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## A STUDY OF *DIPLURUS LONGICAUDATUS* WITH NOTES ON THE BODY FORM AND LOCOMOTION OF THE COELACANTHINI

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### INTRODUCTION

During the last decade a hitherto unknown coelacanth fauna has been discovered in the Upper Triassic Newark series of New Jersey and Pennsylvania. In 1934 Bryant described *Coelacanthus newarki* from the Lockatong formation near North Wales, Pennsylvania, and Schaeffer in 1941 reported on additional specimens from the underlying Stockton formation at North Bergen, New Jersey. The new genus *Osteopleurus* was erected by the latter to include both the Lockatong and the Stockton forms, which were considered to be generically and specifically indistinguishable, but nevertheless quite distinct from *Coelacanthus* as defined by Moy-Thomas and Westoll (1935). On the basis of additional material, Shainin (1943) removed the Stockton coelacanths from *O. newarki* and assigned them to the new species *O. milleri*. He further recognized a distinct subspecies, *O. milleri grantonensis*, on the basis of a caudal fin 1.83 times larger than the mean of known specimens of *O. milleri*.

An as yet undescribed collection of coelacanths from the Lockatong numbering many hundred specimens has recently been made by Dr. G. L. Jepsen in a building excavation on the Princeton University campus. This material has been tentatively assigned to *Osteopleurus*. Additional coelacanth remains have also been discovered by Mr. Wilhelm Bock in the Lockatong at North Wales and appear to represent both *Osteopleurus* and *Diplurus*.

Prior to 1934, *Diplurus longicaudatus* was the only member of

the Coelacanthini known from the Newark series. As the above studies and identifications have been made without having available a detailed description of *Diplurus*, it is most desirable at this time to undertake a reexamination of all the available specimens of this genus obtained by Newberry. This author's original description of *Diplurus* (1878) was based on a single and rather poorly preserved specimen from Boonton, New Jersey, and included several inaccuracies regarding the character of the fins and scales. Specimens collected later under Newberry's direction at Boonton and by S. W. Loper at Durham, Connecticut, presented a clearer picture of the skeletal details. These data were incorporated in Newberry's (1888) second and extended description. A rather perfunctory illustration of the type specimen plus some drawings of scales and a portion of the supplementary caudal fin were published with this report and represent the only figures of *Diplurus* thus far available. Dean's (1895) restoration is inaccurate and incomplete in a number of respects. The descriptions of Eastman (1905 and 1911), incorporating some additional observations, are too brief to be of much value. The diagnosis of Stensiö (1932) included all the trustworthy information in existence at that time.

As far as the writer has been able to determine, all the known specimens of *Diplurus longicaudatus* are in the American Museum with the exception of an incomplete lower jaw and two caudal fin fragments. He is indebted to Dr. J. W. Peoples of Wesleyan University, Middletown, Connecticut, for the loan of the lower jaw and for certain information about the Triassic of the Connecticut Valley. Dr. David H. Dunkle has kindly permitted the examination of the caudal fin specimens belonging to the United States National Museum.

Various parts of this paper were discussed with Dr. Dunkle, Dr. E. H. Colbert, and Dr. N. D. Newell, and the writer is obligated to them for interesting and helpful suggestions. The drawings, requiring much patience and interpretation, were prepared by Mr. J. C. Germann. The photographs were taken by Mr. Elwood Logan of the Photographic Division of this museum.

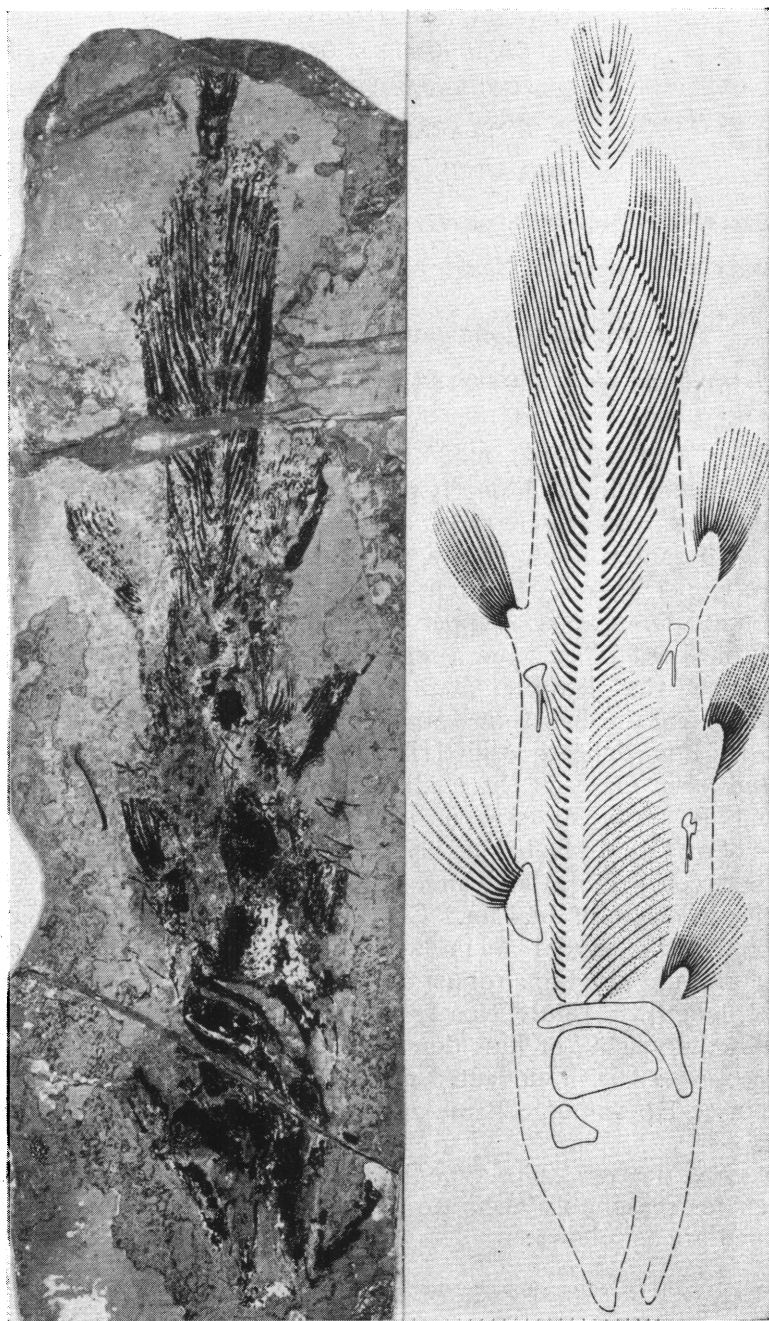


FIG. 1. *Diplurus longicaudatus* Newberry. A. A.M.N.H. No. 630, type specimen,  $\times 1/4$ .  
B. Restoration based on all available specimens.

## TAXONOMY AND DIAGNOSIS

## CROSSOPTERYGII

## COELACANTHINI

## COELACANTHIDAE

## DIPLURUS NEWBERRY

*Diplurus* NEWBERRY, 1878, p. 127.

GENOTYPE: *Diplurus longicaudatus* Newberry.

***Diplurus longicaudatus* Newberry**

*Diplurus longicaudatus* NEWBERRY, 1878, p. 127; NEWBERRY, 1888, p. 70, pl. 20.

TYPE: A.M.N.H. No. 630. Complete fish including supplementary caudal fin, skull poorly preserved.

HORIZONS AND LOCALITIES: Brunswick formation, Upper Triassic, Boonton, New Jersey, and the Anterior and Posterior Shales, Upper Triassic, Durham and Westfield, Connecticut.

GENERIC DIAGNOSIS: Upper Triassic coelacanths attaining a length of about 70 cm. and a maximum depth of approximately one-quarter that length. Skull at least two-sevenths of total length. Neural spines robust, basiventral elements probably not ossified. Long delicate ossified ribs present. Girdles of the paired fins and basal plates of the median fins typical of the Coelacanthidae. Posterior division of pelvis enlarged and triangular. Origin of first dorsal fin behind origin of pectoral fin, pelvic fin midway between pectoral and anal fins, origin of second dorsal fin anterior to origin of anal fin. Caudal fin narrow and elongated, supplementary caudal fin relatively large. Lepidotrichia of paired and unpaired fins robust and jointed for about two-thirds of their length. Minute, closely set barbs on the anterior surface of the lepidotrichia of first dorsal fin. Scales elliptical, exposed surface covered with elongated parallel ridges.

SPECIFIC DIAGNOSIS: Same as for the genus, which is monotypic.

MEASUREMENTS: The type is the only specimen complete enough for reasonably accurate measurement. The dimensions obtained are as follows:

Body length, including supplementary caudal fin.....	69.0
Skull length.....	18.0

## Distance from snout to anterior border of:

First dorsal fin.....	22.5
Second dorsal fin.....	37.5
Pectoral fin.....	20.0
Pelvic fin.....	29.5
Anal fin.....	40.0
Caudal fin.....	45.5
Body depth at anterior border of first dorsal fin (approx.).....	12.0

REFERRED SPECIMENS: 1. A.M.N.H. No. 627, and counterpart. Incomplete specimen including posterior half of skull to beginning of second dorsal fin. Larger individual than type. Durham, Connecticut.

2. A.M.N.H. No. 680, and counterpart. Incomplete supplementary caudal fin. Boonton, New Jersey.

3. A.M.N.H. No. 1529. Portion of caudal fin. Boonton, New Jersey.

4. A.M.N.H. No. 1531. Base of caudal fin. Boonton, New Jersey.

5. A.M.N.H. No. 1532, and counterpart. Portion of caudal fin, isolated rays, well-preserved scales. Durham, Connecticut.

6. A.M.N.H. No. 1533. Skull with pterygoquadrate complex exposed. Durham, Connecticut.

7. A.M.N.H. No. 1536. Skull, poorly preserved. Boonton, New Jersey.

8. A.M.N.H. No. 1537. Portion of trunk area. Boonton, New Jersey.

9. A.M.N.H. No. 4800. Dorsoventrally compressed skull. Durham, Connecticut.

10. U.S.N.M. No. 17095. Part of caudal fin. Westfield, Connecticut.

11. U.S.N.M. No. 17096, with counterpart. Part of caudal fin. Westfield, Connecticut.

12. Wesleyan University Museum No. 846. Lower jaw. Durham, Connecticut.

## DESCRIPTION

**SKULL:** Five poorly preserved and badly crushed skulls are available. In one case (A.M.N.H. No. 4800), the skull is dorsoventrally compressed with the visceral elements spread out on either side of the brain case much as in a specimen of *Undina* figured by Reis (1888, pl. 1, fig. 21). An X-ray of this specimen

has revealed a number of interesting features not otherwise observable in spite of careful preparation (fig. 2). Although the anterior portion of the brain case is missing, much of the parasphenoid is present. It is typically expanded anteriorly and narrowed posteriorly in the region of the basisphenoid. The outline of the basisphenoid area is very similar to that figured for *Wimania* (Stensiö, 1921) and *Rhabdoderma* (Moy-Thomas, 1937). The otic and occipital ossifications are clearly present, although their outlines are confused with those of the roofing bones, presumably intertemporal plus supratemporal. The prootic is expanded posteriorly into a triangular area and behind it, on one side, is a mass that must represent the anterior occipital ossification. There is no evidence of the other occipital ossifications.

The X-rayed specimen possesses peculiar rod-like structures extending laterally on either side from the brain case immediately anterior to the antotic processes. On the basis of their position in relation to the brain case and also to the lower jaws, they appear to represent the thickened border of the vertical ramus of the pterygoid and epipterygoid. The pterygoid, as exposed in another specimen (A.M.N.H. No. 1533), shows the usual thickening of the ascending portion (fig. 3A). This element is broad immediately anterior to the ascending ramus, and the upper edge is gently concave as in *Coelacanthus* and *Macropoma*. In this respect it differs from the markedly concave dorsal border of the *Rhabdoderma* pterygoid. In fact, the shape of the entire pterygoquadrate complex suggests that found in *Coelacanthus* or *Whitea*. A distinct epipterygoid cannot be observed, and it is therefore not possible to determine whether or not it is relatively high as Stensiö (1921, p. 118) points out is characteristic of the later Paleozoic and early Mesozoic types, or low and more or less fused with the pterygoid as in late Mesozoic forms. *Latimeria*, incidentally, has a prominent, high epipterygoid.

The right ceratohyal is completely preserved in the X-rayed specimen and must be in approximately its natural position. It is gently recurved and expanded at both ends as in *Wimania* and *Macropoma* (T. S. Westoll, personal communication). Most of the branchiostegals are apparently present, although the total number is questionable. Four or possibly five can be observed on one side.

The cheek and roofing bones of the skull are not sufficiently well preserved to warrant detailed description. The intertemporals

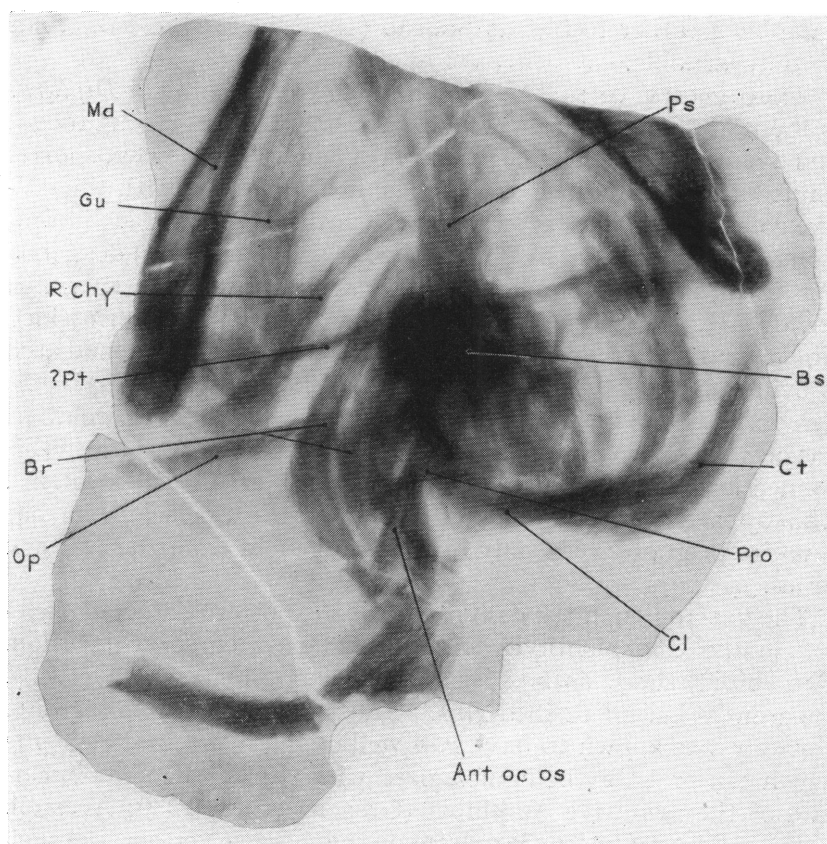


FIG. 2. *Diplurus longicaudatus* Newberry. A.M.N.H. No. 4800, roentgenogram of dorsoventrally compressed skull,  $\times 1/2$ . Abbreviations: Ant oc os, probable anterior occipital ossification; Br, branchiostegals; Bs, basisphenoid; Cl, clavicles; Ct, cleithrum; Gu, gular plate; Md, mandible; Op, opercular; Pro, prootic; Ps, parasphenoid; ?Pt, possible thickened border of pterygoid; R Chy, right ceratohyal.

and frontals are of about the same relative size as in the other Triassic genera. A cheek element, which is very probably the postorbital, is preserved in the type and it resembles the same element in *Whitea* and *Osteopleurus*. The operculum is triangular, tapering rather sharply to the ventral apex.

Although the dentigerous borders of several jaw elements that usually carry teeth appear to be preserved, there is no definite evidence regarding the nature of the dentition. That it must

have been rather feeble, as Stensiö (1921) has suggested, seems quite reasonable.

**AXIAL SKELETON:** The total number of vertebrae in *Diplurus* is about 50. The neural spines in the abdominal region are robust and average about 25 mm. in length. They are somewhat shorter immediately behind the skull. The neural arches, with their V-like conformation, are typically coelacanthid. There is no indication of the presence of ossified basiventrals as have been described for *Coelacanthus granulatus* and *Rhabdoderma*. One specimen (A.M.N.H. No. 627) has well-preserved, long, delicate, ossified ribs, presumably pleural (fig. 4C). Although a single haemal arch is evident in the type (A.M.N.H. No. 630), it is not possible to demonstrate the transition from the ribs to the haemal arches as has been observed in *Coelacanthus*. It is interesting to note in this connection that *Osteopleurus* also has long, ossified pleural ribs. This apparently unique condition among the Coelacanthini has thus far been observed only in the two genera from the Newark series.

The variability in the ossification of the postcranial axial skeleton in the Choanichthyes has received only cursory attention. The rhipidistians, as has been pointed out by Westoll (1943), apparently lacked ossified ribs. Many members of this group, however, are known to have had well-ossified vertebral elements which can probably be homologized with similar elements in certain of the primitive Amphibia (Gregory et al., 1939; Westoll, 1943). Parapophyses are present on the thoracic vertebrae of such genera as *Strepsodus* and *Euthenopteron*, indicating the presence of cartilaginous ribs. In the coelacanth, on the other hand, the only ossified central elements thus far observed are very small paired basiventrals. Short, ossified pleural ribs, however, are often present, and, as pointed out above, may reach a considerable length. In the dipnoans there are no ossified central elements, but well-developed ossified pleural ribs are present which may be quite long, as in *Fleurantia* (Graham-Smith and Westoll, 1937).

The highly variable fate of the primary arcualia in the formation of the vertebrae is thus well illustrated in the Choanichthyes. There is clearly some sort of morphogenetic control established along the notochordal axis that determines, within each vertebral segment, which arcualia or portions thereof will be eliminated or remain as chondrified or ossified units. Such control must also determine the regional differentiation of extensions from certain of



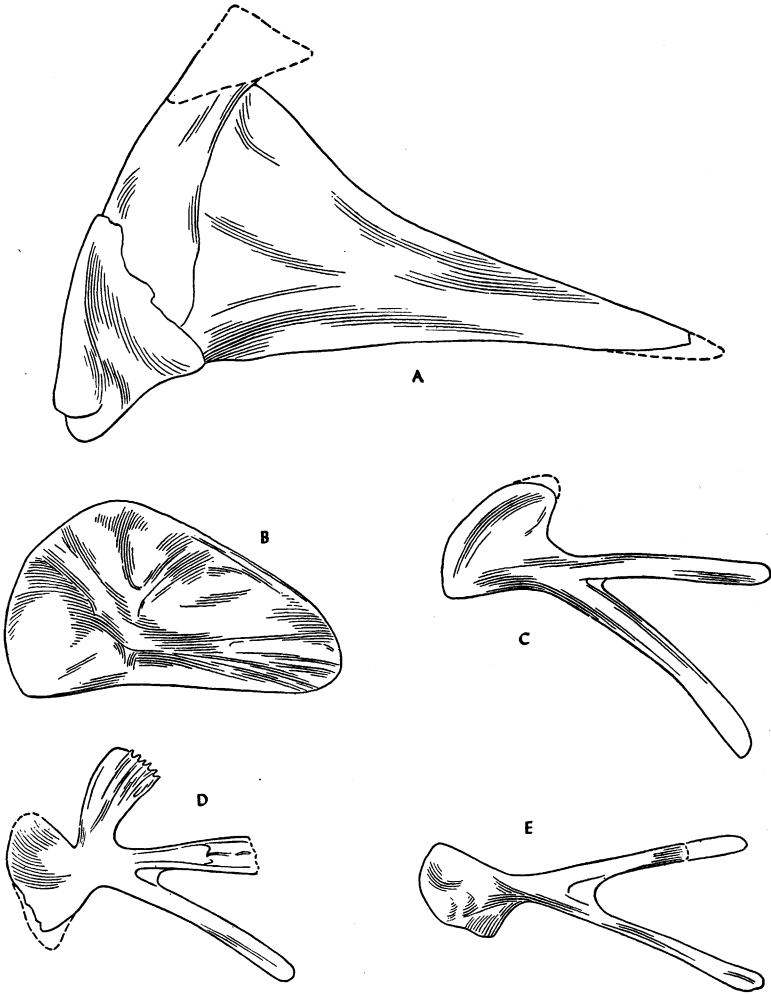


FIG. 3. *Diplurus longicaudatus* Newberry. A. Palatoquadrate complex from A.M.N.H. No. 1533. B. Basal plate of first dorsal fin,  $\times 1$ . C. Basal plate of second dorsal fin,  $\times 1$ . D. Pelvic bone,  $\times 1$ . E. Basal plate of anal fin,  $\times 1$ .

the arcualia, such as the neural spines, ribs, and haemal spines. A biomechanical basis for the differences in the genetic background of such morphogenetic control is difficult to visualize, although it may very well exist.

**GIRDLES AND PAIRED FINS:** The shoulder girdle of *Diplurus* exhibits a cleithrum and clavicle that are firmly united by a long

oblique suture. The supracleithrum is not evident. The X-rayed specimen suggests the presence of an extracleithrum, although a clear-cut suture is lacking between it and the cleithrum proper. The cleithrum is constricted in its middle portion and expanded dorsally for articulation with the supracleithrum and ventrally where it is joined with the endoskeleton of the pectoral fin. The clavicle is triangular and relatively large, rather suggesting the rhipidistid type.

The pectoral fin contains about 19 lepidotrichia arranged along the pre-axial and postaxial borders of the endoskeleton. The rays are long and slender and are jointed for about two-thirds of their length.

The pelvic girdle, of which there are several well-preserved examples, is of the *Coelacanthus* or *Rhabdoderma* type (fig. 3D; fig. 4C). The median process has an expanded, denticulated median border for articulation with its fellow of the opposite side and is directed transversely as in *Rhabdoderma* rather than caudally as in *Osteopleurus milleri*. The posterior division, which articulates with the endoskeleton of the fin, is triangular in shape and relatively larger than in most other pelvic girdles of this type.

The anterior division is composed of two apophyses connected by a delicate bony membrane. These processes appear to be free of the membrane for a much greater distance than the apophyses of either *Coelacanthus* or *Rhabdoderma*. In *Whitea* they are connected for their entire length. The pelvis of *Diplurus* is thus of rather distinctive design, and its shape may be considered as a taxonomic character of some importance. Next to nothing is known, however, of the individual or specific variation of the pelvis within the Coelacanthini. The delicate nature of the pelvic girdle makes it very susceptible to fragmentation, and complete preservation is rare.

The pelvic fin is composed of about 21 lepidotrichia which are jointed to about the same extent as those of the pectoral, and have a similar arrangement. This fin, being opposite the basal plate of the second dorsal fin, has a more posterior position than in the late Paleozoic genera, but agrees in this regard with the Triassic *Osteopleurus* and *Whitea*.

MEDIAN FINS: The basal plate of the anterior dorsal fin (fig. 3B) is triangular as in most other coelacanths (with the exception of *Rhabdoderma* where it is kidney shaped). It is reënforced by localized swellings that radiate from approximately

the center of the plate. The lepidotrichia, numbering about 11, articulate directly with the thickened posterodorsal border and are jointed for two-thirds of their length. The jointed portions of the rays have very small, acute spines on their anterior surfaces. The spines are clearly evident on only one specimen (A.M.N.H. No. 627) and are apparently not present on the other fins as previously reported.

The posterior dorsal fin of *Diplurus* has a typically bifurcated basal plate (fig. 3C) with the apex directed posteriorly. The apical portion is expanded into a nearly circular process. The fin itself is typically lobed, with the basal plate situated about a third of the distance forward between it and the anterior dorsal fin. The actual origin of the fin is about midway between the pelvic and anal fins. It is made up of about 14 lepidotrichia, with all but about two segmented for almost three-fourths of their length.

The basal plate of the anal fin is also bifurcated (fig. 3E), in this respect differing from the late Paleozoic types which have a plate resembling that found in the rhipidistians (Schaeffer, 1941). The bifurcated anal basal plate appears to be characteristic of the Mesozoic genera, with the exception of the curiously elaborated type found in *Laugia*. The anal fin of *Diplurus* consists of about 21 lepidotrichia, of which 16 are divided except for the proximal third.

The caudal and supplementary caudal fins together make up almost a third of the total body length. The caudal proper is composed of about 19 radials and 16 lepidotrichia. The perichondrially ossified radials are expanded proximally for the contact with the neural or haemal spines and distally for the articulation with the lepidotrichia. The lepidotrichia are segmented for about half their length. Each half of the supplementary lobe contains at least 10 lepidotrichia which are likewise jointed for half their length. The asymmetrical relationship between the dorsal and ventral lobes of the caudal fin, which is quite evident in most coelacanth, is not marked in *Diplurus*. Usually the origin of the dorsal lobe is anterior to that of the ventral, resulting in lobes that are clearly different in size and shape (fig. 5).

**SQUAMATION:** The scales are essentially elliptical, and in one specimen where several are isolated they measure about 1.25 by 2.25 cm. The exposed portion is ornamented with 14 to 16 parallel ridges which do not converge posteriorly. The ridges

may be close together or separated enough to show between them fine paralleling striae which cover the entire scale.

Moy-Thomas (1937) has pointed out that variation is evident in the ornamentation of the scales of *Rhabdoderma* from different regions of the body. As mentioned above, some differences are also found in the scales of *Diplurus*, particularly in the spacing and continuity of the ridges (fig. 4A, B). They may either be continuous for the entire length of the exposed part of the scale or divided into two or more overlapping parts. The subdivision is particularly common in the ridges of the central portion of the scale. The ridges are never interrupted in the same fashion as in *Whitea*, however, and tubercles are entirely absent. The scale ridges are more numerous than in *Osteopleurus* and relatively less robust.

#### GEOLOGIC OCCURRENCE AND THE PALEOECOLOGY OF THE NEWARK SERIES

The type and five other incomplete specimens of *Diplurus longicaudatus* were obtained from a black shale horizon in the Brunswick formation of the Newark series at a quarry near Boonton, New Jersey. This quarry is now part of a reservoir and is unfortunately no longer accessible. In addition to the very rare remains of *Diplurus*, this locality yielded hundreds of specimens of the semionotid genus *Semionotus* (*Ischypterus*), representing a number of rather poorly defined species, and an equally large number of two species of the subholostean *Redfieldia* (*Catopterus*).

Five fragmentary specimens of *Diplurus* were collected by S. W. Loper from an exposure of the anterior black shales in a stream bed on the western slope of Totoket Mountain, a part of Durham, Connecticut (Davis and Loper, 1891). Two additional specimens, also discovered by Loper, came from the posterior black shales near Westfield, Connecticut. The Durham locality has likewise yielded a great many examples of *Semionotus* and *Redfieldia* and about 12 specimens of the subholostean *Ptycholepis*.

The possible occurrence of *Diplurus* in the Lockatong formation at North Wales, Pennsylvania, considerably extends the vertical range of this genus. This identification can be considered as only tentative, however, as the remains consist only of isolated scales and rays that clearly indicate a coelacanth of large dimensions with a scale ornamentation similar to that of *Diplurus*. In coelacanths, as already pointed out, the ornamentation of the scales, taken by itself, is hardly a safe criterion of generic or specific affinity.

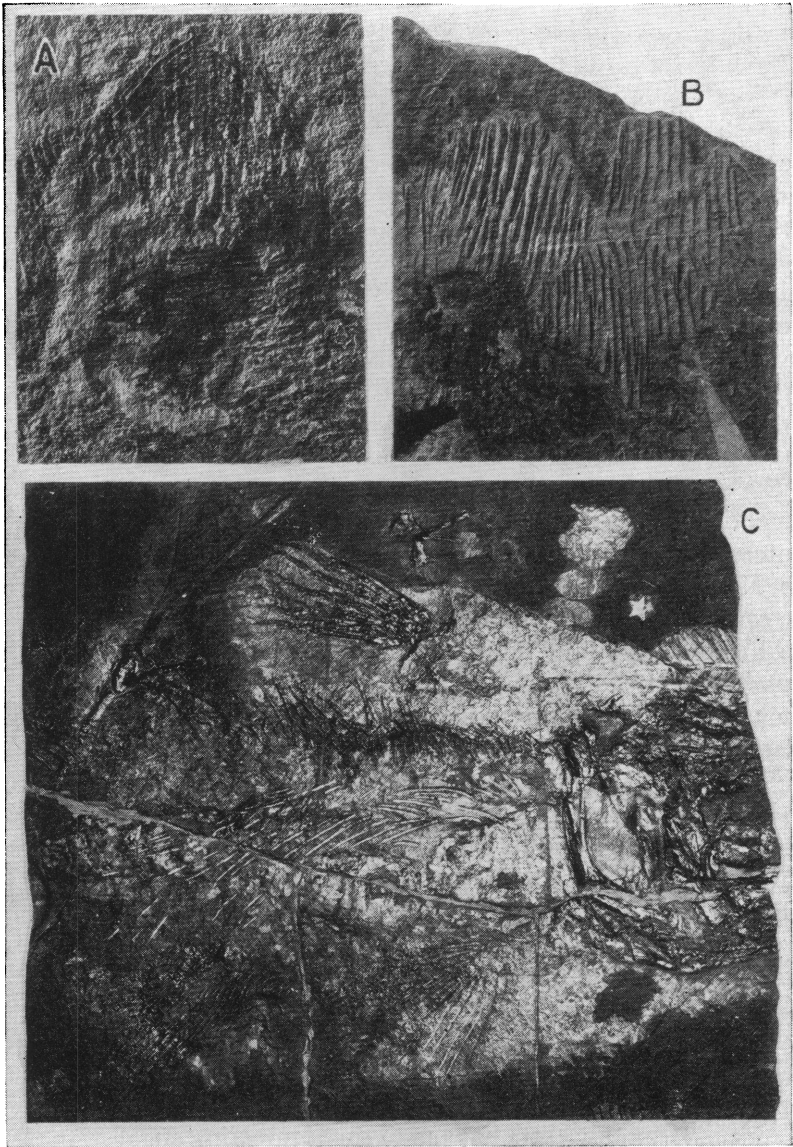


FIG. 4. *Diplurus longicaudatus* Newberry. A. Impression of isolated scale,  $\times$  approx.  $3/1$ . B. Exposed portions of three scales showing nature of ornamentation,  $\times$   $2/1$ . C. A.M.N.H. No. 627, showing ribs, pelvic bone lying above first dorsal fin, and basal plates of first and second dorsal fins,  $\times$   $1/3$ .

The Newark series is composed of a series of isolated deposits of varying size extending from Nova Scotia to North Carolina. The sediments accumulated in long, narrow, down-faulted troughs, and at the time of deposition the deposits probably covered larger areas than they do at the present time. Whether or not any of these basins were originally connected or were continuous is not known, but this must be considered as a distinct possibility.

Several attempts have been made to correlate the formations in the various basins (e.g., Roberts, 1928). The relations of the sediments in the Connecticut Valley and New Jersey have recently been worked out by Colbert (1946) on the hypothesis that these two nearly adjacent basins would probably not independently experience three distinct phases of igneous activity, separated by almost equal periods of inactivity. Thus, the anterior and main trap sheets of the lower Connecticut Valley are considered to be of the same age as the First and Second Watchung extrusives, respectively, of northern New Jersey. The posterior trap is then contemporaneous with the Hook Mountain extrusive near Boonton, New Jersey. On this basis, the anterior shales of Connecticut correspond with that portion of the Brunswick formation between the First and Second Watchung, and the posterior shales to the beds between the Second Watchung and Hook Mountain. The black shales at Boonton, being above the Hook Mountain extrusive, must therefore be correlated with the basal portion of the so-called upper sandstones and shales of Connecticut. On the basis of Colbert's computations, the vertical separation between the *Diplurus* horizons in New Jersey and Connecticut (anterior shales) is  $\pm 2500$  feet.

Fossil fishes have been discovered at a number of localities throughout the Newark series. They represent six genera included in the families Dictyopygidae, Semionotidae, and Coelacanthidae. The semionotids are by far the most common and are all included in the genus *Semionotus* with 10 currently recognized species. Such characteristic European Upper Triassic families as the Belonrhynchidae, Eugnathidae, and Pholidophoridae are not present. Brough (1931) has made the interesting suggestion that the generically limited Newark fauna with apparently a large number of species, particularly in *Semionotus*, is rather characteristic of an endemic fresh-water fish fauna. This conclusion is further supported by the fact that these basins were apparently a last refuge for the catopterids, which had disappeared elsewhere

during the Middle Triassic, and also for the fresh-water coelacanths.

The biased nature and apparent scarcity of the fish fauna throughout the Newark series invite speculation on the nature of the environment in these basins. Longwell (1928) has stated in regard to the Connecticut Triassic that "the deposits themselves testify to piedmont slopes, flood plains, and local flood-plain lakes and swamps," and this interpretation must, in general, be true for all the basins. The piedmont deposits were extensively distributed along the margins of the basins adjacent to the highlands. The basin floors were occupied by a flood-plain environment including more or less transient shallow lakes and swamps. The sediments of the basins in general consist of red sandstones and shales and of gray, yellow, and black shales. In Virginia and North Carolina the black shales are replaced by coal deposits in several basins. The nature of these various types of sediments indicates that there were several distinct ecological niches within each basin, and the presence of coal in certain of the more southern basins suggests environmental conditions peculiar to that area.

A survey of the literature indicates that the formation and subsequent persistence of red sediments are a complex phenomenon for which no single explanation may be entirely adequate. It is generally conceded, however, that laterite-like soils develop for the most part in a warm, humid climate such as must have existed during the Newark interval. The Newark red beds are colored by dehydrated ferric oxide (Dorsey, 1926; Roberts, 1928) or ferric hydroxide (Raymond, 1927). The formation of these compounds is induced by high temperature, a rather heavy plant cover preventing erosion and thus giving the sediments time to undergo chemical change, and finally a porous soil with an oxygen content that is high enough to promote rapid bacterial action. The last must be fast enough to balance the production of humus and largely prevent its formation. The presence of a humus cover results in reduction of the iron to a ferrous state and loss of the red color.

Krynine (1937) is of the opinion that the Newark red beds in Connecticut are a "first-cycle product," formed in an area that was markedly dissected, with extremely rapid erosion and chemical decay, and with seasonal rainfall. Raymond believes, however, that the red soils developed on the Appalachian peneplane prior to the beginning of Newark deposition. In any case, red

sediments accumulated in the basins to a depth of over 10,000 feet under conditions that permitted retention of the red color. This required rapid deposition plus lack of any factors promoting reduction.

Vertebrate remains are relatively rare in the Newark red beds, indicating that disintegration factors were very active in this environment. Although a small number of more or less associated reptile skeletons have been discovered, the writer has thus far seen but a single scale and shoulder girdle fragment of a coelacanth to represent the fish fauna. Invertebrates are represented by three genera of pelecypods from one locality in Pennsylvania and by the presence of *Unio* in Massachusetts.

The gray and yellowish shales of the Virginia basins were analyzed by Roberts (1928) and found to contain ferrous iron. This suggests reduction in stagnant bodies of water probably with an abundance of decaying plant material. Aquatic organisms are occasionally found in these shales. The American Museum collection includes the dissociated remains of a coelacanth in a slab of yellow shale from the Danville basin.

The fresh-water black shale environment has recently been discussed by Twenhofel (1939). The basic requirement for the formation of bituminized shales is quiet water with little or no circulation resulting from through-flowing streams or temperature change. Under such conditions, there will be a deficiency of oxygen, little bacterial activity, and a concentration of humus, with resulting toxic conditions, and a lack of macroscopic and microscopic scavengers. Decompositional bacteria are active only for short periods following "overturn" in a temperate climate. Organic matter will, therefore, be well preserved and contribute to the formation of black muds following rapid reduction of the red sediments. The black shales of the Newark basin undoubtedly derived most of their organic content from plants carried into or growing around the swamps and lakes. Twenhofel points out that if any decomposition occurs, the less resistant parts of plants disappear and a concentration of the more resistant parts will result, producing a bituminous deposit. Humic deposits such as occur in certain basins in Virginia and North Carolina indicate complete lack of overturn. The plant remains from the various basins offer no definite information regarding climatic differences, as the same types seem to be equally distributed at least from Massachusetts to North Carolina. The preserved flora consists



of a mixture of transported upland forms and lowland swamp types.

The environments described briefly above probably represent the major ecological niches that existed with the Newark basins. One of the most interesting problems is the accumulation of fish remains in the most unfavorable environment, which was apparently not capable of supporting any invertebrates susceptible to preservation with the exception of an ostracod which, following Raymond (1946), may be tentatively identified as *Pseudestheria ovata* (Lea). This, or a closely related genus, is found today in stagnant temporary pools and may therefore be considered as another indication of the sort of environment described for black mud formation.

The factors involved in the decomposition of the skeleton of an aquatic or terrestrial vertebrate have not, to the writer's knowledge, been investigated experimentally. Any discussion of this problem must, therefore, be based largely on inference. It is obvious that decomposition is retarded in some environments more than in others and that the opportunity for the fossilization of non-organic bony substance is increased through such retardation. Bacterial activity presumably has little direct effect on the non-organic constituents but may bring about rapid disintegration of all organic parts and thus expose the non-organic skeleton to various chemical and mechanical agents. The action of the latter two will be influenced by the rate of sedimentation and the degree of coarseness and porosity of the sediments.

The vertebrate fossils that have been found in the Newark red beds are rarely badly fragmented. This suggests that the disintegration process in the red bed environment was essentially chemical rather than mechanical (as it would have to be in any case to cause the complete disappearance of bone). The high bacterial activity probably resulted in a rapid decomposition of the soft tissues, while the rapid sedimentation, in some cases, caused partial or complete dissociation of the skeleton. Although the few known fish remains are isolated elements, most of the reptiles are represented by at least partial, and occasionally by almost complete, skeletons. There is thus reason for believing that burial usually took place before complete dissociation was possible. The chemical factors involved are difficult to postulate without an analysis of the composition of the fossil bone from this environment and without any information on the causes of bone

decomposition in a modern red soil environment.

In the environments producing yellowish, gray, and black shales the concentration of organic acids was apparently not great enough to have any effect on the bone. The reduced bacterial activity and the almost complete absence of mechanical factors permitted entire fish to be buried and their hard parts preserved in articulation.

There are several possible explanations to account for the concentration of fossil fishes in the black and probably also the yellowish shales. They may have entered the swamps in schools or individually at various times only to be trapped and finally to succumb to the toxic environment. Such an explanation is favored by the fact that nearly all the known specimens of a given species are of about the same size, suggesting that at least the young developed in a different environment. Some of the black shale deposits may represent the bottom sediments of lakes which were deep enough to have well-oxygenated surface waters but toxic bottom waters. Lastly, it is possible that the fishes inhabiting the basin swamps had special adaptations for aerial respiration. Carter and Beadle (1931) have found that the fishes in the fouled swamps of the Paraguayan Chaco have a number of different types of adaptations specifically for this purpose, and Westoll (1944) has postulated such structural modifications for the Haplolepididae, a palaeoniscoid family restricted to the late Carboniferous coal swamps of North America and Europe. Certain features of the body form and of the orientation of the pectoral fins in these fishes further suggest subsurface swimming associated with aerial respiration. The problem of body form in coelacanths will be discussed in the next section, but it might be pointed out here that such modifications are not evident.

The extreme paucity of *Diplurus* remains in layers containing abundant remains of *Semionotus* and *Redfieldia* suggests that this coelacanth rarely entered the swamp environment of the basins or that it was a more or less solitary type with only a few individuals inhabiting a given swamp at a given time. By contrast, the remains of *Osteopleurus* are exceedingly common at certain black shale horizons in the Granton quarry and also at the Lockatong locality on the Princeton campus, while the other representatives of the Newark fauna are very rare. Palaeoniscoid scales have been found, however, while some from the Granton quarry are quite certainly *Ptycholepis*.

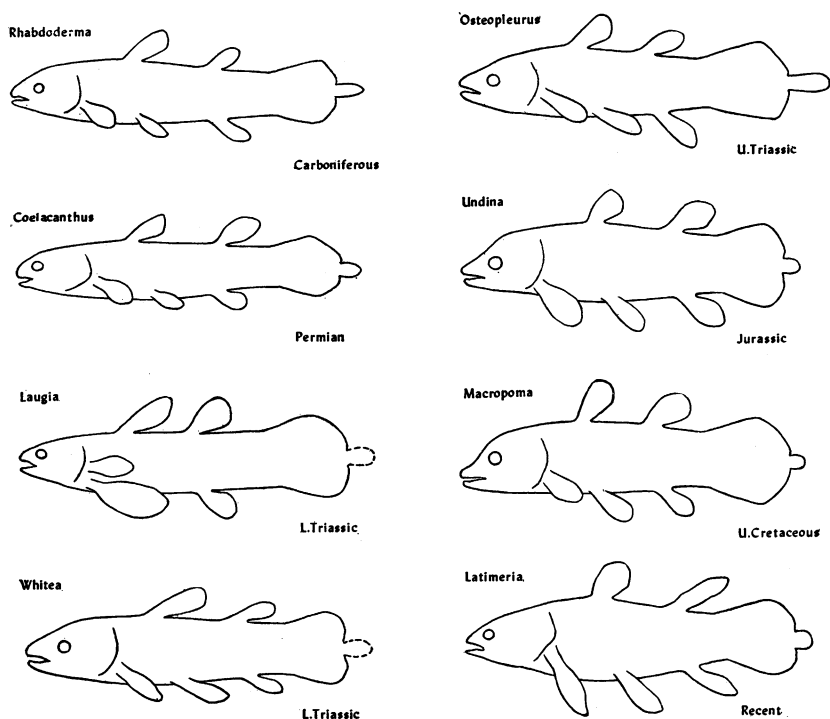


FIG. 5. Restoration of the body outline in various coelacanths. *Rhabdoderma*, *Whitea*, and *Osteopleurus* based on specimens, *Coelacanthus* modified after Moy-Thomas and Westoll, *Laugia* modified after Stensiö, *Undina* modified after Huxley and Woodward, *Macropoma* from specimen and after Huxley, *Latimeria* after Smith. Drawn at unit scale.

#### BODY FORM AND LOCOMOTION IN THE COELACANTHS

During the process of determining the probable body outline and proportions of *Diplurus*, various problems associated with the generalized coelacanthid body form became evident, particularly in relation to the persistence of this body type from the Upper Devonian to the present and its significance in terms of locomotion. The body form outlines (fig. 5) demonstrating this conservatism are based, whenever possible, on a series of specimens of the species represented or on illustrations of such specimens. They appear to be reasonably accurate in their general proportions, while the relative positions of the fins can be determined with considerable accuracy. The arrangement of the outlines is not meant to imply a phylogenetic sequence.

The typical coelacanth body form has remained essentially unchanged for a period of not less than 300 million years. Huxley (1861), Woodward (1898), and Stensiö (1921) have emphasized the long persistence of the Coelacanthini, probably representing a record among the fishes and possibly for the entire vertebrate phylum. Simpson (1944) considers the coelacanths to illustrate one of the more classic examples of low-rate evolution or bradytely.

The Coelacanthini branched off the primitive crossopterygian (rhhipidistian) stock in the Lower or Middle Devonian, attaining their distinctive status no later than the early Upper Devonian. The abrupt appearance of this specialized choanichthoid line, with no described intermediate types, represents an example of high-rate evolution followed by an apparently sudden change to a low rate. This marked change in rate undoubtedly occurred many times during the evolution of the various lines of bradytelic vertebrates. The change in rate represents the attainment of a new, broad, adaptive zone which, in the case of the coelacanths, might be interpreted in terms of a structural organization, as reflected in the skeleton, so stabilized as to be largely resistant to further environmental change. Simpson points out, however, that the attainment of this zone does not always mean a decrease in plasticity and that bradytelic groups can give rise to other lines which in turn may invade somewhat different and more restricted zones. It thus appears possible that the coelacanths, which inhabited several radically different environments during the course of their history, are actually represented by several side branches from a basic marine stock. The differences between these branches could mainly involve, for instance, the organs of respiration and elimination and would therefore not be preserved in the fossil state.

The earliest described coelacanths occur in the Upper Devonian marine sediments of the Rhineland, while the Carboniferous and Permian forms are thus far recorded only from fresh-water deposits. The Triassic genera are more numerous, and this period may represent the peak of coelacanth evolution from the standpoint of generic diversification. They apparently had a world-wide distribution at this time and were all marine with the exception of the endemic Newark forms. The Jurassic and Cretaceous coelacanths were marine as is the Recent *Latimeria*. It is plausible, therefore, that the coelacanths have always been primarily a marine group from which, during the late Paleozoic and early

Mesozoic, one or more fresh-water lines were derived. It is of interest that the Carboniferous *Rhabdoderma* is present in certain fresh-water deposits in Europe and also occurs at the famous Linton locality in North America. In the Permian on the other hand, the Wichita *Spermotodus* is known only from Texas, while the marine Middle Permian-Lower Triassic *Coelacanthus* occurs in Europe and possibly Madagascar. *Spermotodus* (Westoll, 1939) appears to be most closely related to *Coelacanthus*. Thus there is only negative evidence for supposing that the coelacanth was absent from the seas during the late Paleozoic.

Stensiö (1937) points out that the Upper Devonian coelacanth had attained about the same stage of evolution as the post-Devonian forms, although they do possess certain rhipidistian-like characters such as greater ossification of the vertebral arcualia and two large unpaired endocranial ossifications. In the coelacanth, from the Carboniferous on, the arcualia are only perichondrally ossified. There was also a marked reduction and subdivision of the endocranial ossifications, although this appears to have been largely stabilized as early as the Carboniferous. The pattern of the dermal bones of the skull remains essentially the same, with some variation in the shape and relative size of the individual elements, particularly in the cheek region. In fact, the amazingly slight variation within the bounds of a typical primitive coelacanth pattern is characteristic of the entire skeleton, and this pattern has persisted throughout the history of the group in spite of the radically different environments which these fishes have inhabited.

The body form of a fish offers much reliable evidence regarding its general habitus, particularly in relation to locomotion. The coelacanth body is fusiform and, in life, was probably more or less elliptical in cross section as in *Latimeria*. The dorsal angle, between the anterodorsal and posterodorsal slopes, is farther forward than in the rhipidistians, about one-third of the distance from the snout. The first dorsal fin, which in nearly all fishes is immediately posterior to the apex of this angle (the palaeoniscoids and subholosteans are notable exceptions), is consequently anterior to the midpoint of the body. The caudal fin is relatively large and with the supplementary caudal makes up a quarter to a third of the total body length. The dorsal surface of the head is slightly concave in many genera and gently rounded in the others. There appears to be some tendency towards a deepening of the body in the post-Triassic forms, although it is hardly great enough to have any obvious adaptive value.

The dual caudal fin is regarded as a modified diphyccercal type. It evolved independently from the primitive rhipidistian heterocercal tail through enlargement of the epichordal lobe and straightening of the notochordal axis. The epichordal and hypochordal lobes are of about equal size, while the supplementary caudal fin may be long as in *Diplurus* or short as in *Undina*. It is difficult to visualize a separate and distinct function for the supplementary caudal in spite of its morphological discreteness. This lobe might best be considered as a functional part of the main caudal, in other words, the entire caudal was functionally isobatic (Breder, 1926).

Grove and Newell (1936) have experimentally demonstrated that the heterocercal or functionally epibatic tail when undulating elevates the posterior end of the fish. The isobatic type, whether diphyccercal or homocercal, drives the fish forward without elevating or depressing the body. In the sharks and probably the Placodermi, the tendency towards elevation of the posterior end of the body was compensated for by the proper inclination of the pectoral fins which are wide based and low. They are described by Harris (1937) as aerofoil in design. In addition, the pectorals prevent rolling of the body during rapid swimming.

With the development of an air bladder in the Osteichthyes, the specific gravity of the body approached and in many groups almost equaled that of water. Harris (1937) has pointed out that the caudal and pectoral fins were then largely relieved of the necessity of providing a raising force to neutralize the weight of the fish. With the caudal fin thus only concerned with providing a forward momentum to the body, it gradually evolved into the homocercal type, the most efficient shape for such propulsion. The pectoral fins became relatively short based and capable of a wide range of movement, mostly associated with stopping and steering. Grove and Newell (1939) offer further evidence, based on the ontogeny of several teleosts, that the specific gravity of a fish decreases as the air bladder becomes functional and that this change is associated with the transformation of the larval heterocercal tail into the adult homocercal type.

Although an air bladder was presumably present in the most primitive palaeoniscoids known, the isobatic tail lagged behind in its appearance. It developed, however, in the more specialized paleoniscoids and all the other actinopterygian groups. The crossopterygians, on the other hand, retained the heterocercal tail

until Upper Devonian time, as did the Dipnoi. In the terms of the above theory, this relatively slow phylogenetic transformation in tail shape indicates that the specific gravity of the more persistent epibatic types remained greater than that of water. This was possibly associated with the heavy bony skull and bony scale cover. Harris (1937) further points out that in order for the pectorals to function efficiently as brakes and at the same time not cause the fish to initiate a somersault motion when stopping, the pectorals have migrated dorsally nearer the center of gravity, which is located in the air bladder (Breder, 1926). These fins have also increased their drag effect by being reoriented from the more primitive horizontal insertion found in the shark to a more vertical one. The change in the angle of insertion, Harris demonstrates, produces a lift component which tends to elevate the fish during stopping. In order to compensate for this, the action of the pelvics produces a downward force, and if they are far back along the body, this can cause a rotating force around the center of gravity. Thus, as a final expression of maneuvering efficiency, the pelvics, in the acanthopterygians, have migrated to a position under the pectorals.

The Choanichthyes are characterized by having internal nares and an air bladder that undoubtedly had a respiratory function. Available evidence indicates, however, that the coelacanth lacked internal nares (Stensiö, 1921; Jarvik, 1942), and it might be presumed that the bladder had no respiratory function. A number of actinopterygians, which of course lack the internal nares, have a partially respiratory air bladder, and this could have been the case in the coelacanth inhabiting fresh or salt water.

Breder (1926, p. 226) states that a spatulate tail with a wide peduncle normally gives rise to a slow rate of locomotion, but can produce sudden bursts of speed for short distances. The large dual caudal fin of the coelacanth must have offered great resistance to the water when undulating and, without further considering the mechanics of caudal fin propulsion, it appears evident that these fishes were not rapid swimmers, although undoubtedly very powerful ones. The caudal fin region was probably about as flexible as in *Ceratodus*.

In all coelacanth, with the possible exception of the Upper Devonian forms, the pectoral fin was attached to the pectoral girdle somewhat below the middle of the cleithrum. Although the internal skeleton of the fin was rarely ossified, the position of

the ossified fin rays in relation to the girdle indicates that this chain of elements was of varying length. There is also a noticeable size range in the rayed portions of the fin. In most genera, however, the pectoral fin could probably be extended well below the ventral body wall as in *Latimeria*. The pelvic fins, with one known exception, are situated opposite the space between the two dorsal fins. They likewise had a long endoskeletal axis, the elements of which were usually cartilaginous. The first dorsal fin is never lobed, the fin rays being attached directly to the ossified basal plate. The second dorsal and anal fins are lobed, with the axis again usually not ossified.

Until it is possible to make observations on a living specimen of *Latimeria*, it will be necessary to rely on other living types with a somewhat similar fin structure and essentially similar functional pattern for deductions concerning coelacanth locomotion. *Ceratodus* possibly fills these requirements more closely than any other fish among either the Actinopterygii or the Choanichthyes. Dean's (1906) description of the locomotion of this dipnoan indicates that rapid swimming is accomplished by the movement of the caudal fin, with the pectorals and pelvics held close to the body. The body movement is obviously carangiform. Accelerated locomotion in the coelacanths was undoubtedly produced in a similar way, with the dorsal and anal fins acting as stabilizers to prevent body roll. The lobate second dorsal and anal fins were capable of a much greater range of movement than the first dorsal. Their positions opposite one another and near the posterior end of the body suggests that they were of importance in assisting the pectoral fins and the caudal fin in turning movements.

The pectoral fins probably had a rather wide range of movement, including a forward rotation of the pre-axial border into a tetrapod-like position. This assumption is based on the resemblance to the *Ceratodus* pectorals which can be moved into such a position when the fish is resting on the bottom. As in other bony fishes, these fins must also have functioned as brakes, in producing turning movements, in hovering, and in changing the swimming plane. Dr. Breder has suggested to the writer that undulation of the rays around the border of the fin would assist in slow locomotion.

The location of the pelvic fins in the coelacanths, excepting *Laugia*, is similar to their position in many holosteans and isospondyls. Harris states that the pelvics in a posterior position are often able to undulate and oscillate in such a manner as largely



to control the hovering movements of the fish, as well as to produce depressing and elevating forces. Amputation of these fins indicates that, when in this position, they are of no appreciable importance in stopping or in locomotion. Dean's figures of *Ceratodus* demonstrate that the lobate pelvic fins, along with the pectorals, are used in hovering, in rising to the surface, and in slow swimming. They can also be rotated forward like the pectorals to support the fish when resting on, or rising from, the bottom. It is reasonable to suppose that the typical coelacanth pelvic fins were employed in the various ways described above.

The location of the pelvic in *Laugia*, in the typical percoid position below the pectorals, indicates a mechanical relationship between these fins which must have been almost identical with that found in the acanthopterygians (Harris, 1938). A comparison of various coelacanth pectoral girdles (Schaeffer, 1941) indicates that the pectoral fin attachment in *Laugia* is not relatively much higher than in the other members of the group with the exception of the Upper Devonian *Diplocercides* where the attachment is close to the lower border of the cleithrum. It is of further interest that the pelvic fin of *Laugia* is about twice as large as the pectoral fin. This suggests that the downward force produced by the pelvic was greater than is usually produced in the acanthopterygians.

On the basis of the above discussion, the coelacanth may be described as powerful but not normally rapid swimmers. They were probably capable of sudden bursts of speed for relatively short distances. The lobate pectorals and pelvics with their presumably wide range of movement could support the body when resting on the bottom, and the pectorals may have been able to propel the body slowly over the bottom. As in other fishes, the pectorals must have functioned as brakes and for turning movements while swimming, while the pelvics were active during hovering, slow swimming, and during upward and downward movements of the body. The air bladder may or may not have functioned as a respiratory organ, although there is reason for believing that it had a true hydrostatic function.

The functional significance of the ossified layer around the air bladder in the coelacanth is problematical. Among the Osteichthyes, certain catfishes, the loaches, and the peculiar oceanic genus *Kurtus* have a bony capsule entirely or partly surrounding the bladder. These fishes, with the exception of *Kurtus*, inhabit a variety of environments, including mountain streams, rivers,

lakes, and ponds. They are, again excepting *Kurtus*, all bottom living types in which the bladder is much reduced in size and of slight or no value as a hydrostatic organ. There is some evidence that the bladder in the loaches functions in a sensory capacity, possibly in connection with thermal and barometric changes. The air bladder of the coelacanth, however, is large and must have had a hydrostatic function. There is, furthermore, no evidence from the body form that these fishes were or are habitually bottom dwellers. The air bladder of *Latimeria* was not recovered, although J. L. B. Smith (1939) presumes that it was not ossified. The final solution of this problem requires experimental evidence which is not at present available.

#### OSSIFICATION VERSUS CHONDRIFICATION

The early reduction in the ossification of the coelacanth skeleton has been mentioned. In the Osteichthyes generally there was a tendency in this direction in a number of unrelated or distantly allied groups such as the Coelacanthini, Dipnoi, Acipenseroides, Amiidae, and in the Teleostei, although secondary ossification has occurred in some bottom living teleosts. Such a phylogenetic reduction in the degree of ossification of the squamation and of the skeleton, particularly of the skull, has been attributed to the gradual development, at the placoderm level, of an efficient mechanism for the regulation of calcium metabolism (Westoll, 1942). H. W. Smith (1939) has suggested, with the ostracoderms and placoderms in mind, that migration to a marine environment, where there was a greater concentration of salts for maintaining the necessary osmotic equilibrium, would eliminate the need for an extensive non-permeable bony cover. As far as the Osteichthyes are concerned it is difficult to reconcile the latter theory with the fact that the sturgeons, for instance, have never entered salt water.

The work of Grove and Newell and of Harris demonstrates that active locomotion in an aquatic environment requires a lowering of the specific gravity of the fish until it approaches that of water. Heavily ossified types such as the ostracoderms and many placoderms, even with the lifting power of the aerofoil pectoral fin and heterocercal caudal, were essentially bottom living types. In the absence of an air bladder, one way the specific gravity might be reduced would be through a marked reduction in ossification. It appears plausible to assume that the sharks perfected their free

swimming habitus through such reduction, and finally through an efficient regulation of calcium metabolism controlling the degree of calcification of the cartilaginous skeleton.

The development of an air bladder in the Osteichthyes lowered the specific gravity, but apparently not sufficiently in all cases to produce the required buoyancy. Grove and Newell point out, however, that while the heterocercal tail is present in nearly all the primitive choanichthoids and paleoniscoids (*Cornuboniscus* represents an exception), the air bladder buoyed the anterior end of the body so that the aerofoil pectoral was of little functional value and was transformed into the teleost type. The reduction in ossification might then be considered as the last step in lowering the specific gravity to such a degree that the elevating effect of the heterocercal tail was no longer required and the homocercal type was favored. There are, however, a number of exceptions to this thesis. The rhipidistians, with no appreciable reduction in ossification, developed a diphycercal tail. The acipenseroids, in spite of such reduction, retained a heterocercal tail. It appears evident, from a phylogenetic point of view, that there is a rather delicate balance between the shape and position of the pectoral fin, the shape of the caudal, the degree of ossification, and, when present, the efficiency of the air bladder as a hydrostatic organ.

Romer's (1942) thesis that the presence of cartilage in the skeleton of an adult vertebrate represents a neotenic condition is clearly indicated by the known facts. As suggested above, however, the significance of this embryonic retention is far more evasive. A distinction should be made between the persistence of skeletal elements in cartilage and the complete elimination of such elements. Cartilage continues to offer some protection and support, to resist tension and compression forces, as well as to reduce the weight of elements formerly composed of bone. The complete loss of bony or cartilaginous structures, besides resulting in a lighter skeleton, implies, from a functional point of view, that this loss has been compensated for by other structural and/or functional modifications.

Romer further points out that skeletal degeneration, involving in some groups mostly chondrification, in others also loss of dermal bones and bony scales, was progressive, with some exceptions, from the ostracoderms through the amphibians. With the appearance of the amniotes, however, this process was arrested, presumably in response to the mechanical requirements of a completely

terrestrial existence. The general reduction in ossification in the various groups of aquatic vertebrates, as mentioned earlier, might very well be associated with a lowering of the specific gravity of the body, while selective ossification, as in the postcranial axial skeleton of the coelacanth, may, in addition, have some more elusive function implications.

#### COELACANTH CLASSIFICATION

Various authors (e.g., Stensiö, 1932; Schaeffer, 1941) have discussed briefly the relationships of the different coelacanthid genera and have made suggestions regarding the erection of higher categories within this group. Berg (1940) and Romer (1945) are the first actually to attempt such a subdivision, and the difference between the two classifications is mainly one of taxonomic rank. Berg considers the Dipnoi, in spite of their established derivation from the early choanichthid stock, to be in a separate class equivalent to the Teleostomi, the latter being essentially equal to Romer's Osteichthyes. The various categories in Berg's Subclass Crossopterygii, which has about the same diagnosis as Romer's Subclass Choanichthyes, are thus unnecessarily elevated with the result that the Coelacanthini are considered to be a superorder.

The subdivisions within the Coelacanthini are essentially the same for both authors and adequately reflect our present knowledge of the group. Following the classification of Romer, the primitive Devonian genera are grouped into the family Diplocercidae and the Carboniferous-Cretaceous forms into the family Coelacanthidae. The Recent *Latimeria* is the sole representative of the Latimeriidae. The Lower Triassic *Laugia*, with its acanthopterygian-like relationship between the pectoral and pelvic girdles and various other specializations, has been placed in a separate family, the Laugiidae.

It is hardly possible at the present time to formulate a concise and restrictive definition of the family Coelacanthidae. This is due not only to our incomplete knowledge of the osteology of most of the genera, particularly of the skull, but also to the amazing homogeneity of the entire suborder from the Middle Devonian to the Recent. This lack of diversification emphasizes the still somewhat arbitrary basis for any subdivision into families. An attempt at defining the Coelacanthidae is desirable, however, and it might be formulated as follows:

Otico-occipital and ethmo-sphenoid portions of neurocranium

incompletely ossified, with varying number of isolated paired ossifications such as ethmoids, anterior occipitals, and posterior occipitals. Basioccipital, if ossified, connecting reduced prootics. Supraoccipital may or may not be ossified. Pattern and tendency towards reduction of dermal bones of skull not distinctive from other families. Basiventral vertebral elements present in some genera, also ossified ribs. Pectoral girdle not distinctive, pelvic girdle usually composed of an anterior division with one to three apophyses, a median process with denticulated medial border and an expanded posterior division. Pelvic girdle never in contact with pectoral. Basal plate of first dorsal fin essentially triangular, that of second dorsal and anal fins usually forked. Scale ornamentation not distinctive.

On the basis of our present information, this definition eliminates the Diplocercidae because of the complete ossification of the two moieties of the neurocranium. The postcranial skeleton is poorly known. The Laugiidae are excluded by the greater ossification of the otico-occipital portion of the neurocranium, the attachment of the pelvic to the pectoral girdle, and the very specialized basal plate of the anal fin.

The assignment of *Latimeria* to a separate family, however, is difficult to justify on the basis of known morphology, and Berg includes the Latimeriidae and Coelacanthidae in one suborder. He distinguishes the Latimeriidae on the basis of the pedunculate pectoral fins as opposed to the lobed pectorals of the Coelacanthidae. *Latimeria* may also have a greater reduction of endocranial ossification than occurs in the Coelacanthidae. The double articulation of the lower jaw, with both quadrate and symplectic, may or may not be unique.

*Diplurus* is clearly a member of the Coelacanthidae. The few determinable characters of the neurocranium suggest close relationship with *Rhabdoderma* or *Wimania*. The pelvis, with its two diverging apophyses and long median process is very similar to that of *Whitea*. The basal plates of the median fins resemble similar elements in *Osteopleurus milleri*, *Coelacanthus*, and *Undina*.

Coelacanth with long, ossified ribs are thus far known only from the Newark series, and this character may represent another expression of the endemism of the Newark fauna. While it is not possible at present to compare adequately the skulls of *Diplurus* and *Osteopleurus*, there are differences in the squamation, shape of the pelvis, and maximum body size which indicate generic separa-

tion. The exact degree of affinity between these two genera is therefore difficult to determine, although it may be closer than these differences suggest. This is all the more probable in view of the variation in scale ornamentation and the form of the pelvis within the Coelacanthini. The long, ossified ribs must have served some mechanical purpose, and it is tempting to suppose that this is associated in some way with the Newark environment.

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