

The Familial Phylogeny  
of the Tetraodontiformes  
(Acanthopterygii: Pisces)  
as Evidenced by Their  
Comparative Myology

RICHARD WINTERBOTTOM

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## ABSTRACT

Winterbottom, Richard. The Familial Phylogeny of the Tetraodontiformes (Acanthopterygii: Pisces) as Evidenced by Their Comparative Myology. *Smithsonian Contributions to Zoology*, number 155, 201 pages, 185 figures, 1974.—The myology of 46 species of the order Tetraodontiformes is described, the species representing the 11 families initially recognized for the purposes of this study. The data gathered from the descriptions has been interpreted phylogenetically, using only those characters of a shared specialized (synapomorph) nature. This analysis suggests that the Triacanthodidae and Triacanthidae are sister groups, and separated off first from the ancestral stock. The remaining families are divided into two lines. On the one hand, the Balistidae form the sister group of the Monacanthidae, and together form the sister group of the Aracnidae and Ostraciidae. In the other lineage, the Triodontidae separated off first, followed by the Molidae. The Diodontidae form the sister group of the Tetraodontidae plus Canthigasteridae.

In the final analysis, such fossils as are considered pertinent to the understanding of tetraodontiform phylogeny are considered. The information provided by these fossils, combined with the results of the myological interpretations, suggest the following systematic changes in the hierarchical classification of tetraodontiforms in order to bring it into line with the proposed phylogeny: (1) that two suborders be provisionally recognized, the first containing the Triacanthodidae and Triacanthidae, the second consisting of two superfamilies; (2) that a superfamily Balistoidea be recognized to contain the families Balistidae, †Spinacanthidae, and Ostraciidae; (3) that the families Monacanthidae and Aracnidae be treated as subfamilies of the Balistidae and Ostraciidae respectively, and that the †Spinacanthinae of Tyler (1968) be removed from the Triacanthodidae and placed as the sister group of the Balistidae, with equal rank (as †Spinacanthidae); (4) that a superfamily Tetraodontoidea be formed to contain the families †Eoplectidae, Triodontidae, Tetraodontidae, Diodontidae, and Molidae, and, should †*Zignoichthys* prove to be further along the gymnodont line than †*Eoplectus*, as hinted by Tyler (1972) and tentatively preferred here, the †Zignoichthyidae; (5) that the family Canthigasteridae be reduced to subfamilial rank within the family Tetraodontidae, and that the †Eoplectinae of Tyler (1972) be transferred from the Triacanthodidae to the superfamily Tetraodontoidea and raised to familial rank, in keeping with its phylogenetic position.

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# The Familial Phylogeny of the Tetraodontiformes (Acanthopterygii: Pisces) as Evidenced by Their Comparative Myology

*Richard Winterbottom*

## **Introduction**

This paper represents an attempt to elucidate the familial phylogeny of the order Tetraodontiformes, using a comparative myological approach. Past classifications, usually based on external characters, osteology or both, have often been vague concerning the precise interrelationships of the families, although certain family groupings have been almost universally accepted. Since the aim is to resolve the familial phylogeny, the eleven families recognized by Tyler (1970a) are provisionally accepted rather than the seven families proposed by Greenwood, et al. (1966). This approach is used in order to facilitate recognition of evolutionary lines that may become obscured in a more compressed classification.

For a group supposedly derived from a perciform or preperciform stock, the Tetraodontiformes (of which there are some 320 Recent species) are very diverse in size, shape, habits, habitats, and diet. The morphological changes associated with these variations can be expected to be reflected in the anatomy, particularly in the myology. Myological

changes appear to be of a grosser and less subtle nature (and thus more obvious) than those involving other facets of the functional systems.

Since this paper represents one of the first attempts at detailed phylogenetic interpretation from a purely myological standpoint, it seems necessary to outline certain factors influencing myology. The evolutionary mechanism of muscular change may be by the subdivision of new sections from existing muscles, the reduction and ultimate loss of a muscle, or change in fiber direction, since these alterations have functional significances. There are two extreme muscle types (pinnate and parallel), with a complete gradation between them. In pinnate muscles, the fibers converge on a central axis (usually a tendon), while they lie parallel to one another in a parallel fibered muscle. The two types are apparently capable of the same amount of work (Alexander, 1968:19). Perhaps more important than work in an evolutionary context is (are) the advantage(s) conveyed by the different fiber arrangements. Parallel fibered muscles provide maximum excursion, and can be arranged as thin sheets. Pinnation allows the localization of forces, the accommodation of the muscle in an otherwise unsuitable place (e.g., a narrow bony canal), and the possibility of moving the tendon in two planes

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by asymmetric contraction (Gans and Bock, 1965: 141-142). There is no evidence as to which of the two types (if either) is phylogenetically the older in vertebrates. Muscles affect a multidimensional system, and therefore a change in any one muscle is likely to produce changes in other muscles serving the same system. The synergistic interactions of bones, nerves, blood vessels, and ligaments with each other and with the muscles are also subject to this interpretation, of course, although not quite so obviously. The apparent ease with which muscle fibers can migrate and rearrange themselves (as evidenced, for example, by individuals with deformed limbs or jaws), coupled with the rigidity necessary for the application of muscle force at the most suitable point of the lever system makes comparative myology a particularly useful and rewarding field of study.

Although the data gathered here for phylogenetic interpretation can be utilized in a number of other ways (e.g., functional evolution, systematic definition), this lies beyond the scope of this study. The view that interpretations of phylogeny are only meaningful if based on the presence of shared, specialized (synapomorphic) characters is finding increasing acceptance among biologists. This process inevitably results in assumptions about the probable homology and character state (i.e., plesiomorph vs. apomorph) of the characters, and the weighting of these characters is a necessary and integral part of the process. While the utilization of synapomorphic characters in the elucidation of phylogeny is unlikely to produce much disagreement, the incorporation and reflection of that phylogeny in a hierarchical classification is still avoided by certain biologists. I agree with Mayr (1969:78) when he states, "The evolutionist believes that a classification consistent with our reconstruction of phylogeny has a better chance of meeting these objectives. [i.e., maximum information content with maximal ease of retrieval] than any other method of classification." I have therefore attempted to reorganize the classification of the tetraodontiforms to reflect the phylogenetic picture derived from the myology, using the basic methods set out by Hennig (1966) and Brundin (1966, 1968).

Although muscles are described in terms of the bones they attach to (and hence perhaps an osteological summary should be included), the reader is referred to the detailed osteological investigations

of Tyler (1962a, 1962b, 1962c, 1963a, 1963b, 1968, 1970a, 1973) for information on this topic.

Numerous papers contain sparse observations on the muscles of tetraodontiforms, with varying degrees of accuracy. These include the works of Cuvier (1817), E. Geoffroy Saint-Hilaire (1818); I. Geoffroy Saint-Hilaire (1827), Meckel (1828), Goodsir (1841), Cleland (1862), Owen (1866), Thilo (1879, 1896, 1899, 1914, 1920), Sørensen (1883, 1884), Wiedersheim (1887), Borcea (1906), Maurer (1912), Lubosch (1917, 1938), Takahasi (1917), Souché (1932a, 1932b, 1932c, 1935), Gregory and Raven (1934), van Dobben (1935), Edgeworth (1935), Nishi (1938), Raven (1939a, 1939b), Gabriel (1940), van Roon (1942), Kesteven (1943), Monod (1950, 1959a, 1959b, 1960), Le Danois (1958), and Winterbottom (1970).

Of the more detailed papers, Winther (1877), Lubosch (1929), and van Roon and ter Pelkewijk (1940) described the jaw muscles, Dietz (1914) the jaw and branchial muscles, Grenholm (1923) the muscles of the fins, Rosen (1913), Parr (1927), and Winterbottom (1971a) aspects of the body musculature, while Willem (1941, 1942, 1944, 1945, 1947a, 1947b, 1949) and Sarkar (1960) considered the functional workings of the tetraodontiform head. Le Danois (1955, 1959, 1961) has made extensive observations on the myology of the "Orbicates" (a group containing the gymnodonts and ostracioids). Few of these papers contain any reasoned, phylogenetic remarks. Winther (1877:462-463) accepted Cuvier's (1817) Sclerodermi (balistoids and ostracioids), and suggested that the Triacanthidae were specialized relatives. He felt, however, that the gymnodonts were most closely related to the "Discobali" (=Cyclopteridae), a conclusion which has not, as far as I am aware, been supported since then. Lubosch (1929) made certain general conclusions, but these suffer from the wide scope of the work in relation to the number of species examined. The placement of the Acanthuridae between the Balistidae and Triacanthidae in the text may indicate that Lubosch felt them to be tetraodontiforms, but this is not explicitly stated. Grenholm (1923:245), while stating that the tetraodontiforms were a well-defined group (and probably closely related to the Acanthuridae), felt that the separation of the order into scleroderms and gymnodonts was difficult to maintain ("... schwer afrecht zu erhalten"), although he gave no reasons



for this opinion. Willem, in his (1942:19–21) paper, concluded that among the scleroderms, the acanthurids were the most generalized, followed either by the triacanthids or the monacanthids, with the balistids the most specialized. Later (1944), Willem placed the chaetodontid fishes in the tetraodontiforms (=his "Plectognathes").

In her definition of the "Orbiculates"—the ostracioid and gymnodont fishes—Le Danois (1955) regarded the following myological characters as primitive, and used them to define the suborder: musculature complex, subcutaneous and trapezoidal muscles present. As discussed above, it has recently been realized that primitive (symplesiomorph) characters cannot be used to link groups phylogenetically. Additionally, complexity of muscles is a sign of specialization, not of antiquity; subcutaneous muscles are found elsewhere (e.g., Antenariidae), and certainly could not exist where discreet, overlapping scales (surely a "primitive" condition for the teleosts) are present. "Trapezoidal" muscles present somewhat of an enigma. The anteroventral muscle (the "trapèze inférieur" of Le Danois, 1959) is the protractor pectoralis (derived from the levator series of the branchial arches, and innervated by the vagus nerve), while her "trapèze supérieur" is derived from the anterior trunk myomeres, and is innervated by an occipitospinal nerve. The protractor pectoralis occurs regularly throughout the Euteleostei (Division III) of Greenwood, et al. (1966, 1967) except in most, if not all, members of the Protacanthopterygii (sensu Rosen and Patterson, 1969). The levator pectoralis has only been reported as a separate muscle from certain families of Rosen and Patterson's (1969) Series Percomorpha. Thus, the presence of two "trapezoidal" muscles in the "Orbiculates" is more in keeping with an alignment of these fishes with groups of at least the percomorph level of organization, rather than with the "malacopterygian" level (to which Le Danois felt they were related). Parenthetically, it should be noted that the last two of these three myological characters are not found in ostracioids. The comparative reader will find certain discrepancies between Le Danois' myological descriptions and those given here. The phylogenetic conclusions reached by Tyler in his various publications on tetraodontiform osteology will be reviewed in the discussion section of this paper.

**ACKNOWLEDGMENTS.**—This paper represents the major portion of a doctoral dissertation submitted to the School of Graduate Studies, Queen's University, Kingston, Ontario, Canada.

I wish to express my deepest gratitude to Dr. James C. Tyler of the Academy of Natural Sciences, Philadelphia (ANSP), whose stimulating interest and helpful advice has formed the mainspring of this study. He has freely made available his detailed knowledge of the tetraodontiforms, and supplied much unpublished osteological information as well as most of the specimens dissected. Dr. Tyler has generously commented on both the dissertation and much of the manuscript, although he is not necessarily in agreement with the phylogenetic relationships as presented here, and certainly disagrees with the classificatory approach taken by the author.

To Dr. S. H. Weitzman of the Smithsonian Institution, Washington, D.C., I express my thanks for his encouragement to complete the manuscript and to maintain it in its entirety, and for his comments on the text.

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### Materials, Methods, and Terminology

The nomenclature of the muscles used in this paper is taken from a descriptive synonymy of teleostean muscles at present in preparation by the author. In the case of the muscles to the rudimentary balistoid pelvic fin, the nomenclature is based on the assumption that the fin ray elements represent the pelvic spines. In the descriptive section, the muscles have been grouped according to convenient body regions.

Osteological nomenclature is based on Tyler (1962a, 1970a) except for the hyoid arch, where Nelson (1969) has been followed. The suture lines shown in the figures are approximate, and are included for reference purposes only. For accurate outlines of the bones, see Tyler's various publications on tetraodontiform osteology.

Specimens for the most part were dissected under a Wild M-5 stereoscopic research dissecting microscope. Rough pencil drawings were made on bristol board with the aid of a Wild M-5 camera lucida attachment. Detail was filled in freehand from the dissection, the drawing then being inked in. Bone and cartilage—stippled; muscles—lined with long and short dashes; connective tissue—filled with wavy lines; tendons, aponeuroses and ligaments—short dashes; coelom—crosshatched. Bones are only labeled in the figures of species dissected in detail for each family; the muscle abbreviations being underlined for clarity in these figures. Caudal fin rays are numbered from the midline, those above being prefixed by "D", those below by "V". Numerical differences arising from the number of fin rays in any fin are not considered.

The musculature of representatives of the following families, and in the following order, are described: Triacanthodidae, Triacanthidae, Balisti-

dae, Monacanthidae, Aracanidae, Ostraciidae, Triodontidae, Tetraodontidae, Canthigasteridae, Diodontidae, and Molidae. The following group terms are used provisionally to contain more than one family: balistoid (Balistidae + Monacanthidae), ostracioid (Aracanidae + Ostraciidae), tetraodontoid (Tetraodontidae + Canthigasteridae), and triacanthoid (Triacanthodidae + Triacanthidae). The latter group may not be phylogenetically valid, and will be used for convenience only. The Cuvierian term "gymnodont" will be used initially to designate the Triodontidae + Molidae + Diodontidae + tetraodontoids.

The following is a list of the material examined, arranged alphabetically by family. The number in parentheses indicates the number of specimens examined. Catalog abbreviations are clarified in "Acknowledgments."

ARACANIDAE.—*Capropygia unistriata* Kaup: ANSP 109574, (1), 67 mm SL, Kingston, South Australia. *Kentrocabros aculeatus* (Houttuyn): ANSP 117531, (2), 91 and 92 mm SL, no data, received from T. Abe.

BALISTIDAE.—*Balistapus undulatus* (Mungo Park): ANSP 108832, (1), 159 mm SL, Ressource Islands, Indian Ocean; ANSP 117598, (1), 83 mm SL, Inhaca Island, Indian Ocean. *Balistes vetula* Linnaeus: ANSP 105508, (1), 111 mm SL, Estado Sucre, Venezuela; ANSP 117535, (1), 137 mm SL, no data, aquarium specimen. *Melichthys niger* (Bloch): ANSP 117515, (1), 153 mm SL, no data, aquarium specimen. *Odonus niger* (Rüppell): ANSP 102779, (1), 257 mm SL, Amirante Islands, Indian Ocean. *Rhinecanthus aculeatus* (Linnaeus): ANSP 117546, (1), 159 mm SL, Johnston Island, Hawaii; ANSP 117544, (1), 175 mm SL, no data, received from J. H. Wallace.

CANTHIGASTERIDAE.—*Canthigaster margaritatus* (Rüppell): ANSP 117517, (1), 52 mm SL, no data, received from M. M. Smith. *Canthigaster valentini* (Bleeker): ANSP 117534, (1), 45 mm SL, Seychelles Islands, Indian Ocean.

DIODONTIDAE.—*Chilomycterus orbicularis* (Bloch): ANSP 117510, (1), 80 mm SL, no data, received from M. M. Smith. *Chilomycterus schoepfi* (Walbaum): ANSP 117518, (1), 138 mm SL, beach at Kitty Hawk, North Carolina. *Diodon hystrix* Linnaeus: NMC 68-997, (1), 77 mm SL, Tres Maria, Mexico; ANSP 117553, (1), 291 mm SL, Kaneohe Bay, Hawaii.

MOLIDAE.—*Mola mola* Linnaeus: BM(NH) 1938.6.23.38, (1), 287 mm SL, off Chousi, Japan; NMC 67.298, (1), 500 mm SL, off Newfoundland. *Ranzania laevis* (Pennant): ANSP 106723, (1), 93 mm SL, Hawaii.

MONACANTHIDAE.—*Aluterus heudelotii* Hollard: ANSP 103224, (1), 110 mm SL, Guinea, West Africa. *A. monoceros* (Osbeck): ANSP 117498, (1), 160 mm SL, R/V *Oregon* (Station 10523); ANSP 117554, (2), 345 and 350 mm SL, no data, received from J. Field. *A. schoepfi* (Walbaum): ANSP 101843, (1), 106 mm SL, Caribbean, off Columbia. *Anacanthus barbatus* Gray: ANSP 117516, (1), 166 mm SL, Gulf of Thailand. *Cantherhines pardalis* (Rüppell): ANSP 117529, (1), 61 mm SL, Inhaca Island, Indian Ocean; ANSP 117530, (1), 126 mm SL, no data, received from M. M. Smith. *Chaetoderma spinosissimus* (Quoy and Gaimard): ANSP 117514, (1), 42 mm SL, Gulf of Thailand. *Oxymonacanthus longirostris* (Bloch and Schneider): ANSP 117496, (1), 72 mm SL, Zanzibar; ANSP 104791, (1), 72 mm SL, Amirante Islands, Indian Ocean. *Paraluteres prionurus* (Bleeker): ANSP 106644, (1), 57 mm SL, Farquhar Islands, Indian Ocean. *Paramonacanthus barnardi* Fraser-Brunner: ANSP 117506, (1), 78 mm SL, Natal, South Africa. *Pervagor melanocephalus* (Bleeker): ANSP 117500, (2), 66 and 85 mm SL, Taiwan; ANSP 117512, (1), 87 mm SL, Moçambique Island, Indian Ocean. *Pseudalutarius nasicornis* (Schlegel): ANSP 100830, (1), 45 mm SL, Bay of Bengal. *Stephanolepis auratus* (Castlenau): ANSP 117526, (1), 64 mm SL, Delagoa Bay, South Africa; ANSP 117521, (2), 69 and 82 mm SL, Natal, South Africa.

OSTRACIDAE.—*Acanthostracion quadricornis* (Linnaeus): ANSP 98848, (1), 126 mm SL, Atlantic Ocean, off South America. *Lactoria cornuta* (Linnaeus): ANSP 117540, (1), 50 mm SL, Natal, South Africa; ANSP 117538, (1), 92 mm SL, no data, received from M. M. Smith; ANSP 117539, (1), 176

mm SL, no data, received from J. H. Wallace. *Ostracion tuberculatus* Linnaeus: ANSP 117542, (2), 102 and 157 mm SL, no data, received from J. H. Wallace. *Tetrosomus concatenatus* (Bloch): ANSP 117555, (2), 196 and 200 mm SL, no data, received from M. M. Smith.

TETRAODONTIDAE. — *Amblyrhynchotes honckenii* (Bloch): ANSP 117547, (1), 106 mm SL, Cape Province, South Africa. *Arothron immaculatus* (Bloch): ANSP 117528, (1), 68 mm SL, no data, received from M. M. Smith. *Colomesus psittacus* (Bloch and Schneider): ANSP 98887, (1), 117 mm SL, off Surinam. *Lagocephalus lunaris* (Bloch and Schneider): ANSP 113639, (3), 118, 124, and 137 mm SL, Malaysia. *Tetraodon schoutedeni* Pellegrin: ANSP 117501, (1), 62 mm SL, Congo River at Leopoldville. *Xenopterus naritus* (Richardson): ANSP 117495, (2), 102 and 120 mm SL, Bay of Bengal.

TRIACANTHIDAE. — *Triacanthus biaculeatus* (Bloch): ANSP 111536, (1), 111 mm SL, off Kerala State, India. *Tripodichthys oxycephalus* (Bleeker): ANSP 89397, (1), 82 mm SL, Paknam, Siam. *Triphichthys weberi* (Chaudhuri): ANSP 117492, (2), 115 and 122 mm SL, Bay of Bengal.

TRIACANTHODIDAE.—*Halimochirurgus centriscoides* Alcock: ANSP 117494, (1), 114 mm SL, Bay of Bengal. *Hollardia hollardi* Poey: ANSP 117491, (2), 53 and 92 mm SL, off Honduras. *Macrorhamphosodes platycheilus* Fowler: ANSP 117533, (2), 79 and 88 mm SL, Bay of Bengal. *Parahollardia lineata* (Longley): ANSP 101031, (1), 68 mm SL, Gulf of Mexico. *Triacanthodes anomalus* (Schlegel): ANSP 101256, (1), 74 mm SL, Honshu, Japan; ANSP 117493, (1), 87 mm SL, Honshu, Japan. *Tydemania navigatoris* Weber: ANSP 117532, (1), 73 mm SL, Bay of Bengal.

TRIODONTIDAE. — *Triodon macropterus* Lesson: ANSP 103902, (3), 270, 350, and 350 mm SL, Ryukyu Islands, Pacific Ocean; ANSP 98916, (1), 382 mm SL, Bonin Island, Pacific Ocean.

### Myological Descriptions of Representative Triacanthodids

The general body outline of these fishes is represented in Figure 1. The sample size of the two subfamilies is four out of nine genera for the Triacanthodinae and two out of two genera for the Hollardiinae.

The latter subfamily is found mainly in the

Caribbean (with one exception presently recorded only from Hawaii), while the triacanthodins extend broadly from the east coast of Africa to the western Pacific. Triacanthodids are usually benthic or bathypelagic fishes, living well below 100 fathoms.

They appear to feed predominantly on marine

invertebrates, with the exception of *Macrorhamphosodes*, in whose gut nothing but scales of other fishes has yet been found.

The rounded caudal fin and rather deep body of these fishes implies that they are not fast swimmers, while the protractile jaws (of at least the more conservative genera) evidences that their prey is active. The jaws, however, are not protrusile in the percoid manner, since the process here is completely passive (i.e., no active part is played by the maxilla in protruding the premaxilla). They are apparently incapable of closing the mouth with the premaxillae still in the protruded position (the advantages of such a maneuver are discussed by Alexander, 1967).

Figure 48 shows the overall structure of the jaws of *Triacanthodes anomalus* and *Triacanthus biaculeatus* (a triacanthid). The maxilla (Figures 48c,d) is a fairly broad plate, the dorsal region curving inward toward the midline. The fact that it is a broad bone and not rodlike indicates that it is incapable of rotating about its vertical axis, a movement essential in the protrusion of the percoid jaw. The dorsomedial region of the maxilla has developed an external and internal flange. These two flanges together form a groove containing the lateral margin of the ascending process of the premaxilla. From the lateral face of the inner flange of the maxilla there arises a continuous sheet of tough ligamentous tissue (the maxillopremaxilla ligament) which passes dorsomedially to attach to the ventromedial face of the ascending process of the premaxilla. Neither the posteroventral face of the maxilla, nor the anterior surface of the ethmo-vomer region where the maxilla articulates show any evidence of the cartilagenous pad found there in percoids. This indicates that the maxilla can only move in one direction, since in most cases of joints with two degrees of freedom (a higher pair) there is a cartilagenous meniscus or pad allowing this type of movement (Alexander, 1967). It seems, then, that the maxilla cannot function as it does in percoids. From the anterodorsal region of the maxilla the maxilloethmoid ligament passes posteriorly to the ethmoid bone. Immediately beneath its attachment to the maxilla is the anterior process of the palatine, which rests in a concavity in the maxilla (Figure 48b). In perciform fishes with protrusile jaws, the anterior process of the palatine moves medially when the buccal and opercular

cavities are expanded (e.g., when feeding), since it is situated dorsal to the articulation of the palatal arch with the skull. This medial movement locks the cranial condyle of the maxilla in position, which in turn prevents the posterior movement of the premaxilla (since the articular process of the premaxilla jams against the premaxillary condyle of the maxilla). The mouth can thus be closed with the premaxilla in the protruded position (were the processes not present, the premaxillae would be retracted during mouth closing—see Alexander, 1967, for details). In the triacanthoids, medial movement of the palatal process would put some pressure on the maxilla, but since none of the above processes are present, this would be insufficient to lock them in position during closure of the mouth.

Of the two subfamilies, the Hollardiinae are apparently the most generalized (Tyler, 1968:31-33). However, Tyler (1968:30, fig. 6) also indicates in effect, that they, the triacanthids and the balistoids, form the sister group of the triacanthodins.

#### Subfamily TRIACANTHODINAE

##### *Triacanthodes anomalus* (Schlegel)

FIGURES 49-56

#### MUSCLES OF THE CHEEK

**ADDUCTOR MANDIBULAE** (Figure 49: A 1, A 2 $\alpha$ , A 2 $\beta$ ; see also Figure 68a of *Hollardia*).—The adductor mandibulae is well separated into two portions by the path of ramus mandibularis V. The postero-dorsal section (A 2 $\alpha$ ) originates from the anterodorsal face of the hyomandibular and from a sheetlike aponeurosis covering the dorsal surface of the section. Beneath the eye, A 1 begins to develop, increasing in size as it passes anteriorly. The fibers from A 1 grade into a tendon which receives contributions from A 2 $\beta$  and A 3 ventrally. This composite tendon then divides, the dorsal part passing anterodorsally to insert near the medial face of the cranial condyle of the maxilla, beneath its articulation with the palatine, while the ventral part inserts on the anteromedial face of the dentary in the Meckelian fossa. The lateral portion of the ventral fibers contributing to the tendon mentioned above forms A 2 $\beta$ , which originates from the dorsal

preopercle and quadrate and the anterior face of the hyomandibular. The ventromedial section, A 3, originates from the lateral faces of the quadrate, symplectic, and metapterygoid.

**LEVATOR ARCUS PALATINI** (Figure 49: L.A.P).—The muscle originates from the ventral face of the postorbital process of the sphenotic, and inserts on the dorsal and anterodorsal faces of the hyomandibular. It is a pyramidal muscle, whose apex lies dorsally.

**DILATOR OPERCULI** (Figure 49: D.O).—Origin is from the ventrolateral sphenotic and pterotic and the dorsal tip of the hyomandibular. The fibers pass ventrolaterally to insert on the tip of the dorsal process of the opercle. It is a conical muscle, with the apex pointing ventrally.

**LEVATOR OPERCULI** (Figure 49: L.O).—The muscle consists of two portions. The anterior part originates from the ventrolateral face of the pterotic and inserts on the dorsomedial face of the posterior flange of the opercle. The posterior section arises from the lateral pterotic and anteromedial supra-cleithrum and passes ventrally to insert on the posteromedial flange of the opercle just behind the insertion of the anterior part.

**ADDUCTOR ARCUS PALATINI** (Figure 49: A.A.P).—This parallel fibered muscle originates from the ventrolateral surface of the parasphenoid and the lateral prootic. It inserts on the dorsomedial faces of the metapterygoid, mesopterygoid, and hyomandibular.

**ADDUCTOR OPERCULI** (Figure 50: AD.OP).—Origin is from the ventral face of the pterotic, the fibers inserting on the dorsomedial face of the opercle.

#### MUSCLES OF THE HYOID REGION

**INTERMANDIBULARIS** (see Figure 65 of *Hollardia*, *IMD*).—This small muscle connects the halves of the lower jaw, attaching to the dentaries just below the Meckelian fossae.

**PROTRACTOR HYOIDEI** (Figure 49: PR.HY).—Origin is from the inner face of the dentary, both dorsal and ventral to the intermandibularis. The fibers pass posteriorly and split into left and right halves. Each section inserts on the lateral face of the anterohyal as far back as the third branchiostegal ray.

**HYOHYOIDEUS INFERIORIS** (Figures 49, 50: HY.IN).—The muscle is relatively well developed, and passes from a median ventral raphe to the antero-

lateral and ventral surfaces of the anterohyal. The muscle attaches ventrally to the ventrohyals by a pair of ligaments passing anterolaterally from the anteromedial border of the fibers. These are similar, although somewhat weaker, than those figured for *Hollardia* (Figure 65).

**HYOHYOIDEI ABDUCTORES** (Figure 49: H.AB).—There are four sections of this muscle, one to each of the ventral four branchiostegal rays. The section to the first ray originates as a long tendon from the posteroventral face of the ventrohyal, that to the next ray from the base of the first ray. The two following sections arise from the base of the second ray. All insert on the medial faces of the rays distal to their bases.

**HYOHYOIDEI ADDUCTORES** (Figure 49: H.AD).—The muscle passes between the dorsalmost four branchiostegal rays and continues above them as a thin layer of fibers in the membrane lining the opercular cavity, fading out beneath the opercle and subopercle. There is a fairly well-developed section along the posterior border of the opercle in the tissues of the opercular valve. Fibers also continue inward ventrally along the floor of the opercular cavity for a short distance.

**STERNOHYOIDEUS** (Figures 49, 50: STH).—A well-developed muscle, consisting of three bundles of fibers separated by myocommata. The posterolateral region is continuous with the anterolateral fibers of the obliquus inferioris. Origin is from the anteroventral cleithrum and insertion mainly on the posterior and lateral faces of the urohyal. The dorsomedial fibers tend to pass dorsally rather than anterodorsally. The more anterior of these fibers attach to the fascia separating the halves of the sternohyoideus, while the more posterior ones are to a greater or lesser extent continuous with the fibers of the sternobranchialis.

**STERNOBRANCHIALIS** (Figure 50: STB).—The muscle originates from the anteroventromedial face of the cleithrum. It passes dorsally, the anterior fibers intermingling with those of the sternohyoideus, and grades into a broad, flat aponeurosis which fuses with that from the other side. The two sheets then separate and divide into anterior and posterior components. The latter passes dorsally, lateral to the rectus communis, to insert on the ventral faces of the third hypobranchial and fourth ceratobranchial. From the posteromedial face of the anterior portion a tendon arises, fusing briefly

with its antimere before diverging to insert on the ventral surface of the third hypobranchial. It passes medial to the rectus communis. The rest of the anterior sheet continues upward, lateral to the rectus communis, to insert on the ventral surfaces of the first three hypobranchials.

#### VENTRAL BRANCHIAL MUSCLES

**PHARYNGOCLAVICULARIS EXTERNUS** (Figures 50, 51: PHC.E.).—Origin is from the anterodorsal face of the medial region of the cleithrum, the fibers passing dorsomedially to insert on the anteroventral face of ceratobranchial 5.

**PHARYNGOCLAVICULARIS INTERNUS** (Figures 50, 51: PHC.I.).—The fibers arise from the anteromedial face of the cleithrum and pass forward to insert on the ventral border of ceratobranchial 5. The insertion is medial to that of the pharyngoclavicularis externus.

**OBLIQUI VENTRALES I-III** (Figure 51: OBL.V.).—These muscles pass between the ceratobranchials and hypobranchials of the first three arches. The first is small, the second being somewhat better developed. The third muscle attaches to the ventral process of the third hypobranchial. The more posterior fibers of this section attach to the arch-shaped ligament between the left and right hypobranchial processes.

**TRANSVERSI VENTRALES IV-V** (Figure 51: TR.V.).—The muscles pass transversely across the midline, connecting the ventromedial faces of the fourth and fifth ceratobranchials, respectively.

**RECTI VENTRALES I AND IV** (Figure 51: RECT.V.).—The first of these muscles connects the anterolateral face of hypobranchial 1 to the posterolateral face of the dorsohyal. Rectus IV arises from the ventral face of ceratobranchial 4 and passes anteromedially to attach to the posterior surface of the arch-shaped ligament between the third hypobranchials.

**RECTUS COMMUNIS** (Figures 50, 51: R.COMM.).—Origin is from the posterodorsolateral face of the urohyal. The fibers pass posteriorly, the muscle becoming aponeurotic about the level of the third hypobranchial. It inserts on the ventrolateral face of ceratobranchial 5.

#### DORSAL BRANCHIAL MUSCLES

**LEVATORES EXTERNI I-IV** (Figure 50: L.EXT.).—

These four cylindrical muscles insert aponeurotically on the posterodorsal faces of the four epibranchials. They originate from the lateral prootic, and a small part of the pterotic, increasing in size while attaining a more lateral origin as one proceeds posteriorly in the series.

**LEVATORES INTERNI II-III** (Figure 52: L.INT.).—Both muscles originate from the prootic. Levator II inserts on the dorsomedial face of the infrapharyngobranchial 2, while levator III (which originates more dorsolaterally on the prootic) inserts on the anterodorsolateral face of the infrapharyngobranchial 3.

**OBLIQUUS DORSALIS III** (Figure 52: OBL.D.).—The muscle passes from the anterodorsal face of epibranchial 2 to the posterodorsal face of infrapharyngobranchial 3.

**OBLIQUUS POSTERIOR** (Figure 52: OBL.P.).—The muscle connects the anterodorsal face of ceratobranchial 5 to the posterodorsal face of ceratobranchial 4.

**TRANSVERSI DORSALES II-III** (Figures 50, 52: TR.D.).—The anterior muscle originates partly from the ventrolateral surface of the parasphenoid and partly from a raphe with its antimere behind this. It inserts on the dorsal face of epibranchial 2. The posterior muscle arises from a raphe in the dorsal midline and courses laterally to insert on the posterodorsal face of epibranchial 3.

**RETRACTOR DORSALIS** (Figure 52: D.RETR.).—This is a well-developed muscle originating from the ventrolateral surfaces of the basioccipital and the first vertebra. It passes anteroventrally to insert on the dorsal face of infrapharyngobranchial 3.

**ADDUCTORS IV-V** (Figures 50, 52: AD.).—Adductor IV is a small muscle connecting the medial faces of the fourth epi- and ceratobranchials. Adductor V is also small, and passes from the anterodorsal tip of ceratobranchial 5 to the distal tip of epibranchial 4. It lies lateral to the obliquus posterior.

**SPHINCTER OESOPHAGI** (Figures 51, 52: S.O.).—The fibers of the muscle surround the esophagus, attaching mainly to the posteromedial faces of the fifth ceratobranchials. In the ventral midline, it lies dorsal to transversus ventralis V, and develops a raphe at its extreme anterior margin. It is continuous across the dorsal midline, and is attached anteriorly to epibranchial 4 by connective tissue.

## MUSCLES OF THE PECTORAL GIRDLE

**ABDUCTOR SUPERFICIALIS** (Figure 49: ABD.S.).—The fibers originate from the posteroventral face of the cleithrum, and pass posterodorsally to insert by a series of tendons on the dorsolateral bases of the 12 principal fin rays.

**ABDUCTOR PROFUNDUS** (Figures 49, 50, 53: ABD.P.).—Origin is from the posterior face of the cleithrum and the anterior face of the coracoid. The fibers pass dorsally to insert tendinously on the lateral faces of the posteroventral flanges of the 12 principal fin rays and the lateral half of the base of the vestigial fin ray.

**ARRECTOR VENTRALIS** (Figure 49: ARR.V.).—The muscle originates just dorsal to the abductor superficialis on the cleithrum. It courses posterodorsally to insert tendinously on the base of the medial half of the vestigial fin ray.

**ADDUCTOR SUPERFICIALIS** (Figure 53: ADD.S.).—Origin is from the posterior face of the cleithrum and the ventromedial scapula. The fibers insert by a series of 12 tendons on the dorsomedial faces of the principal fin rays. The more medial and dorsal portion of the muscle serves the more ventral fin rays, attaching at right angles to the longitudinal axes of the rays. The more ventral fibers attach to the more dorsal rays with an increasingly parallel orientation. The muscle has thus effectively "folded under" itself.

**ADDUCTOR PROFUNDUS** (Figure 53: ADD.P.).—Origin is from the medial cleithrum and coracoid, the muscle inserting tendinously on the ventromedial flanges of the bases of the 12 principal fin rays.

**ARRECTOR DORSALIS** (Figure 53: ARR.D.).—The muscle originates from the medial face of the scapula and cleithrum, and passes posterodorsally to insert on the medial half of the vestigial fin ray.

**CORACORADIALIS** (Figure 53: COR.R.).—A small muscle, arising from the dorsal face of the posterior process of the coracoid, and inserting on the ventromedial face of the last (ventralmost) radial.

**ADDUCTOR RADIALIS** (see Figure 62 of *Paraholardia*, ADD.R.).—The fibers arise from the ventromedial faces of the middle two radials and insert on the bases of the ventralmost two fin rays. It courses at right angles to the coracoradialis, and lies lateral to the adductor profundus.

**PROTRACTOR PECTORALIS** (Figure 50: P.P.).—Origin is from the ventrolateral pterotic just behind

the hyomandibular fossa, the fibers passing ventrally to insert on the anterodorsal face of the cleithrum.

**LEVATOR PECTORALIS** (Figure 50: TR.).—The muscle arises from the pterotic just behind the protractor pectoralis. The fibers fan out to insert on the medial face of the supracleithrum.

## MUSCLES OF THE PELVIC GIRDLE

**ARRECTOR DORSALIS PELVICUS** (Figures 50, 53: A.D.P.).—Origin is from the anterolateral face of the anterior part of the pelvis, and is bordered ventrally by the lateral flange of the bone. It inserts on the anterolateral aspect of the pelvic spine, dorsal to the articulation with the pelvis.

**ARRECTOR VENTRALIS PELVICUS** (Figure 53: A.V.P.).—The muscle arises from the anteroventral surface of the anterior part of the pelvis. It inserts on the anterolateral aspect of the pelvic spine, ventral to the articulation with the pelvis.

**ADDUCTOR SUPERFICIALIS PELVICUS** (Figures 50, 53: A.S.P.).—Originating on the posteromedial face of the anterior part of the pelvis, the fibers pass posterolaterally to insert on the dorsal surface of the dorsal flange of the pelvic spine.

**ADDUCTOR PROFUNDUS PELVICUS** (Figure 53: A.P.P.).—There are two slips of this muscle, which originate from the dorsomedial face of the pelvis posterior to the adductor superficialis pelvici. Each slip inserts on the dorsomedial surface of a pelvic ray, the larger and more anterior section inserting on the more anterior of the two rays.

## MUSCLES OF THE DORSAL FIN

**INCLINATOIRES DORSALES** (Figures 49, 55a: INC.).—The second to fourth dorsal spines and their pterygiophores receive a sheet of muscle fibers arising from the fascia overlying the epaxialis. The inclinator to the sixth spine and those to the soft dorsal fin rays are separate, inserting only on the bases of the spine or ray. The muscles to the rays are well developed, particularly anteriorly.

**ERECTORES DORSALES** (Figures 49, 54, 55a: EREC.).—All spines and fin rays receive an erector. The fibers arise from the lateral faces of the pterygiophores and associated neural spines, and insert on the anterolateral bases of the spines or

rays. The first erector is extremely powerful and is bipinnate. The size of these muscles in both the spiny and the soft dorsal fins decreases posteriorly.

**DEPRESSORES DORSALES** (Figures 49, 54, 55a: DEPR.).—All spines and rays receive a depressor, which originates from the lateral pterygiophores and neural spines in between the erectors. The muscles are smaller than the erectors, and insert on the posterolateral bases of the spines and rays. They also decrease in size posteriorly in both fins.

**SUPRACARINALIS ANTERIOR** (Figures 49, 54: s. ANT.).—Origin is from the lateral and dorsal faces of the supraoccipital, the fibers inserting on the anterodorsolateral face of the first pterygiophore of the dorsal fin.

**SUPRACARINALIS POSTERIOR** (Figure 56: s.POST.).—Fibers arise from the lateral surface of the last pterygiophore of the dorsal fin, and course posteriorly. The muscle attaches to the dorsolateral tips of the neural spines of the caudal vertebrae, terminating on the neural spine of caudal vertebra 10.

#### MUSCLES OF THE ANAL FIN

**INCLINATOIRES ANALES** (Figure 55b: INC.).—Each anal fin ray receives an inclinator on the lateral face of the fin base, which originates in the fascia overlying the hypaxialis. The anterior muscles are better developed than the posterior ones. There is an additional, residual inclinator muscle originating in front of the first normal inclinator and inserting on the ventrolateral face of the first anal fin pterygiophore.

**ERECTORES ANALES** (Figure 55b: EREC.).—Each fin ray possesses an erector, originating from the lateral faces of the pterygiophores and haemal spines and inserting on the anterodorsal base of the ray.

**DEPRESSORES ANALES** (Figure 55b: DEPR.).—These muscles originate just posterior to the erectors and insert on the posterolateral bases of the fin rays.

**INFRACARINALIS ANTERIOR** (Figures 49, 50, 53: INF.A.).—Fibers arise from the posteroventral extremity of the cleithrum and fan out to insert on the anterolateral face of the pelvis.

**INFRACARINALIS MEDIUS** (Figure 49: INF.M.).—The muscle originates from the anteroventral margin of the first anal pterygiophore and inserts on

the dorsal face of the posterior tip of the pelvis. It consists of two bundles of fibers separated by a myocomma, just posterior to which is a small knot of fibers passing dorsally to join the ventral surface of the obliquus inferioris.

**INFRACARINALIS POSTERIOR** (Figure 56: INF.P.).—Fibers arise from the posteroventral face of the last anal pterygiophore and attach to the ventrolateral tip of the haemal spine of caudal vertebra 10. The medial fibers of the muscle attach to the lateral tips of the haemal spines of the two intervening vertebrae (8 and 9).

#### MUSCLES OF THE CAUDAL FIN

**INTERRADIALIS** (Figure 56a,b: INT.).—The muscle interconnects the caudal fin rays, with a section inserting on the ventrolateral face of each of the six dorsal rays and on the dorsolateral face of each of the six ventral rays. The two strips of muscle thus formed mingle between the rays on either side of the midline.

**HYPCHORDAL LONGITUDINALIS** (Figures 56a,b: H.L.).—Origin is from the lateral face of hypurals 1 and 2, the fibers coursing posterodorsally to insert on the lateral bases of the second to fourth (D 2-4) dorsal fin rays.

**FLEXOR DORSALIS** (Figure 56b: F.D.).—The muscle originates from the lateral surfaces of the neural spines and dorsolateral surfaces of the centra of the ninth to eleventh caudal vertebrae, and the dorsolateral face of the urostyle. The fibers pass posterodorsally to insert on the lateral bases of rays D 2-5.

**FLEXOR DORSALIS SUPERIOR** (Figure 56: F.D.S.).—Origin is from the neural spines of the tenth and eleventh caudal vertebrae, the fibers passing posteriorly to insert on the lateral base of D 6.

**FLEXOR VENTRALIS** (Figure 56b: F.V.).—Fibers arise from the posterolateral faces of the haemal spines and ventrolateral surfaces of the centra of the ninth to eleventh caudal vertebrae, and the ventrolateral face of the urostyle. Fibers pass posteroventrally to insert on the bases of rays V 1-6.

**FLEXOR VENTRALIS EXTERNUS** (Figure 56b: F.V.E.).—The muscle originates from the posterolateral faces of the haemal spines of caudal vertebrae 9-10, and passes posteriorly to insert on the lateral bases of rays V 1-2. It lies directly beneath the hypaxial body musculature.



**FLEXOR VENTRALIS INFERIOR** (Figure 56: F.V.I.).—Origin is from the posterolateral tips of the haemal spines of caudal vertebrae 10–11. Insertion is on the base of ray V 6.

**TRANSVERSUS CAUDALIS** (Figure 56c: TR.C.).—This fan-shaped muscle originates from the dorsolateral face of hypural 5 and the posterolateral surface of the urostyle. It courses posteroventrally beneath the hypochordal longitudinalis to insert on the dorsal base of ray V 1.

#### LATERAL BODY MUSCLES

**EPAXIALIS** (Figures 49, 56a: EPAX.).—The epaxial musculature consists of nineteen myomeres, all vertebrae except the urostyle thus being represented. There are two major directions of the myocommata, and a third direction is present anterodorsally. The first two merge in the posterior region of the body, where they insert by a series of broad aponeuroses on the lateral bases of rays D 1–6. The aponeuroses to rays D 1–3 pass medial to the hypochordal longitudinalis. Anteriorly, the mass of the muscle attaches to the posterior surface of the skull.

**OBLIQUUS SUPERIORIS** (Figures 49, 50, 56a: OBL.S.).—This section forms the main mass of the hypaxialis, and consists of eighteen myomeres. It is poorly developed anteriorly, where it attaches to the extreme posterodorsal tip of the cleithrum. (The anterior section probably contains part of the lateralis superficialis, which usually forms a thin sheet covering both epaxial and hypaxial musculature near the anterior midline. The fibers apparently always pass anteroposteriorly, with little dorsal or ventral angulation. Owing to the extreme difficulty of observing the nature of this subdivision in preserved (or even fresh) material, it will not be considered further. Suffice it to say that a detailed, accurate description of the lateral body muscles in general, and that of the lateralis superficialis in particular, would require serial sectioning of the material. Greene (1913), in his diagnosis of the lateralis superficialis, relies on color and histological criteria.) The obliquus superioris broadens out posteriorly, forming the dorsal and posterior borders of the abdominal cavity. It contributes fibers to the compound section of the hypaxialis inserting on the lateral bases of caudal rays V 1–6.

**OBLIQUUS INFERIORIS** (Figures 49, 56a: OBL.I.).—

The anteroventral portion of this section arises from the ventrolateral face of the cleithrum and the posterolateral pelvis. The anterior fibers are continuous with the sternohyoideus, most of the fibers behind this attaching to the anteroventral margin of the postcleithrum. The anterodorsal fibers arise from the fascia over the midline and epipleurals and course anteroventrally to the posterodorsal surface of the postcleithrum. The fibers become increasingly horizontal posteriorly, and the section separates somewhat from the obliquus superioris before finally fusing with it in the peduncular region. The fibers from this part attach to the bases of caudal fin rays V 1–6. The muscle is made up of sixteen myomeres, the more anterior of which are parallel with the muscle fiber direction.

#### *Tydemanina navigatoris* Weber

##### FIGURE 57

Many of the differences in musculature between this and the preceding species result from the more elongate form of *Tydemanina*. The sections of the adductor mandibulae are somewhat reduced in dorsoventral extent. A 3 is absent, having either fused with A 2 $\beta$  or having degenerated. The origin of A 2 $\beta$  thus now includes the lateral faces of the symplectic, mesopterygoid and metapterygoid. The tendon of A 1 is better developed. The origin of the dilatator operculi is reduced, while that of the anterior part of the levator operculi is larger. Owing to the more dorsal position of the opercle and the smaller size of the dilatator operculi, a hiatus has appeared between that muscle and the anterior portion of the levator operculi.

The intermandibularis is poorly developed, consisting of only a few fibers, and the hyohyoideus inferioris is not as large as in *T. anomalus*. A few fibers of the sphincter esophagi overlie the retractor dorsalis. Origin of the adductor radialis is restricted to the ventral face of the third radial, the fibers inserting only on the ventralmost pectoral fin ray. The adductor profundus pelvis, which inserts on the pelvic fin rays in *T. anomalus*, is absent in all other members of the Triacanthodinae examined. The erectores and depressores dorsales serve only the first three dorsal spines. In this species and the remaining members of the subfamily, the inclinadores dorsales are present only in the soft dorsal fin.

*Macrorhamphosodes platycheilus* Fowler

FIGURES 58-59

The larger specimen had the mouth twisted some 55 degrees to the left, while that of the smaller individual was twisted to a lesser extent to the right. No differences that could be correlated with the side to which the mouth was twisted were found, except in the adductor mandibulae. Here A 1 appears to have completely replaced A 2 $\alpha$ , and includes the anterior faces of the preopercle and hyomandibular in its sites of origin. A 3 is absent. In both examples a single tendon passes anteriorly and splits into two smaller ones. One of these inserts on the anteroventromedial face of the dentary, while the dorsal division attaches to the postero-medial face of the maxilla. The tendon to the maxilla is divided into two sections on the side to which the mouth is twisted, but not on the opposite side.

Owing to the considerably modified snout, the origin of the protractor hyoidei has shifted mainly to the ventral faces of the interopercles and the thick connective tissue surrounding them. The origin extends a third of the way along the snout before grading into a single medial tendon which courses anteriorly between the interopercles to attach broadly to the ventromedial faces of the dentaries. The intermandibularis and hyohyoideus inferioris are as described for *Tydemanina*.

Figure 59 gives a general view of the branchial arch muscles not originating on the arches themselves, and is included to illustrate topographical differences too slight to be discussed in the text. The adductor radialis originates only from the second radial, and inserts on the lowermost pectoral ray. Inclinatores dorsales to the spiny dorsal fin are absent, and only the first two spines have erector and depressor muscles. The interr radialis is better developed, and the flexor dorsalis inserts on caudal rays D 1-6. There is less continuity between the sternohyoideus and the anteroventral component of the obliquus inferioris, mainly because the ventrolateral border of the cleithrum and the dorso-lateral surface of the pelvis are very close to one another.

*Halimochirurgus centriscoides* Alcock

FIGURE 60

The origin of the adductor mandibulae sections

is as for *M. platycheilus*. A single tendon passes anteriorly, inserting only on the posteromedial face of the dentary. The protractor hyoidei is similar to that of *M. platycheilus*, but there is no connection to the dentary. Instead, the fibers fade out in the connective tissue between the interopercles, about halfway up the length of the snout. The comments made in connection with *M. platycheilus* for the remaining muscular systems also apply to *H. centriscoides*.

## Subfamily HOLLARDIINAE

*Parahollardia lineata* (Longley)

FIGURES 61-63

The muscles of the cheek are very similar in disposition and proportion to those described for *T. anomalus*. The hiatus between the dilatator operculi and anterior part of the levator operculi, which was apparent in all the triacanthodins examined except *T. anomalus*, is present in the two species of Hollardiinae dissected. The ligaments attaching the hyohyoideus inferioris to the ventrohyal are somewhat better developed. The adductor radialis inserts on the three ventralmost pectoral rays. The levator pectoralis inserts more on the dorsomedial surface of the cleithrum than on the supracleithrum.

The arrector dorsalis pelvis is virtually continuous with the infracarinalis anterior anteriorly, being separated only by a myocomma. This applies to the arrector ventralis pelvis as well. Two adductor profundus pelvis muscles are present, the section to the second ray passing ventrolaterally as opposed to posteroventrolaterally. An adductor superficialis pelvis originates from the dorsal pelvis between the two slips of the adductor profundus pelvis, and inserts on the tip of the posterodorsal flange of the first pelvic ray.

The inclinatores dorsales do not form a continuous sheet anteriorly, and insert variously on the pterygiophores and spine bases, the precise relationships differing on the left and right sides of the fish. All the spines receive erector and depressor muscles.

The infracarinalis medius consists of four myomeres separated by myocommata. The ventrolateral surface of the first anal pterygiophore receives

fibers from two residual inclinatorea anales, which lie anterior to the first inclinador inserting on a fin ray. The body and caudal fin muscles are as was described for *T. anomalus*.

***Hollandia hollardi* Poey**

FIGURES 64-65, 68a

The powerful tendon of the adductor mandibulae which inserts in the Meckelian fossa develops a few muscle fibers on its dorsal surface. These pass anterodorsally to insert along the medial face of the dentary dorsal to the fossa. The adductor radialis consists of two muscle slips to the ventralmost two pectoral rays.

The first pelvic fin ray receives an adductor profundus pelvificus muscle, all other fin ray musculature being absent.

Five inclinatorea dorsales are recognizable, most of them overlapping from the base of the spine onto the surrounding pterygiophore. The last two spines do not have erector and depressor muscles.

The infracarinalis medius is made up of two sections (as in the other triacanthodids examined,

but not *P. lineata*) in the smaller (53 mm) fish, and of three sections in the larger (92 mm) example. A single anterior residual inclinador analis is present.

Other muscles are as for *P. lineata*, or, if not mentioned in connection with that species, as described for *T. anomalus*.

**Summary of Triacanthodidae**

Certain regions of the body are more prone to variation than others. Among the triacanthodids dissected, significant variations are found in the adductor mandibulae, intermandibularis, protractor hyoidei, levator and dilatator operculi, adductor radialis, the muscles of the pelvic fin rays, and the erector, depressor, and inclinador muscles of the spiny dorsal fin. The last three of these muscles involve numerical differences, and seem to be following a reductive trend. Apart from those outlined above, the triacanthodid muscle plan appears to be rather stable, in spite of the modifications of the two long-snouted genera (*Macrorhamphosodes* and *Halimochirurgus*).

**Myological Descriptions of Representative Triacanthids**

The general body outline of this family is represented in Figure 2. One species from three out of the four recognized genera was dissected. They are fairly slender fishes, with a rather long snout region and a maximum body depth between the bases of the dorsal and pelvic fins. The tapering caudal peduncle ends in a lunate caudal fin. They are evidently capable of some speed and, unlike other tetraodontiforms (except possibly *Triodon*), use the tail as the primary unit of propulsion (see Wickler, 1963).

Triacanthids are relatively shallow-water fishes, their food apparently being composed of soft- and hard-bodied marine invertebrates. They are usually considered to share a common ancestor with the Triacanthodidae, but to be somewhat more specialized.

***Triphichthys weberi* (Chaudhuri)**

FIGURES 66, 67, 69-75

**MUSCLES OF THE CHEEK**

**ADDUCTOR MANDIBULAE** (Figure 66; see also Fig-

ure 68b of *Triacanthus biaculeatus*: A 1, A 2, A 3).—The sections of this muscle are not well separated, particularly in the posterior region. A 1 arises partly from the thick ligamentous fascia covering the muscle beneath the eye, and partly from the anterodorsal face of the hyomandibular (a flange of which overlies the posterodorsal region of the muscle). A small portion of this section inserts on the dorsomedial face of the maxilla. The A 2 section originates from the dorsal and lateral quadrate and preopercle, and the anteroventral hyomandibular. It forms a broad sheetlike tendon anteriorly, which receives a substantial contribution from A 1, and inserts in the Meckelian fossa in the dentary. A 3 is possibly the most distinct section, and originates from the lateral quadrate and preopercle. It lies medial to the tendinous plate in the middle of the adductor mandibulae, and joins the tendon to the Meckelian fossa anteriorly.

**LEVATOR ARCUS PALATINI** (Figure 66: L.A.P.).—The muscle is fairly small, and conical in shape. It originates from the ventral face of the postorbital process of the sphenotic and inserts on the antero-

dorsal face of the hyomandibular, including the flange overlying section A 1 of the adductor mandibulae.

**DILATATOR OPERCULI** (Figure 66: D.O.).—Origin is from the sphenotic-pterotic suture region, the muscle coursing ventrally to insert on the tip of the dorsal process of the opercle. It is relatively well developed.

**LEVATOR OPERCULI** (Figure 66: L.O.).—The muscle consists of two sections. The anterior portion originates from the pterotic and inserts on the dorsomedial flange of the opercle. The posterior part arises from the dorsomedial face of the supracleithrum, and inserts just behind the anterior portion on the dorsomedial opercle.

**ADDUCTOR ARCUS PALATINI** (Figures 66, 67: A.A.P.).—Origin is from the lateral surface of the prefrontal and the ventral flange of the parasphenoid. It inserts on the dorsomedial faces of the mesopterygoid, metapterygoid, and hyomandibular. The muscle is well developed, and extends anterior to the orbit. Here the origin of the fibers becomes relatively more dorsal than the insertion, so that the fibers pass anteroventrolaterally.

**ADDUCTOR OPERCULI** (Figures 69, 71: AD.OP.).—Fibers originate from the ventral surface of the pterotic just behind the origin of the levatores interni. The muscle courses ventrolaterally to insert on the dorsomedial face of the opercle.

#### MUSCLES OF THE HYOID REGION

**INTERMANDIBULARIS**.—This is a small muscle connecting the halves of the lower jaw. It attaches to the dentary below the Meckelian fossa, just anterior to the quadrate.

**PROTRACTOR HYOIDEI** (Figure 66: PR.HY.).—Origin is from the lower jaw both dorsal and ventral to the intermandibularis, the fibers passing posteroventrally. It separates into two halves in front of the ventrohyal, and inserts on the lateral anterohyal. It also overlies the ventral two branchiostegal rays, some fibers arising from the lateral face of the third ray.

**HYOHYOIDEUS INFERIORIS** (Figure 66: HY.IN.).—The muscle arises from the ventrolateral face of the anterohyal, lying for the most part beneath the first two branchiostegal rays, but with a small section overlying the base of the first ray. It lies medial to the protractor hyoidei, and arises from a mid-

ventral raphe with its antimere. The anterior face of each side gives rise to a short ligament which passes anteromedially to attach to the ventrohyal.

**HYOHYOIDEI ABDUCTORES** (Figure 66: H.AB.).—There are four sections of this muscle, which insert on the anteromedial faces of the ventral four branchiostegal rays. The first muscle is well developed, and originates from the posterior face of the ventral flange of the ventrohyal. The second muscle arises from the base of the first ray, the two dorsal muscles originating from the fascia covering the bases of the first two rays.

**HYOHYOIDEI ADDUCTORES** (Figure 66: H.AD.).—A well-developed muscle, interconnecting the four dorsalmost branchiostegal rays. It continues dorsally, but soon fades out in the connective tissue beneath the opercle and subopercle. It also continues inwards on the floor of the opercular cavity for a short distance.

**STERNOHYOIDEUS** (Figures 66, 69: STH.).—The muscle originates from the anterolateral face of the ventral region of the cleithrum. In the extreme anteroventral area there may be some fusion of fibers from the two sides of the body. The posteroventrolateral fibers are continuous with the obliquus inferioris. The muscle, which is made up of three myomeres, inserts on the lateral, posterior, and ventral surfaces of the urohyal.

**STERNOBRANCHIALIS** (Figures 69, 70: STB.).—Origin is from the anteroventral cleithrum. The fibers pass dorsally, and form a broad, sheetlike aponeurosis which fuses briefly with that of the opposite side before diverging again. The sheet then divides into a large anterior section and a smaller posterior part. The former inserts on the posterodorsal urohyal and the three hypobranchials. The posterior sections cross over to the ventral midline and insert on the fourth ceratobranchial of the other side. The aponeurosis from one side passes through the middle of the aponeurosis of the other side in the course of this crossing over. The anterior aponeurosis is thickest in the region of the junction between the first and second hypobranchials.

#### VENTRAL BRANCHIAL MUSCLES

**PHARYNGOCLAVICULARIS EXTERNUS** (Figure 69: PHC.E.).—Fibers arise from the anterodorsal face of the cleithrum and pass slightly posterodorsally to insert on the ventrolateral face of the ceratobranchial 5.

**PHARYNGOCLAVICULARIS INTERNUS** (Figures 69, 70: PHC.I.).—The muscle passes anteriorly from its origin on the anteromedial face of the cleithrum. It splits into a series of tendons (of which the ventralmost is largest) which insert on the ventral surface of ceratobranchial 5.

**OBLIQUI VENTRALES I–III** (Figures 69, 70: OBL.V.).—The oblique muscles connect the ventral surfaces of the cerato- and hypobranchials of the first three arches. Obliquus I is well developed. Part of obliquus III inserts directly on the third hypobranchial. The most ventral fibers contribute to a ligament which passes anteriorly to join that from the other side and attach to the posterodorsal face of the urohyal.

**TRANSVERSI VENTRALES IV–V** (Figure 70: TR.V.).—These two muscles connect the anteromedial faces of the fourth and fifth pairs of ceratobranchials across the ventral midline.

**RECTI VENTRALES I, II, AND IV** (Figures 69, 70: RECT.V.).—The first of these muscles connects the posterolateral face of the dorsohyal to the anterolateral face of hypobranchial 1, the second passing from the dorsolateral surface of the urohyal to the ventral region of ceratobranchial 2. Rectus IV arises from the anteroventromedial face of ceratobranchial 4 and passes anteromedially to attach to the arch-shaped ligament between the ventral processes of the third hypobranchials. There is a partial crossing over of the more medial fibers in this region.

**RECTUS COMMUNIS** (Figure 70: R.COMM.).—The muscle originates from the posterodorsal urohyal. It passes posteriorly, and grades into a tendon at the level of the third hypobranchials. It inserts on the anterolateral surface of ceratobranchial 5, lying lateral to the sections of the pharyngoclaviculares.

#### DORSAL BRANCHIAL MUSCLES

**LEVATORES EXTERNI I–IV** (Figure 69: L.EXT.).—This series of four muscles originates from the lateral surface of the prootic. The muscles become larger, and have a more lateral origin as they pass posteriorly in the series. They insert aponeurotically on the posterodorsolateral faces of epibranchials 1–4, the second levator having a small inner connection to epibranchial 3.

**LEVATORES INTERNI II–III** (Figure 71: L.INT.).—These muscles originate from a depression in the posterodorsal surface of the prootic. Levator II, which has a slightly more lateral origin, inserts on the dorsomedial face of infrapharyngobranchial 2, while levator III inserts on the dorsolateral face of infrapharyngobranchial 3.

**OBLIQUUS DORSALIS III** (Figure 71: OBL.D.).—The muscle passes from the dorsal surface of epibranchial 3 to the dorsomedial face of infrapharyngobranchial 3.

**OBLIQUUS POSTERIOR** (Figure 71: OBL.P.).—The fibers connect the anteromedial face of ceratobranchial 5 to the posterior face of epibranchial 4.

**TRANSVERSI DORSALES II–III** (Figures 69, 71: TR.D.).—The anterior of these two muscles originates from the ventrolateral face of the parasphenoid, and courses laterally to insert on the dorsolateral face of epibranchial 2. A few of the more posterior fibers may fuse with their antimeres. Transversus III arises from a middorsal raphe with its antimeres, and passes laterally to insert on the posterodorsal face of epibranchial 3 beneath obliquus dorsalis III.

**RETRACTOR DORSALIS** (Figure 71: D.RETR.).—Origin is from the ventrolateral surface of the first vertebra, although a few of the more posterior fibers may arise from the anterodorsal tip of the swim bladder. It passes anteroventrally to insert on the posteromedial face of infrapharyngobranchial 3.

**ADDUCTORES IV–V**.—The anterior muscle connects the dorsomedial face of ceratobranchial 4 to the ventrolateral face of epibranchial 4. Adductor V arises from the anterodorsal tip of ceratobranchial 5 and passes anterodorsally to the posterolateral face of epibranchial 4, lateral to the obliquus posterior.

**SPHINCTER OESOPHAGI** (Figures 70, 71: S.O.).—Ventrally the fibers attach to the ventromedial faces of the fifth ceratobranchials, there being a midventral raphe. The fibers pass dorsally around the esophagus, attached to the fifth ceratobranchials, the more dorsal fibers attaching to the fourth epibranchials. A small section overlaps the retractor dorsalis anterodorsally.

#### MUSCLES OF THE PECTORAL REGION

**ABDUCTOR SUPERFICIALIS** (Figure 66: ABD.S.).—Fibers originate from the posterior rim of the cleithrum and course posterodorsally to insert on

the dorsolateral bases of the 13 principal fin rays.

**ABDUCTOR PROFUNDUS** (Figures 66, 69: ABD.P.).—The muscle originates beneath the abductor superficialis from the posteroventrolateral cleithrum and the anterolateral coracoid. It inserts on the posterolateral bases of both the principal and the vestigial fin rays.

**ARRECTOR VENTRALIS** (Figure 66: ARR.V.).—The fibers arise from the posterior face of the cleithrum just above those of the abductor superficialis, and insert on the lateral base of the medial half of the vestigial fin ray.

**ADDUCTOR SUPERFICIALIS** (Figure 73: ADD.S.).—Origin is from the posteromedial face of the cleithrum. The fibers of the dorsomedial part of the muscle serve the more ventral fin rays, those of the more superficial, ventral section inserting on the more dorsal fin rays. Tendons insert on the dorsomedial faces of the principal rays a little distal to their bases.

**ADDUCTOR PROFUNDUS** (Figure 73: ADD.P.).—The muscle originates from the medial faces of the coracoid and cleithrum ventral to the adductor superficialis and inserts on the ventromedial bases of the principal fin rays.

**ARRECTOR DORSALIS** (Figure 73: ARR.D.).—Fibers arise from the medial face of the cleithrum between the two adductor sections. Insertion is on the dorsomedial face of the base of the vestigial fin ray.

**CORACORADIALIS** (Figure 73: COR.R.).—The muscle originates from the fascia covering the adductor profundus and from the posteromedial coracoid. The fibers insert on the posteromedial process of the fourth radial.

**ADDUCTOR RADIALIS**.—This small muscle originates from the medial faces of the middle two radials and passes posteriorly to insert on the bases of the ventralmost two pectoral fin rays.

**PROTRACTOR PECTORALIS** (Figure 69: P.P.).—Fibers arise from the ventrolateral region of the pterotic and insert on the anterodorsal face of the cleithrum.

#### MUSCLES OF THE PELVIC GIRDLE

**ARRECTOR DORSALIS PELVICUS** (Figure 69: A.D.P.).—Origin is from the lateral surface of the anterior region of the pelvis, the fibers inserting on the anterodorsolateral face of the pelvic spine. The muscle is bipinnate.

**ARRECTOR VENTRALIS PELVICUS**.—The muscle is only partially separated from the infracarinalis anterior, and originates from the anteroventral face of the pelvis. Insertion is on the anteroventrolateral face of the pelvic spine.

**ADDUCTOR SUPERFICIALIS PELVICUS** (Figure 69: A.S.P.).—The muscle originates from the posteromedial face of the cleithrum and passes posteroventrally and somewhat laterally to insert on the posterodorsal face of the dorsal flange of the pelvic spine.

#### MUSCLES OF THE DORSAL FIN

**INCLINATOIRES DORSALES** (Figures 66, 74: INC.).—There are three inclinators to the spiny dorsal fin, arising in the fascia over the epaxialis and inserting on the posterolateral bases of the first three pterygiophores. Each fin ray of the soft dorsal fin receives an inclinator attaching to its lateral base, the fibers arising in the spaces between the lateral flanges of the pterygiophores. The inclinators to the spiny dorsal fin are flat and fan-shaped, those to the soft dorsal fin are smaller and more conical.

**ERECTORES DORSALES** (Figures 72, 74: EREC.).—The first five spines of the dorsal fin have erector muscles, of which the powerful, bipinnate muscle to the first spine is very much the largest. The erectors of the spiny fin originate from the lateral faces of the pterygiophores (including the exoccipital in the case of the first muscle), while those to the soft fin arise from the lateral faces of the pterygiophores and the neural spines.

**DEPRESSORES DORSALES** (Figures 66, 72, 74: DEPR.).—Depressors serve the first five spines and all the fin rays, inserting on the posterolateral bases of these elements. Origin is from the lateral faces of the pterygiophores for the muscles serving the spines, and also includes the lateral faces of the neural spines for the sections to the fin rays.

**SUPRACARINALIS ANTERIOR**.—The muscle is short and powerful. It originates from the posterior face of the supraoccipital and inserts on the anterior face of the first basal pterygiophore of the spiny dorsal fin.

**SUPRACARINALIS POSTERIOR** (Figure 75*b*: S.POST.).—The muscle arises from the posterior face of the last dorsal fin pterygiophore and passes posteriorly, attaching to the tips of the neural spines of the seventh to tenth caudal vertebrae, ending on the tenth neural spine.

## MUSCLES OF THE ANAL FIN

**INCLINATOIRES ANALES.**—Each anal fin ray possesses an inclinator muscle, originating in the fascia overlying the hypaxial body musculature and inserting on the lateral base of the ray. An anterior, residual inclinator muscle is present, inserting on the ventrolateral base of the first anal fin pterygiophore.

**ERECTORES ANALES.**—Each fin ray has an erector muscle, which originates from the lateral face(s) of the pterygiophore, haemal spine, or both, and inserts on the anterolateral base of the ray.

**DEPRESSORES ANALES.**—The depressor muscles have the same sites of origin as the erectors, and insert on the posterolateral bases of all the fin rays.

**INFRACARINALIS ANTERIOR** (Figure 69: INF.A.).—The muscle arises from the ventromedial face of the posterior coracoid and from the fascia attached to the posteromedial face of the cleithrum. It inserts on the anteroventral face of the pelvis.

**INFRACARINALIS MEDIUS** (Figure 66: INF.M.).—The fibers connect the posterodorsal face of the pelvis with the ventrolateral tip of the first anal pterygiophore.

**INFRACARINALIS POSTERIOR** (Figure 75*b*: INF.P.).—The fibers arise from the posterior face of the last anal fin pterygiophore, and course posteriorly. The muscle ends on the anterior tip of the haemal spine of the tenth caudal vertebra, the fibers attaching to the haemal spine tips of the intervening vertebra (7-9).

## MUSCLES OF THE CAUDAL FIN

**INTERRADIALIS** (Figure 75*a*: INT.).—The muscle is made up of slips of fibers arising from the ventral bases of the dorsal rays and the dorsal faces of the ventral rays, the resulting muscle bundles intermingling in the midlateral line. All fin rays possess a slip of this muscle.

**PROXIMALIS** (Figure 75*b*: PROX.).—The muscle originates from the lateral face of the centrum of the tenth caudal vertebra. It passes posteriorly to insert on the lateral flange of the ural centrum. (The flange arises from the posterior region of the centrum, and continues posteriorly onto the anterior part of the fused third and fourth hypurals.)

**HYPOCHORDAL LONGITUDINALIS** (Figure 75*a*:

H.L.).—Origin is from the lateral surface of the fused lower hypurals (1 and 2). The fibers pass posterodorsally to insert on the lateral bases of rays D 3-4, lateral to the epaxialis.

**FLEXOR DORSALIS** (Figure 75*b*: F.D.).—The muscle arises from the lateral faces of the penultimate and ural centra and the anterolateral region of fused hypurals 3 + 4. Insertion is on the dorsolateral bases of rays D 1-6.

**FLEXOR DORSALIS SUPERIOR** (Figure 75: F.D.S.).—The muscle originates from the lateral and dorsal faces of the neural spines and centra of the ninth to eleventh caudal vertebra. It inserts tendinously on the anterolateral base of ray D 6.

**FLEXOR VENTRALIS** (Figure 75: F.V.).—Origin is from the posteroventral face of the flange of the ural centrum, the ventrolateral faces of the ural centrum, and the fused hypurals 1 + 2. The muscle inserts on the lateral bases of rays V 1-6.

**FLEXOR VENTRALIS EXTERNUS** (Figure 75*b*: F.V.E.).—The fibers arise from the anteroventral surface of the eleventh caudal vertebra and insert on the lateral bases of rays V 1-2.

**FLEXOR VENTRALIS INFERIOR** (Figure 75: F.V.I.).—The muscle originates from the lateral and ventral faces of the ninth to eleventh caudal vertebra, and inserts on the anteroventral base of ray V 6.

## LATERAL BODY MUSCLES

**EPAXIALIS** (Figures 66, 75*a*: EPAX.).—Two main directions of the myocommata are evident, with a third anterodorsally. In the anterior region, the fibers attach to the posterior face of the skull. Posteriorly the muscle fibers become intermingled with aponeuroses, which gives rise to a tough fascia covering the intrinsic caudal fin musculature. Beneath this fascia the fibers grade into aponeuroses which insert on the lateral bases of caudal rays D 2-6, and lie, for the most part, medial to the hypochordal longitudinalis.

**OBLIQUUS SUPERIORIS** (Figures 66, 69, 75*a*: OBL.S.).—The section is poorly developed anteriorly, but forms the main mass of the hypaxial body musculature posteriorly. In the region of the caudal peduncle, the fibers become intermingled with aponeuroses, which join those of the epaxialis to give rise to the fascia mentioned above. Beneath this, the fibers mingle with those of the obliquus inferioris and grade into a series of aponeuroses

inserting on the lateral bases of rays V 1-6. Anteroventrally, some fibers arise from the fascia overlying the dorsal surface of the swim bladder. In the extreme anterior region, the fibers attach to the posterodorsal tip of the cleithrum.

**OBLIQUUS INFERIORIS** (Figure 66: OBL.I.).—Anteroventrally this section originates from the posterior coracoid and posterior and lateral cleithrum, being continuous anterolaterally with the sternohyoideus. Most of these fibers insert on the anteroventral face of the postcleithrum. Above this, fibers arise from the midline at the level of the epipleurals and pass ventrally to attach to the posterodorsal face of the postcleithrum. The fibers become more horizontally oriented in the posterior region, and begin to mingle with those of the obliquus superioris at about the level of the anal fin, giving rise to the aponeuroses to the caudal fin rays.

**SPINALIS** (Figure 72: SPIN.).—This muscle originates from the posterior face of the strutlike first dorsal pterygiophore and passes posteriorly. It soon grades into a long tendon which attaches to the dorsolateral tips of the neural spines of the second to fifth vertebrae. It is a bilaterally symmetrical muscle, and may represent the first myomere.

#### *Triacanthus biaculeatus* (Bloch)

FIGURES 68b, 76

There are few differences in the musculature. Owing to the shorter snout of *T. biaculeatus*, the overall shape of the adductor mandibulae is somewhat different (compare Figures 66 and 76), although the subdivisions are the same. The hyohyoidei adductores are better developed, some fibers continuing dorsally behind the opercle to attach to the supracleithrum. There are only two inclinator dorsales to the spiny dorsal fin, which insert on the lateral bases of the first two basal pterygiophores.

The spinalis is less well developed than in the preceding species.

#### *Tripodichthys oxycephalus* (Bleeker)

FIGURE 77

The adductor arcus palatini is well developed, being of quite substantial thickness beneath the eye. The adductor operculi possesses a small anterior section which inserts on the posterodorsomedial face of the hyomandibular. The hyohyoidei adductores are as described for *T. biaculeatus*, and the ventralmost muscle of the hyohyoidei abductores is well developed. There is no fusion of the fibers of the sternohyoideus with those of the sternobranchialis. The aponeurotic sheet of the latter muscle is continuous, and the portion inserting on ceratobranchial 4 does not cross over with the section from the other side. The adductor radialis is very small and inserts only on the lowermost pectoral ray.

There are four inclinators dorsales, one to the dorsolateral region of each pterygiophore. The lateral flange on the ural centrum is less well developed, so that the proximalis is scarcely visible superficially. The flexor dorsalis does not have a section to ray D 6.

#### Summary of Triacanthidae

Little variation is apparent in the single species of each of the three genera examined. The inclinators dorsales of the spiny dorsal fin do vary considerably, however, but these muscles appear to have no functional significance since they are very small and insert on the bases of the dorsal pterygiophores. There is also some variation in the extent of development of the hyohyoidei adductores and the adductor radialis, but the family is basically conservative.

#### Myological Descriptions of Representative Balistids

The general body outline of this family is represented in Figure 3. Representative species from five of the eleven genera recognized by Berry and Baldwin (1966) were dissected. Members of this family are very conservative in body form. They

possess a terminal mouth armed with incisiform teeth (and two canines in *Odonus*). The snout region is long, with the eye high up on the head. The first dorsal fin consists of three spines, the heavy, large first spine being locked in position by



the small second spine. Pelvic fins are reduced to rudiments at the end of a long, shaftlike pelvic bone (Tyler, 1962b). The soft dorsal and anal fins are well developed, consisting of many rays. A slightly narrowed caudal peduncle ends in a double emarginate or rounded caudal fin, although other shapes do occur. Scales are large and heavy, and may possess longitudinal ridges (for the functional significance of which, see Wahler and Wahler, 1964). Balistids occur mainly on and around coral reefs, and are diurnal. A few oceanic forms exist, primarily in tropical waters. The food of the family is comprised of both soft- and hard-bodied marine invertebrates (often corals), although certain species show a preference for plant material (see, for example, *Melichthys*, in Randall, 1967).

Fast swimming is accomplished by synchronous side-to-side beating of the dorsal and anal fins, the caudal fin being used for bursts of speed. Slow swimming is achieved by undulations of the dorsal and anal fins. When stationary, the beat passes posteriorly in the dorsal fin and anteriorly in the anal fin. This can be shown by a parallelogram of forces to help in counteracting the larger gravitational forces acting on the head region.

Balistids are supposed to be derived from triacanthid-like fishes, and to have "given rise" to the Monacanthidae. Using a more modern approach, they are apomorph relative to the former, and represent the plesiomorph sister group of the latter. However, recent work (Tyler, 1970a:31) indicates that the ostracioids may have to be included somewhere in this lineage, probably sharing a common ancestor with the balistoids.

### *Balistes vetula* Linnaeus

FIGURES 78-85

#### MUSCLES OF THE CHEEK

**ADDUCTOR MANDIBULAE** (Figures 78, 79; and Figure 87a of *Balistapus undulatus*: A 1 $\alpha$ , A 1 $\beta$ , A 2 $\alpha$ , A 2 $\beta$ , A 2 $\gamma$ , A 3).—Section A 1 is separable into two portions, one superficial (A 1 $\alpha$ ) and the other deep (A 1 $\beta$ ). The former originates from the lateroventral faces of the ethmoid and prefrontal, the infraorbital ligament and the anterodorsal face of the hyomandibular. A 1 $\beta$  is small,

and originates from the lateral metapterygoid and mesopterygoid, being completely overlain by A 1 $\alpha$ . The two sections insert by a common tendon on the posteroventral and ventromedial faces of the maxilla. A 2 is also subdivided into two parts. A 2 $\alpha$  is superficial and originates from the lateroventral ethmoid, the prefrontal, the infraorbital ligament and the lateral hyomandibular. It is separated from A 2 $\beta$  by the path of ramus mandibularis V, which emerges beneath the maxilla. The section largely overlaps the subdivisions of A 1, and also covers the more dorsal portion of A 2 $\beta$ . The latter section originates from the anterior hyomandibular, anterodorsal preopercle, and the lateral metapterygoid. A 2 $\gamma$  develops along the ventrolateral extent of the preopercle. The sections of A 2 insert broadly on the posterodorsomedial face of the dentary, with some fibers of the first two sections inserting on the maxillomandibular ligament. A deep section, arising from the lateral faces of the symplectic, quadrate, and metapterygoid appears to represent A 3. It fuses with the tendon of A 2 $\beta$  anteriorly.

**LEVATOR ARCUS PALATINI** (Figure 78: L.A.P.).—The muscle is fairly small, and originates from the ventral face of the orbital process of the sphenotic and the anterodorsal pterotic. The fibers pass anteroventrally to insert on the anterodorsal face of the hyomandibular.

**DILATATOR OPERCULI** (Figure 78: D.O.).—Normally in the shape of an inverted triangle, this muscle has inverted its shape anteriorly, the somewhat tendinous apex arising from the orbital process of the sphenotic. Some of the medial fibers are continuous with the posterolateral fibers of the levator arcus palatini. The more posterior fibers arise from the ventrolateral face of the sphenotic. Insertion is along the dorsolateral face of the opercle.

**LEVATOR OPERCULI** (Figure 78: L.O.).—Origin is from the anteroventrolateral pterotic and the anterior supracleithrum, the fibers inserting on posterodorsolateral face of the opercle.

**ADDUCTOR ARCUS PALATINI** (Figure 79: A.A.P.).—The fibers arise from the anterolateral ethmoid and the lateral parasphenoid in front of the orbit. The more anterior fibers course in an increasingly anteroventrolateral direction. These fibers are anterodorsally continuous with the anteroventral fibers of the retractor arcus palatini. Insertion is on the

medial and dorsal faces of the mesopterygoid, metapterygoid, and the hyomandibular.

**RETRACTOR ARCUS PALATINI** (Figures 78, 79: R.A.P.).—The muscle originates from the ventral surface of the lateral flange of the ethmoid, the lateral face of that bone, and the lateral parasphenoid. It consists of two subsections. The more anterior, superficial fibers insert on the shaft of the palatine and the ectopterygoid. From the dorsal process of the ectopterygoid, a tendinous fascia passes back to below the prefrontal, separating the subsections completely posteriorly. The posteroventral subsection is covered by a thick fascia, to which many of the fibers attach. It inserts on the dorsal faces of the mesopterygoid and metapterygoid. The fibers mingle with those of the adductor arcus palatini anteroventrally and those of the dorsal subsection anterodorsally. Both subsections are served by the same branch of the ramus buccalis that serves the adductor arcus palatini.

**ADDUCTOR OPERCULI** (Figure 80: AD.OP.).—Origin is from the anterolateral pterotic and lateral prootic. The fibers pass anteroventrolaterally to insert on the dorsomedial face of the opercle.

**ADDUCTOR HYOMANDIBULAE** (Figure 80: A.H.).—The muscle originates behind and above the adductor operculi from the anteroventrolateral faces of the pterotic and prootic. It inserts on the dorsomedial face of the hyomandibular, immediately below the articulation with the skull.

#### MUSCLES OF THE HYOID REGION

**INTERMANDIBULARIS**.—Lying immediately behind the symphysis of the halves of the lower jaw, this muscle (which is wholly dorsal to the protractor hyoidei) connects the posterodorsomedial faces of the left and right dentaries.

**PROTRACTOR HYOIDEI** (Figure 78: PR.HY.).—There appear to be two sections of this muscle. A superficial division originates completely from the skin and joins the deeper section before inserting on the posteroventral margin of the lower jaw. The larger inner portion originates almost entirely from the lateral faces of the branchiostegal rays and the anterohyal. There is some separation into three longitudinal bundles posteriorly. The more ventral fibers meet their artimeres in the ventral midline.

**HYOHYOIDEUS INFERIORIS** (Figure 78: HY.IN.).—The fibers arise from a midventral raphe under-

lying the anteroventral region of the urohyal and pass dorsolaterally to insert along the ventral face of the anterohyal.

**HYOHYOIDEI ABDUCTORES** (Figure 78: H.AB.).—The muscles serve the ventral five branchiostegal rays. The muscle to the first ray is much enlarged and sheetlike. The fibers from the other four sections join that from the first ray and attach anteriorly to the ventromedial faces of the anterohyal, dorsohyal, and ventrohyal.

**HYOHYOIDEI ADDUCTORES** (Figure 78: H.AD.).—The muscle is in the form of a continuous sheet covering the wall of the opercular cavity. Fibers arise from the fascia over the sternohyoideus and sternobranchialis and pass dorsolaterally, fading out in the connective tissue beneath the opercle and subopercle. The branchiostegal rays are buried in the same connective tissue as the muscle fibers, but there is little direct attachment.

**STERNOHYOIDEUS** (Figures 78, 80: STH.).—The posterolateral fibers are continuous with the anterolateral fibers of the obliquus inferioris. The more medial fibers arise from the anteroventral face of the cleithrum. A partially separated bundle of fibers originates from the anteroventral tip of the cleithrum and passes almost dorsally to the posteroventral tip of the urohyal. The muscle inserts broadly on the urohyal, with some attachment to the posteroventromedial face of the ventrohyal.

**STERNOBRANCHIALIS** (Figures 80, 81: STB.).—The muscle originates from the anteroventral face of the cleithrum, and passes vertically upward to split into three sections. The anteriormost inserts on the posteroventral tip of the urohyal, the middle section inserting on the ventromedial face of hypobranchial 3. The third section joins its antimeres ventral to the rectus communis.

#### VENTRAL BRANCHIAL MUSCLES

**PHARYNGOCLAVICULARIS EXTERNUS** (Figures 80, 81: PHC.E.).—Originating from the cleithrum immediately behind the sternobranchialis, the muscle courses posterodorsally to insert on the anteroventral face of ceratobranchial 5.

**PHARYNGOCLAVICULARIS INTERNUS** (Figures 80, 81: PHC.I.).—The muscle originates from the anteromedial face of the cleithrum. It passes anteriorly to insert on the ventromedial bases of ceratobranchials 4 and 5.

**OBLIQUI VENTRALES I-III** (Figure 81: OBL.V.).—These muscles connect the ventral faces of the ceratobranchials and hypobranchials of the first three arches. In the case of obliquus III, most of the fibers from the ceratobranchial attach to the arch-shaped ligament between the ventral processes of the third hypobranchials, the section actually inserting on the ventral process of hypobranchial 3 being fairly distinct.

**TRANSVERSI VENTRALES IV-V** (Figure 81: TR.V.).—The anterior muscle connects the anteroventromedial faces of the fourth ceratobranchials across the ventral midline. There are two sections to the posterior muscle. The anterior of these lies between the extreme anteroventromedial tips of the fifth ceratobranchials and is small. There is a small hiatus between it and the posterior section, which lies ventral to the sphincter oesophagi.

**RECTI VENTRALES I, II, IV** (Figures 80, 81: RECT.V.).—The first rectus joins the anteroventrolateral face of ceratobranchial 1 to the posterodorsal face of the dorsohyal. Some of the posteromedial fibers are continuous with those of obliquus ventralis I. Rectus II arises from the dorsolateral face of the urohyal and attaches to the posterolateral face of ceratobranchial 2. Rectus IV is represented by two sections. The more ventral one arises from the ventral face of ceratobranchial 4 and passes antero-medially to attach to the posterior face of the arch-shaped ligament between the third hypobranchial processes. The other section arises from the dorsolateral face of ceratobranchial 4 and attaches to the dorsomedial face of hypobranchial 3. This latter muscle is apparently a derivative of obliquus ventralis III.

**RECTUS COMMUNIS** (Figures 80, 81: R.COMM.).—Origin is from the dorsolateral urohyal. The fibers pass posteriorly, grading into an aponeurosis at about the level of the third hypobranchial. The tendon lies medial to the pharyngoclavicularis externus and lateral to the pharyngoclavicularis internus, and inserts on the ventrolateral face of ceratobranchial 5.

#### DORSAL BRANCHIAL MUSCLES

**LEVATORES EXTERNI I-V** (Figure 80: L.EXT.).—The first four levators originate from the ventral surface of the prootic shelf and pass ventrally to the dorsolateral faces of epibranchials 1-4. The muscle

to the third arch is not well developed. A fifth levator is present, inserting on the dorsal tip of the fifth ceratobranchial, the more anterior fibers fusing with the posterior region of levator IV. This muscle appears to be divided into two sections by a myocomma, which seems to cast aspersions on a theory postulating its development solely from levator IV.

**LEVATORES INTERNI II-III** (Figure 82: L.INT.).—These muscles originate one on either side of the facial foramen on the ventral surface of the prootic. The anterior muscle inserts on the dorsomedial face of infrapharyngobranchial 2, the posterior one inserting on infrapharyngobranchial 3.

**OBLIQUUS DORSALIS III** (Figure 82: OBL.D.).—There are two sections of this muscle. The anterior one connects the anterodorsal face of epibranchial 3 to the anterior and lateral faces of infrapharyngobranchial 3. The posterior part passes from the dorsal face of epibranchial 3 to the dorsomedial face of infrapharyngobranchial 3.

**OBLIQUUS POSTERIOR** (Figure 82: OBL.P.).—The muscle connects the dorsomedial face of ceratobranchial 5 with the posterolateral face of epibranchial 4.

**TRANSVERSI DORSALES II-III** (Figure 82: TR.D.).—The anterior muscle originates from the ventrolateral parasphenoid, with some posterior fibers from a raphe in the dorsal midline. The fibers insert on the dorsal face of epibranchial 2. The posterior muscle arises from the dorsal midline and inserts primarily on epibranchial 3, with some fibers to epibranchial 4.

**RETRACTOR DORSALIS** (Figure 82: D.RETR.).—A well-developed muscle, arising from the lateral and ventral faces of the basioccipital and inserting on the dorsomedial region of infrapharyngobranchial 3.

**ADDUCTORES IV-V** (Figure 82: AD.).—The muscle of the fourth arch spans the medial side of the articulation between the epibranchial and ceratobranchial. Adductor V connects the anterodorsal tip of ceratobranchial 5 and the posterodorsal face of epibranchial 4.

**SPHINCTER OESOPHAGI** (Figures 81, 82: S.O.).—The muscle encircles the esophagus, attaching mainly to the posterior margins of the fifth ceratobranchials, and lying above transversus ventralis V. Dorsally it attaches to epibranchial 4, with a few fibers passing to infrapharyngobranchial 3. There

is a small bundle of fibers crossing the dorsal midline above the retractor dorsalis.

#### MUSCLES OF THE PECTORAL REGION

**ABDUCTOR SUPERFICIALIS** (Figure 78: ABD.S.).—Origin is from the posterolateral face of the cleithrum, the fibers passing posterodorsally to insert on the dorsal bases of the principal fin rays.

**ABDUCTOR PROFUNDUS** (Figures 78, 80: ABD.P.).—The fibers originate almost exclusively from the anterolateral face of the coracoid, a few fibers coming from the posterolateral cleithrum. The muscle inserts on the ventrolateral bases of the principal fin rays and on the lateral base of the lateral half of the vestigial ray.

**ARRECTOR VENTRALIS** (Figures 78, 80: ARR.V.).—The muscle originates from the posterolateral face of the cleithrum and inserts on the lateral face of the medial half of the vestigial fin ray.

**ADDUCTOR SUPERFICIALIS** (Figure 83: ADD.S.).—Origin is from the anteroventral face of the postcleithrum and the posteromedial face of the dorsal region of the cleithrum. The fibers insert on the dorsomedial faces of the principal rays distal to their bases, the more medial fibers serving the more ventral rays.

**ADDUCTOR PROFUNDUS** (Figure 83: ADD.P.).—The muscle passes from the posterior cleithrum and medial coracoid to insert on the ventromedial flanges of the bases of the principal fin rays.

**ARRECTOR DORSALIS** (Figure 83: ARR.D.).—The fibers originate from the medial cleithrum between the two adductor sections, and insert on the medial base of the vestigial fin ray.

**CORACORADIALIS** (Figure 83: COR.R.).—The muscle originates largely from the fascia overlying the medial surface of the adductor profundus. It attaches to the medial process of the ventral radial.

**PROTRACTOR PECTORALIS** (Figure 80: P.P.).—The fibers fan out from their origin on the ventral tip of the pterotic and insert on the anterodorsal face of the cleithrum. The more anteromedial fibers spread out to cover the posteromedial wall of the branchial chamber.

**LEVATOR PECTORALIS** (Figure 80: TR.).—Origin is from the posteroventral tip of the pterotic, the muscle passing posteriorly to insert on the anterodorsal tip of the cleithrum.

#### MUSCLES OF THE PELVIC GIRDLE

**ARRECTOR VENTRALIS PELVICUS?** (Figure 84: A.V.P.).—The muscle originates in the ventral groove in the pelvis. Just before inserting, the fibers divide into left and right tendons. These continue posteriorly, dorsal to the first and second encasing scales to attach to the ventrolateral faces of the fin ray element.

**ADDUCTOR SUPERFICIALIS PELVICUS?** (Figure 84: A.S.P.).—This bilateral muscle originates in the dorsal groove of the pelvis. Posteriorly, the tendons pass through a tunnel in the dorsal lobe of the pelvis and insert on either side of the dorsal half of the fin ray element.

#### MUSCLES OF THE DORSAL FIN

**INCLINATOIRES DORSALES** (Figure 78: INC.).—There are no inclinators to the spiny dorsal fin. Each ray in the soft dorsal fin receives an inclinator, which inserts on the lateral base of the ray just above the insertion of the erector and depressor muscles. The fibers originate in the fascia overlying the epaxialis.

**ERECTORES DORSALES** (Figures 78, 80: EREC.).—The first erector is very powerful and passes from the dorsal faces of the frontal and supraoccipital to the anterolateral base of the first dorsal spine. The second erector arises from the posterior epiotic and, passing medial to the strut supporting the first spine, inserts on the lateral base of the second spine. There is no erector to the third spine. The erectors of the soft dorsal fin originate from the lateral faces of the posterior halves of the pterygiophores (just behind the lateral flanges) and the neural spines. The fibers reach the centra, and insert on the anterolateral bases of the fin rays.

**DEPRESSORES DORSALES** (Figures 78, 80: DEPR.).—The depressors of the first two spines arise from the epiotic. The first passes medial to the lateral strut of the pterygiophore before turning dorsally to insert on the posterolateral base of the spine, while the second muscle passes lateral to the strut to insert on the anterior face of the elongate, posteroventrally directed base of the second spine, ventral to its articulation with the lateral strut. The depressor of the third spine originates from the anteroventral face of the first pterygiophore of the soft dorsal fin. It passes anterodorsomedially,

through a foramen in the pterygiophore, to insert on the base of the third spine. The depressors of the soft dorsal fin originate from the anterolateral faces of the pterygiophores and the neural spines, and insert on the posterolateral bases of the rays.

**SUPRACARINALIS ANTERIOR** (Figure 78: S.ANT.).—The muscle connects the posterodorsolateral face of the frontal to the anterolateral edge of the first basal pterygiophore of the spiny dorsal fin.

**SUPRACARINALIS MEDIUS** (Figure 80: S.MED.).—The muscle attaches to the posterolateral face of the second pterygiophore and fans out to insert broadly on the anterior face of the first pterygiophore of the soft dorsal fin.

**SUPRACARINALIS POSTERIOR** (Figure 85; S.POST.).—Fibers arise from the posterodorsolateral face of the last pterygiophore of the soft dorsal fin and the tip of the neural spine of the eighth caudal vertebra. The fibers attach to the tips of the ninth and tenth neural spines.

#### MUSCLES OF THE ANAL FIN

**INCLINATOIRES ANALES** (Figure 78: INC.).—Each fin ray possesses an inclinator arising from the fascia overlying the hypaxial body musculature and inserting on the lateral base of the ray. There is a large residual inclinator, which inserts on the base of the first anal pterygiophore. The inclinator decrease in size posteriorly.

**ERECTORES ANALES.**—Each fin ray has an erector muscle, which originates from the lateral faces of the pterygiophore and the haemal spines, and inserts on the anterolateral base of the ray.

**DEPRESSORES ANALES.**—The depressor muscles originate on the lateral faces of the pterygiophores and haemal spines, and insert on the posterolateral bases of each fin ray.

**INFRACARINALIS ANTERIOR** (Figures 78, 80: INF.A.).—The muscle is well developed. It arises from the posteroventral region of the cleithrum and inserts broadly over the lateral face of the pelvic bone. Posteriorly, it passes into a lateral tunnel in the bone, to whose walls fibers attach.

**INFRACARINALIS MEDIUS** (Figures 78, 80: INF.M.).—The fibers arise from the posterolateral face of the pelvic bone and pass posterodorsally to join with the fibers of the obliquus inferioris before acquiring attachment to the first anal pterygiophore. The muscle overlaps the posterior fibers of the

infracarinalis anterior anterolaterally.

**INFRACARINALIS POSTERIOR** (Figure 85: INF.P.).—Fibers arise from the posteroventrolateral tip of the last anal pterygiophore and pass posteriorly, attaching to the tips of the haemal spines of the eighth and ninth vertebrae before ending on the midregion of the anterior face of the haemal spine of the tenth caudal vertebra.

#### MUSCLES OF THE CAUDAL FIN

**INTERRADIALIS** (Figure 85a: INT.).—The muscle consists of a number of bundles of fibers passing between the rays and meeting at the midlateral line. Fibers usually pass over two or three rays before reattaching.

**HYPOCHORDAL LONGITUDINALIS** (Figure 85a: H.L.).—Origin is from the lateral faces of hypural 2 and the urostyle, the fibers coursing posterodorsally to insert on the lateral bases of the fin rays D 2-4.

**FLEXOR DORSALIS** (Figure 85b: F.D.).—The muscle originates from the dorsolateral faces of the tenth caudal vertebral centrum and the urostyle. Fibers insert on the anterolateral bases of the rays D 1-6.

**FLEXOR DORSALIS SUPERIOR** (Figure 85: F.D.S.).—A well-developed muscle, originating from the dorsolateral faces of the neural spines and centra of the eighth and ninth caudal vertebrae, and inserting on the anterodorsolateral base of fin ray D 6.

**FLEXOR VENTRALIS** (Figure 85b: F.V.).—Origin is from the ventrolateral face of the hypural plate, the ural, and the penultimate centrum. The fibers insert on the anterolateral bases of rays V 1-6.

**FLEXOR VENTRALIS INFERIOR** (Figure 85: F.V.I.).—A well-developed muscle, arising from the ventrolateral faces of the haemal spines and vertebral centra of the eighth and ninth caudal vertebrae, with a few fibers from the tenth haemal spine. The muscle inserts on the anteroventrolateral base of ray V 6.

**TRANSVERSUS CAUDALIS** (Figure 85b: TR.C.).—Fibers originate from the dorsolateral face of the hypural plate beneath the urostyle and pass posteroventrally to insert on the anterodorsal base of ray V 1.

#### LATERAL BODY MUSCLES

**EPAXIALIS** (Figures 78, 85a: EPAX.).—Anteriorly

the fibers arise from the supracleithrum, posttemporal, pterotic, epiotic, and exoccipital. The muscle is fairly uniform as it passes posteriorly, the myocommata becoming more horizontally oriented. The fibers grade into a fascia which inserts on the lateral bases of rays D 1-6.

**OBLIQUUS SUPERIORIS** (Figures 78, 85a: OBL.S.).—Anteriorly the fibers lie beneath the anteroventral downgrowth of the fibers of the epaxialis. The section does not reach the pectoral girdle anteriorly, and these fibers are also overlain by the anterodorsal region of the obliquus inferioris. They become exposed posteriorly, where they grade into a fascia with the obliquus inferioris to attach to the lateral bases of rays V 2-6. Dorsomedially, the fibers are attached to the centra of the vertebrae.

**OBLIQUUS INFERIORIS** (Figure 78: OBL.I.).—The anteroventral section of the muscle arises from the posterior face of the coracoid, the lateral fibers being continuous with the sternohyoideus. Most of the fibers from this region attach to the anteroventral face of the postcleithrum. Above the postcleithrum, the fibers arise from the fascia overlying the region of the epipleurals and course anteroventrally to attach to the posterodorsal face of the postcleithrum. The more posterior fibers become increasingly horizontal, and the section apparently fuses with the obliquus superioris to insert compoundly on rays V 2-6.

**SPINALIS** (Figure 80: SPIN.).—Fibers arise from the posterodorsal face of the epiotic and pass posteriorly to attach to the tips of the neural spines of the second and third abdominal vertebrae.

#### CUTANEOUS MUSCLES

**TRANSVERSUS CUTANEOUS** (Figure 78: TR.CUT.).—The fibers of this muscle arise from the fascia overlying the anteroventral portion of the obliquus inferioris and pass ventromedially to attach to the ventrolateral face of the pelvis. The posterodorsal fibers attach to the anteroventral tip of the postcleithrum. The section probably arose from the infracarinalis medius as postulated by Rosen (1913: 3), although he did not distinguish the infracarinalis medius from the obliquus inferioris.

#### *Balistapus undulatus* (Mungo Park)

FIGURES 86, 87a

A 2 $\alpha$  is not as well developed anterodorsally,

thus exposing more of A 1 $\alpha$  in lateral view. Ramus mandibularis V passes through A 2 $\alpha$  dorsal to the division between the two upper A 2 sections. A 2 $\gamma$  is better developed, and is bipinnate.

There is a hiatus between the extreme posterior fibers of the protractor hyoidei and the fibers anterior to them, and the hyohyoideus inferioris is visible externally through the gap.

The medial section of the sternohyoideus has separated completely from the main mass of the muscle. There is, in addition, another section which has separated off from the main mass. It passes horizontally from the cleithrum (lateral to the sternobranchialis) to insert on the urohyal just lateral to the insertion of the vertical section. A myocomma is present across the middle of the length of this horizontal section. Rectus ventralis I has completely separated from obliquus ventralis I.

The first levator externus is better developed and the fifth less well developed than in *B. vetula*. Transversus dorsalis II originates only from the lateral parasphenoid, with no fibers from a mid-dorsal raphe. The arrector ventralis pelvici is as for *B. vetula*, except that the tendons join again before inserting on the fin ray element. The transversus caudalis is not as well developed as in *B. vetula*.

#### *Melichthys niger* (Bloch)

FIGURE 88

A 2 $\beta$  is more exposed posterodorsally, and A 2 $\gamma$  is more obviously bipinnate. The hyomandibular crest is somewhat larger, with the result that there is more of the levator arcus palatini visible laterally.

The cutaneous portion of the protractor hyoidei is much better developed and overlies a greater part of the ventral branchiostegal rays, while the inner and more ventral sections are reduced. There is some development of the horizontal section of the sternohyoideus described in *B. undulatus*. The posterodorsomedial fibers of the sternobranchialis do not meet their antimeres. The pharyngoclavicularis internus has partially divided into two portions. Levator externus V is less well developed than in either of the two previous species, and transversus dorsalis II is as for *B. vetula*. The arrector ventralis pelvici and transversus caudalis are as for *B. undulatus*.

*Rhinecanthus aculeatus* (Linnaeus)

FIGURE 89

The levator arcus palatini is poorly developed, with only a few fibers to the anterodorsal face of the hyomandibular, while the levator operculi is well developed, extending inward beneath the dilatator operculi to the ventral process of the pterotic.

The cutaneous portion of the protractor hyoidei is well developed, and there is a fifth section of the hyohyoidei abductors. The sternohyoideus is as was described for *B. undulatus*.

The fifth levator externus is well developed, and partially fused to the fourth levator anterodorsally. Transversus dorsalis II arises only from the parasphenoid.

The posterior region of the groove in the pelvis which contains the arrector ventralis pelvici has closed over ventrally to form a tube. The tendon remains single throughout its length, but divides immediately before its insertion.

*Odonus niger* (Rüppell)

FIGURE 90

The adductor mandibulae is somewhat reduced in size, particularly sections A 2 $\alpha$  and A 2 $\beta$ . A 3 is also reduced, but A 1 $\alpha$  and A 1 $\beta$  are better developed than in the other balistids examined.

The cutaneous portion of the protractor hyoidei is well developed, with some fibers of the more dorsal portions originating from the dorsal three branchiostegal rays. The sections of the hyohyoidei abductores from the second to fifth rays are much reduced. The horizontal and vertical subdivisions

of the sternohyoideus are present, and the pharyngo-clavicularis externus is poorly developed.

Only the ventral fibers of levator externus V are developed, and these grade into an aponeurotic sheet dorsally, which fuses to the outer face of the midregion of levator IV. Both levatores interni are poorly developed, and transversus dorsalis II is as for *B. vetula*. The protractor pectoralis is well developed. The arrector ventralis pelvici is as for *R. aculeatus*, the movable portion of the pelvis being much reduced. The inclinator analis of the first anal fin ray appears to consist of two sections, and the transversus caudalis is small.

## Summary of Balistidae

In the balistids, there is some variation in the relative development of the sections of the adductor mandibulae, and minor differences in the size of the levator arcus palatini. The development of the cutaneous portion of the protractor hyoidei differs, as does the relative size of the sections of the hyohyoidei abductores. Two subdivisions of the sternohyoideus are usually present (one vertical and the other horizontal). The extent to which levator externus V develops varies, and transversus dorsalis II may or may not have fibers arising from the midline behind its main origin on the parasphenoid. There is some variation in the posterior region of the arrector ventralis pelvici, and the transversus caudalis is usually poorly developed.

While there is more variation in the Balistidae than in either of the two preceding families, it is usually of a minor nature and relatively unimportant at the level of analysis to be used here.

## Myological Descriptions of Representative Monacanthids

The general body outline of representatives of this family is given in Figure 4. Out of the 22 genera recognized by Fraser-Brunner (1941a), species representing 10 genera have been examined. Body form is basically conservative, and similar to balistids, although there are numerous exceptions such as the long snouted *Oxymonacanthus* and the tremendously elongate *Anacanthus*. The scales are spinose. The dorsal spines, of which there are

normally two (the second being able to lock the first in position), vary in position from behind the eye to the anterior snout region. The pelvis may be in evidence externally, as in balistids, or may simply be a movable strut of bone completely covered by skin. Locomotion is mainly by undulations of the soft dorsal and anal fins, turning being achieved by the pectoral fins and flexion of the body. The caudal fin does not seem to be used at

all in *Pseudalutarius* (Wickler, 1962), although it may be brought into play in escape movements. The teeth are much the same as in the balistids, but the general body plan is less robust.

The food of monacanthids is rather varied. Some species are totally herbivorous, others omnivorous, while yet others ingest primarily animal matter. They are usually found around coral reefs and on the sea-grass flats of tropical waters, although some species do occur in colder regions.

### *Pervagor melanocephalus* (Bleeker)

FIGURES 87b, 91-99

#### MUSCLES OF THE CHEEK

**ADDUCTOR MANDIBULAE** (Figures 87b, 91, 92; see also Figure 101 of *Stephanolepis auratus*: A 1 $\alpha$ , A 1 $\beta$ , A 1 $\gamma$ , A 2 $\alpha$ , A 2 $\beta$ , A 3).—The A 1 section of the adductor mandibulae has become considerably modified. A 1 $\alpha$  and A 1 $\alpha'$  arise from the lateral face of the ethmoid (and the ventral surface of the lateral flange) as well as from the prefrontal and the infraorbital ligament (between the prefrontal and hyomandibular). A 1 $\alpha'$  (Figure 91) grades into an aponeurotic sheet which fades into the tissues of the upper lip. It is a fairly distinct subsection, although there is some intermingling of fibers posteriorly. The main mass of A 1 is formed by A 1 $\alpha$ , which inserts on the posteroventrolateral face of the maxilla by a broad aponeurosis. Medial to this are two other sections, arising from the infraorbital ligament. The dorsal of these, A 1 $\gamma$  (see Figure 101) soon grades into a flat aponeurosis which attaches to the lateral process of the ethmoid supporting the palatine, and the palatine itself. Its function is obscure. Beneath this muscle is A 1 $\beta'$  (Figure 101), a smallish, somewhat flattened muscle which develops a tendon anteriorly joining that of A 1 $\alpha$  laterally and that of A 1 $\beta$  medially. A 1 $\beta$  originates from the lateral faces of the mesopterygoid and metapterygoid and inserts on the medial face of the maxilla. A 2 consists of two subdivisions. A 2 $\alpha$  originates from the prefrontal, infraorbital ligament, and the hyomandibular. A 2 $\beta$  is well developed and is separated from A 2 $\alpha$  by ramus mandibularis V. It arises from the anterior hyomandibular, the preopercle, symplectic, quadrate, and posterior metapterygoid. Some of the antero-

ventral fibers originate from the extreme ventral flange of the preopercle, but do not form a distinct section as in the balistids. A 2 $\alpha$  and A 2 $\beta$  insert by a common tendon on the medial face of the dentary. A 3 is completely separate from A 2 except for the shared tendinous insertion on the dentary. It originates from the lateral faces of the metapterygoid and quadrate.

**LEVATOR ARCUS PALATINI**.—The muscle is poorly developed, and no longer visible in superficial lateral view. It originates from the ventromedial face of the orbital process of the sphenotic and the anterolateral prootic. The fibers fan out to insert on the posterodorsal and posterolateral faces of the hyomandibular, the two regions being separated by a thin ridge.

**DILATOR OPERCULI** (Figure 91: D.O.).—Origin is from the ventrolateral face of the orbital process of the sphenotic and the pterotic, the fibers inserting on the anterolateral face and dorsal rim of the opercle.

**LEVATOR OPERCULI** (Figure 91: L.O.).—The muscle originates from the anterodorsal supracleithrum and anterolateral posttemporal and inserts on the posterodorsal ridge of the opercle.

**ADDUCTOR ARCUS PALATINI** (Figure 92: A.A.P.).—Fibers arise from the ventrolateral faces of the vomer and parasphenoid and insert on the dorso-medial hyomandibular and metapterygoid and dorsal mesopterygoid. The anterior region of the pterygoids underlies the parasphenoid, with which it is in contact dorsally. The muscle is not developed in the posterior half of the floor of the orbit.

**RETRACTOR ARCUS PALATINI** (Figures 91, 92: R.A.P.).—The muscle has completely separated from the adductor arcus palatini, and the division of the fibers into anterior and posterior sections as in balistids is not nearly as striking (the ventral aponeurosis of the anterior portion being absent). A small anterolateral bundle arises from the lateral process of the ethmoid. Fibers from this region insert mainly on the cartilagenous plug between the ectopterygoid, maxilla, and vomer, the rest of the muscle inserting predominantly on the ectopterygoid. Origin is entirely from the lateral and ventral surfaces of the dorsal flange of the ethmoid.

**ADDUCTOR OPERCULI** (Figure 95: AD.OP.).—This is a well-developed muscle originating from the lateral prootic and pterotic, and passing lateroventrally in front of the ventral process of the pterotic. It



inserts on the dorsomedial margin of the opercle posterior to that bone's articulation with the hyomandibular.

#### MUSCLES OF THE HYOID REGION

**INTERMANDIBULARIS.**—The muscle crosses transversely between the halves of the lower jaw just behind the symphysis. It lies completely dorsal to the protractor hyoidei.

**PROTRACTOR HYOIDEI** (Figures 91, 92: PR.HY.).—The fibers arise from the posteroventrolateral face of the anterohyal. The dorsal fibers pass anteriorly to the ventromedial face of the dentary. The more ventral fibers originate at an increasingly transverse angle and meet their antimeres in the midventral line. There is an obvious myocomma which passes anteriorly as it proceeds toward the midline in the dorsal region.

**HYOHYOIDEUS INFERIORIS** (Figures 91, 95: HY. IN.).—Origin is from the entire ventral surface of the anterohyal, the fibers passing ventrally to a midventral raphe and attachment on the ventrolateral face of the urohyal.

**HYOHYOIDEI ABDUCTORES** (Figure 91: H.AB.).—Only the three ventral rays possess these muscles. The more dorsal two are small, passing from the medial faces of the rays to the fascia on the medial face of the anterohyal. The ventralmost muscle is broad and flat, arising anteriorly in the region of the urohyal and ventrohyal and inserting along the dorsomedial border of the first ray.

**HYOHYOIDEI ADDUCTORES** (Figures 91, 92: H.AD.).—The fibers arise from the fascia overlying the dorsal surface of the sternohyoideus, and pass posterodorsally, medial to the branchiostegal rays and the preopercle, to fade out in the tissue beneath the opercle and subopercle.

**STERNOHYOIDEUS** (Figures 91, 95: STH.).—The fibers arise mainly from the posterior myocomma separating the muscle from the obliquus inferioris, with only a few medial fibers from the anteroventral cleithrum. There are two myocommata, the fibers inserting anterodorsally by a tendon to the posteroventral face of the ventrohyal and anteroventrally on the posterolateral face of the urohyal. Ventromedially, a small bundle of fibers arises from the anteroventral tip of the cleithrum and inserts on the posteroventral tip of the urohyal. It is very similar to the vertical bundle found in the same

position in balistids, and is probably a homologous structure.

**STERNOBRANCHIALIS** (Figures 94, 95: STB.).—Origin is from the anteroventromedial cleithrum. The fibers pass vertically upward, meeting briefly with their antimeres. The tendon divides into two sections, the anterior of which inserts broadly on the posterodorsal urohyal while the posterior part inserts on the ventral face of hypobranchial 3.

**RETRACTOR INTEROPERCULI** (Figure 93: R.I.).—Origin is from the medial face of the posteroventral flange of the preopercle. The fibers converge to insert on the anterior part of the interopercle-opercle ligament. Just in front of this, the interopercle attaches to the posterohyal and the medial preopercle. The muscle is probably a derivative of the hyochoidei adductores.

#### VENTRAL BRANCHIAL MUSCLES

**PHARYNGOCLAVICULARIS EXTERNUS** (Figures 94, 95: PHC.E.).—The fibers arise from the anterior face of the cleithrum, and diverge as they pass dorsally. The anterior section inserts on the extreme anterolateral tip of ceratobranchial 5, while the tendon of the posterior part joins the dorsal tendon of the coracobranchialis internus to insert on the anteroventral face of ceratobranchial 5.

**PHARYNGOCLAVICULARIS INTERNUS** (Figures 94, 95: PHC.I.).—The muscle originates from the antero-medial face of the dorsal cleithrum, and passes anteriorly. It grades into a tendon which divides into a dorsal section to ceratobranchial 5 (joining the posterior tendon of the pharyngoclavicularis externus) and a main anterior tendon which inserts on the anteroventromedial faces of the fourth ceratobranchials.

**OBLIQUI VENTRALES I, III** (Figure 94: OBL.V.).—Both muscles are small, spanning the joints between the hypobranchials and ceratobranchials of their respective arches. Obliquus II has apparently been modified into a section of rectus II.

**TRANSVERSI VENTRALES III-V** (Figure 94: TR.V.).—The anteriormost of this series connects the ventral faces of the third ceratobranchials, and is single. In the cases of transversi IV and V, certain changes have occurred. Both these muscles consist of two bundles of fibers, crossing each other in the midline at some 30 degrees. The anterior muscles both connect the anteromedial faces of the fourth cerato-

branchials across the midline, the posterior muscles connecting the fifth ceratobranchials in a like manner. In both pairs, the fibers passing from anterior left to posterior right lie ventral to those passing in the opposite direction.

**RECTI VENTRALES I, II, IV** (Figures 94, 95: *RECT. v.*).—Rectus I connects the ventrolateral surface of basibranchial 1 (with some fibers to the posterodorsal face of the dorsohyal) to the anterolateral face of ceratobranchial 1. The main mass of rectus II lies between the anteroventral face of ceratobranchial 2 and the dorsolateral face of the urohyal. A very small lateral section attaches to the posteroventromedial face of ceratobranchial 1. The major section of rectus IV passes between the ventromedial face of hypobranchial 3 and the anterolateral tip of ceratobranchial 4. The posteroventral section found in triacanthoids and balistids is presumably represented by a slip of fibers diverging from the posterior face of transversus ventralis III, and attaching to the dorsal surface of the tendon of the rectus communis.

**RECTUS COMMUNIS** (Figures 94, 95: *R.COMM.*).—The muscle originates from the posterodorsal urohyal and grades into a tendon which inserts on the anterolateral face of ceratobranchial 5. As described above, the tendon receives a small bundle of fibers from the posterior face of the transversus ventralis III.

#### DORSAL BRANCHIAL MUSCLES

**LEVATORES EXTERNI I-IV** (Figure 95: *L.EXT.*).—The four muscles originate from the anteroventral face of the prootic, the origins becoming more lateral posteriorly. Levator III inserts on epibranchials 3 and 4, the other three levators inserting on the epibranchials of their respective arches. The third levator is partially fused to the fourth, and a small aponeurosis connects the latter muscle to the dorsal tip of ceratobranchial 5.

**LEVATORES INTERNI II-III** (Figure 96: *L.INT.*).—Origin is from the prootic posterior to the hyomandibular foramen. Levator II passes anteroventrally to insert on the medial face of infrapharyngobranchial 2, while levator III inserts on the dorsolateral face of infrapharyngobranchial 3.

**OBLIQUUS DORSALIS III** (Figure 96: *OBL.D.*).—There are two sections, the anterior of which passes between the anterodorsal face of infrapharyngo-

branchial 2 and the anterodorsal face of epibranchial 3, lying beneath transversus dorsalis II. The smaller, posterior portion connects the third infrapharyngobranchial to epibranchial 3.

**OBLIQUUS POSTERIOR** (Figure 96: *OBL.P.*).—A small muscle, which passes from the anterodorsal tip of ceratobranchial 5 to the posterodorsal face of epibranchial 4.

**TRANSVERSI DORSALES II-III** (Figure 96: *TR.D.*).—The anterior muscle originates from the lateral parasphenoid and passes out laterally to insert on the posterodorsal face of epibranchial 2. Transversus III crosses the dorsal midline between the dorsal faces of the third epibranchials, with a few of the more anterior fibers arising from the parasphenoid.

**RETRACTOR DORSALIS** (Figure 96: *D.RETR.*).—Origin is from the posterodorsolateral surface of the basioccipital, the fibers coursing anteroventrally to insert on the dorsomedial face of the infrapharyngobranchial 3.

**ADDUCTORES IV-V** (Figure 96: *AD.*).—Adductor IV passes across the angle between the medial faces of the fourth epibranchial and ceratobranchial. Adductor V connects the anterodorsal face of ceratobranchial 5 to the posterodorsal face of ceratobranchial 4.

**SPHINCTER OESOPHAGI** (Figures 94, 95, 96: *S.O.*).—The muscle encircles the esophagus, attaching to ceratobranchial 5, epibranchial 4, and infrapharyngobranchial 3. A fairly large section passes anterodorsal to the retractor dorsalis.

#### MUSCLES OF THE PECTORAL REGION

**ABDUCTOR SUPERFICIALIS** (Figure 91: *ABD.S.*).—Origin is from the ventrolateral and posteroventral cleithrum. The fibers insert on the anterolateral bases of each of the principal fin rays.

**ABDUCTOR PROFUNDUS** (Figure 95: *ABD.P.*).—The fibers arise from the anterolateral face of the coracoid and insert on the bases of the principal fin rays in the region of the posteroventral flange.

**ARRECTOR VENTRALIS** (Figure 91: *ARR.V.*).—The muscle originates from the lateral cleithrum behind the ala laminaris and above the abductor superficialis. The fibers insert on the lateral base of the vestigial fin ray, of which only the medial half remains.

**ADDUCTOR SUPERFICIALIS** (Figure 97: *ADD.S.*).—

Origin is from the dorsomedial face of the cleithrum, the fibers inserting on the dorsomedial faces of the principal rays, a little distal to their bases. The more dorsal fibers serve the more ventral rays, and lie more medially.

**ADDUCTOR PROFUNDUS** (Figure 97: ADD.P.).—The fibers arise from the medial faces of the cleithrum and coracoid, and insert on the posteroventromedial flanges of the principal fin rays.

**ARRECTOR DORSALIS** (Figure 97: ARR.D.).—The muscle originates from the medial face of the cleithrum and passes posterodorsally to insert on the posteromedial flange of the vestigial fin ray.

**CORACORADIALIS** (Figure 97: COR.R.).—This small muscle arises from the anterior face of the medial flange of the coracoid. It passes laterally to insert on the medial face of the ventral (fourth) radial.

**PROTRACTOR PECTORALIS** (Figure 95: P.P.).—The muscle connects the posteroventral tip of the pterotic to the anterodorsal face of the cleithrum.

**LEVATOR PECTORALIS** (Figure 95: TR.).—A somewhat smaller muscle, arising from the ventral process of the pterotic and inserting on the extreme anterodorsal tip of the cleithrum.

#### MUSCLES OF THE PELVIC GIRDLE

**ARRECTOR VENTRALIS PELVICUS** (Figure 98: A.V.P.).—The fibers arise from the midventral groove in the pelvis, the structure becoming somewhat bipinnate posteriorly. A tendon develops (and may be split into left and right components), which inserts on the anteroventral tip of the cartilagenous plug. There did not appear to be a ventral fin ray element, but the specimens were not alizarin stained.

**ADDUCTOR SUPERFICIALIS PELVICUS** (Figure 98: A.S.P.).—The muscle consists of left and right halves, and originates in the trough on the postero-dorsal face of the pelvis in front of the dorsal lobe. The tendons pass posteriorly through a bony canal and insert on the fin ray element, the right tendon also attaching partly to the cartilagenous plug.

#### MUSCLES OF THE DORSAL FIN

**INCLINATORES DORSALES** (Figure 91: INC.).—These muscles serve the soft dorsal fin only. They arise in the fascia between the lateral processes of the distal ends of the pterygiophores and insert on the

lateral bases of the fin rays, decreasing in size posteriorly.

**ERECTORES DORSALES** (Figures 91, 92: EREC.).—The erector to the first spine is large, and originates from the anterolateral face of the pterygiophore, the frontal, and the supraoccipital. It inserts on the anterolateral base of the spine. The erector to the reduced second spine arises from the frontal and inserts on the lateral surface of the main body of the spine. The erectors to the fin rays originate from the posterolateral halves of the pterygiophores and the anterolateral faces of the neural spines. They insert on the anterolateral bases of the rays.

**DEPRESSORES DORSALES** (Figure 91: DEPR.).—The first depressor passes from the frontal to the posterolateral base of the spine, while that to the second spine arises from the frontal and lateral face of the pterygiophore and inserts on the distal tip of the ventrolateral process. The muscles to the fin rays originate from the anterolateral halves of the pterygiophores and posterolateral faces of the neural spines and insert on the posterolateral bases of the rays.

**SUPRACARINALIS MEDIUS** (Figure 91: S.MED.).—The muscle passes from the posterior tip of the first basal pterygiophore to attach in a long, vertical groove in the anterior face of the first pterygiophore of the soft dorsal fin. Some of the more medial fibers attach to the tips of the neural spines of the second and third vertebrae.

**SUPRACARINALIS POSTERIOR** (Figure 99: S.POST.).—The muscle connects the posterodorsal face of the last pterygiophore of the dorsal fin with the anterodorsal tip of the last neural spine. The medial part of the muscle attaches to the dorsolateral tips of the neural spines of the antepenultimate and penultimate vertebrae.

#### MUSCLES OF THE ANAL FIN

**INCLINATORES ANALES** (Figure 91: INC.).—The enlarged, residual first inclinor passes from the fascia overlying the obliquus inferioris to attach to the anteroventral face of the first anal pterygiophore. All the other inclinors, one of which inserts on the lateral base of each ray, arise in the fascia between the lateral pterygiophore processes and the hypaxial body muscles.

**ERECTORES ANALES**.—The erectors originate from the posterior halves of the pterygiophores and in-

sert tendinously on the anterolateral base of each fin ray.

**DEPRESSORES ANALES.**—The fibers arise from the anterolateral halves of the pterygiophores and insert on the posterolateral bases of the fin rays.

**INFRACARINALIS ANTERIOR** (Figures 91, 95: INF. A.).—The muscle originates from the ventromedial coracoid and posteroventral cleithrum. Insertion is in the large ventrolateral groove in the pelvis, the fibers almost reaching the posterior margin of the bone.

**INFRACARINALIS MEDIUS** (Figure 91: INF.M.).—This is a thin, sheetlike muscle extending posteriorly from the lateral face of the pelvis. It joins the ventral fibers of the obliquus inferioris, the more dorsal fibers reaching the posteroventral tip of the postcleithrum, while the posteroventral fibers attach to the ventrolateral face of the first anal pterygiophore.

**INFRACARINALIS POSTERIOR** (Figure 99: INF.P.).—Fibers arise from the posteroventral tip of the last anal pterygiophore. They attach to the tips of the next two haemal spines before ending on the anteroventral tip of the last haemal spine.

#### MUSCLES OF THE CAUDAL FIN

**INTERRADIALIS** (Figure 99a: INT.).—The muscle is made up of slips which pass from the lateral faces of the rays toward the midline. They usually attach to the bases of the rays lying nearer the midline, but cross over each other in the case of the fibers from rays V 1 and D 1.

**HYPCHORDAL LONGITUDINALIS** (Figure 99a: H.L.).—The fibers arise from the ventrolateral face of the hypural plate and divide into three tendons, which insert on the ventrolateral bases of rays D 1–3.

**FLEXOR DORSALIS** (Figure 99b: F.D.).—Origin is from the dorsolateral faces of the 18th and 19th centra, the neural spine of the former, the urostyle, and the epurals. The fibers divide into six tendons, inserting on the bases of rays D 1–6.

**FLEXOR DORSALIS SUPERIOR** (Figure 99: F.D.S.).—Origin is from the dorsolateral faces of the third and fourth last vertebrae and their neural spines, the fibers inserting on the base of ray D 6.

**FLEXOR VENTRALIS** (Figure 99b: F.V.).—The fibers arise from the ventrolateral faces of the antipenultimate and penultimate centra, the haemal spine of

the former and the hypural plate. The muscle inserts on the bases of rays V 1–6.

**FLEXOR VENTRALIS INFERIOR** (Figure 99: F.V.I.).—The muscle originates from the ventrolateral faces of the centra of the third and fourth last vertebrae and their haemal spines and inserts on the base of ray V 6.

**TRANSVERSUS CAUDALIS** (Figure 99b: TR.C.).—Origin is from the dorsolateral face of the hypural plate. The fibers pass posteroventrally to insert on the dorsal base of ray V 1.

#### LATERAL BODY MUSCLES

**EPAXIALIS** (Figures 91, 95, 99a: EPAX.).—The fibers attach anteriorly to the epiotic, exoccipital, and supraoccipital. Posteriorly, the angle of the myocommata increases to a sharp V, whose apex lies posteriorly. Only the section closest to the midline contributes fibers to the insertion tendons serving rays D 1–5. The dorsal portion fades into a fascia covering the whole region, joining with a similar fascia from the obliquus inferioris. A small slip of the ventral section attaches to epural 2.

**OBLIQUUS SUPERIORIS** (Figures 91, 99a: OBL.S.).—The anterior region does not reach the skull, arising from the lateral surface of the vertebral column. The size of the muscle increases posteriorly, the last myomere inserting on the bases of rays D 1 and V 1–5, with a small ventral slip to the posterolateral face of the first hypural.

**OBLIQUUS INFERIORIS** (Figures 91, 95, 99a: OBL.I.).—The anteroventral portion of the muscle arises from the fascia overlying the lateral coracoid-cleithrum region, and is anteriorly continuous with the sternohyoideus. Some fibers arise from the posterolateral face of the coracoid. Most of the fibers from this region attach to the anteroventral face of the postcleithrum. A number of myomeres arise from the lateral midline, the fibers passing anteroventrally to insert aponeurotically on the posterodorsal face of the postcleithrum. Fiber direction gradually becomes horizontal posteriorly, and the muscle grades into a vague aponeurosis which joins that from the dorsal portion of the epaxialis to cover the caudal peduncular region.

**SPINALIS.**—The muscle originates from the posterior face of the epiotic and the first dorsal pterygiophore and inserts on the dorsolateral tips of the neural spines of the second and third vertebrae.

## CUTANEOUS MUSCLES

**TRANSVERSUS CUTANEUS** (Figure 91: TR.CUT).—This is a small muscle arising from the middle of the anteroventral face of the postcleithrum and passing downward to insert on the ventrolateral face of the pelvis.

*Stephanolepis auratus* (Castlenau)

FIGURES 100-101

A 2 $\beta$  is slightly more bulky, and the levator arcus palatini is just visible in lateral view. The ventral portion of rectus ventralis IV is smaller, and the arch-shaped ligament between the ventral processes of the third hypobranchials is lost. The coracoradialis is less well developed, and the medial projection for its insertion on the fourth radial is not as prominent. The adductor superficialis pelvici is single anteriorly but bilaterally symmetrical posteriorly. The depressor of the second spine is larger, and is partially overlain by the epaxialis which attaches to the lateral surface of the pterygiophore between the two spines. The anterodorsal portion of the obliquus inferioris above the postcleithrum inserts muscously on that bone. The spinalis is small and inserts only on the neural spine of the second vertebra.

*Paramonacanthus barnardi* Fraser-Brunner

FIGURE 102

The adductor mandibulae and levator arcus palatini are as for *S. auratus*, and the dilatator operculi is more parallel fibered. The retractor interoperculi is better developed. The adductor superficialis pelvici is single, as is the arrector ventralis pelvici. The erector dorsalis to the first spine is contained in a fairly deep depression and is partially overlain dorsally by a lateral flange of the pterygiophore. The anterodorsal portion of the obliquus inferioris is as for *S. auratus*.

*Chaetoderma spinosissimus* (Quoy and Gaimard)

FIGURE 103

A 1 $\alpha'$  is rather poorly developed, and A 1 $\gamma$  is visible laterally between A 1 $\alpha$  and A 1 $\beta'$ . A 3 is

well developed, and visible anterior to A 2 $\beta$ . The levator operculi originates more from the pterotic and posttemporal than from the supracleithrum.

Rectus ventralis II has developed extra fibers on its medial surface which join their antimeres in the midline. The fibers are separated from the more anterior section by the anterior tendon of the sternobranchialis to hypobranchial 2 (see Figure 111 of *Aluterus* for the extreme of this condition). The ventral portion of rectus ventralis IV is well developed. In both the transversi ventrales, the relative positioning of the sections crossing over each other is reversed; i.e., the anterior left section lies dorsal to the section arising from the anterior right. The muscle fibers of the arrector ventralis pelvici and the adductor superficialis pelvici are virtually absent, but fairly well-developed tendons remain. The residual inclinator of the anal fin is aponeurotic, with no muscle fibers visible. The spinalis is poorly developed, and the transversus cutaneus does not reach the postcleithrum dorsally.

*Paraluteres prionurus* (Bleeker)

FIGURE 104

A 1 $\alpha$  is fairly small, originating primarily from the ethmoid with only a few fibers from the prefrontal. A 1 $\alpha'$  is well developed, while A 1 $\gamma$  has enlarged to take over much of the site of origin of A 1 $\alpha$ . It now originates from the prefrontal and the entire anterodorsal half of the infraorbital ligament. The insertion has also expanded to include the dorsolateral face of the maxilla as well as the ethmoid and palatine. A 1 $\beta$  is larger and visible in superficial lateral view, while A 1 $\beta'$  is small. Another section, A 1 $\beta''$ , has separated from its dorsomedial face and inserts on the maxilla near A 1 $\alpha$ . Both the A 1 $\beta$  sections mentioned originate from the anterior hyomandibular, A 1 $\beta'$  also receiving a few fibers from the infraorbital ligament. A 2 $\alpha$  is much reduced, but A 2 $\beta$  and A 3 are more normal. The adductor arcus palatini is tremendously well developed, and inserts primarily on the entire dorsomedial half of the metapterygoid.

All the fibers of the hyohyoideus inferioris attach to the ventrolateral face of the urohyal, and the dorsal fibers of the hyohyoidei adductores attach to the dorsomedial face of the opercle. The ventro-

medial section of the sternohyoideus is poorly developed, and the insertion of the sternobranchialis is confined to the ventral faces of hypobranchials 2 and 3.

The small lateral section of rectus ventralis II attaches more to hypobranchial 1 than to ceratobranchial 1, and the medial section is as for *C. spinosissimus*. The ventral portion of rectus ventralis IV is absent, and transversus ventralis IV consists only of a single transverse fiber bundle. The arrector ventralis pelvificus and adductor superficialis pelvificus are absent, as they are in all the remaining species except *Cantherhines pardalis*.

The infracarinalis anterior is small, and the infracarinalis posterior and supracarinalis posterior do not attach to the tips of the haemal and neural spines respectively, apart from the spine on which they insert. The last three vertebrae possess well-developed lateral flanges, and the origins of the flexor dorsalis and flexor ventralis have shifted partially onto these surfaces. The spinalis is well developed, and originates mainly from the occipital.

#### *Cantherhines pardalis* (Rüppell)

FIGURE 105

A 1 $\alpha'$  is poorly developed, while A 2 $\alpha$  has expanded its origin dorsally to reach the prefrontal. A 1 $\beta'$  inserts by a broad, aponeurotic sheet over the posterolateral face of the maxilla ventral to the palatine. A 1 $\beta$  is well developed, while A 1 $\gamma$  has a somewhat restricted insertion on the ethmoid and palatine. A 3 is partially fused to A 2 $\beta$  anteroventrally. There are no fibers of A 2 $\beta$  from the ventrolateral flange of the preopercle.

All six branchiostegal rays may receive a slip of the hyohyoidei adductores, but that to the dorsal-most ray may be absent. The halves of the sternobranchialis do not meet in the midline. The pharyngoclavicularis externus is bifid, rectus ventralis II is as for *C. spinosissimus*, and the ventral portion of rectus ventralis IV is well developed.

The abductor profundus is considerably exposed ventrally beneath the abductor superficialis. Both the adductor profundus and the protractor pectoralis are well developed. The arrector ventralis pelvificus appears to be represented by a tendon which just reaches the posteroventral surface of the

pelvis from the canal in which it lies. The adductor superficialis pelvificus is present as a tiny paired muscle on the dorsal surface of the pelvis. It passes through the canal in the dorsal lobe, and both tendons insert on the posterior face of the cartilagenous plug. Some of the more ventral fibers of the infracarinalis medius attach to the thickened dermis around the anus.

The anterodorsal portion of the obliquus inferioris is made up mainly of an aponeurotic sheet, the muscle fibers being confined to a narrow band in the middle of the sheet.

#### *Oxymonacanthus longirostris* (Bloch and Schneider)

FIGURE 106

A 1 $\alpha$  is rather small, passing from the ventral face of the maxilla to its origin at the anterior junction of the frontal and prefrontal. Above A 1 $\alpha'$ , a third subdivision, A 1 $\alpha''$ , is recognizable. It originates along the ventrolateral surface of the ethmoid ridge and passes into the connective tissue of the lips dorsal to A 1 $\alpha'$ . A 1 $\beta'$  has acquired some origin from the prefrontal, and partially overlies A 1 $\gamma$  ventrally. A 1 $\gamma$  itself is well developed with a broad insertion. A 2 $\alpha$  is also well developed, its origin stretching from the prefrontal to the hyomandibular and including the infraorbital ligament. At about the middle of its origin is a gap in the fibers, through which passes a sensory branch of nerve V. There are no fibers of A 2 $\beta$  from the ventrolateral flange of the preopercle (and this is true for all the remaining species). A 3 is poorly developed. The ridge of bone on the posterodorsal surface of the hyomandibular is well developed, the fibers of the levator arcus palatini inserting on either side of it. The lateral wall of the fossa containing the origin of this muscle has broken down, and the muscle is visible laterally between the frontal and sphenotic. A few fibers of the levator operculi arise from the pterotic. The adductor arcus palatini is visible in lateral view, and stretches to the rear of the orbit. The retractor arcus palatini is poorly developed, with no fibers to the palatine.

There is no ventromedial section to the sternohyoideus, and the aponeuroses of the sternobranchialis are more consolidated. The retractor interoperculi is absent.

The pharyngoclavicularis externus is single, and inserts on ceratobranchial 5, while the pharyngoclavicularis internus has been reduced to a strap-like, parallel fibered muscle. Obliquus ventralis I is well developed, being almost the same size as rectus ventralis I. The medial portion of rectus ventralis II is as described for *C. spinosissimus*, and the ventral portion of rectus ventralis IV is absent (as in *P. prionurus*).

The depressor dorsales of the first spine has broken through beneath the lateral strut of the pterygiophore supporting the base of the spine, and has extended its origin into the fossa originally occupied only by the erector dorsalis to the first spine. Erector dorsalis II passes posteromedially to its insertion, while depressor dorsalis II courses posterolaterally to the base of the second spine. Both penetrate the tunnel beneath the flange, but do not extend beyond its anterior margin. The hypochordal longitudinalis inserts only on rays D 2 and 3, and the transversus caudalis is poorly developed. The transversus cutaneous fans out from the posterodorsal face of the pelvis, and attaches to the coracoid anteriorly.

#### *Pseudalutarius nasicornis* (Schlegel)

##### FIGURE 107

The adductor mandibulae complex is very much like that of *O. longirostris*, although the snout is not as elongated. A 1 $\alpha'$  inserts more on the maxilla than the lips, and A 1 $\beta'$  completely overlies A 1 $\gamma$ .

Where *O. longirostris* differs from *P. melanocephalus*, the descriptions also apply to *P. nasicornis*, with the following exceptions.

There is a larger section of the levator operculi originating from the pterotic, and the retractor interoperculi is present. Obliquus ventralis II is apparently absent.

The general positioning of the dorsal branchial levators seems more primitive than in *P. melanocephalus*, since all the origins are from the posterolateral face of the prootic, and none from the poorly developed prootic shelf. The small size of the shelf could, of course, be secondary.

#### *Aluterus monoceros* (Linnaeus)

##### FIGURES 108-113

A 1 $\alpha$  (Figure 108) is a single section, the more

dorsal part of the insertion extending into the tissues of the lips. The origin has expanded enormously to include not only the anteroventral prefrontal, but the entire infraorbital ligament as well. A 1 $\beta'$  is long and thin (Figure 109), while A 1 $\beta$  and A 1 $\gamma$  are more like the generalized condition. A 2 $\alpha$  (Figure 108) is much reduced dorsally, there being no fibers from the infraorbital ligament. A 3 is small. The adductor arcus palatini (Figure 110: A.A.P.) is divided into two sections by the junction between the metapterygoid and the parasphenoid. The retractor arcus palatini is not subdivided at all.

Most of the posteroventral fibers of the protractor hyoidei arise from the fascia over the anteroventral tip of the cleithrum. These fibers are almost at right angles to the ones originating from the posteroventral face of the anterohyal.

Rectus ventralis II (Figure 111: RECT.V.) is well developed. There is a lateral section to hypobranchial 1, an anterior section to the dorsolateral urohyal, and a transverse section across the midline. The anterior tendon of the sternobranchialis inserts on hypobranchial 2 between the two latter sections. The arrangements of the two bundles of fibers forming transversus ventralis IV are as for *P. melanocephalus*, but the relative positions of the bundles is reversed in transversus V. The pharyngoclavicularis externus is bifid, with tendons to ceratobranchials 4 and 5.

The anterior extension of the prootic shelf has carried the origins of the levatores externi with it (Figure 112: L.EXT.). There is some variation in the mode of insertion in levators II and IV. They may insert by a continuous aponeurosis on epibranchials 3 and 4, or separately. If the latter is the case, the anterior tendon may send a small branch to epibranchial 4. The aponeurosis of levator II sends a small section to epibranchial 3. The levatores interni retain their origin from the prootic beneath the hyomandibular foramen. Some fibers of transversus dorsalis III overlap onto the dorsal face of epibranchial 4. Obliquus dorsalis III is somewhat modified. Fibers from infrapharyngobranchial 2 pass to three different points of attachment. The medial fibers pass posteriorly to the dorsal face of infrapharyngobranchial 3. The more lateral fibers attach to epibranchial 3 (as in *P. melanocephalus*), while some of the ventromedial fibers loop around epibranchial 2 and reattach to infra-

pharyngobranchial 2.

The adductor superficialis is well developed (Figure 113: ADD.s.). The supracarinalis medius is present as a pair of cylindrical muscles, rather than the more usual triangular muscle. The erectores and depressores dorsales do not reach the vertebral column ventrally. The infracarinalis medius forms a broad tendon posterodorsally before grading into the fascia beneath the postcleithrum. Both the transversus caudalis and the spinalis are small, the latter muscle arising from the posterodorsal face of the first vertebra. In view of the fact that *A. monoceros* exhibits certain characters not found in any of the other monacanthids examined (particularly in the form of the adductor mandibulae complex), two additional species of the genus were dissected.

#### *Aluterus heudeloti* Hollard

The only difference noted was that there were tough connective tissue strands from the posterodorsolateral face of A 2 $\alpha$  to the prefrontal.

#### *Aluterus schoepfi* (Walbaum)

The findings were the same as for *A. heudeloti*. In the smaller specimen (57 mm SL), A 2 $\alpha$  has relatively larger dorsal extent than in any other *Aluterus* examined, the posterodorsal fibers almost reaching the infraorbital ligament.

#### *Anacanthus barbatus* Gray

FIGURE 114

Various modifications are apparent in the adductor mandibulae complex. A 1 $\alpha'$  originates from the lateral and medial ethmoid. It is partially covered by A 1 $\alpha$  posteriorly, and has a long, thin aponeurosis which crosses the upper jaw to insert in the anterior tissues of the barbel. A 1 $\alpha$  arises from the ethmoid behind A 1 $\alpha'$  and from the prefrontal. It also develops a long aponeurosis, which fades into the tissues of the barbel at its posterior base. These sections are only connected to the upper jaw by connective tissue. A 1 $\beta$  is fairly well developed, and has its normal relationships. A 1 $\beta'$  is absent, and A 1 $\gamma$  is poorly developed, originating from the prefrontal and the infraorbital ligament. The fibers

of the latter section soon become aponeurotic, and insert on the ethmoid and parasphenoid posterior to the retractor arcus palatini. A 2 $\alpha$  and A 2 $\beta$  are not separated posteriorly, but are so anteriorly, where the ramus mandibularis V passes between them. The orbital process of the sphenotic almost reaches the hyomandibular. The levator operculi and levator arcus palatini are very small, but the dilatator operculi remains well developed. The adductor arcus palatini is confined to a region in front of the orbit, but behind the retractor arcus palatini. The latter muscle is very well developed.

Both the hyohyoidei abductores and the hyohyoidei adductores are well developed, the latter muscle attaching to three of the four branchiostegal rays. The hyohyoideus inferioris meets its antimere in the ventral midline, and is not attached to the urohyal.

Rectus ventralis II is single, with the fibers passing anteromedially to the midline, where they join to form two tendons to the urohyal. Obliquus ventralis III is absent, as is the ventral section of rectus IV.

The dorsal ends of the gill arches lie beneath the prootic shelf at the level of the prefrontal. Levatores externus IV inserts only on epibranchial 4. The levatores interni arise from the prootic just before the start of the shelf at the rear of the orbit. They course the length of the orbit before inserting on the infrapharyngobranchials.

The levator pectoralis is very well developed, originating from the elongated ventral process of the pterotic and sphenotic, the medial fibers arising from the posteromedial face of the hyomandibular. It inserts on the supracleithrum and anterodorsal cleithrum. The protractor pectoralis is less well developed, but also more anterior in position.

There is a single dorsal spine, the depressor dorsalis being larger than the erector dorsalis. The supracarinalis medius is muscous at its attachment sites, but aponeurotic in the middle two-thirds, where it attaches to the tips of the neural spines. The infracarinalis anterior has partially fused in the midline. The residual inclinator of the anal fin is very well developed, grading into the infracarinalis medius anteriorly and the obliquus inferioris dorsally. The interradians is well developed, but both the hypochordal longitudinalis and the transversus caudalis are absent.



### Summary of Monacanthidae

The monacanthids exhibit a wide range of variation and progressive specialization, which may or may not be obviously related to the body form. The adductor mandibulae is very variable in both the number of subdivisions and in the relative development of these sections. The basic plan is, however, fairly consistent, with two subdivisions of A 1 $\alpha$  and A 1 $\beta$ , and a single section of unknown function, A 1 $\gamma$ . Section A 2 usually has two subdivisions, separated by the path of ramus mandibularis V, the posterodorsal surface of A 2 $\alpha$  sometimes reaching the prefrontal. The levator arcus palatini may be well developed or almost absent, or it may be visible laterally owing to a breakdown in the lateral wall of the dilatator fossa. The adductor arcus palatini may be well or poorly developed, confined to the region in front of the orbit, stretch half way across it, or it may reach the rear of the orbit. The retractor arcus palatini is well separated from the above muscle, and may be well or poorly developed.

The protractor hyoidei may have a superficial section arising from the fascia overlying the ventral tips of the cleithra, and the hyohyoideus inferioris may arise partially, totally, or not at all from the ventrolateral face of the urohyal. There are minor variations in the extent of development and num-

ber of the sections of the branchiostegal ray musculature. The amount of separation and consolidation of the ventromedial section of the sternohyoideus varies, as does the insertion of the sternobranchialis. The retractor interoperculi is sometimes absent.

The pharyngoclavicularis externus is often bifid, and rectus II shows progressive specialization and subdivision. The ventral fiber bundle of rectus ventralis IV may be absent, and the relative positioning and development of the sections of transversus ventralis IV differs.

The position of origin of the levatores externi depends on the location of the prootic shelf, while that of the levatores interni seems independent of this variable. The muscles serving the fin ray elements of the pelvis are variously developed or absent, the ray elements themselves being absent in certain genera. Muscles attaching to the dorsal spines vary in sites of origin and relative development. The anterodorsal portion of the obliquus inferioris may be muscular or largely aponeurotic, and the sites of origin of the spinalis vary.

At least some of the variation in monacanthids is attributable to the large number of species and genera and the great variety of body form. They would appear to have undergone "explosive" evolution, and form the apomorph sister group of the balistids.

### Myological Descriptions of Representative Aracanids

The general body form of these fishes is illustrated in Figure 5. In his review of the genera of ostracioid fishes, Fraser-Brunner (1935) recognized six genera in what was originally a subfamily, but which he later raised to familial rank (1941b). Representatives of two of these six genera have been dissected for the present study. The fishes are encased in a bony cuirass of modified scales from the snout to the level of the posterior margin of the dorsal and anal fins. Neither this family, nor the succeeding one (Ostraciidae) show any evidence of pelvic fins or girdle. They are presumably slow swimmers, but virtually nothing is known about their life habits. They appear to live in deepish water (down to 100 fathoms). The gut contents of the specimens dissected for this study indicate a diet of small crustacea and worms.

The aracanids are usually considered, in effect, as the plesiomorph sister group of the next family, the Ostraciidae, and derived originally from a common ancestor with the balistids (although it has also been suggested that they arose from a neotenic molid ancestor).

#### *Kentrocapros aculeatus* (Houttuyn)

FIGURES 115, 116 $\alpha$ , 117-124

#### MUSCLES OF THE CHEEK

ADDUCTOR MANDIBULAE (Figures 115, 116, 117: A 1 $\beta$ , A 2 $\alpha$ , A 2 $\beta$ , A 3).—A 2 $\alpha$  is well developed, originating from the dorsolateral parasphenoid, the anterior face of the prootic shelf, and the anterodorsal margin of the hyomandibular. Fibers

also arise from the tendinous sheath on the dorso-medial face of the muscle. The more medial fibers in this region are not completely distinct from the lateral fibers of A 1 $\beta$ ' (Figure 117) posteriorly. A 2 $\beta$  arises from the preopercle and hyomandibular, the fibers passing anterodorsally. They tend to pass more medially than do those of A 2 $\alpha$ , but join to form a common tendon before inserting on the inner face of the dentary. Ramus mandibularis V emerges from beneath A 1 $\beta$ ' and passes lateral to the other sections of A 1 $\beta$ . It appears superficially from beneath the anterior fibers of A 2 $\beta$ . The sections of A 1 are not well separated either from each other or from the overlying A 2. A 1 $\beta$ ' is the dorsalmost section and originates from the anterior face of the prootic shelf. Beneath it, A 1 $\beta'$  (Figure 117) arises from the dorsolateral metapterygoid and anterior hyomandibular. It is poorly separated from A 1 $\beta$ , which arises from the anterolateral face of the hyomandibular. The latter section partly overlies and intermingles with A 3. Anteriorly, these four sections come together to form a tendinous aponeurosis which divides into a strong dorsal component to the medial face of the maxilla and a weaker ventral one to the medial face of the dentary.

**LEVATOR ARCUS PALATINI** (Figures 115: L.A.P.).—This is a short, conical muscle originating from the ventral face of the orbital process of the sphenotic and fanning out to insert on the anterolateral face of the hyomandibular.

**DILATATOR OPERCULI** (Figure 115: D.O.).—The fibers form a long, thin, bipinnate muscle which arises from the dilatator fossa (mainly in the sphenotic) and inserts on the dorsal process of the opercle.

**LEVATOR OPERCULI** (Figure 115: L.O.).—The muscle originates from the ventrolateral posttemporal and inserts on the posterodorsal face of the opercle.

**ADDUCTOR ARCUS PALATINI**.—The muscle is short and thick. It originates from the ventrolateral face of the parasphenoid and inserts mainly on the dorsomedial face of the metapterygoid. The anterior fibers pass outward to their insertion at an increasingly anterolateral angle, and grade imperceptibly into the retractor arcus palatini. The muscle lies wholly in front of the orbit.

**RETRACTOR ARCUS PALATINI** (Figure 117: R.A.P.).—The muscle is fairly well developed, and, as stated, not completely separate from the adductor arcus

palatini. The fibers arise from the anterodorsal parasphenoid and pass anteroventrally to insert on the posterodorsal face of the metapterygoid.

**ADDUCTOR OPERCULI** (Figures 119, 121: AD.OP.).—Fibers arise from the lateral face of the basioccipital and anteroventral exoccipital, and insert on the dorsomedial face of the opercle by a long tendon.

**ADDUCTOR HYOMANDIBULAE** (Figures 119, 121: A.H.).—The muscle lies just above the adductor operculi, and passes more anteriorly to insert on the dorsomedial face of the hyomandibular. Its origin is poorly separated from that of the adductor operculi, the muscle being derived from the more posterodorsal fibers.

#### MUSCLES OF THE HYOID REGION

**INTERMANDIBULARIS**.—This is a small transverse muscle spanning the symphysis between the dentaries, and being closely associated with the anterodorsal fibers of the protractor hyoidei.

**PROTRACTOR HYOIDEI** (Figures 115, 117, 118: PR.HY.).—The muscle originates from the medial face of the dentary near the symphysis and inserts on the lateral faces of the anterohyal, posterohyal, and the bases of the dorsal four branchiostegal rays. The two halves remain separate for most of their length, being joined by a midventral raphe just below the jaws. A myocomma arises in the region of the raphe, and passes posterodorsally. Some of the more dorsal fibers attach to the interopercle.

**HYOHYOIDEUS INFERIORIS** (Figures 115, 118: HY.IN.).—The muscle is rather small, and originates from the posteroventral anterohyal and anteroventral posterohyal beneath the second branchiostegal ray. The fibers pass down to the midline, where they meet their antimeres in a midventral raphe.

**HYOHYOIDEI ABDUCTORES** (Figures 115, 118: H.AB.).—These muscles insert on the medial faces of the first four branchiostegal rays. The section to the first ray arises from the ventromedial face of the ventrohyal, that to the second ray originates from the base of the first ray, while the slips to the other rays arise from the base of the second ray and the surrounding anterohyal.

**HYOHYOIDEI ADDUCTORES** (Figures 115, 117, 118: H.AD.).—The muscle lies mainly in the lateral tissues of the opercular cavity. It attaches dorsally to the sphenotic and prootic shelf. Ventrally, fibers attach to the fascia covering the sternohyoideus

and the ventral surfaces of the branchial arches. The more dorsal branchiostegal rays are partially embedded in the fibers. A small slip of fibers arises from the anteroventral region of the cleithrum and courses dorsally to join the main mass in the vicinity of the opercular valve.

**STERNOHYOIDEUS** (Figures 115, 118, 119: *STH.*).—The muscle consists of two sections. The main lateral portion arises from the myocomma with the obliquus inferioris lateral to the abductors of the pectoral fin. It inserts on the posteroventral face of the ventrohyal. A small, medial section of the muscle originates from the anteroventral tip of the cleithrum and inserts on the lateral face of the small urohyal. It lies medial to the main body of the muscle.

**STERNOBRANCHIALIS** (Figures 118, 119, 120: *STB.*).—The fibers originate from the anteroventral region of the cleithrum and pass dorsally to separate into two tendons. The anterior of these inserts on hypobranchials 2 and 3 and ceratobranchial 3, while the posterior tendon inserts on ceratobranchials 3 and 4.

#### VENTRAL BRANCHIAL MUSCLES

**PHARYNGOCLAVICULARIS EXTERNUS** (Figures 119, 120: *PHC.E.*).—This muscle is very well developed. It originates from the anterior and ventromedial surfaces of the cleithrum, dorsolateral to the origin of the medial section of the sternohyoideus. The fibers pass upward to insert on the ventral surface of ceratobranchial 5.

**PHARYNGOCLAVICULARIS INTERNUS** (Figures 119, 120: *PHC.I.*).—The fibers arise from the anterodorsomedial face of the cleithrum and insert on the ventral face of ceratobranchial 5.

**OBLIQUUS VENTRALIS III** (Figures 119, 120: *OBL.V.*).—The muscle is small, and connects the ventral face of ceratobranchial 3 to the tip of the ventral process of hypobranchial 3. The process is embedded in a flat ligament which passes anteriorly to attach to the posterior face of the urohyal.

**TRANSVERSI VENTRALES IV-V** (Figure 120: *TR.V.*).—These two muscles connect the anteroventromedial faces of the ceratobranchials of the fourth and fifth arches across the ventral midline. The posterior muscle is well developed.

**RECTI VENTRALES I, II, IV** (Figures 119, 120: *RECT.V.*).—The two anterior recti arise from the

ventral surfaces of the ceratobranchial-hypobranchial regions of the first and second arches respectively. Rectus I attaches to the posterodorsal face of the dorsohyal, while rectus II passes anteromedially, fusing partly with its antimeric and partly with the ligament from the ventral process of hypobranchial 3. Rectus IV is well developed, and connects the ventral face of ceratobranchial 4 to the arch-shaped ligament between the third hypobranchials. Some fibers intermingle with those of the other side in the midline.

**RECTUS COMMUNIS** (Figures 119, 120: *R.COMM.*).—The muscle arises from the posterior face of the urohyal and inserts on the ventrolateral face of ceratobranchial 5.

#### DORSAL BRANCHIAL MUSCLES

**LEVATORES EXTERNI I-IV** (Figure 119: *L.EXT.*).—The series is well developed. All the muscles originate from the ventral surface of the prootic shelf, and insert on the dorsal faces of the respective epibranchials. Levators III and IV are completely fused dorsally, the bulk of the fibers affecting the tendon serving the fourth epibranchial. The tendon to epibranchial 3 arises from the anteromedial surface of this bundle.

**LEVATORES INTERNI II, III** (Figures 115, 119, 121: *L.INT.*).—These are both enormously developed, bipinnate muscles, which insert on infrapharyngobranchials 2-4. Levator II originates from the posterolateral prootic, ventral pterotic, lateral exoccipital, and ventrolateral epiotic, and inserts on the posterior face of infrapharyngobranchial 2. Levator III overlies the posteroventral surface of the anterior muscle, and includes the pterotic, epiotic, and exoccipital in its sites of origin. Anteriorly, the muscle divides into two tendons, the anterior of which inserts on infrapharyngobranchial 3, the posterior one attaching to the medial tip of epibranchial 4 and the tough connective tissue which appears to contain the cartilagenous remains of infrapharyngobranchial 4. The posterolateral origin of this muscle is visible in superficial lateral view.

**OBLIQUUS DORSALIS III** (Figures 119, 121: *OBL.D.*).—The muscle connects the dorsal face of epibranchial 3 to the dorsal face of infrapharyngobranchial 3, passing between the two tendons of levator internus III.

**OBLIQUUS POSTERIOR** (Figure 121: *OBL.P.*).—This

is a well-developed muscle, passing from the dorso-medial face of ceratobranchial 5 to the posterior face of epibranchial 4.

**TRANSVERSI DORSALES II, IV** (Figure 121: TR.D.).—Both muscles originate from middorsal raphe with their antimeres. Transversus II passes out laterally behind infrapharyngobranchial 2 to insert on the dorsal face of epibranchial 2. The posterior muscle inserts on the posterodorsal face of epibranchial 4.

**RETRACTOR DORSALIS** (Figures 119, 121: D.RETR.).—Origin is from the lateral face of the basioccipital, the muscle passing anteriorly beneath Baudelot's ligament and the medial process of the supracleithrum to insert in the connective tissue surrounding the cartilagenous remains of infrapharyngobranchial 4 near the medial tip of epibranchial 4.

**ADDUCTOR IV.**—This is a poorly developed muscle, crossing the angle between the medial faces of the fourth epibranchial and ceratobranchial. It is embedded in thick connective tissue.

**SPHINCTER OESOPHAGI** (Figures 119, 120, 121: s.o.).—The muscle surrounds the esophagus, attaching to the posterior faces of ceratobranchial 5 and epibranchial 4. A pair of ligaments arise from the ventral surface and pass posterolaterally to attach to the medial faces of the cleithra.

#### MUSCLES OF THE PECTORAL REGION

**ADDUCTOR SUPERFICIALIS** (Figures 115, 118: ABD.S.).—Origin is from the lateral and posterior faces of the cleithrum and the fascia overlying the abductor profundus. The fibers insert on the anterolateral bases of the principal fin rays.

**ADDUCTOR PROFUNDUS** (Figures 115, 118, 119: ABD.P.).—A well-developed muscle, arising mainly from the broad, lateral surface of the coracoid. The tendons insert on the posteroventral bases of the principal fin rays. There is a section to the lateral base of the vestigial ray that arises from the medial surface of the muscle mass serving the dorsalmost ray.

**ARRECTOR VENTRALIS** (Figure 115: ARR.V.).—The muscle originates from the anterolateral face of the cleithrum and inserts on the anterolateral margin of the medial half of the vestigial fin ray.

**ADDUCTOR SUPERFICIALIS** (Figure 123: ADD.S.).—Origin is from the posterodorsomedial face of the

cleithrum. The muscle inserts on the anteromedial faces of the principal rays distal to their bases. The more ventral fibers pass more dorsolaterally to serve the more dorsal rays.

**ADDUCTOR PROFUNDUS** (Figures 115, 118, 123: ADD.P.).—A well-developed muscle originating from the medial coracoid and posteromedial cleithrum. It inserts on the posteroventromedial flanges of the principal fin rays.

**ARRECTOR DORSALIS** (Figure 123: ARR.D.).—The muscle originates from the medial face of the cleithrum, lying lateral to the adductor profundus and medial to the adductor superficialis. It inserts on the ventromedial base of the vestigial fin ray.

**CORACORADIALIS** (Figure 123: COR.R.).—A small muscle, consisting of only a few fibers from the posterodorsal face of the coracoid to the posteroventral face of the fourth radial.

#### MUSCLES OF THE DORSAL FIN

**ERECTORES DORSALES** (Figure 122: EREC.).—These are greatly expanded muscles, whose origin covers the centra and neural spines of the fourth to twelfth vertebrae as well as the pterygiophores of the dorsal fin. Each erector is partially overlain posterolaterally by the depressor muscle of the same fin ray. The muscles decrease in size posteriorly, and insert tendinously on the anterolateral bases of the fin rays.

**DEPRESSORES DORSALES** (Figure 122: DEPR.).—These muscles share their sites of origin with the erectors, but are somewhat more laterally situated. They insert tendinously on the posterolateral bases of the fin rays, and decrease in size posteriorly.

**SUPRACARINALIS ANTERIOR** (Figures 115, 122: s.ANT.).—Origin is from the posterodorsal face of the supraoccipital and the lateral face of its spine. The fibers pass posteriorly to insert on the tips of the neural spines of the third and fourth vertebrae and the anterior face of the "supraneural" (= basal pterygiophore of the now absent spiny dorsal fin).

**SUPRACARINALIS POSTERIOR** (Figures 122, 124b: s.POST.).—The muscle arises from the posterodorsal face of the neural spine of the thirteenth vertebra and courses posteriorly, attaching to the neural spines of the succeeding vertebrae, to end on the neural spine of the penultimate vertebra.

## MUSCLES OF THE ANAL FIN

**ERECTORES ANALES** (Figure 122: EREC.).—The first three muscles arise from the anterior face of the laterally displaced pterygiophores, the other muscles originating from the posterior and lateral faces of the pterygiophores. Insertion is tendinous on the anterolateral bases of the fin rays, the muscles decreasing in size posteriorly.

**DEPRESSORES ANALES** (Figure 122: DEPR.).—The muscles lie immediately behind the erectors of the respective fin rays, and have the same origins. They insert on the posterolateral bases of the rays, decreasing in size caudally.

**INFRACARINALIS POSTERIOR** (Figures 122, 124b: INF.P.).—The muscle arises from the posteroventral tip of the last anal pterygiophore. It passes posteriorly to attach to the anteroventral margin of the haemal spine of the penultimate vertebra.

## MUSCLES OF THE CAUDAL FIN

**INTERRADIALIS** (Figure 124a: INT.).—The muscle courses dorsoventrally across the fin rays, a slip of the more posterior fibers attaching to the ventrolateral (rays D 1–5) or dorsolateral (rays V 1–6) faces of the rays.

**HYPCHORDAL LONGITUDINALIS** (Figure 124a: H.L.).—The muscle originates from the lateral face of the ventral part of the hypural plate. It inserts beneath the interradias on the ventrolateral bases of rays D 3–5.

**FLEXOR DORSALIS** (Figure 124b: F.D.).—The fibers arise from the dorsolateral faces of the centra and neural spines of the last three vertebrae, and insert on the bases of rays D 1–4. It is poorly separated from the epaxialis laterally and the flexor dorsalis superior dorsally.

**FLEXOR DORSALIS SUPERIOR** (Figure 124: F.D.S.).—Origin is from the dorsolateral surface of the penultimate vertebra, the muscle inserting on the anterolateral base of ray D 5.

**FLEXOR VENTRALIS** (Figure 124b: F.V.).—The muscle originates from the centrum and haemal spine of the penultimate vertebra and the anteroventral border of the hypural plate. It inserts on the anterolateral bases of rays V 1–5.

**FLEXOR VENTRALIS INFERIOR** (Figure 124: F.V.I.).—The fibers arise from the lateral tip of the haemal spine of the penultimate vertebra and insert on the anterolateral base of ray V 6.

**TRANSVERSUS CAUDALIS** (Figure 124b: TR.C.).—The muscle is well developed, and originates from the entire dorsolateral surface of the hypural plate, reaching as far anteriorly as the ural centrum. It inserts by three distinct tendons (the ventral one of which serves two rays) on the dorsolateral bases of rays V 2–5.

## LATERAL BODY MUSCLES

**EPAXIALIS** (Figures 115, 122, 124a: EPAX.).—The two portions of the muscle are well separated anteriorly, but grade into each other posteriorly. The dorsal moiety attaches anteriorly to the posterior faces of the supraoccipital and exoccipital. The ventral section is larger, and arises anteriorly from the lateral faces of the anterior vertebrae. It increases in size posteriorly, where it overlaps both centra and parts of the haemal arches. The muscle inserts on the lateral bases of the dorsal caudal fin rays, and is poorly separated from the flexor dorsalis medially.

**OBLIQUUS SUPERIORIS** (Figures 122, 124a: OBL.S.).—The muscle is poorly developed, particularly anteriorly, where it arises from the ventrolateral face of the epaxialis. Posteriorly, the lateral septum fades out, and it is not clear how much the obliquus superioris contributes to the musculature inserting on the ventral caudal fin rays.

**OBLIQUUS INFERIORIS** (Figures 115, 118, 122: OBL.I.).—The anteroventral section of the muscle passes from the posterolateral face of the coracoid to the anteroventral face of the postcleithrum. It is partially overlain by the sternohyoideus anterolaterally. The anterodorsal section is much reduced. It originates from the ventrolateral ridge of the epiotic (where it shows faint traces of segmentation) and inserts on the dorsal face of the postcleithra. Posteriorly it grades into an aponeurotic fascia overlying the greatly expanded lobes of the liver, which cover the obliquus superioris and epaxialis in this region. Posteroventrally, the muscle is small, and soon grades into an aponeurotic sheet which overlies and intermingles with the obliquus superioris.

*Capropygia unistriata* Kaup

FIGURE 125

A 2 is poorly subdivided, with no clear-cut sep-

aration of parts. It is, however, bipinnate, and could easily have arisen or given rise to the condition in *K. aculeatus*. There is no intermingling of fibers with the underlying A 1 $\beta$ . A 1 $\beta$ " is better separated from the more ventral portions of A 1, and originates exclusively from the prootic shelf. The ventral fibers do not intermingle with those of A 3, although they do share the archlike tendon between the maxilla and dentary. The levator and dilatator operculi are smaller. The retractor arcus palatini is continuous with the adductor arcus palatini anteriorly and ventrally, and merely consists of a more anterior-posterior orientation of these muscle fibers. There is no adductor hyomandibulae.

The sternobranchialis has completely separated into two sections, and its origin just overlaps the ventrolateral face of the cleithrum. Levator externus III is not fused to levator IV, but is closely applied to it. Adductor IV is well developed. The adductor superficialis has some fibers originating from the ventral face of the medial process of the cleithrum. The adductor profundus is better developed, and is partly visible posteroventrally behind the coracoid. The supracarinales anterior are fused in the midline, although a septum is present.

A single, small inclinator dorsalis passes to the ventrolateral face of the first pterygiophore.

A small inclinator analis arises from the fascia over the obliquus inferioris behind the posteroventral surface of the postcleithrum and attaches to the ventrolateral face of the first anal pterygiophore. Behind this, a thin tendon attaches to the anteroventral base of the first fin ray, and passes posterodorsally. The fibers sweep dorsally in a large semicircle to fade into the fascia beneath the posterior half of the dorsal fin, overlying the epaxialis. The muscle appears to represent an extreme modification of the inclinator of the first anal fin ray.

The bulk of the body musculature consists of the more ventral moiety of the epaxialis. This is well separated from the more dorsal portion, and originates anteriorly from the vertebral column and the fascia over the erectores and depressores dorsales. Posteriorly it forms a tendinous sheath attaching to the bases of all the caudal fin rays (although part of the fibers in the ventral region may be derived from the obliquus superioris. Attachment to the two outermost fin rays is mainly derived from the dorsal and ventral portions of the body musculature, and is tendinous.

### Myological Descriptions of Representative Ostraciids

The normal body outline of members of this family is illustrated in Figure 6. Fraser-Brunner (1935, 1941b) recognized seven genera of ostraciids, which he divided (1941b) among two subfamilies. Representatives of four of the seven genera were dissected. These fishes are rather similar to the aracanids, except that the carapace extends behind the base of the anal fin, and, in all but one species, the dorsal fin as well. They are slow swimmers, living on or near coral reefs and sea-grass meadows. Their food is comprised mainly of soft-bodied marine invertebrates, although crabs and other harder bodied organisms are also eaten. The dorsal and anal fins are used for locomotion, being supplemented by the caudal fin in emergencies. Steering is achieved by the pectoral and caudal fins.

As stated above, the ostraciids are considered the more specialized (apomorph) sister group of the aracanids.

#### *Ostracion tuberculatus* Linnaeus

FIGURES 116b, 126-134

#### MUSCLES OF THE CHEEK

ADDUCTOR MANDIBULAE (Figures 116b, 126, 127: A 1 $\beta$ , A 2 $\alpha$ , A 2 $\beta$ , A 3).—The section A 2 is well developed, and superficial in position. It consists of a smallish dorsal section, A 2 $\alpha$ , which originates mainly from the region where the ethmoid, parasphenoid, prefrontal, and prootic meet each other. The main mass is formed by A 2 $\beta$ , which arises from the anterior margin of the prootic shelf, the hyomandibular, and the preopercle. The two subdivisions share a tendinous insertion in the Meckelian fossa on the medial face of the dentary. A 1 consists of three poorly separated subdivisions or "heads." A 1 $\beta$ " (Figure 127) is best developed and originates from the

anterior and ventral faces of the prootic shelf and the lateral parasphenoid. A  $\beta'$  (Figure 127) arises primarily from the metapterygoid, with a few fibers from the mesopterygoid. A  $\beta$  originates from the hyomandibular, ventrolateral metapterygoid, and symplectic. These subdivisions join to insert on the medial face of the maxilla. The tendon curves ventrally in the form of an arch to join with that of A  $\beta$ . A  $\beta$  itself is fairly well developed, originating from the quadrate and symplectic and inserting on the medial face of the dentary (ventral to the insertion of A  $\beta$ ).

**LEVATOR ARCUS PALATINI** (Figure 126: L.A.P.).—The muscle originates from the ventral face of the sphenotic and inserts on the posterodorsal face of the hyomandibular.

**DILATATOR OPERCULI** (Figure 126: D.O.).—Origin is from the dilatator fossa behind the orbit. The fossa is bounded variously by the sphenotic, pterotic, prootic, and frontal. Insertion is along the dorsal rim of the opercle behind its articulation with the hyomandibular.

**LEVATOR OPERCULI** (Figure 126: L.O.).—The fibers arise from the anteroventral posttemporal and insert on the posterodorsal rim of the opercle.

**ADDUCTOR ARCUS PALATINI** (Figure 128: A.A.P.).—The muscle covers a fairly small area in front of the orbit, where it is well developed. Origin is from the ventrolateral parasphenoid, stretching from its suture with the vomer to the flange beneath the prootic shelf. Insertion is on the dorsomedial faces of the mesopterygoid, metapterygoid, and anterior hyomandibular.

**RETRACTOR ARCUS PALATINI** (Figure 128: R.A.P.).—Origin is from the lateral parasphenoid above the adductor arcus palatini. Anteriorly, a tendon attaches to the dorsomedial face of the mesopterygoid. The dorsomedial face of the tendon is joined by a small bundle of fibers originating from the lateral face of the vomer.

**ADDUCTOR OPERCULI** (Figure 129: AD.OP.).—The muscle has a fairly extensive horizontal origin from the lateral faces of the parasphenoid and basioccipital. The fibers converge to form a long, thin tendon which inserts on the dorsomedial face of the opercle.

**ADDUCTOR HYOMANDIBULAE** (Figure 129: A.H.).—This is a broad, short muscle originating from the anterodorsomedial face of the cleithrum, as well as Baudelot's ligament and the posttemporal in

that region. It passes anterolaterally to insert on the anterodorsomedial face of the hyomandibular.

#### MUSCLES OF THE HYOID REGION

**INTERMANDIBULARIS**.—This is a small, short muscle which spans the midline just behind the symphysis between the dentaries. It is closely associated with the anterodorsal fibers of the protractor hyoidei.

**PROTRACTOR HYOIDEI** (Figure 126: PR.HY.).—The muscle arises from the posteroventral corner of the anterohyal and the bases of the dorsalmost four branchiostegal rays. The more ventral fibers join their antimeres in the midline, while the more dorsal fibers sweep upward to insert on the posterior margin of the lower jaw. A myocomma is present in the anterior region.

**HYOHYOIDEUS INFERIORIS** (Figure 126: HY.IN.).—This is a small muscle passing across the ventral midline between the posteroventral margins of the anterohyals. It lies lateral to the hyohyoidei abductores, but medial to the branchiostegal rays.

**HYOHYOIDEI ABDUCTORES** (Figure 126: H.AB.).—This is a series of four muscles inserting on the medial faces of the ventral four branchiostegal rays. The ventralmost originates tendinously from the ventrohyal, the others arising from the base of the second ray and the surrounding anterohyal. They lie medial to the hyohyoideus inferioris.

**HYOHYOIDEI ADDUCTORES** (Figure 126: H.AD.).—The muscle consists of a well-developed sheet of fibers in the lateral wall of the opercular cavity, stretching from the fascia overlying the sternohyoideus to the medial faces of the preopercle, subopercle, opercle, and on up to the prootic shelf. The more dorsal branchiostegal rays are attached to the sheet by connective tissue. There is a small bundle of fibers—arising from the anteroventral cleithrum—which passes dorsally to attach to the main mass of the muscle in the region of the opercular flap.

**STERNOHYOIDEUS** (Figures 126, 127: STH.).—The muscle is subdivided into two distinct sections. The larger, lateral portion arises from the posterolateral face of the coracoid and the posterior continuity with the obliquus inferioris (it has effectively incorporated the anterior myomere of the latter muscle). It inserts on the posteroventral face of the ventrohyal. The medial section originates from the

anteroventromedial face of the cleithrum and inserts on the ventromedial face of the ventrohyal. Some of the more medial fibers attach to the small urohyal.

**STERNOBRANCHIALIS** (Figures 129, 130: STB.).—There are two well-separated sections of this muscle. The larger and more ventral of these originates from the fascia overlying the pectoral fin abductors and the anteroventrolateral face of the cleithrum. Insertion is on the ventromedial face of hypobranchial 2. The dorsomedial section arises almost exclusively from the anteroventral face of the cleithrum and inserts on the ventral faces of hypobranchial 3 and ceratobranchial 4.

#### VENTRAL BRANCHIAL MUSCLES

**PHARYNGOCLAVICULARIS EXTERNUS** (Figures 129, 130: PHC.E.).—The muscle originates from the ventromedial face of the cleithrum and passes dorsally to insert on the ventral part of ceratobranchial 5.

**PHARYNGOCLAVICULARIS INTERNUS** (Figures 129, 130: PHC.I.).—The fibers arise from the medial region of the cleithrum and insert on the ventromedial face of ceratobranchial 5.

**OBLIQUUS VENTRALIS III** (Figures 129, 130: OBL.V.).—The muscle connects the anteroventral region of ceratobranchial 3 to the ventral process of hypobranchial 3 and the arch-shaped ligament behind it. Posteriorly, the fibers mingle somewhat with those of rectus IV.

**TRANSVERSI VENTRALES IV, V** (Figure 130: TR.V.).—The anterior muscle passes across the midline between the anteromedial faces of the fourth ceratobranchials. Transversus V is better developed, and connects the fifth ceratobranchials across the ventral midline.

**RECTI VENTRALES, I, II, IV** (Figures 129, 130: RECT.V.).—The first muscle connects the dorsohyal to ceratobranchial 1. Rectus II passes from the anteroventral face of ceratobranchial 2 to a mid-ventral raphe, the anterior portion of which is firmly attached to basibranchial 1. Rectus IV is a small muscle arising from the anteroventral region of ceratobranchial 4 and attaching to the posterior face of the arch-shaped ligament between the ventral processes of the third hypobranchials.

**RECTUS COMMUNIS** (Figures 129, 130: R.COMM.).—The muscle originates from the posterior face of the urohyal. The fibers grade into a tendon at

about the level of the third hypobranchial and insert on the ventrolateral base of ceratobranchial 5.

#### DORSAL BRANCHIAL MUSCLES

**LEVATORES EXTERNI I-IV** (Figure 129: L.EXT.).—The four muscles arise from the ventrolateral face of the anterior part of the prootic shelf. Levator II is overlain anterolaterally by levator I, and by levators III and IV posterolaterally. The muscles insert on the dorsolateral faces of epibranchials 1-4. Levator II is the smallest, and is poorly separated from levator IV dorsally.

**LEVATORES INTERNI II, III** (Figures 129, 131: L.INT.).—Levator II is well developed and originates from the ventral prootic and pterotic and the lateral parasphenoid. It inserts on the posterodorsal surface of infrapharyngobranchial 2. Levator III is smaller and more flattened, and arises just behind levator II. It includes the exoccipital in its sites of origin, and inserts on the posterodorsal face of infrapharyngobranchial 3.

**OBLIQUUS POSTERIOR** (Figure 131: OBL.P.).—A well-developed muscle, which passes from the dorsomedial face of ceratobranchial 5 to the posterior margin of epibranchial 4.

**TRANSVERSI DORSALES I-IV** (Figures 129, 131: TR.D.).—These four muscles connect the dorsal surfaces of the left and right epibranchials of arches 1-4 across the dorsal midline. Transversus I passes between the levatores interni, and also receives a few fibers from infrapharyngobranchial 3. The third and fourth muscles are not well separated.

**RETRACTOR DORSALIS** (Figures 129, 131, 133: D.RETR.).—This is a well-developed muscle originating from the lateral faces of the first few vertebrae and inserting on the medial face of infrapharyngobranchial 3.

**SPHINCTER OESOPHAGI** (Figures 129, 130, 131: S.O.).—The muscle encircles the esophagus attached to the posterior margin of ceratobranchial 5. It lies dorsal to transversus ventralis V and ventral to the retractor dorsalis.

#### MUSCLES OF THE PECTORAL REGION

**ABDUCTOR SUPERFICIALIS** (Figure 126: ABD.S.).—The mass of the muscle originates from the posterolateral face of the anterolateral flange of the



cleithrum. It inserts on the anterolateral bases of the principal fin rays.

**ABDUCTOR PROFUNDUS** (Figures 126, 129: ABD.P.).—Origin is from the ventrolateral regions of the coracoid and cleithrum. The muscle inserts on the ventrolateral bases of the principal fin rays, with a small tendon to the ventrolateral base of the vestigial fin ray.

**ARRECTOR VENTRALIS** (Figures 126: ARR.V.).—This is a well-developed muscle, originating from the posterior face of the anterolateral flange of the cleithrum and inserting on the anterior base of the vestigial fin ray (of which only the medial half is present, the lateral half having apparently fused with it).

**ADDUCTOR SUPERFICIALIS** (Figure 132: ADD.S.).—The fibers arise from the posterodorsomedial face of the cleithrum and insert on the anteromedial faces of the principal rays distal to their bases. The more ventral fibers serve the more dorsal rays, and lie more laterally.

**ADDUCTOR PROFUNDUS** (Figure 132: ADD.P.).—A well-developed muscle, originating over most of the posteromedial faces of the cleithrum and coracoid. It inserts on the ventromedial bases of the principal fin rays.

**ARRECTOR DORSALIS** (Figure 132: ARR.D.).—Origin is from the posteromedial cleithrum, the muscle inserting on the medial base of the vestigial fin ray.

#### MUSCLES OF THE DORSAL FIN

**ERECTORES DORSALES** (Figure 133: EREC.).—Each fin ray has an erector muscle inserting on its anterolateral base. The fibers originate from the lateral faces of the neural spines and centra of the seventh to thirteenth vertebrae and the lateral pterygiophores. They tend to lie somewhat lateral to the depressores dorsales, and decrease in size posteriorly.

**DEPRESSORES DORSALES** (Figure 133: DEPR.).—The origin of these muscles is similar to that of the erectors, but somewhat more medially. They insert on the posterolateral bases of the fin rays.

**SUPRACARINALIS POSTERIOR** (Figures 133, 134a: S.POST.).—The muscle arises from the posterior and lateral faces of the neural spines of the thirteenth and fourteenth vertebrae and ends on the anterodorsal face of the eighteenth vertebra. It passes be-

tween the bifid neural spines of the intervening vertebrae, and is partially attached to their tips.

#### MUSCLES OF THE ANAL FIN

**ERECTORES ANALES** (Figure 133: EREC.).—The first four muscles arise from the anterior faces of the laterally displaced pterygiophores, the rest of the muscles originating from the lateral faces of the succeeding pterygiophores and the ventrolateral vertebral column. They insert on the anterolateral bases of all the fin rays.

**DEPRESSORES DORSALES** (Figure 133: DEPR.).—These muscles originate just behind the erector of each ray, lying somewhat more medially. They insert on the posterolateral bases of the rays.

**INFRACARINALIS POSTERIOR** (Figure 133: INF.P.).—The fibers arise from the posterior and lateral faces of the haemal spine of the fourteenth vertebra and pass posteriorly to attach to the anteroventral surface of the haemal spine of the eighteenth vertebra.

#### MUSCLES OF THE CAUDAL FIN

**INTERRADIALIS** (Figure 134a: INT.).—The muscle spans the caudal fin rays dorsoventrally, a short distance from their bases. Each ray gives rise to a small bundle of fibers joining the main mass posteriorly, and the more medial rays receive a small fiber bundle anterolaterally.

**HYPOCHORDAL LONGITUDINALIS** (Figure 134: H.L.).—The muscle originates on the ventrolateral surface of the hypural plate, and inserts tendinously on the ventrolateral bases of rays D 3–5.

**FLEXOR DORSALIS SUPERIOR** (Figure 134: F.D.S.).—This is a fairly small muscle, originating from the dorsolateral region of the ural centrum and fused hypural-epural region and inserting on the anterodorsal face of ray D 5.

**FLEXOR VENTRALIS INFERIOR** (Figure 134: F.V.I.).—Origin is from the ventrolateral region of the ural centrum and fused hypural-parhypural region, the muscle inserting on the ventrolateral base of ray V 5.

**TRANSVERSUS CAUDALIS** (Figure 134b: TR.C.).—The fibers originate from the dorsolateral surface of the hypural plate and insert tendinously on the dorsolateral faces of rays V 2–4.

## LATERAL BODY MUSCLES

**EPAXIALIS** (Figures 126, 133, 134a: EPAX.).—The muscle arises anteriorly from the posterodorsal region of the skull. It passes posteriorly, and is only attached to the vertebral column behind the dorsal fin. Here the dorsolateral fibers grade into a tendon that joins a similar tendon from the obliquus inferioris. The cruciform tendon thus formed inserts on the anterolateral bases of the uppermost and lowermost rays of the caudal fin. The remaining fibers of the muscle more or less fuse with the obliquus superioris medially, and insert by a continuous tendinous sheath on the anterolateral bases of the dorsal fin rays (D 1–5).

**OBLIQUUS SUPERIORIS** (Figures 133, 134a: OBL.S.).—The section is much reduced. Anteriorly it arises from the lateral faces of the centra above the swim bladder. Posteriorly, in the urostyle region, the fibers appear to fuse dorsally with the epaxialis. It inserts tendinously on the anterolateral bases of the fin rays. In front of the anal fin the muscle is completely separate from the epaxialis dorsally and the obliquus inferioris ventrally.

**OBLIQUUS INFERIORIS** (Figures 126, 133, 134a: OBL.I.).—The muscle consists of a ventral portion only. Anteriorly, it is laterally continuous with the sternohyoideus, the deeper fibers attaching to the posterior face of the coracoid. Posteriorly, it grades into a tendon that forms the ventral component of the cruciform tendon. Most of the fibers from this tendon pass dorsally to the base of the uppermost fin ray. There is little fusion with the obliquus superioris, and the more ventrolateral fibers have some connection to the carapace.

## SWIM BLADDER MUSCLES

**SWIM BLADDER "a"** (Figure 133: s.BL.a.).—The main mass of the muscle passes across the dorsal surface of the anterior half of the swim bladder. The fibers originate from the lateral faces of the centra and overlying fascia of the middle abdominal vertebrae and pass posterolaterally to insert on the dorsolateral face of the swim bladder.

**SWIM BLADDER "b"**.—The muscle lies beneath swim bladder "a," near the midline. The fibers lie in a longitudinal plane, inclining slightly toward the midline anteriorly. They lie very close to the ventral surface of the seventh abdominal

vertebra, and the muscle as a whole is considerably smaller than swim bladder "a."

The wall of the swim bladder beneath these muscles is very thin, and the bladder is firmly attached to the ventral processes of the first six vertebrae (as described by Tyler, 1963b:159).

*Lactoria cornuta* (Linnaeus)

## FIGURE 135

Certain proportional differences are evident. The shorter snout and more down-tilted mouth are reflected in the shape of A 2 and the dilatator operculi. The sections of A 2 are poorly separated, as are those of A 1 $\beta$ . This is even more apparent in the 50 mm specimen, where both A 1 and A 2 appear as single, undivided muscles. The levator arcus palatini is well developed, and its fibers are not entirely separate from those of the dilatator operculi posteriorly.

There is a slip of the hyohyoidei abductores to the fifth branchiostegal ray. The interradiialis is very well developed, and the hypochordalis longitudinalis inserts only on the base of D 5. The transversus caudalis has a more restricted origin from the hypural plate dorsally, but a more extensive one anteroventrally. Both the flexor dorsalis superior and the flexor ventralis inferior are better developed, and have a more extensive origin, which includes the neural and haemal spines of the penultimate vertebrae respectively.

Both the muscles to the swim bladder are better developed, swim bladder "a" being more firmly attached to the lateral surface of the vertebral column medially.

*Tetrosomus concatenatus* (Bloch)

## FIGURE 136

The subdivision of A 2 is not at all clear, and A 1 $\beta'$  is hardly distinguishable from A 1 $\beta''$ . The levator arcus palatini is fairly small, and there is no dorsal bundle of fibers to the dorsomedial face of the tendon of the retrator arcus palatini. The subdivisions of the sternobranchialis are not as clear as in either of the previous species. Levator internus II is extremely well developed, with a broad insertion on infrapharyngobranchial 2. The obliquus posterior is somewhat reduced. The hy-

pochordal longitudinalis inserts by a broad, undivided tendon on the bases of rays D 3–5, while the transversus caudalis inserts on rays V 3–5.

#### *Acanthostracion quadricornis* (Linnaeus)

FIGURE 137

The sections of A 2 are well separated, and there are two fiber directions in A 2 $\alpha$ . A 1 $\beta$  is well separated from the more ventral fibers, but the other two portions are scarcely distinct. The anterior bundle of fibers of the retractor arcus palatini is well developed. The dilatator operculi has an entirely tendinous insertion on the tip of the dorsal process of the opercle, and the levator arcus palatini is well developed.

The dorsolateral half of the protractor hyoidei passes lateral to the interopercle to insert on the dentary.

The interradialis partly overlies the tendons of the hypochordal longitudinalis, and the transversus caudalis inserts on rays V 3–5. The flexor dorsalis superior and the flexor ventralis inferior are better developed than in *O. tuberculatus*.

The epaxialis and the obliquus superioris insert

on the middle eight caudal fin rays (D 1–4 and V 1–4), there being no tendons to D 5 or V 5.

The swim bladder musculature differs from *O. tuberculatus*. The lateral and more posterior fibers pass dorsally and medially from their insertion on the anterodorsal surface of the swim bladder to their origin on the dorsolateral face of the vertebral column. Anteriorly, the fibers tend to curve ventrally and then posteriorly from their origin on the vertebrae, and lie medial to the outer, more posterior fibers. This leaves a gap between the ventromedial surfaces of the transverse posterior fibers and the dorsolateral surface of the anterior and more longitudinal fibers, giving rise to the "hollow ball of muscles" (Tyler, 1963b:159).

#### Summary of Ostraciidae

The main variation in this family is found in the jaw and caudal fin musculatures. In the former, the differences involve mainly the degree of subdivision of the adductor mandibulae, while in the latter most variation is seen in the sites and number of rays involved in the insertion of the hypochordal longitudinalis and transversus caudalis. Apart from this, this family is conservative in its myology.

#### Myological Description of the Representative Triodontid

The outline of *Triodon*, the monotypic representative of this family, is given in Figure 7. The species inhabits the deeper waters (150–300 meters) of the continental shelves of the Indo-Pacific. Almost nothing is known of the life history and habits of this rare fish. Of the four specimens dissected for this study, only one had anything in its gut. This specimen (270 mm SL) contained the remains of a number of echinoids (?Clypeasteroidea), with occasional carapaces of shrimplike crustaceans. The lunate caudal fin, slender peduncle, and poorly developed dorsal and anal fins suggest that *Triodon* is a fairly fast swimmer, but there is no direct evidence. The pelvic girdle is represented by a long, shaftlike bone, very similar to that of the balistoids. The jaws are massive and beak-like, and form a powerful crushing apparatus, as they do in all the remaining families except the Canthigasteridae (although even here the basic plan remains).

*Triodon* is usually considered to be the pleisomorphic member of the gymnodonts (e.g., Tyler, 1962c), and to form a morphological intermediate between them and the triacanthoids + balistoids + ostracioids.

#### *Triodon macropterus* Lesson

FIGURES 138, 139a, 140–145

#### MUSCLES OF THE CHEEK

ADDUCTOR MANDIBULAE (Figures 138, 139, 140: A 1, A 2 $\alpha$ , A 2 $\beta$ , A 3).—A 1 is a single, undivided muscle which originates beneath the orbit as a flat, aponeurotic sheath attached primarily to the anterodorsal face of the hyomandibular. It inserts on the posteromedial face of the ventral half of the maxilla. A 2 is separated into two parts by the passage of ramus mandibularis V. A 2 $\alpha$  originates exclusively from the anterodorsolateral face of the

hyomandibular—a few fibers may attach to the ventral face of the aponeurosis of A 1 posteriorly. The extreme posterior fibers are covered laterally by the dilatator operculi. A 2 $\beta$ , which lies beneath A 2 $\alpha$ , originates almost entirely from the dorsal and lateral faces of the preopercle. The posterodorsal fibers overlie the posteroventral region of A 2 $\alpha$ . The two subdivisions insert together on the medial face of the dentary above the Meckelian fossa. A 3 is present as a thin sheet of fibers originating from the lateral metapterygoid and symplectic. It inserts medial to A 2 on the dentary by a somewhat sheetlike aponeurosis. It is partially confluent with A 2 $\beta$  posteriorly. A  $\omega$  is well developed, and stretches along the medial surface of the quadrate and anterior metapterygoid. It inserts by a flat aponeurosis on the dentary, lying medial to the insertion of A 3.

**LEVATOR ARCUS PALATINI** (Figures 138, 140: L.A.P.)—From a straplike origin on the ventral sphenotic at the rear of the orbit, the muscle passes downward to insert on the posterodorsolateral face of the hyomandibular. This point lies medial to the dorsolateral flange of that bone, which has developed in association with the origin of A 2 $\alpha$ . The fibers of the muscle fan out before their insertion, this being particularly marked anteriorly.

**DILATATOR OPERCULI** (Figure 138: D.O.)—Origin is from the ventrolateral sphenotic and adjoining pterotic. The muscle narrows to a tendon which inserts on the enlarged anterodorsal process of the opercle.

**LEVATOR OPERCULI** (Figure 138: L.O.)—This is a broad, well-developed muscle, originating in the groove between the pterotic and the large supraclithrum. It inserts broadly on the dorsomedial face of the opercle. A small superficial aponeurosis is present on the midlateral face of the muscle.

**ADDUCTOR ARCUS PALATINI** (Figure 140: A.A.P.)—The muscle is confined to the floor and rear of the orbit. Origin is from the lateral surface of the parasphenoid. Anteriorly it inserts on the dorsomedial face of the mesopterygoid. There is a gap where the fibers end in the tough connective tissue lining the buccal cavity. Posteriorly, the fibers insert on the posterodorsal faces of the metapterygoid and hyomandibular.

**ADDUCTOR OPERCULI** (Figure 142: AD.OP.)—The muscle originates from the prootic beneath the

hyomandibular fossa ventral to, but dorsally continuous with, the origin of the adductor hyomandibulae. The fibers pass out laterally to insert on the dorsomedial face of the opercle, just posterior to its articulation with the hyomandibular.

**ADDUCTOR HYOMANDIBULAE** (Figure 142: A.H.)—The muscle originates from the ventrolateral prootic just above the adductor operculi, and inserts as a more or less flattened sheet on the posterodorsomedial face of the hyomandibular.

#### MUSCLES OF THE HYOID REGION

**VALVULUS**.—The muscle is present as a thin, flattened sheet of fibers, arising from the dorsolateral face of the protractor hyoidei at about the middle of its length and grading into the tissues of the buccal valve anterodorsally.

**PROTRACTOR HYOIDEI** (Figure 138: PR.HY.)—The fibers arise from the posteroventromedial dentary and insert on the posteroventral anterohyal and the adjoining posterohyal. It completely covers the first two branchiostegal rays, and is a long, cylindrical muscle.

**HYOHOIDEUS INFERIORIS**.—The fibers of this muscle are partially fused with those of the protractor hyoidei. It arises from the ventral face of the anterohyal, sharing, to some degree, aponeuroses with the medial region of the protractor hyoidei. The fibers pass anteromedially and fuse with their antimeres. The muscle lies lateral to the origin of the infracarinalis anterior, and there is some intermingling of fibers with those of the protractor hyoidei.

**HYOHOIDEI ABDUCTORES** (Figure 138: H.AB.)—The muscle is made up of three slips. That to the first ray originates from the medial face of the ventrohyal and inserts broadly over the ventromedial face of the ray. The slip to the second ray arises from the expanded dorsolateral surface of the first ray, while that to the third ray originates from the bases of the first and second rays.

**HYOHOIDEI ABDUCTORES** (Figure 138: H.AD.)—This is a well-developed sheet of muscle fibers. It is firmly attached to the dorsomedial face of opercle dorsally, and fades out in the wall of the opercular chamber in the region of the dorsohyal anteroventrally.

**STERNOHYOIDEUS**.—The muscle is small, its origin being confined to the anterodorsal tip of the ventral

part of the cleithrum, including a small fossa in that bone. Anteriorly, the fibers sweep up to insert on the ventral face of the ventrohyal.

#### VENTRAL BRANCHIAL MUSCLES

**PHARYNGOCLAVICULARIS EXTERNUS** (Figure 141: PHC.E.).—This is a straplike muscle originating from the lateral face of the cleithrum and inserting on the anteroventral face of ceratobranchial 5. The fibers pass posterodorsolaterally from their origin.

**PHARYNGOCLAVICULARIS INTERNUS** (Figures 141, 142: PHC.I.).—Origin is from the anterodorsomedial face of the cleithrum, the fibers passing anteriorly to insert on the posterior face of ceratobranchial 5. It is a flattened muscle.

**OBLIQUI VENTRALES II, III** (Figure 141: OBL.V.).—The anterior muscle connects the ventral faces of the ceratobranchial and hypobranchial of the second arch. Obliquus III joins ceratobranchial 3 to the ventral process of hypobranchial 3 and the arch-shaped ligament.

**TRANSVERSI VENTRALES IV, V** (Figure 141: TR.V.).—The anterior muscle connects the anteromedial faces of the fourth ceratobranchials across the ventral midline. Transversus V is well developed, and joins the anteromedial faces of the fifth ceratobranchials.

**RECTI VENTRALES I, IV** (Figure 141: RECT.V.).—Rectus I is a fairly long, straplike muscle which connects the dorsal face of the dorsohyal and the ventrolateral face of the first ceratobranchial and hypobranchial. Rectus IV arises from the anteroventral face of ceratobranchial 4 and passes anteromedially to attach to the posterior surface of the arch-shaped ligament between the ventral processes of the third hypobranchials.

**RECTUS COMMUNIS** (Figure 141: R.COMM.).—The muscle originates anteriorly from the posterior face of the urohyal. The fibers pass posteriorly, grading into an aponeurosis at about the level of the third basibranchial which inserts on the ventrolateral face of ceratobranchial 5.

#### DORSAL BRANCHIAL MUSCLES

**LEVATORES EXTERNI I-IV** (Figure 142: L.EXT.).—The four muscles originate from the prootic just anteroventral to the hyomandibular fossa. They

insert on the dorsal faces of epibranchials 1-4. The first two muscles are not very well developed, the fourth levator being the largest.

**LEVATORES INTERNI II, III** (Figure 142: L.INT.).—The muscles originate from the prootic beneath the hyomandibular fossa, levator II having a more medial origin than levator III. The former inserts partially on the medial face of infrapharyngobranchial 2 but mainly on the anteromedial face of infrapharyngobranchial 3. Levator III inserts on the dorsal face of infrapharyngobranchial 3.

**OBLIQUUS DORSALIS III** (Figure 142: OBL.D.).—Two heads of this muscle arise from the anterolateral face of epibranchial 3. The fibers coalesce and pass medially to attach to the posterodorsal face of infrapharyngobranchial 3.

**OBLIQUUS POSTERIOR** (Figure 142: OBL.P.).—Fibers pass from the dorsomedial face of ceratobranchial 5 to the posterior face of epibranchial 4.

**TRANSVERSI DORSALES II, III** (Figure 142: TR.D.).—The anterior muscle is well developed and partially subdivided. The dorsal layer arises from infrapharyngobranchial 2 and the surrounding connective tissue. The fibers pass posteriorly and then curve toward the midline just behind the basal process of the parasphenoid, and join their antimeres. Beneath this, the ventral layer passes outward from the midline to attach to the anterolateral face of epibranchial 4, the two layers separating completely. Transversus III arises from the dorsal midline and passes laterally to insert on the dorsal face of the medial process of epibranchial 3.

**RETRACTOR DORSALIS** (Figure 142: D.RETR.).—The muscle originates from the lateral face of the first vertebra and passes anteriorly to insert on the ventromedial faces of infrapharyngobranchials 3 and 4.

**ADDUCTORES IV, V** (Figure 142: AD.).—Adductor IV is well developed, and connects the medial faces of epibranchial 4 and ceratobranchial 4. Adductor V is less well developed, and passes from the anteroventral tip of ceratobranchial 5 to the posterolateral face of epibranchial 4.

**SPHINCTER OESOPHAGI** (Figures 141, 142: s.o.).—The anteroventral fibers of this muscle attach to the ventromedial face of ceratobranchial 5. There are two fairly distinct layers dorsally. The ventral one arises from infrapharyngobranchial 2, the fibers passing posteriorly and then medially before fading out in the connective tissue of the esopha-

gus. This is covered posterodorsally by the main mass of the muscle, which does not extend anteriorly beyond the posteromedial face of epibranchial 4.

#### MUSCLES OF THE PECTORAL REGION

**ABDUCTOR SUPERFICIALIS** (Figure 138: ABD.S.).—The muscle arises from the posteroventral surface of the elongated cleithrum and inserts on the anterolateral bases of the principal fin rays.

**ABDUCTOR PROFUNDUS** (Figure 138: ABD.P.).—Origin is from the lateral face of the cleithrum. The fibers insert on the posterolateral bases of the principal rays and on that of the lateral half of the vestigial fin ray.

**ARRECTOR VENTRALIS** (Figure 138: ARR.V.).—The muscle lies above the abductor superficialis and originates from the lateral face of the cleithrum beneath the flange. It inserts on the anterior face of the medial half of the vestigial fin ray. There may be a few fibers attaching to the lateral half of the ray posteriorly.

**ADDUCTOR SUPERFICIALIS** (Figure 143: ADD.S.).—The fibers originate from the anteromedial face of the cleithrum and insert on the dorsomedial faces of the principal rays distal to their bases. The more ventrolateral fibers serve the more dorsal rays.

**ADDUCTOR PROFUNDUS** (Figure 143: ADD.P.).—The muscle is well developed, and originates from the medial face of the cleithrum and coracoid. It inserts on the ventromedial bases of the principal fin rays, the tendons to the ventral two rays being covered medially by the main mass of the muscle.

**ARRECTOR DORSALIS** (Figure 143: ARR.D.).—This is a fairly small muscle, originating from the medial face of the cleithrum and inserting on the base of the medial half of the vestigial fin ray. It is partially covered medially by the adductor profundus.

**CORACORADIALIS** (Figure 143: COR.R.).—A somewhat flattened muscle, arising from the dorsal face of the posterior process of the coracoid and inserting on the ventromedial face of the fourth radial.

**PROTRACTOR PECTORALIS** (Figures 138, 142: P.P.).—The muscle originates from the ventrolateral tip of the pterotic and fans out posteroventrally to attach to the dorsal region of the cleithrum.

**LEVATOR PECTORALIS** (Figure 138: TR.).—Origin is from the posterior face of the pterotic. The fibers pass mainly posteriorly, but also somewhat laterally,

to insert on the extreme posterodorsal tip of the cleithrum. The muscle is almost entirely covered by the supracleithrum, and is closely associated with the fibers of the epaxialis dorsally.

#### MUSCLES OF THE DORSAL FIN

**INCLINATOIRES DORSALES** (Figure 144: INC.).—Each fin ray possesses an inclinator which arises in the fascia between the skin and the epaxialis and inserts on the lateral base of the fin ray a little dorsal to the insertions of the erector and depressor muscles. The inclinators decrease in size posteriorly.

**ERECTORES DORSALES** (Figure 144: EREC.).—There are two small, anterior erectors, which originate from the lateral faces of the first two pterygiophores and insert on the bases of the spines of the spiny dorsal fin. Each fin ray has an erector inserting on its anterolateral base. These muscles arise from the lateral faces of the pterygiophores and the neural spines and centra of the eighth to fourteenth vertebrae.

**DEPRESSORES DORSALES** (Figure 144: DEPR.).—The first dorsal spine only has a depressor muscle, which originates from the lateral base of the first pterygiophore and inserts on the posteroventral base of the spine. Each ray in the soft dorsal fin has a depressor inserting on its posterolateral base. Origin is as for the erectors, the depressor to each ray lying just behind the erector.

**SUPRACARINALIS ANTERIOR**.—This is a well-developed muscle arising from the posterior and lateral faces of the supraoccipital. The fibers pass posteriorly to attach to the anterior face of the first pterygiophore. There is some intermingling of fibers from the left and right sides in the midline.

**SUPRACARINALIS POSTERIOR** (Figures 144, 145: s. POST.).—The muscle stretches from the posterior face of the last pterygiophore of the dorsal fin and the neural spine of the fourteenth vertebra to the anterodorsal regions of the neural spines of the third and fourth last vertebrae.

#### MUSCLES OF THE ANAL FIN

**INCLINATOIRES ANALES** (Figure 144: INC.).—An inclinator arises from the fascia over the obliquus inferioris and inserts on the anterolateral base of each fin ray. The medial fibers of the more anterior inclinators attach to the myocommata of the

obliquus superioris, making separation of the muscle difficult. In addition, there is a large, residual inclinator inserting on the anteroventrolateral base of the first pterygiophore. Its ventromedial region is more or less continuous with the ventral fibers of the obliquus inferioris.

**ERECTORES ANALES** (Figure 144: *EREC.*).—These muscles, which insert on the anterolateral bases of the anal fin rays, originate almost entirely from the lateral faces of the pterygiophores, with only a few fibers from the tips of the haemal spines of the associated vertebrae.

**DEPRESSORES ANALES** (Figure 144: *DEPR.*).—Origin is as for the erectors, the depressor of each fin ray inserting on the posterolateral base of the ray.

**INFRACARINALIS ANTERIOR** (Figure 138: *INF.A.*).—This is a well-developed muscle which originates from the anteroventral tip of the cleithrum and inserts in the anteroventral groove in the pelvis. Evidence of its originally paired nature is visible externally, but the deeper fibers of either side have fused in the midline.

**INFRACARINALIS MEDIUS** (Figure 138: *INF.M.*).—A fairly well-developed section, which attaches to the ventrolateral face of the pelvis just anterior to the middle of its length. It grades into the obliquus inferioris at about the level of the postcleithrum, the more posterolateral fibers intermingling somewhat with those of the residual inclinator analis.

**INFRACARINALIS POSTERIOR** (Figures 144, 145: *INF.P.*).—The muscle arises from the posterolateral faces of the last anal pterygiophore and the haemal spine of the fifteenth vertebra and attaches to the anteroventral face of the haemal spines of the third and fourth last vertebrae.

#### MUSCLES OF THE CAUDAL FIN

**INTERRADIALIS** (Figure 145a: *INT.*).—The muscle is developed between the middle twelve caudal fin rays. The fibers span a few rays between their sites of attachment. Those of the dorsal rays pass anteroventrally, while those of the ventral rays pass anterodorsally.

**HYPCHORDAL LONGITUDINALIS** (Figure 145b: *H.L.*).—The muscle is well developed, and originates from the dorsolateral face of the ural centrum, and the lateral faces of the hypurals 1 and 2, parhypural, and hypurapophysis. The muscle inserts on the bases of rays D 3–5.

**FLEXOR DORSALIS** (Figure 145c: *F.D.*).—Origin is restricted to the lateral faces of the epural, the first uroneural and the dorsal crest of the ural centrum. The tendons insert on the bases of rays D 2–6.

**FLEXOR DORSALIS SUPERIOR** (Figures 145b,c: *F.D.S.*).—The muscle originates from the lateral faces of the epural and the neural spines of the second and third last vertebrae. Insertion is on the lateral base of ray D 7.

**FLEXOR VENTRALIS** (Figure 145c: *F.V.*).—The muscle is fairly well developed, and lies beneath the flexor ventralis externus. Origin is from the lateral faces of the centra and haemal spines of the last three vertebrae (including the ural centrum), the parahypural, and the hypurapophysis. The muscle inserts on the bases of rays V 1–7.

**FLEXOR VENTRALIS EXTERNUS** (Figure 145c: *F.V.E.*).—The fibers arise from the lateral faces of the centra and haemal spines of the third and fourth last vertebrae and pass posteriorly to insert on the bases of rays V 1–2.

**FLEXOR VENTRALIS INFERIOR** (Figure 145b,c: *F.V.I.*).—Origin is primarily from the lateral face of the haemal spine of the penultimate vertebra, the muscle inserting on the lateral base of V 7.

**TRANSVERSUS CAUDALIS** (Figure 145c: *TR.C.*).—The muscle is poorly developed. It originates from the lateral face of the fourth hypural and inserts on the dorsal base of ray V I.

#### LATERAL BODY MUSCLES

**EPAXIALIS** (Figures 138, 145a,b: *EPAX.*). — The subdivision of this muscle into dorsal and ventral moieties is incomplete, particularly medially. Anteriorly, the dorsal section attaches to the posterodorsal faces of the frontal, epiotic, pterotic, supraoccipital, and exoccipital. The myocommata become increasingly oblique posteriorly until they are almost horizontal (behind the dorsal fin). Anteromedially, some of the fibers arise from the neural spines and centra of the vertebrae and the pterygiophores. Posteriorly, the fibers grade into a flattened tendon which joins a similar tendon from the obliquus inferioris. Together, these two tendons form an aponeurotic sheath inserting on the bases of all the procurrent and principal caudal fin rays. The ventral section of the epaxialis is virtually continuous with the obliquus superioris. The fibers arise anteriorly from the posterior faces of the

pterotic and exoccipital. In the posterior region the muscle inserts on the lateral bases of rays D 1-6, the more ventral tendons passing medial to the hypochordal longitudinalis.

**OBLIQUUS SUPERIORIS** (Figures 138, 145*a,b*: OBL. s.).—This section arises anteriorly as a small slip of fibers from the posterodorsal tip of the cleithrum. It fans out posteroventrally, attaching to and between the pleural ribs, with the ventral fibers intermingling with the obliquus inferioris. Behind the anal fin, these two sections are relatively well separated. It inserts tendinously on the bases of rays V 1-6. A large bundle, which appears to be mostly continuous with the obliquus superioris, but which also receives fibers from the epaxialis, passes somewhat dorsally in the peduncular region to insert on the lateral crest of the ural centrum. It is slightly overlain posteriorly by the hypochordal longitudinalis. It is somewhat reminiscent of a proximalis muscle, but is not separated from the body muscles.

**OBLIQUUS INFERIORIS** (Figures 138, 144, 145*a*: OBL. i.).—The muscle has a number of subsections. The anteroventral section arises from the posterior and posteroventral faces of the coracoid and clei-

thrum, and attaches to the anteroventral face of the postcleithra. Two vague myocommata are present, and occasional fibers are to be found in the connective tissue between the ventral border of this section and the infracarinalis medius below it. A thin sheet of fibers passes obliquely upward from the posterodorsal faces of the postcleithra and fades into the fascia overlying the obliquus superioris. Posteroventrally, the fibers become more horizontally oriented, and intermingle with those of the obliquus superioris, infracarinalis medius, and residual inclinator analis. Myocommata, which are continuous with those of the obliquus superioris, are present in the fibers behind the postcleithra. From the ventromedial surface of the posterior myocommata of the eleventh myomere, and closely associated with the medial faces of the infracarinalis medius and the rest of the obliquus inferioris, there arises a short bundle of fibers which passes posterodorsomedially to insert tendinously on the anteroventral face of the haemal spine of the fourteenth vertebra. The fibers pass medial to the obliquus superioris but lateral to the erectores and depressores anales.

### Myological Descriptions of Representative Tetraodontids

The members of this family (see Figure 8 for general outline) as recognized here contain ten genera (representatives of six genera were dissected for this study), which were divided into four families by Fraser-Brunner (1943). Although his families may well represent distinct phyletic lines, the status accorded them by Fraser-Brunner has not been followed by other workers (e.g., Tyler, 1970a).

The skin is smooth or covered with small prickles, and the fish are capable of considerable inflation when threatened. Some forms have an almost lunate caudal fin (e.g., *Lagocephalus*), but a rounded caudal is more common. Dorsal and anal fins are usually small, and normally beat synchronously from side to side. The pectoral fins are large, and often used in locomotion. The powerful beaklike jaws are well adapted for crushing the mollusks and brachyurans which form a major part of the puffer-fish diet. They are generally tropical to subtropical in distribution (with a few fluviatile forms), and are commonly found over

sea-grass meadows, sandy bottoms, and the adjoining coral reefs.

The family is considered to be closely related to the Canthigasteridae (which latter has often been included in the Tetraodontidae), and also close to the Diodontidae.

#### *Lagocephalus lunaris* (Bloch and Schneider)

FIGURES 139*b*, 146-155

#### MUSCLES OF THE CHEEK

**ADDUCTOR MANDIBULAE** (Figures 139*b*, 146, 147, 148, 149: A 1*a*, A 1*β*, A 2*a*, A 2*β*, A 3).—A 1 consists of two well-developed sections. A 1*β* has a complicated fiber structure. Fibers originating from the lateral faces of the palatine, vomer, and ethmoid pass ventrolaterally. They form a bipinnate structure with the fibers arising from the anterior face of the prefrontal (which pass ventromedially).



Fibers from the ventrolateral tip of the prefrontal course anteroventrally, the fibers from the ventral face of that bone at first pass ventrally, and then (as they become more posterior in origin) anteroventrally. The ventral surface is largely aponeurotic. Beneath this, another bundle of fibers is present, arising from the lateral parasphenoid. It is well separated from the above-mentioned aponeurosis posteriorly, but grades into it anteriorly. The muscle inserts on the dorsomedial faces of the premaxilla and maxilla. A 1  $\alpha$  is smaller. It originates from an aponeurosis on the floor of the orbit (attaching posteriorly to the hyomandibular medial to A 2  $\alpha$ ) and from a small head on the posterolateral preopercle. Insertion is on the posteromedial face of the maxilla. A 2  $\alpha$  is very well developed and is expanded ventrally to originate from two heads. The anteroventral one arises from the quadrate, symplectic, lateral preopercle, and the anteroventral tip of the hyomandibular. The other head arises from the dorsolateral preopercle and posterolateral hyomandibular. There is a considerable variety of fiber direction. Anteriorly, a tough aponeurosis joins A 2 $\beta$ . The section lies lateral to ramus mandibularis V apart from a small fiber bundle from the dorsolateral quadrate. A 2 $\beta$ , which lies medial to the above nerve, has shifted dorsally in origin, and lies above A 3. It originates from the lateral parasphenoid and prootic. The fibers pass laterally and anteroventrally to grade into a tendinous aponeurosis which joins that of A 2  $\alpha$ . The two sections insert on the medial face of the dentary. A 3 is a distinct muscle arising from the lateral faces of the metapterygoid, quadrate, and ectopterygoid and inserting by a flat, tendinous aponeurosis on the dorsal surface of Meckel's cartilage. A  $\omega$  is a small muscle (Figures 147, 149). It arises from the anteromedial edge of the ectopterygoid and inserts on the ventral rim of the Meckelian fossa. It lies medial to the tendon of A 3.

**LEVATOR ARCUS PALATINI** (Figures 146, 147: L.A.P.).—The fibers of this muscle are continuous dorsolaterally with the dilatator operculi. Origin is from the ventrolateral tip of the frontal, and the fibers fan out to insert in the fossa on the posterodorsal face of the hyomandibular, just anterior to the articulation with the skull.

**DILATATOR OPERCULI** (Figure 146: D.O.).—This muscle is very well developed. The anterior fibers

are almost parallel, but the muscle becomes bipinnate posteriorly. Origin is from the lateral faces of the frontal and sphenotic, and the dorsolateral hyomandibular about its articulation with the skull. Insertion is on the dorsolateral opercle, mainly around the strong, dorsoventrally oriented crista, but also on the anterolateral surface of the bone. It is overlain dorsally by an aponeurotic sheath from the epaxialis. Anterolaterally, a strap of muscle fibers attaches to the posteroventral face of the preopercle.

**LEVATOR OPERCULI** (Figure 146: L.O.).—This is a flattened muscle, which arises from the anteroventrolateral pterotic and the ventrolateral face of the posterior process of the frontal. It inserts on the posterodorsal face of the opercle and its crista. Some of the ventral fibers are closely associated with the dorsal fibers of the protractor pectoralis.

**ADDUCTOR ARCUS PALATINI** (Figures 147, 148: A.A.P.).—The muscle is extensively developed, particularly anteriorly. It originates from the anteroventral prootic, lateral parasphenoid, and posteroventrolateral vomer. The fibers beneath the vomer stretch across the midline. Insertion is on the medial face of the palatine, and the dorsomedial faces of the ectopterygoid, metapterygoid, and hyomandibular.

**ADDUCTOR OPERCULI** (Figures 147, 150: AD.OP.).—The muscle originates from the anteroventral face of the pterotic and passes outward as a thin sheet to insert on the dorsomedial face of the opercle just medial to the insertion of the levator operculi.

#### MUSCLES OF THE HYOID REGION

**VALVULUS** (Figure 149: VA.).—The muscle, which is not fully separated from the protractor hyoidei posteriorly, arises from the anteroventral surface of the interopercle. It passes anteriorly, and then curves upward to face out in the tissues of the mandibular buccal valve.

**PROTRACTOR HYOIDEI** (Figure 146: PR.HY.).—Origin is from the ventral margins of the dentary, angular, anterior preopercle, and interopercle. The fibers insert on the lateral faces of branchiostegal rays 2–4, and the anterohyal between these rays. The more posterior fibers tend to course more toward the midline from their sites of insertion.

**HYOHYOIDEI ABDUCTORES** (Figures 146, 150: H.AB.).—A bundle of fibers passes posteroventrally

from the base of the second ray to the medial faces of the third and fourth rays. The section serving the second ray arises from the posterior face of the lateral process of the enlarged first ray. The muscle to the first ray is massively developed. The ray forms a flat, horizontal plate extending posteriorly from the anterohyal, which lies lateral to it. The muscle has a large number of fiber directions. The ventral surface of the ray gives rise to a large bundle of fibers that pass anteriorly and a little dorsally to originate from the ventral and lateral anterohyal. The more lateral fibers, including those from the lateral process of the ray, tend to sweep anterodorsally, and then medially to the midline, where they join their antimeres. A large volume of fibers inserts on the dorsomedial face of the ray. They originate from the fascia overlying the sternohyoideus, the lateral face of the first basibranchial and the medial anterohyal. Most of these fibers, however, arise from the midline, where they join with their antimeres. Although undoubtedly functioning as two muscles, there is no physical hiatus, and the fibers from the two bundles intermingle to a considerable extent. The posterodorsomedial edge of the ray gives rise to a small bridge of fibers across the midline, which lies beneath the ventral branchial musculature at about the level of the third basibranchial.

**HYOYOIDEI ADDUCTORES** (Figures 146, 147, 150: H.AD.).—The muscle is somewhat subdivided. The main mass passes dorsoventrally in the lateral wall of the opercular cavity, with a dorsal bundle attaching to the dorsomedial face of the hyomandibular. Ventrally, the fibers (to which the medial faces of branchiostegal rays 2–6 attach) pass anteromedially to meet another sheet of fibers from the medial floor of the opercular cavity, the latter passing anterolaterally. Posterolaterally, a bundle arises from the posteroventral face of the supracleithrum and a myocomma with the anterior part of the obliquus inferioris. These fibers pass anteroventrally and then posteroventrally in a semicircle to attach ventrally to the dorsolateral tip of the coracoid. From the anteroventral margin of this semicircle, a bundle passes anteriorly to attach along the ventrolateral surface of the cleithrum. Anterodorsally, fibers from this arch are continuous with the rest of the muscle. Posterodorsomedially, a bundle passes upward to grade into the posterior fibers of the levator externus IV.

**STERNOHYOIDEUS** (Figures 146, 150: STH.).—The muscle is somewhat conical, and is poorly developed. It originates from the anteroventral tip of the cleithrum and inserts on the dorsomedial face of the anterior region of the anterohyal.

#### VENTRAL BRANCHIAL MUSCLES

**PHARYNGOCLAVICULARIS EXTERNUS** (Figures 150, 151: PHC.E.).—Origin is from the ventromedial face of the cleithrum, the fibers passing dorsally to insert on the anteroventral face of ceratobranchial 5.

**PHARYNGOCLAVICULARIS INTERNUS** (Figures 150, 151: PHC.I.).—The muscle arises from the medial face of the cleithrum, and consists of two sections. The anterior section passes anterodorsally, medial to the pharyngoclavicularis externus, to insert on the posteroventral face of basibranchial 3. The more medial fibers of this section join their antimeres in a midventral raphe, while some of the more dorsal ones arise from ceratobranchial 4 and pass to basibranchial 3. The more posterior section arises from the anteroventromedial cleithrum and inserts on the ventral face of ceratobranchial 5.

**OBLIQUUS VENTRALIS III** (Figure 151: OBL.V.).—The muscle originates from the anteroventral region of ceratobranchial 3 and the posteroventral tip of hypobranchial 3. The fibers pass anteromedially to join with the fibers of rectus IV in an insertion on the anteroventral process of hypobranchial 3.

**TRANSVERSI VENTRALES IV, V** (Figure 151: TR.V.).—These muscles connect the anteromedial faces of the ceratobranchials of the fourth and fifth arches across the ventral midline. Both muscles are small.

**RECTI VENTRALES I–IV** (Figures 150, 151: RECT.V.).—Rectus I is well developed, passing from the dorsolateral face of the anterohyal to the anterolateral surface of hypobranchial 1. The lateral surface of the muscle gives rise to a bundle of fibers passing posterodorsally, which grade into a tendon attaching to the ventromedial face of the hyomandibular just lateral to its articulation with the skull. Recti II and III connect the hypobranchials of the first and second and second and third arches respectively. Rectus IV passes from the anteroventral face of ceratobranchial 4 to the posterior face of the ventral process of hypobranchial 3. The anterodorsolateral fibers are continuous with the anteromedial fibers of obliquus ventralis III.

**RECTUS COMMUNIS** (Figure 151: *r.comm.*).—The muscle arises from the posterior face of the ventrohyal. It passes posteriorly as a tendon, and develops fibers at the level of hypobranchial 1, where it splits into left and right halves. The fibers then pass posteriorly, and grade into tendon at the level of ceratobranchial 4. The tendon inserts on the ventrolateral face of ceratobranchial 5.

#### DORSAL BRANCHIAL MUSCLES

**LEVATORES EXTERNI I-IV** (Figure 150: *L.EXT.*).—These muscles originate from the ventral faces of the prootic and pterotic beneath the hyomandibular fossa. Levator I inserts on the dorsolateral face of epibranchial 1, with a few posterior fibers passing to the anteroventral face of epibranchial 2. Levator II inserts on the dorsolateral faces of epibranchials 2 and 3, and apparently represents fusion with the third levator. Levator IV is well developed. It inserts along the dorsal length of epibranchial 4, and continues in the wall of the opercular cavity behind the bone, reaching the dorsomedial face of the cleithrum.

**LEVATORES INTERNI II, III** (Figure 152: *L.INT.*).—These muscles have altered somewhat from the usual condition. Levator II originates from the posteroventromedial face of the pterotic. It passes anteroventrally to insert partly on the dorsomedial face of infrapharyngobranchial 3, and partly on the dorsolateral face of infrapharyngobranchial 2. The medial face of the muscle shares a strong aponeurosis with the dorsolateral fibers of transversus dorsalis III. Behind this, the muscle passes medial to levator III to its origin. Levator III originates from the ventrolateral sphenotic beneath the hyomandibular fossa. It passes ventrally to insert on the anterodorsolateral face of infrapharyngobranchials 2 and 3.

**OBLIQUUS DORSALIS III** (Figure 152: *OBL.D.*).—A fairly well-developed muscle, which passes anteromedially from the dorsomedial faces of epibranchials 3 and 4 to the posterodorsal face of infrapharyngobranchial 2.

**OBLIQUUS POSTERIOR** (Figure 150: *OBL.P.*).—The muscle appears to be present, but is not clearly separated from the sphincter oesophagi.

**TRANSVERSI DORSALES II, III** (Figure 152: *TR.D.*).—In transversus II, the fibers arise from the ventrolateral face of the parasphenoid. The posterior

fibers almost intermingle with the anterior fibers of the lateral bundle of the sphincter oesophagi. The main mass of the fibers passes laterally and then curves anteriorly. Dorsolaterally, a strong aponeurosis attaches to the medial face of levator internus II. The ventrolateral fibers attach to the dorsal faces of epibranchials 1 and 2 and infrapharyngobranchial 1. The more anterior fibers pass medially to a middorsal raphe, and are not attached to the skull. Posteriorly, the muscle gives rise to a bundle that passes laterally into the posterodorsal wall of the opercular cavity. Transversus III is a well-developed muscle, which passes across the dorsal midline between the third and fourth epibranchials of either side. It lies ventral to transversus II, which covers it both anteriorly and posteriorly.

**RETRACTOR DORSALIS** (Figure 152: *D.RETR.*).—Origin is from the lateral and ventrolateral faces of vertebrae 1 and 2. The fibers course anteroventrally, fuse briefly with their antimeres in the midline, and insert on the posteromedial faces of infrapharyngobranchials 2 and 3. It is overlain dorsally by a small bundle of the sphincter oesophagi.

**ADDUCTORES I-V** (Figures 150, 151, 152: *AD.*).—Adductors I-III all connect the anteromedial faces of ceratobranchials 1-3 to the anterolateral faces of epibranchials 1-3. Adductor IV connects the medial faces of ceratobranchial 4 and epibranchial 4. Adductor V passes from the lateral region of ceratobranchial 5 to the posterior face of epibranchial 4.

**SPHINCTER OESOPHAGI** (Figures 150, 151, 152: *s.o.*).—The muscle has a very complicated form. Ventrally, two longitudinal bundles arise from the posterior face of basibranchial 3. They fuse at the level of ceratobranchial 5, and form a longitudinal sheath on the floor of the esophagus. Beneath this, a thick, almost transverse bundle connects the medial faces of the fifth ceratobranchials. Ventral to the latter bundle is a thin sheet of fibers, also between the fifth ceratobranchials posteriorly, but becoming longitudinally oriented and fading out above transversus ventralis V. Dorsally, three bundles pass anteriorly beneath the infrapharyngobranchials, attaching to the ventromedial faces of infrapharyngobranchials 1-3. They fade out posteriorly in the tissue of the esophagus. The muscle passes across the midline below the retractor dor-

salis posteriorly, except for a small bundle of fibers lying above and in front of the retractor.

#### MUSCLES OF THE PECTORAL REGION

**ABDUCTOR SUPERFICIALIS** (Figures 146, 150: ABD. s.).—The muscle originates from the posterior, medial, and lateral faces of the cleithrum. It passes posteriorly to insert on the lateral faces of the anterodorsal processes of the bases of the principal fin rays.

**ABDUCTOR PROFUNDUS** (Figure 150: ABD.P.).—The muscle originates from the posteroventral cleithrum and lateral faces of the coracoid and actinosts. It inserts on the ventrolateral bases of the principal rays and the lateral base of the lateral half of the vestigial ray.

**ARRECTOR VENTRALIS** (Figure 146: ARR.V.).—Origin is from the ventrolateral face of the dorsal region of the cleithrum. The muscle inserts on the anterolateral base of the medial half of the vestigial fin ray.

**ABDUCTOR SUPERFICIALIS** (Figure 153: ADD.S.).—The muscle originates from the dorsomedial cleithrum. The fibers to the dorsalmost rays pass posteriorly, the slip to each succeeding ray passing increasingly ventromedially. Thus, the slip to the ventralmost ray passes ventrally, and lies medial to all the others. The ventral six rays have dorsal processes, to which the tendons attach, the more dorsal tendons inserting on the dorsomedial faces of the rays distal to their bases.

**ABDUCTOR PROFUNDUS** (Figure 153: ADD.P.).—The muscle originates from the medial faces of the coracoid and the radials, and inserts on the postero-medial flanges of all but the six ventral rays, where insertion is on the ventromedial shaft of the ray.

**ARRECTOR DORSALIS** (Figure 153: ARR.D.).—The muscle is small, arising from the medial face of the scapula, and inserting on the medial face of the medial half of the vestigial fin ray.

**CORACORADIALIS** (Figure 153: COR.R.).—The muscle is poorly developed. It passes from the dorsomedial face of the posterior coracoid process to the posteroventral face of the fourth radial.

**PROTRACTOR PECTORALIS** (Figure 146: P.P.).—From its origin on the ventrolateral pterotic, the muscle passes ventrally to the anteromedial face of the supracleithrum and the posterodorsal cleithrum.

**LEVATOR PECTORALIS** (Figure 146: TR.).—The

fibers pass from the posteroventral face of the pterotic to the extreme dorsolateral tip of the cleithrum medial to the supracleithrum.

#### MUSCLES OF THE DORSAL FIN

**INCLINATOIRES DORSALES** (Figure 154: INC.).—The muscles are represented by a flat sheet of transverse fibers. They have lost their association with the fin rays, and now form the dorsal part of the transverse cutaneous system.

**ERECTORES DORSALES** (Figure 154: EREC.).—The erectors originate from the lateral faces of the pterygiophores and neural spines, and the dorsolateral faces of the sixth to thirteenth centra. They insert on the anterolateral bases of all the fin rays (including the small first ray).

**DEPRESSORES DORSALES** (Figure 154: DEPR.).—These muscles arise in the same area as the erectors, and insert on the posterolateral bases of all the fin rays.

**SUPRACARINALIS ANTERIOR** (Figures 146, 154: s. ANT.).—The muscle is well developed, and arises from the posterior faces of the supraoccipital and epiotic. It passes posteriorly to attach to the anterolateral face of the first dorsal pterygiophore.

**SUPRACARINALIS POSTERIOR** (Figures 154, 155: s. POST.).—The fibers arise from the posterodorsal face of the last dorsal fin pterygiophore, and attach to the dorsolateral faces of the neural spines of the next three vertebrae to end on the neural spine of the seventeenth vertebra.

#### MUSCLES OF THE ANAL FIN

**INCLINATOIRES ANALES** (Figures 146, 154: INC.).—The residual inclinator arises from the posteroventral tip of the postcleithrum and attaches to the lateroventral face of the first pterygiophore of the anal fin. The first inclinator of the fin is well developed, but all the others are poorly so, and do not insert on the fin rays, but on the cartilagenous distal pterygiophores. These muscles arise from the fascia over the obliquus inferioris.

**ERECTORES ANALES** (Figure 154: EREC.).—The muscles originate from the lateral faces of the pterygiophores and the haemal arches and spines of the ninth to thirteenth vertebrae, inserting on the anterolateral bases of all the fin rays.

**DEPRESSORES ANALES** (Figure 154: DEPR.).—The depressors arise just behind the erectors to any particular ray, but insert on the posterolateral bases of the rays.

**INFRACARINALIS ANTERIOR**.—The muscle is apparently represented by fibers arising from the ventral tip of the cleithrum and passing posteriorly in the subdermal tissue to intermingle with those of the *infracarinalis medius*, helping to form the longitudinal cutaneous system.

**INFRACARINALIS MEDIUS** (Figures 146, 154: INF. M.).—It seems likely, as discussed above, that this muscle forms part of the longitudinal cutaneous system. It arises from the first pterygiophore of the anal fin and passes anteriorly into the subdermal tissue.

**INFRACARINALIS POSTERIOR** (Figures 154, 155: INF. P.).—The muscle arises from the posteroventral face of the last anal pterygiophore and its posterior process. Fibers attach to the ventrolateral faces of the haemal spines of the fourteenth to sixteenth vertebrae, ending on the spine of the seventeenth vertebra.

#### MUSCLES OF THE CAUDAL FIN

**INTERRADIALIS** (Figure 155a: INT.).—The muscle passes toward the midline from the lateral faces of the caudal rays, a little distal to their bases. The fibers are superficially continuous.

**HYPOCHORDAL LONGITUDINALIS** (Figure 155: H.L.).—This muscle originates from the dorsal surface of the ridged parhypural and the lateral faces of the ventral fused hypurals, as well as from the ural centrum. It inserts on the ventrolateral faces of rays D 3 and 4.

**FLEXOR DORSALIS** (Figure 155b: F.D.).—Origin is from the dorsolateral faces of the third and fourth last vertebral centra and the anterolateral face of the epural. The tendons insert on the anterolateral bases of rays D 1-4.

**FLEXOR DORSALIS SUPERIOR** (Figure 155: F.D.S.).—A well-developed muscle, originating from the dorsolateral faces of the thirteenth to fifteenth vertebral centra. The fibers give rise to a tendon which joins its antimere before inserting on the anterodorsal base of D 5.

**FLEXOR VENTRALIS** (Figure 155b: F.V.).—The muscle originates from the ventrolateral face of the hypural plate, the ural centrum, and the cen-

trum and haemal spine of the penultimate vertebra. It inserts on the bases of rays V 3 and 4.

**FLEXOR VENTRALIS EXTERNUS** (Figure 155b: F.V. E.).—The fibers arise from the ventrolateral faces of the centra and haemal spines of the second and third last vertebrae and insert on the bases of rays V 1 and 2.

**FLEXOR VENTRALIS INFERIOR** (Figure 155: F.V.I.).—Origin is from the ventrolateral faces of the centra of the thirteenth to fifteenth vertebrae. The fibers give rise to a tendon which meets its antimere before inserting on the base of ray V 5.

**TRANSVERSUS CAUDALIS** (Figure 155b: TR.C.).—The muscle arises from the ventral face of the epural and the lateral surface of the upper part of the hypural plate. It passes posteroventrally as a thin tendon to insert on the dorsolateral face of ray V 3.

#### LATERAL BODY MUSCLES

**EPAXIALIS** (Figures 146, 154, 155a: EPAX.).—Anteriorly, the muscle is attached to the posterior faces of the supraoccipital, exoccipital, pterotic, epiotic, frontal, and supracleithrum. Fibers also arise from the lateral faces of the neural spines and centra of the vertebrae. The dorsal moiety is well separated from the main mass at about the level of the dorsal fin. It passes posteriorly, becoming increasingly aponeurotic, and eventually forms a flat, sheetlike tendon which joins a similar tendon from the *obliquus inferioris* to insert on the lateral bases of all the caudal fin rays. The anterior region covers the anterior part of the *obliquus superioris*. Fiber direction superficially tends to be from anteroventral to posterodorsal. A few of the ventromedial fibers attach to the peritoneum overlying the swim bladder near the vertebral centra. Posteriorly, the fibers grade into a flat aponeurosis which inserts on the lateral bases of rays D 1-4.

**OBLIQUUS SUPERIORIS** (Figures 146, 154, 155a: OBL.S.).—The muscle arises from the posterodorsal tip of the cleithrum. It broadens out rapidly, becoming closely associated with the *epaxialis* dorsally and the vertebral centra and haemal spines medially. Posteriorly, it grades into an aponeurosis which inserts on the lateral bases of rays V 1-4.

**OBLIQUUS INFERIORIS** (Figures 146, 154, 155a: OBL.I.).—The anteroventral section consists of two

well-separated parts. The dorsal one connects the anteroventral face of the postcleithrum to the posterior and ventral faces of the coracoid. Beneath this, the ventral part passes back from the posteroventral cleithrum and coracoid to attach to the medial face of the postcleithrum via the third myocomma, the more posterior fibers being continuous with the anterodorsal part. The anterodorsal portion arises from the fascia overlying the epaxialis, being partly overlain itself by the superficialis lateralis. The fibers attach to the posterodorsal face of the postcleithrum, the more medial ones being continuous with those of the anteroventral section. Posteriorly, the fibers become increasingly horizontally oriented, most of them attaching to the ventrolateral face of the first anal pterygiophore. Some of the posterior fibers join to a myocomma of the deeper section of the obliquus inferioris. This deeper part is continuous anteriorly with the fibers of the infracarinalis medius, and now forms the longitudinal cutaneous system. A small bundle of fibers passes posterodorsomedially from this part of the muscle. It soon grades into a tendon which courses lateral to the erector-depressor complex of the anal fin to attach to the anteroventral tip of the haemal spine of the twelfth centrum.

#### CUTANEOUS MUSCULATURE

This system, which lies immediately below the skin, is very complicated and difficult to follow. These difficulties arise largely because of the numerous elastic connective tissue fibers which intermingle with the muscle fibers. Owing to the difficulty in following the system, only cursory attention will be paid to it. The fibers pass in two main directions, transverse and longitudinal, of which the transverse is the more superficial. The fibers are concentrated in the regions where the spines or prickles are best developed—mainly along the stomach and back. The central bases of the spines are closely associated with the muscle fibers, but histological sections are necessary to determine whether the fibers actually insert on these bases. Transverse fibers are also present behind the dorsal and anal fins, across the midline of the skull, and beneath the eye. The ring of fibers encircling the mouth in the tissues of the lips may also be derived from this system. A well-developed bundle of fibers passes anteriorly from

the dorsal region of the prefrontal to the lips, where it is joined by another bundle arising from the anteroventral corner of the eye.

The longitudinal system is best developed ventrally, between the anus and the lower jaw. This part of the system presumably arose from the fibers of the infracarinales anterior and medius after the loss of the pelvis, while the transverse system may have been initially derived from the inclinators of the dorsal and anal fins. There is an enigmatic bundle (present in this species only of those examined) which arises from the peritoneum overlying the swim bladder and passes anterolaterally between the posterodorsal tip of the cleithrum and the anterior margin of the obliquus inferioris. It grades into the connective tissue overlying the dilatator operculi.

#### *Amblyrhynchotes honckenii* (Bloch)

##### FIGURE 156

A 1 $\alpha$  completely covers A 2 $\alpha$  posterodorsolaterally. The ventral bundle of A 1 $\beta$  is well developed, and reaches as far as the rear of the orbit posteriorly. The separation of the two bundles of A 2 $\alpha$  is more distinct, and A 2 $\beta$  is not as well developed. The anterolateral bundle of the dilatator operculi inserts on the anterodorsal face of the opercle and subopercle.

The pharyngoclavicularis externus consists of two parts, the anterior inserting on basibranchial 3 (where it is partly confluent with the pharyngoclavicularis internus), the posterior part inserting on the anteroventral face of ceratobranchial 5. The obliquus posterior is well developed, and distinct from the sphincter oesophagi. The inclinator analis to the first ray now inserts on the cartilagenous distal pterygiophore and not on the base of the first ray. The infracarinalis medius is somewhat distinct. It attaches anteriorly to the posteroventral tip of the cleithrum, and becomes continuous with the longitudinal cutaneous in the midregion. It separates from the cutaneous again posteriorly to attach to the first anal pterygiophore. The hypochordal longitudinalis inserts on rays D 2-4, while the transversus caudalis inserts on rays V 2-3.

#### *Colomesus psittacus* (Bloch and Schneider)

##### FIGURE 157

A 1 $\alpha$  and A 1 $\beta$  are as for *A. honckenii*. A 2 $\alpha$ ,

which is not particularly well separated into two heads, has a high dorsal origin from the ventral surface of the lateral process of the hyomandibular, and has increased in bulk. A 2 $\beta$  has expanded across what was the dilatator fossa, and extends its origin posterodorsally onto the sphenotic, the posterior tip of the frontal, the supraoccipital, epiotic, and pterotic. The dilatator operculi is well developed, and inserts on the anterodorsal face of the subopercle, posterodorsal interopercle, and the opercle. Origin has greatly expanded to include the dorsal faces of the prefrontal, frontal, supraoccipital, epiotic, and pterotic. The anterior fibers cover the posterodorsomedial fibers of A 2 $\beta$ . The hyomandibular is not included in the sites of origin. The levator arcus palatini is very small.

There is no section of the hyohyoidei adductores to the fourth ray. The posteroventral bundle of the semicircular portion of the hyohyoidei adductores attaches to the ventrolateral face of the fourth radial. Two slips of fibers pass inward to the medial face of the posterodorsal bundle. One passes dorsomedially to attach to the posteromedial face of epibranchial 3, the other passes posteroventrally to fade out lateral to the pharyngoclavicularis internus. Both lie lateral to the posterior fibers of levator externus IV.

There are no fibers from levator externus I to epibranchial 2, and only a few from levator II to the fascia between epibranchials 2 and 3. No other fibers attach to epibranchial 3. Levator externus IV is well developed. No lateral bundle of transversus dorsalis II was found, but it may be represented by a dorsomedial bundle which passes out laterally to join the posterodorsal part of the hyohyoidei adductores.

The hypochordal longitudinalis inserts on rays D 2-4, while the transversus caudalis inserts on rays V 2-3. The flexor ventralis externus inserts on the bases of rays V 1-3, and its origin is expanded distally onto the haemal spines.

### *Xenopterus naritus* (Richardson)

FIGURE 158

The posteroventral portion of A 1 $\beta$  is expanded dorsally and originates from the roof of the orbit, while the dorsal head of A 2 $\alpha$  extends posteriorly beyond the hyomandibular to the anterolateral

face of the pterotic. A 2 $\beta$  is as for *Colomesus*, except that the frontal secondarily roofs the dilatator fossa, and some of the fibers arise from it. The levator arcus palatini inserts on the hyomandibular by a broad, flat aponeurosis.

The hyohyoidei adductores is poorly developed in the outer wall of the opercular cavity, but with the posterodorsal and posteroventral bundles still well developed near their origins. The halves of the sternohyoideus fuse in the anterior midline. A well-developed and distinct intermandibularis is present. It attaches in the fossa of the dentary below the insertion of A 2, lying anterodorsal to the angular.

Levatores externi II and III are fused, and levator internus II is not associated with transversus dorsalis II medially. Adductor I is small. The erectores dorsales and anales lie in a somewhat more lateral position than do the depressores dorsales and anales. Inclinatores anales are attached to the bases of the first and the twenty-first (twentieth in the 124 mm specimen) to twenty-eighth fin rays.

The obliquus inferioris does not separate from the obliquus superioris in the region of the anal fin, and there is thus no anteroventral section joining the fibers arising from the posteroventral tip of the postcleithrum. The posterodorsomedial bundle of fibers attaching to the haemal spine of the twelfth vertebra is absent. The extreme anteroventral fibers of the obliquus inferioris attach to the lateral face of the first branchiostegal ray. A small aponeurosis from the obliquus superioris attaches to the base of ray D 1. The hypochordal longitudinalis and flexor ventralis externus are as for *Colomesus*, and the transversus caudalis inserts on the bases of rays V 1-2.

### *Arothron immaculatus* (Bloch)

FIGURE 159

The posteroventral part of A 1 $\beta$  is expanded along the floor of the orbit, and A 1 $\alpha$  covers A 2 $\alpha$  laterally. A 2 $\beta$  is well developed, and A 3 is much reduced (particularly dorsally). The anterior part of the dilatator operculi inserts on the subopercle and opercle.

The posterodorsal bundle of the hyohyoidei adductores attaches to the anteroventral face of the supracleithrum.

The fibers of levator externus I insert only on epibranchial 1, and adductores II and V are absent.

The residual inclinator analis has fused with the obliquus inferioris, and the first and last anal fin rays have inclinatoris attaching to their bases.

The hypochordal longitudinalis is as for *A. honckenii*. The single tendon of the transversus caudalis attaches to the base of ray V 2. The flexor ventralis attaches to the bases of rays V 1-5.

The posterodorsomedial bundle of the obliquus inferioris fades into an aponeurotic sheet at the level of the anal fin, the sheet attaching to the haemal arches of the thirteenth and fourteenth vertebrae.

#### *Tetraodon schoutedeni* Pellegrin

FIGURE 160

A 1 $\beta$  is well developed, and similar to that of *Xenopterus*, the posteroventral portion having expanded posterodorsally along the roof of the orbit. A 2 $\alpha$  is reduced dorsally, and there is only a thin slip of muscle to the posterodorsolateral face of the hyomandibular beneath the dorsal process of the opercle. The adductor operculi is very well developed. A lateral bundle of the sphincter oesophagi attaches to the anteroventral face of epibranchial 4.

The flexor ventralis externus inserts only on V 1, while the flexor ventralis attaches to V 2-5. The transversus caudalis inserts on V 2.

#### Summary of Tetraodontidae

A number of regions of the body in this family show myological variation. The subdivisions of the adductor mandibulae, while constant in presence and position, show a considerable variation in relative development. This is particularly true of the A 1 sections, and of A 2 $\beta$ . The size and sites of origin of the dilatator operculi differ markedly, as does the insertion of the anterolateral bundle of fibers of this muscle. The lateral fibers of the hyohyoidei adductores vary in size and position. The insertion of the levatores externi shows considerable variation, and there are other minor differences in the dorsal branchial musculature. The number and form of the inclinatores anales differ, and there is some variation in the relative development of the posterodorsolateral bundle of fibers of the obliquus inferioris. The number of insertion tendons (and their relative positions) of the hypochordal longitudinalis, flexor ventralis, flexor ventralis externus, and transversus caudalis varies widely. The remaining muscles are relatively conservative in the members of the family examined.

#### Myological Descriptions of Representative Canthigasterids

The typical body outline of this monogeneric family is illustrated in Figure 9. Fraser-Brunner (1943) recognizes a single genus with 15 species in this family. Representatives of two of the species were dissected for this study.

The head region is higher, narrower, and of less robust construction than in the tetraodontids. Other bodily proportions are similar, and some inflation is possible. These fishes can also raise the skin on the back into a ridge by contraction of the underlying cutaneous musculature. They are usually brightly colored coral reef forms, feeding mainly on sea grasses and soft-bodied marine invertebrates.

As outlined above, they are generally considered to be closely allied to the Tetraodontidae.

#### *Canthigaster margaritatus* (Rüppell)

FIGURES 161-167

#### MUSCLES OF THE CHEEK

ADDUCTOR MANDIBULAE (Figures 161, 162: A 1 $\alpha$ , A 1 $\beta$ , A 2 $\alpha$ , A 2 $\beta$ , A 3).—A 1 $\alpha$  inserts on the posteroventral face of the maxilla. The ventral fibers arise from the posterodorsolateral preopercle. The dorsal region overlies A 2 $\alpha$  (with some fibers arising from the fascia between them), and then passes medial to that muscle to originate from the dorsal metapterygoid. A 1 $\beta$  originates from the ethmoid and the ventral surface of the prefrontal. A ventral extension of this muscle arises from the lateral face of the parasphenoid anterior to the



orbit. The fibers insert on the posterodorsal face of the maxilla, medial to A 1 $\alpha$ . A 2 $\alpha$  originates from the lateral preopercle, metapterygoid, quadrate, and hyomandibular. The muscle becomes tendinous anteriorly, and joins the lateral face of the tendon of A 2 $\beta$ . A 2 $\beta$  arises from the anterior faces of the hyomandibular and prootic and the lateral face of the posterior region of the parasphenoid. The joint tendon with A 2 $\alpha$  inserts on the medial face of the dentary. A 3 originates from the lateral faces of the quadrate, ectopterygoid, and metapterygoid, and inserts tendinously in the Meckelian fossa.

**LEVATOR ARCUS PALATINI** (Figures 161, 162: L.A.P.).—A minute muscle, originating from the ventral face of the postorbital process of the frontal and inserting on the posterodorsolateral ridge of the hyomandibular.

**DILATATOR OPERCULI** (Figure 161: D.O.).—Origin is from the posterolateral frontal (primarily in the gutter formed by the vertical lateral ridge of this bone behind the orbit) and the anterior epiotic. The fibers insert on the posterodorsal face of the interopercle, the anterior opercle, and the dorsal process of the latter bone.

**LEVATOR OPERCULI** (Figure 161: L.O.).—Origin is from the anterolateral face of the lateral process of the pterotic, the fibers inserting on the posterodorsal face of the opercle.

**ADDUCTOR ARCUS PALATINI** (Figure 162: A.A.P.).—The muscle originates from the lateral face of the parasphenoid and passes laterally to insert on the dorsomedial faces of the hyomandibular, metapterygoid, and ectopterygoid. Anteriorly, the fibers cross the midline beneath the anterior part of the parasphenoid and the vomer, attaching to the medial faces of the palatines.

**ADDUCTOR OPERCULI** (Figure 163: AD.OP.).—The muscle arises from the posteroventrolateral face of the pterotic and inserts on the posterodorsomedial face of the opercle.

#### MUSCLES OF THE HYOID REGION

**VALVULUS**.—The muscle originates from the anteroventromedial face of the preopercle, and sweeps forward in a dorsoventral curve to grade into the tissues of the mandibular buccal valve. It lies medial to the interopercle.

**PROTRACTOR HYOIDEI** (Figure 161: PR.HY.).—The muscle is well developed, connecting the anterior elements of the hyoid arch to the posteroventral face of the dentary near the symphysis. The muscle is single anteriorly, and diverges into two halves before attaching to the lateral faces of the anterohyal and ventral branchiostegal rays.

**HYOHYOIDEI ABDUCTORES** (Figure 161: H.AB.).—The form of the muscle is very similar to that described for *Lagocephalus*, with the following differences. The large section to the first ray is faintly subdivided into ventrolateral and dorso-medial bundles. A small bundle attaches to the posteromedial face of basibranchial 1, just in front of the section which fuses with its antimere in the midline beneath hypobranchial 3.

**HYOHYOIDEI ADDUCTORES** (Figure 161: H.AD.).—The form of this muscle is also very similar to that described for *Lagocephalus*, but differs in the following respects. The posterodorsal bundle attaches to the anteroventral face of the supracleithrum. The posterior wall of the branchial (opercular) chamber is formed by fibers from the posterolateral face of epibranchial 3, which pass out laterally in front of epibranchial 4, and a ventral bundle from the ventromedial face of the cleithrum.

**STERNOHYOIDEUS** (Figures 161, 163: STH.).—The muscle is cone-shaped, with a fairly wide origin on the anteroventral cleithrum and an aponeurotic insertion on the ventrohyal. The halves fuse in the anterior midline.

#### VENTRAL BRANCHIAL MUSCLES

**PHARYNGOCLAVICULARIS EXTERNUS** (Figures 163, 164: PHC.E.).—Origin is from the ventromedial face of the cleithrum, the muscle dividing into three bundles. The anterior one inserts on the junction between basibranchial 2 and hypobranchial 2, the middle part inserts on basibranchial 3 and the posterior section attaches to the ventromedial face of ceratobranchial 5.

**PHARYNGOCLAVICULARIS INTERNUS** (Figures 163, 164: PHC.I.).—The muscle arises from the anteroventromedial cleithrum. It passes anterodorsally to insert on basibranchial 3 and ceratobranchial 5. In between the two points of insertion, the fibers sweep across the midline to join their anteriors.

**OBLIQUUS VENTRALIS III** (Figures 163, 164: OBL.v.).—The fibers pass between the anteroventral face of ceratobranchial 3 and the posteroventrolateral tip of the ventral process of hypobranchial 3.

**TRANSVERSUS VENTRALIS V** (Figure 164: TR.v.).—This is a small muscle which crosses the ventral midline between the anteroventromedial faces of the fifth ceratobranchials. There is no transversus IV, but it may have fused with the fibers of the pharyngoclavicularis internus to form the transverse part.

**RECTI VENTRALES I-IV** (Figures 163, 164: RECT.v.).—The first muscle consists of two parts. The more medial section links the dorsomedial face of the anterohyal with the anteroventral face of hypobranchial 1. The lateral portion arises from the dorsomedial surface of the anterohyal and sweeps dorsally to attach to the anteroventrolateral flange of ceratobranchial 1. Recti II and III interconnect the hypobranchials of the first and second, and second and third arches, respectively. Rectus IV passes from the anteroventral face of ceratobranchial 4 to the posteroventral tip of the ventral process of hypobranchial 3.

**RECTUS COMMUNIS** (Figures 163, 164: R.COMM.).—The muscle arises tendinously from the posterior face of the ventrohyal. It passes ventral to basibranchial 1 (lying medial to the basibranchial-hypobranchial ligament), where it develops a belly of muscle fibers, before grading into a tendon which attaches to the anteroventrolateral face of ceratobranchial 5.

#### DORSAL BRANCHIAL MUSCLES

**LEVATORES EXTERNI I-IV** (Figure 163: L.EXT.).—The muscles originate from the prootic and pterotic beneath the hyomandibular fossa. The first muscle inserts on the dorsolateral face of epibranchial 1, while the second inserts on the dorsolateral faces of epibranchials 2 and 3. There is no distinct third levator. Levator IV is well developed, and inserts along the entire dorsal surface of epibranchial 4. It continues posteriorly in the wall of the opercular cavity, the fibers attaching to the dorsomedial face of the cleithrum.

**LEVATORES INTERNI II, III** (Figure 165: L.INT.).—Levator II originates from the posteroventrolateral face of the pterotic, and inserts on the anterodorsal face of infrapharyngobranchial 2. Levator III arises

from the dorsolateral prootic and inserts on the anterolateral face of infrapharyngobranchial 3 and the dorsolateral edge of infrapharyngobranchial 2. Levator II passes medial to levator III, and forms an aponeurotic connection with transversus dorsalis II.

**OBLIQUUS DORSALIS IV** (Figure 165: OBL.D.).—Origin is from the posterior and dorsal faces of epibranchial 4, the fibers passing anteromedially to insert on the posterodorsal face of infrapharyngobranchial 2.

**OBLIQUUS POSTERIOR**.—The fibers of this muscle are not well separated from the sphincter oesophagi, but pass from the dorsal tip of ceratobranchial 5 to the posteromedial face of epibranchial 4.

**TRANSVERSI DORSALES II, IV** (Figure 165: TR.D.).—The anterior muscle arises from the midline and attaches to the connective tissue covering infrapharyngobranchial 2 (there is no direct connection) and to the medial face of levator internus II. Transversus IV crosses the dorsal midline directly beneath the posterior portion of transversus II, connecting the medial faces of the fourth epibranchials.

**RETRACTOR DORSALIS** (Figure 165: D.RETR.).—The muscle originates from the lateral face of the exoccipital and the ventrolateral face of the basioccipital. It inserts on the posterodorsal face of infrapharyngobranchial 2.

**ADDUCTORES I-V** (Figures 163, 164, 165: AD.).—The muscles pass between the anteromedial faces of the ceratobranchials and epibranchials of the first three arches, the medial faces of these bones of the fourth arch, and from the dorsal tip of ceratobranchial 5 to the posterolateral face of ceratobranchial 4.

**SPHINCTER OESOPHAGI** (Figures 164, 165: S.O.).—Dorsally, the muscle consists of a bundle of fibers across the midline, joined by a bundle from epibranchial 4. In addition, the muscle sends out a bundle which attaches to the anterior face of ceratobranchial 4. Ventrally, there is a bundle across the midline behind transversus IV. Immediately above this, the fibers are transverse posteriorly, but become increasingly longitudinally oriented anteriorly. This gives rise to a pair of fiber bundles passing forward beneath the basibranchials to attach to the posteroventral face of basibranchial 1. The anterior section of the pharyngoclavicularis internus inserts between the halves.

## MUSCLES OF THE PECTORAL REGION

**ABDUCTOR SUPERFICIALIS** (Figure 161: ABD.S.).—Origin is from the posterior face of the lateral flange of the cleithrum, the muscle inserting on the anterolateral bases of the principal fin rays.

**ABDUCTOR PROFUNDUS**.—The fibers arise from the lateral face of the coracoid and the ventrolateral cleithrum. Insertion is on the posterolateral bases of the principal fin rays and on the posterolateral face of the lateral half of the vestigial fin ray.

**ARRECTOR VENTRALIS** (Figure 161: ARR.V.).—This is a small muscle, originating from the posterolateral face of the cleithrum beneath the lateral flange. It inserts on the lateral extension of the base of the medial half of the vestigial fin ray.

**ADDUCTOR SUPERFICIALIS** (Figure 153 for *Lagocephalus*, ADD.S.).—Origin is from the dorsomedial face of the cleithrum, the muscle inserting on the dorsomedial bases of the ventral six rays, and the dorsomedial faces of the next nine rays some distance distal to their bases.

**ADDUCTOR PROFUNDUS** (as above, but ADD.P.).—The fibers arise from the medial faces of the cleithrum, coracoid, and scapula. Insertion is on the ventromedial bases of the rays. There is no aponeurosis anteriorly on the body of the muscle as there is in *Lagocephalus*.

**ARRECTOR DORSALIS**.—The muscle originates from the cleithrum beneath the adductor profundus, and inserts on the base of the medial half of the vestigial fin ray.

**CORACORADIALIS**.—The muscle is better developed than in the tetraodontids examined. It passes from the posterior process of the coracoid to the distal ventral tip of the fourth radial.

**PROTRACTOR PECTORALIS** (Figures 161, 163: P.P.).—Origin is from the posterolateral face of the pterotic. The fibers fan out to insert broadly on the dorsal face of the cleithrum and anteroventral supracleithrum.

**LEVATOR PECTORALIS**.—The muscle arises from the pterotic behind the protractor pectoralis and passes posteroventrally to insert on the dorsomedial face of the cleithrum beneath the supracleithrum.

## MUSCLES OF THE DORSAL FIN

**INCLINATOIRES DORSALES** (Figure 166: INC.).—There are two inclinator to the two posteriormost

fin rays, arising in the subdermal fascia and inserting on the posterolateral bases of the rays.

**ERECTORES DORSALES** (Figures 161, 166: EREC.).—The muscles originate from the lateral faces of the pterygiophores and the neural spines of the seventh to tenth vertebrae. They insert on the anterolateral bases of the rays, partially overlying the depressors anteriorly, and completely covering them posteriorly.

**DEPRESSORES DORSALES** (Figures 161, 166: DEPR.).—These muscles originate behind and medial to the respective erectors, and insert on the posterolateral bases of the fin rays.

**SUPRACARINALIS ANTERIOR** (Figures 161, 166: s. ANT.).—Origin is from the supraoccipital and its spine and the exoccipital. The lateral fibers pass posteroventrally to attach to the dorsomedial faces of the bifid neural spines of the first four vertebrae. The dorsomedial fibers pass posteriorly to the anterolateral face of the first pterygiophore of the dorsal fin.

**SUPRACARINALIS POSTERIOR** (Figures 166, 167: s. POST.).—The fibers arise from the last pterygiophore of the dorsal fin and end on the anterodorsal face of the neural spine of the penultimate vertebra. They attach to the tips of the neural spines of the intervening vertebrae.

## MUSCLES OF THE ANAL FIN

**INCLINATOIRES ANALES** (Figures 161, 166: INC.).—There are four of these muscles. The first residual one arises in the fascia overlying the obliquus inferioris and attaches to the anteroventral tip of the first anal pterygiophore. The first and last two fin rays receive inclinator inserting on their lateral bases, the fibers arising in the fascia over the ventral body muscles.

**ERECTORES ANALES** (Figure 166: EREC.).—The muscles originate from the anterolateral faces of the anal pterygiophores, anterolateral to the origins of the depressors, and insert on the anterolateral bases of the fin rays.

**DEPRESSORES ANALES** (Figures 161, 166: DEPR.).—The fibers arise posteromedial to those of the erectors, and insert on the posterolateral bases of the rays.

**INFRACARINALIS ANTERIOR**.—The muscle is apparently represented by a bundle of fibers arising from the ventral tip of the cleithrum, and passing

into the subdermal tissues as part of the longitudinal cutaneous.

**INFRACARINALIS MEDIUS** (Figures 161, 166: INF. M.).—The muscle arises from the anteroventral face of the first anal pterygiophore and grades posteriorly into the longitudinal cutaneous together with the anteroventral bundle of the obliquus inferioris. Its posterodorsal surface gives rise to a posterodorsomedial bundle of fibers attaching to the anterior face of the haemal spine of the twelfth vertebra. This bundle is probably derived from the obliquus inferioris, which (in tetraodontids and triodontids) gives rise to a similar bundle.

**INFRACARINALIS POSTERIOR** (Figures 166, 167: INF. P.).—The fibers arise from the ventrolateral face of the last anal pterygiophore, and insert on the anteroventral face of the haemal spine of the penultimate vertebra. They contact the tips of the haemal spines of the intervening vertebrae.

#### MUSCLES OF THE CAUDAL FIN

**INTERRADIALIS** (Figure 167a: INT.).—The muscle stretches between the fin rays, each ray receiving a more or less distinct slip.

**HYPOCHORDAL LONGITUDINALIS** (Figure 167a: H.L.).—The muscle originates from the lateral face of the fused lower hypurals and inserts on the bases of rays D 1-4.

**FLEXOR DORSALIS** (Figure 167b: F.D.).—The muscle is not well developed. It originates from the lateral faces of the neural spines of the second and third last vertebrae, the epural, and the anterodorsal tip of the urostyle, and inserts on the anterolateral bases of rays D 1-3.

**FLEXOR DORSALIS SUPERIOR** (Figure 167: F.D.S.).—Origin is from the lateral faces of the neural spines and centra of the third to fifth last vertebrae. The fibers sweep posterodorsally, grading into a tendon inserting on the dorsolateral base of ray D 5.

**FLEXOR VENTRALIS** (Figure 167b: F.V.).—The fibers arise from the lateral faces of the second and third last vertebrae and the ural centrum. The muscle inserts on the bases of rays V 1-5. The section to ray V 5 is fairly well separated from the other part, the two bundles being subequal in size. The fibers to V 1, and some of those to V 2 are partially separated from the main mass of the muscle, lying on the medial side and passing posterodorsally instead of posteroventrally.

**FLEXOR VENTRALIS EXTERNUS** (Figure 167b: F.V.E.).—The fibers arise from the lateral face of the haemal spine of the penultimate vertebra, and insert on the lateral bases of rays V 1-2.

**FLEXOR VENTRALIS INFERIOR** (Figure 167: F.V.I.).—Origin is from the lateral faces of the haemal spines of the second to fourth last vertebrae, and the centra of the third and fourth last vertebrae. The muscle inserts on the anterolateral base of ray V 6.

**TRANSVERSUS CAUDALIS** (Figure 167b: TR.C.).—The fibers arise from the dorsolateral face of the hypural plate, and insert on the anterodorsal faces of rays V 1 and 2.

#### LATERAL BODY MUSCLES

**EPAXIALIS** (Figures 161, 167a: EPAX.).—The fibers of this muscle attach variously to the rear of the skull, the centra and neural spines, and the dorsal caudal fin rays. In the posterior region, the dorsal moiety becomes inclined at an increasingly oblique angle to the main section, and gives rise to an aponeurotic sheet which, together with a similar sheet from the obliquus inferioris, forms a superficial aponeurosis to all the caudal fin rays. The main medial portion inserts posteriorly on the bases of rays D 2-5.

**OBLIQUUS SUPERIORIS** (Figures 161, 167a: OBL.S.).—The muscle is small anteriorly, where it arises from the posterodorsal tip of the cleithrum. It broadens out posteriorly behind the abdominal cavity, attaching to the centra and haemal spines of the caudal vertebrae. Posteriorly, it inserts on the bases of rays V 1-4.

**OBLIQUUS INFERIORIS** (Figures 161, 166, 167a: OBL.I.).—As in tetraodontids, the muscle has become extensively subdivided. The main mass arises anteriorly from the coracoid and ventrolateral cleithrum. It passes posteriorly, the more dorsal fibers attaching to the anteroventral faces of the postcleithra, and then continuing posterodorsally to fade aponeurotically into the fascia overlying the midlateral septum. The anterodorsal fibers of this section sweep up to attach to the posterolateral base of the first pterygiophore of the dorsal fin. The more ventral fibers pass beneath the tip of the ventral postcleithrum, joining the fibers from the posteroventral face of that bone to attach to the anteroventral tip of the first anal pterygiophore. The posterior section, which is somewhat separated

from the obliquus superioris, grades into an aponeurotic sheet joining that of the dorsal moiety of the epaxialis as described above. Anteroventrally, this section passes beneath the posterior region of the main anterior mass, and fades out in the subdermal tissue covering the abdominal cavity, where it contributes to the formation of the longitudinal cutaneous. A small bundle passes posteroventrally to join the dorsal surface of the infracarinalis medius.

#### CUTANEOUS MUSCLES

The cutaneous muscular system is as for tetrao-

dontids, the anterior longitudinal bundle of the snout region overlying A 1 $\beta$  and attaching to the dorsal face of the palatine.

#### *Canthigaster valentini* (Bleeker)

FIGURE 168

The ventral portion of A 2 $\beta$  is expanded ventrally to almost completely cover A 3 laterally. The obliquus posterior is well developed, with some slight intermingling of fibers with adductor V at its site of attachment to ceratobranchial 5. The hypochordal longitudinalis inserts on rays D 2-4.

### Myological Descriptions of Representative Diodontids

In his review, Fraser-Brunner (1943) recognized three genera and about 18 species of diodontids (see Figure 10 for body outline). Representatives of two of these genera have been dissected. They are much like the tetraodontids, but covered with spines. The head is broad and flat, and their inflation capabilities often impressive. The jaws are even better developed than in the two preceding families, and the diet is primarily composed of gastropods, hermit crabs, and echinoids. They occur mainly in coral reef and sandy bay environments, and swim almost exclusively by undulations of the well-developed pectoral fins.

Diodontids are usually considered to be closely related to tetraodontids, although they have occasionally been allied with the Molidae.

#### *Diodon hystrix* Linnaeus

FIGURES 169-175

#### MUSCLES OF THE CHEEK

**ADDUCTOR MANDIBULAE** (Figures 169, 170: A 1 $\alpha$ , A 1 $\beta$ , A 2 $\alpha$ , A 2 $\beta$ ).—A 1 originates from the entire lateral margin of the preopercle, the fascia over the opercle-hyomandibular articulation, and the posterodorsolateral edge of the hyomandibular. The more posterior fibers pass anteriorly, while the anteroventral fibers sweep anterodorsally to insert on the ventromedial faces of the maxilla

and premaxilla. The anterolateral face of the muscle gives rise to a short tendon which passes into the tissues of the lips at the corner of the mouth. A 1 $\beta$  (Figure 170) is much reduced. It originates from the posterodorsal palatine and the ethmoid-vomer, and inserts by a sheetlike aponeurosis on the posteromedial face of the maxilla (Winterbottom, 1971a). The remaining sections are greatly modified, primarily through the enlargement of A 2. The fibers of A 2 $\beta$  originate from the ventral faces of the frontal and prefrontal, and the lateral faces of the palatine, mesopterygoid, and parasphenoid (the latter three sites of origin being mainly concerned with the posteroventral extension of the muscle). In addition, the fibers meet their anteriors in the midline across the anteroventral region of the orbit. The posteroventral fibers are continuous with the main mass of A 2 (which probably represents A 2 $\alpha$ ), in which a great variety of fiber direction is found. Fibers originate from the lateral or anterior faces of the preopercle, hyomandibular, quadrate, mesopterygoid, pterotic, sphenotic, frontal, pterosphenoid, prootic, and parasphenoid. The ventromedial section is partially subdivided anteriorly, and the medial portion may represent A 3. Insertion is on the medial face of the dentary. A  $\omega$  is a small muscle from the anterior face of the quadrate and ectopterygoid to the Meckelian fossa.

**LEVATOR ARCUS PALATINI** (Figure 170: L.A.P.).—This is a very small, half aponeurotic muscle,

which arises from the ventral tip of the lateral flange of the sphenotic. It inserts on the medial face of the posterodorsolateral ridge of the hyomandibular, passing between the fibers of both A 2 $\alpha$  and the dilatator operculi.

**DILATATOR OPERCULI** (Figure 169: D.O.).—A well-developed muscle, which originates from the dorsal and ventral faces of the posterolateral flange of the frontal, the lateral sphenotic, and the anterior and posterior faces of the lateral flange of the pterotic. Insertion is mainly on the anterior face of the dorsal crista of the opercle, with a few fibers to the posterior margin of the crista.

**LEVATOR OPERCULI** (Figure 169: L.O.).—The fibers arise from the dorsolateral margin of the pterotic, and pass down to insert on the lateral opercle, and the posterior face of the crista of that bone.

**ADDUCTOR ARCUS PALATINI**.—A small muscle, extending from the lateral parasphenoid and prootic to the dorsomedial faces of the palatine, mesopterygoid, metapterygoid, and hyomandibular. It does not continue anteriorly across the midline.

**ADDUCTOR OPERCULI** (Figure 170: AD.OP.).—The fibers arise from the ventral face of the pterotic and insert along the posterodorsomedial rim of the opercle.

#### MUSCLES OF THE HYOID REGION

**VALVULUS**.—The muscle arises from the postero-medial face of the dentary and the medial face of the angular, and sweeps dorsomedially to fade into the tissues of the mandibular buccal valve.

**PROTRACTOR HYOIDEI** (Figure 169: PR.HY.).—The fibers arise from the lateral faces of branchiostegal rays 2–6 and the lateral surfaces of the anterohyal and posterohyal. The muscle inserts in a groove along the posteroventral face of the dentary.

**HYOHYOIDEI ABDUCTORES** (Figure 169: H.AB.).—The form of these muscles is very similar to that found in tetraodontoids. The sections to rays 2 and 3 are well separated, and originate from the posterior face of the lateral crista of the first ray. The section across the midline is poorly developed and separated.

**HYOHYOIDEI ADDUCTORES** (Figures 169, 170, 171: H.AD.).—The muscle is very well developed in the lateral wall of the opercular cavity, fibers arising

from the anterodorsal face of the opercle, the posterolateral hyomandibular and the fascia beneath the pterotic. Beneath the hyomandibular-opercle articulation, a bundle of fibers arises from the inner face of the lateral wall of the opercular cavity, and passes posteriorly. It fades out on the cleithrum ventral to the insertion of the protractor pectoralis. Posteroventrally in the cavity, fibers arise from the cleithrum, the fascia over the pharyngoclavicularis internus and ceratobranchial 4, and from the fascia over the anterior region of adductor IV. These bundles meet, pass laterally, and join the posterodorsal region of the main mass of the muscle in the lateral wall of the cavity.

**STERNOHYOIDEUS** (Figure 171: STH.).—The muscle originates from the anteroventral face of the cleithrum and passes anteriorly to insert on the posteroventral face of the ventrohyal. The two halves fuse extensively in the midline. The posteromedial fibers pass dorsally, curving inward to meet their antimeres, the posteroventromedial fibers attaching to the cartilagenous knob between the ventral tips of the cleithra.

#### VENTRAL BRANCHIAL MUSCLES

**PHARYNGOCLAVICULARIS EXTERNUS** (Figures 171, 172: PHC.E.).—Origin is from the ventromedial face of the cleithrum, the fibers passing medial to the pharyngoclavicularis internus and the rectus communis to insert on the anteroventral tip of ceratobranchial 5.

**PHARYNGOCLAVICULARIS INTERNUS** (Figures 171, 172: PHC.I.).—The fibers arise from the medial face of the cleithrum and pass anterodorsally to insert on the ventral faces of ceratobranchials 4 and 5, with some connection to basibranchial 3.

**OBLIQUI VENTRALES I–III** (Figures 171, 172: OBL.V.).—The first two muscles connect the hypobranchials and ceratobranchials of the first two arches. Obliquus III passes between the posterior face of the ventral process of hypobranchial 3 and the anteroventral face of ceratobranchial 3.

**TRANSVERSI VENTRALES IV, V** (Figure 172: TR.V.).—The muscles connect the anteroventral faces of the fourth and fifth ceratobranchials across the ventral midline. The posterior muscle is well developed.

**RECTI VENTRALES I–IV** (Figures 171, 172: RECT.V.).—The first muscle in this series passes from the dorsal face of the anterohyal to the antero-

ventrolateral face of ceratobranchial 1. The next three muscles arise from the anteroventral faces of ceratobranchials 2-4, and attach to the posterior faces of hypobranchials 1-3. The last of these muscles attaches to the posterior face of the ventral process of hypobranchial 3.

**RECTUS COMMUNIS** (Figures 171, 172: R.COMM.).—The fibers connect the posterior face of basibranchial 1 to the anteroventral face of ceratobranchial 5. The muscle is fibered throughout, and attaches at both ends by short aponeuroses.

#### DORSAL BRANCHIAL MUSCLES

**LEVATORES EXTERNI I, II, IV** (Figure 171: L.EXT.).—The muscles originate from the ventrolateral prootic and pterotic, and from the ventromedial face of the hyomandibular near its articulation with the skull. They are well developed, and form a sheet of fibers passing posteroventrally to insert on the dorsal faces of epibranchials 1, 2, and 4. Posterior to epibranchial 4 the muscle continues as a thick sheet of fibers which attach to the dorsolateral face of the cleithrum.

**LEVATORES INTERNI II, III** (Figure 173: L.INT.).—Levator II originates from the lateral pterotic behind the hyomandibular fossa and passes anteroventrally, medial to levator III, to insert on the dorsal rim of infrapharyngobranchial 2 and the anterodorsal face of infrapharyngobranchial 3. Levator III arises from the prootic and anteroventral face of the hyomandibular adjacent to the fossa. The fibers course posteroventrally to the dorsolateral face of infrapharyngobranchial 3.

**OBLIQUUS DORSALIS III** (Figure 173: OBL.D.).—The fibers connect the anterodorsal region of epibranchial 3 with the anterodorsal face of infrapharyngobranchial 3.

**OBLIQUUS POSTERIOR** (Figure 173: OBL.P.).—The muscle is well developed, and connects the posteromedial face of epibranchial 4 with the dorsomedial face of ceratobranchial 5.

**TRANSVERSUS DORSALIS II-IV** (Figure 173: TR.D.).—Transversus II has undergone considerable modification. The anterior fibers pass forward to attach to the dorsomedial face of infrapharyngobranchial 2. Behind them, a thinnish aponeurosis attaches to the medial face of epibranchial 2. The fibers join and sweep across the midline. Posterodorsally, some fibers attach to the posterior faces of the

exoccipital and pterotic. Posterolaterally, the fibers sweep outward and downward to attach to the anteromedial face of the cleithrum. This section lies medial to the hyohyoidei adductores and the posterior part of levator externus IV. Transversus III is a small muscle passing across the midline between the dorsomedial faces of the third infrapharyngobranchials. Some of the anterior fibers arise from the anteroventromedial faces of the third epibranchials. Transversus IV connects the anterodorsal faces of the fourth epibranchials across the midline.

**RETRACTOR DORSALIS** (Figure 173: D.RETR.).—The muscle is somewhat subdivided. Origin is from the lateral faces of the centra and neural spines of the fourth to sixth vertebrae. It inserts by a main anterior bundle onto the anteromedial face of infrapharyngobranchial 3. Behind this, a large bundle dissipates in the tissues of the esophagus. A slip of the more posterior fibers inserts on the anterodorsal wall of the swim bladder, in the region of the constriction between the halves.

**ADDUCTORES I-V** (Figures 171, 172, 173: AD.).—The first four muscles connect the anteromedial faces of epibranchials 1-4 to their respective ceratobranchials. Adductor V arises from the ventrolateral face of ceratobranchial 5 and passes dorsally to the posterolateral face of epibranchial 4.

**SPHINCTER OESOPHAGI** (Figures 172, 173: S.O.).—The ventral section passes anteromedially between the ventromedial faces of the fifth ceratobranchials. The dorsal fibers of this part are more longitudinally oriented, and form an anterior bundle to the ventral face of basibranchial 3. Dorsally, the main mass of the muscle connects the ventromedial faces of the fourth epibranchials, the ventral fibers passing out as an aponeurotic sheet over the anterior face of adductor IV. A small bundle arises from the main mass of the muscle behind ceratobranchial 5, and passes dorsomedially to attach to the posteromedial face of epibranchial 4. Medially, the fibers sweep anteriorly in a small bundle to attach to the posteromedial face of infrapharyngobranchial 3.

#### MUSCLES OF THE PECTORAL REGION

**ABDUCTOR SUPERFICIALIS** (Figure 169: ABD.S.).—Origin is from the posterior and lateral faces of the cleithrum beneath the ala laminaris externus.

A tendon inserts on the anterolateral base of each of the principal fin rays. The ventral nine rays possess anterodorsal flanges which overlap the base of the preceding ray, and the tendons attach to these flanges.

**ABDUCTOR PROFUNDUS** (Figure 169: *ABD.P.*).—The muscle originates from the ventrolateral cleithrum, the lateral coracoid, and the ventrolateral faces of the ventral radials. Insertion is on the ventrolateral bases of the principal rays, there being no section to the vestigial ray.

**ARRECTOR VENTRALIS** (Figure 169: *ARR.V.*).—The muscle is fairly well developed, and originates from the posterolateral face of the cleithrum, beneath the *ala laminaris externus*. It inserts on the anterolateral base of the medial half of the vestigial fin ray.

**ADDUCTOR SUPERFICIALIS** (Figure 174: *ADD.S.*).—The muscle has the same form as that described for tetraodontids. The ventral nine tendons insert on the dorsomedial flanges of the respective rays, the other slips inserting on the dorsomedial faces of the rays distal to their bases.

**ADDUCTOR PROFUNDUS** (Figure 174: *ADD.P.*).—The fibers arise from the medial faces of the coracoid and cleithrum and insert on the ventromedial bases of the principal rays.

**ARRECTOR DORSALIS** (Figure 174: *ARR.D.*).—The muscle is poorly developed, arising from the medial face of the cleithrum (lateral to the adductor profundus), and inserts on the base of the medial half of the vestigial fin ray.

**CORACORADIALIS** (Figure 174: *COR.R.*).—The muscle connects the enlarged medial flange of the fourth radial to the posteroventral flange of the coracoid. It is joined by a bundle of the *obliquus inferioris* which arises from the anteroventral face of the ventral postcleithrum.

**PROTRACTOR PECTORIALIS** (Figures 169, 170, 171: *P.P.*).—Origin is from the ventrolateral surface of the winglike process of the pterotic. The fibers pass posteroventrally to insert on the anterolateral face of the dorsal region of the cleithrum.

**LEVATOR PECTORIALIS**.—The muscle arises from the posterior face of the lateral process of the pterotic and inserts on the anterodorsal tip of the cleithrum.

#### MUSCLES OF THE DORSAL FIN

**INCLINATOIRES DORSALES** (Figure 169: *INC.*).—

There is a single inclinador arising from the fascia overlying the dorsal extension of the *obliquus inferioris*. It inserts on the lateral face of the first dorsal fin pterygiophore.

**ERECTORES DORSALES** (Figure 169: *EREC.*).—Origin is from the dorsal faces of the ventrolateral flanges and centra of the tenth to fifteenth vertebrae, and, posteriorly, from the ventrolateral faces of the pterygiophores. The muscles insert on the anterolateral bases of the fin rays, and are partly overlain by the depressors anteriorly, being completely covered by them posteriorly.

**DEPRESSORES DORSALES** (Figure 169: *DEPR.*).—The sites of origin are much the same as for the erectors, but somewhat more lateral. The muscles insert on the posterolateral bases of the fin rays.

**SUPRACARINALIS ANTERIOR**.—The muscle has partially fused with the *epaxialis*. It is contained in the trough formed by the bifid neural spines of the anterior vertebrae, and passes from the supraoccipital to the first pterygiophore of the dorsal fin.

**SUPRACARINALIS POSTERIOR** (Figures 169, 175*b*: *s. POST.*).—The muscle connects the last pterygiophore of the dorsal fin to the anterodorsal face of the neural spine of the penultimate vertebra. It lies between the tips of the neural spines of the intervening vertebrae.

#### MUSCLES OF THE ANAL FIN

**INCLINATOIRES ANALES** (Figure 169: *INC.*).—There are two of these muscles, both arising in the fascia over the *obliquus inferioris* and inserting on the ventrolateral face of the first anal pterygiophore.

**ERECTORES ANALES** (Figure 169: *EREC.*).—Origin is from the ventrolateral faces of the ventrolateral processes of the tenth to fifteenth vertebrae. The muscles insert on the anterolateral bases of the fin rays.

**DEPRESSORES ANALES** (Figure 169: *DEPR.*).—Origin is the same as for the erectors, the depressor of each ray arising behind the respective erector. The muscles insert on the posterolateral bases of the rays, and arise lateral to the erectors.

**INFRACARINALIS MEDIUS** (Figure 169: *INF.M.*).—The fibers arise from the anteroventral face of the first anal pterygiophore, and join with the ventrolateral section of the *obliquus inferioris* before grading into the subdermal tissue as part of the



longitudinal cutaneous system.

**INFRACARINALIS POSTERIOR** (Figure 175*b*: INF.P.).—This muscle connects the posterior face of the last anal pterygiophore and the supporting haemal spine to the anterior margin of the haemal spine of the penultimate centrum.

#### MUSCLES OF THE CAUDAL FIN

**INTERRADIALIS** (Figure 175*a*: INT.).—The muscle interconnects the caudal fin rays just distal to their bases.

**HYPCHORDAL LONGITUDINALIS** (Figure 175*b*: H.L.).—Origin is from the posteroventrolateral hypural plate, the dorsal face of the flange of the ural centrum and the centrum itself, and the neural and haemal spines and centrum of the penultimate vertebra. The muscle inserts on the bases of rays D 3–5.

**FLEXOR DORSALIS** (Figure 175*b*: F.D.).—Origin is from the lateral face of the neural spine of the penultimate vertebra, the muscle inserting on the lateral bases of rays D 3–4.

**FLEXOR DORSALIS SUPERIOR** (Figure 175: F.D.S.).—The fibers originate from the lateral faces of the neural spines of the second to fourth last vertebrae, and the dorsolateral faces of the epural and the hypural plate. The muscle inserts on the dorsolateral base of ray D 5.

**FLEXOR VENTRALIS** (Figure 175*b*: F.V.).—The fibers arise from the ventral face of the flange of the ural centrum, and the dorsolateral and ventromedial faces of the ventrolateral flanges of the second to fourth last vertebrae. Insertion is on the lateral bases of rays V 2–4.

**FLEXOR VENTRALIS EXTERNUS** (Figure 175*b*: F.V.E.).—The muscle arises primarily from the fascia on the lateral surface of the flexor ventralis, with some attachment to the lateral flange of the ural centrum. It inserts on the lateral bases of rays V 1 and 2.

**FLEXOR VENTRALIS INFERIOR** (Figure 175: F.V.I.).—Origin is from the ventrolateral faces of the third and fourth last vertebrae, the muscle inserting on the ventrolateral base of ray V 4.

#### LATERAL BODY MUSCLES

**EPAXIALIS** (Figures 169, 170, 173, 175*a*: EPAX.).—Anteriorly, the fibers arise mainly from the epiotic

and pterotic, and from the lateral faces of the bifid neural spines of the anterior vertebrae (where the fibers are poorly separated from those of the supracarinalis anterior). Posteriorly, the ventral moiety inserts on the lateral bases of caudal fin rays D 1–5. The dorsal moiety is restricted to a section arising from the dorsomedial faces of the bifid neural spines of the fifteenth and sixteenth vertebrae. It joins the aponeurosis from the posterior section of the obliquus inferioris to form an aponeurotic sheet to all the caudal fin rays.

**OBLIQUUS SUPERIORIS** (Figures 169, 175*a*: OBL.S.).—The fibers arise from the ventrolateral region of the seventh vertebra, and increase in size posteriorly. The muscle inserts on the lateral bases of the ventral caudal fin rays.

**OBLIQUUS INFERIORIS** (Figures 169, 174, 175*a*: OBL.I.).—The muscle is considerably modified. The anterodorsal section arises from the fascia over the epaxialis and from the dorsolateral tips of the first and last dorsal fin pterygiophores behind this. Ventrally, a similar attachment occurs on the last anal fin pterygiophore. The more dorsal of these fibers pass to the posterodorsal face of the postcleithrum, the middle ones attach to the posteroventral face of the coracoid, while the ventral fibers pass into the subdermal tissue, contributing to the formation of the longitudinal cutaneous. The anteroventral face of the postcleithrum gives rise to a short section which forms an aponeurosis with the coracoradialis (Figure 174). A ventral section passes posterodorsally, lateral to the erector-depressor complex of the anal fin, to attach to the anteroventral surface of the ventrolateral process of the sixteenth vertebra. This section fuses with the infracarinalis medius anteriorly, and fades into the subdermal tissue. The posteriormost section arises from the ventrolateral process of the sixteenth vertebra, and soon grades into an aponeurosis which joins that of the dorsal moiety of the epaxialis before inserting on the lateral bases of the caudal fin rays.

#### SWIM BLADDER MUSCLES

In addition to the ventral fibers of the retractor dorsalis to the anterodorsal surface of the swim bladder, the posterior border of the bladder is covered by a muscle which passes dorsoventrally across its surface (Figure 173: s.m.).

## CUTANEOUS MUSCLES

The cutaneous muscles are much like those of tetraodontids, although the transverse system is not as well developed (particularly dorsally and posteriorly). The longitudinal system is better developed than in the former group.

*Chilomycterus orbicularis* (Bloch)

## FIGURE 176

The adductor mandibulae is not as well developed as in *D. hystrix*. There is no tendon from the anterolateral face of A 1 $\alpha$  to the lips. A 2 $\alpha$  does not extend beyond the border of the orbit, and A 2 $\beta$  does not meet its antimeres across the midline at the front of the orbit. Since the posterior section of A 2 does not extend behind the orbit, the fibers of the levator arcus palatini no longer pass through the muscle.

The protractor hyoidei arises from branchiostegals 2 and 3, and possesses a distinct longitudinal myocomma about the middle of its width. The origin of the levatores externi is less from the posterodorsomedial face of the hyomandibular. Transversus dorsalis II is better developed, particularly posterolaterally. The retractor dorsalis arises from the lateral faces of the second to seventh vertebrae.

The ventralmost eight pectoral rays only possess anterodorsal processes, with the concomitant change in the insertion of the abductor superficialis. The flexor dorsalis inserts on the bases of rays D 3-4, and the flexor ventralis is subdivided near its origin. The obliquus inferioris is much reduced, being composed of only a few bundles of fibers.

In addition to the swim-bladder muscle mentioned in *D. hystrix*, there is a well-developed muscle from the anterodorsal surface of the bladder which passes forward and ventrally around the anterior end of the bladder as far as its anteroventral tip. The muscle is largely contained in the groove separating the halves of the bladder.

*Chilomycterus schoepfi* (Walbaum)

## FIGURE 177

A 1 $\alpha$  is better developed dorsally than in *D. hystrix*, and has acquired attachment to the head of the hyomandibular and the anterolateral pterotic. This region of origin is somewhat aponeurotic,

and the fibers are inseparable from those of A 2 $\alpha$ . Insertion of the additional fibers is primarily on the ventrolateral face of the maxilla. Anteroventrally, some of the fibers arise from the dentary and articular. A 1 $\beta$  is also better developed, as is the A 2 complex.

The posterodorsal section of the hyohyoidei adductores has a tendon passing posteriorly over the cleithrum to attach to the postcleithrum. The pharyngoclavicularis internus is smaller, while the externus division is larger than in *D. hystrix*. What is apparently transversus ventralis IV is modified to form an aponeurotic sheet to basibranchial 2, i.e., it is obliquely oriented, and the fibers do not meet their antimeres.

The levatores externi are as for *C. orbicularis* and transversus dorsalis II is very well developed posteriorly, with a large section attaching to the dorsomedial cleithrum. Adductor III is small, and the retractor dorsalis originates from the third to seventh vertebrae. No inclinatores dorsales or anales were separable. The anterodorsal origin of the flexor dorsalis superior is more extensive. The flexor dorsalis is also larger, with a thin aponeurosis to ray D 5. The flexor ventralis is not subdivided, and originates mainly from the medial faces of the ventrolateral flanges of the second and third last vertebrae.

The anteroventral section of the obliquus inferioris from the postcleithrum attaches to the coracoid rather than joining the coracoradialis. The section over the abdominal cavity is reduced, although not to the extent seen in *C. orbicularis*. The posterodorsomedial section is bifid, attaching to the lateral flanges of the thirteenth and fourteenth vertebrae. The posteriormost section and the dorsal moiety of the epaxialis are much reduced.

## Summary of Diodontidae

The relative development of the A 1 and A 2 sections of the adductor mandibulae varies fairly considerably, although the basic plan of the subdivisions remains constant. The sites of origin of the levatores externi and the retractor dorsalis vary, as does the relative development of the transversus dorsalis II. Other areas of the musculature showing significant variation are the flexors of the caudal fin and the development of the obliquus inferioris.

### Myological Descriptions of Representative Molids

The body outline of members of this family are illustrated in Figure 11. Two out of the three genera (possibly all monotypic) were dissected for this study, no specimens of *Masturus* being available. The mouth is small, the dorsal and anal fins very high, and rather stiff. The caudal peduncle is aborted, so that the rays of the caudal fin lie in an almost vertical line behind the dorsal and anal fins, and appear to grade into them. The pectoral fins are short. In swimming, the dorsal and anal fins flap synchronously from side to side, steering apparently being accomplished by using the caudal fin as a rudder. The body is high and thin, the shape being ellipsoid or circular. Molids possess the powerful jaws typical of gymnodonts, although their food is reported to consist of coelenterates and pelagic tunicates (*Mola*) or seaweeds (*Ranzania*). They have a worldwide distribution (*Mola* itself occurring in both tropical and cold-temperate waters). Molids are thought to be pelagic, although the possibility that they are bathypelagic cannot be ruled out.

Phylogenetically, they are usually considered to be derived from the gymnodont line before separation of the tetraodontoid and diodontid stocks.

#### *Mola mola* Linnaeus

FIGURES 178-184

#### MUSCLES OF THE CHEEK

**ADDUCTOR MANDIBULAE** (Figures 178, 179: A 1 $\alpha$ , A 1 $\beta$ , A 2 $\alpha$ , A 2 $\beta$ , A 3).—A 1 $\alpha$  is fairly small, arising from the fascia over A 2 beneath the orbit, and inserting on the posteroventral face of the maxilla. A 1 $\beta$  originates from the posterolateral face of the palatine and the lateral parasphenoid. It passes anteroventrally to insert on the posterodorsal face of the maxilla. A 2 $\alpha$  originates from the dorsolateral preopercle, the anterior and dorsal hyomandibular and by a small slip from the ventromedial face of the pterotic. It passes anteriorly, lateral to ramus mandibularis V, to insert with A 2 $\beta$  and A 3 in the Meckelian fossa. A 2 $\beta$  originates from the lateral parasphenoid (some fibers arising as far back as the posterolateral margin of the bone beneath the basioccipital), the antero-

ventral and ventral prootic, and the dorsomedial faces of the hyomandibular and metapterygoid. It lies medial to ramus mandibularis V, and inserts together with A 2 $\alpha$  and A 3 in the Meckelian fossa. A 3 arises from the lateral quadrate, symplectic, mesopterygoid, and hyomandibular and passes forward to join the insertion tendon of the A 2 complex.

**LEVATOR ARCUS PALATINI** (Figure 178: L.A.P.).—This is a small muscle, originating from the ventral face of the sphenotic at the rear of the orbit and passing down to insert on the dorsal face of the hyomandibular medial to the posterior extension of A 2 $\alpha$ .

**DILATATOR OPERCULI** (Figure 178: D.O.).—Origin is from the ventral face of the lateral process of the sphenotic. The fibers insert aponeurotically on the dorsal margin of the opercle.

**LEVATOR OPERCULI** (Figure 178: L.O.).—This is a well-developed muscle, originating from the ventrolateral face of the pterotic and inserting on the posterodorsal face of the opercle.

**ADDUCTOR ARCUS PALATINI** (Figure 179: A.A.P.).—The muscle is well developed, and passes ventrolaterally from its origin on the lateral face of the parasphenoid to insert on the dorsomedial faces of the palatine, mesopterygoid, metapterygoid, and hyomandibular. Posteriorly, the origin is aponeurotic. Anteriorly, a very small bundle of fibers passes anterolaterally from the parasphenoid to the palatine. It possesses a ventral aponeurosis, and R. maxillaris V passes through it. It bears a striking resemblance to the retractor arcus palatini of the balistoids and ostracioids.

**ADDUCTOR OPERCULI** (Figure 180: AD.OP.).—The fibers arise from the ventral face of the pterotic and insert on the posterodorsomedial face of the opercle.

#### MUSCLES OF THE HYOID REGION

**VALVULUS**.—Origin is from the ventromedial face of the angular, the fibers sweeping anterodorsomedially to fade into the tissues of the mandibular buccal valve.

**PROTRACTOR HYOIDEI** (Figure 178: PR.HY.).—The fibers arise from the posteroventral face of the dentary and attach to the lateral faces of the an-

terohyal and posterohyal. The more posteroventral fibers pass medially to a midventral raphe.

**HYOHYOIDEI ABDUCTORES** (Figure 178: H.AB.).—There are three of these muscles. The dorsalmost passes from the anterodorsomedial face of ray 2 to the posteroventromedial face of ray 3, the second has the same sites of attachment, but involving rays 1 and 2, while the third muscle connects the ventromedial face of ray 1 with the ventromedial regions of the anterohyal and ventrohyal. The muscles are well developed.

**HYOHYOIDEI ADDUCTORES** (Figures 178, 180: H.AD.).—The muscle is well developed in the lateral wall of the opercular cavity, where it attaches to the medial faces of branchiostegal rays 2–6. A small anterior slip passes ventrally to attach to the dorsal face of ray 1. Some of the dorsal fibers arise from the medial face of the preopercle and the anterodorsal face of the cleithrum. Ventrally, the fibers attach to the anteromedial face of the cleithrum and the aponeurotic fascia covering the pharyngoclaviculares. Posterodorsally, fibers of the muscle arise from the medial face of the hyomandibular, ventral pterotic, and the fascia covering the wall of the opercular cavity, which, in molids, extends dorsally to the region of the sixth to seventh vertebrae (medial to the posterior part of the pterotic and the supracleithrum). These fibers form the dorsal and medial walls of the cavity between the pterotic and the fifth vertebra, ultimately fading out in the aponeurotic sheet which attaches to the dorsomedial margin of the cleithrum.

**HYOHYOIDEUS INFERIORIS** (Figure 178: HY.IN.).—This muscle is well developed, passing dorsolaterally from the midline to the lateral face of the anterohyal and the base of the first branchiostegal ray.

**STERNOHYOIDEUS** (Figures 178, 180: STH.).—Origin is from the anteroventral face of the cleithrum. The ventral fibers pass medial to the rectus communis to the posterior face of the ventrohyal, while the dorsolateral fibers lie lateral to this muscle, also attaching to the ventrohyal.

#### VENTRAL BRANCHIAL MUSCLES

**PHARYNGOCLAVICULARIS EXTERNUS** (Figures 178, 180, 181: PHC.E.).—The muscle is well developed near its origin from the ventromedial face of

the cleithrum, but fades into an aponeurotic sheet on the inner wall of the opercular cavity, just lateral to the heart. A small ventral bundle continues anterodorsally to insert on the anteroventral face of ceratobranchial 5.

**PHARYNGOCLAVICULARIS INTERNUS** (Figures 180, 181: PHC.I.).—A large bundle of the muscle inserts on the posteroventral margin of ceratobranchial 5. Most of the fibers grade into the fascia formed by the pharyngoclavicularis externus and the hyohyoidei adductores. A small dorsal bundle continues posteriorly to attach to the medial face of the cleithrum.

**OBLIQUI VENTRALES I–III** (Figure 181: OBL.V.).—The muscles span the articulations between the ventral faces of the ceratobranchials and the respective hypobranchials of the first three arches.

**TRANSVERSI VENTRALES IV, V** (Figure 181: TR.V.).—The anterior muscle crosses the midline between the anteroventromedial faces of the fourth ceratobranchials. Transversus V spans the midline between the anteroventromedial faces of the fifth ceratobranchials, and is somewhat larger.

**RECTUS VENTRALIS I** (Figures 180, 181: RECT.V.).—The muscle connects the anterolateral faces of the first ceratobranchial and hypobranchial to the posterodorsal face of the dorsohyal.

**RECTUS COMMUNIS** (Figures 180, 181: R.COMM.).—The fibers arise aponeurotically from the posteroventromedial face of the ventrohyal. They grade into a thin, aponeurotic sheet which inserts on the anteroventral face of ceratobranchial 5.

#### DORSAL BRANCHIAL MUSCLES

**LEVATORES EXTERNI I, III, IV** (Figure 180: L.EXT.).—Origin is from the dorsomedial face of the hyomandibular, and the muscles are small. Levator I inserts on the dorsolateral face of epibranchial 1 and the ligament between the first and second ceratobranchials. Levator III inserts on the dorsolateral faces of epibranchials 2 and 3, with the bulk of the fibers serving the latter bone. Levator IV is best developed, and inserts along the dorsomedial face of epibranchial 4.

**LEVATORES INTERNI II, III** (Figure 180: L.INT.).—Both muscles originate from the posteroventral face of the prootic and pass anteroventrally. Levator II inserts on the lateral face of infrapharyngobranchial 2, while levator III inserts on the

dorsolateral faces of infrapharyngobranchials 2 and 3.

**OBLIQUUS DORSALIS III** (Figure 182: OBL.D.).—The muscle connects the posterodorsal face of epibranchial 3 with the posterodorsal faces of infrapharyngobranchials 2 and 3.

**TRANSVERSI DORSALES II, IV** (Figures 180, 182: TR.D.).—**Transversus II** arises from the midline beneath and including the ventrolateral surface of the parasphenoid. The more anterior fibers have migrated forward along the parasphenoid, so that this part of the muscle passes posterolaterally from its origin. Insertion is on the dorsomedial face of infrapharyngobranchial 2. **Transversus IV** passes across the midline between the medial faces of the fourth epibranchials.

**RETRACTOR DORSALIS** (Figure 182: D.RETR.).—Origin is from the posterodorsolateral faces of the exoccipital and basioccipital, and the neural spine of the first vertebra. The muscle inserts on the posterodorsomedial faces of infrapharyngobranchials 2–4.

**ADDUCTORES IV, V** (Figures 180, 182: AD.).—**Adductor IV** is well developed and connects the medial and posteromedial faces of epibranchial 4 and ceratobranchial 4. **Adductor V** is small, passing from the anterodorsal tip of ceratobranchial 5 to the posterolateral face of epibranchial 4.

**SPHINCTER OESOPHAGI** (Figures 180, 181, 182: S.O.).—The muscle surrounds the esophagus, attaching primarily to the posterior faces of epibranchial 4 and ceratobranchial 5. Dorsally, some fibers become longitudinally oriented, lying both lateral and medial to the retractor dorsalis. They attach to the posteromedial faces of epibranchial 4 and infrapharyngobranchial 3. Ventrally, some fibers also take on a longitudinal orientation, lying dorsal to transversus ventralis V and attaching to the anteromedial face of ceratobranchial 5.

#### MUSCLES OF THE PECTORAL REGION

**ADDUCTOR SUPERFICIALIS** (Figure 178: ABD.S.).—The fibers arise from the anterolateral face of the cleithrum and insert on the dorsolateral faces of the principal fin rays.

**ADDUCTOR PROFUNDUS** (Figure 178: ABD.P.).—Origin is from the lateral faces of the cleithrum and coracoid, the muscle inserting on the posterolateral faces of the principal rays and the lateral

base of the vestigial ray.

**ARRECTOR VENTRALIS** (Figure 178: ARR.V.).—The muscle arises from the lateral cleithrum dorsal to the abductor superficialis, and inserts on the anterodorsal face of the medial half of the vestigial fin ray.

**ADDUCTOR SUPERFICIALIS** (Figure 183: ADD.S.).—The fibers arise from the anterodorsomedial face of the cleithrum, and insert on the anteromedial faces of the principal rays some distance distal to their bases.

**ADDUCTOR PROFUNDUS** (Figure 183: ADD.P.).—Origin is from the medial faces of the cleithrum and coracoid and the posterolateral face of the latter bone. The muscle inserts on the posteromedial faces of the principal rays a little distal to their bases.

**ARRECTOR DORSALIS** (Figure 183: ARR.D.).—This is a small muscle, originating from the medial face of the cleithrum and inserting on the medial face of the medial half of the vestigial fin ray.

**PROTRACTOR PECTORALIS** (Figures 178, 180: P.P.).—The muscle originates from the posterodorsal tip of the hyomandibular and the pterotic behind it. It attaches to the anterodorsal face of the cleithrum. The medial fibers intermingle somewhat with the lateral fibers of the levator pectoralis. The muscle lies lateral to the adductor operculi but medial to the levator operculi.

**LEVATOR PECTORALIS** (Figure 180: TR.).—The fibers of this muscle pass medial to the adductor operculi, and arise from the fascia of the opercular cavity beneath the posterior extension of the hyomandibular. The fibers insert on the anterodorsomedial face of the cleithrum.

#### MUSCLES OF THE DORSAL FIN

**ERECTORES AND DEPRESSORES DORSALES** (Figures 178, 184: EREC. + DEPR.).—Only the erectors and depressors of the first two fin rays have separate tendons. In the next fourteen rays, the erectors and depressors have fused, and insert by a single tendon along the lateral face of each ray a little distal to the base. Origin is from the lateral faces of the vertebral centra and neural spines, the posterodorsal surface of the skull, and the septum in the midline dividing the dorsal and anal fin musculature. The ventral fibers are continuous with the surrounding fibers, particularly anteriorly. The

muscles to the more anterior rays tend to lie nearer the midline, those to middle rays being best developed. The lateral fibers of the more anterior muscles also take origin from the medial face of the thick, subdermal fascia (represented as cut surface in Figure 178, but not in Figure 184).

**SUPRACARINALIS ANTERIOR.**—This is a small muscle which arises from the posterodorsal face of the supraoccipital. The fibers soon grade into a long, thin tendon which attaches to the anterodorsal face of the first dorsal pterygiophore.

#### MUSCLES OF THE ANAL FIN

**ERECTORES AND DEPRESSORES ANALES.** (Figure 184: EREC. + DEPR.).—The first two fin rays have separate erector and depressor tendons, the tendons to the other fourteen fin rays being compound, owing to the fusion of the erector and depressor muscles. Insertion of these tendons is on the lateral faces of the rays a little distal to their bases. The fibers originate from the lateral septum, the centra and haemal spines of the seventh to sixteenth vertebrae, and the basal pterygiophores of the anal fin. The fibers do not encroach on the abdominal cavity, and intermingle in the dorsal region.

#### LATERAL BODY MUSCLES

**EPAXIALIS** (Figures 178, 184: EPAX.).—The muscle is much reduced. Anteriorly, it arises from the posterodorsal tip of the epiotic. It passes posteriorly as a very thin sheet, just below the skin, and gradually becomes broader. It is separated from the erector-depressor complex by a tough fascia, from the medial surface of which the lateral fibers of this latter complex arise. Vague myomeres are recognizable, there being some fifteen of them before the fibers become continuous with the section serving the dorsal eight caudal fin rays. This main posterior section arises from the lateral faces of the caudal fin supporting elements and the centra and neural spines of the fourteenth to sixteenth vertebrae. Insertion is tendinous on the anterolateral bases of the eight dorsal caudal fin rays.

**OBLIQUUS SUPERIORIS** (Figure 184: OBL.S.).—Posteriorly, vague fibers in the subdermal tissue are continuous with the anterodorsolateral surface of the muscle mass serving the ventral caudal fin rays.

The mass of this musculature arises from the lateral faces of the ventral caudal fin supporting elements and the centra and haemal spines of the fifteenth and sixteenth vertebrae. Insertion is tendinous on the anterolateral bases of the eight ventral caudal fin rays.

**OBLIQUUS INFERIORIS** (Figure 178: OBL.I.).—The muscle is reduced to two small fiber bundles. The anteroventral one arises from the posteromedial face of the coracoid, and soon fades out in the fascia overlying the abdominal cavity. The other section arises from the posteroventral tip of the postcleithrum and passes posteroventrally into the subdermal tissue, fading out just above the first pterygiophore of the anal fin. It is just possible that this section represents the residual first inclinator analis, but it seems more likely that it is part of the obliquus inferioris.

#### *Ranzania laevis* (Pennant)

##### FIGURE 185

A 1 $\alpha$  is smaller, while A 1 $\beta$  originates predominantly from the ventrolateral prefrontal and frontal. A 2 $\alpha$  is smaller, without a posterior section along the hyomandibular to the pterotic. A 2 $\beta$  does not reach the rear of the orbit, nor does it extend far in front of it. A 3 appears to be absent. The levator arcus palatini is better developed. The levator operculi originates more from the supracleithrum than from the pterotic. There is no small, anterior bundle of the adductor arcus palatini.

The valvulus arises from the anterodorsal face of the interopercle. Only a small bundle of the hyohyoidei adductores is developed in the dorsolateral wall of the opercular cavity above the sixth branchiostegal ray. Rectus ventralis II joins ceratobranchial 2 to hypobranchial 1 and basibranchial 1. Both sections of the pharyngoclaviculares are more diffuse.

There are four levatores externi. Transversus dorsalis II is more complex, since some of the posterolateral fibers attach to the anteromedial face of epibranchial 3. Obliquus dorsalis II passes from the dorsal face of epibranchial 2 to the dorsolateral region of infrapharyngobranchial 2. This may represent that portion of transversus dorsalis II which usually arises from the epibranchial, and

which has in this case become separated by the dorsal expansion of infrapharyngobranchial 2. The protractor pectoralis grades into a diffuse aponeurosis attaching to the posterodorsal face of the preopercle, and passing lateral to the levator operculi.

The first dorsal fin ray only has both an erector and a depressor. The broad tendons of the rest of the compound muscles overlap onto the base of the preceding ray. The last three tendons pass anterior to the bases of the last three rays, and meet their antimeres in the midline just above the platelike, cartilagenous pterygiophores. No fibers arise from the subdermal fascia.

The muscles to the anal fin rays are as described above for the dorsal fin. Their origin is more extensive, and includes the posteromedial face of the

cleithrum. The fibers virtually cover the abdominal cavity ventrally. The residual inclinator analis arises from the anterolateral base of the first anal pterygiophore, but fades out in the subdermal tissue before reaching the posteroventral tip of the postcleithrum. There are no fibers from the postcleithrum.

The epaxialis is restricted to a well-defined muscle serving the dorsal ten caudal fin rays, with no fibers from the subdermal tissue. The obliquus superioris is likewise well separated from the erector-depressor complex of the anal fin, and inserts on the bases of the ten ventral caudal fin rays. The obliquus inferioris is thus confined to a small bundle of fibers from the posteroventral face of the coracoid which fades out in the fascia over the abdominal cavity.

#### Phylogenetic Significance of Observed Myological Variation

Each muscle is analyzed on the assumption that nothing is known of the phylogeny of the contained units. This approach has certain drawbacks. It precludes, for example, the possibility of any explanation based on parallel or "convergent" evolution, although the former phenomenon is often traceable through the presence of reductive trends. Evidence from muscles which suggest phylogenies other than the one postulated in Figure 44 (which is derived from the evidence of 64 percent of the muscles for which phylogenetic interpretation proved possible) is reinterpreted immediately after the initial analysis of the muscle concerned, and I have attempted to provide plausible explanations for the discrepancies. In this connection, it is of interest to note that the phylogenies initially indicated by these muscles seldom agreed with each other, which is a further justification for their reinterpretation.

It should be stressed that in this interpretive section, all statements concerning phylogeny and character state are based on a consideration of the muscle being reviewed at that time only, and are not intended as generalized or particularized statements of fact outside that context. It should also be noted that one of the major difficulties in deciding character state in fish muscles is due to the lack of reliable, published information on the majority of fish groups.

In the following section, the letters "R.T." indicate that there is some reason to believe that the phylogeny indicated by that muscle may be the result of a reductive trend. The term "R.T. pars" means that only some of the phyletic lines exhibit a reductive trend in the character under consideration. These abbreviations are used whether the indicated phylogeny agrees or disagrees with that postulated in Figure 44. The Hennigian nomenclature to denote character state is used, which roughly corresponds to more widely used terms as follows: apomorph (specialized, derived); autapomorph (specialized in one lineage only—denoted by "A" in Figure 44); plesiomorph (primitive, generalized); symplesiomorph (shared primitive) and synapomorph (shared specialized). The nuances of the Hennigian nomenclature differ slightly from the alternative terms given above—plesiomorph meaning "primitive" for the group under consideration only, and always defined relative to apomorph.

Symbols used in the phylogenetic tree accompanying each muscle (Figures 12–43) are in the "List of Abbreviations." In interpreting the phylogenetic trees accompanying the muscle analyses, the following conventions are used: oblong "boxes" indicate a common ancestor for all the families whose lines arise from the "box" itself; lines which branch are to be interpreted as is usual for phylo-

genetic trees, i.e., they indicate the sequence of branching in relative time; "boxes" with one end open connect up with the similar "box" with the opposite end open, and indicate a common ancestor for the families arising from both parts (they only appear when the analysis of the muscle indicates a sequence of branching differing from the one postulated in Figure 44).

### Interpretation

1. ADDUCTOR MANDIBULAE, SECTION A 1 (Figure 12).—It is probable that the ancestral tetraodontiform condition of this section was such as is found in most perciforms with protrusile jaws—i.e., the section is not subdivided, and inserts high on the posterodorsal face of the maxilla (the anteroventral region being ligamentously continuous with A 2). As such, it is found in all the Triacanthodidae examined except the two long-snouted genera (*Macrorhamphosodes* and *Halimochirurgus*), where the protrusibility of the jaw has been lost with the elongation of the snout.

In triacanthids, the section is more intimately associated with A 2, the tendon to the maxilla lying in an almost horizontal plane, and being much reduced. This is presumably associated with a lesser degree of jaw protrusion and the more incisiform teeth, perhaps indicating that biting and nibbling are important in feeding. The only other family in which A 1 is single is the triodontids, where the muscle inserts broadly on the interdigitated elements of the upper jaw.

There is a fairly clear dichotomy between the other families. In balistoids and ostracioids, a deep subdivision to A 1 develops (A 1 $\beta$ ), lying, for the most part, medial to A 2. In monacanthids, considerable further subdivision of both sections has occurred, but not in balistids. Ostracioids have lost A 1 $\alpha$ , and A 1 $\beta$  develops three heads of origin. It seems likely that the common balistoid-ostracioid ancestor possessed a condition similar to that found in the extant Balistidae. The subdivisions presumably allow more controlled nibbling movements of the upper jaw. It is therefore not surprising to find their greatest development in the more herbivorously inclined monacanthids than in the other more omnivorous groups.

In the gymnodonts (exclusive of triodontids), there are again two subdivisions of A 1. A 1 $\alpha$

(which appears to be homologous with the balistoid A 1 $\alpha$ ) is very well developed in all families except the molids. It reaches the height of its development in the diodontids. A 1 $\beta$  (which does not seem to be homologous with that of balistoids + ostracioids) is a dorsal subdivision of A 1, and, in most cases, acquires attachment to the prefrontal region of the skull. It is well developed in molids, and enormously enlarged in the tetraodontoids, where it extends posteriorly along the parasphenoid beneath the orbit. It is small in diodontids, where most of the area of its origin in the other families has been 'taken over' by A 2 $\beta$ . The small size is probably associated with the lateral migration of the oblique eye muscles (see Winterbottom, 1971a). In these gymnodonts, the feeding emphasis is on grinding and crushing—hence the massive jaws and well-developed musculature.

Phylogenetically, the form of A 1 in the triacanthodids is assumed to be plesiomorph. Triacanthids are autapomorphly specialized, while all the other families are linked by the broad insertion of A 1 $\alpha$  on the maxilla. Triodontids possess a condition similar to what one would expect in the common ancestor of these families. The balistoids and ostracioids are linked by the development of the deep A 1 $\beta$  subdivision (see analysis above), and it appears that the balistoids form the plesiomorph sister group of the ostracioids (where A 1 $\alpha$  is lost). The molids appear to form the plesiomorph sister group of the diodontids and tetraodontoids, in which latter A 1 $\alpha$  is well developed and attaches to the preopercle laterally. Diodontids do not have the well-developed A 1 $\beta$  of the tetraodontids and canthigasterids, but this is probably an autapomorph condition. However, the enlargement of this subdivision (relative to the condition in both diodontids and molids) in the tetraodontoids does seem to be synapomorph, and thus valid as phylogenetic evidence.

2. ADDUCTOR MANDIBULAE, SECTION A 2 (Figure 13).—A 2 consists of two subdivisions in all the families except the triacanthids and the two long-snouted genera of the triacanthodids (*Macrorhamphosodes* and *Halimochirurgus*). In the more generalized tetraodontiforms, A 2 $\alpha$  lies dorsolaterally and A 2 $\beta$  lies ventromedially. The subdivisions are separated by the path of ramus mandibularis V, which passes medial to A 2 $\alpha$  and



lateral to A 2 $\beta$  (except in the ostracioid families where it lies medial to both sections, and may indicate the sister group status of the two families). It is by no means certain whether the ancestral condition of this muscle in the pretetraodontiforms was divided or undivided, and the usefulness of it as a phylogenetic indicator among the more basal groups is thus negligible. The generalized condition of section A 2 as described above is found in the triacanthodids, triodontids, balistoids, and ostracioids. The condition in triacanthids appears to be autapomorph. Balistoids are linked by the development of a ventral section, A 2 $\alpha$ , although this may be absent in certain specialized monacanthid genera. The synapomorphic condition of A 2 unites the gymnodonts (except the triodontids). Here A 2 $\beta$  has expanded dorsally and medially, above A 3, to include the parasphenoid and prootic in its sites of origin. The molids show a lesser (and thus plesiomorph) development of the section anteriorly than is found in the remaining families. Out of these last three families, only the diodontids show an enormous, anterodorsal development of the section to the ventral roof of the orbit, but this is an autapomorph condition.

In functional terms, it seems that the much broader anterior portion of the diodontid cranium is an adaptation to the inequality in the jaw musculature. The muscles to the upper jaw are much weaker, and those to the lower jaw much more powerful than in the tetraodontoids. Thus, there will be greater force tending to push the upper jaw dorsally on the contraction of the jaw musculature, this force being in some measure balanced in tetraodontoids by the almost equal force applied to the upper jaw. Hence, a stronger bracing of the elements of the upper jaw against the skull is required in diodontids, and is reflected in the broader anterior region. The same argument may apply in reverse to the canthigasterids, whose jaw musculature is relatively weaker than that of the tetraodontoids and diodontids. Here the snout region is relatively more elongate than in the other two families.

3. ADDUCTOR MANDIBULAE, SECTION A 3 (Figure 14a).—The section is of little use in phylogenetic interpretations. It is almost uniformly present in all the families (absent in three genera of triacanthodids), but is not always completely separated

from the overlying sections of A 2. In the ostracioids, however, the dorsal fibers are continuous with the ventral region of A 1 $\beta$  indicating that the Aracanidae and Ostraciidae are sister groups.

4. ADDUCTOR MANDIBULAE, SECTION A  $\omega$  (Figure 14b,c).—The section is possibly present in the triacanthodid *Hollardia* (the fibers do not, however, reach the quadrate), and is fully formed in triodontids, diodontids, and tetraodontids. In the three latter families, the muscle originates from the palatal arch (anterior face of quadrate and ectopterygoid in the diodontids and tetraodontids, and the medial face of the quadrate and metapterygoid in triodontids). Since it seems likely that the triodontid condition is autapomorph, we can say nothing further concerning the phylogeny of these three families.

The simplest inference is that the section developed soon after the gymnodont line diverged, and was correlated with the powerful, crushing "beak" of these fishes. Its absence in canthigasterids and molids ties in very nicely with their diet (canthigasterids are mainly herbivorous, or take soft-bodied marine invertebrates—molids apparently feed largely on medusoid coelenterates and salps), where powerful jaws are not necessary. It is thus feasible that the section has been lost separately in the two lineages (Figure 14c).

5. LEVATOR ARCUS PALATINI (Figure 15a).—Little can be deduced about the detailed familial interrelationships from this muscle. It is relatively well developed in triacanthoids, triodontids, and molids. It is rather poorly developed in all the other families (except a few ostraciids), but in somewhat different ways. In balistoids and ostracioids, as a result of the ventral extension of the sphenotic region immediately behind the orbit, the area containing the muscle is reduced. This may be correlated with the presence of the retractor arcus palatini (which appears to perform a similar function anteriorly—see below). In diodontids and tetraodontoids, the hyomandibular extends posterodorsally far behind the orbit. Here again the muscle is small, but this time its reduction is probably associated with the decreased importance of the palatal arch in respiration, and the concomitant increase in the first branchiostegal ray pumping mechanism.

6. DILATATOR OPERCULI (Figure 15b).—In its plesiomorph condition (as found in most perci-

forms), this muscle arises from the dorsolateral surfaces of the sphenotic and pterotic, and inserts tendinously on the tip of the dorsal process of the opercle. As such, it is present in triacanthoids and triodontids. In molids, it inserts on the anterodorsal rim of the much-reduced opercle. It is very well developed in all the other families (it is worth adding here that these are the groups in which the levator operculi is small), but there again appear to be two lines. In balistoids and ostracioids, the origin is low on the skull, and contained in the dilatator fossa (synapomorph), which is particularly well covered laterally by the sphenotic in ostracioids (also synapomorph). The insertion has become specialized in balistoids, and the fibers attach to the dorsolateral surface of the opercle as well as the dorsal rim (the latter site being of less importance in monacanthids). In ostracioids, the muscle attaches to the remains of the dorsal process of the opercle (the more so in the aracanids), this apparently being the plesiomorph condition. The muscle becomes very well developed (particularly in the dorsal region of origin) in diodontids and tetraodontoids. The frontals are included among the sites of origin, and insertion is all around the dorsal process of the opercle. Tetraodontids and canthigasterids are linked synapomorphly by the presence of an anterolateral strap of muscle fibers to the interopercle (canthigasterids), preopercle (*Lagocephalus*), or subopercle (most other tetraodontid genera). The large development of the muscle in the latter three families is again presumably associated with changes in respiratory mechanism, and would allow for more forceful operation of the opercular suction pump.

7. LEVATOR OPERCULI (Figure 16a).—Many perciforms and the triacanthoids exhibit an apparently plesiomorph condition of this muscle. It consists of anterior and posterior parts, the former primarily arising from the pterotic, the latter from the posttemporal. In all other tetraodontiforms, the muscle is single. In the balistoids and ostracioids, it is small, and arises from the secondary portion of the pectoral girdle (posttemporal and, in balistoids, the supracleithrum). In the gymnodonts, however, the muscle is well developed, and originates from the pterotic and some of the bones dorsal to it. There are two possible interpretations. Either the former condition

represents the pars posterior of the muscle and the gymnodont condition the pars anterior, or else (and more likely) the muscle was reduced to a single entity in a postulated common ancestor, this then developing in the directions outlined above. The available evidence does not seem to warrant a firm conclusion in this matter. The gymnodont condition is presumably associated with the increased use of the opercle and subopercle in respiration. Both conditions are synapomorph relative to the triacanthoid state, and indicate a common ancestor for each of the two groups which is not shared by the triacanthoid fishes.

8. ADDUCTOR ARCUS PALATINI (Figure 16b).—The plesiomorph condition, in which the muscle occupies the floor of the orbit, is found in most perciforms, triacanthoids, and triodontids. Triacanthids are somewhat specialized in that the muscle has expanded anterodorsally in front of the orbit. In balistoids, the muscle is largely in front of the orbit, in ostracioids it is completely so. In both, the anterodorsal fibers are to some degree continuous with those of the retractor arcus palatini. The muscle is also plesiomorph in molids. *Mola* (but not *Ranzania*) develops a small, longitudinal, anterior bundle which inserts on the palatine and mesopterygoid. The homology of this bundle is not clear (see below). In diodontids, the muscle is small and confined to the orbit, while the fibers continue anteriorly in tetraodontoids to connect the medial faces of the palatines across the midline beneath the vomer. Phylogenetic interpretation is difficult. The triacanthid condition appears to foreshadow the development of the retractor arcus palatini. It is thus possible that (1) the anterior bundle of *Mola* is a "de novo" development, (2) molids were derived from the ancestral stock before the separation of the triodontids, the molid sister group (i.e., all other gymnodonts) losing the anterior bundle (in which case we cannot explain the absence of the bundle in *Ranzania*), or (3) the incipient retractor arcus palatini has been lost in three separate lineages—triodontids, *Ranzania*, and the diodontids plus tetraodontoids. It seems that the acceptance of the "de novo" development of the bundle in *Mola* is the most parsimonious interpretation. However, the anterior bundle can be of little functional significance at this size, and its morphological similarity to the retractor arcus palatini of balistoids and ostra-

coids adds an element of incredulity to such an acceptance. It seems better to leave this part of the interpretation open to question (although atavism may be involved). Tetraodontoids exhibit a synapomorph condition in the anterior extension of the muscle across the dorsal midline, while there is a partial (balistoids) or complete (ostracioids) migration of the muscle in front of the orbit.

Functional interpretations pose as much of a problem as those of a phylogenetic nature. Presumably the triacanthid condition is a response to the increased length of the snout, which is continued further in the balistoids and ostracioids. However, it is not so easy to postulate a reason for the difference between the tetraodontoid and diodontid conditions, and none will be attempted.

9. **RETRACTOR ARCUS PALATINI** (Figure 17a).—The muscle has only become distinct in the balistoids and ostracioids, although its development is apparently foreshadowed by the dorsal extension of the adductor arcus palatini in triacanthids (see above). The muscle is well separated from the adductor arcus palatini and inserts tendinously on the dorsomedial face of the palatal arch in ostracioids. The muscle is less well separated with a more vertical fiber direction, and inserts on the dorsolateral face of the palatal arch in the balistoids. The balistoid condition is not considered to be wholly plesiomorph, since the muscle is very well developed. In this respect, the ostracioids are more plesiomorph; however, here the orientation of the fibers, the tendinous insertion, and the complete separation of the muscle from the adductor arcus palatini seem to be synapomorph. The condition in *Mola* has been discussed above, but the absence of a well-developed muscle in gymnodonts is scarcely surprising in view of the interdigitation of the palatine with the ethmoid-vomer region of the skull.

The development of this muscle is presumably in response to the elongation of the ethmoid region. Usually, the palatal arch is moved laterally by the contraction of the levator arcus palatini. However, the elongation of the ethmoid region decreases the mechanical advantage of this muscle, since it is situated at the rear of the orbit. The development of the retractor arcus palatini may alleviate this deficiency. The anterior fibers of the adductor arcus palatini in certain chaetodontins and pomacanthins show a somewhat similar orientation to those of

triacanthids (although not so pronounced). In acanthurids (including the Zanclinae) a well-developed retractor arcus palatini is present. The homologies of this with the balistoid-ostracioid muscle are uncertain. In balistids, the posterodorsal force of the muscle causes the arch to rotate outward about its articulation with the palatine. In monacanthids, the fibers are more vertical, and rotation could occur about the cartilagenous ball between the palatine, vomer, and ectopterygoid. In ostracioids, the movement seems to take place between the palatine and vomer.

10. **ADDUCTOR OPERCULI** (Figure 17b).—The muscle is present in all the families examined. It originates from the pterotic, prootic, or both in all except the ostracioids, where the fibers arise from the occipital region. This condition is apomorph, and links the two families.

11. **ADDUCTOR HYOMANDIBULAE** (Figure 18a,b).—The muscle has a somewhat peculiar distribution. It is present in balistids (but not monacanthids), in the aracanid *Kentrocapros* (but not *Capropygia*), in ostraciids, and in triodontids. In perciforms (?thus plesiomorph), origin is from the prootic in front of the adductor operculi. It is not certain whether the tetraodontiform condition is homologous with this, or, indeed, whether it is homologous within the tetraodontiforms themselves. In the ostracioids it originates from the exoccipital (*Kentrocapros*) or from the cleithral region (ostraciids), and this posterior origin is apparently apomorph. Its absence in gymnodonts (other than triodontids) is not surprising, since the hyomandibular becomes increasingly interdigitated with the chondrocranium, and thus less mobile. Its absence in triacanthoids may be due either to the fact that they have independently lost the muscle, or, more likely, because the muscle only developed after they had split off from the other groups (in which case the muscle is not homologous with its perciform counterpart). Its absence in monacanthids could be due to subsequent loss.

In reexamining the situation, I assume that the most generalized condition of the adductor arcus palatini is when it stretches across the posterior part of the floor of the orbit, and inserts on the palatal arch, the hyomandibular, and the opercle (forming the adductor operculi of more advanced fishes). These points of insertion are close together, and it is not unreasonable to assume a "polyphy-

letic" (i.e., independent) occurrence of the adductor hyomandibulae, which occupies the area between the adductor arcus palatini and adductor operculi. It seems probable that the triacanthoid condition, where the muscle is absent, is plesiomorph for the tetraodontiforms. The common balistoid + ostracioid-gymnodont ancestor developed a section (most likely from the adductor operculi, with which the present muscle is in contact) which attached to the hyomandibular. In the balistoid-ostracioid line, the insertion became tendinous (ostracioids), while the muscle was lost in the monacanthids (the reason why this should be so is enigmatic). Among the gymnodonts, triodontids retain what is now the plesiomorph condition, while all the other families have lost the muscle—probably because of the increasing interdigitation of the hyomandibular to the chondrocranium. Reinterpreted in this way, the phylogenetic tree changes to that shown in Figure 18*b*.

12. INTERMANDIBULARIS (Figure 19*a*).—The presence of this muscle is plesiomorph in the Teleostei. It is absent in the gymnodonts dissected, and this is presumably associated with the firm suture or fusion of the halves of the lower jaw, precluding the normal lateral movement of these elements. There is one exception to this general absence—it appears as a healthy, well-developed muscle in the tetraodontid *Xenopterus*. This is inexplicable in normal evolutionary terms—it seems fatuous to assume (1) that *Xenopterus* represents a lone, evolutionary line which split off from the gymnodont stock before any of the other derivatives or (2) that the muscle was present in the tetraodontid line up until *Xenopterus* split off, being subsequently lost in the other species. The situation is perhaps analogous to that found in the pleural ribs of tetraodontiforms—they are found only in *Triodon* and the monacanthid *Pseudaluteres* (Tyler, pers. comm.). The single possible explanation is that an unblocking of the genetic code governing the development of the muscle has occurred, possibly as a result of selection pressures acting on one of the other facets of that gene complex's pleiotropism (i.e., atavism, sensu Rensch, 1959). Although this is not a particularly convincing argument, it is certainly easier to accept than either of the above alternatives.

13. VALVULUS (Figure 19*b*).—The muscle is

present as a "de novo" development in the gymnodonts only. It may arise from the protractor hyoidei as a diffuse sheet (triodontids), or from the interopercle (tetraodontids and the molid *Ranzania*), the angular (diodontids and the molid *Mola*), or the preopercle (canthigasterids). The triodontid condition would seem to be plesiomorph.

14. PROTRACTOR HYOIDEI.—Such variation as occurs in this muscle cannot, at present, be used in phylogenetic interpretation, either because it is too sporadic, or because the character state cannot be satisfactorily determined.

15. HYOHYOIDEUS INFERIORIS (Figure 20*a,b*).—In the apparently plesiomorph condition, the muscle passes from the anterohyal beneath the first few branchiostegal rays to a midventral raphe. It is connected to the ventrohyals by tendons arising from its anterior surface. As such, it is found in triacanthoids. In all other families, the tendons are lost. The muscle is well developed in balistoids (in most monacanthid genera it is partially attached to the urohyal) and poorly so (synapomorph) in the ostracioids. It is partially fused to the protractor hyoidei in triodontids, but absent in all other gymnodonts except molids, where it is well developed.

In diodontids and tetraodontids, the loss (or fusion) of the muscle is presumably associated with the branchiostegal ray pumping mechanism. This mechanism is not found in triodontids, but here the pectoral and pelvic girdles closely underlie the hyoid arch, inhibiting the amount of lateral movement of the arch, and thus decreasing the usefulness of the muscle; that is, it does not necessarily mean that triodontids share an ancestor with diodontids and tetraodontoids, in which groups the reduction has been completed. Figure 20*b* gives the resulting phylogeny.

16. HYOHYOIDEI ABDUCTORES (Figure 21*a*).—Many generalized perciforms possess these muscles to the ventral six branchiostegal rays. Their number is usually four in tetraodontiforms (five in some balistids, three to six in monacanthids). Balistoids are apomorph in that the muscle to the first ray is enlarged, and often passes more dorsally than the other muscles. Triodontids and molids have three muscles, with the first broadly developed. The first branchiostegal ray of diodontids and tetraodontoids is enormously enlarged, and this is accompanied by an equally enormous, apo-

morph development of the muscle serving the ray. Tetraodontoids have developed a medial fiber bundle which crosses the midline beneath the branchial arches above the ventral tip of the cleithrum. This bundle is not as well developed or separated in the diodontids.

17. **HYOHYOIDEI ADDUCTORES** (Figure 21*b*).—In most perciforms, the muscle is usually somewhat diffuse, and lies in the lateral wall of the opercular cavity between and above the branchiostegal rays. As such, it is found in triacanthoids and balistoids. It is fairly well developed in the ostracioids, and there is a ventromedial slip to the anterior face of the cleithrum from the opercular valve. It is well developed in triodontids. In the other gymnodonts, it becomes even better developed, and acquires attachment to the pterotic and hyomandibular dorsally (although it is poorly developed laterally in the molid *Ranzania*). In diodontids and tetraodontoids, it is an extremely powerful muscle, with some fibers passing from the fascia between epibranchials 3 and 4 to the posteromedial wall of the cavity. In tetraodontoids, the posterolateral fibers form a semicircle around the opercular valve, connecting the dorsal cleithrum to the dorsolateral coracoid. Just below this, a bundle passes anteriorly from the coracoid to the cleithrum. The large development of the muscle in gymnodonts (particularly in the last three families) is presumably associated with the increased rigidity of the palatal arch, and the increased role of the opercular cavity in respiration.

18. **STERNOHYOIDEUS** (Figure 22*a*).—In most teleosts, this muscle is posteriorly continuous with the obliquus inferioris body musculature, and inserts on the urohyal. As thus defined, it is found in triacanthoids. In balistoids, a medial subdivision develops which inserts on the ventral tip of the urohyal. There may also be a horizontal subdivision as in some balistids (e.g., *Rhinecanthus*, *Balistapus*) or the medial subdivision may be absent (e.g., the monacanthid *Oxymonacanthus*). Ostracioids also possess this medial subdivision, but here the muscle arises primarily from the fascia between the cleithrum and the coracoid (synapomorph). In gymnodonts, the sternohyoideus is small, and is not laterally continuous with the obliquus inferioris. In diodontids and tetraodontids, the posteromedial fibers tend to sweep more dorsally than anteriorly.

It is possible (but difficult to demonstrate) that the medial section of the sternohyoideus in balistoids and ostracioids is involved in more complex respiratory movements. The small size of the muscle in gymnodonts is again presumably associated with a different breathing mechanism.

19. **STERNOBRANCHIALIS** (Figure 22*b,c*).—The plesiomorph condition of this muscle is probably such as is found among certain perciforms and triacanthoids. Here the posteromedial fibers of the sternohyoideus tend to pass dorsally and become attached (triacanthoids) to the median septum separating the opercular cavities from each other and from the heart. The fibers separate out farther in triacanthids, balistoids, and ostracioids. Insertion is still broad and somewhat diffuse in triacanthids. In balistoids, the anterior aponeurosis attaches to the urohyal, while the posterior one inserts on hypobranchial 3. Two subdivisions are also present in the ostracioids, the first including hypobranchial 3 and the second including ceratobranchial 4 in sites of insertion (these subdivisions in ostracioids are completely separate from each other and the sternohyoideus). Both conditions appear to be synapomorph, apparently arising from different directions of consolidation of the broad aponeurotic sheet probably present in the common ancestor. The muscle is absent in all gymnodonts. In a broad context, this is plesiomorph, for the muscle has seldom been reported in perciforms (although Dietz, 1914:133, reports its presence in gobioids, and the orientation of the posteromedial fibers of the sternohyoideus in many acanthopterygians). If, however, one accepts that the gymnodonts are tetraodontiforms (and the evidence is impressive), then it is true to say that the subsequent loss of the muscle is apomorph.

Since no tetraodontiform possesses well-developed toothed, lower pharyngeals, and since the sternobranchialis attaches anteriorly onto the branchial arches, it seems that its presence must be correlated with respiration (by aiding the depression of the branchial and hence hyoid arches), and its absence may once again be referable to the branchiostegal ray pumping mechanism of the diodontids and tetraodontoids. This latter may not be wholly correct, since the muscle is also absent in triodontids and molids. Possibly it was originally lost by a common ancestor similar to *Triodon*, where the cleithrum closely underlies the branchial

basket (and hence there is little room for vertical movement of the branchial and hyoid arches).

It is also possible that the similarity of the triacanthid and balistoid-ostracioid condition is due to parallel evolution. If the triacanthoid condition is plesiomorph for tetraodontiforms, then the muscle may have become consolidated and separated in those two lines independently. Thus, the common balistoid + ostracioid-gymnodont ancestor may well have retained the triacanthoid condition, and the gymnodonts themselves may never have developed a sternobranchialis. This view is expressed as an alternative in Figure 22c.

20. PHARYNGOCLAVICULARIS EXTERNUS (Figure 23a).—The muscle is consistently present in perciforms, tetraodontiforms, and many other fishes. Variations found in tetraodontiforms were the large development of the muscle in ostracioids, its bifid nature in many monacanthids, the triple insertion in canthigasterids, and the medial position relative to the pharyngoclavicularis internus in diodontids. Only the first has phylogenetic significance, the other variations being autapomorphic.

21. PHARYNGOCLAVICULARIS INTERNUS (Figure 23b).—Normally, this muscle passes horizontally forward from the medial face of the cleithrum to insert on the anteroventral surface of ceratobranchial 5. It is present in this form in triacanthoids, ostracioids, and triodontids. In triacanthids, the insertion is broad and by way of numerous tendons. In molids, the whole muscle is broad and diffuse. Balistoids are linked by the insertion of the muscle on ceratobranchials 4 and 5. Diodontids and tetraodontoids are specialized in that some fibers insert on basibranchial 3. In addition, tetraodontoids possess a section of the muscle which crosses the midline.

22. OBLIQUI VENTRALES (Figure 23c).—In most fishes, there are three pairs of these muscles, which span the ventral articulations between the ceratobranchials and hypobranchials of the first three arches. Fibers of obliquus ventralis III often attach to the arch-shaped ligament between the ventral processes of the third hypobranchials. This condition is met with in triacanthoids and balistoids, with minor variations. In monacanthids, the muscle of the second arch is absent; except in *Oxymonacanthus*; the third muscle is also absent in *Anacanthus*. In ostracioids, only obliquus ventralis III is present—a synapomorph condition link-

ing the two families. Triodontids have lost the muscle of the first arch, but the other two are well developed. All other gymnodonts have lost the arch-shaped ligament between the third hypobranchials. Molids and diodontids have all three obliqui ventrales present, but only the third is present in tetraodontoids. Although this could be interpreted as a link between the tetraodontoids and the ostracioids, I feel that the loss of the arch-shaped ligament and associated muscle fibers is far more subject to the laws of parsimony than the postulated loss, in more than one phyletic line, of muscles whose absence or presence is more labile.

23. TRANSVERSI VENTRALES (Figure 24a).—Most fishes possess two of these muscles, which connect the ventromedial faces of the fourth and fifth ceratobranchials across the ventral midline. There is little variation in them in tetraodontiforms. Transversus ventralis V consists of separate anterior and posterior sections in balistids. In monacanthid, both muscles consist of two sections, which cross over each other in the midline (the relative position of one to the other being variable). In addition, there is a third transversus ventralis between the ventral tips of the third hypobranchials—the muscle apparently being formed from fibers contributed by obliquus ventralis III and rectus ventralis IV. Transversus ventralis IV is single in the monacanthid *Paraluteres*. Canthigasterids possess only the fifth muscle—it seems probable that the fourth has fused with that part of the pharyngoclavicularis internus that crosses the midline just ventral to the fourth ceratobranchials.

24. RECTI VENTRALES (Figure 24b).—These muscles, which interconnect the basal regions of the arches to one another, are of mosaic occurrence in teleosts. The most frequent one (often called the interarcuales III/IV) connects the anterior tip of ceratobranchial 4 to the ventral process of hypobranchial 3, usually with some fibers attaching to the arch-shaped ligament between the hypobranchial processes. Triacanthoids and triodontids have this muscle, as well as one between ceratobranchial 1 and the dorsohyal. Among the molids, *Mola* has only the first rectus, while *Ranzania* also possesses the second muscle. However, neither of them possesses a rectus IV. In the triacanthids, balistoids, and ostracioids, recti I, II, and IV are

present. Rectus II attaches primarily to the urohyal or to its antimere where the urohyal is small or absent (ostracioids). Balistoids are apomorph in the possession of an extra section to the fourth rectus (the original section being absent in the monacanthids *Paraluteres*, *Oxymonacanthus*, *Pseudalutarius*, and *Anacanthus*, and poorly developed in most other monacanthid genera). Diodontids and tetraodontoids possess four rectus muscles, the tetraodontoids being linked by the presence of a lateral division of the first rectus, which attaches to the lateral face of ceratobranchial 1 (canthigasterids) or to the dorsomedial face of the hyomandibular (tetraodontids). Since the arch-shaped ligament between the ventral processes of the third hypobranchials is absent in the last three families mentioned, the fourth rectus attaches to the posterior face of the ventral process of hypobranchial 3.

25. **RECTUS COMMUNIS** (Figure 25a).—The muscle is found throughout the acanthopterygian fishes, and usually passes from the urohyal to the anteroventral face of ceratobranchial 5. It is present in this condition in the triacanthoids, balistoids, ostracioids, and triodontids. In certain monacanthid genera, two small bundles of muscle fibers arise from the posterior face of transversus ventralis III and attach to the dorsal faces of the tendons of this muscle. They apparently represent the remains of the ventral sections of rectus IV, whose posterior sites of attachment have shifted from the anteroventral faces of the fourth ceratobranchials onto these tendons. The remaining families of gymnodonts have lost the urohyal, and the muscle originates from the ventrohyal (except diodontids, where the origin is from the posterior face of basibranchial 1). Tetraodontoids are specialized in that both the origin and insertion are tendinous, the muscle fibers being confined to a belly in the middle of the length of the muscle.

26. **LEVATORES EXTERNI** (Figure 25b).—There are generally four of these muscles, which originate from the prootic region of the skull beneath the hyomandibular fossa and insert on the dorsolateral faces of epibranchials 1-4. Often, as in a number of tetraodontiform families, the manner of insertion varies—e.g., the muscle of the first arch may send a slip of fibers to the second arch. Triacanthoids and triodontids exhibit the presumed plesiomorph condition. Balistoids and ostracioids are

linked by the fact that the origin of the muscles is from the ventral surface of the prootic shelf, which appears to have evolved for this purpose. Ostracioids are apomorph in that the enlargement of the shelf has allowed the anterior migration of the branchial arches and the associated musculature to a position beneath the orbit. Gymnodonts other than triodontids have the fourth levator much enlarged. In molids, the entire origin of these muscles is from the dorsomedial face of the hyomandibular. Diodontids and tetraodontoids have in common the even greater development of levator IV, and the insertion of its posterior fibers on the cleithrum. Origin here includes the pterotic as well as the prootic (some fibers arising from the hyomandibular in diodontids).

27. **LEVATORES INTERNI** (Figure 25c).—The muscles generally originate from the prootic, and, in perciforms, insert on infrapharyngobranchials 2 and 3. They are found as defined above in triacanthoids and balistoids. Levator III usually lies somewhat lateral to levator II, and originates more posteriorly. Ostracioids show an enormous development of these muscles, whose origin has expanded to include not only the prootic, but the pterotic, epiotic, exoccipital, and (ostraciids) parasphenoid as well. Much of the origin is thus from the posterior face of the skull. In triodontids, levator II inserts on infrapharyngobranchials 2 and 3, while in molids levator III inserts on these bones. Diodontids and tetraodontoids are linked by the posterior migration of the origin of levator II to the pterotic, the fibers crossing medial to those of levator III at an angle of about 45 degrees. In the insertion of these muscles, tetraodontoids are similar to molids, and diodontids more like triodontids, but the character state at this level is difficult to determine. Tetraodontoids possess a medial connection of levator II to the lateral face of transversus dorsalis III.

28. **OBLIQUUS DORSALIS** (Figure 26a).—Perciforms usually possess a single such muscle between the infrapharyngobranchial and epibranchial of the third arch. This condition is found in triacanthoids, balistoids (except the monacanthid *Aluteres*), aracanids, triodontids, and diodontids. Balistoids have developed an additional anterior section which connects infrapharyngobranchial 2 to epibranchial 3. Molids show some familial variation. In *Mola*, most of the fibers attach to

infrapharyngobranchial 2, while in *Ranzania* an obliquus dorsalis II has developed between the infrapharyngobranchial and epibranchial of the second arch (possibly being derived from transversus dorsalis II). Tetraodontoids are linked by the fact that epibranchial 4 contributes partially (tetraodontids) or wholly (canthigasterids) to the lateral site of the muscle's attachment. In both these families, fibers pass anteromedial to infrapharyngobranchial 2.

29. **OBLIQUUS POSTERIOR.**—The muscle is present in all the tetraodontiform families except the molids (it is also absent in the monacanthid *Anacanthus*). Frequently, fibers of this muscle intermingle with those of the sphincter oesophagi or adductor V. Nothing could be deduced from it phylogenetically.

30. **TRANSVERSI DORSALES** (Figure 26*b*).—In the plesiomorph condition, there are two such muscles which connect the epibranchial, infrapharyngobranchial, or both elements across the midline between the second and third arches. Triacanthoids and balistoids exhibit this condition, except that most of the fibers of transversus II arise from the lateral face of the parasphenoid instead of from the midline. In the latter group, some fibers of transversus III may attach to epibranchial 4. Ostraciids, on the other hand, have four such muscles, inserting on epibranchials 1–4. The fibers serving epibranchials 3 and 4 are poorly separated from each other. Gymnodonts appear to show almost all possible sites of insertion. In triodontids, the anterior muscle inserts on epibranchial 4 and infrapharyngobranchial 2, the posterior one attaching to epibranchial 3. Molids have an anterior muscle passing posterolaterally from the parasphenoid to infrapharyngobranchial 2 (and epibranchial 3 in *Ranzania*). Diodontids possess the anterior muscle to the third epibranchial and infrapharyngobranchial, while the fibers of the posterior muscle insert on epibranchial 4. In tetraodontids, transversus II arises partially from the parasphenoid, inserting on infrapharyngobranchial 1, epibranchials 1 and 2, the medial face of levator internus II, with some fibers passing to the wall of the opercular cavity. Transversus II inserts on epibranchials 3 and 4. Canthigasterids have the anterior muscle to infrapharyngobranchial 2 and the medial face of levator internus II, and the posterior fibers to epibranchial 4. In view of this incredible diver-

sity, phylogenetic interpretation does not seem warranted, except to state that the tetraodontids and canthigasterids are sister groups, since they share the unique anastomosis of fibers with those of levator internus II.

31. **RETRACTOR DORSALIS** (Figure 27*a*).—This muscle, which, in the plesiomorph condition, connects infrapharyngobranchial 3 to the anterior portion of the vertebral column, is found as such in triacanthoids and ostracioids. All other families have become specialized in the site of insertion, origin, or both, and all (with one exception) in different ways. In both balistoid families, the origin of the muscle has shifted anteriorly onto the lateral face of the basioccipital, the insertion remaining on infrapharyngobranchial 3.

32. **ADDUCTORES** (Figure 27*b*).—In most teleosts, there are two of these muscles, adductor IV connecting the medial faces of the fourth epibranchials and ceratobranchials and adductor V connecting ceratobranchial 5 to epibranchial 5 or, when that bone is absent (as in most fishes), to epibranchial 4. This latter condition is met with in triacanthoids, balistoids, triodontids, and molids. Ostracioids are linked by the loss of adductor V (ostraciids having lost adductor IV as well). In diodontids and tetraodontoids, each arch possesses an adductor (except the tetraodontid *Arothron*, where adductores III and IV are absent).

33. **SPHINCTER OESOPHAGI** (Figure 27*c*).—The normal condition of this muscle, where it simply encircles the esophagus behind the gill arches, is found in the triacanthoids. Balistoids are linked by the possession of a bundle of fibers passing dorsomedially from epibranchial 4 to infrapharyngobranchial 3, while ostracioids possess a pair of ventral tendons attaching to the medial faces of the cleithra, and lack a section of the muscle passing anterodorsal to the retractor dorsalis. Gymnodonts all have a longitudinal bundle of fibers passing posteriorly from at least one infrapharyngobranchial, and all of them except the triodontids have a similar orientation of the anteroventral fibers. Diodontids, canthigasterids, and some tetraodontids possess a lateral bundle passing anterior to (and sometimes attached to) the epibranchial-ceratobranchial region of the fourth arch. In addition, the ventral longitudinal bundle in these three families attaches to the basibranchials (to the third in diodontids and tetraodontids, where it



seems to be plesiomorph, and to the first in canthigasterids). Tetraodontids and canthigasterids have also developed a partial separation between the more dorsal longitudinal bundle and the ventral transverse component of the ventral region of the muscle.

34. **ABDUCTOR SUPERFICIALIS** (Figure 28a).—The fibers originate from the posterior face of the *ala laminaris externus* and the lateral cleithrum behind it. Tendons insert on the anterolateral bases of the principal fin rays. The only variation of phylogenetic significance in tetraodontiforms is found in diodontids and tetraodontoids. Here, some ventral (diodontids, canthigasterids) or all the rays (tetraodontids) develop anterodorsal flanges from their bases, at the same time losing the posteroventral flange. Consequently, the tendon of the abductor superficialis inserts on the flange rather than on the anterodorsal base of the ray. Molids lack flanges on the fin rays, both laterally and medially.

The development of the anterodorsal flange appears to be related to the more vertical axis of the fin, and would seem to allow better control of the fin rays.

35. **ABDUCTOR PROFUNDUS** (Figure 28b).—The muscle arises from the coracoid and posterior cleithrum beneath the abductor superficialis, and inserts on the tips of the posteroventral flanges of the principal and vestigial fin rays. In diodontids and tetraodontoids it inserts on the posteroventral base of the shaft of some ventral or all the rays, for the reasons discussed above. Both monacanthids and diodontids lack a section of the muscle to the vestigial fin ray, but the former do not possess the anterodorsal flanges of the ventral fin rays.

36. **ARRECTOR VENTRALIS**.—Origin is from the lateral face of the cleithrum above and beneath the abductor superficialis, the fibers inserting tendinously on the anterolateral face of the medial half of the vestigial fin ray. No significant variations were noticed in the tetraodontiforms examined.

37. **ABDUCTOR SUPERFICIALIS** (Figure 28c).—There is little variation in the form of this muscle among tetraodontiforms. However, diodontids and tetraodontoids have developed dorsally directed flanges on the ventral six to nine rays, with a concomitant loss of the ventral flanges. The tendons serving these rays insert on the flanges

rather than on the shaft of the rays distal to their bases. The possible explanation is the same as that advanced for the analogous flanges on the lateral halves of the rays, as discussed under the abductor superficialis

38. **ABDUCTOR PROFUNDUS** (Figure 29a).—Once again, little can be said except that the diodontids and tetraodontoids apparently share a common ancestor, the ventral six to nine tendons inserting at the base of the ray instead of on the now non-existent ventral flanges.

39. **ARRECTOR DORSALIS** (Figure 29b).—Origin of the muscle is primarily from the medial face of the cleithrum, the insertion being on the medial face of the vestigial fin ray. All gymnodonts show a considerable reduction of the muscle, which, in addition, becomes covered medially by the adductor muscles (the latter also occurs in aracanids, but here the arrector dorsalis is well developed).

40. **CORACORADIALIS** (Figure 29c,d).—The fibers of this muscle generally connect the posterodorsal region of the coracoid to the posteroventral face of the fourth radial, in the apparently plesiomorph condition. As such, it is found in triacanthodids, monacanthids, aracanids (small), triodontids, and tetraodontids. In balistids and triacanthids it is a well-developed muscle, originating mainly from the fascia over the medial face of the adductor profundus; in ostraciids and molids it is absent; and in diodontids some of the dorsal fibers are continuous with fibers of the *obliquus inferioris*. The two former apparently synapomorph conditions give rise to the phylogeny in Figure 29c.

In the above analysis, the muscle's form was interpreted as linking the triacanthids and balistids as sister groups, and also linking the ostraciids and molids together. To take the latter first, there is a reductive trend in the ostracioids—the muscle is small in aracanids and absent in ostraciids. Molids are unique in possessing an anterior prong of the postcleithrum which articulates with the lateral surfaces of the radials. It is doubtful whether the radials are very mobile under these circumstances (the apparent function of the coracoradialis), and it is not surprising that the muscle is absent in molids.

The large form of the muscle and its position medial to the adductor series in triacanthids and balistids is difficult to explain in terms of the proposed phylogeny. It should theoretically either

be present in this form in all the families (in which case it has reverted to the ancestral condition in four separate lineages—triacanthodids, monacanthids, ostracioids, and gymnodonts), or else it has reached the same modified, enlarged condition separately in triacanthids and balistids. The former seems unlikely. The latter is possible, especially if one could offer an explanation as to why this should occur, and what advantage(s) it confers. However, this cannot be done until the function of the muscle has been accurately determined, and its influence on the mechanism of the pectoral fin defined.

41. **ADDUCTOR RADIALIS** (Figure 30a).—This muscle is present in many perciform groups, and is found in the triacanthoids, where it inserts on a maximum of three rays. It is absent in all other tetraodontiform families.

42. **PROTRACTOR PECTORALIS** (Figure 30b).—The muscle is consistently present in most euteleosts including tetraodontiforms (except the ostracioids). It arises from the pterotic and inserts on the anterodorsal face of the cleithrum. In molids, it is reduced to a thin strip of fibers. In diodontids and tetraodontoids, the muscle inserts on the anterodorsolateral face of the cleithrum, and, in tetraodontoids, part of the muscle attaches to the supracleithrum. This seems to be associated with the operation of the postcleithral apparatus (see Winterbottom, 1971a, for details).

43. **LEVATOR PECTORALIS** (Figures 30c,d).—In most perciforms and triacanthodids, the muscle passes from the pterotic to the supracleithrum, cleithrum, or both. Triacanthids possess a cleithrum which abuts firmly against the skull, and the muscle is absent. It is also absent (apparently for a similar reason) in ostracioids. In balistoids, it attaches to the anterodorsomedial rim of the cleithrum, mainly in front of the supracleithrum. In all gymnodonts, the fibers pass posteromedially to the supracleithrum to insert on the tip of the posterodorsal extension of the cleithrum. In molids, the muscle is much reduced, but still passes medial to the supracleithrum to attach to the cleithrum (Figure 30c).

In the above analysis, the point of disagreement is the linking of the triacanthids and ostracioids by virtue of the absence of the muscle. In both cases, the reason appears to be the very firm attachment of the pectoral girdle to the skull, result-

ing in the decrease or loss of movement of the girdle. However, this seems to have taken place for different reasons. In triacanthids, it is associated with increased support for the pelvis and the pelvic spines. In ostracioids, there is no pelvis, and the increased rigidity results from the close association of the pectoral girdle with the bony cuirass of the exoskeleton, (Figure 30d).

44. **ARRECTOR DORSALIS PELVICUS** (R.T.) (Figure 31a).—This muscle, which is found in most perciforms and a number of other fishes, originates from the dorsolateral face of the pelvis and inserts on the pelvic spine. It is present in triacanthoids, but absent in all other tetraodontiform families. The great development of the muscle relative to the presumed plesiomorph condition in the triacanthoids seems synapomorph. However, the loss of the muscle may be synapomorph, or it may have occurred in more than one lineage. Although the former view is tentatively followed here, the presence of a rather normal-looking pelvis and pelvic fin in the Eocene *Eoplectus* may mean that it has been lost independently in the gymnodont and the balistoid-ostracioid lineages.

45. **ARRECTOR VENTRALIS PELVICUS** (R.T.) (Figure 31b,c).—The fibers of this muscle arise from the ventral face of the pelvis and insert on the pelvic spine. It is extremely well developed in the triacanthoids (more so than in the presumed plesiomorph condition exemplified by perciforms), much reduced (or absent—five genera of monacanthids) in balistoids, and absent in all the other families.

The absence of the muscle in ostracioids and gymnodonts needs reinterpreting, since it is apparently the result of parallel evolution. Ostracioids have lost the pelvic girdle as a result of the development of the exoskeleton; in gymnodonts, its reduction and loss is either associated with the body form (molids) or with the inflatory abilities. It is not certain whether the muscle followed the same reductive processes in the balistoids and ostracioids (i.e., the balistoid condition may be plesiomorph for the two groups), and therefore its presence cannot be used to link the balistids and monacanthids.

46. **ADDUCTOR SUPERFICIALIS PELVICUS** (R.T.) (Figure 32a,b).—In perciforms, the muscle inserts both on the pelvic spine and on the pelvic fin rays. A single slip to a pelvic fin ray was found only in the triacanthodid *Parahollandia*. The sec-

tion to the pelvic spine is very well developed in triacanthoids, much reduced and passing through a bony canal in balistoids (absent in five monacanthid genera), and absent in all the other families.

In the reinterpretation of this muscle, the reasoning used for the arrector ventralis pelvici applies in the same way, except that the passage of the tendon through a narrow, bony canal in balistoids is considered to be synapomorph, and thus links the two families as sister groups.

47. *ADDUCTOR PROFUNDUS PELVICUS* (R.T.) (Figure 32c).—Among the perciforms, this muscle inserts on the bases of the pelvic fin rays. It is found only among members of the Triacanthodidae (but is absent in seven of the genera—see Winterbottom, 1970).

Since this muscle is very much reduced, and frequently absent, in the triacanthoids, the trend in its reduction seems obvious. It is, therefore, better to assume that no phylogenetic information can be deduced from it at present.

48. *INCLINATOIRES DORSALES* (R.T.pars) (Figure 33a,b).—In the apparently plesiomorph condition, these muscles originate from the fascia overlying the epaxialis and insert on the lateral bases of the spines and rays of the dorsal fin. They are present to the spines only in the triacanthoids, where triacanthoids may have up to six (inserting on the spines and the basal pterygiophores) and triacanthids possess two to four (inserting only on the pterygiophores). The muscles attach to all the dorsal fin rays in triacanthoids, balistoids, and triodontids. They are much reduced or absent in all the other families (0–1 in aracanids and diodontids, absent in molids and ostraciids, 2 to the posterior rays in canthigasterids, and continuous with the transverse cutaneous attaching to the pterygiophores in tetraodontids—see Figure 33a).

In the initial interpretation, the ostracioids were linked with the gymnodonts minus triodontids. This was based on the loss or reduction of the muscles in these families. In ostracioids, the loss seems to be associated with the large development of the erector and depressor dorsales muscles, and the reduction and freeing of the dorsal moiety of the epaxialis (their normal site of origin). This is taken a step further in molids, where the epaxialis almost entirely disappears, and the erector and depressor muscles are enormously enlarged. Inclinator muscles are also reduced or absent in diodontids and tetra-

odontids, possibly because the fibers become associated with the transversus cutaneous system. In addition, there may well be an elusive, functional reason. In all cases where the muscles are reduced or absent, the fin is short based, and, when used in locomotion, it flaps synchronously from side to side with the anal fin (Figure 33b).

49. *ERECTORES DORSALES* (R.T.pars) (Figure 34a,b).—Generally, these muscles are fairly small, and insert on the anterolateral base of each spine and fin ray. In the spiny dorsal fin, triacanthoids possess up to six, triacanthids up to five, while there are two in balistoids and triodontids. Since there is overlapping variation in the first two families, these muscles cannot be used to differentiate between them. They are absent in all other families (which do not possess a spiny dorsal fin). Those to the fin rays are much enlarged in ostracioids, and are enormous, being partially to wholly fused to the depressors in molids (Figure 34a).

In the initial analysis, the ostracioids were linked with the gymnodonts (minus triodontids). This is apparently the result of a reductive trend, since the former group would have little use for a spiny dorsal fin (being encased in thick, bony armor) and, as in the gymnodonts mentioned, loss of the spiny dorsal fin may well be associated with the posterior migration and small size of the soft dorsal fin (Figure 34b).

50. *DEPRESSORES DORSALES* (R.T.pars) (Figure 34c,d).—In the most plesiomorph condition, each spine and fin ray receives a depressor muscle. There are up to six in the spiny dorsal fin of triacanthoids, up to five in triacanthids, three in balistids, two in most monacanthids, and one in triodontids. The muscles to the fin rays are enlarged in ostracioids, and fused to the erectors in molids.

Once again, a reductive trend is apparent. The postulated ancestor of the balistoids + ostracioids + gymnodonts must have possessed a spiny dorsal fin. This is retained symplesiomorphly in the balistoids, but lost in the ostracioids (the same reasoning used for the erectors dorsales applies here). Triodontids are plesiomorph in the retention of a single depressor to the spiny dorsal fin, the fin being absent in all the other gymnodonts.

51. *INCLINATOIRES ANALES* (Figure 35a).—These muscles generally insert on the lateral bases of all the anal fin rays. In all families (except most ostracioids) there is a residual inclinator attaching

to the distal face of the first basal pterygiophore. It is well developed in balistoids, and attaches to the tip of the postcleithrum in most tetraodontoids. There are 0-2 normal inclinator in diodontids, and four in canthigasterids. Molids show two extremes in the form of the residual inclinator. In *Ranzania*, the muscle attaches to the base of the pterygiophore and fades into the subdermal connective tissue, while in *Mola* it attaches to the tip of the postcleithrum but does not reach the pterygiophore. It is therefore described as part of the obliquus inferioris, for it seems as likely to be part of this muscle as to be an inclinator. Inclinator to the fin rays are reduced (tetraodontoids) or absent (most ostracioids, some diodontids and molids). In view of the intrafamilial variation, no interpretation will be placed on this facet of the distribution of the muscle.

52. **ERECTORES ANALES** (Figure 35*b*).—The only variation found in this muscle complex is in ostracioids (where the origin is more lateral owing to the divergent nature of the pterygiophores) and in molids (where the muscles are enormously developed, and partially to wholly fused with the depressores anales).

53. **DEPRESSORES ANALES** (Figure 35*c*).—The remarks made in connection with the erectores anales apply to this muscle complex as well.

54. **SUPRACARINALES ANTERIOR (R.T.)** (Figure 36*a,b*).—The muscle usually passes from the supraoccipital region of the skull to the first pterygiophore of the dorsal fin. As such, the muscle is present in triacanthoids, balistids, aracanids, and triodontids. It is absent in monacanthids and ostraciids, being small and largely tendinous in molids. In diodontids and tetraodontoids, the lateral fibers insert on the dorsomedial faces of the first few bifid neural spines (Figure 36*a*).

The reduction and loss of this muscle has occurred in the monacanthids (where the pterygiophore of the spiny dorsal fin has become firmly attached to the cranium) and ostraciids (where the long pterygiophore to which the muscle attaches in aracanids is greatly reduced). Thus, the processes that resulted in the loss of this muscle are different in the two families (Figure 36*b*).

55. **SUPRACARINALIS MEDIUS** (Figure 36*c*).—The muscle appears to have arisen a number of times during the evolution of the teleosts. It occupies the dorsal midline between the two dorsal fins,

where these are separate. In the tetraodontiforms, its presence is apomorph, and it is found only in the balistoids. These two families are the only ones where the anterior migration of the spiny dorsal fin has separated it from the soft dorsal fin. In all other forms (apart from the triacanthoids), the spiny dorsal fin has apparently migrated posteriorly.

56. **SUPRACARINALIS POSTERIOR.**—In the normal teleostean condition, this muscle connects the last pterygiophore of the soft dorsal fin with the neural spine of the last complete vertebra, attaching to the tips of the neural spines of the intervening vertebrae. The variations found in tetraodontiforms are both autapomorphs—the muscle is absent in molids, and attaches to the dorsomedial faces of the bifid neural spines in diodontids.

57. **INFRACARINALIS ANTERIOR (R.T.)** (Figure 37*a,b*).—In the apparent plesiomorph condition (such as is found in most teleosts), the fibers originate from the posteroventral regions of the cleithrum and coracoid and pass posteriorly to insert on the anteroventrolateral face of the pelvis. Triacanthoids are apparently synapomorph in that the muscle has partially fused with both the arrector dorsalis and ventralis pelvici. In balistoids, the muscle inserts in a lateral fossa along the anterolateral face of the pelvis, while in triodontids it inserts on the lateral face of that bone. It is much reduced and intermingles with the longitudinal cutaneous in tetraodontoids, and is absent in ostracioids, molids, and diodontids (in which latter family it has probably become fully incorporated in the longitudinal cutaneous, losing both sites of origin and insertion).

The loss of this muscle in ostracioids is correlated with the loss of the pelvis and the absence of any alternative function for the muscle to perform, such as is found in diodontids and tetraodontoids. This is probably also true of the molids. As pointed out, it seems likely that in the diodontids the muscle has become completely incorporated into the longitudinal cutaneous system.

58. **INFRACARINALIS MEDIUS (R.T.pars)** (Figure 37*c,d*).—The muscle normally connects the posterior edge of the pelvis with the anteroventrolateral face of the first basal pterygiophore of the anal fin. It is usually in intimate contact with the obliquus inferioris dorsally. Triacanthoids are apparently autapomorph in the distinct separation

of the muscle from the obliquus inferioris. In diodontids and tetraodontoids, the fibers join with the obliquus inferioris in giving rise to the longitudinal cutaneous system, the former family having lost the anterior connection of the muscle with the cleithrum. It is absent in ostracioids and molids (Figure 37c).

The absence of the muscle in the two latter groups is probably due to the same causes as postulated in paragraph 57 for the infracarinalis anterior. This involves the independent loss of the pelvis and the concomitant lack of an alternative function for the muscle to perform (with the same explanation of its presence in diodontids and tetraodontoids).

59. *INFRACARINALIS POSTERIOR*.—The muscle connects the last basal pterygiophore of the anal fin to the last haemal spine or the parhypural. The only significant variation noted in tetraodontiforms was the absence of the muscle in molids.

60. *INTERRADIALIS*. (Figure 38a).—In most teleosts, this muscle interconnects the lateral faces of the caudal fin rays together, lying a little distal to their bases. It is absent in molids. In diodontids and tetraodontoids, the fibers tend to course vertically (rather than at an anteriorly inclined angle), and also tend to be superficially continuous.

61. *HYPCHORDAL LONGITUDINALIS*. (Figure 38b).—Origin is from the ventral hypural region, often including the parhypural and the ural centrum. The plesiomorph condition for the tetraodontiforms seems to involve the insertion of the tendons on dorsal caudal rays D 3–5. This condition is found in triacanthodids, triodontids, and ostracioids. In triacanthids, the muscle inserts on rays D 3–4, in balistids on D 2–5, and in monacanthids on rays D 1–3. Diodontids and most tetraodontoids have the tendons inserting on rays D 2–4, and this is apparently apomorph for the group. The muscle is absent in molids.

62. *FLEXOR DORSALIS SUPERIOR* (Figure 38c).—In most perciform fishes, this muscle originates from the centra and neural spines of the last few caudal vertebrae, and inserts on the bases of all the dorsal branched caudal fin rays. This condition is found in triacanthids and balistids. In ostracioids, the muscle is partially (aracanids) or wholly (ostraciids) fused to the overlying epaxialis. Triacanthodids (except the two long-snouted genera) have lost the uppermost and lowermost sections.

In triodontids, the origin is limited to the ural centrum, and there is no tendon to ray D 1. Insertion is variable in diodontids, but is on the ventral three (canthigasterids) or four (tetraodontids) of the dorsal caudal rays in tetraodontoids. The muscle is absent in molids.

63. *FLEXOR DORSALIS SUPERIOR* (Figure 39a,b).—The plesiomorph condition of this muscle is apparently as it is found in perciforms and triacanthodids, where it is small, and originates from the distal tips of the neural spines of the last few vertebrae. In all other tetraodontiforms, at least some fibers arise from the vertebral centra, and the muscle is considerably larger. In all families except triacanthids, the fibers partially cover the flexor dorsalis laterally. In ostracioids, the muscle is fairly small, and inserts on D 5, while in balistoids it is large and originates mainly from the neural spines. The plesiomorph condition here is probably considerably smaller than in the balistoids but larger than in the ostracioids. In diodontids and tetraodontoids, the muscle is well developed, the origin being mainly from the vertebral centra and the neural arches, the insertion usually being on ray D 5. It is absent in molids.

The loss of the muscle in molids is autapomorph, and does not necessarily exclude them from the phylogenetic tree. One other aspect seems to require further analysis. The expansion of the muscle, and its origin (at least partially) from the vertebral centra in all but triacanthodids suggests that these families shared a common ancestor possessing this condition. At present, only one other group of teleosts is known to exhibit this enlargement of the muscle—the Acanthuridae (Monod, 1959c, fig. 10; Winterbottom, 1971b, fig. 2). What this means in terms of the phylogeny of these groups remains, for the moment, an enigma. However, the presence of such a specialized condition in an extremely closely related group of fishes is difficult to ascribe to convergence. In view of the low neural spines of triacanthids, and thus the likelihood of the flexor dorsalis superior contacting the vertebral column (provided, of course, it is not lost as, for example, it is in scombrids and many other forms with slender peduncles and lunate caudal fins), the triacanthid condition seems more likely to be due to convergence than to synapomorphy. The character

can still be used to group the balistoid + ostracioid + gymnodont fishes as a monophyletic lineage whether or not the acanthurids belong to the assemblage, since we are, for the present, only concerned with the interrelationships of the "tetraodontiform" fishes as they are usually conceived (Figure 39b).

64. *FLEXOR VENTRALIS* (Figure 40a).—The muscle forms the ventral counterpart of the flexor dorsalis. Description of the plesiomorph condition is similar—origin is from the centra and haemal spines of the last few vertebrae, the ural centrum, and the ventral hypurals; insertion is on the bases of the branched ventral caudal fin rays. As such, it is found in triacanthoids, balistoids, triodontids, and some tetraodontoids. It is partially (aracanids) or totally (ostraciids) fused to the overlying obliquus superioris in ostracioids. The insertion is reduced to three fin rays in diodontids (and to two in certain tetraodontoids), and the muscle is absent in molids.

65. *FLEXOR VENTRALIS EXTERNUS* (Figure 40b).—The muscle, which in the normal perciform condition connects the haemal spines and centra of the last few vertebrae with the bases of ventral caudal fin rays V 1–2, is present in triacanthoids and gymnodonts (except molids). It shows little variation in these groups, except in two genera of tetraodontids. It is absent in all balistoids and ostracioids, but for a different reason from that in molids, where all intrinsic caudal fin muscles have been lost.

66. *FLEXOR VENTRALIS INFERIOR* (Figure 40c,d).—The plesiomorph condition appears to be for most perciforms, where the origin is from the tip(s) of the haemal spine(s) of the last (few) vertebra(e), and the muscle is small. This state is met with in the triacanthoids. In the other families, it arises from the ventrolateral faces of the centra (triacanthids) or the lateral surfaces of these centra. In balistoids, it is large, with much of the origin from the haemal spines, although many fibers arise from the centra. The origin is not as extensive in ostracioids, and both conditions are apparently synapomorph. It arises more from the centra and the haemal arches (rather than haemal spines) in diodontids and tetraodontoids, and it is absent in molids.

The reasoning followed in the reinterpretation of this muscle is exactly the same as used for the

flexor dorsalis superior (paragraph 63).

67. *TRANSVERSUS CAUDALIS* (Figure 41a,b).—In perciforms which possess this muscle, it arises from the dorsolateral region of the hypurals and inserts on the base of ventral caudal fin ray V 1. It is present in this form in triacanthoids, balistoids, and triodontids. In ostracioids, it inserts on at least three rays, not including V 1. It inserts partially on V 2 in canthigasterids and most tetraodontids. It is absent in diodontids, triacanthids, and molids.

In reinterpreting, the molids can be removed from this group, since they lack all intrinsic caudal fin musculature (in which respect they are autapomorph). In perciforms which possess this muscle, it is usually reduced or absent in forms with a lunate tail fin—presumably because this type of fin requires a more rigid attachment of the fin rays, and hence less movement is possible. It is absent (possibly for this reason) in triacanthids, and is small in the other family with a lunate fin, the triodontids. I can offer no explanation for the absence of the muscle in diodontids, except that I consider Grenholm's explanation (1923:239–240) unlikely. Grenholm suggests that the flattened posterior margin of the hypural plate allows considerable vertical movement of the fin rays, rendering the transversus caudalis redundant. This is, however, a purely destructive criticism.

68. *EPAXIALIS* (Figure 41c).—In most fishes, this division forms the main component of the dorsolateral body musculature. In the plesiomorph condition (found to some degree in the triacanthoids), the anterior myocommata pass posterodorsally near the dorsal midline. The other tetraodontiform families have lost almost all traces of this final change of direction of the myocommata. In ostracioids, the dorsal of the two main moieties (i.e., where the myocommata pass anterodorsally) separates from the ventral section in front of the dorsal fin, and, owing to the enlargement of the erector-depressor complex, few, if any, of the medial fibers attach to the vertebral column. In addition, the ventral fibers tend to fuse with the dorsal fibers of the obliquus superioris posteriorly. In all gymnodonts (except molids, which are autapomorph) the dorsal moiety becomes aponeurotic posteriorly, joining a similar aponeurosis from the obliquus inferioris to insert

on the bases of all the caudal fin rays.

69. **LATERALIS SUPERFICIALIS.**—This muscle, which covers the anterior portions of the epaxialis and obliquus superioris laterally, is undoubtedly present in at least some triacanthoids and balistoids. However, it is an extremely difficult muscle to identify and delimit (the more so in preserved material, where it loses its distinctive red coloration), and usually requires histological examination in order to describe satisfactorily. It will therefore not be considered in the phylogenetic analysis.

70. **OBLIQUUS SUPERIORIS** (Figure 42a).—In the plesiomorph condition for perciforms (not found in tetraodontiforms), this muscle is not separate from the obliquus inferioris. The fibers pass from posteroventral to anterodorsal, coursing in the opposite direction in the latter section. The sections may also be recognized by the direction of the myocommata, which is the same as that of the fibers, but at a greater angle. In tetraodontiforms, these sections are usually well separated and variously modified. The anterior region in all is much reduced, and does not cover the abdominal cavity dorsolaterally. In balistoids and ostracioids, the anterior fibers do not reach the posterodorsal face of the cleithrum. The fibers apparently fuse with the epaxialis posteriorly in ostracioids. In molids, the muscle is absent except for a small posterior section serving the ventral caudal fin rays, and, in *Mola*, a thin, diffuse sheet extending anteriorly in the subdermal tissue. The muscle is much reduced anteriorly in diodontids, and arises from the vertebral centra above the swim bladder.

71. **OBLIQUUS INFERIORIS** (Figure 42b).—The plesiomorph condition of this muscle was described under the obliquus superioris above. It is extensively modified in tetraodontiforms, particularly in those gymnodonts with inflation abilities. It will therefore be discussed under a series of section headings, following Winterbottom (1971a) where applicable.

**Section A:** Present only in tetraodontoids as a small, partially separated division, originating from the posterodorsal process of the coracoid and inserting on the ventral postcleithrum. The fibers forming this section are present in most families of tetraodontiforms, but are not separated from the rest of the muscle.

**Section B:** This portion is present in tetraodontoids and diodontids only. Origin is from the

medial faces of the cleithrum and coracoid, the fibers attaching to the ventral postcleithrum. The more ventral fibers pass medial to section A. and are ventrally continuous with the dorsal fibers of section C.

**Section C:** The dorsal fibers of this section give rise to sections A and B in the forms described above. Thus, in tetraodontoids, only a few fibers of this section attach to the ventral postcleithrum, and none do so in diodontids, where the bone is much reduced.

The fibers in other families arise from the lateral faces of the cleithrum and coracoid (being, in most cases, continuous with the sternohyoideus anteriorly), and pass posteriorly to attach to the postcleithrum dorsally. The more dorsal fibers continue dorsally as section D. In tetraodontoids, the ventral fibers attach to the base of the first pterygiophore of the anal fin. In all forms except molids (where a patch of anterior fibers may remain—*Mola*) and diodontids, the posteroventral fibers continue posteriorly, usually being firmly attached to the ventral region of the obliquus superioris. In diodontids, these fibers arise from the ventrolateral process of the sixteenth vertebra. In all gymnodonts (except molids, where this portion is absent), the fibers grade into an aponeurosis which joins a similar aponeurosis from the dorsal moiety of the epaxialis to form a tendinous sheath inserting on the bases of all the caudal fin rays. In addition, all gymnodonts (except molids and one genus of tetraodontid) possess a posterodorsomedial bundle of fibers which arises from the main mass of the muscle just in front of the anal fin, and courses up and back, medial to all muscles save the erector-depressor complex of the anal fin, to attach tendinously to the tips of one or more haemal spines. Fibers pass anteriorly from the region of the anal fin into the subdermal tissue in diodontids and tetraodontoids (where they contribute to the formation of the longitudinal cutaneous).

**Section D:** The fibers arise from the fascia in the region of the lateral septum, and pass anteroventrally to insert on the posterodorsal face of the postcleithra. The section is well developed in triacanthoids, most balistoids, and gymnodonts (except molids, where it is absent). In diodontids, it attaches to the first and last pterygiophores of the dorsal fin and the last pterygiophore of the

anal fin in some species. In canthigasterids, some fibers reach the first pterygiophore of the dorsal fin. The section is much reduced or absent in ostracioids.

72. *SPINALIS* (Figure 43*a,b*).—Little, if anything, has been reported in the literature about this muscle and its distribution. It is present in triacanthids and balistoids. In the former, it arises from the posterior face of the first pterygiophore of the spiny dorsal fin and attaches to the tips of the neural spines of the second to fifth vertebrae. In balistoids, it originates from the epiotic and inserts primarily on the neural spine of the third vertebra.

Although the muscle appears to indicate the sister group status of triacanthids and balistoids, this is unlikely in view of the large amount of evidence placing the ostracioids as the balistoid sister group, these two then forming the gymnodont sister group. A second alternative is that the triacanthids form the sister group of the balistoid + ostracioid + gymnodont line. This necessitates the postulated loss of the *spinalis* in ostracioids and gymnodonts. In view of the anatomical differences between the muscles in the two groups possessing it, our meager knowledge of its distribution in fishes, and its probable derivation from the anteriormost epaxial myomere, neither alternative is particularly satisfying. The origin of the muscle from the epiotic in balistoids will, for the present, be considered synapomorph (Figure 43*b*).

73. *TRANSVERSUS CUTANEUS* (Figure 43*c*).—This name is used for two, apparently non-homologous muscles. In balistoids, the muscle arises from the lateral face of the pelvis and passes dorsally into the fascia over the obliquus inferioris in the region of the ventral tip of the postcleithrum, to which it may attach. In diodontids and tetraodontoids, it lies in the subdermal tissue, being best developed ventrally.

74. *LONGITUDINAL CUTANEUS* (Figure 43*d*).—The muscle system is present in diodontids and tetraodontoids. It is best developed ventrally, where the *infracarinalis medius* and *obliquus inferioris* contribute to its formation. The tetraodontoids also possess well-developed fibers anterodorsally.

75. *SWIM BLADDER MUSCLES*.—These muscles are present in only two families. They are not homol-

ogous structures. In ostraciids, the anterior region of the swim bladder possesses two layers of fibers passing at different angles to each other. In diodontids, there is a vertical bundle of fibers on the posterior face of the swim bladder, and there may be another bundle anteriorly between the two halves of the bladder.

### Discussion

Of the 75 muscles analyzed in the preceding section, seven (9 percent) yielded no interpretable phylogenetic information, 18 (24 percent) initially disagreed with the hypothesized phylogeny (Figure 44) while 50 (67 percent) confirmed it to greater or lesser extents. Out of the 18 muscles disagreeing with the hypothesis, only five (*sternobranchialis*, *coracoradialis*, *flexor dorsalis superior*, *flexor ventralis inferior*, and *spinalis*) seem to be important, the others being easily explained by normal evolutionary phenomena such as reductive trends. It may well be significant that these five muscles (of which the *coracoradialis* is a dubious member) indicate some sort of connection between the triacanthids and the nontriacanthoid tetraodontiforms. This possibility is analyzed in more detail under "Branch Point 1."

In the weighting of characters, it is apparent that little emphasis can be placed on those subject to parallel evolution, since more than one interpretation is possible. Furthermore, it seems to me that synapomorphs resulting from reduction and "serial homologues" (such as certain branchial arch muscles, and those of the dorsal and anal fins) carry less weight than shifts in origin and insertion, and the development of new muscles. Myers (1958) points out that reduction is one of the chief mechanisms of specialization in teleosts, but since it is apparently easier for two groups to lose a common structure than it is for them to independently develop a morphologically identical one, the latter seems worthy of greater emphasis in the interpretation of phylogeny (see also Weitzman, 1964:150).

One other point seems worthy of specific mention at this stage. We have already seen that groups can only be linked by synapomorph characters. Should the hierarchical units one is dealing with (in this case, families) have evolved so that each of the main branch points ultimately gives



rise to more than one unit, synapomorphs must be present in both these lines. If one line gives rise to, say, families A and B, while the other divides into a number of families, the fact that the families of the second branch may share many synapomorphs indicates only that they themselves share a common ancestor, i.e., it does not tell us whether these families are most closely related to family A, family B, or the ancestor of both A and B. For this reason, the lines of the branch points are labeled "a" and "b" in Figure 44, and the letter after each muscle used in the analysis below indicates the line in which that character is synapomorph. Where the character indicates a common ancestor for the two lines, the letters are omitted; both are included if the muscle is apparently synapomorph in both lines, but does not give any evidence of a common ancestor for these lines. Toward the end point of the branching, where lines contain only two families, synapomorphs linking the members of each of these families to each other are not listed, since this would require examination of all the genera contained in every family to be valid.

The letters "a" and "b" mentioned above appear as suffixes to a parenthesized numeral behind each muscle mentioned. This numeral refers to the number used to denote the muscle in the section on the phylogenetic significance of the myological differences observed.

#### BRANCH POINT 1

The phylogeny proposed from the analysis of the musculature suggests that the families Triacanthodidae and Triacanthidae form the sister group of all the remaining tetraodontiforms. Specialized characters supporting this contention are: section A 1 of the adductor mandibulae (1b); adductor hyomandibulae (11b); adductor radialis (41b); arrector dorsalis pelvici (44a,b); arrector ventralis pelvici (45a); adductor superficialis pelvici (46a); inclinatiores dorsales (48b); erectores dorsales (49b); depressores dorsales (50b); infracarinalis anterior (57a); flexor dorsalis superior (63b); flexor ventralis inferior (66b); and epaxialis (68b).

It is fairly obvious that this collection of synapomorphs is by no means convincing. Although the evidence is good for the sister group status

of the balistoids + ostracioids to the gymnodonts (10 characters), the linking of the triacanthodids and triacanthids as sister groups is very weak (4 characters). Furthermore, these four characters are ones which required reinterpretation. The justification is mainly based on the form of the triacanthoid pelvis. This complex is extremely unusual, possessing large pelvic spines which can be locked in position, and a well-developed posterior elongation of the pelvis behind the articulation of the fin. Should the triacanthodids and triacanthids not be sister groups, then we must postulate that such a structure was present in the tetraodontiform ancestor. This in turn implies that the nontriacanthoid tetraodontiforms have reversed the evolutionary trend, reducing the spines (and ultimately losing them); and exhibiting the posterior migration of the pelvic fin along the posterior elongation of the pelvis.

Furthermore, the fossil *Eoplectus* (see "Alternative Interpretations"), which is an early gymnodont, possesses a normal-looking perciform I 4 pelvic fin (although the presence or absence of a posterior elongation cannot be determined). The presence of this apparently extremely specialized character complex in triacanthodids and triacanthids seems to me to indicate the sister group status of these two families, and that their common ancestor developed this condition after splitting off from the line giving rise to all the other tetraodontiform families. In addition to this, both triacanthoid families possess the same locking mechanism for the large first dorsal spine (a mechanism which differs considerably from that of both balistoids and acanthurids).

It should perhaps be remarked here that the extremely similar dorsal and pelvic spine locking mechanisms of at least some members of the Zeiformes (e.g., *Capros aper*) require further examination, and, until our knowledge of the various anatomical systems of the zeiforms has substantially increased, the possibility of a close relationship between at least some of them and triacanthoids should not be entirely ignored.

There is a certain amount of myological evidence which would appear to indicate a somewhat different picture of the basal evolution of the tetraodontiforms—namely, that the triacanthids form the sister group of the nontriacanthoid families, and that these together form the sister

group of the triacanthodids. Although these possibilities have been discussed in the interpretive section, it seems pertinent to review them here.

The condition of the anterior region of the adductor arcus palatini of triacanthids is somewhat reminiscent of what one would deduce to be the beginnings of the development of a retractor arcus palatini, and thus may suggest that triacanthids form the balistoid-ostracioid sister group. However, the reason for the absence of the muscle in gymnodonts is readily apparent, (i.e., the interdigitation of the palatine to the ethmoid-vomer region of the skull. Furthermore, such an intermediate condition (although not as well developed as in triacanthids) is also found in certain chaetodontin and pomacanthin fishes, and a well-developed and separated retractor arcus palatini is present in acanthurids. It is therefore conceivable that the triacanthid condition is a response to the somewhat elongated ethmoid region rather than being due to synapomorphy.

A sternobranchialis muscle (in varying stages of separation from the sternohyoideus) is present in all families but the gymnodonts. This muscle has only been reported elsewhere in certain gobioids (Dietz, 1914). I feel that the explanation for the absence of the muscle in gymnodonts is satisfactory, and it seems that we can assume that such a muscle, probably in a state of differentiation similar to that found in present-day triacanthodids, was present in the ancestral tetraodontiforms.

The specialized condition of the coracoradialis, too, is of dubious significance, being present only in triacanthids and balistids. If triacanthids did form the sister group of balistoids, balistoids + ostracioids, or of all nontriacanthoid tetraodontiforms, one would nonetheless expect the presence of the specialization in monacanthids, instead of the plesiomorph condition of the muscle, which is what they in fact possess. It appears that this character is somewhat labile, and, as stated, it is necessary to accurately determine its functional role before the significance of the triacanthid-balistid condition can be interpreted.

The presence of a flexor dorsalis superior and a flexor ventralis inferior which have origins at least partially from the vertebral centra in triacanthids and all nontriacanthoid tetraodontiforms is another factor suggesting the sister group relations of these two groups. However, as pointed

out, acanthurids possess a form of these two muscles which is apparently identical to the balistoid condition. Whether this is due to synapomorphy or convergence cannot, for the moment, be ascertained and must await further study. In view of this, and because of the apparent ease with which the triacanthids could exhibit a condition similar to the nontriacanthoid tetraodontiforms (see "Interpretation"), it seems dangerous to place much emphasis on these characters.

Lastly, the spinalis is found in triacanthids and balistoids. This is probably the most telling character. The absence of the muscle in ostracioids and gymnodonts poses little difficulty, since in these fishes the neural spines are broad and plate-like, and do not appear capable of much movement (the apparent function of the spinalis). Should, however, the spinalis prove to be involved in curving the vertebral column, then it is possible that the muscle has differentiated independently in the two lineages, and is perhaps involved in the better positioning of the dorsal spines.

However these muscles are interpreted, I feel that the acceptance of the phylogeny postulated here for these groups involves mental exercises of a less deep-seated nature than would be indulged in if one were to attempt to explain away the pelvic fin and pelvis of the triacanthoids, to say nothing of the synapomorphs linking the nontriacanthoid tetraodontiforms.

#### BRANCH POINT 2

This dichotomy suggests that the balistoids + ostracioids form the sister group of the gymnodonts. Evidence supporting this is derived from the following muscles: section A 1 of the adductor mandibulae (1a); section A  $\infty$  of the adductor mandibulae (4b); levator arcus palatini (5a); dilator operculi (6a); levator operculi (7a,b); adductor arcus palatini (8a); retractor arcus palatini (9a); intermandibularis (12b); valvulus (13b); hyohyoideus inferioris (15a,b); hyohyoidei abductores (16b); hyohyoidei adductores (17b); sternohyoideus (18a,b); sternobranchialis (19a—alternative interpretation); levatores externi (26a); sphincter oesophagi (33b); arrector dorsalis (39b); levator pectoralis (43b); arrector ventralis pelvici (45b); adductor superficialis pelvici (46b); depressores dorsales (50b); flexor ventralis externus

(65a); epaxialis (68b); and obliquus superioris (70a).

Of the 24 muscles listed, 11 have become synapomorph in the balistoids + ostracioids and 15 in the gymnodonts, which indicates that the former are slightly more plesiomorph than the latter. Given, then, that the ancestral species at Branch Point 2 was, in fact, the common ancestor of the balistoids, ostracioids, and gymnodonts, there is convincing evidence that the balistoids and ostracioids form one line, and the gymnodonts the other.

#### BRANCH POINT 3

This branch point separates the balistoids as the sister group of the ostracioids. The synapomorph conditions are present in the following muscles: section A 1 (1b), section A 2 (2a,b), and section A 3 (3b) of the adductor mandibulae; dilatator operculi (6); levator operculi (7a); adductor arcus palatini (8b); retractor arcus palatini (9); adductor operculi (10b); adductor hyomandibulae (11b); hyohyoideus inferioris (15b); hyohyoidei abductores (16a); hyohyoidei adductores (17b); sternohyoideus (18b); sternobranchialis (19—alternative interpretation); pharyngoclavicularis externus (20b); pharyngoclavicularis internus (21b); obliqui ventrales (22b); transversus ventrales (23a); recti ventrales (24a,b); levatores externi (26b); levatores interni (27b); obliquus dorsalis (28a); retractor dorsalis (31a); adductores (32b); sphincter oesophagi (33a,b); coracoradialis (40b); protractor pectoralis (42b); levator pectoralis (43b); arrector ventralis pelvici (45b); adductor superficialis pelvici (46a,b); erectores dorsales (49b); depressores dorsales (50b); inclinatores anales (51a,b); erectores anales (52b); depressores anales (53b); supracarinalis medius (55a); infracarinalis anterior (57a,b); infracarinalis medius (58b); flexor dorsalis (62b); flexor dorsalis superior (63a,b); flexor ventralis (64b); flexor ventralis inferior (66a,b); transversus caudalis (67b); epaxialis (68b); obliquus superioris (70b); obliquus inferioris (71b); spinalis (72a); and transversus cutaneus (73a).

Of the 48 synapomorphs listed above, 16 occur in balistoids and 36 in ostracioids, which clearly places the balistoids as the plesiomorph sister group of the ostracioids.

#### BRANCH POINT 4

The hypothesis presented here is that the Triodontidae form the sister group of the other gymnodont families. The evidence is provided by the following synapomorphs: section A 1 (1b), section A 2 (2b), and section A  $\omega$  (4b) of the adductor mandibulae; adductor hyomandibulae (11b); valvulus (13); hyohyoidei adductores (17); obliqui ventrales (22b); rectus communis (25b); levatores externi (26b); sphincter oesophagi (33); erectores dorsales (49b); depressores dorsales (50); and obliquus inferioris (71).

The evidence seems fairly conclusive, and would probably be more so were it not for the autapomorph loss of the intrinsic caudal fin musculature in molids.

#### BRANCH POINT 5

The hypothesis is that the Molidae form the sister group of the tetraodontoids and diodontids. Synapomorphic evidence is furnished by the following muscles: section A 1 (1), and section A 2 (2a) of the adductor mandibulae; levator arcus palatini (5); dilatator operculi (6a); hyohyoideus inferioris (15a); hyohyoidei abductores (16a); hyohyoidei adductores (17); sternohyoideus (18a); pharyngoclavicularis internus (21a); recti ventrales (24a); levatores externi (26); levatores interni (27a); adductores (32a); sphincter oesophagi (33); abductor superficialis (34a); abductor profundus (35a); adductor superficialis (37a); adductor profundus (38a); protractor pectoralis (42a); inclinatores dorsales (48a); supracarinalis anterior (54a); infracarinalis anterior (57a); infracarinalis medius (58a); transversus cutaneus (73a); and longitudinal cutaneus (74a). There are 25 synapomorphs listed, and it is likely that this number could be greater were it not for the autapomorph condition of the intrinsic caudal fin musculature of the molids.

#### BRANCH POINT 6

This branch point suggests that the Diodontidae form the sister group of the Tetraodontidae and Canthigasteridae. Evidence is derived from the following synapomorphs: section A 1 of the adductor mandibulae (1); dilatator operculi (6a);

adductor arcus palatini (8a); hyohyoidei abductores (16); hyohyoidei adductores (17); pharyngoclavicularis internus (21); obliqui ventrales (22a); recti ventrales (24); rectus communis (25a); levatores interni (27); obliquus dorsalis (28a); transversi dorsales (30a); sphincter oesophagi (33); protractor pectoralis (42); infracarinalis anterior (57); flexor dorsalis (62a); transversus caudalis (67a); obliquus inferioris (71); and longitudinal cutaneous (74).

Of these 19 synapomorphs, the infracarinalis anterior (57) and the transversus caudalis (67) may be autapomorph in diodontids, and hence inadmissible as evidence. Even so, there seems no reason to doubt that the Diodontidae separated off first from the line which ultimately gave rise to the Canthigasteridae and Tetraodontidae.

#### Alternative Interpretations

The vast majority of previous anatomical works on the tetraodontiforms have been taxonomically oriented. Phylogeny is seldom expressed, for although hierarchical levels were established in classifying these fishes, it is only recently becoming recognized that the phylogeny should be reflected in the systematic hierarchy.

Among the more recent works purporting to deal with the phylogeny of the tetraodontiforms, few, if any, have been influenced by synapomorph characters alone, and fewer still seem to have taken reductive trends (with the implied "parallelism") into account. Thus, the family tree presented by Breder and Clark (1947) is largely one of morphological and ontogenetic similarity-dissimilarity, with little attempt to conform the classification to the phylogeny as it is proposed. Fraser-Brunner, even in his last paper on tetraodontiforms (1951), made but few phylogenetic observations, and his planned monograph on these fishes has yet to appear. The quality of Le Danois' work (1955, 1959, 1961) has already been alluded to, and may be dismissed.

The provisional classification of Greenwood, et al. (1966), while it is implicitly phylogenetic, is (in the section on tetraodontiforms) a slight modification of Regan's (1903) system, in which the Triodontidae are placed with the tetraodontoid fishes, and Regan's suborder raised to ordinal status. No evidence is given by Greenwood, et al., but, as they

point out (1966:391), much remains to be done in the sorting out of the perciform and derived families, and the Tetraodontiforms (among others) are specifically mentioned in this respect.

In the more recent works of Tyler (1968, 1970a) on the osteology of tetraodontiforms, some tentative phylogenetic conclusions are drawn, and these will be discussed in detail below.

In examining alternative interpretations of tetraodontiform phylogeny, certain lineages postulated in this study will not be broken down to the family level, either because they are widely accepted, or because the evidence presented here is felt to be virtually conclusive. Thus, neither the balistoids + ostracioids nor the gymnodonts will be considered as other than single entities, each derived from a single common ancestor. The potential problems, then, lie in the basal phylogeny of the order, where the evidence presented here is weakest. There are four extant groups (Triacanthodidae, Triacanthidae, balistoids + ostracioids, and gymnodonts) whose phylogenetic interrelationships are open to different interpretations. To these can be added a fifth, since Tyler (1968, fig. 6) postulates that the subfamily Triacanthodinae forms the sister group of all other living triacanthoids and balistoids. Tyler's views are expressed graphically in Figure 45.

Unfortunately, Tyler's provisional interpretation is based on the autapomorph conditions of the supraoccipital, first anal pterygiophore, and pelvic basin in triacanthodins (i.e., these characters are plesiomorph in the hollardiins and triacanthids, and hence both are invalid as phylogenetic evidence). To prove, however, that the triacanthoid subfamilies are more closely related to each other than to any other living group, one needs to find synapomorphic characters linking them. This becomes extremely difficult where the groups are postulated as being the most plesiomorph members alive today. The triacanthoids are apparently specialized in the complete separation of the infracarinalis medius from the obliquus inferioris, since the muscle is partially continuous with, or at least firmly attached to, the obliquus inferioris in all other tetraodontiforms and most perciforms. In his discussion of the relationships of triacanthoids to the balistoids, Tyler (1968:34) lists a large number of characters shared by triacanthids and balistoids (most, but not all, also being present

in the ostracioids). Nearly all these character conditions may also be found in acanthurids (including the flange of the pterotic overlying the posterodorsal region of the hyomandibular, and the meeting and suturing of the pterosphenoids in the midline). This brings the state of these characters into question—if the acanthurids form the sister (or a close) group to the tetraodontiforms, then it is reasonable to assume the triacanthid-balistoid condition is one of symplesiomorphy (in which case the triacanthodid subfamilies are synapomorph, and the characters cannot be used to link the triacanthids and balistoids phylogenetically). If on the other hand, the characters are specialized, then there is osteological evidence that the acanthurids are more closely related to the triacanthids, balistoids, or both than they are to anything else still extant. It is obvious that a detailed osteomyological study of acanthurids, siganids, chaetodontins, and other related fishes is urgently needed to clear up the state of many of these characters.

It seems necessary at this point to consider the nature of the triacanthoid pelvis in the light of the fossil evidence. As already noted, the pelvis of these fishes has a very well-developed posterior elongation behind the equally well-developed pelvic spine. As stated under "Branch Point 1," one must either postulate (1) that this is a plesiomorph condition for the tetraodontiforms as a whole, or (2) that it represents a shared, specialized character complex strongly suggesting that these two families possessed a common ancestor with this condition, and that this ancestor did not give rise to any other known tetraodontiform group. If the former is the case, then we must postulate a reversal in evolutionary trend, for the balistoid pelvis, while elongate, has, at its distal tip, a bifid structure which probably represents the pelvic spines. In other words, either the pelvic fin itself has migrated backward along the posterior elongation of a triacanthoid-like pelvis, or this posterior elongation has been reduced and resorbed so that the fin lies once more near the distal margin of the pelvis. The second of the above postulates (2) receives some support from the newly described fossil, *Eoplectus bloti* Tyler from the Eocene of Monte Bolca. Although systematically Tyler (1973) places this specimen in the Triacanthodidae, he states that it is phylogenetically closely related to

the gymnodonts, possessing the remarkable combination of jaw and dental features of this group. The incomplete *Zignoichthys oblongus* (Zigno) has been redescribed by Tyler in the same paper (1973). It appears to be closely related to *Eoplectus*, but may be farther along the line toward modern gymnodonts. The two alternatives are given as 4 and 3, respectively, in the phylogenetic tree in Figure 47. In addition to the plesiomorph character of five or six dorsal spines, *Eoplectus* has a perciform-like I 4 pelvic fin, the balistoid-ostracioid condition of the large ventral flange on the parasphenoid, and the second basal pterygiophore of the spiny dorsal fin oriented similarly to that of the balistids. From the evidence provided by these fossils, it seems reasonable to conclude that the common ancestor of the balistoids + ostracioids and the gymnodonts had a pelvic fin of the normal perciform type (less one ray—the condition of the posterior part of the pelvis is unknown); at least five dorsal spines (six if the phylogenetic placement of the Spinacanthinae is correct—see below); the anterior pterygiophores of the spiny dorsal fin relatively far forward and possibly in contact with the skull; the shaft of the second pterygiophore being directed anteroventrally; a large ventral flange on the parasphenoid; pleural ribs with epipleurals; procurrent caudal fin rays; and the maxilla immovably articulated with the premaxilla, which lacked an ascending process. Such a fish, should it have existed, is a far cry from the triacanthoids of today, and it certainly seems quite feasible that the triacanthoids are the result of a single common ancestor that diverged from the line, which gave rise to the other tetraodontiform families.

The relationships of the tetraodontiform families to the Acanthuridae (here conceived as including the Zanclinae, following Tyler, 1970b) poses something of a problem. Although not enough information is at hand to warrant valid conclusions, it seems necessary to hint at the possible relationship of acanthurid fishes to the balistoid-ostracioid-gymnodont lineage, forming the sister group of this assemblage, and together with it forming the sister group of the triacanthoids. In spite of the fact that there is little osteological evidence to support such a contention (indeed much of the evidence is weighted against it—see Tyler, 1970a:42–43; 1970b), there is, on superficial examination, con-

siderable myological evidence (e.g., the form of the adductor mandibulae; a retractor arcus palatini; and the form of the flexor dorsalis superior and flexor ventralis inferior). Whatever the relations of the acanthurids to the tetraodontiforms may be, there is enough information to make it apparent that considerable "convergent" evolution has occurred (i.e., the development of morphologically very similar characters, or the common loss of many osseous elements in independent lines).

Although fossils do not provide myological information, a discussion of such forms as have been discovered is essential to any study purporting to be phylogenetic. Much of the information comes from Tyler's (1968) excellent summary of fossil triacanthoids.

Tyler (1968) placed the Spinacanthinae as a subfamily of the Triacanthodidae, and considered them to be the most basal group of the order (i.e., the sister group of all other tetraodontiforms), mainly on the basis of the extremely well-developed, six-spined dorsal fin. The two monotypic genera, *Spinacanthus* [*S. cuneiformes* (Blainville)] and *Protobalistum* [*P. imperiale* (Massolonga)], are from the upper Eocene of Monte Bolca. Tyler's objections to these fishes having balistoid affinities are the six-spined dorsal fin and the short-based soft dorsal and anal fins. The former objection falls away, since *Eoplectus* has at least five (and probably six) dorsal spines, and this must have been the condition of the common ancestor of the gymnodonts and balistoids + ostracioids. The fact that the spines are better developed than in any other tetraodontiform seems irrelevant, for it could just as easily be an apomorph condition as a plesiomorph one, and besides, dorsal spine reduction is apparent independently in the triacanthoid, gymnodont, and balistoid-ostracioid lines, the spines being better developed in the fossil examples. Short-based soft dorsal and anal fins, while not found in Recent balistoids, are present in ostracioids and gymnodonts (with a few secondary exceptions), and the character is, in the Spinacanthinae, plesiomorph (i.e., the state of the fins is as one would postulate for the ancestor at Branch Point 2), the longer based balistoid fin thus being synapomorphic. Evidence that the Spinacanthinae belong to the balistoid-ostracioid lineage rather than the gymnodont line is provided by the elongate ethmoid region between the upper jaw

and the eye, and the small eye high up on the head. It seems quite possible that the spinacanthins represent the sister group of the modern balistoids for two reasons. First, the dorsal spines have migrated anteriorly onto the skull, whereas the basal pterygiophores of the now-absent spiny dorsal fin in ostracioids have migrated posteriorly. Second, Eocene ostracioid fossils are known from the same formation (having already lost the dorsal spines and pelvis), whereas balistoids are first known from the Oligocene.

The Protacanthodinae (Tyler, 1968:237-238) apparently represent an offshoot of the triacanthoid-like stock leading toward the triacanthids. This agrees basically with Tyler's (1968) concept, except that I would derive the balistoids (and the other nontriacanthoid groups) from a slightly more basal position, before the separation of the protacanthodins. The reduction of all but the first dorsal spine and the elongate soft dorsal and anal fins of protacanthodins are apparently synapomorphic with the triacanthid condition, while they share the form and configuration of the pelvis with triacanthoids generally. Tyler's placement of *Acanthopleurus* and *Marosichthys* in close proximity to the triacanthids seems undeniable.

The last fossil which seems pertinent to this discussion is *Cryptobalistes brevis* (Rath), placed in its own subfamily by Tyler (1968:243-249). Of this extremely confusing Oligocene fossil, Tyler (1968:247) has said, "*Cryptobalistes* simply is not on a lineage which led to any Recent balistids or to any other Recent fishes, even though it has paralleled the fundamental trends within the Triacanthidae-Balistidae line of evolution." The reader is referred to Tyler for the reasoning behind this statement. Concerning the phylogenetic position of the fossil, the apparently synapomorphic nature of the basin-like pelvic shaft with that of Recent triacanthodins seems to be the only pertinent character, and the subfamily is tentatively placed as the extinct sister group of the triacanthodins (although this must imply that the hollardiids diverged somewhat before the Oligocene from the triacanthodins).

Vom Rath's specimens (one in counterpart, the other single) are no longer at Bonn (pers. comm. H. K. Erben, Institute für Paläontologie, Bonn) and every effort to relocate them for reexamination has failed. The description given by vom Rath

(1859) is sparse, but the figure looks much like a balistid with a triacanthoid pelvis and pelvic fin. Should *Cryptobalistes* ultimately prove to be (in spite of Tyler's statement quoted above) a balistoid sister group, it may be that the posterodorsal flange of the balistoid pelvis represents the posterior elongation in the process of resorption. However, such a postulate raises certain difficulties. It seems fairly clear that *Cryptobalistes* would be on the balistoid line rather than the ostracioid or ostracioid + balistoid one if it should prove in any way related to these forms. The 11 synapomorphs listed under "Branch Point 2" which link the ostracioids and balistoids seem to be powerful ones, and the sister group status of these two groups is extremely likely. If so, then balistoids and ostracioids separated from their common ancestor well before the Eocene, for ostracioid fossils, apparently fully differentiated, are known from Monte Bolca. Until more specimens of *Cryptobalistes* are found, or the original specimens rediscovered, it seems safer not to form any firm ideas on the position of the genus, and I have accordingly followed one of Tyler's (1968) interpretations.

There are thus two main likely points of difference from the interpretation of tetraodontiform phylogeny postulated here. One of these involves the sister group status of the triacanthoids and triacanthids, which has been extensively discussed, and, although I believe the triacanthoid pelvis to be a significant synapomorph, it is quite possible that the triacanthoids separated off first from the ancestral stock (thus forming the sister group of all the other tetraodontiform families) and that they were followed soon after by the triacanthids (which thus would form the sister group of all the nontriacanthoid families). The other point is my placement of the gymnodonts as the sister group

of the balistoids + ostracioids. Tyler hinted (1962c:800) that the gymnodonts share a common ancestor with the triacanthoids + balistoids + ostracioids (= his Sclerodermi), but in a later paper (1970a:29) he states that ". . . the Triodontidae have on other grounds been considered as the most generalized family of the suborder Gymnodontes, the latter probably derived from the basal Sclerodermi." By "basal Sclerodermi," Tyler presumably means the triacanthoid fishes, but he does not commit himself as to whether the gymnodonts are derived from a pretriacanthoid, pretriacanthid, or prebalistoid + ostracioid stock. Since the latter case is the one presented here, and since no formulated arguments or alternatives have been proposed to this hypothesis as yet, further discussion awaits new evidence or reinterpretation of the old.

One last point may be mentioned in connection with the postulated sister group status of the balistoids + ostracioids and the gymnodonts—their normal method of locomotion involves the synchronous, side-to-side flapping of the dorsal and anal fins. The possible exception to this is *Triodon*, which has small dorsal and anal fins and a somewhat lunate caudal fin. This is probably a secondary condition (particularly since the caudal fin of †*Eoplectus* and nearly all other gymnodonts is rounded). It therefore seems likely that this method of locomotion was developed by the postulated common ancestor of these fishes. It also appears likely that an in-depth study of the anatomical systems associated with these fins will reveal further synapomorphs linking the two superfamilies, particularly in the fields of neurology, osteology, and myology.

My own views on the phylogenetic positions of the fossil groups discussed above are incorporated in Figure 47.

#### A New Classification of the Tetraodontiformes

The importance of the distinction between phylogeny and systematics has already been emphasized, and the ideal system would appear to be one of phylogenetic systematics, i.e., a classification of animals in a hierarchical manner such that the phylogeny of the components is accurately represented. There is, at present, no method of

doing this. In a hierarchical phylogenetic classification, no taxon (be it species, genus, or family) can contain more than two subtaxa, since the moment a third subtaxon is added, a new rank has to be imposed in order to preserve the phylogenetic information. The use of the classical, hierarchical system results in a number of, say,

families within a superfamily, and it is impossible to deduce the phylogeny of the contained units.

The establishment of a classification based on "coordinate" units poses a number of apparent problems at the present time. Since no taxon can be the evolutionary equivalent (in the strict sense of the word) of any other, it seems that one cannot imply equivalency in the hierarchical ranking of taxa. Logical extension of the Hennigian methods in these directions appears to lead ultimately to a ranking system of classification without the imposition of arbitrary levels of implied equivalency (such as family and genus). Although the naming of all branch points may be the final result, it appears to be unnecessary for the present (unless an immediate purpose is served by doing so). The hierarchical classification presented here is, therefore, provisional, pending the outcome of the attention currently directed to the discussion of these problems. The relative time of branching (i.e., the phylogeny) has been indicated by the development of the following method, which allows for the inclusion of more than two subgroups in any group, the phylogeny of the contained units being indicated by a simple system of numbers (derived from the phylogenetic tree) behind each taxon. The first taxon to diverge is suffixed by 1, the second by 2, and so on. Should any of these lines subsequently radiate, the resulting units could be labeled (if the radiation took place in the lineage labeled, say, 2) 2 in the case of sister groups, or, if there were three resulting lines, 2, 2.1, 2.1, where the units labeled 2.1 are sister groups, and together form the sister group of 2. The above would only arise, of course, if the taxa were to be treated as equivalent hierarchical units. It can be seen from the following example (which contains more units than would normally be encountered) that each prime number contains the taxon (or taxa) whose sister group is composed of all taxa with a larger prime number (Figure 46).

Using the method of interpretation put forward above, we get:

Taxon A (1)	Taxon E (3.2)	Taxon I (5.1)
Taxon B (2)	Taxon F (3.2)	Taxon J (5)
Taxon C (3.1)	Taxon G (4)	Taxon K (6)
Taxon D (3.1)	Taxon H (5.1)	

The main difficulty with this system is that one is forced to make arbitrary decisions as to what constitutes any given hierarchical level. It is obvious that definitions based on morphological dissimilarity will only lead to confusion if used in a phylogenetic classification, since they ignore Hennig's "Rule of Deviation" (1966:207). Hennig's suggestion that hierarchical levels be determined by their geological age is more logical, even if still arbitrary and sometimes clouded by our lack of knowledge. By suggesting only broad stages, Hennig (1966:185) "makes it possible for the time being to reserve the well known category designation ('class' and 'subclass') for the more important and morphologically isolated groups. All possibilities of future refinement of the method remain open." This view can apply equally well to lower categories, and there seems to be no reason why the phylogeny should not be indicated (where necessary) by the numerical suffix method outlined above. Where it has not proved possible to elucidate the phylogeny, there is no cause to reject the system prevailing prior to the investigation. That changes in systematic rank may result in applying phylogenetic findings to the classification is irrelevant, since hierarchical levels are completely arbitrary, and have, in the past, been based solely on the amount of similarity-dissimilarity, without regard for the state of the characters.

The following phylogenetic tree is drawn up from the myological evidence presented in this paper, to which has been added my views on the phylogenetic position of the various fossil groups. Where alternative branch points are shown, the dashed line represents the less likely possibility. The numbers (1 and 2, 3 and 4) are used to indicate the alternatives in the hierarchical classification presented after Figure 47.

The hierarchical arrangement of these groups thus becomes:



1. Suborder Triacanthoidei  
 Family Triacanthodidae  
 Subfamily Triacanthodinae (1)  
 Subfamily? †Cryptobalistinae (1)  
 Subfamily Hollardiinae (2)  
 Family Triacanthidae  
 Subfamily Triacanthinae  
 Subfamily †Protacanthinae
- Suborder Tetraodontoidei  
 Superfamily Balistoidea  
 Family †Spinacanthidae (1)  
 Family Balistidae (1)  
 Subfamily Balistinae  
 Subfamily Monacanthinae  
 Family Ostraciidae (2)  
 Subfamily Aracaninae  
 Subfamily Ostraciinae  
 Superfamily Tetraodontoidea  
 3. Family †Eoplectidae (1)  
 Family †Zignoichthyidae (2)  
 Family Triodontidae (3)  
 Family Tetraodontidae (4)  
 Subfamily Tetraodontinae  
 Subfamily Canthigasterinae  
 Family Diodontidae (4)  
 Family Molidae (5)

The following systematic and hierarchical changes are suggested in order to bring tetraodontiform classification into line with the phylogenetic relationships postulated in this paper:

1. That two suborders be provisionally recognized (Triacanthoidei and Tetraodontoidei), the first containing two families, the second consisting of two superfamilies.
2. That a superfamily Balistoidea be recognized, containing the families †Spinacanthidae, Balistidae, and Ostraciidae.
3. That the families Monacanthidae and Aracanidae be treated as subfamilies of the Balistidae and Ostraciidae, respectively, and that the †Spinacanthinae of Tyler (1968) be removed from the Triacanthodidae and placed as the sister group of the Balistidae, being given equal rank (as †Spinacanthidae).
4. That a superfamily Tetraodontoidea be formed to contain the families †Eoplectidae, Triodontidae, Tetraodontidae, Diodontidae, Molidae, and—should †Zignoichthys prove to be farther along the gymnodont line than †Eoplectus, as hinted by Tyler (1973) and tentatively preferred here—the †Zignoichthyidae.
5. That the family Canthigasteridae be reduced to subfamilial rank within the family

- OR 2. Suborder Triacanthoidei (1)  
 Family Triacanthodidae  
 Subfamily Triacanthodinae (1)  
 Subfamily? †Cryptobalistinae (1)  
 Subfamily Hollardiinae (2)  
 Suborder Triacanthoidei (2)  
 Family Triacanthidae  
 Subfamily Triacanthinae  
 Subfamily †Protacanthinae  
 Suborder Tetraodontoidei (2)

- OR 4. Family †Eoplectidae (1)  
 Family Triodontidae (2)  
 Family Tetraodontidae (3)  
 Subfamily Tetraodontinae  
 Subfamily Canthigasterinae  
 Family Diodontidae (3)  
 Family Molidae (4)

Tetraodontidae,<sup>1</sup> and that the †Eoplectinae of Tyler (1973) be transferred from the Triacanthodidae to the superfamily Tetraodontoidea, and raised to familial rank, in keeping with its phylogenetic position.

It seems unlikely, at this stage of our knowledge, that the Tetraodontiformes is phylogenetically equivalent to the Perciformes, and the sister group of the former order (as alluded to in the text) probably lies among the acanthurid-siganid-chaetodontid fishes. Since these latter groups are presently classified in the order Perciformes, it may well prove necessary to place them in the tetraodontiforms when sufficient evidence to warrant such a change has been assembled. This, however, must await further investigations.

<sup>1</sup> In this paper, the conventional view of the canthigasterids forming the sister group of the tetraodontids has been followed. Recently, Tyler (ms) has demonstrated that the sister group of *Canthigaster* consists of at least *Carinotetrodon*, and quite possibly *Monotreta* and *Chelonodon* as well. No representatives of the latter three genera were dissected for the purposes of this study. Should Tyler's view prove to be correct, the subfamilial rank afforded to *Canthigaster* above would have to be rescinded, and the genus would become completely incorporated within the Tetraodontidae. A detailed study of the generic interrelationships of this family is badly needed.

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## List of Abbreviations

In figures where both muscles and bones are illustrated, muscle abbreviations are underscored

A 1.	Adductor mandibulae A 1, $\alpha$ , $\beta$ , and $\gamma$	Di	Diodontidae
A 2.	Adductor mandibulae A 2, $\alpha$ , $\beta$ , and $\gamma$	D.L.	Dorsal lobe (of pelvis)
A 3.	Adductor mandibulae A 3	D.O.	Dilatator operculi
A $\omega$ .	Adductor mandibulae A $\omega$	D.RETR.	Retractor dorsalis
A.A.P.	Adductor arcus palatini	D.S.	Dorsal spine
ABD.P.	Abductor profundus	EBR.	Epibranchial
ABD.S.	Abductor superficialis	ECTO.	Ectopterygoid
ACT.	Radial	EHY.	Posterohyal (=epihyal)
AD.	Adductores	EOC.	Exoccipital
ADD.P.	Adductor profundus	EP.	Epural
ADD.R.	Adductor radialis	EPAX.	Epaxialis
ADD.S.	Adductor superficialis	EPIP.	Epipleural
AD.OP.	Adductor operculi	E.P.L.	Epihyal-ptyerygoid ligament
A.D.P.	Arrector dorsalis pelvici	EPOT.	Epiotic
A.H.	Adductor hyomandibulae	EREC.	Erectores dorsales or anales
A.M.L.	Articulo-maxilla ligament	ETH.	Ethmoid
ANG.	Angular	F.	Frontal
A.P.P.	adductor profundus pelvici	F.D.	Flexor dorsalis
Ar	Aracnidae	F.D.S.	Flexor dorsalis superior
ARR.D.	Arrector dorsalis	FOR.B.	Blood vessel foramen
ARR.V.	Arrector ventralis	F.R.	Fin ray
ART.	Articular	F.R.E.	Fin ray element
ASC.P.	Ascending process	F.V.	Flexor ventralis
A.S.P.	Adductor superficialis pelvici	F.V.E.	Flexor ventralis externus
A.V.	Abdominal vertebra	F.V.I.	Flexor ventralis inferior
A.V.P.	Arrector ventralis pelvici	H.AB.	Hyohyoidei abductores
Ba	Balistidae	H.AD.	Hyohyoidei adductores
BBR.	Basibranchial	HBR.	Hypobranchial
BHY.	Basihyal	H.L.	Hypochordal longitudinalis
B.L.	Baudelot's ligament	H.S.	Haemal spine
BOC.	Basioccipital	HY.IN.	Hyohyoideus inferioris
B.PT.	Basal pterygiophore	HYOM.	Hyomandibular
B.R.	Branchiostegal ray	HYP.	Hypural
B.V.	Buccal valve	IBR.	Infrapharyngobranchial
C.	Coelom	I.E.L.	Interopercle-epihyal ligament
Ca	Canthigasteridae	IHY.	Interhyal
CART.	Cartilage	IMD.	Intermandibularis
CBR.	Ceratobranchial	INC.	Inclinatores dorsales or anales
CHY.	Anterohyal (=ceratohyal)	INF.A.	Infracarinalis anterior
CL.	Cleithrum	INF.M.	Infracarinalis medius
COR.	Coracoid	INF.P.	Infracarinalis posterior
COR.R.	Coracoradialis	INT.	Interradialis
C.P.	Cartilagenous plug	I.O.L.	Interopercle-opercle ligament
C.S.	Cut surface	IOP.	Interopercle
C.T.	Connective tissue	I.S.L.	Interopercle-subopercle ligament
C.V.	Caudal vertebra	L.A.P.	Levator arcus palatini
DEN.	Dentary	L.CUT.	Longitudinal cutaneous
DEPR.	Depressores dorsales or anales	L.EXT.	Levatores externi
D.HHY.	Dorsohyal (=dorsal hypohyal)	LIG.	Ligament

L.INT.	Levatores interni	R.CAR.	Rostral cartilage
L.O.	Levator operculi	R.COMM.	Rectus communis
MAX.	Maxilla	RECT. V.	Rectus ventralis
Mc	Monacanthidae	R.I.	Retractor interoperculi
M.E.L.	Maxillo-ethmoid ligament	R.MD.	Ramus mandibularis V
MESO.	Mesopterygoid	R.MX.	Ramus maxillaris V
META.	Metapterygoid	S.ANT.	Supracarinalis anterior
MI	Molidae	S.B.	Swim bladder
M.P.L.	Maxillo-premaxilla ligament	S.BL.a.	Swim bladder "a"
N.S.	Neural spine	SCAP.	Scapula
OBL.D.	Obliquus dorsalis	SCL.	Supracleithrum
OBL.I.	Obliquus inferioris	S.M.	Posterior swim bladder muscle
OBL.P.	Obliquus posterior	S.MED.	Supracarinalis medius
OBL.S.	Obliquus superioris	S.N.	Supraneural
OBL.V.	Obliquus ventralis	S.O.	Sphincter oesophagi
O.FOR.	Foramen for olfactory nerve	SOC.	Supraoccipital
O.N.	Olfactory nerve	SOP.	Subopercle
OP.	Opercle	SPIN.	Spinalis
O.R.	Olfactory rosette	S.POST.	Supracarinalis posterior
Os	Ostraciidae	SPOT.	Sphenotic
PAL.	Palatine	STB.	Sternobranchialis
PAS.	Parasphenoid	STH.	Sternohyoideus
PCL.	Postcleithra	SYM.	Symplectic
PEL.	Pelvis	T.	Tendon of . . .
PF.	Prefrontal	Te	Tetraodontidae
PHC.E.	Pharyngoclavicularis externus	Ti	Triacanthidae
PHC.I.	Pharyngoclavicularis internus	To	Triacanthodidae
PM.	Premaxilla	Tr	Triodontidae
POP.	Preopercle	TR.	Levator pectoralis
P.P.	Protractor pectoralis	TR.C.	Transversus caudalis
P.P.L.	Palatino-palatine ligament	TR.CUT.	Transversus cutaneous
P.R.	Pelvic ray	TR.D.	Transversus dorsalis
PR.HY.	Protractor hyoidei	TR.V.	Transversus ventralis
PROT.	Prootic	U.C.	Ural centrum
PROX.	Proximalis	U.HBL.	Urohyal-hypobranchial ligament
P.S.	Pelvic spine	UHY.	Urohyal
PT.	Posttemporal	U.HYL.	Urohyal-hypohyal ligament
PTS.	Pterosphenoid	VA.	Valvulus
PTOT.	Pterotic	V.F.R.	Vestigial fin ray
Q.	Quadrata	V.HHY.	Ventrohyal (=ventral hypohyal)
R.A.P.	Retractor arcus palatini	VOM.	Vomer
R.B.	Ramus buccalis VII		

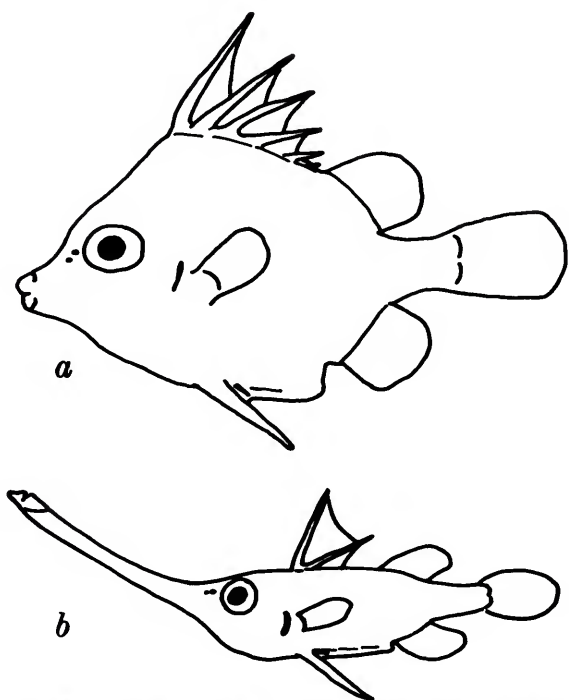


FIGURE 1.—Body outlines of representative triacanthodids: *a*, *Parahollardia* (Hollardiinae); *b*, *Halimochirurgus* (Triacanthodinae).

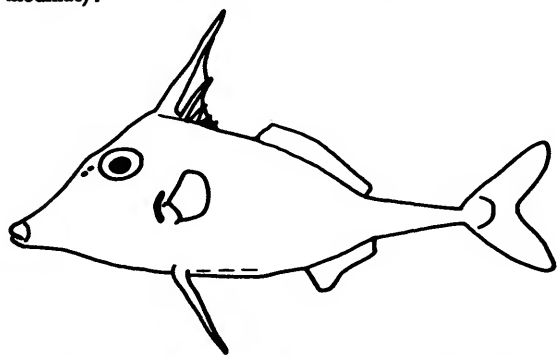


FIGURE 2.—Body outline of a representative triacanthid, *Trixiphichthys*.

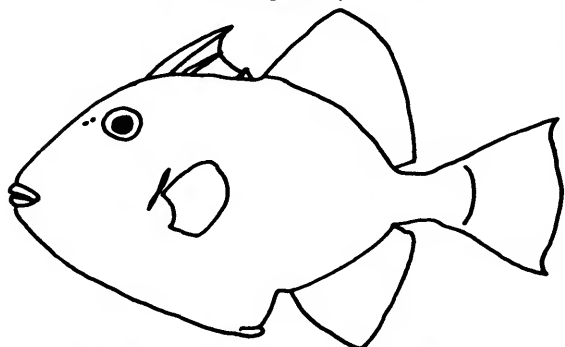


FIGURE 3.—Body outline of a representative balistid, *Balistes*.

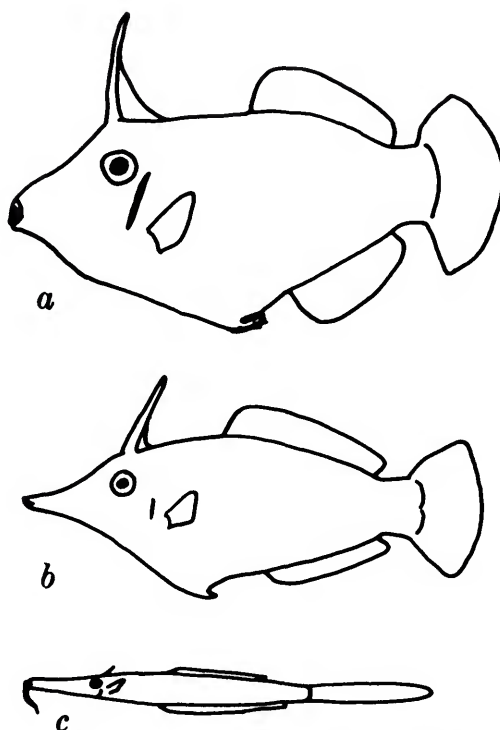


FIGURE 4.—Body outlines of representative monacanthids: *a*, *Pervagor*; *b*, *Oxymonacanthus*; *c*, *Anacanthus*.



FIGURE 5.—Body outline of a representative aracanid, *Aracanostracion*.

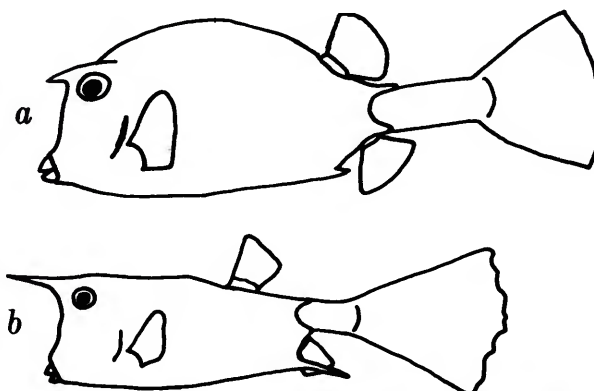


FIGURE 6.—Body outlines of representative ostraciids: *a*, *Acanthostracion*; *b*, *Lactoria*.



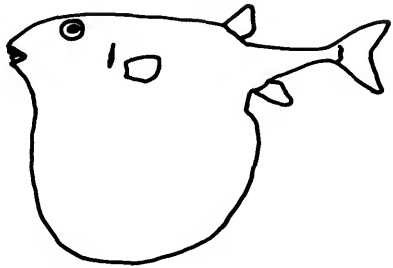


FIGURE 7.—Body outline of *Triodon macropterus*.

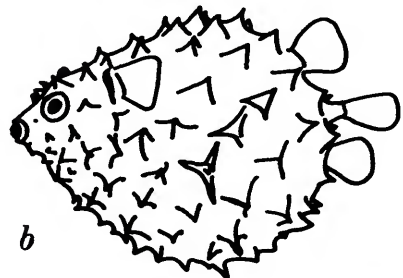
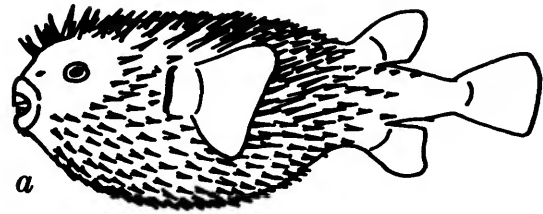


FIGURE 10.—Body outlines of representative diodontids: a, *Diodon*; b, *Chilomycterus*.

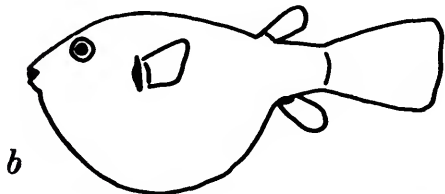
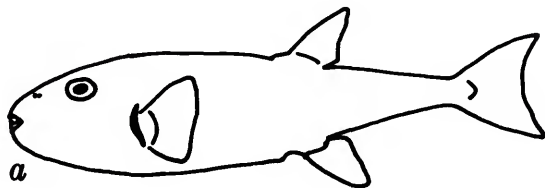


FIGURE 8.—Body outlines of representative tetraodontids: a, *Lagocephalus*; b, *Arothron*.

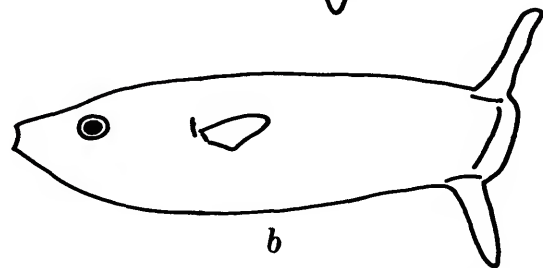
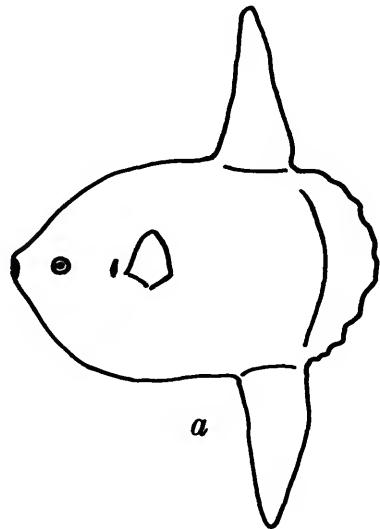


FIGURE 11.—Body outlines of representative molids: a, *Mola*; b, *Ranzania*.

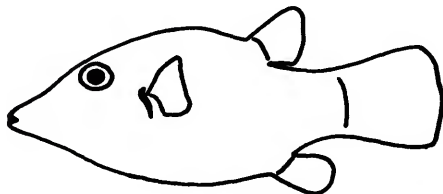


FIGURE 9.—Body outline of a representative canthigasterid, *Canthigaster*.

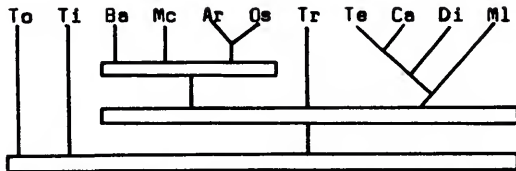


FIGURE 12.—Phylogenetic tree for section A 1 of the adductor mandibulae. (See "List of Abbreviations".)

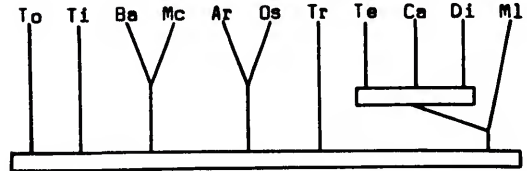
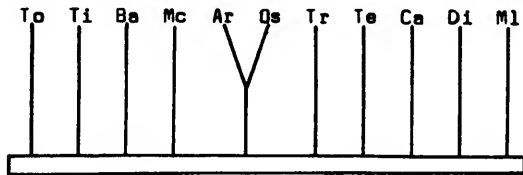
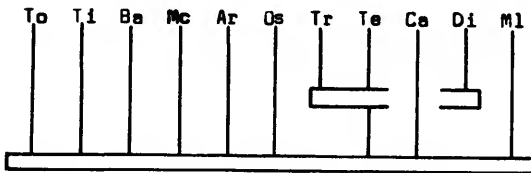


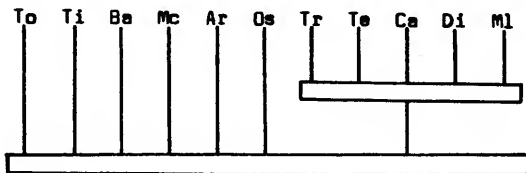
FIGURE 13.—Phylogenetic tree for section A 2 of the adductor mandibulae.



*a*

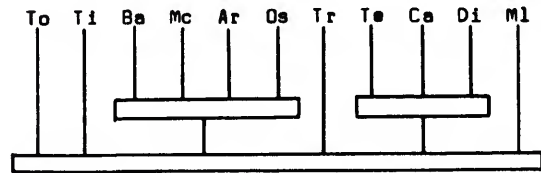


*b*

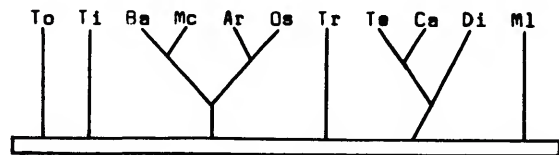


*c*

FIGURE 14.—Phylogenetic trees: *a*, section A 3 of the adductor mandibulae; *b*, A  $\omega$  of the adductor mandibulae; *c*, reinterpreted for section A  $\omega$ .

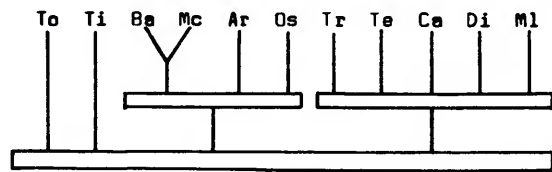


*a*

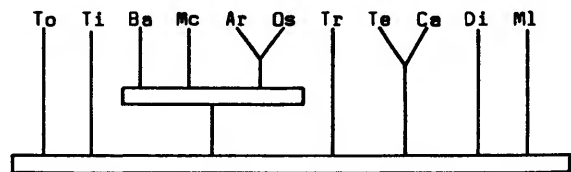


*b*

FIGURE 15.—Phylogenetic trees: *a*, the levator arcus palatini; *b*, the dilatator operculi.



*a*



*b*

FIGURE 16.—Phylogenetic trees: *a*, the levator operculi; *b*, the adductor arcus palatini.

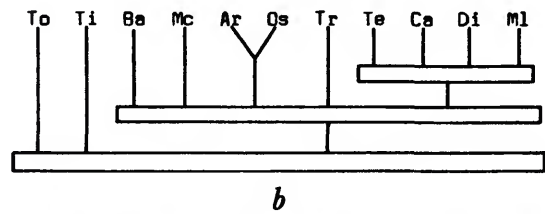
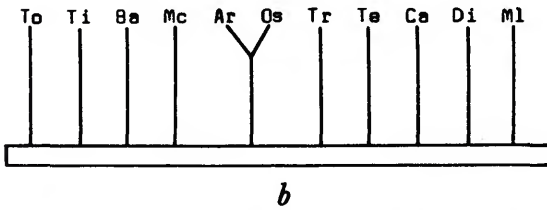
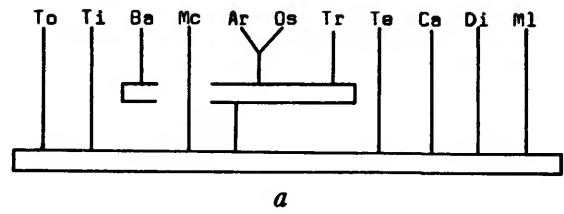
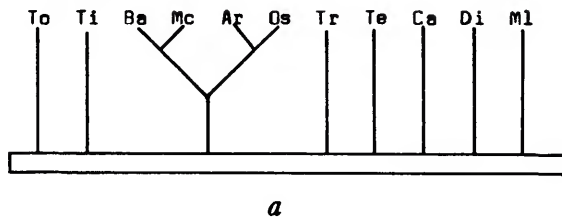


FIGURE 17.—Phylogenetic trees: *a*, the retractor arcus palatini; *b*, the adductor operculi.

FIGURE 18.—Phylogenetic trees: *a*, the adductor hyomandibulae; *b*, reinterpreted for the adductor hyomandibulae.

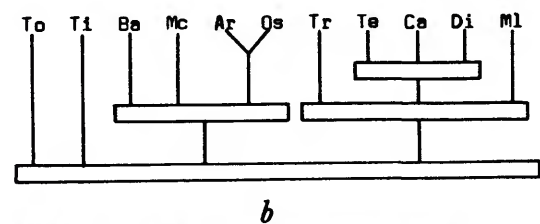
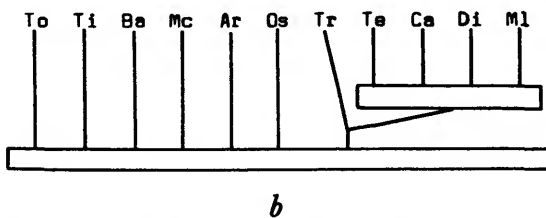
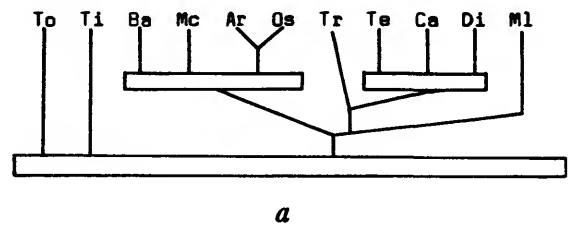
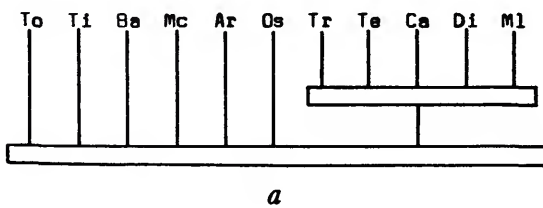


FIGURE 19.—Phylogenetic trees: *a*, the intermandibularis; *b*, the valvulus.

FIGURE 20.—Phylogenetic trees: *a*, the hyohyoideus inferioris; *b*, reinterpreted for the hyohyoideus inferioris.

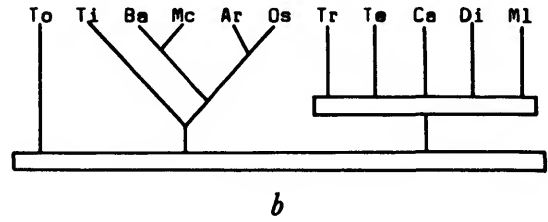
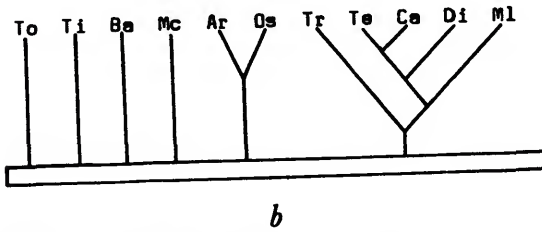
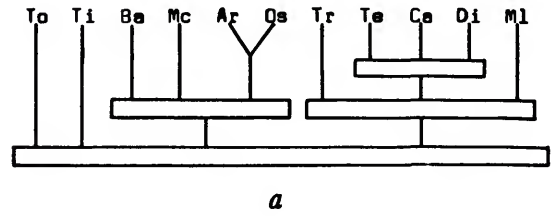
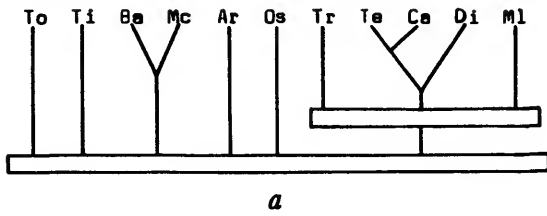


FIGURE 21.—Phylogenetic trees: *a*, the hyohyoidei abductores; *b*, the hyohyoidei adductores.

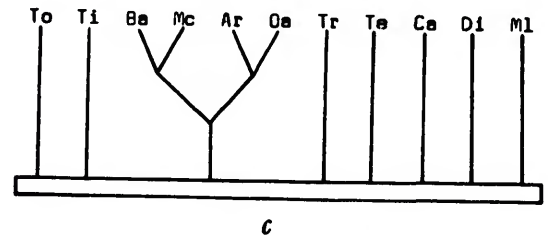
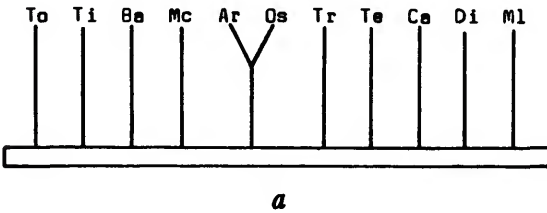


FIGURE 22.—Phylogenetic trees: *a*, the sternohyoideus; *b*, the sternobranchialis; *c*, alternative for the sternobranchialis.

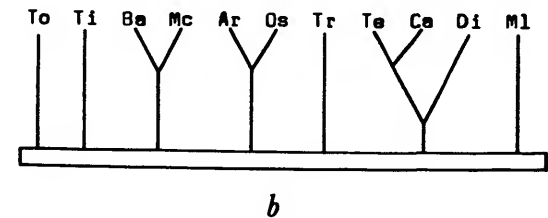
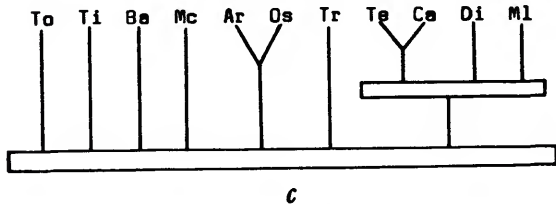
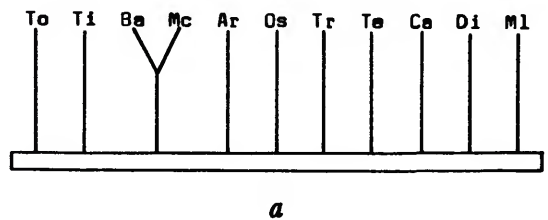
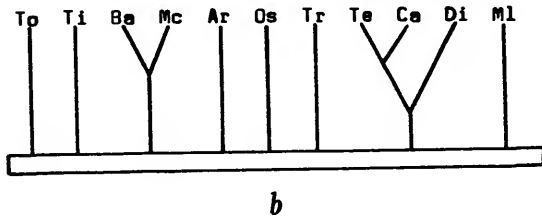


FIGURE 23.—Phylogenetic trees: *a*, the pharyngoclavicularis externus; *b*, the pharyngoclavicularis internus; *c*, the obliqui ventrales.

FIGURE 24.—Phylogenetic trees: *a*, the transversi ventrales; *b*, the recti ventrales.

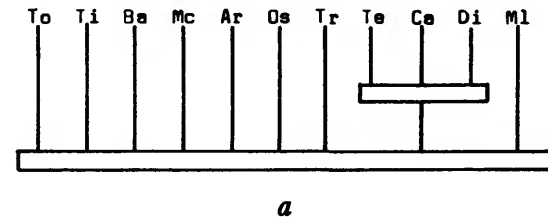
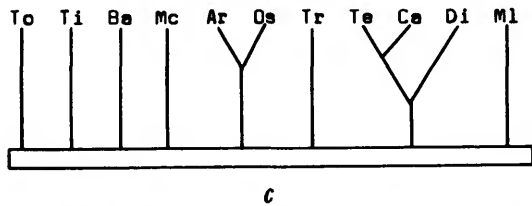
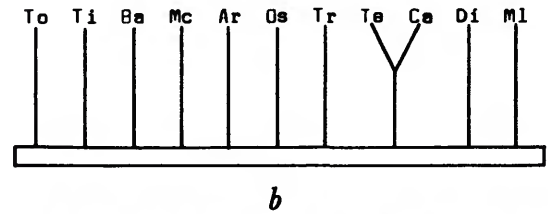
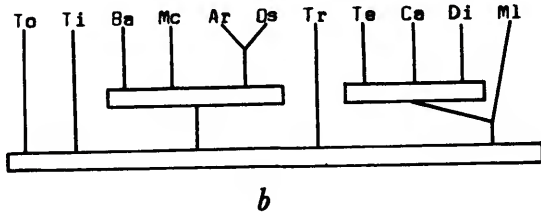
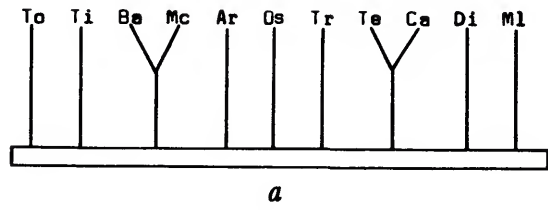
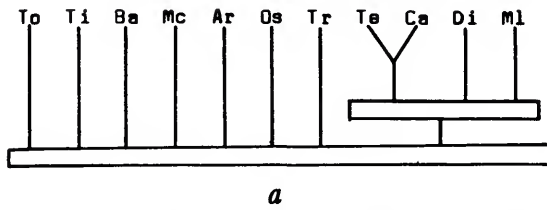


FIGURE 25.—Phylogenetic trees: *a*, the rectus communis; *b*, the levatores externi. *c*, the levatores interni.

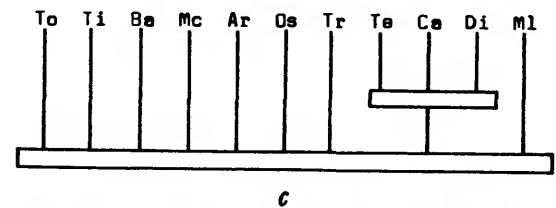
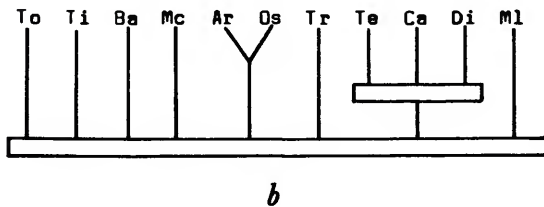
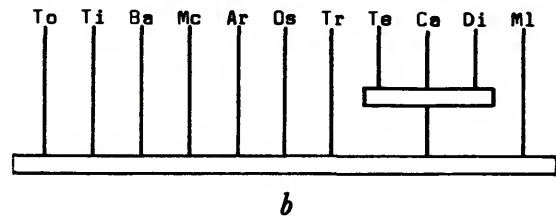
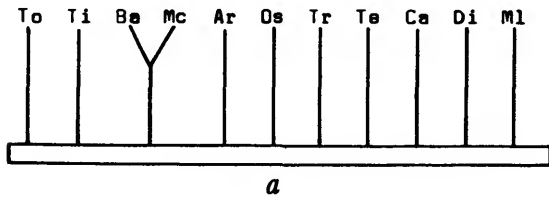
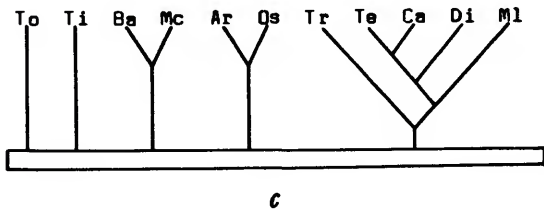


FIGURE 28.—Phylogenetic trees: *a*, the abductor superficialis; *b*, the abductor profundus; *c*, the adductor superficialis.



← FIGURE 27.—Phylogenetic trees: *a*, the retractor dorsalis; *b*, the adductores; *c*, the sphincter oesophagi.

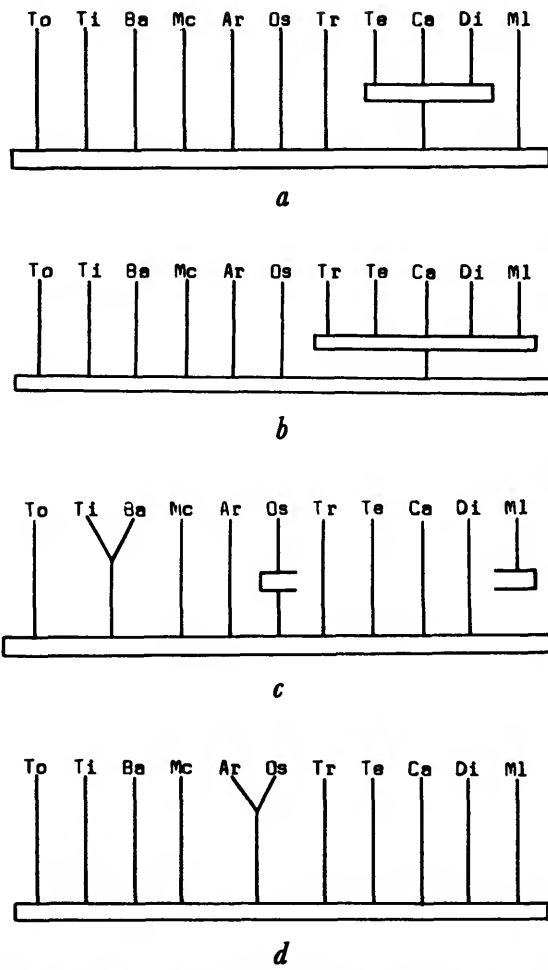


FIGURE 29.—Phylogenetic trees: *a*, the adductor profundus; *b*, the arrector dorsalis; *c*, the coracoradialis; *d*, reinterpreted for the coracoradialis.

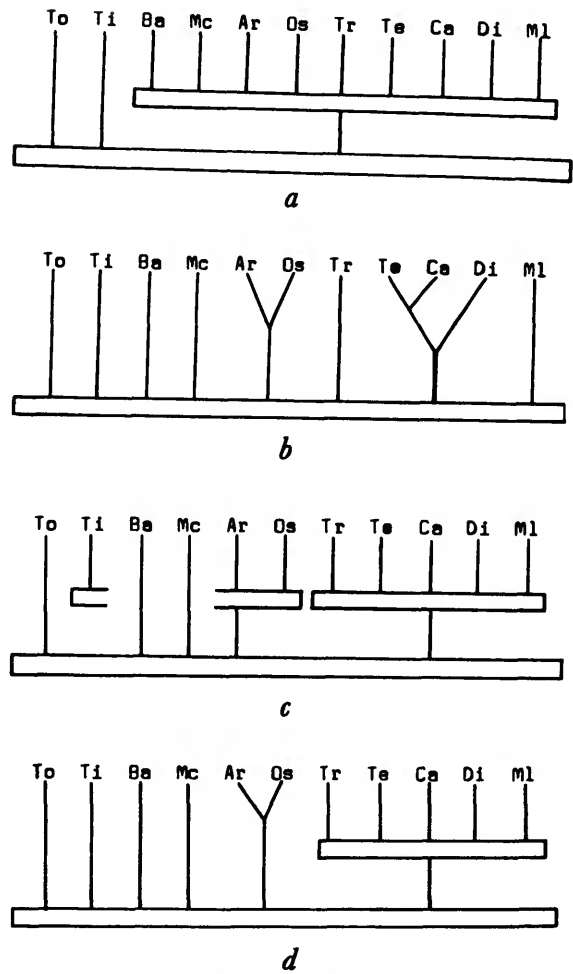


FIGURE 30.—Phylogenetic trees: *a*, the adductor radialis; *b*, the protractor pectoralis; *c*, the levator pectoralis; *d*, reinterpreted for the levator pectoralis.

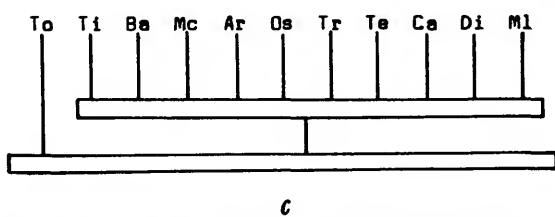
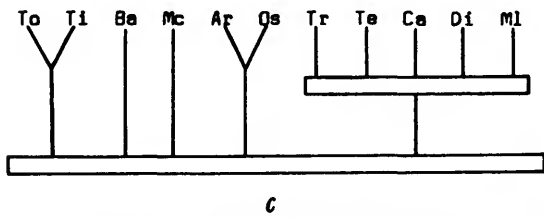
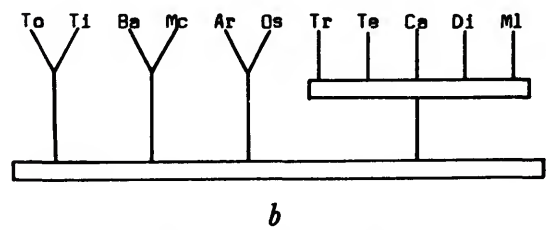
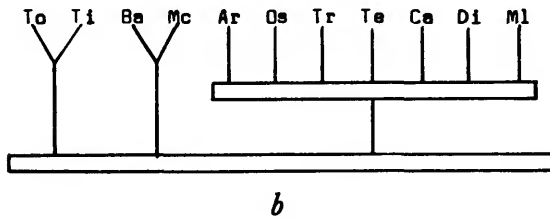
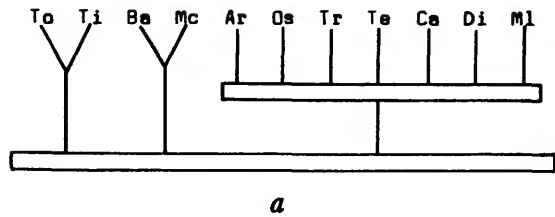
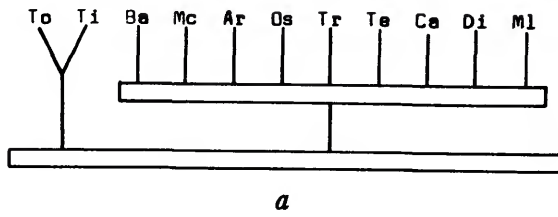


FIGURE 31.—Phylogenetic trees: *a*, the arrector dorsalis pelvificus; *b*, the arrector ventralis pelvificus; *c*, reinterpreted for the arrector ventralis pelvificus.

FIGURE 32.—Phylogenetic trees: *a*, the adductor superficialis pelvificus; *b*, reinterpreted for the adductor superficialis pelvificus; *c*, the adductor profundus pelvificus.

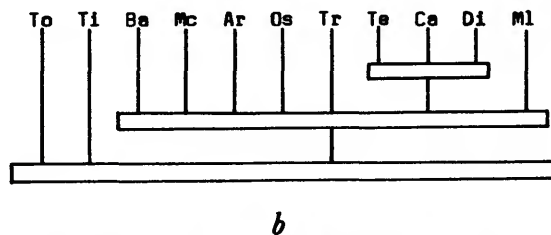
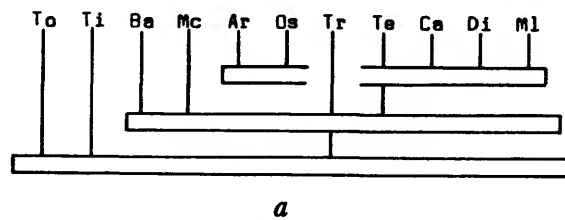


FIGURE 33.—Phylogenetic trees: *a*, the inclinatore dorsales; *b*, reinterpreted for the inclinatore dorsales.

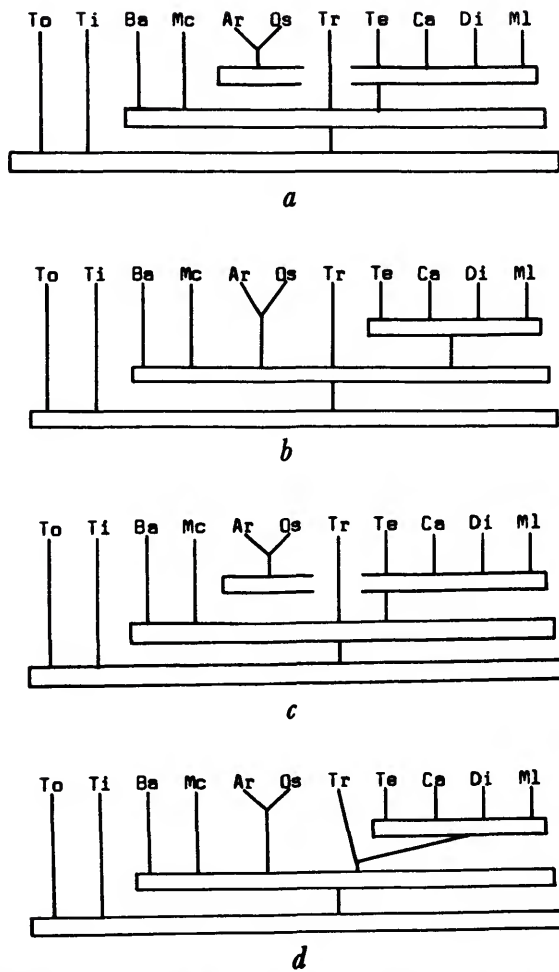


FIGURE 34.—Phylogenetic trees: *a*, the erectores dorsales; *b*, reinterpreted for the erectores dorsales; *c*, the depressores dorsales; *d*, reinterpreted for the depressores dorsales.

FIGURE 36.—Phylogenetic trees: *a*, the supracarinalis anterior; *b*, reinterpreted for the supracarinalis anterior; *c*, the supracarinalis medius.

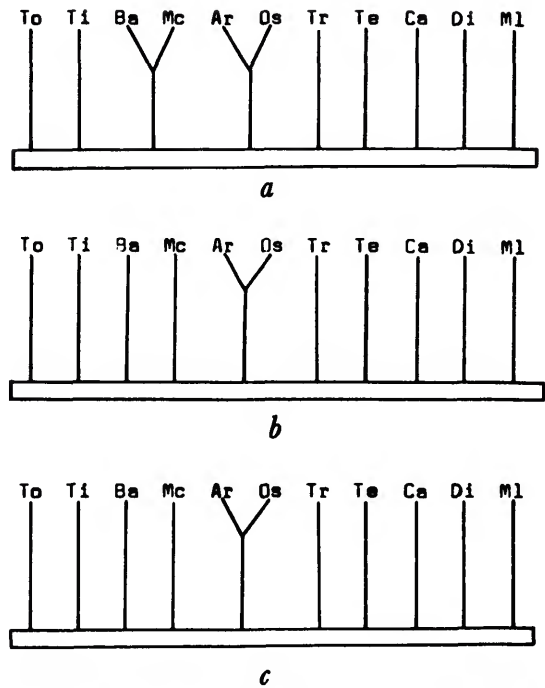
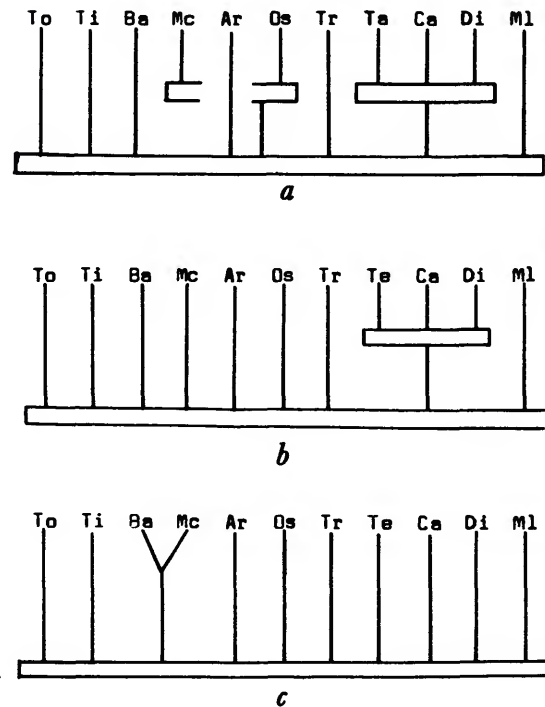


FIGURE 35.—Phylogenetic trees: *a*, the inclinatore anales; *b*, the erectores anales; *c*, the depressores anales.





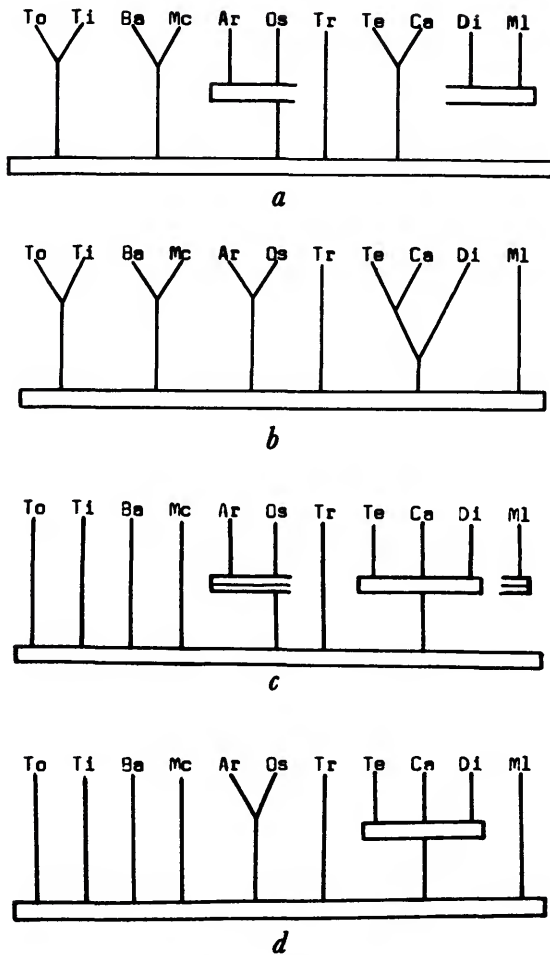


FIGURE 37.—Phylogenetic trees: *a*, the infracarinalis anterior; *b*, reinterpreted for the infracarinalis anterior; *c*, the infracarinalis medius; *d*, reinterpreted for the infracarinalis medius.

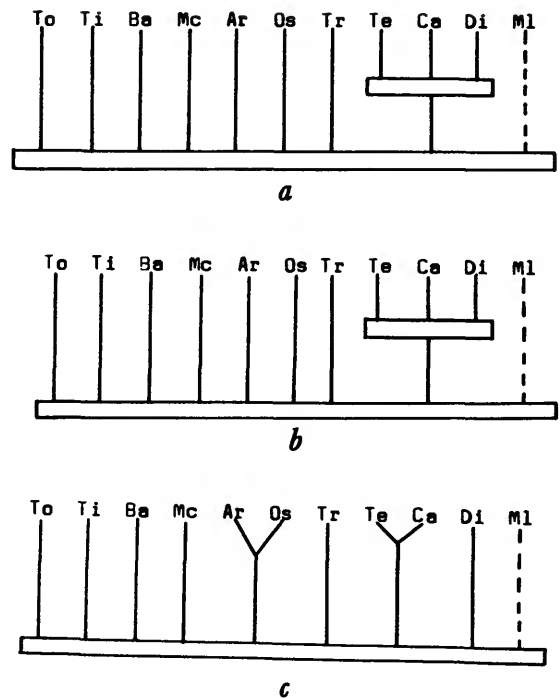


FIGURE 38.—Phylogenetic trees: *a*, the interradialis; *b*, the hypochordal longitudinalis; *c*, the flexor dorsalis.

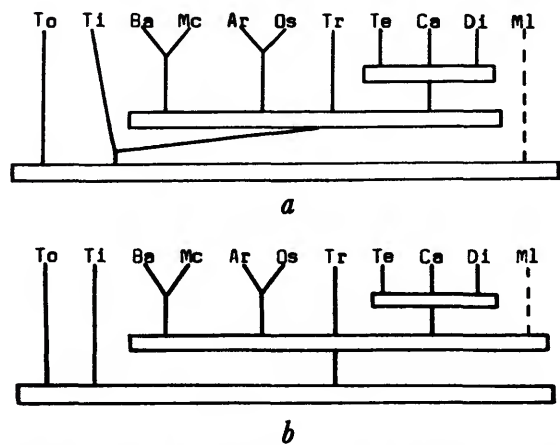


FIGURE 39.—Phylogenetic trees: *a*, the flexor dorsalis superior; *b*, reinterpreted for the flexor dorsalis superior.

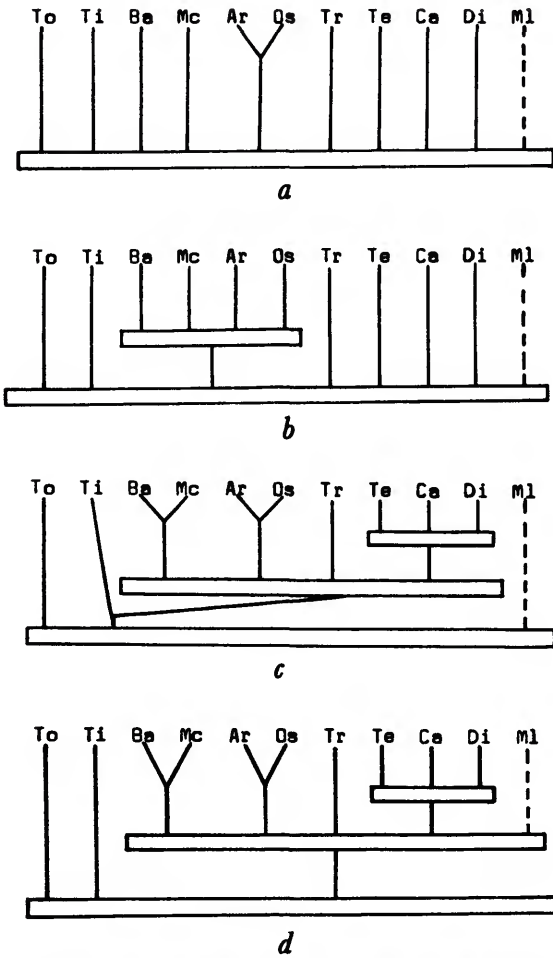


FIGURE 40.—Phylogenetic trees: *a*, the flexor ventralis; *b*, the flexor ventralis externus; *c*, the flexor ventralis inferior; *d*, reinterpreted for the flexor ventralis inferior.

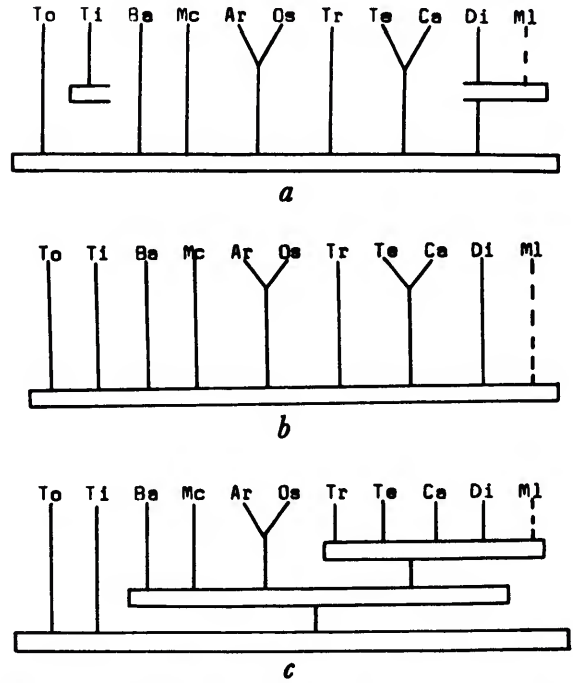


FIGURE 41.—Phylogenetic trees: *a*, the transversus caudalis; *b*, reinterpreted for the transversus caudalis; *c*, the epaxialis.

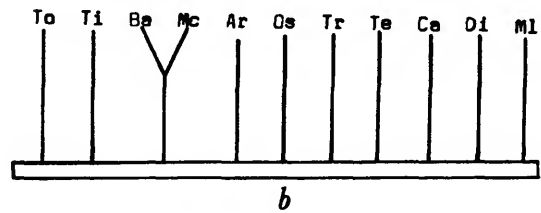
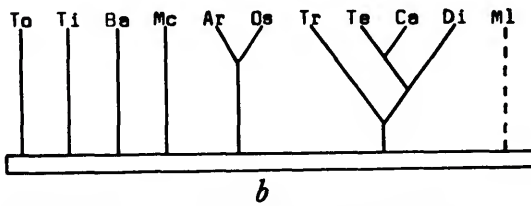
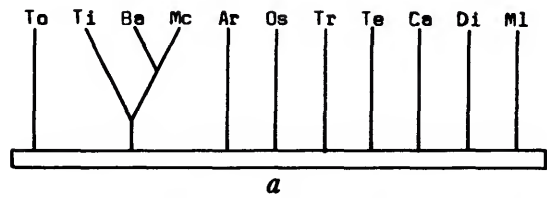
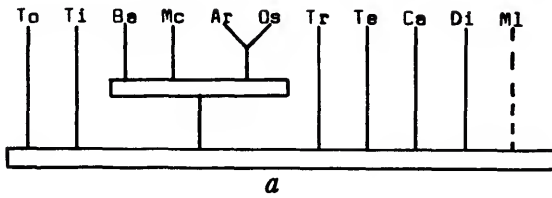


FIGURE 42.—Phylogenetic trees: *a*, the obliquus superioris; *b*, the obliquus inferioris.

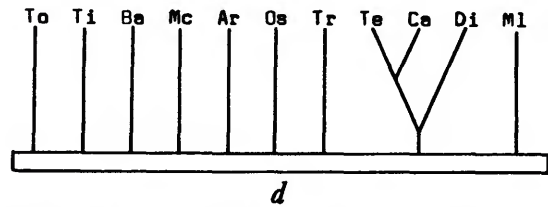
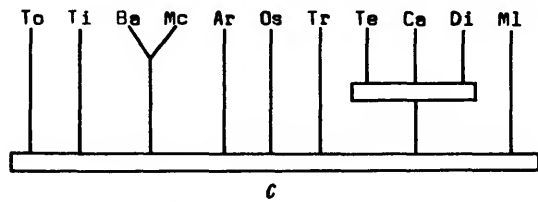


FIGURE 43.—Phylogenetic trees: *a*, the spinalis; *b*, reinterpreted for the spinalis; *c*, the transversus cutaneus; *d*, the longitudinal cutaneus.

FIGURE 44.—A hypothesized phylogeny of the Tetraodontiformes, based on the analysis of those muscles yielding phylogenetic information.

*Solid black:* The phylogeny included in the shaded area is as indicated in the phylogenetic tree. If only two families are linked, the two families are sister groups.

*Wavy lines:* The contained families share a common ancestor, but further subdivision into sister groups is not possible.

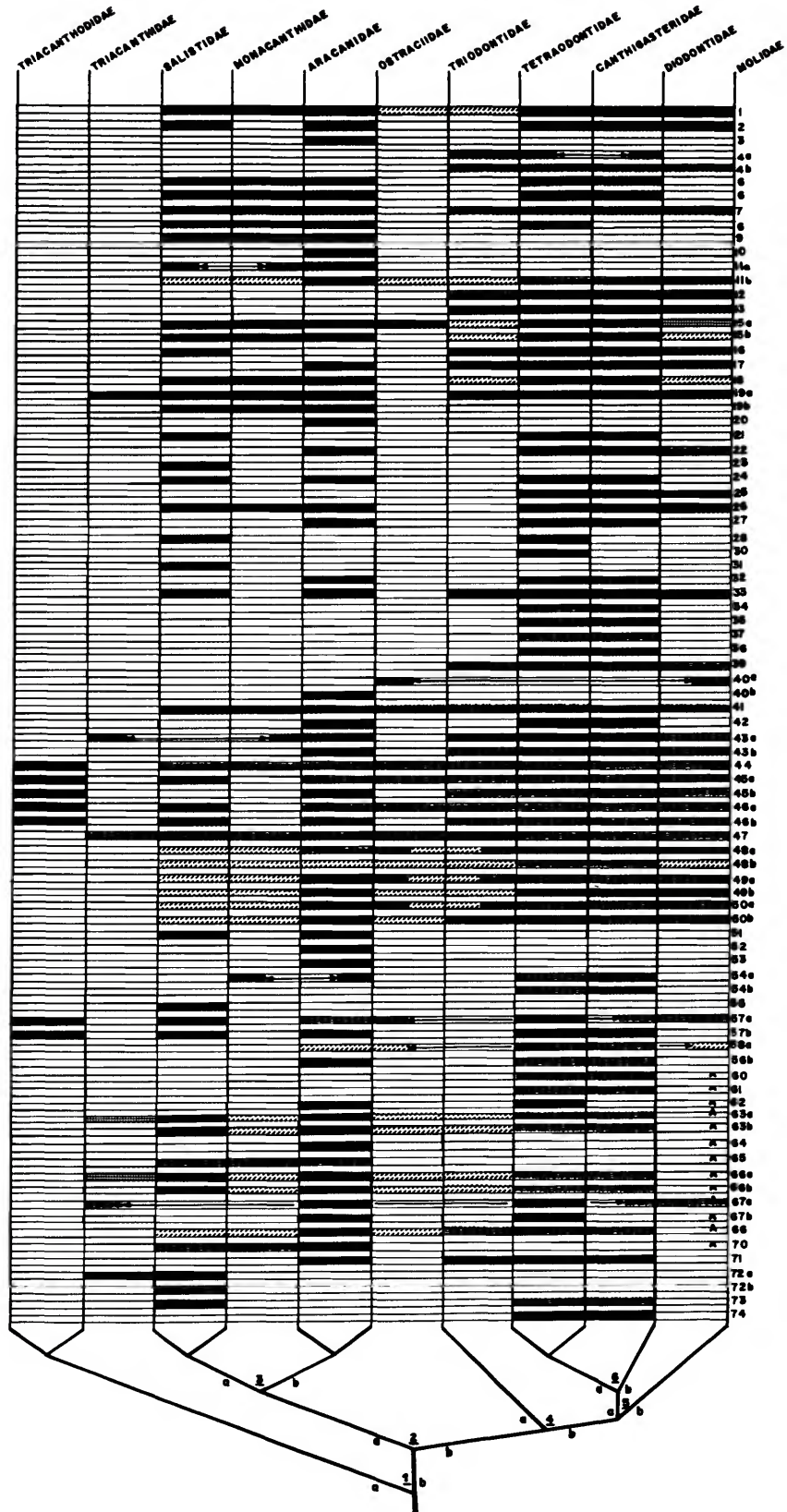
*Oblique dashes:* The common ancestor of the families linked by the wavy lines shares a common ancestor with the families covered by this symbol.

*Dots:* As above, but the next lowest level of application.

*Arrow:* Used to link supposed sister groups where the hypothesized phylogeny is incorrect, if confusion is otherwise likely.

*A:* An autapomorph condition, where this would otherwise affect the interpretation.

*General:* Where symbols extend halfway across the gap separating families and then cease or change, it indicates that the family (-ies) thus implicated should be linked with the family (-ies) which is (are) elsewhere represented by the same half-symbol. It only occurs where the hypothesized phylogeny is incorrect. The numerals in the right-hand margin correspond to the text number used for that muscle. Where a muscle has been reinterpreted, "a" and "b" are appended after the number. The numerals within the tree itself will be used to designate branch points in the discussion. The letters "a" and "b" are used at points of branching to clarify the lines in which the evidence applies.



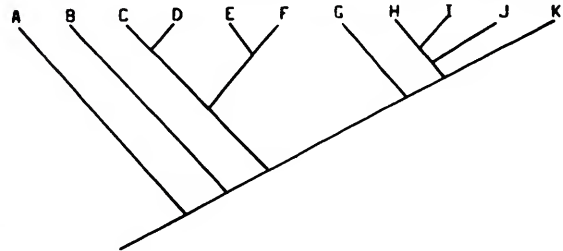
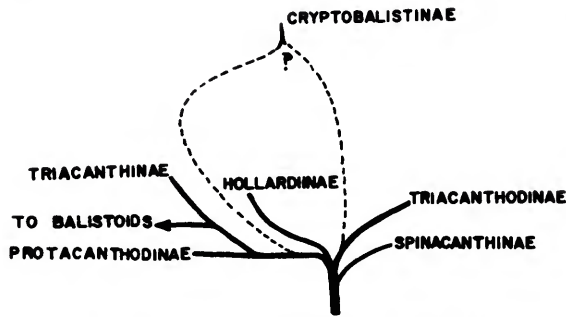


FIGURE 46.—Cladogram for taxa A-K.

FIGURE 45.—The phylogenetic tree of the basal tetraodontiforms. (Drawn from Tyler, 1968, fig. 6.)

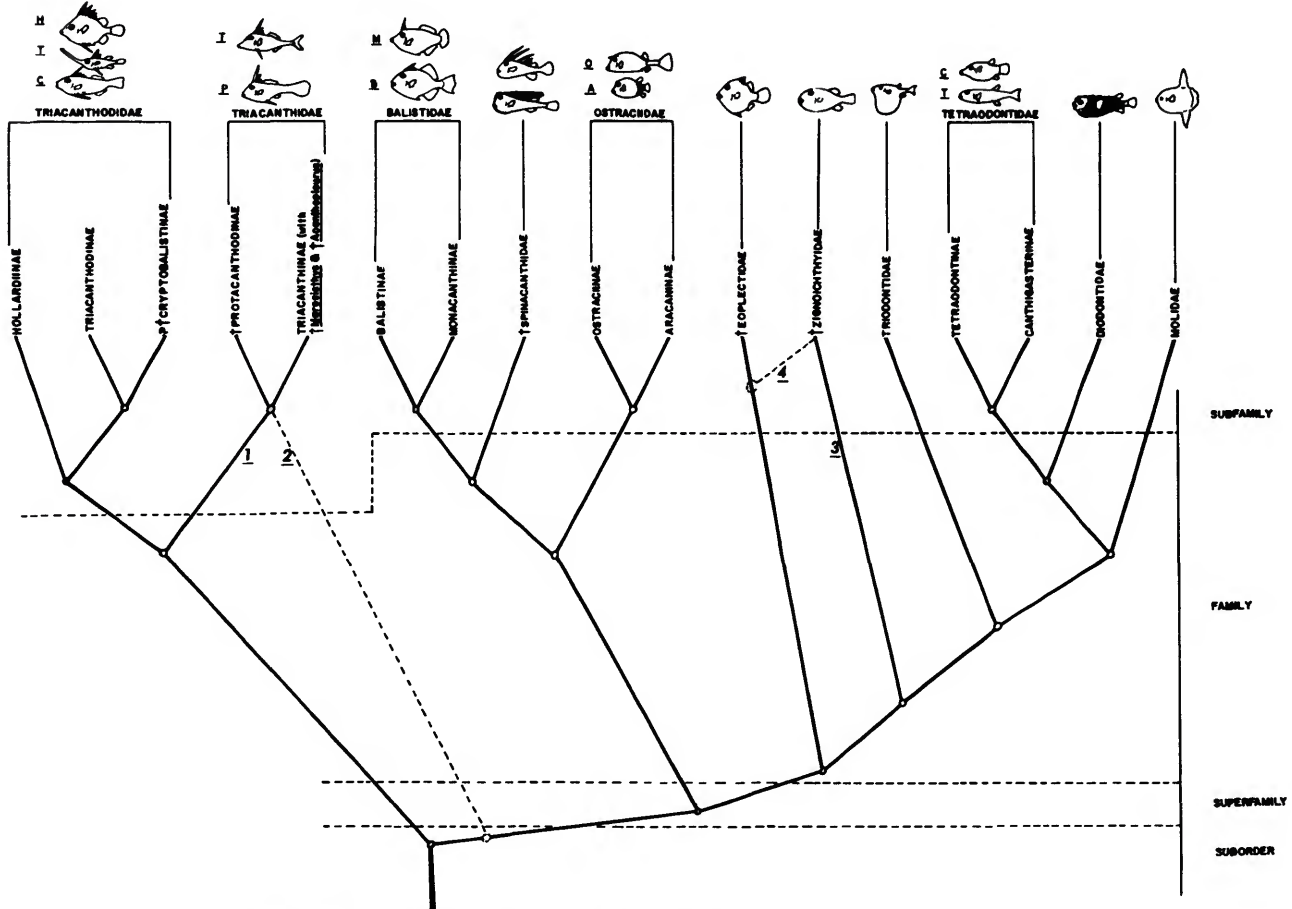


FIGURE 47.—Phylogenetic tree of living and fossil tetraodontiforms. Daggers indicate fossil groups; question mark emphasizes the tentative placement of the Cryptobalistinae as the sister group of the Triacanthodinae; the digits 1 through 4 correspond to the hierarchical alternatives in the classification on p. 99; outline of fossils from Tyler (ms).

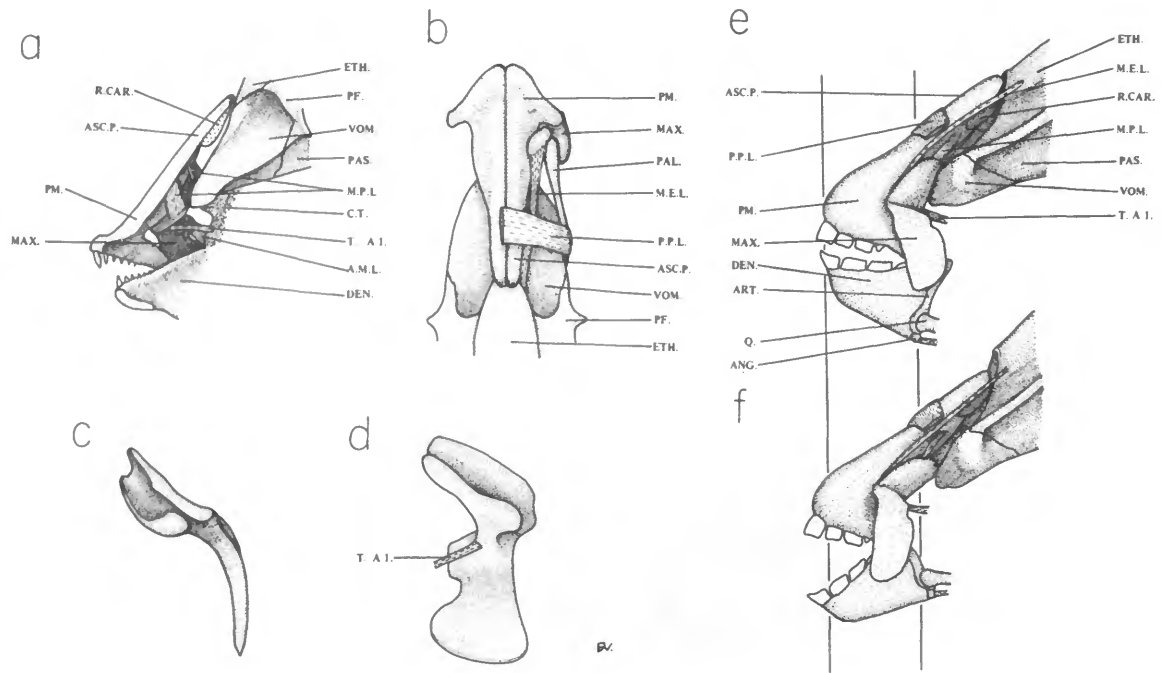


FIGURE 48.—*Triacanthodes anomalous*, ANSP 117493, 87 mm SL: a, medial view of right half of jaw region; b, dorsal view of jaws (left palatine and maxilla removed); c, anterior view of left maxilla; d, medial view of left maxilla. *Triacanthus biaculeatus*, ANSP 111536, 111 mm SL.: e-f, left lateral view of snout region, showing degree of upper jaw protrusion. (See abbreviations list for explanation.)

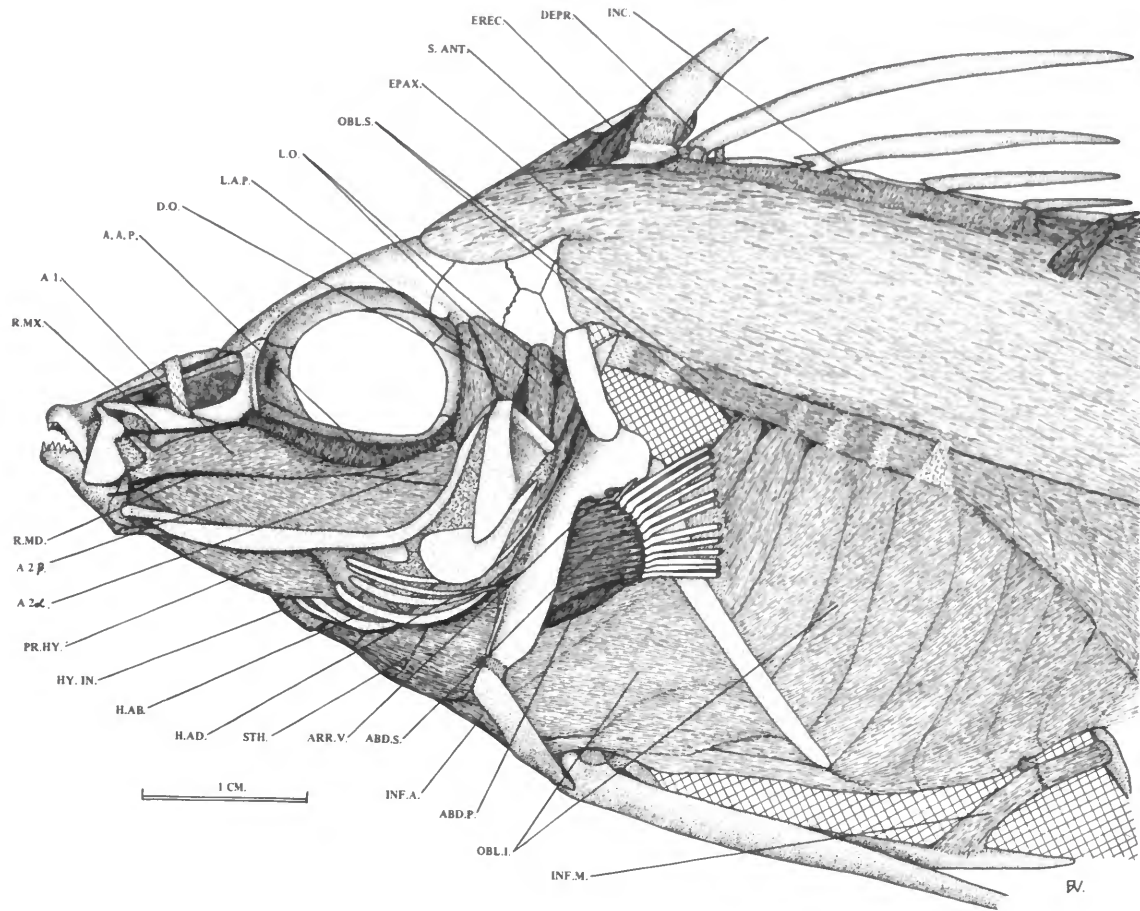


FIGURE 49.—*Triacanthodes anomalus*, ANSP 117493, 87 mm SL, left lateral view of superficial anterior musculature.



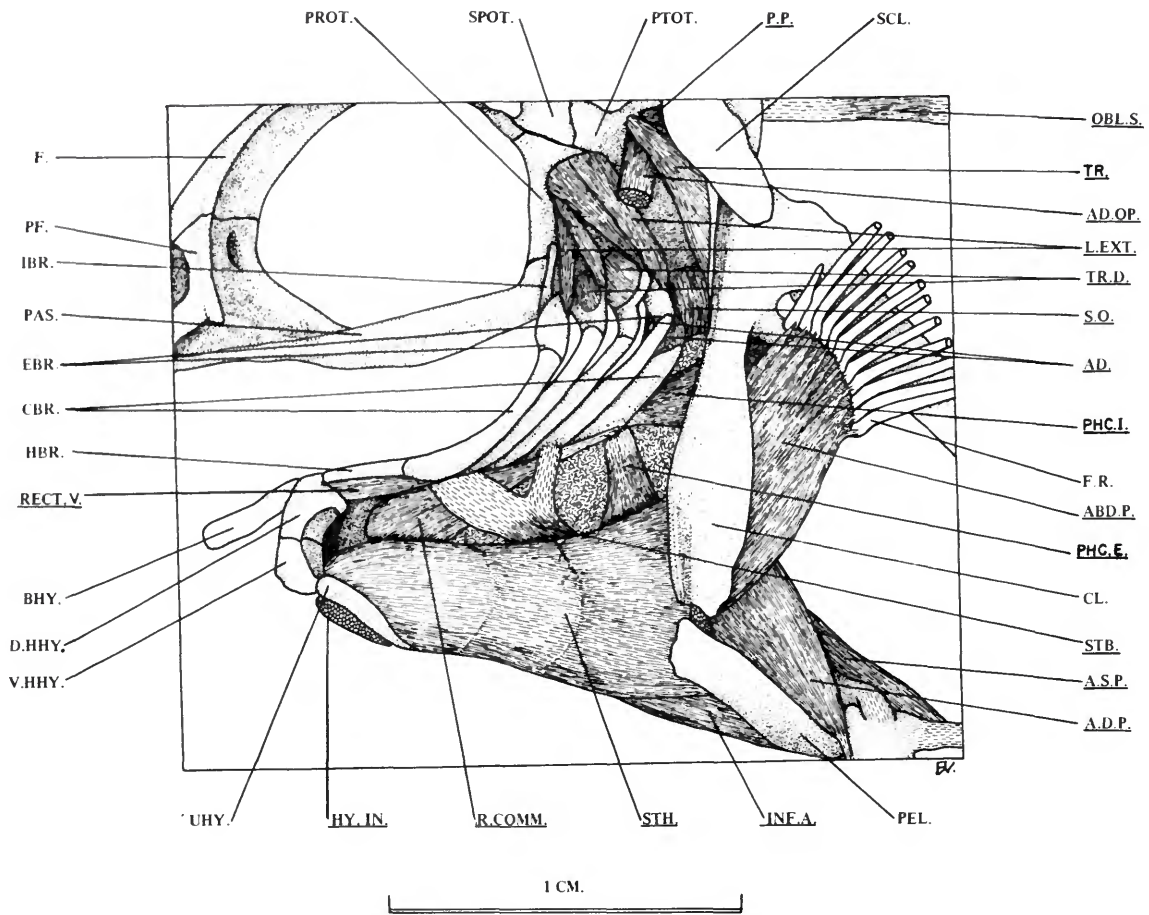


FIGURE 50.—*Triacanthodes anomalus*, ANSP 117493, 87 mm SL, left lateral view of the branchial arch region. (Palatal arch and parts of the hyoid arch removed.)

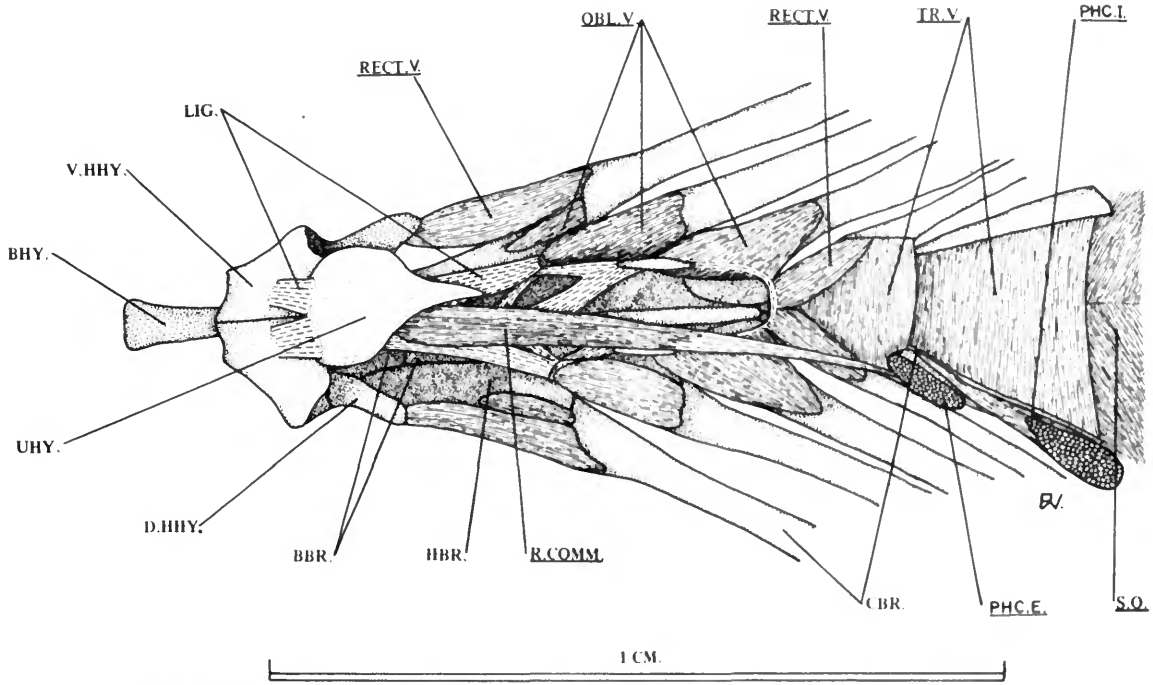
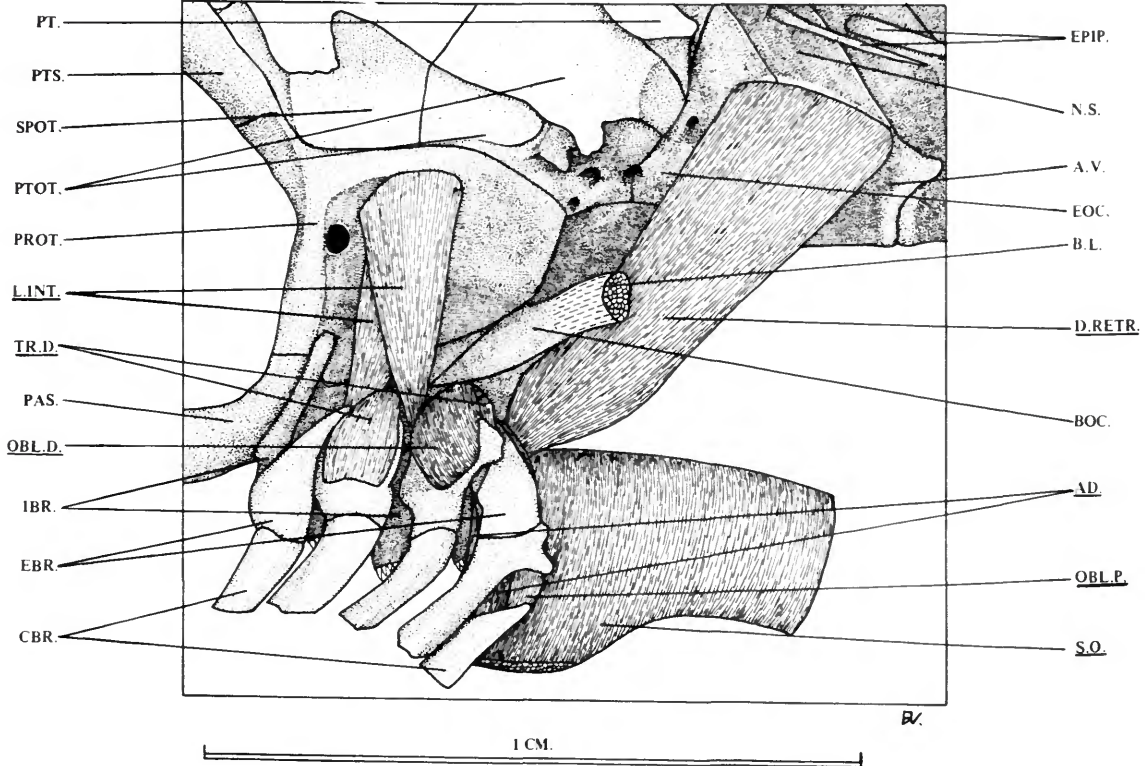


FIGURE 51.—*Triacanthodes anomalus*, ANSP 117493, 87 mm SL, ventral view of branchial arches, urohyal displaced to left. (Left rectus communis and pharyngoclaviculares removed.)

FIGURE 52.—*Triacanthodes anomalus*, ANSP 117493, 87 mm SL, left lateral view of dorsal branchial arch region. (Levatores externi removed.)



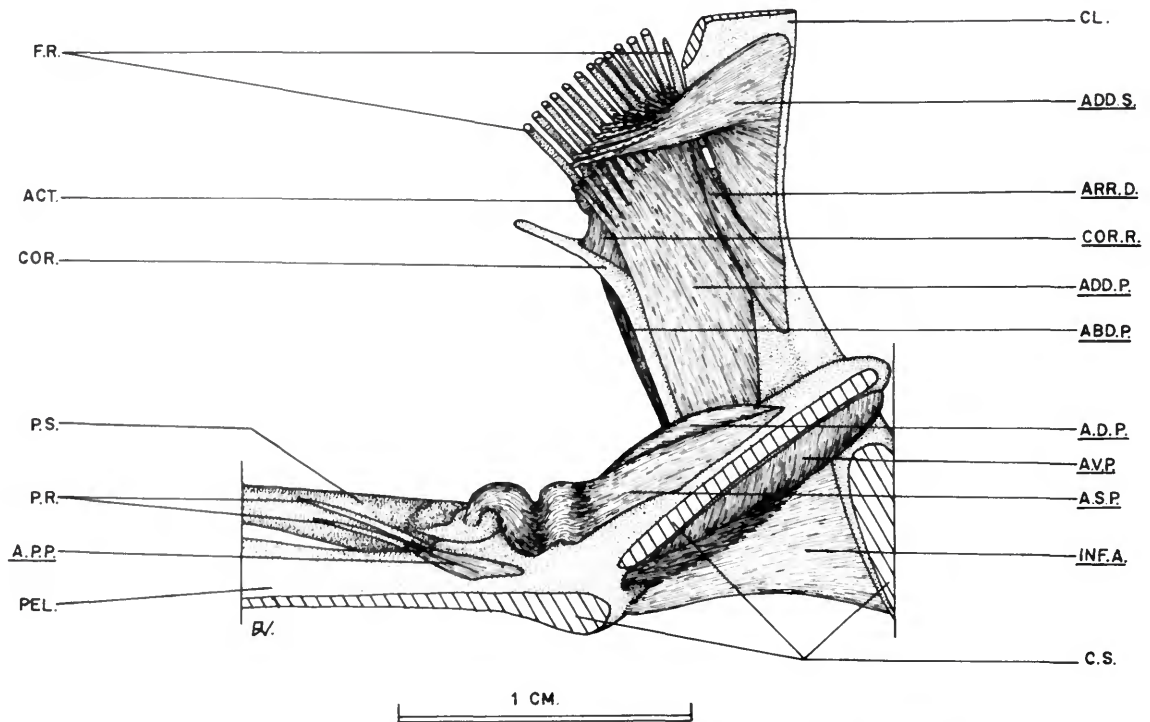


FIGURE 53.—*Triacanthodes anomalus*, ANSP 117493, 87 mm SL, medial view of left pectoral and pelvic girdles and the associated musculature.

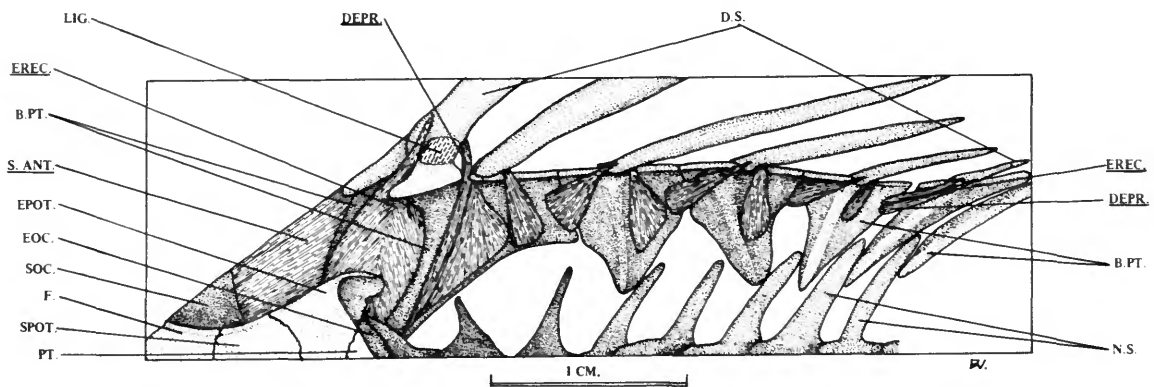


FIGURE 54.—*Triacanthodes anomalus*, ANSP 117493, 87 mm SL, left lateral view of the spiny dorsal fin. (Inclinatores dorsales and the epaxialis removed.)

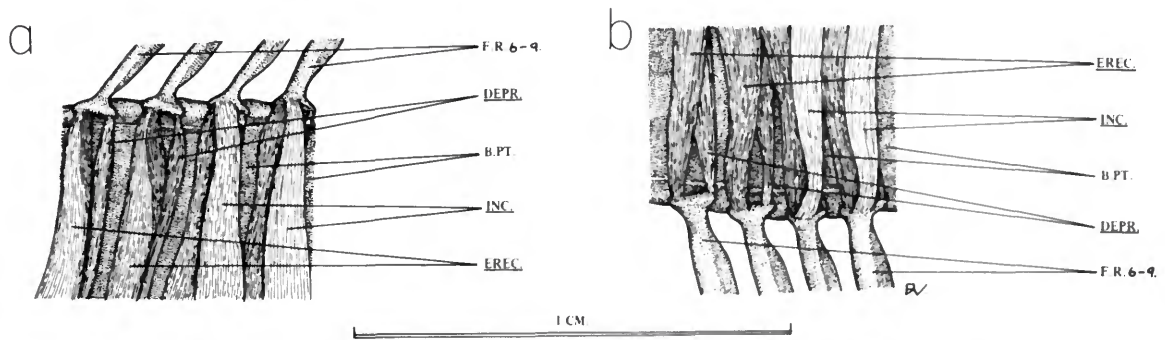


FIGURE 55.—*Triacanthodes anomalus*, ANSP 117493, 87 mm SL, left lateral view of the sixth to ninth fin rays of: *a*, soft dorsal fin; *b*, anal fin. (Body muscles and first two inclinators removed.)

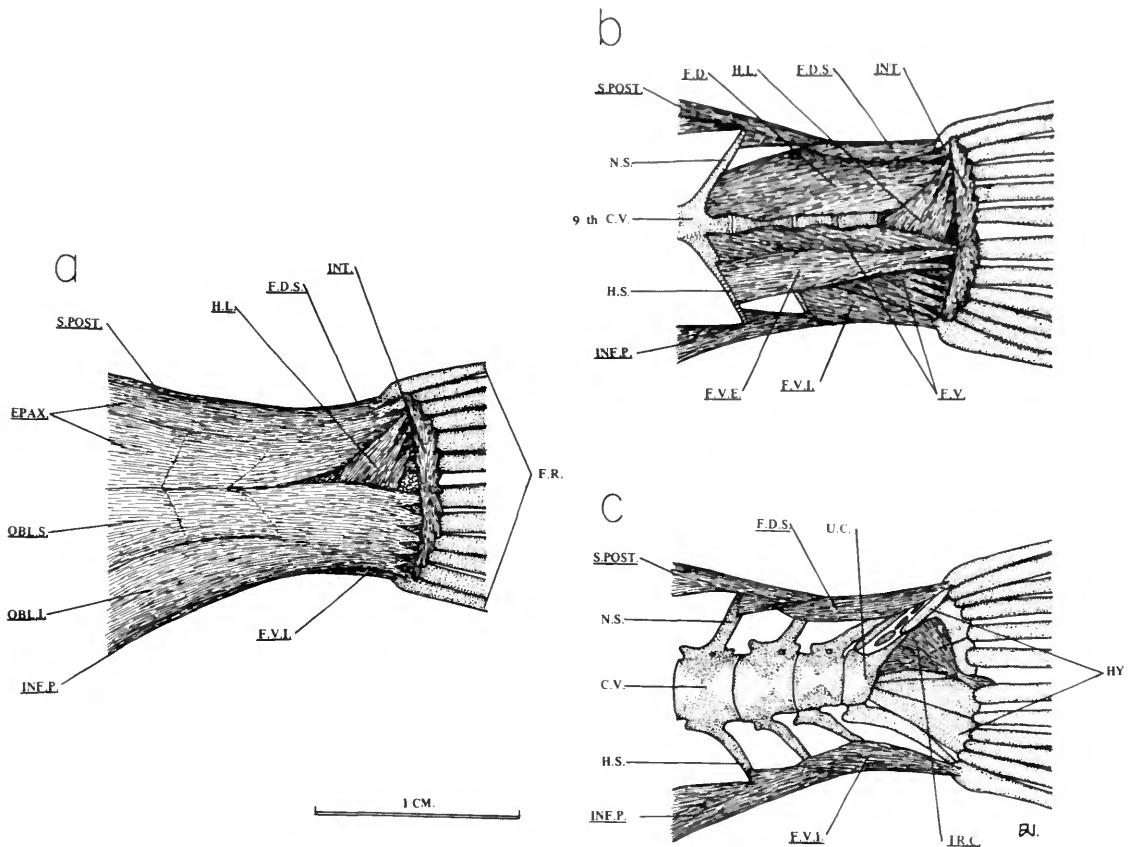


FIGURE 56.—*Triacanthodes anomalus*, ANSP 117493, 87 mm SL, left lateral view of caudal peduncle region: *a*, superficial musculature; *b*, after removal of body musculature; *c*, deep layer of muscle.

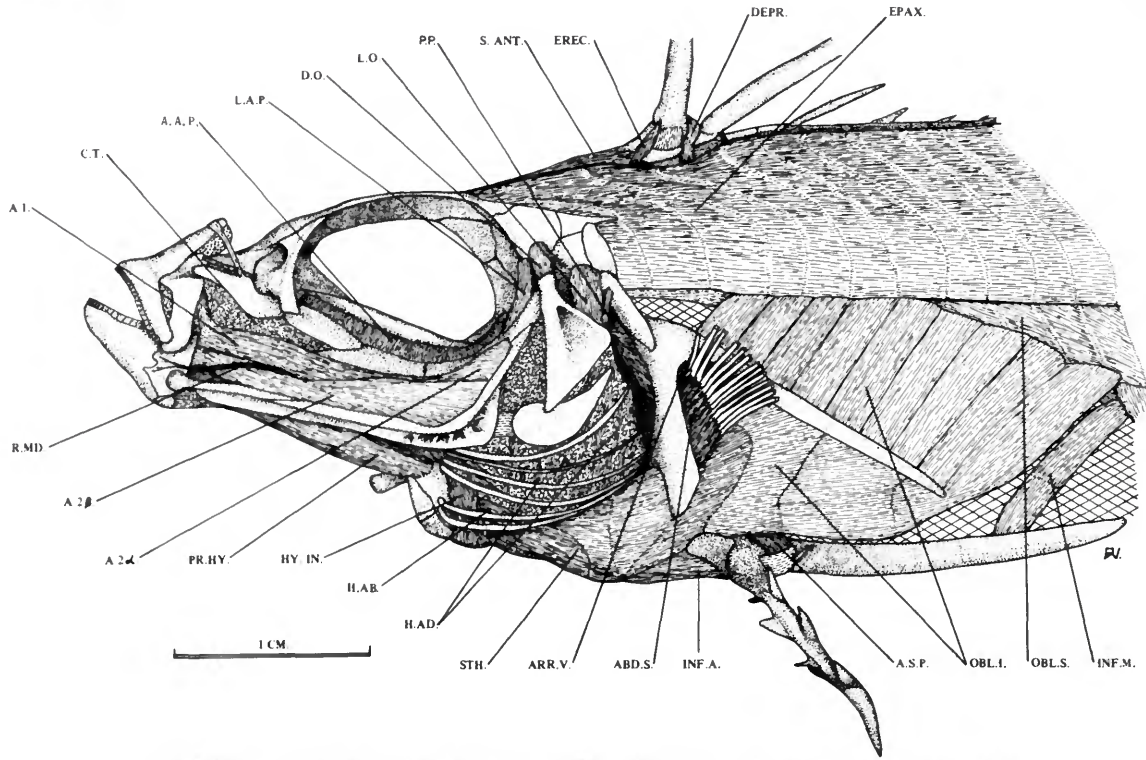


FIGURE 57.—*Tydemania navigatoris*, ANSP 117532, 75 mm SL, left lateral view of superficial anterior musculature.

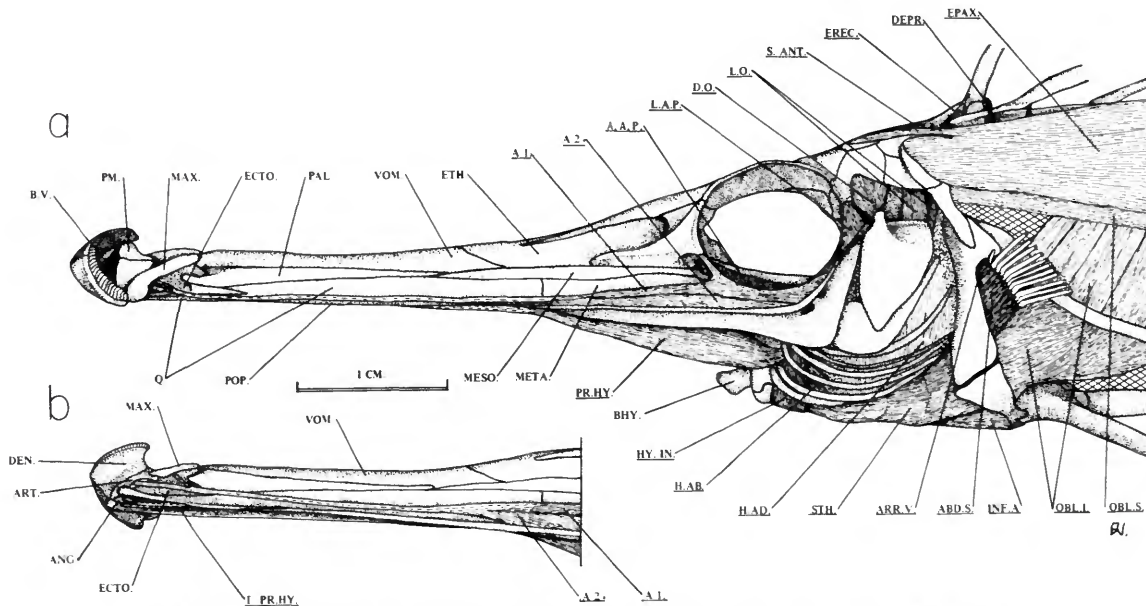


FIGURE 58.—*Macrorhamphosodes platycheilus*, ANSP 117533, 88 mm SL: a, left lateral view of superficial anterior musculature; b, mirror image of right lateral view of anterior snout region.

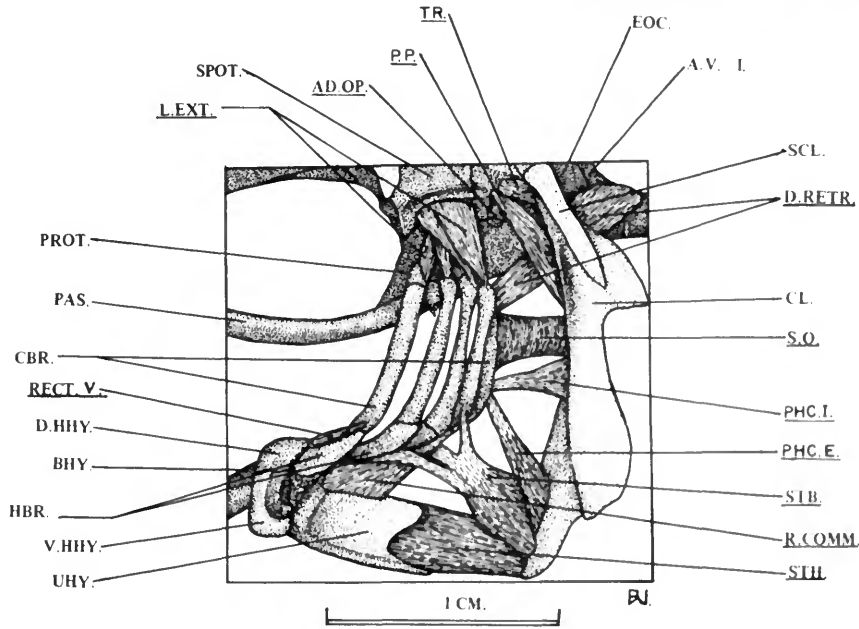


FIGURE 59.—*Macrorhamphosodes platycheilus*, ANSP 117533, 88 mm SL, left lateral view of branchial arch muscles (superficial).

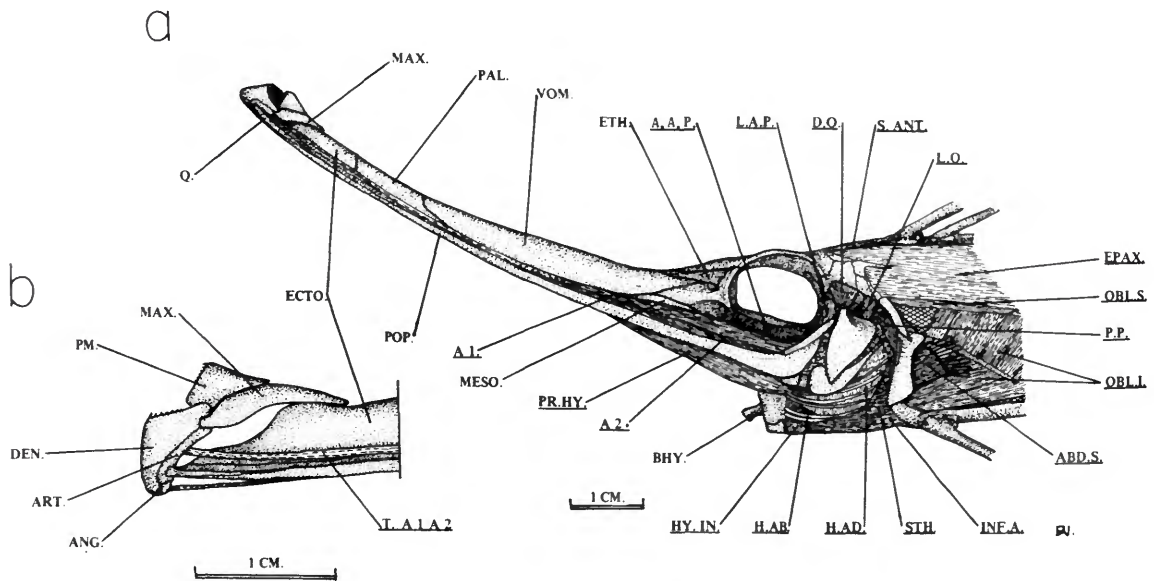


FIGURE 60.—*Halimochirurgus centriscoides*, ANSP 117494, 114 mm SL: a, left lateral view (slightly dorsal) of superficial anterior musculature; b, left lateral view of anterior snout, with mouth fully open.

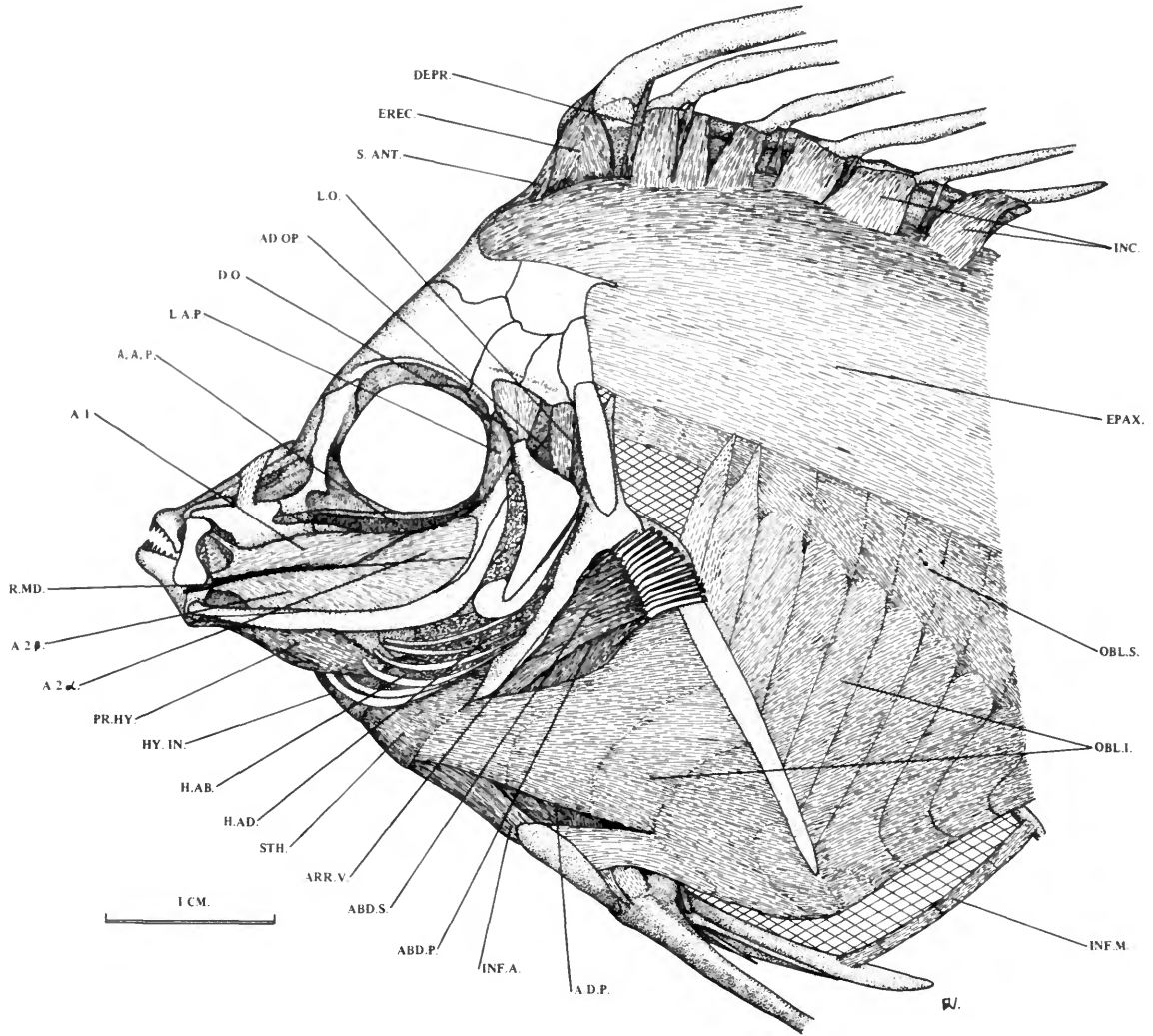


FIGURE 61.—*Parahollardia lineata*, ANSP 101031, 68 mm SL, left lateral view of superficial musculature.

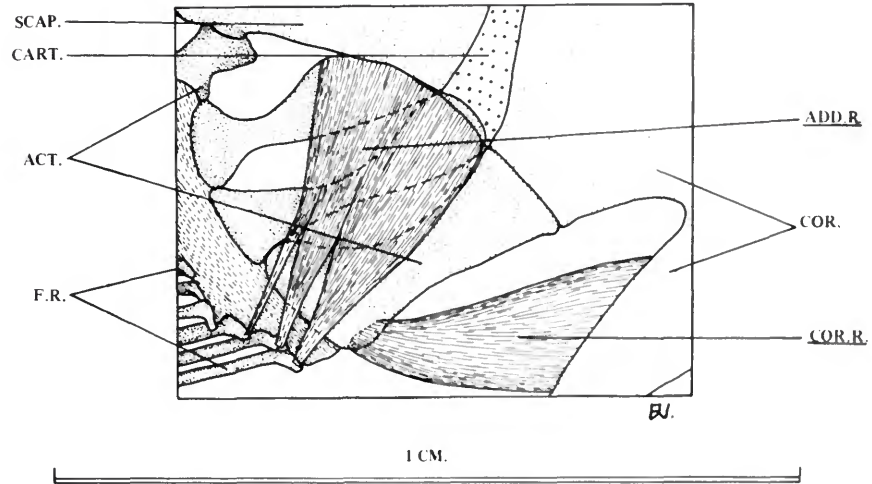


FIGURE 62.—*Parahollardia lineata*, ANSP 101031, 68 mm SL, medial view of left pectoral girdle, in the region of the radials. (Adductor superficialis and profundus removed.)

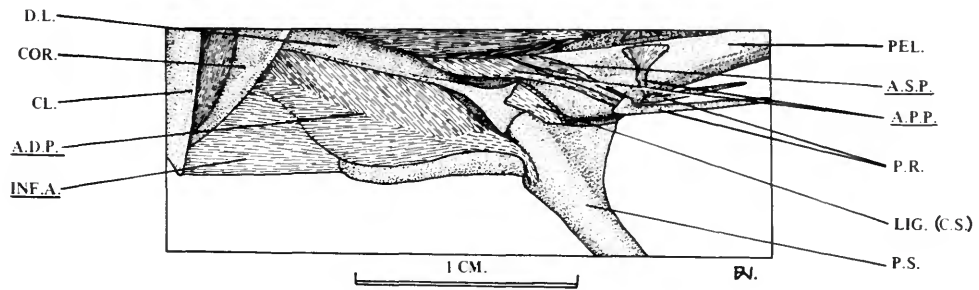


FIGURE 63.—*Parahollardia lineata*, ANSP 101031, 68 mm SL, dorsolateral view of left side of pelvis. (Postcleithrum, obliquus inferioris, and adductor superficialis pelvis section serving the pelvic spine removed.)



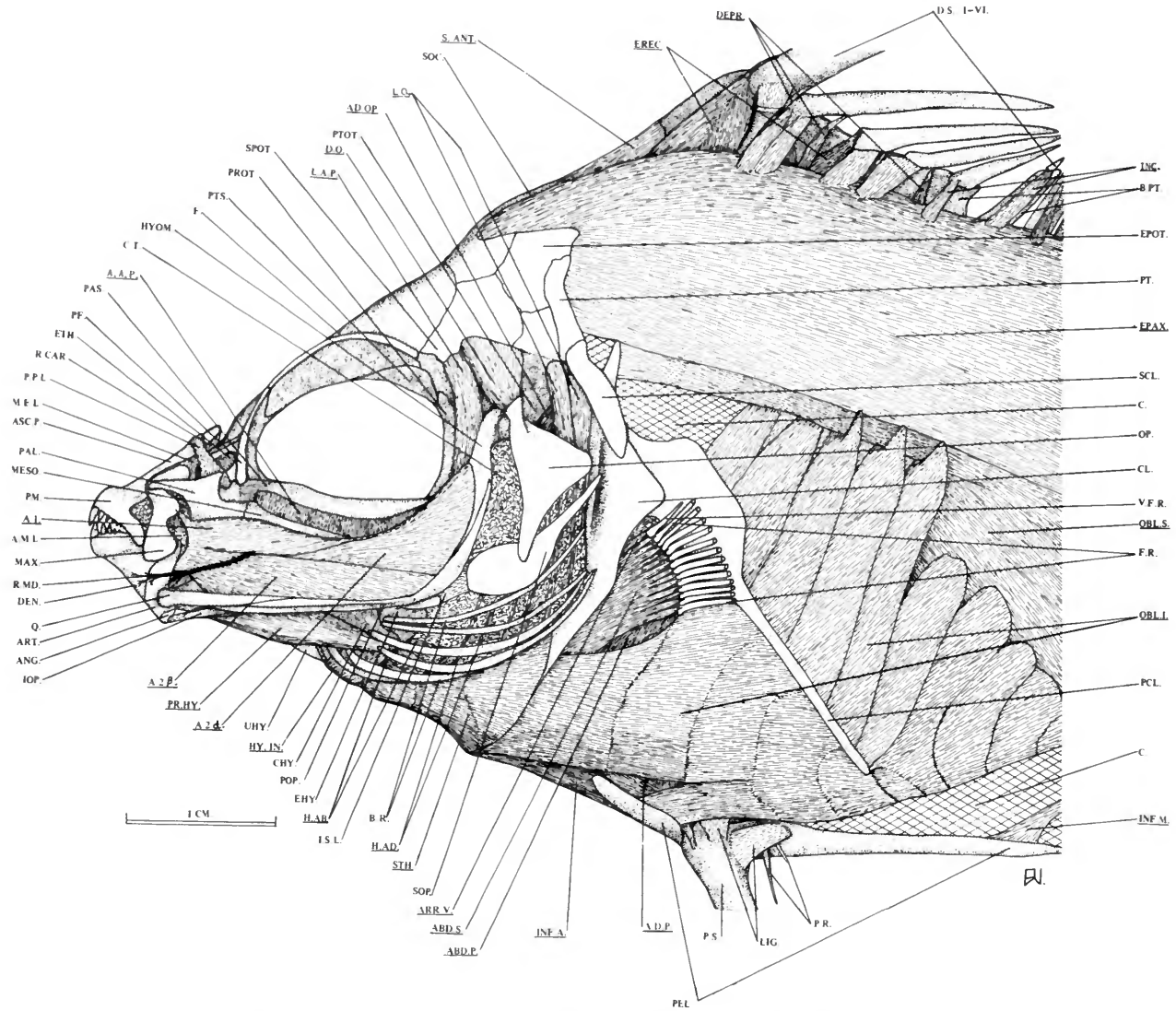


FIGURE 64.—*Hollardia hollardi*, ANSP 117491, 92 mm SL, left lateral view of superficial anterior musculature.

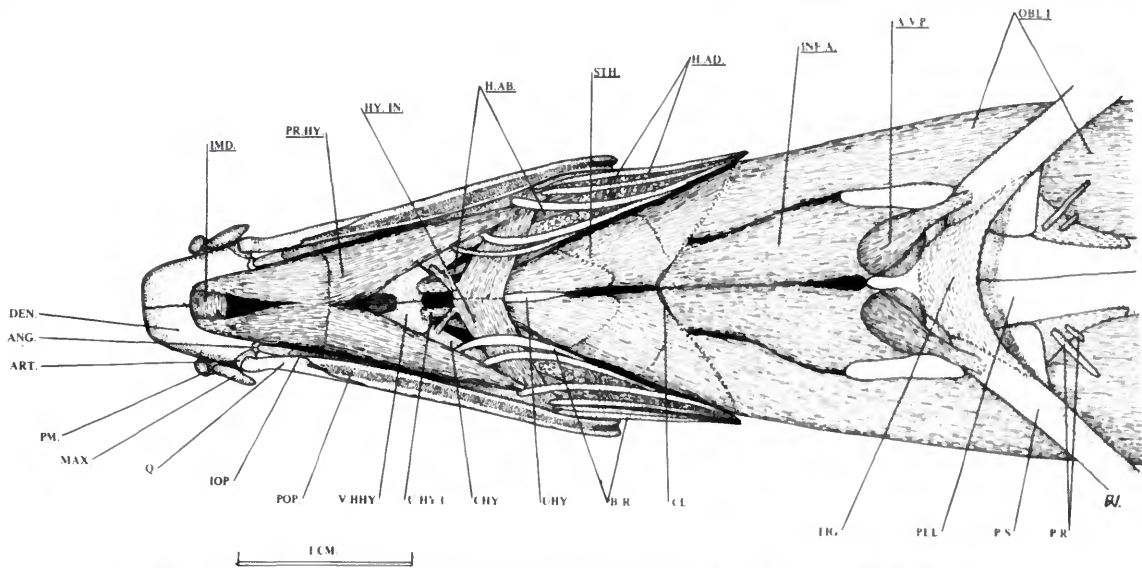
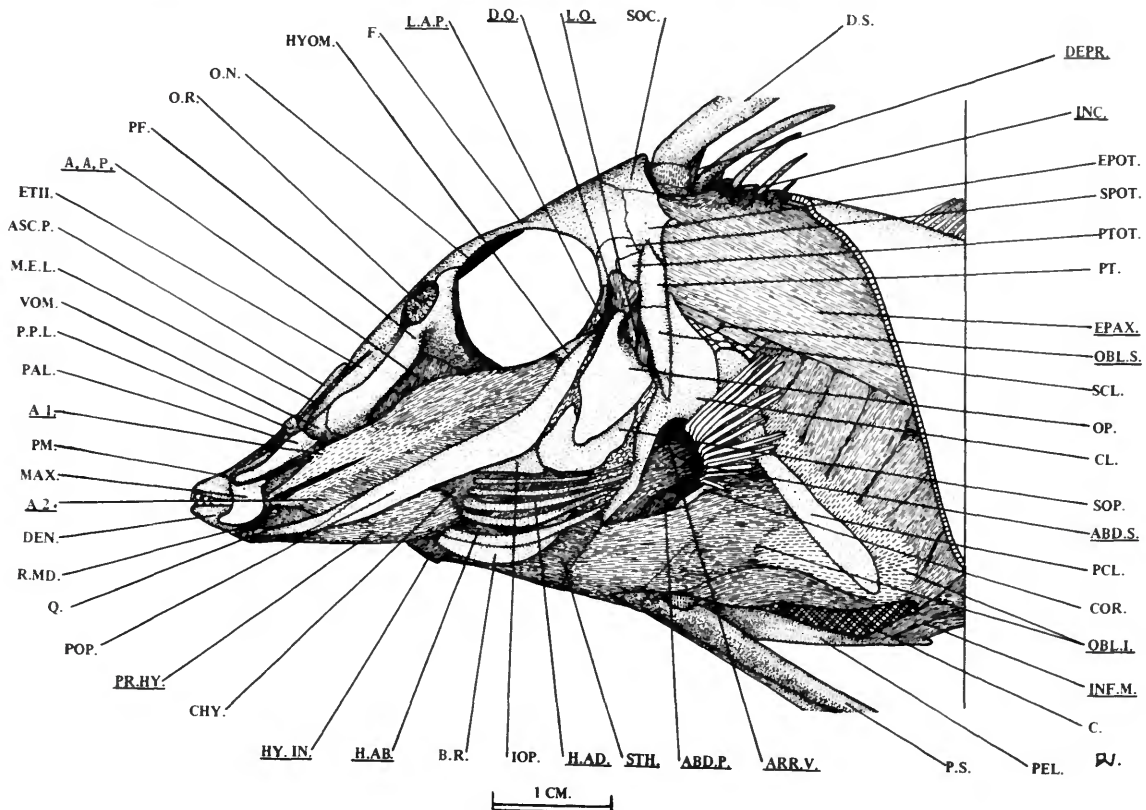


FIGURE 65.—*Hollardia hollardi*, ANSP 117491, 92 mm SL, ventral view of superficial anterior musculature.

FIGURE 66.—*Trixiphichthys weberi*, ANSP 117492, 122 mm SL, left lateral view of superficial anterior musculature.



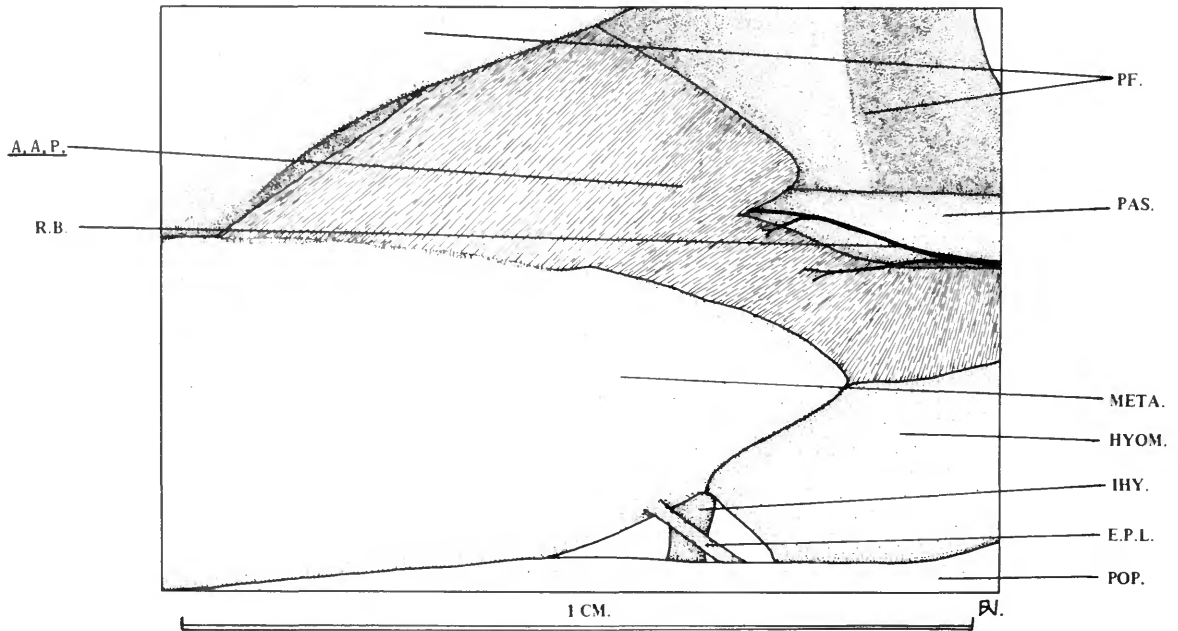
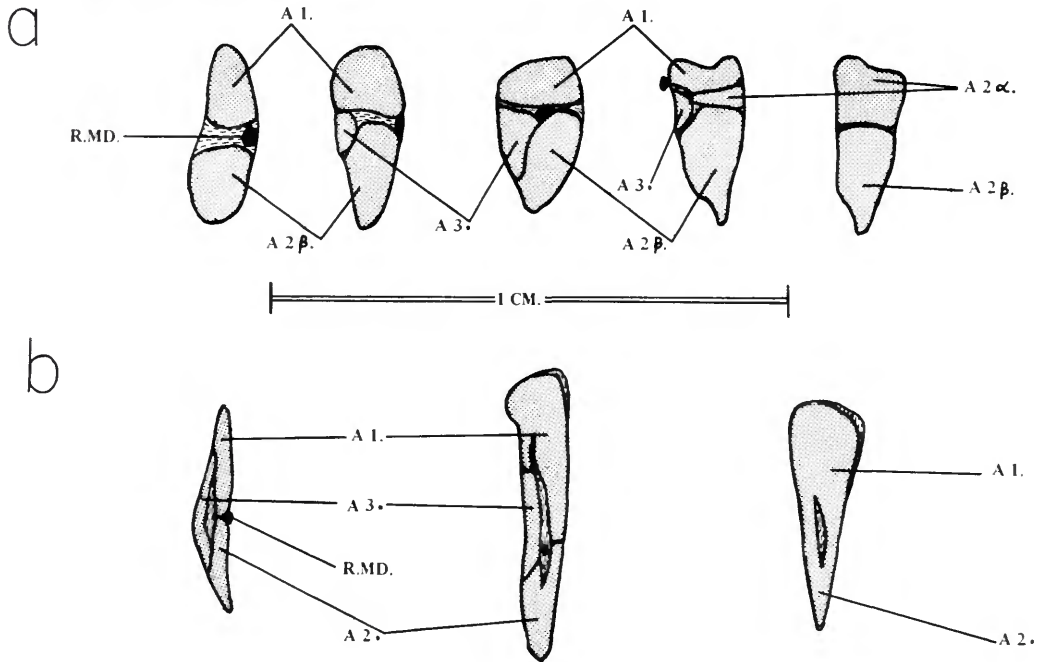


FIGURE 67.—*Trixiphichthys weberi*, ANSP 117492, 122 mm SL, posterolateral view of anterior orbital region. (Adductor mandibulae complex removed.)

FIGURE 68.—Transverse sections progressing posteriorly of the left adductor mandibulae complex, viewed from anterior: a, *Hollardia hollardi*, ANSP 117491, 53 mm SL; b, *Triacanthus biaculeatus*, ANSP 111536, 111 mm SL.



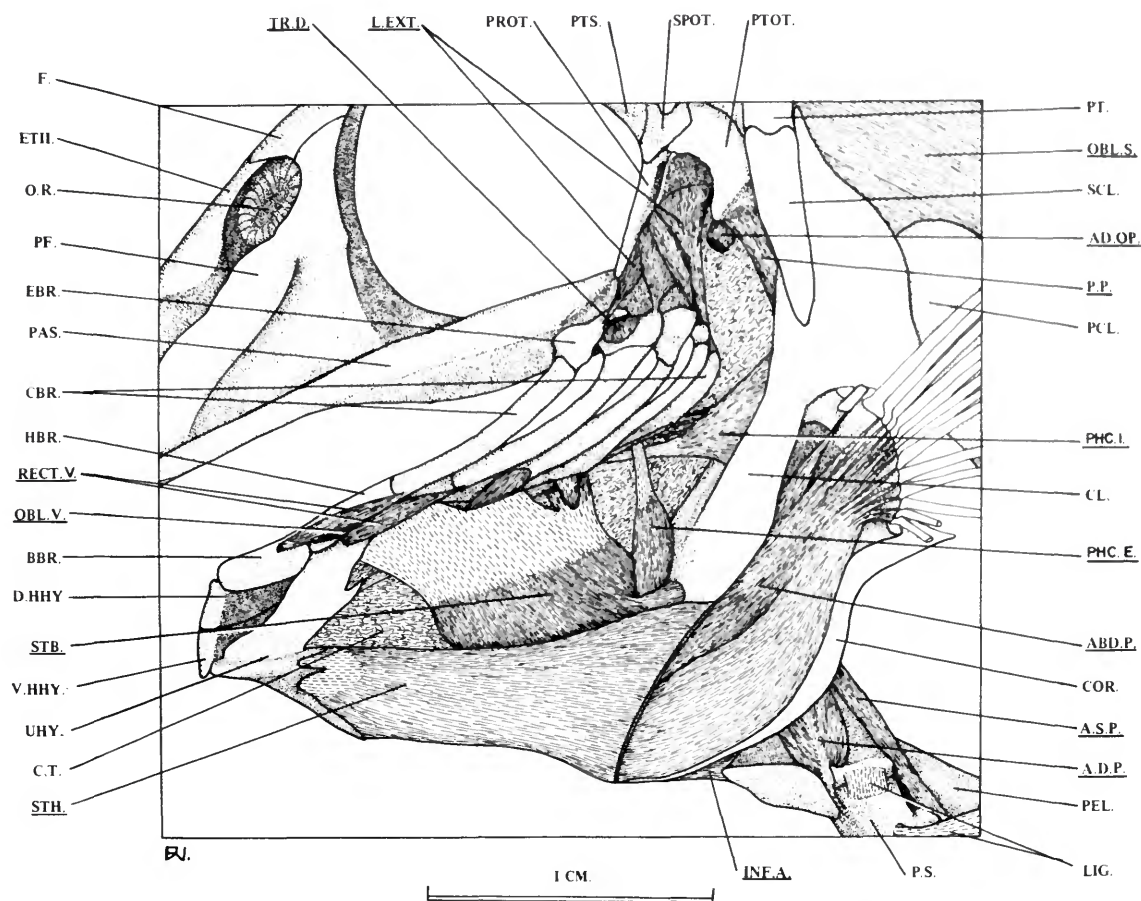


FIGURE 69.—*Trixiphichthys weberi*, ANSP 117492, 122 mm SL, left lateral view of branchial arch region. (The palatal and hyoid arches, and the abductor superficialis removed.)

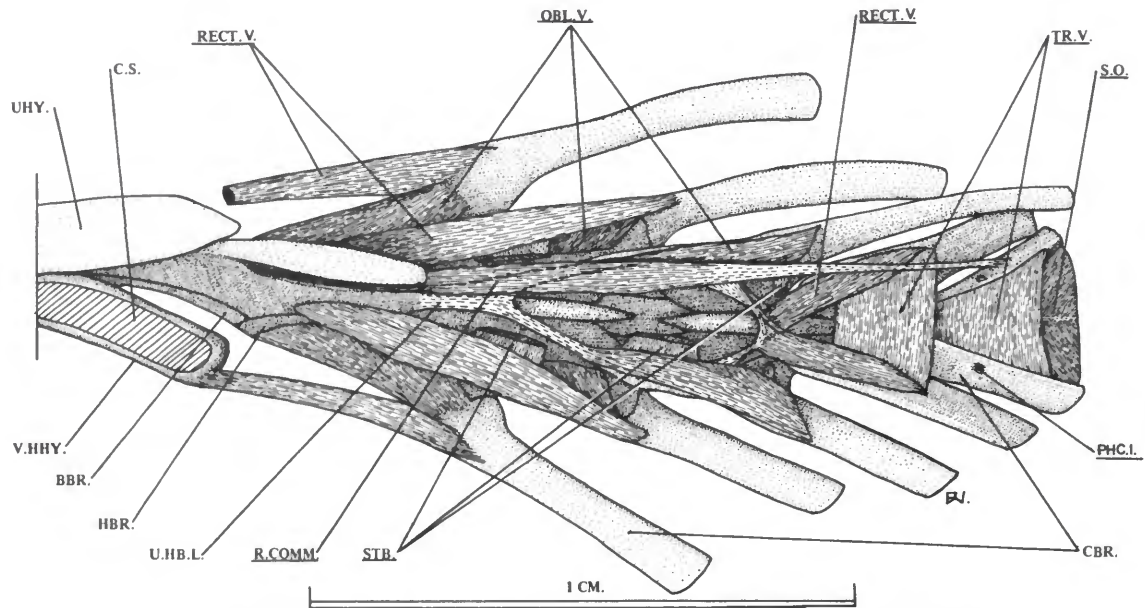
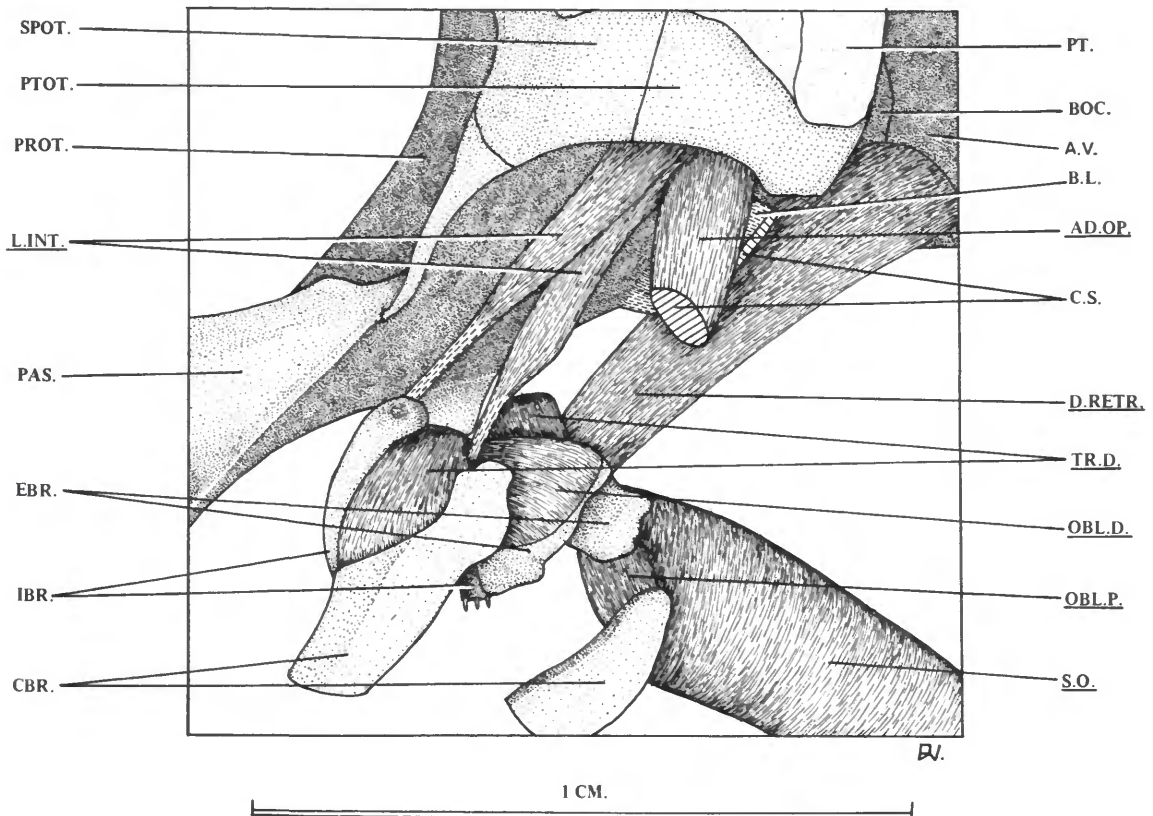


FIGURE 70.—*Trixiphichthys weberi*, ANSP 117492, 122 mm SL, ventral view of branchial arches, urohyal displaced to left. (Pharyngoclasticus externus, right rectus communis, and part of sternobranchialis removed.)

FIGURE 71.—*Trixiphichthys weberi*, ANSP 117492, 122 mm SL, left lateral view of dorsal branchial arch region. (The levatores externi, the first arch, and ceratobranchials 3 and 4 removed.)



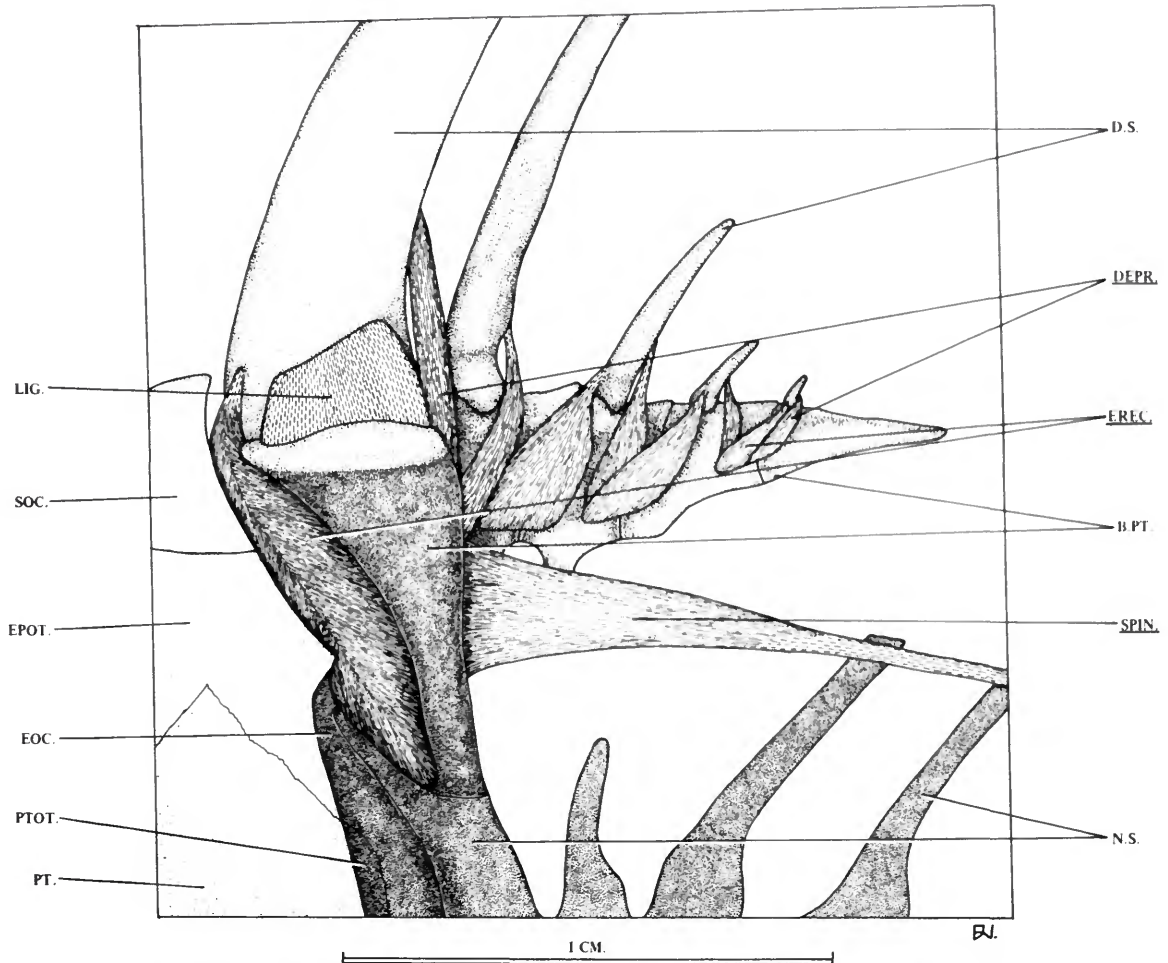


FIGURE 72.—*Trixiphichthys weberi*, ANSP 117492, 122 mm SL, left lateral view of dorsal spine region. (Epaxialis and inclinatore dorsales removed.)

FIGURE 73.—*Trixiphichthys weberi*, ANSP 117492, 122 mm SL, medial view of left pectoral girdle. (Pelvis removed.)

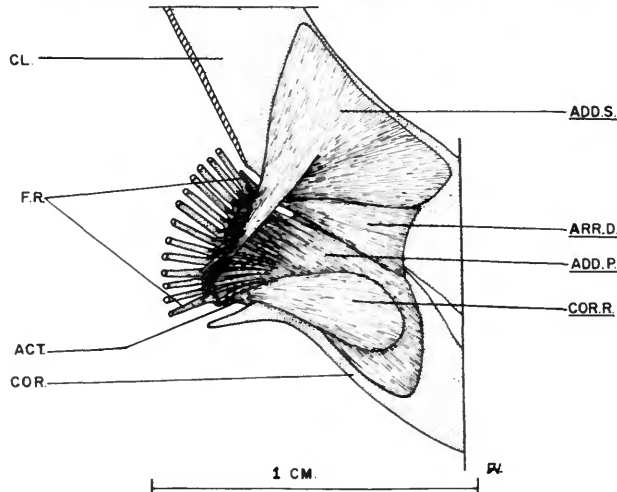
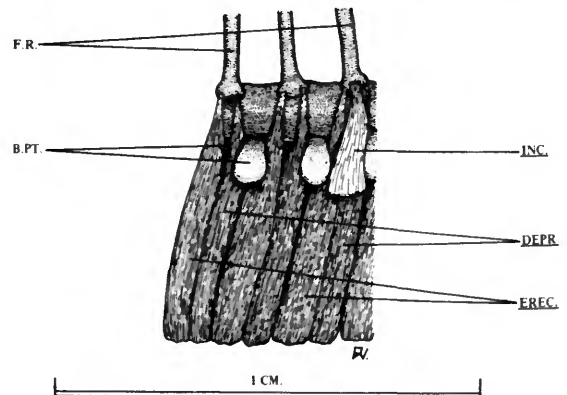


FIGURE 74.—*Trixiphichthys weberi*, ANSP 117492, 122 mm SL, left lateral view of the sixth to eighth dorsal fin rays. (Epaxialis and the sixth and seventh inclinatore dorsales removed.)



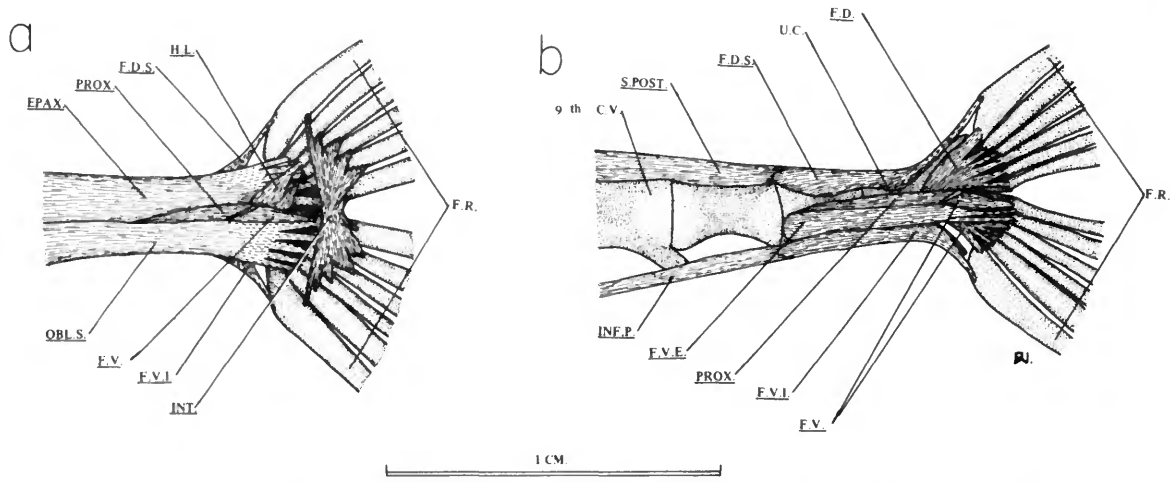


FIGURE 75.—*Trixiphichthys weberi*, ANSP 117492, 122 mm SL, left lateral view of caudal peduncle region: a, superficial musculature; b, deep musculature.

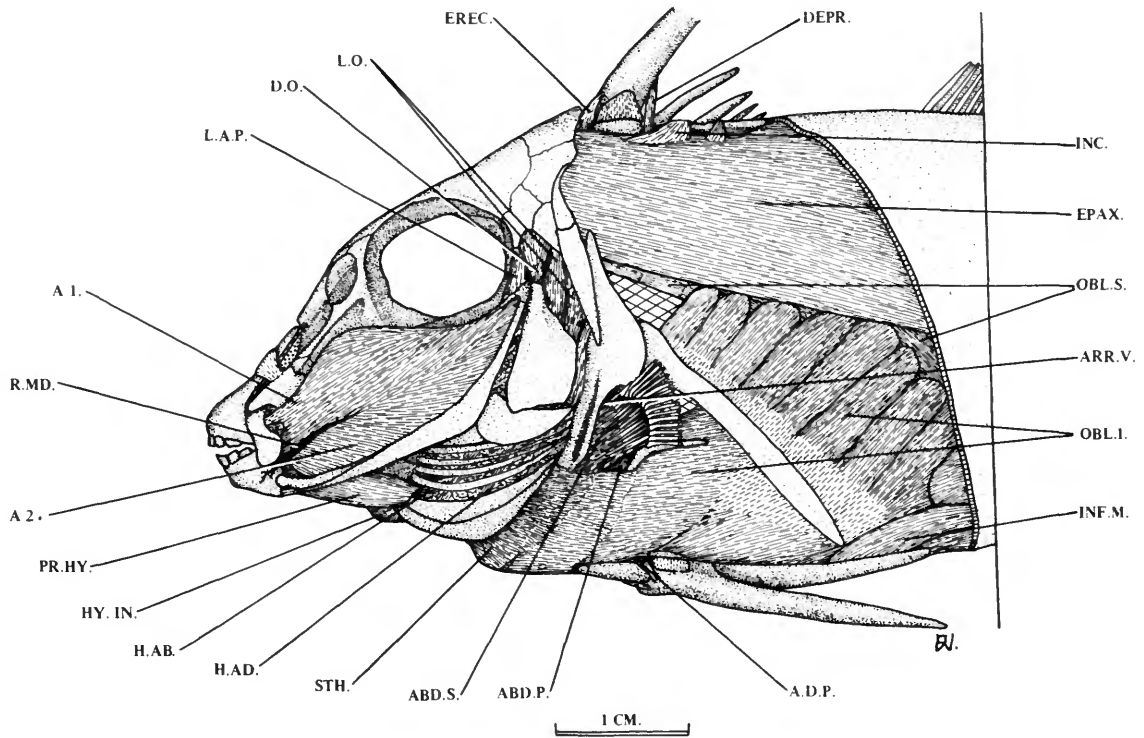


FIGURE 76.—*Triacanthus biaculeatus*, ANSP 111536, 111 mm SL, left lateral view of superficial anterior musculature.

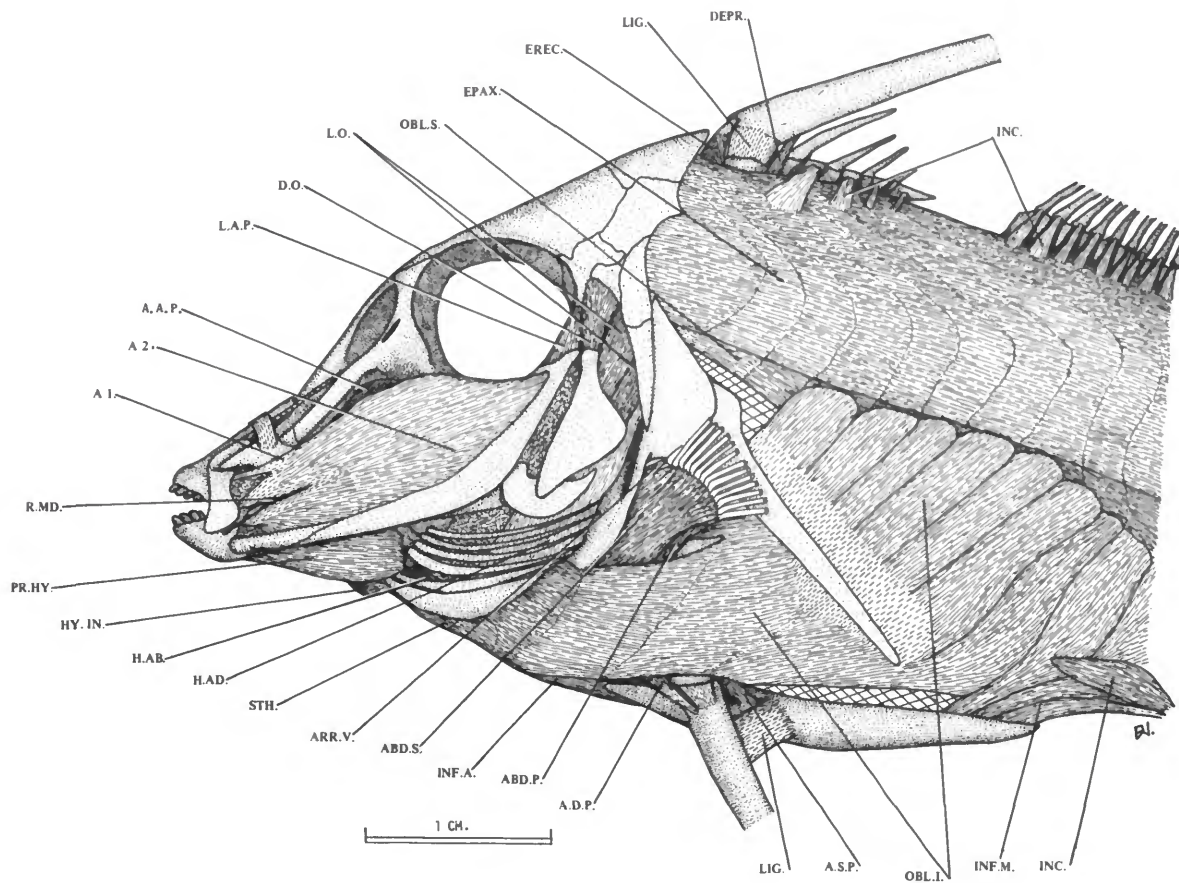


FIGURE 77.—*Tripodichthys oxycephalus*, ANSP 89397, 82 mm SL, left lateral view of superficial anterior musculature.



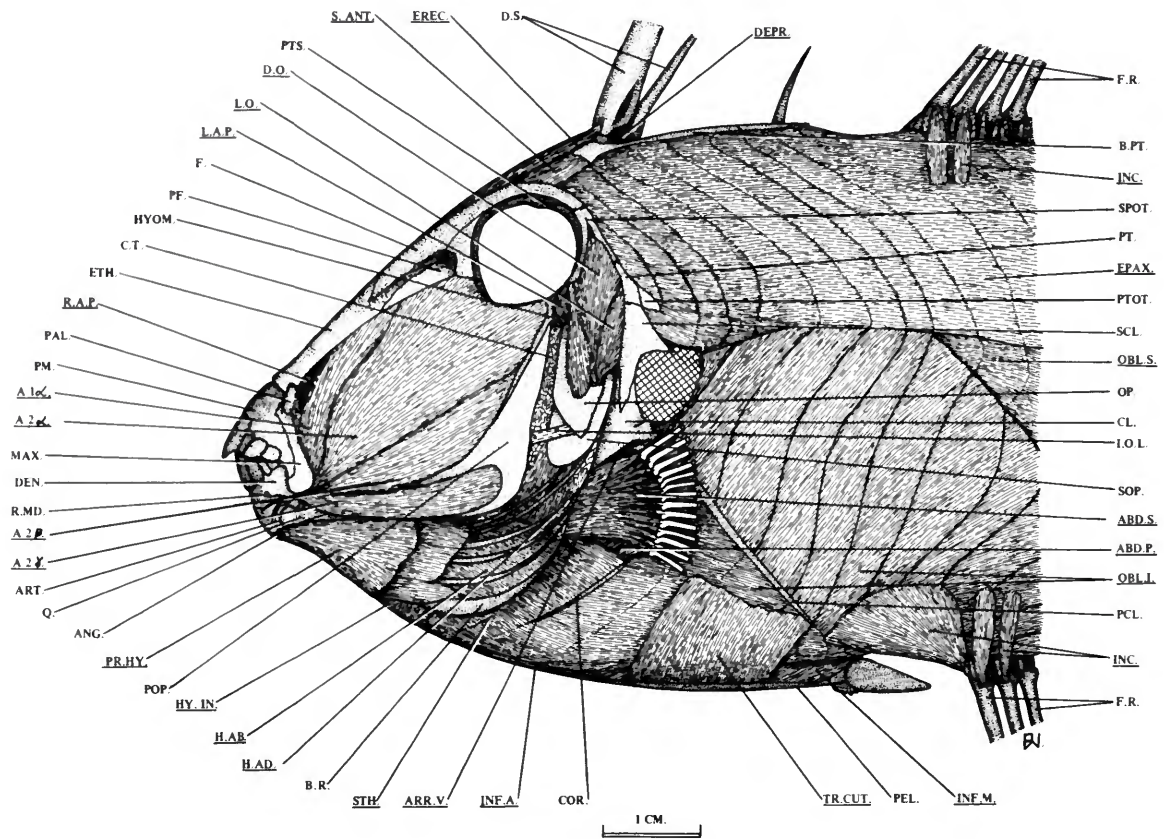


FIGURE 78.—*Balistes vetula*, ANSP 117535, 137 mm SL, left lateral view of superficial anterior musculature.

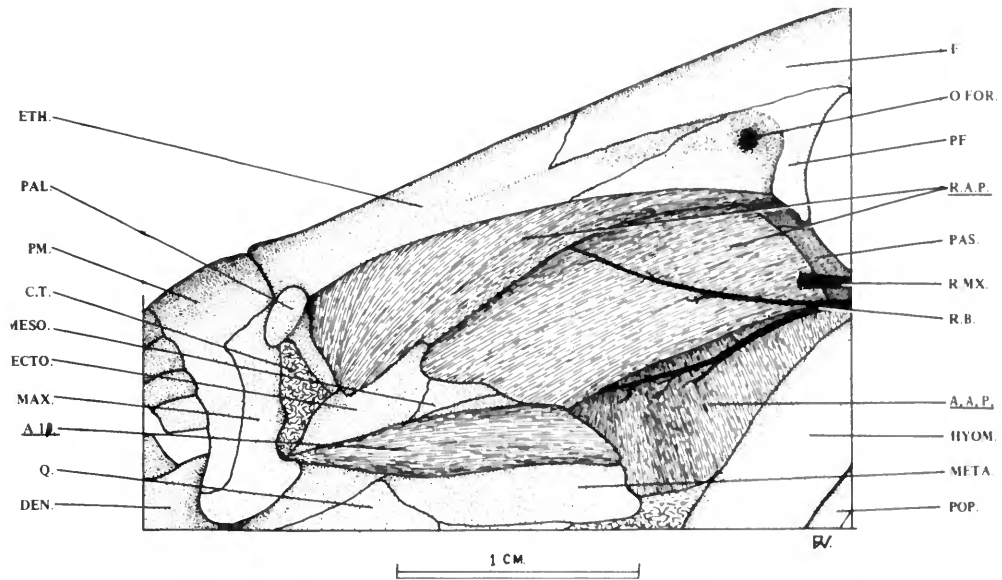
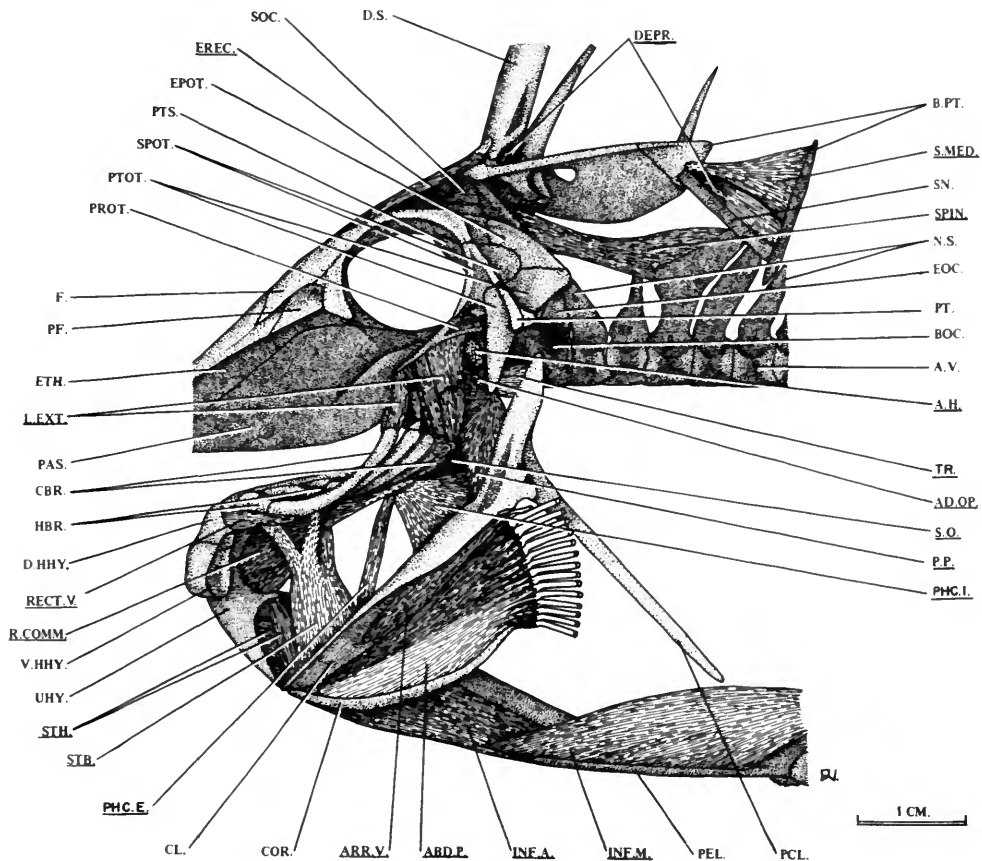


FIGURE 79.—*Balistes vetula*, ANSP 117535, 137 mm SL, left lateral view of snout region. (Most of the adductor mandibulae complex removed.)

FIGURE 80.—*Balistes vetula*, ANSP 117535, 137 mm SL, left lateral view of head region. (Body muscles, abductor superficialis, lateral portion of the sternohyoideus, and the palatal arch removed.)



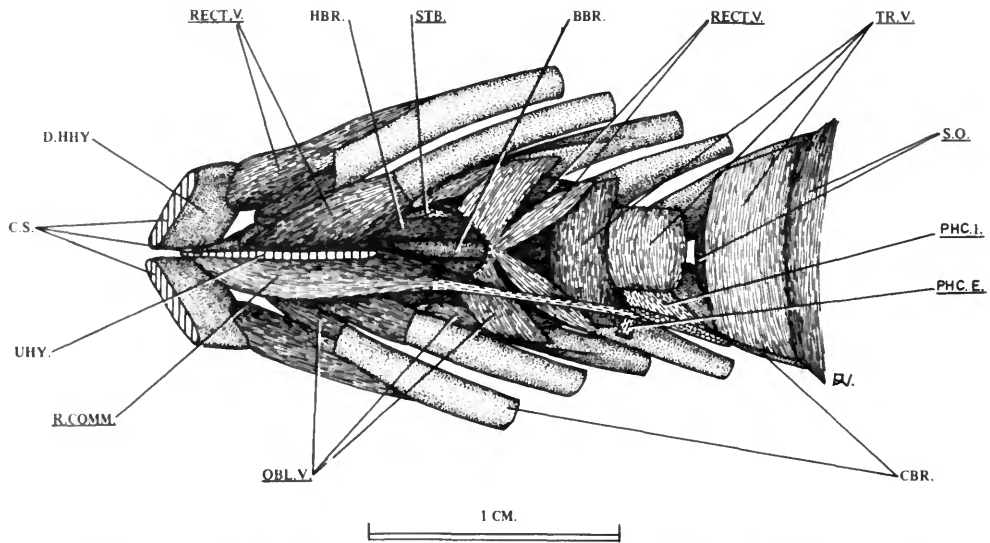


FIGURE 81.—*Balistes vetula*, ANSP 117535, 137 mm SL, ventral view of branchial arches. (Left rectus communis, pharyngoclaviculars and right sternobranchialis removed.)

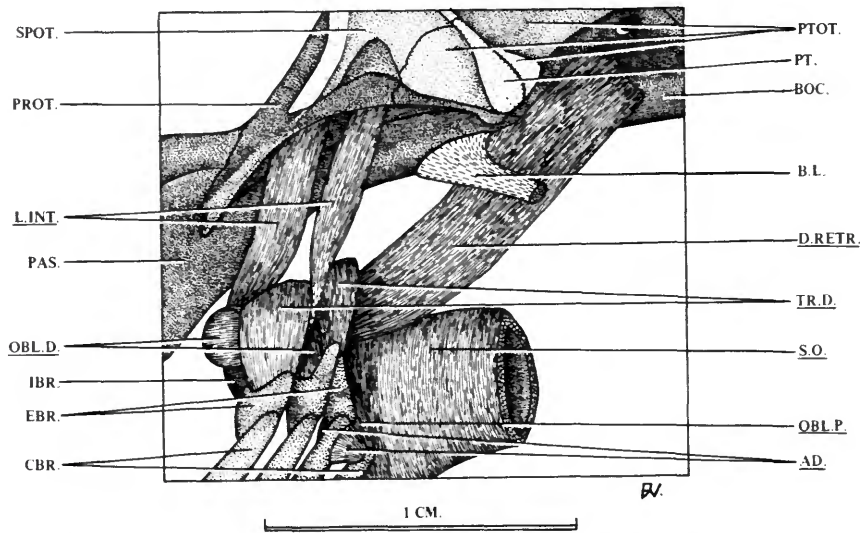


FIGURE 82.—*Balistes vetula*, ANSP 117535, 137 mm SL, left lateral view of dorsal branchial arch region. (First branchial arch, palatal arch, pectoral girdle, and levatores externi removed.)

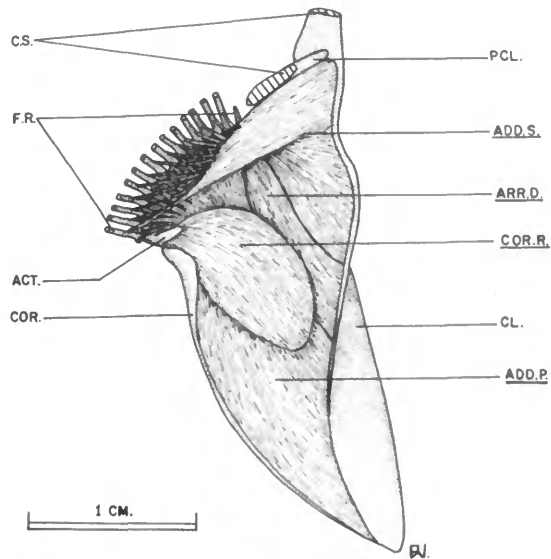


FIGURE 83.—*Balistes vetula*, ANSP 117535, 137 mm SL, medial view of left pectoral girdle and associated muscles.

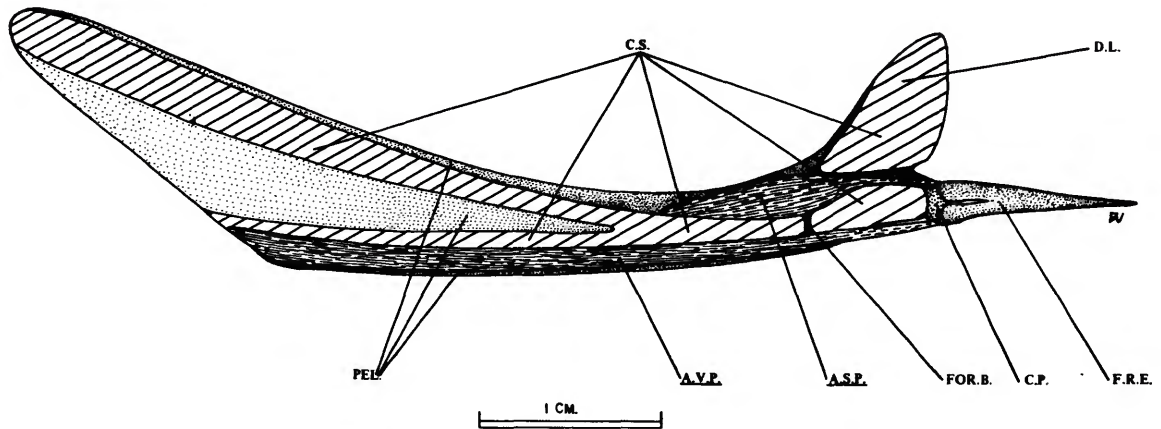


FIGURE 84.—*Balistes vetula*, ANSP 117535, 137 mm SL, left lateral view of pelvis, cut longitudinally slightly to the left of the midline, showing the muscles of the right side.

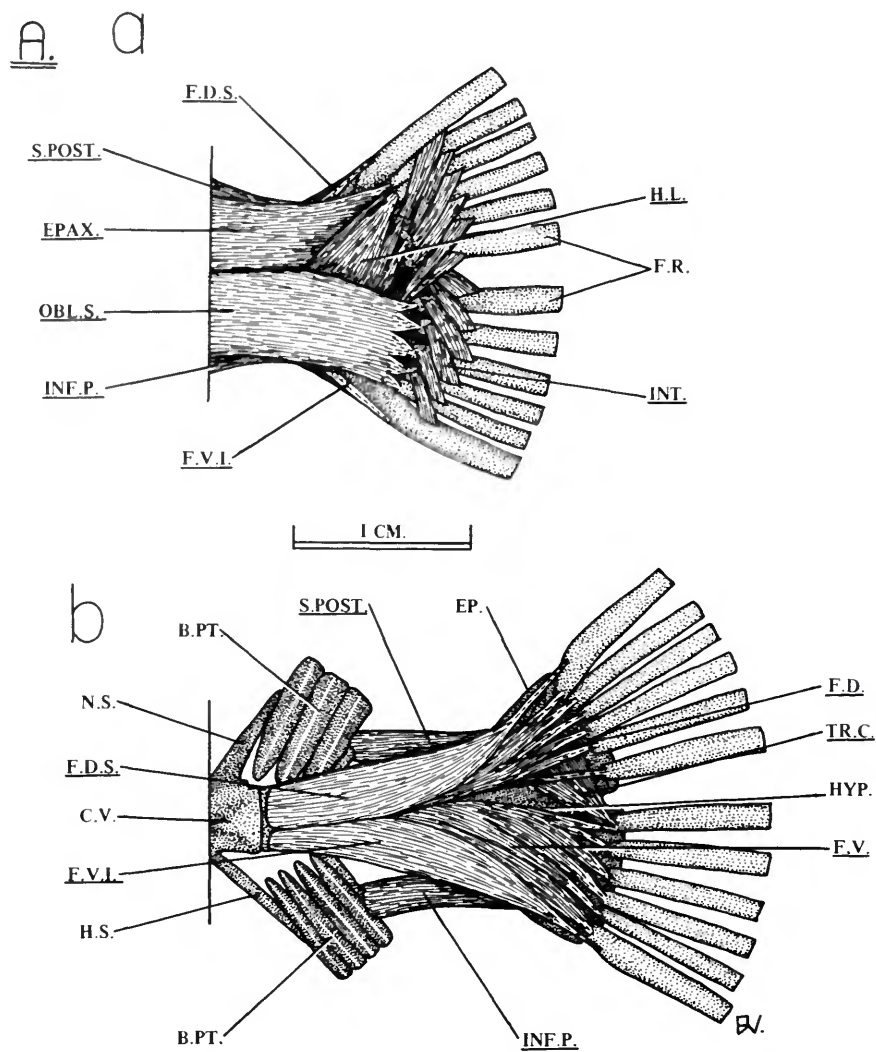


FIGURE 85.—*Balistes vetula*, ANSP 117535, 137 mm SL, left lateral view of caudal peduncle region: a, superficial musculature; b, deep musculature.

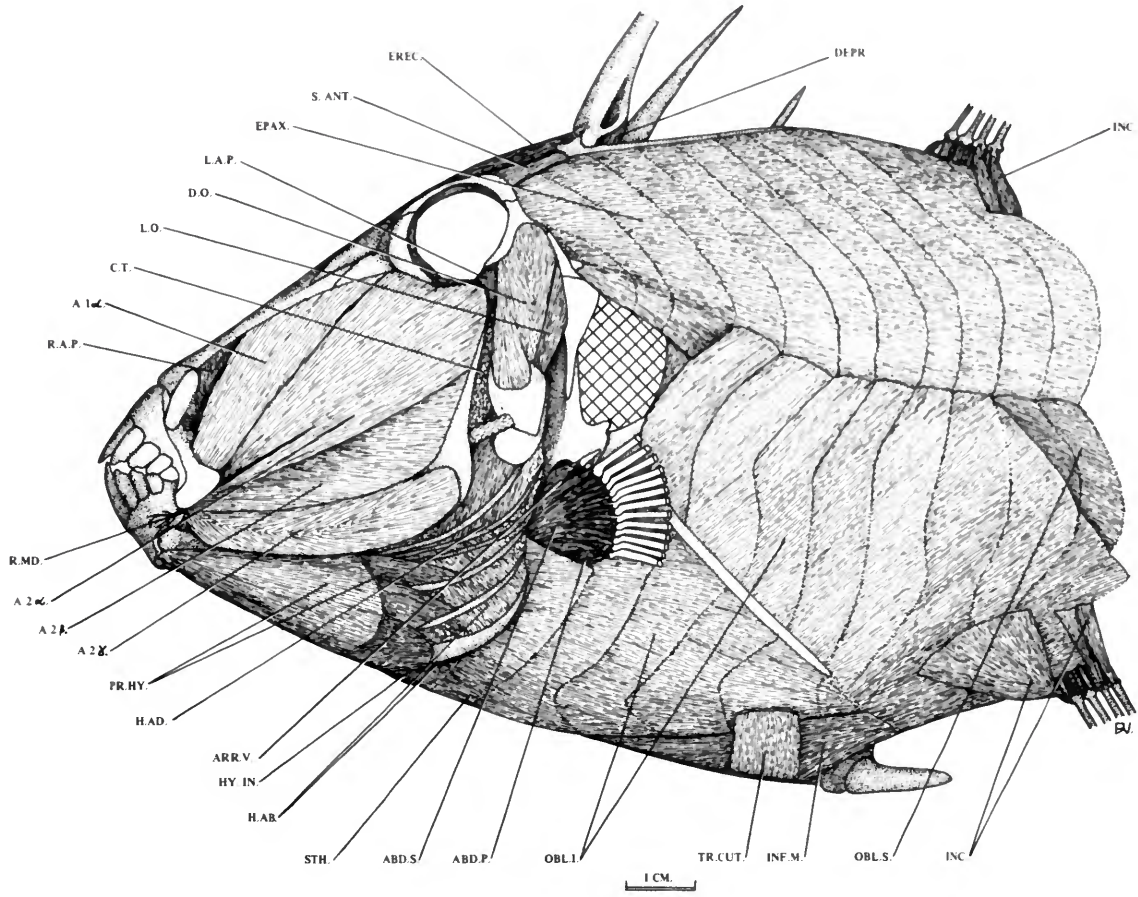


FIGURE 86.—*Balistapus undulatus*, ANSP 117598, 83 mm SL, left lateral view of superficial anterior musculature.

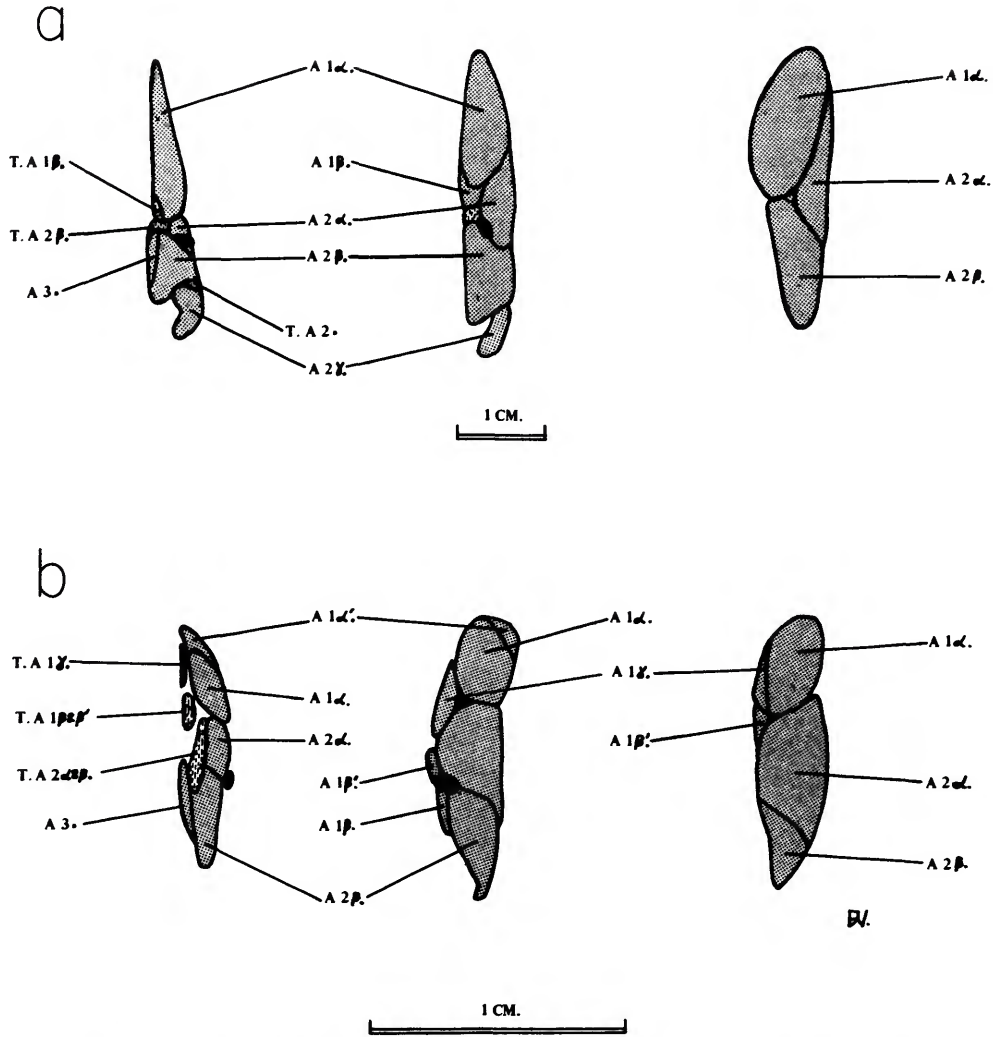


FIGURE 87.—Transverse sections progressing posteriorly of the left adductor mandibulae complex, viewed from anterior: *a*, *Balistapus undulatus*, ANSP 117598, 83 mm SL: *b*, *Pervagor melanocephalus*, ANSP 117500, 85 mm SL.

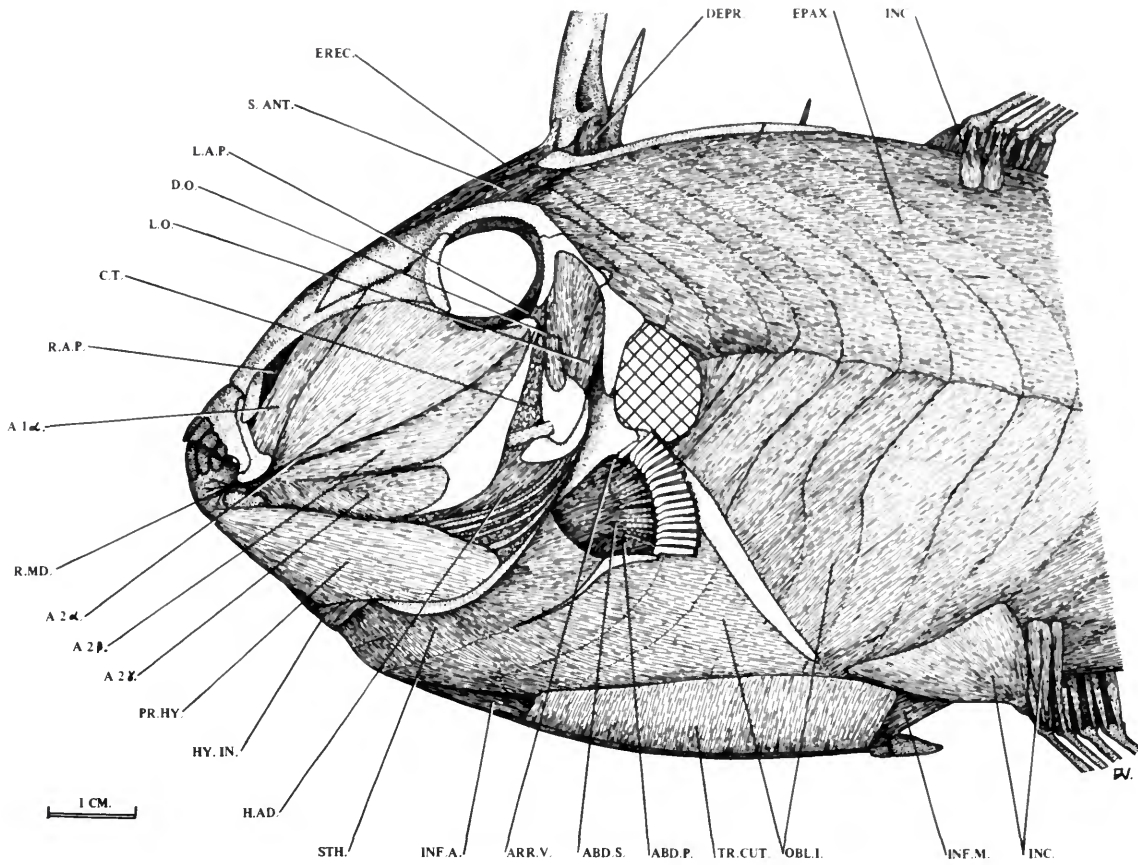


FIGURE 88.—*Melichthys niger*, ANSP 117515, 153 mm SL, left lateral view of superficial anterior musculature.



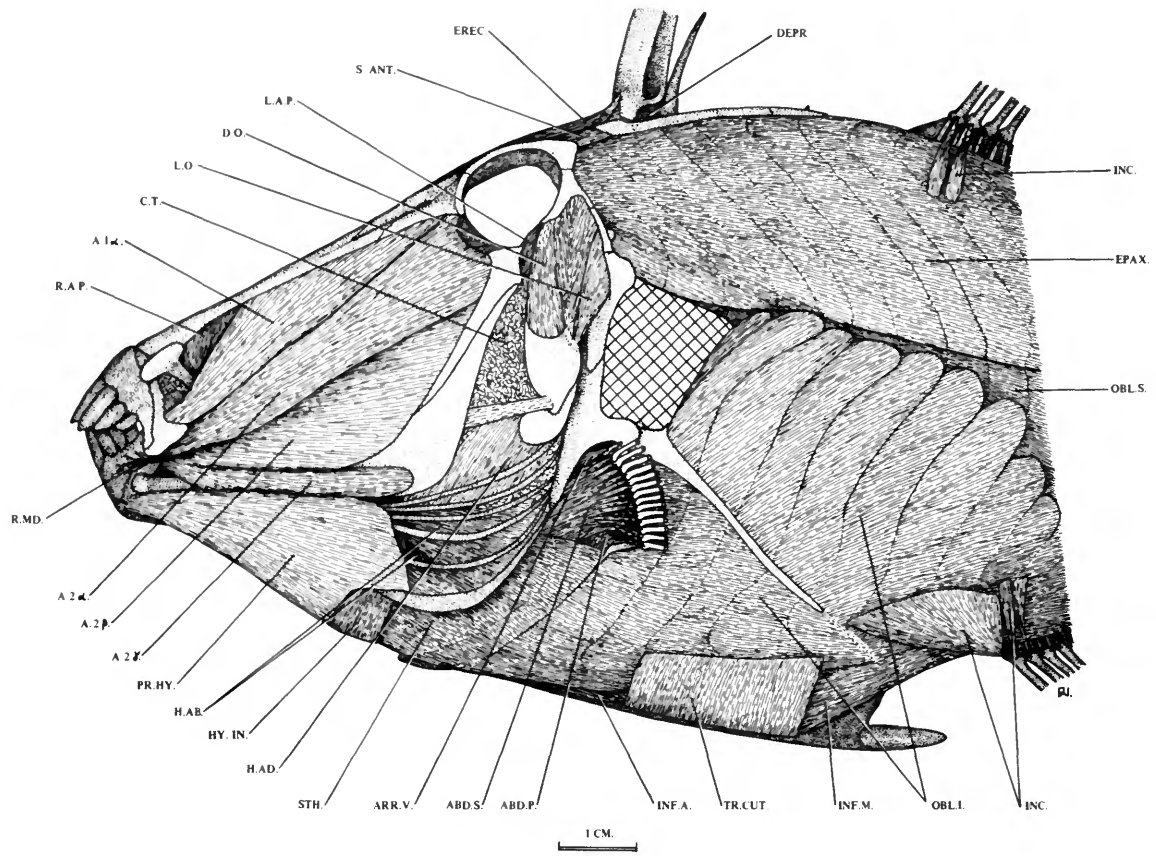


FIGURE 89.—*Rhinecanthus aculeatus*, ANSP 117546, 159 mm SL, left lateral view of superficial anterior musculature.

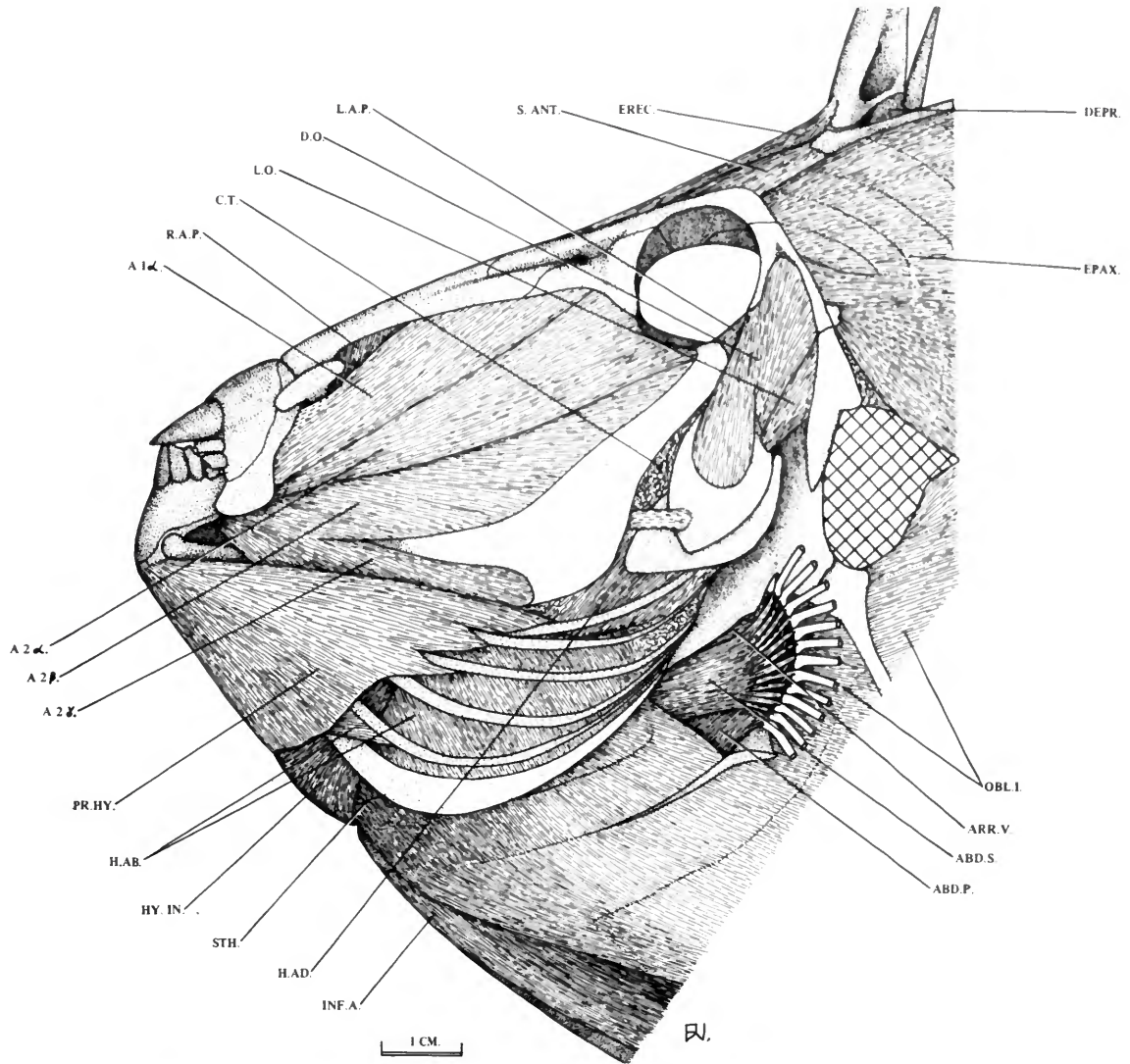


FIGURE 90.—*Odonus niger*, ANSP 102779, 257 mm SL, left lateral view of superficial anterior musculature.

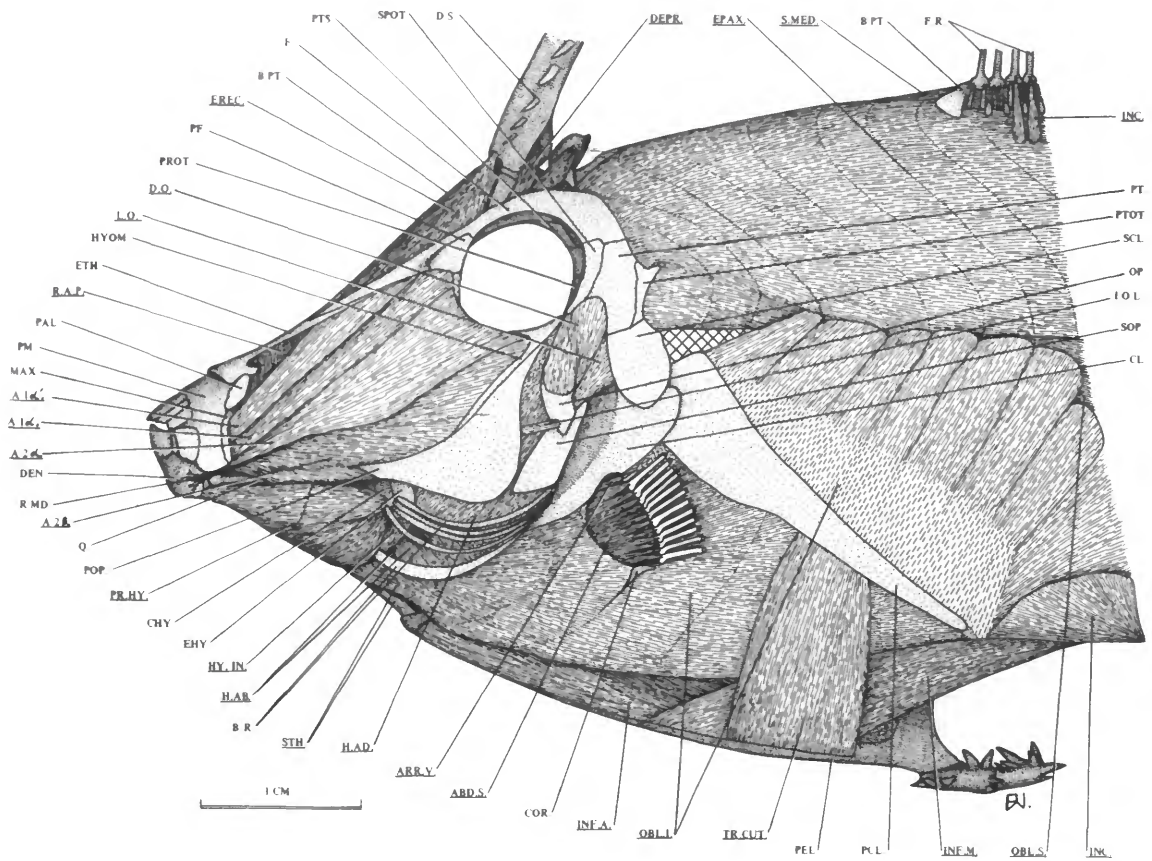


FIGURE 91.—*Pervagor melanocephalus*, ANSP 117512, 87 mm SL, left lateral view of superficial anterior musculature.

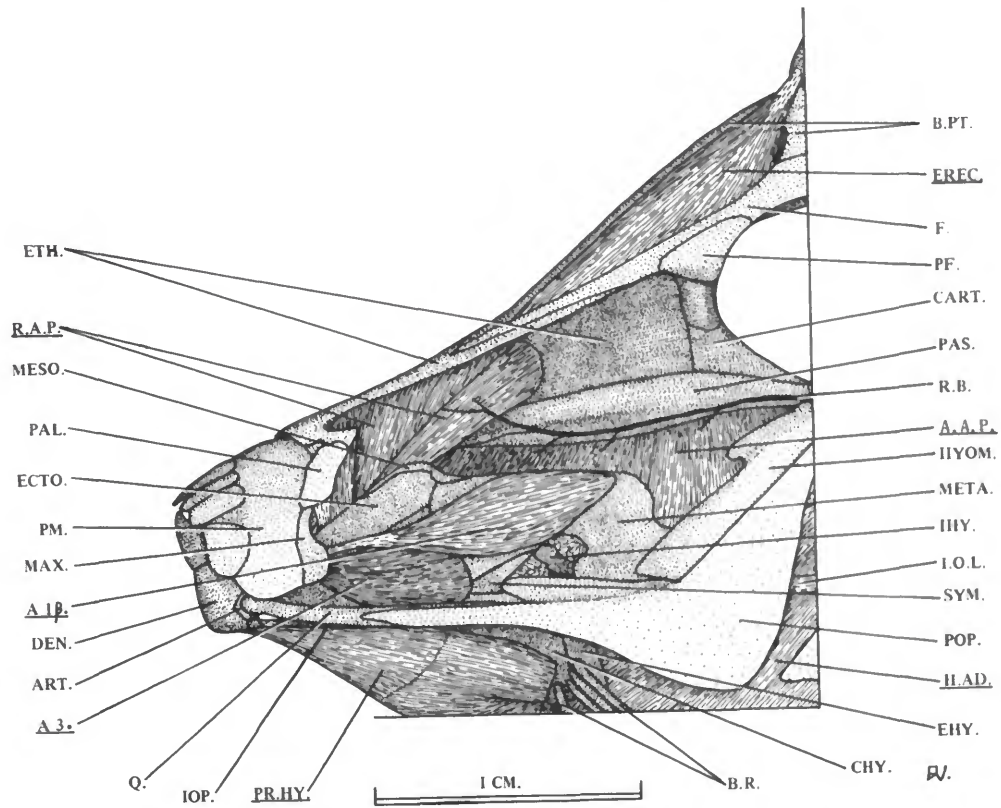
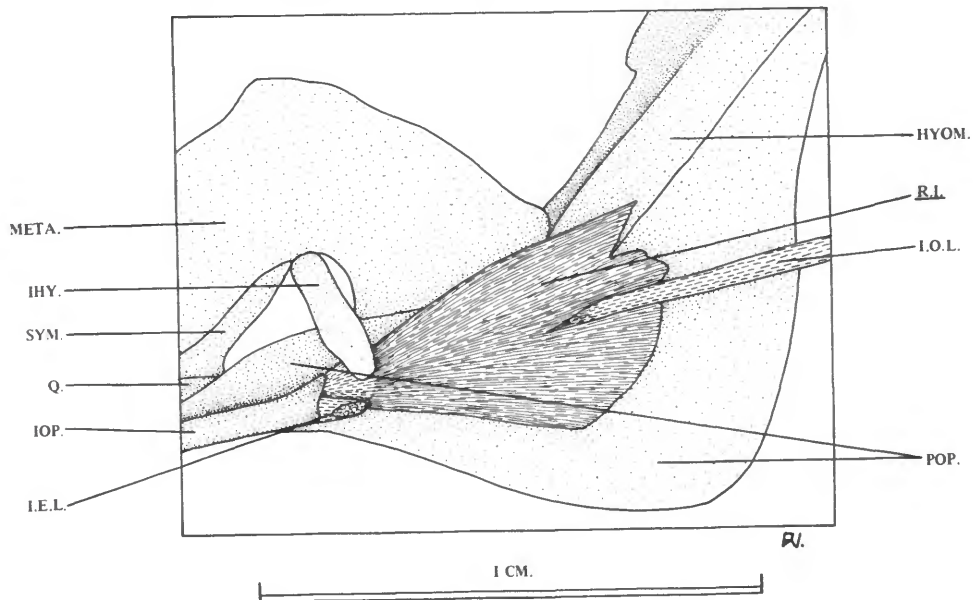


FIGURE 92.—*Pervagor melanocephalus*, ANSP 117512, 87 mm SL, left lateral view of the deep muscles of the cheek. (Most of the adductor mandibulae complex removed.)

FIGURE 93.—*Pervagor melanocephalus*, ANSP 117512, 87 mm SL, medial view of right palatal arch (posteroventral region). (Hyoid arch, except interhyal, removed.)



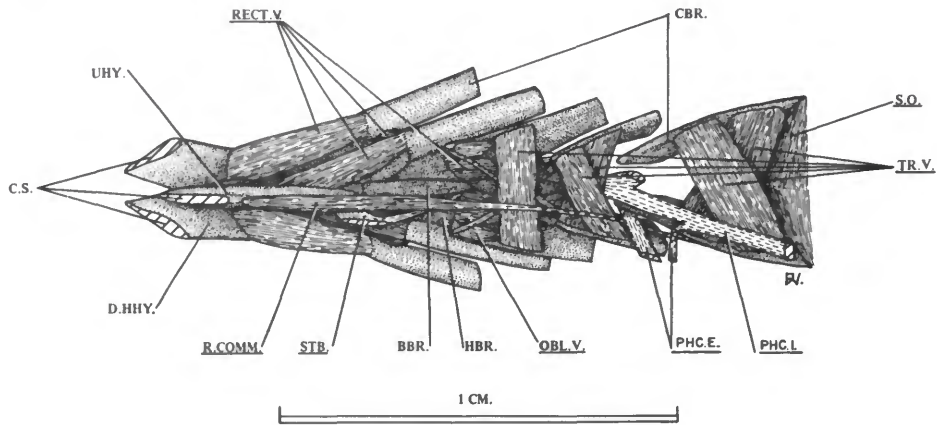


FIGURE 94.—*Pervagor melanocephalus*, ANSP 117512, 87 mm SL, ventral view of branchial arches. (Left rectus communis, sternobranchialis, and pharyngoclavicularis removed.)

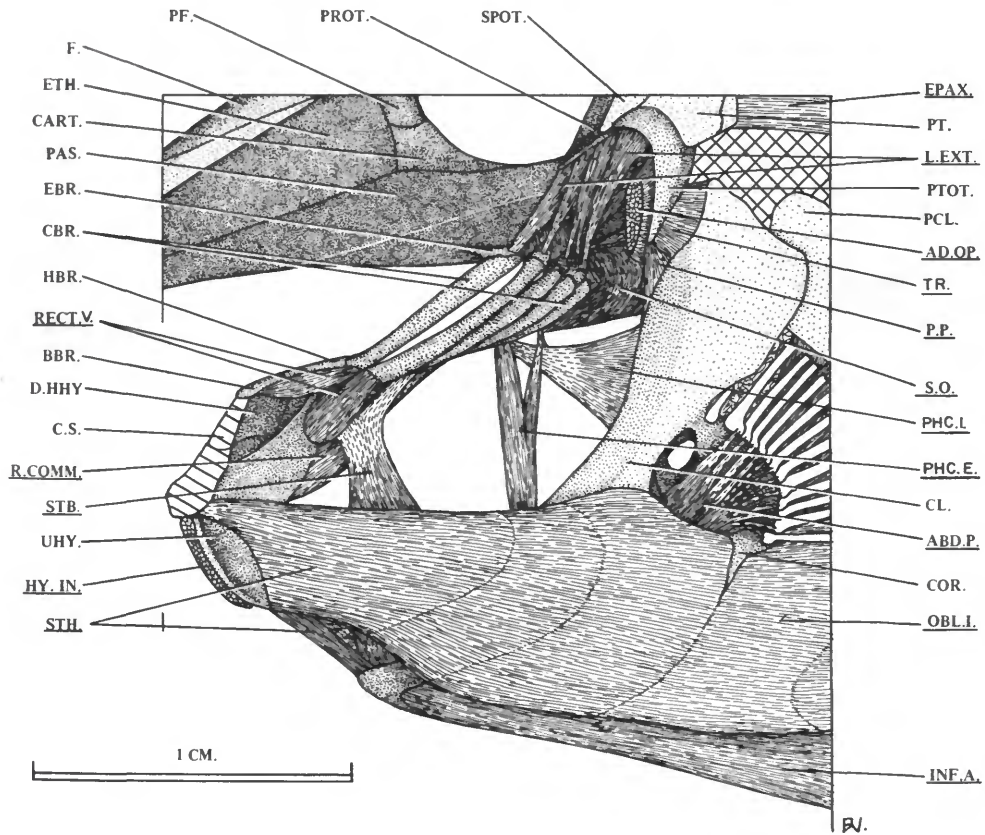


FIGURE 95.—*Pervagor melanocephalus*, ANSP 117512, 87 mm SL, left lateral view of superficial branchial arch musculature. (The palatal and hyoid arches removed.)

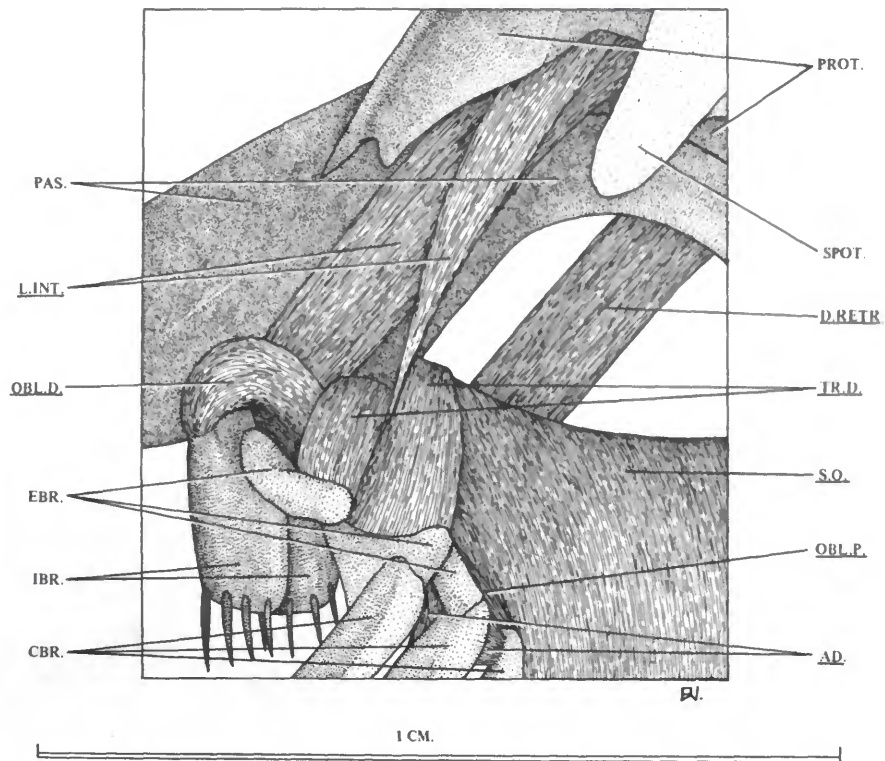


FIGURE 96.—*Pervagor melancephalus*, ANSP 117512, 87 mm SL, dorsolateral view of the dorsal branchial arch region. (The levatores externi, first branchial arch, and ceratobranchial 2 removed.)

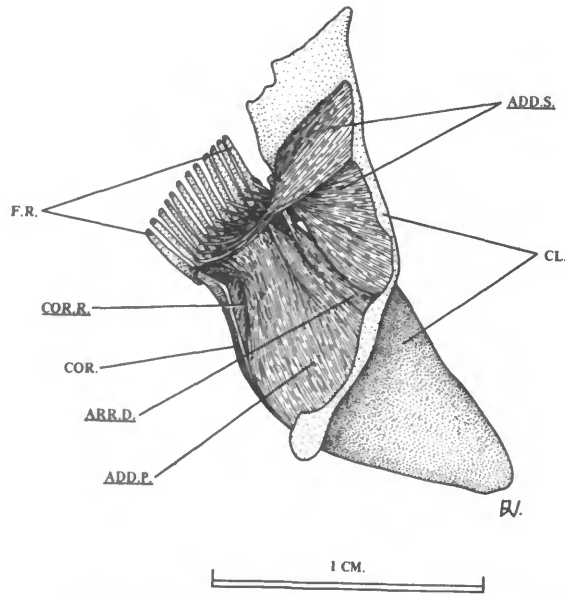


FIGURE 97.—*Pervagor melanocephalus*, ANSP 117512, 87 mm SL, medial view of left pectoral girdle. (Postcleithrum, removed.)

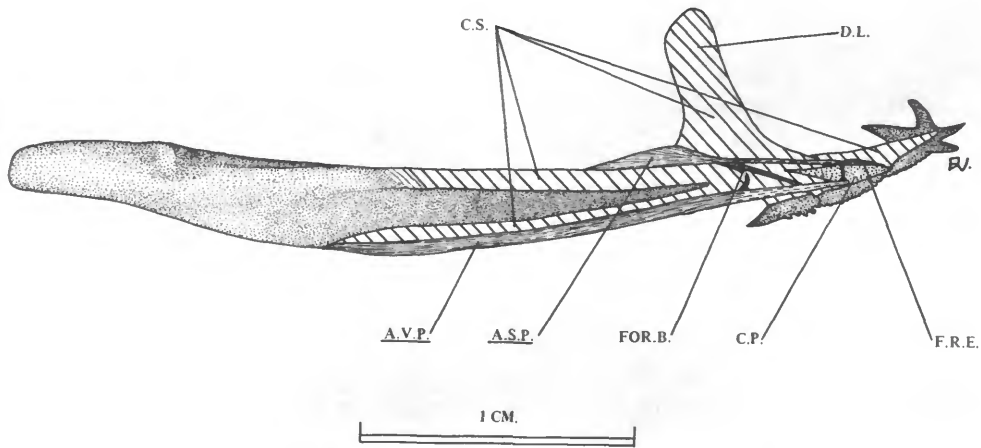


FIGURE 98.—*Pervagor melanocephalus*, ANSP 117512, 87 mm SL, left lateral view of pelvis, cut longitudinally slightly to the left of the midline.

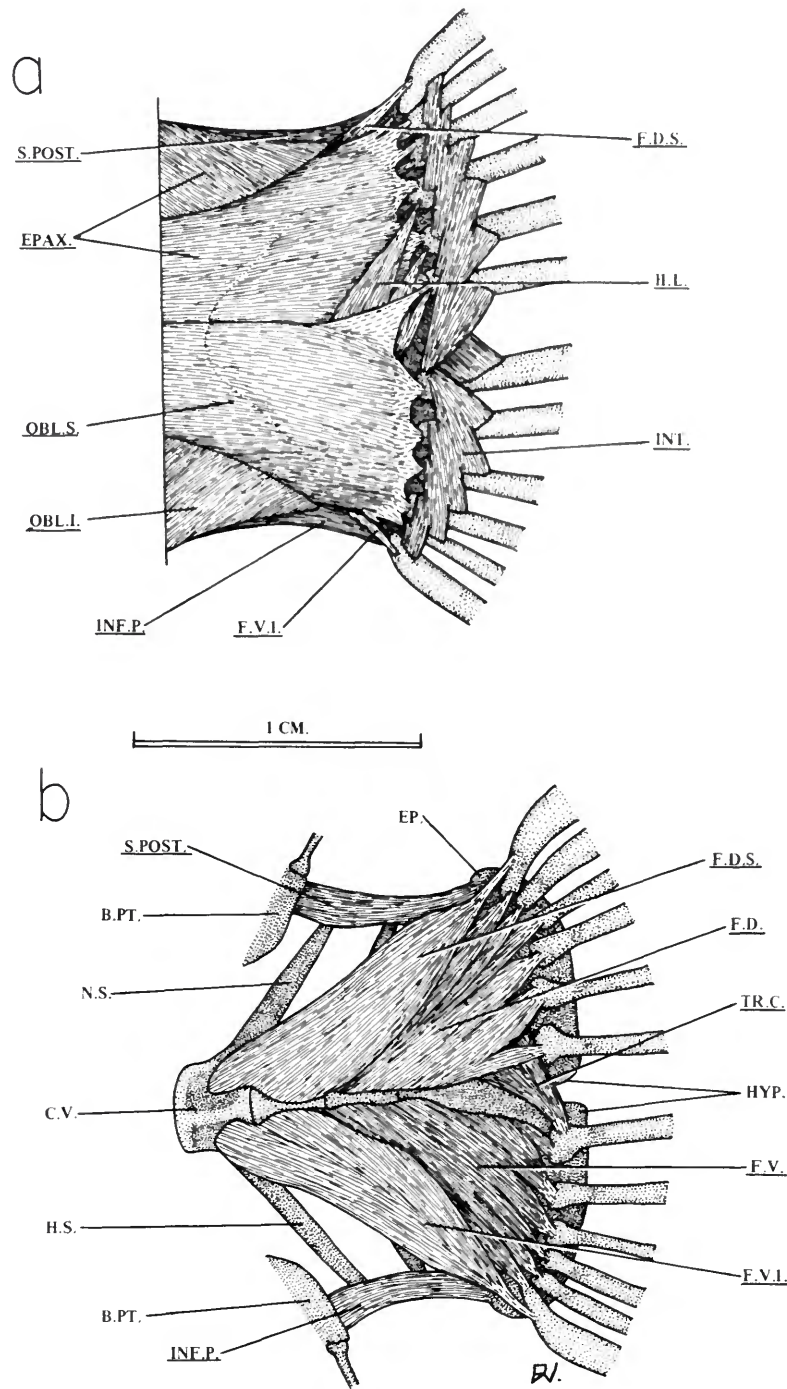


FIGURE 99.—*Pervagor melanocephalus*, ANSP 117512, 87 mm SL, left lateral view of caudal peduncle region: a, superficial musculature; b, deep musculature.



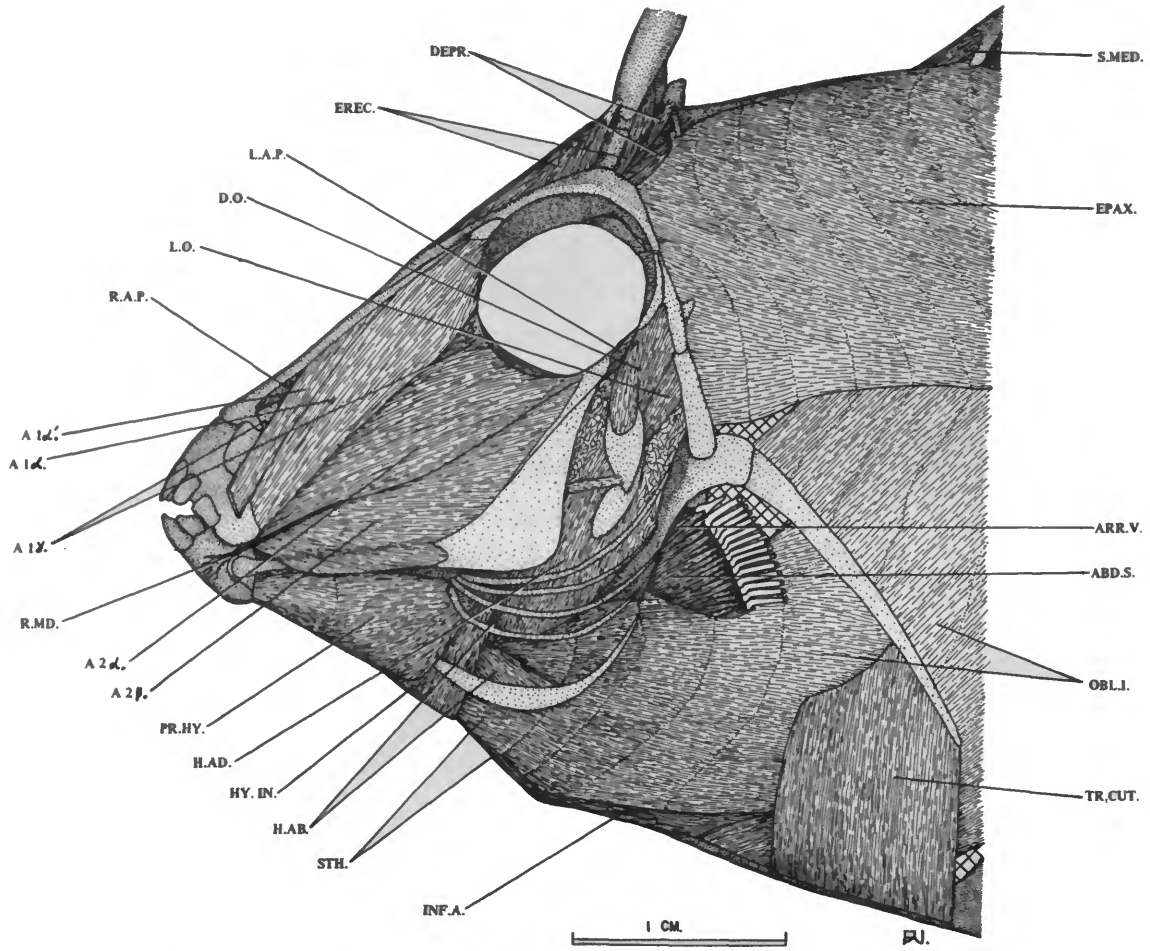
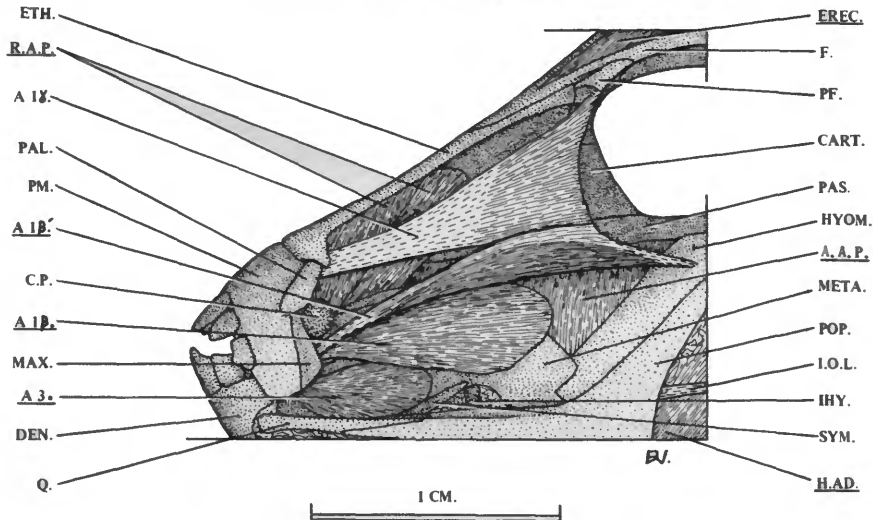


FIGURE 100.—*Stephanolepis auratus*, ANSP 117526, 64 mm SL, left lateral view of superficial anterior musculature.

FIGURE 101.—*Stephanolepis auratus*, ANSP 117526, 64 mm SL, left lateral view of deep cheek musculature. (A 1α, A 1α', and A 2 removed.)



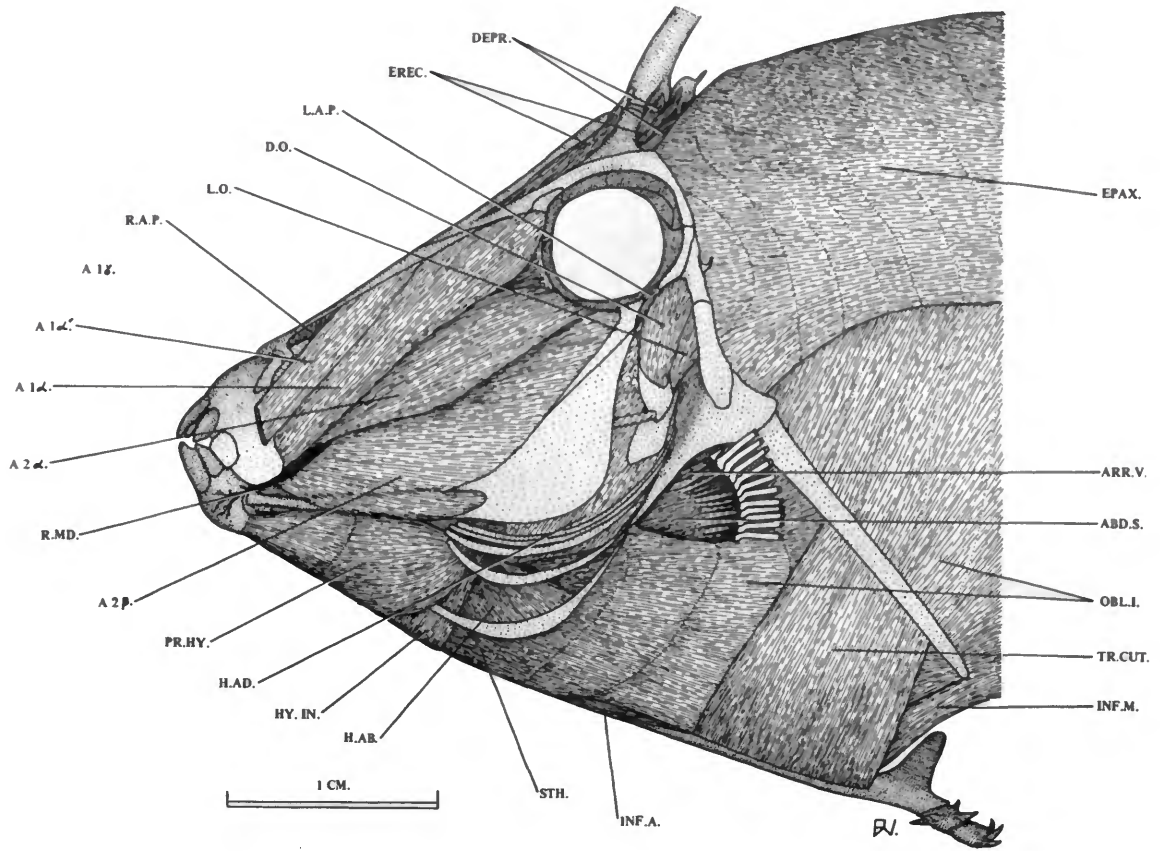


FIGURE 102.—*Paramonacanthus barnardi*, ANSP 117506, 78 mm SL, left lateral view of superficial anterior musculature.

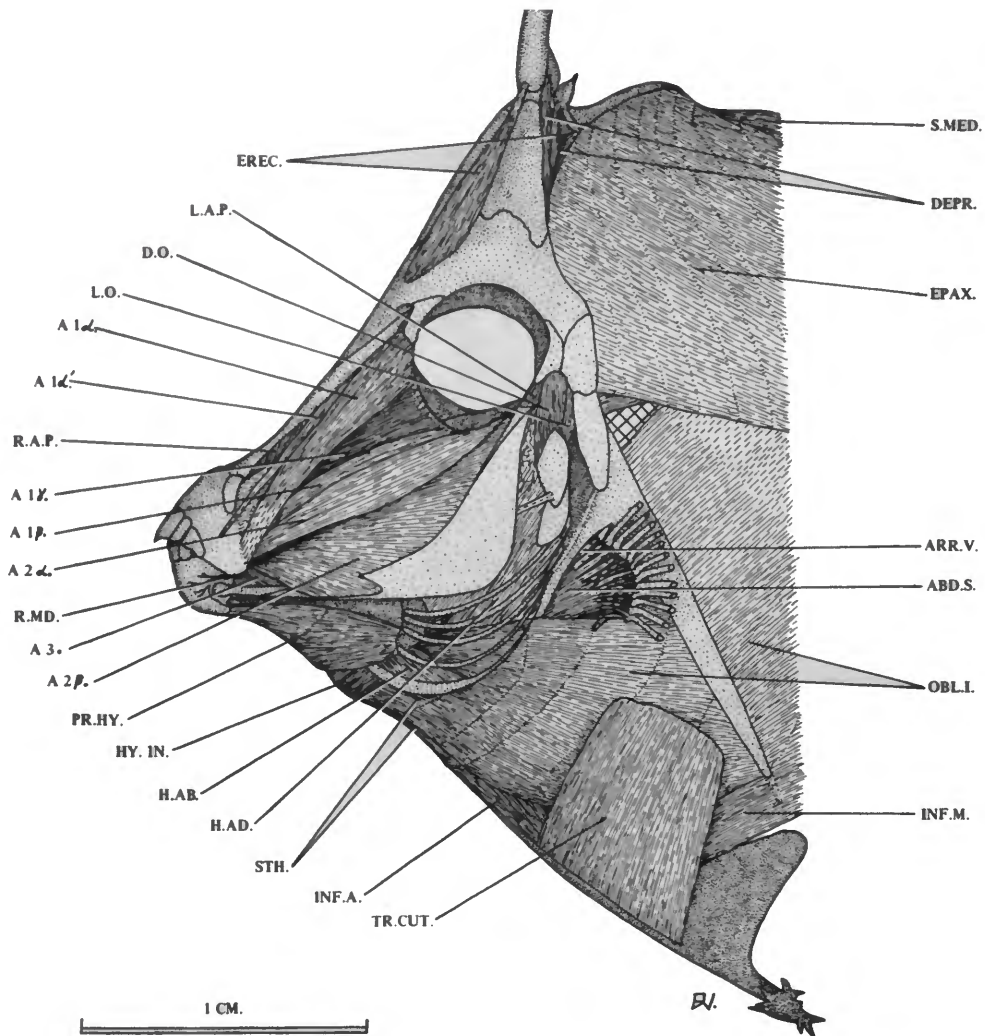


FIGURE 103.—*Chaetoderma spinosissimus*, ANSP 117514, 42 mm SL, left lateral view of superficial anterior musculature.

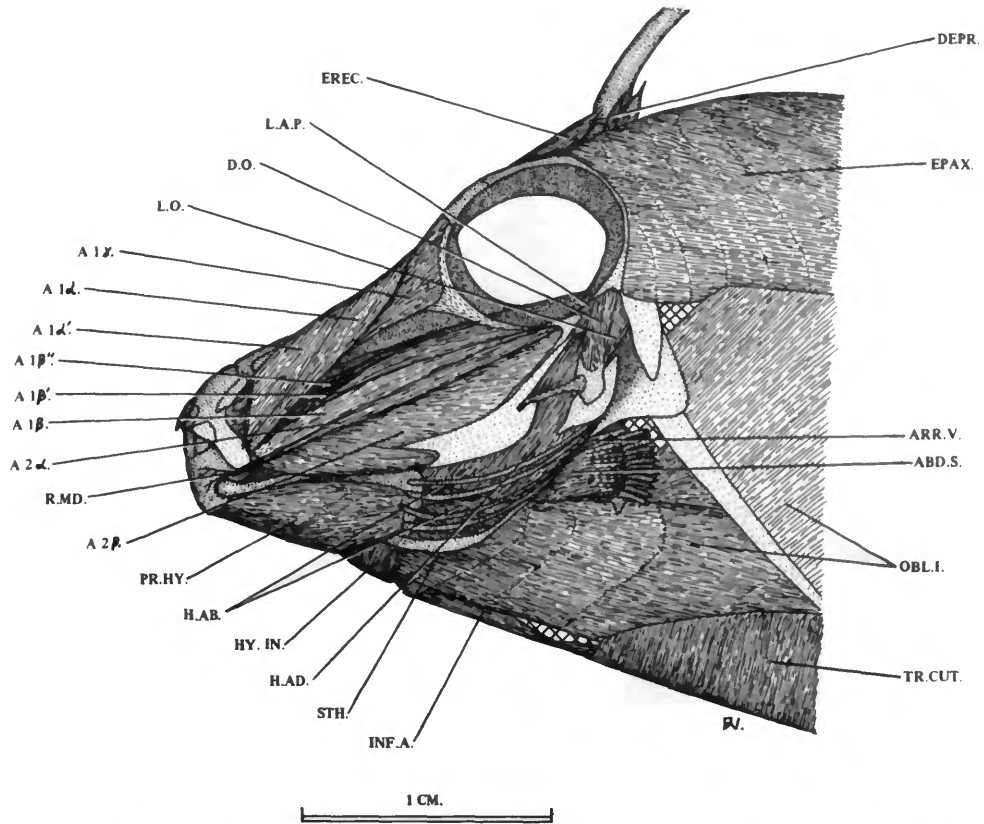


FIGURE 104.—*Paraluteres prionurus*, ANSP 106644, 57 mm SL, left lateral view of superficial anterior musculature.

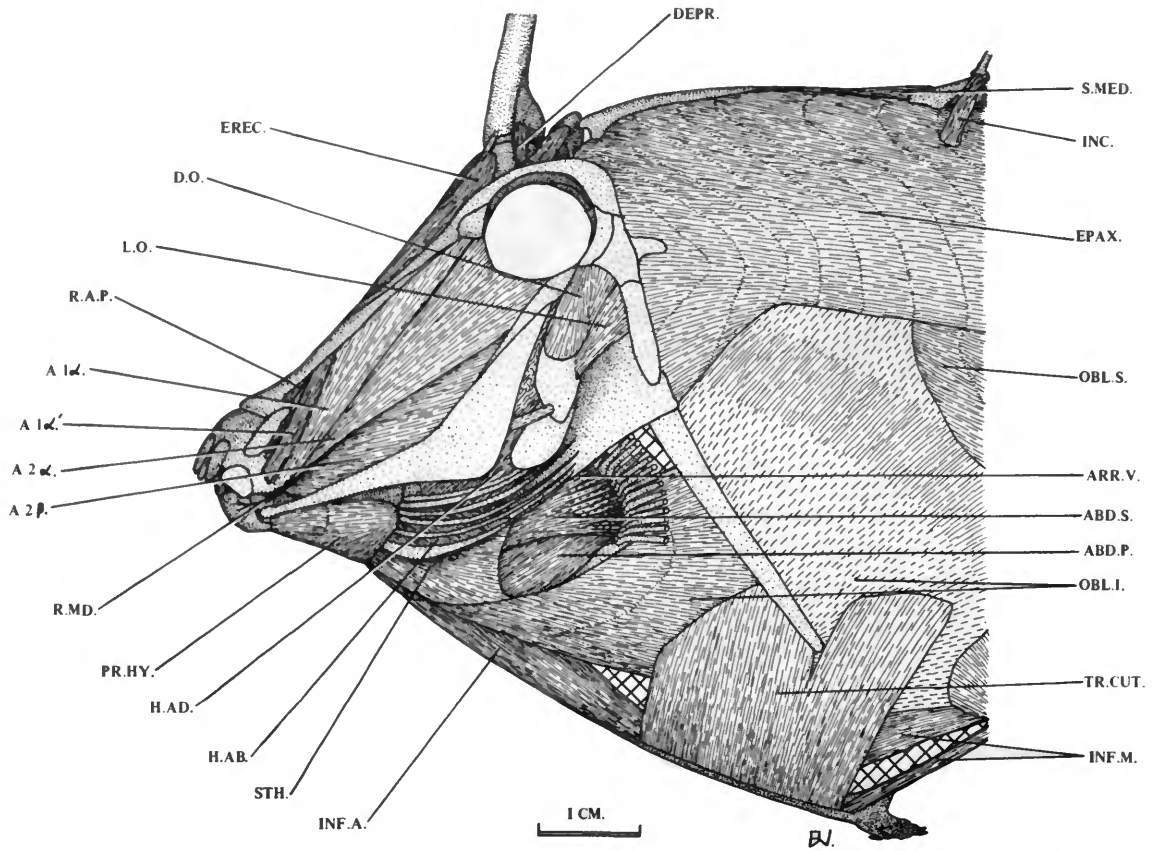


FIGURE 105.—*Cantherhines pardalis*, ANSP 117530, 126 mm SL, left lateral view of superficial anterior musculature.

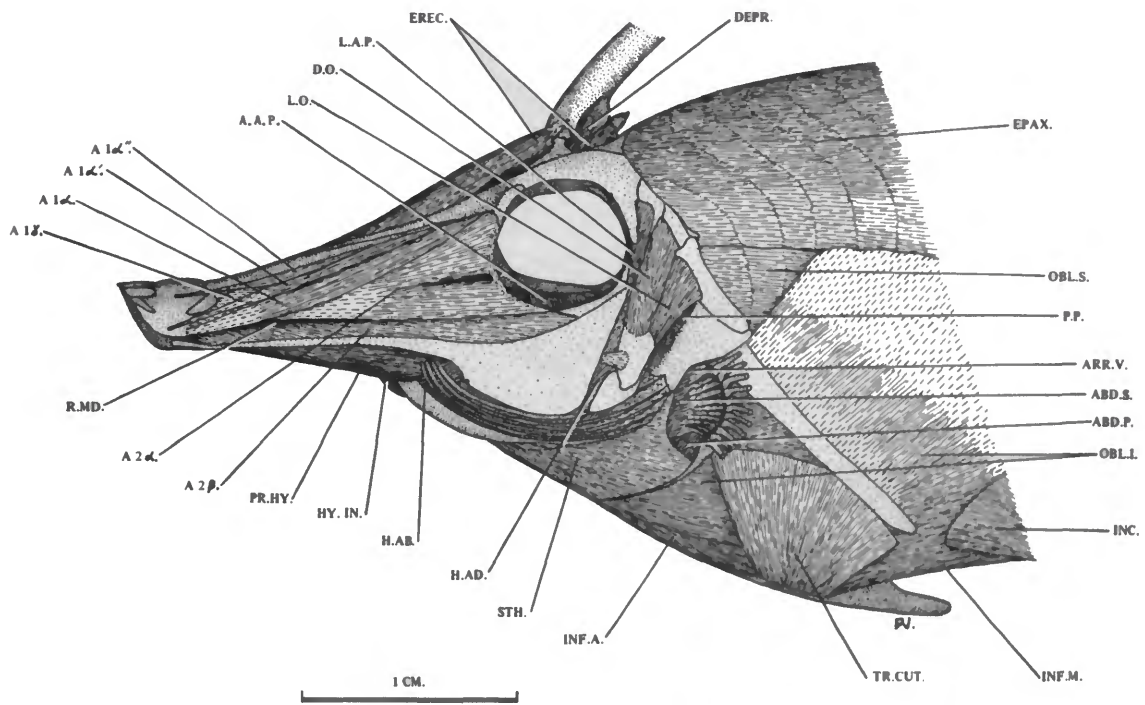


FIGURE 106.—*Oxymonacanthus longirostris*, ANSP 117496, 72 mm SL, left lateral view of superficial anterior musculature.

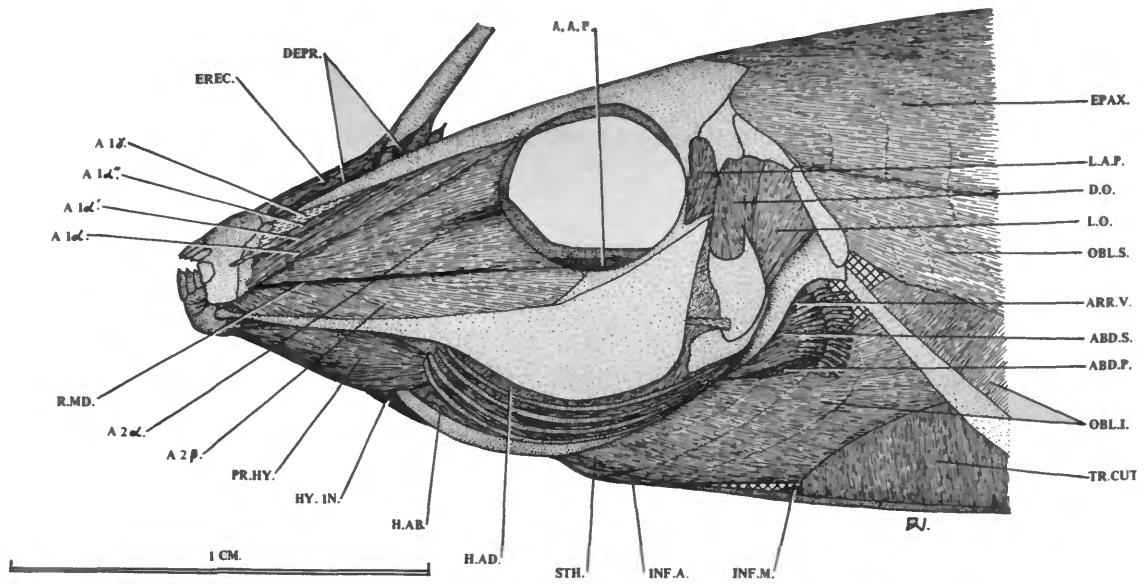


FIGURE 107.—*Pseudalutarius nascornis*, ANSP 100830, 45 mm SL, left lateral view of superficial anterior musculature.

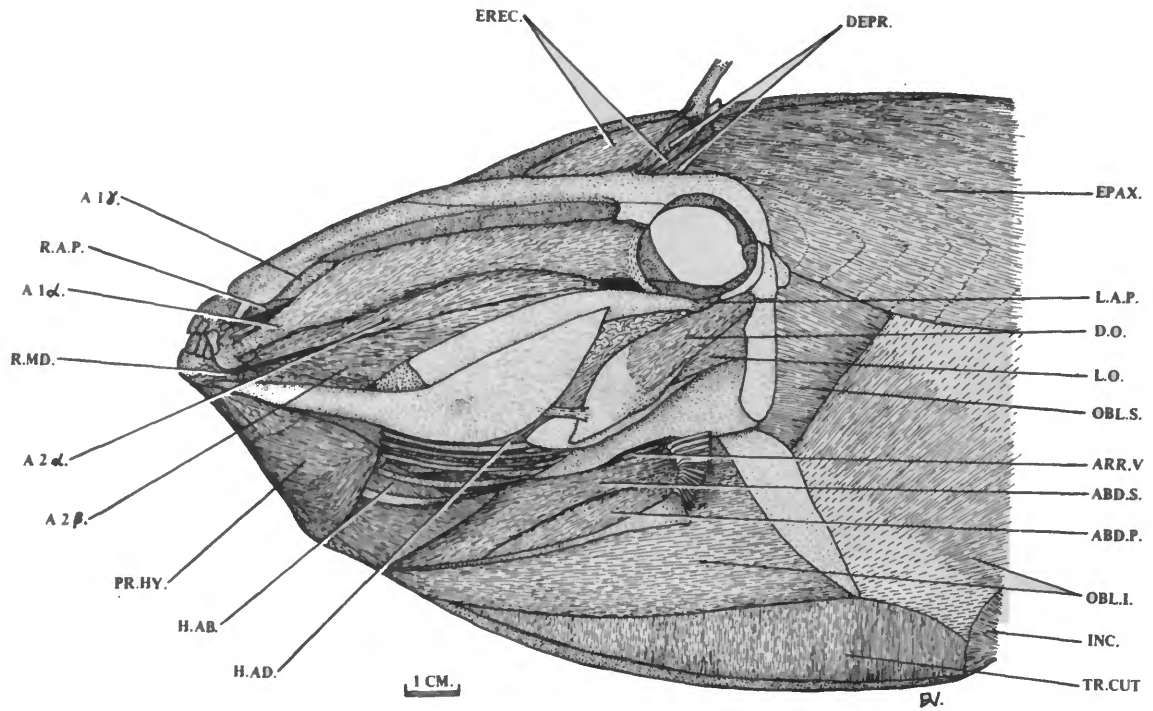


FIGURE 108.—*Aluterus monoceros*, ANSP 117554, 345 mm SL, left lateral view of superficial anterior musculature.

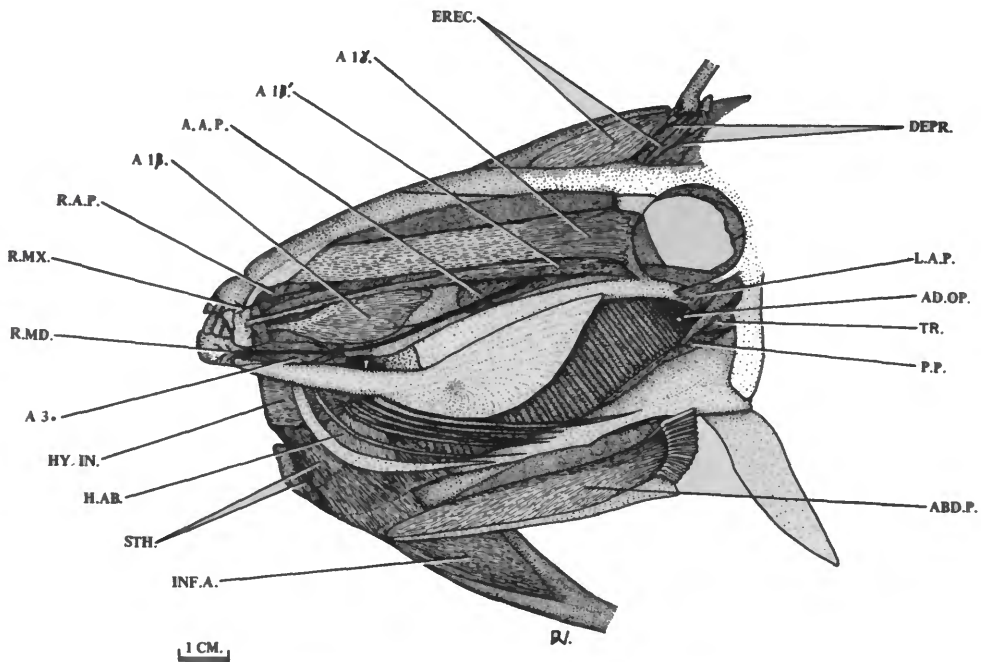


FIGURE 109.—*Aluterus monoceros*, ANSP 117554, 345 mm SL, left lateral view of the deeper muscles in the head region.

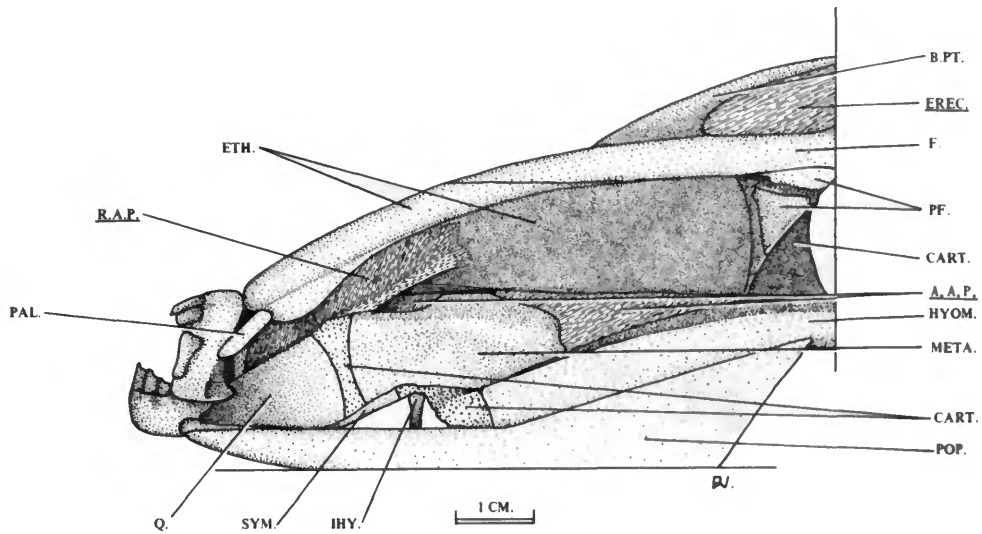


FIGURE 110.—*Aluterus monoceros*, ANSP 117554, 345 mm SL, left lateral view of the cheek. (The adductor mandibulae complex removed.)

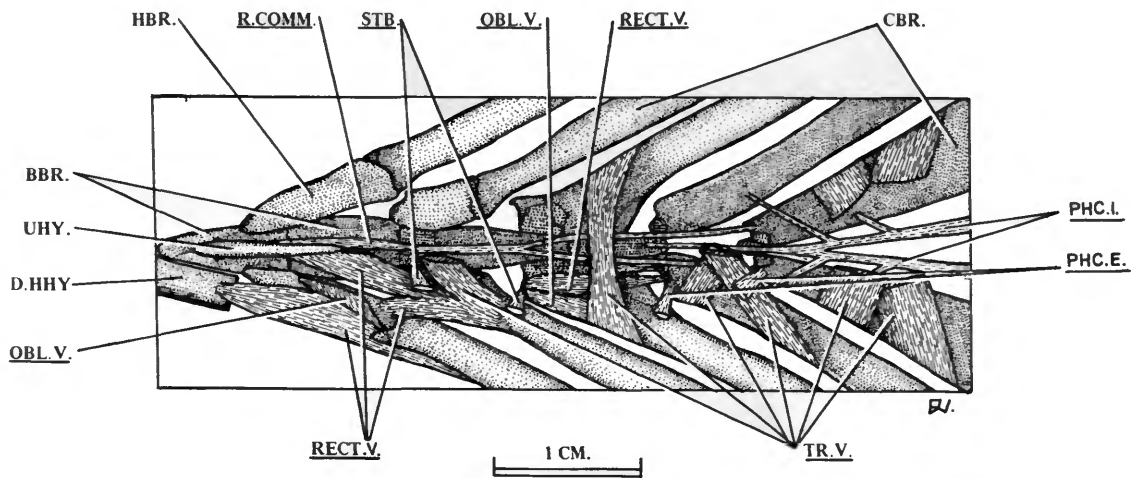


FIGURE 111.—*Aluterus monoceros*, ANSP 117554, 345 mm SL, ventral view of branchial arch musculature. (Most of the muscles of the left side and the right rectus communis removed.)



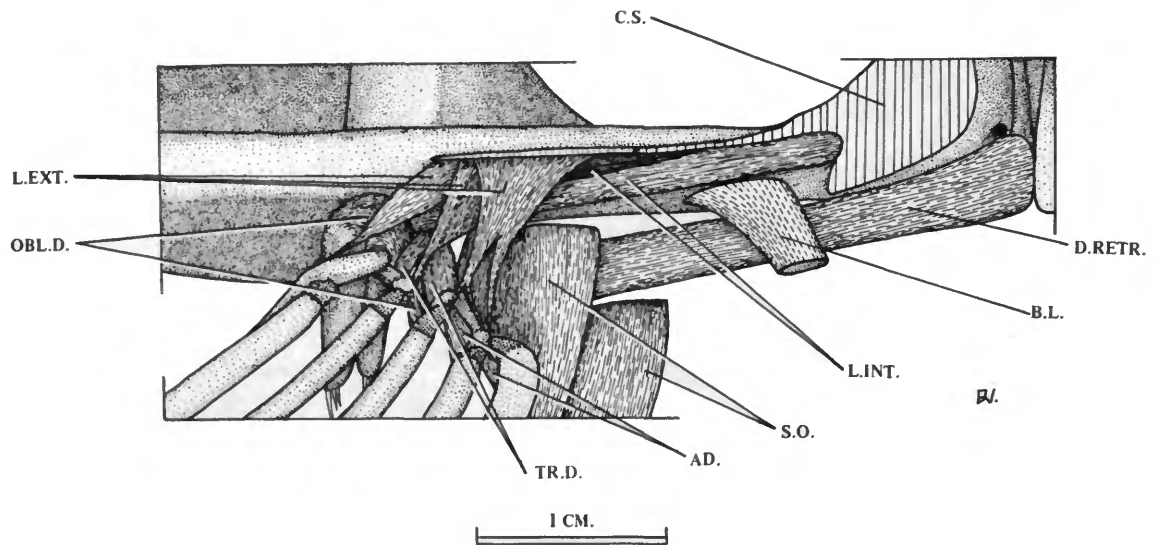


FIGURE 112.—*Aluterus monoceros*, ANSP 117554, 345 mm SL, left lateral view of dorsal branchial arch musculature. (Palatal arch, pectoral girdle, and first infrapharyngobranchial removed.)

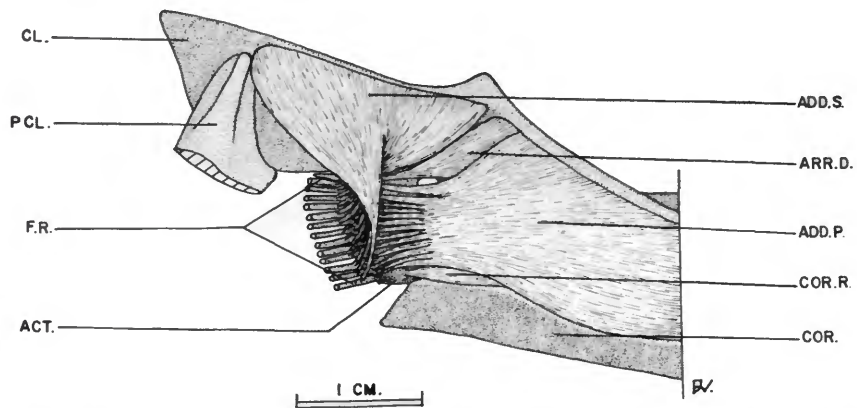


FIGURE 113.—*Aluterus monoceros*, ANSP 117554, 345 mm SL, medial view of the left pectoral girdle and associated muscles.

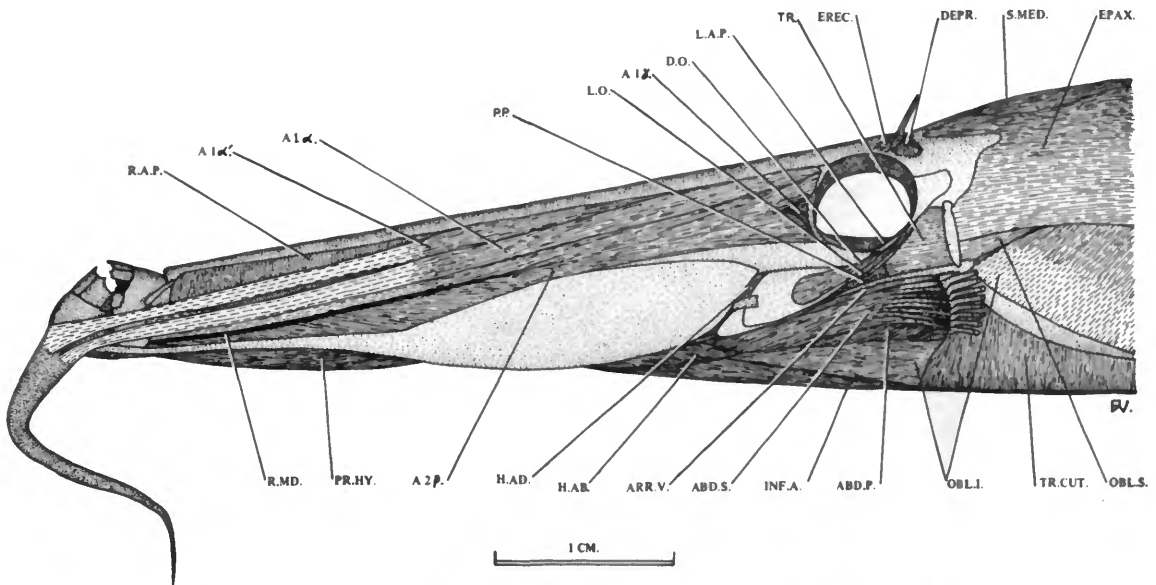


FIGURE 114.—*Anacanthus barbatus*, ANSP 117516, 166 mm SL, left lateral view of superficial anterior musculature.

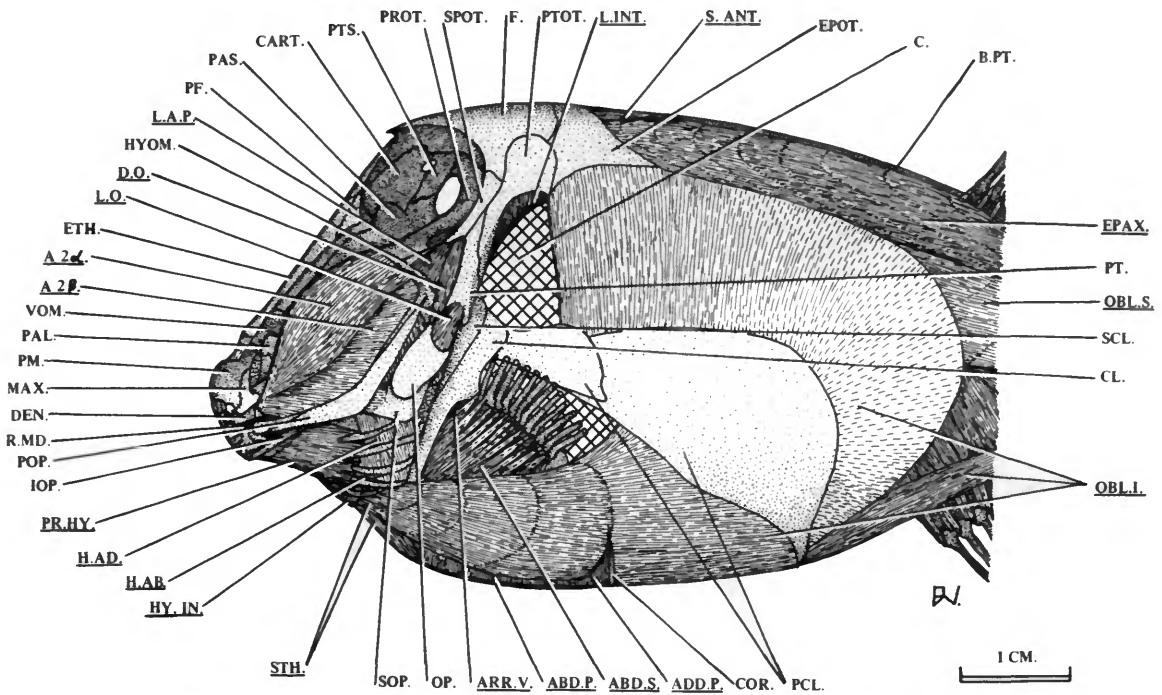


FIGURE 115.—*Kentrocapros aculeatus*, ANSP 117531, 91 mm SL, left lateral view of superficial anterior musculature.

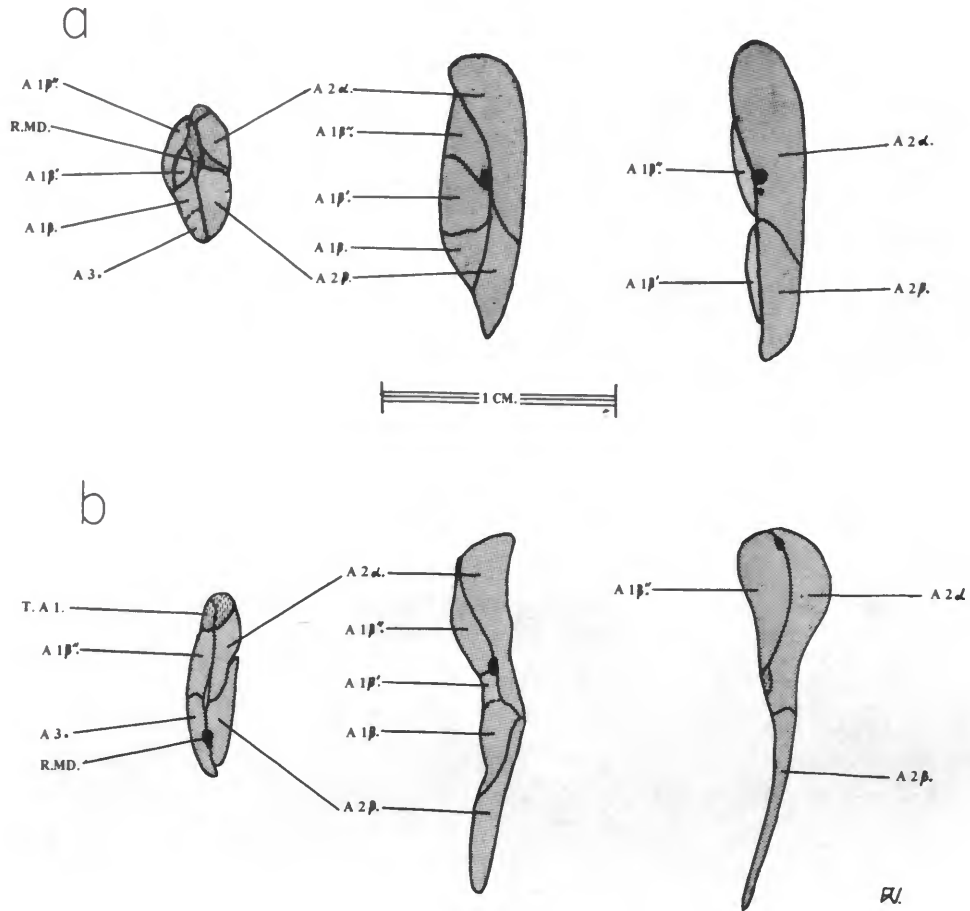


FIGURE 116.—Transverse sections progressing posteriorly of the left adductor mandibulae complex, viewed from anterior: *a*, *Kentrocapros aculeatus*, ANSP 117531, 91 mm SL; *b*, *Ostracion tuberculatus*, ANSP 117542, 102 mm SL.

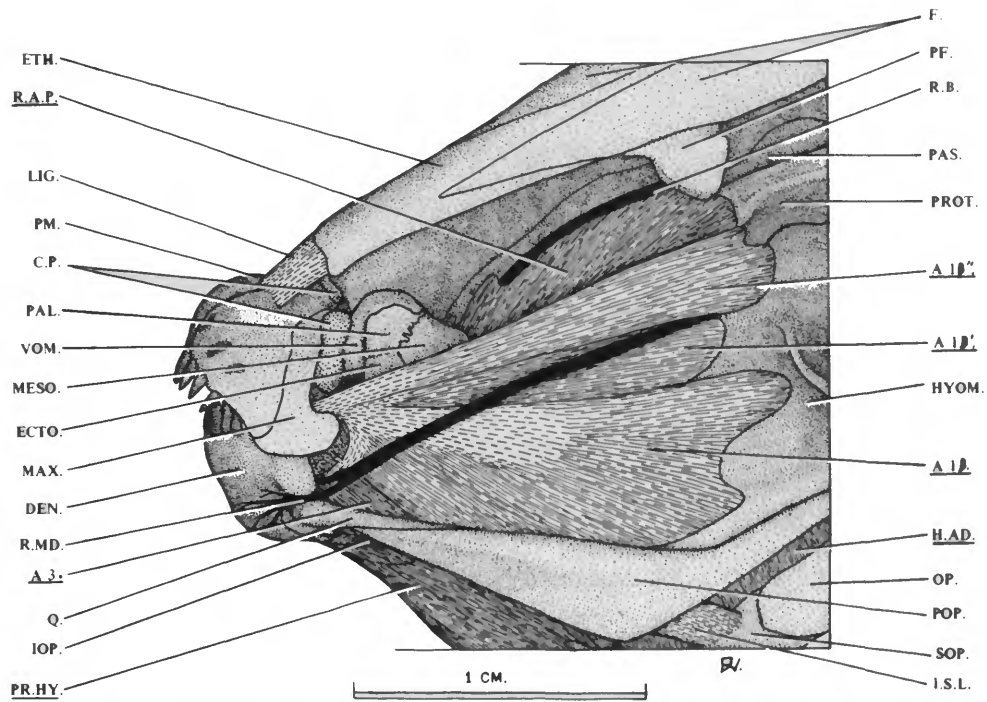
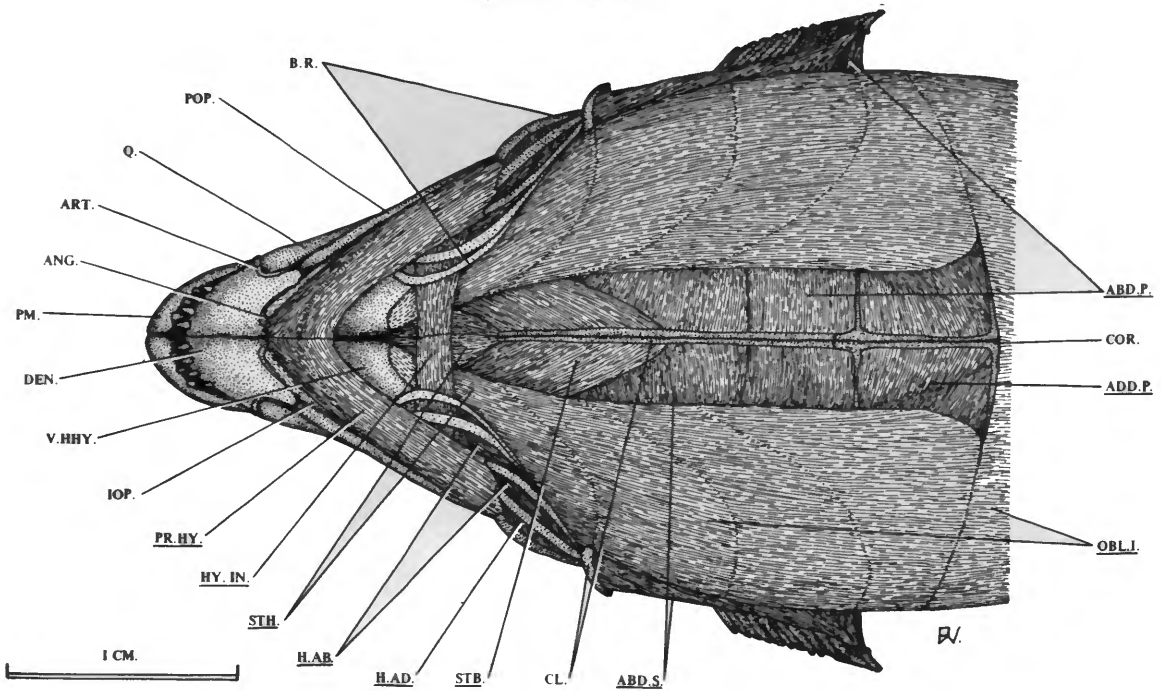


FIGURE 117.—*Kentrocapros aculeatus*, ANSP 117531, 91 mm SL, dorsolateral view of the deep muscles of the cheek.

FIGURE 118.—*Kentrocapros aculeatus*, ANSP 117531, 91 mm SL, ventral view of superficial anterior musculature.



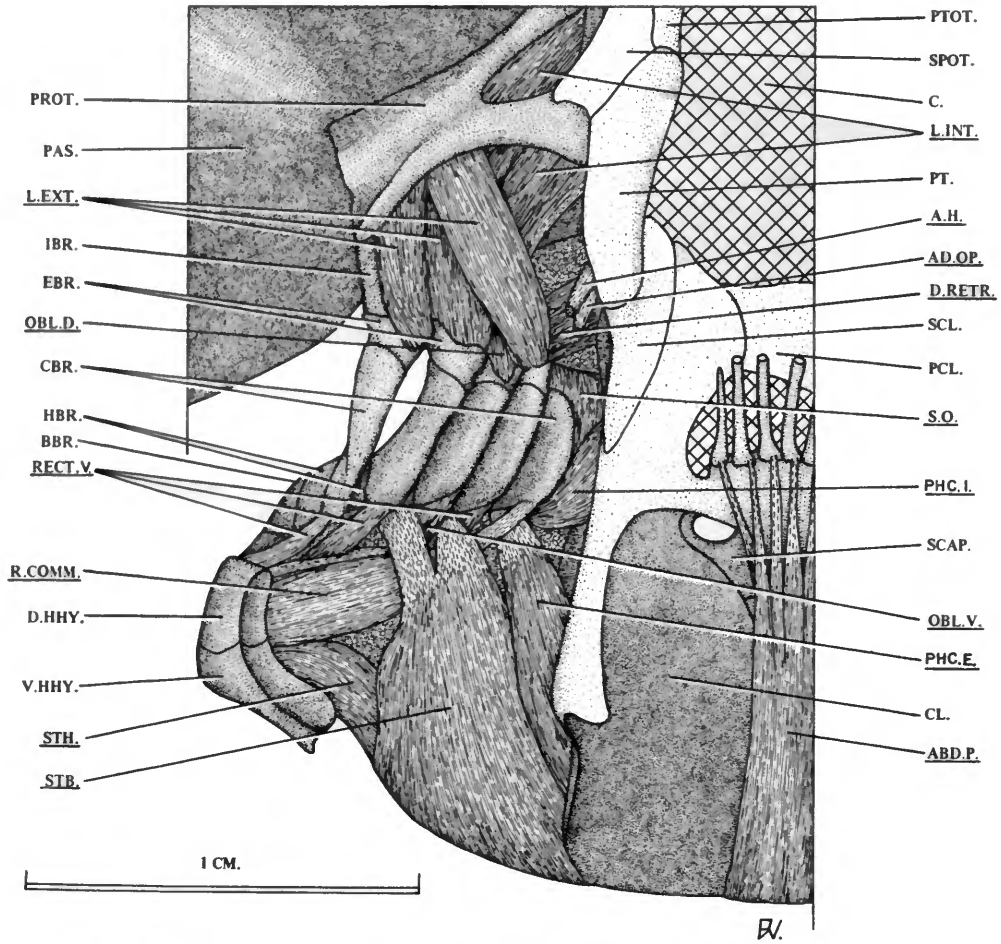


FIGURE 119.—*Kentrocapros aculeatus*, ANSP 117531, 91 mm SL, left lateral view of superficial branchial arch musculature.

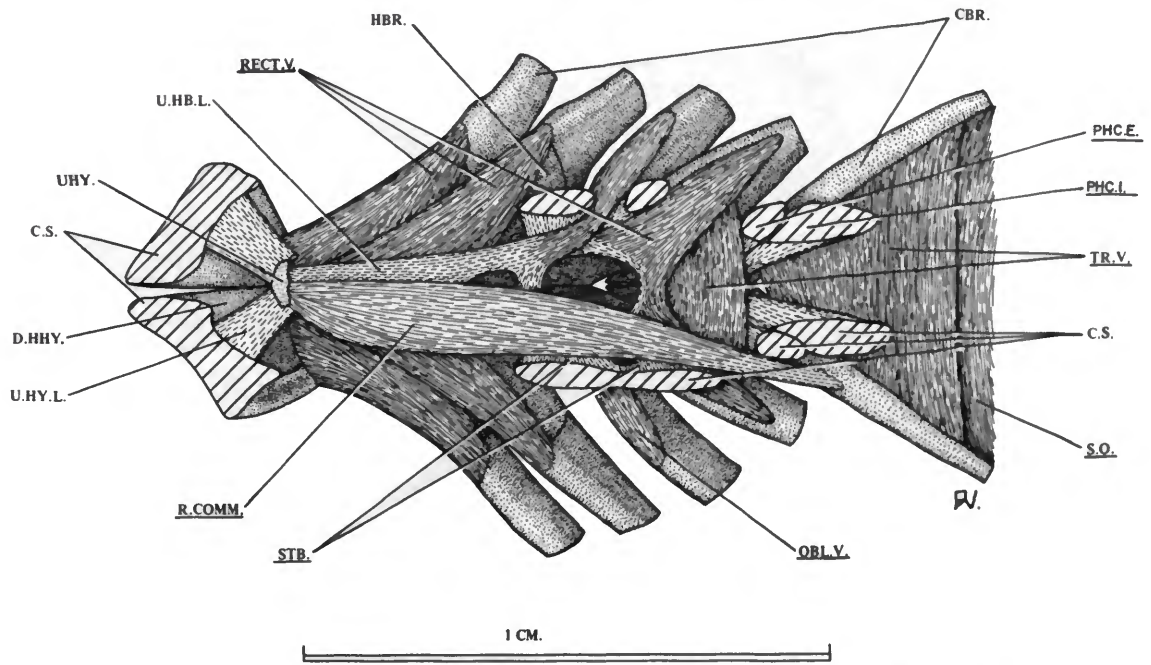


FIGURE 120.—*Kentrocapros aculeatus*, ANSP 117531, 91 mm SL, ventral view of branchial arch musculature.

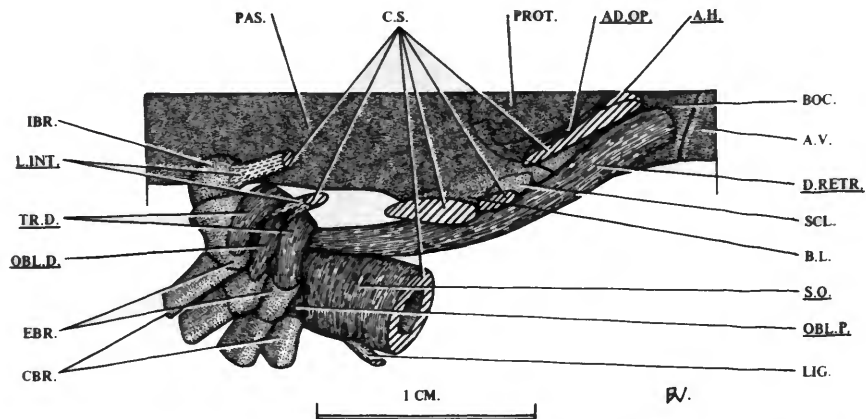


FIGURE 121.—*Kentrocapros aculeatus*, ANSP 117531, 91 mm SL, left lateral view of dorsal branchial arch musculature. (The levatores externi, interni, and the first arch removed.)

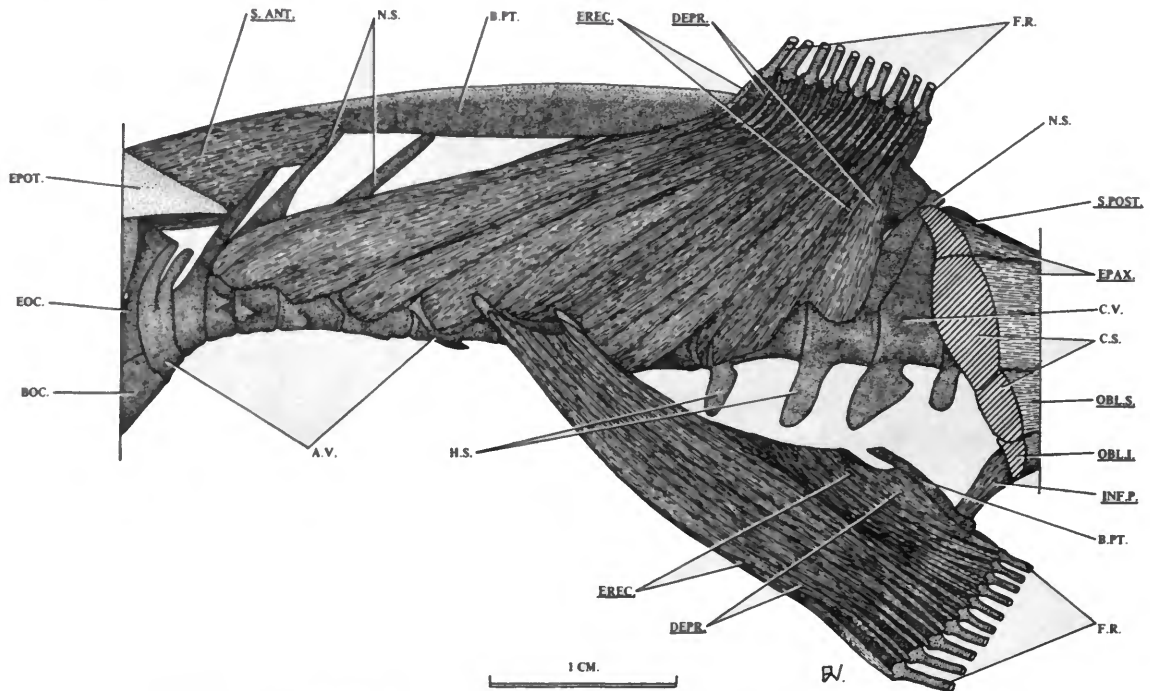


FIGURE 122.—*Kentrocapros aculeatus*, ANSP 117531, 91 mm SL, left lateral view of dorsal and anal fin musculature.

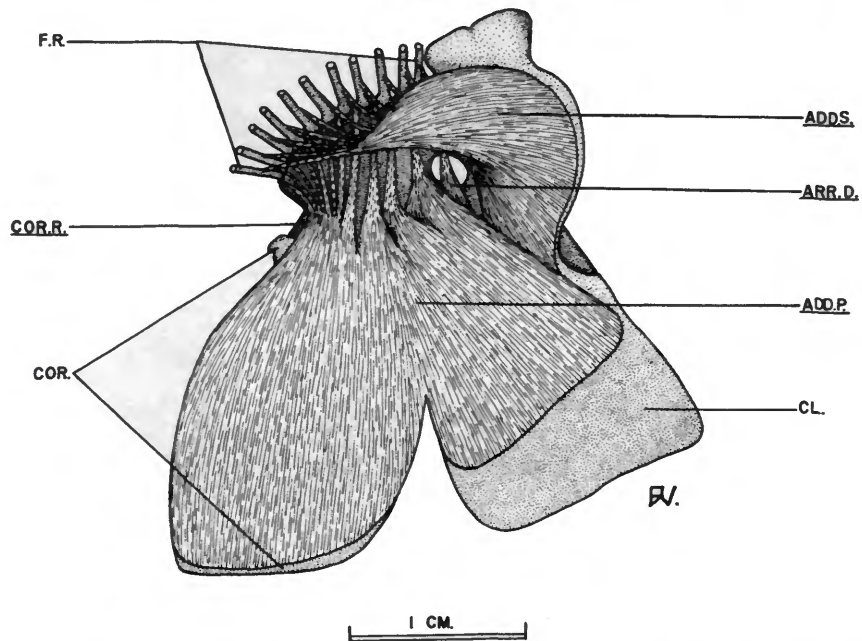


FIGURE 123.—*Kentrocapros aculeatus*, ANSP 117531, 91 mm SL, medial view of left pectoral girdle and associated musculature, from somewhat posterodorsally.

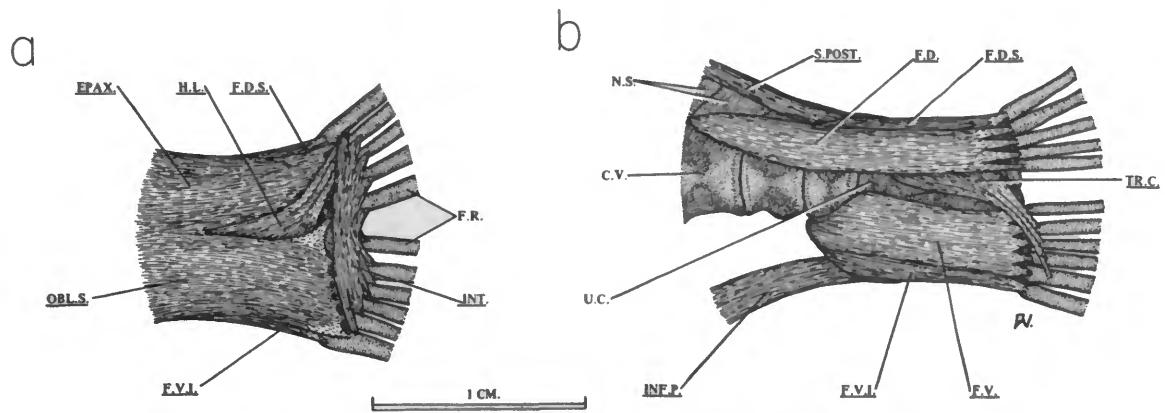


FIGURE 124.—*Kentrocapros aculeatus*, ANSP 117531, 91 mm SL, left lateral view of caudal peduncle region: a, superficial musculature; b, deep musculature.

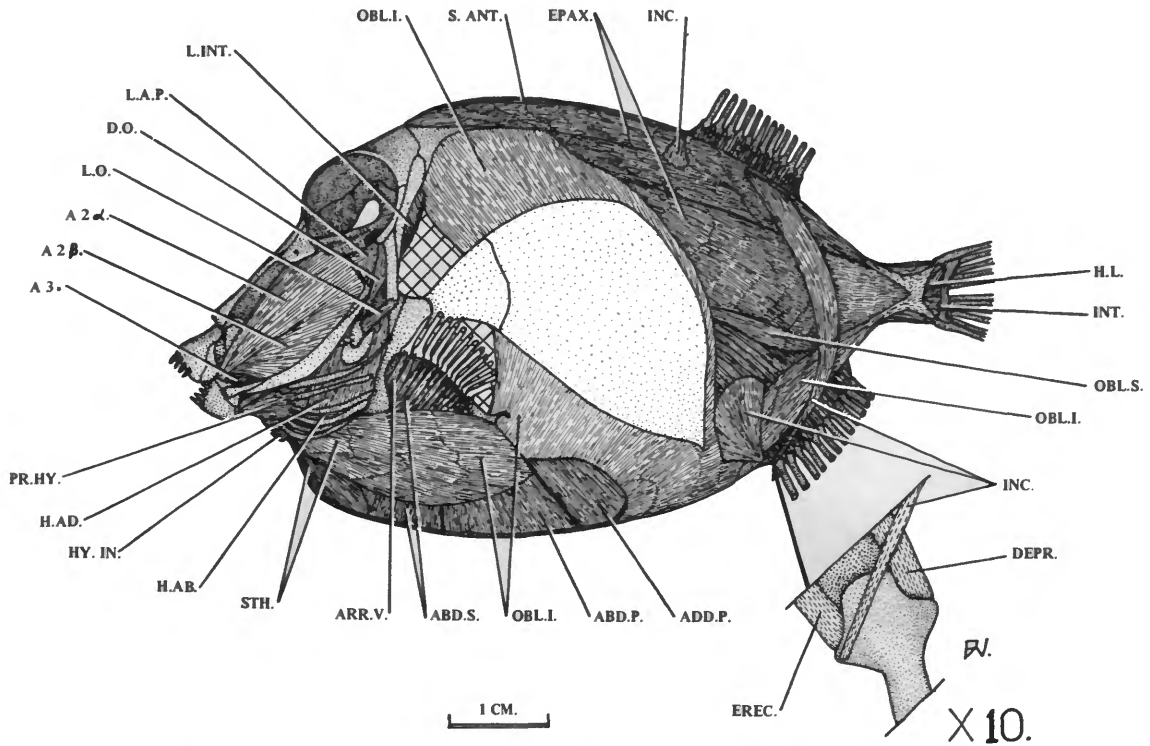


FIGURE 125.—*Capropygia unistriata*, ANSP 109574, 67 mm SL, left lateral view of superficial musculature.



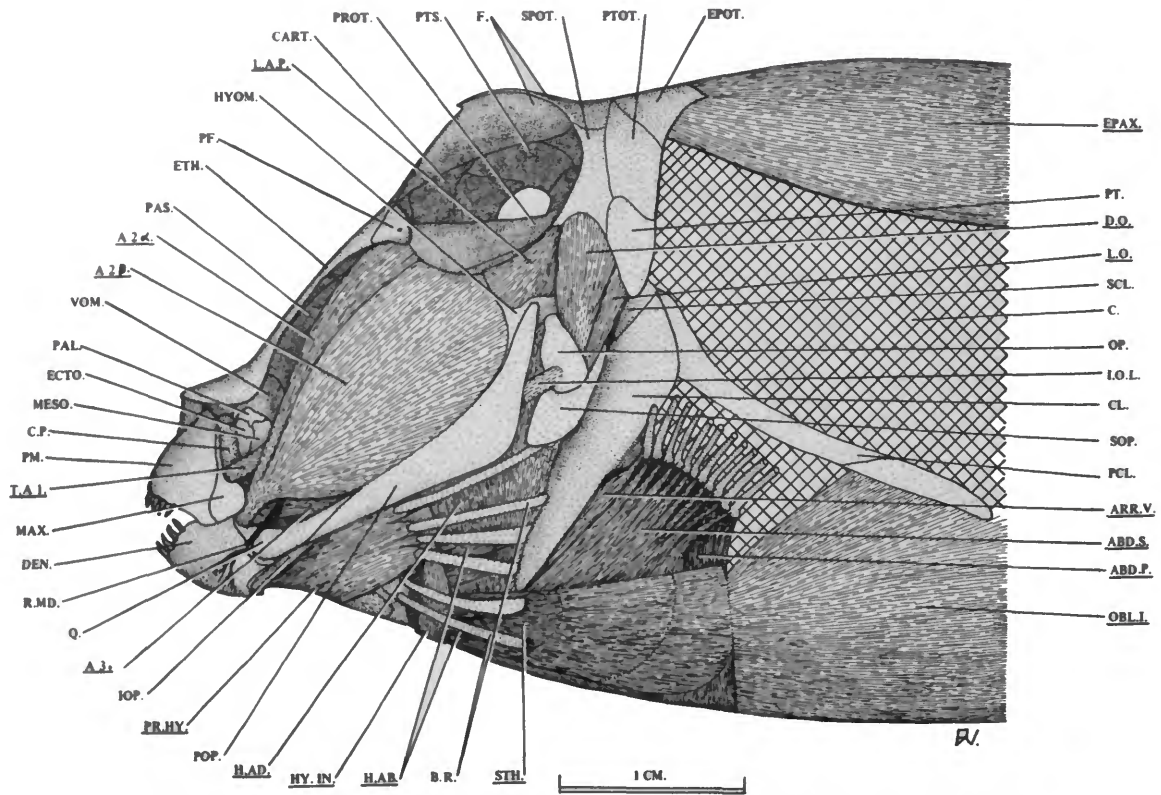
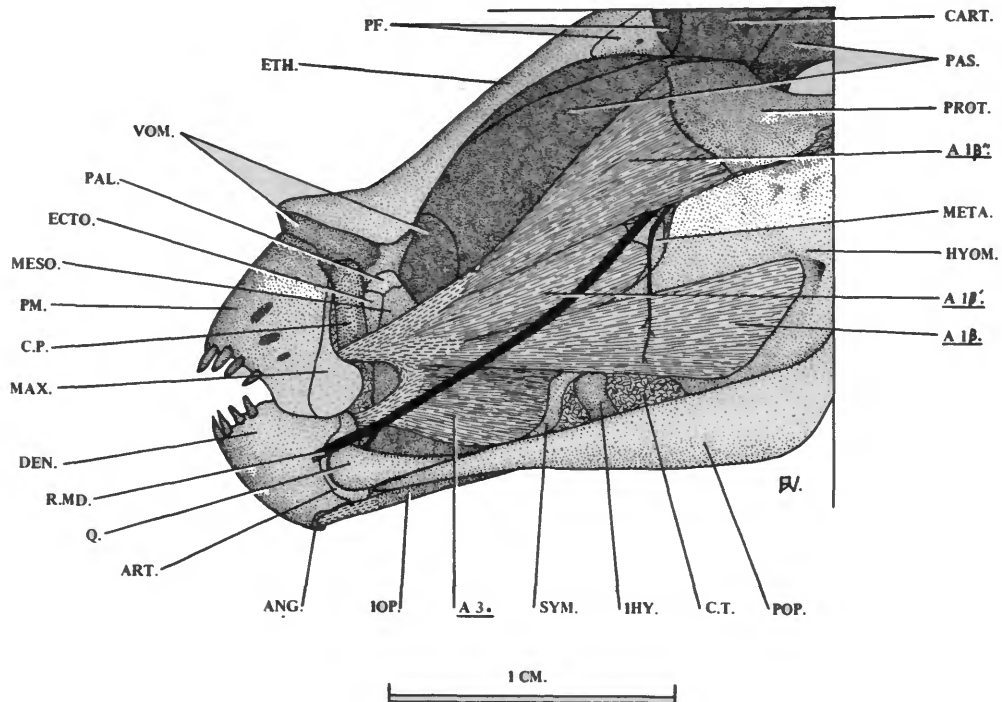


FIGURE 126.—*Ostracion tuberculatus*, ANSP 117542, 102 mm SL, left lateral view of superficial anterior musculature.

FIGURE 127.—*Ostracion tuberculatus*, ANSP 117542, 102 mm SL, left lateral view (slightly dorsally) of the deep check musculature.



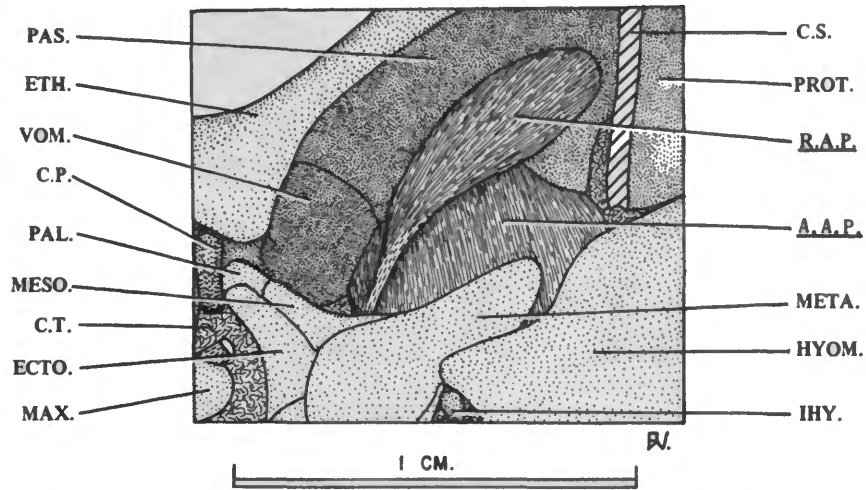


FIGURE 128.—*Ostracion tuberculatus*, ANSP 117542, 102 mm SL, dorsolateral view of snout region after removal of the adductor mandibulae complex.

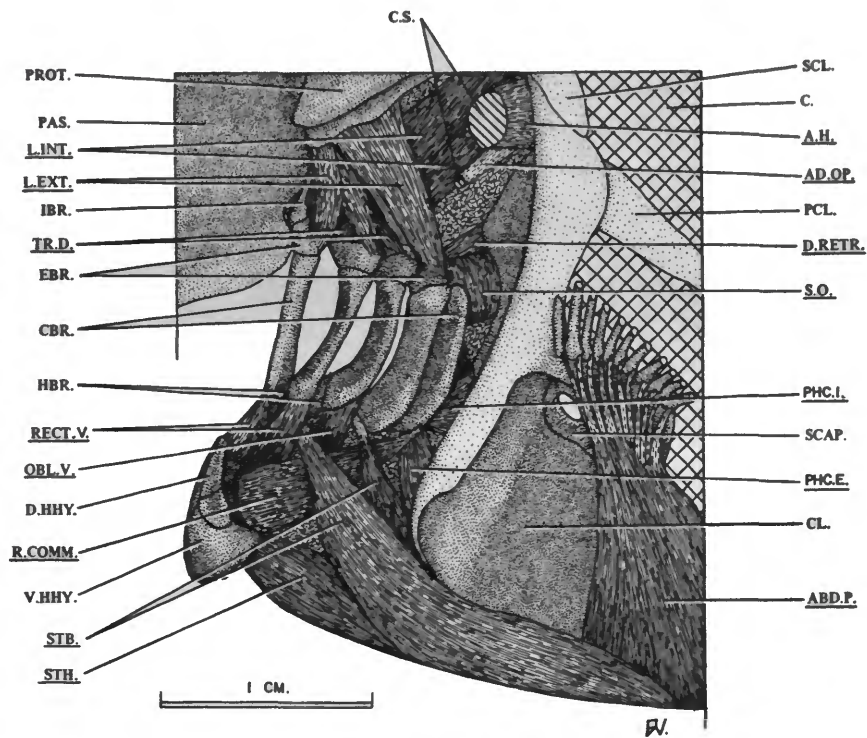


FIGURE 129.—*Ostracion tuberculatus*, ANSP 117542, 102 mm SL, left lateral view of superficial branchial arch musculature.

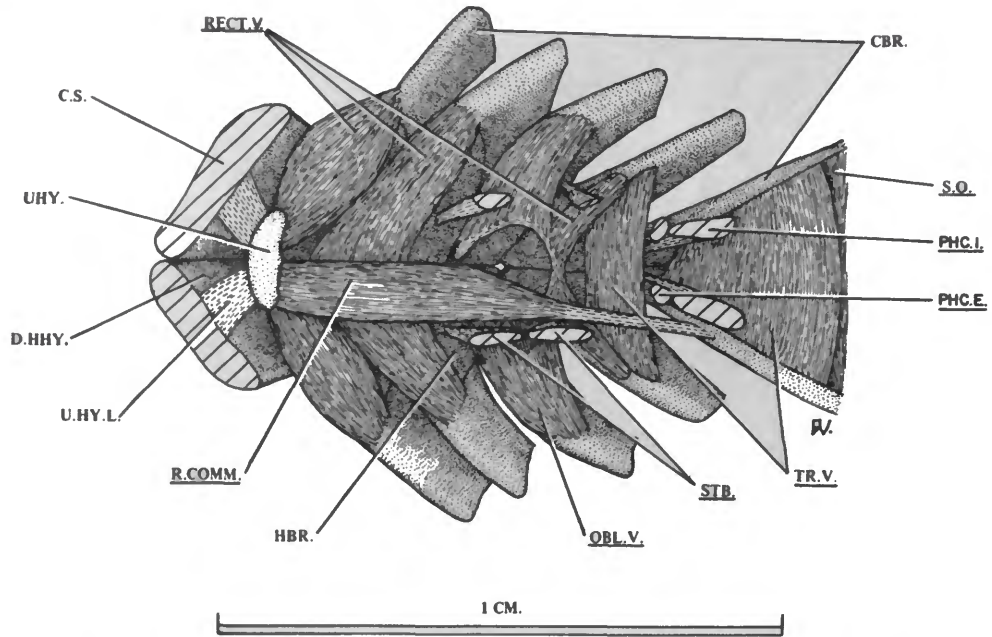


FIGURE 130.—*Ostracion tuberculatus*, ANSP 117542, 102 mm SL, ventral view of the branchial arch musculature. (Left rectus communis removed.)

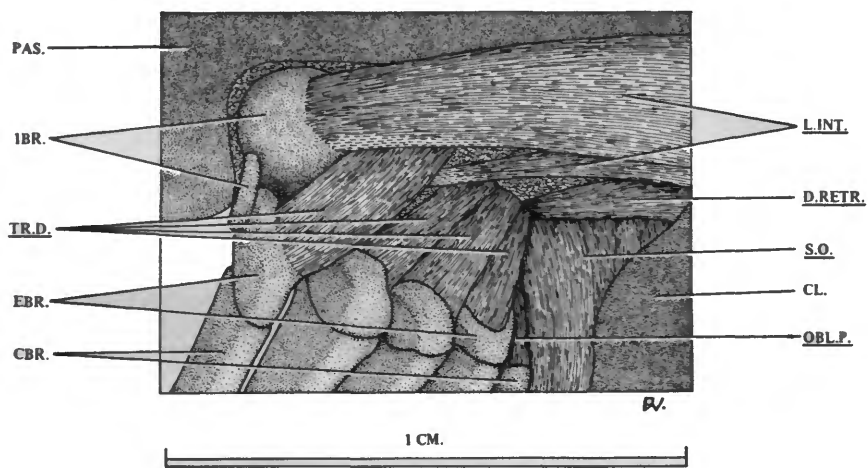


FIGURE 131.—*Ostracion tuberculatus*, ANSP 117542, 102 mm SL, dorsolateral view of dorsal branchial arch musculature. (Levatores externi removed.)

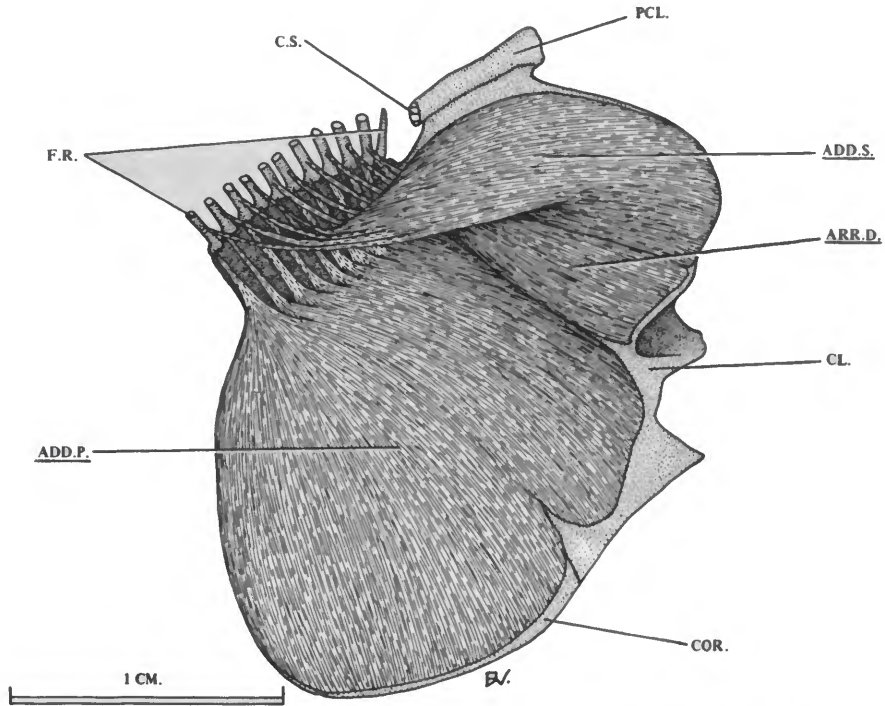


FIGURE 132.—*Ostracion tuberculatus*, ANSP 117542, 102 mm SL, posteromedial view of left pectoral girdle and associated musculature.

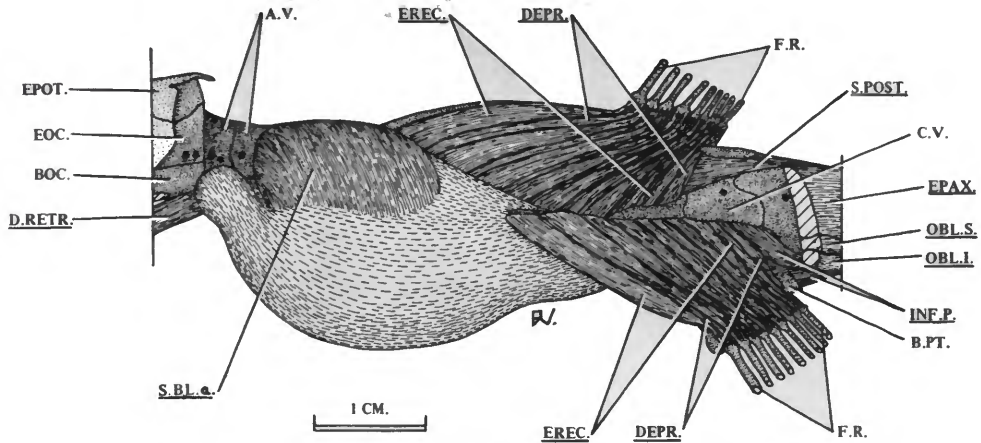


FIGURE 133.—*Ostracion tuberculatus*, ANSP 117542, 102 mm SL, left lateral view of deep body musculature.

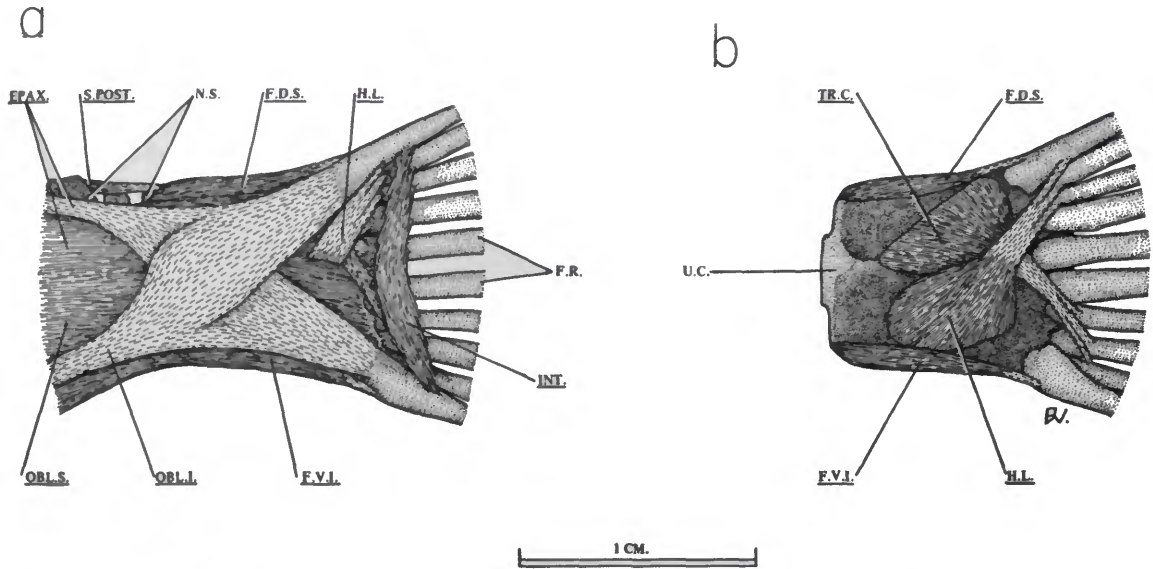


FIGURE 134.—*Ostracion tuberculatus*, ANSP 117542, 102 mm SL, left lateral view of caudal peduncle region: a, superficial musculature; b, deep musculature.

FIGURE 135.—*Lactoria cornuta*, ANSP 117539, 176 mm SL, left lateral view of superficial anterior musculature.

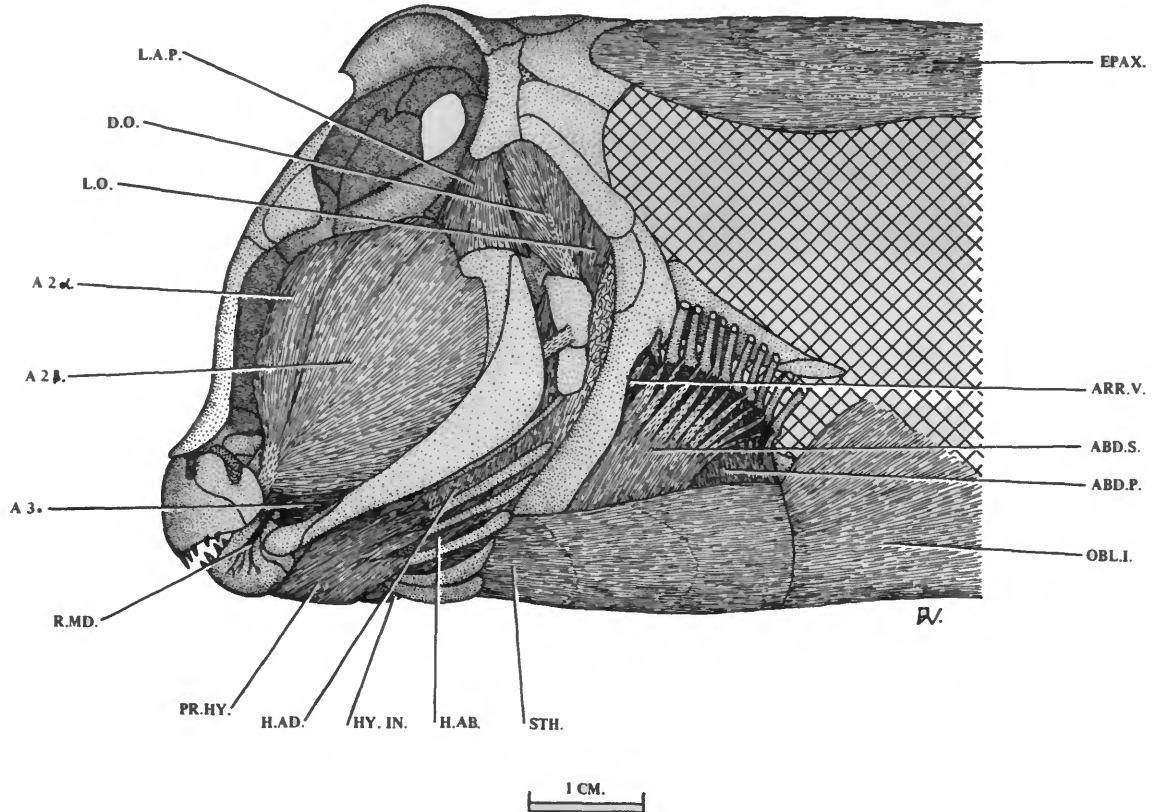


FIGURE 136.—*Tetrosomus concatenatus*, ANSP 117555, 196 mm SL, left lateral view of superficial anterior musculature.

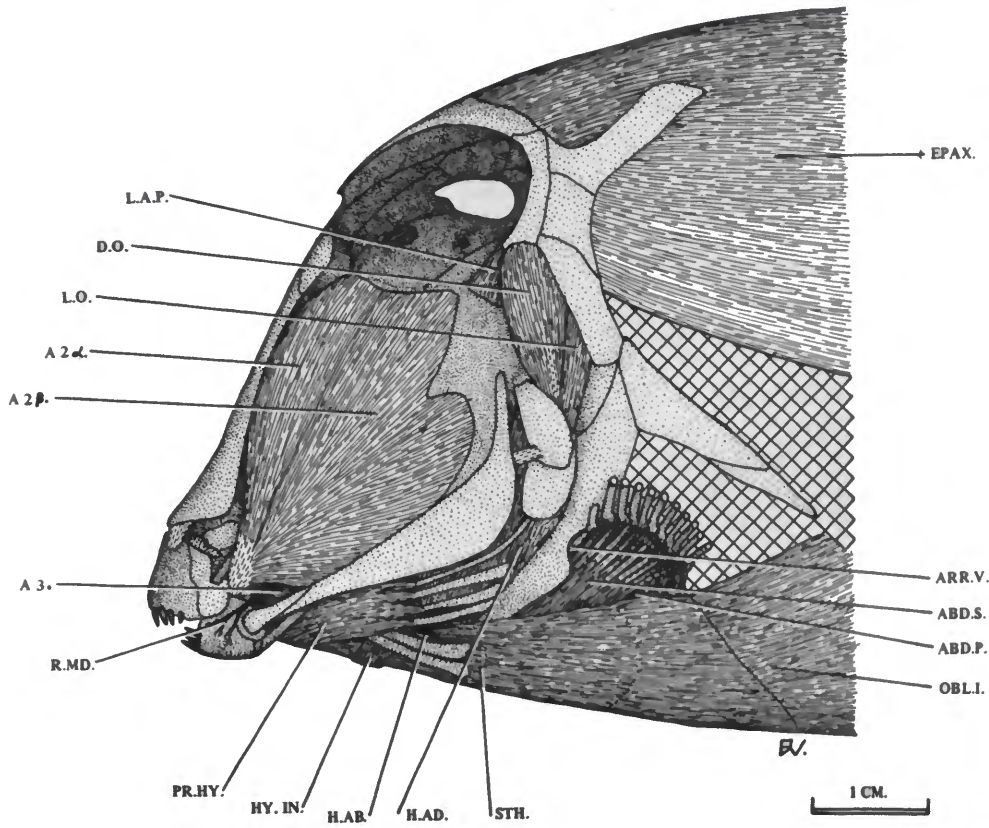
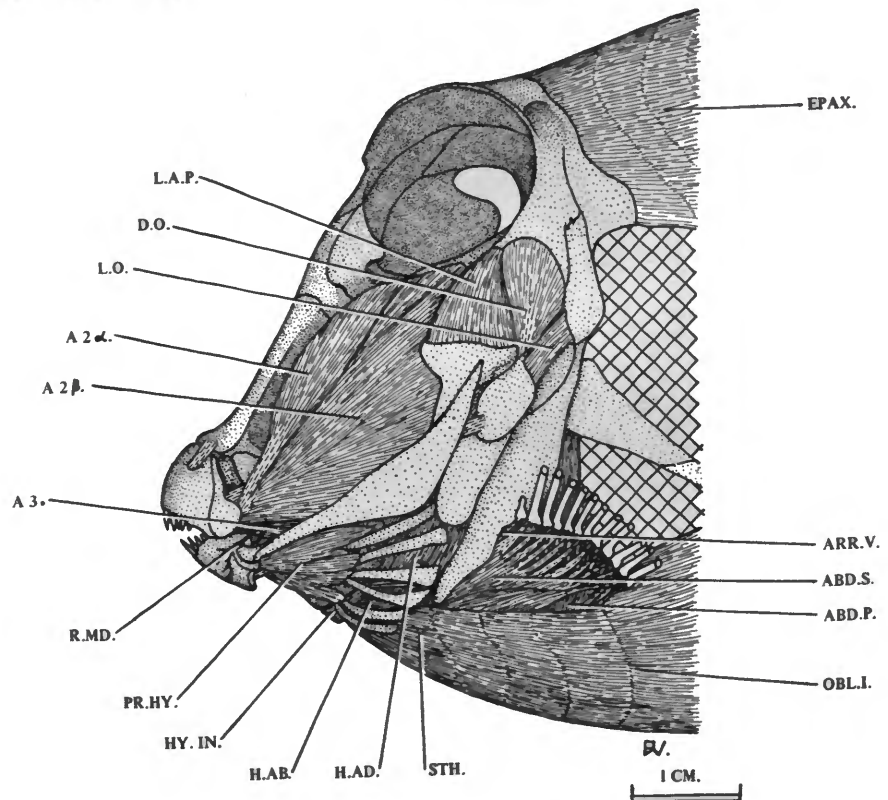


FIGURE 137.—*Acanthostracion quadricornis*, ANSP 98848, 126 mm SL, left lateral view of superficial anterior musculature.



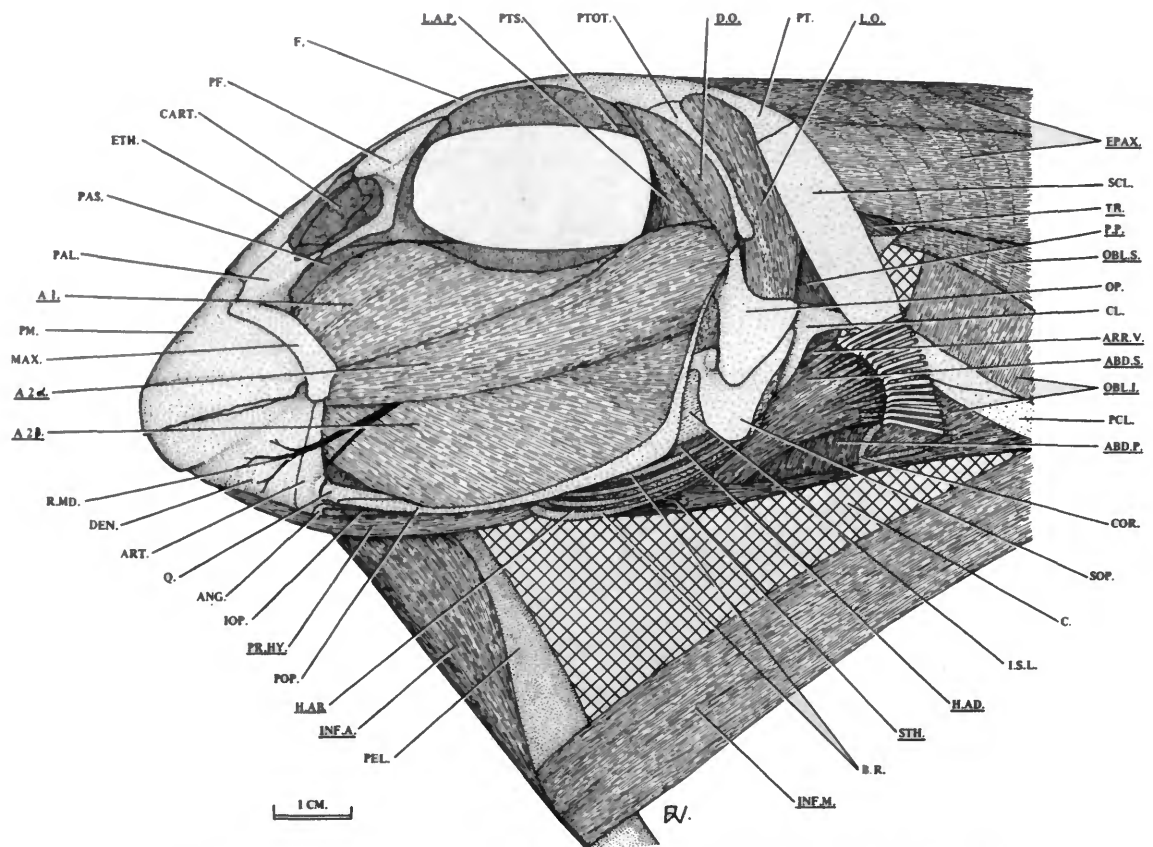


FIGURE 138.—*Triodon macropterus*, ANSP 105902, 270 mm SL, left lateral view of superficial anterior musculature.

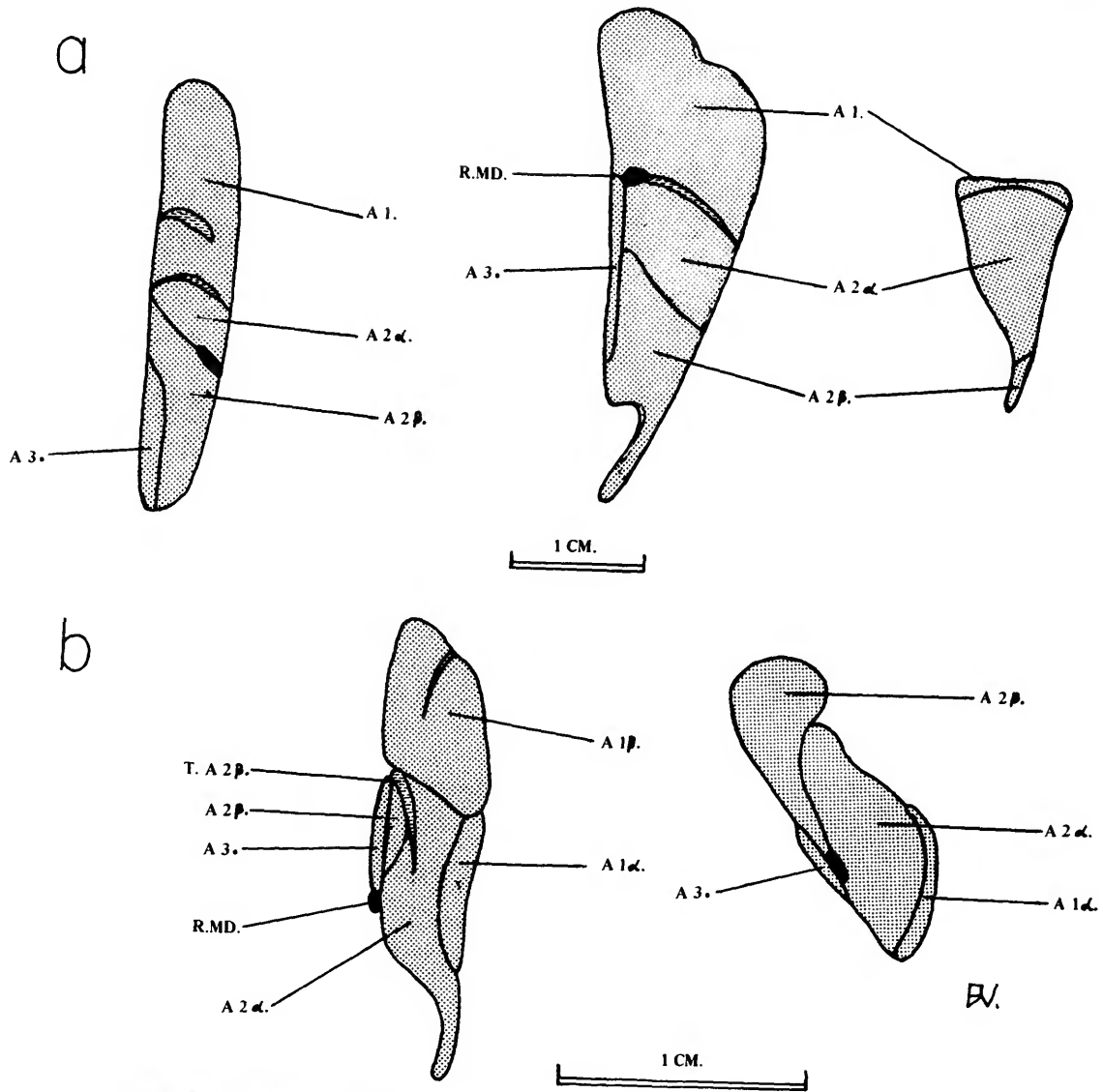


FIGURE 139.—Transverse sections progressing posteriorly of the left adductor mandibulae complex, viewed from anterior: a, *Triodon macropterus*, ANSP 103902, 350 mm SL; b, *Lagocephalus lunaris*, ANSP 113639, 124 mm SL.



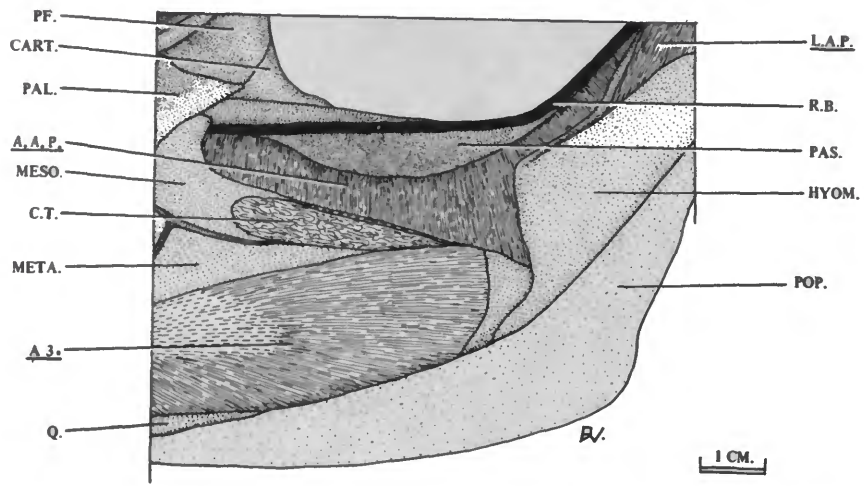


FIGURE 140.—*Triodon macropterus*, ANSP 103902, 270 mm SL, left lateral view of the deep muscles of the cheek.

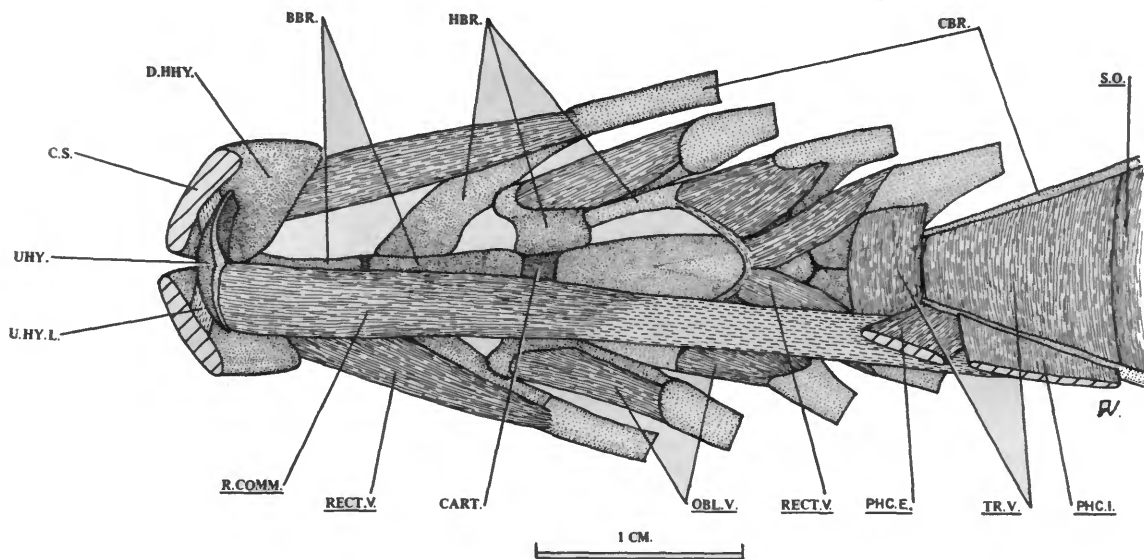


FIGURE 141.—*Triodon macropterus*, ANSP 103902, 270 mm SL, ventral view of branchial arch musculature. (Left rectus communis and pharyngoclaviculares removed.)

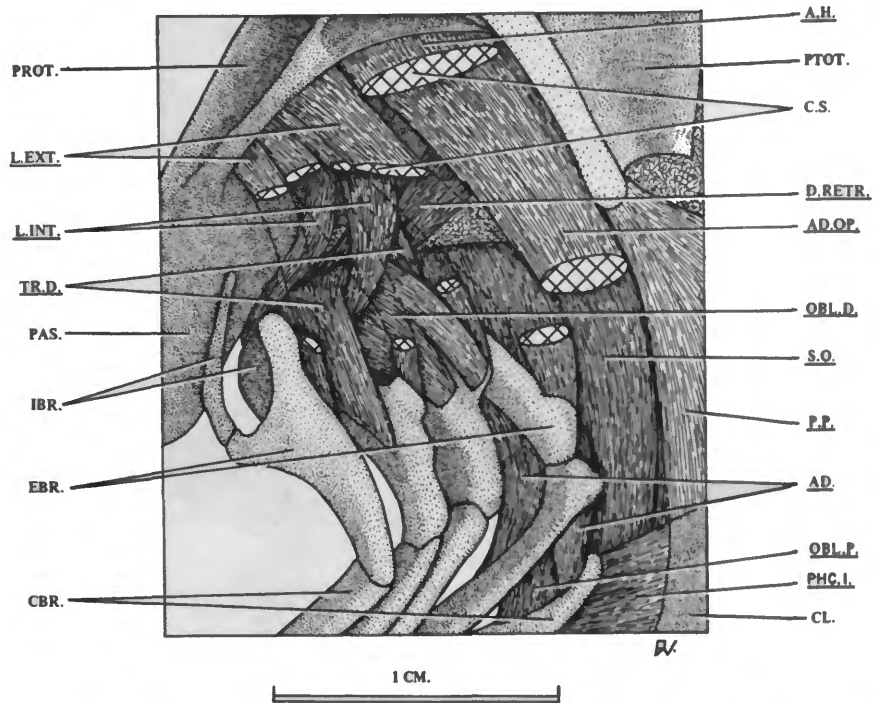


FIGURE 142.—*Triodon macropterus*, ANSP 103902, 270 mm SL, left lateral view of dorsal branchial arch region. (Most of the levatores externi removed.)

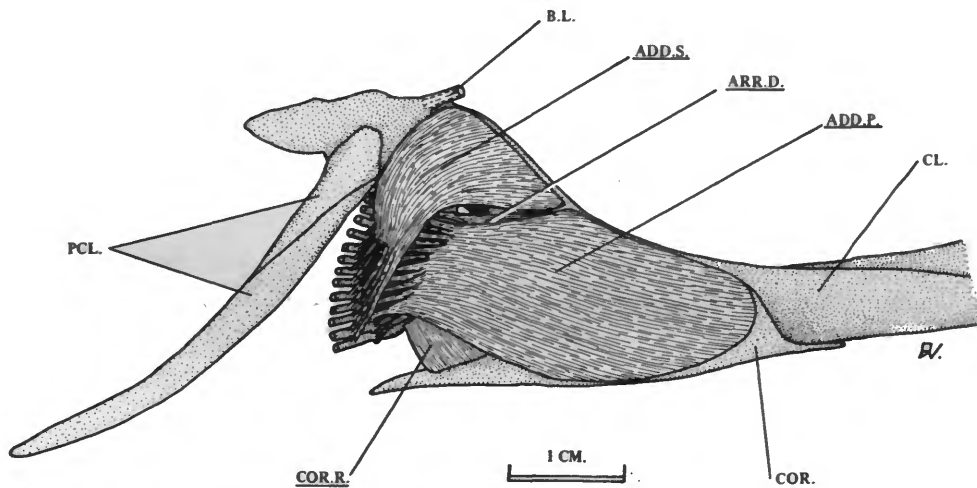


FIGURE 143.—*Triodon macropterus*, ANSP 103902, 270 mm SL, medial view of left pectoral girdle and associated musculature.

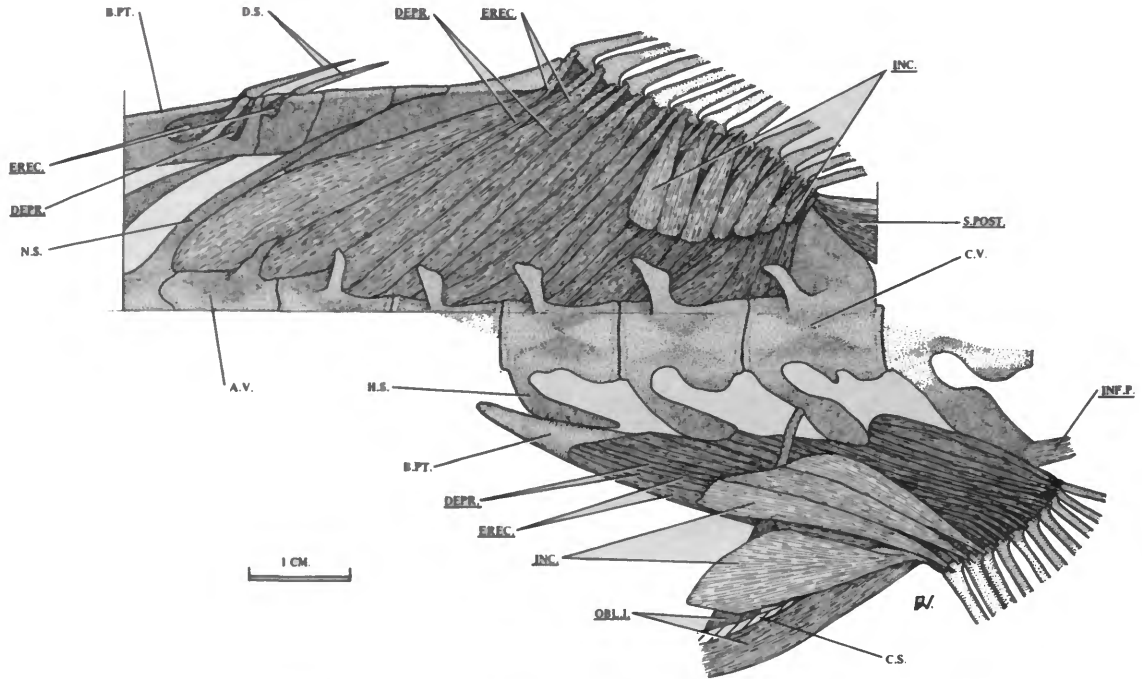
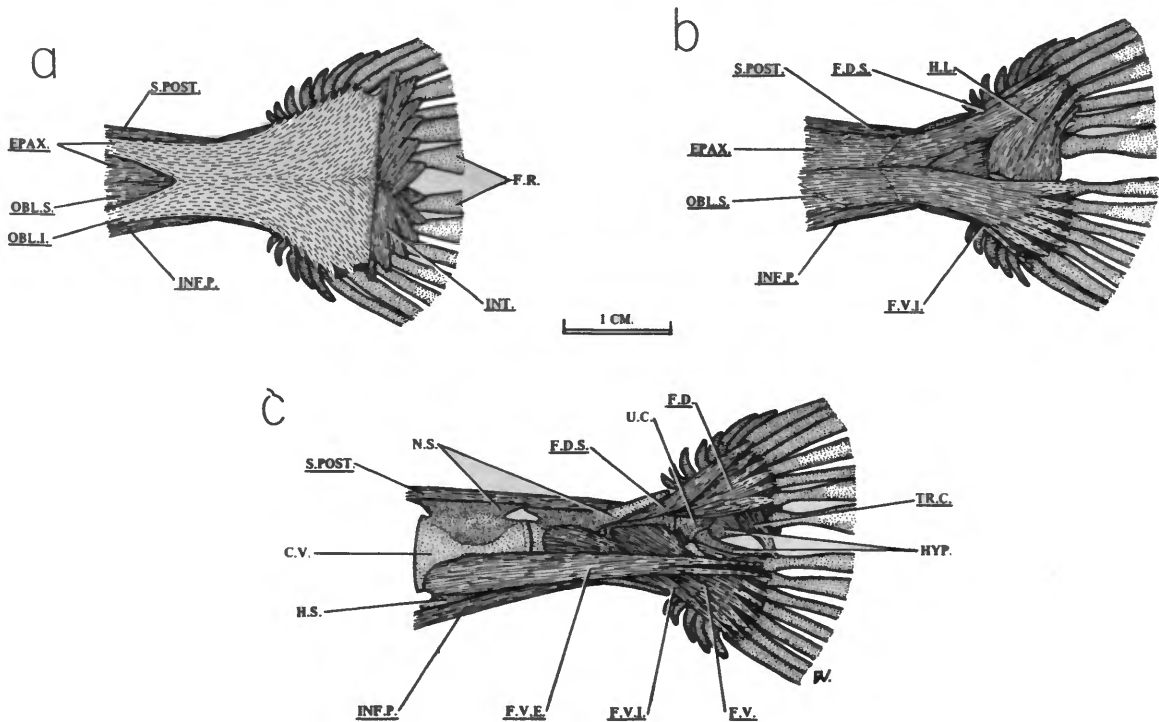


FIGURE 144.—*Triodon macropterus*, ANSP 103902, 270 mm SL, left lateral view of dorsal and anal fin musculature.

FIGURE 145.—*Triodon macropterus*, ANSP 103902, 270 mm SL, left lateral view of caudal peduncle region: a, superficial musculature; b, after removal of the aponeurosis; c, deep musculature.



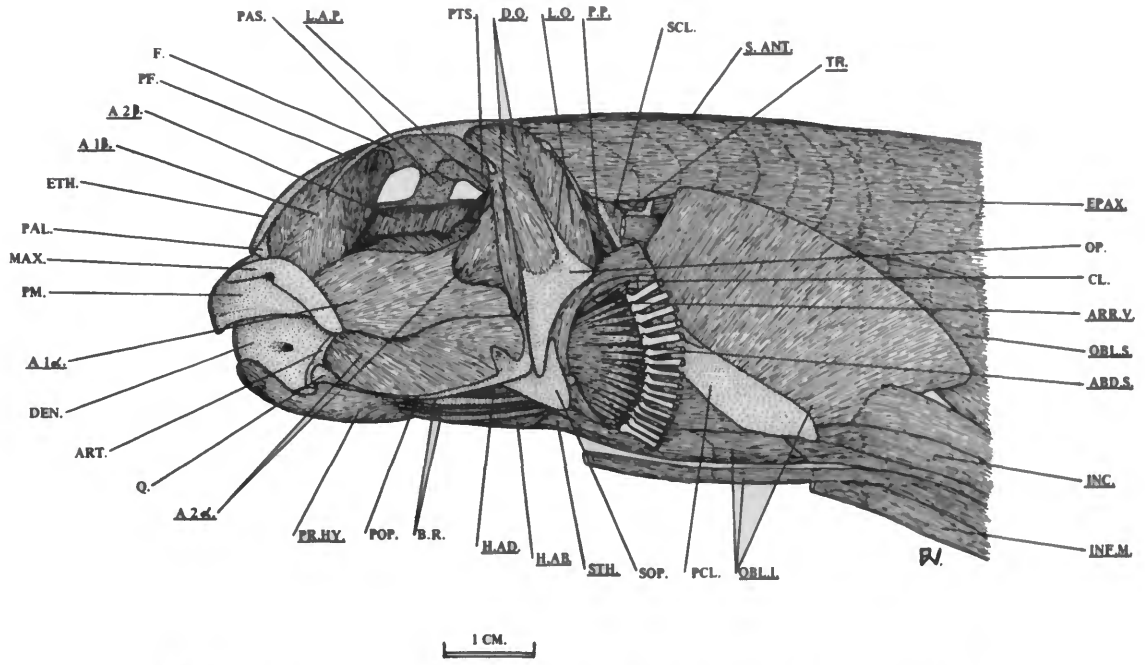
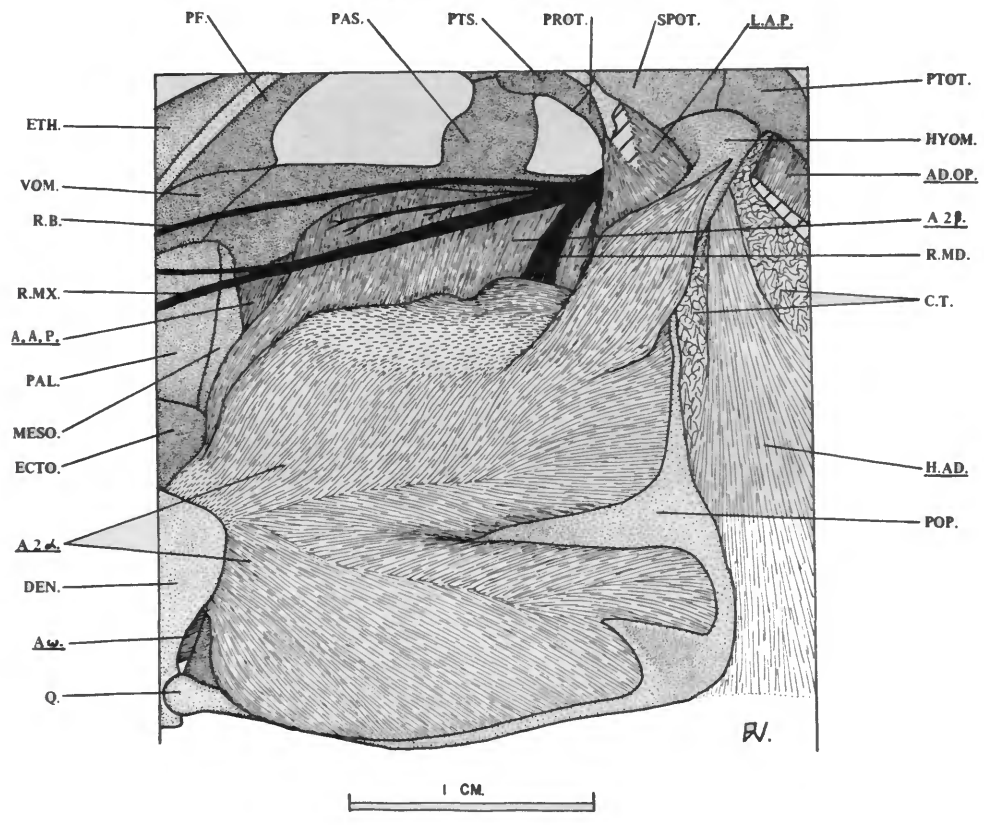


FIGURE 146.—*Lagocephalus lunaris*, ANSP 113639, 124 mm SL, left lateral view of superficial anterior musculature.

FIGURE 147.—*Lagocephalus lunaris*, ANSP 113639, 124 mm SL, left lateral view of cheek musculature after the removal of A 1.



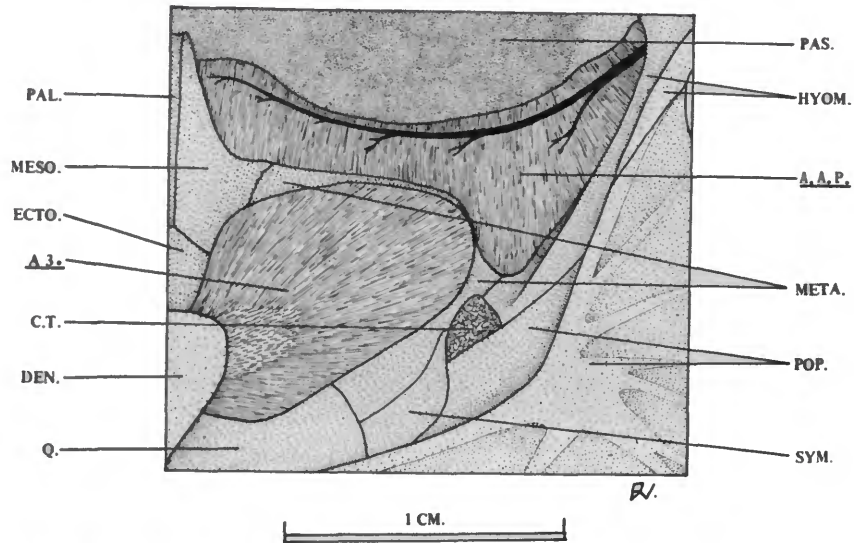


FIGURE 148.—*Lagocephalus lunaris*, ANSP 113639, 124 mm SL, left lateral view of the deep muscles of the cheek.

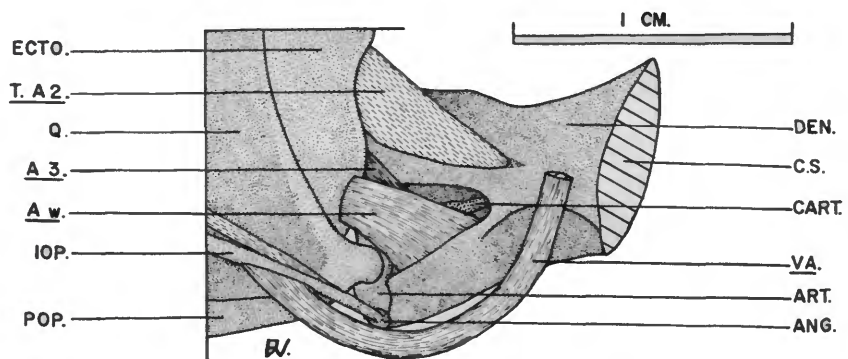


FIGURE 149.—*Lagocephalus lunaris*, ANSP 113639, 124 mm SL, medial view of articulation region of left lower jaw.

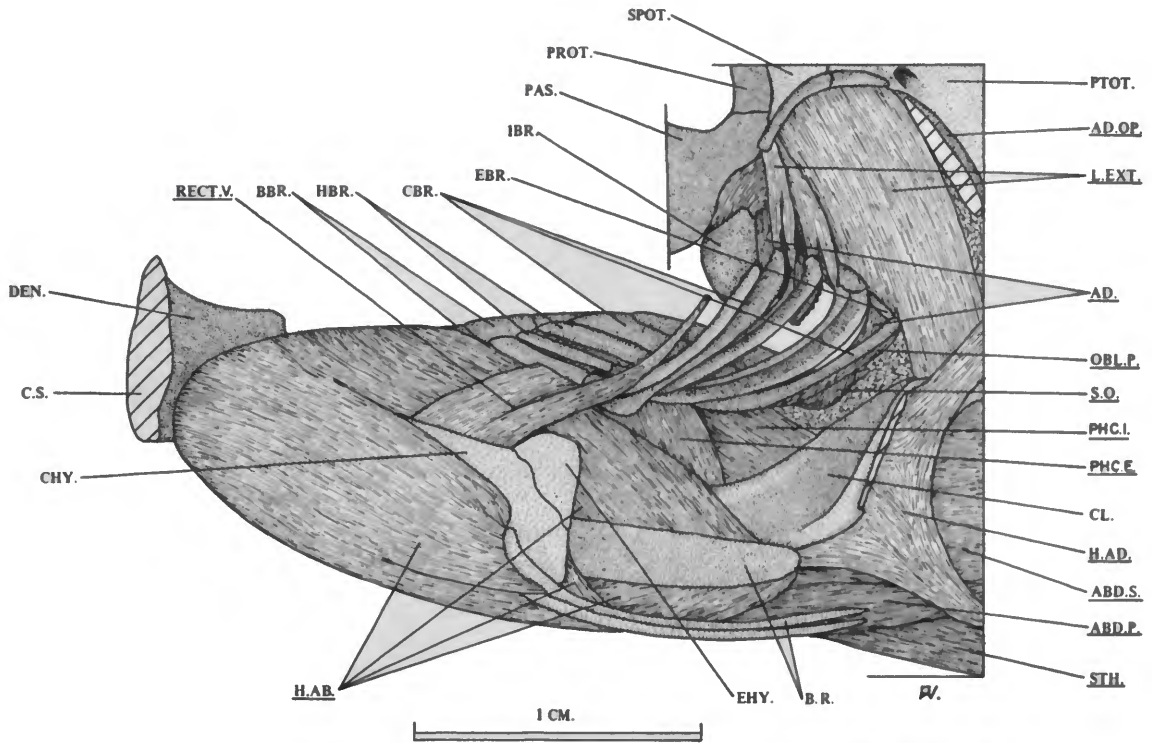
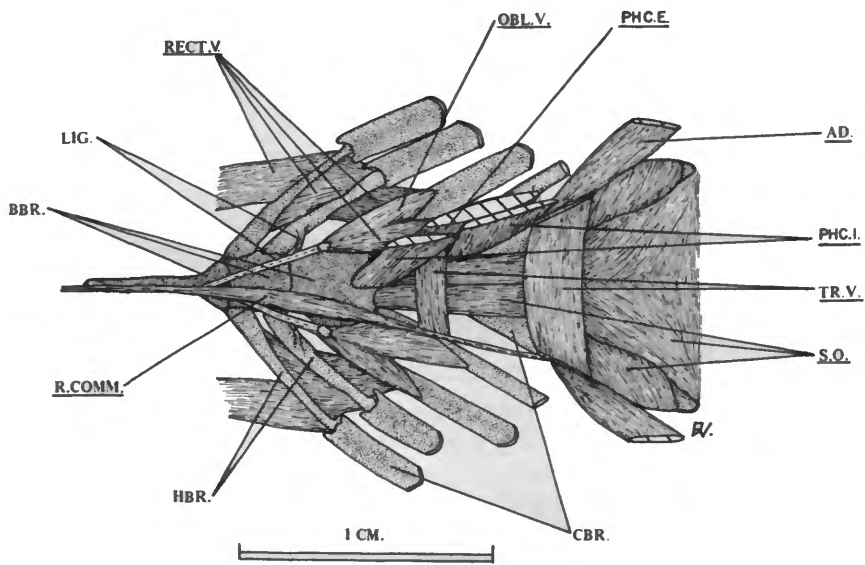


FIGURE 150.—*Lagocephalus lunaris*, ANSP 113639, 124 mm SL, left lateral view of superficial branchial and hyoid arch musculature.

FIGURE 151.—*Lagocephalus lunaris*, ANSP 113639, 124 mm SL, ventral view of branchial arch musculature.



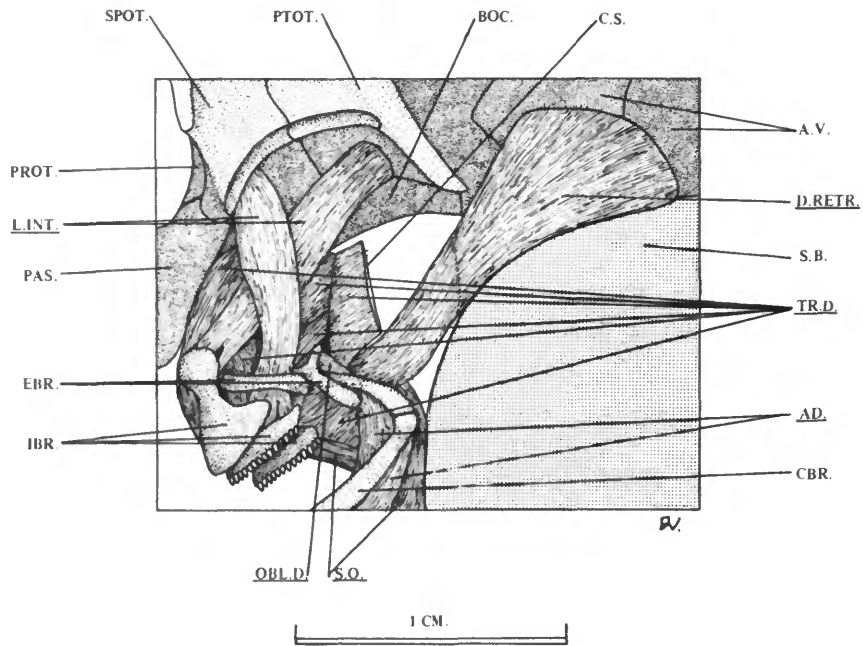
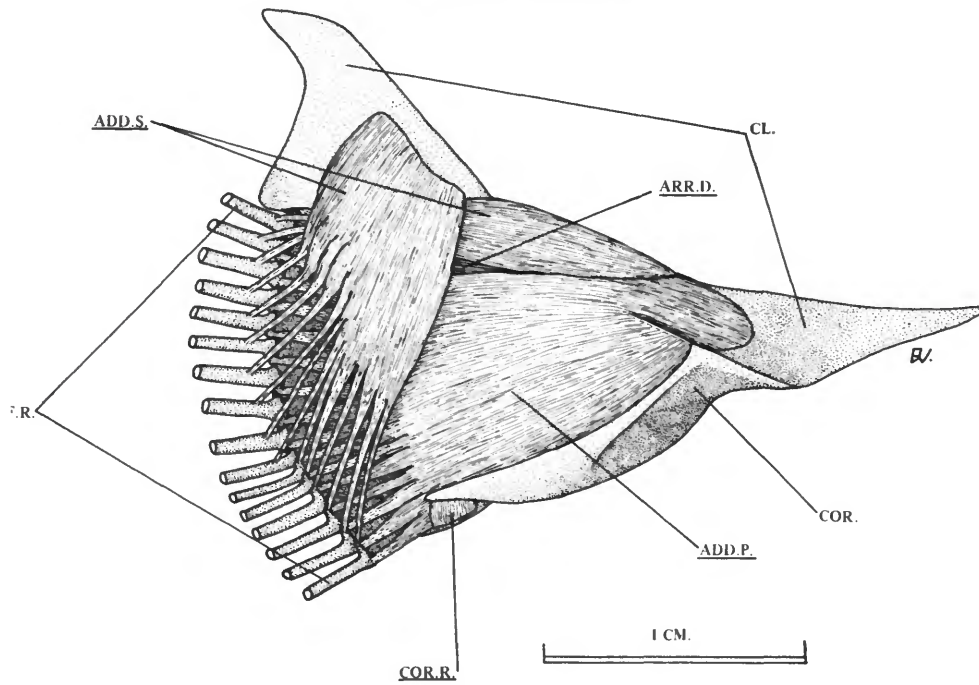


FIGURE 152.—*Lagocephalus lunaris*, ANSP 113639, 124 mm SL, left lateral view of dorsal branchial arch musculature.

FIGURE 153.—*Lagocephalus lunaris*, ANSP 113639, 124 mm SL, medial view of left pectoral girdle and associated musculature.



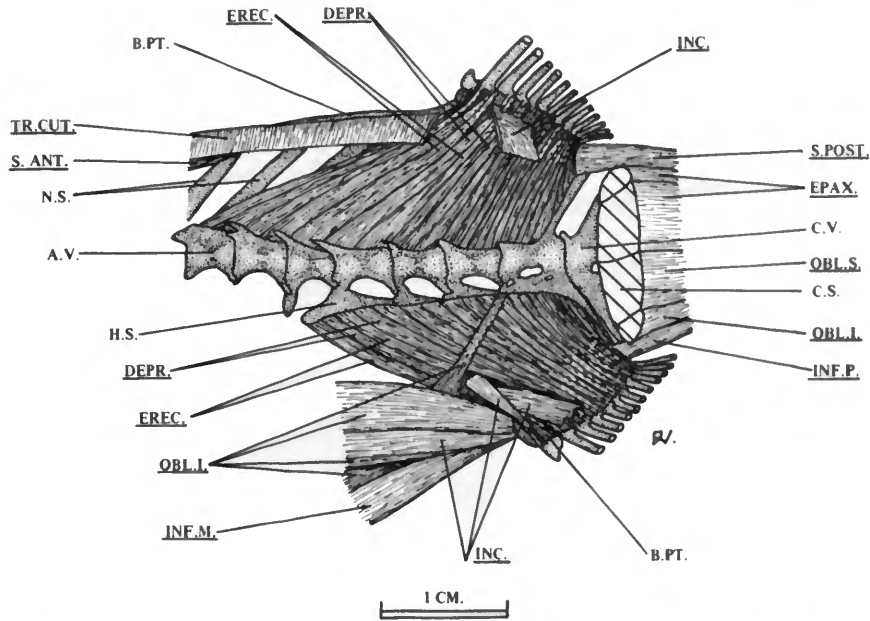


FIGURE 154.—*Lagocephalus lunaris*, ANSP 113639, 124 mm SL, left lateral view of dorsal and anal fin musculature.

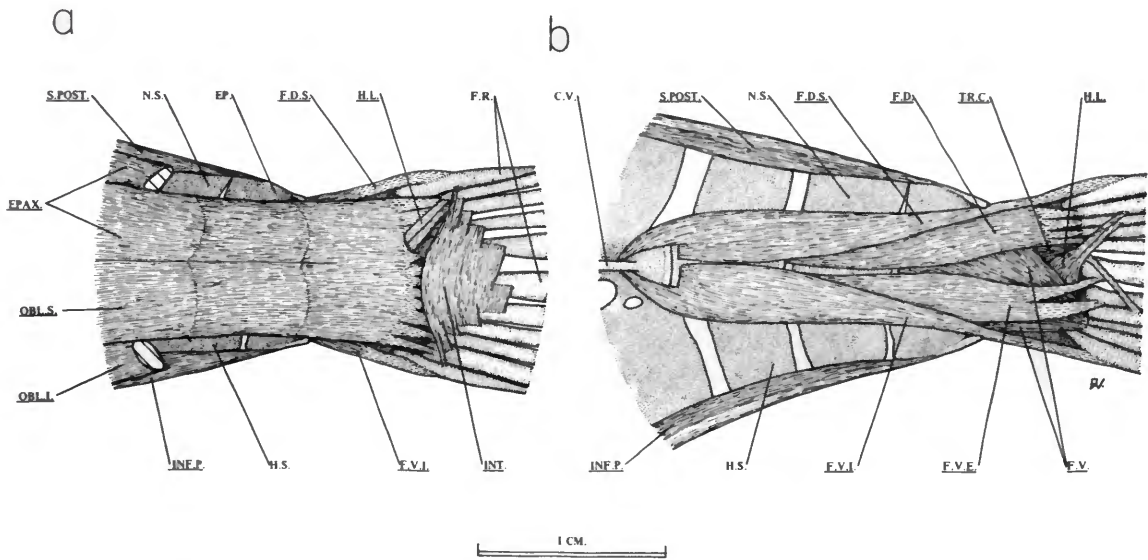


FIGURE 155.—*Lagocephalus lunaris*, ANSP 113639, 124 mm SL, left lateral view of caudal peduncle region: a, superficial musculature; b, deep musculature.



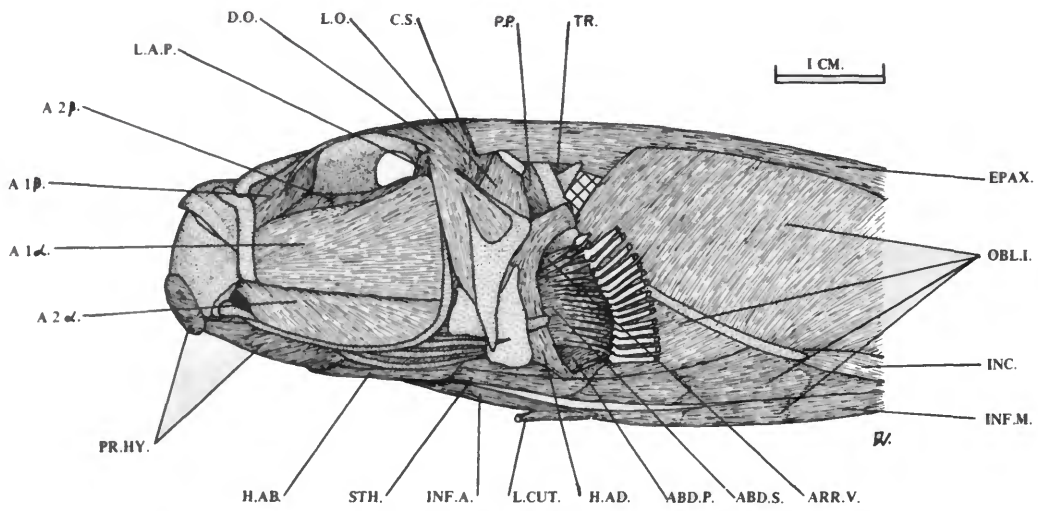


FIGURE 156.—*Amblyrhynchotes honckenii*, ANSP 117547, 106 mm SL, left lateral view of superficial anterior musculature.

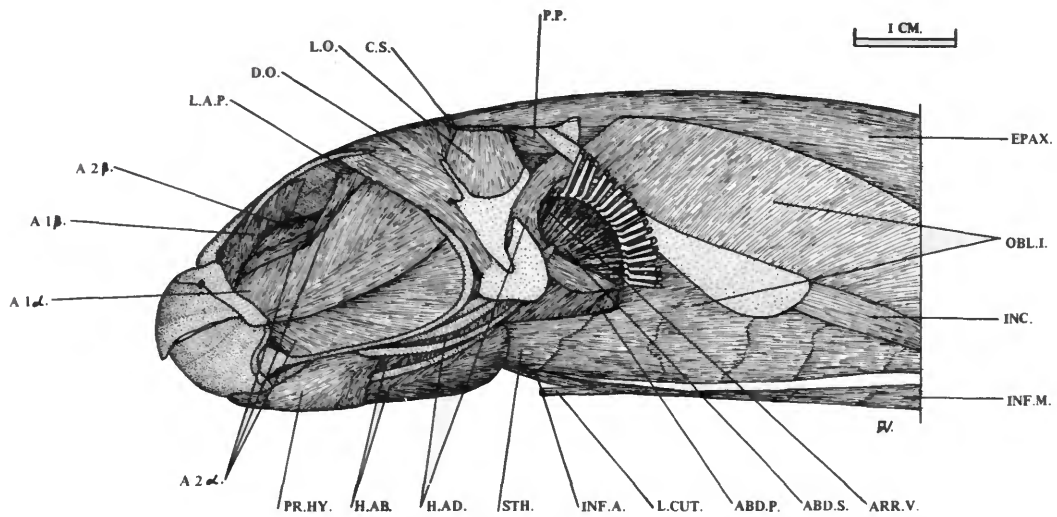


FIGURE 157.—*Colomesus psittacus*, ANSP 98887, 117 mm SL, left lateral view of superficial anterior musculature.

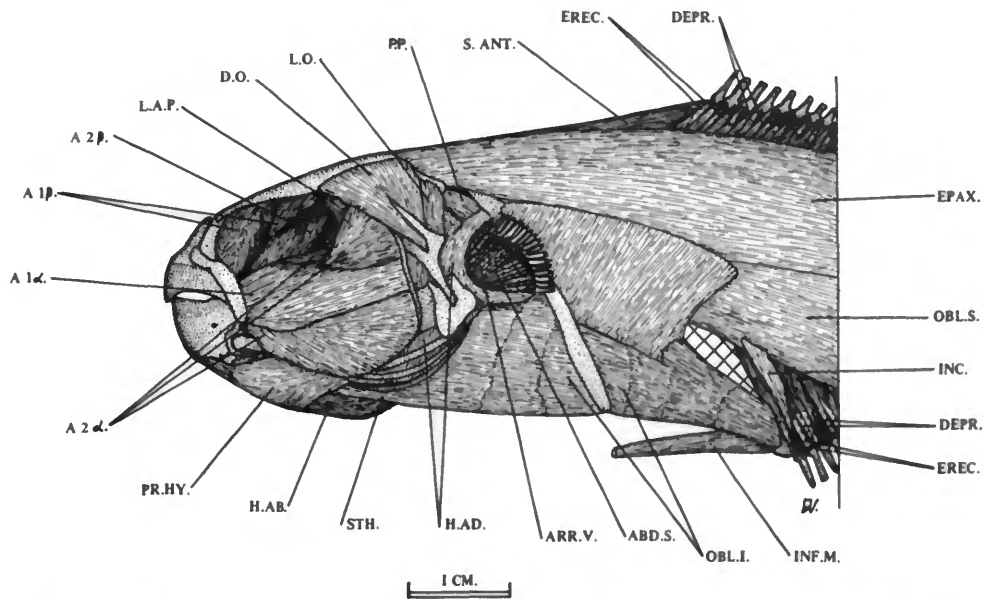


FIGURE 158.—*Xenopterus naritus*, ANSP 117495, 102 mm SL, left lateral view of superficial anterior musculature.

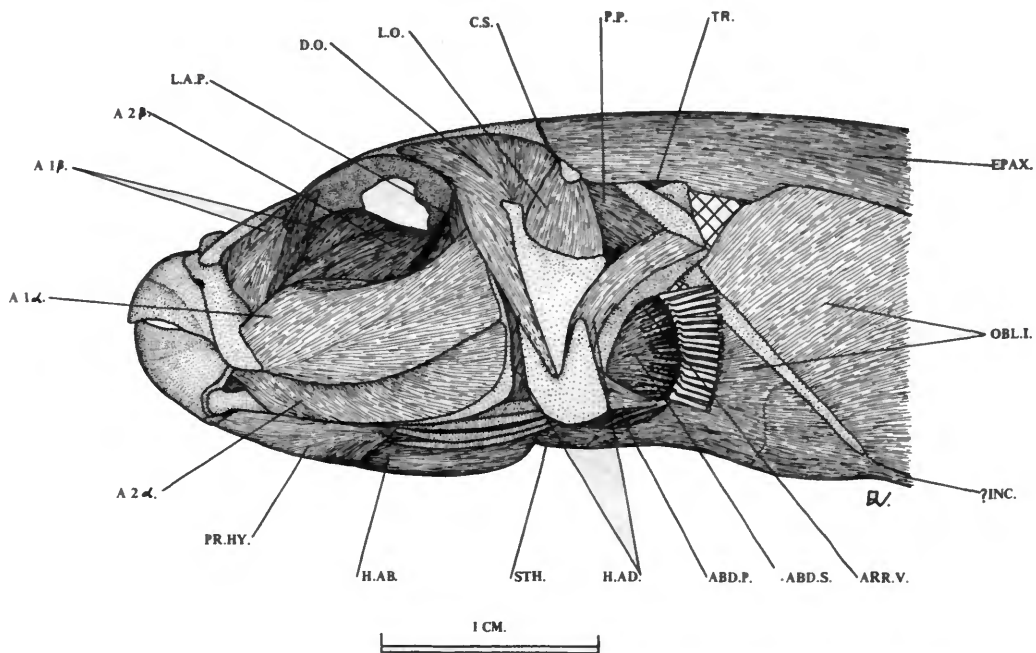


FIGURE 159.—*Arothron immaculatus*, ANSP 117528, 68 mm SL, left lateral view of superficial musculature. ("?INC" implies that the identification of these fibers as part of the inclinator (analis) system is tentative.)

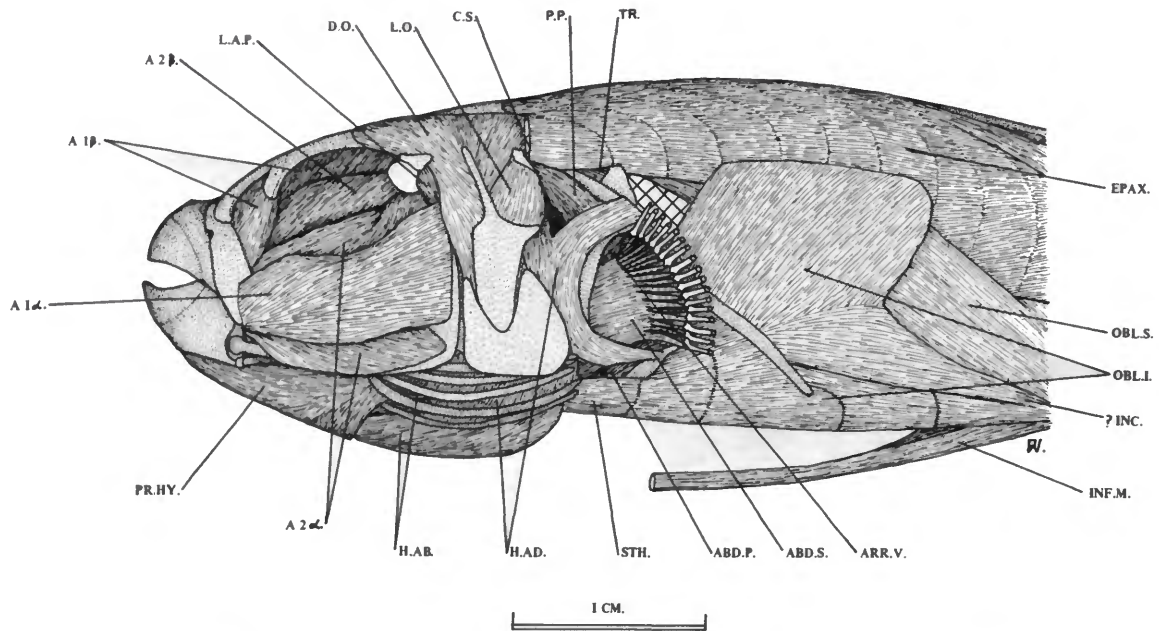


FIGURE 160.—*Tetraodon schoutedeni*, ANSP 117501, 62 mm SL, left lateral view of superficial anterior musculature. ("?INC.", as for Figure 159.)

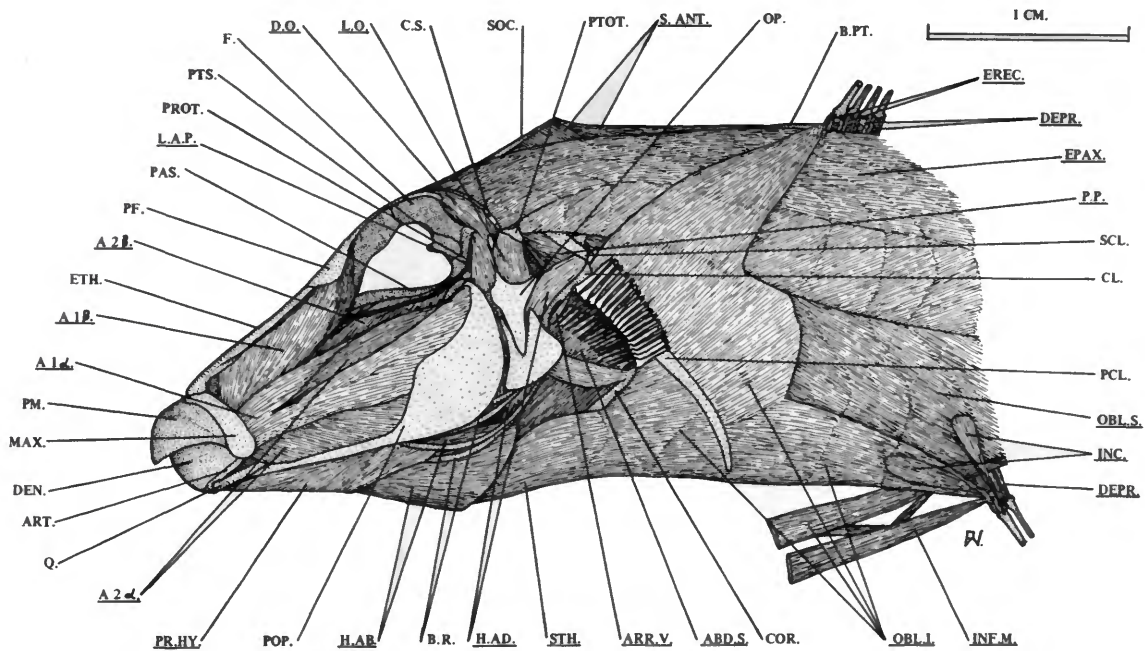


FIGURE 161.—*Canthigaster margaritatus*, ANSP 117517, 52 mm SL, left lateral view of superficial anterior musculature.

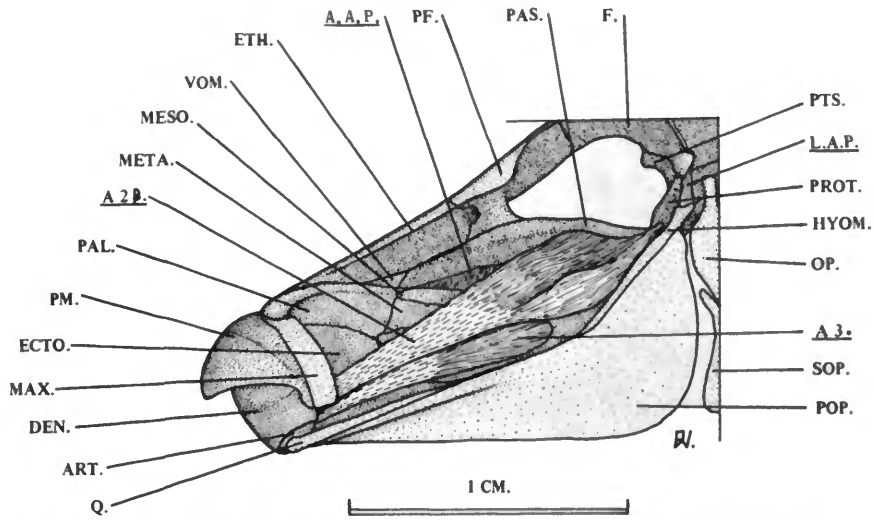
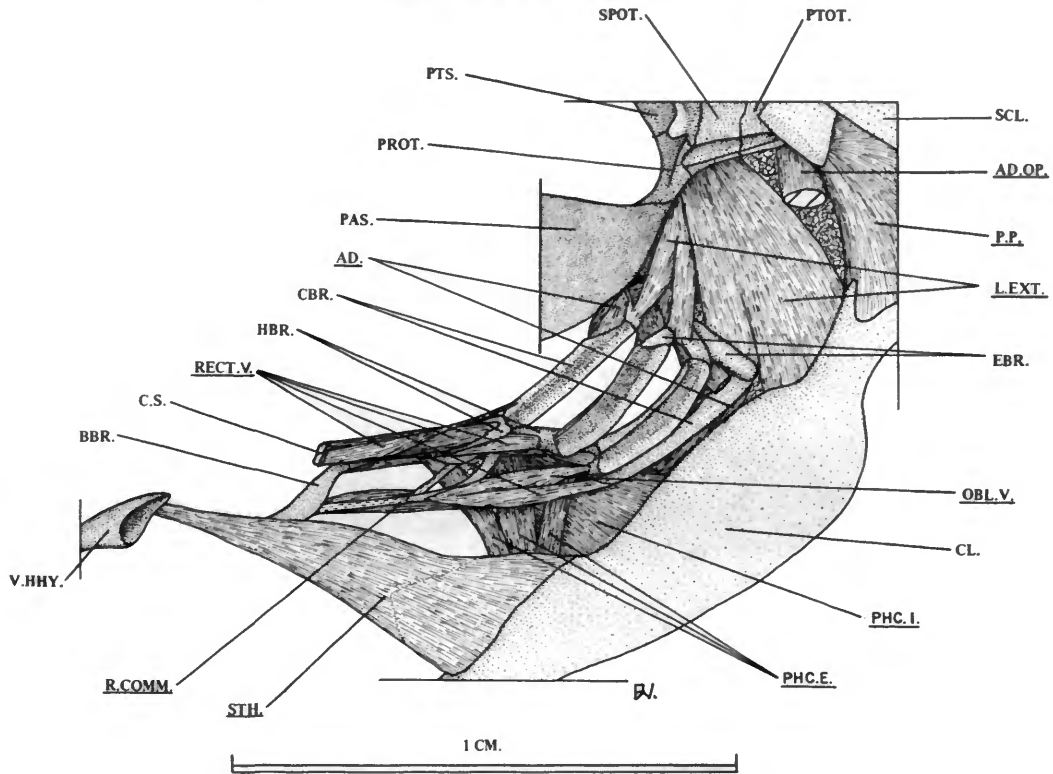


FIGURE 162.—*Canthigaster margaritatus*, ANSP 117517, 52 mm SL, left lateral view of deep muscles of the cheek.

FIGURE 163.—*Canthigaster margaritatus*, ANSP 117517, 52 mm SL, left lateral view of superficial branchial arch musculature.



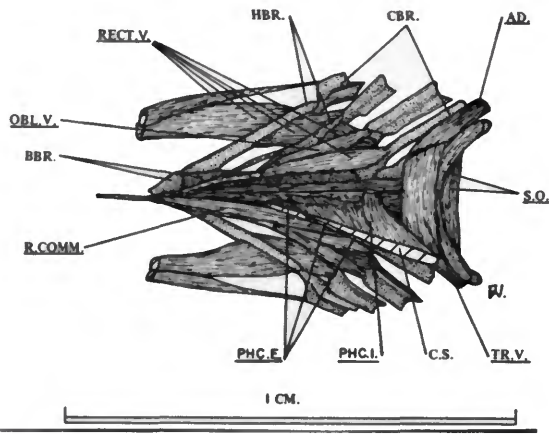


FIGURE 164.—*Canthigaster margaritatus*, ANSP 117517, 52 mm SL, ventral view of branchial arch musculature.

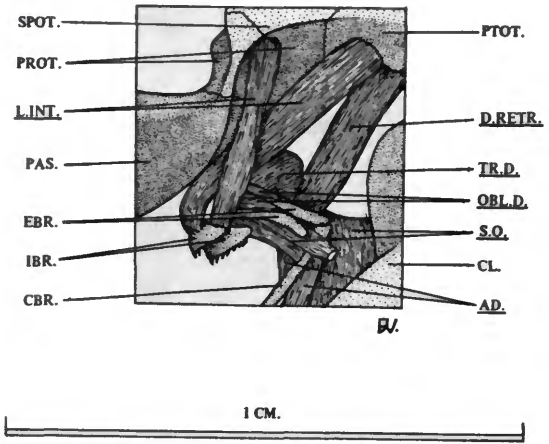


FIGURE 165.—*Canthigaster margaritatus*, ANSP 117517, 52 mm SL, left lateral view of dorsal branchial arch region. (The first infrapharyngobranchial, epibranchials 1 and 2, ceratobranchials 1-3, and the levatores externi removed.)

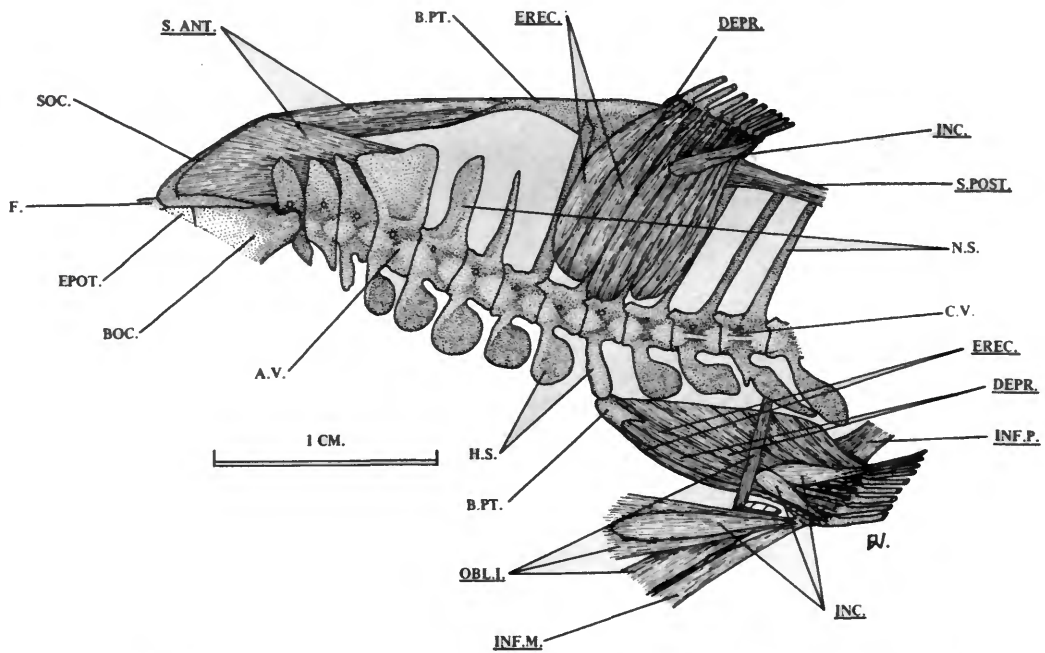


FIGURE 166.—*Canthigaster margaritatus*, ANSP 117517, 52 mm SL, left lateral view of dorsal and anal fin musculature.

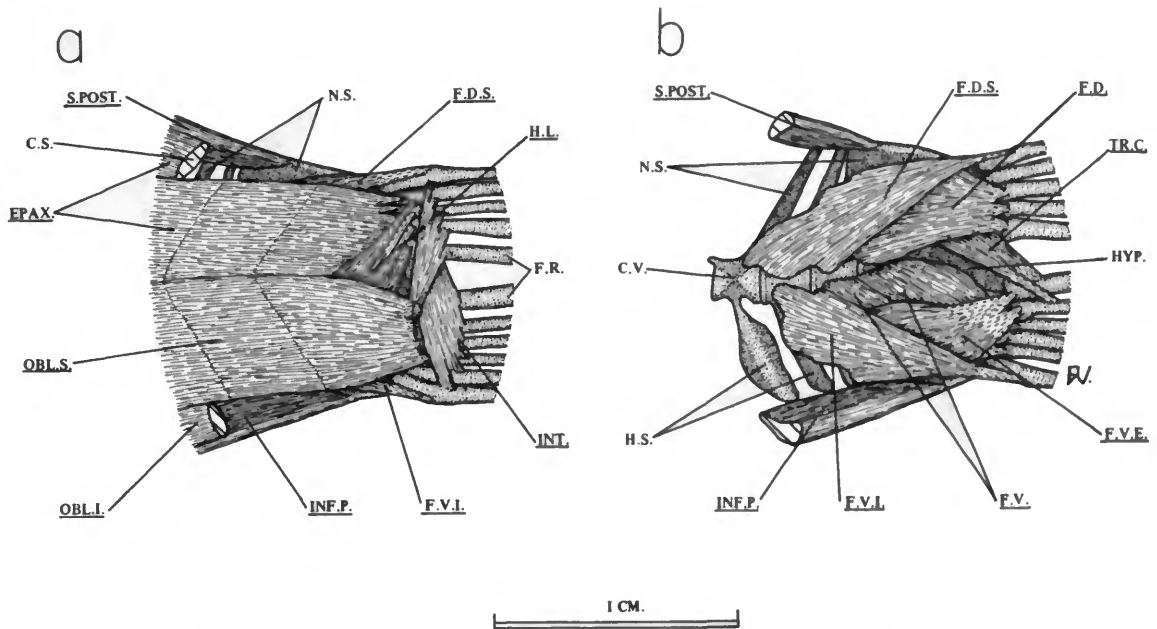
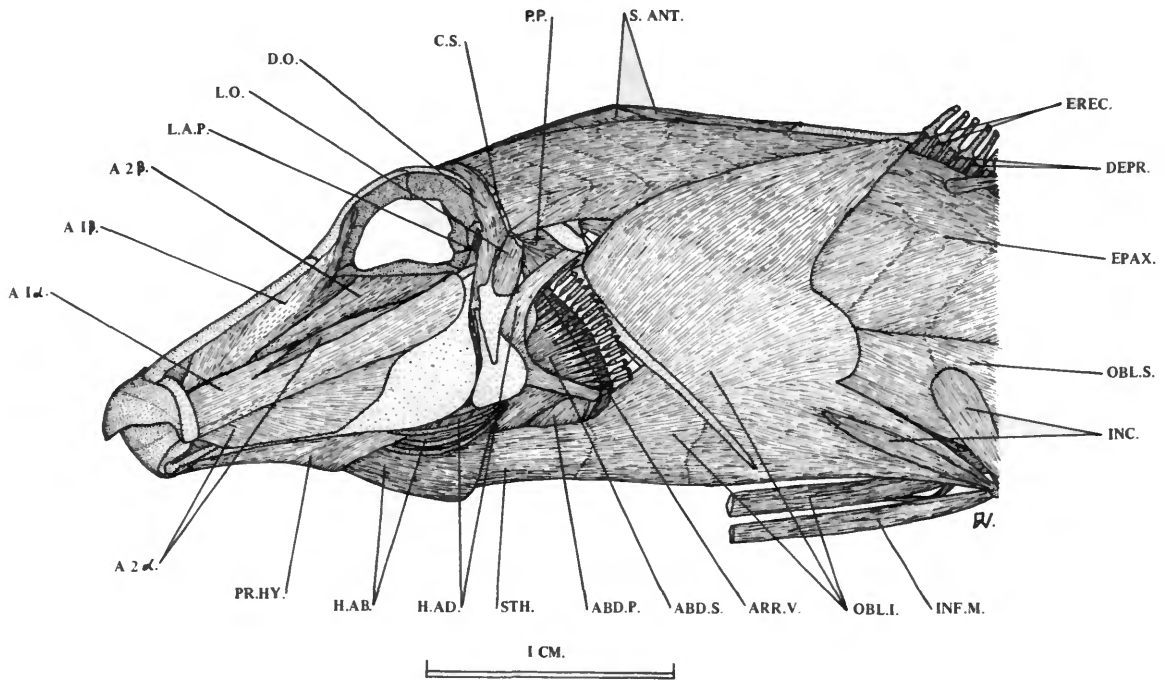


FIGURE 167.—*Canthigaster margaritatus*, ANSP 117517, 52 mm SL, left lateral view of caudal peduncle region: a, superficial musculature; b, deep musculature.

FIGURE 168.—*Canthigaster valentini*, ANSP 117534, 45 mm SL, left lateral view of superficial anterior musculature.



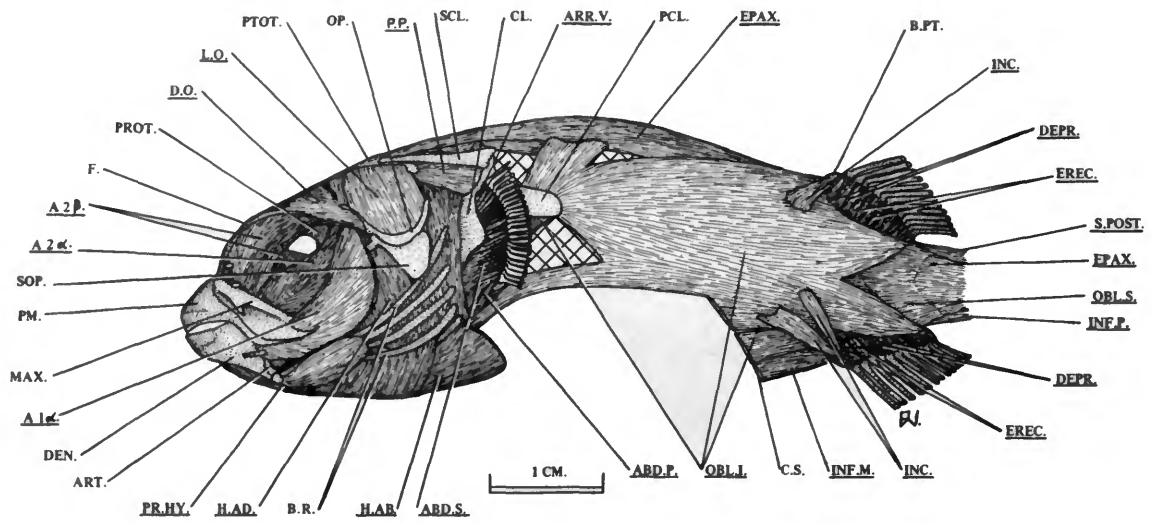


FIGURE 169.—*Diodon hystrix*, NMC 68-997, 77 mm SL, left lateral view of superficial anterior musculature.

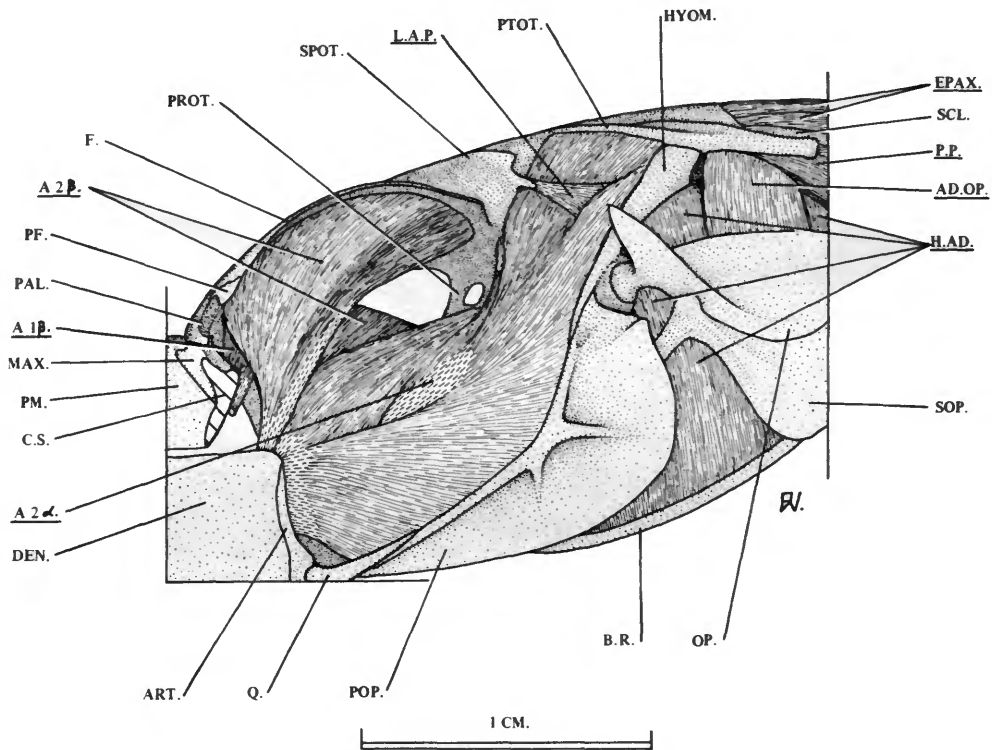


FIGURE 170.—*Diodon hystrix*, NMC 68-997, 77 mm SL, left lateral view of the deep muscles of the cheek.

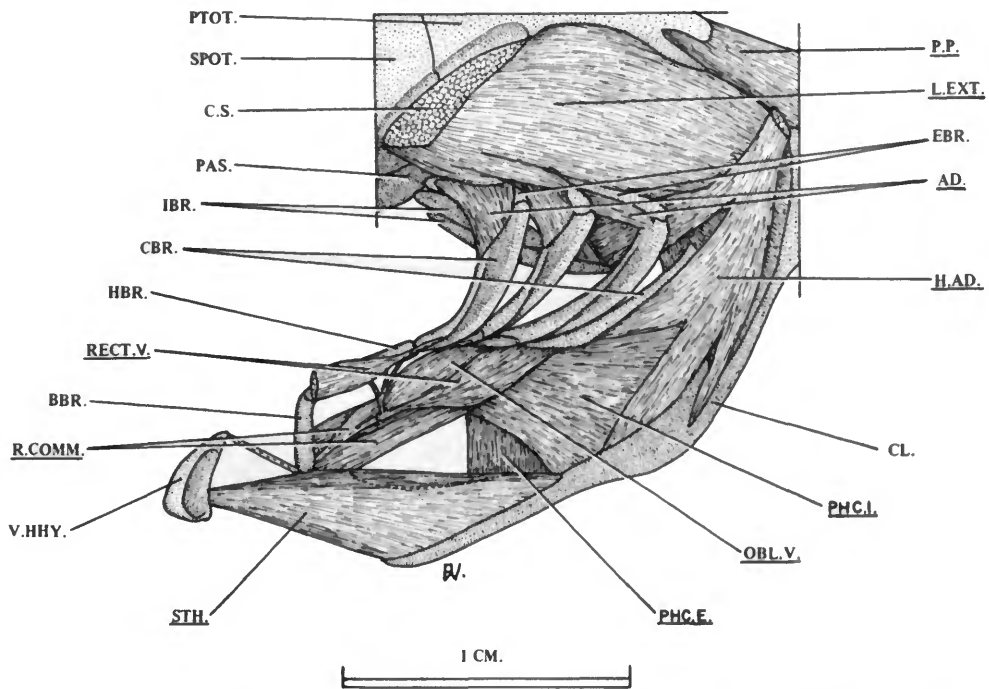


FIGURE 171.—*Diodon hystrix*, NMC 68-997, 77 mm SL, left lateral view of superficial branchial arch musculature.

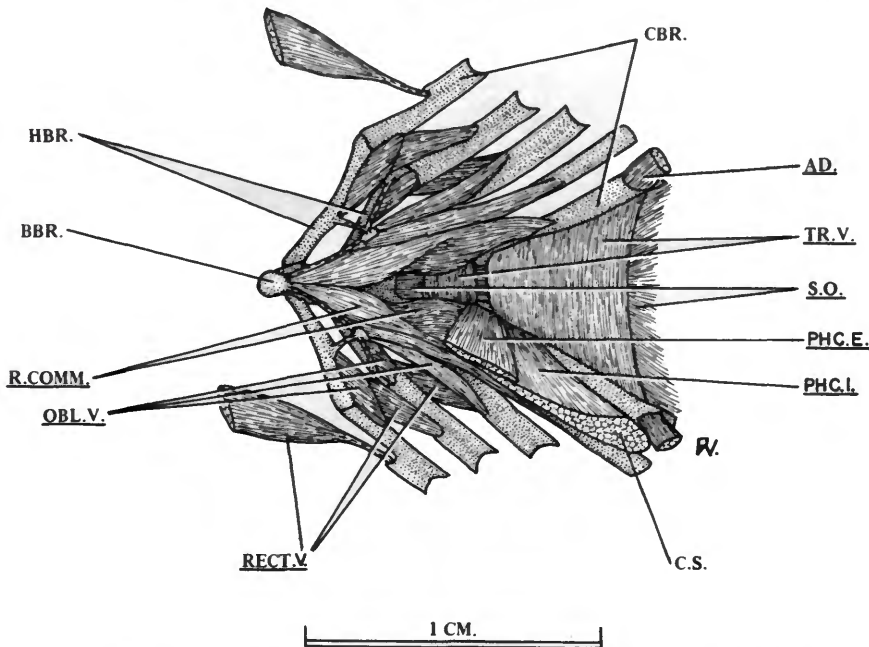


FIGURE 172.—*Diodon hystrix*, NMC 68-997, 77 mm SL, ventral view of branchial arch musculature.



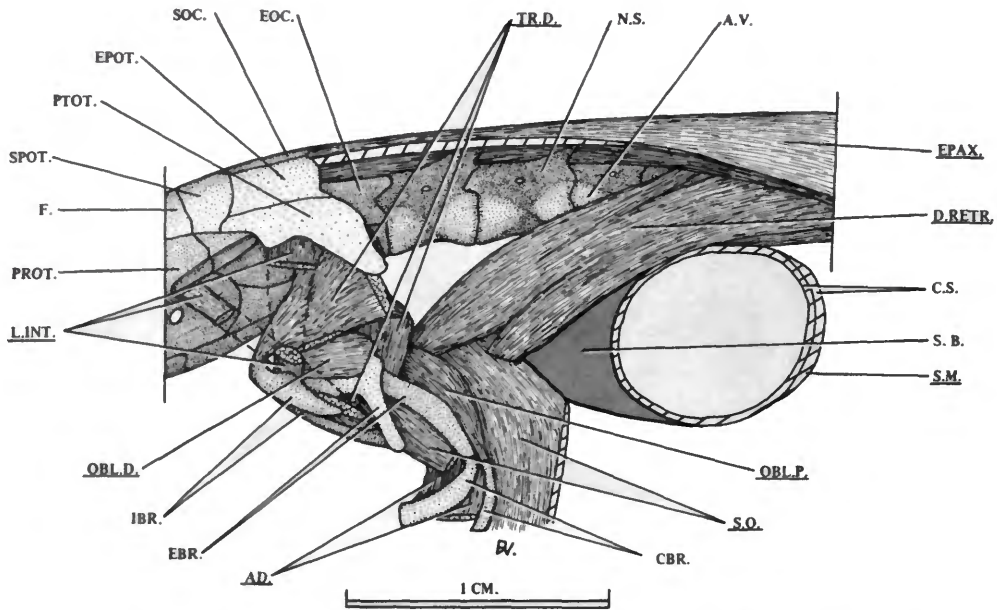


FIGURE 173.—*Diodon hystrix*, NMC 68-997, 77 mm SL, left lateral view of dorsal branchial arch musculature. (Epibranchials 1 and 2, ceratobranchials 1-3, and the levatores externi removed.)

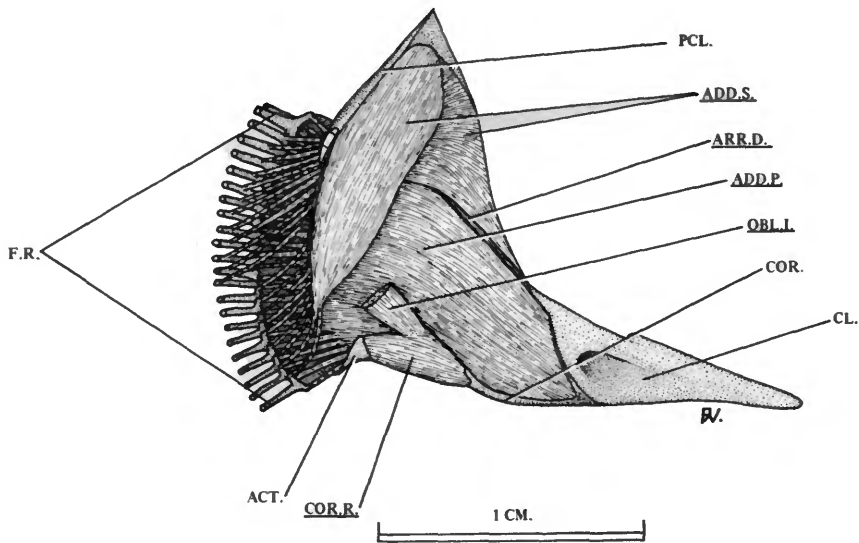


FIGURE 174.—*Diodon hystrix*, NMC 68-997, 77 mm SL, medial view of left pectoral girdle and associated musculature.

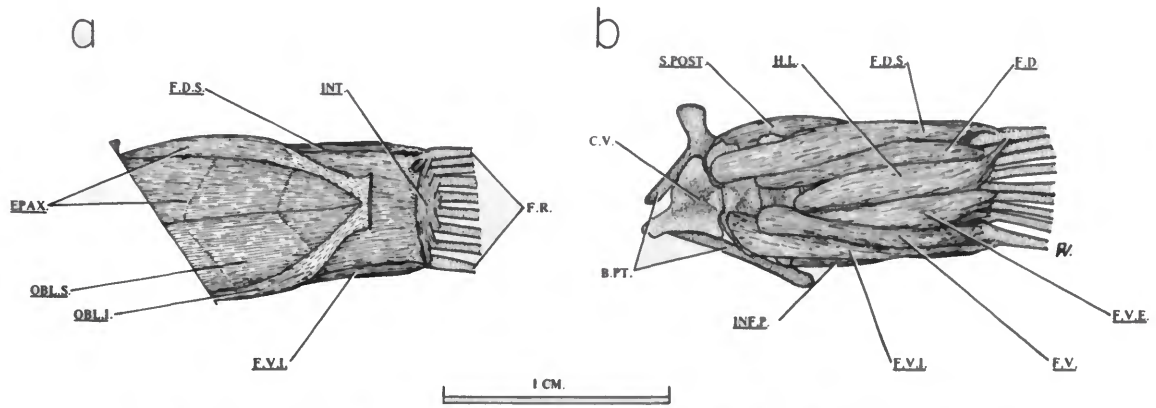


FIGURE 175.—*Diodon hystrix*, NMC 68-997, 77 mm SL, left lateral view of caudal peduncle: a, superficial musculature; b, deep musculature.

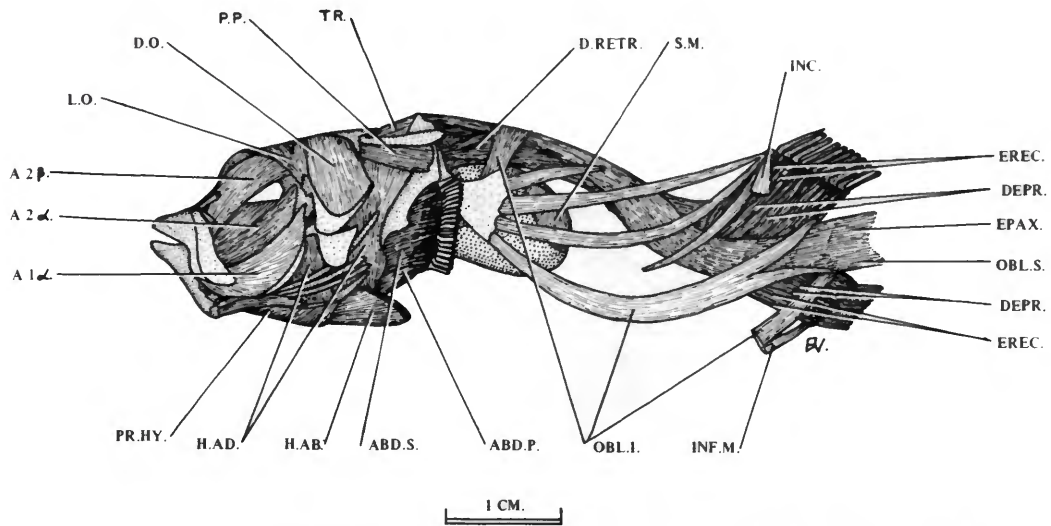


FIGURE 176.—*Chilomycterus orbicularis*, ANSP 117510, 80 mm SL, left lateral view of superficial anterior musculature.

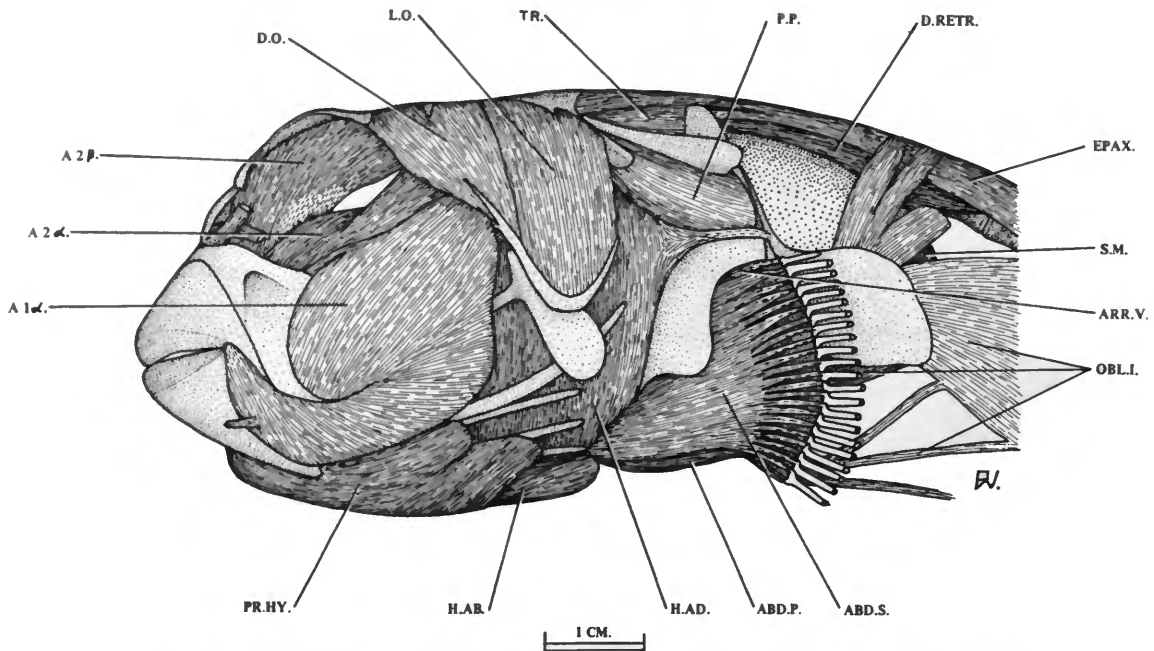
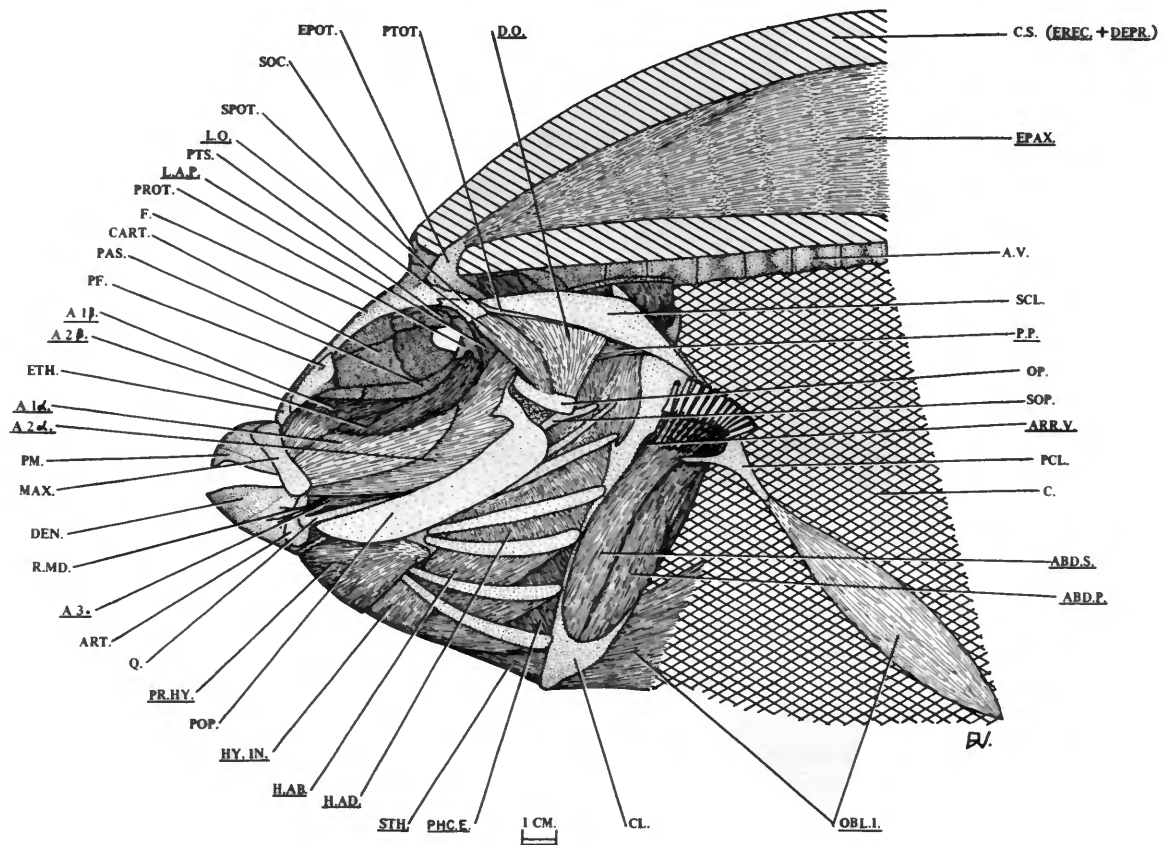


FIGURE 177.—*Chilomycterus schoepfi*, ANSP 117518, 138 mm SL, left lateral view of superficial anterior musculature.

FIGURE 178.—*Mola mola*, BM (NH) 1938.6.23.38, 287 mm SL, left lateral view of superficial anterior musculature.



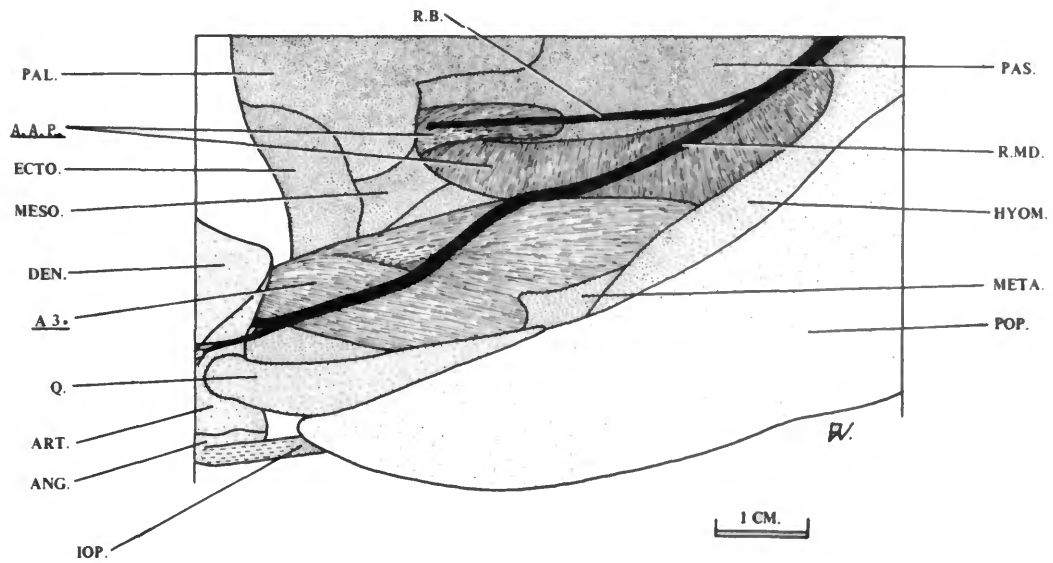
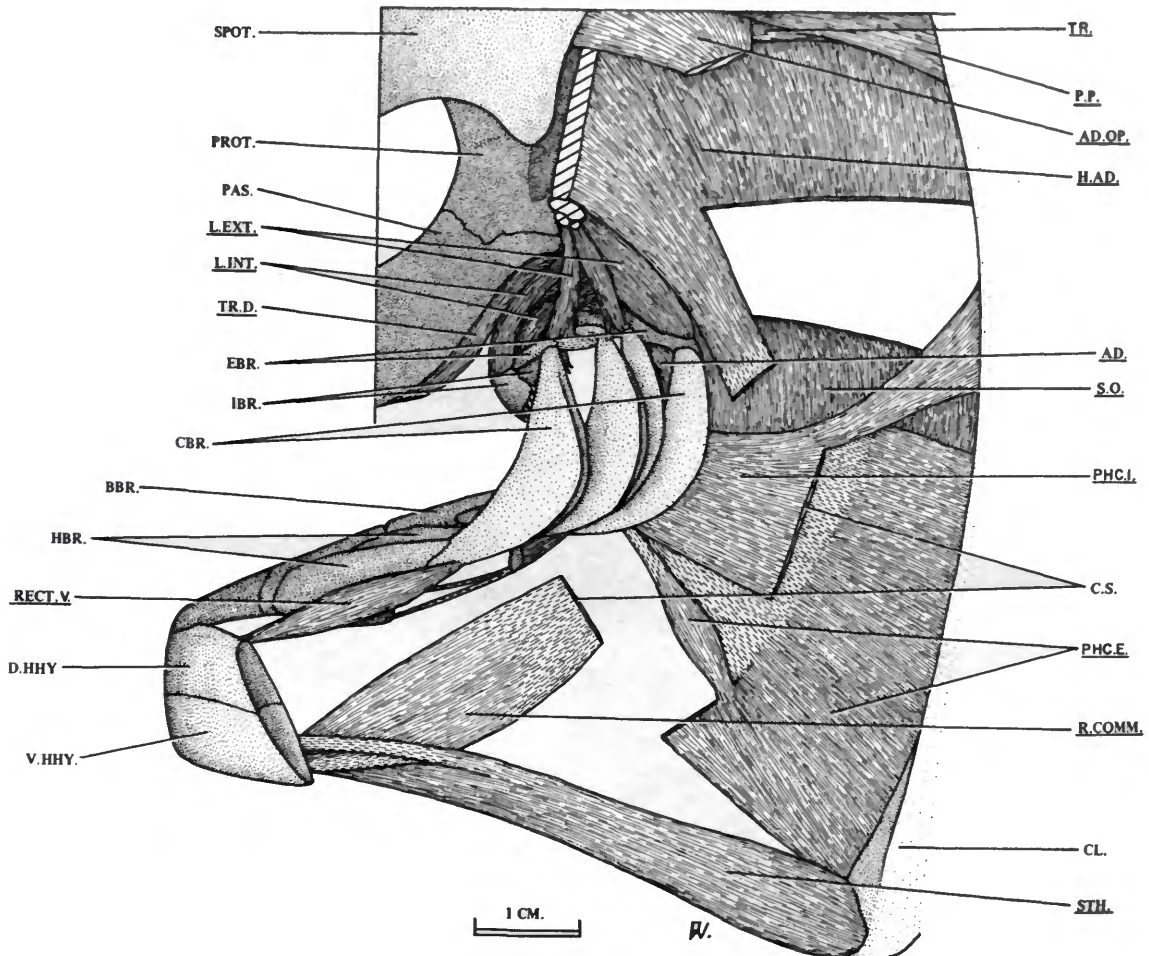


FIGURE 179.—*Mola mola*, BM (NH) 1938.6.23.38, 287 mm SL, left lateral view of the deep muscles of the cheek.

FIGURE 180.—*Mola mola*, BM (NH) 1938.6.23.38, 287 mm SL, left lateral view of superficial branchial arch musculature.



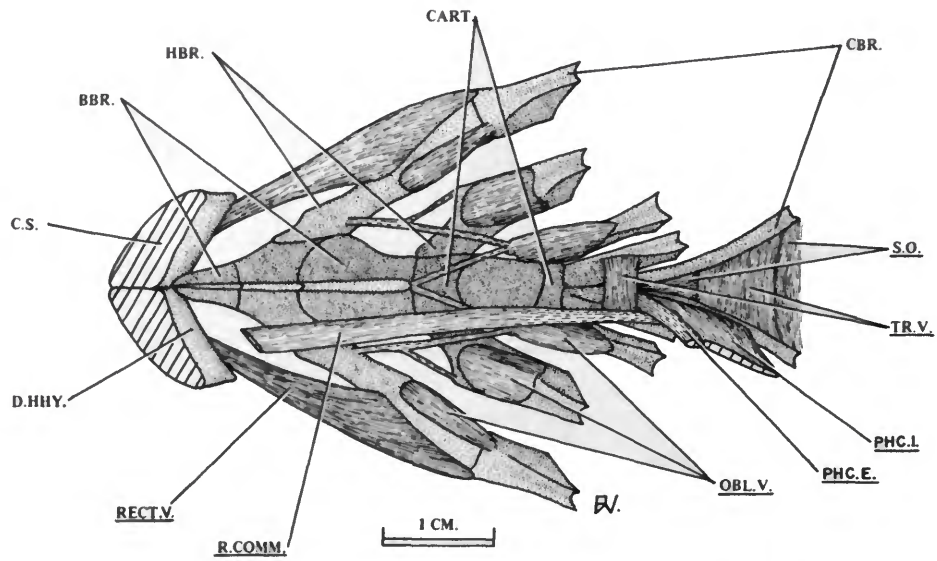


FIGURE 181.—*Mola mola*, BM (NH) 1938.6.23.38, 287 mm SL, ventral view of branchial arch musculature.

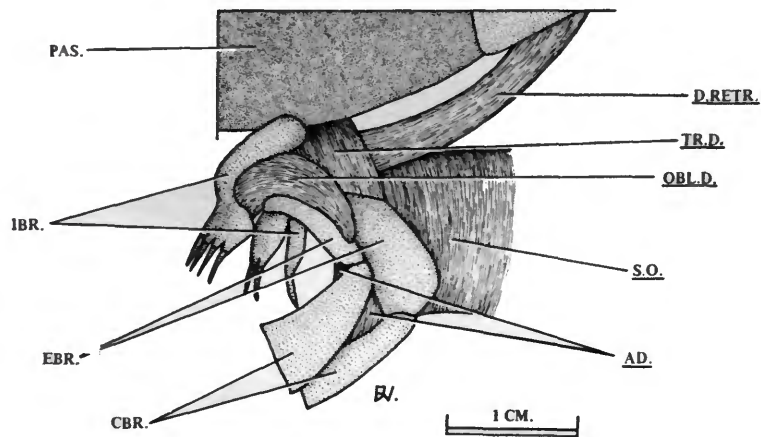


FIGURE 182.—*Mola mola*, BM (NH) 1938.6.23.38, 287 mm SL, left lateral view of dorsal branchial arch musculature. (Epibranchials 1 and 2, ceratobranchials 1-3, and the levatores externi and interni removed.)

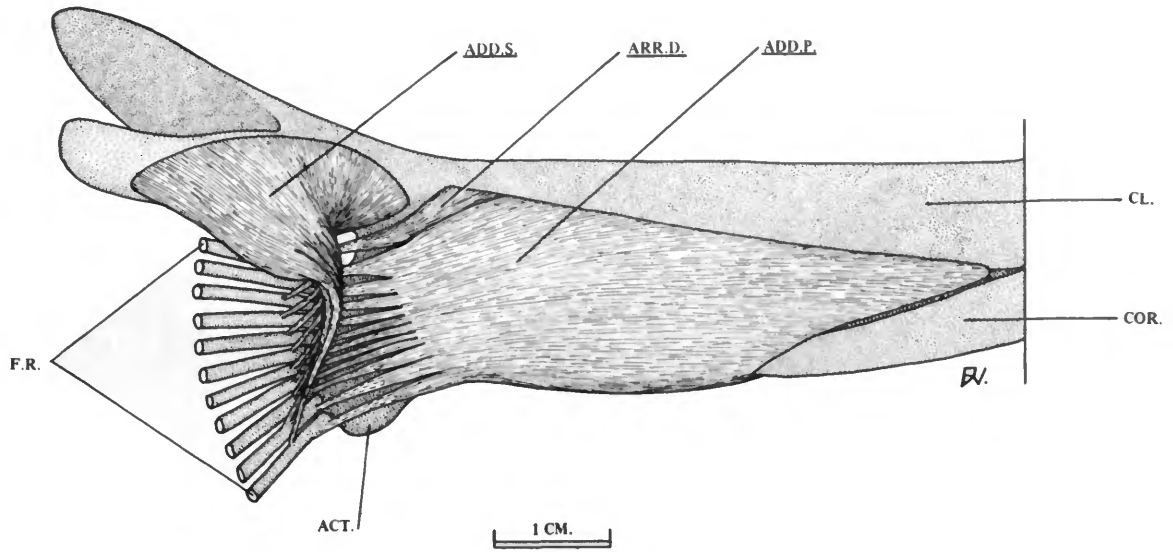
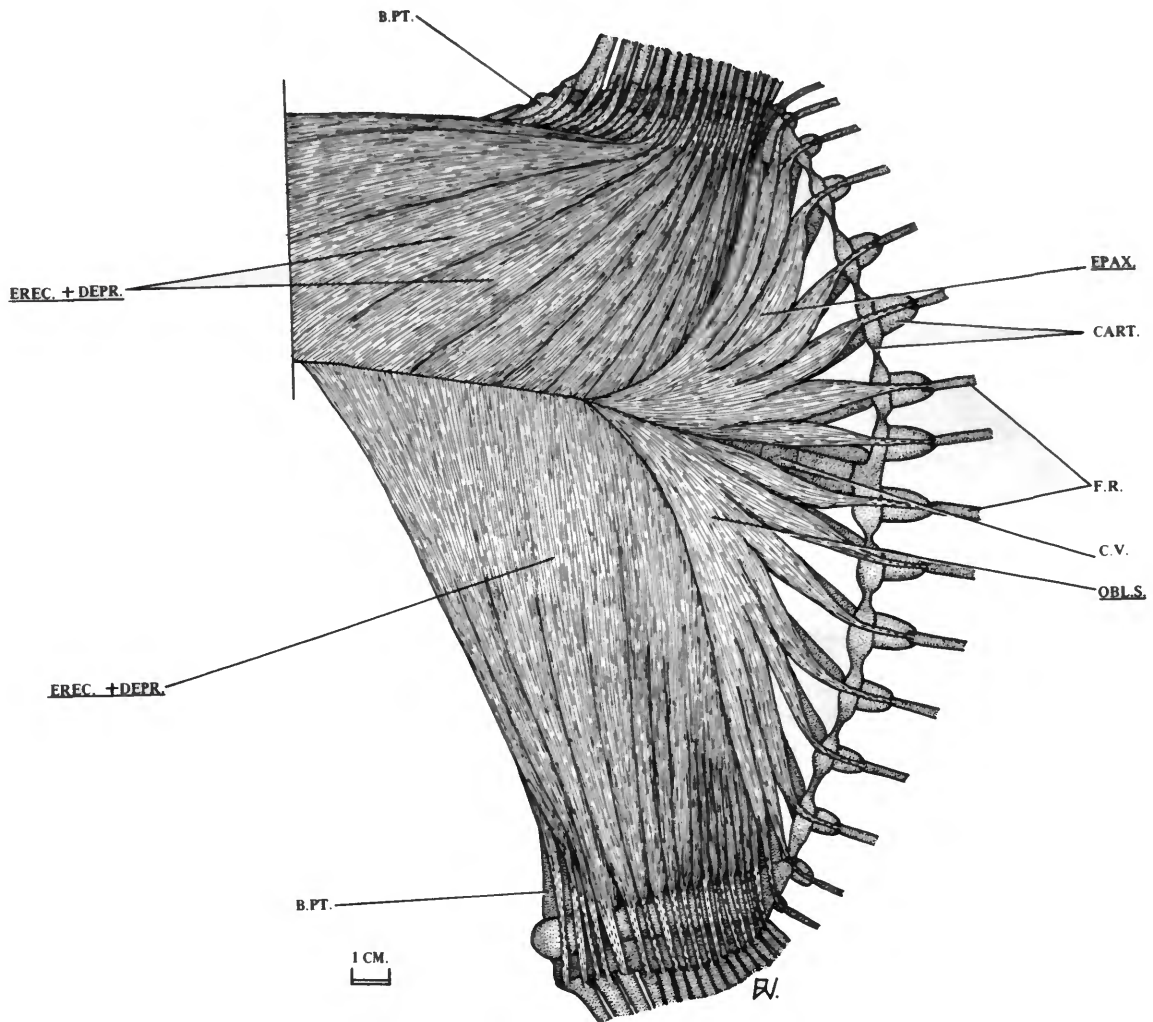


FIGURE 183.—*Mola mola*, BM (NH) 1958.6.23.58, 287 mm SL, medial view of left pectoral girdle and associated musculature.



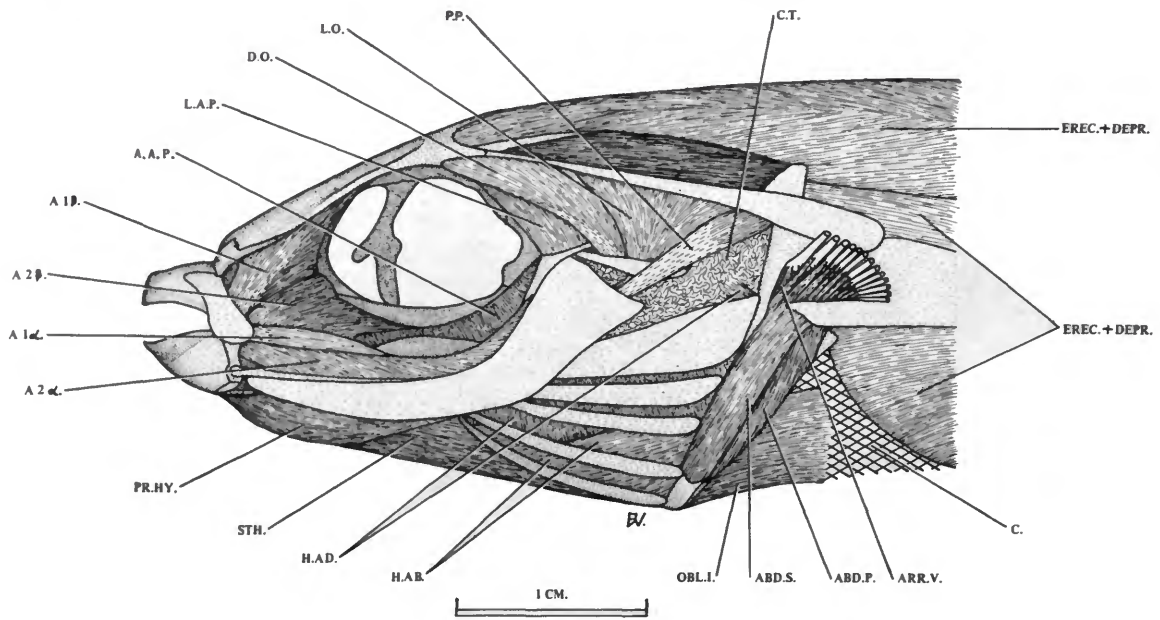


FIGURE 185.—*Ranzania laevis*, ANSP 106723, 93 mm SL, left lateral view of superficial anterior musculature.

← FIGURE 184.—*Mola mola*, BM (NH) 1938.6.23.38, 287 mm SL, left lateral view of dorsal, anal, and caudal fin musculature.









## Publication in *Smithsonian Contributions to Zoology*

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