4, 389-416); Queensland, Cairns; G. McPherson and P. Cooper. USNM 270389, 270391 (2, 400-521); Queensland, off Port Douglas; Sept.-Oct. 1976.

**Solomon Islands** 2 (275-482) from 2 collections. USNM 205078 (1, 482); New Georgia, Gizo I.; W. Chapman; 30 May 1944. AMS I.19435-020 (1, 275); Solomon Is.; G. Smith.

**Caroline Islands** 15 (327-575) from 13 collections. CAS GVF 651 (1, 462); Palau Is., Rattakadakor; Palau 145; 5 Sept. 1955. CAS GVF 933 (1, 439); Palau Is., Velasco Reef; Palau 147; 6 Oct. 1956. CAS GVF 934 (1, 432); Palau Is., Velasco Reef; Palau 148; 6 Oct. 1956. CAS GVF 946 (1, 454); Palau Is., Velasco Reef; Palau 149; 6 Oct. 1956. CAS GVF 1422 (1, 543); Palau Is., Ilruthapel I.; Palau 57-42; 20 Oct. 1957. CAS GVF 1867 (1, 461); Palau Is.; Palau 59-39; 15 April 1959. CAS GVF 1891 (1, 444); Palau Is., Angaur I.; Palau sta. 59-63; 16 June 1959. CAS GVF 1970 (2, 543-575); Palau Is., Kossol Passage, 7°56'18"N, 134°31'55"E; sta. 59-709; 30 July 1959. BPBM 10501 (2, 434-448); Palau; 23

April 1964. USNM 264910 (1, 510); between Ponape and Ant Atoll; R.A. Croft; 1983. CAS GVF (1, 408); Kapingamarangi, 1°6'N, 154°44'W; sta. 108; 4 Aug. 1958. CAS GVF 405 (1, 327); Kapingamarangi; sta. 102; 2 Aug. 1954. CAS GVF 33 (1, 462); Ifaluk; 2 Oct. 1953.

**Marshall Islands** 9 (254-549) from 7 collections. USNM 140986 (2, 419-468); Bikini Atoll lagoon, V. Brock and J. Marr; 2 April 1946. USNM 142054 (2, 503-549); Bikini Atoll lagoon off Bikini I.; V. Brock and J. Marr; 25 March 1946. USNM 142055 (1, 410) Bikini Atoll, W of Boro I., V. Brock; 6 April 1946. USNM 181932 (1, 382); Majuro Atoll; A.F. Bartsch; 1958. BPBM uncat. (1, 254); Majuro Atoll; P. Shiota; 30 Aug. 1972. USNM 270387 (1, 424); Enewetak Atoll; J.E. Randall; 2 April 1976. BPBM 12800 (1, 330); Enewetak; 4 April 1972; J.E. Randall.

**Fiji Islands** 2 (335-426) from 2 collections. USNM 176657 (1, 426); S of Suva; J.K. Howard; 4-15 Dec. 1952. USNM 243969 (1, 335); reef NNE Malamala I., V.G. Springer 82-24; 24 May 1982.

**Rotuma Island** USNM 285517 (396); Rotuma; G.D. Johnson; 14 May 1986.

**Samoan Islands** USNM 305080 (1, 465); American Samoa, East Bank, 12 mi. off E end of Tutuila; 1 July 1989.

### *Grammatorcynus bicarinatus* (Quoy and Gaimard, 1825) Shark mackerel

*Thynnus bicarinatus* Quoy and Gaimard 1825:357 (original description; Baie des Chiens-Marins (= Shark Bay), W. Australia), pl. 61, fig. 1.

*Grammatorcynus bicarinatus*. McCulloch 1915:266-269 (description; off Cook I., near Tweed River Heads, New South Wales; 925 mm FL, 18.75 lbs.), pl. 1, fig. 1. Ogilby 1918:101 (reference to McCulloch 1915; caught off Moreton Bay, Queensland), 105 (30-lb. specimen in Queensland state fish market). McCulloch 1922:106 (New South Wales; rarely captured; to 3 ft.). McCulloch and Whitley 1925:142 (Moreton Bay, Queensland). McCulloch 1929:263-264 (synonymy). Anonymous 1945:7 (listed among marketable fish of Cairns, Queensland area). Whitley 1947:129 (W. Australia). Whitley 1948:24 (listed, W. Australia). Coates 1950:22 (Great Barrier Reef; 25 lbs. maximum; "shark mackerel"), fig. Serventy 1950:20 (common in W. Australia from Geraldton northwards but not extending in waters of the Kimberly Division of W. Australia). Munro 1958a:112 (description; Queensland, N New South Wales, and W. Australia), fig. 748 (after McCulloch). Whitley 1964a:232 (length to 48 in., weight 25 lb.), 239 (fig. 4f, range in Australia only), pl. 4 (fig. b, after McCulloch). Whitley 1964b:48 (listed). Marshall 1964:367 (description, Queensland), color plate 53, fig. 354. Grant 1965:176 (description after Munro 1958a; sought-after market fish in

Queensland), fig. Marshall 1966:205 (description), color plate 53, fig. 354. Munro 1967:197-198 (text is based on Australian *G. bicarinatus*; New Guinea specimens are *G. bilineatus*), fig. 333. Grant 1972:107 (same as 1965), fig. Coleman 1974:42 (color, habits), 43 (underwater color photograph, Heron I., Queensland). Grant 1975:165 (same as 1972), fig. Rohde 1976:50 (Lizard I., Queensland). Anonymous 1978:18 (listed among species being investigated by Queensland Fisheries Service). Grant 1978:195 (same as 1975), fig. Hutchins 1979:83 (may visit Rottneest I., W. Australia). Coleman 1981:268 (Australia, habits), color underwater photo (from Coleman 1974). Lewis 1981:12 (species A, shark mackerel; maximum size 110 cm FL, 13.5 kg) photograph. Grant 1982:632 (same as 1978 plus comments on ammonia smell of flesh). Collette 1983:716-718 (distinguished from *G. bilineatus*), fig. 1B. Collette and Nauen 1983:39-40 (description, range, fig.). Hutchins and Thompson 1983:62, 85 (W. Australia), p. 63 (fig. 290). Russell 1983:146 (Heron I., Barrier Reef based on Coleman 1974). McPherson 1984 (color pattern in Queensland, fig.). Collette and Russo 1985b:547 (in key). Hutchins and Swainston 1986:102 (description, range), 103 (color painting 587), 141 (weight to 11.7 kg). Grant 1987:362 (shark mackerel; Queensland; color photo 768). Allen and Swainston 1988:144 (Geographe Bay north, Western Australia), 145 (color painting 965). Hutchins 1990:275 (sight record, Shark Bay, Western Australia). Randall et al. 1990:433 (description, range), color plate VII-13 (painting).

**Diagnosis** *Grammatorcynus bicarinatus* has fewer gill rakers (12-15 vs. 18-24), a smaller eye (3.1-4.6% vs. 4.1-6.0% FL), small black spots on the lower sides of its body, and reaches a larger maximum size (1100 mm FL) than *G. bilineatus*.

**Description** Dorsal spines 12; rays 10, finlets usually 7, rarely 6 or 8 (Table 4). Anal spines 1, rays 11-13, finlets 6 or 7, usually 7 (Table 5). Pectoral fin rays 21-24,  $\bar{x}$  23.2 (Table 6). Gill rakers on first arch 12-15,  $\bar{x}$  14.1 (Table 3). Upper jaw teeth 14-25,  $\bar{x}$  20.5 (left), 20.9 (right) (Table 2); lower jaw 15-23,  $\bar{x}$  17.5 (left), 17.6 (right) (Table 2). Morphometric data summarized in Table 1.

*Grammatorcynus bicarinatus* has a shorter neurocranium (13% vs. 14-16% FL), shorter parasphenoid flanges (14% vs. 18-21% neurocranium length), a lower maximum number of teeth on the upper (25 vs. 37) and lower (23 vs. 32) jaws, lower posterior edge of shank of maxilla (6-8% vs. 8-11% maxilla length), shorter quadrate process (122-125% vs. 134-145% quadrate length), narrower first postcleithrum (46-52% vs.

55-62% length), wider ethmoid (25-28% vs. 19-21% length), wider vomer (16-18% vs. 13-15% neurocranium length), wider lachrymal (30-35% vs. 27-30% length), longer teeth (maximum 6% vs. 4% dentary length), wider palatine tooth patch (38-42% vs. 26-32% length), wider opercle (72-79% vs. 63-72% length), and a thin posttemporal shelf between the anterior processes.

**Color** General color in life is bright, glowing green above, grading into the silver of the sides and belly, which is marked with scattered small black spots that are absent in *G. bilineatus* (Grant 1987:362). Underwater, it is reported to display a dark band along the lower lateral line (McPherson 1984). Color photographs have been published by Marshall (1964 and 1965: pl. 53, fig. 354) and Grant (1987: photo 768), and there are color paintings in Hutchins and Swainston (1986:103), Allen and Swainston (1988:965), and Randall et al. (1990: plate VIII-13). An underwater photograph was published by Coleman (1974:43 and 1981:268).

**Size** Maximum size is 110-130 cm FL and 11.6-13.5 kg weight (Lewis 1981, Hutchins and Swainston 1986, Allen and Swainston 1988).

**Biology** Shark mackerel form dense concentrations near individual bays and reefs in Barrier Reef waters. With the rising tide, they move into shallow water over the reef flats, feeding on schools of clupeoid fishes (Grant 1982).

**Interest to fisheries** Shark mackerel are fished off Western Australia, the Northern Territory, Queensland, and northern New South Wales (Grant 1987). It is regarded as a light-tackle sportsfish with commercial value in Queensland (McPherson 1984). The name shark mackerel comes from the ammonia-like smell noticed when the fish is being filleted. This odor can be masked by brushing the fillets with lemon juice prior to cooking (Grant 1982, 1987).

**Range** Found over coastal reefs of all Australian warm waters (Grant 1987) with occasional stragglers south to 30° on both east (Cook I., New South Wales) and west (Shark Bay, Western Australia) coasts (Fig. 27) and in the Gulf of Papua (A.D. Lewis, South Pacific Comm., Noumea, pers. commun.). The apparent gap in distribution may be due to ecological reasons, the scarcity of reef habitats along the north coast of Australia, or to historical reasons, as outlined by Springer and Williams (1990).

**Dissections** 4 specimens (563-765 mm FL). USNM 270392 (563), Cairns, Qld., diss. 1-3-83. USNM 316126 (765),

Exmouth Gulf, WA, B. Hutchins, diss. 1-18-83. USNM 316127-8 (2, 625-663), Australia, diss. 7-5-89.

**Material examined** 11 specimens (300-765 mm FL) from 8 collections. USNM 316129 (1, 563), Queensland, Fitzroy I. S of Cairns; Jan. 1984. USNM 176832 (1, 525), Great Barrier Reef; J.K. Howard; 8 April-29 May 1952. AMS IB.5207-8 (2, 306-315), Queensland, Gladstone District; P. Gibson. USNM 316126, uncat. (2, 607-765), Western Australia, Exmouth Gulf. WAM-P 27343 (1, 825), Western Australia, N. Muiron I., 21°39'S, 114°22'E. WAM-P 25821 (1, 320), Western Australia, S. Muiron I., 21°39'S, 114°20'E. WAM-P 22974 (head only, 105 mm), Western Australia, Kendrick I., 20°29'S, 116°22'E; 21 Feb. 1973; B. Hutchins. USNM 316127-8 (2, 625-663), Australia.

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