# A LATE PERMIAN ACTINOPTERYGIAN FISH FROM AUSTRALIA

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ABSTRACT. *Ebenaqua*, a new genus of deep-bodied palaeoniscoid fishes, type species *E. ritchiei* sp. nov., is described from the Late Permian Rangal Coal Measures at Blackwater, central Queensland. It is interpreted as an early member of the Bobasatraniformes. Examination of a large number of characters on specimens from the Kupferschiefer suggests that the genus *Platysomus* is also a bobasatraniform. The homologies of the bones in the suborbital and maxillary regions of members of this order are reinterpreted. A functional study of the jaw mechanics suggests that the forward position of the jaw articulation, the loosely articulated bones of the face, and the markedly upright suspensorium of *E. ritchiei* are adaptations to a distinctive mode of feeding and gill ventilation. These features should not be used to infer halecostome or neopterygian relationships. The pectoral and pelvic fins are vestigial, and their functions in the control of manœuvre and stability are inferred to have been taken over by the dorsal and anal fins, which nevertheless retain a paleoniscoid structure. The versatility of palaeoniscoid fins movements was greater than has been accepted previously.

A COLLECTION of actinopterygian fishes belonging to nine genera has been made from two localities at Blackwater in the Upper Permian Blackwater Group, a coal measure sequence lying between the marine Permian Back Creek Group and the Lower Triassic Rewan Formation (text-fig. 1). The material was first found in outcrop in a complex area where the shales have been baked by a fire in one of the seams. Subsequently, more prolific and better preserved specimens were found in
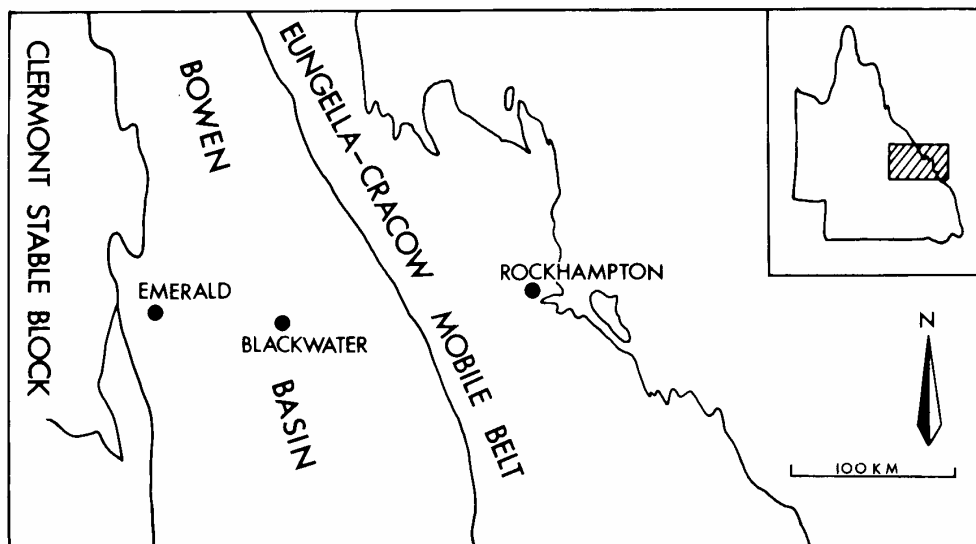


TEXT-FIG. 1. Locality map of Blackwater Mine, Queensland.

position in the Utah Development Company's open-cut mine. The fauna at the two sites is apparently identical.

The assemblage includes members of the Palaeonisciformes, Redfieldiiformes, and Bobasatraniformes. The palaeonisciforms are the most diverse, including seven distinct types, four of which are sufficiently well preserved and distinct to warrant description as new genera. One of the remainder may be a species of *Cycloptychius* Young, a European Carboniferous genus, but no head has been found and this assignment must be tentative.

The most abundant species is the bobasatraniform *E. ritchiei* gen. et sp. nov., described below. It makes up about one-third of the total collection available to us, and the specimens are commonly found completely articulated. The species is important for several reasons. It has some of the most highly specialized features, such as reduced pectoral and pelvic fins and protruding snout, known from the Bobasatraniformes. Its skull bones are well enough preserved to permit a functional analysis to be made, and this analysis suggests that the similarities between bobasatraniforms and holostean, or more advanced, fishes are superficial. The extreme reduction of pectoral and pelvic fins implies that the fish manœuvred by the action of the anal and dorsal fins, which nevertheless retain a primitive structure. The capacity of paleoniscoid fins to produce flexible movements comparable to those of more advanced fishes will therefore need further investigation. And finally, the presence of the genus in freshwater deposits whereas all other occurrences of the Order are marine, poses interesting questions for biogeography.

## STRATIGRAPHY

The stratigraphic sequence in the Blackwater area is shown below (after Staines 1975).

| Lower Triassic | Mimosa Group | Rewan Formation |
|---|---|---|
| *Local minor disconformity* | | |
| Upper Permian | Blackwater Group | ⎰ Rangal Coal Measures ⎱ Burngrove Formation ⎰ Fair Hill Formation |
| Lower to Upper Permian | Back Creek Group | ⎰ MacMillan Formation ⎱ German Creek Formation ⎰ Ingelara Formation ⎱ Freitag Formation |

The fishes are from the Rangal Coal Measures, a unit which is 90–135 m thick in the vicinity of Blackwater. It contains several coal seams that split and rejoin, producing difficulty in correlation and a resultant complex nomenclature which has been stabilized by Staines (1972, 1975). His work is followed here. The chief fossiliferous locality is 6 m above the Argo (or Main Lower) Seam which, as the name implies, lies towards the bottom of the Rangal Coal Measures.

The fishes occur in a light-grey, soft shale in which there is abundant comminuted plant material. On exposure to the weather the shale rapidly breaks down. A similar lithology at the top of the Argo Seam contains more carbonaceous layers from which specimens of *Phyllotheca*, *Glossopteris*, *Vertebraria*, *Taeniopteris*, and equisetalean stems have been recovered. Occasional specimens of *Glossopteris* and *Vertebraria* are found in the fish bed.

A specimen of mudstone from the fish bed was examined for palynomorphs by Dr. Elizabeth Truswell who has supplied the following list. Spores: *Dulhuntyispora dulhuntyi* s.l., and *D. parvithola* (very rare); *Granulatisporites micronodosus*; *Horridotriletes ramosus*; *Granulatisporites* sp.; *Dictyotriletes* sp. nov. (common); *Didecitriletes* cf. *ericianus*; and *Laevigatosporites colliensis*. Pollens: *Marsupipollenites triradiatus*; *Praecolpatites sinuosus*; *Platysaccus* spp.; *Protohapploxypinus limpidus*, *P. amplus*, and *P.* cf. *varius* (common); *Scheuringipollenites* spp.; *Vitreisporites pallidus*; *Striatopodocarpidites* cf. *pantii*; and *Parasaccites* sp. She has indicated that this assemblage implies a position

high in the Upper Stage 5 of Kemp *et al.* (1977), which is at the top of the Permian. There are no distinctive elements of the basal Triassic Trla assemblage.

## SYSTEMATIC PALAEONTOLOGY

Order BOBASATRANIFORMES
Genus *EBENAQUA* gen. nov.

*Derivation of name: Latin ebenus* black; *aqua* (f) water.

*Diagnosis.* Body deeply rhombic in profile, with dorsal and ventral angles approximately equal; laterally compressed. Facial contour steep and with a strongly protruding snout based on an enlarged maxilla. A large suborbital attached to the maxilla and bearing a branch of the lateral line canal. Postspiraculars present. Maxilla and suborbital overlapped by infraorbitals forming a loose junction. Two preoperculars without a lateral line canal. Opercular and subopercular separated by an oblique suture, the subopercular extending almost to the ventral edge of the animal. Branchiostegal rays greatly reduced in number. Mandible small, about two-thirds the length of the maxilla, and slung well forward. Jaws edentulous. Cleithrum strong; supracleithrum present, but no anocleithrum or clavicle. Twenty-seven rows of scales between the posterior end of the cleithrum and the caudal peduncle, and another ten rows extending forward under the pectoral fin. Posterodorsal and posteroventral scale rows much reduced in width, very regular compared with *Bobasatrania*, and running at a low angle to the body margins. Flank scales elongate, rhomboid, with steeply inclined unornamented leading and trailing edges, and only slight overlap; long, spiked scale articulation. Lateral line canal well-defined throughout, and with a regular posteroventral branch and a highly irregular anterodorsal branch on the body; short dorsal and, less commonly, ventral tubules branch from the main canal. Pectoral and pelvic fins small, the pelvic being situated a short distance in front of the ventral angle. Dorsal and anal fins extending from dorsal and ventral angles to the caudal peduncle, and consisting of a group of long rays at their distal extremities, but much shorter, more uniform rays over most of their length; dorsal and anal fin rays more numerous than their baseosts. All fin rays jointed. Tail strongly heterocercal with the scales on the dorsal lobe extending to its extremity; ventral lobe slightly expanded; fin rays on ventral lobe more crowded, stronger and with longer segments than those on the dorsal lobe; outline of the caudal fin symmetrical.

Ebenaqua *and the Bobasatraniformes.* If Westoll's (1941) assessment of *Lekanichthys* is correct, the only genera confidently placed in this group are *Bobasatrania* and *Ecrinesomus*. Several features of *Ecrinesomus* remain unknown—e.g. the details of the caudal fin and of the lower dermal bones of the branchial chamber. However, they have in common the following features: deep body; extended dorsal and anal fins; jaw slung well forward; maxilla large and placed well forward; edentulous; 'suspensorium' vertical; a large suborbital (the supramaxilloquadratojugal of Neilson 1952) between the preoperculars and the maxilla; peculiar development of paired preoperculars, and suboperculars; branchiostegal rays reduced or absent; postspiraculars present; clavicles reduced or absent; flank scales elongated and vertically striated; scale rows swing forward to meet the posterodorsal and anteroventral margins obliquely; pelvic fin small or absent; dorsal and anal fins extended from dorsal and ventral extremities to the caudal peduncle; caudal fin heterocercal, but the approximately symmetrical development of dorsal and ventral lobes.

Of course, not all these features are unique to the Bobasatraniformes, but their combination defines a distinctive group. *Ebenaqua* shares all the above characters. The case for its inclusion in the group is made even stronger by comparison with *Bobasatrania* itself. Both genera have a lateral line canal on the suborbital, the jaw articulation strongly overlapped by the posterior part of the maxilla, long rays at the anterior ends of the dorsal and anal fins, clearly differentiated rays on the dorsal and ventral lobes of the dorsal and anal fins, and a row of spines on the anterodorsal and anteroventral body margins.

The main differences between *Ebenaqua* and *Bobasatrania* are the existence in the latter genus of (*a*) a short rostral region; (*b*) an entirely free suborbital; (*c*) a lacuna in the cheek below the orbit; (*d*) a

lateral line canal on the preoperculars; (e) an elongate pectoral fin; (f) an entire ventral edge with no gap for a pelvic fin; (g) a greatly reduced squamation on the caudal lobe; (h) baseosts approximately equal in number to the rays of the dorsal and anal fins.

These differences are considered to be of generic significance only. It is noted that *Ecrinesomus* is more similar to *Ebenaqua* than *Bobasatrania* in characters b, c, d, and h above.

This relatively straightforward situation is complicated by difficulties with the interpretation of the genus *Platysomus*. As indicated in the Appendix, this genus has to be interpreted on the Permian species which are in urgent need of revision, and not on such Early Carboniferous species as *Platysomus superbus* Traquair, which are almost certainly not congeneric with the Permian forms. Specimens from the Late Permian Kupferschiefer described in the Appendix do not have the head structure figured by Traquair (1879) for *P. gibbosus*; nor do they resemble the reconstructions of *P. parvulus* (Traquair 1879) or *P. superbus* (Moy-Thomas and Bradley Dyne 1938). On the other hand, the skull roof and circumorbital bones, the opercular and preoperculars, the edentulous jaws, the peculiar forward position of the mandible with its distinctive cross-section and its overlapped relation with the maxilla, the shape and arrangement of the scales, the lateral line with its crossbar-like tubules, the overall fine linear ornament that breaks up into pustules on the dorsal parts of the animal, and the shape and position of the ceratohyal, all show similarities with *Ebenaqua* and with Bobasatraniformes. More importantly, there is a lateral-line-bearing bone behind the maxilla, and it has the same shape and relationships as the bone designated as a suborbital in *Ebenaqua*, and by inference in the Bobasatraniforms, the only other groups in which it is known to occur. If further study confirms our interpretation of the Kupferschiefer specimens, and *Platysomus* and the Bobasatraniformes are shown to be more closely related than has been previously accepted, there will be difficulty with the nomenclature of some of the higher taxa covering these groups (see Moy-Thomas and Miles 1971). Meanwhile we propose to assign *Ebenaqua* to the Bobasatraniformes pending further investigation of the Permian platysomids.

*Relationships of the Bobasatraniformes.* We are in agreement with Gardiner's view (1967a, p. 195) that the group is most clearly allied with the palaeoniscoids and did not give rise to any subsequent group. In our view bobasatraniids are essentially primitive fishes with some specialized characters that it would be incorrect to term 'advanced', if by that term is meant having characters in common with holosteans or even teleosts (see Patterson 1973, p. 296).

Evidence of the essentially palaeoniscoid structure of the group is found in the complex development of the dorsal caudal lobes; the small number of baseosts in comparison with the number of dorsal and anal fin rays in *Ebenaqua* and *Ecrinesomus*; the degree of segmentation of the fin rays; the absence of undivided rays in the dorsal and anal fins; the posterior position of the pelvic fin (when present); the well-developed postrostral bone; and the presence of postspiracular bones.

The so-called advanced features that cause most concern are the mobile maxilla and the vertical suspensorium (see Schaeffer and Rosen 1961, for a discussion of the significance of these features). Patterson (1973, p. 296) has indicated that the mobile maxilla of *Bobasatrania* is a halecostome character and that the reduced clavicles, vertical suspensorium, and equal numbers of fin rays and baseosts in both dorsal and anal fins, are neopterygian characters. On the other hand, he goes on to point out (p. 297) that as the maxilla in *Ecrinesomus* is fixed, that bone must have become free more than once in actinopterygians. This is supported by the new evidence from *Ebenaqua*. Moreover, as is shown in the functional section of this work, the peculiar maxilla-suborbital arrangement and the forward jaw articulation are related to distinctive feeding and gill ventilation systems of a kind quite different from the jaw-gape changes associated with evolution of the holosteans. Mobile maxillae *ipso facto* do not indicate relationships, though different styles of mobility *may* do so. As for the upright suspensorium, in the bobasatraniids, as judged from Neilsen's figures, the hyomandibula has completely lost its connection with the jaw suspension and the jaw is articulated, and presumably supported, in a manner different from that shown by neopterygians. Consequently, this feature cannot be regarded as indicating relationships either. Finally, *Ecrinesomus* and *Ebenaqua* show the normal palaeoniscoid baseost numbers relative to fin ray numbers, and the fin rays in *Bobasatrania* are proportionately more numerous and more closely spaced than in neopterygians. Judging from

the close spacing of its baseosts, it seems probable that the approximately equal numbers of baseosts and rays in *Bobasatrania* resulted from an increase in the number of baseosts rather than a decrease in the number of rays as in neopterygians. Consequently, only the reduced clavicles remain from the list of 'advanced' features mentioned by Patterson, and even they may be explained in terms of the narrow ventral body form in bobasatraniids.

Schaeffer and Mangus (1976, p. 559) concluded that in *Bobasatrania* 'the open cheek, free maxilla and vertical suspensorium indicate a holostean–halecostome arrangement of the jaw musculature', though they did not imply that this judgement had taxonomic implications. Our reconstruction of the adductor musculature of Bobasatraniformes is not holostean–halecostome in character (see below).

It goes without saying that suggestions of a relationship between *Bobasatrania*, the pycnodonts and *Dorypterus* (see Westoll 1941, for discussion), were based on convergent characters.

The bobasatraniids, in our view, form an aberrant group retaining many primitive characters, but developing several unique ones that show convergent similarities to holosteans and halecostomes. The question that remains to be discussed is—which palaeoniscoid group is likely to be its closest relative? Gardiner (1967a, p. 195) allied the group with the amphicentrids, and Westoll (1941, p. 47) considered that *Bobasatrania* is probably derived from *Platysomus* or one of its near allies, thus supporting the conclusions of Stensiö (1932) and Woodward (1939). These suggestions will be discussed in turn.

Gardiner's (1967a, p. 195) proposal that bobasatraniids 'are an offshoot from the same palaeoniscoid stock which gave rise to the amphicentrids', rests on 'the make-up of the shoulder girdle and the unpaired fins, and in the much deepened, laterally compressed body'. However, body form is scarcely a differentiating character in this instance, and the other features are too poorly defined to be applicable. It is difficult to escape the conclusion that he preferred an amphicentrid to a platysomid origin because he considered the bobasatraniids to have crushing teeth (see his p. 185 for discussion).

Westoll's assessment of Bobasatraniform relationships was based on comparisons with English Late Permian specimens assigned to *P. gibbosus*, and the similarities he emphasized were the skull roof and circumorbitals, two preoperculars, sigmoid axonosts, elongate rhomboid scales with longitudinal striae, and paired tubules on the body lateral line. As indicated above, we have additional characters indicating a close relationship between at least some Permian forms of '*P. gibbosus*' type and the Bobasatraniformes. This relationship is of importance in the search for possible ancestors because '*P. gibbosus*' is the oldest known member of this group, and it has such features as a few free branchiostegal rays and several suborbitals in front of the preopercular that are not known in *Ebenaqua*, *Ecrinesomus*, or *Bobasatrania*. Assuming that the features these three genera and '*P. gibbosus*' have in common are jointly inherited, it should be possible to infer the minimal characters of an ancestral group. To these should be added those features which, though they are not equally represented in all members of this group, are interpreted as having been modified from an ancestral form of specified type. For example, all four taxa have different branchiostegal plate arrangements, '*P. gibbosus*' being the most complex and *Ecrinesomus* apparently being without plates on the ventral surface apart from the gular. In view of the common occurrence of multiple branchiostegals in Late Palaeozoic actinopterygians, and the fact that the greatest number of plates occurs in the oldest form, we infer that the ancestral group had a number of free branchiostegal rays. A similar argument might be used with respect to the preoperculars of which there are two without a lateral line in the above taxa except *Bobasatrania*. In that genus there is a larger plate that is readily interpreted as a fusion of the second preopercular and the subopercular, and a lateral line occurs on this plate and the isolated preopercular. Since late Palaeozoic actinopterygians normally have a preopercular canal, and since the forward movement of the mandible in the group under discussion has produced a profound modification in the canal system on the lower part of the head, we infer that the ancestral group had two canal-bearing preoperculars.

Using the above approach we conclude that the ancestor of this group had the following features: dermosphenotic, dermopterotic, at least three postspiraculars, paired extrascapulars, two preoperculars with lateral line canal, three or more suborbitals in a postorbital position, clavicles, deep body,

elongate body scales with long spike-and-groove articulation and fine linear ornament, long dorsal and anal fins, caudal fin with ridge scales and rays of ventral lobe strengthened to produce an isobatic structure. In addition, the ancestral group should have structures that can be transformed to give the unique Bobasatraniform structures.

At present, no genus with this group of characters is known, but that causes little concern given the extremely patchy sampling of late Palaeozoic fish faunas and the incomplete descriptions available for many known species. What is clear is that deep-bodied species such as '*Platysomus*' *superbus* Traquair, '*Platysomus*' *parvulus* Williamson, *Chirodopsis geikiei* Traquair, and *Amphicentrum granulosum* Young, which are among the best-known species in the groups cited as possible ancestral groups for the Bobasatraniformes, have little in common with such an hypothetical ancestor.

### *Ebenaqua ritchiei* sp. nov.

*Derivation of name*: In honour of Dr. A. Ritchie.

*Holotype*. F58674 AM and counterpart F58695 AM. Two specimens on the slab, the larger and more complete individual being the holotype.

*Paratypes*. (*a*) F10135 QM, an almost complete fish and the largest specimen available. (*b*) F53871 AM, part and counterpart, preserved in pink, baked shale. (*c*) F58676 AM, an almost complete small individual. (*d*) F58680 AM, part and counterpart, almost complete. (*e*) F56881 AM, a single whole individual. (*f*) F58683 AM and counterpart F58693 AM, three incomplete individuals on a slab. (*g*) F58684 AM, a single large but partly effaced individual. (*h*) F58699 AM, a fragment of a large individual.

*Description*. The specimens are preserved compressed almost into a plane, and when split the shale parts along a surface that approximately corresponds with the median plane of the animal. This means that many specimens are viewed from the inside out. However, in places the split surface passes around one side of the animal or the other, leaving a confusing superimposed set of bones or scales from the two sides. This can usually be detected, but in areas of strong ossification it leads to difficulty of interpretation.

The skeletal material has been completely replaced by kaolinite. The manner of such replacement is difficult to understand, not only because of the mechanism involved, but also because of the fidelity of the structural preservation. The finest surface details of the scales, for example, are recorded. Unfortunately, no details of the bone histology remain, and consequently some important criteria of relationship are unavailable.

The body form of the animal is deep but variable, as is shown in text-figs. 2–3. (The position of the orbit is chosen as the anterior measuring point because several specimens have lost their snouts.) This variation in form is not the result of compression as there has been no shearing of the rock, and opposite sides of the one animal seem to be almost exactly superimposed. The body must have been very slender over almost its entire length. Four reasons may be advanced to support this conclusion. (*a*) The scales have remained almost exactly in contact edge-to-edge on *all* parts of the trunk, and not only along the posterodorsal and posteroventral edges where the scale pattern indicates that the body was blade-like. (*b*) The anterodorsal and anteroventral edges of the body are preserved as only gently convex curves, whereas they would be markedly convex if there were any body swelling. (*c*) The cleithrum has sprung apart at the symphysis with almost no displacement of the scales lying immediately behind it, and with a minimum amount of fracturing. (*d*) The dimensions of the bones flooring the branchial chamber indicate that the animal was narrow in this region.

There is some variation in the straightness of the anteroventral and anterodorsal margins, in general the larger specimens being the more convex. All specimens have gently convex posteroventral and posterodorsal margins.

*Skull roof and cheeks*. The post-temporals are the largest bones in the roof. Their posterior edges swing forward to the mid-line where they are separated by three or four spine-bearing scales. The junctions with all the surrounding bones are strong. No specimens show the sutures opened up, though they are commonly slightly depressed, probably reflecting a life condition.
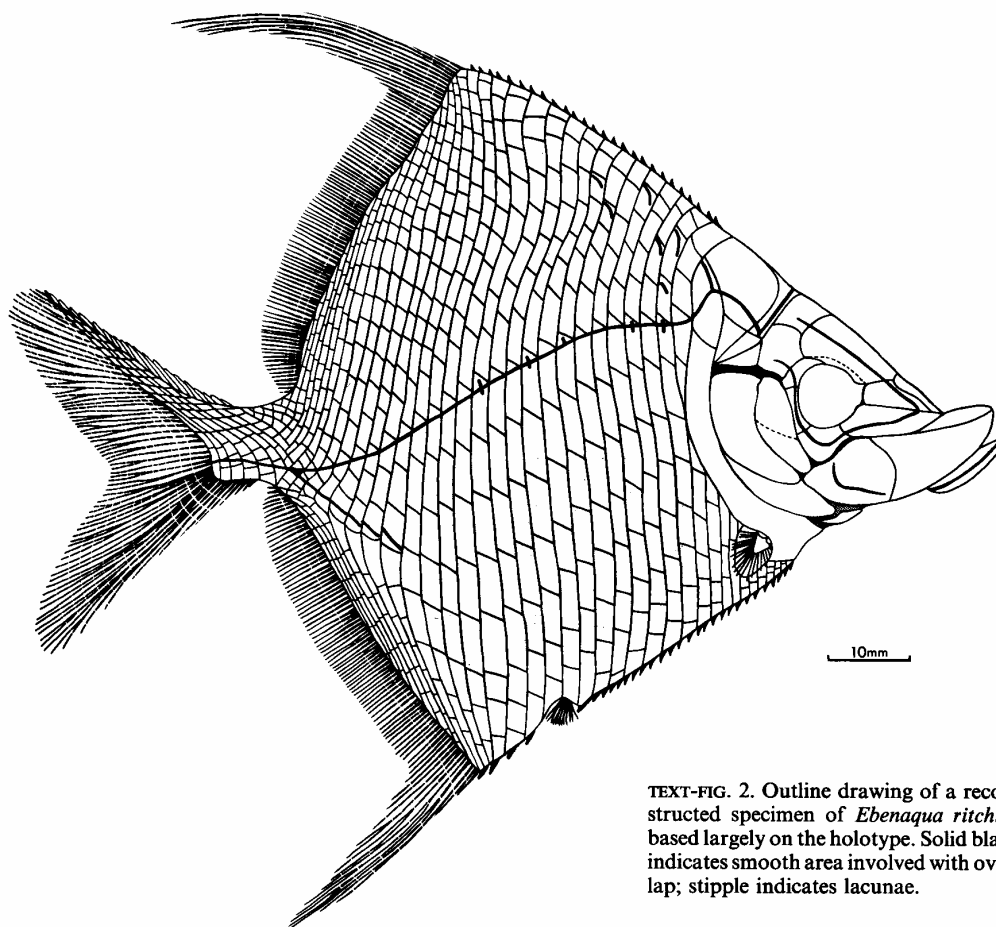
TEXT-FIG. 2. Outline drawing of a reconstructed specimen of *Ebenaqua ritchiei*, based largely on the holotype. Solid black indicates smooth area involved with overlap; stipple indicates lacunae.

The extrascapulars are narrow but expand towards the mid-line, particularly between the post-temporals. On most specimens the suture between the lateral and median components is not clear, but where it is visible the median is the smaller.

The parietal is clearly defined on all specimens, but there is difficulty with the interpretation of the frontal. Lying between the frontal and the orbit on all specimens there is a thickened ridge of bone that is firmly attached to the frontal. It is not common for the frontal to be in contact with the orbit in the deep-bodied palaeoniscoids. However, signs of a suture are seen on three specimens, and a peculiar angular junction against the dermosphenotic has been observed on others. Consequently we have tentatively shown a supraorbital in the reconstruction.

The boundary between the nasal and the frontal is clear on several specimens, lying at the upper edge of the posterior nostril. The anterior nostril cannot be seen clearly on any specimen. The possibility that both nostrils lay within the deep embayment of the orbit has been considered and rejected because of the position of the lateral line canal in front of this embayment. We conclude that the anterior nostril is a very small opening near the anterodorsal corner of the nasal.
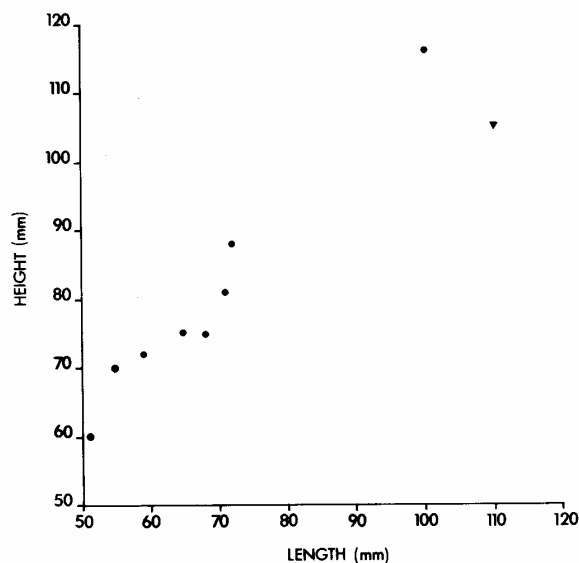
TEXT-FIG. 3. Plot of length/width for nine specimens. The length has been measured from the posterior edge of the orbit to the posterior edge of the caudal peduncle. The large specimen indicated by the triangle is F10135 QM.

The area between the nasal and the rostral projection is not well preserved on any specimen, but there is a long thin bone lying in this area anterior to the frontal. It is not known if this is a single bone crushed on itself or a paired bone. It has no lateral line canal. This, together with its position, indicates that it can only be a postrostral. There is no space for the rostral or for the rostropremaxilla, which are found in this region in *Bobasatrania*. The lateral line passes directly from the nasal to the infraorbital 3 (see below). It may be suspected that the nasal and infraorbital 3 have undetected sutures across them, the front of the so-called nasal being the rostral, and the front of the infraorbital 3 being the rostropremaxilla. Apart from the fact that we cannot detect sutures on these bones, this solution is not reasonable because it places the rostral behind the postrostral. Nor does it take account of the fact that a rostral commissure of the lateral line and canal has not been found. We conclude that this commissure has been lost along with the rostral and rostropremaxilla during remodelling of the rostrum.

The maxilla is a remarkable, elongate bone, most of the lateral surface of which is flat and highly ornamented, but its upper edge is smooth and is overlapped by the infraorbital 3. It is clear that the two bones could move relative to each other. Posteriorly it meets the suborbital, which is also overlapped by the infraorbitals on a similar smooth surface. The posterior boundary of the maxilla is always clear, and is usually represented by a depressed suture whose outline is convex forwards. An occasional specimen is split along the suture. We have little doubt that the two bones were flexibly joined. The ventral edge of the maxilla is markedly convex and edentulous. The best-preserved specimens show a smooth lenticular strip of bone forming the upper edge of the rostrum and running back into the overlapped part of the maxilla. This lenticle must have been thin, but at its anterior end it has a slight swelling. On some specimens it shows a slight emargination where it joins the ornamented part of the maxilla, but on others this junction is even. We can find no suture between it and the maxilla, though it always lies in a plane at an angle to the plane of the main part of the maxilla.

Its upper edge is invariably sharp, so that it must have been sutured against its antimere. Such a suture would have been very weak. There is a natural tendency to regard this structure as a 'rostral' that has become fused to the maxilla, but its continuity with the smooth dorsal overlapped strip of the maxilla, and the absence of a lateral line canal on it, suggest that this explanation is not acceptable. We conclude that it is a differentiated strip of maxilla.

The bone that is clearly homologous with the one labelled 'supramaxillaquadratojugal' by Nielsen (1952), Lehman (1956), and Schaeffer and Mangus (1976), in *Bobasatrania* and *Ecrinesomus*, is a distinctive structure. Schaeffer and Mangus expressed doubt about the homology of this bone, but did not reach any positive conclusions. It has a flat, highly ornamented body, but its upper edge has a smooth overlapped surface separated off by a slight kink, and its posterior edge has a powerful subtriangular smooth projection that is overlapped by the preopercular 2 and fits into a slight notch in the anterior edge of the subopercular. It carries a clearly defined segment of the lateral line canal which runs from a dorsal direction into the bone just below the dorsal overlap, contains an angular bend, and then runs forward without dividing. Anteriorly it runs off the bone near its anteroventral corner, and it is directed towards the mandible. We believe that it is almost certainly the upper part of the mandibular canal. The precise homology of this bone is unlikely to be finally determined without further material intermediate between *Ebenaqua* and its ancestors, but some points can be made.

There seem to be three possible homologies—supramaxilla, quadratojugal, or suborbital—apart from the complex suggestion of Nielson which requires fusions for which we can see no firm evidence. Gardiner (1967b, p. 200) has regarded the bone as a supramaxilla, but he gave no supporting argument. The supramaxilla *sensu stricto* first appeared in Mesozoic holosteans as a consequence of disarticulation of the cheek when the mouth was widely opened, and it lay on the dorsal edge of the maxilla for this reason. In the Bobasatraniformes the bone in question occupied a different position from the supramaxilla and, as explained elsewhere in this article, it originated with a different function and at an earlier time. Consequently, we cannot accept this hypothesis. The second view is that it is a highly modified quadratojugal, a bone known in various palaeoniscoids in which it is usually 'a small, plate-like bone which is in contact with the quadrate and is overlapped externally by the maxilla and preopercular' (Patterson 1973, p. 249). In this position the mandibular lateral line canal from the preopercular to the mandible passed in the soft tissue over its surface. It could be that as the lower jaw moved forwards in Bobasatraniformes the quadratojugal became exposed and greatly enlarged, and incorporated the lateral line connection from the preopercular to the mandible. Then as the distance between preopercular and mandible increased even more, the canal connections were modified. A virtue of this hypothesis is that although the quadratojugal is primitively not a canal bone, it apparently becomes canal-bearing in some palaeoniscoid groups—for example, the Haplolepidae (Westoll 1944). On the other hand, we consider it significant that there are no known Palaeozoic forms with an anteriorly displaced jaw articulation in which there is an exposed quadratojugal with a canal from the preopercular. The hypothesis that the bone is a modified suborbital is supported by the following arguments. Several palaeoniscoids have one or more suborbitals between the infraorbitals, the preopercular, and the maxilla—for example, *Mesopoma* and *Rhadinichthys* (see text-fig. 4). The Late Permian holostean *Acentrophorus* has a short maxilla with a suborbital immediately behind it and out of contact with the quadrate articulation, as is the bone in question in the Bobasatraniformes. And the Late Permian platysomid described in the Appendix has a row of suborbitals forming a series that includes the bone under discussion. Consequently, it would not be surprising if, in a late Palaeozoic form, a suborbital moved forwards to occupy a space created by the progressively more anterior suspension of the mandible. One difficulty with this interpretation is that suborbitals are not lateral line bones, but this is not a fatal objection as canals are able to invade non-canal bones (Graham-Smith 1978). The Bobasatraniform canal, moreover, is unique, in that no other group of fishes has a canal directed towards the infraorbital. We note also that in *Bobasatrania* the preopercular canal is still present though connection with the mandible has been lost. In Nielsen's figure of *B. groenlandica* it is directed ventrally off the bone, suggesting that if such a connection existed it passed in the skin ventral to the bone under discussion. Schaeffer and Mangus (1976, fig. 9) also show the canal rising off the bone in a ventral direction in
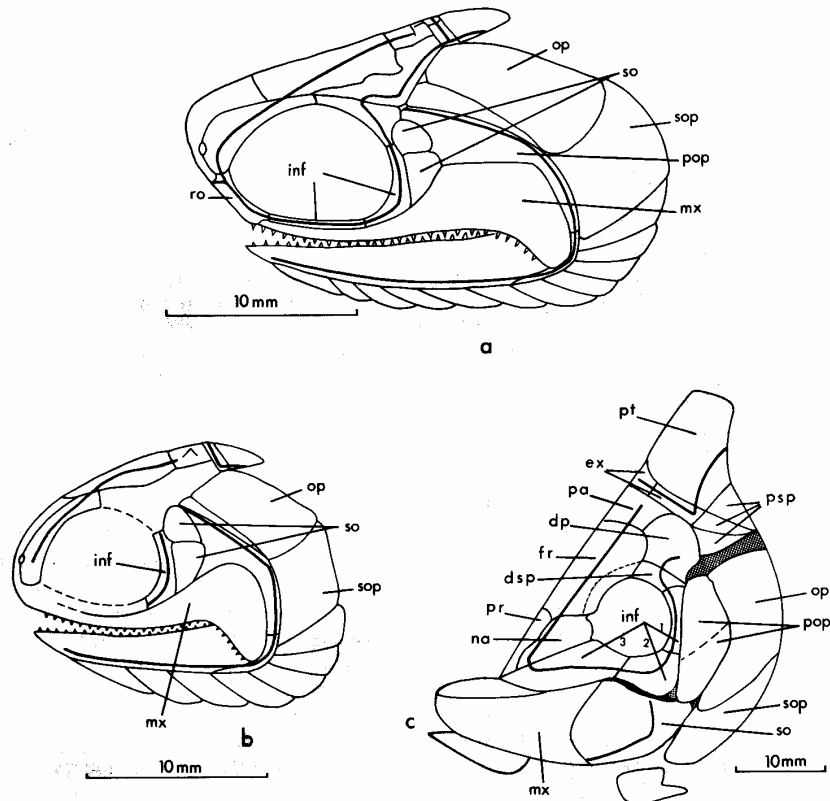
TEXT-FIG. 4. Lateral views of skulls of (a) *Radinichthys*, (b) *Mesopoma*, and (c) *Ebenaqua* to show the position of the suborbital bones. Figures (a) and (b) modified from Moy-Thomas and Dyne 1938. dp, dermopterotic; dsp, dermosphenotic; ex, extrascapulars; fr, frontal; inf 1, 2, 3 infraorbitals; mx, maxilla; na, nasal; op, operculum; pa, parietal; pop, preoperculum; pr, postrostral; psp, postspiracular; pt, post-temporal; ro, rostral; so, suborbital; sop, suboperculum. Solid black indicates smooth area involved with overlap; stipple indicates lacunae.

*B. canadensis.* Presumably this connection in the skin was broken when a new line developed from the infraorbital. As indicated above, we find none of these arguments conclusive, but on balance we prefer the suborbital to the quadratojugal hypothesis.

Below the post-temporal and the extrascapulars is a group of three triangular bones. These are bordered below by the opercular from which they are separated by a gap. Although the three bones are usually preserved in a confused state, F58699 AM shows them all with great clarity. Nielsen (1952, p. 203) refers to the two bones in this position of *B. groenlandica* as postspiraculars, noting that there is a single bone in this position in *Pteronisculus*. There is also a bone in a similar position in *Moythomasia* (Jessen 1968). Although Lehman (1956, pp. 20–21) considered these bones in *B. mahavavica* to be postspiraculars, White (1932) thought that they may be postorbitals, or the bone Y of Traquair. The examples of *Pteronisculus*, *Moythomasia*, and the Bobasatraniformes suggest either that in primitive palaeoniscoids bones were developed in the angle between the shoulder girdle, the cranial roof, and the opercular, but that they were later lost in many genera; or alternatively that

bones developed in this position to fill space as required. (The causal mechanisms for the independent development of these bones may be different in each case.) We cannot choose between these alternatives on the basis of evidence known to us, but for simplicity we refer to these bones as postspiraculars.

Anterior to these is a large bone which is sharply defined around its upper edges, but it is always broken ventrally. We are satisfied that it is a single bone and that it carries the lateral line canal to the dermosphenotic. The reason for the poor preservation seems to be that only the lower part of the plate is well ossified, and on crushing cracks develop across the plate. It can only be the dermopterotic.

The dermosphenotic is a clearly defined thick bone that in structure and form is really one of the circumorbitals. It carried a thick bony crest and is traversed by the lateral line canal in the usual way.

Infraorbital 1 is a long narrow bone also with a thick crest, but infraorbital 2, though thick close to the edge of the orbit, has a wide outer flange that becomes quite thin towards its ventral edge. The boundaries between infraorbital 2 and infraorbitals 1 and 3 are not clear. Infraorbital 3 is a large, flat, triangular bone, the thickened ridge around the orbit having faded away on infraorbital 2. The bone extends forwards to the rostral protuberance, and its junction with the nasal and the postrostral is straight and frequently open. This may be the result of compaction, but we suspect that it was probably a very weak suture. There is no sign of bone overlap along this line.

The opercular and the subopercular can be distinguished on all specimens (see text. fig. 5). The dorsal end of the opercular is quadrate in outline and it is slightly flexed and thickened in its anterodorsal corner where it articulates with the suspensorium. It slightly overlaps the subopercular along a very oblique and somewhat variable junction. In the largest specimen F10135 QM, the junction forms a deep V, whereas in others it is straight or has a slight V at its anteroventral extremity. The subopercular also is almost flat. Along its anterior edge it has a smooth strip which overlaps the suborbital, and at the upper end of this strip there is a thickened flexural notch that seems to articulate with the posterior prominence of the suborbital. The posterior edges of both bones overlap a recessed edge on the cleithrum.

The preoperculars are difficult bones to restore. They are almost always crumpled in appearance, and the posterior end of the parasphenoid with its various processes, as well as the superimposed ceratobranchials, always obscure the detail. However, we believe that two bones are present, separated by a straight oblique suture. The ventral edge of the lower bone is very thin and poorly preserved, but there is clear evidence on F58680 AM (counterpart) that it overlapped the posterior end of the suborbital, and it may also have overlapped infraorbital 2. A difficulty with the interpretation of these bones are preoperculars is that we are unable to recognize the preopercular lateral line on them. This may be the result of bad preservation, but such an explanation is unlikely because the dorsal part of preopercular 1 is frequently well enough displayed to show a canal if one were present. Apparently *Ecrinesomus* has no preopercular canal, though all three species of *Bobastrania* have the canal clearly developed. Schaeffer and Mangus (1976) explored the possibility that in *Ecrinesomus* these bones are suborbitals, but rejected that view in favour of a very guarded confirmation of their status as preoperculars. With this conclusion we are in agreement.
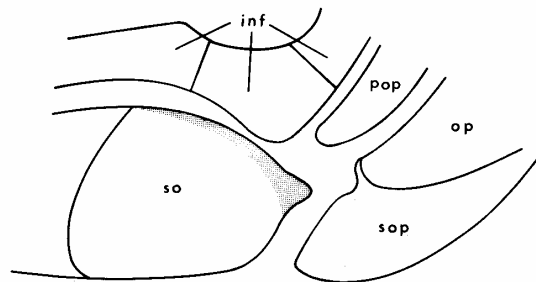


TEXT-FIG. 5. The bones of the cheek and lower opercular region separated to show their interrelationships. Stipple indicates overlapped area on the suborbital.

All specimens with the ventral edge of the head preserved have a characteristic club-shaped bone lying below the subopercular. It has a thick anterior body and a thickened anteromedial edge, but the bone is always preserved in such a way as to prevent its precise pattern of ossification being determined. It is clearly a dermal bone as is shown by the ornament, and consists of three arcuate segments, as shown in text-fig. 6, that seem to unite anteriorly to form one piece. The posterior edge also is weakly lobed in some specimens to correspond with the three segments. The bone would have
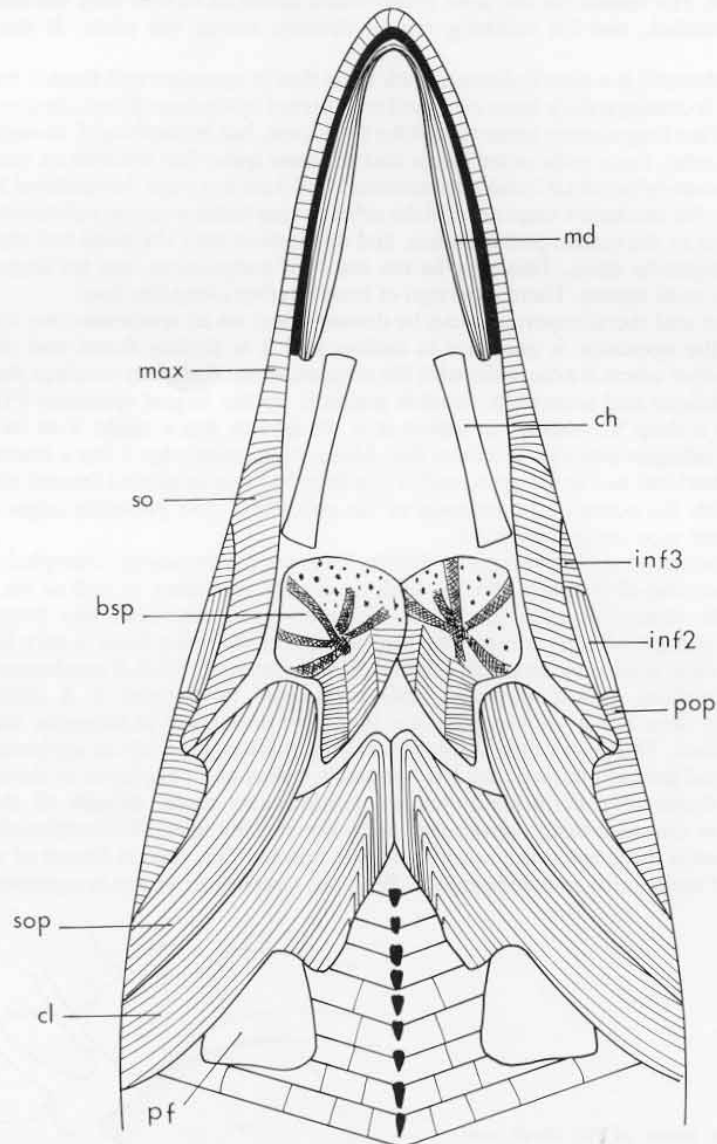
TEXT-FIG. 6. Ventral view of head and shoulder girdle. bsp, branchiostegal plate; ch, ceratohyal; cl, cleithrum; inf 2, 3 infraorbital; md, mandible; max, maxilla; pf, pectoral fenestra; pop, preoperculum; so, suborbital; sop, suboperculum.
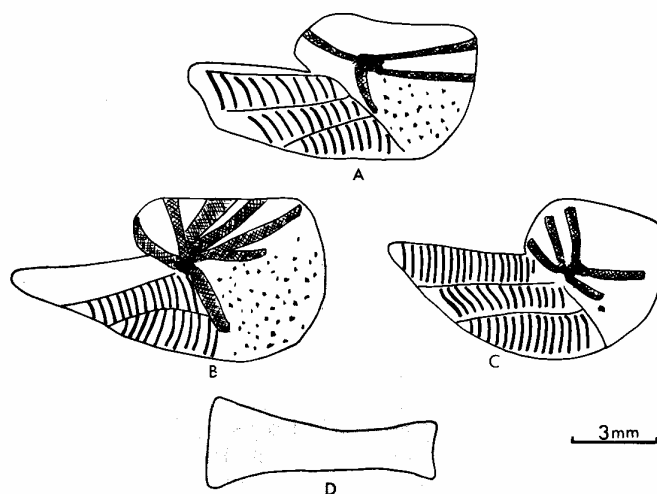
TEXT-FIG. 7. A–C, three branchiostegal plates showing variation in outline and surface detail. Drawn from F58680, F58674, and F53871 AM respectively. D, outline of ceratohyal F58371 AM.

been paired, and in life would have abutted snugly against the suboperculum and the suborbital along its upper edge while overlapping its antimere medially. A bone in such a position would normally be regarded as a branchiostegal ray, but such rays were normally lath-like and functioned as a covering for a broad arch in the body around the flank of the gill chamber. The bone in *Ebenaqua* is single, covers the floor of the gill chamber, and negotiates change in body slope by hinging below the suborbital. It would seem most appropriate, therefore, to refer to this bone as a branchiostegal plate, - and to note that it probably functioned as a second suboperculum (see text-fig. 7).

*Mandible*. Except for the anterior end, the mandible is usually preserved crushed against the inside of the maxilla. Interference between the longitudinal ornament on the two bones causes problems for the interpretation of the outline and the position of the lateral line canal. The best-preserved specimens are F58674 and F58694 (counterparts), F58680, F58683, and F58693 (counterparts) AM. In lateral view the mandible is lancet-shaped anteriorly with an abruptly terminated posterior (see text-fig. 8). Its biting edge is almost straight in lateral view, but its anterior tip is deflected inwards.

On the external surface the sutures are not clear, but there seem to be two divisions. The upper band, which is almost flat and carries a thickened oral edge, is presumably the dentary. The lower band is bulky, forming a subangular keel along most of its length, together with a number of subparallel striations that meet the dentary at an oblique angle. There seems to be a single ossification towards the posterior end of the bone giving rise to the thickenings. The lateral line canal cannot be distinguished with certainty, but it probably runs parallel with the above thickenings. Because this lower bone occurs back to the articulation in the position normally occupied by the angular, we propose to give it this name.

A fragment of the inner surface is seen on F53871 AM. It apparently was almost flat and smooth. Separate bones cannot be distinguished.

The glenoid fossa is a small depression, behind which is a short rounded projection covered by the angular. There is no indication of a coronoid process, and presumably there was a Meckelian cavity between the highest point of the dentary and the articulation.

*Ornament of skull bones*. The ornament of the skull bones consists primarily of a series of closely spaced approximately equidimensional striae that form various patterns—concentric, radial, or straight across the bone. Towards the dorsal edge of all bones the linear pattern breaks down and is
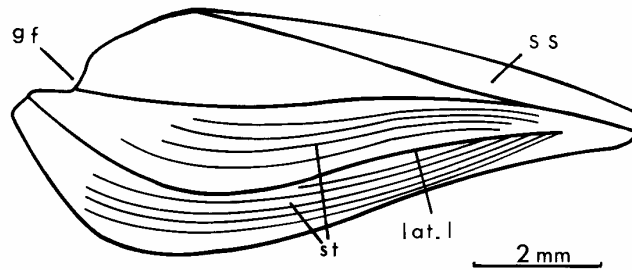
TEXT-FIG. 8. Reconstructed lateral view of mandible. Bones not clearly defined. gf, glenoid fossa; lat. l, lateral line; ss, smooth surface; st, striae.

replaced first by a regular series of pustules, and then by irregular pustules. Though there is variation in the pattern, the various bones have more or less consistent patterns and these are shown in text-fig. 9. Some peculiar variations are known. The maxilla normally has regular vertical striae across the whole bone, but on F10135 QM there is a marked discordance on the posterior quarter where a group of about a dozen striae are parallel with the posterior bone edge. On the opercular and subopercular the striae are invariably oriented dorso-ventrally, but on some, perhaps even most, individuals there is a series of oblique fine radial striae on the upper part of the subopercular. These radiate from a centre placed just behind the articulation with the suborbital. Similar transverse striae sometimes occur on the upper part of the opercular also. Both sets are well developed on F58680 AM. It should be noted that the dominant longitudinal striae are almost always finer on the subopercular than on the opercular. The distance from the dorsal edge, where the breakdown from striae to pustules occurs, varies from specimen to specimen, but particularly between specimens of different ages. For example, on the larger specimens about half the dermopterotic may be covered by pustules whereas on smaller ones its ornament is entirely linear.

*Shoulder girdle.* The shoulder girdle consists of two bones, the cleithrum and the supracleithrum.

The cleithrum is by far the thickest bone in the skeleton, and extends from the mid-ventral line up to the level of the postspiraculars. Its external surface has a powerful ridge running down the bone separating a flattened or slightly concave posterior strip from a steep anterior branchial lamina. This ridge fades gradually towards the supracleithrum and more abruptly at the pectoral embayment. It flares around the lower edge of the pectoral embayment where it is separated from its antimere by four short rows of scales. The symphysis is formed of a short straight sector at the anterior edge of which is a slightly rounded knob. There is no unusual degree of fracturing of the bone towards the symphysis despite the fact that it all now lies in the one plane. This suggests that there was no sharp angular bend from the flank on to the ventral surface which, in the median line, may have been slightly keeled or rounded. The anterior edge of the cleithrum above the symphysis is slightly concave and must have been marginally covered by the branchiostegal plate.

The bone has a peculiar texture at present, consisting of cords of white kaolinite separated by films of black substance. The significance of this is not understoood, but it is probably a function of bone replacement. However, some of the internal structure is reflected by the ribbing on the surface, at least of the lateral surface of the bone, where the ornament is of similar dimensions to that of the opercular.

The supracleithrum, which is also ornamented like the adjacent skull bones with dorsoventrally arranged striae, is a much flatter bone. It is firmly sutured to the post-temporal and the posterior postspiracular.

There is no sign of an anocleithrum on any of our material. However, we note that because the cleithrum is so powerful, the crushing of the left and right sides together and the slight displacement of the two because of the strong ridging, produce marginal overlaps that could be misinterpreted as additional cleithral elements.
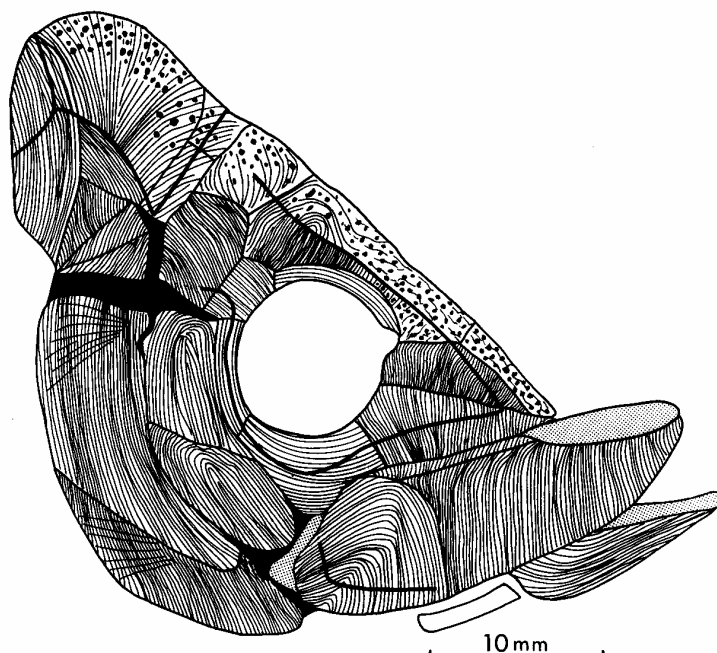
TEXT-FIG. 9. Pattern of ornament on the dermal bones of the skull. The diagram is intended to reflect the patterns commonly seen on the various bones in adult fishes, and it has been prepared from a number of specimens. The density of the lines and dots only approximates the density of the ridges and striae on the bones. The abrupt changes at bone boundaries and across lateral lines are overemphasized and are not seen on all specimens. Fine stipple indicates smooth bone; solid black indicates lacunae.

*Palate.* The only element that can be identified with certainty is the parasphenoid. This is a long narrow bone that extends from the level of the preoperculars almost as far as the level of the anterior end of the orbit. It is well ossified and is preserved on all specimens, lying across the lower quarter of the orbit. It bears no teeth, the surface being apparently quite smooth.

At the posterior end the parasphenoid is abruptly thickened where processes join it. On compression these processes rotate and shatter, making interpretation difficult. In particular, it is impossible to determine the length and attitude of the processes, though they must have been long and thin, arising abruptly from the main body. The centre of ossification is just anterior to the junction of the processes where the hyophysial pit must also be situated, though only doubtful traces of the pit can be observed.

There are two processes on each side, each being formed of a thickened rod flanked by much thinner flanges. Presumably the more posterior of the pair is the ascending process, and it would have stood up steeply. The anterior one may have been a dermal basipterygoid process, which in most genera is very short. Its apparent length is increased in this genus by the very slender stem of the parasphenoid. Moreover, the peculiar conformation of the mouth may have necessitated an unusually long basipterygoid process and a dermal cover for it. As Gardiner and Bartram (1977) have shown, the processes of the parasphenoid are very variable in palaeoniscoids, even in genera with similarly shaped heads. It would not be surprising if unusual forms like *Ebenaqua* showed peculiar structures.

The posterior extension of the parasphenoid behind the processes is very short, presumably

indicating that it covered only the prechordal part of the basicranium. This is said by Gardiner (1973, p. 115) to be a primitive feature of actinopterygians.

It is noted that the posterior end of the parasphenoid shows no structure similar to the blade illustrated by Nielsen (1952, fig. 2) for *B. groenlandica*.

The palatoquadrate is quite unossified, but from what is known of the parasphenoid and the jaw articulation, the pterygoids must have formed a steeply inclined sheet lying obliquely to the suborbital and the maxilla as shown in text-fig. 10.
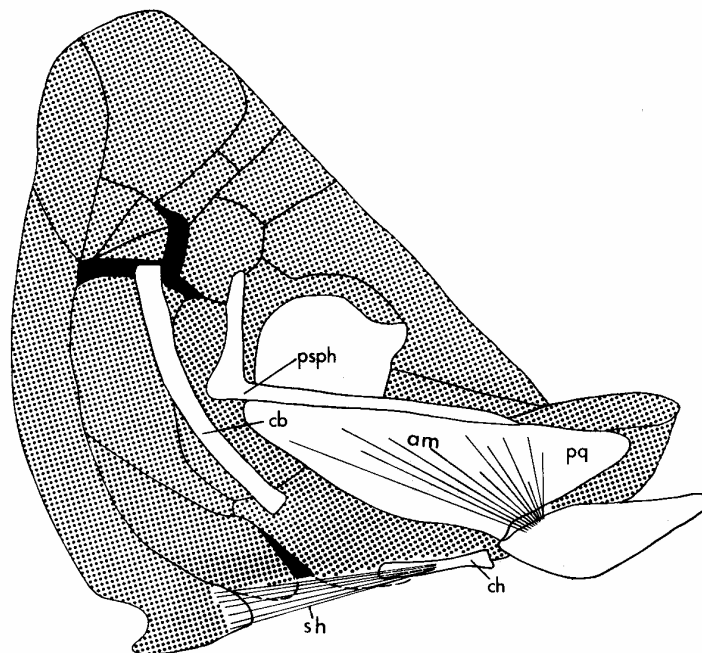


TEXT-FIG. 10. Cutaway diagram showing the dermal bones of the left side of the skull with the superimposed reconstructed parasphenoid (psph), cerato-branchial (cb), ceratohyal (ch), and palatoquadrate (pq). The shape of the palatoquadrate process is largely conjectural, and the shape of the palato-quadrate has been inferred from the preserved position of the mandible and the parasphenoid. The inferred positions of the adductor mandibulae (am) and the sternohyoideus muscles (sh) are shown.

*Visceral arches.* The hyomandibula was apparently unossified or only weakly ossified. The only element of the hyoid arch that can be recognized is the ceratohyal. It is a slightly ossified bone, usually crushed against its counterpart and thus has its shape obscured. It lies between the branchiostegal plate and the jaw articulation and it could be mistaken for another branchiostegal ray. However, its surface carries a few weak longitudinal lines quite unlike the dermal plates, and the cross-section of the bone is rod-like rather than plate-like. The best-preserved structures (F53871 and F58674 AM) are shaft-like and expand slightly towards their extremities. They are approximately half as long as the mandibles.

The ceratobranchials are very lightly ossified, but on several specimens they are strong enough to be impressed into the overlying operculum and preoperculum, obliquely down below the posterior end of the suborbital. This is their position as shown by Nielsen (1952, fig. 2) in *B. groenlandica*.

*Squamation.* The scale pattern of this species is quite distinctive. Although the flank scale rows are predominantly vertical, all specimens show a characteristic forward flexure of the rows in front of the apical angle.

The posterodorsal rows are very oblique to the body margin and the scales become progressively smaller and less ossified towards this margin. In addition, the individual scales in these rows become smaller towards the dorsal ends.
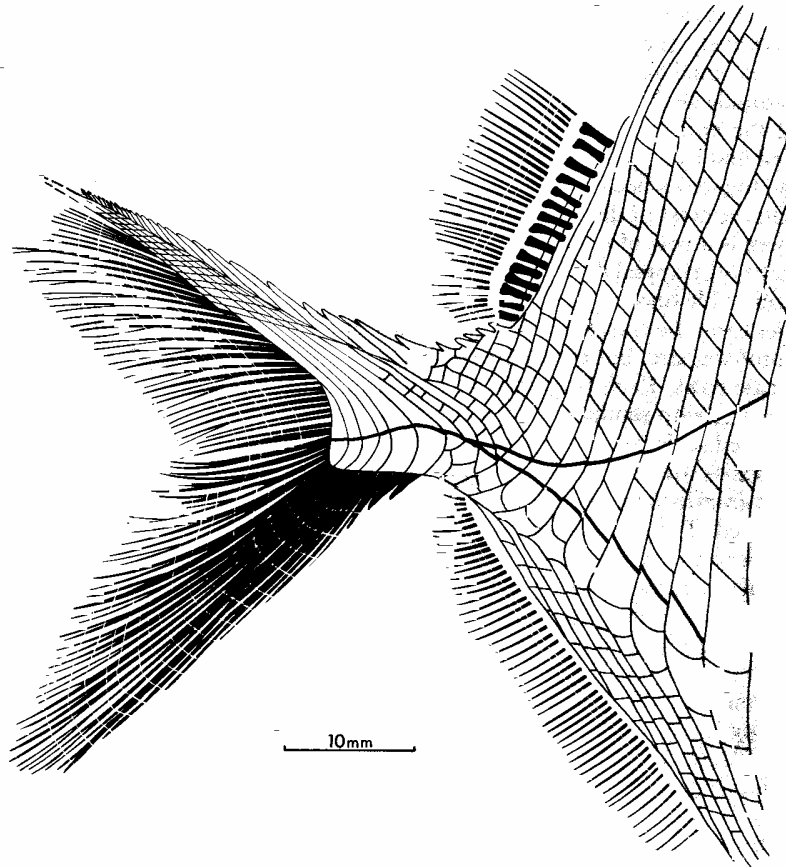


TEXT-FIG. 11. Enlargement of the posterior end of F58681 AM to show the scale and fin patterns, and the baseosts for part of the dorsal fin. The scales on the caudal peduncle are confused on this and other specimens, so that only the row outlines are shown. Those on the dorsal caudal lobe are very fine and confused so that only a generalized pattern is shown.

In the discussion that follows, the scale rows are counted along the lateral line from the first scale row behind the cleithrum. All the rows lying behind the row leading to the ventral angle (row 14 or 15) flex forwards as they approach the posteroventral margin. This flexure progressively increases on the more posterior rows back to about row 22 behind which they do not flex. Instead, the rows of fine ventral scales maintain an independent existence and meet the ends of the dorso-ventral rows abruptly (see text-fig. 11). The most distal three or four rows may meet the margin at each end. The scales in these latter rows are almost totally unossified.

There are seven to eight scale rows in front of the pelvic fin, sixteen to seventeen in front of the dorsal, and fourteen to fifteen in front of the anal. The caudal fin is at the end of a pronounced peduncle on which the scale rows are usually preserved in a confused state, and there is difficulty in distinguishing the first of the caudal rays in some specimens. However, there are twenty-nine to thirty-one rows in front of the caudal fin, though thirty-one to thirty-three scale rows are crossed by the lateral line before it terminates against the caudal fin.

The scale arrangement on the caudal peduncle and on the caudal lobe is also distinctive. Dorsoventral row 25 is the last of the complete rows to meet the ventral margin. Behind that there are five to six progressively shorter dorsoventral rows that are gradually and more or less regularly replaced by rows inclined along the length of the dorsal caudal lobe. On the peduncle the scales are short and occasionally slightly irregular in shape.

Scales extend the entire length of the caudal lobe, the number of rows towards the tip being gradually reduced first by elimination of those on the dorsal side, and then those on the ventral side as well. In addition, the scales become progressively smaller and form more elongated rhombs towards the caudal tip. On the crest of the caudal peduncle and the dorsal lobe, apparently extending right to its extremity, there is a row of overlapping ridge scales that diminish gradually in size and become progressively more overlapped distally. These number at least fifteen, but there are probably several more small uncountable ones on the caudal extremity.

Modified scales form the crest from the back of the skull to the dorsal apex. They are not regularly arranged or of uniform size, but on the best-preserved specimens they seem to alternate in position with the main scale rows. Each bears one or more spines, one being dominant if two or three are present. Similar scales with similar spines occur along the anteroventral margin. In front of the pelvic fin there is a modified scale with a rather stronger spine curved back under the fin base (Pl. 7, fig. 6).

Typical flank scales are rhomboid in form. They are flattened or slightly concave from top to bottom, but their anterior and posterior edges are bent sharply inwards, so that in section they are broadly mesa-shaped. The downturned edges meet only along their margins, leaving deep grooves separating the scale rows and imparting a strongly corrugated appearance to the surface. The amount of overlap between scales in successive rows is slight. The articulation between adjacent scales in the same rows has not been clearly observed, but several specimens (see Pl. 9, figs. 3, 6) show a regular pattern of cross-cutting lines suggesting that a long blade-like spike extends from the posterodorsal corner of a scale up under the scale above. This is very similar to the scales of *Bobasatrania* and *Platysomus*. Ornament on the flank scales consists of vertical striae which maintain their dimensions over the whole length. In structure the scales seem to be formed almost entirely of threads which produce the striae referred to above (see text-fig. 12). They show up similarly on the internal as well as the external surface, but internally they are bonded together by short, slight processes that produce a weak grid pattern.

The scales on the dorsum immediately behind the head are smaller and more irregularly shaped than those elsewhere. This seems to be the result of the flexure of the rows in response to the need to

**EXPLANATION OF PLATE 7**

*Ebenaqua ritchiei* gen. et sp. nov.

Figs. 1–3. An almost complete small specimen, F58676 AM, showing the body form and the pelvic and anal fins.

Fig. 4. Latex cast of part of the head of F53871 AM to show the ornament pattern on the bones of the maxillary and orbital regions, and the smooth convex area along the crest of the maxillary. Position of orbit marked by letter 'O'.

Fig. 5. Head of a well-preserved specimen F58694 AM. Note particularly the form of the jaw region, the ornament on the branchiostegal plate, the parasphenoid, and the row of scales below the pectoral fenestra.

Fig. 6. Part of the ventral edge of F58681 AM to show the pelvic fin in its embayment, and the enlarged spines forming the margin on either side of it.

All scale bars are 10 mm long.

PLATE 7
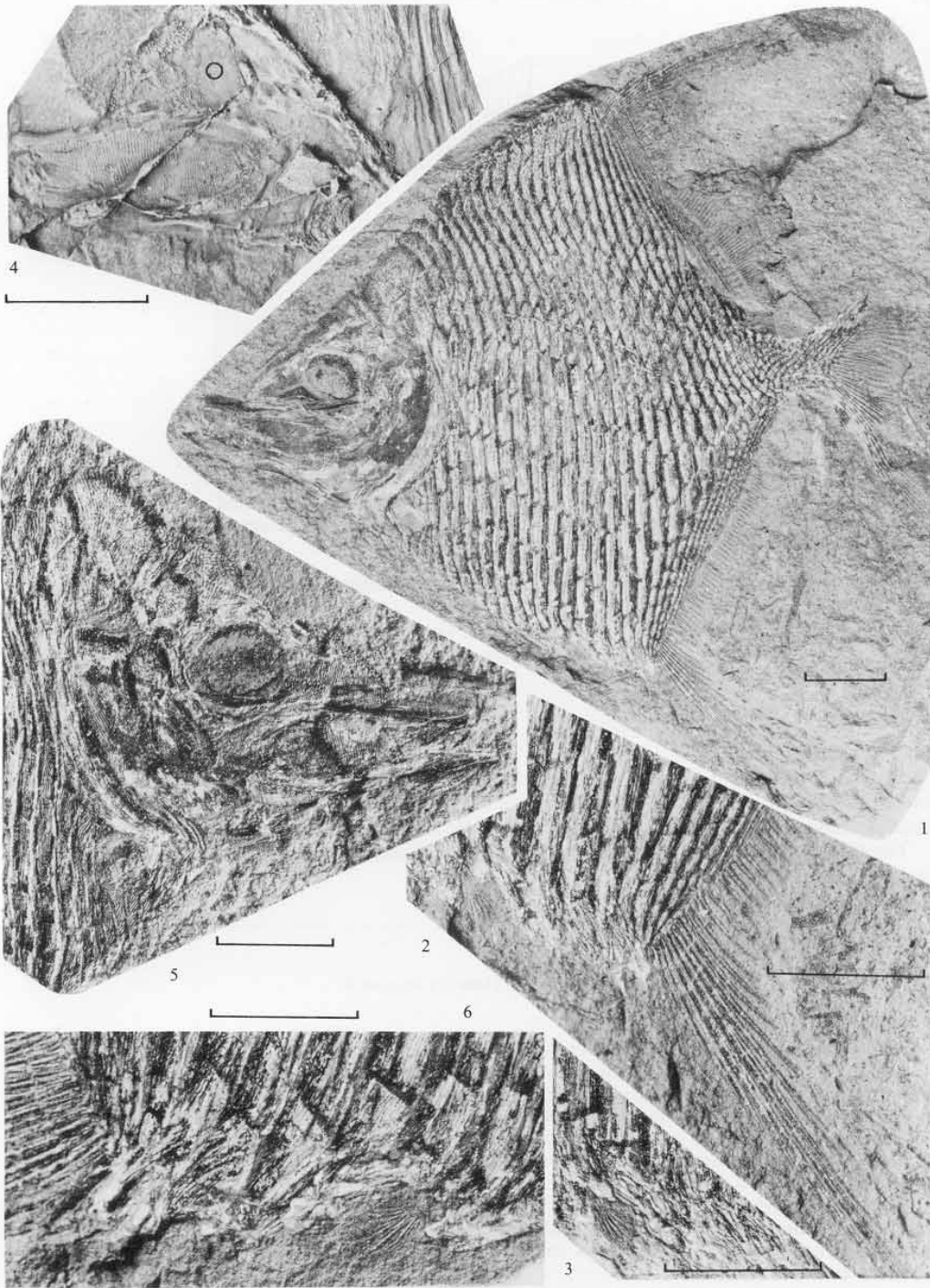


CAMPBELL and PHUOC, Late Permian Actinopterygian fish
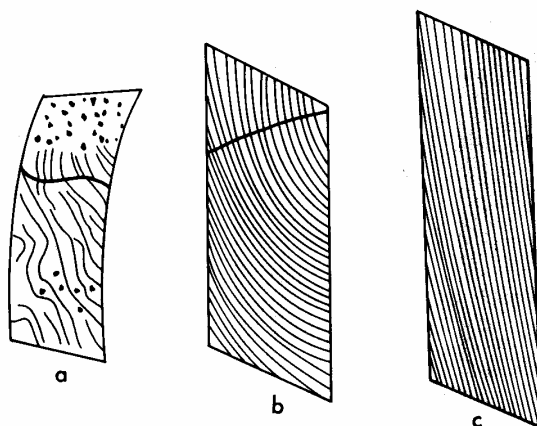
TEXT-FIG. 12. Diagrammatic representation of the shapes and ornament patterns of three scales taken about the mid-length of the body in (a) dorsal, (b) medial, and (c) ventral positions. Solid lines on (a) and (b) indicate lateral lines.

move the head sideways as a unit. There is also some slight modification of scale shape towards the anteroventral margin.

The ornament of the scales on the mid-flank is described above. Approaching the lateral line from below, the ornament pattern changes so that the striae run anteroventrally on the lower part of the scale and bend to run parallel with its margins on the upper part. Above the lateral line the whole scale is ornamented by striae that are oblique to the lower edges. On the uppermost scales the striae tend to become irregular, particularly on the shape specimens, and at the dorsal extremity they break up into rounded pustules.

The scales forming the rows behind the region of maximum depth conform to a similar pattern except that at the dorsal extremities there are no pustules, and the pattern in front of and on the caudal peduncle is quite distinctive (see text-figs. 10 and 11; Pl. 8, figs. 2, 7; Pl. 9, fig. 6).

The ridge scales on the caudal lobe are ornamented with very weak lines subparallel with their length.

EXPLANATION OF PLATE 8

*Ebenaqua ritchiei* gen. et sp. nov.

Figs. 1. Posterior part of F58683 AM. Note particularly the form of the dorsal fin and its lepidotrichs, and the way in which the scale rows are oriented anteroventrally to the caudal peduncle.

Figs. 2, 3. 2, posterior part of a latex cast, F53871 AM. Note the ornament pattern on the scales, the crest of ridge scales on the caudal lobe, and the lepidotrich pattern in the dorsal and caudal fins. 3, enlargement of the dorsal apex of the same specimen to show the spines on the ridge scales in front of the dorsal fin.

Fig. 4. Enlargement of part of the dorsal fin of F58681 AM (see Pl. 9, fig. 3) to show the baseosts.

Figs. 5, 6. 5, the head of the holotype showing almost all the bones. 6, enlargement to show the ornament on the suboperculum and the small basal part of the pectoral fin lying in the pectoral fenestra.

Fig. 7. A fragment, F58699 AM, to show the scale ornament pattern, the main lateral line canal with its crossbars, and the fragmentary irregular anterodorsal canal.

All scale bars are 10 mm long.

PLATE 8
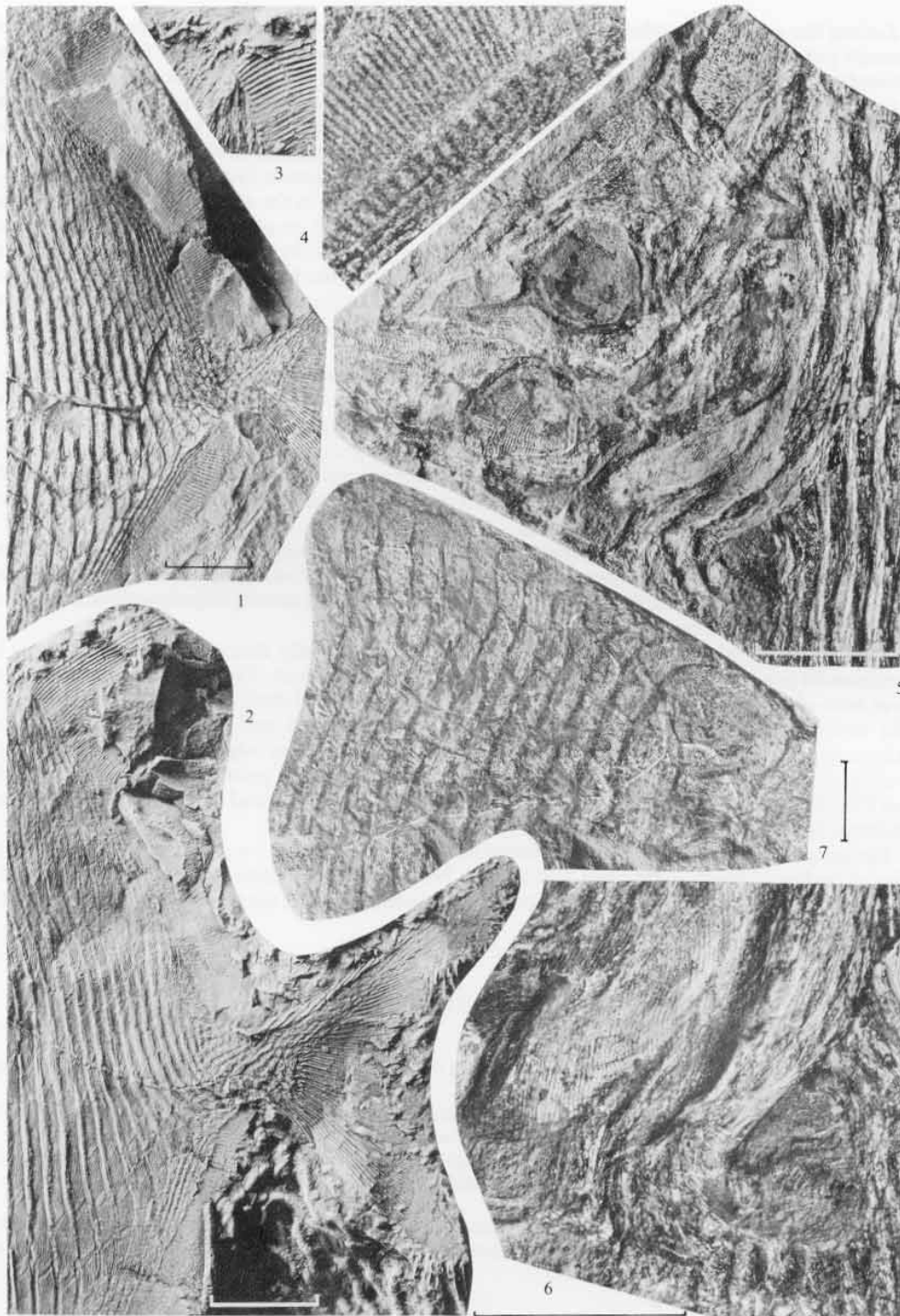


CAMPBELL and PHUOC, Late Permian Actinopterygian fish

*Lateral line canal.* Everywhere the lateral line canal is in a bony sheath, and it opens to the surface through pores, some of which may be seen on F58684 AM. It usually stands out from the surface of the scales and is clearly visible except where it lies parallel with the striae of the surface ornament.

On the flanks the canal consistently follows the pattern shown on text-fig. 2. Its posterior end always lies at the junction between the ventral and dorsal caudal lobes (i.e. at the cleft in the caudal fin). The individual scale segments of the canal are usually straight and lie end to end, though in some specimens they are arcuate or even sigmoid on the first few scale rows. Given off from the body canal at irregular intervals are short dorsal tubules that are confined to the scale on which they originate. They usually occur only on the anterior half of the body, though on occasional specimens they occur further back also. Specimen F58684 AM has fourteen, which is the largest number observed on any one specimen. As many of the scales are incomplete, there could be more. On the largest specimens, F58699 AM and F10135 QM, there are occasional ventral projections matching the dorsal ones, and producing an arcuate crossbar effect similar to that observed in *Platysomus* and *Bobasatrania* by Westoll (1941).

There are two main subsidiary canals on the body. The anterodorsal one originates at the angular flexure of the canal on the supracleithrum, and can usually be traced to the upper edge of that plate, where it disappears. Irregularly on the first five or six scale rows there are discontinuous fragments of lateral line canal (see Pl. 8, fig. 7). These fragments are often curved and tend to be subparallel to the dorsal edge, so that there is some confusion between irregular ornament and the bone-sheathed lateral line canal. It is not possible to determine if these fragments were independently innervated or if they were connected by canals in the skin.

The posteroventral canal is much more regular and forms almost a straight line across eight or nine scale rows. In each row it transverses the scale that lies above the row inflexion. On some specimens the segments on successive scales lie end to end, but on others they are slightly curved and are offset. It divides from the main canal at scale row 23 or 24.

*Fins.* The pectoral fin is very small, consisting of approximately thirty rays only 5 mm long in a specimen 80 mm high. The possibility that the rays were much longer (like those of *Bobasatrania*) and have been obscured by the thick scales, has been considered, but there is no evidence to support it. The endoskeletal supports, seen in F58674 AM (counterpart) and F56881 AM, consist of a subtriangular plate with a broad median line from which about ten ridges radiate on each side (see text-fig. 13). From the free edge of this plate a fringe of short rays is given off all round (F53871 AM and F58674 AM counterpart). The rays are apparently unbranched, and articulations have not been observed (see also Pl. 8, figs. 5, 6).

The pelvic fin is situated in an embayment of the ventral edge. It, too, is very small, consisting of rays up to 4 mm long in a specimen 75 mm high. No endoskeletal supports are preserved, though on the two specimens with observable fins the rays are oriented so that the supports could be seen if they

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**EXPLANATION OF PLATE 9**

*Ebenaqua ritchiei* gen. et sp. nov.

Figs. 1–2. 1, part of the head of the largest specimen F10135 QM. Note particularly the junction between the operculum and the suboperculum. 2, tail of same.

Fig. 3. An almost complete specimen F58681 AM with the rostrum and the anterodorsal edge destroyed. Note the overall scale pattern, the fins and the baseosts in the dorsal fin.

Figs. 4, 5. Two views of the head of F58676 AM in different lighting. Note the bone pattern of the head, the parasphenoid, the ceratohyal, the posterior articulation between the suborbital and the suboperculum, and the ornamented branchiostegal plate.

Fig. 6. The anterior end of the holotype. Note the jaws, the articulation between the suborbital and suboperculum, the branchiostegal plate, the lateral line system, and the row of spines on the ventromedian scales.

All scale bars are 10 mm long.

PLATE 9



CAMPBELL and PHUOC, Late Permian Actinopterygian fish

had been ossified. The open embayment in the body outline is very distinctive, and means that the two fins must have been almost in contact during life. At the base of the fin there are nine or ten rays, the longest and strongest ones being in the middle, and those towards the margins being very weak indeed. The middle rays divide once, or possibly twice. No articulations have been observed.
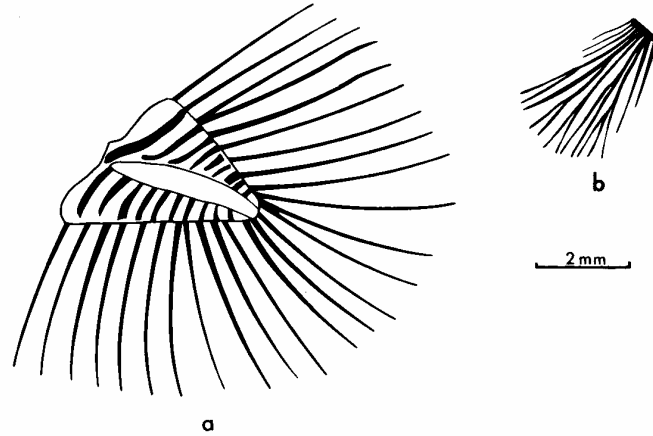


TEXT-FIG. 13. Diagrams of (a) the pectoral and (b) the pelvic fins. In (a) the proximal structure is apparently a solid radially ridged structure as is shown on Pl. 8, fig. 6.

The dorsal and anal fins are similar in shape and structure. Each is markedly elongated towards its extremity and diminishes rapidly in length to produce a fringe of short rays that extends down on to the caudal peduncle. The fins begin immediately behind the dorsal and ventral angles respectively, the rays increasing rapidly in length to a maximum at ray 7 to 8. Only one or two rays and their bifurcations form this elongate sector, and the rapid reduction in ray length then occurs over the next five or six rays. The greatest ray length is approximately 32 mm in a specimen 72 mm high. The longest rays divide twice, but not in a regular fashion. The shorter rays are not bifurcated. At the caudal end the last eight to ten rays gradually decrease in length, producing a rounding off of the fin terminus. In specimens 75 mm high there are approximately seventy-five to eighty rays in both the dorsal and anal fins, through precise counts are not possible for both fins on any single specimen.

Each ray consists of a bony axis which has an angular edge on each side running the length of the ray—i.e. in transverse section the axis of each segment is almost square. Connecting adjacent axes there are clearly preserved membranes which were contiguous with (but perhaps not fused to) their neighbours. They split apart on compression, and in some specimens their edges are clear straight lines, suggesting that they were composed of strong tissue. This is supported by the presence of fine lineations on the membrane parallel with the length of the rays.

The proximal segments are somewhat longer on the long rays than the short ones. The long rays have twenty segments, or possibly more, but the shorter ones have only three or four. On rays of all types, the distal elements are very indistinct.

The caudal fin is heterocercal, equilobate, and posteriorly cleft. As in *Bobasatrania* the rays above and below the cleft are quite different in structure and in disposition. The cleft, of course, corresponds with the junction between the dorsal and ventral lobes. The rays in the dorsal lobe tend to be well separated at their bases and are joined by flanges like those on the median fins. Towards the caudal tip, as they become more oblique to the lobe, they become more closely spaced and the flanges are appropriately reduced. The rays on the dorsal lobe number approximately forty-five in the larger specimens, though counting of the very short rays at the caudal tip is not accurate. They usually

bifurcate once, but occasionally twice. The lepidotrichs are very short and are slightly expanded at their junctions.

The rays on the ventral lobe are so crowded proximally that they are contiguous. They are also more heavily ossified than those on the dorsal lobe, and the degree of ossification increases slightly towards the ventral edge. The most ventral of the rays is very short and they gradually increase in length to the sixth or seventh, after which they gradually decrease towards the cleft. The shorter rays are undivided; those forming the longest part of the fin bifurcate only once towards their distal ends; those further towards the cleft bifurcate twice. Of course, the ossification decreases towards the distal extremities, the segments become less angular, and the membranes produce a webbed structure. So far as we can determine there are no unsegmented rays in this lobe. The proximal segments in the rays adjacent to the cleft are about 1·5–2·0 times as long as those in the equivalent dorsal lobe rays, and they are distinctly expanded at their junctions. There are fifteen to seventeen rays in the ventral lobe.

*Axial skeleton.* The vertebral column must have been completely unossified as no trace of it can be found. The best-preserved structures are the baseosts of the dorsal and anal fins. These are preserved on a number of specimens, but though there is ossification in the larger individuals, they appear mainly as dark stains on the rock in the smaller ones, apparently indicating that they were cartilaginous or weakly ossified. They are most clearly preserved where the scales are thinnest, and this is towards the caudal end of each fin. In these regions the crushed baseosts have a wide, flat, or slightly concave outer edge, are strongly waisted, and are expanded to a lesser extent at their inner ends. In each fin, ten baseosts support twenty-two to twenty-seven fin rays.

Axonosts are very indistinctly preserved. They are infrequently observed as compressions that deform the overlying scales, and are much weaker, when present, than those figured by Schaeffer and Mangus (1976, fig. 9) in *B. canadensis*. They are too vague to warrant description in detail, but they seem to be flat and sigmoid like those of *Bobasatrania*.

## FUNCTIONAL INTERPRETATION

*The environment.* There is no doubt that the animal inhabited a freshwater coal swamp. The sediment is a grey shale that abounds with plant matter, and there is ample evidence from both the nature of the sediment and the distribution of the stratum that the water was quiet. There must have been large quantities of plant material in the water and although much of it had been broken down and degraded before burial, an abundance of finely divided plant tissue would have been available for feeding. Alternatively, soft invertebrates living in the mud of the bottom of the swamp would have provided suitable food. This is important because the other previously recognized members of the Order, *Bobasatrania* and *Ecrinesomus*, are both marine and have been interpreted as nibblers in coral reef environments, and *Platysomus gibbosus* is from the Kupferschiefer, a euxinic deposit.

*Morphology.* There are three main functions that may be investigated using the skeleton—viz. feeding, respiration, and locomotion. All these are, of course, closely interrelated, and hence it is necessary to produce a consistent interpretation of all these functions. We attempt to do this by an examination of the jaws, the buccal and branchial chambers, the body shape, and the fins. The method of analysis has been to establish the possible movements of the preserved elements, then to attempt the restoration of soft tissues, particularly the muscles, in the light of what is known of these structures in living primitive actinopterygians; and then finally to attempt a functional analysis. For the sake of continuity, the presentation below is integrated and does not follow this pattern.

(a) *The face and jaws.* In all specimens the maxilla is a large, flat, highly ornamented plate, surmounted by a smooth segment that is set at an angle to the plane of the ornamented plate. When the two sides of the fish are put together the maxillae have an apse-like form in anterior view. Unornamented bone in this fish occurs either where there is overlap or where the ossification is only slight. Because the upper sector of the rostrum cannot be involved in overlap it was probably slightly ossified, and it may have been encased in skin.

The mandible is situated in about the same position in all specimens. This seems to be the life position because if it is rotated about its articulation the tips of the mandible and maxilla would come

into juxtaposition. The position of the quadrate is thus approximately fixed. It is known that the mandibles are slightly thickened at their tips and turn in slightly, but abruptly, towards the symphysis. It seems probable, therefore, that as the jaws were closed the maxillae would be rotated outwards slightly. This would have two main effects—the edges of the dentary and the maxilla would move past each other like a pair of scissors, and slight lateral expansion would be produced at the anterior end of the mouth to help counterbalance the volume change caused by vertical contraction.
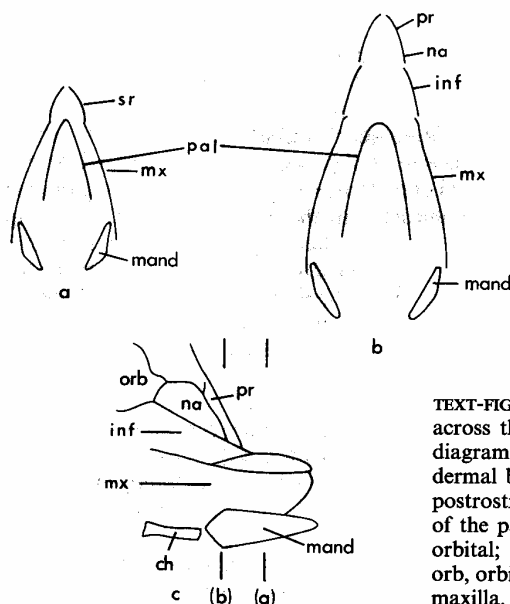


TEXT-FIG. 14. (*a*), (*b*) diagrammatic vertical sections across the snout in the two positions indicated in diagram c, showing the mobile junctions between the dermal bones as gaps and immobile junctions (i.e. postrostral/nasal) as a continuous line. The position of the palate is inferred. ch, ceratohyal; inf, infra-orbital; mand, mandible; max, maxilla; na, nasal; orb, orbit; pr, postrostral; sr, smooth rostral part of maxilla.

The size and strength of the jaws and adductor mandibulae (see below) indicate that the animal ate soft tissues, and these almost certainly included plants and/or small invertebrates. An inflow of water during the bite would then pull food tissues into the mouth while they were cut. This explains two unusual features of the jaw morphology—the depth of the maxilla and the straight edge of the dentary. The deeper the maxilla the greater the proportion of volume expansion of the oral cavity for any given angle of rotation (see text-fig. 14), and hence the production of a relatively greater suction. If the suction was weak, it would be an advantage for the upper edge of the dentary to be concave so as to hold the food in the bite, but this would limit the gape.

The infraorbitals overlap the maxilla and the suborbital. This loose junction did not allow rostro-caudal movement of these bones because the suborbital has an articulation with the suboperculum preventing such movement. Lateral rotation of the maxilla and the suborbital with the line of overlap as an axis would have been possible. In addition, the infraorbital/nasal suture is also open and would have permitted some lateral rotation. The vertical section through the preorbital region of the skull given in text-fig. 14 shows the possible movements of the various bones. For this to be accomplished there can have been no firm connection between the quadrate and the maxilla.

The design of the rostral region therefore seems to be that of an inverted C-spring with most of the resistance to the spreading of the maxilla being provided by skin on the top of the rostrum, supplemented by the strength of the median sutures in front of the orbits and by whatever rigidity existed in the bone overlaps and sutures.

A difficulty with this mechanism is the fact that we can find no evidence of a differentiated biting edge on either the maxilla or the dentary. There is no evidence of bone meeting bone in a biting action

in any group of organisms, and hence one might expect dentine cutting edges on the above bones. The replacement of the skeletal tissue prevents testing this suggestion.

(b) *Adductor mandibulae*. There is no coronoid process, and the evidence is that there is an adductor pit situated just forward of the glenoid fossa. The adductor muscles, as is normal, would have taken origin on the outer face of the palatoquadrate. Lauder (1980a,b) has shown that in primitive modern actinopterygians fibres of the adductor mandibulae run behind and below the orbit, and to the hyomandibula. He postulates that in palaeoniscoids (1980a, fig. 18) there were three components of the adductor mandibulae. In *Ebenaqua*, however, there seem to be mechanical limits to such a scheme. It is unlikely that in such a small jaw a muscle would extend to the postorbital/ hyomandibula region, especially as such a muscle would have no mechanical advantage when the jaw was open, and little advantage when it was closed. It may be that a posterior division of the adductor was lost in this group, but if present it must have been short and have taken its origin from the palatoquadrate below the orbit. The median and anterior divisions would have originated well forwards of the orbit. The arrangement would have been as shown in text-fig. 10. The muscles would have formed a rather thin sheet to fit in the confined space between the maxilla and the palatoquadrate. The palatoquadrate must have been cartilaginous or very poorly ossified, and so presumably was somewhat flexible. The contraction of the adductors would have pushed the quadrate outwards slightly and this would have at least maintained the lateral position of the maxilla, tending to maintain the volume of the front of the mouth during the bite.

During the closing of the mouth the posterior intermandibularis muscles would have been relaxed, allowing full lateral expansion of the mandibular rami.

(c) *Abduction of the jaws*. For several reasons we believe that contraction of the epaxial and hypaxial musculature to produce tilting of the cranium and the shoulder girdle respectively, would have been of no consequence in *Ebenaqua*. The shape of the head and the forward position of the mouth would prevent movement of the cranium having any effect on the size of the gape. In any case the gape would have been small and the hyoid musculature would have been adequate to control it (see Lauder 1980a, 1982, for summary and references) (see text-fig. 15).

The ceratohyal part of the hyoid arch was strong and, as argued above, it was well separated from the hyomandibula, so that the epihyal and interhyal must have been long and cartilaginous, and hence very flexible. The sternohyoids would therefore have been able to produce considerable retraction of the hyoid bar, and some of this movement would have been mediated to the mandible via the tissues of the floor of the chamber. Lauder (1980a) has concluded that a mandibulohyoid ligament was primitive for actinopterygians, and that the sternohyoids functioned in retracting the mandible by the transmission of stress from the hyoid to the mandible via this ligament. It is possible that such a ligament existed in *Ebenaqua*, but it would be situated much further forward than in any of the forms discussed by Lauder. Even if such a mechanism existed, muscles between the hyoid arch and the mandible would also have had an important role, and in view of the distance between the ceratohyal and the mandible, muscles operating independently of the sternohyoids would seem to be necessary to provide the required delicate control over mandible movement. The geniohyoids operate in this way in higher fishes, but Lauder (1980a, p. 312) concluded that palaeoniscoids lacked these muscles. On the other hand, the interhyoideus muscles are part of the primitive actinopterygian hyoid musculature. Contraction of such muscles would not only have provided fine control on the opening of the mandible, but would also have exercised a control on the spread of the mandibular rami and thus on the volume of the buccal cavity. During this phase the intermandibularis posterior muscles would have been contracting, but presumably they did not cause the mandibular rami to move together. Rather, they exerted a control on the rate of spreading of the rami under the influence of the interhyoideus and sternohyoideus muscles.

In passing we note that in *Ebenaqua* there is no possibility of any connection between the action of the levator operculi and mandibular depression, which is said by Lauder to be a halecostome character.

Another important point relates to the absence of gulars, and the lack of a bony cover to the floor of the mouth and the gill chamber in front of the branchiostegal plate. Presumably this was covered
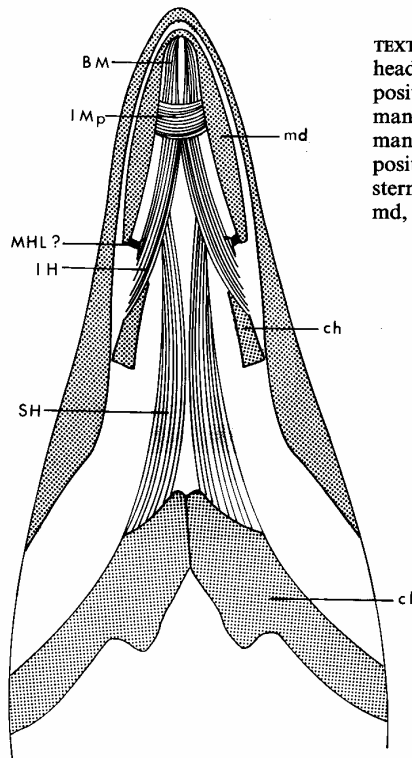
TEXT-FIG. 15. Diagrammatic ventral view of head and shoulder girdle to show the inferred positions of the main muscles. BM, branchio-mandibularis; IH, interhyoideus; IMp, inter-mandibularis posterior; MHL?, possible position of mandibulohyoid ligament; SH, sternohyoideus; ch, ceratohyal; cl, cleithrum; md, mandible.

with loose skin, above which lay the usual intermandibularis and branchiomandibularis or interhyoideus muscles. If the space was covered by soft tissues it would be expected that they would play a passive role and this could be of significance. For example, if the floor of the mouth was covered with gular plates the volume of the buccal cavity would be increased by contraction of the interhyoideus muscles, but decreased when they relaxed and the jaws closed (Lauder 1980a, fig. 18). There would be no such control on volume of the buccal cavity in *Ebenaqua*, though with the soft floor in the mouth one would expect a less rapid decrease in volume as the jaws closed, and this would enhance the effect of the slight spread of the maxillae and suborbitals in controlling the rate of decrease of buccal volume as the jaws closed.

(d) *The posterior buccal and lower branchial cavities*. From an evolutionary point of view the shapes of these cavities have been produced largely by the forward movement of the jaws. The ceratobranchials extend around beneath the suborbital where the mouth and gills are able to occupy the full width of the head unimpeded by the jaw musculature. This is an important feature in an animal with such a narrow head. On the other hand, the dorsal part of the branchial chamber has been reduced slightly in comparision with that of other palaeoniscoids. The overall effect of the forward migration of the jaw has been to displace the main volume of the branchial chamber downwards and forwards.

Under these circumstances one might have expected to find a number of branchiostegal rays, but this is not so. Instead, a large subopercular and an unusual suborbital cover the flanks of the most voluminous part of the branchial chamber. The suborbital is flexibly fixed to the maxilla, which restricts its range of movement to a lateral rotation. Hence the only dermal plates able to move to permit egress of water from the gills are the operculars, suboperculars, and the branchiostegal plates.

It is important to appreciate that the last-mentioned plates give evidence of being compound, and each is formed of at least three branchiostegal rays. There must have been an advantage in forming such a plate to act as what is, in effect, a second suboperculum that could move laterally and also rotate around an axis along the ventral edge of the suborbital, thus widening and opening the chamber from the ventral mid-line of the animal.

Of considerable significance is the process on the posterior end of the suborbital. This articulates into a notch on the subopercular where there may have been a ligament attachment, and it is overlapped by the edge of the preopercular. It is clear, therefore, that lateral movement of the suborbital will result in movement of the whole opercular series of bones and the hyomandibula, which is assumed to have been attached to the preopercular in the usual way.

It is necessary also to reconstruct as much as possible of the hyoid arch. The hyomandibula is not preserved, but assuming the usual actinopterygian relationships between it and the dermal bones, and using Nielsen's work on *B. groenlandica* as a guide, inferences are possible. From the size and position of the preoperculars the hyomandibula would be expected to be large and vertically placed. Such a structure is found in *B. groenlandica*, but its posterior blade is larger than expected. Given the relative sizes of the preoperculars in this species and in *Ebenaqua*, an even broader hyomandibula with a more elongate opercular process could be inferred for the latter.

The ceratohyal is a long bone situated at a distance from the hyomandibula with which it must have been connected by a long cartilaginous epihyal and interhyal. The strength of the ceratohyal together with the powerful cleithrum extending around to its symphysis suggests that the sternohyoideus muscles were strong; what is more, the position of the ceratohyal with its head inside the median part of the ventral edge of the suborbital is ideal to produce maximum lateral movement of that bone on contraction of the sternohyoideus muscles.

(e) *Suspensorium and operculum.* It is necessary now to examine the possibility of interpreting the musculature that activates the suspensorium and the operculum. Many of these muscles originate on the walls of the neurocranium, and hence there is no possibility of reconstructing them; but some originate on the roofing bones and others around the posterodorsal edge of the orbit. A feature of *Ebenaqua* is the thickening of the dermal bones in the area where such muscles would have taken origin—the lower part of the dermopterotic, the dermosphenotic, the supraorbital, and the infraorbitals. This suggests that the muscles would have been powerful. The levator arcus palatini and the levator hyomandibulae would have originated on the dermopterotic and the dermosphenotic, and produced considerable vertical and the lateral expansion of the palate. Presumably they would contract at the same time as the sternohyoideus muscles and reinforce the expansion of the buccal and lower branchial chambers. They sometimes assist with the abduction of the operculum but such could not have been the situation in *Ebenaqua* because as has been shown below, expansion of the lower branchial chamber would have tended to close the operculum. Opening the operculum would then have become a function of the dilator operculi which would have taken origin on the dermosphenotic.

Now the problem becomes one of understanding the mechanism of the dilation and contraction of the branchial chamber, and the synchronization of these movements with the suction activity of the mouth. In attempting to solve this problem the posterior process on the suborbital seems to us to be of critical importance. As indicated above, lateral movement of that plate would lift the subopercular and the lower end of the preopercular, and hence the lower end of the hyomandibula. Note that although the subopercular would be moved laterally, its edge against the cleithrum would be held shut both because its hinge against the preopercular is also being moved laterally, and because the leverage is being applied in front of that hinge. A great deal therefore depends on the means for producing lateral movement in the suborbital.

Lateral movement at the base of the branchial chamber in actinopterygian fishes at all evolutionary grades is produced by contraction of the sternohyoideus muscles acting to draw the hyoid bar backwards and downwards. The bowed hyoid bar pushes laterally and ventrally on the overlying plates, usually the preoperculars and the branchiostegal rays (Alexander 1970, pp. 72–76 for summary). In *Ebenequa* the hyoid bar would push laterally against the lower part of the suborbital and downwards against the branchiostegal plate. The suborbital process would then lift the

subopercular and the preopercular. Note that these movements would not cause the subopercular or the branchiostegal plates to rotate open. The effect of lifting the front of the subopercular would be to close its posterior edge more firmly against the cleithrum, and lifting the anteroventral corner of the operculum would produce the same effect on that bone. Consequently, the effect of dilating the suborbital would be to dilate the branchial chamber as a whole while keeping it firmly closed around its edges.

(f) *Biting/respiration cycle.* The sequence of biting and respiratory movements is extremely difficult to determine from skeletal considerations alone, as the work of Schaeffer and Rosen (1961) and Lauder (1979, 1980*a*, *b*, 1982) has shown. However, what is needed for *Ebenaqua* is the postulation of an internally consistent sequence of movements that would be possible given the proposed skeletal and muscle reconstruction. In proposing this sequence the only other control is what is known of the cycles in primitive modern fishes.

The following cycle of movements and effects seems to be possible given the bone/muscle arrangements postulated above.

1. The jaw begins to drop with relaxation of the adductor mandibulae and the contraction of the sternohyoideus and interhyoideus muscles. The operculum and the hyomandibula are abducted. Water moves through the mouth and into the lower part of the buccal cavity because, although the front of the mouth is laterally contracting a small amount due to the inward movement of the maxillae, it is vertically expanding with the jaw opening and this will probably maintain the volume of the cavity.

2. The further movement of water backwards in the mouth is then accomplished by increasing the volume of the buccal cavity as the hyoid arch pushes the suborbital laterally, thus pushing the opercular series outwards but not opening them, and by expansion of the roof of the mouth on contraction of the levator arcus palatini.

3. The jaw reaches maximum opening and the buccal and lower branchial chambers approach maximum expansion. The operculum remains abducted.

4. The jaw closes rapidly with fast adductor action and relaxation of the interhyoideus and levator arcus palatini muscles. The spreading of the maxillae compensates for the decrease in oral volume caused by the upward movement of the jaws, and at the same time the buccal and lower branchial chambers attain maximum expansion with the sternohyoideus muscles still contracted. A slight sucking of water into the front of the mouth during the completion of the bite holds the soft food in the mouth while it is cut by the scissors-like action of the jaws.

5. The buccal and lower branchial cavities collapse on relaxation of the sternohyoids. The operculum opens on contraction of the dilator operculi and the abduction of the hyomandibula. Because the mouth is closed, water is forced out between the operculum and suboperculum and the cleithrum, and ventrally between the branchiostegal plates. This completes the cycle.

Such a sequence maintains a water flow through the mouth and gill chambers without any reversals; it provides a pump for gill ventilation in a fish that moves slowly and feeds by browsing; it provides a suction in the mouth at the time of biting; and it does not require the action of any anatomical structures that are unknown in living primitive fishes.

The efficacy of the proposed sequence may be thought to depend too heavily on the fine relative timing of the movements—in particular the slight delay in the attainment of maximum expansion of the buccal and lower branchial chambers after the mandible has opened, and the still further delay in the abduction of the operculum. However, such delays have been established in modern fishes at all levels of evolutionary development (Ballantijn and Hughes 1965; Lauder 1979, 1980*a*, *b*, 1982).

Recently Lauder (1980*a*, p. 315) has criticized Hutchinson's suggestion (1973) that redfieldiiform fishes were suction feeders, mainly on the grounds that he had misinterpreted the effects of retraction of the pectoral girdle on pressures in the buccal cavity, but partly on the grounds that these fishes 'lack the morphological features identified here as correlates of a suction-feeding mechanism. The maxilla is fixed to the cheek, an interopercular bone is absent, and a single mechanism exists for mandibular depression.' Similar criticisms could be levelled at our interpretation of *Ebenaqua*, but they have validity only if suction is associated with one type of feeding and is produced by one mechanism.

What we are proposing is a modified set of mechanisms associated with a slow-moving, plant- or soft invertebrate-feeding fish, as opposed to the fast-moving predators studied by Lauder.

(g) *Fins and locomotion.* The striking features of the fins of *Ebenaqua* are: (a) the greatly reduced pectorals and pelvics that have become almost vestigial, and are placed well towards the ventral edge of the animal; (b) the symmetry of the dorsal and anal fins, not only in form and size, but also in the manner of subdivision of the rays; (c) the association of two or three rays with a single baseost, and the increased strength and marginal position of the baseosts towards the posterior ends of both the dorsal and anal fins; (d) the greater length and strength of the rays at the anterior ends of the dorsal and anal fins; (e) the symmetrical outline of the caudal fin; (f) the tendency of the fins to be preserved in similar orientations on most specimens indicating that they had a certain rigidity of ray orientation and were not collapsible.

The effect on movement produced by a heterocercal tail depends primarily on the relative area and flexibility of the dorsal and ventral fin ray lobes (Affleck 1950). In *Ebenequa* the dorsal lobe is long and slender, whereas the ventral lobe has a muscular scale-covered base that bears an array of thick densely clustered rays with long lepidotrichs. These rays together would have given the ventral lobe a rigidity comparable with that of the dorsal lobe. It is interesting to note, therefore, that the distribution of the weaker, more flexible rays with inter-ray membranes tends to be almost symmetrical around the median cleft. The caudal fin, though heterocercal, would have been approximately isobatic.

The swimming capacities of actinopterygians have been summarized recently by Webb (1982), who has emphasized the distinction between steady or time-independent locomotion, and unsteady or time-dependent (acceleration and turning) locomotion. Modern fishes with the general body form of *Ebenaqua*, with their large surface area/volume ratios and poor streamlining, are not adapted to even moderately fast steady locomotion. In addition, the scale rows on *Ebenaqua* stand out from the body producing strong corrugation. Though this is not of sufficient amplitude to penetrate the laminar boundary layer for expected movement velocities if the fish is treated as a rigid body, the thickness of the boundary layer decreases sharply with a flexing body and 'the mean drag of a flexing fish appears to be about 2 to 5 times greater than that of an equivalent non-flexing body' (Webb 1982). Under these circumstances the amplitude of the scale corrugation in *Ebenaqua*, estimated to be about 1 mm on the flanks of a fish 10 cm long, could become significant if the animal engaged in steady locomotion.

On the other hand, *Ebenaqua* has a large caudal fin and body area, long anal and dorsal fins, flexible body, and large muscle mass/body mass ratio, which are considered to be the morphological characters of unsteady movers. The effects of frictional drag are less significant for animals of this kind, inertial drag becoming dominant. Scale corrugation would therefore not be of consequence.

We conclude that *Ebenaqua* belonged to the class of unsteady locomotors, and because it has many of the optimal features of this class it probably had a well-developed capacity to accelerate and produce short darts either to escape predators or to grasp food.

The pectoral and pelvic fins are normally used for manœuvre, balance, and braking. The dorsal and anal fins serve several functions depending on the variety of movements the rays are able to accomplish. When extended they may act with the caudal fin to propel the animal, and in this position they also provide stability in a vertical plane and at the same time they may act as a rudder. In some holosteans and teleosts with long dorsal and anal fins, waves move along extended rays in either direction, and such fin movements provide control on both forward and backward movement, as well as on positive and negative pitch (Harris 1937, 1953; Gosline 1971).

If *Ebenaqua* is an unsteady swimmer, as has been inferred above, there would have been little need for the paired fins to act as brakes. Clearly they were too small, and placed far too low on the body, to be effective in this role in any case. They were also too small to function in any but the smallest equilibrium adjustments. The dorsal and anal fins must therefore have performed these roles. Holosteans and teleosts have flexible fins because of individual muscle control on each ray, but the conventional view is that the fins of primitive actinopterygians, of which *Acipenser* is a modern example, had 'fin muscles arranged like those of sharks and had the same range of fin movements as

sharks' (Alexander 1970, p. 38). If this is true, the range of fin movements in *Ebenaqua* would presumably be too limited to produce the effects required by our analysis. However, no other control mechanism was available in that fish, and therefore we question the conventional view. This is not surprising as the number of living chondrosteans available for observation is very small, and there is no guarantee that they have fin structures representative of the whole group.

In this connection we note that the rays of both dorsal and anal fins become finer and shorter posteriorly, that there is a sudden reduction in ray length and strength after the first few rays, and that the baseosts are apparently strongest and closest to the rays on the posterior parts of the fins. These features suggest to us that both fins were more flexible toward the rear, the site of more powerful muscle insertion on the baseosts. The waves passing along the flexible part of the fin from front to back would decrease in wavelength and presumably provided finer control. The long, relatively less flexible rays towards the anterior extremity of each fin would prevent yawing.

We also note that the orientation of these fins would have promoted positive and negative pitch in an effective fashion. Both fins are set at approximately 60° to the horizontal axis of the fish, and assuming a centre of buoyancy as shown in text-fig. 16 and that the forces produced by undulations act along the length of the fin, these forces would exert a maximum pitching moment.

Waves passing uniformly along each fin from front to back would assist the forward motion produced by the tail. Waves passing uniformly in the reverse direction would act to brake the animal in a straight line or to provide forces to balance the propulsion effects of the respiratory currents and thus allow it to hover in the water. Reverse waves passing at different rates along the two fins would produce braking and either positive and negative pitch (for summary in modern fishes see Lindsey 1978).

This raises the question of buoyancy. Some workers such as Romer (1966) have assumed that chondrosteans were negatively buoyant, and that therefore they had to move at moderate speeds to remain off the bottom. This seems to us to be inherently improbable because many of them were predaceous and had downward driving heterocercal tails, but the pectoral fins were not appropriately placed or shaped to provide lift. Species with these characteristics must have had neutral or positive buoyancy.

Harris (1937, 1953) has shown that asymmetrical undulations caused by movement of the rays at different speeds on opposite sides of the sagittal plane, may produce forces at a high angle to that plane. Large median fins normally produce stability against yaw and roll, but in *Ebenaqua* it may be that they served this function by remaining unflexed when the fish was moving in a straight line, but could induce yaw and roll as required, by wave formation. We believe that they did act in this way because there seem to be no other mechanisms available to produce yaw and roll.
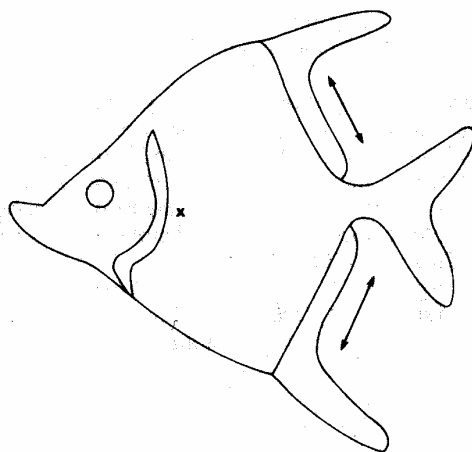


TEXT-FIG. 16. Outline of *Ebenaqua ritchiei* showing directions of movement resulting from the action of the dorsal and anal fins. Note that with the centre of buoyancy placed approximately in the position x on the longitudinal axis, these fins exert maximum torque.

Consequently, we conclude: the animal was a slow mover, capable of short bursts of acceleration; that it had neutral buoyancy; that in the absence of effective pectoral and pelvic fins, the dorsal and anal fins must have been able to brake, pitch, yaw and roll the animal; that to do this requires a capacity to produce waves moving in either direction in each fin; that the arrangement of length and strength of the rays is such as to make these waves possible; that although there are at least two rays to each baseost, this cannot be regarded as inhibiting effective wave formation despite the evidence from living chondrosteans; and that there is no evidence for collapsible dorsal and anal fins.

# APPENDIX

## '*Platysomus gibbosus*' Agassiz

### Plate 10, figs. 1–4; text-fig. 17

Agassiz (1835) nominated five species as members of his new genus, all from the Late Permian in Germany or England. Four of these were placed in synonymy by Woodward (1891) without discussion, and discussed under the specific name *Platysomus gibbosus* (Blainville). The species omitted was *P. macrurus* Agassiz which he had assigned to *Globulodus* Munster, 1842. No systematic review of the remaining species has been attempted, though Schaumberg (1977) continues to use the name *P. striatus* Agassiz, and has figured details of the skull roof, body form, and scales as though the species is distinguishable.

Professor Goujet has sent us photographs of some of Agassiz's figured specimens now housed in the Institute de Paleontologie, Museum National d'Histoire Naturelle, Paris, but these specimens are too poorly preserved to permit interpretations to be made, at least without direct reference to the specimens themselves.

In the absence of a complete analysis of this group, we wish to provide a description of certain Kupferschiefer specimens that are of the *P. gibbosus* type mainly to point out that their relationships are quite different from those currently accepted.

The specimens are: 841-1 Geologisch Paläontologisches Institut und Museum der Universität, Göttingen, from Ilmenau; and 3216–3218 Geological Museum, Copenhagen, from Wolfsberg, Richeldorfer Gebirge.

The Göttingen specimen is preserved as an external impression in a concretion, and hence has some relief. This permits the bone outlines to be traced more easily than on the flattened specimens. The surface detail also is well preserved. The Copenhagen specimens are almost completely flattened in a slightly calcareous siltstone. The bone can be removed with dilute hydrochloric acid causing little damage to the matrix, and this has been done for one head, 3217, with good results.

Emphasis is placed on details of cranial morphology because these indicate the relationships of the species most clearly. Only the main points of postcranial morphology are mentioned. A more complete description, and a discussion of the taxonomy of this species, will await work on the abundant material in European museums.

*Description.* The post-temporal is large, and rather rounded in outline medially. The lateral line canal has an angular bend at its radiation centre, which is below its topographic centre. The two extrascapulars are long and narrow, the median being smaller than the lateral. The parietal and dermopterotic are present but their lateral-line connections are not clear, and the shape of the dermopterotic is apparently different in the two specimens in
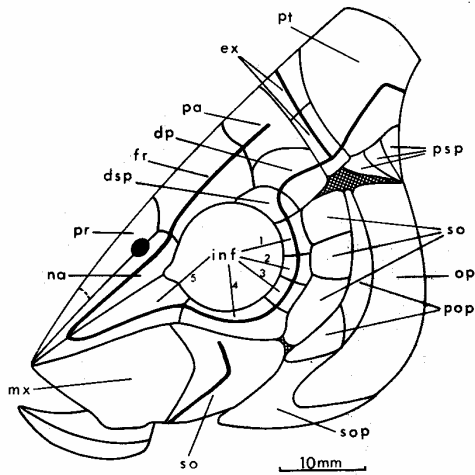
TEXT-FIG. 17. Reconstruction of the head of '*Platysomus gibbosus*' based largely on specimen 841-1 Geologisch-Paläontologisches Institut und Museum, Göttingen.

which it is preserved. The best estimates of outlines and canals are given in text-fig. 17. The frontal is a long bone, and seems to reach to the upper edge of the eye where it forms an inflected flange. The post-rostral and the nasal are both long and splinter-like, their anterior edges being obscured on all our specimens. The anterior naris is well preserved, and lies on the junction between these bones.

Between the rostrum and the dermosphenotic are five infraorbitals, the most anterior one of which is very long. Infraorbitals 4 and 5 have a loose overlapping contact with the maxilla and the bone behind it. The lateral line canal can be distinguished running around the complete set, and sends off short tubules towards the eye on the three bones in the post-orbital position. The canal on to the dermosphenotic is not clear, and text-fig. 17 shows the best estimate of its position. Behind the infraorbitals there are three bones that can only be suborbitals. The upper two are almost square, but the third is elongate and runs ventral to meet the end of the bone behind the maxilla that in *Ebenaqua* we have referred to as a suborbital. As can be seen from the text-figure, it is in series with the suborbitals, and we refer to it in this species as the anterior suborbital. Its suture against the maxilla is convex backwards, unlike that of *Ebenaqua*. The Göttingen specimen shows that the suture is of the overlapping type, and runs concordantly with the ornament so that it is normally difficult to observe. Moreover, it is possible that in adults these bones tend to become fused. The lateral line on this bone is clear. It enters the bone obliquely from the overlying skin, runs ventrally to the ossification centre, and then turns abruptly to run a course to the anteroventral corner.

The maxilla is large and edentulous, and along its ventral edge there is a curved, lenticular expansion that probably added to the slicing effect of the bite.

There are clearly two preoperculars forming a thin boomerang-shaped outline and making contact with the posterior extremity of the anterior suborbital. Apart from the fact that they touch we can add nothing to the relationship between these bones.

On the Göttingen specimen three postspiraculars can be distinguished. The region is badly broken, but there is little doubt that the anterior edge of the middle one is strongly curved. The operculum is a long, narrow,

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**EXPLANATION OF PLATE 10**

'*Platysomus gibbosus*' Agassiz

Figs. 1-3. Latex cast of specimen 841-1 Geol. Pal. Inst. und Mus. der Univ., Göttingen, from Ilmenau. 1, 2, photographed in different lights to show details of the opercular and suborbital regions. 3, shows the detail of the scales on the anteromedian part of the flank. Note the peg and socket arrangement on the lower left.

Fig. 4. Latex cast of specimen 3217 Geological Museum, Copenhagen, to show details of the ornament pattern on the head bones, the overall size of the mandible, and the branchiostegal rays.

All scale bars are 10 mm long.

PLATE 10
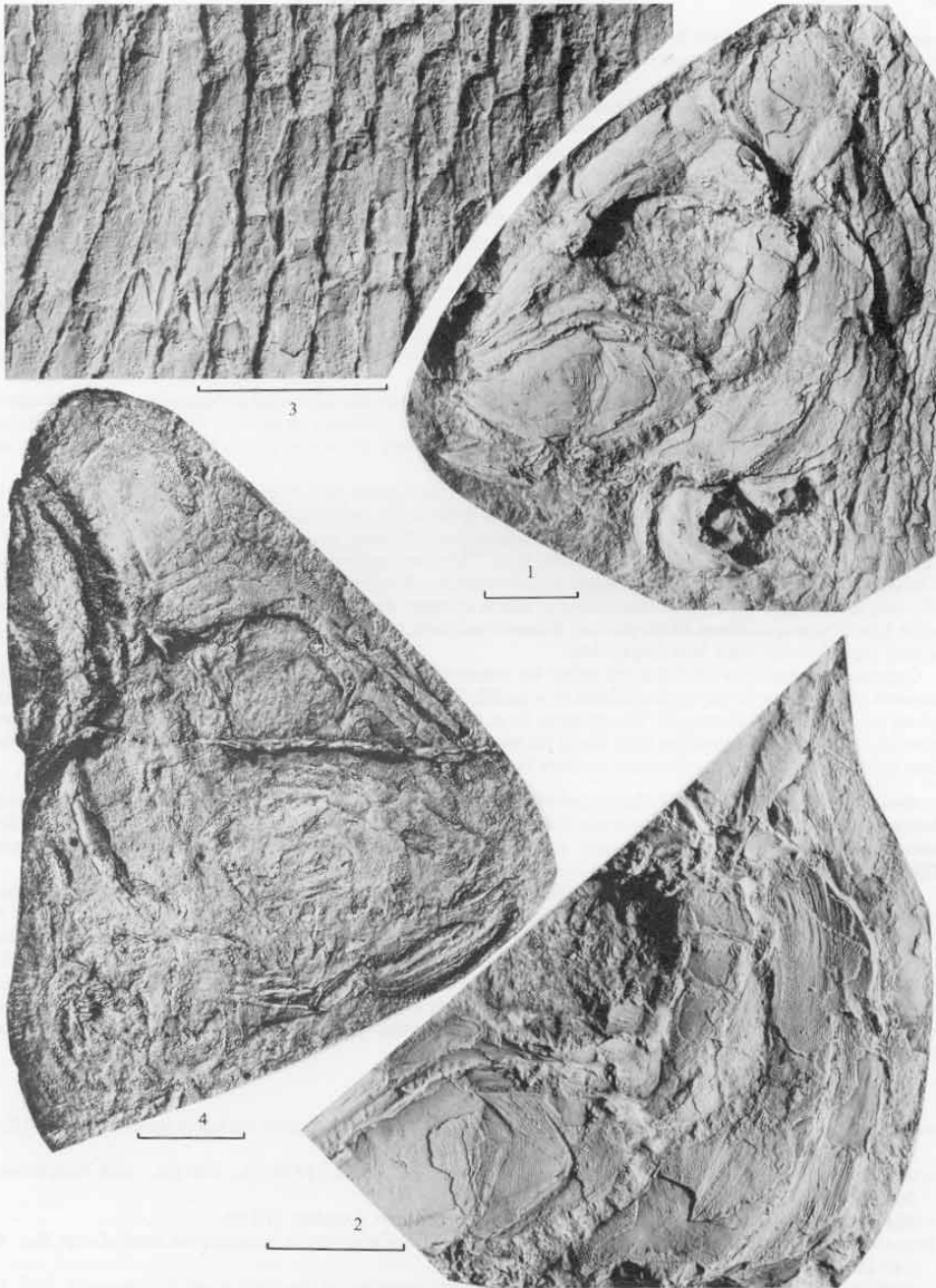


CAMPBELL and PHUOC, Late Permian Actinopterygian fish

approximately parallel-sided bone that extends well round to a point beneath the posterior end of the anterior suborbital. It overlaps, in a deep rounded V, the much smaller suboperculum, which extends around below the anterior suborbital.

Preservation of the bones below the suboperculum is not good, but 3217 in the Copenhagen collection seems to have a broad plate made of about five posteriorly joined branchiostegal elements that are free at their anterior ends, producing a deeply serrated edge. There is probably also at least one free branchiostegal ray.

The cleithrum and supracleithrum are strong bones. Ventrally there is a deep embayment in the cleithrum for the pectoral fin.

The mandible is lancet-like in outline but in section it is narrow dorsally and abruptly expanded ventrally below a keel. The articulation lay beneath the posteroventral end of the maxilla. The individual bones cannot be distinguished but the lateral line is well developed, and runs the full length of the jaw below the keel.

The ornament of the dermal bones is very similar to that of *Ebenaqua*, consisting predominantly of striae on the lower bones of the head, but breaking up into nodes on the upper ones. The operculum is very distinctively ornamented; in addition to the vertical striae that run approximately parallel to its edge, there are finer oblique lines that abruptly strengthen and hook around as they cross the mid-length of the bone forming a pronounced series of invaginated U's.

The body scales and their ornament are also of the same type as *Ebenaqua* and *Bobasatrania*, with evidence of articulation by long blade-like pegs and shallow furrows between scales in the same vertical rows. Posteroventrally the scale rows turn abruptly and run obliquely to the margin. In this they appear to be less regular and more oblique than those of *Ebenaqua*.

The dorsal and anal fins are both situated well behind the deepest part of the body, and the anterior rays in each are the longest. The dorsal fin is short and may have as few as thirty rays, the precise number not being determinable on our material. The anal fin is much longer, extending almost to the caudal peduncle, where the rays form a very short fringe only about 2 mm long. There are approximately seventy to eighty rays in the fin. The dorsal lobe of the caudal fin continues to the extremity. It is long and acute, being 35 mm long in a fish of 125 mm total length. Its crest carries twelve to fifteen strongly overlapping ridge scales. The caudal fin has the same type of construction as *Ebenaqua* and *Bobasatrania* with strong closely packed ventral rays and thin, more widely spaced dorsal ones. It is deeply cleft.

Copenhagen specimen 3218 has the pelvic fin preserved. It is small, being approximately 5 mm long, and consists of sixteen to twenty rays attached to a paddle-like base. It is situated low on the flank about half-way along the posteroventral margin. The pectoral fin is a larger structure consisting of possibly as many as thirty powerful primary rays extending back along the body. Their posterior extent is not shown on our material, but they must extend back some distance, possibly in the manner of *Bobasatrania*.

*Remarks.* Despite the defects in the available material, enough is known to highlight the remarkable similarity between this species and the Bobasatraniformes. Though not mentioned above, there are other features that seem to add to these similarities, such as the position and shape of both the axonosts and baseosts. Unfortunately, they are not well-enough preserved in our material to warrant description.

Attention is drawn to the fin pattern. The pelvic fin is quite unlike that of *Ebenaqua* in both form and position, and *Bobastrania* seems to have lost its pelvic fins. Both dorsal and anal fins are much shorter and weaker in '*P. gibbosus*' than in the above genera, whereas the pectoral fin is much stronger than that of *Ebenaqua* and at least as strong as that of *Bobasatrania*. From a functional point of view, '*P. gibbosus*' was clearly a scissors-type feeder that depended for on its pectoral and pelvic fins for locomotory control more than did *Ebenaqua* and *Bobastrania*. It also has unreduced suborbitals, a relatively undeveloped snout, and a complex branchiostegal arrangement. In all these features, '*P. gibbosus*' is the most primitive-known member of the Bobasatraniformes.

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