MORPHOLOGY, SYSTEMATICS, AND BIOLOGY OF THE SPANISH MACKERELS (*SCOMBEROMORUS*, SCOMBRIDAE)

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ABSTRACT

The Spanish mackerels and seerfishes of the genus *Scomberomorus* constitute the most speciose group of the 44 genera in six families that comprise the suborder Scombroidei. As in higher scombrids, *Scomberomorus*, *Acanthocybium*, and *Grammatorcynus* have a well-developed median keel on the caudal peduncle, but there is no bony support as is present in the Sardini and Thunnini. *Acanthocybium* and *Scomberomorus* share 17 osteological characters and are considered sister-groups. The relationships of *Grammatorcynus* are not clear but it is clearly more primitive than *Scomberomorus*; therefore, we have used it as the outgroup for a cladistic analysis of *Scomberomorus*.

Scomberomorus differ from all other scombrids in having a spatulate anterior extension of the vomer. There are 18 species in the genus, nearly 40% of the 49 species of scombrids: Eastern Atlantic—*tritor* (Cuvier); western Atlantic—*brasiliensis* Collette, Russo and Zavala-Camin, *cavalla* (Cuvier), *maculatus* (Mitchill), and *regalis* (Bloch); eastern Pacific—*concolor* Lockington and *sierra* Jordan and Starks; and Indo-West Pacific—*commerson* (Lacepède), *guttatus* (Bloch and Schneider), *koreanus* (Kishinouye), *lineolatus* (Cuvier), *munroi* Collette and Russo, *multiradiatus* Munro, *niphonius* (Cuvier), *plurilineatus* Fourmanoir, *queenslandicus* (Macleay), *semifasciatus* (Macleay), and *sinensis* (Lacepède). A cladistic analysis of 58 characters shows six monophyletic species-groups in *Scomberomorus*. The *sinensis* group is monotypic and is defined by the presence of an abrupt downward curve in the lateral line under the first dorsal fin and by its retention of a swim bladder. The *commerson* species-group contains *commerson*, *niphonius*, *queenslandicus*, and *cavalla* and is defined by the presence of an intercalar spine of at least moderate length. *Scomberomorus cavalla* and *S. commerson* share two additional specializations, the pterosphenoid bones are close together and the lateral line curves abruptly downward under the second dorsal finlets. The *munroi* species-group is monotypic and is defined by the loss of the anterior process on the outer surface of the head of the maxilla. The *semifasciatus* species-group contains *semifasciatus*, *plurilineatus*, and *lineolatus*, and is defined by the presence of a greatly expanded posterior end of the maxilla. *Scomberomorus lineolatus* and *S. semifasciatus* share an additional specialization, a wide parasphenoid, but this character state appears independently in several other lines. The *guttatus* species-group contains *guttatus*, *multiradiatus*, and *koreanus* and is defined by a high supraoccipital crest. Auxiliary branches extend off the anterior part of the lateral line in *S. guttatus* and *S. koreanus*. The *regalis* species-group contains *regalis*, *tritor*, *maculatus*, *concolor*, *sierra*, and *brasiliensis* and is defined by the presence of nasal denticles. All but the most primitive species in this group (*S. tritor*) have an artery arising from the fourth left epibranchial artery. The four most advanced species (all except *tritor* and *maculatus*) have developed a long posterior process on the pelvic girdle. The three most advanced species (*sierra*, *brasiliensis*, and *regalis*) have a coeliaco-mesenteric shunt connecting the fourth right epibranchial artery with the coeliaco-mesenteric artery.

The purposes of this paper are to define the 18 species of *Scomberomorus*, to clarify their relationships, and to assess the systematic position of *Scomberomorus* within the Scombridae. The methods used are similar to those of Collette and Chao (1975) in a revision of the bonitos and of Gibbs and Collette (1967) in a revision of *Thunnus*, and rely on previous work by Kishinouye (1923), Munro (1943), Mago Leccia (1958), and Devaraj (1977).

The Spanish mackerels have been placed by Collette and Chao (1975) and Collette and Russo (1979) in a tribe (the Scomberomorini) along with *Acanthocybium* and *Grammatorcynus*, intermediate between the more primitive mackerels (Scombrini) and the more advanced bonitos (Sardini). *Acanthocybium* is clearly the specialized sister group of *Scomberomorus*, but the phylogenetic position of *Grammatorcynus* has been unclear.

Until recently, the number of valid species of

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Scomberomorus has been in doubt. In his revision of Australian species, Munro (1943) recognized 15 species in the world (excluding *Cybiosarda elegans*, a bonito, and *Lepidocybium flavobrunneum*, a gempylid). Fraser-Brunner (1950) recognized only nine species, placing five valid species in synonymy. In the course of this revision, we have discovered two previously undescribed species, *S. brasiliensis* (Collette et al. 1978), which was confused with *S. maculatus*, and *S. munroi* (Collette and Russo 1980), which was confused with *S. niphonius*.

Emphasis was placed on obtaining fresh or frozen specimens for dissection from several populations of each species. Standard counts and measurements were taken, color pattern was recorded, and a search made for parasitic copepods. Results of the copepod study have been reported by Cressey and Cressey (1980), and analysis of these data from a host-parasite point of view has been completed (Cressey et al. 1983; Collette and Russo 1985). The viscera were examined and illustrated in situ following removal of an oval portion of the ventral body wall. The viscera then were removed and drawings were made of the liver and other selected organs. The kidneys and anterior parts of the arterial system then were drawn. Counts of ribs and intermuscular bones were made and the specimen was then skeletonized, facilitated by immersion in hot water.

The base measurement for morphometric comparisons of fresh, frozen, and preserved specimens was millimeters fork length (mm FL).

This paper is divided into three major parts. The first part contains descriptions and illustrations of morphometry, meristic characters, soft anatomy, and osteology of the species of *Scomberomorus*. Comparisons with *Acanthocybium solandri* and *Grammatorcynus bilineatus* are included. All references to *Grammatorcynus* in this paper refer to *G. bilineatus*. The validity of the second species, *G. bicarinatus*, was only established recently (Collette 1983). The second part comprises separate species accounts including synonymy, types of nominal species, diagnosis (based on characters from the first section), description, size, color pattern, summaries of published information on biology and interest to fisheries, geographic distribution, and material examined. The most important references to each species are marked with asterisks in the synonymies. The third part is an analysis of the relationships of *Acanthocybium* and the species of *Scomberomorus* based on a cladistic analysis of characters described in the first part, using *Grammatorcynus* as the plesiomorphic out-group.

MATERIAL

The material examined is listed by general locality under four or five headings in the accounts for each of the 18 species of *Scomberomorus*. Comparative material of *Acanthocybium* and *Grammatorcynus* is listed at the end of this section. The numbers under these headings are not additive but are included to give some degree of confidence in the morphological data presented in the body of the paper. "Total specimens" is the total number of individuals examined whether preserved, dissected, or skeletonized. "Dissected" are fresh or frozen specimens for which data on the viscera and usually other characters were recorded. Specimens were subsequently made into skeletons. "Measured and counted" includes specimens that were subsequently dissected as well as the preserved museum specimens used for detailed morphometric and meristic examination. "Counts only" are additional museum specimens used only for meristic examination. "Skeletons" refer to all the skeletal material examined, both specimens that were dissected and additional skeletal material already in museums. Asterisks indicate type-specimens of nominal species.

Material was examined from the following institutions:

AMNH	American Museum of Natural History, New York
AMS	Australian Museum, Sydney
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	British Museum (Natural History), London
CAS	California Academy of Sciences, San Francisco
CSIRO	CSIRO Marine Biological Laboratory, Cronulla, N.S.W., Australia
DASF	Department of Agriculture, Stock, and Fisheries, Port Moresby, Papua New Guinea
FMNH	Field Museum of Natural History, Chicago
HUMZ	Laboratory of Marine Zoology, Hokkaido University, Hakodate, Hokkaido

GCRL	Gulf Coast Research Laboratory and Museum, Ocean Springs, Miss.
LACM	Los Angeles County Museum of Natural History, Los Angeles
MCZ	Museum of Comparative Zoology, Harvard
MNHN	Museum National d'Histoire Naturelle, Paris
MPIP	Museu de Pesca do Instituto de Pesca, Santos
MSUF	Museo de La Specola, Universita di Firenze, Florence
MZUSP	Museu de Zoologia da Universidade de São Paulo, São Paulo
NHMV	Naturhistorisches Museum, Vienna
NMC	National Museum of Natural Sciences, Ottawa
QM	Queensland Museum, Brisbane
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden
ROM	Royal Ontario Museum, Toronto
RUSI	J. L. B. Smith Institute of Ichthyology, Rhodes University, Grahamstown, South Africa
SAM	South African Museum, Capetown
SIO	Scripps Institution of Oceanography, La Jolla, Calif.
TABL	Miami Laboratory (formerly Tropical Atlantic Biological Laboratory), NMFS, Miami, Fla. [Most specimens now at UF.]
UDONECI	Universidad de Oriente, Nueva Esparta, Centro de Investigaciones, Venezuela
UF	Florida State Museum, University of Florida, Gainesville
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
USNM	United States National Museum, Washington, D.C.
WAM	Western Australia Museum, Perth
ZMA	Zoological Museum, Amsterdam
ZMH	Zoologisches Institut und Zoologisches Museum, Hamburg
ZMK	Zoological Museum, Copenhagen
ZSI	Zoological Survey of India, Calcutta

Acanthocybium solandri.—Total 47 (536-1,500 mm FL).

meas.: 26 (536-1,500): W Atlantic (8); St. Helena (1); S. Africa (3); Indian Ocean (4); Caroline Is. (6); Tuamotu Is. (1); E Pacific (3).

heads: 8 (202-380): Bahama Is. (1); St. Helena (2); Australia (1); Marshall Is. (1); E Pacific (2).

counts: 36.

diss.: 11 (943-1,420): W Atlantic (7); Indian O. (3); Revillagigedos (1).

Grammatorcynus bilineatus.—Total 52 (23.5-575 mm FL).

meas.: 34 (226-575): Red Sea (13, **Thynnus bilineatus*); Indian Ocean ? (1); Andaman Sea (3); Celebes (1); New Guinea (3); Australia (8); Philippine Is. (5, **Nesogrammus piersoni*); Solomon Is. (1); Caroline Is. (3); Marshall Is. (8); Fiji (2).

counts: 44.

diss.: 10 (382-453): Indian Ocean ? (1); Timor Sea (2); Bismarck Arch. (1); Marshall Is. (2); Queensland, Australia (4).

Grammatorcynus bicarinatus.—Total 9 (306-825 mm FL).

meas.: 9 (306-825): Western Australia (5); Queensland (4).

counts: 9.

diss.: 2 (521 and 563): Queensland.

KEY TO *GRAMMATORCYNUS*, *ACANTHOCYBIUM*, AND *SCOMBEROMORUS*

1a. Two lateral lines, the lower joining the upper behind the pectoral fin base and at the caudal fin base; interpelvic process single; teeth in jaws slender, conical, not compressed; vertebrae 31 .... *Grammatorcynus* 2

1b. One lateral line; interpelvic process double; teeth in jaws strong, compressed, almost triangular or knife-like; vertebrae 39-64 3

2a. Gill rakers 14-15; small eye, 3-4% FL; frequently with small dark spots on lower sides of body .... *G. bicarinatus* (Quoy and Gaimard)

2b. Gill rakers 19-24; large eye, 7-9% FL; seldom with dark spots on sides of body .... *G. bilineatus* (Rüppell)

3a. Snout as long as rest of head; no gill rakers; 23-27 spines in first dorsal fin; posterior end of maxilla concealed under preorbital bone; vertebrae 62-64 . . . . *Acanthocybium solandri* (Cuvier)

3b. Snout much shorter than rest of head; gill rakers 1-27; 12-22 spines in first dorsal fin; posterior end of maxilla exposed; vertebrae 41-56 . . . . *Scomberomorus* 4

4a. Lateral line abruptly curving down below first or second dorsal fin; vertebrae 41-46 5

4b. Lateral line straight or descending gradually posteriorly; vertebrae 44-56 7

5a. Lateral line abruptly curving down below first dorsal fin; total gill rakers on first arch 12-15; caudal vertebrae 21-22 . . . . *S. sinensis* (Lacepède)

5b. Lateral line abruptly curving down below second dorsal fin; total gill rakers on first arch 2-13; caudal vertebrae 23-27 6

6a. Total gill rakers on first arch 7-13, usually 9 or more; spines in first dorsal fin 12-18, usually 15 or fewer; precaudal vertebrae 16-17 . . . . . . *S. cavalla* (Cuvier)

6b. Total gill rakers on first arch 3-8, usually 6 or fewer; spines in first dorsal fin 15-18, usually 16 or more; precaudal vertebrae 19-20 . . . . *S. commerson* (Lacepède)

7a. Total gill rakers on first arch 21-27; no bars on body . . . . *S. concolor* Lockington

7b. Total gill rakers on first arch 1-18; spots, bars, or other markings usually present on sides of body 8

8a. Anal fin rays 25-29; second dorsal fin rays 21-25, usually 23 or more; gill rakers on first arch 1-4; total vertebrae 54-56; no pattern on body . . . . *S. multiradiatus* Munro

8b. Anal fin rays 15-24; second dorsal fin rays 15-24; total gill rakers on first arch 3-18; total vertebrae 44-53; sides of body usually with spots or other markings 9

9a. Dorsal fin spines 19-22, usually 19 or more 10

9b. Dorsal fin spines 13-19, usually 18 or fewer 11

10a. First dorsal fin black only on first 5-7 interspinous membranes, white posteriorly; intestine straight, with no folds; total vertebrae 48-50 . . . . *S. niphonius* (Cuvier)

10b. First dorsal fin black to, or almost to, posterior end; intestine with 2 loops and 3 limbs; total vertebrae 50-52 . . . . *S. munroi* Collette and Russo

11a. Lateral line with many small auxiliary branches anteriorly 12

11b. Lateral line without auxiliary branches or with only a few anteriorly 13

12a. Dorsal fin spines 15-18, usually 16 or more; intestine with 2 loops and 3 limbs; total vertebrae 47-52, usually 48 or more; head longer, 20.2-21.5% FL; body depth less, 22.8-25.2% FL . . . . *S. guttatus* (Bloch and Schneider)

12b. Dorsal fin spines 14-17, usually 15 or fewer; intestine with 4 loops and 5 limbs; total vertebrae 46-47, usually 46; head shorter, 19.7-20.4% FL; body depth greater, 24.4-26.7% FL . . . . *S. koreanus* (Kishinouye)

13a. Sides of body with spots and at least one stripe, the stripes may be short, wavy or interrupted 14

13b. Sides of body without any stripes, spots usually present 16

14a. One long stripe on sides with spots or interrupted lines above and below the stripe; total vertebrae 47-48, usually 48; total gill rakers on first arch 12-18, usually 15 or more . . . . *S. regalis* (Bloch)

14b. Sides with several short stripes; total vertebrae 44-47, usually 46; total gill rakers on first arch 9-15, usually 14 or fewer 15

15a. Sides with a series of short straight stripes and few if any spots; total gill rakers on first arch usually 11 or fewer; second dorsal fin rays 15-19, usually 18 or fewer; distance from 2D origin to caudal base 46.2-54.5% FL, $\bar{x}$ 50.0% . . . . *S. lineolatus* (Cuvier)

15b. Sides with a series of short wavy markings plus many small spots; total gill rakers on first arch usually 12 or more;

second dorsal fin rays 19-21, usually 20 or more; distance from 2D origin to caudal base 51.8-57.5% FL, $\bar{x}$ 54.8% .. .. *S. plurilineatus* Fourmanoir

16a. Sides with bars or large spots, larger than the diameter of the eye 17
16b. Sides with small round spots, about the diameter of the eye, orange colored in life 19

17a. Sides with large spots or blotches; total gill rakers on first arch 3-9, usually 7 or fewer ...... *S. queenslandicus* Munro
17b. Sides plain or with bars; total gill rakers of first arch 6-15, usually 9 or more .. 18

18a. First dorsal fin spines 13-15; second dorsal fin rays 19-22, usually 20 or more; total gill rakers on first arch 6-13, usually 11 or fewer; total vertebrae 44-46, usually 45; base first dorsal fin 17.0-23.6% FL .... *S. semifasciatus* (Macleay)
18b. First dorsal fin spines 15-18, usually 16 or more; second dorsal fin rays 16-19, usually 17; total gill rakers on first arch 12-15; total vertebrae 46-47, usually 46; base first dorsal fin 23.8-30.4% FL .... *S. tritor* (Cuvier)

19a. Total vertebrae 51-53; second dorsal fin rays 17-20, usually 18 or more .... *S. maculatus* (Mitchill)
19b. Total vertebrae 46-49; second dorsal fin rays 15-19, usually 18 or fewer 20

20a. Pectoral fin rays 21-24, usually 22 or more; pelvic fin short, 2.9-5.9% FL, $\bar{x}$ 4.5% .... *S. brasiliensis* Collette, Russo, and Zavalla-Camin
20b. Pectoral fin rays 20-24, usually 21 or fewer; pelvic fin longer, 3.2-6.4% FL, $\bar{x}$ 5.3% ..... *S. sierra* Jordan and Starks

COMPARATIVE MORPHOLOGY

The morphological characters useful for distinguishing the species of *Scomberomorus* and for evaluating their phylogenetic relationships are divided into six categories: lateral line, nasal denticles, morphometry, meristics, soft anatomy, and osteology.

Lateral Line

In most species of *Scomberomorus*, the lateral line runs posteriorly above the pectoral fin and then gradually descends to the middle of the body at about the level of the second dorsal fin. *Grammatorcynus* differs from *Scomberomorus*, *Acanthocybium*, and all other members of the family by having a second lateral line that joins the upper lateral line at a right angle behind the pectoral fin base and then courses ventrally and posteriorly along the ventral surface of the body to join the dorsal lateral line on the caudal peduncle. In *Acanthocybium* and three species of *Scomberomorus*, the lateral line moves abruptly downward under the first or second dorsal fin. The abrupt downward curve is under the first dorsal fin in *Acanthocybium* and *S. sinensis* (see Figure 68); it is under the second dorsal in *S. cavalla* and *S. commerson* (see Figures 50 and 52).

Scomberomorus guttatus and *S. koreanus* differ from other members of the genus in having many fine branches from the anterior part of the lateral line, both dorsally and ventrally (see Figures 54 and 56). *Acanthocybium* and *S. niphonius* (see Figure 62) may have branches from the lateral line but they are not as numerous or distinct.

Nasal Denticles

Nasal denticles (Fig. 1a, b) are small generalized teeth found within the olfactory chamber on the medial surface surrounding the posterior nares and on the skin covering the anterior surface of the lateral ethmoid. Nasal denticles are similar to the small villiform teeth present within the mouth cavity and adjoining regions of stomadeal origin and on the skin covering the cleithrum (Fig. 1c, d) and on the isthmus where they are contacted by the opercular membrane. These teeth typically fit into sockets in pads of fine spongelike bone. They point posteriorly and are aligned with presumed flow of water from the anterior naris through the olfactory chamber and out the posterior naris. Nasal denticles were found only in the six species of the *Scomberomorus regalis* species-group (*brasiliensis*, *concolor*, *maculatus*, *regalis*, *sierra*, and *tritor*). Nasal denticles are not present in *Acanthocybium* or *Grammatorcynus*. We do not know their function and are not aware of such structures in other fishes.

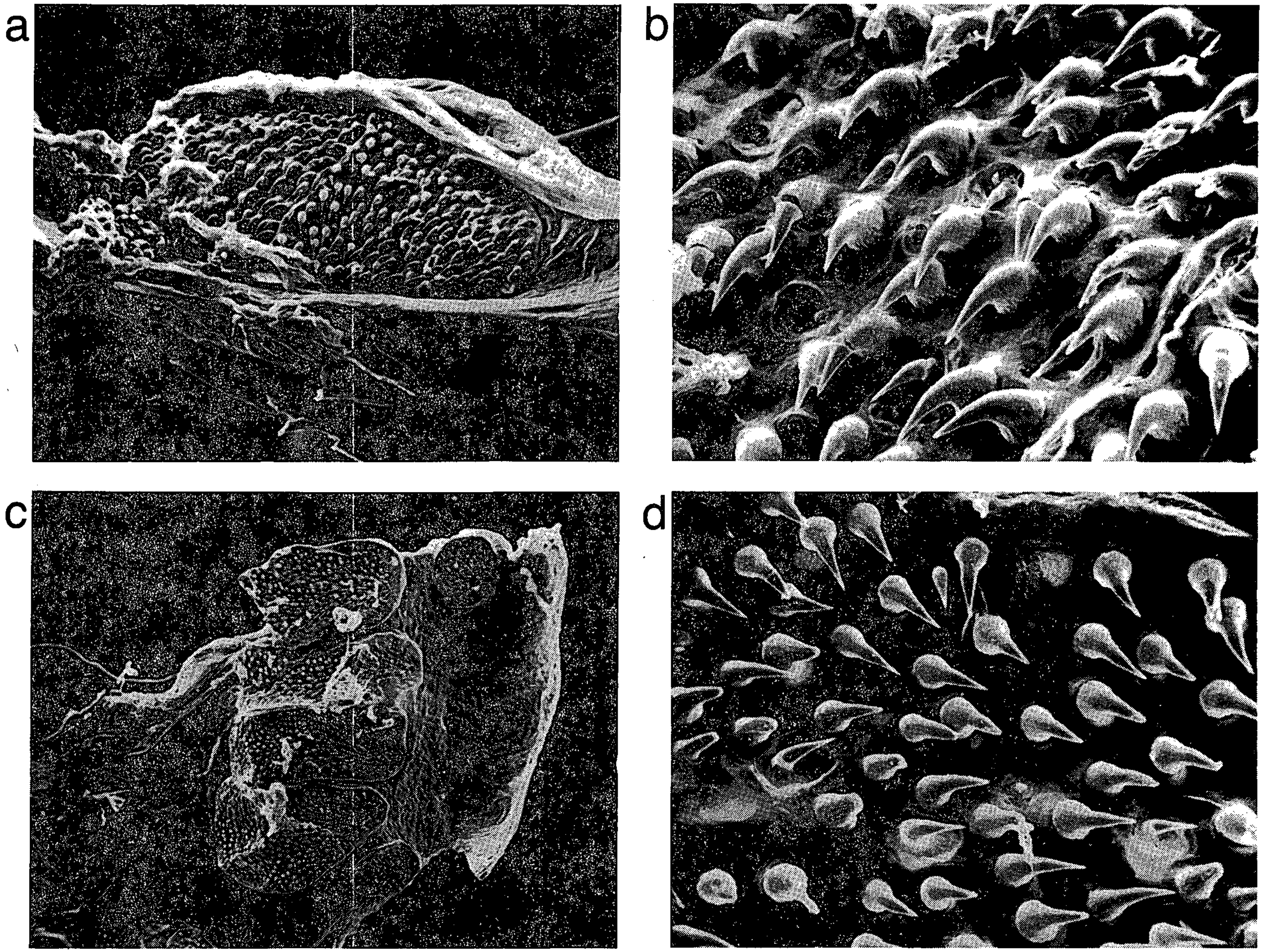


FIGURE 1.—Scanning electron photomicrographs of nasal denticles (a-b) and villiform teeth over the cleithrum (c-d) in *Scomberomorus sierra*, Gulf of California, 353 mm FL, USNM 217368. a, c. 50×. b, d. 250×.

Morphometric Characters

In addition to fork length, 26 measurements routinely were made on all specimens destined to be dissected, to insure that these data would be available if needed. Preserved material also was measured until an adequate sample was obtained. Measurements follow the methods of Marr and Schaefer (1949) as modified by Gibbs and Collette (1967) and Collette and Chao (1975). Morphometric characters can be used to separate species and populations within species. Tables showing the 26 characters as thousandths of fork length and 8 characters as thousandths of head length are presented in the systematic section of the paper (see Tables 13-30). Most of the characters are best used at the species level; therefore, only a summary table of the means of proportions (Table 1) is presented in this section. Where there was sufficient material from two or more potentially different populations, analysis of covariance (ANCOVA) was carried out on the regressions of body parts on fork length. Results are reported, under a section entitled Geographic Variation, in 11 of the 18 species accounts. Tests of significance were made by Newman-Keuls Multiple Range Test.

Meristic Characters

Countable structures are of special value systematically because they are relatively easy to record unambiguously and are easy to summarize in tabular fashion. Meristic characters that have proved valuable systematically in *Scomberomorus* include numbers of fin rays (first dorsal spines, second dorsal rays, dorsal finlets, anal rays, anal finlets, and pectoral rays), gill rakers, teeth on the upper and lower jaws, vertebrae (precaudal, caudal, and total), and lamellae in the olfactory rosettes. Olfactory lamellae are discussed as the next to last section under soft

TABLE 1.—Morphometric comparison of the species of *Scomberomorus*. Means as thousandths of fork length or head length. Species arranged alphabetically by the first three letters of their names. Ranges for the species given in Tables 13-30.

Character	bra	cav	com	con	gut	kor	lin	mac	mul	mun	nip	plu	que	reg	sem	sie	sin	tri	Min. spp.	Max. spp.
Fork length																				
Snout-A	538	539	542	524	517	493	507	536	505	546	563	502	525	548	506	537	584	533	493 kor	584 sin
Snout-2D	511	506	510	507	481	467	501	503	477	528	536	473	501	521	472	510	559	513	467 kor	559 sin
Snout-1D	242	258	243	236	239	242	252	241	249	222	248	221	234	255	245	241	291	246	221 mun, plu	291 sin
Snout-P_2	253	258	257	242	251	248	245	257	243	249	263	233	251	265	250	252	290	266	233 plu	290 sin
Snout-P_1	219	232	237	209	209	210	212	217	213	201	225	193	229	234	219	221	258	222	193 plu	258 sin
P_1-P_2	108	106	96	100	106	114	93	110	102	105	105	103	99	109	105	104	113	111	93 lin	114 kor, sin
Head length	213	223	229	202	205	208	206	212	208	198	216	193	220	223	213	212	255	217	193 plu	255 sin
Max. body depth	198	191	187	187	209	237	181	197	229	190	172	206	188	197	211	190	218	206	172 nip	237 kor
Max. body width	82	89	94	89	93	100	97	.91	95	100	84	97	101	91	94	84	102	90	82 bra	104 mun
P_1 length	123	129	122	125	109	133	139	129	131	109	111	123	120	126	147	123	158	134	109 gut, mun	158 sin
P_2 length	45	65	56	50	59	60	55	52	40	54	68	51	55	56	50	53	83	60	40 mul	83 sin
P_2 insertion-vent	273	271	273	261	251	227	241	263	247	281	285	243	254	267	237	267	273	250	237 sem	285 nip
P_2 tip-vent	225	212	217	212	191	164	185	211	207	225	218	186	198	210	187	222	189	190	164 kor	225 bra, mun
Base 1D	263	245	261	254	235	218	231	256	216	307	282	240	263	257	210	260	260	262	210 sem	307 mun
Height 2D	117	109	103	111	131	166	124	125	167	112	98	148	114	114	159	123	145	126	98 nip	167 kor, mul
Base 2D	118	106	104	127	141	160	114	128	178	115	113	128	113	114	138	120	121	122	104 com	178 mul
Height anal	114	106	100	107	127	160	117	118	164	108	97	135	112	112	156	117	145	125	97 nip	164 mul
Base anal	113	108	100	134	133	154	122	123	216	105	107	125	108	110	145	119	122	120	100 com	216 mul
Snout (fleshy)	82	87	89	72	72	70	81	80	77	77	81	67	86	87	81	79	97	81	67 plu	97 sin
Snout (bony)	72	79	81	63	64	62	74	70	67	70	75	59	80	79	72	70	91	72	59 plu	91 sin
Maxilla length	123	132	131	113	108	111	113	119	125	104	120	96	125	124	119	121	147	123	96 plu	147 sin
Postorbital	95	98	104	96	96	101	91	96	86	90	102	94	102	98	95	98	117	96	86 mul	117 sin
Orbit (fleshy)	37	38	35	32	37	34	32	34	34	25	34	34	31	41	35	33	35	38	25 mun	41 reg
Orbit (bony)	54	51	49	46	53	50	48	51	52	39	47	45	49	56	51	49	52	53	37 mun	56 reg
Interorbital width	57	60	62	49	59	60	57	56	58	56	57	56	63	58	57	55	63	59	49 con	63 que, sin
2D-caudal	490	477	481	484	527	550	500	487	494	468	465	548	496	480	517	475	445	476	445 sin	550 kor
Head length																				
Snout (fleshy)	386	392	390	353	351	339	395	376	372	386	376	348	391	390	378	371	382	376	339 kor	395 lin
Snout (bony)	343	357	355	313	310	301	359	335	321	351	346	306	363	351	339	331	355	333	301 kor	363 que
Maxilla length	581	591	571	555	526	532	547	562	603	521	553	496	568	556	555	570	578	568	496 plu	603 mul
Postorbital	446	438	455	476	464	489	442	454	415	456	473	485	463	439	447	461	460	443	415 mul	489 kor
Orbit (fleshy)	175	168	147	159	174	157	156	160	165	134	150	179	142	178	162	158	138	173	129 mun	178 reg
Orbit (bony)	249	229	211	226	252	238	231	242	252	199	215	232	223	247	238	235	202	245	191 mun	252 gut, mul
Interorbital width	270	268	270	241	284	292	276	266	280	282	264	290	286	262	267	253	249	272	241 con	292 kor

anatomy. The other meristic characters are discussed in the relevant osteological sections of the paper.

Soft Anatomy

The relative position, shape, and size of the various internal organs provide valuable diagnostic characters. For purposes of discussion, the characters in the soft anatomy are divided into five sections: viscera, vascular system, urogenital system, olfactory organ, and pharyngeal muscles.

VISCERA

Emphasis was placed on the appearance of the viscera in ventral view, after removal of an oval segment of the belly wall (Figs. 2, 3). Previous papers on the viscera include Kishinouye (1923, 5 Japanese species of *Scomberomorus*, and *Acanthocybium* and *Grammatorcynus*), Munro (1943, 4 Australian species), Silas (1963, *Grammatorcynus*), Mota Alves and Tomé (1967a, *S. cavalla*), Mota Alves (1969, *S. brasiliensis*), Tongyai (1971a, *S. guttatus* and *S. commerson*), and Collette and Russo (1979, preliminary review of the genus).

The anterior end of the liver abuts the transverse septum anteriorly in the body cavity. The liver has three lobes. The left and right lobes are longer than the middle lobe in all three genera (Fig. 4). The right lobe is longest in *Scomberomorus* and *Grammatorcynus*. The left and right lobes are about equal in length in *Acanthocybium*. Two efferent (venous) vessels lead directly from the anterior surface of the liver into the sinus venosus in all species. The short esophagus leads into the stomach. The stomach is sometimes visible in ventral view but this is dependant on the amount of food present, rather than showing differences between species. The pyloric portion of the intestine arises from the anterior end of the

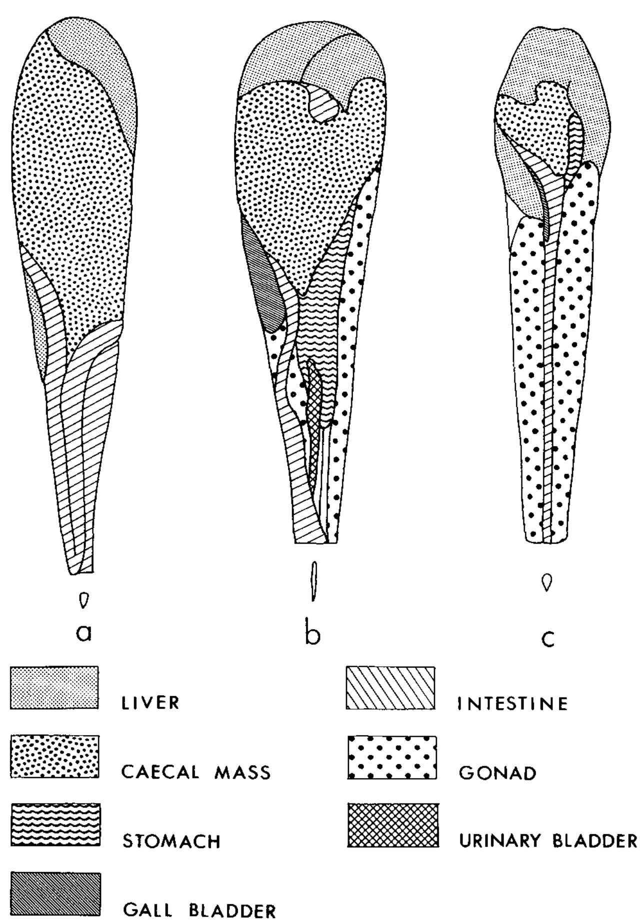


FIGURE 2.—Viscera in ventral view. a. *Scomberomorus maculatus*, Georgia, 290 mm FL. b. *Acanthocybium solandri*, Campeche Banks, Mexico, 1,280 mm FL. c. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL.

stomach. At this point the main branches of the pyloric caeca join the intestine. The caeca branch and form a dense dendritic conglomeration, the caecal mass. Cells in the pyloric caeca are histologically similar to those in the intestine and produce enzymes such as lipase, maltase, trypsin, and pepsin (Mota Alves and Tomé 1970). The intestine continues posteriorly and its course appears to be species-specific. The intestine may be a simple straight tube from stomach to anus, have two descending and one ascending arm, or have four bends with three descending and two ascending arms. The spleen is prominent in ventral view in most species but is hidden in others. The gall bladder, an elongate tubular sac which is usually green, arises from the right lobe of the liver and usually lies along the first descending arm of the intestine on the right side. A swim bladder is present in *Grammatorcynus*, *Acanthocybium*, and *S. sinensis* (Fig. 5) but is absent in the other 17 species of *Scomberomorus*.

The Spanish mackerels can be divided into three groups based on the number of folds in the intestine. *Grammatorcynus*, *Acanthocybium* (Fig. 2b, c), and *S. niphonius* (Fig. 3k) have a straight gut not folded back on itself. *Scomberomorus koreanus* (Fig. 3f) has four folds and five distinct arms. The other species all have two folds and three long arms (Fig. 3). Collette and Russo (1980) used this character to differentiate *S. munroi* from the North Pacific *S. niphonius*.

The spleen is large and centrally located in ventral view in four species: *guttatus*, *koreanus*, *munroi*, and *plurilineatus*. The spleen is smaller and distinctly on the left side in ventral view in seven species: *brasiliensis*, *commerson*, *lineolatus*, *maculatus*, *multiradiatus*, *queenslandicus*, and *sinensis*. It is not visible in ventral view in *Grammatorcynus*, *Acanthocybium*, and seven species of *Scomberomorus*: *cavalla*, *concolor*, *niphonius*, *regalis*, *semifasciatus*, *sierra*, and *tritor*.

VASCULAR SYSTEM

The only published work on the vascular system of the Spanish mackerels is on Japanese species by Kishinouye (1923). No specialized subcutaneous vascular system and no cutaneous arteries or veins are present as they are in the higher tunas, Thunnini, *Auxis* to *Thunnus* (Collette 1979). Therefore, this description will be confined to the anterior portion of the dorsal aorta and the postcardinal vein.

The efferent branchial (epibranchial) arteries and coeliaco-mesenteric artery form a unit at the anterior end of the dorsal aorta (Figs. 6, 7). Two anterior epibranchials on each side unite to form a common trunk, and these trunks join as the "Y" of the aorta beneath the posterior part of the skull or the first or second vertebra. The posterior two epibranchials of each side unite immediately before they join the aorta, usually ventral to the second or third vertebra. As the aorta proceeds posteriorly, it gives rise to the large coeliaco-mesenteric artery on the right side ventral to the second to fourth vertebrae. The coeliaco-mesenteric artery has two or three main branches which lead to the liver and other viscera.

The postcardinal vein runs along the ventral surface of the kidney (Fig. 8) from the vicinity of the first complete haemal arch anteriorly in the median line to the pectoral region. There it curves to the right and discharges into the right Cuvierian duct. Posteriorly, the postcardinal receives a pair of small veins at the level of each vertebra. The postcardinal is composed of two main branches that join anterior to the Y of the ureter. The main branch leaves the haemal arch dorsally and the small branch runs under the surface of the kidney from the urogenital area.

Five species of *Scomberomorus* (*brasiliensis*, *concolor*, *maculatus*, *regalis*, and *sierra*) have unique specializations of the right and/or left fourth epibranchial arteries (Fig. 7c-g). Each of these species has an artery arising from the fourth left epibranchial artery. Other species of the genus (e.g., *S. guttatus* and *S. tritor*, Fig. 7a, b) lack these specializations. In *S. concolor* and *S. brasiliensis* this branch is small and goes into the muscular tissue surrounding the left dorsal portion of the esophagus (Fig. 7d, f). In *S. maculatus* and *S. sierra*, this branch is large and becomes the dorsal left gastric artery (Fig. 7c, e). In *S. regalis* this branch goes into the left lobe of the liver (Fig. 7g, hepatic branch). *Scomberomorus maculatus* and *S. sierra* have lost the connection between the dorsal left gastric artery and the coeliaco-mesenteric artery. It is replaced by a connection to the fourth left epibranchial artery. In *S. regalis*, the left dorsal gastric artery seems to have been reduced.

Scomberomorus brasiliensis, *S. sierra*, and *S. regalis* share a specialization of the right fourth epibranchial artery. In these species an artery connects the fourth right epibranchial artery with a branch of the coeliaco-mesenteric artery (coeliaco-mesenteric shunt, Fig. 7e-g).

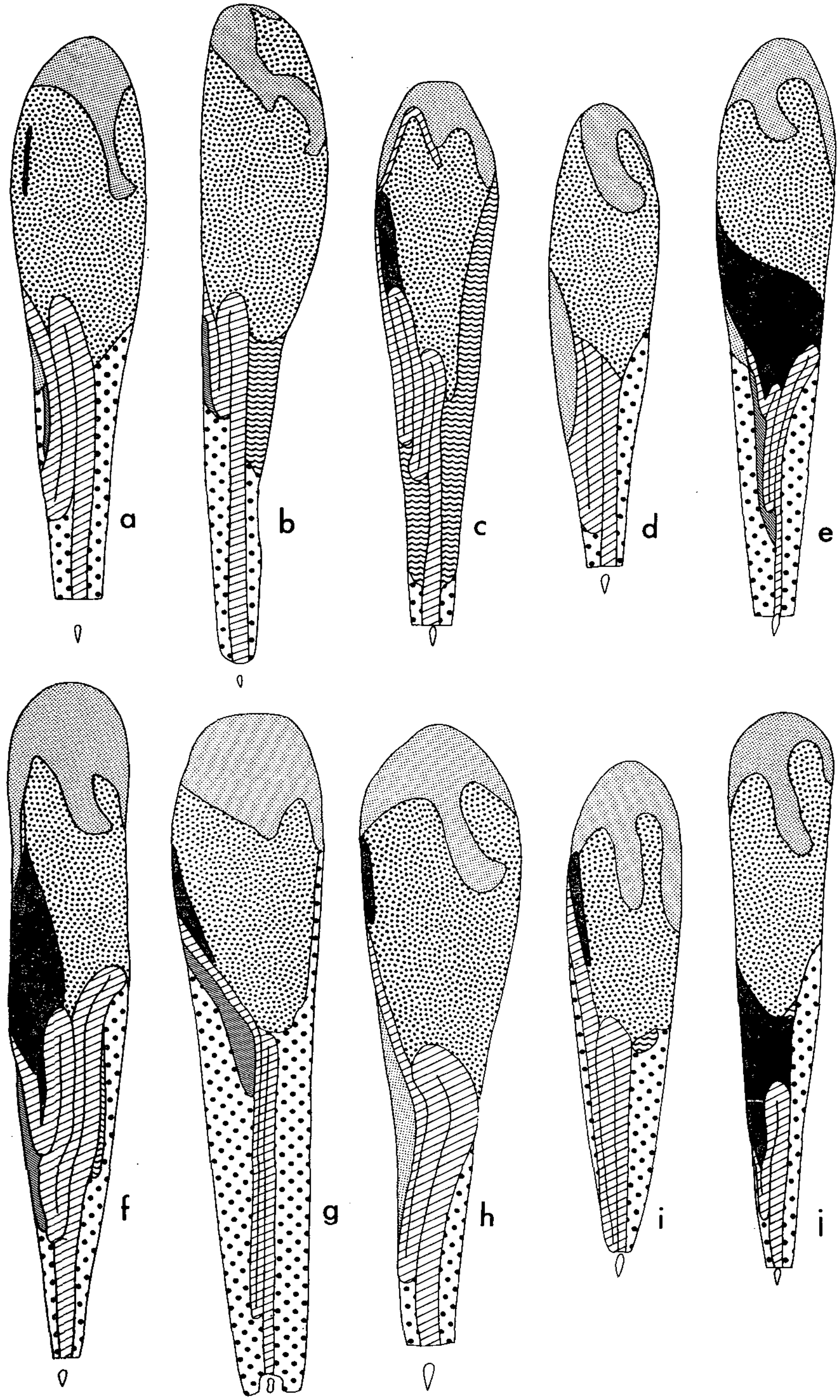
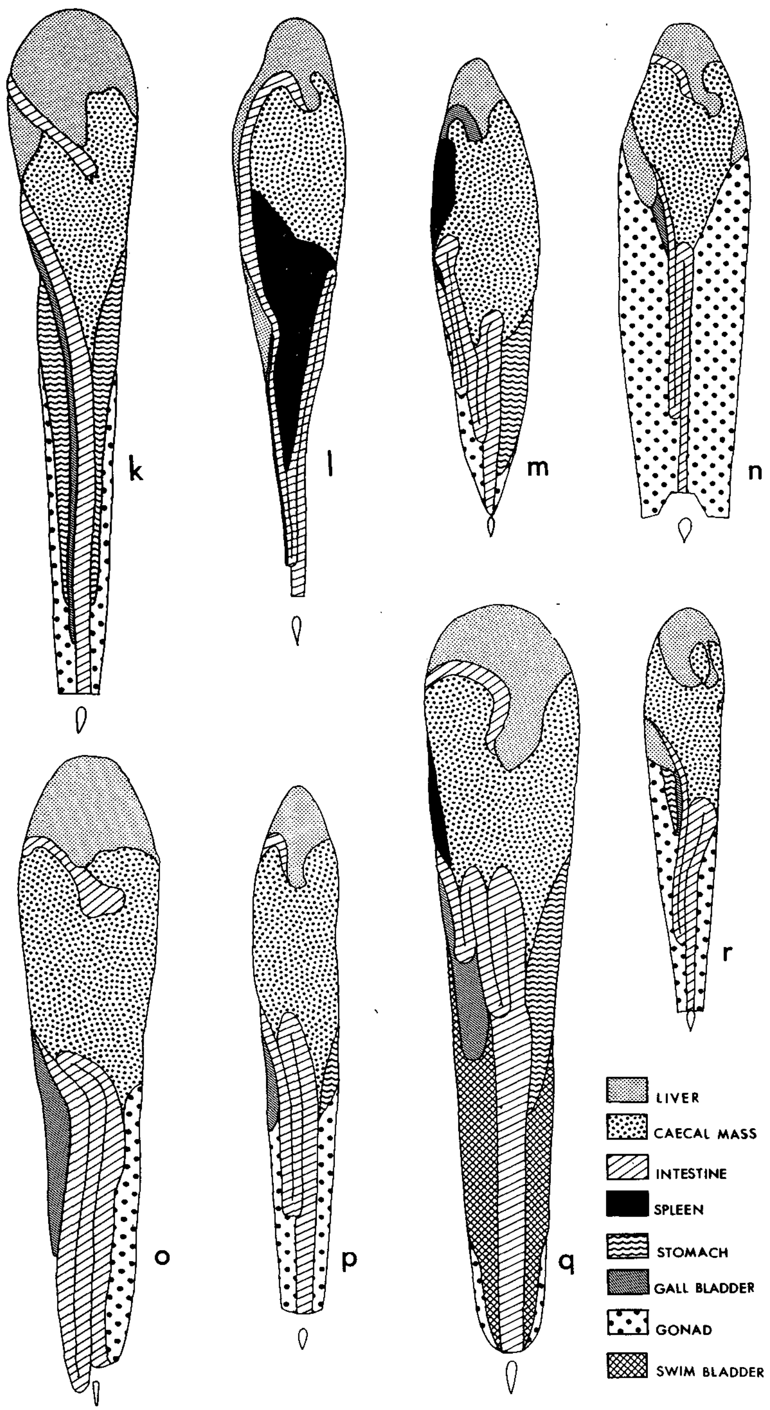


FIGURE 3.—Viscera in ventral view of representative specimens of the 18 species of *Scomberomorus*. a. *S. brasiliensis*, Belém Fish Market, Brazil, 556 mm FL. b. *S. cavalla*, off Miami, Fla., 797 mm FL. c. *S. commerson*, Gulf of Papua, 580 mm FL. d. *S. concolor*, Gulf of California, 495 mm FL. e. *S. guttatus*, Gulf of Mannar, 405 mm FL. f. *S. koreanus*, locality unknown, 812 mm FL. g. *S. lineolatus*, Cochin, India, 786 mm FL. h. *S. maculatus*, St. Andrews Bay, Fla., 323



mm FL. i. *S. multiradiatus*, Gulf of Papua, 272 mm FL. j. *S. munroi*, Gulf of Papua, 512 mm FL, USNM 219374. k. *S. niphonius*, Korea, 235 mm FL. l. *S. plurilineatus*, Durban, S. Africa, 490 mm FL. m. *S. queenslandicus*, Exmouth Gulf, Western Australia, 466 mm FL. n. *S. regalis*, Bahamas, 456 mm FL. o. *S. semifasciatus*, Gulf of Papua, 715 mm FL. p. *S. sierra*, Baja California, 516 mm FL. q. *S. sinensis*, China, 711 mm FL. r. *S. tritor*, Gulf of Guinea, 415 mm FL.

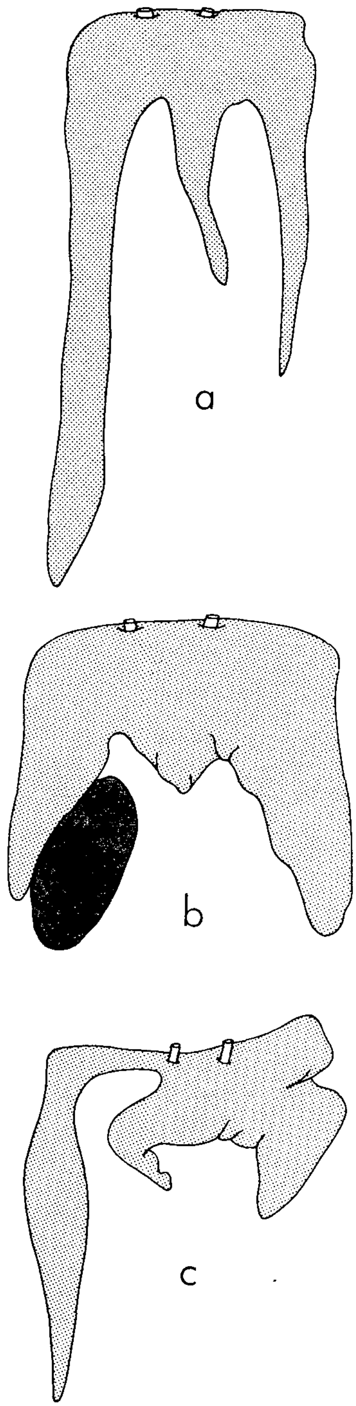


FIGURE 4.—Livers in ventral view. a. *Scomberomorus maculatus*, Florida, 712 mm FL. b. *Acanthocybium solandri*, Florida, 1,403 mm FL. c. *Grammatorcynus bilineatus*, Marshall Is., 444 mm FL.

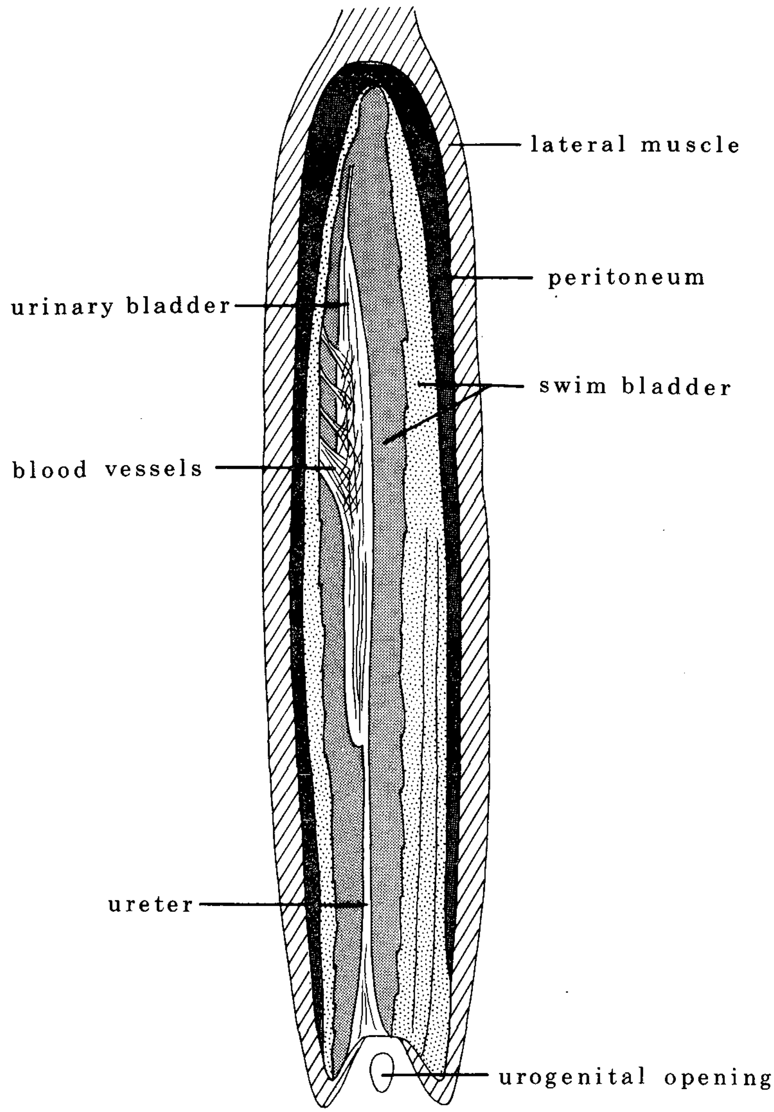


FIGURE 5.—Swim bladder and urinary bladder in ventral view of *Scomberomorus sinensis* (body wall and viscera removed), off Zhoushan Is., China, 714 mm FL, USNM 220856.

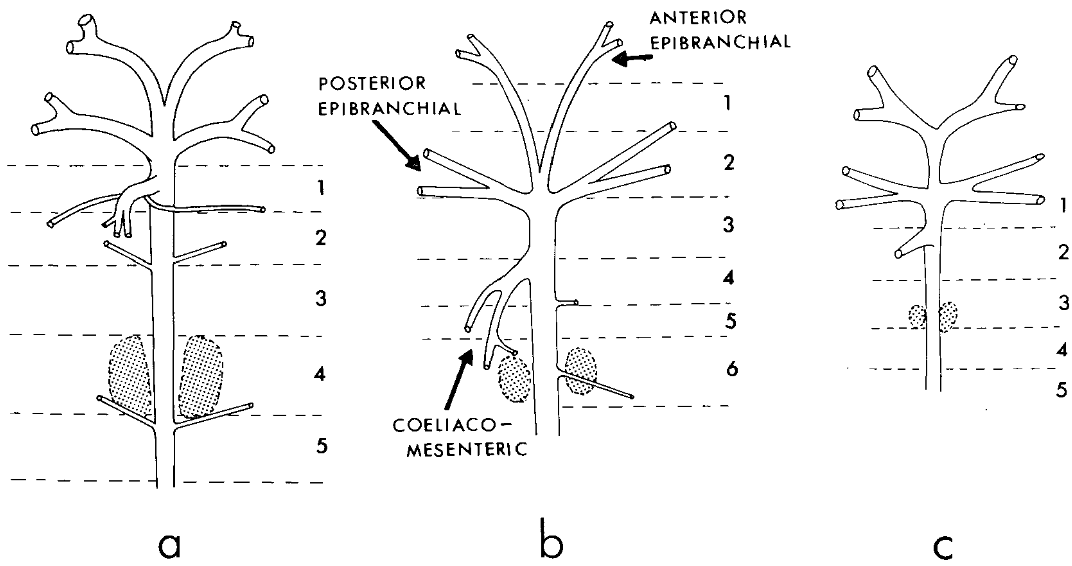


FIGURE 6.—Anterior arterial system in ventral view. Numbers indicate vertebral centra, stippled areas where pharyngeal muscles originate. a. *Scomberomorus multiradiatus*, off the Fly River, Gulf of Papua, 272 mm FL. b. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL. c. *Grammatorcynus bilineatus*, Timor Sea, 453 mm FL.

UROGENITAL SYSTEM

The only reference to the anatomy of the urogenital system in *Scomberomorus* (other than fishery biology studies of the gonads) is Kishinouye (1923) on Japanese species and *Acanthocybium*. The paired gonads lie along the dorsolateral body wall and are visible in ventral view in mature adults. The kidney lies dorsal to the layer of fibrous connective tissue which forms the dorsal wall of the peritoneum. Anteriorly, the kidney divides into a pair of narrow projections which extend along the sides of the parasphenoid and usually reach the posterior end of the "midridge" of the prootic. The anterior ends of the kidney surround the origins of the pharyngeal muscles on the vertebral column and usually separate along the middle of the vertebral column. In the vicinity of the esophagus, the kidney expands laterally and forms two projections which may extend anteriorly to the upper end of the gill slits. Posteriorly, near the posterior fifth of the body cavity, the kidney narrows to an elongate triangle (Fig. 8). The branches of the "ureter" (mesonephric ducts) join to form a common trunk just before entering the urinary bladder. The ureters enter the urinary bladder either at its anterior end or on its dorsal surface. The urinary bladder (Figs. 9, 10) is either ovoid or elongate, depending on degree of inflation, and is located in the mesenteries between the gonads in all species except *S. sinensis*. *Scomberomorus sinensis* has a specialization of the urinary bladder unique to scombrids and, so far as we know, vertebrates in general. In this species the urinary bladder has become hypertrophied and occupies the space inside the swim bladder (Fig. 5). *Acanthocybium* (Fig. 2b) has an elongate urinary bladder that extends anteriorly one-third to two-thirds the length of the visceral cavity.

OLFACTORY ORGAN

Kishinouye (1923) provided a generalized account of the olfactory organ of several scombrids. More detailed studies have been made on *Scomber scombrus* (Burne 1909), *Sarda sarda* (Tretiakov 1939), *Allothunnus fallai* (Nakamura and Mori 1966), *Katsuwonus pelamis* (Gooding 1963), *Thunnus* (Iwai and Nakamura 1964a; Gibbs and Collette 1967), and the bonitos, Sardini (Collette and Chao 1975). As in other scombrids, the olfactory cavity in *Scomberomorus* has a small anterior naris and a slitlike posterior naris. No information on the supplementary sacs, or accessory olfactory cavity (Iwai and Nakamura 1964a), was obtained from the present study comparable with that of Tretiakov (1939), who described three supplementary sacs (middle, maxillary, and rostral sacs) in *Sarda sarda*. The central axis of the

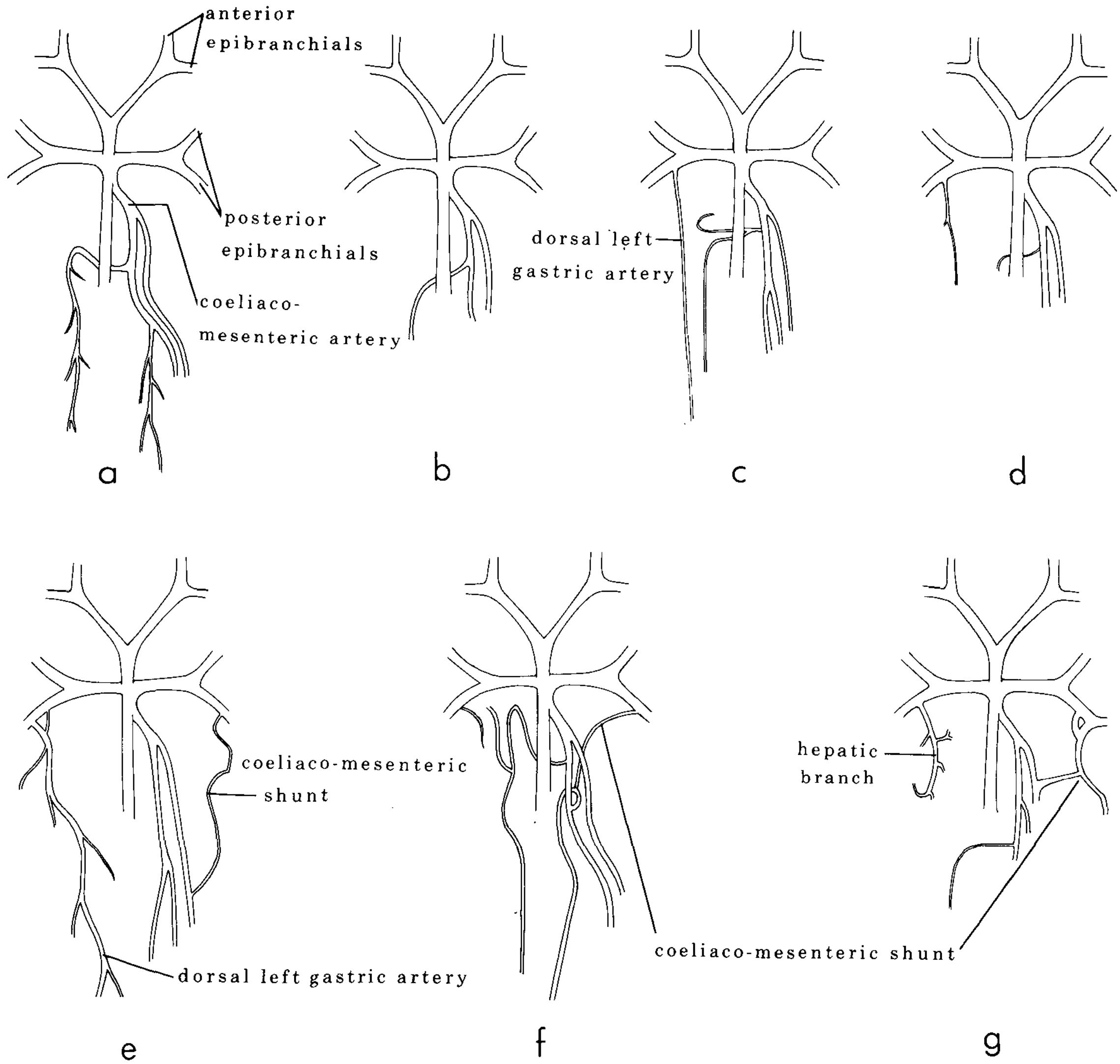


FIGURE 7.—Anterior arterial system in dorsal view of seven species of *Scomberomorus*. a. *S. guttatus*, Pakistan, 545 mm FL. b. *S. tritor*, Gulf of Guinea, 494 mm FL. c. *S. maculatus*, Chesapeake Bay, 312 mm FL. d. *S. concolor*, Gulf of California, 455 mm FL. e. *S. sierra*, Ecuador, 512 mm FL. f. *S. brasiliensis*, Belém market, Brazil, 588 mm FL, USNM 217557, paratype. g. *S. regalis*, Bahama Is., 490 mm FL.

olfactory rosette is located beneath the anterior naris. Leaflike lamellae radiate from the central axis and occupy the anterior dorsal third of the olfactory cavity. Gooding (1963) studied the morphology and histology of the olfactory organ of *Katsuwonus pelamis* and found olfactory cells on the olfactory epithelium of the lamellae. Iwai and Nakamura (1964a) found that the number of lamellae per rosette varies among specimens of species of *Thunnus* but that there were differences among species in the shape of the nasal laminae. Most species of bonitos have 21-39 lamellae in each nasal rosette but *Gymnosarda unicolor* is distinct in the group in having 48-56 (Collette and Chao 1975:532).

The number of olfactory lamellae was counted on both sides in *Scomberomorus* and a wide range of variation was observed, 24-76 (Table 2). In bonitos, the number of lamellae increases from small specimens to adults but does not appear to change after a certain size is reached, as Collette and Chao (1975:532) showed for *Gymnosarda*

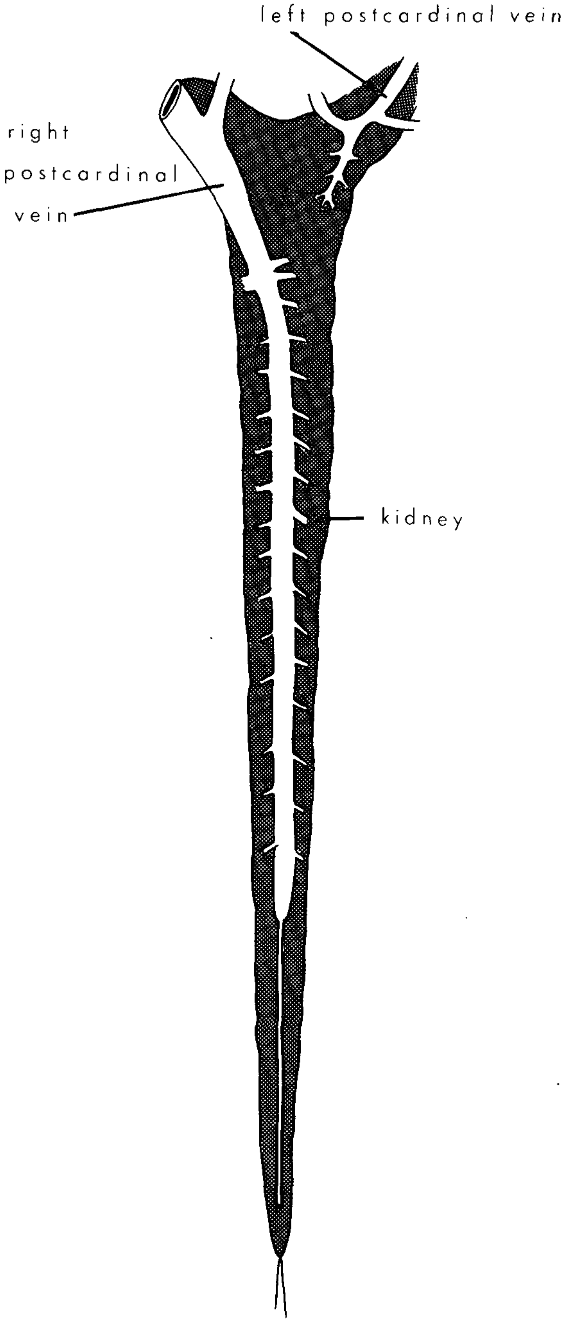


FIGURE 8.—Kidney and postcardinal vein in ventral view of *Scomberomorus queenslandicus*, Palm I., Queensland, 641 mm FL.

TABLE 2.—Number of lamella in nasal rosettes of species of *Scomberomorus*.

Species	Side	Min.	Max.	$\bar{x}$	N	Overall $\bar{x}$	Rank
brasiliensis	L	24	40	33.67	12	33.88	6
	R	25	42	34.08	13		
cavalla	L	30	56	42.92	24	43.13	12
	R	31	55	43.35	23		
commerson	L	42	58	48.92	12	49.32	13
	R	43	60	49.80	10		
concolor	L	26	35	30.92	13	30.92	1
	R	26	34	30.92	13		
guttatus	L	30	76	53.41	27	53.43	16
	R	31	73	53.46	26		
koreanus	L	47	56	50.67	3	54.75	18
	R	48	73	57.20	5		
lineolatus	L	30	35	32.50	4	32.18	3
	R	30	34	32.00	7		
maculatus	L	25	38	33.43	14	33.44	5
	R	30	37	33.45	11		
multiradiatus	L	32	40	36.75	4	36.00	10
	R	25	44	34.50	2		
munroi	L	54	54	54.00	3	53.84	17
	R	54	57	53.67	3		
niphonius	L	25	42	33.67	15	34.41	7
	R	26	42	35.21	14		
plurilineatus	L	45	53	49.50	4	50.50	14
	R	44	56	51.50	4		
queenslandicus	L	43	59	49.75	4	50.67	15
	R	43	61	51.40	5		
regalis	L	28	41	34.00	9	35.11	9
	R	30	43	36.22	9		
semifasciatus	L	31	37	34.00	3	34.78	8
	R	31	38	35.17	6		
sierra	L	30	36	32.64	14	32.07	2
	R	28	34	31.50	14		
sinensis	L	38	38	38.00	1	42.50	11
	R	41	47	44.00	3		
tritor	L	27	48	33.40	10	32.57	4
	R	24	37	31.83	11		

unicolor and *Orcynopsis unicolor.* We have not examined many small *Scomberomorus* nasal rosettes but did find 23 lamellae in an 80 mm FL *S. guttatus*, a species for which the minimum count of lamellae for specimens larger than 100 mm was 30.

Three species of *Scomberomorus* (*koreanus*, *munroi*, and *guttatus*) had high counts, overall means 53.4-54.8. The highest counts per side were for *S. koreanus* (73) and *S. guttatus* (76). Ten species had low counts, overall means 31.0-36.0. These 10 included all 6 species of the *regalis* group as well as *lineolatus*, *multiradiatus*, *niphonius*, and *semifasciatus*.

PHARYNGEAL MUSCLES

The paired pharyngeal (retractor dorsalis) muscles originate on the ventral surface of one or two vertebrae between the third and the sixth abdominal vertebrae and insert on the upper pharyngeal bones (Fig. 2). We did not find any differences between species as Collette and Chao (1975) did for the bonitos.

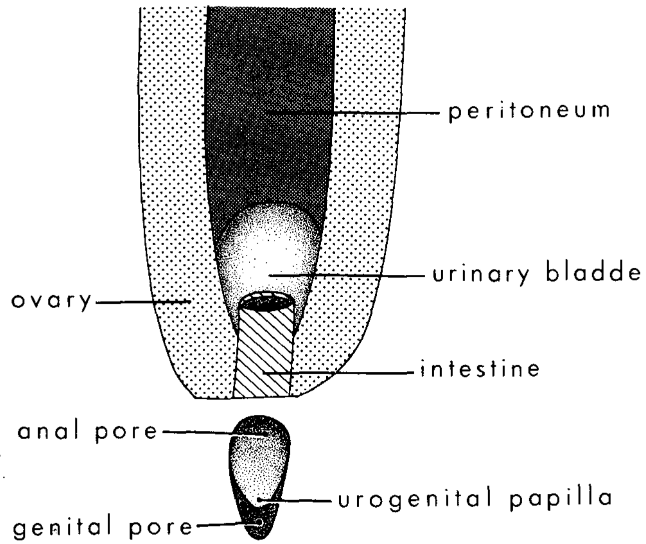


FIGURE 9.—Urogenital system in ventral view of *Scomberomorus* (body wall and viscera removed). Composite illustration.

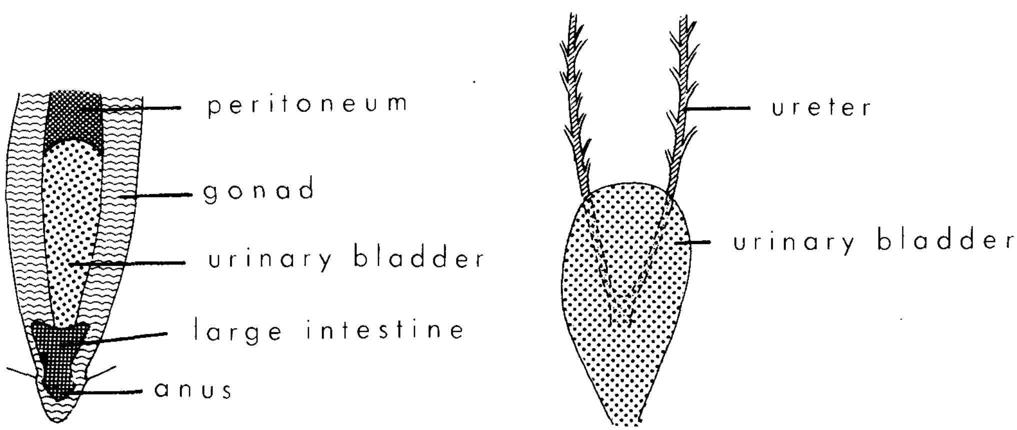


FIGURE 10.—Urogenital system in ventral view of *Scomberomorus queenslandicus*, Palm I., Queensland, 641 mm FL. a. With intestine opened. b. Urinary bladder and ureters.

Osteology

Osteological characters proved to be useful in determining relationships among the 18 species of *Scomberomorus* and between this genus and its presumed closest relatives, *Acanthocybium* and *Grammatorcynus*. The osteological portion of the paper is divided into five sections: skull, axial skeleton, dorsal and anal fins, pectoral girdle, and pelvic girdle. Osteological terminology generally follows Gibbs and Collette (1967) and Collette and Chao (1975). Organization within sections is similar to that of Collette and Chao (1975) and the two earlier papers of most importance to the osteology of *Scomberomorus*: Mago Leccia (1958) on three western Atlantic species (*cavalla*, *maculatus*, and *regalis*) and Devaraj (1977) on four Indian species (*commerson*, *guttatus*, *koreanus*, and *lineolatus*) and *Acanthocybium*.

SKULL

Description of the skull is presented in two sections: neurocranium (Figs. 11-19) 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, the neurocranium of *Scomberomorus* is more or less trapezoidal in shape. It is elongate and flat, particularly at the anterior region and is deepest at the hind end of the orbit. The dorsal surface is marked by a median ridge and three grooves on each side: dilator, temporal, and supratemporal (Allis 1903:49). These grooves are

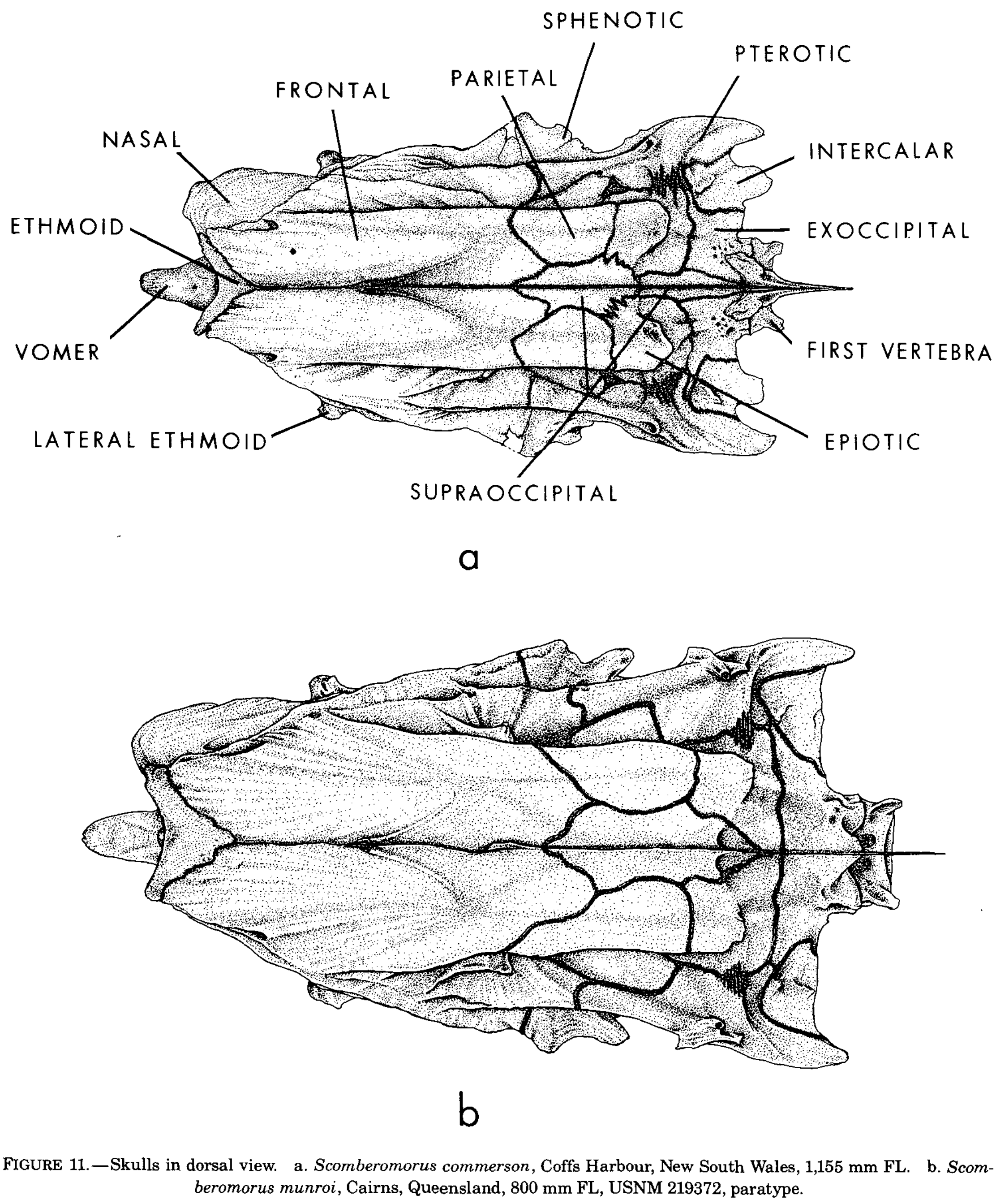


FIGURE 11.—Skulls in dorsal view. a. *Scomberomorus commerson*, Coffs Harbour, New South Wales, 1,155 mm FL. b. *Scomberomorus munroi*, Cairns, Queensland, 800 mm FL, USNM 219372, paratype.

separated from each other by ridges of bone. Thus, there are six grooves and five ridges in all. The median ridge is carried forward on the frontals to the ethmoid and is prolonged posteriorly in a large supraoccipital crest. This crest extends down over the exoccipital suture more broadly than in any other genus of the Scombridae.

The internal ridge or temporal ridge almost reaches anteriorly to the posterior portion of the nasal, and it is not interrupted above the eyes by any transverse ridge. Posteriorly, the ridge ends at the epiotic where the medial process of the posttemporal attaches.

The external or pterotic ridge extends forward to the midlevel of the orbit and develops anteriorly a small auxiliary ridge that extends laterally and posteriorly toward the temporal ridge.

The dilator groove is shorter than the other two

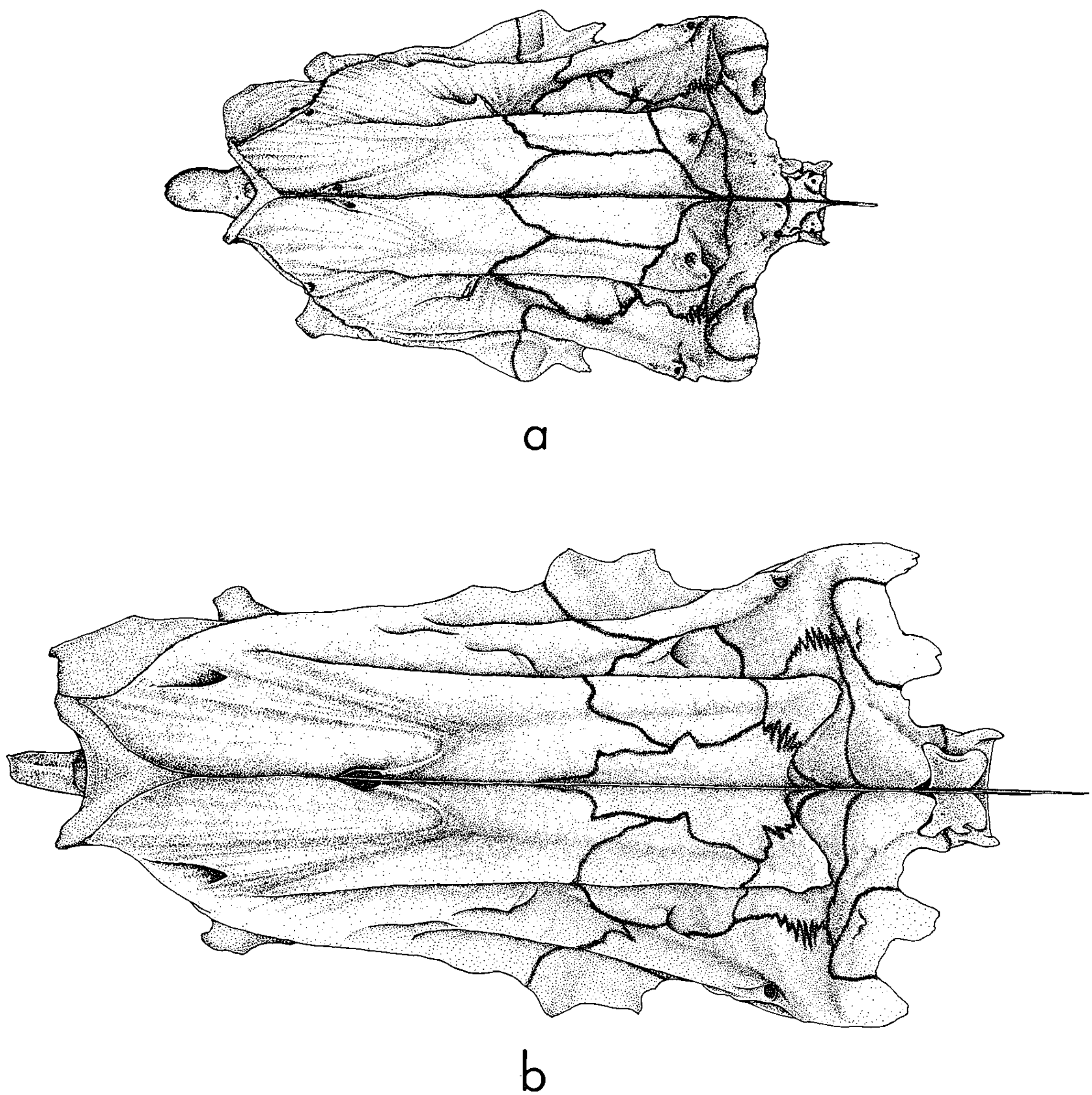


FIGURE 12.—Skulls in dorsal view. a. *Scomberomorus koreanus*, Singapore, 480 mm FL. b. *Scomberomorus concolor*, Gulf of California, 495 mm FL.

and can be detected easily in lateral view. The temporal groove is the middle one and is deeper than either of the other two. The remaining groove, the supratemporal, is the largest of the three and opens posteriorly between the supraoccipital crest and the middle portion of the epiotic.

The interorbital and otic regions are not as broad as in the more advanced genera of the Sardini (Collette and Chao 1975) and Thunnini (Gibbs and Collette 1967). The median and temporal crests are higher in *Scomberomorus* than in other scombrids. The bonitos, particularly *Orcynopsis unicolor* (Collette and Chao 1975:fig. 21),

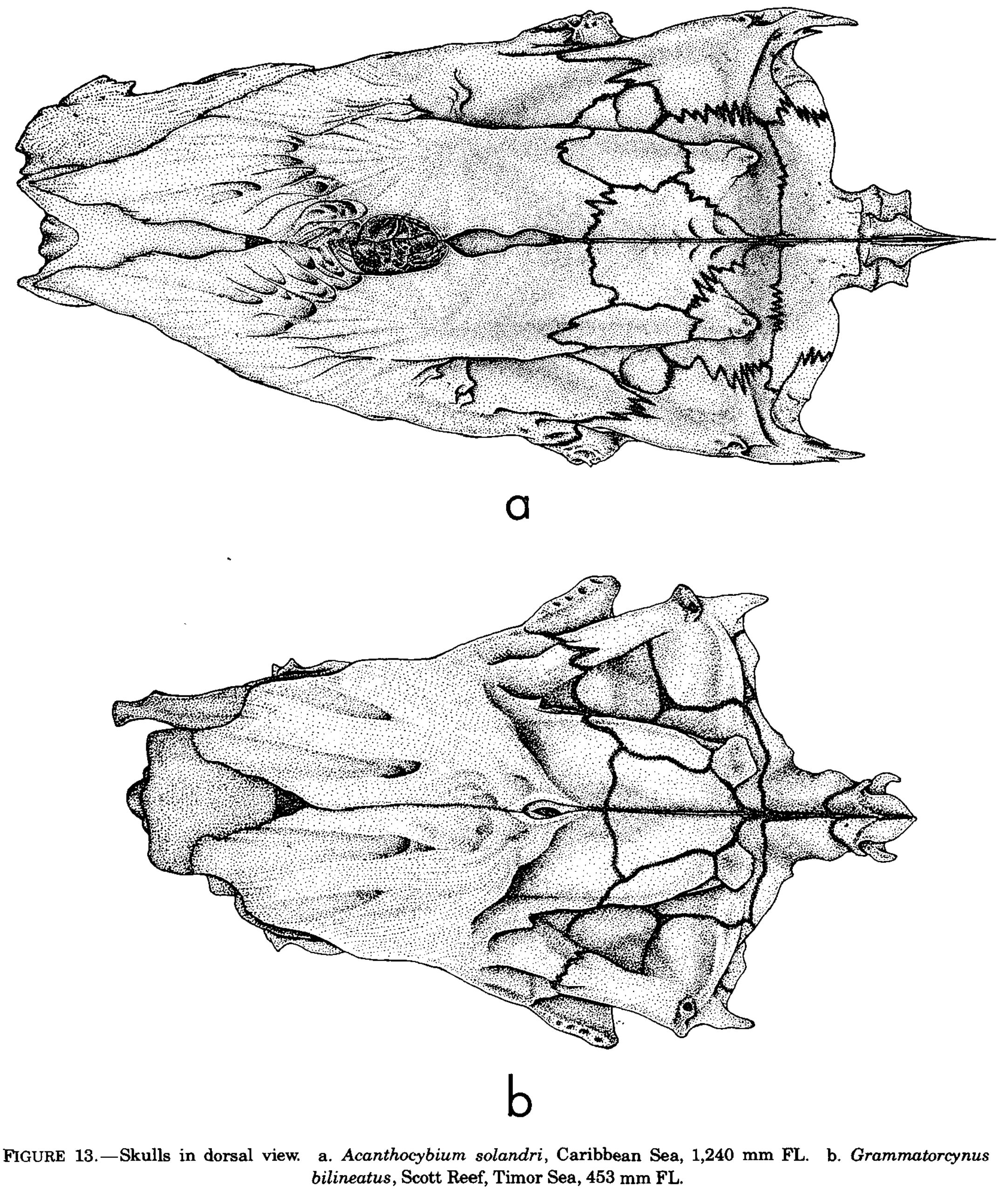


FIGURE 13.—Skulls in dorsal view. a. *Acanthocybium solandri*, Caribbean Sea, 1,240 mm FL. b. *Grammatorcynus bilineatus*, Scott Reef, Timor Sea, 453 mm FL.

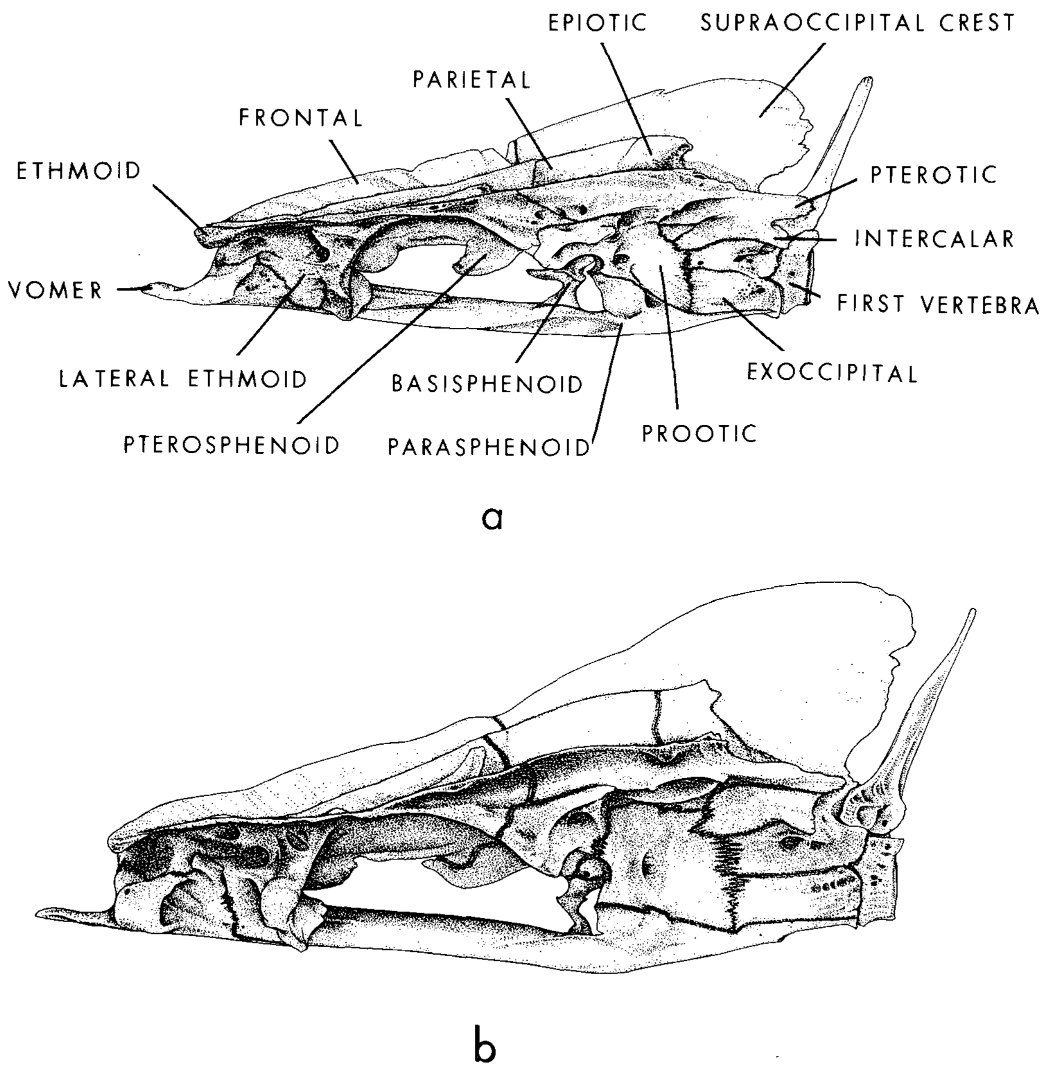


FIGURE 14.—Skulls in lateral view. a. *Scomberomorus commerson*, Coffs Harbour, New South Wales, 1,155 mm FL. b. *Scomberomorus munroi*, Cairns, Queensland, 800 mm FL, USNM 219372, paratype.

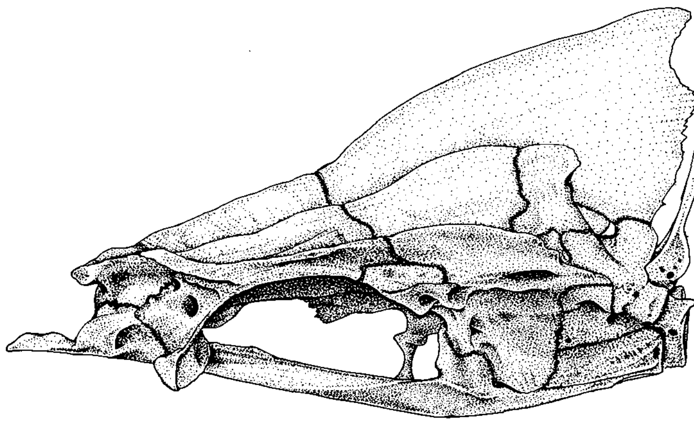
have the next highest crests.

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.

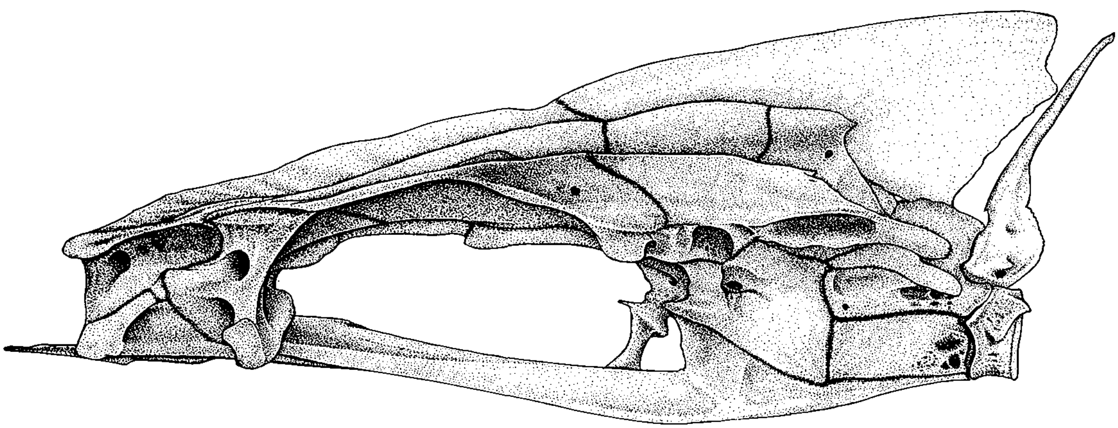
Ethmoid.—The ethmoid (dermethmoid) is a forked median bone overlapped by the frontals above and bounded by the vomer and lateral ethmoid ventrally. The concave anterior surface articulates with the ascending process of the premaxilla. At its anterolateral aspect, the ethmoid bone supports the nasals.

In *Scomberomorus*, only the most anterior part of the ethmoid bone is exposed in dorsal view, while the rest of it is overlapped by the frontals. In *Acanthocybium*, only the lateral aspects of the bone are overlapped by the frontals and a V-shaped dorsal median portion is exposed. The ethmoid bone is longer in *A. solandri* than in *Scomberomorus*.

Lateral ethmoid.—The lateral ethmoids (par-ethmoids) are massive paired bones which form the anterior margin of the orbit and the posterior and mesial walls of the nasal cavity. The lateral portion of each bone extends downward from the middle region of the frontals. The ventral surface of this wall mesially bears an articulating surface for the palatine and laterally another articulating surface for the first infraorbital (lachrymal). The inner walls of the lateral ethmoids come closest to each other at the ventral median line of the skull and contact the anterior edge of the parasphenoid. The median half of each lateral ethmoid extends downward about three-fourths as far as the lateral portion and has a large round foramen for the olfactory nerve which is prominently seen on the anterior surface. On the dorsal surface, they abut the nasals anteriorly, the frontals posteriorly, and articulate with the ethmoid mesially. On the anterior surface, ventral to the foramen, each lateral ethmoid bears a process



a

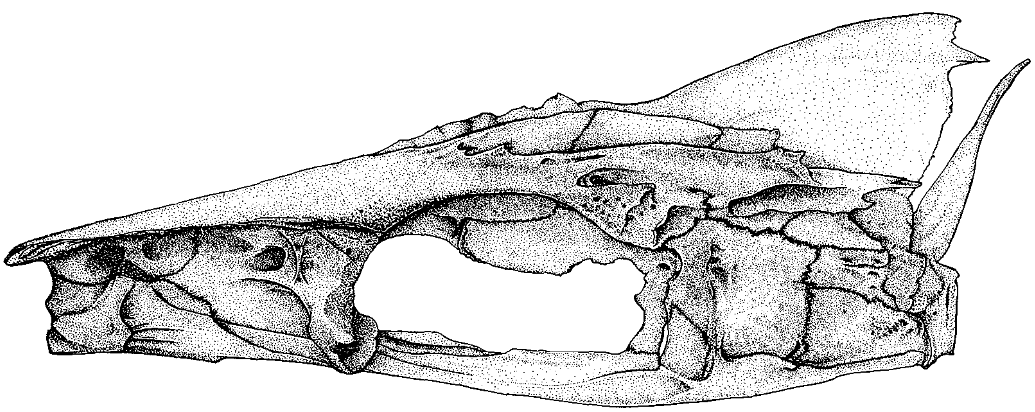


b

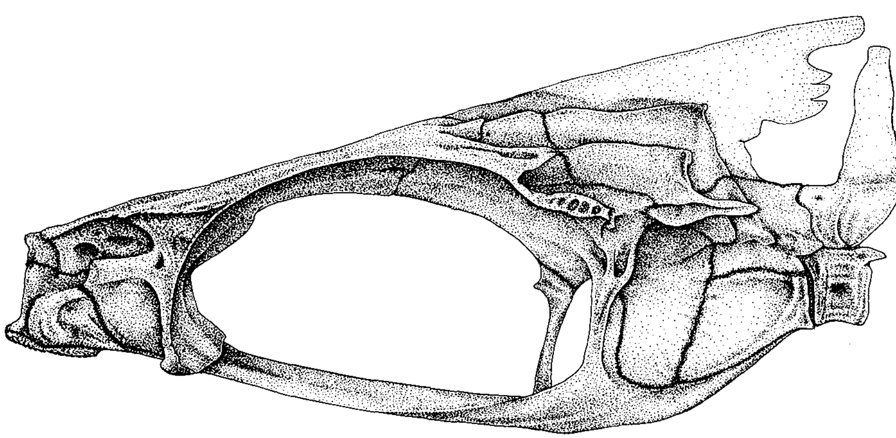
FIGURE 15.—Skulls in lateral view. a. *Scomberomorus koreanus*, Singapore, 480 mm FL. b. *Scomberomorus concolor*, Gulf of California, 495 mm FL.

that extends anteriorly and mesially to contact the dorsolateral surface of the spear-shaped posterior portion of the vomer. No appreciable difference was noted in the lateral ethmoids of the different species.

Vomer.—The vomer is the most anteroventrally located bone of the cranium. The spatula-shaped anterior process bears a large oval patch of fine teeth on its ventral surface. The vomerine tooth patch extends posteriorly as a narrow ridge in some specimens of some species, e.g., *S. concolor* (Fig. 15b). The vomer articulates with the ethmoid dorsally and lateral ethmoid dorsolaterally. The pointed posterior process is firmly ankylosed dorsally with the parasphenoid. On each side of the vomer, dorsolaterally and behind the spatulate anterior process, is a prominent articular surface for a loose articulation with the head of the maxilla. Posterior to this articular surface, facing ventrolaterally, is a prominent sulcus for a similar movable articulation with the ventral branch of the anterolateral fork of the palatine. The spatulate anterior process of the vomer is very long and extends beyond the anterior margins of the nasal and ethmoid bone in *Scomber-*



a



b

FIGURE 16.—Skulls in lateral view. a. *Acanthocybium solandri*, Caribbean Sea, 1,240 mm FL. b. *Grammatorcynus bilineatus*, Scott Reef, Timor Sea, 453 mm FL.

omorus. No other scombrid has such a spatulate anterior extension of the vomer. In fact, the vomer is either not visible in dorsal view or protrudes anteriorly slightly beyond the ethmoid in other scombrid genera.

Nasal.—The nasal bones (Fig. 20) are flat, roughly triangular bones with thickened lateral edges. The mesial edges are irregular and almost serrate in some species to form a firm immovable articulation with the lateral edge of the frontals.

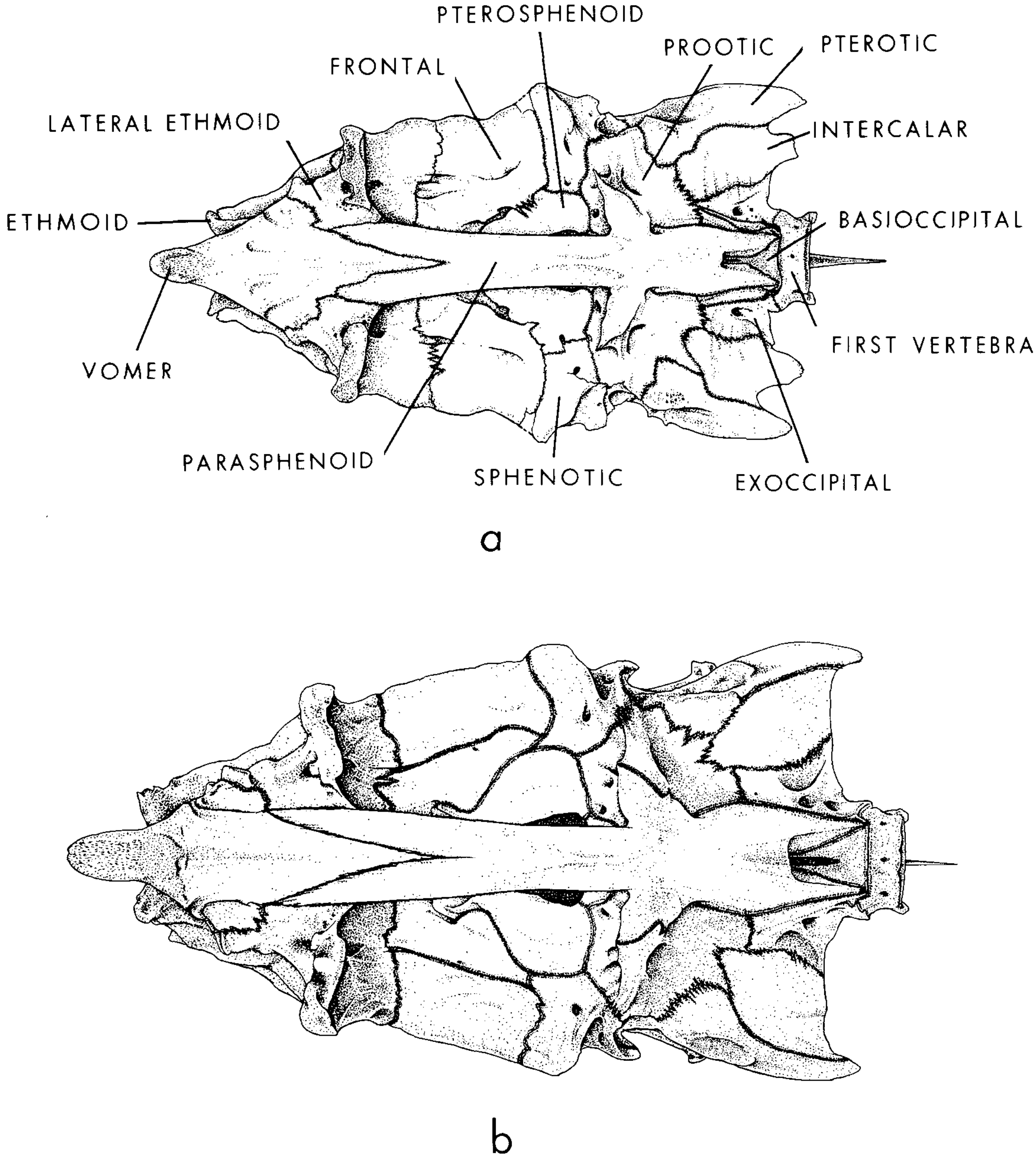
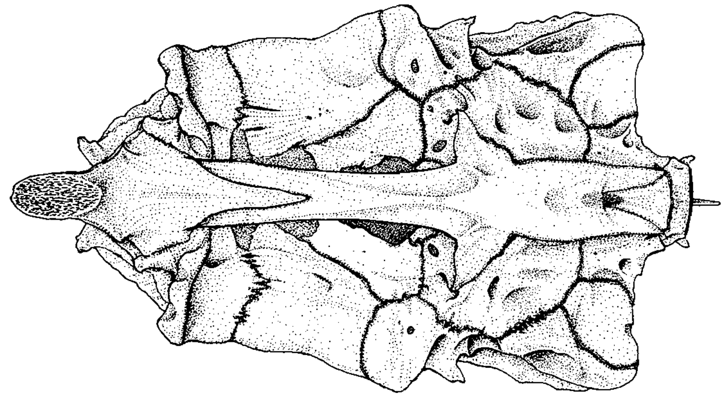


FIGURE 17.—Skulls in ventral view. a. *Scomberomorus commerson*, Coffs Harbour, New South Wales, 1,155 mm FL. b. *Scomberomorus munroi*, Cairns, Queensland, 800 mm FL, USNM 219372, paratype.



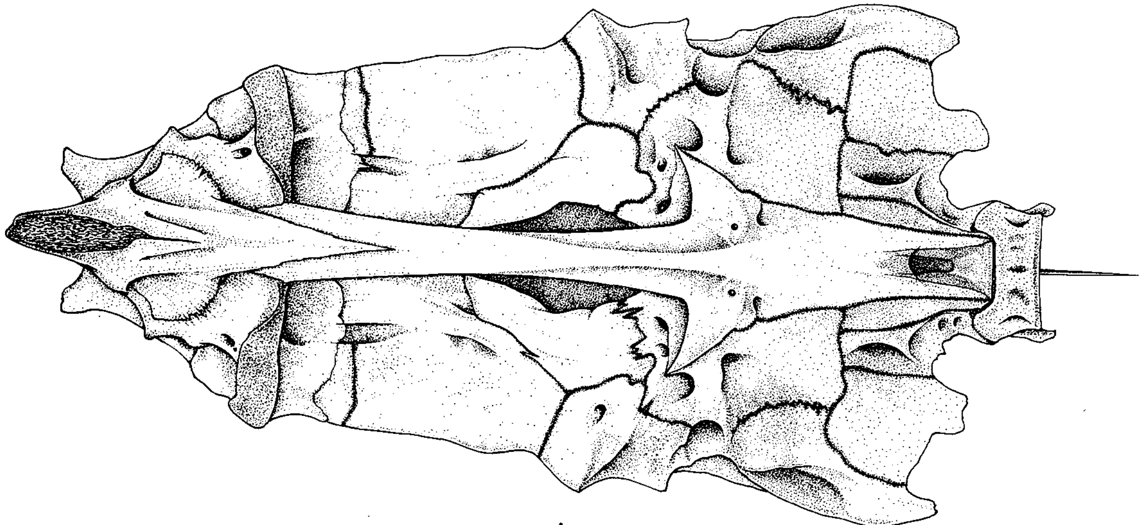


FIGURE 18.—Skulls in ventral view. a. *Scomberomorus koreanus*, Singapore, 480 mm FL. b. *Scomberomorus concolor*, Gulf of California, 495 mm FL.

The anterior margins fit neatly beside the anterior branches of the forked ethmoid bone as can be seen in the dorsal views of the skulls (Figs. 11, 12). They are nonprojecting in that their anterior margin is at the level of the ethmoid bone except in *Grammatorcynus* where they project well beyond the anterior end of the neurocranium (Fig. 13b). Length divided by width ranges from 2.0 to 4.2 in the three genera. The widest nasal bones are in *S. koreanus* (2.0-2.1) and *S. sinensis* (2.0-2.3, Fig. 20b). The most elongate nasals are in *Acanthocybium* (3.1-4.2, Fig. 20c), *Grammatorcynus* (2.8-3.4, Fig. 20d), *S. cavalla* (2.8-3.1, Fig. 20a), and *S. regalis* (2.8-3.0). The other 14 species of *Scomberomorus* are intermediate (2.0-2.9). The anterior end of the nasal bone is rounded and heavy in *Scomberomorus* and *Acanthocybium* (Fig. 20a-c). The anterior end has a short, slightly angled arm in *Grammatorcynus* (Fig. 20d).

ORBITAL REGION.—The orbit is surrounded by the posterior wall of the lateral ethmoid, the ventral side of the frontal, the pterosphenoid, sphenotic, prootic, suborbital, and lachrymal

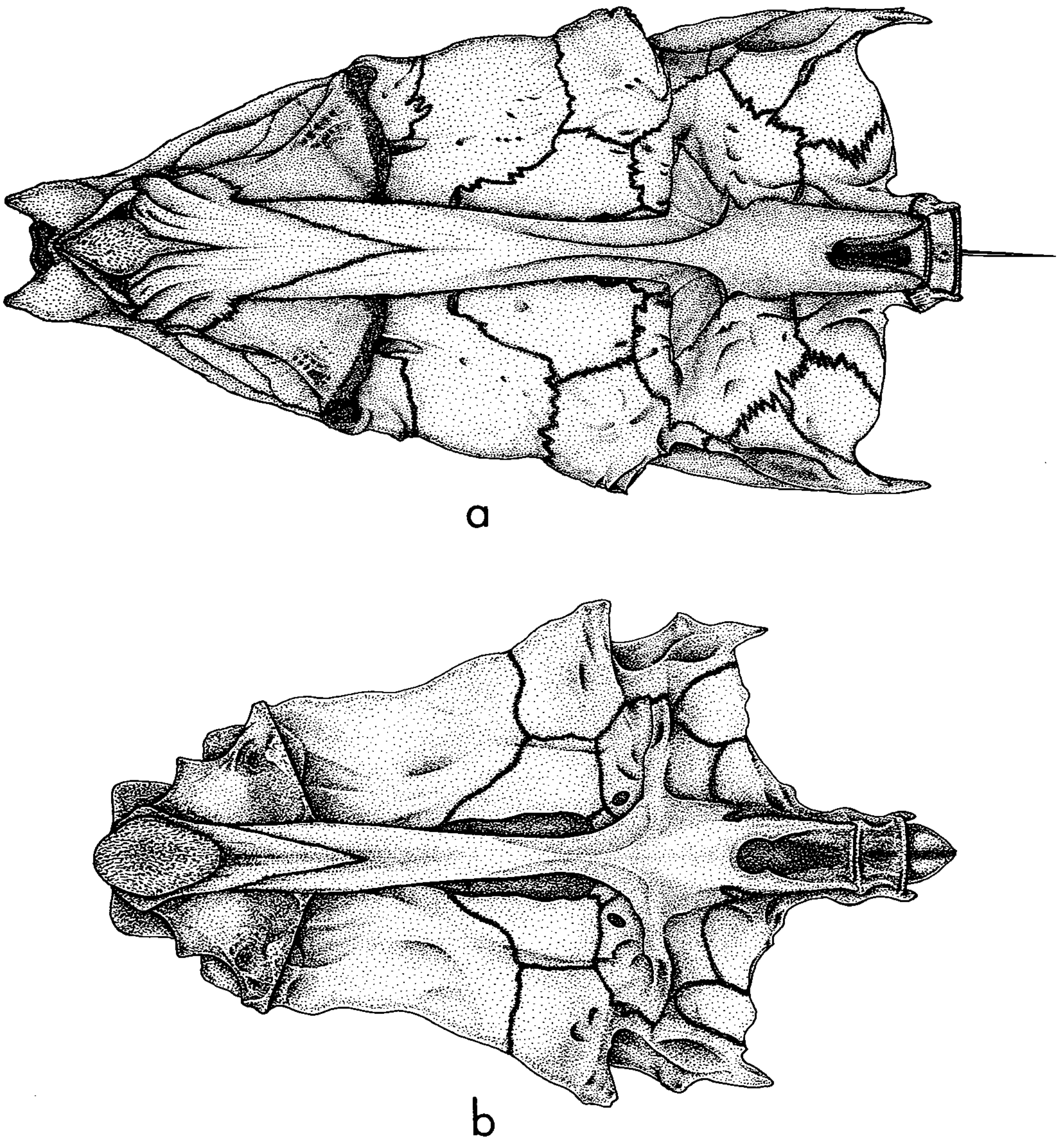


FIGURE 19.—Skulls in ventral view. a. *Acanthocybium solandri*, Caribbean Sea, 1,240 mm FL. b. *Grammatorcynus bilineatus*, Scott Reef, Timor Sea, 453 mm FL.

bones. The left and right orbits are partially separated by the basisphenoid. The sclerotic bones enclose the eyeballs.

Frontal.—The frontals are paired bones that form the largest portion of the dorsal surface of the neurocranium. Anteriorly they are pointed, and posteriorly they become expanded. Anteriorly, the frontals overlap the dorsal surface of the ethmoid bone, the inner edge of the nasals, and the dorsal surface of the lateral ethmoid. The midlateral aspect is thickened to form the orbital roof. Posteriorly, they are bounded by the supraoccipital and parietals. Posterolaterally, they overlap the pterotics and just anterior to the pterotics, cover the sphenotics. Ventrally, each frontal bears a sheet of bone, the orbital lamella, which is bounded by the sphenotic posteriorly, lateral ethmoid anteriorly, and pterosphenoid mesially. On the base of the orbital lamella may be seen a number of small foramina for the branches of the supraorbital nerve trunk. The laterosensory canals of the frontals are evident on the pterotic crests as a series of pores.

In *Acanthocybium*, the frontals are separated from each other by the dorsomedian pineal fenestra lying just in front of the supraoccipital at the level of the pterosphenoids and another anterior fontanel just posterior to the ethmoid bone (Fig. 13a). A smaller, more oval pineal opening is present between the posterior ends of the frontals in *Grammatorcynus* (Fig. 13b). When viewed through the pineal fenestra, a part of the dorsal surface of the parasphenoid is visible through the opening of the brain chamber between the pterosphenoids. There is a deep depression on the frontals mesially, just anterior to the pineal fenestra. This depression becomes shallower anteriorly, becoming confluent with the dorsal surface of the frontals. In *Scomberomorus*, the frontals join mesially along the median line on the neurocranium where they form the anterior half of the median ridge whose posterior half is composed of the supraoccipital crest. In all but three species of *Scomberomorus*, the left and right frontals are attached very closely to each other such that there is no gap between them. However, in *S. commerson* and *S. cavalla*, there is a long narrow slit between the left and right frontals, but it is not a fenestra in the true sense, as the lower parts of the bones are very closely approximated. A third condition is found in *S. sinensis*. Here the anterior part of the median ridge is almost absent and there is a wide gap between the left and right frontals. The interorbital commissures of the lateralis system are developed a little anterior to the middle of each frontal in the form of two pores at the margin of the median ridge which lead into oblique tubes downwards and posteriorly. Another pair of commissures of the lateralis system is developed along the anterolateral margin of the frontals. These sensory canals are not developed in *Acanthocybium* and *Grammatorcynus*.

Pterosphenoid.—The pterosphenoids (alisphenoids) form the posterodorsal region of the orbit. They abut the basisphenoid and prootics posteri-

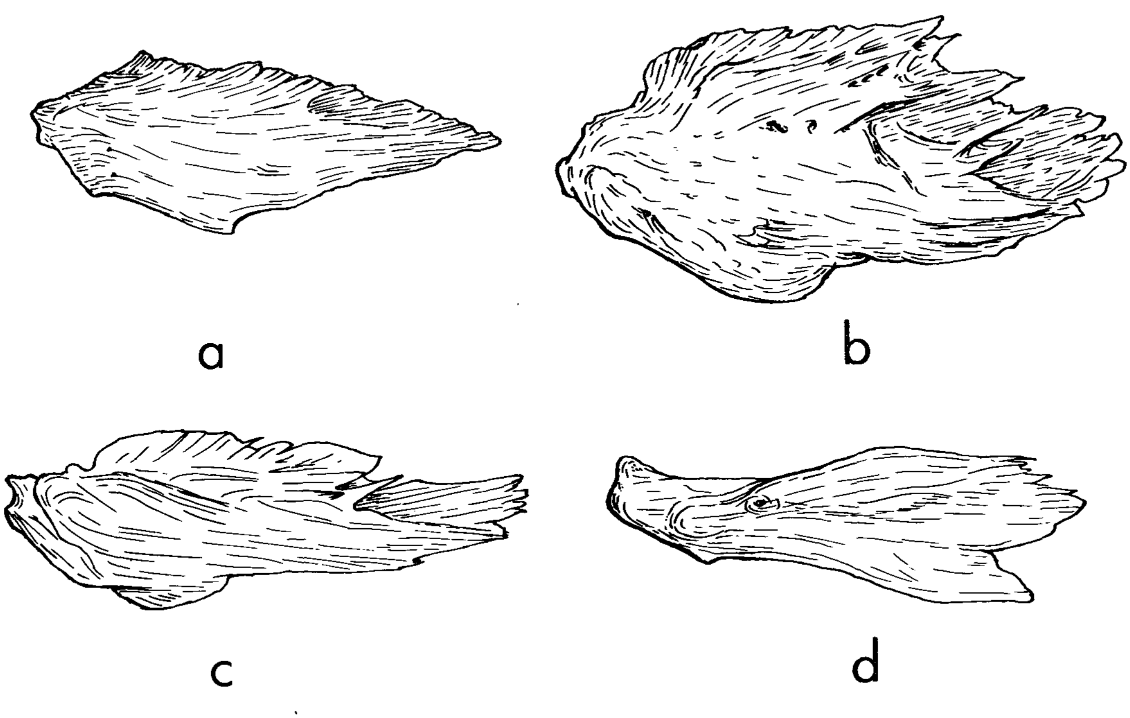


FIGURE 20.—Left nasal bones in lateral view. a. *Scomberomorus cavalla*, Miami, 797 mm FL, 2×. b. *Scomberomorus sinensis*, Tokyo, 1,850 mm FL, 1×. c. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL, 1.5×. d. *Grammatorcynus bilineatus*, Queensland, 521 mm FL, 3×.

orly and the frontals and sphenotics laterally. There is a space between the left and right pterosphenoids opening into the brain chamber just anterior to the basisphenoid. In most species of *Scomberomorus*, there is an anterior medially directed lobe on each pterosphenoid. These lobes meet along the median line or at least come very close to each other in adults of three species: *commerson* (over 1,000 mm FL), *cavalla* (over 550 mm FL), and *lineolatus* (over 750 mm FL). Smaller specimens of these 3 species and all sizes of the other 15 species have a wide gap or fenestra between the left and right lobes. The gap is about equal to the width of the parasphenoid or slightly larger in three species: *brasiliensis*, *koreanus* (Fig. 12a), and *concolor* (Fig. 12b). The gap is largest in *S. multiradiatus*, so large that there is virtually no medially directed lobe. This causes the window into the brain chamber to be almost rectangular in this species.

Sclerotic.—The sclerotic bones consist of two thickened semicircular segments connected by cartilage on the inner lateral surface and by corneal membranes on the outside. The inner rim of the sclerotic bones appears elliptical externally as in the bonitos (Collette and Chao 1975) and *Thunnus* (e.g., *T. atlanticus*, de Sylva 1955:fig. 7). The sclerotic bones of *Grammatorcynus* are relatively larger, thinner, and close to circular. In *Acanthocybium*, the sclerotic bones are elliptical as in *Scomberomorus*, but they are heavier and extend further medially. The only species of *Scomberomorus* that appeared to differ from the other species is *S. sinensis*. The sclerotics are especially thick in this species and there is a thick bony lump in the middle of the posterior surface of one of the two sclerotics. Other species of *Scomberomorus* have a thickening of the bone in the same region but it does not form a distinct protrusion as it does in *S. sinensis*.

Basisphenoid.—The basisphenoid is a small, median, Y-shaped bone that connects the parasphenoid, prootics, and pterosphenoids. The compressed median vertical base bears an anterior median process but lacks a posterior process as is present in other scombrids such as *Thunnus* (Gibbs and Collette 1967) and most bonitos (Collette and Chao 1975). In most species of *Scomberomorus* there is at least a trace of a lateral ridge that extends laterally and posteriorly on each side of the anterior process. There is great variation in the length of the anterior process and in the relative degree of development of the lateral ridges. Both features are best developed in *S. commerson* where the length of the anterior process is greater than the height of the vertical axis of the bone.

Infraorbitals.—The *infraorbital* (suborbital) series of *Scomberomorus* consists of from 9 to 13 elements which enclose the infraorbital branch of the lateral sensory canal system (Fig. 21a). Only 9 elements were observed in *S. munroi*, *S. sierra*, and *S. sinensis*, but 13 elements were observed in *S. brasiliensis*. The canal enters the infraorbital series at what is usually considered the last element (dermosphenotic) and continues around the orbit to terminate on the first infraorbital (lachrymal).

The first infraorbital (lachrymal or IO1) is the first and largest element in the infraorbital series. Anteriorly, several canal tubes open on the laminar, platelike surface of the bone. Posteriorly, the canal tube continues directly to the second infraorbital. The first infraorbital is an elongate bone (length/height = 2.8-3.5) that covers part of the maxilla and is attached to the lateral ethmoid dorsally by a mesially directed articular process. The anterior portion is forked with a thin anterior process. This process is a point of attachment for a ligament connected to the nasal. The projection is present in all species of *Scomberomorus* except *S. lineolatus* and *S. tritor*. The portion posterior to the articular process is elongate, pointed, and longer than the anterior portion. The general shape of the first infraorbital in *Scomberomorus* is similar to that in the bonitos (Collette and Chao 1975:fig. 28), particularly *Cybiosarda elegans*, except that the anterior process is smaller and more dorsally directed than in *Cybiosarda*. *Acanthocybium* differs from *Scomberomorus* in having the posterior portion of the first infraorbital short and broad, shorter than the anterior portion (Fig. 21b). *Grammatorcynus* has a feebly forked anterior end (Fig. 21c), lacking a distinct anterior process such as is present in *Scomberomorus* and *Acanthocybium*.

As Devaraj (1977) noted, the dorsal margin of the anterior part of the first infraorbital is straight, or nearly so, in *S. cavalla* and *S. commerson* but clearly concave in the other species. Mago Leccia (1958:pl. 4, fig. 7) indicated that *S. cavalla* lacked the characteristic anterior projection, but we have found it to be present in our material. In other respects, there seems to be as much variation between individuals of a species

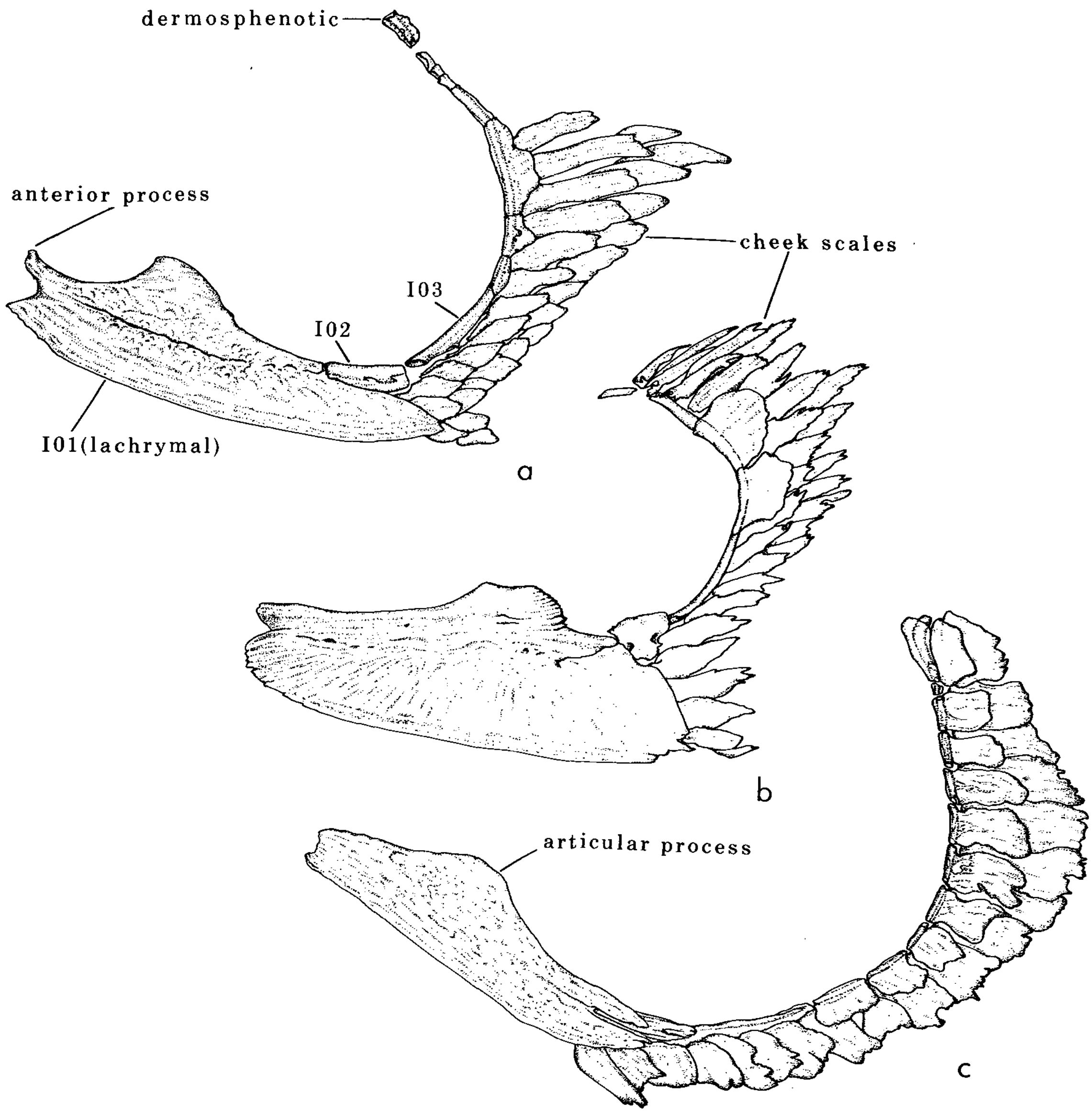


FIGURE 21.—Left infraorbital bones in lateral view. a. *Scomberomorus maculatus*, Cape Hatteras, N.C., 534 mm FL. b. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL. c. *Grammatorcynus bilineatus*, Timor Sea, 453 mm FL.

as between species in the shape of the first infraorbital.

The second infraorbital (IO2) sits firmly on the dorsal edge of the anterior portion of the first infraorbital. It is a flat, somewhat compressed bone.

The third infraorbital (IO3) is an elongate, tubular bone. It has no platelike extensions, but has a large mesial shelflike extension (subocular shelf of Smith and Bailey 1962). Although not reported by those authors, we have found this shelf to occur in all species of *Scomberomorus* as well as in all other genera of scombrids. The shape of this shelf varies among specimens of the same species as well as between right and left sides of a single specimen.

The fourth through the penultimate elements (postorbitals) usually are simple tubelike bones which may have pores accommodating canal tubes to the skin and cheek scales. The fourth through about the seventh elements may be expanded laterally as laminar plates which cover the anterior end of the cheek scales. There may be 10-16 rows of specialized cheek scales posterior to the infraorbitals. These scales originate mesial to the infraorbital canal tubes and extend posteriorly as flat, sometimes pointed, platelike elements. These platelike scales may themselves be covered with more typical cycloid scales and exhibit the same morphology as the corselet scales of higher scombrids. The cheek scales of *Scomberomorus* may represent the primitive condition of the corselet.

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 and the pterotics laterally, sphenotics ventrally, and epiotics posteriorly. The inner lateral crest that originates at the middle of the frontal bones continues through the parietals to terminate at the epiotics. This crest is typical of scombrids and is particularly well developed in *Scomberomorus*. These crests originate on the parietals, instead of the frontals, in *Acanthocybium* and *Grammatorcynus* and are not as high as in *Scomberomorus*. The parietals of all the species of *Scomberomorus* are similar.

There is a gap or fenestra on the dorsal surface of the skull where the parietal, epiotic, and pterotic bones come together. It varies in shape from roughly triangular to rectangular in most species. There is wide variation from specimen to specimen that tends to obscure potential interspecific differences. The gap is very small in some specimens of eight species: *commerson*, *concolor* (Fig. 12b), *koreanus* (Fig. 12a), *maculatus*, *munroi* (Fig. 11b), *plurilineatus*, *queenslandicus*, and *sierra*. It is usually larger in the other species and in most specimens of *S. commerson* (Fig. 11a).

Epiotics.—The epiotics are massive, irregular, and bounded by the parietals anteriorly, the supraoccipital mesially, the exoccipitals posteriorly, and the pterotics laterally. The inner lateral crests terminate at the posterior end of the epiotics. The medial process of the posttemporal bone attaches here on a rough process. There are slight differences between the species of *Scomberomorus* in the attitude of the attachment area and its roughness. In many species, the lateral crest continues posteriorly almost perpendicular to the skull. In some species such as *S. commerson* (Fig. 11a) and *S. queenslandicus*, the area of attachment is flatter. This area is flat and rough in *Acanthocybium* (Fig. 13a) and forms a separate process in *Grammatorcynus* (Fig. 13b).

Supraoccipital.—The supraoccipital forms the dorsomedial portion of the posterior end of the neurocranium and bears a well-developed crest which continues anteriorly on the frontals and is pronounced posteriorly as a strong supraoccipital crest. The supraoccipital can be divided into two parts: a thin, elongate triangular crest and 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, but it is not interposed between the exoccipitals. The hexagonal base is bounded anteriorly by the frontals and laterally by the parietals and epiotics. The crest extends posteriorly over the first vertebral centrum usually to a level past the posterior margin of the centrum (Figs. 14-16). The height of the crest varies among species of *Scomberomorus* and is highest in three species, *S. guttatus*, *S. koreanus* (Fig. 15a), and *S. multiradiatus*. Dividing the height of the supraoccipital crest (ventral margin of supraoccipital to edge of crest) by skull length (tip of vomer to posteroventral margin of basioccipital) gives a ratio of 0.46-0.57 for these three species, compared with 0.34-0.45 in the other 15 species. Low ratios are found in *S. cavalla* and *S. commerson* (0.35-0.40) and in all six species of the *regalis* group (0.34-0.42).

Prootics.—In ventral view, the prootics connect with all bones on the ventral side of the skull which compose the posterior part of the neurocranium (Figs. 17-19). 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 pterosphenoid and basisphenoid. The prootic bones are irregular in shape and meet each other along the ventromedian line of the brain case to form the anterior portion of the posterior myodome. On the ventral surface, extending from the lateral wing of the parasphenoid to the sphenotic, the prootic forms a thick bridge which strengthens the trigemino-facialis chamber (Allis 1903). A prootic foramen is present anterolaterally between the tip of the parasphenoid wing and the sphenotic. There is no trace of the prootic pit characteristic of the Thunnini and *Allothunnus* (Gibbs and Collette 1967; Collette and Chao 1975). Specimens differ in the number and arrangement of foramina leading into the brain cavity from inside the anterior opening of the trigemino-facialis chamber, but these do not seem to be useful interspecific differences.

Pterotics.—The pterotics form the lateral posterior corners of the neurocranium. Posteriorly, each pterotic is produced into a truncate process or pointed spine. The pterotics articulate with the epiotics and parietals medially and with the exoccipitals and intercalars posteriorly. A ridge, the pterotic ridge, originates on the dorsal surface of the posterior third of the frontal and continues posteriorly, diverging to the posterior corner of the pterotic, just anterior to the pterotic spine. In ventral view, the pterotics articulate with the sphenotics anteriorly and the prootics and intercalars medially. Two contiguous fossae, one at the posterior half of the pterotic bone and one at its joint with the sphenotic, seat the dorsal and anterior condyles of the hyomandibula. Three closely situated lateral sensory canal pores open on each pterotic at the posteriormost region of the pterotic crest. The largest pore is the most posterior and opens dorsally; lateral to this is the next largest opening laterally on the outside of the pterotic crest; the smallest is the most anterior of the three, lying along the crest and usually more elongate in shape.

The lengths and widths of the pterotic spines vary among the species. In eight species (*brasiliensis*, *guttatus*, *koreanus* (Fig. 18a), *multiradiatus*, *plurilineatus*, *regalis*, *semifasciatus*, and *tritor*), there is essentially no pterotic spine, merely a rounded posterior area of the skull. In six species (*concolor* (Fig. 18b), *lineolatus*, *maculatus*, *munroi* (Fig. 17b), *niphonius*, and *sierra*), there is a blunt posteriorly projecting spine. *Scomberomorus sinensis* is similar to this group, but the posterior projection is broader and less like a spine. The pterotic spines are longest in three species (*cavalla*, *commerson* (Fig. 17a), and *queenslandicus*), all of which also have prominent posterior projections of the intercalars. *Grammatorcynus* (Fig. 19b) is similar to the latter group, but the spine is thinner and sharper. *Acanthocybium* (Fig. 19a) has a longer and thinner pterotic spine than do *Grammatorcynus* and the species of *Scomberomorus*.

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 segment of the articular fossa for the head of the hyomandibula is afforded by the lateral wall of the sphenotic on the ventral surface. The sphenotic is pierced by a foramen for the ramus oticus nerve (Allis 1903). When viewed dorsally, the sphenotics spread out on both sides more prominently in *Scomberomorus* than in *Acanthocybium*, as noted by Devaraj (1977). Devaraj stated that the "midlateral projection" was large in *koreanus*, *guttatus*, *maculatus*, and *regalis*; small in *lineolatus*, *cavalla*, and *commerson*; and absent in *Acanthocybium*, but we are not clear as to what he was referring.

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 side. Each intercalar bears a protuberance on the dorsal surface to receive the lateral arm of the posttemporal. This protuberance is followed by a posterior projection of the intercalars in some species of *Scomberomorus* but not in *Acanthocybium* or *Grammatorcynus*.

Species of *Scomberomorus* may be roughly divided into three groups based on the size of the posterior projection from the intercalar as Devaraj (1977) noted for Indian species. Eight species lack any posterior projection or have only an insignificant projection: *guttatus*, *koreanus* (Fig. 18a), *lineolatus*, *multiradiatus*, *munroi* (Fig. 17b), *plurilineatus*, *semifasciatus*, and *sinensis*. In each of these species, except *S. multiradiatus*, the pterotic spine protrudes further posteriorly than does the intercalar region. In *S. multiradiatus*, the posterior corners of the skull are rounded and there is no pterotic spine so the intercalars project further posteriorly. Eight species have a distinct posterior projection from the intercalar: *brasiliensis*, *cavalla*, *concolor* (Fig. 18b), *maculatus*, *niphonius*, *regalis*, *sierra*, and *tritor*. The posterior projection is smaller in some specimens of *S. niphonius*, placing it somewhat between groups 1 and 2. The posterior projection is a little longer in *S. cavalla*, between groups 2 and 3. Two species, *commerson* (Fig. 17a) and *queenslandicus*, have a prominent truncate process.

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 (Figs. 17-19) which articulates with the vomer anteriorly and forms the ventral axis of the skull. The lateral wing of the parasphenoid extends dorsolaterally along the ventral ridge of the prootic bones on either side, and has a pointed end which forms part of the anteroventral wall of the posterior myodome. Posteriorly, the parasphenoid bifurcates into two lateral flanges which attach dorsally to the corresponding posteroventral flanges of the basioccipital bone and surround the posterior opening of the posterior myodome. A ventrally projecting median keel is present in the area anterior to the origin of the lateral flanges. In ventral view, the general characteristic of the parasphenoid is a gradual narrowing of the bone from anterior to posterior. The broadest portion of the parasphenoid is located usually at or before the tip of the V-shaped joint with the vomer. Broad parasphenoids are also present in *Acanthocybium* and the bonitos, Sardini (Collette and Chao 1975). In lateral view (Figs. 14-16), the parasphenoid forms the ventral border to the orbits and connects with the lateral ethmoids, basisphenoid, prootics, and basioccipital bones dorsally.

The shaft of the parasphenoid is distinctly wider in seven species: *S. commerson* (Fig. 17a), *lineolatus*, *munroi* (Fig. 17b), *niphonius*, *queenslandicus*, *semifasciatus*, and *sinensis*. Devaraj (1977) included *S. cavalla* along with *S. lineolatus* and *S. commerson* as having a broad parasphenoid, based on Mago Leccia (1958). We find *S. cavalla* to have a broader parasphenoid than some members of the *regalis* species group but not as broad as in the group of seven species listed above.

Basioccipital.—The basioccipital is the most posteroventrally located bone of the skull. It is shaped like an inverted U with lateral flanges on either side of the skull and forms the roof and lateral walls of the posterior myodome. Anteriorly, the basioccipital is attached to the prootic bones and dorsally with the exoccipital bones. Its lateral flanges expand ventrally to meet the flat posterior flanges of the parasphenoid. Posteriorly, the lateral flanges fuse to form a circular margin in a slightly backward oblique position and attach to the margin of the first vertebral centrum. There are a variable number of small pores in a shallow depression on the lateral surfaces of the basioccipital. This depression is deepest in *S. sinensis* but does not approach the basioccipital depression characteristic of the bonitos, Sardini (Collette and Chao 1975).

Exoccipital.—The exoccipitals connect the skull to the first vertebra dorsally. The exoccipital articulates with the epiotic and supraoccipital bones anterodorsally, the intercalar laterally, and with the other exoccipital posterodorsally. In ventral view, the exoccipital articulates with the prootic anteriorly, basioccipital medioventrally, and intercalar laterally. In posterior view, the foramen magnum is framed by the exoccipitals. Laterally, there are two foramina. The small anterior glossopharyngeal foramen (Allis 1903) lies close to the posterior border of the prootic. The large posterior vagal foramen lies just under the overhanging shelf formed by the posterior margin of the exoccipital. Dorsally, a small foramen which opens into the brain cavity is present at the medioposterior corner of the exoccipital.

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 is a useful taxonomic character (see Dentition section).

Dentition.—Large, triangular, laterally compressed teeth are present in the upper and lower jaws of *Scomberomorus*. *Acanthocybium* has similar teeth that are a little blunter and more tightly packed. *Grammatorcynus* has long thin teeth that are slightly compressed laterally. Bonitos have conical teeth that are larger than the conical teeth of the higher tunas (Thunnini). Tooth replacement in *Scomberomorus cavalla* was studied by Morgan and King (1983). The number of jaw teeth in *Scomberomorus* varies widely with a range of 5-39 in the upper jaw, 4-37 in the lower jaw (Tables 3, 4). Two species of *Scomberomorus* stand out from the rest, *S. multiradiatus* with the fewest teeth (5-10, $\bar{x}$ 8.0 on the upper jaw; 5-11, $\bar{x}$ 7.8 on the lower jaw) and *S. concolor* with the most teeth (13-37, $\bar{x}$ 22.2 on the upper jaw; 12-34, $\bar{x}$ 19.7 on the lower jaw). The 18 species can be ranked from lowest to highest as follows (mean for upper jaw followed by mean for lower jaw): 1) *multiradiatus* (8.0, 7.8); 2) *queenslandicus* (13.3, 10.6); 3) *semifasciatus* (12.8, 11.2); 4) *cavalla* (14.0, 10.9); 5) *koreanus* (13.7, 11.2); 6) *commerson* (14.1, 11.3); 7) *sinensis* (13.4, 12.2); 8) *brasiliensis* (14.0, 11.9); 9) *lineolatus* (15.1, 12.9); 10) *guttatus* (16.9, 14.4); 11) *sierra* (17.3, 14.1); 12) *maculatus* (16.8, 14.6); 13) *munroi* (17.5, 15.0); 14) *plurilineatus* (17.9, 15.4); 15) *tritor* (18.6, 15.4); 16) *regalis* (19.3, 15.8); 17) *niphonius* (19.6, 15.9); and 18) *concolor* (22.2, 19.7). The species with the fewest teeth, *S. multiradiatus*, also has the fewest gill rakers (usually 2 or 3, see Table 5), and the species with the most teeth, *S. concolor*, has the most gill rakers (usually 23-25, see Table 5) but the correlation is not so good in the other 16 species (compare Tables 3 and 4 with Table 5).

Premaxilla.—The premaxilla (Fig. 22) is a long, curved bone with a stout, 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 5-39 compressed triangular 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. The 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 32°-61° with the shank, and this process is 31-48% of the total length of the premaxilla. Devaraj (1977:22) noted that *S. lineolatus* had the sharpest angle among the Indian species that he studied (23° as he measured it), and we find that it has the sharpest angle (Fig. 22b) of any of the species in the genus, 32°-36° according to our measurements. The species with the largest angle is *S. guttatus*, 60°-61°. Devaraj included *guttatus* along with *koreanus*, *regalis*, and *maculatus* as species with angles of 40°-43°. Our data for these other three species are 40°-54°. *Scomberomorus com-*

TABLE 3.—Number of teeth in upper jaw in species of *Scomberomorus*.

Species	Side	Min.	Max.	$\bar{x}$	SD	N	Overall $\bar{x}$	Rank
brasiliensis	L	6	25	14.07	3.62	68	14.00	6
	R	8	27	13.93	3.53	69		
cavalla	L	8	29	14.24	5.82	50	14.00	7
	R	6	28	13.74	5.23	46		
commerson	L	5	35	14.15	5.68	110	14.06	8
	R	7	38	13.96	5.28	109		
concolor	L	15	35	22.15	4.94	26	22.20	18
	R	13	37	22.26	5.77	23		
guttatus	L	12	36	16.78	4.13	89	16.88	11
	R	11	35	16.97	4.25	93		
koreanus	L	9	19	14.17	2.76	24	13.71	5
	R	10	16	13.25	2.11	24		
lineolatus	L	10	27	15.28	3.94	29	15.07	9
	R	9	28	14.86	4.19	29		
maculatus	L	10	32	17.04	4.06	55	16.82	10
	R	7	30	16.57	3.80	49		
multiradiatus	L	5	10	7.88	1.24	26	8.04	1
	R	6	10	8.19	1.20	26		
munroi	L	12	20	16.57	2.64	7	17.50	13
	R	12	23	18.22	3.90	9		
niphonius	L	12	26	19.53	2.71	32	19.56	17
	R	14	26	19.58	2.75	33		
plurilineatus	L	16	22	18.25	1.70	24	17.92	14
	R	12	23	17.58	2.52	24		
queenslandicus	L	8	17	13.33	2.43	30	13.29	3
	R	10	18	13.24	2.31	29		
regalis	L	9	31	19.34	5.10	47	19.29	16
	R	10	30	19.25	4.74	48		
semifasciatus	L	10	23	13.03	3.07	33	12.76	2
	R	8	21	12.48	2.92	33		
sierra	L	10	37	17.15	5.79	60	17.32	12
	R	7	39	17.48	7.34	62		
sinensis	L	10	16	13.64	1.69	14	13.43	4
	R	10	17	13.21	1.67	14		
tritor	L	11	30	18.56	3.98	32	18.58	15
	R	11	28	18.59	4.38	32		

TABLE 4.—Number of teeth in lower jaw in species of *Scomberomorus*.

Species	Side	Min.	Max.	$\bar{x}$	SD	N	Overall $\bar{x}$	Rank
brasiliensis	L	7	19	11.96	2.85	70	11.88	7
	R	7	20	11.79	3.04	67		
cavalla	L	6	24	10.94	3.84	50	10.92	3
	R	7	22	10.90	3.78	48		
commerson	L	5	29	11.37	4.40	108	11.27	6
	R	4	27	11.17	3.84	106		
concolor	L	13	30	19.46	3.96	26	19.71	18
	R	12	34	19.96	4.96	25		
guttatus	L	10	25	14.49	3.06	98	14.42	11
	R	9	23	14.34	2.70	97		
koreanus	L	8	17	11.25	2.19	24	11.21	4
	R	9	15	11.17	1.31	24		
lineolatus	L	7	28	12.72	3.69	29	12.93	9
	R	9	26	13.14	3.20	29		
maculatus	L	10	30	14.89	3.70	55	14.64	12
	R	8	26	14.37	3.02	52		
multiradiatus	L	6	11	8.00	1.20	26	7.75	1
	R	5	9	7.50	0.95	26		
munroi	L	11	29	15.88	5.62	8	15.01	13
	R	11	19	14.13	2.75	8		
niphonius	L	12	20	15.55	2.05	33	15.93	17
	R	12	20	16.30	2.05	33		
plurilineatus	L	12	22	15.83	2.08	23	15.37	14
	R	12	20	14.92	1.89	24		
queenslandicus	L	6	14	10.59	1.79	32	10.61	2
	R	7	14	10.64	1.99	28		
regalis	L	10	24	15.72	4.17	46	15.80	16
	R	8	23	15.87	4.10	47		
semifasciatus	L	7	18	11.24	2.98	33	11.23	5
	R	7	18	11.21	2.93	33		
sierra	L	7	37	13.90	5.29	61	14.05	10
	R	7	32	14.19	5.30	62		
sinensis	L	10	15	12.43	1.87	14	12.22	8
	R	10	15	12.00	1.41	14		
tritor	L	10	21	15.24	2.95	33	15.40	15
	R	10	23	15.56	3.19	33		

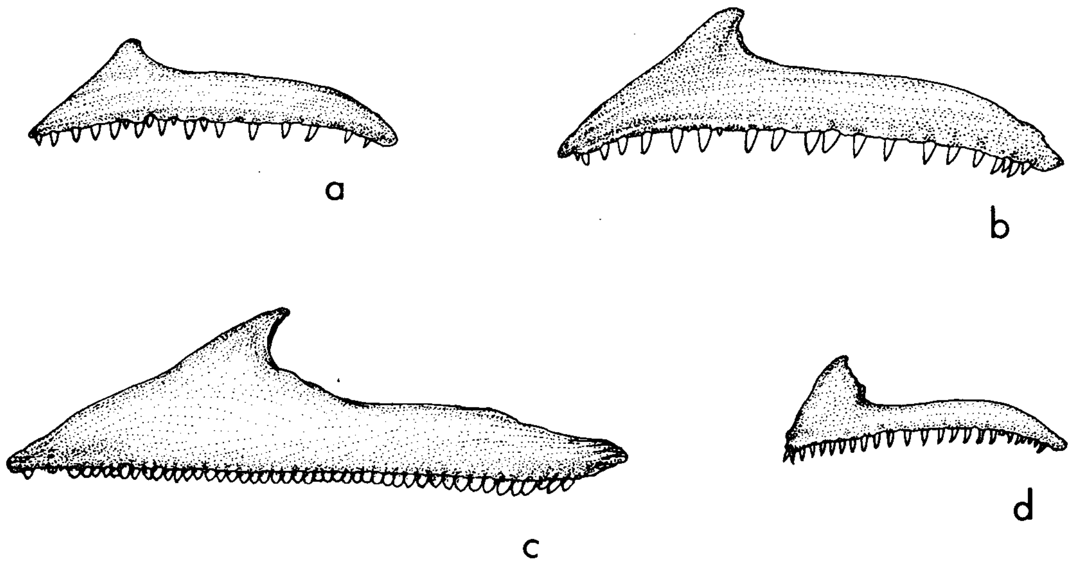


FIGURE 22.—Left premaxillae in lateral view. a. *Scomberomorus semifasciatus*, Port Moresby, New Guinea, 510 mm FL, 2×. b. *Scomberomorus lineolatus*, Cochin, India, 786 mm FL, 2×. c. *Acanthocybium solandri*, Miami, Fla., 1,403 mm FL, 1×. d. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL, 2×.

merson and *S. cavalla* also fall into this intermediate group with angles of 41°-54°. *Acanthocybium* (Fig. 22c) has a sharp angle (34°-37°), like *S. lineolatus*. *Grammatorcynus* (Fig. 22d) has a very large angle, 64°-67°, even greater than *S. guttatus*. The ascending process is longest in *S. lineolatus*, 46-48% of the length of the premaxilla (41-45% according to Devaraj) and *S. sinensis*, 43-46%. The process is shortest in *S. guttatus* and *S. cavalla*, 31-32%. *Acanthocybium* has a longer process than any of the species of *Scomberomorus*, 50% (according to our data and Devaraj 1977).

Maxilla.—The maxilla (Fig. 23) 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 (see *S.*

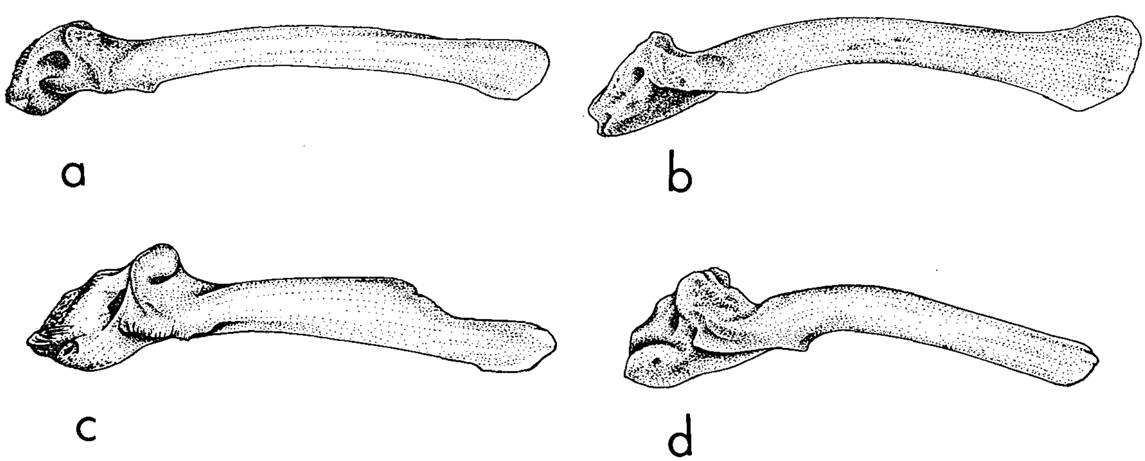


FIGURE 23.—Left maxillae in lateral view. a. *Scomberomorus semifasciatus*, Port Moresby, New Guinea, 510 mm FL, 2×. b. *Scomberomorus munroi*, New Guinea, 512 mm FL, 2×. c. *Acanthocybium solandri*, Miami, Fla., 1,403 mm FL, 1×. d. *Grammatorcynus bilineatus*, Timor Sea, 453 mm FL, 2×.

semifasciatus, Fig. 23a). The former possesses a prominent knob at its dorsolateral aspect that fits into the articular surface of the vomer and an anterior, deep concavity facing the inner wall of the premaxilla. The head is 18-25% of the total length of the maxilla. Immediately posterior to the head is a shallow depression which receives the anterior articulating process of the palatine. The shank of the maxilla is narrow and somewhat flattened. The posterior end expands into a thin, flat plate which is partially covered dorsally by the supramaxilla. The height of the plate is 8-15% of the total length of the maxilla. *Acanthocybium* (Fig. 23c) and *Grammatorcynus* (Fig. 23d) lack any posterior expansion of the maxilla. In fact, in *Acanthocybium* there is a notch in the dorsal margin of the maxilla, and the posterior end is distinctly lower than the middle of the shaft of the bone.

Scomberomorus munroi is the only species in the genus that is distinguishable from the others in characters of the maxilla; it totally lacks the anterior process on the outer surface of the head of the maxilla (Fig. 23b). Devaraj (1977:23) stated that the outer process was "flimsier" in *S. commerson*, but we find that the process varies from small to moderate in our material of the species and that *S. commerson* is not distinct in this aspect.

The head of the maxilla is shorter than in most other species, relative to total length of the maxilla, in the six species of the *S. regalis* group. Starting with the shortest maxilla head length (lowest mean percent), these six species (plus *koreanus* and *multiradiatus*) rank as follows: 1) *concolor*, 18.8; 2) *brasiliensis*, 19.0; 3) *sierra*, 19.8; 4) *tritor*, 19.9; 5) *koreanus*, 20.2; 6) *maculatus*, 20.6; 7) *multiradiatus*, 21.0; and 8) *tritor*, 21.1. The longest heads are found in *niphonius* (24.7), *semifasciatus* (24.1), and *lineolatus* (24.0). The head of the maxilla is a little longer, relative to total maxilla length, in *Grammatorcynus* (26%) and much longer (33%) in *Acanthocybium*.

The posterior expansion of the maxilla is least well-developed (lowest) relative to maxilla length in *S. multiradiatus* (8-9%) and *S. sinensis* (9-11%). The best-developed posterior expansion is in *S. plurilineatus* (15%). The other 15 species range from 11 to 14%. This range of variation is shown in *S. munroi* but the specimen illustrated (Fig. 23b) shows a relatively well-developed posterior expansion. The shape of the posterior expansion varies within and between species, but most of the expansion is usually ventral.

Dentary.—The dentary (Fig. 24) is a large forked bone which forms the major part of the lower jaw. It is laterally flattened and bears a single row of 4-37 compressed triangular teeth on the dorsal margin. Posteriorly, the dentary forms two arms. The ventral arm is relatively narrow and shorter than the dorsal arm, and its inferior margin has a groove which accepts the angular and the anterior end of Meckel's cartilage. The base of the ventral arm has an external series of pores, which seem to be the preoperculomandibular pores (Allis 1903; Mago Leccia 1958) of the lateral line system. The length of the dentary from its anterior margin to the tip of the lower arm is 86-97% of the length to the tip of the upper arm. The figures are similar for *Acanthocybium* (91-96%). However, the lower margin is longer in *Grammatorcynus*, 105-109% of the length of the upper margin (Fig. 24c). The proportions are similar in all 18 species of *Scomberomorus*, with *S. maculatus* having the shortest lower margin (87-89%) and *S. concolor* the longest (92-97%).

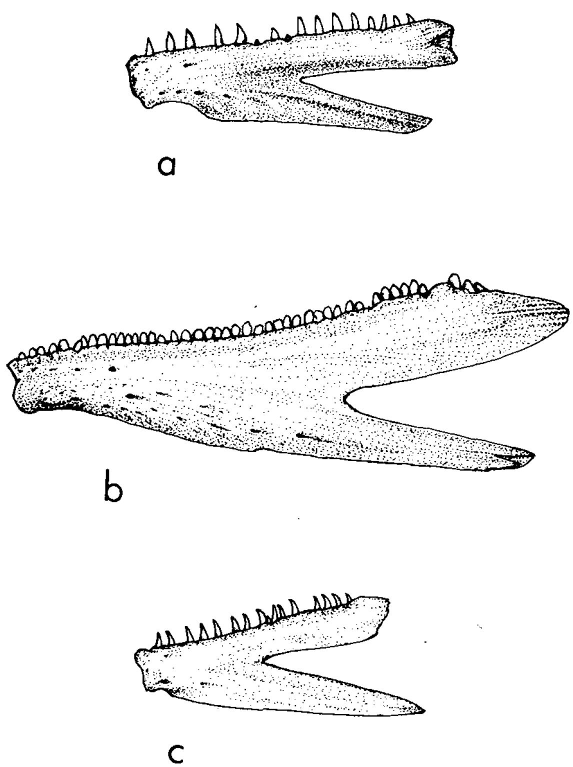


FIGURE 24.—Left dentaries in lateral view. a. *Scomberomorus semifasciatus*, Port Moresby, New Guinea, 510 mm FL, 2×. b. *Acanthocybium solandri*, Miami, Fla., 1,403 mm FL, 1×. c. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL, 2×.

All the species of *Scomberomorus* and *Grammatorcynus* have a notch on the anteroventral margin of the dentary. This notch is absent in *Acanthocybium.* The notch seems to vary as much between specimens of a species of *Scomberomorus* as between species of the genus. *Acanthocybium* has a prominent notch on the anterior margin of the dentary (Fig. 24b) which is indistinct or absent in *Scomberomorus* and *Grammatorcynus.* Devaraj (1977) stated that the anterior notch was distinct in *S. cavalla* and *S. commerson.* The notch may be a little more prominent in *S. commerson* than in the other species, but we cannot confirm this for *S. cavalla.*

Angular.—The triangular anterior end of the angular (frequently called articular) fits into the dentary anteriorly (Fig. 25). The posterior end of

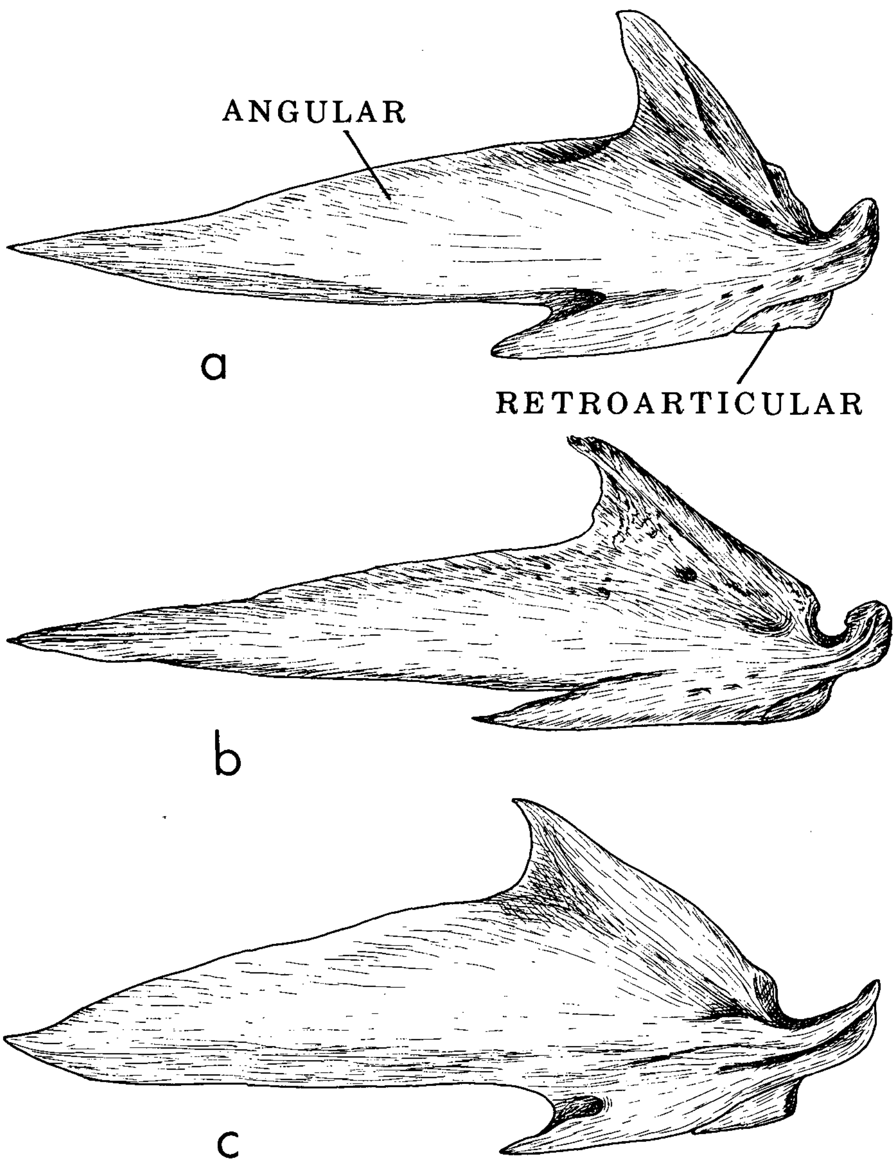


FIGURE 25.—Left angulars and retroarticulars in lateral view. a. *Scomberomorus semifasciatus*, Port Moresby, New Guinea, 510 mm FL, 3.5×. b. *Acanthocybium solandri*, Miami, Fla., 1,403 mm FL, 1×. c. *Grammatorcynus bilineatus*, New Guinea, 382 mm FL, 4.5×.

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. This process is hooked and carries a transverse articular facet for the quadrate. Between the dorsal and ventral processes is Meckel's cartilage which extends directly anterior into the space between the two arms of the dentary. The length of the angular to the tip of the dorsal process is 31-42% of the total length of the bone; the length to tip of the ventral process is 42-53% of the total length. The maximum width of the angular, measured from the tip of the dorsal process to the tip of the ventral process is 34-43% of the total length. Devaraj (1977) stated that the ventral process was longer and narrower in *S. commerson* and *Acanthocybium* than in other Indian species and we confirm this. The ventral process is as long or longer than the dorsal process in *S. commerson* (ventral process 99-162% of the dorsal process), *Acanthocybium* (99-148%), and also in *S. queenslandicus* (115-136%). The next longest ventral processes are in *S. cavalla* (80-104%) and *S. sinensis* (82-97%). The other 14 species of *Scomberomorus* (and *Grammatorcynus*) have shorter ventral processes, 40-85% of the length of the dorsal process. The shortest ventral process is in *S. regalis*, 40-44%.

Retroarticular.—The retroarticular bone (frequently called angular) is rhomboid and attached firmly, but not fused to the posteroventral margin of the angular (Fig. 25). No differences were found among the retroarticulars of the species of *Scomberomorus*.

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 (Fig. 26) is forked both posteriorly and anterolaterally. 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 is cone-shaped or pointed. The exterior branch of the posterior fork carries on its dorsal surface the shank of the ectopterygoid, and the inner, flat, thin branch is attached to the anterior end of the entopterygoid. The lateral aspect of the palatine is roughly triangular and concave, and closely attached to the mesial wall of the maxilla. *Grammatorcynus* (Fig. 26d) differs from *Scomberomorus* (Fig. 26a, b) and *Acanthocybium* (Fig. 26c) in almost lacking the anteriorly directed ventral branch. *Acanthocybium* has a distinct ventral branch but it is shorter than the

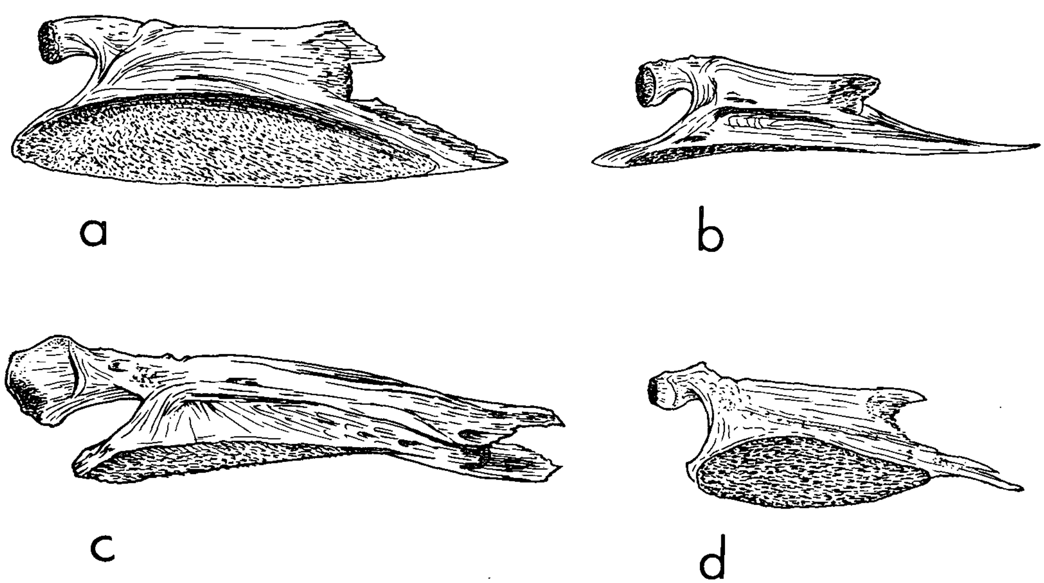


FIGURE 26.—Left palatines in lateral view, slightly rotated to better show tooth patch. a. *Scomberomorus semifasciatus*, New Guinea, 740 mm FL, 2×. b. *Scomberomorus commerson*, New South Wales, 1,155 mm FL, 1×. c. *Acanthocybium solandri*, Miami, Fla., 1,403 mm FL, 1×. d. *Grammatorcynus bilineatus*, Timor Sea, 453 mm FL, 2×.

dorsal branch, as pointed out by Devaraj (1977), whereas the ventral branch is longer than the dorsal branch in all species of *Scomberomorus*. 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 120-123% in *Grammatorcynus*, 112-121% in *Acanthocybium*, and only 87-107% in the species of *Scomberomorus*. *Acanthocybium* differs from both *Scomberomorus* and *Grammatorcynus* in having the posteriorly directed inner branch almost as long as the outer branch. 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 97-99% in *Acanthocybium* and 54-84% in the species of *Scomberomorus* and *Grammatorcynus*. The tooth patch is long and narrow in *Acanthocybium* (Fig. 26c), short and wide in *Grammatorcynus* (Fig. 26d), and with the species of *Scomberomorus* in between these extremes. The teeth are fine in all three genera, but a little larger in *Acanthocybium* and *Grammatorcynus* than in most species of *Scomberomorus*.

The species of *Scomberomorus* show some differences in the length of the ventral branch relative to that of the length of the external branch, the relative length of the outer to the inner branch, the relative width of the tooth patch, and the size of the teeth in the tooth patch. Dividing the length of the ventral margin, from the anterior end of the ventral branch to the end of the external branch, by the length of the dorsal margin, from the tip of the dorsal hook to the end of the ventral branch, shows three species of *Scomberomorus*—*sinensis* (98-107%), *tritor* (100-102%), and *commerson* (94-102%)—to be most similar to *Acanthocybium* (112-121%). The lowest figures are for *S. niphonius* (87-88%). Dividing the length of the dorsal margin by the distance from the tip of the dorsal hook to the end of the inner branch shows four species of *Scomberomorus*—*plurilineatus* (75-84%), *munroi* (77-79%), *lineolatus* (72-74%), and *semifasciatus* (70-73%)—to resemble *Grammatorcynus* (71-75%). The lowest figures are for *S. multiradiatus* (54-56%). The tooth patch is very narrow in *S. commerson* (Fig. 26b), similar to the patch shape in *Acanthocybium* but with finer teeth. The tooth patch is also narrow in a 677 mm FL specimen of *S. sinensis* and reduced to only a single row of teeth in a 1,082 mm specimen. The teeth in *S. sinensis* are larger than in other species of the genus, at least the same size as in *Acanthocybium*. The widest tooth patch is in *S. semifasciatus* (Fig. 26a), almost as wide as in *Grammatorcynus* but with much finer teeth.

Ectopterygoid.—The ectopterygoid (Fig. 27) is a T-shaped bone, the top of the T forming its posterior end. It is joined with the entopterygoid dorsolaterally, the palatine laterally and anteriorly, and the quadrate and metapterygoid posteriorly. The dorsal arm of the ectopterygoid is shorter than the ventral arm in *Scomberomorus* and vice versa in *Acanthocybium* and *Grammatorcynus*. This relationship can be expressed by 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). The range is 85-100% in the species of *Scomberomorus* compared with greater than 100% in *Acanthocybium* (103-109%) and *Grammatorcynus* (110-116%). 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) is shorter relative to the ventral distance in *Acanthocybium* (41-47%) than in the species of *Scomberomorus* (43-63%) and *Grammatorcynus* (64-68%).

The ectopterygoids of the species of *Scomberomorus* are very similar. The shortest ventral distance is in *S. sinensis*, 85-88% of the dorsal distance, the longest in *S. regalis*, 99-100%. The shortest posterior edges are in *S. niphonius* and *S. tritor* (50-51% of the dorsal distance), the longest posterior edges are in *S. koreanus* (61-63%), *S. plurilineatus* (60-63%), and *S. semifasciatus* (59-62%).

Entopterygoid.—The entopterygoid is elongate and oval in shape (width 23-46% of length) (Fig. 28). The outer margin of the entopterygoid is the thickest part of the bone and is attached 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 contacts with other bony elements. The dorsal surface is concave and the smooth convex ventral surface forms the major part of the buccal roof. The anterior end is narrower than the posterior end in most species but a little wider in *S. guttatus* and *S. koreanus*. The entopterygoid is narrowest in *S. commerson* (width 23-28% of length, Fig. 28a) and *S. multiradiatus* (29%). The shortest and widest entopterygoids are in *sinensis* (39-46%,

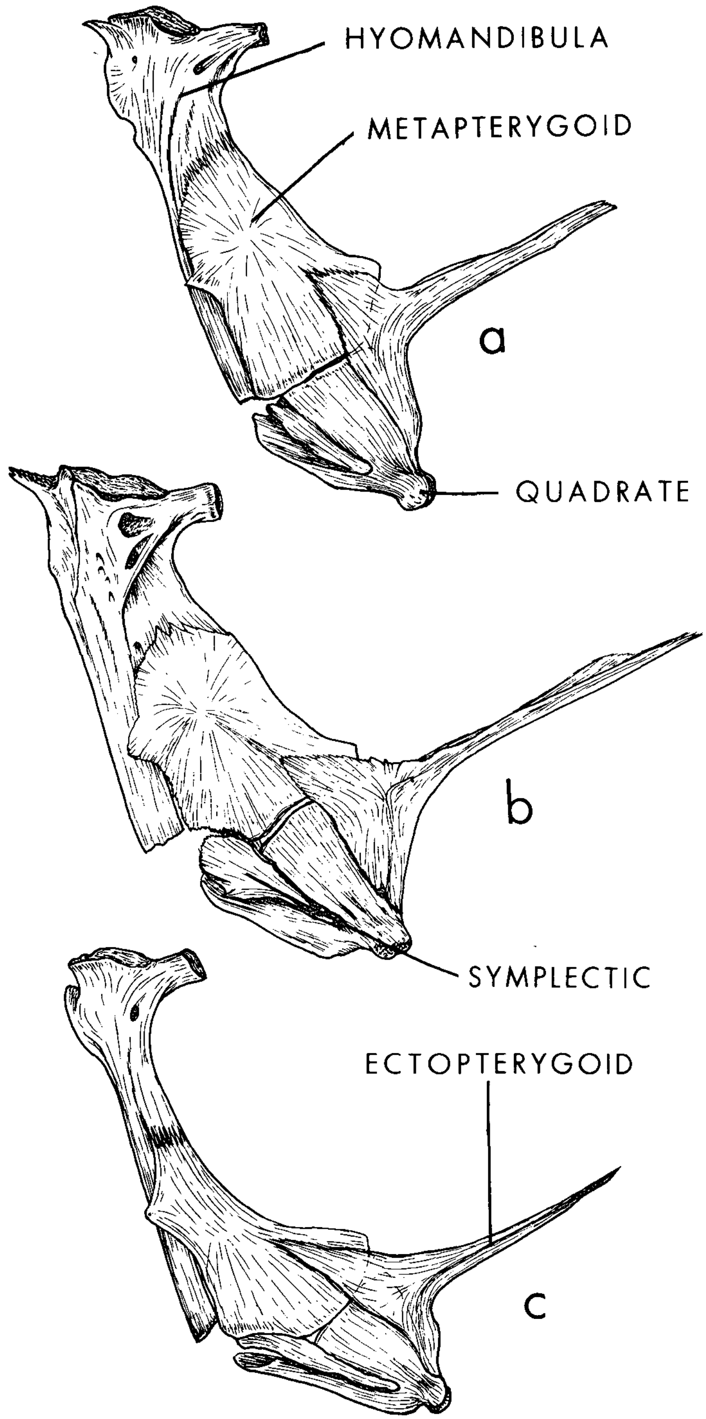


FIGURE 27.—Left suspensoria in mesial view. a. *Scomberomorus semifasciatus*, Port Moresby, New Guinea, 510 mm FL, 2.5×. b. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL, 1.5×. c. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL, 2×.

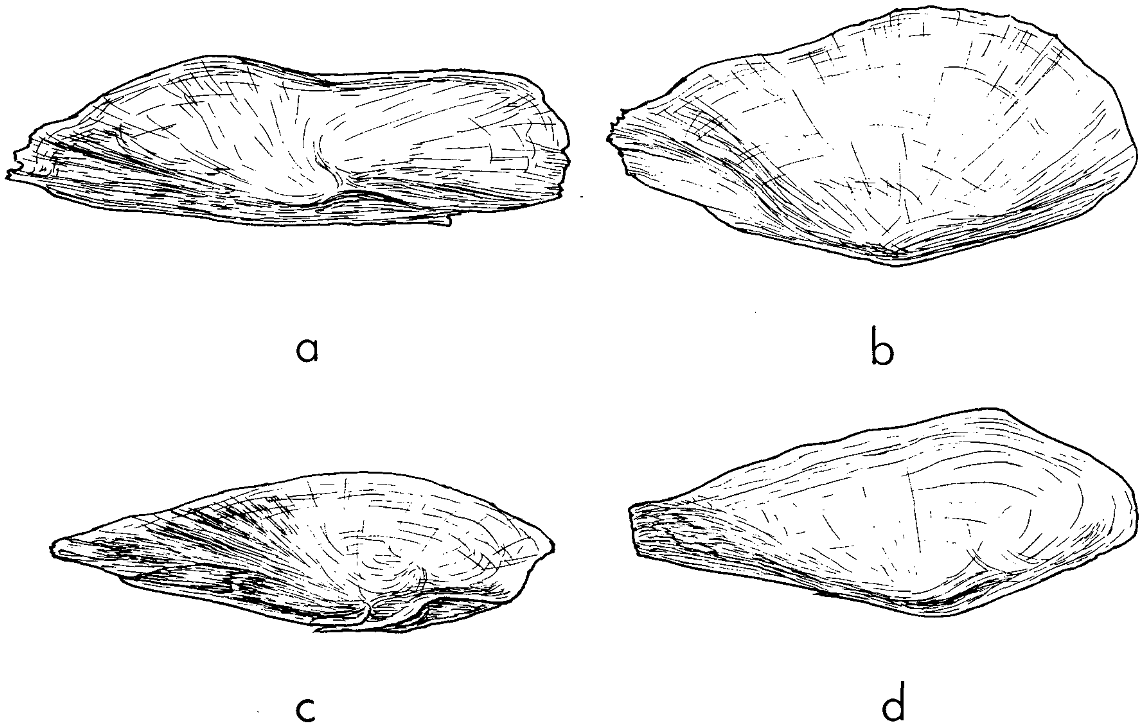


FIGURE 28.—Left entopterygoids in dorsal view. a. *Scomberomorus commerson*, New South Wales, 1,155 mm FL, 1×. b. *Scomberomorus sinensis*, Hong Kong, 677 mm FL, 2×. c. *Acanthocybium solandri*, Indian Ocean, 943 mm FL, 2×. d. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL, 2.5×.

Fig. 28b), *maculatus* (41-42%), and *concolor* (40-42%). *Acanthocybium* (Fig. 28c), *Grammatorcynus* (Fig. 28d), and the other 13 species of *Scomberomorus* are intermediate in width (30-40%).

Metapterygoid.—The metapterygoid (Fig. 27) is a flat, quadrangular or somewhat triangular bone. 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 possesses a triangular-shaped area which 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 *Acanthocybium* and *Grammatorcynus* (Fig. 27b, c), but not in most species of *Scomberomorus* (Fig. 27a). The posterior horizontal part of the ventral border is longer than the anterior oblique part in *Scomberomorus* (anterior part 39-86% of posterior part), but vice versa in *Acanthocybium* and *Grammatorcynus* (anterior part 132-218% of posterior part).

The anterior part of the ventral margin is relatively longer in *S. multiradiatus* (77-78% of posterior part) and *S. maculatus* (65-86%), and relatively shorter in *S. plurilineatus* (41-45%) and *S. regalis* (39-50%). Devaraj (1977) reported differences in the shape of the anterior free border of the metapterygoid, as convex, nearly straight, or concave. We have found similar tendencies but it is difficult to place the species of *Scomberomorus* in specific categories.

HYOID ARCH.—The hyoid arch is the chain of bones that connect the lower jaw and the opercular apparatus with the skull. The arch is composed of the hyomandibula, symplectic, quadrate, hyoid complex (hypohyal, ceratohyal, epihyal, interhyal, and the seven branchiostegal rays), and two median unpaired bones, the glossohyal and urohyal.

Hyomandibula.—The hyomandibula (Fig. 27) is an inverted L-shaped bone that connects the mandibular suspensorium and opercular bones to the neurocranium. There are three prominent condyles on the dorsal end of the hyomandibula. 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 spine. A strong vertical ridge extends from the ventral margin to a little below the dorsal border, thence it curves anteriorly to confluence with the anterior condyle. The portions 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 which is especially well developed in *Acanthocybium*. There are two deep fossae on the inner surface of the hyomandibula of *Acanthocybium* but only one in *Scomberomorus* and *Grammatorcynus*.

The posterodorsal spine is best developed in *Acanthocybium* (Fig. 27b) and *S. commerson*, as pointed out by Devaraj (1977). This spine is also well developed in *S. queenslandicus* and is present but small in the other 16 species of *Scomberomorus* (e.g., *S. semifasciatus*, Fig. 27a). No spine is present in *Grammatorcynus* (Fig. 27c). The total length of the hyomandibula (ventral tip to dorsal margin of dorsal condyle) is greater relative to maximum width (tip of anterior condyle to outer margin of posterior condyle) in *Grammatorcynus* (width 35-36% of length) and *S. multiradiatus* (36-39%). The hyomandibula is shortest relative to width in *S. sinensis* (45-52%). *Acanthocybium* (41-44%) is similar to the majority of species of *Scomberomorus* (39-47%).

Symplectic.—The symplectic is a small bone that fits into a groove on the inner surface of the quadrate (Fig. 27). The symplectic is very narrow in *Scomberomorus*, not filling the groove in the quadrate (Fig. 27a). It is slightly wider in *Grammatorcynus* but the groove is narrower, the symplectic more nearly filling the groove (Fig. 27c). The symplectic is greatly expanded at its dorsal end in *Acanthocybium* (Fig. 27b). In most species of *Scomberomorus*, the symplectic, like the posterior process of the quadrate, extends only a slight distance beyond the dorsal margin of the quadrate. The symplectic is slightly longer than the posterior process in a species with a short process (e.g., *S. multiradiatus*) and in one with a relatively long process (e.g., *S. sinensis*). No bony contact is present between the dorsal end of the symplectic and either the metapterygoid or the hyomandibula in most species of *Scomberomorus*. The metapterygoid is in slight contact with the symplectic in *S. sinensis* and *S. koreanus*. Both *Grammatorcynus* and *Acanthocybium* have much longer symplectics, extending well beyond the dorsal margin of the quadrate and even beyond the dorsal end of the posterior process to make firm contact with the metapterygoids. Devaraj (1977:fig. 11) illustrated the symplectics by themselves for the four Indian species (*koreanus*, *guttatus*, *lineolatus*, and *commerson*) and *Acanthocybium*.

Quadrate.—The lower jaw is suspended from the cranium by means of the articulating facet of the ventral surface of the triangular quadrate. The broad dorsal margin of the quadrate abuts the ventral border of the metapterygoid (Fig. 27). The mesial surface of the quadrate bears a deep groove which accepts the symplectic. There is a strong process on the posterior margin of the quadrate that is attached along the lower anterior arm of the preopercle. The process is relatively short in *Scomberomorus*, extending only a short distance beyond the dorsal margin of the quadrate in most species (e.g., *S. semifasciatus*, Fig. 27a). The process is shortest in *S. multiradiatus*, not reaching the dorsal margin. The process is longest in *S. commerson*, *S. lineolatus*, and *S. sinensis*, but it is still shorter in these three species than in *Acanthocybium* (Fig. 27b) and *Grammatorcynus* (Fig. 27c). An attempt was made to quantify this by measuring from the inside of the articular facet to the tip of the dorsal process and to the tip of the anterior margin of the quadrate. The short process in *S. multiradiatus* is shown by the distance to the anterior margin being about equal (95-103%) to the distance to the tip of the process. In the other species of *Scomberomorus*, the distance to the anterior margin is less than (76-96%) the distance to the tip of the process. This percent is low in *S. lineolatus* (76%), indicative of a long process, but the figures for *S. commerson* (80-83%) and *S. sinensis* (83-85%) are not much lower than those for many other species with shorter processes. The lowest figures are for *Acanthocybium* (72-80%) and *Grammatorcynus* (65-71%), indicative of the long process in these two genera.

Hyoid complex.—This complex includes the two hypohyals (= basihyal of Mago Leccia 1958), ceratohyal, epihyal, and interhyal bones, and the seven branchiostegal rays (Fig. 29). The hypohyals, ceratohyal, and epihyal are closely associated and form a functional unit.

Hypohyals.—The hypohyals are composed of separate dorsal and ventral elements joined longitudinally. In lateral view, the ventral hypohyal is clearly larger than the dorsal hypohyal in all species of *Scomberomorus* and in *Grammatorcynus* (Fig. 29a, c). The ventral hypohyal is about three times larger than the dorsal in *Acanthocybium* (Fig. 29b). Devaraj (1977:29) stated that the dorsal and ventral hypohyals were of equal size in *S. commerson*, but we find the ventral larger in lateral view, as in the other species of the genus. In mesial view, the dorsal and ventral hypohyals in *S. commerson* and the other 17 species are about equal in size. The ventral hypohyal is perhaps a little larger than the dorsal in mesial view in *S. multiradiatus* and *S. queenslandicus*. Laterally, the suture between the dorsal and ventral hypohals runs almost horizontally in *Acanthocybium* but curves ventrally at various angles in *Scomberomorus* and *Grammatorcynus*. Devaraj (1977) stated that it formed "an upward curve anteriorly in *S. koreanus*, *S. lineolatus*, *S. regalis*, and *S. niphonius* and runs nearly straight in the other species including *A. solandri*." The specimen of *S. commerson* that he illustrated (figure 12D) does show a straight suture, but in our material a downward curve usually is present. Mesially, a pointed lateral process at the anterodorsal end of the dorsal hypohyal forms a symphysis with the glossohyal, urohyal, basibranchial, and the process of the hypohyal from the opposite side in *Scomberomorus* and *Grammatorcynus*. *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. The groove extends anteriorly 29-54% of the length of the dorsal hypohyal before becoming a covered tunnel in *Scomberomorus* and *Grammatorcynus* or a foramen in *Acanthocybium* leading to the inner side of the dorsal hypohyal. The opening on the inner side appears as a small to moderate pit usually located in the ventral portion of the dorsal hypohyal in *Scomberomorus* and *Grammatorcynus*. The pit lies astride the junction of the dorsal and ventral hypohyals in *S. brasiliensis* and extends slightly into the ventral hypohyal in *S. maculatus* and *S. sierra*. The pit also is larger in these species.

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 *Scomberomorus* (Fig. 29a) the fifth branchiostegal ray usually is attached to the most posterior part of the ceratohyal or on the space between the ceratohyal and epihyal, not on the anterior part of the epihyal as stated by Devaraj (1977) and Mago Leccia (1958:pl. 4). In *Acanthocybium* and *Grammatorcynus*, the fifth ray is on the anterior part of the epihyal (Fig. 29b, c). The hyoidean groove runs the length of the ceratohyal on its lateral surface. The groove is so deep in some specimens of some species that it forms a thin slit through the bone, the ceratohyal window or beryciform foramen. Slits are common in 10 species of *Scomberomorus*: *brasiliensis*, *commerson*, *concolor*, *multiradiatus*, *munroi*, *niphonius*, *queenslandicus*, *semifasciatus*, *sierra*, and *tritor*; rare in four, *cavalla*, *plurilineatus*, *maculatus*, and *sinensis* plus *Acanthocybium* and *Grammatorcynus*; and occasional in the other four species:

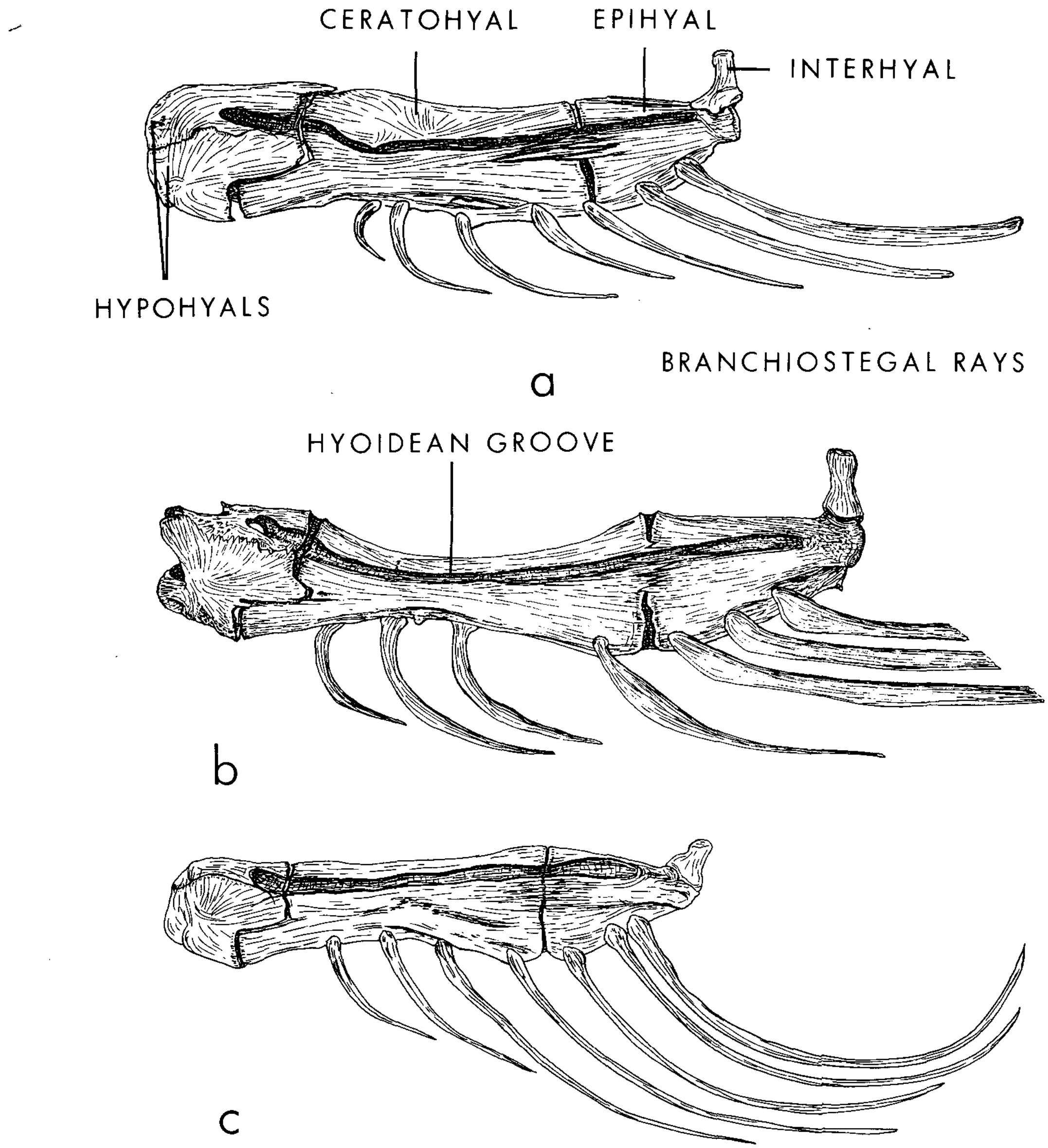


FIGURE 29.—Left hyoid complexes in lateral view. a. *Scomberomorus commerson*, New South Wales, 1,155 mm FL, 1×. b. *Acanthocybium solandri*, Miami, Fla., 1,403 mm FL, 1×. c. *Grammatorcynus bilineatus*, Timor Sea, 453 mm FL, 2×.

guttatus, *koreanus*, *lineolatus*, and *regalis*. Both large (*S. commerson*) and small (*S. multiradiatus*) species have slits. Smaller specimens of a species sometimes have slits (*guttatus*, *plurilineatus*, *queenslandicus*, *regalis*, and *semifasciatus*), while larger specimens lack them; sometimes the situation is reversed (*koreanus*, *lineolatus*, and *tritor*). The dorsal margin of the ceratohyal is deeply concave and very much constricted in *Acanthocybium* such that the dorsal margin of the bone comes closer to the groove for the hyoidean artery. The margin is straight in *Grammatorcynus* and varies in *Scomberomorus*. Devaraj (1977:30-31) stated that the dorsal margin of the ceratohyal is convex in some species (*koreanus* and *lineolatus*), almost straight in others (*gut-*

tatus and *niphonius*), and slightly concave in most (*commerson*, *maculatus*, *regalis*, and *cavalla*). We find similar tendencies, but there is extensive variation even in small samples. Six species tend to have the dorsal margin convex: *guttatus*, *koreanus*, *lineolatus*, *multiradiatus*, *plurilineatus*, and *semifasciatus*; seven species tend to have the dorsal margin concave: *cavalla*, *commerson*, *maculatus*, *munroi*, *queenslandicus*, *regalis*, and *sinensis*; and five usually have the dorsal margin nearly straight: *brasiliensis*, *concolor*, *niphonius*, *sierra*, and *tritor.*

Epihyal.—The epihyal is a triangular bone which interlocks anteriorly with the ceratohyal. It has a posterior process which articulates with the interhyal. In *Scomberomorus*, two branchiostegal rays are seated on the ventral portion of the epihyal, not three as stated by Devaraj (1977) or shown by Mago Leccia (1958). Three branchiostegal rays do articulate with the epihyal in *Acanthocybium* and *Grammatorcynus.* The depth of the epihyal is least in *Acanthocybium*, 58-62% of the length from the smooth anterior margin of the bone to the tip of the posterior process. Two species of *Scomberomorus* (*commerson* and *cavalla*) have relatively low epihyals, 68-71% of length. *Grammatorcynus* also has a relatively low epihyal, 66-77% of length. The deepest epihyals are in four species of *Scomberomorus*: *koreanus* (90-98%), *concolor* (86-94%), *plurilineatus* (87-91%), and *guttatus* (87-90%).

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

Glossohyal.—The glossohyal (basihyal) (Fig. 30) is a median bone that supports the tongue and overlies the first basibranchial bone at the anterior end of the branchial arch. In *Scomberomorus*, the glossohyal is roughly rod-shaped or conical in most species. Its width is 35-54% of its length. It generally has a flat or narrowed anterior end and broadens posteriorly, but terminates in a small posterior cone or flattened projection. The glossohyal protrudes ventrally adjacent to the posterior articulation. The glossohyal of *Acanthocybium* is flattened and spatulate with a broad anterior end, a narrow posterior end, and no ventral protrusion (Fig. 30c). *Grammatorcynus* differs in having a quadrangular to oval tooth plate fused to and covering the dorsal surface of the bone (Fig. 30d). Two bonitos, *Cybiosarda* and *Orcynopsis*, have a similar condition but there are two separate oval tooth patches in these genera (Collette and Chao 1975:fig. 43a, b). Another bonito, *Gymnosarda*, has what appears to be a single tooth plate on the glossohyal, but this plate is actually composed of left and right portions that fit over the bone rather than being fused to it (Collette and Chao 1975:fig. 43f). The glossohyal is a little wider in *Grammatorcynus* than in *Acanthocybium* or most species of *Scomberomorus*, 47-55% of length.

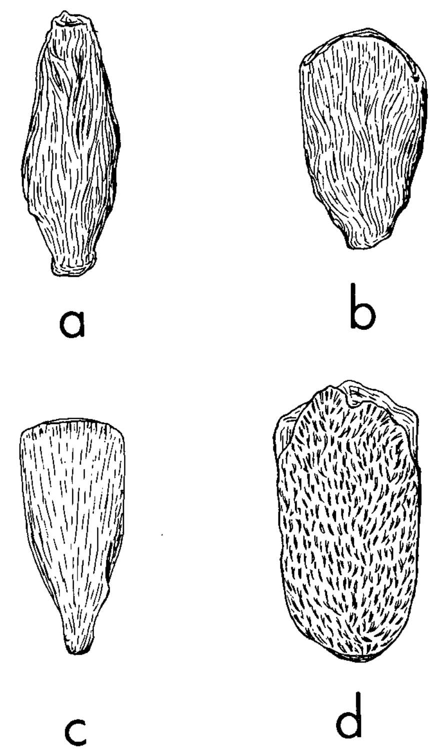


FIGURE 30.—Glossohyals in dorsal view. a. *Scomberomorus plurilineatus*, Natal, 910 mm FL, 4×. b. *Scomberomorus munroi*, New Guinea, 512 mm FL, 5×. c. *Acanthocybium solandri*, Indian Ocean, 1,088 mm FL, 2×. d. *Grammatorcynus bilineatus*, Queensland, 521 mm FL, 4×.

The size of the ventral protrusion varies among the species of *Scomberomorus.* It is greatest in *S. sinensis*, *commerson*, and *cavalla.* The glossohyal is narrowest in *S. multiradiatus* and *plurilineatus* (Fig. 30a), 35-36% of width. It is widest in *S. sierra* and *munroi* (Fig. 30b), 52-54%. The anterior end is widest in *S. niphonius* and *sinen-*

sis, narrowest in *brasiliensis*, *cavalla*, and *commerson*.

Urohyal.—The urohyal (Fig. 31) is a compressed, median, unpaired bone. The anterior end of this element lies between, and is connected with, the hypohyals of the left and right sides. The dorsal and ventral margins are thickened. The anterior end has an articulation head and the posterior end is deep. The maximum depth posteriorly is 13-24% of the length of the dorsal margin. The urohyal is not as deep in *Acanthocybium* as in the species of *Scomberomorus*, depth 13-15% of the length of the dorsal margin compared with 16-24%. *Grammatorcynus* also has a low urohyal, depth 15-17% of length. The length of the ventral margin is 68-91% of the length of the dorsal margin. The ventral margin of the urohyal does not extend as far posteriorly in *Grammatorcynus*, only 68-69% of the length of the dorsal margin compared with 80-91% in *Acanthocybium* and *Scomberomorus*. Both Mago Leccia (1958:322) and Devaraj (1977:32) stated that the posterior end of the dorsal margin was pointed but it ends in a distinct fork in all species of *Scomberomorus* and in *Acanthocybium* (Fig. 31c). The major difference in *Grammatorcynus* is that the shape of the posterior end of the dorsal

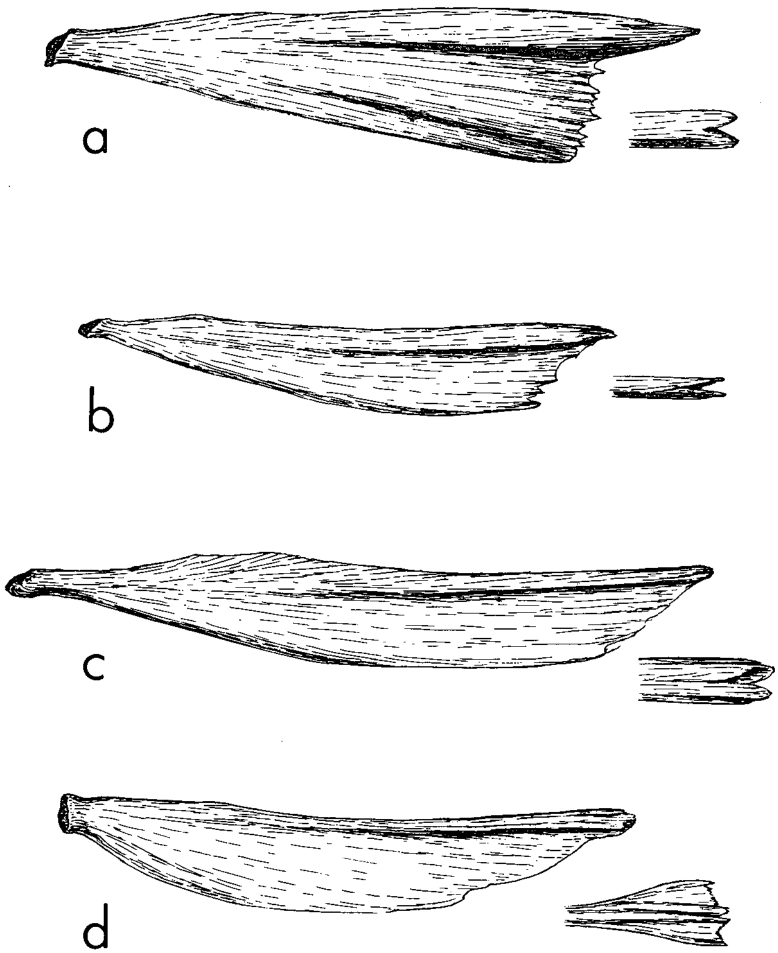


FIGURE 31.—Urohyals in left lateral view. a. *Scomberomorus queenslandicus*, Queensland, 641 mm FL, 2×. b. *Scomberomorus munroi*, New Guinea, 512 mm FL, 2×. c. *Acanthocybium solandri*, Indian Ocean, 1,088 mm FL, 1×. d. *Grammatorcynus bilineatus*, New Guinea, 382 mm FL, 3×. Inset to right is the posterior end of the dorsal margin, in dorsal view.

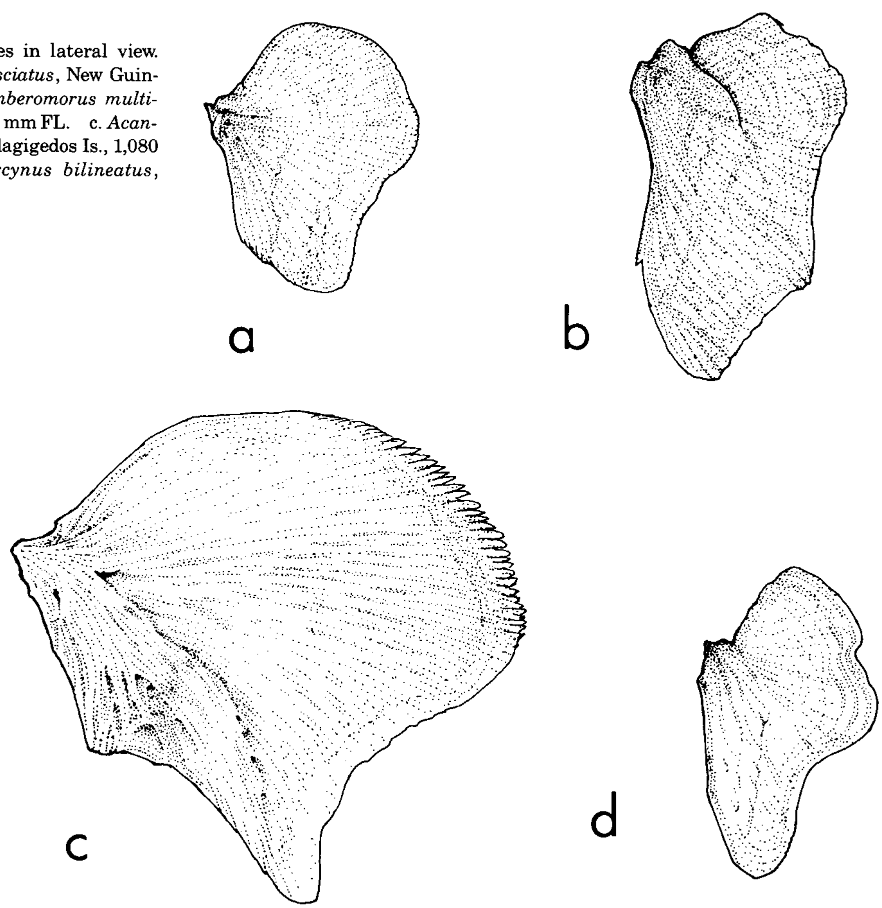
margin is tripartite (Fig. 31d) instead of forked. Some specimens of *Acanthocybium* differ from the other two genera by having a slight indentation in the anterior end of the urohyal.

OPERCULAR APPARATUS.—Four wide flat bones (opercle, preopercle, subopercle, and interopercle) fit together to form the gill cover which protects the underlying gill arches.

Opercle.—The opercle is broad (Fig. 32), and it is overlapped laterally on its anterior margin by the posterior half of the preopercle. The narrow, elongate, articular facet for the opercular process of the hyomandibula is located on the mesial surface of the anterodorsal corner of the opercle. *Grammatorcynus* (Fig. 32d) and most species of *Scomberomorus* have a weak process at the posterodorsal corner. This process appears to be absent in *Acanthocybium* (Fig. 32c) and *Scomberomorus sinensis*. In several species of *Scomberomorus* (*cavalla*, *regalis*, and *tritor*), there is also a weak anteroventral process. Instead of a distinct process at this point, *Acanthocybium* and the other species of *Scomberomorus* have an angle where the anterior margin meets the anteroventral margin. The posterior margin and/or the posteroventral margin of the opercle are fimbriate in *Acanthocybium* and most species of *Scomberomorus* (*brasiliensis*, *koreanus*, *lineolatus*, *maculatus*, *niphonius*, *queenslandicus*, *semifasciatus* (Fig. 32a), *sinensis*, and *tritor*). *Grammatorcynus* (Fig. 32d) has a much narrower and more elongate opercle than do *Acanthocybium* or the species of *Scomberomorus*. The most elongate opercle among *Scomberomorus* species is in *S. multiradiatus* (Fig. 32b). The broadest is in *Acanthocybium*.

Preopercle.—The preopercle (Fig. 33) is a large crescent-shaped flat bone, broadest at the lower posterior angle. The anterior portion of the bone

FIGURE 32.—Left opercles in lateral view. a. *Scomberomorus semifasciatus*, New Guinea, 510 mm FL. b. *Scomberomorus multiradiatus*, New Guinea, 294 mm FL. c. *Acanthocybium solandri*, Revillagigedos Is., 1,080 mm FL. d. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL.



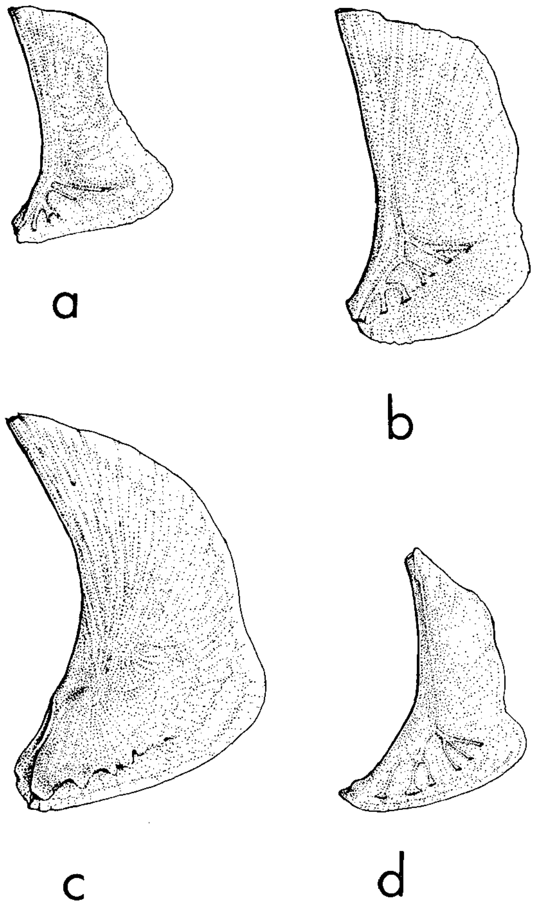


FIGURE 33.—Left preopercles in lateral view. a. *Scomberomorus semifasciatus*, New Guinea, 510 mm FL. b. *Scomberomorus multiradiatus*, New Guinea, 294 mm FL. c. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL. d. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL.

is thickened into a bony ridge. A series of 5-7 pores along the lower margin of the ridge represents the preopercular canal of the lateral line system which continues into the dentary. On the mesial side, the 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* (Fig. 33c) that is not present in *Scomberomorus* (Fig. 33a, b) or *Grammatorcynus* (Fig. 30d). Devaraj (1977:34) referred to this as a groove. The canals leading to the preopercular pores are visible through the bone in *Scomberomorus* and *Grammatorcynus* but cannot be seen in *Acanthocybium* due to the thickness of the bone. The posterior margin of the preopercle is distinctly concave in *Grammatorcynus* and most species of *Scomberomorus*. Devaraj (1977:34) stated that the posterior margin was convex in *S. commerson* and *Acanthocybium*. We find it to be nearly straight in *Acanthocybium* and very slightly concave in *S. commerson*. The concave posterior border makes the upper and lower parts appear as two limbs, the lower of which is longer. As Devaraj (1977:34) noted, the lower portion is longer in *S. guttatus* than in the other species, the distance from the anterior margin of the bony ridge to the posterior end of the lower lobe being 74-80% of the height of the preopercle measured from the ventral margin to the dorsal tip of the bone. Other species with long lower portions include *S. munroi* (73-78%), *S. plurilineatus* (69-79%), *S. niphonius* (73-75%), and *Grammatorcynus* (68-75%). Devaraj (1977:34) stated that the anterior ridge was forked at its upper part in all the Indian species of *Scomberomorus* except *S. commerson* in which the fork is either indistinct or absent, and that the fork was completely absent in *Acanthocybium*. We are unable to confirm this observation and find no differences between *Scomberomorus* and *Acanthocybium*. In these genera, and in *Grammatorcynus*, the anterodorsal margin terminates in a pore similar to the preopercular lateral line canal pore at the anteroventral margin of the bone.

Subopercle.—The subopercle is a flat triangular bone with a prominent anterior projection (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 stronger than the ventral ridge and extends over the main part of the subopercle as a discrete shelf. The much weaker ventral ridge is difficult to detect in some species. The angle between the anterior projection and the anterior margin of the subopercle varies from approximately a right angle in *Acanthocybium* (Fig. 34c) and most species of *Scomberomorus* to acute in *Grammatorcynus* (Fig. 34d) and *Scomberomorus multiradiatus* (Fig. 34b). The length of the anterior projection varies from 20 to 45% of the length of the anterior margin dorsal to the projection. The projection is longest in *Acanthocybium* (36-45%), *S. sierra* (37-43%), and *S. koreanus* (33-41%). It is shortest in *S. commerson* (20-25%), *S. semifasciatus* (21-23%, Fig. 34a), and *S. queenslandicus* (21-

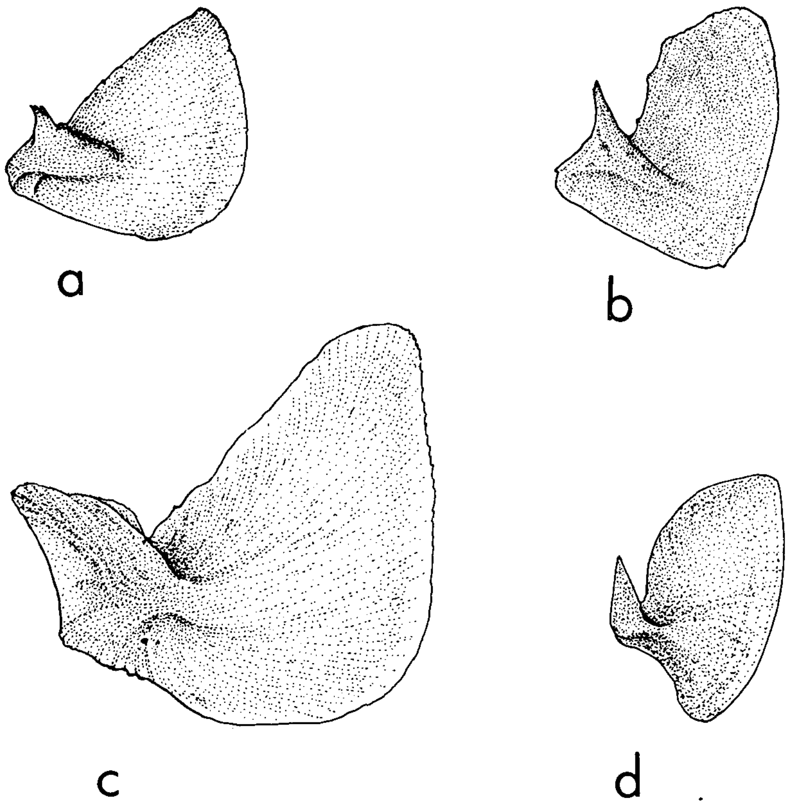


FIGURE 34.—Left subopercles in lateral view. a. *Scomberomorus semifasciatus*, New Guinea, 510 mm FL. b. *Scomberomorus multiradiatus*, New Guinea, 294 mm FL. c. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL. d. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL.

27%). It is also short, relative to the long, narrow subopercle, in *Grammatorcynus* (25-26%). Devaraj (1977:33) mentioned differences in the shape of the posteroventral margin and the dorsal edge of the subopercle, but we have not noted any consistent differences between species in these regions.

Interopercle.—The interopercle (Fig. 35) is roughly oval in shape with a crest on the superior margin. There is a well-developed facet on the mesial side to receive the articular process of the interhyal. The depth of the interopercle varies from 37 to 61% of the length of the bone. The deepest interopercles are in *Scomberomorus sinensis* (54-61%, Fig. 35b) and *S. sierra* (57-58%). The interopercles are moderately deep (50-58%) in seven species: *brasiliensis*, *commerson*, *koreanus*, *lineolatus*, *multiradiatus*, *queenslandicus*, and *tritor*. *Grammatorcynus* (37-42%, Fig. 35d) and *Acanthocybium* (40-49%, Fig. 35c) have lower interopercles than most species of *Scomberomorus* (Fig. 35a, b). The shallowest interopercles in this genus are in *S. plurilineatus* (45-47%), *S. munroi* (47-49%), *S. niphonius* (47-49%), and *S. semifasciatus* (47-51%, Fig. 35a). A well-formed notch anterior to the crest on the sloping anterior margin in *Scomberomorus* and *Grammatorcynus* is relatively poorly developed in *Acanthocybium*, rendering the superior margin nearly straight. The posterior margin is rounded in *Scomberomorus* and *Grammatorcynus* but divided into two by a notch in *Acanthocybium*.

BRANCHIAL APPARATUS.—The branchial apparatus is composed of the five pairs of gill arches, gill filaments, gill rakers, pharyngeal tooth patches, and supporting bones. The general arrangement in the Scomberomorini (Fig. 36) is similar to that found in other scombrids such as

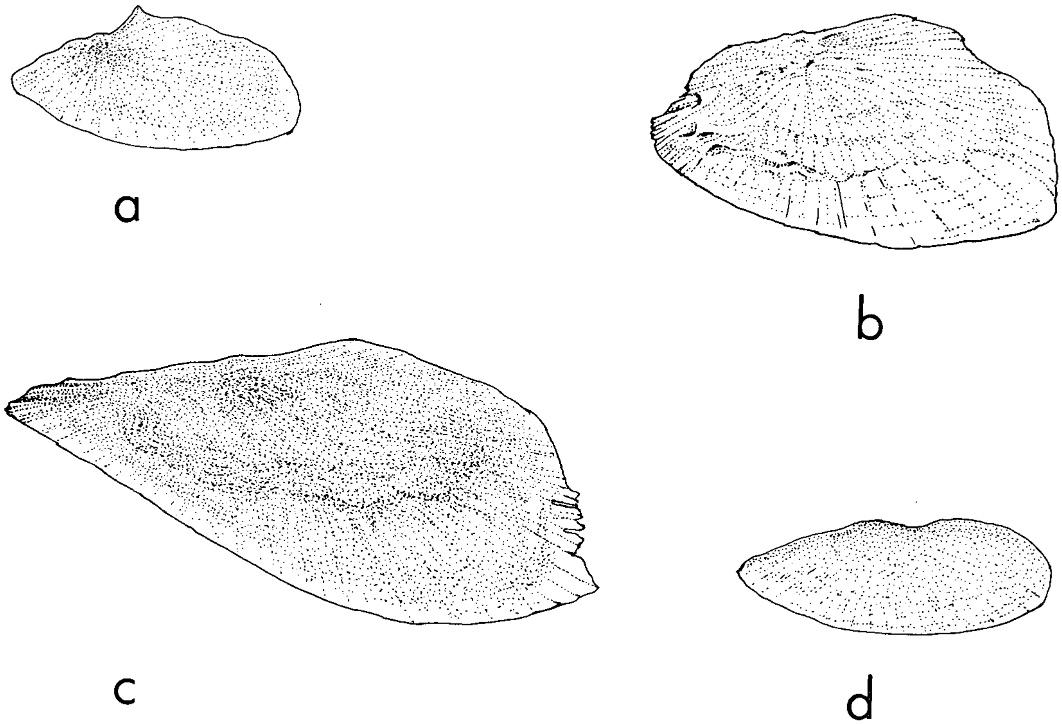


FIGURE 35.—Left interopercles in lateral view. a. *Scomberomorus semifasciatus*, New Guinea, 510 mm FL. b. *Scomberomorus sinensis*, Hong Kong, 677 mm FL. c. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL. d. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL.

the Sardini (Collette and Chao 1975), *Thunnus* (Iwai and Nakamura 1964b:22, fig. 1; de Sylva 1955:21, fig. 40), *Scomberomorus* (Mago Leccia 1958:327, pl. 12), and *Rastrelliger* (Gnanamuttu 1971:14, fig. 6). Within the Scomberomorini, the most useful differences are in the number of gill rakers. Most of the 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 *Scomberomorus*, it is short with a wide base where it joins with the second basibranchial but it is much more elongate in *Acanthocybium* and *Grammatorcynus*. The second basibranchial has a prominent notch in the ventral margin and a distinct groove laterally which extends from the anteroventral margin to the middorsal 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 which accepts the medial anterior end of the second hypobranchial. A section of cartilage extends posteriorly to articulate with the fourth and fifth ceratobranchials.

Hypobranchials.—Three hypobranchials are present. The first is interposed between the second basibranchial and the first ceratobranchial. The second hypobranchial 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 is divided into two processes: the anterior process attaches to the second pharyngobranchial and the posterior process is coupled with the third pharyngobranchial by way of an elongate cartilage. This process is much more elongate in *Grammatorcynus* than in *Acanthocybium* or *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. The fourth epibranchial is larger than

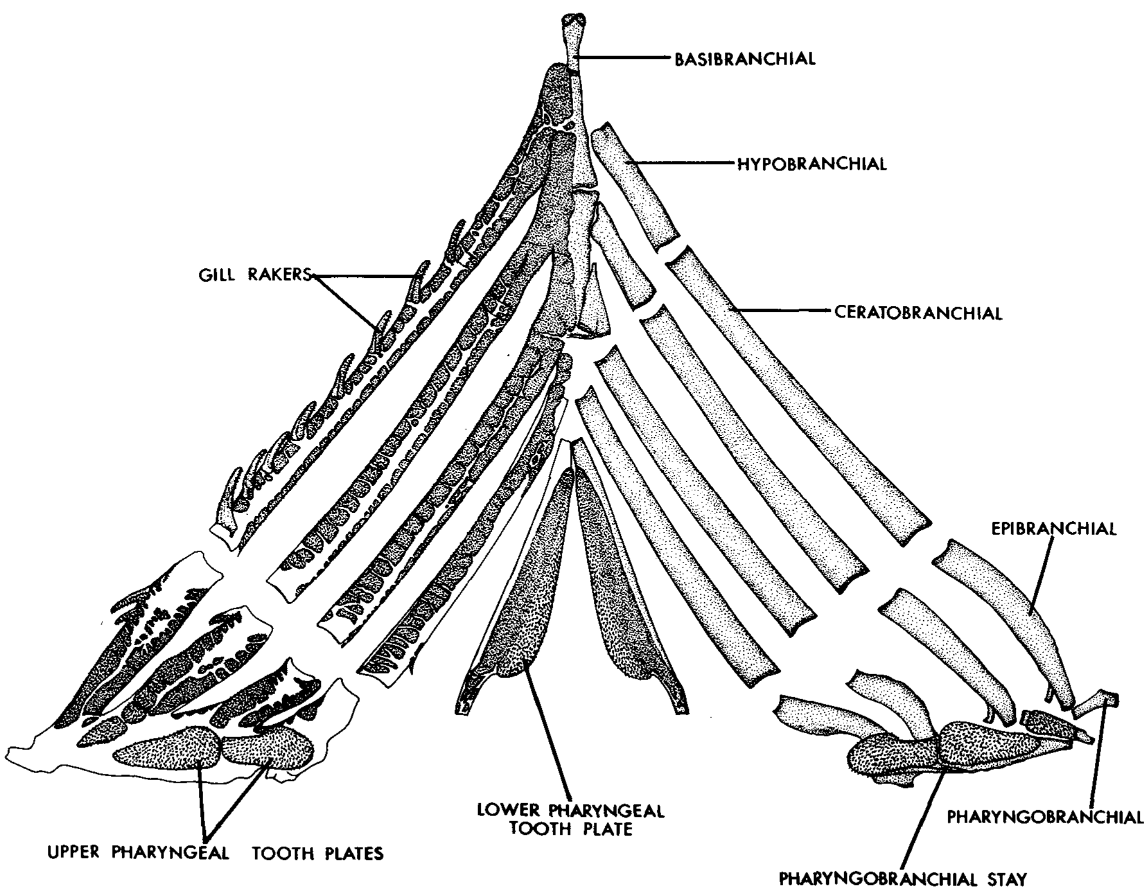


FIGURE 36.—Branchial apparatus of *Scomberomorus semifasciatus*, New Guinea, 510 mm FL. Dorsal view of the gill arches with the dorsal region folded back to show their ventral aspect. Epidermis removed from right hand side to reveal underlying bones.

the third and is interposed between the fourth ceratobranchial and pharyngobranchial. It may be described as a curved bone with the angle formed by the lateral and medial arms being much more acute in *Grammatorcynus* than in *Acanthocybium* or *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 1964b). 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. The third pharyngobranchial of *Scomberomorus* is much more elongate than those of *Acanthocybium* and *Grammatorcynus*. 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 more elongate in *Scomberomorus* than in *Acanthocybium* and *Grammatorcynus*.

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. There is a correlation between numbers of gill rakers, gap between gill rakers, and size of food items, as Magnuson and Heitz (1971) have clearly shown for a number of species of Scombridae. The number of gill rakers is easily countable and is a useful taxonomic character in Spanish mackerels as well as among other groups of the Scombridae.

Acanthocybium differs from *Grammatorcynus*, *Scomberomorus*, and the other genera of Scombridae by completely lacking gill rakers. Three species of *Scomberomorus* have greatly reduced numbers of gill rakers (Table 5): *multiradiatus* (1-4, sometimes only a single gill raker present, at the junction of the upper and lower arches), *commerson* (1-8), and *queenslandicus* (3-9). One species, *concolor*, stands out from the rest of the genus in having many gill rakers, 21-27. *Grammatorcynus* has more gill rakers (19-24) than 17 species of *Scomberomorus* but fewer than *S. concolor*. There is a correlation between number of gill rakers and number of jaw teeth (Tables 3, 4) in *Scomberomorus*. The species with the fewest gill rakers, *S. multiradiatus*, also has the fewest jaw teeth ($\bar{x}$ 8.0 on the upper jaw, 7.8 on the lower jaw) and the species with the most gill rakers, *S. concolor*, has the most teeth ($\bar{x}$ 22.2, 19.7).

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 (ab-

TABLE 5.—Total number of gill rakers on the first arch in *Acanthocybium*, *Grammatorcynus*, and the species of *Scomberomorus*.

Species	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	*N*	$\bar{x}$
S. brasiliensis												1	9	49	37	22	11												129	13.8
S. cavalla								3	8	30	22	1	1	1															66	9.3
S. commerson		1	0	37	28	27	12	3	2																				110	4.3
S. concolor																						1	2	10	10	9	4	3	39	24.2
S. guttatus									3	7	24	53	25	9	2														123	11.1
S. koreanus												5	4	3	11	4													27	13.2
S. lineolatus								1	0	3	9	12	3	1															29	10.5
S. maculatus											1	4	16	27	13	5	1												67	13.0
S. multiradiatus		2	12	10	3																								27	2.5
S. munroi											3	4	1																8	10.8
S. niphonius												3	18	14	2	1													38	12.5
S. plurilineatus													10	15	8	1													34	13.0
S. queenslandicus				2	3	3	11	13	1	1																			34	6.2
S. regalis													1	2	4	19	13	6	1										46	15.4
S. semifasciatus							1	1	1	11	9	5	3	1															32	9.8
S. sierra													1	5	15	33	22	6											82	15.1
S. sinensis												1	7	6	1	1													16	12.6
S. tritor													7	18	11	5													41	13.3
Acanthocybium	30																												30	0
Grammatorcynus																				3	9	17	8	5	1				43	21.1

dominal) and caudal (Tables 6-8). 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. Of the three genera, *Acanthocybium* has the most vertebrae (62-64), *Grammatorcynus* the least (31), with the species of *Scomberomorus* falling between (41-56). The same situation exists with precaudal vertebrae (*Acanthocybium* 30-32, *Scomberomorus* 16-23, *Grammatorcynus* 12) and caudal vertebrae (*Acanthocybium* 31-33, *Scomberomorus* 20-36, *Grammatorcynus* 19). 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.

Within *Scomberomorus*, *S. multiradiatus* has the most vertebrae (54-56), followed by *S. maculatus* (51-53), *S. munroi* (50-52), and *S. guttatus* (47-52). The fewest vertebrae are found in *S. cavalla* (41-43) and *S. sinensis* (41-42). Vertebral counts are useful in distinguishing species that had previously been confused (Collette and Russo 1979); *S. koreanus* (46) from *S. guttatus* (usually 48-51) as shown by Devaraj (1976); *S. brasiliensis* (47-49) from *S. maculatus* (51-53) as shown by Collette et al. (1978); and *S. munroi* (50-52) from *S. niphonius* (48-50) as shown by Collette and Russo (1980). In general, low vertebral number is considered primitive in the genus, high vertebral number advanced.

Species with similar total numbers of vertebrae may differ in numbers of precaudal and caudal vertebrae. Both *S. cavalla* and *S. sinensis* have

TABLE 6.—Number of precaudal vertebrae in *Acanthocybium*, *Grammatorcynus*, and the species of *Scomberomorus*.

Species	12	/ /	16	17	18	19	20	21	22	23	/ /	30	31	32	*N*	$\bar{x}$
S. brasiliensis						4	78	1							83	20.0
S. cavalla			1	28											29	17.0
S. commerson						41	69								110	19.6
S. concolor					1	14	5								20	19.2
S. guttatus						1	14	43	2						60	20.8
S. koreanus							24								24	20.0
S. lineolatus					2	13	1								16	18.9
S. maculatus								30	3						33	21.1
S. multiradiatus							9	16							25	20.6
S. munroi								2	10						12	21.8
S. niphonius								4	23	1					28	21.9
S. plurilineatus						1	12								13	19.9
S. queenslandicus						1	13								14	19.9
S. regalis						1	9								10	19.9
S. semifasciatus					1	21									22	19.0
S. sierra						3	45	3							51	20.0
S. sinensis						9	3								12	19.3
S. tritor					2	24									26	18.9
Acanthocybium												2	4	2	8	31.0
Grammatorcynus	14														14	12.0

TABLE 7.—Number of caudal vertebrae in *Acanthocybium*, *Grammatorcynus*, and the species of *Scomberomorus*.

Species	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	*N*	$\bar{x}$
S. brasiliensis									7	72	4								83	28.0
S. cavalla						1	27	1											29	25.0
S. commerson					11	33	49	7	9										109	24.7
S. concolor									2	13	5								20	28.2
S. guttatus										12	17	28	3						60	29.4
S. koreanus								22	2										24	26.1
S. lineolatus							1	3	11	1									16	26.8
S. maculatus												15	18						33	30.5
S. multiradiatus																10	13	2	25	34.7
S. munroi										2	8	2							12	29.0
S. niphonius									23	5									28	27.2
S. plurilineatus							2	10	1										13	25.9
S. queenslandicus										10	4								14	28.3
S. regalis										10									10	28.0
S. semifasciatus							1	17	4										22	26.1
S. sierra								1	9	36	5								51	27.9
S. sinensis			2	9															11	21.8
S. tritor									23	3									26	27.1
Acanthocybium													1	4	2				7	32.1
Grammatorcynus	14																		14	19.0

TABLE 8.—Total number of vertebrae in *Acanthocybium*, *Grammatorcynus*, and the species of *Scomberomorus*.

Species	31	/ /	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	/ /	62	63	64	*N*	$\bar{x}$
S. brasiliensis									11	67	5												83	47.9
S. cavalla			2	28	1																		31	42.0
S. commerson				7	16	34	39	15															111	44.4
S. concolor								1	11	8													20	47.4
S. guttatus									1	8	5	16	28	2									60	50.1
S. koreanus								23	2														25	46.1
S. lineolatus						1	3	13															17	45.7
S. maculatus													13	19	2								34	51.7
S. multiradiatus																1	15	9					25	55.3
S. munroi												3	9	1									13	50.8
S. niphonius										3	20	6											29	49.1
S. plurilineatus							2	12															14	45.9
S. queenslandicus										12	3												15	48.2
S. regalis									1	9													10	47.9
S. semifasciatus						1	23	3															27	45.1
S. sierra								1	8	38	4												51	47.9
S. sinensis			10	1																			11	41.1
S. tritor								25	1														26	46.0
Acanthocybium																				2	3	2	7	63.0
Grammatorcynus	16																						16	31.0

41-43 vertebrae, but *S. cavalla* has 16-17 precaudal and 24-26 caudal, while *S. sinensis* has 19 or 20 precaudal and 21-22 caudal vertebrae (compare Tables 6 and 7).

Vertebral Column

The neural arches and spines are stout and compressed on the first to the fifth or sixth vertebrae in most species of *Scomberomorus*. Compressed neural spines extend to the seventh vertebra in *S. commerson* and *Acanthocybium* but only to the fourth vertebra in *Grammatorcynus*. 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). Neuropophyses are present on all centra except the last one or two. The neural prezygapophyses on the first vertebra are modified to articulate with the exoccipital where the vertebral axis is firmly articulated with the skull. They are stronger at the anterior portion of the vertebrae and are spurlike spines on the peduncular vertebrae and in the caudal complex. 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 6-8 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).

Variable characters are found on the haemal arches and haemapophyses. Laterally directed parapophyses, arising from the middle of the centrum, appear on the fourth to sixth 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 7th-9th vertebra in *Scomberomorus*, usually the 8th, on the 6th-7th in *Grammatorcynus*, 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* (Fig. 37d), 10th-16th in *Scomberomorus* (Fig. 37a, b), and 25th-28th in *Acanthocybium* (Fig. 37c). This location is correlated with the total number of vertebrae (Table 8). Among the species of *Scomberomorus*, the first closed haemal arch is most anterior in *S. cavalla* (10th-11th vertebra, Fig. 37a) and *S. sinensis* (12th), the two species with the fewest vertebrae (40-43). The most posterior first haemal arch is on the 15th-16th vertebra in *S. munroi* and *S. niphonius* (Fig. 37b) and on the 14th-15th in *S. multiradiatus*, species with many vertebrae (48-56). The other 13 species, including *S. guttatus* and *S. maculatus* with high vertebral counts (47-53), have the first haemal arch located at an intermediate position, on the 13th-14th vertebra. 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 Inter-

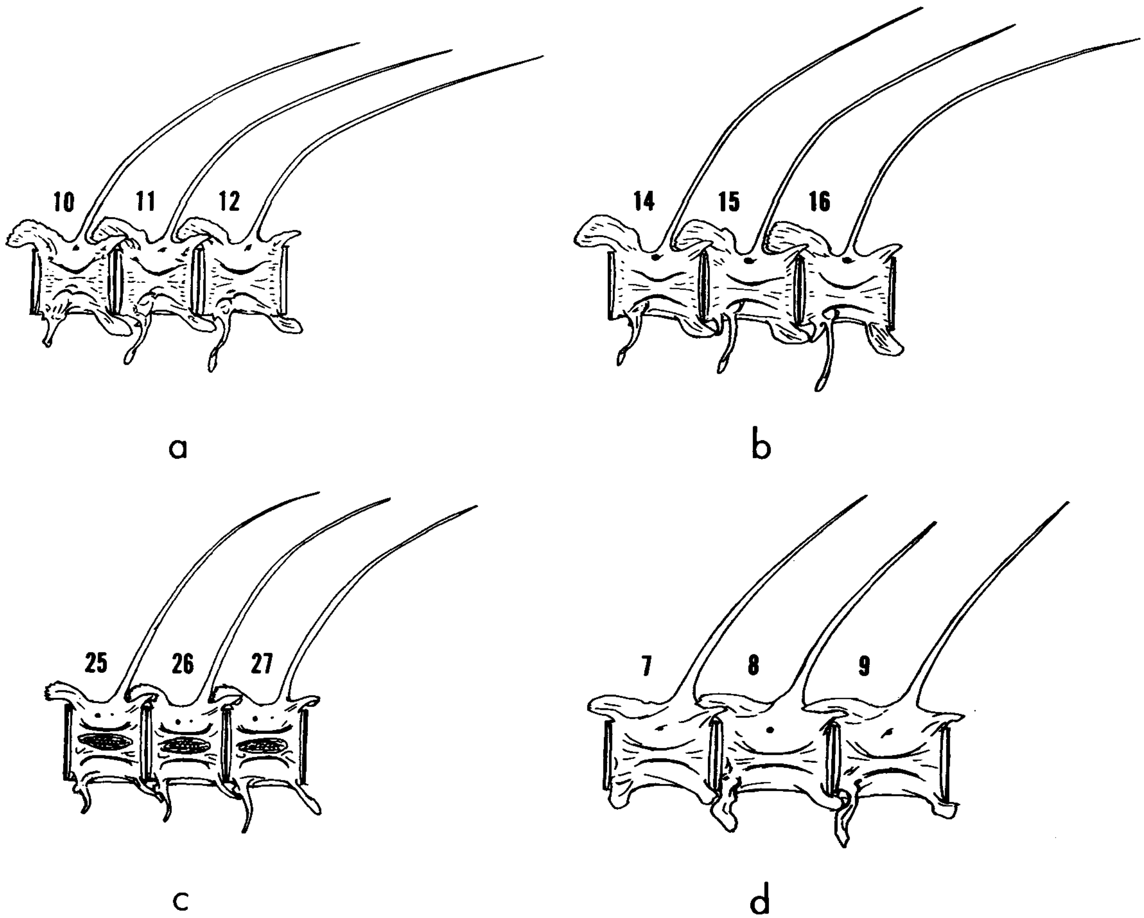


FIGURE 37.—Vertebra bearing first closed haemal arch in left lateral view (middle vertebra of each set of three). Vertebrae numbered from anterior. a. *Scomberomorus cavalla*, Chesapeake Bay, 672 mm FL, 1.5×. b. *Scomberomorus niphonius*, Japan, 683 mm FL, 1.5×. c. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL, 1×. d. *Grammatorcynus bilineatus*, Queensland, 521 mm FL, 1.5×.

muscular Bones) attach to the distal ends of the parapophyses and arches and extend posteriorly to the last precaudal vertebra. Symmetrically with the neural arches and spines on the caudal vertebrae, the haemal arches and spines bend posteriorly at the caudal peduncle and then merge into the caudal complex.

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*, and they reach their maximum length at about the junction of the precaudal and caudal vertebrae (Fig. 38). 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-22d in *Scomberomorus*, and the 23d-25th in *Acanthocybium*. The most anteriorly located prezygapophyses in *Scomberomorus* are in *S. cavalla*, on the 10th-12th vertebra. The most posteriorly located are in *S. sinensis* (22d), *S. queenslandicus* (18th-20th), *S. multiradiatus* (18th-19th), and *S. maculatus* (17th-20th). The other 15 species have the first haemal prezygapophyses on the 13th-19th vertebra. The data from Devaraj (1977) for the four Indian species fall in the interme-

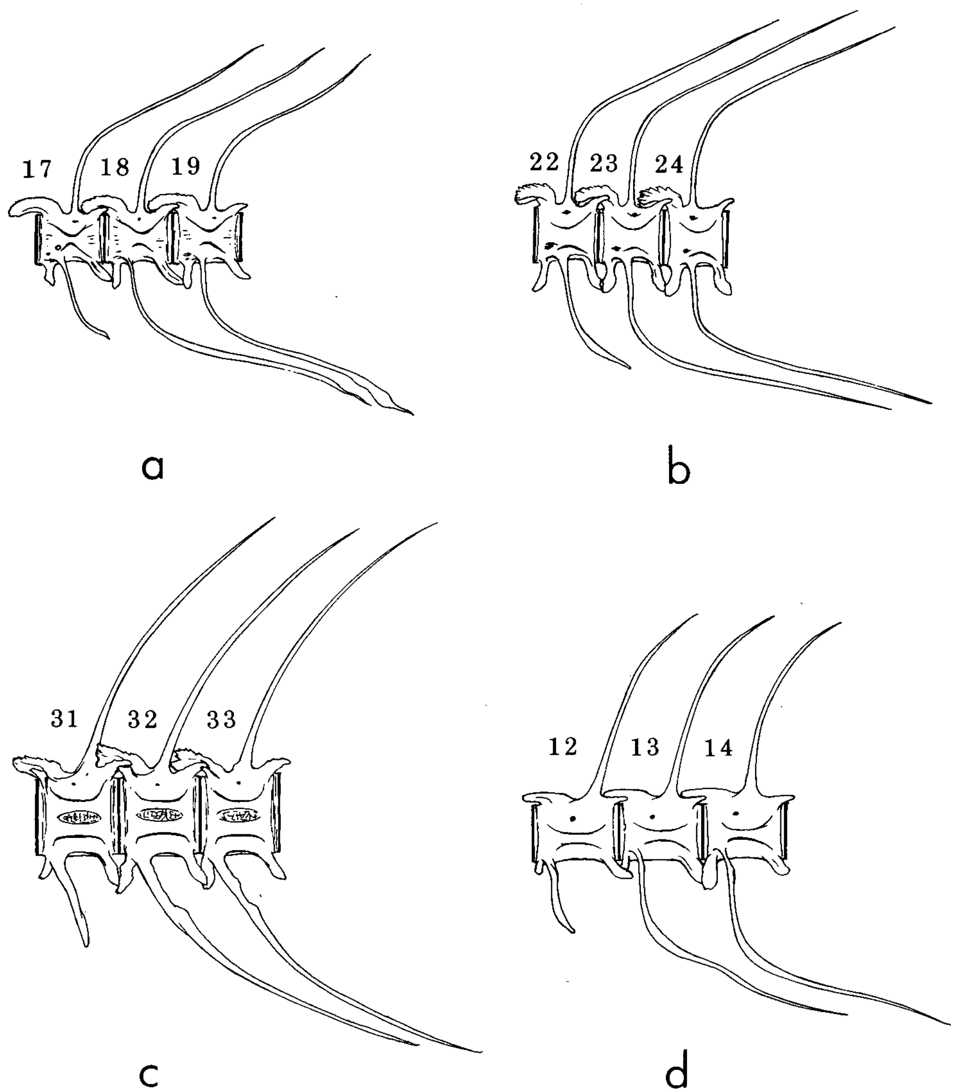


FIGURE 38.—Junction of precaudal and caudal vertebrae in left lateral view (middle vertebra of each set of three is first caudal vertebra). Vertebrae numbered from anterior. a. *Scomberomorus cavalla*, Florida, 688 mm FL, 1×. b. *Scomberomorus munroi*, Cairns, Queensland, 800 mm FL, 1×. c. *Acanthocybium solandri*, Miami, Fla., 1,242 mm FL, 1×. d. *Grammatorcynus bilineatus*, Timor Sea, 453 mm FL, 1.5×.

diate group, but we found more variation, usually a range of three or four vertebrae, than Devaraj did. As do their counterpart neural prezygapophyses, the haemal prezygapophyses persist symmetrically into the caudal complex.

Struts between the haemal arch and the centrum form the inferior foramina. Foramina are present from the 18th-19th to the 27th-28th vertebra in *Grammatorcynus*, the 21st-33d to the 35th-52d in *Scomberomorus*, and the 49th-51st to the 56th-57th in *Acanthocybium*. Devaraj (1977) found only one inferior foramen in *Acanthocybium*, on the 49th vertebra, but we found them on 7-9 vertebrae in 10 specimens from the Atlantic, Indian, and Pacific Oceans. In *Scomberomorus*, inferior foramina begin furthest anteriorly and extend furthest posteriorly in *S. multiradiatus*, from the 21st-23d to the 51st-52d vertebra. They begin furthest posteriorly in *S. maculatus* (29th-33d), *S. niphonius* (27th-33d), and *S. concolor* (26th-38th). They extend posteriorly only to the 35th-36th vertebra in *S. cavalla*.

Ribs and Intermuscular Bones

Pleural ribs are present from the 2d or 3d vertebra posterior to the 12th-31st vertebra, depending on the species. Intermuscular bones start on the back of the skull or the first vertebra and extend to the 10th-30th vertebra.

Correlated with its high number of vertebrae, *Acanthocybium* has the most pleural ribs (30 pairs) of the three genera. Similarly, *Grammatorcynus* has the fewest pleural ribs (10 pairs) in agreement with its low number of vertebrae. Species of *Scomberomorus* are intermediate in number of vertebrae and pleural ribs (15-21 pairs). The first pleural rib articulates with the centrum of the third vertebra in *Grammatorcynus* and most specimens of *Scomberomorus*. The first rib articulates with the centrum of the second vertebra in *Acanthocybium*, as noted by Devaraj (1977:44), and in one or two specimens of at least three species of *Scomberomorus*: *commerson* (1 of 5), *maculatus* (2 of 10), and *sinensis* (our only specimen). Pleural ribs extend posteriorly usually to about the last precaudal vertebra. They extend to the 31st vertebra in *Acanthocybium*, to the 17th-23d in *Scomberomorus*, and only to the 12th in *Grammatorcynus*. Of the species of *Scomberomorus*, the most ribs are found in *S. munroi* (20-21 pairs), *S. guttatus* (20), *S. brasiliensis* (18-20), and *S. maculatus* (18-20). The fewest are in *S. cavalla* (15 pairs), *S. semifasciatus* (15-17), and *S. concolor* (16-18). Ribs extend back furthest in the same four species with the most pleural ribs, *S. munroi* (to the 22d-23d), *S. guttatus* (20th-22d), *S. brasiliensis* (20th-22d), and *S. maculatus* (17th-22d). They extend back the shortest distance in *S. cavalla* (to the 17th) and *S. semifasciatus* (17th-19th). As Devaraj (1977:44) noted, the anterior ribs in *Acanthocybium* are very broad compared with those in *Scomberomorus*.

Intermuscular bones start on the first vertebra in *Acanthocybium*, *Grammatorcynus*, 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. This appears to be the usual condition in three species, *S. concolor*, *S. koreanus* (also noted by Devaraj 1977), and *S. sierra*. At least three other species usually appear to have the first intermuscular bone attached to the first vertebra: *S. guttatus*, *S. munroi*, and *S. niphonius*. The condition in the remaining 12 species either varies or is based on only a single specimen. The greatest number of intermuscular bones are found in *S. guttatus*, 26-30 pairs. Counts as high as 27 are found in *S. koreanus*, *S. maculatus*, and *S. multiradiatus*. Except for *S. koreanus*, the other three species with high numbers of intermuscular bones also have high vertebral counts. The fewest intermuscular bones in *Scomberomorus* are found in *S. cavalla* and *S. sinensis*, 20 pairs, and *S. lineolatus*, *S. niphonius*, and *S. semifasciatus*, 20-23 pairs each. *Grammatorcynus* has relatively few intermuscular bones (19-21 pairs) and *Acanthocybium*, unexpectedly, has the fewest (10 pairs) among the genera under discussion. This seems odd in view of its high number of vertebrae and pleural ribs. Intermuscular bones extend back furthest in the four species with the highest number, *S. guttatus* (to the 25th-29th), *S. koreanus* (24th-29th), *S. maculatus* (22d-27th), and *S. multiradiatus* (26th). They extend back the shortest distance in *S. cavalla* (to the 19th), the species with the fewest intermuscular bones. Correlated with their low number in *Grammatorcynus* and *Acanthocybium*, the bones extend back to the 19th-21st and to the 10th vertebra respectively.

Caudal Complex

The supporting bones of the caudal fin (Fig. 39) consist of four or five preural centra in *Scomberomorus*. Having four preural centra supporting the caudal fin is not a diagnostic character of the family as stated by Potthoff (1975). Only three preural centra support the caudal fin in *Grammatorcynus*, *Scomber*, and *Rastrelliger*. Five centra support the caudal fin in *Acanthocybium*. In *Scomberomorus* and *Acanthocybium*, preural centra 4 and 3 bear stout haemal and neural spines. Preural centrum 2 has an epural. Preural centra 2 and 3 each have autogenous haemal spines. 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. Dorsally, the urostyle bears an autogenous epural and ventrally, the autogenous parhypural. Preural centra 2-4 are compressed in *Scomberomorus* and *Acanthocybium* but not so much as in the bonitos and tunas (Collette and Chao 1975; Gibbs and Collette 1967). Preural centrum 4 is not at all shortened in *Grammator-*

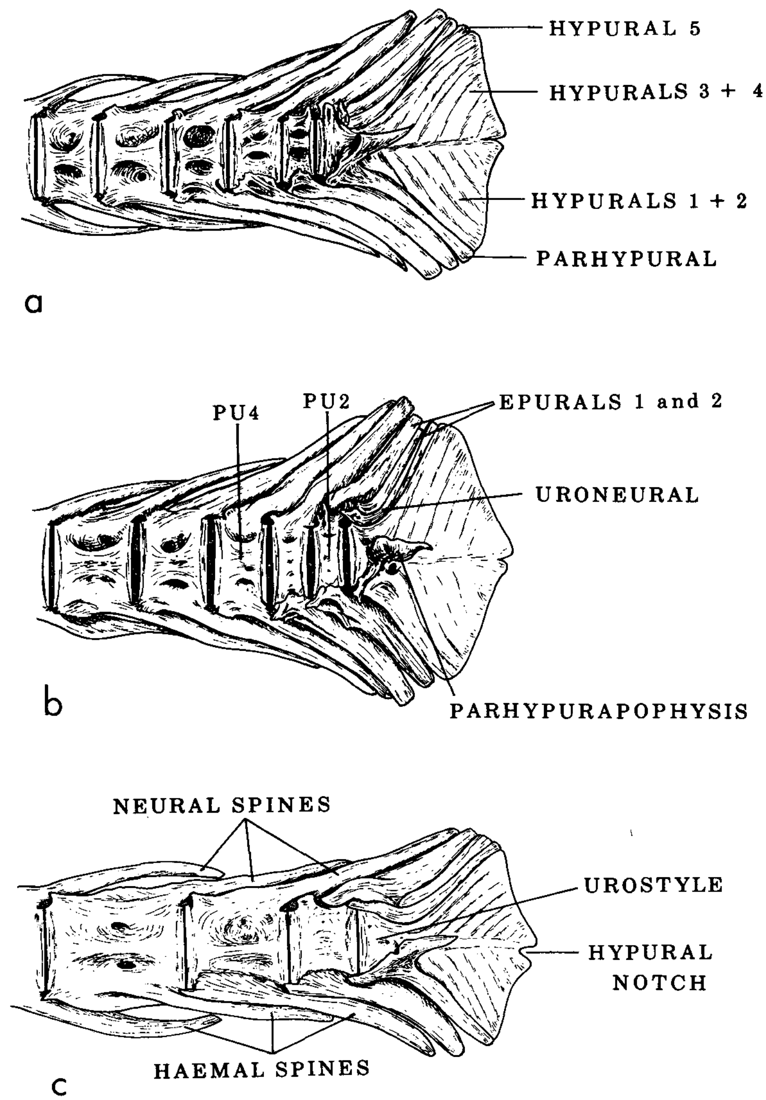


FIGURE 39.—Caudal complex in left lateral view. a. *Scomberomorus semifasciatus*, New Guinea, 510 mm FL, 3×. b. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL, 2×. c. *Grammatorcynus bilineatus*, New Guinea, 382 mm FL, 4×.

cynus and preural centrum 3 is only slightly shortened (Fig. 39c). In *Scomberomorus* and *Acanthocybium*, the posterior three neural and three haemal spines bend abruptly away from the vertebral axis and parallel the dorsal and ventral edges of the hypural plate. Only one neural and one haemal spine do so in *Grammatorcynus*.

The triangular hypural plate is composed of 4-5 fused hypural bones (Potthoff 1975). The dorsalmost (hypural 5) is not fused with the dorsal part of the hypural plate (hypurals 3 and 4). The primitive hypural notch is present on the middle of the posterior margin of the hypural plate (Fig. 39). This notch is a remnant of the fusion of the dorsal part of the hypural plate with the ventral part (1 and 2). The notch is absent in the more advanced bonitos and tunas (Collette and Chao 1975). In two larger specimens of *Grammatorcynus* (453 and 521 mm FL), the fifth hypural is partially fused to the dorsal hypural plate instead of being separate as in three smaller specimens (382-410 mm FL, Fig. 39c). One of the diagnostic characters of the Scombridae is that the bases of the caudal rays completely cover the hypural plate instead of only extending part way over the plate as is true of the Gempylidae and Trichiuridae with caudal fins.

The parhypural is separate from the ventral hypural plate in *Scomberomorus* and *Grammatorcynus* but is fused with it in *Acanthocybium*

(Fig. 39b). This fusion was also noted by Conrad (1938), Fierstine and Walters (1968), and Devaraj (1977). The parhypural appears to be partially fused with the hypural plate in *Scomberomorus niphonius* (see Kishinouye 1923:figure 41) and *S. plurilineatus*. The two haemal arches preceding the parhypural are autogenous in the three genera although Devaraj (1977) stated that the two haemal arches 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 upwards in a similar manner in *Scomberomorus* and *Grammatorcynus* but has a right angle and then a level projection in *Acanthocybium*. Devaraj (1977:44) claimed that "the hypurapophysis is reduced to a small process" in *Acanthocybium*, and his figure seems to show that. This conclusion must be based on a damaged specimen because the parhypurapophysis is well developed in our specimens (Fig. 39b). The concentrations of tendons and muscular bands between the parhypurapophysis and caudal rays in scombroids were described by Fierstine and Walters (1968), but no specific study of this aspect was made during our work.

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

Illustrations of the caudal complex of *Acanthocybium* and 11 species of *Scomberomorus* have been provided by several authors: *S. sinensis* and *S. niphonius* (Kishinouye 1923:pl. 23, fig. 40, pl. 24, fig. 41); *S. cavalla*, *S. maculatus*, and *S. regalis* (Mago Leccia 1958:pl. 15, figs. 1-3); *S. tritor* (Monod 1968:fig. 736); *S. koreanus*, *S. guttatus*, *S. lineolatus*, and *S. commerson* (Devaraj 1977:fig. 15); *S. semifasciatus* (Collette and Russo 1979:fig. 4B); and *Acanthocybium* (Kishinouye 1923:pl. 23, fig. 39; Conrad 1938:fig. 8; and Monod 1968:fig. 737). There are problems with nomenclature and labelling of various elements in these papers, as discussed by Potthoff (1975).

DORSAL AND ANAL FINS

Scombrids have two dorsal fins. The first dorsal fin is composed of stiff spines and is separated from the second dorsal by a short distance, except in *Rastrelliger*, *Scomber*, and *Auxis* which have a greater distance between the fins. The second dorsal fin is composed of soft rays and is followed by a series of free finlets, 6-11 in *Scomberomorus*. The anal fin is located approximately opposite the dorsal fin and is composed largely of soft rays followed by a series of anal finlets similar to the dorsal finlets, 5-12 in *Scomberomorus*. Some scombrids have a free or partially free spine preceding the anal fin, but in *Scomberomorus* it is difficult to tell if the anterior elements are spiny or soft rays; therefore, all are included as "anal rays". Numbers of fin rays are useful characters in distinguishing groups of species in *Scomberomorus*.

The range in number of spines in the first dorsal fin is 11-27 among *Scomberomorus*, *Acanthocybium*, and *Grammatorcynus* (Table 9). The

TABLE 9.—Number of spines in the first dorsal fin of *Acanthocybium*, *Grammatorcynus*, and the species of *Scomberomorus*.

Species	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	*N*	$\bar{x}$
S. brasiliensis							61	67	2									130	17.5
S. cavalla		1	3	6	42	2	3	1										58	14.9
S. commerson					3	50	107	5										165	16.7
S. concolor					1	3	20	7										31	17.1
S. guttatus					6	30	59	7										102	16.7
S. koreanus				2	20	5	1											28	15.2
S. lineolatus					2	10	15	1										28	16.5
S. maculatus							10	40	7									57	17.9
S. multiradiatus						1	8	14	4									27	17.8
S. munroi										6	8	1						15	20.7
S. niphonius									4	29	5							38	20.0
S. plurilineatus					12	17	2											31	15.7
S. queenslandicus						8	24	2										34	16.8
S. regalis						9	31	6										46	16.9
S. semifasciatus			1	11	17													29	14.6
S. sierra					1	3	36	39										79	17.4
S. sinensis					1	7	6											14	16.4
S. tritor					3	7	19	11										40	17.0
Acanthocybium													2	2	7	19	4	34	25.6
Grammatorcynus	2	42	1															45	12.0

usual variation for a species is 3 or 4 spines. *Acanthocybium* has the most dorsal spines, 23-27. Of the species of *Scomberomorus*, *munroi* (20-22) and *niphonius* (19-21) both usually have 20 or 21 dorsal spines, more than the other 16 species in the genus, and this is one reason that *S. munroi* was not described until recently (Collette and Russo 1980). Four species of *Scomberomorus* have low counts: *cavalla* 12-18, usually 15; *semifasciatus* 13-15; *koreanus* 14-17, usually 15; and *plurilineatus* 15-17. *Grammatorcynus* has even fewer dorsal spines, 11-13, usually 12. Dorsal spine counts are roughly correlated with vertebral number (Table 8). *Acanthocybium* has the highest counts of precaudal and total vertebrae; *S. munroi* and *S. niphonius* have the highest precaudal vertebral counts, but not highest total vertebral number; *S. cavalla* has the lowest precaudal and total counts in the genus; and *Grammatorcynus* has the fewest precaudal, caudal, and total vertebrae.

The range in number of second dorsal fin rays is 10-25 in the three genera (Table 10). The usual variation for a species is 4 or 5 rays. Five species of *Scomberomorus* have high counts: *multiradiatus* 21-25, usually 23 or 24; *koreanus* 20-24, usually 22 or 23; *guttatus* 18-24, usually 20-22; *semifasciatus* 19-22, usually 20; and *plurilineatus* 19-21, usually 20. The lowest counts in *Scomberomorus* are in *sinensis*, 15-17 rays. *Acanthocybium* (12-16) and *Grammatorcynus* (10-12, usually 11) have even fewer second dorsal fin rays. Vertebral counts (caudal and total) are highest in *S. multiradiatus* and lowest in *S. sinensis*. *Grammatorcynus* has the fewest vertebrae.

Dorsal finlets number 6-11 in the three genera (Table 10). The usual variation for a species is 3 or 4 finlets. The highest counts are in *S. commerson* and *S. queenslandicus*, both usually 9 or 10 finlets. The lowest counts, 6 or 7, are in *S. sinensis* and *Grammatorcynus*. The next fewest dorsal finlets, 7 or 8, rarely 9, are found in *S. multiradiatus*. The low number of finlets and high number of second dorsal fin rays in this species may indicate an extension of the fin at the expense of the number of finlets.

Anal fin rays (Table 11) show a similar trend to that of dorsal fin rays. The range in the three genera is 11-29; the usual variation for a species is 4-6 rays. Four of the five species of *Scomberomorus* with high counts of second dorsal fin rays also have high counts of anal fin rays: *multiradiatus* 25-29; *koreanus* 20-24, usually 22 or 23; *guttatus* 19-23, usually 20-22; and *semifasciatus* 19-22, usually 21 or 22. No species of *Scomberomorus* stands out with very low counts but six species usually have 17-19 anal fin rays, lower than the other species of the genus: *brasiliensis*, *cavalla*, *commerson*, *munroi*, *niphonius*, and *sinensis*. *Acanthocybium* (11-14) and *Grammatorcynus* (11-13, usually 12) again have the fewest rays in this fin.

Anal finlets range 5-12 in the three genera (Table 11) with the usual variation for a species being 4 finlets. The most finlets are found in *S. queenslandicus* (9-11, usually 10) followed by *commerson* and *lineolatus* usually having 9 or 10 finlets, similar to the situation with dorsal finlets. The lowest counts, usually 6 finlets, are found in *S. multiradiatus*, *S. sinensis*, and *Grammatorcynus*, just as with dorsal finlets. Again the anal fin of *S. multiradiatus* appears to have

TABLE 10.—Number of second dorsal fin rays and dorsal finlets in *Acanthocybium*, *Grammatorcynus*, and the species of *Scomberomorus*.

	Dorsal rays																		Finlets							
Species	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	*N*	$\bar{x}$	6	7	8	9	10	11	*N*	$\bar{x}$
S. brasiliensis						1	11	52	48	13							125	17.5			29	89	12		130	8.9
S. cavalla						4	12	25	19								60	17.0		1	15	35	6		57	8.8
S. commerson						1	21	61	67	11	1						162	17.4			12	76	72	4	164	9.4
S. concolor							1	2	10	16	2						31	18.5	1	7	21	1			30	7.7
S. guttatus									3	5	24	40	24	7	1		104	21.0		6	52	43	4		105	8.4
S. koreanus											1	4	8	13	1		27	22.3		7	17	4			28	7.9
S. lineolatus						1	4	9	11	2	0	1	1				29	17.6		2	7	18	2		29	8.7
S. maculatus								5	19	25	7						56	18.6		2	29	25			56	8.4
S. multiradiatus												3	4	10	8	2	27	23.1		15	10	2			27	7.5
S. munroi								3	8	3	1						15	18.1				11	4		15	9.3
S. niphonius						1	12	12	12	1							38	17.0		9	22	7			38	7.9
S. plurilineatus										6	22	8					36	20.1			12	20	3		35	8.7
S. queenslandicus								10	11	10							31	18.0				12	17	2	31	9.7
S. regalis							2	12	28	5							47	17.8		2	39	6			47	8.1
S. semifasciatus										6	18	5	3				32	20.2			9	19	3		31	8.8
S. sierra							2	29	41	6							78	17.7		2	43	33	1		79	8.4
S. sinensis						4	9	1									14	15.8	8	6					14	6.4
S. tritor							6	25	9	1							41	17.1		1	33	7			41	8.1
Acanthocybium		1	3	21	7	1	2										35	13.3		6	16	11	3		36	8.3
Grammatorcynus	5	37	1														43	10.9	40	5					45	6.1

TABLE 11.—Number of anal fin rays and anal finlets in *Acanthocybium*, *Grammatorcynus*, and the species of *Scomberomorus*.

Species	Anal rays																					Finlets									
	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	*N*	$\bar{x}$	5	6	7	8	9	10	11	12	*N*	$\bar{x}$
S. brasiliensis						6	35	30	44	9										124	18.1			1	41	84	2			128	8.7
S. cavalla						1	9	27	21	1										59	18.2			4	33	19	4			60	8.4
S. commerson						8	29	72	43	12	1									165	18.2			1	17	84	57	4	2	165	9.3
S. concolor									1	17	9	2	1							30	20.5		1	15	15					31	7.5
S. guttatus									2	23	49	26	3							103	21.0			20	63	17	4			104	8.0
S. koreanus										1	3	13	11	1						29	22.3			17	11	1				29	7.4
S. lineolatus							2	0	7	17	2	1								29	19.7			2	2	14	11			29	9.2
S. maculatus							4	11	24	18										57	19.0			1	33	21	1			56	8.4
S. multiradiatus															3	7	8	8	1	27	26.9		18	8	1					27	6.4
S. munroi							8	5	2											15	17.6				2	10	3			15	9.1
S. niphonius						1	12	20	3	1										37	17.8		1	7	20	10				38	8.0
S. plurilineatus									4	16	13	1								34	20.3			1	15	17	2			35	8.6
S. queenslandicus						2	1	6	14	8										31	18.8					8	21	2		31	9.8
S. regalis					1	1	4	15	24	1										46	18.4			3	34	8	1			46	8.2
S. semifasciatus									1	4	17	11								33	21.2			1	11	19	2			33	8.7
S. sierra						3	6	19	33	17	1									79	18.7			6	48	23	1			78	8.2
S. sinensis						1	3	9	1											14	17.7	2	9	3						14	6.1
S. tritor							5	20	14	2										41	18.3			6	27	8				41	8.0
Acanthocybium	1	11	14	8																34	12.9			13	12	7	2			34	7.9
Grammatorcynus	5	22	17																	44	12.3	1	39	4						44	6.1

extended posteriorly to reduce the number of anal finlets.

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. 40) is a flat elliptical bone with two sturdy anterior processes that attach the pectoral girdle to the neurocranium. The median (dorsal) process is concave at its dorsal surface and 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 between the median and lateral processes in

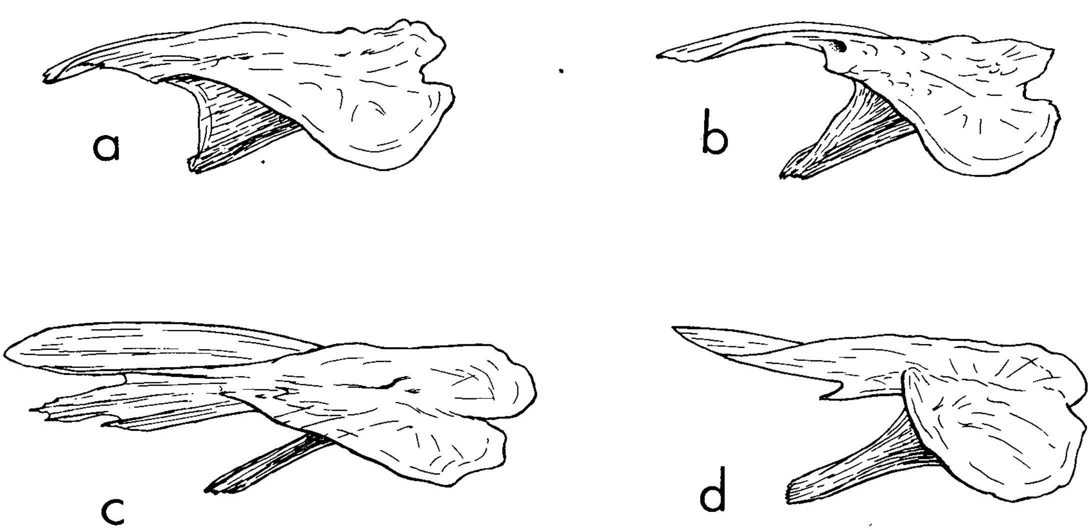


FIGURE 40.—Left posttemporals in lateral view. a. *Scomberomorus cavalla*, Chesapeake Bay, 672 mm FL, 1.5×. b. *Scomberomorus plurilineatus*, South Africa, 910 mm FL, 1×. c. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL, 1×. d. *Grammatorcynus bilineatus*, Queensland, 521 mm FL, 1.5×.

Scomberomorus (Fig. 40a, b) but this shelf is absent in *Acanthocybium* (Fig. 40c) and *Grammatorcynus* (Fig. 40d). A variably sized notch is present at the middle of the posterior edge of the flat body of the bone. *Grammatorcynus* has a prominent, 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 auxiliary 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 auxiliary process as the median process.)

The lengths of the median and lateral processes vary among the species under discussion. To compare the species quantitatively, we made two sets of measurements and divided them by the total length of the posttemporal, from the anterior tip of the median process to the posterior margin of the bone. We measured to the tips of the median and lateral processes from the most posterior point on the shelf between the two processes. Largely because of the lack of a shelf between the processes in *Acanthocybium* and *Grammatorcynus*, both processes appear to comprise a larger proportion of total posttemporal length than they do in the species of *Scomberomorus*, 53-65% vs. 36-51% for the median process and 27-40% vs. 15-36% for the lateral process. The median process is longer in *Acanthocybium* than in *Grammatorcynus*, 56-65% vs. 53-60%, but the lateral process is slightly longer in *Grammatorcynus* than in *Acanthocybium*, 35-40% vs. 27-37%. Among the species of *Scomberomorus*, the longest median processes (48-51% total length) are found in *S. commerson*, *plurilineatus*, and *sierra*; the shortest (36-40%) in *cavalla*, *semifasciatus*, and *sinensis*. The longest lateral processes are in *koreanus* (36%) and *plurilineatus* (30-31%); the shortest (15-19%) in *cavalla*, *munroi*, *niphonius*, *queenslandicus*, and *tritor*.

To eliminate the confounding factor of the shelf between the median and lateral processes, measurements also were made on the inner surface of the bone, from the point where the two processes diverge to the tips of the processes. Measured this way, the longest median processes (74-79% of total length of the posttemporal) are in *Acanthocybium* and six species of *Scomberomorus*. The shortest median processes (63-68%) are in three species of *Scomberomorus*: *multiradiatus*, *niphonius*, and *semifasciatus*. *Grammatorcynus* also has a short median process (66-71%). Measured this way, the longest lateral processes are in *koreanus* (53-55%), *sierra* (52%), *plurilineatus* and *regalis* (50-51%), *guttatus* (49-55%), and *Grammatorcynus* (48-52%). The shortest lateral processes are in *munroi* (37-40%), *tritor* (41-42%), and *cavalla* and *niphonius* (41-44%). *Acanthocybium* also has a relatively short lateral process (42-51%).

Still another way of comparing relative lengths of the processes among species is to divide the length of the lateral process by the length of the median process, both measured on the inner surface of the posttemporal. By this technique, relatively greater proportional measurements of the lateral processes are found in *S. koreanus* (75-77% of median process), *S. semifasciatus* (76%), *Grammatorcynus* (71-74%), *S. multiradiatus* (70-73%), and *S. guttatus* (69-71%). Relatively shorter proportional measurements of these lateral processes (55-63%) are found in *Acanthocybium* and five species of *Scomberomorus*: *cavalla*, *munroi*, *niphonius*, *queenslandicus*, and *tritor*.

Another difference lies in the presence and, if present, in the shape of a spine or process at the base of the lateral process on the inner surface of the posttemporal. It appears to be absent in seven species of *Scomberomorus*: *cavalla*, *guttatus*, *maculatus*, *queenslandicus*, *regalis*, *semifasciatus*, and *tritor*. It is small and inconspicuous in six species: *brasiliensis*, *concolor*, *koreanus*, *lineolatus*, *multiradiatus*, and *sierra*. It is broader, usually shaped more like a shelf with a point in the remaining five species of the genus: *commerson*, *munroi*, *niphonius*, *plurilineatus*, and sometimes in *sinensis*. The process has the form of a wide flap in *Grammatorcynus* and of a long blunt process in *Acanthocybium*. Devaraj's (1977) data for Indian species correspond well with ours.

Supracleithrum

The supracleithrum (Fig. 41) is an ovate bone, overlapped dorsolaterally by the posttemporal and overlapping the anterior part of the dorsal winglike extension of the cleithrum. The anterior border of the bone on the mesial side is thickened into a ridge. Dorsally there is a small handle-shaped process which curves into the posterior margin to end in a notch at the posterodorsal aspect. 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 42 to 75% of the total length of the bone in the three genera. The supracleithrum is widest in *Grammatorcynus* (72-75% of length), *Scomberomorus niphonius* (55-62%), and *S. lineolatus* (53-57%). It is narrowest in *S. multiradiatus* (43-53%), *sinensis* (45-46%), *semifasciatus* (46-51%), and *sierra* (45-49%). Specimen size is a factor because the smallest species of *Scomberomorus* (*S. multiradiatus*) and small specimens of large species tend to have narrower supracleithra than large species and large specimens. For example, the percentages for a series of five *S. commerson* are as follows: 354-364 mm FL, 38-43%; 493 mm, 42%; 1,052 mm, 39-44%; 1,155 mm, 47%.

The dorsal process is prominent in *Acanthocybium* (Fig. 41c), *Grammatorcynus* (Fig. 41d), *S. cavalla*, *commerson*, and *lineolatus* (Fig. 41a). It is small but distinct in *S. multiradiatus* (Fig. 41b). In most of the other species of *Scomberomorus*, it tends to be less sharply set off from the main body of the supracleithrum.

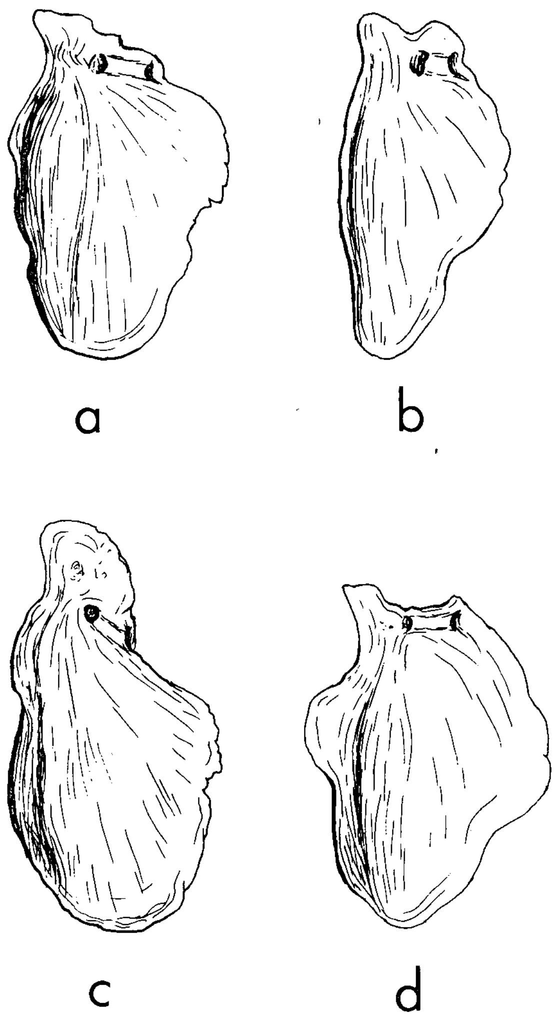


FIGURE 41.—Left supracleithra in lateral view. a. *Scomberomorus lineolatus*, Cochin, India, 786 mm FL, 1.5×. b. *Scomberomorus multiradiatus*, New Guinea, 294 mm FL, 3×. c. *Acanthocybium solandri*, Caribbean Sea, 1,240 mm FL, 1×. d. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL, 2×.

Supratemporal

The supratemporal (Fig. 42) is a thin flat triangular bone lying just underneath the skin where its lateral process articulates with a dorsal articular surface on the pterotic. Mago Leccia (1958:324) failed to find the supratemporal in his specimens. The anterior margin is concave and the convex posterior margin slightly overlaps the dorsal arm of the posttemporal. The supratemporal is deeper (from the tip of the median anterior arm to the base) than wide (tip of lateral anterior arm to tip of posterior arm), width 49-84% of depth in *Scomberomorus* and *Acanthocybium*. However, the supratemporal is wider than deep in *Grammatorcynus* (Fig. 42d), width 101-113% of length. *Acanthocybium* (Fig. 42c) has a wider supratemporal (84-93% of depth) than do the species of *Scomberomorus* (49-79%). The widest supratemporals in *Scomberomorus* are in *niphonius* (73%), *guttatus* (67-79%), *sierra* (69-74%), and *semifasciatus* (63-72%). The narrowest supratemporals are in *multiradiatus* (49-50%), *koreanus* (54%), *brasiliensis* (53-59%), *queenslandicus* (55-60%), and *sinensis* (54-62%).

The supratemporal bears a prominent lateral line canal that extends out almost to the tips of all three arms. Devaraj (1977:45) did not specifically mention the presence of this canal. In *Scomberomorus*, the canal along the anterior margin of the bone is the longest and best developed, and the canal along the lateral side the next longest. In most species of the genus, the first canal has three or four posteriorly directed branches. Specimens of *S. niphonius* and *S. semifasciatus* (Fig. 42a) had five or six branches. Two specimens of *S. multiradiatus* had only a single posterior branch. A specimen of *S. munroi* had no posterior

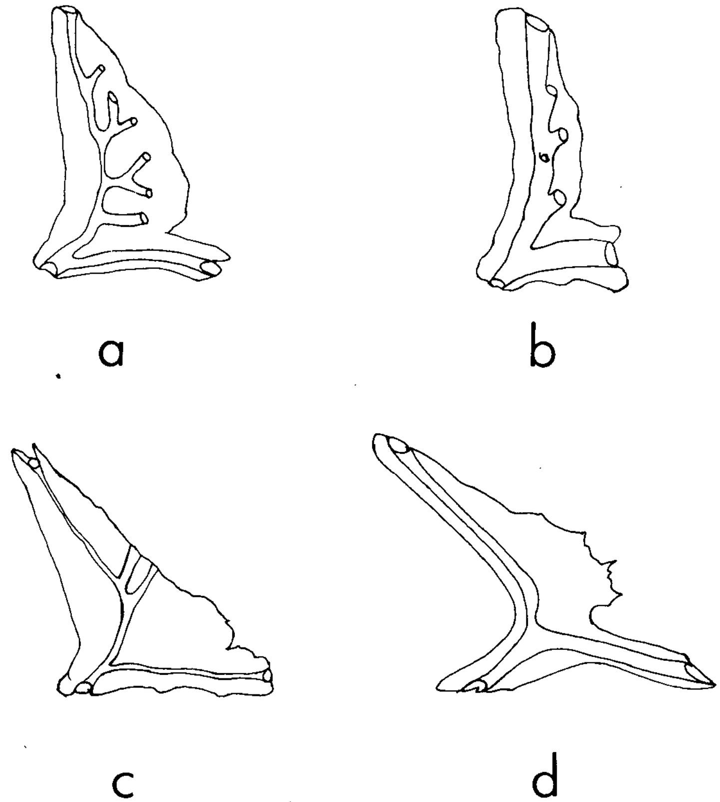


FIGURE 42.—Left supratemporals in lateral view. a. *Scomberomorus semifasciatus*, New Guinea?, 740 mm FL, 1.5×. b. *Scomberomorus multiradiatus*, New Guinea, 224 mm FL, 5×. c. *Acanthocybium solandri*, Caribbean Sea, 1,240 mm FL, 1×. d. *Grammatorcynus bilineatus*, New Guinea, 382 mm FL, 3×.

branches, but it did have four pores along the main part of the canal. *Acanthocybium* has a single short posterior branch that opens into a very large pore (Fig. 42c). *Grammatorcynus* (Fig. 42d) lacks a distinct posterior branch but has a relatively longer canal on the lateral side of the bone.

Cleithrum

The main body of the cleithrum is crescent-shaped with an anterodorsal spine and a posteriorly projecting plate at the upper end, as in other scombrids (Fig. 43). The angle between the spine and the plate is wider in *Acanthocybium* (Fig. 43c) than in *Grammatorcynus* (Fig. 43d) and the species of *Scomberomorus*. The bonitos have wider angles (Collette and Chao 1975:fig. 61), except for *Gymnosarda*. The spine extends about as far dorsally as the plate does in *Acanthocybium* and all the species of *Scomberomorus*, except *S. sinensis* in which the spine extends well past the dorsal margin of the plate. In *Grammatorcynus*, the spine does not extend all the way to the margin of the plate (Fig. 43d). The plate becomes narrower posteriorly in most species of *Scomberomorus* and in *Grammatorcynus*. The posterior plate is longer and of uniform width in *Acanthocybium* (Fig. 43c).

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. As Devaraj (1977: 46) pointed out, this slit is hidden in lateral view in the species of *Scomberomorus* by the great width of the lateral wall of the cleithrum. This portion of the cleithrum is narrower in *Acanthocybium* and *Grammatorcynus*, and consequently the upper part of the slit is visible in lateral view.

Coracoid

The coracoid is elongate and more or less triangular in shape (Fig. 43). It connects with the scapula along its dorsal edge and with the mesial shelf of the cleithrum anterodorsally and anteroventrally. There is a prominent elongate slit between the cleithrum and the coracoid that is

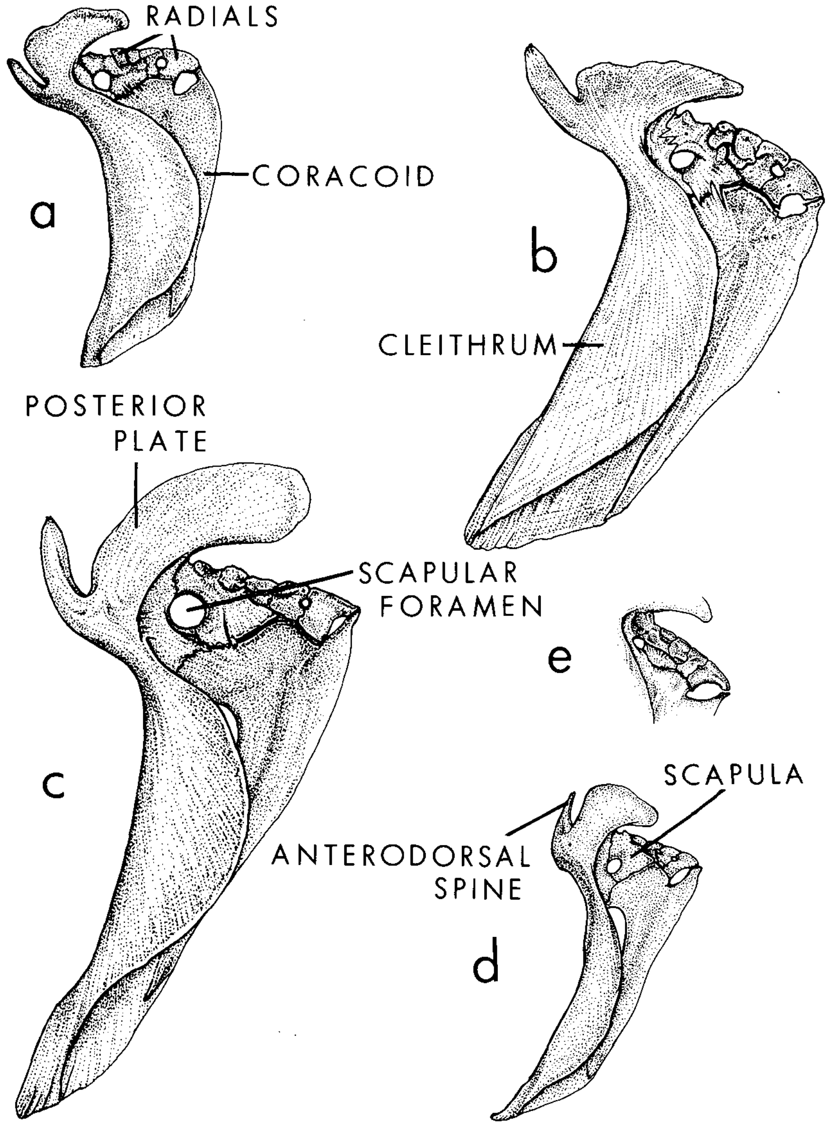


FIGURE 43.—Left pectoral girdles in lateral view. a. *Scomberomorus semifasciatus*, New Guinea, 510 mm FL. b. *Scomberomorus sinensis*, Hong Kong, 677 mm FL. c. *Acanthocybium solandri*, Revillagigedos Is., 1,086 mm FL. d. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL. e. *Scomberomorus koreanus*, Indonesia, 480 mm FL, inset of scapular and interradial foramina.

visible laterally in *Acanthocybium* and *Grammatorcynus* but is concealed by the lateral shelf of the cleithrum in *Scomberomorus.* The coracoid is relatively narrower in *Acanthocybium* than in *Grammatorcynus* and the species of *Scomberomorus.* We did not find the coracoid to be significantly narrower in *S. commerson*, as reported by Devaraj (1977:47).

Scapula

The anterior margin of the scapula connects to the mesial shelf of the cleithrum (Fig. 43). This attachment extends to the posterior projecting plate anterodorsally. The scapula is attached to the coracoid posteriorly and with the first two and part of the third upper radials posterodorsally. The posterodorsal margin of the scapula is drawn out into a facet which 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 from the scapular foramen to the ventral margin of the scapula. The foramen is largest in *Acanthocybium* (Fig. 43c), *Scomberomorus brasiliensis*, and *S. regalis*. It is smallest in *S. guttatus* and *S. niphonius*. We did not find it very large in *S. koreanus* (Fig. 43e), as stated by Devaraj (1977: 47). It is intermediate in size in *Grammatorcynus* (Fig. 43d) and the other species of *Scomberomorus* (e.g., *S. semifasciatus* and *S. sinensis*, Fig. 43a, b).

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 ranges from 19 to 26 in the three genera (Table 12). Most species of *Scomberomorus* usually have 22 or 23 rays. Five species average fewer, with a mode of 21 rays: *concolor*, *guttatus*, *maculatus*, *sierra*, and *tritor*. The two species in the genus with the most pectoral rays are *S. plurilineatus* (21-26, $\bar{x}$ 23.1) and *S. semifasciatus* (22-25, $\bar{x}$ 23.3). *Acanthocybium* and *Grammatorcynus* have slightly higher counts than do the species of *Scomberomorus*, 22-26, mostly 24 or 25.

Within the Scombridae, the number of pectoral fin rays increases from the more primitive members of the family to the more advanced: Scombrini 18-21, Scomberomorini 19-26, Sardini 21-28, Thunnini (except for *Thunnus*) 22-29, *Thunnus* 30-36.

TABLE 12.—Number of pectoral fin rays in *Acanthocybium*, *Grammatorcynus*, and the species of *Scomberomorus*.

Species	19	20	21	22	23	24	25	26	*N*	$\bar{x}$
S. brasiliensis			9	38	21	1			69	22.2
S. cavalla			6	27	18				51	22.2
S. commerson			18	52	32	8			110	22.3
S. concolor	1	8	21	4					34	20.8
S. guttatus		20	57	11	1				89	20.9
S. koreanus		1	4	13	7	3			28	22.3
S. lineolatus		4	2	6	10	3			25	22.2
S. maculatus		8	33	14	1				56	21.1
S. multiradiatus		1	10	10	6				27	21.8
S. munroi			4	4	1				9	21.7
S. niphonius			9	22	5				36	21.9
S. plurilineatus			1	9	14	5	3	1	33	23.1
S. queenslandicus			5	19	5	0	1		30	22.1
S. regalis		1	17	21	4	1			44	21.7
S. semifasciatus				4	15	13	1		33	23.3
S. sierra		16	38	17	1	1			73	21.1
S. sinensis			2	8	3				13	22.1
S. tritor		3	22	13					38	21.3
Acanthocybium				3	4	17	12	1	37	24.1
Grammatorcynus				1	8	13	17	3	42	24.3

Radials

The four radials differ in size and shape and are attached directly to the thickened posterior edges of the scapula and coracoid (Fig. 43). The size of the radials increases posteroventrally. Small foramina are located between the second and third, and the third and fourth radials counting posteriorly. In *Scomberomorus* and *Acanthocybium* (Fig. 43a-c), the first two radials and the upper third of the third radial attach to the scapula; the ventral third of the third plus the fourth radial attach to the coracoid. In *Grammatorcynus* the first two radials attach to the scapula, the second two to the coracoid (Fig. 43d). 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. The process on the fourth radial is only slightly developed in *Grammatorcynus* (Fig. 43d). The foramen is considerably larger than the scapular foramen in five species of *Scomberomorus*: *guttatus*, *koreanus* (Fig. 43e), *lineolatus*, *niphonius*, and *plurilineatus*. It is slightly larger than the scapular foramen in seven species: *commerson*, *concolor*, *maculatus*, *multiradiatus*, *munroi*, *queenslandicus*, and *tritor*. The two foramina are about equal in size in six species of *Scomberomorus* (*brasiliensis*, *cavalla*, *regalis*, *semifasciatus* (Fig. 43a), *sierra*, and *sinensis* (Fig. 43b)) and *Grammatorcynus* (Fig. 43d). The scapular foramen is much larger than the foramen following the fourth radial in *Acanthocybium* (Fig. 43c).

Postcleithra

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 (Fig. 44) is kidney-shaped with a narrow upper end, rounded lower margin, concave anterior border and convex posterior margin. In *Grammatorcynus* (Fig. 44d), the first postcleithrum is very wide and short with a notch in the dorsal margin instead of a pointed end, width/maximum length = 55-62%. It is wider (47-48%) in *Acanthocybium*

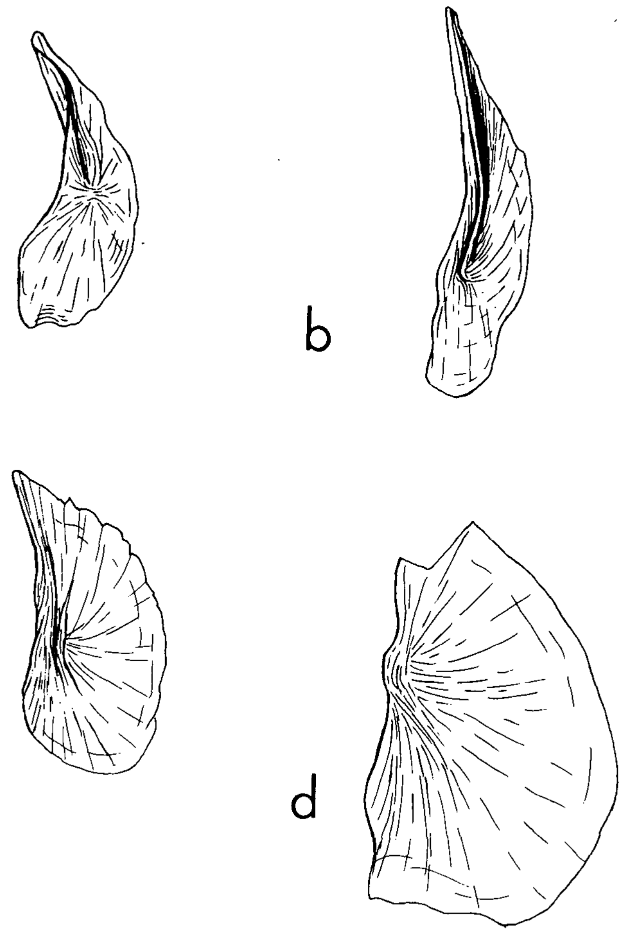


FIGURE 44.—Left first postcleithra in lateral view. a. *Scomberomorus sinensis*, Hong Kong, 677 mm FL, 1×. b. *Scomberomorus koreanus*, Indonesia, 480 mm FL, 2×. c. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL, 1×. d. *Grammatorcynus bilineatus*, Queensland, 521 mm FL, 2×.

(Fig. 44c) than in the species of *Scomberomorus* (24-41%). Three species of *Scomberomorus* have wide first postcleithra (37-41%): *commerson*, *sinensis* (Fig. 44a), and *tritor.* Three species have narrow first postcleithra: *koreanus* (24-26%, Fig. 44b), *lineolatus* (28-29%), and *guttatus* (28-31%). The other 12 species have moderately wide first postcleithra, 30-39%. Devaraj (1977:48) reported long, narrow first postcleithra in the same three species (plus *S. maculatus* and *S. regalis* from Mago Leccia's 1958 work) and wider ones in *S. commerson* and *S. cavalla.*

The second postcleithrum (Fig. 45) is broad and lamellar at the upper part with a short pointed ascending process and a long styliform descending process. *Grammatorcynus* (Fig. 45d) differs strikingly from *Acanthocybium* and *Scomberomorus* in having a sharp process extending anteriorly from the broad lamellar portion of the bone. Inclusion of this process in measurements of the width of the bone makes the second postcleithrum appear much wider in *Grammatorcynus*, 37-42% of total length compared with 16-27% in the other two genera. The widest second postcleithra in *Scomberomorus*, 22-27% of total length, are in *lineolatus*, *maculatus*, *plurilineatus*, and *queenslandicus* (Fig. 45a). The narrowest ones are in *guttatus* and *koreanus* (15-20%, Fig. 45b), and *cavalla*, *sierra*, and *sinensis* (19-20%). *Acanthocybium* (Fig. 45c) and the other nine species of *Scomberomorus* are intermediate, 20-24%. The ascending process appears longer in 6 species of *Scomberomorus* (*brasiliensis*, *cavalla*, *maculatus*, *queenslandicus*, *regalis*, and *tritor*) than in *Acanthocybium*, *Grammatorcynus*, and the other 12 species of *Scomberomorus.*

PELVIC GIRDLE

The pelvic fin rays (I, 5) attach directly to the paired basipterygia which make up the pelvic girdle. The bones are united along the midline and are imbedded in the ventral abdominal wall free from contact with any other bones. Each

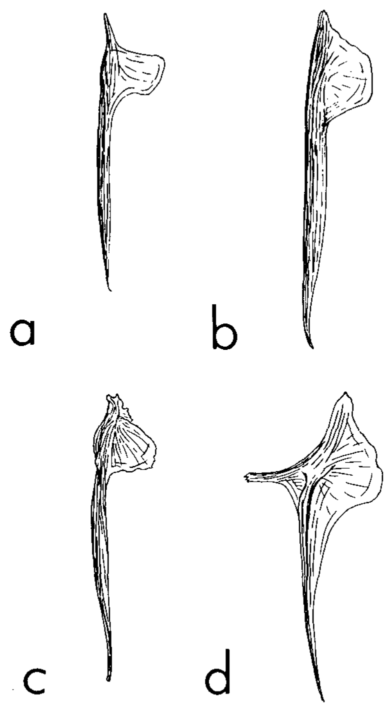


FIGURE 45.—Left second postcleithra in lateral view. a. *Scomberomorus queenslandicus*, Great Barrier Reef, 641 mm FL, 1×. b. *Scomberomorus koreanus*, Indonesia, 480 mm FL, 1.5×. c. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL, 1×. d. *Grammatorcynus bilineatus*, New Guinea, 382 mm FL, 2×.

basipterygium is composed of three main parts (Fig. 46): a wide anterodorsal plate; a thin, flat anterior process (anterior xiphoid process of de Sylva 1955, anteromesial process of Devaraj 1977); and a strong posterior process (posterior xiphoid process of de Sylva 1955). There are three wings to the anterodorsal plate (Kishinouye 1923): lateral (external), mesial (internal), and ventral (vertical). Anteriorly, the lateral wing turns into the same vertical plane and merges into the ventral wing. The mesial wing and the lateral wing meet in one plane posteriorly along a ridge.

To compare the pelvic girdles, the lengths of all three parts were measured from their bases to their tips. The anterior process comprised 15-52% of the length of the anterodorsal plate. The longest anterior processes were in *Grammatorcynus* (46-51%, Fig. 46d), *Acanthocybium* (35-47%, Fig. 46c), and seven species of *Scomberomorus*: *sierra* (38-52%), *concolor* (36-44%), *regalis* (31-44%, Fig. 46a), *semifasciatus* (35-36%), *sinensis* (35%), *tritor* (32-36%), and *maculatus* (28-36%). The shortest anterior processes were in three species of *Scomberomorus*: *koreanus* (15-30%), *multiradiatus* (21-26%), and *lineolatus* (23-33%, Fig. 46b), but there is a large range of variation within species. The posterior process comprised 20-85% of the length of the anterodorsal plate. The longest posterior processes were in four American species of *Scomberomorus*: *regalis* (78-90%), *brasiliensis* (81%), *sierra* (62-85%), and *concolor* (67-68%). The other two species that belong to this group have shorter posterior processes: *maculatus* (38-48%) and *tritor* (36-50%). The shortest posterior processes were in five

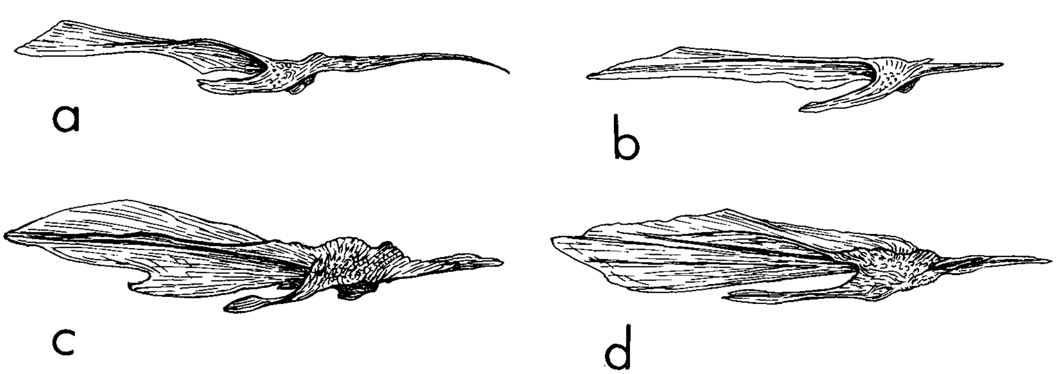


FIGURE 46.—Right basipterygia of the pelvic girdle in mesial view. a. *Scomberomorus regalis*, Miami, Fla., 469 mm FL, 1.5×. b. *Scomberomorus lineolatus*, Palk Strait, India, 428 mm FL, 2×. c. *Acanthocybium solandri*, Miami, Fla., 1,403 mm FL, 1×. d. *Grammatorcynus bilineatus*, Queensland, 521 mm FL, 1.5×.

species of *Scomberomorus*: *guttatus* (20-41%), *koreanus* (25-29%), *lineolatus* (29-35%), *multiradiatus* (27-33%), and *munroi* (28-44%), plus *Grammatorcynus* (29-33%) and *Acanthocybium* (30-39%).

Grammatorcynus and some individuals of *Acanthocybium* and at least seven species of *Scomberomorus* have longer anterior processes than posterior processes. The lengths of the anterior process as a percentage of the posterior process are *Grammatorcynus* (154-158%), *Acanthocybium* (91-156%), and the seven species of *Scomberomorus*: *sinensis* (121%), *semifasciatus* (111-116%), *munroi* (84-120%), *guttatus* (80-116%), *plurilineatus* (89-113%), *koreanus* (57-105%), and *tritor* (66-100%). The shortest anterior processes were in *brasiliensis* (42%), *concolor* (52-65%), and *sierra* (56-62%).

Devaraj (1977:48) alluded to differences in the relative depth of the anterior end of the anterodorsal plate, but we have found this very difficult to assess owing to different sizes and conditions of our material. Devaraj appears to be correct in stating that the anterior end is particularly narrow in *S. lineolatus*. The broadest anterior end is certainly in *Grammatorcynus* (Fig. 43d), which Devaraj did not study.

As Devaraj (1977:48) pointed out, a notch is present on the ventral wing of the anterolateral plate before it joins the other wings in *Acanthocybium* (Fig. 46c) but is absent in *Scomberomorus* (and also in *Grammatorcynus*).

Except for *Grammatorcynus*, no differences were found among the three genera in the fleshy bifid interpelvic process that is ventral to the paired posterior processes of the basipterygia. *Grammatorcynus* differs from *Scomberomorus* and *Acanthocybium* in having a single interpelvic process. *Auxis* and *Gymnosarda* also have a single interpelvic process, the former very large, the latter of moderate size. However, there is a posterior process from each basipterygium regardless of whether the fleshy interpelvic process is single or bifid.

SPECIES ACCOUNTS

Scomberomorus Lacepède

Scomberomorus Lacepède 1801:292 (type-species: *Scomberomorus plumierii* Lacepède 1801 by monotypy, = *Scomberomorus regalis* (Bloch 1793)).

Polipturus Rafinesque 1815:84 (replacement name for *Scomberomorus* Lacepède, therefore, takes the same type-species, *Scomberomorus plumierii* Lacepède 1801).

Cybium Cuvier 1829:199 (type-species: *Scomber commerson* Lacepède 1800 by subsequent designation of Gill 1862:126).

Apolectus Bennett 1831:146 (type-species: *Apolectus immunis* Bennett 1831 by monotypy, = *Scomberomorus tritor* (Cuvier *in* Cuvier and Valenciennes 1831)).

Apodontis Bennett 1832:169 (replacement name for *Apolectus* Bennett, preoccupied by *Apolectus* Cuvier *in* Cuvier and Valenciennes 1831, Pisces).

Chriomitra Lockington 1879a:133 (type-species: *Chriomitra concolor* Lockington 1879a by monotypy).

Sierra Fowler 1905:766 (type-species: *Cybium cavalla* Cuvier 1829 by original designation and monotypy).

Sawara Jordan and Hubbs 1925:214 (type-species: *Cybium niphonium* Cuvier *in* Cuvier and Valenciennes 1831 by original designation and monotypy).

Pseudosawara Munro 1943:68 (type-species: *Cybium kuhlii* Valenciennes 1831 by original designation, = *Scomberomorus guttatus* (Bloch and Schneider 1801)).

Indocybium Munro 1943:68-69 (type-species: *Cybium semifasciatum* Macleay 1884a by original designation).

Diagnosis.—*Scomberomorus* differs from all other scombrids in possessing a spatulate vomer that projects anteriorly well beyond the anterior margin of the neurocranium.

Scomberomorus differs from both *Acanthocybium* and *Grammatorcynus* in a series of 12 osteological characters: 1) posterior horizontal edge of metapterygoid longer than anterior oblique edge (anterior oblique edge longer in *Grammatorcynus* and *Acanthocybium*); 2) dorsal arm of ectopterygoid shorter than ventral arm (dorsal arm longer or equal); 3) lateral wall of cleithrum wide, space between cleithrum and coracoid not visible in lateral view (narrow, space visible in lateral view); 4) epiotic crests originate on anterior part of frontal bones (originate behind midfrontal region); 5) many (more than 11) vertebrae with inferior foramina (few, less than 11); 6) first basibranchial short (long); 7) strut on fourth pharyngobranchial elongate (not elongate); 8) symplectic short, not in contact with metapterygoid (long, in contact); 9) ventral hypohyal at least three times larger than dorsal hypohyal (less than three times larger); 10) fifth branchiostegal ray on suture between epihyal and ceratohyal (on epihyal); 11) no shelf present between dorsal and ventral arms of posttemporal (shelf present); and 12) epihyal much longer than deep, depth 58-62% of length (depth 66-98% of length).

In three additional characters, *Scomberomorus* differs from *Acanthocybium* and *Grammatorcynus* but is closer to the former than the latter: ventral branch of palatine equal to or longer than (87-107%) dorsal branch (slightly shorter, 112-121%, in *Acanthocybium*; much shorter, 120-123%, in *Grammatorcynus*); supratemporal much deeper than wide, 49-79% (deeper, 84-93%; wider than deep, 101-113%); and first postcleithrum very narrow, 24-41% of length (narrow, 47-48%; wide, 55-62%). *Scomberomorus* has a deep urohyal; it is moderately deep in *Grammatorcynus* and shallow in *Acanthocybium. Scomberomorus* has a moderate to high number of vertebrae (40-56) compared with other members of the family, more than *Grammatorcynus* (31), but less than *Acanthocybium* (62-64).

Scomberomorus and *Acanthocybium* agree with each other but differ from *Grammatorcynus* in a series of 16 osteological characters: 1) supracleithrum narrow, 42-62% of length (wide, 72-75% in *Grammatorcynus*); 2) pores present on dorsal arm of supratemporal (absent); 3) nasals do not protrude far beyond ethmoid region (protrude far beyond); 4) posterior end of dorsal margin of urohyal forked (tripartite); 5) glossohyal without teeth fused to bone (large tooth patch fused to bone); 6) hyomandibula wide, 36-52% of length (narrow, 35-36%); 7) angle of lateral and medial arms of fourth epibranchial less acute (more acute); 8) anterior process of second epibranchial not elongate (elongate); 9) four or five vertebrae supporting caudal fin rays (three); 10) no anterior process on second postcleithrum (prominent spinelike process present); 11) anterior end of first postcleithrum pointed (notched); 12) base of third pectoral radial on suture between coracoid and scapula (completely on coracoid); 13) jaw teeth compressed and triangular (conical); 14) ventral surface of parasphenoid convex (concave); 15) upper margin of dentary longer than lower margin (lower longer); and 16) posterior edge of ectopterygoid short, 41-63% of ventral distance (long, 64-68%).

Scomberomorus brasiliensis Collette, Russo, and Zavalla-Camin Serra Spanish Mackerel

Figure 47

Scomberomorus maculatus. Not of Mitchill 1815. Ribeiro 1915:134-135 (Brazil). Lowe 1962:679-686 (British Guiana continental shelf). Cervigón 1966:720-721 (description, fishery; Venezuela), fig. 303. Bastos 1966: 113-117 (counts and measurements). Nomura 1967:29-39 (biology; Ceará, Brazil). Mota Alves and Tomé 1968a:25-30 (sexual development). Mota Alves and Tomé 1968b:139-140 (sperm). Fonteles Filho 1968:133-137 (fishery; Ceará, Brazil). Nomura and Costa 1968:95-99 (length-weight relationship). Costa and Paiva 1969:89-95 (maximum size 125 cm FL; Ceará, Brazil). Mota Alves 1969:167-171 (digestive tract). *Menezes 1970:171-176 (food). Dahl 1971:278-279 (Colombia), photograph. Alcan-

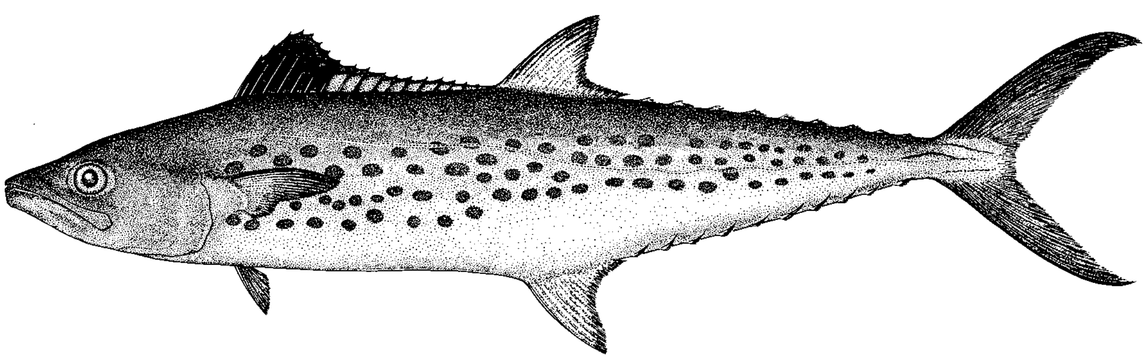


FIGURE 47.—*Scomberomorus brasiliensis*. Belém market, Brazil, 502 mm FL, USNM 217550, holotype.

tara Filho 1972a (gill net fishery; Ceará, Brazil). *Gesteira 1972:117-122 (reproduction and fecundity). Menezes 1972:86-88 (number of gill rakers). Bastos et al. 1973 (canning, Brazil). Costa and Almeida 1974:115-122 (length frequencies). Menezes 1976:45-48 (size, sex-ratio; NE Brazil). Fonteles-Filho and Alcantara-Filho 1977 (gill net mesh selectivity curve; Ceará, Brazil). *Sturm 1978:155-172 (biology, Trinidad). Ximenes 1983 (age and growth; Ceará, Brazil).

Scomberomorus brasiliensis Collette, Russo, and Zavalla-Camin 1978:273-279 (original description; Brazil). Manooch et al. 1978 (annotated bibliography). Collette 1979:29 (characters). Collette and Russo 1979:8-11 (diagnostic characters, range). Cressey et al. 1983:264 (host-parasite list, 4 copepod species). Collette and Nauen 1983:60-61 (description, range, fig.).

Types.—Holotype: USNM 217550 (502 mm FL); Belém market; 22 May 1975; B. B. Collette 1642. D XVIII + 17 + X; A 19 + IX; P_1 22; RGR_1 3 + 1 + 10 = 14; vertebrae 19 + 28 = 47. Paratypes: 103 specimens (110-630 mm FL) from 54 Brazilian collections (see Collette et al. 1978:276-278).

Diagnosis.—This species possesses nasal denticles as do the other five species of the *regalis* group (*concolor*, *maculatus*, *regalis*, *sierra*, and *tritor*), has the artery that branches from the fourth left epibranchial artery as do all the species in the group except *S. tritor*, and shares a specialization of the fourth right epibranchial artery (Fig. 7f) with *S. sierra* and *S. regalis*. In these three species an artery connects the fourth right epibranchial with a branch of the coeliaco-mesenteric artery. *Scomberomorus brasiliensis* has shorter pelvic fins than do the other members of the *regalis* group (Fig. 48), 3.6-5.9% FL compared with 4.7-6.4 in *S. sierra* and 4.4-6.3 in *S. regalis*. Together with three other species of the *regalis* group (*concolor*, *regalis*, and *sierra*), *S. brasiliensis* has a long posterior process on the pelvic girdle, 62-90% of the length of the anterior plate. Differs from *S. sierra* by essentially lacking pterotic spines. Intercalar spine absent as in the other five species of the *regalis* group and *S. niphonius*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3a). Spines in first

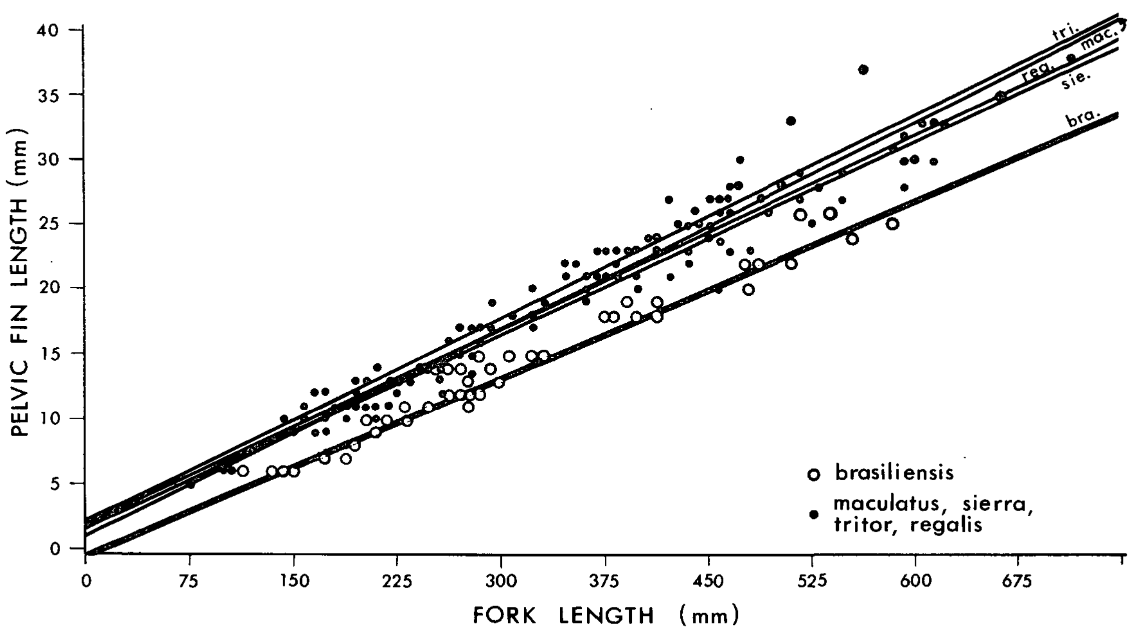


FIGURE 48.—Regression of pelvic fin length on fork length in five species of *Scomberomorus*. The regression line for *S. brasiliensis* is significantly different from those for *S. maculatus*, *S. sierra*, *S. tritor*, and *S. regalis*. The regression lines for the latter four species do not differ significantly from each other. Therefore, the same symbol is used for plotting specimens of these four species. (From Collette et al. 1978:fig. 1.)

dorsal fin 17 or 18, rarely 19 (Table 9); second dorsal fin rays 15-19, usually 17 or 18 (Table 10); finlets 8-10, usually 9 (Table 10); anal fin rays 16-20, usually 17-19 (Table 11); finlets 7-10, usually 9 (Table 11); pectoral fin rays 21-24, usually 22 or 23 (Table 12). For a sample of 90 Brazilian *S. brasiliensis*, Bastos (1966) found the following numbers of fin rays to be most common: dorsal spines 18 (86.6%), rays 18 (76.6%), finlets 9 (75.3%); anal rays 18 (100%), finlets 9 (79.8%), pectoral rays 22 (98.9%). Precaudal vertebrae 19-21, usually 20 (Table 6); caudal vertebrae 27-29, usually 28 (Table 7); total vertebrae 47-49, usually 48 (Table 8). The counts of 46 or 47 reported by Bastos (1966) presumably exclude the hypural plate which we include in our counts. Gill rakers on first arch (1-3) + (9-13) = 11-16, usually 2 + (11-12) = 13-15 (Table 5). For a large sample from Brazil (225 males, 275 females), Menezes (1972) found a similar range, 11-17, and a "typical" count of 3 + 1 + 11 = 15. Morphometric characters are given in Table 13.

Size.—Maximum size 125 cm FL (Costa and Paiva 1969, Ceará, Brazil). Of 16,170 fish measured in Ceará from 1962 to 1966, 9 exceeded 95.0 cm FL, more than 60% each year from 1962 to 1968 were in the size range 40-65 cm (Brazilian records summarized by Collette et al. 1978). Sexual maturity is reached at age III or IV, 46 cm FL in Ceará (Gesteira 1972). The shortest mature male in Trinidad was 38 cm, the shortest ripe female 45 cm (Sturm 1978). The length-weight relationship for the Brazilian population was given by Nomura (1967). Males and females grew at roughly equal rates up to 4 yr of age but then females grew faster on to age XIV (Ximenes 1983).

TABLE 13.—Summary of morphometric data of *Scomberomorus brasiliensis*. FL = fork length, HL = head length.

Character			N	Min.	Max.	Mean	SD
Fork length			69	111	710	317	136
Snout-A	‰	FL	68	508	692	538	24
Snout-2D	‰	FL	68	483	672	511	23
Snout-1D	‰	FL	68	196	337	242	20
Snout-P_2	‰	FL	69	217	359	253	22
Snout-P_1	‰	FL	69	191	317	220	20
P_1-P_2	‰	FL	68	83	159	108	11
Head length	‰	FL	69	121	309	213	22
Max. body depth	‰	FL	69	164	263	197	15
Max. body width	‰	FL	67	54	114	81	11
P_1 length	‰	FL	68	97	143	123	9
P_2 length	‰	FL	66	29	59	45	5
P_2 insertion-vent	‰	FL	66	234	349	272	18
P_2 tip-vent	‰	FL	62	193	298	226	17
Base 1D	‰	FL	68	232	360	263	18
Height 2D	‰	FL	62	92	139	118	11
Base 2D	‰	FL	69	93	153	118	10
Height anal	‰	FL	61	83	149	115	12
Base anal	‰	FL	68	97	142	113	10
Snout (fleshy)	‰	FL	69	69	120	82	8
Snout (bony)	‰	FL	65	59	102	73	7
Maxilla length	‰	FL	68	104	188	124	13
Postorbital	‰	FL	69	84	127	95	6
Orbital (fleshy)	‰	FL	69	27	57	37	6
Orbital (bony)	‰	FL	69	33	77	53	8
Interorbital	‰	FL	69	48	107	57	7
2D-caudal	‰	FL	67	427	594	490	31
Head length			69	33	140	66	25
Snout (fleshy)	‰	HL	69	354	596	386	29
Snout (bony)	‰	HL	65	300	546	344	31
Maxilla length	‰	HL	68	541	937	581	47
Postorbital	‰	HL	69	387	758	446	43
Orbit (fleshy)	‰	HL	69	136	286	175	24
Orbit (bony)	‰	HL	69	172	408	249	31
Interorbital	‰	HL	69	240	564	269	44

Color pattern.—Sides with several rows of round yellowish-bronze (in life) spots (Fig. 47) similar to *S. maculatus* and *S. sierra* but without any lines or streaks such as are present in *S. regalis*. Number of yellowish-bronze spots on sides of body increases with size of fish; young specimens (200 mm) have about 30 spots; adults more, 45 spots (422 mm), 47(455), 46(470), 45(516), and 58(530) (Collette et al. 1978). Spots arranged in three or four rows (sometimes in two rows). The rows are not very well defined but it is possible to recognize them. First dorsal fin black in the anterior half (first seven membranes), posterior half white with upper edge black. Pectoral fin dusky; pelvic and anal fins white.

There is a black and white photograph of a specimen from Colombia in Dahl (1971:278) and a drawing of a Venezuelan specimen in Cervigón (1966:fig. 303).

Biology.—No extensive migrations are known for *S. brasiliensis*, and it is available to the fishery in northeastern Brazil all year round. There does appear to be some seasonal movement around Trinidad (Sturm 1978). There is a spawning peak in the Gulf of Paria, Venezuela, in October-April followed by a postspawning feeding migration away from Venezuela with a period of maximum abundance in Trinidad waters May-September. Some spawning takes place in the Gulf of Paria throughout the year with a peak in October-April (Sturm 1978). Ripe fish are taken on the Guyana continental shelf in September (Lowe 1962). Spawning takes place all year round off northeastern Brazil with a peak in the third trimester, July-September (Gesteira 1972). Spawning probably takes place mostly offshore beyond the main fishing areas. There appear to be no references to eggs or larvae of *S. brasiliensis*. As with other species in the genus, food consists largely of fishes with smaller quantities of penaeoid shrimps and loliginid cephalopods. The most important component of the food of 1,020 individuals (17.5-87.5 cm FL) from northeastern Brazil was the thread herring, *Opisthonema oglinum*, (more than 25%) followed by Engraulidae, Carangidae, Hemiramphidae, and Pomadasyidae (Menezes 1970).

Interest to fisheries.—This is an important food fish throughout its range—Colombia (Dahl 1971), Venezuela (Cervigón 1966), Trinidad (Sturm 1978), the Guianas (Gines and Cervigón 1968), and especially in northeastern Brazil. The fishery is concentrated in June-August in Trinidad (Sturm 1978) but is conducted year round in northeastern Brazil (Alcantara Filho 1972a). The fishing grounds are 5-16 mi offshore in Brazil (Fonteles Filho 1968; Alcantara Filho 1972a). Most of the catch previously reported as *S. maculatus* from Fishing Area 31 (Western Central Atlantic) for Colombia, Trinidad and Tobago, and Venezuela is *S. brasiliensis* as is also a large proportion of the Brazilian catch of *Scomberomorus* spp. In Trinidad, it is taken by drift gill nets that are fished overnight and with beach seines (Sturm 1978). There are two major fisheries in Brazil. One employs gill nets (rede-de-pesca) from wooden boats not over 10 m long powered by gasoline engines (Fonteles Filho 1968; Alcantara Filho 1972a). The other method is trolling from rafts (Fonteles Filho 1968; Costa and Almeida 1974). Most of the catch is consumed fresh, but in Brazil some has been salted (Paiva and Costa 1966) and some has been canned (Bastos et al. 1973).

Distribution.—Caribbean and Atlantic coasts of Central and South America from Belize at least as far south as Lagoa Tramandai, Rio Grande do Sul, Brazil (Fig. 49). Previously confused with, but not known to overlap the range of, *S. maculatus* which occurs in the Gulf of Mexico and along the Atlantic coast of the United States. Replaced in the West Indies by *S. regalis*.

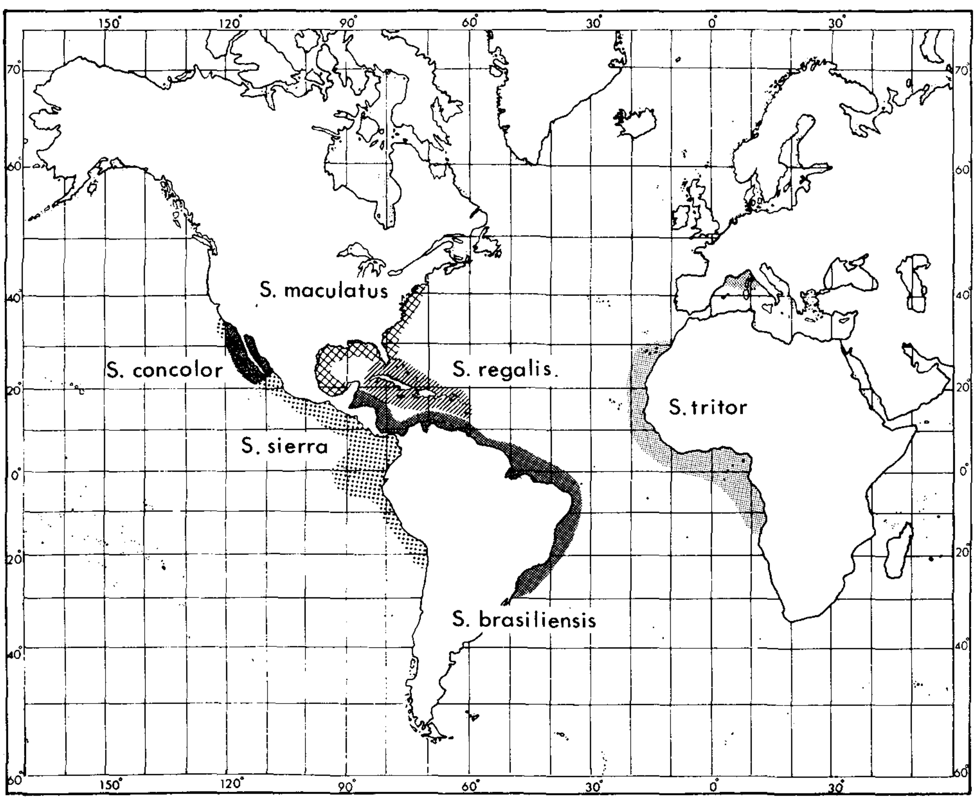


FIGURE 49.—Ranges of the *regalis*-group of *Scomberomorus*: *S. tritor*, *S. maculatus*, *S. regalis*, *S. brasiliensis*, *S. sierra*, and *S. concolor.* (Range of *S. regalis* more extensive, see text.)

Geographic variation.—Morphometric data from two populations of *S. brasiliensis* were compared by ANCOVA: Central America (n = 9-11) and Brazil (n = 39-44). Null hypotheses that the 2 sets of regressions are coincident were accepted for 24 of 26 regressions. The two populations were different in Sn-P_2 and 2D-C. Comparison of meristic characters for central and northern South America versus Brazil did not reveal any differences (Collette et al. 1978:tables 1-3).

Material examined.—Total 146 (89-710 mm FL).

meas.: 69 (111-710): Belize (2); Honduras (1); Costa Rica (3); Panama (5); Colombia (1); Venezuela (3); Trinidad (2); Guyana (2); Surinam (4); French Guiana (2); Brazil (44, **S. brasiliensis*).
counts: 146.
diss.: 6 (363-639): French Guiana (2); Belem, Brazil (4).

Scomberomorus cavalla (Cuvier)
King Mackerel
Figure 50

Guarapucu. Marcgrave 1648:178 (Brazil).
Cybium cavalla Cuvier 1829:200 (original description after Marcgrave's Guarapucu; Brazil).
Cybium caballa. Cuvier *in* Cuvier and Valenciennes 1831:187-190 (description; Brazil, West Indies). Günther 1860:373 (synonymy, description; West Indies). Poey 1865:322 (Brazil, Puerto Rico; *C. caballa* is the juvenile of *C. acervum*). Poey 1875:147 (description; Cuba). Poey 1878:3-4 (synonymy, characters).
Cybium immaculatum Cuvier *in* Cuvier and Valenciennes 1831:191 (original description, no locality). Günther 1860:370. Poey 1878:5 (after Cuvier).
Cybium acervum Cuvier *in* Cuvier and Valenciennes 1831:186 (original description, Martinique, Santo Domingo, Cuba). Poey 1865: 322 (Cuba; color pattern of juveniles). Poey 1868:362 (description; Cuba). Poey 1875:147 (after Cuvier *in* Cuvier and Valenciennes 1831). Poey 1878:4 (unable to find this species in Cuba).
?*Cybium clupeoidum* Cuvier *in* Cuvier and Valenciennes 1831:178 (original description, "Île de Norfolk, Nouvelle Hollande").
Scomberomorus caballa. Jordan and Gilbert 1882:427 (synonymy, range). Goode 1884:316 (range, size), pl. 94.
Scomberomorus cavalla. Meek and Newland 1884:233, 235 (description, synonymy, range). Dresslar and Fesler 1889:442 (in key), 444-445 (synonymy, range), pl. 11 (specimen from Woods Hole). Jordan and Evermann 1896b: 875-876 (description, synonymy). Evermann and Marsh 1902:124 (description, synonymy; Puerto Rico). Jordan and Evermann 1902: 287-288 (description, range), photograph. Bean 1903:400-401 (synonymy, description, range). Fowler 1905:766-767 (placed in new subgenus *Sierra*; description, Santo Domingo and St. Martins). Smith 1907:193-194 (diagnosis, range; few or no records from North Carolina). Sumner et al. 1913:750 (references, occurrence; Menemsha Bight and Quisset Harbor, Mass.). Ribeiro 1915:135-136 (description; range S to Angra dos Reis, Brazil). Meek and Hildebrand 1923:322-323 (description, synonymy). Schroeder 1924:7 (maximum weight 75 lb; Fla. Keys), fig. 5. Nichols and Breder 1927: 124 (description, range), fig. 172. Nichols 1929:230-231 (range, description), fig. 84. Beebe and Hollister 1935:213 (Union I., Grenadines). Baughman 1941:16-17 (Texas records). Munro 1943:69, 71-72 (placed in subgenus *Sierra*). La Monte 1945:26 (description, range),

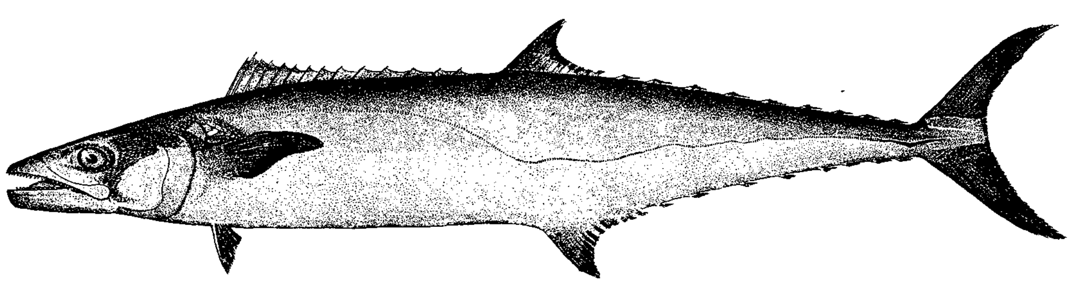


FIGURE 50.—*Scomberomorus cavalla*. Woods Hole, Mass., 1,000 mm FL, USNM 19418. (From Goode 1884:pl. 94.)

color pl. 11. Breder 1948:127 (range), fig. Erdman 1949:301 (West Indies). Fraser-Brunner 1950:160-161 (range), fig. 33. Baughman 1950: 243-244 (previous Texas records). Knapp 1950:141-142 (food in Texas, shrimps, squids, fishes). Rivas 1951:224-225 (synonymy, diagnosis, range). Taylor 1951:270 (popular anglers' fish taken by trolling; North Carolina). La Monte 1952:50 (description, range). Bigelow and Schroeder 1953:349 (description, range; Gulf of Maine record, N Truro, Cape Cod), fig. 184. Pew 1954:26 (description, range, habits), fig. 22. Mather 1954:292 (13 specimens, about 70 cm FL, in trap; Quisset, Mass.). Mather and Gibbs 1957:243 (9 specimens, 600-700 mm FL; Buzzards Bay, Mass.). Briggs 1958:287 (range). *Mago Leccia 1958 (osteology, comparisons with *S. maculatus* and *S. regalis*), figs. Butz and Mansueti 1962:130-135 (description; N Chesapeake Bay; comparison with specimens from Mass. and Fla.), fig. 2 (head). Moe 1963:108-109 (most sought fish in Fla. charter boat fishery). Collette 1966:365-367 (types of *C. acervum* and *C. immaculatum*; both names synonyms of *S. cavalla*). Nomura and Costa 1966:11-13 (length-weight of 666 specimens; Ceará, Brazil). Cervigón 1966:718-719 (description; Venezuela). Randall 1967:753-754 (food of 22 West Indian specimens, 92.3% fishes). Nomura and Rodriguez 1967:79-85 (age and growth, condition factor, 1,504 specimens, 30-120 cm FL; Ceará, Brazil), fig. 1 (sagitta). Mota Alves and Tomé 1967a:103-108 (anatomy and histology of the digestive tract), figs. 1, 2 (arrangement of viscera), figs. 3-7 (histology of gut). Mota Alves and Tomé 1967b:1-9 (histology of gonads), figs. 1-11 (photomicrographs). Mota Alves and Tomé 1967c: 173-175 (anatomy and histology of the liver and gall bladder). Mota Alves and Tomé 1968c: 31-32 (sperm). Fonteles Filho 1968 (fishery; NE Brazil). Nomura and Costa 1968:95-99 (length-weight relationship, 104 males and 90 females; Ceará, Brazil). Randall 1968:119 (description, range, habits), fig. 136. Lyles 1969: 16-21 (summary of U.S. landings, 1880-1967). Menezes 1969a:15-20 (food of 798 specimens; Ceará, Brazil; fishes compose main diet). Menezes 1969b:175-178 (meristic characters, osteology; NE Brazil). Mota Alves and Tomé 1970:181-184 (histology and enzymes of pyloric caeca). Beardsley and Richards 1970:5 (length-weight of 197 specimens, 585-1,500 mm FL, 1.47-32.09 kg; Florida). Wollam 1970 (development, pigmentation, counts, and measurements; 49 larvae and juveniles (3.3-31.0 mm SL), figs. 4, 5, 6B (larvae and juveniles, 3.3-23 mm SL)). Dahl 1971:277 (uncommon in Colombia), fig. Ivo 1972:27-29 (gonadal stages of 4,346 females; Ceará, Brazil). Moe 1972:16-17 (migrations; Florida). Alcantara Filho 1972b (gill net and trolling fisheries; NE Brazil). Richards and Klawe 1972:13 (range), 89 (reference to Wollam 1970). Miyake and Hayasi 1972:III:3 (in key), IV:11 (common names). Dwinell and Futch 1973 (139 larvae and juveniles, 2.8-13.5 mm SL, all months; NE Gulf of Mexico). Bastos et al. 1973 (canning; NE Brazil). *Beaumariage 1973 (age, growth, food, reproduction; Florida). Ivo 1974 (fecundity; Ceará, Brazil). Berrien and Finan 1977a (species synopsis). Erdmann 1977:150 (in spawning condition mainly in July and Aug.; NE Caribbean). Klawe 1977:2 (common name, range). DeVane 1978 (stomach contents; North Carolina). Fritzsche 1978:121-125 (description, larval development), figs. 66-69 (larvae). Collette 1978: Scombm 4 (description, range), figs. Manooch et al. 1978 (annotated bibliography). Lima and Oliveira 1978:6, 23 (common name "cavalla" in Brazil). Collette 1979:29 (characters, range). Collette and Russo 1979:9 (diagnostic characters, range). Manooch 1979 (commercial U.S. catches averaged 2,541 t/yr over last 17 yr, recreational catch statistics are inadequate). Meaburn 1979 (heavy metal contamination). McEachran et al. 1980 (larvae off Texas coast). Fischer 1980:1-21 (size, length-weight, sex ratio; Louisiana). Sutherland and Fable 1980 (annual migration from S Florida N to NE Gulf of Mexico and W to S Texas in the spring). MacGregor et al. 1981 (significant correlation found between gonadosomatic indices and serum estrogens in females and with serum androgens in males). Fable et al. 1981 (temperature effects on catches; NW Florida). Lubbock and Edwards 1981:150 (Saint Paul's Rocks). Richardson and McEachran 1981 (larvae 2.0-2.9 mm SL, pigment characters, measurements; Gulf of Mexico), fig. 2A (2.3 mm larva). Naughton and Saloman 1981 (stomach contents of 139 juveniles, 103-309 mm FL; Cape Canaveral, Fla.; diet mainly clupeoids). Sacchi et al. 1981:3 (French Antilles). Trent et al. 1981 (size composition and sex ratio; SE U.S.). Ximenes et al. 1981 (age and growth; NE Brazil). Morgan and King 1983 (tooth replacement). Johnson et al. 1983 (age, growth, and mortality; SE U.S.). Cressey et al. 1983:264 (host-parasite list, 4 copepod species). Collette and Nauen 1983:61-62 (description, range), fig. Saloman and Naughton 1983a (food in SE U.S.).

Types of nominal species.—*Cybium cavalla* Cuvier, 1829 is based on Marcgrave's description and figure (1648:179) of the "Guarapucu"; there are no extant types for this name.

Cybium acervum Cuvier *in* Cuvier and Valenciennes, 1831. Lectotype: MNHN A.5781; Santo Domingo; Ricord; 130 mm FL; selected by Collette (1966:365); D XV+17+VIII; A 18+VIII; RGR_1 1+1+7=9; vertebrae 17+25=42; upper jaw teeth 8-11; lower jaw teeth 7-8. Paralectotypes: MNHN B.2508, out of A.5781; Santo Domingo; Ricord; 2(133-138 mm FL). A photograph of one of the syntypes was published by Blanc and Bauchot (1964: pl. 1, fig. 1, upper fig.).

Cybium immaculatum Cuvier *in* Cuvier and Valenciennes, 1831. Lectotype: MNHN A.5720; Martinique; Plée; 157 mm FL; selected by Collette (1966:366); D XV+17+IX; A 17+IX; P_1 23; RGR_1 1+1+7=9; vertebrae 17+25=42; upper jaw teeth 9-11; lower jaw teeth 9-12. Paralectotypes: MNHN B.2509; out of A.5720; Martinique; Plée; 147 mm FL; and MNHN A.5780; Martinique; Plée; 164 mm FL. Photographs of two of the syntypes were published by Blanc and Bauchot (1964:pl. 2, fig. 12).

Cybium clupeoidum Cuvier *in* Cuvier and Valenciennes, 1831. Holotype: MNHN A.5784; "Île de Norfolk, à l'oeust de la Nouvelle-Hollande"; Broussonet collection; 302 mm FL; D XV+17+IX; A 18+VIII; RGR_1 1+1+7=9; vertebrae 17+25=42; upper jaw teeth 13-13; lower jaw teeth 11-12. A photograph of the type was published by Blanc and Bauchot (1964:pl. 1, fig. 3). The high gill raker count and low vertebral number show the type to be a specimen of the western Atlantic *S. cavalla* as supposed by Bauchot and Blanc (1961) and Blanc and Bauchot (1964) rather than *S. commerson* as presumed by Collette (1966) based on geography. The locality has been supported by Bauchot (1969), but the data or the specimen must have been mixed with the western Atlantic species sometime in the past.

Diagnosis.—This species shares with *S. commerson* an abrupt downward curve in the lateral line under the second dorsal fin (Fig. 50). *Scomberomorus sinensis* also has an abrupt downward curve in the lateral line under the first dorsal fin but the lateral line gradually descends in the other 15 species. *Scomberomorus cavalla* differs from *S. commerson* in having fewer vertebrae (41-43, usually 42 or fewer compared with 42-46, usually 43 or more) and more gill rakers (7-13, usually 8 or more compared with 1-8, usually 7 or fewer). Ventral process of angular moderate, 87-93% of dorsal process as in *S. sinensis*. Ascending process of premaxilla short as in *S. guttatus*. Anterior ends of pterosphenoid close together as in *S. commerson*. Intercalar spine well developed as in *S. commerson* and *S. queenslandicus*.

Description.—Intestine with two folds and three limbs (Fig. 3b). Spines in first dorsal fin 12-18, usually 15 (Table 9); second dorsal fin rays 15-18, usually 17 or 18 (Table 10); dorsal finlets 7-10, usually 9 (Table 10); anal fin rays 16-20, usually 18 or 19 (Table 11); anal finlets 7-10, usually 8 (Table 11); pectoral fin rays 21-23, usually 22 or 23 (Table 12). Precaudal vertebrae 16 or 17, usually 17 (Table 6); caudal vertebrae 24-26, usually 25 (Table 7); total vertebrae 41-43, usually 42 (Table 8). Gill rakers on first arch (1-2)+(6-11)=7-13, usually 1+(8-9)=9-10 (Table 5). Counts for a large Brazilian sample (353 individuals, Menezes 1969b), were (0-2)+1+(5-9)=6-11, usually 1+1+7=9. Morphometric characters are given in Table 14.

Size.—Maximum size 172.5 cm FL (female, 37.2 kg; Beaumariage 1973); common to 70 cm. The all-tackle angling record is a 40.8 kg fish taken off Key West, Fla., in 1976. In Florida, females usually mature in their fourth summer at a mean length of 83.7 cm, males in the third summer at 73 cm (Beaumariage 1973). In Brazil, females mature at age V-VI, about 77 cm according to Ivo (1972), at age IV and 63 cm according to Gesteira and Mesquita (1976). Males and females grow at roughly equal rates up to age V but then females grow faster (Ximenes et al. 1981). They reach an age of at least XIV (Ximenes et al. 1981; Johnson et al. 1983). Length-weight relationships have been published for Brazil (Nomura and Costa 1968; Ximenes et al. 1981), Florida (Beaumariage 1973), and Louisiana (Fischer 1980).

Color pattern.—Adults have plain silvery sides without bars or spots, juveniles have bronze spots smaller than the pupil of the eye in five or six irregular rows (Randall 1968:119). Adults have no

TABLE 14.—Summary of morphometric data of *Scomberomorus cavalla*. FL = fork length, HL = head length.

		United States					West Indies					South America					Total				
Character		*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD
Fork length		10	560	1,160	769	179	20	126	710	323	209	23	147	860	326	183	54	126	1,160	405	257
Snout-A	‰ FL	10	510	562	535	15	20	519	582	547	23	23	463	568	533	21	54	463	582	539	21
Snout-2D	‰ FL	10	474	521	499	14	20	486	534	512	12	23	430	524	504	18	54	430	534	505	16
Snout-1D	‰ FL	10	225	266	241	11	20	247	297	268	13	23	210	273	256	15	54	210	297	258	16
Snout-P_2	‰ FL	8	223	260	236	11	20	239	290	266	14	23	205	293	256	21	52	205	293	257	20
Snout-P_1	‰ FL	10	199	241	212	12	20	212	260	243	14	23	194	252	231	14	54	194	260	232	17
P_1-P_2	‰ FL	5	86	103	93	7	13	91	136	107	15	22	73	135	107	15	41	73	136	105	15
Head length	‰ FL	10	192	229	203	10	20	206	250	231	13	23	177	246	224	17	54	177	250	223	17
Max. body depth	‰ FL	7	149	173	159	10	10	153	258	198	37	22	147	237	197	25	40	147	258	190	30
Max. body width	‰ FL	8	95	109	102	5	11	78	101	89	9	21	70	126	85	13	41	70	126	89	12
P_1 length	‰ FL	10	114	138	124	7	15	108	143	129	12	23	111	142	130	7	49	108	143	129	9
P_2 length	‰ FL	10	53	62	58	3	12	54	95	68	10	21	36	85	66	12	44	36	95	64	11
P_2 insertion-vent	‰ FL	8	264	294	281	9	15	245	309	277	17	22	211	298	266	18	46	211	309	272	18
P_2 tip-vent	‰ FL	8	205	237	222	11	12	187	236	214	14	21	162	289	208	26	42	162	289	212	21
Base 1D	‰ FL	9	221	255	242	11	19	224	267	246	11	23	207	269	247	14	52	207	269	245	13
Height 2D	‰ FL	9	85	108	95	7	14	76	127	108	13	20	79	128	114	12	44	76	128	108	13
Base 2D	‰ FL	10	78	103	93	7	14	82	124	105	12	23	81	135	112	15	48	78	135	106	14
Height anal	‰ FL	8	89	102	95	5	11	81	122	107	12	17	89	127	110	9	37	81	127	105	11
Base anal	‰ FL	10	87	111	98	9	17	92	123	107	10	23	83	129	112	12	51	83	129	108	12
Snout (fleshy)	‰ FL	10	74	103	84	8	17	83	98	89	4	23	72	92	86	5	51	72	103	87	6
Snout (bony)	‰ FL	10	68	96	78	8	17	73	86	81	4	22	68	85	78	4	50	68	96	79	5
Maxilla length	‰ FL	10	108	137	117	8	20	120	152	138	9	23	103	147	132	11	54	103	152	132	12
Postorbital	‰ FL	7	86	99	92	4	17	89	112	99	6	23	81	104	98	6	48	81	112	98	6
Orbital (fleshy)	‰ FL	10	24	43	30	5	17	33	58	41	8	23	27	54	39	6	51	24	58	38	7
Orbital (bony)	‰ FL	10	28	48	41	6	17	42	73	55	10	23	38	65	52	6	51	28	73	51	9
Interorbital	‰ FL	10	52	68	55	4	20	56	66	62	3	23	48	66	60	5	54	48	68	60	4
2D-caudal	‰ FL	7	485	527	506	13	13	452	500	473	14	23	445	516	472	18	44	445	527	477	20
Head length		10	112	266	158	45	20	32	151	72	44	24	36	152	73	35	55	32	266	88	51
Snout (fleshy)	‰ HL	10	362	451	415	25	17	350	424	391	25	24	354	422	384	17	52	350	451	392	24
Snout (bony)	‰ HL	10	355	417	384	20	17	305	388	353	27	23	318	388	351	19	51	305	417	358	26
Maxilla length	‰ HL	10	546	604	576	18	20	577	613	598	10	24	570	609	590	10	55	546	613	591	14
Postorbital	‰ HL	7	428	485	453	22	17	408	463	434	16	24	395	463	437	16	49	395	485	439	18
Orbit (fleshy)	‰ HL	10	123	210	147	24	17	152	233	176	24	24	147	220	171	18	52	123	233	168	24
Orbit (bony)	‰ HL	10	138	238	204	28	17	191	305	237	31	24	201	265	231	15	52	138	305	229	27
Interorbital	‰ HL	10	256	295	272	11	20	248	284	267	10	24	254	281	269	7	55	248	295	269	9

black area in the anterior part of the first dorsal fin as do many species of *Scomberomorus*.

Black and white photographs are given by Jordan and Evermann (1902) and Randall (1968: fig. 136). The drawing published by Goode (1884: pl. 94) is included here as Figure 50.

Biology.—A summary of biological information has been presented by Berrien and Finan (1977a) and there is also a useful annotated bibliography by Manooch et al. (1978). King mackerel appear to be present all year in Louisiana (Fischer 1980) and in the state of Ceará in northeastern Brazil. Some populations appear to be resident in south Florida waters as they are available to the recreational fishery throughout the year. However, the large schools that are found in south Florida waters during January and February move north along both coasts in the spring (Moe 1972). Schools that occur offshore of Palm Beach and Martin Counties on the east coast of Florida in winter and early spring move north. They appear off North Carolina in April and remain until fall (DeVane 1978). On the west coast of Florida, king mackerel move north to the Naples-Ft. Myers or St. Petersburg-Tampa areas by April and Cape San Blas in May (Sutherland and Fable 1980). The main run usually arrives in Panama City, Fla., in late May or early June. The westward migration along the northern Gulf of Mexico ends off west Texas in June-July (Sutherland and Fable 1980). Return migration in the fall from summer feeding grounds in the northwest Gulf to winter feeding grounds off southern Florida has been confirmed by recaptured tagged fish (Sutherland and Fable 1980). Based on gonad development and larval distribution, spawning takes place in the northeastern Gulf of Mexico and in the Atlantic offshore of Cape Kennedy, Fla., and northward in late summer (Moe 1972). According to Beaumariage (1973), spawning in Florida may be protracted as indicated by successive increase in vitellogenic oocyte size during the summer. Spawning takes place in May-September in the western Gulf of Mexico, especially in September in waters 35-183 m deep over the middle and outer continental shelf (McEachran et al. 1980). In the northeastern Caribbean, spawning peaked in July and August (Erdman 1977). Spawning is year round offshore of Ceará, northeastern Brazil (Ivo 1972). Larvae and juveniles (139 specimens, 2.8-28.8 mm SL) were taken off the northwest coast of Florida from June to October with larvae <3.1 mm taken in June, August, and September (Dwinell and Futch 1973). Most of these larvae and juveniles were taken in surface plankton tows at surface temperatures of 26.3°-31.0°C and salinities of 26.92-35.0‰. Larvae were taken in increasing numbers from May to September (35% or more of larvae in September of each year) in the western Gulf of Mexico, particularly over the middle and outer continental shelf (McEachran et al. 1980). Larvae and juveniles have been described and illustrated by Wollam (1970; 3 figures, 3.3-23 mm SL), Fritzsche (1978; 12 figures, 2.98-17 mm), and Richardson and McEachran (1981, 2.3 mm SL). As with other members of the genus, food consists primarily of fishes with smaller quantities of penaeoid shrimps and squids (Knapp 1950, Texas; Randall 1967, Caribbean; Menezes 1969a, northeastern Brazil; Beaumariage 1973, Florida; DeVane 1978, North Carolina; Saloman and Naughton 1983a, United States). Clupeids such as *Opisthonema*, *Harengula*, *Sardinella*, and *Brevoortia* are particularly important (Randall 1967; Menezes 1969a; Beaumariage 1973; DeVane 1978; Saloman and Naughton 1983a), even in juveniles 103-309 mm FL (Naughton and Saloman 1981). Other fishes commonly consumed include Carangidae (particularly *Decapterus*), Lutjanidae, Pomadasyidae, and Hemiramphidae (Randall 1967; Menezes 1969a; Beaumariage 1973; Saloman and Naughton 1983a).

Interest to fisheries.—The king mackerel is an important species for recreational, commercial, or artisanal fisheries throughout its range from southeastern United States to northeastern Brazil. North of southern Florida, the fishery is concentrated in the summer months. In North Carolina, sport fishing is carried out from April to December (DeVane 1978) but is concentrated in spring and fall (Taylor 1951). In the Panama City area of the Florida panhandle, fish are taken from April to November and are most often caught in August and September (Fable et al. 1981). From December to March the fishery along the east coast of Florida is concentrated from Jupiter Inlet to Palm Beach Inlet, the rest of the year the fishery is further north from Ft. Pierce to Sebastian Inlet (Beaumariage 1973). There is a winter commercial fishery in the Florida Keys (Beaumariage 1973). King mackerel are taken all year in Louisiana with a maximum in November-January (Fischer 1980). King mackerel is the main species of commercial interest along the coast of northeastern Brazil where they are taken all year (Nomura and Rodrigues 1967). The main fishing grounds in northeastern Brazil are 6-16 nmi from the coastline (Fonteles Filho 1968). An historical summary of the fishery in the United States has been presented by Lyles (1969). Commercial catches in the United States have averaged 2,541 t a year with a value of $1.3 million over 17 yr with a peak in 1974 of 4,764 t (Manooch 1979). The bulk of these landings were made in Florida by hook and line and gill net fisheries (Manooch 1979). Data on the large recreational catch are inadequate. The catch reported from Fishing Area 31 (Western Central Atlantic) totalled 7,122 t in 1982 (FAO 1984) but is higher than this because much of the catch of 1,105 tons of unclassified *Scomberomorus* species is *S. cavalla* (or *S. regalis*). It is fished for with hook and line in all the southeastern United States (Trent et al. 1981). In addition, there is a commercial fishery using snapper hooks and line in Mississippi, a commercial gill net fishery in southern Florida, and commercial hook and line fisheries in North Carolina and southern Florida (Trent et al. 1981). The gill net fishery has employed power block retrieval since 1963 and aerial spotting is sometimes used (Beaumariage 1973). The king mackerel is the staple of the charter boat industry in Florida and is the most sought fish by private boats (Moe 1963). In Florida it is most often fished at the surface with trolled lure or small bait fish (Moe 1963). It is less commonly caught than is *S. brasiliensis* across the northern coast of South America (Dahl 1971; Cervigón 1966; Gines and Cervigón 1968). Both gill nets and trolling are used in northeastern Brazil, the former catching 87.6% II-IV yr fish and the latter 78.2% IV-VI yr fishes (Alcantara Filho 1972b). The Brazilian fishery is also carried out from rafts with hooks baited with thread herring (Fonteles Filho 1968). Most of the catch is processed into steaks or sold fresh (Lyles 1969), but it has been canned (Bastos et al. 1973) and salted (Paiva and Costa 1966) in northeastern Brazil.

Distribution.—Western Atlantic Ocean from Massachusetts to Rio de Janeiro, Brazil (Fig. 51). There are several summer records from the southern side of Cape Cod (Dresslar and Fesler 1889; Sumner et al. 1913; Mather 1954; Mather and Gibbs 1957) but only one stray is known to have moved around to the north side of Cape Cod, to North Truro in the Gulf of Maine (Bigelow and

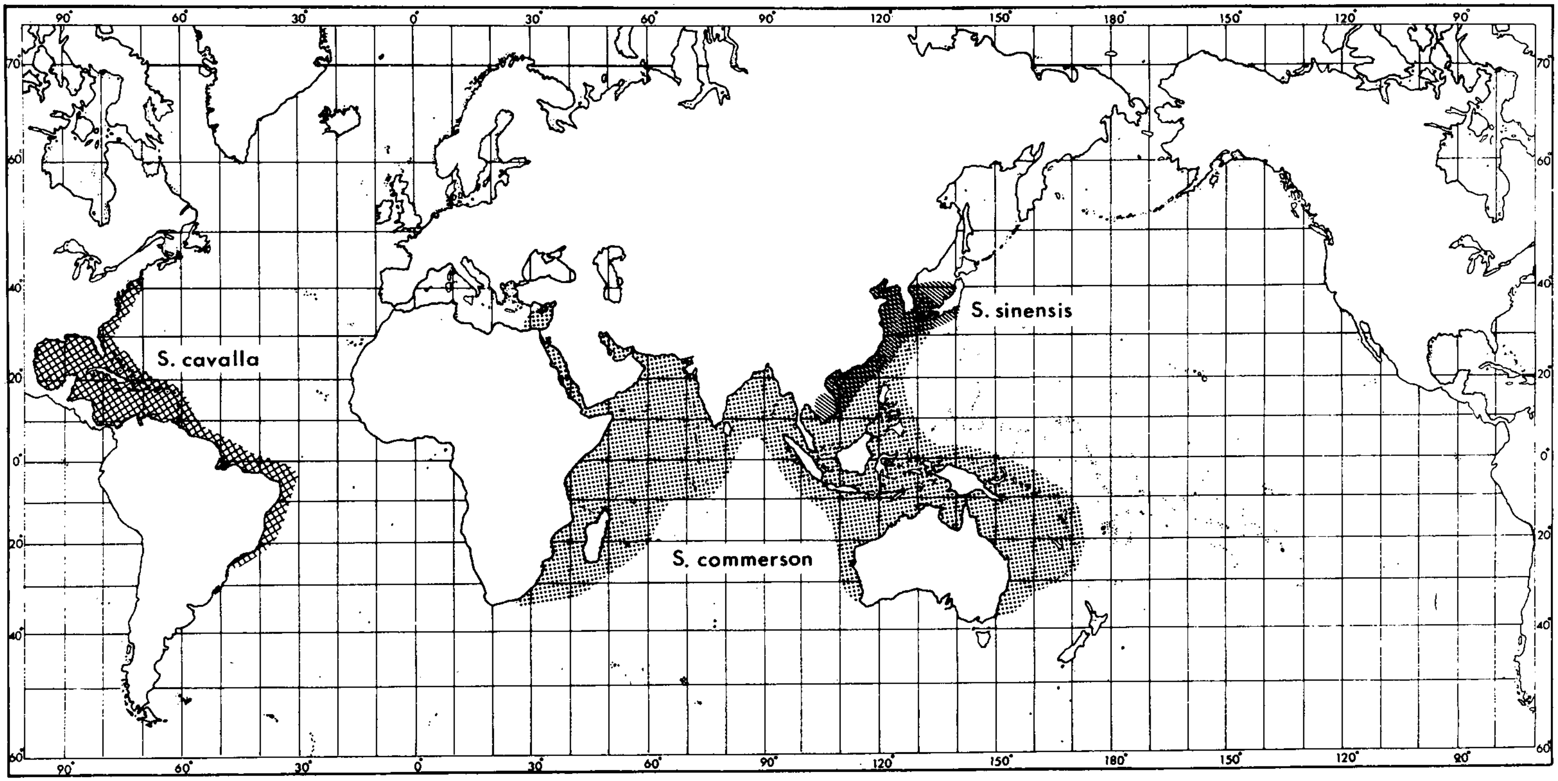


FIGURE 51.—Ranges of *Scomberomorus cavalla*, *S. commerson*, and *S. sinensis*.

Schroeder 1953:349; MCZ 37041, 560 mm FL). Abundant in the West Indies. The range extends south to at least Rio de Janeiro (Angra dos Reis, Ribeiro 1915; Rio de Janeiro, MCZ 17269, BMNH 1903.6.9.79).

Geographic variation.—Samples were adequate to compare the morphometric data of three populations of *S. cavalla* by ANCOVA (Table 14): United States (n = 7-10), West Indies (n = 11-20), and South America (n = 17-23). Null hypotheses that the 3 sets of regressions are coincident were accepted for only 10 of 26 regressions, rejected for the other 16. For 12 regressions (Sn-A, Sn-2D, Sn-1D, Sn-P_2, Sn-P_1, P_1-P_2, Hd L, Sn (fleshy and bony), maxilla L, postorbital, and interorbital), all three populations were significantly different from each other by the Newman-Keuls Multiple Range Test. For these 12 regressions, there is a cline from the United States to the West Indies to South America, a decreasing cline in slopes. The United States and West Indies populations differed in one additional regression (2D-C) and the South America and the West Indies populations differed in two additional regressions (maximum depth and Ht 2D). No meristic differences were found between the three populations, all usually had 15 spines in the first dorsal fin, 9 or 10 gill rakers on the first arch, and 42 vertebrae.

Material examined.—Total 76 (126-1,160 mm FL).

meas.:	54 (126-1,160): E United States (3); Fla. (7); Veracruz (1); West Indies (20) (**C. acervum* Cuvier, **C. immaculatum* Cuvier), Trinidad (3); Guyana (10); Suriname (3); Brazil (7).
counts:	76.
diss.:	7 (557-909): Chesapeake Bay (1); Miami (4); Panama City, Fla. (2).

Scomberomorus commerson (Lacepède) Narrow-Barred King Mackerel

Figure 52

Scomber commerson Lacepède 1800:598, 600-603 (original description after a figure from Commerson's manuscripts), pl. 20, fig. 1.

Scomber Konam Russell 1803:27-28 (description; Vizigapatam, Coromandel coast of India), pl. 135.

Scomber Commersonii. Shaw 1803:589 (description after Lacepède), pl. 85 (bottom fig.).

Scomber Maculosus Shaw 1803:592 (original description based on the Konam of Russell 1803, pl. 135).

Cybium Commerson(i)(ii). Cuvier 1829:200 (listed in footnote after *Sc. Commersonii* Lacepède). Cuvier *in* Cuvier and Valenciennes 1831:165-170 (description, earlier references; Pondichery and Malabar, India; Mauritius). Richardson 1846:268 (range, references). Bleeker 1853:42 (Malabar and Pondichery, India; Mauritius, Red Sea, China). Günther 1860:370 (synonymy, description; Malayan Peninsula and Cape Seas). Playfair and Günther 1866:67 (Zanzibar and E coast of Africa). Klunzinger 1871:494-495 (description, range). Bleeker 1873:131 (China, listed). Bleeker 1874:100 (Mauritius, listed). Day 1878:255-256 (synonymy, description, range), pl. 56, fig. 5. Bleeker 1879:18 (Mauritius, listed). Castelnau 1879:352 (Port Jackson, Australia; listed). Kent 1893:229 (Great Barrier Reef, Australia), pl. 46, fig. 1. Kishinouye 1923:416-418 (synonymy, *C. multifasciatum* Kishinouye a synonym of *C. commerson*; description, anatomy; Japan, Taiwan, and S China), pl. 22, fig. 36 (adult). Reeves 1927:8 (NE China and Korea; listed). Umali 1936:98-99 (food fish; Philippine Is.), fig. 59. Umali 1938:182 (fishery;

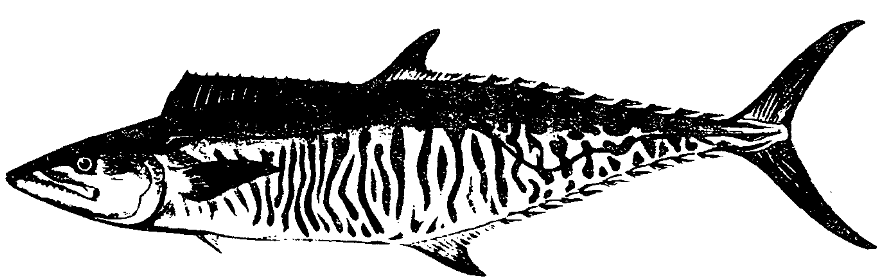


FIGURE 52.—*Scomberomorus commerson.* Queensland, 968 mm FL. (From Munro 1943:pl. 6B.)

Ragay Gulf, Luzon, Philippine Is.). Domantay 1940:379 (important species; Margosatubig, Zamboanga, Philippine Is.). Chevey and Durand 1945:27 (description, food fish; Indochina), fig. Chacko 1949:89 (stomach contents of 12 specimens, 21-43 cm FL; Gulf of Mannar, India; mostly clupeoids such as *Stolephorus* and *Dussumiera*). Chacko 1950:171 (characters of eggs and larvae; Krusadai I., Gulf of Mannar, India). Mori 1952:136 (Fusan, Korea; listed). La Monte 1952:51 (description, range), color pl. 19. Gopalan Nayar 1958:49-51 (fishery; Vizhingam, S India). Munro 1958b:262-263 (many records; New Guinea region). Fourmanoir and Crosnier 1964:386-387 (found along the entire coast of Madagascar; one of most important food fishes; occasional in lagoon at Mayotte, Comores Is.). Chacko et al. 1967:1007-1008 (drift net fishery; Madras State).

Cybium Konam Bleeker 1851a:357 (original description, Batavia). Bleeker 1852:39-40 (description; Batavia). Bleeker 1853:42 (Coromandel, India; East Indies). Kner 1865:144 (description; Manila).

Scomberomorus commerson(*i*)(*ii*). Jordan and Seale 1906:228 (New Guinea, East Indies; listed). Jordan and Seale 1907:13 (description; Cavite, Luzon, Philippine Is.). Jordan and Dickerson 1908:610 (Suva market; Fiji). Fowler 1918:63 (Philippine Is.; listed). Whitley 1927:5 (Fiji; listed). Herre 1931:33 (Philippine localities). Whitley 1932:289 (Snapper I., Great Barrier Reef). Herre 1933:7 (Dumaguete, Philippine Is.; listed). Hardenberg 1936: 252 (mouth of Kapuas R., W Borneo). *Munro 1942:33-48 (spawning, eggs, early larvae; N Queensland), pls. 2-4, figs. 1-17 (eggs and early larvae). *Munro 1943:67, 71-72 (placed in subgenus *Cybium*), 74-82 (description, anatomy, synonymy, occurrence in Australia); pl. 6, fig. B (968 mm Fl specimen; Queensland); fig. 2.4 (viscera); pl. 8, fig. 3 (368 mm FL immature specimen; N Queensland). Chapman 1946:169 (off New Caledonia). Herre and Umali 1948 (common names in several languages and dialects; Philippine Is.). Barnard 1948:380 (49-in, 24-lb specimen; False Bay, South Africa). Norman and Fraser 1949:153-154 (range). Fraser-Brunner 1950:161 (synonymy, range), fig. 34. Umali 1950:9 (found throughout the Philippines in open sea, bays, and gulfs). Warfel and Manacop 1950:42 (in otter-trawl catches; Philippine Is.). Warfel 1950:2 (regularly found in fresh fish market, Philippine Is.). Herre 1953:245-246 (synonymy; Philippine records). Ommanney 1953:66 (off Marie Louise I., S Amirante Is.). Devanesen and Chidambaram 1953:32-36 (names, description, fishery, economic importance), fig. 34. Tham 1953:49 (Singapore Straits). Fowler 1959:167 (description, synonymy, locality records; Suva, Fiji), 583 (additional references). Jones et al. 1960: 136 (Andaman-Nicobar Is. waters). Jones 1962:113-117 (larvae and juveniles; S Kerala, India), figs. 9-14 (postlarvae and juveniles 14.4-278 mm). Bauchot and Blanc 1961:370 (description of "neosyntypes"). Kaikini 1961:357 (largest species in the seerfish fishery at Malwan, India, reaching 17.24 kg). Venkataraman 1961:292 (teleosts in stomachs of 2 specimens; Calicut, India). Kumaran 1964:586-587 (stomach contents 283 specimens, 17-225 mm FL; Vizhingam, W coast of India; 79% small fishes, 43% *Anchoviella*). Baissac 1964:186 (now scarce in Mascarene waters). Boeseman 1964:467 (types of *C. konam* = *S. commersonii*), pl. 4, fig. 16 (lectotype of *S. konam*). Blanc and Bauchot 1964:444-445 ("neosyntypes" of *C. commersonii*), pl. 1-2, figs. 4-7. Gorbunova 1965a:53 (spawning season). George and Athanassiou 1965:1-4 (St. George Bay, Lebanon; first Mediterranean records; description), fig. 1 (49.0 and 60.3 cm TL specimens). Collette 1966:369 (Bauchot and Blanc's "neosyntypes" invalid). Kamohara 1967:44 (description; Japan), color pl. 22, fig. 4. George and Athanassiou 1967:238 (listed among species entering the Mediterranean through the Suez Canal). Anonymous 1967:46 (off NW coast of Borneo). Maugé 1967:120 (listed from Smith's Fishes of South Africa). Arnoult and Fourmanoir 1967:134, 139 (juveniles in mangrove swamp; Nossi-Bé, Madagascar). Ben-Tuvia 1968:35 (commercially important fish; several caught trolling in Dahlak Archipelago; many from coast of Ethiopia, common in Eilat). Ben-Yami 1968:37 (caught by trolling and purse seine; Ethiopia). Wongratana 1968 (trawl survey; Thailand). Silas 1967:1096 (leaping out of the water; Gulf of Mannar), 1,113-1,115 (length-weight). Merçeron 1970:72-81 (length-weight, maturity, food mostly anchovies, movements; Cambodia). *Tongyai 1970 (distribution, peak fishing months, migrations, food, fishery; Thailand). Collette 1970:3, 5 (Mediterranean coast of Israel). *Prado 1970:91-116 (synonymy; description; biology, length-frequency, food, sex ratio, reproduction; Madagascar). Ben-Tuvia 1971: 20-21 (3 specimens from Mediterranean coast of Israel). Tongyai 1971a:9-13 (description), pl. II (photograph), pl. III (viscera). Tongyai 1971b:3 (economically important; Thailand), pl. 7, 8, 10, 13 (photographs). Dhawan et al. 1972: 183 (trolling line operations; Goa; feed on sardines). Nagabhushanam and Chandrasekhara Rao 1972:303 (Minimoy Atoll, Laccadive Archipelago). Shiino 1972:71 (common name). Richards and Klawe 1972:13 (range), 90-91 (references to eggs, larvae, and juveniles). Magnuson 1973:350 (short pectoral fin). Orsi 1974: 175 (Vietnam; listed). Ronquillo 1974 (caught by light fishing; Philippine Is.). Lewis et al. 1974:82-85 (93 specimens, 53.7-144.5 cm FL; ova diameters, maturity of ovaries; Bismark Archipelago, Papua New Guinea). Van der Elst 1976:25 (important predator on *Pomatomus saltatrix*; Natal, South Africa). Baissac 1976:216 (Mauritius). *Devaraj 1977 (osteology). Klawe 1977:2 (common names, range). Randall et al. 1978:166 (Persian Gulf: photograph), 212 (color photograph 56). Uchida 1978:13, 17, 20 (fishery resource; Cook Is., New Caledonia; Wallis and Futuna Is.). Collette 1979:29 (characters, range). Collette and Russo 1979:9, 13 (diagnostic characters, range). Golani and Kredo 1981:41 (fishery; Mediterranean coast of Israel). Hutchins 1979:83 (Rottnest I., off Perth, W. Australia). Joubert 1981: 5 (minor component of shore angler's catch; Natal, South Africa). McPherson 1981 (biology, migrations; Queensland). Van der Elst 1981:274 (photograph, description, natural history, range). Kyushin et al. 1982:227 (description, photograph). *Devaraj 1982 (age and growth). Sivasubramaniam and Mohamed 1982:65 (Qatar, Persian Gulf). Lewis and Endean 1983 (presence of a ciguatoxin-like substance in Queensland specimens caught between lat. 24°S and 26°S). Lewis et al. 1983: 14-21 (biology; Fiji). Cressey et al. 1983:264 (host-parasite list, 10 copepod species). Lee and Yang 1983:229-230 (Taiwan), fig. 19 (580 mm FL). Collette and Nauen 1983:63-64 (description, range), fig. Jenkins et al. 1984:348-351 (62 larvae, 3.5-9.3 mm SL; off Townsville, Qld.), fig. 3 (6 larvae, 3.7-9.1 mm SL).

Cybium multifasciatum Kishinouye 1915:9 (original description; Yamaguchi Prefecture, Japan), pl. 1, fig. 3.

Scomberomorus konam. Herre 1953:246 (synonymy).

Types of nominal species.—*Scomber commerson* Lacepède, 1800 is based on a figure from Commerson's manuscript; no types of this name are extant.

Scomber Maculosus Shaw 1803 is based on the "konam" of Russell (1803:pl. 135); no types of this name are extant.

Cybium konam Bleeker 1851b. Lectotype: RMNH 6051; Batavia; P. Bleeker; 444 mm FL; selected by Boeseman (1964:467); D XVII+18+VIII; A 18+IX; P_1 22-22; RGR_1 0+1+2=3; upper jaw teeth 15-16; lower jaw teeth 15-12. A photograph of the lectotype was published by Boeseman (1964:pl. 4, fig. 16). Paralectotypes: RMNH 24087; 12 specimens; in part. The original description was based on 12 specimens 90 to 490 lines (= mm) long from Batavia. Boeseman (1964) found more than 12 specimens in RMNH 6051, selected the largest specimen as lectotype, removed 2 specimens that were below the minimum size of the type-series, and recatalogued the remainder of the material as RMNH 24087.

Cybium multifasciatum Kishinouye 1915. The original description was based on a specimen from Yamaguchi Prefecture, Japan in 1914 and is probably no longer extant. Data from the original description show this name to be a junior synonym of *S. commerson*: D XVII+15+IX; A 14+IX; GR 1+2=3; vertebrae 20+24=44; and lateral line forming a deep bend. The author himself (Kishinouye 1923:416) subsequently placed *multifasciatum* in synonymy.

Diagnosis.—This species shares with *S. cavalla* an abrupt downward curve in the lateral line under the second dorsal fin (Fig. 52). One species, *S. sinensis*, has an abrupt downward curve in the lateral line under the first dorsal fin but the lateral line descends gradually in the other 15 species. It differs from *S. cavalla* in having more vertebrae (42-46, usually 43 or more compared with 41-43, usually 42 or fewer) and fewer gill rakers (1-8, usually 7 or fewer compared with 7-13, usually 8 or more). Posterodorsal spine of hyomandibula large as in *S. queenslandicus* and *Acanthocybium*. Palatine tooth patch very narrow (Fig. 23b) as in *S. sinensis* and *Acanthocybium*. Ventral process of angular long, 117-126% of dorsal process, as in *S. queenslandicus* and *Acanthocybium*. Anterior ends of pterosphenoid close together (Fig. 17a) as in *S. cavalla*. Intercalar spine well developed (Fig. 11a) as in *S. cavalla* and *S. queenslandicus*.

Description.—Intestine with two folds and three limbs (Fig. 3c). Spines in first dorsal fin 15-18, usually 17 (Table 9); second dorsal fin rays 15-20, usually 17 or 18 (Table 10); dorsal finlets 8-11, usually 9 or 10 (Table 10); anal fin rays 16-21, usually 18 or 19 (Table 11); anal finlets 7-12, usually 9 or 10 (Table 11); pectoral fin rays 21-24, usually 22 or 23 (Table 12). Precaudal vertebrae 19 or 20, usually 20 (Table 6); caudal vertebrae 23-27, usually 24 or 25 (Table 7); total vertebrae 42-46, usually 44 or 45 (Table 8). Gill rakers on first arch (0-2)+(1-8)=1-8, usually (0-1)+(3-4)=3-5 (Table 5). Morphometric characters given in Table 15.

Size.—Maximum size 230 cm FL and 59 kg; commonly 60-120 cm (Lewis 1981). The all-tackle angling record is a 44.9 kg fish taken at Scottburgh, Natal, South Africa, in 1982. Sexual maturity is attained at a length of 70-80 cm FL in Madagascar (Prado 1970), Papua New Guinea (Lewis et al. 1974), and Fiji (Lewis et al. 1983), but not until 90-100 cm in South Africa (van der Elst 1981). Females attain larger sizes than males (Prado 1970; Lewis et al. 1974, 1983).

Color pattern.—Munro (1943:75) presented a good description of Australian specimens. Sides pale silver gray marked with transverse vertical bars of a darker gray. Bars narrow and slightly wavy, sometimes breaking up into spots ventrally. Bars number 40-50 in adults but are usually fewer than 20 in juveniles up to 450 mm FL. Munro reported the cranial regions and upper regions of the back to be mottled with iridescent blue and green. Cheeks, lower jaw, and belly silvery white. First dorsal fin bright blue rapidly fading to blackish blue. Pectoral fin light grey turning to blackish blue. Caudal fin lobes, second dorsal, anal, and dorsal and anal finlets pale grayish white turning to dark gray. Juveniles have the anterior membranes of the first dorsal jet black contrasting with pure white posteriorly (Munro 1943:pl. 8, fig. 3).

There is an excellent illustration of an adult *S. commerson* from Japan in Kishinouye (1923:pl. 22), of an adult (968 mm FL, here reproduced as Figure 52), and a juvenile (368 mm) from Australia in Munro (1943), and of an adult from India in Jones and Silas (1962:fig. 2). There are color paintings in La Monte (1952:pl. 19) and Grant (1982:627) and color photographs of a specimen

TABLE 15.—Summary of morphometric data of *Scomberomorus commerson*. FL = fork length, HL = head length.

			Red Sea					Indian Ocean					East Indies					Total				
Character			*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD
Fork length			12	266	854	346	162	34	180	1,085	443	275	22	94	628	234	132	119	94	1,155	403	247
Snout-A	‰	FL	12	530	559	549	8	33	426	575	535	26	22	521	635	563	26	117	426	635	543	23
Snout-2D	‰	FL	12	491	525	506	8	34	405	538	501	22	22	500	545	522	13	118	405	625	509	20
Snout-1D	‰	FL	12	233	255	245	8	34	188	261	237	17	22	231	273	258	12	118	188	273	243	16
Snout-P_2	‰	FL	12	247	269	259	6	33	201	321	256	21	22	229	299	269	18	117	201	321	257	18
Snout-P_1	‰	FL	12	228	258	243	8	34	185	260	233	18	22	226	274	254	13	118	185	274	238	17
P_1-P_2	‰	FL	12	89	103	96	4	31	70	105	90	8	22	83	119	99	10	112	70	123	96	9
Head length	‰	FL	12	218	239	230	6	34	177	251	226	18	22	215	261	240	12	119	177	261	229	15
Max. body depth	‰	FL	12	174	202	188	9	32	141	215	177	15	22	165	234	193	19	115	141	235	187	18
Max. body width	‰	FL	12	76	99	87	6	31	74	118	95	10	22	64	142	85	17	109	64	142	93	12
P_1 length	‰	FL	11	118	148	124	8	33	103	137	124	7	22	86	135	108	11	114	86	153	122	12
P_2 length	‰	FL	12	47	67	57	5	33	46	71	56	6	22	38	127	61	16	115	38	127	56	10
P_2 insertion-vent	‰	FL	12	264	285	275	7	33	207	386	270	27	22	269	320	288	14	117	207	386	273	19
P_2 tip-vent	‰	FL	12	203	233	220	10	33	170	238	210	15	22	209	278	231	17	115	170	278	217	16
Base 1D	‰	FL	12	248	276	261	7	33	210	286	257	14	22	243	285	265	11	117	210	286	261	13
Height 2D	‰	FL	12	98	125	108	7	31	91	119	104	8	21	76	108	91	9	102	76	135	103	11
Base 2D	‰	FL	12	87	123	104	14	33	81	130	99	11	22	78	171	106	18	117	78	171	104	14
Height anal	‰	FL	11	90	117	100	7	32	89	120	102	8	21	70	114	91	12	103	70	128	100	10
Base anal	‰	FL	12	89	108	98	6	33	81	113	97	8	22	80	119	98	10	116	80	164	100	11
Snout (fleshy)	‰	FL	12	80	91	88	3	33	66	99	88	7	22	84	100	93	5	117	66	100	89	6
Snout (bony)	‰	FL	12	72	82	77	3	33	61	136	82	12	22	77	91	84	4	117	61	136	81	7
Maxilla length	‰	FL	12	119	137	130	5	32	101	147	129	13	22	115	163	142	13	117	101	163	131	13
Postorbital	‰	FL	12	100	111	104	3	33	81	119	104	9	21	98	109	104	3	114	81	119	104	6
Orbital (fleshy)	‰	FL	12	28	38	34	3	32	21	47	33	6	22	28	50	40	6	115	21	50	34	6
Orbital (bony)	‰	FL	12	35	53	48	5	33	31	81	48	10	22	38	64	54	7	116	31	81	49	8
Interorbital	‰	FL	12	59	66	63	2	33	47	66	60	5	22	58	69	64	3	115	47	71	62	4
2D-caudal	‰	FL	12	458	520	474	20	33	380	540	491	31	21	420	489	454	18	109	380	540	480	27
Head length			12	61	186	79	34	34	41	214	96	50	22	24	135	55	28	119	24	242	89	48
Snout (fleshy)	‰	HL	12	351	402	381	14	33	326	408	388	15	22	356	412	389	12	117	326	424	390	15
Snout (bony)	‰	HL	12	324	372	338	14	33	333	571	362	39	22	329	371	349	10	117	316	571	354	25
Maxilla length	‰	HL	12	548	596	566	13	32	518	610	569	20	22	533	651	593	29	117	518	651	570	23
Postorbital	‰	HL	12	436	483	455	15	33	418	496	461	18	21	397	497	436	22	114	397	504	455	21
Orbit (fleshy)	‰	HL	12	128	167	147	10	32	111	189	144	17	22	129	200	166	18	115	101	224	147	21
Orbit (bony)	‰	HL	12	161	232	209	18	33	155	352	210	35	22	179	256	223	22	116	147	352	211	28
Interorbital	‰	HL	12	256	303	275	12	33	245	286	265	8	22	246	289	266	11	115	245	316	270	12

from Kuwait in Kuronuma and Abe (1972:pl. 17), a Japanese specimen in Masuda et al. (1975:79), a Persian Gulf specimen in Randall et al. (1978: 212), a South African specimen in van der Elst (1981:274), a Queensland specimen in Grant (1982:pl. 325), and a 344 mm specimen from the South China Sea in Kyushin et al. (1982:248).

Biology.—Adults frequently undertake lengthy seasonal longshore migrations (Lewis 1981). Migrations occur along the entire eastern coast of Queensland (McPherson 1981). Tongyai (1970:fig. 4) has mapped the migration route in the Gulf of Thailand; from the Cambodian border in October to the northernmost part of the Gulf of Thailand in December to February, then south along the west coast of the gulf in April. At least some individuals are present year round in some areas, e.g., Cambodia (Merçeron 1970) and East Africa (Williams 1964). Spawning apparently occurs over a long period in some regions, e.g., October to July in East Africa (Williams 1964), July to December in Papua New Guinea (Lewis et al. 1974). Spawning times have been reported as spring in Taiwan (Kishinouye 1923), October-December on the Great Barrier Reef (Munro 1942), October to February, peaking in December and January in Fiji (Lewis et al. 1983), May to July in the coastal waters of Madras State (Chacko et al. 1967), and December-February in Madagascar (Fourmanoir and Crosnier 1964). Munro (1942) described and illustrated the development of artificially fertilized eggs and early larvae from the Great Barrier Reef. Jones (1962) described and illustrated five postlarvae and juveniles (14.4-54.4 mm) from Vizhingam along the coast of southern Kerala taken in shore seines from February to June. The most complete larval description is by Jenkins et al. (1984) of 62 larvae (3.5-9.3 mm SL) from the shelf waters of the Barrier Reef. Tongyai (1970) reported that juveniles 100-450 mm were taken in waters of high turbidity and salinity in the Gulf of Thailand. Juveniles were caught with dip nets in Papua New Guinea waters in July, October, November, and December (Lewis et al. 1974). Like other species of the genus, *S. commerson* feeds primarily on small fishes particularly anchovies such as *Anchoviella* and *Stolephorus* and clupeids such as *Sardinella* (South Africa—van der Elst 1981; Madagascar—Prado 1970; Madras—Chacko et al. 1967; Waltair, east coast of India—Rao 1964; Vizhingam, southern India—Kumaran 1964; Gulf of Manaar—Chacko 1949; and Cambodia—Merçeron 1970). Other food items mentioned by these authors include small carangids, *Leiognathus*, squids such as *Loligo*, and penaeoid shrimps. Feeding apparently takes place day and night (Tongyai 1970).

Interest to fisheries.—This species is taken throughout its range by commercial, artisanal, and recreational fisheries. Although it may be present the year round, e.g., in the coastal water of Madras State (Chacko et al. 1967), fisheries are usually concentrated in some seasons, particularly those with the best weather conditions for fishing. Peak fishing seasons in some areas are as follows: Taiwan—spring (Kishinouye 1923); Great Barrier Reef—August to September (Grant 1978); Cambodia—the dry season, October to April (Merçeron 1970); Gulf of Thailand—October to May (Tongyai 1970); Waltair, northeastern India—March-April, June-July, and December (Venkata Subba Rao et al. 1981); Vizhingam, southeastern India—September to April (Gopalan Nayar 1958); and Malwan, south of Bombay—February to March and October to December (Kaikini 1961). There are important fisheries in Fishing Areas 51, 57, and 71. The total catch fluctuated between 63,290 and 79,047 t/yr in 1979-82 (FAO 1984). The five countries with the largest reported catch in this period were Indonesia, Philippines, Sri Lanka, Yemen, and Pakistan. The landings in Queensland were around 1,000 tons/yr during the mid-1970's but have dropped to 730-770 tons in 1978-80 (McPherson 1981). The 1982 catch in Fiji probably exceeded 300 tons (Lewis et al. 1983). There is also an important drift net fishery in India, but the catch is not identified to species in the statistics. Drift nets (gill nets) that are usually fished over night appear to be the most important gear used for *S. commerson* in Thailand, Malaysia, and India (Tongyai 1970; Pathansali 1968; Kaikini 1961; Chacko et al. 1967, respectively); other gear includes shore seines in Taiwan and India (Kishinouye 1923; Gopalan Nayar 1958), trolling lines in Taiwan, Malaysia, India, and East Africa (Kishinouye 1923; Pathansali 1968; Dhawan et al. 1972; Williams 1964, respectively). Hand lines (bett-tok) baited with mackerel (*Rastrelliger*) or squid (*Loligo*) and trotlines (bett-laak) with spoons are also employed in the Gulf of Thailand (Tongyai 1970). It is taken fairly commonly in the inshore fishery along the Mediterranean coast of Israel with trammel nets and occasionally with purse seines (A. Ben-Tuvia[3]). The yearly catch will be about 20 t out of the 2,000 t taken in the inshore fisheries according to A. Ben-Tuvia and D. Golani.[4] It is a highly regarded species that commands a good price in the Philippine Islands, Thailand, India, Madagascar, and East Africa (Warfel 1950; Tongyai 1971b; Devanesen and Chidambaram 1953; Fourmanoir and Crosnier 1964; Williams 1964, respectively). It is a prime target of the Natal ski-boat fishermen and is pursued by sport and commercial anglers in South Africa, using lures, feathers, clupeids, and anchovies as bait (van der Elst 1981). It is marketed fresh, on ice, or salted and dried (Gopalan Nayar 1958; Fourmanoir and Crosnier 1964; Williams 1964; Tongyai 1971b; McPherson 1981). A lipid-soluble toxin similar to ciguatoxin has been found in the flesh of *S. commerson* between lat. 24° S and 26° S along the east coast of Queensland (Lewis and Endean 1983). From 1976 to 1980, at least 38 toxic *S. commerson*, resulting in 217 poisonings, came from this area.

Distribution.—Widespread throughout the Indo-West Pacific from South Africa and the Red Sea east through the Indo-Australian Archipelago to Australia and Fiji and north to Hong Kong, Formosa, and Japan (Fig. 51). The northernmost record is from the northern coast of Yamaguchi Prefecture, southern Honshu, on the Sea of Japan (Kishinouye 1923:417). Its range extends farther out into the Pacific islands than any of the other species of *Scomberomorus*, throughout the Philippine Islands, to New Caledonia (Chapman 1946; Fourmanoir and Laboute 1976; Uchida 1978) and Fiji (Jordan and Dickerson 1908; Whitley 1927; Fowler 1959). Records from Wallis and Futuna Islands and Cook Islands (Uchida 1978) are doubtful and need to be verified. In Australia the range extends south to Sydney (Castelnau 1879; AMS I.9693) and, rarely, even to Victoria and Tasmania (Munro 1958a; Whitley 1964a) on the east coast and to Rottnest Island off Perth, Western Australia (Hutchins 1979). From Australia and the East Indies, the range extends along the coast of the Indian Ocean including the Persian Gulf and Red Sea to False Bay, Cape Town, South Africa (Barnard 1948). The range includes many major offshore island groups in the Indian Ocean: Andamans and Nicobars (Jones et al. 1960), Laccadives (Nagabhushanam and Chandrasekhara Rao 1972), Amirantes (Ommanney 1953), Comores and Madagascar (Fourmanoir and Crosnier 1964), and Mauritius (Bleeker 1874; Baissac 1976). It has strayed into the South Atlantic because we have examined the head of a specimen (BMNH 1965.12.1.104) collected by Arthur Loveridge from Egg Island, St. Helena. It has even traversed the Suez Canal and entered the eastern Mediterranean Sea where it is now known from Lebanon (George and Athanassiou 1965) and Israel (Collette 1970; USNM 226334; Golani and Kredo 1981).

Geographic variation.—Samples were adequate to compare the morphometric data of three populations of *S. commerson* by ANCOVA (Table 15): Red Sea (n = 12), Indian Ocean (n = 31-34), and East Indies (n = 21-22). Null hypotheses that the three sets of regressions are coincident were accepted for 11 of 26 regressions, rejected for the other 15. For one set, interorbital width, the regressions for all three populations differed significantly in slope. The Red Sea population differs significantly from the Indian Ocean population in six regressions: Sn-1D, Sn-P_1, Ht 2D, Base 2D, Ht A, and interorbital width. The Indian Ocean population differs from the East Indies population in eight regressions: P_1-P_2, Hd L, P_2 tip-vent, Ht 2D, Sn (fleshy), Sn (bony), maxilla L, and interorbital width.

There are also geographic differences in meristic characters. Populations in the Red Sea and Persian Gulf tend to have fewer vertebrae (23-24 caudal, 43 total) and fewer rays in the second dorsal and anal fins (usually 16-17 second dorsal and 17-18 anal) than other populations (24-27 caudal, 44-46 total vertebrae; 17-18 second dorsal, 18-19 anal rays). Populations in the East Indies and Gulf of Thailand tend to have more vertebrae (25-27 caudal, 45-46 total) and anal finlets (mode 10 rather than 9). Gill rakers tend to be fewer in the East Indies, Gulf of Thailand, and South China Sea (2-6, usually 3 or 4) compared with other populations (3-8, usually 4-6).

Material examined.—Total 262 (94.2-1,155).

meas.: 120 (94.2-115): Israel (2); Red Sea (12); Gulf of Aden (2); St. Helena (1); W Indian Ocean (14); Arabian Sea (14); Bay of Bengal (5); Andaman Sea (7); Gulf of Thailand (14); East Indies (22, **C. ko-*

[3]A. Ben-Tuvia, Professor of Zoology, Zoology Department, The Hebrew University, 91904 Jerusalem, Israel, pers. commun. October 1982.

[4]A. Ben-Tuvia, Professor of Zoology, and D. Golani, Zoology Department, The Hebrew University, 91904 Jerusalem, Israel, pers. commun. October 1982.

nam Bleeker), New Guinea (2); Australia (5); Philippine Is. (6); South China Sea (8); Fiji (5).

counts: 262.

diss.: 14 (260-1,155): Israel (1); W Indian Ocean (2); Pakistan (1); New Guinea (2); New South Wales, Australia (2); Philippine Islands (2); Hong Kong (4).

Scomberomorus concolor (Lockington) Monterey Spanish Mackerel

Figure 53

Chriomitra concolor Lockington 1879a:134-136 (original description; Monterey Bay, Calif.). Lockington 1879b:34 (uncommon; San Francisco market).

Scomberomorus concolor. Jordan and Gilbert 1881a:456 (Monterey Bay; *Chriomitra* placed in synonymy of *Scomberomorus*). Jordan and Jouy 1881:13 (specimens from Soquel, Calif.; USNM 27205; distributed as duplicates). Jordan and Gilbert 1881b:45 (Monterey Bay). Jordan and Gilbert 1882:425-426 (description). Meek and Newland 1884:232-233 (synonymy, description). Goode 1884:316 (Soquel, Monterey Bay; occurrence, price). Dresslar and Fesler 1889:442-443 (synonymy, description). Jordan and Evermann 1896a:341 (listed). Jordan and Evermann 1896b:873-874 (description, synonymy). Jordan and Evermann 1902:284 (description). Starks 1918:121 (not reported from Monterey Bay in 40 yr). Meek and Hildebrand 1923:325-326 (description; Soquel, Calif.). Jordan et al. 1930:257 (listed). Phillips 1932:99 (Monterey Bay; first record in more than 40 yr). Breder 1936:12 (2 specimens, 491-520 mm SL; from Gulf of California; measurements). Croker 1937:245-246 (Long Beach). Walford 1937:25-26 (description, occurrence). Roedel 1939:341 (Long Beach; fifth record of recent years). Munro 1943:69, 71-72 (placed in subgenus *Chriomitra*). Fowler 1944:498 (listed; Mexico; Panama Bay record probably *S. sierra*). Fitch 1948:134 (Santa Monica Bay; sixth specimen since 1880's). *Fitch and Flechsig 1949:275-280 (history of previous captures; description), fig. 75. Fraser-Brunner 1950:157-158 (description), fig. 26. Clothier 1950:53 (47-48 vertebrae). Fitch 1950:70 (Newport Harbor; seventh California record since 1880's; comparison with *S. sierra*). Roedel 1951:510 (Long Beach; 8th to 10th specimens since 1880's; may have spots). Fitch 1952:560 (Los Angeles Harbor). Roedel 1953:85 (occasional in S California). Radovich 1961:21, 30 (years of California captures). Collette et al. 1963:54 (compared with *S. sierra*; previous California records of *S. sierra* = *S. concolor*). Clemens and Nowell 1963:260 (Gulf of California). Fitch and Craig 1964:202, fig. 5 (otolith). Klawe 1966:445 (compared with *S. sierra*; more gill rakers on upper and lower arches). Fitch 1969:65 (jaw fragments and teeth; Chumash Indian village archaeological site; Ventura, Calif.). Castro-Aguirre et al. 1970:156-157 (abundant in Gulf of California). Fitch and Lavenberg 1971:131, 168 (listed). Miller and Lea 1972:192 (description; range Gulf of California to Soquel, Calif.), fig. Buen 1972:291 (Mexico). Bullis et al. 1972:75 (bionumeric code number). Richards and Klawe 1972:13 (range), 91 (references to juveniles). Magnuson 1973:350 (short pectoral fin). Sharp 1973: 384, fig. 3 (hemoglobin electrophoretic patterns

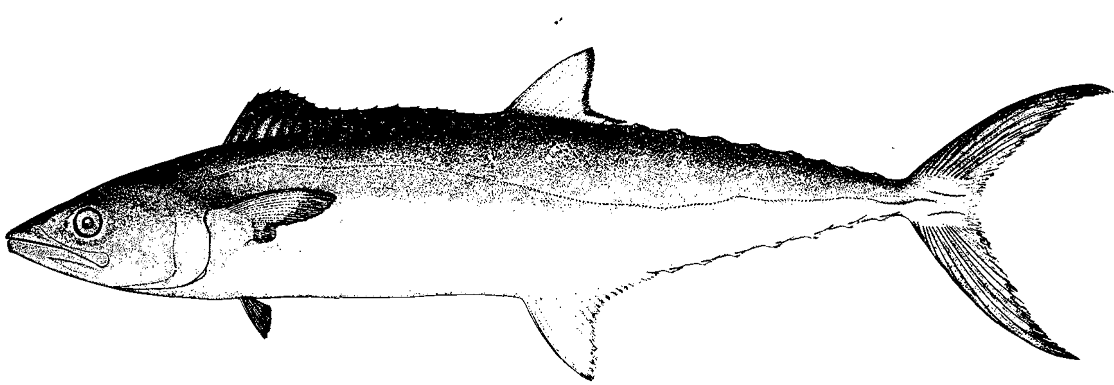


FIGURE 53.—*Scomberomorus concolor.* Gulf of California, 440 mm FL, USNM 233681.

of *S. sierra*, *S. concolor*, and *Acanthocybium* identical or very similar). Johnson 1975:20 (procurrent spur not present). Shiino 1976: 231 (common name). Thomson and McKibbin 1976:46 (description; Gulf of California). Klawe 1977:2 (common name, range). Fitch and Schultz 1978:85, fig. 4G (otolith). Horn and Allen 1978:39 (range lat. 36°N to 32°N along California coast). Collette 1979:29 (characters, range). Collette and Russo 1979: 13 (diagnostic characters, range). Cressey et al. 1983:264 (host-parasite list, 3 copepod species). Collette and Nauen 1983:64-65 (description, range), fig.

Types.—*Chriomitra concolor* Lockington 1879a. Description based on a 21-in FL (533 mm FL) specimen obtained in the San Francisco market and probably originating in Monterey Bay. Lockington stated that the specimen was "in the possession of the Cal. Acad. of Sciences", but it is not now present in the CAS collection. Data from the original description are "D XV + 17 + VII; A 18 + VIII. Body color dark steel blue above, becoming silvery below; no streaks".

Diagnosis.—The species of *Scomberomorus* with the most gill rakers, a total of 21-27 on the first arch, compared with 1-18 in the other 17 species. It possesses nasal denticles as do the other five species of the *regalis* group (*brasiliensis*, *maculatus*, *regalis*, *sierra*, and *tritor*). Like *S. maculatus*, *S. concolor* lacks the artery that goes from the fourth right epibranchial artery to the coeliaco-mesenteric artery (Fig. 7d), but it has the artery that comes off the fourth left epibranchial artery as do all the species in the group except *S. tritor*. Together with three other species of the *regalis* group (*brasiliensis*, *regalis*, and *sierra*), *S. concolor* has a long posterior process on the pelvic girdle, 62-90% of the length of the anterior plate. Intercalar spine absent as in the other five species of the *regalis* group and *S. niphonius*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3d). Spines in first dorsal fin 15-18, usually 17 (Table 9); second dorsal fin rays 16-20, usually 18 or 19 (Table 10); dorsal finlets 6-9, usually 8 (Table 10); anal fin rays 19-23, usually 20 (Table 11); anal finlets 6-8, usually 7 or 8 (Table 11); pectoral fin rays 19-22, usually 21 (Table 12). Precaudal vertebrae 18-20, usually 19 (Table 6); caudal vertebrae 27-29, usually 28 (Table 7); total vertebrae 46-48, usually 47 or 48 (Table 8). Gill rakers on first arch (4-8) + (15-21) = 21-27, usually (6-7) + (17-18) = 23-25 (Table 5). Morphometric characters given in Table 16.

TABLE 16.—Summary of morphometric data of *Scomberomorus concolor*. FL = fork length, HL = head length.

Character		*N*	Min.	Max.	Mean	SD
Fork length		34	134	685	401	139
Snout-A	‰ FL	34	504	547	524	10
Snout-2D	‰ FL	34	488	534	506	12
Snout-1D	‰ FL	34	220	258	236	10
Snout-P_2	‰ FL	34	192	287	242	18
Snout-P_1	‰ FL	34	124	263	209	21
P_1-P_2	‰ FL	30	89	116	100	6
Head length	‰ FL	34	185	230	202	10
Max. body depth	‰ FL	29	164	220	187	16
Max. body width	‰ FL	32	70	111	89	10
P_1 length	‰ FL	34	116	137	125	6
P_2 length	‰ FL	31	41	61	50	4
P_2 insertion-vent	‰ FL	32	222	294	261	16
P_2 tip-vent	‰ FL	29	173	248	212	18
Base 1D	‰ FL	34	210	292	254	15
Height 2D	‰ FL	26	98	129	111	9
Base 2D	‰ FL	33	108	153	128	10
Height anal	‰ FL	25	26	137	108	20
Base anal	‰ FL	33	107	171	135	14
Snout (fleshy)	‰ FL	33	53	83	72	5
Snout (bony)	‰ FL	33	57	76	64	3
Maxilla length	‰ FL	33	103	128	113	6
Postorbital	‰ FL	29	85	101	96	4
Orbital (fleshy)	‰ FL	33	25	47	32	7
Orbital (bony)	‰ FL	30	34	63	46	8
Interorbital	‰ FL	34	44	55	49	3
2D-caudal	‰ FL	30	413	524	484	24
Head length		34	31	134	80	27
Snout (fleshy)	‰ HL	33	276	389	353	19
Snout (bony)	‰ HL	33	273	355	314	16
Maxilla length	‰ HL	33	532	575	555	11
Postorbital	‰ HL	29	419	524	475	22
Orbit (fleshy)	‰ HL	33	125	212	158	26
Orbit (bony)	‰ HL	30	175	285	226	32
Interorbital	‰ HL	34	220	274	242	12

Size.—Maximum size 76.2 cm FL, 2.3-3.6 kg (Goode 1884).

Color pattern.—According to Walford (1937), males are steel blue on the back, silvery on the sides and below, and are without streaks or spots. Females are darker, with two alternate series of brown spots on sides. The spots on the sides of the females are gold in life (Fitch and Flechsig 1949).

A black and white photograph of *S. concolor* is included in Fitch and Flechsig (1949:fig. 75).

Biology.—Little is known about the biology of *S. concolor*. In the 1880's, they appeared in Monterey Bay in September and disappeared in November (Goode 1884). There are no references to eggs, larvae, or juveniles (Richards and Klawe 1972).

Interest to fisheries.—Some accounts indicate that *S. concolor* was of considerable commercial importance in Monterey Bay in the 1870's and 1880's, in great demand and at a high price, 30-50 cents a pound according to Goode (1884). According to other authors, such as Lockington (1879a, b), it was not abundant even then. No longer of any commercial significance.

Distribution.—An eastern Pacific endemic originally described from Monterey Bay, Calif. (Lockington 1897a). This apparently was the northern limit of the range, and there have been only about 10 recent records from the California coast (Long Beach, Santa Monica Bay, Newport Harbor; Fitch and Flechsig 1949; Radovich 1961). Its present range is concentrated in the Gulf of California (Castro-Aguirre et al. 1970; Miller and Lea 1972; Collette and Russo 1979:13, fig. 8).

Material examined.—Total 34 (134-685 mm FL).

meas.:	34 (134-685): Soquel, Calif. (6); Gulf of California (27).
counts:	30.
diss.:	6 (420-495): Gulf of Calif.

Scomberomorus guttatus (Bloch and Schneider) Indo-Pacific King Mackerel

Figure 54

Scomber guttatus Bloch and Schneider 1801:23-24 (original description; Tranquebar, India), pl. 5.

Scomber wingeram Russell 1803:26-27 (description; Coromandel coast of India), pl. 134.

Scomber leopardus Shaw 1803:591-592 (original description based on the wingeram of Russell 1803:pl. 134).

Cybium guttatum. Cuvier 1829:200 (listed in footnote from *Sc. guttatus* Bloch and Schneider). Cuvier *in* Cuvier and Valenciennes 1831:173-176 (description). Richardson 1846:268 (synonymy, range). Cantor 1849:1093-1095 (synonymy, description, range; Pinang). Bleeker 1852:38, 39 (synonymy, description; East Indies). Bleeker 1853:42 (India). Bleeker 1860:13 (Borneo). Günther 1860:371 (synonymy, description). Bleeker 1861a:52 (Singapore; listed). Bleeker 1861b:74 (Pinang; listed). Kner 1865:143-144 (description). Day 1873:225 (description, range). Bleeker 1873:131 (China; listed). Day 1878:255 (synonymy, description, range), pl. 55, fig. 1 (young), pl. 56, fig. 4 (adult). Tirant 1885:46 (Cambodia; listed). Kishinouye 1923:419-420 (description, anatomy), pl. 34, fig. 61 (adult). Chabanaud 1926:22 (Côte d'Annam, Tonkin; listed). Hardenberg 1931:141 (Sumatra). Delsman 1931:402 (vertebrae $20+25=45$), figs. 1-9 (eggs and larvae). Morice 1953:37 (villiform tongue teeth present). Gopalan Nayar 1958:49-51 (fishery; Vizhingam, S India).

Cybium interruptum Cuvier *in* Cuvier and Valenciennes 1831:172-173 (original description; Pondichery, India). Günther 1860:371 (description after Cuvier). Day 1873:225 (description, range). Day 1878:254-255 (synonymy, description), pl. 56, fig. 3.

Cybium Kuhlii Cuvier *in* Cuvier and Valenciennes 1831:178-179 (original description; Bombay). Hardenberg 1931:140 (often found in river mouths; Sumatra). Delsman 1931:402 (vertebrae $20+25=45$), 407 (commonest species of *Cybium* at Bagan Si Api Api).

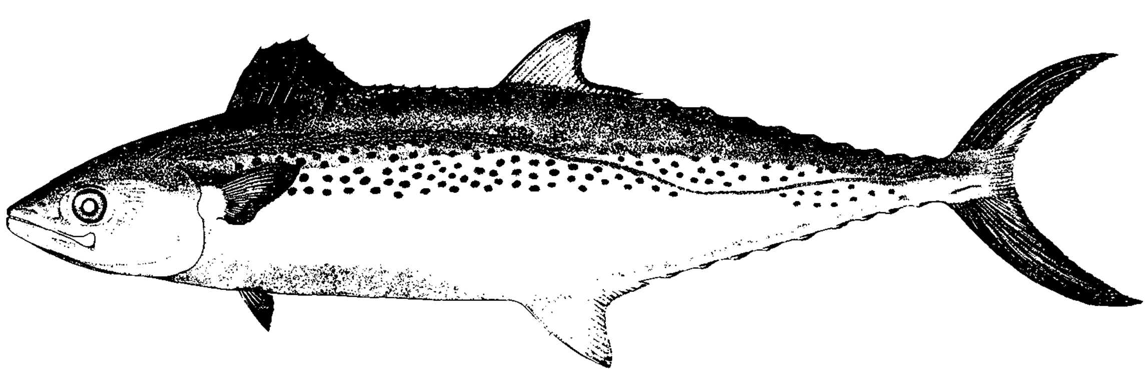


FIGURE 54.—*Scomberomorus guttatus.* Gulf of Thailand, 459 mm FL, CAS GVF Reg. 1512.

Cybium Croockewitii Bleeker 1851b:161 (original description; Banka). Bleeker 1852:37-38 (description). Günther 1860:372 (description after Bleeker).

Scomberomorus guttatus. Fowler 1905:766 (Sumatra; ANSP 27490-91). Jordan and Richardson 1909:177 (Formosa; FMNH 59284). Reeves 1927:8 (Swatow, China). Fowler 1928:109 (Bombay). Chevey 1934:45-46 (Tirant's *C. guttatum* = *S. guttatus*). Delsman and Hardenberg 1934:341-342 (description; East Indies), fig. 247 (adult), fig. 248 (larva, with myomeres 15 + 35 = 50). Hardenberg 1934: 311 (Sumatra; listed). Hardenberg 1936:252 (mouth of Kapuas R., Borneo). Hardenberg 1937:12 (mouth of Kumai R., Borneo). Herre and Myers 1937:21 (Singapore). Munro 1943: 68, 71 (placed in subgenus *Indocybium*). Quraishi 1945:28 (pyloric caeca arranged in dendritic pattern). Norman and Fraser 1949: 153 (Indo-Pacific species). Fraser-Brunner 1950:160 (synonymy in part, range), fig. 31. Tham 1950:21 (feeds largely on *Stolephorus*). de Beaufort 1951:232-234 (synonymy, description, range). Tham 1953:49 (Singapore Straits), 50 (correlation of catch with physical factors and presence of food fishes such as *Stolephorus*). Vijayaraghavan 1955:360-372 (commonest species of genus in Madras; eggs, larval development). Krishnamoorthi 1957:236 (second in importance among fishes landed at Rameswaram I., Palk Bay), 239-242 (catch), 251 (value of catch). Krishnamoorthi 1958:270-281 (spawning season and fisheries; Rameswaram I., SE India). Venkataraman 1961: 287, fig. 4C (food of 133 specimens; Calicut, India; mostly teleosts). Kaikini 1961:361 (seerfish fishery; Malwan, India). Jones and Silas 1962:195-197 (synonymy, description, range), fig. 3 (533 mm adult), fig. 5D (head, not 5C as labelled), fig. 6C (gill arch), fig. 7C (caudal peduncle keels). Jones 1962:107-113 (development, 14.8-239 mm), figs. 2-6 (specimens 14.8, 22.9, 41.2, 66.8, and 239 mm long). Misra 1962:295-296 (description, distribution), fig. 181 (size given as "1828 mm"). Jones and Kumaran 1964:344-346 (larval development), figs. 1-3 (from Jones 1962). Kumaran 1964: 587-589 (postlarval and juvenile fishes form most of diet of juveniles; W coast of India). Blanc and Bauchot 1964:449 (specimens examined by Cuvier). Boeseman 1964:468 (syntypes of *C. kuhlii*), pl. V, fig. 18 (photograph of syntype). Rao 1964:592-597 (teleosts predominate in food of juveniles and adults; Waltair coast, India). Gorbunova 1965a:52-53 (spawning). Gorbunova 1965b:174-175 (spawning; Gulf of Tonkin), fig. 6 (4.3 and 5.8 mm larvae). Menon 1966:396 (Tranquebar, India). Thiemmedh 1966:129, 140 (Thai names). Tongyai 1966a:7-13 (synonymy, occurrence in Thailand, biology), pl. 2C. Tongyai 1966b:3-17 (length frequency; Andaman Sea). Collette 1966:368-369 (*Cybium kuhlii* a junior synonym of *S. guttatus*, lectotype of *C. kuhlii* selected). Jones 1968:998 (seerfish fishery; India). Pathansali 1968:1001-1002 (fishery on east and west coasts of Malaya). Tongyai 1970:559 (distribution; Thai waters), 561 (spawning), 561-562 (food). Merçeron 1970:75-81 (length-weight; Cambodia). Tongyai 1971a:13-16 (description), pl. I (viscera), pl. IV (photograph). Tongyai 1971b: 3 (undetermined economic potential; Thailand), pl. 8, 13 (photographs). Latiff 1971:92 (description; Penang waters; photograph). Banerjee and Chakrubarty 1972 (drift gill netting; Lower Sundarbans, W Bengal). Fernando 1972:524, 530 (incidental catches in trawls; Wadge Bank, Ceylon). Kuronuma and Abe 1972:105 (description; Kuwait), color pl. 17. Richards and Klawe 1972:13-14 (range), 91-92 (references to eggs, larvae, and juveniles). Magnuson 1973: 350 (small pectoral fin). Banerji 1973:129-130 (seerfish fishery; India). Orsi 1974:175 (listed; Vietnam). Roy and Roy 1974:44, 51, 53 (a principal species in gill net fishery; Balashore, India). Shenoy and James 1974 (ice storage). Devaraj 1976:80-85 (distinguished from *S. koreanus*), fig. 4 (vertebrae), 5 (preopercle and liver). Rao 1976:63-78 (biometric comparison of 5 Indian populations). Shiino 1976: 231 (common names). *Devaraj 1977 (osteology). Rao and Ganapati 1977:107-111 (comparison with postlarvae and juveniles of *S. lineolatus* and *S. commerson*). Klawe 1977:2 (common name, range). Randall et al. 1978: 167 (Persian Gulf; photograph). Collette 1979: 29 (characters, range). Collette and Russo 1979:13 (diagnostic characters, range). Zhang and Zhang 1981:104 (range in part). Nakamura and Nakamura 1982:446 (3 specimens, description; Sea of Japan), fig. 1B. *Devaraj 1982 (age and growth). Sivasubramaniam and Mohamed 1982:64 (Qatar, Persian Gulf). Cressey et al. 1983:264 (host-parasite list, 4 copepod species). Lee and Yang 1983:230-231 (Taiwan), fig. 21 (353 mm FL). Collette and Nauen 1983:65-66 (description, range), fig.

Scomberomorus guttatum. Malpas 1926:72-74 (87 specimens; length, weight, gonads, stomach contents; Ceylon). Scott 1959:113 (description; Malaya), photograph.

Scomberomorus kuhlii. Chevey 1934:20 (Tirant's *C. kuhlii* = *S. kuhlii*). Hardenberg 1934:311 (listed; Sumatra). Hardenberg 1936: 252 (mouth of Kapuas R., Borneo). Hardenberg 1937:12 (mouth of Kumai R., Borneo). Munro 1943:68, 71 (placed in subgenus *Pseudosawara*). Herre and Herald 1951:339 (Sandakan market; N Borneo). Bauchot and Blanc 1961:372 (types of *C. kuhlii*; recognized as valid species). Blanc and Bauchot 1964:447 (types of *C. kuhlii*), pl. III, fig. 14 (photograph of type-specimens). Orsi 1974:175 (listed; Vietnam).

Scomberomorus croockewiti. de Beaufort 1951: 234-235 (description), fig. 40 (drawing made for Bleeker). Boeseman 1964:467 (holotype), pl. V, fig. 17 (photograph of holotype).

Indocybium guttatum. Munro 1955:221 (description; Ceylon), fig. 652. Chacko et al. 1967: 1006 (fishery; Madras).

Scomberomorus lineolatus. Not of Cuvier, 1831. Bauchot and Blanc 1961:371 (type of *C. interruptum*). Blanc and Bauchot 1964:446-447 (type of *C. interruptum*), pl. III, fig. 13 (photograph of holotype of *C. interruptum*).

Scomberomorus guttatus guttatus. Jones and Silas 1964:62-63 (synonymy, description, range), pl. VII, fig. B. Silas 1964:325-329 (synonymy, description, range; *C. koreanum* considered a subspecies of *S. guttatus*).

Types of nominal species.—*Scomber guttatus* Bloch and Schneider 1801. The original description was based on a specimen from Tranquebar, India. No types are known to be extant. The figure in the original description leaves little doubt as to the identity of the name.

Scomber leopardus Shaw 1803 was based on the "wingeram" of Russell (1803:pl. 134); no types are extant.

Cybium interruptum Cuvier *in* Cuvier and Valenciennes 1831. Holotype: MNHN A.5522; Pondichery, India; Leschenault; 375 mm FL; D ?+?+IX; A ?+VII; lateral line branched anteriorly; dried, dorsal fin badly damaged. A photograph of the type was published by Blanc and Bauchot (1964:pl. 3, fig. 13).

Cybium kuhlii Cuvier *in* Cuvier and Valenciennes 1831. Lectotype: MNHN A.5771; Java; Kuhl and van Hasselt; 108 mm FL; selected by Collette (1966:368); D XVII+21+VIII; A 21+VIII; P_1 22; RGR_1 2+1+9=12; vertebrae 21+30 =51. A photograph of the lectotype was published by Blanc and Bauchot (1964:pl. 3, fig. 14, upper fish). Paralectotypes: RMNH 1239 (1, 190 mm FL) and 1241 (1, 108 mm FL); Java; Kuhl and van Hasselt; and MNHN A.5715 (1, 115 mm FL); Bombay; Dussumier. Photographs of RMNH 1239 and MNHN A.5715 have been published by Boeseman (1964:pl. 5, fig. 19) and Blanc and Bauchot (1964:pl. 3, fig. 14, lower fish), respectively.

Cybium Croockewitii Bleeker 1851. Holotype: RMNH 6054; Banka, Strait near Muntok, East Indies (= Indonesia); J. H. Croockewit; D XV+24 +VII; A 23+VII; P_1 21-21; RGR_1 2+1+9=12; lateral line with fine branches anteriorly. A photograph of the type was published by Boeseman (1964:pl. 5, fig. 18).

Diagnosis.—This species shares with *S. koreanus* the presence of numerous fine auxiliary branches from the anterior part of the lateral line (Fig. 54). It differs from *S. koreanus* in having the usual two loops and three limbs to the intestine instead of four loops and five limbs. Anterior end of premaxilla forms a blunt rather than intermediate or acute angle. Ascending process of premaxilla short as in *S. cavalla*. Scapular foramen small as in *S. koreanus* and *S. niphonius*. Supraoccipital crest high as in *S. koreanus* and *S. multiradiatus*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 2e). Spines in first dorsal fin 15-18, usually 16 or 17 (Table 9); second dorsal fin rays 18-24, usually 20-22 (Table 10); dorsal finlets 7-10, usually 8 or 9 (Table 10); anal fin rays 19-23, usually 20-22 (Table 11); anal finlets 7-10, usually 8 (Table 11); pectoral fin rays 20-23, usually 21 (Table 12). Precaudal vertebrae 19-22, usually 21 (Table 6); caudal vertebrae 28-31, usually 29 or 30 (Table 7); total vertebrae 47-52, usually 50 or 51 (Table 8). Gill rakers on first arch (1-2)+(7-12)=8-14, usually 2+(9-10)=11-12 (Table 5). Morphometric characters given in Table 17.

Size.—Maximum size 76 cm FL. Size at first maturity 48-52 cm TL in southern India (Krishnamoorthi 1958), 41-45 cm TL in Thailand (Tongyai 1966b).

Color pattern.—Nakamura and Nakamura (1982)

TABLE 17.—Summary of morphometric data of *Scomberomorus guttatus*. FL = fork length, HL = head length.

			Indian Ocean					East Indies					Gulf of Thailand					China					Total				
Character			*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD
Fork length			22	109	545	309	144	24	107	515	242	100	17	173	459	331	84	31	63	760	291	167	143	63	760	317	128
Snout-A	‰	FL	20	495	568	519	19	24	503	559	524	14	17	494	518	505	7	28	468	568	517	20	138	468	568	516	17
Snout-2D	‰	FL	22	452	509	483	14	24	454	504	481	12	17	459	494	479	9	28	463	510	481	10	140	451	512	481	11
Snout-1D	‰	FL	22	224	273	242	12	22	225	260	241	10	17	219	248	232	9	29	220	275	238	13	123	219	275	238	11
Snout-P_2	‰	FL	19	228	285	253	17	22	231	278	255	12	17	225	358	248	31	26	225	296	248	20	116	224	358	250	19
Snout-P_1	‰	FL	22	193	241	213	13	23	191	235	212	12	17	190	225	201	8	29	186	245	207	19	124	185	245	208	14
P_1-P_2	‰	FL	19	94	126	109	8	22	93	119	107	7	17	92	120	104	7	25	95	129	106	9	114	89	129	106	8
Head length	‰	FL	22	188	234	211	13	24	188	221	208	9	17	190	218	199	8	31	185	259	207	19	143	185	259	205	13
Max. body depth	‰	FL	19	171	326	218	30	19	190	229	208	10	16	99	226	202	29	30	191	236	209	9	129	99	326	209	18
Max. body width	‰	FL	15	69	125	92	16	15	69	106	88	10	16	85	104	93	6	22	71	106	91	8	92	69	146	93	12
P_1 length	‰	FL	17	92	130	113	9	20	89	130	107	11	11	93	122	107	7	23	89	133	108	9	99	89	133	109	9
P_2 length	‰	FL	13	47	70	63	6	16	47	69	59	5	13	47	62	57	4	20	48	74	59	5	88	41	74	59	6
P_2 insertion-vent	‰	FL	14	224	270	250	16	22	240	279	257	11	15	231	268	245	12	23	218	269	248	13	101	218	288	251	13
P_2 tip-vent	‰	FL	10	158	208	187	17	14	178	223	196	13	12	174	209	187	12	22	167	211	189	13	81	158	229	191	15
Base 1D	‰	FL	22	203	253	232	13	21	210	258	234	13	17	208	256	240	12	29	216	246	232	8	122	203	270	234	12
Height 2D	‰	FL	18	113	153	138	11	20	103	167	124	16	10	114	169	132	15	22	117	155	132	10	113	103	254	131	17
Base 2D	‰	FL	22	125	161	146	11	23	121	156	136	10	17	113	157	136	13	29	100	170	144	13	124	100	170	141	12
Height anal	‰	FL	15	109	165	135	13	16	93	166	122	18	13	107	170	127	15	24	109	153	125	11	106	93	170	127	14
Base anal	‰	FL	22	115	165	138	13	23	83	154	127	13	17	111	147	130	10	29	116	146	134	7	124	83	171	133	12
Snout (fleshy)	‰	FL	22	60	81	72	5	24	64	80	72	3	17	61	75	69	4	29	61	170	75	19	125	60	170	72	10
Snout (bony)	‰	FL	22	56	73	64	4	24	57	69	64	3	17	54	68	61	4	29	48	161	66	19	125	47	161	63	10
Maxilla length	‰	FL	22	92	130	110	9	24	86	121	111	9	17	90	118	102	9	28	95	132	108	11	124	86	132	108	9
Postorbital	‰	FL	22	85	112	97	7	24	87	100	95	4	17	79	105	93	5	29	88	112	95	6	123	79	112	95	5
Orbital (fleshy)	‰	FL	22	25	50	36	7	24	28	56	40	6	17	29	41	34	3	29	23	52	35	8	125	23	56	36	7
Orbital (bony)	‰	FL	22	37	70	53	10	24	47	69	57	6	17	41	60	48	5	29	38	71	52	8	124	37	71	52	8
Interorbital	‰	FL	22	55	66	60	3	24	55	62	59	2	17	52	62	57	3	29	53	63	58	3	124	52	66	58	3
2D-caudal	‰	FL	22	481	552	519	23	23	491	558	534	14	17	480	553	507	23	28	465	579	528	34	138	465	579	527	26
Head length			22	25	125	64	29	24	24	98	50	18	17	38	88	65	15	31	16	145	58	30	143	16	145	64	24
Snout (fleshy)	‰	HL	22	296	383	344	21	24	319	368	344	12	17	319	365	345	12	29	310	734	364	72	125	296	734	351	38
Snout (bony)	‰	HL	22	265	328	303	15	24	281	334	306	12	17	282	320	304	12	29	245	694	320	74	125	232	694	309	38
Maxilla length	‰	HL	22	455	564	523	23	24	451	564	530	26	17	463	550	512	30	28	497	565	531	17	124	451	565	525	23
Postorbital	‰	HL	22	412	499	463	20	24	410	496	457	20	17	413	502	469	25	29	393	563	470	34	123	382	563	465	26
Orbit (fleshy)	‰	HL	22	118	217	173	30	24	148	253	193	24	17	151	198	168	13	29	121	220	169	26	125	118	253	174	27
Orbit (bony)	‰	HL	22	158	306	253	41	24	240	314	275	19	17	214	275	242	18	29	197	304	252	26	124	158	314	252	30
Interorbital	‰	HL	22	244	325	284	16	24	258	298	284	8	17	272	296	284	8	29	254	301	284	13	124	244	325	285	12

described fresh specimens taken in Wakasa Bay in the Sea of Japan. Body greyish blue dorsally, silvery white laterally and ventrally. Several longitudinal rows of small brownish spots scattered rather densely along lateral median line. First dorsal fin membrane black. Pectoral, second dorsal, and caudal fins dark brown. Pelvic and anal fins silvery white.

There are good illustrations of a specimen from the North Pacific in Kishinouye (1923:fig. 61) and of one from India in Jones and Silas (1962:fig. 3). There are photographs of specimens of *S. guttatus* from India in Jones and Silas (1964:pl. 7) and Silas (1964:pl. 2), and there is a good photograph of a specimen from the Sea of Japan in Nakamura and Nakamura (1982:fig. 1B). A good color photograph of a specimen from the Persian Gulf is included in Kuronuma and Abe (1972: pl. 17).

Biology.—Little is reported in the literature about movements and migration of *S. guttatus* but it appears to be less migratory than *S. commerson.* Possible movements in the Gulf of Thailand might be deduced from seasonal changes in peak fishing months along the coast of Thailand. These peaks are November-December in eastern Thailand, late December-January in the northern part of the Gulf, and January-March in the western part of the Gulf (Tongyai 1970). Based on occurrence of ripe females and size of maturing eggs, spawning probably occurs from April to July around Rameswaram Island between India and Sri Lanka (Krishnamoorthi 1958). Ripe females 32.5-46.5 cm FL were taken in Thai waters in May. Larvae and juveniles have been reported from Indonesian and Indian waters but apparently the only certain accounts are those of Jones (1962) and Jones and Kumaran (1964) who illustrated four postlarvae (14.8, 22.9, 41.2, and 66.8 mm). As with other species of *Scomberomorus*, the food is primarily fishes. Juveniles in India feed mainly on teleosts, particularly clupeoids such as *Anchoviella* (Venkataraman 1961; Kumaran 1964; Rao 1964). Adults also feed mainly on teleosts with small quantities of crustaceans and squids (Thailand—Tongyai 1970, India—Rao 1964). Anchovies are particu-

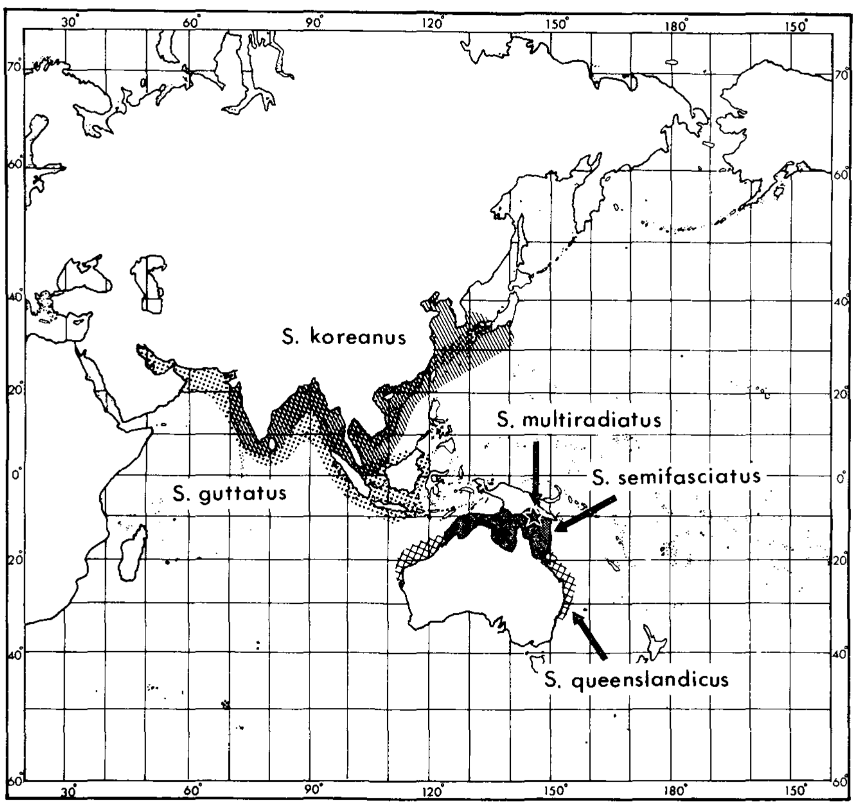


FIGURE 55.—Ranges of five Indo-West Pacific species of *Scomberomorus*: *S. guttatus*, *S. koreanus*, *S. semifasciatus*, *S. queenslandicus*, and *S. multiradiatus*.

larly important: *Stolephorus* in Singapore Straits (Tham 1950, 1953) and *Anchoviella* in Waltair, India (Rao 1964).

Interest to fisheries.—There are commercial or artisanal fisheries for *S. guttatus* in Cambodia (Merçeron 1970), Thailand (Tongyai 1971b), Malaysia (Pathansali 1968), and India, particularly in the lower Sundarbans, West Bengal (Banerjee and Chakrubarty 1972), the Balashore coast (Roy and Roy 1974), around Madras (Vijayaraghavan 1955), the Gulf of Mannar-Palk Bay area (Krishnamoorthi 1957), and Malwan, south of Bombay (Kaikini 1961). It is caught all year round in some areas (Cambodia—Merçeron 1970; Ramaswaram I., India—Krishnamoorthi 1957) but there are peaks of abundance that differ from region to region. It is taken in the non-monsoon months (September-May) along the Balashore coast south of Calcutta with the catch increasing from October to February (Roy and Roy 1974). Catches peak in September-October, December-February, and May in Waltair near Vishakhapatnam further south along the west coast of the Bay of Bengal (Venkata Subba Rao et al. 1981). The season extends from September-October to March-April in Vizhingam, southern India, (Gopalan Nayar 1958) with the peak catches usually in September or October. It is one of the principal species in the drift net seerfish fishery in India, but the catch is not identified to species in the statistics. Indonesia reported the only catch identified as *S. guttatus* (4,254-5,249 t/yr) in 1979-82 (FAO 1984). The primary gear in most areas appears to be the drift gill net which is set overnight, but it is also taken in bamboo stake traps and with hand lines in Thailand (Tongyai 1970) and by trolling or with hook and line in India and Malaysia (Rao 1964; Jones 1968; Pathansali 1968). It is utilized fresh or salted in most areas (India—Jones 1967; Cambodia—Merçeron 1970; Thailand—Tongyai 1971b). It can be stored on ice for 10-13 d (Shenoy and James 1974). Although less abundant than the Indian mackerels (*Rastrelliger* spp.), it is highly esteemed for food and commands a higher price in Thailand and India (Tongyai 1966a; Pathansali 1968).

Distribution.—Indo-West Pacific from Taiwan to the Gulf of Thailand, Java, and Sumatra west around the Bay of Bengal and Arabian Sea into the Persian Gulf (Fig. 55). The northernmost records are from Wakasa Bay, Japan (Nakamura and Nakamura 1982), Taiwan (FMNH 59284), Amoy (BMNH 1860.7.20.110), and Swatow, China (Reeves 1927). There are many records and specimens from Indochina, the Gulf of Thailand, and the East Indies. There are records and specimens of *S. guttatus* from Borneo (Bleeker 1860; Hardenberg 1936; Herre and Herald 1951; ANSP 72282) and Makassar, Celebes (RMNH 24096). The range extends further out in the East Indies than that of either *S. lineolatus* or *S. koreanus*, at least to Bali. The report of *S. guttatus* from Western Australia (McKay 1970) is based on a specimen (HUMZ F-423) of *S. queenslandicus*. Earlier reports of *S. guttatus* from Australia (Macleay 1881; Stead 1906, 1908; Rendahl 1923) are also based on *S. queenslandicus* (Munro 1943: 86). Early reports from New Zealand are based on "a damaged specimen of a *Cybium*, probably *C. guttatum*, was obtained at the Chatham Islands. . . ." (Hutton 1895). This report has led to subsequent records (Hutton 1904; Phillipps 1927; Whitley 1968). We concur with Whitley's conclusion that this record is "very doubtful". The range extends west into the Persian Gulf (Kuronuma and Abe 1972; ZMK 3-4).

Geographic variation.—Morphometric data for five populations of *S. guttatus* were compared with ANCOVA (Table 17): Arabian Sea (n = 7-13), Bay of Bengal (n = 5-9), East Indies (n = 14-24), Gulf of Thailand (n = 10-17), and China (n = 22-31). Null hypotheses that the 5 sets of regression lines are coincident were accepted for 18 sets, rejected for 8 sets: Sn-1D, Sn-P_1, Head L, maximum depth, maxilla L, orbit (fleshy), interorbit, and 2D-C. The five populations were arranged geographically from west to east as listed above. No significant differences were found between populations in the Arabian Sea and Bay of Bengal, but there were significant differences between all other adjacent populations: Bay of Bengal vs. East Indies (Sn-P_1), East Indies vs. Gulf of Thailand (Interorbital), Gulf of Thailand vs. China (Sn-1D, interorbital, and 2D-C). The Arabian Sea and Bay of Bengal populations were combined, the regressions rerun, and compared with the other three populations with ANCOVA. Null hypotheses that the 4 sets of regression lines are coincident were accepted for 15 sets, rejected for 11 sets: Sn-1D, Sn-P_1, Head L, maximum body depth, Base 1D, Base 2D, Base A, maxilla L, orbit (fleshy), interorbital, and 2D-C. The Newman-Keuls Multiple Range Test was able to distinguish populations that differed significantly for 7 sets of regressions but could not do so for 4:

maximum body depth, Base 1D, Base 2D, and Base A. Significant differences were found between the Indian Ocean population and that in the East Indies and Gulf of Thailand population in one (interorbital); and between the Gulf of Thailand and China populations in two (Sn-1D and maxilla L).

One meristic difference was found between populations of *S. guttatus*. The Indian Ocean population has a mode of 50 vertebrae while populations in the East Indies, Gulf of Thailand, and China have modes of 51. Gill rakers were usually 11 and second dorsal rays 21 in all four populations.

Material examined.—Total 149 (63.3-760).

meas.: 144 (80.0-760): Persian Gulf (2); N Arabian Sea (6); Malabar coast of India (25); Gulf of Mannar (7); Coromandel Coast of India (6, **C. interruptum* Cuvier); "India" (4); Burma (2); Andaman Sea (3); East Indies (31, **C. croockewitii* Bleeker); Gulf of Thailand (17); China (33).
counts: 143.
diss.: 14 (367-548): Karachi, Pakistan (6); Cochin, India (1); Gulf of Mannar (4); Hong Kong (2).

Scomberomorus koreanus (Kishinouye)
Korean Seerfish
Figure 56

Cybium kuhlii. Not of Cuvier, 1831. Day 1878: 254 (description, synonymy), pl. 46, fig. 2. Delsman 1931:402, 407 (vertebrae 20 + 25 = 45). Hardenberg 1931:140 (common, often found in river mouths; Bagan Si Api Api, Sumatra).
Cybium koreanum Kishinouye 1915:11 (original description; Korea), pl. 1, fig. 6. Kishinouye 1923:420-421 (description), pl. 21, fig. 35. Mori 1928:5 (Fusan, Korea; listed). Morice 1953:37 (villiform teeth on tongue).
Sawara koreanum. Soldatov and Lindberg 1930:112 (description after Kishinouye).
Cybium guttatum. Not of Bloch and Schneider 1801. Delsman 1931:402, 407 (vertebrae 20 + 25 = 45). Hardenberg 1931:141 (Bagan Si Api Api, Sumatra).
Scomberomorus guttatus. Not of Bloch and Schneider 1801. Hardenberg 1934:311 (Sumatra). Delsman and Hardenberg 1934:340-343 (in part, description, fishery), fig. 248 (in part, myomeres 13 + 33 = 46).
Scomberomorus koreanus. Munro 1943:68, 71 (placed in subgenus *Pseudosawara* Munro). Okada 1955:150 (description), fig. 137 (after Kishinouye). Kamohara 1967:43-44 (description, range), color pl. 22, fig. 3. Shiino 1972:71 (common name). Magnuson 1973:350 (short pectoral fin). *Devaraj 1976:79-87 (description, validation of species, comparison with *S. guttatus* and *S. semifasciatus*, synonymy), fig. 2 (745 mm adult; Palk Bay, India), fig. 3 (second dorsal and anal fins), fig. 4 (vertebral column), fig. 5 (preopercle and liver). Shiino 1976:231 (common name). Klawe 1977:2 (common name, range). *Devaraj 1977 (osteology). Collette 1979:24 (characters, range). Collette and Russo 1979:13 (diagnostic characters,

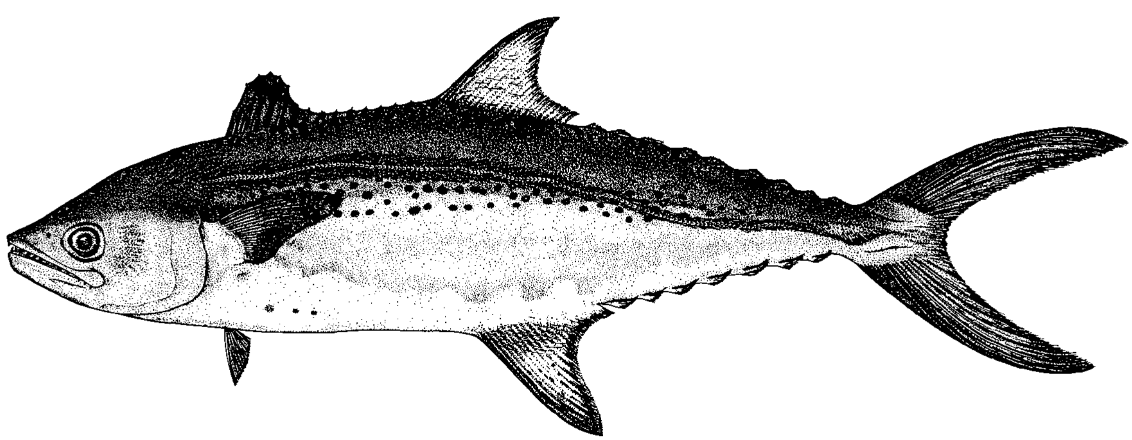


FIGURE 56.—*Scomberomorus koreanus.* Ning Po, China, 525 mm FL, NHMV uncat.

range). Nakamura and Nakamura 1982:445-446 (3 specimens; Wakasa Bay, Sea of Japan; description), figs. 1A, 2A. Kyushin et al. 1982: 249 (description, photograph). Cressey et al. 1983:264 (host-parasite list, 3 copepod species). Lee and Yang 1983:231 (Taiwan), fig. 22 (550 mm FL). Collette and Nauen 1983:66-67 (description, range), fig.

Scomberomorus semifasciatus. Not of Macleay 1884. Fraser-Brunner 1950:159 (*C. koreanus* placed in synonymy of *S. semifasciatus*).

Sawara koreana. Mori 1952:136 (listed; Fusan and Chinnampo, Korea).

Scomberomorus guttatus koreanus. Silas 1964: 313-314, 325-326, 328-329 (description and range in part).

Types.—*Cybium koreanum* Kishinouye 1915 was based on a specimen collected by Yojiro Wakiya on the west coast of Korea in 1913. There is no evidence to indicate that the specimen is still extant. Data from the original description: D XIV+18-21+IX; A 18-21+VIII; GR 3+10=13; vertebrae 20+26=46.

Diagnosis.—The only species of *Scomberomorus* with four loops and five limbs to the intestine (Fig. 3f). Other species have two loops and three limbs or a straight intestine. It shares with *S. guttatus* the presence of numerous fine auxiliary branches that branch from the anterior part of the lateral line on the body (Fig. 56). Scapular foramen small (Fig. 43e) as in *S. guttatus* and *S. niphonius*. Supraoccipital crest high (Fig. 15a) as in *S. guttatus* and *S. multiradiatus*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Spines in first dorsal fin 14-17, usually 15 (Table 9); second dorsal fin rays 20-24, usually 22 or 23 (Table 10); dorsal finlets 7-9, usually 8 (Table 10); anal fin rays 20-24, usually 22 or 23 (Table 11); anal finlets 7-9, usually 7 or 8 (Table 11); pectoral fin rays 20-24, usually 22 or 23 (Table 12). Precaudal vertebrae 20 (Table 6); caudal vertebrae 26 or 27, usually 26 (Table 7); total vertebrae 46 or 47, usually 46 (Table 8). Gill rakers on first arch (1-2)+(9-12)=11-15, usually 2+(11-12)=13-14 (Table 5). Morphometric characters given in Table 18.

Size.—Maximum size 150 cm FL and 15 kg in weight; matures at 75 cm and 2.25 kg (Kishinouye 1923); common to 60 cm.

Color pattern.—Nakamura and Nakamura (1982) described fresh specimens taken in Wakasa Bay in the Sea of Japan. Body greyish blue dorsally, silvery white laterally and ventrally. Several longitudinal rows of small brownish spots rather sparsely scattered along lateral median line. First dorsal fin membrane black. Pectoral, second dorsal, and caudal fins dark brown. Pelvic and anal fins silvery white.

There are good drawings of *S. koreanus* from Japan in Kishinouye (1923:pl. 21) and from India in Devaraj (1976:fig. 2), and there is a good photograph of a specimen from the Sea of Japan in Nakamura and Nakamura (1982:fig. 1A). There is a good color illustration of *S. koreanus* in Kamohara (1967:pl. 22) and a color photograph of a 411 mm specimen from the South China Sea in Kyushin et al. (1982:249).

Biology.—Little is known of the migrations or movements of *S. koreanus*. Kishinouye (1923) reported that it spawns at the mouth of Daidoko, near Chinnanpo, Korea, in July. Feeds on sardines, anchovies, and shrimps (Kishinouye 1923).

TABLE 18.—Summary of morphometric data of *Scomberomorus koreanus*. FL = fork length, HL = head length.

Character			*N*	Min.	Max.	Mean	SD
Fork length			30	160	812	386	201
Snout-A	‰	FL	30	443	547	493	20
Snout-2D	‰	FL	30	427	512	467	15
Snout-1D	‰	FL	30	215	254	241	9
Snout-P_2	‰	FL	29	224	267	247	11
Snout-P_1	‰	FL	29	189	223	209	9
P_1-P_2	‰	FL	28	99	127	114	7
Head length	‰	FL	30	187	224	207	11
Max. body depth	‰	FL	30	185	263	236	16
Max. body width	‰	FL	26	83	115	101	9
P_1 length	‰	FL	30	112	157	134	11
P_2 length	‰	FL	26	44	67	60	7
P_2 insertion-vent	‰	FL	29	192	265	227	19
P_2 tip-vent	‰	FL	26	135	197	165	19
Base 1D	‰	FL	29	198	270	217	14
Height 2D	‰	FL	26	112	190	165	21
Base 2D	‰	FL	30	120	189	161	14
Height anal	‰	FL	26	96	184	160	19
Base anal	‰	FL	30	100	171	154	15
Snout (fleshy)	‰	FL	30	63	77	70	3
Snout (bony)	‰	FL	30	56	68	62	3
Maxilla length	‰	FL	30	93	120	110	8
Postorbital	‰	FL	29	94	114	101	5
Orbital (fleshy)	‰	FL	30	21	42	33	7
Orbital (bony)	‰	FL	30	32	61	50	9
Interorbital	‰	FL	30	52	69	61	4
2D-caudal	‰	FL	29	508	586	550	21
Head length			30	35	152	78	37
Snout (fleshy)	‰	HL	30	310	367	340	13
Snout (bony)	‰	HL	30	271	335	300	12
Maxilla length	‰	HL	30	484	565	531	17
Postorbital	‰	HL	29	459	536	488	18
Orbit (fleshy)	‰	HL	30	110	197	157	27
Orbit (bony)	‰	HL	30	170	286	238	33
Interorbital	‰	HL	30	259	350	293	22

Interest to fisheries.—The fishery for this species was begun in Daidoko, Korea, by Japanese fishermen in 1917; it is caught in summer and autumn with drift nets and pound nets (Kishinouye 1923). It is usually not distinguished from other species of seerfishes but comprises an important part of the drift net fishery in Palk Bay and the Gulf of Mannar between southeastern India and Sri Lanka (Devaraj 1976).

Distribution.—Continental Indo-West Pacific from Japan, Korea, and China south to Singapore and Sumatra and west to Bombay, India (Fig. 55). The northern limit of the range is Wakasa Bay in the Sea of Japan (Nakamura and Nakamura 1982). This species usually does not occur north of the west and south coasts of Korea (Kishinouye 1923). Specimens obtained in the Tokyo markets apparently are usually imported from Korea (Okada 1955). There are museum specimens from Ningpo (MNHN 5513), Swatow, and Hong Kong (BMNH 1939.1.17.48) along the coast of China. There appear to be few specimens or records from the coast of Indochina or the Gulf of Thailand, but we have examined specimens from "Cochinchine" (MNHN A.6827). There are several reports and specimens from Sumatra (Bagan Api Api, Hardenberg 1931 as *Cybium kuhlii*; Delsman and Hardenberg 1934 as *S. guttatus*; ZMA 114.593), but the range apparently does not extend out further into the East Indies. Dependable Indian records are from Pondicherry (USNM 216698), Palk Bay, and the Gulf of Mannar (Devaraj 1976) on the east coast, and Bombay (ANSP 88360) on the west coast.

Geographic variation.—Morphometric data were compared by ANCOVA for three small samples of *S. koreanus*: India (n = 5), East Indies (n = 9), and Japan and China (n = 8-12). Null hypotheses that the 3 sets of regression lines are coincident were accepted for 25 sets, rejected only for body width. The Newman-Keuls Multiple Range Test showed that the population from Japan and China differed significantly in slope from that in the East Indies. The population in the East Indies did not differ significantly from that in India so these two populations were combined and retested. The only significant difference was again maximum body width and the combined India-East Indies population differed significantly from the Japan-China population (slopes 0.090, 0.123, Q = 5.987**). No meristic differences were found between populations.

Material examined.—Total 30 (160-812 mm FL).

meas.:	30 (160-812) Tokyo market (4); Hong Kong (4); Swatow and Ning-Po (4), China; Indochina (1); Sumatra (8); Indonesia (1); India (5).
counts:	30.
diss.:	6 (420-812): Tokyo market, probably Korean fish (4); Indonesia (1); Hong Kong? (1).

Scomberomorus lineolatus (Cuvier)
Streaked Seerfish

Figure 57

Cybium lineolatum Cuvier *in* Cuvier and Valenciennes 1831:170-172 (original description; Malabar, India). Cantor 1849:1092-1093 (description, range; Pinang). Bleeker 1852:40-41 (description, synonymy; East Indies). Bleeker

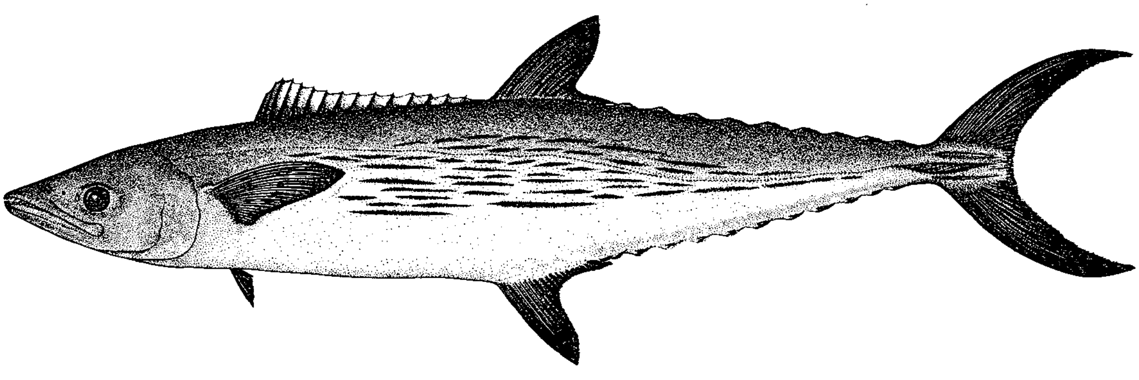


FIGURE 57.—*Scomberomorus lineolatus*. Cochin, India, 588 mm FL, USNM 223538.

1853:42 (India). Günther 1860:370 (description; Malaya). Bleeker 1861a:52 (Singapore; listed). Bleeker 1861b:74 (Pinang, Malaya; listed). Day 1873:225 (description, range). Day 1878:256 (description).

Scomberomorus lineolatum. Malpas 1926:74 (3 males, 54.5-82.5 cm TL, 1.1-3.4 kg, Ceylon). Frost 1928:329 (otolith similar to that of *S. regalis*).

Scomberomorus lineolatus. Munro 1943:68, 70 (placed in subgenus *Indocybium*; vertebral count of 21 + 29 = 50 pertains to another species of *Scomberomorus*, such as *S. guttatus*). De Beaufort 1951:235-236 (synonymy, description, range). Tham 1953:49 (Singapore Straits), 50 (correlation of catch with physical factors and presence of food fishes such as *Stolephorus* and *Clupea*). Scott 1959:114 (description; Malaya), photograph. Bauchot and Blanc 1961:372 (types of *Cybium lineolatum*). Jones 1962:117-119 (eggs, larvae, and juveniles). Jones and Silas 1961:197-198 (description, range), fig. 4 (680 mm adult), fig. 5C (not 5D as legend reads, lateral view of head), fig. 6D (gill arch), fig. 7E (caudal peduncle keels). Jones and Silas 1964: 58-61 (synonymy, description, range), pl. 7, fig. A (photograph of 740 mm specimen). Silas 1964:317, 323-324 (specimens from India only). Jones and Kumaran 1964:347 (larvae as yet undescribed). Blanc and Bauchot 1964:447 (types of *Cybium lineolatum*), pl. III, figs. 15, 16 (photographs of type-specimens). Rao 1964: 592-594 (teleosts constitute 97% of diet of juveniles, Waltair coast of India). Thiemmedh 1966:140 (common names). Collette 1966:367-368 (type of *Cybium lineolatum*). Tongyai 1966a:7-10 (synonymy, occurrence, Thailand), pl. 2D. Tongyai 1966b:3-15 (5 specimens, 46.5-76.5 cm FL; Terutao Is., Andaman Sea). Pathansali 1968:1002-1003 (fishery; Malaya). Silas 1968:1114 (fishery; Gulf of Mannar), pl. 3A (photograph of adult). Rajan et al. 1969:90 (outer channel; Chilka Lake, India). Tongyai 1970:559-561 (found in areas of low turbidity and high salinity offshore; Thailand). Merçeron 1970:72 (specimens from near Sihanoukville, Cambodia). Tongyai 1971a:16-18 (Thailand). Fernando 1972:524, 530 (incidental catches in trawls; Wadge Bank, Ceylon). Richards and Klawe 1972:14 (range), 92 (references to larvae and juveniles). Banerji 1973:129-130 (seerfish fishery; India). Magnuson 1973:350 (short pectoral fin). Orsi 1974:175 (listed; Vietnam). Tham 1974 (possible predator of *Stolephorus*). Shiino 1976:231 (common name). *Rao and Ganapati 1977:101-111 (postlarvae and juveniles; India). Klawe 1977:2 (common name, range). *Devaraj 1977 (osteology). Collette 1979:29 (characters). Collette and Russo 1979:13 (diagnostic characters, range). *Devaraj 1982 (age and growth). Cressey et al. 1983:264 (host-parasite list, 3 copepod species). Collette and Nauen 1983:68 (description, range), fig.

Scomberomorus guttatus. Not of Bloch and Schneider 1801. Fraser-Brunner 1950:160 (*Cybium lineolatum* placed in synonymy of *Scomberomorus guttatus*).

Indocybium lineolatum. Munro 1955:221 (description; Ceylon); fig. 651. Chacko et al. 1968: 1006 (fishery; Madras).

Types.—Holotype: MNHN A.6866; Malabar coast of India; Dussumier; 707 mm FL; D about XVII + 17 + IX; A 19 + X; P_1 21; RGR_1 2 + 1 + 8 = 11; pattern of three rows of elongate streaks still visible on type in 1975. Photograph of type published by Blanc and Bauchot (1964:pl. 3, fig. 15). Paratype: MNHN 6357; Mahé (Malabar Coast), Belenger; only head and tail of a fish about 710 mm FL (judging from head length of 145 mm). Photograph of paratype published by Blanc and Bauchot (1964:pl. 3, fig. 16).

Diagnosis.—The only species of *Scomberomorus* that has a pattern of short lines on its sides (Fig. 57). Other species have some spots, blotches, or bars, or are plain. Posterior end of maxilla greatly expanded as in *S. plurilineatus* and *S. semifasciatus.* Anterior end of premaxilla forms an acute angle (Fig. 22b). Ascending process of premaxilla very long as in *S. sinensis* and *Acanthocybium.* Supracleithrum wide (Fig. 41a), 53-57% of length, as in *S. niphonius.* Foramen between last pectoral radial and coracoid larger than in any other species of *Scomberomorus.*

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3g). Spines in first dorsal fin 15-18, usually 16 or 17 (Table 9); second dorsal fin rays 15-22, usually 17 or 18 (Table 10); dorsal finlets 7-10, usually 9 (Table 10); anal fin rays 17-22, usually 20 (Table 11); anal finlets 7-10, usually 9 or 10 (Table 11); pectoral fin rays 20-24, usually 23 (Table 12). Precaudal vertebrae 18-20, usually 19 (Table 6); caudal vertebrae 25-28, usually 27 (Table 7); total vertebrae 44-46, usually

46 (Table 8). Gill rakers on first arch (1-2) + (6-11) = 7-13, usually 2 + (8-9) = 10-11 (Table 5). Morphometric characters given in Table 19.

TABLE 19.—Summary of morphometric data of *Scomberomorus lineolatus*. FL = fork length, HL = head length.

Character			N	Min.	Max.	Mean	SD
Fork length			31	144	786	434	191
Snout-A	‰	FL	30	464	540	507	16
Snout-2D	‰	FL	29	453	525	502	17
Snout-1D	‰	FL	30	214	284	253	17
Snout-P_2	‰	FL	27	209	268	245	13
Snout-P_1	‰	FL	30	175	237	213	14
P_1-P_2	‰	FL	27	81	104	93	6
Head length	‰	FL	31	174	231	207	13
Max. body depth	‰	FL	27	153	211	181	11
Max. body width	‰	FL	25	65	117	96	13
P_1 length	‰	FL	28	117	156	140	11
P_2 length	‰	FL	20	45	70	56	7
P_2 insertion-vent	‰	FL	24	216	276	240	14
P_2 tip-vent	‰	FL	20	156	223	184	15
Base 1D	‰	FL	24	198	270	231	15
Height 2D	‰	FL	23	87	168	124	19
Base 2D	‰	FL	29	89	155	113	15
Height anal	‰	FL	22	80	148	118	15
Base anal	‰	FL	28	100	150	123	14
Snout (fleshy)	‰	FL	30	64	88	82	6
Snout (bony)	‰	FL	30	55	83	74	6
Maxilla length	‰	FL	30	93	136	113	11
Postorbital	‰	FL	30	75	108	92	8
Orbital (fleshy)	‰	FL	30	23	43	33	6
Orbital (bony)	‰	FL	29	34	64	48	9
Interorbital	‰	FL	29	47	61	57	3
2D-caudal	‰	FL	29	462	545	500	23
Head length			31	33	147	88	35
Snout (fleshy)	‰	HL	30	325	438	395	24
Snout (bony)	‰	HL	30	276	398	358	28
Maxilla length	‰	HL	30	473	596	547	24
Postorbital	‰	HL	30	404	512	443	24
Orbit (fleshy)	‰	HL	30	131	215	157	24
Orbit (bony)	‰	HL	29	188	284	231	30
Interorbital	‰	HL	29	255	292	275	10

Size.—Maximum size 80 cm FL.

Color pattern.—Body dark bluish dorsally, silvery white ventrally, marked with several rows of elongate lines (Fig. 57). First dorsal fin black anteriorly, white posteriorly.

There is a good drawing of a specimen from India in Jones and Silas (1962:fig. 4). There are also poor photographs in Jones and Silas (1964:pl. 7) and Silas (1968:pl. 3).

Biology.—Little has been reported in the literature on the biology of *S. lineolatus*. A ripe male (82.5 cm TL, 3.4 kg) was taken on Wadge Bank, off southern India on 2 October (Malpas 1926). A running ripe female (76.5 cm, 4.4 kg) was caught in January in the Bay of Bengal off Satun, Thailand, near the border with Malaysia (Tongyai 1966b). Postlarvae and juveniles (18.4-99.5 mm) were described from Waltair on the east coast of India by Rao and Ganapati (1977). Early stages were taken in shore seines in February-April, more advanced stages from boat seine catches in July-September. Juveniles feed on teleosts in India (Venkataraman 1961; Rao 1964).

Interest to fisheries.—There are small fisheries for *S. lineolatus* in the waters around Thailand, Malaysia, and India. It is taken from October to November in Thai waters of the Indian Ocean (Tongyai 1970). It is less abundant than either *S. commerson or S. guttatus* in the Gulf of Thailand and along the Thai coast of the Bay of Bengal being found in areas of lower turbidity and higher salinity than the other two species (Tongyai 1970). Fished for on both coasts of Malaysia, on the west coast from November to February in the north and March to July in the south, and on the east coast from February to March and August to November (Pathansali 1968). Species of *Scomberomorus* are taken on both coasts of Malaysia mainly by gill nets, but hand lines and trolling lines are also important on the east coast (Pathansali 1968). In India, there is an important coastal fishery for the three species of seerfishes of which *S. lineolatus* is the least common (Silas 1968). Small individuals, up to 50 cm, are taken, together with *S. commerson* and *S. guttatus*, during the multiple troll fishery season (May-September) in gill nets 5-12 mi off Tuticorin in the Gulf of Mannar, India (Silas 1968). Gill nets, hook and line, and trolling are the most important gear types in India (Silas 1968). *Scomberomorus* spp., or pla in-see in Thai, are highly esteemed foodfishes in Thailand and are consumed as spicy fish-burgers (tod-mun pla in-see) or high-quality salted fish (Tongyai 1966a). A monthly average of about 100 t, fresh or salted, is consumed in Bangkok alone (Tongyai 1966a). Seerfishes form a much smaller proportion of the catch in India than mackerels (*Rastrelliger* spp.), but are much in demand both fresh and salt-cured (Jones 1968).

Distribution.—Gulf of Thailand and Java west around India at least to Bombay (Fig. 58). There are records and specimens from Cambodia (Merçeron 1970) and Thailand (Tongyai 1966b, 1971a; CAS-GVF 60-286) in the Gulf of Thailand and from both coasts of Malaysia (Cantor 1849; Bleeker 1861b; Scott 1959; CAS SU 14100; BMNH 1860.3.19.215), Singapore Straits (Tham 1953), Java (USNM 72632), and Sumatra (NHMV 1874.I; ZMA 114.595). Central Indian Ocean reports and specimens are from Madras (ZSI 2156-7), Palk Bay (Devaraj 1977; dissections), Sri Lanka (Fernando

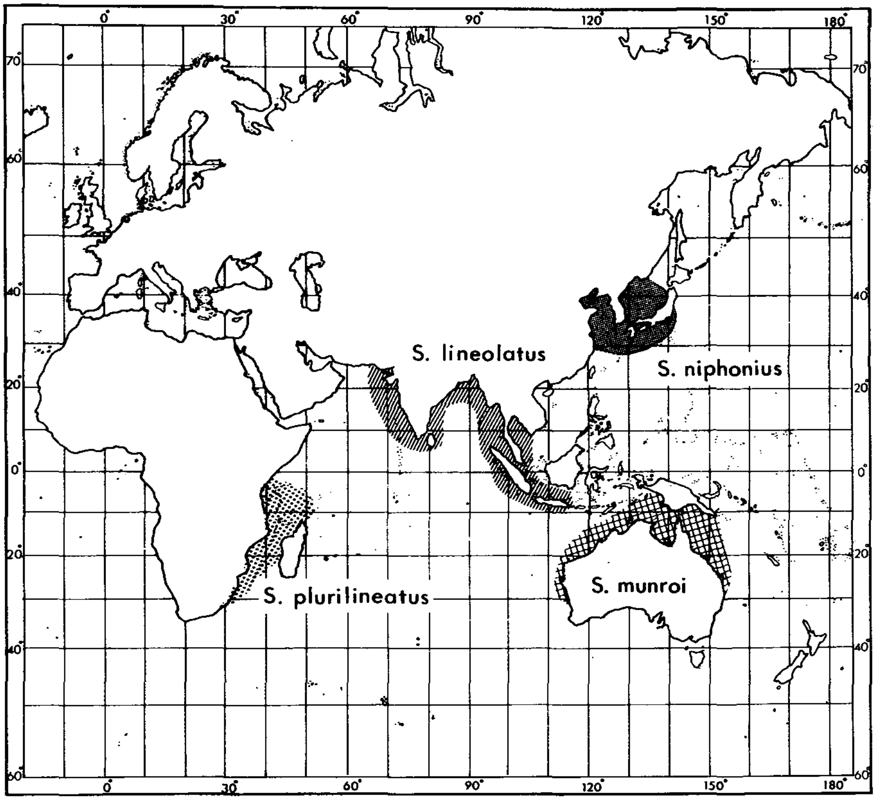


FIGURE 58.—Ranges of four Indo-West Pacific species of *Scomberomorus*: *S. lineolatus*, *S. plurilineatus*, *S. niphonius*, and *S. munroi*.

1972), Wadge Bank south of India (Malpas 1926), the Malabar coast (MNHN A.6866, holotype of *C. lineolatum*), Cochin (5 specimens measured, 1 dissected), and Bombay (MNHN A.5783). Records of *S. lineolatus* from East Africa (Williams 1960) are referrable to *S. plurilineatus*. The report of *S. lineolatus* from Western Australia (McKay 1970) was based on a specimen (HUMZ F-422) of *S. munroi*.

Geographic variation.—Comparisons of morphometric data by ANCOVA were made for four small samples of *S. lineolatus*: Arabian Sea (n = 7-12), Bay of Bengal (n = 4-6), Gulf of Thailand (n = 3-5), and East Indies (n = 4-6). No significant differences were found. No meristic differences were found between populations.

Material examined.—Total 31 (160-786 mm FL).

meas.: 31 (160-786): India, Arabian Sea (8, *C. *lineolatum* Cuvier), Bay of Bengal (7); Andaman Sea (4); Gulf of Thailand (5); East Indies (7).
counts: 31.
diss.: 5 (417-786): Palk Strait (4); Cochin (1).

Scomberomorus maculatus (Mitchill) Spanish Mackerel

Figure 59

Scomber maculatus Mitchill 1815:426-427 (original description; New York), pl. 6, fig. 8.
Cybium maculatum. Cuvier 1829:200 (listed in footnote after *Sc. maculatus* Mitchill). Cuvier *in* Cuvier and Valenciennes 1831:181 (description; New York). Storer 1855:146-147 (synonymy, description; exceedingly rare in Massachusetts, 1 from Lynn and 4 from Provincetown), pl. 13, fig. 1. Holbrook 1860:68-72 (synonymy, description, color, anatomy, range in part), pl. 9, fig. 1. Günther 1860:372 (synonymy, description). Poey 1878:4 (synonymy, description).

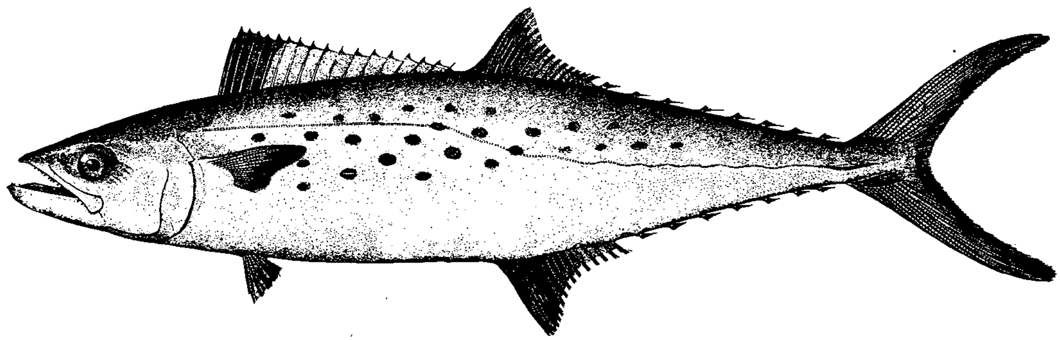


FIGURE 59.—*Scomberomorus maculatus.* New York market, 270 mm FL, USNM 15582. (From Goode 1884:pl. 93.)

Smiley 1881 (distribution, fishery). Ryder 1882 (gonads, embryology, development), pl. 1-4 (eggs, embryos, and larvae). Earll 1883 (name, description, distribution, movements, reproduction, fishery, artificial propagation), pl. 1.

Scomberomorus maculatus. Jordan and Gilbert 1882:426 (synonymy, range in part). Goode 1884:307-315 (range, fishery, reproduction), pl. 93. Meek and Newland 1884:232-234 (description, synonymy, range in part). Dresslar and Fesler 1889:442 (in key), 443 (synonymy and range in part), pl. 9. Jordan and Evermann 1896b:874 (description, synonymy in part). Jordan and Evermann 1900:pl. 134, fig. 368 (specimen from New York market). Jordan and Evermann 1902:285-286 (description, range), fig., photograph. Bean 1903:396-398 (synonymy, description, range in part, occurrence in New York). Smith 1907:190-192 (diagnosis, size, range, catch, price; North Carolina), fig. 77. Sumner et al. 1913:750 (references, occurrence, parasites; Buzzards Bay and Vineyard Sound, Mass.). Schroeder 1924:6-7 (most valuable food fish in the Florida Keys, range in part), fig. 3. Nichols and Breder 1927:123-124 (description, range, biology), fig. 170. Frost 1928 (sagitta similar to that of *S. regalis*). Hildebrand and Schroeder 1928:203-205 (description, range, biology, synonymy; Chesapeake Bay), fig. 115. Nichols 1929:229-230 (synonymy, range, description), fig. 82. Hildebrand and Cable 1938:508-518 (development of larvae and postlarvae; Beaufort, N.C.), figs. 2-10 (larvae and juveniles, 2.75-97 mm). Baughman 1941:17 (migratory off Texas coast). Munro 1943:67, 71-72 (placed in subgenus *Scomberomorus*). Fowler 1945:185-186 (synonymy, description; South Carolina). Gunter 1945:55 (occurrence, Texas), 145 (monthly production, 1937-42; Texas). La Monte 1945:26, 28 (description, range), color pl. 11. Breder 1948:127 (range in part, biology), fig. Erdman 1949:301 (range confined to coastal America and the N coast of Cuba; other West Indian records are misidentifications). Fraser-Brunner 1950: 159 (synonymy and range in part), fig. 29. Baughman 1950:244 (numerous Texas records throughout the year). Knapp 1950:142 (458 stomach contents, Texas). Rivas 1951:225-226 (synonymy in part, diagnosis, range). Taylor 1951:116-118 (biology, occurrence in North Carolina), 271-272 (angling in North Carolina). La Monte 1952:50 (description, range), color pl. 18. Bigelow and Schroeder 1953:347-348 (description, range in part, only a stray in the Gulf of Maine), fig. 182. Pew 1954:26 (description, range, habits), fig. 23. Mather and Day 1954: 185 (comparison of W and E Atlantic specimens; *S. tritor* at best racially distinct from *S. maculatus*). Briggs 1958:286 (range in part). Springer and Pirson 1958:175 (catch in Texas). *Mago Leccia 1958 (osteology, comparisons with *S. regalis* and *S. cavalla*), figs. *Klima 1959 (distribution, biology). Moe 1963: 109 (second most fished for species by private boats in Florida). Jorgensen and Miller 1968: 9, 13 (SL-FL-TL conversions). *Mendoza 1968 (biology; Veracruz). Lyles 1969:1-15 (landings, in part). Wollam 1970 (development, pigmentation, counts, and measurements; 175 larvae and juveniles, 3.1-25 mm SL, from the Gulf of Mexico), figs. 2, 3, 6A (larvae and juveniles, 3.1-25 mm SL). Beardsley and Richards 1970:5 (length-weight of 35 specimens from SE Florida, 330-770 mm FL, 0.45-4.76 kg). Farragut 1972 (use of antioxidants to prevent rancidity during frozen storage). Richards and Klawe 1972:14 (range in part), 92-93 (references to eggs and larvae). Miyake and Hiyasi 1972:III-3 (in key); IV-11 (common names). Dwinell and Futch 1973 (188 larvae and juveniles, 2.8-42.2 mm SL, caught in June, Aug., and Sept., NE Gulf of Mexico). Márquez 1973 (distribution, biology, fishery). *Powell 1975 (age, growth, reproduction; Florida). *Berrien and Finan 1977b (in part; species synopsis). Klawe 1977:2 (common names, range). Fritzsche 1978:126-132 (description, larval development), figs. 70-74 (eggs, larvae, and juveniles). Collette 1978: Scombm 5 (description, range), figs. Collette et al. 1978:274-275 (comparison with other American species of *Scomberomorus*). Manooch et al. 1978 (annotated bibliography). Pristas and Trent 1978:582-588 (most abundant spring-fall; St. Andrew Bay, Fla.). Collette 1979:29 (characters, range). Collette and Russo 1979:13 (diagnostic characters, range). Trent and Anthony 1979 (commercial and recreational fisheries in U.S.). Doi and Mendizábal 1979 (Mexican catch). Meaburn 1979 (heavy metal contamination). Hale 1979 (preservation technology). Amezcua-Linares and Yáñez-Arancibia 1980:86-90 (Campeche, Mexico). McEachran et al. 1980 (larvae off Texas coast). Sutherland and Fable 1980 (annual migration from wintering grounds off S Florida and Campeche to summer grounds along the N coast of the Gulf of Mexico, return migration in fall). Deardorff and Overstreet 1981 (larvae of 4 forms of the anisakid nematode *Hysterothylacium* found in mesentary of specimens from the Gulf of Mexico). Johnson 1981 (electrophoresis; NW Florida). Skow and Chittenden 1981 (differences between Atlantic coast and Gulf of Mexico populations by hemoglobin electrophoresis). Richardson and McEachran 1981 (larvae 1.8-2.9 mm SL, pigment characters, measurements; Gulf of Mexico), fig. 1B (2.1 mm larva). Naughton and Saloman 1981 (stomach contents of 344 juveniles, 117-432 mm FL; Cape Canaveral, Fla., and Galveston, Tex.; diet mainly clupeoids). Adkins and Bourgeois 1982:12-13, 32-35, 48 (gill net; Louisiana). Cressey et al. 1983:264 (host-parasite list, 4 copepod species). Collette and Nauen 1983:69-70 (description, range), fig. Saloman and Naughton 1983b (food in U.S. waters).

Types.—*Scomber maculatus* Mitchill 1817 was based on a 19-in (482.6 mm) fish from New York. No types known to be extant. The figure (pl. 6, fig. 8) and description (about 20 yellowish spots decorate sides; more than half anterior part of first dorsal fin black, remainder white) leave no doubt as to identity of name.

Diagnosis.—*Scomberomorus maculatus* possesses nasal denticles as do the other five species of the *regalis* group (*brasiliensis*, *concolor*, *regalis*, *sierra*, and *tritor*) and has an artery branching from the fourth left epibranchial artery as do all the species in the group except *S. tritor.* Like *S. concolor*, *S. maculatus* lacks the shunt from the fourth right epibranchial artery to the coeliacomesenteric artery (Fig. 7c). It also has more vertebrae (51-53) than any of the other five species in the group (46-49). Intercalar spine absent as in the other five species of the *regalis* group and *S. niphonius*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3h). Spines in first dorsal fin 17-19, usually 18 (Table 9); second dorsal fin rays 17-20, usually 18 or 19 (Table 10); dorsal finlets 7-9, usually 8 or 9 (Table 10); anal fin rays 17-20, usually 19 or 20 (Table 11); anal finlets 7-10, usually 8 or 9 (Table 11); pectoral fin rays 20-23, usually 21 (Table 12). Precaudal vertebrae 21 or 22, usually 21 (Table 6); caudal vertebrae 30 or 31 (Table 7); total vertebrae 51-53, usually 51 or 52 (Table 8). Gill rakers on first arch (1-4)+(8-13)=10-16, usually 2+(10-11)=12-14 (Table 5). Morphometric characters given in Table 20.

Size.—Maximum size 77 cm FL, 4.8 kg (Beardsley and Richards 1970). Sexual maturity in Florida is attained by age II, at 25-32 cm FL for females, 28-34 cm for males (Klima 1959). Length-weight equations have been presented for populations in Florida (Powell 1975) and Veracruz (Doi and Mendizábal 1979).

Color pattern.—Dark bluish above, silvery below, sides marked with about three rows of round to elliptical dark spots (Fig. 59), orange in life. First dorsal fin black anteriorly and at distal margin posteriorly, basal part of posterior membranes white.

There is a color painting of an *S. maculatus* in La Monte (1945:pl. 11, 1952:pl. 18), and a black and white photograph of one in Jordan and Evermann (1902). The drawing published by Goode (1884:pl. 93) is included here as Figure 59.

Biology.—Summaries of biological information have been presented by Mendoza (1968), Márquez (1973), and Berrien and Finan (1977b). There is also a useful annotated bibliography by Manooch et al. (1978). The Spanish mackerel is clearly a migratory species that moves north from Florida along the Atlantic coast of the United States and north and west along the coast of the Gulf of Mexico in the spring and returns in the fall, but the details of the migration are not completely known. There are large concentrations in the winter in Florida and the Florida Keys (Beaumariage 1970) which move north to reach Charleston, S.C., in late March, North Carolina in April, Chesapeake Bay in May, and Sandy Hook, N.J., to Narragansett Bay, R.I., by late July (Earll 1883; Beaumariage 1970). Schools also move north along the Gulf coast of Florida in the spring (Moe 1972), and west across the northern Gulf from Panama City, Fla., to Mobile, Ala. (Sutherland and Fable 1980), and possibly on into Texas reaching Galveston in early March and Port Aransas in late March (Baughman 1941). There is also north-south migration along the Mexican coast, from south to north in March-April, north to south in August-November (Mendoza 1968). Tag returns support the Panama City to Mobile and Port Aransas to Veracruz *migrations* (Sutherland and Fable 1980). Spawning takes place in New York-New Jersey late August-late September, in Chesapeake Bay mid-June to the end of summer, and in the Carolinas starting in April (Earll 1883). Ripe females were found in Florida from July to September by Klima (1959) and from April to September by Powell (1975). Powell felt that individuals spawned repeatedly in a prolonged spawning season in Florida. Spanish mackerel spawn from May to September in waters <50 m over the inner continental shelf of Texas (McEachran et al. 1980). Spawning in Veracruz takes place in July-September (Mendoza 1968). Early studies on developing eggs and larvae (to 6 d old) were carried out by Ryder (1882) in North Carolina. Larvae have been described from North Carolina (14-20 mm, Hildebrand and Cable 1938; some misidentified, see Wollam 1970), the west coast of Florida (3.1-35.0 mm, June-September, Wollam 1970), the northeastern Gulf of Mexico (2.8-42.2 mm SL, June-September, Dwinell and Futch 1973), and Texas (1.8-11.5 mm SL, May-September, McEachran et al. 1980). Most were taken over the middle and

TABLE 20.—Summary of morphometric data of *Scomberomorus maculatus*. FL = fork length, HL = head length.

Character			Atlantic					Gulf of Mexico					Total				
			N	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD
Fork length			24	163	712	330	137	36	152	593	307	95	60	152	712	316	113
Snout-A	‰	FL	24	515	570	538	14	36	507	565	534	14	60	507	570	536	14
Snout-2D	‰	FL	24	478	540	505	14	36	466	543	502	16	60	466	543	503	15
Snout-1D	‰	FL	24	227	260	240	10	36	226	258	242	7	60	226	260	241	8
Snout-P_2	‰	FL	22	216	279	249	14	32	228	300	263	17	54	216	300	257	17
Snout-P_1	‰	FL	24	199	247	217	14	36	193	261	217	12	60	193	261	217	13
P_1-P_2	‰	FL	21	95	121	108	8	34	97	132	111	9	55	95	132	110	9
Head length	‰	FL	24	195	281	213	18	36	195	227	211	9	60	195	281	212	13
Max. body depth	‰	FL	18	168	232	194	19	33	178	228	198	12	51	168	232	197	15
Max. body width	‰	FL	18	70	110	89	12	36	65	137	92	15	54	65	137	91	14
P_1 length	‰	FL	24	114	146	131	7	35	107	140	129	8	59	107	146	129	8
P_2 length	‰	FL	21	43	66	55	6	33	35	68	50	9	54	35	68	52	8
P_2 insertion-vent	‰	FL	22	241	305	270	16	33	223	299	259	19	55	223	305	263	19
P_2 tip-vent	‰	FL	21	186	246	215	18	31	175	233	208	13	52	175	246	211	15
Base 1D	‰	FL	24	236	288	258	13	36	222	286	254	14	60	222	288	256	13
Height 2D	‰	FL	21	92	153	124	14	28	108	141	125	10	49	92	153	125	12
Base 2D	‰	FL	24	109	150	128	10	35	110	158	128	11	59	109	158	128	11
Height anal	‰	FL	23	97	140	117	13	31	88	133	119	12	54	88	140	118	12
Base anal	‰	FL	24	100	157	122	14	36	101	147	124	10	60	100	157	123	12
Snout (fleshy)	‰	FL	24	73	86	78	3	36	74	90	80	4	60	73	90	80	4
Snout (bony)	‰	FL	24	59	78	69	4	23	63	84	72	5	47	59	84	70	5
Maxilla length	‰	FL	24	108	134	117	7	36	110	136	120	6	60	108	136	119	6
Postorbital	‰	FL	23	87	108	98	5	36	84	101	95	4	59	84	108	96	4
Orbital (fleshy)	‰	FL	24	24	47	34	7	35	26	47	34	4	59	24	47	34	5
Orbital (bony)	‰	FL	24	41	62	50	7	36	40	65	52	6	60	40	65	51	7
Interorbital	‰	FL	24	51	60	56	2	36	52	63	57	3	60	51	63	56	3
2D-caudal	‰	FL	23	462	521	493	19	36	438	524	483	22	59	438	524	487	21
Head length			24	38	147	69	27	36	34	129	65	20	60	34	147	67	23
Snout (fleshy)	‰	HL	24	271	401	369	25	36	346	416	381	16	60	271	416	376	21
Snout (bony)	‰	HL	24	237	360	327	25	23	325	385	343	15	47	237	385	335	22
Maxilla length	‰	HL	24	401	572	552	34	36	546	628	568	15	60	401	628	562	25
Postorbital	‰	HL	23	317	496	461	37	36	407	486	450	16	59	317	496	454	27
Orbit (fleshy)	‰	HL	24	103	204	159	27	35	121	216	160	17	59	103	216	160	21
Orbit (bony)	‰	HL	24	153	284	234	29	36	186	308	246	27	60	153	308	242	28
Interorbital	‰	HL	24	204	296	264	20	36	234	296	268	13	60	204	296	266	16

inner continental shelf, over depths from 12 to 50 m, off Texas at surface water temperatures of 19.6°-29.8° C and salinities of 28.3-37.4‰ (McEachran et al. 1980). Summaries of previous larval work and illustrations of larvae 2.6-13.5 mm and of juveniles 14-97 mm are contained in Fritzsche (1978). As with other members of the genus, food consists chiefly of small fishes with lesser quantities of penaeoid shrimps and cephalopods. Clupeoids such as menhaden (*Brevoortia*), alewives (*Alosa*), thread herring (*Opisthonema*), Spanish sardine (*Sardinella*), and anchovies (*Anchoa*) are particularly important in North Carolina, Florida, Texas, and Veracruz (Earll 1883; Knapp 1950; Miles and Simmons 1951; Klima 1959; Mendoza 1968; Naughton and Saloman 1981; Saloman and Naughton 1983b). Juveniles (100-400 mm FL) ate more anchovies (Naughton and Saloman 1981; Saloman and Naughton 1983b) than adults did. Other fishes commonly consumed include Carangidae, Mugilidae, and Trichiuridae (Klima 1959; Saloman and Naughton 1983b).

Interest to fisheries.—The Spanish mackerel is a valued fish to recreational or commercial fisheries throughout its range. The fishery along the Atlantic coast of the United States north of southern Florida is seasonal (Klima 1959): late July to September from Rhode Island to New Jersey (Earll 1883), May or June to September in Chesapeake Bay (Hildebrand and Schroeder 1928), April to June on the way north, and September-October on the way south through the Carolinas (Smith 1907; Taylor 1951). The fishery in southern Florida is concentrated in the winter months, October-February or March (Klima 1959; Beaumariage 1970). In northwest Florida, the fishery peaks March-April (Beaumariage 1970); in Louisiana in June and October (Adkins and Bourgeois 1982); and in Texas March-April and July-September (Springer and Pirson 1958). As in the Carolinas, there are two major capture seasons in Veracruz: 45% of the annual production is taken March-April during the northward migration and 30% October-December in the southward migration (Doi and Mendizábal 1979). The beginnings of the Spanish mackerel fishery in the United States were discussed by Earll (1883) and a historical summary of the U.S. catch from 1887 to 1967 was provided by Lyles (1969). The commercial fishery began along the middle Atlantic and Chesapeake Bay areas before 1850, and by 1880 about 86% of the total U.S. catch of 1.9 million pounds was landed in the Chesapeake Bay area (Trent and Anthony 1979). Since 1950, over 92% of the total U.S. catch has been landed in Florida (Trent and Anthony 1979). In 1976 about 18 million pounds valued at about $3.2 million were landed by commercial fishermen in the United States; in 1970 an estimated 23 million pounds were landed by recreational fishermen (Trent and Anthony 1979). Spanish mackerel is second in volume among Mexico's Gulf of Mexico fisheries with an average annual production from 1968 to 1976 of 4,900 t (Doi and Mendizábal 1979). Most of this (80%) is produced in the state of Veracruz with lesser amounts from Campeche (15%) and Yucatan (5%). The early fishery in the United States utilized trolling lines, gill nets, and pound nets (Earll 1883). The commercial fishery in Florida utilizes stab or floating gill nets, which capture fish of age II-III, 30-65 cm FL (52% 36-41 cm), and hook and line, which captures smaller fish, age I-II, 21-69 cm FL (38% 33-35 cm) (Klima 1959). Larger vessels now entering the fishery have power-rollers to retrieve the nets which are mostly nylon; airplane spotter pilots locate the fish (Trent and Anthony 1979). Recreational anglers catch Spanish mackerel from boats while trolling or drifting and from boats, piers, jetties, and beaches by casting, livebait fishing, jigging, and drift fishing (Trent and Anthony 1979). Fishermen in Veracruz employ beach seines (chinchorros playeros), gill nets (redes agalleras), trolling spoons (curricanes), and trap nets (almadrabas) (Doi and Mendizábal 1979). Nearly all the catch is consumed fresh, frozen, or smoked (Lyles 1969). A few attempts have been made at canning Spanish mackerel but the product has not been widely accepted (Earll 1883; Lyles 1969). Frozen fish begin to show signs of rancidity after as little as 3 mo time in frozen storage, a problem which has been treated with antioxidants and EDTA (Farragut 1972; Hale 1979).

Distribution.—Western Atlantic Ocean from Massachusetts south along the Atlantic coast of the United States and the coast of the Gulf of Mexico from Florida to Yucatan, Mexico (Fig. 49). There are several summer records from the southern side of Cape Cod, Buzzards Bay, Woods Hole, and Vineyard Sound (Sumner et al. 1913; Bigelow and Schroeder 1953), but only strays are known from further north. Storer (1855) recorded the capture of an individual at Lynn in Massachusetts Bay and stated that individuals had been obtained at Provincetown, at the tip of Cape Cod, and at Monhegan Island in Maine. There do not appear to be any extant specimens to verify these records; there is one specimen labelled only as "Cape Cod" (MCZ 23929). The known southern limit of the range is Progreso, Yucatan (MCZ 32894); it is replaced by *S. brasiliensis* from Belize to Rio de Janeiro and by *S. regalis* in the Bahamas and West Indies. Reports of *S. maculatus* from the West Indies (except for the north coast of Cuba) are referrable to *S. regalis* (Erdman 1949), those from the eastern Pacific are based on *S. sierra*, and those from the eastern Atlantic on *S. tritor*.

Geographic variation.—Morphometric characters were compared for two populations of *S. maculatus* by ANCOVA (Table 20): Atlantic coast of the United States (n = 18-24) and Gulf of Mexico (n = 28-36). Null hypotheses that the 2 sets of regression lines are coincident were accepted for 20 sets of regressions and rejected for 6: Sn-1D, Sn-P_2, P_1L, Snout (fleshy), Snout (bony), and maxilla length.

There is also a difference in vertebral numbers between the eastern U.S. and Gulf of Mexico populations. The eastern U.S. population usually has 31 caudal and 52 total vertebrae ($\bar{x}$ 30.4, 51.5), the gulf population has 30 or 31 caudal and 51 or 52 total vertebrae ($\bar{x}$ 30.9, 52.1).

The Gulf of Mexico and eastern U.S. populations also differ electrophoretically. Skow and Chittenden (1981) found differences in hemoglobin phenotypes between samples from Port Aransas, Tex., and Beaufort, N.C.

Material examined.—Total 69 (152-712 mm FL).

meas.: 60 (152-712): Atlantic coast of U.S. (24); Gulf of Mexico coast of U.S. (35); Yucatan (1).
counts: 67.
diss.: 16 (281-712): Va.-N.C. (3); Ga.-Fla. (7); St. Andrews Bay, Gulf of Mexico, Fla. (6).

Scomberomorus multiradiatus Munro
Papuan Seerfish
Figure 60

Scomberomorus multiradiatus Munro 1964:168-169 (original description; Gulf of Papua off mouth of Fly R.), fig. 12 (holotype). Munro 1967:200 (description), fig. 339. Magnuson 1973:350 (short pectoral fin). Kailola 1975:235 (4 specimens listed; Orokolo Bay, Tureture, 17 mi W of Fly R.). Klawe 1977:2 (range, common name). Kailola and Wilson 1978:34 (trawled in Gulf of Papua), 60 (number of fin rays). Collette 1979:29 (diagnostic characters). Collette and Russo 1979:13 (diagnostic characters, range). Lewis 1981:16 (photograph, biology). Cressey et al. 1983:264 (host-parasite list, 2 copepod species). Collette and Nauen 1983: 70-71 (description, range), fig.

Types.—Holotype: CSIRO C.3172; off northern mouth of Fly River, Papua New Guinea; MV *Fairwind*; 1948-50; 232 mm FL; D XVII + 23 + VIII; A 28 + VI; P_1 23-23; RGR_1 0 + 1 + 2 = 3; vertebrae 20 + 35 = 55; no spots or vertical bars. Holotype illustrated by Munro (1964:fig. 12, 1967:fig. 339).

Diagnosis.—The species of *Scomberomorus* with the most vertebrae (54-56) and the fewest gill

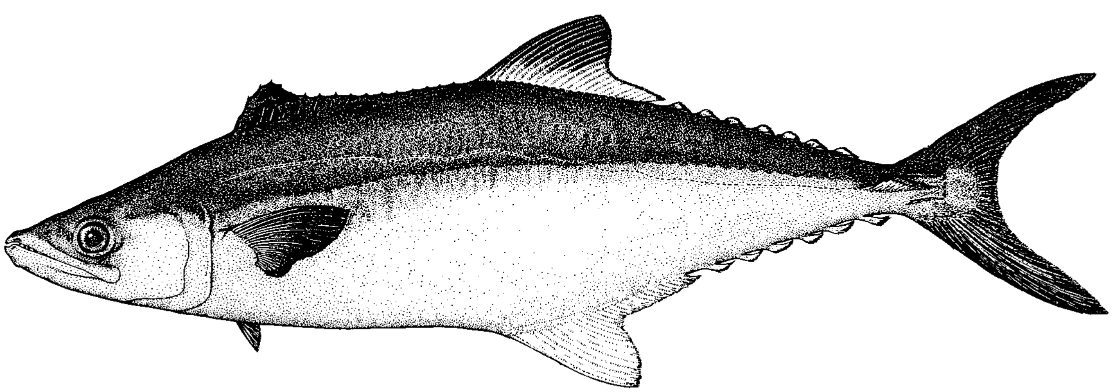


FIGURE 60.—*Scomberomorus multiradiatus*. Gulf of Papua, 312 mm FL, USNM 233696.

rakers (1-4) compared with the other 17 species (vertebrae 41-53, gill rakers 1-27). It has the most rays in the anal fin (25-29, compared with 15-24 in the other 17 species). Posterior end of maxilla only slightly expanded as in *S. sinensis*. Supraoccipital crest high as in *S. guttatus* and *S. koreanus*. Supracleithrum narrow (Fig. 41b), 43-53% of length as in *S. sinensis*, *semifasciatus*, and *sierra*. Foramen between last pectoral radial and coracoid smaller than in any other species of *Scomberomorus*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3i). Spines in first dorsal fin 16-19, usually 17 or 18 (Table 9); second dorsal fin rays 21-25, usually 23 or 24 (Table 10); dorsal finlets 7-9, usually 7 or 8 (Table 10); anal fin rays 25-29, usually 26-28 (Table 11); anal finlets 6-8, usually 6 (Table 11); pectoral fin rays 20-23, usually 21 or 22 (Table 12). Precaudal vertebrae 20 or 21 (Table 6); caudal vertebrae 34-36, usually 34 or 35 (Table 7); total vertebrae 54-56, usually 55 or 56 (Table 8). Gill rakers on first arch 0 + (1-4) = 1-4, usually 0 + (2-3) = 2-3 (Table 5). Morphometric characters given in Table 21.

TABLE 21.—Summary of morphometric data of *Scomberomorus multiradiatus*. FL = fork length, HL = head length.

Character			*N*	Min.	Max.	Mean	SD
Fork length			27	203	350	253	39
Snout-A	‰	FL	27	471	540	505	15
Snout-2D	‰	FL	27	448	508	477	15
Snout-1D	‰	FL	27	230	268	249	9
Snout-P_2	‰	FL	27	228	255	243	7
Snout-P_1	‰	FL	27	201	229	213	7
P_1-P_2	‰	FL	26	93	118	102	6
Head length	‰	FL	27	198	247	208	8
Max. body depth	‰	FL	27	205	265	228	16
Max. body width	‰	FL	27	81	113	95	9
P_1 length	‰	FL	22	121	143	131	5
P_2 length	‰	FL	25	29	56	40	6
P_2 insertion-vent	‰	FL	26	204	299	247	19
P_2 tip-vent	‰	FL	24	160	269	207	24
Base 1D	‰	FL	25	188	243	216	13
Height 2D	‰	FL	17	144	186	167	12
Base 2D	‰	FL	27	154	198	177	13
Height anal	‰	FL	20	151	178	164	8
Base anal	‰	FL	27	176	268	216	18
Snout (fleshy)	‰	FL	27	70	84	77	3
Snout (bony)	‰	FL	27	59	74	67	4
Maxilla length	‰	FL	27	117	134	125	3
Postorbital	‰	FL	27	77	96	86	6
Orbital (fleshy)	‰	FL	27	30	41	34	3
Orbital (bony)	‰	FL	27	43	60	52	4
Interorbital	‰	FL	27	51	71	58	5
2D-caudal	‰	FL	24	470	522	494	15
Head length			27	42	73	53	9
Snout (fleshy)	‰	HL	27	317	407	372	18
Snout (bony)	‰	HL	27	278	349	321	19
Maxilla length	‰	HL	27	514	630	603	21
Postorbital	‰	HL	27	339	469	415	35
Orbit (fleshy)	‰	HL	27	121	195	165	16
Orbit (bony)	‰	HL	27	190	287	252	23
Interorbital	‰	HL	27	257	342	280	22

Size.—Maximum size 35 cm FL, 0.5 kg, the smallest species in the genus, sexually mature at < 30 cm (Lewis 1981).

Color pattern.—Dark bluish black dorsally, silvery white ventrally, with no spots, blotches, or bars (Fig. 60). First dorsal fin black anteriorly and along distal edge posteriorly with some white at base of fin posteriorly. The only previously published figures were of the holotype by Munro (1964:fig. 12, 1967:fig. 339) and a photograph by Lewis (1981:16).

Biology.—Schooling and other behavior unknown (Lewis 1981).

Interest to fisheries.—Trawled in the Gulf of Papua but too small to be of any commercial significance.

Distribution.—Restricted to shallow turbid waters of the Gulf of Papua off the mouth of the Fly River (Fig. 55). The western known limit is Tureture village, 12 mi west of Daru (Kailola 1975; DASF FO 2851), and the eastern limit Freshwater Bay at Kerema (lat. 8°12′ S, long. 145°59′ E; Kailola 1975; several dissected specimens, USNM).

Material examined.—Total 28 (203-350 mm FL).

meas.: 27 (203-350): off Fly R., Gulf of Papua (**S. multiradiatus*).
counts: 28.
diss.: 4 (224-323).

Scomberomorus munroi Collette and Russo
Australian Spotted Mackerel

Figure 61

Scomberomorus niphonius. Not of Cuvier 1831. Munro 1943:86-90 (first Australian record, description, range) pl. vii, fig. A. Serventy 1950: 19 (throughout N Australia, S to Kimberly). Roughley 1951:110 (description), pl. 45 (fig. after Munro 1943). Taylor 1964:282 (Arnhem Land; listed after Munro 1958a). Marshall 1964:364-365 (description after Munro 1943), pl. 50, fig. 351. Marshall 1966:205 (description), pl. 50, fig. 351. Kailola 1974:72 (description, first record from Papua New Guinea). Kailola 1975: 237 (listed, fish reference collection). Zhang and Zhang 1981:104 (Australia).

Sawara niphonia. Not of Cuvier 1831. Munro

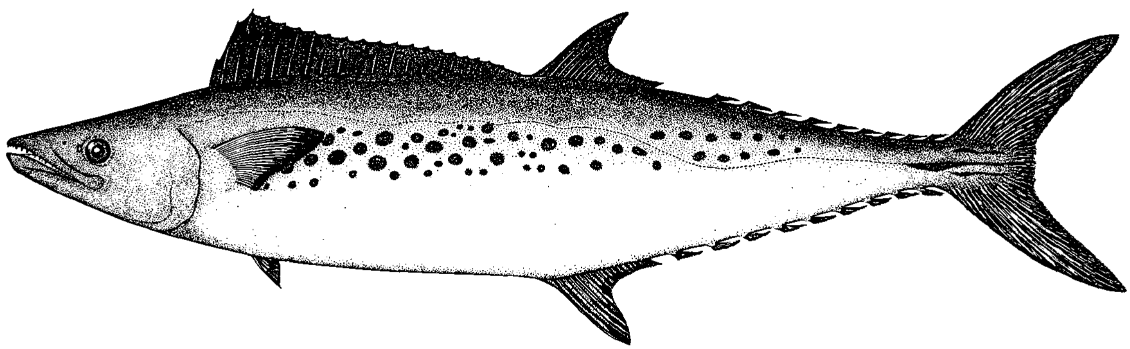


FIGURE 61.—*Scomberomorus munroi.* Deception Bay, Queensland, 740 mm FL, USNM 218387, holotype.

1958a:20 (description; new record for W Australia); fig. Whitley 1964a:240 (fig. 5, range), 252 (range, size). Whitley 1964b:48 (listed). Grant 1965:175 and 1972:104 (description after Munro 1958a), fig. Grant 1975:162 (description), 163 (color pl. 41). Grant 1978:190 (description), 191 (color pl. 73).

Sawara niphonius. Not of Cuvier 1831. Rohde 1976 (no monogenes found on 1 specimen from Coffs Harbour, N.S.W.).

Scomberomorus sp. Collette 1979:29 and Collette and Russo 1979:13 (Australian population referred to *S. niphonius* actually an undescribed species).

Scomberomorus munroi Collette and Russo 1980: 243-248 (original description; Australia, Papua New Guinea), fig. 1 (holotype). Lewis 1981: 18 (photograph, biology). Grant 1982:622 (description), 623 (color pl. 323). Cressey et al. 1983:264 (host-parasite list, 4 copepod species). Collette and Nauen 1983:71-72 (description, range), fig.

Types.—Holotype: AMS I.21029-001; Deception Bay N of Brisbane, Queensland; M. Dredge; 15 May 1975; 705 mm FL; D XXI + 18 + X; A 18 + X; $P_1$22; RGR_1 2 + 1 + 7 = 10; vertebrae 22 + 30 = 52. Paratypes: 10 (373-820 mm FL) from Queensland and southern coast of Papua New Guinea (see Collette and Russo 1980:247).

Diagnosis.—This species differs from all other species of *Scomberomorus* in lacking an anterior process on the outer surface of the head of the maxilla (Fig. 23b). It is superficially similar to *S. niphonius* in being spotted and having many spines (20-22) in the first dorsal fin. It differs from *S. niphonius* in having the usual two loops and three limbs to the intestine instead of having a straight intestine, and in having more vertebrae (50-52, usually 51 vs. 48-50, usually 49).

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3j). Spines in first dorsal fin 20-22, usually 20 or 21 (Table 9); second dorsal fin rays 17-20, usually 18 (Table 10); dorsal finlets 9 or 10, usually 9 (Table 10); anal fin rays 17-19, usually 17 or 18 (Table 11); anal finlets 8-10, usually 9 (Table 11); pectoral fin rays 21-23, usually 21 or 22 (Table 12). Precaudal vertebrae 21 or 22, usually 22 (Table 6); caudal vertebrae 28-30, usually 29 (Table 7); total vertebrae 50-52, usually 51 (Table 8). Gill rakers on first arch 2 + (8-10) = 10-12, usually 8 + (8-9) = 10-11 (Table 5). Morphometric characters given in Table 22.

Size.—Maximum size 100 cm FL, 8 kg; more commonly 50-80 cm and 4.5 kg in weight (Lewis 1981); size at first maturity 50-55 cm (A. D. Lewis[5]). A 9.1 kg fish was caught near Rockhampton, Queensland, in 1976 (G. McPherson[6]).

Color pattern.—Sides with several poorly defined rows of round spots, larger than pupil but smaller than diameter of eye (Fig. 61). *Scomberomorus niphonius* has more numerous, smaller spots, usually about size of pupil. Munro (1943:87) reported sides of freshly caught specimens light silvery grey, upper part of back and inner surface of pectoral fin dark blue, cheeks and belly silvery

[5]A. D. Lewis, Principal Fisheries Officer, Department of Agriculture & Fisheries, P.O. Box 358, Suva, Fiji, pers. commun. February 1983.

[6]G. McPherson, Fishery Biologist, Northern Fisheries Service, Queensland Fisheries Service, % Post Office, Bungalow, Cairns, Qld. 4870, Australia, pers. commun. February 1983.

white, anal fin light silvery grey, and anal finlets silvery grey. First dorsal fin black (bright steely blue in fresh specimens according to Munro) with blotches of white toward bases of more posterior membranes in some specimens. First dorsal fin membranes entirely black in holotype (Fig. 61). Most other species of *Scomberomorus* with more extensive white areas on posterior half or middle third of dorsal fin.

An excellent black and white illustration of *S. munroi* drawn by Munro has appeared several times in the literature (Munro 1943, 1958a; Roughley 1951; Marshall 1964, 1966) and another drawing by George Coates has been published by Grant (1965 and subsequent editions). We (Collette and Russo 1980) illustrated the holotype with the same figure that is included here. Grant has included a color photograph of a freshly caught specimen in the last three editions of his book (1972:pl. 41, 1978:pl. 73, 1982:pl. 323). A photograph was included by Lewis (1981:18).

Biology.—At the end of summer in the Southern Hemisphere (December to April or May), large schools of *S. munroi* move close inshore along the coast of Queensland from Double Island Point to Southport (Grant 1982). Other biological information is lacking on this species.

TABLE 22.—Summary of morphometric data of *Scomberomorus munroi*. FL = fork length, HL = head length.

Character			*N*	Min.	Max.	Mean	SD
Fork length			19	296	820	517	177
Snout-A	‰	FL	17	521	572	547	12
Snout-2D	‰	FL	17	507	545	527	10
Snout-1D	‰	FL	17	198	237	222	10
Snout-P_2	‰	FL	17	228	267	249	10
Snout-P_1	‰	FL	17	178	222	202	11
P_1-P_2	‰	FL	18	95	126	105	7
Head length	‰	FL	18	176	213	198	8
Max. body depth	‰	FL	19	169	203	189	9
Max. body width	‰	FL	15	85	122	100	9
P_1 length	‰	FL	14	100	126	108	7
P_2 length	‰	FL	15	48	59	54	4
P_2 insertion-vent	‰	FL	16	261	308	282	14
P_2 tip-vent	‰	FL	13	200	244	225	12
Base 1D	‰	FL	17	281	322	307	12
Height 2D	‰	FL	12	99	125	111	7
Base 2D	‰	FL	17	106	128	116	8
Height anal	‰	FL	12	93	120	108	8
Base anal	‰	FL	18	87	125	105	9
Snout (fleshy)	‰	FL	18	70	85	76	4
Snout (bony)	‰	FL	18	63	77	70	4
Maxilla length	‰	FL	18	91	115	103	5
Postorbital	‰	FL	19	73	100	90	6
Orbital (fleshy)	‰	FL	19	20	36	26	4
Orbital (bony)	‰	FL	19	30	50	39	6
Interorbital	‰	FL	19	52	63	56	3
2D-caudal	‰	FL	19	435	521	468	25
Head length			18	62	151	98	29
Snout (fleshy)	‰	HL	18	354	426	386	19
Snout (bony)	‰	HL	18	314	389	351	19
Maxilla length	‰	HL	18	486	544	521	16
Postorbital	‰	HL	18	390	496	456	29
Orbit (fleshy)	‰	HL	18	113	174	134	18
Orbit (bony)	‰	HL	18	163	242	199	23
Interorbital	‰	HL	18	256	318	282	16

Interest to fisheries.—Together with *Grammatorcynus* and three other species of *Scomberomorus*, mackerel fishing is Queensland's second major finfishery with an annual output of about 1,000 tons of whole and filleted fish (Anonymous 1978). The best catches are made by drifting or anchoring over inshore Queensland reefs and fishing with lines baited with small fish on a gang of three or four linked hooks (Grant 1982). Also taken by trawlers in the Gulf of Papua.

Distribution.—Inshore coastal waters of the northern coast of Australia (Fig. 58) from Abrolhos Islands region in Western Australia to Coffs Harbour and Kempsey in northern and central New South Wales (Munro 1943, 1958a; Serventy 1950; Whitley 1964a; Lewis 1981) and Gulf of Papua along southern coast of Papua New Guinea from Kerema to Port Moresby (Kailola 1974, 1975). Previously referred to as *S. niphonius* in Australia (Munro 1943).

Material examined.—Total 19 (296-820 mm FL).

meas.: 19 (296-820): Papua New Guinea (12); Australia: N. Territory (3); Queensland (3, **S. munroi*); W. Australia (1).
counts: 19.
diss.: 4 (373-800): New Guinea (3); Queensland (1).

Scomberomorus niphonius (Cuvier)
Japanese Spanish Mackerel
Figure 62

Cybium niphonium Cuvier *in* Cuvier and Valenciennes 1831:180-181 (original description based on a figure of a specimen from Japan). Temminck and Schlegel 1844:101-102 (description), pl. 53, fig. 2 (color painting of adult). Richardson 1846:268 (Sea of Japan). Günther 1860:371 (description after Cuvier and Temminck and Schlegel). Günther 1880:66 (Inland Sea, Japan). Kitahara 1897:3 (description), fig. 11. Kishinouye 1915:10 (description), pl. 1, fig. 4. *Kishinouye 1923:421-424 (description, biology), pl. 15, fig. 6 (soft anatomy in color); pl. 16, fig. 9 (transverse section of vertebrae); pl. 20, fig. 32 (adult); pl. 24, fig. 41 (skull and vertebral

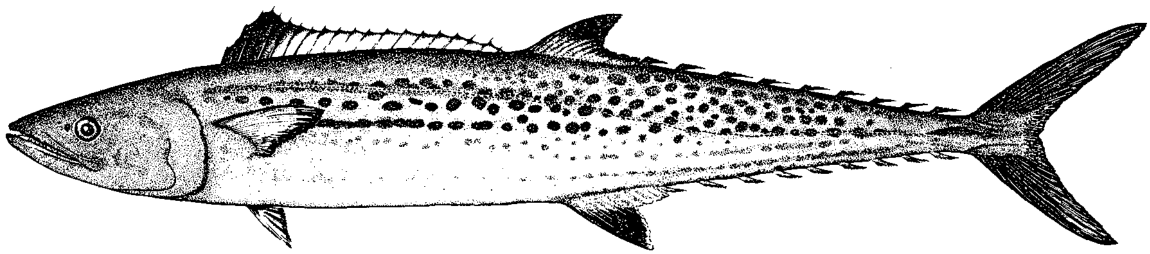


FIGURE 62.—*Scomberomorus niphonius.* Japan, 719 mm FL, USNM 268909.

column). Boeseman 1947:95-96 (specimens in Burger's collection).

Cybium gracile Günther 1873:378-379 (original description; Cheefo, China). Morice 1953:37 (tongue smooth).

Scomberomorus niphonius. Steindachner and Döderlein 1884:180-181 (description; Japan). Jordan et al. 1913:121 (Japanese common names). Kamiya 1922:14-15, 26-32 (eggs and larvae; Japan), pl. IV-V, figs. 1-24 (developmental sequence of eggs and larvae). Kamiya 1924:35 (eggs). Tanaka 1927:154-157 (description from 530 mm specimen from Tokyo market), pl. 42, figs. 163 and 164, pl. 44, fig. 173. Soldatov 1929:5 (listed). Munro 1943:67-68, 71 (subgenus *Sawara*). Fraser-Brunner 1950: 157-158 (description, range; "*Scomber" gracile* a synonym of *S. niphonius*), fig. Okada 1955: 149 (description, range, biology), fig. 136 (after Kishinouye). Mori 1956:23 (Kasumi, Hamada; S. Japan Sea). Mito 1960:79, 93 (eggs compared with those of *S. commerson*). Mito 1961:457 (eggs and larvae). Tominaga 1964:vol. 1, pl. 198 (figure; anatomy), vol. 3:256-257 (description, habits, distribution). Jones and Silas 1964:52-54 (description, synonymy, range; in part, only Chinese and Japanese specimens). Gorbunova 1965a:53 (spawning season). Sha et al. 1966:1-12 (eggs and larvae), figs. Mito 1966:22-23 (fig. 15a, egg), 46-47 (fig. 26, larva). Mito 1967:41 (vertical distribution of larvae). *Hamada and Iwai 1967:1013-1020 (fishing seasons, length-weight, growth; Inland Sea of Japan), pl. 1 (otoliths). Kamohara 1967:43 (description, range in part), color pl. 22, fig. 2. Tokida and Kobayashi 1967:158 (identification of *C. niphonium* from Uchimura's unpublished 1884 manuscript). Kim 1970:37-40 (age determination; Korea). Uyeno 1971:79 (Japan Sea). Richards and Klawe 1972:14 (range), 93 (references to eggs and larvae). Shiino 1972:71 (common name). Magnuson 1973:350 (short pectoral fin). Kusaka 1974:146 (urohyal), fig. 269. Anonymous 1975:184 (description, range), map of fishery, color fig. Masuda et al. 1975:79 (fig. G, color photograph), 256 (range). Uyeno and Fuji 1975:14 (characters of caudal complex). Shiino 1976:231 (common name). Klawe 1977: 2 (common name, range). Collette 1979:24 (characters, range). Collette and Russo 1979: 13 (diagnostic characters, range). Liu 1981: 129-137 (age and growth). Zhang and Zhang 1981:104 (range in part). *Liu et al. 1982:170-178 (age and growth; Yellow Sea). *Wang 1982:51-55 (catch, length-weight, management; Yellow Sea). Cressey et al. 1983:264 (host-parasite list, 4 copepod species). Lee and Yang 1983:230 (Taiwan), fig. 20 (619 mm FL). Collette and Nauen 1983:72-73 (description, range), fig. Ye and Zhu 1984 (bioeconomics).

Sawara niphonia. Jordan and Hubbs 1925:214 (new genus *Sawara*; specimen from Kobe market). Reeves 1927:9 (Ningpo, Peitaiho, China; listed). Mori 1928:5 (Fusan, Korea). Soldatov and Lindberg 1930:112 (synonymy, description, range). Suyehiro 1942:123-124 (intestine straight), fig. 78 (pyloric caeca). Honma 1952: 143 (Echigo Prov. = Niigata Pref., Japan). Mori 1952:136 (Fusan, Masan, Quelpart I., Korea; listed). Nalbant 1970:58 (Kamchatka?).

Scomberomorus gracileus (sic). Reeves 1927:8 (Cheefo, Chinwangtao, China; listed).

Types of nominal species.—*Cybium niphonium* Cuvier *in* Cuvier and Valenciennes 1831 was based on a figure of a specimen from Japan, no type-specimens extant (Blanc and Bauchot 1964:449).

Cybium gracile Günther 1873. Holotype: BMNH 1873.9.23.4; Cheefoo, N China; R. Swinhoe; 547 mm FL; D XX + 16 + IX; A 18 + VIII; P_1 22-23; RGR_1 2 + 1 + 10 = 13; vertebrae 22 + 27 = 49.

Diagnosis.—The only species of *Scomberomorus* with a straight intestine (Fig. 3k). The other species have two or four loops. Scapular foramen small as in *S. guttatus* and *S. koreanus*. Intercalar spine absent as in the six species of the *regalis* group. Supracleithrum wide, 55-62% of length, as in *S. lineolatus*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Spines in first dorsal fin 19-21, usually 20 (Table 9); second dorsal fin rays 15-19, usually 16-18 (Table 10); dorsal finlets 7-9, usually 8 (Table 10); anal fin rays 16-20, usually 17 or 18 (Table 11); anal finlets 6-9, usually 8 or 9 (Table 11); pectoral fin rays 21-23, usually 22 (Table 12). Precaudal vertebrae 21-23, usually 22 (Table 6); caudal vertebrae 27 or 28, usually 27 (Table 7); total vertebrae 48-50, usually 49 (Table 8). Gill rakers on first arch (2-3)+(9-12)=11-15, usually 2+(10-11)=12-13 (Table 5). Morphometric characters given in Table 23.

Size.—Maximum size 100 cm FL, 4.5 kg in weight (Kishinouye 1923). Age and growth studies have been published by Hamada and Iwai (1967), Kim (1970), and Liu et al. (1982).

Color pattern.—Kishinouye (1923:422) described *S. niphonius* as shining with a metallic lustre. Dorsum light greyish blue washed with green, belly silvery. Seven or more rows of longitudinal spots on the sides. Some spots connected together (Fig. 62). There are more numerous, smaller spots than in *S. munroi*, about pupil size (Collette and Russo 1980). Anterior quarter of first dorsal fin and a narrow distal margin of the rest of the dorsal fin black, most of basal membranes of posterior three-quarters of fin white.

There are color paintings of *S. niphonius* in Kamohara (1967:pl. 22) and Anonymous (1975:pl. 184), a color photograph in Masuda et al. (1975:79), and a good black and white illustration in Kishinouye (1923:fig. 32). We (Collette and Russo 1980: fig. 1b) included the drawing that is presented here in the paper describing *S. munroi*.

Biology.—There are two migrations in the Inland Sea of Japan, a spawning migration in the spring (March to June) and feeding migration in the fall (September to November) according to Hamada and Iwai (1967). The spawning season in Japan is from April to May (Kishinouye 1923). The ripe

TABLE 23.—Summary of morphometric data of *Scomberomorus niphonius*. FL = fork length, HL = head length.

Character			Japan and Korea					China					Total				
			N	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD
Fork length			13	157	788	439	200	16	105	623	280	167	32	105	788	351	197
Snout-A	‰	FL	11	539	574	553	10	16	558	605	573	14	30	484	605	563	22
Snout-2D	‰	FL	12	505	563	535	17	16	523	576	542	13	31	427	576	536	25
Snout-1D	‰	FL	12	202	271	239	21	16	224	278	256	16	31	202	278	248	20
Snout-P_2	‰	FL	12	227	307	255	23	15	232	305	269	20	29	227	307	263	22
Snout-P_1	‰	FL	12	184	252	216	20	16	197	264	232	18	31	184	264	225	20
P_1-P_2	‰	FL	12	89	125	100	11	13	95	129	109	12	26	89	129	105	12
Head length	‰	FL	13	180	249	207	18	16	192	252	223	18	32	180	252	215	19
Max. body depth	‰	FL	11	148	203	167	17	11	152	190	172	13	23	148	211	171	17
Max. body width	‰	FL	10	77	95	88	6	12	71	92	80	7	25	71	103	84	8
P_1 length	‰	FL	12	87	122	105	9	16	104	125	115	6	31	87	125	111	9
P_2 length	‰	FL	11	51	76	62	7	15	56	127	74	16	29	45	127	68	14
P_2 insertion-vent	‰	FL	12	243	318	283	25	13	258	321	290	18	27	232	321	285	23
P_2 tip-vent	‰	FL	11	186	256	221	23	12	188	245	216	17	25	186	256	218	20
Base 1D	‰	FL	12	271	320	293	17	16	259	310	280	14	31	219	320	282	20
Height 2D	‰	FL	12	66	110	92	10	13	95	112	101	5	28	66	124	98	10
Base 2D	‰	FL	12	90	131	104	12	16	94	132	113	11	31	90	189	113	19
Height anal	‰	FL	9	84	108	92	7	15	63	106	97	11	27	63	124	97	11
Base anal	‰	FL	11	92	117	105	9	16	93	135	106	11	30	92	147	107	12
Snout (fleshy)	‰	FL	13	66	88	78	7	16	70	95	84	7	32	66	95	81	8
Snout (bony)	‰	FL	13	59	83	72	7	16	62	89	77	7	32	56	89	75	8
Maxilla length	‰	FL	13	94	136	114	13	16	103	145	125	11	32	93	145	119	14
Postorbital	‰	FL	13	91	104	98	4	16	89	115	104	7	31	89	115	102	7
Orbital (fleshy)	‰	FL	13	19	41	28	6	16	25	51	36	7	32	19	51	33	8
Orbital (bony)	‰	FL	13	29	59	41	9	16	36	65	51	8	32	29	65	47	10
Interorbital	‰	FL	13	51	63	56	4	16	54	61	57	2	32	51	63	57	3
2D-caudal	‰	FL	12	412	490	459	27	15	420	488	468	16	29	412	490	465	21
Head length			13	39	142	88	34	16	27	120	60	30	32	27	142	72	35
Snout (fleshy)	‰	HL	13	351	401	377	16	16	362	393	378	11	32	345	401	376	14
Snout (bony)	‰	HL	13	314	373	346	15	16	325	365	348	12	32	294	373	346	16
Maxilla length	‰	HL	13	504	582	549	23	16	538	582	560	14	32	484	582	553	22
Postorbital	‰	HL	13	417	511	477	26	16	405	518	470	26	31	405	518	473	26
Orbit (fleshy)	‰	HL	13	103	170	136	19	16	122	204	158	21	32	103	204	150	23
Orbit (bony)	‰	HL	13	161	250	194	28	16	188	257	230	23	32	161	257	215	30
Interorbital	‰	HL	13	248	294	271	14	16	226	285	258	18	32	226	303	264	18

eggs are large, about 1.5 mm in diameter and number about 550,000-870,000 (Kishinouye 1923). Immature fish of about 30 mm are found in April and May (Kishinouye 1923). Eggs and larvae up to 35 mm TL are described by Sha et al. (1966) from plankton net samples from Kiaochow Bay, Tsingtao, China. Although it feeds on small fishes (Kishinouye 1923), no detailed food studies seem to have been published.

Interest to fisheries.—In the Inland Sea of Japan, the main fishing seasons are from March to June and from September to November (Hamada and Iwai 1967). Angling and gill nets are important gear in this region. There are also important fisheries in the Huanghai Sea (Yellow Sea) and Bohai Sea (Liu et al. 1982). Ye and Zhu (1984) have developed a bioeconomic model for this fishery, estimating maximum revenue, optimum economic effort, and optimum energy consumption. The annual catch reported by China, Japan, and Korea varied from 60,733 to 77,356 t between 1979 and 1982 (FAO 1984).

Distribution.—Confined to temperate and subtropical waters of the western North Pacific, Japan, Korea, and northern China (Fig. 58). The northernmost locality is Vladivostok, U.S.S.R., in the Sea of Japan (BMNH 1893.1.27.10-12). In Japan, it is found from southern Hokkaido to Honshu, Shikoku, and Kyushu, west to Pusan, Korea (CAS SU 31263), and Ningpo, Peitaiho (Reeves 1927; ZMA 114.597), Cheefo (= Yentai) (Günther 1873; BMNH 1873:9.23.40; UMMZ 167374), and Tsingtao (USNM 130474) on the Shantung Peninsula of northern China. Records of *S. niphonius* from northern Australia and southern Papua New Guinea are referrable to the recently described *S. munroi* (Collette and Russo 1979).

Geographic variation.—Morphometric characters were compared for two populations of *S. niphonius* by ANCOVA (Table 23): Japan and Korea (n = 9-13) and China (n = 11-16). Null hypotheses that the 2 sets of regression lines are coincident were accepted for 21 regressions and rejected for 5 sets: Sn-A, Sn-1D, maximum body width, P_1L, and orbit (bony). No meristic differences were found between the two populations.

Material examined.—Total 38 (86.5-788 mm FL).

meas.: 31 (97.5-705): Japan (8); Korea (5); China (16); unknown locality (2).
counts: 38.
diss.: 2 (683-788): Japan.

Scomberomorus plurilineatus Fourmanoir
Queen Mackerel or Kanadi Kingfish

Figure 63

Cybium lineolatum. Not of Cuvier 1831. Gilchrist and Thompson 1911:41 (description; Durban).

Scomberomorus lineolatum. Not of Cuvier 1831. Gilchrist and Thompson 1917:395 (Natal).

Scomberomorus lineolatus. Not of Cuvier 1831. Barnard 1927:803 (description; Natal). Fowler 1934:441 (Durban). Smith 1935:210-211 (description; Port Alfred, South Africa). *Williams 1960:183-192 (description, synonymy, range), pl. 2. *Williams 1964:151-154 (distribution, fishery biology). Merrett and Thorpe 1966:371-372 (references, range, size, biology).

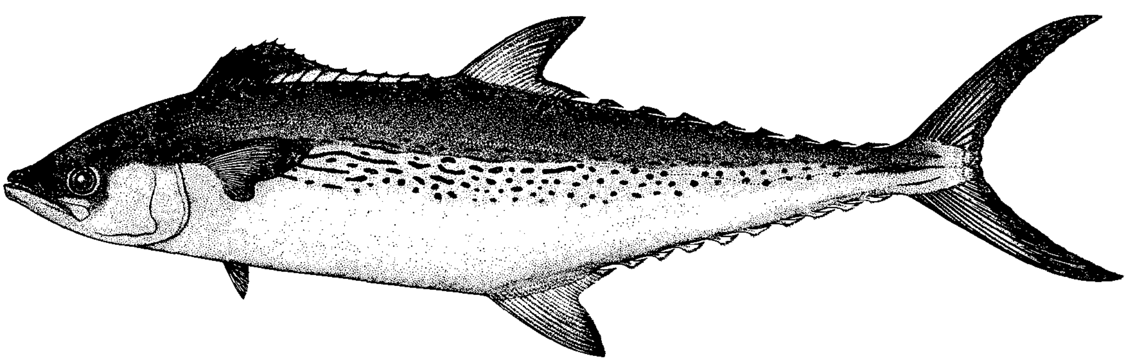


FIGURE 63.—*Scomberomorus plurilineatus.* Durban, South Africa, 598 mm FL, USNM 264809.

Scomberomorus leopardus. Not of Shaw 1803. Fowler 1929:254 (description; Natal). Smith 1949, 1953, 1961:301 (description, range), fig. 841, pl. 64. Morrow 1954:815 (near Shimoni and Pemba I., East Africa). Talbot 1965:469 (Mafia area, Tanganyika). Maugé 1967:234 (Anakao, Tulear region, Madagascar). Shiino 1976:231 (common name).

Scomberomorus sp. Williams 1956:44 (Kenya).

Scomberomorus guttatus. Not of Bloch and Schneider 1801. Smith 1956:722 (Aldabra). Smith and Smith 1963:43 (Seychelles), pl. 30B. Smith 1964:176-177 (description; Durban and Delagoa Bay), pl. 8, figs. 3-5. Silas 1964: 314-328 (western Indian Ocean population only). Smith and Smith 1966:72 (Natal), color pl. 841.

Cybium leopardus. Not of Shaw 1803. Fourmanoir 1957:227 (description; Mozambique Channel).

Cybium lineolatus. Not of Cuvier 1831. Fourmanoir and Crosnier 1964:387-388 (Madagascar).

Scomberomorus plurilineatus Fourmanoir 1966: 223-226 (original description; Madagascar), fig. 1. Klawe 1977:2 (range, common name). Collette 1979:29 (characters). Collette and Russo 1979:13 (diagnostic characters, range). *Van der Elst 1981:275 (description, natural history, range, photograph). Joubert 1981:5 (minor component of shore angler's catches; Natal, South Africa). Cressey et al. 1983:264 (host-parasite list, 5 copepod species). Collette and Nauen 1983:73-74 (description, range), fig.

Types.—*Scomberomorus plurilineatus* Fourmanoir 1966 was based on a 740 mm specimen collected near Nossi-Bé, Madagascar, in 1965. The type was supposed to be transferred from the O.R.S.T.O.M. collections to the MNHN collection but apparently was inadvertently discarded (M.-L. Bauchot and P. Fourmanoir[7]).

Diagnosis.—The only species of *Scomberomorus* that has a pattern of short wavy lines and spots on its sides (Fig. 63). Other species have straight lines, spots, blotches, or bars on the side or are plain. Posterior end of maxilla greatly expanded as in *S. lineolatus* and *S. semifasciatus*.

[7]M.-L. Bauchot, Curator of Fishes, Laboratoire d'Ichtyologie Générale et Appliquée, Muséum National d'Histoire Naturelle, 43 Rue Cuvier, 75231 Paris Cedex 05, France, and P. Fourmanoir, Office de la Recherche Scientifique et Technique Outre-Mer, Institut Français d'Oceanie, Nouméa, B.P. 4, Nouvelle-Calédonie, pers. commun. December 1974.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 31). Spines in first dorsal fin 15-17, usually 15 or 16 (Table 9); second dorsal fin rays 19-21, usually 20 (Table 10); dorsal finlets 8-10, usually 9 (Table 10); anal fin rays 19-22, usually 20 or 21 (Table 11); anal finlets 7-10, usually 8 or 9 (Table 11); pectoral fin rays 21-26, usually 22 or 23 (Table 12). Precaudal vertebrae 19 or 20, usually 20 (Table 6); caudal vertebrae 25-27, usually 26 (Table 7); total vertebrae 45 or 46, usually 46 (Table 8). Gill rakers on first arch (2-3) + (9-13) = 12-15, usually 2 + (10-11) = 12-13 (Table 5). Morphometric characters given in Table 24.

TABLE 24.—Summary of morphometric data of *Scomberomorus plurilineatus*. FL = fork length, HL = head length.

Character			N	Min.	Max.	Mean	SD
Fork length			37	144	910	547	211
Snout-A	‰	FL	36	478	614	502	22
Snout-2D	‰	FL	36	446	622	473	28
Snout-1D	‰	FL	36	202	247	221	12
Snout-P_2	‰	FL	36	207	261	232	12
Snout-P_1	‰	FL	37	176	228	192	11
P_1-P_2	‰	FL	26	96	117	103	5
Head length	‰	FL	37	175	222	193	11
Max. body depth	‰	FL	32	184	225	205	11
Max. body width	‰	FL	20	76	123	97	13
P_1 length	‰	FL	31	98	140	123	10
P_2 length	‰	FL	35	44	66	51	6
P_2 insertion-vent	‰	FL	24	223	257	244	9
P_2 tip-vent	‰	FL	23	158	207	187	15
Base 1D	‰	FL	23	219	256	240	11
Height 2D	‰	FL	29	122	166	148	11
Base 2D	‰	FL	27	101	156	128	11
Height anal	‰	FL	27	91	155	135	14
Base anal	‰	FL	27	111	143	126	9
Snout (fleshy)	‰	FL	35	61	75	67	3
Snout (bony)	‰	FL	25	48	67	58	4
Maxilla length	‰	FL	36	83	113	96	7
Postorbital	‰	FL	36	81	107	94	6
Orbital (fleshy)	‰	FL	37	22	139	34	19
Orbital (bony)	‰	FL	27	33	60	45	8
Interorbital	‰	FL	36	46	67	56	4
2D-caudal	‰	FL	25	518	575	549	15
Head length			37	31	159	104	37
Snout (fleshy)	‰	HL	35	309	371	348	13
Snout (bony)	‰	HL	25	256	327	305	15
Maxilla length	‰	HL	36	469	529	496	14
Postorbital	‰	HL	36	413	527	485	23
Orbit (fleshy)	‰	HL	37	121	769	179	104
Orbit (bony)	‰	HL	27	178	276	231	27
Interorbital	‰	HL	36	253	352	290	21

Size.—Maximum size 120 cm FL, South African angling record 10.0 kg, sexual maturity attained at about 80 cm FL (van der Elst 1981).

Color pattern.—Williams (1960) published a good description of fresh specimens from Zanzibar. Head blue-grey above, silvery white below, except for lower jaw tip, preorbital area and maxillary groove dusky to black. Pupil of eye black, rest silvery. Body iridescent blue-grey above lateral line, silver below becoming whitish ventrally. A series of about six to eight interrupted horizontal black lines on sides of body much narrower than interspaces. Anteriorly, usually only one of these lines above lateral line; replaced posteriorly by a number of short oblique black lines becoming somewhat confused, and only two or three continue through to caudal peduncle. Horizontal black lines on body interrupted to varying degrees, beginning almost intact in places, but broken up into a series of small rectangular "spots" in others. Juveniles have spots but develop adult pattern of interrupted lines by the time they reach a length of 400 mm (Smith 1964:177). Upper areas of caudal peduncle and median keel black, lower areas dusky. First dorsal fin black except lower areas of membrane may be pale posteriorly. Second dorsal fin with leading edge and tips of rays dusky, rest silver to pale; finlets dusky with a silver area at center. Anal fin, leading edges and tips of rays dusky, rest silvery; finlets white with a dusky central area. Pectoral fins black inside, as is axil; dusky outside with edges black; pelvic fins pale whitish with outside of midrays dusky, groove on body a little dusky. Caudal fin basally pale, rest of fin dusky to black.

Black and white photographs of *S. plurilineatus* have been published by Williams (1960:pl. 2, 640 mm Zanzibar specimen) and Fourmanoir (1966: fig. 1, 740 mm holotype from Madagascar). Illustrations of a spotted 300 mm juvenile and two adults over 1 m long were presented by Smith (1964:pl. 8). A colored figure of the juvenile is included in Smith and Smith (1966:fig. 841).

Biology.—Large schools are present in the Zanzibar Channel from March-April until August-September, average weight 3.2-3.5 kg (Williams 1960). Angling statistics point to a peak abundance in Natal, South Africa, during May (van der Elst 1981). Spawning probably takes place in August-September in the Zanzibar Channel (Williams 1964). There do not appear to be any published references to eggs or larvae of *S. plurilineatus*. This species feeds mainly on anchovies (*Anchoviella* sp.), clupeids (*Amblygaster* sp., *Sardinella fimbrata*, *S. perforata*), other small fishes, squids, and mantis shrimps (Williams 1964; Merrett and Thorp 1966; van der Elst 1981).

Interest to fisheries.—In the Malindi area of Kenya, catches of *S. plurilineatus* are mainly made by trolling and hand lines, while in the Zanzibar Channel all methods are used but the gill net prevails (Williams 1964). On the west coast of Zanzibar a trap net called the mensab is used to intercept fish on their projected paths of movements (Williams 1964). More recently, tuna purse seines are used in Zanzibar with catches of several tons reported off the northwest coast (Merrett and Thorp 1966). In Natal, South Africa, it is a popular gamefish with ski-boat fishermen and also with spearfishermen (van der Elst 1981).

Distribution.—Common in coastal waters, especially near rocky and coral reefs. Western Indian Ocean along the coast of East Africa from Kenya (lat. 1°30′S) and Zanzibar (Williams 1964) to Natal, South Africa (Fig. 58). The southernmost records are from Algoa Bay (Smith and Smith 1966). Also found in the Seychelles Islands (Smith and Smith 1963) and along the west coast of Madagascar.

Material examined.—Total 37 (165-910 mm FL).

meas.:	37 (165-910): Natal, South Africa (25); Mozambique (1); Kenya (1); Zanzibar (10, F. Williams' data).
counts:	37.
diss.:	5 (490-910): South Africa (4); Kenya (1).

Scomberomorus queenslandicus Munro
Queensland School Mackerel

Figure 64

Cybium guttatum. Not of Bloch and Schneider 1801. Macleay 1880:559 (description; Port Jackson, Australia). Ogilby 1887:30 (listed; Port Jackson).

Scomberomorus guttatus. Not of Bloch and Schneider 1801. Waite 1904:42 (New South Wales). Stead 1906:165-166 (N.S.W.). Stead 1908:98 (description; N.S.W.). McCulloch 1922:105 (N.S.W.). McCulloch 1929:264-265 (range in part; Queensland, N.S.W.).

Scomberomorus (Cybium) queenslandicus Munro 1943:82-86 (original description; Queensland and west Australia), pl. 7, fig. B, pl. 8, fig. 1. Coates 1950:24 (description), fig. Roughley 1951:110 (description), pl. 45, top fig. (after Munro). Jones and Silas 1962:202 (may turn up in Indian waters), fig. 8 (after Munro). Jones and Silas 1964:61-62 (description, range), fig. 11 (after Munro). Taylor 1964:282 (listed after Whitley 1954). Marshall 1964:363-364 (description; Qld.), pl. 49, fig. 350 A and B (after

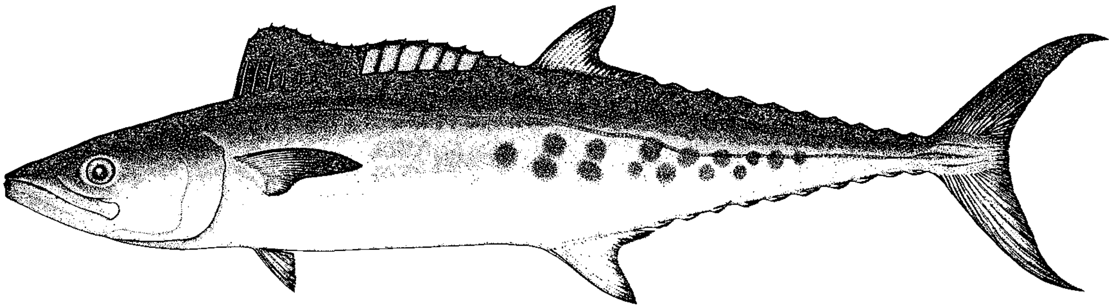


FIGURE 64.—*Scomberomorus queenslandicus.* Exmouth Gulf, Western Australia, 635 mm FL, USNM 268910.

Munro). Marshall 1966:205 (Qld.), pl. 49, fig. 350 A and B (after Munro). Richards and Klawe 1972:14 (range), 94 (references to juveniles). Magnuson 1973:350 (short pectoral fin). Kailola 1974:71 (description; Gulf of Papua; range extension). Kailola 1975:237 (specimen in Kanudi Fisheries collection). Shiino 1976:231 (common name). Klawe 1977: 2 (common name; range). Kailola and Wilson 1978:35 (trawled in Gulf of Papua), 60 (number of fin rays). Collette 1979:29 (characters, range). Collette and Russo 1979:13 (diagnostic characters, range). Grant 1982:624 (description, fishery in S Qld.), 625 (color pl. 324). Rainer and Munro 1982:1046 (inshore group, Gulf of Carpentaria), 1050-1051 (avoids low salinity areas in the southern Gulf). Cressey et al. 1983:264 (host-parasite list, 5 copepod species). Collette and Nauen 1983:74-75 (description, range), fig. Jenkins et al. 1984:348-351 (193 larvae, 3.5-9.9 mm SL; off Townsville, Qld.), fig. 4 (6 larvae, 3.6-9.5 mm SL).

Cybium queenslandicum. Whitley 1947:129 (W. Australia). Whitley 1948:24 (W. Australia). Whitley 1954:27 (Parry Shoal, N. Territory). Whitley 1964a:251-252 (description; W. Australia and N. Territory). Whitley 1964b:48 (listed).

Cybium queenslandicus. Munro 1958a:112 (description, range), fig. 750 (after Munro). Grant 1965:174 (description after Munro; Moreton Bay, Queensland), fig. Grant 1972:103, 1975:161, 1978:194 (description after Munro; fishery in S Qld.), fig.

Types.—Holotype: QM I.6588; Cape Cleveland, N Queensland, Australia; G. Coates; 463 mm FL; D XVII + 18 + IX; A 20 + IX; P_1 23; RGR_1 1 + 1 + 4 = 6.

Diagnosis.—This species has relatively few large spots (larger than the diameter of the eye) on its sides (Fig. 64). In having few gill rakers (3-9), it is superficially similar to *S. commerson* but differs in lacking an abrupt downward curve in the lateral line under the second dorsal fin and in having more vertebrae (48 or 49 vs. 42-46). Posterodorsal spine of hyomandibula large as in *S. commerson* and *Acanthocybium.* Ventral process of angular long, 117-126% of dorsal process, as in *S. commerson* and *Acanthocybium.* Intercalar spine well developed as in *S. cavalla* and *S. commerson.*

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3m). Spines in first dorsal fin 16-18, usually 17 (Table 9); second dorsal fin rays 17-19 (Table 10); dorsal finlets 9-11, usually 9 or 10 (Table 10); anal fin rays 16-20, usually 19 (Table 11); anal finlets 9-11, usually 10 (Table 11); pectoral fin rays 21-23, rarely 25 (Table 12). Precaudal vertebrae 19 or 20, usually 20 (Table 6); caudal vertebrae 28 or 29, usually 28 (Table 7); total vertebrae 48 or 49, usually 48 (Table 8). Gill rakers on first arch (0-2) + (3-8) = 3-9, usually 1 + (5-6) = 6-7 (Table 5). Morphometric characters given in Table 25.

Size.—Maximum size 100 cm FL, 8 kg in weight, commonly 50-80 cm (Lewis 1981).

Color pattern.—In his original description of the species, Munro (1943) provided a good description of freshly caught specimens from Queensland. Cranial regions and upper part of back iridescent bluish green, cheeks and belly silvery white. In adult fish, sides marked with about three indefinite rows of indistinct bronze-grey blotches, each a little larger than orbit. Membrane of first dorsal fin jet black with large contrasting areas of

TABLE 25.—Summary of morphometric data of *Scomberomorus queenslandicus*. FL = fork length, HL = head length.

Character			N	Min.	Max.	Mean	SD
Fork length			28	156	641	392	123
Snout-A	‰	FL	28	502	558	525	12
Snout-2D	‰	FL	28	470	518	502	11
Snout-1D	‰	FL	28	219	254	234	10
Snout-P_2	‰	FL	27	234	273	252	11
Snout-P_1	‰	FL	27	211	252	228	10
P_1-P_2	‰	FL	27	85	118	99	7
Head length	‰	FL	28	203	245	220	10
Max. body depth	‰	FL	25	161	207	188	11
Max. body width	‰	FL	26	81	118	101	11
P_1 length	‰	FL	24	103	135	119	8
P_2 length	‰	FL	23	44	62	55	5
P_2 insertion-vent	‰	FL	24	233	275	254	12
P_2 tip-vent	‰	FL	22	178	222	198	13
Base 1D	‰	FL	28	239	283	263	11
Height 2D	‰	FL	18	89	136	114	12
Base 2D	‰	FL	28	80	135	113	11
Height anal	‰	FL	17	94	157	112	15
Base anal	‰	FL	28	89	141	108	12
Snout (fleshy)	‰	FL	28	78	97	86	4
Snout (bony)	‰	FL	27	73	125	80	9
Maxilla length	‰	FL	27	109	146	125	8
Postorbital	‰	FL	28	90	110	102	5
Orbital (fleshy)	‰	FL	28	23	41	31	5
Orbital (bony)	‰	FL	27	39	66	49	8
Interorbital	‰	FL	28	56	74	63	5
2D-caudal	‰	FL	17	440	532	496	22
Head length			28	36	141	85	25
Snout (fleshy)	‰	HL	28	357	423	390	17
Snout (bony)	‰	HL	27	331	554	363	41
Maxilla length	‰	HL	27	526	597	568	17
Postorbital	‰	HL	28	410	502	463	21
Orbit (fleshy)	‰	HL	28	112	171	141	16
Orbit (bony)	‰	HL	27	183	283	222	29
Interorbital	‰	HL	28	259	330	287	17

intense white between sixth and last spines. Second dorsal fin, finlets, and caudal fin pearly grey with darker margins. Pelvic fins, anal fin, and anal finlets white. Pectoral fins greyish, darkest on inner surface. Munro also noted the absence of characteristic blotches in a 95 mm juvenile.

Munro (1943:pl. 7, 8) provided excellent illustrations of adult (545 mm FL) and juvenile (140 mm FL) specimens from Queensland. There is also a figure drawn by George Coates in Grant (1982 and previous editions). A photograph of two juveniles (about 300 mm FL) was included in Lewis (1981: 15). A color photograph of a 230 mm specimen was added to the fifth edition of Grant (1982:pl. 324).

Biology.—Schools move into bays and estuaries and inshore coastal waters the length of the entire coast of Queensland during midwinter and early spring in the Southern Hemisphere (Grant 1982). A female 450 mm FL with mature ovaries was collected in Moreton Bay, Queensland, in January 1980 (Lewis, footnote 5). Information on eggs (Richards and Klawe 1972) and on spawning and food habits is lacking. Larvae (3.5-9.5 mm SL) were described and illustrated by Jenkins et al. (1984).

Interest to fisheries.—Caught by recreational and commercial line-fishermen trolling with lures and spoons, and using cut baits along the coast of Queensland (Grant 1982). They also form the basis of a substantial net fishery, using set nets by day or night. Considerable quantities of juveniles are trawled in parts of Moreton Bay during autumn (March-May). Together with *Grammatorcynus* and three other species of *Scomberomorus*, mackerel fishery is Queensland's second major finfishery with an annual output of about 1,000 tons of whole and filleted fish (Anonymous 1978). It was known to south Queensland fishermen as school mackerel for over 60 yr prior to its formal description by Munro (1943). Trawled in the Gulf of Papua.

Distribution.—Confined to inshore coastal waters of southern Papua New Guinea and the northern three quarters of Australia (Fig. 55). The westernmost records are from Shark Bay (Munro 1943) and Onslow (AMS IB.1576, WAM P. 8669-8678), Western Australia. The range extends south to Port Jackson (USNM 4795, AMS I.15026) and Botany Bay (USNM 47948) in the Sydney area. A tentative record from Fiji (Collette and Russo 1979) was based on small specimens of *S. commerson* (USNM 227183, 203-242 mm FL) with less dip in the lateral line than is usual in the species. The origin of a specimen of *S. queenslandicus* (USNM 213539, 215 mm FL) that was purchased in the Anbon market in the Moluccas is unknown but joint venture trawlers which fish in the Arafua Sea unload at Anbon (Lewis footnote 5).

Geographic variation.—Comparisons were made of morphometric characters of three small samples of *S. queenslandicus* by ANCOVA: Western Australia (n = 5-9), eastern Australia (n = 9-13), and southern New Guinea (n = 3-5). Null hypotheses that the 3 sets of regression lines are coincident were accepted for 24 sets of regressions and rejected for 2 sets: orbit (fleshy) and orbit (bony). In both cases, the Western Australian population was significantly different by the Newman-Keuls Multiple Range Test from the population in eastern Australia (intercepts 5.140, 2.847, Q = 5.630** for fleshy orbit; intercepts 8.380, 1.951, Q = 4.562** for bony orbit) and the population in eastern Australia was not significantly different from that in New Guinea. No significant meristic differences were found between populations.

Material examined.—Total 35 (156-641 mm FL).

meas.: 28 (156-641): New South Wales, Australia (5); Queensland (8, *S. queenslandicus*); W. Australia (9); New Guinea (5); Anbon market (1).
counts: 35.
diss.: 6 (354-641): Queensland (4); W. Australia (1); New Guinea (1).

Scomberomorus regalis (Bloch)
Cero
Figure 65

Scomber regalis Bloch 1793:38-43 (original description, after a drawing by Plumier; Martinique), color pl. 333. Bloch 1797:31-34 (French translation of original description), color pl. 333. Bloch and Schneider 1801:22 (description after Bloch). Shaw 1803:583 (after Bloch). Lacepède 1803:711 (Scomberomore plumier is the same as *Scomber regalis*).

Scomberomorus Plumierii Lacepède 1802:292-294 (original description after Plumier's drawing; Martinique).

Cybium regale. Cuvier 1829:200 (listed in footnote from *Sc. regalis* Bloch; *Scomberomorus plumieri* a synonym). Cuvier *in* Cuvier and Valenciennes 1831:184-185 (description; Santo Domingo). Castelnau 1855:23 (Bahia, Brazil). Günther 1860:372-373 (synonymy, description; Jamaica). Poey 1865:322 (description; Santo Domingo). Kner 1865:144 (description; Rio de Janeiro). Poey 1868:362 (description; Cuba). Poey 1875:147 (description; Cuba). Poey 1878: 4 (synonymy, characters).

Scomberomorus regalis. Jordan and Gilbert 1882:426 (description, synonymy). Jordan and Gilbert 1883c:573 (*Scomberomorus plumierii* identical with *Scomber regalis*). Goode 1884: 316 (size; Fla. Keys), pl. 94. Meek and Newland 1884:233-234 (description, synonymy, range). Jordan 1884:120 (description; Key West). Dresslar and Fesler 1889:442 (in key), 444 (synonymy, range Cape Cod to Brazil), pl. 10. Jordan and Evermann 1896b:875 (description, synonymy). Jordan and Evermann 1900:pl. 135, fig. 369 (Key West specimen). Evermann and Marsh 1902:124 (description, synonymy in part; Puerto Rico), fig. 28. Jordan and Evermann 1902:286-287 (description, range), fig. Bean 1903:398-400 (synonymy, description, range). Fowler 1905:766 (description; Santo Domingo). Smith 1907:192 (diagnosis; North Carolina record from Yarrow 1877), fig. 78. Sumner et al. 1913:750 (references, occurrence; Buzzards Bay, Mass.). Ribeiro 1915:135 (description, range S to Angra dos Reis, Brazil). Meek and Hildebrand 1923:323-324 (description, synonymy). Schroeder 1924:7 (Fla. Keys), fig. 4. Nichols and Breder 1927:124 (description, distribution, biology), fig. 171. Frost 1928:329-330 (sagittae), pl. 12, fig. 7 (sagitta). Beebe and Tee-Van 1928:97 (description; Port-au-Prince Bay, Haiti), fig. Hildebrand and Schroeder 1928:205 (description, range in part, biology; Chesapeake Bay), fig. 116. Nichols 1929:230 (range, description; Puerto Rico), fig. 83. Beebe and Hollister 1935:213 (Union I., Grenadines). Hubbs 1936:253 (description of 4 juveniles, 36-50 mm, from Yucatan). Baughman 1941:17-18 (Texas records). Munro 1943: 67, 71-72 (placed in subgenus *Scomberomorus*). Fowler 1945:186 (synonymy, description; Charleston, S.C.), 290 (Florida). La Monte

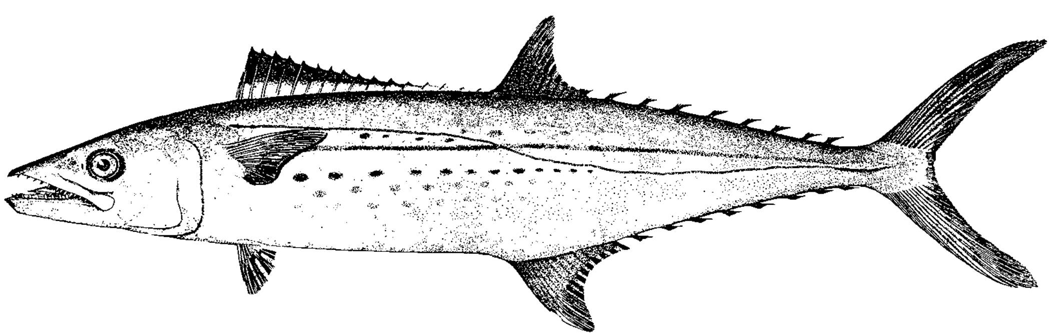


FIGURE 65.—*Scomberomorus regalis.* Key West, Fla., 625 mm FL, USNM 12527. (From Goode 1884:pl. 94.)

1945:28 (description, range). Breder 1948: 127 (range), fig. Erdman 1949:301 (frequently found in the West Indies). Fraser-Brunner 1950:160 (synonymy in part, range), fig. 32. Baughman 1950:244 (previous Texas records). Rivas 1951:225 (synonymy, diagnosis, range). La Monte 1952:50-51 (description, range). Bigelow and Schroeder 1953:348 (description; one record from Gulf of Maine, Monomoy, Cape Cod), fig. 183. Pew 1954:26, 28 (description, range, habits; 3-ft specimen from Port Aransas, Tex.), fig. 24. *Erdman 1956:317 (range, spawning periods; Puerto Rico). Briggs 1958: 286 (range). *Mago Leccia 1958 (osteology, comparisons with *S. maculatus* and *S. cavalla*), figs. Cervigón 1966:720-721 (description; Venezuela). *Randall 1967:754 (food of 116 West Indian specimens, 96.1% fishes). Böhlke and Chaplin 1968:573 (description, range), fig. Randall 1968:117-118 (description, range, habits), fig. 134 (photograph of Virgin Is. specimen). Beardsley and Richards 1970:5 (length-weight of 58 specimens, 213-835 mm FL, 0.13-4.88 kg; Florida). Dahl 1971:278 (common in Colombia), fig. Richards and Klawe 1972:14 (range), 94 (reference to Hubbs 1936). Miyake and Hayasi 1972:III-3 (in key), IV-11 (common names). Klawe 1977:2 (common name, range). Erdman 1977:150 (spawn virtually all year; NE Caribbean). Collette et al. 1978:274-275 (comparison with other American species of *Scomberomorus*). Fritzsche 1978:133-135 (description, larval development), figs. 75-76 (larvae). Collette 1978:Scombm 6 (description, range), figs. Lima and Oliveira 1978:13, 24 (common name "sierra-penincho" in Brazil). Manooch et al. 1978 (annotated bibliography). Collette 1979:29 (characters, range). Collette and Russo 1979:13 (diagnostic characters, range). Sacchi et al. 1981:3 (French Antilles). Köster 1981:55 (Isla Rosario, Colombia). Cooper 1982 (fishery in Jamaica). Cressey et al. 1983:264 (host-parasite list, 7 copepod species). Garzon and Acero 1983:18 (Isla Providencia, Colombia). Collette and Nauen 1983:75-76 (description, range), fig. Finucane and Collins 1984 (reproductive biology, Fla.).

Types of nominal species.—Both *Scomber regalis* Bloch 1793 and *Scomberomorus plumierii* Lacepède 1802 are based on Plumier's drawing of a specimen from Martinique, and there are no known type-specimens extant. The pattern of spots and lines in the color plate published by Bloch (color pl. 333) leaves no doubt as to the identity of the species.

Diagnosis.—The only species of *Scomberomorus* that has a stripe on its sides (which may be broken into several segments) with small dots above and below the stripe (Fig. 65). Other species have lines, spots, blotches, or bars, or are plain. *Scomberomorus regalis* possesses nasal denticles as do the other five species of the *regalis* group (*brasiliensis*, *concolor*, *maculatus*, *sierra*, and *tritor*), has an artery that comes off the fourth left epibranchial artery as do all the species in the group except *S. tritor*, and shares a specialization of the fourth right epibranchial artery (Fig. 7g) with *S. brasiliensis* and *S. sierra*. In these three species an artery connects the fourth right epibranchial with a branch of the coeliaco-mesenteric artery. Together with three other species of the *regalis* group (*brasiliensis*, *concolor*, and *sierra*), *S. brasiliensis* has a long posterior process on the pelvic girdle (Fig. 46a), 62-90% of the length of the anterior plate. Intercalar spine absent as in the other five species of the *regalis* group and *S. niphonius*. Pectoral fin covered with scales.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3n). Spines in first dorsal fin 16-18, usually 17 (Table 9); second dorsal fin rays 16-19, usually 17 or 18 (Table 10); dorsal finlets 7-9, usually 8 (Table 10); anal fin rays 15-20, usually 18 or 19 (Table 11); anal finlets 7-10, usually 8 (Table 11); pectoral fin rays 20-24, usually 21 or 22 (Table 12). Precaudal vertebrae 19 or 20, usually 20 (Table 6); caudal vertebrae 28 (Table 7); total vertebrae 47 or 48, usually 48 (Table 8). Gill rakers on first arch (2-4) + (10-14) = 12-18, usually 3 + (12-13) = 15-16 (Table 5). Morphometric characters given in Table 26.

Size.—Maximum size 83.5 cm FL, 4.9 kg (Beardsley and Richards 1970). Sexual maturity in Florida is attained at about 350 mm FL for males, 380 mm for females (Finucane and Collins 1984).

Color pattern.—Bluish green on back, sides silvery, with a midlateral row of yellow streaks of variable length and small yellow spots above and below this row (Randall 1968). Distal part of anterior lobe of first dorsal fin black, rest of fin white.

Bloch (1793:pl. 333) included a color plate in his original description of *Scomber regalis*. There is a

TABLE 26.—Summary of morphometric data of *Scomberomorus regalis*. FL = fork length, HL = head length.

Character			N	Min.	Max.	Mean	SD
Fork length			53	77	544	329	121
Snout-A	‰	FL	53	509	583	548	14
Snout-2D	‰	FL	53	489	560	520	14
Snout-1D	‰	FL	53	226	285	254	11
Snout-P_2	‰	FL	49	210	306	264	16
Snout-P_1	‰	FL	53	195	286	233	16
P_1-P_2	‰	FL	50	96	128	109	7
Head length	‰	FL	53	190	258	222	11
Max. body depth	‰	FL	49	113	231	197	18
Max. body width	‰	FL	45	56	176	91	18
P_1 length	‰	FL	51	87	166	125	12
P_2 length	‰	FL	49	40	63	55	5
P_2 insertion-vent	‰	FL	50	238	304	267	16
P_2 tip-vent	‰	FL	48	187	252	210	17
Base 1D	‰	FL	53	227	283	258	12
Height 2D	‰	FL	45	75	145	115	11
Base 2D	‰	FL	53	94	135	116	9
Height anal	‰	FL	44	84	138	112	10
Base anal	‰	FL	53	89	130	111	10
Snout (fleshy)	‰	FL	53	72	98	86	5
Snout (bony)	‰	FL	52	64	88	78	5
Maxilla length	‰	FL	53	105	145	123	7
Postorbital	‰	FL	52	87	128	97	6
Orbital (fleshy)	‰	FL	53	31	63	40	6
Orbital (bony)	‰	FL	53	40	73	55	6
Interorbital	‰	FL	53	49	64	58	3
2D-caudal	‰	FL	51	416	509	480	23
Head length			53	20	119	72	25
Snout (fleshy)	‰	HL	53	357	426	390	16
Snout (bony)	‰	HL	52	316	383	351	17
Maxilla length	‰	HL	53	528	606	556	15
Postorbital	‰	HL	52	376	569	440	26
Orbit (fleshy)	‰	HL	53	150	248	178	20
Orbit (bony)	‰	HL	53	199	292	247	21
Interorbital	‰	HL	53	220	286	262	13

good black and white photograph of a 400 mm specimen from the Virgin Islands in Randall (1968:fig. 134) and a small color photograph in Walls (1975:fig. 410). The drawing published by Goode (1884:pl. 94) is included here as Figure 65.

Biology.—Little is known about migrations or movements of *S. regalis*. Young adults are taken throughout the year in small numbers over the Jamaica shelf (Cooper 1982). Around Puerto Rico, spawning takes place virtually all year (Erdman 1977). Spawning takes place from April to October at California Bank, south of Jamaica (Cooper 1982). The majority of fish appeared to be sexually mature during most of the period between August and October in the coastal waters of southern Florida (Finucane and Collins 1984). Fecundity estimates for 20 females 380-800 mm FL ranged from 161,000-2,234,000 (Finucane and Collins 1984). The only published reference to eggs and larvae is by Fritzsche (1978:133-135) based on C. A. Mayo's Ph.D. thesis. Food in the West Indies is 96% fishes, particularly small schooling clupeoids (*Harengula*, *Jenkinsia*, and *Opisthonema*) and atherinids (*Allanetta*) but also including squids and shrimps (Randall 1967).

Interest to fisheries.—Taken commercially with gill nets and on lines in Florida, the West Indies, and the Bahama Islands. Also a valued sportfish taken by trolling with cut bait. It is taken by trolling and with hooks baited with live bait in Jamaica (Cooper 1982). Only 76-106 t identified as *S. regalis* were reported from Fishing Area 31 (Western Central Atlantic) in 1979-82, all from the Dominican Republic (FAO 1984), but the actual catch is higher because an additional 985-1,108 t of unidentified *Scomberomorus* was also reported from this area and this is *S. cavalla* and *S. regalis*.

Distribution.—Most abundant in clear waters around reefs in southern Florida, the Bahamas, and West Indies (Fig. 49), but there are scattered records from Cape Cod to Brazil. The northernmost records appear to be Monomoy at the southern elbow of Cape Cod (Bigelow and Schroeder 1953:348) and Buzzards Bay on the south shore of Cape Cod (Sumner et al. 1913). There are also records from Chesapeake Bay (Hildebrand and Schroeder 1928) and further south along the Atlantic coast of the United States. Several authors have reported occurrences in Texas (Baughman 1941, 1950; Pew 1954). Reports are scattered from the northern coast of South America-Isla Providencia, Colombia (Garzon and Acero 1983); Colombia (Dahl 1971; USNM 94766), Venezuela (Cervigón 1966; USNM 123081). The southern end of the range is apparently about at Rio de Janeiro (Ribeiro 1915; BMNH 1903.6.9.80).

Material examined.—Total 60 (76.5-544 mm FL).

meas.: 53 (76.5-544): Florida (3); Bahamas (6); Cuba (5); Hispaniola (3); Jamaica (4); Puerto Rico (2); Virgin Is. (13); Antigua (1); St. Eustatius (2); Martinique (1); Barbados (5); Colombia (1); Curacao (1); Venezuela (1); Brazil (3); Mexico (1).
counts: 60.
diss.: 5 (456-544): Florida (2); Bahamas (3).

Scomberomorus semifasciatus (Macleay)
Broad-barred Spanish Mackerel

Figure 66

Cybium semifasciatum Macleay 1884a:205-206 (original description; Burdekin R., Queensland). Macleay 1884b:28 (Burdekin R.). Whitley 1936:40-42 (description in part; AMS IA.1598 and IA.6573 = *S. queenslandicus* (Munro 1943:

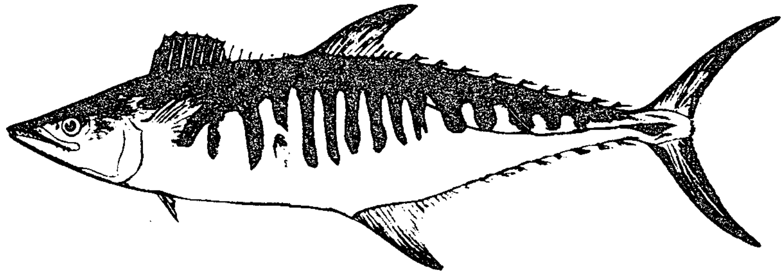


FIGURE 66.—*Scomberomorus semifasciatus.* Queensland, 451 mm FL. (From Munro 1943:pl. 6A.)

95); *C. tigris* a synonym of *S. semifasciatum*); fig. 3 (holotype of *C. semifasciatum*), fig. 4 (holotype of *C. tigris*).

Cybium tigris De Vis 1884:545 (original description; Cape York).

Scomberomorus semifasciatum. McCulloch and Whitley 1925:142 (Burdekin R.; after Macleay 1884a, b).

Scomberomorus tigris. McCulloch and Whitley 1925:142 (Cape York; after De Vis 1884). McCulloch 1929:265 (Cape York; after De Vis 1884).

Scomberomorus semifasciatus. McCulloch 1929: 264 (Burdekin R.; after Macleay 1884). *Munro 1943:91-95 (description, range, synonymy), pl. 6A (451 mm FL specimen from Mackay Dist., N Queensland), fig. 4 (45 and 58 mm juvs., Townsville, N Qld.). Coates 1950:23 (description), fig. Fraser-Brunner 1950:159 (description, range and synonymy in part). Roughley 1951, 1953:110-111 (description), pl. 45, fig. C (after Munro). Jones and Silas 1964:57-58 (description, range), fig. 10 (after Munro). Taylor 1964:282 (description, references, specimens from Nightcliffe, N. Territory). Marshall 1964:365-366 (description; Qld.), pl. 50, figs. 350 A & B (after Munro). Marshall 1966:205 (Qld.), pl. 50, figs. 350 A & B (after Munro). Richards and Klawe 1972:14 (range), 95 (references to juveniles). Magnuson 1973:350 (short pectoral fin). Kailola 1975:237 (3 collections from Gulf of Papua in Kanudi Fisheries collection). Shiino 1976:231 (common name). Klawe 1977:2 (common name, range). Collette 1979:29 (characters, range). Collette and Russo 1979:13 (diagnostic characters, range). Grant 1982:630 (description, fishery in Qld.), 631 (color pl. 328). Cressey et al. 1983:264 (host-parasite list, 5 copepod species). Collette and Nauen 1983:76-77 (description, range), fig. Jenkins et al. 1984:345, 348-351 (101 larvae, 3.3-10.5 mm SL; off Townsville, Qld.), fig. 2 (6 larvae, 3.8-10.5 mm SL).

Indocybium semifasciatus. Fraser 1953:6 (abundant along NW coast of Western Australia).

Indocybium semifasciatum. Whitley 1947:129 (Western Australia). Whitley 1948:24 (W. Australia). Whitley 1954:27 (between Darwin and Pt. Charles, Northern Territory). Munro 1958a:112 (description, range), fig. 752. Whitley 1964a:252 (description, range in part; material from Qld., N. Territory, W. Australia). Whitley 1964b:48 (listed). Grant 1965:173 (description after Munro), fig. Grant 1972: 106, 1975:164, 1978:194 (description after Munro; fishery in Qld.), fig.

Types of nominal species.—*Cybium semifasciatum* Macleay 1884a. Holotype: AMS I.18288; lower Burdekin River, Queensland, Australia; A. Morton; Aug. 1883; 285 mm FL; D ? + 20 + VIII; A 21 + VIII; P_1 24-24; RGR_1 2 + 1 + 6 = 9; vertebrae 19 + 26 = 45.

Cybium tigris De Vis 1884. Holotype: QM I.119; Cape York, Queensland, Australia; K. Broadbent; 286 mm FL; D XIV + 19 + IX; A 21 + IX; P_1 24-24; RGR_1 2 + 1 + 7 = 10.

Diagnosis.—This species has wider lateral keels on the caudal peduncle than other species in the genus, but this is difficult to quantify and so is not a very useful diagnostic character. Superficially similar to *S. commerson* in having prominent vertical bars on the sides (specimens over 700 mm FL lose their bars), but the bars are much wider (Fig. 66) than the many narrow bars of *S. commerson.* Also differs in lacking an abrupt downward curve in the lateral line under the second dorsal fin, in having fewer spines in the first dorsal fin (15 or fewer vs. usually 16 or 17), and in having more gill rakers on the first arch (6-13, usually 9 or more vs. 1-8, usually 6 or less). Palatine tooth patch wider (Fig. 26a) than in any other species of *Scomberomorus*. Posterior end of maxilla expanded (Fig. 23a) as in *S. lineolatus* and *S. plurilineatus*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3o). Spines in first dorsal fin 13-15, usually 14 or 15 (Table 9); second dorsal fin rays 19-22, usually 20 (Table 10); dorsal finlets 8-10, usually 9 (Table 10); anal fin rays 19-22, usually 21 or 22 (Table 11); anal finlets 7-10, usually 8 or 9 (Table 11); pectoral fin rays 22-25, usually 23 or 24 (Table 12). Precaudal vertebrae 18 or 19, usually 19 (Table 6); caudal vertebrae 25-27, usually 26 (Table 7); total vertebrae 44-46, usually 45 (Table 8). Gill rakers on first arch (1-2)+(5-11)=6-13, usually 2+(7-9)=9-10 (Table 5). Morphometric characters given in Table 27.

Size.—Maximum size 120 cm FL, 10 kg (Lewis 1981).

Color pattern.—Munro (1943) provided good descriptions of the colors of juveniles and adults from Queensland. Juveniles (<100 mm) with cranial regions and upper regions of the back pale green with a bronze sheen and marked with 12-20 broad vertical dark grey bands. Bars confined to region of body above lateral line, number increasing with age. Cheeks and belly silver white. Snout dark slate grey, patch of green above orbit. First dorsal fin jet black with contrasting areas of white in central region. Second dorsal fin cream with yellow anteriorly. Anal fin and finlets transparent white. Caudal flukes creamy white at margins and dusky or blackish near hypural. Pectoral fins dusky.

With increase in size the bronze-green coloration of the back turns greenish blue. The vertical bands on the back are most marked in specimens < 500 mm and in larger fish there is a tendency for these markings to become less distinct, break into spots or fade out more or less completely. Above 700 mm, dead fish assume a drab greyish-yellow blotchy appearance with little or no evidence of markings. This uniform grey color apparently accounts for the vernacular "grey mackerel" of Queensland fishermen as applied to older age groups of the species.

Munro included excellent illustrations of a 451 mm specimen and a 140 mm juvenile in his 1943 paper (pl. 6, 8). The illustration of the larger individual has been reproduced in Grant (1982 and previous editions) and herein (Fig. 66). There is a color photograph of a 470 mm specimen in Grant (1982:pl. 328).

TABLE 27.—Summary of morphometric data of *Scomberomorus semifasciatus*. FL = fork length, HL = head length.

Character			N	Min.	Max.	Mean	SD
Fork length			31	142	840	344	217
Snout-A	‰	FL	31	477	533	505	16
Snout-2D	‰	FL	31	452	495	472	11
Snout-1D	‰	FL	30	212	261	245	12
Snout-P_2	‰	FL	29	195	273	249	18
Snout-P_1	‰	FL	31	183	248	219	15
P_1-P_2	‰	FL	29	85	116	104	7
Head length	‰	FL	31	180	236	212	14
Max. body depth	‰	FL	29	190	231	210	10
Max. body width	‰	FL	29	71	121	94	13
P_1 length	‰	FL	30	132	166	147	10
P_2 length	‰	FL	28	36	59	50	6
P_2 insertion-vent	‰	FL	22	198	271	237	13
P_2 tip-vent	‰	FL	19	168	210	187	10
Base 1D	‰	FL	30	170	236	210	14
Height 2D	‰	FL	25	112	177	160	13
Base 2D	‰	FL	30	119	211	138	18
Height anal	‰	FL	23	135	220	156	17
Base anal	‰	FL	29	124	168	145	11
Snout (fleshy)	‰	FL	30	72	89	81	4
Snout (bony)	‰	FL	30	63	80	72	4
Maxilla length	‰	FL	30	92	134	118	11
Postorbital	‰	FL	29	84	109	95	6
Orbital (fleshy)	‰	FL	30	23	46	35	7
Orbital (bony)	‰	FL	31	34	63	51	8
Interorbital	‰	FL	31	48	80	56	5
2D-caudal	‰	FL	25	470	565	518	34
Head length			31	33	156	70	39
Snout (fleshy)	‰	HL	30	355	409	379	17
Snout (bony)	‰	HL	30	289	409	340	26
Maxilla length	‰	HL	30	496	596	554	21
Postorbital	‰	HL	29	385	486	448	24
Orbit (fleshy)	‰	HL	30	122	202	162	24
Orbit (bony)	‰	HL	31	176	269	237	24
Interorbital	‰	HL	31	242	357	266	20

Biology.—Little is known of the biology of this species other than it forms small schools. Juveniles ranging in size from 45 to 100 mm are common along the beaches in the vicinity of Townsville, Queensland, during November and grow to twice this size by January (Munro 1943). Larvae (3.3-10.5 mm SL) were described and illustrated by Jenkins et al. (1984).

Interest to fisheries.—Fish of 60-90 cm are caught on fishing grounds north of Yeppoon, Queensland, in November while smaller age groups are caught in estuaries along the Queensland coast north of Moreton Bay (Munro 1943). It is taken by setnetting as well as by trolling and is popularly fished by Queensland anglers in small outboard-powered boats trolling with small lures or cut bait (Grant 1982). Together with *Grammatorcynus* and three other species of *Scomberomorus*, mackerel fishing is Queensland's second major finfishery with an annual output of about 1,000 tons of whole and filleted fish (Anonymous 1978). Also trawled in the Gulf of Papua.

Distribution.—This is the most estuarine of the species of *Scomberomorus* in Australia. It is confined to estuarine and coastal waters of northern Australia from Shark Bay, Western Australia, through the Northern Territory, and Queensland to northern New South Wales (Whitley 1964a:252, fig. 5f; Lewis 1981:17) and southern Papua New Guinea (Fig. 55). Reports of specimens collected by D. G. Stead from Thailand and Malaya (Whitley 1964a:252) are based on misidentifications.

Geographic variation.—Comparisons of morphometric characters for three small samples of *S. semifasciatus* were made with ANCOVA: Queensland (n = 3-4), Northern Territory (n = 3-5), and New Guinea (n = 13-22). Null hypotheses that the 3 sets of regression lines are coincident were accepted for 23 sets, rejected for 3 sets: Base 1D, orbit (fleshy), and orbit (bony). The Newman-Keuls Multiple Range Test showed that the Queensland and New Guinea populations differed significantly from each other in Base 1D (slopes 0.256 and 0.211, Q = 4.392**) and that the New Guinea population differed from the Northern Territory population in fleshy orbit (slopes 0.020 and 0.030, Q = 5.492**) and bony orbit (slopes 0.034 and 0.046, Q = 7.523**).

Material examined.—Total 34 (142-840 mm FL).

meas.:	31 (142-840): Queensland, Australia (4, **C. semifasciatus*, **S. tigris*); N. Territory, Australia (5); New Guinea (22).
counts:	33.
diss.:	6 (406-840): New Guinea.

Scomberomorus sierra Jordan and Starks
Sierra

Figure 67

Scomberomorus maculatus. Not of Mitchill 1815. Jordan and Gilbert 1882:426 (in part; E. Pacific). Jordan and Gilbert 1883a:106 (Mazatlan). Jordan and Gilbert 1883b:110 (Panama). Meek and Newland 1884:234 (synonymy in part; E. Pacific). Dresslar and Fesler 1889:443 (synonymy in part; E. Pacific). Evermann and Jenkins 1891:128 (not previously reported N of Mazatlan), 137 (important food fish; Guaymas, Mexico). Meek and Hildebrand 1923:324-325 (in part; Pacific coast of Panama; *S. sierra* considered a synonym of *S. maculatus*). Herre 1936:105 (description, several specimens; Albemarle I., Galapagos; *S. sierra* considered a synonym of *S. maculatus*). Fowler 1938:30-31 (synonymy in part, description; specimen from Charles I., Galapagos). Hildebrand 1946:376-377 (synonymy in part; 14 specimens, 100-606 mm SL, from Gulf of Guayaquil; comparison of Atlantic and Pacific populations, "...at most different races for the opposite coasts"). Fraser-Brunner 1950:159 (*S. sierra* considered a synonym of *S. maculatus*). Bini and Tortonese 1955:32 (specimens from several localities in Peru). Ricker 1959:13 (Petalco Bay and San Blas I., Mexico). Castro-Aguirre et al. 1970: 156 (Gulf of California). Sánchez T. and Lam C. 1970:58-59 (length-weight; weights of body parts; diagram of vertebral column, 19+28=47); photograph. León 1973:22 (Puntarenas, Costa Rica). Amezcua-Linares 1977:10 (lagoon system; Sinaloa, Mexico). Kong 1978:6-9 (Antofagasta, Chile). Yañez-Arancibia 1980:111-

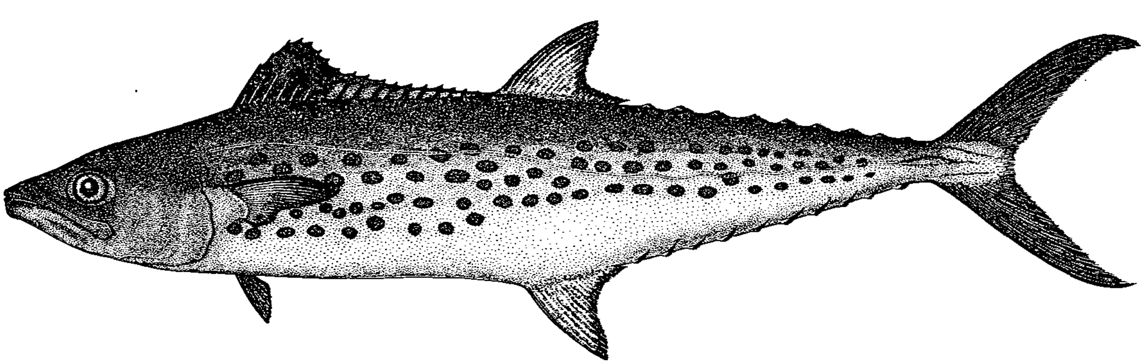


FIGURE 67.—*Scomberomorus sierra*. Gulf of California, 354 mm FL, USNM 217368.

112 (Guerrero, Pacific coast of Mexico), pl. 29, fig. 1.

Scomberomorus sierra Jordan and Starks *in* Jordan 1895:428-429 (original description; Mazatlan, Mexico; also found in Panama). Jordan and Evermann 1896a:341 (listed). Jordan and Evermann 1896b:874-875 (description). Jordan and Evermann 1902:286 (description). Gilbert and Starks 1904:68-69 (description; Panama Bay; comparison with *S. maculatus*). Snodgrass and Heller 1905:360 (Albemarle I., Galapagos). Starks 1910:89-90 (osteology, vertebrae 19+30=49). Kendall and Radcliffe 1912:96 (2 specimens from Panama Bay; description). Osburn and Nichols 1916:158 (Agua Verde Bay; Gulf of California). Evermann and Radcliffe 1917:55-56 (synonymy, description; specimen from Paita, Peru). Starks 1918:120-121 (description, occurrence), fig. 64. Higgins 1920:33-34 (imported to San Diego from Mexico). Craig 1926:167 (used locally; Calexico, Mexico). Ulrey 1929:6 (Gulf of California). Jordan et al. 1930:257 (listed). Croker 1933:14-15 (fishery), fig. 3, fig. 59 (yearly deliveries to San Diego and San Pedro by California boats fishing off Baja California). Breder 1936:11 (specimen taken by second "Pawnee" expedition). Walford 1937:24-25 (description, range, angling notes), color pl. 39. Seale 1940:16-17 (taken along the coast of Mexico and in the Galapagos Is.). Munro 1943:67, 71-72 (placed in subgenus *Scomberomorus*). Fowler 1944: 172-173 (synonymy, description, specimen from Balboa Harbor, Panama). Nichols and Murphy 1944:240 (Bay of Malaga, and Buenaventura, Colombia; more spots than in *S. maculatus*). La Monte 1945:29 (common names, range). Eckles 1949:247-250 (description of 12 juveniles, 21-71 mm FL, 9 from Costa Rica, 3 from the Gulf of California; vertebrae (19-20)+28=(47-48), fig. 2 (21 mm specimen), fig. 3 (71 mm specimen). Fitch and Flechsig 1949:278 (compared with *S. concolor*). Fitch 1950:70 (comparison of 17 *S. sierra* with 30 *S. concolor*). Clothier 1950:52-53 (vertebrae 47-49), pl. X (outline of axial skeleton). Roedel 1951:510 (comparison with *S. concolor*). Mead 1951:121 (2 ripe females, Gulf of California). Roedel 1953:85 (Mexican species; California records of *S. sierra* probably refer to *S. concolor*). Clemens 1956:76, 78 (14 postlarvae, 12-22 mm SL, caught at lat. 08°06′N, long. 79°06′W; 2 survived in shipboard aquaria for 13 d), fig. 2 (postlarvae 16.5 and 54.0 mm SL). Clemens 1957:306 (specimens taken with bait net and night light; Panama, Nicaragua). Collette et al. 1963:53-54 (594 mm FL specimen, La Jolla, first California record, comparison with *S. concolor*), fig. 1. Clemens and Nowell 1963:260 (19 stations, Gulf of California, off Baja California, Mexico, Costa Rica, Gulf of Panama, Gulf of Guayaquil). Fitch and Craig 1964:202 (sagitta similar to that of *S. concolor*). Quiroga and Orbes 1964 (fishery; Esmeraldas Prov., Ecuador). Klawe 1966:445-451 (occurrence of young and spawning; E. Pacific), fig. 2 (11 mm specimens). Fierstine and Walters 1968:4 (localities), 12 (aspect ratio of caudal fin; vertebral counts), fig. 12D (caudal fin complex). Lindsey 1968:1988-1990 (muscle temperature 1.15°C higher than surface water temperature). Matsumoto 1968:309-310 (jaw development compared with that in *Acanthocybium*). Wollam 1970:22 (larval differences between *S. maculatus* and *S. sierra* warrant recognition of *S. sierra*). Erdman 1971:68 (gonads ripe late Aug. to end of Nov., Gulf of Nicoya, Costa Rica; *S. sierra* distinct from *S. maculatus*). *Artunduaga Pastrana 1976 (species synopsis, Colombia). Miller and Lea 1972:192 (description, range), fig. Richards and Klawe 1972:14 (range), 95 (references to larvae and juveniles). Magnuson 1973:350 (short pectoral fin). Sharp 1973:384 (electrophoretic patterns of hemoglobin the same as in *S. concolor*). Shiino 1976: 231 (common name). Thomson and McKibbin 1976:46 (description; Gulf of California), fig. Klawe 1977:2 (common name, range). Collette et al. 1978:274-275 (comparison with *S. brasiliensis* and other American species of *Scomberomorus*). Horn and Allen 1978:41 (California range lat. 33°N to 32°N). Collette 1979:29 (characters, range). Collette and Russo 1979: 13 (diagnostic characters, range). Phillips 1981:54 (El Salvador). Cressey et al. 1983:264 (host-parasite list, 3 copepod species). Collette and Nauen 1983:77-78 (description, range), fig.

Cybium concolor. Not of Lockington, 1889. Boulenger, 1899:3 (Golfe de Panama).

Scomberomorus maculatus sierra. Chirichigno 1969:75 (common names, Ecuador, Peru, and Chile). Chirichigno 1974:325 (in key), fig. 641, 349 (range—S. Calif. to Bahía de Pisco, Peru and Galapagos Is.).

Types.—The original description was based on at least two specimens: "Types, 1720, L. S. Jr. Univ. Mus.; the largest 24 inches long" (Jordan 1895:

429). Böhlke (1953:105) considered SU 1720 to be the holotype of the species but there is a specimen in the British Museum (BMNH 1895.5.24.104) which is also labelled as "type". To clarify the issue, we hereby select CAS SU 1720 as lectotype: Mazatlan, Mexico; D. S. Jordan; 332 mm FL; D XVIII+17+IX; A 19+VIII; P_1 22; RGR_1 4+1+11=16; 3 rows of faint small spots visible on both sides in 1962, size of spots about equal to half diameter of eye. Paralectotype: BMNH 1895.5.24.104; Mazatlan, Mexico; D. S. Jordan; tin tag with no. 1720 attached to specimen; 550 mm FL; D XVII+17+IX; A 16+IX; P_1 21-22; LGR_1 3+1+10=14; 3 rows of spots on sides.

Diagnosis.—This species possesses nasal denticles (Fig. 1a, b) as do the other five species of the *regalis* group (*brasiliensis*, *concolor*, *maculatus*, *regalis*, and *tritor*), has an artery branching off the fourth left epibranchial artery as do all the species in the group except *S. tritor*, and shares a specialization of the fourth right epibranchial artery (Fig. 7e) with *S. brasiliensis* and *S. regalis*. In these three species, an artery connects the fourth right epibranchial with a branch of the coeliaco-mesenteric artery. *Scomberomorus sierra* has a longer pelvic fin (Fig. 48) than does *S. brasiliensis* (4.7-6.4% FL vs. 3.6-5.9%) and lacks the lateral stripe that is the diagnostic feature of the pigment pattern of *S. regalis*. Together with three other members of the *regalis* group, *S. sierra* has a long posterior process on the pelvic girdle, 62-90% of the length of the anterior plate. Differs from *S. brasiliensis* by having distinct pterotic spines. Intercalar spine absent as in the other five species of the *regalis* group and *S. niphonius*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3p). Spines in first dorsal fin 15-18, usually 17 or 18 (Table 9); second dorsal fin rays 16-19, usually 17 or 18 (Table 10); dorsal finlets 7-10, usually 8 or 9 (Table 10); anal fin rays 16-21, usually 18-20 (Table 11); anal finlets 7-10, usually 8 or 9 (Table 11); pectoral fin rays 20-24, usually 21 (Table 12). Precaudal vertebrae 19-21, usually 20 (Table 6); caudal vertebrae 26-29, usually 28 (Table 7); total vertebrae 46-49, usually 48 (Table 8). Gill rakers on first arch (2-4)+(9-14)=12-17, usually 3+(12-13)=15-16 (Table 5). Morphometric characters given in Table 28.

TABLE 28.—Summary of morphometric data of *Scomberomorus sierra*. FL = fork length, HL = head length.

Character		Mexico					Panama					Colombia					Total				
		N	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD
Fork length		36	163	615	344	139	21	98	596	349	154	14	180	266	226	22	97	68	621	340	139
Snout-A	‰ FL	35	518	565	539	13	21	519	560	536	12	14	510	562	526	13	95	510	616	537	17
Snout-2D	‰ FL	35	496	534	513	10	21	466	529	507	14	14	489	511	504	6	95	466	586	510	14
Snout-1D	‰ FL	36	222	268	245	13	21	221	266	242	12	14	216	251	237	11	97	213	276	241	14
Snout-P_2	‰ FL	36	224	297	255	18	20	238	286	257	15	14	250	264	257	5	96	198	330	252	22
Snout-P_1	‰ FL	36	195	249	222	14	21	205	245	220	11	14	211	227	219	5	97	181	260	220	15
P_1-P_2	‰ FL	31	93	118	106	8	20	93	123	104	8	14	91	111	105	5	91	89	123	104	8
Head length	‰ FL	36	190	246	216	14	21	197	237	212	9	14	206	219	213	4	97	183	260	212	14
Max. body depth	‰ FL	34	157	205	191	12	19	164	210	184	14	14	190	221	205	9	93	157	221	190	15
Max. body width	‰ FL	32	53	111	84	13	19	63	104	86	11	14	64	86	74	8	90	53	115	84	12
P_1 length	‰ FL	36	110	141	123	7	21	102	140	123	11	14	117	135	127	6	97	78	145	123	9
P_2 length	‰ FL	36	40	64	53	4	19	36	64	53	9	14	50	61	55	3	94	32	64	53	6
P_2 insertion-vent	‰ FL	35	215	318	268	23	20	239	294	271	16	14	235	277	255	11	95	193	339	267	25
P_2 tip-vent	‰ FL	35	162	264	216	20	19	194	262	221	18	14	183	216	200	10	93	162	284	221	22
Base 1D	‰ FL	35	232	286	261	11	20	206	280	253	18	14	238	288	260	12	95	206	306	259	16
Height 2D	‰ FL	35	103	139	120	8	18	109	139	124	8	13	127	141	135	5	88	103	146	123	10
Base 2D	‰ FL	36	69	142	118	13	21	105	140	120	10	14	109	144	125	8	97	69	184	120	14
Height anal	‰ FL	35	103	130	115	7	20	106	135	123	8	14	121	136	128	5	93	91	136	118	9
Base anal	‰ FL	36	97	163	121	12	21	103	157	121	12	14	115	131	122	5	97	88	163	119	12
Snout (fleshy)	‰ FL	36	69	91	81	6	21	73	89	80	4	14	73	78	76	2	97	62	92	79	6
Snout (bony)	‰ FL	33	43	82	72	7	19	65	78	71	4	9	62	69	66	2	85	43	150	70	11
Maxilla length	‰ FL	36	103	146	124	11	21	115	139	122	6	14	114	129	120	4	97	99	150	121	10
Postorbital	‰ FL	31	91	107	100	4	21	90	102	97	3	14	94	101	98	2	92	85	116	98	5
Orbital (fleshy)	‰ FL	36	25	49	34	7	21	23	48	34	7	14	34	43	39	2	97	2	53	34	7
Orbital (bony)	‰ FL	31	39	64	50	8	21	37	64	50	8	14	50	61	54	3	92	16	77	50	9
Interorbital	‰ FL	36	29	62	56	6	21	52	59	54	2	14	51	58	54	2	97	2	65	54	7
2D-caudal	‰ FL	30	430	520	476	25	20	436	509	471	18	14	443	511	467	18	89	234	580	475	38
Head length		36	40	135	73	26	21	23	122	73	31	14	39	57	48	5	97	18	135	71	26
Snout (fleshy)	‰ HL	36	350	405	375	13	21	345	434	379	23	14	344	370	358	7	97	338	434	371	16
Snout (bony)	‰ HL	33	182	375	332	30	19	310	373	336	21	9	299	320	308	8	85	182	576	332	37
Maxilla length	‰ HL	36	540	610	573	18	21	561	610	578	13	14	542	592	566	12	97	531	610	570	17
Postorbital	‰ HL	31	403	502	458	26	21	415	497	460	22	14	446	472	460	8	92	388	509	461	26
Orbit (fleshy)	‰ HL	36	124	200	156	22	21	114	203	158	27	14	160	196	182	11	97	9	232	158	27
Orbit (bony)	‰ HL	31	184	278	226	25	21	173	292	234	33	14	228	280	256	15	92	81	337	235	35
Interorbital	‰ HL	36	143	284	257	22	21	220	288	257	14	14	241	270	254	8	97	11	288	253	33

Size.—Maximum size 96.5 cm FL, 5.44 kg; of 271 sierra caught in the Gulf of Nicoya, Costa Rica, 50 measured more than 63.5 cm and weighed more than 5.4 kg (Erdman 1971). Size at first maturity 26-32 cm FL in Colombia (Artunduaga Pastrana 1976). A length-weight regression curve has been published for 310 Colombian specimens 15-63 cm, 0.03-2.4 kg (Artunduaga Pastrana 1976:fig. 6).

Color pattern.—Bluish above, silvery white ventrally, sides with numerous round brownish (orange in life) spots, three rows below lateral line, one above (Fig. 67). First dorsal fin black distally, white at base. Second dorsal tinged with yellow, margins black. Anal white.

There is a color painting of *S. sierra* by Malmquist in Walford (1937:pl. 39), and there is a good black and white underwater photograph of several specimens in the Gulf of California in Thomson et al. (1979:fig. 115).

Biology.—Spawning probably takes place near the coast over most of its range (Klawe 1966). Spawning occurs off Mexico in July-September (Klawe 1966). Ripe males and females were found from late August to the end of November in the Gulf of Nicoya, Costa Rica (Erdman 1971). The maximum incidence of ripe females extends from November to April in Colombia with a peak in February-April (Artunduaga Pastrana 1976). Larvae and juveniles, 4.5-139 mm FL, of *S. sierra* have been taken from Baja California to Peru during January-April and July-September (Klawe 1966:fig. 1, table 1). The smallest larvae were taken off Baja California July-September: 4.5-9.5 mm FL, 13 September; 4.8 mm, 12 August; 8.4 mm, 9 July (Klawe 1966:table 1). Food of adults consists of small fishes (Walford 1937). In Colombia (Artunduaga Pastrana 1976), the commonest fishes in stomach contents were anchovies (Engraulidae, *Anchoa* and *Cetengraulis*) and clupeids (*Odontognatus* and *Opisthonema*).

Interest to fisheries.—According to Walford (1937), *S. sierra* seems to be the most abundant game fish along the Pacific coasts of Mexico and Central America. It is an excellent food fish frequently taken by anglers and abundant enough to support a commercial fishery (Eckles 1949). Statistics are reported from Fishing Areas 77 and 87; the bulk of the catch is reported for Mexico 4,028-11,999 t/yr and for Peru 320-579 t/yr in 1979-82 (FAO 1984). No specific commercial fishery exists for *S. sierra* in Colombia, but it is taken by the shrimp fleet and by artisanal fishermen for a total catch in 1971 of 127 tons (Artunduaga Pastrana 1976).

Distribution.—Eastern Pacific (Fig. 49) from La Jolla, southern California (Collette et al. 1963) south past Payta, Peru (Collette and Russo 1979: fig. 8) to Antofagasta, Chile (lat. 23°24′S, long. 70°26′W, Kong 1978). Also found around the Galapagos Islands.

Geographic variation.—Comparisons were made of morphometric data for three populations of *S. sierra* by ANCOVA (Table 28): Mexico (n = 31-36), Panama (n = 18-21), Colombia (n = 9-14). Null hypotheses that the 3 sets of regression lines are coincident were accepted for 18 sets, rejected for 8 sets: Sn-1D, Sn-P_2, Head L, maximum body depth, Ht 2D, Ht A, Snout (fleshy), and maxilla L. The Newman-Keuls Multiple Range Test identified populations that were significantly different for 6 sets of regressions. Five of these (Sn-1D, Sn-P_2, Head L, Ht A, and maxilla L) indicated that the populations from Mexico and Panama were significantly different, one (maximum depth) that the Panama and Colombia populations were significantly different. The samples from Panama and Colombia were then combined and the combined regressions were compared with those for Mexico. Null hypotheses were rejected for 7 of the 26 sets of regression lines; the same ones as were rejected in the first test except for maximum body depth. No meristic differences were found between populations.

Material examined.—Total 123 (68-621 mm FL).

meas.: 97 (68-621): California (1); Mexico (39, **S. sierra*); El Salvador (1); Costa Rica (5); Panama (21); Colombia (14); Ecuador (7); Peru (6); Galapagos Is. (3).
counts: 123.
diss.: 13 (368-590): Mexico (2); Panama (5); Ecuador (5).

Scomberomorus sinensis (Lacepède)
Chinese Seerfish

Figure 68

Scomber sinensis Lacepède 1800:599 (original description). Lacepède 1802:23 (description based on a Chinese drawing). Günther 1860: 369 (footnoted as dubious species).

Cybium chinense Cuvier *in* Cuvier and Valenciennes 1831:180 (original description based on

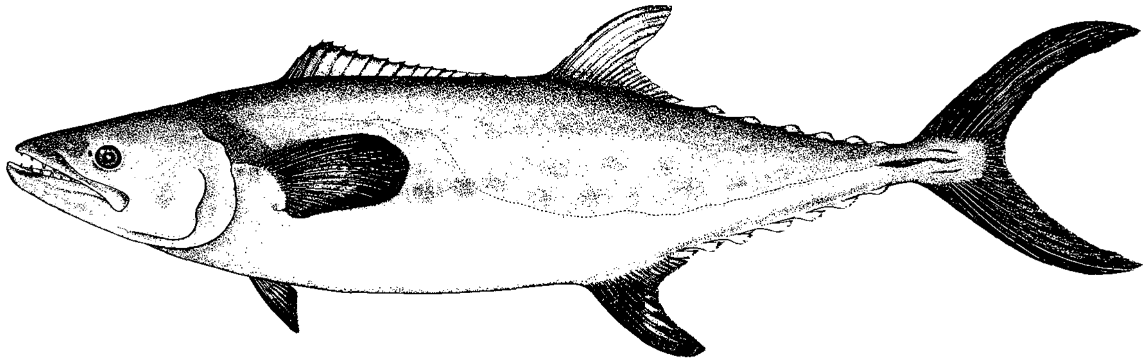


FIGURE 68.—*Scomberomorus sinensis*. Shanghai, China, 714 mm FL, USNM 220856.

same figure used by Lacepède). Temminck and Schlegel 1844:100-101 (description), pl. 53, fig. 1 (color painting of adult). Richardson 1846:268 (synonymy; seas of China and Japan). Günther 1860:369 (footnoted as dubious species). Bleeker 1873:131 (China; listed). Kishinouye 1915:11 (description), pl. 1, fig. 5. *Kishinouye 1923:418-419 (description, range), pl. 21, fig. 34 (adult), pl. 23, fig. 40 (skull, vertebral column). Kishinouye 1924:92 (26 mm juvenile from skipjack stomach). Boeseman 1947:95 (identification of Burger's plate). Morice 1953: 37 (villiform tongue teeth present).

Scomberomorus sinensis. Jordan and Snyder 1900:352 (Tokyo; listed). Jordan and Snyder 1901:64 (Japanese localities). Reeves 1927:8 (Chefoo, China; listed). Mori 1928:5 (Fusan, Korea; listed). Soldatov and Lindberg 1930:111 (synonymy, description, range). Munro 1943: 69, 71 (placed in subgenus *Sierra*; *C. cambodgiense* Durand a junior synonym of *S. sinensis*). Mori 1952:137 (Fusan, Korea; listed). Mori 1956:23 (Kasumi and Hamada, S Japan Sea; listed). Blanc et al. 1965:121-123 (*C. cambodgiense* Durand a junior synonym of *S. sinensis*). *D'Aubenton and Blanc 1965:233-243 (description, range, biology), fig. 1 (191 mm juvenile), fig. 2 (1,170 mm adult). Kamohara 1967:43 (comparison with *S. niphonius*). Tokida and Kobayashi 1967:158 (identification of *C. chinense* of Uchimura's unpublished 1884 manuscript). Sugiura 1970:205 (Bonin Is., listed). Richards and Klawe 1972:15 (range), 95-96 (reference to Blanc et al. 1965 and D'Aubenton and Blanc 1965). Shiino 1972:71 (common name). Magnuson 1973:350 (short pectoral fin). Orsi 1974: 175 (Vietnam; listed). Shiino 1976:231 (common name). Klawe 1977:2 (common name, range). Zama and Fujita 1977:118 (Ogasawara Is., listed after Sugiura 1970). Collette 1979: 29 (characters, range). Collette and Russo 1979:13 (diagnostic characters, range). Ohe et al. 1981:42-43 (comparison with Miocene *Acanthocybium* from Japan). Zhang and Zhang 1981:104 (range). Lee and Yang 1983:229 (Taiwan), fig. 18 (1,056 mm). Cressey et al. 1983: 264 (host-parasite list, 3 copepod species). Collette and Nauen 1983:78 (description, range), fig.

Scomberomorus chinensis. Jordan et al. 1913: 122 (Japanese common names). Norman and Fraser 1949:153 (China and Japan). Devaraj 1977:56-57 (*S. chinensis* intermediate between *Acanthocybium* and other species of *Scomberomorus*).

Cybium cambodgiense Durand 1940:37-38 (original description; Phnom Penh, Cambodia), pl. 6.

Scomberomorus cavalla (not of Cuvier 1829). Fraser-Brunner 1950:160-161 (*Cybium sinensis* placed in synonymy of *S. cavalla* and considered a subspecies of it).

Scomberomorus chinense. Richards and Klawe 1972:13 (range), 90 (reference to Kishinouye 1924).

Scomberomorus sp. Kawamoto et al. 1972:49 (description; Mekong Delta, Vietnam), fig. 96.

Scomberomorus cambodgiense. Orsi 1974:174 (Vietnam; listed).

Types of nominal species.—Both *Scomber sinensis* Lacepède 1800 and *Cybium chinense* Cuvier *in* Cuvier and Valenciennes 1831 are based on a Chinese drawing; no types are extant (Blanc and Bauchot 1964:449).

Cybium cambodgiense Durand 1940. The original description was based on a 215 mm specimen taken in Phnom Penh, Cambodia, 28 January 1939. Because this specimen is not known to still exist, data are presented from the original description: D XVI + 16 + VII; A 19 + VI; P_1 22; GR 3 + 9 = 12. The figure (pl. 6) accompanying the original description clearly shows the deep dip in the lateral line under the posterior part of the first dorsal fin.

Diagnosis.—The only species of *Scomberomorus* that has a swim bladder and the only species with an abrupt downward curve in the lateral line beneath the first dorsal fin (Fig. 68). Two species, *S. cavalla* and *S. commerson*, also have abrupt downward curves in the lateral line but they are under the second dorsal fin. The lateral line in the other 15 species descends gradually without any prominent dips. The pectoral fins are large and rounded rather than pointed as in the other 17 species. Palatine tooth patch very narrow as in *Scomberomorus commerson* and *Acanthocybium*. Ventral process of angular moderate, 87-93% as long as the dorsal process, as in *S. cavalla*. Posterior end of maxilla only slightly expanded as in *S. multiradiatus*. Ascending process of premaxilla very long as in *S. lineolatus* and *Acanthocybium*.

Description.—Intestine with two folds and three limbs (Fig. 3q). Spines in first dorsal fin 15-17, usually 16 or 17 (Table 9); second dorsal fin rays 15-17, usually 15 or 16 (Table 10); dorsal finlets 6-7 (Table 10); anal fin rays 16-19, usually 17 or 18 (Table 11); anal finlets 5-7, usually 6 (Table 11); pectoral fin rays 21-23, usually 22 (Table 12). Precaudal vertebrae 19 or 20 (Table 6); caudal vertebrae 21 or 22, usually 22 (Table 7); total vertebrae 41 or 42, usually 41 (Table 8). Gill rakers on first arch (1-3) + (10-12) = 11-15, usually 2 + (10-11) = 12-13 (Table 5). Morphometric characters given in Table 29.

Size.—Maximum size 200 cm FL, 80 kg in weight (Kishinouye 1923). A length-weight graph for fish up to 120 cm FL and 18 kg was published by D'Aubenton and Blanc (1965:fig. 4).

Color pattern.—Back greenish blue, belly silvery, fins mostly blackish. Pelvic and anal fins with blackish margins, anal finlets colorless (Kishinouye 1923). Large (larger than the diameter of the eye), round, indistinct spots on sides in two poorly defined rows in adults (Fig. 68). Juveniles with saddlelike blotches extending down to about middle of body (D'Aubenton and Blanc 1965:fig. 2).

There is an excellent figure of *S. sinensis* in Kishinouye (1923:fig. 34) and there are drawings of a juvenile (191 mm FL, fig. 1) and an adult (1,017 mm FL, fig. 2) of *S. sinensis* from the Mekong River in Cambodia in D'Aubenton and Blanc (1965).

Biology.—No information is available on the movements of *S. sinensis*. Although it penetrates great distances up the Mekong River, D'Aubenton and Blanc (1965) reported that they failed to find the slightest trace of sexual activity in Cambodian freshwater specimens and so they concluded that *S. sinensis* must reproduce exclusively in the sea. No information is available on eggs or larvae (Richards and Klawe 1972), but D'Aubenton and Blanc (1965) did report on juveniles as small as 166 mm FL from Tonle Sap, Cambodia.

Interest to fisheries.—No catches were reported as *S. sinensis* by FAO for the period 1979-82 (FAO 1984). However, it is a prized food fish in Japan and probably in China as well. Kishinouye (1923)

TABLE 29.—Summary of morphometric data of *Scomberomorus sinensis*. FL = fork length, HL = head length.

Character			N	Min.	Max.	Mean	SD
Fork length			18	157	714	330	176
Snout-A	‰	FL	14	573	605	584	11
Snout-2D	‰	FL	14	526	571	558	13
Snout-1D	‰	FL	16	268	309	292	9
Snout-P_2	‰	FL	16	270	318	290	12
Snout-P_1	‰	FL	16	234	279	259	11
P_1-P_2	‰	FL	16	101	128	113	7
Head length	‰	FL	18	230	264	255	8
Max. body depth	‰	FL	16	201	231	218	10
Max. body width	‰	FL	16	77	127	102	14
P_1 length	‰	FL	18	133	186	157	14
P_2 length	‰	FL	16	75	89	83	5
P_2 insertion-vent	‰	FL	15	254	295	273	13
P_2 tip-vent	‰	FL	15	161	216	189	17
Base 1D	‰	FL	16	230	282	260	12
Height 2D	‰	FL	15	130	164	145	10
Base 2D	‰	FL	15	99	137	121	11
Height anal	‰	FL	16	129	164	145	10
Base anal	‰	FL	16	99	149	122	12
Snout (fleshy)	‰	FL	16	86	106	97	5
Snout (bony)	‰	FL	16	77	99	90	5
Maxilla length	‰	FL	16	131	159	147	7
Postorbital	‰	FL	16	104	126	117	7
Orbital (fleshy)	‰	FL	16	25	40	35	5
Orbital (bony)	‰	FL	16	40	61	52	7
Interorbital	‰	FL	16	54	72	63	5
2D-caudal	‰	FL	13	394	469	445	27
Head length			18	41	173	83	41
Snout (fleshy)	‰	HL	16	360	414	382	14
Snout (bony)	‰	HL	16	335	387	355	14
Maxilla length	‰	HL	16	561	603	578	12
Postorbital	‰	HL	16	404	482	460	24
Orbit (fleshy)	‰	HL	16	104	155	138	17
Orbit (bony)	‰	HL	16	157	236	202	23
Interorbital	‰	HL	16	208	289	249	23

reported that 2 or 3 dozens of this species were often caught on an autumn day in pound nets on the southern coast of Korea. It is caught in the Mekong River of Cambodia and commanded a high price in the Phnom Penh market in 1964 (D'Aubenton and Blanc 1965:242).

Distribution.—Western Pacific from Japan and China south to Cambodia and Vietnam where it enters the Mekong River (Fig. 51). The northern limit is Akita, Honshu, in the Sea of Japan and the Chiba-Tokyo area on the Pacific coast (Kishinouye 1923:418). There are records or specimens from Pusan, Korea (Mori 1928, 1952), Cheefo (= Yentai) on the Shantung Peninsula (Reeves 1927), the Zhoushan Islands (lat. 30°N, long. 122°E, USNM 220856), Foochow (ZMH 11384), Amoy (USNM 221277), and Hong Kong (CAS GVF HK 127). A record from the Bonin (or Ogasawara) Islands (Sugiura 1970; repeated by Zama and Fujita 1977) has not been verified and seems very far offshore for this species. It has been taken on the coast of Vietnam at Nha Trang (Blanc et al. 1965). *Scomberomorus sinensis* is the only species of the genus and of the family to move any significant distance into freshwater. It was described as a distinct species, *Cybium cambodgiense*, by Durand (1940) from material from Phnom Penh, Cambodia, about 300 km up the Mekong River. Specimens (MNHN 1965-286-9) have come from Tonle Sap (or Grand Lac) which is even further up the Mekong River (Blanc et al. 1965).

Geographic variation.—Morphometric data for two small samples of *S. sinensis* were compared with ANCOVA: China (n = 7-10) and the Mekong River, Cambodia (n = 6). Null hypotheses that the 2 sets of regression lines are coincident were accepted for all but 1 set of the 26 sets, Sn-P_2 (intercepts 7.552 and 8.385 respectively). The Chinese sample had slightly fewer gill rakers on the first gill arch (11-14, mode 12, $\bar{x}$ 12.30) than the Mekong sample (12-15, mode 13, $\bar{x}$ 13.17). No other meristic differences were found.

Material examined.—Total 19 (157-714 mm FL).

meas.:	18 (157-714): China (10); Mekong R., Cambodia (6); Cochinchine (2).
counts:	18.
diss.:	1 (plus 1 head, 431 mm).

Scomberomorus tritor (Cuvier)
West African Spanish Mackerel
Figure 69

Cybium tritor Cuvier *in* Cuvier and Valenciennes 1831:176-177 (original description; Gorée, Sénégal), pl. 218. Günther 1860:372 (description after Cuvier). Rochebrune 1882:96 (very common; Gorée, Dakar). Osorio 1898:197 (Principe). Pellegrin 1908:75 (Dakar). Chabanaud and Monod 1927:278 (Port-Étienne), fig. 30 A. Cadenat 1947:15 (common names; W. Africa). Postel 1954:357-358 (stomach contents of 286 specimens), 362 (gonosomatic index). A. Postel 1955:60-61, fig. 3 (lower jaw teeth 10-21, upper jaw teeth 13-27; 190 specimens), 63, fig. 5 (number of jaw teeth in males and females). *Postel 1955a:4-158 (distribution, size, reproduction), pl. II, bottom figure. Postel 1955b: 31-32 (sex ratio, maximum size, number of eggs). Frade and Postel 1955:35 (histology of

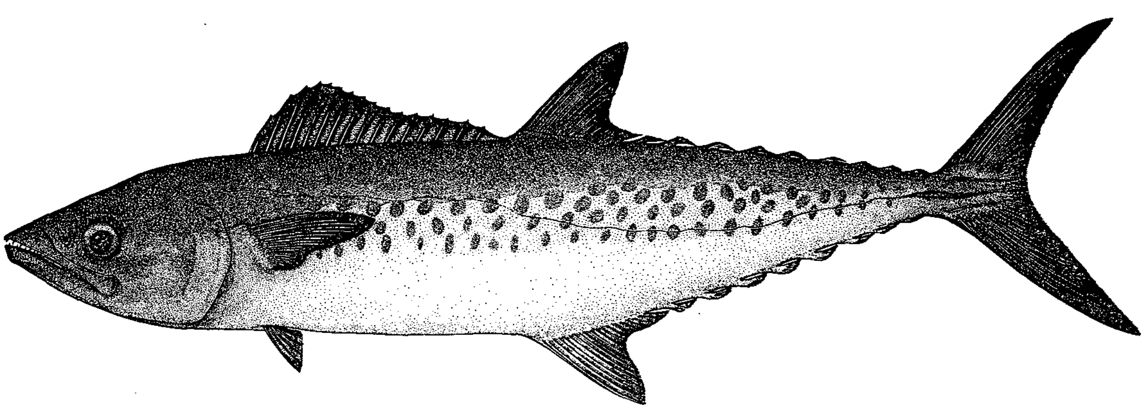


FIGURE 69.—*Scomberomorus tritor.* Liberia, 430 mm FL, USNM 193178.

gonads; mature in June), fig. 7 (oocytes). Postel 1958:107-111 (summary of Postel 1955a). Postel 1959:163 (listed). Postel 1960:257 (Cap Blanc to Senegambie). Marchal 1961:106 (lat. 9°12′N, long. 13°42′W). Franca 1964:table 3 (Angola). Daget and Iltis 1965:280-281 (Ebrie and Abi lagoons, Ivory Coast), fig. 178. Sanches 1966:146 (Angola). Blache et al. 1970:375 (in key), fig. 960 (not fig. 961). Conand 1970:40 (distribution of larvae).

Apolectus immunis Bennett 1831:146 (original description; "Atlantic Coast of North Africa").

Cybium maculatum. Not of Mitchill 1815. Stassano 1890:44 (Spanish Sahara). Vinciguerra 1890:100-103 (synonymy). Osorio 1898:197 (São Thome).

Scomberomorus argyreus Fowler 1905:764-765 (original description, "West Africa"), pl. 51.

Scomberomorus maculatus. Not of Mitchill 1815. Fowler 1936:628-629. Cadenat 1937:482 (Dakar). Scaccini 1941:19 (synonymy in part; Mauritania). Navarro 1943:131 (Cabo Barbas and Blanco, Banco Arguín, Mauritania). Tortonese 1949:65 (accidental in Mediterranean Sea). Sanz Echeverría 1950:1-2 (sagitta compared with other scombrids), pl. 1, figs. 1-4 (photographs of sagittae). Mather and Day 1954:182, 185 (Sierra Leone, Dakar, Canary Is.; *S. tritor* not specifically distinct from *S. maculatus*). Tortonese 1956:7 (accidental in Mediterranean Sea). Poll 1959:104-106 (description; S to Baie des Tigres, Angola), fig. 34. Maurin et al. 1970:19 (Nouakchott, NW Africa). Lozano Cabo 1970:158 (Sahara coast). Fagade and Olaniyan 1973:212, 220, 224 (piscivorous, feeding largely on *Ethmalosa fimbriata* in Lagos). Fagade and Olaniyan 1974:249 (caught in Lagos Lagoon when water was brackish). Tortonese 1975:354-355 (description, Italy), fig. 155.

Scomberomorus tritor. Munro 1943:67-71 (placed in subgenus *Scomberomorus*). Irvine 1947: 186-187 (Accra, Ghana), fig. 108. Fraser-Brunner 1950:158 (synonymy in part), fig. 27. Chaine 1957:504-509 (otoliths), pl. IV (otoliths). Gras 1961:583 (Lagune de Cotonou and Lac Nokoue, Dahomey). Bauchot and Blanc 1961: 372-373 (types). Blanc and Bauchot 1964:448 (types), pl. IV, figs. 19-20 (photographs of types). Gorbunova 1965a:54 (spawning season). Collette 1966:367 (types). Williams 1968:436, table 593 (taken from Gambia to the Congo during the Guinean Trawling Survey). Collette 1970: 4-5 (in key; Mediterranean Sea). Richards and Klawe 1972:15 (range), 96 (references to larvae). Miyake and Hayasi 1972:III-3 (in key), IV-10 (common names). Magnuson 1973:350 (short pectoral fin). Klawe 1977:2 (common name; range). Penrith 1978:187 (Baia dos Tigres, Angola). Collette et al. 1978:274-275 (comparison with W. Atlantic species). Collette 1979: 29 (characters, range). Collette and Russo 1979:13 (diagnostic characters, range). Collette 1981:Scombm 7 (description, range), fig. Seret and Opic 1981:332-333 (description), fig. Cressey et al. 1983:264 (host-parasite list, 4 copepod species). Collette and Nauen 1983:79 (description, range), fig.

Types of nominal species.—Holotype: MNHN A.6871; Gorée, Sénégal; Rang; 658 mm FL; D XV+17+VIII; A 17+VIII; P_1 21; RGR_1 2+1+10 =13. Paratype: MNHN A.6868; Gorée; Sénégal; Rang; 505 mm FL. Photographs of the holotype and paratype were published by Blanc and Bauchot (1964:pl. 4, figs. 19, 20).

Scomberomorus argyreus Fowler 1905. Holotype: ANSP 11400; west coast of Africa; Dr. Savage; 148 mm FL; D XVII+17+VIII; A 19+VIII; P_1 22-22; RGR_1 2+1+11=14; vertebrae 18+28=46.

Diagnosis.—This species possesses nasal denticles as do the other five species of the *regalis* group (*brasiliensis*, *concolor*, *maculatus*, *regalis*, and *sierra*) but lacks the artery branching from the fourth left epibranchial artery that is present in the other species (Fig. 7b). Intercalar spine absent as in the other five species of the *regalis* group and *S. niphonius*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3r). Spines in first dorsal fin 15-18, usually 17 or 18 (Table 9); second dorsal fin rays 16-19, usually 17 (Table 10); dorsal finlets 7-9, usually 8 (Table 10); anal fin rays 17-20, usually 18 or 19 (Table 11); anal finlets 7-9, usually 8 (Table 11); pectoral fin rays 20-22, usually 21 (Table 12). Precaudal vertebrae 18 or 19, usually 19 (Table 6); caudal vertebrae 27 or 28, usually 27 (Table 7); total vertebrae 46 or 47, usually 46 (Table 8). Gill rakers on first arch (1-3)+(10-13)=12-15, usually 2+(11-12)=13-14 (Table 5). Postel (1955a) reported a range of 10-15 gill rakers for 240 males and 520 females, 94% of both sexes 12-14. Morphometric characters given in Table 30.

Size.—Maximum size of males 83.9 cm FL, females 97.5 cm FL; commonly 50-70 cm; age at first maturity of both sexes 45 cm (Postel 1955a).

Color pattern.—Upper parts of body bluish, belly silvery, sides marked with several poorly defined rows of elongate spots (Fig. 69). First dorsal fin black anteriorly and along distal margin posteriorly, white at base.

There are drawings of *S. tritor* in Postel (1955a: pl. 2) and Poll (1959:fig. 34), Collette (1981: Scombm 7), and Seret and Opic (1981:333).

Biology.—Sexual maturity in both sexes of *S. tritor* occurs from April to October in Sénégal (Postel 1955a). Postel (1955a) reported 1 million eggs in a 95 cm FL female. Juveniles have been seined along the shore near Dakar in July (Postel 1955a). Seven larvae 3.5-8.1 mm were caught in September, December, February, and March, south of the Ivory Coast at water temperatures of 23.2°-26°C and salinities of 34.38-35.45‰ (Zhudova 1969). Three larvae identified as *S. tritor* were reported from a station track from Dakar to Recife (Zharov and Zhudova 1967), but this distribution seems highly unlikely. In Lagos Lagoon, Nigeria, stomach contents of 24 of 26 specimens of *S. tritor* with food contained the clupeid *Ethmalosa fimbriata* (Fagade and Olaniyan 1973). No sexually mature stages of *S. tritor* were found in the lagoon so Fagade and Olaniyan concluded that the lagoon served as a feeding ground for this and other piscivorous fishes that could tolerate the reduced salinity of the lagoon.

TABLE 30.—Summary of morphometric data of *Scomberomorus tritor.* FL = fork length, HL = head length.

Character			*N*	Min.	Max.	Mean	SD
Fork length			40	102	658	347	151
Snout-A	‰	FL	40	506	567	533	15
Snout-2D	‰	FL	39	482	551	513	14
Snout-1D	‰	FL	39	190	276	246	13
Snout-P_2	‰	FL	40	237	301	266	17
Snout-P_1	‰	FL	40	197	247	222	13
P_1-P_2	‰	FL	40	95	138	111	11
Head length	‰	FL	40	199	242	217	10
Max. body depth	‰	FL	38	166	240	206	21
Max. body width	‰	FL	36	67	110	90	11
P_1 length	‰	FL	39	110	152	134	9
P_2 length	‰	FL	38	48	71	60	6
P_2 insertion-vent	‰	FL	39	213	304	250	18
P_2 tip-vent	‰	FL	38	146	243	190	17
Base 1D	‰	FL	38	238	304	262	14
Height 2D	‰	FL	31	97	161	126	14
Base 2D	‰	FL	40	101	144	122	10
Height anal	‰	FL	36	92	159	125	13
Base anal	‰	FL	40	93	139	119	10
Snout (fleshy)	‰	FL	40	73	93	81	5
Snout (bony)	‰	FL	40	64	86	72	5
Maxilla length	‰	FL	40	110	143	123	8
Postorbital	‰	FL	39	89	107	96	4
Orbital (fleshy)	‰	FL	40	26	52	38	6
Orbital (bony)	‰	FL	40	28	68	53	8
Interorbital	‰	FL	40	51	68	59	4
2D-caudal	‰	FL	38	432	534	476	29
Head length			40	23	145	74	31
Snout (fleshy)	‰	HL	40	332	409	376	18
Snout (bony)	‰	HL	40	290	388	333	21
Maxilla length	‰	HL	40	541	608	568	14
Postorbital	‰	HL	39	399	474	443	20
Orbit (fleshy)	‰	HL	40	124	233	173	23
Orbit (bony)	‰	HL	40	133	307	245	32
Interorbital	‰	HL	40	230	301	272	13

Interest to fisheries.—Taken throughout the Gulf of Guinea, but catches are reported only for Ghana and Angola in the period 1979-82. Most of the catch is reported for Ghana, 1,569 to 4,412 t/yr (FAO 1984).

Distribution.—Eastern Atlantic, concentrated in the Gulf of Guinea from the Canary Islands (Mather and Day 1954; MCZ 26416), West Sahara (Stassano 1890), and Dakar, Sénégal (original description), south to Baia dos Tigres, southern Angola (Fig. 49). Accidental and rare in the Mediterranean Sea (Tortonese 1949, 1956), with several extant specimens from Nice (NHMV 14599, MSUF M.1665), Villefranche, and Palermo (Tortonese 1975).

Material examined.—Total 49 (69-658 mm FL).

meas.: 40 (102-658): N. Mediterranean (2); Canary Is. (1); Spanish Sahara (1); Sénégal (4, **C. tritor*), Guinea (1); Sierra Leone (5); Liberia (5); Ivory Coast (10); Ghana (5); Nigeria (4); Angola (2); "West Africa" (1, **S. argyreus* Fowler).

counts: 49.

diss.: 10 (394-600): Ivory Coast.

RELATIONSHIPS

After comparing the species of *Scomberomorus* with each other and with *Grammatorcynus* and *Acanthocybium* (Comparative Morphology), all the characters that differentiated species or genera were listed. Character polarities were determined by considering the character state present in *Grammatorcynus* to represent the plesiomorphous condition. *Scomberomorus*, *Acanthocybium*, the Sardini, and the Thunnini have 4 or 5 caudal vertebrae supporting the caudal fin and 37 or more total vertebrae. These derived characters indicate that these taxa form a monophyletic group within the Scombridae. *Grammatorcynus* lies between the Scombrini and the higher scombrids and is clearly more primitive than *Scomberomorus* because it has, as in the

Scombrini, only 3 vertebrae supporting the caudal fin and only 31 total vertebrae. Therefore, we have used it as the outgroup for comparison with *Scomberomorus*. Of the 72 characters that differentiated at least 1 taxon from the others, 14 were autapomorphies of *Acanthocybium*. These cannot contribute to an understanding of relationships within *Scomberomorus* and were omitted from the analysis. The remaining 58 characters were employed to generate a cladogram using a computer program (WAGNER 78) written by J. S. Farris (following Farris 1970 and Farris et al. 1970). The order of the taxa was "shuffled" to determine if another equally parsimonious tree would be generated. Another cladogram was produced with the same total length, 112 steps. The first cladogram has a deviation ratio (sum of the homoplasies between all pairwise combinations of terminal taxa divided by the sum of the character changes between all pairwise combinations of terminal taxa) of 0.24, the second 0.21. The difference is due to characters 3 and 17. We feel that the first cladogram (Fig. 70) more reasonably reflects our concepts of evolution within the genus. A summary of the character states with references to the relevant figures is presented as Appendix 1.

We recognize six species groups within *Scomberomorus* (Fig. 70, Table 31): *sinensis* from node 17; *commerson* from node 15; *munroi* from node 11; *semifasciatus* from node 9; *guttatus* from node 8; and *regalis* from node 5.

The *sinensis* group is monotypic. It is defined by the presence of an abrupt downward curve in the lateral line under the first dorsal fin (character 19, state 1). A similar abrupt downward curve is present in two species of the *commerson* group but the curve is under the second dorsal in those two species. *Scomberomorus sinensis* is the only species in the genus with a well-developed swim bladder (character 18, state 0), but this is a plesiomorphous character. This species is restricted to the northwestern Pacific from Cambodia to Japan. There is no genus-group name available for this group.

The *commerson* group contains four species: *niphonius*, *queenslandicus*, *cavalla*, and *commerson*. This group is defined by the presence of an intercalar spine of at least moderate length (character 17, state 1). Three species (*queenslandicus*, *cavalla*, and *commerson*) have a long (state 2) intercalar spine. *Scomberomorus cavalla* and *S. commerson* share two additional specializations: the pterosphenoid bones are close together (character 13, state 1) and there is an abrupt downward curve in the lateral line under the second dorsal fin (character 19). Three of these species are Indo-West Pacific: *niphonius* from China, Korea, and Japan; *queenslandicus* from off northern Austra-

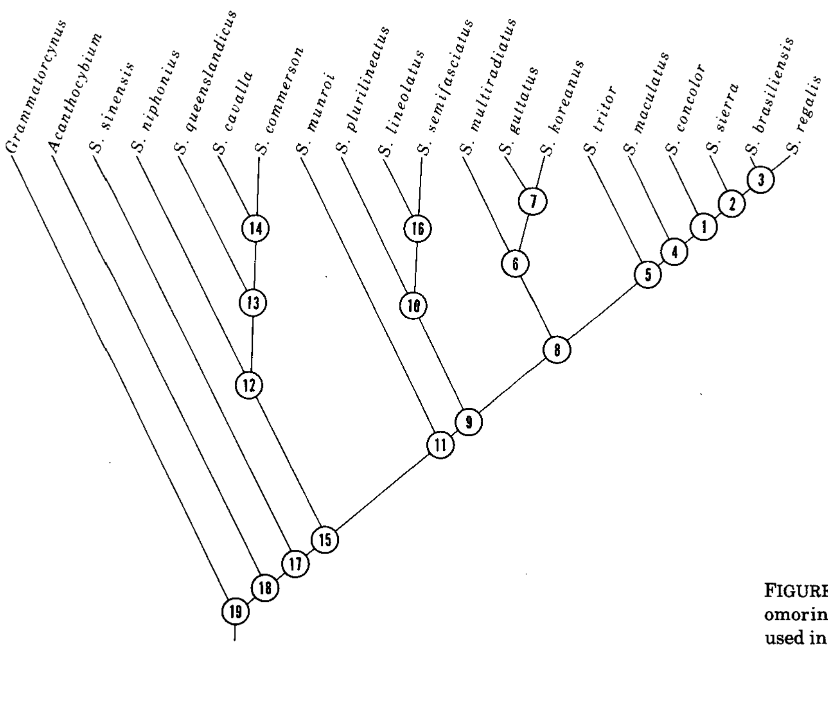


FIGURE 70.—Cladogram of the Scomberomorini, node numbers refer to numbers used in Table 31.

TABLE 31.—Changes in character states based on the most parsimonious cladogram in Figure 70. Numbers under acquisition and reversal columns refer to nodes, three-letter mnemonics refer to species of *Scomberomorus*, and four-letter mnemonics refer to genera, i.e., ACAN = *Acanthocybium*. Two or more components per cell indicate independent acquisition or loss of a character state. Two or more states of the same character acquired at a single node assume that the more primitive state was transitional during the acquisition of the more advanced state.

Character	State	Acquisition	Reversal	Character	State	Acquisition
1	0	19		26	0	19
	1	18			1	18
	2	ACAN, 13	CAV		2	17
2	0	19		27	0	19
	1	18	SEM		1	18
	2	COM, 18	15		2	ACAN
3	0	8, 17	11	28	0	ACAN
	1	19			1	19
	2	ACAN			2	17
4	0	19		29	0	19
	1	13, 18	15		1	17
	2	13, ACAN	CAV	30	0	19
5	0	19			1	17
	1	17		31	0	19
	2	15	MUL		1	17
	3	10		32	0	19
6	0	8	GUT		1	17
	1	17	NIP, 16	33	0	19
	2	19			1	17
	3	ACAN		34	0	19
7	0	19			1	17
	1	16, 18	CAV, 9	35	0	19
8	0	19			1	17
	1	18	GUT	36	0	19
	2	ACAN, LIN			1	17
9	0	CAV, GUT		37	0	19
	1	19			1	17
	2	18, LIN	15	38	0	19
10	0	19			1	17
	1	5	BRA	39	0	19
11	0	ACAN			1	17
	1	19		40	0	19
	2	NIP, 7			1	17
12	0	19		41	0	19
	1	17			1	18
	2	17	14	42	0	19
13	0	19			1	18
	1	LIN, 14		43	0	19
14	0	19			1	18
	1	6		44	0	19
15	0	19			1	18
	1	3, 9	LIN, 4	45	0	19
16	0	19			1	18
	1	1		46	0	19
17	0	19			1	18
	1	5, 12		47	0	19
	2	13			1	18
18	0	19		48	0	19
	1	15			1	18
19	0	19		49	0	19
	1	14, 18	15		1	18
20	0	19		50	0	19
	1	7			1	18
21	0	19		51	0	19
	1	5			1	18
22	0	19		52	0	19
	1	4			1	18
	2	2		53	0	19
23	0	19			1	18
	1	17	MUL	54	0	19
	2	LIN			1	18
24	0	19		55	0	19
	1	18			1	18
	2	17		56	0	19
25	0	19			1	18
	1	18		57	0	19
	2	17			1	18
				58	0	17
					1	19

lia and southern Papua New Guinea; and *commerson* widespread throughout the Indo-West Pacific. The fourth, *cavalla*, is restricted to the western Atlantic. The genus-group name *Cybium* Cuvier (type-species *S. commerson*) is available for this group.

Scomberomorus niphonius is the only species in the genus with a straight gut. This species has very small scapular foramina (character 11, state 2), a character state also found, evidently homoplasiously, in *S. guttatus* and *S. koreanus*. It is restricted to the northwestern Pacific from China, Korea, and Japan. The genus-group name *Sawara* Jordan and Hubbs is available for *S. niphonius*.

The *munroi* group is monotypic. It is defined by the loss of the anterior process on the outer surface of the head of the maxilla. It is restricted to northern Australia and southern Papua New Guinea. There is no genus-group name available for this group.

The *semifasciatus* group contains three species: *plurilineatus*, *lineolatus*, and *semifasciatus*. This group is defined by the presence of a greatly expanded posterior end of the maxilla (character 5, state 3). Two species, *S. lineolatus* and *S. semifasciatus*, share an additional specialization, a wide parasphenoid (character 7, state 1). This character state appears independently in several other lines. All are Indo-West Pacific species, *plurilineatus* along the coast of East Africa plus Madagascar, *lineolatus* along the continental coast from India to Indonesia, and *semifasciatus* in northern Australia and southern Papua New Guinea. The genus-group name *Indocybium* Munro (type-species *S. semifasciatus*) is available for this group.

The *guttatus* group contains three species: *multiradiatus*, *guttatus*, and *koreanus*. This group is defined by a high supraoccipital crest (character 14, state 1). Two species, *guttatus* and *koreanus*, share the presence of auxiliary branches of the lateral line (character 20, state 1). They also have very small scapular foramina (character 11, state 2), a character state shared homoplasiously with *S. niphonius*. All are Indo-West Pacific species, *guttatus* and *koreanus* along the coast of Asia and *multiradiatus* confined to a small section of the Gulf of Papua off the mouth of the Fly River. The genus-group name *Pseudosawara* Munro (type-species *S. guttatus*) is available for this group.

The *regalis* group contains six Atlantic and eastern Pacific species: *tritor*, *maculatus*, *concolor*, *sierra*, *brasiliensis*, and *regalis*. This group is defined by the presence of nasal denticles (character 21, state 1), a synapomorphy unique to the group. All species also have a moderately long intercalar spine (character 17), but this is also present in *S. niphonius*. All species in the group have a vomerine ridge (character 10, state 1) except for *S. brasiliensis* in which it has been secondarily lost. The five most advanced species (all except *S. tritor*) have an artery arising from the fourth left epibranchial artery (character 22, state 1). The four most advanced species (all except *S. tritor* and *S. maculatus*) have developed a long posterior process on the pelvic girdle (character 16, state 1). The three most advanced species (*sierra*, *brasiliensis*, and *regalis*) have a coeliaco-mesenteric shunt connecting the fourth right epibranchial artery with the coeliaco-mesenteric artery (character 22, state 2). The two most advanced species (*brasiliensis* and *regalis*) have lost the pterotic spine (character 15, state 1) but this spine has also been independently lost in other lines. The genus-group name *Scomberomorus* Lacepède sensu stricto (type-species *S. regalis*) applies to this group.

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APPENDIX 1.

Characters used in analysis of *Scomberomorus* relationships

1) Posterodorsal spine of hyomandibula (Fig. 27). Plesiomorphous condition: absent. Character states: 0(absent), 1(present and small), 2 (large).

2) Palatine tooth patch (Fig. 26). Plesiomorphous condition: wide. Character states: 0(wide), 1(narrow), 2(very narrow).

3) Inner process of palatine bone. Plesiomorphous condition: short. Character states: 0(very short, distance from dorsal hook of palatine to end of inner process 54-72% of length to end of outer process), 1(short, 70-84%), 2(long, 97-99%).

4) Ventral process of angular (Fig. 25). Plesiomorphous condition: short. Character states: 0(short, 42-80% of length of dorsal process), 1 (moderate, 87-93%), 2(long, 117-126%).

5) Posterior expansion of maxilla (Fig. 23). Plesiomorphous condition: no expansion. Character states: 0(no posterior expansion of maxilla), 1 (slight expansion), 2(moderate expansion), 3 (marked expansion).

6) Length of head of maxilla. Plesiomorphous condition: long. Character states: 0(short), 1 (medium), 2(long), 3(very long).

7) Width of parasphenoid. Plesiomorphous condition: narrow. Character states: 0(narrow), 1(wide).

8) Angle of margins of anterior end of premaxilla (Fig. 22). Plesiomorphous condition: blunt. Character states: 0(blunt), 1(intermediate), 2 (acute).

9) Length of ascending process of premaxilla (Fig. 22). Plesiomorphous condition: moderately long. Character states: 0(short), 1(moderately long), 2(very long).

10) Vomerine ridge (Figs. 17-19). Plesiomorphous condition: absent. Character states: 0 (absent), 1(present).

11) Relative size of scapular foramen (Fig. 43). Plesiomorphous condition: medium-sized. Character states: 0(large), 1(medium), 2(small).

12) Pineal foramen (Figs. 11-13). Plesiomorphous condition: present. Character states: 0 (present), 1(reduced), 2(absent).

13) Anterior ends of pterosphenoids (Figs. 17-19). Plesiomorphous condition: far apart. Character states: 0(far apart), 1(close together).

14) Height of supraoccipital crest (Figs. 14-16). Plesiomorphous condition: low. Character states: 0(low), 1(high).

15) Pterotic spine (Figs. 11-13). Plesiomorphous condition: well developed. Character states: 0 (well developed), 1(essentially absent).

16) Pelvic girdle: relative length of posterior process (Fig. 46). Plesiomorphous condition: short to moderate-sized posterior process. Character states: 0(short to moderate posterior process, 20-50% of length of anterior plate), 1(long posterior process, 62-90% of length of anterior plate).

17) Spine on intercalar (Figs. 17-19). Plesiomorphous condition: absent. Character states: 0(absent), 1(moderate length), 2(long).

18) Swim bladder. Plesiomorphous condition: present. Character states: 0(present), 1(absent).

19) Curvature of lateral line (Figs. 50, 52, 68). Plesiomorphous condition: no abrupt curve. Character states: 0(no abrupt curve), 1(abrupt downward curve).

20) Auxiliary branches off lateral line (Figs. 54, 56). Plesiomorphous condition: absent. Character states: 0(absent), 1(present).

21) Nasal denticles (Fig. 1). Plesiomorphous condition: nasal chamber without denticles. Character states: 0(denticles absent), 1(nasal denticles present).

22) Anterior epibranchial artery (Fig. 7). Plesiomorphous condition: unmodified. Character states: 0(unmodified), 1(esophageal artery arises from fourth epibranchial), 2(coeliaco-mesenteric shunt arises from fourth epibranchial).

23) Relative size of foramen between last radial and coracoid (Fig. 43). Plesiomorphous condition: small. Character states: 0(small), 1(large), 2(very large).

24) Length of branches of palatine bone (Fig. 26). Plesiomorphous condition: ventral branch much shorter than dorsal branch. Character states: 0(ventral branch much shorter than dorsal branch, 120-123%), 1(ventral branch slightly shorter, 112-121%), 2(ventral branch equal to or longer than dorsal branch, 87-107%).

25) Width of supratemporal (Fig. 42). Plesiomorphous condition: wider than deep. Character states: 0(wider than deep, 101-113%), 1(deeper than wide, 84-93%), 2(much deeper than wide, 49-79%).

26) Width of first postcleithrum (Fig. 44). Plesiomorphous condition: wide. Character states: 0(wide, 55-62% of length), 1(narrow, 47-48%), 2(very narrow, 24-41%).

27) Total number of vertebrae (Table 8). Plesiomorphous condition: few (31). Character states: 0(few, 31), 1(moderate number, 41-56), 2(many, 62-64).

28) Depth of urohyal (Fig. 31). Plesiomorphous condition: moderately deep. Character states: 0(shallow), 1(moderately deep), 2(deep).

29) Shape of metapterygoid (Fig. 27). Plesiomorphous condition: anterior oblique edge longer than posterior horizontal edge. Character states: 0(anterior oblique edge longer than posterior horizontal edge), 1(posterior horizontal edge longer than anterior oblique edge).

30) Length of arms of ectopterygoid (Fig. 27). Plesiomorphous condition: dorsal arm longer than or equal to ventral arm. Character states: 0(dorsal arm longer than or equal to ventral arm), 1(dorsal arm shorter than ventral arm).

31) Vomer (Figs. 17-19). Plesiomorphous condition: not spatulate. Character states: 0(not spatulate), 1(spatulate, extending beyond anterior margin of ethmoid complex).

32) Width of lateral wall of cleithrum (Fig. 43). Plesiomorphous condition: lateral wall narrow. Character states: 0(lateral wall narrow, space between cleithrum and coracoid visible in lateral view), 1(lateral wall wide, space between cleithrum and coracoid not visible in lateral view).

33) Epiotic crests (Figs. 11-13). Plesiomorphous condition: originate behind midfrontal region. Character states: 0(originate behind midfrontal region), 1(originate on anterior part of frontals).

34) Vertebrae with inferior foramina. Plesiomorphous condition: few. Character states: 0 (few, <11), 1(many, more than 11).

35) Size of first basibranchial. Plesiomorphous condition: elongate. Character states: 0(elongate), 1(short).

36) Strut on fourth pharyngobranchial. Plesiomorphous condition: not elongate. Character states: 0(not elongate), 1(elongate).

37) Length of symplectic (Fig. 27). Plesiomorphous condition: long. Character states: 0(long, in contact with metapterygoid), 1(short, not in contact with metapterygoid).

38) Size of dorsal and ventral hypohyals (Fig. 29). Plesiomorphous condition: ventral < 3 times larger than dorsal. Character states: 0(ventral hypohyal < 3 times larger than dorsal hypohyal in lateral view), 1(ventral hypohyal > 3 times larger than dorsal).

39) Position of fifth branchiostegal ray (Fig. 29). Plesiomorphous condition: located on epihyal. Character states: 0(completely on epihyal), 1(on suture between epihyal and ceratohyal).

40) Posttemporal shelf (Fig. 40). Plesiomorphous condition: no shelf present. Character states: 0(no shelf present between dorsal and ventral arms of posttemporal), 1(shelf present).

41) Width of supracleithrum (Fig. 41). Plesiomorphous condition: wide. Character states: 0 (wide, 72-75% of length), 1(narrow, 42-62%).

42) Supratemporal pores (Fig. 42). Plesiomor-

phous condition: no pores. Character states: 0(no pores), 1(pores present on dorsal arm).

43) Position of nasals (Figs. 11-13). Plesiomorphous condition: protrude beyond ethmoid region. Character states: 0(protrude far beyond ethmoid region), 1(do not protrude, located adjacent to ethmoid region).

44) Shape of posterior end of dorsal margin of urohyal (Fig. 31). Plesiomorphous condition: tripartite. Character states: 0(tripartite), 1 (forked).

45) Glossohyal teeth (Fig. 30). Plesiomorphous condition: glossohyal teeth present. Character states: 0(patch of teeth fused to dorsal surface of glossohyal), 1(no glossohyal teeth).

46) Width of hyomandibula (Fig. 27). Plesiomorphous condition: narrow. Character states: 0(narrow, width 35-36% of length), 1(wide, width 36-52% of length).

47) Angle of lateral and medial arms of fourth epibranchial. Plesiomorphous condition: more acute. Character states: 0(more acute), 1(less acute).

48) Anterior process of second epibranchial. Plesiomorphous condition: elongate. Character states: 0(elongate), 1(not elongate).

49) Preural centra 2-4 (Fig. 39). Plesiomorphous condition: not shortened and compressed. Character states: 0(not compressed), 1(compressed).

50) Number of vertebrae supporting caudal fin. Plesiomorphous condition: 3 vertebrae support caudal fin. Character states: 0(3 vertebrae support caudal), 1(4 or 5 vertebrae).

51) Anterior process on second postcleithrum (Fig. 45). Plesiomorphous condition: elongate process present on anterior margin of second postcleithrum. Character states: 0(process present), 1(process absent).

52) Anterior end of first postcleithrum (Fig. 44). Plesiomorphous condition: notched. Character states: 0(notched), 1(pointed).

53) Position of third pectoral fin radial (Fig. 43). Plesiomorphous condition: base of third radial completely on coracoid. Character states: 0(completely on coracoid), 1(on suture between coracoid and scapula).

54) Tooth shape. Plesiomorphous condition: conical. Character states: 0(conical), 1(triangular and compressed).

55) Parasphenoid contour. Plesiomorphous condition: concave ventrally. Character states: 0(concave), 1(convex).

56) Relative length of arms of dentary (Fig. 24). Plesiomorphous condition: lower arm longest. Character states: 0(lower arm longer than upper arm), 1(upper arm longer than lower arm).

57) Length of posterior edge of ectopterygoid (Fig. 27). Plesiomorphous condition: posterior edge long. Character states: 0(posterior edge long, 64-68% of ventral distance), 1(posterior edge short, 41-63%).

58) Shape of epihyal (Fig. 29). Plesiomorphous condition: not much longer than deep. Character states: 0(depth 68-98% of length), 1(much longer than deep, 58-62% of length).