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NOAA Technical Report NMFS Circular 450

The Utility of Developmental Osteology in Taxonomic and Systematic Studies of Teleost Larvae: A Review

Jean R. Dunn

June 1983

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
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Malcolm Baldrige, Secretary
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John V. Byrne, Administrator
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William G. Gordon, Assistant Administrator for Fisheries

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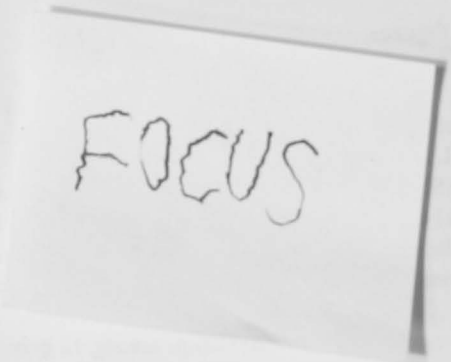
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The Utility of Developmental Osteology in Taxonomic and Systematic Studies of Teleost Larvae: A Review

JEAN R. DUNN[1]

ABSTRACT

Numerous examples from the literature indicate that cartilaginous and bony structures aid in the taxonomy of teleost larvae. The vertebral column, neural and haemal spines, ribs, predorsal bones, basal supports, and constituent bones of the median and paired fins, and the bones of the skull have all been used to varying degrees in larval fish taxonomy. The size, number, and morphology of cartilaginous or bony structures and their sequence of ossification have been employed to elucidate identification of larvae. Such structures have been used as characters at every taxonomic level, although no single structure has been found to be useful at all levels.

Various methods for preparing and studying cartilaginous or bony structures are available (e.g., clearing and staining, and radiography). The use of biological stains for detecting cartilage and/or bone, however, is the technique most commonly used for larval fishes.

Studies of developmental osteology have been used only recently to infer phylogenetic relationships of teleosts. Morphological characters and their development have great systematic utility at all hierarchical levels. Osteological studies of fish larvae and rigorous documentation and analyses of such studies in the primary literature have the potential to notably increase our understanding of teleost phylogeny.

INTRODUCTION

Due to similarities in appearance, fish larvae of some groups are difficult to identify—using either pigment patterns or morphology. Examples of such difficult groups occurring in the marine environment include (but are not limited to) clupeids, scorpaenids, gadids, scombrids, cottids, and hexagrammids. Because of the problems encountered when attempting to identify larvae of these groups, detailed studies of developmental osteology are often required.

Ossified structures may be defined as those skeletal structures composed of bone (e.g., skull and trunk bones); in practice they are distinguished in the laboratory by their uptake of biological stains, usually Alizarin Red. Endochondral bone is preformed in cartilage, whereas dermal bones ossify directly from membrane (Wake 1979). Cartilaginous structures may also be distinguished by their uptake of vital stains, usually Alcian or Toluidine Blue, allowing one to count or examine the structure of bones which may not ossify until late in the larval period, until well into the juvenile stage, or never (e.g., epurals, predorsal bones, radials of pterygiophores, etc.). Meristic segments, those structures commonly defined as countable structures normally occurring in a series (e.g., vertebrae, neural and haemal spines, fin spines and rays and their supporting bones), are often a powerful tool for identifying teleost larvae (e.g., Matsumoto et al. 1972; Richards and Potthoff 1974; Berrien 1978; Potthoff 1980; Fritzsche and Johnson 1980). Analysis of osteological structures can also help place unknown fish larvae in the correct order, suborder, and, sometimes, family (Ahlstrom and Moser 1976). Osteological structures are of demonstrable value in phylogenetic studies and can be of great utility in elucidating systematic relationships based on studies of teleost larvae (Moser and Ahlstrom 1970; Ahlstrom et al. 1976; Kendall 1976, 1979; Potthoff et al. 1980).

Taxonomy is here taken as the study of groups of organisms, their identification and variation; systematics as the study of the relationships of organisms, their distribution, classification, and evolution (Blackwelder 1967; see also Simpson 1961 and Mayr 1969 for alternate definitions). Phylogeny (following Mayr 1969) is the study of the lines of evolution of a group of organisms—the origin and evolution of higher taxa.

Much of the activity of larval fish taxonomists today is so-called alpha taxonomy (Mayr et al. 1953), identifying fish larvae to species. In the eastern subarctic Pacific, only about 50% of the larvae collected can be identified to species (Kendall et al. 1980[2])—due primarily to such abundant, species-rich, and poorly known families as Scorpaenidae, Cottidae, Stichaeidae, and Agonidae. Increased examination of osteological structures and their documentation in the formal literature may expand our understanding of the relationships of teleosts as well as enable the specific identification of a larger proportion of larvae.

The utility of developmental osteology in taxonomic and systematic studies of teleost larvae has not previously been reviewed. Therefore, in addition to describing laboratory methods commonly used to facilitate the study of cartilaginous and bony structures and in reviewing pertinent structures of the axial skeleton, median and paired fins, and cranium, I have attempted to synthesize the available knowledge regarding the value of these structures in taxonomic and systematic studies of fish larvae. In preparing this review, I have drawn freely upon previously published papers on taxonomic aids in larval fish studies (Berry and Richards 1973; Ahlstrom and Moser 1976) as well as on unpublished notes from classes conducted by the late E. H. Ahlstrom[3].

[1]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[2]Kendall, A. W., Jr., J. R. Dunn, R. J. Wolotira, Jr., J. H. Bowerman, Jr., D. B. Dey, A. C. Matarese, and J. E. Munk. 1980. Zooplankton, including ichthyoplankton and decapod larvae, of the Kodiak shelf. Unpubl. manuscr., 393 p. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98112.

[3]Ahlstrom, E. H. (deceased), Southwest Fish. Cent. La Jolla Laboratory, Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, class notes taken by J. R. Dunn, August 1971, and class notes recorded by Beverly Vinter, NWAFC, March-April 1976.

METHODS OF PREPARING LARVAL FISHES FOR SKELETAL STUDY

In working with larval fishes, it is necessary to know the counts of meristic structures in the adults. Because data are often not available and details of the structure of cartilaginous or bony parts are absent from the literature, the investigator must often collect his own data from adults. Erroneous identifications occur throughout the literature; therefore, caution is necessary in extracting data or working with unfamiliar groups.

There are several methods for preparing larval fishes for cartilage and bone study. The most common method involves clearing the flesh and staining the skeleton with bone- and/or cartilage-specific stains. The uptake of Alizarin Red stain, perhaps the most widely used bone-specific stain, is apparently not the first indication of ossification (Meyer and O'Rahilly 1958), but for practical purposes the uptake of this stain is usually considered to represent the onset of ossification. The Schultze method (1897) and its derivatives (e.g., Dawson 1926; Hollister 1934) include: 1) using potassium hydroxide (KOH) to digest the flesh of specimens; 2) staining ossified structures with Alizarin Red; 3) clearing the tissue in a succession of baths of glycerin and dilute KOH; and 4) storing in pure glycerin. The Schultze method and its variants have the advantage of being fairly rapid, particularly on small specimens. However, when using KOH, large specimens often swell or rupture (Taylor 1967)—probably due to osmotic pressures within the bodies of the organisms. Sometimes these specimens cannot be used for osteological study due to their disintegration. A method using enzyme (trypsin) digestion in place of alkaline maceration was introduced by Taylor (1967); he noted that problems may arise in producing good transparent specimens when using the Schultze method or its modifications. Taylor's method is usually satisfactory, but slower (e.g., days for larvae and a few weeks for juveniles) than the Schultze procedure for clearing and staining fish larvae. However, results from Taylor's procedure are often superior. Problems encountered using this method, such as persistent opacity of skin or difficulty in destaining specimens, were noted by Miller and Van Landingham (1969) who recommended alternate procedures, such as the use of carbon tetrachloride to dissolve fat and glacial acetic acid in glycerin to correct overstaining. Taylor's method was modified by Paxton (1972) who used ethyl alcohol to dissolve undigested fat and, instead of KOH-based Alizarin stain, used an alcohol-based stain to prevent specimen disarticulation.

Cartilage stain (Toluidine Blue) in conjunction with bone-specific Alizarin Red was in use over 40 yr ago (Williams 1941), but results with this method were often unpredictable. A modification of the Simons and Van Horn (1971) procedure for staining cartilage blue and bone red was introduced by Wassersug (1976) who utilized Alcian Blue, Alizarin Red, and KOH maceration. Taylor's enzyme method was modified by Dingerkus and Uhler (1977) to permit differential staining of bone and cartilage in fishes using Alcian Blue to stain cartilage. This technique offers the advantages of enabling one to trace the ossification of cartilage structures. Unfortunately, some workers (Nelson[4]; Dunn pers. obs.) have noticed problems with the Dingerkus-Uhler method, such as staining ossified structures blue (teeth, spines and rays, and scutes). Problems associated with the Dingerkus-Uhler method were discussed by Taylor and Van Dyke (1978[5]) who suggested modifications of the former procedure. These problems include the deossification of bones, due to excess acidity during specimen fixation, and the possibility that washing of specimens following fixation and prior to cartilage staining may render cartilage unstainable. More research is needed, both on cartilage and bone stains and on methods of preserving teleost larvae, if we are to rely on the specificity of cartilage and bone stains.

Ono (1980) described a modification of the Winkelmann and Schmit (1957) silver impregnation technique to demonstrate muscle-bone-cartilage relationships in small fishes. This technique is claimed to be faster than the usual double-staining techniques, and, since muscles stain, their location and origin can be located.

A number of microscopic techniques may be used to enhance one's ability to observe structures in cleared and stained specimens. Transfer of specimens from pure glycerin to solutions of about 60% glycerin in KOH increases the translucence of the specimen (Miller and Van Landingham 1969). The use of polarizing filters also aids in detecting structural details of the specimen (Miller and Van Landingham 1969). Changing light intensity and the angle of the substage mirror helps viewing unstained cartilage (Potthoff et al. 1980). The use of a closed-circuit television unit attached to a microscope is valuable when detailed examination of particular structures is desired in cleared and stained larvae. Bones may be dissected out of an intact specimen (Weitzman 1974), although dissection difficulty increases with decreasing size of the specimen.

Uptake of stain in individual fish may be variable. Decalcification of bone occurs with length of time in Formalin preservative. Stain may rapidly leach from ossified structures in specimens which have been preserved over a period of time. The examination of specimens shortly after they have been put through the clearing and staining process is often necessary (Dunn pers. obs.). We routinely attempt to make counts of meristic structures in specimens as soon as they are placed in 70% glycerin. The specimen-fixation problem in relation to uptake of Alizarin Red was reviewed by Taylor (1977). He offered recommendations on preservation techniques, including the use of powdered limestone instead of sodium borate as a buffer in Formalin.

Radiography is a rapid method of examining bony structures. The applicability of "soft" X-rays for radiography of larval and juvenile fishes was reviewed by Miller and Tucker (1979). The use of Agfa-Gevaert RP1 (Curex or Osray) medical film for juvenile and adult fishes is relatively inexpensive and results in a negative superior to that obtained by the use of mammography film. Excellent results using various other films have been reported (Miller and Tucker 1979). A medical/dental film processor produces quality negatives consistently and rapidly.

Radiographs offer limited benefits in studying incompletely ossified fish larvae. Cartilage does not show in radiographs, and radiography may cause erroneous conclusions as to the presence or absence of structures which may ossify in the late larval or juvenile stage. Radiographs may also be hard to interpret, as in the discrimination of vertebrae into precaudal and caudal groups. In nomeid fishes, the backward bending and crowding together of haemal spines and ribs on caudal vertebrae made difficult the differentiation of precaudal and caudal vertebrae from radiographs although not on cleared and stained specimens (Ahlstrom et al. 1976).

Counts of fin spines, fin rays, branchiostegal rays, and scales can be made without resorting to radiographs or clearing and staining, but interpretation of such counts may sometimes be difficult. For example, a factor easily overlooked when examining larval fishes not cleared and stained is whether or not the last two dorsal or anal fin rays arise from a single pterygiophore—a character easily detected on cleared and stained material. Larvae may be immersed

[4]D. W. Nelson, College of Fisheries, Univ. Wash., Seattle, WA 98195, pers. commun. January 1982.

[5]Taylor, W. R., and G. C. Van Dyke. 1978. Staining and clearing small vertebrates for bone and cartilage study. Unpubl. manuscr., 19 p. Natl. Mus. Nat. Hist., Wash., DC 20560.

in Alizarin stain and 1% KOH for a few hours to enable more accurate counting of fin rays and branchiostegal rays.

Electron microscopy (scanning and transmission) may be of value in the study of bony parts, but apparently has not been extensively used on larval fishes (Meyer-Rochow 1972). Examples of the use of electron microscopy include study of the ultrastructure of otoliths in juvenile fishes (Dunkelberger et al. 1980), the development of fins and their structure (Yamamoto and Egami 1974; Géraudie 1978), and the development and organization of scales (Hughes 1981).

Other methods are available for defleshing the skeleton of fishes, but these are not useful on small and fragile larvae. Examples include the use of enzyme "pre-soakers" to produce disarticulated (Ossian 1970) and articulated (Konnerth 1965) skeletons or dermestid beetles (Knudsen 1966) for defleshing skeletons.

SKELETAL STRUCTURES OF TELEOST LARVAE AS TAXONOMIC AIDS AND SYSTEMATIC CHARACTERS

Vertebral Column and Associated Bones

The number, morphology, and sequence of ossification of the vertebral column and associated bones of the vertebral centra and their appendages, of the neural and haemal spines, and of the ribs and intermuscular bones are useful as taxonomic aids and are of systematic importance. The manner of formation of vertebral centra, arches, and ribs was described for herring by Manavala Ramanujam (1929), for haddock (*Gadus aeglefinus* = *Melanogrammus aeglefinus*) by Faruqi (1935), and for *Lebistes reticulatus* by Mookerjee et al. (1940).

Vertebrae (or myomeres) are one of the basic meristic characters used in identification of larval fishes (Table 1). Myomeres form in the embryo (Fowler 1970) and are considered to be nearly, if not exactly, equivalent to the number of vertebrae. Possible exceptions to this generality have been suggested by Hempel and Blaxter (1961) and by Berry and Richards (1973). Myomeres may be difficult to count, particularly those near the skull or near the end of the caudal peduncle. The use of polarized light, immersion of the specimen in glycerin, or staining the larvae in alcohol-based stains (Russell 1976) often aid in precise myomere counts. Stains apparently have not been developed which differentially show myosepta and myomeres, although such stains appear potentially feasible.

When counting vertebrae, some authors (e.g., Berry and Richards 1973) include the ural bones (or urostyle) as a single unit, irrespective of the number of constituent elements: others (e.g., Cohen and Nielsen 1978) do not include ural bones in their counts. Partial counts of vertebrae (or myomeres) are useful when applied to certain groups of fishes. Preanal, postanal, predorsal, and postdorsal myomere counts were used by Houde et al. (1974) in their description of the scaled sardine, *Harengula jaquana*. Predorsal and preanal myomeres were counted in ophichthyid eels by Fahay and Obenchain (1978), whereas preanal and nephric myomeres were utilized by Leiby (1979). The possibility of fin or vent migration in relation to the myomeres should not be overlooked when using such counts, because these counts may change during ontogeny (Richards et al. 1974).

In addition to vertebral counts, the gross morphology of the vertebral column or its centra may be of taxonomic importance. Obvious examples are the ostariophysin fishes in which the anteriormost four or more vertebrae are modified into the Weberian apparatus. These vertebrae are commonly included in the precaudal counts

Table 1.--Characters of pelagic life history stages that aid in identification to order or suborder (from Ahlstrom and Moser 1976).

Character	Pleuronectiformes	Myctophiformes	Beryciformes	Perciformes	Scorpaeniformes	Clupeiformes	Argentinoidei	Stomiatoidei	Anguilliformes	Gadiformes
Larvae Predominant body shape	Various, markedly Compressed	Various, often elongate	Slender to stubby	Various, usually stubby	Various, usually stubby	Elongate, slender	Elongate, slender	Elongate, slender	Leptocephalus	Various, elongate to deep-bodied
Snout to anus length	Usually <40%SL	ca. 40-70%SL	ca. 30-60%SL	Various, 20-60%SL	ca. 35-60%SL	65-95%SL	70-90%SL	30-95%SL (usually long)	40-95%SL	Usually <50%SL
Character of gut	Coiled	Straight, variously shaped	Coiled	Various, usually coiled	Coiled	Straight	Straight	Straight	Straight or looped	Usually coiled
Trailing gut	Not trailing, but gut can be distended from body	Seldom trailing, reverse can apply; gut gradually increases in relative length on larvae	Not trailing	Not trailing	Not trailing	Not trailing	Not trailing	Often trailing, sometimes markedly	Seldom trailing (markedly trailing on some congrids)	Not trailing
Number of vertebrae	25 to 65	Myctophids 28 to 45, others 29 to 121	Usually 23 to 33	ca. 20 to 100+, often 24 to 28	ca. 25 to 65	ca. 40 to 60	ca. 40 to 85	ca. 30 to 100+	68 to 400+ (most 100 to 250)	ca. 40 to many (Macruridae)
Larval stage characters Larval eyes	Round	Round to markedly narrowed; often choroid tissue under eye, infreq. stalked	ca. Round	Usually round, can be narrowed with choroid tissue	ca. Round	ca. Round	Round or narrowed, sometimes stalked	Round to markedly narrowed (stalked in Idiacanthus)	Round or moderately narrowed (telescopic: 2 families) choroid tissue under eye (sev. families)	ca. Round
Larval head spination	Frequently-various, useful in ident.	Various-none to markedly heavy	Various-none to markedly heavy	Various-none to markedly heavy	Usually-useful in ident.	None	None	None	Usually none	Usually none
Early forming fin rays or spines (often ornate)	Often: 1 to 12 ant. D rays Sometimes: 2 or 3 V rays	Occasionally P fin rays	Often V & ant. D	Sometimes 1 or more 1st D sp. and V sp. & rays	No, but P fin can be quite large	No	No	Occasionally (P in Ichthyococcus)	No	V fins (sometimes)
Transformation stage	Marked (1 eye shifts to right or left)	Various, often marked, sometimes delayed sometimes prolonged	Usually gradual	Usually gradual	Gradual	Marked D, A & V fins move, anchovy snout forms	Marked	Marked, photophore formation can be prolonged	Marked	Gradual
Early juvenile stage (prejuvenile of Hubbs, 1958)	No, but larval stage can be markedly prolonged	In some forms (ex. Macristiella stage)	Sometimes marked (ex. Holocentrids)	Sometimes (in var. families)	Pelagic juvenile stage (ex. some scorpaenids)	No	No	No	No	No

(Hubbs et al. 1974; Williams and Bond 1980). The sometimes-diagnostic surface features of centra have been used by archeologists and paleontologists for taxonomic identification (Casteel 1976). However, like other structures, centra undergo ontogenetic changes in shape even after ossification has occurred (Clothier 1946, 1950; Bond and Uyeno 1981).

The length of individual centra may vary according to stage of development (Kramer 1960); in *Scomber japonicus*, centra near the middle of the vertebral column initially outgrew those more anterior or posterior. In some fishes sexual dimorphism occurs in the structure of vertebral elements, such as in the relative size of the haemal canal of the first caudal vertebra in *Labrus mixtus* (Ford 1937). Other variations in structure, such as the size and shape of the first haemal spine and the modifications of neural and haemal spines, were included by Clothier (1950) in his key to adult fishes and noted by Matsumoto (1963) and Potthoff (1974) for the first haemal spine in *Thunnus alalunga*.

The separation of vertebral counts into precaudal (abdominal) and caudal components (Fig. 1) has useful application in the taxonomy of a number of groups of larvae, even at the species level (Potthoff 1974; Sumida et al. 1979). As commonly defined, the caudal centra lack pleural ribs and possess medial haemal spines (Hubbs and Lagler 1949; Berry and Richards 1973). In various taxa, the haemal spine of the first caudal vertebra is anterior to, or articulates with, the first anal pterygiophore (Fig. 1, 2A). In some species of nomeid fishes, from one to five caudal vertebrae bear both a haemal arch and a pair of pleural ribs (Ahlstrom et al. 1976). These authors defined caudal vertebrae in nomeids as those possessing a haemal spine regardless of the presence of ribs. They noted that precise determination of precaudal and caudal vertebrae could easily be made in cleared and stained specimens by following the sequence of ossification of samples because the haemal spines ossify earlier than the ribs.

Vertebral counts are of great value in separating larvae which are superficially similar but phylogenetically remote, such as clupeids and pholids (Russell 1976); vertebral counts also aid in identification of closely related taxa such as species of clupeids (Houde et al. 1974). The intraspecific variation in vertebral counts must be known when using this character to separate closely related taxa (Berry and Richards 1973). Unfortunately, few lists of vertebral counts and their intraspecific variation are available in the literature. Vertebral counts for about 553 species of fishes occurring in the eastern Pacific Ocean were listed by Clothier (1950) and Clothier and Baxter (1969[6]). Hotta (1961) listed vertebral counts for 266 species in 106 families of fishes in Japanese waters, while Takahashi (1962) listed such counts for 256 species in 100 families. Meristic characters (including precaudal and caudal vertebral counts) for 642 species of marine fishes of the northwest Atlantic Ocean were listed by Miller and Jorgenson (1973), and means (and range of means) of vertebral counts of 3,137 fish species belonging to 118 families were presented by Lindsey (1975). Lists also exist for certain specific groups such as North Pacific blennioids (Makushok 1958) and cottids (Howe and Richardson 1978[7]).

The shape and structure of projecting processes of the vertebrae, termed "apophyses" (Wake 1979), can be of taxonomic significance. Neurapophyses are dorsal projections from the centrum which join to form the neural arch; haemapophyses are ventrolateral projections from the centrum which join to form the haemal arch (Fig. 2A). Parapophyses are bony projections on each side of the precaudal centra to which pleural ribs are attached; zygapophyses are projections of the centra which, in some fishes, may interlock with each other and give rigidity to the vertebral column (Fig. 2B). These may be separated into neural and haemal pre- and postzygapophyses (Clothier 1950). The size and shape of the apophyses were used as a taxonomic character by Clothier (1950) and Clothier and Baxter (footnote 6) in their keys to adult California fishes based on the vertebral column. Potthoff (1974) described the ontogeny of apophyses in tunas (*Thunnus*) and used the position of the first haemal postzygapophyses as one of several characters to separate three species of *Thunnus*. Bond and Uyeno (1981) used the remarkable changes in parapophysis shape which occur during growth in *Scombrolabrax heterolepis* as one character justifying placement of this monotypic species in a separate suborder and family.

The number, size, and shape of neural and haemal spines may be useful taxonomic characters in larval fishes as they have been

[6]Clothier, C. R., and J. L. Baxter. 1969. Vertebral characters of some Californian fishes with notes on other Eastern Pacific species. Unpubl. manuscr., 264 p. Calif. Dep. Fish Game, Sacramento.

[7]Howe, K. M., and S. L. Richardson. 1978. Taxonomic review and meristic variation in marine sculpins (Osteichthyes: Cottidae) of the Northeast Pacific Ocean. Unpubl. manuscr., 142 p. School of Oceanography, Oregon State Univ., Corvallis, OR 97331.

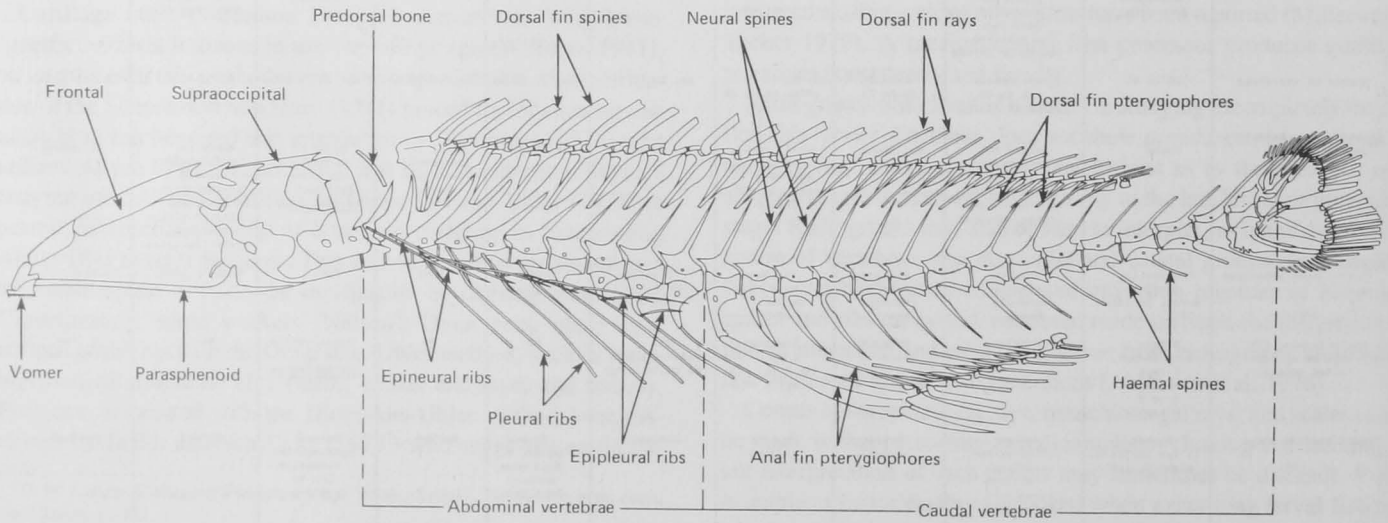


Figure 1.—Skeletal structure of *Sebastes* sp.

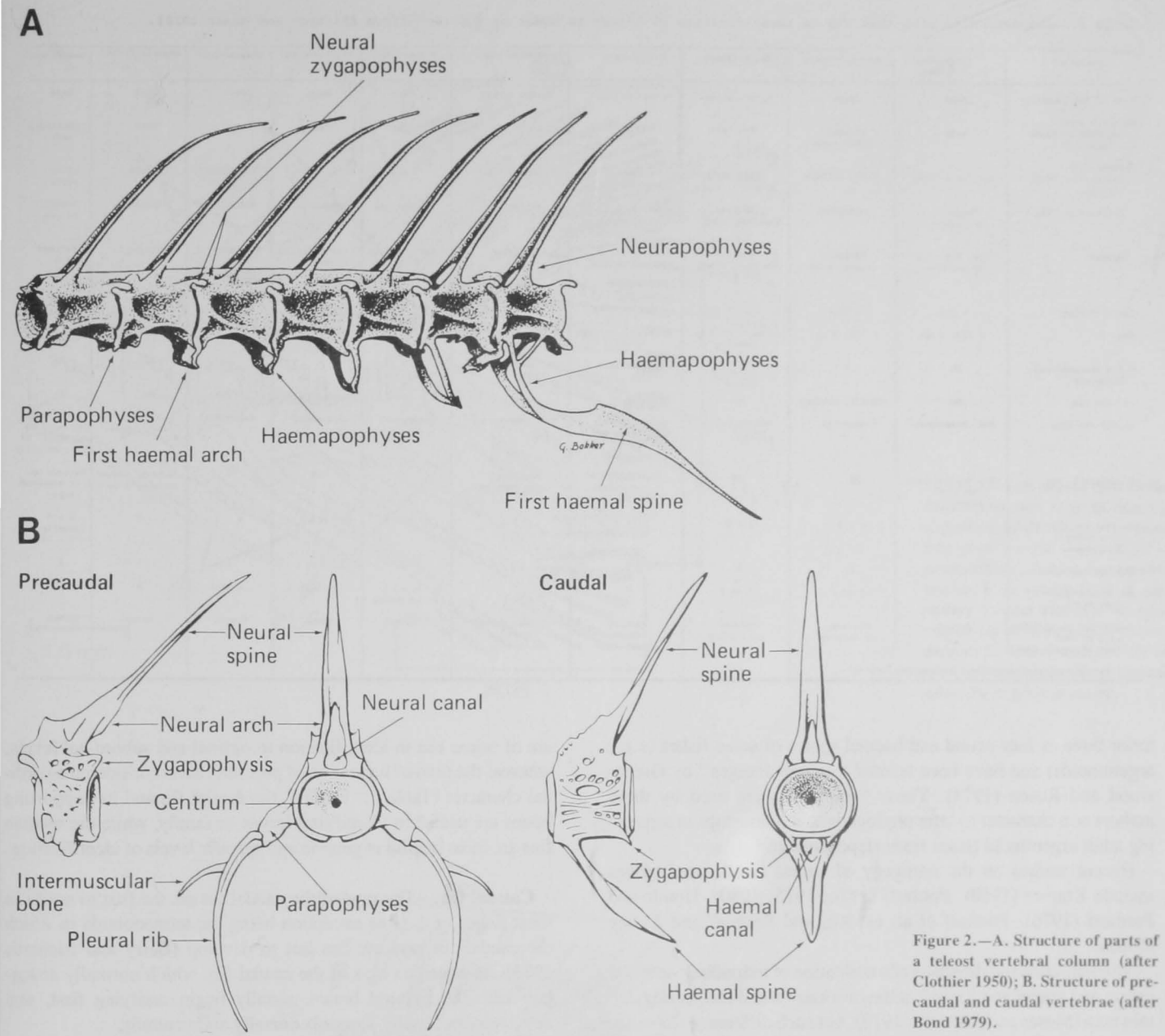


Figure 2.—A. Structure of parts of a teleost vertebral column (after Clothier 1950); B. Structure of precaudal and caudal vertebrae (after Bond 1979).

shown to be for adult fishes by Clothier (1950) and Clothier and Baxter (footnote 6) from which the following has been extracted. In adults, the most anterior neural spines may differ in shape, length, and width from the more posterior spines. The neural and haemal spines may be modified into plates (as in *Gymnothorax mordax*), or the first few anterior neural spines may be fused into a bony plate (e.g., *Verrunculus polylepis*). The terminal three or so neural or haemal spines may be truncated distally and laterally broadened, whereas those anteriorly situated may be more spinous. In the cottid *Icelinus quadriseriatus*, the last three neural and haemal spines are enlarged into wide plates. In bothid and pleuronectid flatfishes, the first haemal spine is distinctively strong and heavy, and its structure varies interspecifically. Whether or not the centra adjacent to the ural centrum (or centra) bears a neural spine is a taxonomic character of value at the ordinal level (Ahlstrom and Moser 1976), as shown in Table 2. If reduced or lacking, this is often termed the "rudimentary neural arch" (Greenwood and Rosen 1971) and, when enlarged or variously shaped and ankylosed to other bones, is called the "supraneural lamina" by these authors.

The first haemal spine and first haemal arch may occur on the same vertebra in some fishes (e.g., *Engraulis mordax, Synodus lucioceps, Merluccius productus*), according to Clothier (1950), but more commonly the first haemal spine occurs posterior to the first haemal arch (Fig. 2A). The position of these two characters was used in a key to adult fishes based on skeletal elements by Clothier (1950) and Clothier and Baxter (footnote 6). According to Clothier (1950), the first haemal spine may be indeterminate when it is only a minute process, with subsequent spines becoming gradually longer (*Sarda, Thunnus, Neothunnus*), or because the haemal process fuses proximally only and remains bifurcate distally (*Albula vulpes*). In some atherinids (*Atherinops, Atherinopsis*, and *Leuresthes*), the position of the first haemal spine is obscured by the "haemal funnel" (Clothier 1950). In atherinids this structure begins 6 to 10 vertebrae in front of the first haemal spine and is essentially a double arch, the lowermost part of which does not fuse until the first haemal spine forms. Other variations in structure of neural and haemal spines are documented by Ford (1937), Clothier (1950), and Clothier and Baxter (footnote 6).

The posteriormost one or more haemal spines may be autogenous or ankylosed to the centra. Flanges may be present on the pos-

Table 2.--Characters of fins that aid in identification of larvae to order or suborder (from Ahlstrom and Moser 1976).

Character	Pleuronecti-formes	Myctophiformes	Beryciformes	Perciformes	Scorpaeniformes	Clupeiformes	Argentinoidei	Stomiatoidei	Anguilliformes	Gadiformes
Type of fin elements	Rays	Rays	Spines & rays	Spines & rays	Spines & rays	Rays	Rays	Rays	Rays	Rays
Pectoral rays* Sequence of formation	Late	Various; often early	Not late	Not late	Not late	Late	Late	Late	Late	Sometimes late
Ventral fins Sequence of formation	Sometimes early	Early to late	Often early	Various; sometimes early	Intermediate	Late	Rel. late	Rel. late	Absent	Often early
Position on body	Thoracic to jugular	Abdominal	Various Thor.-abd.-jug.	Usually thoracic, sometimes abd. or jug.	Thoracic	Abdominal	Abdominal	Abdominal	Absent	Thoracic or jug
Formula	6/6, 5/5, 0/4 or various	Various, usually 8-10	Not 1,5 various, often 1,6 1,7	1,5 or fewer	1,5 or fewer	Var. usually 7-10	Var. usually 8-12	Var. usually 5-6 (Bathophilus 4-26	Absent	Various 2-8
Dorsal fin(s)	1 fin	1 fin	1 or 2 fins	1 or 2 fins	1 or 2 fins	1 fin	1 fin	1 fin	1 fin	1 to 3 fins
Anal fin	1 fin, 0 sp.	1 fin, 0 sp.	1 fin, 1 to 4 sp. usually	1 fin, 1 to 3 sp. usually	1 fin, 0 to 3 sp.	1 fin, 0 sp.	1 fin, 0 sp.	1 fin, 0 sp.	1 fin, 0 sp.	1 or 2 fins, 0 sp.
D & A terminal ray-bifurcate	No	+	+	+, sometimes -	+, sometimes -	+	+	+	No	No
Adipose fin	No	Usually present	No	No	No	No	Usually	Often	No	No
Caudal fin type	Mod. homocercal	Homocercal	Homocercal	Homocercal (sometimes mod.)	Mod. homocercal	Homocercal	Homocercal	Homocercal	Reduced homo. prob.	Gadoid type; few rays on hypurals, br. rays dorsally
Principal C. rays	Var. no. br. rays Var. no. total rays	19	19	17 (sometimes fewer)	Variable, less than 17	19	19	19	Reduced number, usually 5 to 11	Various no. of branched rays
Maximum no. hypurals (including parhypural)	3 + 3	4 + 3	4 + 3	3 + 3	3 + 3	4 + 3	4 + 3	4 + 3	?	3 + 3 (usually 1 + 2)
Maximum no. epurals	2	3	3	3	3	3	3	3	?	2
No. ural centra (see text)	1	2 or 1	2 or 1	1	1	3, 2, 1 (occasionally 4)	3, 2 or 1	2 or 1	2	2
Neural sp. on vertebra adj. to ural (pu2 of Monod, 1968)	Normal	Reduced or lacking	Reduced or lacking	Lacking (some exceptions)	Various, normal reduced or lacking	Normal	Normal	Normal	Normal	Normal

(*) (Larval pectoral fins always early forming).

terior three or four neural and haemal spines of some fishes (e.g., argentinoids) and have been termed "preural flanges" by Greenwood and Rosen (1971). These "flanges" were used by these authors as a character to infer phylogenetic relationships in separating adult argentinoid fishes from alepocephalid fishes.

Recent studies on the ontogeny of neural and haemal spines include Kramer (1960), Potthoff (1974, 1975, 1980), Houde and Potthoff (1976), Potthoff et al. (1980), and Potthoff and Kelley (1982).

The sequence and direction of ossification of individual vertebral centra and neural and haemal spines are known to differ among certain taxa (Moser and Ahlstrom 1970), but such differences have not yet been analyzed. Such an analysis might offer considerable insight into phylogenetic affinities.

Ribs (pleural, epipleural, and epineural—Fig. 1, 2B), as well as intermuscular bones, are seldom-used characters of potential taxonomic and systematic value, but their use is poorly documented in the literature. Emeliĭanov (1935) described the origin and morphology of ribs in a number of fish species. Intermuscular bones (Fig. 2B) were used as a diagnostic character by Amaoka (1969) in distinguishing adult bothid and paralichthyid flatfishes, and the presence or absence of intermuscular bones was used by Hensley (1977) in his generic analysis of bothids. The ontogeny of pleural and epipleural ribs in the Pacific mackerel (*Pneumatophorus diego* = *Scomber japonicus*) was described by Kramer (1960), in the sea bream, *Archosargus rhomboidalis*, by Houde and Potthoff (1976), and in *Scombrolabrax heterolepis* by Potthoff et al. (1980).

Fins and Their Supports

The number, structure, position, and sequence of development of the fins are useful in identification of larvae at all taxonomic levels. Ahlstrom and Moser (1976) indicated that caudal and pelvic fins are of prime use in identification to ordinal and subordinal levels, whereas the time of formation of pectoral fins is considered an ordinal character (Table 2). Further, the caudal fin and its supporting bones are useful in identifying larvae to family, while the median fins are most helpful at generic and specific levels of identification.

Caudal fin.—The rays of the caudal fin are the first to ossify in most fishes, a notable exception being the tetraodontids in which the caudal fin rays are the last to develop (Berry and Richards 1973). The median rays of the caudal fin, which normally articulate with the hypural bones, usually begin ossifying first, and development usually proceeds dorsally and ventrally.

Generally, principal caudal rays (Figs. 3, 4) in adult fishes have been defined as the number of branched rays plus the adjacent dorsal and ventral unbranched rays (Hubbs and Lagler 1949). However, this definition does not apply to all fishes because some (e.g., Clinidae, footnote 3) possess no branched rays or the branching develops late (e.g., juvenile and adult cottids, Howe[8]) and is often of limited use in larval taxonomy. The number of rays articulating with the hypural bones, however, is often a useful taxonomic character. In some gadids the number of rays on the superior hypural is a generic character (Matarese et al. 1981), while the number of rays on the second hypural may be a taxonomic character at the specific or generic level (Dunn pers. obs.).

Secondary (procurrent) caudal rays are generally located anterior of the principal caudal rays, and normally do not articulate with hypural bones. These vary in number among phylogenetic groups and usually are the last rays of the caudal complex to ossify. In some taxa they may be of taxonomic utility. Among the cottids (footnote 8), the counts for dorsal and ventral secondary rays are distinctive

[8]K. M. Howe, College of Fisheries, Univ. Wash., Seattle, WA 98195, pers. commun. December 1980.

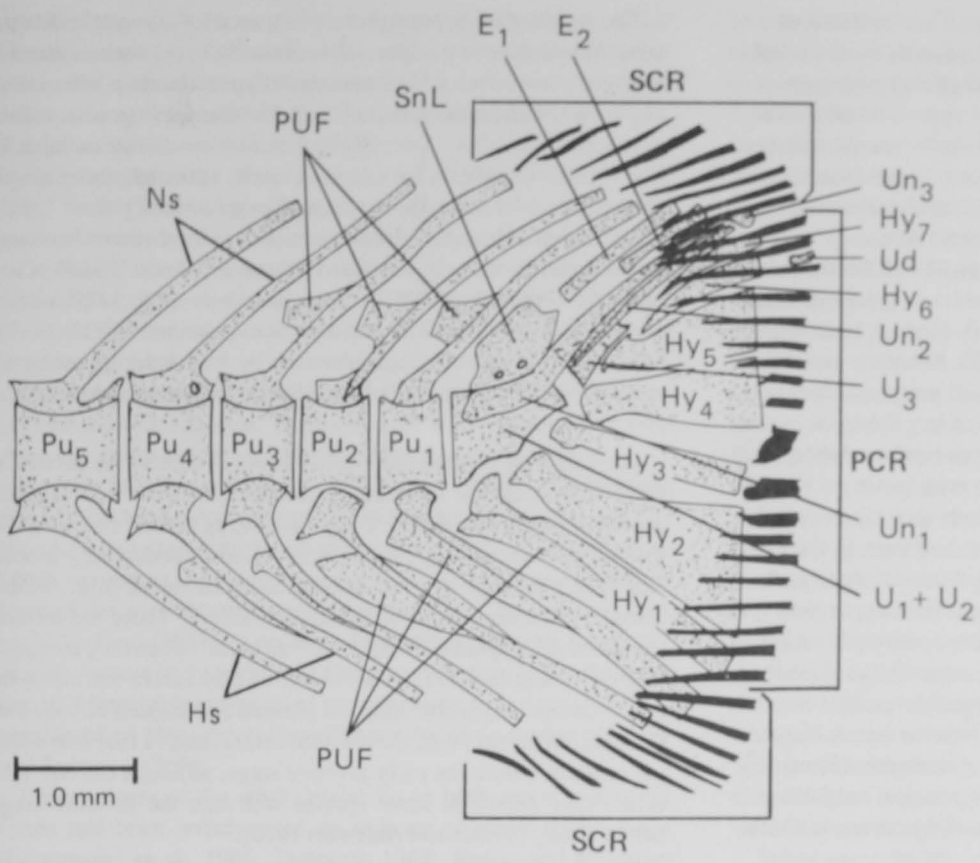


Figure 3.—Left lateral view of the caudal complex of a 38 mm SL *Argentina silus*. Clockwise from left: Ns = neural spine; PUF = preural flange; SnL = supraneural lamina; E = epural; SCR = secondary caudal ray; Un = uroneural; Hy = hypural; Ud = urodermal; U = ural centra; PCR = principal caudal ray; Hs = haemal spine; Pu = preural centra.

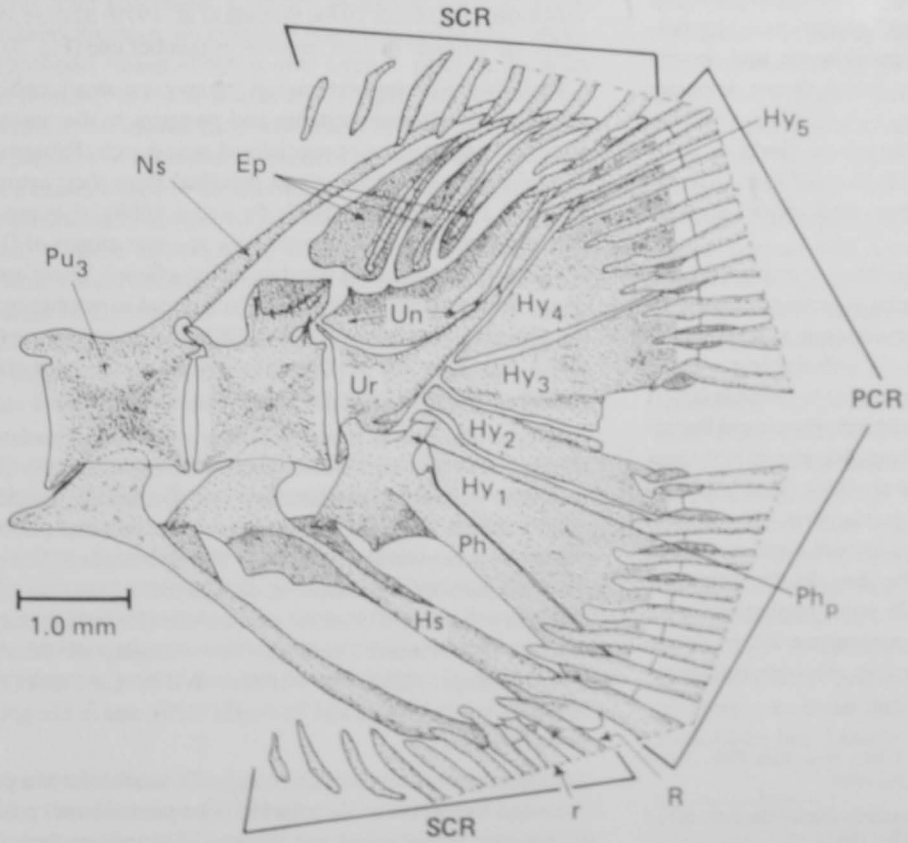


Figure 4.—Left lateral view of the caudal complex of a 68.1 mm SL *Scombrolabrax heterolepis* from the Atlantic Ocean (after Potthoff et al. 1980). Clockwise from left: Pu = preural centra; Ns = neural spine; Ep = epural; SCR = secondary caudal ray; Hy = hypural; PCR = principal caudal ray; Ph_p = parhypurapophyses; Ph = parhypural; R = secondary ray with procurrent spur; r = secondary forestunted ray; Hs = haemal spine; Ur = urostyle; Un = uroneural.

for some fishes, e.g., 6–8 dorsal, 6–8 ventral in *Hemilepidotus*; 11 dorsal, 7 ventral in *Chitonotus*; and 10–12 dorsal, 9–10 ventral in *Scorpaenichthys*. The related agonids and cyclopterids appear to possess few secondary caudal rays, but the ventral count is often 1 or 2 less than the dorsal count (footnote 8). In the scorpaenids (and hexagrammids), the dorsal and ventral secondary caudal counts are usually equal (footnote 8). The distribution and variation of secondary rays have not been investigated in most taxa.

The homocercal caudal fin is generally considered a conservative structure, and the distribution of upper and lower principal caudal rays is usually consistent within broad phylogenetic groups (Gosline 1960; Berry and Richards 1973; Ahlstrom and Moser 1976). The count of 10 (upper) and 9 (lower) principal caudal rays occurs in almost all clupeiform and salmoniform fishes, as well as in most berycoids. Perciforms have 9 + 8 principal caudal rays and scorpaeniforms vary but have 17 or fewer principal rays, whereas pleuronectiforms have highly variable counts ranging from 10 to 23 principal caudal rays. Exceptions occur, however. In the cottid genus *Ascelichthys*, the count of principal caudal rays is 6 + 7 (Matarese[9]), and a greater number of lower than upper principal caudal rays may occur in other cottid genera (footnote 8) as it also occurs in ceratiods (footnote 3) and in some catfishes (Lundberg and Baskin 1969). The distribution of principal caudal rays on hypural bones may vary among genera, as in some cottids (footnote 8), or among species, as in the Hexagrammidae (Kendall[10]). Detailed examination of the distribution of principal caudal rays in various groups of teleosts may result in useful taxonomic characters.

Departures from the normal homocercal caudal fin of teleosts are taxonomically helpful both in hypural structure and the distribution of the associated rays. The isocercal (gadoid) caudal fin is unique among teleosts in that the hypural bones support relatively few branched rays, some of which may occur dorsad of the hypurals (Ahlstrom and Counts 1955). Leptocercal caudal fins in eels are markedly reduced, as are those in some blennies. Molids possess a unique "pseudocaudal," termed a "clavus" characterized by failure of the notochord to flex, a lack of hypural bones, and possession of bones posterior to the last centrum which do not articulate directly with fin ray bases (Leis 1977). Much descriptive caudal-fin morphology remains to be completed, although the works on adult fishes provide a good basis (Hollister 1936; Gosline 1961; Monod 1968; Patterson 1968; Rosen and Patterson 1969; Nybelin 1963, 1971; Rosen 1973).

Hypural bones lie ventrad to the ural centrum or centra (or urostyle if fused) and support principal caudal rays in most teleosts (Figs. 3, 4). Counts of hypural bones are made from ventral to dorsal, but are usually expressed as superior plus inferior (e.g., 2 + 2, 4 + 3, etc.). The anteriormost hypural bone in some fishes is called the "parhypural" by some authors (Monod 1968; Rosen and Patterson 1969; Potthoff 1975, 1980) but not others (Moser and Ahlstrom 1970; Ahlstrom et al. 1976; Richardson et al. 1980; Markle 1980). As defined by Nybelin (1963), the parhypural differs from the following hypural bones in that it contains a haemal canal and more closely resembles a typical haemal spine than do the following hypural bones (see also Monod 1968). In some phylogenetically diverse groups of fishes, the parhypural possesses a lateral flange usually terminating in a point posteriorly (Fig. 4)—the parhypurapophysis of Nursall (1963).

[9]A. C. Matarese, Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98112, pers. commun. December 1980.

[10]A. W. Kendall, Jr., Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98112, pers. commun. November 1980.

The number of hypural bones is generally consistent among related phylogenetic groups, and variation from the norm is a useful systematic character. A high number of hypural bones is often taken as a primitive character (i.e., seven in *Elops* and salmonids); reduction is advanced (i.e., four in pleuronectids) as shown in Table 2. The hypural bones may be variously fused, ultimately into a single plate in adults of some species, e.g., *Coryphaena* (Potthoff 1980). When fusion of hypural bones occurs, it may be observed in ontogeny in some fishes (e.g., *Thunnus atlanticus*, Potthoff 1975; *Coryphaena*, Potthoff 1980) but not in others (e.g., *Ophichthus gomesi*, Leiby 1979; *Microgadus proximus*, Matarese et al. 1981). This reduction of constituent elements by fusion during ontogeny may be useful in analyzing relationships at the generic level (Moser and Ahlstrom 1970).

The centra supporting the hypural bones in teleosts are generally believed to undergo reduction in numbers by fusion during the course of evolution. Again, a high number is usually considered a primitive character (e.g., three in salmonids, occasionally four in clupeoids); a single centrum is considered advanced (e.g., Perciformes, pleuronectids) as indicated in Table 2. These are termed "ural centra" (Nybelin 1963) or the "urostyle" when they are fused into one (Gosline 1971). The fusion of ural centra can often be observed in ontogenetic series of cleared and stained larvae. For example, in myctophids, the two ural centra usually fuse into a single centrum before the early juvenile stage, although the two free centra may persist in some species well into the juvenile stage before fusing (Moser and Ahlstrom 1970).

Nybelin (1963) and Monod (1968) suggested that the urostyle consists of a fusion of a number of ural centra and preural centrum one. Hence, in certain groups of fishes some investigators consider the ultimate preural centrum as number two and the urostyle to be a fusion of preural centrum one and of the ural centra (Rosen and Patterson 1969; Houde and Potthoff 1976; Potthoff 1975, 1980) as shown in Figure 4. Other investigators (Moser and Ahlstrom 1970; Ahlstrom and Moser 1976; Sumida et al. 1979; Markle 1980) consider the ultimate preural centrum as number one (Fig. 3).

Epurals, which support epaxial fin rays, are small median bones dorsal to the ultimate vertebra and posterior to the posteriormost complete neural spine or specialized neural arch (Patterson 1968). Considered to be neural spines detached from their neural arches (Gosline 1960; Nybelin 1963; Patterson 1968), they are of taxonomic and phylogenetic significance in some groups of fishes and are generally constant in number within species. There are usually one to three epurals, but they may be reduced in number or size during ontogeny (Richardson et al. 1980), fusion can occur (Potthoff 1980), they may not ossify until well into the juvenile stage as in some bathylagids (Dunn 1983), or they may be lacking.

Uroneurals, paired bones generally occurring dorsolaterally to the ultimate vertebra, are often the first bones to ossify in the caudal complex. According to Patterson (1968) they are modified ural neural arches. They frequently fuse to the terminal centrum, and the anterior uroneural may expand during ontogeny. The presence of three pairs of uroneurals is considered a primitive character, whereas reduction in numbers or even loss (Pleuronectidae) is considered an advanced character. The ontogeny of uroneurals in *Hiodon, Elops,* and *Salmo* was described by Cavender (1970), in *Archosargus* by Houde and Potthoff (1976), and in *Coryphaena* by Potthoff (1980).

The presence of urodermals or stegurals is considered a primitive character. Urodermals (Nybelin 1963) are medial bones posterior to the urostyle (Greenwood and Rosen 1971) and are thought to be

modified scales (Patterson 1968). Stegurals may be defined as the incorporation of the first ural neural arch and usually the first preural neural arch into the first uroneural. The definition of stegural differs among authors (Monod 1968; Greenwood and Rosen 1971), and questions remain as to the homology of "stegurals" among different groups of fishes (Rosen and Patterson 1969). In some fishes (e.g., some gadoids, cynoglossids), medial bones occur dorsally and/or ventrally anterior to the last neural and haemal spines. These are termed "dorsal (or ventral) accessory bones" (Marshall and Cohen 1964; Rosen and Patterson 1969) or "X" and "Y" bones (Monod 1968), and may be taxonomically significant at the generic or subfamily level.

Other characteristics of the caudal fin may be of taxonomic or phylogenetic significance. The procurrent spur of the caudal fin of some perciform fishes was described by Johnson (1975) who discussed its phylogenetic implications (Fig. 4). Nursall (1963) defined the hypurapophysis as "a lateral process of the anterior hypural bone associated with the terminal vertebra (of Gosline 1960), serving as the anterolateral portion of the proximal attachment of the hypochordal longitudinal muscle." This process was noted by Ford (1937) to occur in 24 families; Nursall found this process present in 11 additional families. Whether or not the anteriormost hypural (parhypural of some authors) is free proximally is considered of phylogenetic significance by some workers (Rosen and Patterson 1969).

The structure of the adult caudal fin in both recent and fossil fishes has been widely used to indicate phyletic relationships (Greenwood et al. 1966; Patterson 1968; Rosen and Patterson 1969; Gosline 1971; Greenwood and Rosen 1971; Rosen 1973). Relatively few authors have analyzed caudal fin ontogeny, and even fewer have attempted to interpret the phylogenetic significance of the development of this fin.

Several recent papers on the development of the caudal fin in teleost larvae indicate the structure differs from that commonly accepted for adult specimens. Contrary to accepted interpretation of adult caudal structure, no evidence was observed during ontogeny of a two-part fusion of the ventral hypural plate in *Thunnus atlanticus* (Potthoff 1975). Matarese et al. (1981) noted the absence of uroneurals in the caudal fin development of *Microgadus proximus*, the presence of which was considered by Rosen and Patterson (1969) as a characteristic of the Gadiformes. *Isopsetta isolepis* also lacked uroneurals according to Richardson et al. (1980), a structure considered by some authors to be characteristic of Pleuronectiformes (Rosen and Patterson 1969; Amaoka 1969). The two pairs of uroneurals in *Coryphaena* fused during ontogeny into a single pair (Potthoff 1980). Based on examination of adult caudal fin morphology, the absence (i.e., fusion or loss) of the posterior pair of uroneurals could be considered an evolutionary advance (Fraser 1972).

The reported absence of uroneurals in *Microgadus* and *Isopsetta* does not necessarily imply that fusion or absorption of these structures into the ural centrum (or centra) did not occur during evolutionary history. Similarly, the reported absence of ontogenetic fusion (as in the ventral hypural plate of *T. atlanticus*) does not refute the hypothesis that this plate is derived from the fusion of two elements. Absence of such structures in adult fishes is still an evolutionary advance, even if it occurs by ontogenetic fusion or deletion.

Dorsal and anal fins.—The number of dorsal and anal fins, and whether the fins are composed of rays only or of spines and rays, are useful taxonomic characters and can be indicators of phyletic position (Table 2). The number of spines in dorsal or anal fins is often constant in many families or genera, but the number of rays may vary inter- or intraspecifically. In fishes possessing fins with both spines and rays, care should be taken in discriminating between the two. Separation of the two types based on the adult complement does not always apply to larvae. Spines and soft rays may be fimbriated at the terminus in larvae, but these are replaced later in spines by blunt or pointed tips according to Berry and Richards (1973). Segmentation of soft rays does not occur until after the ray has formed. In certain fishes (e.g., *Morone saxatilis*), some soft rays may become spines during or after the larval stage (Mansueti 1958). In *Sebastes*, the posteriormost dorsal spine and the third anal spine first form as soft rays and then transform to spines, beginning at the base and continuing distally (Moser et al. 1977; Richardson and Laroche 1979); these were termed "prespines" by Richardson and Laroche (1979). In many fishes the terminal soft ray of the dorsal and anal fins consists of an anterior and posterior part but is associated with a single pterygiophore (Table 2) and should be counted as one ray (Berry and Richards 1973).

Transient ossified structures occurring in dorsal and anal fins of certain groups may aid in identification. Larvae of some epinepheline serranids possess extremely elongate dorsal spines which become reduced during ontogeny (Kendall 1979). Such distinctive elongate dorsal spines also are characteristic of a number of other groups including holocentrids, acanthurids, and balistids. Distinctive elongate dorsal rays occur in bothids, lophiids, and bregmacerotids, and elongate anal rays are present in some lophiids.

When using the structure, shape, and position of dorsal and anal fins as taxonomic characters, one should keep in mind that in some fishes (e.g., clupeids) these fins may migrate anteriorly or posteriorly during ontogeny (Houde et al. 1974). Additionally, dorsal and anal fins may form in the fin fold and attach to the body by "streamers," as in argentinoids (Ahlstrom 1969; Moser [1981]).

In some phylogenetically distant groups of fishes, the dorsal and anal fins may form early (e.g., *Engraulus*, some stromatiids, *Syacium*), whereas in other groups these fins may not ossify until transformation to the juvenile stage (e.g., *Leuroglossus schmidti*, Dunn 1983). Dorsal fins may form before or after the anal fin or they may form simultaneously. In species with more than one dorsal or anal fin, the sequence of ossification of the various fins may differ among taxa. The second dorsal fin forms (simultaneously with the anal) before the first dorsal fin in *Scomber japonicus, Trachurus symmetricus, Scombrolabrax heterolepis*, and *Archosargus rhomboidalis* (Kramer 1960; Ahlstrom and Ball 1954; Houde and Potthoff 1976; Potthoff et al. 1980). In *Merluccius productus* the first dorsal fin forms before the second dorsal fin and the anal fin (Ahlstrom and Counts 1955), as it does in most gempylids and all scombrids, except *Scomber* and *Rastrelliger* (Potthoff[11]; Matsumoto 1959, 1962, 1967; Voss 1954). In *Microgadus proximus*, the first anal fin is the first to form (after larval pectoral fins) followed by the second anal fin. Nearly simultaneously, the third, second, and first dorsal fins develop (Matarese et al. 1981). In a related gadid, *Theragra chalcogramma*, anal fins one and two and dorsal fin three form together, followed by the second and then the first dorsal fin (Dunn, pers. obs.) The sequence of ossification of spines and/or rays of the dorsal and anal fins varies among different groups of fishes. Ossification may begin in the center of the fin and progress anteriorad and/or posteriorad (e.g., *Sebastes crameri*, Richardson and Laroche 1979; *Coryphaena*, Potthoff 1980) or it

[11]T. Potthoff, Southeast Fish. Cent. Miami Laboratory, Natl. Mar. Fish. Serv., NOAA, Miami, FL 33149, pers. commun. January 1982.

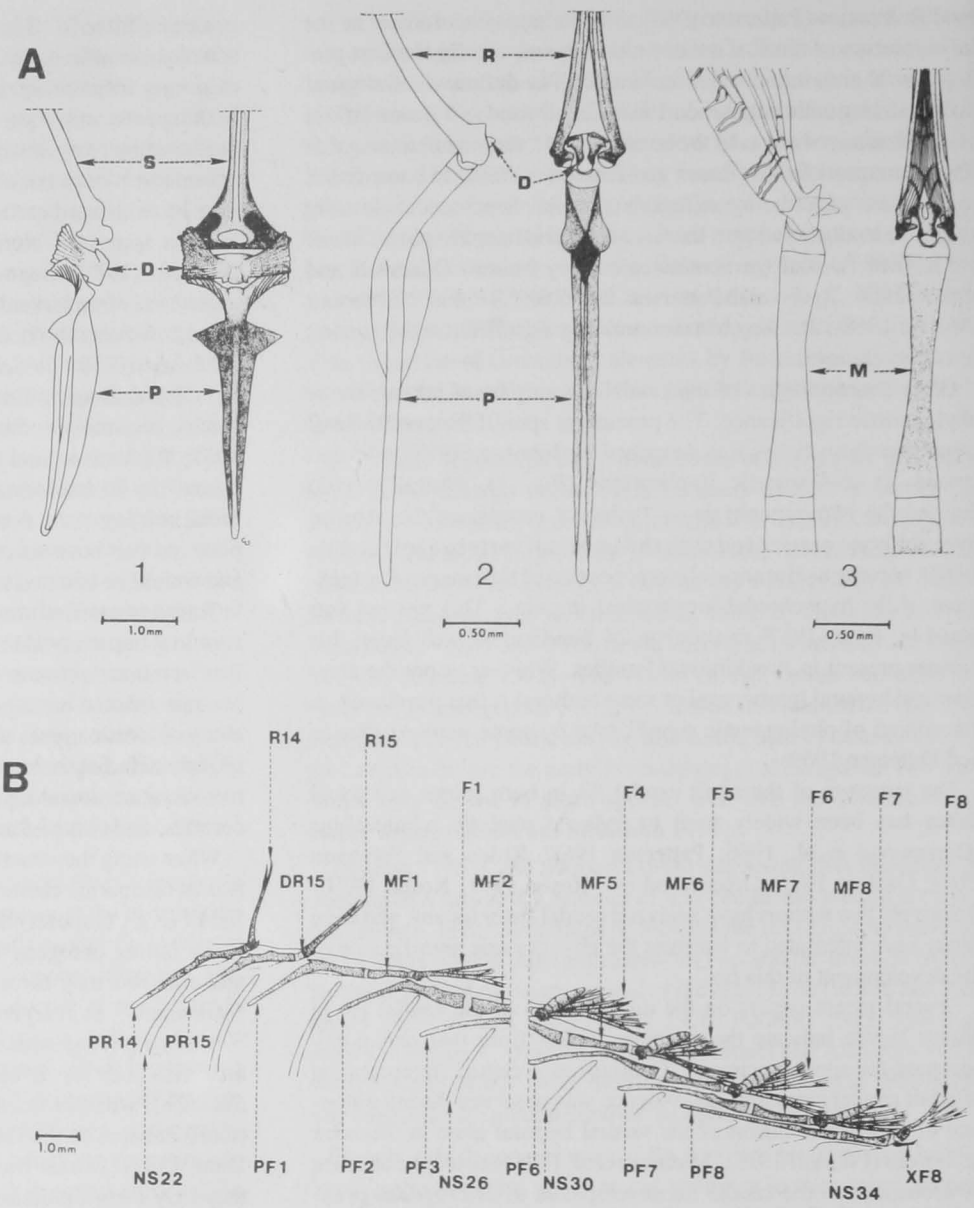


Figure 5.—A. Lateral and anterior views of the serial association between pterygiophore and fin ray from an 85.0 mm SL *Thunnus atlanticus*. 1) Fifth spiny ray of the first dorsal fin and its serial pterygiophore, lateral view on left and anterior view on right; 2) Eleventh ray of the second dorsal fin and its serial pterygiophore, lateral view on left and anterior view on right; 3) Third finlet and parts of its serial pterygiophore, lateral view on left and anterior view on right. S = spiny ray; D = distal radial; P = proximal radial; R = ray; M = middle radial (from Potthoff 1975). B. Lateral view of pterygiophores of the dorsal finlets from an 85.0 mm SL *Thunnus atlanticus*. Left to right: PR14 = Proximal radial serial with the 14th ray of the second dorsal fin; NS22 = neural spine of the 22nd centrum; PF1 = proximal radial serial with the first finlet; DR15 = distal radial serial with the last (15th) ray of the second dorsal fin, partly hidden by the base of the ray; R15 = last ray (15th) of the second dorsal fin; MF1 = middle radial serial with the first finlet; F1 = first finlet; XF8 = fourth radial or stay of the last (8th) finlet (from Potthoff 1975).

may be initiated at the anterior (*Merluccius productus*, Ahlstrom and Counts 1955; *Citharichthys*, Ahlstrom and Moser 1975) or posterior (*Idiacanthus fasciola*, Beebe 1934) portions of the fins. In those species possessing spines in the dorsal and anal fins, development may begin at or near the origin of the fins (Berry and Richards 1973) as it does for gempylids and scombrids (footnote 11).

The ontogeny of dorsal and anal finlets in the carangid, *Elagatus bipinnulata*, was discussed by Berry (1969), in scombrids, *Thunnus atlanticus*, by Potthoff (1974), and in *Scomber japonicus* by Kramer (1960).

The supporting structures of the dorsal and anal fins, called "pterygiophores" (Eaton 1945) or, by some authors, "interneurals" (e.g., Kramer 1960), are generally composed of three parts: Proximal, middle, and distal radials (also called pterygiophores; Wake 1979; Fink and Weitzman 1982) as shown in Figure 5. The presence of three components is considered a primitive character (e.g., salmonids, Norden 1961; bathylagids, Borodulina 1969); the middle and proximal radials, however, may be fused into a single structure (e.g., *Scomber japonicus*, Kramer 1960; *Coryphaena*, Potthoff 1980)—considered an advanced character. In some cases the three components may be fused into a single structure (e.g., *Tilapia macrocephala*, Eaton 1945; Blenniidae and Labridae, Lindsey 1955); a fourth radial, called a "stay," may be present (Fig. 5), as in the last finlet of *Thunnus* (Potthoff 1975). The number of pterygiophores is usually smaller than the number of fin rays or spines, in that the anteriormost or posteriormost pterygiophore may support one or more fin elements (Fig. 1). In *S. japonicus*, the pterygiophores are continuous between the first and second dorsal fins, but some do not support fin spines (Kramer 1960); such interneurals are also found between fins in some gadids (Dunn pers. obs.). Some pterygiophores (usually the first or last) may be bifurcate or variously expanded (e.g., tetraodontids, Tyler 1980); and fusion of adjacent pterygiophores may also occur (e.g., *T. atlanticus*, Potthoff 1975). The anteriormost dorsal and anal pterygiophores represent a fusion of two in many Perciformes (Potthoff 1975; Fritzsche and Johnson 1980).

The number of pterygiophores in the first interneural space differed between two species of *Coryphaena*, according to Potthoff (1980). Pterygiophore ontogeny has been described for *S. japonicus* (Kramer 1960), *Thunnus atlanticus* (Potthoff 1975), *Archosargus rhomboidalis* (Houde and Potthoff 1976), *Morone* spp. (Fritzsche and Johnson 1980), *Scombrolabrax heterolepis* (Pot-

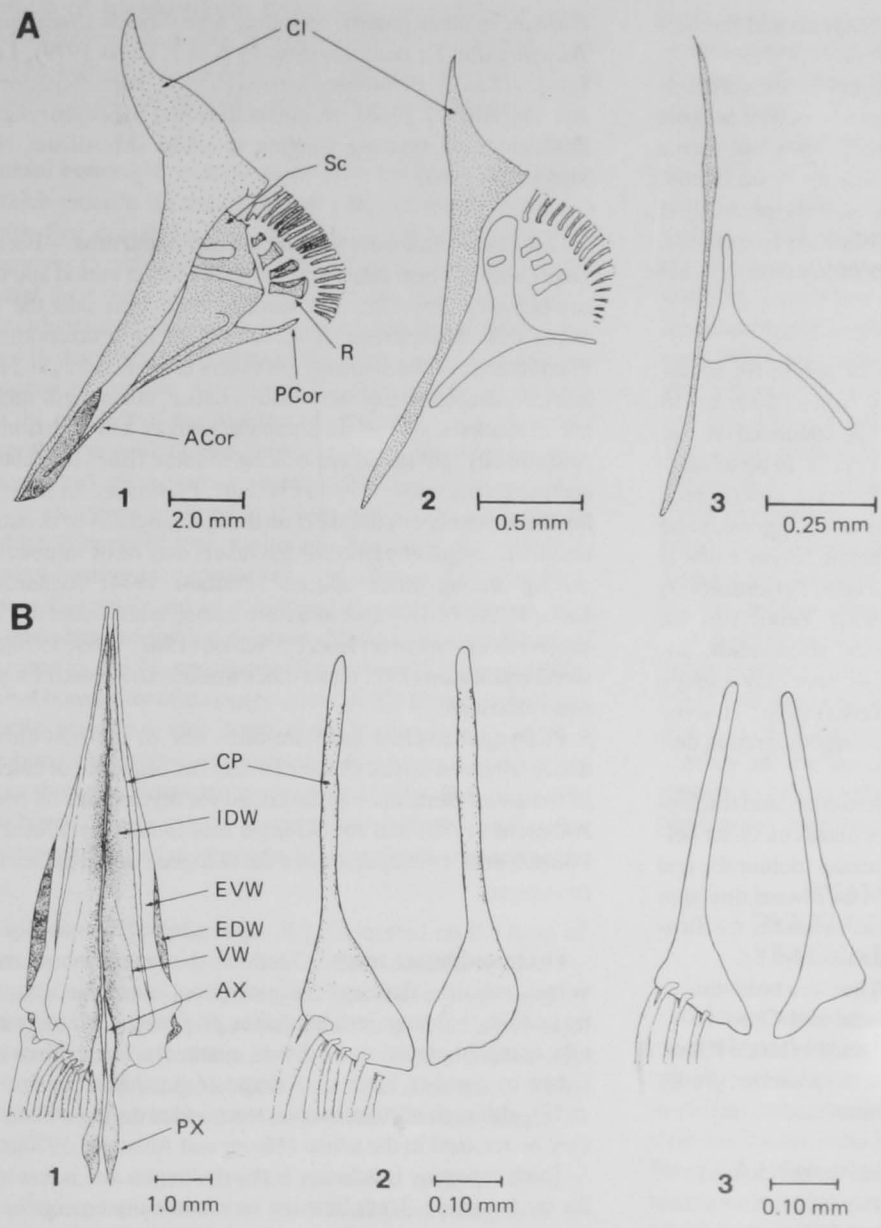


Figure 6.—A. Lateral view of ontogeny of left pectoral girdle from *Scombrolabrax heterolepis*: 1) 68.1 mm SL; 2) 10.4 mm SL; 3) 4.2 mm SL. Top to bottom: CL = cleithrum; Sc = scapula; R = radial; PCor = posterior process of coracoid; ACor = anterior process of coracoid. Cartilage, white; ossifying, stippled (from Potthoff et al. 1980). B. Ventral view of left and right basipterygia from *Scombrolabrax heterolepis*, showing their ontogeny: 1) 68.1 mm SL; 2) 7.3 mm SL; 3) 5.2 mm SL. Fin rays from the left basipterygium have been removed. Top to bottom: CP = central part; IDW = internal dorsolateral wing; EVW = external ventral wing; EDW = external dorsolateral wing; VW = ventral wing; AX = anterior xiphoid process; PX = posterior xiphoid process. Cartilage, white; ossifying, stippled (from Potthoff et al. 1980).

thoff et al. 1980), and *Coryphaena* (Potthoff 1980). The ontogeny of dorsal and anal finlets in the carangid *Elagatis bipinnulata* was discussed by Berry (1969); in the scombrids, *Thunnus atlanticus*, by Potthoff (1974); and in *Scomber japonicus* by Kramer (1960). In addition to its use as a taxonomic character, pterygiophore morphology may be an important tool in phylogenetic studies (Potthoff 1975; Potthoff et al. 1980).

Pectoral fins and their supports.—Generally pectoral fins form later in the larval stage than median fins (Table 2) and, therefore, are somewhat less valuable as a taxonomic aid in the identification of larval fishes. In some myctophid larvae, pectoral fins may be large, conspicuous appendages which become reduced in size during ontogeny (Moser and Ahlstrom 1970; Moser [1981]). Pectoral buds are the first fins to form in most larvae, but development of rays usually lags behind those of other fins (Tables 1, 2). However, in the molid *Ranzania* the pectoral fins are the first to develop rays (Leis 1977). Early developing pectoral fins are also found in some *Sebastes* (Moser et al. 1977) and in lophiids (footnote 3). In some anguilliforms, larval pectoral fins are lacking, whereas in *Tactostoma, Idiacanthus*, and some malacosteids the larval pectorals are lost at transformation (footnote 3). As noted by Moser and Ahlstrom (1970), the count of pectoral fin rays in larvae of some myctophid genera may be greater than in adults. During transformation as many as six pectoral fin rays (in *Loweina*) are lost (resorbed?).

The presence in larvae of elongate spines and rays in pectoral fins is a valuable taxonomic aid in a number of groups of fishes. Elongate pectoral fin rays are present in larvae of some myctophids, e.g., *Tarletonbeania* and *Loweina* (Moser and Ahlstrom 1970). In many fishes the sequence of ossification of the pectoral fins occurs dorsoventrally (e.g., *Coryphaena*, Potthoff 1980; *Morone*, Fritzsche and Johnson 1980).

The bones of the pectoral girdle and its suspensorium (Fig. 6A) have been widely used as characters in systematic investigations of adult fishes (e.g., myctophids, Paxton 1972; sternoptychids, Weitzman 1974; Lophiiformes, Pietsch 1974, 1981; Tetraodontiformes, Tyler 1980). Starks (1930) described the anatomy of the primary shoulder girdle (i.e., those parts preformed in cartilage, the scapula, coracoid, mesocoracoid, and radials) of adult fishes of a number of families. However, relatively few developmental studies have been made on the pectoral fin and its supports (Houde and Potthoff 1976 for *Archosargus rhomboidalis*; Potthoff 1980 for

Coryphaena; Potthoff et al. 1980 for *Scombrolabrax*; and Potthoff and Kelley 1982 for *Xiphias gladius*).

The reduction or total atrophy during ontogeny of the cartilaginous posterior process of the coracoid apparently occurs in most fishes (Swinnerton 1906; Starks 1930; Potthoff 1980), but such a process is lacking in developing *Theragra chalcogramma* (Dunn, pers. obs.). The number of supporting elements of the pectoral fin (radials) may be a generic character in some fishes. As an example, they range from two to five in various genera of lophiiform fishes (Pietsch 1981).

Pelvic fins and their supports.—Counts of pelvic fin spines and/or rays are taxonomically useful in many fishes (Table 2). In most perciform families, pelvic fin counts are stabilized at one spine and five rays (I, 5) according to Regan (1913). In pleuronectids and bothids the pelvic fin counts are stabilized at 6 rays (in each fin), whereas in soleids the count is 5–5 and in cynoglossids the count is 0–4 (footnote 3). In myctophids the pelvic fin ray count is usually 8, but in some genera the count is reduced to 7 (*Gonichthys*) or 6 (*Notolychnus*) (Moser and Ahlstrom 1970). Pelvic fins are absent in a number of fishes (e.g., trichiurids, stromateids, stichaeids, *Ammodytes*, and some lophiids); others have only a single spine and no rays as seen in some balistids (Nelson 1976). In some fishes (e.g., clupeoids) the pelvic fins may undergo migration during ontogeny (Russell 1976).

Elongate pelvic rays are found in gadids, macrourids, and trachipterids, and in some serranids and ceratioids; whereas elongate pelvic spines are present in some serranids, lutjanids, trichiurids, and others (footnote 3). Pelvic fins often ossify in an inward direction (*Scombrolabrax*, Potthoff et al. 1980); in some fishes the ossification of all pelvic fin rays occurs nearly simultaneously.

The pelvic bone or basipterygium (Fig. 6B) has also been used as a systematic character in adult fishes (Collette and Chao 1975; Tyler 1962, 1980), but has rarely been investigated in larval fishes. Sewertzoff (1934) discussed the pelvic bone among various groups of fishes, while Gosline (1961) discussed the structure of the pelvic bone in adult "lower" fishes.

In many teleosts, radials are present between the pelvic rays and the pelvic girdle (Gosline 1961), but they may be lost in various diverse groups (Gosline 1961; Potthoff 1980). Additionally the pelvic bones may be fused (e.g., some tunas, Collette and Chao 1975), they may be highly modified (some balistoids, Tyler 1962, 1980), or lost (e.g., *Mola*, Tyler 1980).

The ontogeny and structure of pelvic bones were described by Potthoff (1980) for *Coryphaena* and Potthoff et al. (1980) for *Scombrolabrax*, while Fritzsche and Johnson (1980) briefly described the ontogeny of the basipterygia in *Morone*.

Other Skeletal Structures

Teleosts possess a great number of other skeletal structures, particularly of the head and axial skeleton, which may be of taxonomic and systematic use when applied to fish larvae.

Branchiostegal rays.—Branchiostegal rays often form their adult complement relatively early in the larval period, and their position and number are of value in separating some groups of fishes, particularly in taxa considered advanced (McAllister 1968). Numbers of branchiostegal rays may vary in some groups, whereas in other groups they may be relatively constant. For example, number of branchiostegal rays varies from 7 to 19 in engraulids, 5 to 24 in stomiatoids, and 17 to 51 in ophichthid eels. They are relatively constant in other groups, including argentinoids (*Nansenia* 3 to 4, *Bathylagidae* 2), percoids (usually 6 to 7; Bond 1979), Lampridiformes (5 to 7), Pleuronectiformes (6 to 8), Batrachoidiformes (6), etc. (McAllister 1968). In giganturids and Saccopharyngiformes, branchiostegal rays are wanting in adults (McAllister 1968; see also Orton 1963).

Gill rakers and pharyngobranchial apparatus.—Because gill rakers usually form relatively late in the larval period and the adult complements are often not reached until well into the juvenile stage, this characteristic is sometimes of little taxonomic value. The presence of rudimentary gill rakers in some fishes and the difficulty of distinguishing them from adjacent normal gill rakers have led to inconsistency in the literature (Moser and Ahlstrom 1970). Additionally, gill rakers are lacking in some fishes (Giganturoidea) and extremely reduced in others (e.g., *Psettodes*). In some groups, however, counts of gill rakers on the epibranchials or ceratobranchials or the length of particular gill rakers may be of value in discriminating among allied species (Potthoff 1974; Richardson and Laroche 1979). Gill arch structure among adult fishes has been the subject of extensive reviews by Nelson (1967, 1969, 1970), Greenwood and Rosen (1971), and other workers in a search for phylogenetic affinities.

Pharyngobranchial teeth are often one of the first elements to ossify in teleost larvae (Moser 1972). The sequence of calcification of branchial elements was described for myctophids by Moser and Ahlstrom (1970) and for *Sebastes macdonaldi* by Moser (1972). Potthoff et al. (1980) described the ontogeny of gill arches in *Scombrolabrax*.

Oromandibular teeth.—Teeth on the maxillary, premaxillary, vomer, palatine, dentary, and glossohyal bones are often used as taxonomic characters in adult fishes. In general, the adult and juvenile complement of teeth differs markedly from those in larval fishes in number, size, and shape (e.g., Ahlstrom and Counts 1958), although in some species teeth added during metamorphosis may be retained in the adults (Moser and Ahlstrom 1970).

Tooth ontogeny in teleosts is poorly known and is a subject ripe for further study. Teeth in many larvae initially emerge in a single series, but as more teeth are added they tend to emerge between existent teeth and often form multiple rows. Teeth apparently are added slowly during transformation in some species (*Scomber japonicus*, Kramer 1960) and more rapidly in others (*Isopsetta isolepis*, Richardson et al. 1980). Leptocephalus larvae of some fishes (e.g., Elopiformes, Anguilliformes, and Notacanthiformes) possess fang-like teeth in the upper and lower jaws; they are apparently not homologous with teeth in adult eels and are shed or resorbed during metamorphosis (Smith 1979). In larvae of *Scopelosaurus*, teeth on the maxillary are apparently shed or resorbed, as they are not present in adults (Berry 1964). In the bathylagid *Leuroglossus schmidti* teeth on the glossohyal disappear during transformation; hence the common name "smoothtongue" (Dunn 1983).

It is generally believed (Scott and Symons 1964; Jollie 1973; Fink 1981) that teeth of teleosts are continuously replaced, but questions apparently remain as to such replacement (Hildebrand 1974). The tooth-replacement mechanism may also differ among kinds of fishes (Lawson and Manly 1973; Holmbakken and Fosse 1973; see also Edmund 1960).

Fink (1981) described four major tooth-attachment modes in actinopterygian fishes and concluded that paedomorphic tooth development can be associated with major phylogenetic groups of teleost fishes. Suga et al. (1981) analyzed the fluoride concentra-

tion in teeth of tetradontiform fishes and compared the levels observed with the phylogenetic tree proposed for the order by Tyler (1980). The authors concluded that the fluoride concentration in the enameloid is closely related to the proposed phylogeny.

Predorsal bones.—Predorsal bones are usually slender splinter bones which precede the pterygiophores supporting the spines or rays of the first dorsal fin (Fig. 1). Thought to be derived from pterygiophores (Smith and Bailey 1961), they insert in interneural spaces, and their number and arrangement are in some groups of fishes a taxonomic aid as well as a character relating to phylogeny. Smith and Bailey (1961) investigated the relationships of predorsal bones, dorsal fin spines, and dorsal fin pterygiophores in adult fishes in the families of the superfamily Percoidea and illustrated some hypothetical evolutionary trends in dorsal fin supports. Predorsal bones and spine-bearing pterygiophores in adult serranoid fishes were examined by Kendall (1976) who found phylogenetic relationships. Counts of predorsal bones and their relationship to spine- or ray-bearing pterygiophores were used by Ahlstrom et al. (1976) as a diagnostic aid in separating stromateoid larvae. The position and shape of predorsal bones differed between larvae of *Morone saxatilis* and *M. americana* (Fritzsche and Johnson 1980).

Predorsal bones may often ossify either in late larvae or well into the juvenile stage but may form early in cartilage. Use of a cartilage-bone stain will enable detection of predorsal bones when formed, as shown by Fritzsche and Johnson (1980). Discriminating predorsal bones by radiography is sometimes difficult, but Kendall (1976) successfully used radiographs in his study of adult serranids.

Head spines and sculpturing.—Spines located on the head of teleost larvae may be an important diagnostic character (Table 1). Ridges, crests, or various sculpturing of head bones may occur in some larvae and be useful in specific, generic, or familial identification. Some head spines are transient, whereas others (particularly opercular spines) may persist into the juvenile or adult stage. These spines, crests, or ridges may vary intraspecifically in size, shape, or sculpturing.

Spines, crests, or ridges are often associated with the opercle bones, supraoccipital, pterotic, or other head bones; they may be located on the nuchal, snout , or supraoccular regions and are found in a number of diverse groups of fishes such as melamphids, scorpaenids, serranids, istiophorids, carangids, and pleuronectids.

A number of authors have used head spination as a diagnostic character. Examples for scorpaenid larvae are Moser et al. (1977), Richardson and Laroche (1979), and Laroche and Richardson (1980); for serranid larvae Kendall (1979); for carangid larvae Aboussouan (1975); and for cottid larvae Richardson and Washington (1980).

Scales and lateral line pores.—Scales rarely develop until the juvenile stage and hence are of small value in identification of larvae. A number of exceptions occur including some serranids (Kendall 1979), chiasmodontids (footnote 11), *Xiphias gladius* (Potthoff and Kelley 1982), holocentrids, and branchiostegids (Okiyama 1964) in which scales form during the larval period. The count of lateral line pores or of diagonal scale rows in juveniles, however, may be an important tool in identification of juveniles and adults which can be traced back to the larvae (e.g., Laroche and Richardson 1980).

Cranial bones.—Osteology of the teleost skull has long been used in taxonomic and phylogenetic studies of adult fishes. As demonstrated most recently by Fritzsche and Johnson (1980), the ontogeny of cranial bones can provide diagnostic differences at the species level.

The structure and shape of cranial bones (particularly the supraoccipital, epiotic, prootic, alisphenoid, and parasphenoid) were used by Clothier (1950) as a taxonomic character in his key to southern California adult fishes. The lack of an orbitosphenoid and the presence of antorbitals in adult *Leuroglossus schmidti* were noted by Borodulina (1969), who used these trenchant characters for removing *Leuroglossus* from the synonomy of *Bathylagus*. Paxton (1972) separated myctophids into two subfamilies based on photophore arrangement and adult osteology (including jaw length and unsculptured circumorbitals with an extensive orbital shelf). These two subfamilies corresponded closely to the classification independently proposed by Moser and Ahlstrom (1970) based on larval morphology, particularly eye shape. Recently Fritzsche and Johnson (1980) compared the early ossification of two species of *Morone* and noted osteological differences between them, including the shape of the ethmoid cartilage.

A number of workers have described the ontogeny of cranial bones in teleosts; some examples include Weisel (1967) for *Catostomus* and *Poecilia*, Moser and Ahlstrom (1970) for myctophids, Aprieto (1974) for carangids, and Mook (1977) for *Archosargus*.

Study of the development of cranial bones in teleost larvae appears to offer a valuable avenue of pursuit, and its increased use could assist in differentiating closely related taxa.

EXAMPLES OF THE USE OF DEVELOPMENTAL OSTEOLOGY IN SYSTEMATIC STUDIES OF TELEOSTS

Ahlstrom and Moser (1976) pointed out that a combination of morphological and meristic characters is not only of value in identifying larval fishes to order, suborder, and often to family, but that such characters can be used to infer phylogenetic affinities. As shown in Tables 1 and 2, morphological and meristic characters can be used to assign unknown larvae to order or suborder. The characteristics of fin position, development, and structure are particularly useful in taxonomy and systematics.

Although a number of authors have used characteristics of larval fishes as a means of analyzing phylogenetic affinities above the species level (e.g., for ceratioids, Bertleson 1951; for myctophids, Moser and Ahlstrom 1970, 1972, 1974; for serranids, Kendall 1979; for coryphaenids, Potthoff 1980; and for Scombrolabracidae, Potthoff et al. 1980), few workers have attempted to analyze phylogenetic affinities in a rigorous, quantitative manner. Even fewer have used developmental osteology in such analyses. A few examples of such attempts follow.

Employing an approach previously used on adult fishes by Ebeling and Weed (1973), Okiyama and Ueyanagi (1978) analyzed 12 of the 14 genera of the subfamily Scombrinae (Scombridae) according to a sequence of primitive to advanced character states. A "character" may be defined as any attribute of an organism, and a "character state" as the qualitative and quantitative description of the character in question (Sneath and Sokal 1973). Okiyama and Ueyanagi (1978) assigned coded values to 13 characters (Table 3) including head spination, size and shape of premaxillary teeth, presence or absence of a cartilaginous pad on lower jaw, and myomere counts. By summing the character-state code values (Table 4), they arrived at an index of primitiveness which allowed them to construct a dendrogram depicting morphological relationships

Table 3.—Larval characters (chiefly advanced postlarval or early juvenile stages) presumed phylogenetically important as coded states for comparison of 12 genera of the subfamily Scombrinae (from Okiyama and Ueyanagi 1978).

Char. index	Character	Coded state 1	2	3
1	Supraoccipital spine	absent	—	present
2	Head	small; < 1/3 of SL	—	large; > 1/3 of SL
3	Viscera and vent	compact; wide space from anal fin	—	elongated; vent just in front of anal fin
4	Snout	rounded	pointed	elongated
5	Premaxillary teeth	minute	large	large; some fang-like
6	Jaw	equal size	equal or unequal size	unequal; distinct upper jaw projection
7	Preopercular spine	absent	—	present
8	Spiny supra-orbital crest	absent	present or absent	present
9	Pterotic spine	absent	—	present
10	Cartilaginous pad on lower jaw	absent	present or absent	present
11	Dorsal body pigmentation	heavier	—	lighter
12	Post vent pigmentation	present, extensive	absent or a few dots	absent
13	Myotome counts	low; 30–31	middle; 38–41	[1]high; 40–65

[1]Exceptional low vertebral count of *Scomberomorus sinensis* is responsible for this unclearly discreted coded state.

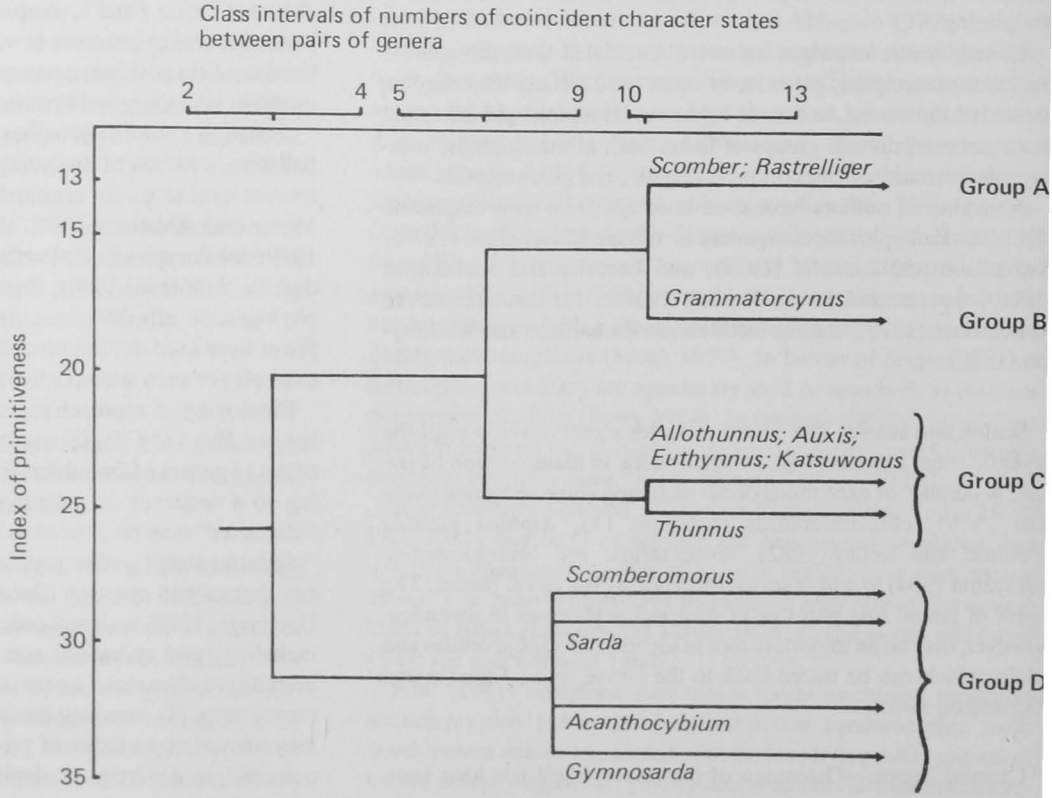
among the 12 genera studied (Fig. 7). Groups "A," "B," "C," and "D" of Figure 7 correspond well to generic affinities previously postulated by Richards (1973) on the bases of myomere counts and pigment patterns, as well as to affinities postulated by Collette and Chao (1975) based on characters of adult fishes.

Using larval as well as adult characters, Johnson (1974) analyzed generic relationships of Scopelarchidae. He analyzed primitive and advanced states of six larval characters in addition to 15 adult characters, including several osteological characters: 1) extent of peritoneal pigment; 2) presence or absence of accessory pigment spots; 3) gradual or abrupt metamorphosis; 4) position of pelvic fin buds in relation to the dorsal fin; 5) precocious or nonprecocious appearance of the pectoral fin; and 6) head length relative to standard length. He also determined the length of the basihyal, and whether

Table 4.—Comparisons of 12 genera of the subfamily Scombrinae. For the 13 characters and their coded state, see Table 3 (from Okiyama and Ueyanagi 1978).

Genus	Coded character states by character number 1	2	3	4	5	6	7	8	9	10	11	12	13	Total score
Scomber	1	1	1	1	1	1	1	1	1	1	1	1	1	13
Rastrelliger	1	1	1	1	1	1	1	1	1	1	1	1	1	13
Grammatorcynus	1	3	1	2	1	1	3	1	1	1	1	1	1	18
Scomberomorus	3	3	1	3	2	2	3	2	2	2	1	1	3	28
Acanthocybium	1	3	3	3	2	3	3	1	3	3	3	1	3	32
Sarda	1	3	1	3	2	2	3	3	3	1	3	1	3	29
Gymnosarda	1	3	1	3	3	3	3	3	3	3	3	3	2	34
Allothunnus	1	3	1	2	2	1	3	1	1	1	3	3	2	24
Auxis	1	3	1	2	2	1	3	1	3	1	3	1	2	24
Euthynnus	1	3	1	2	2	1	3	1	3	1	3	1	2	24
Katsuwonus	1	3	1	2	2	1	3	1	3	1	3	1	2	24
Thunnus	1	3	1	2	2	1	3	1	3	1	3	2	2	25

Figure 7.—Numerically constructed dendogram depicting larval morphological relationships among 12 genera of the subfamily Scombrinae (from Okiyama and Ueyanagi 1978). Groups A–D represent related genera, based on data in Table 3 as coded in Table 4. Group A is considered the most primitive group; Group D the most derived.



or not teeth were present. Johnson used these characters and character states to infer relationships among species and to group scopelarchid species into genera.

Certain larval characters were used by Zahuranec (1980) in his cladistic analysis of myctophids of the genus *Nannobrachium*. In addition to using a number of adult characters, he analyzed ontogenetic characters to establish criteria of polarity of characters (i.e., from primitive to derived). Larval characters used by Zahuranec were: 1) Pectoral fin size and shape; 2) direction of orientation of pectoral fins; 3) pectoral ray thickness; 4) pectoral ray fusion to the edge of the cleithrum during ontogeny; 5) larval snout shape; 6) presence or absence of a swim bladder in larvae; and 7) presence of a fat-filled or gas-filled swim bladder. The adult and larval characters were used to construct a Wagner tree (Kluge and Farris 1969; Farris 1970) to hypothesize phylogenetic relationships of species in *Nannobrachium*.

Washington (1981) used 11 larval characters in a Wagner tree analysis (Farris 1970; Farris et al. 1970) of larvae of three cottid genera, *Artedius, Clinocottus,* and *Oligocottus*. She used the following characters: 1) Number of preopercular spines; 2) size of preopercular spines; 3) presence or absence of basal spines on preopercular spines; 4) number of auxiliary spines on inner shelf of preopercle; 5) presence or absence of bubble of skin at nape; 6) presence, absence, and size of gut diverticula; 7) number and modification of parietal spines; 8) presence or absence of melanophores on nape; 9) snout pointed or round; 10) presence or absence of trailing gut and, if present, the configuration and length of the trailing gut; and 11) number of pelvic fin rays.

Based on these characters, Washington (1981) erected a cladogram inferring systematic relationships of the three genera and 13 species. She concluded that two sister groups exist within the genera examined: 1) Those with multiple preopercular spines, and 2) those sharing two derived characters—basal preopercular spines and pointed snouts.

The investigation of phylogenetic relationships following the cladistic approach of Hennig (1966) has stimulated an intense debate in systematics (see, for example, the last 10 or more years of the journal *Systematic Zoology*). This conceptual approach has been little used with larval fishes, yet larval fishes possess a rich suite of characters and character states. In many groups of fishes, the larval stages exist in habitats distinctly different from adults (e.g., planktonic larval pleuronectids vs. demersal adult pleuronectids).

Hennig (1966) proposed that ontogeny should be used as a criterion for analyzing phylogenetic relationships and establishing the polarity (direction) of character states from primitive to derived. Eldredge and Cracraft (1980), in their presentation of cladistic methods, restated Hennig's ideas concerning ontogeny and stated that it is surprising that little attention has been directed toward using ontogenetic data in systematics.

Listed in Table 5 are a number of characters of potential value in analyzing phylogenetic affinities among teleost larvae. A number of other characters might also lend themselves to study and analysis, the most notable of which are bones of the neurocranium (see Fraser 1972 for examples of character states of adult apogonids). A combination of osteological and other character states would be useful in any such analysis.

Analyses of character states such as were done by Okiyama and Ueyanagi (1978) can be of value in estimating phylogenetic affinities at generic and higher levels, depending upon the particular suite of characters chosen and how they are analyzed. More rigorous quantitative approaches to phylogenetic analysis (Kluge and Farris 1969; Smith and Koehn 1971; Marx and Rabb 1972; Baird and Eckardt 1972; Estabrook et al. 1977; Straugh 1978; Presch 1980) such as used by Washington (1981) have rarely been attempted exclusively with larval fishes.

Table 5.—Potential characters for analysis of phyletic affinities of teleost larvae; character usually of value (+) and sometimes of value (−) at indicated hierarchical level.

Characters	Hierarchical level			
	Order/ Suborder	Family	Genus	Species
Morphological				
Pigment pattern		−	−	+
Predominant body shape	+	−	−	
Snout-anus length	+	+	+	
Characteristics of gut	−	−		
Pelvic fin position	+	+		
Larval eye shape	−	−	−	−
Transformation stage	+	+		
Prejuvenile stage present	+	+		
Osteological				
Number of vertebrae		+	+	+
Number of branchiostegals	+	+	+	−
Dorsal fin(s): Number	+		+	
Type of elements	+			
Formula				+
Sequence of formation		+	+	
Anal fin(s): Number	+		+	
Type of elements	+	+		
Formula				+
Sequence of formation		+	+	
Last dorsal and anal ray bifurcate	+	−		
Pectoral fin rays:				
Sequence of formation	+	+		
Formula				+
Pelvic fin rays:				
Sequence of formation	+			
Formula				+
Caudal fin: Type	+	−		
Principal caudal rays	+		−	+
Maximum number hypurals	−			
Maximum number epurals	−	−		
Number of ural centra	+	+		
Neural spine on vertebrae adjacent to urals	+	−		
Fin spines or rays elongate	+	+	+	
Head spines present in larvae	+			+
Predorsal bones present		+	+	
Oromandibular teeth		+	+	

Increased use of developmental osteology should increase our understanding of fishes and their relationships.

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LITERATURE CITED

ABOUSSOUAN, A.
1975. Oeufs et larves de Téléostéens de l'Ouest africain. XIII. Contribution à l'identification des larves de *Carangidae*. Bull. Inst. Fondam. Afr. Noire, Ser. A Sci. Nat. 37:899–938.

AHLSTROM, E. H.
1969. Remarkable movements of oil globules in eggs of bathylagid smelts during embryonic development. J. Mar. Biol. Assoc. India 11:206–217.

AHLSTROM, E. H., and O. P. BALL.
1954. Description of eggs and larvae of jack mackerel (*Trachurus symmetricus*) and distribution and abundance of larvae in 1950 and 1951. U.S. Fish Wildl. Serv., Fish. Bull. 56:209–245.

AHLSTROM, E. H., J. L. BUTLER, and B. Y. SUMIDA.
1976. Pelagic stromateid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions, and early life histories and observations on five of these from the northwest Atlantic. Bull. Mar. Sci. 26:285–402.

AHLSTROM, E. H., and R. C. COUNTS.
1955. Eggs and larvae of the Pacific hake, *Merluccius productus*. U.S. Fish Wildl. Serv., Fish. Bull. 56:295–329.
1958. Development and distribution of *Vinciguerria lucetia* and related species in the eastern Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 58:363–416.

AHLSTROM, E. H., and H. G. MOSER.
1975 Distributional atlas of fish larvae in the California Current region: Flatfishes, 1955 through 1960. Calif. Coop. Oceanic Fish. Invest. Atlas 23, 207 p.
1976. Eggs and larvae of fishes and their role in systematic investigations and in fisheries. Rev. Trav. Inst. Peches Marit. 40:379–398.

AMAOKA, K.
1969. Studies on the sinistral flounders found in the waters around Japan—taxonomy, anatomy, and phylogeny. J. Shimonoseki Univ. Fish. 18:65–340.

APRIETO, V. L.
1974. Early development of five carangid fishes of the Gulf of Mexico and the south Atlantic coast of the United States. Fish. Bull., U.S. 72:415–443.

BAIRD, R. C., and M. J. ECKARDT.
1972. Divergence and relationship in deep-sea hatchetfishes (Sternoptychidae). Syst. Zool. 21:80–90.

BEEBE, W.
1934. Deep-sea fishes of the Bermuda oceanographic expeditions. Family Idiacanthidae. Zoologica 16:149–241.

BERRIEN, P. L.
1978. Eggs and larvae of *Scomber scombrus* and *Scomber japonicus* in continental shelf waters between Massachusetts and Florida. Fish. Bull., U.S. 76:95–115.

BERRY, F. H.
1964. Aspects of the development of the upper jaw bones in teleosts. Copeia 1964:375–384.
1969. *Elagatis bipinnulata* (Pisces: Carangidae): Morphology of the fins and other characters. Copeia 1969:454–463.

BERRY, F. H., and W. J. RICHARDS.
1973. Characters useful to the study of larval fishes. *In* A. L. Pacheco (editor), Proceedings of a workshop on egg, larval, and juvenile stages of fish in Atlantic coast estuaries, p. 48–65. Tech. Publ. 1, Middle Atl. Coastal Fish Cent., Natl. Mar. Fish. Serv., NOAA, Highlands, NJ 07732.

BERTELSEN, E.
1951. The Ceratioid fishes. Ontogeny, taxonomy, distribution and biology. Dana-Rep., Carlsberg Found. 7(39), 276 p.

BLACKWELDER, R. E.
1967. Taxonomy, a text and reference book. Wiley, N.Y., 698 p.

BOND, C. E.
1979. Biology of fishes. W. B. Saunders Co., Phila., 514 p.

BOND, C. E., and T. UYENO.
1981. Remarkable changes in the vertebrae of perciform fish *Scombrolabrax* with notes on its anatomy and systematics. Jpn. J. Ichthyol. 28:259–262.

BORODULINA, O. D.
1969. Osteology of *Leuroglossus stilbius schmidti* Rass (Bathylagidae). Prob. Ichthyol. 9:309–320.

CASTEEL, R. W.
1976. Fish remains in archaeology and paleo-environmental studies. Acad. Press, N.Y., 180 p.

CAVENDER, T. M.
1970. A comparison of coregonines and other salmonids with the earliest known teleostean fishes. *In* C. C. Lindsey and C. S. Woods (editors), Biology of coregonid fishes, p. 1–32. Univ. Manitoba Press, Winnipeg.

CLOTHIER, C. R.
1946. Vertebral variation with size in *Clevelandia ios*. Copeia 1946:113–116.
1950. A key to some southern California fishes based on vertebral characters. Calif. Dep. Fish Game, Fish Bull. 79, 83 p.

COHEN, D. M., and J. G. NIELSEN.
1978. Guide to the identification of genera of the fish order Ophidiiformes with a tentative classification of the Order. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 417, 72 p.

COLLETTE, B. B., and L. N. CHAO.
1975. Systematics and morphology of the bonitos (*Sarda*) and their relatives (Scombridae, Sardini). Fish. Bull., U.S. 73:516–625.

DAWSON, A. B.
1926. A note on the staining of the skeleton of cleared specimens with alizarin red S. Stain Technol. 1:123–124.

DINGERKUS, G., and L. D. UHLER.
1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Technol. 52:229–232.

DUNKELBERGER, D. G., J. M. DEAN, and N. WATABE.
1980. The ultrastructure of otolithic membrane and otolith in the juvenile mummichog, *Fundulus heteroclitus*. J. Morphol. 163:367–377.

DUNN, J. R.
1983. Development and distribution of the young of northern smoothtongue, *Leuroglossus schmidti* (Bathylagidae), in the northeast Pacific, with comments on the systematics of the genus *Leuroglossus* Gilbert. Fish. Bull. U.S. 81:23–40.

EATON, T. H., Jr.
1945. Skeletal supports of the median fins of fishes. J. Morphol. 76:193–212.

EBELING, A. W., and W. H. WEED III.
1973. Order Xenoberyces (Stephanoberyciformes). *In* D. M. Cohen (editor), Fishes of the Western North Atlantic. Mem. Sears Found. Mar. Res., Yale Univ. 1 (Part 6):397–478.

EDMUND, A. G.
1960. Tooth replacement phenomena in the lower vertebrates. R. Ont. Mus., Contrib. 52, 190 p.

ELDREDGE, N., and J. CRACRAFT.
1980. Phylogenetic patterns and the evolutionary process. Method and theory in comparative biology. Columbia Univ. Press, N.Y., 349 p.

EMELIANOV, S. W.
1935. Die Morphologie der Fishrippen. Zool. Jahrb. Abt. Anat. 60:133–262.

ESTABROOK, G. F., J. G. STRAUCH, Jr., and K. L. FIALA.
1977. An application of compatability analysis to the Blackiths' data on orthopteroid insects. Syst. Zool. 26:269–276.

FAHAY, M. P., and C. L. OBENCHAIN.
1978. Leptocephali of the ophichthid genera *Ahlia*, *Myrophis*, *Ophichthus*, *Pisodonophis*, *Callechelys*, *Letharchus*, and *Apterichtus* on the Atlantic continental shelf of the United States. Bull. Mar. Sci. 28:442–486.

FARRIS, J. S.
1970. Methods for computing Wagner trees. Syst. Zool. 19:83–92.
FARRIS, J. S., A. G. KLUGE, and M. J. ECKARDT.
1970. A numerical approach to phylogenetic systematics. Syst. Zool. 19:172–189.
FARUQI, A. J.
1935. The development of the vertebral column in the haddock (*Gadus aeglifinus*). Proc. Zool. Soc. Lond. 1935:313–332.
FINK, W. L.
1981. Ontogeny and phylogeny of tooth attachment modes in actinopterygian fishes. J. Morphol. 167:167–174.
FINK, W. L., and S. H. WEITZMAN.
1982. Relationships of the stomiiform fishes (Teleostei), with a description of *Diplophos*. Bull. Mus. Comp. Zool. 150:31–93.
FORD, E.
1937. Vertebral variation in teleostean fishes. J. Mar. Biol. Assoc., U.K. 22:1–60.
FOWLER, J. A.
1970. Control of vertebral number in teleosts—an embryological problem. Q. Rev. Biol. 45:148–167.
FRASER, T. H.
1972. Comparative osteology of the shallow water cardinal fishes (Perciformes: Apogonidae) with reference to the systematics and evolution of the family. Rhodes Univ., Dep. Ichthyol., Ichthyol. Bull. 34:1–105.
FRITZSCHE, R. A., and G. D. JOHNSON.
1980. Early osteological development of white perch and striped bass with emphasis on identification of their larvae. Trans. Am. Fish. Soc. 109:387–406.
GÉRAUDIE, J.
1978. Scanning electron microscope study of the developing trout pelvic fin bud. Anat. Rec. 191:391–394.
GOSLINE, W. A.
1960. Contributions toward a classification of modern isospondylous fishes. Bull. Br. Mus. (Nat. Hist.) Zool. 6:325–365.
1961 Some osteological features of modern lower teleostean fishes. Smithson. Misc. Collect. 142:1–42.
1971. Functional morphology and classification of teleostean fishes. Univ. Hawaii Press, Honolulu, 208 p.
GREENWOOD, P. H., and D. E. ROSEN.
1971. Notes on the structure and relationships of the alepocephaloid fishes. Am. Mus. Novit. 1971(2473), 41 p.
GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, and G. S. MYERS.
1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist. 131:341–455.
HEMPEL, G., and J. H. S. BLAXTER.
1961. The experimental modification of meristic characters in herring (*Clupea harengus* L.). J. Cons. Perm. Int. Explor. Mer 26:336–346.
HENNIG, W.
1966. Phylogenetic systematics. Univ. Illinois Press, Chicago, 251 p.
HENSLEY, D. A.
1977. Larval development of *Engyophrys senta* (Bothidae), with comments on intermuscular bones in flatfishes. Bull. Mar. Sci. 27:681–703.
HILDEBRAND, M.
1974. Analysis of vertebrate structure. Wiley, N.Y., 710 p.
HOLLISTER, G.
1934. Clearing and dyeing fish for bone study. Zoologica 12:89–101.
1936. Caudal skeleton of Bermuda shallow water fishes. I. Order Isospondyli: Elopidae, Megalopidae, Albulidae, Clupeidae, Dussumieriidae, Engraulidae. Zoologica 21:257–296.
HOLMBAKKEN, N., and G. FOSSE.
1973. Tooth replacement in *Gadus callarias*. Z. Anat. Entwicklungsgesch. 143:65–79.
HOTTA, H.
1961. Comparative study of the axial skeleton of Japanese teleostei. Bull. Tohoku Reg. Fish. Res. Lab., 155 p.
HOUDE, E. D., and T. POTTHOFF.
1976. Egg and larval development of the sea bream *Archosargus rhomboidalis* (Linnaeus): Pisces, Sparidae. Bull. Mar. Sci. 26:506–529.
HOUDE, E. D., W. J. RICHARDS, and V. P. SAKSENA.
1974. Description of eggs and larvae of scaled sardine, *Harengula jaguana*. Fish. Bull., U.S. 72:1106–1122.
HUBBS, C. L.
1958. *Dikellorhynchus* and *Kanazawaichthys*: nominal fish genera interpreted as based on prejuveniles of *Malacanthus* and *Anntennarius*, respectively. Copeia 1958:282–285.
HUBBS, C. L., and K. F. LAGLER.
1949. Fishes of the Great Lakes Region. Cranbrook Inst. Sci. Bull. 26, 186 p.
HUBBS, C. L., R. R. MILLER, and L. C. HUBBS.
1974. Hydrographic history and relict fishes of the North-Central Great Basin. Calif. Acad. Sci. Mem. 7, 259 p.
HUGHES, D. R.
1981. Development and organization of the posterior field of ctenoid scales in the Platycephalidae. Copeia 1981:596–606.
JOHNSON, G. D.
1975. The procurrent spur: An undescribed perciform caudal character and its phylogenetic implications. Occas. Pap. Calif. Acad. Sci. 121, 23 p.
JOHNSON, R. K.
1974. A revision of the alepisauroid family Scopelarchidae (Pisces: Myctophiformes). Fieldiana Zool. 66, 249 p.
JOLLIE, M.
1973. Chordate morphology. R. E. Krieger Publ. Co., N.Y., 478 p.
KENDALL, A. W., Jr.
1976. Predorsal and associated bones in serranid and grammistid fishes. Bull. Mar. Sci. 26:585-592.
1979. Morphological comparisons of North American sea bass larvae (Pisces: Serranidae). U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 428, 50 p.
KLUGE, A. G., and J. S. FARRIS.
1969. Quantitative phyletics and the evolution of anurans. Syst. Zool. 18:1–32.
KNUDSEN, J. W.
1966. Biological techniques: collecting, preserving and illustrating plants and animals. Harper and Row, N.Y., 525 p.
KONNERTH, A.
1965. Preparation of ligamentary articulated fish skeletons. Curator 8:325–332.
KRAMER, D.
1960. Development of eggs and larvae of Pacific mackerel and distribution and abundance of larvae, 1952–56. U.S. Fish Wildl. Serv., Fish. Bull. 60:393–438.
LAROCHE, W. L., and S. L. RICHARDSON.
1980. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes flavidus* and *Sebastes melanops* (Scorpaenidae) off Oregon. Fish. Bull., U.S. 77:901–924.
LAWSON, R., and B. F. J. MANLY.
1973. Tooth growth and replacement in *Ctenolucius hujeta*, a neotropical characoid fish. J. Morphol. 141:383–394.
LEIS, J. M.
1977. Development of the eggs and larvae of the slender mola, *Ranzania laevis* (Pisces, Molidae). Bull. Mar. Sci. 27:448–466.
LEIBY, M. M.
1979. Leptocephalus larvae of the eel family Ophichthidae. I. *Ophichthus gomesi* Castelnau. Bull. Mar. Sci. 29:329–343.
LINDSEY, C. C.
1955. Evolution of meristic relations in the dorsal and anal fins of teleost fishes. Trans. R. Soc. Can. 49:35–49.
1975. Pleomerism, the widespread tendency among related fish species for vertebral number to be correlated with maximum body length. J. Fish. Res. Board Can. 32:2453–2469.
LUNDBERG, J. G. and J. N. BASKIN.
1969. The caudal skeleton of the catfishes, order Siluriformes. Am. Mus. Novit. 2398, 49 p.
MAKUSHOK, V. M.
1958. The morphology and classification of the northern blennioid fishes (Stichaeoidae, Blennioidei, Pisces). Akad. Nauk SSSR, Tr. Zool. Inst. 25:3–129. [In Russ.]. (Transl. by A. R. Gosline and W. A. Gosline, 1959, 105 p., avail. U.S. Dep. Inter., Fish. Wildl. Serv., Ichthyol. Lab., Wash., D.C.)
MANAVALA RAMANUJAM, S. G.
1929. The study of the development of the vertebral column in teleosts, as shown in the life history of the herring. Proc. Zool. Soc. Lond. 1929:365–414.
MANSUETI, R.
1958. Eggs, larvae and young of the striped bass, *Roccus saxatilis*. Chesapeake Biol. Lab., Contrib. 112, 35 p.
MARKLE, D. F.
1980. A new species and a review of the deep-sea fish genus *Asquamiceps* (Salmoniformes: Alepocephalidae). Bull. Mar. Sci. 30:45–53.
MARSHALL, N. B., and D. M. COHEN.
1964. Order Anacanthini (Gadiformes): Characters and synopsis of families. *In* D. M. Cohen (editor), Fishes of the Western North Atlantic. Mem. Sears

Found. Mar. Res., Yale Univ., I (Part 6):479–495.
MARX, H., and G. B. RABB.
1972. Phyletic analysis of fifty characters of advanced snakes. Fieldiana Zool. 63, 321 p.
MATARESE, A. C., S. L. RICHARDSON, and J. R. DUNN.
1981. Larval development of Pacific tomcod, *Microgadus proximus*, in the northeast Pacific Ocean with comparative notes on larvae of walleye pollock, *Theragra chalcogramma*, and Pacific cod, *Gadus macrocephalus* (Gadidae). Fish. Bull., U.S. 78:923–940.
MATSUMOTO, W. M.
1959. Descriptions of *Euthynnus* and *Auxis* larvae from the Pacific and Atlantic Oceans and adjacent seas. Dana-Rep., Carlsberg Found. 9(50), 34 p.
1962. Identification of larvae of four species of tuna from the Indo-Pacific region I. Dana-Rep., Carlsberg Found. 10(55), 16 p.
1963. Unique shape of the first elongate haemal spine of albacore, *Thunnus alalunga* (Bonnaterre). Copeia 1963:460–464.
1967. Morphology and distribution of larval wahoo *Acanthocybium solandri* (Cuvier) in the central Pacific Ocean. U.S. Fish Wildl. Serv., Fish. Bull. 66:299-322.
MATSUMOTO, W. M., E. H. AHLSTROM, S. JONES, W. L. KLAWE, W. J. RICHARDS, and S. UEYANAGI.
1972. On the clarification of larval tuna identification particularly in the genus *Thunnus*. Fish. Bull., U.S. 70:1–12.
MAYR, E.
1969. Principles of systematic zoology. McGraw-Hill, N.Y., 428 p.
MAYR, E., E. G. LINSLEY, and R. L. USINGER.
1953. Methods and principles of systematic zoology. McGraw-Hill, N.Y., 336 p.
McALLISTER, D. E.
1968. Evolution of branchiostegals and classification of teleostome fishes. Natl. Mus. Can., Bull. 221, 239 p.
MEYER, D. B., and R. O'RAHILLY.
1958. Multiple techniques in the study of the onset of prenatal ossification. Anat. Rec. 132:181–183.
MEYER-ROCHOW, V. B.
1972. A scanning electron microscope study of marine fish larvae. J. Microsc. (Paris) 13:169-172.
MILLER, G. L., and S. C. JORGENSON.
1973. Meristic characters of some marine fishes of the western Atlantic Ocean. Fish. Bull., U.S. 71:301–312.
MILLER, J. M., and J. W. TUCKER, Jr.
1979. X-Radiography of larval and juvenile fishes. Copeia 1979:535–538.
MILLER, R. V., and J. W. VAN LANDINGHAM.
1969. Additional procedures for effective enzyme clearing and staining of fishes. Copeia 1969:829–830.
MONOD, T.
1968. Le complex urophore des poissons teleosteens. Mem. Inst. Fondam. d'Afrique Noire 81, 705 p.
MOOK, D.
1977. Larval and osteological development of the sheepshead, *Archosargus probatocephalus* (Pisces: Sparidae). Copeia 1977:126–133.
MOOKERJEE, H. K., G. N. MITRA, and S. R. MAZUMDAR.
1940. The development of the vertebral column of a viviparous teleost, *Lebistes reticulatus*. J. Morphol. 67:241-269.
MOSER, H. G.
1972. Development and geographic distribution of the rockfish, *Sebastes macdonaldi* (Eigenmann and Beeson, 1893), family Scorpaenidae, off southern California and Baja California. Fish. Bull., U.S. 70:941–958.
[1981]. Morphological and functional aspects of marine fish larvae. *In* R. Lasker (editor), Marine fish larvae: Morphology, ecology, and relation to fisheries, p. 90-131. Univ. Wash. Press, Seattle.
MOSER, H. G., and E. H. AHLSTROM.
1970. Development of lanternfishes (family Myctophidae) in the California Current. Part I. Species with narrow-eyed larvae. Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 7, 145 p.
1972. Development of the lanternfish, *Scopelopsis multipunctatus* Brauer 1906, with a discussion of its phylogenetic position in the family Myctophidae and its role in a proposed mechanism for the evolution of photophore patterns in lanternfishes. Fish. Bull., U.S. 70:541–564.
1974. Role of larval stages in systematic investigations of marine teleosts: The Myctophidae, a case study. Fish. Bull., U.S. 72:391–413.
MOSER, H. G., E. H. AHLSTROM, and E. M. SANDKNOP.
1977. Guide to the identification of scorpionfish larvae (family Scorpaenidae) in the eastern Pacific with comparative notes on species of *Sebastes* and *Helicolenus* from other oceans. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 402, 71 p.
NELSON, G. J.
1967. Epibranchial organs in lower teleostean fishes. J. Zool. (Lond. 153:71–89.
1969. Gill arches and the phylogeny of fishes, with notes on the classificatio of vertebrates. Bull. Am. Mus. Nat. Hist. 141:475–552.
1970. Gill arches of some teleostean fishes of the families Salangidae an Argentinidae. Jpn. J. Ichthyol. 17:61–66.
NELSON, J. S.
1976. Fishes of the world. Wiley, N.Y., 416 p.
NORDEN, C. R.
1961. Comparative osteology of representative salmonid fishes, with particu lar reference to the grayling (*Thymallus arcticus*) and its phylogeny. J. Fish Res. Board Can. 18:679–791.
NURSALL, J. R.
1963. The hypurapophysis, an important element of the caudal skeleton Copeia 1963:458–459.
NYBELIN, O.
1963. Zur Morphologie und Terminologie des Schwanskelettes der Actinop terygier. Ark. Zool., Ser. 2, 15:485–516.
1971. On the caudal skeleton in *Elops* with remarks on other teleostea fishes. Acta Regiae Soc. Sci. Litt. Gothob. Zool. 7:1–52.
OKIYAMA, M.
1964. Early life history of the Japanese blanquillos, *Branchiostegus japon cus japonicus* (Houttuyn). Bull. Jpn. Sea Reg. Fish. Res. Lab. 13:1–14.
OKIYAMA, M., and S. UEYANAGI
1978. Interrelationships of scombroid fishes: an aspect from larval morpho ogy. Bull. Far Seas Fish. Res. Lab. (Shimizu) 16:103–113.
ONO, R. D.
1980. A silver impregnation technique to demonstrate muscle-bone-cartilag relationships in fishes. Stain Technol. 55:67–70.
ORTON, G. L.
1963. Notes on larval anatomy of fishes of the Order Lyomeri. Copei 1963:6–15.
OSSIAN, C. R.
1970. Preparation of disarticulated skeletons using enzyme-based laundr "pre-soakers." Copeia 1970:199–200.
PATTERSON, C.
1968. The caudal skeleton in Lower Liassic pholidophorid fishes. Bull. B Mus. (Nat. Hist.) Geol. 16:201–239.
PAXTON, J. R.
1972. Osteology and relationships of the lanternfishes (Family Myctoph dae). Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 13, 81 p.
PIETSCH, T. W.
1974. Osteology and relationships of ceratioid anglerfishes of the famil Oneirodidae, with a review of the genus *Oneirodes* Lütken. Bull. Los Ang Cty. Mus. Nat. Hist. Sci. 18, 113 p.
1981. The osteology and relationships of the anglerfish genus *Tetrabrachiu* with comments on lophiiform classification. Fish. Bull., U.S. 79:387–419
POTTHOFF, T.
1974. Osteological development and variation in young tunas, genus *Thunnu* (Pisces, Scombridae), from the Atlantic Ocean. Fish. Bull., U.S 72:563–588.
1975. Development and structure of the caudal complex, the vertebr column, and the pterygiophores in the blackfin tuna (*Thunnus atlanticus*, Pi ces, Scombridae). Bull. Mar. Sci. 25:205–231.
1980. Development and structure of fins and fin supports in dolphin fish *Coryphaena hippurus* and *Coryphaena equiselis* (Coryphaenidae). Fish Bull., U.S. 78:277–312.
POTTHOFF, T., and S. KELLEY.
1982. Development of the vertebral column, fins and fin supports, branchio tegal rays and squamation in the swordfish (*Xiphias gladius*). Fish. Bull U.S. 80:161–186.
POTTHOFF, T., W. J. RICHARDS, and S. UEYANAGI.
1980. Development of *Scombrolabrax heterolepis* (Pisces, Scombrolabrac dae) and comments on familial relationships. Bull. Mar. Sci. 30:329–357
PRESCH, W.
1980. Evolutionary history of the South American microteiid lizards (Teiida Gymnophthalminae). Copeia 1980:36–56.
REGAN, C. T.
1913. The classification of percoid fishes. Ann. Mag. Nat. Hist., Ser. 8 12:111–145.
RICHARDS, W. J., R. V. MILLER, and E. D. HOUDE.
1974. Egg and larval development of the Atlantic thread herring, *Opi thonema oglinum*. Fish. Bull., U.S. 72:1123–1136.
RICHARDS, W. J., and T. POTTHOFF.
1974. Analysis of the taxonomic characters of young scombrid fishes, genu

Thunnus. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 623–648. Springer-Verlag, N.Y.

RICHARDSON, S. L., J. R. DUNN, and N. A. NAPLIN.
1980. Eggs and larvae of butter sole, *Isopsetta isolepis* (Pleuronectidae), off Oregon and Washington. Fish. Bull., U.S. 78:401–417.

RICHARDSON, S. L., and W. A. LAROCHE.
1979. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes crameri*, *Sebastes pinniger*, and *Sebastes helvomaculatus* (family Scorpaenidae) off Oregon. Fish. Bull., U.S. 77:1–46.

RICHARDSON, S. L., and B. B. WASHINGTON.
1980. Guide to the identification of some sculpin (Cottidae) larvae from marine and brackish waters off Oregon and adjacent areas in the Northeast Pacific. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 430, 56 p.

ROSEN, D. E.
1973. Interrelationships of higher euteleostean fishes. *In* P. H. Greenwood, R. S. Miles, and C. Patterson (editors), Interrelationships of fishes, p. 397–513. Acad. Press, N.Y.

ROSEN, D. E., and C. PATTERSON.
1969. The structure and relationships of the paracanthopterygian fishes. Bull. Am. Mus. Nat. Hist. 141:357–474.

RUSSELL, F. S.
1976. The eggs and planktonic stages of British marine fishes. Acad. Press, N.Y., 524 p.

SCHULZTE, O.
1897. Veber Hersteilung un Conservirung Durchich-tiger Embryonen zum Studium der Skeletbildung. Anat. Anz. 13:3–5.

SCOTT, J. H., and N. B. B. SYMONS.
1964. Introduction to dental anatomy. E&S Livingstone, Ltd., Lond., 406 p.

SEWERTZOFF, A. N.
1934. Evolution der Bauchflossen der Fische. Zool. Jahrb., Anat. 58:415–500.

SIMONS, E. V., and J. R. VAN HORN.
1971. A new procedure for whole-mount alcian blue staining of the cartilaginous skeleton of chicken embryos, adapted to the clearing procedure in potassium hydroxide. Acta Morphol. Neerl.-Scand. 8:281–292.

SIMPSON, G. G.
1961. Principles of animal taxonomy. Columbia Univ. Press, N.Y., 247 p.

SMITH, C. L., and R. M. BAILEY.
1961. Evolution of the dorsal-fin supports of percoid fishes. Pap. Mich. Acad. Sci., Arts Lett. 46:345–363.

SMITH, D. G.
1979. Guide to the leptocephali (Elopiformes, Anguilliformes, and Notocanthiformes). U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 424, 39 p.

SMITH, G. R., and R. K. KOEHN.
1971. Phenetic and cladistic studies of biochemical and morphological characteristics of *Catostomus*. Syst. Zool. 20:282–297.

STARKS, E. C.
1930. The primary shoulder girdle of the bony fishes. Stanford Univ. Publ. Biol. Sci. 6:149–239.

STRAUGH, J. G., Jr.
1978. The phylogeny of the Charadriiformes (Aves): a new estimate using the method of character compatibility analysis. Trans. Zool. Soc. Lond. 34:263–345.

SUGA, S., K. WADA, and M. OGAWA.
1981. Fluoride concentration in teeth of tetraodontiform fishes and its phylogenetic significance. Jpn. J. Ichthyol. 28:304–312.

SUMIDA, B. Y., E. H. AHLSTROM, and H. G. MOSER.
1979. Early development of seven flatfishes of the eastern North Pacific with heavily pigmented larvae (Pisces, Pleuronectiformes). Fish. Bull., U.S. 77:105–145.

SWINNERTON, H. H.
1906. A contribution to the morphology and development of the pectoral skeleton of teleosteans. Q. J. Microsc. Sci. 49:363–383.

TAKAHASHI, Y.
1962. Study for the identification of species based on the vertebral column of Teleostei in the inland sea and its adjacent waters. Bull. Nankai Reg. Fish. Res. Lab. 16:1–72.

TAYLOR, W. R.
1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122:1–17.
1977. Observations on specimen fixation. Proc. Biol. Soc. Wash. 90:753–763.

TYLER, J. C.
1962. The pelvis and pelvic fin of plectognath fishes; a study in reduction. Proc. Acad. Nat. Sci. Phila. 114:207–250.
1980. Osteology, phylogeny, and higher classification of the fishes of the Order Plectognathi (Tetraodontiformes). U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 434, 422 p.

VOSS, N. A.
1954. The postlarval development of the fishes of the family Gempylidae from the Florida Current. I. *Nesiarchus* Johnson and *Gempylus* Cuv. and Val. Bull. Mar. Sci. Gulf Caribb. 4:120–159.

WAKE, M. H. (Editor).
1979. Hyman's comparative vertebrate anatomy. 3d ed. Univ. Chicago Press, Chicago, 788 p.

WASHINGTON, B. B.
1981. Identification and systematics of larvae of *Artedius*, *Clinocottus*, and *Oligocottus* (Scorpaeniformes: Cottidae). M.S. Thesis, Oregon State Univ., Corvallis, 206 p.

WASSERSUG, R. J.
1976. A procedure for differential staining of cartilage and bone in whole formalin-fixed vertebrates. Stain Technol. 51:131–134.

WEISEL, G. F.
1967. Early ossification in the skeleton of the sucker (*Catostomus macrocheilus*) and the guppy (*Poecilia reticulata*). J. Morphol. 121:1–18.

WEITZMAN, S. H.
1974. Osteology and evolutionary relationships of the Sternoptychidae with a new classification of the stomiatoid families. Bull. Am. Mus. Nat. Hist. 153:329–478.

WILLIAMS, J. E., and C. E. BOND.
1980. *Gila boraxobius*, a new species of cyprinid fish from southeastern Oregon with a comparison to *G. alvordensis* Hubbs and Miller. Proc. Biol. Soc. Wash. 93:291–298.

WILLIAMS, T. W., Jr.
1941. Alizarin red S and toluidine blue for differentiating adult and embryonic bone and cartilage. Stain Technol. 16:23–25.

WINKELMANN, R. K., and R. W. SCHMIT.
1957. A simple silver method for nerve axoplasm. Proc. Staff Meet. Mayo Clin. 32:217–222.

YAMAMOTO, M., and N. EGAMI.
1974. Fine structure of the surface of the anal fin and the processes on its fin rays of male *Oryzias latipes*. Copeia 1974:262–265.

ZAHURANEC, B. J.
1980. Zoogeography and systematics of the lanternfishes of the genus *Nannobrachium* (Lampanyctini: Myctophidae). Ph.D. Thesis, George Washington Univ., Wash., D.C., 331 p.