VIMS Articles

1975

Systematics And Morphology Of Bonitos (Sarda) And Their Relatives (Scombridae, Sardini)

Bruce B. Collette

Labbish N. Chao

Recommended Citation

SYSTEMATICS AND MORPHOLOGY OF THE BONITOS (*SARDA*) AND THEIR RELATIVES (SCOMBRIDAE, SARDINI)[1]

BRUCE B. COLLETTE[2] AND LABBISH N. CHAO[3]

ABSTRACT

The bonitos constitute the scombrid tribe Sardini, consisting of eight species placed in five genera. They differ from the more primitive mackerels and Spanish mackerels in lacking a notch in the hypural plate and in having a bony lateral keel on the posterior caudal vertebrae. From the higher tunas, they differ in having the bony keel only incompletely developed and in lacking a specialized subcutaneous vascular system. The monotypic Australian endemic *Cybiosarda elegans* shares several characters with the monotypic eastern Atlantic endemic *Orcynopsis unicolor* (structure of the bony caudal keel; relative lengths of liver lobes; position and size of spleen) that distinguish them from *Gymnosarda unicolor* and the species of *Sarda. Sarda* contains four allopatric species, which differ from each other in such characters as numbers of fin rays, gill rakers, vertebrae, and teeth: the Atlantic *S. sarda*; the southeastern Australian *S. australis*; the tropical Indo-Pacific *S. orientalis*; and the eastern temperate Pacific *S. chiliensis*. The monotypic Indo-West Pacific reef species *Gymnosarda unicolor* is the only member of the Sardini that has a swim bladder and lacks intermuscular bones on the back of the skull. The monotypic Southern Ocean *Allothunnus fallai* differs from all other scombrids in having laterally extended prootic wings. It is more closely related to the bonitos than to any other scombrids. *Allothunnus* resembles the higher tunas in having a prootic pit but lacks the subcutaneous vascular system. Tables of meristic characters, diagrams of the soft anatomy, and drawings of most bones are included in the first part of the paper. The second part of the paper includes sections on synonymy, comparative diagnosis, types of nominal species, and distribution for each species.

The purpose of this paper is to clarify the relationships of the Sardini at the generic and specific level. This work is part of a continuing study of the systematics of the Scombridae. The methods used are similar to those used by Gibbs and Collette (1967) in a revision of *Thunnus* and rely heavily on the classic work of Kishinouye (1923) and Godsil (1954, 1955).

The bonitos (*Sarda*) and their relatives form a tribe (Sardini) of the subfamily Scombrinae intermediate between the primitive mackerels (Scombrini) and Spanish mackerels (Scomberomorini), and the more advanced tunas (Thunnini) (see Collette and Gibbs 1963a; Gibbs and Collette 1967). Five genera are treated in this paper. The status of the related monotypic genera *Orcynopsis*, *Cybiosarda*, and *Gymnosarda* has been unclear; for example, Fraser-Brunner (1950) placed *Cybiosarda* in the synonymy of *Gymnosarda*. The

systematic position of the monotypic *Allothunnus* has been still more confused—whether it is closer to *Thunnus* (Fraser-Brunner 1950), to *Sarda* (Fitch and Craig 1964), or strikingly different from all other scombrids (Nakamura and Mori 1966). There has been no agreement on the number of species of *Sarda*. Fraser-Brunner (1950) recognized three species: *chiliensis*, *orientalis*, and *sarda*. Godsil (1955) believed that there were two basic groups of species—*sarda-chiliensis* and *orientalis-velox*. Some authors have considered *S. australis* as a valid species, others as a subspecies of *S. chiliensis*.

This project was initiated at the request of the FAO (Food and Agriculture Organization of the United Nations) panel of Experts for the Facilitation of Tuna Research at its Fourth Session in La Jolla, Calif. in November 1971, and should be considered as a report from the Working Party on Tuna and Billfish Taxonomy. Bonitos, as a group, are one of the few underexploited groups of tunalike fishes; therefore, research on their systematics is a necessary predecessor of successful management.

According to the FAO Yearbook of Fishery Statistics for 1972 (Food and Agriculture Or-

ganization of the United Nations 1973), the two species of bonitos that are presently of economic importance are *Sarda chiliensis* and *S. sarda*. Peruvian fishermen landed 54,000-73,000 metric tons per year of the southeast population of *S. chiliensis* in 1965-1972. Smaller catches by Chile and of the northeast Pacific population by Mexico and the United States made the total 65,000-94,000 metric tons per year during that period. *Sarda sarda* is fished particularly by Turkey in the Mediterranean and the Black Sea where 11,700-55,200 metric tons per year were landed in 1965-1972. Other catches of *S. sarda* by Spain, Portugal, Greece, Angola, Argentina, and Brazil made the total 25,000-65,000 metric tons per year in 1965-1972. Both the Japanese and the Koreans fish for *S. orientalis* and there are smaller catches elsewhere throughout its range. *Sarda australis* comes into the markets in Sydney and probably elsewhere in southeastern Australia. In 1971, Morocco was reported to have landed 600 metric tons of *Orcynopsis* and we have seen *Orcynopsis* in the markets in Tunis. We have seen specimens of *Cybiosarda* in the Sydney fish market mixed with *S. australis*. The only commercial catch of *Allothunnus* was the 230 tons taken with purse seines off eastern Tasmania in June 1974 (Webb and Wolfe 1974). *Gymnosarda* occurs around coral reefs where it is taken by fishermen on hook and line.

Emphasis was placed on obtaining fresh or frozen specimens from each population of each species for dissection. Standard counts and measurements were taken, color pattern was recorded, and a search was made for parasitic copepods. Results of the copepod study will be reported on later by Roger F. Cressey (United States National Museum, USNM). The viscera were examined and drawn in situ following removal of an oval portion of the ventral body wall. The viscera were then removed and drawings were made of the liver and other selected organs. The kidneys and anterior parts of the arterial system were then drawn. Counts of ribs and intermuscular bones were made and the specimen was then skeletonized. Specimens were immersed in hot water to assist removal of the flesh.

For morphometric comparisons, the base measurement used for fresh, frozen, and preserved specimens was millimeters fork length (mm FL). Skeletal material was measured in millimeters skeletal length, the distance from the anterior margin of the ethmoid to the posterior tip

of the hypural plate, a distance somewhat shorter than fork length. Skulls were measured from the anterior margin of the ethmoid to the posteroventral junction of the skull with the first vertebral centrum.

This paper is divided into two major sections. The first part describes and illustrates the squamation, morphometry, meristic characters, soft anatomy, and osteology of the Sardini. The second part treats the genera and species separately including synonymy, diagnosis (based on characters from the first section), types of nominal species, geographical distribution, and, for some species, geographic variation.

MATERIAL

Abbreviations used for the institutions cited herein are as follows:

AB — Northwest Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, Auke Bay, Alaska.

AMS — Australian Museum, Sydney.

ANSP — Academy of Natural Sciences, Philadelphia, Pa.

BMNH — British Museum (Natural History), London.

BPBM — Bernice P. Bishop Museum, Honolulu, Hawaii.

CAS — California Academy of Sciences, San Francisco.

CBL — Chesapeake Biological Laboratory, Solomons, Md.

CSIRO — CSIRO Marine Biological Laboratory, Cronulla, N.S.W., Australia.

DM — Dominion Museum, Wellington, New Zealand.

FMNH — Field Museum of Natural History, Chicago, Ill.

HUJ — Hebrew University, Jerusalem.

LACM — Los Angeles County Museum of Natural History, Los Angeles, Calif.

MACN — Museo Argentina de Ciencias Naturales, Buenos Aires.

MCZ — Museum of Comparative Zoology, Harvard.

MNHN — Muséum National d'Histoire Naturelle, Paris.

MSNG — Museo di Storia Naturale, Genoa.

MSUF — Museo de La Specola, Universita di Firenze, Florence.

NHMV - Naturhistorisches Museum, Vienna.
NMC   - National Museum of Natural Sciences, Ottawa.
QM   - Queensland Museum, Brisbane.
RMNH - Rijksmuseum van Natuurlijke Historie, Leiden.
RUSI - J. L. B. Smith Institute of Ichthyology, Rhodes University, Grahamstown.
SAM   - South African Museum, Capetown.
SFRS - Sea Fisheries Research Station, Haifa, Israel.
SIO   - Scripps Institution of Oceanography, La Jolla, Calif.
SMF   - Senckenberg Museum, Frankfurt-am-Main.
TABL - Southeast Fisheries Center, National Marine Fisheries Service, NOAA (formerly Tropical Atlantic Biological Laboratory), Miami, Fla.
UBC   - Institute of Fisheries, University of British Columbia, Vancouver.
UCLA - University of California, Los Angeles.
UMML - Rosenstiel School of Marine and Atmospheric Science, Miami, Fla.
UMMZ - University of Michigan Museum of Zoology, Ann Arbor.
USNM - United States National Museum, Washington, D.C.
WAM   - Western Australia Museum, Perth.
WHOI - Woods Hole Oceanographic Institution, Woods Hole, Mass.
ZMK   - Zoological Museum, Copenhagen.
ZMO   - Zoological Museum, Oslo.

The material examined is listed by general locality under four or five headings for each species (except *Sarda chiliensis*, *S. orientalis*, and *S. sarda* which are subdivided into two populations each). The numbers in each category 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 skeletons. "Measured and counted" includes specimens that were subsequently dissected and the preserved museum specimens used for detailed morphometric and meristic examination. "Counts only" are the additional museum specimens used only for meristic examination. "Skeletons" refer to all the skeletal material examined, specimens that were dissected plus skeletal museum material.

Allothunnus fallai. Total 8 specimens (451-787 mm FL).
Dissected 4 (680-778). Tasmania (3); California (1).
Measured and counted 7 (642-787). Tasmania (4); California (1); New Zealand (2).
Skeletons 5 (451-778). Tasmania (3); California (1); South Africa (1).

Cybiosarda elegans. Total 22 specimens (250-422 mm FL).
Dissected 5 (355-422). Perth, Western Australia (1); Macleay River, New South Wales (4).
Measured and counted 21 (250-422). New South Wales (11); E. Queensland (7, including holotype of *Scomberomorus (Cybiosarda) elegans* Whitley); Gulf of Carpentaria (1); Western Australia (2).
Examined 1 (380). New South Wales.
Skeletons 5 (355-422). Western Australia (1); New South Wales (4).

Gymnosarda unicolor. Total 38 specimens (71.6-1,080 mm FL).
Dissected 6 (522-787). Amirante Islands (2); Truk Islands, Caroline Islands (3); Bikini, Marshall Islands (1, partial).
Measured and counted 31 (71.6-1,040). Red Sea (5, including holotype of *Thynnus unicolor* Rüppell); Comoro Islands (1); Amirante Islands (2); Madagascar (1); New Britain (1); Solomon Islands (2); Gilbert Islands (1); Japan (3); Palau Islands (1); Caroline Islands (7); Marshall Islands (5); Society Islands (1); Marquesas Islands (1).
Examined 1 (267-mm head of 1,080-mm specimen). Pitcairn Group.
Skeletons 11 (about 625-1,013). Amirante Islands (2); Marshall Islands (4); Truk Islands (3); unknown locality (2).

Orcynopsis unicolor. Total 55 specimens (164-960 mm FL).
Dissected 11 (332-645). Israel (5, partial); Tunisia (6, complete).
Measured and counted 43 (164-960). Lebanon (12, 242-325); Israel (12, 285-735); Egypt (5, 164-280); Tunisia (7, 312-645); Nice (1, 553); Mauritania (2, 400-410); Senegal (2, 405-960); Norway (2, 565-570, types of *Thynnus peregrinus* Collett).
Counts only 12 (417-950). Pizza (1, ca. 950); Elba (1, ca. 790); Gulf of Genoa (1, 670); Rimini, Adriatic (1, ca. 600); Egypt (6, 417-556); locality unknown (2).
Skeletons 11 (332-645). Israel (5); Tunisia (6).

Sarda australis. Total 21 specimens (195-495 mm FL).

Dissected 3 (360-495). New South Wales, Australia.

Measured and counted 21 (195-495). Norfolk Island (1); New South Wales (20, including holotype of *Pelamys australis* Macleay).

Skeletons 3 (360-495). New South Wales.

Sarda chiliensis—northeast Pacific. Total 91 specimens (207-643 mm FL).

Dissected 4 (401-472). La Jolla, Calif.

Measured and counted 24 (207-587). California: La Jolla; San Diego (including holotype of *Pelamys lineolatus* Girard); Los Angeles; San Pedro; Santa Barbara; Oceanside. Baja California: Coronados Island; Natividad Island; Cedros Island; Blanca Bay.

Counts only 21 (220-625). Vancouver, British Columbia (1); Alaska (2); S. California (17); Revillagigedos Island (1).

Skeletons 50 (310-643). S. California (including holotype of *Sarda stockii* (David)).

Sarda chiliensis—southeast Pacific. Total 44 specimens (57.2-672 mm FL).

Dissected 7 (437-571). Callao, Peru.

Measured and counted 23 (94.1-672). Valparaiso, Chile (holotype of *Pelamys chiliensis* Cuvier). Arica Bay, Chile. Peru: Callao; Foca Island; San Lorenzo Island; Pachacamac Island; Guañape Island; San Gallán Island.

Counts only 9 (57.2-636). Peru: San Lorenzo Island; San Gallán Island; Foca Island; Callao.

Skeletons 18 (437-571). Callao, Peru.

Sarda orientalis—Indo-West and central Pacific. Total 31 specimens (150-645 mm FL).

Dissected 5 (341-500). Tokyo (3); Hawaii (2).

Measured and counted 27 (150-645). South Africa (2); Seychelles Islands (1); Red Sea (2); Cochin, India (1); Western Australia (paratype of *Sarda orientalis serventyi* Whitley); China (4); Japan (12, including types of *Pelamys orientalis* Temminck and Schlegel); Hawaii (4).

Counts only 3 (223-370). Muscat (2); Ceylon (1).

Skeletons 6 (341-500). Muscat (1); Tokyo (3); Hawaii (2).

Sarda orientalis—eastern Pacific. Total 21 specimens (354-447 mm FL).

Dissected 4 (354-447). Navidad Bay, Mexico (1); Piñas Bay, Panama (2); Pearl Islands, Panama (1).

Measured and counted 12 (354-447). Mexico (1); Panama (8, including holotype of *Sarda velox* Meek and Hildebrand); Galapagos Islands (2); Gulf of Guayaquil (1).

Counts only 7 (429-650). Cabo San Lucas and Las Tres Marias Islands, Mexico (4); Galapagos Islands (3).

Skeletons 6 (354-447). Mexico (2); Panama (3); unknown locality (1).

Sarda sarda—western Atlantic. Total 86 specimens (118-637 mm FL).

Dissected 2 (333). New Jersey (1); Miami, Fla. (1).

Measured 29 (228-637). North America 12 (257-637): Massachusetts (4); New York (3); Chesapeake Bay (2); Florida (1); Cuba (1). Gulf of Mexico 5 (228-321): Florida (1); Texas (4). South America 12 (202-450): Gulf of Carioca, Venezuela (6); Brazil (5); Mar del Plata (1).

Counts only 51 (118-572). North America 39 (118-572): Massachusetts (24); Rhode Island (3); New York (3); New Jersey (1); Chesapeake Bay (2); Maryland (3); Florida (1). Gulf of Mexico 11 (103-400): Florida (3); Mississippi delta (3); Texas (1). South America 5 (214-570): Venezuela (1); Brazil (3); Mar del Plata (1).

Skeletons 9 (333-577). Massachusetts (2); Connecticut (1); New York (1); New Jersey (1); Florida (1); exact locality unknown (3).

Sarda sarda—eastern Atlantic. Total 62 specimens (104-680 mm FL).

Dissected 5 (363-504). Azores (3); Tunisia (1); Gulf of Guinea (1).

Measured and counted 30 (260-600). Atlantic Europe 9 (418-600): Norway (5); Spain (1); Azores (3). Mediterranean 8 (260-564). Black Sea 1 (550). Gulf of Guinea 10 (305-478). Port Elizabeth, South Africa 2 (447-517).

Counts only 31 (104-680). Europe 2 (482-670). Mediterranean 18 (187-487). Black Sea 9 (104-680). Gulf of Guinea 2 (366-375).

Skeletons 6 (363-504). Azores (3), Tunisia (1); Gulf of Guinea (2).

ACKNOWLEDGMENTS

KEY TO THE SPECIES OF SARDINI

1a. Jaw teeth tiny, 40-55 on each side of upper and lower jaws; gill rakers fine and numerous, total of 70-80 on first arch; body elongate, snout to second dorsal 610-654 thousandths of fork length; maxilla short, 354-379 thousandths of head length . . . . . *Allothunnus fallai* Serventy

1b. Jaw teeth larger and more prominent, 10-30 on each side of upper and lower jaws; total gill rakers on first arch 8-27; body less elongate, snout to second dorsal 481-610 thousandths of fork length; maxilla longer, 431-557 thousandths of head length 2

2a. Five to ten narrow, dark, longitudinal stripes on upper part of body; no teeth on the tongue; spleen prominent in posterior third of body cavity in ventral view .... *Sarda* 3
2b. Body either without stripes or with dark spots above the lateral line and longitudinal dark stripes below; two patches of teeth present on tongue; spleen either concealed or located in anterior third of body cavity in ventral view 6
3a. Spines in first dorsal fin 20-23; total vertebrae 50-55 .... *S. sarda* (Bloch)
3b. Spines in first dorsal fin 17-19; total vertebrae 43-46 4
4a. Total gill rakers on first arch 8-13; supramaxilla narrow (see Figure 32e) ....
.... *S. orientalis* (Temminck and Schlegel)
4b. Total gill rakers on first arch 19-27; supramaxilla wider (see Figure 32c-d) 5
5a. Total gill rakers on first arch 19-21; pectoral rays 25-27, modally 26; teeth sometimes present on vomer; length of first dorsal base 315-343 thousandths of fork length; maxilla 503-539 thousandths of head length .... *S. australis* (Macleay)
5b. Total gill rakers on first arch 23-27; pectoral rays 22-26, modally 24 or 25; teeth never present on vomer; length of first dorsal base 267-314 thousandths of fork length; maxilla 460-503 thousandths of head length .... *S. chiliensis* (Cuvier)
6a. Body with dark spots above lateral line and dark longitudinal stripes below (see Figure 1a); spines in first dorsal fin 16-18 .... *Cybiosarda elegans* (Whitley)
6b. Body without a prominent pattern of stripes or spots (see Figure 2); spines in first dorsal fin 12-15 ....
7a. Pectoral rays 21-23; small conical teeth in jaws; total gill rakers on first arch usually 14 or more; interpelvic process bifid; spleen not visible in ventral view; laminae in olfactory rosette 25-28; interorbital width 239-310 thousandths of head length ....
.... *Orcynopsis unicolor* (Geoffroy St. Hilaire)
7b. Pectoral rays 25-28; jaw teeth very large and conspicuous; total gill rakers on first arch usually 13 or fewer; interpelvic process single; spleen visible on right side of body cavity in ventral view; laminae in olfactory rosette 48-56; interorbital width 321-400 thousandths of head length .... *Gymnosarda unicolor* (Rüppell)

PART 1.
COMPARATIVE MORPHOLOGY

The morphological characters useful for distinguishing the species of bonitos and for evaluating their phylogenetic relationships are divided into six categories: color pattern, scales, morphometry, meristics, soft anatomy, and osteology.

Color Pattern

The most strikingly colored species of the Sardini, and perhaps the entire family Scombridae, is clearly *Cybiosarda elegans* (Figure 1a). The light venter has several stripes reminiscent of the skipjack tuna, *Katsuwonus pelamis* (Linnaeus). The dorsum is covered with black spots over a deep blue background. The high first dorsal fin is jet black anteriorly and white posteriorly. The anal and second dorsal fins are yellow. *Orcynopsis unicolor* (Figure 1b) has a high black first dorsal fin as in *Cybiosarda*, but there the similarity ends because adult *Orcynopsis* have only a faint mottled pattern

that has been deliberately exaggerated in the figure. All species of *Sarda* (Figure 1c) have stripes along their backs but the number of stripes and their alignment varies both interspecifically and intraspecifically. *Sarda australis* has stripes on the venter as well as on the dorsum. *Sarda* also has a black first dorsal fin but it is lower and longer than in *Cybiosarda* and *Orcynopsis*. *Gymnosarda unicolor* (Figure 2a) is deep blue without any distinct pattern; *Allothunnus fallai* (Figure 2b) also lacks distinctive markings.

Color plates have been published of all the species of bonitos except *Allothunnus*. Paintings of three Australian species by George Coates were published by Marshall (1964, 1966): *Cybiosarda elegans* (fig. 345), *Sarda australis* (fig. 348), and *Gymnosarda unicolor* (fig. 342). Color illustrations of *Orcynopsis unicolor* were published by Lozano y Rey (1952, pl. 41, fig. 2—800-mm adult and fig. 3—150-mm juvenile) and by Bini (1968:39). *Sarda sarda* was illustrated by La Monte (1945, pl. 8; 1952, pl. 17), Lozano y Rey (1952, pl. 39, fig. 4—500-mm adult), and Bini (1968:37). Walford (1937, pl.
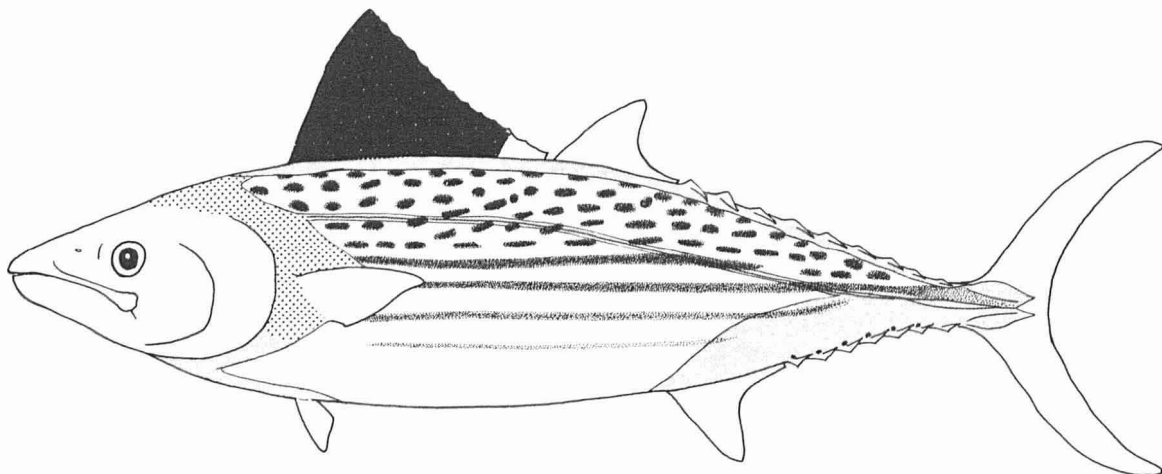
a
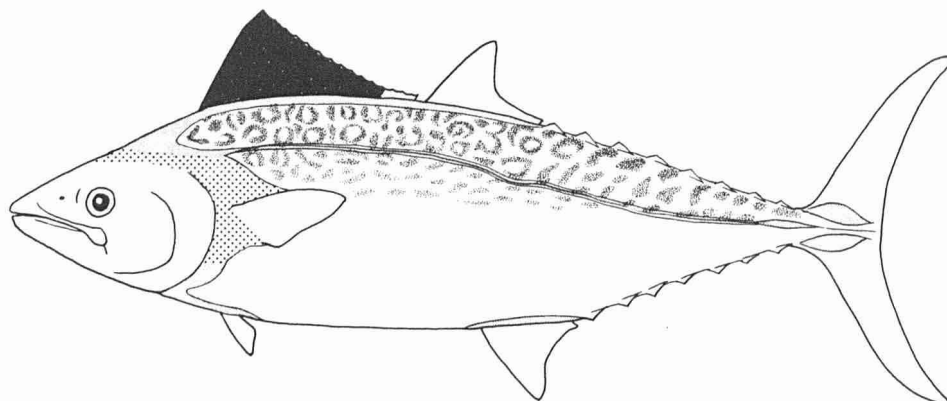
b

c

FIGURE 1.–Diagramatic lateral views of three species of Sardini to show general pigment pattern, extent of corselet (coarse stippling), and parts of the body covered by smaller scales (fine stippling). a. *Cybiosarda elegans*, New South Wales, 337 mm FL, USNM 259407-F2. b. *Orcynopsis unicolor*, Tunisia, 312 mm FL, USNM 206526. c. *Sarda sarda*, Gulf of Mexico, 287 mm FL, USNM 118646.

38) includes color photographs of a northeastern Pacific *Sarda chiliensis* and an eastern Pacific *S. orientalis*.

Scales

In bonitos, the body scales are cycloid and usually small. Those on the corselet, along the fin bases, and along the lateral line are larger and more elongate. The predorsal and opercular scales are larger and are embedded under the skin. No scales are present on the snout, the interorbital area, or on the fins. Posterior to the corselet, the distribution of scales differs among the genera of bonitos (Figures 1, 2). Species of *Sarda* have their body completely covered with small scales except for the distal portion of the caudal keels (Figure 1c). *Allothunnus* has the dorsal half of the body covered with scales (Figure 2b), but they do not extend onto the caudal keels, although they do cover the base of the caudal fin. Serventy (1948) described the type of *Allothunnus fallai* as having its whole body covered with scales. But later authors, Talbot (1960), Olsen (1962), and Nakamura and Mori (1966), all indicated that the minute scales of *Allothunnus* are present only on

a

b
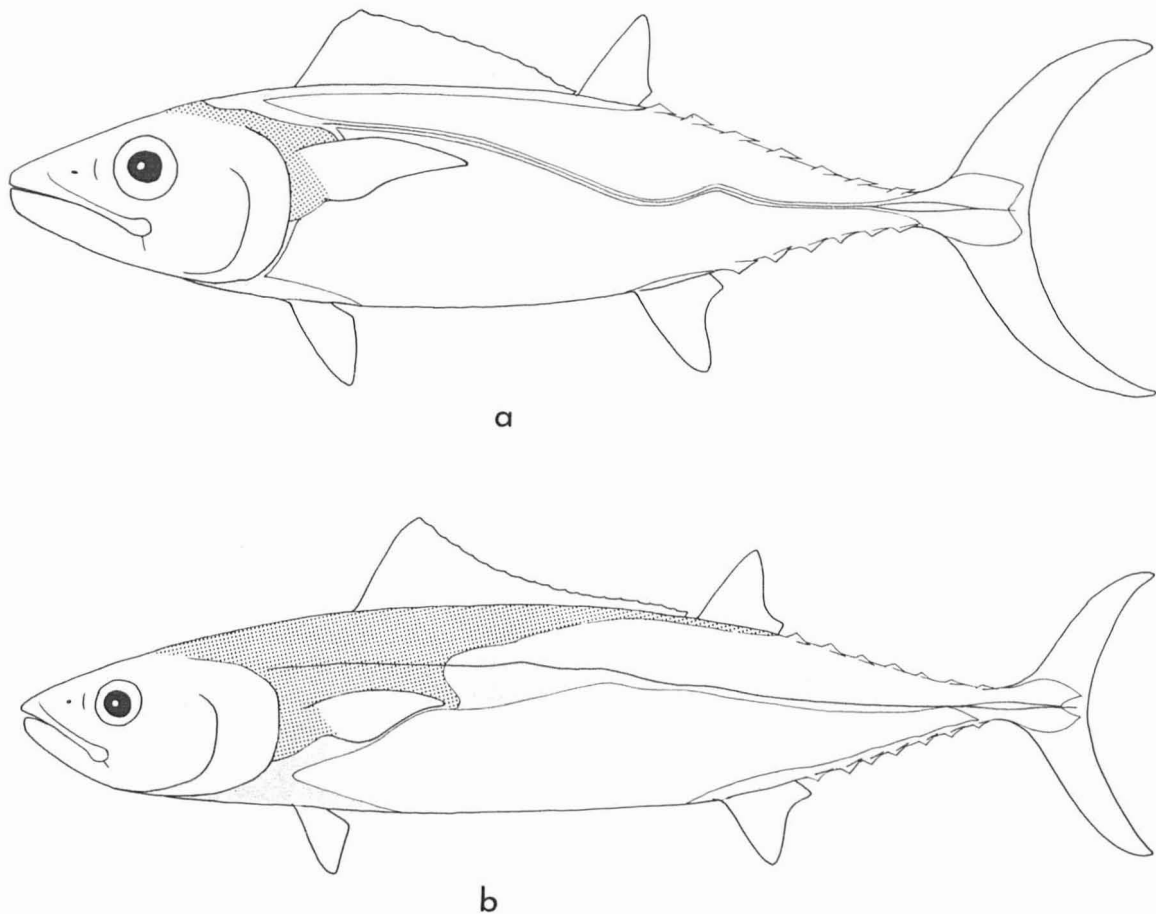
FIGURE 2.–Diagrammatic lateral views of two species of Sardini to show extent of corselet (coarse stippling) and parts of body covered by smaller scales (fine stippling). a. *Gymnosarda unicolor*, Tahiti, 446 mm FL, ANSP 93818. b. *Allothunnus fallai*, New Zealand, 642 mm FL.

the dorsal half of the fish. A patch of scales is also present around the base of the pelvic fins. *Cybiosarda* has a band of scales dorsally extending along the entire midline (Figure 1a). Ventrally, scales are present around the base of the pelvic fins and a broad band of scales extends from the anal fin origin posterodorsally to the caudal peduncle. The peduncular region is entirely covered with scales except for the distal margin of the caudal keel. *Orcynopsis* (Figure 1b) has fewer scales than *Cybiosarda*. The band of scales along the dorsal midline is narrower and ends at the dorsal finlets. Ventrally, *Orcynopsis* has scales around the bases of the pelvic and anal fins. The caudal peduncle is naked except for the caudal keel. *Gymnosarda* is completely naked posterior to the corselet except for the lateral line, dorsal fin base, and caudal keel (Figure 2a).

The corselet, composed of enlarged scales, is well defined in the pectoral region of bonitos. It extends from the dorsal end of the gill slit to the tip of the pectoral fin, except in *Sarda* and *Allothunnus*. Anterior and ventral to the pectoral fin base, the scales are smaller than on other parts of the corselet in bonitos. In *Sarda*, an extra wing of the corselet extends dorsally toward the origin of the first dorsal fin. *Allothunnus* has the most extensive corselet, covering most of the area between the first dorsal fin base and the pectoral fin.

Morphometric Characters

Twenty-six measurements, in addition to fork length, were routinely made on all specimens destined to be dissected to insure that these data would be available if needed. Preserved material was also measured until an adequate sample was obtained. Measurements follow the methods of Marr and Schaefer (1949) as modified by Gibbs and Collette (1967). Morphometric characters can be used to separate genera, 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. 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.

Orcynopsis is short-bodied and short-headed. It has shorter snout-anal and snout-second dorsal distances than do the other bonitos. *Cybiosarda* is also relatively short-bodied. *Allothunnus* is the most elongate of the bonitos and has the greatest distances between the snout and the origins of the anal and second dorsal fins. *Cybiosarda* and *Orcynopsis* both have high first dorsal, second dorsal, and anal fins compared to other bonitos. *Gymnosarda* has a differently shaped head than do other bonitos: the interorbital distance is much wider, the eyes are larger, the postorbital distance is shorter, and the distance between the origins of the pectoral and pelvic fins is much larger. In addition, *Allothunnus* has large eyes and a very short snout and maxilla.

Because of small sample size, restricted geographical distribution, or both, morphometric data were combined for each of four species: *Cybiosarda elegans*, *Sarda australis*, *Gymnosarda unicolor*, and *Allothunnus fallai*. Three populations of *Orcynopsis unicolor* are compared: Israel, Lebanon, and Tunisia. The southeast Pacific population of *Sarda chiliensis* (nominal *S. c. chiliensis*) is compared with the northeast Pacific population (*S. c. lineolata*). The population of *Sarda orientalis* in the eastern tropical Pacific (nominal *S. o. velox*) is compared with the only other sufficiently large sample, northwest Pacific. Three populations of *S. sarda* are compared: western Atlantic, Mediterranean Sea (including the Black Sea), and the Gulf of Guinea.

Meristic Characters

Countable structures are of special value systematically because they are relatively easy to record unambiguously and because they are easy to summarize in tabular fashion. Meristic characters that have proved valuable systematically in the Sardini include numbers of fin rays (first dorsal spines, second dorsal rays, dorsal finlets, anal rays, anal finlets, pectoral rays), gill rakers, teeth (especially on the upper and lower jaws), vertebrae, and laminae in the olfactory rosettes. Olfactory laminae are discussed as the last section under soft 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. Within the genus *Sarda*, these characters are useful at the species level. For purposes of discussion, the characters in the soft anatomy are divided into five sections: viscera, vas-

TABLE 1.—Morphometric comparison of species and populations of Sardini. Means as thousandths of fork length or head length.

Character	Cybiosarda elegans	Orcynopsis unicolor Israel	Lebanon	Tunisia	Sarda australis	Sarda chiliensis NE Pacific	SE Pacific	Sarda orientalis NW Pacific	E Pacific	Sarda sarda NW Atlantic	Mediterranean	Gulf of Guinea	Gymnosarda unicolor	Allothunnus fallai
Fork length														
Snout — A	652	577	587	578	674	665	654	694	678	668	660	657	629	676
Snout — 2D	531	499	511	481	586	566	569	606	582	582	579	578	557	628
Snout — 1D	273	247	253	246	263	269	279	286	288	270	266	298	285	306
Snout — P_2	299	273	284	270	296	295	303	303	310	296	288	275	285	284
Snout — P_1	267	238	247	229	267	266	275	281	290	269	263	265	264	269
P_1 — P_2	125	113	122	—	116	123	118	113	114	111	104	111	139	110
Head length	266	235	243	231	267	263	272	278	284	264	259	271	261	258
Max. body depth	227	246	255	240	231	210	210	234	213	214	205	217	224	223
Max. body width	133	124	123	130	141	131	134	146	144	135	131	—	151	164
P_1 length	138	138	135	142	121	116	—	115	127	115	116	130	160	129
P_2 length	82	63	61	64	85	78	84	76	86	79	82	83	103	78
P_2 insertion-vent	327	294	288	300	390	353	341	392	367	366	370	357	332	371
P_2 tip-vent	262	230	228	233	290	276	269	311	280	282	285	266	229	293
Base 1D	254	246	248	241	326	297	286	306	292	311	311	311	262	319
Height 2D	108	128	117	126	86	83	97	78	94	80	95	91	102	93
Base 2D	121	117	133	120	103	93	94	93	95	96	104	107	77	72
Height anal	107	126	118	125	81	74	92	73	89	77	79	85	99	90
Base anal	91	114	111	106	78	71	74	73	79	73	78	80	62	72
Caudal spread	251	261	270	213	259	246	258	214	236	222	247	253	304	226
Snout (fleshy)	98	89	94	91	96	94	95	96	101	94	93	96	107	75
Snout (bony)	82	76	80	83	81	78	81	86	86	82	78	82	98	65
Maxilla length	130	113	123	112	139	126	130	145	150	136	131	138	138	93
Post orbital	136	112	117	—	130	139	142	139	146	136	132	138	101	139
Orbit (fleshy)	29	28	31	31	39	31	31	42	37	35	31	34	51	45
Orbit (bony)	58	51	57	52	66	57	56	56	64	57	57	60	73	63
Interorbital width	73	68	66	72	66	63	70	71	71	64	62	63	92	—
Head length														
Snout (fleshy)	367	381	387	396	361	357	348	344	357	358	358	353	410	292
Snout (bony)	308	326	328	358	305	297	299	308	303	309	303	301	374	252
Maxilla length	489	483	505	483	518	481	477	522	528	514	505	509	527	361
Post orbital	511	478	484	—	492	526	523	503	512	516	511	506	381	545
Orbit (fleshy)	109	121	129	107	137	119	115	136	130	133	118	122	196	175
Orbit (bony)	218	218	236	211	246	218	205	220	226	217	220	220	279	244
Interorbital width	273	289	272	297	249	239	257	256	251	242	238	231	353	224

cular system, pharyngeal muscles, urogenital system, and olfactory organ.

VISCERA

Emphasis was placed on the appearance of the viscera in ventral view, after removal of an oval segment of the belly wall (Figure 3). Important papers on the viscera of bonitos include Kishinouye (1923 - *Sarda* and *Gymnosarda*), Godsil (1954, 1955 - *Sarda*), Postel (1954 - *Orcynopsis*), Blanc and Postel (1958 - *Gymnosarda*), Silas (1963 - *Gymnosarda*), and Nakamura and Mori (1966 - *Allothunnus*).

General Description. —The anterior end of the liver abuts against the transverse septum anteriorly in the body cavity. There are usually three lobes to the liver: the middle lobe is conspicuous in ventral view in all bonitos, whereas one or both lateral lobes are visible only in *Gymnosarda* and *Sarda*. No striations are present on the surface of the liver as they are in four species of *Thunnus* (see Gibbs and Collette 1967). 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 intestine arises from the anterior end of the stomach which extends posteriorly as a blind sac. The caecal mass covers 22-81% of the anterior part of the body cavity and opens into the intestine immediately posterior to the junction of intestine and stomach. The intestine forms a loop anteriorly. The remainder of the digestive tract is straight in *Sarda*, but two additional loops are present in the mid-intestine of *Cybiosarda*, *Gymnosarda*, and *Orcynopsis*.

The spleen is prominent in ventral view in *Gymnosarda* and *Sarda*, but is hidden by the liver and caecal mass in *Allothunnus*, *Cybiosarda*, and
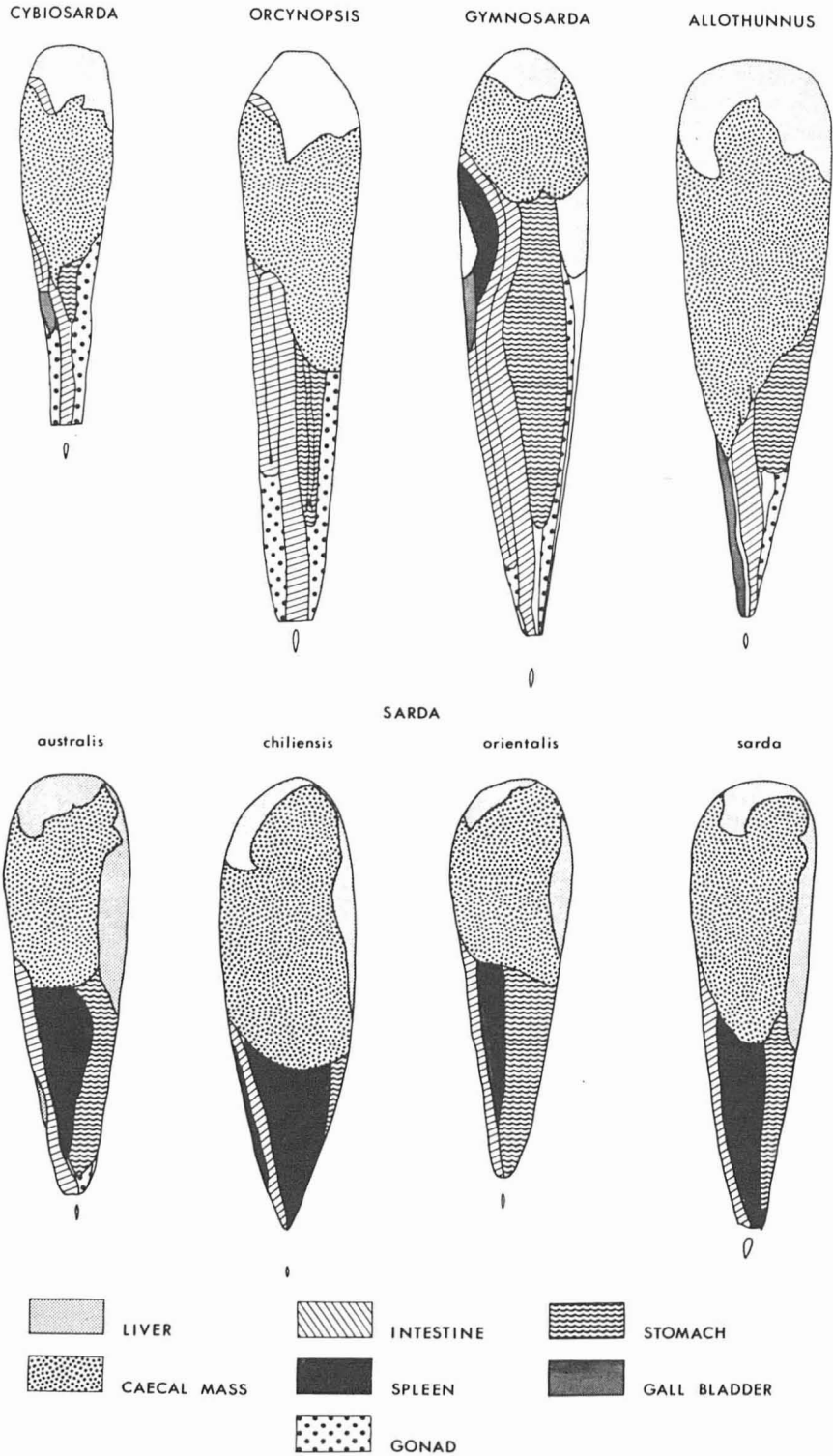
FIGURE 3.—Viscera, in ventral view, of the eight species of Sardini.

Orcynopsis. The gall bladder, an elongate tubular sac which is usually green in color, arises from the right lobe of the liver and usually lies along the intestine on the right hand side. The stomach extends further posteriorly and is more prominent in ventral view when it is full. The mature ovary is sometimes large enough to cover the stomach ventrally. A swim bladder is absent in all bonitos except *Gymnosarda.*

Specific Characters.—The bonitos are divided into three groups based on the shape of the liver (Figure 4). *Sarda* and *Gymnosarda* have three distinct liver lobes; both lateral lobes are elongate and much longer than the middle lobe; the right lateral lobe is always longer than the left lateral lobe. All three lobes in *Gymnosarda* are visible ventrally if the dissection extends far enough laterally. In addition, the connection of middle and left lobes is visible anteroventrally in *Sarda. Orcynopsis* and *Cybiosarda* have an elongate right lateral lobe and a very short left lateral lobe which tends to fuse with the middle lobe. *Allothunnus* differs from the other genera in having three subequal lobes, as in the bluefin tuna group of species of *Thunnus.*

The bonitos can be divided into three groups based on the relative length of the caecal mass. *Allothunnus* has the longest caecal mass (71-81% of body cavity length, $\bar{x}$ 76.4%) of any of the bonitos followed by *Cybiosarda* (65-72%, $\bar{x}$ 69.2%) and *Orcynopsis* (46-59%, $\bar{x}$ 56.3%). *Gymnosarda* has the shortest caecal mass (22-30%, $\bar{x}$ 25.2%). The species of *Sarda* are intermediate between these two groups, most having the caecal mass about half the length of the body cavity (*S. australis* 44-55%, $\bar{x}$ 49.7; *S. sarda* 38-58%, $\bar{x}$ 48.3; and *S. orientalis* 41-50%, $\bar{x}$ 46.7). There is significant geographic variation in the fourth species, *S. chiliensis.* Three northeast Pacific specimens have a distinctly longer caecal mass (61-65%, $\bar{x}$ 62.3) than six southeast Pacific specimens (40-53%, $\bar{x}$ 48.5). This

FIGURE 4.—Ventral view of excised livers of eight species of Sardini. Spleen shown in black for *Cybiosarda* and *Orcynopsis.*

tendency supports the findings of Godsil (1955). However, a seventh southeast Pacific specimen had a considerably longer caecal mass (70%) than our other six specimens.

The position and size of the spleen are distinctive among the genera. Species of *Sarda* have a large spleen, the major portion of which is located in the posterior half of the body cavity between the intestine and the stomach in ventral view. The spleen of *Gymnosarda* is also visible ventrally, but it is smaller than in *Sarda* and located in the anterior half of the body cavity. In *Orcynopsis* and *Cybiosarda*, the spleen is hidden by the right lobe of the liver and caecal mass. The spleen was visible in ventral view in one specimen of the four *Allothunnus* examined.

The number of loops in the intestine separates *Sarda* and *Allothunnus* from the other three genera of bonitos. In *Sarda* and *Allothunnus*, the intestine leaves the stomach and then moves posteriorly along the right side of the body cavity straight to the anus (Figure 5a). In the other genera, the intestine makes a loop at about the level of the posterior end of the stomach, runs
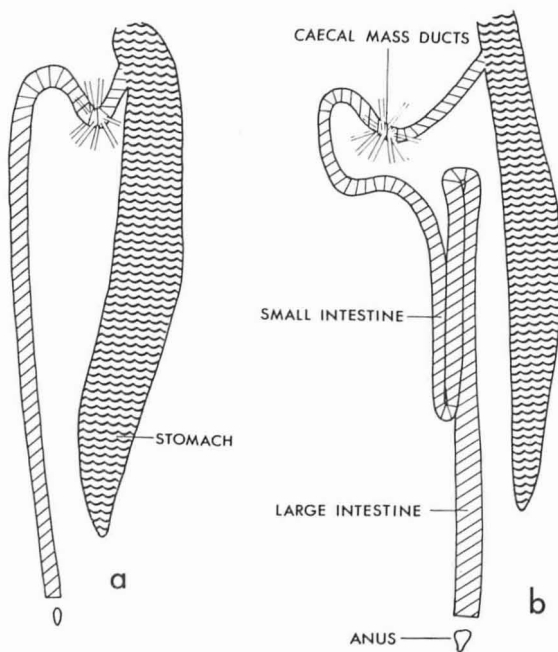
anteriorly almost to where it came off the stomach, forms another loop, and then goes straight posteriorly to the anus (Figure 5b).

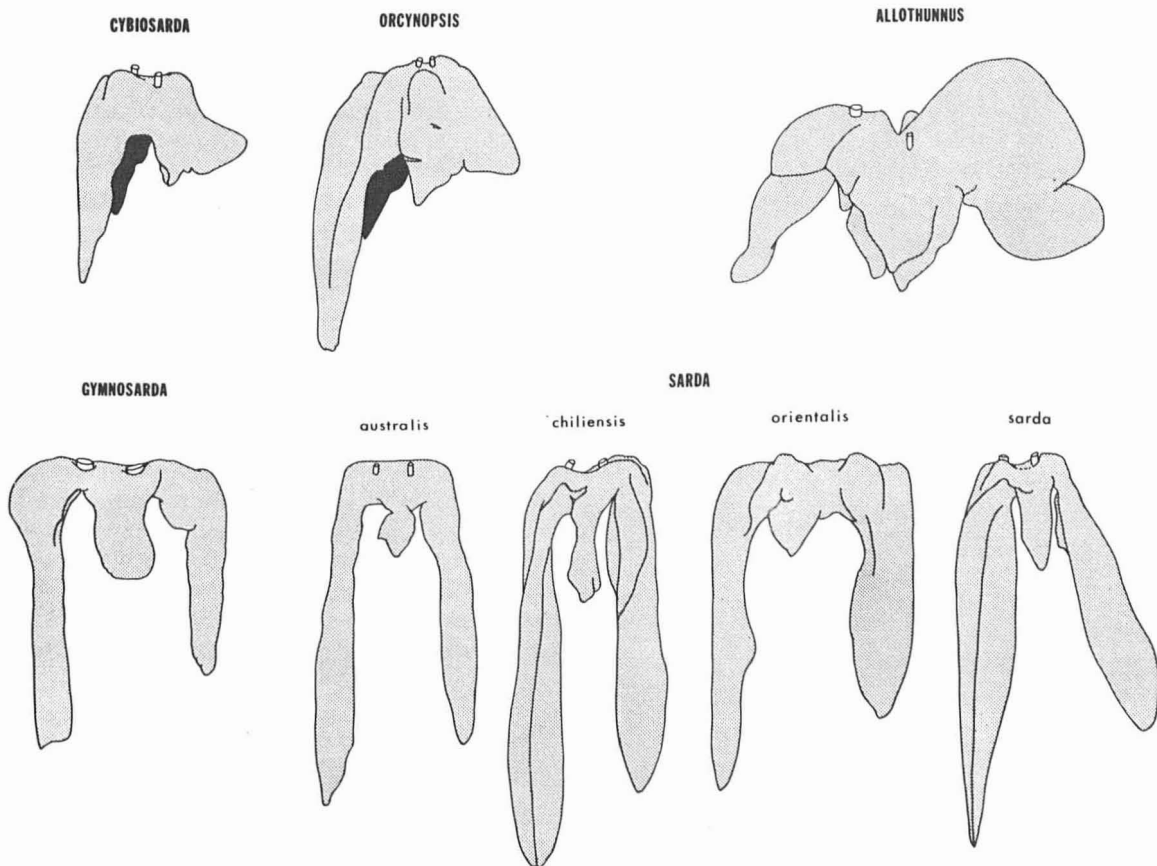The caecal mass is connected to the anterior part of the intestine by 6-9 ducts as shown diagrammatically in Figure 5. Each of the main ducts branches into numerous smaller ducts within a short distance from the intestine. We did not count the number of ducts often enough to determine the systematic value of this character and so merely present the results for six specimens: *Cybiosarda*—3 anterior and 5 posterior ducts in one specimen, 3 anterior and 6 posterior in another; *Sarda australis*—3 anterior and 4 posterior; *S. chiliensis*—2 anterior and 4 posterior; *S. orientalis*—3 anterior and 4 posterior; and *Gymnosarda*—a total of 6 ducts.

VASCULAR SYSTEM

The only published work on the vascular system of the bonitos is on the Pacific species *Sarda orientalis* by Kishinouye (1923) and Godsil (1954, 1955) and on *S. chiliensis* by Godsil (1954, 1955). No specialized subcutaneous vascular system and no cutaneous arteries or veins are present as they are in the higher tunas, *Auxis* to *Thunnus*. Therefore, this description will be confined to the anterior portion of the dorsal aorta and the postcardinal vein.

General Description.—The efferent branchial (epibranchial) arteries and coeliaco-mesenteric artery form a unit at the anterior end of the dorsal aorta (Figure 6). Two anterior epibranchials on each side unite to form a common trunk, and these trunks join as the "Y" of the aorta beneath 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 vertebra. The coeliaco-mesenteric

FIGURE 5.—Course of intestine from stomach, through area where the ducts of the caecal mass empty into the intestine, to the anus in two species of Sardini, ventral view (diagrammatic). a. *Sarda orientalis*, Tokyo, 341 mm FL. b. *Cybiosarda elegans*, New South Wales, 365 mm FL.

FIGURE 6.—Anterior part of arterial system in seven species of Sardini. Numbers indicate vertebral centra; stippled areas show where pharyngeal muscles originate. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 543 mm FL. c. *Sarda australis*, New South Wales, 408 mm FL. d. *Sarda orientalis*, Tokyo, 500 mm FL. e. *Sarda sarda*, eastern United States, 388 mm FL. f. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. g. *Allothunnus fallai*, Tasmania, 764 mm FL.

528
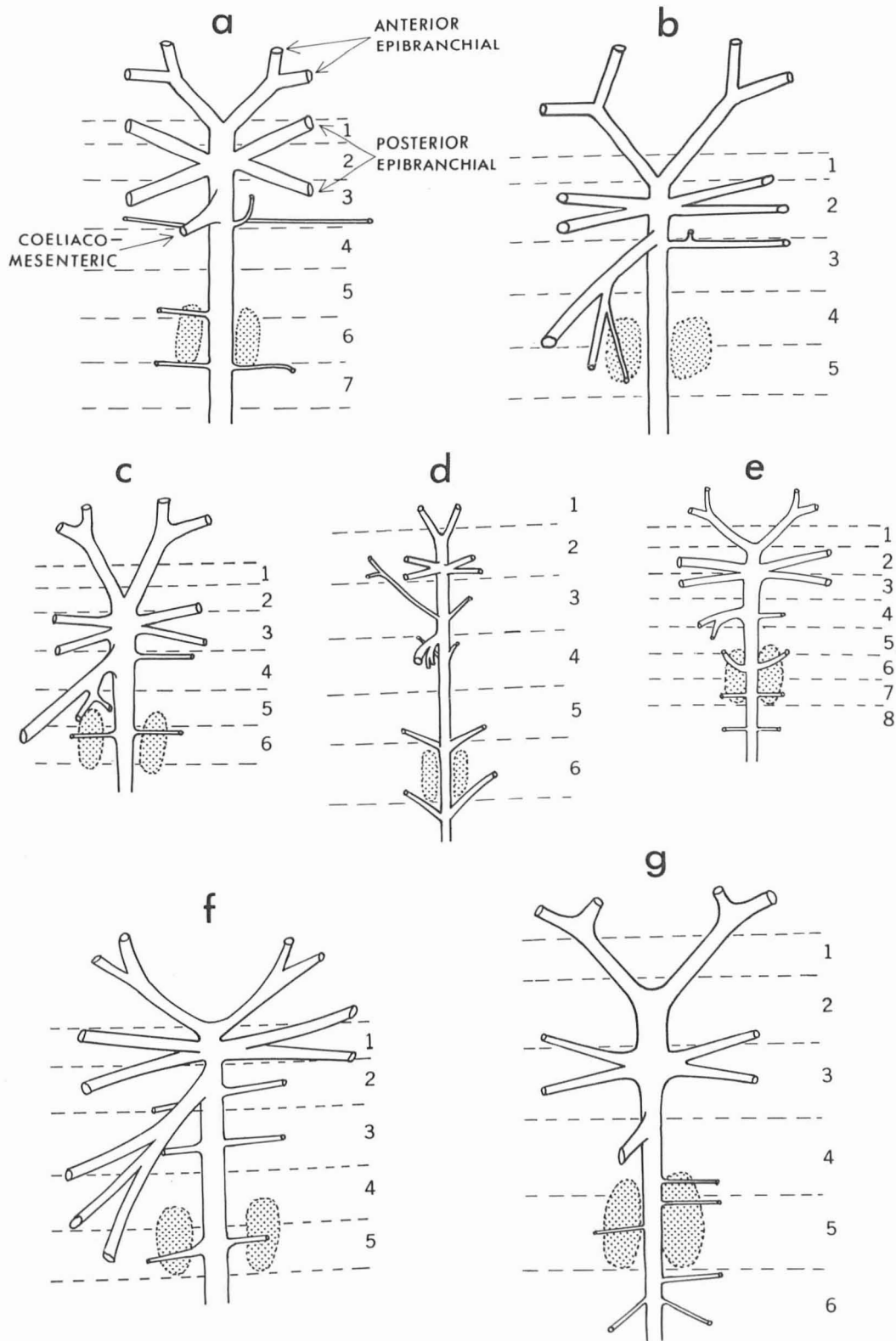
has two or three main branches which lead to the liver and other viscera. Godsil (1954, 1955) illustrated and described the branches of the coeliaco-mesenteric in great detail.

The postcardinal vein runs along the ventral surface of the kidney (Figure 7) 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.

Specific Characters.—Variation was found in the location of the components of the anterior part of the arterial system (Table 2). *Orcynopsis* and *Gymnosarda* tend to have both the epibranchials and coeliaco-mesenteric more anterior than in the other bonitos (ventral to first vertebra vs. second, second vs. third, respectively).

To locate which haemal arch the dorsal branch of the postcardinal enters, a pin was forced into the vertebral column at the point where the postcardinal came up to the surface of the kidney. The number of the vertebra bearing this haemal arch was then determined at the end of the dissection. The number of the vertebra varied as follows:

Cybiosarda   15, 16, 17, 17

Orcynopsis   16
Sarda australis   17, 18
S. chiliensis   16, 17, 17, 19, 21
S. orientalis   15, 16, 18, 19
S. sarda   18, 19, 20
Gymnosarda   16, 16, 17
Allothunnus   21

PHARYNGEAL MUSCLES

The paired pharyngeal (retractor dorsalis) muscles are included on the figures of the anterior part of the arterial system (Figure 6). The muscles originate on the ventral surface of one to three vertebrae between the fourth and the seventh and insert on the upper pharyngeal bones.

The pharyngeal muscles insert on the fourth and fifth vertebra in *Gymnosarda* and are mostly on the fifth or sixth vertebra in the other bonitos. The data are as follows: *Cybiosarda* 6 (3 specimens), 5 (1 specimen), 7 (1 specimen); *Orcynopsis* 5 extending onto 4 (4 specimens); *Sarda australis* 6 (3 specimens, extending onto 7 in 1 specimen); *S. chiliensis* NE Pacific 6 and 7 (2 specimens); *S. chiliensis* SE Pacific 5 (5 specimens, extending onto 6 in 3); *S. orientalis* Indo-West Pacific 6 (2 specimens), 5 extending onto 4 (1 specimen), 6 extending onto 7 and 5 (1 specimen); *S. orientalis* eastern Pacific 6 (4 specimens, extending onto 7 in all 4, onto 5 in 1); *S. sarda* 6 (3 specimens, extending onto 7 in 2 specimens, onto 5 in 1); *Gymnosarda* 4 extending onto 5 (3 specimens); and *Allothunnus* 5 extending onto 4 (1 specimen).

TABLE 2.—Location of "Y" of aorta, posterior epibranchials, and the coeliaco-mesenteric artery, in the eight species of Sardini.

Structure under vertebra no.	Cybiosarda elegans	Orcynopsis unicolor	Sarda australis	Sarda chiliensis		Sarda orientalis		Sarda sarda	Gymnosarda unicolor	Allothunnus fallai
				SE Pac.	NE Pac.	Indo-W Pac.	E Pac.			
Y of aorta										
skull									1	
skull-1	3	1		2					2	
1	2	5	1	1	1	2	1	2	1	1
1-2		2	—	2	2	—	2	1	—	1
2			2			3	1	2	1	2
2-3										
Posterior epibranchials										
1		2		1					2	
1-2		3		1					2	
2	3	2		2	2	3	2	2	1	
2-3	1		1	1		1	1	1		2
3	1		2			1	1	1		1
Coeliaco-mesenteric										
1-2		1								
2		1							3	
2-3		3		1					1	
3	2	3		2	3	2	1		1	1
3-4	2		1	—		1	1	1		1
4	1		2	2		2	2	3		1

FIGURE 7.—Ventral view of posterior part of kidney showing postcardinal vein, junction of ureters, and urinary bladder in eight species of Sardini. Posterior ends of gonads shown in some figures. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Cybiosarda elegans*, New South Wales, 360 mm FL. c. *Orcynopsis unicolor*, Tunisia, 567 mm FL. d. *Orcynopsis unicolor*, Tunisia, 593 mm FL. e. *Sarda australis*, New South Wales, 355 mm FL. f. *Sarda chiliensis*, La Jolla, Calif., 472 mm FL. g. *Sarda orientalis*, Tokyo, 500 mm FL. h. *Sarda sarda*, Tunisia, 504 mm FL. i. *Gymnosarda unicolor*, Truk Islands, 787 mm FL. j. *Allothunnus fallai*, Tasmania, 764 mm FL.

UROGENITAL SYSTEM

The only references to the anatomy of the urogenital system are those of Kishinouye (1923) on *Sarda orientalis* and Godsil (1954, 1955) on *S. orientalis* and *S. chiliensis*.

General Description.—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 layer 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 "mid-ridge" 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. The kidney may be absent in the area between the vertebrae and where the epibranchial arteries join to form the aorta. In some cases in each species, the kidney is well developed dorsal to this area and even covers the posterior end of the parasphenoid. In the vicinity of the esophagus, the kidney expands laterally and forms two projections which may reach 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 (Figure 7). The branches of the ureter join to form a common trunk which leads to the urinary bladder between the gonads. The distance between the junction of the ureters and the urinary bladder and the size of ureters varies intraspecifically. The urinary bladders appear similar in all the bonitos, but no detailed study was made of them.

OLFACTORY ORGAN

General Description.—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), and *Thunnus* (Iwai and Nakamura 1964b; Gibbs and Collette 1967). As in other scombrids, the olfactory cavity in bonitos has a small anterior naris and a slitlike posterior naris. No information on the supplementary sacs, or accessary olfactory cavity (Iwai and Nakamura 1964b), was obtained from the present study comparable to that of Tretiakov (1939), who described three supplementary sacs (middle, maxillary, and rostral sacs) in *S. sarda*. The central axis of the olfactory rosette is located beneath the anterior naris. Leaflike laminae 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 laminae. Iwai and Nakamura (1964b) were the first to use the number of laminae to distinguish species of scombrids, but Gibbs and Collette (1967:91) felt additional material was necessary to validate the character in *Thunnus*.

We counted the number of olfactory laminae (by averaging both sides and rounding upward) in bonitos and found a rather wide range of variation (Table 3). Gooding (1963) also found a wide variation in *Katsuwonus*: 38-47 laminae per rosette in 38 skipjack olfactory rosettes. The number of laminae increases from small specimens to adults but does not appear to change after a certain size is reached. For example, 15 specimens of *Orcynopsis unicolor* (242-645 mm FL) had 25-28 laminae, a 178-mm specimen had 22, and a 164-mm specimen had 23. Twelve *Gymnosarda unicolor* (400-940 mm FL) had 48-56 laminae; a 306-mm specimen, 45; a 215-mm specimen, 43; and a 71.6-mm specimen, 27. Looking only at adults and subadults (Table 3), *Gymnosarda* has the highest number of olfactory laminae (48-56) and is completely separated from the other bonitos (21-39) in this character. *Orcynopsis*, *Cybiosarda*, and *Sarda australis* form a series with increasing numbers of laminae.

The pigmentation of the olfactory rosette varied in preserved specimens. In *S. australis* and *Orcynopsis* the dorsal margins of the olfactory laminae were pigmented and gave a radial pigmentation to the olfactory rosette. Black spots were found on the laminae of a specimen of *Cybiosarda* (Figure 8a). The fleshy ring of *S. sarda* showed grayish pigmentation in large specimens. No specific pigmentation was noted in other species of bonitos. The morphology of each olfactory lamina (Figure 8) is similar in each olfactory rosette, but decreased in size anteriorly. The olfactory cavity and accessary cavity are similar in all bonitos, except in *Cybiosarda* where the opening of the accessary sac was more dorsally located and led interiorly rather than interior-ventrally as in other bonitos.

TABLE 3.—Number of laminae in olfactory rosettes in species of Sardini. (Means based on original data not combined frequency distribution.)

Species	20-1	22-3	24-5	26-7	28-9	30-1	32-3	34-5	36-7	38-9	40-1	42-3	44-5	46-7	48-9	50-1	52-3	54-5	56-7	N	x̄
Orcynopsis unicolor			2	8	5															15	26.9
Cybiosarda elegans					1	5	3													9	30.8
Sarda australis								1	1	4										6	37.2
S. chiliensis:																					
NE Pacific	1	2	8	7	1	1														20	25.4
SE Pacific		3	4	6	2															15	25.5
S. orientalis:																					
Red Sea - Indian Ocean			2	—	—	2	2	4												10	31.4
NW Pacific			2	—	1	1	1													5	28.0
Cent. Pacific			1	—	—	1			1											3	30.7
E Pacific						1	4	3	4											12	34.3
S. sarda:																					
North America		1	3	2	3	2	4													15	27.5
South America					2															2	28.5
Mediterranean - Black Sea		2	5	—	—	2														9	25.1
Gulf of Guinea - South Africa		1	3	1	2															7	25.4
Gymnosarda unicolor															4	1	3	3	1	12	51.6
Allothunnus fallai					2	1														3	29.0

Specific Characters.—A fleshy ring (Iwai and Nakamura 1964b) was found along the posterior margin of the olfactory rosettes in some bonitos. This fleshy ring is the continuation of the well-developed distal end of the olfactory laminae and forms a fleshy elevated area in species of *Sarda*. In *S. sarda* the fleshy ring usually develops in larger specimens (over 360 mm FL) as a folded fleshy pad (Figure 8h). Different developmental stages of the fleshy pad were found in all species of *Sarda* except in *S. c. chiliensis* which had no apparent rings. No fleshy ring or pad was found in *Cybiosarda* or *Orcynopsis* (Figure 8a, b). In *Gymnosarda*, a very definite fleshy ring surrounds all the olfactory laminae (Figure 8i) except in a juvenile specimen (71 mm FL), which had an elongated oval rosette with only 27 laminae. Nakamura and Mori (1966) found the olfactory rosette of *Allothunnus* to have labial fleshy rings around the olfactory laminae, similar to our observations (Figure 8j).

Osteology

Osteological characters proved to be very useful in determining how many genera of Sardini should be recognized. The osteological description is divided into five sections: skull, axial skeleton, dorsal and anal fins, pectoral girdle, and pelvic girdle. Osteological terminology generally follows de Sylva (1955) and Gibbs and Collette (1967) with a few changes to bring this nomenclature into closer agreement with more modern terminology.

SKULL

Description of the skull is presented in two sections: neurocranium and branchiocranium. Figure 9 shows an articulated skull of *Gymnosarda unicolor* in lateral view to provide orientation for the descriptions of the individual bones.

Neurocranium

Following a general description of the neurocranium, the four major regions are discussed: ethmoid, orbital, otic, and basicranial. Descriptions of the otoliths are included at the end of this section.

General Characteristics.—In dorsal view, the neurocranium of bonitos is roughly triangular in shape. The interorbital and otic regions are not as
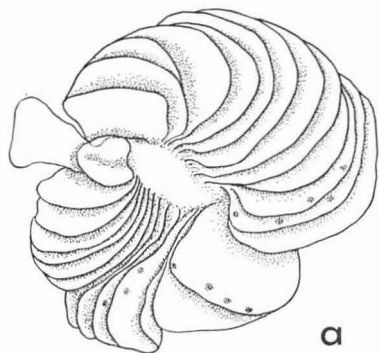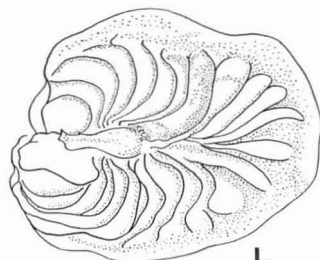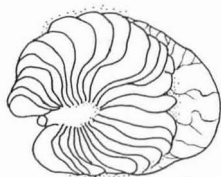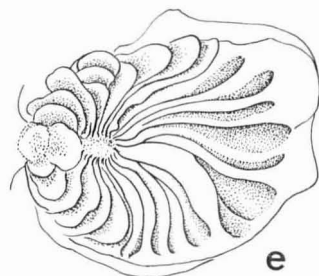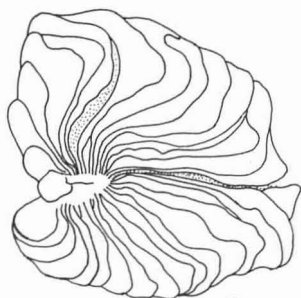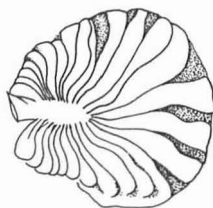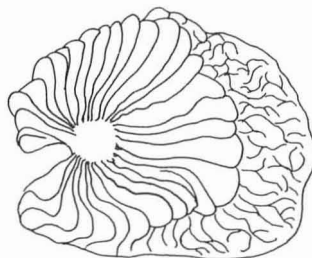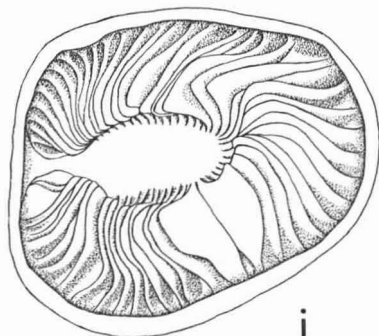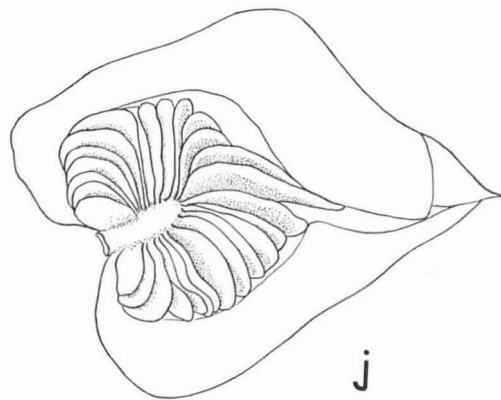
FIGURE 8.—Olfactory rosettes (left) of eight species of Sardini. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, USNM 59881, 332 mm FL. d. *Sarda chiliensis*, Santa Barbara, Calif., USNM 31104, 335 mm FL. e. *Sarda chiliensis*, Callao, Peru, 571 mm FL. f. *Sarda orientalis*, Pearl Island, Panama, USNM 128644, 505 mm FL. g. *Sarda sarda*, Portuguese Guinea, 361 mm FL. h. *Sarda sarda*, Chesapeake Bay, 436 mm FL. i. *Gymnosarda unicolor*, Bikini, USNM 140980. j. *Allothunnus fallai*, New Zealand, DM 2472, 740 mm FL.

broad as in the most advanced scombrid genera—*Thunnus, Euthynnus, Katsuwonus*, and *Auxis* (Kishinouye 1923; de Sylva 1955; Gibbs and Collette 1967), but are broader than in the more primitive genera—*Scomber, Rastrelliger, Grammatorcynus, Scomberomorus*, and *Acanthocybium* (Allis 1903; Kishinouye 1923; Conrad 1938; Mago Leccia 1958; Gnanamuttu 1971), except in *Gymnosarda* which has a broad and short skull (Figure 10; Kishinouye 1923, fig. 38). *Allothunnus* has a more elongate and narrow skull (Figure 11) than do other bonitos. Bonitos lack the prominent frontoparietal foramen (Gibbs and Collette 1967) which is present on each side of the dorsal surface

of the skull at (or near) the junction of the frontal, parietal, and supraoccipital bones of the three most advanced genera of Scombridae: *Euthynnus, Katsuwonus*, and *Thunnus*. The corresponding junction in bonitos does have a small hole and/or an area of very thin dermal bone (see Figure 12 of *Sarda sarda*). Two prominent dorsolateral crests are present on each side of the neurocranium (Figures 10-14). The inner crest arises at the anterolateral edge of the frontal bone, extends along the frontal and parietal bones, and terminates at the posterolateral corner of the epiotic bone. This crest is a thin bony process in all bonitos except *Allothunnus*, in which it arises from the posterior half of the frontal bones and has a much thicker and wider anterior half than do the other scombrid genera mentioned above. The primitive scombrid *Grammatorcynus* resembles *Allothunnus* in this character. The outer crest (Figure 11), which constitutes the posterolateral margins of the neurocranial roof, is formed by the edges of the frontal and pterotic bones. It originates at the posterolateral region of the frontal bones and extends posteriorly as a flat pterotic spine. The
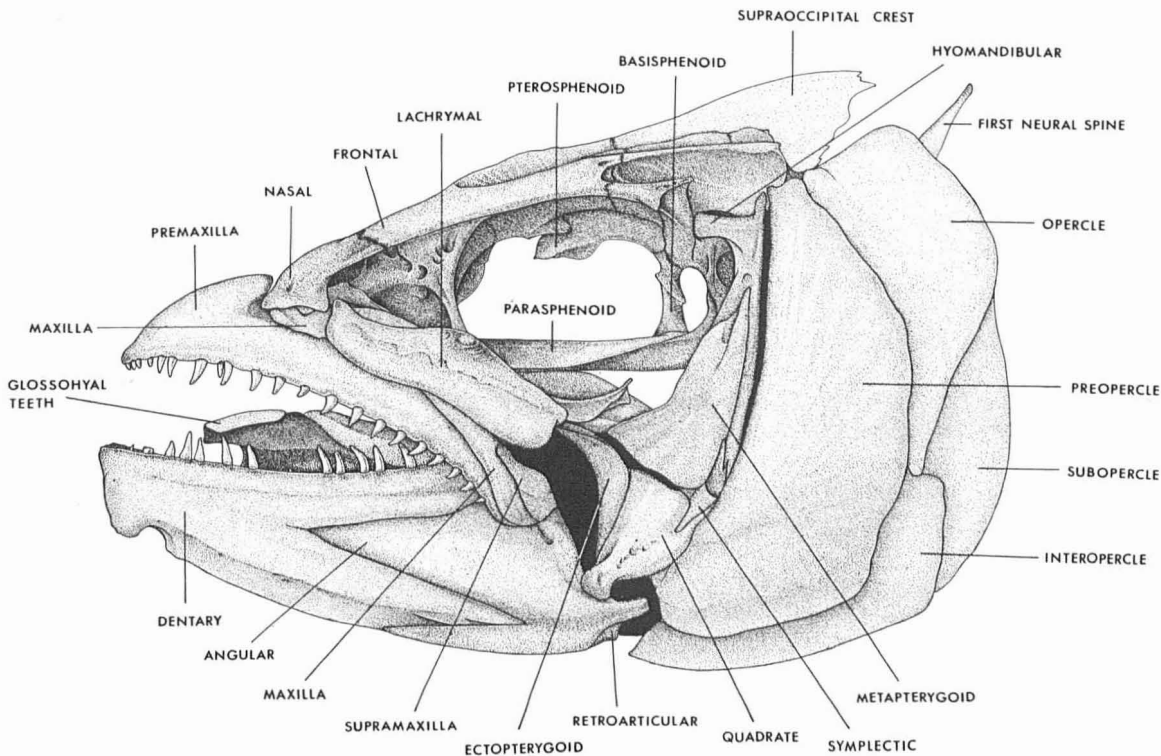
FIGURE 9.—Lateral view of head of *Gymnosarda unicolor*, Bikini, Marshall Islands, USNM 11478, 750 mm FL.

535
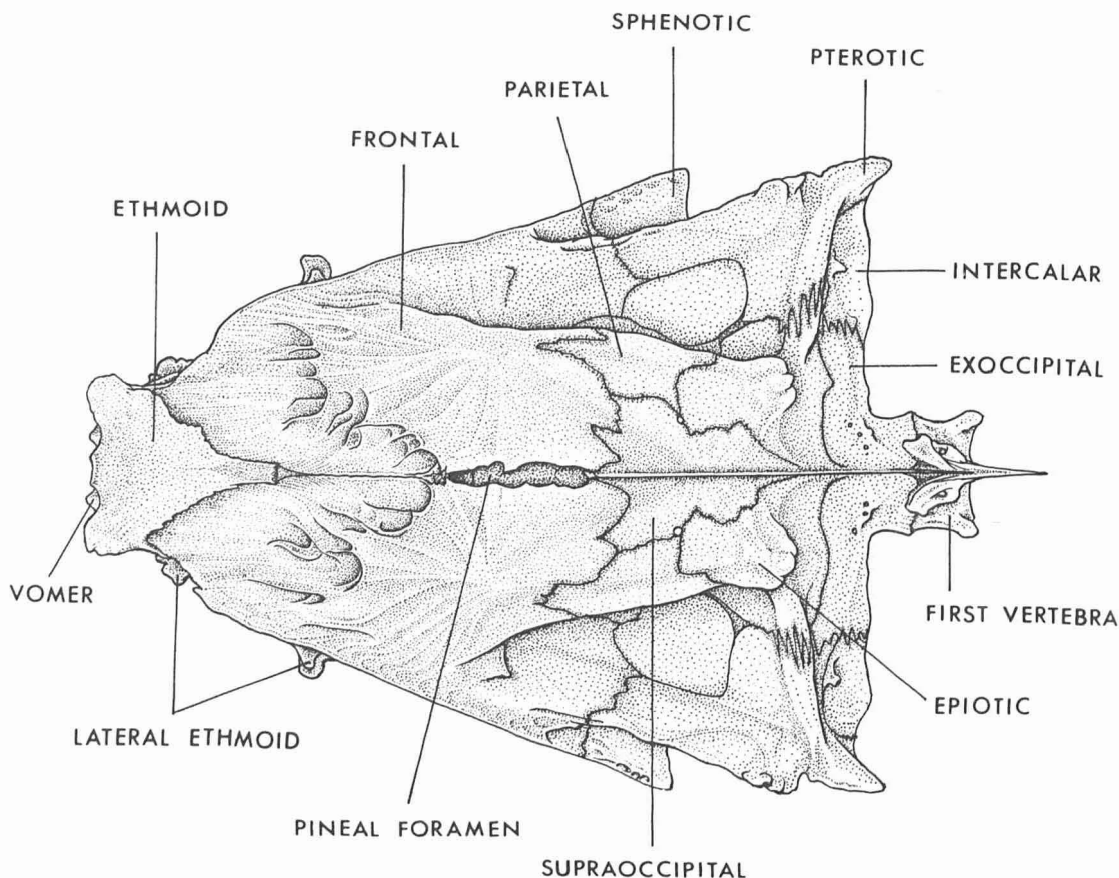
FIGURE 10.—Dorsal view of skull of *Gymnosarda unicolor*, Truk Islands, 696 mm FL.

supraoccipital crest is high and usually does not extend posteriorly past the tip of the first neural spine.

A prominent pineal foramen (Figures 10-14) is present anterior to the supraoccipital crest between the median edges of the frontal bones. Among the bonitos, it is most prominent in *Allothunnus*. Other scombrids either have a reduction in the thickness of the bone in this area (*Scomber*, *Rastrelliger*, and *Scomberomorus*) or a similar pineal foramen (*Grammatorcynus*, *Acanthocybium*, *Auxis*, *Euthynnus*, *Katsuwonus*, and *Thunnus*). In life, the pineal foramen is filled with a translucent cartilaginous lens and is covered by a layer of skin usually having an unpigmented window dorsal to the cartilage. Rivas (1953) hypothesized that, by permitting light to reach the pineal body, the pineal apparatus in *Thunnus* could be instrumental in controlling phototactic movements involved in migration. Holmgren (1958) concluded that while there are

morphological indications of light sensitivity in the pineal area of *T. thynnus*, there is not enough physiological evidence to be sure of possible hormonal control by this area.

Ventrally (Figures 15-19), the prelateral ethmoid region of bonitos is shorter and broader than in other scombrids. The ventral surface of the skull is formed by the vomer, lateral ethmoids, and parasphenoid and is broader than that of more advanced scombrids. The anterior three-fifths of the parasphenoid is almost flat, there is a medial, ventral keel in the next fifth, and posteriorly it is thin and smoothly curved into lateral flanges which enclose a parasphenoidal chamber (Kishinouye 1923). The lateral wings of the parasphenoid project dorsolaterally from the posterior half of the ventral keel to form the anteroventral part of the posterior myodome. The ventral surface of the brain case is formed by the frontal, pterosphenoid, sphenotic, prootic, basioccipital, exoccipital, intercalar, and pterotic bones.
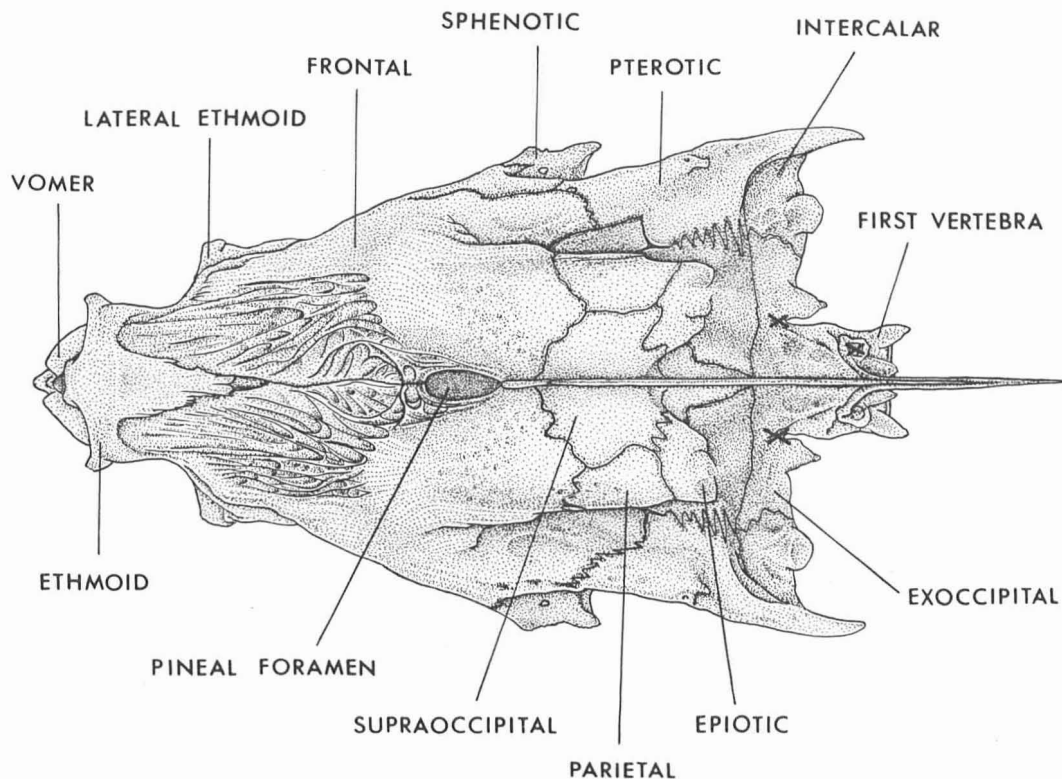
FIGURE 11.—Dorsal view of skull of *Allothunnus fallai*, California, 680 mm FL. X's indicate the points of attachment of intermuscular bones.

In lateral view (Figures 20-24), bonito skulls are similar to more advanced scombrids, but are more elongate and have the roof of the orbit less fully arched. *Allothunnus* (Figure 24) is most distinct in having a more pointed anterior end and a deeper posterior portion. The pterosphenoids project ventrally from the roof of the skull and form a partial interorbital septum which never fuses with the parasphenoid as in large *Thunnus thynnus* (see Gibbs and Collette 1967). In the posterior part of the orbit, the basisphenoid bisects the orbital capsule by connecting the pterosphenoids and prootic bones to the parasphenoid. The orbit is formed by the posterior edge of the lateral ethmoid, the ventral surface of the frontal and pterosphenoid, the parasphenoid, basisphenoid, and the anterior edge of the prootic. As expressed by the ratio of orbit height to length (see section on orbital region), the orbit is low and elongate in bonitos (Table 4); *Cybiosarda, Orcynopsis*, and *Sarda* have the lowest orbits as in *Scomberomorus* and *Acanthocybium. Gymnosarda* and *Allothunnus* each have a more highly arched orbit resembling that in *Scomber, Grammatorcynus,*

TABLE 4.—Ratio of orbit height to length in species of Sardini.

Species	Range	$\bar{x}$	N	Skull length (mm)	Fork length (mm)
Orcynopsis unicolor	3.85-4.60	4.32	6	43.2-71.2	323-620
Cybiosarda elegans	3.83-5.37	4.49	4	48.6-64.3	355-422
Sarda australis	3.03-3.70	3.33	3	23.1-29.6	363-495
Sarda chiliensis:					
SE Pacific	3.78-6.69	5.12	17	26.7-86.7	437-571
NE Pacific	3.10-5.78	4.12	37	24.3-92.3	332-570
Sarda orientalis:					
Indo-W Pacific	3.67-4.30	4.06	3	47.8-68.8	340-500
E|Pacific	3.20-5.09	4.03	7	50.9-68.0	354-497
Sarda sarda	3.42-5.00	3.92	7	45.6-66.1	333-504
Gymnosarda unicolor	2.26-2.68	2.45	5	102-120	625-772
Allothunnus fallai	2.94-3.40	3.19	4	72.4-114	406-778

Rastrelliger, Auxis, Euthynnus, Katsuwonus, and *Thunnus* (Allis 1903; Kishinouye 1923; Mago Leccia 1958; Gibbs and Collette 1967; Gnanamuttu 1971).

The posterior part of the base of the cranium is formed by the lateral flanges of the parasphenoid (ventral profile) and basioccipital (posterior profile). Along the dorsal profile, a crest formed anteriorly by the joint between the frontals is most distinctive in *Sarda*, as in *Scomberomorus*

537
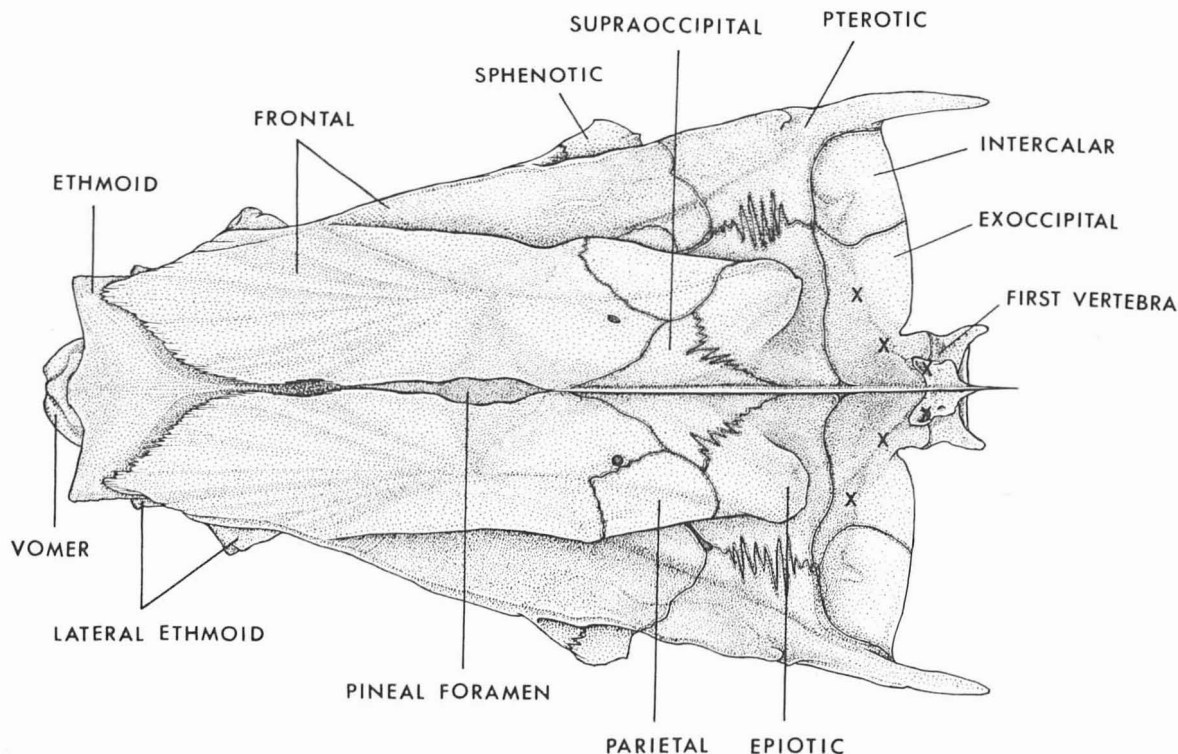
FIGURE 12.—Dorsal view of skull of *Sarda sarda*, eastern United States, 388 mm FL. X's indicate the points of attachment of intermuscular bones.

(Mago Leccia 1958), *Katsuwonus*, and *Thunnus*. In *Cybiosarda* and *Orcynopsis*, these anterofrontal crests are merely visible laterally as in *Auxis* and *Euthynnus*. No anterofrontal crest is present in *Gymnosarda* and *Allothunnus* (Figures 22, 24) and it is also absent in *Grammatorcynus* and *Acanthocybium*.

The first vertebral centrum has modified neural prezygapophyses (Figure 25) that firmly attach the first vertebra to the modified exoccipital and basioccipital region (Figure 26) of the skull. The anterior circular margin of the first centrum is smaller than its posterior margin and is in a forward oblique position to meet the posterior margin of the modified basioccipital which is in a backward oblique position. The strong first neural spine, with its tubular base, sits on the junction of the first centrum and exoccipital and it is not fused to the first centrum. No bony shelf is present in the neural canal (Figure 25a) to divide it into dorsal and ventral portions as is the case in *Auxis*, *Euthynnus*, and *Katsuwonus*. An intermuscular bone is attached to the center of each exoccipital in the bonitos (also see section on ribs and intermus-

cular bones) except in species of *Sarda* (Figure 26) which have an additional pair of intermuscular bones attached to the exoccipital just anterior to the first neural prezygapophyses and *Gymnosarda* which lacks cephalic intermuscular bones.

The prootic pits (Godsil 1954) of the more advanced scombrids are incipient in bonitos except in *Allothunnus*, which has a larger pouchlike concavity on each side of the ventral surface of the cranium. Part of the roof, floor, and sides of the prootic pit are formed by the prootic and pterotic bones. The branchial musculature originates in these pits in *Thunnus* (Gibbs and Collette 1967). The posterior end of the orbital region extends into a deep median depression, the posterior myodome, which is surrounded by the prootic anterodorsally, the parasphenoid ventrally, and the basioccipital postdorsally and postlaterally, and then opens at the back of the skull between the posterior flanges of the parasphenoid, or communicates with a posterior or parasphenoidal chamber (Kishinouye 1923). The rectus muscles of the eyes attach in the posterior myodome (Gibbs and Collette 1967).
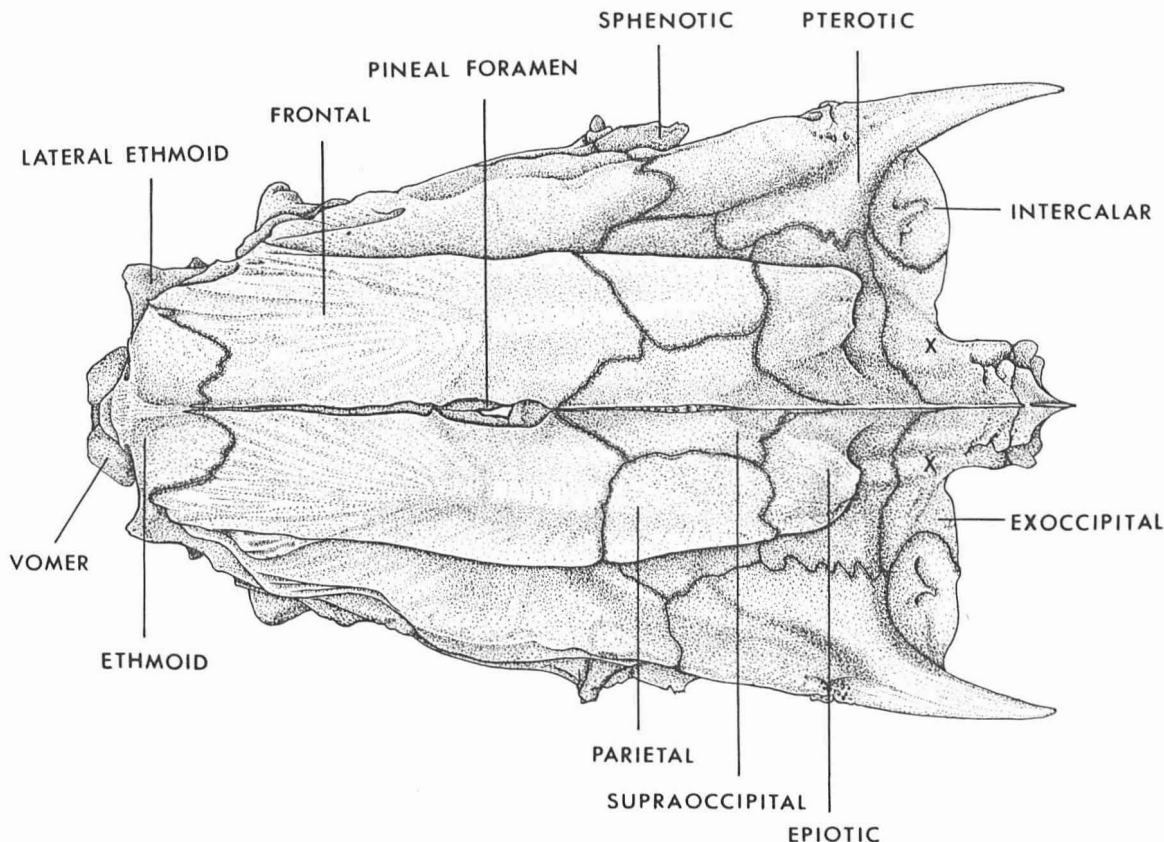
FIGURE 13.—Dorsal view of skull of *Cybiosarda elegans*, Western Australia, 422 mm FL. X's indicate the points of attachment of intermuscular bones.

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 the most anterodorsally located bone of the neurocranium. It has a smooth flat dorsal surface, slightly convex at the median posterior end, to receive the frontal bones. It connects ventrally to the vomer and posteriorly to the lateral ethmoids with rough and porous sutures. The anterior border of the ethmoid is nearly straight in *Orcynopsis* (Figure 14), but is concave in the other genera with an anteromedian projection and an anterolateral horn on each side.

Lateral Ethmoid.—The paired lateral ethmoids (parethmoids) form the posterolateral wall of the ethmoid region and the anterior wall of the orbit with an olfactory foramen on each side. The lateral

ethmoid articulates with the ethmoid anterodorsally, with the frontal bone posterodorsally, with the parasphenoid posteroventrally, and with the vomer anteroventrally. The posterolateral process of the lateral ethmoid serves as an articulating surface for the lachrymal, ectopterygoid, and the entopterygoid. In ventral view, this articulating surface area is small in *Cybiosarda*, slightly larger in *Allothunnus*, and most expanded in the species of *Sarda*, (Figures 15, 18, 19). In *Orcynopsis* and *Gymnosarda*, it is an elongate narrow strip (Figures 16, 17). The lateral expansions of the lateral ethmoids in bonitos resemble those of more primitive scombrids in being wider than in more advanced genera.

Vomer.—The vomer is the most anteroventrally located bone of the cranium. It is located beneath the ethmoid and the lateral ethmoids. Its pointed posterior end fits into the V-shaped anterior projection of the parasphenoid to form the sup-

539
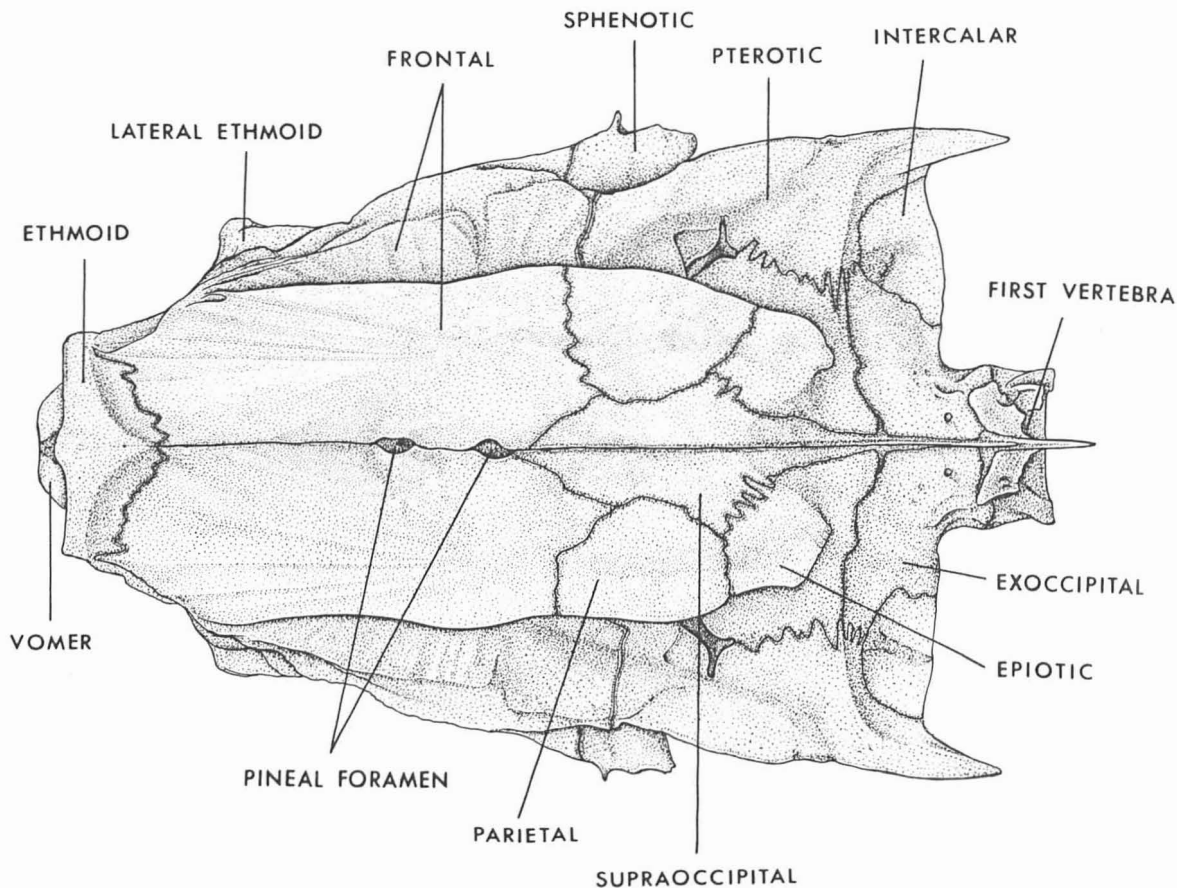
FIGURE 14.–Dorsal view of skull of *Orcynopsis unicolor*, Tunisia, 543 mm FL.

porting axis of the roof of the mouth. Ventrally, the vomer of *Cybiosarda* and *Orcynopsis* (Figures 15, 16) has a blunt anterior edge and bears a patch of villiform teeth. *Sarda australis* and *S. sarda* frequently have a few small teeth on the middle of the expanded part of the vomer, but vomerine teeth are absent in the other bonitos. Some specimens of *S. chiliensis* have a ridge along the midline of the vomer but most have this area flat or convex. The variation is individual, not geographic: 3 of 12 southeastern specimens have a ridge; 6 of 26 northeastern specimens have a ridge. Godsil (1955) mentioned that the ventral surface of the expanded portion of the vomer was flat in Indo-West Pacific *S. orientalis* and that of eastern Pacific specimens was slightly cupped or concave ventrally. We found that this character is not consistent in our material. The anterolateral edges of the vomer are prominent and project ventrally in *Gymnosarda*. The anterior one-third of the vomer

in *Allothunnus* projects ventrally with an axelike anterior end and is porous in the middle of the ventral surface. The pointed posterior end of the vomer is more elongate in *Sarda* than in other genera of bonitos.

The bonitos fall into three groups based on vomerine dentition. *Allothunnus*, *Sarda orientalis*, and *S. chiliensis* lack vomerine teeth. A few small teeth are frequently present on the head of the vomer in *S. sarda* and *S. australis* and sometimes in *Gymnosarda*. Both *Orcynopsis* and *Cybiosarda* have a small patch of teeth on the head of the vomer and a few teeth usually extend posteriorly a short distance on the shaft of the vomer.

Nasal.–The anterior end of the nasal, which reaches the premaxilla posterodorsally, is thickened in all bonitos and has an expanded hammerlike head except in the species of *Sarda* (Figure 27). The nasal gradually becomes thinner

towards its posterior margin which attaches to the frontal bone. *Gymnosarda* has the strongest nasal bone, with serrations along its anteroventral margin. The nasal in *Allothunnus* is more elongate than in other bonitos and its constricted midportion is more prominent.

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

Godsil (1955) found a difference in the ratio of orbit height to length between southeastern and northeastern populations of *Sarda chiliensis*. The ratio in his material varied from 5.83 to 6.83 in 5 southeastern specimens (606-659 mm FL) and from

3.40 to 4.50 in 6 northeastern specimens (439-563 mm FL). Following Godsil's definitions, length was measured along the shaft of the parasphenoid, from its juncture with the lateral ethmoid to the point where the lateral wing of the parasphenoid begins. Orbit height is the least distance between the anterior ventral projection of the pterosphenoid and the shaft of the parasphenoid. The range of variation in this ratio (Table 4) indicates that this is not a useful diagnostic character within the genus *Sarda*, although the means for the populations of *S. chiliensis* show the same trend that Godsil found. *Orcynopsis* and *Cybiosarda* have the highest ratios, which indicate the most elongate and narrow orbits and the most ventrally projecting pterosphenoids. *Allothunnus* and *Gymnosarda* have the lowest ratios due to their slightly higher arched orbits and the smooth ventral margins of the pterosphenoids.
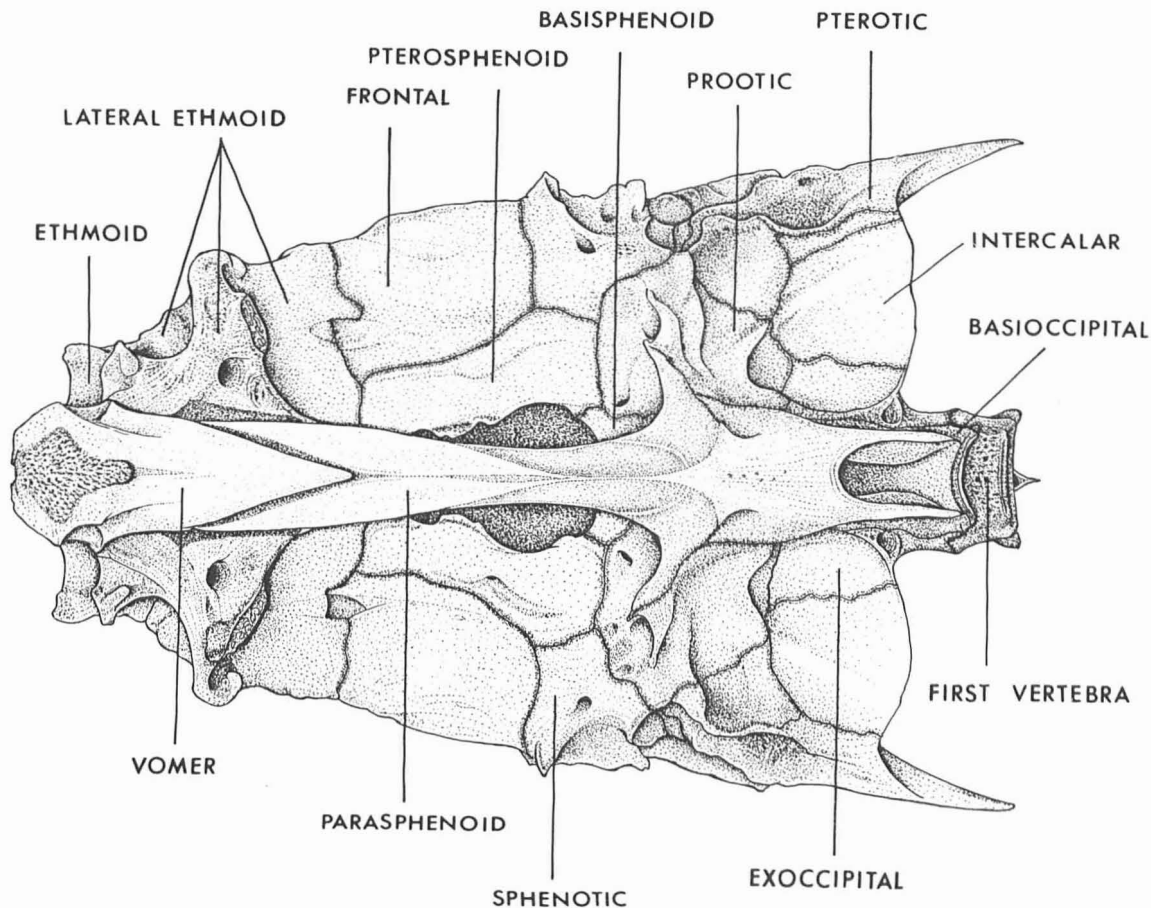
FIGURE 15.—Ventral view of skull of *Cybiosarda elegans*, Western Australia, 422 mm FL.
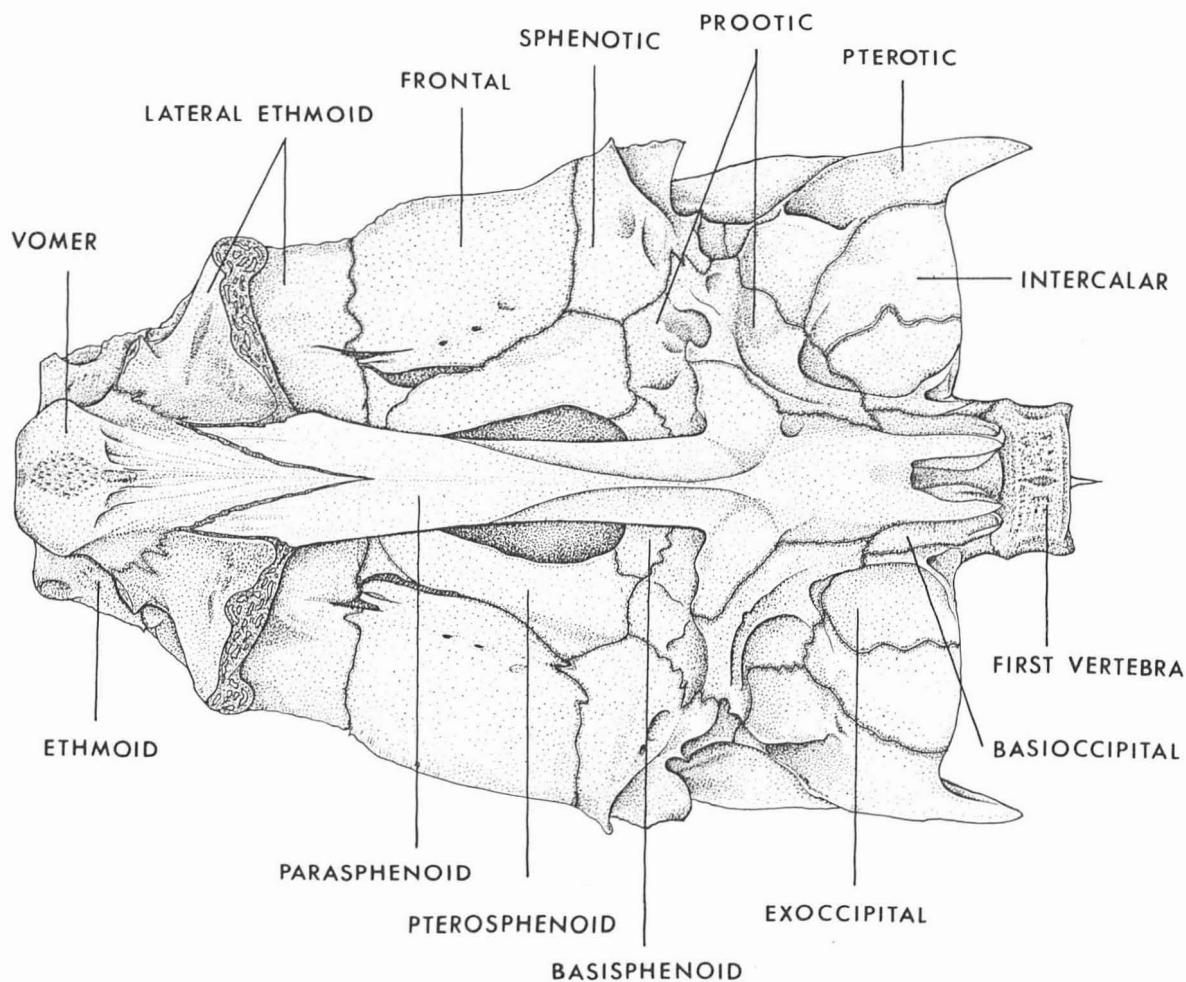
FIGURE 16.—Ventral view of skull of *Orcynopsis unicolor*, Tunisia, 543 mm FL.

Frontal.—Most of the dorsal surface of the cranium is covered by large concave frontal bones. In dorsal view, the anterior ends of the frontals overlap the posterior part of the ethmoid. Posteriorly, they articulate with the sphenotic, pterotic, parietal, and supraoccipital bones. The frontal bones are thickened laterally to form the roof of the orbit; they become thinner where they meet along the median line of the skull and form a crest. A thin bony inner lateral crest begins at the middle of each frontal bone and continues along the parietal to the epiotic bone. A pineal foramen is present immediately anterior to the supraoccipital crest. The pineal foramen is slitlike and filled with cartilage in most bonitos. *Allothunnus* has the largest and thickest frontal bones; they are concave dorsally, with deep conspicuous radiating ridges and lack a frontal crest. A deep round depression, lined with bony ridges, is present anterior to the oval pineal foramen. This feature of *Allothunnus* is similar to that in *Acanthocybium* (Conrad 1938). *Grammatorcynus* also has many conspicuous shallow radiating ridges on the frontal bones. In ventral view, the frontal bone articulates with the lateral ethmoid anteriorly, the pterosphenoid medially, and the sphenotic posteriorly. The ratio of the length of the external edge of the frontal bone to the length of the skull (anterior edge of the vomer to the articulation of the first centrum) varies from 30.9 to 33.3% in *S. australis* (3 specimens 363-495 mm FL) and thus differs from other species of *Sarda*, whose ratios were less than 28%. Laterally, the frontal bone divides into two shelves posteriorly
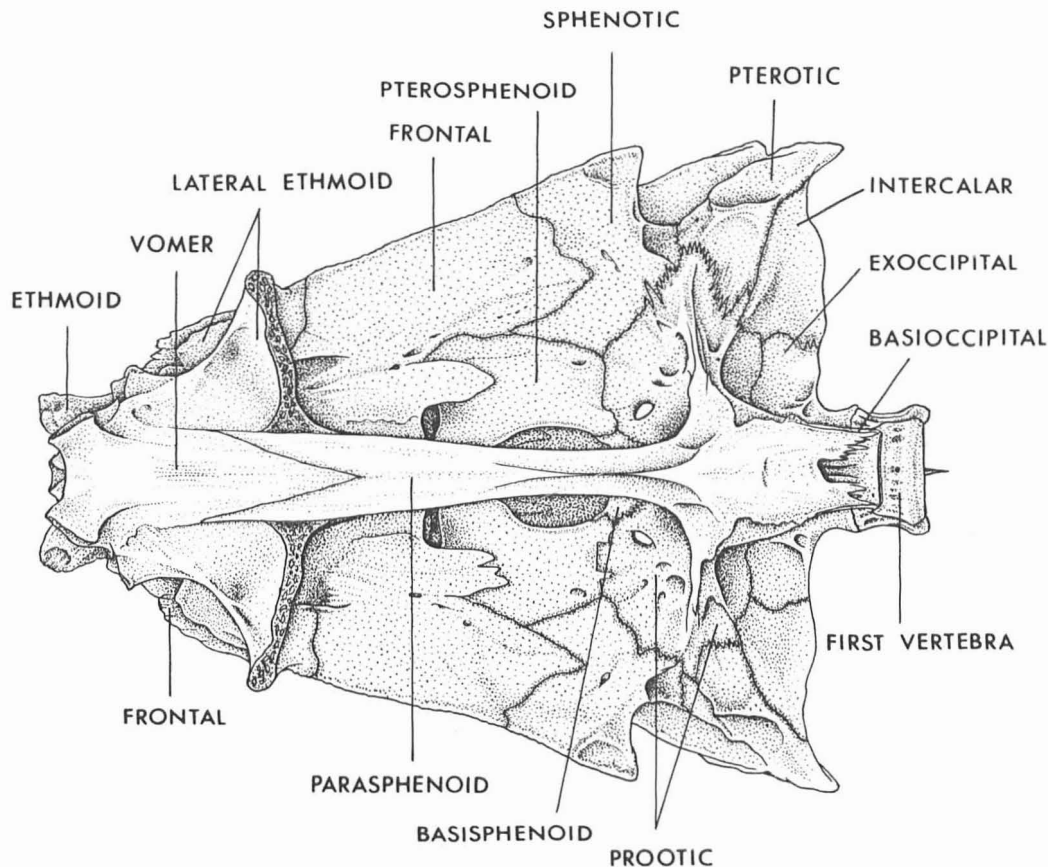
FIGURE 17.—Ventral view of skull of *Gymnosarda unicolor*, Truk Islands, 696 mm FL.

where the upper shelf meets the pterotic and the lower shelf meets the sphenotic. The frontal crest is absent in *Allothunnus* (Figure 24), indistinct in *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* (Figures 20-22), and is most prominent in the species of *Sarda* (Figure 23).

Basisphenoid.—The basisphenoid is a Y-shaped bone, connected dorsally to the prootics and the pterosphenoids. In anterior view, the basisphenoid bisects the entrance of the myodome, with an anteriorly and a posteriorly directed process in its upper half (Figures 20-24), except in *Allothunnus* (Figure 25). Ventrally, the basisphenoid extends toward the parasphenoid to which it is connected in all the bonitos except *Allothunnus*.

Godsil (1954) studied possible differences between the basisphenoids of eastern Pacific *Sarda chiliensis* and *S. orientalis*. He concluded that the lower portion of the basisphenoid in *S. chiliensis* is generally a narrow bone, only slightly expanded, and firmly ankylosed to the parasphenoid. In *S. orientalis*, the lower extremity of the basisphenoid is greatly expanded and it is apparently only loosely attached to the parasphenoid. We agree with his statements in part. In *S. orientalis* from the eastern Pacific and the Indo-West Pacific, the lower extremities of the basisphenoid are expanded and firmly attached to the parasphenoid. In northeast and southeast populations of *S. chiliensis*, the lower portions of the basisphenoid are narrow or slightly expanded and are either firmly or loosely ankylosed to the parasphenoid. In general, the lower extremities of the basisphenoid in *S. chiliensis* are less expanded and less firmly attached to the parasphenoid than in *S. orientalis*.

The angle of the long axis of the basisphenoid relative to the parasphenoid in bonitos is less variable than in *Thunnus* (Gibbs and Collette 1967), but no specific differences were found among the bonitos, except in *Allothunnus*. The

543

basisphenoid curves posteriorly as it approaches the parasphenoid and is not attached to the parasphenoid in *Allothunnus* (Figure 25). This may explain why the basisphenoid was lost in three of the four skulls that we prepared. The angle of the anterior basisphenotic process was used as a character in *Thunnus* by de Sylva (1955:32-35), but Gibbs and Collette (1967:73) found it too variable to be useful. In bonitos, the axes of the anterior and the posterior processes of the basisphenoid are straight, with the anterior process slightly directed downward in some specimens. *Allothunnus* has no basisphenotic process and the anterior process in *Orcynopsis* and *Cybiosarda* is not as prominent as in the other bonitos. The angle between the axis of the process and the vertical axis of the basisphenoid is similar in all bonitos except for *Gymnosarda* (Figure 19). In *Gymnosarda*, a ridge is present along the axis of the process and the posterior process is more ventrally directed.

Among other scombrids, *Thunnus* and *Scomberomorus* lack a prominent posterior process on the basisphenoid (Gibbs and Collette 1967; Mago Leccia 1958, pl. 3), *Allothunnus* and *Rastrelliger* have no process on the basisphenoid (Nakamura and Mori 1966; Gnanamuttu 1971, fig. 1), *Acanthocybium*, *Auxis*, *Euthynnus*, and *Katsuwonus* have both the anterior and the posterior process. If the shape of the basisphenoid bone is used as a diagnostic character in scombrid classification (Kishinouye 1923; Godsil 1954; de Sylva 1955; Gibbs and Collette 1967), its high intraspecific variability must be taken into account.

Pterosphenoid.—The pterosphenoid (alisphenoid) articulates with the edges of the frontal, sphenotic, prootic, and basisphenoid on the ventral surface of the brain case. Anteriorly, the pterosphenoids are connected to the lateral ethmoids directly or indirectly by a cartilaginous membrane. The paired pterosphenoid bones meet each other anteriorly along the median ventral line forming a pterosphenotic window that differs

FIGURE 18.—Ventral view of skull of *Sarda sarda*, eastern United States, 388 mm FL.
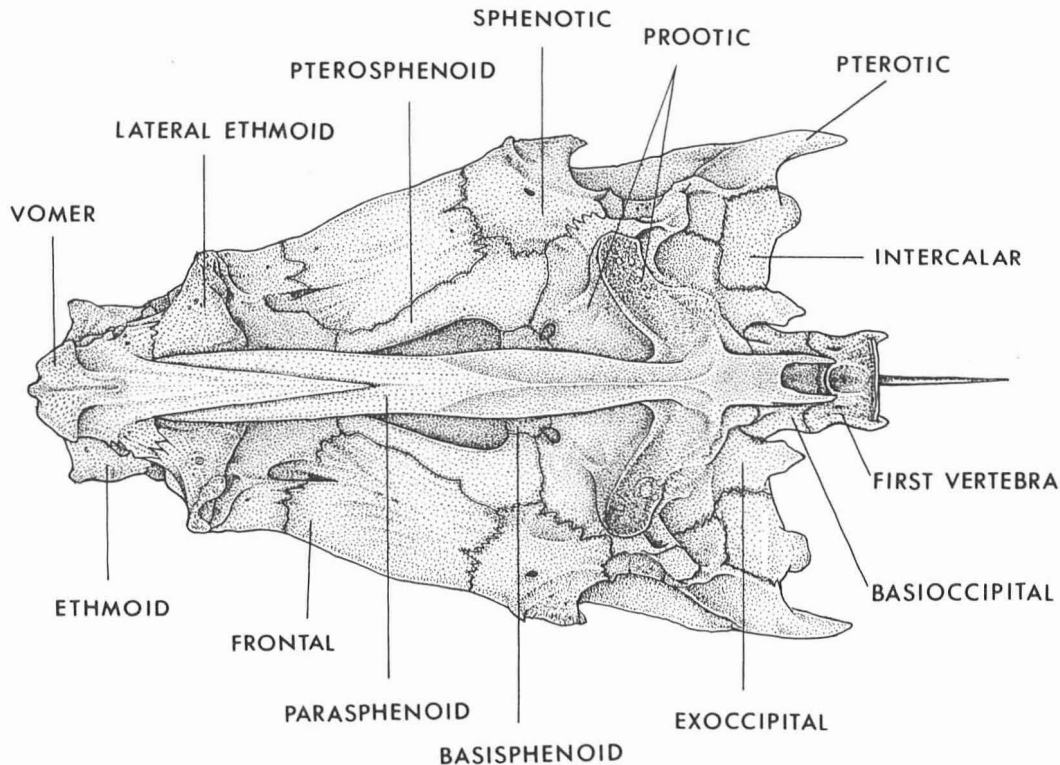
FIGURE 19.—Ventral view of skull of *Allothunnus fallai*, California, 680 mm FL.

slightly among the bonitos in shape. *Cybiosarda, Orcynopsis,* and *Gymnosarda* have a beer bottle-shaped window; it is roughly triangular with a broad arched posterior margin in *Sarda.* In *Allothunnus,* a thin bony membrane is present along the inner edge of the pterosphenoid toward the center of the window. The pterosphenoids do not fuse with the parasphenoid, as they frequently do in large specimens of *Thunnus thynnus* (Gibbs and Collette 1967).

Lachrymal.—The lachrymal is an elongate bone that covers up part of the maxilla and is attached to the lateral ethmoid by means of a dorsal projection on its inner surface (Figure 9). This process is most pronounced in *Gymnosarda* and most flattened in *Allothunnus.* The anterior margin of the lachrymal has an indentation with an anteriorly projecting process on the dorsal margin of the indentation (Figure 28). The margin is slightly concave in *Sarda* and *Gymnosarda* compared to the deep notch present in the other bonitos, *Cybiosarda* has the longest anterior process, much longer and thinner than in *Orcynopsis.*

Gymnosarda has a wide blunt process. The lachrymal is relatively shorter and stronger in *Gymnosarda* and it is extremely heavy and sculptured at the dorsal projection and along the posterodorsal margin.

Suborbital bones.—Nakamura and Mori (1966) stated that the first and second suborbital bones are inconspicuously developed and not much differentiated from the scales on the cheek in *Allothunnus.* Suborbital bones are present in the bonitos, but we have made no special effort to study them.

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 in all bonitos as in *Thunnus atlanticus* (de Sylva 1955, fig. 7).

OTIC REGION.—This region encloses the otic chamber inside the skull, and is formed by the
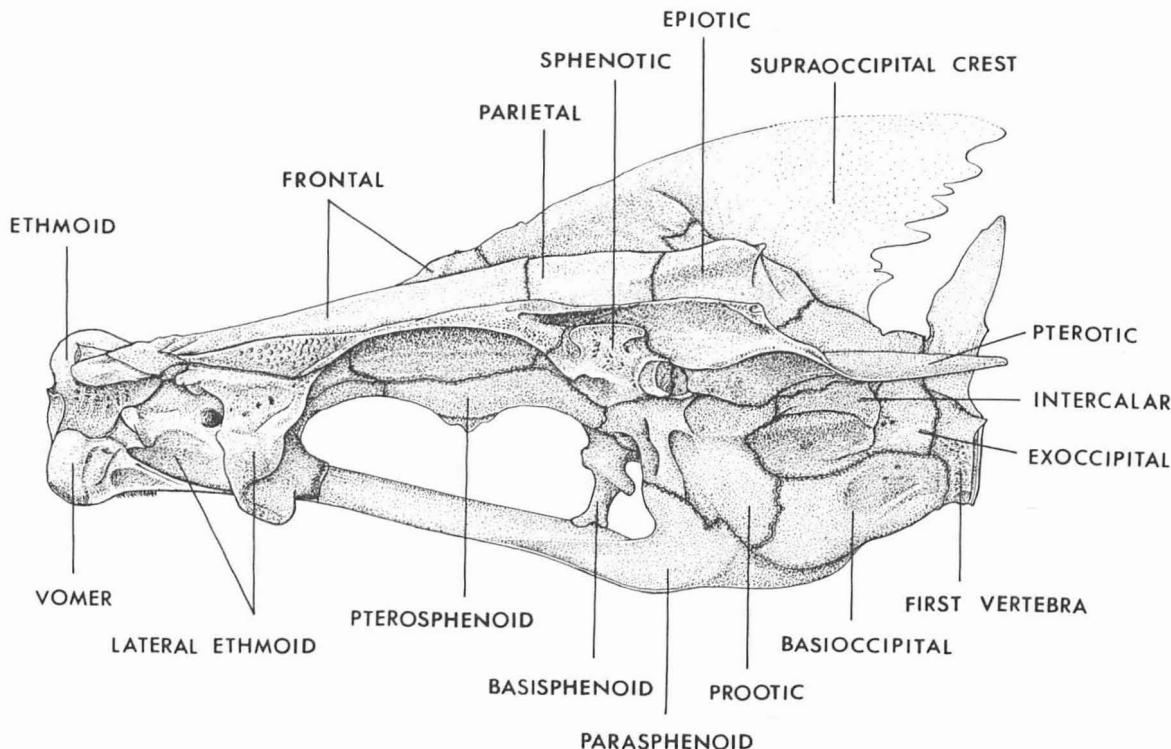
FIGURE 20.—Lateral view of skull of *Cybiosarda elegans*, Western Australia, 422 mm FL.

parietal, epiotic, supraoccipital, pterotic, prootic, sphenotic, and intercalar (opisthotic) bones.

Parietal.—The parietal articulates with the frontal anteriorly, the supraoccipital and the pterotic laterally, sphenotic ventrally, and epiotic 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 but is less developed in *Grammatorcynus* and in *Scomber* (Allis 1903).

Epiotic.—The epiotic is massive, irregular, and bounded by the parietal anteriorly, the supraoccipital mediolaterally, the exoccipital posteriorly, and the pterotic distolaterally. The inner lateral crest terminates at the posterior end of the epiotic. The medial process of the posttemporal bone is also attached here. The epiotic bones of all the bonitos are similar.

Supraoccipital.—The supraoccipital can be divided into two parts: a thin, elongate triangular crest and a roughly hexagonal shaped base. The

supraoccipital crest arises just behind the pineal foramen and extends posterodorsally. In bonitos, the crest extends posteriorly over the first neural spine but usually not over the posterior margin of the first centrum. In *Allothunnus* the crest extends posteriorly over the second centrum. In dorsal view, the hexagonal base articulates with the frontal bones anterolaterally, the parietals laterally, and the epiotic posteriorly. *Cybiosarda* and *Orcynopsis* have the narrowest and most elongate supraoccipital base; *Allothunnus* has the shortest and widest.

Pterotic.—Dorsally, the pterotic is the most posterolaterally located bone. The pterotic articulates with the epiotic and parietal medially and with the exoccipital and intercalar posteriorly. A sharp posteriorly pointed process is characteristic of the pterotic bone of the bonitos as well as other scombrids. In ventral view, the pterotic articulates with the sphenotic anteriorly and the prootic and intercalar medially. Two 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. A deep

depression continues from the interspace of the posterior frontal shelves and separates the pterotic from the sphenotic. In bonitos, the size of both fossae varies only slightly; they tend to be deeper and larger in *Gymnosarda* and *Allothunnus*.

Prootic.—In ventral view, the prootic connects with all ventral bones which compose the posterior part of the neurocranium (Figures 15-19). The prootic bones are irregular in shape and meet each other along the ventral median line of the brain case to form the anterior portion of the posterior myodome. A prootic foramen is present anterolaterally between the tip of the parasphenoid wing and the sphenotic. The strut forming the outer part of the foramen is absent in *Allothunnus* forming a deep groove. The prootic pit of the more advanced scombrids (Gibbs and Collette 1967) is present in *Allothunnus* and absent or incipient in the other bonitos. In addition to the distinct prootic pit in *Allothunnus*, there is a very peculiar thick bony wing which is developed

laterally; this twisted wing has a smooth convex anterior surface and a concave posterior surface.

Sphenotic.—The sphenotic bone forms the most posterior dorsolateral part of the roof of the orbit. It forms a continuation of the outer lateral shelf from the frontal bones and articulates with the pterosphenoid medially and the prootic and pterotic posteriorly. The lateral process of the sphenotic serves as an attachment for the outer process of the supratemporal. This process is pointed in *Cybiosarda*, *Orcynopsis*, *Gymnosarda*, and *Allothunnus*, and is less sharp in the species of *Sarda*. There are differences in the outlines of the joints around the sphenotic bone with the adjacent bones, but these are probably individual variations.

Intercalar.—The intercalar (opisthotic) bone fits between the pterotic and exoccipital bones (Figures 10-14) and bears a dorsal protuberance which connects to the lateral process of the post-
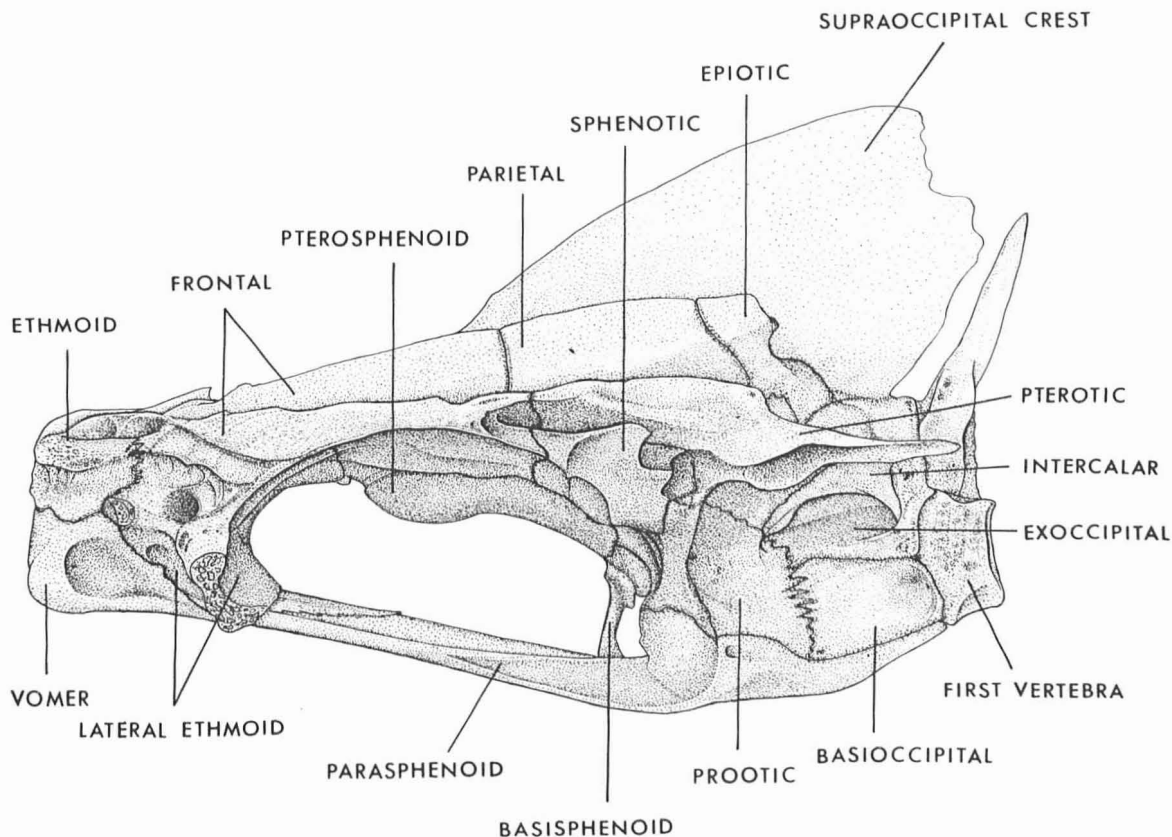
FIGURE 21.—Lateral view of skull of *Orcynopsis unicolor*, Tunisia, 543 mm FL.
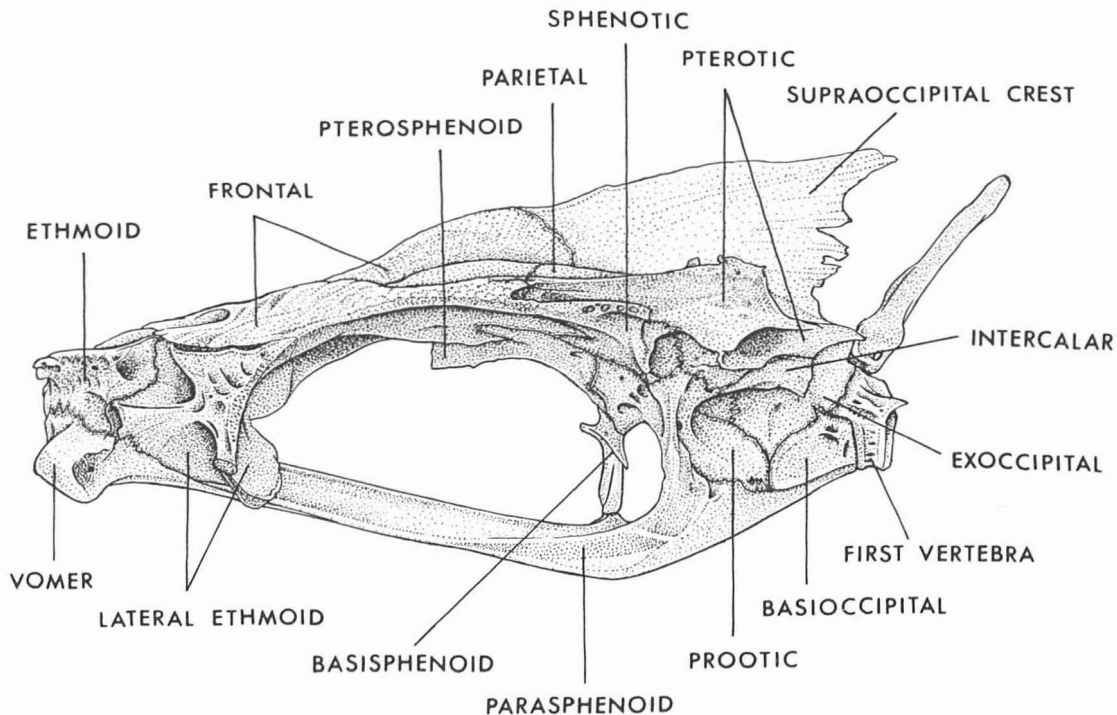
FIGURE 22.–Lateral view of skull of *Gymnosarda unicolor*, Truk Islands, 696 mm FL.
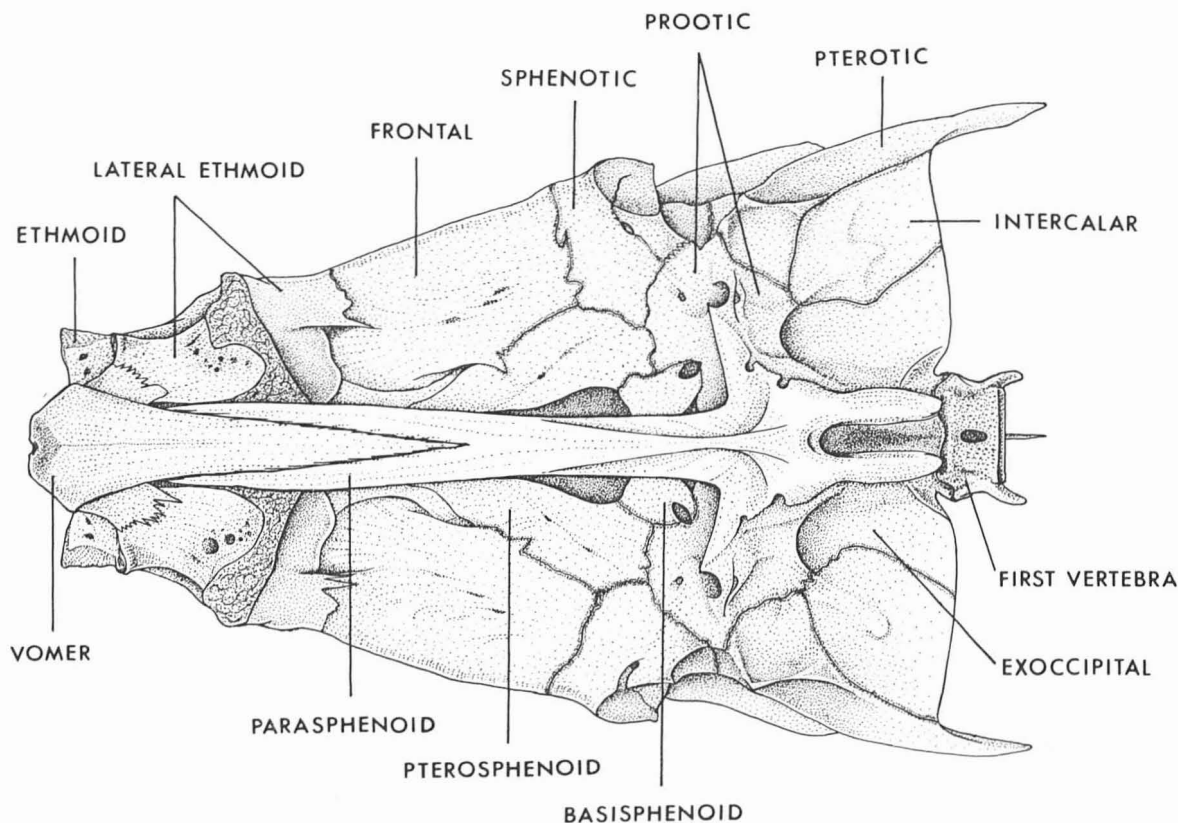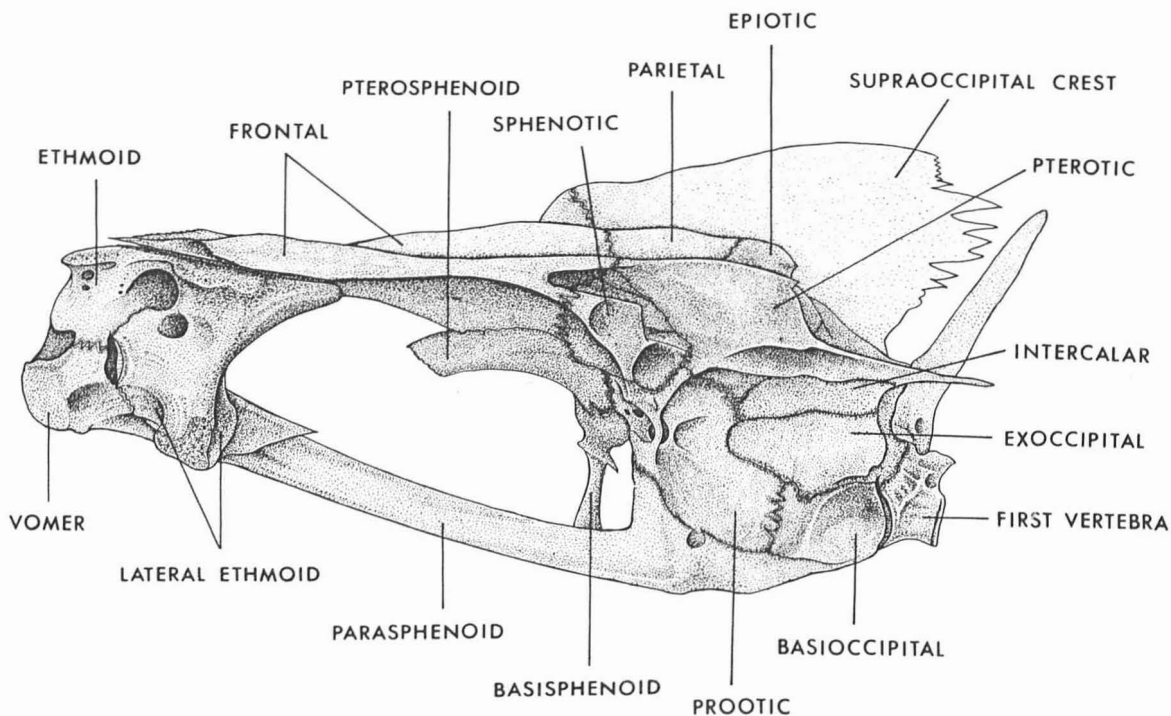

FIGURE 23.–Lateral view of skull of *Sarda sarda*, eastern United States, 388 mm FL.
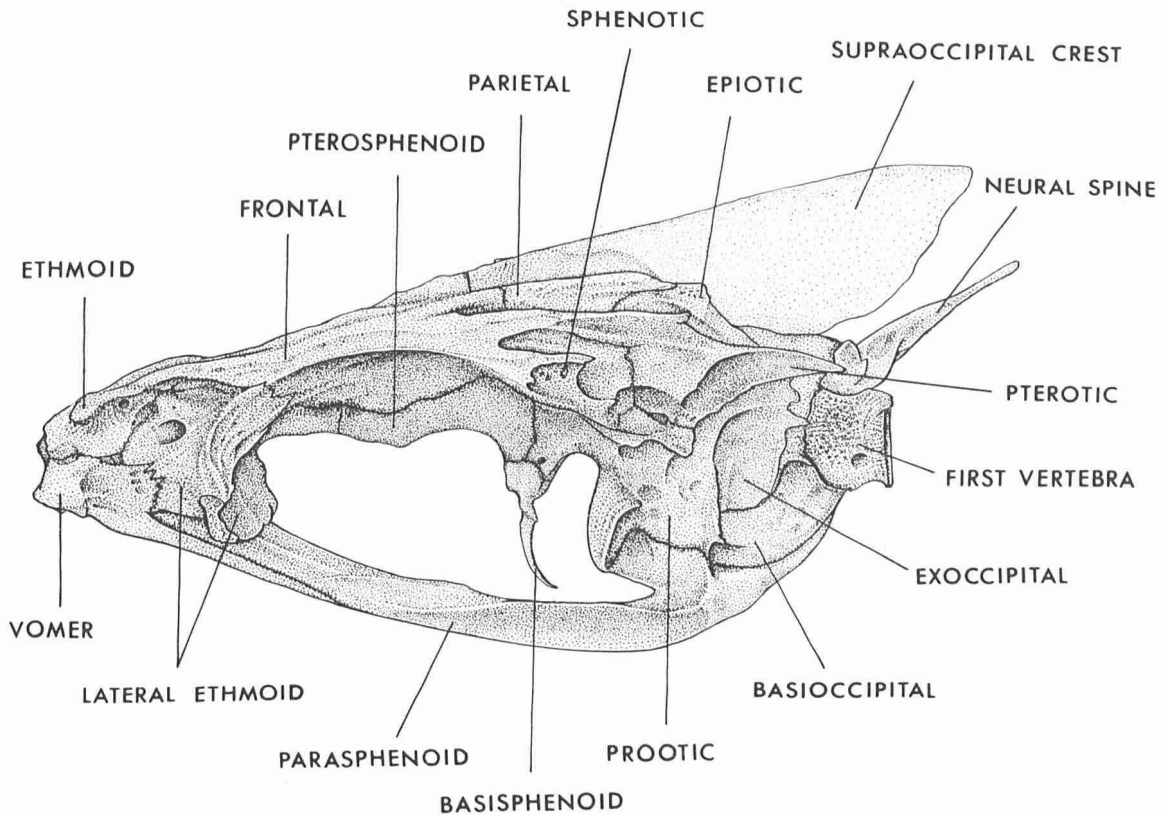
FIGURE 24.—Lateral view of skull of *Allothunnus fallai*, California, 680 mm FL.
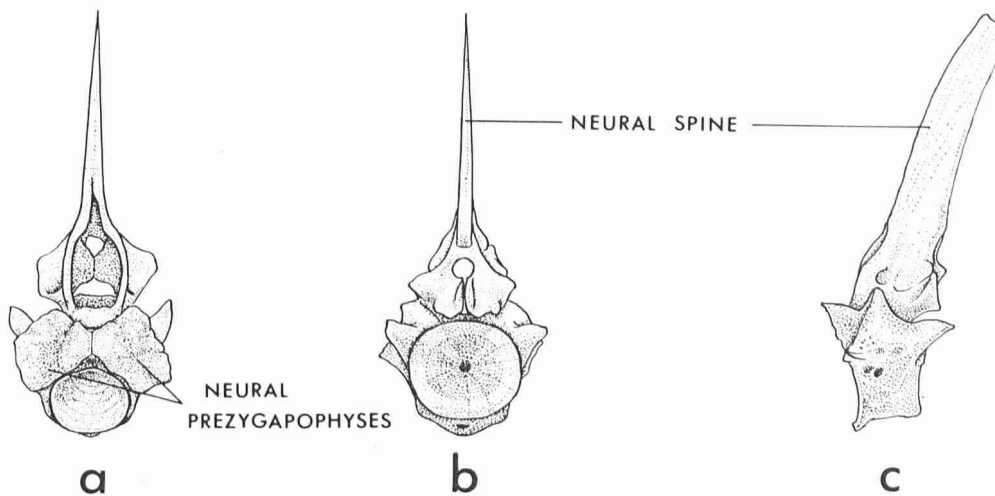
FIGURE 25.—First vertebra of *Sarda chiliensis*, Callao, Peru, 571 mm FL. a. Anterior view. b. Posterior view. c. Lateral view.
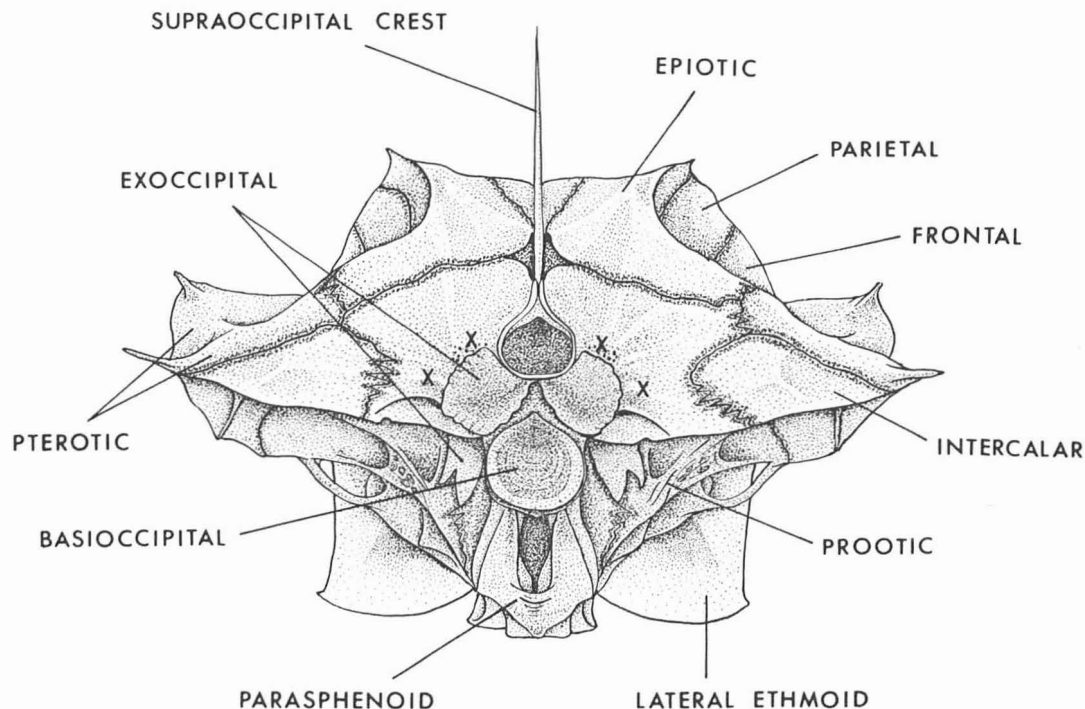
FIGURE 26.—Rear view of skull of *Sarda chiliensis*, Callao, Peru, 571 mm FL. X's indicate the points of attachment of intermuscular bones.

temporal. In *Allothunnus*, this protuberance projects out from the posterior outline of the skull, while in other bonitos this outline is smooth. Ven-

FIGURE 27.—Nasals of six species of Sardini, left external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda chiliensis*, Callao, Peru, 442 mm FL. d. *Sarda sarda*, Florida, 333 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, Tasmania, 775 mm FL. a–d drawn twice as large as e and f.

trally, the intercalar articulates with the prootic bone anteriorly and the exoccipital and pterotic bones laterally (Figures 15-19).

BASICRANIAL REGION.—This region consists of the parasphenoid, basioccipital and exoccipital bones, and forms the posteroventral base of the skull.

Parasphenoid.—Ventrally, the parasphenoid is a long cross-shaped bone (Figures 15-19) 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 keel is present along the posterior two-fifths of the parasphenoid. The V-shaped joint connecting the parasphenoid with the vomer anteriorly is most
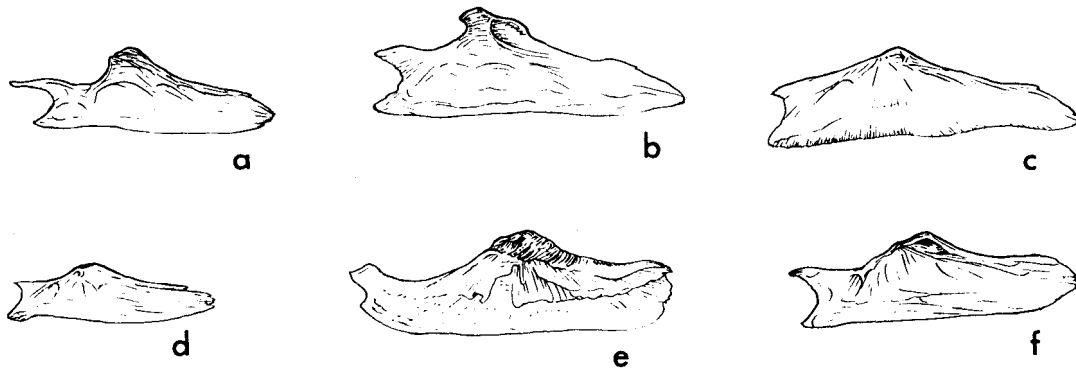
FIGURE 28.—Larchrymals of six species of Sardini, left lateral view. a. *Cybiosarda elegans*, New South Wales, 360 mm FL. b. *Orcynopsis unicolor*, Tunisia, 495 mm FL. c. *Sarda orientalis*, Tokyo, 350 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, California, 680 mm FL. a, b, and c drawn twice as large as d, e, and f.

elongate in *Allothunnus* and the species of *Sarda* (also see vomer). In ventral view, the general characteristic of the parasphenoid is a gradual narrowing of the bone from anterior to posterior. *Orcynopsis* has the widest and strongest parasphenoid; species of *Sarda* have the weakest. Broad parasphenoids are also present in *Scomberomorus* and *Acanthocybium*; narrower parasphenoids in *Auxis, Euthynnus, Katsuwonus*, and *Thunnus*. The broadest portion of the parasphenoid is usually located at or before the tip of the V-shaped joint with the vomer in all bonitos except *Allothunnus*. In five skulls (406-778 mm FL) of *Allothunnus*, the broadest portion of the parasphenoid is in the posterior half of the bone, about at the beginning of the ventral keel. This is in contradiction to Nakamura and Mori (1966, fig. 4B), whose illustration of a specimen (876 mm FL) shows the parasphenoid as similar to other bonitos.

The anterior edge of the lateral wings of the parsphenoid is smoothly concave forward and forms a dorsolaterally directed shelf, visible ventrally in all bonitos except *Allothunnus*. In *Allothunnus* (Figure 19), the anterior edge of the lateral wing is deeply concave and the wing projects vertically along the prootic wing toward the roof of the skull, as in the more advanced scombrids. The posterior opening, between the lateral flanges of the parasphenoid, is usually elongate and the lateral flange does not extend beyond the juncture of the skull with the first centrum (Figures 15-19). In our *Gymnosarda* skulls, this opening is much smaller than in the other bonitos (Figure 17). A thin layer of bone covers the anterior portion of the opening, perhaps

indicating additional ossification in larger individuals of this particular species.

In lateral view (Figures 20-24), the parasphenoid forms the ventral border of the orbit and connects with the lateral ethmoid, basisphenoid, prootic, and basioccipital bones dorsally. The ventral keel projects further ventrally in *Gymnosarda* and *Allothunnus* than in *Orcynopsis* and *Cybiosarda*. The posterior one-third of the parasphenoid and its lateral flanges are strongly convex in *Allothunnus*, forming the unique posteroventral outline of its skull (Figure 24). A middorsal ridge is also present in all bonitos. This ridge arises from the juncture of the lateral ethmoids, where the ridge projects the most, and merges into the main axis of the parasphenoid posteriorly at about the beginning of the ventral keel. Usually, a triangular piece of cartilage, connecting with the lateral ethmoid, covers the most anterior end of the dorsal ridge. The middorsal ridge is least prominent in *Cybiosarda*.

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 (Figure 25). In lateral view, a distinct deep concave pit is

present at the posterodorsal corner of the basioc-cipital in all bonitos (Figures 20-24). Godsil (1954) first noted this feature, "a deep-rimmed, crater-like depression in the basioccipital," and stated that "This character is sufficient to separate *Sarda* from any species of the Plecostei." In 1955, Godsil modified this statement to ". . . it is not a positive diagnostic generic character." In comparing this basioccipital depression with other scombrids, we found it to be diagnostic of bonitos. In *Auxis*, *Euthynnus*, *Katsuwonus*, and *Thunnus* only a shallow concave surface is present; *Scomberomorus* and *Acanthocybium* have small foramina on the corresponding position of the basioccipital. *Grammatorcynus* has a similar depression but it is much shallower.

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. Dorsally, a small foramen is present at the medioposterior corner of the exoccipital and it opens into the brain cavity. The exoccipital bones are similar, with an intermuscular bone attached, in all bonitos except *Gymnosarda* which has none and *Sarda* which has two (Figure 12).

OTOLITHS.—The first figures of bonito otoliths were presented by Shepherd (1910a, b) who illustrated the asteriscus and sagitta of *Sarda sarda* along with other miscellaneous eastern Atlantic species, but his figures are too small and poorly defined to be of any comparative value. Chaine (1957) published good figures of the sagittae of *Sarda sarda* as well as two species of *Scomber*, two of *Thunnus*, and *Scomberomorus tritor*. Bauzá Rullán (1961:155-156, pl. 1, figs. 7-10) also illustrated the sagitta of *S. sarda*. Two studies include information about intraspecific variation in the shape of bonito sagittae. Chaine (1957) discussed variation in *S. sarda*; Kuo (1970:125, fig. 7) showed considerable variation with outline sketches of sagittae from the left and right sides of 47 *S. chiliensis* from California in an age and growth study. Fitch and Craig (1964) made the first comparative study of scombrid otoliths when they compared the sagittae of eastern Pacific scombrids

in an attempt to assess the relationships of *Allothunnus fallai*. They found that scombrid sagittae, except for *Scomber japonicus*, have a long thin rostrum, finely serrate margins, and a deep sulcus on the inner face. Among bonitos, they compared the otoliths of *Allothunnus* and three species of *Sarda* (*chiliensis*, *orientalis*, and *sarda*). *Allothunnus* and *S. chiliensis* were illustrated.

Specific Characters.—We calculated proportions of the sagittae as percent of the otolith (sagitta) length (OL) in fork length and the greatest height (H) in length of sagitta and in length of rostrum (R).

	FL (mm)	OL/FL (%)	H/OL (%)	H/R (%)
Orcynopsis	576	1.54	48.3	1.3-1.4 ($n=3, \bar{x}=1.39$)
Cybiosarda	365	1.56	44.6	1.0-1.2 ($n=4, \bar{x}=1.09$)
Sarda sarda	418	1.17	35.7	0.9
S. orientalis	350	1.10	33.8	0.8
Gymnosarda	789	0.91	44.4	1.2
Allothunnus	775	0.92	44.8	1.2

($n=1$ unless otherwise noted)

The sagitta of *Orcynopsis* is the largest among the bonitos relative to fork length. It has a ridge extending from the postdorsal part of the outer surface to the middle of the otolith. It also has the shortest and widest rostrum and the deepest sulcus of any bonito (Figure 29b).

The sagitta of *Cybiosarda* is larger and heavier than *Sarda*. It is similar in size to *Orcynopsis* but has a longer and thinner rostrum. *Cybiosarda* has two ridges extending from the middorsal and posteroventral parts of the sagittae toward the ventral and middorsal areas respectively (Figure 29a). The latter one seems to be weaker. Both *Cybiosarda* and *Orcynopsis* are distinct in having a winglike flange which extends outward and forms a small platform at the posterodorsal margin on the inner side.

The sagittae in the species of *Sarda* are small and have similar outlines (Figure 29c, d). A pyramidlike ridge is present in the middle of the posterior half of the sagitta. They also have the

FIGURE 29.—Sagittae of six species of Sardini, upper figure of each pair is the outer view, lower figure the inner view. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Tunisia, 567 mm FL. c. *Sarda orientalis*, Tokyo, 350 mm FL. d. *Sarda sarda*, Azores, 418 mm FL. e. *Gymnosarda unicolor*, Marshall Islands. f. *Allothunnus fallai*, Tasmania, 775 mm FL. (Scale indicates 1 mm.)
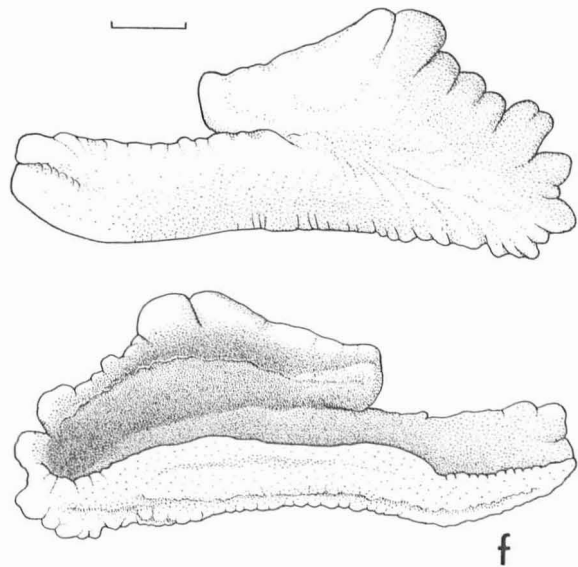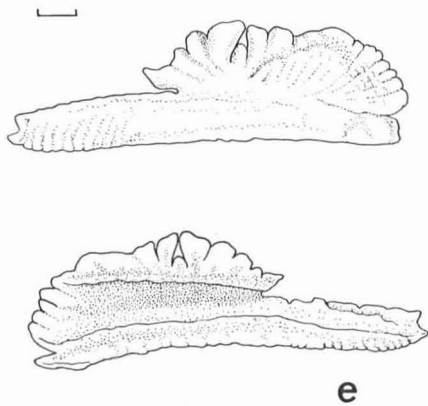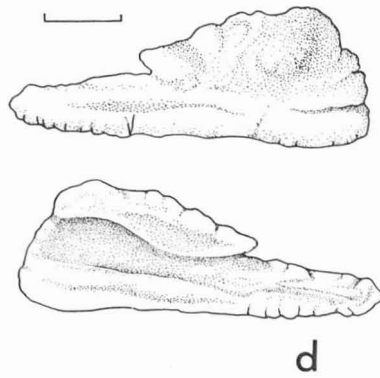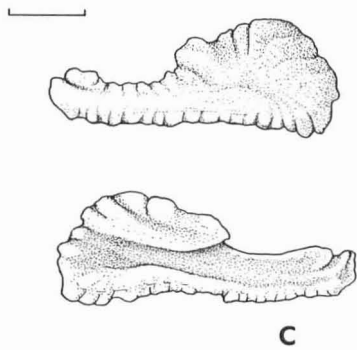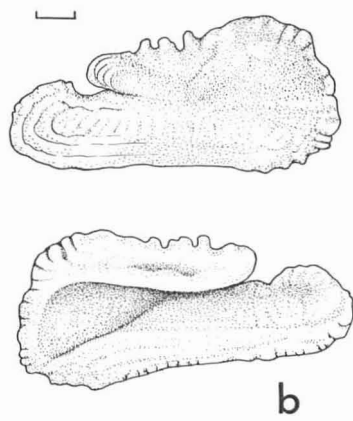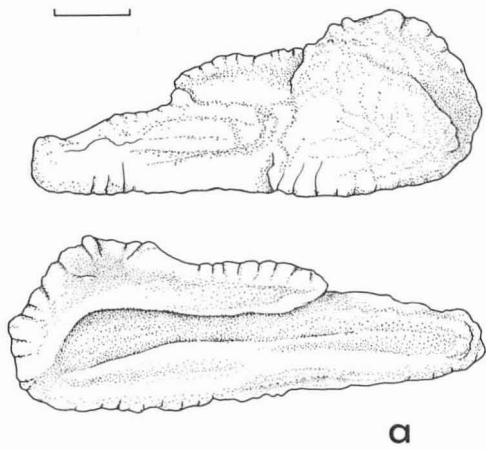
longest and narrowest rostra among bonitos. The dorsal process above the rostrum seems to vary considerably inter- and intraspecifically (see Kuo 1970, fig. 7).

The sagittae of *Gymnosarda* are distinct from those of all other bonitos by their extreme curvature when viewed in situ from above, by their concave ventral margin (sagittae of all other bonitos have relatively straight ventral margins), and by the fact that except for minor protuberances and other irregularities the dorsal margin, in the posterior half of the otolith, roughly parallels the ventral margin, giving a sameness of height to the otolith in this region. The sulcus is more distinctive on the inner surface. The posterior dorsal margin is deeply serrate. No pyramidlike ridge is present in the middle of the posterior half. Laterally, the deepest part of the sagitta is in front of the middle of the posterior half.

The sagitta of *Allothunnus* is small and similar in size to the species of *Sarda*. It has a very distinctive triangular outline; with an acute posteroventral angle and no prominent ridges on the outer surface. The inner surface of the sagitta has a deep sulcus with a very prominent dorsal ridge.

Branchiocranium

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

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.

Dentition.—Conical teeth are present on the upper and lower jaws in all bonitos. These teeth differ from the laterally compressed teeth with serrate edges found in Spanish mackerels (Scomberomorini) and are generally larger than the tiny conical teeth of the higher tunas (Thunnini). In addition to jaw and palatine teeth,

TABLE 5.—Number of teeth in the upper jaw in species of Sardini. (Mean of left and right sides rounded off upwards to nearest whole number.)

Species	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	N	x̄
Cybiosarda elegans		1	2	1	2	1	5	4	4	1	1										22	17.9
Orcynopsis unicolor:																						
E Mediterranean								2	3	2	5	5	5	6	3	2						33	22.2
Cent. Mediterranean									1	—	—	3	—	—	1	1	1				7	23.3
Atlantic											2	—	1	2							5	22.6
Total								2	4	2	7	8	6	8	4	3	1				45	22.4
Sarda australis				2	3		2	7	2	2	1										19	18.7
Sarda chiliensis:																						
NE Pacific									2	9	11	15	16	11	6	2	—		2	2	76	23.7
SE Pacific							3	3	3	—	5	9	7	2	6	2	1				41	23.0
Total							3	3	5	9	16	24	23	13	12	4	1		2	2	117	23.5
Sarda orientalis:																						
Indian Ocean		1	3	—	3	1	2	1													11	15.9
NW Pacific	1	2	2	4	4	1															14	14.8
Cent. Pacific	1	—	1	2																	4	14.0
E Pacific		2	3	1	4	4	3	1	1												19	16.2
Total	2	5	9	7	11	6	5	2	1												48	15.5
Sarda sarda:																						
North America							8	4	18	12	10	6									58	19.5
South America						1	—	—	1	2	2	6	3								15	21.2
NE Atlantic							2	1	—	—	—	—	5	1							9	22.2
Mediterranean-Black Sea					1	1	1	—	5	6	8	5	4								31	21.4
(Demir 1964, Turkey)			(1	2	2	4	17	18	19	12	14	11	11	5	2)						(118)	(20.6)
Gulf of Guinea-S. Africa								3	2	5	4	3	3	5	1						26	20.4
Total						2	12	9	25	23	21	23	13	10	1						139	20.5
Gymnosarda unicolor:																						
Indian Ocean			2	—	4	1	—	—	—	—	—	1	—	1							9	18.4
W Pacific		1	3	3	1	2	3	3	2	—	1	1	—	—	1	—	—		1	1	23	19.8
Total		1	5	3	5	3	3	3	2	—	1	2	—	1	1	—	—		1	1	32	19.4
Allothunnus fallai													(40-42-44-51-54-55)								6	47.7

patches of teeth are present on the vomer and tongue in some genera. *Allothunnus* has many very small teeth (40-55) on each of the upper and lower jaws, compared to a range of 12-31 on the upper jaw and 10-25 on the lower jaw in other bonitos (Tables 5, 6). *Orcynopsis* averages more teeth in both upper and lower jaws than does *Cybiosarda*. Both *Gymnosarda* and *Sarda australis* have a very wide range in the number of jaw teeth. In the eastern Pacific, the tropical *Sarda orientalis* differs from the south and north temperate *S. chiliensis* in having fewer upper (13-20, $\bar{x}$ 16.2 vs. 18-30, $\bar{x}$ 23.5) and lower (10-17, $\bar{x}$ 13.2 vs. 14-25, $\bar{x}$ 19.2) jaw teeth. Numbers of jaw teeth and gill rakers are correlated: note especially *Allothunnus* with 70-80 gill rakers and *Orcynopsis* with more gill rakers than *Cybiosarda* (Table 7).

Premaxilla.—The premaxilla (Figure 30) is a long curved bone with a stout arrowhead-shaped anterior end and teeth on the ventral margin. The angle between the oblique anterior and the ventral margin of the premaxilla is most acute in *Gymnosarda* and *Orcynopsis*, similar to *Scomberomorus*. It is almost perpendicular with a small anterior projection in *Allothunnus* (Figure 30f), as in *Thunnus*. The sharp anterior dorsal process of the premaxilla in the species of *Sarda* separates them from the other bonitos (Figure 30c, d). The posterior end of the premaxilla in *Allothunnus* is also similar to *Thunnus*, sharper and thinner than in the other bonitos. The main axis of the premaxilla is curved more in *Gymnosarda*, *Cybiosarda*, and *Orcynopsis* than in *Sarda* and *Allothunnus*.

Maxilla.—The maxilla (Figure 31) is a long curved bone with two irregularly shaped condyles which join the premaxilla anterodorsally. The main axis of the maxilla is most curved in *Orcynopsis* and most flattened in *Gymnosarda* and *Allothunnus* (as in *Thunnus*). A process from the lower condyle of the anterior portion of the maxilla protrudes ventrally in *Cybiosarda* and the species of *Sarda*. This projection is not present in *Scomberomorus* or *Thunnus*. The posterior ends of the maxillae of *Gymnosarda* and *Allothunnus* are broader than in other bonitos. The anterior ends of

TABLE 6.—Number of teeth in the lower jaw of species of Sardini. (Mean of left and right sides rounded off upwards to nearest whole number.)

Species	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	N	$\bar{x}$
Cybiosarda elegans	2	1	7	8	1	1	2	1									23	13.0
Orcynopsis unicolor:																		
E Mediterranean			1	1	2	3	6	3	9	5	1	2					33	17.1
Cent. Mediterranean							1	1	2	1							5	17.6
Atlantic						1	—	1	1	1	1						5	17.8
Total			1	1	2	4	7	5	12	7	2	2					43	17.2
Sarda australis		1	2	2	5	5	2	1	—	—	1						19	14.5
Sarda chiliensis:																		
NE Pacific						2	2	7	18	16	9	10	8	2	1	2	77	19.4
SE Pacific					1	3	4	5	8	7	4	2	5	4			43	18.9
Total					1	5	6	12	26	23	13	12	13	6	1	2	120	19.2
Sarda orientalis:																		
Indian Ocean		2	4	3	—	2											11	12.6
NW Pacific		2	3	5	3	1											14	12.9
Cent. Pacific				3	1												4	13.3
E Pacific	2	1	3	6	2	3	1	1									19	13.2
Total	2	5	10	17	6	6	1	1									48	13.0
Sarda sarda:																		
North America			3	4	12	18	15	3	2	1							58	15.0
South America					2	2	4	3	3								14	16.2
NE Atlantic						1	—	4	—	1	2	—	—	—	1		9	18.4
Mediterranean-Black Sea				1	2	4	6	3	10	4	1						31	16.9
(Demir 1964, Turkey)			(1	6	9	21	18	22	18	16	3	3	1)				(118)	(16.7)
Gulf of Guinea-S. Africa				1	5	3	7	6	2	2							26	16.0
Total			3	6	21	28	32	19	17	8	3	—	—	—	1		138	16.0
Gymnosarda unicolor:																		
Indian Ocean	1	—	2	4	—	—	—	1	—	1							9	13.5
W Pacific	2	5	4	3	4	1	1	1	—	—	—	1	1	—	1		24	13.9
Total	3	5	6	7	4	1	1	2	—	1	—	1	1	—	1		33	13.8
Allothunnus fallai											(41-42-49-53)						4	46.3

TABLE 7.—Total number of gill rakers on the first arch in species of Sardini.

Species	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	N	x̄
Cybiosarda elegans					3	12	4	1													20	13.2
Orcynopsis unicolor:																						
E. Mediterranean						1	8	18	8	1											36	15.0
Cent. Mediterranean					1	—	1	3	1												6	14.5
(Postel 1956a, Tunisia)						(2	51	96	34	6)											(189)	(15.0)
Atlantic							1	4	1												6	15.0
Total					1	1	10	25	10	1											48	14.9
Sarda australis												3	10	5							18	20.1
Sarda chiliensis:																						
NE Pacific																3	9	12	10	6	40	25.2
(Kuo 1970)															(1	28	226	229	25	1)	(510)	(24.5)
SE Pacific																3	4	9	10	3	29	25.2
(Kuo 1970)																(6	41	44	1)		(92)	(24.4)
Total																6	13	21	20	9	69	25.2
Sarda orientalis																						
Indian Ocean			2	4	2	1															9	11.2
NW Pacific		2	4	3	1	1															11	10.0
Cent. Pacific			4																		4	10.0
E Pacific	1	—	2	7	4	3															17	11.3
Total	1	2	12	14	7	5															41	11.0
Sarda sarda:																						
North America									6	25	14	7	2	—	1						55	17.6
South America										2	6	2	2	2							14	18.7
NE Atlantic											3	—	4	4							11	19.8
Mediterranean-Black Sea											1	5	7	5	12	2					32	20.9
(Demir 1964, Turkey)									(1	2	31	172	427	247	112	7	1)				(1,000)	(20.3)
Gulf of Guinea-S. Africa											1	1	11	4	10	1					28	20.9
Total									6	27	25	15	26	15	23.	3					140	19.3
Gymnosarda unicolor:																						
Indian Ocean						3	4	1													8	12.7
W Pacific					1	7	13														21	12.6
Total					1	10	17	1													29	12.6
Allothunnus fallai																	(72-73-74-75-76-80)				6	75.0

FIGURE 30.—Left premaxillae of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

FIGURE 31.—Left maxillae of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

the maxillae of *Cybiosarda* and *Orcynopsis* are more pointed than in the other bonitos.

Supramaxilla.—The supramaxilla covers the posterior part of the maxilla and is partly covered anteriorly by the lachrymal (see Figure 9). It has a flat oval posterior main body and an anterior process which forms a shelf on the inner surface of the bone that continues as a ridge posteriorly. *Allothunnus* has a smoother dorsal margin and a more gradual transition between the process and the body giving the bone a more triangular shape (Figure 32h). The posterior edge of the supramaxilla of *Gymnosarda* is more curved and the anterior process is blunter (Figure 32g). *Orcynopsis* has a much deeper main body than *Cybiosarda*. Godsil (1954) used the width of this bone (called auxiliary maxillary) to separate *Sarda chiliensis* from *S. orientalis* in the eastern Pacific. He found the bone to be much narrower in relation to length in *S. orientalis* (ratio of width to length 4.1-4.4) than in northeast Pacific *S. chiliensis* (ratio 3.0-3.1). We also found that the main body of the supramaxilla is broader in *S. chiliensis* and narrower in *S. orientalis*. There do not appear to be any significant differences between northeast and southeast Pacific populations of *S. chiliensis* or between Indo-West Pacific and eastern Pacific *S. orientalis* in this character. *Sarda sarda* and *S. australis* have the supramaxilla intermediate in width between the wide bone present in *S. chiliensis* and the narrow bone in *S. orientalis*.

Dentary.—The dentary divides posteriorly into a dorsal dentigerous branch and a ventral branch,

which are usually about equal in length, although the ventral branch is slightly longer in *Gymnosarda* and *Allothunnus* and sometimes in *Sarda* (Figure 33e, f). *Allothunnus* has a row of numerous (40-50) tiny teeth on the dentary while the other genera have fewer (10-25) strong conical teeth. The number of teeth varies among genera and species (Table 6). The shape of the anterior margin of the dentary can be used to divide the bonitos into three distinct groups. The anterior margin of the bone forms an acute angle with the dentigerous dorsal margin in *Sarda*, and there is a notch present at the upper portion of the anterior margin. The notch is deeper and located in the middle of the margin in *Allothunnus* (Figure 33f). *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* lack an anterior notch (Figure 33a, b, e). Another notch is present in *Gymnosarda*, on the anterior part of the ventral margin; there is a slight depression in this position in the other genera of bonitos. In overall shape and size, the dentary of *Sarda* is more elongate, especially that of *S. orientalis*. The angle between the dorsal and ventral arms of the dentary is slightly greater in *Gymnosarda*. The dorsal branch is wider, flatter, and thinner in *Allothunnus*.

Angular and Retroarticular.—The triangular anterior end of the angular (frequently called articular) fits into the dentary anteriorly (Figure 9). *Allothunnus* has the most elongate angular (Figure 34f). The strongest angular is found in *Gymnosarda* (Figure 34e) followed by *Cybiosarda* and *Orcynopsis* (Figure 34a, b). An anteriorly projecting spine is present on the ventral edge of the angular. This spine is thin and weak in
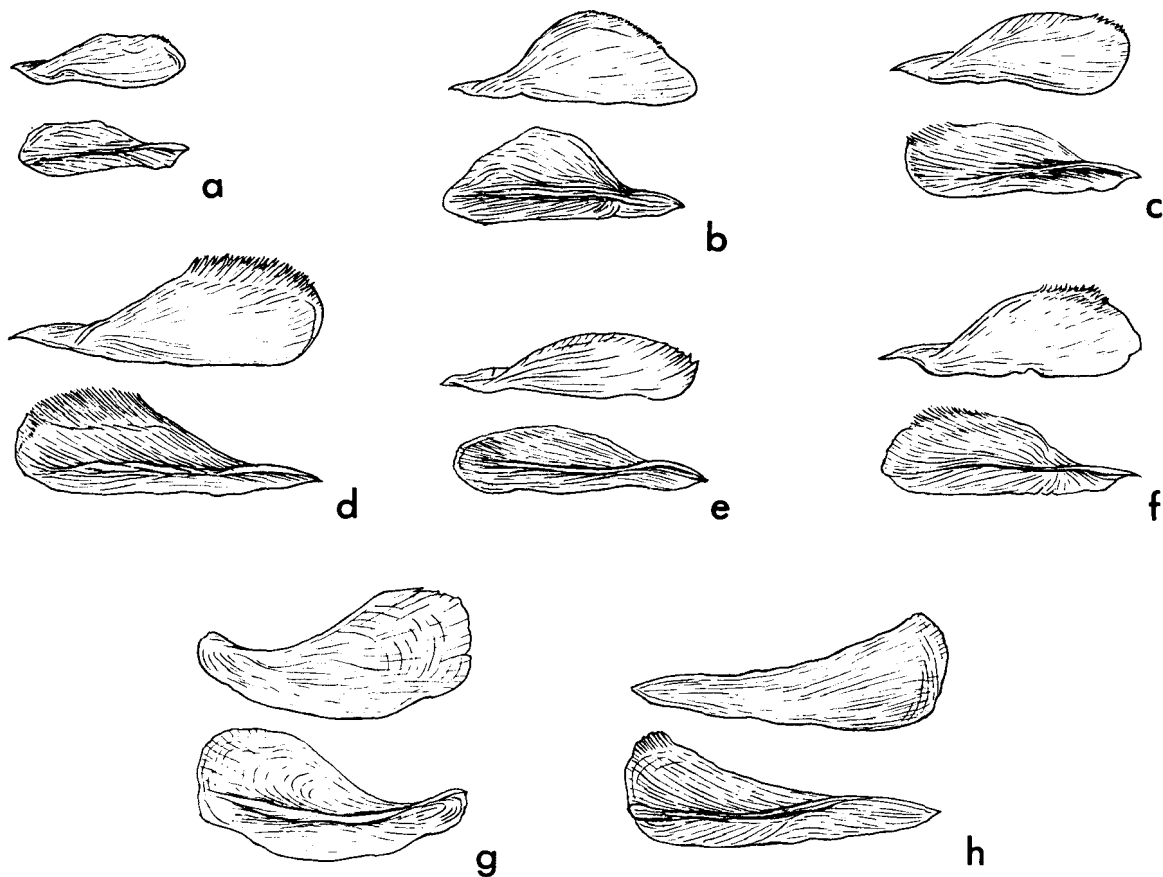
FIGURE 32.—Left supramaxillae of eight species of Sardini, upper figure of each pair is the external view, lower the internal view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 453 mm FL. d. *Sarda chiliensis*, Callao, Peru, 571 mm FL. e. *Sarda orientalis*, Jalisco, Mexico, 434 mm FL. f. *Sarda sarda*, Tunisia, 504 mm FL. g. *Gymnosarda unicolor*, Truk Islands, 787 mm FL. h. *Allothunnus fallai*, Tasmania, 775 mm FL.
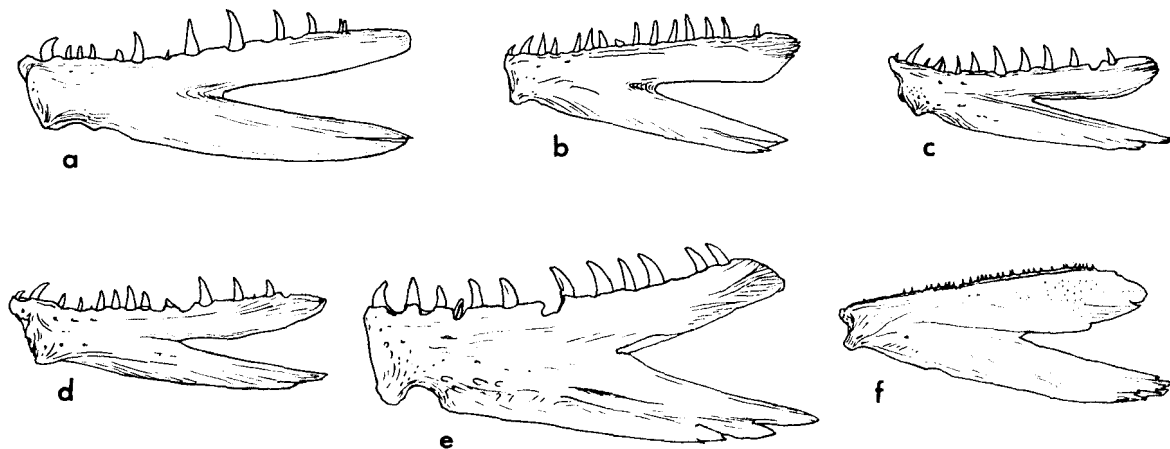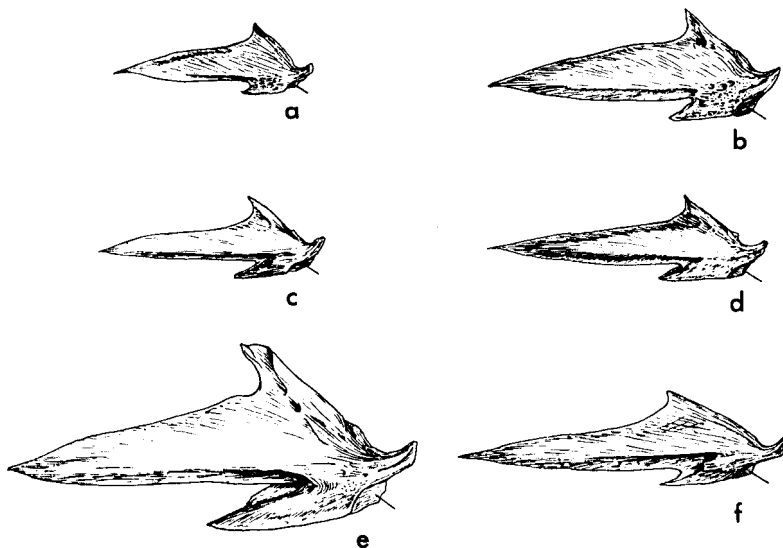
FIGURE 34.—Left angulars and retroarticulars of six species of Sardini, external view. Line indicates position of retroarticular. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

Allothunnus as in *Thunnus*. There is also an anterodorsally projecting spine on the dorsal edge of the angular. This spine has a sharp point in the bonitos, except in *Gymnosarda* where the spine is heavier and blunt as in *Scomberomorus*. The retroarticular bone (frequently called angular) is rhomboid and attached firmly to the posteroventral margin of the angular. No differences were found among the retroarticulars of the bonitos.

PALATINE ARCH.—The palatine arch consists of four pairs of bones in the roof of the mouth: palatine, ectopterygoid, entopterygoid, and metapterygoid.

Palatine.—For illustration (Figure 35), the palatine bones were placed flat with the external side up and tipped so that when viewed from above the palatine teeth and part of the anterior end of dorsal ridge were exposed. A longer ventral ridge and a shorter dorsal ridge are present as in *Thunnus*. *Cybiosarda, Orcynopsis, Gymnosarda,* and
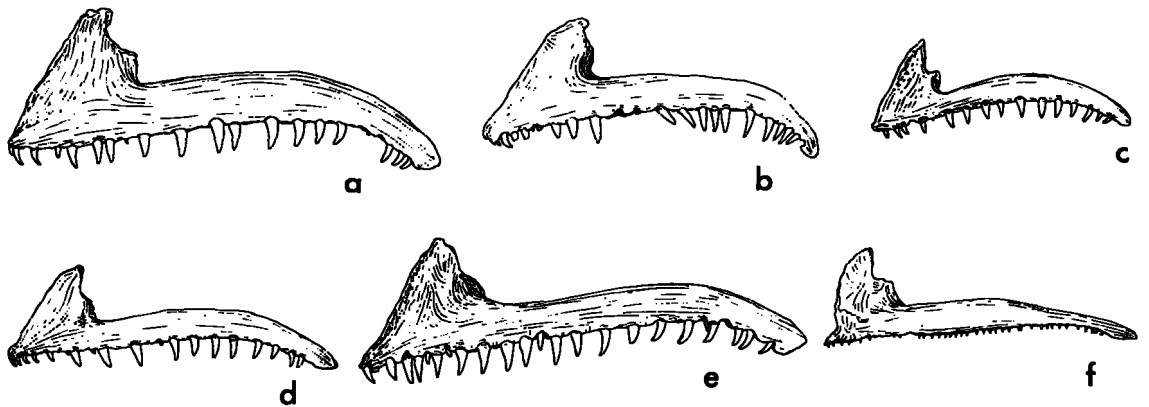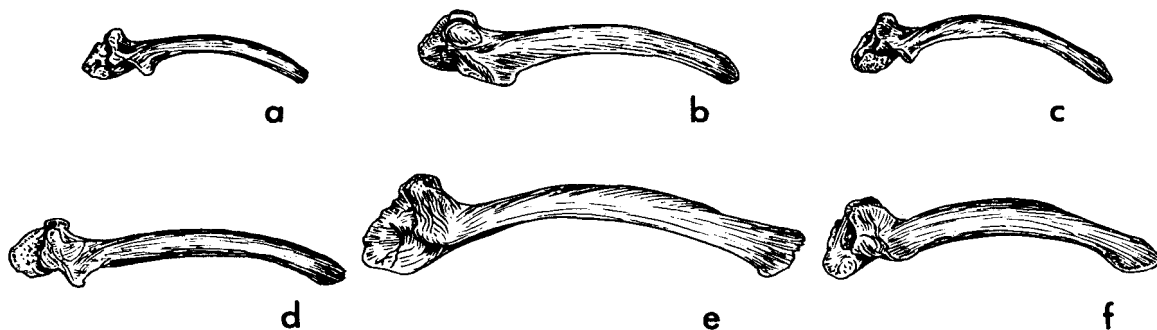
FIGURE 33.—Left dentaries, external view, of six species of Sardini. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 495 mm FL. d. *Sarda orientalis*, Tokyo, 500 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 775 mm FL. f. *Allothunnus fallai*, Tasmania, 775 mm FL.

Allothunnus have slightly elongated dorsal ridges compared to *Sarda* (Figure 35c, d). The anterior process of the dorsal ridge is hooked in all bonitos except *Allothunnus* in which the distance between the process and the front of the ventral ridge is greater (Figure 35f).

Teeth are located along the inferior margin of the ventral ridge. Palatine teeth vary from a relatively few, large, conical teeth curved posteriorly and arranged in a single row to a broad roughened patch of tiny villiform teeth. Species of *Sarda* have one row of small conical teeth, the number of teeth varying from 7 to 22, usually 10-18. *Sarda chiliensis* has the most palatine teeth (9-22, $\bar{x}$ 15.2) but it broadly overlaps with the other three species: *S. sarda* (8-21, $\bar{x}$ 12.3), *S. orientalis* (8-19, $\bar{x}$ 11.9), and *S. australis* (7-14, $\bar{x}$ 10.7). *Cybiosarda* has about 50 small teeth in two or three rows; *Orcynopsis* about 75 tiny teeth in a patch one or two rows wide posteriorly and about five rows anteriorly; and *Gymnosarda* has an elongate oval tooth patch with hundreds of tiny teeth. There are even more and smaller teeth in *Allothunnus*, so small that Nakamura and Mori (1966) thought they were absent.

Ectopterygoid.—All bonitos have a slender T-shaped ectopterygoid (Figure 36). The ventral

FIGURE 35.—Right palatines of six species of Sardini, internal view rotated slightly to better show palatine teeth. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda orientalis*, Tokyo, 500 mm FL. d. *Sarda chiliensis*, Callao, Peru, 549 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL.
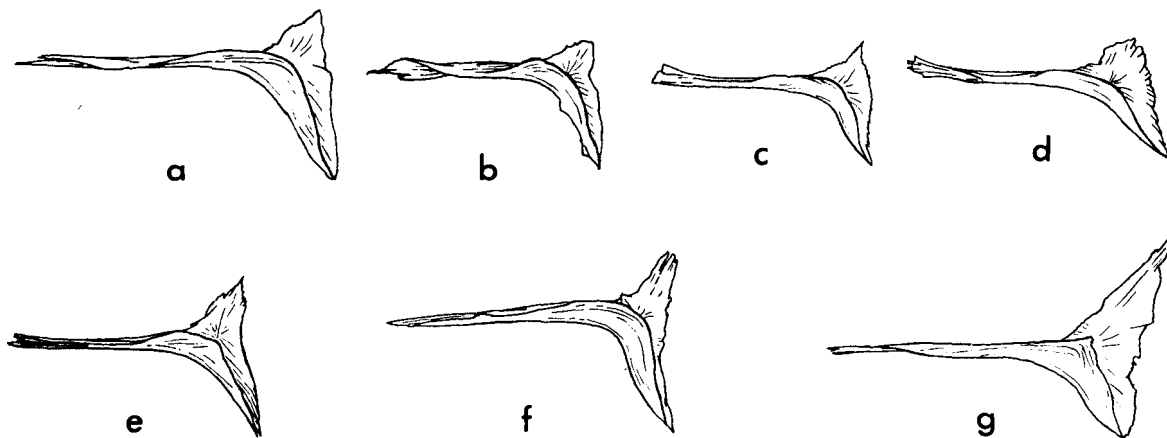
FIGURE 36.—Left ectopterygoids of seven species of Sardini, external lateral view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda sarda*, Tunisia, 504 mm FL. d. *Sarda orientalis*, Tokyo, 500 mm FL. e. *Sarda chiliensis*, Callao, Peru, 549 mm FL. f. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. g. *Allothunnus fallai*, California, 680 mm FL.

projection of the ectopterygoid is longer than the dorsal projection except in *Allothunnus* which has a larger dorsal projection. The ridge extending from the main axis to the tip of the ventral projection has a sharper angle in *Allothunnus* compared to the smooth curve in the other bonitos. The main shaft of the ectopterygoid is thicker and higher in *Gymnosarda* than in the other bonitos. *Sarda orientalis* has the dorsal projection slightly expanded instead of pointed as in the other species of *Sarda*.

Entopterygoid.—The entopterygoid is elongate oval in shape in all the bonitos (Figure 37). The external margin of the entopterygoid is the strongest and thickest part of the bone, and there is a bent posterior end which attaches to the ectopterygoid externally. *Allothunnus* has a more elongate entopterygoid and *Gymnosarda* has a broader one than the other bonitos.
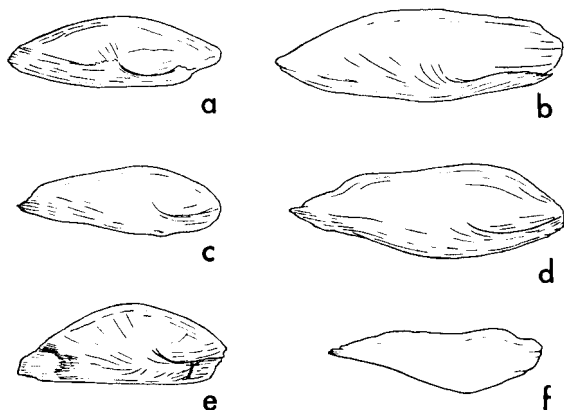
FIGURE 37.—Left entopterygoids of six species of Sardini, dorsal view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 573 mm FL. c. *Sarda australis*, New South Wales, 363 mm FL. d. *Sarda sarda*, Azores, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL. a-d drawn twice as large as e and f.

Metapterygoid.—The posterior and dorsal margins of the metapterygoid articulate with the hyomandibula (Figure 9). A groove is present on almost the entire posterior margin in all bonitos except *Allothunnus*, which has a deeper and wider groove on the upper half of the posterior margin, as in *Thunnus*. *Cybiosarda*, *Orcynopsis*, and *Sarda* have a thin projection along the upper half of the posterior margin extending from the internal surface of the metapterygoid (Figure 38). These three genera also have a posteroventral notch on

the inner surface of the bone into which the anterodorsal process of the symplectic fits. The metapterygoid of *Gymnosarda* is more elongate and triangular in shape and has no projection along the posterior margin. In *Allothunnus*, the anteroventral and posteroventral margins are very similar to those in *Thunnus* (Gibbs and Collette 1967, fig. 7).

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 (basihyal, ceratohyal, epihyal, interhyal,
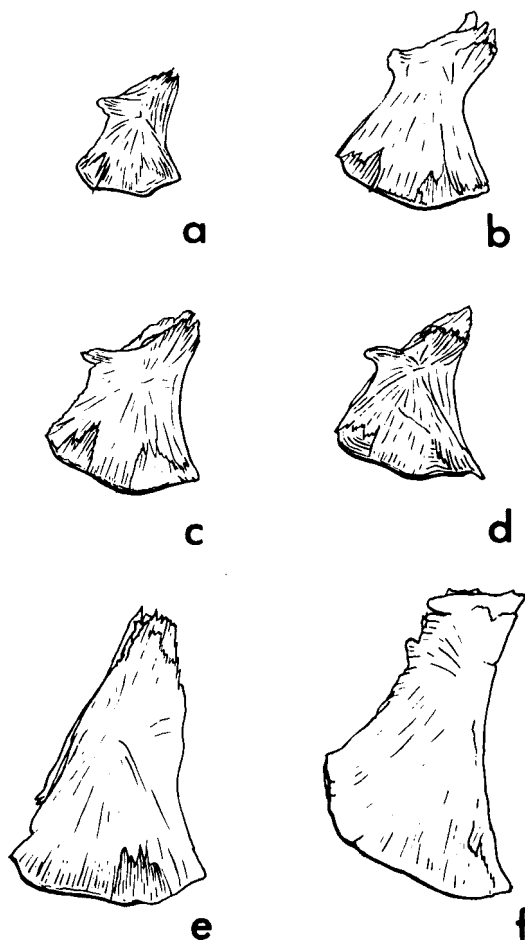
FIGURE 38.—Left metapterygoids of six species of Sardini, internal view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda orientalis*, Tokyo, 500 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL.

561

and the seven branchiostegal rays), and two median unpaired bones, the glossohyal and urohyal.

Hyomandibula.—The hyomandibula is an inverted L-shaped bone that connects the mandibular suspensorium and opercular bones to the neurocranium (Figure 9). Dorsally, there are three prominent condyles. The longest and anteriormost forms the base of the L and fits into the fossa at the junction of the pterotic and sphenotic bones. The dorsal condyle articulates with the ventral fossa of the pterotic and the lateral process is attached to the inside of the opercle. Anterolaterally the hyomandibula joins the metapterygoid; posterolaterally it has a long articulation with the preopercle.

Godsil (1954, 1955) found two differences between the hyomandibula in *Sarda orientalis* and *S. chiliensis*. In both species a spine protrudes posteriorly from the center condyle. The spine forms an angle of 90° or less with the major axis of the hyomandibula in *S. orientalis* and greater than 90° in *S. chiliensis*. We confirm this difference and use the character to divide the bonitos into groups. *Sarda chiliensis, Cybiosarda* (Figure 39a), and *Orcynopsis* (Figure 39b) have the angle greater than 90°; *Gymnosarda* and *Allothunnus* probably belong in this group based on the angle, but the spines are greatly reduced in both genera. *Sarda orientalis* has the angle 90° or less. *Sarda sarda* (Figure 39c) and *S. australis* are intermediate between the two groups in having the angle about 90°.

Godsil used the length of the spine on the ridge of bone next to the groove into which the preopercle fits as a second character to distinguish *S. orientalis* from *S. chiliensis*. The spine is much longer in *S. orientalis* and projects beyond the center condyle when the spine is placed flat with the internal side down. Again we can confirm this difference and note that *S. sarda* agrees with Godsil's description of *S. orientalis*. *Sarda australis* and *S. chiliensis* have the spine short and not protruding. Godsil (1955:34) noted that on one
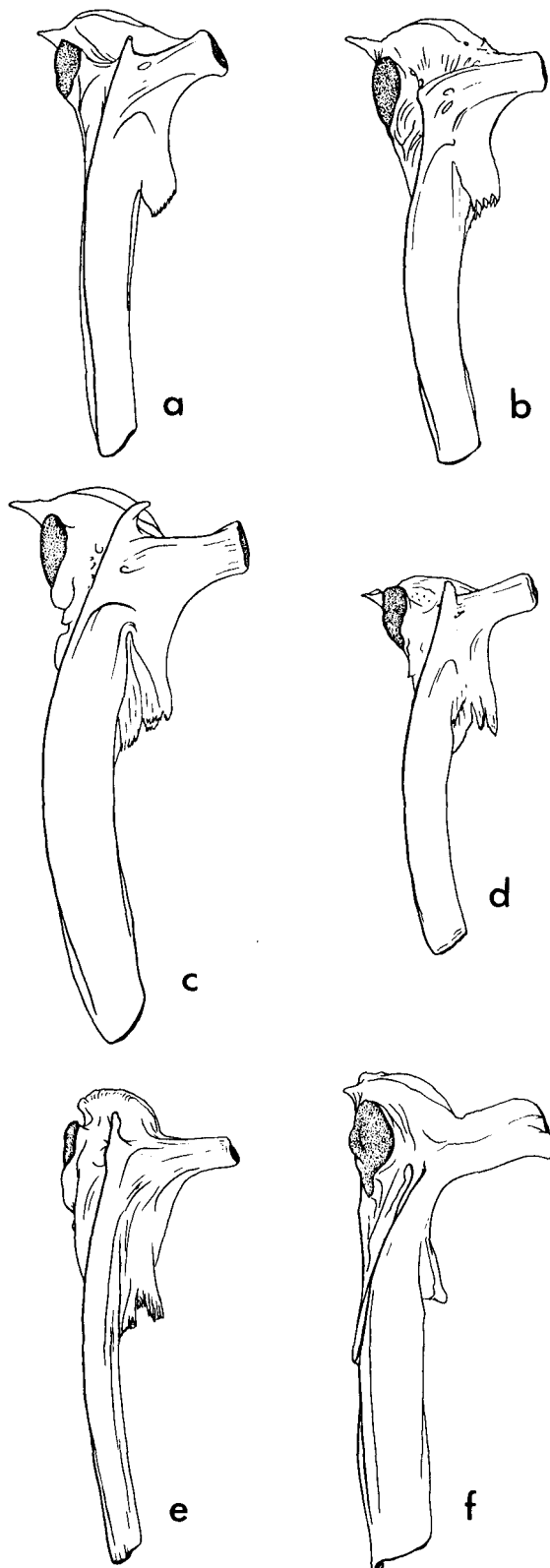
FIGURE 39.—Right hyomandibulae of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda sarda*, Tunisia, 504 mm FL. d. *Sarda australis*, New South Wales, 495 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL. a and c drawn twice as large as e and f, b and d drawn 1.5 times as large.

side of one hyomandibula of a Tokyo specimen of *S. orientalis*, the spine was short as in *S. chiliensis*. We found one specimen of *S. chiliensis* from Callao, Peru in which the spine projected as in *S. orientalis*. Thus, this difference is not absolute but "corroboratory" as Godsil has noted. *Cybiosarda* (Figure 39a) and *Gymnosarda* (Figure 39e) resemble *S. chiliensis* but the spine is still shorter. The ridge forms an angle but no spine is present in *Orcynopsis* (Figure 39b) and *Allothunnus* (Figure 39f).

The lateral condyle is broader in *Allothunnus* than in other bonitos, and its lower anterior vertical margin, where the metapterygoid attaches, does not project as far (Figure 39f). Also, the groove into which the preopercle fits is more curved in *Allothunnus*.

Symplectic.—The symplectic is a small bone that fits into a groove in the quadrate (Figure 9). Bonitos fall into three groups based on the shape of the symplectic. *Orcynopsis*, *Cybiosarda*, and *Sarda* (Figure 40a-d) have a wider upper part with a pointed or "flared" anterodorsal projection as in *Thunnus*. *Gymnosarda* has a rather thick upper part and only a slight lateral expansion about the middle of the anterior margin (Figure 40e). The anterolateral expansion of the symplectic is better developed in *Allothunnus* (Figure 40f) than in *Gymnosarda*, but there is no anterior projection at the upper end.

In external view, there is a longitudinal axis to the symplectic which is shaped differently in the three groups. *Gymnosarda* has a much thicker upper end. The upper part is also thick but somewhat flattened in *Allothunnus* as also noted by Nakamura and Mori (1966). *Orcynopsis*, *Cybiosarda*, and *Sarda* all have a notch at about the middle of the axis on the external surface of the bone which is absent in *Gymnosarda* and *Allothunnus*.

Quadrate.—The lower jaw is suspended from the cranium by means of the articulating facet of the ventral surface of the triangular quadrate (Figure 9). The quadrates are similar in all bonitos, with a deep groove where the symplectic fits along the inner posterior margin and a posterodorsal process (Figure 41). The quadrate of *Allothunnus* has a distinctly longer posterodorsal process resembling those in *Thunnus*. The process in *Gymnosarda* (Figure 41e) has a slightly broader tip and also its
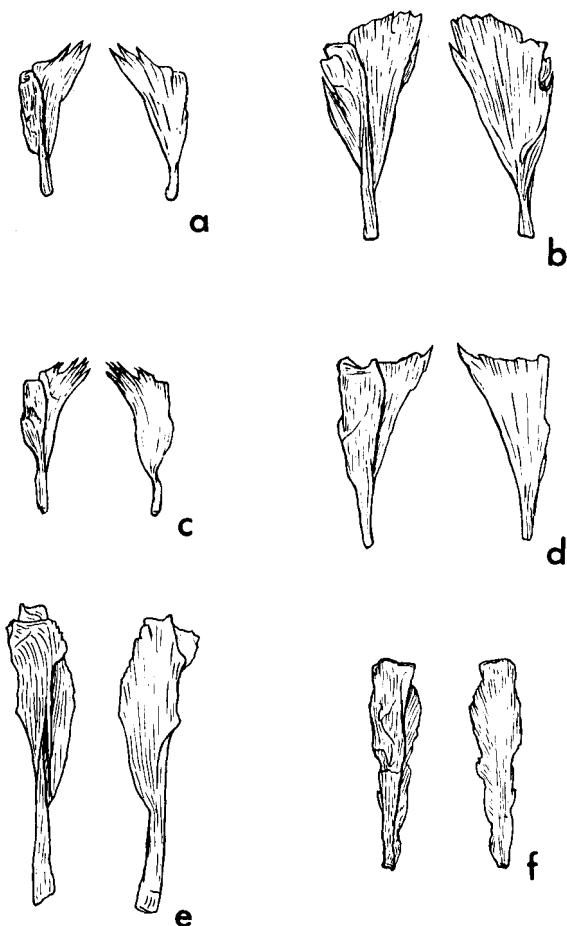
FIGURE 40.—Right symplectics of six species of Sardini, left figure of each pair is the external view, right the internal view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 573 mm FL. c. *Sarda australis*, New South Wales, 363 mm FL. d. *Sarda chiliensis*, Callao, Peru, 437 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 775 mm FL. f. *Allothunnus fallai*, Tasmania, 775 mm FL. a-e drawn twice as large as f.
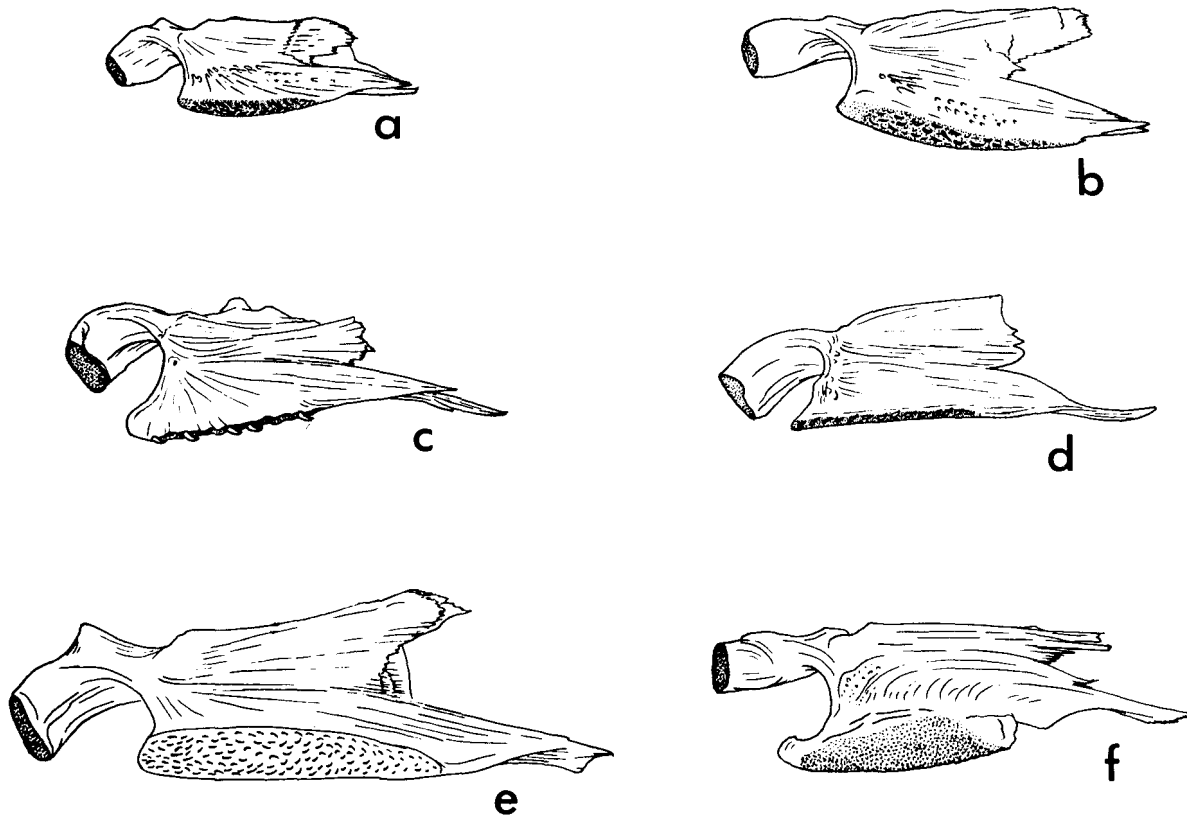
base is expanded more than in other genera of bonitos.

Hyoid Complex.—This complex, as discussed here, includes the hypohyal, ceratohyal, epihyal, and interhyal bones and the seven branchiostegal rays (Figure 42). The external view of the four bones in *Sarda orientalis* and *Gymnosarda unicolor* has been previously illustrated by Kishinouye (1923:326) along with the hyoid arches of six other genera of Scombridae.

The hypohyal is composed of a dorsal and a ventral segment fused longitudinally along a

FIGURE 41.—Right quadrates of six species of Sardini, internal view to show groove for symplectic. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda sarda*, Florida, 333 mm FL. d. *Sarda australis*, New South Wales, 495 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

elliptical ceratohyal window (Nakamura and Mori 1966, fig. 6), except for *Sarda orientalis* which has only a trace of a depression at the appropriate site (Figure 42d). A deep groove extends along the upper third of the ceratohyal from the depression of the hypohyal to the middle of the epihyal in *Gymnosarda*, but there is only a slight trace of this groove in the other bonitos.

The epihyal is a triangular bone which interlocks medially with the ceratohyal. This serrated interlocking suture is limited to the inner surface of the bone in *Cybiosarda*, *Orcynopsis*, and *Sarda* (Figure 42 a-d); there are only cartilaginous connections between these two bones on the outer surface, as in *Thunnus* (de Sylva 1955, fig. 36). *Gymnosarda* and *Allothunnus* also have well-developed interlocking sutures on the outer surface (Figure 42 e, f). The epihyal bears a small condyle on its posterior end that articulates with the inner surface of the interopercle. The fifth to seventh branchiostegal rays are attached to the outer surface of the ventral margin of the epihyal. The fifth branchiostegal is at the junction of the epihyal and ceratohyal in *Gymnosarda* and is a short distance behind the junction in other bonitos.

The interhyal is a small bone with an expanded ventral end that is attached to the epihyal dorsal to the epihyal condyle. The interhyal is attached, with connective tissue, to the symphysis of the hyomandibula, quadrate, symplectic, metapterygoid, and preopercle. The interhyal also articulates above the interopercular fossa posteriorly.

Glossohyal.—The glossohyal is a spatulate bone underlying the tongue and overlying the first basibranchial bone at the anterior end of the branchial arch (see Figure 49). *Cybiosarda* and *Orcynopsis* have a pair of oval tooth patches on the dorsal surface of the glossohyal (Figure 43a, b). *Gymnosarda* also has a pair of tooth patches on the tongue, but they are on plates over the glossohyal and are not fused to the bone (Figure 43f). The ventral surface of the tooth patches of *Gymnosarda* have a deep longitudinal ridge which fits the ventral ridge of the glossohyal laterally. On the dorsal surface of the glossohyal of *Gymnosarda*, there is a prominent longitudinal ridge on which the paired tooth patches meet. The size of the tooth patches may vary from one side to the other as in the specimen of *Orcynopsis unicolor* illustrated (Figure 43b). *Sarda* lacks tooth patches (Figure

serrated suture that is most prominent in *Gymnosarda* (Figure 42e). There is a depression on the outer surface at the posterior half of the suture in all bonitos, as in *Thunnus*. Internally, a lateral process at the anterodorsal end forms a symphysis with the glossohyal, urohyal, basibranchial, and the process of the hypohyal from the opposite side.

The ceratohyal is a long flat bone, broader at the posterior end and with an anteroventral projection that articulates with the posteroventral notch of the hypohyal. The middle portion of the ceratohyal is concave dorsally in all bonitos. There are three notches along the ventral margin where the anterior three branchiostegal rays attach. Bonitos have no notch at the site of attachment of the fourth branchiostegal ray. All bonitos have an

FIGURE 42.—Hyoid complex (hypohyal, ceratohyal, epihyal, and interhyal) and branchiostegal rays of six species of Sardini, external view of left side. Unlabelled line points to ceratohyal window. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 543 mm FL. c. *Sarda australis*, New South Wales, 495 mm FL. d. *Sarda orientalis*, Panama, 415 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 787 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL.

43c-e) and the shape and proportions of the glossohyal is extremely variable both inter- and intraspecifically as Godsil (1955) has pointed out for *S. chiliensis* and *S. orientalis*. A slightly concave anterior margin is present on the glossohyal of *Allothunnus*. A depression on the ventral surface of the proximal portion of the glossohyal is present in most bonitos except for *Sarda orientalis* (Godsil 1954, 1955) and *Gymnosarda*.

Urohyal.—The urohyal is a median unpaired bone. The anterior end of this element lies between, and is connected with, the hypohyals of the left and right sides. The urohyals of the bonitos have a thickened anteroventral margin which gradually narrows posteriorly (Figure 44). *Gymnosarda* has a distinctive thickened posterodorsal margin, which starts at the anterior third of the bone and forms a flattened platform at the posterior end. A similar tendency was found occasionally in other bonitos, especially *Orcynopsis*, but the thickening was limited to the middle portion of the dorsal margin. *Cybiosarda, Orcynopsis,* and *Gymnosarda* have relatively deep urohyals; *Sarda* and *Allothunnus* have relatively elongate urohyals.

565
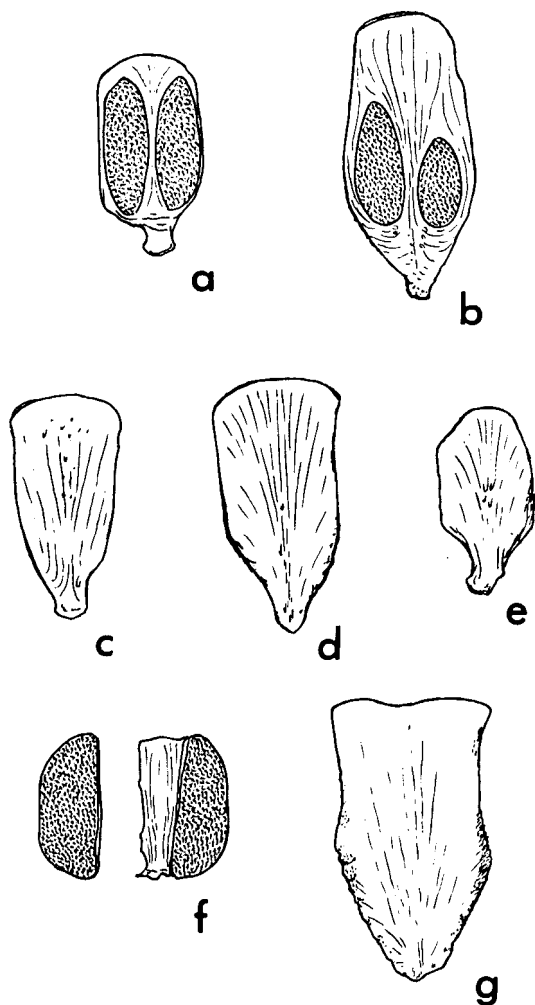
FIGURE 43.—Dorsal view of glossohyals of seven species of Sardini. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL, note unequally developed tooth patches. c. *Sarda australis*, New South Wales, 495 mm FL. d. *Sarda chiliensis*, Callao, Peru, 549 mm FL. e. *Sarda sarda*, Tunisia, 504 mm FL. f. *Gymnosarda unicolor*, Truk Islands, superficial tooth plate removed from left side of bone. g. *Allothunnus fallai*, California, 680 mm FL. a-e and g drawn twice the size of f.

FIGURE 44.—Urohyals of five species of Sardini, in left lateral view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda chiliensis*, Callao, Peru, 549 mm FL. d. *Gymnosarda unicolor*, Truk Islands, 787 mm FL. e. *Allothunnus fallai*, California, 680 mm FL. a drawn twice as large as b-e.

projections which extend beyond the posterior notch and their dorsal margins are flat or slightly concave (Figure 45a-d). *Allothunnus* has no distinct lower projection (Figure 45f).

Subopercle.—The subopercle is similar among bonitos and generally resembles those of scombrids such as *Thunnus*. *Cybiosarda*, *Orcynopsis*, and *Sarda* (Figure 46a-d) have two ridges that converge posteriorly from the anterior projection. 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 ridges are much stronger

OPERCULAR APPARATUS.—Four wide flat bones fit together to form the gill cover which protects the underlying gill arches.

Opercle.—The opercle is broad and more or less rectangular in shape in all bonitos except *Gymnosarda*, in which it is narrower, elongate, and more triangular (Figure 45e). *Cybiosarda*, *Orcynopsis*, and *Sarda* have similar lower posterior
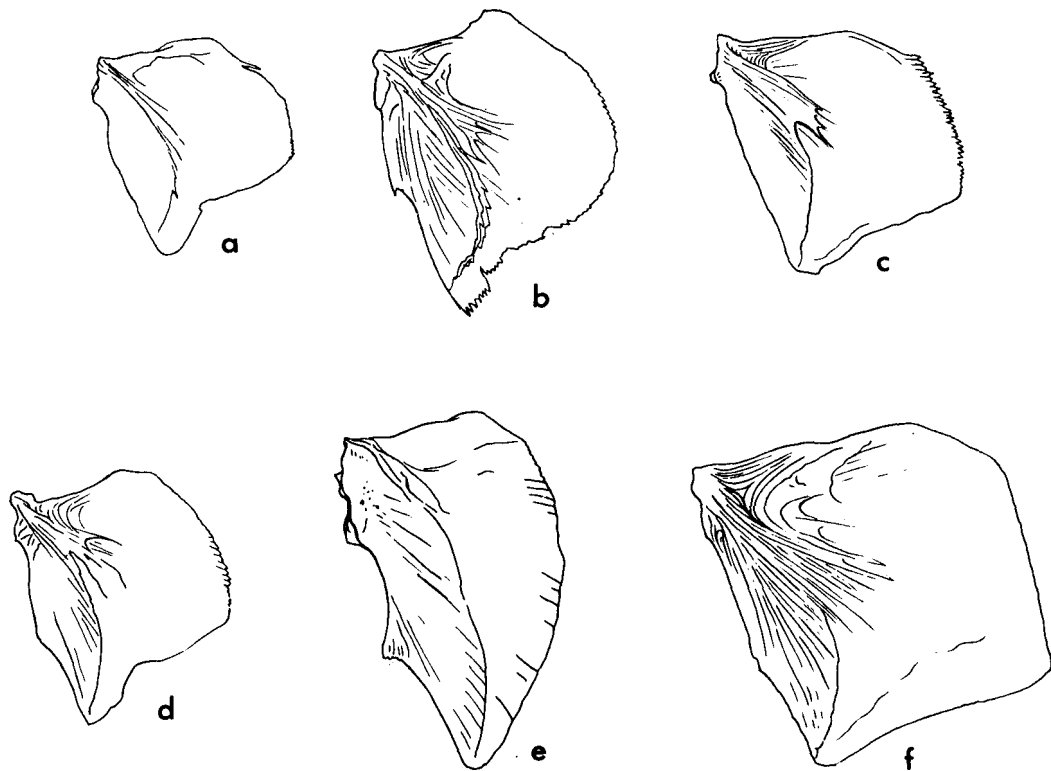
FIGURE 45.—Left opercles of six species of Sardini, external view. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda orientalis*, Tokyo, 500 mm FL. d. *Sarda australis*, New South Wales, 495 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

in *Cybiosarda* and *Orcynopsis* than in the species of *Sarda*. A trace of these ridges is discernible in *Allothunnus* and the bone is much thinner than in other genera. *Gymnosarda* (Figure 46e) has no ridges and the entire subopercle is more elongate than in other bonitos.

Preopercle.—The elongate preopercle is thickened along its inner surface for attachment with the hyomandibula (see Figure 9). The preopercles are similar in *Cybiosarda*, *Orcynopsis*, and the species of *Sarda* (Figure 47a-d). The dorsal projecting arm is somewhat longer and narrower in the species of *Sarda* than in *Cybiosarda* and *Orcynopsis*. As is true of the subopercle, the preopercle of *Gymnosarda* (Figure 47e) is long and narrow compared to the previous three genera. *Allothunnus* (Figure 47f) has a preopercle much more similar to *Thunnus* (de Sylva 1955:17, fig. 28)

than to other bonitos. It is divided into superior and inferior arms which are approximately equal in length instead of the superior arm being longer than the inferior arm.

Interopercle.—The interopercle is roughly shaped like an elongate triangle, with a narrow anterior end. Most of the outer surface of the anterodorsal portion of the interopercle is covered by the preopercle. On the inner surface, beneath the middle of the anterodorsal margin of the interopercle, there is a condyle, which articulates with the posterior end of the epihyal and the interhyal. The anterior and posterior ends of the interopercle are narrowest in *Allothunnus* and broadest in *Gymnosarda* (Figure 48). The thinnest part of the interopercle is along the ventral margin, and a weak fimbriate posterior margin is present in all the bonitos as in *Thunnus*.

567
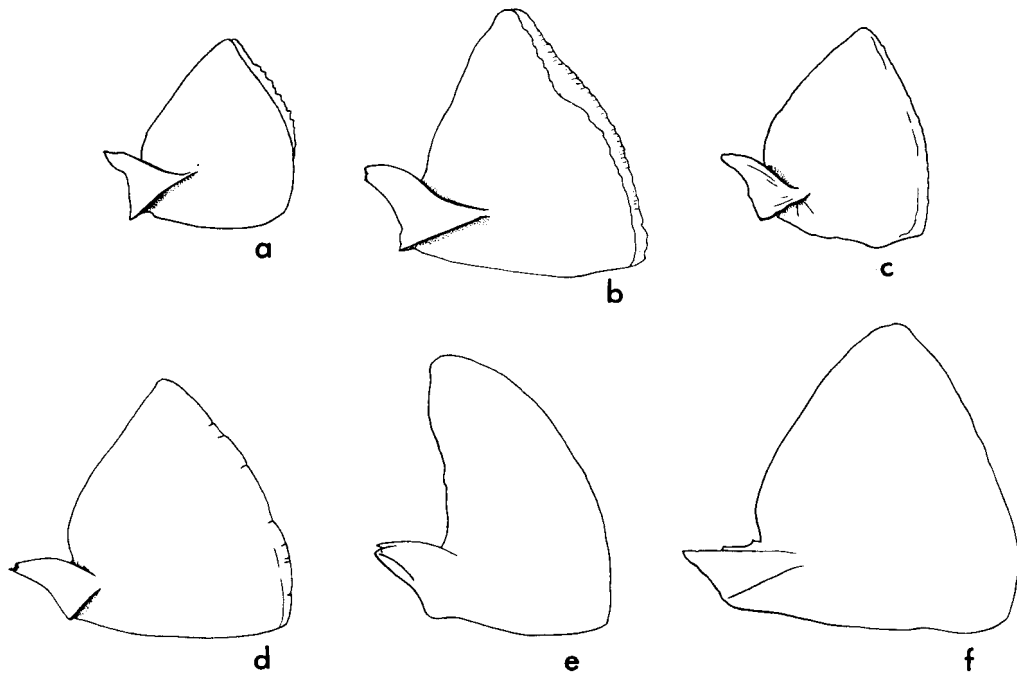
FIGURE 46.—Left subopercles of six species of Sardini, external view. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 405 mm FL. d. *Sarda chiliensis*, Callao, Peru, 549 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

BRANCHIAL ARCH.—The branchial arch is composed of the five pairs of gill arches: gill filaments, gill rakers, pharyngeal tooth patches, and supporting bones. The general arrangement in the Sardini (Figure 49) is similar to that found in other scombrids such as *Thunnus* (Iwai and Nakamura 1964a: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 Sardini, the most important generic and specific differences are in the number of gill rakers. All of the branchial bones bear patches of tiny teeth.

Basibranchials.—The three basibranchials form a chain from anterior to posterior. The first and second are about the same size and considerably shorter than the third. The first basibranchial is covered dorsally by the broad, flattened glossohyal which is dentigerous in *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* as described in the hyoid arch section.

In lateral view (Figure 50), the first basibranchial has an expanded anteroventral end and is curved downward except in *Allothunnus* (Figure 50f). The second basibranchial has a prominent notch in the ventral margin that is absent in *Allothunnus*. The third basibranchial has an expanded anterior end at its junction with the second basibranchial and then tapers posteriorly. A section of cartilage extends posteriorly to articulate with the fourth ceratobranchial and lower pharyngeal.

Hypobranchials.—The first three arches have hypobranchials which connect with the ceratobranchials. The first hypobranchial is attached to the second basibranchial; the second and third hypobranchials are attached to the third basibranchial. The first two hypobranchials are longer than the third.

Ceratobranchials.—The ceratobranchials are the longest bones in the branchial arch and support most of the gill filaments and gill rakers. The first three are morphologically similar and articulate

FIGURE 48.—Left interopercles of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 573 mm FL. c. *Sarda australis*, New South Wales, 475 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

FIGURE 47.—Left preopercles of six species of Sardini, external view. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 495 mm FL. d. *Sarda chiliensis*, Callao, Peru, 517 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

with small conical teeth that are directed slightly posteriorly. *Allothunnus* has the smallest pharyngeal teeth among the bonitos.

Epibranchials.—The four epibranchials are attached basally to the ceratobranchial of their respective gill arch. They vary in shape with the first one being long and slender like a short ceratobranchial, the second and third shorter and stubbier, and the fourth one almost V-shaped.

Pharyngobranchials.—There are four pharyngobranchials attached basally to the epibranchial of their respective gill arch. The recurved first one articulates dorsally with the parasphenoid and is frequently referred to as the suspensory pharyngeal (Iwai and Nakamura 1964a). The triangular second pharyngobranchial bears a patch of small teeth. The third and fourth pharyngobranchials both have dermal tooth plates fused to them and are termed upper pharyngeal bones.

Gill Rakers.—The hypobranchial, ceratobranchial, and epibranchials 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. Gill rakers prevent food loss through the opercular gap. There is a correlation between numbers of gill rakers, gap between gill rakers, and size of food items as

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

569
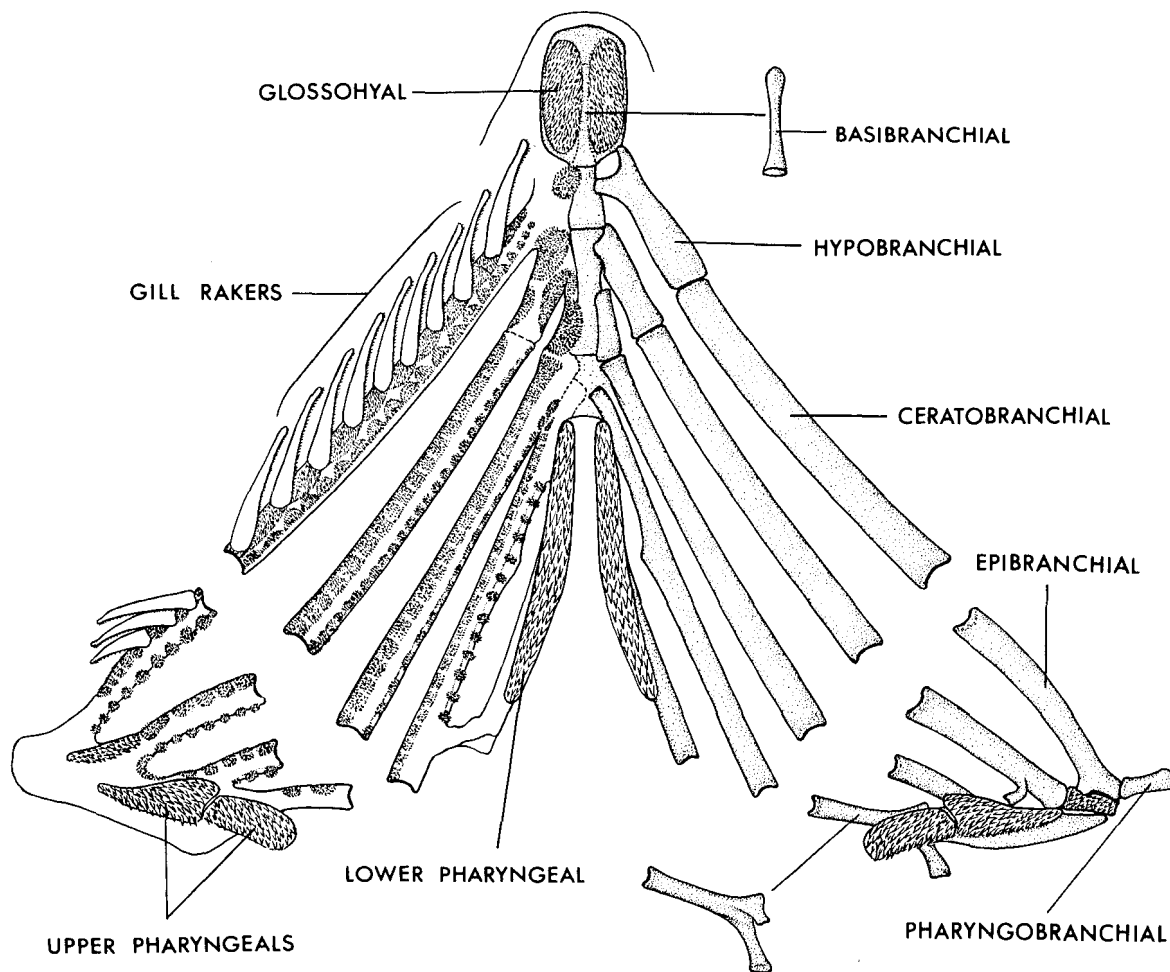
FIGURE 49.—Branchial arch of *Cybiosarda elegans*. Dorsal view of the gill arches with the dorsal halves folded back to show their ventral aspect. Epidermis removed from right hand side to reveal underlying bones.
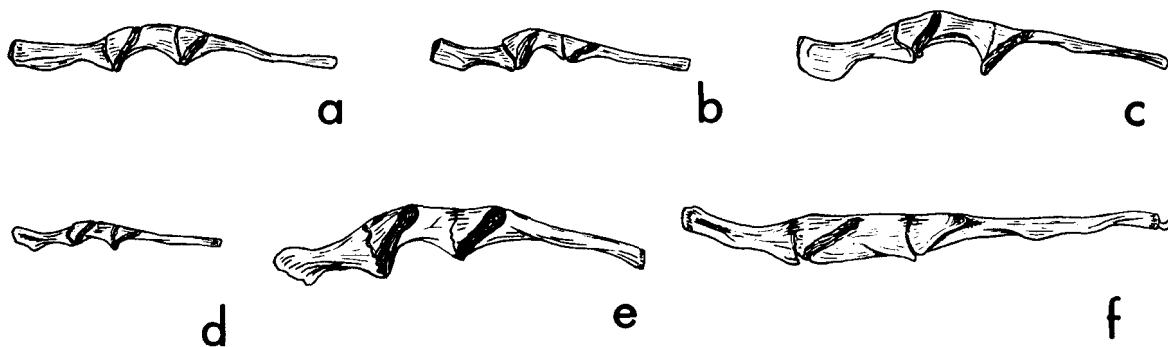
FIGURE 50.—Left lateral view of the three basibranchial bones in six species of Sardini. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 593 mm FL. c. *Sarda sarda*, Azores, 418 mm FL. d. *Sarda australis*, New South Wales, 407 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL. a-c drawn twice as large as d-f.

Magnuson and Heitz (1971) have clearly shown for a number of species of Scombridae. The number of gill rakers is easily countable and is an important taxonomic character in the Sardini as well as among other groups of the Scombridae.

Allothunnus differs strikingly from other bonitos in having many more gill rakers on the first arch, 72-80 compared to 8-27 (Table 7). The only other scombrids that approach this high number of gill rakers are *Katsuwonus pelamis* with 53-63 and two species of the genus *Rastrelliger*, *R. kanagurta* (Cuvier) and *R. brachysoma* (Bleeker), with 48-68. As discussed under dentition, the high number of gill rakers in *Allothunnus* is correlated with a high number of teeth in both upper and lower jaws.

Cybiosarda, *Orcynopsis*, and *Gymnosarda* all have few gill rakers (11-17), fewer than any other bonitos except *Sarda orientalis* (8-13).

Number of gill rakers is a valuable character within the genus *Sarda*. The largest difference is between *S. orientalis* (8-13) and *S. chiliensis* (23-27), which is particularly useful in the eastern Pacific where the tropical *S. orientalis* can be separated from *S. chiliensis* to the north and south on the basis of fewer gill rakers (and, in a similar fashion, jaw teeth). *Sarda australis*, which has been considered a subspecies of *S. chiliensis* by many authors, is intermediate in number of gill rakers (19-21) between *S. chiliensis* and *S. orientalis* but completely separated from both. There are also differences below the species level: *Sarda sarda* in the western Atlantic averages fewer (North America, 17.6; South America, 18.7) gill rakers than the other four populations, especially

the Mediterranean—Black Sea (20.9) and Gulf of Guinea (20.9).

Inner Gill Rakers.—The inner surface of the hypobranchial, ceratobranchial, and epibranchial bones of the first gill arch supports a series of tubercles, the inner gill rakers. The strongest tubercle usually occurs at or near the junction of the upper and lower arches on the lower arch. The number of inner gill rakers (Table 8) is correlated with the number of gill rakers on the first gill arch (Table 7). *Allothunnus* has the longest, thickest, and most numerous inner gill rakers (49-56). In many specimens of *Cybiosarda elegans* and *Sarda orientalis* the inner gill rakers are degenerate with only a few small tubercles present. We agree with Godsil (1954, 1955) that the counts are difficult to make in *Sarda* with any consistency. Godsil used the presence of the inner gill rakers ("gill teeth") as a character to distinguish *Sarda chiliensis* from *S. orientalis* in the eastern Pacific. *Gymnosarda* completely lacks inner gill rakers, but many small conical teeth are present around the base of the gill rakers. These small teeth are also present around the base of the gill rakers in the other bonitos but they are much smaller than in *Gymnosarda*.

AXIAL SKELETON

This section is divided into six parts: vertebral number, vetebral column, infracentral grooves, ribs and intermuscular bones, caudal peduncle keels, and caudal complex.

TABLE 8.—Total number of inner gill rakers on the first gill arch in species of Sardini.

Species	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	$\bar{x}$
Cybiosarda elegans		1	1	—	—	1	—	—	—	—	2	1	—	—	1											7	10.6
Orcynopsis unicolor														2	3	2	1	3	—	2	2	—	—	—	1	16	19.8
Sarda australis												1	—	—	2	2	3	4	2	2	1	1				18	18.6
Sarda chiliensis:																											
NE Pacific															4	3	7	4	1	3	—	1				23	18.4
SE Pacific												1	1	1	2	1	2	3	2	4	1	1	1			20	19.9
Total												1	1	5	5	8	6	4	5	4	2	1	1			43	19.1
Sarda orientalis:																											
Indo-West Pacific	1	1	1	—	—	—	—	—	—	—	—	—	—	1	1											5	9.0
E Pacific		1	—	—	1	—	1	1	1	1	1	—	—	—	—	—	—	—	—	—	—	1				8	12.4
Total	1	2	1	—	1	—	1	1	1	1	1	—	—	1	1	—	—	—	—	—	—	1				13	10.8
Sarda sarda:																											
W Atlantic							3	—	3	1	4	1	9	3	—	3	2	1								30	14.3
E Atlantic											2	1	1	2	4	2	2	2	—	2						18	17.4
Total							3	—	3	1	6	2	10	5	4	5	4	3	—	2						48	15.5
Allothunnus fallai																		(49-52-54-55-56)								5	53.2

Vertebral Number

Vertebrae may be divided into precaudal (abdominal) and caudal. The first caudal vertebra is defined as the first vertebra that bears a notably elongated haemal spine and lacks pleural ribs. Vertebral counts include the ural centrum which bears the hypural plate.

As with dorsal spines, the bonitos fall into three groups based on total number of vertebrae (Table 9): few vertebrae (37-39) in *Orcynopsis, Gymnosarda,* and *Allothunnus;* moderate number (42-48) in *Cybiosarda* and three species of *Sarda;* and many (50-55) in *S. sarda.* These groups can be

further subdivided by dividing the total count into precaudal plus caudal. *Orcynopsis* usually has $18 + 20 = 38$; *Gymnosarda* $19 + 19 = 38$; and *Allothunnus* $20 + 19 = 39$. *Cybiosarda* has more, usually $(22\text{-}23) + (24\text{-}25) = 47$, than the middle group of *Sarda* species, which usually have $(23\text{-}25) + (20\text{-}22) = 44\text{-}45$. Precaudal, caudal, and total counts all vary more in *S. sarda* than in other species of bonitos.

Vertebral Column

The neural arches and spines are stout and laterally flattened on the first to fifth vertebrae in

TABLE 9.—Numbers of precaudal, caudal, and total vertebrae in species of Sardini.

Species	Precaudal vertebrae
	17	18	19	20	21	22	23	24	25	26	27	28	N	x̄
Orcynopsis unicolor	2	27											29	17.9
Cybiosarda elegans						5	6	2					13	22.8
Sarda australis							1	11					12	23.9
Sarda chiliensis:														
NE Pacific							2	34	9				45	23.2
SE Pacific							5	13	1				19	22.8
Total							7	47	10				64	23.0
Sarda orientalis:														
Indo-W Pacific								1	7	6			14	24.4
E Pacific								2	6	7			15	24.3
Total								3	13	13			29	24.3
Sarda sarda:														
W Atlantic										15	16	1	32	26.6
Mediterranean-Black Sea											11	4	15	27.3
Gulf of Guinea-S. Africa											8	9	17	27.5
Total										15	35	14	64	27.0
Gymnosarda unicolor			17										17	19.0
Allothunnus fallai				7									7	20.0

Species	Caudal vertebrae
	19	20	21	22	23	24	25	26	27	N	x̄
Orcynopsis unicolor	1	26	2							29	20.0
Cybiosarda elegans						2	5	5	1	13	24.4
Sarda australis			10	2						12	21.2
Sarda chiliensis:											
NE Pacific		1	14	26	3					44	21.7
SE Pacific			10	8	1					19	21.5
Total		1	24	34	4					63	21.7
Sarda orientalis:											
Indo-W Pacific		9	4	1						14	20.4
E Pacific		8	4	2						14	20.6
Total		17	8	3						28	20.5
Sarda sarda:											
W. Atlantic					2	13	16	1		32	24.5
Mediterranean-Black Sea						3	9	3		15	26.0
Gulf of Guinea-S. Africa							11	6		17	25.4
Total					2	13	30	16	3	64	25.1
Gymnosarda unicolor	17									17	19.0
Allothunnus fallai	7									7	19.0

TABLE 9.—CONTINUED.

Species	Total vertebrae																			N	$\bar{x}$
	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55		
Orcynopsis unicolor	3	24	3																	30	38.0
Cybiosarda elegans											11	2								13	47.2
Sarda australis								11	1											12	45.1
Sarda chiliensis:																					
NE Pacific							1	8	34	4										47	44.9
(Kuo 1970)							(1	14	54	4)										(73)	(44.8)
SE Pacific							1	17	4	1										23	44.2
(Kuo 1970)						(9	29	23	4	1)										(66)	(43.4)
Total							2	25	38	5										70	44.7
Sarda orientalis:																					
Indo-W Pacific								2	12											14	44.9
E Pacific								1	14											15	44.9
Total								3	26											29	44.9
Sarda sarda:																					
W Atlantic														4	25	4	1			34	51.1
NE Atlantic															3					3	51.0
Mediterranean-Black Sea																	11	4		15	53.3
(Demir 1964, Turkey)																(6	71	34	1)	(112)	(53.3)
Gulf of Guinea-S. Africa																2	14	—	1	17	53.0
Total														4	28	6	26	4	1	69	52.0
Gymnosarda unicolor		17																		17	38.0
Allothunnus fallai						7														7	39.0

all bonitos except *S. sarda* (first to seventh). Posteriorly, towards 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). Neurapophyses are present on all centra. 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 with prezygapophyses posteriorly. The postzygapophyses progressively merge into the neural spine in the peduncular region. The basic structure and elements of the neural arches and neurapophyses are similar in bonitos (Figures 51-53) to those of other scombrids (Kishinouye
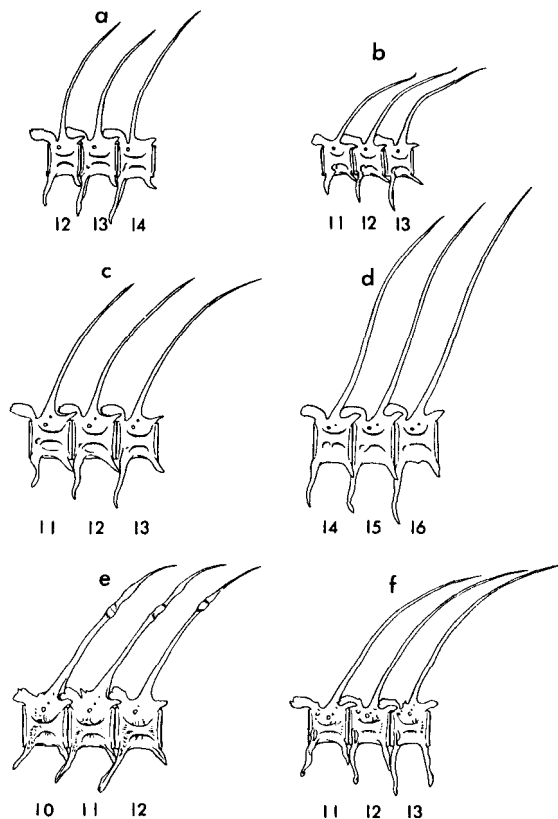
FIGURE 51.—Left lateral view of vertebra bearing first closed haemal arch (middle vertebra of each set of three) in six species of Sardini. Vertebrae numbered from anterior. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Israel, 545 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL (lumps on neural spines are anomalies). f. *Allothunnus fallai*, California, 680 mm FL.
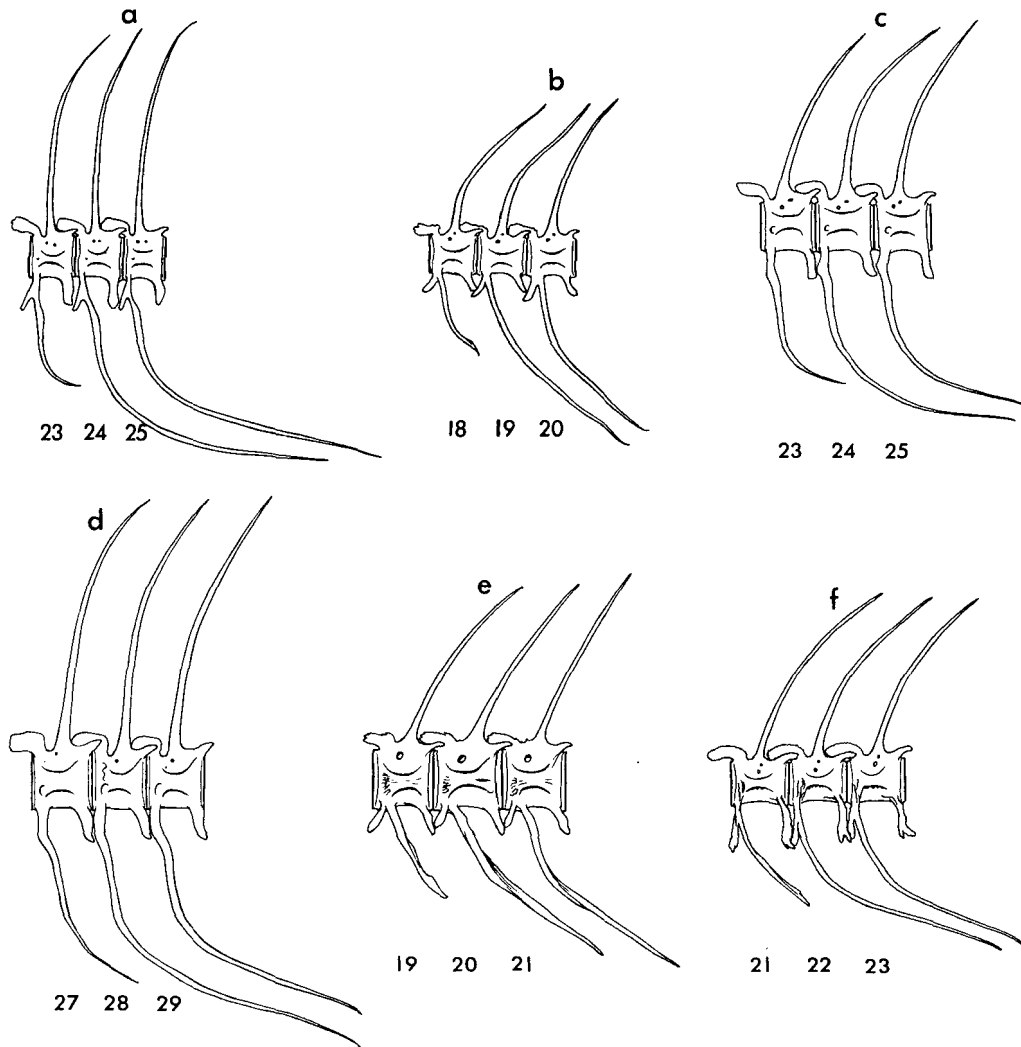
FIGURE 52.—Junction of precaudal and caudal vertebrae (middle vertebra of each set of three is first caudal vertebra) in six species of Sardini, left lateral view. Vertebrae numbered from anterior. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Israel, 545 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

1923; Conrad 1938; Mago Leccia 1958; Nakamura 1965; Gibbs and Collette 1967).

Variable characters are found on the haemal arches and haemapophyses in bonitos. Laterally directed parapophyses, arising from the middle of the centrum, appear distinctively on the third to fifth 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 8th to 10th vertebrae as described by Godsil (1954) for eastern Pacific *Sarda chiliensis* and *S. orientalis*. Posteriorly, the distal ends of the paired parapophyses meet on the 11th to 15th vertebrae forming the first closed haemal arch as Godsil (1954) found in eastern Pacific *S. chiliensis*. Nakamura (1965) suggested that the location of the first closed haemal arch can be used to assess relationships within the Thunnini. In the bonitos,
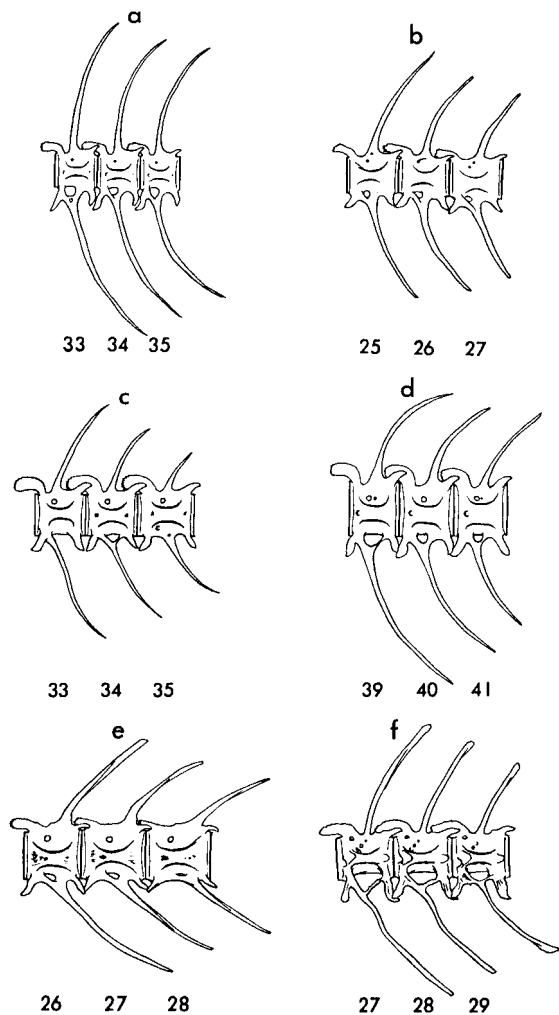
FIGURE 53.—Inferior foramina on caudal vertebrae in six species of Sardini, left lateral view. Vertebrae numbered from anterior. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Israel, 545 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

the first closed haemal arch is at the 11th to 13th vertebra in *Orcynopsis*, 13th in *Cybiosarda*, 13th to 15th in *Sarda sarda*, 12th to 14th in the other species of *Sarda*, 11th in *Gymnosarda*, and 12th in *Allothunnus*. This position is correlated with the number of vertebrae (Table 9). The first closed haemal arch is pointed anteriorly or posteriorly (Figure 51). The haemal spines become elongate and point posteriorly until they abruptly elongate on the first caudal vertebra. The paired pleural ribs (see section on ribs and intermuscular bones) at-

tach to the distal end 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 post-zygapophyses but their relative positions are different from those of the neurapophyses, and they do not overlap in the bonitos. Haemal arches and haemapophyses are best developed in *Allothunnus*. The first haemal postzygapophyses arise posteroventrally from the eighth or ninth centrum, and they reach their maximum length at about the junction of the precaudal and caudal vertebrae (Figure 52). They begin at the fourth vertebra in *Thunnus* (Gibbs and Collette 1967) and the eighth vertebra in *Scomberomorus* and *Acanthocybium* (Mago Leccia 1958; Conrad 1938). The haemal postzygapophyses fuse with the haemal spine in the caudal peduncle region. The haemal prezygapophyses arise from the anterior base of the haemal arches on the 14th to 23rd vertebra, depending on the species. They begin at the 12th to 18th vertebra in "Thunninae" (Nakamura 1965; Gibbs and Collette 1967; Potthoff 1974) and at the 16th in *Acanthocybium* (Conrad 1938). As do their counterpart neural prezygapophyses, the haemal prezygapophyses persist symmetrically into the caudal complex.

The relative position and contacts between pre- and postzygapophyses of both neuro- and haemapophyses, especially the latter, vary in different regions of the vertebral column (Figures 51-53). Godsil (1954) compared haemal pre- and postzygapophyses of eastern Pacific *Sarda chiliensis* and *S. orientalis*. We believe that comparisons should be made within specific regions of the vertebral column. The haemal post-zygapophysis of the last precaudal vertebra and the haemal prezygapophysis of the first caudal vertebra (Figure 52) abut each other in *Orcynopsis*, *Sarda orientalis*, and *Allothunnus*. A space between these two elements is present in other bonitos. The haemal prezygapophysis is longer than the postzygapophysis at the junction (Figure 52) of precaudal and caudal vertebrae in *Cybiosarda*, *Orcynopsis*, *S. chiliensis*, and *S. orientalis*. The opposite condition is found in *S. sarda*, *S. australis*, and *Allothunnus*.

Struts between the haemal arch and the centrum form the inferior foramina. These are variably developed on 3 to 12 vertebrae anterior to the

caudal peduncle, depending on the species (Figure 53). *Cybiosarda* has the most inferior foramina, on 10 to 12 vertebrae; *Orcynopsis* has 9 to 10; *Sarda* 3 to 7; and *Gymnosarda* 6 to 7. *Allothunnus* has the largest inferior foramina on 7 to 9 vertebrae.

Infracentral Grooves

Nakamura and Kikawa (1966) described three types of infracentral grooves on the ventral side of the vertebral centra in tunas. They placed *Sarda orientalis* in type C, with a single groove, and this is the category of all species of *Sarda*, *Cybiosarda*, and *Orcynopsis* (Figure 54). *Gymnosarda* (Figure 54e) has the type C infracentral grooves on the centra, but the grooves are much deeper and a shallow transverse septum is present in the middle of each groove. Nakamura and Kikawa (1966) did not place *Allothunnus* in any of the three categories. The precaudal vertebrae of *Allothunnus* have type A, with two separate infracentral grooves per centrum, but these are not distinct posteriorly as shown in Figure 54f. Some of the
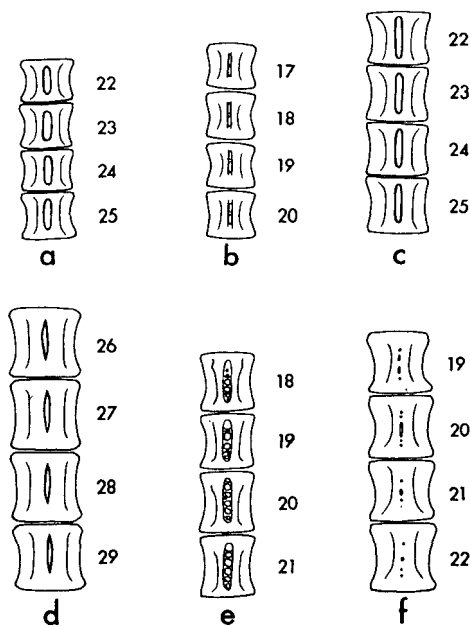
FIGURE 54.—Infracentral grooves on the ventral surface of four vertebrae including the last precaudal and first caudal vertebra in six species of Sardini. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Israel, 545 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, Tasmania, 775 mm FL. a, c, and d drawn twice as large as b, e, and f.

grooves may be covered with a layer of thin bone, especially on the anterior precaudal vertebrae. In all the bonitos, the grooves are very irregular on the first several vertebrae.

Ribs and Intermuscular Bones

Pleural ribs are present from the third vertebra posterior to the 18-27th vertebra, depending on the species. Intermuscular bones start on the back of the skull and extend to the 19-39th vertebra.

Sarda differs from other bonitos in having two cephalic intermuscular bones attached to the exoccipital on each side of the skull (Figures 12, 26). One is attached to the center of the exoccipital. The other one is attached to the exoccipital just anterior to the first neural prezygapophysis close to the midline of the skull. *Orcynopsis*, *Cybiosarda*, and *Allothunnus* have the median cephalic intermuscular bone, but the lateral one is represented only by an unossified ligament. *Gymnosarda* completely lacks cephalic intermuscular bones and also lacks a ligament in the lateral position. A ligament is present in the comparable position of the median cephalic intermuscular bone.

Sarda has more pleural ribs than do other genera, 19-24 pair; *Cybiosarda* has 20, *Allothunnus* 18, *Gymnosarda* 17, and *Orcynopsis* 16. These numbers are well correlated with vertebral number except that *Cybiosarda* has fewer than would be predicted.

The same general trend is apparent in the number of intermuscular bones but several genera are not in corresponding order. *Sarda sarda* has the most (36-45 pair) followed by other species of the genus (32-36). Following are *Allothunnus* (28-29) and *Gymnosarda* (25-28) with more than expected; *Cybiosarda* (23-24) with fewer than expected; and *Orcynopsis* (19-20) with the fewest.

Caudal Peduncle Keels

We believe that there is a general evolutionary trend within the Scombridae in the relative development of keels on the caudal peduncle. The Gasterochismatinae and the primitive members of the Scombrinae (Scombrini—mackerels and Scomberomorini—Spanish mackerels) lack supporting bony keels and have only external fleshy keels on the caudal peduncle. Starting with the bonitos, bony keels are developed under the largest pair of fleshy keels to strengthen and support them. They are developed in two different ways in
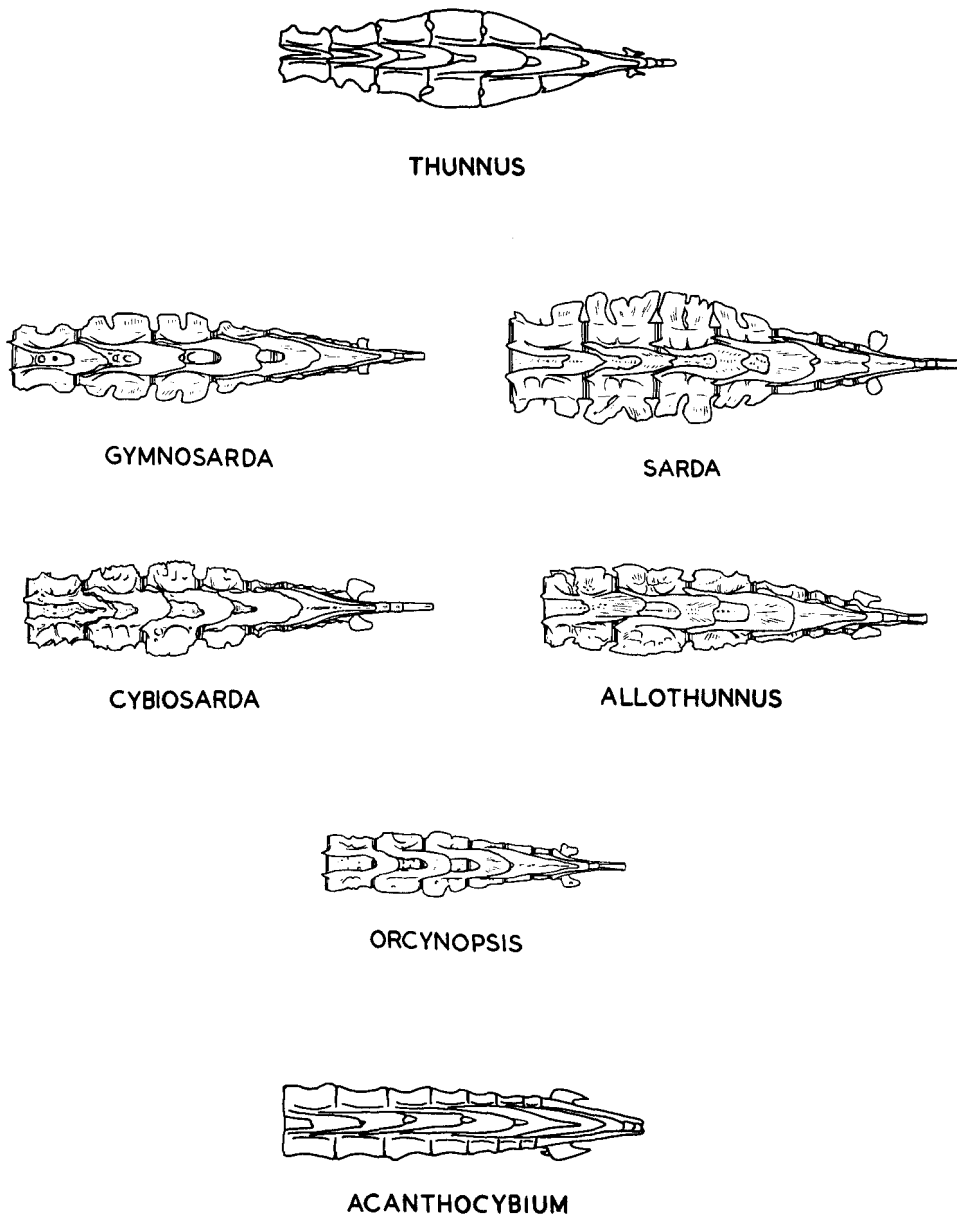
FIGURE 55.—Dorsal view of last seven or eight preural centra to show structure of bony caudal keels in the five genera of Sardini plus *Acanthocybium* and *Thunnus* representing a more primitive (Scomberomorini) and a more advanced tribe (Thunnini) respectively.

the bonitos. *Orcynopsis*, *Cybiosarda* (Figure 55), and *Allothunnus* have low keels running the entire length of the vertebrae involved. *Sarda* and *Gymnosarda* have wider keels, as in the higher tunas, but they are divided into two segments on each vertebra, one on the anterior part of the vertebra and one on the posterior part. The higher tunas (Thunnini—*Auxis* through *Thunnus*) have a wide flattened plate that acts as a single functional unit over several vertebrae.

Within the bonitos, there are minor differences as to which vertebrae bear the bony caudal keel. Counting anteriorly from preural centrum one, *Orcynopsis* differs from *Cybiosarda* in having keels concentrated on the fourth to sixth preural vertebrae instead of on the fifth to seventh.

577

Allothunnus has keels on the fourth to seventh; *Gymnosarda, Sarda australis, S. orientalis,* and *S. chiliensis* all have them on the four vertebrae between the fourth and eighth. Correlated with its greatly increased number of vertebrae (Table 9), *Sarda sarda* has keels on the 5th to 10th preural vertebrae.

Caudal Complex

Posterior to the peduncular vertebrae, the supporting bones of the caudal fin (Figure 56) consist of four preural centra. Preural centra four and three bear stout haemal and neural spines. Preural centrum two has a haemal spine and a fused epural. The urostyle represents a fusion of preural centrum one and the ural centrum (Potthoff 1975). The urostyle is fused with a triangular plate posteriorly and with the uroneural anteriorly. Dorsally, the urostyle bears an autogenous epural and ventrally, the autogenous parhypural. Preural centra two to four are compressed in all bonitos, as in *Thunnus*. Usually, two neural and three haemal spines bend abruptly away from the vertebral axis on these preural centra and parallel the dorsal and ventral edges of the hypural plate. Exceptions are found in some specimens of *S. sarda* and *S. chiliensis* (Figure 56c), which have an additional pair of neural and haemal spines from preural centrum five supporting caudal rays. The figure of *S. sarda* presented by Monod (1968, fig. 749) has two haemal spines on preural centrum three which is an anomaly. Other elements of the preural centra are described in the sections on the vertebral column and caudal peduncle keels.

The triangular hypural plate is composed of five fused hypural bones (Potthoff 1975). The dorsalmost (hypural 5) is not completely fused with the hypural plate in the bonitos (Figure 56c) or in the higher tunas, *Auxis* to *Thunnus*. The primitive hypural notch is absent from the middle of the posterior margin in all bonitos except for a vestige in *Gymnosarda*. The anterior epural (epural one) resembles the neural spine of the adjacent preural centrum three because it is secondarily fused to the neural arch of the second preural centrum. The posterior epural (epural two) is a free splint located between the anterodorsal margin of the hypural plate and the anterior epural in the Sardini (Figure 56b). It is absent (or may be secondarily fused to the anterior epural) in one Tunisian specimen of *S. sarda* (Figure 56d), which is an anomaly.

The parhypural has a strong hooked process, the parhypurapophysis, at its proximal end. As in *Thunnus*, it is located between the first haemal spine and the anteroventral margin of the hypural plate in all bonitos, except *Gymnosarda*. In *Gymnosarda* (Figure 56e), the parhypural is fused with the hypural plate as in *Acanthocybium* and some species of *Scomberomorus*. Kishinouye's (1923) figures of *Gymnosarda* (fig. 38) and *Acanthocybium* (fig. 39) are similar to our observations, but the caudal complex is upside down in his figure of *Gymnosarda*. Fusion of the parhypural with the hypural plate in *Acanthocybium* was also noted by Conrad (1938) and Fierstine and Walters (1968). In *Scomberomorus niphonius*, we also find this fusion, which is in agreement with Kishinouye's (1923) fig. 41. However, the parhypural is not fused with the hypural plate in *Scomberomorus chinense* (Kishinouye 1923, fig. 40) and the three western Atlantic species of *Scomberomorus* described by Mago Leccia (1958). The shape of the parhypurapophysis separates *Cybiosarda, Orcynopsis,* and *Gymnosarda* from *Sarda* and *Allothunnus*. The former have a smooth oblique anterior margin and the latter are concave. 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.

One of the diagnostic characters of the Scombridae is that the bases of the caudal rays cover the hypural plate (Figure 57), instead of only extending part way over the plate as is true of the Gempylidae and Trichiuridae. Another diagnostic character of the Scombridae is that four preural centra support the caudal rays (Figure 57). In the Gempylidae, Carangidae, and Coryphaenidae, only three preural centra support the caudal fin rays (Berry 1969; 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, 6-10 in the Sardini. The anal fin is located approximately opposite the dorsal fin and is composed largely of soft rays
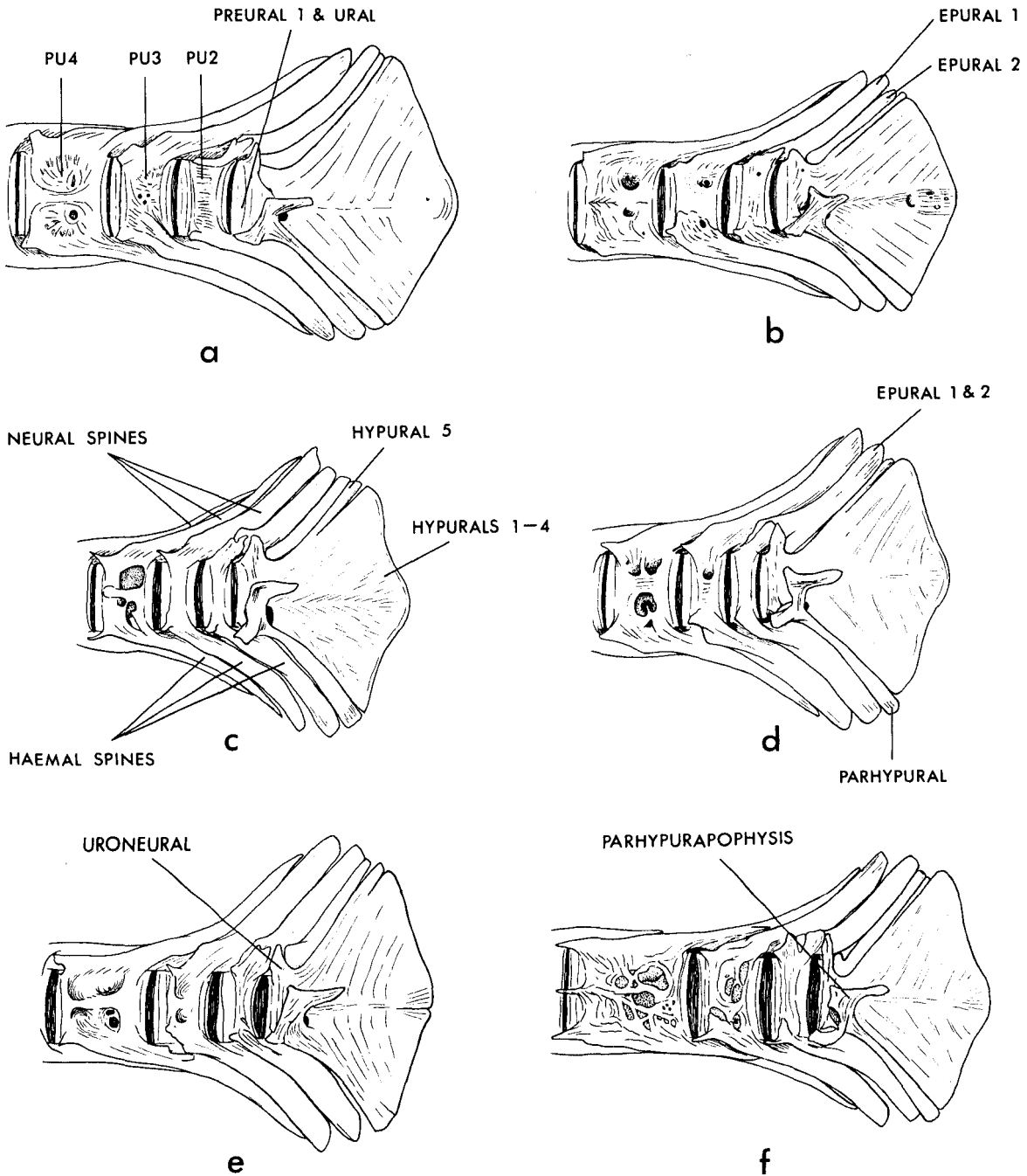
FIGURE 56.–Left lateral view of caudal complex of six species of Sardini. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 573 mm FL. c. *Sarda chiliensis*, Callao, Peru, 571 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL (with anomalous fusion of the two epurals). e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, California, 680 mm FL. a is drawn twice as large as b, e, and f, and c and d are 1.5 times as large as b, e, and f.
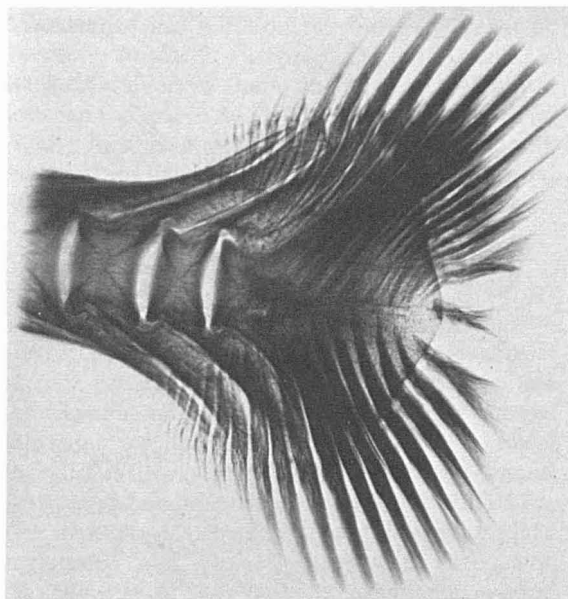
FIGURE 57.–Radiograph of the caudal complex with the bases of the caudal fin rays covering the hypural plate. *Orcynopsis unicolor*, Dakar, 960 mm FL.

followed by a series of anal finlets similar to the dorsal finlets. Some scombrids have a free or partially free spine preceding the anal fin, but in the Sardini it is difficult to tell if the anterior elements are spiny or soft rays so all are included as "anal rays." Numbers of fin rays are useful taxonomic characters in the Sardini.

Using the number of dorsal spines (Table 10), bonitos can be divided into three groups: few spines (12-15) in *Orcynopsis* and *Gymnosarda*; moderate numbers (16-19) in *Cybiosarda*, *Allothunnus*, and three species of *Sarda*; and many (20-23) in *S. sarda*. The difference between these groups is correlated with the number of vertebrae. Intraspecifically, eastern Atlantic specimens of *Sarda sarda* have modally higher counts (22) than western Atlantic specimens (21).

The most distinctive bonito in counts of second dorsal elements is *Cybiosarda*, with a high count of 17-19 rays (Table 11). *Orcynopsis*, *Gymnosarda*, and *Allothunnus* have low counts (15 or fewer). *Sarda australis* has, modally, one more second dorsal ray than do *S. orientalis* and *S. chiliensis*.

TABLE 10.–Number of spines in the first dorsal fin of species of Sardini.

Species	11	12	13	14	15	16	17	18	19	20	21	22	23	N	$\bar{x}$
Cybiosarda elegans						12	9	1						22	16.5
Orcynopsis unicolor:															
E Mediterranean		1	28	7										36	13.2
Cent. Mediterranean			10											10	13.0
(Postel 1956a, Tunisia)	(3	22	161	3)										(189)	(12.9)
Atlantic			4	2										6	13.3
Total		1	42	9										52	13.2
Sarda australis							7	12						19	18.0
Sarda chiliensis:															
NE Pacific							19	16						35	18.5
(Kuo 1970)						(20	420	69	2)					(511)	(18.1)
SE Pacific							5	19	7					31	18.1
(Kuo 1970)						(8	77	5)						(90)	(18.0)
Total							5	38	23					66	18.3
Sarda orientalis:															
Indian Ocean							10							10	18.0
NW Pacific							11	4						15	18.3
Cent. Pacific							2	2						4	18.5
E Pacific						4	11	1						16	17.8
Total						4	34	7						45	18.1
Sarda sarda:															
North America										6	46	8	1	61	21.1
South America										6	8			14	20.6
NE Atlantic										2	2	8		12	22.2
Mediterranean-Black Sea											5	21	4	30	22.0
(Demir 1964, Turkey)						(1	1		2	38	351	558	49)	(1,000)	(21.6)
Gulf of Guinea-S. Africa											6	22		28	21.8
Total										14	67	59	5	145	21.4
Gymnosarda unicolor:															
Indian Ocean			4	3	2									9	13.8
W Pacific			2	16	3									21	14.1
Total			6	19	5									30	13.9
Allothunnus fallai					1	4	1	1						7	16.3

TABLE 11.—Number of second dorsal rays, dorsal finlets, and total second dorsal rays in species of Sardini.

Species	Second dorsal rays										Dorsal finlets							Total second dorsal rays										
	12	13	14	15	16	17	18	19	N	$\bar{x}$	6	7	8	9	10	N	$\bar{x}$	19	20	21	22	23	24	25	26	27	N	$\bar{x}$
Cybiosarda elegans						11	8	3	22	17.6			4	17	1	22	8.9							1	9	12	22	26.5
Orcynopsis unicolor:																												
E Mediterranean	1	6	16	7					30	14.0		3	22	11		36	8.2		1	4	16	7	1				29	22.1
Cent. Mediterranean		1	5	2					8	14.1			6	2		8	8.3			1	4	2	1				8	22.4
(Postel 1956a, Tunisia)												(7	140	42)		(189)	(8.2)											
Atlantic			3	2					5	14.4			6			6	8.0				3	2					5	22.4
Total	1	7	24	11					43	14.0		3	34	13		50	8.2		1	5	23	11	2				42	22.2
Sarda australis				5	11	3			19	15.9	15	4				19	7.2				4	9	6				19	23.1
Sarda chiliensis:																												
NE Pacific		4	10	15	6				35	14.7	5	28	2			35	7.9			5	10	14	6				35	22.6
(Kuo 1970)		(1	42	260	195	12)			(510)	(15.3)	(73	411	28)			(512)	(7.9)											
SE Pacific		3	18	9					30	14.2	12	18	1			31	7.6		1	8	14	7					30	21.9
(Kuo 1970)			(29	53	10)				(92)	(14.8)	(22	65	1)			(88)	(7.8)											
Total		7	28	24	6				65	14.4	17	46	3			66	7.8		1	13	24	21	6				65	22.3
Sarda orientalis:																												
Indian Ocean			1	5	4				10	15.3		9	1			10	8.1				1	4	5				10	23.4
NW Pacific			2	6	6	1			15	15.4	1	14				15	7.9				2	7	5	1			15	23.3
Cent. Pacific				2	2				4	15.5		3	1			4	8.3				1	2	—	1			4	23.3
E Pacific			1	7	8				16	15.4	1	12	3			16	8.1				2	3	11				16	23.6
Total			4	20	20	1			45	15.4	2	38	5			45	8.1				6	16	21	2			45	23.4
Sarda sarda:																												
North America		1	1	17	33	3	1		56	15.7		4	34	19		57	8.3				3	14	26	11	2		56	23.9
South America			1	3	8	2			14	15.8		1	9	4		14	8.2				1	2	7	4			14	24.0
NE Atlantic				1	7	2			10	16.1		1	6	4		11	8.3					1	5	3	1		10	24.4
Mediterranean-Black Sea				2	4	10	2		18	16.7		2	10	6		18	8.2					1	5	8	3	1	18	24.9
(Demir 1964, Turkey)		(2	4	17	87	114	25	1)	(250)	(16.5)	(1	15	530	439	15)	(1,000)	(8.5)											
Gulf of Guinea-S. Africa				2	7	13	5		27	16.8		7	18	2		27	7.8						3	7	15	2	27	24.6
Total		1	2	25	59	30	8		125	16.1		15	77	35		127	8.2				4	21	50	41	8	1	125	24.3
Gymnosarda unicolor:																												
Indian Ocean	1	7	1						9	13.0	1	8				9	6.9	2	6	1							9	19.9
W Pacific		13	9						22	13.4	2	20				22	7.0		15	7							22	20.3
Total	1	20	10						31	13.3	3	28				31	6.9	2	21	8							31	20.2
Allothunnus fallai	3	4							7	12.6	1	5	1			7	7.0	3	4								7	19.6

Cybiosarda has, modally, nine dorsal finlets; *Gymnosarda*, *Allothunnus*, and *S. australis* have seven; and the other four species have eight. Thus, in total number of second dorsal elements, *Cybiosarda* is high (25-27), *Gymnosarda* and *Allothunnus* are low (19-21), and the other species are intermediate.

Anal rays (Table 12) follow a similar trend to that of dorsal rays. *Cybiosarda* has many anal rays (15-17) and total anal elements (21-24). *Gymnosarda* has few anal rays (12-13) and total anal elements (18-19). Modally, *Cybiosarda*, *Orcynopsis*, *Allothunnus*, *Sarda chiliensis*, and *S. sarda* have seven anal finlets; *Gymnosarda*, *Sarda australis*, and *S. orientalis* have six finlets.

PECTORAL GIRDLE

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

Posttemporal

The posttemporal bones of the bonitos are generally similar with two anterior processes and a flat posterior body (Figure 58). The median process is thin and flat and articulates with the epiotic. The lateral process is rounded and rodlike and articulates with the intercalar anteroventrally. *Cybiosarda*, *Orcynopsis*, *Sarda*, and *Allothunnus* each have a well-developed shelf connecting the median and lateral processes while *Gymnosarda* (Figure 58e) has the shelf greatly reduced. The shelf extends posteriorly and forms a posteriorly directed spine beneath the body in all bonitos. *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* have a shorter body than do *Sarda* and *Allothunnus*. There is a notch at the middle of the posterior edge of the body of the bone. The dorsal profile of the posttemporal is more or less flat in all the bonitos except in *Gymnosarda*, which has the margin convex posteriorly.

Supratemporal

The supratemporal bones of the bonitos are thin with two anterior processes and an elongated posterior body (Figure 59). The dorsal process lies free beneath the skin and the ventral process is firmly attached with connective tissue. The posterior body of the supratemporal overlaps externally the lateral process and part of the posterior body of the posttemporal. Lateral line canals are present on the internal surfaces of the
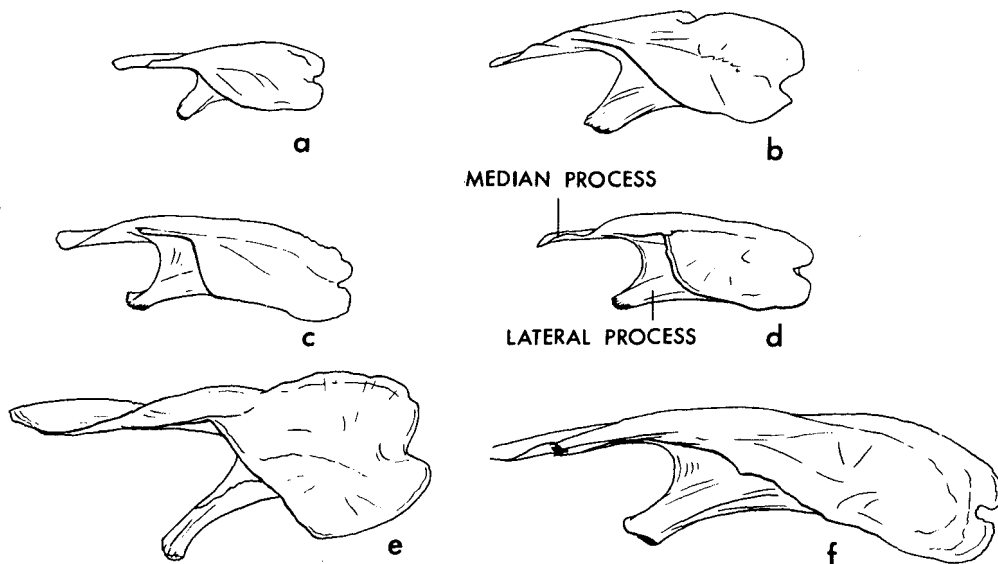
FIGURE 58.—External view of left posttemporals of six species of Sardini. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda sarda*, Tunisia, 504 mm FL. d. *Sarda australis*, New South Wales, 363 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 784 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

TABLE 12.—Number of anal rays, anal finlets, and total anal rays in species of Sardini.

Species	Anal rays										Anal finlets							Total anal rays								
	11	12	13	14	15	16	17	18	N	$\bar{x}$	5	6	7	8	9	N	$\bar{x}$	18	19	20	21	22	23	24	N	$\bar{x}$
Cybiosarda elegans					1	8	12		21	16.5	5	16				21	6.8				1	2	7	11	21	23.3
Orcynopsis unicolor:																										
E Mediterranean				1	17	9			27	15.3		9	23	2		34	6.8				1	25	1		27	22.0
Cent. Mediterranean				1	4	3			8	15.3		1	5	1		7	7.0					5	2		7	22.3
(Postel 1956a, Tunisia)												(16	150	23)		(189)	(7.0)									
Atlantic				1	3	1			5	15.0			5			5	7.0				1	3	1		5	22.0
Total				3	24	13			40	15.3		10	33	3		46	6.9				2	33	4		39	22.1
Sarda australis				1	14	4			19	15.2	1	17	1			19	6.0		1	—	13	5			19	21.2
Sarda chiliensis:																										
NE Pacific		2	11	17	5				35	13.7		10	23	2		35	6.8		3	16	12	4			35	20.5
(Kuo 1970)	(3	100	269	124	13)				(509)	(13.1)		(51	427	34)		(512)	(7.0)									
SE Pacific		2	10	17	2				31	13.6		18	12	1		31	6.4	1	5	14	10				30	20.1
(Kuo 1970)	(2	40	42	8)					(92)	(12.6)		(27	65)			(92)	(6.7)									
Total		4	21	34	7				66	13.7		28	35	3		66	6.6	1	8	30	22	4			65	20.3
Sarda orientalis:																										
Indian Ocean				3	7				10	14.7		8	2			10	6.2			1	9				10	20.9
NW Pacific				7	9				16	14.6		15	1			16	6.1			6	10				16	20.6
Cent. Pacific				2	2				4	14.5		4				4	6.0			2	2				4	20.5
E Pacific				4	10	2			16	14.9		12	4			16	6.3			1	12	3			16	21.1
Total				16	28	2			46	14.7		39	7			46	6.2			10	33	3			46	20.8
Sarda sarda:																										
North America				18	37	7			62	14.8		14	42	5		61	6.9			1	22	35	3		61	21.7
South America				2	10	2			14	15.0		3	11			14	6.8			1	2	10	1		14	21.8
NE Atlantic				1	9				10	14.9		2	7	1		10	6.9				3	6	1		10	21.8
Mediterranean-Black Sea				1	10	7			18	15.3		4	11	3		18	6.9				3	10	5		18	22.1
(Demir 1964, Turkey)			(2	8	66	88	24	5)	(193)	(15.7)	(2	98	730	164	6)	(1,000)	(7.1)									
Gulf of Guinea-S. Africa				2	9	14	2		27	15.6		8	19			27	6.7					5	9	13	27	22.3
Total				24	75	30	2		131	15.1		31	90	9		130	6.8				2	35	70	23	130	21.9
Gymnosarda unicolor:																										
Indian Ocean		6	3						9	12.4		9				9	6.0	6	3						9	18.4
W Pacific		4	17						21	12.8		21				21	6.0	4	17						21	18.8
Total		10	20						30	12.7		30				30	6.0	10	20						30	18.7
Allothunus fallai			3	4					7	13.6		2	5			7	6.7		1	3	3				7	20.3

FIGURE 59.—Left supratemporals of six species of Sardini, external lateral view. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Tunisia, 503 mm FL. c. *Sarda sarda*, New Jersey, 375 mm FL. d. *Sarda chiliensis*, Peru, 473 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 607 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL.

supratemporal bones in all bonitos. *Orcynopsis*, *Cybiosarda*, and *Gymnosarda* have a shorter posterior body than do *Sarda* and *Allothunnus*. The thin edges of the supratemporal vary slightly among species of *Sarda* (Figure 59) and within each species of bonito. *Allothunnus* has the most elongate posterior body.

Supracleithrum

The supracleithrum lies in between the posttemporal and the cleithrum. *Cybiosarda*, *Orcynopsis*, and *Sarda* have relatively narrow and elongate supracleithra compared to *Gymnosarda* and *Allothunnus*. A dorsally projecting process is set off from the main body of the supracleithrum by a notch or angle on the anterodorsal part of the outer surface of the bone. *Sarda australis* and *Allothunnus* have the notch almost right-angled (Figure 60f, h). The other species of *Sarda* have a more poorly developed notch with a wider angle.

FIGURE 60.—Left supracleithra of eight species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda chiliensis*, Callao, Peru, 549 mm FL. d. *Sarda orientalis*, Panama, 415 mm FL. e. *Sarda sarda*, Tunisia, 504 mm FL. f. *Sarda australis*, New South Wales, 495 mm FL. g. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. h. *Allothunnus fallai*, California, 680 mm FL. a drawn twice as large as other figures.

Gymnosarda has a comparatively deep notch but the dorsally projecting process points more anteriorly than in any other bonito (Figure 60g). There is only a slight notch in *Cybiosarda* and no indentation at all on the anterodorsal edge of the bone in *Orcynopsis*. A ridge extends along the length of the inner surface of the supracleithrum. The ridge gradually merges into the main body of the bone dorsally. It stops abruptly about two-thirds of the way toward the dorsally projecting tip and is almost absent anteriorly in *Allothunnus*, as in *Thunnus*.

Cleithrum

The main body of the cleithrum in bonitos is crescent-shaped with an anterodorsal spine and a posteriorly projecting plate at the upper end, as in other scombrids (Figures 61, 62). The angle between the spine and the dorsal margin of the plate is smallest in *Gymnosarda* and widest, almost a right angle, in the species of *Sarda*. The angle is intermediate in *Cybiosarda*, *Orcynopsis*, and *Allothunnus*, similar to the condition in *Thunnus*. Godsil (1954) stated that the posteriorly projecting plate in *S. velox* (= *S. orientalis*) has a bluntly rounded distal end compared to *S. chiliensis*, which has the plate tapered distally. We found that this character is not consistent in *S. orientalis*, but *S. chiliensis* does have a more tapered distal portion than do the other species of *Sarda*. The main body of the cleithrum consists of an inner and an outer shelf, which join at the main axis, and a ridge at the anterior margin of the main axis on its inner surface. *Cybiosarda*, *Orcynopsis*, and *Sarda* have a poorly developed ridge along the anterior margin of the outer shelf (Figure 61a-d) as does *Thunnus* (de Sylva 1955, fig. 34). It is present only along the posterior edge of the upper two-thirds of the inner shelf of *Gymnosarda*. In *Allothunnus* (Figure 64f), the ridge becomes a broad well-developed inner shelf which extends internally from the outer shelf and at right angles to the inner shelf along the upper two-thirds of the main body. *Orcynopsis* has an expanded lower portion of the inner shelf; in
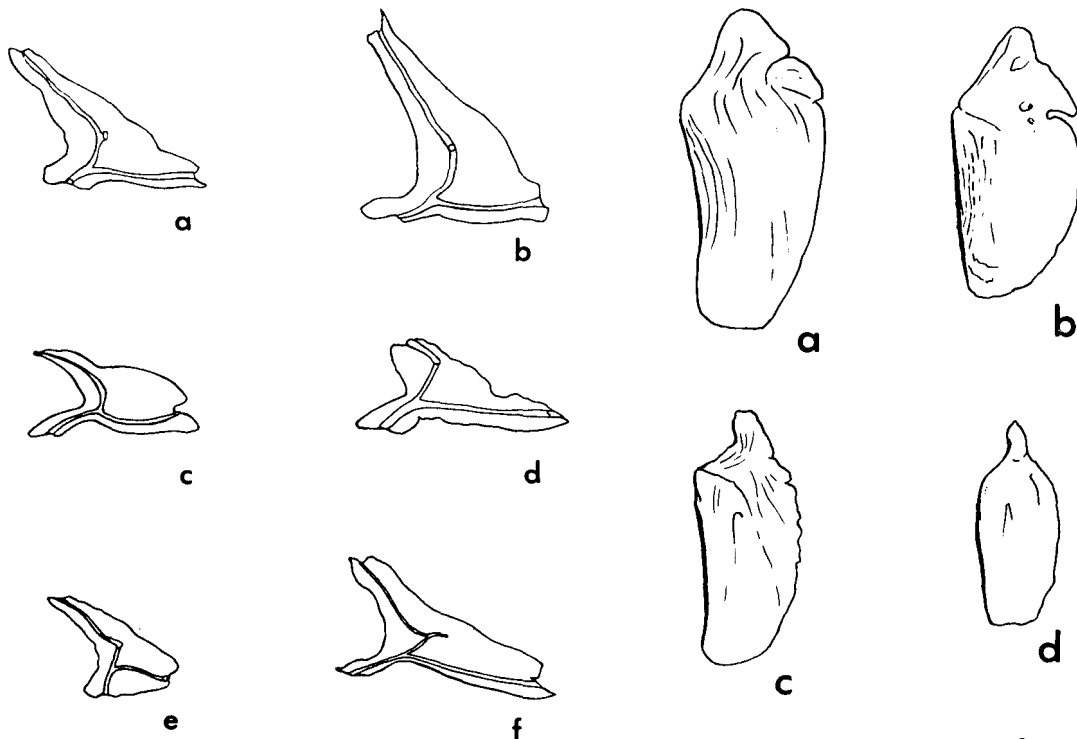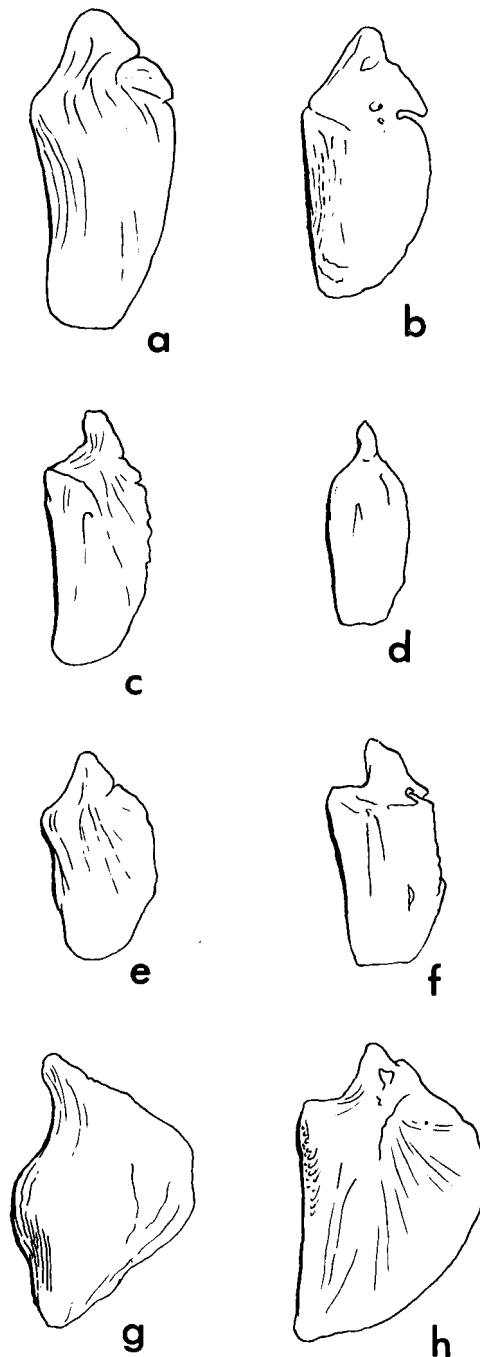

FIGURE 61.–Left cleithra of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 495 mm FL. c. *Sarda australis*, New South Wales, 495 mm FL. d. *Sarda chiliensis*, La Jolla, Calif., 453 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, Tasmania, 680 mm FL.
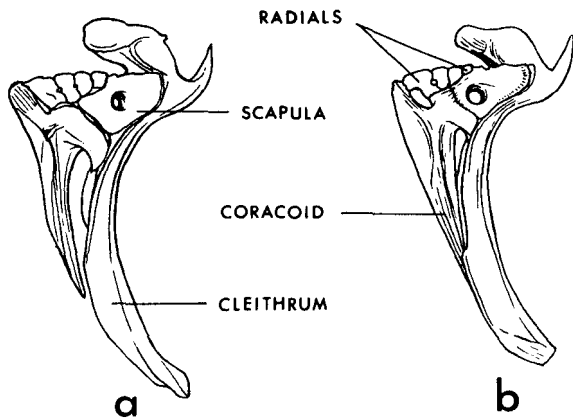
FIGURE 62.—Left pectoral girdles of two species of Sardini, internal view. a. *Sarda sarda*, Azores, 418 mm FL. b. *Cybiosarda elegans*, New South Wales, 360 mm FL.

Gymnosarda the inner shelf stops abruptly at the middle portion where the marginal ridge begins.

Scapula

The anterior margin of the scapula fits into the inner shelf of the cleithrum (Figure 62). This attachment extends to the posterior projecting plate anterodorsally. The scapula is attached with the coracoid posteriorly and dorsally it is attached with the first two and part of the third upper radials (Figure 63). The posterior margin of the scapula is drawn out into a facet which accepts the anterior ray of the pectoral fin. A suture bisects the scapula through the scapular fenestra. The general features of the scapula are similar among the bonitos. The scapular fenestra of *Gymnosarda* (Figure 63e) is relatively larger, and that of the species of *Sarda* (Figure 63c, d) is smaller, than the other bonitos.

Coracoid

The coracoid is elongated and more or less triangular in shape (Figure 63). It is connected with the scapula along its flat dorsal edge in *Allothunnus* (Figure 63f). In all other bonitos, this margin is interrupted ventral to the scapular fenestra and extends dorsally as an interdigitating suture. The ventral wing of the coracoid is xiphoid with a V-shaped depression along the midline. The coracoid has two points of attachment with the cleithrum, the first along the anterior margin near the scapula, and the second at the anterior end of the ventral wing. The mar-

gin of the coracoid, between its articulations with the cleithrum, is curved inward. This curvature is more pronounced in *Gymnosarda* (Figure 63e) than in the other bonitos, which resemble *Thunnus*.

Radials

The four radials differ in size and shape and are attached directly to the thickened posterior edges of the scapula and coracoid (Figures 62, 63). The size of the radials increases ventrally. Two small foramina are located between the second and third, and the third and fourth radials, counting downward. The first two radials and the upper half of the third radial attach to the coracoid; the ventral half of the third plus the fourth radial attach to the scapula. A fenestra is present between the dorsoposterior end of the coracoid and the largest radial, which has a prominent posteroventral process in all bonitos except *Sarda* and *Allothunnus*. In both characters, the fenestra and the last radial process, *Sarda* and *Allothunnus* resemble *Thunnus*; the other bonitos resemble *Acanthocybium*.

Pectoral Fin Rays

The first (and largest) pectoral ray articulates directly with a posterior process of the scapula. The other rays attach to the radials. 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 20-25, Sardini 21-28, Thunnini (except for *Thunnus*) 22-29, *Thunnus* 30-36. Within the Sardini (Table 13), *Orcynopsis* and *Cybiosarda* have the fewest pectoral fin rays (modes of 22 and 23, respectively). *Gymnosarda* has the most (25-28), followed by one species of *Sarda* (*S. australis*, 25-27), and *Allothunnus* (24-26). The other three species of *Sarda* are intermediate with species modes of 24 or 25.

Postcleithrum 1 and 2

The posterior projecting plate of the cleithrum has its posterior end attached to the curved first postcleithrum, which connects to another bone, the second postcleithrum. Both postcleithra are thin and bent. Postcleithrum 1 (the upper one) has a narrow anterodorsal end and a broad posteroventral body (Figure 64). *Gymnosarda* has a pointed

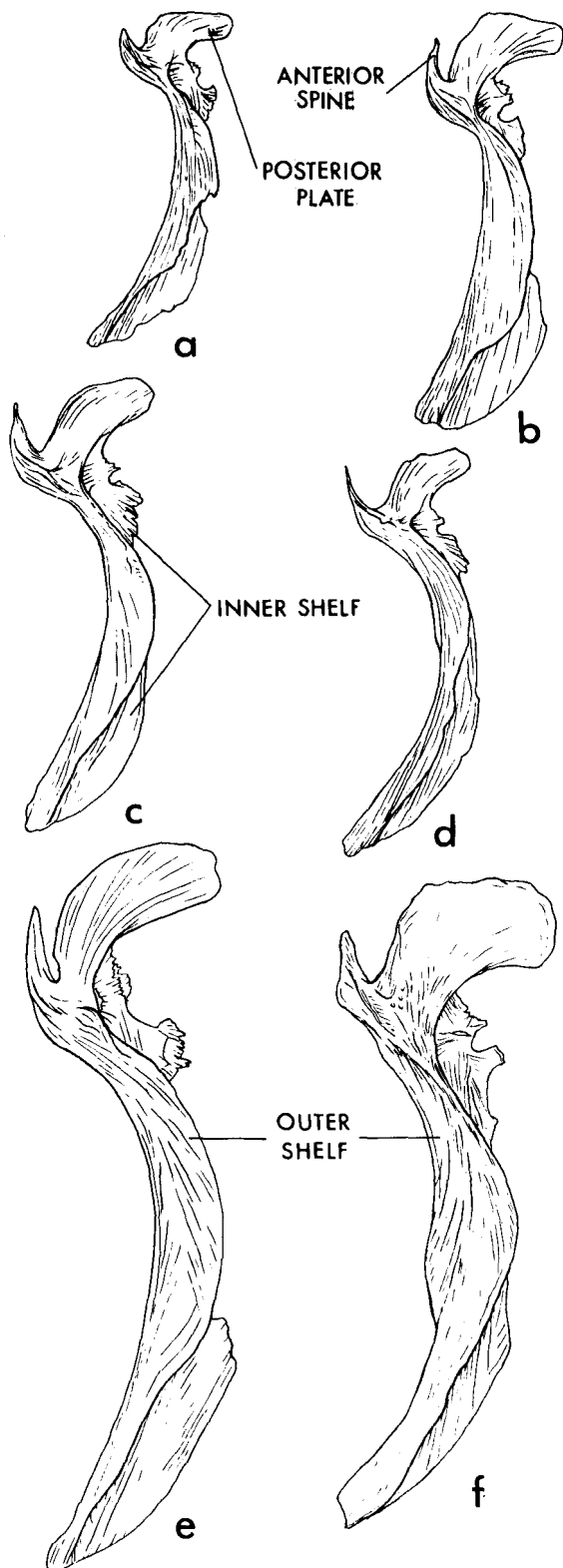FIGURE 63.—Left pectoral girdles (minus cleithra) of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda chiliensis*, California, 472 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, California, 680 mm FL. a drawn twice as large as b-f.

TABLE 13.—Number of pectoral rays in species of Sardini.

Species	21	22	23	24	25	26	27	28	N	$\bar{x}$
Orcynopsis unicolor:										
E Mediterranean	6	17	7						30	22.0
Cent. Mediterranean		5	3						8	22.4
Atlantic		3	5						8	22.6
Total	6	25	15						46	22.2
Cybiosarda elegans		1	15	5					21	23.2
Sarda australis					6	9	4		19	25.9
Sarda chillensis:										
NE Pacific		1	6	9	12	3			31	24.3
(Kuo 1970)		(1	28	226	229	25	1)		(510)	(24.5)
SE Pacific		2	4	13	10	3			32	24.2
(Kuo 1970)			(6	41	44	1)			(92)	(24.4)
Total		3	10	22	22	6			63	24.3
Sarda orientalis:										
Indian Ocean			2	4	2	1			9	24.2
NW Pacific			2	10	3				15	24.1
Cent. Pacific				2	2				4	24.5
E Pacific			2	6	6				14	24.3
Total			6	22	13	1			42	24.2
Sarda sarda:										
North America			9	27	21	4			61	24.3
South America			1	3	3	1			8	24.5
NE Atlantic				4	5	2			11	24.8
Mediterranean-Black Sea			2	11	5				18	24.2
(Demir 1964, Turkey)		(1	12	51	34	7)			(105)	(24.3)
Gulf of Guinea-S. Africa			6	13	7				26	24.0
Total			18	58	41	7			124	24.3
Gymnosarda unicolor:										
Indian Ocean					3	5	—	1	9	25.9
W Pacific					3	8	9	1	21	26.4
Total					6	13	9	2	30	26.2
Allothunnus fallai				2	1	3			6	25.2

anterodorsal end on postcleithrum 1, which is unique among bonitos. Postcleithrum 1 in *Orcynopsis* and *Cybiosarda* is elongate and broad at the upper end. The general features of postcleithrum 1 of *Sarda* species are similar to those of *Thunnus*. *Allothunnus* has the broadest postcleithrum 1. Postcleithrum 2 (the lower one) is a spinelike structure with both ends pointed and a broad upper process (Figure 65). These bones are similar in all bonitos except for minor variations. Postcleithrum 2 of *Gymnosarda* has an elongate upper end and a curved lower portion. The broad process of postcleithrum 2 is much enlarged in *Allothunnus* as in *Thunnus*.

PELVIC GIRDLE

The pelvic fin rays (I, 5) attach directly to the paired basipterygia which make up the pelvic girdle. The bones are fused together along the midline and are imbedded in the ventral abdominal wall free from connections with any other bones. Each basipterygium is composed of three main parts (Figure 66): a wide anterodorsal plate and two processes: an anterior process (anterior xiphoid process of de Sylva 1955) and a shorter, stronger, posteriorly directed styliform process (posterior xiphoid process of de Sylva 1955). There are three wings to the anterodorsal plate (Kishinouye 1923): external, internal, and vertical (ventral). Anteriorly, the external wing turns into the same vertical plane and merges into the vertical wing. The internal wing and the external wing meet in one plane posteriorly along a ridge. A "valleylike" depression is present in the posterior half of the anterodorsal plate in all the bonitos except *Allothunnus* (Figure 66f). The internal wing of *Allothunnus* attaches to the vertical wing horizontally at a right angle which is completely separate from the external wing, as in *Thunnus* (de Sylva 1955, figs. 50-52). The vertical wing is the largest and most variable character of the bonito basipterygium. The vertical wings of *Orcynopsis*, *Cybiosarda*, and *Sarda* are elongate and have pointed anterior ends. *Gymnosarda* and *Allothunnus* have vertical wings that are shorter
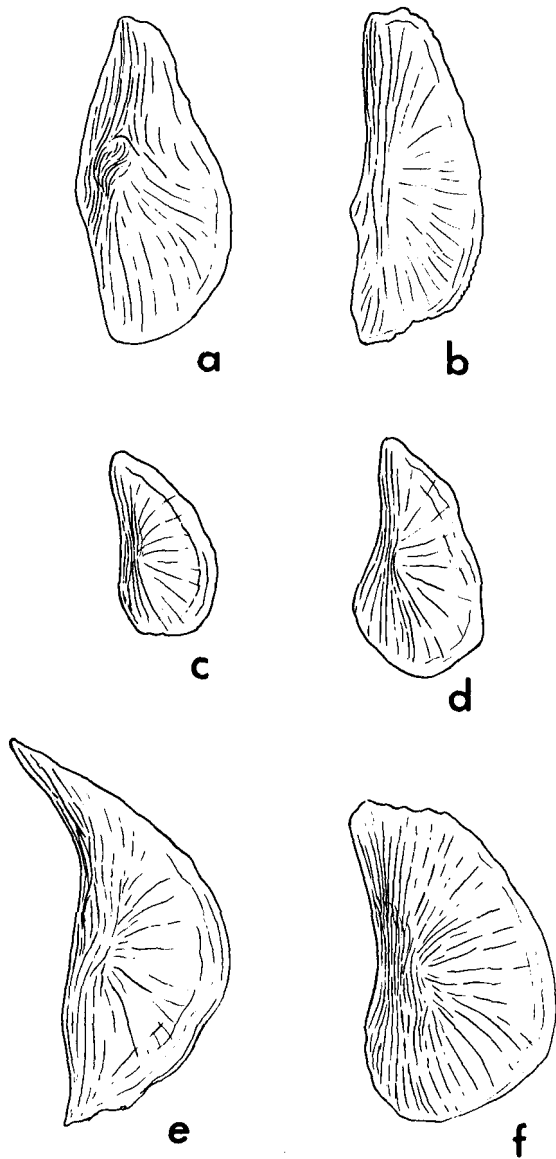
FIGURE 64.—Left first postcleithra of six species of Sardini. a. *Cybiosarda elegans*, New South Wales, 360 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 774 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.
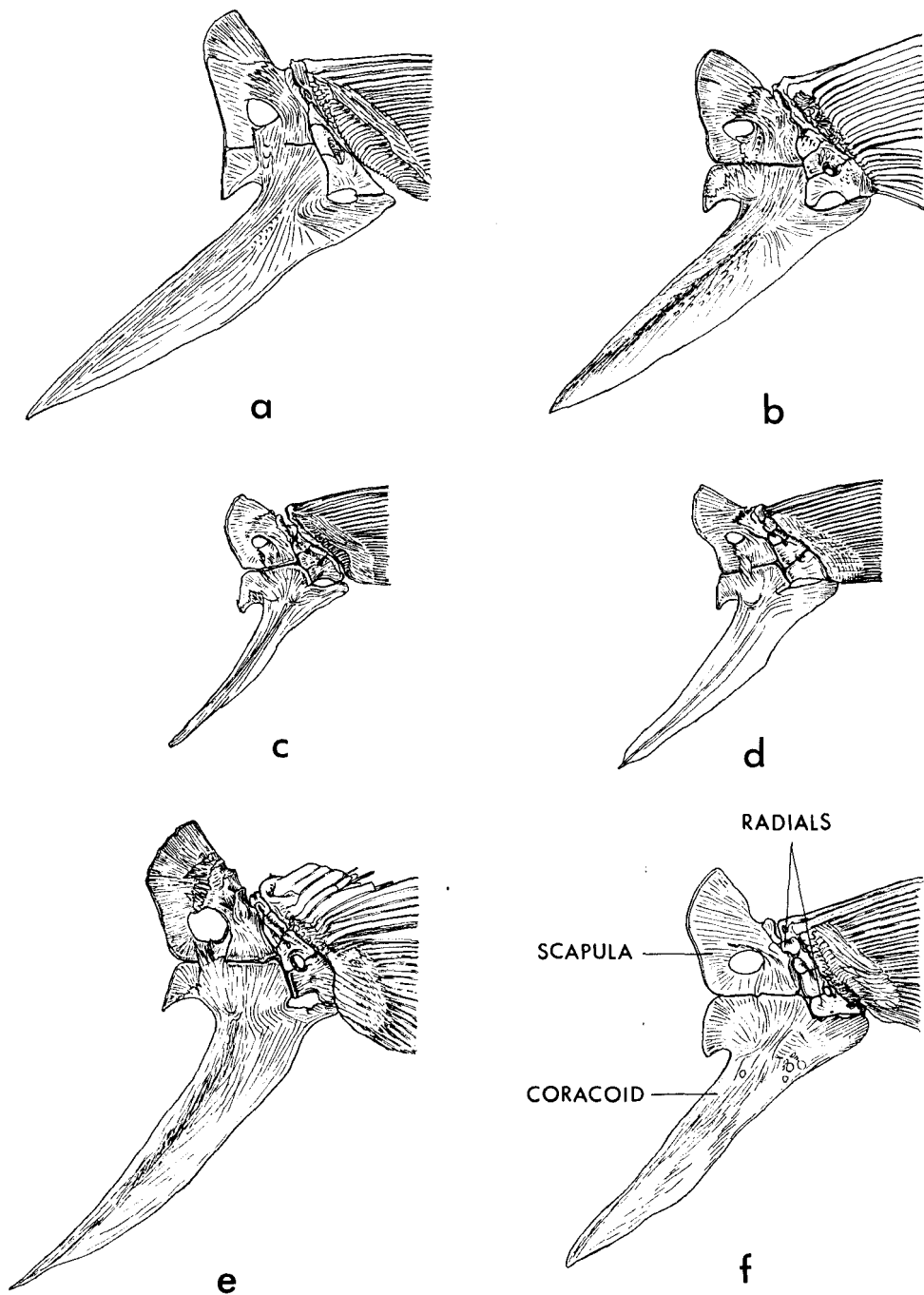
FIGURE 65.—Left second postcleithra of six species of Sardini, external lateral view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 545 mm FL. c. *Sarda sarda*, New Jersey, 375 mm FL. d. *Sarda orientalis*, Jalisco, Mexico, 434 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 607 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

and broader in the midanterior portion. The portion above the internal wing is even better developed in *Allothunnus* than in *Thunnus* (de Sylva 1955, fig. 51). The internal and external wings of *Allothunnus* are less prominent than in the other bonitos. Among the species of *Sarda*, *S. orientalis* has a narrower and longer vertical wing.

The anterior process of the basipterygium extends anteriorly to about the middle of the anterodorsal plate. The posterior styliform process is shorter and stronger than the anterior process in the bonitos. Except for *Gymnosarda*, no differences were found among the bonitos in the fleshy bifid interpelvic process that is supported by the paired posterior styliform process of the basipterygia

589
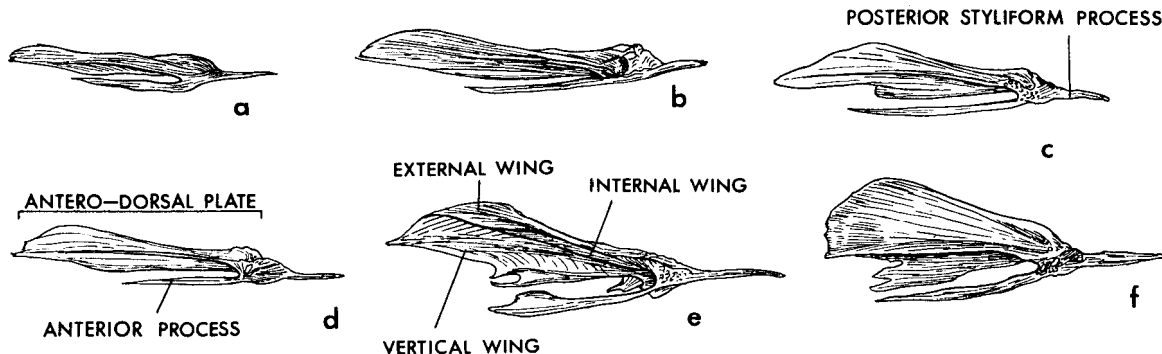
FIGURE 66.—Lateral view of inner surface of right basipterygium of pelvic girdles of six species of Sardini. a. *Cybiosarda elegans*, Western Australia, 442 mm FL. b. *Orcynopsis unicolor*, Tunisia, 620 mm FL. c. *Sarda chiliensis*, Callao, Peru, 437 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL.

(Figure 67). *Gymnosarda* differs from the other bonitos in having a single interpelvic process. *Auxis* and *Grammatorcynus* also have a single interpelvic process, the former very large, the latter small. However, there is a posterior styliform process from each basipterygium regardless of whether the fleshy interpelvic process is single or bifid.
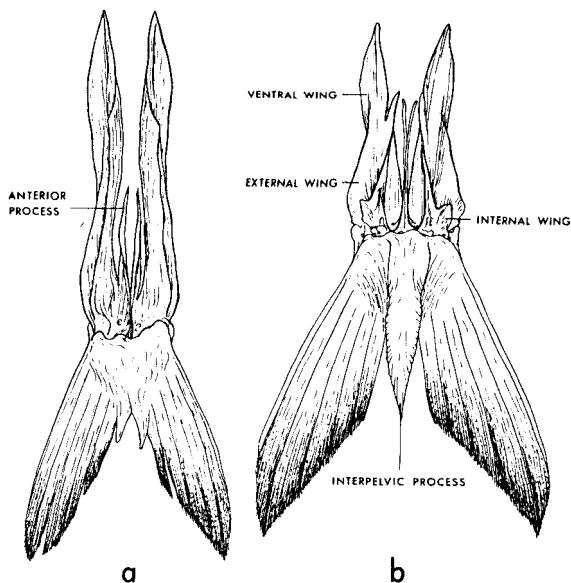
FIGURE 67.—Ventral view of pelvic girdles and fins of two species of Sardini. a. *Orcynopsis unicolor*, Tunisia, 495 mm FL. b. *Gymnosarda unicolor*, Truk Islands, 787 mm FL. a drawn twice as large as b.

PART 2. SYSTEMATICS

The family Scombridae can be divided into two subfamilies: the Gasterochismatinae, which contains only the aberrant *Gasterochisma melampus* Richardson, and the Scombrinae. The Scombrinae is composed of two groups of tribes (Figure 68). The more primitive mackerels (Scombrini — *Scomber* and *Rastrelliger*) and Spanish mackerels (Scomberomorini—*Grammatorcynus*, *Scomberomorus*, and *Acanthocybium*) have a distinct notch in the hypural plate, lack any bony support for the fleshy caudal peduncle keels (Figure 56), and do not have preural centra two and three greatly shortened. The bonitos comprise a tribe (Sardini, Starks 1910) of five genera and eight species. The bonitos differ from the higher tunas (Thunnini—*Auxis*, *Euthynnus*, *Katsuwonus*, and *Thunnus*) in lacking any trace of a specialized subcutaneous vascular system, in lacking dorsally projecting lateral cartilaginous ridges on the tongue, and in having the bony caudal keel only partially developed instead of complete. The Sardini lack the prominent paired frontoparietal foramina characteristic of the Thunnini (except *Auxis*). Except for *Allothunnus*, the Sardini also differ from the Thunnini in lacking prominent prootic pits. In this character, and in its tiny conical teeth, *Allothunnus* is similar to the Thunnini. The Sardini agree with *Thunnus* and with the Scombrini and Scomberomorini in lacking the bony shelf that divides the neural canal of the anterior six vertebrae into dorsal and ventral portions. This bony division is characteristic of the

other three genera of Thunnini—*Katsuwonus*, *Euthynnus*, and *Auxis*.

Five genera, four of them monotypic, are recognized as a result of analyzing the morphology described in the first part of this paper. A sample
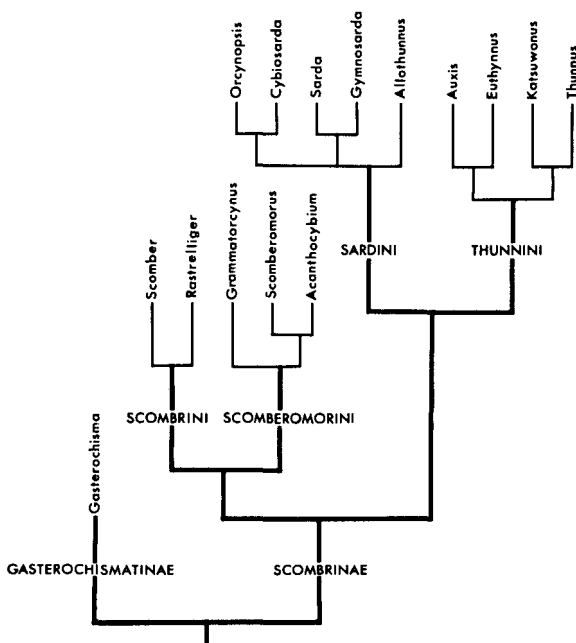
FIGURE 68.—The subfamilies, tribes, and genera of the Scombridae.

of some of the more important characters is summarized in Table 14. *Orcynopsis* and *Cybiosarda* form a pair of related genera in characters such as the poor development of the bony caudal keels, location of the spleen, presence of a pair of tooth patches fused to the glossohyal bone, and length of the liver lobes. They differ sharply in vertebral number; *Orcynopsis* usually has 18 precaudal plus 20 caudal vertebrae compared to (22-23) + (24-25) = 47 in *Cybiosarda*. In some respects, *Sarda* and *Gymnosarda* also form a pair of related genera. However, characters of *Gymnosarda* such as the well-developed swim bladder, curved sagitta, large number of olfactory laminae, paired glossohyal tooth plates, location of the spleen, lack of cephalic intermuscular bones, and parhypural fused to the hypural plate demonstrate that *Gymnosarda* is very different from the other genera of Sardini. *Allothunnus* differs strongly from the other bonitos in liver shape, presence of prootic wings, and shape of pineal foramen, but shares more characters in common with the Sardini than with the Thunnini as previously noted.

Orcynopsis Gill

Orcynopsis Gill 1862:125 (type-species *Scomber unicolor* Geoffroy St. Hilaire; misspelled *Orycnopsis*).

TABLE 14.—Summary of characters distinguishing the five genera of Sardini.

Character (reference)	Orcynopsis	Cybiosarda	Sarda	Gymnosarda	Allothunnus
Intestine (Fig. 5)	folded	folded	straight	folded	straight
Tongue teeth (Fig. 43)	2 patches fused to glossohyal	2 patches fused to glossohyal	none	2 patches free from glossohyal	none
Prootic pit	absent	absent	absent	absent	present
Prootic wings	absent	absent	absent	absent	present
Bony caudal keels (Fig. 55)	low and poorly developed	low and poorly developed	well-developed and divided into 2 parts	well-developed and divided into 2 parts	low and poorly developed
Length of liver lobes (Fig. 4)	right lobe longest	right lobe longest	right and left lobes equally long	right and left lobes equally long	3 subequal lobes
Spleen (in ventral view) (Fig. 3)	small and concealed under liver	small and concealed under liver	large and prominent posteriorly	present on right side anteriorly	not visible
Cephalic intermuscular bones	1 on each side of skull	1 on each side of skull	2	none	1
Pineal foramen (Fig. 10-14)	elongate and slit-shaped	elongate and slit-shaped	elongate and slit-shaped	elongate and slit-shaped	large and oval
Swim bladder	absent	absent	absent	well-developed	absent
Sagitta	flat	flat	flat	curved	flat
Opercular bones (Fig. 45-47)	not elongate	not elongate	not elongate	elongate	not elongate
Olfactory laminae (Table 3)	25-28	28-33	21-39	48-56	28-30
Vertebrae (Table 9)	18+20=38	(22-23)+(24-25)=47	43-46; 50-55	19+19=38	20+19=39
Pectoral rays (Table 13)	22-23	23-24	23-26	25-27	24-26
Dorsal spines (Table 10)	12-14	16-17	17-23	13-15	15-18
Parhypural (Fig. 56)	free from hypural plate	free from hypural plate	free from hypural plate	fused to hypural plate	free
Interpelvic process (Fig. 67)	small paired processes	small paired processes	small paired processes	single large process	small and paired
Total first arch gill rakers (Table 7)	12-17	12-15	8-27	11-14	72-80

Pelamichthys Giglioli 1880:25 (type-species *Scomber unicolor* Geoffroy St. Hilaire by original designation).

Comparative Diagnosis.—The monotypic genera *Orcynopsis* and *Cybiosarda* share several important characters that distinguish them from *Sarda* and *Gymnosarda*: low and poorly developed bony caudal keels versus well-developed caudal keels divided into anterior and posterior sections; right lobe of liver longest versus right and left lobes much longer than the middle lobe; spleen small and not visible in ventral view versus large and prominent in ventral view. Both genera have high first dorsal fins (Figure 1a, b) and are relatively more compressed (almost like *Scomberomorus*) than fusiform. *Orcynopsis*, *Cybiosarda*, and *Gymnosarda* have two patches of tongue teeth, but the patches are attached to the glossohyal bone in *Orcynopsis* and *Cybiosarda* and are on separate plates that fit over the glossohyal in *Gymnosarda*.

Orcynopsis differs from *Cybiosarda* most obviously in lacking the bold pattern of stripes and blotches on the body of the latter. *Orcynopsis* has lower counts than does *Cybiosarda*: vertebrae 37-39 vs. 47-48; dorsal spines 12-14 vs. 16-18; second dorsal rays 12-15 vs. 17-19; pleural ribs 16 vs. 20; and intermuscular bones 19-20 vs. 24-25.

Orcynopsis unicolor is a short-bodied and short-headed species (Table 15). It has a shorter snout-anal and snout-second dorsal distance than do other bonitos. The snout-first dorsal and snout-pelvic fin origin distances are shorter than in other bonitos except *Gymnosarda unicolor* and *Sarda australis*. The snout-pectoral fin origin, pelvic fin insertion-vent, and pelvic fin tip-vent distances are all shorter than in other bonitos except *Gymnosarda*. The fins are high compared to fork length, the second dorsal and anal fins are higher than in other bonitos except for the second dorsal in *Cybiosarda*. The bases of the second dorsal and

TABLE 15.—Comparison of morphometric characters of three populations of *Orcynopsis unicolor*. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

Character	Israel Range	$\bar{x}$	N	Lebanon Range	$\bar{x}$	N	Tunisia Range	$\bar{x}$	N
Fork length (mm)	285-735	404	12	242-325	287	11	312-645	539	7
Fork length									
Snout — A	555-597	577	12	573-598	587	11	556-597	578	7
Snout — 2D	481-522	499	12	496-530	511	11	400-503	481	7
Snout — 1D	239-253	247	12	248-262	253	11	229-257	246	7
Snout — P_2	265-282	273	12	276-293	284	11	263-285	270	7
Snout — P_1	231-243	238	12	240-257	247	11	219-239	229	7
P_1 — P_2	109-116	113	7	118-129	122	11			
Head length	226-246	235	12	239-251	243	11	224-241	231	7
Max. body depth	221-268	246	11	240-272	255	11	226-248	240	7
Max. body width	106-140	124	9	113-135	123	11	116-139	130	7
P_1 length	125-153	138	12	131-140	135	11	135-148	142	7
P_2 length	57- 68	63	12	55- 64	61	11	62- 66	64	6
P_2 insertion - vent	278-307	294	12	266-296	288	11	280-315	300	7
P_2 tip - vent	218-241	230	12	209-242	228	11	216-241	233	7
Base 1D	235-255	246	10	241-259	248	11	230-255	241	7
Height 2D	109-148	128	10	108-124	117	10	116-150	126	7
Base 2D	107-126	117	12	107-140	133	11	108-149	120	7
Height anal	111-148	126	10	107-126	118	11	119-131	125	7
Base anal	94-128	114	11	98-131	111	10	95-120	106	7
Caudal spread	236-275	261	6	249-297	270	10	239-259	244	5
Snout (fleshy)	76- 95	89	11	92- 98	94	11	90- 94	91	6
Snout (bony)	65- 80	76	11	77- 83	80	11	76-111	83	7
Maxilla length	101-118	113	11	116-129	123	11	104-119	112	6
Post orbital	109-115	112	7	113-122	117	11			
Orbit (fleshy)	24- 32	28	11	29- 34	31	11	23- 66	31	7
Orbit (bony)	46- 58	51	11	53- 61	57	11	44- 69	52	7
Interorbital width	65- 74	68	11	59- 70	66	11	67- 83	72	6
Head length									
Snout (fleshy)	327-405	381	11	376-392	387	11	385-406	396	6
Snout (bony)	280-353	326	11	316-335	328	11	329-480	358	7
Maxilla length	431-508	483	11	485-517	505	11	456-495	483	6
Post orbital	453-490	478	7	462-515	484	11			
Orbit (fleshy)	107-133	121	11	120-137	129	11	98-121	107	7
Orbit (bony)	204-249	218	11	221-254	236	11	192-222	211	6
Interorbital width	256-308	289	11	239-288	272	11	262-310	297	6

anal fins are longer than in any bonitos except *Cybiosarda.*

Orcynopsis unicolor Geoffroy St. Hilaire

Scomber unicolor E. Geoffroy St. Hilaire 1817: pl. 24, fig. 6 (original description). I. Geoffroy St. Hilaire 1827:331-332 (description; Alexandria, Egypt). Guichenot 1850:58-59 (description; Algeria).

Cybium commersoni (not of Lacépède, 1800). Bonaparte 1845:74 (listed after Verany; Italy).

Cybium Bonapartii Verany 1847:493 (original description; Genoa, Italy).

Pelamys Bonaparte. Filippi and Verany 1859:194 (description, comparison with *S. sarda*), fig. 4. Moreau 1881:434-436 (synonymy, description; very rare, Nice). Liebman 1934:325 (Israel).

Pelamys unicolor. Günther 1860:368 (synonymy, description). Canestrini 1870:103 (description, rare in Italian waters). Rochebrune 1882:95-96 (Senegal). Stassano 1890:32-33 (Spanish Sahara). Griffini 1903:398-399 (synonymy; description; Italy).

Cybium altipinne Guichenot in Duméril 1858:262 (nomen nudum, listed; Senegal).

Orycnopsis unicolor. Gill 1862:126 (original description of *Orcynopsis*, misspelled *Orycnopsis*).

Thynnus peregrinus Collett 1879a:20-30 (original description; Christiania (now Oslo) Norway), pl. 1.

Orcynopsis unicolor. Collett 1879b:1-3 (*Thynnus peregrinus* Collett a synonym of *O. unicolor*). Ninni 1882:264 (Adriatic). Dresslar and Fesler 1889:434-435 (description; synonymy). Vinciguerra 1890:98-100 (synonymy; Cabo Blanco, Spanish West Africa). Carus 1893:659-660 (synonymy; description). Gruvel and Bouyat 1906:150 (Cabo Yubi to Cabo Blanco, Spanish West Africa). Lozano 1916:298-302 (description; Melilla, Spanish Morocco). Parona 1919:91-95 (synonymy, description; Italy), pl. 10-11. Ehrenbaum 1924:12 (Alexandria). Chabanaud 1925:197-200 (comparison with *Sarda* and *Gymnosarda*), fig. 1 (lingual and pharyngeal teeth), 2 (vomerine teeth). Chabanaud and Monod 1927:278-279 (common; Port Étienne, Mauritania), fig. 30B. Buen 1930a:46-47 (description, synonymy), pl. 2, fig. 5. Dieuzeide 1930:141-144 (synonymy, description, Algeria). Buen and Frade 1932:72 (in key), fig. 5. Frade and Buen 1932:70 (in key).

Le Gall 1934a:288 (description), fig. (after Smitt). Jensen 1937:11-12 (Collett's 1879 records from the Skagerak). Fraser-Brunner 1950:148-149 (description), fig. 14. Postel 1950:63-66 (description; reproduction; food; length-weight; Cape Verde), 64 (fig. of viscera). Lozano y Rey 1952:527-531 (description), pl. 40, fig. 1, col. pl. 41, figs. 2 and 3. Morice 1953a:37 (dentition; gill rakers), 41 (generic key). Postel 1954:357-358 (stomach contents), 359 (parasites), 361 (gonosomatic index). Dieuzeide et al. 1955:145-146 (description, fig.; Algeria). Dollfus 1955:55 (listed), 141 (references to occurrence in Atlantic Morocco; Rabat market). Frade and Postel 1955:35 (gonads; spawning season; Cape Verde), fig. 6 (ovary). A. Postel 1955:59-60, 65, table 2, fig. 2 (number of teeth on upper and lower jaws, 100 Tunisian specimens). Postel 1955b:31-32 (sex ratio by months, maximum size by sexes, number of eggs). Postel 1956a:1220-1248 (synonymy, relationships, distribution, morphometry, meristics, anatomy, reproduction, food, parasites), fig. 3 (distribution map), fig. 4 (drawing), figs. 9, 10 (viscera). Postel 1956b:52 (common names). Postel 1956c:67-68 (abundant in Gulf of Gabes, Tunisia). Tortonese 1956:7 (Mediterranean). Postel 1960:257 (distribution). Collette and Gibbs 1963a:26 (relationships). Šoljan 1963:147-148 (description; figs.; Adriatic Sea). George et al. 1964:21 (rare, Lebanon). Postel 1964:220 (listed, North Africa). Collette 1966:370 (*Cybium altipinne* a synonym of *O. unicolor*). Zharov 1967:220 (relationships of scombroids). Bini 1968:39-40 (synonymy; description), color plate. Williams 1968:436 (Ghana). Blache et al. 1970:375 (in key; fig. 961, not fig. 960 which is *Scomberomorus tritor*). Collette 1970:4 (Israel). Ben-Tuvia 1971:20 (Israel). De Groot and Nijssen 1971:8 (Arguin Bank, Mauritania). Lozano Cabo 1970:158 (North Africa). Economidis 1972:526 (Greece). Magnuson 1973:350 (maximum size, no swim bladder, short pectoral fin). Postel 1973:474-475 (range, synonymy).

Pelamichthys unicolor. Giglioli 1880:25 (original description of *Pelamichthys*, Italy).

Cybium Veranyi. Giglioli 1880:25 (description, Italy).

Sarda unicolor. Smitt 1892:102-104 (synonymy; description; rare in Scandinavia), fig. 29. Fowler 1936:625-626 (synonymy; description;

compiled), fig. 283 (after Smitt). Cadenat 1937:482 (Sénégal). Navarro 1943:131 (Arguin Bank, Mauritania), pl. 19, fig. B (photograph). Tortonese 1949:65 (permanent resident, Mediterranean Sea). Tortonese and Trotti 1949:87 (Ligurian Sea).

Types of Nominal Species.—*Scomber unicolor* E. Geoffroy St. Hilaire 1817: pl. 24, fig. 6. No type-specimens, text published by Isidore Geoffroy St. Hilaire in 1827 ". . . sont extraits des notes prises en Egypte par mon pére. Je n'ai pu me procurer ni cette especé, ni celle qui est figurée dans l'Atlas sous le nom de *Maquereau unicolore*; . . . trouvee dans le Méditerranée."

Cybium Bonapartii Verany 1847:493. The type was examined in the Museo della R. Universita di Genova by Collett (1879b) and the name placed in the synonymy of *O. unicolor* (along with *Thynnus peregrinus* Collett). The present whereabouts of the type, if extant, are unknown. It is not listed in the type catalog of the Museo Civico di Storia Naturale di Genova (Tortonese 1963) which absorbed the University collections. The original description was based on a specimen from the Genoa market taken on 31 May 1847. It had eight dorsal finlets, seven anal finlets, conical teeth, and lacked spots on the body.

Cybium altipinne Guichenot in Duméril 1858. Apparently a nomen nudum as there is no description and we cannot find a description by either Guichenot or Duméril elsewhere. Also considered a nomen nudum by Postel (1973). Previous authors (Fraser-Brunner 1950; Bauchot and Blanc 1961) have considered *C. altipinne* to be a synonym of *Scomberomorus tritor* (Cuvier) but the specimen labelled as type is clearly *O. unicolor* as Collette (1966) has shown.

Thynnus peregrinus Collett 1879a:20-30, pl. 1. Placed in the synonymy of *Orcynopsis unicolor* later in the same year (Collett 1879b). Lectotype (herein selected): ZMO J4632; 565 mm FL; Norway, Christianiafjord (Oslo), Naesøen; 26 Aug. 1876. Prof. Esmark. Paralectotype: ZMO J4631; 570 mm; same data as lectotype. The smaller syntype is selected as lectotype because the dorsal spine count of 13 matches the original description and because the two patches of teeth on the tongue are the usual size for *O. unicolor*. The paralectotype has two very small patches of tongue teeth. Counts for the lectotype (paralectotype in parentheses): dorsal fin rays XIII + 14 + VIII (XIV + 14 + VIII); anal fin rays 15 + VII (15 + VII); pectoral fin rays (left-right) 23-21 (23-22); gill rakers 3 + 1 + 11 = 15 in both; upper jaw teeth (left-right) 23-25 (20-22); lower jaw teeth 20-20 (16-17).

Distribution.—*Orcynopsis unicolor* is an eastern Atlantic endemic whose range is centered in the Mediterranean Sea but extends south to Dakar, Sénégal and north to Oslo, Norway (Figure 69). It was first described from Egypt by Geoffroy St. Hilaire (1817) and most subsequent records have come from the southern Mediterranean: Lebanon (George et al. 1964; 12 USNM specimens), Israel (Liebman 1934; Collette 1970; Ben-Tuvia 1971; 5 USNM specimens; SFRS 1686, 2009, BT-1767, BT-1582, BT-1986), Egypt (Ehrenbaum 1924; 10 NHMV specimens), Tunisia (Postel 1956c; 7 USNM specimens), Algeria (Guichenot 1850; Dieuzeide 1930; Dieuzeide et al. 1955), and Morocco (Lozano 1916). Records from the northern Mediterranean are scarcer: Genoa, Italy (Verany 1847; MSNG 1987); Ligurian Sea (Tortonese and Trotti 1949); Adriatic Sea (Ninni 1882; Šoljan 1963; MSUF 495D); Elba (MSUF coll. 1172); Nice, France (Moreau 1881; NHMV 1884.I.204). The Norwegian record is based on the two types of *Thynnus peregrinus* Collett, taken at Naesøen, Christianiafjord (= Oslofjord) in August 1876. There are several records for the Atlantic coast of North Africa south to Dakar, Sénégal: Rabat, Morocco (Dollfus 1955); Spanish West Africa (Stassano 1890; Vinciguerra 1890; Gruval and Bouyat 1906); Mauritania (Chabanaud and Monod 1927; Navarro 1943; de Groot and Nijssen 1971; USNM uncat.); and Cape Verde and Dakar, Sénégal (Duméril 1858; Rochebrune 1882; Postel 1950; Frade and Postel 1955; MNHN A.5797). There is one record from further south, in the Gulf of Guinea. Williams (1968:436) reported that a specimen was taken off Ghana during the Guinean Trawling Survey. The specimen was apparently not saved, the identification was probably based on the first draft of the illustrated key by Blache et al. (1970) which has the figures of *Scomberomorus tritor* and *Orcynopsis unicolor* transposed, and the record is well out of the normal range of the species. Therefore, the record must be considered highly questionable unless confirmed by additional specimens.

Cybiosarda Whitley

Scomberomorus (*Cybiosarda*) Whitley 1935:236 (type-species *S.* (*C.*) *elegans* Whitley by monotypy).
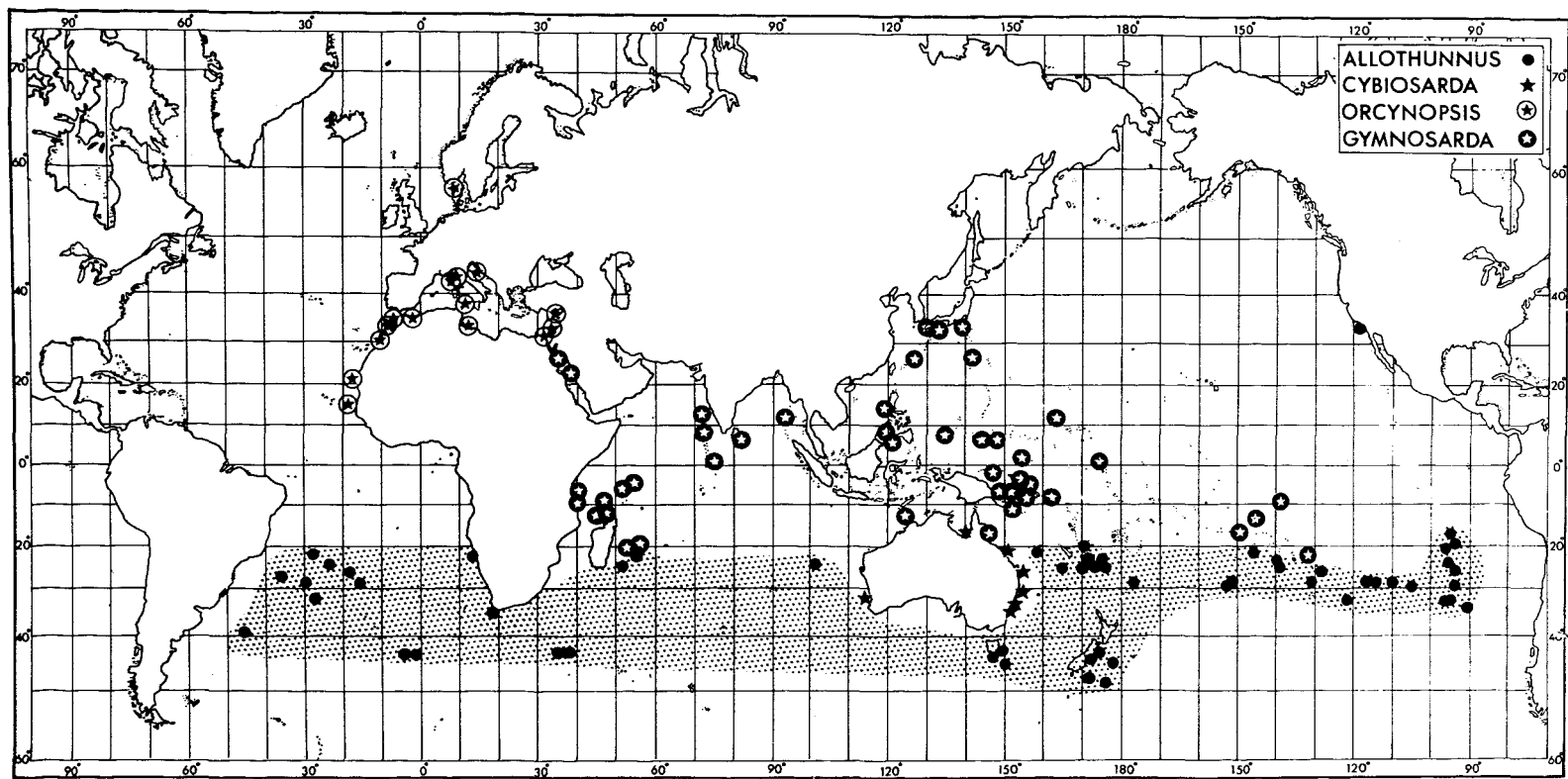
FIGURE 69.—Distribution of *Orcynopsis unicolor*, *Gymnosarda unicolor*, *Cybiosarda elegans*, and *Allothunnus fallai* based on specimens personally examined and literature records.

Comparative Diagnosis.—The monotypic genera *Cybiosarda* and *Orcynopsis* share several characters that distinguish them from *Sarda* and *Gymnosarda*: low and poorly developed bony caudal keels instead of well developed, but divided into anterior and posterior parts; right lobe of liver much longer than middle and left lobes instead of both right and left lobes elongate; spleen small and not visible in ventral view versus spleen large and prominent in ventral view. Both have one intermuscular bone on the back of the skull compared to none in *Gymnosarda* and two in *Sarda*. Both genera have high first dorsal fins and are relatively more compressed (almost like *Scomberomorus*) than fusiform. *Orcynopsis*, *Cybiosarda*, and *Gymnosarda* have a pair of tooth patches on the tongue, but these are attached to the glossohyal bone in the first two genera and are on separate plates that fit over the glossohyal in *Gymnosarda*. Osteologically, the two genera also show many similarities.

Cybiosarda differs from *Orcynopsis* most obviously in its prominent pattern of blotches above the lateral line and stripes below it (Figure 1a). *Cybiosarda* has higher counts than does *Orcynopsis*: vertebrae 47-48 vs. 37-39; dorsal spines 16-18 vs. 12-14; second dorsal rays 17-19 vs. 12-15; pleural ribs 19 vs. 16; and intermuscular bones 23-24 vs. 19-20. *Cybiosarda* has a smaller sagitta with a longer and thinner rostrum than does *Orcynopsis*.

Cybiosarda is a relatively short-bodied bonito (Table 16). The snout-second dorsal distance is shorter than in other bonitos except *Orcynopsis* and *Sarda chiliensis*, the first dorsal fin base is shorter than in the others except *Orcynopsis* and *Gymnosarda*. The second dorsal and anal fins are higher than in *Sarda* and *Allothunnus* and the second dorsal fin is also higher than in *Gymnosarda*.

Cybiosarda elegans (Whitley)

Scomberomorus (*Cybiosarda*) *elegans* Whitley 1935:236-237 (original description; Moreton Bay, Queensland, Australia).
Cybiosarda elegans. Whitley 1936:42-45 (redescription of type; anatomy; pl. 4, fig. 1; text fig. 5; Queensland). Whitley 1939:274 (New South Wales). Serventy 1941a:43 (description, New South Wales and Western Australia), pl. 4, bottom fig. Whitley 1948:24 (listed; Western Australia). La Monte 1952:48, 50 (description). Munro 1958a:113-114

TABLE 16.—Morphometric characters of *Cybiosarda elegans*. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

Character	Range	$\bar{x}$	N
Fork length (mm)	250-422	347	19
Fork length			
Snout — A	638-678	652	19
Snout — 2D	509-547	531	18
Snout — 1D	260-284	273	19
Snout — P_2	289-317	299	18
Snout — P_1	258-291	267	18
$P_1 — P_2$	113-136	125	18
Head length	259-280	266	19
Max. body depth	199-252	227	16
Max. body width	105-168	133	17
P_1 length	128-148	138	19
P_2 length	76- 88	82	19
P_2 insertion - vent	344-363	327	17
P_2 tip - vent	240-282	262	17
Base 1D	229-270	254	19
Height 2D	101-118	108	19
Base 2D	112-133	121	18
Height anal	97-118	107	18
Base anal	82-100	91	19
Caudal spread	219-275	251	16
Snout (fleshy)	94-104	98	19
Snout (bony)	79- 87	82	19
Maxilla length	125-140	130	19
Post orbital	128-146	136	19
Orbit (fleshy)	26- 34	29	19
Orbit (bony)	54- 61	58	9
Interorbital width	65- 78	73	19
Head length			
Snout (fleshy)	352-383	367	19
Snout (bony)	299-323	308	19
Maxilla length	475-501	489	19
Post orbital	489-551	511	19
Orbit (fleshy)	98-125	109	19
Orbit (bony)	204-232	218	9
Interorbital width	244-292	273	19

(description; Queensland, New South Wales, Western Australia), fig. 756 (after Serventy). Jones and Silas 1961:379 (compiled), fig. 5 (after Fraser-Brunner). Collette and Gibbs 1963b:28 (description), pl. 7 (after Fraser-Brunner). Jones and Silas 1963:1786-1787 (compiled). Jones and Silas 1964:24-25 (description). Marshall 1964:357-358 (summary), col. pl. 52, fig. 345. Whitley 1964a:228-229 (summary), pl. 2, fig. b (Western Australia specimen), text fig. 4c (distribution). Whitley 1964b:48 (listed). Marshall 1966:204, col. pl. 52. Grant 1972:113 (description; Queensland), fig. (after Serventy).
Gymnosarda elegans. Fraser-Brunner 1950:149 (description), fig. 15.

Types.—*Scomberomorus* (*Cybiosarda*) *elegans* Whitley 1935:236-237. Original description repeated with additional locality data and the QM catalog number for the type plus more information on the species by Whitley (1936). Holotype: QM

I.5413; 356 mm FL; Queensland, Moreton Bay, Goat Island; G. W. Watson. A second specimen (QM I.5142) is labelled as a paratype and is mentioned as having been collected with the first specimen by Whitley (1936:42). However, it is not mentioned in the original description where the statement is made "Described from a specimen in the Queensland Museum from Moreton Bay, Queensland"; therefore, it should not be considered as a paratype. Counts for the holotype: dorsal fin rays XVI + 17 + IX; anal fin rays 17 + VII; pectoral fin rays (left-right) 24-24; gill rakers 4 + 10 = 14; upper jaw teeth (left-right) 17-20; lower jaw teeth 12-12.

Distribution.—*Cybiosarda elegans* is restricted to the northern three quarters of Australia (Figure 69). It was first described by Whitley (1935) from Moreton Bay, Queensland, and then reported from New South Wales by Whitley (1939) and from Western Australia by Serventy (1941a). We have examined specimens from near Perth, Western Australia, and several localities along the east coast (Shellharbour and Maclean, New South Wales, and Moreton Bay and Lindeman Island, Queensland). In addition, we have examined a 250-mm specimen (AMS I.15557-095) taken by the CSIRO shrimp survey in the Gulf of Carpentaria at lat. 16°40′S, long. 139°50′E.

Sarda Cuvier

Sarda Cuvier 1829:199 (type-species *Scomber sarda* Bloch 1793 by monotypy).

Pelamys Cuvier in Cuvier and Valenciennes 1831:149 (type-species *Scomber sarda* Bloch 1793 by original designation).

Palamita Bonaparte 1831:173 (substitute name for *Pelamys* Cuvier 1831 preoccupied by *Pelamys* Oken 1816 in Reptilia, Hydrophiidae; therefore, takes the same type-species *Scomber sarda* Bloch 1793).

Creotroctes Gistel 1848:p. x (type-species *Scomber sarda* Bloch 1793; substitute name for *Sarda* Cuvier 1829).

Comparative Diagnosis.—The species of *Sarda* all have several stripes dorsally, ranging from horizontal to oblique in orientation. *Sarda* (and *Allothunnus*) differ from the other genera of bonitos in having the intestine run straight from the stomach to the anus (versus having two additional loops, Figure 5) and two intermuscular

bones on each side of the back of the skull (*Gymnosarda* has none, the other three genera have one on each side).

Sarda and *Gymnosarda* share a number of characters that distinguish them from *Orcynopsis* and *Cybiosarda*: the bony caudal peduncle keels are well developed as in higher tunas, but are divided into anterior and posterior sections on each vertebra; the spleen is large and prominent in ventral view versus small and not visible in ventral view; the right and left lobes of the liver are both much longer than the middle lobe versus only the right lobe elongate. Both *Sarda* and *Gymnosarda* are fusiform in body shape instead of being more laterally compressed.

Sarda (Figure 1c) differs from *Gymnosarda* (Figure 2a) in being completely covered with fine scales posterior to the corselet (instead of being naked posteriorly); in lacking a swim bladder; in having the spleen centrally located in the posterior half of the body cavity in ventral view (instead of on the right side of the anterior half); in having fewer lamellae in the olfactory rosettes (21-39 vs. 48-56); more vertebrae (42-55 vs. 38); and in lacking a pair of tooth patches on the glossohyal bone.

Species of *Sarda*.—Four allopatric species of *Sarda* are recognized based on the morphological characters described in the first part of this paper (a summary of 26 of these characters is presented in Table 17). *Sarda australis* is similar to the other three species in the genus in 11-15 characters. *Sarda chiliensis* and *S. orientalis* resemble each other in 12 characters. *Sarda sarda* stands out as being very different from *S. chiliensis* and *S. orientalis*, sharing only eight or nine characters with each. Many of the meristic differences between *S. sarda* and the other species of *Sarda* are correlated with its greater number of body segments as reflected by having 50-55 vertebrae (compared to 43-46). Thus, *S. sarda* also has more dorsal spines, pleural ribs, intermuscular bones, vertebral keels, and the first closed haemal arch is further posterior. *Sarda sarda* is most similar to *S. australis* in numbers of anal rays, gill rakers, upper and lower jaw teeth, occasional presence of vomerine teeth, angle of the hyomandibular spine and the condyle, width of the supramaxilla, and relative length of the haemal pre- and post-zygapophyses on the first caudal vertebra. If the several differences between *S. australis* and *S. sarda* that are correlated with the higher number of body segments are considered as one character, the two species would appear even more similar.

TABLE 17.—Summary of characters distinguishing the four species of *Sarda*.

Character (reference)	S. sarda	S. australis	S. chillensis	S. orientalis
Lamellae in nasal rosettes (Table 3)	22-33 ($\bar{x}$ 26.5)	34-39 ($\bar{x}$ 37.2)	21-30 ($\bar{x}$ 25.4)	25-36 ($\bar{x}$ 31.9)
Vomerine teeth present	sometimes	sometimes	never	never
Upper jaw teeth (Table 5)	16-26	16-26	18-30 ($\bar{x}$ 23.5)	12-20 ($\bar{x}$ 15.5)
Lower jaw teeth (Table 6)	12-24 ($\bar{x}$ 16.0)	11-20 ($\bar{x}$ 14.5)	14-25 ($\bar{x}$ 19.2)	10-17 ($\bar{x}$ 13.0)
Palatine teeth	8-21 ($\bar{x}$ 12.3)	7-14 ($\bar{x}$ 10.7)	9-22 ($\bar{x}$ 15.2)	8-19 ($\bar{x}$ 11.9)
Supramaxilla width (Fig. 32)	intermediate	intermediate	wide	narrow
Ectopterygoid-dorsal portion (Fig. 36)	pointed	pointed	pointed	slightly expanded
Hyomandibular spine-condyle (Fig. 39)	projects beyond condyle	short	short	projects beyond condyle
Angle of hyomandibular spine (Fig. 39)	about 90°	about 90°	greater than 90°	less than 90°
Elliptical ceratohyal window (Fig. 42)	present	present	present	only slight depression
Ventral surface of glossohyal (Fig. 43)	depression present	depression present	depression present	no depression
Gill rakers (Table 7)	16-23	19-21	23-27	8-13
Vertebrae (Table 9)	50-55	43-46	43-46	43-46
Pleural ribs	24	19-23	19-23	19-23
Intermuscular bones	31-45	32-36	32-36	32-36
Keels on vertebrae number	5-10	5-8	5-8	5-8
First closed haemal arch (Fig. 51)	13th-15th vertebra	13th-15th vertebra	12th-14th vertebra	12th-14th vertebra
Length of haemal prezygapophyses and postzygapophyses at precaudal-caudal junction (Fig. 52)	postzygapophyses longer than prezygapophyses	postzygapophyses longer than prezygapophyses	prezygapophyses longer than postzygapophyses	prezygapophyses longer than postzygapophyses
Dorsal spines (Table 10)	20-23	17-19	17-19	17-19
Dorsal finlets (Table 11)	modally 8	modally 7	modally 8	modally 8
Anal rays (Table 12)	14-17 (modally 15)	14-17 (modally 15)	12-15 (modally 14)	14-16 (modally 15)
Anal finlets (Table 12)	modally 7	modally 6	modally 7	modally 6
Total anal elements (Table 12)	19-23 (modally 21-22)	19-23 (modally 21-22)	18-22 (modally 20)	20-22 (modally 21)
Supracleithral notch (Fig. 60)	wide angle	almost 90°	wide angle	wide angle
Pectoral rays (Table 13)	23-26	25-27 (modally 26)	22-26 (modally 24-25)	22-26 (modally 24-25)
Vertical wing of pelvic girdle (Fig. 66)	shorter and wider	shorter and wider	narrower and longer	narrower and longer

Sarda australis (Macleay)

Pelamys australis Macleay 1880:557 (original description; Port Jackson, Sydney, Australia). Ogilby 1887:29 (listed, New South Wales; should be compared with *P. chilensis*). McCoy 1888:208 (compared with *P. schlegeli*). Stanbury 1969:206 (holotype in Macleay Museum, University of Sydney).

Pelamys schlegeli McCoy 1888:207-208 (original description from one specimen from Prince Phillip Bay, Victoria), col. pl. 155.

Pelamys chilensis (not of Cuvier, 1831). Ogilby 1893:97-98 (synonymy, description; New South Wales), pl. 26.

Sarda chilensis (not of Cuvier 1831). Waite 1904:42 (listed, New South Wales). Stead 1906:163-164 (New South Wales and Victoria), fig. 59. Stead 1908:94-95 (New South Wales), pl. 54.

Sarda chilensis (not of Cuvier 1831). McCulloch 1922:105 (New South Wales), pl. 33, fig. 291a.

Sarda orientalis (not of Temminck and Schlegel 1844). Lord 1927:15 (listed, Tasmania).

Sarda australis. Walford 1936:9 (in key as valid species of *Sarda*). Serventy 1941a:42-43 (description; Eastern Australia), pl. 4, middle fig. Serventy 1941b:7 (summer visitor to Victoria). Laevastu and Rosa 1963:1844 (fig. 7, map of distribution and fishing areas, in part). Whitley 1964a:236 (common from the Capricorn Islands, Great Barrier Reef to Sydney), fig. 2 (distribution map). Whitley 1964b:48 (listed).

Sarda chiliensis australis. Roughley 1951:121-122 (description; Australia), plate 49b. Munro 1958a:113 (description; Queensland, New South Wales, and Victoria), fig. 754. Grant 1972:114 (description; Queensland), fig. (after McCoy).

Sarda chilensis australis. Silas 1964:296 (in key, map, *S. chilensis* divided into an eastern Pacific *S. c. chilensis* and an Australian *S. c. australis*).

Comparative Diagnosis.—*Sarda australis* shows 11-15 similarities each, among characters considered (Table 17), with *S. sarda*, *S. chiliensis*, and *S. orientalis*. It differs from all of them in having slightly fewer pectoral rays (25-27, modally 26 vs. 22-26, modally 24-25) and in having a 90° angle in

the supracleithral notch instead of a much wider angle. *Sarda australis* resembles *S. sarda* in characters such as the numbers of anal rays, gill rakers, and upper and lower jaw teeth, occasional presence of vomerine teeth (vs. never), having a 90° angle between the hyomandibular spine and condyle, having the haemal postzygapophyses longer than the prezygapophyses at the precaudal-caudal vertebral junction, and having a supramaxilla of intermediate width between the wide one in *S. chiliensis* and the narrow one in *S. orientalis. Sarda australis* resembles *S. chiliensis* in having a short hyomandibular spine that does not project beyond the condyle.

Morphometrically (Tables 1, 18), *Sarda australis* is very similar to the other species of *Sarda*. It has a longer first dorsal fin base (315-343 thousandths of FL) than either *S. chiliensis* (267-314) or eastern Pacific *S. orientalis* (282-302) but overlaps with Indo-West Pacific *S. orientalis* (285-327) and *S. sarda* (291-330). The maxilla is longer (503-539 thousandths of head length) than in *S. chiliensis* (460-503).

Types.—*Pelamys australis* Macleay 1880:557. Holotype: AMS Macleay Mus. F-333; 405 mm FL; Australia, New South Wales, Sydney, Port Jackson. Counts: dorsal fin rays XIX + 16 + VII; anal fin rays 15 + VI; pectoral fin rays 25-25; gill rakers 6 + 1 + 13 = 20; upper jaw teeth (left-right) 14-19; lower jaw teeth 13-10; palatine teeth about 10 in one long row; vertebrae 24 + 21 = 45; head length 82.9 mm, maxilla length 43.2 mm.

Distribution.—*Sarda australis* has the most restricted range of any species of bonito: the east coast of Australia plus Norfolk Island (Figure 70). Munro (1958a) gave the range as Queensland, New South Wales, and Victoria. Whitley (1964a) stated that *S. australis* ". . . is common at practically all times off eastern Australia from about the Capricorns [Queensland] to Sydney or even Gabo Island . . ." [just south of New South Wales—Victoria border]. There are specific literature reports from Victoria (McCoy 1888; Serventy 1941b) and Tasmania (Lord 1927), as well as from New South Wales. Except for one specimen from Norfolk Island (AMS I.10751), all the material we have examined has come from New South Wales (from north to south: Macleay River, Broughton Island off Port Stephens, Laurieton, New Castle, Sydney, Woolongong). Sherrin (1886) and others have reported *Sarda* from New Zealand, but it seems

TABLE 18.—Morphometric characters of *Sarda australis*. First set of numbers are measurements expressed in thousandths of fork length, second set as thousandths of head length.

Character	Range	$\bar{x}$	N
Fork length (mm)	195-526	349	21
Fork length			
Snout — A	662-698	674	20
Snout — 2D	581-605	586	20
Snout — 1D	251-276	263	20
Snout — P_2	281-312	296	20
Snout — P_1	258-281	267	20
$P_1 — P_2$	104-125	116	19
Head length	259-279	267	20
Max. body depth	221-240	231	16
Max. body width	127-169	141	17
P_1 length	112-135	121	19
P_2 length	76-118	85	20
P_2 insertion - vent	340-393	374	18
P_2 tip - vent	260-311	290	18
Base 1D	315-343	326	20
Height 2D	77-95	86	19
Base 2D	88-118	103	20
Height anal	72- 92	81	20
Base anal	48- 88	78	20
Caudal spread	238-277	259	11
Snout (fleshy)	88-103	96	20
Snout (bony)	76- 88	81	20
Maxilla length	131-150	139	20
Post orbital	120-136	130	20
Orbit (fleshy)	32- 41	37	19
Orbit (bony)	56- 84	66	20
Interorbital width	58- 72	66	19
Head length			
Snout (fleshy)	342-381	361	20
Snout (bony)	291-324	305	20
Maxilla length	503-539	518	20
Post orbital	478-508	492	20
Orbit (fleshy)	134-148	137	19
Orbit (bony)	231-287	246	20
Interorbital width	226-266	249	19

likely that these reports were based on misidentified specimens of *Allothunnus fallai* which was not described until 1948.

Sarda chiliensis (Cuvier)

Two subspecies of *S. chiliensis* are recognized: *S. c. chiliensis* (Cuvier) for the southeastern Pacific population and *S. c. lineolata* (Girard) for the northeastern Pacific population.

Sarda chiliensis chiliensis (Cuvier)

Pelamys chiliensis Cuvier in Cuvier and Valenciennes 1831:163 (original description; Valparaiso, Chile).
Pelamys chilensis. Günther 1860:368 (in part; description).
Sarda chilensis. Starks 1906:784 (Callao, Peru). Meek and Hildebrand 1923:318-319 (in part; description; Peru). Hildebrand 1946:372-374 (description; 13 Peruvian
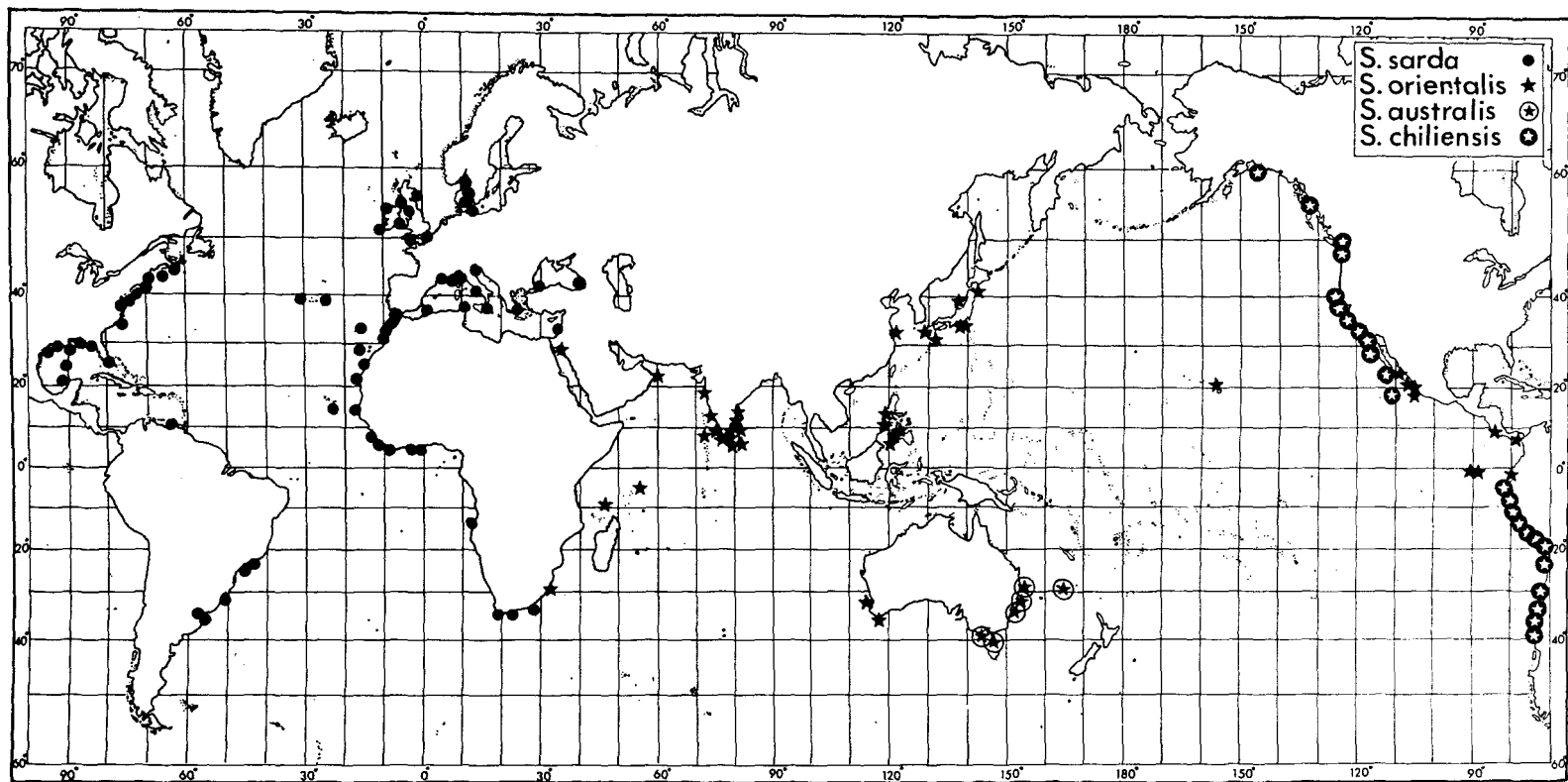
FIGURE 70.—Distribution of the four species of *Sarda* based on specimens personally examined and literature records.

specimens [USNM]). Fraser-Brunner 1950:146-147 (in part). La Monte 1952:44 (description), pl. 15. Mann 1954:298 (description, distribution; Chile). Vildoso 1960:1-75 (sexual maturity and reproduction; Peru). Bauchot and Blanc 1961:373 (type of *P. chiliensis*). Ancieta 1963:1607-1619 (fishery in Peru). Laevastu and Rosa 1963:1844, (fig. 7, in part; map of distribution and fishing areas). Vildoso 1963a:1143-1152 (reproduction; Peru). Blanc and Bauchot 1964:449, fig. 21 (type of *P. chiliensis*). Ancieta 1964:17-49 (species synopsis; Peru).

Sarda chiliensis. Walford 1936:8-10 (description; comparison with other species of *Sarda*). Chabanaud 1944:1-6 (in part; description; synonymy; all Indo-Pacific species considered synonyms of *S. chiliensis*). Godsil 1955:7-21, figs. 1-6, table 1-3 (description; anatomy; 5 Peruvian specimens). Pinkas 1961:175-188 (in part; 8 Peruvian juveniles, 38.0-201 mm). Klawe 1961b:487-493 (in part; juveniles from Peru and Chile), fig. 4 (160-mm Peruvian specimen).

Sarda sarda chiliensis. Buen 1958:12-17 (synonymy; description; fishery; range south to Talcahuano, Chile). Chirichigno 1969:75 (common name), 79 (fig. 147).

Sarda chilensis chilensis. Vildoso 1963b:1549-1556 (Peru; subspecifically distinct from *S. c. lineolata* based on vertebral number). Silas 1964:296-297 (in key, map, *S. chilensis* divided into an eastern Pacific *S. c. chilensis* and an Australian *S. c. australis*).

Sarda sarda chiliensis. Sánchez and Lam 1970:42-43 (length-weight; weights of parts of body; fig. of vertebral column; photograph; Peru).

Sarda chiliensis chiliensis. Kuo 1970:2805-2806 (taxonomy, growth, maturation).

Sarda chiliensis lineolata (Girard)

Pelamys lineolata Girard 1859:106 (original description, San Diego, Calif.).
Pelamys chilensis. Günther 1860:368 (in part).
Sarda chilensis. Jordan and Gilbert 1882:428 (in part; description; synonymy). Jordan and Evermann 1896:872-873 (in part; description; synonymy). Starks 1910:91-93 (osteology; Puget Sound specimen). Meek and Hildebrand 1923:318-319 (in part; description; synonymy). Hildebrand 1946:374 (*S. lineolata* a synonym

of *S. chilensis*). Fraser-Brunner 1950:146 (in part). Morice 1953a:37-39 (dentition; number of gill rakers and vertebrae). Ricker 1959b:6 (Revillagigedos Island, new record).

Sarda lineolata. Walford 1936:8-10 (key to species of *Sarda*; description). Walford 1937:22-23 (description). Clothier 1950:52-53 (vertebrae), pl. 10 (vertebral column). Godsil 1954:30-43, figs. 12-19, tables 4-5 (anatomy). Clemens and Wilby 1961:226-227 (description; north to northern end of Vancouver Island), fig. 131. Manzer 1965:853-855, fig. 1 (description; record from east coast of Vancouver Island).

Sarda stockii David 1943:31-33 (original description; Santa Monica Mountains, Calif.; Modelo formation, Upper Miocene), pl. 4 (holotype), 155 (additional specimen from Lompoc).

Sarda chilensis. Chabanaud 1944:1-6 (description, in part; recognizes Atlantic *S. sarda* and Indo-Pacific *S. orientalis*). Fraser-Brunner 1950:146 (in part). Godsil 1955:38-42 (*S. lineolata* a synonym of *S. chilensis*). Pinkas 1961:175-188 (in part; 27 juveniles 16.7-54.5 mm, from California and Baja California), fig. 4 (16.7-mm juvenile), fig. 5 (33.0-mm juvenile). Klawe 1961b:487-493 (in part; juveniles from California and Baja California), fig. 3 (42-mm juvenile). Radovich 1961:22, 31 (records north of Point Conception). Klawe 1962:180 (92-mm juvenile, Baja California). Laevastu and Rosa 1963:1844 (fig. 7, in part, map of distribution and fishing areas). Fitch and Craig 1964:201 (fig. 4, outline of sagitta), 202 (sagittae of three species of *Sarda* almost identical). Quast 1964:448 (11 specimens from coastal Alaska). Patten et al. 1965:298-299 (Puget Sound records). Magnuson and Prescott 1966:54-67 (courtship, locomotion, feeding). Fierstine and Walters 1968:1-31 (vertebral counts, myology, aspect ratio of caudal fin). Magnuson and Heitz 1971:363-365 (gill raker apparatus and filtering area). Pinkas et al. 1971:64-82 (food habits in southern California and Baja California). Hart 1973:373-374 (description, distribution, fig.).

Sarda chilensis lineolata. Kuo 1970:2805-2806 (taxonomy, growth, maturation).

Comparative Diagnosis.—*Sarda chilensis* is most similar to *S. orientalis* and *S. australis* and most different from *S. sarda* (Table 17). It differs from all three other species in having fewer anal fin rays (12-15, modally 14 vs. 14-17, modally 15)

and fewer total anal elements (18-22, modally 20 vs. 19-23, modally 21 or 22). *Sarda chiliensis* also has the greatest number of palatine teeth (9-22 vs. 7-14 in *S. australis*, 8-21 in *S. sarda* and *S. orientalis*) and the widest supramaxillary (slightly wider than in *S. sarda* and *S. australis*, much wider than in *S. orientalis*). *Sarda chiliensis* resembles *S. orientalis* and differs from *S. sarda* and *S. australis* in always lacking teeth on the vomer; *S. chiliensis* and *S. australis* both have a short hyomandibular spine that does not project beyond the condyle.

Morphometrically (Tables 1, 19), *Sarda chiliensis* has the shortest maxilla (463-489 thousandths of head length in the southeast Pacific population, 460-503 in the northeast Pacific), much shorter than *S. australis* (503-539) and *S. orientalis* (510-529) and the North American population of *S. sarda* (503-529), but overlapping with the eastern

Atlantic populations of this species (497-511, 494-523). It has a shorter first dorsal base (267-314 thousandths of fork length) than *S. australis* (315-343) and differs from the northwest Pacific population of *S. orientalis* in snout-second dorsal and pelvic origin to vent distances.

Types of Nominal Species.—Pelamys chiliensis Cuvier in Cuvier and Valenciennes 1831:163. Holotype: MNHN A.5608; 672 mm FL; Chile, Valparaiso; d'Orbigny. Type previously considered by Bauchot and Blanc (1961), Blanc and Bauchot (1964, photograph-fig. 21), and Collette (1966). Counts: dorsal fin rays XVIII + 14 + VIII; anal fin rays 12 + VI; pectoral fin rays 24; gill rakers missing; upper jaw teeth 23; lower jaw teeth (left-right) 16-19.

Pelamys lineolata Girard 1859:106. Holotype: USNM 688; 266 mm FL; California, San Diego; A. Cassidy. Counts: dorsal fin rays XIX + 14 + VIII; anal fin rays 12 + VII; pectoral fin rays (left-right) 26-26; gill rakers 9 + 1 + 17 = 27; upper jaw teeth (left-right) 23-22; lower jaw teeth 18-19; palatine teeth 18-17; vertebrae 24 + 21 = 45; lamellae in nasal rosette 26.

Sarda stockii David 1943:31-33, pl. 4. Holotype: LACM 1035/1059A; originally Calif. Inst. Technol. 10039; ca. 522 mm FL; California, Santa Monica Mountains, quarry near Mulholland Drive, locality 1035; Modelo Formation; Upper Miocene. Counts from holotype: dorsal fin rays XVIII or XIX + 13 or 14 + VI; anal fin rays 12 + VI; vertebrae 24 or 25 + 21-22 = 45 or 46. Caudal rays cover the hypural plate; teeth not visible; lower jaw with anteroventral notch similar to *Sarda*.

Distribution.—Sarda chiliensis is restricted to the eastern Pacific Ocean. Its range is divided into north and south temperate populations by a tropical population of *S. orientalis* (Figure 70). The southern *S. chiliensis chiliensis* was originally described from Valparaiso, Chile, and has been reported as far south as Talcahuano by Buen (1958) and Valdivia at lat. 39°48'S, long. 79°13'W by Kŭo (1970). Its northern limit is at Mancora, Peru (Ancieta 1964), at lat. 4°09'S, long. 81°01'W, immediately south of the Gulf of Guayaquil, Ecuador. Most of our material comes from near Callao, Peru.

The northern subspecies, *S. c. lineolata* was originally described by Girard (1859) from San Diego, Calif. It regularly reaches south to Magdalena Bay, Baja California (Radovich 1961; CAS

TABLE 19.—Comparison of morphometric characters in two populations of *Sarda chiliensis*, northeast Pacific (*S. c. lineolata*) and southeast Pacific (*S. c. chiliensis*). First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

Character	Northeast Pacific			Southeast Pacific		
	Range	$\bar{x}$	N	Range	$\bar{x}$	N
Fork length (mm)	207-587	375	24	325-672	498	18
Fork length						
Snout — A	642-674	656	23	631-672	654	18
Snout — 2D	553-595	573	24	551-585	569	18
Snout — 1D	243-281	269	24	268-290	279	18
Snout — P_2	275-318	295	24	280-323	303	18
Snout — P_1	247-279	266	24	260-300	275	18
$P_1 — P_2$	106-121	112	21	105-131	118	16
Head length	248-275	263	24	259-292	272	18
Max. body depth	179-232	210	24	177-230	210	13
Max. body width	98-167	131	22	116-154	134	10
P_1 length	99-132	116	24	125-152	138	18
P_2 length	65- 87	78	24	65- 91	84	18
P_2 insertion - vent	329-367	353	24	327-368	346	16
P_2 tip - vent	248-331	276	24	237-352	269	17
Base 1D	278-314	297	24	267-303	286	16
Height 2D	64- 98	83	23	82-116	97	17
Base 2D	71-115	93	23	80-109	94	18
Height anal	58- 89	74	23	77-107	92	18
Base anal	61- 84	71	24	61- 88	74	18
Caudal spread	196-300	234	20	228-289	258	11
Snout (fleshy)	87-119	94	24	86-102	95	18
Snout (bony)	71- 83	78	24	75- 89	81	18
Maxilla length	115-136	126	24	121-143	130	18
Post orbital	125-144	139	21	131-150	142	16
Orbit (fleshy)	25- 44	31	24	27- 36	31	18
Orbit (bony)	47- 63	57	22	47- 63	56	18
Interorbital width	57- 69	63	24	62- 82	70	18
Head length						
Snout (fleshy)	339-368	353	23	331-363	348	18
Snout (bony)	283-308	297	24	279-329	299	18
Maxilla length	460-503	481	24	463-489	477	18
Post orbital	499-548	526	21	504-544	523	16
Orbit (fleshy)	102-168	119	24	102-141	115	18
Orbit (bony)	190-238	218	22	174-229	205	18
Interorbital width	213-278	239	24	233-302	257	18

SU 61662, Blanca Bay, lat. 24°46′30″N, long. 112°15′W), and occasionally to Cabo San Lucas at the tip of Baja California (lat. 22°20′N, long. 112°27′W). There is one specimen (Ricker 1959b; UBC 57-149) from Socorro Island in the Revillagigedos Islands 250 miles south of Cabo San Lucas. It is not common north of Point Conception, Calif., but there are several scattered records: off the Farallon Islands and off Eureka, Calif. (Radovich 1961); Puget Sound (Starks 1910, Patten et al. 1965); east coast of Vancouver Island, British Columbia (Manzer 1965; UBC 64-394); and coastal Alaska (Quast 1964) in Clarence Strait northwest of Ketchikan (USNM 213494) and off the Copper River at lat. 60°16′N, long. 145°32′W (USNM 213495).

Geographic Variation.—Although the temperate northeast (c. lineolata) and southeast (c. chiliensis) Pacific populations of Sarda chiliensis are completely separated from each other by the tropical eastern Pacific population of S. orientalis (Figure 70), there are few differences between the two populations; anatomically they are virtually identical. The caecal mass extends posteriorly for more than half the length of the body cavity in ventral view in the northeast population; less than half this distance in the southeast population.

Walford (1936) used the posterior extent of the corselet to distinguish the northeast Sarda lineolata (pectoral fin extends scarcely beyond corselet) from the southeast S. chiliensis (pectoral fin extends an eye diameter further). Hildebrand (1946) considered this character entirely unreliable in separating the two populations. Kuo (1970) measured the extent of the corselet in 380 specimens from southern California and 49 from Callao, Peru. He found that the corselet does extend further posteriorly in the southern population but that the interpopulational differences were not significant at the 5% level. He concluded that the character was not reliable even for subspecific separation of the two populations.

Morphometrically, there are some differences in the ranges and means between the two populations (Table 19), but these are smaller than those between some populations of S. sarda and S. orientalis. Kuo (1970) found, through covariance analyses and scatter diagrams, significant differences at the 1% level between the two populations in such morphometric characters as head length, predorsal length, prepelvic length,

and the distance from the origin of the second dorsal and anal fins to the caudal base.

Among meristic characters, the total number of vertebrae is the best distinguishing character between the southeast and northeast populations of Sarda chiliensis. The northeast population has more vertebrae (Table 9) with means of 44.9 for our data, 44.8 for Kuo (1970), and 45 ± 0.47 for a sample of 19 reported by Vildoso (1963b). Our data for 23 southeast specimens ($\bar{x}$ 44.2) agrees with that reported by Vildoso (1963b) for two samples, 44.15 ± 0.40 for 38 specimens, and 44.21 ± 0.40 for a sample of 100. Kuo (1970), however, found even fewer: a range of 42-46 with a mode of 43 and a mean of 43.4 compared to our range of 43-46, mode 44, mean 44.2. The reasons for the discrepancies between our data and that of Vildoso on the one hand, and that of Kuo on the other are not known. We have reexamined seven of Kuo's southeastern specimens and find totals of 43 (1 specimen), 44 (5), and 45 (1).

There are also differences in the highly variable number of teeth in the upper and lower jaws (Tables 5, 6) with the northeast Pacific population having slightly more: upper jaw 20-30, $\bar{x}$ 23.7 vs. 18-28, $\bar{x}$ 23.0; lower jaw 15-25, $\bar{x}$ 19.4 vs. 14-23, $\bar{x}$ 18.9.

The available data does not convince us that the northeast and southeast Pacific populations are subspecies. However, as the populations are genetically isolated from each other and there are some significant differences, there is practical value in using the available subspecific names, and there is ample historical precedent for the name lineolata for the northeast population. Therefore, we have emphasized comparisons between the two geographic populations by labelling the populations northeast and southeast Pacific in the tables but have retained the subspecies designations in the formal synonymies.

Sarda orientalis (Temminck and Schlegel)
Indo-West Pacific

Pelamys orientalis Temminck and Schlegel 1844:99 (original description, Japan), pl. 52. Richardson 1846:268 (Sea of Japan). Günther 1860:368 (description). Tirant 1885:46 (Cambodia).
Pelamys chilensis (not of Cuvier 1831). Day 1878:253-254 (description; Bombay), pl. 56, fig. 1.
Sarda chilensis var. *orientalis*. Steindachner and Döderlein 1884:179 (description; Japan).

Sarda orientalis. Jordan and Snyder 1900:352 (Tokyo). Jordan and Snyder 1901:64 (Tokyo, Nagasaki). Kishinouye 1923:424-426 (description, anatomy; Japan, southern species abundant around Kyushu, juvenile from Aomori, Honshu), figs. 11, 17, 33, 42. Jordan and Hubbs 1925:215 (not uncommon in Japanese markets). Walford 1936:9 (*S. orientalis* separate species from *S. velox*). Tortonese 1939:323-324 (Yokohama, Japan). Boeseman 1947:94-95 (lectotype of *P. orientalis* selected). Smith 1949:299 (description; south to Durban, South Africa). Warfel 1950:18 (description; Philippine Islands), 21 (fig. 14, fish, gill arch, excised liver). Fraser-Brunner 1950:147-148 (description), fig. 12. Honma 1952:143 (Echigo Province, Honshu, Japan). Herre 1953:251 (Philippine Islands). Morice 1953a:37-39 (dentition; number of gill rakers and vertebrae), fig. 5 (after Warfel 1950). Godsil 1955:22-35, figs. 7-13, tables 4-6 (description, anatomy, five Japanese specimens). Smith 1956:721 (Aldabra). Munro 1958a:113 (Western Australia), fig. 755. Jones 1961:343,346, fig. 10 (158 mm. juvenile, fig. 11 (80 mm juvenile). Jones and Silas 1961:379-380 (Vizhingam and Cape Comorin, Western India), fig. 6 (juvenile and adult). Collette and Gibbs 1963b:30 (Indian Ocean), pl. 9, upper fig. Jones and Silas 1963:1787 (distribution in Indian Ocean). Kikawa et al. 1963:147-156 (species synopsis). Thomas and Kumaran 1963:1667 (diet in Indian waters mostly fish). Boeseman 1964:465, pl. 3, fig. 11 (lectotype of *P. orientalis*). Jones and Kumaran 1964:357-358, 360, fig. 60 (after Jones 1961). Jones and Silas 1964:26 (description), pl. 8A. Kumaran 1964:605 (diet 98% fish). Rao 1964:736 (ripe ovaries). Nakamura and Kikawa 1966:60-62 (infracentral grooves on vertebrae). Sivasubramaniam 1967:29 (catch in Ceylon), 44 (fig. 14, length-weight). Gnanamuttu 1968:365 (Madras). Sivasubramaniam 1969:73-77 (description, biology; Ceylon), pl. 1 (photos of juvenile and adult). Nair et al 1970:13-17 (biology, description; India). Nagabhushanam and Chandrasekhara Rao 1972:303 (Minicoy Atoll, Laccadive Archipelago).

Sarda chilensis (not of Cuvier 1831). Jordan and Snyder 1904:125 (description; Honolulu). Jordan et al. 1913:121 (Japan). Jordan and Jordan 1922:32 (occasional at Hawaii). Barnard 1927:801 (description; Natal coast, South Africa). Fowler 1928:134-135 (Hawaii). Chevey 1934:45-46 (Tirant's Cambodia record). Tinker 1944:160-161 (Hawaii). Brock 1949:275 (in key to Hawaiian scombrids).

Sarda chiliensis (not of Cuvier 1831). Fowler 1938:277 (Honolulu). Fowler 1949:73 (Honolulu).

Sarda orientalis serventyi Whitley 1945:41 (original description; Western Australia). Whitley 1947:146, pl. 11, fig. 4 (holotype). Whitley 1948:24 (range in Western Australia). Whitley 1964a:236, 242 (Western Australia). Whitley 1964b:48 (listed).

Sarda orientalis
Eastern Pacific

Sarda chilensis (not of Cuvier 1831). Gilbert and Starks 1904:68 (description; Panama City).

Sarda chiliensis (not of Cuvier 1831). Herre 1936:107 (Galapagos). Erdman 1971:68-69 (Gulf of Nicoya, Costa Rica).

Sarda velox Meek and Hildebrand 1923:320-321 (original description; Panama City), pl. 24. Walford 1936:8-10 (description; recognized as valid species). Walford 1937:23 (description), col. pl. 38a. Schmitt and Schultz 1940:3 (Galapagos Islands [USNM 107055]). Fowler 1944:342 (Galapagos Islands [ANSP 82007, 89065]). Hildebrand 1946:374-375 (description; Gulf of Guayaquil, Peru [USNM 127907]; Galapagos; Pearl Islands, Panama). La Monte 1952:44, 46 (description), pl. 15. Morice 1953a:37 (listed). Godsil 1954:44-59 (description; anatomy; 4 Galapagos specimens), tables 6, 7 (counts and measurements), figs. 21-27 (morphometrics), figs. 28-33 (anatomy), figs. 35-41 (osteology). Vildoso 1963b:1549-1556 (description; range). Laevastu and Rosa 1963:1844 (fig. 7, distribution map).

Sarda orientalis. Fraser-Brunner 1950:147 (*S. velox* a synonym of *S. orientalis*). de Sylva 1955:38, fig. 61 H (dorsal view of skull). Godsil 1955:36-42 (no significant anatomical differences between *S. velox* and *S. orientalis*). Ricker 1959a:13 (S. Baja California; Las Tres Marías Islands). Silas 1964:296 (in part; in key and on range map). Fitch and Craig 1964:202 (sagittae of three species of *Sarda* almost identical).

Comparative Diagnosis.—*Sarda orientalis* is similar to *S. australis* and *S. chiliensis* in an equal

number of characters (Table 17). It differs from the other species of *Sarda* in having the lowest number of gill rakers (8-13 vs. 16-27); a very narrow supramaxillary; the dorsal projection of the ectopterygoid slightly expanded versus pointed; only a trace of a depression in the position of the elliptical ceratohyal window; no depression on the ventral surface of the proximal portion of the glossohyal; the haemal postzygapophyses of the last precaudal vertebra and the haemal prezygapophyses of the first caudal vertebra abutting against each other; gall bladder not visible in ventral view between the intestine and spleen; and a narrower and longer vertical wing to the pelvic girdle. *Sarda orientalis* is similar to *S. sarda* in having a long hyomandibular spine that projects beyond the condyle and in having a low number of palatine teeth (8-19 vs. 8-21). *Sarda orientalis* is sharply differentiated from *S. chiliensis* in having fewer gill rakers, a much narrower supramaxillary, and also in having fewer larger teeth (upper jaw 12-20, $\bar{x}$ 15.5 vs. 18-30, $\bar{x}$ 23.5; lower jaw 10-17, $\bar{x}$ 13.0 vs. 14-25, $\bar{x}$ 19.2).

Morphometrically (Tables 1, 20), *Sarda orientalis* is generally similar to the other species of *Sarda*. It does have a longer maxilla (141-149 and 146-156 thousandths of fork length in the northwest and eastern Pacific populations, respectively) than *S. chiliensis* (115-143) and *S. sarda* (125-145). The base of the first dorsal fin (285-327, 282-302) is shorter than that of *S. australis* (315-343).

Types of Nominal Species.—*Pelamys orientalis* Temminck and Schlegel 1844:99, pl. 52. There are three syntypes in Leiden of which Boeseman (1947:94-95; 1964:465, pl. 3, fig. 11) selected the largest as lectotype. Lectotype: RMNH 2286; about 560 mm FL, stuffed and mounted; Japan; 1830; Burger. Paralectotypes: RMNH 842; about 470 mm, stuffed and mounted; Japan; Burger. RMNH 1244; 451 mm, stuffed but preserved in alcohol; Japan; 1824-29. Counts for lectotype (paralectotypes in parentheses): dorsal fin rays XVIII + 14 + VIII (XVIII + 14 + VIII, XIX + 15 + VIII); anal fin rays ca. 14 + VI (ca. 13 + VI, 15 + VI); pectoral fin rays 24 (23-23, 25-24); gills missing in all three; upper jaw teeth ca. 14 (ca. 13-11, 15-17); lower jaw teeth (left-right) 12-12 (?, 12-13).

Sarda velox Meek and Hildebrand 1923:320-321, pl. 24. Holotype: USNM 81060; 364 mm FL; Panama City market; 19 Jan. 1912; S. E. Meek and

TABLE 20.—Comparison of morphometric characters in populations of *Sarda orientalis* from Japan and the eastern tropical Pacific. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

Character	Japan			East tropical Pacific		
	Range	$\bar{x}$	N	Range	$\bar{x}$	N
Fork length (mm)	342-560	432	7	354-613	472	10
Fork length						
Snout — A	674-703	694	5	662-703	678	10
Snout — 2D	596-614	606	5	569-596	582	10
Snout — 1D	273-308	286	7	274-311	288	10
Snout — P_2	293-316	303	5	299-321	310	10
Snout — P_1	272-292	281	7	277-299	290	10
$P_1 — P_2$	109-118	113	5	105-118	114	10
Head length	268-286	278	7	266-294	284	10
Max. body depth	221-244	234	4	193-236	213	10
Max. body width	143-151	146	4	127-153	144	10
P_1 length	104-125	115	7	119-134	127	10
P_2 length	70- 78	76	5	81- 91	86	10
P_2 insertion - vent	374-419	392	7	353-384	367	10
P_2 tip - vent	305-322	311	7	265-302	280	10
Base 1D	285-327	306	7	282-302	292	10
Height 2D	75- 82	78	7	89-101	94	8
Base 2D	85-111	93	7	88-107	95	9
Height anal	61- 85	73	7	84- 97	89	8
Base anal	66- 78	73	7	73- 83	79	9
Caudal spread	168-234	214	4	192-259	236	5
Snout (fleshy)	86-103	96	7	98-105	101	10
Snout (bony)	80- 97	86	7	83- 91	86	10
Maxilla length	141-149	145	6	146-156	150	10
Post orbital	128-147	139	7	141-151	146	10
Orbit (fleshy)	32- 60	42	7	34- 40	37	10
Orbit (bony)	29- 65	56	7	60- 68	64	10
Interorbital width	67- 73	71	6	65- 79	71	10
Head length						
Snout (fleshy)	306-368	344	7	348-369	357	10
Snout (bony)	288-344	308	7	291-317	303	10
Maxilla length	510-529	522	6	512-557	528	10
Post orbital	476-525	503	5	494-553	512	10
Orbit (fleshy)	102-152	136	7	120-147	130	10
Orbit (bony)	210-234	220	7	210-238	226	10
Interorbital width	251-263	256	6	230-283	251	10

S. F. Hildebrand. Counts: dorsal fin rays XVIII + 15 + VIII; anal fin rays 15 + VI; pectoral fin rays (left-right) 25-24; gill rakers 3 + 1 + 8 = 12; upper jaw teeth (left-right) 17-19; lower jaw teeth 13-11; vertebrae 25 + 20 = 45; lamellae in nasal rosette 34-32.

Sarda orientalis serventyi Whitley 1945:41. Holotype figured in Whitley (1947:pl. 11, fig. 4). Holotype: WAM P.3512; 265 mm FL; Western Australia, Perth. Paratype: WAM P.2568; 480 mm; Western Australia, Busselton. The holotype could not be located when Collette visited Perth in 1970. Counts for paratype: dorsal fin rays XVIII + 14 + VIII; anal fin rays 14 + VI; pectoral fin rays 24-24; no gills; upper jaw teeth (left-right) 19-17; lower jaw teeth 15-14; palatine teeth 13.

Distribution.—*Sarda orientalis* is widespread in the Indo-Pacific but there are two reports from the Atlantic Ocean. Nichols and Breder (1927) record-

ed it (as *S. velox*) from Block Island, R.I., based on a drawing (Stillman 1921). We do not believe a positive identification of a species of *Sarda* can be based solely on a drawing. Fraser-Brunner (1950) "confirmed" the presence of *S. orientalis* in the Atlantic based on a specimen from the Gold Coast (Ghana), but reexamination of this specimen (BMNH 1939.7.12.31) shows it to be a perfectly normal *S. sarda*.

There appear to be large gaps between populations in the tropical Indo-West Pacific (Figure 70). In the western Indian Ocean, it is recorded from along the coast of Natal, South Africa (Barnard 1927; ANSP 91185), south to Durban (Smith 1949; BMNH 1920.7.23.59). It occurs at Aldabra (Smith 1956) and in the Seychelles Islands (Smith and Smith 1963; BMNH 1927.4.14.81). We have examined specimens from Eilat at the northern end of the Gulf of Aqaba in the Red Sea (SFRS 704/1-2) and from Muscat at the entrance to the Persian Gulf (BMNH 1888.12.129-131). Day (1878) gave an early report from Bombay. Silas (1964, fig. 7) mapped the occurrence and fishery areas for *Sarda orientalis* in the eastern Arabian Sea along the southwest coast of India and Nagabhushanam and Chandrasekhara Rao (1972) listed it among the fauna of Minicoy Atoll, Laccadive Archipelago. Sivasubramaniam (1967, 1969, 1970) recorded it as one of the least abundant tunas in the inshore water of Sri Lanka (Ceylon); we have examined a juvenile from there (UBC 57-183). Small quantities were taken in gill nets off Madras in 1966 (Gnanamuttu 1968). We have not seen any records or specimens from the eastern Indian Ocean except for the southwest tip of Australia from where Whitley (1945) described *S. orientalis serventyi* (Albany and Busselton, Western Australia; WAM P. 2568).

There appear to be no records or museum specimens of *Sarda orientalis* from Indonesia or elsewhere in the East Indies. There is an old published record for Cambodia (Tirant 1885), but we have seen no specimens from the Gulf of Thailand or South China Sea in any collections including the extensive series of scombrids collected by the George Vanderbilt Expedition. Warfel (1950) and Herre (1953) reported it from the Philippine Islands and there are specimens from Shanghai (MNHN 91-628; NHMV uncat.). Starting with its original description by Temminck and Schlegel in 1844, there have been numerous reports from Japan where it is not uncommon in many markets (Jordan and Hubbs

1925): Richardson 1846 (Sea of Japan); Jordan and Snyder 1900 (Tokyo); Jordan and Snyder 1901 (Tokyo and Nagasaki); Tortonese 1939 (Yokohama). Kishinouye (1923) reported *S. orientalis* as abundant around the island of Kyushu and he recorded a juvenile from north as far as Aomori Prefecture (about lat. 41°N) at the north end of Honshu. According to Kikawa et al. (1963), this remains the northernmost record of the species in Japan. Honma (1952) listed it from Sado Island (about lat. 38°N), Niigata Prefecture, in the Sea of Japan. Carl L. Hubbs obtained specimens (UMMZ uncat.) from Suruga Bay and Sagami Bay in 1923 and Collette purchased specimens in the Tokyo market in 1966. There appears to be a large gap in the range from Japan and China on the north and the Philippine Islands further south all the way east to the Hawaiian Islands where it is not common (Jordan and Snyder 1904; Jordan and Jordan 1922; Fowler 1928; Tinker 1944; Brock 1949); however, we have examined two preserved Hawaiian specimens (USNM 58527; ANSP 82258) and have dissected two recently collected specimens.

The eastern Pacific population is confined to the tropical coasts of Middle America and Ecuador and also occurs in the Galapagos Islands. This population was described as *Sarda velox* by Meek and Hildebrand in 1923 from Panama City specimens and several other records are also from Panama and the Pearl Islands (Gilbert and Starks 1904; Hildebrand 1946; CAS SU 12824; USNM 81060, 128643-5). The range extends south to the Galapagos (Herre 1936; Schmitt and Schultz 1940; Fowler 1944; Hildebrand 1946; Godsil 1954; ANSP 82007, 89065; CAS SU 4885; USNM 107055, 119781) and the Gulf of Guayaquil, Ecuador (Hildebrand 1946; USNM 127907). To the north, there are records from the Gulf of Nicoya, Costa Rica (Erdman 1971) and from the coast of Mexico at Banderas Bay, Las Tres Marías Islands, and Cape San Lucas (NMC 68-0710) at the southern tip of Baja California (Ricker 1959a).

Geographic Variation.—The distribution of *Sarda orientalis* (Figure 70) is disjunct and, therefore, subspecific or populational differences are possible. Two forms have been named—the population in southwestern Australia (*S. orientalis serventyi* Whitley) and the tropical eastern Pacific population (*S. velox* Meek and Hildebrand). Based on the scattered material available, there appear to be no significant anatomical or meristic

differences between any populations of the species. Morphometrically, there appear to be some differences between the small samples from Japan and the eastern Pacific (Table 20), in such characters as snout-second dorsal distance, pelvic fin tip to vent, height of anal and second dorsal fins. Until more material is examined, there does not seem to be adequate data to support recognition of subspecies in *S. orientalis*. However, to facilitate entry into the literature, the synonymies have been divided into Indo-West Pacific (including Hawaii) and tropical eastern Pacific.

Sarda sarda (Bloch)

Pelamis Belon 1553:177-179 (description).
Amia Rondelet 1554:238-241 (description, fig.).
Pelamyde vera Rondelet 1554:245-248 (description, fig.)
Pelamyde sarda Rondelet 1554:248 (description, fig.).
Thunnus authoris primus Aldrovandi 1613:313 (fig.).
Pelamys sarda Willughby 1686:179 (description).
Scomber pelamis Brünnich 1768:68-69 (original description; Adriatic Sea; preoccupied by *Scomber pelamis* Linnaeus, 1758 [= *Katsuwonus pelamis*]).
Bonite Duhamel du Monceau 1769: pl. 7, fig. 2.
Thonin sorte de pélamide Duhamel du Monceau 1769: pl. 7, fig. 5.
Scomber sarda Bloch 1793:44-48 (original description; pre-Linnean synonymy; Europe) pl. 334. Bloch and Schneider 1801:22-23 (description; Mediterranean and Atlantic). Risso 1810:168-169 (description; Nice).
Scomber mediterraneus Bloch and Schneider 1801:23 (substitute name for *Scomber pelamis* Brünnich; description). Delaroche 1809:336 (description; Balearic Islands and Mediterranean coast of Spain).
Scomber palamitus Rafinesque 1810:44-45 (original description; Palermo, Sicily), pl. II, fig. 2.
Scomber ponticus Pallas 1811:217 (original description; Crimea).
Thynnus pelamis. Risso 1826:415-416 (synonymy; description; Nice).
Thynnus sardus. Risso 1826:417 (synonymy; description; Nice).
Thynnus brachypterus Cuvier 1829:198 (original description based on the *pelamyde vera* of Rondelet (1554:245) and the thonin sorte de

pélamide of Duhamel du Monceau (1769:pl. 7, fig. 5).
Sarda sarda. Cuvier 1829:199 (original description of *Sarda*). Dresslar and Fesler 1889:440-441 (synonymy; description; Woods Hole, Mass.), pl. 8. Berg 1895:41 (Mar del Plata, Argentina). Jordan and Evermann 1896:872 (description; synonymy). Ihering 1897:52 (Rio Grande do Sul, Brazil). Fowler 1915:532 (Trinidad). Miranda Ribeiro 1918:766 (Santos, Brazil). Schroeder 1924:6 (uncommon in Florida Keys). Chabanaud 1925:199-200 (vertebral number; West Africa), fig. (dentition). Fowler 1926:268 (Buenos Aires). Barnard 1927:800 (description; Cape Seas, South Africa). Chabanaud and Monod 1927:279 (Port Étienne, Mauritania). Nichols and Breder 1927:122-123 (description; Western Atlantic north to Casco Bay, Maine) fig. 169. Buen 1930a:40 (pl. 1, fig. 4), 46 (synonymy; description; Spain). Buen 1930b:1-32 (larvae and juveniles; Mediterranean Sea), figs. Dieuzeide 1930:134-140 (synonymy; description; Algeria), pl. 2. Le Gall 1934b:287 (description), fig. (after Smitt). Pozzi and Bordale 1935:162 (lat. 35-38°S, Argentina). Vladykov 1935:7-8 (Nova Scotia). Fowler 1936:626-627 (synonymy; description; Italian and New Jersey specimens). Walford 1936:9 (key to species of *Sarda*). Cadenat 1937:482 (Cape Verde, Sénégal). Lovén 1938:274-280 (Scandinavian records), 275 (fig. 1), 276 (fig. 2, map). McKenzie 1939:16 (St. Margaret's Bay, Nova Scotia). Baughman 1941:18 (Texas [USNM 118644-6]). Jensen 1941:201-202 (14 locality records from the Kattegat off Denmark). Redeke 1941:212-213 (description; Netherlands). Chabanaud 1944:3-6 (*S. sarda* a distinct species). La Monte 1945:20-21, col. pl. 8. Irvine 1947:185-186 (description; Accra, Ghana). Poll 1947:284-285 (description), fig. 183. Molteno 1948:23 (abundant off Angola and South West Africa; summer schools from Cape Point to Mosselbaai, South Africa). Smith 1949:299 (occasional at Cape Point, South Africa), col. pl. 66, fig. 833. Tortonese and Trotti 1949:86 (common in Ligurian Sea). Cadenat 1950:134 (Cape Verde Islands). Fraser-Brunner 1950:146-147 (key; range), fig. 11. Postel 1950:59-62 (description; length-frequency; biology; Cape Verde Islands). Rivas 1951:223 (synonymy; description; Western Atlantic). La Monte 1952:46 (description; range), col. pl.

17. Lozano y Rey 1952:523-527 (synonymy; description), col. pl. 39, fig. 4. Bigelow and Schroeder 1953:337-338 (description; habits; range in Gulf of Maine), fig. 180 (after Smitt). Morice 1953a:37-41 (anatomy), p. 58 (fig. 5 after Dresslar and Fesler 1889). Morice 1953b:72 (fig. 6, liver). Belloc 1954:297-310 (description; synonymy; Mediterranean distribution; biology; fishery). Collins 1954:27 (Azores). Mather and Day 1954:182 (Spanish Sahara). Pew 1954:28-30 (Texas), fig. 27. Postel 1954:357-358 (stomach contents); 359 (parasites), 361 (gonosomatic index). Dieuzeide et al. 1955:147-148 (description; range; fig.; Algeria). Dollfus 1955:55 (listed), 141 (references; Atlantic coast of Morocco). Frade and Postel 1955:34 (gonads; spawning season; Cape Verde Islands), 35 (fig. 5, ovary). Hildebrand 1955:206 (common sports fish in northwest Gulf of Mexico; 6 trawled west of Campeche). Nümann 1955:75-127 (migrations in the Black Sea and Sea of Marmara). A. Postel 1955:57-67 (number of teeth in 503 specimens; Tunisia). E. Postel 1955a:1-167 (summary of biology in the tropical eastern Atlantic). E. Postel 1955b:31-32 (sex ratio; maximum size). Springer and Bullis 1956:71 (Arcas Cay, off Campeche, Mexico). Mather and Gibbs 1957:243 (Shag Harbour, Nova Scotia). Ionescu et al. 1958:165-186 (biology; Roumania). Klawe and Shimada 1959:111 (2 juveniles, 64-67 mm; Gulf of Mexico), 112 (fig. 6, 67-mm juvenile). Gordon 1960:47-48 (summer visitor to Block Island Sound, R.I. Bauzá Rullán 1961:155-156 (otoliths), pl. 1 (figs. 7-10, sagittae). Klawe 1961a:154 (34-mm juvenile off Charleston, S.C.). Mansueti 1962:47-49 (description; Chesapeake Bay). Nunes-Ruivo 1962:17 (copepod *Caligus pelamydis* from Angolan specimen). Collette and Gibbs 1963a:26 (species of *Sarda*). Demir 1963:101-129 (description, synonymy; range; biology, especially in the Black Sea). Idyll and de Sylva 1963:755-760 (biology; western Atlantic). Laevastu and Rosa 1963:1844 (fig. 7, map of distribution and fishing areas). Bănărescu 1964:805-809 (synonymy; description; ecology; Roumania), fig. 355 (adult), fig. 356 (larvae). Demir 1964:455-457 (meristics of 1,000 specimens; Black Sea and Sea of Marmara). Fitch and Craig 1964:202 (sagittae of three species of *Sarda* almost identical). George et al. 1964:21 (Lebanon, rare). Postel 1964:220 (summary of biology, North Africa). Svetovidov 1964:389-395 (extensive synonymy; description; biology; Black Sea), fig. 125 (adult), fig. 126 (juvenile). Boschung 1966:227-228 (Gulf of Mexico records; stomach contents). Rodrígues-Roda 1966:269-279 (biology; Spanish trap net fishery 1958-1964). Jensen 1967:45-46 (central and western Gulf of Guinea). Padoa 1967:479-483 (eggs and larvae), figs. 308-312 (eggs and larvae). Bini 1968:37-38 (description; col. fig.). Granier 1968:325 (Golfe d'Aigues-Mortes, Golfe du Lion, France). Rae and Pirie 1968:212 (Montrose, east coast of Scotland). Went 1968:37-38 (Streedagh, near Grange, County of Sligo, Ireland; previous Irish records). Williams 1968:436 (Gulf of Guinea). Dornescu and Mişcalencu 1968:15 (perciform type of branchial apparatus). Muir 1969:168 (gill dimensions). Rae and Pirie 1969:279 (Garlieston, Scotland). Went 1969:149 (7 previous Irish records). Wheeler and Blacker 1969:327 (British seas 1966-67). Lozano Cabo 1970:158 (Spanish Morocco). Mago Leccia 1970:109 (Venezuela). Muir 1970:22 (measurements of branchial vessels of second gill arch). Carey et al. 1971:136 (body temperature). Dahl 1971:276-277 (Colombia). De Groot and Nijssen 1971:8 (Arguin Bank, Mauritania). Went 1971:44 (Irish records). Adamicka 1972:308-331 (functional anatomy of the head), figs. 1-4 (head muscles). Wheeler and Blacker 1972:162 (British seas, 1968-69). Postel 1973:475 (synonymy; distribution).

Pelamys sarda. Cuvier in Cuvier and Valenciennes 1831:149-162 (synonymy; description; Cape Verde Islands and Brazil); pl. 217. Rathke 1837:335 (*Scomber ponticus* Pallas a synonym of *P. sarda*). Bonaparte 1845:74 (synonymy). Guichenot 1850:58 (synonymy; Algeria). Lowe 1850:248 (Madeira). Storer 1855:141-143 (description; Massachusetts), pl. 11, fig. 5. Günther 1860:367 (synonymy; description). Duméril 1858:262 (Cape Verde Islands). Steindachner 1865:401 (Canary Islands). Steindachner 1868:358-360 (description; Iberian Peninsula and Canary Islands). Canestrini 1870:103 (description; Italy). Collett 1879a:19-20 (description; Christiana (= Oslo), Norway). Giglioli 1880:25 (Italy). Moreau 1881:430-434 (synonymy; description; France). Ninni 1882:264 (Adriatic). Rochebrune 1882:95

(Cap Vert). Hilgendorf 1888:208 (Azores Islands). Osorio 1890:56 (Angola). Vinciguerra 1893:93 (Canary Islands). Griffini 1903:398 (description; Italy). Pellegrin 1908:89-90 (Dakar), fig. 6. Shepherd 1910a:59, fig. 13 (asteriscus). Shepherd 1910b:293, fig. 1 (sagitta). Parona 1919:84-91 (synonymy; common names; description; distribution; Italy; col. pl. 8). Farran 1923:106 (Ireland). Sanzo 1932:3-9 (eggs and larvae; Italy; col. pl. with 7 figs. of egg and developing embryo). Athanassopoulos 1934:315-316 (Greece; Sea of Marmora). Liebman 1934:325 (Israel).

Palamita sarda. Bonaparte 1831:173 (original description of *Palamita*, substitute name for *Pelamys* Cuvier, preoccupied).

Pelamis sarda. Valenciennes 1844:49-50 (Canary Islands). Verany 1847:493 (Liguria, Italy). Ehrenbaum 1924:10-11 (vertebral counts; description of 7.2-mm larva from Oran, Algeria); fig. 3a (7.2-mm larva) and 3b (preopercle of larva).

Sarda pelamys. Gill 1862:126 (type-species of *Sarda*). Jones 1879:88 (Halifax, Nova Scotia).

Sarda mediterranea. Jordan and Gilbert 1882:427-428 (description; both sides of Atlantic; synonymy). Carus 1893:659 (Mediterranean). Šoljan 1963:147 (description; figs.; Adriatic Sea).

Sarda pelamis. Smitt 1892:105-107 (synonymy; description; occasional visitor to Scandinavia), fig. 30. Sanz Echeverría 1926:150 (sagitta). Jensen 1937:10-11 (a summer visitor to the Skagerak and Kattegat). Otterstrøm 1943:125-126 (summary of previous records from Denmark, photograph).

Comparative Diagnosis.—*Sarda sarda* is the most distinct species in the genus and can be distinguished from the other three species by higher counts in several characters (Table 17). Dorsal spines number 20-23 compared to 17-19; vertebrae 50-55 vs. 43-46; pleural ribs 24 vs. 19-23; intermuscular bones 31-45 vs. 32-36; keels on vertebrae number 5-10 (counting from hypural plate anteriorly) vs. 5-8. *Sarda sarda* is closest to *S. australis* in several characters: numbers of anal rays, gill rakers, upper and lower jaw teeth, occasional presence of vomerine teeth, angle of the hyomandibular spine and the condyle, width of the supramaxilla, and relative length of the haemal pre- and postzygapophyses on the first caudal vertebra. As in *S. australis*, the supramaxilla is in-

termediate in width, wider than in *S. orientalis*, but narrower than in *S. chiliensis*. *Sarda sarda* resembles *S. orientalis* in having a long hyomandibular spine, projecting beyond the condyle.

Morphometrically (Tables 1, 21), *Sarda sarda* is similar to the other species of *Sarda* but has a shorter first dorsal base (291-330 thousandths of fork length, $\bar{x}$ 311 vs. 315-343, $\bar{x}$ 326) and smaller orbit (35-64 vs. 60-80, $\bar{x}$ 66) than *S. australis*. The first dorsal fin base is longer than in *S. chiliensis* (329-368) as is also the maxilla (494-529 thousandths of head length vs. 463-503). *Sarda sarda* differs from *S. orientalis* in averaging a longer head and greater distances from snout to anal origin and snout to pelvic fin origin.

Types of Nominal Species.—*Scomber pelamis* Brünnich 1768:68-69. Adriatic Sea. No types known to be extant. Counts from the original description (dorsal fin rays XXIII + 15 + VIII; anal fin rays 15 + VII; pectoral fin rays 24) leave little doubt about the description being of *S. sarda*.

Scomber sarda Bloch 1793:44-48, pl. 334. Europe. No types known to be extant. The plate leaves little doubt as to the identity of the description. Counts from the original description: dorsal fin rays XXI + 15 + VII; anal fin rays 14 + VI.

Scomber palamitus Rafinesque 1810:44-45, pl. 2, fig. 2. Palermo, Sicily. No types known to be extant. Original description states that there are 20 spines in the first dorsal fin and the figure is of *S. sarda*.

Scomber ponticus Pallas 1811:217. Black Sea. No types known to be extant. Original description includes counts of dorsal fin rays XXII + 14 + IX; anal finlets VIII; and pectoral fin rays 25.

Thynnus brachypterus Cuvier 1829:198. The original description is not based on specimens but on pre-Linnean authors—the "pelamyde vera" of Rondelet (1554:245-248) and the "thonin sorte de pélamide" of Duhamel du Monceau (1769:pl. 7, fig. 5). The large teeth, general body shape, and broad vertical bands show both figures to be of juvenile *Sarda*. The specimens used by Cuvier (in Cuvier and Valenciennes 1831) in the redescription of *T. brachypterus* and considered by Bauchot and Blanc (1961) and Blanc and Bauchot (1964) as types are not types. (As Collette 1966, pointed out, four of these specimens are *Thunnus thynnus* and one is *Euthynnus alletteratus*).

Distribution.—*Sarda sarda* occurs along the tropical and temperate coasts of the Atlantic

TABLE 21.—Comparison of morphometric characters in populations of *Sarda sarda* from North America, the Mediterranean Sea, and the Gulf of Guinea. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

Character	North America			Mediterranean			Gulf of Guinea		
	Range	$\bar{x}$	N	Range	$\bar{x}$	N	Range	$\bar{x}$	N
Fork length (mm)	228-500	362	17	260-504	376	7	305-443	379	9
Fork length									
Snout — A	646-690	668	13	641-685	660	7	648-666	657	9
Snout — 2D	570-594	582	13	563-593	579	7	570-585	578	9
Snout — 1D	262-275	270	13	257-284	266	7	262-306	298	9
Snout — P_2	286-304	296	12	280-302	288	6	267-284	275	9
Snout — P_1	259-284	269	13	255-274	263	7	253-273	267	9
$P_1 — P_2$	105-118	111	12	94-114	104	7	107-118	111	8
Head length	256-272	264	13	251-268	259	7	253-278	271	8
Max. body depth	200-224	214	8	197-216	205	5	195-228	217	8
Max. body width	96-171	135	10	115-148	131	6			
P_1 length	96-138	115	13	105-127	116	6	120-136	130	9
P_2 length	73- 84	79	12	76- 86	82	7	77- 87	83	9
P_2 insertion - vent	348-403	366	13	356-379	370	7	341-388	357	9
P_2 tip - vent	269-302	282	12	269-297	285	7	252-293	266	9
Base 1D	291-330	311	13	301-323	311	7	298-323	311	9
Height 2D	68- 90	80	10	85-117	95	5	81- 99	91	9
Base 2D	85-113	96	13	93-112	104	5	92-112	107	9
Height anal	68- 98	77	11	68- 85	79	6	77- 91	85	9
Base anal	63- 86	73	13	69- 90	78	7	66- 89	80	9
Caudal spread	204-235	222	5	226-270	247	4	223-289	253	3
Snout (fleshy)	76-100	94	13	88- 98	93	7	88-101	96	9
Snout (bony)	78- 93	82	13	74- 83	78	7	75- 85	82	9
Maxilla length	131-141	136	13	127-136	131	7	125-145	138	9
Post orbital	130-142	136	11	126-136	132	7	133-144	138	9
Orbit (fleshy)	27- 40	32	17	27- 34	31	7	31- 36	34	9
Orbit (bony)	35- 64	57	13	53- 62	57	6	53- 64	60	9
Interorbital width	59- 73	64	13	59- 64	62	7	58- 65	63	9
Head length									
Snout (fleshy)	354-374	360	17	346-367	358	7	346-366	353	9
Snout (bony)	289-342	309	13	289-312	303	7	293-308	301	9
Maxilla	503-529	514	13	497-511	505	7	494-523	509	9
Post orbital	494-541	516	11	503-521	511	7	489-519	506	9
Orbit (fleshy)	100-149	121	17	104-133	118	7	116-132	122	9
Orbit (bony)	203-248	222	16	210-232	220	6	204-228	220	9
Interorbital width	216-275	242	13	231-245	238	7	212-245	231	9

Ocean, including the Gulf of Mexico and the Mediterranean and Black seas (Figure 70). Its usual northern limit in the western North Atlantic is Cape Ann, Mass. (Bigelow and Schroeder 1953), but there are records north to Casco Bay, Maine (Nichols and Breder 1927) and to several localities along the outer coast of Nova Scotia (from north to south): Cape Breton Island (McKenzie 1939); Halifax (Jones 1879); Lunenberg (McKenzie 1939); Shag Harbour (Mather and Gibbs 1957); and Pubnico (Vladykov 1935). It is common along the east coast of the United States but becomes uncommon around Miami (D. P. de Sylva, pers. commun.) and the Florida Keys (Schroeder 1924). Although Rivas (1951) stated that there were no records of *S. sarda* from the Gulf of Mexico or Caribbean Sea, there are now several such reports; northern Gulf of Mexico (Boschung 1966) off Pensacola, Fla. (USNM 30692; CAS IU 7825), Dauphin Island, Ala. and the Mississippi Delta (USNM 188420; UMML

7745); Texas (Baughman 1941; Pew, 1954; Hildebrand 1955; USNM 118644-6; CAS SU 18003); the middle of the Gulf (Klawe and Shimada 1959); and Campeche, Mexico (Hildebrand 1955; Springer and Bullis 1956). We have also examined a specimen that was collected by Poey and labelled "Cuba" (MCZ 17047). *Sarda sarda* is apparently absent from most of the Caribbean Sea but is recorded from Colombia (Dahl 1971) and Venezuela (Röhl 1942; Mago Leccia 1970), and we have examined a series of specimens from the Gulf of Cariaco, Venezuela, collected by the RV *Geronimo* in 1966. Fowler (1915) stated that several were seen in the fish market of Port-of-Spain, Trinidad but none were preserved. Published records and museum specimens become more common south of the Amazon: Rio de Janeiro (BMNH 1903.6.9.77, 1923.7.30.303); Santos (Mirando Ribeiro 1918); Rio Grande do Sul (Ihering 1897; MCZ 4739); Argentina from lat. 35° to 38°S (Pozzi and Bordale 1935);

Buenos Aires (Fowler 1926); and Mar del Plata, Argentina (Berg 1895; MACN 5151; MSNG 27472).

Sarda sarda extends further north and south in the eastern than in the western Atlantic, from near Oslo, Norway to Port Elizabeth, South Africa. In Scandinavia it has been taken in Oslo Fjord (Collett 1879a; five ZMO specimens, 425-600 mm FL) and along the Swedish and Danish coasts of the Kattegat (Smitt 1892; Jensen 1937; Lovén 1938; Jensen 1941; Otterstrøm 1943). There is one record from the Netherlands (Hubrecht 1879; Redeke 1941) and there are records from Scotland (Montrose on the east coast, Rae and Pirie 1968; Wigtown on the west coast, Rae and Pirie 1969) and from many counties in Ireland (Farran 1923; Went 1968, 1969, 1971; Wheeler and Blacker 1969, 1972). It is common throughout most of the Mediterranean (Belloc 1954) including the Adriatic Sea (Brünnich 1768; Ninni 1882; Šoljan 1963), Aegean Sea, Sea of Marmora, and the Black Sea (Pallas 1811; Athanassopoulos 1934; Nümann 1955; Demir 1963, 1964; Bănărescu 1964; Svetovidov 1964; MNHN A.6870; USNM 199648; BMNH 1864.4.25.13, 1888.2.3.53). There are records from the four major groups of islands off Europe and Africa: the Azores (Hilgendorf 1888; Collins 1954; USNM skeletons), Madeira (Lowe 1850; BMNH uncat.), Canaries (Valenciennes 1844; Steindachner 1865, 1868; Vinciguerra 1893), and Cape Verdes (Cuvier and Valenciennes 1831; Duméril 1858; Cadenat 1950; Postel 1950). Along the coast of North Africa, there are records from Spanish Morocco (Lozano Cabo 1970), Morocco (Dollfus 1955); Spanish West Africa (Mather and Day 1954); Port Étienne and d'Arguin Bank, Mauritania (Chabanaud and Monod 1927; De Groot and Nijssen 1971); Cape Verde, Sénégal (Rochebrune 1882; Pellegrin 1908; Cadenat 1937; Frade and Postel 1955). *Sarda sarda* is also present in the Gulf of Guinea from Sénégal to Ghana (Irvine 1947; BMNH 1939.7.12.31; Jensen 1967; 23 USNM specimens from the Guinean Trawling Survey; Williams 1968); along the coasts of Angola (Osorio 1890) and South-West Africa (Molteno 1948) through the "Cape Seas" (Barnard 1927) to the Cape of Good Hope (Smith 1949), Mosselbaai (Molteno 1948), and Port Elizabeth, South Africa (SAM uncat.), in the southwestern corner of the Indian Ocean.

Geographic Variation.—For purposes of comparison, *Sarda sarda* was divided into five populations: North America, South America (no vertebral counts available), northeast Atlantic (Scandinavia, Atlantic Europe, and the Azores), Mediterranean Sea (including the Black and Adriatic seas), and Gulf of Guinea (extending south to South Africa). Comparison of meristic characters shows that the two western Atlantic populations are similar to each other as are the Mediterranean and Gulf of Guinea populations. There are differences in a number of characters between combined eastern and combined western Atlantic populations, mostly correlated with higher vertebral counts in the eastern Atlantic. The small northeast Atlantic sample is similar to the other two eastern Atlantic populations but resembles the western Atlantic populations in some characters.

The North American population has 50-53 vertebrae, mode 51, $\bar{x}$ 51.1, compared to a range of 52-55, mode 53, $\bar{x}$ 53.3, for the Mediterranean-Gulf of Guinea (Table 9). Three specimens from the Azores have 51 vertebrae, thus resembling the western Atlantic population. Correlated with vertebral counts, there are fewer fin rays in the western Atlantic (Tables 10-12): dorsal spines modally 21 vs. 22; second dorsal rays modally 16 vs. 17; total second dorsal elements 24 vs. 25; anal rays modally 15 vs. 15 or 16; total anal elements modally 22 skewed toward 21 vs. 22 or 23 skewed toward 22. Independently, there are also fewer gill rakers (Table 7) in the western Atlantic (North America modally 17, $\bar{x}$ 17.6, South America modally 18, $\bar{x}$ 18.7) compared to the eastern Atlantic (Mediterranean and Gulf of Guinea, $\bar{x}$ 20.9)

Based on admittedly small samples, there seems to be a difference between western and eastern Atlantic specimens of *S. sarda* in the size of the caecal mass. Western Atlantic specimens have the caecal mass extending posteriorly for more than half the length of the body cavity in ventral view; eastern Atlantic specimens less than half this distance.

Study material was adequate to compare three areas morphometrically: western Atlantic, Mediterranean Sea, and Gulf of Guinea. There appear to be differences in three characters (Table 21). The western Atlantic population has a lower second dorsal fin (68-90 thousandths of fork length, $\bar{x}$ 80) and a smaller caudal spread (204-235, $\bar{x}$ 222) than do the two eastern Atlantic populations (85-117, $\bar{x}$ 95 and 81-99, $\bar{x}$ 91 for the second dorsal height of the Mediterranean and Gulf of Guinea populations, respectively; 226-270, $\bar{x}$ 247 and 223-289, $\bar{x}$ 253 for the caudal spread). In the snout-

pelvic fin origin distance, the western Atlantic and Mediterranean populations have a longer distance (286-304, $\bar{x}$ 296 and 280-302, $\bar{x}$ 288 respectively) than does the Gulf of Guinea population (267-284, $\bar{x}$ 275).

Of the three widespread species of *Sarda*, there is at least as much justification for recognition of subspecies in *S. sarda* as in *S. chiliensis*. However, there appears to be no available name for the western Atlantic population, the Azores specimens appear intermediate in some characters, and the differences are not great enough to warrant recognition of this population as a distinct subspecies at this time. Additional study is needed on this problem.

Gymnosarda Gill

Gymnosarda Gill 1862:125 (type-species *Thynnus unicolor* Rüppell 1838 by original designation).

Comparative Diagnosis.—The monotypic genus *Gymnosarda* differs from other bonitos in having a well-developed swim bladder, in lacking any intermuscular bones on the back of the skull, and in having more olfactory lamellae (48-56 vs. 21-39 in the other Sardini). It is the only bonito with 19 precaudal and 19 caudal vertebrae. *Gymnosarda* has a differently shaped head than do other bonitos (Tables 1, 22); the interorbital distance is much wider, the eyes are larger, the postorbital distance is shorter, and the distance between the origins of the pectoral and pelvic fins is much larger. The opercular bones are more elongate in *Gymnosarda* than in other bonitos.

Gymnosarda and *Sarda* share characters that distinguish them from *Orcynopsis* and *Cybiosarda*: the bony caudal peduncle keels are well developed, but each keel is divided into anterior and posterior portions on each vertebrae; the spleen is large and prominent in ventral view versus small and not visible in ventral view; the right and left lobes of the liver are both much longer than the middle lobe versus only the right lobe being greatly elongate.

The two genera also differ in several characters. *Gymnosarda* has a pair of glossohyal tooth plates which are absent in *Sarda*. *Gymnosarda* has a naked body; *Sarda* is covered with tiny scales behind the anterior corselet. *Gymnosarda* lacks the horizontal stripes characteristic of *Sarda*. The intestine makes a loop before reaching the anus in *Gymnosarda*; the intestine runs straight from the stomach to the anus in *Sarda*. In ventral view, the

TABLE 22.—Morphometric characters of Pacific *Gymnosarda unicolor*. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

Character	Range	$\bar{x}$	N	Kapingamarangi specimens	
Fork length (mm)	240-1040	597	18	875	930
Fork length					
Snout — A	612-651	632	18	650	651
Snout — 2D	545-580	560	18	554	554
Snout — 1D	267-303	292	18	292	303
Snout — P_2	276-306	292	18	298	278
Snout — P_1	251-283	270	18	276	278
$P_1 - P_2$	123-154	139	16	151	154
Head length	251-275	267	18	297	271
Max. body depth	200-254	222	15	~231	~217
Max. body width	139-176	153	14	—	—
P_1 length	127-188	163	18	180	182
P_2 length	97-120	107	18	120	120
P_2 insertion - vent	321-358	320	18	348	349
P_2 tip - vent	219-251	233	17	—	—
Base 1D	234-284	265	18	258	234
Height 2D	76-121	105	15	120	121
Base 2D	64-102	77	18	73	75
Height anal	76-128	102	17	128	120
Base anal	56- 68	63	18	59	62
Caudal spread	272-344	318	12	328	344
Snout (fleshy)	104-118	109	18	108	108
Snout (bony)	96-106	100	18	98	97
Maxilla length	133-151	140	18	139	136
Post orbital	92-110	101	17	103	103
Orbit (fleshy)	41- 64	53	18	57	57
Orbit (bony)	63- 88	75	16	82	84
Interorbital width	88-110	96	18	104	110
Head length					
Snout (fleshy)	385-430	409	18	403	393
Snout (bony)	355-397	374	18	368	355
Maxilla length	496-550	526	18	524	496
Post orbital	360-409	380	17	388	375
Orbit (fleshy)	161-231	197	18	212	209
Orbit (bony)	232-320	281	16	307	307
Interorbital width	321-400	359	18	391	400

spleen is visible on the right side in *Gymnosarda*; it is centrally located in the posterior half of the body cavity in *Sarda*.

Remarks.—There has been a question as to the valid name for the species in this monotypic genus—*unicolor* Rüppell or *nuda* Günther. The problem arose when Günther placed both *Scomber unicolor* Geoffroy St. Hilaire 1817 and *Thynnus (Pelamis) unicolor* Rüppell 1838 in the genus *Pelamys* Cuvier 1831. This action made *P. unicolor* Rüppell a junior secondary homonym of *P. unicolor* Geoffroy St. Hilaire so Günther replaced the former name with *P. nuda* Günther. Gill (1862) eliminated the homonomy by describing new genera for both *unicolor* Geoffroy St. Hilaire (*Orcynopsis*) and *unicolor* Rüppell (*Gymnosarda*). We recognize *unicolor* Rüppell as the valid name for the type-species of *Gymnosarda*. Review of the following synonymy shows equal usage of the

names *unicolor* (22 references) and *nuda* (23 references) so there is no reason to favor either name on the grounds of stability.

Gymnosarda unicolor (Rüppell)
Dogtooth Tuna

Thynnus (Pelamis) unicolor Rüppell 1838:40-41 (original description; Jiddah, Red Sea; pl. 12, fig. 1).

Pelamys nuda Günther 1860:368 (replacement name for *Thynnus unicolor* Rüppell 1838 preoccupied in *Pelamys* by *Scomber unicolor* Geoffroy St. Hilaire 1817). Klunzinger 1871:443-444 (description; Koseir, Red Sea).

Gymnosarda unicolor. Gill 1862:125 (original description of *Gymnosarda*). Chabanaud 1925:198-200 (comparison with *Sarda* and *Orcynopsis*). Fraser-Brunner 1950:149-150 (description), fig. 16. Smith 1956:721 (Aldabra Island), 722 (photograph). Blanc and Postel 1958:370-371 (description, Réunion Island), fig. 1 (viscera), fig. 2 (excised liver). Jones and Silas 1961:380-381 (Port Blair, Andaman Islands; Minicoy Island, Laccadive Archipelago), fig. 7 (after Fraser-Brunner). Jones et al. 1960:136 (Port Blair, Andaman Islands). Postel et al. 1960:392-393 (description; Réunion Island). Collette and Gibbs 1963a:26 (relationships). Collette and Gibbs 1963b:29 (compiled). Gorbunova 1963:87-89, fig. 13, table 11 (19 larvae 8.0-14.0 mm, Indian Ocean). Silas 1963:877-899 (synonymy, description, range, anatomy, biology). Smith and Smith 1963:41 (Seychelles), pl. 31H. Baissac 1964:185-186 (Mascarene waters). Williams 1964:122-124 (Mafia Island, Tanganyika). Talbot 1965:469 (Tutia Reef, Tanganyika). Merrett and Thorp 1966:375 (St. Lazarus Bank, East Africa). Jonklaas 1967:1134 (Maldive Islands), pl. 1 (underwater photo). Jones 1969:26 (Laccadive Archipelago). Nagabhushanam and Chandrasekhara Rao 1972:299, 317, 321 (Laccadive Archipelago). Fukusho and Fujita 1972:32-33 (description, 27 juveniles; Tsushima Island, Korea Straits), fig. 1 (42.9 cm FL juvenile).

Gymnosarda nuda. Kishinouye 1923:426-428 (anatomy; Ryukyu and Ogasawara [Bonin] Islands). Chabanaud 1925:198-199 (comparison

with *Sarda* and *Orcynopsis*). Jordan and Hubbs 1925:215 (description; Tokyo market). Fowler 1938:139-140 (description; Tahiti [ANSP 93818]). Marshall 1941:61-62 (first Australian record, Townsville, Queensland). Herre 1945:148 (several records from Philippine Islands). Coates 1950:22 (Barrier Reef), fig. Serventy 1950:19 (Cartier Island and Woodbine Bank, Timor Sea). Warfel 1950:11, 14 (description, Philippine Islands), 15 (fig. 9, lateral view of fish, gill arch, excised liver), 16 (fig. 10, distribution map). La Monte 1952:40 (description), pl. 12. Dung and Royce 1953:tables 93-96 (morphometric data for specimens from Japan, Marshall Islands, Caroline Islands, and Philippine Islands). Herre 1953:248-249 (Philippine records). Fourmanoir 1957:224 (Madagascar, Mauritius, and Comoro Islands), pl. 14, fig. B. Munro 1958b:264 (new records for the New Guinea region: Louisiade Archipelago, Solomon Islands, Woodlark Island, Laughlan Island, Carteret Island, New Ireland, New Britain, Admiralty Islands). Schultz 1960:416-417 (description; Marshall Islands [USNM 140980]). Ronquillo 1963:1723, 1725, 1738, 1739 (length-weight; Philippine Islands), 1732-1733 (gonad index). Marshall 1964:355-356 (description, N. Queensland, Australia), col. pl. 51, fig. 342. Marshall 1966:204, col. pl. 51, fig. 342. Munro 1967:203 (description; New Guinea), pl. 17 (fig. 344). Kami et al. 1968:123 (Guam). Lewis 1968:56 (copepod *Caligus pseudokalumai* described from Eniwetok specimen). Fourmanoir and Griessinger 1971:484 (Rangiroa, Tuamotus). Grant 1972:112 (description; Barrier Reef), col. pl. 17. Bablet 1972:62, 87 (Tuamotu Archipelago).

Misidentification.—*Sarda orientalis*. Smith and Pope 1907:464-465 (77-mm specimen from Urado, Japan [USNM 59638]).

Types.—*Thynnus (Pelamis) unicolor* Rüppell 1838:40-41, pl. 12, fig. 1. Holotype: SMF 2739; 473 mm FL stuffed specimen; Red Sea, Jiddah; 1834; E. Rüppell. Counts: dorsal fin rays XIII + 13 + VI, but there is probably one more spine concealed in the groove to make the count XIV + 13 + VI; anal fin rays 12 + VI; pectoral fin rays 26; gill rakers cannot be counted (if still present); upper jaw teeth 18; lower jaw teeth (left-right) 14-12.

Distribution.—*Gymnosarda unicolor* is a coral reef species of the tropical Indo-West Pacific (Figure 69). It was originally described by Rüppell (1838) from Jiddah in the Red Sea and was reported by Klunzinger (1871) from Koseir, also in the Red Sea. Western Indian Ocean records include: Tanzania (Mafia Island, Williams 1964; Tutia Reef, Talbot 1965; St. Lazarus Bank, Merrett and Thorp 1966); the Seychelles Islands (Smith and Smith 1963); Amirante Islands (USNM uncat.); Aldabra Island (Smith 1956); Madagascar, Mauritius, and the Comoro Islands (NMC 73-244; Fourmanoir 1957); Réunion Island (Blanc and Postel 1958; Postel et al. 1960) and Mascarene waters (Réunion, Mauritius, and Rodrigues; Baissac 1964). There are records from the Laccadive Archipelago (Jones and Silas 1961; Jones 1969; Nagabhushanam and Chandrasekhara Rao 1972), the Maldive Islands (Jonklaas 1967), Sri Lanka (Ceylon) (Sivasubramaniam 1970), and the Andaman Islands (Jones and Silas 1961; Jones et al. 1960). The only records from the Indonesian area appear to be from Cartier Island and Woodbine Reef in the Timor Sea (Serventy 1950). *Gymnosarda unicolor* is known from several localities in the Philippine Islands (Herre 1945, 1953; Warfel 1950; Dung and Royce 1953; Ronquillo 1963); the New Guinea region—Louisiade Archipelago, Solomon Islands, Woodlark Island, Laughlan Island, Carteret Island, New Ireland, New Britain, and the Admiralty Islands (Munro 1958b); and the northern part of Australia's Great Barrier Reef (Townsville, Marshall 1941; Coates 1950; Marshall 1964). (The record from off Scotland Island, New South Wales (Whitley 1964a) is based on a specimen (AMS IB. 4291) of *Scomberomorus*.) The northern limit of the range is the Sagami Sea (CAS SU 24080, 97 mm FL) and Urado, near Kochi, Shikoku, Japan (USNM 59638, 72 mm FL), the Ryukyu and Bonin islands south of Japan (Kishinouye 1923), and the Straits of Korea (Fukusho and Fujita 1972). To the southeast, there are records or specimens from Guam in the Mariana Islands (Kami et al. 1968), the Palau Islands (CAS GVF), the Carolines (Kapingamarangi and Ifalik, CAS GVF; Pikelot Island in the Truk Islands group, 5 uncataloged USNM specimens; Dung and Royce 1953; Marshalls (Dung and Royce 1953; Schultz 1960; USNM 140980); Gilberts (AMS IB. 5660); Society Islands (Tahiti—Fowler 1938; ANSP 93818); Marquesas Islands (SIO 59-282-43a); Rangiroa Atoll, Tuamotu Archipelago (Fourmanoir and Griessinger 1971;

Bablet 1972); and Oeno Island in the Pitcairn Group (BPBM 16966).

Remarks.—Two large specimens from Kapingamarangi Atoll (CAS GVF, 930 and 875 mm FL) require special mention. They have a higher number of very small teeth on the upper (left side, right side 31-29+, 31-30) and lower jaws 22-22, 25-22) than other *Gymnosarda* (Tables 5, 6). Morphometrically, these two Kapingamarangi specimens have distinctly greater snout-anal origin, pectoral to pelvic origin, pelvic fin length, height of second dorsal, height of anal fin, and greater interorbital widths than 18 *Gymnosarda* (240-1,040 mm FL) from throughout the range. The specimens are not very well preserved, but we feel confident that the morphometric differences are real. The differences are not great enough to require the description of a new species, but we cannot fully account for the differences that exist. Additional material, over a wider size range, from Kapingamarangi will be necessary to solve this problem.

Allothunnus Serventy

Allothunnus Serventy 1948:132 (type-species: *Allothunnus fallai* Serventy 1948, by monotypy).

Comparative Diagnosis.—The monotypic genus *Allothunnus* differs from all other scombrids in its very high number of gill rakers. It is the most elongate species of bonito and so has the greatest distances between the snout and the origins of the dorsal and anal fins (Tables 1, 23). The snout and maxilla are shorter than in any other bonito.

Allothunnus differs from all other scombrid genera in having the prootics remarkably extended laterally as wings that frame the posterior margin of the orbit. A pair of dorsolateral processes extend from the parasphenoid up to the prootic wing. *Allothunnus* resembles the Thunnini and differs from all other bonitos in having a prootic pit. Only *Gymnosarda* has a trace of the prominent ridges present on the frontals of *Allothunnus*. The pineal foramen is large and oval in *Allothunnus*, elongate and slit-shaped in all other Sardini and Thunnini. The otoliths are more similar to those of *Sarda* than to those of other bonitos.

The liver has three subequal lobes like *Thunnus*; other bonitos have the right lobe or both right and

left lobes longer than the middle lobe. The nasal rosettes are also more similar to those of *Thunnus* than to those of other bonitos.

Allothunnus fallai Serventy

Allothunnus fallai Serventy 1948:132-135 (original description; Timaru, South Island, New Zealand), fig. 1 (photograph of holotype), fig. 2 (internal gill rakers), fig. 3 (ventral view of liver). Fraser-Brunner 1950:148 (description), fig. 13. Parrott 1958:30-31 (after Serventy). Moreland 1959:30 (New Zealand endemic). Talbot 1960:258-259 (description; Cape Peninsula, South Africa). Olsen 1962:95-96 (description; 4 specimens from southern Tasmania). Collette and Gibbs 1963a:26 (relationships). Collette and Gibbs 1963b:31 (compiled), pl. 9 (after Fraser-Brunner). Jones and Silas 1963:1795 (compiled). Jones and Silas 1964:43-44 (compiled), fig. 8 (after Serventy). Talbot 1964:191-192 (description; anatomy; rela-

TABLE 23.—Morphometric characters of *Allothunnus fallai*. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

Character	Range	$\bar{x}$	N
Fork length (mm)	642-787	734	6
Fork length			
Snout — A	654-688	676	6
Snout — 2D	607-654	628	6
Snout — 1D	291-315	306	6
Snout — P_2	274-294	284	6
Snout — P_1	257-285	269	6
P_1 — P_2	102-116	110	4
Head length	248-272	258	6
Max. body depth	199-239	223	6
Max. body width	159-172	164	4
P_1 length	119-142	129	6
P_2 length	69- 83	78	6
P_2 insertion - vent	356-382	371	6
P_2 tip - vent	276-306	293	6
Base 1D	305-341	319	6
Height 2D	88- 97	93	6
Base 2D	59- 88	72	6
Height anal	82- 98	90	6
Base anal	66- 77	72	6
Caudal spread	210-246	226	3
Snout (fleshy)	70- 79	75	6
Snout (bony)	60- 69	65	6
Maxilla length	91- 96	93	6
Post orbital	136-144	139	4
Orbit (fleshy)	40- 67	45	6
Orbit (bony)	61- 65	63	6
Interorbital width	29- 66	57	6
Head length			
Snout (fleshy)	283-301	292	6
Snout (bony)	242-263	252	6
Maxilla length	354-379	361	6
Post orbital	540-554	545	4
Orbit (fleshy)	153-246	175	6
Orbit (bony)	232-252	244	6
Interorbital width	108-255	224	6

tionships), pl. 1, fig. 1. Fitch and Craig 1964:199-201 (description; relationships based on otoliths; figs. 3, 5A; California). Whitley 1964a:227 (compiled). Whitley 1964b:48 (listed; Australia). Smith 1965:23 (description; 4 specimens off Walvis Bay, South West Africa), pl. 3, figs. A-B. Nakamura and Kikawa 1966:59-62 (comparison of vertebrae with other scombrids). Nakamura and Mori 1966:67-83 (anatomy, relationships, figs. 1-14; Tasman Sea). Watanabe et al. 1966:85-94 (description of larvae; 100 specimens, 3.2-10.5 mm TL; Indian and South Pacific oceans), figs. 1-5 (larvae 4.0-10.5 mm TL), fig. 6 (distribution map). Tominaga 1966:44-46 (description; specimens from Uruguay and Tasmania), fig. 1B (photo of 870-mm Tasmanian specimen), fig. 2B (first gill arch). Mori 1967a:105-111 (description of 36 larvae from South Atlantic Ocean), figs. 1, 2 (larvae 5.5-13.3 mm TL). Mori 1967b:113-120 (description of 40 juveniles, 96-290 mm FL from stomachs of tunas and marlins from South Pacific), fig. 1 (distribution map). Zharov 1967:220 (*Allothunnus* included in Sardidae). Fierstine and Walters 1968:12 (aspect ratio of caudal fin). Whitley 1968:72 (listed; New Zealand). Ueyanagi 1969:193 (fig. 16e, relationship between occurrence of larvae and ocean structure near New Caledonia). Magnuson 1973:350 (maximum size, no swim bladder, short pectoral fins). Mori 1972:29-31 (juveniles from istiophorid stomach contents; SE of Palau Islands and off South-West Africa), fig. 1 (219-mm juvenile). Warashina and Hisada 1972:51-75 (adults found south of lat. 38°S in the Atlantic, Indian, and Pacific oceans; larvae between lat. 20° and 30°S; juveniles between lat. 25° and 35°S; length-frequency data on 652 specimens 650-960 mm FL). Webb and Wolfe 1974:5-7 (230 tons taken with purse seines off eastern Tasmania, June 1974; fig.).

Types.—*Allothunnus fallai* Serventy 1948:132-135. Holotype: Canterbury Museum; 616 mm FL female; New Zealand, South Island, Timaru; 17 July 1916. Two other specimens from the Canterbury Museum are mentioned in the original description and so may be considered paratypes: a cast of a specimen from Kaiapoi, north of Christchurch, dated 4 October 1911 and measuring 920 mm TL and a specimen, 840 mm FL, from Akaroa, Banks Peninsula, dated 4

February 1938. We have not examined any of these and report the counts of the holotype from Serventy's original description: dorsal fin rays XVII + 12 + VII; anal fin rays 14 + VII; pectoral fin rays 25; gill rakers (left-right) 25 + 48 = 73, 24 + 51 = 75.

Distribution.—*Allothunnus fallai* is found around the world in the Southern Ocean (Figure 69). It was originally described from the South Island of New Zealand in 1948, then reported from Cape Peninsula, South Africa, by Talbot (1960), South-West Africa by Smith (1965), and from Tasmania by Olsen (1962). Fitch and Craig (1964) reported the most unusual record, a 680-mm FL specimen from the Los Angeles-Long Beach harbor complex, the only adult specimen that had been taken north of lat. 35°S. Subsequent to this, Nakamura and Mori (1966) studied several specimens from the Tasman Sea and a series of Japanese authors (Watanabe et al. 1966; Mori 1967a, b; Ueyanagi 1969; Mori 1972) reported juveniles from the southern parts of the Atlantic, Indian, and Pacific oceans to complete our present knowledge of the range of the species. Another scombrid, *Gasterochisma melampus*, and probably also *Thunnus maccoyii*, has a similar distribution in the northern part of the South Ocean around the world.

Food.—One of the Tasmanian specimens reported on by Webb and Wolfe (1974) had its stomach filled with euphausiids. Edward Brinton (SIO) has kindly identified these as *Nyctiphanes australis*, a species endemic to eastern Australian and New Zealand neritic and slope waters.

LITERATURE CITED

ADAMICKA, P.
  1972. Funktionsanatomische Untersuchungen am Kopf von Akanthopterygiern (Pisces, Teleostei): *Sarda sarda, Pterois volitans, Chrysophrys aurata*. Teil I: Einleitung und *Sarda sarda*. [Engl. abstr.] Zool. Jahrb. Anat. 89:301-331.
ALDROVANDI, U.
  1613. De piscibus libri v. et de cetis lib. unus. Bononiae, 732 p.
ALLIS, E. P., JR.
  1903. The skull, and the cranial and first spinal muscles and nerves in *Scomber scomber*. J. Morphol. 18:45-328.
ANCIETA CALDERON, F.
  1963. La pesquería del bonito en el Perú. [Engl. and Fr. abstr.] FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:1607-1619.

  1964. Sinopsis sobre la biología y pesquería del "bonito" *Sarda chilensis* (Cuvier y Valenciennes) frente a la costa del Perú. Rev. Fac. Cienc. Biol., Univ. Nac. Trujillo 1(1):17-49.
ATHANASSOPOULOS, G.
  1934. Sur la présence des pelamydes (*Pelamys sarda* Bl.) dans la Méditerranée orientale. Comm. Int. Explor. Sci. Mer Médit., Rapp. P.-V. Reun., New Ser., 8:315-316.
BABLET, J. P.
  1972. Faune ichtyologique des atolls. *In* Le monde vivant des atolls Polynésie française, Tuamotu-Gambier. Publ. Soc. Océan. 28:57-94.
BAISSAC, J. DE B.
  1964. The scombroid fishes of Mascarene waters. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:185-186.
BĂNĂRESCU, P.
  1964. Pisces-Osteichthyes (peşti ganoizi şi ososi). Fauna Repub. Pop. Rom., Vol. 13, 959 p.
BARNARD, K. H.
  1927. A monograph of the marine fishes of South Africa. Part II. Ann. S. Afr. Mus. 21:419-1065.
BAUCHOT, M. L., AND M. BLANC.
  1961. Catalogue des types de Scombroidei (poissons téléostéens Perciformes) des collections du Muséum National d'Histoire Naturelle de Paris. Bull. Mus. Nat. Hist. Nat. Paris, Ser. 2, 33:369-379.
BAUGHMAN, J. L.
  1941. Scombriformes, new, rare, or little known in Texas waters with notes on their natural history or distribution. Trans. Tex. Acad. Sci. 24:14-26.
BÁUZA RULLÁN, J.
  1961. Contribuciones al conocimiento de los otolitos de peces actuales. Bol. Real Soc. Esp. Hist. Nat. (B) 59:153-168.
BELLOC, G.
  1954. Les thons de la Méditerranée. Première note: germon, pélamide et melva. Proc. Tech. Pap. Gen. Fish. Counc. Medit., FAO (Food Agric. Organ. U.N.) 2:283-318.
BELON, P.
  1553. De aquatilibus, libri duo cum eiconibus ad vivam ipsorum effigiem, quoad eius fieri potuit, expressis. Paris, 448 p.
BEN-TUVIA, A.
  1971. Revised list of the Mediterranean fishes of Israel. Isr. J. Zool. 20:1-39.
BERG, C.
  1895. Enumeración sistemática y sinonímica de los peces de las costas Argentina y Uruguaya. An. Mus. Nac. Buenos Aires 4:1-120.
BERRY, F. H.
  1969. *Elegatis bipinnulata* (Pisces: Carangidae): Morphology of the fins and other characters. Copeia 1969:454-463.
BIGELOW, H. B., AND W. C. SCHROEDER.
  1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53:1-577.
BINI, G.
  1968. Atlante dei pesci delle coste Italiane, Vol. VI. Osteitti. Mondo Sommerso Editrice, Milan, 177 p.
BLACHE, J., J. CADENAT, AND A. STAUCH.
  1970. Clés de détermination des poissons de mer signalés dans l'atlantique oriental entre le 20e parallèle Nord et le 15e parallèle Sud. Faune Tropicale XVIII, O.R.S.T.O.M., Paris, 480 p.

BLANC, M., AND M. L. BAUCHOT.

1964. Les Scombroidei (poissons téléostéens Perciformes) du Muséum National d'Histoire Naturelle de Paris. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:443-458.

BLANC, M., AND E. POSTEL.

1958. Sur une petite collection de poissons de la Réunion. Mém. Inst. Sci. Madagascar, Ser. F, Oceanogr. 2:367-376.

BLOCH, M. E.

1793. Naturgeschichte der äuslandischen Fische. Königl. Akad. Kunst. J. Morino Comp., Berlin, Part 7, 144 p.

BLOCH, M. E., AND J. G. SCHNEIDER.

1801. Systema Ichthyologiae. Berlin, 584 p.

BOESEMAN, M.

1947. Revision of the fishes collected by Burger and Von Siebold in Japan. Zool. Meded Rijksmus. Nat. Hist. Leiden 28:1-242.

1964. Scombroid types in the Leiden Museum collection. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:461-468.

BONAPARTE, C. L.

1831. Saggio d'una distribuzione metodica degli animali vertebrati a sangue freddo. Gior. Arcad. Sci. Lett. Art., Rome 53:129-209.

1845. Catalogo metodico dei pesci Europei. Atti Sci. Ital. 1845:1-95.

BOSCHUNG, H. T., JR.

1966. The occurrence of the common bonito, *Sarda sarda*, in the northern Gulf of Mexico. Trans. Am. Fish. Soc. 95:227-228.

BROCK, V. E.

1949. A preliminary report on *Parathunnus sibi* in Hawaiian waters and a key to the tunas and tuna-like fishes of Hawaii. Pac. Sci. 3:271-277.

BRÜNNICH, M. T.

1768. Ichthyologia Massiliensis, sistens piscium descriptiones eorumque apud incolas nomina. Accedunt Spolia Maris Adriatici. Hafnea et Lipsiae, 110 p.

BURNE, R. H.

1909. The anatomy of the olfactory organ of teleostean fishes. Proc. Zool. Soc. Lond. 1909:610-663.

BUEN, F. DE.

1930a. Ictiología española. I. Scombriformes y Thunniformes. Bol. Oceanogr. Pesca Madrid 15(162):34-53.

1930b. Estados larvarios y juveniles de la *Sarda sarda* (Bloch). Inst. Español Oceanogr. Trabajos 3:32 p.

1958. Peces del suborden Scombroidei en aguas de Chile. Rev. Biol. Mar., Valparaiso 7:3-38.

BUEN, F. DE, AND F. FRADE.

1932. Clef dichotomique pour une classification rapide (d'après les caractères de coloration et très apparents de la morphologie externe). Comm. Int. Explor. Sci. Mer Medit. Rapp. P.-V., New Ser., 7:71-74.

CADENAT, J.

1937. Recherches systématiques sur les poissons littoraux de la Côte Occidentale d'Afrique, récoltés par le navire *Président Théodore-Tissier*, au cours de sa 5e croisière (1936). Rev. Trav. Off. Sci. Tech. Pêch. Marit. 10:425-562.

1950. Notes sur quelques Scombridae des Îles du Cap-Vert. Congr. Pêches Pêcheries, l'Union Fr. d'Outre-Mer, p. 131-134.

CANESTRINI, G.

1870. Pesci. *In* E. Cornalia (editor), Fauna d'Italia.

CAREY, F. G., J. M. TEAL, J. W. KANWISHER, AND K. D. LAWSON.

1971. Warm-bodied fish. Am. Zool. 11:135-143.

CARUS, J. V.

1893. Prodromus faunae Mediterraneae. Vertebrata. 1. Class. Pisces. E. Schweiz., Stuttg. 2:498-711.

CHABANAUD, P.

1925. Sur quelques Scombroides de la côte occidentale d'Afrique. Bull. Soc. Zool. Fr. 50:197-201.

1944. *Sarda chiliensis* (C.V.). Remarques diverses. Bull. Inst. Océanogr. Monaco 860:1-6.

CHABANAUD, P., AND T. MONOD.

1927. Les poissons de Port-Étienne. Bull. Comit. Etud. Hist. Sci. Afr. Occident. Fr. 1926:225-287.

CHAINE, J.

1957. Recherches sur les otolithes des poissons. Étude descriptive et comparative de la sagitta des téléostéens. Description des espèces. Bull. Cent. Étud. Rech. Sci. Biarritz 1:463-557.

CHEVEY, P.

1934. Révision synonymique de l'oeuvre ichtyologique de G. Tirant. Inst. Océanogr. Indochine, Stn. Mar. Cauda, Note 7, 291 p.

CHIRICHIGNO F., N.

1969. Lista sistematica de los peces marinos comunes para Ecuador, Peru, y Chile. Conf. Explot. Conserv. Riquezas Marit. Pac. Sur, 108 p.

CLEMENS, W. A., AND G. V. WILBY.

1961. Fishes of the Pacific coast of Canada. 2nd ed. Fish. Res. Board Can., Bull. 68, 443 p.

CLOTHIER, C. R.

1950. A key to some southern California fishes based on vertebral characters. Calif. Div. Fish Game, Fish Bull. 79, 83 p.

COATES, G.

1950. Fishing on the Barrier Reef and inshore. T. Willmett and Sons, Townsville, 72 p.

COLLETT, R.

1879a. Meddelelser om Norges Fiske i Aarene 1875-1878. Forh. Vidensk.-Selsk. Christ. 1:1-107.

1879b. Om den saakaldte *Thynnus peregrinus*, Coll., 1879. Forh. Vidensk.-Selsk. Christ. 15, 3 p.

COLLETTE, B. B.

1966. Revue critique des types de Scombridae des collections du Muséum National d'Histoire Naturelle de Paris. [Engl. summ.] Bull. Mus. Natl. Hist. Nat. Paris, Ser. 2, 38:362-375.

1970. *Rastrelliger kanagurta*, another Red Sea immigrant into the Mediterranean Sea, with a key to the Mediterranean species of Scombridae. Bull. Sea Fish. Res. Stn. Haifa 54, p. 3-6.

COLLETTE, B. B., AND R. H. GIBBS, JR.

1963a. A preliminary review of the fishes of the family Scombridae. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:23-32.

1963b. Preliminary field guide to the mackerel- and tuna-like fishes of the Indian Ocean (Scombridae). Smithson. Inst., 48 p.

COLLINS, B. L.

1954. Lista de peixes dos mares dos Açores. Açoreana 5(2):103-142.

CONRAD, G. M.

1938. The osteology and relationships of the wahoo (*Acanthocybium solandri*), a scombrid fish. Am. Mus. Nat. Hist. Novit. 1000, 32 p.

CUVIER, G.
1829. Le règne animal. Nouvelle ed. tom. II. Deterville, Paris, 406 p.
CUVIER, G., AND A. VALENCIENNES.
1831. Histoire naturelle des poissons, Vol. 8. F. G. Levrault, Paris, 375 p.
DAHL, G.
1971. Los peces del norte de Colombia. INDERENA, Bogotá, 391 p.
DAVIP, L. R.
1943. Miocene fishes of southern California. Geol. Soc. Am., Spec. Pap. 43, 193 p.
DAY, F.
1878. The fishes of India; being a natural history of the fishes known to inhabit the seas and fresh waters of India, Burma, and Ceylon, 1:1-320. Bernard Quaritch, Lond.
DE GROOT, S. J., AND H. NIJSSEN.
1971. Notes on the fishes collected by the R. V. "Tridens" on the north west African Shelf, 19-25 January 1969. Bijdr. Dierkd. 41:1-9.
DELAROCHE, F. E.
1809. Suite du mémoire sur les espèces de poissons observées a Iviça. Ann. Mus. Hist. Nat. Paris 13:313-361.
DEMIR, M.
1963. Synopsis of biological data on bonito Sarda sarda (Bloch) 1793. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:101-129.
1964. Distribution of meristic counts of common bonito (Sarda sarda Bl.) from Turkish waters. [Fr. abstr.] Proc. Tech. Pap. Gen. Fish. Counc. Medit., FAO (Food Agric. Organ. U.N.) 7:455-457.
DE SYLVA, D. P.
1955. The osteology and phylogenetic relationships of the blackfin tuna, Thunnus atlanticus (Lesson). Bull. Mar. Sci. Gulf Caribb. 5:1-41.
DIEUZEIDE, R.
1930. Sur quelques scombriniens des côtes algériennes. Bull. Trav. Stn. Aquicult. Pêche, Castiglione, Alger [1929], fasc. 2, p. 127-167.
DIEUZEIDE, R., M. NOVELLA, AND J. ROLAND.
1955. Catalogue des poissons des côtes algériennes. III. Ostéoptérygiens. Bull. Stn. Aquicult. Pêche Castiglione, New Ser. 6, 384 p.
DOLLFUS, R. P.
1955. Première contribution a l'établissement d'un fichier ichthyologique de Maroc Atlantique de Tanger a l'embouchure de l'oued Dra. Trav. Inst. Sci. Chérifien, Zool. Sér. 6, 227 p.
DORNESCU, G. T., AND D. MIȘCALENCU.
1969. Cele trei tripuri de branhii ale Teleosteenilor. [Russ. and Fr. summ.] Anal Univ. București, Ser. Stiint. Nat. Biol. 17:11-20.
DRESSLAR, F. B., AND B. FESLER.
1889. A review of the mackerels (Scombrinae) of America and Europe. Bull. U.S. Fish Comm. 7:429-446.
DUHAMEL DU MONCEAU, H. L.
1769. Traité général des pêches, et histoire des poissons qu'elles fournissent. . . . Paris.
DUMÉRIL, A.
1858. Reptiles et poissons d l'Afrique occidentale. Arch. Mus. Hist. Nat. Paris 10:137-268.
DUNG, D. I. Y., AND W. F. ROYCE.
1953. Morphometric measurements of Pacific scombrids. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 95, 170 p.

ECONOMIDIS, P. S.
1972. Catalogue des poissons de la Grèce. [In Greek, Fr. summ.] Hellenic Oceanol. Limnol. 11:421-598.
EHRENBAUM, E.
1924. Scombriformes. Rep. Dan. Oceanogr. Exped. 1908-1910, II (Biology) A, 11, 42 p.
ERDMAN, D. S.
1971. Notes on fishes from the Gulf of Nicoya, Costa Rica. Rev. Biol. Trop. 19(1, 2):59-71.
FARRAN, G. P.
1923. Rare fishes in Irish Waters. Irish Nat. (Dublin) 33(10):106-107.
FIERSTINE, H. L., AND V. WALTERS.
1968. Studies in locomotion and anatomy of scombroid fishes. Mem. South. Calif. Acad. Sci. 6:1-31.
FILIPPI, F. DE, AND G. B. VERANY.
1859. Sopra alcuni pesci nuovi o poco noti del Mediterraneo. Mem. Reale Accad. Sci. Torino, Ser. 2, 18:187-199.
FITCH, J. E., AND W. L. CRAIG.
1964. First records for the bigeye thresher (Alopias superciliosus) and slender tuna (Allothunnus fallai) from California, with notes on eastern Pacific scombrid otoliths. Calif. Fish Game 50:195-206.
FOOD AND AGRICULTURAL ORGANIZATION OF THE UNITED NATIONS.
1973. Catches and landings, 1972. FAO Yearb. Fish. Stat. 34, 560 p.
FOURMANOIR, P.
1957. Poissons téléostéens des eaux malgaches du Canal de Mozambique. Mém. Inst. Sci. Madagascar, Ser. F, Oceanogr. 1:1-316.
FOURMANOIR, P., AND M. GRIESSINGER.
1971. Poissons de Rangiroa. Cah. O.R.S.T.O.M., Sér. Océanogr. 9:475-489.
FOWLER, H. W.
1915. The fishes of Trinidad, Grenada, and St. Lucia, British West Indies. Proc. Acad. Nat. Sci. Phila. 67:520-546.
1926. Fishes from Florida, Brazil, Bolivia, Argentina, and Chile. Proc. Acad. Nat. Sci. Phila. 78:249-285.
1928. The fishes of Oceania. Mem. Bernice P. Bishop Mus. 10, 540 p.
1936. The marine fishes of West Africa based on the collection of the American Museum Congo expedition, 1909-1915. Part II. Bull. Am. Mus. Nat. Hist. 70:607-1493.
1938. The fishes of the George Vanderbilt South Pacific expedition, 1937. Acad. Nat. Sci. Phila., Monogr. 2, 349 p.
1944. The fishes. In Results of the fifth George Vanderbilt Expedition (1941) (Bahamas, Caribbean Sea, Panama, Galápagos Archipelago and Mexican Pacific Islands), p. 57-529. Acad. Nat. Sci. Phila., Monogr. 6.
1949. The fishes of Oceania—Supplement 3. Mem. Bernice P. Bishop Mus. 12(2):37-185.
FRADE, F., AND F. DE BUEN.
1932. Poissons Scombriformes (excepté la famille Scombridae). Clef de classification principalement d'après la morphologie interne. Comm. Int. Explor. Sci. Mer Mèdit. Rapp. P.-V. Reun. 7:69-70.
FRADE, F., AND E. POSTEL.
1955. Contribution à l'etude de la reproduction des scombridés et thonidés de l'Atlantique tropical. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 137:33-35.
FRASER-BRUNNER, A.
1950. The fishes of the family Scombridae. Ann. Mag. Nat. Hist., Ser. 12, 3:131-163.

FUKUSHO, K., AND S. FUJITA.

1972. Notes on the young of dogtooth tuna caught in the waters of Tsushima Island. [In Jap., Engl. abstr.] Jap. J. Ichthyol. 19:32-33. (Natl. Mar. Fish. Serv. Syst. Lab. Transl. 70)

GEOFFROY SAINT-HILAIRE, E.

1817. Poissons de la Mer Rouge et de la Méditerranée. In Description de l'Egypte. . . ., Paris, Planches Histoire Naturelle, 1, Poissons, pl. 18-27.

GEOFFROY SAINT-HILAIRE, I.

1827. Histoire naturelle des poissons de la Mer Rouge et de la Méditerranée. Description de l'Egypte. . ., Paris, Histoire Naturelle 1:311-340.

GEORGE, C. J., V. A. ATHANASSIOU, AND I. BOULOS.

1964. The fishes of the coastal waters of Lebanon. Am. Univ. Beirut, Misc. Pap. Nat. Sci. 4, 27 p.

GIBBS, R. H., JR., AND B. B. COLLETTE.

1967. Comparative anatomy and systematics of the tunas, genus Thunnus. U.S. Fish. Wildl. Serv., Fish. Bull. 66:65-130.

GIGLIOLI, E. H.

1880. Elenco dei mammiferi, degli uccelli e dei rettili ittifagi apparetenenti alla fauna italica e catalogo degli anfibi e dei pesci italiani. Espos. Int. Pesca Berlin, 1880, 55 p.

GILBERT, C. H., AND E. C. STARKS.

1904. The fishes of Panama Bay. Mem. Calif. Acad. Sci. 4, 304 p.

GILL, T. N.

1862. On the limits and arrangement of the family of scombroids. Proc. Acad. Nat. Sci. Phila. 1862:124-127.

GIRARD, C.

1859. Fishes. In Reports of explorations and surveys to survey the most practical and economical route for a railroad from the Mississippi River to the Pacific Ocean. Vol. X.

GISTEL, J.

1848. Naturgeschichte des Thierreichs. Für höhere Schulen. Scheitlin and Krais, Stuttgart, 216 p.

GNANAMUTTU, J. C.

1968. On the occurrence of the oriental bonito, Sarda orientalis (Temminck and Schlegel) along the Madras coast. J. Mar. Biol. Assoc. India 8:365.

1971. Osteology of the Indian mackerel, Rastrelliger kanagurta (Cuvier). Indian J. Fish. 13:1-26.

GODSIL, H. C.

1954. A descriptive study of certain tuna-like fishes. Calif. Dep. Fish Game, Fish Bull. 97, 185 p.

1955. A description of two species of bonito, Sarda orientalis and S. chiliensis and a consideration of relationships within the genus. Calif. Dep. Fish Game, Fish Bull. 99, 43 p.

GOODING, R. M.

1963. The olfactory organ of the skipjack Katsuwonus pelamis. [Fr. and Span. abstr.] FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:1621-1631.

GORBUNOVA, N. N.

1963. Larvae of scombroid fishes (Pisces, Scombriformes) from the Indian Ocean. [In Russ., Engl. summ.] Tr. Inst. Okeanol. Akad. Nauk SSSR 62:68-95.

GORDON, B. L.

1960. The marine fishes of Rhode Island. Book and Tackle Shop, Watch Hill, R.I., 136 p.

GRANIER, J.

1968. Les Scombres dans le Golfe d'Aigues-Mortes. Bull. Mens. Soc. Linn. Lyon 37(8):324-330.

GRANT, E. M.

1972. Guide to fishes. 2nd ed. Queensland Dep. Primary Ind., Brisbane, 472 p.

GRIFFINI, A.

1903. Ittiologia italiana. Ulrico Hoepli, Milan, 469 p.

GRUVEL, A., AND A. BOUYAT.

1906. Les pêcheries de la côte occidentale d'Afrique. A. Challamel, Paris, 280 p.

GUICHENOT, A.

1850. Histoire naturelle des reptiles et des poissons. Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842. Sci. Phys., Zool. Vol. 5 (3), 128 p.

GÜNTHER, A.

1860. Catalogue of the acanthopterygian fishes in the collection of the British Museum. Vol. 2, 548 p.

HART, J. L.

1973. Pacific fishes of Canada. Fish. Res. Board Can., Bull. 180, 740 p.

HERRE, A. W.

1936. Fishes of the Crane Pacific Expedition. Field Mus. Nat. Hist., Zool. Ser., 21:1-472.

1945. Additions to the fish fauna of the Philippine Islands. Copeia 1945:146-149.

1953. Check list of Philippine fishes. U.S. Fish Wildl. Serv., Res. Rep. 20, 977 p.

HILDEBRAND, H. H.

1955. A study of the fauna of the pink shrimp (Penaeus duorarum Burkenroad) grounds in the Gulf of Campeche. Publ. Inst. Mar. Sci., Univ. Tex. 4(1):169-232.

HILDEBRAND, S. F.

1946. A descriptive catalog of the shore fishes of Peru. U.S. Natl. Mus. Bull. 189, 530 p.

HILGENDORF, F. M.

1888. Die Fische der Azoren. Arch. Naturgesch. 54(1):205-213.

HOLMGREN, U.

1958. On the pineal organ of the tuna, Thynnus thynnus L. Breviora 100, 5p.

HONMA, Y.

1952. A list of the fishes collected in the Province of Echigo, including Sado Island. [In Jap.] Jap. J. Ichthyol. 2:138-146.

HUBRECHT, A. A. W.

1879. [Mededeeling over de vangst van Pelamys sarda C V in Juni 1878 nabij Bergen-op-Zoom] Tweede Jaarversl. Zool. Stn. Tijdschr. Ned. Dierk. Ver. 4:9.

IDYLL, C. P., AND D. P. DE SYLVA.

1963. Synopsis of biological data on bonito Sarda sarda (Bloch) 1793 (Western Atlantic). FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:755-760.

IHERING, H. VON.

1897. Os peixes da costa do mar no Estado do Rio Grande do Sul. Rev. Mus. Paulista 2:25-63.

IONESCU, N., N. GADIDOV, AND S. STĂNESCU.

1958. Contribuţii la cunoaşterea biologiei, şi perscuitului pălămidei (Sarda sarda Bloch), în apele Romîneşti ale Mării Negre în perioada 1954-1956. Hidrobiologia 1:165-186.

IRVINE, F. R.

1947. The fishes and fisheries of the Gold Coast. Crown Agents for the Colonies, Lond., 352 p.

IWAI, T., AND I. NAKAMURA.

1964a. Branchial skeleton of the bluefin tuna, with special reference to the gill rays. Bull. Misaki Mar. Biol. Inst., Kyoto Univ. 6:21-25.

619

1964b. Olfactory organs of tunas with special reference to their systematic significance. Bull. Misaki Mar. Biol. Inst., Kyoto Univ. 7:1-8.

JENSEN, A. J. C.
    1937. Seasonal guests in transition area. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 102(6):1-18.

JENSEN, A. S.
    1941. Om nogle for den danski fauna nye eller sjaeldne fiskearter. Vidensk. Medd. Dan. Naturhist. Foren. Kbh. 104:179-206.

JENSEN, A. C.
    1967. Observations on pelagic fishes off the west coast of Africa. Bull. Mar. Sci. 17:42-51.

JONES, J. M.
    1879. List of the fishes of Nova Scotia. Proc. Trans. N. S. Inst. Nat. Sci. 5(1):87-97.

JONES, S.
    1961. Notes on eggs, larvae and juveniles of fishes from Indian waters. VI. Genus *Auxis* Cuvier. VII. *Sarda orientalis* (Temminck & Schlegel). Indian J. Fish. 7:337-347.
    1969. Catalogue of fishes from the Laccadive Archipelago in the reference collections of the Central Marine Fisheries Research Institute. Bull. Cent. Mar. Fish. Res. Inst. 8, 32 p.

JONES, S., AND M. KUMARAN.
    1964. Eggs, larvae and juveniles of Indian scombroid fishes. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:343-378.

JONES, S., AND E. G. SILAS.
    1961. Indian tunas-A preliminary review, with a key for their identification. Indian J. Fish. 7:369-393.
    1963. Tuna and tuna-like fishes from the Indian seas. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:1775-1796.
    1964. A systematic review of the scombroid fishes of India. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:1-105.

JONES, S., E. G. SILAS, AND E. DAWSON.
    1960. New records of scombroid fishes from the Andaman-Nicobar waters. J. Mar. Biol. Assoc. India 2:136-137.

JONKLAAS, R.
    1967. Scombroid fishes and fisheries of the Maldive Islands with special reference to the tuna fishery. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:1132-1138.

JORDAN, D. S., AND B. W. EVERMANN.
    1896. The fishes of North and Middle America. Bull. U.S. Natl. Mus. 47, 1240 p.

JORDAN, D. S., AND C. H. GILBERT.
    1882. Synopsis of the fishes of North America. Bull. U.S. Natl. Mus. 16, 1018 p.

JORDAN, D. S., AND C. L. HUBBS.
    1925. Record of fishes obtained by David Starr Jordan in Japan, 1922. Mem. Carnegie Mus. 10:93-346.

JORDAN, D. S., AND E. K. JORDAN.
    1922. A list of the fishes of Hawaii, with notes and descriptions of new species. Mem. Carnegie Mus. 10:1-92.

JORDAN, D. S., AND J. O. SNYDER.
    1900. A list of fishes collected in Japan by Keinosuke Otaki, and by the United States steamer Albatross, with descriptions of fourteen new species. Proc. U.S. Natl. Mus. 23:335-380.
    1901. A preliminary check list of the fishes of Japan. Annot. Zool. Jap. 3(2-3):31-159.

    1904. Description of a new species of fish (*Apogon evermanni*) from the Hawaiian Islands, with notes on other species. Proc. U.S. Natl. Mus. 28:123-126.

JORDAN, D. S., S. TANAKA, AND J. O. SNYDER.
    1913. A catalogue of the fishes of Japan. J. Coll. Sci., Imp. Univ., Tokyo 33(1):1-497.

KAMI, H. T., I. I. IKEHARA, AND F. P. DeLeon.
    1968. Check-list of Guam fishes. Micronesica 4:95-131.

KIKAWA, S., AND STAFF.
    1963. Synopsis of biological data on bonito *Sarda orientalis* Temminck and Schlegel 1842. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:147-156.

KISHINOUYE, K.
    1923. Contributions to the comparative study of the so-called scombroid fishes. J. Coll. Agric., Imp. Univ., Tokyo 8:293-475.

KLAWE, W. L.
    1961a. Young scombroids from the waters between Cape Hatteras and Bahama Islands. Bull. Mar. Sci. Gulf Caribb. 11:150-157.
    1961b. Notes on larvae, juveniles, and spawning of bonito (*Sarda*) from the eastern Pacific Ocean. Pac. Sci. 15:487-493.
    1962. Bonito juvenil (*Sarda chiliensis*) en las aguas del sur de Baja California. Ciencia (Mexico) 21:180.

KLAWE, W. L., AND B. M. SHIMADA.
    1959. Young scombroid fishes from the Gulf of Mexico. Bull. Mar. Sci. Gulf Caribb. 9:100-115.

KLUNZINGER, C. B.
    1871. Synopsis der Fische des Rothen Meeres. II. Verh. Zool.-Bot. Ges. Wien 21:441-668.

KUMARAN, M.
    1964. Studies on the food of *Euthynnus affinis affinis* (Cantor), *Auxis thazard* (Lacépède), *Auxis thynnoides* Bleeker and *Sarda orientalis* (Temminck and Schlegel). Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:599-606.

KUO, C.-M.
    1970. Taxonomic, growth, and maturation studies on the bonitos of the temperate eastern Pacific Ocean. Ph.D. Thesis, Univ. California, San Diego, 321 p.

LAEVASTU, T., AND H. ROSA, JR.
    1963. Distribution and relative abundance of tunas in relation to their environment. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:1835-1851.

LA MONTE, F.
    1945. North American game fishes. Doubleday, Doran and Company, Inc., Garden City, N.Y., 202 p.
    1952. Marine game fishes of the world. Doubleday & Company, Inc., Garden City, N.Y., 190 p.

LE GALL, J.
    1934a. *Orcynopsis unicolor*. Species account 287. Cons. Perm. Int. Explor. Mer, Faune Ichthyol. Atl. Nord., Vol. 15.
    1934b. *Sarda sarda*. Species account 288. Cons. Perm. Int. Explor. Mer, Faune Ichthyol. Atl. Nord., Vol. 15.

LEWIS, A. G.
    1968.Copepod crustaceans parasitic on fishes of Eniwetok Atoll. Proc. U.S. Natl. Mus. 125:1-78.

LIEBMAN, E.
    1934. Contributions to the knowledge of Palestine sea fishes. Comm. Int. Explor. Sci. Mer. Médit., Rapp. P.-V. Réun., New Ser., 8:317-327.

LORD, C. E.
  1927. A list of the fishes of Tasmania. J. Pan-Pac. Res. Inst. 2(4):11-16.
LOVÉN, M.
  1938. Den ryggstrimmiga pelamiden *Sarda sarda* Bloch och dess förekomst i nordiska farvatten. Fauna Flora 33(6):274-280.
LOWE, R. T.
  1850. An account of fishes discovered or observed in Madeira since the year 1842. Proc. Zool. Soc. Lond. 18:247-253.
LOZANO, L.
  1916. Sobre el hallazgo de un *Orcynopsis unicolor* (Geoffr.) en Melilla. Bol. R. Soc. Esp. Hist. Nat. 16:298-302.
LOZANO CABO, F.
  1970. Caractéristiques zoogéographiques de la faune ichthyologique des côtes de îles Canaries, du Maroc, du Sahara espagnol et de la Mauritanie avec une étude speciale des poissons côtiers. Rapp. P.-V. Réun., Cons. Perm. Int. Explor. Mer 159:152-164.
LOZANO Y REY, L.
  1952. Peces fisoclistos, subserie toracicos. Segunde parte. Mem. R. Acad. Cienc. Exactas. Fís. Nat., Madr. Ser. Cienc. Nat. 14:387-703.
MACLEAY, W.
  1880. Descriptive catalogue of the fishes of Australia. Part II. Proc. Linn. Soc. N.S.W. 5(4):510-629.
MAGNUSON, J. J.
  1973. Comparative study of adaptations for continuous swimming and hydrostatic equilibrium of scombroid and xiphoid fishes. Fish. Bull., U.S. 71:337-356.
MAGNUSON, J. J., AND J. G. HEITZ.
  1971. Gill raker apparatus and food selectivity among mackerels, tunas, and dolphins. Fish. Bull., U.S. 69:361-370.
MAGNUSON, J. J., AND J. H. PRESCOTT.
  1966. Courtship, locomotion, feeding, and miscellaneous behaviour of Pacific bonito (*Sarda chiliensis*). Anim. Behav. 14:54-67.
MAGO LECCIA, F.
  1958. The comparative osteology of the scombroid fishes of the genus *Scomberomorus* from Florida. Bull. Mar. Sci. Gulf Caribb. 8:299-341.
  1970. Lista de los peces de Venezuela, incluyendo un estudio preliminar sobre la ichtiogeografía del país. Minist. Agric. Cria, Of. Nac. Pesca, Caracas, 283 p.
MANN F., G.
  1954. La vida de los peces en aguas Chilenas. 2nd ed. Ministerio de Agricultura, Santiago de Chile, 339 p.
MANSUETI, R. J.
  1962. The Atlantic bonito, *Sarda sarda*, in northern Chesapeake Bay, and comments on the seaside fishery of Maryland. Chesapeake Sci. 3:47-49.
MANZER, J. I.
  1965. *Sarda lineolata* (Girard), a Pacific bonito in the Strait of Georgia, British Columbia. J. Fish. Res. Board Can. 22:853-855.
MARR, J. C., AND M. B. SCHAEFER.
  1949. Definitions of body dimensions used in describing tunas. U.S. Fish Wildl. Serv., Fish. Bull. 51:241-244.
MARSHALL, T. C.
  1941. New ichthyological records. Mem. Queensl. Mus. 12:53-64.
  1964. Fishes of the Great Barrier Reef and coastal waters of

Queensland. Angus and Robertson, Sydney, 566 p. Also 1965, Livingston Publishing Company, Narbeth, Pa.
  1966. Tropical fishes of the Great Barrier Reef. Angus and Robertson, Sydney, 239 p.
MATHER, F. J. III, AND C. G. DAY.
  1954. Observations of pelagic fishes of the tropical Atlantic. Copeia 1954:179-188.
MATHER, F. J. III, AND R. H. GIBBS, JR.
  1957. Distributional records of fishes from waters off New England and the middle Atlantic states. Copeia 1957:242-244.
MCCOY, F.
  1888. Prodromus of the zoology of Victoria. 1(16):203-251. Gov. Printer, Melbourne.
MCCULLOCH, A. R.
  1922. Check list of the fish and fish-like animals of New South Wales. Part 3. Aust. Zool. 2:86-130.
MCKENZIE, R. A.
  1939. Some marine fish and salp records. Proc. Nova Scotia Inst. Sci. 20:13-20.
MEEK, S. E., AND S. F. HILDEBRAND.
  1923. The marine fishes of Panama. Field Mus. Nat. Hist., Publ. 215, Zool. Ser. 15, Part 1, 330 p.
MERRETT, N. R., AND C. H. THORP.
  1966. A revised key to the scombroid fishes of East Africa with new observations on their biology. Ann. Mag. Nat. Hist., Ser. 13, 8:367-384.
MIRANDA RIBEIRO, A. DE
  1918. Lista dos peixes Brasileiros do Museu Paulista. 3ª Parte. Rev. Mus. Paul. 10:763-783.
MOLTENO, C. J.
  1948. The South African tunas - a preliminary study of the economic potentialities. S. Afr. Fish. Ind. Res. Inst., Cape Town, 34 p.
MONOD, T.
  1968. Le complexe urophore des poissons téléostéens. Mém. Inst. Fond. Afr. Noire 81, 705 p.
MORÉAU, E.
  1881. Histoire naturelle dès poissons de la France, vol. 2. G. Masson, Paris, 570 p.
MORELAND, J.
  1959. The composition, distribution and origin of the New Zealand fish fauna. Proc. N. Z. Ecol. Soc. 6:28-30.
MORI, K.
  1967a. Occurrence of the larvae of *Allothunnus fallai* Serventy in the South Atlantic Ocean. Rep. Nankai Reg. Fish. Res. Lab. 25:105-111.
  1967b. Record of occurrence and some notes on young slender-tuna (*Allothunnus fallai* Serventy) from the stomachs of longline tunas and marlins in the South Pacific Ocean. Rep. Nankai Reg. Fish. Res. Lab. 25:113-120.
  1972. Records of juveniles of slender tuna, *Allothunnus fallai*, from the equatorial western Pacific and the South Atlantic Ocean. [In Jap., Engl. abstr.] Jap. J. Ichthyol. 19:29-31. [Natl. Mar. Fish. Serv., Syst. Lab. Transl. 70.]
MORICE, J.
  1953a. Essai systématique sur les familles des Cybiidae, Thunnidae et Katsuwonidae, poissons Scombroïdes. Rev. Trav. Inst. Sci. Tech. Pêches Marit. 18(1):35-63.
  1953b. Un caractère systématique pouvant servir à séparer les espècies de Thunnidae atlantiques. Rev. Trav. Inst. Sci. Tech. Pêches Marit. 18(1):65-74.

MUIR, B. S.

1969. Gill dimensions as a function of fish size. J. Fish. Res. Board Can. 26:165-170.

1970. Contribution to the study of blood pathways in teleost gills. Copeia 1970:19-28.

MUNRO, I. S. R.

1958a. Handbook of Australian fishes, No. 28:113-116. Fish. Newsl. 17(10):17-20.

1958b. The fishes of the New Guinea region. Papua New Guinea Agric. J. 10(4):97-369.

1967. The fishes of New Guinea. Dep. Agric., Stock, Fish., Port Moresby, New Guinea, 650 p.

NAGABHUSHANAM, A. K., AND G. CHANDRASEKHARA RAO.

1972. An ecological survey of the marine fauna of Minicoy Atoll (Laccadive Archipelago, Arabian Sea). Mitt. Zool. Mus. Berl. 48:265-324.

NAIR, R. V., K. VIRABHADRA RAO, AND K. DORAIRAJ.

1970. The tunas and tuna-like fishes of India. Bull. Cent. Mar. Fish. Res. Inst. 23, 93 p.

NAKAMURA, I.

1965. Relationships of fishes referrable to the subfamily Thunninae on the basis of the axial skeleton. Bull. Misaki Mar. Biol. Inst., Kyoto Univ. 8:7-38.

NAKAMURA, I., AND S. KIKAWA.

1966. Infra-central grooves of tunas with special reference to the identification of young tunas found in the stomachs of large predators. Rep. Nankai Reg. Fish. Res. Lab. 23:55-66.

NAKAMURA, I., AND K. MORI.

1966. Morphological study on the slender tuna, *Allothunnus fallai* Serventy obtained from the Tasman Sea. Rep. Nankai Reg. Fish. Res. Lab. 23:67-83.

NAVARRO, F. D. P.

1943. La pesca de arrastre en los dondos del Cabo Blanco y del Banco Arguin (Africa Sahariana). Trab. Inst. Esp. Oceanogr. 18, 225 p.

NICHOLS, J. T., AND C. M. BREDER, JR.

1927. The marine fishes of New York and southern New England. Zoologica (N.Y.) 9:1-192.

NINNI, A. P.

1882. Sopra una forma di tonna nuova per l'Adriatico. Atti Soc. Ital. Sci. Nat. Mus. Civ. Stor. 25:261-264.

NÜMANN, W.

1955. Die Pelamiden des Schwarzen Meeres, des Bosporus, der Marmara und der Dardanellen (*Sarda sarda*). Publ. Hydrobiol. Res. Inst., Univ. Istanbul 3B:75-127.

NUNES-RUIVO, L.

1962. Copépodes parasitas de peixes das costas de Angola. (Lista faunística). Notas Mimeogr. Cent. Biol. Piscat. 33, 28 p.

OGILBY, J. D.

1887. Catalogue of the fishes of New South Wales with their principal synonyms. Fisheries of the Colony. Rep. Comm. Fish. N.S.W. 1886, Append. 6, 1-67.

1893. Edible fishes and crustaceans of New South Wales. Gov. Printer, Syd., 212 p.

OLSEN, A. M.

1962. *Allothunnus fallai* Serventy—a new record for Australian waters. Pap. Proc. R. Soc. Tasmania 96:95-96.

OSORIO, B.

1890. Estudos ichthyologicos ácerca da fauna dos dominios portuguezes na Africa. 2.a nota.—Peixes maritimos d'Angola. J. Sci. Math. Phys. Nat., Ser. 2, 5:50-60.

OTTERSTRØM, C. V.

1943. Rygstribet pelamide (*Sarda pelamis* Brünn.). Flora Fauna 49(4-5):125-126.

PADOA, E.

1967. Eggs, larva and juvenile stages of the Scombriformes (in part) of the Gulf of Naples. [In Ital.] Fauna e Flora del Golfo di Napoli 38:471-521. [Natl. Mar. Fish. Serv., Trop. Atl. Lab. Transl. 12.]

PALLAS, P. S.

1811. Zoographia Rosso-Asiatica, sistens omnium animalium in extenso Imperio Rossico et adjacentibus maribus observàtorum recensionem, domicilia, mores et descriptiones, anatomen atque icones plurimorum. Petropoli, vol. 3, 428 p.

PARONA, C.

1919. Il tonno e la sua pesca. Mem. R. Com. Talassogr. Ital. Venice 68, 265 p.

PARROTT, A. W.

1958. Big game fishes and sharks of New Zealand. Hodder and Stoughton, Lond., 127 p.

PATTEN, B. G., D. T. RODMAN, AND K. D. WALDRON.

1965. The Pacific bonito *Sarda chiliensis* (Cuvier) in Puget Sound, Washington. Calif. Fish Game 51:298-299.

PELLEGRIN, J.

1908. Mission des pêcheries de la côte occidentale d'Afrique. Poissons (2ᵉ Memoire). Actes Soc. Linn. Bordeaux 62:71-102.

PEW, P.

1954. Food and game fishes of the Texas coast. Tex. Game Fish Comm., Mar. Lab. Bull. 33, Ser. IV, 68 p.

PINKAS, L.

1961. Descriptions of postlarval and juvenile bonito from the eastern Pacific Ocean. Calif. Fish Game 47:175-188.

PINKAS, L., M. S. OLIPHANT, AND I. L. K. IVERSON.

1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dep. Fish Game, Fish Bull. 152, 105 p.

POLL, M.

1947. Poissons marins. Faune de Belgique, Bruxelles, 452 p.

POSTEL, A. E.

1955. Considerations biometriques sur la denture des Cybiidés (dents maxillaires). Bull. Stn. Océanogr. Salammbo 51:57-67.

POSTEL, E.

1950. Note sur les thonidés de la presqu'ile du Cap Verte. Bull. Serv. Élev. Ind. Anim. Afr. Occ. Fr. 3(2-3):41-76.

1954. Contribution à l'étude des thonidés de l'Atlantique tropical. J. Cons. 19:356-362.

1955a. Contribution à l'étude de la biologie de quelques Scombridae de l'Atlantique tropico-oriental. Ann. Stn. Océanogr. Salammbo 10:1-167.

1955b. Contribution à l'étude des thonidés de l'Atlantique tropical (deuxième note). Rapp. P.-V. Réun., Cons. Perm. Iné. Explor. Mer 137:31-32.

1956a. Essai sur la palomette, *Orcynopsis unicolor* (Geoffroy Saint-Hilaire, 1809). Bull. Inst. Fr. Afr. Noire 18A(4):1220-1248.

1956b. Données biométriques sur quelques scombridés tunisiens. Bull. Stn. Océanogr. Salammbo 53:50-63.

1956c. Les affinités tropicales de la faune ichtyologique du golfe de Gabès. Bull. Stn. Océanogr. Salammbo 53:64-68.

1960. Liste commentée des poissons signalés dans l'Atlantique tropico-oriental nord, du Cap Spartel au Cap Roxo, suivie d'un bref aperçu sur leur répartition bathyme-

trique et geographique. Bull. Soc. Sci. Bretagne 34(3-4):241-281.

1964. Les thonides d'Afrique de Nord. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:211-220.

1973. Scomberomoridae. CLOFNAM - Check-list of the fishes of the northeastern Atlantic and of the Mediterranean. UNESCO (U.N. Educ., Sci. Cult. Organ.) 1:473-475.

POSTEL, E., P. FOURMANOIR, AND P. GUEZE.

1960. Sur quelques thons (sensu lato) de la Réunion, en collection au Laboratoire des Pêches Outre-Mer. Bull. Mus. Natl. Hist. Nat. Paris, Ser. 2, 32:392-394.

POTTHOFF, T.

1974. Osteological development and variation in young tunas, genus Thunnus (Pisces, Scombridae), from the Atlantic Ocean. Fish. Bull., U.S. 72:563-588.

1975. Development and structure of the caudal complex, the vertebral column, and the pterygiophores in the blackfin tuna (Thunnus atlanticus, Pisces, Scombridae). Bull. Mar. Sci. 25:205-231.

POZZI, A. J., AND L. F. BORDALE.

1935. Cuadro sistemático de los peces marinos de la República Argentina. An. Soc. Cient. Argent. 120:145-189.

QUAST, J. C.

1964. Occurrence of the Pacific bonito in coastal Alaskan waters. Copeia 1964:448.

RADOVICH, J.

1961. Relationships of some marine organisms of the Northeast Pacific to water temperatures particularly during 1957 through 1959. Calif. Dep. Fish Game, Fish Bull. 112, 62 p.

RAE, B. B., AND S. F. PIRIE.

1968. Scottish records of rare fishes-1966. Ann. Biol. 23:212.

1969. Scottish records of rare fishes-1969. Ann. Biol. 26:279.

RAFINESQUE, C.

1810. Caratteri di alcuni nuovi generi e nuove specie di animali e piante della Sicilia. San Filippo, Palermo, 105 p.

RAO, K. V. N.

1964. An account of the ripe ovaries of some Indian tunas. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:733-743.

RATHKE, H.

1837. Beitrag zur Fauna der Krym. Mém. Acad. Imp. Sci. Saint-Pétersbourg Etrang. 3:291-454.

REDEKE, H. C.

1941. De visschen van Nederland. A. W. Sijthoff, Leiden, 331 p.

RICHARDSON, J.

1846. Report on the ichthyology of the seas of China and Japan. Rep. Br. Assoc. Adv. Sci., 15th Meet., p. 187-320.

RICKER, K. E.

1959a. Mexican shore and pelagic fishes collected from Acapulco to Cape San Lucas during the 1957 cruise of the "Marijean". Univ. B.C. Inst. Fish., Mus. Contrib. 3:1-18.

1959b. Fishes collected from the Revillagigedo Islands during the 1954-1958 cruises of the "Marijean". Univ. B.C. Inst. Fish., Mus. Contrib. 4:1-10.

RISSO, A.

1810. Ichthyologie de Nice ou histoire naturelle des poissons du département des Alpes Maritimes. F. Schoell, Paris, 388 p.

1826. Histoire naturelle des poissons de la Méditerranée qui fréquentent les côtes des Alpes Maritimes, et qui vivent dans le Golfe de Nice. In Histoire naturelle des principales productions de l'Europe méridionale, 3:97-480. Levrault, Paris and Strasbourg.

RIVAS, L. R.

1951. A preliminary review of the western North Atlantic fishes of the family Scombridae. Bull. Mar. Sci. Gulf Caribb. 1:209-230.

1954. The pineal apparatus of tunas and related scombrid fishes as a possible light receptor controlling phototactic movements. Bull. Mar. Sci. Gulf Caribb. 3:168-180.

ROCHEBRUNE, A. T. DE.

1882. Faune de la Sénégambie. Poissons. Actes Soc. Linn. Bordeaux 36, Ser. 4, 6:23-188.

RODRÍGUEZ-RODA, J.

1966. Estudio de la bacoreta, Euthynnus alleteratus (Raf.), bonito, Sarda sarda (Bloch) y melva, Auxis thazard (Lac.), capturados por las almadrabas españolas. Invest. Pesq. Barc. 30:247-292.

RÖHL, E.

1942. Fauna descriptiva de Venezuela (vertebrados). Tipogr. Am. (Caracas), 431 p.

RONDELET, G.

1554. Libri de piscibus marinis. Lugdini Mathiem Bonhomme, Lyons, 583 p.

RONQUILLO, I. A.

1963. A contribution to the biology of Philippine tunas. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:1683-1752.

ROUGHLEY, T. C.

1951. Fish and fisheries of Australia. Angus and Robertson, Sydney, 343 p.

RÜPPELL, E.

1938. Neue Wirbelthiere zu der Fauna von Abyssinien gehörig. Fische des Rothen Meeres. Frankfurt am Main, 148 p.

SÁNCHEZ T., J., AND R. LAM C.

1970. Algunas característicus físicas y químicas de las principales especies para consumo humano y sus rendimientos en productos pesqueros, en el Perú. Inst. Mar Perú, Callao, Inf. 33, 92 p.

SANZ ECHEVERRÍA, J.

1926. Datos sobre el otolito sagita de los peces de España. Bol. R. Soc. Esp. Hist. Nat. 26(2):145-160.

SANZO, L.

1932. Uova e primi stadi larvali di Pelamys sarda C.V. R. Com. Talassogr. Ital. Mem. 188:3-9.

SCHMITT, W. L., AND L. P. SCHULTZ.

1940. List of the fishes taken on the Presidential Cruise of 1938. Smithson. Misc. Collect. 98(25):1-10.

SCHROEDER, W. C.

1924. Fisheries of Key West and the clam industry of Southern Florida. Rep. U.S. Comm. Fish., 1923, append. 12:1-74. (Doc. 962.)

SCHULTZ, L. P.

1960. Suborder Scombrina. Family Scombridae: Tunas. In L. P. Schultz, W. M. Chapman, E. A. Lachner, and L. P. Woods. Fishes of the Marshall and Marianas Islands. Bull. U.S. Nat. Mus. 202(2):410-417.

SERVENTY, D. L.

1941a. The Australian tunas. Counc. Sci. Ind. Res., Div. Fish. Rep. 104, 48 p.

1941b. Victorian tunas and some recent records. Victorian Nat. 58:51-55.

1948. Allothunnus fallai, a new genus and species of tuna from New Zealand. Rec. Canterbury Mus. 5:131-135.

623

1950. Tuna survey of north Australia. Fish. Newsl. (Aust.) 9(3):18-20.

SHEPHERD, C. E.
1910a. The "asteriscus" in fishes. Zoologist (Lond.), Ser. 4, 14(158):57-62.
1910b. Comparisons of otoliths found in fishes. Zoologist (Lond.), Ser. 4, 14(164):292-298.

SHERRIN, R. A. A.
1886. Handbook of the fishes of New Zealand. Wilsons and Horton, Auckland, 307 p.

SILAS, E. G.
1963. Synopsis of biological data on dogtooth tuna *Gymnosarda unicolor* (Rüppell) 1838 (Indo-Pacific). FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:877-899.
1964. Aspects of the taxonomy and biology of the oriental bonito *Sarda orientalis* (Temminck and Schlegel). Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:283-308.

SIVASUBRAMANIAM, K.
1967. Distribution and length-weight relationships of tunas and tuna-like fishes around Ceylon. Bull. Fish. Res. Stn. Ceylon 19(1-2):27-41.
1969. Occurrence of oriental bonito (*Sarda orientalis* Temminck and Schlegel) in the inshore waters of Ceylon. Bull. Fish. Res. Stn. Ceylon 20(1):73-77.
1970. Surface and subsurface fisheries for young and immature yellowfin tuna (*T. albacares*) around Ceylon. Bull. Fish. Res. Stn. Ceylon 21(2):113-122.

SMITH, H. M., AND T. E. B. POPE.
1906. List of fishes collected in Japan in 1903, with descriptions of new genera and species. Proc. U.S. Natl. Mus. 31:459-499.

SMITH, J. L. B.
1949. The sea fishes of southern Africa. Central News Agency, Ltd., South Africa, 550 p.
1956. The fishes of Aldabra. Part V. Ann. Mag. Nat. Hist., Ser. 12, 9(106):721-729.
1965. New records and descriptions of fishes from Southwest Africa. Rhodes Univ., Dep. Ichthyol. Occas. Pap. 3:13-23.

SMITH, J. L. B., AND M. M. SMITH.
1963. The fishes of Seychelles. Rhodes Univ., Dep. Ichthyol., Grahamstown, S. Afr., 215 p.

SMITT, F. A.
1892. A history of Scandinavian fishes by B. Fries, C. U. Ekström, and C. Sundevall. 2nd ed. revised and completed by F. A. Smitt. Part 1. P. A. Norstedt and Söner, Stockh., 566 p.

ŠOLJAN, T.
1963. Fishes of the Adriatic. Fauna et Flora Adriatica, volume 1, Pisces. Publ. for Dep. Inter. and Natl. Sci. Found., Wash., D.C. by Nolit Publ. House, Belgrade, Yugosl., 428 p.

SPRINGER, S., AND H. R. BULLIS, JR.
1956. Collections by the *OREGON* in the Gulf of Mexico. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 196, 134 p.

STANBURY, P. J.
1969. Type specimens in the Macleay Museum, University of Sydney. I. Fishes. Proc. Linn. Soc. N.S.W. 93:203-210.

STARKS, E. C.
1906. On a collection of fishes made by P. O. Simons in Ecuador and Peru. Proc. U.S. Natl. Mus. 30:761-800.

1910. The osteology and mutual relationships of the fishes belonging to the family Scombridae. J. Morphol. 21:77-99.

STASSANO, E.
1890. La pesca sulle spiagge atlantiche del Sahara. Ann. Agrar. Roma 1890:7-59.

STEAD, D. G.
1906. Fishes of Australia: A popular and systematic guide to the study of wealth within our waters. Wm. Brooks and Co., Ltd., Sydney, 278 p.
1908. The edible fishes of New South Wales: Their present importance and their potentialities. Gov. Printer, Sydney, 123 p.

STEINDACHNER, F.
1865. Vorläufiger Bericht über die an der Ostküste Tenerife's bei Santa Cruz gesammelten fische. Sitzber. Akad. Wiss. Wien 51(1):398-404.
1868. Ichthyologischer Bericht über eine nach Spanien und Portugal unternommene Reise. V. Übersicht der Meeresfische an den Küsten Spanien's und Portugal's. Sitzber. Akad. Wiss. Wien 57:351-424.

STEINDACHNER, F., AND L. DÖDERLEIN.
1884. Beiträge zur Kenntniss der Fische Japan's [III]. Denkschr. Akad. Wiss. Wien 49:171-212.

STILLMAN, C. K.
1921. A reconstructed fish. Bull. Am. Game Prot. Assoc. 10(1):15.

STORER, D. H.
1855. A history of the fishes of Massachusetts. Mem. Am. Acad. Arts Sci., New Ser., 5:122-168.

SVETOVIDOV, A. N.
1964. The fishes of the Black Sea. [In Russ.] Zool. Inst. Akad. Nauk, Opred. Faune SSSR 86:552 p.

TALBOT, F. H.
1960. Additions to the South African Museum collections of marine fishes. Ann. S. Afr. Mus. 45:257-259.
1964. The South African tunas. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:187-209.
1965. A description of the coral structure of Tutia Reef (Tanganyika Territory, East Africa), and its fish fauna. Proc. Zool. Soc. Lond. 145:431-470.

TEMMINCK, C. J., AND H. SCHLEGEL.
1844. Pisces. *In* P. F. von Siebold, Fauna Japonica . . . 1823-30, Part 3, p. 73-112. Lugduni Batavorum.

THOMAS, P. T., AND M. KUMARAN.
1963. Food of Indian tunas. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:1659-1667.

TINKER, S. W.
1944. Hawaiian fishes. Tongg Publ. Co., Honolulu, 404 p.

TIRANT, G.
1885. Notes sur les poissons de la Basse-Cochinchine et du Cambodge. Excur. Reconnais. Cochinchine Française 9:413-438 and 10:91-198. Repr. 1929, Serv. Océanogr. Pêch Indochine, Stn. Mar. Cauda, Note 6:43-163.

TOMINAGA, Y.
1966. On two tuna-like fishes captured in waters at about 40°S Lat. [In Jap., Engl. summ.] Jap. J. Ichthyol. 14:41-48.

TORTONESE, E.
1939. Risultati ittiologici del viaggio di circumnavigazione del globo della R. N. "Magenta" (1865-68). Boll. Mus. Zool. Anat. Comp. Univ. Torino 47, Ser. 3, 100:177-421.
1949. Identificazione di due Sgombroide (pesci) accidentali nel Mediterraneo. Boll. Zool. Torino 16(1-3):61-66.

1956. Brevi considerazioni sui pesci Mediterranei del Sottordine Sgombroidi. Boll. Inst. Mus. Zool. Univ. Torino 5(3):3-11.

1963. Catalogo dei tipi di pesci del Museo Civico di Storia Naturale de Genova (Parte III). Ann. Mus. Civ. Stor. Nat. Genova 73:333-350.

TORTONESE, E., AND L. TROTTI.
1949. Catalogo dei pesci del Mare Ligure. Atti Accad. Ligure Sci. Lett. 6(1):1-118.

TRETIAKOV, D. K.
1939. Olfactory organ in *Sarda sarda* C. V. Dokl. Akad. Nauk SSSR 22(4):202-205.

UEYANAGI, S.
1969. Observations on the distribution of tuna larvae in the Indo-Pacific Ocean with emphasis on the delineation of the spawning areas of albacore, *Thunnus alalunga*. [In Jap., Engl. synop.] Far Seas Fish. Res. Lab. Bull. 2:177-256.

VALENCIENNES, A.
1844. Ichthyologie des îles Canaries. *In* P. B. Webb and S. Berthelot, Histoire Naturelle des îles Canaries, Vol. 2, 109 p.

VERANY, J. B.
1847. Aggiunta al catalogo de'pesci della Liguria. Atti Sci. Ital. Genova 8:492-494.

VILDOSO, A. C. DE.
1960. Estudios sobre la reproducción del "bonito" *Sarda chilensis* (C. y V.) en aguas adyacentes a la costa peruana. Ser. Divulg. Cient. Perú 14:1-75.

1963a. Estudios sobre la reproducción del bonito *Sarda chilensis* (C. y V.) en aguas adyacentes a la costa peruana. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:1143-1152

1963b. Especies del genero *Sarda* en el Pacifico oriental. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:1549-1556.

VINCIGUERRA, D.
1890. Intorno ad alcune specie di pesci raccolte dal dottore Enrico Stassano presso la costa occidentale del Sahara. Ann. Agrar. Roma 1890:61-103.

1893. Catalogo dei pesci delle Isole Canarie. Atti Soc. Ital. Sci. Nat. Milan 34:295-334.

VLADYKOV, V. D.
1935. Some unreported and rare fishes for the coast of Nova Scotia. Proc. Nova Scotia Inst. Sci. 19(1):1-8.

WAITE, E. R.
1904. A synopsis of the fishes of New South Wales. Mem. NSW Nat. Club 2:59 p.

WALFORD, L. A.
1936. On the bonitos (*Sarda*) of the Pacific Ocean. St. Barbara Mus. Nat. Hist., Occas. Pap. 4(3):8-10.

1937. Marine game fishes of the Pacific coast from Alaska to the equator. Univ. Calif. Press, Berkeley, 205 p.

WARASHINA, I., AND K. HISADA.
1972. Geographical distribution and body length composition of two tuna-like fishes, *Gasterochisma melampus* Richardson and *Allothunnus fallai* Serventy, taken by Japanese tuna longline fishery. [In Jap., Engl. synop.] Far Seas Fish. Res. Lab. Bull. 6:51-74.

WARFEL, H. E.
1950. Outlook for development of a tuna industry in the Philippines. U.S. Fish Wildl. Serv., Res. Rep. 28, 37 p.

WATANABE, H., M. YUKINAWA, S. NAKAZAWA, AND S. UEYANAGI.
1966. On the larva probably referrable to slender tuna, *Allothunnus fallai* Serventy. [In Jap., Engl. summ.] Rep. Nankai Reg. Fish. Res. Lab. 23:85-94.

WEBB, B. F., AND D. C. WOLFE.
1974. Commercial catches of slender tuna in Tasmanian waters. Aust. Fish. 33(8):5-7.

WENT, A. E. J.
1968. Rare fishes taken in Irish waters in 1967. Ir. Nat. J. 16(2):35-39.

1969. Rare fishes taken in Irish waters in 1968. Ir. Nat. J. 16(6):147-150.

1971. Interesting fishes from Irish waters in 1970. Ir. Nat. J. 17(2):41-45.

WHEELER, A., AND R. W. BLACKER.
1969. Rare and little-known fishes in British seas in 1966 and 1967. J. Fish. Biol. 1:311-331.

1972. Rare and little-known fishes in British seas in 1968 and 1969. J. Fish. Biol. 4:141-170.

WHITLEY, G. P.
1935. Studies in ichthyology. No. 9. Rec. Aust. Mus. 19:215-250.

1936. More ichthyological miscellanea. Mem. Queensl. Mus. 11:23-51.

1939. Studies in ichthyology. No. 12. Rec. Aust. Mus. 20:264-277.

1945. New sharks and fishes from Western Australia. Part 2. Aust. Zool. 11(1):1-42.

1947. New sharks and fishes from Western Australia. Part 3. Aust. Zool. 11(2):129-150.

1948. A list of the fishes of Western Australia. W. Aust. Fish. Dep., Fish. Bull. 2, 35 p.

1964a. Scombroid fishes of Australia and New Zealand. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:221-253.

1964b. A survey of Australian ichthyology. Proc. Linn. Soc. N.S.W. 89:11-127.

1968. A check-list of the fishes recorded from the New Zealand region. Aust. Zool. 15(1):102 p.

WILLIAMS, F.
1964. The scombroid fishes of East Africa. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India. Symp. Ser. 1:107-164.

1968. Report on the Guinean Trawling Survey. Volume I. Gen. Rep. Org. Afr. Unity, Sci., Tech. and Res. Comm., Lagos, Nigeria. OAU/STRC Publ. 99, 828 p.

WILLUGHBY, F.
1686. Historia piscium libri quatuor . . . Totum opus recog novit, coaptavit, supplevit, librum etiam prjmum et secundum integors adjecit Johannes Raius. Oxonii, 343 p.

ZHAROV, V. L.
1967. Classification of scombroid fishes (Suborder Scombroidei, Order Perciformes). [In Russ.] Vopr. Ikhtiol. 43:209-224. (Transl. Natl. Mar. Fish. Serv. Hawaii Area Fish. Cent.)