COMPARATIVE ANATOMY AND SYSTEMATICS OF THE TUNAS, GENUS *THUNNUS* [1]

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ABSTRACT

The taxonomic status of the tunas of the world, often placed in the genera *Thunnus, Germo, Neothunnus, Parathunnus,* and *Kishinoella,* is assessed through the use of external morphological and internal anatomical characters. Seven species, all included in the single genus *Thunnus,* are considered valid: *T. thynnus,* the bluefin tuna; *T. alalunga,* the albacore; *T. obesus,* the bigeye tuna; and *T. albacares,* the yellowfin tuna, are circumglobal in distribution; *T. atlanticus,* the blackfin tuna, and *T. tonggol,* the longtail tuna, are restricted to the western Atlantic and the Indo-West Pacific, respectively; *T. maccoyii,* the southern bluefin tuna, is known in the southern Pacific and Indian oceans and off northwestern Australia. Two subspecies of *T. thynnus* are recognized: *T. t. thynnus* in the Atlantic and *T. t. orientalis* in the Pacific.

In Part 1 the comparative anatomy is described and characters are given for differentiating the species by means of counts and measurements and by comparison of the skeletal, visceral, and vascular systems. In Part 2 the genus *Thunnus* is characterized with respect to other genera of Scombridae, and for each species a synonymy, a résumé of distinctive characters, discussion of type specimens and nomenclatural problems, and a review of known geographic distribution are given.

The purpose of this paper is to demonstrate that there are, at most, seven species of tunas in the world, and that they should be placed in the single genus *Thunnus* which is circumglobal in distribution and constitutes one of the most important groups of commercial fishes. Much time and money have been expended in gathering meristic, morphometric, anatomical, distributional, and life-history data, yet the systematic and nomenclatural status of the group remains unsatisfactory. Over the years, 10 generic names and 37 specific names have been applied to the seven species which we recognize. The confusion is due, at least in part, to the pelagic habits of all of the species and to their large adult size, which makes specimens difficult to preserve and store and

requires that observations be made at the time of collection, often under adverse conditions. Study material over the great size range is not easily obtained, so that growth changes are hard to evaluate. The economic importance of the group has led many biologists to dabble in tuna taxonomy, using variable characters and different means of counting and measuring. Provincialism has caused otherwise competent workers to believe that the kinds of tunas in their home areas are unique and to cling tenaciously to locally established names despite contrary evidence.

Our studies have been built upon the work of a number of previous investigators. We have come to realize, as many of these workers have, the great value of internal anatomical characters as a means of distinguishing tuna species. In this field, Kishinouye (1915, 1917, 1923) pioneered. The most extensive

and painstaking anatomical descriptions are found in his works and those of Godsil and Byers (1944) and Godsil and Holmberg (1950).

This paper is divided into two major sections. The first part describes and compares the osteology, viscera, vascular system, meristic characters, morphometry, and coloration among the species. The second part considers the systematic position of the genus *Thunnus*. Each species is treated separately, including a synonymy, diagnosis (based on characters from the first section), discussion of nominal species, and outline of geographical distribution.

MATERIALS AND ACKNOWLEDGMENTS

We have examined, measured, and made counts on numerous specimens of all Western Atlantic species. Many specimens taken in pound nets in Cape Cod Bay were made available through the courtesy of John E. Vetorino, Mike Goulart, and Adam Rupkus. Most material for dissection and a large share of the total specimens examined were collected on exploratory longline cruises, by the Bureau of Commercial Fisheries vessels *Delaware* in the Gulf Stream and adjacent waters east to the Azores and *Oregon* in the Gulf of Mexico and Caribbean Sea. For saving valuable specimens and for allowing us to participate in many cruises, we are particularly indebted to Harvey R. Bullis, Peter C. Wilson, and James L. Squire. The late Al Pflueger of Miami, Fla., and Frank J. Mather III of Woods Hole Oceanographic Institution (WHOI), gave us a number of specimens. Edward C. Raney lent us skeletons from Cornell University. Margaret E. Watson of WHOI and Donald P. de Sylva of the University of Miami Institute of Marine Science allowed us to examine other specimens.

Southeast Pacific specimens of *T. obesus* and *T. albacares* were dissected during our participation in cruise 14 of the *Anton Bruun*, part of the South East Pacific Biological Oceanographic Program sponsored by the National Science Foundation. Australian and Japanese tunas were examined in the fish markets of Tokyo and Yaizu. We obtained whole specimens or skeletal material of Pacific species from the Inter-American Tropical Tuna Commission (M. B. Schaefer and Craig Orange); California State Fisheries Laboratory (Phil Roedel and Harold B. Clemens); Bureau of Commercial Fisheries Biological Laboratory, Honolulu (John C. Marr); Nankai Regional Fisheries Laboratory, Kochi, Japan (Hir-

oshi Nakamura and Shoji Ueyanagi); Tokyo University (Tokiharu Abe); Kyoto University, Maizuru, Japan (Izumi Nakamura and Tamotsu Iwai); Institut Français d'Océanie, Noumea, New Caledonia (Michel Legand); and C.S.I.R.O. Marine Laboratory, Cronulla, Australia (J. C. Moore and J. P. Robins).

Specimens from the Indian Ocean were received from the Nankai Laboratory and from cruises of the *Anton Bruun* made during the U.S. Program in Biology of the International Indian Ocean Expedition. Frank H. Talbot and Michael Penrith provided South African specimens and skeletons.

We examined specimens and skeletons of both Atlantic and Pacific forms at the California Academy of Sciences (W. I. Follett); Stanford University (George S. Myers and Warren C. Freihofer); University of California at Los Angeles (Wayne J. Baldwin); Scripps Institution of Oceanography (Richard H. Rosenblatt); and the U.S. National Museum and skeletons of Pacific and Indian Ocean specimens at Kyoto University, Maizuru (Tamotsu Iwai and Izumi Nakamura) and the Nankai laboratory (Shoji Ueyanagi).

All available types were examined at the Muséum National d'Histoire Naturelle (MNHN), Paris (M. L. Bauchot and C. Roux); at the Rijksmuseum van Natuurlijke Historie (RMNH), Leiden (M. Boeseman); and at the Academy of Natural Sciences, Philadelphia (ANSP) (James E. Böhlke). We received information on types in the Australian Museum in Sydney and the Dominion Museum in Wellington from Frank H. Talbot and J. Moreland, respectively.

We made thorough examinations of viscera and blood vessels on the following (sizes in mm.):

Thunnus alalunga 9 Atlantic (780–1,250), 1 Pacific (992), 2 Indian (ca. 900–970)
Thunnus albacares 15 Atlantic (600–1,515), 4 Pacific (670–941), 11 Indian (601–895)
Thunnus atlanticus 21 (322–665)
Thunnus obesus 17 Atlantic (697–1,545), 5 Pacific (851–1,614), 2 Indian (630–680)
Thunnus maccoyii 3 (742–1,442)
Thunnus thynnus thynnus 10 (316–2,315)
Thunnus thynnus orientalis 3 (614–1,450)
Thunnus tonggol 4 (373–924)

The following complete skeletons (most of which are now in the U.S. National Museum) provide the basis for our analysis. These include a large share of the material of Godsil and Byers (1944) and Godsil

and Holmberg (1950). Range of skull lengths, in mm., in parentheses.

Thunnus alalunga 19 Atlantic (125–167), 26 Pacific (99–152), 2 Indian (146–157)

Thunnus albacares 21 Atlantic (98–196), 26 Pacific (49–149), 12 Indian (101–127)

Thunnus atlanticus 26 (51–111)

Thunnus obesus 21 Atlantic (119–215), 5 Pacific (97–237), 4 Indian (112–178)

Thunnus maccoyii 9 Australia (111–219), 4 South Africa (128–218), 4 SE. Pacific (207–238)

Thunnus thynnus thynnus 21 Atlantic (76–335), 1 South Africa (322)

Thunnus thynnus orientalis 40 (34–294), 1 SE. Pacific (290)

Thunnus tonggol 2 East Australia (122–128), 6 Indian (56–99).

Details were corroborated by numerous partial dissections of all species. We also examined many additional skulls, postcranial skeletons, and radiographs.

We are grateful to Daniel M. Cohen, J. A. F. Garrick, Brian J. Rothschild, Donald W. Strasburg, Frank H. Talbot, and Stanley H. Weitzman for making comments on various drafts of the manuscript. Mildred H. Carrington and Gale G. Pasley made most of the figures from our sketches. Alice Holland typed many drafts of the manuscript. John E. Fitch made it possible to use the plate blocks from Godsil and Byers (1944) for figures 20 and 21.

METHODS

Dissections.—Although numerous partial dissections of both preserved and fresh specimens were made, the most thorough work was done with fresh specimens on shipboard or, more often, with frozen specimens in the laboratory. After the fish thawed, colored latex was injected into the arteries and veins through the lateral cutaneous branches that had been exposed by removing the thick skin behind the pectoral fin base. Often the injection mass did not reach the posterior ends of the cutaneous vessels or the posterior commissure, but these vessels ordinarily could be followed rather easily. In the other direction, the injection mass seldom penetrated beyond the liver, partly because the deeper regions were not completely thawed. After the latex had set, the lateral cutaneous system was studied. The ventral wall of the body cavity was then removed and the viscera drawn in situ. The ventral organs were then turned aside or removed to expose the swim-

bladder, and this, in turn, was removed and the dorsal fibrous connective tissue cut to expose the kidney and ureters. The most difficult aspect of the dissection involved exposing and tracing the anterior arteries, which lie so far forward and are so deep that they are difficult to reach without mutilating the branchial region. After the appropriate observations were completed, the specimen was fleshed and the skeleton cleaned.

Counts and measurements.—Most external counts and measurements were made on fresh or frozen specimens, some on preserved material, according to the methods described by Marr and Schaefer (1949), with the following exceptions. Our fork length is what they called "total length." We measured length of bony orbit rather than diameter of iris; in our comparisons, therefore, we used only our own data for this character. (We do not recommend this procedure for future workers.) We did not measure "pectoral insertion to insertion first dorsal," or "length longest dorsal finlet," but we made the following measurements not mentioned by Marr and Schaefer: Snout to insertion of pectoral fin, maximum width of body, pelvic fin length, insertion of pelvic fin to vent, tip of depressed pelvic fin to vent (all of which are self-explanatory), snout length (snout tip to front edge of bony orbit), and interorbital width (least distance between dorsal rims of bony orbits formed by frontal bones).

Measurements made by the same worker of the same specimen before and after freezing may differ enough to negate a morphometric difference between species, therefore, all morphometric characters should be used only with rather wide margins for error.

Skeletons.—Skull length was measured from the anterior tip of the vomer to the lower posterior end of the ankylosed first vertebral centrum. Individual bones of the skull, pectoral girdle, and pelvic girdle were compared simultaneously in all species, and measurements were made only when proportional differences were suspected. The only significant differences requiring measurements for definition were among those already pointed out by Godsil and Byers (1944) or Godsil and Holmberg (1950). Dial calipers were used in most cases, and articulation cartilages were removed from skull bones. The methods of mensuration follow.

Anterior articulating head of hyomandibula (See fig. 6). Length (B) was measured from the end of the horizontal articulation surface (pterotic head) to the most anterior point of the anterior articulation

surface (sphenotic head). Least width (A) and greatest width were measured vertically on the anterior (sphenotic) head.

Metapterygoid (See fig. 7). The transition from anteroventral (C) to posteroventral (D) margin is usually an arc. Each margin was measured to the midpoint of the arc.

Quadrate (See fig. 8). Length (G) was measured from the most ventral part of the articular condyle to the tip of the spine. Width of horizontal edge (F) was measured along the horizontal dorsal edge to the point where it forms a slight depression before the spine. Total width (E) was measured from the anterior point of the horizontal dorsal edge along a projection of the line of this edge to the posterior margin of the spine.

36th vertebra. Length was measured along the axis of the centrum from the outer anterior rim to the outer posterior rim. Width was measured vertically on the lateral surface at the narrowest part of the centrum and does not include the neural or haemal arches.

Bone terminology is that of de Sylva (1955), which has been used for tuna osteology by most other recent workers. A number of names differ from those accepted by many fish osteologists.

PART 1. COMPARATIVE ANATOMY

The morphological characters useful for distinguishing the species of *Thunnus* fall into seven groups: osteology, viscera, vascular system, olfactory organ, meristic characters, morphometric characters, and coloration. These will be discussed in this order in this section of the paper. The first three groups, osteology, viscera, and vascular system, include the most important characters.

OSTEOLOGY

Osteological characters are very important in distinguishing species of *Thunnus*. They have an advantage over characters in the soft anatomy in that the bones can be saved so future workers can reexamine the material on which a study is based. We have used a large amount of the material Godsil and his co-workers reported on. Four groups of osteological characters will be considered: neurocranium, branchiocranium, pectoral and pelvic girdles, and vertebral column. The most useful characters are in the skull and the vertebral column. Each of the four groups will be discussed separately, giving a general osteological description followed by an enumeration of the specific characters.

Neurocranium

General characteristics.—Details of the general neurocranial structure of tunas have been illustrated by Masterman (1894), Kishinouye (1923), Frade (1932), Gregory (1933), Godsil and Byers (1944), de Sylva (1955), and Nakamura (1965). The accompanying labeled figures of an albacore (*Thunnus alalunga*) skull show the bones of the neurocranium (figs. 1–3). Photographs of the skulls of six of the seven species of *Thunnus* are presented in appendix figs. 1–3.

The skull of a tuna, compared with that of most typical percoid fishes, is short and wide. In dorsal view (fig. 2), at its anterior end, the dermethmoid (= ethmoid) is wide and its anterior margin only slightly curved. The interorbital region is broad, and the otic region broader still. A prominent dorsolateral crest is formed on each side by the frontal, parietal, and epiotic bones; each of the epiotics bears a short, posteriorly directed process. The lateral edges of the frontal and pterotic, making up the sides of the roof of the neurocranium, form a more prominent and rather flat sharp crest on each side which extends posteriorly as a long plate-like pterotic spine. The supraoccipital crest is high and extends posteriorly over the first few vertebrae.

Ventrally, the dentigerous vomer (= prevomer) is flanked by broad processes of the parethmoids (= lateral ethmoids). Most of the base of the skull is formed by the parasphenoid, which is flat or slightly concave in its anterior two-fifths, bears a medial, ventrally directed crest in the next two-fifths, and posteriorly is first convex, then deeply concave, with dorsomesially curved lateral flanges that enclose a parasphenoid chamber. Lateral wings project dorsad from near the end of the ventral crest to form part of the posterior myodome.

In lateral view, the alisphenoids (= pterosphenoids) form a partial interorbital septum extending ventrad from the roof of the skull. In extreme cases (large *Thunnus thynnus*) this septum may be fused with the parasphenoid, to form a bony septum partially separating the orbits. In the posterior part of the
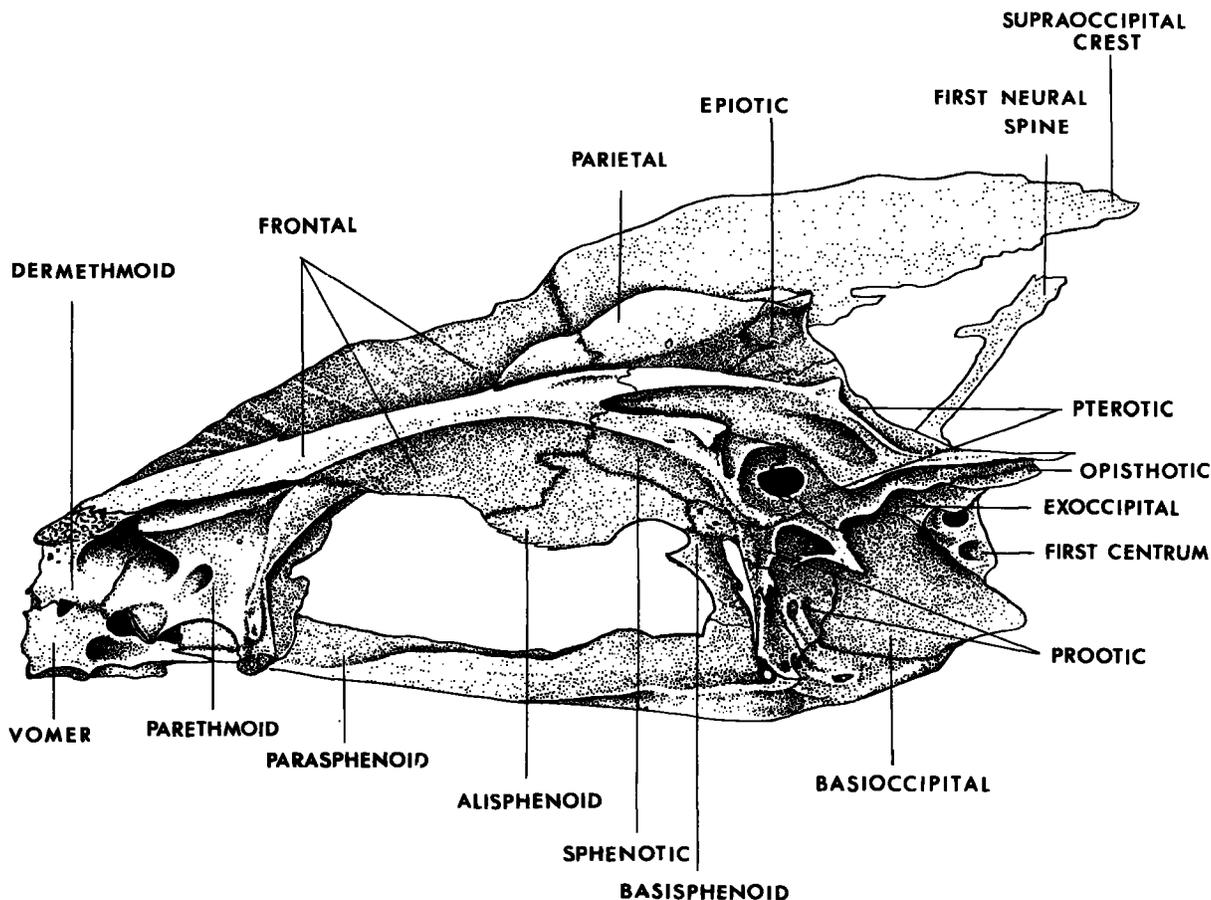
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FIGURE 1.—Skull of *Thunnus alalunga*. Lateral view.

orbital region is a median, vertically oriented basisphenoid, which usually has an anteriorly directed process near its dorsal end. The posterior base of the cranium is formed by the end of the parasphenoid (ventral profile) and the lateral flanges of the basioccipital (posterior profile). The first vertebra articulates firmly, partly by a jagged suture, with the occipital region and forms an integral part of the skull. One end of Baudelot's ligament attaches to the basioccipital, the other end to the supracleithrum.

The prootic pits (Godsil, 1954) are large pouchlike concavities on each side of the ventral surface of the cranium, opening posteriorly and separating the pterotic bones from the brain case. Part of the roof, floor, and sides of each prootic pit is formed by the prootic bone, and the anterior wall by the sphenotic. The pits function as areas of attachment for the branchial musculature. These pits are characteristic of the most advanced scombrids—*Thunnus, Euthynnus, Katsuwonus, Auxis,* and *Allothunnus*—

and are incipient in *Sarda* (Starks, 1910; Godsil, 1954).

The posterior myodome is a deep median depression opening anteriad at the posterior end of the orbital region. Its anterolateral walls and roof are formed by the prootics, its floor and ventrolateral walls by the parasphenoid, and its posterior concave wall by the basioccipital. The posterior myodome functions as a place of attachment for the rectus muscles of the eyes. The narrow basisphenoid lies just anterior to the anterior opening of the posterior myodome. There is a posterior or parasphenoidal chamber (Kishinouye, 1923), which communicates with the posterior myodome and is formed by the upcurved walls of the posteriormost end of the parasphenoid.

A large triangular fronto-parietal foramen (lateral parietal foramen of Masterman, 1894) is present on each side of the dorsal surface of the skull, at the junction of the frontal, parietal, and supraoccipital
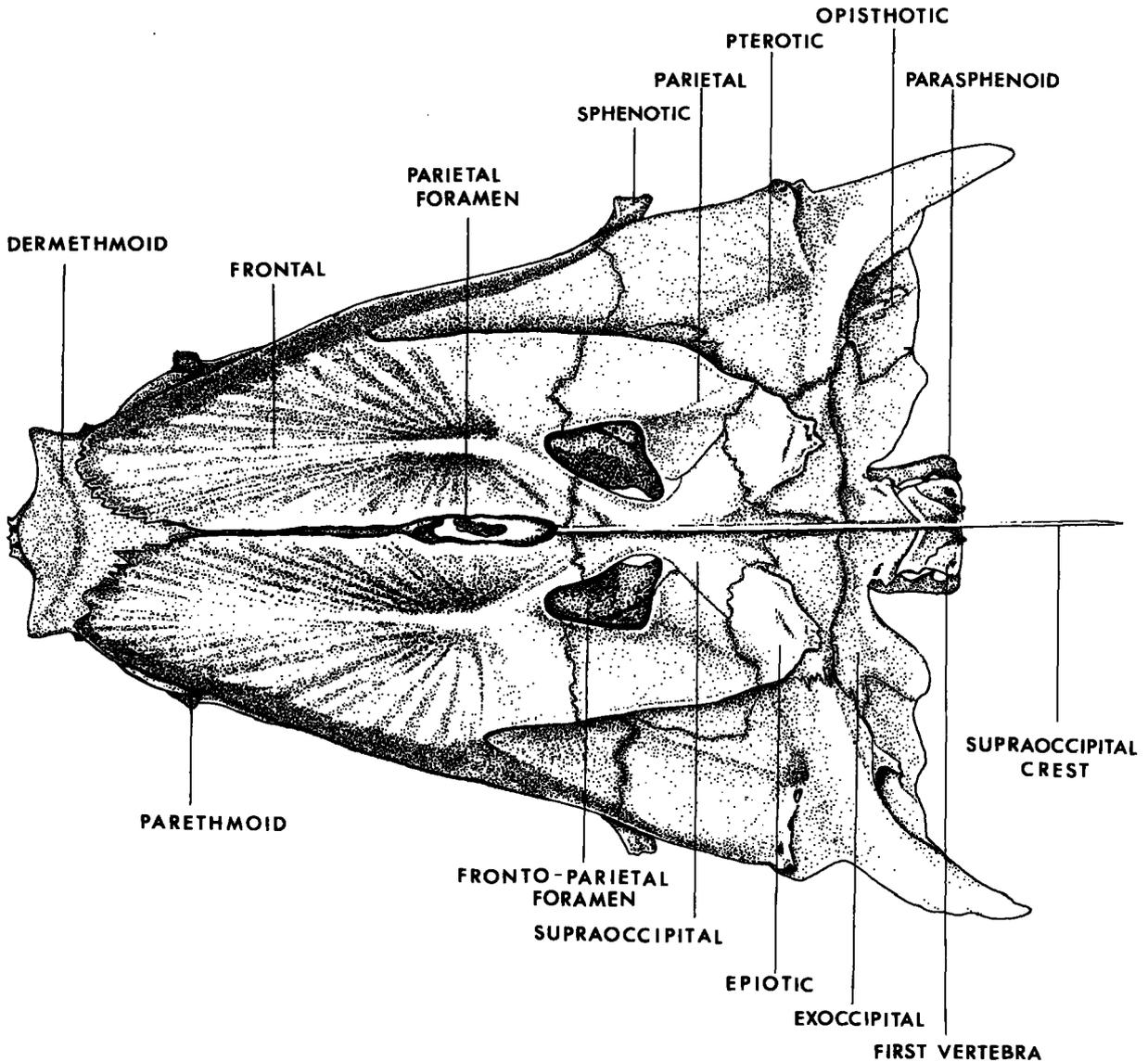
FIGURE 2.—Skull of *Thunnus alalunga*. Dorsal view. [The pineal foramen is incorrectly labeled as parietal foramen.]

bones. In life these foramina are covered by a tough membrane and are not passages for nerves or blood vessels. We were unable to determine their function. Fronto-parietal foramina are characteristic of *Thunnus*, *Euthynnus*, and *Katsuwonus*, and the bone is thin in this area in several other scombrids.

There is a prominent medial pineal foramen between the edges of the frontal bones, just anterior to the supraoccipital crest. Rivas (1954a) has suggested that in *T. thynnus* light can pass through the transparent "window" in the skin over this foramen and then down to the brain through the carti-laginous lens that fills the foramen in life. He postulated that the pineal apparatus has a phototropic function involved in migration. Holmgren (1958) also studied the pineal apparatus of *T. thynnus* but could find no evidence of a photoreceptive role for the pineal organ. The pineal foramen is characteristic of the more advanced members of the Scombridae and is absent or represented by only a small slit in the more primitive genera such as *Scomber*, *Rastrelliger*, and *Scomberomorus* (Allis, 1903; Kishinouye, 1923; Mago Leccia, 1958).

Specific Characters.—Four neurocranial characters

70

DERMETHMOID

PARETHMOID

FRONTAL

ALISPHENOID

SPHENOTIC

PROOTIC

OPISTHOTIC

BASIOCCIPITAL

VOMER

PARASPHENOID
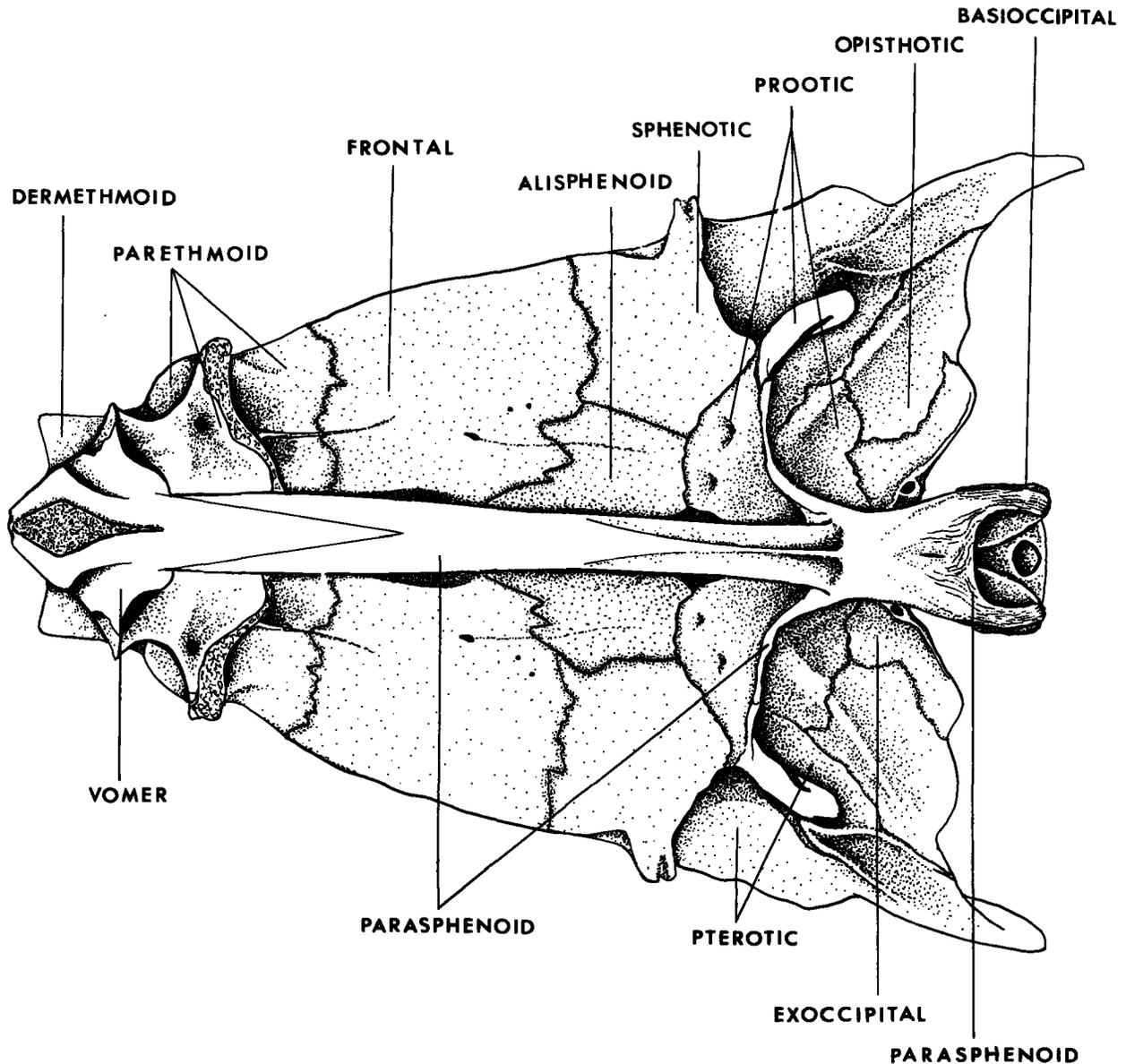
PTEROTIC

EXOCCIPITAL

PARASPHENOID

FIGURE 3.—Skull of *Thunnus alalunga:* Ventral view.

have been found useful in distinguishing the species of *Thunnus:* the alisphenoids, posterior parasphenoid margin, supraoccipital crest, and ventral paraesphenoid shaft. They are characteristic of specimens from all oceans.

Alisphenoids (fig. 4). The alisphenoids meet in the median line and extend ventrad into the orbit. They approach the parasphenoid more closely in *T. thynnus* and *T. maccoyii* than in the other tunas. The greatest height of the anterior part of the orbit, B, measured from dorsal parasphenoid to upper

median part of parethmoid, was divided by the least distance between alisphenoid and parasphenoid, A. In 46 skulls of *T. thynnus*, 16 have the alisphenoids fused to the parasphenoids; in the remaining 30, A goes into B 2–15 times; with a mean ($\bar{x}$) of 4.8, only in 6 specimens is the ratio less than 2.5. No fusion was observed in *T. maccoyii;* in 17 skulls the ratio was 2.0–10.3, $\bar{x}$ 4.8. By contrast, in all other species, A goes into B 1–3 times. Among 122 skulls of the other species, only 3 *T. albacares* and 2 large *T. tonggol* have a ratio of 2.5 or greater. Mean
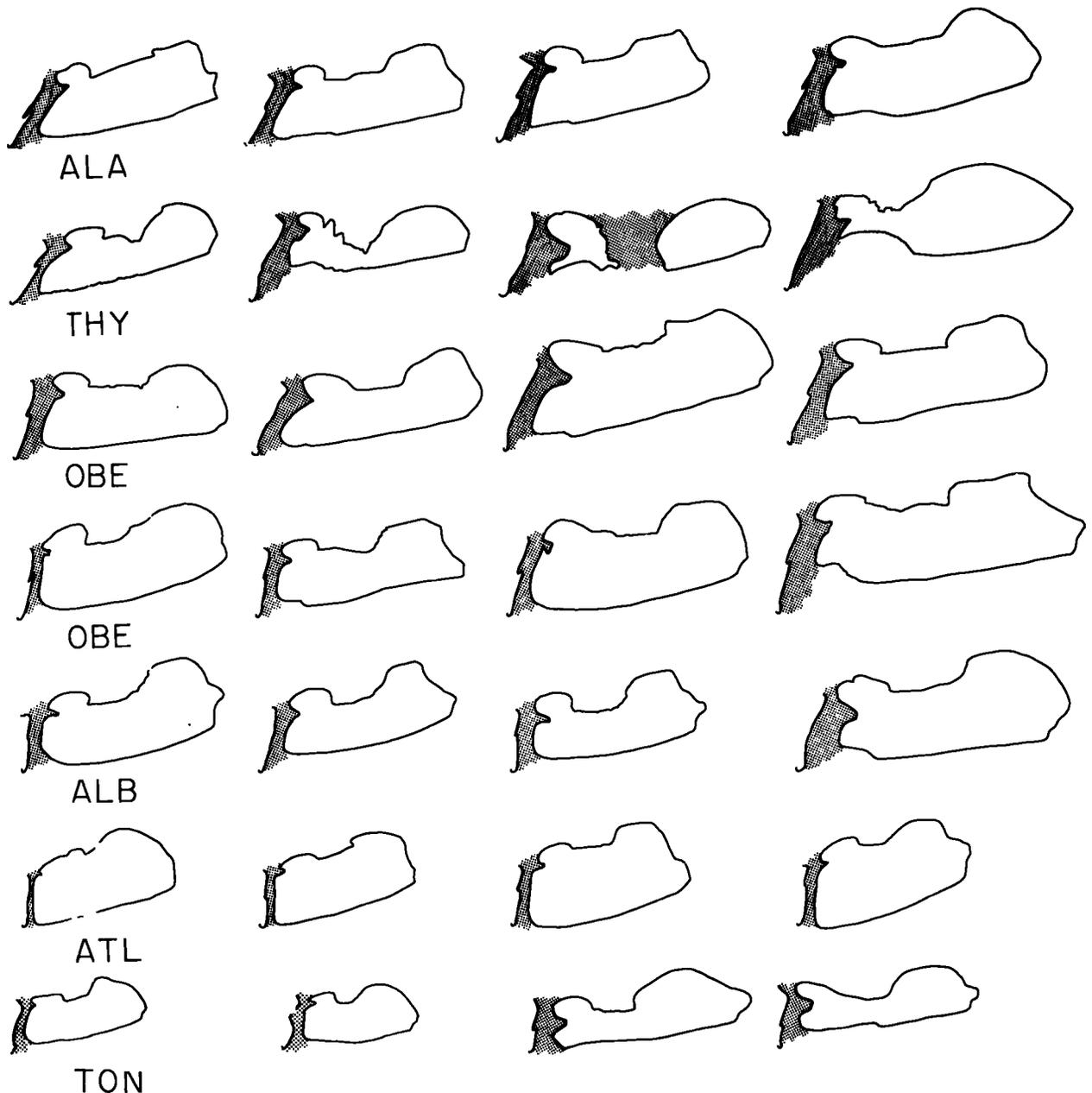
FIGURE 4.—Skulls of *Thunn.*   Right lateral view of orbital region of neurocranium showing conformation of basisphenoid (stippled) and aₙₚᵣ ₙₙd.   Arrangement within each species in order of increasing skull lengths from left to right: ALA—*T. alalunga*, 131, 138, 150, 167 mm.   ALB—*T. albacares*, 103, 116, 122, 179 mm.   ATL—*T. atlanticus*, 51, 80, 97, 102 mm.   OBE—*T. obesus:* upper-Atlantic, 170, 181, 185, 207 mm.; lower-Pacific, 97, 142, 147, ca. 240 mm. THY—*T. thynnus*, 76, 139, 231, ca. 320 mm.   TON—*T. tonggol*, 57, 61, 122, 128 mm.

values are: *T. tonggol* (*N*=8) 2.0; *T. albacares* (*N*=43) 1.8; *T. obesus* (*N*=32) 1.6; *T. alalunga* (*N*=27) 1.6; *T. atlanticus* (*N*=14) 1.2.

Posterior parasphenoid margin (fig. 5). The portion of the parasphenoid forming the walls of the parasphenoidal chamber is partially covered laterally by the basioccipital. Together the margins of these bones extend ventrad from the first vertebra, either vertically or slanting forward or backward; anteriorly the parasphenoid alone forms the margin. With due consideration for growth changes and individual variation, the profile formed at this part of the skull
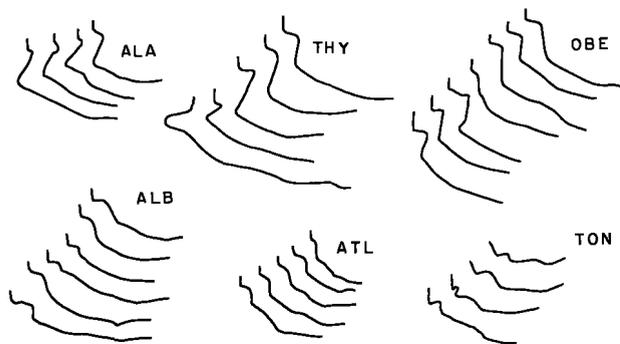
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FIGURE 5.—Skulls of *Thunnus* species. Right lateral view of posteroventral part of neurocranium showing conformation of posterior parasphenoid margin. Arrangement within each species in order of increasing skull length from right to left. ALA—131, 138, 150, 167 mm. ALB—103, 107, 116, 122, 169, 179 mm. ATL—51, 80, 88, 97, 102 mm. OBE—Pacific, 97, 141, 143, 146, 165, 189, 210 mm. THY—76, 139, 230, 335 mm. TON—57, 61, 122, 127 mm.

is quite characteristic of some species.

In *T. thynnus*, *T. maccoyii*, and *T. alalunga* a decided angle is formed by the posterior parasphenoid margins. The acuity of the angle and its posterior extent generally increase with size in *T. thynnus* (fig. 5), and extreme development of the angle is found in very large specimens. Within its observed size range (skull length 88–167 mm.), *T. alalunga*, however, displays a more acute angle than does *T. thynnus* of similar size. *T. maccoyii* resembles *T. thynnus* in this respect.

In relatively large specimens of *T. obesus* the angle is apparent but not as acute as in *T. thynnus*, *T. maccoyii*, and *T. alalunga*. Observations of Pacific specimens indicate probable changes with growth. The two smaller eastern Pacific specimens reported by Godsil and Byers (1944) and again by de Sylva (1955) have rounded margins, but other eastern Pacific specimens within the same size range show a definite angle.

T. albacares, *T. atlanticus*, and *T. tonggol* exhibit great variation. Some have unmistakably rounded margins; others are somewhat angulate but have a very short distance from the first vertebral centrum to the apex of the angle, so that the angle itself is never obvious.

Supraoccipital crest. In *T. alalunga* (fig. 1) the supraoccipital crest is relatively more slender than in any of the other species of *Thunnus* and is longer, nearly always reaching at least to the centrum of the third vertebra. In the other six species the crest rarely extends beyond the second vertebra.

Ventral parasphenoid shaft. In *T. atlanticus* the anterior portion of the parasphenoid shaft is concave ventrally (de Sylva, 1955). In *T. tonggol* we found it concave in three small specimens (skull length 57–99 mm.) and flat in two larger specimens (skull length 122–128 mm.). It is most commonly flat or slightly convex in the other species, but a degree of concavity has been observed in individuals, especially young, of all except *T. obesus*.

Other characters.—Godsil and Byers (1944) cited several additional neurocranial characters that are supposedly useful in distinguishing among the species. In our estimation, none of these is valid for the following reasons.

The parietal crest in *T. albacares* was described as extending farther forward than in *T. obesus* so that a projection of the curvature of the lateral edge of the parethmoid (prefrontal of Godsil and Byers) would be continuous with the parietal crest in *T. obesus* but would run below it in *T. albacares*. Our material shows both conditions in all species.

The angle of the long axis of the basisphenoid relative to the parasphenoid is highly variable and not reliable as a specific character. The width of the basisphenoid relative to its height is not only variable within any given size range but also changes with growth.

The anteriorly directed process at the upper end of the basisphenoid was used by de Sylva as a distinguishing character (1955: 32–35). He described the process in *T. albacares* and *T. "sibi"* (Pacific *T. obesus*) as being directed obliquely ventrad so that a line drawn through its axis would transect the parasphenoid at or behind the junction with the parethmoid; in *T. thynnus*, *T. alalunga*, and *T. atlanticus* such a line would more nearly parallel the parasphenoid and would not cross it. We find this character variable within a species. Furthermore, in larger fishes, the entire bone becomes relatively shorter and wider, whereas, the process becomes broader and more rounded.

The head of the vomer in *T. alalunga* was described as having a thin bony ridge behind the dentigerous anterior portion, a similar ridge being present in some *T. thynnus*, but not in *T. albacares* or *T. obesus*. Actually, all the species may have such a ridge. In *T. alalunga* teeth are generally restricted to the anterior end; the posterior end is very thin. The other species usually, but not always, bear teeth along the entire ridge, and the posterior portion is wider. In *T. atlanticus* the ridge is usually absent.

These tendencies exist, but frequent exceptions render the character uncertain.

A depression in the dorsal profile just anterior to the supraoccipital, reported to be present in all species but most pronounced in *T. thynnus*, is related to the pineal foramen. We find this variable in all species and distinctive in none.

In the contour of the posterior margin of the sphenotic as seen in ventral view, we can detect no difference among the species. A concave curvature of the margin, held by Godsil and Byers to be characteristic of *T. alalunga* and *T. thynnus*, is not only slight but may be present or absent in all species.

Branchiocranium

General description.—The branchiocranium includes the branchial bones, opercular apparatus, jaws, and associated bones. On each side the dentigerous premaxilla forms the upper jaw, and the maxilla is located dorsomesial to it. A small supramaxilla is attached to the posterior end of each maxilla. The lower jaw includes the dentary, which bears teeth; the articular, forming the rear end of the jaw and articulating with the condylar region of the quadrate; and a small angular at the posteroventral corner of the articular. The suspensorium begins with the hyomandibula, which articulates at its upper end with the otic region of the neurocranium and with the opercle. The ventral limb of the hyomandibula articulates with the metapterygoid, and the ventral portion of the latter in turn articulates with the symplectic and quadrate. To the anteroventral part of the metapterygoid are joined the basal portions of the endopterygoid and ectopterygoid. At their anterior ends, these are joined to the short, dentigerous palatine, which articulates with the condyle of the anterior end of the maxilla.

In addition to the hyomandibula, the hyoid arch is composed of two median and four paired bones. A glossohyal supports the tongue, and a urohyal lies below and between the two sides of the arch. The paired bones include small basihyals, large ceratohyals that articulate with smaller epihyals by jagged, toothlike sutures on the mesial side only, and small interhyals posteriorly joining the operculum.

In the branchial arches are three median basibranchials (a small cartilage posterior to the third may represent a fourth basibranchial, see Iwai and Nakamura, 1964a) and on each side three hypobranchials, five ceratobranchials, four epibranchials, and four pharyngobranchials. The posteriormost

ceratobranchials and mesial three pairs of pharyngobranchials bear villiform teeth. The anterior surfaces of the first four arches bear gill rakers, and, as supports for the gill filaments, so-called gill bars are found on the posterior surfaces (Iwai and Nakamura, 1964a).

Specific Characters.—Differences worthy of note have been described for only six bones by Kishinouye (1923) or Godsil and Byers (1944). These are the hyomandibula, metapterygoid, quadrate, subopercle, interopercle, and ceratohyal. We concur in their observations on the first four only.

The anterior (sphenotic) articulating head of the hyomandibula (fig. 6) is relatively longer and nar-
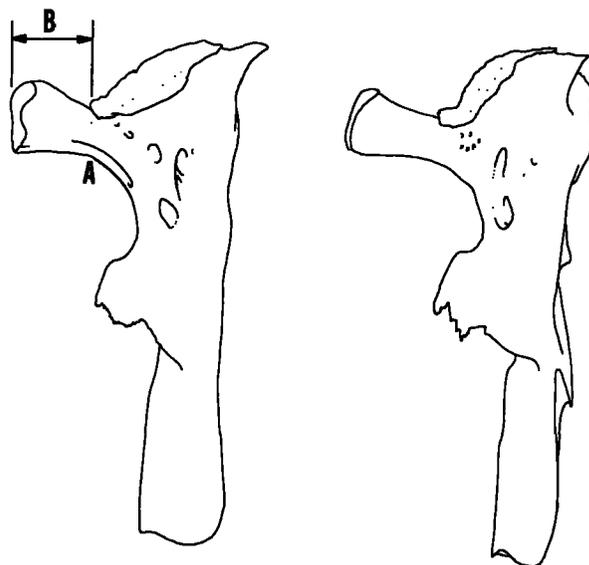

FIGURE 6.—Hyomandibula of (left) *Thunnus thynnus*, skull length 139 mm., (right) *T. alalunga*, skull length 150 mm. Measurements of anterior articular head include A—least width, B—length.

rower in *T. alalunga* than in the other species. The proportion of length to least width in our specimens ranged as follows: *T. alalunga* (N=35) 1.7–2.7, $\bar{x}=2.2$; *T. thynnus* (N=44) 1.3–2.1, $\bar{x}=1.7$; *T. maccoyii* (N=17) 1.6–2.3, $\bar{x}=1.9$; *T. obesus* (N=36) 1.3–1.9, $\bar{x}=1.5$; *T. atlanticus* (N=18) 1.3–2.2, $\bar{x}=1.7$; *T. albacares* (N=58) 1.2–1.9, $\bar{x}=1.6$; *T. tonggol* (N=4) 1.4–1.8, $\bar{x}=1.6$. These proportions are close to those given by Godsil and Byers (1944: 86), who reported 1.7–3.0 for Pacific *T. alalunga* and 1.2–1.5 for Pacific *T. albacares*, and stated that Pacific *T. thynnus* and *T. obesus* are similar to *T. albacares*.

74

Kishinouye (1923: 322) stated that the anterior head is "more or less roundish in cross-section in *Thunnus;* but more or less flattened in *Parathunnus* and *Neothunnus*. . . ." We can find no significant difference among any of the species in this character. Furthermore, we cannot confirm de Sylva's contention (1955:14) that the process is oblique to the vertical limb in *T. atlanticus* but forms a right angle in the other species.

In *T. alalunga* the metapterygoid (fig. 7) is narrower than in other species. This condition can be indicated by the proportion of the length of the anteroventral margin to the posteroventral margin
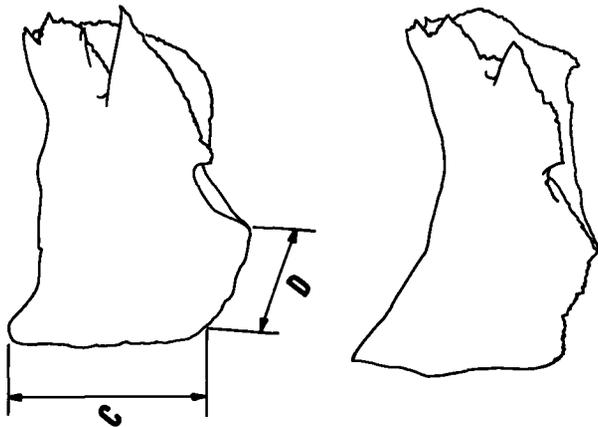

FIGURE 7.—Metapterygoid of (left) *Thunnus thynnus*, (right) *T. alalunga*, same specimens as in fig. 6, showing measurements of C—anteroventral margin, D—posteroventral margin.

(measured in each case to the midpoint of the arc of the posteroventral edge.) In our material, this proportion is as follows: *T. alalunga* ($N=32$) 1.1–1.8, $\bar{x}=1.4$; *T. thynnus* ($N=43$) 1.6–2.6, $\bar{x}=2.0$; *T. maccoyii* ($N=17$) 1.4–2.7, $\bar{x}=1.9$; *T. obesus* ($N=37$) 1.5–3.1, $\bar{x}=2.0$; *T. atlanticus* ($N=19$) 1.4–2.1, $\bar{x}=1.7$; *T. albacares* ($N=58$) 1.5–3.1, $\bar{x}=2.1$; *T. tonggol* ($N=4$) 1.8–2.2, $\bar{x}=2.0$. These proportions are similar to those given by Godsil and Byers (1944: 86) for Pacific tunas, but provide even better distinction. Godsil and Byers measured each margin to the "most ventral point," which seemed more nebulous to us than the midpoint of the arc. Their figures of 1.0–1.5 for *T. alalunga* and 1.3–1.9 for *T. albacares* and the other species include slightly lower proportions than were found in our specimens, but the conclusions are nevertheless similar.
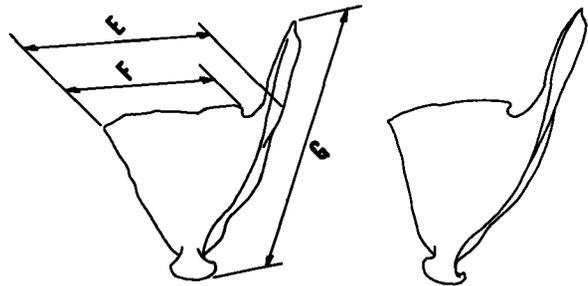

FIGURE 8.—Quadrate of (left) *Thunnus thynnus*, (right) *T. alalunga*, same specimens as in fig. 6, showing measurements of E—total width, F—width of horizontal edge, G—length.

Again, in *T. alalunga* the quadrate (fig. 8) is slightly narrower than in the other species. The proportion of length to total width in our specimens is as follows: *T. alalunga* ($N=35$) 1.5–2.1, $\bar{x}=1.8$; *T. thynnus* ($N=44$) 1.2–1.6, $\bar{x}=1.4$; *T. maccoyii* ($N=16$) 1.3–1.5, $\bar{x}=1.4$; *T. obesus* ($N=37$) 1.4–1.7, $\bar{x}=1.5$; *T. atlanticus* ($N=20$) 1.3–1.8, $\bar{x}=1.6$; *T. albacares* ($N=57$) 1.4–1.8, $\bar{x}=1.5$; *T. tonggol* ($N=4$) 1.4–1.6, $\bar{x}=1.5$. The proportions of the same length to width of the horizontal dorsal edge are: *T. alalunga* ($N=35$) 2.1–2.7, $\bar{x}=2.5$; *T. thynnus* ($N=44$) 1.6–2.1, $\bar{x}=1.9$; *T. maccoyii* ($N=16$) 1.6–2.0, $\bar{x}=1.9$; *T. obesus* ($N=37$) 1.8–2.2, $\bar{x}=2.0$; *T. atlanticus* ($N=20$) 2.0–2.3, $\bar{x}=2.1$; *T. albacares* ($N=57$) 1.8–2.2, $\bar{x}=2.0$; *T. tonggol* ($N=4$) 1.8–2.2, $\bar{x}=2.0$. We are not certain where Godsil and Byers (1944: 87) measured the width, but they gave proportions of 1.8–2.3 for Pacific *T. alalunga* and 1.6–1.8 for other species. Thus there is agreement in order of magnitude, but their proportions are generally higher than our first and lower than our second.

The subopercle of *T. thynnus* and *T. maccoyii* (fig. 9) differs, with few exceptions, from that of the other species in being relatively narrow and in having the anterodorsal margin almost vertical in its lower two-fifths to one-half, followed by a decided change in slope of the upper portion. In the other species there may be a very short perpendicular portion, less than one-fifth of the length, before the oblique slope begins, or, most often, there is an almost straight or very slightly convex oblique edge. This finding conforms with the observations of Godsil and Byers (1944: 101) for the Pacific forms and presumably also with the observations of Kishinouye (1923: 325), although his statement is less clear.
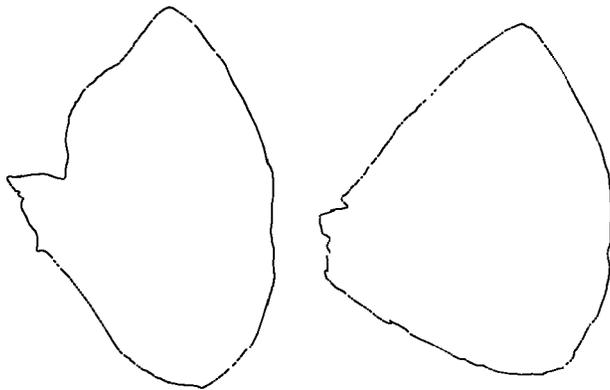
FIGURE 9.—Subopercle of (left) *Thunnus thynnus*, (right) *T. alalunga*. Same specimens as in fig. 6.

We are unable to confirm two other characters mentioned by Kishinouye (1923: 325, 327). In Japanese *T. thynnus* the posterior margin of the interopercle was described as being convex, whereas in other Japanese tunas it is nearly straight. In our material the shape of the margin is variable; most of the species have both types and variants thereof. Kishinouye also described a groove for blood vessels along the dorsolateral edge of the ceratohyal. The groove was present in *T. thynnus*, *T. alalunga*, and *T. obesus* but hardly visible in *T. albacares*. This groove is present in all species and is generally more apparent in larger specimens. In small specimens of most species the groove is indistinct or absent.

Pectoral and Pelvic Girdles

The pectoral girdle is composed of a series of bones connecting the skull and the pectoral fin. The two-armed supratemporal, not really a functional part of the pectoral girdle, is closely applied to the skin beside the otic region of the neurocranium. A larger, also two-armed, posttemporal articulates with the skull, followed by a supracleithrum and the large, curved, bladelike cleithrum. Baudelot's ligament runs from the supracleithrum to the basioccipital. From the posterior margin of the supracleithrum extend two flattened postcleithra, the second of which has an attenuated posteriorly directed process. The long curved blade of the cleithrum forms a thin-walled trough that opens posteriorly. The thickened, somewhat rectangular scapula is borne dorsally, on the mesial side. Below the scapula, the bladelike coracoid is attached. The lower, posterior end of the scapula and the uppermost posterior edge of the coracoid are thickened and flattened; they form articular surfaces for four pterygials, on which the fin rays are borne.

The pelvic girdle includes a pair of winglike basi-pterygia that join posteriorly in the median line. Anteriorly each bone has a flattened lateral wing and a long narrow mesial process. Posteriorly a long mesial process extends between the fin rays. There are no pterygials.

No differentiating characters are apparent in either the pectoral or the pelvic girdle.

Vertebral Column

General description.—Important papers describing the vertebral column in species of *Thunnus* include: Starks (1910), Kishinouye (1923), Frade (1932), Godsil and Byers (1944), Godsil and Holmberg (1950), Clothier (1950), de Sylva (1955), and Nakamura (1965).

The vertebral column usually has 39 vertebrae, including the hypural plate. The first vertebra is articulated firmly with the rear of the skull. Neural arches and spines are present on all except the hypural plate. The spines are erect and laterally flattened on the first six vertebrae. On the seven vertebrae anterior to the hypural plate, both the neural and haemal spines are wide and depressed and lie on top of the next posterior centrum, forming a strong and rigid tail section. Laterally directed transverse processes (parapophyses) appear as small projections on the third vertebra, become longest and broadest on about the sixth, shorter and more canted on the next two or so, and usually become both longer and ventrally directed on the eighth or ninth. By the 10th or 11th vertebra, the first closed haemal arch is formed by the meeting of the distal ends of the parapophyses. The ventral ends of the haemal arches become progressively longer, forming haemal spines. Ribs are attached, beginning with the 3d vertebra, to each parapophysis or to the end of each haemal arch or spine until the 18th or 19th vertebra. Posteriorly, haemal spines are present, but ribs are absent. Dorsal to the ribs, intermuscular bones (epipleurals) articulate either on the neural arch or the centrum of each of the vertebrae from the 1st to the 31st.

Beginning at the 12th to 18th vertebra, each haemal arch bears on each side a process directed obliquely ventrad which has been called a haemal prezygapophysis (de Sylva, 1955). On succeeding vertebrae this process is longer, then shorter and

76

more dorsally situated; by the 20th to 25th vertebra it comes to arise from the anterior end of the centrum rather than from the haemal arch.

Beginning at about the fourth vertebra, a process which has been called a haemal postzygapophysis (de Sylva, 1955) arises on each side from the posterior end of each centrum. On the anterior centra it is small and laterally directed. This process becomes ventrally directed on the eighth vertebra, and its distal end meets the parapophysis; farther posteriorly it meets the upper part of the haemal arch or the haemal prezygapophysis when it is formed. On approximately the last eight vertebrae the haemal spines are situated so posteriorly that they obliterate the haemal postzygapophyses.

From some or all of the 20th to the 33d vertebrae, the blood vessels and nerves that emerge from the haemal canal exit through ventrolateral foramina. The anterior foramina are formed by struts running from the haemal arch to the centrum near the base of the haemal postzygapophyses. They become smaller posteriorly and are separate from and anterior to the haemal arches; the latter in this region gradually become located toward the posterior end of the centra. On the 32d to 36th vertebrae, flattened lateral processes form a horizontal bony keel. The sizes of the individual vertebrae vary considerably, and regional differences are emphasized in older specimens. The length increases regularly to the 35th vertebra; the 36th is slightly shorter, the 37th and 38th are very short, and the 39th is incorporated into the wide, triangular hypural plate. The depth of the vertebra increases regularly to about the 25th, beyond which there is a gradual decrease to the hypural plate. A simple splintlike bone (epural) is closely applied to the anterodorsal surface of the hypural plate. A similar bone (hypural) bearing a spinous process on each side is present along the anteroventral surface of the hypural plate. The terminology and derivation of these two bones are in doubt.

Specific Characters.—The vertebrae typically total 39 in all species. Godsil and Byers (1944) reported, and we have reexamined, a California *T. thynnus* with only 38, in which 1 vertebra near the hypural is obviously missing. Among more than 200 skeletons of the seven species, we found only three additional abnormalities, all due to recognizable fusion of two adjacent centra. Frade (1932) reported, among 110 *T. thynnus*, 8 with 38 vertebrae, 6 with 40, and 1 with 41. We doubt the counts of

40 and 41 but cannot explain them. All but one species have 18 precaudals and 21 caudals, the first long haemal spine occurring on the 19th vertebra. The same count was given by de Sylva (1955) for *T. atlanticus*, but, as Watson (1964) has shown, this species differs from all other *Thunnus* in having 19 precaudals and 20 caudals. Exceptions may be expected in all species; we have examined *T. atlanticus* with counts of 18+21 and 20+19, *T. obesus* and *T. albacares* with 17+22, and *T. thynnus* and *T. obesus* with 19+20; and Godsil and Byers (1944: 86) reported one *T. alalunga* with 20+19.

The position of the first (anteriormost) ventrally directed parapophyses appears to show almost no variability within a species or subspecies; only one exception has been noted. These parapophyses occur on the 8th vertebra in *T. thynnus*, on the 10th in *T. tonggol*, and on the 9th in the other species. In *T. alalunga* none of the parapophyses is directed quite so obviously ventrad as in the other species; those on the ninth vertebra that we regarded as ventrally directed are much shorter than in any other species and seem almost twisted, never becoming completely ventrally oriented. In other species, there is variation in the ventral extent of the preceding parapophyses. As long as these were more or less flattened and rounded, their relative location was not considered. The first ventrally directed ones are definitely elongated in a ventral direction (compare the eighth vertebra in *T. thynnus* and *T. maccoyii*, fig. 10).

The first (closed) haemal arch usually occurs on the 11th vertebra in *T. albacares*. *T. atlanticus*, *T. tonggol*, and *T. obesus*, and usually on the 10th vertebra in *T. alalunga*, *T. maccoyii*, and *T. thynnus*. In all species except *T. alalunga* and *T. maccoyii* we observed the first closed arch occasionally either one vertebra anterior or one vertebra posterior to the usual position. Godsil and Byers (1944: 68, 101) observed notable variation in Pacific *T. albacares* and in *T. thynnus*. In most of the species the parapophyses on the vertebra preceding the one that bears the first haemal arch approach each other so closely in the median line that it appears to be a matter of chance whether or not they or the next pair fuse. In many specimens in which the haemal arch was formed anterior to its usual position, its shape was noticeably different (fig. 10, OBE).

In *T. alalunga* the first haemal arch is directed forward, with an angle of about 45° or less between it and the vertebral axis. In all of the other species
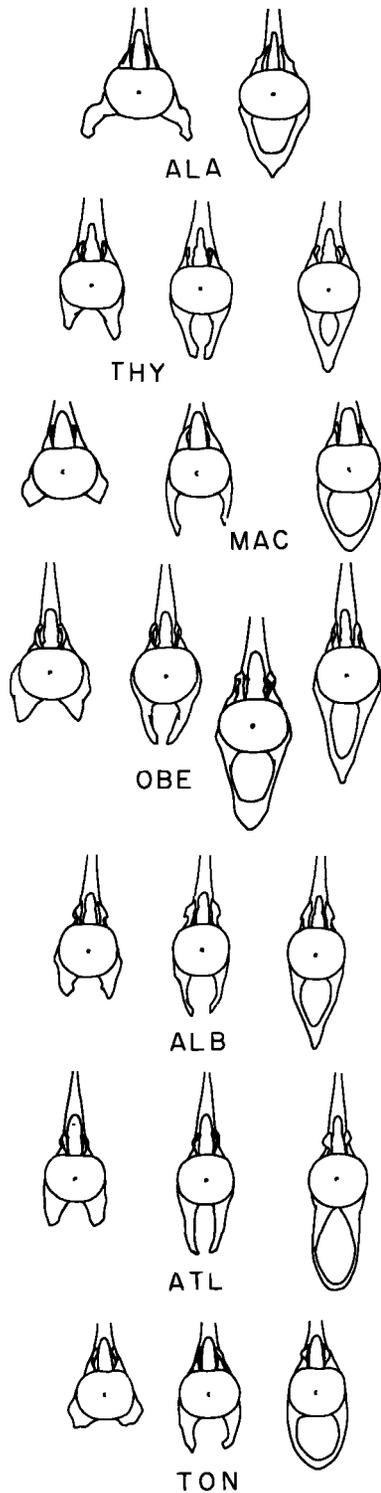
FIGURE 10.—Anterior view, first closed haemal arch and preceding vertebrae of *Thunnus* species. ALA—vertebrae 9–10, ALB—9–11, ATL—9–11, MAC—8–10, OBE—9–11 (the one slightly below the main row shows shape of first closed haemal arch when located on 10th vertebrae), THY—8–10, TON—9–11.

FIGURE 11.—Left lateral view of vertebrae of *Thunnus* species showing first ventrally directed parapophyses (left vertebra) and first closed haemal arch (right vertebra). ALA—vertebrae 9–10, ALB—9–11, ATL—9–11, OBE—9–11, THY—8–10, TON—10–12.

78

FIGURE 12.—Left lateral view of vertebrae of *Thunnus* species,
showing development of anteriormost haemal pre- and post-
zygapophyses.   ALA—vertebrae 13–16, ALB— 14–16,
ATL—14–18, OBE—14–17, THY—14–16, and TON—14–17.

it may range from almost perpendicular to a 60°
angle (fig. 11).   The shape of the first haemal arch
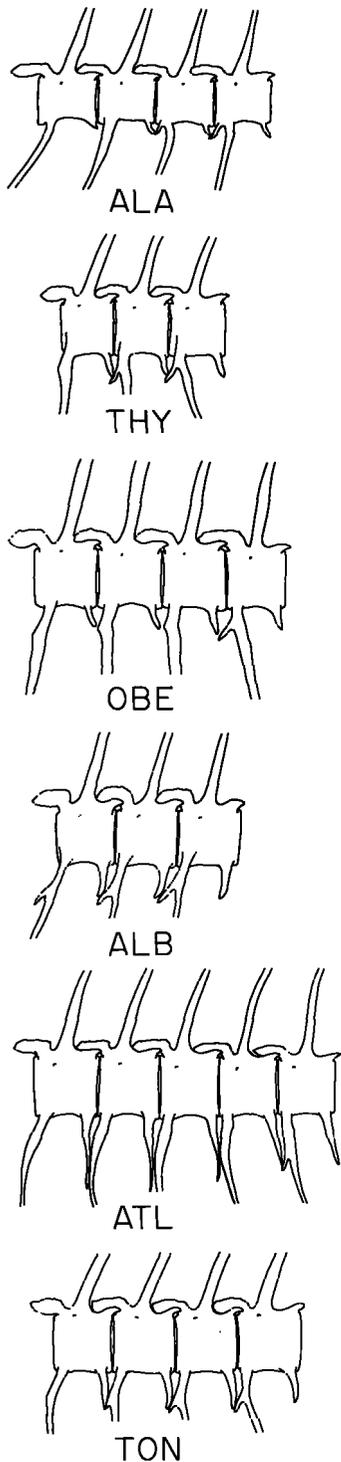and the dimensions of its bony parts vary consider-
ably, but in *T. atlanticus, T. tonggol*, and *T. maccoyii*
the bony portions are thinner and the sides more
bowed than in the other species (fig. 10).

As shown by Yabe et al. (1958), by Matsumoto
(1963), and by Yoshida (1965), the heamal spine of
the first caudal vertebra is always laterally flattened
and winglike in *T. alalunga* but in the other species
resembles the other haemal spines and is not flattened.

The length of the haemal prezygapophyses and
the distance of their origin from the centrum vary
among the species of *Thunnus*.   In *T. alalunga* the
haemal prezygapophyses all originate at the centrum
or extremely close to it.   Correlated with this, the
anterior haemal postzygapophyses are relatively
short (fig. 12).   In the other species the anterior
haemal prezygapophyses arise from the sides of the
haemal arches of 3 to 12 vertebrae before they begin
to arise from the centra, and the posterior haemal
postzygapophyses are relatively longer.   In *T. ala-
lunga, T. obesus, T. maccoyii*, and *T. thynnus* the
haemal prezygapophyses arise high on the neural
arch, so that only the first two or three at most can
be regarded as clearly on the arch.   Correspondingly,
the associated haemal postzygapophyses hardly dif-
fer in length from those on the posterior vertebrae.
By contrast, in *T. atlanticus, T. albacares*, and *T.
tonggol* the haemal prezygapophyses arise far more
ventrad on the haemal arch, from one-fourth to
one-half the distance to the ventral tip, and there is
no question that at least five (usually more) are
definitely on the arch, not on the centrum.   The
associated haemal postzygapophyses in these species
are longer than in the other three, although less so
in *T. albacares* than in *T. atlanticus* and *T. tonggol*.
In *T. atlanticus* and *T. tonggol* the longest haemal
postzygapophyses are equal to or longer than the
length of the centra; in *T. albacares* they may be
about three-fourths the centrum length.

The species differ in the development of the ventro-
lateral foramina that are found on some or all of the
20th to the 33d vertebrae (fig. 13).   These foramina
are best developed anteriorly and in this region
appear to arise through the formation of a bony strut
from the haemal postzygapophyses to the dorsal
part of the haemal arch.   They diminish in size
posteriorly and are absent on the last several ver-
tebrae.   In *T. atlanticus, T. albacares*, and *T. tonggol*
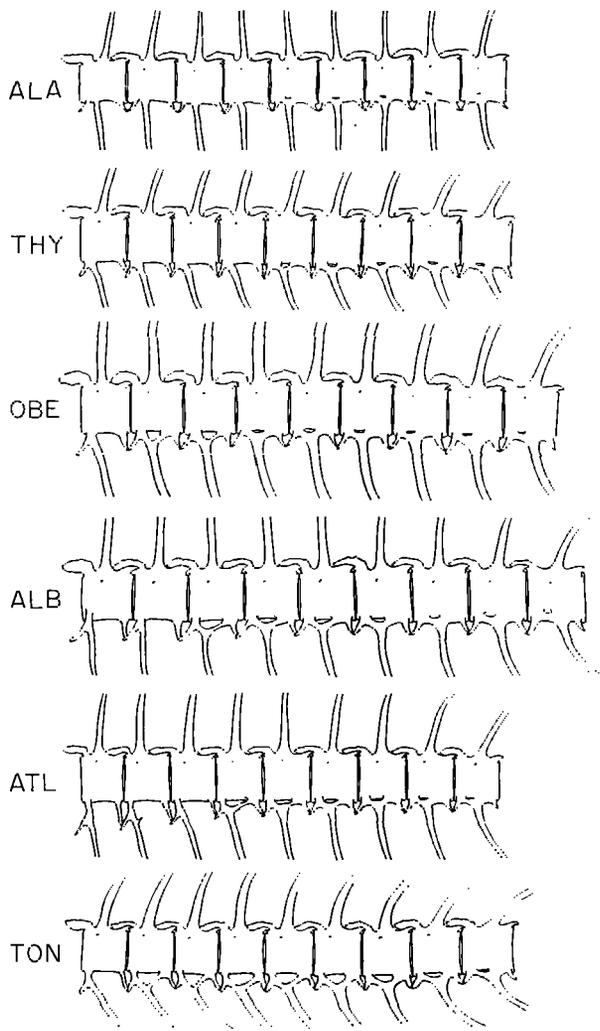the anterior openings are large, longer than wide,

FIGURE 13.—Left lateral view of vertebrae 20-28 of *Thunnus* species, showing development of inferior foramina.

the largest usually three times or more as long as the horizontal width of the base of the corresponding haemal spine. In *T. obesus*, *T. maccoyii*, *T. thynnus*, and *T. alalunga* the size of the openings is variable, usually small, and the largest opening is rarely more than about 1.5 times as long as the width of the adjoining bony neural arch.

T. atlanticus, *T. albacares*, and *T. tonggol* are distinguishable by the development of vertebral processes and openings, which approach the ornate trelliswork seen in *Auxis*, *Euthynnus*, and *Katsuwonus; T. alalunga* shows the least development, and *T. obesus*, *T. maccoyii*, and *T. thynnus* are intermediate.

The first haemal prezygapophysis tends to be found more anteriorly in *T. albacares* and *T. tonggol*, most commonly on vertebra 13 or 14 (range 12-15) in *T. albacares*. In *T. maccoyii* it usually occurs on 14 or 15 (range 14-16), in *T. alalunga* and *T. obesus* on 15 or 16 (range 14-17), and in *T. atlanticus* on 16 or 17 (range 15-18). *T. thynnus* displays a wider range of variation (12-17), and overlap is considerable between it and the other species.

While this paper was in press, Nakamura and Kikawa (1966) described specific differences in the infra-central grooves on the ventral side of the centra of vertebrae 10-30. These infra-central grooves were categorized into three types: type A with two separate infra-central grooves; type B with two grooves connected by a canal; type C with a single, usually elongate, groove. We have reexamined our skeletal material, which comprises many more specimens than the total of 19 used by Nakamura and Kikawa, and we conclude that the infra-central grooves are a useful character, but show variation that often precludes positive species identification. Our conclusions are as follows:

Thunnus albacares (24 specimens, fork length 280-1,430 mm.) has type C infra-central grooves that tend to be divided by a thin septum anteriorly but that posteriorly are undivided or occupied by a honeycomb-like network of bony material. In this character, *T. albacares* is distinctive, but is approached by some specimens of *T. maccoyii*.

Thunnus maccoyii (16 specimens, 742-1,445 mm.) is the most variable of all the species. Very few have type C (undivided) grooves, as described by Nakamura and Kikawa. Typically, all the vertebrae have two grooves (type A) that are divided by very thin septa or a honeycomb of septa. This condition resembles that of the anterior grooves of *T. albacares*. Only an occasional undivided groove occurs among the divided ones in *T. maccoyii*, whereas most of the grooves are undivided in *T. albacares*. Some specimens, particularly the six from Australia that were used by Godsil and Holmberg (1950), were almost impossible to distinguish from *T. thynnus*.

Thunnus thynnus thynnus (7 specimens, 316-2,315 mm.) and *T. t. orientalis* (18, 530-1,450 mm.) have type A grooves, two grooves per centrum, that tend to be round or oval anteriorly and become longer and narrower posteriorly. The distance between the two grooves on the anterior centra is highly variable. When the grooves are narrowly separated, the specimens resemble some *T. maccoyii*.

Thunnus obesus (7 Atlantic specimens, 697-1,360 mm.; 3 Indian Ocean, 630-1,270 mm.; 1 eastern Pacific, 1,600 mm.) have type A grooves and could not be distinguished from *T. thynnus*.

Thunnus alalunga (20 specimens, 520-1250 mm.), like *T. thynnus* and *T. obesus*, have type A grooves, but, although the grooves vary greatly in width, they tend to be much narrower than in the latter two species. Usually the grooves are widely separated, but in a few specimens, the partitions are narrow.

Thunnus tonggol (4 specimens, 373-924 mm.) have type B grooves, two grooves per centrum, quite variable in size, with a shallow canal connecting them. The grooves tend to be larger than those of *T. atlanticus* and smaller than those of *T. thynnus* or *T. obesus*. In the two larger specimens, the anterior grooves strongly resemble those of *T. thynnus* or *T. obesus* in being larger and close together.

Thunnus atlanticus (20 specimens, 322-665 mm.) have type B grooves, with two very small pits on each centrum connected by a very narrow canal. The canal is not evident in some specimens, giving the impression that the two grooves are separated by a sharp ridge. In this respect *T. atlanticus* is distinctive. The largest specimens, however, closely resemble small *T. tonggol*, with small grooves connected by an obvious canal, the grooves becoming elongate posteriorly.

The proportion of length to depth of the 36th vertebra is relatively greatest in *T. albacares* ($N = 60$) 1.2-1.9, $\bar{x} = 1.4$ and in *T. alalunga* ($N = 40$) 1.1-1.7, $\bar{x} = 1.5$. In *T. alalunga* the vertebrae are often considerably smaller anteriorly than posteriorly (fig. 14), accounting for the high ratio. In the other species, this proportion is: *T. thynnus* (N = 58) 0.8-1.3, $\bar{x} = 1.1$; *T. maccoyii* ($N = 16$) 0.8-1.3, $\bar{x} = 1.0$; *T. obesus* ($N = 30$) 0.9-1.4, $\bar{x} = 1.2$; *T. atlanticus* ($N = 23$) 1.0-1.4, $\bar{x} = 1.3$; *T. tonggol* ($N = 8$) 1.1-1.5, $\bar{x} = 1.3$.

VISCERA

The relative position, shape, and size of the various internal organs provide excellent diagnostic characters (fig. 15). These organs are treated here by systems. Important works on the viscera of *Thunnus* include those of Eschricht and Müller (1837), Kishinouye (1923), Frade (1925), Serventy (1942), Godsil and Byers (1944), and Godsil and Holmberg (1950).
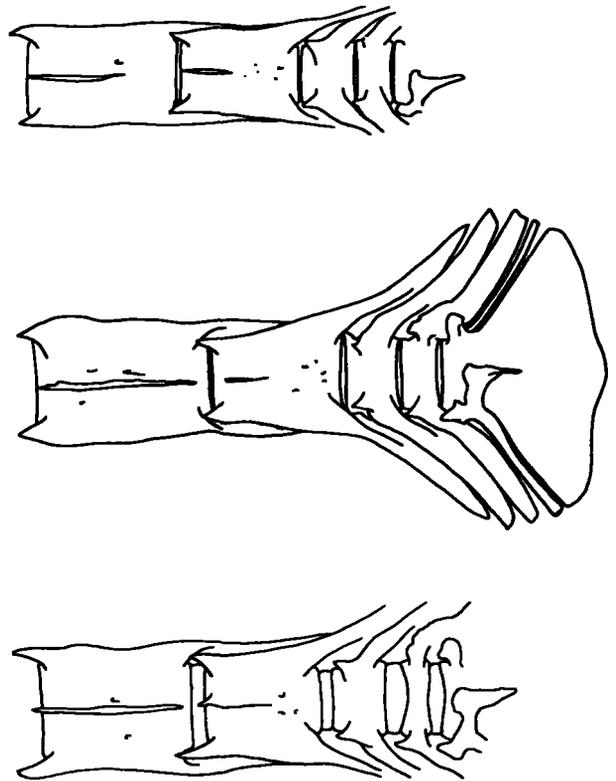

FIGURE 14.—Left lateral view of vertebrae 35–39, showing differences in proportions of vertebra 36. (top) *Thunnus albacares*, (middle) *T. alalunga*, (bottom) *T. obesus*, typical of other species not illustrated.

Digestive System and Associated Organs

General Description.—At the anterior end of the body cavity the liver abuts against the transverse septum and caps the other organs. It is usually composed of three lobes, only the middle of which is plainly visible in ventral view; the other two lobes lie along the lateral body wall, hidden by the other organs. The ventral surface of the liver of some species appears striated owing to the parallel arrangement of blood vessels (both arterial and venous) near its surface. The species with striated livers also possess, on the dorsal surface of the liver, several large "vascular cones," each comprising numerous vessels bound in a common sheath. These are absent in species with unstriated livers. In all species (Morice, 1953, to the contrary) there are two efferent (venous) vessels leading directly from the anterior surface of the liver into the sinus venosus. The esophagus merges indistinguishably (in external view) into the stomach, which forms a blind sac posteriorly. The intestine rises from the anterior

Legend:

- URINARY BLADDER
- SWIMBLADDER
- GONAD
- LIVER
- CAECAL MASS
- SPLEEN
- STOMACH
- INTESTINE
- GALL BLADDER
- BODY WALL

ALA

THY
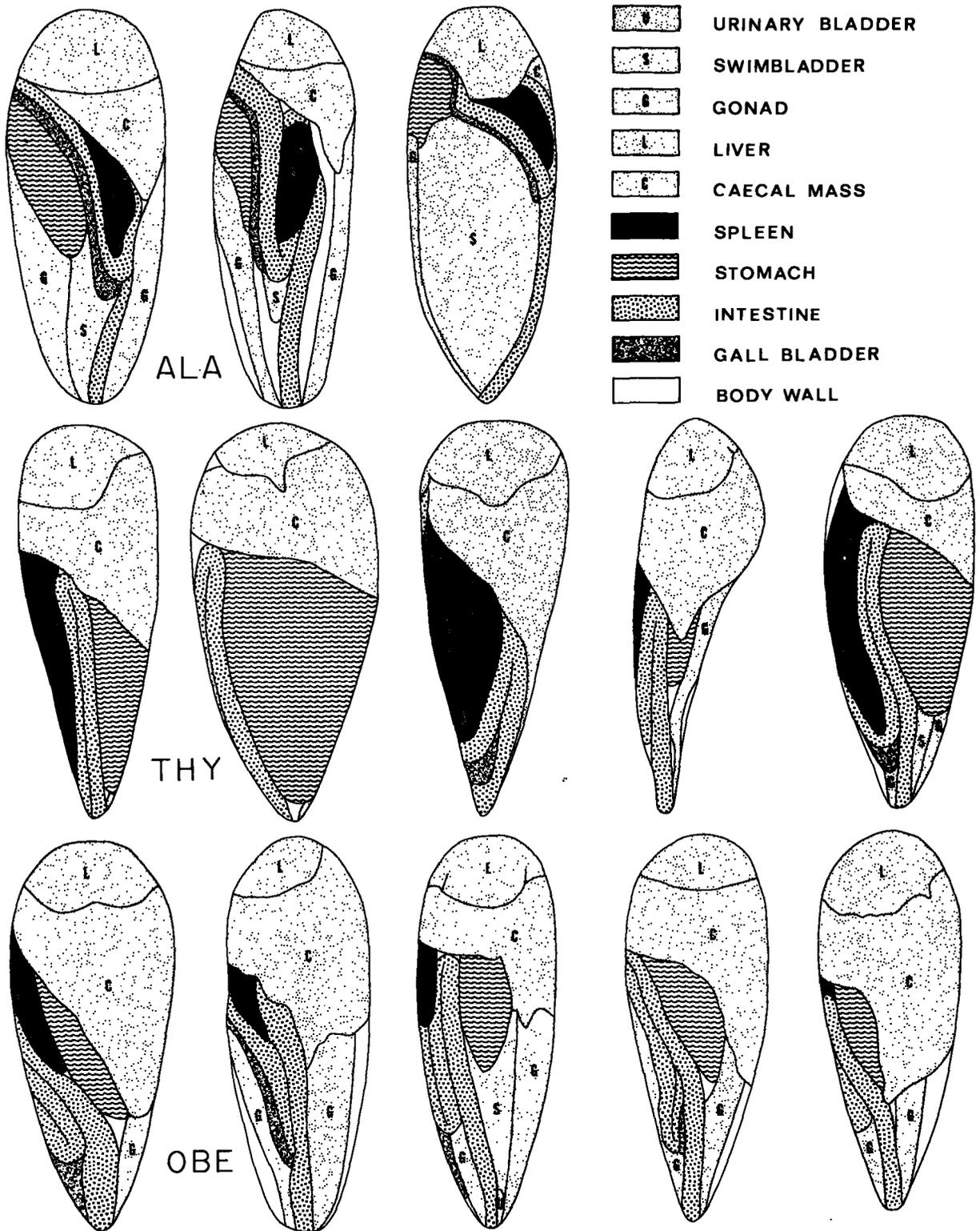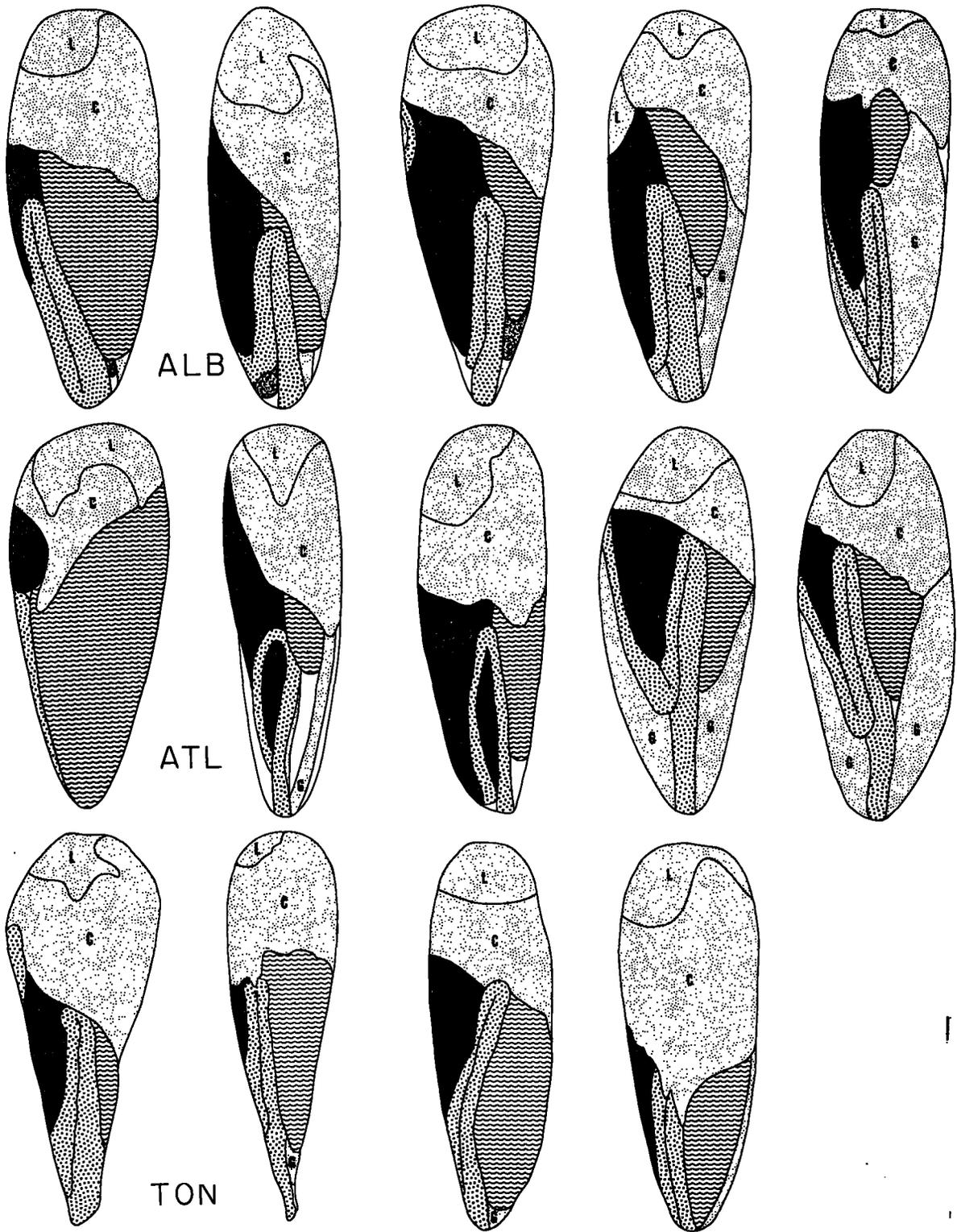
OBE

FIGURE 15.—Ventral view of in situ visceral patterns of *Thunnus* species. Arranged from left to right in order of increasing fork length. ALA—780, 875, 1,030 mm.; ALB—637, 700, 808, 1,340,

ALB

ATL

TON

1,420 mm.; ATL—337, 438, 513, 563, 650 mm.; OBE—1,250, 1,310, 13,50 1,450, 1,540 mm.; THY—457, 750, 872, 1,050, 1,670 mm.; TON—373, 392, 910, 924 mm.

ANATOMY AND SYSTEMATICS OF TUNAS

end of the stomach, and a very large caecal mass is attached to its origin by several ducts that are not externally apparent. The intestine proceeds caudad for half or more the length of the body cavity (straight intestine), forms a loop, runs craniad (ascending portion) almost to the pylorus, then forms another loop and continues in a nearly straight line (descending portion) to the anus. The spleen is located between the straight and ascending portions. The gall bladder is a long, tubular sac rising from the right lobe of the liver, attached to the dorsal wall or the left side of the straight intestine. A swimbladder, when present, is situated dorsad to the main visceral mass, and may be rudimentary or well developed.

Specific Characters.—The ventral surface of the liver (fig. 16) is striated in *T. alalunga, T. maccoyii, T. thynnus,* and *T. obesus.* These striations give the impression of being denser and extending farther toward the center of the middle lobe in *T. alalunga, T. maccoyii,* and *T. thynnus* than in *T. obesus,* but this difference is not easy to detect. We have seen only one instance of striations being limited to the peripheral margins, at least of the middle lobe, as described by Kishinouye (1923) and Godsil and Byers (1944) for Pacific, and by Morice (1953) for Atlantic *T. obesus.* The peripheral nature of these striations has been used as a major diagnostic character of the nominal genus *Parathunnus.* In *T. albacares, T. atlanticus,* and *T. tonggol* the liver lacks striations.

In *T. alalunga, T. maccoyii, T. thynnus,* and *T. obesus* the three liver lobes are subequal in length, the lateral lobes most often slightly shorter than the middle lobe. In *T. albacares, T. atlanticus,* and *T. tonggol* the right lobe is much longer and narrower than the middle or left lobe.

Correlated with the ventral striations on the livers of *T. alalunga, T. maccoyii, T. thynnus,* and *T. obesus,* vascular cones are associated dorsally with each lobe. The middle lobe always has a single large cone; the other lobes usually have two or more, and these may be somewhat difficult to distinguish from ordinary blood vessels. In the left lobe, we recorded two to five cones in *T. alalunga;* two to six, usually two or three, in *T. thynnus;* two to four in *T. maccoyii;* one to six, usually one or two, in *T. obesus.* In the right lobe we found: two to eight, usually two, in *T. alalunga;* one or two, usually two, in *T. thynnus;* two in *T. maccoyii;* one to four, usually one or two, in *T. obesus.*
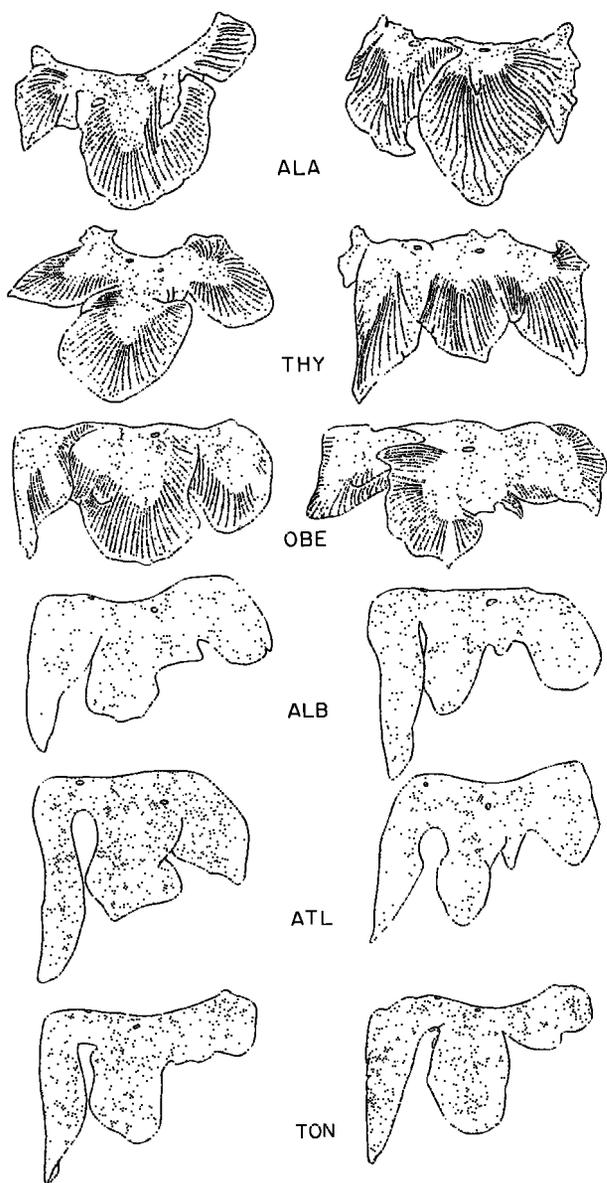
FIGURE 16.—Ventral view of livers of *Thunnus* species, showing shape and presence or absence of striations. Fork lengths (left, right): ALA—875, 1,030 mm.; ALB—700, 1,175 mm.; ATL—568, 650 mm.; OBE—1,450, 1,540 mm.; THY—457, 757 mm.; and TON—910, 924 mm.

Morice (1953) described the liver of *T. albacares* as having two efferent vessels at the anterior end, but noted only a single vessel in *T. alalunga, T. thynnus,* and *T. obesus.* He probably overlooked the vessel in the right lobe near the junction with the middle lobe, because this vessel is smaller than the one in the middle lobe. All specimens that we examined had two such efferent vessels.

84

Thunnus alalunga has the spleen on the left side and the stomach on the right. In the other species these positions are reversed (fig. 15).

Godsil and Byers (1944) attached considerable importance to their observation that the straight intestine in *T. alalunga* crosses from the right to the left side, and the descending portion lies on the left side. This course is obviously correlated with the position of the stomach in this species. We found that the intestine often does not cross over so obviously and that the descending portion is commonly near the middle. Thus there is little or no difference between *T. alalunga* and the other species in position of the descending intestine, although the side on which the intestine originates is different.

The relative position of the first loop of the intestine (where the straight intestine forms the ascending portion) differs to a degree among the species (fig. 15). In *T. alalunga* this loop is shortest and is located about one-half to two-thirds the distance between the posterior margin of the middle liver lobe and the anus. In the other six species the loop may reach from about three-fourths to nine-tenths of the liver-anus distance. In Pacific forms, *T. alalunga* is reported by Godsil and Byers (1944) to have a short "fold" (27–41 percent of body cavity), *T. albacares* a slightly longer "fold" (36-61 percent), and *T. thynnus orientalis* and *T. obesus* a long "fold." Their illustrations and measurements, and our observations, indicate such a wide range of variation that only *T. alalunga* can be regarded as distinct in this character.

One Atlantic specimen of *T. obesus* among our study material had two intestinal loops, a situation never before reported to our knowledge.

The length of the spleen (fig. 15) is normally short, seldom reaching beyond half the distance from caecal mass to end of body cavity in *T. alalunga*, *T. obesus*, and *T. atlanticus*, but usually long, reaching at least three-fourths of this distance in *T. thynnus*, *T. maccoyii*, and *T. albacares; T. tonggol* is variable. In all species there are exceptions.

The gall bladder (fig. 15) in *T. alalunga* is normally exposed along the entire right side of the straight intestine. In the other species it is usually either entirely hidden or a small portion may appear posterior to the first intestinal loop; in the few specimens in which it was largely exposed, the visceral mass seemed to be distorted.

The swimbladder (fig. 17) appears to be invariable and distinctive only in *T. obesus*, in which it is long,

usually slender, beginning near the transverse septum, and tapering to a point that reaches the posterior end of the body cavity.
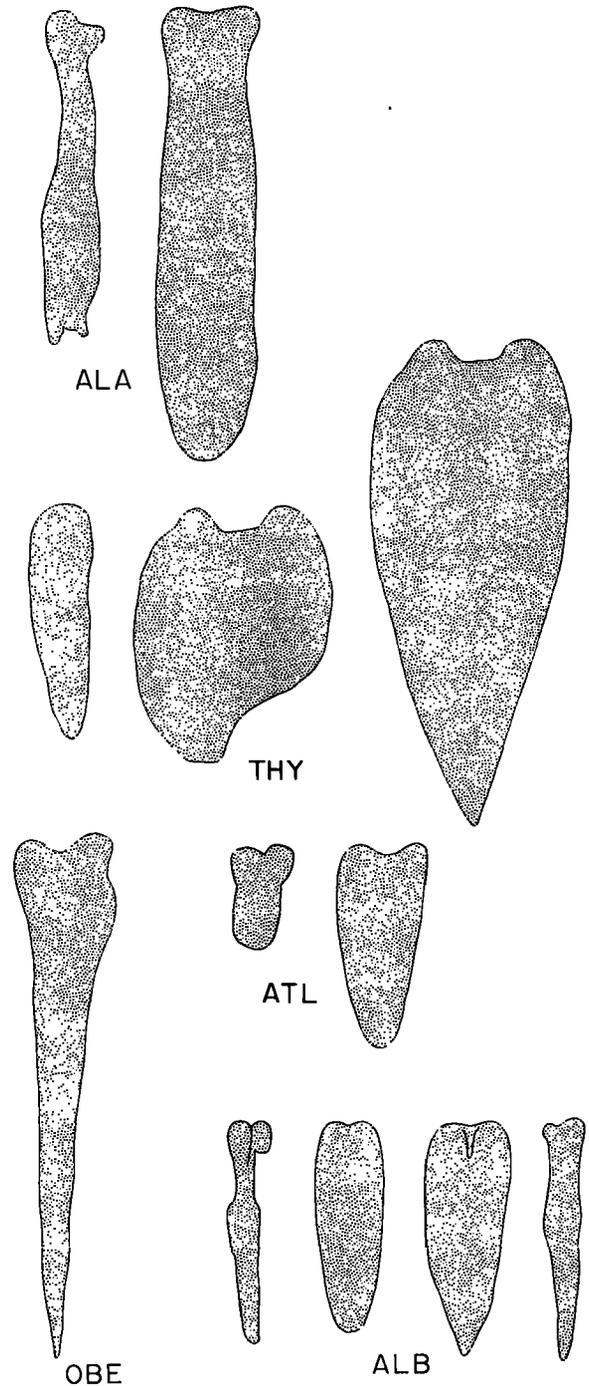

FIGURE 17.—Ventral view of swimbladder shapes of *Thunnus* species. Fork lengths (left to right): ALA—875, 1,030 mm.; ALB—637, 700, 1,175, 1,420 mm.; ATL—650, 664 mm.; OBE—1,250 mm.; and THY—954, 1,050, 1,670 mm.

Absence of a functional swimbladder in *T. tonggol* may be regarded as a useful diagnostic character, but in most specimens we discovered a tiny swimbladder, about 4 mm. in diameter, which could easily have been overlooked. A very small swimbladder (ca. 20 mm. long) also was present in two *T. maccoyii* (742 and 764 mm.).

Variation in the other five species is considerable (fig. 17). In *T. atlanticus* the swimbladder may be short, oblate, lying far anterior in the body cavity; or it may approach the length of a poorly developed swimbladder of *T. albacares*. In the latter case, the swimbladder is comprised of two chambers divided by a transverse membrane, with the anterior chamber probably representing the small type of swimbladder, the posterior chamber an addition. In *T. albacares* the swimbladder is moderately long, usually reaching about the level of the 14th or 15 vertebra (range 12–17). In *T. alalunga* it varies from narrow, only moderately long, and deflated, to fully the length of the body cavity and inflated to fill much of the cavity.

In *T. thynnus* and *T. maccoyii* variation in swimbladder dimensions may be correlated with growth. The changes in swimbladder dimensions were recognized by Serventy (1956a:10), and were suggested but not recognized by Godsil and Holmberg (1950: 21). Smaller specimens (457–954 mm.) have rudimentary swimbladders that are slender, deflated, and short (about 6 vertebrae long), about a quarter of the length of the body cavity, and do not reach the depression anterior to the dorsal bulge. In two *T. maccoyii* the swimbladder was tiny and could easily have been missed in a casual dissection. In a 1,060-mm. specimen of *T. t. thynnus* the organ was inflated and occupied about half the body cavity (fig. 17). In specimens 1,390-mm. and larger the swimbladder extends from the depression anterior to the kidney almost or quite to the posterior end of the body cavity; it is as wide as the body cavity in its anterior half and posteriorly tapers almost to a point.

Urogenital System

General Description.—The paired gonads are frequently visible in ventral view. They lie along the dorsolateral body wall, their posterior ends forming ducts which open on each side of the urinary papilla. The kidney is anterior in position and dorsal to the layer of fibrous connective tissue overlying the swimbladder. Its anterior margin usually follows the edges of the depression anterior to the hump formed

by the haemal arches, and lateral extensions reach forward in a semicircle and sometimes nearly meet anteriorly. Depending upon the species, a posterior extension ("tail") may reach about as far as the level of the 16th vertebra; and *T. albacares* sometimes has accessory masses of kidney tissue posterior to the main mass. In the anterolateral extensions of the kidney, the urinary ducts ("ureters") arise and join within or just posterior to the kidney substance, and the resulting single duct proceeds posteriorly. Just before the anus, the duct enters a small but prominent urinary bladder, which may lie within the mesenteries of the gonads or project freely into the body cavity, depending upon the species. The urinary bladder empties through a urinary papilla behind the anus.

Specific Characters (fig. 18).—The kidney of *T. alalunga* is unique in lacking a "tail," the end reaching the level of the 7th to 9th vertebra (11th in one specimen). In *T. thynnus* and *T. maccoyii* the tail is relatively short, reaching the 8th to 11th vertebra. Its configuration varies in Atlantic specimens from tapering to truncate, encompassing all the forms used by Godsil and Holmberg (1950) to differentiate *T. maccoyii* from Atlantic and Pacific *T. thynnus*. None of our *T. maccoyii* had truncate kidneys. In *T. obesus* the tail is slightly longer than in *T. thynnus*, reaching the 11th to 14th vertebra, is narrower, and is more distinctly delimited from the anterior kidney mass. The kidney of *T. albacares* has a long tail, tapering gradually from the anterior kidney mass and reaching the 12th to 16th vertebra; accessory kidney masses are often present posteriorly. In *T. atlanticus* the kidney mass is bulky anteriorly and has a long, narrow tail that reaches the 12th to 17th vertebra. In *T. tonggol* there is a large anterior portion and a long, narrow tail that reaches the 15th to 17th vertebra.

The branching of the ureters varies considerably, but shows some general tendencies that, together with the shape of the kidney, are useful in distinguishing species (fig. 18). In the tailless kidney of *T. alalunga*, the two main branches are widely divergent, joining at the posteriormost end of the kidney substance. In *T. thynnus* and *T. maccoyii* the junction may occur at the posterior end, at some distance craniad, or just posterior to the kidney. The angle formed by the branches is small when the junction is well posterior, large when far anterior. In *T. obesus* the branches converge to run close together and almost parallel for a considerable dis-
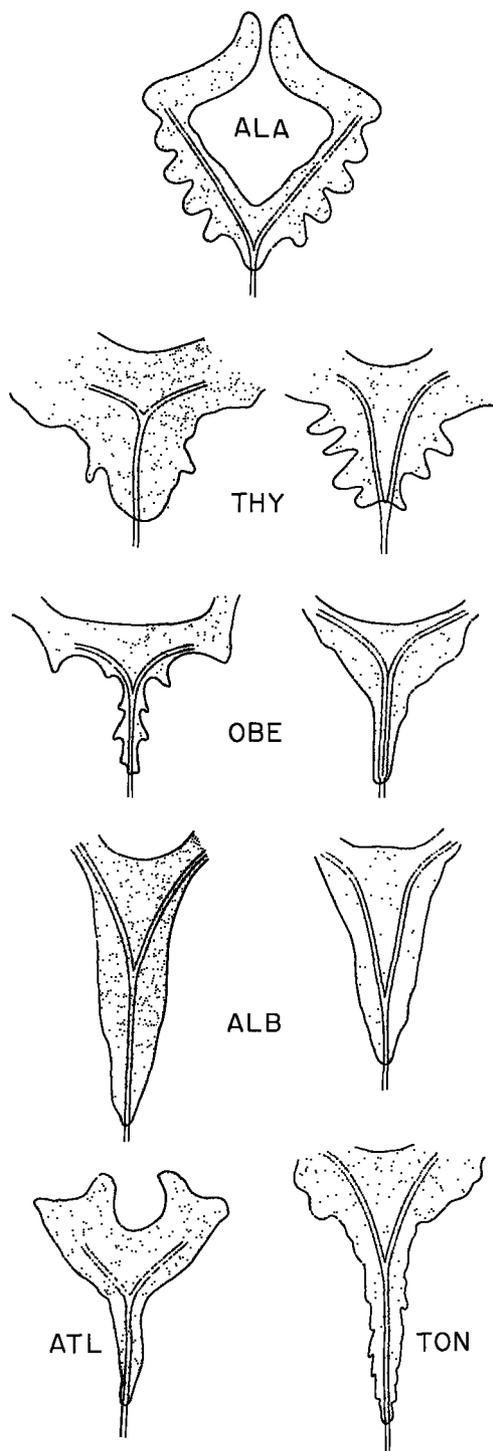
FIGURE 18.—Ventral view of kidney and ureter of *Thunnus* species. Forward extent shown only in ALA and ATL. Fork lengths (left, right): ALA—875 mm.; ALB—700, 1,175 mm.; ATL—533 mm.; OBE—1,310, 1,350 mm.; THY—457, 872 mm.; and TON—910 mm.

tance before they join at the posterior end of the kidney. In those specimens in which the junction occurs well forward, the angle between the branches is less than in *T. thynnus* or *T. maccoyii*. In *T. albacares* and *T. tonggol* the branches usually converge gradually, at a very slight angle, and join at some distance craniad from the end of the kidney tail. When the junction is almost at the posterior end of the tail, the branches may be almost parallel for a short distance. The junction of the branches in *T. atlanticus* usually occurs far anteriorly, and the angle between the branches is usually large. Some specimens, however, resemble *T. albacares*.

Our observations on the urinary bladder are few, but they suggest more variation than was implied by Godsil and Byers (1944). The extent to which the bladder is embedded in the dorsal body wall or projects freely into the body cavity seems to be partly a matter of interpretation. In all species, most of the bladder was contained in the membrane between the left and right gonads. Some *T. thynnus* and *T. alalunga* had much of the posterior part closely attached to the body wall, but the anterior part was separated from the body wall and contained in the membrane of the gonads. The anterior tip of the bladder actually projected free of the membrane in some specimens of *T. obesus*. In all three of these species, at least some specimens had the bladder, except for its posteriormost end, entirely within the membrane, not attached to the body wall, and without a freely projecting anterior tip; this was the only condition observed in the other four species.

Dorsal Connective Tissue

Covering most of the dorsal body wall, dorsal to the peritoneum but ventral to the kidney, is a region of tough, white fibrous connective tissue. In *T. alalunga* the sheet becomes extremely thick posteriorly. In *T. albacares* a thick raised median cord forms in the anterior half. The other species have a rather uniform thin sheet of tissue, perhaps slightly thickened posteriorly.

VASCULAR SYSTEM

Important papers on the circulatory system of *Thunnus* include those of Kishinouye (1923), Godsil and Byers (1944), and Godsil and Holmberg (1950).

General Description

The pericardial cavity is separated from the pleuroperitoneal cavity by a transverse septum, the walls

of which are formed posteriorly by peritoneum, anteriorly by pericardium and the walls of the sinus venosus and the ducts of Cuvier, which enter the sinus. No specific differences have been observed in these structures or in the heart itself.

After leaving the heart, blood is carried in the ventral aorta, which sends an afferent branchial artery into each of the gill arches. After circulating in the capillaries of the gill lamellae, the blood from each gill arch enters an efferent branchial (epibranchial) artery. The anterior two epibranchials of each side unite to form a common trunk, and these trunks join as the "Y" of the aorta, usually beneath the second vertebra, to form the dorsal aorta (fig. 19). The posterior two epibranchials of each side also unite, and their short common trunks join the dorsal aorta, usually beneath the third vertebra. The dorsal aorta continues posteriorly along the dorsal body wall to the first haemal canal. The coeliaco-
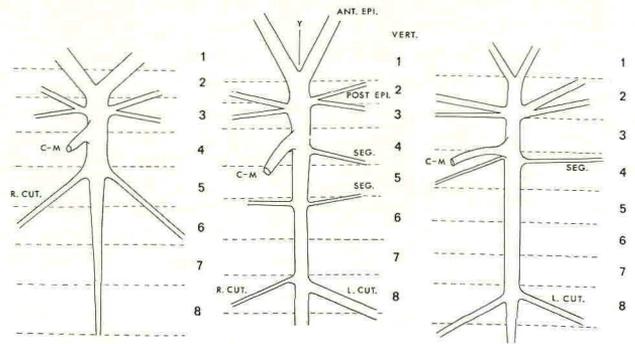
FIGURE 19.—Representative patterns of anterior branches of dorsal aorta in *Thunnus* species. (Left) *T. alalunga;* (middle) *T. atlanticus;* (right) *T. tonggol.* Y: Y of aorta. ANT EPI: anterior epibranchials. POST EPI: posterior epibranchials. C–M: coeliaco-mesenteric. SEG: segmental. L. CUT and R. CUT: Left and right cutaneous. VERT: vertebrae separated by dashed lines.

FIGURE 20.—Cutaneous system of arteries (red) and veins (blue) of *Thunnus obesus.* (upper) Course of cutaneous vessels in superficial musculature. (A) Enlarged transverse section. (B) Enlarged partial view of C, with portions of the arterial walls cut away to show origin of arterioles and venules. (C) Enlarged lateral view of cutaneous vessels. (D) Posterior course of cutaneous vessels; no posterior commissure. From Godsil and Byers, 1944 (fig. 66).

mesenteric artery arises from the dorsal aorta beneath the third to fourth vertebra and forms two or three main branches that go to the liver, supply the vascular cones when present, and give off branches to the other visceral organs. The paired cutaneous arteries rise posterior to the origin of the coeliaco-mesenteric artery and course laterad almost or quite perpendicular to the aorta; they penetrate the lateral body musculature, and on each side form two branches beneath the skin that almost parallel one another to the caudal peduncle (fig. 20, 21). At about the level of the 30th vertebra, a posterior commissure may connect the dorsal and ventral branches of each side. Along their length, the lateral branches give off into their interspace arterioles, which are so dense that they seem to form a solid sheet penetrating the dark muscle (chiai).

Cutaneous veins accompany the arteries; the two parallel lateral branches join anteriorly on each side (fig. 22) to form a large vein that enters the duct of Cuvier, which in turn enters the sinus venosus.

If a post-cardinal vein is present it emerges from the first closed haemal arch, runs toward the right side in the kidney mass, and joins the right cutaneous vein. There is usually a cross-connection between the post-cardinal and left cutaneous veins.

Specific Characters

The coeliaco-mesenteric artery usually has two branches in *T. thynnus*, *T. maccoyii*, *T. alalunga*, and *T. atlanticus*, and three branches in *T. albacares* and *T. tonggol*. In *T. obesus* either two or three branches may be present in both Atlantic and Pacific specimens. Exceptions were noted in *T. albacares* and *T. atlanticus*.

A connecting branch near the liver between two of the coeliaco-mesenteric branches is present in *T. maccoyii*, may be present or absent in *T. thynnus*,
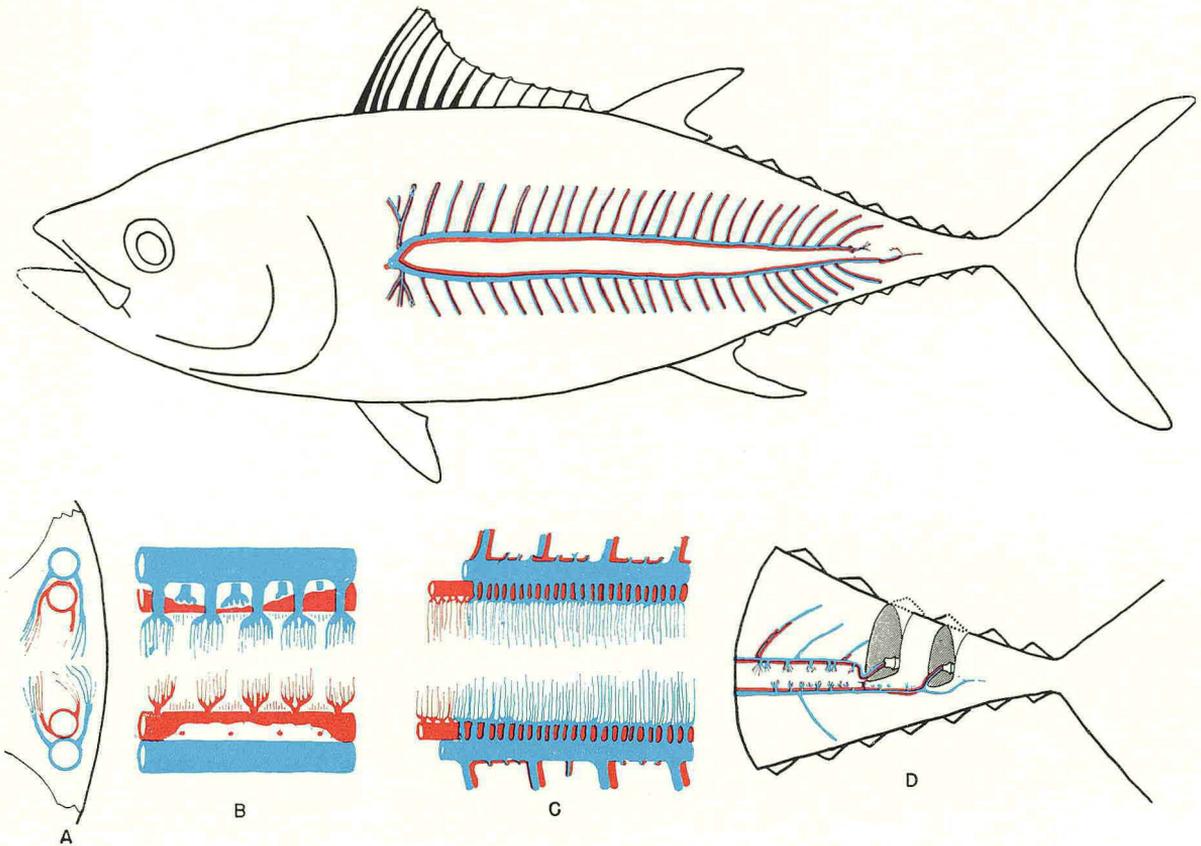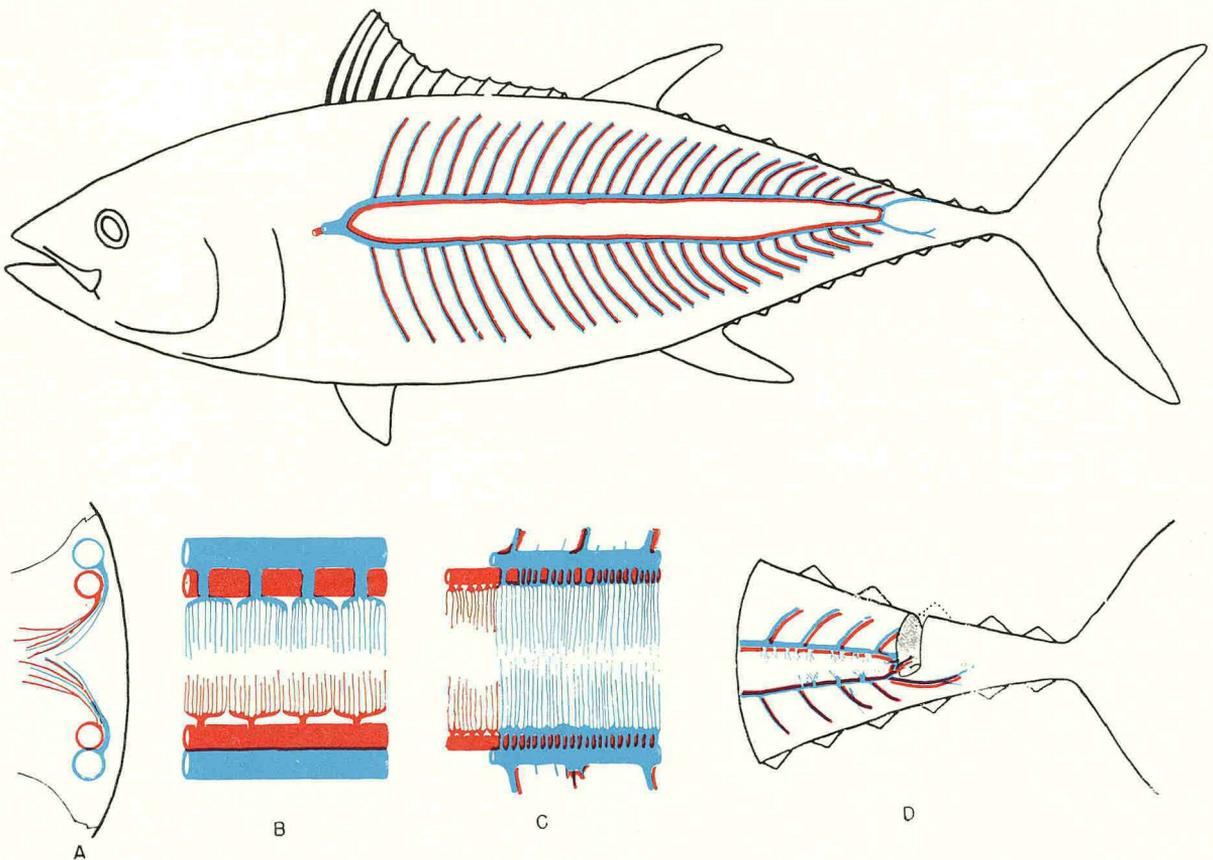

FIGURE 21.—Cutaneous system of arteries (red) and veins (blue) of *Thunnus albacares*. (upper) Course of cutaneous vessels in superficial musculature. (A) Enlarged transverse section. (B) Enlarged partial view of C, to show origin of venules (dorsal) and arterioles (ventral). (C) Enlarged lateral view of cutaneous vessels. (D) Posterior commissure. From Godsil and Byers, 1944 (fig. 31).
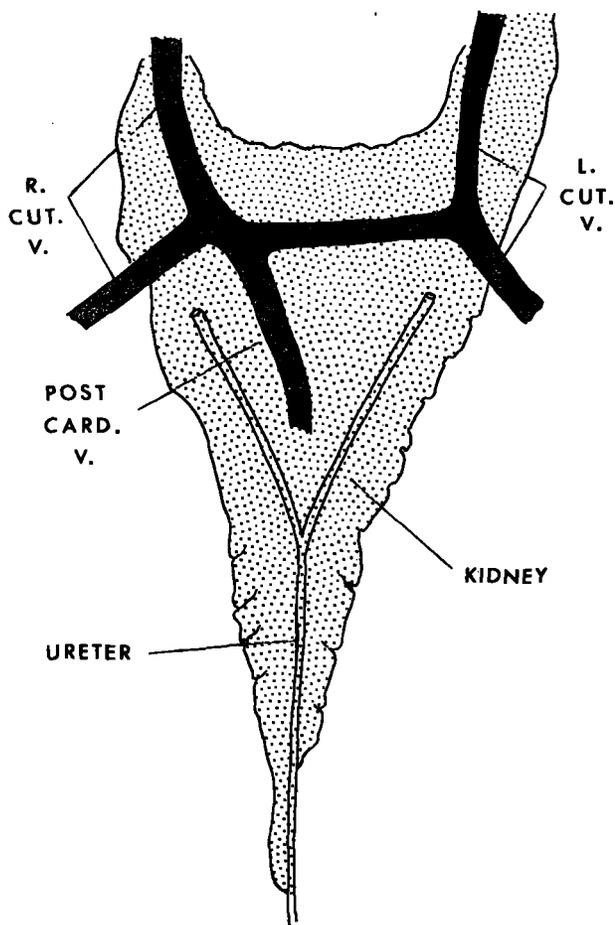
FIGURE 22.—Post-cardinal vein in relation to cutaneous veins and kidney in *Thunnus atlanticus.* Also typical of *T. obesus, T. albacares,* and *T. tonggol.*

T. obesus, and *T. albacares;* and appears to be absent in *T. alalunga, T. atlanticus,* and *T. tonggol.* Godsil and Byers (1944) implied that this connection is always, or nearly always, present in Pacific *T. albacares.* Godsil and Holmberg (1950) used its supposed absence in Atlantic *T. t. thynnus* as one character that differentiates Atlantic from Pacific specimens (*T. t. orientalis*), a conclusion which our observations do not support.

The cutaneous artery usually originates at the level of the third or fourth vertebra in *T. thynnus, T. maccoyii,* and *T. alalunga,* and at the sixth to eighth vertebra in *T. albacares, T. obesus, T. atlanticus,* and *T. tonggol.*

The cutaneous arteries pass laterally between the third and fourth ribs in all *T. thynnus, T. maccoyii,* and *T. alalunga* examined by us (also between the second and third according to Godsil and Holmberg,

1950); in *T. albacares, T. obesus, T. tonggol,* and *T. atlanticus* they pass between the fifth and sixth ribs, or occasionally between the fourth and fifth. Branching occurs between the fourth and fifth intermuscular bones in *T. thynnus, T. maccoyii,* and *T. alalunga,* and between the sixth and seventh in *T. albacares, T. obesus, T. tonggol,* and *T. atlanticus.* Godsil and Holmberg (1950) reported more *T. maccoyii* with branching between the fifth and sixth, and we observed this in one specimen of *T. t. thynnus.* In a significant number of our *T. albacares,* as well as two *T. obesus,* branching occurred between the seventh and eighth intermuscular bones.

A posterior commissure is present in *T. thynnus, T. maccoyii, T. albacares* (fig. 21), *T. tonggol,* and *T. atlanticus,* but absent in *T. alalunga.* In *T. obesus* it is present or absent (fig. 20). In all species except *T. albacares* and *T. maccoyii,* we encountered specimens in which we could not ascertain the presence of a commissure.

We noted the number and position of the rows of arterioles and venules arising from the lateral cutaneous vessels in relatively few specimens of each species (see fig. 23). *T. alalunga, T. albacares* (fig. 21), *T. atlanticus,* and *T. tonggol,* have one row from each vessel; in *T. alalunga* it originates on the mesial side, and in the other species on the lateral side. In *T. thynnus, T. maccoyii,* and *T. obesus* (fig. 20) two rows, one mesial and one lateral, arise from each vessel. Kishinouye (1923) reported two rows of venules and a single row of arterioles in Japanese *T. thynnus orientalis.* California specimens have two rows of arterioles (Godsil and Byers, 1944, and our observations). We feel certain that Kishinouye either was mistaken or relied on an unusual specimen.

In *T. albacares* large parallel trunks connect the posterior epibranchial and the cutaneous arteries on
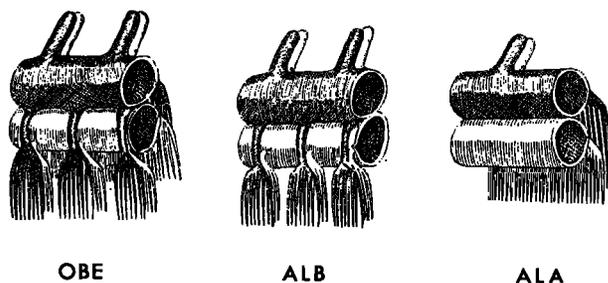

OBE   ALB   ALA

FIGURE 23.—Relationships of arterioles and venules to cutaneous artery (light) and vein (dark). Three patterns represented by *T. obesus* (OBE), *T. albacares* (ALB), and *T. alalunga* (ALA). Lateral view. After Kishinouye (1923).

each side; they are absent in the other species.

A post-cardinal vein joins the right cutaneous vein in *T. albacares, T. obesus, T. atlanticus,* and *T. tonggol;* it is absent in *T. thynnus, T. maccoyii,* and *T. alalunga.*

OLFACTORY ORGAN

As this manuscript was being completed, Iwai and Nakamura (1964b) described their use of the olfactory rosette to distinguish species of *Thunnus.* In each nasal cavity beneath the anterior naris is an olfactory rosette, consisting of numerous laminae arranged radially around a central axis. According to Iwai and Nakamura, *T. alalunga* is unique in having a pair of fleshy labia surrounding the short laminae. The laminae in *T. obesus* are described as smooth, greatly expanded distally with adipose tissue, and often partly fused distally. In *T. thynnus* the laminae in small specimens are smooth and of uniform thickness to the distal edge, whereas in larger specimens the laminae are smooth and distally expanded, but with little evident adipose tissue. *Thunnus maccoyii* is differentiated from *T. thynnus* by the presence, in some specimens, of slight fringing in the distal ends of the laminae. In *T. albacares* and *T. tonggol* the laminae are entirely fringed on their distal edges; and in large *T. albacares* the basal half of the rosette is densely spotted with pigment; however, Iwai and Nakamura admit that the rosettes of *T. tonggol* and small *T. albacares* resemble each other, and, from their figure 3, also resemble those of *T. maccoyii.* On the basis of admittedly insufficient material, Iwai, Nakamura, and Matsubara (1965) indicate that the nasal rosettes of *T. atlanticus* closely resemble those of *T. tonggol* except that the laminae of the former tend to have the distal ends folded inward.

We have examined very few nasal rosettes, but our observations indicate a need for more careful scrutiny of this character, with respect to normal variation and growth changes, before it is used widely. A specimen of *T. alalunga* and two of *T. obesus* agreed with Iwai and Nakamura (1964b), but in one *T. obesus* the laminae were lightly pigmented and had short, flat fimbriae along their entire length. Two specimens of *T. albacares* were distinctive in the abundance of pigment in the laminae, but while in one the fimbriae were very pronounced and finger-like, in the other they were less developed and flatter. Rosettes of one *T. atlanticus* and one *T. tonggol* were virtually identical and were similar to those of *T. albacares,* with dense, short, flat fimbriae on the laminae, but had less abundant pigment; folding of the distal ends of the laminae was not apparent in either species. In a larger specimen of *T. thynnus* from Cape Town, South Africa, the laminae were almost uniform in thickness to the distal edge and bore prominent flattened fimbriations along most of their length. These observations are enough at variance with those of Iwai and Nakamura that they clearly show the need for further study.

MERISTIC CHARACTERS

The species of *Thunnus* are essentially identical in the number of fin rays (table 1). The number of gill rakers is the only meristic character that we have found valuable in separating species of *Thunnus* (table 2).

Species Differences.—T. atlanticus has fewer gill rakers (19–25) than any other species of *Thunnus* in the Atlantic, and *T. tonggol* has fewer (19–26, rarely to 28) than any other *Thunnus* in the Indo-Pacific (table 2). *T. thynnus* and *T. maccoyii* have the greatest number of gill rakers in the genus (31–43). The other three species fall between these two groups with a combined range 23–35. The overlap between species with low, medium, and high numbers of gill rakers is very slight. The *T. thynnus-maccoyii* complex shows differences of some magni-

TABLE 1.—Range of variation in fin-ray counts in the species of *Thunnus*
[Based on original and published data]

Fin	Species					
	T. alalunga	*T. albacares*	*T. atlanticus*	*T. obesus*	*T. thynnus*	*T. tonggol*
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
Dorsal spines	12–14	12–14	12–14	13–14	12–14	11–14
Second dorsal rays	13–16	13–16	12–15	14–16	13–15	14
Dorsal finlets	7–9	8–10	7–9	8–10	8–10	9
Total second dorsal rays	21–24	22–24	20–23	22–24	22–24	23
Anal rays	13–15	12–15	11–15	11–15	13–16	14
Anal finlets	7–9	7–10	6–8	7–10	7–9	8
Total anal rays	20–23	21–23	19–22	21–23	21–24	21–23
Pectoral rays	31–36	33–36	31–35	31–35	30–36	30–35

TABLE 2.—Total number of gill rakers on the first arch in the species of *Thunnus*

Number of rakers	T. tonggol			T. atlanticus	T. obesus			
	West Indian-Red Sea	SE Asia	Australia	West Atlantic	West Atlantic	East Atlantic	Central-West Pacific	East Pacific
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
19			3	1				
20		2	18	7				
21	1	2	43	29				
22		2	86	59				
23	4	4	54	21			1	
24	1	2	19	2			5	1
25	3		2	1	5	1	27	3
26	10				13	4	159	26
27	1				15	6	147	28
28	1				17	3	70	17
29					4	4	23	12
30						1	14	
31						1	2	
Number of fish	21	12	225	120	55	20	448	87
Average	25.1	21.7	22.0	21.9	27.3	27.6	26.9	27.1
Sources	6, 15, 17	6	6, 13, 25	2, 6, 12, 17	6, 12	6	3, 5, 30	5, 6, 8, 30

Number of rakers	T. alalunga					T. albacares				
	West Atlantic	East Atlantic	Indian Ocean	Central-West Pacific	East Pacific	West Atlantic	East Atlantic	West Indian Ocean	Central-West Pacific	East Pacific
25	1								1	
26	1	4	1	6	1		2	2	3	
27	10	18	5	45	6	6	3	7	24	2
28	20	55	9	142	21	11	11	22	73	8
29	15	50	15	176	26	33	51	54	194	20
30	6	27	11	96	8	37	88	58	242	50
31	2	4	1	15	2	30	126	23	202	51
32				1		9	80	5	93	24
33						1	23		21	6
34							7		2	
35							1			
Number of fish	55	158	42	481	64	127	392	171	855	161
Average	28.3	28.6	28.8	28.8	28.6	29.8	30.8	29.5	30.0	30.5
Sources	6, 12	6, 10, 11	14, 28, 29	5, 8, 29, 30	5, 8, 30	6, 12, 17	6, 11, 23	6, 19, 28	5, 8, 21, 22, 30	5, 8, 20, 30

Number of rakers	T. maccoyii		T. t. orientalis		T. t. thynnus	
	South Africa	Australia	Central-West Pacific	East Pacific	West Atlantic	East Atlantic-South Africa
31	1	10				
32	2	62		2		
33	3	84		2		
34	5	89		2	3	
35	1	54	3	14	2	4
36	1	25	6	10	12	8
37		6	2	11	32	40
38			1	2	63	88
39				2	102	105
40		1	1		40	74
41					29	36
42					4	7
43					1	4
Number of fish	13	331	13	45	288	366
Average	33.5	33.7	36.4	35.8	38.8	38.9
Sources	26	1, 5, 6, 9, 24	5, 6	6, 9, 12	6, 7, 9, 12	6, 18, 26, 27

Source:
1—Abe, 1955; 2—Beebe and Tee-Van, 1936; 3—Brock, 1949; 4—Crane, 1936; 5—Dung and Royce, 1953; 6—Gibbs and Collette, original data; 7—Ginsburg, 1953; 8—Godsil and Byers, 1944; 9—Godsil and Holmberg, 1950; 10—Letaconnoux, 1951; 11—Marchal, 1959; 12—Mather, 1064; 13—Munro, 1957; 14—Postel et al., 1960; 15—Ranade, 1961; 16—Rivas, 1954b; 17—Rivas, 1961; 18—Robins, 1957; 19—Royce, 1965; 20—Schaefer, 1948; 21—Schaefer, 1952; 22—Schaefer, 1955; 23—Schaefer and Walford, 1950; 24—Serventy, 1956a; 25—Serventy, 1956b; 26—Talbot, 1964; 27—Tiews, 1963; 28—Williams, 1964; 29—Yoshida and Otsu, 1963; 30—Japan Fishery Agency, 1964.

tude among populations in both the means (Atlantic 38.9, Pacific 35.9, *T. maccoyii* 33.7) and the modes (39, 35, 34). These differences and others can be used to separate the two subspecies, *T. thynnus thynnus* in the Atlantic and *T. thynnus orientalis* in the Pacific, and *T. maccoyii* in the southern Pacific

and Indian oceans. Populations of *T. tonggol* in the Red Sea and western Indian Ocean appear to have more gill rakers than those to the eastward.

MORPHOMETRIC CHARACTERS

Relative lengths of body parts have limited value in species identification of tunas, although they have been widely used by many investigators. Allometric growth has been demonstrated for many, if not most, body parts and has been responsible for many misconceptions. A classic example of allometry involves the dorsal and anal fins of *T. albacares* which become relatively much longer in large specimens. Furthermore, the length attained by these fins varies geographically in a complex fashion (Royce, 1965). Lack of consideration of these factors has resulted in the description of numerous nominal species. Many limited analyses have shown statistically significant differences between populations of widely distributed species (cf. Kurogane and Hiyama, 1957b, 1958a, 1959 for *T. alalunga*).

Of the many measurements that can be made, only the following appear to be of importance in distinguishing tuna species: dorsal and anal fin heights, pectoral fin length, placement of second dorsal fin, greatest body depth, and diameter of eye (or orbit).

Our conclusions are based, as often as possible, on data from many parts of the range of each species. Where these data have shown no noteworthy geographic differences, we consider them together as a single unit. Otherwise, the differences are mentioned. In addition to our original data, we have leaned heavily upon Dung and Royce (1953) for raw data, and have used many other sources. Our information has significant gaps that can be filled only by future work or by use of unpublished data from other workers. All species are more or less deficient in morphometric data for specimens below 400 mm. For the Atlantic, such data are few or lacking for *T. alalunga* less than 900 mm.; for *T. atlanticus* larger than 650 mm.; and for *T. obesus* less than 1,000 mm. For the Pacific and Indian Oceans, *T. maccoyii* is represented by data on only four specimens outside the 650-750 mm. range, and our sparse Indian Ocean data for all species are almost entirely from specimens sent to us as a result of cruises of the R/V *Anton Bruun* during the International Indian Ocean Expedition. Our interpretations must be judged with these deficiencies in mind.

Heights of the second dorsal and anal fins have received much attention, especially in *T. albacares*, in which the positive allometry of both these fins relative to fork length, apparently characteristic of all species, is most pronounced. This allometry has led to the description of long-finned nominal species in both the Atlantic and Pacific and even to the establishment of a new genus (*Semathunnus*). The species are compared in figs. 24 and 25, in which the large *T. albacares* are western Atlantic specimens. The few data for *T. maccoyii* fall in the range of *T. thynnus* and are not discussed separately.

As many workers have shown and as Royce (1965) has most recently demonstrated, different popula-
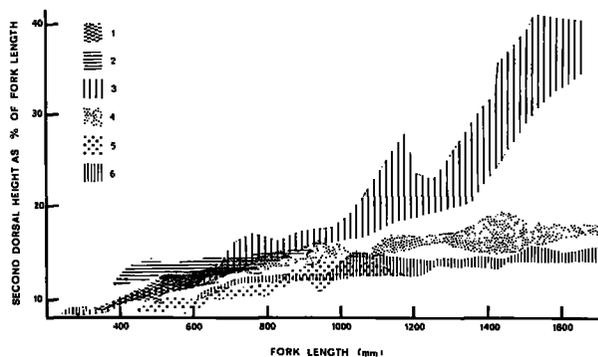
FIGURE 24.—Relative height of second dorsal fin in *Thunnus* species. Data, in addition to our own, include Dung and Royce (1953: tables 27, 28, 42). 1—*T. atlanticus;* 2—*T. tonggol;* 3—*T. albacares;* 4—*T. obesus;* 5—*T. alalunga;* 6—*T. thynnus.*
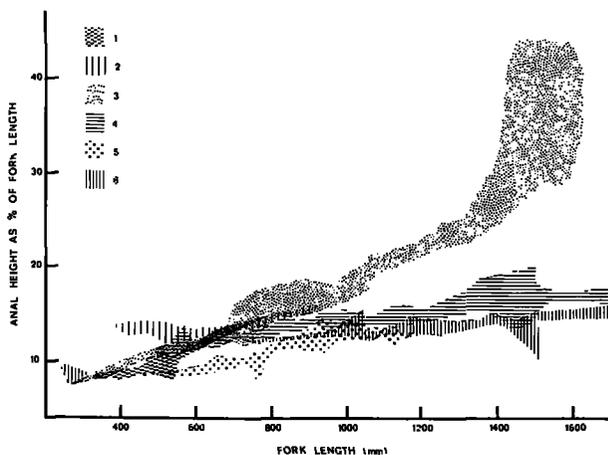
FIGURE 25.—Relative height of anal fin in *Thunnus* species. Data, in addition to our own, include Dung and Royce (1953: tables 27, 28, 42). 1—*T. atlanticus;* 2—*T. tonggol;* 3—*T. albacares;* 4—*T. obesus;* 5—*T. alalunga;* 6—*T. thynnus.*

tions of *T. albacares* show different regressions, but in adults of this species the fins always become higher than in any other species of *Thunnus*. In the equatorial Pacific the fin heights vary in clinal fashion from highest in the west to lowest in the east. Western Atlantic specimens have very high fins, thereby resembling those from the western equatorial Pacific; eastern Atlantic (Angola) specimens have lower fins, as do those from the eastern Pacific.

At sizes between 350 and 600 mm., *T. tonggol* appears to have higher fins than any other species of *Thunnus*. From about 500 to 800 mm., *T. alalunga* has the lowest fins. The other five species are difficult to distinguish until about 700 mm. Beyond 800 mm., *T. albacares* clearly develops the highest fins, *T. thynnus* and *T. alalunga* remain the shortest, and *T. obesus* and *T. tonggol* are intermediate.

The pectoral fin shows a growth pattern that is probably similar in all species, but which differs among the species in size of fin and fork length at times of inflection. Simply stated, the pectoral fin undergoes a period or stanza of increase in length relative to fork length in juveniles, followed by an isometric period that leads into a final and continuous stanza of relative decrease in length (fig. 26). Size range of the stanzas is shown in table 3 for each adequately represented species. The smallest *T. tonggol* for which data were available are probably in the size range at which the distinction between


FIGURE 26.—Relative length of pectoral fin in *Thunnus* species. Data, in addition to our own, include Dung and Royce (1953: tables 12, 21, 27, 28, 42, 45–50), Godsil and Holmberg (1950: 54–55), and Serventy (1956b). 1—*T. atlanticus;* 2—*T. tonggol;* 3—*T. albacares;* 4—*T. obesus;* 5—*T. alalunga;* 6—*T. thynnus;* 7—*T. maccoyii.*

increasing relative fin size and isometry is difficult to distinguish; hence the stanzas could not be determined.

TABLE 3.—*Approximate range in fork length of growth stanzas of pectoral fins in species of* Thunnus. *Smallest size limited by available data*

Species	Increase	Isometric	Decrease
	Millimeters	*Millimeters*	*Millimeters*
alalunga	450–700	700–900	900 +
obesus (Indo-Pacific)	350–700	700–900	900 +
obesus (Atlantic)	?	?650–1,000	1,000 +
albacares	250–500	500–650	650 +
atlanticus	? –350	350–500	500 +
tonggol	?	?	?400 +
thynnus	150–850	850–1,600	1,600 +
maccoyii	?	?650–1,450	?

At less than 500 mm., only *T. thynnus* is distinct, with pectorals 21 percent of fork length or less. Data for *T. maccoyii* are lacking. All other species overlap more or less in the 25–31 percent range, although between 400 and 500 mm. species distinctions begin to be apparent (viz. Pacific *T. obesus* pectorals become relatively longer, those of *T. tonggol* shorter).

The marked positively allometric growth of the pectorals of *T. alalunga* and Pacific *T. obesus* makes these two forms clearly distinctive from all others between 500 and 1,200 mm. (fig. 26). Most specimens have fins 34–46 percent of fork length. Up to 700 mm., *T. alalunga* has slightly shorter fins than Pacific *T. obesus*, but from 700–1,200 mm. they are virtually identical. Atlantic *T. obesus* in the 650–1,200 mm. range (no data were available for smaller specimens) appear to have significantly shorter pectorals than Pacific specimens: 29–35 percent at sizes of 650–1,000 mm., then gradually decreasing until no suggestion of difference is seen above 1,300 mm.

In *T. albacares* a gradual negative allometry after 600 mm. keeps the pectorals shorter than in *T. alalunga* or either Atlantic or Pacific *T. obesus* until about 1,100 mm., when overlap with *T. obesus* begins to increase.

Whereas the pectorals of *T. atlanticus* are, at first, very similar in length to those of *T. albacares*, the more rapid decline in relative length makes them at sizes above 600 mm. even shorter than in *T. albacares*.

The greatest negative allometry is seen in T. *tonggol*, which, at 500 mm., already shows the trend that brings the pectoral length into the ranges of *T. maccoyii* and *T. thynnus* between 650 and 900 mm. The fins are the shortest of all the species at fork
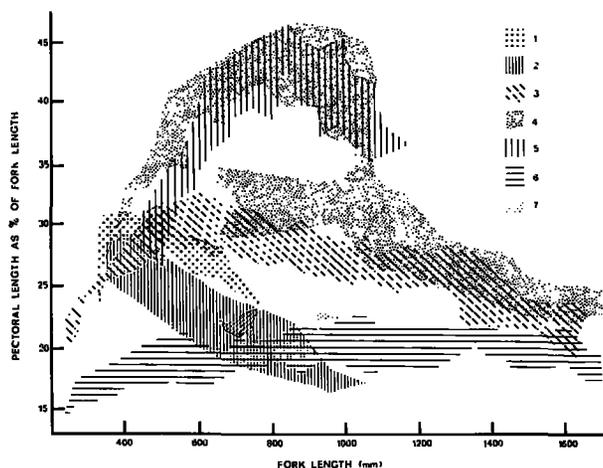
lengths from 900 to 1,050 mm. (the maximum size of *T. tonggol* for which data were available).

Except for the size range where *T. tonggol* overlaps it, *T. thynnus* has pectorals consistently shorter than those of other species, the longest on record being about 23 percent of fork length.

Although more data are needed for *T. maccoyii*, it appears that this species has a slightly longer pectoral fin than *T. thynnus*. From 650–750 mm. fork length, for which a fair amount of data is available, the fin of *T. maccoyii* is 20–24 percent of fork length, that of *T. thynnus* 17–21 percent. A few specimens of *T. maccoyii* between 900 and 1,000 mm., and one of 1,445 mm. have pectorals 22–23 percent of fork length, also slightly longer than those of similar sized *T. thynnus*. The ranges given by Iwai, Nakamura, and Matsubara (1965: 31, 33) of 4.8–6.0 in fork length (= 16.7–21.7 percent) for *T. thynnus* and 4.4–4.5 in fork length (= 22.2–22.7 percent) for *T. maccoyii* suggest a distinctness of separation that is not upheld by our data, although the basic species differences in pectoral length appear to be real.

The distance from snout to second dorsal origin relative to fork length (fig. 27) shows a negative regression in all species of *Thunnus* over 400 mm. When size is taken into account, this measurement provides a reliable separation of some species, but a simple statement of range is inadequate. For example, *T. tonggol* appears distinct throughout its size range (maximum around 1,000 mm.) but larger *T. albacares*, *T. obesus*, and *T. thynnus* all have a distance that is the same as that of smaller *T. tonggol*.

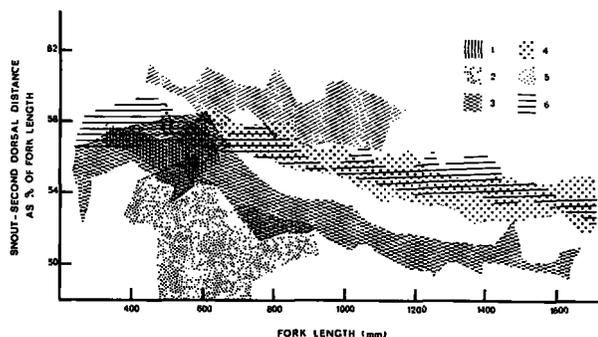Throughout the size ranges examined by us (fig. 27) the distance is greatest in *T. alalunga* and least in

FIGURE 27.—Relative distance from snout to second dorsal origin in *Thunnus* species. Data, in additon to our own, include Dung and Royce (1953: tables 12, 21, 28, 42, 50–54). 1—*T. atlanticus;* 2—*T. tonggol;* 3—*T. albacares;* 4—*T. obesus;* 5—*T. alalunga;* 6—*T. thynnus.*

T. tonggol. Two intermediate groups can be categorized: one with a shorter distance that includes *T. atlanticus* and *T. albacares*, and one with a longer distance that includes *T. obesus* and *T. thynnus*. The meager data for *T. maccoyii* fall in the range of *T. thynnus*. Below a fork length of about 600 mm. there is so much overlap that the usefulness of snout-second dorsal distance in species distinction is doubtful, but above 600 mm. it appears to be useful.

Greatest body depth is shown in fig. 28. This
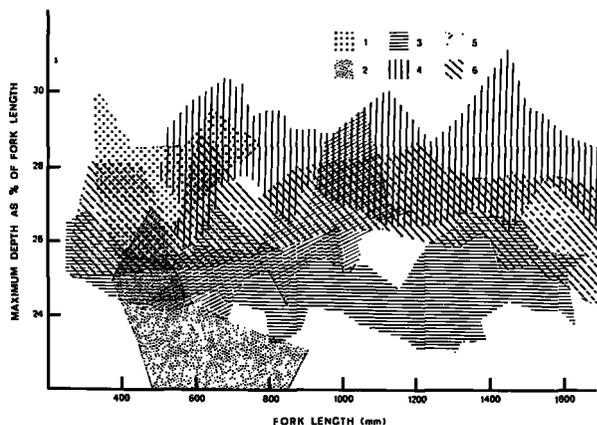
FIGURE 28.—Relative greatest body depth in *Thunnus* species. Data, in addition to our own, include Dung and Royce (1953: tables 27, 28, 42). 1—*T. atlanticus;* 2—*T. tonggol;* 3—*T. albacares;* 4—*T. obesus;* 5—*T. alalunga;* 6—*T. thynnus.*

character is so variable that it should not be used by itself. Rather, there are tendencies which, with other characters, can be helpful in species determination.

In specimens less than about 600 mm. fork length, overlap is particularly evident, but two categories can be based on greatest depth: deep-bodied species, including *T. obesus*, *T. thynnus*, and *T. atlanticus*, with depths usually 26–30 percent of fork length; and slender species, including *T. albacares*, *T. tonggol*, and *T. alalunga*, with depths usually 23–26 percent of fork length. The few data for *T. maccoyii* fall in with *T. thynnus*.

There appears to be little change in depth relative to fork length from 600 to 1,500 mm. in any species except *T. alalunga*, in which the relative depth increases gradually until specimens over 1,000 mm. are clearly in the deep-bodied category.

The two species that commonly become larger than 1,500 mm., *T. obesus* and *T. thynnus*, exhibit

increased variability at these larger sizes. In *T. thynnus* this is particularly evident; specimens over 2,000 mm. fork length (not shown in fig. 28) appear randomly distributed over a range of body depths from 22–29 percent of fork length, which is almost the entire range of all species combined.

The greatest body depth is found in individuals of *T. obesus* at all sizes over 600 mm., but the species overlaps with *T. atlanticus*, *T. thynnus*, or *T. alalunga* throughout its known size range.

Eye size, in combination with other characters, is a useful species criterion, but the negative allometry must be considered. Because we measured the bony orbit, our data are not comparable with most other published data. We recommend that future workers use iris diameter.

Fig. 29 compares the species. Both *T. alalunga* and *T. atlanticus* exhibit wide variation in eye diameter, making categorical statements difficult. At less than 600 mm. fork length the smallest orbit diameter is found in *T. thynnus* and *T. tonggol*, the largest in *T. atlanticus* and *T. alalunga*, and intermediate in *T. albacares*; *T. obesus* is not represented.

At sizes greater than 600 mm., *T. obesus* clearly has the largest orbit diameter. Variation in *T. alalunga* covers the range from largest to smallest. The other species have so much overlap with one another that species distinctions are impossible.

COLORATION

Colors and color patterns of tunas have limited use in tuna systematics because they show great individual and age variation, and because they may be lost after death and preservation. Nevertheless, there are some excelle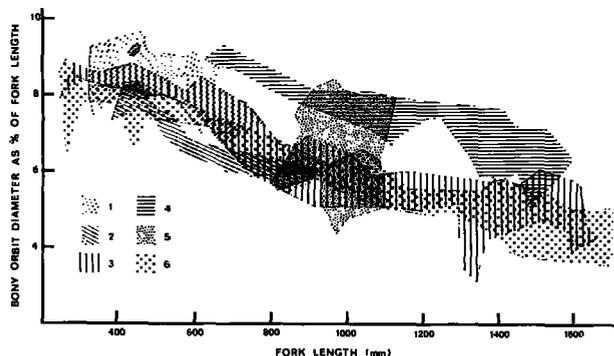nt color characters, in spite of the difficulty in verbal expression of many of them. Many of the descriptions are taken from Mather (1964).

Body. Most *Thunnus* species are iridescent dark blue above and silvery below. *T. albacares* is the most brilliantly colored, with a shining golden lateral band. *T. atlanticus* also has a prominent gold lateral band, but its body is usually very dark compared with other species. *T. obesus* may display a trace of a gold band, but the band is apparently absent in *T. thynnus* and *T. tonggol* and is replaced by an iridescent blue band in *T. alalunga*.

Small specimens of all species may display a pattern of white spots or streaks ventrolaterally. In *T. tonggol* these markings consist of horizontally elongated spots. The other six species have rounded spots that are either randomly distributed or tend to become arranged in vertical rows that alternate with vertical white lines; horizontally elongated spots are sometimes seen on the caudal peduncle but rarely farther anteriorly. This pattern is usually lost in large individuals, although it may be retained in specimens of *T. albacares* and *T. thynnus* up to 1,500–1,600 mm.

In *T. maccoyii*, alone among the species of *Thunnus*, the caudal keels are an unmistakable bright yellow. In the fish markets of Japan, we were able to recognize *T. maccoyii* from a considerable distance on the basis of this character. However, we suspect the keels may lose their yellow in larger adults.

Fins. The color of the first dorsal fin is variable. It may be entirely white, or there may be a yellow suffusion, and the distal margin may be black. Too few observations have been made to enable us to characterize the species. The second dorsal and anal fins usually have yellow tips in all but *T. alalunga* and *T. atlanticus*, which have dark fins with white distal margins. The dorsal and anal finlets are usually bright yellow with black margins in all except *T. alalunga* and *T. atlanticus*. In *T. albacares* the black margin is usually very narrow, while in *T. obesus* it is wider. *T. alalunga* may have yellow in the dorsal and some anal finlets, but the anal finlets are commonly all silvery or dusky. Both the dorsal and anal finlets of *T. atlanticus* are almost invariably dusky with white margins; yellow has been observed in these finlets only in frozen specimens. June (1952b) reported black dorsal and anal finlets in an unusual specimen of *T. albacares* from the central Pacific.

FIGURE 29.—Diameter of bony orbit relative to fork length in *Thunnus* species. Only our data used. 1—*T. atlanticus;* 2—*T. tonggol;* 3—*T. albacares;* 4—*T. obesus;* 5—*T. alalunga;* 6—*T. thynnus.*

The caudal fin of *T. alalunga* has a narrow, white trailing margin that distinguishes it from all other *Thunnus*, in which the white margin is lacking.

Specific Characters. The uniformly white-margined dusky finlets of *T. atlanticus*, the white caudal margin of *T. alalunga*, the horizontally elon-gated ventrolateral spots of *T. tonggol*, and the yellow caudal keels of *T. maccoyii* are the only color characters we regard as generally useful in distinguishing species, and confusing examples of other species with these same characters have been observed.

PART 2. SYSTEMATICS

Workers have differed in their interpretations of the suprageneric relationship of tunas and the mackerel-like fishes. Regan (1909) and Starks (1910) placed all of these fishes in the single family Scombridae. Kishinouye (1915, 1917, 1923) recognized four families: Scombridae, Cybiidae, Katsuwonidae, and Thunnidae, the last two of which he (1917, 1923) recognized as an order Plecostei, separate from the Teleostei, in which he included all other higher bony fishes. Takahashi (1924, 1926) disagreed with the recognition of a distinct order but did not alter the four families. More recently, Fraser-Brunner (1950) placed the tuna-like and mackerel-like fishes back in the Scombridae. Berg (1940, 1955) is one of the few recent taxonomists who followed Kishinouye in placing the tunas in a separate order Thunniformes. For reasons outlined elsewhere (Collette and Gibbs, 1963), we follow Regan, Starks, and Fraser-Brunner in placing all of the tunas and other mackerel-like fishes in the family Scombridae.

It is possible to divide the Scombridae into smaller units. *Gasterochisma* is so different from the other scombrids that it deserves at least subfamily status. Fraser-Brunner (1950) recognized only the subfamilies Gasterochismatinae and Scombrinae. Nakamura (1965) considered *Thunnus* and *Euthynnus* (including *Katsuwonus*) as a third subfamily, Thunninae. In the comparative diagnosis of the genus *Thunnus* which follows, we give suggestions of other possible subdivisions. Until a thorough anatomical study is completed, however, we do not wish to present formally a revised family classification.

THUNNUS SOUTH, 1845

Thynnus Cuvier, 1817: 313 (type-species: *Scomber thynnus* Linnaeus, 1758, by absolute tautonymy; preoccupied by *Thynnus* Fabricius, 1775, a genus of Hymenoptera).

Orcynus Cuvier, 1817: 314 (type-species: *Scomber germo* Lacépède, 1800 [= *Scomber alalunga* Bonnaterre, 1788], by subsequent designation of Jordan,

1888: 180; preoccupied by *Orcynus* Rafinesque, 1815, a substitute for *Scomberoides* Lacépède).

Thunnus S. D. W., 1837 (emendation of *Thynnus* Cuvier, 1817, therefore taking the same type-species: *Scomber thynnus* Linnaeus, 1758; suppression in favor of *Thunnus* South, 1845 requested by Collette and Gibbs, 1964).

Thunnus South, 1845 (emendation of *Thynnus* Cuvier, 1817, therefore taking the same type-species: *Scomber thynnus* Linnaeus, 1758).

Orycnus Cooper, 1863: 77 (substitute name for *Thynnus* Cuvier, 1817, and therefore taking the same type-species: *Scomber thynnus* Linnaeus, 1758; not *Orycnus* of Gill, 1861, a misprint for *Orcynus* Cuvier, 1817).

Albacora Jordan, 1888: 180 (substitute name for *Thynnus* Cuvier, 1817, therefore taking the same type-species: *Scomber thynnus* Linnaeus, 1758).

Germo Jordan, 1888: 180 (substitute name for *Orcynus* Cuvier, 1817, therefore taking the same type-species: *Scomber germo* Lacépède, 1800 [= *Scomber alalunga* Bonnaterre, 1788]).

Parathunnus Kishinouye, 1923: 442 (type-species: *Thynnus mebachi* Kishinouye, 1923 [= *Thynnus obesus* Lowe, 1839], by monotypy).

Neothunnus Kishinouye, 1923: 445 (type-species: *Thynnus macropterus* Temminck and Schlegel, 1844 [= *Scomber albacares* Bonnaterre, 1788] by subsequent designation of Jordan and Hubbs, 1925: 218).

Kishinoella Jordan and Hubbs, 1925: 219 (type-species: *Thynnus rarus* Kishinouye, 1923 [= *Thynnus tonggol* Bleeker, 1851] by original designation).

Semathunnus Fowler, 1933: 163 (type-species: *Semathunnus guildi* Fowler, 1933 [= *Scomber albacares* Bonnaterre, 1788] by original designation).

Comparative Diagnosis

The tunas, genus *Thunnus*, comprise a group of seven closely related species representing the most advanced members of the family Scombridae

(sensu Regan, 1909; Starks, 1910; and Fraser-Brunner, 1950). The subfamily Scombrinae of Fraser-Brunner, which includes all Scombridae except *Gasterochisma*, is divisible into two major groups (Collette and Gibbs, 1963). The more primitive *Scomber, Rastrelliger, Scomberomorus, Grammatorcynus,* and *Acanthocybium* have a posterior notch in the hypural plate and lack a bony lateral keel on the caudal vertebrae. The more advanced group, consisting of *Gymnosarda, Orcynopsis, Sarda, Cybiosarda, Auxis, Euthynnus, Katsuwonus, Allothunnus,* and *Thunnus,* lack a hypural notch and have a bony caudal keel. Within the latter group another category may be recognized as including *Allothunnus, Auxis, Euthynnus, Katsuwonus,* and *Thunnus* (the Plecostei of Kishinouye, 1917, 1923), characterized by the presence of well-developed prootic pits and (except *Allothunnus*) a subcutaneous vascular system. Within this group of higher scombrids, the genus *Thunnus* is characterized by the presence of fronto-parietal foramina, a particularly well-developed subcutaneous vascular system with two long lateral branches on each side, and the body fully covered with scales. *Auxis* and *Allothunnus* lack fronto-parietal foramina. *Auxis, Euthynnus,* and *Katsuwonus* have the body squamation limited to an anterior corselet and do not have the subcutaneous vascular system as well-developed as in *Thunnus;* the lower lateral branch is either short, or, if long as in *K. pelamis,* it meets the upper branch mesial to the ribs.

Validity of Nominal Genera

Cuvier (1817: 312–314) was the first to divide the large Linnaean genus *Scomber.* For the tunas he proposed *Thynnus* for *T. thynnus* and *Orcynus* for *T. alalunga.* Later (in Cuvier and Valenciennes, 1831) he placed his subgenus *Orcynus* in the synonymy of *Thynnus.* Several subsequent workers independently realized that *Thynnus* Cuvier was preoccupied by *Thynnus* Fabricius in insects. Thus Cooper (1863) accepted Gill's (1861) *Orycnus,* a misspelling of *Orcynus,* as a replacement name for *Thynnus* Cuvier (see also Gill, 1889). Jordan (1888) overlooked this action and proposed *Albacora* to replace *Thynnus,* and *Germo* to replace *Orcynus.* Gill (1894) settled matters by showing that South (1845) had previously suggested *Thunnus* to replace *Thynnus* Cuvier. Most subsequent workers have used *Thunnus* South either for *T. thynnus* alone or for several or all of the seven species we refer to *Thunnus.*

Whitley (1955) recently discovered an earlier modification of *Thynnus* Cuvier, namely *Thinnus* S.D.W., 1837. S.D.W. (perhaps S. D. Wood, according to Whitley) emended a number of names by changing y to i, ph to f, ... As far as we can determine, only Abe (1955) followed Whitley in the usage of *Thinnus* S. D. W. In order to stabilize the consistent usage of *Thunnus* South from about 1890 to the present, we have applied to the International Commission of Zoological Nomenclature to suppress *Thinnus* S. D. W. (Collette and Gibbs, 1964).

Other nominal genera have been proposed, based on anatomical data. Kishinouye (1923) described two additional genera: *Parathunnus* based on *T. obesus* (as *mebachi*) and *Neothunnus* which included *albacares* (as *macropterus*) and *tonggol* (as *rarus*). He based this division on anatomical characters such as liver striations, the level at which the subcutaneous blood vessels pass through the myomere, and presence or absence of the postcardinal vein. Jordan and Hubbs (1925) then proposed *Kishinoella* for *T. tonggol* (as *rarus*), the only tuna that generally lacks a swim bladder. We have summarized these differences and others that have been used to distinguish genera or subgenera (table 4). A large number of different arrangements can be made depending on which characters one wishes to emphasize as "basic." *Thunnus* can be divided into two groups using the area of origin of the cutaneous artery, the level at which it passes between the ribs, and the intermuscular bones between which it divides: *T. alalunga, T. maccoyii,* and *T. thynnus* in one and *T. obesus, T. albacares, T. tonggol,* and *T. atlanticus* in the other. On the basis of number of arteriolar rows, *T. thynnus, T. maccoyii,* and *T. obesus* stand out from the other species. The presence of liver striations and vascular cones and the length of the liver lobes place *T. alalunga, T. maccoyii, T. thynnus,* and *T. obesus* in one group, the remaining three species in another. The absence of a swimbladder distinguishes *T. tonggol* from the other species, but the swimbladder may be rudimentary in *T. maccoyii,* and a swimbladder has been observed in small *T. tonggol. T. atlanticus* is unique in *Thunnus* in having 19 instead of 18 precaudal vertebrae. *T. atlanticus* and *T. tonggol* fall together on the basis of their low number of gill rakers, and *T. thynnus* stands out with the highest number in the genus. *T. alalunga* is unique in the position of spleen and stomach, in the shape of the first ventrally directed parapophysis,

TABLE 4.—*Comparison of diagnostic characters of the species of* Thunnus

Character	T. alalunga	T. thynnus	T. maccoyii	T. obesus	T. albacares	T. atlanticus	T. tonggol
Cutaneous artery orginates at vertebra number	3-4	3-4	3-4	6-8	6-8	6-8	6-8
Cutaneous artery passes between ribs number	3-4	3-4	3-4, 2-3	5-6	5-6	5-6	5-6
Cutaneous artery divides between intermuscular bones number	4-5	4-5	4-5, 3-4	6-7	6-7	6-7	6-7
Number of arteriolar rows from cutaneous artery	1	2	2	2	1	1	1
Post-cardinal vein	absent	absent	absent	present	present	present	present
Liver striations and vascular cones	present	present	present	present	absent	absent	absent
Liver lobes	subequal	subequal	subequal	subequal	right long	right long	right long
Swimbladder	present	present	present	present	present	present	absent or rudimentary
Spleen position	right	left	left	left	left	left	left
First haemal arch on vertebra number	10	10(11)	10	11(10)	11(10, 12)	11(10)	11(12)
First ventrally directed parapophysis on vertebra	9	8	9	9	9	9	10
Anterior haemal prezygapophysis position	on centrum	near centrum	near centrum	near centrum	well ventrad	well ventrad	well ventrad
Anterior haemal postzygapophysis length	short	short	short	short	long	long	long
Ventrolateral foramina size	small	small	small	small	large	large	large
Number of precaudal vertebrae	18	18	18	18	18	19	18
Posterior parasphenoid margin	angulate	angulate	angulate	angulate	non-angulate	non-angulate	non-angulate
Pectoral length	long	short	short	long to medium	medium	medium	medium to short
Gill raker number	25-31	34-43	31-40	23-31	26-34	19-25	19-28

and in the flattened haemal spine of its first caudal vertebra.

Not only is the subdivision of *Thunnus* into genera or subgenera an arbitrary matter, but such subdivision obscures the close relationship among the species. In this concept we agree with such workers as Rivas (1951, but not 1961), de Sylva (1955), and Iwai, Nakamura, and Matsubara (1965). *Thunnus* can be divided into as many as six groups, but these are essentially species, not subgenera or genera (table 4). However, based on the 18 characters in table 4 (excluding pectoral fin length), there do appear to be two groups of species. *T. alalunga*, *T. thynnus*, and *T. maccoyii* are similar to each other in 14-16 characters; *T. albacares*, *T. atlanticus*, and *T. tonggol* are similar to each other in 15-16 characters; and *T. obesus* is in between the two groups, sharing 12 characters with *T. maccoyii* and 10 with *T. albacares*. This agrees with the intra-generic relationships presented by Iwai et al. (1965) and Nakamura (1965). It disagrees with Watson's (1964) groups where she placed *T. obesus* in the first group. *T. obesus* is similar to the first group in several liver and vertebral characters but fits with the second group in position of the cutaneous artery, presence of the post-cardinal vein, and position of the first haemal arch.

The synonymy of each species includes all the combinations of names we have found, together with selected references containing information on anatomy, morphometry, and distribution. Readers wishing more references should consult tuna bibliographies such as Corwin (1930), Shimada (1951), and

volume 4 of the "Proceedings of the World Scinetific Meeting on the Biology of the Tunas and Related Species" (Bernabei, 1964).

THUNNUS ALALUNGA (Bonnaterre, 1788) ALBACORE

Scomber pinnis pectoralibus longissimis Cetti, 1777: 191-193 (Sardinia, *alalunga* in vernacular).

Scomber alalunga Bonnaterre, 1788: 139 (original description based on Cetti). Walbaum, 1792: 222. Risso, 1810: 169-170.

Scomber alalunga Gmelin, 1789: 1330 (original description based on Cetti; "*alatunga*" a misprint for "*alalunga*"; date of publication according to Cat. Books British Mus. is 1789, not 1788). Lacépède, 1800: 599 and 1802: 21-22.

Scomber germo Lacépède, 1800: 598 (original description in table of species of *Scomber;* misspelled *S. germon*). Lacépède, 1802: 1-8 (description: S. Pacific Ocean, 17° S., 103° W.; based on Commerson's manuscript).

Orcynus germon, Cuvier, 1817: 314.

Orcynus alalonga, Risso, 1826: 419-420 (Mediterranean).

Thynnus alalonga, Cuvier *in* Cuvier and Valenciennes, 1831: 87-95 (Atlantic), fig. 215. Lowe, 1839: 78 and 1849: 2 (Madeira). Günther, 1860: 366. Cunningham, 1910: 109-110 (synonymy, description; St. Helena), fig. 3.

Thynnus pacificus Cuvier *in* Cuvier and Valenciennes, 1831: 96-97 (substitute name for *Scomber germo* Lacépède, 1800).

Thunnus alalonga, South, 1845: 622.

Thunnus pacificus, South, 1845: 622.

Orcynus pacificus (not of Cuvier) Cooper, 1863: 75–77 (original description; California), fig. 19.

Orcynus germo, Lütken, 1880: 468–472, 596 (synonymy in part), pl. 3, figs. 1–2 (young). Kitahara, 1897: 2 (description; Japan), pl. 2, fig. 3.

Germo alalonga, Jordan, 1888: 180. Barnard, 1927: 799 (S. Africa). Morice, 1953: 68–69, fig. 3 (description of liver; E. Atlantic).

Albacora alalonga, Dresslar and Fesler, 1889: 438–439 (synonymy in part), pl. 6.

Germo alalunga, Jordan and Evermann, 1896: 871 (description; synonymy in part; Atlantic and Pacific). Jordan and Jordan, 1922: 33 (Hawaii). Meek and Hildebrand, 1923: 316–317 (description; synonymy in part). Jordan and Evermann, 1926: 15 (Atlantic). Buen, 1930: 48 (synonymy in part), fig. 6. Jordan, Evermann, and Clark, 1930: 260 (synonymy in part). Fowler, 1936: 621–623 (synonymy in part; description), fig. 280. Walford, 1937: 14–17 (description; a single world-wide species of albacore), color pl. 35. Fowler, 1944: 498 (W. of Chile). Tinker, 1944: 158–159 (Hawaii), pl. 1, fig. 6. Brock, 1949: 267 (in key to Hawaiian tunas). Le Gall, 1949 (synonymy, description, biology). Smith, 1949, 1953: 299 (S. Africa), pl. 66, fig. 835. Fernandez-Yepez and Santaella, 1956: 12, fig. 3, pls. 1, 5, (Venezuela). Tucker, 1955 (British Seas). Otsu, 1960 (migration, growth; N. Pacific). Frade and Vilela, 1962: 17–59 (morphology, biology; E. Atlantic). Postel, 1963 (description, biology; E. Atlantic).

Thynnus alalunga, Clarke, 1900 (Scotland).

Germo germon, Fowler, 1905: 761–763 (Sumatra).

Germo germo, Jordan and Seale, 1906: 228 (Samoa). Jordan and Hubbs, 1925: 217 (Japan). Jordan and Evermann, 1926: 16 (Pacific), pl. 3, fig. 1. Jordan et al., 1930: 260 (synonymy).

Thunnus alalunga, Jordan, Tanaka, and Snyder, 1913: 120 (Japan). Kishinouye, 1915: 18 (description; Japan). Fraser-Brunner, 1950: 142 (key to *Thunnus*), 143 (synonymy in part; distribution), fig. 5. Rivas, 1951: 222–223 (synonymy, description; Atlantic). de Sylva, 1955: 33 (relationships, osteology), fig. 56 (neurocranium). Bullis and Mather, 1956 (counts, measurements; key to Caribbean *Thunnus*), fig. 3. Kurogane and Hiyama, 1957b (morphometry; NW. Pacific). Gosline and Brock, 1960: 259–260 (description; Hawaii), 336–337 (synonymy), fig. 257i. Mather and

Gibbs, 1957: 242–243 (39° 45′ N., 73° 00′ W.). Jones and Silas, 1960: 382–383 (Indian Ocean), fig. 9. Talbot and Penrith, 1962: 558 (S. Africa). Jones and Silas, 1963: 1790–1791 (Indian Ocean). Rodrigues Lima and Wise, 1963 (distribution; W. tropical Atlantic). Squire, 1963 (distribution; NW. Atlantic). Talbot and Penrith, 1963: 609–616 (description, biology; S. Africa). Iwai and Nakamura, 1964: 6, fig. 3a (olfactory rosettes). Williams, 1964: 121 (E. Africa). Iwai et al., 1965: 3–5 (synonymy), 28–30 (description), figs. 13, 14, 15. Nakamura, 1965: 13–17, figs. 1, 2, 3A, 4, 5A (osteology). Merritt and Thorp, 1966: 377 (E. Africa). Nakamura and Kikawa, 1966 (infracentral grooves).

Thunnus germo, Kishinouye, 1923: 434 (anatomy; Japan), figs. 20, 46, 52. Serventy, 1941: 23–24 (Australia), pl. 2. Godsil and Byers, 1944: 70–87 (anatomy; comparison of Pacific specimens), figs. 36–47. Godsil, 1948 (morphometric comparison of Japanese, Hawaiian, and American specimens). Alverson, 1961 (distribution; NE. Pacific). Clemens, 1961 (migration, age, growth; N. Pacific). Clemens, 1963 (migration; N. Pacific). Yoshida and Otsu, 1963 (biology; Pacific and Indian oceans). Otsu and Uchida, 1963 (migration; Pacific). Jones and Silas, 1964: 34–36 (Indian Ocean).

Germo germon steadi Whitley, 1933: 81–83 (original description; New South Wales), pl. 11, fig. 1.

Thunnus germon, Tortonese, 1939: 324–325 (W. coast S. America).

Thunnus alalunga germo, Munro, 1958: 111 (Australia).

Types of Nominal Species

Scomber alalunga Bonnaterre, 1788. No type specimens. Original description based on Cetti, 1777 (*Scomber pinnis pectoralibus longissimus*).

Scomber alatunga Gmelin, 1789. No type specimens. Original description based on Cetti, 1777. Specific name, published as *alatunga*, a misprint.

Scomber germo Lacépède, 1800. No type specimens. Original description based on manuscript by Commerson. Specific name spelled *germon* in table of species of *Scomber* (1800), spelled *germo* in description (1802).

Thynnus pacificus Cuvier, *in* Cuvier and Valenciennes, 1831. No type specimens. Original description based on Lacépède's *Scomber germo* (1800) and on Commerson's manuscript. The specimen,

MNHN A. 6862, considered as the holotype by Bauchot and Blanc (1961, p. 377) and Blanc and Bauchot (1964, p. 456) is, therefore, not a type (Collette, 1966).

Orcynus pacificus Cooper, 1863. No type specimen, although mention is made of "State collection, species 1033."

Germo germon steadi Whitley, 1933. Holotype Australian Museum, Sydney, IA 2457, New South Wales, a misshapen skin, 960 mm. FL, preserved in formalin with most of the fins broken. Pectoral fin about 45 percent of fork length. Figured by Whitley (1933, pl. xi, fig. 1).

Characters

Pectoral fin very long, usually reaching nearly or quite to second dorsal finlet, usually 31 percent of fork length or longer (similar to *T. obesus*). Body depth greatest near dorsal and anal origins. A narrow white posterior margin on caudal fin. Anal finlets silvery or dusky.

Gill rakers 25-31 (similar to *T. obesus* and *T. albacares*).

Liver with striations on ventral surface, its three lobes subequal in length, vascular cones present on its dorsal side (as in *T. thynnus*, *T. maccoyii*, and *T. obesus*). Spleen located on left side, stomach on right. Straight intestine short, the first loop located at about half to two-thirds the distance between middle liver lobe and anus. Gall bladder exposed in ventral view along right side of straight intestine. Connective tissue on dorsal wall of body cavity much thickened posteriorly. Kidney short, without posterior "tail," reaching level of vertebrae 7-9.

Cutaneous arteries usually originating at level of vertebra 3-4, passing laterally between ribs 3 and 4, and branching between intermuscular bones 4 and 5 (as in *T. thynnus* and *T. maccoyii*); no posterior commissure. A single row of arterioles and venules arising from each main lateral cutaneous branch (as in *T. albacares*, *T. tonggol*, and *T. atlanticus*) but from vertebral side of vessels. Post-cardinal vein absent (as in *T. thynnus* and *T. maccoyii*).

Posterior parasphenoid margin forming an acute angle (not as extreme as in large *T. thynnus* but more acute than in large *T. obesus*). Supraoccipital crest relatively slender and long, reaching at least to centrum of vertebra 3.

Anterior articulating (sphenotic) head of hyomandibula relatively long and narrow, proportion of length to least width 1.7-2.7. Metapterygoid rela-

tively narrow, proportion of length of anteroventral margin to posteroventral margin 1.1-1.8. Quadrate relatively narrow, proportion of length to width of horizontal dorsal edge 2.1-2.7.

Vertebrae 18+21 (as in all *Thunnus* except *T. atlanticus*). First ventrally directed parapophysis on vertebra 9 (as in all except *T. thynnus* and *T. tonggol*), appearing twisted and not extending strongly ventrad. First closed haemal arch on vertebra 10 (as in *T. thynnus*, *T. maccoyii*, and occasionally in other species), forming an angle of 45 degrees or less with the vertebral axis. All haemal prezygapophyses arising from centra, not from haemal arches. All haemal postzygapophyses less than one-fourth centrum length. Anteriormost ventrolateral foramina small, their width not greater than basal width of haemal spine. Least height of centrum of 36th vertebra 1.1-1.7, usually 1.4-1.6, in centrum length (similar to *T. albacares*), centrum commonly tapering, with least depth at anterior end (in the other species the vertebra is of nearly equal height throughout). Haemal spine of first caudal vertebra flattened, wing-like.

Nominal Species

Although no one seems to have reported any important differences between Atlantic and Pacific populations of *T. alalunga*, at least since Jordan and Evermann (1926), many recent authors still refer to the Pacific populations as *T. germo*. Even Jordan and Evermann (1926) admitted that the slight differences they noted in body proportions and coloration would probably not be valid when more specimens were examined. Our data on *T. alalunga* confirm the view that the Atlantic and Pacific populations belong to the same species. Godsil (1948) and Kurogane and Hiyama (1958a, 1959) found slight population differences within the Pacific, but intermingling of a significant portion of the eastern and western Pacific populations of *T. alalunga* was indicated by tag returns reported by Ganssle and Clemens (1953) and Blunt (1954), and demonstrated by more recent works, including those of Otsu (1960), McGray, Graham, and Otsu (1961), Clemens (1961, 1963) and Otsu and Uchida (1963).

Range

In the western Atlantic, *T. alalunga* is known from south of New England to southern Brazil. Squire (1963) presented seven records north of 40° N., the most northerly 42°18' N., 64°02' W. Le Danois

(1951) reported the species off the coast of Venezuela. Rodrigues Lima and Wise (1963) reported catches from 10° N. to 32° S. off the coast of Brazil, with a concentration near 15° S. There are no records for the Gulf of Mexico. In the eastern Atlantic, it has been found from the Orkney Islands north of Scotland (Clarke, 1900; Tucker, 1955), south to Angola off west African coast (Vilela and Monteiro, 1959) and in the Mediterranean Sea. The range may extend south to South Africa, because Talbot and Penrith (1962, 1963) have found a continuous distribution around South Africa. On the other hand, the South African population may be of Indian Ocean origin.

The distribution in the Indian and Pacific oceans was mapped by Yoshida and Otsu (1963) and by Suda, Koto, and Kume (1963). *T. alalunga* is found across the Indian Ocean from East Africa to Australia between about 10° N. and 30° S. Its range in the western Pacific extends from about 45° N., off the coast of Hokkaido, south to 40° S., off the southern tip of Australia. Longline fishing has indicated a fairly continuous distribution between 30° N. and 20° S., eastward past the Hawaiian Islands. In the eastern Pacific, it is known from about 50° N., off Vancouver Island, British Columbia (Cowan, 1938; Samson, 1940), south to about 42° S. (Japan Fishery Agency, 1964, 1965).

THUNNUS ALBACARES (Bonnaterre, 1788)
YELLOWFIN TUNA

Albacores or *Thynni* Sloane, 1707: 11 (description; Madeira), fig. 1.

Scomber albacares Bonnaterre, 1788: 140 (original description based on drawing by Sloane).

Scomber albacorus Lacépède, 1800: 599 and 1802: 48–49 (substitute name for *Scomber albacares* Bonnaterre, 1788).

Thynnus argentivittatus Cuvier *in* Cuvier and Valenciennes, 1831: 97–98 (original description; Atlantic and Pacific). Günther, 1860: 366.

Scomber Sloanei Cuvier *in* Cuvier and Valenciennes, 1831: 148 (original description based on Sloane).

Thynnus albacora Lowe, 1839: 77–78 (original description; Madeira) and 1849: 2 (repeat of original description). Günther, 1860: 365. Cunningham, 1910: 110–112 (synonymy, description; St. Helena), fig. 4.

Thynnus macropterus Temminck and Schlegel, 1844: 98–99 (original description; Japan), pl. 51.

Kishinouye, 1915: 19 (description, anatomy; Japan), pl. 1, fig. 12.

Thunnus argentivittatus, South, 1845: 622. Rivas, 1951: 221–222 (synonymy).

Orcynus subulatus Poey, 1875: 145–146 (original description; Cuba), pl. 3, fig. 4 (head), fig. 5 (scale).

Orcynus albacora, Poey, 1875: 145.

Orcynus macropterus, Kitahara, 1897: 2 (description; Japan), pl. 2, fig. 3.

Germo macropterus, Jordan and Snyder, 1901: 64 (Nagasaki). Jordan and Seale, 1906: 228 (Samoa). Jordan and Jordan, 1922: 32–33 (Hawaii).

Thunnus macropterus, Jordan et al., 1913: 121 (Japan). Kishinouye, 1915 (description, anatomy; Japan). de Beaufort, 1951: 223–225 (synonymy, description), fig. 39. Ginsburg, 1953: 8–10 (restriction of name *macropterus* to W. Pacific yellowfin).

Thunnus allisoni Mowbray, 1920: 9–10 (original description; Miami, Fla.), figure (unnumbered).

Germo argentivittatus, Nichols and Murphy, 1922: 507 (Peru).

Germo allisoni, Nichols, 1923: 3 (Christmas Island).

Neothunnus macropterus, Kishinouye, 1923: 446–448 (anatomy; Japan; placed in new genus *Neothunnus*), figs. 13, 19, 23, 45, 51. Jordan and Hubbs, 1925: 219 (Japan). Jordan and Evermann, 1926: 20–21 (description), pl. 5. Herre, 1936: 106–107 (synonymy; Galapagos, Philippines, Japan; no species differences between long- and short-finned yellowfin). Walford, 1937: 3–7 (description; Pacific Allison tuna merely old yellowfin), color pl. 33. Serventy, 1941: 25–26 (description; Australia), pl. 2. Godsil and Byers, 1944: 46–69 (anatomy; comparison of Pacific specimens), figs. 20–35, 70–76. Tinker, 1944: 159–160 (Hawaii), pl. 1, fig. 5. Godsil, 1948 (morphometry; Japan, Hawaii, E. Pacific). Schaefer, 1948 (morphometry; Pacific Costa Rica). Brock, 1949: 276 (key to Hawaiian tunas). Schaefer and Walford, 1950 (comparison of yellowfin from Angola and Pacific coast of Central America). Godsil and Greenhood, 1951 (comparison of E. and central Pacific specimens). Schaefer, 1952 (comparison of Hawaiian and W. Pacific specimens). Royce, 1953 (morphometry; Pacific; an east-west cline across the Pacific in some characters). Tsuruta, 1954 (morphometry; SW. Pacific). Schaefer, 1955 (comparisons of specimens from SE. Polynesia,

Central America, and Hawaii). Tsuruta, 1955 (morphometry; southwest Great Sunda Island; yellowfins probably a single worldwide species with many sub-populations). Kurogane and Hiyama, 1957a (morphometry; equatorial Pacific). Kurogane and Hiyama, 1958b (morphometry; Indian Ocean). Munro, 1958: 111 (Australia). Nakagome, 1958 (morphometry; Indian Ocean). Broadhead, 1959 (morphometry; E. tropical Pacific). Klawe, 1959 (reidentification of juvenile called *T. thynnus* by Fowler, 1944). Gosline and Brock, 1960: 260–261 (description; Hawaii), 337 (synonymy), fig. 257j. Jones and Silas, 1960: 385–386 (Laccadive Sea, Gulf of Mannar, Ratnagiri), fig. 12. Legand, 1960 (measurements, counts; New Caledonia; east-west cline in gill rakers across Pacific). Tsuruta and Tsunoda, 1960 (morphometry; Indian Ocean). Talbot and Penrith, 1962: 558 (S. Africa). Mimura et al., 1963a (biology; Indian Ocean). Talbot and Penrith, 1963: 617–623 (description, biology; S. Africa).

Thunnus subulatus, Jordan and Evermann, 1926: 11–12 (repeat of Poey's original description). Jordan et al., 1930: 260. Ginsburg, 1953: 6–8 (synonymy, description; the name *subulatus* used for W. Atlantic yellowfin). Fernandez-Yepez and Santaella, 1956: 6 (Venezuela; in key as a species of bluefin).

Neothunnus catalinae Jordan and Evermann, 1926: 19 (original description; Santa Barbara Islands, S. California), pl. 4. Jordan et al., 1930: 260. Nichols and La Monte, 1941: 31, fig. 1.

Neothunnus albacora, Jordan and Evermann, 1926: 21–22. Frade, 1929: 235–241 (morphometry, swimbladder; Canary Islands), pl. 5, fig. 2. Buen, 1930: 49–50, fig. 8. Bini, 1931: 31–36 (morphometry; Canary Islands), figs. 12, 13. Frade, 1931a: 123–126 (synonymy, morphometry; E. Atlantic). Nichols and La Monte, 1941: 30 (synonymy in part), fig. 2. Barnard, 1948: 378–380 (S. Africa), pl. 11. Bellón and Bardán de Bellón, 1949 (morphometry; Canary Islands). Morice, 1953: 71–73, fig. 5 (liver; E. Atlantic). Postel, 1955 (biology, morphometry; E. Atlantic). Fernandez-Yepez and Santaella, 1956: 15 (in key to Atlantic tunas). Marchal, 1959 (morphometry; E. Atlantic). Vilela and Monteiro, 1959: 30–53 (morphometry; Angola). Tsuruta, 1961 (morphometry; SW. Indian Ocean). Vilela and Frade, 1963 (biology; E. Atlantic).

Neothunnus itosibi Jordan and Evermann, 1926:

22–23 (original description; Hawaii), pl. 6. Smith, 1935: 207–209 (S. Africa), fig. 4. Phillips, 1932: 231 (New Zealand). Powell, 1937: 80–81 (New Zealand), pl. 17, figs. 2, 3. Jones and Silas, 1960: 387–388 (Madras; recognized as distinct from *N. macropterus*), fig. 13.

Neothunnus albacores, Jordan and Evermann, 1926: 23–24 (description). Jordan et al. 1930: 260. Fernandez-Yepez and Santaella, 1956: 17–18 (Venezuela), fig. 6, pl. 8.

Neothunnus allisoni, Jordan and Evermann, 1926: 24 (description). Jordan et al., 1930: 260. Nichols and La Monte, 1941: 30–31 (synonymy), fig. 3. Fernandez-Yepez and Santaella, 1956: 16 (Venezuela), fig. 5, pl. 7.

Kishinoella zacalles Jordan and Evermann, 1926: 27 (original description, Honolulu fish market), pl. 7.

Semathunnus guildi Fowler, 1933: 163–164 (original description; Tahiti), pl. 12.

Semathunnus itosibi, Fowler, 1933: 164. Tinker, 1944: 160 (Hawaii).

Neothunnus argentivittatus, Beebe and Tee-Van, 1936: 184–192 (synonymy, description; West Indies), fig. 5 (copy of fig. in Cunningham), figs. 6–12 (photographs), fig. 13 (copy of fig. in Sloane). Fowler, 1944: 498 (Mexico, Ecuador, Peru).

Germo albacora, Fowler, 1936: 623-624 (synonymy, description), fig. 282. Smith, 1949, 1953: 299 (S. Africa), pl. 66, fig. 835.

Thunnus albacora, Tortonese, 1939: 326 (off Brazil). Fraser-Brunner, 1950: 142 (key to *Thunnus*), 144–145 (synonymy), fig. 7. Morrow, 1954: 16 (29 E. African specimens similar to Pacific specimens).

Germo itosibi, Smith, 1949, 1953: 299 (S. Africa), pl. 65, fig. 834.

Neothunnus albacora brevipinna Bellón and Bardán de Bellón, 1949: 12–19 (original description; as *Neothunnus albacora* forma *brevipinna;* Canary Islands).

Neothunnus albacora longipinna Bellón and Bardán de Bellón, 1949: 12–19 (new name for long-finned *T. albacares* of East Atlantic; as *Neothunnus albacora* forma *longipinna;* Canary Islands).

Neothunnus macropterus macropterus, Bellón and Bardán de Bellón, 1949: 15 (Pacific short-finned form; as *Neothunnus macropterus* forma *macropterus*).

Neothunnus macropterus itosibi, Bellón and Bardán de Bellón, 1949: 15 (Pacific long-finned form; as *Neothunnus macropterus* forma *itosibi*).

Neothunnus brevipinna, Postel, 1950: 67–74 (description, biology; considered a good species distinct from *N. albacora*).

Thunnus zacalles, Fraser-Brunner, 1950: 142 (key to *Thunnus*), 146, fig. 9.

Thunnus albacares, Ginsburg, 1953: 3–6 (synonymy, description; the name *albacares* restricted to the E. Atlantic yellowfin). de Sylva, 1955: 33–40 (osteology, relationships), fig. 58 (neurocranium). Bullis and Mather, 1956 (counts, measurements, key to Caribbean *Thunnus*), fig. 2. Mather and Gibbs, 1957:242 (off New England). Rivas, 1961: 136–139 (synonymy, range). Schaefer, Broadhead, and Orange, 1963 (biology; Pacific). Squire, 1963 (distribution; NW. Atlantic). Iwai and Nakamura, 1964: 6, figs. 3G, H (olfactory rosettes). Tsuruta, 1964: 59–66 (morphometry; Pacific and Indian oceans). Williams, 1964: 115–120 (E. Africa). Iwai et al., 1965: 11–15 (synonymy), 36–38 (description), figs. 20, 21. Nakamura, 1965: 20–22, figs. 3E, 9B, 10 (osteology). Royce, 1965 (morphometry). Merritt and Thorp, 1966: 375–376 (E. Africa). Nakamura and Kikawa, 1966 (infracentral grooves).

Thunnus catalinae, Ginsburg, 1953: 8 (name used for E. Pacific yellowfin).

Neothunnus albacares, Mather, 1954: 292 (SE. of New York). Mather and Day, 1954: 184–185 (N. Brazil and W. Africa).

Thunnus albacores, Le Danois, 1954: 283–287 (history of nomenclature), 285–286 (partial synonymy), 288–294 (biology; Pacific yellowfin recognized as *Thunnus albacores* variety *argentivittatus*).

Neothunnus albacora macropterus, Schultz, 1960: 414–415 (description of Bikini and Marianas specimens), pl. 122 A.

Thunnus albacares macropterus, Jones and Silas, 1963: 1793–1794 and 1964: 40–42 (Indian Ocean).

Thunnus itosibi, Jones and Silas, 1963: 1794–1795 and 1964: 42–43 (Indian Ocean).

Types of Nominal Species

Scomber albacares Bonnaterre, 1788. No type specimens. Original description based on Sloane (1707, pp. 11–12; table 1, fig. 1).

. *Scomber albacorus* Lacépède, 1800. Substitute name for *Scomber albacares* Bonnaterre, 1788.

Thynnus argentivittatus Cuvier *in* Cuvier and Valenciennes, 1831. Syntypes MNHN A.5567 (a stuffed whole skin; collected in the Atlantic Ocean by Quoy and Gaimard) and A.5572 (a half skin, with glass eye, mounted on a board; sent by Dussumier from the Indian Ocean). A third specimen, A.5814, designated by Schaefer and Walford (1950) as lectotype, is not a syntype because it was not mentioned by Cuvier in the original description (cf. Bauchot and Blanc, 1961, p. 376; Blanc and Bauchot, 1964, p. 454). We have examined both syntypes and cannot be certain what species they represent (see discussion under Nominal Species).

Scomber sloanei Cuvier *in* Cuvier and Valenciennes, 1831. No type specimens. Original description clearly based on Sloane (1707), plate 1, fig. 1, but also referring to page 28, where Sloane refers to a different fish (*Scombrus major torosus*). Cuvier stated that *Scomber albacorus* Lacépède, 1800, is not the same as *Scomber sloanei*, because Lacépède's description refers to page 11 of Sloane. This, however, is the description of the fish, from the illustration of which Cuvier drew his description.

Thynnus albacora Lowe, 1839. No type specimens.

Thynnus macropterus Temminck and Schlegel, 1844. Original description clearly based on the specimen figured in plate 51, and not on the specimen in the Rijksmuseum van Natuurlijke Historie, Leiden, number 2552, considered by Boeseman (1947, 1964) as the holotype. In particular, Temminck and Schlegel refer to the long second dorsal and anal fins, which the presumed holotype (fork length 670 mm. as measured by Gibbs in 1962) is too small to have developed.

We believe that this specimen should not have been considered as holotype of this species. The specimen (a stuffed skin) is not a yellowfin tuna at all, but is *T. tonggol*. The pectoral fin is 22 percent of fork length and the snout to second dorsal distance is 50.7 percent, both characteristic of *T. tonggol*.

Since we do not believe this specimen was used in the original description and, therefore, is not a type, we are saved the necessity of having to consider the name *tonggol* Bleeker, 1851 as a junior synonym of *macropterus*, which has been used more often than has any other name for Pacific yellowfin tuna.

Orcynus subulatus Poey, 1875. No type specimens known to us. Original description from an 1,800-mm. specimen, of which the head is figured and might have been saved.

Thunnus allisoni Mowbray, 1920. No type specimen known to us. Original description from three specimens: one taken by spearing in Biscayne Bay, Miami, Fla. for which counts, proportions of body parts, and color are given, but the length noted as a

little larger than the second specimen; a second specimen, 5 feet 9 inches long (1,753 mm.), "taken in the Gulf Stream," but "badly torn by sharks"; and a third specimen weighing 135 pounds (61 kg.).

Neothunnus catalinae Jordan and Evermann, 1926. Type originally designated as "No. 597, Mus. Calif. Acad. Sci., a photograph of a fish taken off Santa Catalina Island, California," weight 157½ pounds (71 kg.). This photograph was published earlier as *Germo macropterus* by Jordan and Starks (1907: 69). The fish appears to be a mounted specimen.

Neothunnus itosibi Jordan and Evermann, 1926. Type originally designated as "No. 598, Mus. Calif. Acad. Sci., a photograph . . . of a specimen weighing 321 pounds in Honolulu market." The specimen is no longer extant.

Kishinoella zacalles Jordan and Evermann, 1926. Type originally designated as "No. 599, Mus. Calif. Acad. Sci., a photograph of a specimen examined in the Honolulu market . . ., 2¼ feet long, . . . weighing 14 pounds." The characters given in the key to species (p. 26) are based on the specimen photographed; the text description is based on another specimen. Jordan and Evermann described *zacalles* as lacking a swimbladder, and they and subsequent workers (Serventy, 1942; Fraser-Brunner, 1950) have placed it close to *T. tonggol*. Jordan and Evermann, however, gave for their *zacalles* a gill-raker count of 30, which is completely outside the known range for *T. tonggol* (19–28, Table 2). It is our experience that the swimbladder may be quite difficult to find in some specimens of most species of *Thunnus*, and we believe that Jordan and Evermann probably overlooked it in their specimens of *zacalles*. They can not have been describing *T. thynnus*, as this species has more gill rakers and a much shorter pectoral fin than they show in their photograph of *zacalles*. Of the three remaining Pacific species, *T. alalunga* may be quickly eliminated because it has a much longer pectoral fin and an entirely different coloration. *T. obesus* has a much larger eye than that shown for *zacalles*, and the swimbladder is well developed in all specimens that we observed. The description of *Kishinoella zacalles* fits *T. albacares* in number of gill rakers (mean for Pacific *T. albacares* 30.2, table 2), length of pectoral fin, coloration, and general body proportions. Also, Jordan and Evermann, in their original description, reported about a dozen specimens of *zacalles*, all from Hawaii, and no specimen of it (or of *T. tonggol*) has since been reported from there. In view of the great

fishery and research program on tunas in the Pacific, it seems highly unlikely that a valid species has been overlooked.

Neothunnus albacora brevipinna Bellón and Bardán de Bellón, 1949. No type specimens. Original description based on 11 specimens from the Canary Islands.

Neothunnus albacora longipinna Bellón and Bardán de Bellón, 1949. No type specimens. Presumed to be a new subspecific designation for the typical subspecies of *N. albacora* Lowe (1839).

Semathunnus guildi Fowler, 1933. Holotype ANSP 55982, a dried skin with skull intact, from Tahiti. Fowler stated, "Length 1,830 mm." Our measurement of fork length was about 1,460 mm., of length to end of caudal lobes about 1,680 mm. The specimen is obviously a yellowfin tuna, with high dorsal and anal fins, and the pectoral reaching to the middle of the second dorsal base.

Characters

Pectoral fin intermediate in length, usually reaching beyond second dorsal origin but not beyond end of its base, usually 22–31 percent of fork length (generally similar to *T. atlanticus* and large *T. obesus*). Dorsal and anal fins very long in large specimens, becoming well over 20 percent of fork length.

Gill rakers 26–35 (overlapping with *T. alalunga* and *T. obesus*).

Liver without striations on ventral surface, its right lobe longer and narrower than the others; vascular cones not present on dorsal side (as in *T. atlanticus* and *T. tonggol*). Spleen located on right side, and stomach on left (as in all except *T. alalunga*). Connective tissue on dorsal wall of body cavity thickened at anterior end to form a prominent raised cord. Kidney long, tapering, reaching level of vertebra 12–14, often with accessory masses posterior to main kidney.

Cutaneous artery usually originating at level of vertebra 6–8, passing laterally between ribs 5 and 6, and branching between intermuscular bones 6 and 7 (as in *T. atlanticus* and *T. tonggol*) or 7–8. A single row of arterioles and venules arising from each main lateral cutaneous branch (as in *T. alalunga*, *T. tonggol*, and *T. atlanticus*) but from lateral sides of vessels (as in *T. tonggol* and *T. atlanticus*). Vessels present on each side parallel to dorsal aorta connecting posterior epibranchial to cutaneous artery. Postcardinal vein present, joining right cutaneous vein (as in *T. atlanticus*, *T. tonggol*, and *T. obesus*).

Posterior parasphenoid margin variable in shape, rounded, concave, or somewhat angulate (as in *T. atlanticus* and *T. tonggol*) but never with a pronounced angle.

Vertebrae 18+21 (as in all *Thunnus* except *T. atlanticus*). First ventrally directed parapophysis on vertebra 9 (as in all *Thunnus* except *T. thynnus* and *T. tonggol*). First closed haemal arch usually on vertebra 11 (as in *T. atlanticus*, *T. tonggol*, *T. obesus* and often in *T. thynnus*). Anteriormost haemal prezygapophyses arising far ventrad on haemal arch (as in *T. atlanticus* and *T. tonggol*). Haemal postzygapophyses long (as in *T. atlanticus* and *T. tonggol*), the longest about 75 percent of its centrum length (somewhat shorter than in *T. atlanticus* and *T. tonggol*). Anteriormost ventrolateral foramina large, their width three or more times that of haemal spine (as in *T. atlanticus* and *T. tonggol*). Least height of centrum of 36th vertebra 1.2–1.9, usually 1.3–1.5 in centrum length (resembling *T. alalunga*, but in that species the vertebrae taper, whereas in *T. albacares* they are of nearly equal width throughout).

Nominal Species

More names have been proposed for supposedly different populations and individual variants of *T. albacares* than for all other species in the genus. Jordan and Evermann (1926) took the most extreme position in recognizing seven species: *catalinae*, from the California coast; *macropterus*, from the central and western Pacific; *itosibi*, a long-finned form from Hawaii and Japan; *albacora*, from the eastern Atlantic; *albacores*, from Madeira and the West Indies; *allisoni*, a western Atlantic long-finned form; and *zacalles* from Hawaii (which has heretofore been considered as most closely related to *T. tonggol*, see above). The main characters that they used to separate these forms were the lengths of the second dorsal and anal lobes. Using the same characters, Ginsburg (1953) distinguished an eastern Atlantic *albacares*, a western Atlantic *subulatus*, an eastern Pacific *catalinae*, and a central and western Pacific *macropterus*. It became apparent to us that *T. albacares* is an extremely variable species morphometrically, from our own data and from the many detailed morphometric studies on populations of *T. albacares*, especially in the Pacific, by workers such as Godsil (1948), Schaefer (1948, 1952, 1955), Schaefer and Walford (1950), Godsil and Greenhood

(1951), Royce (1953), Tsuruta (1954, 1955, 1961), Kurogane and Hiyama (1957a, 1958b), Nakagome (1958), Broadhead (1959), Legand (1960), and Frade (1931a, for the eastern Atlantic).

Statistical analysis of morphometric data indicates that many subpopulations of *T. albacares* are differentiated, but certainly not to a species or subspecies level. Royce (1965), in a monumental study of the morphometry of *T. albacares*, showed conclusively that it is a single, locally variable, pantropical species. He found that the differences between eastern Atlantic and eastern Pacific specimens were less than the differences between eastern Pacific and Caroline Islands specimens, and that several characters change clinally from west to east in the equatorial Pacific.

There has been considerable confusion concerning the name *Thynnus argentivittatus* Cuvier. The original description (Cuvier, *in* Cuvier and Valenciennes, 1831: 97–98) was based on two specimens now at the MNHN in Paris: one from the Atlantic, collected by Quoy and Gaimard (MNHN A.5572) and one from the Indian Ocean, sent by Dussumier (MNHN A.5567). Schaefer and Walford (1950) reported that, according to information received from L. Bertin, the description was based on three specimens: the two already mentioned and a third from the Indian Ocean, coast of Malabar, sent by Dussumier (MNHN A.5814; given erroneously as A.5816 by Schaefer and Walford). A.5814, a specimen in alcohol, was designated the lectotype by Schaefer and Walford (1950, p. 441), who thus recognized the Indian Ocean yellowfin as *Neothunnus argentivittatus*, the Pacific form as *N. macropterus*, and the Atlantic form as *N. albacora*. Based on A.5814 being the lectotype, Rivas (1961) used the name *argentivittatus* for an Indian Ocean tuna which he tentatively placed in the subgenus *Parathunnus*, and regarded as different from *Neothunnus albacares*, the yellowfin tuna, which he considered to be a single, pantropical species.

We have examined the supposed lectotype (A.5814) and believe it, and the other specimens in Rivas' (1961) account, actually to be *T. tonggol*. Watson (1964) reached the same conclusion, and suggested that *T. argentivittatus* be synonymized with *T. tonggol*. This action, to begin with, is inappropriate, for *argentivittatus* has priority over *tonggol*. A.5814, however, cannot be considered as the lectotype of *Thynnus argentivittatus*, as it is nowhere men-

tioned by Cuvier in the original description, whereas the two proper syntypes are noted (Bauchot and Blanc, 1961, p. 376; Blanc and Bauchot, 1964, p. 454). The lectotype must be selected from A.5567, a stuffed whole specimen, and A.5572, a dried half specimen mounted on a board. Although both of us examined the two syntypes and independently made counts and measurements, we do not feel that we can make a selection. Even if the appropriate measurements could be considered accurate, which they certainly cannot, they do not indicate that the syntypes are *T. albacares*, but rather leave the possibility that they could be *T. tonggol* or *T. atlanticus*. The distance from snout to second dorsal origin appears to eliminate *T. thynnus*, *T. alalunga*, and *T. obesus* from consideration. We do not believe that these specimens can be definitely identified, unless a new and better character is found.

Range

As Royce (1965) has shown, *T. albacares* is a pantropical species. In the western Atlantic, it is known from about 42° N. (Squire, 1963) south through the Sargasso Sea to the Gulf of Mexico and the Caribbean Sea (Wathne, 1959) and off the coast of South America from about 10° N. to 32° S. (Rodrigues Lima and Wise, 1963). In the eastern Atlantic, it is recorded from the coasts of Spain and Portugal south to Angola (Vilela and Monteiro, 1959; Vilela and Frade, 1963) but not from the Mediterranean Sea. Talbot and Penrith (1962, 1963) have shown that *T. albacares* has a continuous distribution around South Africa, but the origin of these fish is uncertain.

It is abundant in East African waters (Williams, 1964) and is known from 20° N. to 30° S. in the Indian Ocean (Mimura et al., 1963a). In the western Pacific *T. albacares* occurs from 40° N., off the coast of Japan, to 30° S., off the coast of Australia, between the 70° F. September isotherm to the north and 75° F. February isotherm to the south (Schaefer et al., 1963). The distribution extends across the Pacific in a broad belt from about 30° N. to 20° S., between the same isotherms, and as far as 40° S. (Japan Fishery Agency, 1965).

THUNNUS ATLANTICUS (Lesson, 1830)
BLACKFIN TUNA

Thynnus atlanticus Lesson, 1830: 165–166 (original description; Trinidade Is. off Brazil). Günther, 1860: 362 (in footnote as dubious species).

Thynnus coretta Cuvier *in* Cuvier and Valenciennes· 1831: 102–104 (original description; Martinique)· Günther, 1860: 363.

Thynnus balteatus Cuvier *in* Cuvier and Valenciennes, 1831: 136–137 (original description based on Lesson's unpublished drawing).

Thunnus balteatus, South, 1845: 622.

Thunnus coretta, South, 1845: 622 (description). Jordan and Evermann, 1926: 11 (description). Jordan et al., 1930: 260.

Orcynus balteatus, Poey, 1868: 361–362 (Cuba). Poey, 1875: 145 (Cuba).

Parathunnus rosengarteni Fowler, 1934: 354, 356 (original description; Key Largo, Fla.), figs. 3–5.

Parathunnus ambiguus Mowbray, 1935 (original description; Bermuda).

Parathunnus atlanticus, Beebe and Hollister, 1935: 213–214 (Union Is., British West Indies). Beebe and Tee-Van, 1936: 178–184 (synonymy, description; Bermuda and West Indies), figs. 1–4. Fowler, 1944: 102–103 (synonymy, description; W. Caribbean), fig. 149. Schuck and Mather, 1951: 248 (N. Carolina). Mather and Schuck, 1952: 267 (Martha's Vineyard; NW. Caribbean). Mather and Day, 1954: 183–184 (off coasts of Brazil and Bermuda).

Thunnus atlanticus, Rivas, 1951: 219–220 (synonymy, description). de Sylva, 1955 (osteology, relationships, generic status), figs. 1–54, 57 (osteology). Bullis and Mather, 1956 (counts, measurements, key to Caribbean *Thunnus*). Rivas, 1961: 129–131 (synonymy, description). Iwai et al., 1965: 15–16 (synonymy), 38–39 (description), fig. 22. Nakamura, 1965: 23–24, figs. 3F, 9C, 11 (osteology). Nakamura and Kikawa, 1966 (infracentral grooves).

Misidentifications

The specimen reported as *Parathunnus obesus* by Beebe and Tee-Van (1928: 100) from Haiti is *T. atlanticus* as they (Beebe and Tee-Van, 1936: 181) later pointed out. Fernandez-Yepez and Santaella (1956: 19) reported specimens from Venezuela as *Parathunnus obesus*, but these are probably *T. atlanticus* as indicated by Rivas (1961: 130).

The International Game Fish Association (1965) listed the world record *T. atlanticus* as a 44 pound, 8 ounce, specimen from Cape Town, South Africa. This record is obviously in error and has been corrected (1966).

Types of Nominal Species

Thynnus atlanticus Lesson, 1830. No type specimens. Original description based on a specimen 28 inches total length (711 mm.), with a pectoral fin 6 inches long (152 mm.). Subtracting 50 mm., we obtain a fork length of about 660 mm. The pectoral is about 23 percent of fork length; too short for either *T. albacares* or *T. atlanticus* (see fig. 26), but is nearer the latter. Lesson mentioned only two other characters useful in identifying the species: a coppery-red lateral band, and blue-slate colored fins (presumably also finlets). These appear sufficient to associate the name *atlanticus* with the blackfin tuna, and we follow Beebe and Tee-Van (1936) and later authors in doing so.

Scomber coretta Cuvier, 1829. No type specimen. The first use of the name *coretta* for a tuna is usually credited to Cuvier *in* Cuvier and Valenciennes (1831), where he described *Thynnus coretta*. The original description, however, consists of a footnote on page 198 of the second edition of Règne Animal (1829), which refers only to Sloane (1707, vol. 1, plate 1, fig. 3). Sloane's figure is of *"Scomber Major torosus,"* and there is no way of associating it with any known species, but this indication prevents the name from being considered a nomen nudum. *Scomber coretta* Cuvier, 1829 must be regarded as a nomen dubium.

Thynnus coretta Cuvier *in* Cuvier and Valenciennes, 1831. This later use of the name *coretta* is based on a preserved specimen, MNHN A.5380, 263 mm. fork length from Martinique. It is a blackfin tuna with 19+20 vertebrae and a gill-raker count of 6+17 (left) and 7+17 (right).

Thynnus balteatus Cuvier *in* Cuvier and Valenciennes, 1831. No type specimens. Original description based on an unpublished illustration by Lesson of the same specimen from which *Thynnus atlanticus* was described, and, therefore, a synonym of that species.

Parathunnus rosengarteni Fowler, 1934. Holotype ANSP 60174, a stuffed skin 629 mm. fork length. A count of gill rakers was impossible, but our measurements show the pectoral fin to be 25.8 percent of fork length, characteristic of *T. atlanticus.*

Parathunnus ambiguus Mowbray, 1935. No type specimens. Original description based on Bermuda specimens; gill rakers noted as 6+17, swimbladder "simple, broader than long, well forward," finlets dusky with a trace of yellow. These characters

unquestionably refer this nominal species to the synonymy of *T. atlanticus.*

Characters

Pectoral fin intermediate in length (generally similar to *T. albacares* and large *T. obesus*), usually 22–31 percent of fork length. Dorsal and anal finlets in fresh specimens lacking yellow.

Gill rakers 19–25, resembling only *T. tonggol.*

Liver without striations on ventral surface, right lobe long and narrow, no vascular cones on dorsal surface (as in *T. albacares* and *T. tonggol*). Spleen located on right side, and stomach on left (as in all except *T. alalunga*).

Swimbladder either small, oblate, situated far anteriorly, or resembling a poorly developed *T. albacares;* when long, anterior and posterior chambers divided by a membrane.

Cutaneous arteries usually originating at level of vertebra 6–8, passing laterally between ribs 5 and 6, branching between intermuscular bones 6 and 7 (as in *T. albacares, T. tonggol,* and *T. obesus*). A single row of arterioles and venules arises from each main lateral cutaneous branch (as in *T. albacares, T. tonggol,* and *T. alalunga*), but from the lateral side of each vessel (as in *T. albacares* and *T. tonggol*). Post-cardinal vein present, joining right cutaneous vein (as in *T. albacares, T. tonggol,* and *T. obesus*).

Posterior parasphenoid margin rounded, concave, or somewhat angulate (as in *T. albacares* and *T. tonggol*), never with a pronounced angle. Parasphenoid concave in its anterior portion (seen occasionally in small specimens of all other species).

Vertebrae 19+20, with rare exceptions. First ventrally directed parapophysis on vertebra 9 (as in all except *T. tonggol* and *T. thynnus*). First closed haemal arch usually on vertebra 11 (as in all except *T. alalunga* and some *T. thynnus*). Haemal arches narrow, bowing widely, forming a large, ovate canal (as in *T. tonggol*). Anterior haemal prezygapophyses arising far ventrad on haemal arch (as in *T. tonggol* and *T. albacares*). Longest haemal postzygapophyses equal to or longer than centrum (only *T. tonggol* and *T. albacares* approach this). Anteriormost ventrolateral foramina large, more than three times width of haemal spine (as in *T. albacares* and *T. tonggol*).

Nominal species

Beebe and Tee-Van (1936) established the validity of *T. atlanticus* and placed *Thynnus balteatus, Para-*

thunnus rosengarteni, and *P. ambiguus* in its synonymy. *Thynnus coretta,* which was placed in the synonymy of *T. thynnus* by Fraser-Brunner (1950) and Rivas (1951), is also a synonym of *T. atlanticus,* as Rivas (1961) has recently shown. Morice (1953), Frade (1960), and others have mistakenly plac Ted. *atlanticus* in the synonymy of *T. obesus.*

Range

Thunnus atlanticus is known only from the western Atlantic, from off Martha's Vineyard, Mass. (Mather and Schuck, 1952), and Cape Hatteras (Schuck and Mather, 1951), throughout the West Indies (Beebe and Tee-Van, 1936) and the northern Caribbean (Bullis and Mather, 1956), south to Trinidade Island off the coast of Brazil (Lesson, 1830) and off Rio de Janeiro at 22°21′ S., 37°37′ W. (Mather and Day, 1954).

THUNNUS OBESUS (Lowe, 1839)
BIGEYE TUNA

Thynnus obesus Lowe, 1839: 78 (original description; Madeira). Lowe, 1849: 2 (copy of original description). Günther, 1860: 362 (in footnote as dubious species). Cunningham, 1910: 112 (synonymy, description; St. Helena), fig. 5.

Thynnus sibi Temminck and Schlegel, 1844: 97–98 (original description; Japan), pl. 50. Günther, 1860: 362 (in footnote as dubious species).

Orcynus sibi, Kitahara, 1897: 1–2 (description; Japan), pl. 1, fig. 2.

Thynnus sibi, Jordan and Snyder, 1901: 64 (*Germo sibi;* Nagasaki), 125 (supplementary note: the "Shibi" should be a species of *Thynnus, T. sibi*). de Beaufort, 1951: 222–223 (synonymy, description). de Sylva, 1955: 34–40 (osteology, relationships), fig. 59 (neurocranium). Rivas, 1961: 135–136 (synonymy, description; a valid Indo-Pacific species).

Germo sibi, Jordan and Snyder, 1901: 64 (listed; in supplementary note, p. 125 as *Thynnus sibi*). Jordan and Jordan, 1922: 33 (Hawaii).

Thynnus mebachi Kishinouye, 1915: 19 (original description; Japan).

Parathunnus mebachi, Kishinouye, 1923: 442–445 (description, anatomy; placed in the new genus *Parathunnus*), figs. 4, 22, 47, 49. Godsil and Byers, 1944: 104–119 (anatomy; E. Pacific). Mimura et al., 1963b (biology; Indian Ocean).

Parathunnus sibi, Jordan and Hubbs, 1925: 218 (description; Japan). Jordan and Evermann,

1926: 17 (description), pl. 3, fig. 2. Tinker, 1944: 159 (Hawaii). Brock, 1949 (description; Hawaii). Shimada, 1954 (distribution in Pacific). Gosline and Brock, 1960; 261 (description; Hawaii), 337 (synonymy). Alverson and Peterson, 1963 (biology; Pacific).

Parathunnus obesus, Jordan and Evermann, 1926: 17 (description). Frade, 1929: 229–235 (morphometry, swimbladder; Canary Is.), pl. 5, fig. 1. Buen, 1930: 50, (Spain) fig. 9. Bini, 1931: 27–30 (morphometry; Canary Is.). Frade, 1931a (morphometry, swimbladder; E. Atlantic). Beebe and Tee-Van, 1936: 181 (comparison with *T. atlanticus*). Morice, 1953: 70–71, fig. 4 (liver; E. Atlantic.) Frade, 1960: 1–74 (description, distribution, biology, bibliography), pl. 1–7.

Thunnus obesus, Fraser-Brunner, 1950: 142 (key to *Thunnus*), 144 (synonymy, in part), fig. 6. Rivas, 1951: 220 (comparison with *T. atlanticus* and *T. alalunga*). Bullis and Mather, 1956 (counts, morphometry, key to Caribbean species of *Thunnus*), fig. 2. Mather and Gibbs, 1958: 23 (NW. Atlantic). Rivas, 1961: 133–135 (description, synonymy; restricted to Atlantic). Talbot and Penrith, 1961: 240 and 1962: 558 (S. Africa). Talbot and Penrith, 1963: 624–629 (description, biology; S. Africa). Iwai and Nakamura, 1964: 6, fig. 3B (olfactory rosettes). Iwai et al., 1965: 9–11 (synonymy), 34–36 (description), fig. 19. Nakamura, 1965: 18–19, figs. 3D, 8, 9A (osteology). Merritt and Thorp, 1966: 376–377 (E. Africa). Nakamura and Kikawa, 1966 (infracentral grooves).

Parathunnus obesus mebachi, Jones and Silas, 1960: 383–384 (Indian Ocean), fig. 10.

Thunnus obesus sibi, Jones and Silas, 1963: 1791–1792 (Indian Ocean).

Thunnus obesus mebachi, Jones and Silas, 1964: 36–38 (Indian Ocean).

Misidentification

The 1,450-mm. specimen reported as *T. thynnus* by Fernandez-Yepez and Santaella (1956) is probably *T. obesus* as indicated by Mather and Gibbs (1958: 238) and by Rivas (1961: 134).

Types of Nominal Species

Thynnus obesus Lowe, 1839. No type specimens. Original description rather vague, but definitely referring to the species as now recognized. Apparently based on large specimens from Madeira. Differentiated from *T. thynnus* (as *Thynnus vulgaris*)

"by the larger eye and shorter thickset figure." Pectoral fins described as reaching end of second dorsal fin, longer than in *T. albacares* (as *Thynnus albacora*).

Thynnus sibi Temminck and Schlegel, 1844. Lectotype, RMNH 2327 (a mounted skin, 600 mm. fork length), and paralectotype, RMNH 799 (right side of mounted skin, backed by cardboard, 557 mm. fork length) designated by Boeseman (1947). Measurements made by Gibbs in 1962 fall in the range of *T. albacares* rather than *T. obesus*, but mounted specimens could be expected to be unreliable for this purpose. The description by Temminck and Schlegel likewise offers little aid in identifying the species. They note that the pectoral fin is shorter than in *T. alalunga* (as *Thynnus alalonga* or *T. pacificus*) and approaches in length that of *T. albacares* (as *T. argentivittatus*), and their illustration shows a pectoral fin resembling that of a fairly small Pacific *T. obesus*. On this basis, we follow other authors in considering *T. sibi* a synonym of *T. obesus*. If the measurements of the lectotype and paralectotype were taken at face value, *T. sibi* would have to be regarded as a synonym of *T. albacares*, but we prefer for the present to disregard these specimens.

Thynnus mebachi Kishinouye, 1915. No type specimens. Original description clearly referable to *T. obesus*, apparently based on a number of specimens.

Characters

Pectoral fin intermediate in length (22–31 percent of fork length) in specimens longer than 1,100 mm. (as in *T. albacares* and *T. atlanticus*), as long as in *T. alalunga* (greater than 31 percent) in specimens less than 1,100 mm. from the Pacific.

Gill rakers 23–31 (generally similar to *T. albacares* and *T. alalunga*).

Liver with striations on ventral surface (not restricted to margins, fig. 30), its three lobes subequal in length, vascular cones present on its dorsal side (as in *T. thynnus*, *T. maccoyii*, and *T. alalunga*). Spleen on right side, stomach on left (as in all except *T. alalunga*). Swimbladder as long as body cavity, with two globular dorsal heads anteriorly, tapering gradually to a point posteriorly. Kidney with a short tail, reaching the level of vertebra 11–13.

Cutaneous artery usually originating at level of vertebra 6–8, passing laterally between ribs 5 and 6, branching between intermuscular bones 6 and 7 (as in *T. albacares*, *T. tonggol*, and *T. atlanticus*). Two

rows of arterioles and venules arising from each main lateral cutaneous branch (as in *T. thynnus* and *T. maccoyii*). Post-cardinal vein present, joining right cutaneous vein (as in *T. albacares*, *T. tonggol*, and *T. atlanticus*).

Posterior parasphenoid margin either rounded (in some small specimens) or forming a slightly obtuse angle (not as acute as in *T. alalunga*, *T. maccoyii*, or *T. thynnus*).

Vertebrae 18+21 (as in all *Thunnus* except *T. atlanticus*). First ventrally directed parapophysis on vertebra 9 (as in all except *T. tonggol* and *T. thynnus*). First closed haemal arch usually on vertebra 11 (as in *T. albacares*, *T. atlanticus*, *T. tonggol*, and some *T. thynnus*). Haemal prezygapophyses arising high on haemal arch (as in *T. thynnus* and *T. maccoyii*). All haemal postzygapophyses short, less than half centrum length (as in *T. alalunga*, *T. thynnus*, and *T. maccoyii*). Anteriormost ventrolateral foramina small, not more than $1\frac{1}{2}$ times width of haemal spine (as in *T. alalunga*, *T. thynnus*, and *T. maccoyii*).

Nominal species

Three names have been applied to this species: *Thunnus obesus* for the Atlantic population and *T. sibi* and *T. mebachi* for the Pacific population, both latter names based on Japanese specimens. Fraser-Brunner (1950) correctly placed *sibi* and *mebachi* in the synonymy of *T. obesus* but also mistakenly included *Thunnus maccoyii*, *T. phillipsi* (= *T. maccoyii*), and *Parathunnus rosengarteni* (= *T. atlanticus*) as was pointed out by Rivas (1961). Jones and Silas (1960) stated that they could find no notable differences between Atlantic and Pacific populations, but referred to their Indian Ocean specimens as *Parathunnus obesus mebachi*. Because the name *sibi* has priority over *mebachi*, this should be *T. obesus sibi* if the Indo-Pacific population is subspecifically differentiated, and the latter name was used by Jones and Silas (1963).

Rivas (1961) claimed that the Pacific populations ("*sibi*") can be distinguished from the Atlantic *T. obesus* at lengths of about a meter by a much longer pectoral fin, but admitted difficulty in differentiating large specimens. His conclusion was based on a single small Atlantic specimen (746 mm., pectoral 29.4 percent of fork length) and 10 small specimens (data from Dung and Royce, 1953: 74) from the western Marshall Islands (600–835 mm., pectoral 38.8–44.9 percent).
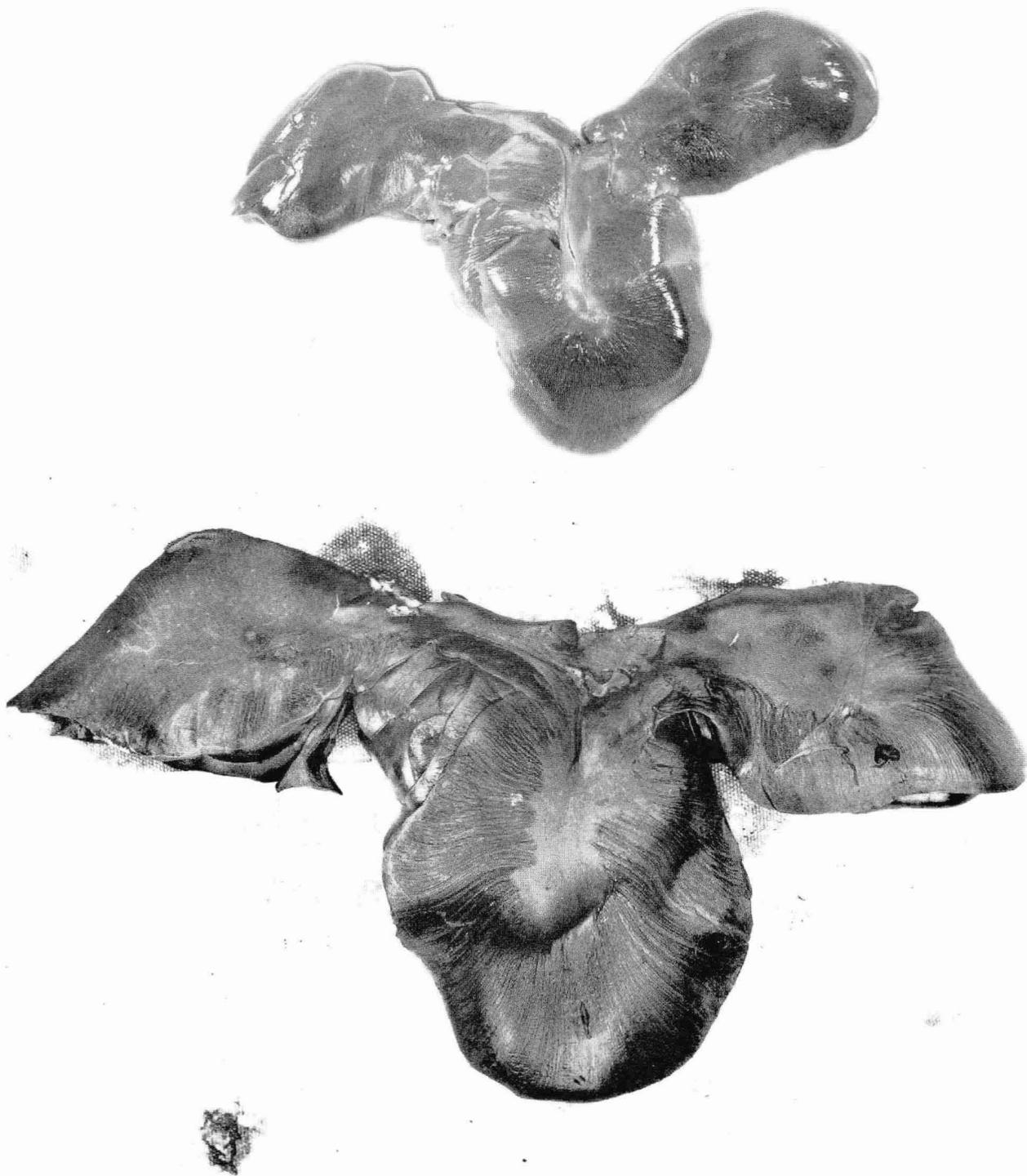
FIGURE 30.—Livers of Atlantic *Thunnus obesus*, ventral view. (Top) from specimen 715 mm. fork length; (bottom) from specimen 1,433 mm. fork length (photographed by P. C. Wilson).

Although abundant data are available for Pacific *T. obesus* from 400 mm. and up (Dung and Royce, 1953), very few Atlantic specimens smaller than 1,000 mm. have been recorded. These data, nevertheless, indicate that the pectoral fin in Atlantic *T. obesus* does not become as long as that of the Pacific populations and that, in fact, the length of this fin in Atlantic *T. obesus* approaches *T. albacares* more closely than Pacific *T. obesus* at intermediate sizes (650–1,000 mm). Some Pacific and Indian Ocean specimens, however, have shorter pectorals than the majority and overlap with Atlantic specimens (fig. 31).
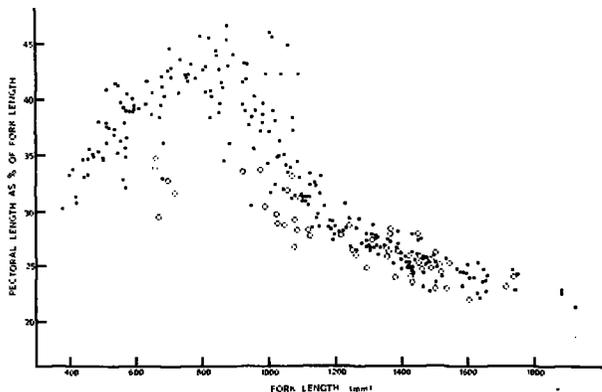

FIGURE 31.—Relative length of pectoral fin in *Thunnus obesus*. Dots, Indian and Pacific ocean specimens; open circles, Atlantic specimens.

It seems, therefore, that the Atlantic population of *T. obesus* is differentiated from the Pacific population, perhaps on a subspecific level, but much more data on sizes smaller than 1,000 mm. will be necessary to establish the level of differentiation.

Range

The distribution of *T. obesus* in the western Atlantic, as summarized by Mather and Gibbs (1958), includes the area from 42°18′ N., 64°02′ W. south along the coast of the United States to Florida; Bermuda; the Caribbean Sea around the West Indies; south to Margarita Island, Venezuela (reported as *T. thynnus* by Fernandez-Yepez and Santaella, 1956, but considered to be *T. obesus* by Mather and Gibbs). Nagai and Nakagome (1958) reported *T. obesus* from the north equatorial and Brazil currents off the coast of South America. In the eastern Atlantic it has been taken off Portugal,

Spain, the Azores, and Madeira, south to Angola (Vilela and Monteiro, 1959) but it is absent from the Mediterranean Sea. There is a report of its occurrence from the Gulf of Gascogne (Legendre, 1936), but this needs confirmation. Talbot and Penrith (1961, 1962, 1963) have shown the distribution to be continuous around the tip of South Africa, but the fish could originate either in the Atlantic or Indian ocean.

T. obesus, like *T. albacares*, is found throughout the Indian Ocean from 20° N. to 30° S. (Mimura et al., 1963b). Its range in the western Pacific is also similar to that of *T. albacares*, extending from about 40° N. to about 30° S. (Alverson and Peterson, 1963). In the eastern Pacific it extends to 40° S. (Japan Fishery Agency, 1965).

**THE BLUEFIN TUNA COMPLEX:
T. MACCOYII AND *T. THYNNUS***

In recent years, various authors have attempted to recognize as distinct species the populations of bluefin tuna in Japan and the western Pacific (*T. orientalis*), Australia (*T. maccoyii*), eastern Pacific (*T. saliens*), western Atlantic (*T. secundodorsalis*), and eastern Atlantic (*T. thynnus*). Frade (1925) noted that the eastern Atlantic form had two rows of cutaneous arterioles, whereas Kishinouye (1923) pictured a single row in his Japanese specimen. Godsil and Byers (1944) found California bluefin similar to Kishinouye's descriptions of the form, except for two major characters. According to Kishinouye, the swimbladder of the Japanese form is short, broad, and heart-shaped, whereas that of California specimens "is rudimentary and of a different shape in small fish, and so erratic in large specimens that no constant pattern is discernible" (Godsil and Byers, 1944: 102). In California specimens, there are two rows of cutaneous arterioles and, according to Kishinouye, but a single row in Japanese fish. Godsil and Holmberg (1950) described numerous anatomical differences among California, Australian, and western Atlantic specimens, finally concluding that the Australian form (*T. maccoyii*) is distinct from the California and western Atlantic forms (*T. thynnus*) and that the latter are also distinct, but not quite so trenchantly. On the basis of published accounts of Japanese and eastern Atlantic populations (Kishinouye, 1923; Frade, 1925), Godsil and Holmberg tentatively concluded that eastern and western Atlantic forms are conspecific but that the Japanese form is different. On the basis of

112

counts and measurements, Ginsburg (1953) recognized as species the eastern Atlantic, western Atlantic, and eastern Pacific populations but did not consider those from other geographic regions. Serventy (1956a) recognized only a single worldwide species, pointing out the ontogenetic increase in relative size of the swimbladder and suggesting that other distinguishing characters shown by Godsil and Holmberg (1950) may also be eliminated when size differences are considered. Serventy (1956a) suggested, however, that the populations from European seas, North American Atlantic coast, South Africa, North American Pacific coast, Asiatic coast of the North Pacific, and Australia-New Zealand, respectively, each be recognized as subspecies, largely on the basis of modal differences in gill-raker counts. We have previously recognized a single species with only two subspecies (Collette and Gibbs, 1963). Iwai et al., (1965) considered *T. maccoyii* and *T. thynnus* as distinct species, with no commitment as to subspecies of the latter.

When individual and ontogenetic variations are considered, almost every anatomical, morphometric, and meristic character has proved to be similar in all populations. The only exceptions are the number of gill rakers, length of pectoral fin, a few skeletal characters, the shape of the dorsal wall of the body cavity, and the color of the caudal peduncle keels. On the basis of these characters, we tentatively recognize two species of bluefin tuna: *T. maccoyii*, mainly from the Southern Ocean south of about 30° S., but including an area off northwestern Australia; and *T. thynnus*, with one subspecies, *T. t. thynnus*, in the Atlantic, and another, *T. t. orientalis* in the Pacific.

We were long reluctant to recognize *T. maccoyii* as a separate species, and even now we do so only with reservation. The only convincing characters that provide evidence of species status are the posi-

tion of the first ventrally directed parapophysis (on the 9th vertebra in *T. maccoyii*, as opposed to the 10th, in *T. thynnus*) and the color of the fleshy caudal keels (yellow in *T. maccoyii*, dark in *T. thynnus*). The few other characters, none of them affording complete separation, are given in table 5.

The presence of *T. thynnus orientalis* in the southeastern Pacific and the northeastern Indian Ocean (Nakamura and Warashina, 1965), and of *T. thynnus thynnus* off Cape Town (Talbot and Penrith, 1963) in the same geographical areas as *T. maccoyii* gives biological support to considering *T. maccoyii* as a separate species, although it is not known whether the two actually spawn in the same areas.

Differences in the configuration of the dorsal wall of the body cavity are not apparent in specimens less than about 1,300 mm. As described by Godsil and Holmberg (1950), numerous western Atlantic specimens (*T. t. thynnus*) examined by us in the field and laboratory had a wide anterior bulge without a lateral concavity and had a deep, narrow trough lateral to the bulge (fig. 32). Our only large specimen of *T. maccoyii* (1,450 mm.) was similar to the western Atlantic forms. Eastern Pacific specimens of *T. t. orientalis*, 1,390 and 1,450 mm., confirm the differences described by Godsil and Holmberg. The anterior bulge is comparatively narrow, with a lateral concavity, and with a wide trough lateral to the bulge (fig. 32). Although we have dissected no large Japanese specimens, we are confident they will resemble those from the eastern Pacific.

Godsil and Holmberg (1950) eliminated a large number of characters from systematic consideration. We can substantiate almost all of their conclusions, and our observations invalidate most of their remaining differential characters.

The tubules of the caecal mass of *T. t. thynnus* and *T. t. orientalis* were said to be relatively large and

TABLE 5.—*Comparison of* Thunnus maccoyii *and the subspecies of* T. thynnus

[Mean values given in parentheses]

| Character	T. t. thynnus	T. t. orientalis	T. maccoyii
Number of gill rakers	34–43 (38. 9)	32–40 (35. 9)	31–40 (33. 7)
First ventrally directed parapophysis on vertebra number	8	8	9
9th vertebra: parapophysis height/least distance apart	1. 2–29. 6 (8. 1)	1. 1–12. 7 (4. 1)	0. 8–3. 2 (1. 6)
10th vertebra: canal height/least width of processes	1. 9–5. 4 (3. 5)	1. 0–9. 0 (4. 1)	6. 0–15. 9 (11. 3)
10th vertebra: canal height/canal width	1. 5–3. 2 (2. 2)	1. 4–4. 8 (2. 0)	0. 9–1. 7 (1. 3)
Depth of anterior haemal canals	first increase, then decrease	first increase, then decrease	decrease
Shape of dorsal wall of body cavity in large specimens	wide bulge with no lateral concavity; deep, narrow lateral trough	narrow bulge with lateral concavity; wide lateral trough	wide bulge with no lateral concavity; deep, narrow lateral trough
Pectoral length as percent fork length (600–1,000 mm.)	17. 0–21. 7	16. 8–20. 8	20. 2–23. 0
Color of caudal keels	dark	dark	yellow
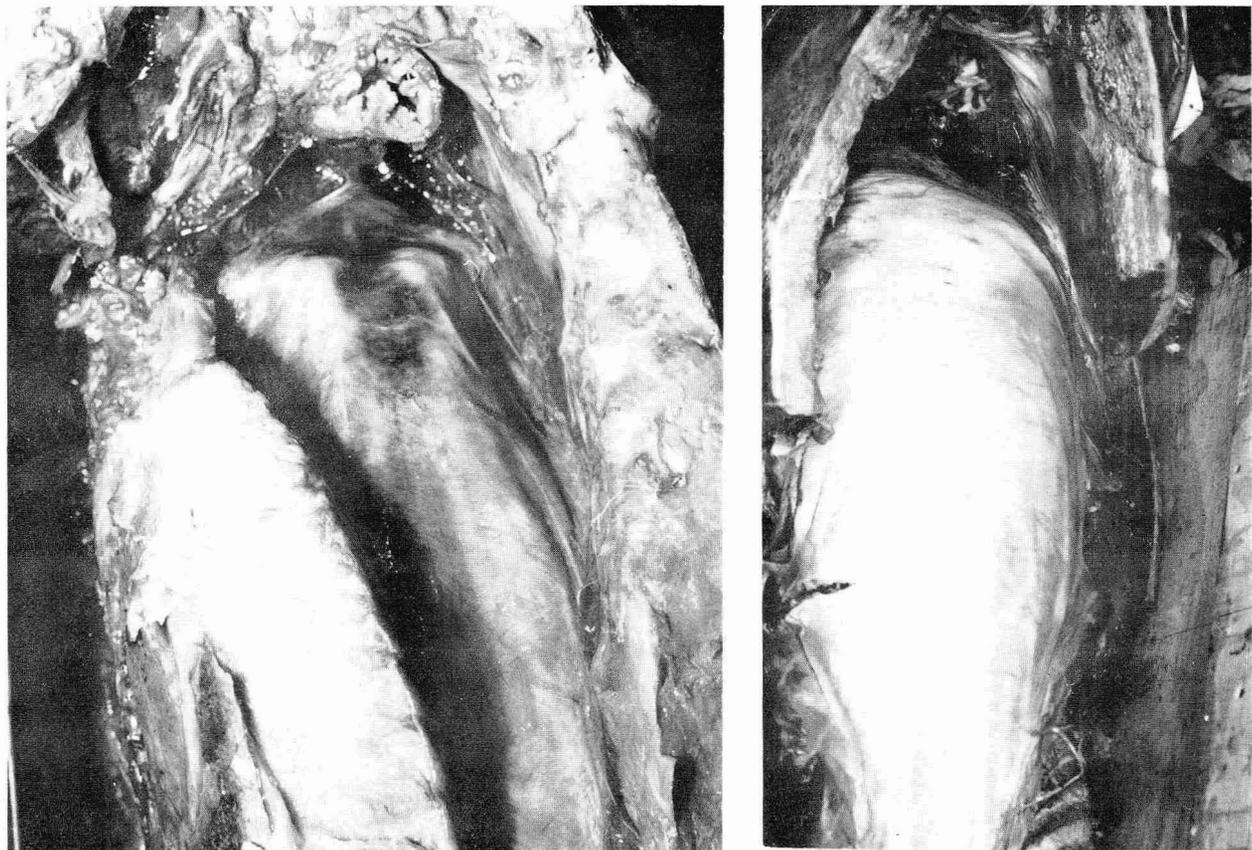
FIGURE 32.—Dorsal wall of body cavity of *Thunnus thynnus*. Ventral view with viscera removed and head end to the left. Left: *T. t. orientalis*, 1,450 mm. fork length, from California, showing the comparatively narrow anterior bulge with lateral concavity and wide lateral trough. Right: *T. t. thynnus*, 1,850 mm. fork length, from the western North Atlantic, showing the wide anterior bulge without a lateral concavity.

coarse compared with *T. maccoyii*. We could detect no differences.

The caecal mass is so variable in size that its dimensions cannot be used to differentiate populations.

The relative length of the lateral liver lobes of western Atlantic specimens encompasses the differences in lobe lengths suggested by Godsil and Holmberg.

The stomach length cannot logically be used as a specific character, since this is a highly distensible organ, the dimensions of which will vary under different physiological states.

Swimbladder dimensions vary with size, becoming larger with growth, as shown by Serventy (1956a) for *T. maccoyii* from Australia and by us for western Atlantic *T. t. thynnus* and eastern Pacific *T. t. orientalis*. Abe (1955) reported that the swimbladder was well developed in a 1,470-mm. specimen thought

to be *T. maccoyii* from the eastern Indian Ocean. Kishinouye (1923) and Frade (1925) illustrated swimbladders for western Pacific and eastern Atlantic specimens, respectively, that are very similar to those of larger specimens from other regions, and Kishinouye noted that the swimbladder is short and very narrow in immature specimens of Japanese *T. thynnus orientalis*, but short and wide in adults.

Godsil and Holmberg described the posterior end of the kidney of *T. maccoyii* specimens as truncate. This condition was observed in several specimens of western Atlantic *T. t. thynnus*, which displayed all variations that have been described, but our specimens of *T. maccoyii* did not show this condition.

The branching of the ureter of *T. maccoyii* was said to differ in that the branching occurred well anterior in the kidney mass. We observed this condition in both *T. t. thynnus* and *T. t. orientalis;* in

two of our three specimens of *T. maccoyii* the branching occurred near the end of the tail of the kidney.

In *T. maccoyii*, the dorsal aorta was reported to be usually conspicuously constricted behind the origin of the cutaneous arteries. We observed this condition in both *T. t. thynnus* and *T. t. orientalis*, but size did not decrease in our specimens of *T. maccoyii*.

The presence of a connecting branch between the two main branches of the coeliacomesenteric artery was said to distinguish *T. t. orientalis* and *T. maccoyii* from *T. t. thynnus*; however, Godsil and Holmberg (1950) did not find the branch in one Australian specimen and they were uncertain as to its presence in another. Furthermore, we observed this connection in several western Atlantic specimens.

The cutaneous artery in *T. maccoyii* was said to pass laterally most often between ribs 2 and 3 (rather than 3 and 4) and to divide usually between intermuscular bones 5 and 6 (rather than 4 and 5). Godsil and Byers (1944) recorded this condition as rare in *T. t. orientalis*, and Godsil and Holmberg (1950) noted the same for *T. t. thynnus*. In all our material, including *T. maccoyii*, the artery passed between ribs 3 and 4, and divided between intermuscular bones 4 and 5 (between 5 and 6 in one specimen of *T. t. thynnus*).

The place of attachment of the internal wing of the pelvic girdle was said to be different in each of the three forms (Godsil and Holmberg, 1950). We found the condition in all three similar to their descriptions of *T. maccoyii*.

THUNNUS MACCOYII (Castelnau, 1872)
SOUTHERN BLUEFIN TUNA

Thynnus maccoyii Castelnau, 1872: 104–105 (original description; Melbourne market).

Thunnus phillipsi Jordan and Evermann, 1926: 13 (original description; New Zealand), pl. 2, fig. 4.

Thunnus maccoyii, Jordan and Evermann, 1926: 13 (description). Serventy, 1941: 27–33 (description; Australia), fig. 5, pl. 2. Godsil and Holmberg, 1950 (comparison of Australian with New England and California specimens; anatomy). Mimura and Warashina, 1962. Iwai and Nakamura, 1964: 6, figs. 3E, F (olfactory rosettes). Iwai et al., 1965: 9 (synonymy), 33–34 (description), fig. 18. Nakamura, 1965: 18, figs. 3C, 5C, 7 (osteology). Nakamura and Kikawa, 1966 (infracentral grooves).

Thunnus obesus, Fraser-Brunner, 1950: 144 (*T. maccoyii* in synonymy).

Thunnus thynnus maccoyi, Serventy, 1956a (counts, distribution around Australia). Munro, 1958: 111 (Australia). Robins, 1963 (biology; Australia).

Thunnus thynnus subspecies, Serventy, 1956a: 13 (probably a separate subspecies in S. Africa).

Thunnus thynnus orientalis, Jones and Silas, 1960: 381–382 (Indian Ocean), fig. 8. Collette and Gibbs, 1963: 28. Jones and Silas, 1963: 1788–1790 (Indian Ocean). Talbot and Penrith, 1963: 630–636 (description, biology; S. Africa). Jones and Silas, 1964: 30–34 (Indian Ocean).

Types of Nominal Species

Thynnus maccoyii Castelnau, 1872. No type specimens. Bauchot and Blanc (1961: 377) reported that a type specimen was catalogued in the collections of the Museum National d'Histoire Naturelle, Paris, in 1877, as number 515, but that the specimen cannot be located. Original description based on several specimens, fresh and dried, from the Melbourne, Australia, market, the largest 23 inches (585 mm.) long. This description is inadequate, but the short pectoral (two-thirds of head) suggests one of the bluefin tunas or *T. tonggol*, and the locality rules out all except *T. maccoyii* as now recognized.

Thunnus phillipsi Jordan and Evermann, 1926. Type originally designated as "A photograph, No. 596, Mus. Calif. Acad. Sci. . . . of a specimen taken in the Bay of Islands, New Zealand." This photograph is of a pug-headed mounted specimen in the Dominion Museum, Wellington. The cast is 1,575 mm. FL. The pectoral fin is short (295 mm.), which makes *T. maccoyii* the only reasonable assignment for this nominal species, *T. tonggol* not being known to occur in New Zealand. According to J. Moreland (pers. comm.), the pug-headedness appears to be the result of the fish being stood on its head forcing the processes of the premaxillaries up over the frontals where they remained when the cast was made.

Characters

Pectoral fin short, not more than 80 percent of head length, 20–23 percent of fork length in specimens 650–1,450 mm. (overlapping *T. tonggol*; slightly longer than *T. thynnus*). Caudal keels yellow in most specimens; this color possibly lost in larger adults.

Gill rakers 31–40, more numerous than in any other species of *Thunnus* except *T. thynnus*.

Liver with striations on ventral surface, its three lobes subequal in length, and with vascular cones on its dorsal side (as in *T. alalunga, T. obesus,* and *T. thynnus*). Spleen located on right side, and stomach on left (as in all except *T. alalunga*). Kidney with a very short "tail," reaching to the level of vertebra 8–12 (as in *T. thynnus*).

Cutaneous arteries originating at level of vertebra 4–5, passing laterally between ribs 2 and 3 or 3 and 4, and dividing between intermuscular bones 4 and 5 (as in *T. alalunga* and *T. thynnus*). Two rows of arterioles and venules arising from each main lateral cutaneous branch (as in *T. obesus* and *T. thynnus*). Post-cardinal vein absent (as in *T. alalunga* and *T. thynnus*).

Posterior parasphenoid margin forming an angle, becoming acute in large specimens (as in *T. alalunga, T. thynnus,* and, to a lesser degree, in *T. obesus*), occasionally rounded in small specimens. Alisphenoids extending far ventrad into orbital cavity; distance from most ventral part of alisphenoid to nearest point on parasphenoid goes into greatest height of anterior part of orbit two times or more (only *T. thynnus* and larger specimens of *T. tonggol* have a similar condition). Alisphenoids not known to fuse with parasphenoid as is the case in some *T. thynnus*. Subopercle relatively slender, its upper anterior margin usually almost vertical in its lower two-fifths or more, sloping posteriad in its upper portion (as in *T. thynnus*); rarely, there is no vertical portion.

Vertebrae 18+21 (as in all except *T. atlanticus*). First ventrally directed parapophysis on vertebra 9 (as in all except *T. thynnus* and *T. tonggol*). First closed haemal arch on vertebra 10 (as in *T. alalunga*, *T. thynnus*, and, rarely, all others except *T. tonggol*). Anterior haemal prezygapophyses arising high on haemal arch (as in *T. alalunga, T. thynnus,* and *T. obesus*). All haemal postzygapophyses short, less than half centrum length (as in *T. alalunga, T. thynnus,* and *T. obesus*). Ventrolateral foramina small, not more than one and one-half times width of haemal spine (as in *T. alalunga, T. thynnus,* and *T. obesus*).

Comparisons with *T. thynnus* are given in table 5.

Range

Thunnus maccoyii is apparently mainly restricted to the Southern Ocean, although it is impossible to evaluate many records. This species is best recognized at present by skeletal characters, although the yellow caudal keel is also diagnostic. We have examined skeletal material from Tasmanian waters reported by Godsil and Holmberg (1950); from western South Africa, reported by Talbot and Penrith (1963); additional specimens from the Sydney, Australia, market; from west of southern Australia; and from off the coast of Chile. The presence of *T. maccoyii* in the Pacific and Indian oceans off both sides of southern Australia and off Chile, and in the Atlantic off South Africa is thus definitely established. The geographic distribution summarized by Robins (1963) included waters north of New Zealand and areas off western Australia north almost to the Indonesian Islands. These records are probably correct, but need confirmation through osteological studies. Southeastern Pacific catches are reported by Japanese expeditions (Japan Fishery Agency, 1964). If these unconfirmed records are accepted, it seems likely that *T. maccoyii* will be found throughout the Southern Ocean south of 30° S.

THUNNUS THYNNUS (Linnaeus, 1758)
BLUEFIN TUNA

The synonymy of each of the two subspecies is presented separately. The diagnosis of the species, discussion of nominal species and subspecies, and summary of the range consider both subspecies.

THUNNUS THYNNUS THYNNUS (Linnaeus, 1758)
ATLANTIC BLUEFIN TUNA

Scomber pinnulis octo vel novem in extremo dorso ex sulco ad pinnas ventrales Artedi, 1738a: 31 (description) and 1738b: 141–142 (references to Aristotle, Ovid, Pliny, etc.).

Scomber thynnus Linnaeus, 1758: 297–298 (original description; based on Artedi, 1738). Bonnaterre, 1788: 139, pl. 58, fig. 228. Gmelin, 1789: 1330–1331 (description, synonymy). Lacépède, 1800: 598, 605–632 (description, synonymy). Risso, 1810: 163 (Nice).

Thynnus thynnus, Cuvier, 1817: 313 (Mediterranean). Günther, 1860: 362–363 (synonymy, description; Atlantic and Mediterranean).

Thynnus mediterraneus Risso, 1826: 414–415 (substitute name for *Scomber thynnus* Linnaeus, 1758; Nice).

Thynnus vulgaris Cuvier *in* Cuvier and Valenciennes, 1831: 42–71 (substitution of new name for *Scomber thynnus* Linnaeus, 1758), pl. 210.

116   **U.S. FISH AND WILDLIFE SERVICE**

Thunnus vulgaris, South, 1845: 620–621 (description, natural history).

Thynnus secundo-dorsalis Storer, 1967: 65–67 (original description; Massachusetts Bay), pl. 12, fig. 4.

Orcynus thynnus, Poey, 1875: 144–145. Lütken, 1880: 460–464, 595–596 (in part; development). Buen, 1925 (migrations, biology; E. Atlantic).

Orcynus secondidorsalis, Poey, 1875: 145 (Cuba).

Albacora thynnus, Jordan, 1888. Dresslar and Fesler, 1889: 439–440 (synonymy in part), pl. 7.

Thunnus thynnus, Jordan and Evermann, 1896: 870 (description, synonymy in part; a single worldwide species of bluefin). Meek and Hildebrand, 1923: 314–315 (description, synonymy in part). Jordan and Evermann, 1926: 10 (synonymy; Europe). Barnard, 1927: 798–799 (S. Africa). Buen, 1930: 49 (synonymy), fig. 7. Frade, 1931b (biometrics; Portugal). Frade, 1931c (meristics; E. Atlantic). Crane, 1936 (description; Gulf of Maine). Fowler, 1936: 619–620 (synonymy, description). Tortonese, 1939: 324 (Yokohama). Bellón and Bardán de Bellón, 1949: 8–11 (Canary Is.). Smith, 1949, 1953: 298 (S. Africa), pl. 66, fig. 831. Godsil and Holmberg,.1950 (anatomy; New England). Fraser-Brunner, 1950: 142 (key to *Thunnus*), 143 (synonymy in part), fig. 4. Rivas, 1951: 217–219 (description, synonymy). Ginsburg, 1953: 1 (the name *thynnus* restricted to the E. Atlantic population of bluefin). Morice, 1953: 67–68, figs. 1, 2 (liver; E. Atlantic). Bellón, 1954 (description, relationships, biology, anatomy, distribution). Mather and Day, 1954: 181 (W. Atlantic). Rivas, 1954b: 302–322 (spawning in straits of Florida), figs. 1–3. Rivas, 1955 (comparison between Gulf of Maine and Florida specimens). de Sylva, 1955: 33–40 (osteology, relationships), fig. 55 (neurocranium). Bullis and Mather, 1956 (key to Caribbean species of *Thunnus*). Robins, 1957 (counts on dorsal and anal fins, gill rakers; one species of bluefin in the Atlantic). Mather and Schuck, 1960 (growth; NW. Atlantic). Frade and Vilela, 1962: 17–58 (morphology, biology; E. Atlantic). Tiews, 1963 (biology; Atlantic.)

Thunnus secundodorsalis, Jordan and Evermann, 1926: 12 (description). Jordan et al., 1930: 260. Ginsburg, 1953: 1–3 (W. Atlantic; summary of meristics from various authors).

Thunnus thynnus thynnus, Serventy, 1956a: 11–13 (subspecies found along Atlantic coast of Europe).

Talbot and Penrith, 1963: 633–640 (description, biology; S. Africa).

Thunnus thynnus coretta, Serventy, 1956a: 11–13 (subspecies found along Atlantic coast of America).

Misidentification

Thynnus brachypterus Cuvier (1829) was based on illustrations by Rondelet (1554) and Duhamel du Monceau (1769). Collette (1966) has indicated that this name is a synonym of *Sarda sarda* (Bloch). Although Cuvier (*in* Cuvier and Valenciennes, 1831) based his later description of *T. brachypterus* on specimens, four of which are *T. thynnus* and one *Euthynnus alletteratus*, this can not be regarded as the original description, and these specimens are not types.

Types of Nominal Species

Scomber thynnus Linnaeus, 1758. No type specimens. Original description not diagnostic, but based on Artedi (1738a, p. 31), who stated: "Longitude 7 pedum circiter." This could only refer to the bluefin tuna.

Thynnus mediterraneus Risso, 1826. Substitute name for *Scomber thynnus* Linnaeus, 1758, and taking the same type.

Thynnus vulgaris Cuvier *in* Cuvier and Valenciennes, 1831. Substitute name for *Scomber thynnus* Linnaeus, 1758, and taking the same type.

Thynnus secundodorsalis Storer, 1867. No type specimens. Original description based on two specimens, 8 feet, 6 inches (1,590 mm.) and 9 feet, 3 inches (1,820 mm.) total length. The pectorals "about one seventh of length of fish," the size and the locality (Mass.) unquestionably assign this nominal species to the synonymy of *Thunnus thynnus thynnus*.

THUNNUS THYNNUS ORIENTALIS
(Temminck and Schlegel, 1844)
PACIFIC BLUEFIN TUNA

Thynnus orientalis Temminck and Schlegel, 1844: 94–95 (original description; Japan). Günther, 1860: 362 (in footnote as dubious species).

Orcynus schlegelii Steindachner *in* Steindachner and Döderlein, 1884: 10–11 (original description; Tokyo), pl. 3, fig. 1.

Thunnus thynnus, Jordan and Evermann, 1896: 870 (description and synonymy in part). Jordan et al., 1913: 121 (Japan). Walford, 1937: 7–13 (description; Pacific specimens; possibility of a single worldwide species of bluefin), color pl. 34.

Brock, 1938 (Washington). Godsil and Byers, 1944: 88–102 (anatomy; E. Pacific), figs. 48–58. Tinker, 1944: 151 (Hawaii), pl. 1, fig. 8. Brock, 1949: 276 (key to Hawaiian tunas). Fraser-Brunner, 1950: 142–143 (synonymy in part), fig. 4. Godsil and Holmberg, 1950 (anatomy; California). June, 1952a (Hawaii). Buen, 1953 (Chile; but might be *T. maccoyii*). Iwai and Nakamura, 1964: 6, figs. 3C, D (olfactory rosettes). Iwai et al., 1965: 3, 6–8 (synonymy), 31–33 (description), fig. 16. Nakamura, 1965: 17–18, figs. 3B, 5B, 6 (osteology). Nakamura and Warashina, 1965: 9–10 (E. Indian and SE. Pacific oceans). Nakamura and Kikawa, 1966 (infracentral grooves).

Orcynus thynnus, Kitahara, 1897: 1 (description; Japan), pl. 1, fig. 1.

Thunnus schlegelii, Jordan and Snyder, 1900: 352 (Tokyo). Jordan and Snyder, 1901: 64 (Yokohama).

Thunnus orientalis, Kishinouye, 1915: 17 (description, anatomy; Japan), pl. 1, fig. 9. Kishinouye, 1923: 437–442 (anatomy; Japan), figs. 3, 21, 43, 44, 50. Jordan and Hubbs, 1925: 216–217 (Japan). Jordan and Evermann, 1926: 14 (description). Tinker, 1944: 157–158 (Hawaii). Brock, 1949: 276 (key to Hawaiian tunas). Gosline and Brock, 1960: 259 (description; Hawaii), 336 (synonymy), fig. 257h. Yamanaka et al., 1963 (biology; Japan).

Thunnus saliens Jordan and Evermann, 1926: 10–11 (original description; California), pls. 1–2, figs. 1–3. Jordan et al., 1930: 259. Ginsburg, 1953: 3 (*saliens* recognized as American Pacific species of bluefin). Neave, 1959 (N. end Vancouver Is.). Bell, 1963 (biology; E. Pacific).

Thunnus thynnus orientalis, Serventy, 1956a: 11–13 (the subspecies found along Asiatic coast of N. Pacific).

Thunnus thynnus saliens, Serventy, 1956a: 11–13 (the subspecies found along Pacific coast of N. America). Buen, 1958: 24–25 (Chile; but might be *T. maccoyii*).

Types of Nominal Species

Thynnus orientalis Temminck and Schlegel, 1844. Holotype RMNH 794, 450 mm. fork length, a mounted specimen from Japan with a pectoral fin 18.4 percent of fork length.

Orcynus schlegelii Steindachner, 1884. Holotype (not seen by us) presumably in Vienna Museum, 360 mm. fork length. The pectoral of barely more than half the head length and the locality (Japan) enable referral of this nominal species to the synonymy of *T. thynnus orientalis* (Temminck and Schlegel, 1844).

Thunnus saliens Jordan and Evermann, 1926. Type originally designated as "No. 595, Mus. Calif. Acad. Sci., a photograph of a specimen weighing 157½ pounds taken ... off Catalina, California." The photograph is clearly of a tuna with short pectoral fins; Jordan and Evermann (1926) recorded the fin length as 5½ (p. 9) or 5 (p. 10) in (standard) length, or about 20 percent. The locality allows referral to the synonymy of *T. thynnus orientalis*.

Characters

Pectoral fin short, not more than 80 percent of head length, less than 23 percent of fork length, slightly shorter than in *T. maccoyii* at a given size (fig. 33), overlapped by *T. tonggol*.

Gill rakers 34–43 in *T. t. thynnus*, 32–40 in *T. t. orientalis*, more numerous than in any other species of *Thunnus* except *T. maccoyii*.
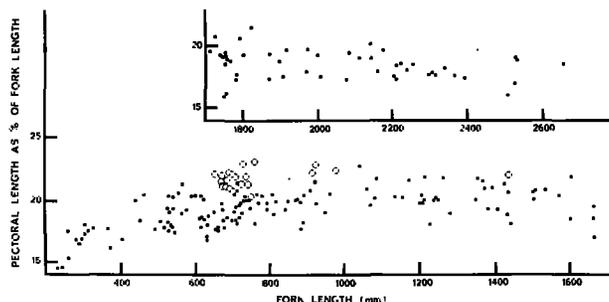

FIGURE 33.—Relative length of pectoral fin in *Thunnus thynnus* (dots) and *T. maccoyii* (open circles).

Liver with striations on ventral surface, its three lobes subequal in length, and with vascular cones on its dorsal side (as in *T. alalunga*, *T. obesus*, and *T. maccoyii*). Spleen located on right side, stomach on left (as in all except *T. alalunga*). Kidney with a very short tail, reaching to level of vertebra 8–11 (as in *T. maccoyii*).

Cutaneous arteries originating at level of vertebra 3–6 (usually 4 or 5), passing laterally between ribs 3 and 4 (occasionally 2 and 3) and dividing between intermuscular bones 4 and 5 or 5 and 6 (as in *T. alalunga* and *T. maccoyii*). Two rows of arterioles and venules arising from each main lateral cutaneous branch (as in *T. obesus* and *T. maccoyii*). Post-

cardinal vein absent (as in *T. alalunga* and *T. maccoyii*).

Posterior parasphenoid margin forming an angle, becoming acute in large specimens (as in *T. alalunga, T. maccoyii*, and, to a lesser degree, in *T. obesus*), occasionally rounded in small specimens. Alisphenoids extending far ventrad into orbital cavity; distance from most ventral part of alisphenoid to nearest point on parasphenoid goes into greatest height of anterior part of orbit two times or more (only *T. maccoyii* and larger specimens of *T. tonggol* have a similar condition). Alisphenoids fused to parasphenoid in some larger specimens. Subopercle (see fig. 9) relatively slender, its upper anterior margin usually almost vertical in its lower two-fifths or more, sloping posteriad in its upper portion (as in *T. maccoyii*); rarely there is no vertical portion.

Vertebrae 18+21 (as in all except *T. atlanticus*). First ventrally directed parapophysis on vertebra 8. First closed haemal arch usually on vertebra 10 (as in *T. alalunga* and *T. maccoyii*), sometimes on 11 (as in the other five species). Anterior haemal prezygapophyses arising high on haemal arch (as in *T. maccoyii* and *T. obesus*). All haemal postzygapophyses short, less than half the centrum length (as in *T. maccoyii* and *T. obesus*). Ventrolateral foramina small, not more than one and one-half times width of haemal spine (as in *T. alalunga, T. maccoyii*, and *T. obesus*).

Comparisons with *T. maccoyii* are given in table 5.

Range

T. thynnus thynnus has been found in the western Atlantic from Hamilton Inlet, Labrador (La Monte, 1946: 22), and Newfoundland, south along the Atlantic coast of the United States into the Gulf of Mexico and Caribbean Sea (Wathne, 1959). It is known off Venezuela (Fernandez-Yepez and Santaella, 1956), and south to northeastern Brazil. In the eastern Atlantic, *T. t. thynnus* is found from the Lofoten Islands of Norway (about 70° N.), south along the coast of Europe and north Africa, south to the Canary Islands. Records from near Cape Verde Islands, Angola, and Republic of South Africa have been questioned (Tiews, 1963), but gill-raker counts given by Talbot and Penrith (1963) for large specimens caught from January to March suggest convincingly that *T. t. thynnus* does occur west of the Cape Peninsula of South Africa, and we have examined one specimen from there.

Tag returns have shown that there is at least some interchange between eastern and western North Atlantic *T. t. thynnus*. Mather (1960) reported two specimens tagged off Martha's Vineyard, Mass., and recaptured in the Bay of Biscay 2 to 5 years later. Two large specimens tagged off Cat Cay, Bahamas, were recaptured off Bergen, Norway, a distance of over 4,000 miles, after 118 and 119 days at large (Mather, 1962).

T. thynnus orientalis has been reported in the eastern north Pacific from the Shelikof Straits, north of Kodiak Island, in the Gulf of Alaska (Radovich, 1961), off Vancouver Island (Neave, 1959), off Willapa Bay and the mouth of the Columbia River (Brock, 1938), regularly off southern California and the length of Baja Calif. (Bell, 1963). In the western north Pacific, *T. t. orientalis* is known from the island of Sakhalin in the southern Okhotsk Sea, southward on both sides of Japan, to the northern Philippines; eastward from Japan between about 30°–40° N. to about 160° W.; and eastward between about 5°–10° N. from about 135°–175° E. (Yamanaka et al., 1963). It is taken occasionally in Hawaiian waters (Jordan and Jordan, 1922; Fowler, 1928; June, 1952a).

The contention that both eastern and western north Pacific *T. thynnus* constitute a single subspecies is supported by the recapture off Japan of at least three specimens that had been tagged 2 to 5 years previously near Guadalupe Island, Mexico (Orange and Fink, 1963; Anonymous, 1964).

Thunnus thynnus has been recorded from the Galapagos area (Snodgrass and Heller, 1905; Herre, 1936), but there is no supporting evidence which would eliminate *T. maccoyii* or any other species from consideration.

Nakamura and Warashina (1965) reported *T. thynnus orientalis* (as *T. thynnus*) from two areas previously not verified. Two specimens, 2,657 mm. and 2,200 mm., were taken in the Indian Ocean off western Australia at 28°24′ S., 105°56′ E. and 27°43′ S., 102°25′ E., respectively. Another, 2,206 mm., was captured in the southeastern Pacific at about 37°11′ S., 114°41′ W. Specimens from Chile had previously been reported by Buen (1953, 1958), as *T. thynnus saliens*. These are areas from which *T. maccoyii* is known. Nakamura and Warashina gave measurements of one specimen from each locality. Converting their figures for pectoral length into percent of fork length (their "total length") gives 18.6 and 17.5 percent, falling below our data for smaller *T. maccoyii* and agreeing well with *T.*

thynnus orientalis (table 5). All three, however, are much larger than the largest reliably identified *T. maccoyii* (1,748 mm.; Iwai and Nakamura, 1964b: 2). It is entirely possible that the two best external diagnostic characters—color of caudal keel and length of pectoral fin—may no longer be distinct at large sizes. At the present time only examination of vertebral characters can offer assurance of their identity.

We examined the skull and vertebral column of the specimen from 37°11′ S., 114°41′ W. The skull (290 mm.) is larger than any we have examined of *T. maccoyii* and has the alisphenoids fused to the parasphenoids, a condition we have found only in large specimens of *T. thynnus*. The first ventrally directed parapophyses are on the eighth vertebra and the first closed haemal arch is on the tenth vertebra as in *T. thynnus*. Three other vertebral characters useful in distinguishing *T. thynnus* from *T. maccoyii* have the following values: 9th vertebra: parapophysis height divided by least distance apart —4.2; 10th vertebra: canal height divided by least width of processes—2.9; and 10th vertebra: canal height divided by canal width—1.8. The first and third are higher and the second is well below the range we have found for *T. maccoyii*, and all agree well with our data for *T. t. orientalis* (table 5). Unfortunately, skeletons of the suspect Indian Ocean specimens are not available, but specimens from this region, observed by us in the Yaizu market, appeared to have the dorsal bulge of the body cavity as in *T. thynnus*.

THUNNUS TONGGOL (Bleeker, 1851)
LONGTAIL TUNA

Thynnus tonggol Bleeker, 1851: 356–357 (original description; Batavia Sea). Günther, 1860: 364.

Thunnus rarus Kishinouye, 1915: 28 (original description; Tokyo market), pl. 1, fig. 13.

Neothunnus rarus, Kishinouye, 1923: 448–450 (anatomy), figs. 24–48, 64. Herre, 1940: 39 (Malaya). Nichols and La Monte, 1941: 32 (synonymy in part).

Kishinoella rara, Jordan and Hubbs, 1925: 219 (placed in the new genus *Kishinoella*). Jordan and Evermann, 1926: 26 (description). Herre, 1945: 148 (Zamboanga, Philippines).

Neothunnus tonggol, Jordan and Evermann, 1926: 22.

Thunnus nicolsoni Whitley, 1936: 30–31 (original description; Queensland), fig. 2.

Thunnus tonggol, Tortonese, 1939: 326 (Java Sea).

Fraser-Brunner, 1950: 142 (key to *Thunnus*), 145–146 (synonymy), fig. 8. de Beaufort, 1951: 225–226 (synonymy; description; Bleeker's types checked). Iwai and Nakamura, 1964: 6, fig. 31 (olfactory rosettes). Jones and Silas, 1964: 38–40 (Indian Ocean). Iwai et al., 1965: 16–17 (synonymy), 39–40 (description), fig. 23. Nakamura, 1965: 24, figs. 3G, 12, 13A (osteology). Nakamura and Kikawa, 1966 (infracentral grooves).

Kishinoella tonggol, Serventy, 1941: 33–38 (description; Australia), figs. 6–9, pl. 2. Serventy, 1942 (description, anatomy, synonymy; Australia), fig. 1, pls. 3–5. Serventy, 1956b (counts, distribution; Australia). Munro, 1958: 111 (Australia.) Jones and Silas, 1960: 384–385 (west coast of India), fig. 11. Ranade, 1961 (description; Arabian Sea). Jones, 1963 (biology; Indian Ocean). Jones and Silas, 1963: 1792–1793 (Indian Ocean).

Misidentifications

Munro (1957) reported a specimen of tuna as *Parathunnus mebachi* from southern Queensland. Rivas (1961) considered this specimen to be the same as his *T. argentivittatus,* but as we have shown under the account of *T. albacares,* Rivas' account and that of Schaefer and Walford (1950) is based on a specimen of *T. tonggol.* Judging from the low number of gill rakers (7+16=23), pectoral length, and distance from snout to second dorsal origin reported by Munro (1957), his specimen was also *T. tonggol.* His later account (Munro, 1958) confirms this opinion. Serventy (1942, 1956b), Fraser-Brunner (1950), and others have considered *Kishinoella zacalles* Jordan and Evermann (1926) as close to or a synonym of *T. tonggol,* but *zacalles* is a synonym of *T. albacares,* as we show under the account of that species.

Types of Nominal Species

Thynnus tonggol Bleeker, 1851. No type specimens known to us. The designation of a neotype by Boeseman (1964) was not in accordance with the International Code of Zoological Nomenclature (1964, Article 75), which states, among other things, that a neotype is to be designated only in connection with revisionary work, and that the designator of a neotype must give his reasons for believing all original type material to be lost or destroyed and the steps that have been taken to trace it. Since designation of a neotype would solve no nomenclatorial problems, and since we have not exhaustively sought

type material, we do not deem it necessary or proper to take this action ourselves.

Bleeker's original description was based on a single specimen, 650 mm. long, from "Batavia, in mari," with a pectoral fin shorter than the head and no swimbladder. The description obviously applies to the species for which the name is now used.

Thunnus rarus Kishinouye, 1915. No type specimens. Original description based on a single specimen, 28.8 inches (ca. 730 mm.) long, from Nagasaki. The gill-raker count of 6+17, short pectoral fins (no measurements given), and lack of swimbladder show this nominal species to be a synonym of *T. tonggol*.

Thunnus nicolsoni Whitley, 1936. Holotype Australian Museum IA. 6553, a 189 mm. head of a specimen originally 30 inches (762 mm.) total length caught between Lindeman and Maher Islands, Cumberland Group, North Queensland, Australia. The gill raker count of 6+16 and pectoral shorter than head establish this as a synonym of *T. tonggol*.

Characters

Pectoral fin (see fig. 26) varying in length from medium (22–31 percent of fork length) in specimens less than 600 mm. to short (16–22 percent) in those over 600 mm. (the latter resembling only *T. thynnus* and *T. maccoyii*). Tail region comparatively long, longest in large specimens; distance from snout to second dorsal origin 49–55 percent of fork length, decreasing with size (consistently lower than in any other *Thunnus* species).

Gill rakers 19–26 (rarely to 28), fewer than in any other *Thunnus* species except *T. atlanticus*.

Liver without striations on ventral surface, its right lobe long and narrow, without vascular cones on its dorsal side (as in *T. albacares* and *T. atlanticus*). Spleen on right side, stomach on left (as in all except *T. alalunga*). Kidney with a bulky anterior mass and a long, narrow tail, reaching vertebra 15–17.

Swimbladder absent or rudimentary.

Cutaneous arteries originating at the level of vertebra 7–8, passing laterally between ribs 4 and 5 or 5 and 6, dividing between intermuscular bones 6 and 7 (as in *T. albacares*, *T. obesus*, and *T. atlanticus*). A single row of arterioles and venules arising from each cutaneous branch (as in *T. alalunga*, *T. albacares*, and *T. atlanticus*), but arising from the lateral side of each vessel (as in *T. albacares* and *T. atlanticus*).

Post-cardinal vein present (as in *T. albacares*, *T. atlanticus*, and *T. obesus*).

Posterior parasphenoid margin not angulate (similar to *T. albacares* and *T. atlanticus*).

Vertebrae 18+21 (as in all except *T. atlanticus*). First ventrally directed parapophysis usually on vertebra 10. First closed haemal arch usually on vertebra 11 (as in *T. atlanticus*, *T. albacares*, *T. obesus*, occasionally *T. thynnus*) or 12. Anterior haemal prezygapophyses arising well ventrad on haemal spines (as in *T. albacares* and *T. atlanticus*). Haemal postzygapophyses long, the longest about equal to or longer than centrum length (as in *T. atlanticus*, slightly longer than in *T. albacares*). Anteriormost ventrolateral foramina large, more than three times as wide as haemal spine (as in *T. albacares* and *T. atlanticus*).

Nominal Species

There appear to be only two synonyms of *T. tonggol*: *Thunnus rarus* Kishinouye from Japan and *T. nicolsoni* Whitley from Queensland. Rivas (1961) placed *T. nicolsoni* in the synonymy of *T. albacares* but the gill raker count of 6+16=22 alone (Whitley, 1936) is enough to show that this is incorrect.

Range

T. tonggol is limited to the Indo-West Pacific. It is found from the western and southern coasts of Kyushyu and the southwestern part of the Japan Sea (Kishinouye, 1923, p. 449), south through the Batavia Sea (Bleeker, 1851, p. 356) to New Guinea, New Britain, and the entire north coast of Australia (Serventy, 1956b). On the Australian east coast, it is reported at least as far south as Twofold Bay, New South Wales; on the west coast it reaches at least to Cockburn Sound in the Freemantle area. Its range in the Indian Ocean (Jones, 1963) includes the Indo-Australian Archipelago, Andaman Islands, both coasts of India, southern Arabia, the Somalia coast, and the Red Sea, but it was not reported from East African waters by Williams (1964) or Merrett and Thorp (1966).

Gill-raker counts indicate differences between populations in the western Indian Ocean, with a modal number of 26, and those in the eastern Indian Ocean and western Pacific, with a mode of 23. More data are necessary to corroborate this.

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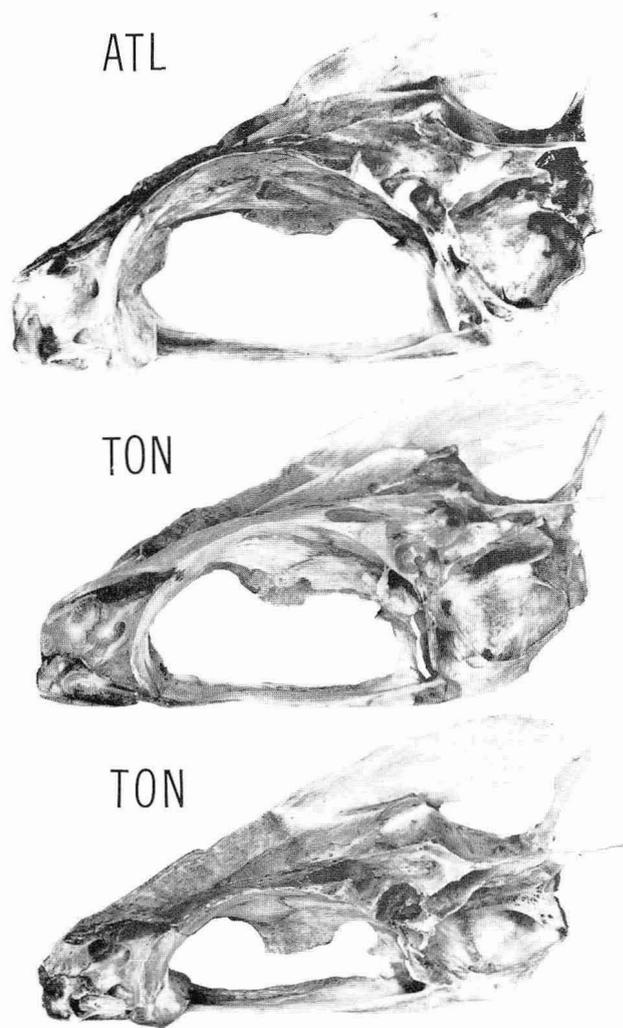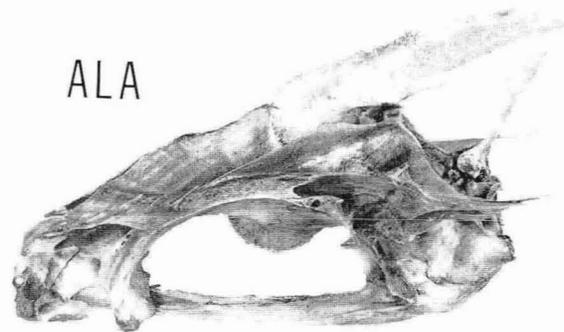
APPENDIX

FIGURE A-1.—Lateral view of skulls of *Thunnus* species. (top) *T. atlanticus*, skull length 88 mm.; (middle) *T. tonggol*, 56 mm.; (bottom) *T. tonggol*, 122 mm.
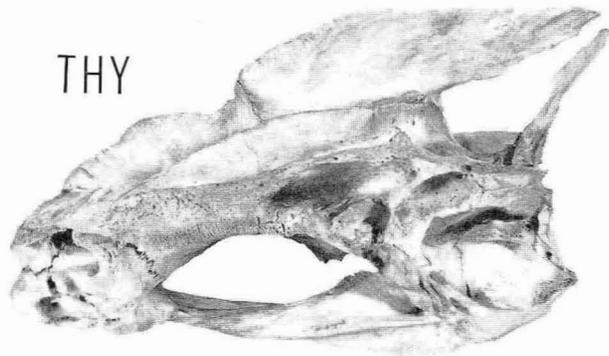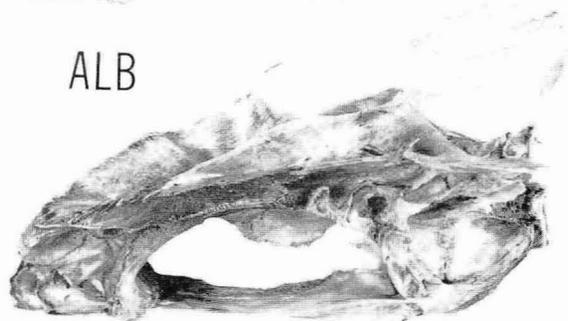
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FIGURE A-2.—Lateral view of skulls of *Thunnus* species. (top) *T. alalunga*, skull length 151 mm.; (middle) *T. thynnus*, 103 mm.; (bottom) *T. thynnus*, 335 mm.

FIGURE A-3.—Lateral view of skulls of *Thunnus* species. (top) *T. obesus*, skull length 200 mm.; (middle) *T. albacares*, 113 mm.; (bottom) *T. albacares*, 164 mm.