

Resumen por el autor, Carl L. Hubbs,
Universidad de Illinois.

Estudio comparado de los huesos que forman la serie opercular
en los peces.

Aunque la estructura y disposición de los huesos que forman la serie opercular de los peces han sido descritas en ciertos grupos por muchos anatómicos, ninguno parece haber consolidado todavía las pruebas obtenidas, mediante un estudio comparado. Después de examinar la estructura de estos huesos en una extensa serie de peces, el autor ha llegado a la conclusión de que son de tipo diferente en los Malacopterigios más primitivos, por una parte, y en los Acantopterigios más especializados y sus parientes más próximos, por otra. Los Isospondyli, el grupo más primitivo de peces teleósteos (tal como se definen generalmente), tienen placas operculares y radios branquióstegos bastante semejantes a los de Amiatus, que bajo este aspecto como en tantos otros, constituye la forma de transición que llena el hueco existente entre los Ganoideos y Teleósteos. En los otros grupos principales de peces con radios blandos (Ostariophysi, Stomiatoidae, Apodes, Heteromi, Lyopomi, Synentognathi, Haplomi, Iniomi) los opérculos y los radios branquióstegos son de tipos derivables aparentemente de los presentes en los Isospondyli. Hay sin embargo una extensa variación en la forma y disposición de estos huesos, en armonía con su posición generalizada. Los grupos más especializados de los teleósteos, por otra parte, (los Microcyprini, Labyrinthici, Hemibranchii, Symbranchii, Opisthomi, Salmopercae y el vasto conjunto comprendido en los Percoidea o relacionados con este grupo) retienen constantemente una disposición peculiar fija en los radios branquióstegos.

Translation by José F. Nonidez
Carnegie Institution of Washington

A COMPARATIVE STUDY OF THE BONES FORMING THE OPERCULAR SERIES OF FISHES

CARL L. HUBBS

Although the structure and arrangement of the bones comprising the opercular series of certain species or groups of fishes have been described by many anatomists, no one seems to have consolidated the evidence in a comparative study. After examining their structure in a wide range of fishes, the writer has concluded that they are of a different type in the more primitive malacopterygians, on the one hand, and the specialized acanthopterygians and their relatives, on the other hand. The Isospondyli, the most primitive of the teleosts (as usually defined), have opercular plates and branchiostegal rays similar to those of *Amia*, which, in this respect as in many others, bridges the gap between ganoids and teleosts. In the other chief groups of soft-rayed fishes—Ostariophysi, Stomiatoidea, Apodes, Heteromi, Lyopomi, Synentognathi, Haplomi, Iniomi—the opercula and branchiostegals are of types apparently derivable from that of the Isospondyli. There is a wide variation in the form and arrangement of these bones in these groups, however, as one might expect from their generalized nature. In the higher groups of teleosts, on the other hand—the Microcyprini, Labyrinthici, Hemibranchii, Symbranchii, Opisthomi, Salmopercae, and in that vast assemblage of modern types comprising in the Percoidea, or clustering about that group—there is maintained a peculiarly constant arrangement of the branchiostegal rays. From a taxonomic standpoint, the results of this study are most significant in confirming many of the recent refinements, particularly those suggested by Mr. C. Tate Regan, in the classification of the Teleostei.

The primitive structure of the membrane bones which support the outer wall of the branchial cavity, and thus protect the

branchiae, is retained in certain extinct groups of ganoids, such as the Palaeoniscidae. Their structure in this family has been described by Traquair and others. On each side is a curved series of homologous, suturally conjoined plates, of which the upper two or three are dilated to form the opercular bones, while the lower anterior ones, narrower and less modified, comprise the branchiostegal rays (or branchiostegals); the lowest or most anterior pair, enlarged to form the plates which may be termed the branchigulars (or branchigular plates), are suturally united posteriorly with one another, and anteriorly with the median gular plate (or intergular), which extends forward between the mandibular rami to their symphysis.

In *Amia calva* the bones of the opercular series are modified in several respects. Each of the upper five plates is imbricate over the one next below. The gular plate largely covers the most anterior branchiostegal rays of the left side, which in turn overlap those of the right side—a feature due to the definite asymmetric folding of the branchial membranes, an asymmetry which is more or less definitely retained throughout the entire teleost series. The uppermost and largest bone of the opercular series in *Amia* is the operculum, a large subquadrate plate, incurved and thickened along its dorsal and anterior edges, and provided inside the anterior edge with an oval socket, into which a peg-like condyle of the hyomandibular fits, allowing considerable lateral movement of the operculum. The suboperculum, the next lower element of the series, is broadly incised by a downward extending arm of the operculum; its dorsal edge slips just under the lower margin of the operculum, while its lower edge is closely joined by membrane with the triangular interoperculum. The anterior edges of these three plates fit into a posterior groove of the preoperculum, which is not regarded as a member of the opercular series. A free dermal fold connecting the opercular membrane with the mandible, and extending along the lower edge of the sub- and interoperculum, may be termed the subopercular fold. The fourth bone of the series, fitting between the sub- and interoperculum, but widely exposed, being nearly one-third as wide as long, extends downward and forward, lying free in a conspicuous fold, continuous with the lower edge of the

mandible. This plate, bearing as much resemblance to the opercula as to the branchiostegals, may be named the branchioperculum; its fold, the branchiopercular fold. The remaining ten plates of the series are attached to the ceratohyal element of the hyoid arch, near the lower edge of its outer face. Except for its pointed, rather than truncate anterior edge, the uppermost of the ten is similar in form to the branchioperculum, which overlies its dorsal edge. Both this plate and the next, which is similar, though only about half as wide, are imbricate on the one next below, having free folds along their lower edges. The lower anterior seven branchiostegals form a continuous even surface, each, except the uppermost, fitting tightly into a groove along the lower outer face of the one next above; they increase in width anteroventrally. The most anterior branchiostegal, which is wider on the left or outer than on the right side, may be homologous with the branchigular plate of the Palaeoniscidae, or may represent two or three fused branchiostegals. The current allocation of *Amia* in a position intermediate between the typical ganoids and the teleosts is confirmed by the study of its opercular and branchiostegal plates.

The Isospondyli, comprising the oldest and most primitive¹ of the teleosts, retain certain generalized features of the opercular series. Thus, in *Elops* an intergular plate is developed, and in *Albula*, although the plate itself is lacking, the intergular fold remains. The branchiostegals of the typical Isospondyli (at least the upper ones), persist as thin wide plates. The uppermost and widest ray (which may be termed the branchioperculum, as it seems to be homologous with the plate in *Amia* to which that name is here applied) is attached closely to the inner margin of the sub- and interoperculum; not having become concealed under these bones, it remains visible from the side. The whole series, in fact, remaining scarcely at all folded together after the fashion of a fan, is visible from below,² though the branchial membranes

¹ Excepting of course *Lepidosteus* and *Amia*, if these be included in the Teleostei.

² In the clupeoid fishes the expanded preoperculum covers the larger portion of the middle rays, and all of the rays are mostly concealed in *Chirocentrus dorab*.

are separate (as they usually are). The plates of the opercular series in the isospondylous fishes differ from those of *Amia* in the following respects: the reduction of the suboperculum, so that the interoperculum and operculum are in contact anteriorly;³ the proximal (or anterior) attachment of branchioperculum and branchiopercular fold to the hyoid arch; the more complete imbrication of all the rays; the attachment of branchiostegals to the epihyal as well as to the ceratohyal; the frequent reduction of the rays below the main hyoid suture to rather slender rods, and the occasional attachment of these reduced rays to the edge of the ceratohyal, rather than to its outer face. These last two features are apparently caused by the strong development of the musculus geniohyoideus of the lower jaw, which is attached to the hyoid arch near the suture separating the ceratohyal from the epihyal. The number of the larger and flatter rays attached to the outer surface of the epihyal (the lowermost sometimes on the suture) varies widely in the Isospondyli and related orders; the writer has counted one in *Bathylagus pacificus*; two in *Pterothrissus gissu*, *Hiodon tergisus*, *Osmerus thaleichthys*, *Osmerus attenuatus*, *Arius gadora*, and *Amiurus nebulosus*; three in *Amphiodon alveoides*, *Ethmidium maculatum*,⁴ *Alepocephalus agassizii*, *Coilia ectenes*, and *Hypomesus olidus*; either three or four in *Albula vulpes*; four in *Chirocentrus dorab*, *Salvelinus fontinalis*, *Osmerus mordax*, *Mallotus villosus*, *Plagyodus ferox*, *Lestidiops sphyraenopsis*, *Bathysaurus ferox*, *Chlorophthalmus chalybeius*, and *Neoscolepis macrolepidotus*; five in *Etrumeus micropus*, *Felichthys felis*, and *Dallia pectoralis*; six in *Oncorhynchus nerka*, *Saurida gracilis*, and *Bathypterois pectoralis*; either six or seven in *Trachinocephalus myops*; seven in *Esox lucius*, *Aulopus japonicus*, and *Synodus intermedius*; eight in *Esox americanus* and *Synodus*

³ According to Woodward's restoration of the primitive extinct genera *Lep-tolepis* and *Holcolepis*, these genera bridge the gap between *Amia* and *Elops* in the character of the opercula. These bones apparently show no significant variation among living teleosts, though certain ones are reduced or increased in size in certain genera; the interoperculum is especially liable to variation, being occasionally absent.

⁴ All but the lowermost of the six on the ceratohyal are of similar shape to those of the epihyal in *Ethmidium maculatum*.

lucioceps; nine in *Elops affinis* and *Harpodon microchir*; ten in *Megalops atlanticus*. The total number of branchiostegals is three in the Cyprinidae and others, twenty-four to thirty-six in the several species of *Elops*. Many other figures might be added, but these are enough to illustrate clearly the inconstancy of the number of branchiostegal rays in the generalized malacopterygian fishes.

In the groups of soft-rayed fishes other than the Isospondyli, the branchiostegals are variable in form and attachment, but they show many points of similarity to those of the Isospondyli. In the Ostariophysi the number of rays varies widely, but the uppermost, at least, remains like that of the isospondylous fishes. To take several examples from the Nematognathi, there are six branchiostegals in *Arius gogora*, seven in *Pseudeutropius garna* and *Saccobranchus fossilis*, nine in *Ictalurus punctatus*, *Amiurus nebulosus* and *Shilbe mystus*, eleven in *Macrones aor*. The characins have only three to five branchiostegals, the cyprinids, constantly three. This low number of branchiostegals in certain malacopterygian fishes is usually correlated with the broad union of the branchial membranes and with a fresh-water habitat. Similarly, there are only three branchiostegals in *Haplochiton*, *Phractolaemus*, *Kneria*, and *Cromeria*, and but four in the *Gonorhynchidae*, *Chanidae*, and *Salangidae* (in all of these, excepting *Gonorhynchus*,⁵ the uppermost ray remains visible below the margins of the opercles). In the *Mormyridae* and *Notopteridae* the branchiostegals are modified in various ways, as Doctor Ridewood ('04, pp. 191-195, 199, 205) has demonstrated; in *Notopterus* there are six to nine branchiostegals, in *Xenomystus* but three, according to Boulenger.

The stomiatoid fishes, formerly confused with the Iniomi, have the branchiostegals short, slender, little curved, evenly spaced, not folded together, attached to the external surface of the hyoid arch near its ventral edge (each opposite a photophore), and largely covered by the opercula. In the *Apodes* (eels), *Heteromi*

⁵ In *Gonorhynchus* there are four branchiostegals, attached beneath the opercles on the outer face of the club-shaped end of the hyoid arch, all above the suture between the ceratohyal and epihyal.

and Lyopomi, the rays are also all slender, usually numerous and long, and frequently curved upward posteriorly about the free margin of the opercular bones. The branchiostegals of the Synentognathi (Belonidae, Scombresocidae, Hemirhamphidae, Exocoetidae) are wholly similar to those of the typical Isospondyli; they are rather numerous (ten in *Euleptorhamphus*), but not constant in number, flat, imbricate plates; the uppermost skirting the lower margins of the opercula, and all with their lower edges exposed. The characters of the branchiostegal rays of the Synentognathi strongly confirm Regan's view that the resemblance between these fishes and the Percesoces is purely fictitious: the group should be placed among the typical soft-rayed fishes. In the Haplomi (*Esox*, *Umbra*, and *Dallia*), but not in the poeciloid fishes which have been confused with them, the branchiostegals are like those of the Isospondyli. In the Iniomi (the Synodont fishes and their allies) the branchiostegals vary greatly in number (from six to twenty, four to eight attached to the suture between ceratohyal and epihyal, two to twelve below the suture); in *Plagyodus* the uppermost ray, as in the Isospondyli, is not wholly concealed, but in most of the genera several of the upper rays are covered by the opercula; when the rays are numerous several of the upper ones are closely approximated basally.

The group of the ribbon fishes (*Taeniosomi*) has been accorded very different positions among fishes, the current tendency being to place it much lower in the series than formerly, a disposition of the group which is doubtfully confirmed by the arrangement of the branchiostegal rays. In *Regalecus*, according to Parker's figure ('86), there are six slender, saber-shaped branchiostegals, all attached to the outer face of the hyoid arch near its lower margin; the uppermost, the only one attached to the epihyal, curving around the lower margin of the interoperculum. In the still more extremely aberrant genus *Stylephorus*, as described by Starks ('08), the five rays are inclined upward from their origin near the upper edge of the ceratohyal, as in no other known fish. In *Trachipterus arcticus*, as described by Meek ('90), the branchiostegal rays differ to no considerable degree from those of *Regalecus*. As in that genus, they are six in number; the uppermost

borders the lower margin of the interoperculum; all seem to arise from the outer face of the hyoid arch, but the anterior two are somewhat separated from the upper posterior four, which, unlike those of *Regalecus*, are largely covered by the expanded preoperculum. In *Trachypterus rex-salmonorum* the branchiostegals are concealed by the interoperculum as well, and the lower two rays, considerably separated from the upper four, are attached to the outer side of a ligament which extends as a chord across the concave anteroventral margin of the hyoid arch.

The *Ammodytoidea* are another group which has been placed by some ichthyologists among the higher teleosts, by others among the lower. The branchiostegals in *Ammodytes personatus* resemble those of the *Acanthopteri* in most of their characters: they are six in number, and are folded up behind the opercula; the upper four arise from both the cerato- and epihyal behind a prominent angle of the arch. The lower two rays, however, arise from the outer surface of the arch, and are closely approximated to the upper four.

The *Microcyprini* (*Poeciliidae* and *Amblyopsidae*) were long confused with the *Haplomi*, but have recently been shown to have a more advanced organization. The structure of the branchiostegal rays in the two groups confirms this view: those of the *Haplomi* are quite like those of the *Isospondyli*, whereas those of the *Microcyprini* are similar to those of the *Acanthopteri*. In the *Poeciliidae* there are six, or fewer, branchiostegals, which are folded up behind the operculum and above its lower margin. The upper four saber-shaped rays are attached to the outer surface of both the ceratohyal and epihyal, postero-superior to the prominent angle of the hyoid arch; the lower rays arise from the inner face of the ceratohyal. In examples of the *Ophicephalidae* and *Anabantidae* at hand (representing the order *Labyrinthici*), there are four plus two branchiostegal rays, arranged as in the *Microcyprini* and *Acanthopteri*.

Many of the aberrant fishes referred to the order *Hemibranchii* have the branchiostegals reduced in number, but in *Fistularia* there are four plus one rays, arranged as in typical *Acanthopteri*. "Most *Lophobranchs* have two branchiostegals, but *Nerophis* has

only one which distally bifurcates" (Jungersen, '10). In other respects also the hyoid apparatus of the *Lophobranchii* is reduced, probably from a condition like that of *Fistularia*.

The *Symbranchia* were long considered a group of true eels, but lately have been accorded a distinctly higher position. The character of the branchiostegals are in harmony with the latter view. In *Monopterus javanensis*, the rather narrow hyoid arch bears two groups of slender branchiostegals: an upper cluster of four and a lower inner pair, widely separated from the others. An essentially similar condition is developed in *Symbranchus marmoratus*, but in this species the two groups of branchiostegals are less widely separated.

The curious *Opisthomi* (*Mastacembelidae*) of southern Asia and Africa have been variously located in the teleost series; lately Boulenger and Regan agree in placing them among the higher teleosts, considering them as bearing a relation toward the spiny-rayed fishes analogous to that which the *Apodes* bear toward the soft-rayed group. This view is sustained by the branchiostegals in *Mastacembelus pancelas*. From the outer surface near the lower edge of the ceratohyal and epihyal, along the upper widened portion of the hyoid arch, four rays arise in close proximity; they are curved upward posteriorly, as in some of the *Apodes*, between the operculum and the branchial aperture; on the inner surface of the arch, near the concave anterior ventral margin, the two lower anterior rays are inserted.

The *Salmopercae*, long considered as intermediate between the soft-rayed and spiny-rayed fishes, have six branchiostegals, arranged exactly as in the *Acanthopteri*. Both of the species usually referred to this group, *Percopsis omiscomaycus* and *Columbia transmontana*, have been examined. *Aphredoderus sayanus*, referred by Regan to the same group, has branchiostegals in all essential respects similar to those of *Percopsis* and the following groups.

A definite fixed type of branchiostegal structure has been retained, almost without deviation, throughout the great groups of spiny-rayed fishes which flourish so abundantly in the modern seas, and with peculiar constancy in the numerous highly special-

ized offshoots of the typical Acanthopteri. In fact, it seems safe to assert that none other of the known characters which separate this series from the lower teleosts has been more conservatively maintained throughout the entire group. This statement may be emphasized by the naming of a few of the more aberrant types which differ in some notable way—primitive, specialized, or degenerate—from the group as a whole, yet which agree with one another and with the more typical members of the series in the essential characters of their branchiostegal apparatus: *Atherina*, *Stephanoberyx*, *Plectrypops*, *Cepola*, *Psettus*, *Toxotes*, *Monacanthus*, *Lactophrys*, *Tetraodon*, *Diodon*, *Agonus*, *Cyclopterus*, *Cephalacanthus*, *Echeneis*, *Solea*, *Callionymus*, *Xiphidion*, *Scytalina*, *Gobiesox*, *Coryphaenoides*, *Antennarius*, *Ogcocephalus*, etc. Broad union of the branchial membranes or their complete separation, membranous or fleshy character of the branchiostegal membranes, narrow lateral restriction or wide development of the branchial aperture, and countless other modifications of these higher teleosts occur—modifications affecting almost every part and structure of the body, as well as the branchial membranes—nevertheless, the essential characters of the branchiostegals remain unaltered.⁶

The characteristically stout hyoid arch is strongly angulated⁷ at some distance below and before the (typically) dentate suture between the ceratohyal and the epihyal, the angle forming the hinder border of a concavity in which the *musculus geniohyoideus* is attached. The strong development of this muscle not only modifies the form of the hyoid arch, but also modifies the structure and attachment of the branchiostegal rays, as it also does, usually

⁶ Certain of the individual rays may become reduced or specialized: for example, in *Tetraodon* the uppermost ray basally is an unossified ligament, while the lowest ray (as in *Diodon*) is greatly expanded; in *Holotrachys* the third to the seventh branchiostegals are strongly armed externally by rows of spinules; in *Polymixia* the lower three rays are modified, according to Starks, into a skeletal support for the barbel.

⁷ The hyoid arch is also angulated, but in not quite the same way, in a few of the soft-rayed types, notably in *Brevoortia*, *Dorosoma*, *Notopterus*, and *Gonorrhynchus*. In most of the lower teleosts the hyoid arch is a thin plate, and the suture between the epihyal and the ceratohyal is straight and often margined with cartilage.

to a lesser degree and without constancy, in the lower teleosts. The upper four saber-shaped branchiostegals are always attached to the outer surface of both epihyal and ceratohyal, at and above the angle of the arch, and are folded together like a fan above and behind the opercular margins (except in those cases in which the branchiostegal membranes are drawn taut by their broad union ventrally). Below (and before) the angle of the arch, to its edge or inner surface, usually two or three shorter and slenderer rays are attached; these may be reduced to one, or, very rarely, to none, and are increased, in certain berycoids and blennioids to four, but never to a higher number. Thus, the branchiostegals of the Acanthopteri and related groups are usually four plus two or four plus three in number, rarely four plus one or four plus four, and very rarely four plus nought or even three plus nought.⁸

In formulating the generalizations outlined in the preceding paragraph, one to many species of each of the families of higher teleosts, named in the following list, were examined. The variations in the characters of the branchiostegals rays were found to be so slight that for present purposes detailed descriptions are unnecessary.

BIBLIOGRAPHY

- BOULENGER, G. A. 1909 Catalogue of the fresh-water fishes of Africa in the British Museum. London.
- JUNGENSEN, H. F. E. 1909 On the osteology of the Lophobranchii. Report Brit. Assoc. Adv. Sci.
- MEEK, ALEXANDER 1890 On the structure of *Trachypterus arcticus*. Studies Dundee College Museum, vol. 1.
- PARKER, T. J. 1886 Studies in New Zealand ichthyology. I. On the skeleton of *Regalecus argenteus*. Trans. Zool. Socy. London, vol. 12, figs. 6 and 15.
- RIDEWOOD, W. G. 1904 On the cranial osteology of the fishes of the families Mormyridae, Notopteridae, and Hyodontidae. Jour. Linn. Socy. London (Zool.), vol. 29.
- STARKS, E. C. 1908 The characters of *Atelaxia*, a new suborder of fishes. Bull. Mus. Comp. Zool., vol. 52.

⁸ A number recorded only for certain cirrhitiform percoids, so far as the writer has determined.

A list of the families of the spiny-rayed fishes (Acanthopteri) and their derivatives examined⁹

Atherinidae	Cepolidae	Gobiidae ¹²
Mugilidae	Cirrhitidae	Echeneidae
Sphyraenidae	Embiotocidae	Bothidae
Stephanoberycidae	Cichlidae	Pleuronectidae
Polynemiidae	Pomacentridae	Soleidae ¹³
Zeidae	Labridae	Trachinidae
Berycidae	Scaridae	Nototheniidae
Holocentridae	Scorpididae	Pteropsaridae
Polymixiidae	Toxotidae	Bathymasteridae
Scombridae	Ephippidae	Uranoscopidae
Carangidae	Ilarchidae	Callionymidae
Coryphaenidae	Acanthuridae	Clinidae
Leiognathidae	Siganidae	Blenniidae
Centrarchidae	Balistidae	Stichaeidae
Percidae	Monacanthidae	Xiphiidae
Apogonidae	Ostraciidae	Lumpenidae
Centropomidae	Tetraodontidae	Pholididae ¹⁴
Serranidae	Diodontidae	Anarhichadidae
Lobotidae	Scorpaenidae	Scytalinidae
Priacanthidae	Anaplopomatidae	Zoarcidae
Lutianidae	Hexagrammidae	Ophidiidae
Haemulidae	Platycephalidae	Brotulidae
Sparidae	Cottidae	Batrachoididae
Gerridae	Agonidae	Gobiesocidae
Kyphosidae	Cyclopteridae	Gadidae
Mullidae ¹⁰	Cyglogasteridae	Coryphaenoididae
Sciaenidae	Triglidae	Lophiidae
Champsodontidae	Cephalacanthidae	Antennariidae
Malacanthidae	Eleotridae ¹¹	Ogcocephalidae

⁹ The sequence of families adopted by Doctor Jordan in his Guide to the Study of Fishes ('05) is here followed.

¹⁰ Branchiostegals four plus naught in the species examined.

¹¹ Branchiostegals four plus two or four plus three in all the genera examined, Eviota excepted.

¹² Branchiostegals four plus one in the numerous genera studied.

¹³ The branchiostegals of all the flat fishes examined are of a very similar type.

¹⁴ The writer follows Regan in the classification of the blennioid fishes.