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## A REVISION OF *COELACANTHUS NEWARKI* AND NOTES ON THE EVOLUTION OF THE GIRDLES AND BASAL PLATES OF THE MEDIAN FINS IN THE COELACANTHINI

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### INTRODUCTION

The existence of coelacanth fishes in the Upper Triassic of North America has long been known from the description by Newberry (1878, 1888) of the very poorly preserved *Diplurus longicaudatus*. Since then, Lambe (1916) has described *Coelacanthus banffensis* from a single fin and more recently Bryant (1934) has reported *Coelacanthus newarki* from the Newark Series. From a new locality much more abundant material of a form that is exceedingly close to *C. newarki* has become available; and in view of the scarcity of coelacanth remains from the Triassic of North America, it is desirable to report this material in some detail.

It has been pointed out by Stensiö (1921) and Moy-Thomas (1937) that a great number of the coelacanths referred to the genus *Coelacanthus* possess characters that are quite distinct from those of the genotype, which is the Permian *Coelacanthus granulatus* of Agassiz (1839). In view of this fact, and for reasons to be mentioned later, it seems advisable to establish a new genus for the reception of the species from the Upper Triassic of Pennsylvania, described as *Coelacanthus newarki* by Bryant, and also for the material to be described in this paper, which is referred to the same genus and species.

The name *Osteopleurus* (Gr. osteon, bone, and Gr. pleuron, rib) is herewith proposed for this genus in allusion to the long, ossified ribs. It will tentatively contain just one species, *newarki*. The type is Prin. Univ. Pal. Mus. No. 13695.

The author is indebted to Dr. G. M. Kay of the Department of Geology, Columbia

University, for the discovery and presentation of the first specimens from this latter site, to Mr. V. E. Shainin for the presentation of the very fine specimens in his possession, and particularly to Professor A. W. Pollister of the Department of Zoölogy for permission to study his private collection and for much helpful advice. He also wishes to thank Dr. G. L. Jepsen for permission to study the type specimen, Professor W. K. Gregory and Mr. H. C. Raven for critically reading the manuscript and finally Dr. A. J. Ramsay for his assistance with certain of the photographs. All the specimens collected in the Granton Quarry have been presented to The American Museum of Natural History and catalogued as A.M.N.H. No. 15222.

### OSTEOPLEURUS, NEW GENUS

GENOTYPE.—*Coelacanthus newarki* Bryant.

DIAGNOSIS.—Long, ossified, pleural ribs. Pelvic fin midway between first and second dorsal fins. Plates of pelvic girdle quadrilateral in shape. Basal plate of anal fin bifurcated. Basal plate of first dorsal, triangular. Basal plate of second dorsal, deeply bifurcated. Scales possessing about five prominent parallel ridges.

### HORIZONS AND LOCALITIES

The Pennsylvania material (one complete specimen and several fragments) was collected by Dr. Jepsen in the Upper Triassic shales of the Newark Series in an exposure of the Lockatong formation, near the town of North Wales. The New Jersey specimens were found in the Upper Triassic black shales of the Stockton formation of the Newark Series in the Granton Quarry at North Bergen, New Jersey. The character of the sediments and the presence of

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the phyllopod *Estheria ovata* Lea indicate that both formations are quite probably fresh water and less likely brackish water deposits.

### MEASUREMENTS

There are no observable qualitative characters which can be used to separate the forms from the Lockatong and the Stockton. There are, however, quantitative differences which at first were considered to be of specific significance. An attempt was made to use quantitative methods outlined by Simpson and Roe (1939) for comparing small samples and single specimens in an effort to determine whether we are dealing with a single species or two separate species. This was not successful, however, since nothing is known concerning relative ontogenetic growth in coelacanth in general, and since the number of measurable specimens of *Osteopleurus* is very small. As Dr. Simpson pointed out, it is impossible to determine in this case whether the quantitative differences are specific differences or merely different stages in the growth of a single species. Therefore, until more well-preserved material is obtained, all of the specimens are referred to the one species, *newarki*.

#### MEASUREMENTS IN MILLIMETERS

	New Jersey Speci- mens	Pennsyl- vania Speci- mens (approx.)
Body length (minus supplementary caudal)	110	71
Head length	30	19
Length post. border of head to ant. border of caudal	45	26
Length first caudal	35	26
Length first plus second caudal	45	?
Fin locations, mm. from anterior end to:		
First dorsal	35-40	22
Second dorsal	62	36
Pelvic	45	25-26
Anal	68	40
Caudal	80	45
Body depth at ant. end of first dorsal (approx.)	24	15

### SQUAMATION

Each scale appears to be an elongated oval. The exposed portion possesses about

five prominent longitudinal ridges, the middle one being the longest and largest. There are also fine striae which converge in the covered portion. Annular rings are present which tend to break the continuity of the striae. The details of ornamentation are well preserved in the scale illustrated in Fig. 2,A.

### SKULL

Due to crushing it is impossible to make out the detailed structure of the skull in any of the specimens. Some features of importance can be determined in one of the specimens from the Stockton (Fig. 1,A), and, also, from numerous isolated plates. The opercular is a large bone, as it is in most coelacanth. An isolated example shows that it is oval in outline and lacks ornamentation. The outline of the postorbital cannot be determined in the preserved skull. An isolated plate (Fig. 4,B), which has a different shape than the opercular, has been tentatively identified as the postorbital, although it may be relatively too large to be this bone. The lack of a lateral line canal would seem to indicate that the medial surface is exposed. The postorbital lateral line canal is, however, very prominent in the preserved skull. That the squamosal, opercular, preopercular, and subopercular are missing from this skull is indicated by the presence of a depressed region (Fig. 1,A,x) behind the orbit. Furthermore, the squamosal branch of the postorbital lateral line canal is not evident.

The angular bone can be readily identified, as the mandibular branch of the lateral line runs over it. The dentary, splenial, and coronoid are not distinct. The gular plates possess the long, oval shape characteristic of the coelacanthids. They are ornamented with fine ridges which follow the outline of the bone. One end has a wide, shallow groove which tapers to a point in the middle of the plate. They are 11 mm. in length and 2.7 mm. in width (Fig. 2,C).

The suture between the frontals and intertemporals is very evident, the bones having been abnormally separated during

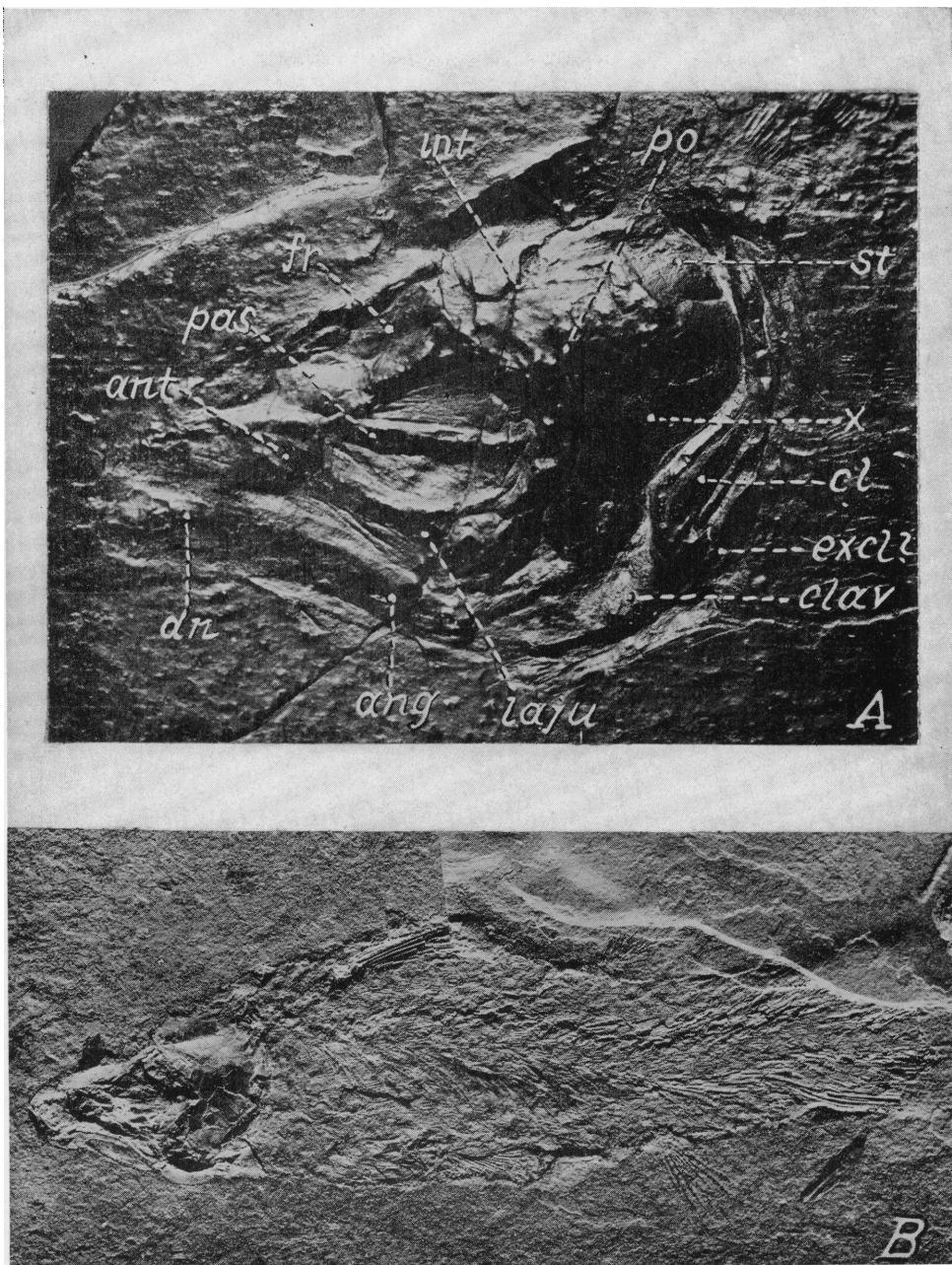


Fig. 1. *Osteopleurus newarki*.

A. Lateral view of skull.  $\times 2.8$ . *ang.*, angular; *ant.*, antorbital; *clav.*, clavicle; *cl.*, cleithrum; *dn.*, dentary; *excl.*, extracleithrum; *fr.*, frontal; *int.*, intertemporal; *laju.*, lacrimo-jugal; *pas.*, parasphenoid; *po.*, postorbital; *st.*, supratemporal; *x.*, opercular region.

B. Lateral view of almost complete specimen showing position of all the fins, scale imprints, and ossified ribs.  $\times 1.1$ .

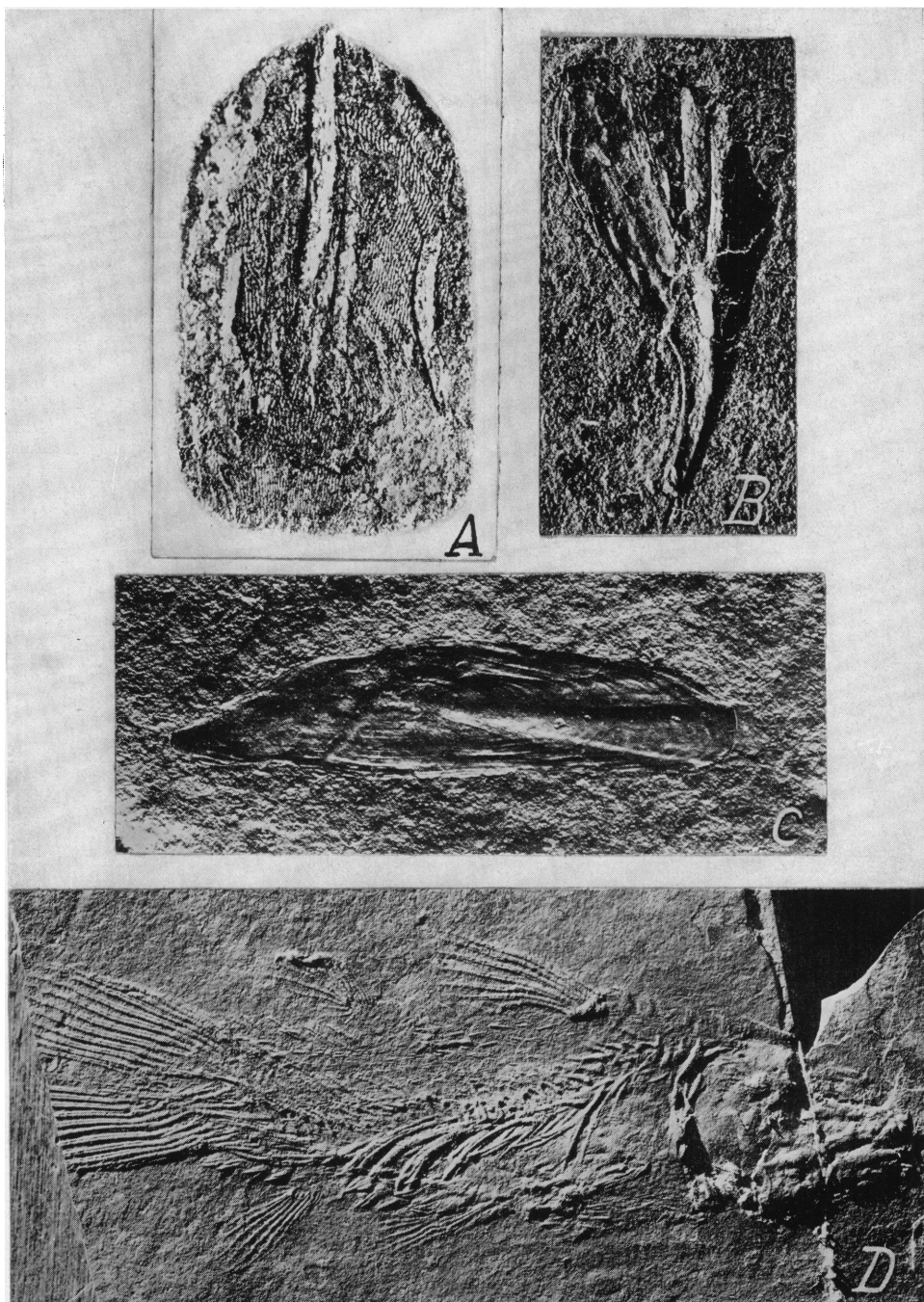


Fig. 2. *Osteopleurus newarki*.

- A. Isolated scale showing details of sculpturing.  $\times 18.0$ .
- B. Unidentified plate.  $\times 9.6$ .
- C. Gular plate.  $\times 7.4$ .
- D. Lateral view of a second almost complete specimen showing well-preserved neural arches.  $\times 1.4$ .

preservation. The supratemporal and extrascapulars cannot be distinguished from the intertemporal, although the supratemporal is undoubtedly present as a poorly defined plate lying just dorsal to the opercular region. What appears to be an anteorbital is present as a small triangular bone on the anterior rim of the orbit. The postrostrals and premaxillary are crushed and their outlines cannot be determined. The circumorbital plates have not been preserved. The lacrimojugal characteristically frames the ventral rim of the orbit.

A bar of bone running lengthwise through the orbit may be the somewhat dorsally displaced parasphenoid. It resembles that part of the bone between the more posterior expanded portion and the ethmoid ossification, as figured by Moy-Thomas (1937) for *Rhabdoderma*.

The ossified part of the neurocranium (Fig. 4,C) is poorly preserved in dorsal aspect on one of the slabs in the Princeton collection (P.U.P.M. No. 13826). The parasphenoid has its edges upturned to a greater degree than in *Wimania*. On each side of the channel thus formed a bony wing projects sideways, as in the *Undina* parasphenoid (Aldinger, 1930). Very fragmentary bits of bone anterior to the parasphenoid have been identified as the ethmoid ossifications. The location of the basisphenoid, proötic, and basioccipital is indicated, but it is impossible to make out any of the structural details. There are several examples of a well-preserved isolated plate of constant shape which cannot be positively identified (Fig. 2,B). It is possibly a part of the ossified neurocranium, or even of the pterygoid complex.

#### PAIRED FINS AND GIRDLES

The pectoral fin is barely indicated on Mr. Shainin's specimen, lying on what may be the remains of the ossified swim bladder (Fig. 2,D). One specimen has a well-preserved pectoral girdle (Fig. 1,A). The cleithrum is apparently quite similar to that found in *Rhabdoderma*. Externally, there is a ridge which runs from the upper posterior border to the lower anterior border. A curved clavicle is indicated

which meets the ventral border of the cleithrum.

A pelvic fin is preserved in place in two of the specimens, but the pelvic girdle is covered with a layer of matrix which cannot be removed. It is preserved in the type, being well ossified, quadrilateral in outline, and with concave margins. The fin has about twelve lepidotrichia and is relatively further behind the pectoral girdle than the pelvic fin of *Coelacanthus granulosus*.

#### UNPAIRED FINS

The anterior dorsal fin including the basal plate is well preserved in several specimens (Fig. 3,A). This plate has a more or less triangular shape, with the apex pointed anteriorly. The lepidotrichia, about nine in number, are attached directly to the plate, the proximal ends being forked to fit over the plate. The former are grooved and flattened laterally and are not broken up into segments, except at their distal ends.

The basal plate of the posterior dorsal fin is preserved in the complete Pennsylvania specimen. As Bryant states, the plate is bifurcated. The lower process, however, is about the same length as the upper, as can be seen in the example figured in Pl. VIII, fig. 1, of Bryant's paper. The fin contains about twelve lepidotrichia.

The basal plate of the anal fin (Fig. 9,E) is also only known from the type specimen. It is deeply bifurcated, the forks being more slender than those on the basal plate of the posterior dorsal. The process with which the fin rays articulated is quite narrow but somewhat expanded posteriorly.

Both the epichordal lobe and the hypochordal lobe of the caudal fin contain about ten to twelve lepidotrichia. The supplementary caudal fin is beautifully preserved in negative in one of the New Jersey specimens (Fig. 3,B). It is relatively longer than the one found in *Undina* and consists of dermal rays in the usual tuft.

#### AXIAL SKELETON

The neural arches are robust forked structures with fairly long, spinous processes which are apparently rather well ossified (Fig. 2,D). There are about thirty

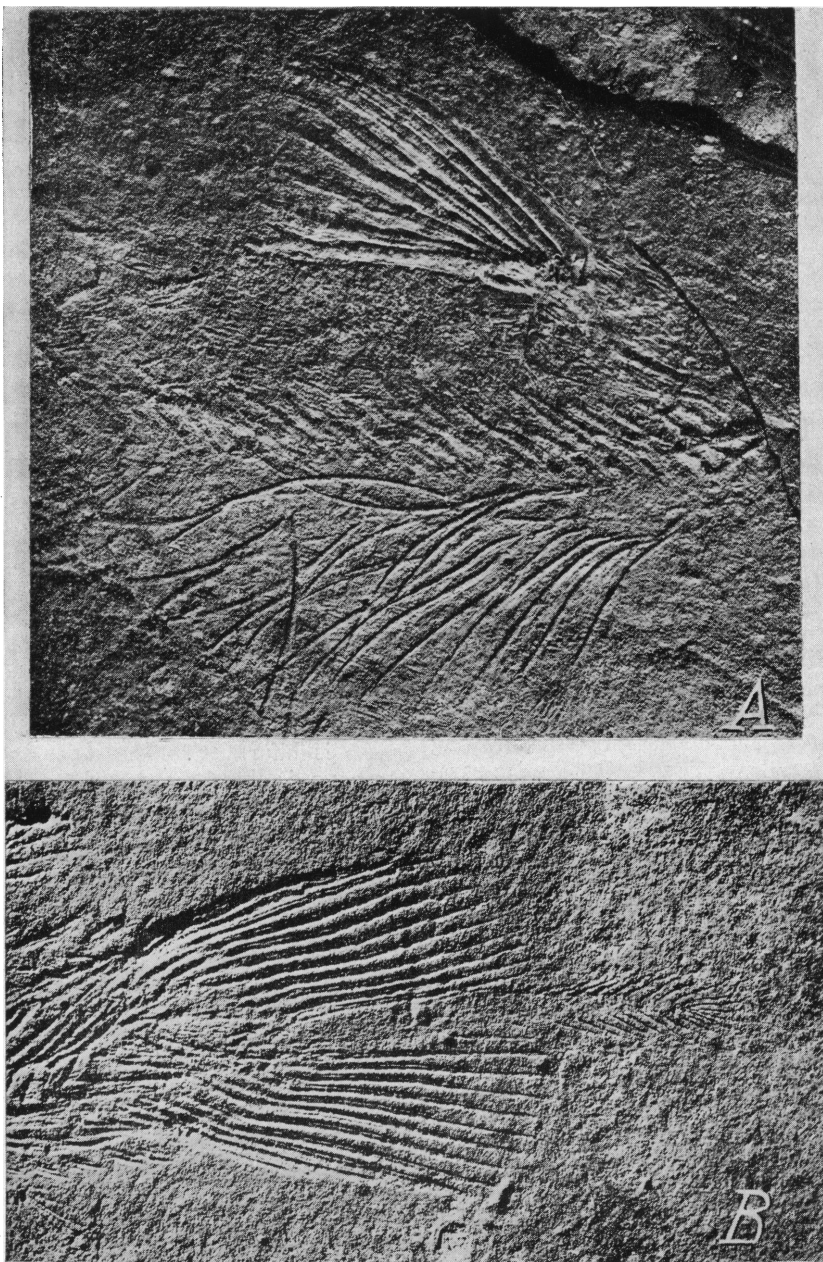


Fig. 3. *Osteopleurus newarki*.

- A. Trunk region showing first dorsal fin, with its basal plate, neural arches, and ossified ribs.  $\times 2.9$ .  
 B. Specimen showing caudal fin and well-preserved supplementary caudal fin.  $\times 2.3$ .



pairs of long, ossified pleural (subperitoneal) ribs (Fig. 2,D and Fig. 3,A). This is an important character which, above all others, separates *Osteopleurus* from the genotype of the genus *Coelacanthus*, which has very short, pleural ribs. Haemal arches are evident posterior to the last rib (Fig. 2,D).

With regard to the Upper Triassic coelacanth from North America, *Coelacanthus banffensis* (Lambe, 1916), from Alberta, is, as Moy-Thomas points out, far too fragmentary for generic determination.

*Diplurus longicaudatus* (Newberry, 1878) from the Brunswick Formation of the Upper Triassic of New Jersey is quite distinct from *Osteopleurus*. It reaches a length of three feet and lacks ossified ribs. The

scales have a great number of fine longitudinal ridges. The only observable resemblance between the two is the triangular shape of the basal plate of the first dorsal, which, as will be shown, is a character common to most members of the order.

By establishing the new genus *Osteopleurus* for the identifiable remains of coelacanthus other than those of *Diplurus* from the Triassic of Pennsylvania and New Jersey, it is hoped that a further contribution has been made toward a more natural classification of the Coelacanthini. The evidence indicates that *Osteopleurus* is probably most closely related to *Coelacanthus*, although, as pointed out above, the pelvic plates have a very different shape. Until better preserved skull material is found, it is unsafe to speculate further.

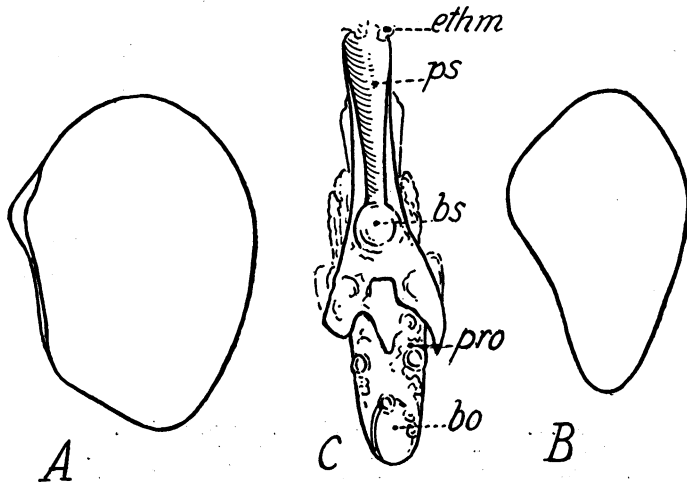


Fig. 4. *Osteopleurus newarki*.

- A. Outline of opercular plate.  $\times 3.5$ .  
 B. Outline of plate tentatively identified as postorbital.  $\times 3.8$ .  
 C. Dorsal view of neurocranium.  $\times 8.1$ . eth., ethmoid; ps., parasphenoid; bs., basisphenoid; pro., proötic; bo., basioccipital.

#### THE EVOLUTION OF THE GIRDLES AND BASAL PLATES OF THE MEDIAN FINS IN THE COELACANTHINI

In an attempt to determine the possible affinities of *Osteopleurus* a comparative study of the paired and unpaired fin supports has been undertaken. It is well known that in most respects the coelacanthus are a very homogeneous and rather conservative order. Stensiö has pointed out

(1932, p. 46), however, that the group shows a much greater range of variation than formerly suspected and that it is possible to distinguish several natural groups of genera. There are some striking variations in the pelvis and in the basal plates of several of the median fins. These varia-

tions must be considered along with the skull in dividing the Coelacanthini (Actinistia) into smaller categories. Up to the present time, no attempt has been made to subdivide the order or to construct at least a tentative phylogeny. Such an attempt is made in this paper.

Moy-Thomas has suggested (1937) that it may be fused with the cleithrum in many cases, i.e., *Rhabdoderma*.

The supracleithrum is evidently loosely united by ligaments to the cleithrum in all but a few genera, such as *Coelacanthus* and possibly *Osteopleurus*, in which it appears

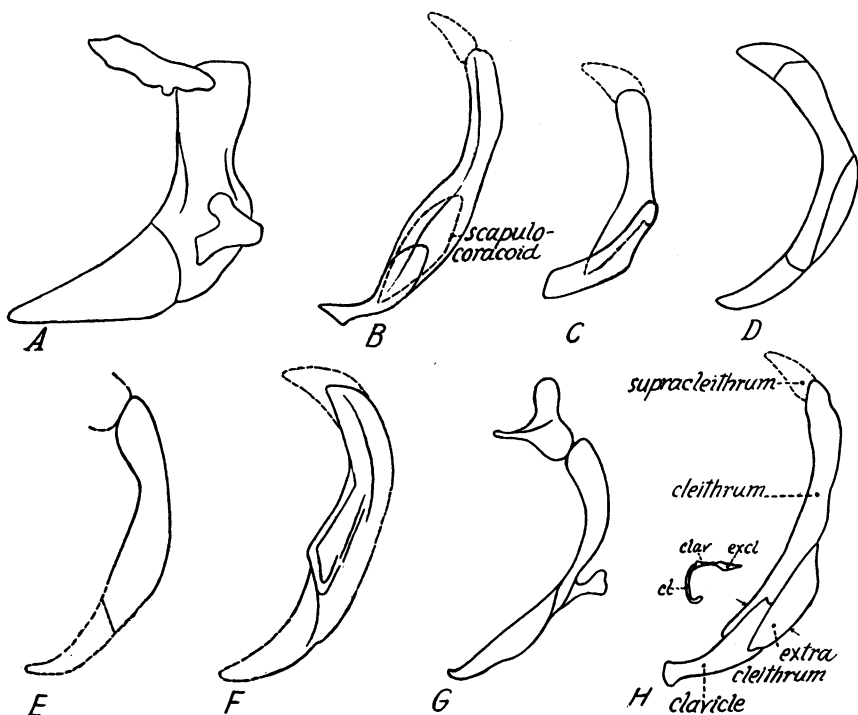


Fig. 5. Series of pectoral girdles. Scales various.

- A. *Eusthenopteron foordi*. Upper Devonian. Medial view (after Bryant).
- B. *Diplocercides kayseri*. Upper Devonian. Lateral view (after Stensiö).
- C. *Rhabdoderma elegans*. Upper Carboniferous (composite, after Huxley and Moy-Thomas).
- D. *Coelacanthus granulatus*. Permian. Lateral view (after Moy-Thomas and Westoll).
- E. *Laugia groenlandica*. Lower Triassic (after Stensiö).
- F. *Osteopleurus newarki*. Upper Triassic (original).
- G. *Macropoma speciosum*. Cretaceous (after Reis).
- H. *Latimeria chalumnae*. Recent. Lateral view and cross-section at level of arrows (after Smith).

### THE PECTORAL GIRDLE

The pectoral girdle (Fig. 5) in all coelacanth consists of the following dermal elements: a somewhat triangular supracleithrum, a dominant cleithrum, and a clavicle which is never as long or as wide as the cleithrum. The endoskeletal portion of the girdle is but rarely distinguishable.

to be suturally united. It is interesting to note in this connection that there is considerable variation in the intimacy of the union between the supracleithrum and the cleithrum in the teleosts.

The cleithrum is quite constant in shape, the variations being of minor importance. It is, in general, the longest bone of the



girdle and is in most cases rather narrow. It is relatively much narrower than the same bone in the rhipidistians. In *Latimeria* (Smith, 1940) the cleithrum is curved about its long axis as can be seen in the cross-section in Fig. 5,H. This is apparently not a general feature, for in *Rhabdoderma* it is a strongly ridged but essentially a flat plate.

The coelacanth clavicle has its greatest extent in the same vertical axis with the cleithrum. It lacks the prominent horizontal portion which is present in the rhipidistian clavicle. The clavicle of the Upper Devonian *Diplocercides* does possess a fairly wide horizontal ramus, approaching the condition in *Eusthenopteron*. In all genera the clavicles meet in the midventral line. In *Latimeria* each clavicle has a distinct facet for articulation with its fellow. There is no evidence of the presence of an interclavicle as recently described by Gross (1936) in certain rhipidistians.

One of the most interesting features of the pectoral girdle is the presence of a dermal bone apparently not found in any other vertebrate. This bone, named by Moy-Thomas the extracleithrum, has so far been observed only in *Coelacanthus granulatus* (Fig. 5,D) and in *Latimeria chalumnae* (Fig. 5,H), although it may have been present in *Osteopleurus*. It is located on the lateral surface of the girdle behind the cleithrum, contacting the clavicle ventrally. The phylogenetic history of the extracleithrum is at present unknown. It does seem odd that it should appear as a neomorph in only a few genera. Moy-Thomas (1935) does not believe it to be homologous with the postcleithrum of actinopterygians since it is ventral to the endoskeletal portion of the girdle. In any case the very distant affinities of the coelacanth and teleosts seem to preclude any possibility of determining its origin and homologies in that manner. It appears extremely unlikely that the extracleithrum is a new element in the coelacanth. Very probably it is indistinguishably fused with the cleithrum in most cross-sections at an early stage in ontogeny. In *Latimeria*, it is situated superficially to the cleithrum and the

clavicle and is very slightly overlapped by them on its anterior margin.

The earliest coelacanthid pectoral girdle known, that of *Diplocercides*, possesses a separately ossified scapulo-coracoid element of relatively large size. As mentioned above, the endoskeletal portion of the girdle is not as independent of the dermal as it is in the rhipidistians. In *Diplocercides*, it consists of a flat, lenticular plate very intimately associated with the cleithrum and clavicle. Besides the suggestion of Moy-Thomas that it may be fused with the cleithrum, the possibility that it was often but poorly ossified must be considered. In *Undina* and *Macropoma*, the endoskeleton has a posterior projection which extends beyond the cleithrum. This process is quite characteristic of these Mesozoic genera. To it was attached the skeleton of the pectoral fin. In no case is it possible to distinguish the scapular element from the coracoid, as they are completely co-ossified.

There is considerable variation in the location of the scapulo-coracoid plate, and hence, in the pectoral fin in relation to the cleithrum and the pectoral girdle as a whole. In *Diplocercides* the plate is located on the lower extremity of the cleithrum, even overlapping the clavicle to a considerable degree. In nearly all other coelacanth the endoskeleton has apparently migrated, at least relatively, dorsward to the middle of the cleithrum. In *Macropoma* and *Undina*, the same positional result is obtained by a relative increase in the length of the clavicle. It would appear that the various positions of the pectoral fin were specializations associated with the different modes of living in the Coelacanthini. For instance, the pectoral fin of *Laugia* could only have been used for maneuvering movements while swimming, while that of *Diplocercides*, like *Eusthenopteron*, was probably also used for propelling the body over the sea floor. Unfortunately, the endoskeletal girdle of *Latimeria* was not recovered, but Smith (1940) is of the opinion that it is situated just inside the dorsal apex of the extracleithrum, as in *Coelacanthus granulatus*, or at about the

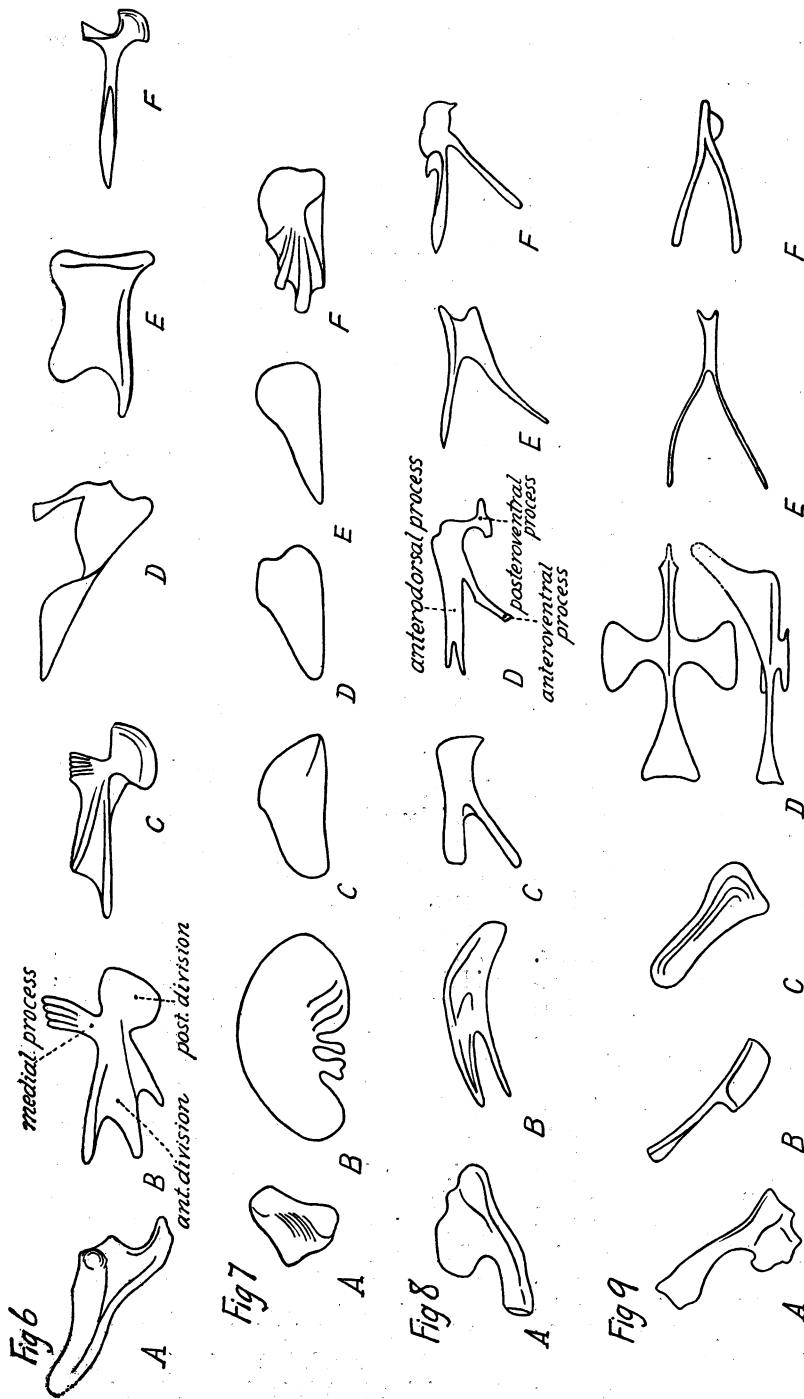


Fig. 6. Pelvic plates. Ventral surface. Left side.

A, *Eusphenopteron foordi* (original). B, *Rhabdoderma elegans* (after Moy-Thomas). C, *Coelacanthus granulatus* (after Moy-Thomas and Westoll). D, *Laugia groenlandica* (after Stensiö). E, *Osteolepiscus newarki* (original). F, *Undina minuta* (after Reis).

Fig. 7. Basal plates of first dorsal fin from left side. A to E as in Fig. 6; F, *Undina pinnulata* (after Reis).

Fig. 8. Basal plates of second dorsal fin from left side. A to E as in Fig. 6; F, *Undina pinnulata* (after Reis).

Fig. 9. Basal plates of anal fin from left side. A to E as in Fig. 6; *Undina gulo* (after Woodward). In D, upper figure of basal plate, dorsal view. Scales various.

middle of the cleithrum. The pectoral fin, however, has a rather long, fleshy portion, thus carrying the fin well down below the ventral surface of the body. This suggests that it can be used for pulling the body over the ocean floor.

### THE PELVIC GIRDLE

The variation in the shape of the pelvic plates results in a natural division into three types represented by the plates of *Rhabdoderma*, *Laugia*, and *Osteopleurus* (Fig. 6). Unfortunately the pelvis has been described or preserved in but few of the known genera and the differences between these known types are extreme enough to indicate that the range of variation must have been rather great. Although the pelvis is unknown in the Upper Devonian forms, it is well preserved in the Carboniferous *Rhabdoderma*. This probably represents a very close approach to the primitive type. The resemblance to the pelvis of *Eusthenopteron* is not too great but is close enough to indicate a derivation from the rhipidistian type. Through the kindness of Professor Gregory and Mr. Raven I am permitted to include a figure of the second known specimen of a pelvic plate of *Eusthenopteron* which will be described by them in detail at a subsequent time. It suffices here to note that this plate does not resemble very closely the one figured by Goodrich (1901) but does agree more closely with the *Rhabdoderma* type.

The *Rhabdoderma* type of pelvic plate is also found in *Coelacanthus granulatus*, *Undina*, *Macropoma*, and *Wimania*. The part of the plate showing the greatest amount of variation in this group is the medial process. This process may (*Rhabdoderma*) or may not (*Undina*) possess a denticulated medial border. It varies in size from little more than a serrated region on the medial border between the anterior and posterior divisions in *Wimania* (Stensiö, 1921, Pl. VIII, fig. 7) to a very prominent process in *Rhabdoderma*. This process articulated with its counterpart of the opposite side to produce a girdle which in transverse section was either perfectly

horizontal, as in the Rhipidistians, or slightly V-shaped. In such forms as *Wimania* and *Coelacanthus* the space between the adjoining pelvic plates would be a mere slit, while in *Rhabdoderma* and *Undina* it would be relatively quite large.

The anterior and posterior divisions (so-called by Stensiö, 1932) were expanded to various degrees for the attachment of the body and fin musculature. The proximal radial(s) of the pelvic fin articulated with the posteroventral region of the posterior division.

The pelvis of *Laugia* is situated so far forward that it evidently made a ligamentous connection with the clavicle of the pectoral girdle. This very percomorph-like position plus the great size of the pelvic fins were probably responsible for the very different shape of the plates of this girdle. In spite of the specializations, it is possible to recognize homologous parts in the pelvic plates of *Laugia* and *Rhabdoderma*. A plate of the former has triangular anterior and posterior divisions with a prominent but not denticulated medial process springing from the latter. As in the percomorphs, the pelvic girdle is hence not only anchored by the hypaxial musculature but also by attachment to the pectoral girdle. This condition undoubtedly evolved along with the enlargement of the pelvic fin which, incidentally, extends posteriorly almost to the base of the anal fin. Such a large fin would offer great resistance to the water during movement, necessitating the coincidental development of such a bracing mechanism. A pelvic plate of *Laugia* is further specialized in having the anterior division twisted medially and the medial and lateral borders of the posterior division turned more or less dorsally, thus offering the most advantageous positions for the attachment of the fin and body muscles.

Stensiö considers the pelvis of *Laugia* to be suggestive of the *Rhabdoderma* type, particularly of *Rhabdoderma elegans*. It was probably derived from a form with a rather well-developed medial process.

The pelvis of the *Osteopleurus* is at present quite baffling. A study of Bryant's

original material has not revealed with certainty which is the lateral and which the medial borders of the plates. Until this point can be definitely settled it is unwise to make detailed comparisons. In any event, the pelvic plates are very unlike anything previously described and if found alone would certainly not be considered as coelacanthid. A plate is quadrilateral in outline, rather than pentagonal as Bryant states, with a rather short anterior projection. The border of each side is slightly concave.

#### BASAL PLATE OF THE FIRST DORSAL FIN

In most genera the basal plate of the first dorsal fin (Fig. 7) is triangular with the apex directed forward. One observed exception to this is found in *Rhabdoderma*, in which the plate is oval or kidney-shaped. The ventral border is notched in some species of this genus for articulation with the neural spines. The other exception is found in *Scleracanthus* in which the plate, while being essentially triangular, is slightly forked at its anterior end. In the rhipidistians, the basal plate of this fin is simply a rod with no anteroposterior expansion (Moy-Thomas, 1939, Fig. 22,A). A single radial is situated between this plate and the lepidotrichia of the fin. In the coelacanth, on the other hand, the lepidotrichia articulate directly with the dorsal border of the fin.

#### BASAL PLATE OF THE SECOND DORSAL FIN

The basal plate of the second dorsal fin (Fig. 8) is without exception a bifurcated structure. The open part of the V is always directed forward. In *Eusthenopteron* the anterodorsal process is very short and rounded, while the anteroventral process is much longer and quite robust. Such a plate could very well be the structural ancestor of the same plate in the coelacanth.

In the latter, the two processes are more nearly the same size. The anterodorsal process is in all cases on the same longitudinal axis with the posterior expanded portion of the plate, while the anteroventral process meets the posterior division at an angle of about thirty-five degrees. The posterior portion reaches its greatest extent in *Rhabdoderma*, in which the anterior processes are relatively quite short. In *Osteopleurus*, on the other hand, the processes are relatively long and narrow and the posterior division is reduced. *Laugia* has a well-developed posteroventral process. This extension is indicated in *Coelacanthus granulatus*, *Undina penicillata*, and in *Mawsonia minor* (Woodward, 1908). The basal plate of the second dorsal fin is certainly one of the diagnostic structures, along with the caudal fin, of the postcranial skeleton.

#### BASAL PLATE OF THE ANAL FIN

The variation in the shape of this plate (Fig. 9) is, indeed, very extreme. In *Rhabdoderma* it resembles that of *Eusthenopteron* rather closely and for that reason the former may approach the primitive type. The simple quadrilateral plate of *Coelacanthus granulatus* may represent the posterior expanded portion of the *Rhabdoderma* type. In *Osteopleurus*, *Undina*, and *Macropoma*, the plate is deeply bifurcated like the basal plate of the second dorsal fin. This type must have arisen by the development of an anteroventral process from the posterior expanded division. The basal plate of this fin in *Laugia* is so utterly unlike any of the others that its origin is not ascertainable. In the ventral view, it is cross-shaped. A large median keel projects dorsally at right angles to the horizontal portion. These various extensions certainly anchored the plate firmly in the ventral musculature, and their development must have been associated with some sort of torsion acting on the plate during fin movement.

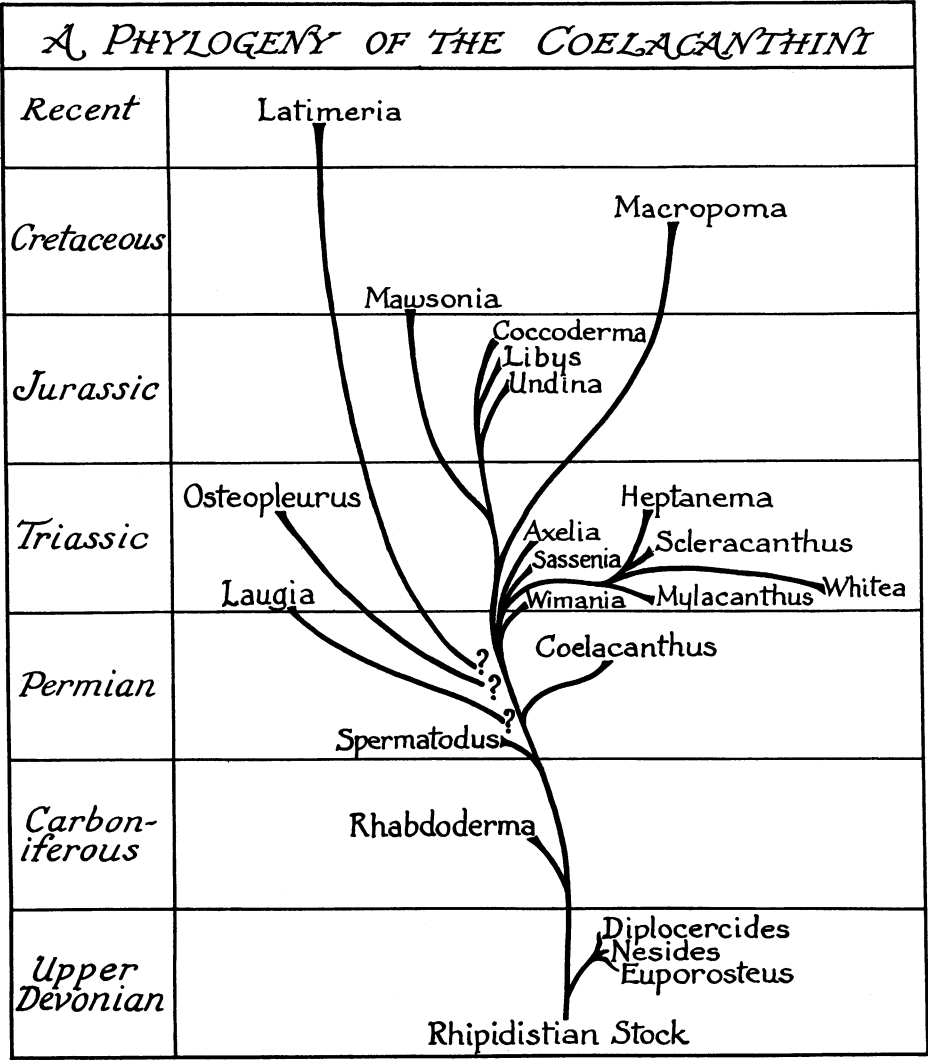


Figure 10.

CLASSIFICATION AND PHYLOGENY

The accompanying phylogeny of the Coelacanthini (Fig. 10) is simply a very tentative attempt to indicate the relationships between certain of the better known genera. As Stensiö (1932) has pointed out, certain of the genera do fall together in natural groups, possibly into families or superfamilies. The characters which establish the coelacanth as a separate order

within the Crossopterygii have been recently summarized by Moy-Thomas (1939) and will only be incidentally mentioned here.

The Upper Devonian forms from Germany, *Diplocercides*, *Nesides*, and *Euporoosteus*, are certainly a natural and primitive group. The neurocranium is ossified in two separate parts and a true basiptyergoid

process is present on the basisphenoid. Both of these characters are present in the rhipidistians. Furthermore, the presence of a horizontal limb on the clavicle is a primitive rhipidistian feature not found in later coelacanth.

Moy-Thomas (1937) has done a great service by revising the Carboniferous and Permian coelacanths of the British Isles and thus eliminating a vast amount of synonymy. Although all the Carboniferous forms have been referred to the genus *Rhabdoderma*, Moy-Thomas himself admits that in the future this genus may have to be subdivided into several genera. This group may then constitute a family. *Rhabdoderma* illustrates a further step in the evolution of the order in the employment of the antotic process (extending laterally from the dorsal border of the basisphenoid) as the articular contact of the neurocranium with the metapterygoid. There is some reduction in the size of the basiptyergoid process. The neurocranium is subdivided into a series of ossifications instead of two major ones. All later coelacanths have a similarly constructed neurocranium. The pelvis of *Rhabdoderma* is the most ancient known and appears to represent the primitive coelacanthid type, showing very distinct but derivable differences from rhipidistians. The same is true for the endoskeletal supports of the other fins, paired and unpaired (except possibly the basal plate of the first dorsal).

Now that the genus *Coelacanthus* has been properly defined (Moy-Thomas and Westoll, 1935), it may, in the future, form the nucleus of a Permian family. It is further evolved from the *Rhabdoderma* stage by the loss of the basiptyergoid process and the presence of only the antotic process. This condition holds for all later coelacanths. *Coelacanthus*, although more progressive, differs markedly from *Rhabdoderma* only in the presence of an extracleithrum. *Spermatodus* appears to be most closely related to *Coelacanthus* (Moy-Thomas, 1939). Besides other similarities in the construction of brain case, both show a reduction in the ossification of the orbital region.

Our present knowledge indicates that the

coelacanths flowered in the Triassic. The number of known distinct Triassic genera is certainly greater than in any other period (Fig. 11). The forms from Spitzbergen *Axelä*, *Sassenia*, *Scleracanthus*, and *Myäacanthus* are apparently a natural group branching off the line leading to the later Mesozoic forms. There are numerous details of the neurocranium which demonstrate this relationship (Stensiö, 1921, pp. 120-129), and also the close affinities of this entire group to *Coelacanthus* on the one hand and the later Mesozoic genera on the other.

*Scleracanthus* has a dentition adapted for crushing. It is closely related to *Axelä* but has a more robust pterygoid, more specialized dentition and differently shaped scales. *Myäacanthus* is closely related to *Axelä* in having a less specialized dentition. *Heptanema* is very difficult to distinguish (Moy-Thomas, 1935) from *Scleracanthus*, while the latter is also considered by the same author to be very close to *Whitea*. A basic character uniting this *Axelä* group is the shape and configuration of the pterygoquadrate complex. In *Axelä*, the pterygoid is large and thick with a very broad posterior vertical limb and a long, thin anterior horizontal limb. In *Myäacanthus* the posterior limb is narrow but longer; in *Scleracanthus* it is also long but wider. The latter is also true of *Whitea* and *Heptanema*. The metapterygoid and quadrate are strongly and independently ossified in this group.

*Wimania*, while it may belong to the *Axelä* group, shows more definite affinities to *Coelacanthus* and *Rhabdoderma* and may have to be placed in a separate family. This conclusion is based on the shape of the parasphenoid, the pterygoid, the cheek plates, and the large opercular.

Stensiö considers *Laugia* to be very suggestive of *Coelacanthus*, the neurocranium exhibiting about the same degree of ossification. He points out that the neurocranium is certainly intermediate between the condition found in *Diplocercides* and such later forms as *Axelä* and *Macropoma*. In a number of the characters of the postcranial skeleton, previously enumerated,

GEOLOGICAL AND GEOGRAPHICAL DISTRIBUTION OF THE COELACANTHINI											
	North America	Brazil	Greenland	Spitzbergen	British Isles	Germany, German and Italian	France, Spain, Belgium	U.S.S.R.	Syria (Mt. Lebanon)	S. Africa, Madagascar	Australia
Recent										Latimeria	
Cretaceous					Macropoma	Macropoma			Macropoma		
Jurassic		Mawsonia			Coccoderma	Macropoma, Coccoderma Libys	Undina				"Coelacanth"
Triassic	Osteolepiscus, Diplurus			(Lower Triassic) Wimmeria, Xosania, Axella, Mucracanthus, Scleracanthus		Graphiurus, Heptanema				"Coelacanth" Coelacanthus, Whitea	
Permian			Laugia		Coelacanthus	Coelacanthus					
Carboniferous	Spermatodus, Rhabdoderma				Rhabdoderma	Rhabdoderma	Rhabdoderma	Rhabdoderma			
Upper Devonian						Diplocercides, Nesides, Euporoosteus					
Spott, Brindley, del.											

Figure 11.



*Laugia* is quite specialized and must represent an offshoot from the *Coelacanthus* type in the Permian.

*Osteopleurus* resembles *Coelacanthus* with respect to the postcranial skeleton except for the apparent very great difference in the shape of the pelvic plates. The former must represent a line isolated from the more central types in the Permian.

*Coccoderma*, *Libys*, and *Undina* appear to be rather closely related. For instance, in each the dermopalatine is an independent bone along the anterior limb of the pterygoid. In other forms it is fused with the pterygoid. Other details of the skull also bear out this conclusion. The direct derivation of this group from the *Coelacanthus* type is indicated not only by the construction of the skull, but also by the details of the postcranial skeleton.

There are a number of minor details in the construction of the dermal cranial roof which indicate relationship between *Macropoma* and the *Azelia* group. For instance, *Macropoma* and *Whitea* have a very similar supraorbital series. The shape of the pelvic plates is another example.

*Mawsonia* seems to be most closely related to *Undina*, more distantly to *Macropoma*. Both have the metapterygoid partially fused with the pterygoid. Other details of the skull are very similar.

*Latimeria* is considered by Smith to be more closely related to a *Rhabdoderma-Wimania* type than to *Macropoma*, although it bears a strong superficial resemblance to the latter. This conclusion appears to be supported by the pattern of the dermal cheek bones, the method of lower jaw suspension, and the presence of an extracleithrum.

The method of lower jaw suspension in

*Latimeria* is worthy of further comment, as it not only articulates in the usual manner with the quadrate, but also separately with the symplectic. Smith points out that two distinct sockets can be observed in the lower jaw of *Diplocercides*, and he has tentatively identified the symplectic in *Wimania* and *Azelia*, indicating a similar type of jaw suspension in these forms. That this condition is common to all coelacanth is doubtful as there is no evidence of its existence in the well-known *Macropoma* (Watson, 1921) or in *Undina*. The symplectic bone likewise articulates with the lower jaw in *Amia*, making a joint which is functionally more important than that formed with the quadrate. There is no evidence, however, to support Smith's suggestion that this relationship between the mandibular and hyoid arches in *Latimeria* is "the typically primitive one." It appears quite certain that this double suspension of the lower jaw has been independently acquired in the coelacanth and the amioids.

The hyomandibular, which is very well developed in *Latimeria*, has been generally considered to be reduced in all coelacanth. Smith considers an element in *Wimania*, identified by Stensiö as an epiphyal, to be an ossified portion of the hyomandibular. In any case, there is now good evidence for believing that the coelacanth hyomandibular was much larger than has been formerly supposed, although it may have been mostly cartilaginous as in *Latimeria*. The hyomandibular, representing the more dorsal part of the same embryonic mass which gives rise to the symplectic, necessarily supports the latter and hence could not have been reduced, at least in the forms having the double suspension of the lower jaw.

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