THE TRIASSIC COELACANTH FISH
DIPLURUS, WITH OBSERVATIONS
ON THE EVOLUTION OF THE
COELACANTHINI

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A STUDY BASED ON SPECIMENS COLLECTED
AT PRINCETON UNIVERSITY

CONTENTS

INTRODUCTION

WITH THE PUBLICATION of this paper the number of coelacanth genera recognized from North America is reduced from four to three. They are *Rhabdoderma* from the Mississippian and Pennsylvanian, *Spermatodus* from the early Permian, and *Diplurus* from the late Triassic. Westoll (1943b) has mentioned an important new form from the Upper Devonian of Canada, and Welles (1947) has figured some coelacanth bones from the Lower Triassic that are probably too fragmentary for identification. *"Coelacanthus" banffensis* (Lambe, 1916) is not generically determinable. *Rhabdoderma* has been defined by Moy-Thomas (1937) to include a number of European as well as American species that formerly were placed in several other genera; *Rhabdoderma* is, however, probably only a form-genus. *Spermatodus*, after a checkered career as a crossopterygian and an actinopterygian, has been definitely identified as a coelacanth by Westoll (1939).

The known remains of *Diplurus longicaudatus* were redescribed by the writer in 1948. Prior to that time, the descriptions of Newberry (1878, 1888) formed the basis for most of the remarks on this form (Eastman, 1905, 1911; Stensiö, 1932). The genus *Osteopleurus* (Schaeffer, 1941) was erected for certain coelacanths from the Newark group, which were at that time considered to be generically distinct from *Diplurus*. The reëxamination of the original Newberry material of *Diplurus*, which was not available until after the last war, cast doubt upon this generic distinction, and the present study indicates that *Osteopleurus* must be regarded as a synonym of *Diplurus*.

In February, 1946, typical black and gray argillites near the base of the Lockatong formation of the Newark series were exposed in the southeast corner of an excavation for the new Firestone Library on the Princeton University campus. Examination of this exposure by various members of the Princeton Geology Department revealed abundant examples of the ostracods *Estheria* and *Candona*, together with plant fragments identified by Dr. Erling Dorf as typical cycads and conifers of Newark age. The possibility of discovering fossil vertebrates prompted continued searching as the rock was removed. Early in March of that year Dr. G. L. Jepsen and Dr. A. F. Buddington were rewarded by finding remains of coelacanth fishes at a horizon about 12 feet below ground level.

The discovery of the fossil fishes aroused much interest within the university community and among the residents of Princeton. In an article for the New Jersey State Museum, Dr. Jepsen (1949) records the following: "Dr. Julian Boyd, Librarian, immediately reported the discovery to the architect, Mr. R. B. O'Connor, who, with the contractor made it possible to proceed with the scientific work. Mr. H. A. Schroedel, superintendent for the Turner Construction Co., arranged to have workmen remove the rock above the fossiliferous layer and to keep heavy machinery out of the southeast corner of the excavation until the fossils had been collected. Truck drivers and other members of the excavating crew became interested, after their original scepticism about fishing with shovel, hammer, chisel and brush, and found some of the best specimens.

"Many students in the University and other local schools enthusiastically joined in the search. Classes in paleontology were held at the site where methods and purposes of collecting fossils were illustrated as they were described. Dozens of faculty members and other Princeton residents became temporary geologists and visited the dig which soon was dubbed 'the old aquarium.'"

Mr. R. V. Witter removed a number of large slabs from the fish layer which were subsequently split by Mr. Frank Goto, disclosing many hundred additional specimens. A number of these slabs show a maximum concentration of about 12 coelacanths per square foot on one bedding plane.

The fish fauna at the Princeton locality includes a rare palaeoniscoid, perhaps several species of *Semionotus*, some fragmentary remains of *Diplurus longicaudatus*, and the abundant specimens of the smaller coelacanth, at that time referred to *Osteopleurus*. Many specimens of the smaller form are in an unusually fine state of preservation, and much of the morphological detail described in this paper has been obtained from them.

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In 1857 (p. 45) Ebenezer Emmons described some isolated fish scales from the "Chatham series" of North Carolina, which he believed to be coelacanth and to which he applied the name *Rabdiolepis specious*. Later in that year, Isaac Lea reported on a fish scale found by him in 1855 at Gwynedd, Pennsylvania, which he referred to Emmons' genus and species. In 1860 (fig. 167) Emmons illustrated, without accompanying description, additional fish remains from the Triassic of North Carolina that are unquestionably coelacanthid. The scales in this figure are referred to a second species, *R. elegans*. The other remains are a basibranchial ossification or a urohyal and a pterygoid (upside down). The specimen represented in figure 166-5 is identified as an entomostracan, *Stylorhynchus unsymmetricus*, but it appears to be a coelacanth cleithrum.

These discoveries were not mentioned by Newberry (1888) or Eastman (1905, 1911) in their reports on the fishes of the Newark group, although Wheatley (1861) listed *Rabdiolepis* in a report on a Triassic bone bed at Phoenixville, Pennsylvania, and Cope (1875) mentioned it in a synopsis of the fossil vertebrates of North Carolina. Woodward (1891, p. 354) considered the scale ornamentation of *Rabdiolepis* to be somewhat similar to that of the Carboniferous osteolepid *Strepsodus*. In 1902 (p. 368) Hay, for reasons unknown, transferred *Rabdiolepis elegans* to the palaeoniscoid genus *Elonichthys*. Except for brief mention by several other authors, there has been no further consideration of the status of *Rabdiolepis* in the literature. Attempts to locate Emmons' specimens at several likely institutions have not been successful. The various scales and bones illustrated by him show a stong resemblance to similar structures in *Diplurus*, and none of them are definitely palaeoniscoid. In the absence of the actual specimens, however, *Diplurus* is not considered to be a synonym of *Rabdiolepis*. If and when the Emmons' specimens are found, this step may be necessary, but until that time *Rabdiolepis*, in the writer's opinion, must remain taxonomically indeterminate.

The writer is greatly indebted to Dr. G. L. Jepsen for the opportunity to describe the unusually fine coelacanth collection obtained on the Princeton University campus. These specimens include the best-preserved coelacanth skulls yet found in the Newark series and, with the possible exception of *Spermatodus*, in North America. A representative series of specimens has been presented to the American Museum. Dr. Jepsen's interest in the vertebrate fauna of the Newark series is also responsible for the discovery of the type of *Diplurus newarki* and the only specimen of a Newark hybodont shark, both from the Lockatong formation. The writer is also indebted to Dr. D. H. Dunkle for the loan of the skull of *Diplurus longicaudatus* from the collection of the United States National Museum.

The figures, based on camera lucida drawings, were prepared by Mr. John R. Le Grand, who also assisted in checking various observations and measurements. Except where noted, the figures of *Diplurus* are composite, and no scale is given. Dr. J. L. B. Smith kindly checked the drawings of the *Latimeria* skull in figures 14 and 15. The photographs were taken by Mr. Elwood Logan.

The following abbreviations have been utilized for catalogued specimens:

A.M.N.H., the American Museum of Natural History

P.U.G.M., Princeton University Geological Museum

U.S.N.M., United States National Museum

ENDOCRANIUM AND PARASPHENOID

THE PARASPHENOID OF *Diplurus* (fig. 1) has the general spatulate appearance found in most coelacanths. It is moderately constricted in its middle portion and is widest in the anterior half where the sides are slightly upturned. The dorsal surface is gently convex back to the constriction, where a slight median depression appears. This depression extends into the posterior half as a groove with its borders delimited by raised ridges. The ridges are essentially parallel for a short distance and then diverge slightly and increase in height to form a shovel-like extension that supports the basisphenoid. The extended portion is truncated posteriorly and is the narrowest portion of the bone.

The ventral surface of the parasphenoid is covered with granular teeth that are not restricted to an elevated tooth plate as in *Spermatodus* and certain other genera. The distribution of the teeth is more suggestive of the condition in *Axelia* (Stensiö, 1921). The center of ossification is located just behind the median constriction. There is no indication of a hypophysial opening such as Westoll (1939) describes for *Spermatodus*, but it may be small and nearly occluded.

The ethmoid ossification (ectethmoid; fig. 2) is either crushed or displaced in all the specimens in which it has been observed, and its relationships to the other snout structures are difficult to determine. The main body of the bone is divided into a narrow horizontal lamina from which projects caudally a relatively long, finger-like process, and a larger,
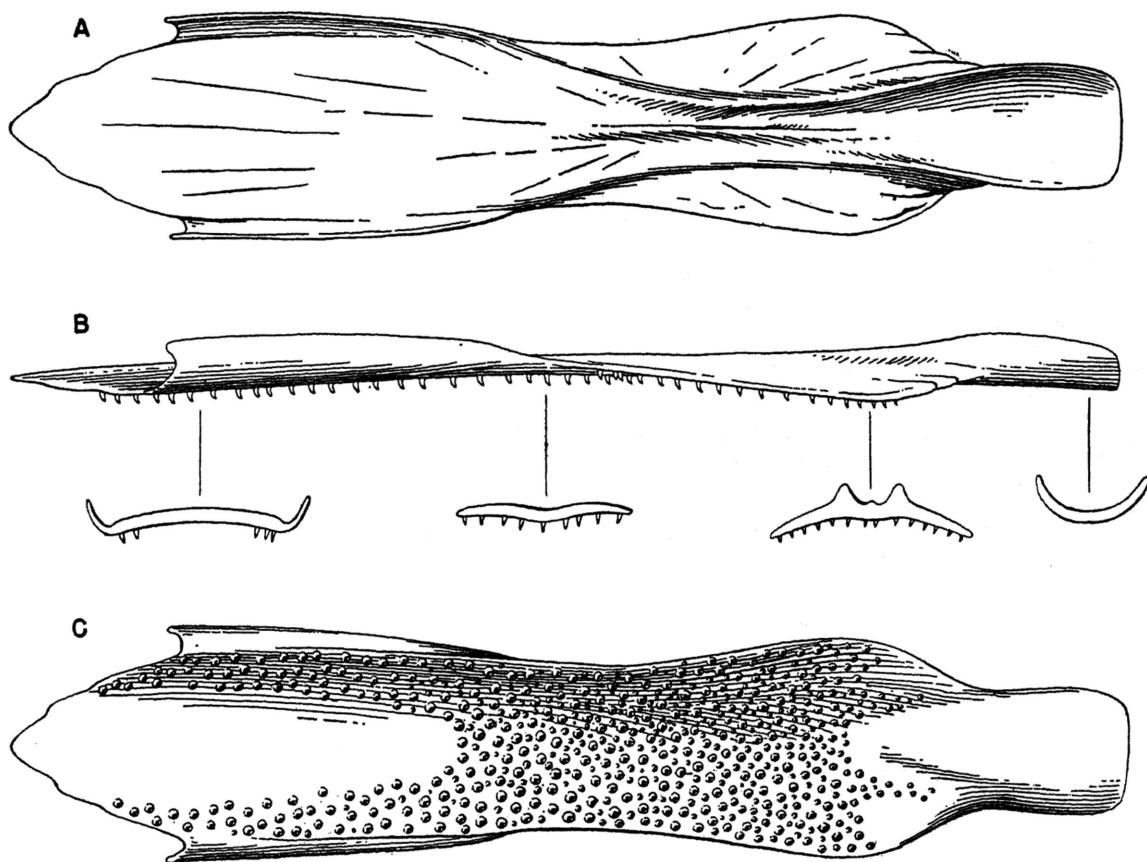

FIG. 1. *Diplurus newarki*. Parasphenoid. A. Dorsal view. B. Lateral view and cross sections. C. Ventral view.
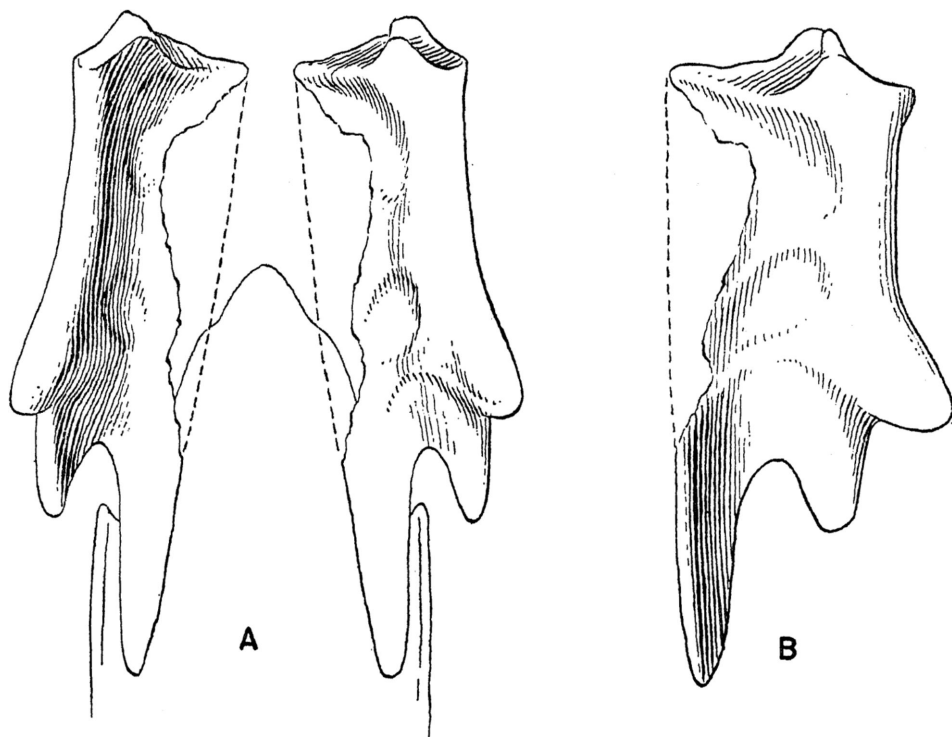
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FIG. 2. *Diplurus newarki*. Ectethmoid, based mainly on A.M.N.H. No. 9451.
A. Dorsal view. B. Median view. ×14.

more vertical lamina that terminates pos-teriorly in two short, diverging processes. The horizontal lamina apparently overlaps the anterior end of the parasphenoid, and the finger-like process fits into the lateral groove on the dorsal surface of the parasphenoid. A small concave facet on the anterodorsal bor-der of the vertical component presumably ar-ticulated with the lateral rostral bone (Niel-sen, 1936, fig. 14). According to Jarvik (1942), the ethmoid ossification in the Meso-zoic coelacanths forms part of the ventral and ventrolateral wall of the nasal cavity. Stensiö (1932, p. 30) has pointed out that the ectethmoid either has a direct articulation with the autopalatine or is situated immedi-ately anterior to some unkown autopalatine-ethmoid connection.

The basisphenoid ossification (fig. 3; pl. 16) has been removed in one specimen (A.M.N.H. No. 9458) and, although it is in-complete, most of the essential details are revealed. It is also preserved in several other specimens, but unfortunately not in natural association with the parasphenoid. In the

terminology of Westoll (1939), the basisphe-noid is composed of a ventral corpus that ar-ticulates with the parasphenoid, paired la-teral lamellae extending forward from the corpus, and paired antotic processes that ex-tend to the dermal skull roof. The antotic processes are joined along their anterior bor-ders by a bony bridge, called the dorsum sellae, that overhangs the pituitary fossa.

The posteroventral surface of the corpus is ovoid, with a rounded and elevated border. In the center of this area, as in *Spermatodus*, there is a small projection that may represent the termination of the notochord. Above the ovoid area, there is a pair of knob-like struc-tures which are very similar to those in *Spermatodus*. In dorsal aspect, the basisphe-noid of *Diplurus* approaches that of *Axelia* in the wide separation of the antotic processes. They are, however, considerably longer and more divergent than in the other genera in which they have been described. The proc-esses extend forward from the corpus as relatively long, flattened, ovoid, and hori-zontal laminae. On the anterior borders of
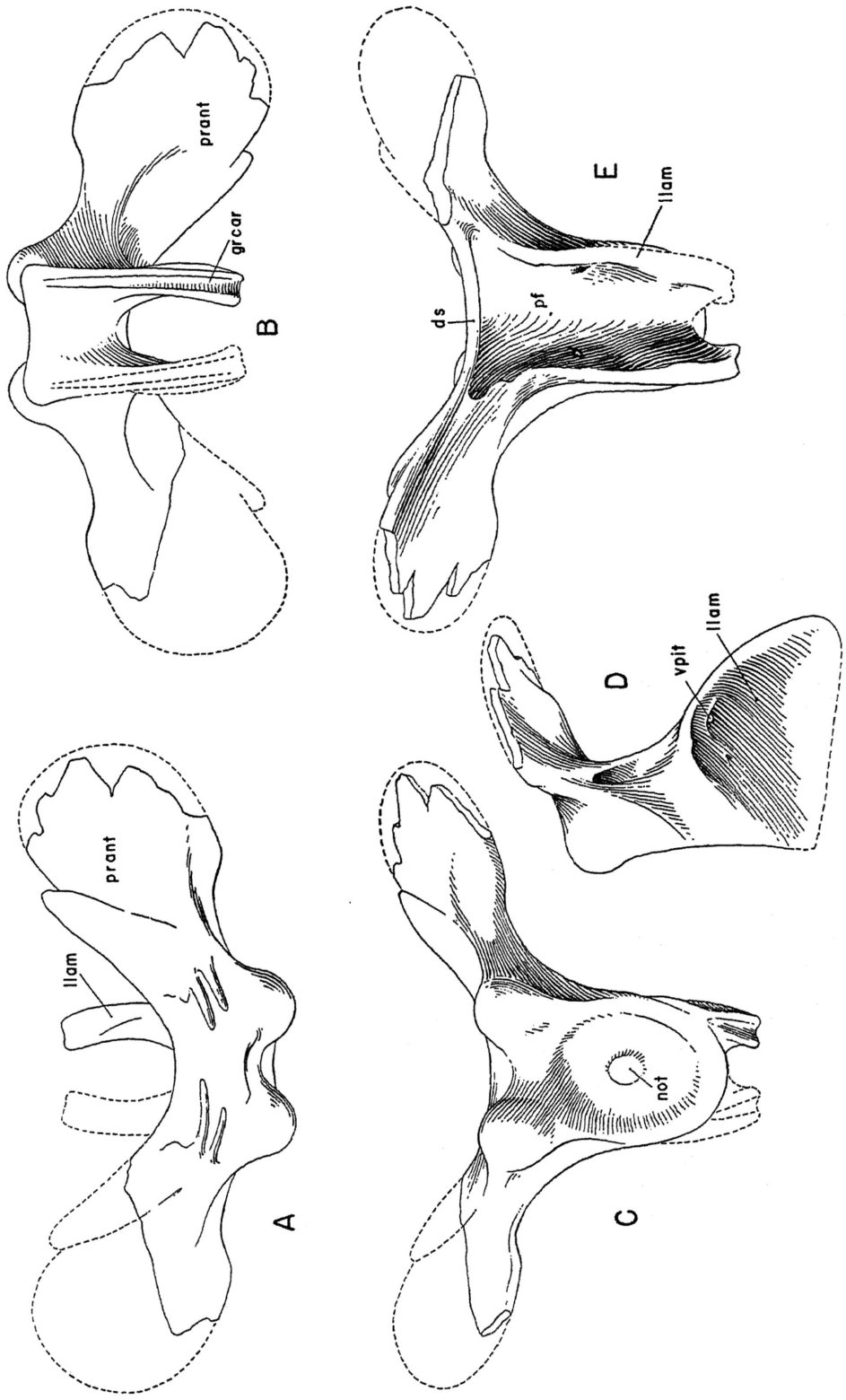
FIG. 3. *Diplurus newarki.* Basisphenoid, A.M.N.H. No. 9458. A. Dorsal view. B. Ventral view. C. Posterior view. D. Lateral view. E. Anterior view. ×9. For abbreviations used in illustrations, see page 78.

the antotic processes there are partially separated spurs that resemble the dorsal extensions of the lateral laminae in *Wimania* (Stensiö, 1921, fig. 22). In *Diplurus*, however, these spurs do not pass directly into the laminae but merge with the dorsum sellae. The nature of the articulation between the frontal processes ("alisphenoids") and the basisphenoid cannot be exactly determined. The situation in *Wimania* (*op. cit.*, fig. 20) suggests, however, that the frontal processes articulated with the spurs, while the antotic processes articulated directly with the frontals.

The lateral laminae are narrow dorsally but expand rapidly ventrally. The extent of their divergence and the nature of their ventral borders cannot be definitely ascertained because of crushing and fragmentation. In order to unite with the "shovel" of the parasphenoid, however, the laminae must have been curved somewhat as indicated in figure 3. A foramen pierces the lamina near its anterior border, about midway between the level of the dorsum sellae and ventral border. This is similar in position to a foramen in the *Spermatodus* lamella that serves for the passage of the pituitary vein (Westoll, 1939).

The pituitary fossa is shallow immediately under the dorsum sellae but increases in depth with the widening of the lamellae. There is no evidence that the floor of the fossa was produced by a bony forward extension of the corpus as in *Spermatodus*. On the ventral surface of the corpus there are lateral grooves that extend forward along the ventral borders of the lamellae. They are probably identical with similarly situated grooves in *Spermatodus*, which Westoll points out may have contained the internal carotid arteries. The basisphenoid was not fused with the parasphenoid.

Comparison of the coelacanth pituitary region with that of the rhipidistian reveals several differences. In *"Megalichthys"* (Romer, 1937), in addition to the greater ossification of the region, the dorsum sellae is not developed as an anterior projection from the bony wall between the pituitary fossa and the anterior notochordal attachment. If this is the primitive condition in crossopterygians, the so-called dorsum sellae in coelacanths may be a new development. Among the rhachitomous amphibians a dorsum sellae is apparently absent in *Edops* (Romer and Witter, 1942, fig. 10) but is present in *Eryops* (Sawin, 1941). As Romer and Edinger note (1942, p. 381), the pituitary fossae of *Edops* and *"Megalichthys"* compare very closely.

In the coelacanths the pituitary fossa presumably housed the saccus vasculosus, the pars intermedia, and the pars nervosa of the pituitary body. A large portion of the pars anterior, however, must have been situated in the groove on the dorsal surface of the parasphenoid, extending at least as far anteriorly as the region of the hypophysial opening in *Spermatodus*. Jarvik (1942, p. 607) has commented on the resemblance between the anterior part of the parasphenoid in the coelacanths and *Polypterus*. This resemblance includes the presence of a hypophysial opening and, to some extent, the configuration of the dorsal surface. The relationship of the pituitary to the parasphenoid in *Polypterus* is figured in longitudinal section by De Beer (1926, fig. 69).

The prootic ossifications are present in several specimens (pl. 7). In general they resemble the prootics of *Rhabdoderma* and *Wimania*, but their poor preservation prevents detailed consideration. There are no specimens that reveal the nature of the occipital ossifications, although apparently they were present.

DERMAL BONES OF SNOUT AND SKULL–ROOF

For the purpose of this discussion, the bone terminology of Moy-Thomas (1937) is employed, with only slight modification. The problem of dermal bone nomenclature in the coelacanth skull is considered at various places in the description and also in another section.

The dorsal surface of the snout (fig. 4; pl. 8) is covered by a mosaic of small rostral bones that occupy the area bounded by the lateral rostrals, the postrostrals, and the premaxillaries. The rostrals unfortunately have not been found in their natural position in any specimen, and consequently it is not

possible to determine their exact number or arrangement. There is a suggestion, however, of some large sensory pores in the snout area similar to those figured by Nielsen (1936) for the unnamed Greenland coelacanth.

The *Diplurus* lateral rostral,[1] as described for the unnamed Greenland form, can be divided into two parts: an anterodorsal process, and a marginal portion that extends along the upper jaw margin and contains the infraorbital sensory canal. The U-shaped opening between the anterodorsal process and the marginal portion resembles a similarly situated gap in the lateral rostral of *Latimeria* and of *Nesides* (Jarvik, 1942, fig. 77). The anterior part of the marginal portion has a medioventral expansion probably corresponding to the anteroventral lamina in *Diplocercides* (*ibid.*, p. 568) and to the ventral extension in the unnamed Greenland form (*ibid.*, p. 584), which meets the ectethmoid.

The anterodorsal process, according to Jarvik, abuts against the dorsal edge of the fenestra leading into the nasal cavity (in the Devonian forms with a fully ossified ethmosphenoid). Jarvik is of the opinion (*ibid.*, p. 605) that in coelacanths in general, the anterodorsal process divides the upper portion of the fenestra into openings for the anterior and posterior nasal tubes. In fossil coelacanths, he believes (*ibid.*, p. 589) that an anterior external nares was located just anterior to the anterodorsal process of the lateral rostral, while, as pointed out above, the two posterior external nares were in, or near, the posterior tectal. In 1921 Stensiö identified the openings in the "antorbital" of *Axelia* as anterior and posterior nasal apertures (= posterior nasal openings of Jarvik), and Nielsen (1936) concurred in this opinion on the basis of his investigation of *Whitea* and the unnamed Greenland form. Moy-Thomas (1937) figures two openings in the "antorbital" of the Madagascar *Whitea* but none in the "antorbital" of *Rhabdoderma;* he does not comment on the meaning of their presence or absence. Should Jarvik's observations regarding the location of the coelacanth external nares prove to be correct, it would appear to follow that in forms such as

Diplurus, which lack the "antorbital," the posterior narial opening, or openings, must be immediately behind the anterodorsal process, or else behind the anterior end of the lacrimo-jugal and in the anterior part of the orbit. In this connection, it is of interest to note that Watson (1921) regarded the large opening immediately above the posterior end of the lateral rostral in *Macropoma* as a sensory canal pore. Unfortunately, the available *Diplurus* specimens do not further elucidate this problem, nor do they confirm (Nielsen, 1936) or deny (Jarvik, 1942) the presence of internal nares.

The premaxillaries (fig. 4; pls. 8, 9) are small, dentigerous elements resembling those of the unnamed Greenland form (Nielsen, 1936, fig. 14). They are widest medially and taper almost to a point at their presumed attachment with the lateral rostrals. In one specimen (P.U.G.M. No. 14944) the premaxillaries are associated with the rostrals and appear to meet at the center of the upper jaw margin. Although the premaxillaries resemble the ectopterygoids of other coelacanths, their relationship with the rostrals does not favor such an identification. In another specimen (P.U.G.M. No. 14943), one premaxillary is preserved, again in association with the rostrals. Here the posterior end of this element is shoved under the anterior portion of the lateral rostral. The premaxillary in the unnamed Greenland form articulates with the ventral extension on the marginal portion of the lateral rostral, and such may be the case in *Diplurus.*

The cranial roof (fig. 4; pls. 10, 11) is variously preserved in about a dozen specimens, and in several of these it is possible to observe the number and arrangement of the individual bones. The fronto-ethmoidal shield is composed of two pairs of frontals and one pair of postrostrals. These elements lack ornamentation of any kind but occasionally show suggestion of growth ridges, indicating the position of the ossification centers. The free edges have shallow embayments, one for each of the supraorbitals.

The postrostrals are firmly incorporated into the skull roof. They are of variable size, depending on the nature of the anterior frontals, and in several specimens they are partially divided by incomplete, transverse su-

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[1] Westoll (1943a, p. 90) objects to Jarvik's name "lateral rostral" in the osteolepids on the basis that the bone in question is not a rostral but rather a "prenarial."
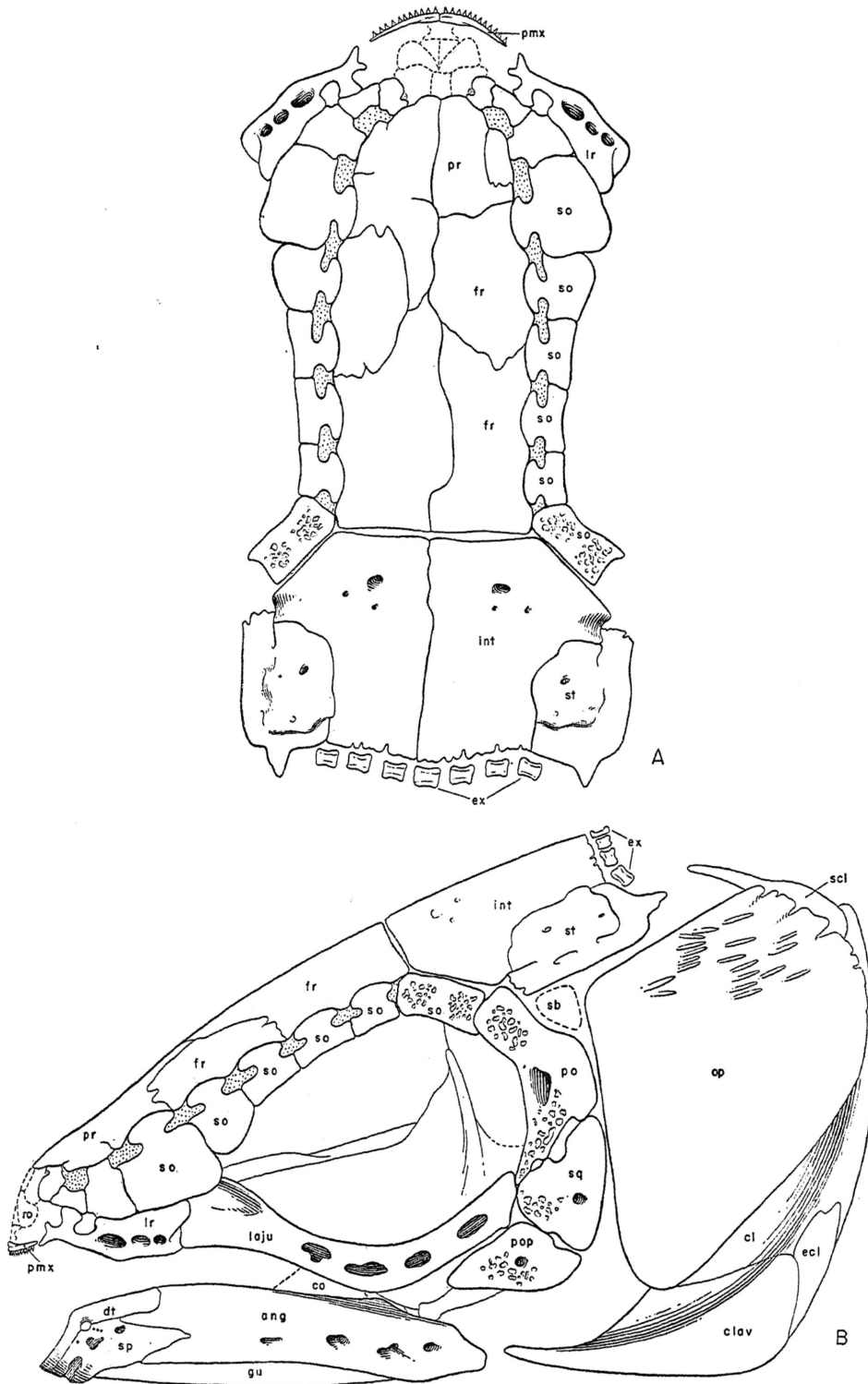
FIG. 4. *Diplurus newarki*. Reconstruction of the skull and shoulder girdle. A. Dorsal view of skull roof flattened to include snout region. B. Lateral view. For abbreviations used in illustrations, see page 78.
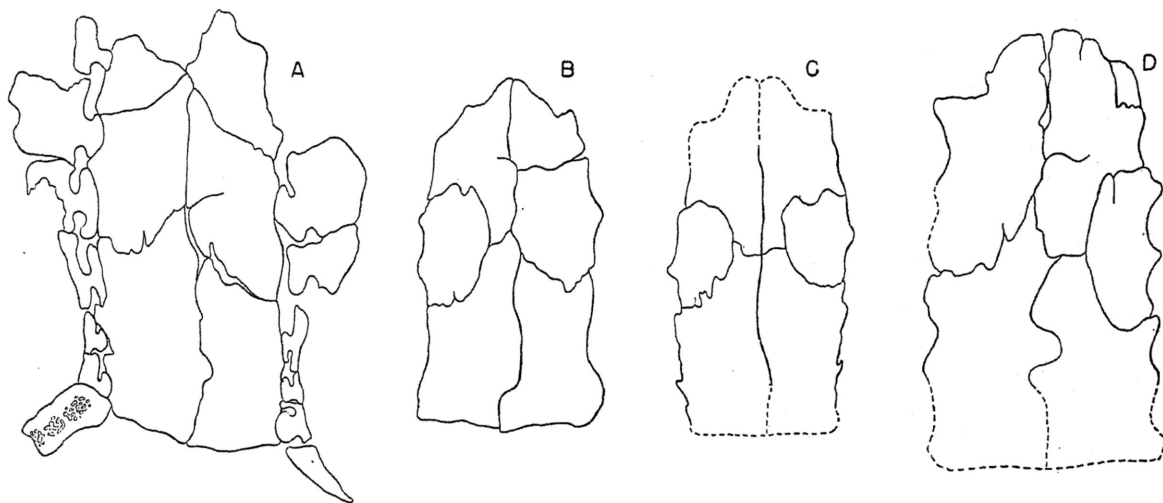
FIG. 5. *Diplurus newarki.* Variation in the bone pattern of the fronto-ethmoidal shield. A. A.M.N.H. No. 9452, including the supraorbitals. B. A.M.N.H. No. 9455. C. P.U.G.M. No. 14939. D. A.M.N.H. No. 9451.

tures. The so-called anterior frontals are also variable in size, shape, and number (fig. 5). They may or may not meet along the middorsal line of the skull roof. In several skulls, both are excluded from the middorsal line, while in at least two other specimens only one bone is excluded, with the postrostral and the posterior frontal meeting. When the anterior frontals do not meet at the middorsal line, they appear to be relatively smaller than either the postrostrals or the posterior frontals. The posterior frontals are the largest elements in this series and, like the others, are longer than wide.

The frontals and the postrostrals are preserved in ventral aspect in one specimen (P.U.G.M. No. 14926, pl. 14). Although the sutures are obscured, it is evident that there are low and essentially parallel ridges extending the full length of the anterior and posterior frontals, close to their lateral borders. These ridges increase in depth caudally and are extended beyond the posterior limits of the shield as distinct processes. Similar processes, but apparently without the elongated ridges, have been described for *Wimania* and *Axelia* (Stensiö, 1921), *Mawsonia libyca* (Weiler, 1935), and *Latimeria* (Smith, 1939). In *Diplurus*, the ridges and processes are fused with the frontals, and there is no indication that they represent separate ossifications, as

Smith states is the case in *Latimeria*.

On the basis of their relationship with the posterior frontals and presumably with the antotic process of the basisphenoid, each of these projections must represent the "alisphenoid" (Stensiö ,1921), or the "alisphenoid ridge" (Stensiö, 1932) or the "ventral process of the fronto-dermosphenotic, which represents the dorsal half of the alisphenoid swelling" (Holmgren and Stensiö, 1936). It does not seem probable that they are derived from any portion of the alisphenoid swellings in, for instance, *Dictyomosteus* (Holmgren and Stensiö, 1936, fig. 265), which is now considered to be a coelacanth (Jarvik, 1942) rather than a rhipidistian. In *Diplurus*, at least, they appear to be simply ventral projections of the posterior frontal that have become enlarged to abut against the basisphenoid, thus functionally uniting this portion of the fronto-ethmodial shield with the braincase.

As here defined, the supraorbital series consists of seven elements. The posterior member of the series is essentially rectangular and joins the frontal only at its anteromedian corner. The median border of this bone, as in *Laugia*, is in contact with the intertemporal and the posterior border with the postorbital. In 1921, Stensiö identified this bone as the dermosphenotic (or dermal postfrontal) of

the rhipidistian skull. Nielsen (1936) has pointed out that, in *Whitea*, is does not contain the dorsal portion of the infraorbital canal, and he therefore regards it as the posterior member of the supraorbital series. He believes that the dermosphenotic has been incorporated into the intertemporal. Stensiö (1937) and Westoll (1939) concur in this opinion. Weiler (1935) considers the dermosphenotic of *Mawsonia libyca* to be fused with the frontal, while Saint-Seine (1949) believes it is a separate bone in *Undina*. Moy-Thomas (1937) called the posterior circumorbital the dermosphenotic in both *Rhabdoderma* and *Whitea*, apparently on the basis that it includes the branching of the infraorbital canal. De Beer (1937, p. 498) points out that in fishes there is no evidence that the so-called dermosphenotic was ever the "dermal representative" of the sphenotic and that, whatever its fate, it should be called "postfrontal." It seems desirable, in the present state of knowledge, to follow Nielsen and call the posterior element of the supraorbital series a supraorbital.

The other supraorbitals are deeply notched on their anterior and posterior borders, with adjacent notches forming ovoid sensory canal apertures that are open dorsally to the lateral margins of the frontals. This is merely a variation of the more usual coelacanth condition, in which the borders of the supraorbital sensory canal pores are formed to a greater extent by the frontal. Isolated supraorbitals show a transverse groove between the pores, which must have formed part of the supraorbital canal. A similar groove has been described by Nielsen (1936) for the unnamed coelacanth from the Triassic of East Greenland. In this form, both the lateral borders of the frontals and the opposing borders of the supraorbitals have dorsal and ventral lamellae that meet to form a canal. The presence of a groove on the frontals of *Diplurus* is not in clear evidence.

An "antorbital," similar to the one in *Rhabdoderma* and *Whitea*, is absent in all specimens in which the cheek region is well preserved. The largest member of the supraorbital series, which is situated at the anterior corner of the orbit, articulates directly with the lacrimo-jugal as in *Undina* and *Macropoma*. Saint-Seine (1949) states specifically

that the "antorbital" is absent in *Undina*, and it is evident that the pattern of the "antorbital area" is subject to considerable variation among the genera in which it is known. The supraorbital which is in contact with the lacrimo-jugal in *Diplurus* lacks the openings considered to be posterior narial apertures by Jarvik (1942), and their exact location cannot be determined. In front of the supraorbital just mentioned, there is a smaller, similarly shaped bone which is part of the supraorbital series but is excluded from the orbital margin. It is equivalent to one of the nasals of *Whitea* (Nielsen, 1936) or to the tectals as defined by Jarvik. In addition, there is a small bone filling an embayment in the anterolateral corner of the postrostral, which may be in the same series, although there is evidence that it is fused with postrostral in some specimens.

In 1937 Westoll pointed out that the "antorbital" of *Amia* is associated with the ethmoid commissure and the infraorbital sensory canal, which is not the case in the rhipidistians. He believes, therefore, that the name "antorbital" has been incorrectly used for certain bones in the rhipidistian skull. Jarvik (1942) agrees with this conclusion and introduces the term "tectal" for the bones that are situated on the roof of the nasal cavity (tectum nasi). He regards them as dermal bones not related "primarily" to any sensory canals (*ibid.*, p. 249) and defines the tectals (*ibid.*, p. 351) as a "series of bones in the anterior prolongation of the series of supraorbitals." Jarvik points out that, in coelacanths, the posterior tectal contains the posterior nares. In *Latimeria*, however, he believes that the posterior nares are excluded from the posterior tectal because of a reduction in its ventral portion. In this genus the posterior tectal (Jarvik, 1942, fig. 35) is associated with the supraorbital canal. The bone that has been named "antorbital" in *Rhabdoderma* and *Whitea* (Moy-Thomas, 1937) is not a sensory canal element but is nevertheless regarded by Jarvik as the posterior tectal. The Devonian *Nesides* (Stensiö, 1937) has an "antorbital" in the same position as that of *Whitea*, and it lacks a sensory canal association. Jarvik states (*ibid.*, p. 351, footnote) that in later coelacanths the posterior tectal may have a secondary association with

the supraorbital sensory canal by fusion of this element with an adjacent supraorbital.

The "parietal" shield of *Diplurus* has the typical coelacanth complement of paired intertemporals meeting in the middorsal line and paired posterolateral supratemporals. The intertemporals are unusual in attaining their greatest width a short distance behind the fronto-ethmoidal shield and in having this dimension almost equal to their greatest anteroposterior length. A large pore near the anterior border of each intertemporal has about the same position as the terminus of a transverse branch of the supraorbital canal in *Laugia* and the Greenland *Whitea*, which Nielsen (1936, figs. 11, 12) identifies as the anterior pitline in the latter. From the region of this pore, which is apparently close to the center of ossification, several low ridges radiate posteriorly, one usually extending onto the supratemporal. The posterior borders of the intertemporals, when preserved, show a distinct and irregular indentation.

The nearly rectangular supratemporals fit into wide embayments in the intertemporals and have about the same relationships with these elements as in *Whitea*. The posterior borders, except for blunt projections, do not extend beyond the limits of the intertemporals. The dorsal surface of the supratemporals has a somewhat thickened and irregular central area, presumably associated with the sensory canal, which is surrounded laterally and posteriorly by a narrow border of smooth bone.

A longitudinal perpendicular lamella such as Stensiö (1921) found on the ventral surface of the intertemporal in *Wimania* and *Axelia* is absent in *Diplurus* (pl. 14). In both *D. newarki* and *D. longicaudatus* (P.U.G.M. No. 14955) there is a strong ridge arising near the anteromedian corner of the intertemporal, which extends obliquely to the lateral border immediately in front of the supratemporal embayment. In *D. longicaudatus* (pl. 15), it also extends along the entire length of the lateral border of the embayment. At the place where the ridge meets the anterior border of the supratemporal, it is enlarged and subdivided but does not appear to extend onto the supratemporal. It was perhaps here that the "parietal" shield was connected with an anterior dorsal process of the prootic as in *Rhabdoderma* (Moy-Thomas, 1937, fig. 3). The apparent absence of an ossified perpendicular lamella on the intertemporal and the supratemporal of *Diplurus* is an unusual condition. The lamella is well developed in *Rhabdoderma*, *Undina* (Aldinger, 1930), *Macropoma* (Watson, 1921), and *Latimeria* (Smith, 1939).

The extrascapulars are reduced to small ossifications surrounding the supratemporal commissural canal. They were probably not in direct contact with the "parietal" shield, although in several specimens they are preserved on top of the shield along its posterior border.

CHEEK REGION

The lacrimo-jugal, as in other coelacanths, forms the entire ventral border of the orbit. The front end is expanded and grooved much as in *Macropoma*. It extends forward below the largest supraorbital to meet the posterior border of the lateral rostral. The posterior end, which is but little expanded, meets the postorbital and the squamosal at their junction, about as in *Laugia*, *Undina*, *Macropoma*, and *Latimeria*.

The postorbital bone is long and narrow, with a relatively small, rounded expansion midway along the posterior border. The sensory pores are deep and relatively large. Because of the large posterior supraorbital, the contact between the postorbital and the intertemporal is greatly reduced; the posterior supraorbital extends almost to the anterior border of the supratemporal. The presence of a spiracular bone (suprasquamosal) is indicated in several specimens, but its shape or size cannot be determined.

The squamosal and preopercular are roughly triangular. The squamosal has an irregular outline and contains large sensory canal pores. The anterior border of the preopercular extends along the posteroventral border of the lacrimo-jugal, although these elements may not have been in actual contact. There is no positive indication of a

subopercular. A portion of the ceratohyal frequently underlies the place where this element should be situated, and it is difficult to distinguish between a possible subopercular and a fractured portion of the ceratohyal.

The opercular has a straight anterior and an almost straight dorsal border. The rounded posteroventral border is frequently crenate locally, in association with low radiating striae. This type of ornamentation, when present, is always confined to the posterior border. The striae, however, may have a more general distribution. In a few specimens of *D. newarki* from the Princeton locality, there are five to 20 short ridges on the dorsal half of the opercular and, according to Shainin (1943), some specimens of this species from Granton may have sparsely distributed tubercles. Operculars of *D. longicaudatus*

from North Bergen, Princeton, and Virginia are heavily ornamented with ridges. The "fine granulations" on the opercular reported by Bryant (1934) for the type specimen of *D. newarki* from North Wales are actually granulations in matrix over the opercular region. The variations in opercular ornamentation of *D. newarki* are clearly not of taxonomic significance.

The sensory canals, as in most coelacanths, are wide, and many of the sensory pores, particularly on the lateral rostral, lacrimo-jugal, postorbital, and angular are large. The canals appear to be arranged in the typical coelacanth pattern (fig. 14G), although the preservation of the bone does not permit their preparation. The relationship of the posterior supraorbital to the infraorbital canal has not been determined.

VISCERAL SKELETON

The palatoquadrate complex is preserved in lateral and medial aspect in a number of specimens from the Princeton locality (fig. 6; pls. 7, 13, 14, 15). In the light of this material, it is evident that the previously published restoration of the pterygoid of *D. longicaudatus* (Schaeffer, 1948), which was based on several badly crushed specimens, is incorrect in several details.

The pterygoid (endopterygoid) may be divided into an anterior horizontal limb and a posterior vertical limb. The angle between the two limbs is roughly 130 degrees, making it wider than in any other figured coelacanth pterygoid. The lateral surface of the horizontal limb is bordered ventrally by a strong, rounded ridge that continues along the posterior edge of the vertical limb. Another somewhat stronger but narrower ridge branches from the vertical one and runs obliquely to the anterodorsal corner of the vertical limb immediately in front of the metapterygoid. The extensive development of the lamina in front of and above the ridges, particularly on the vertical limb, appears to be characteristic of *Diplurus* and can be duplicated in only a few other genera such as *Axelia*.

The external pterygoid ridges have essentially the same orientation in all coelacanths and are better developed than any comparable

ridges on the rhipidistian pterygoid. They apparently evolved in association with the metapterygoid-antotic articulation, which is peculiar to coelacanths, and with the reduction of the basipterygoid process. The size and arrangement of the ridges are probably related to the distribution of forces between the antotic, quadrate, and palatine articulations. From a functional point of view, it would seem that the angle between the vertical and horizontal pterygoid ridges is more important than that between the vertical and horizontal limbs. The ridge angle, which is less than 90 degrees in *Diplurus*, is in fairly close agreement with the similar angle in a number of other genera, such as *Rhabdoderma, Coelacanthus, Wimania, Macropoma,* and *Latimeria*.

The medial surface of the horizontal limb is covered with granular teeth, which extend to the dorsal border.

The metapterygoid (epipterygoid) articulates with the lateral surface of the pterygoid. The antotic facet of the metapterygoid, which is well preserved in P.U.G.M. No. 14942, is narrow anteroposteriorly and overhangs both the medial and the lateral surfaces of this element. It slopes somewhat medially, in confirmation with the orientation of the antotic process. The anterior border of the metapterygoid forms a ridge which is parallel
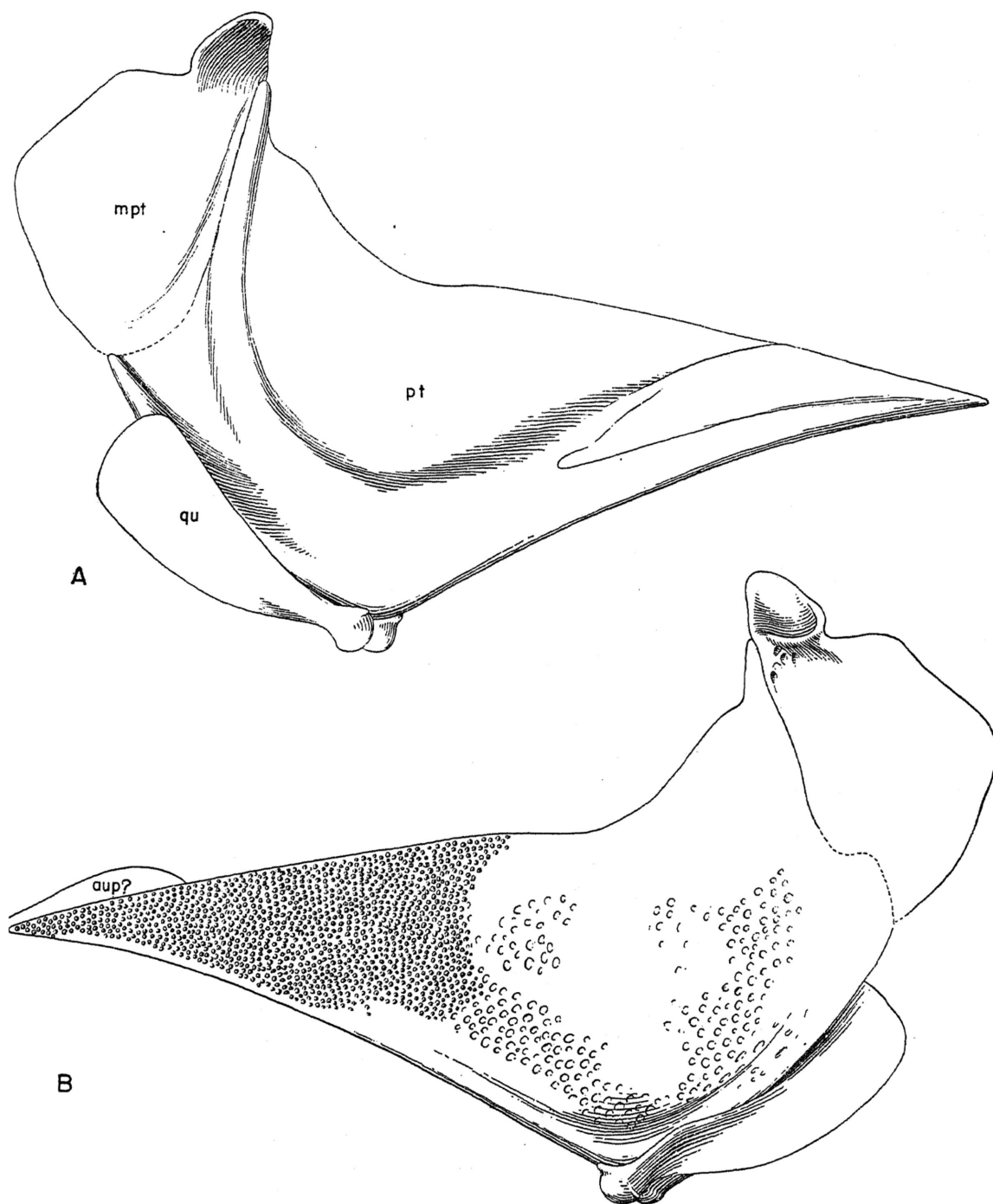
FIG. 6. *Diplurus newarki*. Palatoquadrate complex. A. Lateral view. B. Median view, based mainly on
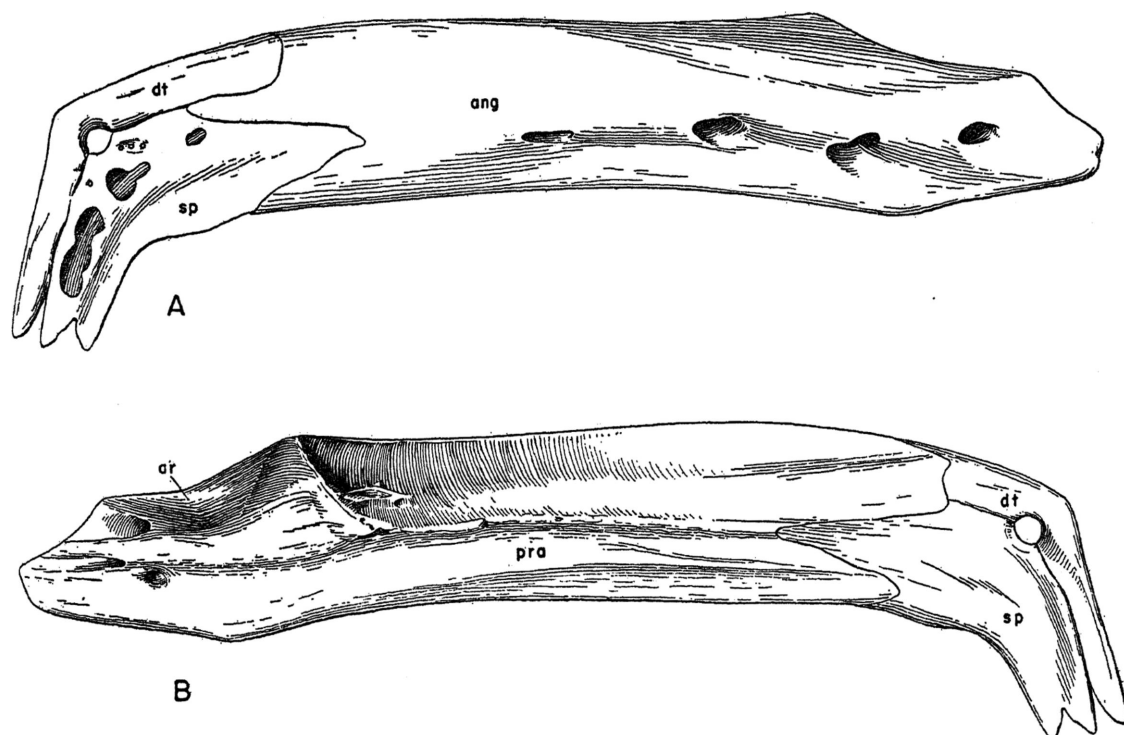P.U.G.M. No. 14942. For abbreviations used in illustrations, see page 78.

FIG. 7. *Diplurus newarki*. Lower jaw, lacking coronoid, with the dentary and spenial flattened as usually preserved. A. Lateral view. B. Median view. For abbreviations used in illustrations, see page 78.

to, and immediately behind, the anterior vertical ridge of the pterygoid.

The quadrate of *Diplurus* is triangular and is in contact with most of the posterior margin of the pterygoid. The condyles are separated from the rest of the bone by a marked constriction and project slightly below the ventral border of the pterygoid. An external ridge of the lower half of the quadrate overlaps the lower posterior border of the pterygoid. There is no evidence of a cartilaginous connection between the quadrate and the metapterygoid, as Stensiö (1921) has postulated for *Axelia*. About one-third of the outer surface of the quadrate is overlapped by the pterygoid, in contrast to the usual coelacanth condition where the superposition is more complete.

The autopalatine has not been identified, unless it is represented by a structure at the front end of the pterygoid, which has a low, rounded, dorsal border and appears to be partly fused with the pterygoid.

In several specimens a long, slender bone

(pl. 9, fig. 1, pl. 13, fig. 1) with a rounded anterior end is situated below the ventral border of the anterior pterygoid limb. It tapers gradually to a point posteriorly. From its position it would appear to be the ectopterygoid. The surface that is exposed lacks teeth, although they are present on the probable ectopterygoid of P.U.G.M. No. 14918a (pl. 5, fig.1). Other small, disassociated, tooth-bearing bones are present in some specimens, which very probably represent the dermopalatines.

The short lower jaw (fig. 7) is composed of a distinctly shaped dentary and splenial, a relatively large angular, a prearticular, and an articular which appears to be fused with both the angular and the prearticular. The dentary may be divided into two rami that meet in a wide angle. The posterior ramus is toothless and overlaps the angular for a short distance. The anterior, as preserved, is consistently directed downward along with the main body of the splenial. At the junction of the two rami, there is a large semicircular

notch that is completed ventrally by the splenial to form a large opening of undetermined significance. In one specimen there is a suggestion of minute teeth on the anterior portion, but their presence is by no means certain. The splenial has somewhat the same shape as the dentary but is broader and has a V-shaped articulation with the angular. There are three or more large pores on its outer surface for the mandibular sensory canal.

In several specimens there is evidence that the downturned portions of the dentaries and splenials were curved medially in life to form a U-shaped anterior jaw margin. If so, the anterior portion of the dentary and the corresponding portion of the splenial would have an almost horizontal orientation. There is no evidence that the rostral area was extended ventrally to produce a mormyrid-like snout, a fact also favoring this sort of articulation. It does seem probable, however, that there was some sort of upper labial fold that fitted into the trough-like depression in the lower jaw. Although the dentaries and splenials of *Diplocercides* and *Whitea* have a different shape, the front part of the lower jaw probably had a somewhat similar trough-like structure. In both these genera, the dentary rises sharply from the symphysis and then slopes more gradually until it meets the angular. In anterior view, the opposite dentaries would form an open U. In *Whitea* (as restored by Moy-Thomas, 1937) there is no conformity between the orientation of the premaxillary and dentary margins, in contrast to the situation in *Latimeria*, and presumably in *Macropoma* and *Undina*. No exact counterpart of the *Diplurus* condition has been found in living fishes with jaws of comparable length. The gymnotid *Eigenmannia* has a similar trough arrangement that involves the entire dorsal margin of the lower jaw. Since the mandibles are very short in this genus, the occlusion presents no particular problem.

The outer surface of the *Diplurus* angular is smooth and slightly convex dorsoventrally. There are four large sensory canal pores distributed along the posterior surface. The medial surface, between the dorsal border and the angular-prearticular contact, is concave as in *Diplocercides* (Stensiö, 1937). This concavity is probably the adductor fossa

(*ibid.*, fig. 7). The junction between the angular and the prearticular is represented by a longitudinal ridge that turns dorsally to define the posterior limit of the fossa.

The posterior limit of the prearticular cannot be accurately determined. There is some evidence, however, that it extends all the way to the posterior border of the mandible, thus covering the lower portion of the articular. A narrow, shallow groove is present on the anterior half of the prearticular which is immediately below, and parallel to, the adductor fossa. The quadrate facet on the articular is shallow and poorly defined. Immediately behind the facet, there is a large foramen that leads into a large canal, suggesting that the foramen may be the entrance for N. mandibularis VII. This foramen is in essentially the same position as a depression on the articular of *Diplocercides* (Stensiö, 1937, pl. 3), which Smith (1939) believes may be a "symplectic" articulation resembling the one in *Latimeria*. Stensiö does not discuss the meaning of this depression in *Diplocercides*; there is no evidence of a double lower jaw articulation in *Diplurus*.

The posterior coronoids were loosely attached to the dorsal borders of the prearticulars and have not been observed in place. In A.M.N.H. No. 9451 (pl. 7) two isolated triangular bones are probably these elements. Precoronoids have not been found.

In most coelacanths the articulation of the lower jaw is situated below the preopercular (fig. 14), and the quadrate is in a nearly vertical position. The unusually short mandible of *Diplurus* implies that the articulation in this genus was in front of the preopercular and that the quadrate was inclined forward.

The hyoid arch in *Diplurus* consists only of the ceratohyal (pl. 7, pl. 9, fig. 1). It agrees in most details with the same element described for such genera as *Wimania*, *Axelia*, and *Undina*. The truncated posterior end is about twice as broad as the anterior. The ventral process is lobate and is skewed posteriorly. The presence of other hyoid ossifications, such as the epihyals described by Stensiö (1921) in *Wimania*, cannot be demonstrated.

The gill skeleton is well preserved in one specimen of *D. newarki* (A.M.N.H. No. 9456; fig. 8; pl. 12, fig. 2) and also in a speci-
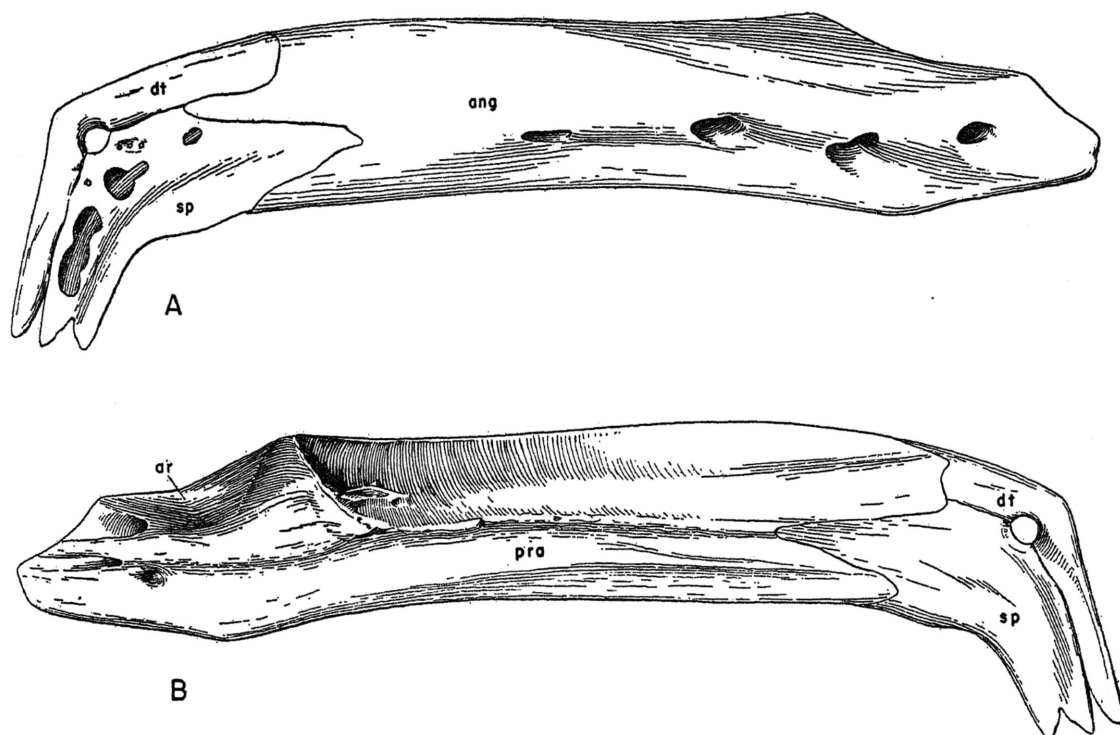
FIG. 7. *Diplurus newarki.* Lower jaw, lacking coronoid, with the dentary and spenial flattened as usually preserved. A. Lateral view. B. Median view. For abbreviations used in illustrations, see page 78.

to, and immediately behind, the anterior vertical ridge of the pterygoid.

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The short lower jaw (fig. 7) is composed of a distinctly shaped dentary and splenial, a relatively large angular, a prearticular, and an articular which appears to be fused with both the angular and the prearticular. The dentary may be divided into two rami that meet in a wide angle. The posterior ramus is toothless and overlaps the angular for a short distance. The anterior, as preserved, is consistently directed downward along with the main body of the splenial. At the junction of the two rami, there is a large semicircular
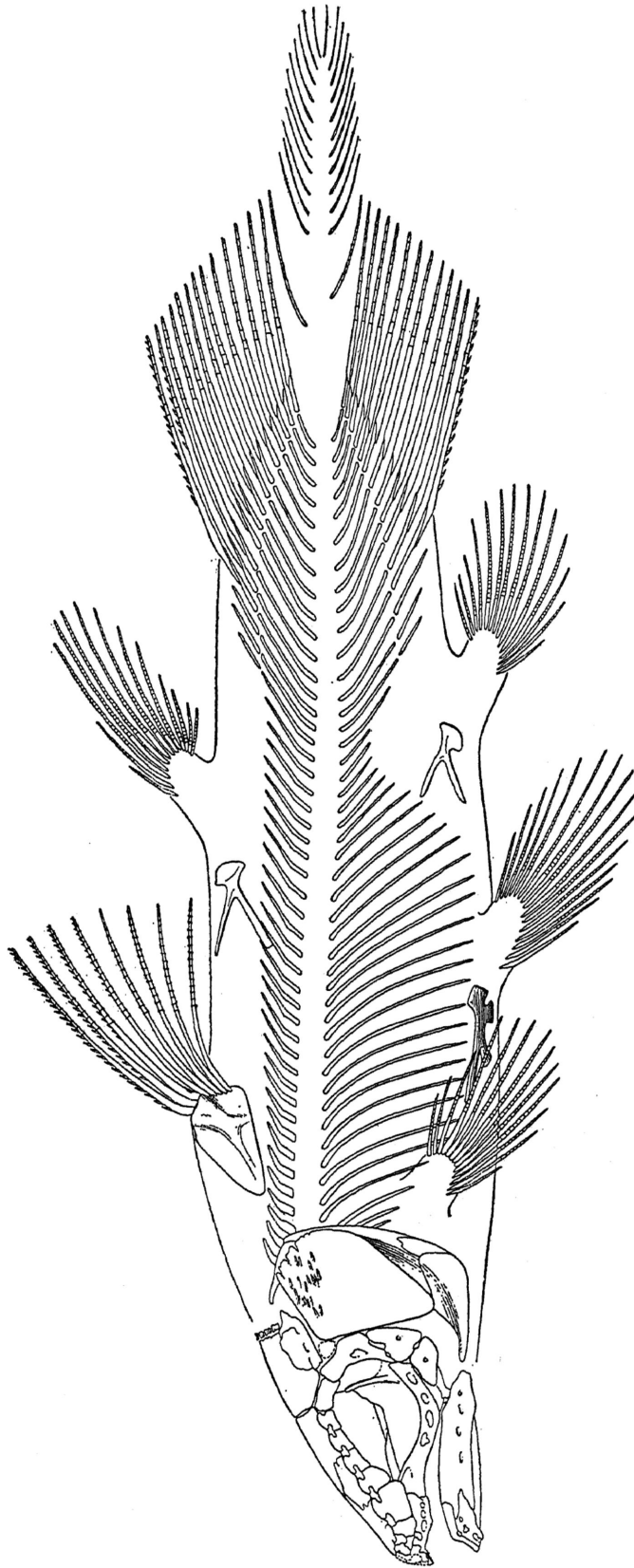
Fig. 9. *Diplurus newarki*. Reconstruction of entire skeleton, based on the proportions of individuals about 10 to 12 cm. in over-all length.

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in cross section, with a grooved posterior surface. The inner surfaces of the ceratobranchials are covered with one or more rows of fine teeth, apparently attached directly to the arch.

AXIAL SKELETON

The axial skeleton, with the exception of the long ribs, is typically coelacanthid and does not require full description. There are about 46 neural arches in *D. newarki* and perhaps 50 in *D. longicaudatus*. In spite of the abundant material of the smaller species, it is difficult to obtain an accurate count of the arches, and this number may be somewhat closer to that obtained for *D. longicaudatus*. The number of arches for most genera has not been recorded, and no information is available on the amount of variation at the individual, specific, or generic levels. On the basis of the published figures, there are about 71 neural arches in *Coelacanthus granulatus* (Moy-Thomas and Westoll, 1935), 59 in *Laugia* (Stensiö, 1932), and 63 in *Macropoma mantelli* (Woodward, 1909).

The anterior eight or 10 neural arches in *Diplurus* are relatively broad and have short spines as in *Laugia*. In the center of the column, the spines are about twice the height of the arches, and in the caudal fin three times that height.

The greatly elongated pleural ribs of *Diplurus* are apparently peculiar to this genus. The functional significance of this elongation is obscure (see Schaeffer, 1948, p. 8). There are about 28 or 30 pairs of ribs; the last five or six are short and were apparently directed caudoventrally in the same manner as the haemal spines. The change from pleural rib to haemal arch is apparently abrupt, as in *Ceratodus*. The ribs are nearly round in cross section and are solidly ossified, in constrast to the neural arches and haemal spines. Basiventral ossifications are absent.

GIRDLES AND PAIRED FINS

The pectoral girdle of *Diplurus* consists of a clavicle, cleithrum, extracleithrum, and supracleithrum (anocleithrum of Jarvik, 1944). In the rhipidistian shoulder girdle, according to Jarvik, there is a bone between the anocleithrum and the posttemporal (suprascapular), which he calls the supracleithrum. The presence of this element in the coelacanth girdle has not yet been conclusively demonstrated, and there is no indication of it in *Diplurus*.

The clavicle consists of a horizontal lamina, which presumably met its fellow of the opposite side anteriorly, and a thin, external, vertical lamina, which increases in depth and curves medially as it approaches the cleithrum.

The cleithrum is typically narrow dorsally, although the ventral part is unusually wide in lateral aspect for a coelacanth cleithrum. Extending medio-anteriorly from the outer anterior margin there is a broad, concave lamina, which resembles the medial lamina of the *Acipenser* cleithrum. *Diplocercides* has a similar but much narrower "anterior face"

(Stensiö, 1937, fig. 19). As in *Acipenser*, this lamina presumably formed part of the posteroventral wall of the branchial chamber. On the median surface of the cleithrum there is a narrow vertical groove, the dorsal portion of which is covered by a thin layer of bone. The canal thus formed ends blindly, about at the junction of the dorsal and ventral portions (fig. 10B; pl. 13, fig. 3). A similar groove and canal are present in *Latimeria*, involving the clavicle and extracleithrum as well as the cleithrum (Smith, 1939, pl. 31). They are also present in a coelacanth cleithrum from the Upper Moenkopi formation figured by Welles (1947, fig. 38, A).

The extracleithrum is oblong, pointed at both ends, and divided on its outer surface by a low curved ridge that passes from the anterodorsal to the posteroventral border. The area that is dorsal to the ridge fits into a similarly shaped depression on the posterior border of the cleithrum. This depression is also present on the Moenkopi cleithrum. The ventral portion is apparently overlapped by the clavicle to a far greater extent than in,
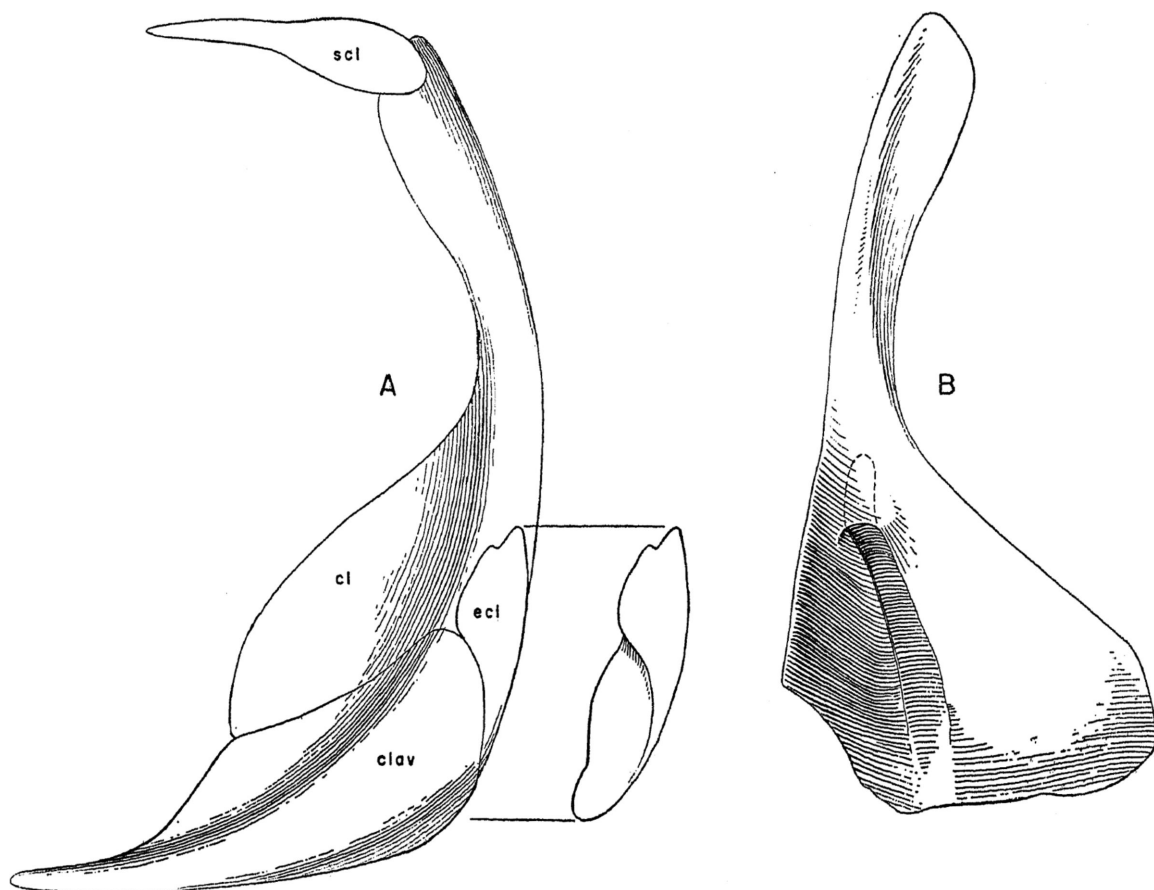
FIG. 10. *Diplurus newarki*. Shoulder girdle. A. Reconstruction of entire girdle in lateral view, extra-cleithrum shown in position and isolated. B. Cleithrum in median view.

for instance, *Latimeria*, and very little of it is exposed laterally. The extracleithrum is thus associated with both the cleithrum and the clavicle as in *Latimeria*, rather than only with the cleithrum as in *Coelacanthus* (Moy-Thomas and Westoll, 1935).

The supracleithrum, or anocleithrum, is a wedge-shaped bone, widest where it is in contact with the cleithrum and acuminate anteriorly.

The pectoral fin presumably was attached to the unossified endoskeleton at the upper limit of the extracleithrum. It consists, in *D. newarki*, of about 13 rays, most of which are segmented for over one-half of their length; the pectoral of *D. longicaudatus* has about 19 rays.

The pelvic girdle (fig. 11C) of *D. newarki* is very similar to that described for *D. longi-*

caudatus (Schaeffer, 1948). The median process is perhaps relatively shorter, and there is no indication that it has a denticulated median border. These apparent differences, however, may be due to the less satisfactory preservation of the pelvic elements in *newarki*. A reëxamination of the impression of a pelvic plate described by Shainin (1943) from the Granton locality indicates that it has two anterior apophyses rather than three; it resembles the one here figured in all essential details. The elements identified as pelvic plates in the type specimen of *D. newarki* (pl. 6, fig. 1) from the North Wales locality have been regarded as quite distinct for those found at Granton (Shainin, 1943). Unfortunately there is only one specimen from North Wales showing these structures. In an individual of about the same size from Prince-
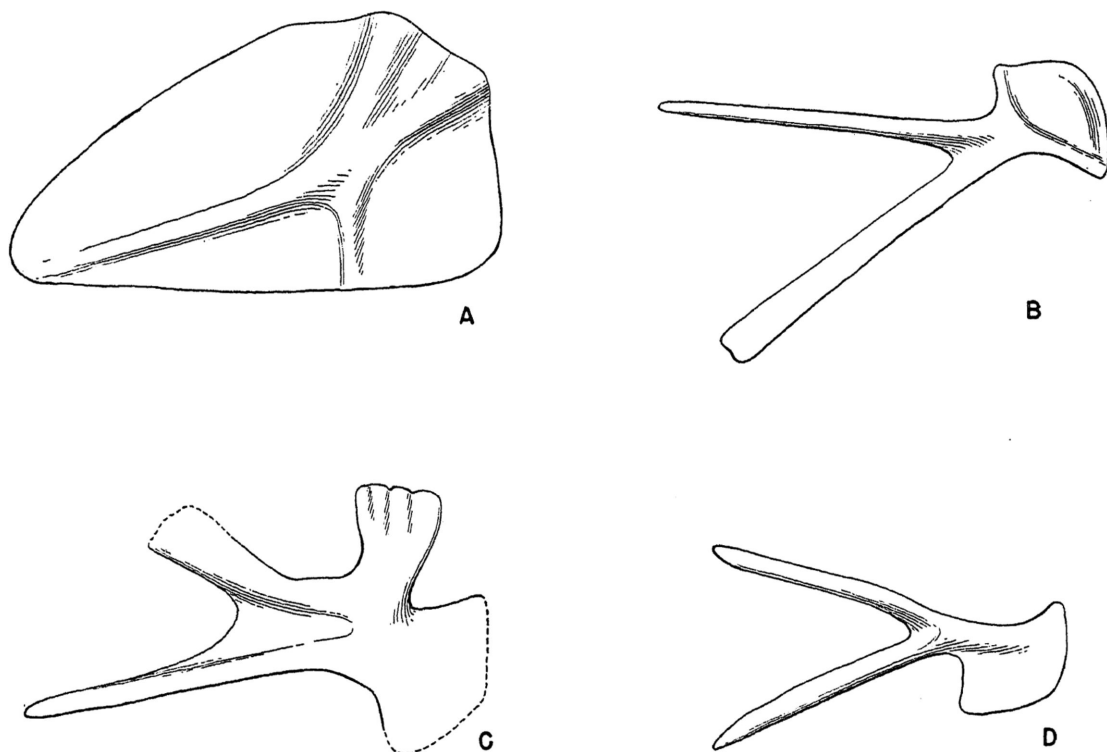
FIG. 11. *Diplurus newarki.* A. Basal plate of anterior dorsal fin. B. Basal plate of posterior dorsal fin. C. Pelvic bone. D. Basal plate of anal fin.

ton (P.U.G.M. No. 14945), the pelvic plates have two anterior apophyses and obviously resemble the figure. There is, however, in the manner of preservation, a resemblance to "pelvic" elements in the North Wales specimen, which suggests that the latter may be only oddly preserved pelves of the usual coelacanthid type. Further preparation of the type specimen tends to support this conclusion. In view of this probability, it would appear undesirable at this time to follow Shainin in regarding the North Wales specimens as taxonomically distinct on the basis of differences in the shape of these plates.

The pelvic fins of *D. newarki* have about 15 rays, all of which are segmented for two-thirds of their length. Those of *D. longicaudatus* have 21 rays. In both species, the pelvic fins are situated about midway between the pectoral and the anal fins.

UNPAIRED FINS

The anterior dorsal fin of *D. newarki* is supported by a triangular basal plate (fig. 11A) that is identical with the one in *D. longicaudatus* (Schaeffer, 1948). A strong ridge extends from the posterodorsal border where the rays are attached to the anteroventral apex. At the posterodorsal border, the ridges of both sides unite to form an ovoid shelf with a slightly concave surface. The first three fin rays, which have rounded rather than forked bases, articulate with this shelf.

The anterior dorsal fin of *D. newarki* is composed of eight relatively robust rays, segmented for about one-half of their length. The last five rays have forked bases which fit over the posterodorsal border below the shelf. A varying number of rays, at least in

D. newarki, have acute spines attached to both the segmented and the unsegmented portions. On the lepidotrichial segments, the spines are frequently paired. In one specimen the spines occur on about six of the rays,while in other specimens of almost equal size they are restricted to the first few rays. In a number of specimens, particularly those under about 9 cm. in length, no spines are in evidence. Some of this variation is undoubtedly related to preservation, although the distribution of the spines is clearly not uniform.

The summit of the dorsal curvature of the body in many coelacanths is at the origin of the anterior dorsal fin. This is, in part at least, related to the size of the basal plate. In certain genera, such as *Coelacanthus, Laugia*, and *Diplurus*, the posterior lepidotrichia appear to articulate with the basal plate well below the dorsal body surface. In such circumstances, the dorsal fin could be completely depressed only if the proximal portions of the posterior rays were situated in a median dermal fold which extended ventrally almost to the basal plate. The mackerel exhibits this condition in an extreme form, the fold entirely concealing the dorsal fin when it is completely depressed. It appears probable that a fold of this sort was present in *Diplurus* and at least a few other genera, assuming that this fin was not more or less permanently erect, which seems unlikely. There is no evidence of a fold in *Latimeria*.

The forked basal plate of the posterior dorsal fin (fig. 11B) is practically identical in both species. In *D. newarki* this fin has about 13 rays, and in *D. longicaudatus* about the same number. The rays are segmented for two-thirds of their length; there are no spines. The anal fin likewise has a basal plate (fig. 11 D) that is very similar in both species. In *D. newarki* the anal consists of about 14 rays, in *D. longicaudatus* of about 21. The degree of segmentation is about the same as in the posterior dorsal.

The caudal and supplementary caudal fins together equal about one-third of the total body length. The caudal fin in *D. newarki* has about 13 lepidotrichia in both lobes, and in *D. longicaudatus* about 16. Each lobe is preceded by three radials that do not support lepidotrichia. The lepidotrichia are segmented for about one-half of their length, and the first two or three of each lobe are spinous along their anterior borders. As Saint-Seine (1949) has noted in the case of *Undina*, there is evidence of paired spines on a number of lepidotrichial segments. In *Undina* the proximal ends of the caudal lepidotrichia are forked. The distal ends of the radials apparently do not fit into these bifurcations but overlap the anterior borders of the lepidotrichia. There is evidence of similar bifurcation in *Diplurus*, but the lepidotrichia overlap and partly cover the anterior border of the radials, much as in *Laugia* (Stensiö, 1932, fig. 21).

The supplementary caudal fin projects unusually far beyond the posterior border of the caudal proper. It is composed of about 22 segmented lepidotrichia in both species. There is an additional, single pair of rays without basal supports forming part of the caudal. They are situated just anterior to the first rays of the supplementary caudal.

SQUAMATION

The scales (fig. 12; pl. 6, figs. 2, 3) are widely to narrowly ovate or elliptical, depending on their location on the body. In most areas the exposed portions of the scales have a varying number of elongated, partially hollow ridges. The orientation of the ridges is subject to much variation. They may be parallel or arranged at slight angles to each other. Frequently the ridges are of different lengths in the center of the exposed portion, and one shorter ridge may only slightly overlap those adjacent to it or abut against another in line with it. On the anterior portion of the body, above and around the pectoral fin, the scales have relatively few ridges. On the flank region, from below the anterior dorsal fin and posteriorly to the caudal fin, the scales of *D. newarki* usually have five to 13 ridges. In this area the central ridge is frequently elevated posteriorly, partly freed from the scale surface, and pointed. In the area between the dorsal and ventral lobes of the caudal fin, and on the lobed fins, the scales are smaller, and have only two or three
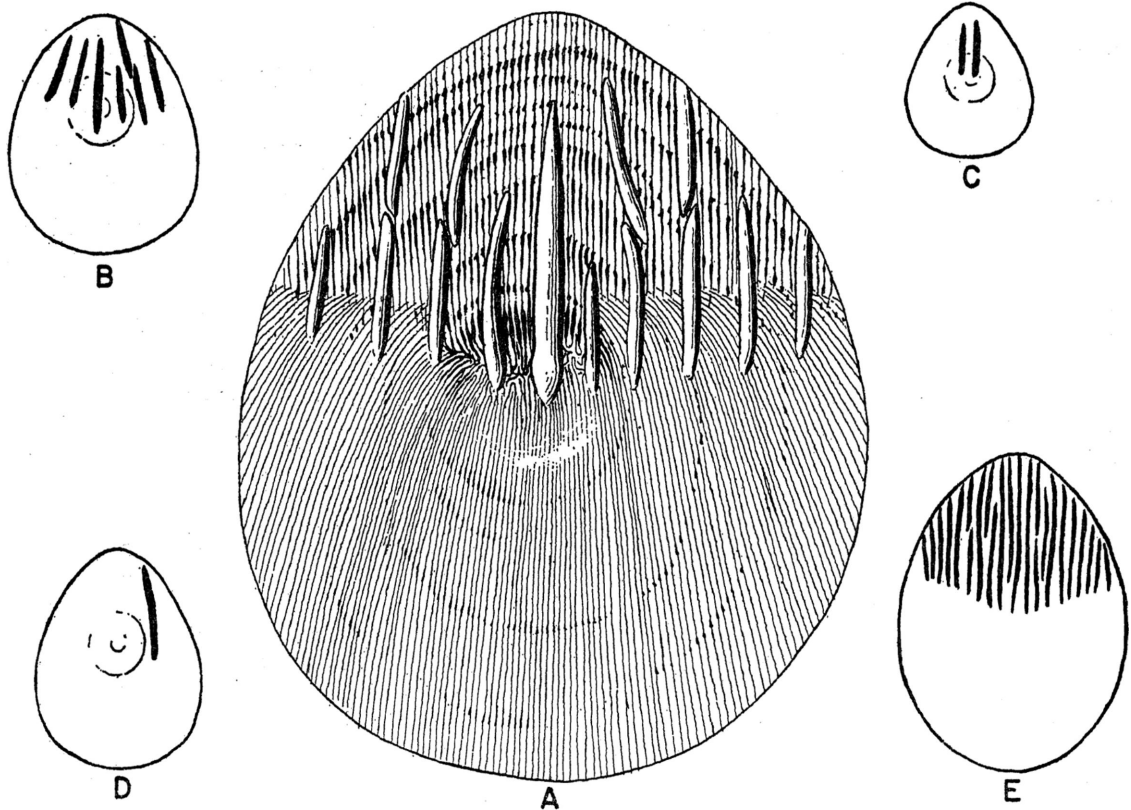
FIG. 12. *Diplurus newarki.* A. Scale from area immediately below anterior dorsal fin, with details of ornamentation. B. Outline of scale from ventral portion of body between pelvic and anal fins. C. Outline of scale situated between dorsal and ventral lobes of caudal fin. D. Outline of scale from pectoral fin area. E. Outline of scale from the dorsal portion of the body of *D. longicaudatus.*

ridges. The scales of the supplementary caudal lobe are much reduced and lack ridges. On the flank area of *D. longicaudatus* the scales may have as many as 27 ridges. These ridges are relatively thinner and more closely spaced than in *D. newarki.*

In addition to the ridges, the scales are covered with fine, parallel striae. The striae on the embedded portion of the scale are finer and more numerous than those of the exposed portion, and in some isolated scales they appear to end abruptly rather than to continue onto the exposed portion. When the surface of the exposed portion is not obscured

by numerous ridges, well-defined "annuli" are in evidence. These are irregularly spaced, localized thickenings of the striae. A focus or nucleus is occasionally seen; it is centrally located and slightly elevated.

The preservation of the histological structure of the scales and bones is poor in the few examples examined in thin section. The bones, and apparently also the scales, are covered with a thin layer of enamel. The presence or absence of enamel on the ridges cannot be ascertained. The layers of trabecular bone and isopedin are difficult to separate, and the cosmine cannot be clearly differentiated.
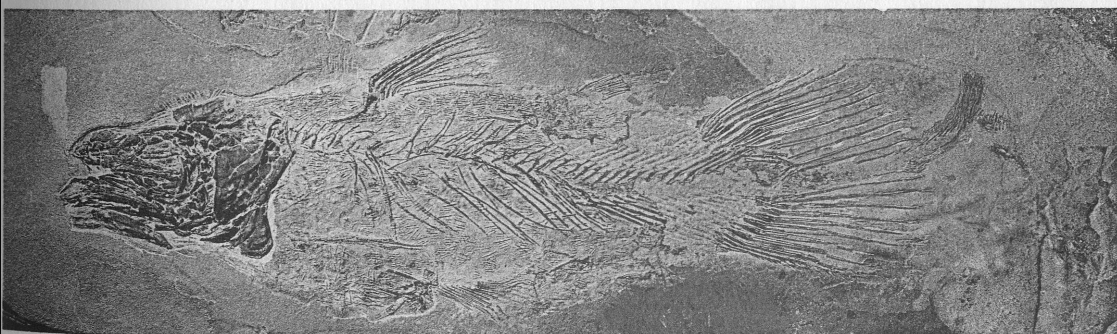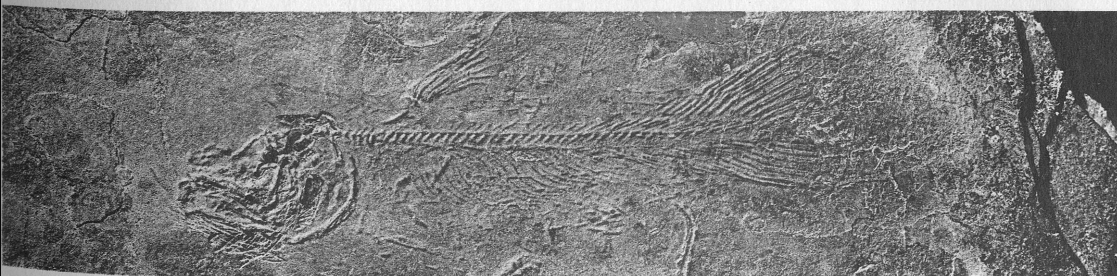
…us newarki. Complete specimens. 1. P.U.G.M. No. 14918a. 2. A.M.N.H. No. 9450. 3. P.U.G.M. 4. P.U.G.M. No. 14927. All natural size
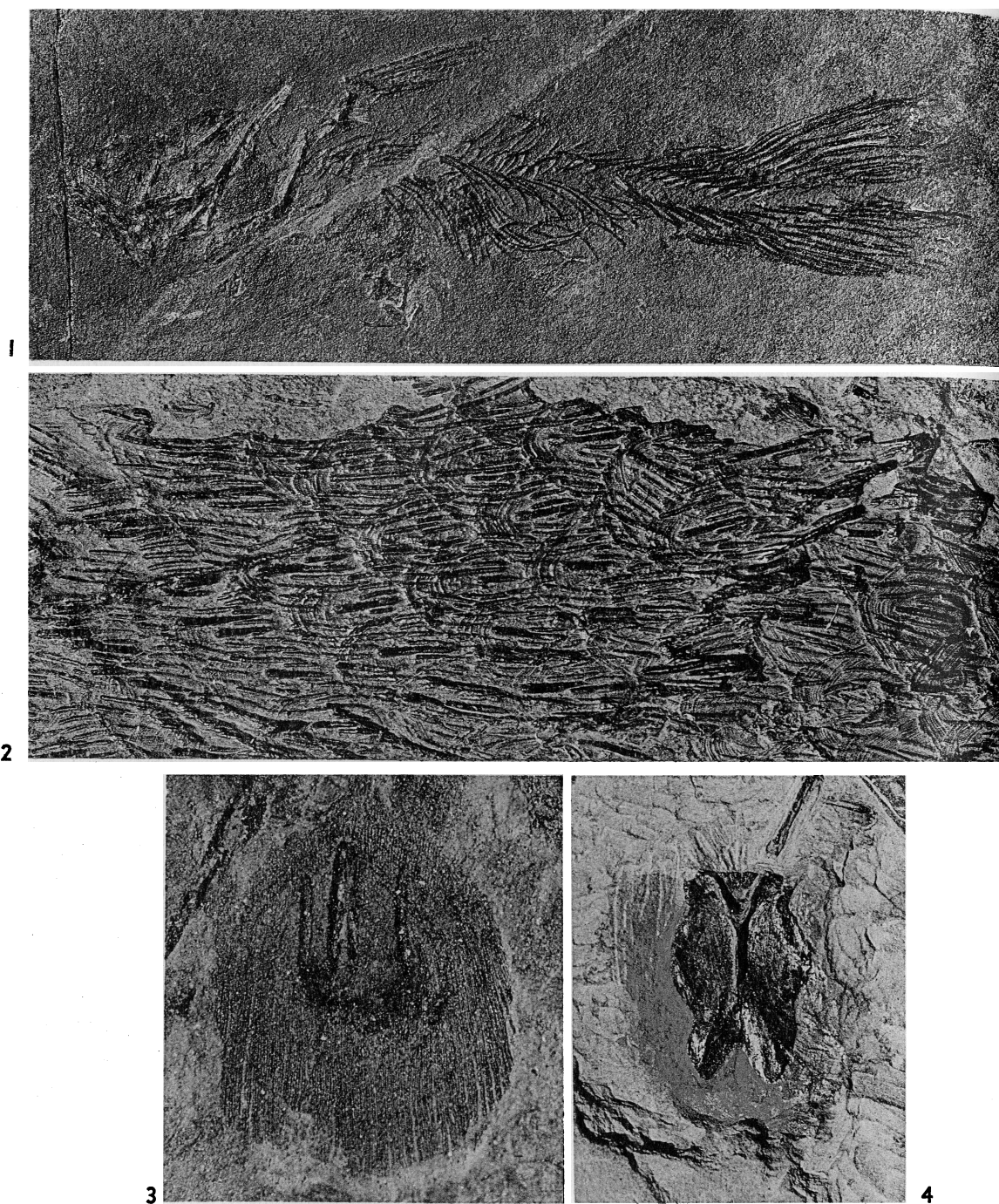
Diplurus newarki. 1. P.U.G.M. No. 13695, type specimen, × 2. 2. P.U.G.M. No. 14943b. Scales on dorsal portion of body between anterior and posterior dorsal fins, × 4. 3. Isolated scale, × 20. 4. A.M.N.H. No. 9451. Presumed urohyal, × 4

Diplurus newarki. P.U.G.M. No. 14943a. Lateral view of skull, × 4
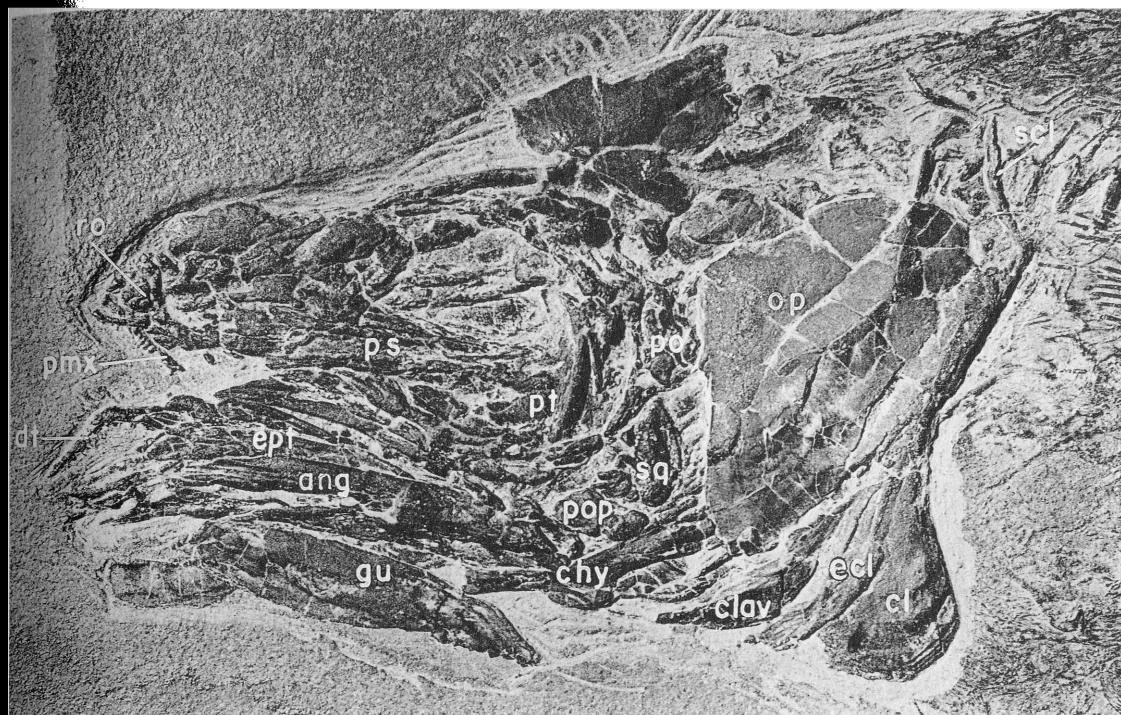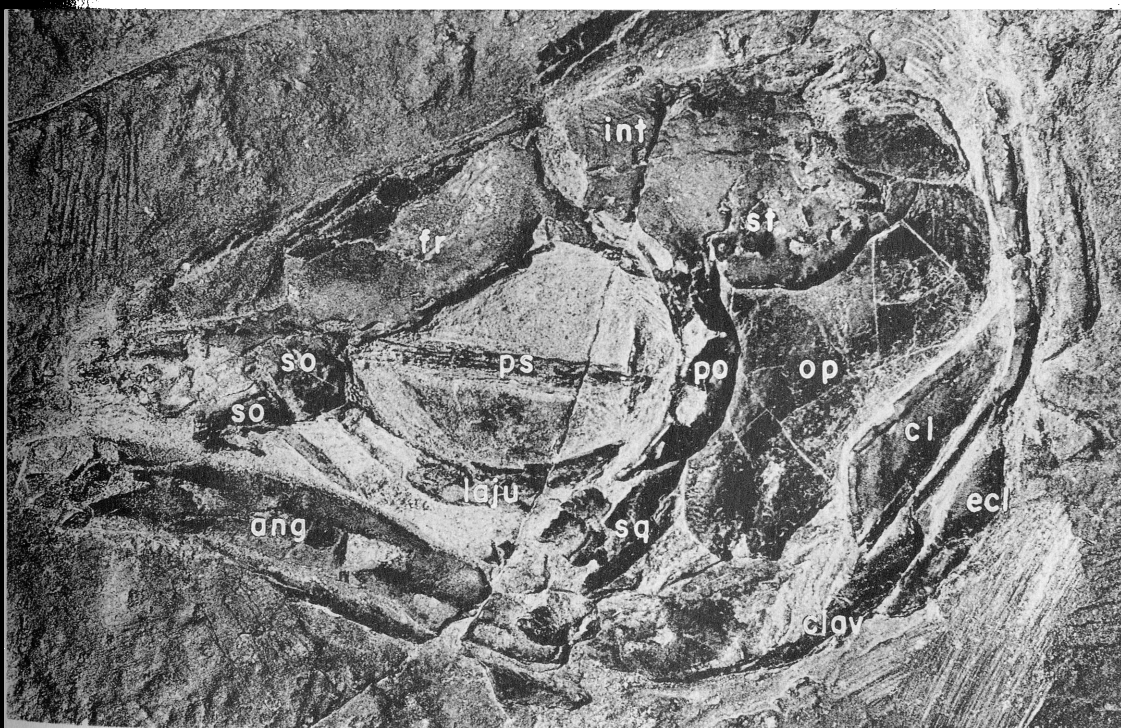
lurus newarki. 1. P.U.G.M. No. 14944. Lateral view of skull, × 4. 2. P.U.G.M. No. 14558. Lateral of skull from Granton Quarry, × 4
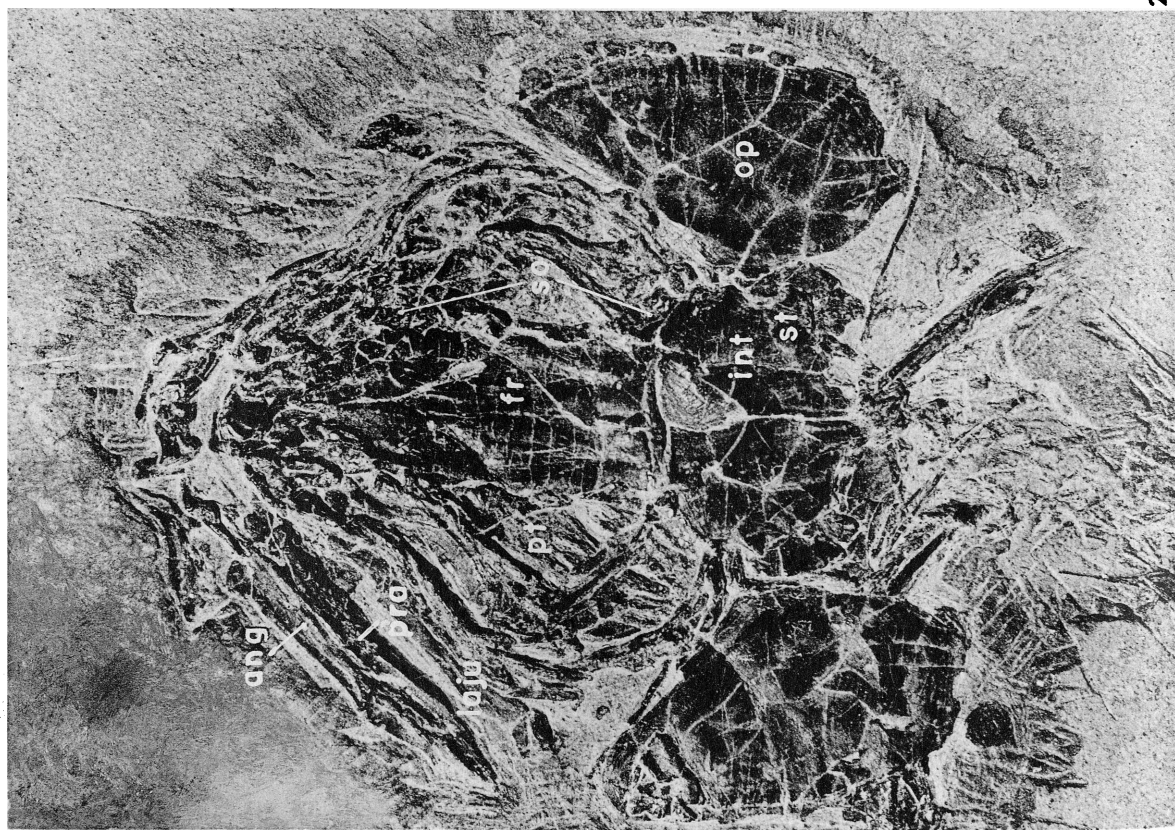
Diplurus newarki. A.M.N.H. No. 9454. 1. Skull in dorsal view, × 4. 2. A.M.N.H. No. 9452. Skull in dorsal view, × 4

newarki. 1. A.M.N.H. No. 9455. Skull roof, × 4. 2. A.M.N.H. No. 9453. Skull in dorsal and lateral
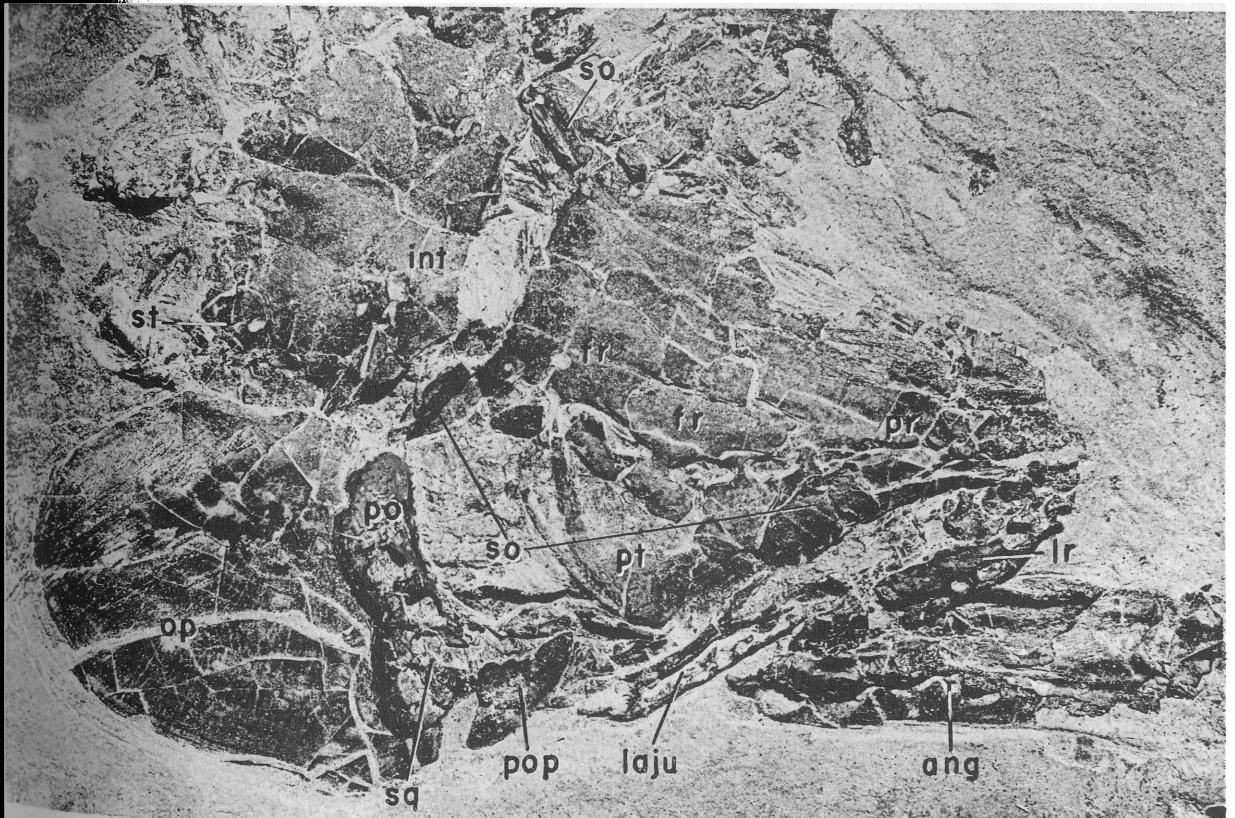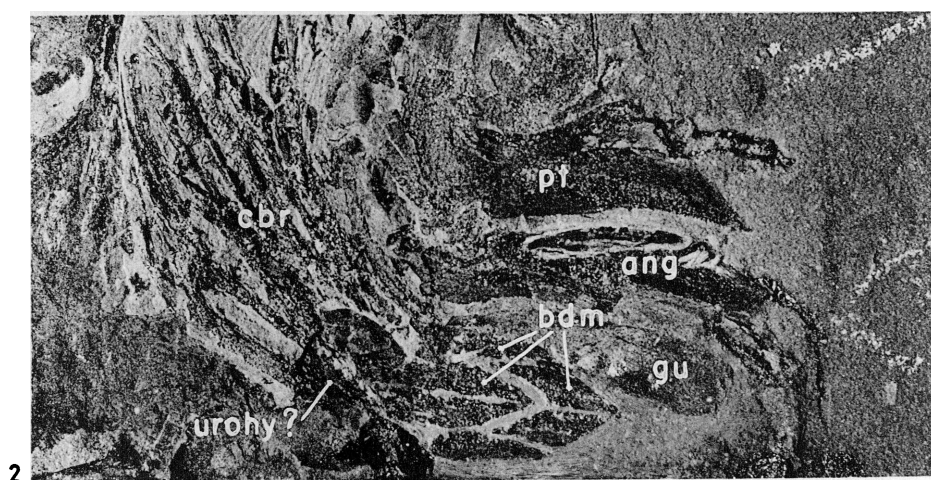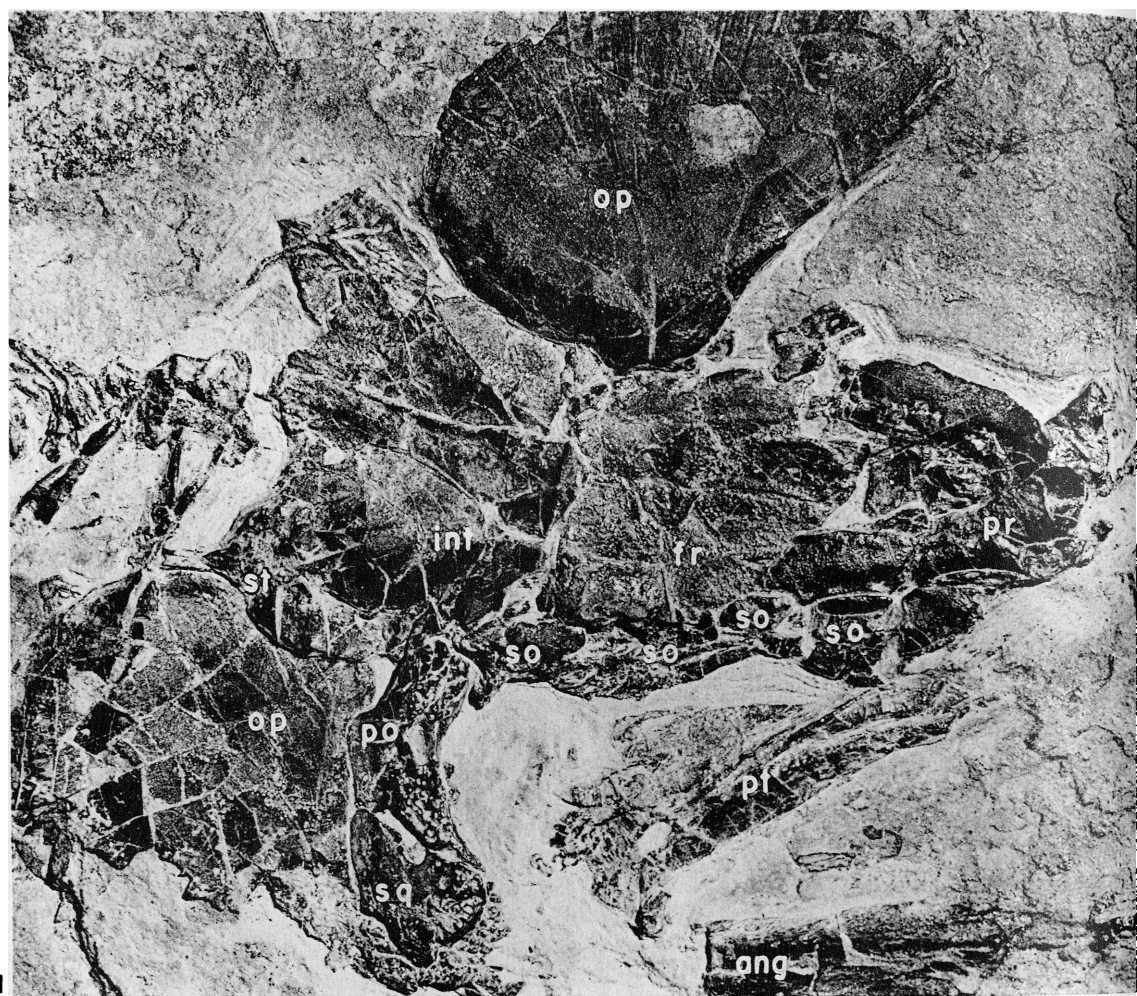
Diplurus newarki. 1. P.U.G.M. No. 14958b. Dorsal view of skull, × 4. 2. A.M.N.H. No. 9456. Gill skeleton in dorsal view, × 4
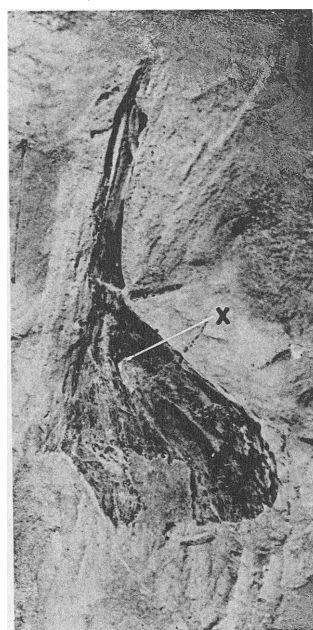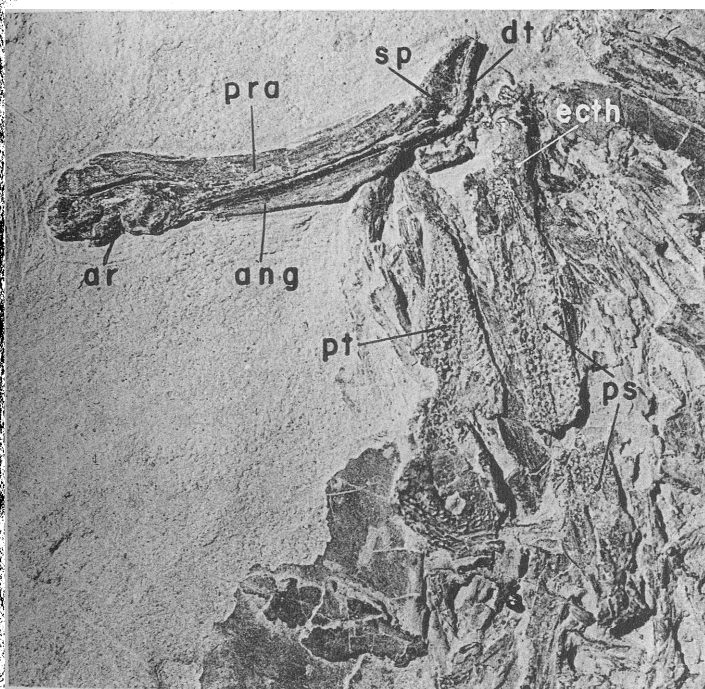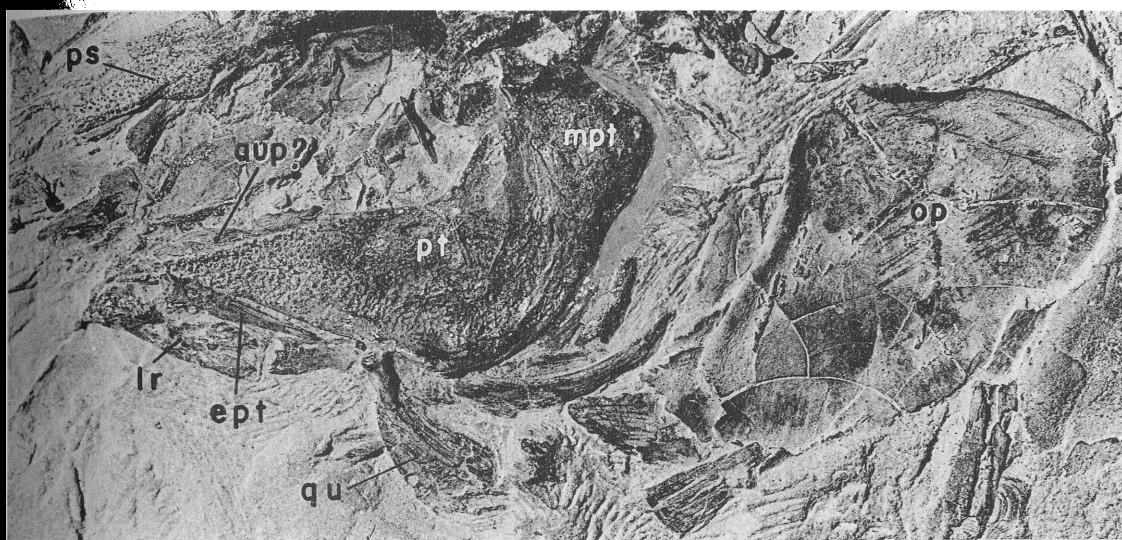
plurus newarki. 1. P.U.G.M. No. 14942. Median view of palatoquadrate complex, × 4. 2. P.U.G.M. 14935. Median view of lower jaw, ventral view of ectethmoid and parasphenoid, × 4. 3. A.M.N.H. 451. Median view of cleithrum; × indicates groove and canal on median surface of cleithrum
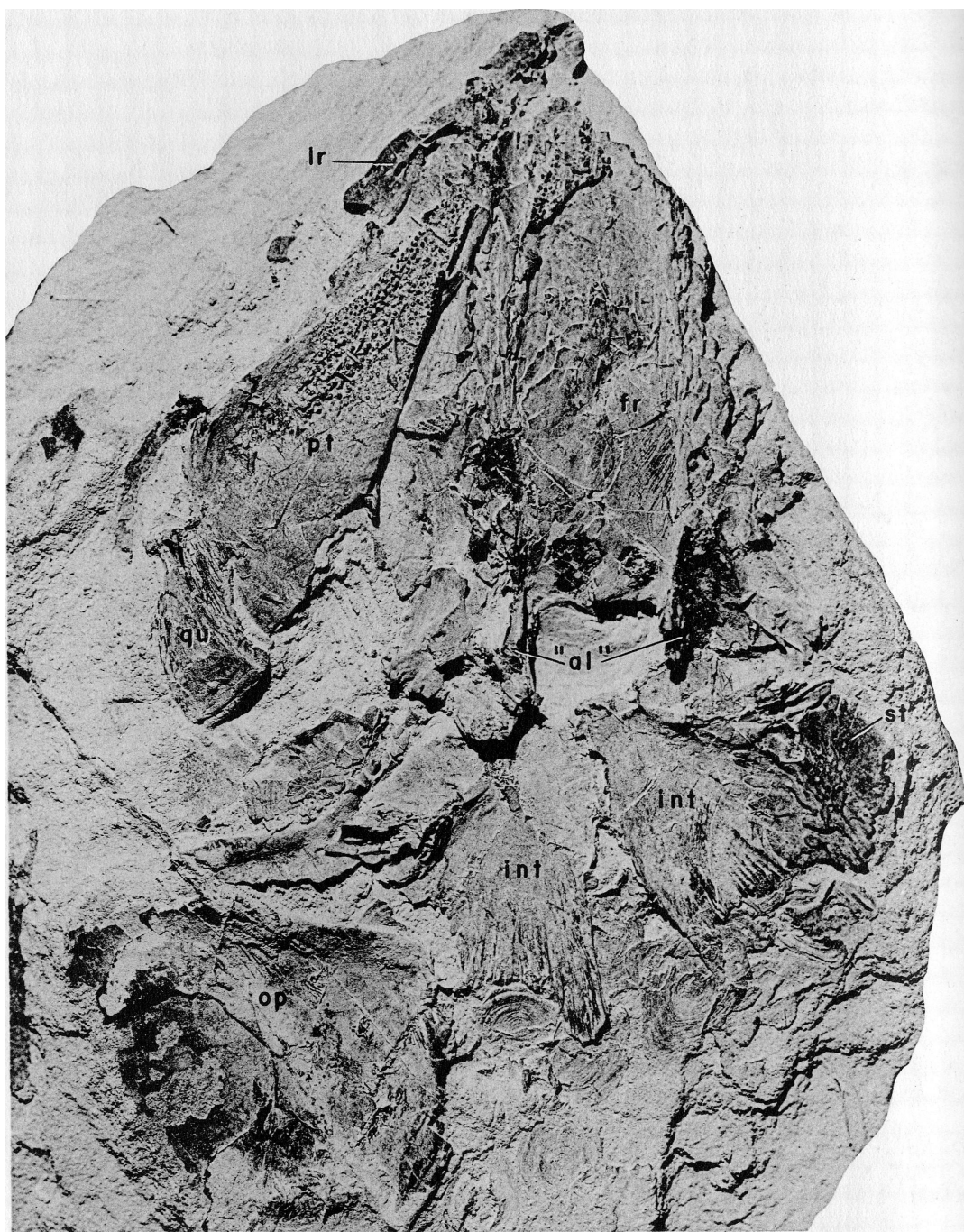
Diplurus newarki. P.U.G.M. No. 14926. Ventral view of skull roof, × 4

Diplurus longicaudatus. P.U.G.M. No. 14955. Partial, dissociated skull, × 1/2
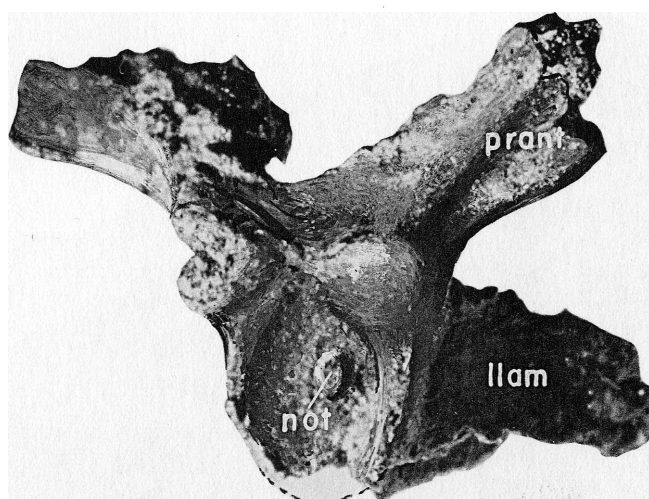
1. *Diplurus newarki*. A.M.N.H. No. 9458. Posterolateral view of basisphenoid, × 12. 2. *Diplurus longicaudatus*. U.S.N.M. No. 18476. Lateral view of partial skull and shoulder girdle, × 1/2

ORDER **CROSSOPTERYGII**

SUBORDER **COELACANTHINI**

FAMILY **COELACANTHIDAE**

DIPLURUS NEWBERRY

Diplurus NEWBERRY, 1878, Trans. New York Acad. Sci., vol. 1, p. 127.

Coelacanthus Agassiz, 1836, (in part) BRYANT, 1934, Proc. Amer. Phil. Soc., vol. 73, p. 323.

Osteopleurus SCHAEFFER, 1931, Amer. Mus. Novitates, no. 1110, p. 1.

GENOTYPE: *Diplurus longicaudatus* Newberry.

HORIZON: Newark group, Upper Triassic, eastern North America.

GENERIC DIAGNOSIS: Upper Triassic coelacanths differing from other members of the family Coelacanthidae by the following combination of characters: braincase incompletely ossified as in other post-Devonian genera; anterior ethmoid with three posterior projections, one of which articulates with parasphenoid; basisphenoid with large, divergent, ovoid antotic processes; otic and occipital ossifications present. Parasphenoid with narrow, shovel-shaped posterior portion, not fused with basisphenoid; parasphenoid teeth not grouped on dental plate. Dermal bones of skull apparently lacking ornamentation except for ridges of tubercles of opercular which may be absent on *D. newarki*. Rostral area partly covered with small bones, presumably in close articulation. Premaxillary small, splint-like, with teeth. Fronto-ethmoid shield usually composed of three paired bones, subequal in size; the middle pair, here called anterior frontals, may or may not meet in middorsal line, and one or possibly both may be absent as separate elements. Supratemporals rectangular, not extending posteriorly beyond intertemporals. Posterior supraorbital ("dermosphenotic") large, its median border against the intertemporal. Extrascapulars reduced to small ossifications surrounding commissural canal. No separate "antorbital." No ossified circumorbital plates. Postorbital and squamosal of distinctive shape, with large sensory canal pores; subopercular not observed and possibly absent. Lower jaw short; dentary and splenial elongated anteromedially; anterior margin of lower jaw concave, symphysis nearly horizontal. Ribs elongated, nearly reaching ventral border; basiventrals not ossified. Cleithrum with large median lamina. Extracleithrum separate. Pelvic plates with two anterior apophyses. Spines on one or more lepidotrichia of anterior dorsal and both lobes of caudal fin. Supplementary caudal fin elongated, about one-eighth of total body length. Scales elliptical, with variable number of elongated ridges, the central ridge frequently elevated and spine-like in the flank area.

Diplurus longicaudatus Newberry, 1878

Diplurus longicaudatus NEWBERRY, 1878, Trans. New York Acad. Sci., vol. 1, p. 127.

TYPE: A.M.N.H. No. 630. Complete fish, including supplementary caudal fin, skull poorly preserved. From Brunswick formation, Newark group, Boonton, New Jersey. (Figured in Schaeffer, 1948, fig. 1.)

SPECIFIC DIAGNOSIS: *Diplurus longicaudatus* differs from *D. newarki* in the following characters: maximum known size about three and one-half times greater (69 cm.) than that of *D. newarki*. Opercular ornamented with numerous radiating ridges and tubercles. About 50 neural arches. Pectoral fin with about 19 lepidotrichia, pelvic about 21, anterior dorsal 11, posterior dorsal 14, anal 21, caudal (both lobes) 32, supplementary caudal 20. Exposed portion of scales in flank area covered with a maximum of about 27 elongated ridges which are relatively more slender than in *D. newarki*.

HORIZONS AND LOCALITIES: Although remains of this species are still far less common than those of *D. newarki*, they have a somewhat greater known stratigraphic and geographical distribution within the Newark group. The distribution is as follows:

"Anterior shales" of Meriden formation, in southern part of Durham on western slope of Totoket Mountain, Connecticut

"Posterior shales" of Meriden formation, Durham (east of Pistapaug Mountain), and Westfield, Connecticut

Stockton formation, Granton Quarry, North Bergen, New Jersey

Lockatong formation, Princeton, New Jersey, and Gwynedd, Pennsylvania

Brunswick formation, Boonton, New Jersey

TABLE 1

MEASUREMENTS (IN CENTIMETERS) OF SPECIMENS OF *Diplurus newarki*
AND *Diplurus longicaudatus*

| | D. newarki | | | | D. longicaudatus |
	P.U.G.M. No. 14945	A.M.N.H. No. 15222	P.U.G.M. No. 14918	P.U.G.M. No. 14959	A.M.N.H. No. 630
Total body length	6.88	9.79	12.60	14.50	69.0
Body length minus supplementary caudal fin	6.15	8.62	11.00	13.10	64.0
Length supplementary caudal fin, including portion overlapped by caudal	.80	1.30	1.69	1.80	8.5
Distance from snout to anterior border of:					
Anterior dorsal fin	2.17	2.78	3.82	4.28	22.5
Posterior dorsal fin	3.64	4.90	6.31	7.36	37.5
Pectoral fin	1.81	2.41	3.34	±3.38	20.0
Pelvic fin	2.58	3.75	4.80	5.65	29.5
Anal fin	3.75	5.30	7.01	—	40.0
Caudal fin	4.50	6.22	8.00	9.38	45.5
Body depth at anterior border of first dorsal fin (approx.)	1.65	1.98	2.60	±2.60	+12.0
Skull length (snout to widest point on opercular)	1.42	2.07	2.75	3.10	18.0

?Bull Run shale, Midland, Fauquier County, Virginia

REFERRED SPECIMENS: In addition to those previously listed (Schaeffer, 1948), the following specimens have been recently collected:

A.M.N.H. No. 9459. Partial opercular, mandible, and gular. Granton Quarry, North Bergen, New Jersey

P.U.G.M. No. 14955. Partial skull including branchial arches, basibranchial ossifications, palate, "parietal" shield, and cleithra. Firestone Library excavation, Princeton University, Princeton, New Jersey

Wilhelm Bock collection, Academy of Natural Sciences of Philadelphia. Dissociated scales and ribs. Railroad cut on Reading Railroad at Gwynedd, Montgomery County, Pennsylvania

U.S.N.M. No. 18476. Partial skull and shoulder girdles. Licking Run, 2 miles northwest of Midland, Fauquier Country, Virginia

Diplurus newarki (Bryant, 1934), new combination

Coelacanthus newarki BRYANT, 1934, Proc. Amer. Phil. Soc., vol. 73, p. 323.

Osteopleurus newarki SCHAEFFER, 1941, Amer. Mus. Novitates, no. 1110, p. 1.

Osteopleurus milleri SHAININ, 1943, Jour. Paleont., vol. 17, p. 272.

Osteopleurus milleri grantonensis SHAININ, 1943, Jour. Paleont., vol. 17, p. 274.

TYPE: P.U.G.M. No. 13695. Partial skeleton; paired fins, posterior dorsal and anal fins missing; skull poor. From Lockatong formation, Newark group, Reading Railroad cut, three-quarters of a mile south of North Wales, Pennsylvania.

SPECIFIC DIAGNOSIS: *Diplurus newarki* differs from *D. longicaudatus* by the following characters: Maximum known size under 20 cm. Opercular lacking ornamentation or with relatively few ridges and frequently crenulated along part of posterior border. About 48 neural arches. Pectoral fin with about 13 lepidotrichia, pelvic 15, anterior dorsal 8, posterior dorsal 13, anal 14, caudal (both lobes) 25, supplementary caudal 22. Exposed portion of scales covered with variable number of ridges, maximum number about 13.

HORIZONS AND LOCALITIES: In contrast to *D. longicaudatus*, this species usually occurs in some abundance at nearly all the localities where it has been discovered. The known distribution is as follows:

Stockton formation, Granton Quarry, North Bergen, New Jersey

Lockatong formation, Princeton, New Jersey; North Wales and Gwynedd, Pennsylvania

?Bull Run shale, near Chatham, Virginia

REFERRED SPECIMENS: The following specimens are referred:

A.M.N.H. No. 9071. Dissociated bones on a single slab of shale. From Newberry collection. Collected "6 miles east of Chatham, Va."

A.M.N.H. No. 15222. Entire series from Granton Quarry, North Bergen, New Jersey, including specimens figured by Schaeffer (1941) and Shainin (1943)

A.M.N.H. Nos. 9450–9458. Firestone Library excavation, Princeton University, Princeton, New Jersey

P.U.G.M. No. 14558. Complete fish with well-preserved skull. Granton Quarry, North Bergen, New Jersey. Figured by Schaeffer (1941, fig. 1)

P.U.G.M. No. 13825. Isolated scales. North Wales, Pennsylvania

P.U.G.M. No. 13826. Dissociated bones including parasphenoid. North Wales, Pennsylvania

P.U.G.M. Nos. 14918, 14920–14925, 14932–14949. Firestone Library excavation, Princeton University, Princeton, New Jersey. This series includes most of the best specimens from the Princeton locality and many of them are figured in this paper

Specimens in Wilhelm Bock collection, Academy of Natural Sciences of Philadelphia. Cut on Reading Railroad at Gwynedd, Montgomery County, Pennsylvania

THE SPECIES OF COELACANTH FISHES have been defined largely on non-meristic characters. These include the ornamentation of the scales and of the various dermal bones of the skull, the shape of the parasphenoid and of certain skull bones such as the opercular, the structure of the girdles of the paired fins and the basal plates of the median fins. In general, the fins and vertebral segments of crossopterygians are rarely well enough preserved to permit accurate counting in sufficiently large samples of a given species. Jarvik (1948) has been able to employ scale counts in separating species of *Osteolepis*.

The range of variation in ornamentation characters for a given coelacanth species has rarely received consideration, except in relation to scale ornamentation on different regions of the body. As noted elsewhere, the operculars of *D. newarki* from the Princeton locality may be entirely free of ornamentation or may have a small number of ridges on the posterodorsal surface; the crenulation of the posterior border of the opercular shows the same sort of variation. The operculars of *D. longicaudatus*, on the other hand, all show evidence of abundant tubercles and ridges on at least the dorsal half. The variation in *D. newarki* is mostly in the number of ridges rather than in the degree of development of the ridges. It is suggestive of weak selection towards any constancy in the expression of the amount of ornamentation.

The question of whether or not the specimens of *D. longicaudatus* simply represent very large individuals of *D. newarki* requires consideration. Lagler (1947) has pointed out that the total number of ctenii, radii, and ridges on scales may increase with age in the actinopterygians. The number of ridges on the upper flank scales of *D. longicaudatus* is significantly greater than on similarly situated scales in *D. newarki*. There is also some evidence of increase in the number of ridges in the *D. newarki* series with increase in size, but the amount of increase is difficult to determine, as the scales of small individuals are very thin and poorly preserved. In any case, the differences in ridge number and relative ridge size in the two species are great enough, in the absence of any known inter-

mediate growth stages, to distinguish the scales when isolated. The differences in meristic characters are, for certain of the fins, perhaps great enough to be significant. The sample of *D. longicaudatus* with well-preserved fins is, however, much too small to present entirely satisfactory evidence. There are other observable differences in *D. longicaudatus*, such as the more robust teeth on the basibranchial dermal plates and the tendency towards greater emphasis of various ridges and other bony prominences that can be related to greater size.

The size range of measurable specimens of *D. newarki* makes it possible to consider ontogenetic changes in skull dimensions and in the positions of the various fins. Only nearly complete specimens were measured; no allowance was made for crushing. On the basis of these regressions (fig. 13) and several others not included here, it is evident that no taxonomic distinction can be made between individuals of different sizes, or from different localities or horizons in the Stockton or Lockatong formations. Apparent variations in relative skull size, fin position, or body length reflect only growth stages of a single species.

The type of *D. longicaudatus* is the only specimen of this species complete enough to yield a comparable series of measurements. These measurements appear to extend the scatter diagrams of *D. newarki* and suggest that within the genus *Diplurus* there is a positive allometric relationship between fin position and size increase that is the same for both species. Additional measurements of *D. longicaudatus* might indicate, however, that separate, but very similar growth gradients are involved, as Shapiro (1943) has observed for the length-width body relationship in various species of scombroid fishes.

In view of these considerations, the two species of *Diplurus* are only tentatively separable. The observed differences between them, however, are constant on the basis of the known evidence, and specific separation is, at present, therefore justified.

Shainin (1943) described a separate "variety," which he called *Osteopleurus milleri grantonensis*, on the basis of a single caudal
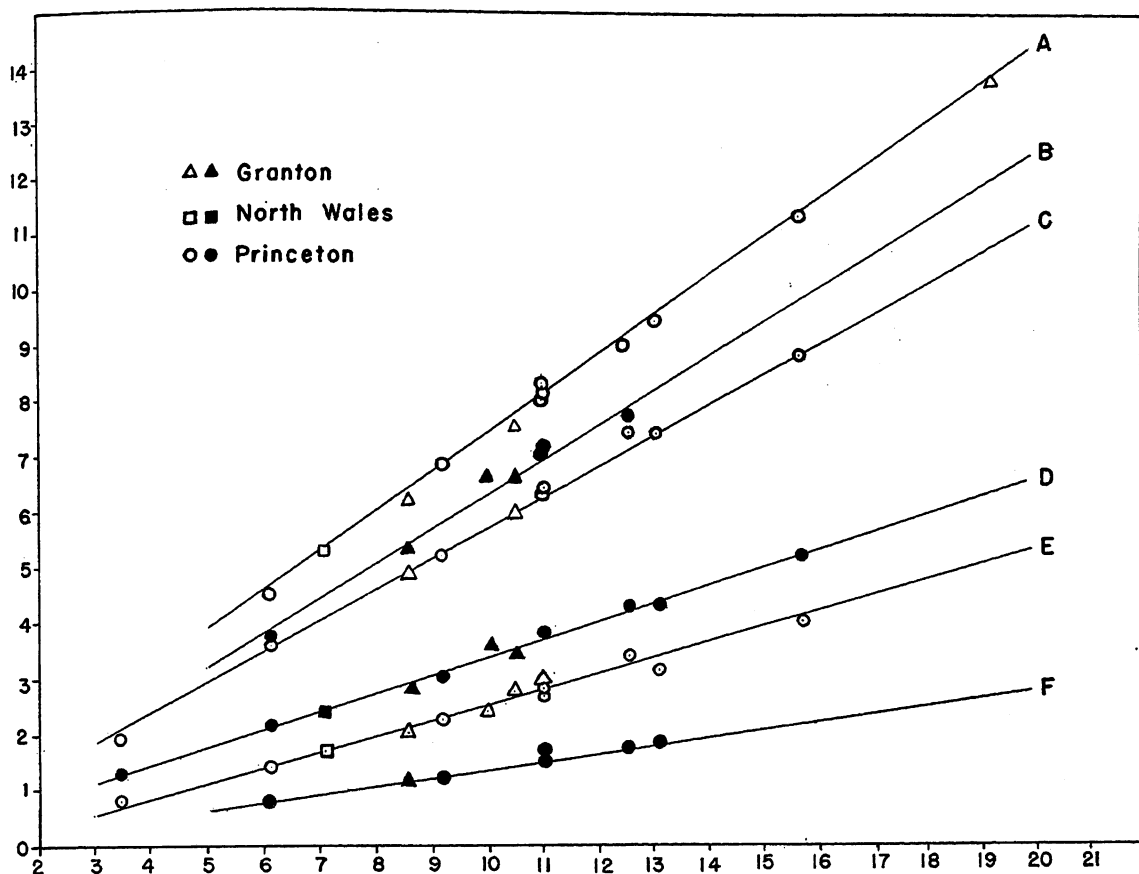
FIG. 13. *Diplurus newarki*. Graph, in centimeters, of body length minus the supplementary caudal fin (horizontal axis), and of the distances from (A) tip of snout to origin of dorsal lobe of caudal fin, (B) tip of snout to origin of anal fin, (C) tip of snout to origin of posterior dorsal fin, (D) tip of snout to origin of anterior dorsal fin, (E) tip of snout to posterior border of opercular bone, and of (F) the length of supplementary caudal fin.

fin, minus the supplementary caudal. It has a length of 5.5 cm. He measured 12 specimens of *O. milleri* (= *D. newarki*) from the Granton Quarry and found the mean ratio between body length and caudal fin length to be 10.5/3.0. Shainin then computed, on this basis, the body length of "variety" *grantonensis* to be 19.2 cm. (or, without the caudal, 13.7 cm.). Since the computed body length was found to be 1.83 times greater than the mean body length for *O. milleri*, he concluded that this specimen must represent a new "variety." When Shainin's data are plotted on the proper regression (fig. 13A), it is evident that this caudal fin belongs to a large specimen of *D. newarki*. There is no detectable morphological difference.

Diplurus is a member of the Coelacanthidae as this family is at present broadly defined. Its relationships within the family are, however, obscure. None of the other Triassic genera has a similar squamosal and preopercular. Numerous other characters, such as the shape of the dentary and the splenial, the broad and divergent antotic processes, the median lamina on the cleithrum, and the elongated ribs, are unique to this genus. There is enough basic resemblance in the structure of the skull and the postcranial skeleton to suggest derivation from an early Triassic type resembling *Whitea*. *Diplurus* is obviously specialized in a number of features, which may reflect a long period of isolation in the pre-Newark and early Newark environment.

Diplurus IS KNOWN from three separate areas of the Newark group. These are the Connecticut Valley area, the New York-Virginia area, and the Danville area. It is reasonable to suppose, however, that this genus occurred in most or all of the eastern Triassic basins, including the Acadian, as it is a typical member of the generally distributed Newark fish fauna. The available evidence indicates that *D. newarki* lived in ponds, lakes, and swamps in great abundance. The relative rarity of *D. longicaudatus* in the same type of beds containing *D. newarki* and other members of the Newark fish fauna suggests that it usually inhabited a different environment, at least in the adult stages. Young individuals of *D. longicaudatus* have not been identified, although it is possible that at least some of the specimens assigned to the smaller species are actually juveniles of the larger. The problem of specific separation is discussed in the section on systematics.

In the New York-Virginia area, both species of *Diplurus* occur in the upper portion of the Stockton formation at the Granton (formerly the Belmont-Gurnee) Quarry in North Bergen, New Jersey. The section exposed in the quarry is about 2100 feet above the base of the Stockton. It is capped by an intrusive sill, the base of which is about 350 feet from the top of the Palisade diabase. The thickness of the Stockton in this part of New Jersey is approximately 2300 feet, placing the Granton locality very near the top of the formation. Below the Granton sill, which is about 40 feet thick, the Stockton consists of alternating layers of dark shales and sandstones. The fish are known to occur in four different black shale layers, 2 to 3 feet in thickness, which probably represent pond or swamp deposits. A columnar section of the rocks exposed in the quarry has been published by Shainin (1943).

The transitional Stockton-Lockatong contact runs through the town of Princeton, and the Firestone Library locality is less than 200 feet above the contact. The Lockatong dips 10 degrees north in this area and is about 1500 feet thick. The fish occur in a layer 6 inches thick. At numerous levels within this layer the argillite has broken down

along the bedding planes, forming bands of soft limonitic clay. The fish embedded in the clay frequently can be exposed with a soft brush, and specimens preserved in this manner have yielded most of the morphological data. Those in the unaltered argillite are, by contrast, very difficult to prepare.

The various fish localities between North Wales and Gwynedd in Montgomery County, Pennsylvania, are, for the most part, in the upper half of the Lockatong formation. The fish occur in thin layers of dark shale which are interbedded with thicker layers of red shale. The thickness of the Lockatong in this area has not been reported, but it must be in the nature of several thousand feet.

The famous fish locality at Boonton, New Jersey, is in a black shale bed near the top of the Brunswick. On the basis of McLaughlin's (1950) estimates this exceedingly fossiliferous horizon may be as much as 10,000 feet above the Lockatong localities in Pennsylvania.

McLaughlin and Willard (1949) discuss in some detail the posssible sequence of deposition in the northern portion of the New York-Virginia basin. They are of the opinion that the Stockton and the Brunswick represent partly contemporaneous facies at the beginning of Newark time, the former deriving its sediments from the east and the latter from the west. With simultaneous sedimentation from these two sources, there was presumably an intergrading near the axis of the basin. By middle Newark time the basin had widened, and Stockton sediments were spread farther eastward. The center of the basin became lacustrine and swampy, and in this environment *D. newarki* became abundant, while the adults, at least, of *D. longicaudatus* perhaps inhabited the surrounding streams. The Lockatong was deposited in the lakes and swamps near the middle of the basin. It grades into the Stockton on the southeast and passes into the Brunswick by gradation and interfingering under the Cretaceous northeast of Princeton and in Berks, Montgomery, and Chester counties, Pennsylvania. In late Newark time the red beds of the Brunswick covered the Lockatong, and the lacustrine environment was essentially terminated. Where the Lockatong was appar-

ently not deposited, as in northern New Jersey and New York, the Brunswick directly overlapped the Stockton. At various times during the deposition of the Brunswick transitory ponds and swamps were formed, and the Boonton fish deposit must represent such an environment.

The specimen of *Diplurus longicaudatus* from near Midland, Fauquier County, Virginia, was obtained in a thin layer of black fissile shale near the base of the Bull Run shale (Baer and Martin, 1949). According to McLaughlin (1950), the underlying Manassas sandstone, with a thickness of 2000 feet, is equivalent to the Stockton, while the Bull Run shale, about 8000 feet in thickness, is correlated with the Lockatong and Brunswick. It is possible, therefore, that this *Diplurus* locality is equivalent to the early Lockatong in age. The single specimen from the Danville area in Virginia presumably comes from shales near the top of that section; no satisfactory correlation has been made with the southern portion of the New York-Virginia area.

The Connecticut Valley area has yielded remains of *D. longicaudatus* but not of *D. newarki*. These have been found in the dark shales of the lower sedimentary division (anterior shales) and upper sedimentary division (posterior shales) of the Meriden formation (Krynine, 1950). In southern Connecticut, the dark shales of the lower sedimentary division are, according to Krynine, about 75 feet thick and begin a varying distance, up to about 115 feet, above the lower lava flow. The dark shales in the upper sedimentary division from which the fish presumably came are about 600 feet above the middle lava flow. They are interbedded with limestones, arkose, and red shale layers.

The history of the Connecticut Valley during Newark time has been summarized by Krynine (*ibid.*, pp. 117–123). The eastern edge of the area is bordered by the Great Fault, along which movement occurred during a greater part of the deposition, producing a wedge-shaped trough. The basal New Haven arkose consists mainly of arkose, sandstone, some siltstone, and very little shale; it is about 6000 to 8000 feet in thickness, and 45 per cent is represented by red sediments. The presence of cross-bedding, mud cracks, and ripple marks indicates essentially a flood-

plain environment, with alternating wet and dry seasons. The absence of fishes in the New Haven can probably be related to the lack of proper conditions for preservation and fossilization. Remains of terrestrial and semiaquatic reptiles have been found at several localities. The alternating shales, arkoses, and siltstones of the Meriden formation, attaining a thickness of between 1150 and 2800 feet, were deposited on the New Haven in a lacustrine-swamp environment. At the end of New Haven time there was apparently a downwarping of the basin, involving changes in drainage pattern and associated with a reduction in the coarseness of the sediments. The near-gradient drainage permitted the formation of large swamps and lakes as in the Lockatong interval. In these, various species of *Semionotus* and *Redfieldia* were abundant; *Ptycholepis* and *Diplurus longicaudatus* were relatively rare. The overlying Portland arkose consists of about 4000 feet of arkoses, siltstones, some shales, and conglomerates. Mud cracks, ripple marks, and footprints indicate in general a return to the flood-plain conditions of New Haven time.

Darton was apparently the first to consider the lava flows in the Brunswick and the Meriden as contemporaneous. This hypothesis has recently been considered by Colbert (1946) and McLaughlin (1950). Aside from the presence of three separate lava flows in each area, there is little other evidence that favors or disfavors such equivalence. McLaughlin cites the presence of fish-bearing shales above the upper lava at Boonton and immediately below the upper lava flow in the Meriden as supporting evidence. Fish-bearing beds are present at a number of levels in the Meriden and probably also occur in the Brunswick lower than the Boonton horizon, indicating either long-continued or recurrent lacustrine-swamp conditions which were favorable for fish preservation. Such beds, therefore, would appear to be of little value for correlation. The apparent absence of *D. newarki* in the Meriden and the Brunswick is negative evidence that is likewise not reliable for correlation purposes. McLaughlin's correlation of the various Newark areas is based on extensive field work in the New York-Virginia area and on reconnaissance of the others but, as he states, it must be regarded as tentative.

DERMAL-BONE NOMENCLATURE IN THE COELACANTH SKULL-ROOF

WITHIN THE LIMITS of an apparent ancestral basic plan, the various dermal bone patterns of the skull-roof in the Osteichthyes may be relatively simple, involving a small number of bones, or they may be relatively complex and include a much larger number of elements. Particular pattern types are constant enough to be of systematic importance at various supraspecific levels. In some groups, however, there is a high degree of intraspecific variation in the number and arrangement of the bones in several different areas of the skull-roof. Although the supraspecific variation indicates adaptive pattern uniformity at a particular taxonomic level, the intraspecific variation implies weak selection towards constancy in pattern detail.

A primary function of the skull-roof is to provide an adequate dermal-bone covering for the braincase and, when the endocranium is incompletely ossified, to play a greater role in skull biomechanics. This dual function is apparently not closely related to the skull-roof pattern, as the various patterns and the minor variations within them seem to meet equally well the same basic biomechanical requirements. The skull-roof can therefore be regarded as a functional unit that may be composed of a varying number of bones arranged in a variety of major and minor patterns.

Within the broad limits imposed by the functional requirements, three major skull-roof patterns have evolved within the Osteichthyes: the crossopterygian, the dipnoan, and the actinopterygian. Various attempts have been made to homologize the individual bones among these three types and with the primitive tetrapods. The disposition of the sensory canals has played an important role in postulating such homologies. In the case of the dipnoans the early efforts were unsuccessful, and in recent years the bone names have been replaced by a system of letters and numbers. The osteolepid skull-roof has been reinterpreted (Westoll, 1943a, and earlier), making possible a more direct comparison with the stegocephalian skull. This modification has been generally accepted, except by the Swedish school (Jarvik, 1942, p. 343). It has not yet been applied to the coelacanth skull, nor have its implications for the actinopterygian skull been discussed. Furthermore, Parrington (1949, 1950) has formulated a new hypothesis on the relationship between sensory canals and dermal bones which, if substantiated, will also affect the problem of dermal-bone homology in the Osteichthyes.

The question of sensory canal and general dermal-bone fusion versus elimination has an important place in these considerations. Jarvik (1948, pp. 76–85) defends the fusionist view of the Swedish school, pointing out that compound bone names represent "an attempt at analysis," while a single name frequently must be arbitrary. Both the fusionists and the eliminationists have employed the paths of the sensory canals to determine bone homologies. Both will agree, for instance, that since the otic sensory canal is associated with the median, paired bones in the coelacanth "parietal" shield, the rhipidistian "interparietals" are involved. The fusionists call these bones parieto-intertemporals or even fronto-parieto-intertemporo-dermosphenotics, while the eliminationists regard them as simply intertemporals.

Westoll (1949) has found evidence in the dipnoans indicating that fusion does occur between sensory canal bones but not between them and general dermal bones. Parrington (1950) points out that, since sensory canal bones appear earlier in development than general bones, there is a greater opportunity for fusion. The fusion may be due to the more rapid growth of the sensory canal bones in relation to the surrounding tissues. Parrington describes two cases in *Dipterus* in which a general bone apparently "captured" the supraorbital canal, and the sensory canal bone normally containing this canal is absent. From this he concludes that certain sensory canal bones may require a neuromast for their development.

The embryological data, with support from the paleontological, have indicated that there is some sort of causal relationship between the developing sensory canals of the head and certain dermal bones. In a general review of this problem, Moy-Thomas (1938) noted

that the available embryological evidence indicates that the lateral line placodes are "responsible for the precocious localization of bone-formation in their vicinity." He pointed out, however, that experimental evidence might indicate that the role of the sensory canal organs has been overemphasized.

Westoll (1944, p. 68) is of the opinion that the presumed absence of the parietals in certain haplolepid paleoniscoids is due to the "degeneration" of the posterior part of the supraorbital sensory canal. He defines degeneration as a failure of the sensory canal to invaginate, with the sensory organs remaining at the surface as pit organs. Under such conditions the stimulus provided by the degenerated parts of the canals for the formation of the parietals was reduced, and their place was taken by the dermopterotics. He believes that the posterior portions of the supraorbital canals in the crossopterygians were degenerated and that, although the "parietals" still persisted in the osteolepids, the degeneration accounts for their absence in the holoptychiids and the coelacanths. The "parietals" are replaced by the more laterally situated sensory canal elements, either the "intertemporals," or the "supratemporals," or both.

An experimental approach has been made by Moy-Thomas (1941) and Devillers (1947, 1950). The former, working with *Salmo*, concluded that there is no causal relationship between sensory canal organs and associated dermal bones, thus reversing his earlier (1938) opinion. The latter, using mainly *Salmo*, is of the opinion that such a relationship does exist, and he concludes, on the basis of transplant experiments, that the neuromast organ induces the formation of dermal bone.

Parrington's (1949) hypothesis is based on the possibility that the neuromast organs do not determine the dermal-bone pattern, but rather that the dermal-bone precursors are responsible for the location of the sensory-canal primordia. He points out that if morphogenetic fields are established with their centers at the centers of future dermal-bone ossification, these fields may attract sensory-canal primordia. Thus in *Holoptychius*, if the "intertemporals" (or supratemporals) are considered to be absent, and the median elements of the "parietal" shield are regarded

as the "parietals" (postparietals), the otic sensory canals appear to have been deflected through the nearest ossification centers, namely, those in the "parietals." If the fields are for some reason relatively weak and are unable to attract the sensory-canal primordia, the canals may develop close to or along bone sutures, as in the case of the supraorbital canal in coelacanths. Parrington emphasizes the fact that this hypothesis can only be tested experimentally, which must be done before the sensory-canal primordia have reached their permanent positions. He considers at some length the various other theories, and the reader is referred to his 1949 paper for a fuller consideration than is given here.

The osteolepid braincase structures utilized by Westoll (1943a, fig. 3) in determining the homologies of the dermal bones in the osteolepid and stegocephalian skull-roof are similarly located in the well-ossified late Devonian coelacanth endocranium. It follows, therefore, that the revised osteolepid demal-bone terminology may be applied to the coelacanth skull-roof. The fronto-ethmoid shield will include the fronto-nasal series and the parietals. The intertemporals might be regarded as the posterior supraorbitals, as missing, or as fused with the main elements of the "parietal" shield. The "parietal" shield will consist of the large paired supratemporals, assuming the postparietals to be absent, and the tabulars.

On the basis of Parrington's conclusions regarding the "parietal" shield in *Holoptychius*, the coelacanth intertemporals of Moy-Thomas (1937), following the revised osteolepid terminology, will become the postparietals. The large, paired, medial ,bones in the coelacanth "parietal" shield thus have a number of possible names, depending on which interpretation is accepted—parietal, "parietal," parieto-intertemporal, fronto-parieto-intertemporal, fronto-parieto-intertemporo-dermosphenotic, intertemporal, "parieto"-dermopterotic, supratemporal, or postparietal. In rejecting a single-name terminology, Jarvik (1948, p. 81) claims that such bones must be compound structures which, in many cases, are probably not "even approximately identical with correspondingly named bones in tetrapods."

It appears obvious that any names applied to the skull-roof bones of coelacanths must, at the present time, be considered as arbitrary. Which names are "closer to the truth" is also a matter of opinion, even if Westoll's conclusions are accepted. The same problem is involved in the terminology of the cheek elements. If Parrington's hypothesis is carried a bit farther, and the jugal sensory canal is not exclusively employed to determine homology, the coelacanth cheek pattern can be compared readily with the osteolepid by taking into account the loss of the maxillary and possibly the subopercular.

There are two fundamental interrelated issues involved in this confused picture. One is the nature of the relationship between sensory canals and dermal bones. The other is under what conditions sensory canal and anamestic bones fuse with their own kind or possibly with each other, subdivide, remain independent, or disappear in a genetic sense. Until some or all of these problems can be resolved experimentally, the homology question will never be entirely settled. Occasion-ally, important transitional types are discovered, such as *Elpistostege*, which do greatly elucidate the dermal-bone identifications and homologies in groups having an ancestor-descendent relationship. Perhaps an intermediate stage between the osteolepids and the coelacanths (not *Dictyonosteus*) may go a long way towards resolving this problem in the coelacanths.

The history of dermal bone nomenclature in the coelacanth skull, exclusive of the mandible, is traced in table 2. Although the terminologies of certain early workers on the group have been omitted, an attempt has been made to include the various opinions expressed in the more recent papers. It will be noted that while some bones have retained the same name for a long period, implying general agreement on homology, others have suffered a variety of single and compound labels. The last two columns represent interpretations based on Westoll's revised osteolepid terminology and on this plus possible conclusions from Parrington's hypothesis.

TABLE 2
PARTIAL HISTORY OF DERMAL-BONE NOMENCLATURE IN THE COELACANTH SKULL[a]

Woodward, 1909	Stensiö, 1921	Watson, 1921	Stensiö, 1932	Moy-Thomas, 1935	Nielsen, 1936	Moy-Thomas, 1937	Stensiö, 1937	Smith, 1939	Westoll, 1939	Jarvik, 1942	Stensiö, 1947	Saint-Seine, 1949	Interpretation based on Westoll, 1937, 1940, 1943; Romer, 1945	Interpretation based on preceding, plus Parrington, 1949
—	—	Premaxilla	Rostralo-pre-maxillary (*Laugia*)	"Premaxilla"	Premaxillary	Premaxillary	Rostralo-premaxillary (in *Macropoma*)	Rostral	—	Premaxillary	—	Premaxillary	Premaxillary	Premaxillary
Ethmoid dermal plates	Rostral	Median parafrontal		—	Rostral+ interrostral	—	(Rostral)	(Rostro-nasal complex)	—	Median rostral+post-rostral (=interrostral)	—	Rostral and interrostral	Rostral complex	Rostral complex
	Interrostral+ postrostral	—	Postrostral	Posterior rostral	Postrostral	Postrostral	Postrostral+ naso-post-rostral		—	Nasal	—	—	Post-rostral (median)+ fronto-nasal series	Post-rostral+ fronto-nasal series
Frontal	Fronto-dermosphenotic (fused)	Frontal (one pair)	Frontal (one pair)	Frontal (anterior and posterior)	Fronto-postrostral+frontal (one pair)	Frontal (anterior and posterior)	Frontal (one pair)	Frontal (anterior and posterior)	Frontal	Frontal (one pair)	"Frontal"	Frontal (anterior and posterior)	Parietal	Parietal
Parafrontal	Supraorbital	Parafrontal	Supraorbital	Supraorbital	Nasal+ supraorbital	Supraorbital	Supraorbital	Parafrontal+ parafronto-antorbital+ naso-antorbital)	—	Anterior tectal +supraorbital	Supraorbital	Nasal and supraorbital	Supraorbital (prefrontal-postfrontal series)	Supraorbital (prefrontal-postfrontal in part)
—	(Dermosphenotic fused with fr. in Spitzbergen forms)	—	Dermosphenotic	Dermosphenotic	Supraorbital	Dermosphenotic	Supraorbital	Dermosphenotic fused with frontal?	Dermosphenotic may be fused with "parietal"	—	Dermosphenotic not independent	Dermosphenotic	?Intertemporal	?Intertemporal
—	Sclerotic ring	—	—	Circum-orbital plates	—	Circumorbital plates	—	—	—	—	—	Sclerotic plates	—	—
Parietal	Parieto-intertemporal	Parietal	Parieto-intertemporal	Parietal	Fronto-parieto-intertemporal[b]	Intertemporal	Parieto-intertemporal (may incl. dermosphenotic)	Intertemporal	"Parietal"	—	"Parieto"-dermosphenotic	Intertemporal (parietal)	Supratemporal	Postparietal
—	Supratemporo-extrascapular	Supratemporal	Supratemporal	Supratemporal	Supratemporo-extrascapular	Supratemporal	Supratemporal	Supratemporal	Supratemporal	—	Posterior dermopterotic	Supratemporal	Tabular	Tabular
—	Extrascapular+ suprascapular	—	Extrascapular	Extrascapular	Extrascapular+ suprascapular	Extrascapular	Extrascapular	Extrascapular	—	—	Extrascapular	Extrascapular	Extrascapular	Extrascapular
—	—	—	—	—	Lateral rostral	Rostral	Lateral rostral	Latero-rostro-nasal	—	Lateral rostral	Lateral rostral	Lateral rostral	Lateral rostral (=?prenarial)	Lateral rostral (=?prenarial)
—	Nasalo-antorbital	—	Nasalo-antorbital	—	Antorbital	Antorbital	Antorbital	Antorbital fused with a parafrontal and a nasal	—	Posterior tectal	Posterior tectal	—	"Antorbital"	"Antorbital"
Suborbital	Lacrymo-jugal	Suborbital	Lacrymo-jugal	Lacrimo-jugal	Lacrymo-jugal	Lacrymo-jugal	Lacrymo-jugal	Lacrymo-jugal or suborbital	Lacrymo-jugal	—	Postorbito-infraorbital	Lacrymo-jugal	Lacrymo-jugal	Lacrymo-jugal
Upper postorbital	Postorbital	Postorbital	Postorbital	Postorbital	Postorbital	Postorbital	Postorbital	Postorbital	Postorbital	—	Postorbital	Postorbital	Postorbital	Postorbital
—	—	—	—	Suprasquamosal	Suprasquamosal	Spiracular bone	Supra-squamosal	Postspiracular	Supra-squamosal	—	Prespiracular plate	—	Spiracular	Spiracular
Lower postorbital	Squamoso-preopercular	(Squamosal)	Squamosal	Squamosal	Squamoso-preopercular	Squamosal	Squamoso-preoperculum	Squamosal	Squamosal	—	"Squamoso-pre-operculum" or dorsal preoperculum	Squamosal	Squamosal	Squamosal
Lower postorbital	Preoperculo-quadratojugal (in *Wimania*)	Quadrato-jugal	Quadrato-jugal	Preoperculo-quadratojugal	Preoperculo-quadratojugal	Preopercular	Preoperculo-quadratojugal	Preopercular	Preopercular	—	Preoperculo-quadratojugulo-supramaxillary or preoperculo-quadrato-jugal	Preopercular	Preopercular	Quadratojugal
—		(Preopercular)	—	Preopercular	Subopercular	Subopercular	Subopercular or branchiostegal plate	Subopercular	Subopercular	—	Suboperculum	Subopercular	Subopercular	Preopercular
Opercular	Opercular	(Opercular)	Opercular	Opercular	Opercular	Opercular	Opercular	Opercular	Opercular	—	Operculum	Opercular	Opercular	Opercular
			—	—	—	—	—	Interopercular	—	—	—	—	—	—

[a] Because of pattern differences between the various genera, a bone-for-bone comparison is not always possible. Inferred bone-names not specifically mentioned by the author or in explanatory notes are in parentheses. Dashes indicate either that the bone, or bones, are absent in the form considered or else are not identified.

[b] Or fronto-parieto-intertemporo-dermosphenotic.

ALTHOUGH THE ARRANGEMENT of the dermal bones in the skulls of various coelacanth genera has been discussed by Moy-Thomas (1935, 1937), Stensiö (1921, 1932, 1937), Westoll (1939), Nielsen (1936), Jarvik (1942), and others, no attempt has been made to assemble figures of the better known forms for a general comparative survey. The reconstructions in figures 14 and 15 include skulls of most of the genera that are known in sufficient detail to warrant consideration. Certain of the dorsal views are based on published lateral views and they may be inaccurate in some details.

Perhaps the most striking feature of the skull-roof series is the variation in the form and number of the bones in the various genera. In spite of the fact that the basic design has remained essentially unaltered from at least the late Devonian to the Recent, there is a pattern peculiar to nearly every genus that has, with few exceptions, no obvious adaptational significance. These pattern differences do not reflect the reduction in the ossification of the endocranium that occurred by the Mississippian, nor do they reflect the current subdivision of the Coelacanthini into four families. Throughout the long history of the group there has been no clear-cut, long-range trend in the dermal skull-roof towards increase or reduction in the number of bones or towards detailed pattern fixation at the family level.

The fronto-ethmoid shield is composed of a series of paired median bones, a series of lateral elements, and a rostral complex that may include a few or numerous paired and unpaired ossifications. Each series has a characteristic, although variable, pattern at the generic level; the variations, as far as known, have no specific value. In a number of genera, such as *Whitea*, the unnamed Greenland Triassic form, *Undina*, *Macropoma*, and *Latimeria*, the median series includes two pairs of relatively large, more or less elongated bones. In *Whitea*, Moy-Thomas (1935) states that these elements represent the subdivided frontals because the sutures between them project backward, suggesting the secondary subdivision of a single bone. Nielsen (1936) agrees with Moy-Thomas, since the two

pairs of frontals "have the same rostro-caudal extent as the single pair of frontals found in for instance *Wimania* and *Axelia*." In the unnamed Triassic form, Nielsen calls the anterior pair fronto-rostrals and the posterior pair frontals. Saint-Seine (1949) recognizes two pairs of frontals in *Undina*, again because of a backwardly projecting suture between the anterior and posterior pairs.

In *Diplurus*, the two pairs of "frontals" have about the same relationships as in the above-mentioned genera. When one of the anterior frontals is missing as a separate element, the postrostral on that side is enlarged. The fate of the missing anterior frontal cannot be positively determined. In view of the unstable pattern in this area, it is possible that the anterior frontal fused with the postrostral at an earlier stage in ontogeny. This conclusion is strengthened by the tendency, in both *Diplurus* and the unnamed Triassic form, for the postrostrals to show various degrees of subdivision and fusion. A transverse suture may extend half the distance from the median longitudinal suture to the lateral border and then disappear. The anterior frontals may share a similar susceptibility towards fusion and separation.

The postrostral region in coelacanths includes the bones in the median series between the "frontals" and the premaxillary (*Rhabdoderma*) or between the "frontals" and a group of smaller rostral elements covering the snout (unnamed Greenland form). Jarvik (1942, pp. 351–353) is of the opinion that the bones called postrostrals must now be regarded as nasals on the basis of their association with the supraorbital sensory canal and their similarity to the rhipidistian nasals. In *Latimeria* (*ibid.*, p. 35) he recognized six pairs of independent nasals, the posterior members of the series equaling the anterior frontals of Smith (1939). In 1937 Moy-Thomas suggested that it would be desirable to speak of the "frontonasal series." He did not state, however, whether or not the paired elements called by him postrostrals should be included in this series. The median interrostrals are regarded by Jarvik as postrostrals. Jarvik's conclusions permit a more direct comparison with the osteolepid snout,
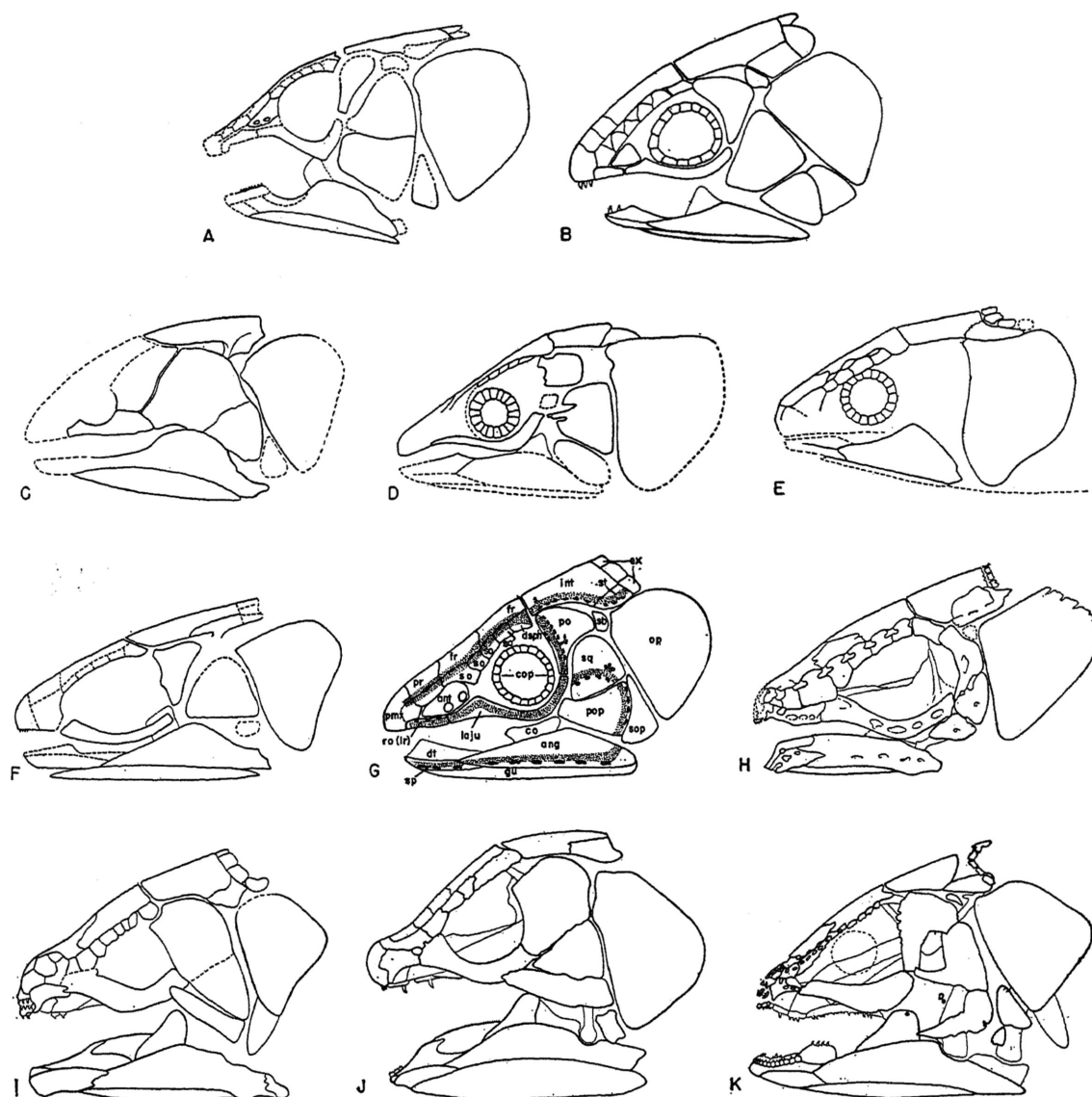
FIG. 14. Series of coelacanth skulls in lateral view. A. *Nesides schmidti* (after Stensiö, 1937). B. *Rhabdoderma elegans* (after Moy-Thomas, 1937). C. *Spermatodus pustulosus* (after Westoll, 1939, and specimens). D. *Wimania sinuosa* (after Stensiö, 1921). E. *Axelia robusta* (after Stensiö, 1921). F. *Laugia groenlandica* (after Stensiö, 1921, and Nielsen, 1936). G. *Whitea* sp. (after Moy-Thomas, 1935, 1937, and Nielsen, 1936), showing typical arrangement of sensory canals. H. *Diplurus newarki*. I. *Undina cirinensis* (modified after Saint-Seine, 1949). J. *Macropoma mantelli* (after Watson, 1921, Westoll, 1939, and specimens). K. *Latimeria chalumnae* (based on Smith, 1939). For abbreviations used in G, see page 78.
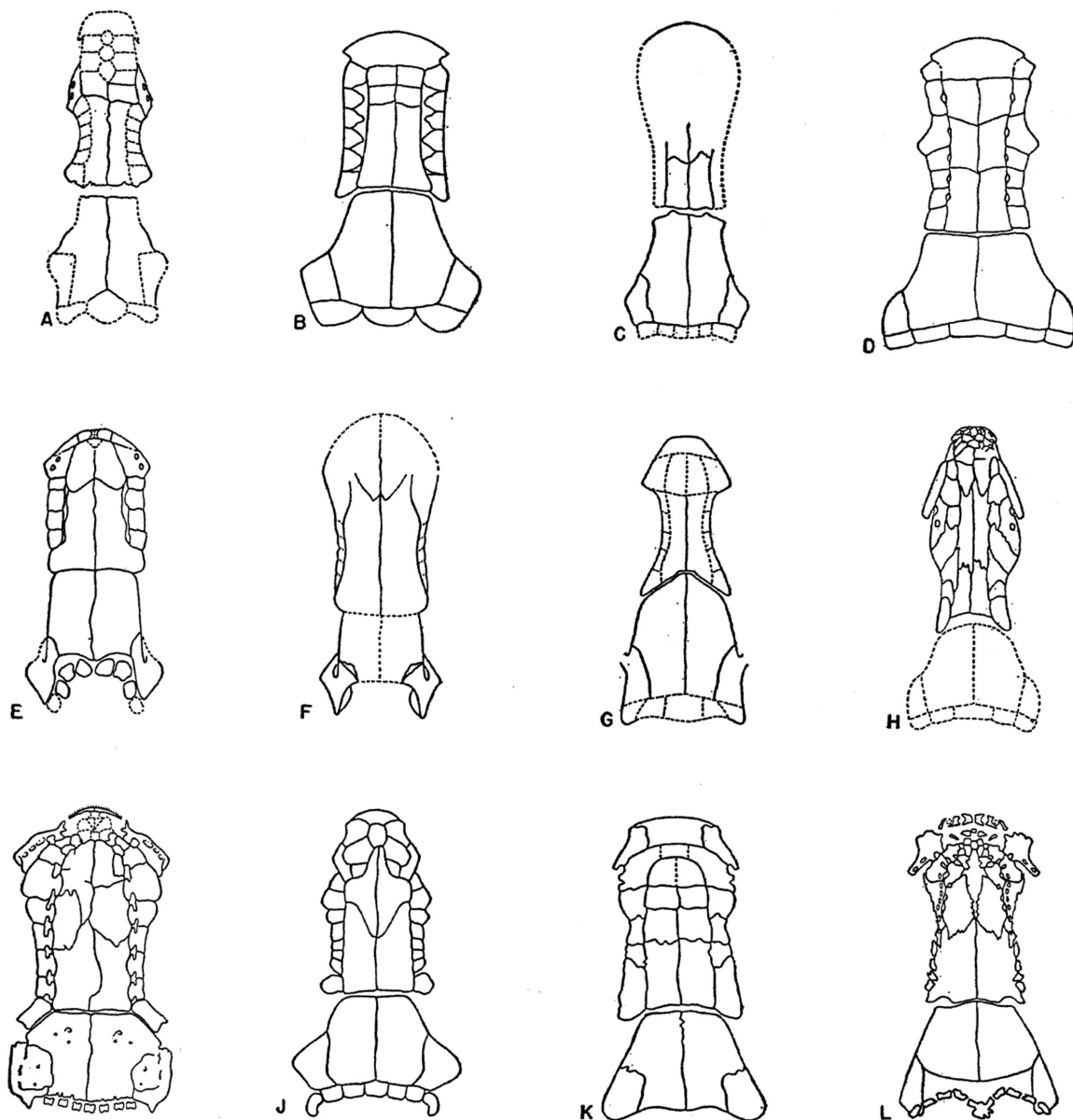
FIG. 15. Series of coelacanth skull-roofs in dorsal view, based on references cited in figure 14 and additional ones given here. B, J, and K prepared from published lateral views and specimens. A. *Nesides schmidti.* B. *Rhabdoderma elegans.* C. *Coelacanthus granulatus* (after Moy-Thomas and Westoll, 1935). D. *Whitea* sp. E. *Axelia robusta.* F. *Wimania sinuosa.* G. *Laugia groenlandica.* H. Undetermined coelacanth from East Greenland (after Nielsen, 1936). I. *Diplurus newarki.* J. *Undina cirinensis.* K. *Macropoma mantelli.* H. *Latimeria chalumnae.*

but in forms like *Rhabdoderma* and *Whitea*, separate interrostrals or postrostrals must then be regarded as absent.

The front part of the snout is completely known in only a few genera. Apparently the small rostral elements, which Jarvik (1942) believes are associated with a rostral commissural canal, are absent in *Rhadboderma*, in several of the Triassic genera, and in *Undina* and *Macropoma*. Since the rostral commissural canal has not been generally observed, it is actually impossible to separate rostrals from postrostrals (or nasals), and Saint-Seine (1949) makes no distinction between them in *Undina*. The rostral area in the unnamed Triassic form, in *Latimeria*, and perhaps in *Diplurus* is covered with a number of small elements, between which are large sensory pores. To what extent this rostral subdivision occurs throughout the Coelacanthini is at present unknown.

The coelacanth premaxillary varies considerably in shape and relative size among the various genera in which it has been found. In the Coelacanthidae, the premaxillaries are frequently fused and have a large, exposed, anterodorsal portion that caps the front end of the snout, as in *Whitea* or *Macropoma*. In the unnamed Greenland form, which Nielsen (1936) states is similar to *Whitea*, and in *Diplurus*, the premaxillary is apparently relatively narrow and without a marked anterodorsal expansion. In *Latimeria* the premaxillaries are represented by a series of separate dentigerous elements, called rostral dental plates by Smith (1939), but regarded as premaxillary components by Jarvik (1942, p. 349). Stensiö (1937) labels the premaxillary of *Macropoma* "rostro-premaxillary," implying that the anterodorsal portion is composed of fused rostral elements.

The supraorbital series, including its forward extension on the snout, contains at least five elements, and frequently as many as seven, arranged in a more or less linear manner. These bones vary considerably in relative size and shape among the different genera and to a lesser extent within a species (*Diplurus newarki*). The median borders are usually grooved to accommodate, in part, the supraorbital canal, and they are frequently notched to provide a series of large sensory pores. Those members of the series situated over the

nasal cavity have been called nasals by Nielsen (1936), but, as discussed earlier, have been renamed tectals by Jarvik (1942). The posterior supraorbital ("dermosphenotic") may oppose the anterior border of the intertemporal (*Whitea*), or it may have an extensive contact with the lateral margin of the intertemporal (*Diplurus*).

The so-called tectal elements include the first two or three members of the supraorbital series, plus the posterior tectal or "antorbital." In the absence of a separate "antorbital," the lacrimo-jugal articulates directly with the supraorbital series, except in *Latimeria*. Jarvik implies that the absence of a separate "antorbital" in coelacanths is due to fusion of this bone with a supraorbital. This fusion has not been demonstrated, although Jarvik (1942) supports his argument by the fact that the prefrontal (supraorbito-tectal) of *Eusthenopteron* may be horizontally subdivided into what he calls an anterior supraorbital and a posterior tectal. Of the forms without a separate "antorbital," only *Undina* and *Macropoma* show evidence of being closely related. The affinities of *Diplurus* and *Latimeria* remain to be determined. There is thus the probability that the loss of the "antorbital," however it occurred, was accomplished independently in several different genera.

The coelacanth "parietal" shield is exceptional in having remained nearly static in its pattern since the middle Devonian. This early fixation in the arrangement and number of the elements must have some functional significance which can be most logically related to the persistent ossification of the otic portion of the braincase. The subdivision of this shield into paired "intertemporals" meeting in the midline, and posterolaterally situated "supratemporals" occurs apparently without variation. There is some variation in the number and relative size of the extrascapulars. Westoll (1939) has pointed out that the "parafrontals" figured by Watson (1921) on the "parietal" shield of *Macropoma* are absent, and that a suture between the intertemporals and supratemporals is present.

In most genera, including *Diplocercides*, the entire median border of the supratemporal articulates with the intertemporal, and

the posterior borders of these elements form a nearly straight, transverse line. In *Wimania*, *Axelia*, and *Latimeria*, however, the contact between the intertemporal and the supratemporal is greatly reduced, and the supratemporal projects beyond the posterior limit of the intertemporal for the greater part of its length. In the rhipidistians, the occipital portion of the braincase projects caudally beyond the dermal skull-roof (Romer, 1937), and in several coelacanth genera there is evidence of the same condition. On the basis of Moy-Thomas' (1937) restoration of *Rhabdoderma*, it appears that the entire supraoccipital ossification is situated behind the posterior border of the "parietal" shield; this is also the case in *Wimania* (Stensiö, 1921). In *Macropoma*, on the other hand, Watson's reconstruction places the supraoccipital almost entirely under the shield. To what extent the freeing of the supratemporals and the greater exposure of the braincase in these few genera are related to a decrease in the size of the intertemporals is difficult to determine. The rather constant relationship between the supratemporals and the opercular complex in the various genera with and without projecting supratemporals suggests, however, that the intertemporals did undergo a relative reduction in length. The greater exposure of the occipital area may be related to an enlargement of the attachment area for the epaxial musculature, as in certain actinopterygian fishes.

The pattern of the cheek elements in coelacanths varies sufficiently from genus to genus to be of primary taxonomic value. In all the genera in which the cheek area is known, except one, the postorbital and, when present, the spiracular bone exclude the squamosal from contact with the "parietal" shield. In *Spermatodus* (Westoll, 1939), however, the enlarged squamosal meets the shield, and the postorbital is reduced (fig. 14C). This convergence towards the rhipidistian condition is further exemplified by the anteriorly placed orbit and the oblique suspensorium, which, as Westoll notes, is unusul among coelacanths. The preopercular usually has a contact with the lacrimo-jugal, but it may be separated from this bone by the squamosal (*Rhabdoderma*) or by its general disposition (*Latimeria*). The subopercular may lie either behind or under the preopercular or be absent (*Laugia* and possibly *Diplurus*). The variation in the shape, size, arrangement, and even the number of cheek elements in front of the opercular indicates that this portion of the cheek complex has little functional significance. The absence of all the cheek bones in *Axelia* (Stensiö, 1921; Westoll, 1937), except for the opercular and two tubular ossifications around the sensory canals, further supports this conclusion. The opercular is without exception well developed and of a characteristic triangular shape.

The general pattern of the lower jaw is fairly constant. Perhaps the greatest deviation is found in *Diplurus* with the relatively large angular and curiously shaped dentary and splenial. The elevation of the plate-like coronoid, already typically coelacanthid in *Nesides* and the other Devonian forms, may be related to the loss of the maxillary. As Smith (1939) states, its principal function perhaps was to limit lateral motion of the mandible, which is prevented in the rhipidistians by the maxillary and the quadratojugal.

SUMMARY OF TRENDS IN COELACANTH EVOLUTION

THE OSTEOLEPID-COELACANTH TRANSITION was essentially completed by or in the early Middle Devonian. The selective factors involved in channeling this trend are difficult to visualize. The coelacanth design, in spite of its many highly characteristic features, is not in its entirety obviously adapted for any particular type of aquatic environment, for any specific type of food, or for any specialized mode of locomotion. As pointed out previously (Schaeffer, 1948), coelacanths have inhabited a variety of fresh-water and marine environments since their origin, without much apparently related structural change. The dentition is generally rather feeble, although a few genera have a dentition or jaw structure suggesting predation or food crushing. The problem of body-form and locomotion has also been considered (*ibid.*, pp. 19–26); except for the interesting specialization exhibited by *Laugia* (Stensiö, 1932), there is no clear suggestion of alteration in locomotor pattern since the Devonian.

The evolution of another choanichthyid group with a comparable time range, the Dipnoi, has been considered in a very illuminating paper by Westoll (1949). Although the origin of the dipnoans is less certain than that of the coelacanths (either from the rhipidistians or from a common ancestral group which also gave rise to the rhipidistians), there is clear evidence of progressive evolutionary change from the late early Devonian to the appearance of the now-living genera in the Tertiary. There are a number of genera, called "normal" by Westoll, that range throughout the history of the group and exhibit this progressive change. A few from the late Devonian and early Permian are specialized off-shoots. For each character complex or morphological entity studied, Westoll worked out a series of evolutionary stages, to each of which he assigned a numerical value. By adding these values for each genus, he arrived at a total value expressing the relative evolutionary level of each genus. These totals were then plotted against time to show graphically the loss of ancestral characters. The graph does not show the rate of loss per unit of time, but this can be readily computed from Westoll's data.

A similar analysis might be made to evaluate evolutionary change within the Coelacanthini, but it would be much more subjective and, in the writer's opinion, not particularly revealing. The most radical change occurred during the osteolepid-coelacanth transition, which is as yet poorly documented. Since relatively few of the trends exhibited within the Coelacanthini are of long duration, it is perhaps more useful to list the major skeletal changes in chronological sequence. The phylogenetic relationships of the known coelacanth genera are obscure, and the more "normal" genera, for many features, can be arranged for the most part only in a morphological series. The "normal" and specialized genera are considered together at their particular time levels.

The following genera have been fully described by the authors cited and represent the basis for these tabulations. They are not all restricted to, but are characteristic of, the periods designated. A number of late Triassic, Jurassic, and Cretaceous genera have not been adequately treated, or are poorly known, and cannot properly be considered here.

Middle and Late Devonian: *Euporosteus*, *Diplocercides*, *Nesides* (Stensiö, 1932; Jarvik, 1942); *Dictyonosteus* (Stensiö, 1918, 1921; Jarvik, 1942)

Mississippian-Pennsylvanian: *Rhabdoderma* (Moy-Thomas, 1937)

Permian: *Coelacanthus* (Moy-Thomas and Westoll, 1935); *Spermatodus* (Westoll, 1939)

Triassic: *Whitea* (Moy-Thomas, 1935; Nielsen, 1936); *Wimania*, *Axelia*, *Mylacanthus*, *Scleracanthus*, *Sassenia* (Stensiö, 1921); *Diplurus* (Schaeffer, 1941, 1948, and this paper); *Laugia* (Stensiö, 1932), unnamed East Greenland form (Nielsen, 1936; Jarvik, 1942)

Jurassic: *Undina* (Aldinger, 1930; Saint-Seine, 1949)

Cretaceous: *Macropoma* (Woodward, 1909; Watson, 1921); *Mawsonia* (Weiler, 1935; Stromer, 1936)

Recent: *Latimeria* (Smith, 1939)

ENDOCRANIUM

LATE DEVONIAN: Completely ossified; divided into trabecular and parachordal moieties as in rhipidistians. Antotic and basipterygoid processes well developed. Noto-

chordal canal in occipital region of para-chordal moiety. Differs from rhipidistian endocranium in *possible* loss of internal nares (Jarvik, 1942), loss of pineal foramen, probably fewer occipital arches incorporated into parachordal moiety, development of median róstral cavity in internasal wall, nasal cavity with single large fenestra in lateral nasal wall, and relative elongation of trabecular moiety.

CARBONIFEROUS: Marked decrease in ossification of both moieties. Trabecular moiety represented by small, paired ethmoid ossifications and large basisphenoid ossification with strongly developed antotic processes. Basipterygoid process reduced and probably nonfunctional. Parachordal moiety represented by paired prootic ossifications and a number of occipital elements.

PERMIAN: Extent of ossification about as above; basipterygoid process absent.

TRIASSIC: As above, except for secondary increase in ossification of interorbital region and possibly parachordal moiety in *Laugia*.

JURASSIC-CRETACEOUS: No significant change.

RECENT: Incompletely known, but little evidence of further reduction in extent of ossification.

PALATE

LATE DEVONIAN: Metapterygoid (epiterygoid of rhipidistians) enlarged to form an antotic articulation in addition to the median contact with basipterygoid process. Quadrate swung forward to a position nearly under or not far behind metapterygoid. Suspensorium slightly oblique instead of markedly so as in rhipidistians. Quadrate triangular, with ventrally projecting, rounded condyles. Pterygoid triangular. Autopalatine with essentially same relationships to postnasal wall and ethmosphenoid area as in rhipidistians. Areas occupied by vomers (*Euporosteus*) ovoid and relatively large; vomers did not extend posteriorly along parasphenoid as in rhipidistians. Parasphenoid running entire length of trabecular moiety and expanded anteriorly; hypophysial opening generally present.

CARBONIFEROUS: As above except for loss of basipterygoid articulation. Pterygoid widely emarginated on dorsal border. Epi-pterygoid and dermopalatine ossifications are present; they were undoubtedly present in the Devonian forms. Vomers presumably situated on ethmoid ossifications. Parasphenoid as above, articulating anteriorly with ethmoid ossifications and posteriorly with basisphenoid, to which it may be fused. Hypophysial opening not recorded.

PERMIAN: No change except for secondary backward projection of the pterygoid in *Spermatodus*, producing a rhipidistian-like obliquity to the suspensorium. Vomers relatively smaller than in *Euporosteus*. Parasphenoid as above, hypophysial opening (in *Spermatodus*) near center of growth of parasphenoid and relatively farther forward than in Devonian forms.

TRIASSIC-RECENT: No major change; some variation in emargination of dorsal border of pterygoid and in slope of suspensorium. Vomers small. Parasphenoid as above; hypophysial opening not recorded.

DERMAL BONES OF SNOUT

LATE DEVONIAN: Rhipidistian maxillaries lost. Premaxillaries and other anterior snout bones unknown. Nasals (postrostrals) and postrostrals (interrostrals) numerous and arranged much as in rhipidistians, but supraorbital canals follow lateral margins of nasals. Tectal portion of supraorbital series not preserved. "Antorbital" (posterior tectal) with two narial apertures. Lateral rostral presumably homologous with similarly situated element in some rhipidistians and containing passage for infraorbital sensory canal. Anterodorsal process of lateral rostral separates lateral fenestra of nasal cavity into anterior and posterior narial openings. The anterior opening, according to one interpretation, gave exit to anterior nasal tube and posterior opening to posterior nasal tube which, in turn, had two openings in the posterior tectal (Jarvik, 1942, fig. 79). In *Eusthenopteron* (*ibid.*, fig. 59), the posterior nasal tube passed through the posterior nasal wall; this condition has not been reported in "*Megalichthys*" (Romer, 1937).

CARBONIFEROUS: Premaxillaries capping end of snout as in rhipidistians. Separate small rostral elements absent. Tectal portion of supraorbital series extending forward to premaxillaries. "Antorbital" with paired

narial openings as above. Lateral rostral presumably as above. Nasals (postrostrals) present; no separate interrostrals reported.

PERMIAN: Snout unknown.

TRIASSIC: Premaxillaries capping end of snout or reduced to smaller marginal element. Other rostral dermal bones variously "subdivided" or absent. "Antorbital" present with paired openings, or absent. Lateral rostral with ventral process meeting ethmoid ossification, relations essentially as above. Commissure between supraorbital and infraorbital canals.

JURASSIC–CRETACEOUS: Premaxillaries capping end of snout. Rostral bone pattern variable, as above. "Antorbital" absent. Narial apertures presumably associated with lateral rostral.

RECENT: Premaxillaries represented by series of small plates. Rostral series associated with infraorbital commissure. Nasals (postrostrals) and tectal elements numerous, arranged on either side of supraorbital canal. Postrostrals (interrostrals) present. Separate "antorbital" absent. Lateral rostral similar in relationships to Triassic forms. Anterior narial openings in rostral series; posterior narial openings probably along anterodorsal border of orbit. Origin of nasal tubes in doubt; according to Smith they issue from median rostral cavity, but Woodward (1940) and Jarvik (1942) suspect, more logically, that they arise from nasal cavities. Sensory canal commissures further elaborated.

SKULL–ROOF

LATE DEVONIAN: Typical coelacanth pattern, differing from rhipidistian in multiplication of supraorbitals, shift of supraorbital sensory canal to position between supraorbital and frontonasal series, loss of dermosphenotic or incorporation into "parietal" shield, absence of one pair of elements in "parietal" shield associated with otic sensory canal in rhipidistians. Median paired elements of "parietal" shield variously interpreted, usually called intertemporals.

CARBONIFEROUS: No important change, variation in "subdivision" of fronto-nasal series. Along with reduction of parachordal moiety a ventral process developed on supratemporal articulating with prootic.

PERMIAN–CRETACEOUS: Variation in number and relative size of bones in fronto-eth-

moid shield.

RECENT: No major change in pattern; median fontanelle present in anterior part of fronto-ethmoid shield.

CHEEK AREA

LATE DEVONIAN: Rhipidistian lacrimal and jugal presumably fused. Quadratojugal lost and preopercular shifted to a position under squamosal. Subopercular moved behind or under preopercular. Postorbital and spiracular bone exclude squamosal from contact with "parietal" shield. Spiracular bone may be same as postspiracular of Eusthenopteron (Jarvik, 1944). Opercular relatively larger than in rhipidistians and with a characteristic triangular shape. In contrast to the rhipidistian condition, the cheek bones are loosely associated or apparently actually separated. Circumorbital plates unknown, possibly not ossified. Disposition of sensory canals, on basis of above homologies, essentially as in rhipidistians.

CARBONIFEROUS: No significant change. Circumorbitals ossified.

PERMIAN: In Spermatodus only, postorbital secondarily reduced and squamosal in contact with "parietal" shield as in rhipidistians. Circumorbitals. unknown.

TRIASSIC: Variable reduction in degree of ossification of cheek bones in the Spitzbergen genera and Laugia. In Axelia space between lacrimo-jugal and opercular without bones except for two very small tubular ossifications on infraorbital and jugal canals. In Diplurus subopercular may be absent. Circumorbitals ossified in most genera.

JURASSIC–CRETACEOUS: No reduction in ossification; cheek patterns in Undina and Macropoma very similar. Bones in closer contact. Circumorbitals (sclerotics?) present in Undina.

RECENT: No marked reduction, but distinctive pattern. Subopercular and particularly "interopercular" may be modified scales in opercular membrane. Circumorbitals unknown.

MANDIBLE

LATE DEVONIAN: Radical modification from the rhipidistian type in development of short dentary overlying single splenial, greatly elongated angular (angulo-surangular), and posterior coronoid enlarged and projecting

above dorsal margin of jaw. Anterior coronoid smaller, dentigerous. Prearticular covering most of the inner mandibular surface. Extensive adductor fossa between angular and coronoid. Articular exposed behind and above posterior border of angular, with well-defined quadrate facet. Presence of "symplectic" facet questionable.

MISSISSIPPIAN–CRETACEOUS: Minor variation in angle of dentigerous border of dentary, in size and number of anterior coronoids, and in width of angular. Ventromedian elongation of dentigerous portion of dentary and associated part of splenial in *Diplurus* apparently unique. "Symplectic" facet on articular in *Macropoma* and *Mawsonia* (Woodward, 1940).

RECENT: Dentary supporting inner and outer series of small dentigerous plates. Anterior coronoid large, bearing teeth. Articular with quadrate and "symplectic" facets.

HYOID AND GILL ARCHES

LATE DEVONIAN: Unknown, except for urohyal, which has not been described in rhipidistians, and paired gulars. Median gular absent.

MISSISSIPPIAN–CRETACEOUS: Hyoid arch represented by ossified "epihyal" (ossification in the hyomandibular?) and ceratohyal. There are five branchial arches consisting of ossified ceratobranchials and in some forms also of epibranchials. A large median basibranchial ossification is present in the unnamed Triassic form, covered with a series of dentigerous plates. A similar element has been observed in *Eusthenopteron*. The ossified dentigerous plates are probably generally present, but the basibranchial must have been frequently cartilaginous. Urohyal and paired gulars generally present.

RECENT: Hyomandibular cartilaginous except for central ossified portion. It is attached dorsally to ventral process of supratemporal and posteriorly to opercular. Position of hyomandibular in relation to exits for hyomandibular branch of facial nerve and jugular vein apparently as in *Megalichthys* (Romer, 1941). "Symplectic" ossification not definitely known in earlier genera, and its identity in *Latimeria* has not been clearly established. Evidence of only four gill arches (also the case in *Macropoma*?). Basibranchial ossification covered with two pairs of dentigerous

plates. Ceratohyals and urohyal not preserved. Gulars paired.

DENTITION

LATE DEVONIAN–RECENT: Generally much weaker than in rhipidistians, but with about the same distribution, except for absence of maxillary. Teeth are usually small, pointed, conical or somewhat spheroidal; occasionally more tusk-like on jaw margins and on certain palatal elements. Distribution includes premaxillaries, parasphenoid, pterygoids, ectopterygoids, dermopalatines, vomers, dentary, coronoids, prearticular, basibranchial dermal plates, hyoid and gill arches. They may be absent on the premaxillaries and the coronoids (*Whitea*). In some Triassic genera (*Axelia*, *Mylacanthus*, *Scleracanthus*) the teeth are robust and presumably adapted for crushing. The basibranchial dentition of *Diplurus longicaudatus* is very well developed. In *Latimeria*, there are two rows of dentigerous plates on the dentary, and the marginal dentition is generally suggestive of predation. There may be a rough inverse correlation between the development of teeth on the jaws and on the rest of the visceral skeleton as in some teleosts.

AXIAL SKELETON

LATE DEVONIAN–RECENT: Notochord not surrounded by ring-shaped intercentra as in rhipidistians; small basiventral ossifications present in a few genera. Neural arches are united and V-shaped; more strongly ossified and with complete neural canal in Devonian forms (*Diplocercides*). Neural and haemal spines perichondrally ossified. Ossified pleural ribs are usually either very short or absent; elongated only in *Diplurus*. Haemal arches V-shaped and haemal spines elongated.

PAIRED FINS AND GIRDLES

LATE DEVONIAN–RECENT: Pectoral girdle basically the same as in rhipidistians except for loss of interclavicle and addition of extracleithrum, which may fuse with cleithrum. Endoskeletal portion may be separate or fused with cleithrum and clavicle. Cleithrum generally narrower than in rhipidistians, but may develop median lamina (*Diplocercides*, *Diplurus*). Three dermal bones of girdle associated with lateral line in rhipidistians

(Jarvik, 1944), not yet confirmed in coelacanths.

Pectoral fin unknown in Devonian forms, otherwise lobate or pedunculate and somewhat higher on body (except in *Laugia*) than in rhipidistians. Endoskeletal axis of fin modified archipterygial type with rhipidistian radials lost, or much reduced, and formed of mesomeral segments (Westoll, 1943b, p. 391). Mesomeral segments rarely ossified. Lepidotrichia not completely segmented.

Pelvic girdle unknown in Devonian genera, otherwise modified from rhipidistian type by development of median process, one to three anterior apophyses and expanded posterior division. Pelves mid-abdominal in position, in contrast to their more posterior location in rhipidistians; in *Laugia* only, pelvic plates in contact with clavicles.

Pelvic fin lobate. Endoskeletal axis modified as in pectoral fin. Mesomeral segments rarely ossified. Lepidotrichia not completely segmented.

UNPAIRED FINS

LATE DEVONIAN: Poorly known, except for Westoll's (1943) statement that in a specimen from Canada they rather resemble the rhipidistians in structure. Caudal fin as below in *Diplocercides*.

CARBONIFEROUS–RECENT: Anterior dorsal fin in front of center of body rather than behind as in rhipidistians. Lepidotrichia articulate directly with ovoid or triangular basal plate. Radials absent. Lepidotrichia robust and incompletely segmented, ornamented with spines or tubercles in some genera.

Posterior dorsal fin somewhat anterior to anal, lobate or pedunculate (*Latimeria*). Basal plate forked anteriorly. Endoskeleton consists of a main segmented radial, with anterior and posterior radials rudimentary (ossified in *Laugia*). Lepidotrichia partly segmented.

Anal fin lobate or pedunculate (*Latimeria*). Basal plate rod-like in known Carboniferous and Permian genera, forked in all later genera except *Laugia*, which has a highly specialized "flying-bird" type. Endoskeletal axis as in posterior dorsal fin; known to be ossified only in *Laugia*. Lepidotrichia not entirely segmented.

Caudal fin of modified diphycercal type, with the middle lobe separated as a supplementary caudal fin. As Reis and Dollo pointed out, it could be an extreme development of the diphycercal form occurring in *Eusthenopteron*. Lepidotrichia of main caudal fin supported by intercalated radials which are considered to be distal segments of neural and haemal spines (Stensiö, 1921). Each lepidotrich is supported by single neural or haemal spine plus radial, in contrast to condition in *Eusthenopteron* (Gregory and Raven, 1941) where one radial is attached to as many as five lepidotrichia. Hence in coelacanths there is a greater number of endoskeletal supports but fewer lepidotrichia than in rhipidistians. Lepidotrichia partly segmented and may have spines or tubercles on anterior border.

Supplementary caudal fin of variable length. Lepidotrichia attached directly to notochordal sheath and partly segmented.

SQUAMATION AND DERMAL BONE STRUCTURE

MIDDLE DEVONIAN–RECENT: Scales thin and cycloidal, exposed portion covered with ridges (striae) or tubercles of varying length which may converge posteriorly, be almost parallel, or be outwardly divergent. Number and orientation of the ridges vary with age and with the region of the body.

Scales and dermal bones are of a modified cosmine type, with the cosmine (dentine) restricted to fine ridges and tubercles (Moy-Thomas, 1937), rather than forming a continuous layer as in rhipidistians. Exposed parts of scales and dermal bones covered with continuous layer of enamel. The enamel may be absent on the ridges and tubercles. The layers of trabecular (vascular) and laminated bone (isopedin) are well differentiated. Openings for vascular canals not observed.

BODY-FORM

LATE DEVONIAN: More or less rhipidistian-like in form from Canada (Westoll, 1943b); otherwise poorly known.

CARBONIFEROUS–RECENT: Fusiform to deeply fusiform; otherwise no great variation. Some differences in head profile. Body generally wider in relation to length than in rhipidistians. Dorsal profile frequently highest at anterior border of dorsal fin; in rhipidistians it is at about the middle of the trunk.

On THE BASIS of the above tabulations, it is possible to note about 52 characters or character complexes that had acquired a distinctly coelacanthid form in the late Middle or early late Devonian. By the early Mississippian there were six or seven additional modifications. The three changes observed in the early Permian forms and the two in the early Triassic are actually end-stages of trends initiated earlier. From the Triassic to the Recent, no modifications occurred that can be included in a general consideration of coelacanth evolution.[1]

Any method of analyzing morphological change that cannot be placed on a strictly quantitative basis is subject to a certain amount of individual interpretation. The selection of definitive coelacanth characters that can be observed in the Devonian genera will vary to some extent according to the consideration of the lesser morphological details or, as Westoll (1949) states, to the "weighting" of the various components of a character complex. Although the number of character changes for any given time interval may be somewhat increased or decreased, the fact remains that by far the greatest amount of change occurred by the late Devonian, with the coelacanth pattern becoming practically fixed after that time, as noted by Moy-Thomas (1939).

Westoll (1943b, p. 391) mentions a specimen from the basal Upper Devonian with "a coelacanth head and squamation but a body form and median fins showing more or less normal rhipidistian conditions." Although no additional information is yet available on this form, it suggests that the median fins evolved towards the typical coelacanth condition at a slower rate than the rest of the skeleton. Variations in evolutionary rate for different character complexes are evident in the dipnoans as well as in other parts of the coelacanth skeleton, particularly in the skull. Generally, character complexes that are closely related functionally evolve at about the same rate.

[1] The character modifications are not listed separately. The interested reader is invited to make his own counts on the basis of the preceding section as a check on the method here employed.

In computing the general morphological evolutionary rate of the Coelacanthini, no account has been taken of the various short-range (generic) specializations that are especially evident in certain Triassic forms, and no attempt has been made to evaluate the variations in the skull-roof and cheek patterns. The rate has been obtained by computing the number of morphological changes per million years for each time interval, regardless of length, during which significant change occurred. This interval may represent the time elapsed between the first appearance of two different genera, or it may include the ranges of a number of genera that show definable, long-continued modification.

Assuming that the coelacanth trend was initiated about 14,000,000 years prior to the appearance of the earliest known coelacanth genera, and that these genera have 52 definitive coelacanth characters, the rate of character change per million years was 3.7 by the late Devonian. This rate, with perhaps minor fluctuations, obviously rose to this level from zero changes per million years (in a coelacanth direction) at the beginning of the trend. From the late Devonian to the early Mississippian, representing a time interval of about 17,000,000 years, the rate dropped to about 0.1, where it perhaps remained until the early Triassic. Shortly thereafter it dropped nearly to zero. Although Tertiary coelacanths are as yet unknown, the conditions in *Latimeria* imply that the rate remained at about this level to the Recent.

It must be emphasized that the rate values are approximations; they are nevertheless significant in providing the basis for a graph (fig. 16), the pattern of which is believed to be valid. The graph, which is obtained by plotting rate against time, demonstrates the relatively short duration of the tachytelic portion of the curve, the bradytelic representing over three-quarters of the entire time-span of the group. The graph pattern indicates accelerated evolution during the osteolepid-coelacanth transition, in other words during the period of initial specialization, with a sharp decrease in rate once this level of specialization was attained. Simpson
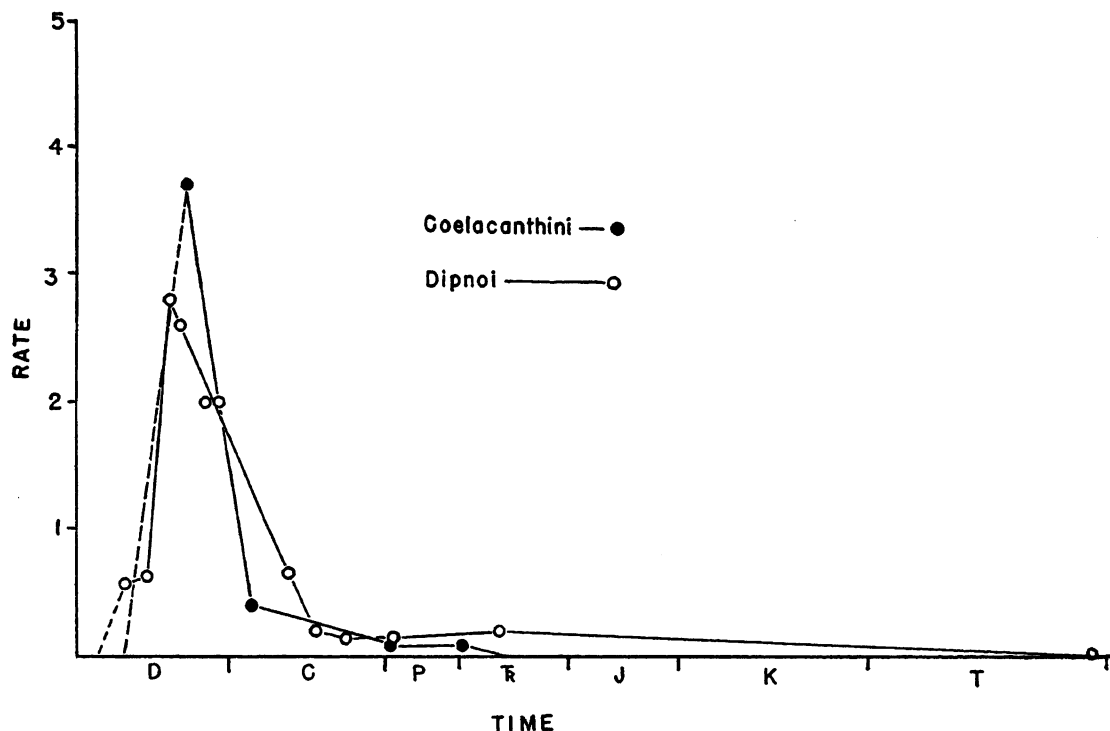
FIG. 16. Graph showing rate of acquisition of coelacanth and dipnoan characters. The dipnoan curve is based on data from Westoll (1949).

(1944, p. 148) has noted that bradytelic lines "are not primitive when they first appear, but are then progressive and normally result from rapid evolution."

A similar rate curve has been plotted for the Dipnoi, based on Westoll's data (1949). In order to make this graph comparable to the one for the Coelacanthini, it has been necessary to compute numerical grades representing the development of advanced characters in each genus (presumed ancestral rating of 100, minus the rating for retained ancestral characters per genus). The pattern of this curve is essentially similar to the coelacanth one in spite of the different method employed in evaluating the morphological change. The primitive *Dipnorhynchus* is remarkably close to Westoll's hypothetical pre-osteolepid (1949, fig. 10 D) and is perhaps a transitional form. The accelerated rate between *Dipnorhynchus* and *Dipterus* supports this conclusion. Westoll states (1949, p. 177) that the change between *Dipterus* and *Phaneropleuron* was very rapid.

Although this is true in terms of morphological specialization, the rate of change per million years was decreasing.

The various major coelacanth specializations such as the loss of the maxillary, the change in the articulation of the palate, the nearly vertical suspensorium, the possible loss of the internal nares, the structure of the lower jaw, the modifications in the pattern of the cheek, the change in the internal skeleton of the fins, the structure of the caudal fin, and the general body form are all presumably more or less interrelated responses to the unknown selective factors that obviously had a profound effect on the population involved in the transition from the ancestral rhipidistian stock. In the dipnoans, the relationship between the development of a triturating dental mechanism, with associated skull modifications, and a sluggish locomotor habitus is clearly described by Westoll, suggesting continuously successful occupation of a particular ecologic niche. The early, rapid fixation of the coelacanth

structural plan indicates a similar successful occupation of some yet-to-be-determined niche. The tolerance limits of the fixation, however, were broad enough to permit some subsequent adaptive radiation in the dentition, in the angle of the suspensorium, in the position of the paired fins, and in certain other features. The occupation of various different environments was also possible, as the structural radiation implies, but frequently this was accomplished with no observable alteration in the morphology of the skeleton.

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ABBREVIATIONS USED IN ILLUSTRATIONS

"al," alisphenoid process of frontal
ang, angular
ant, antorbital
ao, anterior occipital ossification
ap, antotic process
ar, articular
aup?, possible autopalatine
bdm, basibranchial tooth-bearing bones
bsph, basisphenoid
cbr, ceratobranchial
chy, ceratohyal
cl, cleithrum
clav, clavicle
co?, possible coronoid
cop, circumorbital plates
dp, dermopalatine
ds, dorsum sellae
dsph, dermosphenotic
dt, dentary
ecl, extracleithrum
ecth, ectethmoid
ept, ectopterygoid
ex, extrascapular
fl, anterior dorsal process of prootic
fr, frontal
grcar, groove for internal carotid artery
gu, gular
int, intertemporal

laju, lacrimo-jugal
llam, lateral lamina
lr, lateral rostral
mpt, metapterygoid
not, notochordal scar
op, opercular
pf, pituitary fossa
pmx, premaxillary
po, postorbital
pop, preopercular
pr, postrostral
pra, prearticular
prant, antotic process
pro, prootic
ps, parasphenoid
pt, pterygoid
qu, quadrate
ro, rostral
sb, spiracular bone
scl, supracleithrum
so, supraorbital
soc?, possible supraoccipital ossification
sop, subopercular
sp, splenial
sq, squamosal
st, supratemporal
urohy?, possible urohyal
vpit, foramen for pituitary vein