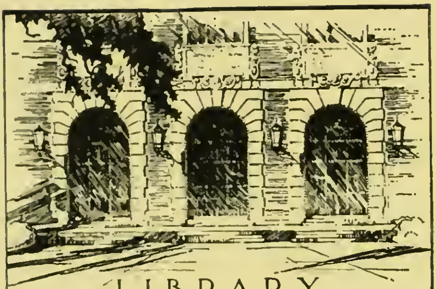

The Comparative Osteology and Phylogeny of the Anabantoidei (Teleostei, Pisces)

KAREL F. LIEM

ILLINOIS BIOLOGICAL MONOGRAPHS: *Number 30*

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CONTENTS

INTRODUCTION

The anabantoid fishes have been grouped with the ophicephalid fishes in a separate order Labyrinthici by many early workers: Day (1876), Regan (1909), Weber and de Beaufort (1922), Jordan (1923), Deraniyagala (1929), Gregory (1933), and Smith (1945). Boulenger (1904) did not recognize the order Labyrinthici, but placed the family Anabantidae in the order Percesoces whereas the families Osphronemidae and Luciocephalidae were included in the order Perciformes. Berg (1940 and 1958) made radical changes in the systematics of the anabantoid fishes, placing the ophicephalids in a separate order Ophicephaliformes whereas the anabantoids and luciocephalids were classified as two separate suborders of the order Perciformes. Recent authors, for example Forselius (1957), Bertin and Arambourg (1958), Darlington (1957), and Herald (1961) tend to follow Berg's classification, although most of our knowledge of the taxonomy of the anabantoids is based on the monographs of Weber and de Beaufort (1922), Boulenger (1916), and Barnard (1943). Further knowledge has gradually accumulated through faunal studies, nomenclatural revisions, or reports on isolated collections, for example Day (1876), Regan (1909), Myers (1923 and 1926), Herre (1924), Deraniyagala (1929), Prashad and Mukerji (1929), Shih (1936), Krull (1939), Smith (1945), Nichols (1943), and Tweedie (1952).

The only osteological studies available are incomplete and scattered. Gill (1893) figured and discussed the hyobranchial apparatus of *Osphronemus goramy,* and Gregory (1933), with some inaccuracies, the skulls of *Anabas* and *Osphronemus.* Berg (1958) presents a lateral view of the skull of *Anabas,* and Schneider (1941) a lateral view of the neurocranium of *Macropodus* in her discussion on hearing in anabantids. Zograff (1888), Henninger (1908), and Bader (1937) studied the comparative morphology of the "labyrinth organ" in great detail. The functional anatomy of the pelvic girdle of *Trichogaster* is discussed by Steinbach (1950). Marathe (1959) has described the cranial osteology of *Trichogaster trichopterus.* Starks (1926) studied the ethmoid region in *Anabas* and *Ophicephalus.* The osteology of the Ophicephaliformes has been studied in great detail by Day (1914), Bhimachar (1932), and Srinivasachar (1955).

The objectives of this study may then be stated as follows:

1. To present an illustrated description of the osteology of the repre-

sentative families, subfamilies, and genera of the anabantoids. The illustrations will supply future students of both recent and fossil acanthopteran fishes with a basis for comparison.

2. To reclassify the supergeneric groups of anabantoid fishes into well-defined families and subfamilies on osteological grounds.
3. To postulate the phylogeny of the anabantoids in the light of osteological evidence, fossil records, and zoogeography.
4. To analyze evolutionary trends in several morphological units of the anabantoids and their adaptive significance.
5. To redefine the suborder Anabantoidei and to reallocate *Luciocephalus*.
6. To compare the Anabantoidei, Ophicephaliformes, and Luciocephaloidei.

In the absence of large series of specimens, a revision of taxonomy at the specific level has not been attempted, but a basis for anabantoid phylogeny and classification has been proposed for future workers in teleost morphology, physiology, and ethology.

The phylogenetic position of the Anabantoidei and Luciocephaloidei in relation to the other members of the Perciformes remains problematical.

Material and Methods

Detailed studies of the osteology were confined to a total of 123 specimens belonging to 26 representative species of 14 genera (Table 1). *Malpulutta, Parasphaerichthys,* and *Parosphromenus* have been described from a very limited number of specimens and are the only genera not available for osteological studies. The absence of these three genera does not seriously limit phylogenetic considerations since they are closely related and seemingly very similar to other genera adequately represented. All specimens have been cleared and the bones and calcified cartilage stained with sodium alizarin sulfonate (Davis and Gore, 1936). Radiographs of several specimens have also been made. The specimens were dissected and disarticulated under a stereoscopic microscope. The drawings were made freehand at successive stages of dissection, taking great care to show correct proportions.

The nomenclature for the skull bones is that of Harrington (1955) and Devillers (1958). To facilitate the descriptions and illustrations the skull has been subdivided into two highly arbitrary divisions: the neurocranium and branchiocranium, as defined by Gregory in 1933. The nomenclature of Merriman (1940) has been followed for the postcranial axial skeleton and pectoral girdle. The homology and terminology for the different processes of the pelvic girdle are based on Shelden (1937) and Sewertzoff (1934). Of these, the later proved the most useful.

Table 1. List of Specimens Studied.

Taxa	Museum[a] number	Locality	Number of specimens
Anabantidae			
Anabas testudineus (Bloch)	UIMNH	?	8
“	MZB 311	Celebes	2
“	MZB 318	Java	1
Ctenopoma muriei (Blgr.)	SNHM 51345	Uganda	2
Ctenopoma multispinis (Peters)	RUDI	Victoria Falls	3
Sandelia bainsii (Castelnau)	RUDI	S. Africa	3
“	TVM 8742	S. Africa	2
Sandelia capensis (Cuv. & Val.)	USZI	S. Africa	4
“	RUDI	S. Africa	6
“	TVM 19821	S. Africa	2
Osphronemidae			
Osphronemus goramy Lacépède	MZB 433	Java	1
Helostomatidae			
Helostoma temmincki Cuv.	MZB 510	Java	2
“	AR	—	4
Belontiidae			
Belontia hasselti (Cuv. & Val.)	RNHL 10490	—	1
Belontia signata (Günther)	SNHM 30172	Ceylon	1
Betta anabatoides Bleeker	RNHL 7902	—	1
Betta picta (Cuv. & Val.)	MZB 293	Situ Gunung	1
Betta splendens Regan	AR	—	6
Betta taeniata Regan	MZB 296	Riouw	1
Betta unimaculata (Popta)	MZB 294	Borneo	1
Colisa fasciata (Bloch & Schneider)	AR	—	6
Colisa labiosa (Day)	AR	—	6
Colisa lalia (Hamilton Buchanan)	AR	—	6
Macropodus opercularis (L.)	AR	—	6
Macropodus chinensis Bloch	RNHL 17408	—	1
Macropodus cupanus (Cuv. & Val.)	AR	—	6
Sphaerichthys osphromenoides Can.	RNHL 20897	—	2
“	SNHM 39450	Malaya	2
Trichopsis pumilus (Arnold & Ahl)	RNHL 20980	—	1
Trichopsis vittatus (Cuv. & Val.)	MZB 292	Java	5
“	MZB 297	Banda	2
“	RNHL 16883	—	1
Trichogaster leeri (Bleeker)	AR	—	6
Trichogaster trichopterus (Pallas)	AR	—	6
“	MZB 321	Pager Alam	3
“	MZB 317	Pager Alam	7
Luciocephaliformes			
Luciocephalus pulcher (Gray)	RNHL 6371	—	1
“	SNHM 35689	Malaya	2
Ophicephaliformes			
Ophicephalus striatus Bloch	RNHL 11875	—	2

[a] AR: aquarium raised; MZB: Museum Zoologicum Bogoriense, Java; RNHL: Ryksmuseum van natuurlyke historie, Leiden; SNHM: Stanford Natural History Museum; RUDI: Rhodes University Department of Ichthyology; TVM: Transvaal Museum, S. Africa; UIMNH: University of Illinois Museum of Natural History; USZI: University of Stellenbosch Zoological Institute.

Since otoliths have distinct patterns in suborders, families, or even genera, they were of some value in the study of interrelationships of the Anabantoidei. The otoliths of nearly all genera have been removed and studied under a binocular microscope after softening the bone with potassium hydroxide. The nomenclature of Adams (1940) has been followed closely.

DESCRIPTIVE OSTEOLOGY

A. ANABANTIDAE

1. NEUROCRANIUM

Nasal region (figs. 1-3, 14-16, 40-42). The *nasals* in *Anabas* and *Ctenopoma* are large bones, suturally united to each other and overlying the ethmoid. In *Sandelia* the nasals are narrow and elongate, separated from each other by a fontanelle.

The *prefrontal* and *lateral ethmoid* are fused as a complex bone separating the nasal and orbital regions. Right and left bones are widely separated by the ethmoid. Ventrally they rest on the parasphenoid. The olfactory foramen is located near the median border of the prefrontal-lateral ethmoid complex. There are no palatine facets, although the palatine articulates against the lateral surface of the complex bone and the prevomer.

The single *ethmoid* is a triangular cap interposed between the prefrontal ethmoids, widely separating them. The front of the triangle slopes anteroventrad toward the prevomer.

The *prevomer* tapers posteriorly as a point entering a shaft of the parasphenoid. Two rows of well-developed conical teeth are present on the anteroventral surface of the prevomer. Dorsomedially the bone is raised to a blunt ridge.

Orbital region (figs. 1-3, 14-16, 27-30, 40-42). The paired *frontals* form a large portion of the roof of the cranial cavity and the central roof and margin of the orbital chamber. In *Anabas* they are joined by a dentate suture, whereas in *Sandelia* a fontanelle separates the anterior halves. *Ctenopoma* and *Sandelia* exhibit extensions of the frontals embracing the supraoccipital, which is not the case in *Anabas*. The frontals in *Anabas* and *Ctenopoma* possess on the ventral surface prominent orbital processes, articulating with the pterosphenoids with which they form an incomplete interorbital septum.

The *pterosphenoid* forms a ventral keel on the frontal and contributes to the posterior border of the orbit. It articulates with the sphenotic, prootic, and basisphenoid. Left and right pterosphenoids do not meet.

The *basisphenoid* is well developed and supported directly by the pterosphenoid and prootic. Its ventral process is joined to the parasphenoid in *Anabas* and *Sandelia*, but not in *Ctenopoma*.

The *lachrymal* (suborbital 1) is an elongate bone bordering the anteroventral portion of the orbit. It articulates with the prefrontal-lateral ethmoid by means of a medial spur. In *Anabas* the lachrymal is bordered by long radiating spines; in *Ctenopoma muriei* it is very weakly serrate, whereas in *Ctenopoma multispinis* and *Sandelia* there is no trace of any serration. There are five *suborbitals* (including the lachrymal) in *Anabas* and *Ctenopoma.* This number has been reduced to four in *Sandelia.* A very well-developed suborbital shelf is formed by prominent medial projections of all suborbitals in the three representative genera. In *Anabas* suborbitals 2-4 are very large and suturally united with the preopercular. *Ctenopoma muriei* shows an intermediate stage, in which the suborbitals are broad plates, reaching to nearly half the distance between orbit and preopercular. *Ctenopoma multispinis* and *Sandelia* exhibit a greater reduction, the suborbitals being narrow elongate bones.

Otic region (figs. 1-3, 14-16, 27-30, 40-42, 52-54). The *sphenotic* is a trapezoid plate bordered by the frontal anteriorly and medially. Posteriorly it is joined by the supratemporal. The sphenotic does not meet the parietal and rests ventrally on the pterosphenoid and prootic.

The *parietals* in *Anabas* are elongate bones, approximately of the same length as the supraoccipital, whereas in *Ctenopoma* and *Sandelia* they are half as long. The parietal in *Anabas* and *Ctenopoma* is joined medially with the supraoccipital, anteriorly with the frontal, laterally with the supratemporal, and posteriorly with the suprascapular. In *Sandelia,* however, the posterior edge of the parietal is bordered mainly by the posttemporal fossa; the extrascapular articulates only with the extreme posterior corner of the parietal.

The *extrascapular* is best developed in *Anabas* and *Ctenopoma,* covering the epiotics completely. It articulates anteriorly with the supratemporal and parietal, and medially with the supraoccipital. The posttemporal fossa is absent in *Anabas* and *Ctenopoma.* In *Sandelia* the extrascapular is somewhat reduced. It overlaps the epiotic partially and does not reach the supraoccipital. A posttemporal fossa is present in *Sandelia.*

The *supratemporal* is an elongate plate forming nearly half of the lateral border of the cranium. It is bounded anteriorly by the sphenotic and frontal, medially by the frontal and parietal, posteriorly by the extrascapular, and ventrally by the exoccipital, prootic, and intercalary.

The *prootic* is an irregularly shaped bone with an anterolaterally directed ridge extending from near its cranial border. The ventral half of this ridge forms the lateral wall of the *myodome* and also provides a slot into which the ascending process of the parasphenoid fits. Anteriorly the prootic is sutured to the pterosphenoid, with the foramen of the trigeminal nerve partly intervening, and to the dorsal portion of the basisphenoid. Dorsally the prootic is united to the sphenotic and supratemporal, and posteriorly to the basioccipital, exoccipital, and in *Anabas* also to the ventral keel of the supraoccipital. Ventrally it is bordered by the parasphenoid. There is a very prominent bulla acustica or saccular swelling. The suture between the prootic and basioccipital is dentate in *Anabas* and irregular in *Ctenopoma* and *Sandelia.*

The *epiotic* in *Anabas* and *Ctenopoma* is completely, in *Sandelia* only partly, overlain by the extrascapular. The bone is cone-shaped, forming the posterodorsal corner of the cranium. Dorsally it possesses an articulation facet for reception of the posttemporal. Medially the epiotic articulates with the supraoccipital, anterolaterally with the supratemporal, and posteroventrally with the intercalary and exoccipital. The epiotics do not reach the foramen magnum. The posttemporal fossa is absent in *Anabas* and *Ctenopoma.* The fossa is present in *Sandelia,* although rather small and shallow.

The *intercalary* (opisthotic) is a cone-shaped bone forming in *Anabas* and *Ctenopoma* the posteroventral corner of the cranium. In *Sandelia* the intercalary is a small plate situated between the posterior extremity of the supratemporal and the lateral wing of the exoccipital. Dorsally the intercalary is covered by the extrascapular. The posttemporal articulates by means of its lower fork with the intercalary in all three genera.

The *supraoccipital* is a hexagonal bone. There is no supraoccipital crest, except for a median keel on the posterior aspect of the skull. The supraoccipital does not reach the foramen magnum. In *Anabas* the supraoccipital possesses a very prominent ventral keel which articulates with the exoccipital and prootic, enlarging the suprabranchial chamber (fig. 14).

The *exoccipital* is connected posterodorsally to the epiotic and intercalary, anterodorsally to the supratemporal, anteriorly to the prootic, and ventrally to the basioccipital. A large foramen exoccipitale is located on the lateral wall of the exoccipital. In life this foramen is covered by a tympanumlike membrane. It is also a passage for the glossopharyngeal nerve. The vagus nerve emerges from a smaller foramen just posterior and dorsal to the foramen exoccipitale. The posterior surface of each exoccipital forms a rounded condyle for articulation with the first vertebra. Dorsal wings from the exoccipitals unite above the small foramen magnum, forming an arch over the spinal cord. The suture between the exoccipital and epiotic is dentate in *Anabas,* partially dentate in *Ctenopoma,* and straight in *Sandelia.*

The *posttemporal* in *Anabas* is comparatively small and slightly forked, whereas in *Ctenopoma* and *Sandelia* the forks are well differentiated. The upper fork articulates directly with the epiotic. The lower fork is connected to the intercalary.

Basicranial region (figs. 40-42, 52-54). The *basioccipital* in *Anabas* is bordered ventrally by the parasphenoid to a greater extent than in *Ctenopoma* and *Sandelia*. The posterior end forms a condylar articulation with the first vertebra. The basioccipital forms nearly the whole posterior half of the otic capsule. Near its posterior end a ventrolateral pharyngeal process is differentiated at either side of the basioccipital, functioning as a support for the hyobranchial apparatus. From the posterior aspect (figs. 52-54) these pharyngeal processes of the basioccipital appear as horizontal wings. Ventrally the basioccipital is bordered by the parasphenoid, anteriorly by the prootic, and dorsally by the exoccipital.

The *parasphenoid* extends from the prevomer to near the posterior extremity of the basioccipital, underlying the greater part of the basioccipital. Dorsally the parasphenoid sends a process to form the floor of the myodome. Near its posterior end the parasphenoid possesses very characteristic toothed transverse processes. In *Anabas* the conical teeth are very large, arranged in single rows of five. On the body of the parasphenoid five large teeth are present in a distinct pattern (fig. 40). In *Ctenopoma* and *Sandelia* the number of teeth has increased; in the latter genus the teeth are arranged in two rows (figs. 41, 42).

2. BRANCHIOCRANIUM

Hyobranchial region. The *interhyal* is a small rod-shaped bone connecting the posterodorsal margin of the epihyal to the cartilaginous block between the symplectic and the hyomandibular (figs. 76-78). The *epihyal* is triangular and joined loosely by a straight suture to the elongate *ceratohyal*. The dorsal and ventral *hypohyals* attach to the ceratohyal with an irregular suture. The unpaired *basihyal* is rod-shaped, and its posterior end joins the apices of the dorsal parts of the hypohyals. The three *basibranchials* lie in the mid-ventral line of the pharynx. The first is situated between the hypohyals and extends anteriad ventral to the basihyal. The second basibranchial is hourglass-shaped, whereas the third is elongate. The anterior ends of the first and second *hypobranchials* curve mesad and articulate with the constricted side of the second and third basibranchials. The third hypobranchial in *Anabas* is a large plate articulating with the third basibranchial, hypobranchial, and fourth ceratobranchial. In *Ctenopoma* and *Sandelia* the third hypobranchial is a curved bone. The first four *ceratobranchials* are slender, curved, rod-shaped bones. The fifth ceratobranchials approximate each other and are covered dorsally by numerous teeth, which are arranged in ten to fourteen rows in *Anabas*, ten rows in *Ctenopoma*, and six to seven rows in *Sandelia*. In *Anabas* the first *epibranchial* is modified into a labyrinthine suprabranchial organ. The suprabranchial organ is less complex in *Ctenopoma,* consisting of a stem and two folded lamellae. In *Anabas* the stem carries at least three folded lamellae. The first epibranchial in *Sandelia* is merely an enlarged but unfolded bony plate. The second and third epibranchials are rod-shaped. The third epibranchial in *Anabas* possesses a dorsal process. The fourth epibranchial in *Anabas* is a trapezoid bone. It is a more slender and rod-shaped bone in both *Ctenopoma* and *Sandelia.* The first *pharyngobranchial* is wanting. The second is a curved element bearing four teeth on the ventral surface. Pharyngobranchials 3-4 are fused indistinguishably; the ventral surface is covered with well-developed teeth arranged in four transverse rows. The *urohyal* is a thin elongate bone with a longitudinal ridge. Six *branchiostegal rays* are present in *Anabas* and *Ctenopoma,* and five in *Sandelia.* In *Anabas* the two most posterior rays articulate with the epihyal; in *Ctenopoma* only the sixth ray joins the epihyal. The last branchiostegal ray in *Sandelia* is situated between the epihyal and ceratohyal.

Opercular series (figs. 27-30). The *opercular* has a nearly vertical anterior border which joins the posterior border of the preopercular along its entire length. The posterier border of the opercular in *Anabas* is deeply serrate and has two well-developed spines. In *Ctenopoma* the degree of serration has decreased, whereas in *Sandelia* there are two distinct serrate patches, each with approximately five teeth. The ventral border is at a slight angle from the horizontal. Auricular and articular processes are wanting (figs. 27-30).

The *subopercular* has a dorsal border which corresponds to the ventral border of the opercular by which it is overlapped laterally. A rather short process is found at the anterodorsal corner. The posterior and ventral borders are deeply serrate in *Anabas,* serrate in *Ctenopoma,* and smooth in *Sandelia.*

The *interopercular* overlaps laterally with its posterior border the anterior end of the subopercular. The posteroventral border is deeply serrate in *Anabas,* faintly in *Ctenopoma.* In *Sandelia* there is just a slight indication of serration on the ventral border.

The *preopercular* is crescent-shaped. The element widens in the bend, except in *Anabas. Anabas* is unique in having the anterior border of the preopercular suturally united with postorbitals 2-4.

Oromandibular region (figs. 64-66). The oromandibular bones are movably suspended from the neurocranium by the palatines anteriorly and by the hyomandibulars posteriorly.

The *palatine* is a rather narrow bone bearing teeth along its anteroventral border in *Ctenopoma* and *Sandelia.* There are no teeth on the palatine of *Anabas.* A slender ethmoid process originates at the anterodorsal corner of the palatine. This ethmoid process is joined to the lateral ethmoid by means of a ligament. Ventrally the palatine is joined to the ectopterygoid and entopterygoid.

The *ectopterygoid* is a slender toothless bone tapering to a point at its anterodorsal end. It articulates with the palatine, entopterygoid, and quadrate.

The *entopterygoids* are large elements joined medially by a membrane to form the roof of the buccal cavity. The entopterygoid is bounded by the palatine, ectopterygoid, quadrate, and metapterygoid.

The *metapterygoid* is the largest of the cheek bones. Posterodorsally it is intimately joined with the symplectic process of the hyomandibular. Anteroventrally it is bounded by the entopterygoid and quadrate. Posteroventrally it articulates with the symplectic.

The *symplectic* is a long curved bone the distal half of which rests on the posterior process of the quadrate. In *Anabas* and *Ctenopoma* the dorsal end of the symplectic articulates with the symplectic process of the hyomandibular, whereas in *Sandelia* it joins the block of cartilage which lies between the symplectic process and interhyal.

The *quadrate* possesses a condyle on its anteroventral corner for articulation with the angular. The posterior margin is deeply incised with a slot into which the symplectic is wedged. The spinelike process caudal from the condylar region receives on its ventral surface the preopercular. Dorsally it articulates with the ectopterygoid, entopterygoid, and metapterygoid.

The dorsal surface of the *hyomandibular* is faintly differentiated into an anterior and posterior head, which articulate respectively with the sphenotic and supratemporal. A short posterior process affords an articulating surface for the opercular.

The *premaxillary* forms the anterior border of the mouth. The ascending process of the premaxillaries is variable in length: one-fifth of the body of the premaxillary in *Ctenopoma*, one-half to one-third in *Sandelia*, and one-third in *Anabas*. The processes from both sides are more or less closely conjoined in the midline and fit into a notch formed by the nasals, ethmoid, and palatines. Articular processes are wanting. The ventral surface of the premaxillary bears several rows of teeth.

The toothless *maxillary* does not contribute to the edge of the mouth. Its narrow anterior end forms a prominent notch. The rounded inner fork slides on the prevomer. The maxillary carries the ascending process of the premaxillary with the groove between the rounded inner fork and slender (in *Anabas* short and rounded) outer fork.

The *angular* is lodged in the posterior notch of the dentary. It lacks an ascending process.

The *dentary* bears teeth on the anterior three-fourths of its dorsal surface. The ascending process of the dentary appears merely as a rounded corner.

The *retroarticular* is a small irregular-shaped bone attached to the posteroventral corner of the angular, ventral to the condyle.

3. PECTORAL GIRDLE (figs. 91, 92)

The *supracleithrum* is more or less spatulate. It is partly covered by the ventral corner of the posttemporal in *Ctenopoma* and *Sandelia*, but not in *Anabas*. The supracleithrum overlaps the dorsal portion of the cleithrum.

The *cleithrum* is the largest element. Its ventral extension curves craniad and joins its partner on the opposite side by a short ligament, forming part of the floor of the hyobranchial apparatus. It possesses a very well-developed ala laminaris externa, concealing part of the postcleithrum, scapula, and coracoid from a lateral view.

The *postcleithrum* is divided into a dorsal and ventral portion. The dorsal one is elliptical, whereas the ventral element is elongate and tapers into a point ventrally.

The *scapula* fits into a groove on the inner ridge of the cleithrum. There is a large foramen. Three and a half *radials* articulate with its posterior margin.

The *coracoid* consists of a more or less rectangular dorsal portion articulating with the inner surface of the cleithrum and an elongate ventral portion which terminates in a short spine and extends anteriad to meet the ventral end of the cleithrum.

4. PELVIC GIRDLE (figs. 91, 92)

The two *basipterygia* are firmly united across the midline, forming a bilaterally symmetrical unit. There is a lateral ridge, the *rachis,* running more or less longitudinally along each basipterygium. Medial to this ridge arises another winglike process, the *processus medialis anterior,* which is longer in *Ctenopoma* and *Sandelia* than in *Anabas*. Originating from the posteromedial corner of the basipterygium are two distinct processes: an anteriorly directed *processus medialis* and a posteriorly directed *processus medialis posterior*. A prominent *processus lateralis* is present at the posterolateral corner of the basipterygium in *Anabas;* in *Ctenopoma* and *Sandelia* it is very reduced. The conjoined anterior tips of the basipterygia are attached to the cleithral symphysis by means of a ligament.

B. BELONTIIDAE

1. NEUROCRANIUM

Nasal region (figs. 6-11, 19-26, 45-51). The shape of the *nasals* varies considerably among the different members of the family. In *Trichogaster* and *Colisa* they are large and suturally united with each other in the midline, overlying the ethmoid. In *Belontia,* the nasals do not meet in the midline, but are widely separated by the dorsoanterior portion of the ethmoid. A similar condition is found in *Macropodus,* but the nasals here are more or less circular in shape. In *Betta* the pear-shaped nasals are also separated, but not by the ethmoid. In *Trichopsis* the nasals are elongate tubular bones, widely separated from each other and articulating only with the frontals. Similar long and narrow tubular nasals are found in *Sphaerichthys.* In the latter, however, the nasals articulate posteriorly with the frontals, and laterally and medially with the prefrontal-lateral ethmoid complex. Wedged between the nasals of *Sphaerichthys* is the prominent ethmoid.

The left and right *prefrontal-lateral ethmoid* complexes are separated by the ethmoid. The olfactory foramen is contained in the complex. Articular facets are wanting.

The *ethmoid* in *Betta, Belontia,* and *Trichogaster* is interposed between the prefrontal-lateral ethmoid complexes. It is a subvertical plate which bends forward to the prevomer on its anteroventral portion. In *Betta* the ethmoid possesses a process which extends posteriorly into the orbit supporting the interorbital septum. In *Trichogaster* the ethmoid is covered dorsally by the nasals. In *Betta* and *Belontia* the dorsal portion of the ethmoid is exposed between the notches in the anteromedial corner of the frontals. A concavity in the superior part of the ethmoid for the reception of the ascending processes of the premaxillaries is present in *Betta, Belontia,* and *Trichogaster.* In *Sphaerichthys, Trichopsis,* and *Macropodus* the ethmoid is widened dorsally but tapers off in its anteroventral extension to join the prevomer. The widened dorsal portion of the ethmoid, in *Sphaerichthys* and *Trichopsis,* forms a rather deep fossa in which the ascending processes of the premaxillaries fit. The ethmoid is fully exposed on the dorsal surface and extends relatively farther posteriorly in *Trichopsis* than in *Sphaerichthys.* In *Macropodus* the ethmoid also possesses a dorsal enlargement with a concavity in which the ascending processes of the premaxillaries are lodged. The ethmoid is covered by the joined nasals and frontals in *Macropodus cupanus. Macropodus opercularis* differs in this respect (fig. 10). In *Macropodus cupanus* the ethmoid possesses at its posteromedial corner a winglike process which extends nearly halfway into the orbit, forming an incomplete interorbital septum. This process articulates with the dorsal surface of the parasphenoid. *Colisa* exhibits a unique condition. The ethmoid is cup-shaped, with a deep wedge-shaped cavity which is closed posteriorly. The cup-shaped ethmoid runs back between the eyes to about the middle of the orbital cavity and receives the long ascending processes of the premaxillaries. The ethmoid does not articulate with the parasphenoid in *Colisa.*

The *prevomer* is a more or less flat toothless bone with a laterally expanded head and a shaft which tapers posteriorly, penetrating the parasphenoid. In *Macropodus cupanus* and *Belontia* the prevomer has a dorsomedial ridge.

Orbital region (figs. 6-11, 19-26, 32-39, 45-51). The *frontals* form three-fourths of the roof of the skull in *Trichogaster, Colisa,* and *Sphaerichthys,* two-thirds in *Macropodus chinensis* and *opercularis, Trichopsis,* and *Betta,* less than two-thirds in *Belontia* and *Macropodus cupanus.* A distinct notch exposing the superior concave part of the ethmoid is present at the anteromedial corner in *Betta, Trichopsis, Macropodus, Sphaerichthys,* and *Belontia.* Ventrally an orbital process of the frontal which is continuous with the pterosphenoid is present in *Betta* and *Macropodus cupanus.* Posteriorly the frontals reach the extreme anteromedial tip of the supratemporal.

The *pterosphenoid* is bounded dorsally by the sphenotic, posteriorly by the prootic, and posteroventrally by the anterolateral corner of the body of the basisphenoid. Its ventral edge forms part of the boundary of the orbital opening of the braincase, and is notched for the exit of the optic nerves. The anterior border of the pterosphenoid articulates with the ventral flangelike orbital process of the frontal in *Betta* and *Macropodus cupanus;* in *Belontia* the pterosphenoids of the right and left side are united by winglike processes which run transversely across the orbit, forming the orbital roof.

The *basisphenoid* is Y-shaped with one fork curved anteroventrally toward the parasphenoid. The ventral fork is sometimes united to the parasphenoid, the condition being variable within the species. In *Betta* the anterior border of the body of the basisphenoid sends out a prominent process supporting the interorbital septum. In *Trichopsis* the ventral fork is wanting. The ventral fork divides the anterior opening of the myodome into two parts, and its anterior edge receives the posteroventral edge of the membranous interorbital septum. The body of the basisphenoid is supported by the sphenotic and prootic.

The long axis of the *lachrymal* is nearly vertical in *Macropodus, Betta,* and *Belontia.* In the remaining genera it is horizontal. The ventral border of the lachrymal is serrate except in *Betta.* The lachrymal articulates with the prefrontal-lateral ethmoid complex as in the family Anabantidae. The remaining *suborbitals* are five in number. Laterally they appear as a chain of narrow tubular bones traversed by the infraorbital branch of the cephalic lateral line system. The suborbital shelf is well developed in all genera (fig. 10). In *Trichopsis, Macropodus, Belontia,* and *Betta* the suborbital shelf is built by prominent medial winglike processes of suborbitals 2-5, which are rigidly united with each other.

Otic region (figs. 6-11, 19-26, 45-51, 57-63). In ventral view the *sphenotic* is more or less hexagonal and forms part of the postorbital process. There is a prominent flangelike ridge on the ventral surface, continuous with a similar ridge on the anterolateral wall of the prootic. On the ventrolateral surface there is often an articular facet for the anterior head of the hyomandibular. The extreme posteromedial corner of the sphenotic articulates with the parietal, except in *Trichogaster* and *Macropodus cupanus,* in which the sphenotic is widely separated from the parietal.

The *parietals* are elongate bones with the long axis arranged more or less anterolaterally. The parietals articulate posteromedially with the supraoccipital, posteriorly with the epiotic, and laterally with the supratemporal. Anteriorly the parietals are joined to the frontals and the posteromedial corner of the sphenotic except in *Trichogaster* and *Macropodus cupanus*. In the latter two the parietals do not reach the sphenotic. A prominent longitudinal ridge runs from the anteromedial corner of the parietal to the posterolateral corner. The parietal forms the anteromedial wall of the posttemporal fossa.

The *supratemporal* forms the posterolateral corner of the skull, contributing to a part of the lateral wall of the neurocranium and the greater portion of the floor of the posttemporal fossa. It joins the frontal with its anteromedial corner. Anteriorly it articulates with the sphenotic, and medially with the parietal, epiotic, and exoccipital. Posteromedially the supratemporal is united with the intercalary. At the anterior portion of the supratemporal an articular facet for the posterior head of the hyomandibular is present ventrolaterally. Ventrally the supratemporal is united with the exoccipital and prootic (figs. 45-51).

The *prootics* are large bones articulating ventrally with the parasphenoid, posteriorly with the exoccipital and basioccipital, anteriorly with the body of the basisphenoid and pterosphenoid, and dorsolaterally with the sphenotic and supratemporal. Near its cranial border the prootic possesses a prominent anterolaterally directed process. This process joins the ascending process of the parasphenoid except in *Trichopsis*, *Betta*, and *Macropodus*. In the latter three genera the process extends over the ascending process of the parasphenoid, forming a more or less transverse septum which separates the orbital region from the otic region. The prootic also houses the greater part of the funnel-shaped myodome. The orbital opening of the *myodome* is triangular and is bisected by the ventral fork of the basisphenoid. The opening is surrounded ventrally by the parasphenoid, laterally by the ascending process of the parasphenoid, and dorsally by the body of the basisphenoid and the medial processes of the prootics. The myodome expands dorsolaterally, reaching the ventral surface of the trigemino-facialis chamber. Posteriorly the myodome narrows rapidly and ends in the anterior quarter of the prootic. Just posterior to the ascending process of the parasphenoid is a foramen for the internal carotid artery, which enters the myodome at this point. After entering the myodome the internal carotid artery turns dorsally in front of the basisphenoid, penetrating the cranial cavity.

The *epiotic* is a somewhat conical bone which adjoins the parietal anteriorly, the supraoccipital medially, and the supratemporal laterally. Ventrally it articulates with the exoccipital. In *Sphaerichthys, Trichogaster,* and *Colisa* the epiotic reaches the foramen magnum and forms part of its roof (figs. 61-63). On the dorsal aspect a rather prominent epiotic process arises at the posterolateral corner of the epiotic. The epaxial trunk muscles attach to these epiotic processes by means of a tendon. The processes are wanting in *Sphaerichthys.* The lateral wall of the epiotic forms the medial wall of the posterior half of the posttemporal fossa.

The *intercalary* is a more or less triangular bone, wedged between the supratemporal and exoccipital. The bone is very small in *Sphaerichthys, Trichogaster,* and *Colisa.* In *Belontia* the bone reaches the posterolateral corner of the neurocranium. The intercalary has an articular facet for articulation with the ventral fork of the posttemporal bone.

The *supraoccipital* consists of two portions: a dorsosuperior and a posteroinferior portion. The superior portion is diamond-shaped in *Belontia,* rhomboidal in *Sphaerichthys,* elongate and narrow in *Trichopsis,* and hexagonal in *Macropodus, Betta, Trichogaster,* and *Colisa.* A well-developed supraoccipital crest is found only in *Belontia* (figs. 6-13). The posteroinferior portion of the supraoccipital is narrow in *Belontia.* In *Betta, Macropodus,* and *Trichopsis* the posteroinferior portion is wide dorsally and tapers ventrally, reaching the foramen magnum with its pointed ventral end (figs. 57-60). In *Sphaerichthys, Colisa,* and *Trichogaster* the supraoccipital narrows ventrally to a much lesser extent and forms the greater part of the roof of the foramen magnum (figs. 61-63). In *Sphaerichthys, Colisa,* and *Trichogaster* the supraoccipital does not articulate with the exoccipital. In the remaining genera the supraoccipital adjoins the exoccipital along the ventral half of its posteroinferior portion.

The *exoccipital* is bounded posterodorsally by the epiotic, laterally and anterodorsally by the intercalary and supratemporal respectively. Anteriorly it is joined to the prootic and ventrally to the basioccipital. A large foramen exoccipitale is present in the anteroventral corner. This foramen serves partly as a passage for the glossopharyngeal nerve. The vagus nerve emerges from a smaller foramen dorsoposteriorly to the foramen exoccipitale. The posterior portion of the exoccipital forms in *Belontia* a rounded condyle, whereas it is elongate in all the remaining genera. The dorsal wings of the exoccipitals do not unite above the foramen magnum (figs. 57-63), but are separated by the posteroinferior portion of the supraoccipital. In *Betta, Trichopsis, Macropodus,* and *Belontia* the foramen magnum is medium-sized and more or less triangular, whereas in *Sphaerichthys, Trichogaster,* and *Colisa* the foramen is large and more or less heart-shaped. In the latter three genera the exoccipitals do not articulate with the supraoccipital (figs. 61-63).

The *posttemporal* is distinctly forked. The dorsal fork articulates with an articular surface on the dorsolateral corner of the epiotic; the ventral fork is connected to an articular facet on the intercalary.

Basicranial region (figs. 45-51, 57-63). The *basioccipital* is more or less fan-shaped. Its posterior end is modified to form a vertebralike condyle for articulation with the first vertebra. Ventrally the basioccipital possesses a very prominent bilobed pharyngeal process. In *Belontia, Macropodus,* and *Trichopsis* the pharyngeal process of the basioccipital does not articulate with a similar process of the parasphenoid (figs. 19-23). In *Sphaerichthys* the dorsal quarter of the pharyngeal process of the basioccipital is joined to the pharyngeal process of the parasphenoid (fig. 24), whereas in *Trichogaster* and *Colisa* nearly its entire length is joined to the parasphenoid. In the latter two genera only the distal bilobed portion of the pharyngeal process is free (figs. 25, 26). In *Sphaerichthys, Colisa,* and *Trichogaster* the anterior portion of the basioccipital is not underlain by the paraspheniod, but articulates anteriorly with the parasphenoid. In *Belontia, Trichopsis, Macropodus,* and *Betta* the anterior half of the basioccipital is underlain by the posterior portion of the parasphenoid.

The *parasphenoid* covers the ventral surface of the neurocranium through about four-fifths of its entire length in *Belontia, Betta, Trichopsis,* and *Macropodus,* and about two-thirds in *Sphaerichthys, Colisa,* and *Trichogaster* (figs. 45-51). The bone consists of a long narrow body and two dorsolateral ascending processes. The concave anterior edge of the process forms the lateral wall of the orbital opening of the myodome. In the angle between the prootic and the posterior edge of the ascending process lies the foramen for the internal carotid artery. At its posterior end the parasphenoid develops a prominent ventrally directed pharyngeal process. The transverse process of the parasphenoid is absent. The pharyngeal process is, in *Sphaerichthys, Colisa,* and *Trichogaster,* a thin keellike structure extending far ventrally at an angle of nearly 90° with the horizontal axis. In *Belontia, Betta, Macropodus,* and *Trichopsis* the pharyngeal process is stout but does not extend as far ventrally, and is at an angle between 15° and 70° with the horizontal axis (figs. 19-26). In *Belontia* the process is oval from a ventral view (fig. 45) and bears strong teeth arranged in a circle; in *Betta* the process is elongate and has five teeth of which the posterior one is stout (fig. 46); a similar condition is found in *Trichopsis* but the number of teeth has been reduced to four; in *Macropodus* the teeth are weakly developed and vary in number between two and four; in *Sphaerichthys* the keellike process possesses only one tooth; in *Colisa* the teeth are very rudimentary and vary in number between zero and two; in *Trichogaster,* finally, the teeth are completely lost (figs. 45-51).

2. BRANCHIOCRANIUM

Hyobranchial region (figs. 81-87). The hyoid apparatus is similar to that of the Anabantidae. The structure and arrangement of the three *basibranchials* is also as described for the Anabantidae, except in *Colisa, Trichogaster,* and *Sphaerichthys,* in which the third basibranchial is much more elongate and rod-shaped. Three *hypobranchials* are present: the first articulates with the second basibranchial, and the second and third with the third basibranchial. The anterolateral corner of the third hypobranchial is produced into a process which articulates with the preceding hypobranchial. The first four rodlike *ceratobranchials* are more slender and elongate in *Colisa* and *Trichogaster.* The anteromedial ends of the fifth ceratobranchials approximate each other. The dorsal surface is covered with well-developed teeth which are arranged in ten transverse rows in *Belontia,* five rows in *Macropodus* and *Betta,* and four rows in *Trichopsis.* In *Sphaerichthys, Colisa,* and *Trichogaster* the teeth are weakly developed; they are arranged in a patch of two to four rows in *Sphaerichthys* and two rows in *Colisa* and *Trichogaster.* The first *epibranchial* is modified in all genera. In *Sphaerichthys* it consists simply of an enlarged curved plate with an epibranchial process which articulates with the saccular swelling of the prootic. In all other genera the first epibranchial is labyrinthine, varying in complexity in the different genera. *Belontia* is unique in having a very elongate suprabranchial organ; it is as long as the entire length of the hyobranchial apparatus, lodged in a suprabranchial cavity which extends posteriorly as far as the sixth vertebra, dorsal to the pleuroperitoneal cavity. The suprabranchial cavity is supported dorsally by the first four epipleural ribs, which have shifted dorsally, articulating with the neural arches of the first four vertebra, and ventrally by the fifth and sixth epipleural ribs. A similar posterior extension of the suprabranchial cavity is lacking in all other anabantoids. The first epibranchial consists, in all genera, basically of a central stem in the form of a median plate with the epibranchial process, which articulates with the prootic. Attached to this central stem is a varying number of folded plates: two in *Belontia,* one in *Trichopsis* and *Betta,* three in *Macropodus,* three in *Trichogaster,* and two in *Colisa.* The remaining three rod-shaped epibranchials decrease in length from the second to the fourth. Dorsal processes are on each of the epibranchials, in various degrees of development. The first *pharyngobranchial* is absent. The second pharyngobranchial is a slender and slightly curved bone. The ventral surface bears eight to fifteen teeth in *Belontia,* four to seven in *Trichopsis,* two in *Betta,* seven in *Macropodus,* three in *Sphaerichthys,* six in *Trichogaster,* and four in *Colisa.* A well-developed dorsal process on the second pharyngobranchial is present in *Macropodus, Betta,* and *Trichopsis.* The other genera lack similar processes. The third and fourth pharyngobranchials are fused. The dorsal surface has an articular surface for the articulation with the pharyngeal process of the basioccipital. The ventral surface is covered with teeth arranged in a varying number of transverse rows in the different genera: seven in *Belontia,* five in *Betta,* four in *Trichopsis, Macropodus,* and *Sphaerichthys,* and four rows of rudimentary teeth in *Colisa* and *Trichogaster.* The *urohyal* consists of a simple plate which gives off two lateroventral winglike processes. A cross section of the urohyal would resemble an inverted Y. In *Belontia, Macropodus, Trichopsis,* and *Betta* the urohyal is relatively short. The urohyal is more slender and elongate in *Sphaerichthys, Colisa,* and *Trichogaster.* The anterodorsal corner of the urohyal is produced into a short process. The *branchiostegal rays* are well developed. Six branchiostegal rays are found in *Belontia, Betta, Trichopsis,* and *Macropodus.* The number of branchiostegal rays is reduced to five in *Sphaerichthys, Colisa,* and *Trichogaster.* In *Belontia,* the sixth branchiostegal ray articulates with the epihyal. In the remaining genera all the branchiostegal rays articulate with the ceratohyal.

Opercular series (figs. 32-39). In *Belontia* the anterior border of the *opercular* is relatively vertical and articulates along its entire length with the posterior border of the preopercular. In all other belontiids the anterior border of the opercular is more or less rounded and articulates only partly with the posterior border of the preopercular. The posterodorsal corner is produced into an auricular process of variable size and shape, as either a posterior or a dorsal extension of the posterodorsal corner. In *Sphaerichthys, Colisa,* and *Trichogaster* the dorsal border of the opercular is distinctly rounded. The opercular is not serrate.

The ventral border of the *subopercular* is not serrate except in *Trichogaster trichopterus.* A prominent process is found at the anterodorsal corner. Posteriorly the subopercular is produced into a long and slender process in *Colisa, Sphaerichthys, Trichogaster, Betta,* and *Belontia.*

The elliptical *interopercular* is not serrate and is overlapped dorsally by the preopercular for about three-fourths of its surface.

The ventral border of the *preopercular* is serrate along its entire length in *Trichogaster* and *Colisa,* along half its length in *Sphaerichthys, Trich-*

opsis, Belontia, and *Macropodus,* and not serrate in *Betta.* The preopercular is crescent-shaped and widens in the bend.

Oromandibular region (figs. 69-75). The *palatine* consists of two components: the slender and curved ethmoid process, directed anterodorsally, articulates with the prefrontal-lateral ethmoid complex, and the body articulates ventrally with the quadrate and posteriorly with the entopterygoid. The body of the palatine is somewhat variable in shape; mostly it is elliptical, but in *Trichopsis* it is triangular and in *Betta* irregular.

The *ectopterygoid* is wanting.

The *quadrate* is a more or less quadrangular bone with its anteroventral corner modified into a condyle. The dorsal border of the bone is convex (except in *Macropodus cupanus*) and articulates with the palatine and entopterygoid. The posterior edge is deeply notched and ventrally produced into a prominent posterior process. The notch lodges the ventral fourth of the symplectic and may be considered as dividing the quadrate into a main body and a posterior process.

The *entopterygoid* is a large thin bone of variable shape. Anteriorly it is bounded by the palatine, ventrally by the quadrate and metapterygoid, and posteriorly by the metapterygoid.

The *metapterygoid* is also variable in shape. It articulates ventrally and posteriorly with the symplectic, and anteriorly with the quadrate and entopterygoid. The metapterygoid does not reach the hyomandibular except in *Belontia,* in which it is joined with the symplectic process of the hyomandibular.

The *symplectic* is a rather large, elongate, curved bone. Its dorsal end is bounded by the interspace of cartilage that lies between itself, the interhyal, and symplectic process of the hyomandibular. The anterior quarter of the symplectic rests on the posterior process of the quadrate.

The *hyomandibular* consists of a body with a symplectic process anteroventrally and an articular process posteroventrally. The angle between the two stout processes in *Colisa* and *Trichogaster* is between 90° and 110°, whereas in the remaining genera it is between 30° and 70°. The dorsal surface is more or less differentiated into an anterior and posterior head, articulating respectively with the sphenotic and supratemporal. The well-developed articular process is connected to an articular facet which is situated on the medial surface in the anterodorsal corner of the opercular.

The *angular* is dartlike in appearance. It has a prominent process anteriorly. The posterior end of the ventral arm of the dentary fits into the angle between the anterior process and the body of the angular. At the dorsal corner of the angular there is a prominent ascending process which reaches its highest development in *Colisa, Sphaerichthys,* and

Trichogaster. The angular is traversed by the posterior part of the mandibular lateral canal.

The *retroarticular* is a small irregular bone that fits against the posteroventral corner of the angular, immediately ventral to the articular facet for the quadrate.

The *dentary* is a strong V-shaped bone. The dorsal edge of the dorsal arm of the V is lined with small conical teeth. The posterodorsal corner of the dorsal arm of the V is produced into a well-developed ascending process of the dentary.

The *premaxillary* has a well-developed ascending process, but no articular process. The ascending processes from both sides are closely conjoined and fit into a notch formed by the ethmoid and the prefrontal-lateral ethmoid complex. The ascending process is as long as the body of the premaxillary in *Belontia,* one-half the length of the body in *Betta, Trichopsis* and *Macropodus cupanus,* twice the length of the body in *Sphaerichthys,* and more than twice the length of the body in *Trichogaster* and *Colisa.*

The toothless *maxillaries* are shorter and more stout than in the Anabantidae. The relationships of the inner and outer forks are identical to those of the Anabantidae.

3. PECTORAL GIRDLE

The *supracleithrum* (figs. 96-101) is a small elliptical bone which articulates with the medial surface of the posttemporal. It is large in *Belontia,* overlapping the lateral surface of the dorsal portion of the cleithrum and postcleithrum.

The *cleithrum* is the largest element in the pectoral girdle. The bone consists of a posterodorsal and anteroventral portion. The anteroventral portion curves craniad and joins its partner from the opposite side. A prominent ala laminaris externa as described for the Anabantidae is present only in *Belontia.* The process is reduced to a flangelike outgrowth in the bend of the cleithrum; it continues as a ridge on the dorsal edge of the anteroventral portion of the cleithrum. A facet for the articulation of the basipterygium is present on the mesial surface of the cleithrum about in the middle of the anteroventral portion in *Trichopsis, Macropodus, Betta, Sphaerichthys,* and *Belontia.* In *Trichogaster* and *Colisa* a distinct fingerlike articular process is present mesially on the cleithrum, near the proximal border of the coracoid, for articulation with the basipterygia.

The *postcleithrum* is divided into a dorsal and ventral element. The dorsal element is spindle-shaped in *Colisa, Trichogaster, Belontia, Betta,* and *Trichopsis.* In *Sphaerichthys* and *Macropodus* the dorsal element possesses a large vane on its posterior surface. The ventral element is elongate and tapers to a point ventrally.

The *coracoid* consists of a dorsal, proximal, and elongate ventral portion which terminates posteriorly in a spine in *Sphaerichthys, Colisa, Trichogaster,* and *Betta,* but not in the remaining genera. The ventral portion of the coracoid extends anteriad to meet the ventral end of the cleithrum. The posterodorsal corner of the coracoid articulates with the largest radial. There are four hourglass-shaped *radials.* In *Sphaerichthys* the radials are elongate rodlike structures.

The *scapula* articulates with three and a half *radials.* The foramen in the scapula is large in *Macropodus, Belontia,* and *Colisa,* small in *Betta, Sphaerichthys,* and *Trichopsis.*

4. PELVIC GIRDLE

Belontia exhibits the most primitive stage, resembling the condition in *Sandelia* and *Ctenopoma.* In *Betta* and *Macropodus* the *basipterygia* are separated. The *rachii* of the basipterygia are also widely separated. The rachii (figs. 96-101) are directed dorsolaterally and articulate respectively on the mesial surface of the right and left cleithrum. The *processus medialis anterior* is a well-developed ridge medial to the rachis; the *processus medialis* is long and spinelike, whereas the *processus medialis posterior* is a distinct projection at the posteromedial corner; the *processus lateralis* is wanting. In *Trichopsis* the processus medialis anterior is well developed and wing-shaped, the processus medialis posterior is very prominent, and the processus lateralis appears as a distinct earlike projection. The most complex pelvic girdle is found in *Colisa* and *Trichogaster.* The dorsally directed rachii are slender and articulate with a fingerlike projection on the medial surface of the cleithrum. The processus medialis anterior is better developed in *Colisa* than in *Trichogaster.* In *Colisa* the processus medialis anterior is directed anteromedially and has a vanelike appendage anteriorly. The distal end of the processus medialis is curved laterally in *Colisa,* but not in *Trichogaster.* The processus lateralis is a highly developed earlike projection; the processus medialis posterior is a pointed projection in *Trichogaster,* whereas in *Colisa* it is a broad platelike process forming the larger part of the posterior border of the pelvic girdle. *Trichogaster* and *Colisa* are unique in having a *processus medialis accessorius,* originating from the basipterygium at the level of the origin of the processus medialis anterior. The accessory medial process is arranged nearly transversely and is better developed in *Colisa* than in *Trichogaster.*

C. OSPHRONEMIDAE

1. NEUROCRANIUM

Nasal region (figs. 4, 17, 43). The *nasals* are elongate, slightly curved bones, widely separated form each other. The area between the nasals is abruptly depressed to form a deep fossa for the reception of the ascending processes of the premaxillaries. Posteriorly the nasal articulates with the frontal and prefrontal-lateral ethmoid complex.

The *prefrontal-lateral ethmoid* complex possesses an orbital wing with a weakly developed palatine facet. The complex bone expands ventrally, joining the prevomer. Dorsally the complex reaches the posterolateral corner of the nasal. The olfactory foramen is contained in the lateral ethmoid. The complex bones are separated by the ethmoid.

The *ethmoid* forms the anterior two-thirds of the floor of the fossa between the nasals and is but little covered by the frontals. It has a horizontal position and does not articulate with the prevomer. Its suture with the anteromedial portion of the frontal is dentate.

The toothless *prevomer* has dorsal wings which articulate with the prefrontal-lateral ethmoid complex, forming dorsally a distinct rostral fossa. Anteriorly the prevomer curves upward and forms a distinct head. Posteriorly the shaft of the prevomer penetrates the parasphenoid.

Orbital region. The *frontals* articulate anteriorly with the ethmoid, nasals, and prefrontal-lateral ethmoid complex, laterally with the sphenotics and supratemporal, and posteriorly with the parietals and supraoccipital. The anteromedial portion of the frontal is depressed abruptly to form the posterior third of the floor of the fossa. The posterior portion of the frontals also forms a distinct depression for the insertion of the epaxial muscles.

The *lachrymal* is serrate along its ventral border. It is a rhomboidal bone with its long axis directed anterodorsally, overlapping the dorsal portion of the maxillary. The remaining four *suborbitals* are narrow tubular bones. The second and third suborbitals are also serrate, a unique feature among the anabantoids. Another characteristic feature of the Osphronemidae is the absence of a suborbital shelf.

The *pterosphenoid* is deeply serrate along its ventral border. Its relationship with the surrounding bones is identical to the condition found in the Belontiidae.

The *basisphenoid* is a relatively large Y-shaped bone. The shank of the Y is vertical and is joined to the parasphenoid.

Otic region (figs. 4, 17, 43, 55). The *sphenotic* is a relatively large bone, forming the entire postorbital process. It adjoins the frontal anteriorly and medially and the supratemporal posteriorly. At its posterolateral surface the sphenotic possesses a shallow depression for articulation with the anterior head of the hyomandibular. It also bears a ventrolateral ridge which is continuous with a similar ridge on the prootic.

The *supratemporal* is an extremely large bone exceeding the frontals in length (fig. 4). It lies at a lower level than the sphenotic and forms the greater part of the floor of the posttemporal fossa. The supratemporal is bounded anteriorly by the sphenotic, medially by the frontal, parietal, and intercalary, and ventrally by the anterior portion of the exoccipital and the prootic.

The *intercalary* is wedged between the supratemporal and exoccipital. Dorsally it appears as a relatively small bone with a distinct articular facet for the ventral fork of the posttemporal. Ventrally the full extent of the bone is visible (fig. 43). The intercalary does not reach the prootic.

The large *parietal* appears in dorsal view as an inverted V. The lateral arm of the V articulates with the frontal and supratemporal, whereas the medial arm articulates with the supraoccipital and epiotic. The posttemporal fossa is situated in the angle of the V. A prominent ridge runs along the lateral side of the medial arm of the V. The ridge is continuous with a similar structure on the epiotic and serves as an insertion for the epaxial muscles.

The *prootic* resembles that of the Belontiidae.

The large spatulate *supraoccipital* is of the same length as the frontal (fig. 4). It possesses a very prominent supraoccipital crest. The posteroinferior portion forms the roof of the foramen magnum, separating the exoccipitals widely from each other.

The *epiotic* is conical. It forms, together with the parietal, the lateral wall of the posttemporal fossa. An epiotic process is wanting. The posterolateral corner forms a distinct articular process for articulation with the dorsal fork of the posttemporal (fig. 4). The epiotic articulates ventrally with the exoccipital, anteriorly with the parietal, and medially with the supraoccipital. The epiotics do not reach the relatively small foramen magnum.

The *exoccipital* forms posteriorly a small triangular condyle for articulation with the first vertebra. The left and right exoccipitals are widely separated by the posteroinferior portion of the supraoccipital. The exoccipitals form the lateral walls of the foramen magnum. A large foramen exoccipitale is present (fig. 17).

Basicranial region (figs. 17, 43, 55). The *parasphenoid* consists of an elongate narrow body with dorsolateral ascending processes. The orbital portion of the parasphenoid has a dorsal, median, serrate ridge which forms, together with the pterosphenoid, an incomplete interorbital septum. Posteriorly the parasphenoid is differentiated into a stout pharyngeal process at an angle of about 80° with the horizontal axis. The pharyngeal process bears eight stout conical teeth.

The *basioccipital* is a rather large bone articulating ventrally with the parasphenoid, anteriorly with the prootic, and dorsally with the exoccipital. Posteriorly it forms a vertebralike condyle for articulation with the first vertebra. Ventrally it is produced into a short and stout bilobed pharyngeal process. The anterior border of the pharyngeal process does not articulate with the posterior border of the pharyngeal process of the parasphenoid.

2. BRANCHIOCRANIUM

Hyobranchial region (fig. 79). The hyoid apparatus is identical to that of the Anabantidae. The three *basibranchials* are hourglass-shaped. The *hypobranchials* resemble those of *Anabas.* The first four *ceratobranchials* are curved elongate elements. The fifth ceratobranchial is more or less triangular and bears numerous well-developed teeth. The first *epibranchial* is modified into a labyrinthine suprabranchial organ. It is attached to the prootic by means of an epibranchial process. The suprabranchial organ consists of a main stem to which are attached three highly folded bony lamellae. The remaining epibranchials lack articular processes. The second *pharyngobranchial* is slightly curved and has two spinelike projections on its dorsal surface. Ventrally it bears a single row of well-developed teeth. The third and fourth pharyngobranchials are fused indistinguishably into one rectangular bone. It possesses an articular surface on its dorsal side for articulation with the pharyngeal process of the basioccipital. The pharyngobranchials bear numerous conical teeth on their ventral surfaces. The *urohyal* is identical to that of the Anabantidae. The sixth *branchiostegal ray* articulates with the epihyal, the fifth is situated between the epihyal and ceratohyal. The remaining four articulate with the ceratohyal.

Opercular series (fig. 67). The *opercular* is oval and possesses neither an auricular nor an articular process. Its anterior border articulates only to a very limited extent with the posterior border of the preopercular.

The *subopercular* is serrate, with about five projections. The anterodorsal corner is produced into a process. Posteriorly the subopercular does not terminate in a process.

The spatulate *interopercular* is serrate along its ventral border.

The *preopercular* is crescent-shaped and expanded at its bend, the ventral edge serrate.

Oromandibular region (fig. 67). The palatine adjoins the ectopterygoid ventrally and the entopterygoid posteriorly. It articulates medially with the orbital wing of the prefrontal-lateral ethmoid complex. Anterodorsally the palatine is produced into an ethmoid process.

The *ectopterygoid* is somewhat triangular but its dorsal border is concave. It articulates dorsally with the palatine, posteroventrally with the quadrate, and posterodorsally with the entopterygoid.

The *entopterygoid* is the largest element in the oromandibular apparatus. Anteriorly it meets the palatine and ectopterygoid, and ventrally the quadrate and metapterygoid.

The *metapterygoid* is somewhat rectangular and articulates posteriorly with the symplectic process of the hyomandibular. Dorsally it is bounded by the entopterygoid, ventrally by the symplectic, and anteriorly by the quadrate.

The *quadrate* has a convex dorsal border. Posteroventrally it is produced into a long, slender, posterior process. Anteroventrally the quadrate is modified into a condyle.

The dorsal portion of the curved *symplectic* articulates with the symplectic process of the hyomandibular. Its anterior half rests on the posterior process of the quadrate.

The *premaxillary* possesses an ascending process which is slightly longer than the length of the horizontal limb.

The *maxillary* is identical to that found in the Belontiidae.

The *dentary* is rather stout and bears three rows of teeth. Posterodorsally it is produced into a broad, rounded, ascending process. Posteriorly the dentary is distinctly notched, to receive a process of the angular.

The *angular* is more or less dart-shaped. Dorsally it bears a pointed ascending process.

The *retroarticular* is a small irregular-shaped bone at the posteroventral corner of the angular.

3. PECTORAL GIRDLE

The pectoral girdle resembles that of *Belontia.*

4. PELVIC GIRDLE

The *rachii* of the *basipterygia* are very long and directed dorsomedially. A dorsal ridge on the basipterygium (fig. 93) represents the *processus medialis anterior.* A long, slender, anterior projection arises from the posteromedial corner of the basipterygium and represents the *processus medialis.* The *processus medialis posterior* is very small. A distinct *processus lateralis* is not differentiated. The *processus medialis accessorius,* characteristic of *Colisa* and *Trichogaster,* is wanting.

D. HELOSTOMATIDAE

1. NEUROCRANIUM

Nasal region (figs. 5, 18, 44). The *nasals* are widely separated by the ethmoid. The nasal is bounded medially by the ethmoid, posteriorly by the frontal, and laterally by the prefrontal-lateral ethmoid complex (fig. 5).

The *prefrontal-lateral ethmoid* complexes are separated by a ventral keel of the ethmoid. From a dorsal view (fig. 5) the complex bone appears as a long and rather narrow element directed anteromedially toward the posterolateral corner of the nasal. It possesses an orbital wing which forms part of the anterior border of the orbit; there are no articular facets. Ventrally the complex bone exhibits a unique shape (fig. 44). Posteriorly it articulates with the pterosphenoid, medially with the ventral keel of the ethmoid, and anteriorly with the dorsal wing of the prevomer. The olfactory foramen is located near the medial border of the complex bone.

The *ethmoid* consists of a nearly horizontal body and a platelike ventral keel, separating the prefrontal-lateral ethmoid complexes. Posteroventrally the ventral keel projects into the anteroventral corner of the orbit, resting on the parasphenoid. The body of the ethmoid lies at the same level as the surrounding bones, the nasals and frontals. From a dorsal view the ethmoid exhibits a very characteristic pattern (see fig. 5).

The toothless *prevomer* is a large bone with very prominent dorsolateral winglike processes which articulate with the nasals and the prefrontal-lateral ethmoid complexes. Posteriorly the prevomer tapers off abruptly into a point which enters a channel at the anterior end of the parasphenoid.

Orbital region (figs. 5, 18, 31, 44). The *frontals* are joined anteriorly by the ethmoid, nasals, and prefrontal-lateral ethmoid complex, posteromedially by the supraoccipital, posteriorly by the parietal and supratemporal, and laterally by the sphenotic and fifth suborbital. The part of the frontal posterior to the postorbital processes lies at a lower level than the anterior part, contributing to the extensive fossa for the insertion of the large epaxial muscles.

The *lachrymal* is serrate along its ventral border. Dorsally it is joined to the nasal and prefrontal-lateral ethmoid complex. The lachrymal is attached to the outer edge of the orbital wing of the prefrontal-lateral ethmoid complex. The remaining four *suborbitals* appear in a lateral view as a chain of narrow tubular bones. The suborbital shelf is absent.

The *pterosphenoids* are large bones, forming an incomplete interorbital septum. The anteroventral border is deeply serrate. Anterodorsally it articulates with the most posterior border of the prefrontal-lateral ethmoid complex. Posteriorly it is bounded by the prootic and posteroventrally by the basisphenoid. The pterosphenoid does not meet the small sphenotic.

The *basisphenoid* is a stout Y-shaped bone. The shank of the Y lies vertically in the midplane of the neurocranium and joins the parasphenoid. The arms of the Y are much broader than the shank. Anterodorsally the basisphenoid meets the pterosphenoid and posterodorsally the prootic.

Otic region (figs. 5, 18, 31, 44, 56). The *sphenotic* is a rather small bone which does not articulate with the pterosphenoid. A shallow depression on the posterolateral border serves as an articular facet for the anterior head of the hyomandibular. Anteriorly the sphenotic is bounded by the fifth suborbital, posteriorly by the supratemporal, and medially by the prootic. Ventrally it possesses a prominent ridge which is continuous with a similar ridge on the prootic. At the dorsal surface of the skull the sphenotic does not reach the parietal, and lies at a lower level than the fifth suborbital.

The *supratemporal* forms the posterolateral corner of the skull and contributes to the greater part of the floor of the posttemporal fossa. In length the supratemporal equals the frontal. It is bounded posteromedially by the intercalary, anteroventrally by the prootic, anterolaterally by the sphenotic, anteromedially by the frontal and parietal, and medially by the epiotic. A unique feature is the fact that the supratemporal is not united to the exoccipital. The latter is widely separated from the former by the large intercalary.

The *intercalary* is a relatively large bone wedged between the exoccipital, supratemporal, and prootic. The intercalary also contributes to the floor of the posttemporal fossa. The ventral fork of the posttemporal rests on the dorsal surface of the intercalary.

The *parietal* is a crescent-shaped bone contributing to a part of the medial wall of the posttemporal fossa. The parietal does not articulate with the sphenotic. It is bounded medially by the epiotic, anteriorly by the frontal, and laterally by the supratemporal.

The *prootics* are large and more or less hexagonal bones. Each articulates posteriorly with the exoccipital and basioccipital, ventrally with the parasphenoid, anteriorly with the basisphenoid and pterosphenoid, laterally with the frontal, sphenotic, and supratemporal, and posterolaterally with the intercalary. The articulation with the intercalary and with the frontal are certainly unique features. A prominent ridge is present on the prootic at the level of the sphenotic, joining the ascending process of the parasphenoid. The prootic also houses a relatively small funnel-shaped *myodome* which opens posteriorly through a large foramen located at the hind edge of the ascending process of the parasphenoid. The myodome does not reach the basioccipital.

The *exoccipital* articulates ventrally with the basioccipital, anteriorly with the prootic, laterally with the intercalary, and dorsally with the epiotic by means of a dentate suture. Posteriorly the exoccipital forms a condyle with a characteristic shape (fig. 56). The exoccipitals are widely separated from each other by the epiotics and supraoccipital (fig. 56). They form the lateral walls of the relatively large foramen magnum. The foramen exoccipitale, found in all other anabantoid families, is absent.

The *epiotics* are conical bones, articulating medially with the supraoccipital, anteriorly with the parietals, laterally with the supratemporals, and ventrally with the exoccipitals. The epiotic contributes to the medial wall of the posttemporal fossa. Posteriorly it is produced into a long, slender, slightly curved epiotic process. Just lateral to the epiotic process is an articular facet for articulation of the dorsal fork of the posttemporal. The epiotics contribute to the roof of the foramen magnum.

The *supraoccipital* is a very large bone, extending anteriorly as far as the level of the postorbital processes. It possesses an extremely well-developed supraoccipital crest. It adjoins the frontals anteriorly and the parietal and epiotic laterally. Its posteroinferior portion reaches the foramen magnum, contributing to the latter's roof. The supraoccipital does not articulate with the exoccipitals.

The *posttemporal* consists of a somewhat rectangular body and two very distinct forks. The dorsal fork is attached by means of a ligament to the articular facet of the epiotic, just lateral to the epiotic process. The ventral fork rests on the dorsal surface of the intercalary. The body of the posttemporal overlaps the dorsal tip of the supracleithrum.

Basicranial region (figs. 18, 44, 56). The *parasphenoid* covers the ventral surface of the neurocranium for about four-fifths of its entire length. The long narrow bone gives off dorsolaterally directed ascending processes which form part of the lateral wall of the orbital opening of the myodome. It possesses a very prominent median keel, extending to the dorsal keels of the basibranchials, dividing the buccopharyngeal cavity nearly into two halves. The ventral keel reaches its maximum height at the level of the anterior tip of the basisphenoid. From this point the keel diminishes gradually in height and disappears at a level just posterior to the ascending process. At its posterior end the parasphenoid is produced into a prominent keel-shaped pharyngeal process, which occasionally bears two to four very rudimentary teeth. The pharyngeal process projects as far ventrally as the median keel at its maximum height. At the anteroventral corner on either side of the pharyngeal process arises a very well-differentiated, slender, and toothless transverse process (fig. 56). Laterally the transverse process extends nearly to the level of the lateral border of the saccular swelling.

The *basioccipital* is a more or less fan-shaped bone. Posteriorly it forms a vertebralike condyle for articulation with the first vertebra. Ventrally the basioccipital sends out a long, flat, pharyngeal process, which extends as far downward as the pharyngeal process of the parasphenoid. The distal end of the process is bilobed. The pharyngeal process of the basioccipital articulates along its anterior border with the posterior border of that of the parasphenoid. The basioccipital articulates anteroventrally with the parasphenoid, anteriorly with the prootic, and dorsally with the exoccipital.

2. BRANCHIOCRANIUM

Hyobranchial region (fig. 80). The *basihyal* is a rather short bone, expanded dorsoventrally. It contributes to the vertical partitioning of the buccopharyngeal cavity into two halves. The *hypohyal* is somewhat rectangular and articulates with a deep facet of the first basibranchial. It is composed of a dorsal and ventral portion. The *ceratohyal* is rather stout and articulates posteriorly with the somewhat triangular *epihyal.* All the elements in the hyoid apparatus are expanded dorsoventrally. The *interhyal* connects the hyoid apparatus with the cartilaginous block between the symplectic process of the hyomandibular and the symplectic. The first *basibranchial* is hourglass-shaped. The remaining two basibranchials, on the other hand, are rod-shaped. Each basibranchial possesses a very prominent median keel. These keels, together with the keel of the basihyal, the ventral keel of the parasphenoid, and the pharyngeal processes of the parasphenoid and basioccipital, divide the buccopharyngeal cavity into a right and left half. The first four *ceratobranchials* are rod-shaped, slightly curved, and elongate bones. The fifth ceratobranchial is roughly triangular. Contrary to the condition in other anabantoids, the fifth ceratobranchial is toothless. The first *epibranchial* is modified into a labyrinthine suprabranchial organ, which articulates with the prootic by means of a distinct epibranchial process. It is composed of a central stem to which are attached four folded bony lamellae. The remaining three epibranchials are simple elements without any processes. The *pharyngobranchials* are very small. The second pharyngobranchial is reduced to a pear-shaped toothless ossicle. The third and fourth pharyngobranchials are fused indistinguishably. They are also toothless, but bear four rows of bristlelike structures which aid in the filtering mechanism. The *urohyal* possesses a ventrolaterally directed ridge on either side. The six *branchiostegal rays* are large and slightly curved bony plates. The first four articulate with the ceratohyal, the fifth is situated between the ceratohyal and epihyal, and the sixth articulates with the epihyal.

Opercular series. The *opercular* is a large oval bone (fig. 31). A well-differentiated auricular process is not present. The articular process appears as a dorsal earlike projection at the anterodorsal corner of the bone. The entire anterior border of the opercular articulates with the posterior border of the preopercular. The anteroventral corner of the opercular is notched to receive a process from the subopercular.

The *subopercular* is serrate along its ventral border. Posteriorly it is produced into a long fingerlike projection. Anterodorsally the subopercular sends out a prominent process which fits into the anteroventral notch of the opercular.

The *interopercular* is spatulate and serrate along the posterior third of its ventral border. Posteriorly it overlaps the anterior end of the subopercular.

The *preopercular* is sickle-shaped, and possesses three to four rudimentary spines along its posteroventral border. The preopercular overlaps the dorsal half of the interopercular.

Oromandibular region (fig. 68). The large *palatine* possesses an anteriorly directed ethmoid process, which articulates with the orbital wing of the prefrontal-lateral ethmoid complex and also with the inner fork of the maxillary. The palatine articulates ventrally with the ectopterygoid and posteriorly with the entopterygoid.

The *ectopterygoid* is a prominent spindle-shaped bone, partly overlapped by the quadrate. Posterodorsally it is bounded by the entopterygoid.

The large *entopterygoid* adjoins the palatine and ectopterygoid anteriorly, the quadrate and part of the metapterygoid ventrally, and the metapterygoid posteriorly.

The relatively small *metapterygoid* does not articulate with the symplectic process of the hyomandibular.

The *symplectic* is a large, elongate, curved bone. It articulates with the symplectic process of the hyomandibular, the metapterygoid, and the quadrate. The anterior two-thirds of the symplectic rests on the posterior process of the quadrate.

The *quadrate* is convex along its dorsal border. Its posterior border bears two notches. The pointed distal end of the symplectic fits into the ventral notch. Posteroventrally the quadrate is produced into a long and slender posterior process, which supports the anterior two-thirds of the symplectic. Anteriorly the quadrate forms a condyle for articulation with the angular.

The *premaxillary* is a small toothless bone with a knoblike ascending process of approximately the same length as the horizontal limb of the premaxillary.

The *maxillary* is dorsally differentiated into an inner fork which articulates with the ascending process of the premaxillary and the ethmoid process of the palatine and the prevomer.

The *dentary* is highly modified and toothless. Posteriorly it is distinctly notched, forming a movable hingelike joint with the blunt anterior process of the angular.

The *angular* is also very modified. Its vertical position is unique among the anabantoids. Anteriorly the angular sends out a blunt process, which forms a highly movable hinge joint with the dentary. The ascending process of the angular is seemingly wanting, but a very prominent dorsolateral process is differentiated near the posteroventral corner. Ventrally the angular adjoins the small *retroarticular.*

The *hyomandibular* possesses a long symplectic and a short articular process. The processes are at a 90° angle to each other. The symplectic process is expanded along its anterodorsal border and articulates with the symplectic only. Dorsally the hyomandibular is differentiated into a smaller anterior head articulating with the sphenotic and a larger posterior head articulating with the supratemporal.

3. PECTORAL GIRDLE

The spatulate *supracleithrum* is small (fig. 94).

The *cleithrum* possesses a very well-developed ala laminaris externa.

The *postcleithrum* consists of a dorsal and ventral element. The dorsal one is oval, whereas the ventral element is elongate and tapers to a pointed ventral end.

The *scapula* articulates with three *radials.*

The *coracoid* has a slender anterior process which articulates with the lateral surface of the ventral portion of the cleithrum. Posteroventrally the coracoid is not produced into a process. Its posterodorsal corner articulates with one *radial.*

4. PELVIC GIRDLE

The *basipterygia* (fig. 95) are not fused. The *rachis* of the basipterygium is directed anteromedially and is joined to the cleithrum of the corresponding side by a ligament. Ventromedially the rachis gives rise to a prominent winglike *processus medialis anterior.* Two processes originate from the posteromedial corner of the basipterygium: an anteriorly directed slender *processus medialis* and a posteriorly directed earlike *processus medialis posterior.* The *processus lateralis* is wanting.

E. Vertebral Column and Unpaired Appendages

All the vertebrae, with the exception of the first two trunk and caudal vertebrae, have centra which are quite uniform in size and form. The first centrum possesses three points of articulation with the skull: a median basal one for the basioccipital and three dorsolateral ones for the exoccipitals. Neural arches are present and complete on all vertebrae. The neural arch of the first vertebra is rather weakly attached to the centrum. The *prezygapophyses* are short anterodorsal projections from the neural arch. The prezygapophyses are not developed on the first centrum and the centra supporting the caudal fin. The *postzygapophyses* are posterodorsal spinelike projections on the neural arch. They gradually diminish in size in the posterior half of the caudal region. The *basapophyses* are lacking on the first three vertebrae in the Anabantidae, the first two in *Belontia,* and the first one in all other anabantoids. The basapophyses are present on the other trunk vertebrae and the first caudal vertebra. In the most anterior part of the vertebral column the basapophyses are located higher on the centrum, but proceeding posteriorly there is a gradual shift to a ventrolateral position. The first hemal arch possesses a very prominent hemal spine supporting the anal fin. The anterior surface of the first hemal spine has a groove for articulation with the pterygiophores from the anterior end of the anal fin. There is a gradual decrease in size of the hemal spines proceeding caudad. Table 2 summarizes the vertebral counts made in this study. Following Schultz (1958), the first vertebra with a fully developed hemal spine, or one that reaches past the tips of the first anal pterygiophores, was considered as the first caudal vertebra.

Three vertebrae are involved in the support of the caudal fin. Their centra are somewhat shorter than those of the preceding caudal vertebrae. The vertebra anterior to the antepenultimate has a hemal spine which represents a transitional stage between typical hemal spines and hypurals. The antepenultimate vertebra possesses a typical neural spine and an elongate curved hypural. The penultimate vertebra has a neural arch with a long pointed spine. The hypural of the penultimate vertebra is broader than that of the antepenultimate. The ultimate vertebra is modified posteriorly for the support of the hypurals. The third hypural does not articulate with the ultimate vertebra in *Anabas, Sandelia, Belontia, Trichogaster,* and *Colisa.* The third hypural is ankylosed to the ultimate vertebra in *Sphaerichthys, Macropodus, Betta,* and *Helostoma.* Hypurals 4-8 articulate with the ultimate vertebra in all Anabantoidei. Dorsal to the ultimate vertebra are two (in *Helostoma,* one) rod-shaped epurals. The morphology of the pterygiophores conforms with the condition in the Perciformes (Dineen and Stokely, 1956). The number of interneurals and pterygiophores is summarized in Table 3.

Two kinds of ribs are present: the epipleural ribs, which are ossifications in the horizontal skeletogenous septum, and the pleural ribs, which are preformed in cartilage between the celomic wall and the hypaxial muscles. All trunk vertebrae carry epipleural ribs, except in *Anabas* and *Sandelia.* In the latter two the epipleurals are absent from the first two trunk vertebrae. In *Belontia* the first four epipleurals originate from the neural arches and the next two from the basapophyses. The first two trunk vertebrae lack pleural ribs in *Anabas, Trichogaster, Trichopsis, Macropodus, Betta,* and *Sandelia.* In *Sphaerichthys, Helostoma,* and *Belontia,* all trunk vertebrae but the first bear pleural ribs. Pleural ribs are found on all the trunk vertebrae in *Colisa.* Table 4 summarizes the counts on the pleural and epipleural ribs.

Table 2. Number of Vertebrae in the Anabantoidei.

Taxa	Trunk vertebrae						Caudal vertebrae							Total vertebrae						
	9	10	11	12	13	14	15	16	17	18	19	20	21	25	26	27	28	29	30	31
Anabantidae																				
Anabas testudineus	—	8	—	—	—	—	8	—	—	—	—	—	—	8	—	—	—	—	—	—
Ctenopoma muriei	—	1	—	—	—	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—
Ctenopoma multispinis	—	3	—	—	—	—	3	—	—	—	—	—	—	3	—	—	—	—	—	—
Sandelia capensis	—	4	—	—	—	—	4	—	—	—	—	—	—	4	—	—	—	—	—	—
Sandelia bainsii	—	3	—	—	—	—	3	—	—	—	—	—	—	3	—	—	—	—	—	—
Belontiidae																				
Belontia hasselti	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	1	—	—	—	—
Betta anabatoides	—	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1	—	—
Betta splendens	—	6	—	—	—	—	—	—	—	—	6	—	—	—	—	—	—	6	—	—
Trichopsis pumilus	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—	—	—
Trichopsis vittatus	9	—	—	—	—	—	—	—	—	—	9	—	—	—	—	—	9	—	—	—
Macropodus cupanus	6	—	—	—	—	—	—	—	—	6	—	—	—	—	—	6	—	—	—	—
Macropodus opercularis	6	—	—	—	—	—	—	—	1	4	1	—	—	—	1	4	1	—	—	—
Sphaerichthys osphromenoides	2	—	—	—	—	—	—	2	—	—	—	—	—	2	—	—	—	—	—	—
Trichogaster trichopterus	—	6	—	—	—	—	—	—	—	—	—	3	3	—	—	—	—	—	3	3
Colisa fasciata	5	1	—	—	—	—	—	1	5	—	—	—	—	—	—	6	—	—	—	—
Colisa labiosa	4	2	—	—	—	—	2	4	—	—	—	—	—	—	—	6	—	—	—	—
Colisa lalia	—	6	—	—	—	—	—	6	—	—	—	—	—	6	—	—	—	—	—	—
Helostomatidae																				
Helostoma temmincki	—	—	—	—	—	6	6	—	—	—	—	—	—	—	—	—	—	6	—	—
Osphronemidae																				
Osphronemus goramy	—	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1	—	—

TABLE 3. NUMBER OF INTERNEURALS AND PTERYGIOPHORES OF THE ANABANTOIDEI.

Taxa	Interneurals	Dorsal pterygiophores	Anal pterygiophores
Anabantidae			
Anabas testudineus	2	26	19
Ctenopoma multispinis	3	22	17
Sandelia capensis	3	21	13
Belontiidae			
Macropodus cupanus	4	20–21	29–30
Macropodus opercularis	3–4	20–21	29–34
Belontia hasselti	3	30	27
Trichopsis vittatus	11	9	33
Sphaerichthys osphromenoides	4–5	17	28
Trichogaster leeri	9	14	44
Betta splendens	9	11	28
Colisa lalia	1	23	35
Helostomatidae			
Helostoma temmincki	1–2	30–31	30–32
Osphronemidae			
Osphronemus goramy	4	25	32

TABLE 4. NUMBER OF PLEURAL AND EPIPLEURAL RIBS IN SOME ANABANTOIDEI.

	Pleural ribs			Epipleural ribs		
Taxa	Trunk	Caudal	Total	Trunk	Caudal	Total
Anabantidae						
Anabas testudineus	8	12–13	20–21	8	5	13
Ctenopoma multispinis	9	13	22	10	3	13
Sandelia capensis	8	13	21	10	4	14
Belontiidae						
Belontia hasselti	9	2	11	10	1	11
Betta splendens	8	15	23	10	8	18
Trichopsis vittatus	7	3–0	7–10	9	6–0	9–15
Macropodus cupanus	7	8–9	15–16	9	8–9	17–18
Macropodus opercularis	7	8–9	15–16	9	6	15
Sphaerichthys osphromenoides	8	0	8	9	4	13
Trichogaster leeri	8	16	24	10	0	10
Colisa lalia	9	12–13	21–22	10	7–9	17–19
Helostomatidae						
Helostoma temmincki	13	9	22	13–14	0	13–14
Osphronemidae						
Osphronemus goramy	10	11	21	9	7	16

F. OTOLITHS

Three types of otoliths can be recognized: the *utriculith, sacculith,* and *lagenolith,* located respectively in the utriculus, sacculus, and lagena of the inner ear. In the Anabantoidei the utriculith and lagenolith prove to be of little value in establishing relationships since they are subject to intraspecific variation. The sacculith, on the other hand, proves to be useful in determining phylogenetic relationships, and is therefore the only otolith described in this study.

Anabantidae (figs. 88, 90). The outer face is concave, the inner convex. The horizontal sulcus opens on the anterior rim and does not reach the posterior one. The sulcus has a short wide ostium and a long narrow cauda. Distinct colliculi are present. The ventral border is distinctly scalloped.

Belontiidae. The outer face is slightly concave, the inner convex. The horizontal sulcus opens on the anterior border. It does not open posteriorly. The ostium and colliculi are wanting. The dorsal border is distinctly indented. The anterior half of the dorsal border is indented in *Belontia, Sphaerichthys, Colisa,* and *Trichogaster.* In *Betta* and *Macropodus* only the anterior third of the dorsal rim is indented. *Betta* is unique in having a posterior indentation in addition to the anterior one. The posterior rim is scalloped in *Betta, Sphaerichthys, Colisa,* and *Trichogaster.*

Osphronemidae. The sacculith of *Osphronemus* resembles that of *Colisa* in many details.

Helostomatidae. The sacculith of *Helostoma* has a very characteristic shape. It is much deeper bodied than the sacculith of other Anabantoidei. The inner face is convex, the outer slightly concave. The horizontal sulcus opens at the anterior rim and does not reach the posterior border. The entire border of the sacculith is distinctly scalloped. A deep

TABLE 5. SCALE TYPES FOUND IN SOME ANABANTOIDEI.[a]

Taxa	Trunk	Top of head	Throat	Dorsal fin	Anal fin
Anabantidae					
Anabas testudineus	t	t	t	t	t
Ctenopoma multispinis	t	y	t	t	t
Sandelia capensis	y	y	y	y	y
Belontiidae					
Belontia hasselti	t	y	t	t	t
Sphaerichthys osphromenoides	t	t	t	t	t
Trichogaster trichopterus	t	t	t	t	t
Colisa labiosa	t	t	t	t	t
Helostomatidae					
Helostoma temmincki	t	y	t	t	t
Osphronemidae					
Osphronemus goramy	t	t	t	t	t

[a] t = ctenoid; y = cycloid.

notch is present at the dorsoanterior corner. The lagenolith has a specific shape (fig. 88 D).

G. Scales

In all Anabantoidei the whole trunk, head, cheeks, dorsal, anal, pectoral, and caudal fins are covered with scales. Berg (1958) stated that the scales in the Anabantoidei are characteristically ctenoid. This generalization is incorrect (Table 5).

DISCUSSION

A. INTERRELATIONSHIPS AND DISTINCTIONS OF ANABANTOID FAMILIES

Many authors, among others Günther (1880), Regan (1909), Weber and de Beaufort (1922), Giltay (1933), Romer (1945), Bertin and Arambourg (1958), Darlington (1957), Berg (1958), and Herald (1961), recognize one family within the Anabantoidei, the Anabantidae. Gill (1893) subdivided the Anabantoidei into the Anabantidae, Osphronemidae, and Luciocephalidae. Boulenger (1904) considers the Anabantidae as a family of the order Percesoces, and the Osphronemidae as a family of the Perciformes. He included *Luciocephalus* in the osphronemids. Jordan (1923) distinguishes six families among the Labyrinthici: Luciocephalidae, Ophicephalidae, Helostomatidae, Polyacanthidae, Osphronemidae, and Anabantidae.

All previous workers have based their classification on external features and the "labyrinth organ" without proper judgment of the taxonomic values of the characters used. Consequently the phylogeny, relationships, and distinctions of the Anabantoidei appear misinterpreted and poorly understood. Recent authors, for example Forselius (1957), Nikolski (1957), Bertin and Arambourg (1958), Darlington (1957), and Herald (1961), tend to follow Berg's classification (1940), in which he classified the Anabantoidei as a suborder of the Perciformes, with the Anabantidae as the only family. Berg separated *Luciocephalus* from the Anabantoidei, for the first time giving the aberrant genus a subordinal rank, Luciocephaloidei, among the Perciformes. The status of *Luciocephalus* will be discussed in a separate section.

The osteological evidence obtained in this study requires distinction of four major groups among the Anabantoidei:

Anabantidae: *Anabas*, *Ctenopoma*, and *Sandelia*.

Belontiidae: *Belontia*, *Betta*, *Trichopsis*, *Macropodus*, *Sphaerichthys*, *Colisa*, *Trichogaster*, *Malpulutta*, *Parasphaerichthys*, and *Parosphromenus*.[1]

Helostomatidae: *Helostoma*.

Osphronemidae: *Osphronemus*.

FAMILY ANABANTIDAE BONAPARTE

Anabantidae Bonaparte, 1839, Mém. Soc. Sci. Neuchâtel, 2: 13-14.

The family Anabantidae (type genus *Anabas* Cuvier) may be con-

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[1] The last three were not examined osteologically.

sidered modern remnants of the more generalized ancestral forms. It can be easily distinguished from the remaining Anabantoidei by the following characters:

1. The prevomer bears two rows of conical teeth (fig. 40).
2. Extrascapulars are present, overlying the epiotics and intercalaries.
3. Distinct posttemporal fossae are absent.
4. The foramen magnum is small. Its lateral walls and roof are formed by the exoccipitals (fig. 52).
5. The parasphenoid underlies the greater part of the basioccipital (fig. 40).
6. The pharyngeal processes of the basioccipital are short and stout, extending laterally from the posteroventral corner of the basioccipital.
7. The parasphenoid possesses a well-developed and toothed transverse process (fig. 14).
8. The entire straight anterior border of the opercular is united with the posterior border of the preopercular (fig. 27).
9. The posterior border of the opercular is serrate, and so is the posteroventral border of the interopercular.
10. An ectopterygoid is present (fig. 64).
11. The metapterygoid is united with the symplectic process of the hyomandibular.
12. The length of the ascending process of the premaxillary is one-fifth to one-half that of the horizontal body of the premaxillary.
13. The angular and dentary lack distinct ascending processes.
14. The basipterygia are firmly joined, forming a bilateral symmetrical unit (fig. 91).
15. The conjoined anterior tips of the basipterygia are united to the cleithral symphysis by a ligament.
16. Total number of vertebrae is 25.
17. The sacculith is not indented anteriorly and possesses an ostium and colliculi.

The Anabantidae appears to be the most primitive and may have given rise to the Helostomatidae, Osphronemidae, and Belontiidae. The presence of teeth on the prevomer and the palatine is, as a rule, characteristic of the least specialized representatives of the teleosts. This fact has, as most authors (Myers, 1958, and Makushok, 1958) have pointed out, auxiliary importance for the establishment of relationships. The well-developed extrascapulars, overlying the epiotics and intercalaries, resemble those described in *Amia* by Shufeldt (1885). The toothed transverse processes of the parasphenoid, palatines, and prevomer indicate that these fishes are carnivorous, as indeed is reported by Vaas, Sachlan, and Wiraatmadja (1953) for *Anabas testudineus.* The mouth is relatively large and the ascending processes of the premaxillaries are very short. The protrusility of the jaws is consequently very limited. This type of jaw represents a primitive condition among the acanthopterans as described by Gregory (1933) for *Lates niloticus*. The oromandibular apparatus is complete and has a well-developed ectopterygoid (fig. 64). Other primitive features are the articulation of the metapterygoid with the symplectic process of the hyomandibular, the connection of the ankylosed basipterygia to the cleithral symphysis by means of a ligament, and the presence of an ostium and colliculi and absence of an anterior indentation on the sacculith. The primitive phylogenetic features in their totality seem to indicate that the Anabantidae resemble the ancestral stock in many important ways.

FAMILY BELONTIIDAE N. FAM.

The Belontiidae (type genus *Belontia* Myers), the largest group of the Anabantoidei, is characterized by the following features:

1. No teeth on the prevomer (figs. 45-51).
2. Extrascapulars are wanting (figs. 6-13).
3. The posttemporal fossae are well developed.
4. The posteroinferior portion of the supraoccipital forms part of the roof of the relatively large foramen magnum (figs. 57-63).
5. A prominent, bilobed, pharyngeal process of the basioccipital is present (figs. 45-51, 57-63).
6. Transverse processes of the parasphenoid are wanting.
7. The parasphenoid has a well-developed pharyngeal process (figs. 19-26).
8. The interopercular is not serrate (figs. 32-39).
9. The ectopterygoid is wanting (figs. 69-75).
10. Distinct ascending processes are present on the angular and dentary.
11. The length of the ascending processes of the premaxillaries is one to two and a half times that of the horizontal body of the premaxillary.
12. The sacculith is indented anteriorly. It lacks an ostium and colliculi.

The Belontiidae forms the largest group of the Anabantoidei. There is a large morphological gap between the Belontiidae and the Anabantidae. The belontiids form a more specialized group. The specialization amounts to the total loss of the extrascapulars in the otic region, and the ectopterygoid in the oromandibular region (figs. 6-13, 69-75). Other specialized features are the reduction in size of the gape of the mouth, the increase in length of the ascending processes of the premaxillaries, dentary, and angular, the acquisition of a protrusile jaw mechanism, the loss of teeth on the prevomer and palatine, the development of ventrally directed pharyngeal processes of the parasphenoid and basioccipital, and the presence of an anterior indentation and loss of ostium and colliculi on the sacculith. These morphological distinctions can be traced invariably in all representatives of the group. The establishment of a family for this homogenous group seems to be well supported by the new osteological data. Jordan (1923) proposed the family Polyacanthidae with *Polyacanthus hasselti* as the type and only species. *Polyacanthus*, however, type species *opercularis* (L.), is a synonym of *Macropodus* (see Myers, 1923). *Polyacanthus hasselti* therefore needed a new name, and in 1923 Myers proposed *Belontia* for it. According to Article 5 of the International Code of Zoological Nomenclature as quoted by Schenk, McMasters, Keen, and Muller (1956), the family name Polyacanthidae should be changed to Belontiidae, because the name of the type genus has been changed from *Polyacanthus* to *Belontia*. This view appears to be valid under the 1961 Code also. The Belontiidae include all genera of Jordan's family Osphronemidae, with the exception of *Osphronemus*. The latter resembles the belontiids superficially but, as discussed in the following section, the resemblances are due to convergence rather than phylogenetic relationships.

FAMILY OSPHRONEMIDAE BLEEKER

Osphronemoidei Bleeker, 1859, Enumeratio Specierum Piscium Archipelago Indico: 18.

The Osphronemidae (type genus *Osphronemus* Lacépède) resembles the belontiids in several ways, but can be distinguished by the following characters:

1. The ethmoid is horizontal and does not articulate with the prevomer.
2. Posteriorly the shaft of the prevomer does not taper to a point; the prevomer forms dorsally a rostral fossa (fig. 43).
3. The second and third suborbitals are serrate.
4. A distinct suborbital shelf is wanting.
5. The parietals are large and appear as inverted V's (fig. 4).
6. The supraoccipital forms the roof of the relatively small foramen magnum, separating the exoccipitals widely (fig. 55).
7. The subopercular, interopercular, and preopercular are serrate (fig. 67).
8. The ectopterygoid is present (fig. 67).
9. The metapterygoid articulates with the symplectic process of the hyomandibular.
10. The very elongate basipterygia are directed dorsomedially and are directly connected to the cleithra (fig. 93).
11. There are 29 vertebrae.
12. All scales are ctenoid.

The Osphronemidae are only distantly related to the belontiids despite the close superficial resemblances between the two groups. Jordan (1923) did not recognize the phylogenetic heterogeneity of his family Osphronemidae. The osphronemids seem to be an early offshoot of the anabantid stock. They are readily distinguished from the belontiids by the following characters: the presence of well-developed ectopterygoids, the serrated interoperculars, second and third suborbitals, and vestigial suborbital shelf, and failure of the ethmoid to articulate with the prevomer. The retention of the ectopterygoid in the oromandibular region suggests that the osphronemids form one of the three main evolutionary lines derived from the Anabantidae. The loss of the suborbital shelf is also an indication that the osphronemids represent a different evolutionary line from the belontiids, in which the extensive suborbital shelf is retained. The Osphronemidae *sensu novo* thus encompasses only one genus, *Osphronemus.*

FAMILY HELOSTOMATIDAE JORDAN

Helostomidae Jordan, 1923, Stanford Univ. Publ. Biol. Ser., 3: 132.

The family Helostomatidae (type genus *Helostoma* Cuvier) is composed of only one monotypic, highly specialized genus, *Helostoma,* which can be characterized as follows:

1. The toothless prevomer possesses prominent dorsolateral wings which articulate with the nasals and prefrontal-lateral ethmoid complex (fig. 18).
2. The pterosphenoid articulates with the prefrontal-lateral ethmoid complex (fig. 44).
3. The epiotics and supraoccipital form the roof of the large foramen magnum (fig. 56).
4. The parasphenoid possesses a keel-shaped pharyngeal process and long, slender, transverse processes (figs. 18, 44, 56).
5. The fifth ceratobranchial and second, third, and fourth pharyngobranchials are toothless (fig. 80).
6. An ectopterygoid is present (fig. 68).
7. The metapterygoid does not articulate with the symplectic process of the hyomandibular.
8. The premaxillary is toothless (fig. 68).
9. The toothless dentary forms a hingelike, highly movable joint with the angular (fig. 68).
10. The suborbital shelf is wanting.

The elaborate filter apparatus of the gill arches has been described by Seitz (1937). Böker (1937), and Vaas, Sachlan, and Wiraatmadja (1953) classify *Helostoma* principally as a plankton feeder. The helostomatids resemble the belontiids and osphronemids in the loss of the extrascapulars and the development of a pharyngeal process on the parasphenoid. The group, on the other hand, differs significantly from the other Anabantoidei in the following specialized characters: the prevomer articulates with the nasals, and the parasphenoid possesses both the pharyngeal and transverse processes, the toothless buccopharyngeal cavity, and the highly movable hinge joint between the dentary and angular. The presence of a well-developed ectopterygoid and both the pharyngeal and transverse processes on the parasphenoid suggests that the helostomatids originated independently from the osphronemids and belontiids.

B. Interrelationships Among Anabantid Genera

Boulenger (1916) placed the Asiatic genus *Anabas* with the African *Ctenopoma* under the former name. De Beaufort (1951), Kosswig (1954), Steinitz (1954), and Darlington (1957) followed Boulenger's view. But several authors do distinguish the two separate genera (Regan, 1909, Jordan, 1923, Krull, 1939, Forselius, 1957, and Bertin and Arambourg, 1958). The two genera are undoubtedly distinct from each other and can be separated easily by the osteological characters tabulated below:

Anabas (figs. 27, 40, 64).	*Ctenopoma* (figs. 28, 29, 41, 65).
Lachrymal possesses long radiating spines.	Lachrymal weakly serrate; in *Ctenopoma multispinis* no serration.
Suborbitals 2-4 suturally united with preopercular.	Suborbitals 2-4 do not articulate with preopercular.
Posttemporal slightly forked.	Posttemporal distinctly forked.
Transverse process of parasphenoid short with five teeth.	Transverse processes of parasphenoid long with numerous small teeth.
Fifth and sixth branchiostegal rays articulate with epiphyal.	Only sixth branchiostegal ray articulates with epihyal.
Opercular deeply serrate and with two spines.	Opercular serrate, no spines.
Palatine toothless.	Teeth on palatine.
Ascending process of premaxillary one-third of body of premaxillary.	Ascending process of premaxillary one-fifth of body of premaxillary.
Basipterygium with a prominent processus lateralis.	Processus lateralis on basipterygium vestigial.

Myers (1926) stated that *Ctenopoma multispinis* may be congeneric with the Asiatic *Anabas* because of the strongly denticulate subopercular. From the above mentioned differences it is evident that *multispinis* is not congeneric with *Anabas*. The serration of the subopercular cannot be considered as a characteristic of the genus *Anabas*.

It is generally assumed (Forselius, 1957) that *Anabas* is a recent representative of an ancestral form of anabantid fish and is less specialized than *Ctenopoma* and *Sandelia*. Regan (1909) considers *Ctenopoma* to be more closely related to *Anabas* than to *Sandelia*.

There is sufficient osteological evidence to assume safely that *Anabas* and *Ctenopoma* resemble the ancestral anabantid stock very closely. Regan's hypothesis that *Anabas* is a recent representative of an ancestral anabantid is, however, difficult to support. *Anabas* is specialized in several ways, and originated from the hypothetical ancestral stock during the Lower Tertiary (see subsequent discussion). *Ctenopoma* is more primitive than *Anabas* in several features: the presence of teeth on the palatines, the shorter ascending process of the premaxillary, and the large number of teeth on the parasphenoid. *Anabas,* on the other hand, appears to be more archaic in the following characters: the posttemporal is only slightly forked, the fifth and sixth branchiostegal rays articulate with the epihyal, and the suborbitals are suturally united to the preopercular. *Ctenopoma* and *Anabas* seem to be derived from a common ancestral stock, which possessed the primitive characters exhibited in both genera.

The genus *Sandelia* can be distinguished from *Ctenopoma* as follows:

Sandelia	*Ctenopoma*
Nasals separated (fig. 3).	Nasals suturally joined (fig. 2).
Very shallow posttemporal fossa present.	No posttemporal fossa.
Extrascapulars do not articulate with supraoccipital and cover epiotics partly (fig. 3).	Extrascapulars cover epiotics and articulate with supraoccipital (fig. 2).
Intercalary small, wedged between supratemporal and exoccipital.	Intercalary cone-shaped, forming posteroventral corner of neurocranium.
First epibranchial a rectangular plate.	First epibranchial labyrinthine-shaped.
Five branchiostegal rays (fig. 78).	Six branchiostegal rays (fig. 77).
Subopercular not serrate (fig. 30).	Subopercular serrate (figs. 28, 29).
Ascending process of premaxillary one-half to one-third of body of premaxillary.	Ascending process of premaxillary one-fifth of body of premaxillary.
Scales cycloid.	Scales ctenoid and cycloid.

Regan's hypothesis that *Ctenopoma* is more closely related to *Anabas* than to *Sandelia* is supported by the data tabulated above. The loss of one branchiostegal ray, the separation of the nasals, and the simple first epibranchial are certainly specialized characters separating *Sandelia* widely from *Ctenopoma*. *Sandelia* seems to have developed in isolation in the southern tip of Africa (Barnard, 1943). The simple form of the suprabranchial organ seems to indicate that the air-breathing capacity of *Sandelia* is less efficient than that of its tropical predecessors. *Sandelia* is probably not exposed to such austere habitats as *Ctenopoma* is in the tropical swamps of central Africa. Air-breathing is of great survival value in habitats which are subjected to periodic droughts. *Sandelia* has penetrated into temperate habitats in which severe periodic droughts do not occur. In these habitats air-breathing may not be a selective advantage, since it has lost most of its survival value. It is, therefore, to be expected that the labyrinthine suprabranchial organ could disappear during the course of evolution in environments in which the original adaptive value of air-breathing is lost. Regression of the suprabranchial respiratory organs has also been recorded in some Clariidae (Greenwood, 1961). Greenwood considers the variation of suprabranchial organs of the clariids as an example of cyclic evolution. A similar theory may be suggested for the anabantids. Jordan (1923) has apparently misplaced *Sandelia* in the family Helostomatidae. The differences between *Sandelia* and *Helostoma* are plainly evident from the previous section on the interrelationships of the anabantoid families.

C. Interrelationships Among Belontiid Genera

The more conservative representative of the belontiids appears to be the genus *Belontia*. It retains several ancestral features: the articulation of the entire straight anterior border of the opercular with the posterior border of the preopercular (fig. 32), the metapterygoid joined to the symplectic process of the hyomandibular (fig. 69), the relatively short ascending process of the premaxillary, and the ankylosed basipterygia with the conjoined rachii (fig. 96). These well-marked differences between *Belontia* and the other belontiids point to a long period of independent existence. Opposed to the above mentioned conservative features, a number of specialized modifications are exhibited in *Belontia*. Among these are the prominent posterior extension of the suprabranchial cavity, which is supported by the first six epipleural ribs, the large supraoccipital with a high crest, and the development of longitudinal ridges on the parietals and epiotics for additional insertion of the epaxial muscles (fig. 19). *Belontia* seems to be an isolated genus representing the end product of a sterile evolutionary line.

Originating from the same ancestor of *Belontia* is another branch of the family, of which *Betta* appears to be the most primitive. *Betta* is easily distinguished from the other genera by the loss of serration of the lachrymal and preopercular (fig. 33), the presence of a process on the ethmoid and basisphenoid supporting the interorbital septum (fig. 20), and the anterior and posterior indentations of the dorsal rim of the sacculith.

In *Trichopsis*, the widely separated nasals become elongate and tubular (fig. 8), the ventral fork of the basisphenoid is lost (fig. 21), and the number of teeth on the pharyngeal process is reduced from five, as in *Betta*, to four.

A third evolutionary line which probably originated from the ancestor of *Betta* has been more flexible, giving rise to several divergent groups. The closely related genera *Macropodus, Parosphromenus,* and possibly *Malpulutta* constitute one group. *Macropodus* is disturbingly diverse but I am not now convinced that its partition at the generic level would be advisable. *Macropodus cupanus* is widely different in osteology from *Macropodus chinensis* and the type species *Macropodus opercularis:*

M. opercularis and *M. chinensis*	*M. cupanus*
Nasals widely separated (fig. 10).	Nasals suturally united (fig. 9).
Ethmoid exposed dorsally.	Ethmoid covered dorsally by frontals and nasals.
Ethmoid lacks processes (fig. 23).	Ethmoid possesses a posterior keel-like process extending into orbit (fig. 22).

These osteological distinctions, combined with the resemblance of the breeding behavior to that of *Betta splendens* (Seleuthner, 1950, as quoted by Gilch, 1957) and the absence of oil containers in the eggs (Oelschlager, 1925, and Seleuthner, 1950, as quoted by Gilch, 1957), collectively suggest that *cupanus* represents a separate genus or subgenus. Seleuthner (1950, as quoted by Gilch, 1957) suggested that *cupanus* represents an intermediate stage between *Betta* and *Macropodus.* The species *cupanus* is definitely more primitive than the other forms examined of *Macropodus,* but it also differs significantly from *Betta. Polyacanthus* is not available since its type is *Chaetodon chinensis* Bloch, a synonym of *Labrus opercularis* L. The type of *Macropodus* is *M. viridi-auratus,* which is, however, conspecific with *Labrus opercularis* (Myers, 1923). Accordingly a new name would be required if *cupanus* were to be regarded as distinct generically or subgenerically from other species now assigned to *Macropodus.* I here refrain from erection for *cupanus* of (*a*) a new genus because *chinensis* is in several ways intermediate in osteology between *cupanus* and *opercularis,* and (*b*) a new subgenus because the differences are not in my opinion commensurate with the conventionally accepted requirements for a monotypic group.

Macropodus is more specialized than *Betta* and *Trichopsis* because it acquired a greater reduction in size and number of teeth on the pharyngeal process of the parasphenoid and a greater angle between the pharyngeal process of the parasphenoid and the horizontal axis of the basioccipital.

The position of *Malpulutta* and *Parosphromenus* is still uncertain. The lack of material for anatomical study renders impossible determination of the exact relationships. Deraniyagala (1937) stated that *Malpulutta* is related to *Belontia* and *Macropodus,* and that *Sphaerichthys* is the genus most closely related to *Malpulutta.* There is, however, no supporting evidence for this hypothesis. *Belontia* and *Macropodus* are very distantly related to each other, as shown in the beginning of this section. *Sphaerichthys* differs in many ways from *Macropodus. Malpulutta* and *Parosphromenus* are tentatively placed between *Macropodus* and *Sphaerichthys.*

The rest of the belontiids belongs to an evolutionary line which, seemingly, has been derived from an ancestral *Macropodus.* This evolutionary line is comprised of the genera *Sphaerichthys, Parasphaerichthys, Colisa,* and *Trichogaster. Sphaerichthys* probably originated from a *Macropodus*-like stock and became specialized as follows: the nasals became long, narrow, tubular, and widely separated (fig. 11); the ethmoid became fully exposed dorsally; the epiotic processes were lost; the keellike pharyngeal process of the parasphenoid turned to a straight angle with the horizontal axis of the basioccipital (fig. 24); the number of teeth on the pharyngeal process of the parasphenoid was reduced to one; the dorsal quarter of the pharyngeal process of the basioccipital acquired a connection with that of the parasphenoid; the radials became elongate rod-shaped structures; the number of vertebrae became reduced to 25; and the pleural and epipleural ribs were lost in the caudal region.

In the second evolutionary line, derived from the *Macropodus*-like stock and leading to *Colisa* and *Trichogaster,* the nasals remain large plates overlying the ethmoid completely, the pleural ribs in the caudal region are retained, and the number of vertebrae increases.

An accentuation of the evolutionary trend already present in *Sphaerichthys* can be traced in the following morphological characters: the pharyngeal process of the basioccipital is joined along its entire anterior border to that of the parasphenoid, the pharyngeal process of the parasphenoid possesses zero to two vestigial teeth (figs. 25, 26), and the number of teeth on the fifth ceratobranchial is greatly reduced (figs. 86, 87).

Trichogaster and *Colisa* can be separated as follows:

Trichogaster	*Colisa*
Ethmoid subvertical and not cup-shaped.	Ethmoid vertical and cup-shaped, extending posteriorly between eyes to middle of orbit.
No teeth on pharyngeal process of parasphenoid.	Pharyngeal process of parasphenoid with one to two vestigial teeth.
Second pharyngobranchial bears six teeth.	Second pharyngobranchial bears four teeth.
Five pelvic fin rays and spine present.	One pelvic fin ray, spine rudimentary.
Six to ten interneurals.	One to two interneurals.
Total number of vertebrae 30 to 31.	Total number of vertebrae 26 to 29.
Epipleural ribs not present in caudal region.	Seven to nine epipleural ribs in caudal region.

The ancestral *Macropodus*-like stock may have separated into two lines. One of these, the genus *Colisa,* shows a tendency toward a posterior shift and modification of the ethmoid, a marked reduction in number of interneurals, a retention of the epipleurals in the caudal region, and a reduction in the number of pelvic fin rays. In the other line of development, the genus *Trichogaster,* the ethmoid remained subvertical, the number of interneurals increased, the epipleural ribs in the caudal region were lost, and all five pelvic fin rays were retained. Many important similarities between *Colisa* and *Trichogaster,* as for example the large size of the foramen magnum, the articulation of the pharyngeal process of the basioccipital with that of the parasphenoid, and the contribution of the epiotics in the formation of the roof of the foramen magnum, strongly indicate the close relationship of the two genera.

The status of *Parasphaerichthys* remains to be investigated. Prashad and Mukerji (1929) stated that it is closely related to *Sphaerichthys.* They summarize the two genera as follows:

Sphaerichthys	*Parasphaerichthys*
Jaws equal.	Jaws unequal.
Lateral line vestigial.	Lateral line absent.
Dorsal fin with 8 to 12 spines and 7 to 10 rays.	Dorsal fins with 4 spines and 6 rays.
Anal fin with 8 to 10 spines and 18 to 22 rays.	Anal fin with 13 spines and 12 rays.
Ventrals originate slightly before pectorals.	Ventrals originate slightly behind pectorals.

Parasphaerichthys is here tentatively placed close to *Sphaerichthys.*

Within the Belontiidae, then, three well-defined groups can be recognized. The establishment of three new subfamilies not only illustrates the natural relationships between the belontiids, but also represents the three major evolutionary lines of the family. The three new subfamilies are:

1. Belontiinae n. subfam., which includes just one genus, *Belontia.*
2. Macropodinae n. subfam., comprised of the following genera: *Betta, Trichopsis, Macropodus, Parosphromenus,* and *Malpulutta.*
3. Trichogasterinae n. subfam., which encompasses *Sphaerichthys, Parasphaerichthys, Colisa,* and *Trichogaster.*

The morphological distinctions between the three subfamilies, constituting their diagnoses, are tabulated below (figs. 19-26, 32-39, 45-51, 57-63, 69-75, 81-87, 96-102):

Belontiinae	Macropodinae	Trichogasterinae
Eight to ten teeth on pharyngeal process of parasphenoid.	Two to five teeth on pharyngeal process of parasphenoid.	Zero to two rudimentary teeth on pharyngeal process of parasphenoid.
Pharyngeal process of basioccipital does not articulate with that of parasphenoid.	As in Belontiinae.	Pharyngeal process of basioccipital articulates with that of parasphenoid.
Entire anterior border of opercular articulates with preopercular.	Anterior border of opercular articulates partly with preopercular.	As in Macropodinae.
Metapterygoid articulates with symplectic process of hyomandibular.	Metapterygoid does not articulate with hyomandibular.	As in Macropodinae.
Ascending process of premaxillary shorter than its body.	Ascending process of premaxillary one to one and a half times its body.	Ascending process of premaxillary at least twice as long as its body.
Posterior extension of suprabranchial cavity supported by first six epipleurals.	No posterior extension of suprabranchial cavity.	As in Macropodinae.
Pterosphenoids united.	Pterosphenoids separated.	As in Macropodinae.
Six branchiostegal rays, of which sixth is joined to epihyal.	Six branchiostegal rays joined to ceratohyal.	Five branchiostegal rays joined to ceratohyal.
Suborbital shelf formed by suborbitals 2-5.	As in Belontiinae.	Suborbital shelf formed by suborbital 2.
Epiotics do not reach foramen magnum.	As in Belontiinae.	Epiotics reach large foramen magnum.
Supraoccipital articulates with exoccipitals.	As in Belontiinae.	Supraoccipital does not articulate with exoccipitals.
Supraoccipital crest present.	Supraoccipital crest absent.	As in Macropodinae.

The evolution of the belontiids may be briefly reviewed as follows. The Belontiinae may have separated at an early stage from the ancestral anabantid stock, retaining several anabantid features: the articulation of the entire straight border of the opercular with the posterior border of the preopercular, the union of the metapterygoid to the symplectic process of the hyomandibular, and the articulation of the sixth branchiostegal ray with the epihyal. The Belontiinae acquired several specializations during their course of evolution: the suprabranchial cavity extends far posteriorly and is supported by the first six epipleural ribs, the pterosphenoids are united, and the supraoccipital crest becomes well differentiated. The Macropodinae may have a common ancestral origin with the Belontiinae. The Macropodinae, however, became specialized in a different way: the suprabranchial cavity becomes reduced in size and shifts into a more ventral position, the supraoccipital crest is not differentiated, the jaws become more protrusile, the teeth on the parasphenoid become vestigial and reduced in number. The Trichogasterinae originated most likely from a *Macropodus*-like ancestor and became modified in the following characters: branchiostegal rays are reduced to five, the teeth on the pharyngeal process of the parasphenoid are vestigial or lost, the supraoccipital is separated from the exoccipitals by the epiotics, the suborbital shelf becomes limited to suborbital 2, and the epiotics reach the very large foramen magnum.

D. Phylogenetic Trends in the Anabantoidei

Gosline (1959) has stressed the importance of a proper understanding of the mode of life and functional morphology for the student of phylogenetic histories of teleosts. A thorough knowledge of the functional systems is especially crucial in the phylogenetic studies of modern teleosts. It seems therefore appropriate to analyze the phylogenetic trends in some morphological and functional units of the Anabantoidei before entering into the final synthesis of the phylogeny.

Protrusility of the jaws (figs. 64-75). The incipient stage is found in the family Anabantidae. In *Ctenopoma* the ascending process of the premaxillary is very short, not exceeding one-fifth of the length of the horizontal body of the premaxillary. The length of the ascending process in *Anabas* and *Sandelia* varies between one-third and one-half of that of the body of the premaxillary. The relatively short ascending processes are more or less conjoined in the midline, forming an inverted V, the top of which articulates with a notch formed by the nasals and ethmoid. The conjoined ascending processes form a "sliding stalk" (Delsman, 1925). This stalk slides forward and backward in the rostral notch. The sliding of the stalk takes place automatically when the dentary and angular are depressed, because of the presence of a ligament on each side which links the freely movable premaxillary with the lower jaw. The adductor mandibulae muscles consist of two parts: A_1 inserts on the medial face of the maxillary, retracting it and indirectly the mandible and premaxillary; A_2 inserts on the ascending processes of the dentary and angular, and pulls on the mandible in closing the mouth. The jaw mechanism is thus of the type common to most acanthopteran fishes (Eaton, 1943). The short ascending processes of the premaxillaries in the primitive Anabantidae limit the protrusility of the jaw to a minimum, because the degree of protrusility of the jaws is directly proportional with the length of the ascending processes of the premaxillaries (Delsman, 1925, Gregory, 1933, and Eaton, 1943).

A nicely graded series toward increased protrusility of the jaws can be followed in the Belontiidae. *Betta* and *Trichopsis* represent the most primitive belontiids. The mouth is of moderate size. The ascending process of the premaxillary in *Betta* is slightly longer than its horizontal body. In *Trichopsis* the length of the ascending process is approximately one and a half times that of the body. *Macropodus* represents an intermediate stage between the moderately protrusile jaws of *Betta* and *Trichopsis* and the highly protrusile jaws of the Trichogasterinae, in which the ascending process is at least twice as long as the body of the premaxillary. Correlated with the increased protrusility is a gradual development of the ascending processes of the dentary and angular for insertion of part A_2 of the adductor mandibulae muscle. Increased protrusility of the jaws is usually accompanied by an increase in size of the mouth (Al-Hussaini, 1947, Delsman, 1925, and Eaton, 1943). In the belontiids the opposite is true. In the sequence leading from the Anabantidae to the Trichogasterinae, the relatively long slender anabantid jaws become greatly shortened. A similar trend has been described for many actinopteran fishes by Gregory (1933).

In the Osphronemidae the mouth is relatively large and the length of the ascending process of the premaxillary is about one and a half times that of the body. This "sliding stalk" fits in the rostral notch formed by the ethmoid. The premaxillary is moderately protrusile.

Helostoma (fig. 68) represents an aberrant form, which, seemingly, has split at an early evolutionary stage from the ancestral anabantid stock. The edentulous premaxillary and dentary are very reduced in size. The jaws are highly protrusile. The protrusility has been established by a highly movable hinge joint between the dentary and angular. The movement between the dentary and angular is accomplished by the differentiation of a unique dorsolateral process on the angular. The dorsolateral process of the angular serves as an insertion for part A_2 of the adductor mandibulae muscles. The only function of the premaxillary is to support the thick "lips." Its role in controlling the degree of protrusility of the mouth has been taken over by the modified dentary and angular.

Dentition (figs. 40-51, 64-75, 76-87). The most primitive condition is found in *Ctenopoma* and *Sandelia,* in which both the prevomer and palatine bear teeth. The teeth on the prevomer are retained in *Anabas,* but in the latter the palatine has lost any trace of dentition. The anabantids possess many well-developed teeth on the parasphenoid, premaxillary, and dentary. In the three divergent lines derived from the ancestral anabantids there is a definite evolutionary trend toward reduction in size and number of teeth. In the osphronemids the prevomer and palatine are devoid of any teeth, whereas the parasphenoid bears eight stout conical teeth. The helostomatids exhibit an extreme edentulous stage. The premaxillary, dentary, and palatine have lost their teeth, and the parasphenoid bears occasionally one to two vestigial teeth. A similar edentulous condition has been developed independently in various unrelated teleosts, as for example in *Brevoortia* (Gregory, 1933), *Clupea* (Kirchhoff, 1958), *Aeoliscus, Hippocampus,* and *Syngnathoides* (Al-Hussaini, 1947).

A gradual and progressive reduction in dentition can be traced in the evolutionary line leading from the anabantids to the Belontiinae, Macropodinae, and Trichogasterinae. In all three subfamilies the teeth are retained on the premaxillary and dentary, whereas the teeth on the prevomer and palatine are lost. The Belontiinae represent the most "primitive" stage in having eight strong teeth on the parasphenoid. Among the Macropodinae *Betta* possesses five teeth on the parasphenoid, *Trichopsis* has four, and *Macropodus* has two to four. The Trichogasterinae appear to be the most advanced group. *Sphaerichthys* possesses one tooth on the parasphenoid, and *Colisa* has zero to two vestigial teeth. The most progressive evolutionary stage is represented by *Trichogaster,* in which the dentition of the parasphenoid has been lost completely.

The evolutionary trend toward reduction in dentition of the prevomer, palatine, and parasphenoid seems widely spread among teleosts. It has been traced in many evolutionary sequences, leading to specialization (Gregory, 1933, Myers, 1958, and Makushok, 1958). It is also generally accepted that the predaceous type of mouth is primitive, from an evolutionary point of view, but this generalization is not necessarily true in all cases. In anabantids the complete armament of teeth on the margins of the mouth, on the palate, and in the pharynx is highly adapted to a predaceous behavior. Vaas, Sachlan, and Wiraatmadja (1953) reported that *Anabas testudineus* is typically carnivorous in its natural habitat, feeding mainly on insects and small fish. The same workers reported that *Osphronemus goramy,* in which the palatal teeth are lost, is predominantly herbivorous. The planktonic feeding behavior of *Helostoma temmincki,* which possesses an edentulous mouth, palate, and pharynx, was well established by Böker (1937), Seitz (1937), and Vaas, Sachlan, and Wiraatmadja (1953). The latter three authors made a careful analysis of the natural feeding habits in nature of only three members of the belontiids. *Betta unimaculata,* with five rather well-developed teeth on the parasphenoid, seems to be carnivorous. Its diet consists mainly of insects obtained at the surface and in the adjacent air. The

Table 6. Number and Form of Gill Rakers in Some Representative Anabantoids.

Taxa	Few and course	Many, moderately course	Many fine	Extremely numerous, very fine
Anabantidae				
Anabas	*			
Ctenopoma	*			
Sandelia	*			
Osphronemidae				
Osphronemus		*		
Belontiidae				
Belontia		*		
Betta		*		
Trichopsis		*		
Macropodus		*		
Sphaerichthys		*		
Colisa			*	
Trichogaster			*	
Helostomatidae				
Helostoma				*

stomach contents of *Trichogaster trichopterus* and *Trichogaster leeri*, in which the dentition of the parasphenoid is lost, are composed of plant parts, filamentous algae, and detritus. The stomach contents of several specimens of *Belontia hasselti*, *Trichopsis vittatus*, and *Macropodus opercularis* have been analyzed. All three species appear to be omnivorous, feeding on plant parts, epiphytes, and insects. Insects, small fish, and shrimp were found in the stomach of one specimen of *Ctenopoma* and four specimens of *Sandelia*.

Evolutionary patterns, similar to those of the buccal and palatal dentition, are found in the hyobranchial apparatus. Table 6 summarizes the data obtained by the study of the gill rakers.

A definite correlation exists between the structure of the gill rakers and pharyngeal teeth on one hand, and feeding habits on the other hand (Suyehiro, 1941, Al-Hussaini, 1947, and Girgis, 1952). In the carnivorous anabantids the gill rakers are few and coarse, and the teeth on the third, fourth, and fifth pharyngobranchials and fifth ceratobranchials are numerous and stout. That this anatomical arrangement is adapted to predaceous feeding habits has been confirmed by the study of stomach contents. In the herbivorous osphronemids the pharyngeal teeth are still numerous and stout, aiding efficiently in grinding plant parts; the many gill rakers are moderately coarse to protect the gill filaments. The gill rakers form a straining mechanism which bars the entry of food particles into the gill filaments. The omnivorous Belontiinae and Macropodinae resemble the osphronemids very closely, but the teeth on the pharyngeal elements become more villiform. In the Trichogasterinae the pharyngeal skeleton becomes much more slender, the gill rakers much finer and more numerous, and the pharyngeal teeth decrease in size and number, obviating much of the grinding capacity and adapting to fine soft food. *Helostoma* is highly specialized to planktonic feeding habits. Both the buccal cavity and pharynx are devoid of any teeth. The gill rakers form a very efficient straining mechanism, collecting microscopic food particles (described in great detail by Seitz, 1937). *Helostoma* also scrapes algae from stones, etc., by means of highly movable "lips" which possess small horny teeth.

A definite correlation between diet and dentition has been found in the anabantoids. Barrington (1957), however, pointed out that many species of fishes can clearly make use of a wide variety of foods and that the ecological situation of fishes may often favor a generalized rather than a highly specialized digestive system. Observations on the feeding behavior of several members of the belontiids confirm Barrington's statements, although unquestionably some species are adapted predominantly to particular categories of food. The dentition, size of the mouth, and structure of the hyobranchial apparatus impose definite limitations on the size and structure of the food and a definite evolutionary trend toward the loss of teeth is present in all three families derived from the predaceous anabantids. The Belontiinae and Macropodinae are likely capable of omnivorous feeding habits. This phenomenon should not be considered as a preadaptive polyphagous stage in the sense of Cuénot (1951), but rather as a broadly adaptive character which may permit a narrowing in realization of prospective functions. The condition in the Trichogasterinae, which are derived from the Macropodinae, illustrates beautifully the narrowing in function or specialization from omnivorously adapted forms to purely herbivorously adapted forms.

The evolution of the dentition and the hyobranchial apparatus can be briefly explained by assuming a more or less simultaneous divergence of three evolutionary lines, the osphronemids, helostomatids, and belontiids, from a similar ancestral adaptive type, represented by the carnivorous anabantids. The three independent lines enter into three diverging adaptive zones. The helostomatids became very specialized plankton feeders, the osphronemids purely herbivorous, and the belontiids mainly omnivorous. Within the belontiids there is a trend toward a progressive occupation of new herbivorous zones by the Trichogasterinae, which have originated from the prospectively adapted omnivorous Macropodinae. It would seem that the adaptive zones of the Trichogasterinae and osphronemids overlap. This is, however, not the case. The osphronemids feed on much larger food than the Trichogasterinae, which are characterized by a very small mouth and a nearly edentulous palate and pharynx. The Trichogasterinae are adapted to fine and soft herbivorous food, approaching the planktonic type.

Suprabranchial cavity (figs. 14-26). The suprabranchial cavity houses the suprabranchial organ, which is able to perform air-breathing functions (Zograff, 1888, Henninger, 1908, and Bader, 1937). In the incipient stage the suprabranchial cavity extends far dorsally and is enclosed medially by the exoccipitals, supraoccipital, and prootics, dorsally by the frontal, supratemporal, and parietal, posteriorly by the epiotic and intercalary, and laterally to a great extent by the supratemporal and sphenotic. This extreme dorsal position of the suprabranchial cavity is found in *Anabas,* and to a lesser extent in *Ctenopoma* and *Sandelia.* In the latter two genera there is a tendency toward a more ventral position and a reduction in size of the cavity, which is bounded laterally by the hyomandibular and opercular. The supratemporal and sphenotic form the roof rather than the lateral wall of the cavity. There is a definite trend toward a ventral shift of the suprabranchial cavity in all three phyletic lines derived from the ancestral anabantid stock.

Among the belontiids, the Belontiinae are unique. The suprabranchial cavity has shifted slightly to a more ventral position, but also extends far posteriorly, where it is supported by the first six epipleural ribs. In the Macropodinae the gradual ventral shift of the suprabranchial cavity is acquired by the development of pharyngeal processes of the parasphenoid and basioccipital. The gradual development of the processes, accompanied by the ventral shift of the suprabranchial cavity, is well illustrated in the sequence *Betta, Trichopsis,* and *Macropodus.* The peak of this evolutionary trend is reached in the Trichogasterinae. With the differentiation of the pharyngeal processes, the hyobranchial apparatus, which is suspended mainly from the pharyngeal processes of the basioccipital, shifts, correspondingly, to a more ventral position. Concomitant with the ventral shift of the hyobranchial apparatus and suprabranchial cavity is the gradual change from a cylindrical skull to a deep-bodied compressed skull. Gregory's (1933) statement that the opercular region becomes enlarged in *Osphronemus* and other anabantoids in connection with the development of the suprabranchial organ seems to be erroneous.

In *Anabas* the adductor arcus palatini and second levator arcus branchialis muscles form the contractile floor of the suprabranchial cavity. The modified muscles represent the principle components of air ventilation. It is evident that, in *Anabas,* the large dorsal portion of the suprabranchial cavity, which is enclosed by a bony capsule formed by the supratemporal and sphenotic, epiotic, and intercalary, will account for a large volume of residual air. In the three families derived from the ancestral anabantids the noncontractile bony capsule is gradually eliminated. In the osphronemids, helostomatids, and belontiids, the bony posterior wall has disappeared, and the supratemporal and sphenotic form only the dorsal wall of the suprabranchial cavity. Bader (1937) noted that the well-differentiated musculature of the suprabranchial cavity in *Macropodus, Trichopsis, Colisa,* and *Trichogaster* extends dorsolaterally and posteriorly. A similar condition is found in *Helostoma* and *Osphronemus.* The contractile and muscular lateral, posterior, and ventral walls of the suprabranchial cavity in the osphronemids, helostomatids, and belontiids resulted, undoubtedly, in a more efficient ventilation than in the ancestral anabantids. The volume of residual air in the belontiids, helostomatids, and osphronemids (Bader, 1937) seems to be smaller than in the anabantids. A mechanical concomitant of these anatomical changes in the suprabranchial cavity is the reduction in size of the pharyngeal cavity, which in turn controls the size limit of the food particles.

Body form. Myers (1958) listed the deepening and compression of the body as one of the evolutionary trends leading from generalized teleosts to more specialized ones. This trend can also be followed in the evolution of the anabantoid fishes. The ancestral anabantids are short-bodied. The osphronemids and helostomatids are compressed, deep-bodied fishes. The gradual deepening of the body can be traced in the sequence leading from the anabantids to the Trichogasterinae. Among the Macropodinae the most primitive short-bodied forms are represented by *Betta* and *Trichopsis.* A slight deepening and compression of the body is found in *Macropodus,* which forms an intermediate stage between *Betta* and the distinctly compressed and deep-bodied *Sphaerichthys,* and *Colisa.* The Belontiinae, although primitive in many ways, are compressed and deep-bodied.

The body form seems to be correlated with the degree of development of the pharyngeal processes of the parasphenoid and basioccipital. Parallel with the deepening of the body is the differentiation of posttemporal fossae. The fossae are wanting in the short-bodied *Anabas* and *Ctenopoma,* in which the epaxial muscles are inserted on the posterior surface of the skull, formed by the supraoccipital, epiotics, intercalaries, and exoccipitals. In *Sandelia* the posttemporal fossae are in a rudimentary stage. The epaxial muscles pass ventral to the extrascapulars, inserting on the shallow fossa formed by the supratemporals, epiotics, and intercalaries. In the osphronemids and helostomatids the extrascapulars are lost. The neurocranium is better adapted to resist the stresses caused by the thrusts coming from the locomotory, masticatory, and respiratory apparatus as discussed for the generalized percoid skull by Gregory

(1933). The neurocranium is also more compact than that of the anabantids because the epaxial muscles pass above the dermal skull roof, inserting on the frontals, supraoccipital, epiotics, and intercalaries. The posttemporal fossae are well developed and appear as distinct depressions on the posterolateral corners of the skull roof. The posteriorly projecting epiotic processes play a very important role in conveying wrenching and pulling forces from the pectoral girdle. Among the belontiids, the Belontiinae are unique in having very prominent longitudinal ridges on the parietals, epiotics, and supraoccipital. The Macropodinae and Trichogasterinae have well-differentiated posttemporal fossae and epiotic processes, which are lacking in *Sphaerichthys*. In none of the belontiids do the epaxial muscles extend as far anteriorly as in the helostomatids and osphronemids. Correlated with the appearance of posttemporal fossae is the increase in size of the foramen magnum. A nicely graded series is present: in the anabantids the foramen is very small and is surrounded by the exoccipitals; in *Betta* and *Trichopsis* the foramen is slightly larger and surrounded by the exoccipitals and supraoccipital; *Macropodus* represents an intermediate stage; the foramen becomes very large in the Trichogasterinae, in which the epiotics form part of the roof of the foramen.

Suborbital shelf. The suborbital shelf is a bony platform formed by fused medial wings of the suborbitals. The function of the shelf is still unknown (Makushok, 1958, and Smith and Bailey, 1962).

In the incipient stage represented by the anabantids, suborbitals 2-5 contribute to the formation of the extensive and rigid suborbital shelf. During the evolution of the belontiids there is a gradual decrease in rigidity and extent of the suborbital shelf. The Belontiinae and Macropodinae represent a more primitive condition, in which suborbitals 2-5 still join in the formation of the rather extensive suborbital shelf. In the Trichogasterinae the less extensive suborbital shelf is made up only by suborbital 2. Suborbitals 3 and 5 are tubular and have lost their medial winglike processes. The helostomatids resemble the osphronemids in respect to the structure of the suborbital shelf. In the evolutionary lines leading to the osphronemids and helostomatids the suborbital shelf becomes vestigial. In *Osphronemus* the suborbital shelf consists of an insignificant medial projection of the second suborbital.

Branchiostegal rays (figs. 76-87). In the primitive genus *Anabas* the first four branchiostegal rays articulate with the ceratohyal and the two posterior ones with the epihyal. A gradual forward shift of the branchiostegal rays can be traced. In *Ctenopoma* only the last branchiostegal ray articulates with the epihyal; the anterior five are joined to the ceratohyal. In *Sandelia* all five branchiostegal rays are connected with the ceratohyal. Among the belontiids, *Belontia* represents an archaic stage in having the last branchiostegal ray joined to the epihyal. In the remaining belontiids the branchiostegal rays articulate solely with the ceratohyal. In the osphronemids and helostomatids the sixth branchiostegal ray is connected to the epihyal, the fifth is situated between the epihyal and ceratohyal, and the remaining four are joined to the ceratohyal.

Loss of skull elements and polyisomerism. A progressive reduction in the number of skull elements can be traced in the series Anabantidae-Macropodinae-Trichogasterinae. The evolutionary significance of this phenomenon is still unknown. In the Belontiinae and Macropodinae the extrascapulars and ectopterygoids are lost. Correlated with the loss of the extrascapulars is an increase in size of the supratemporal, epiotics, and posttemporal fossae. The place of the lost ectopterygoid is taken by the enlarged body of the palatine and entopterygoid. The most advanced stage is represented by the Trichogasterinae, in which not only the extrascapulars and ectopterygoids are lost, but also one of the branchiostegal rays. Hubbs (1919) stated that the Acanthopterygii have, almost without deviation, typically six branchiostegal rays. The general arrangement described for the Acanthopterygii is also found in the anabantoids, with the exception of the Trichogasterinae and *Sandelia,* in which the number of branchiostegal rays has been reduced to five.

In the osphronemids and helostomatids the loss of skull elements has been restricted to the extrascapulars.

Gregory (1951) observed that secondary polyisomerism frequently occurs in the teleostean vertebral column. Secondary polyisomeres arise by budding or by subdivision of older polyisomeres. Secondary polyisomerism seems to occur in the evolution of the postcranial axial skeleton of the anabantoids. The anabantids resemble the ancestral percoids very closely in having 10 trunk and 15 caudal vertebrae. The ancestral percoids possess 10 trunk and 14 caudal vertebrae (Gregory, 1951). In all three phyletic lines derived from the anabantids there is a definite trend to increase the total number of vertebrae (Table 2). The osphronemids and helostomatids possess a total of 29 vertebrae. *Helostoma* is unique in having secondary polyisomerism in the trunk region only. The trunk vertebrae in *Helostoma* increased in number to 14. In all remaining anabantoids secondary polyisomerism is restricted to the caudal region. The belontiids exhibit a rather wide variation in number of vertebrae. *Belontia, Macropodus, Colisa fasciata,* and *Colisa labiosa* possess 27 vertebrae. In *Trichopsis, Betta,* and *Trichogaster* the total number of vertebrae has increased to, respectively, 28, 29, 31. *Sphaerichthys* and *Colisa lalia* form remarkable exceptions in this otherwise graded series. *Sphaerichthys* has the same number of vertebrae as the anabantids, namely 25, whereas *Colisa lalia* possesses 26 vertebrae. The latter two genera have probably evolved from a *Macropodus*-like stock with 27 vertebrae by the loss of one to two vertebrae, returning to the condition found in the ancestral anabantids. This seems to indicate that reversed evolution or negative anisomerism as defined by Gregory (1951) has taken place. The reduction of vertebrae may be correlated with the small size of *Sphaerichthys* and *Colisa lalia.* Myers (1958) observed that there are morphological trends correlated with small size in teleosts, as for example reduction in number of fin rays and scales, and reduction or suppression of the lateral line. The lateral line of *Sphaerichthys* is vestigial. The low number of vertebrae in *Sphaerichthys* and *Colisa* is also correlated with the quick-dodging method of locomotion. Members with a high number of vertebrae, as for example *Trichogaster, Betta,* and *Trichopsis,* move in a more sinuous or eellike way.

Secondary polyisomerism can also be traced in the evolution of the anal pterygiophores (Table 3). In the ancestral anabantids the total number of anal pterygiophores varies between 13 and 19. This number has increased in all three derivatives of the anabantids, as follows: Belontiidae, 28-35, Helostomatidae, 30-32, and Osphronemidae, 32. In studying the evolutionary changes in the postcranial axial skeleton of teleosts it is essential to take the environmentally induced variations into consideration. Lindsey (1954) has studied the temperature-controlled meristic variation in *Macropodus opercularis.* His results indicate that at developmental temperatures of 31° C, 28° C, and 24° C the average total number of vertebrae is, respectively, 28.78, 28.00, and 28.49. Lindsey included the ultimate vertebra in his counts. In my counts I have omitted the ultimate vertebra. Taning (1950) also showed that there is a definite influence of temperature on the number of vertebrae in teleosts. The variation in vertebral counts in the anabantoids, however, does not seem to be induced environmentally, because of the following two reasons: the anabantoids occur in the tropical habitat, in which there is a rather uniform temperature, and the degree of variation is much greater than the experimentally induced differences.

Pelvic girdle (figs. 91-102). The position of the pelvic girdle in the anabantids is nearly horizontal. It is attached indirectly to the cleithral symphysis by means of a ligament. This arrangement is characteristic of the ancestral percoid and represents the incipient stage in the evolution of the anabantoid pelvic girdle. The pelvic girdle in the Belontiinae resembles that of the anabantids rather closely, but differs in the direct attachment of the conjoined rachii of the basipterygia to the cleithral symphysis. A progressive change in the position of the basipterygia, accompanied by the development of various processes, can be found in the Macropodinae and Trichogasterinae. The rachii of the basipterygia are projected dorsolaterally and articulate with the cleithra of the corresponding sides in *Betta, Trichopsis, Macropodus,* and *Sphaerichthys.* The approximate angle between the horizontal axis and the dorsolaterally directed rachii in *Betta, Trichopsis, Macropodus,* and *Sphaerichthys* is, respectively, 30°, 45°, 60°, and 75°. Concomitant with the change in form and position of the rachii is the differentiation of a prominent processus medialis anterior and a marked elongation of the first pelvic fin ray. This anatomical arrangement enables the fish to move the pelvics anteriorly at an angle of 90° with the long axis of the body. The functional significance of this mobility of the pelvics has not been experimentally studied. The bright colors on the pelvics indicate that it may play a role in the reproductive and aggressive behavior of these fishes. *Trichogaster* and *Colisa* represent the most specialized stage in this evolutionary series. The elongate rachii of the basipterygia are directed straight dorsally and articulate with a special fingerlike process on the cleithra. The processus medialis anterior is extremely well developed in *Colisa.* A new process, the processus medialis accessorius, is developed in service as the origin of the superficial abductor muscles. The first fin ray is very elongate in both genera. The remaining pelvic fin rays become vestigial in *Trichogaster* and are completely lost in *Colisa.* Steinbach (1950) studied the mechanical aspects of the pelvic appendages of *Trichogaster.* Both *Trichogaster* and *Colisa* can move the elongated fin ray in any direction. Scharrer, Smith, and Palay (1947) described taste buds on the elongate pelvic fin ray which is innervated by the facial nerve. The new function of the pelvic fins of *Trichogaster* and *Colisa* is both gustatory and tactile. Taste buds have not been found in the other belontiids. The new adaptive structure, the modified pelvic fin ray in *Trichogaster* and *Colisa,* has developed by an intensification of a former morphological trend already present in its ancestors, as for example in *Macropodus.* The new adaptive structure serves a quite different function from the original locomotory and ethological purposes. The morphological trend involves a hypertrophy of the first pelvic fin ray and atrophy of the remaining four rays. This evolutionary trend furnishes an example whereby a structure adaptive in one way in an ancestral group, namely the typical locomotory function of the pelvics in the anabantids, is transformed to serve a different function in a descendent group, in this case the combined tactile and gustatory pelvics in *Trichogaster* and *Colisa.* In the helostomatids the rachii are widely separated and articulate directly with the cleithra at an angle of approximately 15°. The pelvic fin rays of the osphronemids exhibit a superficial resemblance to that of *Trichogaster.* The first pelvic fin ray is very elongate and the remaining rays vestigial. The internal anatomy of the girdle, however, differs considerably from that of *Trichogaster.* The processus medialis accessorius is lacking, the processus medialis anterior is merely a ridge on the basipterygium, the rachii of the basipterygia are directed dorsomedially, and the pelvic spine is well developed. The evolution of the pelvic girdle seems to indicate that the belontiids and osphronemids have arisen independently from each other.

General remarks. It should be emphasized that the evolutionary trends discussed do not occur singly. It is a general rule that a change in one character almost always carries others along with it, by genetic correlations, by ontogenetic mechanisms, and by adaptive correlations. As Simpson (1953) pointed out, the interdependency in the total adaptive situation is generally too complex to permit definite determination of whether a given trend is really primary in an absolute sense or that one of two simultaneous trends is independent and the other dependent.

It is plainly evident that the trends in protrusility of the jaws and the dentition are closely related to each other and produced by functional and adaptive mechanisms. It is a congruence of functions correlated with a change in feeding habits. It is, however, quite possible that the change in position and extent of the suprabranchial cavity is correlated with the changes in dentition and protrusility. The change in size and position of the suprabranchial cavity is made possible by the development of the pharyngeal processes, which in turn limits the size of the food. In *Sandelia* and *Ctenopoma* the suprabranchial cavity has shifted to a slightly more ventral position without the development of pharyngeal processes. The development of the pharyngeal processes on the parasphenoid and basioccipital is accompanied by a simultaneous shift and reduction in size of the suprabranchial cavity in all three phyletic lines derived from the anabantid stock. This fact seems to indicate a definite correlation between the two changing features. The development of the posttemporal fossae and the deepening of the body are certainly correlated. The ventral shift of the suprabranchial cavity is a mechanical concomitant with the formation of the posttemporal fossae, which takes the space formerly occupied by the cavity. An immediate result of these interdependent trends is a gradual deepening of the skull, which in turn depends on the shape of the body (Gregory, 1933). The body form is probably controlled by an ontogenetic mechanism, namely a distinctive growth pattern, which changes because of genetic alterations produced by selection. The simultaneous changes in dentition, protrusility of the jaws, the shift and extent of the suprabranchial cavity, the development of the posttemporal fossae, and the body form seem to provide a complex example of correlated changes in which genetic, ontogenetic, and functional correlations are simultaneously involved. The attempt to isolate intricately interdependent features and factors is therefore highly artificial.

An apparent uniformity of trends is present in the phylogeny of the anabantoids. Parallel changes in dentition, position and size of the suprabranchial cavity, posttemporal fossae, body form, arrangement of branchiostegal rays, and secondary polyisomerism in the vertebral column occur in all three phyletic lines derived from the ancestral anabantid stock. Simpson (1953) indicated that the occurrence of similar trends among members of a given group is quite common. The phenomenon that diverse descendent lines of common origin show parallel trends is often called "programme evolution" (George, 1948).

An apparent basis for parallel changes in related forms lies in the fact that the organisms share a rather similar genotype. A group of related and genetically similar forms would be similar in their phenotypical expression (Bock, 1960).

The interdependence between the different structures should not be interpreted to mean that they do not change independently. The independent changes of structure within evolving groups are well known under the concept of mosaic evolution. The dependency and interdependency of evolving structures have an important bearing on their taxonomic usefulness. Interdependence is related to grouping of structures into functional complexes. Independence, on the other hand, is shown by the fact that functional complexes can break down and can be reorganized during evolutionary change.

E. The Phylogeny of the Anabantoidei

The proposed phylogeny of the anabantoids, based on the morphological data and interpretations outlined in previous sections, is summarized in figs. 103 and 104.

The anabantids represent the most primitive family of the Anabantoidei. The presence of large extrascapulars, the toothed prevomer, palatine, and parasphenoid, and the articulation of the metapterygoid with the symplectic process of the hyomandibular are indicative of the initial stage in anabantoid phylogeny. *Anabas testudineus* is known from Pliocene and Pleistocene deposits of Java (Sanders, 1934). A well-preserved specimen of *Osphronemus goramy*[2] has been found in Sumatran marl shales dating from the early Tertiary (Sanders, 1934). According to Romer (1945), a wide variety of teleosts evolved in the Cretaceous, and all major teleost groups were established by the Eocene. The possible occurrence of the highly specialized *Osphronemus goramy* in the early Tertiary suggests that the four anabantoid families were already differentiated by that time. The ancestral anabantids seem to have originated from a percoid stock during the Upper Cretaceous or Paleocene, in the tropical portion of the Oriental region. The great abundance and di-

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[2] The possibility that this fossil does not represent *Osphronemus goramy* but that it has paralleled this species closely must be left open.

versity of the recent Anabantoidei in Asia supports the hypothesis that the geographical origin of this group has been most likely tropical Asia (Darlington, 1957). It is also generally accepted that the representation of *Anabas* (erroneously taken to include *Ctenopoma*) in Africa is evidence of a late post-Tethys immigration of the anabantids into Africa (Kosswig, 1954, and Steinitz, 1954). But it has been shown that *Anabas* and *Ctenopoma* are widely separated genera. *Anabas* is not represented in Africa. *Anabas* is certainly not the direct ancestor of *Ctenopoma,* since it possesses several specialized features not found in *Ctenopoma.* The hypothesis that *Anabas* and *Ctenopoma* are derivatives of a common ancestral anabantid stock is supported with strong osteological evidence. It is assumed that this ancestral form evolved during the Upper Cretaceous or Paleocene in the tropical part of the Oriental region, from where it radiated into Africa. The invasion into Africa probably occurred in the early Tertiary (Darlington, 1957). Darlington also pointed out that from the Mesozoic into the Tertiary the Tethys Sea stretched across the whole of southern Europe and Asia to the East Indies. But the Tethys was not a stable sea, and the region was constantly changing, with changing barriers and bridges, and an immense changing frontage between salt and fresh water. There is considerable evidence from mammalian fossils in the Upper Eocene and Lower Oligocene of El Faiyum (northern Egypt) that Africa and Eurasia were united in the late Eocene. Picard (1943) also pointed out that land seems to have existed in the higher parts of Transjordan and Cisjordan since the Upper Eocene. The ancestral anabantid form seems to have invaded Africa during the Upper Eocene. It differentiated into the genus *Ctenopoma* in Africa, whereas in Asia it gave rise to (1) *Anabas,* known since the Pliocene and Pleistocene, (2) the osphronemids, known from the early Tertiary (Sanders, 1934), (3) the helostomatids, and (4) the belontiids. No fossil records exist of the latter two families. Steinitz (1954) pointed out that the majority of the fishes found in both Asia and Africa supports the hypothesis of a connection between the two continents during the Miocene. Kosswig (1954) favors a Pliocene land connection. Steinitz remarked that a continuous land mass between the Asiatic and African continents became established only during the Lower Miocene. It should be emphasized, however, that the Tethys Sea was unstable, and that the bridges and barriers were constantly changing. The ancestral anabantid form might have been able to cross barriers which were inaccessible to other fresh-water fishes. *Anabas* and *Ctenopoma* are extraordinarily hardy fish, surviving in spite of very poorly oxygenated water because of their remarkable air-breathing capacity. They are able to live for prolonged periods outside the water. *Anabas testudineus* has more than usual salt tolerance (Weber and de Beaufort, 1922, Giltay, 1933, Sanders, 1934, and Delsman, 1951). Numerous specimens are collected daily from the Bay of Djakarta (Java). *Anabas* behaves as a secondary division fresh-water fish and is, very likely, able to cross narrow sea barriers as reported for *Aplocheilus, Rasbora,* and *Puntius* (Myers, 1951, and Darlington, 1957). The assumption that *Anabas* has been carried by man across Wallace's line to the eastern part of the Indo-Australian Archipelago (Myers, 1937) is difficult to support. *Osphronemus goramy,* which is as hardy a fish as *Anabas* but is far superior as a food fish, has not been carried across Wallace's line by man. *Osphronemus* would probably be preferred above *Anabas* for transportation by the natives. It seems therefore less questionable to ascribe the wide distribution of *Anabas* to its exceptional physiological characteristics. Similar physiological traits would enable the ancestral anabantid form to invade Africa during the Eocene whether there was a continuous land bridge between Africa and Asia as proposed by Darlington (1957) or not, as hypothesized by Steinitz (1954). The presence of a broad connection, Lemuria, between Africa, Madagascar, and India in the Tertiary has been conclusively disproved (de Beaufort, 1951).

Following the paleogeographic suggestions by Steinitz (1954) we may assume that the ancestral anabantid stock migrated into Africa during the Miocene. After the complete breakdown of Africa's land connection with Asia by the Erythrean Rift Valley in the Pliocene, the ancestral stock differentiated into the genus *Ctenopoma* in Africa and *Anabas* in Asia. The presence of *Osphronemus goramy* in the early Tertiary does not support this hypothesis, unless we assume that the ancestral anabantid had already split into the three more specialized families before or during the period of radiation.

Darlington (1957) favors an early Tertiary migration of the ancestral anabantid stock into Africa. The westbound migration of the ancestral form would have taken place simultaneously with the differentiation of the osphronemids, helostomatids, and belontiids in Asia. Parallel evolutionary patterns are found in the Ostariophysi (Darlington, 1957). The evolution of the Anabantoidei corresponds with the general evolutionary patterns of fresh-water fishes on the Asiatic and African continents. Africa has been relatively stable, favoring the survival of archaic forms, whereas Asia has somehow favored the evolution of new groups of fishes. There is decisive evidence against the direct derivation of the osphronemids, helostomatids, and belontiids from *Anabas*. *Anabas* probably evolved from the ancestral stock after Africa's land connection with Asia was broken down during the Lower Pliocene (Steinitz, 1954). *Osphronemus goramy* was already present during the Lower Tertiary; these facts indicate that *Osphronemus* evolved before *Anabas,* from a common anabantid stock. The osteological and zoogeographical evidence seems to indicate that the archaic recent Anabantidae, the specialized Osphronemidae, Helostomatidae, and Belontiidae arose during the Lower Tertiary from a common ancestral anabantid stock. No attempt has been made to reconstruct the hypothetical common ancestor. The set of characters found in both *Ctenopoma* and *Anabas* may be regarded as those which the group owed to its common ancestor. The common ancestor constructed by abstraction from known forms represents an archetype as understood by the *Naturphilosophen* and Owen, and may differ considerably from the actual common ancestor.

The genus *Sandelia,* isolated on the southern tip of South Africa (Barnard, 1943), has been derived from *Ctenopoma. Sandelia* exhibits several specializations, as for example the loss of one branchiostegal ray, the reduction in size of the suprabranchial cavity, the simple first epibranchial, and the separated nasals. But the toothed palatine and prevomer, the spineless serrate opercular, and the arrangement of the pharyngeal processes on the basioccipital indicate the close relationship with *Ctenopoma.* There is also strong zoogeographical evidence for the direct derivation of *Sandelia* from *Ctenopoma.* The present distributional pattern of the African anabantids indicates that *Ctenopoma* has spread along a principal route which leads from an extensive, favorable area of the African tropics into a smaller, less favorable area of temperate South Africa. The expanding *Ctenopoma* population apparently crossed the climatic barrier with difficulty and the group across the barrier became isolated and differentiated independently from its ancestors. As Darlington (1957) remarked, the South African fauna as a whole has been formed by southward extension of parts of the tropical African fauna. It appears that *Anabas* and *Ctenopoma* evolved by schistic (Smith, 1956 and 1960) evolution or splitting from a common ancestor. Geographic isolation seems to have brought about differences between the two separated populations. *Sandelia,* on the other hand, evolved by phyletic evolution from *Ctenopoma.* A progressive change in some features can be followed in the series *Ctenopoma muriei* from central tropical Africa, *Ctenopoma multispinis* from the Zambezi River system, and *Sandelia* from temperate South Africa: the lachrymal is weakly serrate in *muriei,* not serrate in *multispinis* and *Sandelia;* suborbitals extend to nearly half the distance between orbit and preopercular in *muriei,* suborbitals narrow in *multispinis,* suborbitals very narrow in *Sandelia;* a gradual but progressive reduction in size of the suprabranchial cavity and an increase in length of the ascending process of the premaxillary in the sequence *muriei, multispinis,* and *Sandelia.*

During the Lower Tertiary three divergent lines radiated more or less simultaneously from the ancestral anabantid stock. In the first line, the osphronemids, the transverse processes of the parasphenoid are lost, the ectopterygoids retained, the suborbital shelf becomes greatly reduced, the basipterygia and first pelvic fin ray greatly elongate, and the metapterygoid is divested of its articulation with the symplectic process of the hyomandibular. The second line is represented by the highly specialized helostomatids, in which transverse processes and pharyngeal processes of the parasphenoid are retained, the ectopterygoid is not lost, the dentition is completely lost, the dentary and angular acquire a highly movable hinge joint, and the metapterygoid does not articulate with the symplectic process of the hyomandibular. The third line represents the largest group, the belontiids, in which the ectopterygoids are lost and the transverse processes of the parasphenoid are not retained. The three groups seem to have originated by schistic evolution from the same ancestral adaptive type, entering into diverging adaptive zones. *Osphronemus goramy* made a rather sudden appearance in the Lower Tertiary, most likely the Upper Eocene, and has not changed since. The fossil specimen resembles the recent forms in great detail (Sanders, 1934). If we assume that the fossil is actually *Osphronemus goramy* then the species did not change during a period of approximately 36 million years. The rather sudden appearance of the osphronemids from the ancestral anabantids and the complete absence of intermediate stages seem to indicate that the change from the carnivorous ancestral adaptive type to the large-sized omnivorous forms might have taken place quickly. This evolutionary change at an exceptionally high rate might be considered as tachytelic. Tachytely often occurs when populations shift from one major adaptive zone to another (Simpson, 1953). In this particular case the shift is from purely predaceous feeding habits to omnivorous adaptive types. The very elongate first pelvic fin ray, proven to be gustatory and tactile, probably evolved as a concomitant of the feeding behavior. The possible tachytelic line leading toward the differentiation of the osphronemids became bradytelic. *Osphronemus* has not changed morphologically since the Upper Eocene. *Osphronemus* is rather broadly adapted: it can live on a variety of foods (Weber and de Beaufort, 1922), is able to survive in poorly oxygenated water, and has a high salt tolerance. Environmental factors may therefore fluctuate greatly without requiring any adaptive change for survival. These factors may have contributed to the arrested evolution of *Osphronemus* since the Upper Eocene.

Helostoma temmincki represents the most specialized member of the anabantoids. The morphological gap between *Helostoma* and the ancestral stock is exceptionally large. The edentulous condition, the unique movable hinge joint between the dentary and angular, and the elaborate filtering apparatus in the hyobranchial region are, undoubtedly, advanced features adaptive to a highly specialized feeding behavior.

Transitional forms between *Helostoma* and the predaceous ancestral stock are lacking. This sudden evolutionary change from the predaceous adaptive zone to the planktonic adapted forms seems to indicate that an all-or-none reaction is involved whereby no intermediate stages persisted. Once the direction of evolution of the feeding mechanism was established, natural selection continuously acted in that direction until completion of the trend. We are possibly confronted with a beautiful example of quantum evolution. The all-or-none element in quantum evolution arises in general from discontinuity between adaptive zones. It seems that the direction of the relatively rapid change in the evolutionary history of *Helostoma* was rigidly adaptive as a result of strong selection pressure. In this case quantum evolution has, possibly, led to a group of fish whose adaptive zone and correlated morphology are such that a family rank should be established. After penetration into the specific adaptive zone during the Lower Tertiary, the evolution of the helostomatids seems to have been arrested. *Helostoma* seems to be perfectly adapted to its narrow zone. It has been pointed out by Simpson (1953) for animals and Stebbins (1949) for plants that the lines with arrested evolution were specialized when their evolution was arrested. The evolutionary pattern of *Helostoma* seems to fit the generalization that the most slowly evolving groups seem to be very highly and specifically adapted to a particular zone.

The third evolutionary line originating from the ancestral anabantid stock gave rise to the Belontiidae. The evolutionary pattern of the belontiids is mainly a combination of phyletic and schistic evolution. The Belontiinae have several features in common with the ancestral anabantid stock, among which the closely conjoined basipterygia and the articulation of the metapterygoid with the symplectic process of the hyomandibular are the most important. *Belontia* seems to resemble an intermediate stage between the ancestral anabantid stock and the more advanced belontiids. Some specialized features not found in any other belontiid, as for example the posterior extension of the suprabranchial cavity supported by the first six epipleurals and the high supraoccipital crest, indicate strongly that *Belontia* forms an early, sterile, side branch of the main evolutionary line. The main line, originating from the same ancestral stock as the Belontiinae, leads to a progressively changing series, which consists of *Betta*, *Trichopsis*, and *Macropodus*. The latter genera represent the subfamily Macropodinae, which differs from the Belontiinae in lacking a posterior extension of the suprabranchial cavity and a distinct supraoccipital crest, and the loss of the articulation between the metapterygoid and the symplectic process of the hyomandibular. These differences suggest that the Belontiinae and Macropodinae represent two divergent lines. In the belontiine line there is a tendency toward deepening of the skull by the differentiation of a high supraoccipital crest and a posterior extension of the suprabranchial cavity, whereas in the macropodine line the deepening of the skull is the result of the development of pharyngeal processes on the parasphenoid and basioccipital. We can trace the following gradual and progressive changes: reduction in dentition of the parasphenoid, deepening of the body, increase in protrusility of the jaws, and increase in size of the pharyngeal processes of the parasphenoid and basioccipital. These progressive changes are evidently nonrandom and cumulative and apparently adaptive. The morphological changes are correlated with the changing feeding habits. The Macropodinae are omnivorous, and there is a trend toward specialization for eating small-sized food. It should be emphasized that the macropodine evolutionary pattern is not purely phyletic, but the longest line leading to *Malpulutta* takes a branch from *Trichopsis,* which was produced by splitting as indicated by the aberrant elongate and tubular nasals.

The Trichogasterinae forms a homogenous group in which the trends present in the Macropodinae reach their peaks. The group probably originated from a *Macropodus*-like stock, by an intensification of the trends already present in the Macropodinae. The occupation of contiguous and successively higher and narrower zones by a sequence of populations splitting off from the next lower zones seems to have taken place during the evolution of the Macropodinae and Trichogasterinae. The progressive specialization culminated in the penetration of the narrow adaptive zone by the herbivorous Trichogasterinae, which feed on a diet of small plant parts, epiphytes, plankton, filamentous algae, and detritus. It seems that all zones remain in existence and are occupied. In the line leading from *Betta* to the Trichogasterinae, we can trace a sequential occupation of zones decreasing in width. *Betta* is omnivorous, whereas the Trichogasterinae are herbivorous and nearly planktonic. The morphological differences between the Macropodinae and the Trichogasterinae are of such magnitude that the rank of subfamilies should be recognized.

The position of the anabantoids among the Perciformes is still questionable. The ancestors of the anabantoids are still unknown, but are perhaps to be found among the Percoidei, which occupies a central place in the order Perciformes. The anabantoids arose during a major episode of proliferation of teleostean suborders, families, and genera. During this "explosive phase" of adaptive radiation (Upper Cretaceous and Lower Tertiary) of teleosts there was, probably, a considerable phyletic divergence among the evolving lineages, penetrating into a great variety of adaptive zones by successive quantum shifts. Among the crowding lines parallelism and convergence were at work. The phylogeny of teleosts and phylogeny in general are very poorly understood. In this discussion I have attempted to analyze some of the interwoven modes and factors of the evolution of the anabantoids. But as Simpson states, relative to adaptive radiation: "The total process cannot be made simple, but it can be analyzed in part. It is not understood in all its appalling intricacy, but some understanding is in our grasp, and we may trust our own powers to obtain more."

THE STATUS OF *LUCIOCEPHALUS PULCHER* (GRAY)

The taxonomic status of the monotypic genus *Luciocephalus* among the teleosts seems to be problematical. Earlier workers (Day, 1876, Regan, 1909, and Weber and de Beaufort, 1922) lumped *Luciocephalus* with the anabantoids. Boulenger (1904), however, established a separate family Luciocephalidae. Berg (1940) made a study of the skeleton of *Luciocephalus,* using two radiographs from one specimen. He assigned it to a new monotypic suborder, the Luciocephaloidei.

A full description of the structure of *Luciocephalus* with a discussion on its taxonomic status will be presented elsewhere (Liem, unpublished). Only a brief comparison with the Anabantoidei is given here:

Luciocephalus	Anabantoidei
Median gular element present.	Median gular element absent.
No pharyngeal processes on parasphenoid and basioccipital.	Pharyngeal processes present on parasphenoid and basioccipital.
No swim bladder.	Swim bladder extending into caudal region.
No dorsal and anal spines.	Dorsal and anal fins with spines.
Suprabranchial organ rectangular, articulating directly with prootic.	Suprabranchial organ labyrinthine, articulating by means of an epibranchial process.
No ethmoid process on palatine.	Ethmoid process present on palatine.
Anteroventral and posteroventral corners of sacculith distinctly indented (fig. 90 D).	Dorsoanterior corner of sacculith indented.

Luciocephalus has been classified with or near the anabantoids because of the presence of a suprabranchial organ. Previous workers made the assumption that the suprabranchial organ provides a good character for establishing relationships of the ophicephalids, anabantoids, and luciocephaloids. It has been pointed out (Bock, 1960) that the taxonomic value of a structure depends upon the nature of the controlling selection forces. If these selection forces have a tight control over the structure and if they have arisen repeatedly then that structure has little taxonomic value. In order to evaluate the proper taxonomic relationships between the anabantoids and *Luciocephalus* we have to distinguish between homology and convergence among the similarities present in the two groups. Air-breathing has evolved, independently, in many bony fishes, as an adaptation to environmental conditions which render aquatic respiration impossible or inefficient. A great variety of organs became transformed into air-breathing organs (Carter, 1957), as for example the pharyngeal epithelium and diverticula of the pharynx in *Periophthalmus, Electrophorus,* and *Monopterus;* swim bladder and lungs in

Polypterus, Amia, the recent Dipnoi, *Lepisosteus, Umbra, Erythrinus,* and *Gymnarchus;* the esophagus in *Monopterus* (Liem, 1961); stomach and intestine in *Misgurnus, Doras,* etc.; the skin in *Anguilla, Periophthalmus,* and *Boleophthalmus;* and diverticula of the branchial chamber in *Clarias, Saccobranchus, Channa, Luciocephalus,* and the anabantoids. In the South African genus *Sandelia* the suprabranchial organ became secondarily reduced, indicating that the controlling selection forces have reversed their direction during the evolution of the anabantoids. It seems that the controlling selection forces guiding the evolution of the diverticula of the branchial chamber have arisen repeatedly and have reversed their direction several times. Therefore, one has to ascribe little value to the suprabranchial organ in showing relationships between *Luciocephalus,* anabantoids, and ophicephalids. Independent convergent adaptations to air-breathing have evidently evolved in many bony fishes of quite different ancestries. Convergence generally involves adaptations to ecologically similar conditions by various groups of oganisms of distinct ancestries (Simpson, 1961). *Luciocephalus* resembles the anabantoids superficially in respect to the modified first epibranchial, which is specifically adaptive to environments in which air-breathing has a great selective value. The two groups resemble each other only in one way, specifically adaptive to a shared ecology. In characteristics not related to that adaptation, for example the otoliths, the oromandibular apparatus, and the form and extent of the frontals, the two groups differ greatly. The resemblance between *Luciocephalus* and the anabantoids seems, therefore, to be a case of convergence without any bearing on propinquity of descent.

It is impossible, at this stage, to determine the taxonomic status of *Luciocephalus* with any certainty. There is evidence that *Luciocephalus* is not related to the anabantoids. The combination of primitive isospondylous and advanced acanthopteran characters gives *Luciocephalus* a unique position among the teleosts. It is well known that many originally soft-rayed stocks have progressed in certain features toward the spiny-rayed stage of evolution, producing parallelisms and convergence on a grand scale in many different lines. *Luciocephalus* might represent a relict of the original soft-rayed stock which has progressed in certain features toward the spiny-finned stage of evolution. It seems possible that we are dealing with a form with ordinal affiliation.

RELATIONSHIPS OF THE ANABANTOIDEI AND THE OPHICEPHALIFORMES

Many authors unite the ophicephalids with the anabantoids (Gregory, 1951). The osteology of the Ophicephaliformes (Channiformes) has been described in great detail by Day (1914) and Bhimachar (1932). The morphological differences between the anabantoids and the Ophicephaliformes are:

Ophicephaliformes	Anabantoidei
Fins without spines.	Fins with spines.
Metapterygoid articulates with frontal and sphenotic.	Metapterygoid small, widely separated from sphenotic and frontal.
Pharyngeal processes of parasphenoid and basioccipital absent.	Pharyngeal process present on parasphenoid and basioccipital.
First epibranchial modified, articulating with supratemporal.	First epibranchial modified, articulating with prootic.
Frontals articulate with parasphenoid.	Frontals do not articulate with parasphenoid.
Outer wall of otic bulla formed almost completely by prootics.	Outer wall of otic bulla formed by prootics, basioccipital, and exoccipital.

These osteological differences support Berg's (1940) proposal of a new order Ophicephaliformes. The inclusion of the ophicephalids in the anabantoids was based solely on the presence of a modified first epibranchial. The modification is an adaptive device for air respiration, which provides a considerable selective advantage in natural selection for fishes in general, especially in habitats with periodic droughts during which high temperatures decrease the availability of oxygen in the water. The superficial resemblance between the ophicephalids and anabantoids is limited to one structure which is specifically adaptive to a shared ecology. A closer study of the morphology of the suprabranchial organ of the two groups reveals several significant differences. In the Ophicephaliformes the suprabranchial organ is formed by the epibranchial and an expansion of the hyomandibular and articulates with the supratemporal. In the anabantoids the suprabranchial organ is formed by the first epibranchial only and articulates with the prootic. The first epibranchial becomes modified in different ways in the anabantoids, luciocephalids, and Ophicephaliformes. Functionally, the first epibranchial is not associated with the digestive system as is the case in the three remaining epibranchials. The first epibranchial seems therefore "immediately available" for performing a respiratory function without affecting the digestive mechanisms. The Ophicephaliformes and the anabantoids differ in many features which are not related to the shared ecology. Berg's (1940) observation that the Ophicephaliformes and anabantoids are not related and that their resemblance is due to convergence is strongly supported by the new morphological evidence. The Ophicephaliformes resemble the Perciformes in lacking an orbitosphenoid, the absence of the mesocoracoid in the pectoral girdle, and the arrangement of the premaxillary and maxillary. But they possess several primitive features which separate them from the Perciformes, as for example the absence of spines in the fins, the fact that the pelvic girdle is not directly attached to the cleithra, and the arrangement of the branchiostegal rays.

The loss of spines in the fins and the separation of the basipterygium from the cleithrum might have occurred secondarily. It seems that speculation on the ordinal affiliation of the ophicephalids is premature at the present time. A knowledge of the different selection forces which were operative during the evolution of the different anatomical structures of the ophicephalids is essential for determining the proper taxonomic value of the structures. The "labyrinth organ" should not be used as the sole character for determining relationships between the ophicephalids and anabantoids. There seems to be some indication that the selection forces have a tight control over the "labyrinth organ." The modified epibranchial would therefore have little taxonomic value. The use of a large number of different taxonomic characters will reduce the chance of error considerably. The Ophicephaliformes (Channiformes) differ significantly from the anabantoids in characters which are not related to the adaptation to air-breathing. The taxonomic distinctness of the ophicephalids from the anabantoids is evident from the articulation of the metapterygoid with the frontal and sphenotic, the absence of the pharyngeal processes of the parasphenoid and basioccipital, the connection between the frontals and the parasphenoid, and the construction of the otic bulla by the prootic. The taxonomic position of the ophicephalids as a separate order as advocated by Berg seems to be justified, although more supporting evidence is necessary.

CONCLUSIONS

1. Based on the obtained osteological data the suborder Anabantoidei is recharacterized as follows. A suprabranchial organ, sometimes labyrinthine, is formed by expansion of first epibranchial. Nasals variable in shape and size, united or separated. Swim bladder divided posteriorly, extending into caudal region. Opercular bones serrate or entire. Pharyngeal processes present on parasphenoid and basioccipital. Ventrals thoracic, I 1-5, spine sometimes vestigial. Dorsals and anals always with spines. Scales ctenoid and cycloid. Vertebrae 25-31.

2. Four families are recognized within the Anabantoidei:

a) Anabantidae, including the genera *Anabas, Ctenopoma,* and *Sandelia.* Characterized by teeth on prevomer, extrascapulars, toothed transverse processes on parasphenoid, ectopterygoids, and suborbital shelf present.

b) Osphronemidae, including the genus *Osphronemus.* Characterized by no teeth on prevomer, no extrascapulars, toothed pharyngeal process on parasphenoid, transverse processes of parasphenoid absent, ectopterygoids present, and suborbital shelf vestigial.

c) Helostomatidae, including the genus *Helostoma.* Characterized by premaxillaries, dentaries, palate and pharynx devoid of teeth, dentary and angular articulate by a hinge joint, pharyngeal and transverse processes present on parasphenoid, ectopterygoids present, suborbital shelf absent.

d) Belontiidae, n. fam., characterized by the absence of teeth on prevomer, no extrascapulars, pharyngeal process present on parasphenoid, ectopterygoids absent. Three new subfamilies are proposed within the Belontiidae:

(1) Belontiinae, n. subfam., including one genus, *Belontia.* Distinguished by: metapterygoid articulates with symplectic process of hyomandibular, suprabranchial cavity extends far posteriorly, supported by six first epipleurals, supraoccipital crest well developed, epiotics do not reach foramen magnum, six branchiostegal rays, last of which articulates with epihyal, and suborbital shelf formed by suborbitals 2-5.

(2) Macropodinae, n. subfam., including the genera *Macropodus, Betta, Trichopsis, Parosphromenus,* and *Malpulutta.* Distinguished by: metapterygoid does not articulate with symplectic process of hyomandibular, suprabranchial cavity not supported by epipleurals, no supraoccipital crest, epiotics do not reach foramen magnum, six branchiostegal rays articulating with ceratohyal, suborbital shelf formed by suborbitals 2-5.

(3) Trichogasterinae, n. subfam., which includes *Sphaerichthys, Parasphaerichthys, Colisa,* and *Trichogaster.* Distinguished by: metapterygoid does not reach symplectic process of hyomandibular, suprabranchial cavity not supported by epipleurals, no supraoccipital crest, epiotics reach foramen magnum, five branchiostegal rays articulating with ceratohyal, suborbital shelf formed by second suborbital.

3. *Macropodus opercularis* differs significantly from *Macropodus cupanus,* but neither generic nor subgeneric segregation is here recommended.

4. Phylogenetic trends have been traced in three evolutionary lines derived from the anabantids in respect to (*a*) a gradual and progressive increase in the protrusility of the premaxillary; (*b*) a gradual reduction in dentition; (*c*) an increase in number of gill rakers; (*d*) a ventral shift and reduction in size of the suprabranchial cavity; (*e*) an increase in size and change in position of the pharyngeal processes of the parasphenoid and basioccipital; (*f*) a progressive change from short-bodied cylindrical to deep-bodied compressed forms; (*g*) a gradual development of posttemporal fossae; (*h*) a reduction in the extent of the suborbital shelf; (*i*) a forward shift of the branchiostegal rays; (*j*) a reduction in number of bones in the skull with increasing individuality of those remaining; (*k*) polyisomerism in the vertebral column and anal pterygiophores; (*l*) a gradual change in position and form of the basipterygia.

5. The complex interdependency in the total adaptive situation is discussed. Parallel changes occur in the three lines derived from the anabantids.

6. The phylogeny of the Anabantoidei is summarized (figs. 103, 104).

7. The anabantids resemble the ancestral stock from which the osphronemids, helostomatids, and belontiids evolved during the Lower Tertiary.

8. The presence of *Osphronemus goramy* in the Upper Eocene seems to indicate that the original tachytelic line became bradytelic.

9. The Helostomatidae seems to have evolved by a rapid shift into a new zone. The discontinuity between the adaptive zones, correlated with the large morphological gap without any intermediate stages, seems to indicate that the shift took place by quantum evolution.

10. Several aspects of the paleogeography and zoogeography have been incorporated in the discussion of the phylogeny.

11. The suprabranchial organ of the anabantoids differs significantly from that of the luciocephalids and Ophicephaliformes.

12. Supporting morphological evidence is given for Berg's proposal that the Ophicephaliformes represent a separate order.

13. The resemblance of the Anabantoidei, luciocephalids, and Ophicephaliformes is due to convergence rather than phylogenetic relationship.

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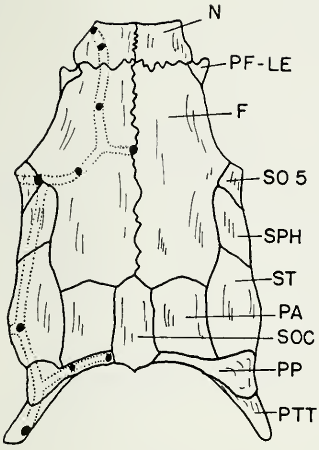
PLATES

PLATE 1

Fig. 1. Dorsal aspect of skull of *Anabas testudineus*. Right sensory canals omitted.
Fig. 2. Dorsal aspect of skull of *Ctenopoma muriei*. Right sensory canals omitted.
Fig. 3. Dorsal aspect of skull of *Sandelia capensis*. Right sensory canals omitted.
Fig. 4. Dorsal aspect of skull of *Osphronemus goramy*.

Abbreviations: E, ethmoid; EO, epiotic; F, frontal; IC, intercalary; L, lachrymal; LE, lateral ethmoid; MX, maxillary; N, nasal; PA, parietal; PF, prefrontal; PM, premaxillary; PP, extrascapular; PTF, posttemporal fossa; PTT, posttemporal; SO_5, suborbital; SOC, supraoccipital; SPH, sphenotic; ST, supratemporal.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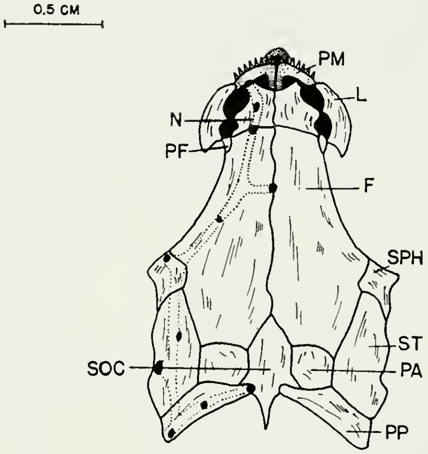
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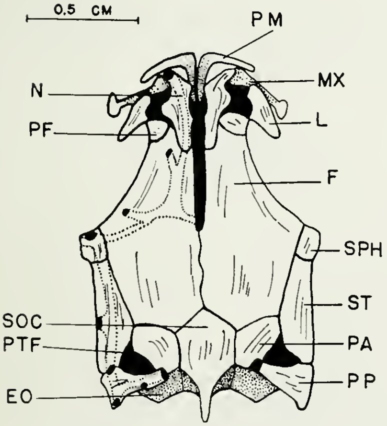
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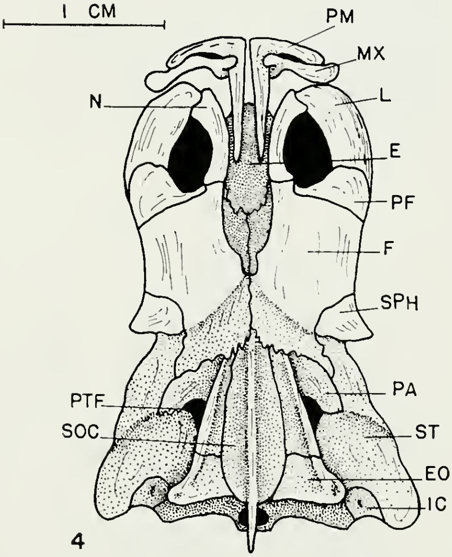
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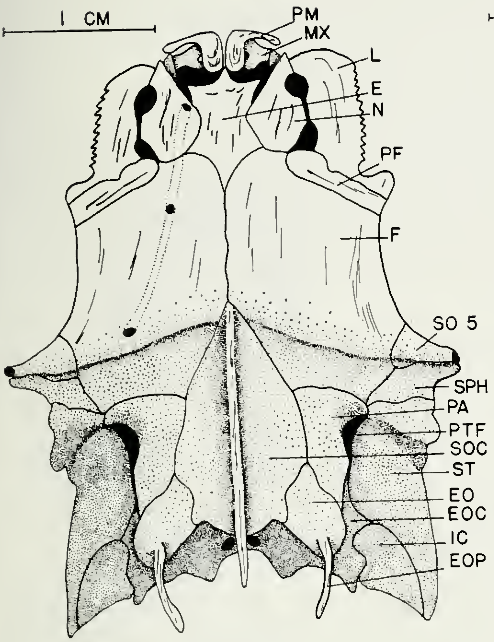
PLATE 2

Fig. 5. Dorsal aspect of skull of *Helostoma temmincki.* Right sensory canals omitted.
Fig. 6. Dorsal aspect of skull of *Belontia hasselti.* Right sensory canals omitted.
Fig. 7. Dorsal aspect of skull of *Betta splendens.*
Fig. 8. Dorsal aspect of skull of *Trichopsis vittatus.* Right sensory canals omitted.
Fig. 9. Dorsal aspect of skull of *Macropodus cupanus.* Right sensory canals omitted.

Abbreviations: D, dentary; E, ethmoid; EO, epiotic; EOC, exoccipital; EOP, epiotic process; F, frontal; IC, intercalary; L, lachrymal; MX, maxillary; N, nasal; PA, parietal; PF, prefrontal; PM, premaxillary; PTF, posttemporal fossa; SO_5, suborbital; SOC, supraoccipital; SPH, sphenotic; ST, supratemporal.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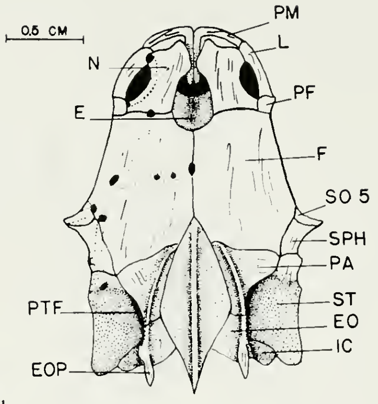
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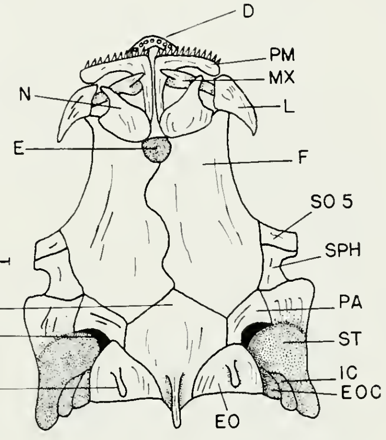
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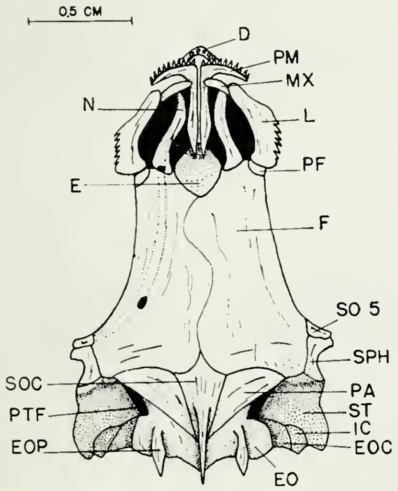
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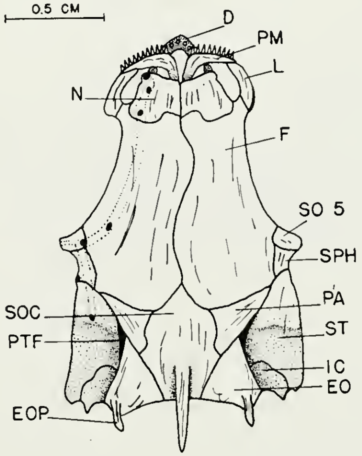
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PLATE 3

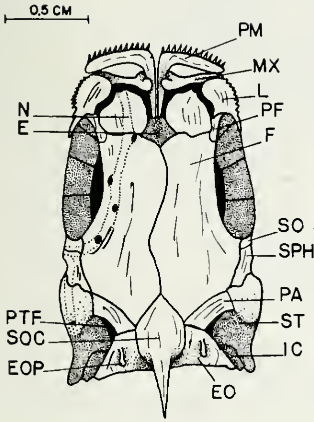
Fig. 10. Dorsal aspect of skull of *Macropodus opercularis*. Right sensory canals omitted.

Fig. 11. Dorsal aspect of skull of *Sphaerichthys osphromenoides*. Left lachrymal and right sensory canals omitted.

Fig. 12. Dorsal aspect of skull of *Colisa fasciata*. Right sensory canals omitted.

Fig. 13. Dorsal aspect of skull of *Trichogaster trichopterus*. Right sensory canals omitted.

Abbreviations: D, dentary; E, ethmoid; EO, epiotic; EOC, exoccipital; EOP, epiotic process; F, frontal; IC, intercalary; L, lachrymal; LE, lateral ethmoid; MX, maxillary; N, nasal; P, palatine; PA, parietal; PF, prefrontal; PM, premaxillary; PTF, posttemporal fossa; SO_5, suborbital; SOC, supraoccipital; SPH, sphenotic; ST, supratemporal.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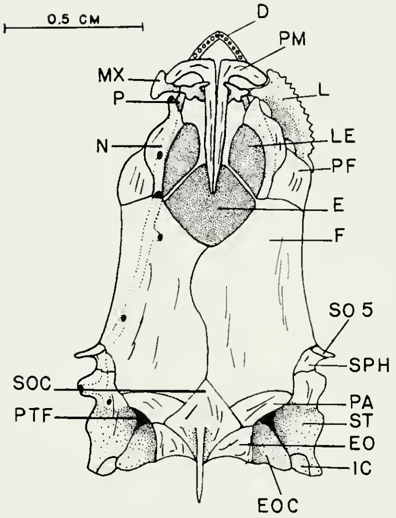
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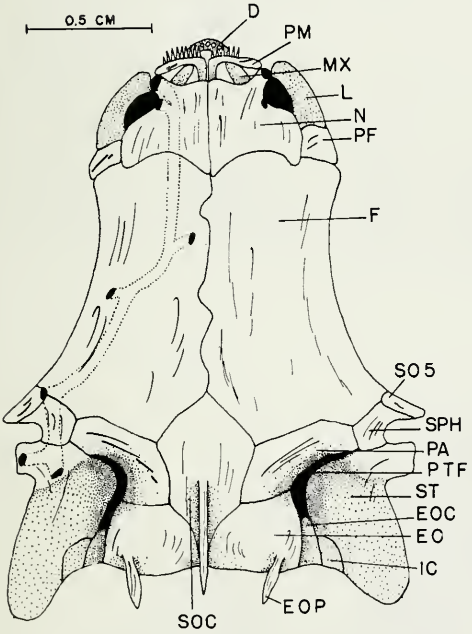
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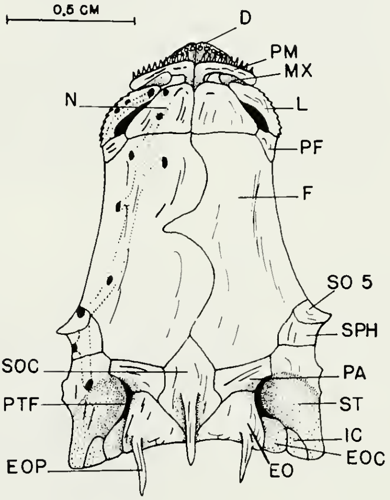
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PLATE 4

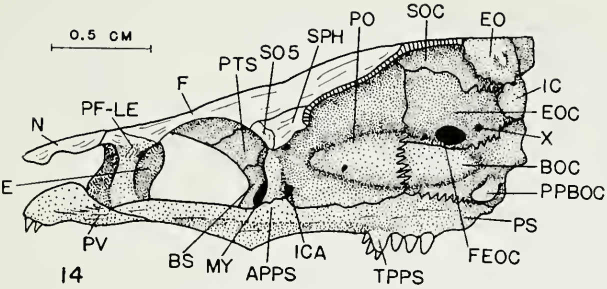
Fig. 14. Lateral aspect of neurocranium of *Anabas testudineus*. Supratemporal-intertemporal removed.

Fig. 15. Lateral aspect of neurocranium of *Ctenopoma multispinis*.

Fig. 16. Lateral aspect of neurocranium of *Sandelia capensis*. Extrascapular omitted.

Fig. 17. Lateral aspect of neurocranium of *Osphronemus goramy*.

Abbreviations: APPS, ascending process of parasphenoid; BOC, basioccipital; BS, basisphenoid; E, ethmoid; EO, epiotic; EOC, exoccipital; F, frontal; FEOC, foramen exoccipitale; IC, intercalary; ICA, internal carotid artery; LAG, lagenar swelling; LE, lateral ethmoid; MY, myodome; N, nasal; PA, parietal; PF, prefrontal; PO, prootic; PP, extrascapular; PPBOC, pharyngeal process of basioccipital; PPPS, pharyngeal process of parasphenoid; PS, parasphenoid; PTF, posttemporal fossa; PTS, pterosphenoid; PV, prevomer; S, swelling of sacculus; SO_5, suborbital; SOC, supraoccipital; SPH, sphenotic; ST, supratemporal; TPPS, transverse process of parasphenoid; U, swelling of utriculus; X, foramen of vagus nerve.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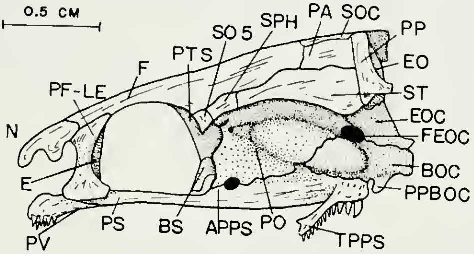
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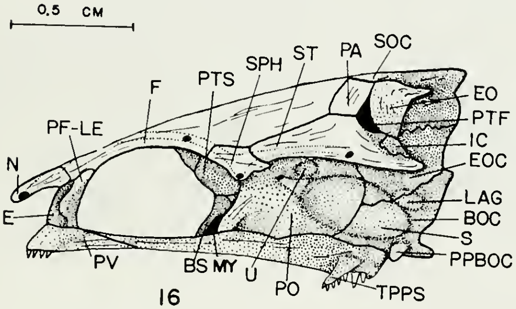
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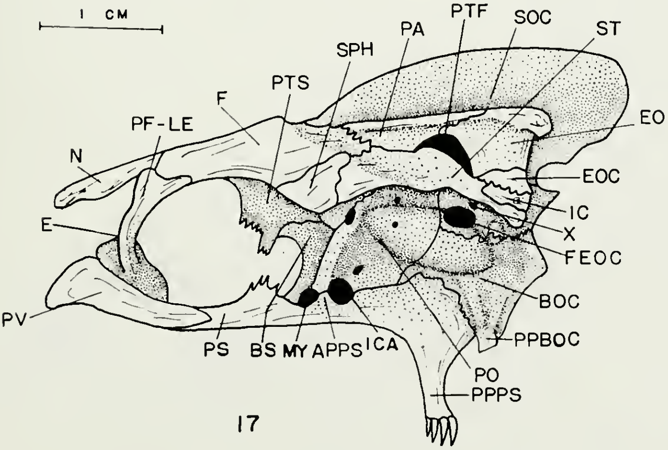
16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BOC
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PPPS

17

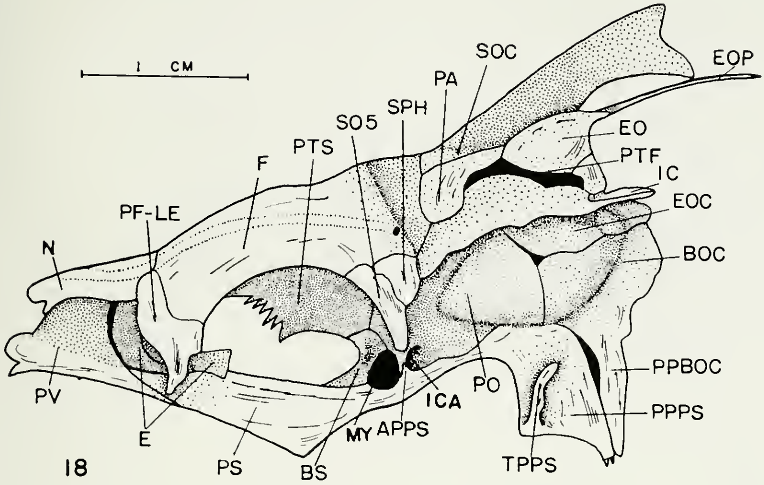
Plate 5

Fig. 18. Lateral aspect of neurocranium of *Helostoma temmincki.*

Fig. 19. Lateral aspect of neurocranium and first six vertebrae of *Belontia hasselti.*

Fig. 20. Lateral aspect of neurocranium of *Betta splendens.*

Abbreviations: APPS, ascending process of parasphenoid; BAP, basapophysis; BOC, basioccipital; BS, basisphenoid; C, centrum; DPT, dorsal pterygiophores; E, ethmoid; EO, epiotic; EOC, exoccipital; EOP, epiotic process; EPLR, epipleural ribs; F, frontal; FEOC, foramen exoccipitale; IC, intercalary; ICA, internal carotid artery; IN, interneural; LE, lateral ethmoid; MY, myodome; N, nasal; NS, neural spine; PA, parietal; PF, prefrontal; PLR, pleural ribs; PO, prootic; POZ, postzygapophysis; PPBOC, pharyngeal process of basioccipital; PPPS, pharyngeal process of parasphenoid; PRZ, prezygapophysis; PS, parasphenoid; PTF, posttemporal fossa; PTS, pterosphenoid; PV, prevomer; SO_5, suborbital; SOC, supraoccipital; SPH, sphenotic; ST, supratemporal; TPPS, transverse process of parasphenoid.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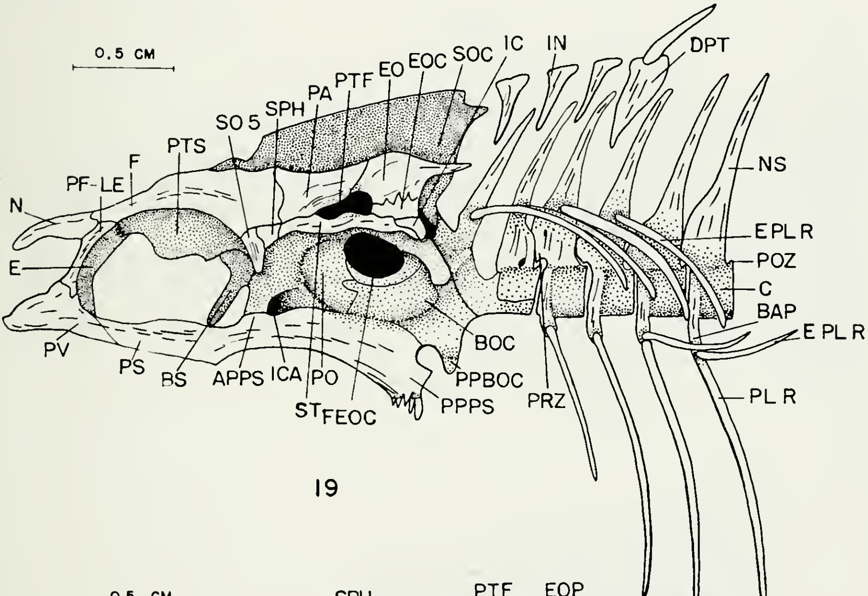
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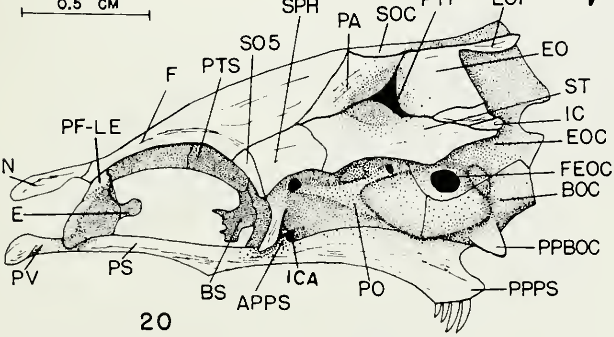
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APPS
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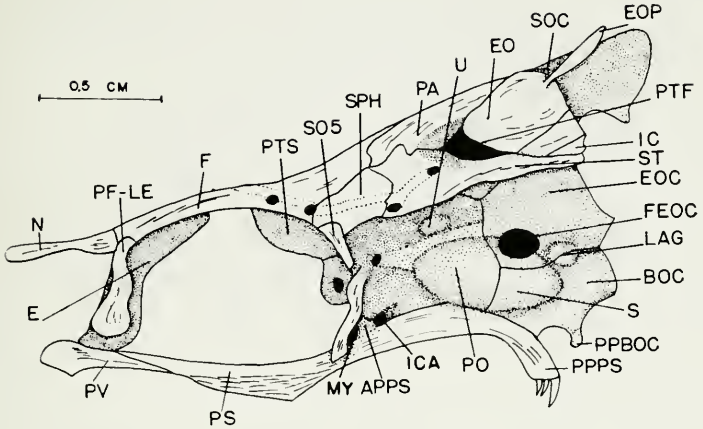
Plate 6

Fig. 21. Lateral aspect of neurocranium of *Trichopsis vittatus.*
Fig. 22. Lateral aspect of neurocranium of *Macropodus cupanus.*
Fig. 23. Lateral aspect of neurocranium of *Macropodus opercularis.*
Abbreviations: APPS, ascending process of parasphenoid; BOC, basioccipital; BS, basisphenoid; E, ethmoid; EO, epiotic; EOC, exoccipital; EOP, epiotic process; F, frontal; FEOC, foramen exoccipitale; IC, intercalary; ICA, internal carotid artery; LAG, lagenar swelling; LE, lateral ethmoid; MY, myodome; N, nasal; PA, parietal; PF, prefrontal; PO, prootic; PPBOC, pharyngeal process of basioccipital; PPPS, pharyngeal process of parasphenoid; PS, parasphenoid; PTF, posttemporal fossa; PTS, pterosphenoid; PV, prevomer; S, swelling of sacculus; SO_5, suborbital; SOC, supraoccipital; SPH, sphenotic; ST, supratemporal; U, swelling of utriculus; X, foramen of vagus nerve.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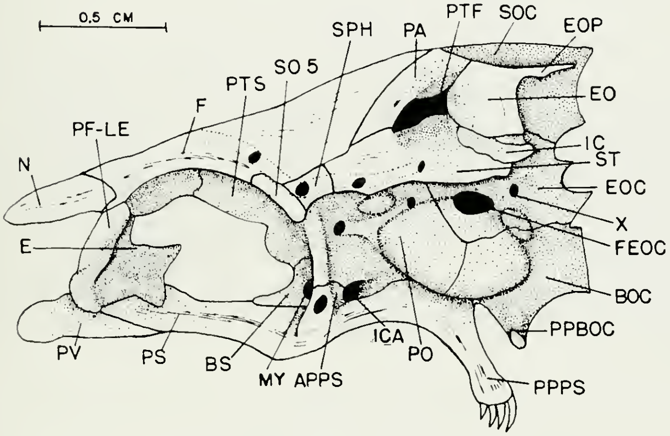
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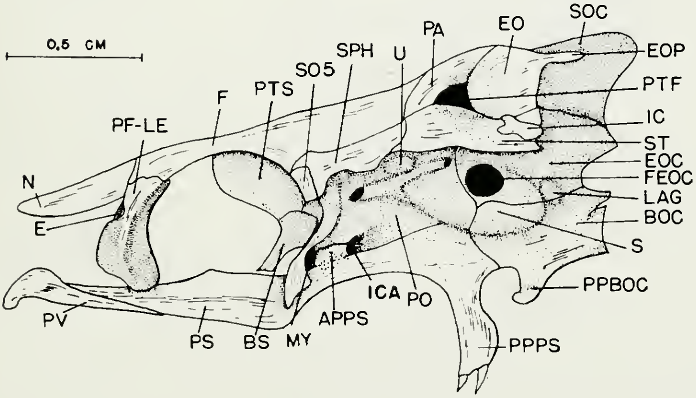
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S
PPBOC
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APPS
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BS
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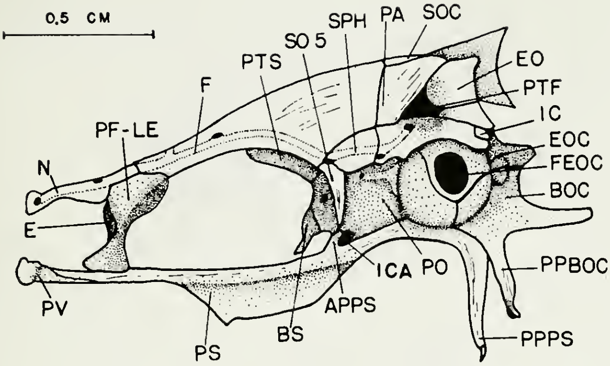
PV

23

PLATE 7

Fig. 24. Lateral aspect of neurocranium of *Sphaerichthys osphromenoides.*
Fig. 25. Lateral aspect of neurocranium of *Colisa lalia.*
Fig. 26. Lateral aspect of neurocranium of *Trichogaster trichopterus.*

Abbreviations: APPS, ascending process of parasphenoid; BOC, basioccipital; BS, basisphenoid; E, ethmoid; EO, epiotic; EOC, exoccipital; EOP, epiotic process; F, frontal; FEOC, foramen exoccipitale; IC, intercalary; ICA, internal carotid artery; LE, lateral ethmoid; N, nasal; PA, parietal; PF, prefrontal; PO, prootic; PPBOC, pharyngeal process of basioccipital; PPPS, pharyngeal process of parasphenoid; PS, parasphenoid; PTF, posttemporal fossa; PTS, pterosphenoid; PV, prevomer; SO_5, suborbital; SOC, supraoccipital; SPH, sphenotic; ST, supratemporal.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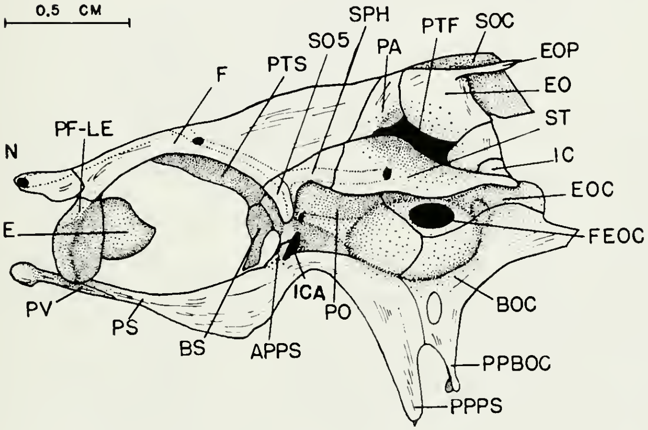
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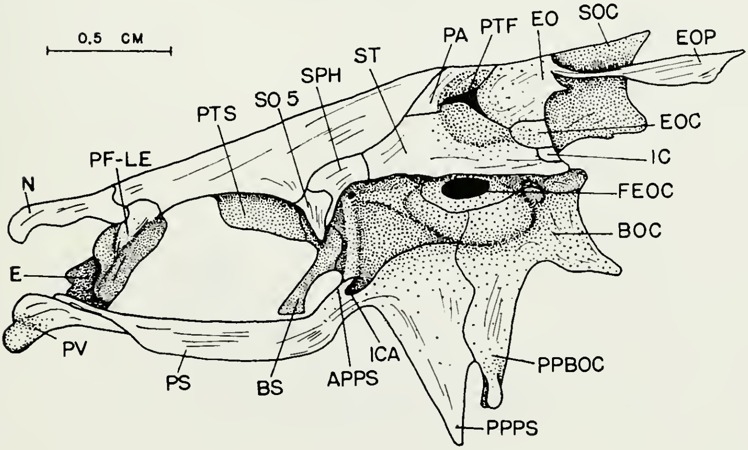
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Plate 8

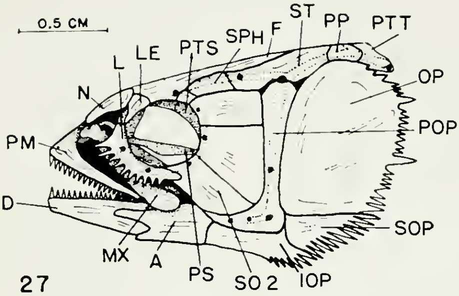
Fig. 27. Lateral aspect of intact skull of *Anabas testudineus*. Suborbitals 3-5 unlabeled.

Fig. 28. Lateral aspect of intact skull of *Ctenopoma muriei*. Suborbitals 3-5 unlabeled.

Fig. 29. Lateral aspect of intact skull of *Ctenopoma multispinis*. Suborbitals 3-5 unlabeled.

Fig. 30. Lateral aspect of intact skull of *Sandelia capensis*. Suborbitals 3-5 unlabeled.

Abbreviations: A, angular; BS, basisphenoid; D, dentary; ECT, ectopterygoid; ENT, entopterygoid; EO, epiotic; F, frontal; HM, hyomandibular; IOP, interopercular; L, lachrymal; LE, lateral ethmoid; MPT, metapterygoid; MX, maxillary; N, nasal; OP, opercular; PA, parietal; PF, prefrontal; PM, premaxillary; POP, preopercular; PP, extrascapular; PS, parasphenoid; PTS, pterosphenoid; PTT, posttemporal; Q, quadrate; RA, retroarticular; SO_2, suborbital; SOC, supraoccipital; SOP, subopercular; SPH, sphenotic; ST, supratemporal; SY, symplectic.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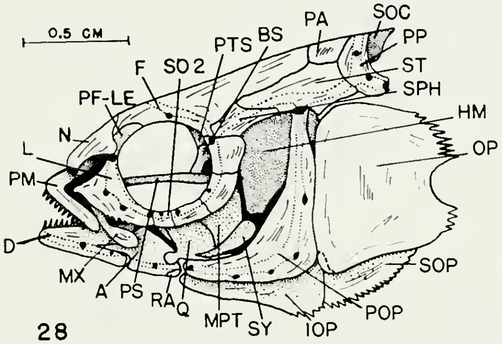
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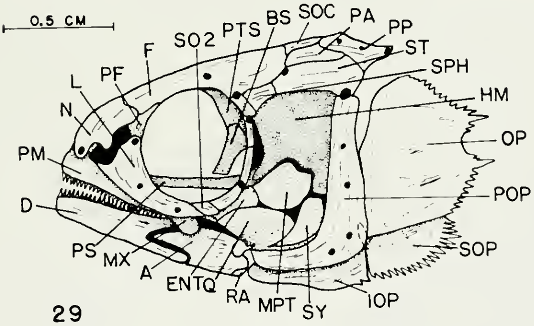
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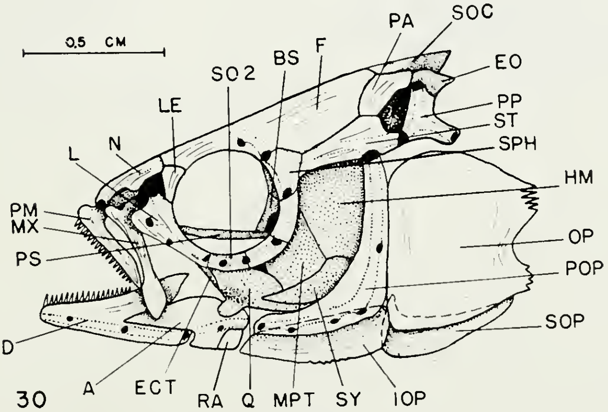
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30

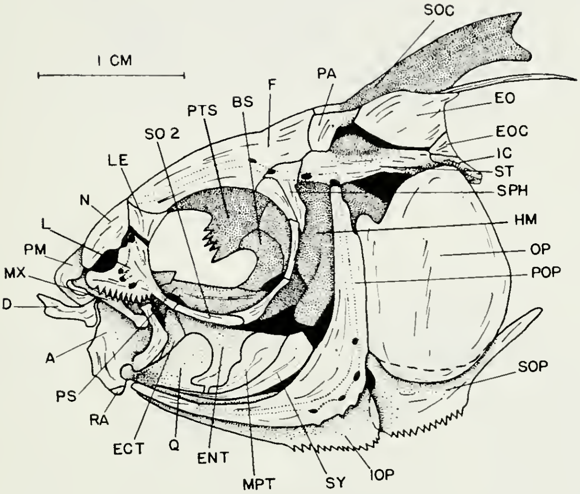
PLATE 9

Fig. 31. Lateral aspect of intact skull of *Helostoma temmincki*. Suborbitals 3-5 unlabeled.

Fig. 32. Lateral aspect of intact skull of *Belontia hasselti*. Suborbitals 3-5 unlabeled.

Fig. 33. Lateral aspect of intact skull of *Betta splendens*. Suborbitals 3-5 unlabeled.

Abbreviations: A, angular; BS, basisphenoid; D, dentary; E, ethmoid; ECT, ectopterygoid; ENT, entopterygoid; EO, epiotic; EOC, exoccipital; F, frontal; HM, hyomandibular; IC, intercalary; IOP, interopercular; L, lachrymal; LE, lateral ethmoid; MPT, metapterygoid; MX, maxillary; N, nasal; OP, opercular; PA, parietal; PM, premaxillary; POP, preopercular; PS, parasphenoid; PTS, pterosphenoid; Q, quadrate; RA, retroarticular; SO_2, suborbital; SOC, supraoccipital; SOP, subopercular; SPH, sphenotic; ST, supratemporal; SY, symplectic.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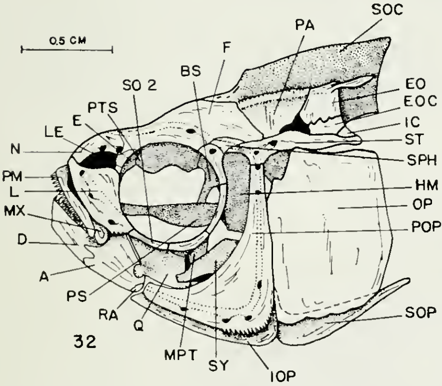
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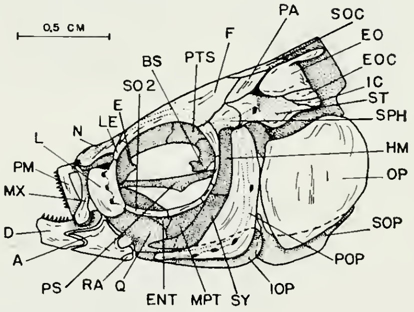
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IOP

33

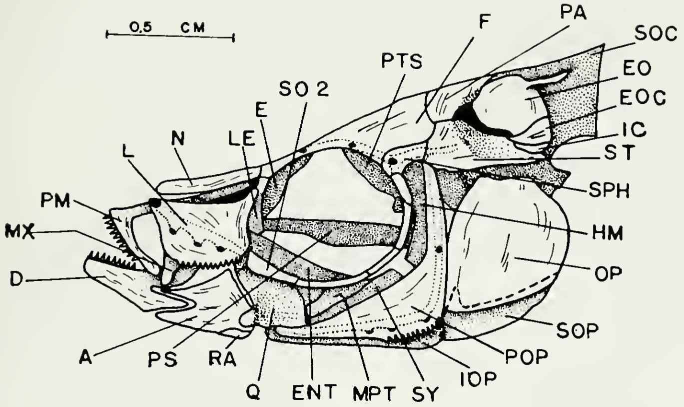
PLATE 10

Fig. 34. Lateral aspect of intact skull of *Trichopsis vittatus*. Suborbitals 3-5 unlabeled.

Fig. 35. Lateral aspect of intact skull of *Macropodus opercularis*. Suborbitals 3-5 unlabeled.

Fig. 36. Lateral aspect of intact skull of *Sphaerichthys osphromenoides*. Suborbitals 3-5 unlabeled.

Abbreviations: A, angular; BS, basisphenoid; D, dentary; E, ethmoid; ENT, entopterygoid; EO, epiotic; EOC, exoccipital; F, frontal; HM, hyomandibular; IC, intercalary; IOP, interopercular; L, lachrymal; LE, lateral ethmoid; MPT, metapterygoid; MX, maxillary; N, nasal; OP, opercular; P, palatine; PA, parietal; PM, premaxillary; POP, preopercular; PS, parasphenoid; PTS, pterosphenoid; Q, quadrate; RA, retroarticular; SC, sensory canal; SO_2, suborbital; SOC, supraoccipital; SOP, subopercular; SPH, sphenotic; ST, supratemporal; SY, symplectic.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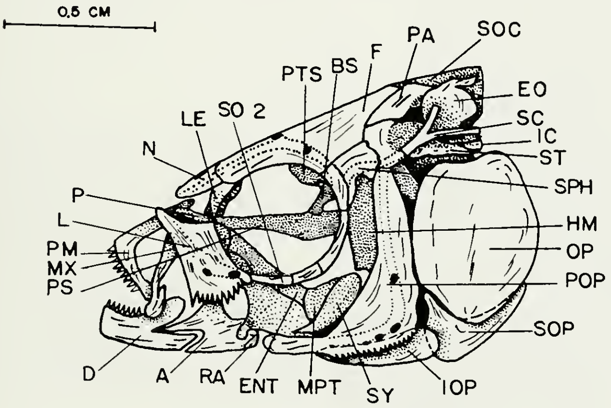
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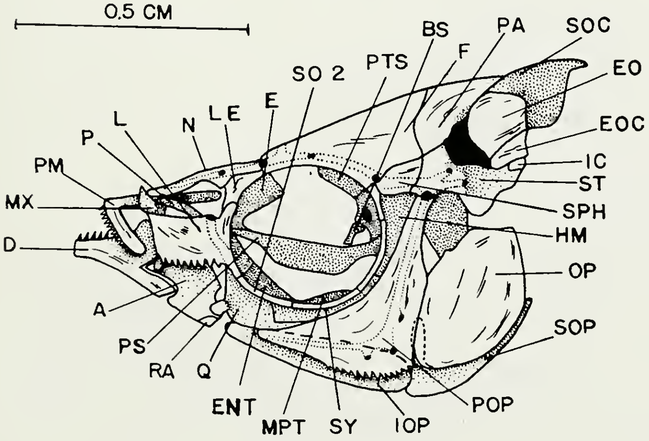
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36

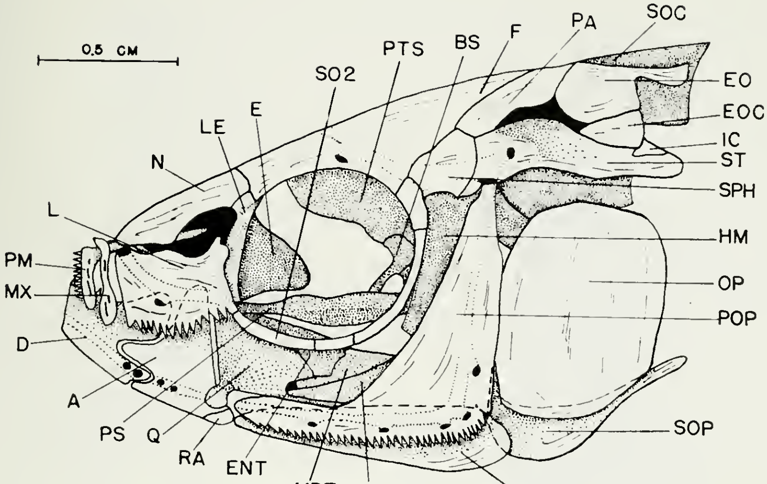
Plate 11

Fig. 37. Lateral aspect of intact skull of *Trichogaster trichopterus*. Suborbitals 3-4 unlabeled.

Fig. 38. Lateral aspect of intact skull of *Trichogaster leeri*. Suborbitals 3-4 removed.

Fig. 39. Lateral aspect of intact skull of *Colisa fasciata*. Suborbitals 3-5 unlabeled.

Abbreviations: A, angular; BS, basisphenoid; D, dentary; E, ethmoid; ENT, entopterygoid; EO, epiotic; EOC, exoccipital; EOP, epiotic process; F, frontal; HM, hyomandibular; IC, intercalary; IOP, interopercular; L, lachrymal; LE, lateral ethmoid; MPT, metapterygoid; MX, maxillary; N, nasal; OP, opercular; PA, parietal; PF, prefrontal; PM, premaxillary; POP, preopercular; PS, parasphenoid; PTF, posttemporal fossa; PTS, pterosphenoid; Q, quadrate; RA, retroarticular; $\mathrm{SO}_{2\text{-}5}$, suborbital; SOC, supraoccipital; SOP, subopercular; SPH, sphenotic; ST, supratemporal; SY, symplectic.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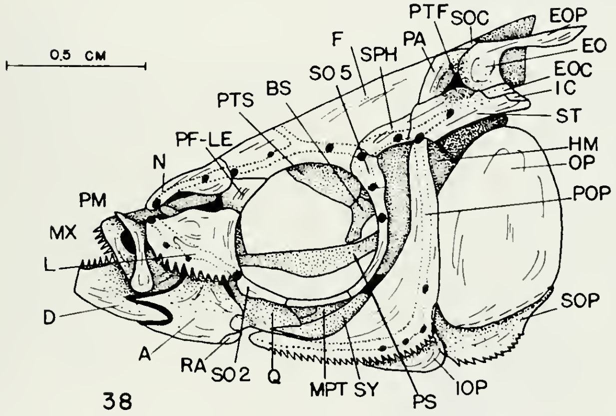
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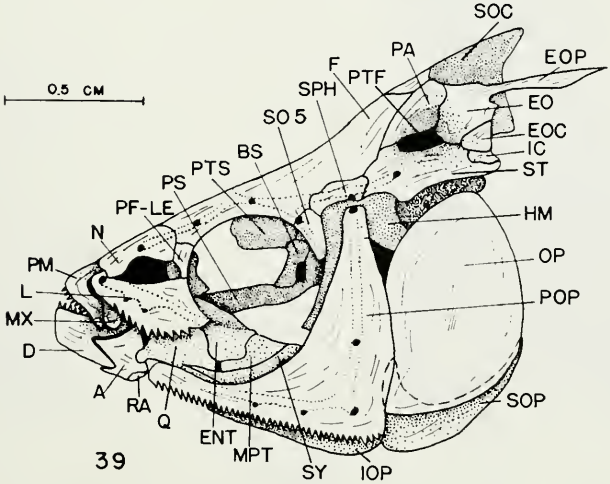
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IOP
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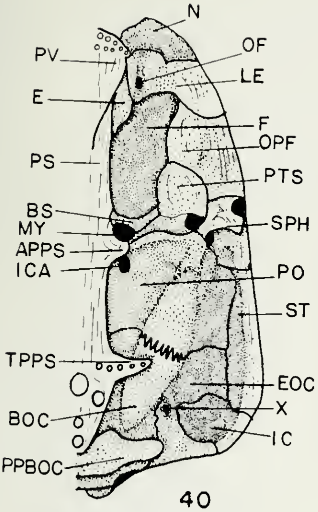
39

Plate 12

Fig. 40. Ventral aspect of left half of neurocranium of *Anabas testudineus.*
Fig. 41. Ventral aspect of left half of neurocranium of *Ctenopoma multispinis.*
Fig. 42. Ventral aspect of left half of neurocranium of *Sandelia capensis.*
Fig. 43. Ventral aspect of left half of neurocranium of *Osphronemus goramy.*
Fig. 44. Ventral aspect of left half of neurocranium of *Helostoma temmincki.*

Abbreviations: APPS, ascending process of parasphenoid; BOC, basioccipital; BS, basisphenoid; E, ethmoid; EOC, exoccipital; F, frontal; IC, intercalary; ICA, internal carotid artery; LAG, lagenar swelling; LE, lateral ethmoid; MY, myodome; N, nasal; OF, olfactory foramen; OPF, orbital process of frontal; PO, prootic; PPBOC, pharyngeal process of basioccipital; PPPS, pharyngeal process of parasphenoid; PS, parasphenoid; PTS, pterosphenoid; PV, prevomer; S, swelling of sacculus; SO_5, suborbital; SPH, sphenotic; ST, supratemporal; TPPS, transverse process of parasphenoid; X, foramen of vagus nerve.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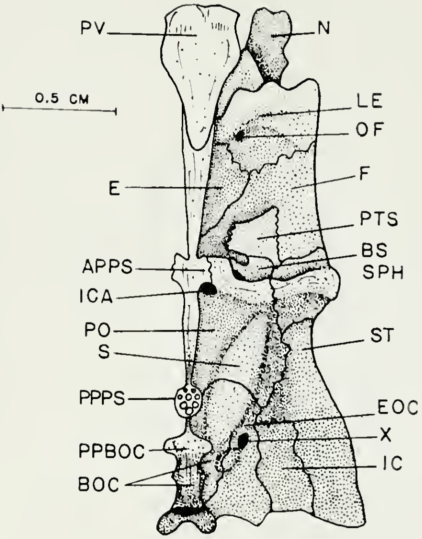
40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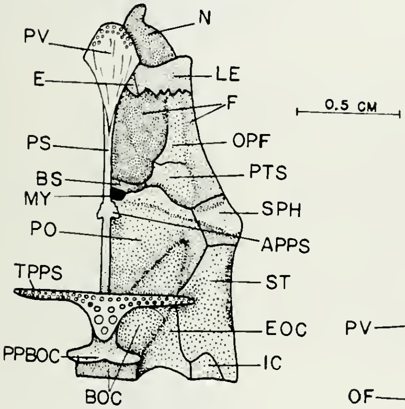
43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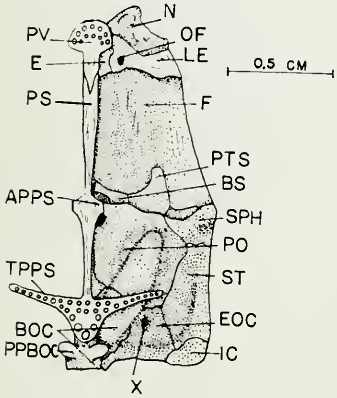
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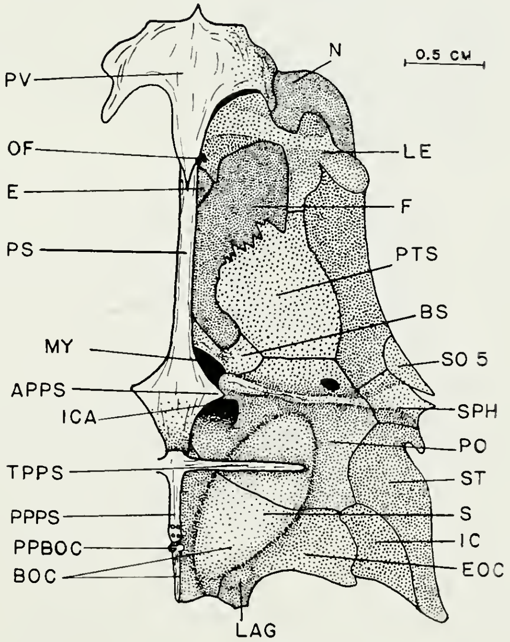
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BOC
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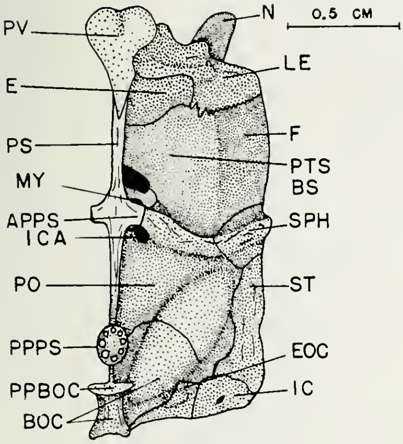
44

PLATE 13

Fig. 45. Ventral aspect of left half of neurocranium of *Belontia hasselti.*
Fig. 46. Ventral aspect of left half of neurocranium of *Betta splendens.*
Fig. 47. Ventral aspect of left half of neurocranium of *Trichopsis vittatus.*
Fig. 48. Ventral aspect of left half of neurocranium of *Macropodus opercularis.*
Abbreviations: APPS, ascending process of parasphenoid; BOC, basioccipital; BS, basisphenoid; E, ethmoid; EOC, exoccipital; F, frontal; IC, intercalary; ICA, internal carotid artery; LAG, lagenar swelling; LE, lateral ethmoid; MY, myodome; N, nasal; OF, olfactory foramen; OPF, orbital process of frontal; PO, prootic; PPBOC, pharyngeal process of basioccipital; PPPS, pharyngeal process of parasphenoid; PS, parasphenoid; PTS, pterosphenoid; PV, prevomer; S, swelling of sacculus; SPH, sphenotic; ST, supratemporal; U, swelling of utriculus; X, foramen of vagus nerve.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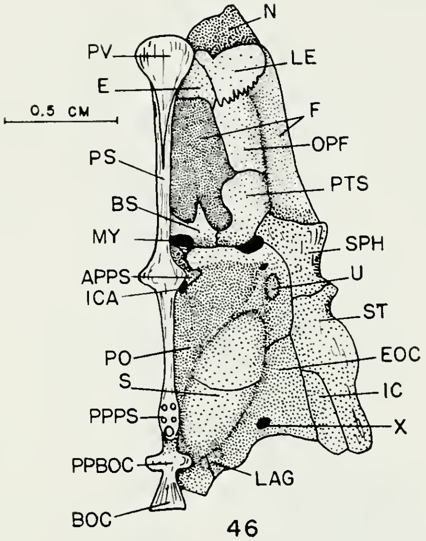
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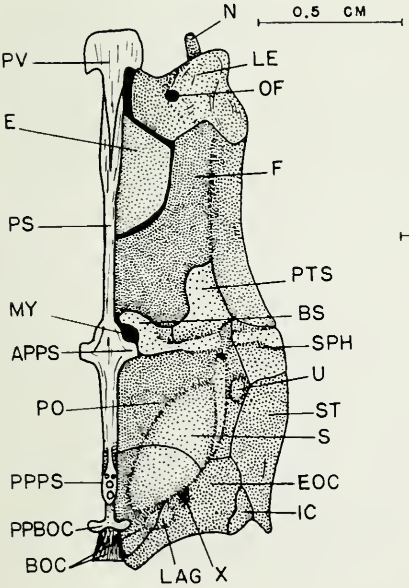
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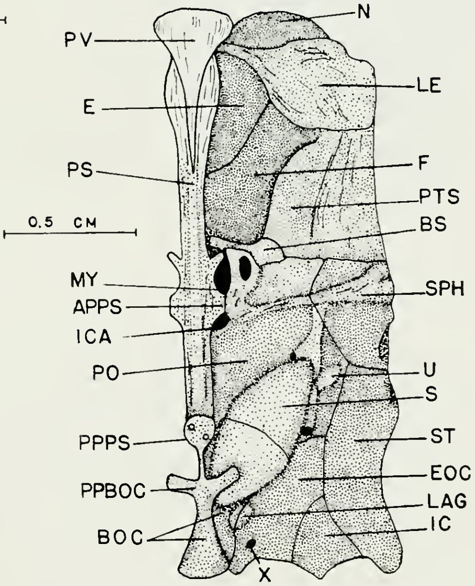
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48

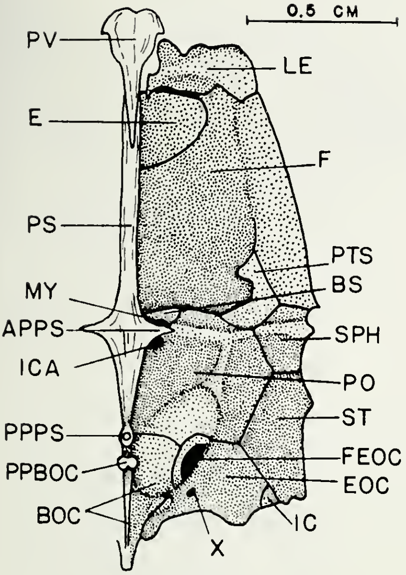
PLATE 14

Fig. 49. Ventral aspect of left half of neurocranium of *Sphaerichthys osphromenoides.*

Fig. 50. Ventral aspect of left half of neurocranium of *Colisa fasciata.*

Fig. 51. Ventral aspect of left half of neurocranium of *Trichogaster trichopterus.*

Abbreviations: APPS, ascending process of parasphenoid; BOC, basioccipital; BS, basisphenoid; E, ethmoid; EOC, exoccipital; F, frontal; FEOC, foramen exoccipitale; IC, intercalary; ICA, internal carotid artery; LAG, lagenar swelling; LE, lateral ethmoid; MY, myodome; N, nasal; OF, olfactory foramen; PO, prootic; PPBOC, pharyngeal process of basioccipital; PPPS, pharyngeal process of parasphenoid; PS, parasphenoid; PTS, pterosphenoid; PV, prevomer; S, swelling of sacculus; SPH, sphenotic; ST, supratemporal; U, swelling of utriculus; X, foramen of vagus nerve.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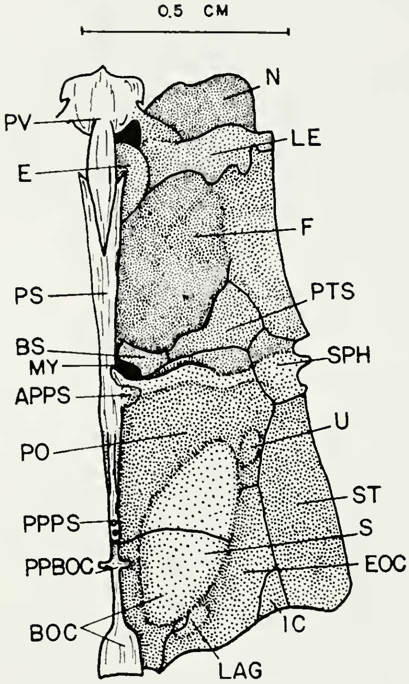
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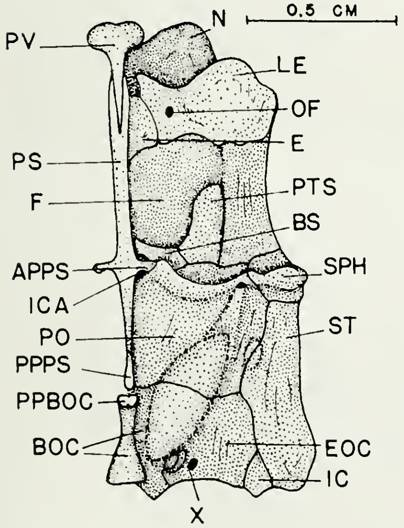
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X

51

PLATE 15

Fig. 52. Posterior aspect of neurocranium of *Anabas testudineus*. Left extrascapular and posttemporal removed.

Fig. 53. Posterior aspect of neurocranium of *Ctenopoma multispinis*. Right extrascapular omitted.

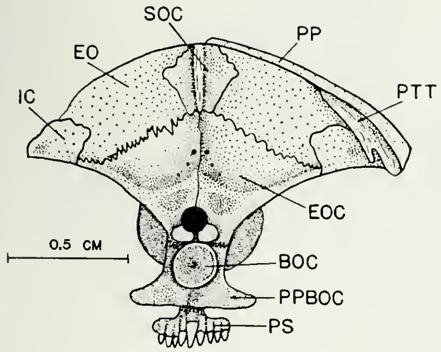
Fig. 54. Posterior aspect of neurocranium of *Sandelia capensis*. Left extrascapular removed.

Fig. 55. Posterior aspect of neurocranium of *Osphronemus goramy*.

Fig. 56. Posterior aspect of neurocranium of *Helostoma temmincki*.

Fig. 57. Posterior aspect of neurocranium of *Belontia hasselti*.

Abbreviations: BOC, basioccipital; EO, epiotic; EOC, exoccipital; EOP, epiotic process; FEOC, foramen exoccipitale; IC, intercalary; PO, prootic; PP, extrascapular; PPBOC, pharyngeal process of basioccipital; PPPS, pharyngeal process of parasphenoid; PS, parasphenoid; PTF, posttemporal fossa; PTT, posttemporal; SOC, supraoccipital; ST, supratemporal; TPPS, transverse process of parasphenoid.



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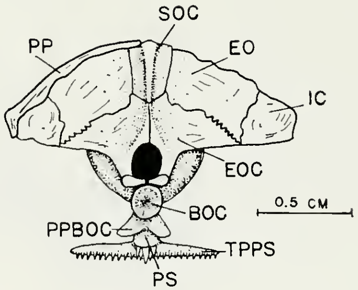

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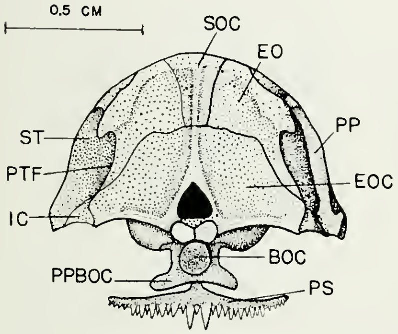

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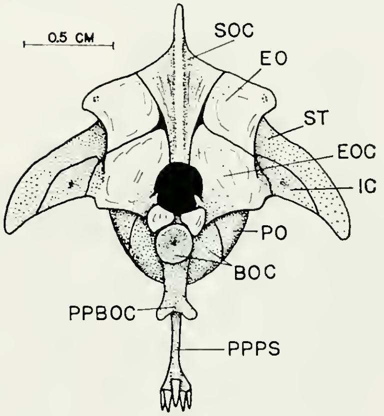

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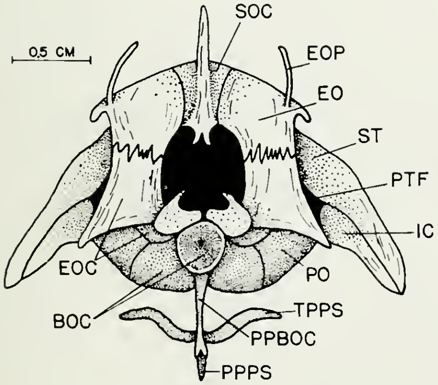

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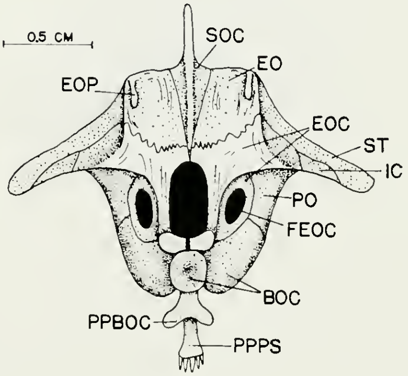
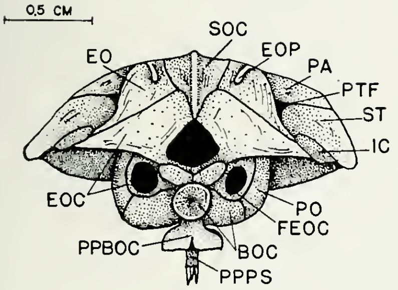


57

PLATE 16

Fig. 58. Posterior aspect of neurocranium of *Betta splendens.*
Fig. 59. Posterior aspect of neurocranium of *Trichopsis vittatus.*
Fig. 60. Posterior aspect of neurocranium of *Macropodus opercularis.*
Fig. 61. Posterior aspect of neurocranium of *Sphaerichthys osphromenoides.*
Fig. 62. Posterior aspect of neurocranium of *Colisa fasciata.*
Fig. 63. Posterior aspect of neurocranium of *Trichogaster leeri.*

Abbreviations: BOC, basioccipital; EO, epiotic; EOC, exoccipital; EOP, epiotic process; FEOC, foramen exoccipitale; IC, intercalary; PA, parietal; PO, prootic; PPBOC, pharyngeal process of basioccipital; PPPS, pharyngeal process of parasphenoid; PTF, posttemporal fossa; SOC, supraoccipital; ST, supratemporal.



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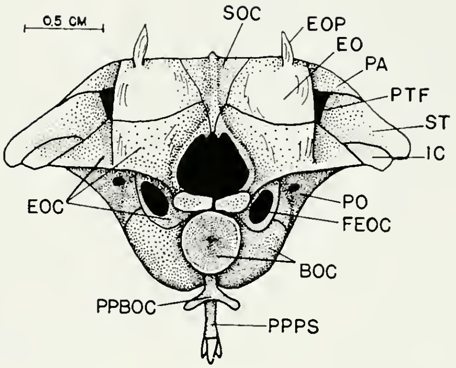

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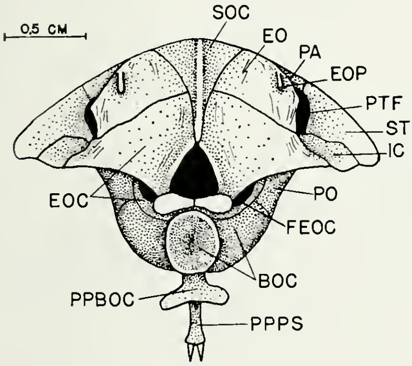

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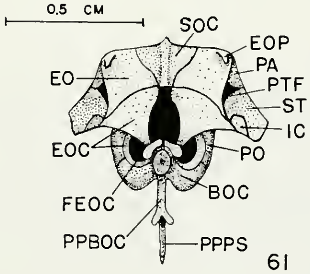

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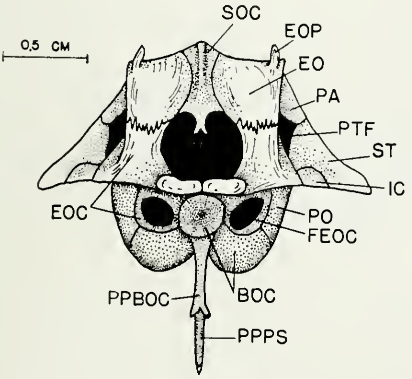

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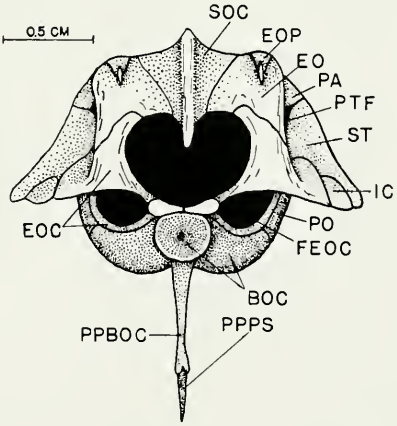

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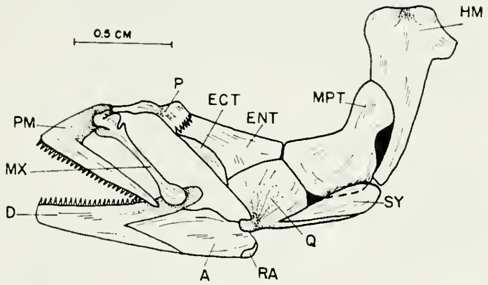
PLATE 17

Fig. 64. Lateral aspect of oromandibular region of *Anabas testudineus.*
Fig. 65. Lateral aspect of oromandibular region of *Ctenopoma multispinis.*
Fig. 66. Lateral aspect of oromandibular region of *Sandelia capensis.*
Fig. 67. A. Lateral aspect of oromandibular region of *Osphronemus goramy.* B. Opercular series of *Osphronemus goramy.*

Abbreviations: A, angular; APA, ascending process of angular; APD, ascending process of dentary; APPM, ascending process of premaxillary; D, dentary; ECT, ectopterygoid; ENT, entopterygoid; EPP, ethmoid process of palatine; HM, hyomandibular; IOP, interopercular; MPT, metapterygoid; MX, maxillary; OP, opercular; P, palatine; PM, premaxillary; POP, preopercular; Q, quadrate; RA, retroarticular; SOP, subopercular; SY, symplectic.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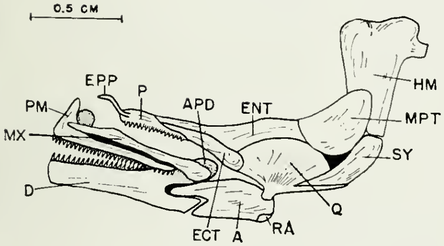
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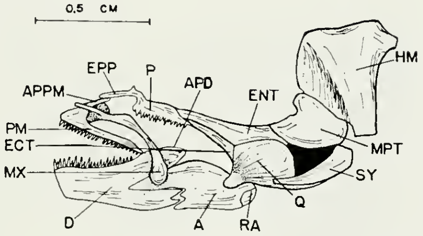
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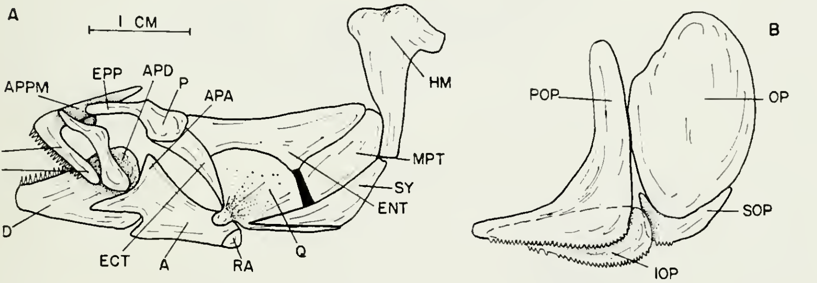
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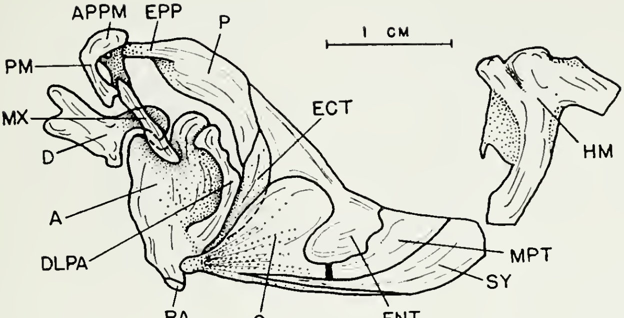
67

PLATE 18

Fig. 68. Lateral aspect of oromandibular region of *Helostoma temmincki.*
Fig. 69. Lateral aspect of oromandibular region of *Belontia hasselti.*
Fig. 70. Lateral aspect of oromandibular region of *Betta splendens.*
Fig. 71. Lateral aspect of oromandibular region of *Trichopsis vittatus.*
Abbreviations: A, angular; APA, ascending process of angular; APD, ascending process of dentary; APPM, ascending process of premaxillary; D, dentary; DLPA, dorsolateral process of angular; ECT, ectopterygoid; ENT, entopterygoid; EPP, ethmoid process of palatine; HM, hyomandibular; MPT, metapterygoid; MX, maxillary; P, palatine; PM, premaxillary; Q, quadrate; RA, retroarticular; SY, symplectic.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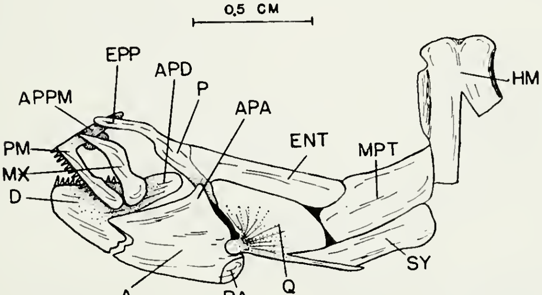
68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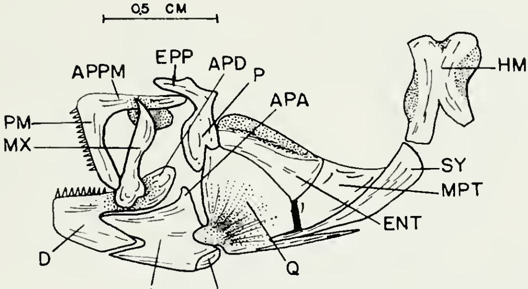
69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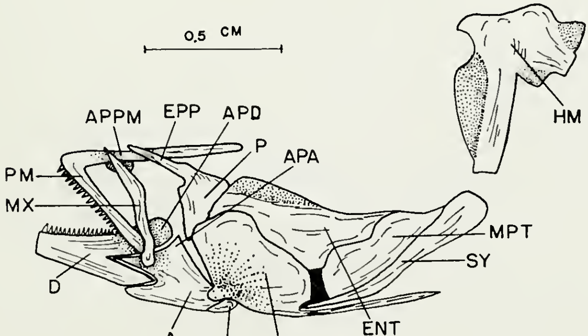
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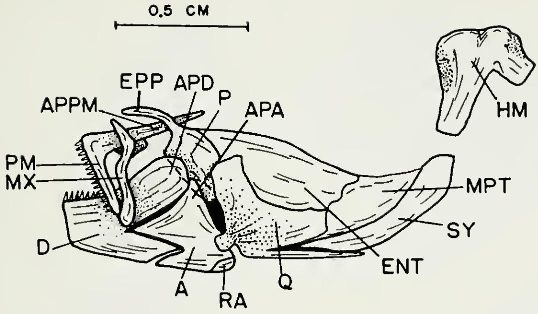
A
RA
Q

71

PLATE 19

Fig. 72. Lateral aspect of oromandibular region of *Macropodus cupanus.*
Fig. 73. Lateral aspect of oromandibular region of *Sphaerichthys osphromenoides.*
Fig. 74. Lateral aspect of oromandibular region of *Colisa fasciata.*
Fig. 75. Lateral aspect of oromandibular region of *Trichogaster leeri.*
Abbreviations: A, angular; APA, ascending process of angular; APD, ascending process of dentary; APPM, ascending process of premaxillary; D, dentary; ENT, entopterygoid; EPP, ethmoid process of palatine; HM, hyomandibular; MPT, metapterygoid; MX, maxillary; P, palatine; PM, premaxillary; Q, quadrate; RA, retroarticular; SY, symplectic.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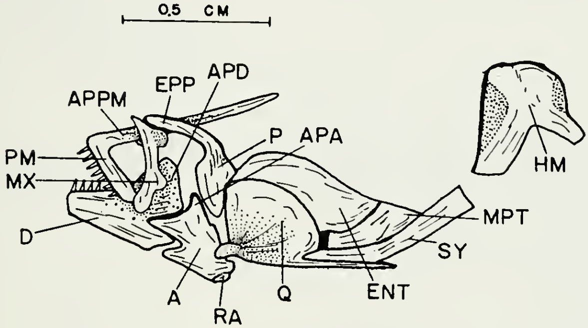
72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RA

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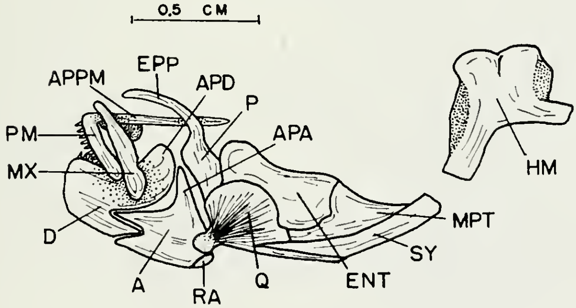
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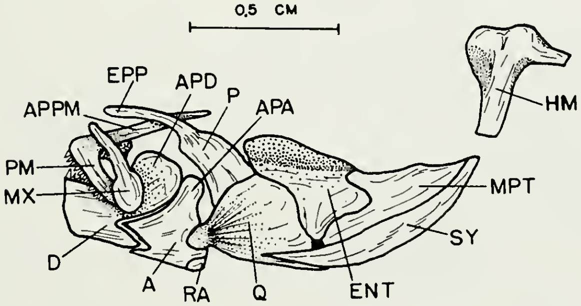
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A
RA
Q
ENT

75

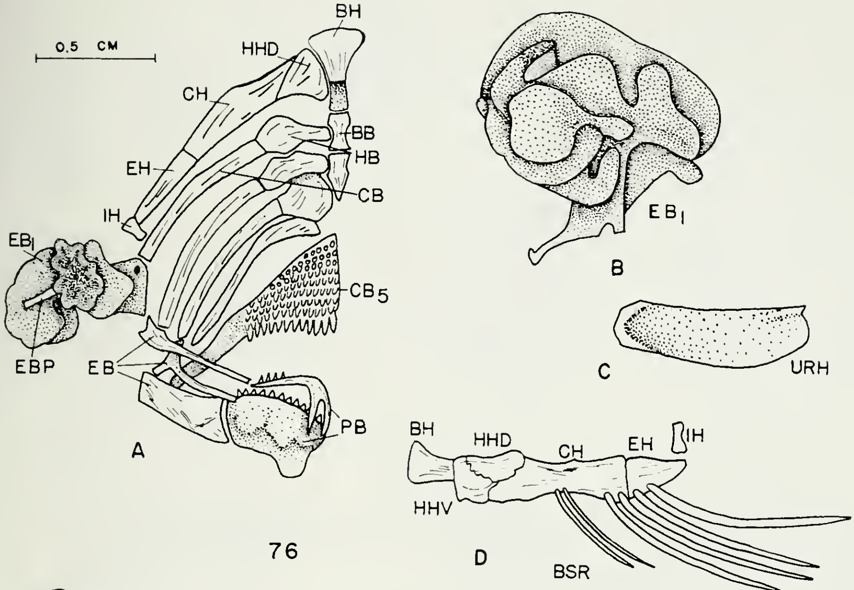
PLATE 20

Fig. 76. Hyobranchium of *Anabas testudineus.*
- A. Dorsal aspect of left half of hyobranchium, first epibranchial reflected laterally.
- B. Lateral aspect of modified first epibranchial (suprabranchial organ).
- C. Lateral aspect of urohyal.
- D. Lateral aspect of hyoid apparatus.

Fig. 77. Hyobranchium of *Ctenopoma multispinis.*
- A. Dorsal aspect of left half of hyobranchium, first epibranchial seen from the medial aspect.
- B. Lateral aspect of modified first epibranchial.
- C. Ventral aspect of pharyngobranchials.
- D. Lateral aspect of hyoid apparatus.
- E. Lateral aspect of urohyal.

Fig. 78. Hyobranchium of *Sandelia capensis.*
- A. Lateral aspect of modified first epibranchial.
- B. Dorsal aspect of left half of hyobranchium.
- C. Ventral aspect of pharyngobranchials.
- D. Lateral aspect of hyoid apparatus.
- E. Lateral aspect of urohyal.

Abbreviations: BB, basibranchial; BH, basihyal; BSR, branchiostegal rays; CB, ceratobranchial; CH, ceratohyal; EB, epibranchial; EBP, epibranchial process; EH, epihyal; HB, hypobranchial; HHD, dorsal hypohyal; HHV, ventral hypohyal; IH, interhyal; PB, pharyngobranchial; URH, urohyal.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B
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C
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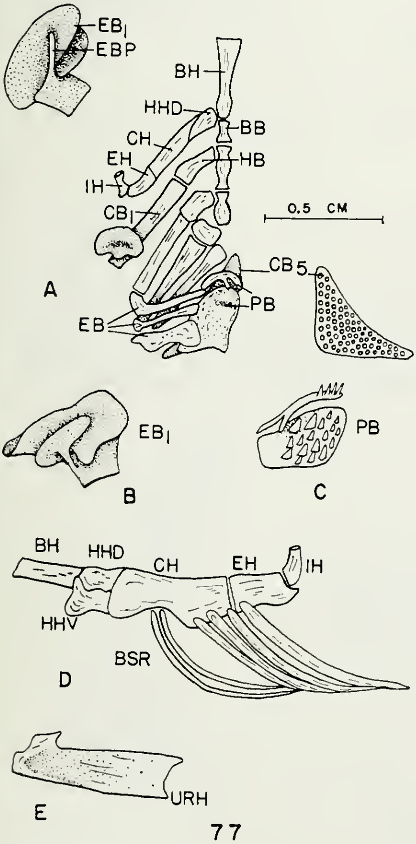
HHD
CH
EH
IH
HHV
D
BSR

76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BH
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CH
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IH
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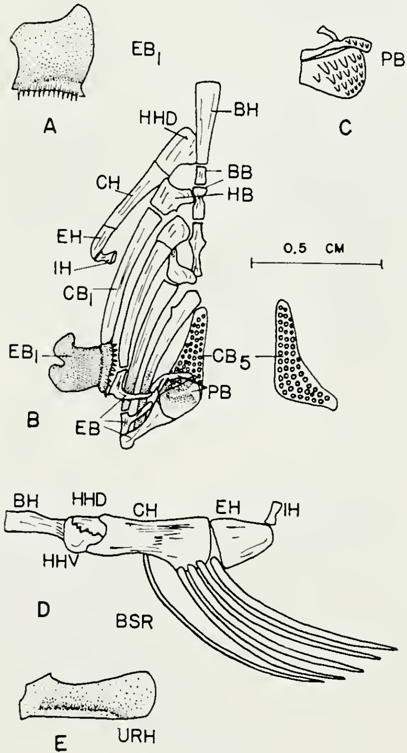
BSR
D
E
URH

77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BH
BB
CH
HB
EH
0.5 CM
IH
CB1
EB1
CB5
PB
B
EB
BH
HHD
CH
EH
IH
HHV
D
BSR
E
URH

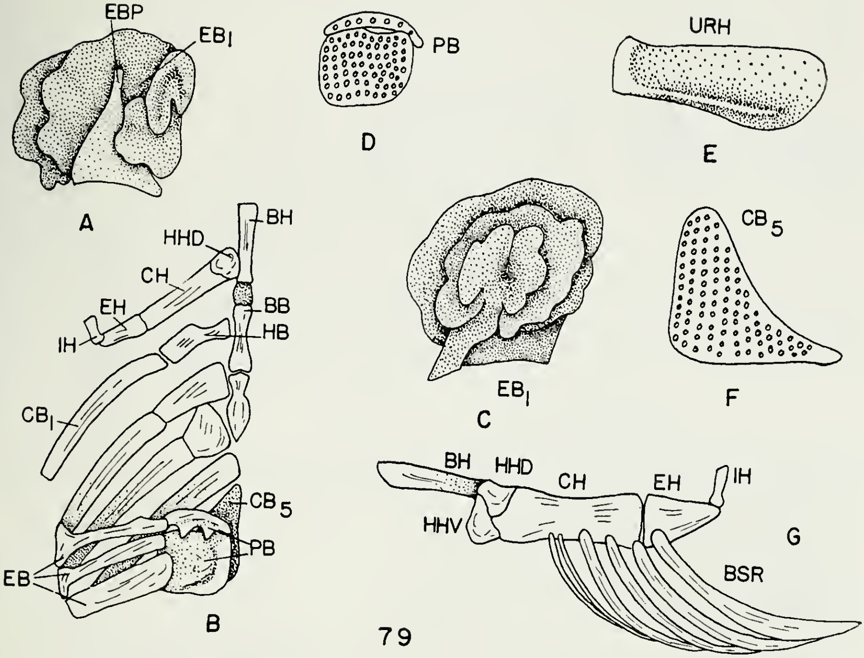
78

PLATE 21

Fig. 79. Hyobranchium of *Osphronemus goramy.*
  A. Medial aspect of modified first epibranchial (suprabranchial organ).
  B. Dorsal aspect of left hyobranchium.
  C. Lateral aspect of first epibranchial.
  D. Ventral aspect of pharyngobranchials 2-4.
  E. Lateral aspect of urohyal.
  F. Dorsal aspect of fifth ceratobranchial.
  G. Lateral aspect of hyoid apparatus.

Fig. 80. Hyobranchium of *Helostoma temmincki.*
  A. Medial aspect of modified first epibranchial (suprabranchial organ).
  B. Dorsal aspect of left hyobranchium.
  C. Lateral aspect of first epibranchial.
  D. Ventral aspect of epibranchials 2-4 and pharyngobranchials.
  E. Dorsal aspect of fifth ceratobranchial.
  F. Lateral aspect of hyoid apparatus.
  G. Lateral aspect of urohyal.

Abbreviations: BB, basibranchial; BH, basihyal; BSR, branchiostegal rays; CB, ceratobranchial; CH, ceratohyal; EB, epibranchial; EBP, epibranchial process; EH, epihyal; HB, hypobranchial; HHD, dorsal hypohyal; HHV, ventral hypohyal; IH, interhyal; MR, median ridge of basibranchials; PB, pharyngobranchial; URH, urohyal.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PB
D
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E
BH
HHD
CH
EH
IH
BB
HB
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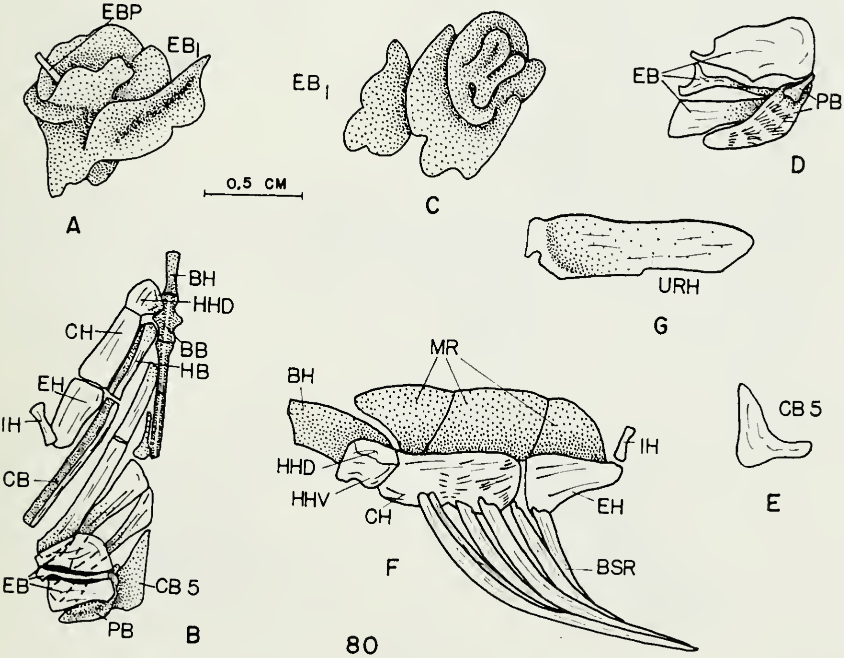
IH
HHV
G
BSR

79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EB1
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0.5 CM
EB1
C
EB
PB
D
URH
G
BH
HHD
CH
BB
HB
EH
IH
CB
EB
CB 5
PB
B
MR
BH
IH
HHD
HHV
CH
EH
BSR
F
CB 5
E

80

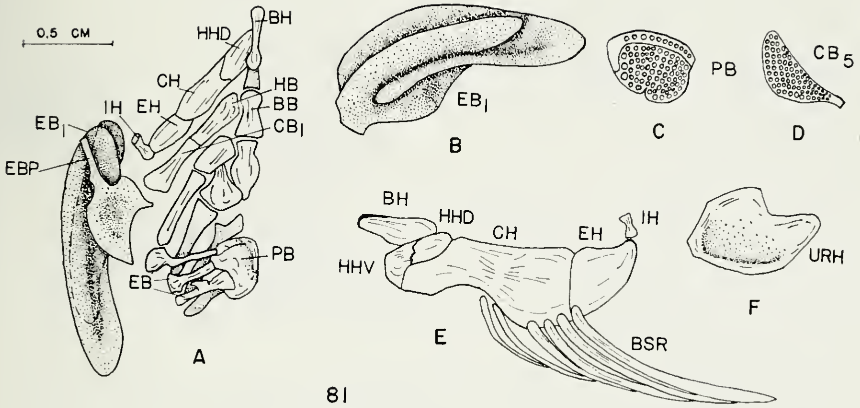
PLATE 22

Fig. 81. Hyobranchium of *Belontia hasselti.*
- A. Dorsal aspect of left half of hyobranchium, first epibranchial reflected laterally.
- B. Lateral aspect of modified first epibranchial (suprabranchial organ).
- C. Ventral aspect of pharyngobranchials.
- D. Dorsal aspect of fifth ceratobranchial.
- E. Lateral aspect of hyoid apparatus.
- F. Lateral aspect of urohyal.

Fig. 82. Hyobranchium of *Betta splendens.*
- A. Dorsal aspect of left half of hyobranchium, first epibranchial reflected laterally.
- B. Lateral aspect of modified first epibranchial (suprabranchial organ).
- C. Ventral aspect of pharyngobranchials.
- D. Dorsal aspect of fifth ceratobranchial.
- E. Lateral aspect of urohyal.
- F. Lateral aspect of hyoid apparatus.

Fig. 83. Hyobranchium of *Trichopsis vittatus.*
- A. Lateral aspect of modified first epibranchial.
- B. Dorsal aspect of left half of hyobranchium.
- C. Ventral aspect of pharyngobranchials.
- D. Lateral aspect of hyoid apparatus.
- E. Lateral aspect of urohyal.

Abbreviations: BB, basibranchial; BH, basihyal; BSR, branchiostegal rays; CB, ceratobranchial; CH, ceratohyal; EB, epibranchial; EBP, epibranchial process; EH, epihyal; HB, hypobranchial; HHD, dorsal hypohyal; HHV, ventral hypohyal; IH, interhyal; PB, pharyngobranchial; URH, urohyal.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EH
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EB1
EBP
PB
EB
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EB1
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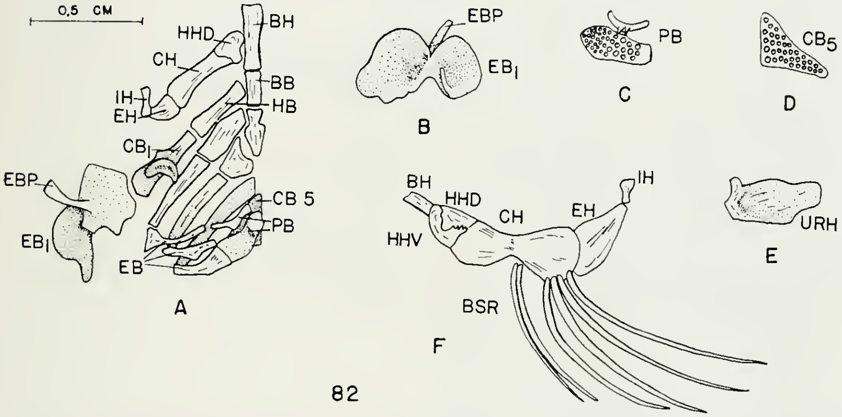
PB
C
CB5
D
BH
HHD
CH
EH
IH
HHV
E
BSR
URH
F

81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EB1
CB 5
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CB5
D
BH
HHD
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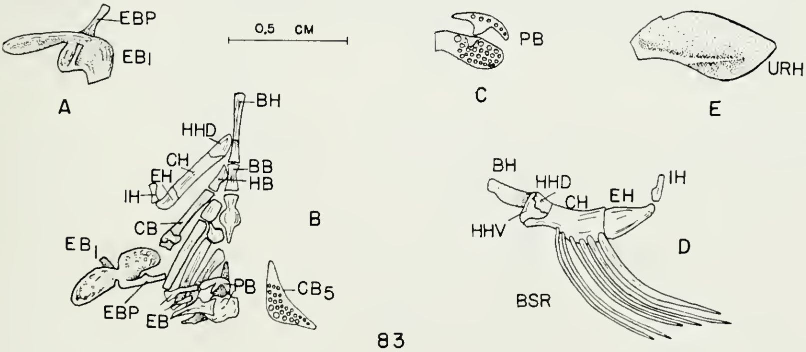
EH
IH
HHV
BSR
F
URH
E

82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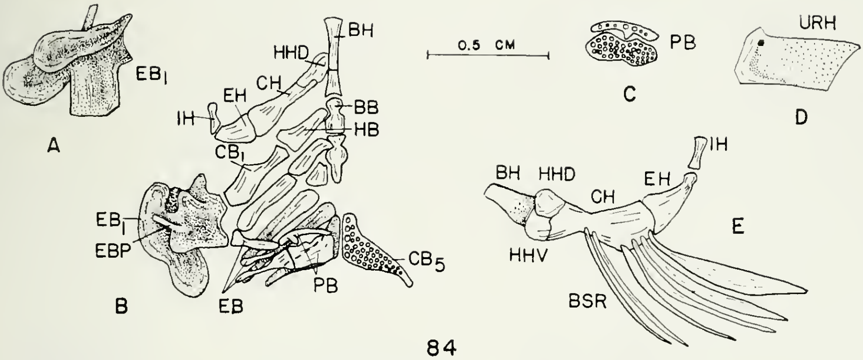
IH
CB
B
EB1
PB
CB5
EBP
EB
BH
HHD
IH
CH
EH
HHV
D
BSR

83

Plate 23

Fig. 84. Hyobranchium of *Macropodus opercularis.*
  A. Lateral aspect of modified first epibranchial (suprabranchial organ).
  B. Dorsal aspect of left half of hyobranchium, first epibranchial reflected laterally.
  C. Ventral aspect of pharyngobranchials.
  D. Lateral aspect of urohyal.
  E. Lateral aspect of hyoid apparatus.
Fig. 85. Hyobranchium of *Sphaerichthys osphromenoides.*
  A. Posterior aspect of modified first epibranchial (suprabranchial organ).
  B. Lateral aspect of first epibranchial.
  C. Dorsal aspect of left half of hyobranchium.
  D. Ventral aspect of epibranchials 2-4 and pharyngobranchials.
  E. Dorsal aspect of fifth ceratobranchial.
  F. Lateral aspect of hyoid apparatus.
Fig. 86. Hyobranchium of *Colisa lalia.*
  A. Medial aspect of modified first epibranchial (suprabranchial organ).
  B. Dorsal aspect of hyobranchium. Branchial element from right side not shown.
  C. Lateral aspect of modified first epibranchial.
  D. Ventral aspect of pharyngobranchials.
  E. Dorsal aspect of fifth ceratobranchial.
  F. Lateral aspect of hyoid apparatus.
  G. Lateral aspect of urohyal.

Abbreviations: BB, basibranchial; BH, basihyal; BSR, branchiostegal rays; CB, ceratobranchial; CH, ceratohyal; EB, epibranchial; EBP, epibranchial process; EH, epihyal; HB, hypobranchial; HHD; dorsal hypohyal; HHV, ventral hypohyal; IH, interhyal; PB, pharyngobranchial; URH, urohyal.



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BH
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HB
CB$_1$
EB$_1$
EBP
B
EB
PB
CB$_5$
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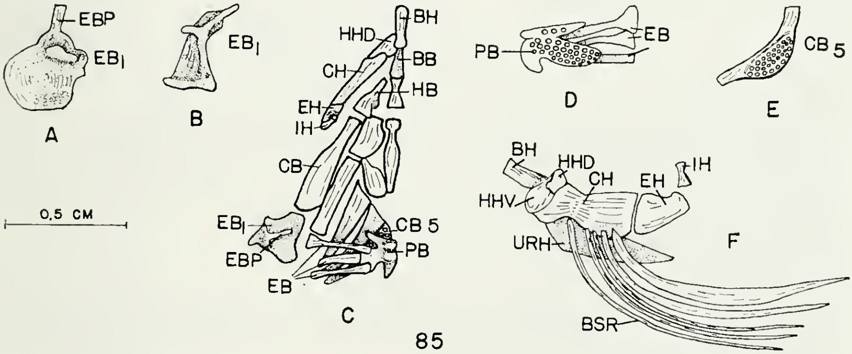
BH
HHD
EH
CH
E
HHV
BSR

84



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EB$_1$
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CB 5
EBP
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D
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E
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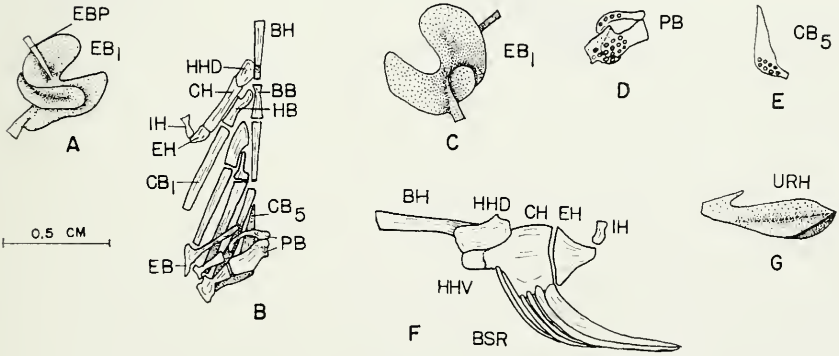
BSR

85



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B
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C
PB
D
CB$_5$
E
BH
HHD
CH
EH
IH
HHV
F
BSR
URH
G

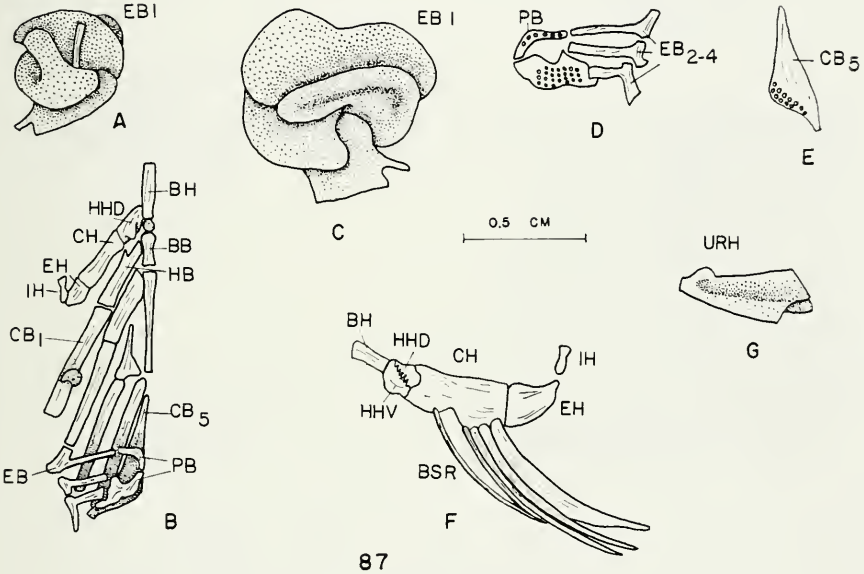
86

PLATE 24

Fig. 87. Hyobranchium of *Trichogaster trichopterus.*

A. Medial aspect of modified first epibranchial (suprabranchial organ).
B. Dorsal aspect of hyobranchium. Branchial elements from right side not shown.
C. Lateral aspect of first epibranchial.
D. Ventral aspect of epibranchials 2-4 and pharyngobranchials.
E. Dorsal aspect of fifth ceratobranchial.
F. Lateral aspect of hyoid apparatus.
G. Lateral aspect of urohyal.

Abbreviations: BB, basibranchial; BH, basihyal; BSR, branchiostegal rays; CB, ceratobranchial; CH, ceratohyal; EB, epibranchial; EH, epihyal; HB, hypobranchial; HHD, dorsal hypohyal; HHV, ventral hypohyal; IH, interhyal; PB, pharyngobranchial; URH, urohyal.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EB 1
C
PB
EB2-4
D
CB5
E
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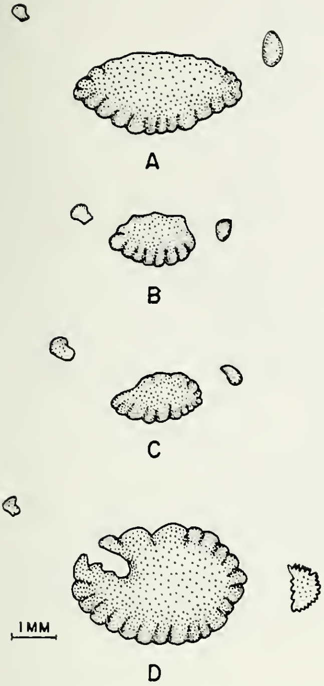
HHD
CH
BB
EH
HB
IH
CB1
CB 5
PB
EB
B
0.5 CM
URH
G
BH
HHD
CH
IH
HHV
EH
BSR
F

87

PLATE 25

Lateral aspects of left otoliths. Sequence of otoliths from left to right is: utriculith (lapillus), sacculith (sagitta), lagenolith (asteriscus).

Fig. 88. A. *Anabas testudineus.*
B. *Ctenopoma muriei.*
C. *Sandelia capensis.*
D. *Helostoma temmincki.*
Fig. 89. A. *Belontia hasselti.*
B. *Macropodus opercularis.*
C. *Betta splendens.*
D. *Sphaerichthys osphromenoides.*
Fig. 90. A. *Colisa lalia.*
B. *Trichogaster trichopterus.*
C. *Ctenopoma multispinis.*
D. *Luciocephalus pulcher.*



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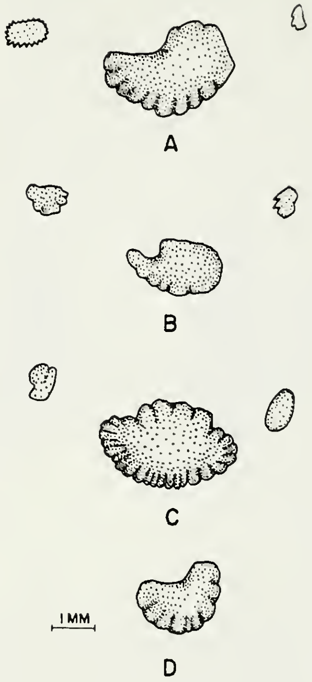

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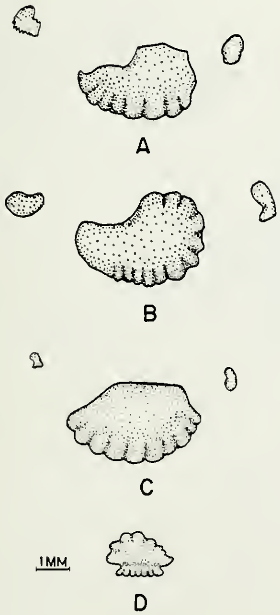
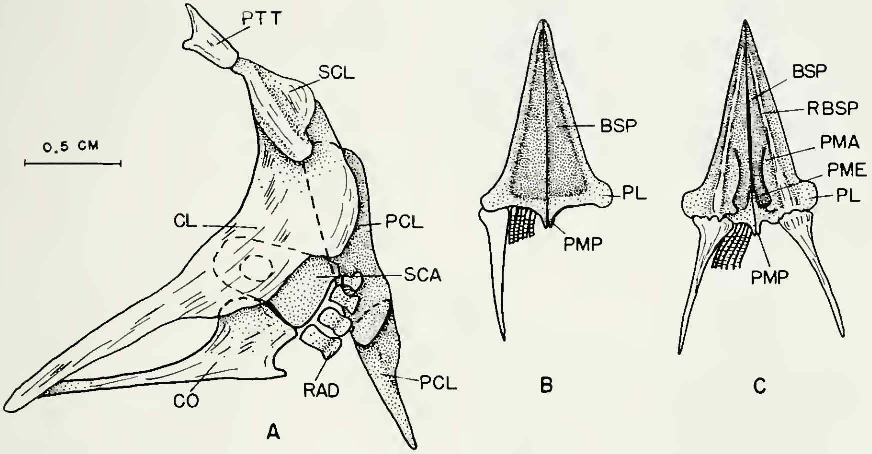


90

PLATE 26

Fig. 91. Pectoral and pelvic girdles of *Anabas testudineus.*
A. Lateral aspect of pectoral girdle.
B. Dorsal aspect of pelvic girdle.
C. Ventral aspect of pelvic girdle.
Fig. 92. Pectoral and pelvic girdles of *Sandelia capensis.*
A. Lateral aspect of pectoral girdle.
B. Ventral aspect of pelvic girdle.
C. Dorsal aspect of pelvic girdle.
Abbreviations: BSP, basipterygium; CL, cleithrum; CO, coracoid; PCL, postcleithrum; PL, processus lateralis; PMA, processus medialis anterior; PME, processus medialis; PMP, processus medialis posterior; PTT, posttemporal; RAD, radial; RBSP, rachis of basipterygium; SCA, scapula; SCL, supracleithrum.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PME
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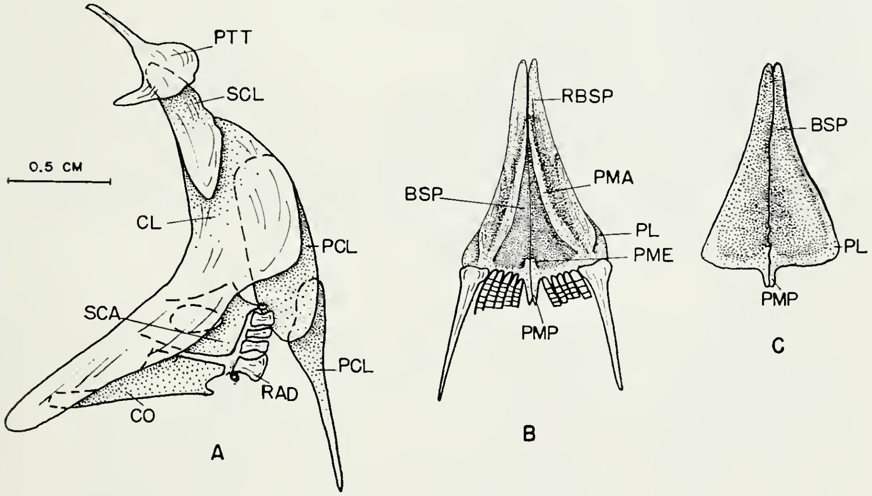
PMP
C

91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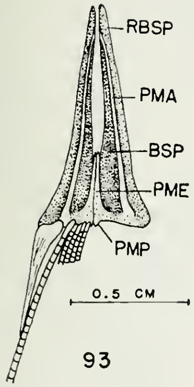
SCA
PCL
RAD
CO
A
RBSP
BSP
PMA
PL
PME
PMP
B
BSP
PL
PMP
C

92

PLATE 27

Fig. 93. Ventral aspect of pelvic girdle of *Osphronemus goramy.*
Fig. 94. Pectoral girdle of *Helostoma temmincki.*
  A. Lateral aspect.
  B. Medial aspect.
Fig. 95. Pelvic girdle of *Helostoma temmincki.*
  A. Ventral aspect.
  B. Dorsal aspect.
Fig. 96. Pectoral and pelvic girdles of *Belontia hasselti.*
  A. Lateral aspect of pectoral girdle.
  B. Ventral aspect of pelvic girdle.
Fig. 97. Pectoral and pelvic girdles of *Trichopsis vittatus.*
  A. Lateral aspect of pectoral and pelvic girdles.
  B. Ventral aspect of pelvic girdle.

Abbreviations: BSP, basipterygium; CL, cleithrum; CO, coracoid; PCL, postcleithrum; PL, processus lateralis; PMA, processus medialis anterior; PME, processus medialis; PMP, processus medialis posterior; PTT, posttemporal; RAD, radial; RBSP, rachis of basipterygium; SCA, scapula; SCL, supracleithrum.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PMP
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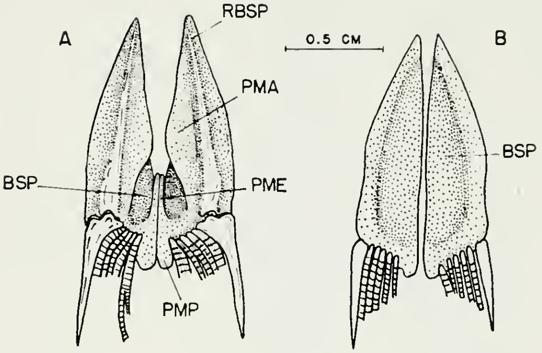
93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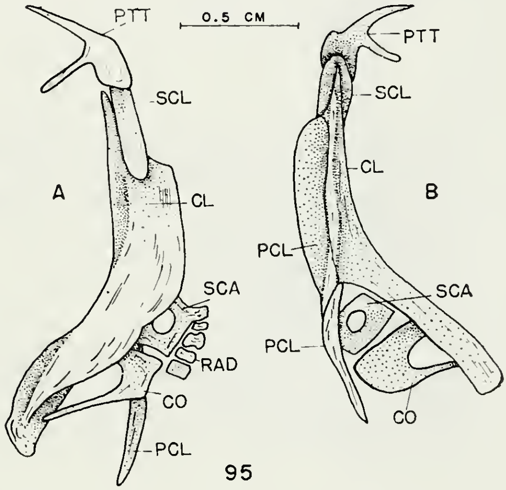
B
BSP

94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SCA
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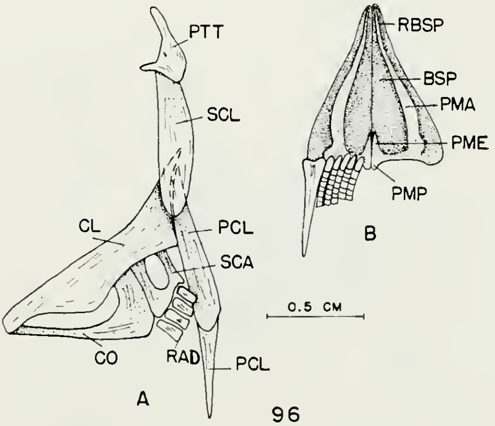
CO

95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PME
PMP
B
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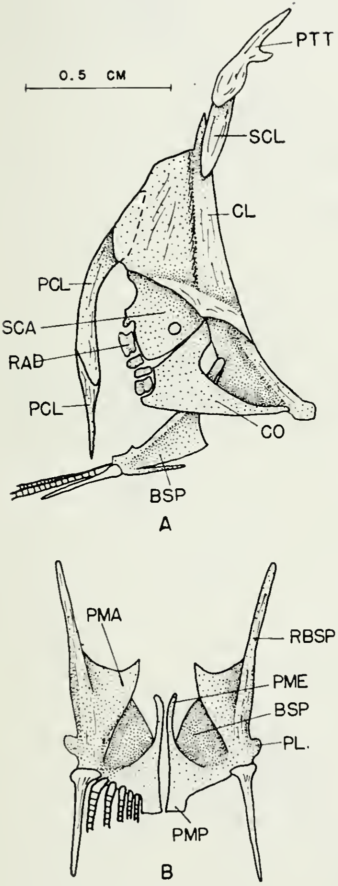
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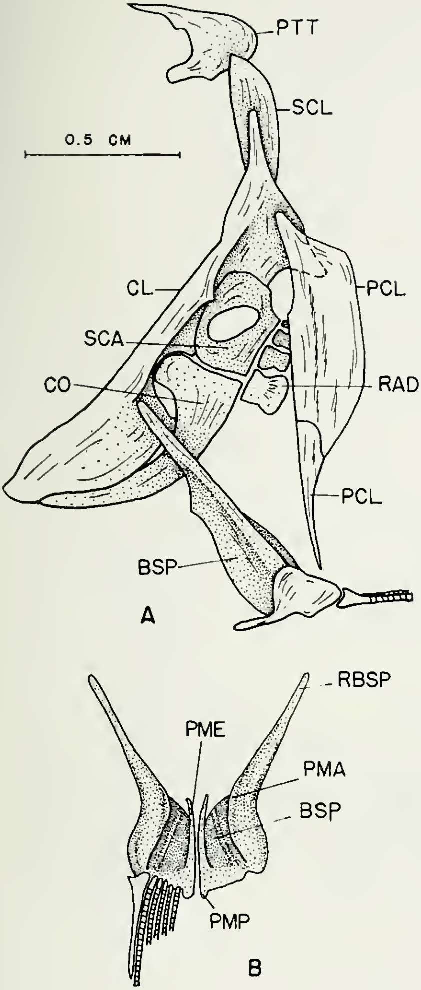
Plate 28

Fig. 98. Pectoral and pelvic girdles of *Macropodus opercularis.*
A. Medial aspect of pectoral and pelvic girdles.
B. Ventral aspect of pelvic girdle.
Fig. 99. Pectoral and pelvic girdles of *Sphaerichthys osphromenoides.*
A. Medial aspect of pectoral and pelvic girdles.
B. Ventral aspect of pelvic girdle.
Fig. 100. Pectoral and pelvic girdles of *Colisa lalia.*
A. Medial aspect.
B. Lateral aspect.

Abbreviations: BSP, basipterygium; CL, cleithrum; CO, coracoid; PCL, postcleithrum; PL, processus lateralis; PMA, processus medialis anterior; PMAS, processus medialis accessorius; PME, processus medialis; PMP, processus medialis posterior; PTT, posttemporal; RAD, radial; RBSP, rachis of basipterygium; SCA, scapula; SCL, supracleithrum.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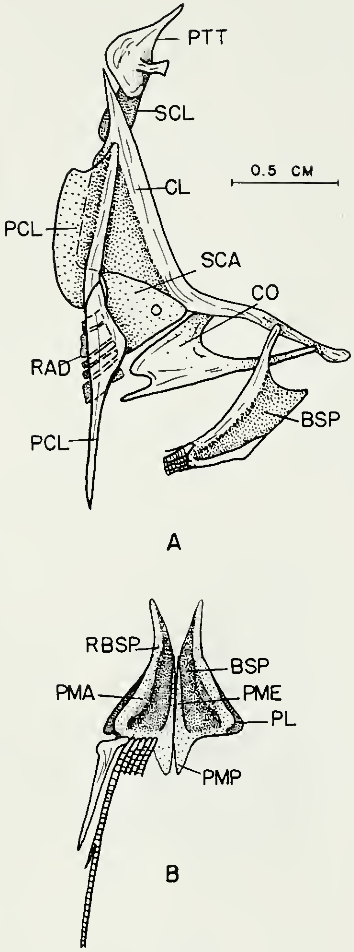
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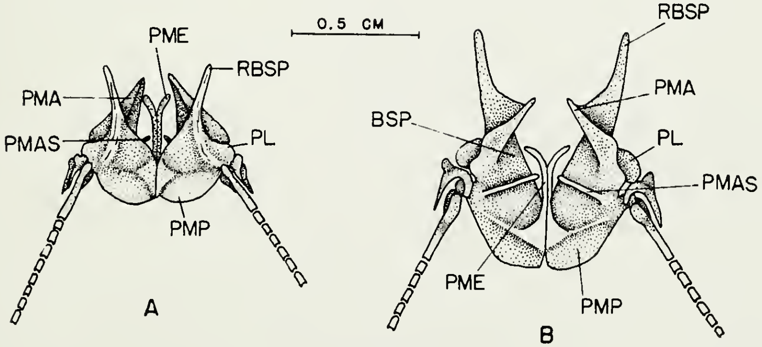
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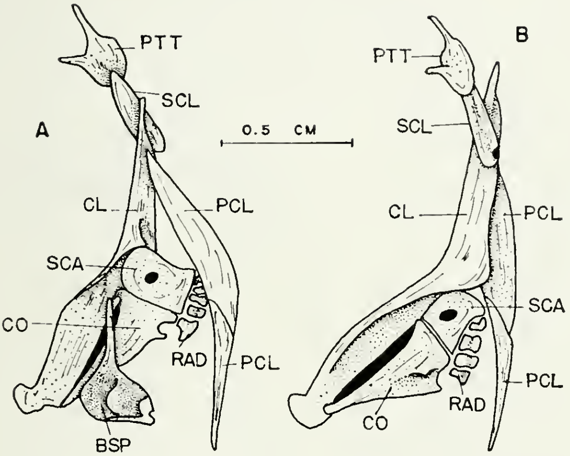
Plate 29

Fig. 101. Pelvic girdle of *Colisa lalia*.
A. Dorsal aspect.
B. Ventral aspect.

Fig. 102. Ventral aspect of pelvic girdle of *Trichogaster leeri.*

Abbreviations: BSP, basipterygium; CL, cleithrum; CO, coracoid; PCL, postcleithrum; PL, processus lateralis; PMA, processus medialis anterior; PMAS, processus medialis accessorius; PME, processus medialis; PMP, processus medialis posterior; PTT, posttemporal; RAD, radial; RBSP, rachis of basipterygium; SCA, scapula; SCL, supracleithrum.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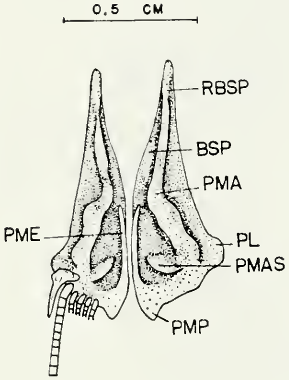
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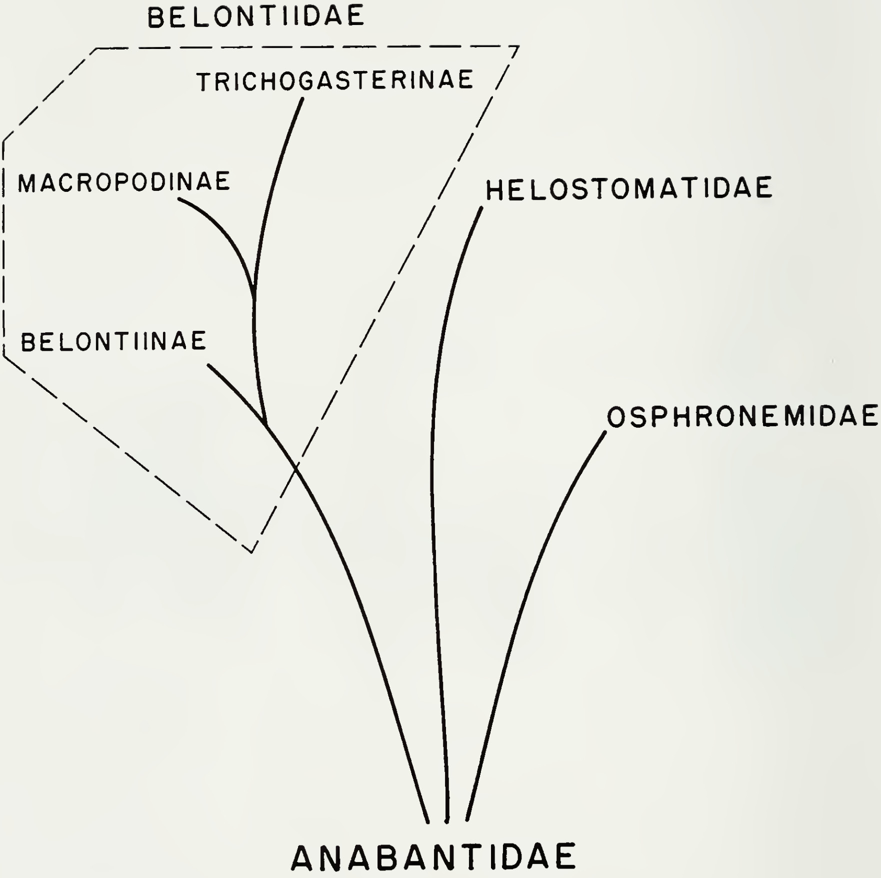

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Fig. 103. The proposed phylogeny of the anabantoid families and subfamilies.

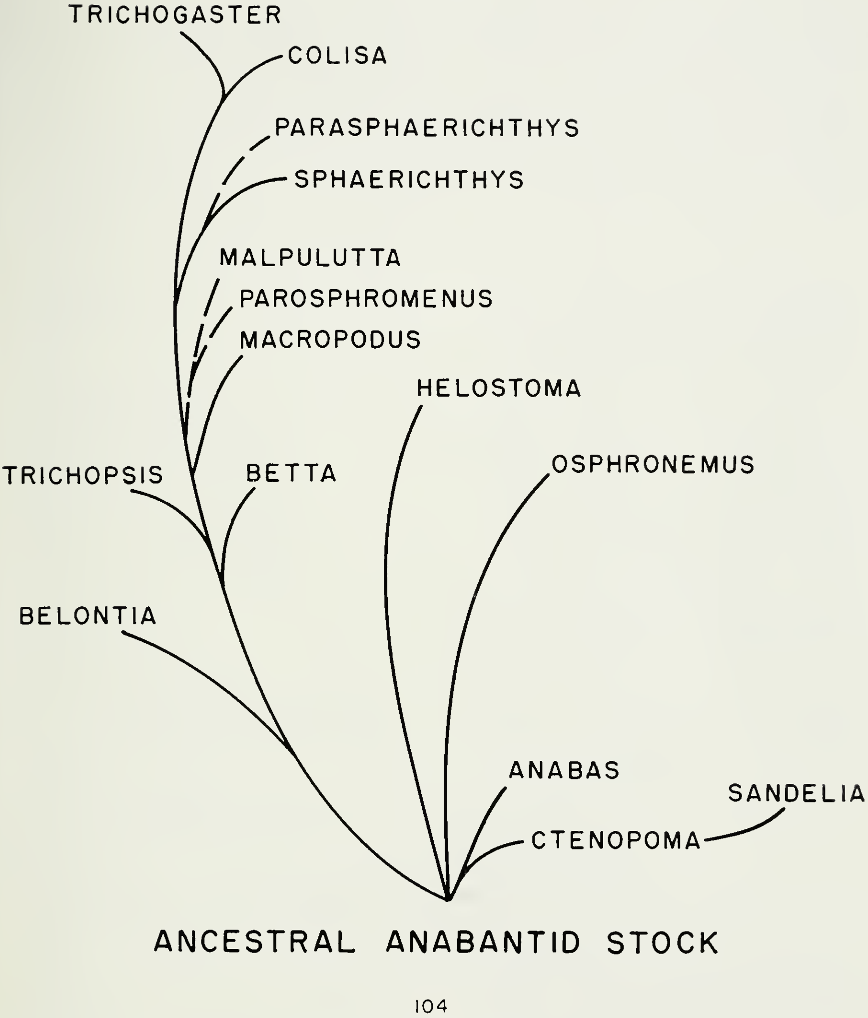

Fig. 104. The proposed phylogeny of the anabantoid genera.

INDEX

Note: Since the 26 species and 14 genera of anabantoids are mentioned on numerous pages, entries in the following index refer only to important discussions and plates. Less important mentions of generic and specific names are entered collectively under family names. All page references to illustrations are restricted to specific names and are entered in boldface type. Taxonomic names appearing in tables, names of bony elements in the legends of figures, authors listed in the bibliography, and chapter titles are not included in this index.

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