THE OSTEOLGY OF *Luvurus imperialis*, a Scombroid Fish: a Study in Adaptive Evolution

By William K. Gregory and G. Miles Conrad

BULLETIN
OF
THE AMERICAN MUSEUM OF NATURAL HISTORY
New York
Issued June 11, 1943
Article II.—THE OSTEOLGY OF LUVARUS IMPERIALIS, A
SCOMBROID FISH: A STUDY IN ADAPTIVE EVOLUTION

BY WILLIAM K. GREGORY AND G. MILES CONRAD

Figures 1 to 38

CONTENTS

<table>
<thead>
<tr>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTRODUCTION</td>
</tr>
<tr>
<td>OSTEOLGY OF Luvarus</td>
</tr>
<tr>
<td>Median Fins and &quot;Contour Bones&quot;</td>
</tr>
<tr>
<td>Caudal Fin</td>
</tr>
<tr>
<td>Dorsal Fin and Dorsal Truss</td>
</tr>
<tr>
<td>Anal Fin and Ventral Truss</td>
</tr>
<tr>
<td>Vertebral Column</td>
</tr>
<tr>
<td>Vertebral Numbers</td>
</tr>
<tr>
<td>Caudal Vertebrae</td>
</tr>
<tr>
<td>&quot;Abdominal&quot; Vertebrae and Ribs</td>
</tr>
<tr>
<td>Summary of Vertebral Regions</td>
</tr>
<tr>
<td>Paired Fins and Girdles</td>
</tr>
<tr>
<td>Pelvic Fin and Pelvis</td>
</tr>
<tr>
<td>Pectoral Fin and Girdle</td>
</tr>
<tr>
<td>Opercular Region</td>
</tr>
<tr>
<td>Jaws and Suspensorium</td>
</tr>
<tr>
<td>Hyobranchial Complex</td>
</tr>
<tr>
<td>Neurocranium</td>
</tr>
<tr>
<td>Anteroposterior Arches</td>
</tr>
<tr>
<td>Supraoccipital-epiotic Ridge</td>
</tr>
<tr>
<td>Ethmo-nasal Complex</td>
</tr>
<tr>
<td>Alisphenoids</td>
</tr>
<tr>
<td>Prootic-occipital Complex</td>
</tr>
<tr>
<td>Vomer-parasphenoid Brace</td>
</tr>
<tr>
<td>Transverse Arches</td>
</tr>
<tr>
<td>Hypsiloid Brace</td>
</tr>
<tr>
<td>Occipito-otic Braces</td>
</tr>
<tr>
<td>LARVAL STAGES</td>
</tr>
<tr>
<td>DISCUSSION AND SUMMARY</td>
</tr>
<tr>
<td>Structural and Functional Characters</td>
</tr>
<tr>
<td>Phylogeny and Classification</td>
</tr>
<tr>
<td>REFERENCES TO THE LITERATURE</td>
</tr>
<tr>
<td>ABBREVIATIONS USED IN FIGURES</td>
</tr>
</tbody>
</table>

INTRODUCTION

The skeleton which is described below was prepared from a specimen of louvar (Luvarus imperialis) which was caught off Cayo Costa Island, Florida, April 25, 1941, by Eugene Spearman, a commercial fisherman. It weighed 200 pounds. It was brought to Dr. Marshall F. Bishop of Yale University and a representative of the New York Aquarium Field Station at Palmetto Key, Florida, for identification. Dr. Bishop notified Dr. Charles M. Breder, Jr., Director of the New York Aquarium, who presented this specimen to The American Museum of Natural History. A cast and life-sized model were made for the Hall of Fishes by Mr. L. Ferraglio, under the joint direction of Mr. J. T. Nichols, Curator of Recent Fishes, and Dr. J. L. Clark, head of the Department of Preparation and Installation. The skeleton was prepared for study by Mr. Andrew Johnson.

This fish closely resembles the one which was captured on the shore near East
Fig. 1. Lutjanus jocutensis Balf. Model of left side, based on cast made from 200-pound specimen caught at Cayo Costa, Florida, 1941. Ca. x 1/5.
Hampton, New York, on August 2, 1940, by Messrs. Bertil Johanssen and Walter Babinski. Through their efforts that specimen, which weighed about 210 pounds, was studied and described by J. T. Nichols and William T. Helmuth, 3d, in American Museum Novitates (No. 1085, October 11, 1940). This was the first record of the occurrence of Luvarus on the American coast of the Atlantic, the subject of the present paper being the second. The third is documented by a vertebra, undoubtedly of Luvarus, which was taken from a mud flat at Pattaguansett River, Black Point, near Niantic, Connecticut, by Mr. F. Tebbut.

This genus and species is extremely rare, only thirty adults in all being recorded, mostly from the North Atlantic and Mediterranean, the Indian Ocean off the coast of Mozambique, the Pacific Ocean off the coasts of California (Bolin, 1940) and Australia (Waite, 1902; Whitley, 1940).

The skeleton of Luvarus was briefly described by Albert Günther (1866) and by Tate Regan (1903). The latter concluded that "Luvarus must be considered to be a most abnormal and specialized Scombrid..." and explained many of its peculiar skeletal characters by comparison with less specialized conditions in Thunnus. Meanwhile Waite (1902) gave a succinct description of a large skeleton of Luvarus which was mounted under his direction in the Australian Museum, Sydney, New South Wales.

Fig. 2. Head on and rear views, based on photographs of the model.

Roule (1924) brought together and described the larval and young stages of the Mediterranean Luvarus, showing the transformation of the minute scales from a bicuspid stage through the tricuspid and stelliform into the fungiform stage of the adult and following step by step the "hypermetamorphosis" from the 6-mm. "Hystricinella," a short, deep-bodied larva with relatively huge head and great spikes on the anterior dorsal and pelvic fins, through the "Astrodermella" and "Luva-
Fig. 3. Dorsal and ventral views of model.

rela’ stages in which the body lengthens, a dorsal keel develops, the fins lose their long spikes and the pelvic fins shrink to their nearly vestigial adult condition. Roule disputed the reference of *Luarus* to the scombriform series, suggested its independent derivation and raised the “Luvariformes” of Jordan (1923) to full ordinal rank. These conclusions will be considered below (p. 280).

*Luarus* is a pelagic fish probably descending to considerable depths, seeking its
food chiefly by sight. The very small mouth and delicate edentulous jaws suggest that small crustaceans and jellyfishes form at least an important part of the food. This is in accord with earlier records, but in our specimen the stomach was empty (Raven, in MS).

The body form of the adult (Fig. 1) is superficially tuna-like except for the small mouth and the great dorsal hump which extends from the snout to the long low dorsal fin; the posterior half is more tunny-like in spite of the lack of distinct dorsal and anal finlets. The relative
fixation of the dorsal and ventral contours by the interlocking of the prolonged bases of the interneural and interhaemal rods suggests relatively slight lateral flexures. On the other hand, the specialization of a pivot vertebra at the root of the tail (see p. 236) would permit a wide sweep of the large tail, the height of which is greater than that of the body.

The skeleton as a whole (Fig. 5) is delicate and fragile, the principal exceptions being certain extremely dense, almost ivory-like parts of the braincase just in front of the first vertebra, which receive the thrusts from the locomotor system. There are large spaces in the ethmoid region which were presumably filled with cartilage.

A detailed osteography of the adult skeleton of Luvarus must necessarily run to considerable length, for there is hardly a single feature which is not worthy of careful consideration, especially since our object is not only to give an adequate description of the osteology of this fish but also to develop the comparative, functional, systematic and phylogenetic implications of the observed details. We have not here followed the custom of describing first the skull and then the axial and appendicular parts, because the skull, having been profoundly modified in correlation with the locomotor parts, may be more easily understood after the main locomotor adaptations have been set forth.

**OSTEOLOGY OF LUVARUS**

**MEDIAN FINS AND "CONTOUR BONES"**

**CAUDAL FIN**

The broad and strong caudal fin (Figs. 4, 5) includes seventeen rays in the dorsal and thirteen in the ventral moiety. Of these, the first nine in the dorsal moiety and the first five in the ventral moiety are unbranched. On either side of the midline each ray fans out distally into small branches, while proximally the rays broadly overlap the hypural fan. A nubbin of bone at the base of the cleft between the dorsal and ventral moieties, attached to the dorsal hypural but directed backward and downward, seems to represent an aborted fin ray. Perhaps the nearest resemblance in form of the tail is to _Acanthocybium._

**DORSAL FIN AND DORSAL TRUSS**

The dorsal fin of Luvarus includes thirteen rays, of which the first two are much stoutier than the rest. Only the last four of the bony rays show even a slight trace of distal branching. This fin has evidently been derived from the "_Hystricinella_" and "_Astrodermella_" larval stages (Fig. 37). The dorsal fin of the former, as noted by Roule (1924), is provided with two very large spikes and from fifteen to twenty rays. In later "_Hystricinella_" the number rises to seventeen, then to twenty.

In "Astrodermella" the two large spines seem to have dwindled so that they are shorter than those behind them, while in the adult they have disappeared entirely, along with seven others, so that the fin proper begins with the eighth of the larval series. In the adult again the first two of the rays have become quite stout and considerably higher than the rest, so that Waite calls them "spines." Thus even in the ontogeny of the existing species the dorsal fin undergoes a marked transformation. Roule has noted that none of the rays in the adult is distally branched as the rays are in the soft dorsal of primitive percoinds and scombroids. Very probably this spiny condition of all the dorsal rays is quite secondary, as it is in the bennies and some other highly specialized teleosts.

Each bony ray of the adult dorsal fin of Luvarus rests upon a strong bony base (Figs. 5, 6) forming part of the great longitudinal truss. This base, hereafter called the "beam," is continued below into a thin median crest, from the middle of which springs the delicate stem. Each beam is prolonged anteriorly and posteriorly into extremely long zigzags which interlock with those of the preceding and following beam. In the dried skeleton
Fig. 6. Zigzag fin supports of *Lusarus* compared with pterygiophores of normal percoid (*Haemulon*).

these zigzags seem so tightly interlocked that the longitudinal truss is very stiff, but when softened in hot water the zigzags permit slight lateral movements and thus serve somewhat like the long overlapping zygapophyses in the caudal part of the column of the marlins.

After extended search we have been unable to find any exact precedent in other fishes for such zigzag articulations between adjacent pieces of the interneurals. Somewhat analogous are the anteroposteriorly-directed spicules on the expanded bases of the neural and haemal arches in the pyenodont *Coelodus* (Woodward, 1898, Fig. 72), or the zigzag sutures between adjacent pectoral actinosts of *Dactylagnus* (Starks, 1930, Fig. 35). Jaggedly serrated edges appear on the zygapophysial laminae of the dorsals and caudals of the scombroid *Acanthocybium solandri*. Close overlapping of the distal segments of the interneurals in *Haemulon* (Fig. 6) might supply a favorable initial stage for the extended...
overlapping and zigzag articulations of *Luvarus*.

The parts of the excessively specialized interneurals of *Luvarus* may be equated with those of the normal teleosts as follows:

**Typical Percoid**

<table>
<thead>
<tr>
<th><strong>Luvarus</strong></th>
<th><strong>Fin ray</strong></th>
<th><strong>Distal piece (3)</strong></th>
<th><strong>Middle piece (2)</strong></th>
<th><strong>Proximal piece (1)</strong></th>
</tr>
</thead>
</table>

By comparison with larval stages (Fig. 37) we may infer that as the lateralis group of myomeres increased both in length and height, the fin spines became more widely spaced and their bases (originally close) became elongated. The zigzag contacts must have been developed at the period between the late "*Hystricinella*" and the early "*Astrodermella*" stages, for in the latter the long dorsal spines are becoming well spaced at the bases. Still later the first nine fin spines shorten and disappear, but their elongate basal beams are left to form more than half the length of the dorsal truss.

**Anal Fin and Ventral Truss**

The ventral truss (Fig. 5) closely resembles the dorsal one in its general construction, even in the details of its zigzag interdigitations. At the posterior end both trusses are inserted between the strong, deeply forked neural and haemal spines of the anchor vertebra (No. 18). Anteriorly the dorsal truss ends in a large forked piece of which the stem or posterior branch impinges lightly against the forward and upward slope of the nuchal plane of the occiput, while the delicate anterior fork, continuing forward far above the top of the skull, tapers downward and is attached (at least in Waite's specimen) to the dorsal process of the forwardly displaced supraoccipital. The ventral truss bears the anal fin on fourteen of its seventeen segments. The first two anal "spines" are thick but short, the others feeble but slender at the tips; their bases, however, swell out laterally where the lateral muscles were inserted. In front of the two "spines" the pieces of the ventral arch become elongate with slender backwardly directed stems. The first interhaemal, enlarged into a long beam, continues forward beneath the posterior end of the pectoral girdle. The anterior end of this beam is attached to a pair of tendons that form the rim of the vent, to be attached to the distal end of the pelvis. This first interhaemal beam probably serves for the attachment of the retractor ischii (or protractor analis) muscles.

If we assume that in the remote ancestors of *Luvarus* the stem of the first interhaemal rod was inclined downward and backward to the column at an angle of 145°, as it is in the tuna, then this stem has swung forward through an arc of 121° to reach its measured position with reference to the column in *Luvarus*. The main part of the so-called first interhaemal of *Luvarus* represents not the stem but the widely extended intermediate or formerly spine-bearing segment, or "beam."

The difficulty in locating a truly ancestral stage for the dorsal and ventral truss is that in all the tunnies, which on other grounds may be nearly related, the posterior part of the dorsal fin is broken up into distinct finlets, whereas in *Luvarus* there is no trace of finlets, but the small unbranched spines are enclosed in a continuous web. If *Luvarus* is a highly specialized derivative of the tunny group, we must then suppose that the "organizers" which produce the elevated part of the dorsal fin became accelerated in development and remolded the finlet series so that the anterior ray of each finlet alone survived and their basal supports were lengthened; also that the numbers of units were reduced in the dorsal from perhaps twenty-eight (*Auxis maru*) to twenty-two, and in the anal from twenty to seventeen. However, while there is evidence that the finlets are a differentiated portion of the soft dorsal which appears early in larval stages, there is no evidence for reversal or dedifferentiation. On the other hand, the expanded pterygiophores (Fig. 6) of the dorsal and anal fins of certain carangoids (e.g., *Trachurus*) make an ideal structural starting point for those of *Luvarus*. 
Fig. 7. Peduncular caudal vertebrae of *Luvarus*. A¹, anterior view of vertebra 19; A², posterior view of vertebra 19; B, anterior view of vertebra 20; C, lateral views of vertebrae 19, 20, 21, 22; D, longitudinal section of vertebrae 21, 22. Ca. × 7/3.
VERTEBRAL NUMBERS

Luvarus is unique among scombroid fishes in the low number of its vertebrae (twenty-three to twenty-four) as compared with thirty to thirty-one in Scomber, thirty-nine in Thunnus, Katsuwonus and their allies, sixty-six to sixty-eight in Acanthocybium and thirty-two to one hundred and sixty in Trichiiformes. The low number in Luvarus is approached only in the swordfish (Xiphias), with twenty-six vertebrae, and in the sailfish-marlin family (Istiophoridae), with twenty-four to twenty-five vertebrae. Among the carangoids the primitive number is twenty-four. From this and other data it is plain that while the number of vertebrae may often be diagnostic for determination of family rank, it may in this case have much less value as an ordinal character.

An exceptionally low number of vertebrae (fourteen to sixteen) is found in the coffer fishes (Ostraciidae), in which the body is rigid and the caudal peduncle adapted for sculling. In Luvarus there is probably an appreciable lessening of lateral movements of the body as a result both of the marked height of the back and of the fastening of the dorsal and ventral contour stays to the eighteenth vertebra. Moreover the adult Luvarus has passed through the "Hystricinella" stage (Fig. 37), in which the exceptionally deep body seems from Roule's Fig. 2 to have but few vertebrae (see p. 273 below).

CAUDAL VERTEBRAE

We may begin with the caudal vertebrae because they clearly indicate the principal method of locomotion, which in turn is conditioned also by the rest of the column.

In the caudal peduncle and hypural fan (Fig. 7) there is even more marked consolidation and differentiation than in the tunnies and their allies. In the adult Luvarus this bony fan has doubtless arisen from the coalescence of: (a) seven hypural rods of the larval stage (Roule, 1924, p. 154. Fig. 18); (b) three or four larval epurals and (c) at least two larval pre-terminal centra. In the mackerels and tunnies there is a wide range of structure, starting in Scomber with the gradual transition from typical caudal to terminal vertebra, without crowding or coalescence of vertebrae, and culminating in Auxis, Thunnus, Katsuwonus and their allies in a sharp regional differentiation and tendency toward crowding and coalescence of three preterminal segments, including neural and haemal processes (cf. Kishinouye, 1923, Pls. xix-xxxiii). Whether or not Luvarus represents a highly aberrant tunny, the gradations in the caudal complex of the tunny group ("Plecostei" of Kishinouye) appear to throw light upon the morphology of this region in Luvarus.

The bony hypural fan of our Luvarus is essentially similar to the tunny type with the important difference that it bears a conspicuous notch just beneath the median protuberance (Fig. 7C, D). A sagittal section from the twenty-first through the fan reveals clear traces of the two epineurals, two fan-shaped hypurals, one greatly flattened hypural centrum. The neural tube runs up over the top of the twenty-second centrum and then expands into a downwardly directed cavern, which ends below in an exceptionally large foramen leading toward the caudal muscles. No visible trace of the foetal urostyle remains. On the outer side of the coalesced twenty-second vertebra a small exostosis or bony wart on either side of the centrum near the junction with the hypural fan probably represents the center of convergence of the tendons of the caudal fin muscles.

The twenty-first vertebra forms a firm block-like base for the hypural complex, its sides being nearly vertical. Its neural arch is very wide and concave anteriorly, where it is broadly overlapped by the neural arch of the twentieth vertebra. Posteriorly it tapers and slopes upward to form the anterior border of the coalesced hypural fan. The haemal arch of this vertebra, although attached and appressed to the lower border of the hypural fan, is not fused with the latter. It is somewhat
movably articulated with the posteroventral face of its own vertebra (21) by a large ball-and-socket articulation, the socket being on its dorsal face, the ball on the ventral surface of the centrum. The hollow anterior intracentral cone of this vertebra is very large and extends backward almost to the posterior end, its apex nearly meeting that of the shallow cone of the posterior end of the vertebra. These hollow notochordal cones are lined with smooth white membrane showing concentric growth rings—all essentially as in the tunnies.

In Waite's specimen (his Pl. xliv) there is clear evidence that the twenty-first vertebra was distinct from the hypural complex and that a small vertebra, the twenty-second, lay between the hypural and the twenty-first, whereas in ours the twenty-first is so firmly coalesced with the elements behind it that the contact is no longer visible externally. In the twentieth vertebra (Fig. 7C, B) of Lucanus the large centrum forms a firm block flattened on both sides as well as on the top and bottom and diminishing gently in transverse diameter posteriorly. Its very large neural and haemal processes are prolonged almost directly backward and like splints over and beneath the terminal complex (vertebra 21 plus). They prevent vertical dislocation of the tail piece but permit slight lateral swing. Thus they serve like a rudder-stock to support the tail and resist its rudder-like and sweeping thrusts. A slight horizontal swelling on either side near the anterior end of the centrum and lying beneath the fleshy peduncular keels may represent the last trace of the scoliod bony flanges. The large neural tunnel just behind the anterior rim of this vertebra dips sharply downward, expanding into a cavern and giving off lateral tunnels for the spinal nerves. These issue on the opposite sides of the centrum near its middle just above the vestigial horizontal keel. The haemal tunnel is also large but passes more horizontally from this vertebra to the next. This twentieth vertebra is amphicoelous, but in contrast with the twenty-first the tip of its posterior cone is near the front end of the vertebra, the anterior cone (Fig. 7B) being shallow.

The articular surfaces between these peduncular vertebrae form conspicuous circular rings of yellowish chondroid tissue, whereas in a large tunny these rings are well ossified.

The centrum of the nineteenth vertebra (Figs. 5, 7A), hereafter called the "pivotal vertebra," is much shorter (26.5 mm.) than that of the twentieth (38.7 mm.), and the entire construction seems more compact. Its posterior face for articulation with the twentieth is widely oval, the outer zone very broad and convex, the central depressed cone very small and shallow, the anterior hollow cone very deep. This vertebra was the main pivot for the movement of the tail complex upon the relatively stiff column in front of it. The dorsal and haemal arches of this pivotal vertebra (No. 19) contrast widely with those of the peduncular vertebra (No. 20, Fig. 7B), being small and erect. The neural tunnel of No. 19 dips sharply downward much as in the tunnies, and the spinal nerve and vessels issued from conspicuous foramina above and below the lateral ridge. The lateral bony crests are represented by stout tuberosities which may have served both for the insertion of one of the larger tendons from the lateral muscles and for the anterior end of the fleshy horizontal keels.

Among the tunnies and their allies, Auxis maru as figured by Kishinouye (Pl. xxxiii, fig. 6) shows an incipient differentiation of an "anchor" vertebra, where the dorsal and anal fins converged onto the column, and a "pivot" vertebra, in front of the dorsoventrally depressed peduncular vertebrae. Even the attachment to the vertebral column of the bony rods supporting the dorsal and anal fin is almost attained or at least suggested in Kishinouye's figure of the skeleton of a Thunnus orientalis (Pl. xxiv, fig. 44).

In the eighteenth, or "anchor," vertebra (Fig. 7), the centrum is intermediate in length between the short pivotal centrum and the long "anterior caudal" centra. Its exceptionally strong but short neural and haemal arches point forward rather than backward, the reverse of the condi-
tions either in the tunnies or in ordinary fishes. To these forwardly directed processes are attached the strong "contour bones," which evidently act as longitudinal trusses for the entire body. The anterior cone of this centrum is evidently deeper than the shallow posterior one, much as in the pivotal vertebra. The sides of the anchor vertebra are strengthened by two stout longitudinal ridges respectively below and above the insertions of the dorsal and ventral trusses. Just in front of the posterior articular zone of the centrum is a short but strong lateral tuberosity, probably for the insertion of a longitudinal tendon.

The five vertebrae in front of the eighteenth (Fig. 5), namely, Nos. 17–13 inclusive, all have relatively elongate centra which are deeply constricted laterally in the middle part. Their large anterior and posterior hollow cones are about equally developed and leave only their circular rims for articulation with each other. The deep neural groove runs between longitudinal bony laminae, each of which is perforated by a foramen for a spinal nerve. Above this foramen the lamina gives off a long slender neural spine which curves gently backward. The anterior and posterior zygapophysial processes are incipient in vertebrae 17, 16, but increase slowly in size up to vertebra 8. Running along the middle ventral surface of centra 17–13 inclusive there is a longitudinal gutter for the main dorsal aorta and cardinal vein; the front half of the gutter is bordered by laminae; these are suddenly prolonged downward into nearly vertical delicate haemal arches and processes. On Nos. 12 and 11 the haemal processes curve forward, bounding the body cavity posteriorly. In the eleventh vertebra the paired haemal processes become short and are spread widely apart so that they project below the outer ventral side of the centrum. In the tenth vertebra the "haemal" process is more like a short parapophysis, and in the ninth it does become a forwardly directed parapophysis arising immediately below and in front of the conspicuous central pit for the head of the rib.

"Abdominal" Vertebrae and Ribs

The ninth vertebra (Fig. 5), bearing a true rib, may be regarded as the last of the "abdominals," the tenth as the first "caudal." The seven ribs (Fig. 5), although very light and fragile, are unusually large, somewhat sabre-like, flattened proximally, pointed distally. No ribs are indicated for the first two vertebrae. On the lateral face of the third centrum there is a prominent pit on each side just above the middle, into which the flattened head of the rib is closely attached by bony fibers. This rib is directed downward and backward and is bowed sharply outward; in a dorsolateral view it is slightly convex in its upper half and gently concave in its lower half, thus being faintly sigmoid. Measured along the outer curve this rib is about 320 mm. long. The anterolateral border is strengthened by a rounded rim. Posterolateral to this rim is a flat blade in the upper half of the rib. On the medial surface a prominent strengthening ridge gives a roundly triangular cross section. The lower part of the rib tends to be oval in section; the lower extremity is bluntly pointed. The following rib, on the fourth vertebra, is slightly longer, but the rib of the ninth vertebra is much shorter (length about 220 mm.). The triangular cross section flattens out on the ribs of the seventh and eighth vertebrae and is absent on that of the ninth, this rib being flattened lateromedially.

The ribs of Luvarus as compared with those of scombroids are much larger, more sabre-like and bowed more widely outward; they also differ in relative lengths, those of centra 3, 4, 5 and 6 being very large, whereas even in Auxis the corresponding ribs are small and delicate. These features seem to be correlated in part with the great development of the dorsal musculature in Luvarus. No intermuscular bones (epipleurals) were observed by our preparators.

Except for the ribs, the more posterior abdominals are but little different from the "caudals."

As noted above, in the rib bearing vertebrae the centra are constricted cylinders, deeply amphicoelus, with small anterior
and posterior zygapophyses; on the third vertebra, however, there is a large anterior zygapophysis. The second, or axis, vertebra (Fig. 8) has a huge anterior zygapophysis which is confluent posteriorly with a long, curved, neural spine; this spine is notably less slender than those of the vertebrae behind it. The great anterior of the tunnies and their allies, which have numerous short centra with large lateral pits lying above and below strong horizontal ridges.

The centrum of the first vertebra (Fig. 8) is closely appressed and bound to the occipital base. Viewed from above, it forms a strong wedge, the sides of which

zygapophysial crest of the second vertebra doubtless supports the thick muscular part of the dorsal hump, as does also the roof of the skull and the forwardly displaced supraoccipital crest.

All the centra that lie between the eighteenth, or "anchor," and the first, or atlanteal, are exceedingly unlike those articulate with the oblique faces of the exoccipitals; these lateral facets are widely flattened, but their surfaces bear the traces of interdigitating sutures. Ventrally the narrow median ventral segment abuts against the downwardly produced basioccipital. The large posterior hollow cone extends nearly to the anterior limit of the

Fig. 8. Interlocking relations between occiput and vertebral column. Ca. x 1/4.
vertebra. Immediately in front of and beneath its tip lies a very small chamber which may represent a vestige of the anterior hollow cone; there is a similar small pocket in the basioccipital, and the two pits may together mark the position of the embryonic notochord. Thus even in this highly specialized fish the tripartite character of the occipito-atlanto-axial joint, which is a general acanthopterygian character, may still be traced.

The neural canal of the first vertebra (Fig. 8) is exceedingly small, its lumen being about 2.4 mm. in diameter. It dips downward and forward to the general horizontal axis at an angle of about 20°. Its straight, strongly compact floor forms the roof of the posterior hollow cone of the first centrum. It is protected latero-anteriorly by a pair of small, much depressed pedicles (Fig. 32) with expanded top and bottom and rounded constricted middle. These little pillars appear to represent modified anterior zygapophyses and they do indeed articulate anteriorly with the exoccipitals. Their dorsal surfaces make contact with and partly support the large separate neural spine of this segment.

The posterior zygapophyses of this vertebra form large, thick and strong posteriorly divergent V-shaped processes (Fig. 22, post. zyg.a.), which articulate above partly with the neural arch of the first vertebra but mainly (Fig. 8) with the great pole-ax portion of the combined anterior zygapophysis plus neural spine of the second, or "axis," vertebra. The centrum of the first vertebra of *Luvarus* closely resembles that of the tunnies, but the neural arch is much more specialized in being lifted dorsad off the centrum and in failing to enclose the spinal cord both laterally and ventrally; whereas in typical percoids, carangoids and scromboids the limbs of the neural arch of the first vertebra do enclose the spinal cord and often meet below it, projecting into a pair of pits or a median pit on the dorsal surface of the first centrum.

**Summary of Vertebral Regions**

According to criteria adopted by Bou-enger, vertebrae 1 to 10 inclusive would be classed as "abdominals," 11 to 22 or 23 as "caudals." If we consider its functional aspects the vertebral column of *Luvarus* may be subdivided into the following regions:

1. — "Cervico-thoracic" including:
   
   (a) The "atlas," or centrum 1, closely appressed to occiput much as in the tunnies; neural canal extremely constricted and inclined downward and forward; neural spine long, distinct from centrum;
   
   (b) The "axis," or second vertebra, with hatchet-like anterior blade of the neural spine; centrum a large constricted cylinder without paraphyses or ribs;
   
   (c) Vertebr a 3, with large anterior zygapophysis articulating with "axis"; paraphophysis absent, rib present;
   
   (d) Vertebræ 4 to 9 inclusive with large ribs, probably homologous with the ribs of percomorphs and tunnies.

2. — "Abdominal-caudal": vertebrae 10 to 18 inclusive. Of these No. 10 is transitional; in No. 11 the haemal arches are well developed. In all these vertebrae the haemal channel for the cardinal arches is well developed. In all these vertebrae the haemal channel for the cardinal arches is well developed. In all these vertebrae the haemal channel for the cardinal arches is well developed. In all these vertebrae the haemal channel for the cardinal arches is well developed. In all these vertebrae the haemal channel for the cardinal arches is well developed.

3. — "Peduncular-hypural" section: beginning with

   (a) the "pivotal" vertebra (No. 19) and including

   (b) the two "rudder-stock" vertebrae (Nos. 20, 21), which form a slightly movable base for

   (c) the "hypural fan," which in turn may represent two or possibly three epural, haemal and hypural bars.

With regard to the derivation of *Luvarus*, the conditions both in the peduncular-caudal and in the atlas-axis sections may easily have been derived from those seen in the tunnies and their allies, but the
Fig. 9. Pelvis and pelvic fins of *Luvarus*. A, pelvis, dorsal view; B, left side; C, ventral; D, oblique ventral; E, coalesced pelvic fins (operculum ani), outer side; F, inner side, × 1.

Intervening vertebrae (Nos. 3–18 inclusive) together with their ribs and haemal arches, are so widely different from the conditions in the tunnies, or indeed in any known scombroids, that if these facts alone were decisive only the most remote relationship of *Luvarus* to the scombroid group might be admitted.

However, in view of the many striking resemblances in the endocranium and certain other regions between *Luvarus* and the tunnies, it may be well to keep before us the hypothesis that after the dorsal and anal contour bones became firmly fastened to the anchor vertebra, a revolutionary change in locomotor habits and structures was made possible, involving a great reduction in number of abdominal-caudal vertebrae and considerable readjustment of muscular segments.
PAIRED FINS AND GIRDLES

PELVIC FIN AND PELVIS

The pelvic fins, as stated above, are reduced to a small lanceolate operculum ani (Fig. 9E, F). The morphology of the pelvis has been extremely difficult to decipher, but we trust that the solution offered in Figs. 9 and 10 may be sometime confirmed by dissection of the pelvic protractor and retractor ischii muscles, which would assist in movements of the pectoral and pelvic arches and possibly of the ventral part of the body cavity, would be relatively huge (Fig. 9D). The pelvic fins in the early "Hystricinella" stage (Fig. 37) are very large and bear huge anterior spines, and since the marked

![Fig. 10. Suggested derivation of Luvarus pelvis, ventral and rear views. A, normal percoid (Roccus); B, C, hypothetical stages leading to Luvarus (Fig. 9C), showing the supposed divergence of the medial ischial processes and the convergence of the acetabular facets forming a tunnel (Fig. 9D) for the protractor ischii muscle.]

muscles which we have assumed to be present after extensive comparisons with other types of fish pelves and with the aid of the works of Grenholm (1923) and Shelden (1937). In brief it seems highly probable that with the great reduction of the pelvic fins, their muscles, including the adductors, protractors and arrectors, would all be correspondingly small, while the reduction in size of the pelvic fins begins in the late "Hystricinella" stage and is completed in the later larvae ("Luvarella"), we may infer that the highly peculiar specialization of the pelvis itself arose at the same time as did the transformation of the bases of the dorsal and anal fins into the dorsal and ventral trusses.

In brief the outstanding specializations
of the pelvis in the adult *Luvarus* are: (1) the strengthening of the opposite pelvic bones and enlargement of the symphysis pubis; (2) lateral diversion and outgrowth from the medial ischial processes of two very large ischial tuberosities for the attachment of the ligaments and muscles bounding the vent; (3) downward and inward displacement of the opposite condylar articulation for the pelvic fins; (4) development of a median groove or tunnel above the condylar junction, presumably for the protractor ischi on its way to the laterally displaced ischial tuberosities; (5) great reduction in size of the fossae for the arrector and protractor muscles of the pelvic fins.

PECTORAL FIN AND GIRDLE

The pectoral fin and its skeletal frame (Figs. 5, 11) are perhaps the least specialized of any part of the skeleton. The anterior ray is short with unbranched tip. The second is more than twice as long, also with pointed tip; then follow sixteen rays all branching and dichotomizing distally; the longest rays are the fourth, fifth and sixth. This pectoral fin is essentially like those of the tunnies and their allies. The first pectoral ray (Fig. 11A) ends proximally in a transversely spreading bony trochlea, with concave depressed middle and elevated lateral and median knuckles.

On the medial side of both pectorals the knuckle of the first ray is separated from the shaft of the ray by an unossified layer. Possibly this knuckle may be secondarily separating from its shaft after the manner of an epiphysis and thus producing a pseudopterygiophore in front of the normal first pterygiophore. The trochlea of the first pectoral ray articulates with the "pectoral condyle" on the posterior border of the scapula. The trochlear surface of
this condyle is placed vertically and permits both vertical and lateral movements of the pectoral fin. The remaining fin rays are collectively supported by four actinosts which increase in anteroposterior diameter from the small rounded first actinost to the much larger fourth, which is constricted in the middle and expanded both proximally and distally. The third actinost articulates with the scapulocoracoid border opposite the horizontal suture between the scapula and the coracoid.

In these and in other features the pectoral girdle and fins of *Luvarus* conform to the typical percoid (including scombroid) condition as described by Starks (1930, p. 199). Among the distinctive characters, however, may be noted the marked posterior prolongation of the ventroposterior process of the coracoid below and behind the pectoral fin base; the transverse width and concavity of the opercular border of the cleithrum; the truncation of the dorso-posterior blade of the cleithrum, this blade in typical scombroids being very pronounced; the loss of the supraleithrum and of the pterotic branch of the supratemporal; the firm fastening of the exoccipital branch of the posttemporal, which is coalesced with a process from the exoccipital.

**Opercular Region**

In *Luvarus* the whole opercular region (Figs. 5, 12) appears to be produced downward and backward, and the opercular slit, although in its normal morphologic relations to the opercular apparatus, gives the impression of being “restricted” (Regan).

All the operculars (opercular, pre-, sub- and inter-) are much like those of the scombroids in being broad, rounded, delicate, thin-edged and without spikes. In the crescentic preoperculum (Fig. 12) the lower limb is produced far forward, following the quadrato-articular joint and fastened by ligament to the articular. The anterosuperior border bears a prominent articular face, passing down into a notch which increases in width from above downward and ends near the center of growth in a large conspicuous depression. The latter receives dorso-posteriorly the large cartilaginous epiphysis on the lower end of the posterior branch of the stem of the hyomandibular and anteroventrally it supports the face of the upper end of the symplectic. Just below this depression on the preoperculum is the transversely oval facet for the epihyal (Fig. 13) on the upper border of the interoperculum.

The crescentic lower limb of the preopercular (Fig. 12) runs closely parallel to, and broadly overlaps, the somewhat similar upper lateral surface and anterior horn of the interoperculum, while the upper limb of the preopercular crescent overlaps the operculum. Thus it happens that in the lateral view the preoperculum exposes the whole of its crescentic surface, since it overlaps the hyomandibular, operculum, suboperculum and interoperculum, while in the medial view (Fig. 13), the exposed portion of the preoperculum is limited to a relatively small triangle. All this again is astonishingly similar to the conditions in the tunnies, especially *Auxis*. The only contact of the preoperculum around its triangular mesial exposure, which is found in *Auxis* but not in *Luvarus*, is that with the metapterygoid, due to the forward displacement of the latter.

The operculum (Figs. 12, 13), instead of flaring upward and inward above the level of the hyomandibular, has a straight-edged strong upper border, which is directed obliquely downward and backward. By comparison with the opercula of various scombroids as figured by Kishinouye (1923, p. 324), it is evident that the dorso-ventral spread of the operculum of *Luvarus* has become markedly restricted. The opercular angles (cf. Kishinouye, *loc. cit.*) are as follows:
On the medial side (Fig. 13) of the opercular in line with the dorsal border there is a long process which points up-
ward, forward and inward toward the posteroventral face of the pterotic. Hence this process, together perhaps with the rough triangular area that is lateral to it, may serve for the insertion of the levator operculi muscle, while a similar but shorter process on the outer face of the opercular (Fig. 12) just laterad to the articulation in the tunny. Even the nutrient grooves on the inner and outer surfaces are similar to those in the scombroids.

The very large right suboperculum in lateral view (Fig. 13) is like an L with a rounded foot and a narrow stem. The rounded heel is directed downward and the stem and foot diverge anteriorly and
posteriorly, respectively. The posterior margin of the stem fits closely onto the anteroventral border of the opercular. The almost crescentic upper part of the “foot” is broadly overlapped laterally by the distoventral blade of the opercular. This thin translucent “foot” of the sub-operculum abounds in delicate bony fibers, which are crowded together in the growth center along the stem and then stream outward over the thin blade or foot. In type, seen by us in Acanthocybium and Auxis, namely, it is a thin, scale-like bone radiating from a growth center around the facet for the epihyal.

The sabre-like branchiostegals (Fig. 16) are four in number, all attached to the lower border of the cerato-epihyal behind the “angle” of the ceratohyoidal. The fourth is very large and extends all the way along the lower medial border of the inter-, sub- and opercular bones. The

these minute structural features the sub-operculum of Luvarus is essentially identical with those of scombroids, while in general shape this bone may readily have been derived from such a one as that of Auxis maru (Kishinouye, 1923, p. 324, Fig. D 8) merely by further reduction of the blade and emphasis of the concavity of the dorsal border.

The large interoperculum (Figs. 12, 13) is convincingly similar to the scombroid third is about a third shorter than the fourth and extends only to below the heel of the subopercular; the first is less than one-third the length of the fourth. These four correspond to the upper four of percoids and scombroids.

The anterior branchiostegals in percoids are usually three and attached to the ceratohyal in front of the angle. These may possibly be represented in Luvarus by a now disconnected fragment, containing
one long slender branchiostegal-like bone, with a recurved proximal end, and behind it a much larger curved bone which we at first mistook for an expanded thin maxilla. If these are really branchio-

tegals, they must have partly covered the floor of the throat, simulating paired gulars, but verification in a preserved Luvarus is needed.

Articular facets of the right quadrate bones

Articular facets of the left articular bones

Roccus Thunnus Luvarus

Fig. 14. Functional relations at the quadrate-articular joint.

JAWS AND SENSORSORIUM

Luvarus has a remarkably small, edentulous, thick-lipped mouth, much smaller than in any other scombroid. This central fact conditions many other marked peculiarities of the bones of the jaws and suspensorium. In contrast to the tunnies, which have more or less elongated, toothed, predaceous jaws, the "maxillary" of Luvarus (Fig. 12) is short, vertically deep and, including in this term both pre-

maxilla and maxilla, extremely thin, although embedded in a thick lip. The main parts of the premaxillae have been destroyed in our skeleton except the median proximal ends, which are small but well ossified and were continued laterally, as if to form rod-like margins. The leaf-like maxillae are paper-thin and transparent except for delicate streaks of bone, radiating from the growth center. This blade-
like bone is certainly a maxilla because it is fastened to a projecting finger-like process of the palatine in the manner of normal maxillae. As preserved it ends abruptly posteriorly in an irregular faintly ossified dorsal strip and a jagged vertical edge. Thus the maxilla of our fish contrasts widely with the outline of the maxilla of the large Luvarus figured by Waite (1902, Pl. XLVI), and after considering many possible solutions, we are unable to account for this apparent discrepancy. Carangoids also have small mouths, but the premaxillae and the maxillae are far nearer to the typical percoid type and show no special approach to Luvarus.

Only the posterior part of the dentary (Fig. 12) is preserved, but in previously described specimens it is figured as very short and deep. The articular with its steeply ascending surangular process is likewise very high in proportion to its length. Although the bone is thin and delicate, its large webbed ascending ramus is provided with trabeculae which converge toward the articular surface and were evidently sufficiently strong for the fairly large adductor mandibulae muscles.

Posteriorly the articular bone has no retroarticular process (in contrast with scombroids), but the angular bone, which is somewhat produced posteriorly, does bear a short and blunt retroarticular process and forms the medioventral part of the articular surface for the quadrate trochlea (Fig. 14). The angular is also extended anteriorly and fits into the posterior part of a groove on the ventral margin of the articular (Fig. 12). In most other fishes, even the scombroids, it is far less extended anteroposteriorly. In the anterior portion of this same groove lies the ventral ramus of the dentary. Immediately above this groove the Meckelian cartilage is present as a long strap-like tract on the medial side, which may have been inserted anteriorly into a pit on the posterior margin of the dentary. A sesamoid articular (Starks, 1916) probably was present but is not preserved.

The articular surface of the articular bone (Fig. 14) is concave transversely and faces posteriorly, rolling on the convex, forwardly facing condyle of the quadrate bone. On the medial side of the articular bone a similar but smaller and transversely compressed process receives the medial convex trochlea from the quadrate. This medial small facet of the articular is separated from the larger lateral facet by a deep notch, which when the mandible is closed receives the ventroanterior edge of the quadrate-ectopterygoid border and helps to prevent lateral dislocation. This entire arrangement of the trochlear surfaces permits the mandible to be depressed about 45° and facilitates the upward slant of the closed mouth.

The primary upper jaw (palato-pterigo-quadrat complex) has lost none of its elements. The palatine (Figs. 12, 25) has an exceptionally large and elongate anterior ramus or hook which curves over the vomer, to which it is fastened below, and is continued forward into a cylindrical process; this in turn overlaps the leaf-like maxilla. The posterosuperior mallet-like process of primitive percoids (sessile or absent in scombroids) is here represented by an elongate oval tuberosity. The anterior hook is appressed to and articulated with the ethmoid medially and with the vomer ventrally. The posterior descending flange bears a narrow dentigerous oval pad (Fig. 15) beset with minute denticles and facing medially. As compared with that of the tunny group the palatine is basically similar but is distinguished by its greatly elongated maxillary hook (correlated with the elongation of the ethmoid) and by the more ventral position of the dentigerous pad.

Posteriorly the palatine is connected with the ento- and ectopterygoids. The splint-like ectopterygoid (Fig. 15, ptr) has a nearly straight oblique anterior edge, rather than the usual gentle concavity of this border. The entopterygoid is a fairly large ovoid thin shell radiating from a conspicuous growth center. In transverse section it is rather sharply curved downward toward the lateral margin, while the dorsal contour is concave medially and sharply convex laterally. Its palatal surface bears a long dentigerous tract, beginning at the front end. It extends
Fig. 15. Right hyomandibular and associated elements, lateral views. For abbreviations, see p. 282.
forward above the quadrate to its contact with the palatine, but, perhaps on account of the forward displacement of the quadrate, it has lost its contact with the ectopterygoid.

The metapterygoid (Figs. 13, 15) has been dragged forward with the forward displacement of the entire suspensorium. Also its dorsal fork, which in percoids (Fig. 15, Roccus) forms a V with divergent medial and lateral laminae, has here been so firmly united with the enlarged and forwardly slung hyomandibular that the space between the forks of the V has been obliterated. The metapterygoid is easily derived from that of the tunnies in the manner just suggested. Owing in part to the sharp forward bend and prolongation of the lower part or stem of the hyomandibular, the quadrate bone lies no longer immediately beneath, but far in front of, the hyomandibular.

The quadrate bone (Figs. 12, 15) is quite large, and its fan-like surface is spread over an arc of about 110° as compared with 60° in a large tunny and about the same angle in a large serranid (Promicrops). Probably the wider spread of the Luvarus quadrate is correlated with the lesser depth of the quadrate-articular joint below the horizontal and with the marked forward displacement of that joint (see Gregory, 1933, pp. 412–422).

The trochea of the quadrate in anteroventral view (Fig. 14) is relatively wide in proportion to its height, as compared with the tunny, and has a conspicuous carina on the mesial side. Moreover, there is a prominent pit, bordered below by a horizontal semicircular swelling on the inner border of the angular bone, which articulates with the inner trochea of the quadrate. The apparent homologue of this pit is well developed in the tunny, but it lies far below the medial articular process of the quadrate and probably serves there for the insertion of a ligament. In Acanthocybium, which has long jaws, the entire suspensorium including the quadrate is more nearly vertical, and the trochea of the quadrate faces more downward, whereas in Luvarus the lower limb of the suspensorium is prolonged far forward, and the trochea of the quadrate faces more forward and is more sharply convex anteroposteriorly.

The hyomandibular (Fig. 15) differs sharply from that of typical fishes in that the sphenotic-articular facet is sessile, enlarged and confluent with the pterotic facet, whereas in scombroids (Kishinouye, 1923, p. 321) the pterotic facet is relatively small and set on a narrow peduncle. This character in Luvarus is associated with the obliquity of the sphenotic-pterotic facets on the skull and with the backward and downward displacement of the opercular-preopercular flap (Fig. 5). The apparently sessile character of the sphenotic facet of the hyomandibular (Fig. 15) may have resulted in part from the backward growth of the entire sphenotic bone (Fig. 34), the pterotic and sphenotic facets of the skull becoming nearly confluent with each other. The two facets together were evidently provided with a thick cartilaginous epiphysis.

While the diaphysis or stem of the hyomandibular is directed downward and backward (Fig. 15), its anteroventral branch curves downward and forward and is broadly continuous onto the metapterygoid, as above noted. The posteroverentral branch is of exceptionally large size and ends in a large cartilaginous epiphysis into which is inserted first, the symplectic and second, the interhyal, carrying a good part of the hyobranchial complex.

In the tunnies and their allies (Kishinouye, 1923, p. 321) on the anterior margin of the hyomandibular, some distance below the sphenotic peduncle, there is a prominent downwardly directed anteromedial process (Fig. 15) for articulation with the top of the medial fork of the metapterygoid V mentioned above. In Luvarus, with the total obliteration of the space between the limbs of the fork, the process above noted has probably extended downward and lost its distinction from the hyomandibular stem—another progressive specialization beyond the scombroids.

The lateral flange of the hyomandibular (Fig. 15, l.f.) to which the preoperculum is
attached posteriorly is exceptionally prominent and bears a thick rounded border, which contrasts with the sharp border in percoids and scombroids. This curving flange, together with the large metapterygoid and the preopercular, forms part of a great anteriorly concave tract, from which the complex adductor muscles converged toward the mandible. Toward the upper end of the hyomandibular, just in front of the root of the lateral flange, or preopercular crest of the hyomandibular, was inserted the protractor hyomandibularis. Tunnels for branches of the facial nerve may be indicated by large pits and smaller foramina on the medial surface of the shaft of the hyomandibular (Fig. 13), but as we were unable to pass a delicate wire sound through any of them, their identification is doubtful.

The symplectic (Figs. 12, 13, 15) is a fairly elongate bar arising from the cartilaginous epiphysis of the hyomandibular and extending downward and forward in the usual groove on the posterior part of the quadrate, and just in front of the preoperculum. It has an unusually elongate and quite firm sutural contact with the metapterygoid. All these relations may be easily derived from the conditions in the scombroids.

The opercular peduncle of the hyomandibular (Fig. 15) is excessively large and directed downward and backward, whereas in the tunnies it faces more laterally.

The main lower segments (cerato- and epiphyal) of the hyoid arch (Fig. 16) are remarkably deep in proportion to their length, the basihyals are large, the glossohyal short. These characters are all readily derivable from the conditions in the scombroids, especially in *Auxis*, by antero-posterior shortening and deepening of the
bones, correlated in part with the forward extension of the lower bar of the hyomandibular.

There are five branchial arches, the first four with long coarse gills ranging up to 75 mm. in length, the fifth short and without a gill. The gill rakers are short, widely and irregularly spaced, some bearing minute irregular bristles; twelve or more erect, thumb-like gill rakers on upper border of first gill arch, not paired with those on inner border; on the second, third, fourth and fifth arches the gill rakers shorten to rounded fleshy palps or protuberances, forming with those on the facing arch and with the accessory row beneath the main row, a coarse strainer. The superior pharyngeals bear loosely inserted bristles with delicate tips curvied mesially, similar bristles in long triangular patches on hypobranchials and inferior pharyngeals, the latter not united along the midplane. A bony sliver in the mid-plane considerably beneath the basibranchials may represent the urohyal. An essentially similar piece is present in a small Auxis species. In the latter the gills are relatively shorter and the gill rakers relatively much longer, forming a sort of baleen-like sieve; the suprapharyngeal bristles are relatively finer and more closely set.

Fig. 17. Syncranium of typical percoid. After Gregory, 1933.

**Neurocranium**

In a central percoid type (Fig. 17) the neurocranium in sagittal section forms a more or less elongate wedge with shallow anterior and deeper posterior parts. The anterior part comprises the ethmo-vomer block and the ethmoid roof. Behind this come the elongate orbits, lying beneath the frontals which form the interorbital bridge. Behind the orbits lies the cranial vault or braincase, comprising the sphenoid,
Fig. 18. Forward migration of supraoccipital and epiotic. Longitudinal section, medial views. *Scomber*, after Allis, 1903.
otic and occipital divisions. On top of the cranial vault is a long median crest on the supraoccipital bone, the latter being in contact anteriorly with the frontals. Behind and above the orbits comes the sphenotic-pterotic crest, which projects slightly above the hyomandibular and opercular complex.

On either side of the basicranial axis the large semicircular canals are roofed and exoccipitals to the base. In cross section another series of trusses distributes the lateral thrusts downward to the base and upward to the fronto-occipital roof (see p. 255). The braincase articulates posteriorly with the vertebral column by means of a tripartite condyle, the basioccipital bearing a circular median facet, the exoccipitals, two laterally extending lateral facets.

By the epiotics; these are pyramidal bones, to the tips of which are attached the dorsal fork of the posttemporal.

From an engineering viewpoint the neurocranium of a typical fish skull in longitudinal section may be regarded as consisting of a simple truss, the base being formed by the vomer-parasphenoid-basioccipital series; the anterior limb of the truss passes through the ethmoid and frontal, the posterior limb through supra-

**Fig. 19.** Skull of *Thunnus*, dorsal view. After Gregory, 1933.

All these and other parts and fundamental traits of the percoid skull may be recognized in *Luvarus*, but they are more or less distorted or otherwise specialized. The same is true of the individual skull bones of *Luvarus*; although most of them may be readily identified, they are all likewise disguised by specializations, even to such a degree that the identity of certain bony elements (nasal, rostral) is still in some doubt.
In the following analysis of the characters of the *Luarus* skull we shall attempt to interpret morphologic details in reference to both their functional and phylogenetic significance.

**Anteroposterior Arches**

**Supraoccipital-epiotic Ridge.**—Among the numerous peculiar features of somewhat doubtful homology which may represent enlarged and fused nasals.

2.—Posterolaterally the supraoccipital crest is supported by the enlarged, sharply upturned flanges of the frontals (Fig. 25), so that in cross section in front of the orbit the frontals and supraoccipital together form a high Gothic arch (Fig. 21).

3.—Posteriorly the supposed supra-

---

*Thunnus*

Fig. 20. Skull of *Thunnus*, ventral view. After Gregory, 1933.

the *Luarus* skull which seem to be correlated with the forward extension and great height and strength of the musculature of the dorsal hump (Figs. 1, 5) are the following:

1.—The supraoccipital crest (Fig. 18) has moved far forward and is supported anteroventrally by a median crest of occipital bone is wedged between the enlarged, forwardly displaced epiotics (Fig. 22).

4.—Seen in median sagittal section (Figs. 23, 24) the supraoccipital extends in a great longitudinal arch of trabecular bone; beneath this arch in the dried skull is a spacious but now empty vault, which may have been partly filled with cartilage or
other connective tissue. The extreme forward extension of the supraoccipital and its crest is approached in Brama, Poronotus, Coryphaena and other carangoids (sensu lato) but is not found in any scombroid. Nevertheless the conditions in the tunnies (Figs. 19, 21, 30), where the supraoccipital base is already well extended toward the front of the cranial vault, seem favorable as a point of departure for the Luvarus specialization.

5.—The epiotics, greatly enlarged and extending forward and upward postero-laterally to the supraoccipital crest (Fig. 22), form most of the forwardly sloping and nearly flat skull roof; anteriorly they

Fig. 21. Front views of skulls. Thunnus, after Gregory, 1933. Dark areas = unossified parts.
Fig. 22. Dorsal view of skull of _Luvarus_, with attached first vertebra. _Cq._ x 11/20.

_Luvarus_

*post. zyga.*
Fig. 23. Longitudinal section of skull of *Luvarus*, showing longitudinal arches.

**Luvarus imperialis**

Fig. 24. Longitudinal section of skull.
spread out laterally and give attachment to the long dorsal fork of the pectoral girdle (see “posttemporal” above, p. 242). Beneath each epiotic in the lateral aspect (Figs. 25, 26) is a huge, vertically expanded bony area, apparently for the trapezius muscle. As seen from above (Fig. 22) the conjoined epiotics become narrower transversely behind the posttemporal attachment. A mesial longitudinal section of the skull (Figs. 23, 24) shows the epiotic forming the longer posterior limb of the huge truss which supports the great dorsal hump. The entire vault formed by the supraoccipital and epiotics is continued aspects. The frontosphenotic roof (Fig. 25) has had its lateral margin markedly depressed, while the ascending lamina of the frontal has extended sharply upward.

7.—The originally V-shaped “trapezius” area (Fig. 26) between the “epiotic-parietal” and “pterotic-frontal” crests has been greatly expanded, the apex of the V being enlarged into an enormous horizontally placed U.

8.—The parietal has either been lost or united with the suprafrontal wing of the epiotic.

9.—The pterotic has been extended laterally (Fig. 22) so that it far overhangs below, anteriorly by the ascending wing of the frontals, laterally by the sphenotics, medially by the enlarged “alisphenoids,” posteriorly and laterally by the pterotics, posteromedially by the conjoined prootics and opisthotics.

6.—The extreme forward growth of the dorsal hump has also influenced the front part and lateral roof of the braincase. The dermethmoid and its olfactory chamber have been markedly elongated, producing a longitudinal fossa in front of the orbits (Fig. 25). The prefrontal (parethmoid) has also been elongated in both lateral (Fig. 25) and mesial (Fig. 28) the articular facet for the hyomandibular (Fig. 33) and posteriorly (Fig. 25) behind the posterior face of the first vertebra.

10.—The sphenotic (Figs. 25, 33) has been shifted posterolaterally, withdrawing from the inner wall of the braincase (Figs. 24, 29, 30) and crowding the prootic posteriorly. Many of these specializations are more or less connected with the anteroposterior stiffening of the skull against thrusts generated by the forward drive of the entire locomotor musculature and by the pressure of the water reacting against such thrusts. The dorsal longitudinal

---

Fig. 25. Neurocranial, right side, x 1/2.
arch shown in Fig. 23 forms the upper limb of a great truss, the base of which lies in the series of bones which may now be described.

Ehthmo-nasal Complex.—Seen from above the dermethmoid and prefrontal (parethmoid) together form a thick-limbed V pointing forward. Owing partly to the elongation of the dorsal hump, the V as a whole is much narrower than in the tunnies (Fig. 27).

In an anterior view of a tunny skull (Fig. 21) there is an anterolateral depression in the surface of the parethmoid just above the vomer and partly roofed by a down-curved rim from the dorsal surface of the parethmoid. In Luvarus (Fig. 25) the homologous dorsal rim of the ethmoid is continued downward, forming the lateral wall of a bony passageway, here called the anterior olfactory groove, which leads downward, forward and inward to a point above the junction of the opposite premaxillae. If we may judge from the comparative material described by Burne (1909) and Derscheid (1924), there must be one or more large nasal sacs in Luvarus, occupying the long fossa in the lateral wall of the parethmoid and ethmoid (Figs. 25, 27). One of these sacs was continued downward and forward through the anterior olfactory groove to

---

**Luvarus**

Fig. 26. Diagram showing “trapezius area.”
anterior nasal tube may safely be regarded as a high specialization derived from more normal percoid and scombroid conditions. The appearance of this specialization in an early stage may be another indication not of the primitiveness of such a larval stage but of tachygenesis or acceleration.

The interior of the dermethmoid in the tunny (Fig. 28) is composed of a series of radiating and branching trabeculae, which appear to spring from a center of growth which is on the middle of the dorsal anterior convexity or roof. Behind this growth center is an elongate interior chamber with smooth walls and without known exits, rapidly widening backward and outward and continued into the anterior part of the prefrontal. By analogy with somewhat similar conditions in Xiphias we may infer that this chamber and the spongy tissue around it served for the storage of fatty material. In Luvarus (Fig. 28) even the presence of this median chamber is not definitely proved in our specimen, but if present it may have occupied the space between the diverging limbs of the V (Fig. 27). In the front view (Fig. 21) the diverging limbs of the dermethmoid V support the upraised frontals. Posterodorsally (Fig. 24) the same widening limbs of the V end in a wide transverse contact between the parenthroids and the alisphenoids (see below, p. 265).

No trace of an orbitosphenoid has been found nor would it be expected in a derivative of the percoid stock.

ALISPHENOIDS.—These bones (Figs. 8, 24, 28, 29, 30, 33), meeting below in the midline, form the thick basal and lower lateral walls of the cranial vault. In the mesial aspect (Fig. 29B) the growth center of the alisphenoid is lateral to the prominent exit of the olfactory nerve (1). From this center radiate five main strengthening ridges or elevations (Fig. 29B, 1–5) and several subordinate ones: the first anterocentral, the second dorsolateral, the third posterolateral, the fourth posterior, in position; a fifth, or basal, process (5) forms the floor of the conjointed alisphenoid chamber. The latter is strengthened in front of the olfactory foramen by a finely cellular transverse plate (1), and behind that foramen by a more densely crowded cellular plate (5). The whole surface of the lateral, basal, dorsal and posterior walls of the cranial vault is covered with a smooth, glistening white, thin layer; this may indicate that the cranial vault was filled with collagenous tissue, as it is in another deep-water fish, Acrotus (H. C. Raven).

In the dried skull just in front of the thick floor of the alisphenoid (Fig. 29B, ?en. for.) there is a large transverse passageway which runs laterally to a large aperture beneath the frontal roof of the

Fig. 27. Relations of the olfactory sacs to the skull.
Fig. 28. Left ethmoid complex, medial section, × 1. Compare Fig. 21.
orbit. This may represent part of the great jugular venous system, which would be necessarily enlarged in order to drain the relatively huge spongy walls of the anterior part of the skull.

The alisphenoid extends transversely outward (Fig. 29A) into a very thick wall which is overlapped anteriorly by the posterior vertical flange of the frontal, dorsally by the supraoccipital and epiotic, posterolaterally by the sphenotic and posteriorly by the prootic.

Near the middle of the alisphenoid floor is a small, transversely extended fossa or depression (Fig. 29B, olf.) probably for the ventral surface of the olfactory bulb; immediately in front of this is a tunnel (I) for the olfactory nerves, of oval cross

Fig. 29. A, left alisphenoid, lateral; B, right alisphenoid, medial. Ca. × 1/4.
section, leading downward and forward along the ventral surface of the alisphenoid and pointing toward the olfactory foramen on the posterior face of the parethmoid.

Posterolateral to the olfactory foramen and immediately behind the center of growth is a small but conspicuous foramen (Fig. 29, ્ant. cer. v.) leading into a small transverse tunnel (probably for the anterior cervical vein), which opens near the middle of the orbital surface of the alisphenoid (Fig. 33).

The dorsoposterior limit of the alisphenoid on the endocranial surface (Fig. 29) forms a boldly jagged suture with the lateral wall of the enlarged epiotic. The same jagged suture is continued downward, marking the posterior contact of the alisphenoid with the proötic.

In the front view the alisphenoid as preserved is sharply truncated, probably by the removal of a thick marginal cartilage.

In the lateral view (Fig. 29A) the alisphenoid exhibits a system of large, radially arranged, spongy cones with their apices converging toward the center of the bone. This system faced an opposite but similar
set in the sphenotic, the apices in both bones being directed away from the irregular surface of contact. This extremely delicate system of cells is far more elaborate than the simple spongy tissue of the alisphenoid of the tuna.

In comparison (Fig. 30) with the alisphenoid of the tuna, that of Luvarus has inherited the following basic features:

1.—Although the alisphenoid forms the floor of the anterior extension of the brain-

1.—In the tuna the sphenotic forms much of the anterolateral wall of the cranial vault, whereas in Luvarus the alisphenoid seems to have extended dorsally, excluding the sphenotic from the wall of the endocranial vault. This is partly the result of the great forward growth of the epiotic and the correlated retreat of the orbitosphenoid, which, however, still articulates with the posterolateral portion of the alisphenoid (Fig. 29A).

---

**Fig. 31.** Location of foramina for the cranial nerves in *Thunnus*; medial view of cranial vault and related parts.

---

2.—The unossified condition of the front part of the alisphenoid also increases the difficulty in homologizing the parts of this region in Luvarus and the tuna (Fig. 30).

3.—In the dried skull of the tuna and all other true scombroids there are large paired fenestrae (hereafter called dorsal fenestrae) visible in the dorsal view (Fig. 19) on either side of the sagittal crest; they are bounded by the frontals or supraoccipitals, parietals, sphenotics and ali-
sphenoids, and lead downward and backward into the cranial vault. In Luvarus (Fig. 22), perhaps as a result of the extreme forward displacement of the supraoccipital and epiotics, these fenestrae, if ever present, have been roofed over; but they may be represented by an unossified space in the dried skull lying dorsoposteriorly to the supraoccipital and mesially to the posterior ascending flange of the frontals.

4.—In Luvarus an apparently new ar-...
strongly built to withstand relatively heavy longitudinal and shearing forces. Laterally it receives thrusts from the sphenotic, which are delivered by the massive hyomandibular from the jaws and opercular series, while ventrally the opposite proötics are prolonged downward into a pair of stout pillars, to which the basioccipital contributes the dorsoposterior and the parasphenoid the ventroposterior portion. These pillars serve in part for the support of the pharyngeal roof, in part for the stiffening of the floor of the neurocranium. Above all else the proötic, with its stout walls and buttresses, affords a strong box wherein the brain is suspended and thus protected from all shocks.

Anterolaterally (Fig. 32) the interior of the proötic wall where it joins the alisphenoid is likewise constructed of cancellous tissue grouped into cones and irregular cells. The same is true of its dorsolateral contact with the epiotic. Internally it is likewise lined with glistening tissue. Ventrolaterally it is pierced by a large circular funnel (Fig. 32) containing foramina for several branches of the fifth and seventh nerves, as shown by comparison with Thunnus (Fig. 31) and Scomber (Allis, 1903, Pl. v, fig. 11, and Pl. xi, fig. 63).

Anteroventrally, in the midline, the proötic bears a large notch which forms the posterior half of the optic foramen, the anterior half being supplied by the alisphenoid.

Very probably the trochlear nerve issued through the dorsolateral corner of the optic foramen. In Scomber this nerve has a separate minute foramen immediately lateral to the optic foramen (Allis, 1903, Pl. xi, fig. 63); in the tuna there is a small semicircular notch on the dorsolateral border of the optic foramen; although no such notch is present in Luvarus, we can find no probable place for the exit of the trochleus except the optic foramen.

Just behind the large optic foramen is a small median pituitary foramen (Fig. 32). The basisphenoid, if present at all, must have been a thin sliver pointing downward and backward, a part of the membranous anterior wall of the pituitary fossa.

Posteroventrally the proötic bears first a vertical wall of extreme density lying behind the large funnel for the fifth and seventh nerves. This wall is penetrated by a small funnel (Fig. 32, VI) for the abducent nerve which passes obliquely ventrolaterally, issuing (Fig. 33, VI) ventrolaterally to the vertical wall. Ventrolaterally the proötic is continued downward, and there is a long squamous overlap on the ascending ramus of the parasphenoid.

Laterally the inner face of the proötic bears a prominent longitudinal (Fig. 32, *) swelling which joins a similar stiffening ridge on the cranial wall of the alisphenoid (Fig. 29, 4). Just behind this ridge is a prominent V-shaped bastion on the cranial wall, with low but sharply defined walls. Possibly the seat of the ampulla (†) of the anterior vertical canal may be represented by a depression just behind the apex of the V. The canal itself may have passed through membranous tissue. At the posterior corner of the bastion is a foramen which leads to the excessively small horizontal semicircular canal (Fig. 32, ant. for. of horiz. can.). A nearly vertical but very high groove running up the rear wall of the proötic onto that of the epiotic apparently indicates the locus of the posterior vertical canal.

The posterodorsal wall of the proötic is firmly fused with that part of the exoccipital which both roofs and floors the small chamber for the medulla (Fig. 32). In this region the bone is exceedingly dense and solid. This chamber is not more than 6.1 mm. high in the midline. Its axis is sharply inclined downward and forward; it is continuous with the even smaller neural tube above the junction of the basioccipital with the first vertebra (see p. 238).

In either side of the chamber for the medulla is a small oval depression in the cranial floor which probably represents the greatly reduced remnant of the saccular fossa. Behind this fossa is a prominent foramen probably for the vagus.

The extremely dense base of the basioccipital sends downward a strong median pillar (Fig. 24) to support the stem of the
parasphenoid; proximally this median pillar bears a prominent facet for the ventral wedge of the first vertebra, while laterally the exoccipital bears a very large, transversely oval, flat facet for the lateral surface of the same vertebra.

The excessively small size of the neural passageway immediately in front of the first centrum (Fig. 8) has been noted above (p. 266). This passageway is roofed not by any part of the skull but by the lower end of the neural spine of the first vertebra. The minute foramen magnum (Fig. 22, f.m.) is bounded by a low ridge on the nuchal surface of the exoccipital, (b) Its contact with the ethmoid above is largely cartilaginous;

(c) In the dried skull the stem of the vomer is far below the ventral surface of the parethmoid and if there were a contact, all trace of the intervening cartilage is now missing; and

(d) The connection between the stem of the vomer and the parasphenoid is also weak, the interdigitation with the parasphenoid being dorsoventrally flattened.

All these characters are specializations beyond the conditions in the tunny and far beyond the primitive percoid stage.

The stem of the parasphenoid of Luvarus

upon which the anterior part of the spine of the first vertebra rests.

VOMER-PARASPHENOID BRACE.—Below the main stiffening axis of the cranium there is another longitudinal arch (Figs. 23, 24) formed by the vomer in front, the parasphenoid below and the descending pillars of the proótic and basioceciptal at the rear. This arch runs along the midline of the roof of the mouth and gives attachment to the dorsal branches of the branchial apparatus.

The vomer of Luvarus is chiefly remarkable because:

(a) Its ascending process for articulation with the ethmoid is greatly reduced;

(b) Its contact with the ethmoid above is largely cartilaginous;

(c) In the dried skull the stem of the vomer is far below the ventral surface of the parethmoid and if there were a contact, all trace of the intervening cartilage is now missing; and

(d) The connection between the stem of the vomer and the parasphenoid is also weak, the interdigitation with the parasphenoid being dorsoventrally flattened.

All these characters are specializations beyond the conditions in the tunny and far beyond the primitive percoid stage.

The stem of the parasphenoid of Luvarus

is overlapped anterolaterally on each side by a posterior process of the parethmoid, which is far longer than it is in the tunny.

This entire ventral arch is clearly foreshadowed in the tunnies (Figs. 20, 30), in which, however, the parasphenoid is less produced downward and backward. In the tunnies also this ventral arch is further strengthened by the junction of a strong median ascending process from the parasphenoid (Fig. 30) with a transversely U-shaped arch descending from the basisphenoid. No trace of this basisphenoid-parasphenoid brace is evident in the Luvarus skeleton.

This median brace in the tunny sepa-
rates the opposite myodomes, which are relatively shallow dorsoventrally and diverge widely in front. In *Luvarus* (Fig. 33), where the median brace is absent, the opposite myodomes are squeezed together into a rapidly narrowing chamber between the descending pillars of the proötic and basiöcipital. The tunnels for the dorsal aortae, which are conspicuous in the tunny (Fig. 20), are absent or not identified in *Luvarus*.

Behind and below the proötic pillars the parasphenoid gives off two very large paired processes (Figs. 25, 34, 36) directed
Fig. 35. Progressive shortening in Caranx, Thunnus, Luvarus, of occipito-otic region and posterior displacement of hypsiloid brace. Horizontal hachure represents sphenotic facet for hyomandibular; vertical hachure, pterotic facet.

backward and outward. By comparison with a dried skeleton of Auxis we see that these very probably served for the suspension of the branchial series, and we are therefore naming them branchial tuberosities. In all these peculiar specializations Luvarus is far more advanced than the tunnies, including Auxis.

**Transverse Arches**

The section of the skull across the middle of the frontals reveals a contour of Gothic arch type (Fig. 21), the keystone being the supraoccipital. This arch, which is based on the broad pachemoids, is relatively high and narrow.

The transverse bracing of the posterior
part of the cranium is well seen from the rear (Fig. 36).

**Hypsiloïd Brace.**—As seen from the side (Fig. 34), vertical and transverse bracing is effected by a system of groins or radiating crests on the external surface of the alisphenoid, sphenotic, proötic and exoccipital; this converges downward upon a vertical column on the lateral surface of the descending pillar of the proötic.
This transverse vertical flange meets the ascending ramus of the parasphenoid ventrally and forms the stem of a conspicuous Y, which is hereafter called the hypsiloid brace; its forks include the enlarged sphenotic and pterotic facets for the hyomandibular (Figs. 34, 35). The anterior fork is deeply grooved laterally and perforated by foramina for the ophthalmic, mandibular and facial nerves. Other pits in the same groove may indicate branches of the jugular vein. The two large foramina on either side of the fork of the Y open from the trigemino-facialis chamber (Figs. 34, 36). The tunnels leading from these foramina into the cranial cavity indicate that they are the facial (VII) and trigeminal foramina (cf. Allis, 1903, Pl. iii, figs. 7, 8, 9).

Occipito-otic Braces.—In the rear view of the skull (Fig. 36, sphot) the conspicuous postorbital process of the sphenotic projects laterally in front of the transverse hypsiloid brace.

The large rounded facet for the sphenotic head of the hyomandibular (Fig. 34) is anterolateral to the much larger pterotic facet. At the junction of the two facets is a deep vertical crease, lying between the forks of the hypsiloid brace. These very large hyomandibular facets receive the transverse thrusts coming by way of the hyomandibular from the opercular series, and its muscles, from the adductors of the mandible and from the entire oral and branchial complex. They are very strongly braced against the endocranial vault by expanded cancellous contacts with the sphenotic, prootic and exoccipital as well as by the transverse and hypsiloid ridges already mentioned.

Immediately behind and beneath the hyomandibular facets on the sphenotic and pterotic is a shallow recess (Fig. 34, phr), hereafter called the posthypsiloid recess, at the junction between the pterotic, sphenotic and exoccipital. The roof of this recess, running inward, is continuous internally with the extremely dense posterior cranial wall formed by the ex- and basioccipital. This roof is bounded posteriorly by a low oblique ridge immediately below the middle of the pterotic facet; it corresponds perfectly to a far larger, deeper and more sharply defined posthypsiloid recess in the tunny (Fig. 34, phr), which has its apex at the junction of the sphenotic, epiotic and pterotic. But in the tunny the sphenotic and pterotic facets (Figs. 34, 35) are widely separated, and there is immediately behind the sphenotic facet a conspicuous oval fenestra, while in Luvarus, owing to the great size of both facets, this fenestra is reduced to a narrow cleft, and the delicate bony bridge which in the tunny forms the posterior fork of the hypsiloid brace is here much thickened and appressed toward the pterotic facet.

Behind the posthypsiloid recess of Luvarus and beneath the lateral wing of the exoccipital, is a prominent obliquely placed but shallow trough or depression (Fig. 36, sub. sty. tr.), here called the substyloid trough, bounded anteriorly (Fig. 34) by the pterotic facet and posteromedially by a substyloid ridge beneath the large styloid process that connects the inner fork of the posttemporal with the transverse extension of the exoccipital. The conspicuous exit of the tunnel for the vagus nerve (Fig. 34, X) is located immediately behind the substyloid trough. The form and placement of the latter could readily be derived from the conditions seen in the tunny (Fig. 34, opo) by strongly shortening the basioccipital region and by swinging the substyloid ridge posteromedially.

The foregoing details support the general inference that in the ancestors of Luvarus there has been an anteroposterior shortening of the postorbital part of the cranial vault and a posterior displacement of the hypsiloid brace with reference to the sphenotic and pterotic facets, as plainly indicated in Fig. 35.
LARVAL STAGES

The larval stages (Fig. 37) differ so widely from the adults in appearance that they have been given several different names, and some of them were referred to the Coryphaenidae. Roule (1924), however, supplementing and greatly extending the work of his predecessors, brought all the available data together in a beautiful memoir, “Étude sur l’Ontogénèse et la Croissance avec Hypermétamorphose de Lurvarus imperialis Rafinesque, Poisson rapporté à l’ordre des Scambriiformes.” The phenomenon of hypermetamorphosis which Roule describes is of the greatest importance in problems relating to the ordinal classification and derivation of this fish.

In comparing the construction of larval and adult stages we can start only from the 6-mm. “Hystricinella” larva figured by Roule (1924). This stage, however, is already far advanced from the unknown true embryonic stages; in such early embryonic stages many other spiny-rayed teleosts (cf. Bigelow and Welch, 1925) are more or less eel-like embryos with spineless fin folds and bulging brains, whereas the “Hystricinella” is a deep bodied, free living fishlet with very large dorsal and pelvic fin spines and brain deeply buried beneath the huge dorsal hump. Evidently the “Hystricinella” stage is already far more specialized away from embryos of normal spiny-rayed fishes than are the early larvae of Scomber.

From a study of Roule’s data we may say that whatever may be the remote phylogenetic stock of Lurvarus our first query is, By what steps were the adult conditions derived from the larval stages?

In the “Hystricinella” larval stages of 6 mm. to 26 mm. the head is relatively huge; for example, in Roule’s 6-mm. stage A, the distance from the tip of the snout to the posterior border of the operculum is about 40 per cent of the total length. Moreover, the general form of the head at this stage at first sight suggests the adult contour. The posterior half of the body, on the other hand, seems far shorter in relation to depth than in the adult.

Comparison of the contours (Fig. 38) indicates a marked later growth in the region between the pectoral fin base and the base of the tail. In Roule’s stage B, as figured, there are about nine myomeres in front of the hypurals to a point above the seventh anal ray. Assuming that all the adult vertebrae are already represented, this would leave sufficient space for about thirteen or fourteen vertebral segments from the point named above to the occiput. In any case there is convincing evidence that the middle part of the body became markedly elongated, not by an increase in the number of segments but by the elongation of a relatively small number of segments, since (except the nineteenth vertebra) the twenty-two adult vertebrae in front of the hypurals have quite long centra.

According to Roule (1924, Fig. 18), the early larval tail is internally heterocercal with seven slightly expanded hypurals which fuse into one fan-shaped mass in the adult. In the earlier larval stages the caudal fan is convex posteriorly and about one-half to one-third the greatest body depth. In the adult it is deeply forked and distinctly larger than the greatest body depth.

More in detail, the great apparent depth of the preorbital region in the early larvae superficially suggests the adult condition but is largely due to the much greater proportional vertical distance from the front of the upper “lip jaw” to the tip of the snout (anterior point of the mesethmoid) in the larva. Indeed the vertical growth of this part slows up sharply in the later larvae. On the other hand, the steep anterior slope of the dorsal hump of the adult has grown up from the gently sloping rostral and supraorbital convexity of the early larva.

The eye of the earlier larvae is relatively large, about one-tenth of the total body length, whereas the adult eye is about one-twenty-fifth the total body length. However, the position of the eye seems to have been relatively constant from early larva to adult.

The supraorbital ridge of the adult
Fig. 37. Larval stages of *Luvarus*. After Roule, 1924.
Fig. 38. Ontogeny of Luvarus, showing changes in proportion from early larvae to adult. Lower figure original, others based on Roule, 1924.
The opercular region is quite distinct in the "Hystricinella" stage and differs from the adult condition in that it is not sharply prolonged downward and backward. The same is true of the pectoral girdle, which at neither the lower nor the upper end has been subject to the obvious specialization of the adult. The pectoral fin is relatively much larger in the "Hystricinella" than in the adult. The rays vary in number from eighteen to twenty (Roule); in our adult, eighteen.

The dorsal fin in "Hystricinella" is supported by two very large spines bordered with little thorns, followed by fifteen rays in stage A, seventeen in B, twenty in C and later stages. The two great spines dwindle at their distal ends even before the "Astrodermella" stage, in which they have already lost their thorns and become shorter than the rays behind them. Still later, in the "Luwarella" stages the shortening and eventual elimination of the free spines extend back to the ninth fin base or pterygiophore.

Although the pectoral and caudal fin rays branch distally as in normal teleosts generally, the dorsal and anal fin rays are unbranched and pointed, even in "Hystricinella" A. This must be deemed a sign of high specialization, as in certain blennies.

Although pterygiophores of the median fins are not visible in Roule's figures, their presence even in the "Hystricinella" stage is indicated not only by the well-developed fin rays but also by the retention of pterygiophores as the adult contour bones, long after the elimination of the first nine spines in the dorsal fin.

The anal fin of the "Hystricinella," apart from the lack of branching in its rays, looks very normal but lacks enlarged spines such as those of the dorsal and pelvic fins. It begins immediately behind the vent, which is posterior in position, whereas in the adult the vent has moved far forward beneath the scapulo-coracoid. Therefore we may infer that the anlage of the first interhaemal rod of the "Hystricinella," if present, was of ordinary dimensions and lay in a nearly vertical position, whereas in the adult it has become a great horizontal beam, like a ship's keel, extending forward to the anteriorly placed vent. The anal rays number eighteen in all but the "Astrodermella" stage A (Roule, 1924, p. 139), where there are seventeen, as in our adult.

The pelvic fin in the earliest "Hystricinella" consists of one very large thorny spine and four long slender rays. In the adult the pelvic fin is extremely reduced and joined with its fellow to produce a lanceolate flap or operculum for the vent. In the dying Luwarian observed by Nardo (1827) this organ worked spasmodically and thus suggested the generic name, Proctostegus (vent, cover). In intermediate stages of "Hystricinella" and "Astrodermella" the pelvic fin spines become reduced, while the soft rays first lengthen
and then rapidly shorten to the minute stage in the adult. The probable phylogenetic transformation of the pelvis itself is treated above (p. 241).

In the caudal fin of the "Hystricinella" stage Roule (1924, p. 154) observed that there were seven visible hypurals and that the fin rays did not encroach upon them, whereas in a larval tunny ("Orcynus thynnus") of 20 mm. length, the hypural region was represented only by two very large fan-shaped areas while the dermal rays already extended more than halfway across the hypurals, thus approaching the condition seen in adult tunnies. He concludes therefore (loc. cit.) that the striking resemblance between the caudal fins of the adult tunny and Luvarus is an expression of convergence, so that he finds it difficult to accept the usual classification of Luvarus as a member of the scrombiform series.

However, further consideration suggests that his "Hystricinella" and tunny larvae represent quite different ontogenetic stages, the "Hystricinella" being accelerated in the anterior part and retarded in the caudal, while in its larval tunny the hypural region is much nearer its adult condition. Assuredly the profound and intimate resemblance between the adult caudal skeletons of the two genera is not to be hastily ascribed to convergence on the evidence of a single difference in different larval stages.

Thus from Roule's data it is evident that although the Hystricinella stages suggest the adult Luvarus in a general way, as well as in certain particular features such as the small size and toothless condition of the mouth and the marked anterior position of the suspensorium, yet they differ in so many other features that on the whole the transformation of a Hystricinella into a Luvarus has been aptly termed by Roule a hypermetamorphosis. By this he means a degree of metamorphosis which is rare among vertebrates except perhaps among deep-sea fishes. The question then arises whether, or to what extent, the Hystricinella stage is a really primitive larva or whether it has acquired some of its unusual characters by "acceleration" (tachygenesis) and others (such as the huge larval spines) as mere larval structures not inherited from earlier adult stages.

**Summary and Comparison of the "Hystricinella" and Adult Stages**

<table>
<thead>
<tr>
<th>Body form</th>
<th>&quot;Hystricinella&quot;</th>
<th>Adult</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head</td>
<td>Very large</td>
<td>Long</td>
</tr>
<tr>
<td>Eye</td>
<td>Very large</td>
<td>Small</td>
</tr>
<tr>
<td>Mouth</td>
<td>Very small, toothless</td>
<td>Moderately large</td>
</tr>
<tr>
<td>Suspensorium</td>
<td>Produced far forward</td>
<td>Very small, toothless</td>
</tr>
<tr>
<td>Opercular series</td>
<td>More normal</td>
<td>Produced far forward</td>
</tr>
<tr>
<td>Branchial chamber</td>
<td>More normal</td>
<td>Produced downward and backward</td>
</tr>
<tr>
<td>Dorsal hump</td>
<td>Prominent</td>
<td>Lengthened anteroposteriorly</td>
</tr>
<tr>
<td>Supraoccipital crest</td>
<td>Presumably above occiput</td>
<td>Extremely prominent</td>
</tr>
<tr>
<td>Pterygiophores of median fins</td>
<td>Presumably normal</td>
<td>Displaced far forward above rostrum</td>
</tr>
<tr>
<td>Pectoral fin</td>
<td>Relatively large</td>
<td>Giving rise to dorsal and anal contour bones</td>
</tr>
<tr>
<td>Dorsal and anal fin bases</td>
<td>Apparently well separated</td>
<td>Relatively smaller but in similar relation to eye</td>
</tr>
<tr>
<td>Caudal fin complex</td>
<td>Internally heterocercal with seven distinct hypural rods</td>
<td>Posterior ends closely attached to vertebral column</td>
</tr>
<tr>
<td>Pelvic fins</td>
<td>Very large with strong thorny spine</td>
<td>Internally almost symmetrical with complex hypural fan</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Forming very small operculum ani</td>
</tr>
</tbody>
</table>
DISCUSSION AND SUMMARY

STRUCTURAL AND FUNCTIONAL CHARACTERS

Among the most peculiar characters of the adult louvar are the extremely small and delicate scales, each of which is shaped somewhat like a tree with a very flat irregular top, a short delicate stem and a radiating system of roots. Possibly these minute scales may serve to keep a watery envelope or film around the body and thus lessen friction against the medium.

In external appearance the plump body of the louvar recalls the rounded contours of a dirigible balloon. In the front view the dorsal swelling of the body suggests that the fish may be able to roll over easily on one side or another under the combined action of its large caudal and pectoral fins. This dominating dorsal hump is filled with large segmental muscles which by their rhythmic contraction bend the body slightly from side to side. The dorsal division of the body musculature is based on the vertebral column but is also attached above to the sides of the strong chain of contour bones forming the dorsal truss (p. 231), which extends backward from the snout. The opposing or cooperating muscle masses on either side below the column are attached to the ventral truss (p. 233). Each of these trusses, made from the expanded interlocking bony bases of the dorsal and anal fins, affords a strong but jointed keel. At its anterior end the dorsal keel is tied onto and supported by the front part of the skull roof; posteriorly it is tied to the eighteenth or anchor vertebra; the ventral keel is tied anteriorly by ligament to the lower part of the shoulder girdle and posteriorly to the anchor vertebra. Thus in the louvar the body as a whole is strengthened by three longitudinal jointed axes, namely, the vertebral column and the dorsal and ventral trusses.

The vertebral centra are strongly braced, elongate constricted cylinders, but the neural and haemal arches are very delicate, having been largely superseded by the dorsal and ventral trusses.

The very large lunate tail is supported by a perfected fan-like hypural complex, which in turn is movably articulated into two very remarkable rudder-stock vertebrae, certain parts of which are overlapped so as to permit sufficient lateral movement of the tail fan without danger of dorso-ventral dislocation. Anteriorly the first rudder-stock vertebra is movably articulated with the short nineteenth centrum which we have called the “pivot” and which in turn is based on the eighteenth, or “anchor,” vertebra.

The dorsal and anal fins are long and low, the pectoral fins large; the pelvics are reduced to a lanceolate flap covering the vent. The pectoral girdle is large but delicate. The pelvis is a long narrow rod attached to the inner sides of the opposite cleithra.

In a louvar weighing 200 pounds by far the greater part of the weight must be due to the above-named muscles of locomotion, which are divided into four main groups: one dorsal, one ventral, on each side. Consequently the backbone, the dorsal and ventral trusses and the braincase must all be sufficiently strong to resist powerful pulling, pushing, bending and shearing forces.

Apparently the maximum bending and shearing forces operate around the occipital base and its junction with the vertebral column, for in this region the bone is extremely dense and hard. The interior of the front part of the skull, on the contrary, is either completely spongy or entirely lacking in the dried skull. Nevertheless it is probable that in life these boneless and spongy areas were bounded by tough membranes and kept turgid by the cumulative pressure exerted by the heart pump acting on the fluids of the body.

In connection with the mechanical conditions noted above for rapid progress through water at considerable depths, we find many structural features in the braincase which have been noted in some detail in the foregoing text. Here may be mentioned the three trusses or arches that run longitudinally, first, along the roof of the skull (p. 254), secondly, along
the floor of the braincase (p. 267) and, thirdly, through the downwardly bowed parasphenoid to the descending pillar of the basioccipital (p. 263). There is also a series of transverse and obliquely directed braces, converging from the lateral borders of the skull roof toward the base of the occiput (p. 269). Here belong also the groin-like ridges, including what we have called the hypsiloïd brace (p. 270), on the side of the braincase, beneath the laterally projecting roof.

In the midst of this complex system of bony trusses and braces lies the strong walled cranial vault and in the middle of this vault in turn was suspended the very small brain. This was prolonged posteriorly into a medulla oblongata of less than 3 mm. diameter. Extremely small also is the horizontal semicircular canal, while the sacculus for the main otolith left only a minute oval depression on either side of the floor of the short occipital tunnel. The anterior and posterior semicircular canals may perhaps have been many times larger than the horizontal canal, but they have left little if any indisputable evidence of their presence. The eyes were, however, fairly large, and the optic lobes of the brain, as figured by Haller (1881), were well developed. The pituitary must have been very small, while the olfactory foramen was not large. The olfactory troughs on the lateral surfaces of the ethmoid bone were continued forward and downward to the small anterior nares lying near the midline immediately above the mouth. Thus the sense of smell, although doubtless adequate, does not seem to be overdeveloped, and sight must have been the predominant sense, supplemented no doubt especially by the organs of the lateral line system. These were lodged in conspicuous pits running along the sides of the skull roof.

With this unequally developed sensory equipment, in cooperation with its powerful and efficient locomotor apparatus, the louvar may have traveled long distances in a leisurely way, on the lookout for schools of copepods, ocean shrimps or medusae, which it easily sucked into its very small and toothless mouth.

Its jaw bones, although extremely delicate and translucent, are nevertheless moved by an elaborate system of muscles which arise from an arc-like path along the outer side of the hyomandibular and pterygoid bones. The small size of the mouth is partly conditioned by the markedly anterior prolongation of the lower bar of the "susceptorium," including parts of the hyomandibular, quadrate, pterygoid, mesopterygoid and palatine bones. The branchial apparatus of the louvar is of the normal teleost type, with no conspicuous specializations. The gill rakers are like delicate recurved hooks, in contrast with the long sifter type of typical plankton feeders.

The branchial chamber is unusually far below the braincase. It is covered with a normal series of opercular elements, including opercular, sub-, inter- and pre-operculars with four thin sabre-like and two leaf-like branchiostegals on the lower border of the opercular fold. The members of the opercular series are all more or less delicate, with rounded contours lacking spikes or projections along their posterior borders.

Altogether the defenseless, delicately constructed but plump louvar would apparently be an easy prey for aggressive predators of much smaller size. Presumably its ancestors once bore normally toothed jaws and were among the swift swimming predators near the surface, but due in part to genetic mutations their teeth became smaller and their jaws more feeble, although retaining the basic arrangements for jaws that bite. Meanwhile other mutations, accumulated during many millions of years, were enabling them to detect and follow suitable food in the dim twilight zone and to live under gradually increasing pressures.
PHYLOGENY AND CLASSIFICATION

As in many other cases where habitus characters tend to obscure ordinal heritage, the high specializations of the louvar are merely modifications of basic morphologic patterns of which the general palaeontological history is already well documented. Were it not for the limitations of a restricted objective, it would require only the necessary labor to record what is already plainly indicated regarding the history of every organ and bone from the stage of the lower Devonian palaeoniscoids, up through the protospondyl ganoids of the Mesozoic order Holostei, into the more primitive isospondyl, berycoid and spiny-rayed stocks of the late Mesozoic. The circumstance that the exact phylogenetic interrelationships of some of the numerous families may perhaps never be fully settled need not prevent us from appreciating the general course of events which set the stage for the emergence of *Lucasius imperialis*.

Thus it has happened, for example, that this highly peculiar fish exhibits the full complement of the bones of the primary upper jaw that were present in the Devonian basal teleostomes; that the *Lucasius* hyomandibular retains all its primitive contacts with surrounding elements and that its opercular fold contains the preoperculum, operculum, sub- and interoperculum and branchiostegals. Nor do we need to designate the bones of its endocranium or of any other part of its skeleton by any other names than those already listed for other teleosts in the works of Parker, Allis, Starks and others.

In brief, *Lucasius* is a derivative of the primitive spiny-rayed teleosts and shares with other moderns the broad heritage of the classic perch type, while even its most peculiar features are foreshadowed in varying degrees among the numerous carangoid and scombroid families to which it still appears to be genetically related.

Coming closer to the main taxonomic problem, we are confronted with the following different solutions:

1. That *Lucasius* is an offshoot of the basic carangoid stock;
   (2) That it is a modified scombroid, its nearest relative being the tuna (Regan);
   (3) That it is the sole known representative of a distinct order, Luvariformes (Jordan), and that its resemblances to carangoids and scombroids are due to convergence (Roule).

1.—If the low number of vertebrae (twenty-three) were to be taken as of major importance in classification, the louvar would be referred to the carangoid division of the percomorph order, and the same result would ensue if we placed a high value upon the general form of the body, which, with its nearly equal dorsal and ventral contours, is not unlike the basic carangoid type. Moreover, in the carangoids the dorsal and ventral trusses are present in an early stage of evolution, and the wide pterygiophores that support the dorsal and anal fins in *Trachinotus* would appear to afford a favorable starting point for the zigzag interlocking between adjacent “beams” of the dorsal and ventral trusses of *Lucasius*. Other rather significant points of resemblance of *Lucasius* to the carangoids are: its dorsal and anal fins are each continuous, not broken up posteriorly into a row of finlets as they are in the scombroids; further, its ribs are broad, few in number and sessile, springing from the sides of the vertebrae as in the carangoid *Trachinotus* rather than from ventrally prolonged haemal arches as in scombroids. Again, the carangoids have very long narrow pelvic rods from which the still narrower pelvis of *Lucasius* might well be derived, while the great forward development of the dorsal hump above the skull is approached in all the carangoids and especially in *Coryphaena*. Nor would the small mouth and short jaws of the louvar be difficult to derive by further specialization from those of the carangoids, and the same is true regarding the shapes of the palatine and other elements of the primary upper and lower jaws. Even the loss of the basisphenoid-parasphenoid column may be
foreshadowed by its very small size in the carangoids.

2.—In favor of the view that the louvar is only a specialized relative of the tunny is the fact that both the caudal region and the entire skull abound in many and detailed specializations which may readily be conceived as stages beyond those of the tunnies (Thunnus) and bonitos (Auxis). Here belong all the points mentioned by Regan (1903) as well as others described above (pp. 235–271). However, after again comparing the Luvarus braincase with those of several carangoids, we now realize that some of the special resemblances between Luvarus and the tunny may be partly due to the large size of both these forms, while some of the differences between Luvarus and the carangoids may be conditioned by the small size of the latter.

Perhaps the chief difficulty in deriving the skeleton of Luvarus from that of any of the tunny group (Thunnidae, Katsuwonidae) would be that if, as seems highly probable, the vertebral formula in primitive perciforms was $10 + 14$, the numbers would have to be increased to thirty-nine in Auxis and then decreased again to $9 + 12$ in Luvarus. That there has been a secondary reduction in the number of vertebrae in the ancestry of the ocean sunfishes (Molidae) is evident from H. C. Raven’s study of that family (1939), and if there were known forms of scombroids and carangoids whose vertebral numbers indicated a corresponding reduction in the ancestral line leading to Luvarus, we might well accept such evidence rather than invoke the ambiguous and often abused doctrine of irreversibility of evolution.

Unpublished experimental evidence by Mordecai Gabriel of Columbia University proves that in the case of Fundulus heteroclitus the number of segments may be decreased by raising the temperature of the medium in which development takes place. This suggests that in Luvarus and the carangoids the temperatures of their breeding grounds are higher than those of the scombroids and that a considerable shift in number of vertebrae either way would in the long run be due in part to a shift in the temperatures of the breeding grounds either through change in the environments or migration to new localities or horizons. Perhaps this is why the mackerel, which breeds near the relatively cold waters of the Gulf of Maine and the Gulf of St. Lawrence (Bigelow and Welsh, 1925, pp. 191, 206) has relatively many vertebrae, while the louvar, which breeds in or near the warm waters of the Mediterranean (Roule) has few vertebrae. Whatever may be the ultimate answers to these problems, the fact remains that among the existing or fossil scombroids (excluding the Ziphiiformes) none is known in which the vertebral formula even remotely approaches that of Luvarus and the carangoids. Consequently we feel obliged to give this fact its due weight in the present discussion.

3.—As noted above, Roule (1924) has correlated the data and material relating to the development of the louvar from the minute 5-mm. “Hystricinella” to the “Lowarella” stage which is approaching the mature Luvarus. Partly because the early larval stages of the louvar are exceedingly unlike those of the tunny, Roule implies that such resemblances as there may be between the adult stages of these forms may be attributed entirely to convergence. He therefore (ibid., p. 155) raises the division Luvariformes of Jordan to full ordinal rank and suggests that many orders of teleosts were derived independently and ab initio from primitive fishes that retained a cartilaginous skeleton. By implication the louvar, possessing a largely cartilaginous skeleton, may have been derived quite independently from the scombroids with which it shows only a convergent resemblance! The contrary view that cartilaginous fishes have in most cases been derived from fishes with well-ossified skeletons was not mentioned by Roule but has since been developed with cumulative evidence by Stensiö.

In short, partly on the basis of a certain difference between the larvae of the louvar and the tunny in the mode of development of the hypural region of the tail, Roule creates, at least by implication, a vast and entirely imaginary phylogenetic
tree of the modern teleosts, disregarding the cumulative evidence of positive agreements in basic morphologic skeletal patterns and attempting to solve all major taxonomic problems at once by the magic of three mystic words: polyphytism, parallelism and convergence. It seems strange that the author who contributed the most brilliant demonstration of "hypermetamorphosis" should have failed to realize that the long continued application of this principle could bring about profound differences between the larval stages of such originally related families as the Carangidae, the Luvaridae and the Scombrids.

We therefore return with greater confidence to the foregoing analysis of morphologic patterns of the skeleton, first as wholes and then point by point, in the search for the ancestral connections of *Luvarus imperialis*.

REFERENCES TO THE LITERATURE

**ALLIS, EDWARD PHELPS, JR.**

**BERG, LEO S.**

**BERGER, E.**

**BIGelow, H. B., AND WELSH, W. W.**

**BOLIN, ROLF L.**

**BULLMORE, W. K.**

**BURN, R. H.**

**COLLENETTE, A.**

**CONRAD, G. MILES**

**CONSTABLE, W. J.**

**CORNISH, T.**

**COUCH, JONATHAN**

**DELAUGE, Y.**

**DERSHEID, J. M.**

**GREGORY, WILLIAM K.**

**GREENHOLM, A.**

**GULIA, GIOVANNI**

**GUNther, A. C.**

**HALLEB, B.**

HOLDER, C. F.
1901. A Rare Fish. Scientific American, LXXXV, p. 415.

JORDAN, DAVID STARR

KISHINOUYE, K.

NARDO, G. D.

NICHOLS, J. T., AND HELMUTH, WILLIAM T., 3d

NINNI, E.

RAVEN, HENRY C.

1943. Notes on the Digestive Tract of Luvarus imperialis. (In manuscript.)

REGAN, C. TATE

ROULE, L.

SCHARRF, R. F.

SEWERTZOFF, A. N.

SHELDEN, FREDERICK F.

STARKS, E. C.


TROIS, E. F.


VAILLANT, L. L.

WAITE, E. R.

WHITLEY, GILBERT
1940. The Second Occurrence of a Rare Fish (Luvarus) in Australia. Rec. Australian Mus., XX, pp. 325–326.

WOODWARD, A. S.

ABBREVIATIONS USED IN FIGURES

alsp. = alisphenoid
ang. = angular
ant. cer. v. = anterior cerebral vein
ant. md. pr. = anterior median process
ant. vert. sem. c. can. = anterior vertical semi-circular canal
art. = articular
bh. = basihyal
boc. = basiopticul
br. = branchiostegals
br. tub. = branchial tuberosity
bsph. = basisphenoid
cer. = ceratohyal
clt. = cleithrum
cor. = coracoid
dent. = dentary
deb. = dermohyal
ef. br. art. = efferent branchial artery
eph. = epihyal
enpt. = entopterygoid
<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>epiot.</td>
<td>epitotic</td>
</tr>
<tr>
<td>exo.</td>
<td>exoccipital</td>
</tr>
<tr>
<td>f. ju.</td>
<td>foramen for branch of jugular vein</td>
</tr>
<tr>
<td>f.m.</td>
<td>foramen magnum</td>
</tr>
<tr>
<td>for.</td>
<td>foramen</td>
</tr>
<tr>
<td>fr.</td>
<td>frontal</td>
</tr>
<tr>
<td>horiz. sem.c. can.</td>
<td>horizontal semicircular canal</td>
</tr>
<tr>
<td>hyom.</td>
<td>hyomandibular</td>
</tr>
<tr>
<td>ih.</td>
<td>interhyal</td>
</tr>
<tr>
<td>int.</td>
<td>internal</td>
</tr>
<tr>
<td>iop.</td>
<td>interoperculum</td>
</tr>
<tr>
<td>lat.</td>
<td>lateral</td>
</tr>
<tr>
<td>l.f.</td>
<td>lateral flange</td>
</tr>
<tr>
<td>m.</td>
<td>muscle</td>
</tr>
<tr>
<td>mtp.</td>
<td>metapterygoid</td>
</tr>
<tr>
<td>mx.</td>
<td>maxillary</td>
</tr>
<tr>
<td>olf.</td>
<td>depression for olfactory bulb</td>
</tr>
<tr>
<td>op.</td>
<td>operculum</td>
</tr>
<tr>
<td>opo.</td>
<td>opisthotic</td>
</tr>
<tr>
<td>op. ped.</td>
<td>opercular pedicle</td>
</tr>
<tr>
<td>pa.</td>
<td>parietal</td>
</tr>
<tr>
<td>pal.</td>
<td>palatine</td>
</tr>
<tr>
<td>pareth.</td>
<td>parethmoid</td>
</tr>
<tr>
<td>pas.</td>
<td>parasphenoid</td>
</tr>
<tr>
<td>pel.</td>
<td>postcleithrum</td>
</tr>
<tr>
<td>phr.</td>
<td>posthypsploid recess</td>
</tr>
<tr>
<td>pit.</td>
<td>pituitary fossa</td>
</tr>
<tr>
<td>pmx.</td>
<td>premaxillary</td>
</tr>
<tr>
<td>po.</td>
<td>posthypophysial</td>
</tr>
<tr>
<td>pop.</td>
<td>preoperculum</td>
</tr>
<tr>
<td>post. orb. proc.</td>
<td>posterior orbitoital process</td>
</tr>
<tr>
<td>post. vert. sem.c. can.</td>
<td>posterior vertical semicircular canal</td>
</tr>
<tr>
<td>post. zyga.</td>
<td>posterior zygapophysis</td>
</tr>
<tr>
<td>proc. med. ischii</td>
<td>median ischial process</td>
</tr>
<tr>
<td>prot.</td>
<td>prootic</td>
</tr>
<tr>
<td>ptm.</td>
<td>posttemporal</td>
</tr>
<tr>
<td>pto.</td>
<td>pterotic</td>
</tr>
<tr>
<td>pm.</td>
<td>pterygoid</td>
</tr>
<tr>
<td>qu.</td>
<td>quadrate</td>
</tr>
<tr>
<td>scap.</td>
<td>scapula</td>
</tr>
<tr>
<td>socal.</td>
<td>supraoccipital</td>
</tr>
<tr>
<td>sop.</td>
<td>suboperculum</td>
</tr>
<tr>
<td>sphot.</td>
<td>sphenotic</td>
</tr>
<tr>
<td>sub. sty. r.</td>
<td>substyloid ridge</td>
</tr>
<tr>
<td>sub. sty. tr.</td>
<td>substyloid trough</td>
</tr>
<tr>
<td>sym.</td>
<td>symplectic</td>
</tr>
<tr>
<td>trig.-fac. rec.</td>
<td>trigemino-facialis recess</td>
</tr>
<tr>
<td>ven. for.</td>
<td>venous (or jugular) foramen</td>
</tr>
<tr>
<td>vert.</td>
<td>vertebra, vertebrae</td>
</tr>
<tr>
<td>vo.</td>
<td>vomer</td>
</tr>
<tr>
<td>I-XII</td>
<td>cranial nerves</td>
</tr>
<tr>
<td>1-5</td>
<td>strengthening ridges on the alisphenoid bones</td>
</tr>
</tbody>
</table>