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Coelacanth Fishes from the Continental Triassic of the Western United States

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Remains of coelacanth fishes from the continental Triassic of the western United States are rare and usually fragmentary. There is now enough evidence, however, to demonstrate that these fishes are present in both the lower (Moenkopi) and the upper (Chinle and Dockum) Triassic beds of this region. The first identified fragments were collected in 1925 by E. C. Case in the Dockum formation of Crosby County, Texas. They consist of an associated quadrate and partial pterygoid tentatively referred to *Macropoma* by Warthin (1928).

The purpose of the present paper is to provide descriptions of the other coelacanth specimens known to us which have been collected since the initial discovery. In spite of the general rarity of fishes in the Moenkopi, Dockum, and Chinle formations, important finds have been made in recent years which will considerably increase our knowledge of both the Moenkopi and the Chinle-Dockum fish assemblages.

We are obligated to Dr. S. P. Welles for permission to describe the coelacanth remains from the Moenkopi formation, and to Dr. Donald Baird for the loan of a pterygoid of *Rhabdoderma elegans* in the Princeton University Geological Museum. Mr. Colin Patterson has kindly supplied us with unpublished drawings of the basisphenoid of *Macropoma praecursor* based on a specimen in the British Museum (Natural History). Sketches of the basisphenoid of *Undina cirinensis* and *Coccoderma suevicum*, also not yet published, were generously provided by Mr. Rolf Schweizer from specimens in the Geologisch-paläontologisches Institut, Tübingen. Dr. Erik Jarvik kindly furnished illustrations of the neurocranium of *Nesides*

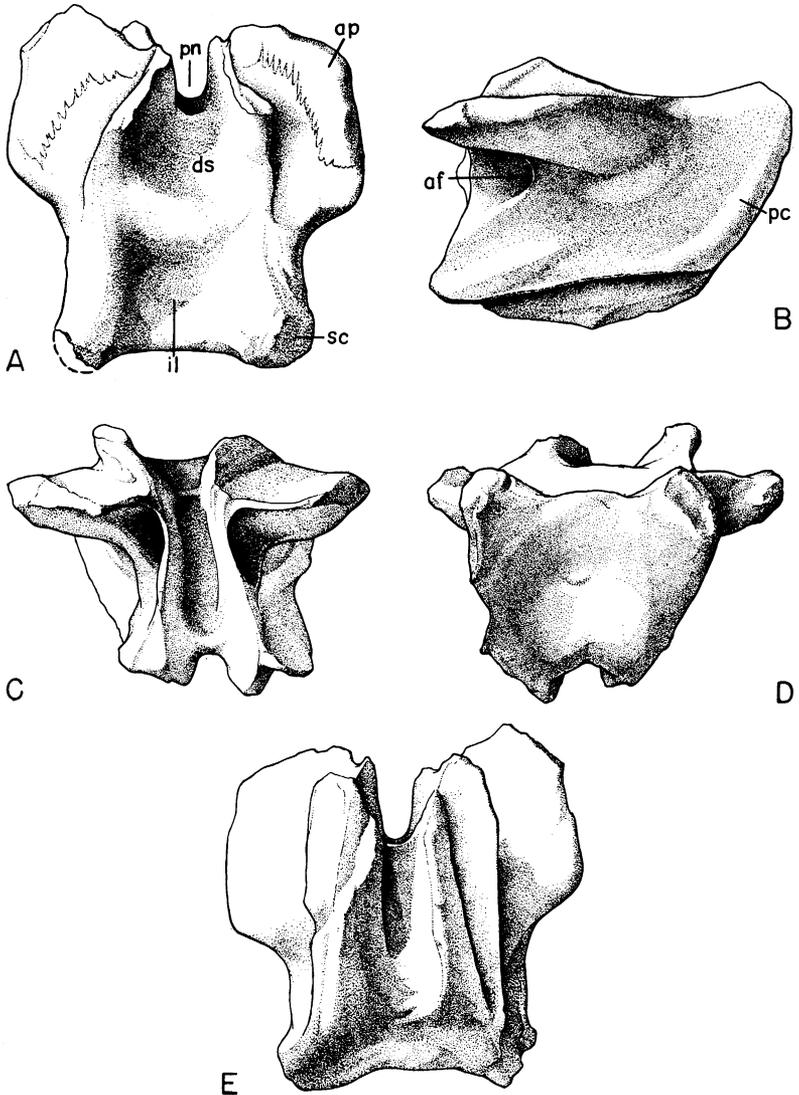


FIG. 1. *Moenkopia welllesi*, U.C.M.P. No. 36193, basisphenoid bone. A. Postero-dorsal view. B. Lateral view. C. Anterior view. D. Posterior view. E. Ventral view. *Abbreviations*: af, adductor fossa; ap, presumed articular area on antotic process for the pleurospenoid; ds, dorsum sellae; il, depression for intracranial ligament; pc, processus connectens; pn, pituitary notch; sc, sphenoid condyles. Three-fourths natural size.

schmidti. The drawings for this paper were made by Mr. Michael Insinna, and the photographs were taken by Mr. Chester Tarka.

The following abbreviations have been used for catalogued specimens:

A.M.N.H., the American Museum of Natural History
M.P.U.M., Museum of Paleontology, University of Michigan
P.U.G.M., Princeton University Geological Museum
U.C.M.P., University of California Museum of Paleontology
Y.P.M., Yale Peabody Museum

REMAINS FROM THE MOENKOPI FORMATION

The large collection of vertebrates obtained by Welles from the upper part of the Moenkopi formation includes numerous isolated coelacanth bones. These coelacanth remains were not so identified by Welles (1947) but were subsequently recognized as such by Westoll (letter to Welles) from the illustrations. They include a number of basisphenoids, several fragments of the parasphenoid, quadrates, incomplete pterygoids, a ceratohyal, possibly mandibular fragments, and two nearly complete cleithra. It may be reasonably assumed that all these elements, which show a considerable range in size, belong to the same genus.

The form of the coelacanth basisphenoid appears to be more or less distinctive for each genus in which it has been described, particularly in the shape and relative size of the antotic processes. Although it is possible that closely related genera are rather similar in this regard, the published illustrations and available examples of the basisphenoid indicate that these differences may have taxonomic significance. The antotic processes and certain other characters of the basisphenoid in the Moenkopi form are sufficiently different from those in any described genus to warrant the erection of a new taxon.

TAXONOMY AND DIAGNOSIS

FAMILY COELACANTHIDAE

MOENKOPIA, NEW GENUS

GENERIC DIAGNOSIS: A genus at present distinguished from other genera in the family Coelacanthidae mainly by the structure of the basisphenoid bone, which exhibits the following characters: Dorsum sellae plus corpus long anteroposteriorly. Sphenoid condyles rounded and prominent; process connectens moderately elevated. Antotic process nearly rectangular in posterodorsal aspect, with articular area for pleurosphenoid. Pituitary notch between antotic processes unusually narrow. Profundus

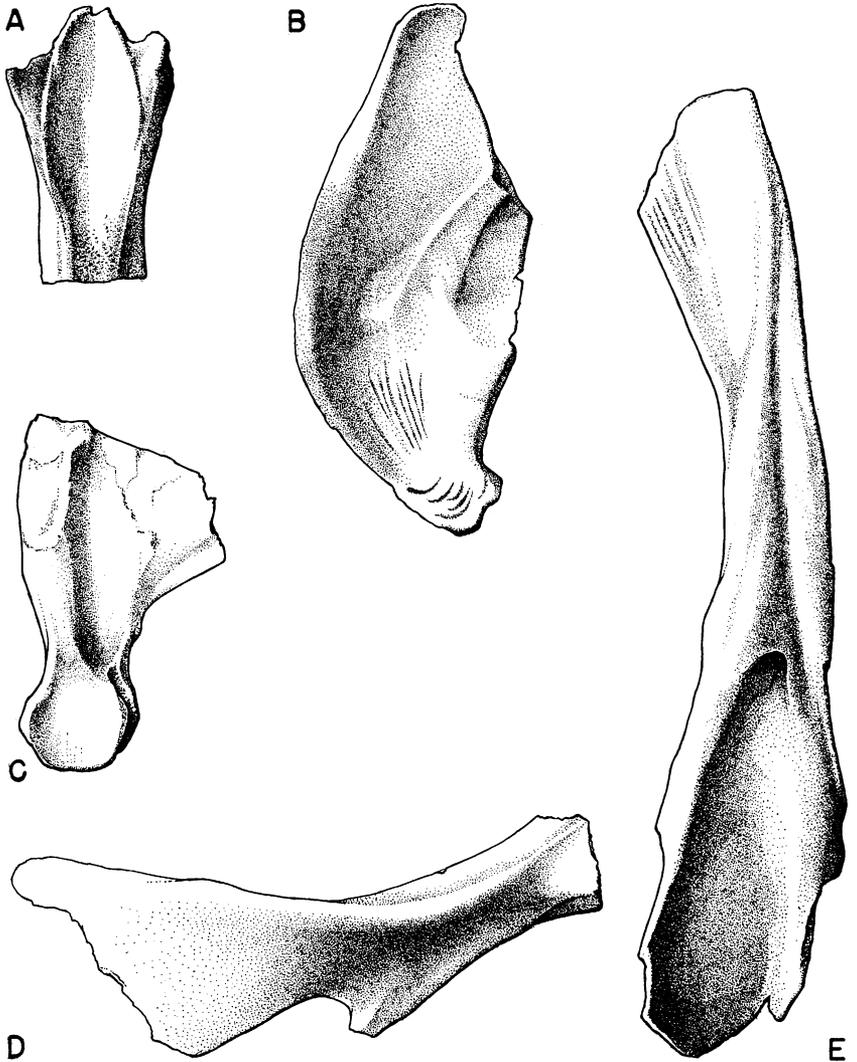


FIG. 2. *Moenkopia wellsi*. A. U.C.M.P. No. 56228, anterior portion of parasphenoid in ventral view. B. U.C.M.P. No. 37788, posterior portion of right pterygoid in lateral view. C. U.C.M.P. No. 37791, right quadrate in lateral view, with fragment of pterygoid attached. D. U.C.M.P. No. 56078, incomplete right ceratohyal in lateral view. E. U.C.M.P. No. 37806, right cleithrum in median view. All $\times 0.6$.

canal and abducens foramen apparently absent. Adductor fossa on lateral lamina well developed.

GENERIC TYPE: *Moenkopia wellesi*, new genus and species.

Moenkopia wellesi, new genus and species

HORIZON AND LOCALITY: From the Holbrook member of the Moenkopi formation (lower Anisian), 6 miles west of Holbrook, Arizona, in the NE. $\frac{1}{4}$ sect. 31, T. 18 N., R. 20 E., Arizona Highway Planning Map, Coconino County. The coelacanth remains, along with those of shark, palaeoniscoid, labyrinthodont, and pseudosuchian, occur in a channel deposit of greenish, limy siltstone and sandstone. The bone fragments are isolated and frequently water-worn (Welles, 1947).

SPECIFIC DIAGNOSIS: Same as for genus.

TYPE: U.C.M.P. No. 36193, complete basisphenoid.

REFERRED SPECIMENS: All the specimens listed below are in the Museum of Paleontology of the University of California at Berkeley. Except as noted, all are about the same size as the corresponding elements in an adult *Latimeria*. There are numerous other fragments in the collection which may be coelacanth, but they have not been positively identified.

Series of basisphenoids: (U.C.M.P. Nos. 37801, 36234, 36235, 36197). These specimens range in size from about one-quarter of that of the type to approximately the same dimensions as the type. Although all of them are incomplete or distorted, it is evident that the shape of the antotic processes changed somewhat with increase in size. In the smallest specimen the processes resemble those in *Wimania* (see fig. 2D), with only a slight indentation on the posterior border. In the progressively larger examples, the sigmoid curve forming the posterior border of the antotic processes becomes more accentuated.

Partial parasphenoid (U.C.M.P. No. 56228).

Incomplete pterygoids (U.C.M.P. Nos. 37788, 37789, 37790, 37793).

Quadrate (U.C.M.P. No. 37791).

Ceratohyal (U.C.M.P. No. 56078).

Cleithra (U.C.M.P. Nos. 73805, 73806).

DESCRIPTION

The largest example of the *Moenkopia* basisphenoid (fig. 1) is equal in size to the basisphenoid of an adult *Latimeria*. It is, however, more massive and more elongated anteroposteriorly. The distance from the anterior border of the dorsum sellae to the dorsal border of the notochordal face is unusually great in comparison with the total length of the

bone, including the antotic processes. The lateral lamina is nearly rectangular.

The antotic processes are essentially rectangular in posterodorsal aspect, with an articular area on the dorsal surface presumably for a bone regarded by Millot and Anthony as the pleurosphenoid. This separate ossification in the pila antotica has been found in *Latimeria* (Millot and Anthony, 1958) but is otherwise unreported in the Crossopterygii. It overlaps the anterior two-thirds of the antotic process and is embedded anteriorly in the ethmosphenoid cartilage. In the rhipidistians and in the Devonian coelacanths such as *Nesides* (Jarvik, 1954, fig. 4), the pleurosphenoid may be incorporated into the completely ossified ethmosphenoid portion of the neurocranium. Failure to distinguish this bone in the later Paleozoic and the Mesozoic coelacanths is probably the result of its close association with the antotic process. It may be the same element as the "alisphenoid" of Stensiö (1921). Isolated basisphenoids of some genera, such as *Spermatodus*, also have a clearly defined articular area on the antotic process, apparently for the pleurosphenoid.

The antotic processes in *Moenkopia* are elevated medially to form ridges which border the narrow pituitary notch. As in *Latimeria*, these ridges must have continued anterodorsally in cartilage to form buttresses for the skull roof. Part of the intracranial ligament extending between the two moieties of the braincase was attached to the basisphenoid in the characteristic depression behind the dorsum sellae. The sphenoid condyles which articulated with the prootic are strongly developed, knob-like prominences capped in life with cartilage. The processus connectus, which defines the lateral border of the notochordal face, is moderately developed. It was presumably covered with cartilage, as in *Latimeria*, to form the principal articulation with the prootic.

A well-defined fossa, in the lateral lamina, opens anterolaterally immediately beneath the anterior part of the antotic process. In *Latimeria*, this fossa is the origination area for the adductor palatoquadrate. Also in the living genus, the profundus nerve passes through a canal in the basisphenoid which begins on the medial surface of the lateral lamina just anterior to the front edge of the dorsum sellae and has its exit in the posterior wall of the adductor fossa. The profundus canal has been identified in the Permian *Spermatodus* (A.M.N.H. No. 3200), in the lower Triassic *Axelia* and *Wimania* (Stensiö, 1921), and in *Macropoma* (Watson, 1921). There is, however, no evidence of its presence in any of the available *Moenkopia* basisphenoids, either on the median surface of the lamina or in the back wall of the adductor fossa. There is likewise no visible foramen for the oculomotor nerve in its usual position below the fossa. The absence

of these openings is puzzling. It suggests that in this genus, at least, the profundus and oculomotor nerves had a different relationship with the basisphenoid.

The ventral surface of the basisphenoid has a shallow median depression, which was probably filled with cartilage, and lateral longitudinal grooves into which fitted vertical flanges of the parasphenoid. Millot and Anthony (1958, p. 7) have demonstrated that the internal carotid arteries do not run between the basisphenoid and the parasphenoid as postulated by Westoll (1939) and Schaeffer (1952). In *Latimeria* the carotid foramen is situated in the sphenoid cartilage near the junction of the anterior border of the lateral lamina and the parasphenoid. Entering the braincase at this point, the internal carotids run posterodorsally over the dorsum sellae to the brain.

The other bones referred to *Moenkopia* are too fragmentary for proper description or comparison with similar elements in other genera. The anterior portion of a parasphenoid (fig. 2A) has a well-defined, long, ovoid tooth plate on the ventral surface. The posterior third of a pterygoid (entopterygoid) (fig. 2B) has dimensions about equal to this element in *Latimeria* (Millot and Anthony, 1958, pl. 38). Several incomplete quadrates and cleithra (fig. 2C, D) are in the same size range, as is a ceratohyal (fig. 2E) of rather distinctive shape.

In summary, the remains referred to *Moenkopia* indicate that it is the largest Triassic coelacanth yet described. It is exceeded only by *Mawsonia libyca* (Weiler, 1935) from the Cenomanian of Egypt which on the basis of quadrate size perhaps attained a length of 10 feet.

GENERAL REMARKS ON THE COELACANTH BASISPHEOID

The series of basisphenoids illustrated in figure 3 demonstrates the diversity in the form of this element at the generic level. The differences involve not only the shape of the antotic processes and the thickness of the corpus but also the shape and extent of the lateral laminae. If it be assumed that these examples are all from adult specimens or from genera in which the shape of the antotic processes does not change appreciably with increase in size, at least three types can be recognized.

In the first type, illustrated by *Nesides* (fig. 3A) and presumably by the other Devonian forms, the basisphenoid is a part of the well-ossified sphenethmoid moiety of the braincase. The dorsum sellae is apparently not differentiated, and the canals for the profundus and the superficial ophthalmic nerves are close together. The differences in the shape and

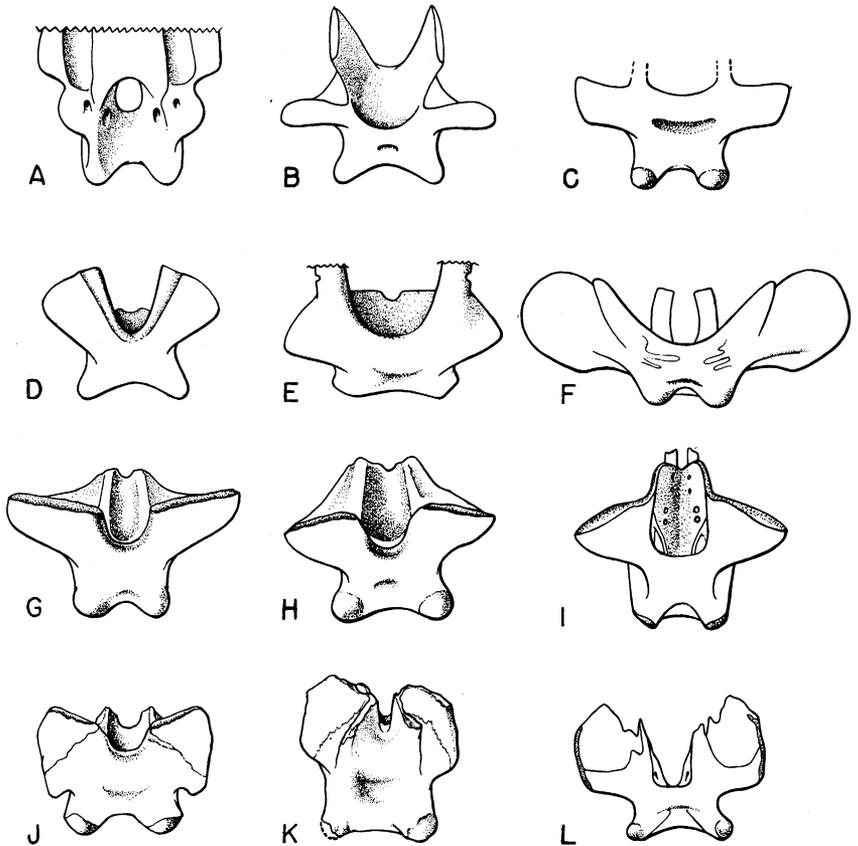


Fig. 3. Comparative series of coelacanth basisphenoids in posterodorsal view. A. *Nesides schmidtii* (after Stensiö). B. *Rhabdoderma elegans* (after Moy-Thomas). C. *Coelacanthus granulatus* (after Moy-Thomas). D. *Wimania sinuosa* (after Stensiö). E. *Axelia robusta* (after Stensiö). F. *Diplurus newarki*. G. *Coccoderma suevicum* (after Schweizer, unpublished). H. *Undina cirinensis* (after Schweizer, unpublished). I. *Macropoma praecursor* (after Patterson, unpublished). J. *Spermatodus pustulosus*. K. *Moenkopia wellsi*. L. *Latimeria chalumnae* (after Millot and Anthony).

relative size of the antotic processes may be related in various ways to the nature of the articulation with the metapterygoid. These processes in *Nesides* appear to be smaller than in any of the post-Devonian genera. Their size is probably correlated with the presence of functional basiptyergoid processes which were involved along with the antotic ones in the suspension of the palate. By the Carboniferous, the basiptyergoid processes

were reduced and subsequently disappeared. The antotic processes consequently became larger and, in general, projected farther laterally as they became the main posterior support for the palate.

In types two and three, including all the post-Devonian forms, the basisphenoid and presumably the pleurospenoid are the only ossifications in the posterior part of the sphenethmoid moiety. A dorsum sellae is always present. The canal for the superficial ophthalmic is situated either anterior to the pleurospenoid ossification as in *Latimeria* (fig. 3L) or perhaps lateral to it as in *Axelia* (fig. 3E). The second type, including the genera illustrated as B through J in figure 3, have mostly triangular antotic processes. This type can perhaps be further subdivided by the form of the presumed pleurospenoid ossification. It is apparently bar-like in B through E, and more plate-like but possibly not ossified in F through I. The third type, represented in figure 3 by *Spermatodus*, *Moenkopia*, and *Latimeria*, has nearly rectangular antotic processes, with an extensive overlap area for the pleurospenoid.

The significance of these basisphenoid types in relation to the phylogeny and classification of the coelacanth remains to be determined. It is obvious, however, that the characters of this element should receive important consideration in future work on coelacanth systematics.

BRAIN SIZE IN COELACANTHS

As the *Moenkopia* basisphenoid and hence the entire braincase attained a size equal to that of the adult *Latimeria*, it may be assumed that *Moenkopia* had a disparity between brain size and endocranial capacity similar to that in the living genus. In *Latimeria* the phenomenally small brain is situated above and behind the basisphenoid, and the hypophysis is far removed from the pituitary fossa. A strand of connective tissue extends from the floor of the pituitary fossa between the lateral laminae and over the dorsum sellae to the hypophysis. Millot and Anthony (1956) consider this to be the greatly elongated remnant of Rathke's pouch.

Most of the known fossil coelacanth were small compared with *Latimeria* or *Moenkopia*, with a braincase rarely exceeding 10 cm. in length. The few studies that have been made on brain growth in the Osteichthyes demonstrate that there is, in general, a differential growth relationship between brain size and skull size. Geiger (1956) has shown the relative decrease in the size of the brain during the ontogeny of *Esox lucius*. In a skull 3 cm. long¹ the ratio of skull length to brain length² is 5/1; for an

¹ From the tip of the snout to the posterior border of the opercular.

² Measured on the illustrations from the posterior border of the cerebellum to the olfactory lobes.

18-cm. skull, 12/1; and for a 35-cm. skull, 18/1. The coelacanth endocranial cavity must increase in size at about the same rate as the entire neurocranium, as it always extends the full length of the neurocranium. This relationship in the actinopterygians has apparently not been investigated, but the *Esox* data suggest a similar growth rate, although the actinopterygian endocranial cavity is relatively smaller. It may therefore be concluded that small adult osteichthyans usually have a brain which nearly fills the endocranial cavity and that with increase in adult size the brain becomes proportionately smaller. In view of this evidence, it seems unnecessary to postulate other mechanisms for the skull-brain disparity in *Latimeria* and, by inference, in the large extinct coelacanths (see Millot and Anthony, 1956; 1958, pp. 108-109).

It is probable that a young *Latimeria* has a relatively larger brain than the adult. In very small individuals the hypophysis may be in front of and below the dorsum sellae. This supposition is further supported by the path of Rathke's cord. It is also probable, if not provable, that the small, fossil coelacanths (*Rhabdoderma*, *Coelacanthus*, *Macropoma*, and others) had a brain that more or less filled the cranial cavity and a hypophysis in the typical vertebrate position. Increase in size, which occurred sporadically during coelacanth history, was associated with a relatively smaller brain. *Moenkopia*, *Mawsonia* (Weiler, 1935), and *Latimeria* represent the extremes in this direction.

REMAINS FROM THE DOCKUM FORMATION

In addition to the partial quadrate and pterygoid described by Warthin, the Dockum formation has yielded the badly weathered skull of a large coelacanth (fig. 4). The specimen was found in Palo Duro Canyon, Texas, in 1950 by K. E. Black of Canyon and is now in the Peabody Museum collection (Y.P.M. No. 3928). Although the sandstone concretion preserves the external form of the skull, most of the dermal bones are incomplete, and their shape and form cannot be determined. The intractable, siliceous matrix has prevented preparation of the basisphenoid, which is probably the only complete, unweathered part of the skull of diagnostic value. Because the determination of the systematic position must await discovery of more completely preserved remains, the specimen is not named at the present time, and the description is confined here to those features that are clearly indicated.

LOCALITY: The skull was found on the surface near the foot of the Triassic badland slope close to the center of the head of the second important draw on the north side of Gold Canyon, a west side tributary of North Sunday Canyon. The mouth of the gulch is about $\frac{3}{4}$ mile west of the

mouth of Gold Canyon by trail. Sunday Canyon is accessible through Palo Duro Canyon State Park east of Canyon, Texas, by a road that turns west just below the first ford of Palo Duro or Prairie-dog-town Creek in the Park. The locality itself lies outside the park boundaries, near the center of the east side of the SW. $\frac{1}{4}$ sect. 123, Randall County, Texas.

GEOLOGIC OCCURRENCE: The place of discovery is a few feet above the contact of the Dockum with the brick-red Quartermaster formation of Permian age. The sandstone matrix on the specimen, however, is more suggestive of the massive sandstones that are present in the upper half of the Dockum formation in Palo Duro Canyon than of the lower 200 feet of many-colored shales, although its derivation from a small sandstone lens within the lower shales cannot be excluded. Thus far efforts to locate the outcrop of the fish-bearing bed have not met with success.

The upper Triassic age of the entire Dockum formation in this area is indicated by remains of phytosaurs and metoposaurs at many levels. On the surface of the slope from which the skull was obtained a number of these characteristic late Triassic fragments were collected.

Deposition of the Dockum under subaerial, continental conditions on extensive flood plains is indicated by the lenticular nature of the coarse, cross-bedded sandstone and conglomerate beds, which have the character of old stream-channel fillings and which are abruptly coarser than the surrounding siltstones and clay shales. The oxidized condition of the bright red to variegated flood-plain clays also supports subaerial deposition. The possibility of a marine or brackish water tongue seems remote; none is known in the extensive Chinle deposits of the Colorado Plateau, which were formed contemporaneously with the Dockum and which lie between Texas and the Triassic seaway of the Cordilleran geosyncline. It is a reasonable inference that this coelacanth was a fresh-water, river-dwelling species.

DESCRIPTION

As preserved, the skull resembles that of *Whitea* (Lehman, 1952) in general form and proportions. It is, however, about four times longer than the largest reported skull in that genus, or approximately 20 cm. from the snout to the posterior border of the operculum. Such a skull size suggests that the entire fish was somewhat over 3 feet in length.

The details of the skull roof are obscure, but it is evident that the frontals were long and narrow as in *Whitea*. The front of the snout is missing, and it is not possible to determine the arrangement and number of the nasal and rostral elements. The intertemporals (parietodermopterotics) are characteristically wider than the frontals, but un-

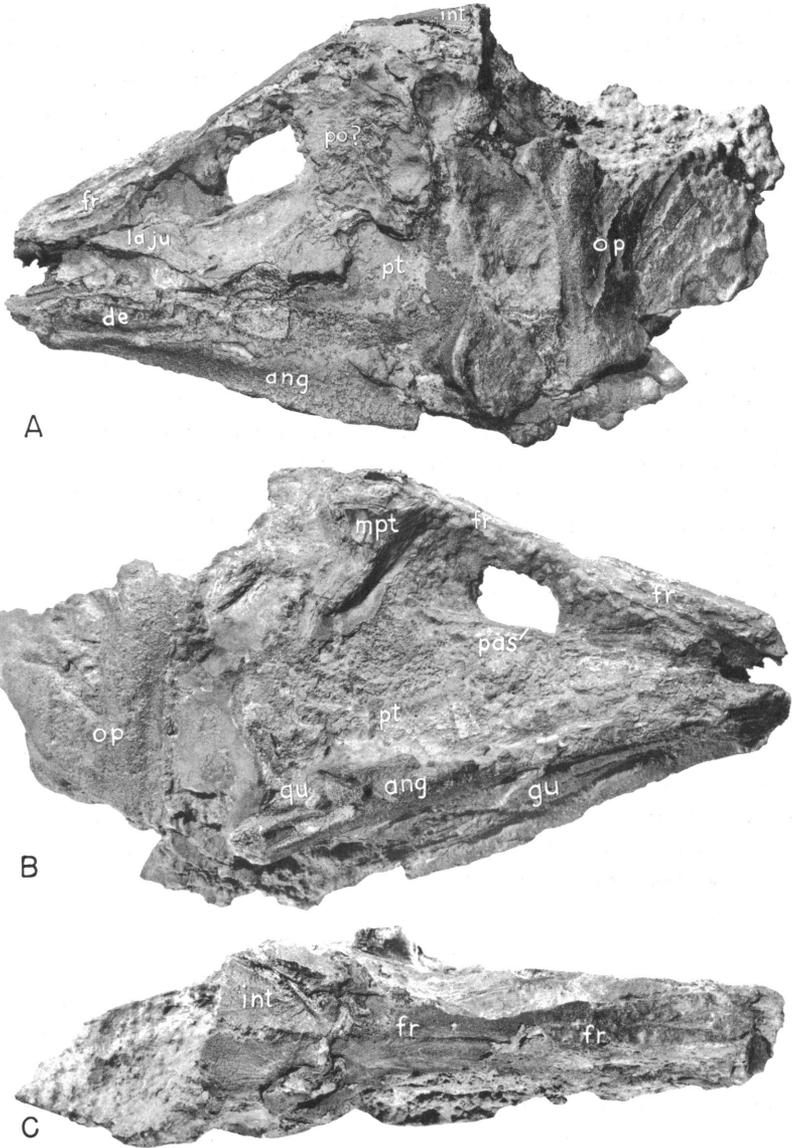


FIG. 4. Skull of unnamed coelacanth from the Dockum formation, Y.P.M. No. 3928. A. Lateral view, left. B. Lateral view, right. C. Dorsal view. *Abbreviations:* ang, angular; de, dentary; fr, frontal; gu, gular; int, intertemporal; laju, lacrimo-jugal; mpt, metapterygoid; op, opercular; pas, parasphenoid; po?, postorbital?; pt, pterygoid; qu, quadrate. One-half natural size.

fortunately they are broken off anterior to their contact with the supra-temporals, so that the pattern in this area cannot be ascertained.

In lateral aspect it is possible to distinguish a large remnant of the postorbital. On the right side there is an impression of the posterior supraorbital, which appears to overlap the intertemporal slightly and thus bridge the transverse joint. The anterior, triangular portion of the lacrimojugal (infraorbital) is preserved and is similar to that of *Whitea*. From the impression of the posterior portion of this bone, it is evident that it curved upward rather sharply to form the lower part of the posterior border of the orbit as in *Whitea* and several other genera. Except for partial impressions of the typically triangular operculars, identifiable indications of the other lateral dermal elements are absent.

The proportions of the lower jaw, as preserved, are also suggestive of *Whitea*. Teeth are present on the dentary for a distance of about 5 cm. back from the symphysis. They are low-crowned, conical, and apparently ankylosed to the jaw. An expansion behind the quadrate articulation presumably represents the articular, although a notch for the symplectic articulation is not evident.

Impressions of the pterygoids (entopterygoid) can be seen on both sides of the skull, along with remnants of these bones. Remains of pterygoid teeth, large just below the posterior part of the orbit and smaller elsewhere, are visible on the right side. The upper part of the metapterygoid, with a well-developed ascending process, is also exposed on the right side. Preserved fragments of both quadrates demonstrate that the condyles, as in most members of this group, were situated well below the pterygoids.

In the absence of really diagnostic characters, it is not possible to present any conclusions regarding the affinities of this unique specimen. Certain resemblances to genera such as *Whitea* or *Laugia* in the narrowness of the frontals or in general skull proportions can have little significance until more and better specimens are discovered.

The fragment of a quadrate and pterygoid from Crosby County, Texas, described by Warthin (1928, pp. 17-18, pl. 1, figs. 2, 3) as *Macropoma* sp. (M.P.U.M. No. 9360) came from a slightly smaller skull than the Palo Duro Canyon specimen. No significant comparisons between the two specimens are possible. As Warthin pointed out, reference to the Cretaceous genus *Macropoma* is improbable; it is more likely to represent the unnamed species described above.

Although the locality in Crosby County from which this fragment was collected is not known, vertebrate fossils are most abundant in this area in a zone of irregular lenticular deposits near the base of the Dockum. This

zone is exposed at all the important localities along Sand Creek, Davidson Creek, and Home Creek. Variegated, often purplish, lenses underlying thin limestones in the reddish claystones and siltstones abound in coprolites, ganoid fish scales, and phytosaur and metoposaur teeth and bone fragments. These deposits, which may be seen in three dimensions in the badland exposures, strongly suggest pond fillings. Massive, cross-bedded, stream-channel sandstones occur nearby but seldom yield fossils. The occurrence suggests that the fossils accumulated in ponds or backwater pools on a flood plain rather than in the river channel itself.

REMAINS FROM THE CHINLE FORMATION

The sharp impression of a pterygoid (A.M.N.H. No. 3201) is the first and only positive indication to date¹ of the presence of coelacanths in the Chinle formation (fig. 5). It was found in 1958 associated with a variety of other bone fragments, some of which may be coelacanthid, while others are undoubtedly actinopterygian.

LOCALITY: The Dolores River canyon locality is southwest of Bedrock, Montrose County, Colorado, in sect. 36, T. 47 N., R. 12 W. It is about 3 miles via the canyon road from the intersection of this road with State Highway 90 which runs along the south side of Paradox Valley.

GEOLOGIC OCCURRENCE: The fish remains occur in a highly resistant layer of sandy dolomitic limestone about 1 foot thick and about 50 feet below the base of the cliff-forming Wingate sandstone. This layer probably occurs in beds equivalent to the Church Rock member of the Chinle (Stewart, 1957; Stewart *et al.*, 1959).

DESCRIPTION

Aside from being the impression of a typical coelacanth pterygoid in lateral aspect, this specimen appears to offer little that requires special comment. A survey of the literature (fig. 6) suggests, however, that the shape and proportions of the pterygoid may differ sufficiently from genus to genus to make this element of some diagnostic significance. It is doubtful, however, that these differences are distinctive enough to warrant the erection of a new genus on the basis of an isolated example.

The Chinle pterygoid seems to be unusual in the gentle, uninterrupted curvature of the dorsal border forward from the point where it meets the vertical ridge. In most genera, this border is either curved more sharply immediately in front of the ridge, as in *Axelia*, or it is nearly straight to

¹ Additional and more complete coelacanth remains have recently been discovered at two Chinle localities. They will be described in a subsequent paper.

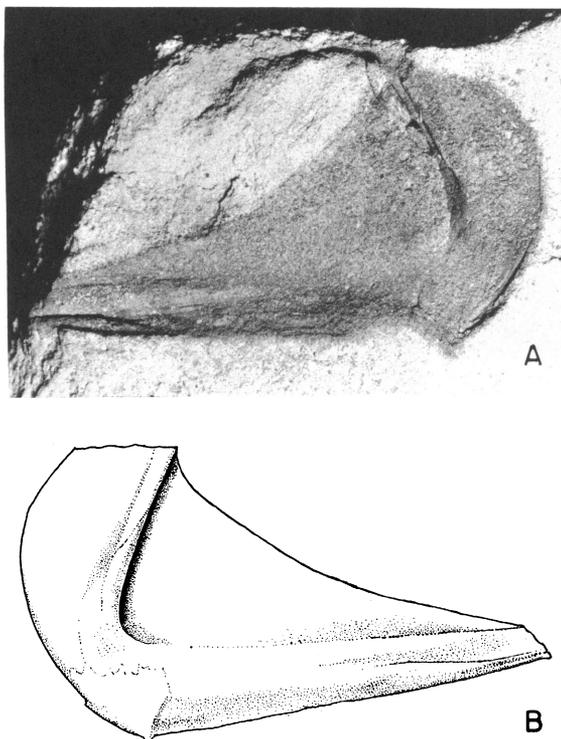


FIG. 5. Coelacanth pterygoid from the Chinle formation, A.M.N.H. No. 3201. A. Original impression. B. Drawing based on latex peel of original. $\times 1.2$.

slightly convex, meeting the ridge in a fairly sharp angle, as in *Mylacanthus* and *Latimeria*.

The articular surfaces for the quadrate and the metapterygoid are rather clearly defined. There is a broad horizontal groove anteriorly for the articulation with the autopalatine and below it, a narrower groove for the ectopterygoid. These features are typical but important in the identification of the specimen. The portion of the vertical ridge that extends dorsally along the anterior border of the metapterygoid is not preserved, and the dorsal extent of the metapterygoid cannot be determined.

SUMMARY

There is now conclusive evidence that coelacanth is present in both the lower and the upper Triassic continental beds of the western United States. The scarcity of their remains is, in part, related to the factors that

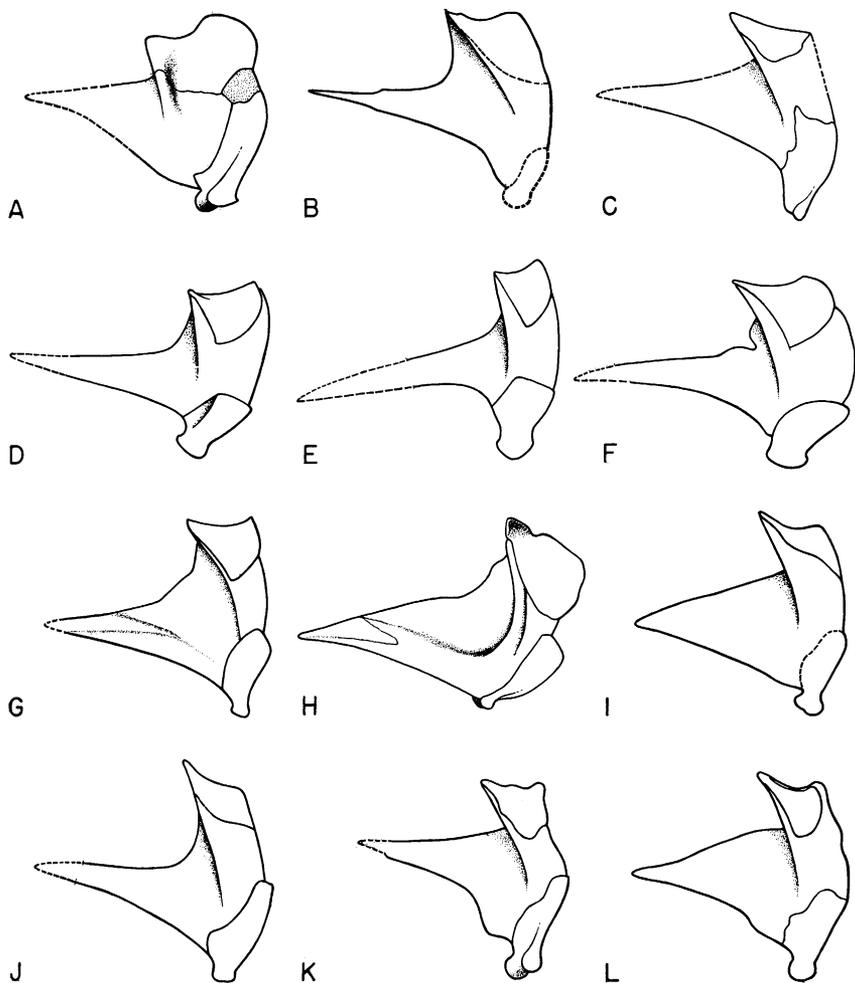


FIG. 6. Comparative series of coelacanth palates in lateral view. A. *Nesides schmidti* (after Jarvik). B. *Rhabdoderma elegans* (P.U.G.M. No. 17170). C. *Coelacanthus granulatus* (after Moy-Thomas). D. *Axelia robusta* (after Stensiö). E. *Mylacanthus lobatus* (after Stensiö). F. *Wimania sinuosa* (after Stensiö). G. *Whitea woodwardi* (after Lehman). H. *Diplurus newarki*. I. *Undina acutidens* (after Reis). J. *Coccoderma nudum* (after Reis). K. *Macropoma mantelli* (after Watson). L. *Latimeria chalumnae* (after Millot and Anthony).

are responsible for the general rarity of fishes in these formations. The broad, flat, flood-plain environment in which the Moenkopi and Chinle-Dockum sediments were deposited (McKee, 1954; Stewart *et al.*, 1959)

was apparently more favorable for the preservation of terrestrial than of aquatic vertebrates. Metoposaur and phytosaur remains are much more abundant and more widely distributed than fish remains. The latter are restricted, as might be expected, to channel and lacustrine deposits. Although isolated actinopterygian scales are reasonably common in such deposits, associated fish remains are extremely rare.

At a few localities in the Chinle complete fishes have been found in great abundance. These usually occur in lacustrine deposits in concentrations suggestive of periodic mass mortality. The apparent rarity of coelacanth remains in these concentrations suggests that they were not common in the lakes and ponds of the Chinle flood plain. On the other hand, there is no positive evidence that they were, in general, restricted to rivers and streams. Except for the Moenkopi occurrence, which is quite clearly fluvial, the paleoecologic picture is unsettled.

Isolated coelacanth bones from the Moenkopi formation include distinctive basisphenoids, the morphology of which provides the basis for establishing a new genus and species, *Moenkopia wellsi*. Specimens thus far recovered from the late Triassic Dockum and Chinle formations are too incomplete to permit generic identification.

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