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Postilla

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GLYPTOLEPIS FROM THE MIDDLE DEVONIAN OF SCOTLAND

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INTRODUCTION

The Rhipidistia (Osteichthyes, Crossopterygii) comprise three superfamilies of Paleozoic fossil fishes, the Holoptychoidea, Osteolepoidea and Rhizodontoidea. Of these the members of the Holoptychoidea (families Holoptychidae and Porolepidae) are by far the least well known, and consequently there exists a considerable gap in our knowledge of the evolution of the Rhipidistia as a whole. The aim of this paper is to fill a small part of this gap by describing an unusually well-preserved specimen belonging to the holoptychid genus *Glyptolepis*. The specimen shows a considerable portion of the cranial anatomy, particularly the skull roof, and provides new information which is useful in determining the relationships of *Glyptolepis* to other members of the Rhipidistia.

DESCRIPTION

The subject of this short description is a single specimen, number RSM 1964.18, in the collections of the Department of Geol-

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ogy, Royal Scottish Museum, Edinburgh. No locality record exists for this specimen which was probably collected in the last century. It is preserved in a rather hard grey sandstone and comparison of the matrix with other specimens from the collections of the Royal Scottish Museum suggests most strongly that the specimen comes from one of the Middle Devonian Old Red Sandstone localities in Caithness, Scotland and that it was probably collected on the East Foreshore at Thurso.

The specimen consists of the skull and a small anterior portion of the trunk of a very large rhipidistian fish belonging to the family Holoptychidae. In life the fish would have measured about one metre in total length. The structure of the scales (judged according to Ørvig, 1957) and general structure show that it belongs to the genus *Glyptolepis*. The Middle to Upper Devonian genus *Glyptolepis* is currently known to be represented in the Old Red Sandstone of Scotland by two species, *G. leptopterus* Agassiz and *G. paucidens* (Agassiz), of which only the latter is found at Thurso (among other places). One or more species of *Glyptolepis* occur in the famous Upper Devonian deposits of Scaumenac Bay, Quebec Province, Canada (see Ørvig, 1957), and fragmentary remains, the taxonomic position of which is uncertain, are known from localities in East Greenland and continental Europe (see Jarvik, 1950). Except for the single feature of its extremely large size the specimen described here accords very well with material of *G. paucidens* that I have studied. However, in view of the rather unsatisfactory state of our knowledge of the holoptychoid Rhipidistia, the uncertainty of the exact provenance of the specimen, and its unusually large size, it seems best to refer the specimen provisionally to the taxon *Glyptolepis* cf. *paucidens*.

The dorsal surface of the specimen was partially obscured by a thin film of matrix which was removed in the laboratory by slow etching with dilute formic acid.

The ornament of the dermal bones of the skull roof and cheek consists of a large number of irregularly but closely spaced separate tubercles. In the ornamentation of the external surfaces of the dermal bones of the lower jaw and gular series the tubercles have a tendency to become joined together to form an anastomosing network of ridges arranged so as to enclose a series of small

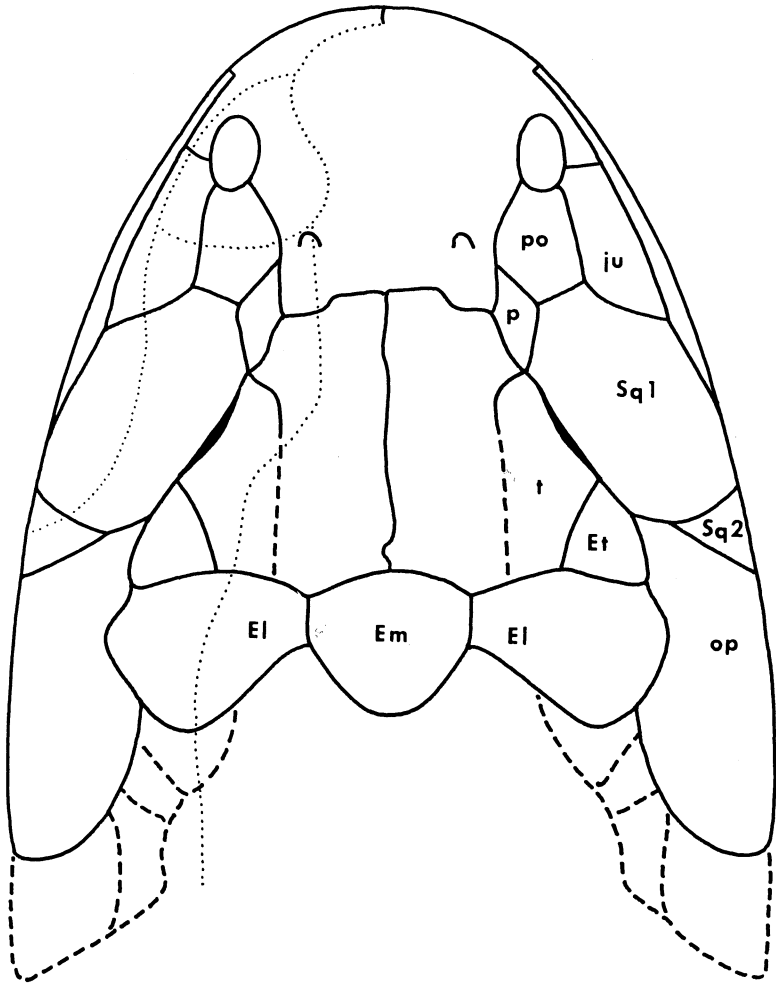


Figure 1. *Glyptolepis* cf. *paucidens*. Restoration of skull in dorsal view. $\times \frac{2}{3}$.

Abbreviations for this and following figures

add 1,2,3	Adductor mandibulae muscles 1,2,3	p	prespiracular plate
El	lateral extrascapular	po	postorbital
Em	median extrascapular	pp	preopercular
Et	Extratemporal	pq	palatoquadrate
ju	jugal	qj	quadratojugal
mx	maxilla	Sq	squamosal
op	operculum	Sq 1,2	squamosal 1,2 (Holoptychoidea)

depressions in a manner more closely resembling the pattern of ornamentation seen in rhizodontoid Rhipidistia.

Throughout the whole specimen suture lines are rather difficult to discern, and it seems that most of the dermal bones had become fused one to another at least superficially. However a few traces of the sutures and the location of some of the pit-lines and of portions of the lateral line system enable us to determine the general dermal bone arrangement. Unfortunately no details in the ethmoid region could be seen.

Plates 1 and 2 give a general view of the specimen and in Figures 1 and 2 an attempt has been made to reconstruct the whole skull. The illustrations will serve *in lieu* of a lengthy verbal description, but special note may be taken of certain of the more interesting structural features, which are of interest in interpreting the morphology of other holoptychoid Rhipidistia.

DISCUSSION

The skull of holoptychoid fishes, as far as is known, differs in several interesting ways from that of the osteolepoid or rhizodontoid Rhipidistia. As clearly shown in the specimen of *Glyptolepis* described here, there is no separate intertemporal bone in the skull roof and similarly a supratemporal is lacking — apparently it is combined with the postparietals. A dermal element found in holoptychoids but absent in the other Rhipidistia is the small bone which Jarvik (1948) terms the “prespiracular plate.” This lies between

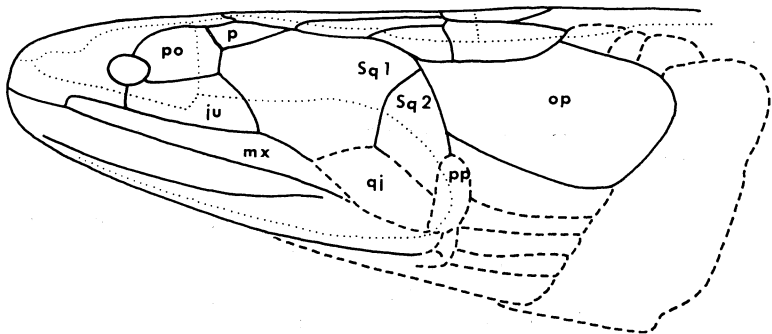


Figure 2. *Glyptolepis* cf. *paucidens*. Restoration of skull in left lateral view. $\times \frac{1}{3}$ approx.



Plate 1. *Glyptolepis* cf. *paucidens*.
Skull in dorsal view.
RSM 1964.18 $\times \frac{1}{3}$.



Plate 2. *Glyptolepis* cf. *paucidens*.
Ventral view of specimen
shown in Plate 1.
RSM 1964.18 $\times \frac{1}{3}$.

the parietal and postparietal shields and the postorbital and squamosal. In *Holoptychius* (family Holoptychidae), as described by Jarvik (1948, 1950, 1963), a short, blind branch of the supraorbital lateral line canal passes backwards onto the prespiracular plate from the union of the supraorbital and infraorbital lateral lines in the 'intertemporal' region of the parietal shield (Fig. 3). Jarvik (1950) states that this short unit of the lateral line system is not found in other holoptychoids and I am able to confirm that it is absent in the specimen described here and all other material of *Glyptolepis* that I have studied. It is interesting to note the differences in size and position of the prespiracular bone that occur within the Holoptychoidea. In the Lower Devonian (or possibly Middle Devonian, see Jarvik, 1950, p. 124) *Porolepis* (family Porolepidae) from Spitzbergen (Figure 3) the prespiracular is very large and has a contact with the extratemporal (Jarvik, 1950); in the Middle Devonian *Laccognathus* (family Holoptychidae) (Figure 3) and the Middle Devonian *Glyptolepis leptopterus* (Figure 3) and especially the specimen of *Glyptolepis* cf. *paucidens* (Figure 1) the prespiracular plate is slightly smaller, but in all three genera it extends anteriorly beyond the parietal-postparietal suture. In the Upper Devonian *Holoptychius* (Figure 3) the prespiracular plate extends only very slightly in front of the line of the parietal-postparietal suture; it is small (although not as small as in *Glyptolepis* cf. *paucidens*) and moreover contains the lateral line canal previously mentioned. It is difficult to determine the functional or adaptive significance of such a considerable change within this superfamily, especially when the pattern of the skull roof in other Rhipidistia is generally rather more stable. One point which may be of importance, however, is that reduction of the size and anterior extent of the prespiracular in the series *Porolepis-Laccognathus-Glyptolepis-Holoptychius* (this is not postulated as a direct phyletic sequence) seems to be accompanied by an increase in the relative size and a progressively more posterior position of the orbit.

The Upper Devonian genus *Holoptychius* is the only member of the holoptychoid superfamily in which the structure of the dermal cheek complex region has been described in detail (see Westoll, 1937; Jarvik, 1948, 1950, 1963). In *Holoptychius* (Figure 3) the "squamosal" region of the cheek is made up of more than one

element and the jugal lateral line canal passes along two main bones, squamosals 1 and 2, before turning ventrally to the infradentary series of the lower jaw through a "preopercular" bone. This last element lies posterior to both the "squamosal 2" and the quadratojugal and does not appear to be homologous with the preopercular of other fishes. In the specimen of *Glyptolepis* discussed here and most other holoptychoid material the postero-lateral corner of the cheek has not been well preserved and it is difficult therefore to see whether a preopercular of the kind seen in *Holoptychius* is present or not. However, the shape and size of the "squamosal 2" bone in our specimen of *Glyptolepis* clearly suggest that if such a bone were present it must have been of small size, as restored

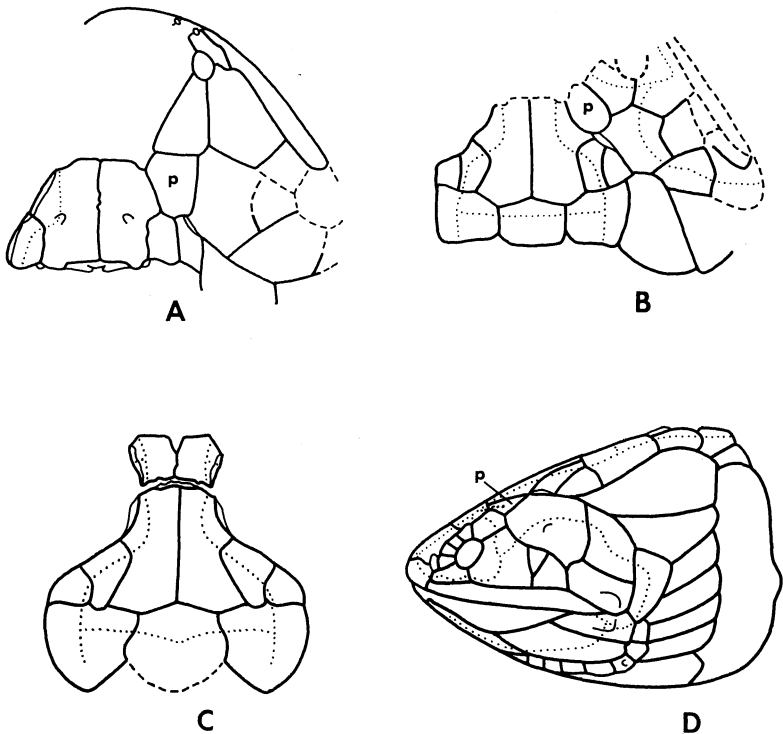


Figure 3. Dorsal aspect of the skull in holoptychoid fishes. A. *Poro-lepis* sp. B. *Laccognathus panderi*. C. *Glyptolepis leptopterus*. D. *Holoptychius flemingi*. (A, B and C redrawn from Jarvik, 1950 and D redrawn from Jarvik, 1963.)

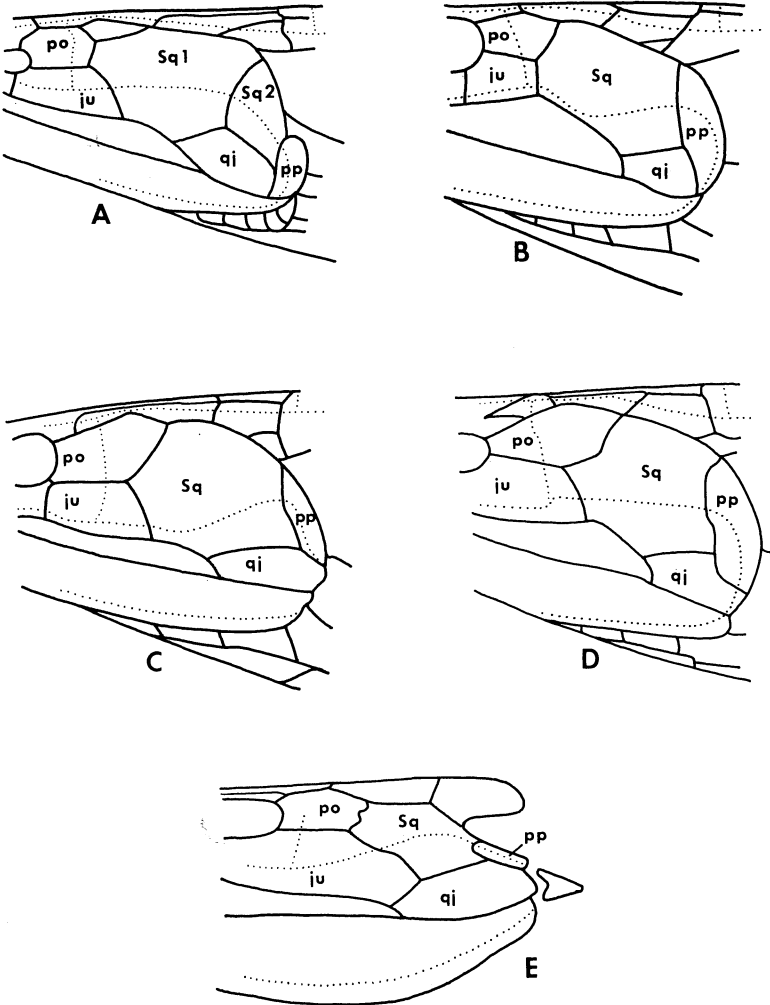


Figure 4. Lateral view of posterior cheek plate of A. *Glyptolepis* cf. *paucidens*. B. *Osteolepis macrolepidotus*. C. *Gyroptychius agassizi*. D. *Eusthenopteron foordi*. E. *Ichthyostega* sp. (B and C redrawn from Jarvik, 1948; D redrawn from Jarvik, 1944, E redrawn from Jarvik, 1952.)

in Figure 4. Comparison of the cheek in *Glyptolepis* with that of Rhipidistia of the other superfamilies (Figure 4) suggests that the bone termed "squamosal 2" in holoptychoids is homologous with the preopercular of other forms and that the holoptychoid preoper-

cular is lost. The course of the lateral line canal in the cheek in various Rhipidistia gives support to this hypothesis. Thus in the Middle to Upper Devonian *Osteolepis* (Säve-Söderbergh, 1933) the preopercular bone is of fair size and extends ventrally behind the quadrato-jugal so that the preopercular lateral line passes from preopercular to infradentary without passing through another bone (Figure 4B). Apparently, as Säve-Söderbergh suggests, the lateral line was continued in soft tissues behind the quadrato-jugal. In apparently more advanced osteolepoids such as the Upper Devon-

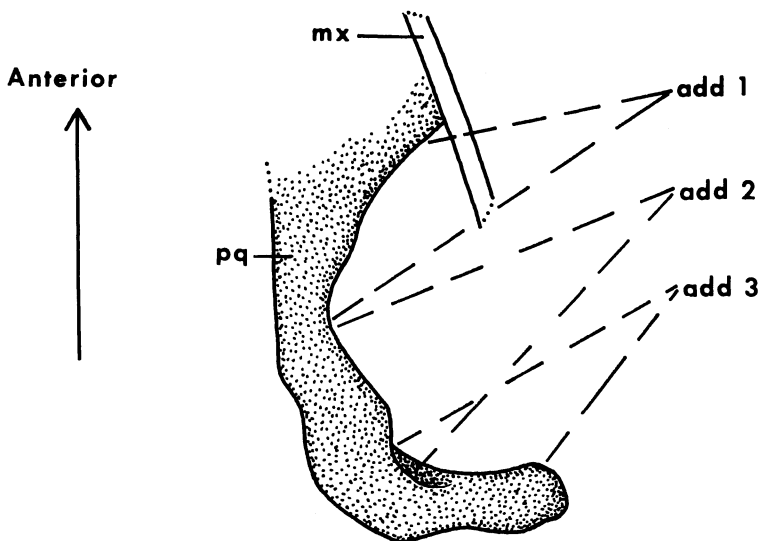


Figure 5. *Glyptolepis* cf. *paucidens*. Ventral view of left subtemporal fossa.

ian genus *Gyroptychius*, as exemplified by *G. agassizi* (Figure 4C), the preoperculum is more directly comparable in size and extent to the squamosal 2 of holoptychoids and it does not extend ventrally behind the quadrato-jugal. Since the lateral line canal emerges from the posterior margin of the preopercular it is thus separated from the infradentary bone by a considerable gap. In rhizodontoids, such as *Eusthenopteron*, as described by Jarvik (1944) the preoperculum is slightly smaller than in *Gyroptychius* and the lateral line canal now turns ventrally to pass through the

posterior corner of the quadrato-jugal in its passage to the infradentary bone series (Figure 4D). It is interesting (but probably irrelevant) to observe that in the amphibian *Ichthyostega* (Figure 4E) the preopercular is much reduced but the preopercular lateral line canal is arranged much as in *Gyroptychius* and does not enter the quadratojugal.

The specimen shows almost the whole of the palato-quadrate rim of the subtemporal fossa and is sufficiently large and well preserved to show some detailed structure in this region. The anterior corner of the fossa in *Glyptolepis*, unlike that of an osteolepid such as *Ectosteorhachis*, has the shape of an acute angle. This indicates that the anterior sections of the adductor mandibulae musculature must have acted at an angle to the maxilla, whereas in *Ectosteorhachis*, where the anterior corner of the fossa is a smooth surface perpendicular to the maxilla, the line of action of these muscles was more directly in line with the maxilla and mandible. Various markings on the rim of the fossa (Figure 5) suggest that the adductor mandibulae musculature was arranged in three portions corresponding approximately to the anterior, middle and posterior pterygoids of tetrapods (cf. Olson, 1961, p. 209).

The result of this study is to show that, despite significant differences in structure between the three superfamilies of Rhipidistia, a general evolutionary continuity may be discerned linking all three groups in a common morphological framework.

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