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RHINOPTERASPIS CORNUBICA (McCOY), WITH NOTES ON THE CLASSIFICATION AND EVOLUTION OF THE PTERASPIDS

Abstract. — The snout and mouth-parts of *Rhinopteraspis cornubica* (McCoy) (syn. *R. dunensis* (Roemer)) are described for the first time in specimens from Daleszyce (Central Poland) and Overath (Rhineland). An analysis is made of the various types of snout known in the pteraspids, and diagnoses are given of important genera based on this feature. Evolutionary trends within the pteraspids are outlined, and it is demonstrated that the long-snouted condition was achieved in two distinct ways. It is suggested that the possession of double nasal sacs excludes the pteraspidomorphs (heterostraci) from the ancestry of the myxinoid cyclostomes.

INTRODUCTION

As a result of their detailed work on the pteraspids in recent years, White and Stensiö have demonstrated the importance of the characters of the snout region when considering the taxonomy of the order. For this reason, the discovery of a snout of *Rhinopteraspis cornubica* in the Holy Cross Mountains of Central Poland (Tarlo, 1958) is of some significance, as the mouth-parts and pre-oral region hitherto unknown in this species are well preserved and a full diagnosis can be given of the genus of which it is the type species. At the same time, it is the first pteraspid to be identified from the Placoderm Sandstone of the region, and enables the correlation of the latter with the Emsian of Western Europe.

The snout was originally identified as belonging to *Pteraspis dunensis* (Roemer). However, a subsequent comparison of the types of *Pteraspis cornubica* (McCoy) and *P.dunensis* confirmed Lankester's (1868) view that they represent a single species and that *P.cornubica* has priority, and this name must therefore be used both for the new specimen and for material previously referred to *P.dunensis*. In addition, so many different forms of pteraspid are now known that it is no longer feasible to retain them all within the single genus *Pteraspis* and, as will be shown, the characters of the snout of *P. cornubica* require that it be placed within a separate

genus. The generic name *Rhinopteraspis* which was proposed by Jaekel (1919) for *P. dunensis* has since become established in the literature, and it is therefore considered appropriate to retain it here for *P. cornubica*.

Modern knowledge of the pteraspids is largely due to the work of White (1935, 1938, 1950, 1956, 1958, 1960) who established a classification based on the general proportions of the carapace and in particular of the rostral and cornual plates, as well as on the characters of the ventral surface of the snout. In the main this classification has been followed by Denison (1953, 1960) and Schmidt (1959). In 1958 however, Stensiö published an extensive account of the morphology of the pteraspids, with particular emphasis on the snout region, and on the basis of this information he introduced many new generic and specific names. As the introduction of so many new names unrelated to White's classification is extremely confusing, an attempt is made in this paper to produce a synthesis of the two systems, and diagnoses are given of the more important genera.

Although it has long been recognized that the earliest pteraspids were small and narrow with blunt snouts, and that the late ones were of two main types — broad and blunt snouted, and narrow and long snouted — hitherto no attempt has been made to trace the manner in which the two contrasting shapes could have evolved. The main evolutionary trends are here given in outline, and with the aid of the Polish specimen it is established that the long-snouted condition evolved independently in two distinct ways.

Finally, the arrangement of the mouth parts of *R. cornubica* is seen to be relevant to a discussion of Stensiö's theory on the internal structure of the pteraspid snout, and it is felt that the evidence does not support his view that the heterostracans (pteraspidomorphs) gave rise to the myxinoid cyclostomes.

DESCRIPTIONS

Family **Pteraspidae** Huxley, 1858

Genus *Rhinopteraspis* Jaekel, 1919

Rhinopteraspis cornubica (McCoy)

(pl. I, II; text-fig. 1, 2 *c*, *d*, 3)

1847. „A striated piece of fish"; C. W. Peach, On the fossil geology..., pl. 2, fig. 7, 8.
1851. *Steganodictyum cornubicum* n. sp.; F. McCoy, On some new..., p. 482-3.
1854. *Steganodictyum cornubicum* McCoy; F. McCoy, Contributions..., p. 233-4.
1854. *Palaeonteuthis daunensis* n. sp.; F. Roemer, Über die Ergebnisse..., p. 650 (name only).
1855. *Steganodictyum cornubicum* McCoy; F. McCoy, British Palaeozoic... pl. 2 A, fig. 1-3.

1855*a*. *Palaeoteuthis dunensis* n. sp.; F. Roemer, Palaeoteuthis..., p. 72-4, pl. 13.
1855*b*. *Archaeoteuthis dunensis* (Roemer); F. Roemer, Kohlen-Periode..., p. 520.
1858. *Archaeoteuthis dunensis* (Roemer); F. Roemer, Notitz..., p. 55-6.
1861. *Pteraspis dunensis* (Roemer); T. H. Huxley, Pteraspis dunensis..., p. 163-6.
1868—70. *Scaphaspis dunensis* (Roemer); E. R. Lankester, The Cephalaspidae, p. 19-20, text-fig. 10.
1868. *Scaphaspis cornubicus* (McCoy) (syn. *Pteraspis (Archaeoteuthis) dunensis* (Roemer)); H. Woodward, Fish remains..., p. 247-8.
1868. *Scaphaspis cornubicus* (McCoy) (syn. *Scaphaspis dunensis* (Roemer)); E. R. Lankester, On the discovery..., p. 547.
1880. *Scaphaspis cornubicus* (McCoy) (syn *Scaphaspis dunensis* (Roemer)); C. W. Peach, On fossils..., p. 94-5.
1882. *Scaphaspis cornubicus* (McCoy); J. E. Lee, Notice..., p. 104-6, pl. 3, fig. 2, 3.
1891. Pteraspid gen. indet. *dunensis* Roemer; A. S. Woodward, Catalogue..., p. 174.
1891. Pteraspid gen. indet. *cornubicus* McCoy; A. S. Woodward, *Ibid.*, p. 175.
1893. *Pteraspis cornubicus* (McCoy); J. H. Collins, A working list..., p. 477.
1899. *Pteraspis cornubica* (McCoy); A. S. Woodward, On some new specimens..., p. 229-232.
1900*a*. *Pteraspis cornubica* (McCoy); H. Fox, Geological notes, p. 356, pl. 16, fig. 7, 8.
1900*b*. *Pteraspis cornubica* (McCoy); H. Fox, Notes on the geology..., p. 148, pl. 7, fig. 7, 8.
1904. *Pteraspis dunensis* (Roemer); F. Drevermann, Über Pteraspis..., p. 275-89, pl. 19-21.
1906. *Pteraspis cornubicus* (McCoy); R. H. Traquair, Notes on fish remains..., p. 11.
1906. *Pteraspis cornubica* (McCoy); C. Reid & J. B. Scrivenor, The geology..., p. 5, 8
1909. *Pteraspis cornubica* (McCoy); W. A. E. Ussher, G. Barrow & D. A. McAlister, The geology..., p. 14.
1912. *Pteraspis cornubica* (McCoy); W. A. E. Ussher, The geology..., p. 24.
1919. *Rhinopteraspis dunensis* (Roemer); O. Jaekel, Die Mundbildung..., p. 74, text-fig. 1 D.
1933*a*. *Pteraspis dunensis* (Roemer); W. Gross, Die unterdevonischen Fische..., p. 44-52, pl. 1, fig. 1, 5; pl. 2; pl. 3, fig. 1-5; text-fig. 1-3, 4 A-G.
1933*b*. *Pteraspis dunensis* (Roemer); W. Gross, Die Wirbeltiere..., p. 7, 8.
1935. *Pteraspis cornubica* (McCoy); E. I. White, The ostracoderm..., p. 443.
1937. *Pteraspis dunensis* (Roemer); W. Gross, Die Wirbeltiere..., p. 7-9, pl. 1, fig. 6.
1938. *Pteraspis (Rhinopteraspis) dunensis* (Roemer); E. I. White, New pteraspids..., p. 87, 110—112, text-fig. 26.
1938. *Pteraspis cornubica* (McCoy); E. I. White, *Ibid.*, p. 112.
1948. *Pteraspis (Steganodictyum) cornubica* (McCoy); H. Dewey, South-west England, p. 17, pl. 12, fig. 1.
1952. *Pteraspis (Archaeoteuthis) dunensis* (Roemer); G. Wängsjö, Morphologic and systematic studies..., p. 583.
1956. *Pteraspis (Rhinopteraspis) dunensis* (Roemer); E. I. White, Preliminary note..., p. 1-10, text-fig. 4.
1956. „*Pteraspis cornubica*" (McCoy), E. I. White, *Ibid.*, p. 4.
1957. *Pteraspis dunensis* (Roemer); K. Fahlbusch, Pteraspis..., p. 1-56, pl. 1-7, text--pl. 1-7, text-fig. 1-27.
1958. *Rhinopteraspis dunensis* (Roemer); E. I. White, Original environment..., p. 230-2, text-fig. 8.
1958. *Pteraspis dunensis* (Roemer); L. B. Tarlo, Specimens of ostracoderms..., p. 8, 9.

1959. *Pteraspis (Rhinopteraspis) dunensis* (Roemer); Wo. Schmidt, Grundlagen..., p. 7, 23-6, 41-52, pl. 2, fig. 8, text-fig. 1(4), 3, 4(1), 7, 8.
1960. *Pteraspis (Rhinopteraspis) dunensis* (Roemer); E. I. White, Notes on pteraspids..., p. 8, 134, text-fig. 5, 6.
1960. *Rhinopteraspis dunensis* (Roemer); L. B. Tarlo, The Downtonian ostracoderm..., p. 224, text-fig. 7 b.

Lectotype (here chosen): Dorsal median plate A. 6955a, housed in Sedgwick Museum, Cambridge, part figured by McCoy (1855, pl. 2 A, fig. 3), re-figured by Dewey (1948, pl. 12, fig. 1), complete specimen figured in present paper (pl. I).

Type locality and horizon: Lantic and Lantwit Bays (Llantivet Bay), near Polperro, Cornwall, England; Black Devonian Shale (Dartmouth Slates), Siegenian — Emsian, Lower Devonian.

Diagnosis. — Pteraspid with elongated, blade-like snout; triangular pre-oral field formed as single synchromorial unit; well developed ascending lamella; oral plates stoutly built; olfactory grooves present; coarse ornamentation of dentine ridges (3—6 mm).

History of the species

Although Peach recorded fish remains from the Devonian slates of Cornwall in 1843, and figured a recognizable fragment of a pteraspid in 1847, similar fish remains were described by McCoy (1851) as polyzoa. He erected the new genus *Steganodictyum* for them and recognized two species — *S. cornubicum* and *S. carteri*, and despite the fact that McCoy was alone in assigning this material to an invertebrate phylum, the names he introduced remain valid. Later *S. carteri* was referred by Lankester (1868) to *Cephalaspis*, but a re-examination of the type material now establishes that it should be placed within the genus *Drepanaspis*.

The type species *S. cornubicum* was also referred by Lankester (1868) to *Scaphaspis* (= *Pteraspis*, see White, 1935) and at the same time he pointed out that there were no grounds for distinguishing *Scaphaspis cornubicus* from *Pteraspis dunensis* (Roemer, 1855). This view was accepted by H. Woodward (1868) and by Peach, Huxley and Symonds (1880), and it is confirmed by an examination of McCoy's type material, here figured as plate I. The ornamentation is identical to that found in *P. dunensis*, in which the density of the dentine ridges is very characteristic, and hence, as Lankester pointed out, material formerly referred to *P. dunensis* most now bear the specific name *P. cornubica*, since McCoy's name has priority.

It has been the practice in the past to refer all Cornish pteraspids to *P. cornubica*, but White (1956) noted that three distinct species — *P. dunensis*, *P. leachi* and a species of *Protaspis* — have all been included under this name. His forthcoming detailed description of the Cornish pteraspids will therefore be of considerable value, as it will clarify this confused situation.

Similarly, in the Ardennes-Rhineland region, the name *P. dunensis* has been used indiscriminately for all large pteraspids, and in particular for the long-snouted forms. But White (1956) again brought order to this confusion, as he was able to show for example, that material ascribed to *P. dunensis* by Leriche (1912, 1924, 1925, 1926, and 1948) actually belonged to *P. leachi*.

Since recent work has shown that it is no longer convenient to retain the different forms of pteraspid within the single genus *Pteraspis*, considerable difficulty has arisen in establishing the correct generic designation of important species. Jaekel (1919) proposed the new genus *Rhinopteraspis* for *P. dunensis* (Roemer) and this name has become established in the literature, although Roemer's earlier generic name *Archaeoteuthis* had priority. White and Ball (1955) gave cogent reasons for the validation of the generic name *Rhinopteraspis* by the suppression of *Archaeoteuthis*, but as *P. dunensis* is now shown to be a synonym of *P. cornubica*, *Archaeoteuthis* automatically becomes a synonym of *Steganodictyum*. However, as the arguments employed by White and Ball apply with even greater cogency to the suppression of *Steganodictyum*, which has found no place whatsoever in the literature, it is proposed to accept Jaekel's genus *Rhinopteraspis* as valid, and *R. cornubica* thus becomes the type species of this genus.

Description of Polish specimen

The specimen which is preserved as a natural mould, comes from the Placoderm Sandstone of Daleszyce, near Kielce, Central Poland (Tarlo, 1957). Originally, all that could be seen, was the natural cast of the inside of the snout and the lateral margins of the ventral surface. When latex casts were made however, the internal part of the snout broke away and revealed the presence of the entire ventral surface of the rostrum, including the pre-oral field, ascending lamella and oral plates[1] (see pl. II and text-fig. 1).

The posterior part of the rostral plate can be seen in ventral view, while the dorsal surface of the rostrum, which is considerably longer than the ventral part, is seen in internal view. The lateral margins of the rostral plate gradually converge anteriorly, and on the ventral surface a well marked groove can be seen on either side. These grooves which are near the edge of the plate,run parallel to the lateral margins. The posterior part of the ventral surface is occupied by a raised triangular area, the pre-oral field, from which the ascending lamella slopes away to

[1] Terminology used in the description of the pteraspid snout varies from one author to another. It is proposed therefore to use Stensiö's term *ascending lamella* for Kiaer's „maxillary plate", and White's *pre-oral field* for Stensiö's „sub-rostral lamella of the rostral plate". The term *para-oral plate* will be used for the plate so named by Stensiö.

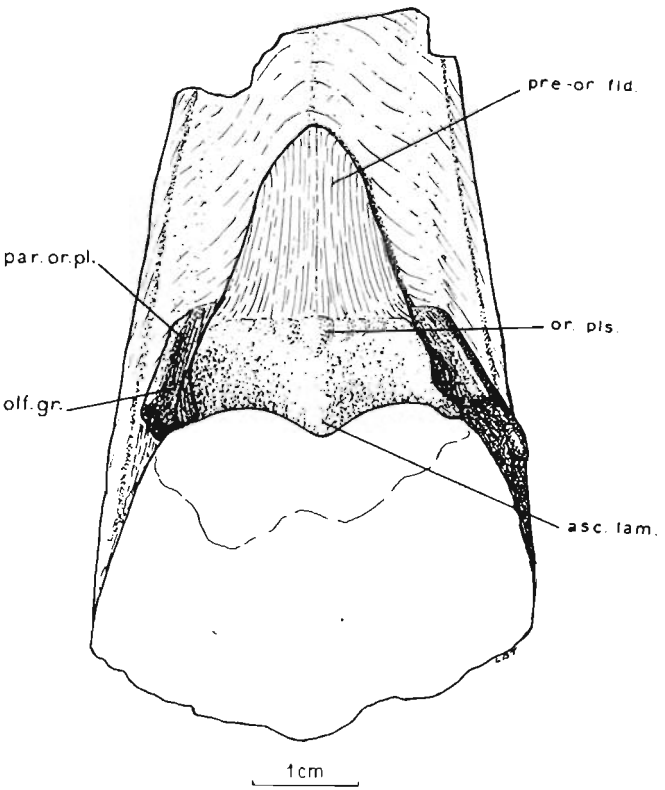

Fig. 1. — *Rhinopteraspis cornubica* (McCoy), D. 1145 from Placoderm Sandstone, Daleszyce, near Kielce, Holy Cross Mts. Original specimen preserved as a natural mould; sketch based on latex cast prepared by Dr. J. Kulczycki

asc. lam. ascending lamella, *olf. gr.* olfactory groove with sensory canal in floor of groove, *or pls.* oral plates, *par. or. pl.* para-oral plate, *pre-or. fld.* pre-oral field.

form the anterior part of the roof of the mouth and buccal cavity. This lamella is gently folded, so that in section the central part forms a median ridge, and its lateral margin is raised to form a sharp angle. On either side of the lamella the anterior portion of an elongated triangular para--oral plate can be seen, and there is a deep groove running between this plate and the lateral margin of the lamella. This would appear to be an olfactory groove which directed water towards the olfactory organs situated at the sides of the mouth.

The ornamentation of the pre-oral field consists of longitudinal dentine ridges, an arrangement not previously observed in the pteraspids, and it has been shown (Tarlo, 1960) that this area was produced as a single unit (i.e. synchronomorially). The ridges on the remainder of the ventral surface of the rostrum are arranged in arcuate rows, and zones of growth are clearly visible. It is clear that the rostrum increased in length by the addition of areal zones of cyclomorial growth on its posterior margin, which were nevertheless anterior to the pre-oral field.

There is a sharp line separating the ornamented pre-oral field from the ascending lamella which is devoid of ornament, and a row of oral plates adhering to the lamella abut against this junction. There are 7 oral plates in all, the median of which is the largest, and in anterior view it appears triangular with its apex directed ventrally. The remaining plates, which are also somewhat triangular in section, diminish in size towards the sides of the mouth. The plates are ornamented by concentric dentine ridges and their ventral surface tends to be abraded (see text--fig. 2). The shape of these plates is reminiscent of those described by Stensiö (1958) in *Mylopteraspis robusta*, although in the Polish specimen the central plate is less elongated than in *Mylopteraspis*, and is blunt rather than pointed. It is not possible, however, to establish the identity of these two sets of oral plates since Stensiö's specimen is known only in dorsal view, having been dissected out from the dorsal side, while in the Polish specimen the plates are known in ventral view only. As these are preserved as natural moulds, there can be no possibility of ascertaining their appearance in dorsal view.

Normally, oral plates are found attached either to the ventral median plate or to the post oral covers (Kiaer, 1928;; White, 1935), but in this instance there is no sign of these elements. When the animal died the oral plates must have been closed against the posterior edge of the pre-oral field, and they subsequently adhered to the ascending lamella where they became preserved, the post oral elements being lost. The perfect alignment of the 7 individual oral plates suggests that they are in the position of

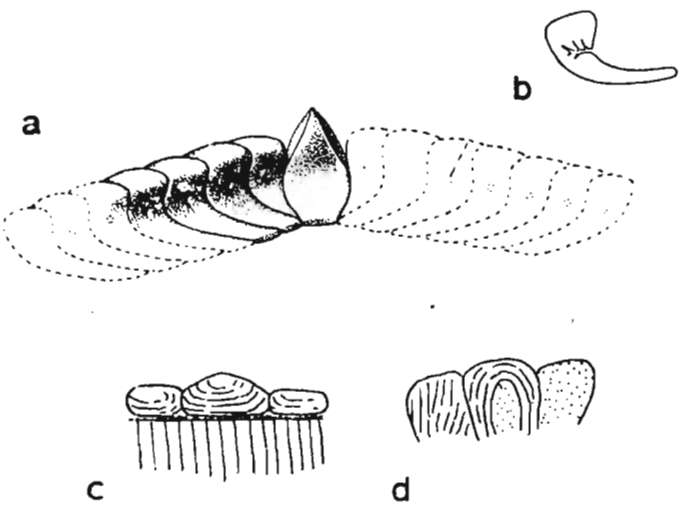

Fig. 2. — Oral plates of *Mylopteraspis robusta* Stensiö. *a* dorsal view, *b* longitudinal vertical section; × 3 (from Stensiö, 1958, p. 263, fig. 142 C, D). Oral plates of *Rhinopteraspis cornubica* (McCoy): *c* anterior view, abutting on the longitudinal dentine ridges of the pre-oral field, *d* ventral view; × 3.

natural articulation; if this condition were due to an accident, they would of necessity have suffered some displacement.

Description of Rhineland specimens

In the Palaeontological Museum, Berlin, there is an immature specimen of *R. cornubica* (G-P. M. B. 133) from Overath in which the ornamentation of the ventral surface of the snout consists of longitudinal dentine ridges. In the posterior part of this surface there is a raised triangular area which again possesses longitudinal dentine ridges (see text-fig. 3). Although this area is somewhat ill defined, it seems likely that it represents the original pre-oral field which was formed synchronomorially at the time when the first ossification took place in the carapace. Subsequently the snout increased in length by the addition of alternate dentine ridges immediately anterior to the post oral region, giving a characteristic chevron pattern such as White (1956) described in the same species. A further increase in length was accomplished by the addition of zones of arcuate dentine ridges posterior to the chevron pattern, identical to those seen in the Polish specimen.

Also in the Berlin Museum there is an adult snout (G-P.M.B. 110), also from Overath, the ventral surface of which is divided into three well-marked zones; an anterior one, in which the ornamentation consists of longitudinal dentine ridges; a middle zone with the chevron arrangement; and a posterior one, in which the dentine ridges are arcuate (see text-fig. 3). This seems to demonstrate that the differences are due to the age of the individual and have no value in themselves as diagnostic characters of the species.

This specimen was further developed in an attempt to reveal the pre-oral field, but only the triangular so-called „oral sinus" of Fahlbusch (1957) could be seen. This sinus would appear to mark the position which in the Polish specimen is occupied by the triangular pre-oral field and ascending lamella. As the snout is increased in length by the addition of dentine ridges on its posterior border, but anterior to the pre-oral field, there is a zone of growth rather like an epiphysis between the main part of the snout and the pre-oral field. This would naturally be a point of weakness, and normally the pre-oral field falls away after death, so that its presence in the Polish specimen is of considerable importance.

Classification of the pteraspids

White (1956) although recognizing that the sub-genera[2] of *Pteraspis* (*Protopteraspis, Belgicaspis,* and *Rhinopteraspis*) were originally based on misunderstandings, nevertheless was able to show by developing the mouth and cornual regions that the diversions were in fact well founded.

[2] Sub-genera are here raised to generic rank as it is felt that the differences between them warrant this.

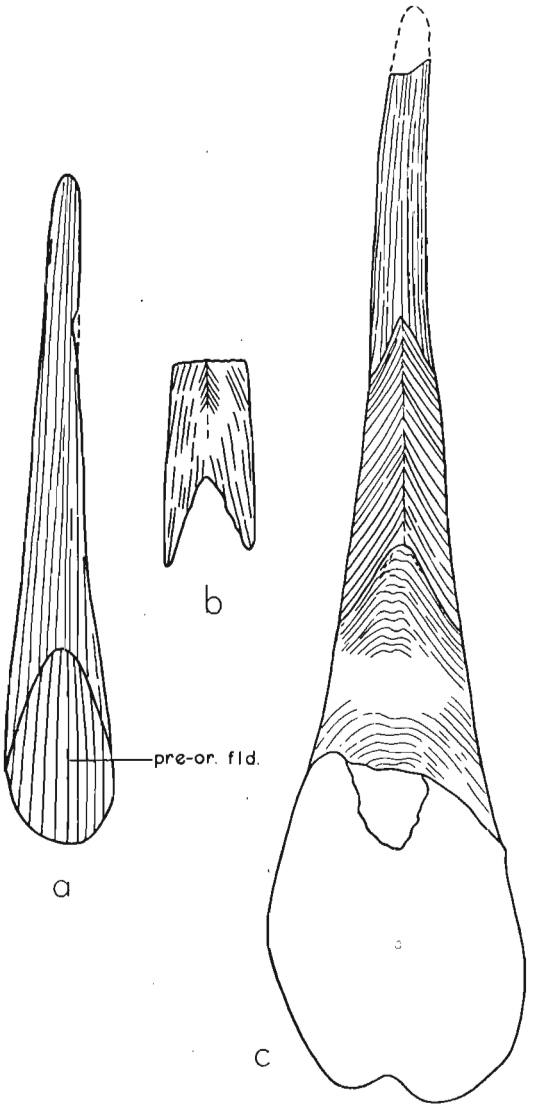

Fig. 3. — Ornamentation of the ventral surface of the snout in *Rhinopteraspis cornubica* (McCoy): *a* immature snout, G-P.M.B. 133, formed as a single synchronomorial unit, with pre-oral field distinguished, × 0.5; *b* young snout B.M., P. 22043, showing chevron arrangement of dentine ridges (from White, 1956, p. 7, fig. 4), × 0.6; *c* adult snout, G-P.M.B. 110, showing three clearly defined zones of growth: the first and most anterior — zone of synchronomorial growth with longitudinally arranged dentine ridges (as in fig. 3*a*); the middle zone — dentine ridges arranged in characteristic chevron (as in fig. 3*b*); posterior zone — dentine ridges arranged arcuately (as in fig. 1); × 0.5.

Note: In this adult specimen the pre-oral field has been lost.

This was a major step towards establishing a modern classification of the pteraspids. Subsequently, White (1960) restored Zych's sub-genus *Althaspis* as a valid name, and introduced the new sub-genus *Cymripteraspis* for the reception of *Pteraspis leachi*.

White's classification, which was accepted by Schmidt (1959), was based on material from the Anglo-Welsh Province and the Ardennes — Rhineland geosyncline. In 1958 however, Stensiö, using material from Podolia (Ukraine), introduced many new generic names for the pteraspids, based in the main on the characters of the snout region and, in particular, on the types of growth exhibited there. Unfortunately, since he was primarily concerned with morphology, Stensiö gave no diagnoses or descriptions of these new forms, nor did he indicate how they were related to species already described from Podolia. As a consequence of the ensuing complicated taxonomic situation, there is a very real danger that Stensiö's fundamental contribution to our knowledge of the pteraspids will be ignored. There is also a danger that two entirely separate classifications will be employed for the pteraspids, one based on Podolian material and the other on material from Western Europe.

The differences in the characters of the snout region recognized by Stensiö are of fundamental importance in any understanding of the pteraspids, and the generic distinctions based on them would seem to be justified. Nevertheless it is necessary to show the relationship between these new genera and those already established, and such a synthesis is attempted here. In this way it is hoped to produce an outline classification which combines features of those proposed by White and Stensiö. Diagnoses of the genera here accepted as valid are given below, together with a short discussion of each.

Genus *Penygaspis* Stensiö, 1958

Type species: *Penygaspis dixoni* (White, 1938)
(text-fig. 4)

1938. *Pteraspis dixoni* n. sp.; E. I. White, New pteraspids..., p. 100-110, text-fig. 11-25.
1958. *Penygaspis dixoni* (White); E. A. Stensiö, Les Cyclostomes..., p. 278, 292, 326, text-fig. 147 C-F.
1960. *Penygaspis dixoni* (White); L. B. Tarlo, The Downtonian ostracoderm..., p. 224, text-fig. 6.

Holotype: Dorsal median plate P. 20155-6, housed in British Museum (Nat. Hist.) London, figured by White (1938, text-fig. 15).

Type horizon and locality: Lower Old Red Sandstone, ? Senni Beds, Pen-y-gau Farm, near Ferryside, Carmarthenshire.

Diagnosis. — Small-sized pteraspid, length of dorsal median plate less than 4.0 cm; dorsal and ventral median plates composed of large central synchronomorial unit ornamented by coarse longitudinal dentine

ridges, with surrounding zone of cyclomorial growth composed of concentric dentine ridges.

Remarks. — This genus represents the most primitive condition found in the pteraspids. The median plates are composed of a large synchronomorial unit surrounded by a comparatively narrow zone of cyclomorial growth, thus contrasting with all other pteraspids in which the growth of the main plates is entirely cyclomorial. Although this form

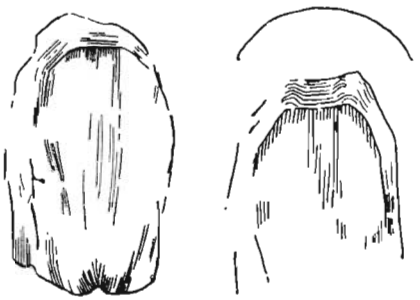

Fig. 4. — *Penygaspis dixoni* (White), ventral median plates showing central synchronomorial unit with surrounding zone of cyclomorial growth (from White, 1938, p. 106, fig. 18, 19).

was originally described from the Lower Siegenian, a fragment belonging to this genus is known from the Lower Gedinnian (*Traquairaspis* zone) (White, 1946, p. 212). This genus is a small snub-nosed form and in this respect is similar to *Protopteraspis*, but it has a striking ornament which is sufficient to warrant generic distinction.

Genus *Protopteraspis* Leriche, 1924
(syn. *Simopteraspis* White, 1950)
Type species: *Protopteraspis gosseleti* Leriche, 1906
(text-fig. 5)

1906. *Pteraspis gosseleti* n. sp.; M. Leriche, Contribution à l'étude,..., p. 26, pl. 1, fig. 6-9, text-fig. 8.

1924. *Pteraspis (Protopteraspis) gosseleti* Leniche; M. Leriche, Les Pteraspis..., p. 149.

1950. *Pteraspis (Simopteraspis) gosseleti* (Leriche); E. I. White, Pteraspis..., p. 82, text-fig. 15-17, 19.

1959. *Pteraspis (Protopteraspis) gosseleti* Leriche; W. Schmidt, Grundlagen..., p. 32, 34.

Lectotype: Carapace in dorsal view, figured by White (1960, text-fig. 15), housed in University of Lille.

Type horizon and locality: Psammites de Lievin, Pas-de-Calais.

Diagnosis. — Small-sized pteraspid with blunt rounded snout; small triangular pineal plate widely separated from orbitals; pre-oral field not developed; narrow ascending lamella; oral plates articulating with ventral median plate.

Remarks. — This genus is characterized by its small size and its short, blunt-ended snout. In ventral view there is a very narrow border anterior to the oral opening, and a very narrow ascending lamella. There is no sign of a pre-oral field.

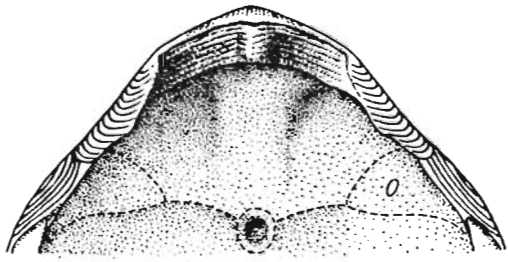

Fig. 5. — *Protopteraspis primaeva* (Kiaer), ventral view of snout region showing narrow ascending lamella (after Stensiö, 1958, p. 262, fig. 141 A).

Genus *Zascinaspis* Stensiö, 1958
(syn. *Brotzenaspis* Stensiö, 1958)
Type species: *Zascinaspis heintzi* (Brotzen)
(text-fig. 6)

1936. *Brachipteraspis heintzi* n. sp.; F. Brotzen, Beiträge..., p. 46-7, pl. 7, fig. 3, text-fig. 16.

1958. *Zascinaspis heintzi* (Brotzen); E. A. Stensiö, Les Cyclostomes..., p. 255, 339, text-fig. 189.

1958. *Zascinaspis obtusirostra* n. sp.; E. A. Stensiö, *Ibid.*, p. 339, text-fig. 189 (invalid).

Holotype: Dorsal carapace P. 112, housed in Geological Survey, Stockholm, figured by Brotzen (1936, pl. 7, fig. 3).

Type horizon and locality: Dittonian, Uścieczko, Podolia.

Diagnosis. — Broad medium-sized pteraspid; wide pentagonal pineal plate adjoining median projection of orbital; pre-oral field not developed; wide and deep ascending lamella.

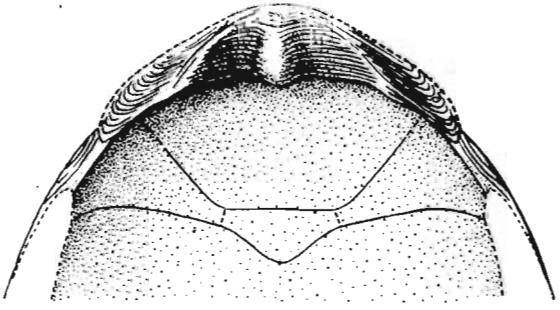

Fig. 6. — *Zascinaspis heintzi* (Brotzen), ventral view of snout region showing well developed ascending lamella (after Stensiö, 1958, p. 339, fig. 189 A).

Remarks. — Although Brotzen originally included *Z. heintzi* in *Brachipteraspis*, the structure of the ventral surface of the snout of *Z. heintzi* shows that it is quite different from the type species of *Brachipteraspis*, i.e. *B. latissima* (Zych), the main distinguishing feature of *Zascinaspis* being the marked development of the ascending lamella. In addition, this form is broad and blunt-snouted and is clearly a precursor of such later forms as *Protaspis*, *Zascinaspis carmani* (Denison) being very close to *Protaspis*.

Genus *Althaspis* Zych, 1931
(syn. *Lericheaspis* Zych, 1931; *Pseudopteraspis* Stensiö, 1958; *Cymripteraspis* White, 1960)
Type species: *Althaspis samsonowiczi* n. nom.
(text-fig. 7)

1927. *Pteraspis lerichei* n.sp. *elongata* n.mut.; W. Zych, Old-Red..., p. 55, pl. 4, fig. 1, 5; pl. 5, fig. 2-4, text-fig. 7.
1931. *Podolaspis (Althaspis) elongata* (Zych); W. Zych, Fauna ryb..., p. 89, text-fig. 41, 50.
1933. *Pteraspis elongata* Zych; F. Brotzen, Die Silurischen..., p. 456-9, text-fig. 16.
1936. *Rhinopteraspis elongata* (Zych); F. Brotzen, Beiträge..., p. 7.
1958. *Pseudopteraspis elongata* (Zych); E. A. Stensiö, Les Cyclostomes..., p. 266, 282, text-fig. 144, 157.
1960. *Pteraspis (Althaspis) elongata* (Zych); E. I. White, Notes on pteraspids..., p. 2.
1960. *Pseudopteraspis elongata* (Zych); L. B. Tarlo, The Downtonian..., p. 224, text-fig. 7c.

Lectotype: Carapace figured by Zych, 1927, pl. 5, fig. 2.
Type horizon and locality: Upper Dittonian, Dźwinogród, Podolia, Ukraine.

Diagnosis. — Long-snouted pteraspid; wide pineal plate adjoining narrow median projection of orbital; para-oral plate; ventral surface of snout ornamented by transverse dentine ridges produced by cyclomorial growth; ascending lamella developed.

Remarks. — Zych (1931) introduced the name *Althaspis* as a sub-genus of *Podolaspis*, including in it *P. elongata* Zych. Subsequently, Brotzen (1933) also referred the authorship of *Pteraspis elongata* to Zych, White (1935) however, recognized that *Pteraspis elongata* (Alth) had priority, despite the fact that he believed a single species was represented. Reference to the original descriptions shows that in fact two species are present. Subsequently reference has erroneously been made to *Pteraspis elongata* Zych, and since this name is pre-occupied, it is necessary to rename this species. The new name *P. samsonowiczi* is here proposed, in honour of the late Professor J. Samsonowicz, Warsaw University, Poland.

Brotzen (1936) referred this species to *Rhinopteraspis* by virtue of

its elongated snout, and White (1938) noted the similarity between *Pteraspis elongata* Zych (= *P. samsonowiczi*) had his *P. leachi*. Stensiö (1958) proposed the new genus *Pseudopteraspis* for this same form on account of the type of growth seen in the snout region, but White (1960) recognized that Zych's name *Althaspis* was still available, and there was no need to introduce a new generic name. *Althaspis* now becomes the valid genus, with *A.samsonowiczi* its type species.

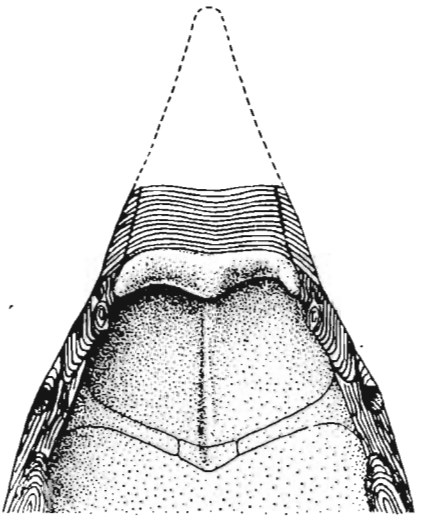

Fig. 7. — *Althaspis samsonowiczi* n.nom., ventral view of snout region showing ascending lamella and transverse dentine ridges (after Stensiö, 1958, p. 282, fig. 157 A).

The growth of the snout of *P. leachi* (White, 1938) enables this species also to be included in *Althaspis*. White (1960) however, proposed the new genus *Cymripteraspis* for this species, separating it from *Althaspis* on account of the small area of concentric cyclomorial growth at the posterior margin of the ventral surface of the rostrum. However, since the greater part of the growth consists of normal zones of cyclomorial growth, identical to those seen in *Althaspis*, the development of this small round „plate" at a late stage of development is not here considered sufficient to warrant the erection of a new genus.

Genus *Podolaspis* Zych, 1931
(syn. *Plesiopteraspis* Stensiö, 1958)
Type species: *Podolaspis lerichei* (Zych, 1927)
(text-fig. 8)

1927. *Pteraspis lerichei* n.sp. *rostrata* n.mut.; W. Zych, Old-Red..., p. 54, pl. 2, fig. 7, 9; pl. 3, fig. 3; text-fig. 5.

1927. *Pteraspis sturi* Alth *rostrata* n.mut.; W. Zych, *Ibid.*, p. 52-3, pl. 2, fig. 6; pl. 3. fig. 3.
1931. *Podolaspis rostrata* (Zych); W. Zych, Fauna ryb..., p. 91, phot. 14.
1933. *Pteraspis lerichei* Zych; F. Brotzen, Die Silurischen..., p. 445-7, text-fig. 9.
1935. *Pteraspis major* Alth; E. I. White, The Ostracoderm..., p. 443.
1958. *Plesiopteraspis* sp.; E. A. Stensiö, Les Cyclostomes..., p. 267-8, 271, text-fig. 145 A, B, 148.

Lectotype: Anterior part of dorsal carapace, figured by Zych (1927, pl. 3, fig. 3).

Type horizon and locality: Downtonian, Mogielnica, Podolia, Ukraine.

Diagnosis. — Broad pteraspid; pineal wide, semicircular in outline, not adjoining orbitals; pre-oral field developed but not clearly differentiated from ascending lamella.

Remarks. — Zych (1927) described the „mutations" *Pteraspis lerichei* n.sp. *rostrata* n.mut., and *Pteraspis sturi* Alth *rostrata* n.mut., and the specimen he figured on pl. 3 fig. 3, under both names is here selected as the lectotype. Zych (1931) described similar material as *Podolaspis rostrata,* and White (1960) selected this species as the type species of *Podolaspis.* In 1933 Brotzen described this same form as *Pteraspis lerichei* Zych, which meant that he had selected *P.lerichei rostrata* as the typical

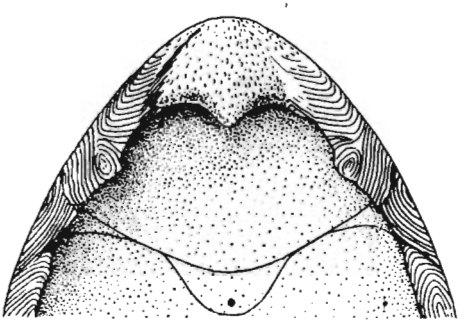

Fig. 8. — *Podolaspis lerichei* (Zych), ventral view of snout region showing the development of the pre-oral field from the ascending lamella (after Stensiö, 1958, p. 272, fig. 148 B).

form of *P.lerichei.* In 1935 however, White claimed that *P.lerichei* was a synonym of *Pteraspis major* Alth, for which he selected as lectotype the specimen figured by Alth (1874, pl. 3, fig. 3-5) which Zych had included in his synonymy of *Pteraspis lerichei rostrata.* A comparison of Alth's and Zych's figures shows that in fact two forms are represented, and hence Brotzen was justified in using *P.lerichei.* Stensiö (1958) has described pteraspids from Podolia with the same type of pre-oral region as *P.lerichei rostrata,* which he has placed in the new genus *Plesiopteraspis.* The differences are in fact sufficient to warrant generic distinction from

Pteraspis, and he was justified in introducing a new generic name. However, since White (1960) selected *Podolaspis rostrata* Zych (*Pteraspis lerichei rostrata* Zych; *P.lerichei* Zych) as the type species of *Podolaspis,* then the generic name *Podolaspis* became available and because it has priority it must replace Stensiö's *Plesiopteraspis.* The only specific name available for the type species is *P.lerichei* Zych, as Brotzen (1933) recognized, and therefore the valid name for this form is *Podolaspis lerichei* (Zych).

Genus *Loricopteraspis* nov.
Type species: *Loricopteraspis althi* (Stensiö, 1958)
(text-fig. 9)

1958. *Pteraspis althi* n.sp.; E. A. Stensiö, Les Cyclostomes..., p. 277, text-fig. 152 A.
1960. *Pteraspis althi* Stensiö; L. B. Tarlo, The Downtonian..., p. 224, text-fig. 7a.

Holotype: Snout C. 1559 housed in Swedish Museum of Nat. Hist. Stockholm, figured by Stensiö (1958, text-fig. 152 A).

Type horizon and locality: Downtonian, Podolia, Ukraine.

Diagnosis. — Blunt-snouted pteraspid; pre-oral field composed of small synchronomorial units some ornamented with dentine ridges aligned longitudinally, and others with transverse ridges.

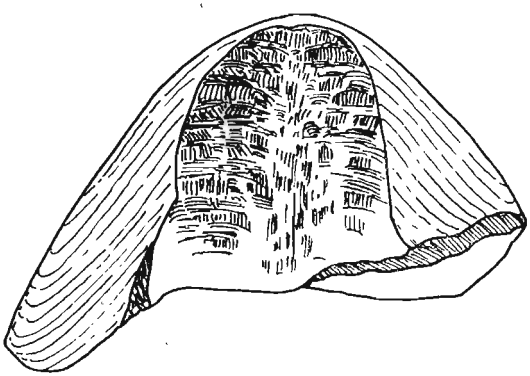

Fig. 9. — *Loricopteraspis althi* (Stensiö), ventral view of snout region showing pre-oral field composed of small scale-like synchronomorial units (schematic representation after fig. 152 A of Stensiö, 1958, p. 277).

Remarks. — Stensiö (1958) considered that this type of pre-oral field could be included in the type genus *Pteraspis,* but as White (1935, 1956) has shown, in the type species of *Pteraspis,* the pre-oral field is ornamented by small pustules, and these contrast with the arrangement described by Stensiö. It is therefore felt that this new form of pre-oral field described by Stensiö should be generically separated from *Pteraspis,* and as the synchronomorial units appear rather scale-like the new name *Loricopteraspis* is here proposed.

Genus *Pteraspis* Kner, 1847
(syn. *Scaphaspis* Lankester, 1864; *Belgicaspis* Zych, 1931; *Brachipteraspis* Brotzen, 1936; *Parapteraspis* Stensiö, 1958)
Type species: *Pteraspis rostrata* (Agassiz, 1835)
for details see White, 1935
(text-fig. 10)

Holotype: Internal cast of dorsal carapace, 21444, housed in Geological Survey Museum, London.

Diagnosis. — Typical pteraspid with triangular snout which may be elongated anterior to the pre-oral field; pre-oral field well developed, ornamented by small pustules; ascending lamella present; oral plates slender, articulating with post-oral covers.

Fig. 10. — *Pteraspis rostrata* (Agassiz), ventral view of snout showing pre-oral field with granular ornament, ascending lamella, oral plates and post-oral cover (after White, 1935, p. 384, fig. 1a).

Remarks. — *Belgicaspis* Zych cannot be generically distinguished from *Pteraspis* itself, as its pre-oral field and ascending lamella are essentially the same as those in *Pteraspis rostrata*. The characteristic elongation of the snout in *Belgicaspis* is also merely a further development of the condition seen in *Pteraspis rostrata*. *Belgicaspis* is therefore here included as a synonym of *Pteraspis*. Similarly, *Parapteraspis* Stensiö cannot be generically distinguished from *Pteraspis* and is also included in its synonymy.

Genus *Mylopteraspis* Stensiö, 1958
Type species: *Mylopteraspis robusta* Stensiö, 1958
(fig. 11)

1958. *Mylopteraspis robusta* n.sp.; E. A. Stensiö, Les Cyclostomes..., p. 263, 280; text-fig. 142, 156.

Holotype: Snout with associated oral plates C. 1546, housed in Swedish Museum of Nat. Hist., Stockholm, figured by Stensiö (1958, text-fig. 142, 156).

Type horizon and locality: Dittonian, Podolia, Ukraine.

Diagnosis. — Triangular snout; pineal produced laterally to meet orbitals; pre-oral field well developed; ascending lamella present; posterior corners of ventral surface of rostrum project medially; oral plates stoutly built.

Remarks. — This genus is very similar to *Pteraspis,* but is generically distinguished from it by its possession of highly specialized mouth-parts.

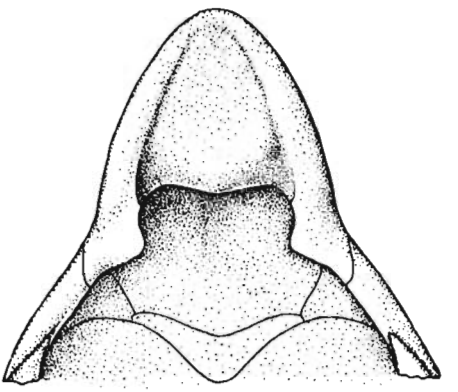

Fig. 11. — *Mylopteraspis gracilis* Stensiö, ventral view of snout showing median projection of postero-lateral margins of the ventral surface of the rostral plate, and well marked pre-oral field (after Stensiö, 1958, p. 259, fig. 139 A).

Genus *Rhinopteraspis* Jaekel, 1919
(syn. *Steganodictyum* McCoy, 1851; *Palaeoteuthis* Roemer, 1855; *Archaeoteuthis* Roemer, 1855)
Type species: *Rhinopteraspis cornubica* (McCoy, 1851)
(pl. I, II)
For details — see above pp. 368-376 and text.-figs. 1, 2 *c*, *d*, 3.

EVOLUTION OF THE PTERASPIDS

It is well known that the earliest pteraspids were small, blunt--snouted forms, while the latest were of two markedly contrasting kinds — one having a very broad carapace and blunt snout, the other being narrower with a greatly elongated snout. However, this simple picture is more complicated than was formerly realized, Stensiö's new information on the growth of the snout region enabling the recognition of separate lineages, which were not previously apparent. This is based on the fact that the characters of the snout region indicate phylogenetic relationships, whereas the proportions of the different plates in the carapace merely

appear to change with geological age, and are therefore satisfactory only when considering overall evolutionary trends. Using the characters of the snout region it can be shown that both the long-snouted and broad--carapaced forms were arrived at in two independent ways, and an attempt is made below to trace the manner in which this took place.

As can be seen in text-fig. 12, three major lines can be traced from a common primitive form, such as *Protopteraspis* and the first of these

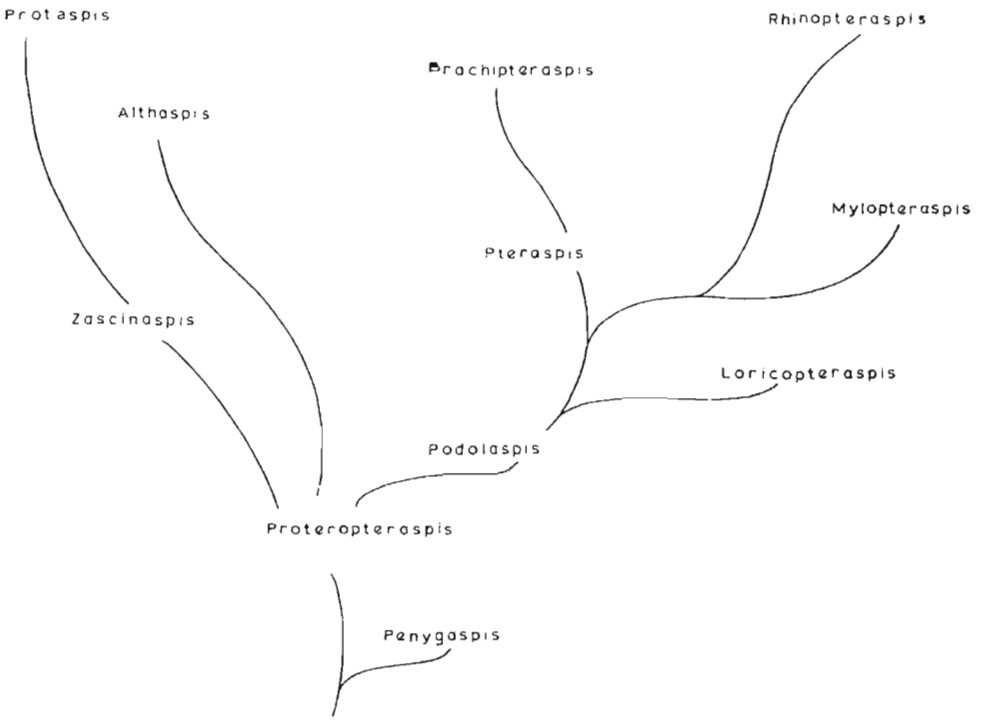

Fig. 12. — Outline phylogeny of the pteraspids.

lead to one of the broad, blunt-snouted forms. In this line little change occurred in the snout region, which remained essentially the same throughout. *Protopteraspis* was small with a blunt snout, and an ascending lamella not strongly developed, and from it one can easily envisage the derivation of *Zascinaspis* which was somewhat broader, and had an increased development of the ascending lamella. Finally, it seems likely that this form gave rise to *Protaspis* by way of a species such as *Zascinaspis carmani* (Denison). It should be noted that although Denison (1960) described this species under the genus *Pteraspis* and considered it to be intermediate between *Pteraspis* and *Protaspis*, it is clear from his figures of the ventral part of the snout that it bears no relation to *Pteraspis*,

but is instead on the *Zascinaspis-Protaspis* line. It is however excluded from *Protaspis* itself on account of the characters of the cornual region.

The next line can also be derived from *Protopteraspis,* but this time it leads to one of the long-snouted forms. The increase in the length of the snout was achieved by the addition on the posterior margin of the rostral plate, of zones of cyclomorial growth in which the dentine ridges were aligned transversely, the zone of growth in all probability being anterior to the ascending lamella. All pteraspids with this type of growth are included in the genus *Althaspis,* the long-snouted *A. samsonowiczi* being reached by way of *A.kujdanowiensis* (Stensiö) with its triangular snout, and *A.vimiensis* White which has a snout intermediate between the two. As there was likely to be a point of weakness where such growth takes place, this may account for the apparent absence of the ascending lamella in specimens of *A.leachi,* as it might easily have fallen away after death.

In contrast to the previous two lines, the third line which can also be derived from *Protopteraspis* is characterized by the development of an entirely new structure on the ventral surface of the rostrum. This is the triangular pre-oral field which in the early blunt-snouted forms such as *Podolaspis,* was not demarcated from the ascending lamella, and in fact can be considered as an anterior production of it in the plane of the rostral plate. This leads to the condition seen in *Pteraspis* where the pre-oral field was clearly differentiated from the ascending lamella. In this genus the resulting triangular snout could also be increased in length by the addition of zones of cyclomorial growth on the posterior margin of the rostral plate, but anterior to the pre-oral field, as for example in *P.rostrata* and *P.crouchi.* Such growth reaches a climax in *Rhinopteraspis,* examples of which have proportions similar to those known in the later forms of *Althaspis.*

Although Brotzen (1936) erected the new genus *Brachipteraspis* for *Pteraspis latissima* Zych, a pteraspid with a broad carapace, which was different from *Protaspis* in the cornual region, Stensiö (1958) pointed out that in fact the ventral surface of the snout in *Brachipteraspis* was of the same type as that seen in *Pteraspis.* Thus it is clear that within this third lineage, both long-snouted and broad-carapaced forms evolved.

It should be noted that *Rhincpteraspis* and *Loricopteraspis* are generically separated from *Pteraspis* itself on account of the type of ornament seen in the pre-oral field, and *Mylopteraspis* on account of its specialized mouth-parts.

Thus it is clear that both long-snouted and broad-carapaced forms developed in different lineages, the animals having been selected in two main directions, and this was probably reflected in their modes of life. The long-snouted forms may well have used their snouts for stirring

up mud containing organic debris and small invertebrates, like the present-day sturgeon, while the broad-carapaced forms glided over the substratum rather like the modern skate.

AFFINITIES OF THE PTERASPIDS

Stensiö's (1927) classic work on the cephalaspids established beyond any doubt their close zoological affinity to the modern lampreys. However, his contention that the heterostracans (pteraspidomorphs) were related to the hag-fishes (myxinoid cyclostomes), has not met with the same ready acceptance. Stensiö drew attention to the fact that the cephalaspids and lampreys both had a dorsal naso-hypophysial opening, and a single nasal sac, and that their branchial pouches had their own individual external openings. He also noted that the heterostracans and hag-fishes both possessed a ventral naso-hypophysial opening, and that there was a common external opening for their branchial pouches.

In 1924 however, Kiaer had proposed a division of the ostracoderms into two major groupings based on the presence of a single nostril in one group — the cephalaspids and anaspids, and double nasal sacs in the other — the heterostracans. White (1935) accepted Kiaer's contention that the heterostracans had double nasal sacs, but he did not feel that this condition was of great taxonomic value. Stensiö on the other hand claimed that the pteraspids like the myxinoids must have had single nasal sacs, but only Zych (1937) agreed with this although in 1931 even he had reported the occurrence of olfactory grooves at the sides of the ventral surface of pteraspid snouts.

The whole question of the relation of the heterostracans to modern cyclostomes has again been broached as a result of the publication by Stensiö (1958) of hypothetical reconstruction of the internal anatomy of the pteraspids. In order to substantiate his claim that the pteraspids had single nasal sacs, Stensiö was obliged to postulate the existence also of a cartilaginous pad on which would be set a row of upper labial plates against which the oral plates would occlude. This was in order that a pre-nasal sinus (which would represent the single naso-hypophysial opening) could be accommodated between the ascending lamella and the oral plates (see text-fig. 13).

Previously, both Kiaer (1928) and White (1935) suggested that the oral plates occluded directly against the ascending lamella, and the new Polish specimen of *R.cornubica* lends support to this opinion. The mouth plates have been remarkably well preserved, and as they are in perfect alignment, this suggests that they were undisturbed after death. Thus the sharpness of the junction between the plates and the posterior margin

of the pre-oral field, which can be taken as the natural position of occlusion, precludes the possibility of the intervention of the hypothetical elements postulated by Stensiö, hence doubt is cast on his basic premise that there is only a single nasal capsule present.

With regard to the case for double nasal sacs, in the Polish specimen paired grooves can be seen situated between the para-oral plate and the

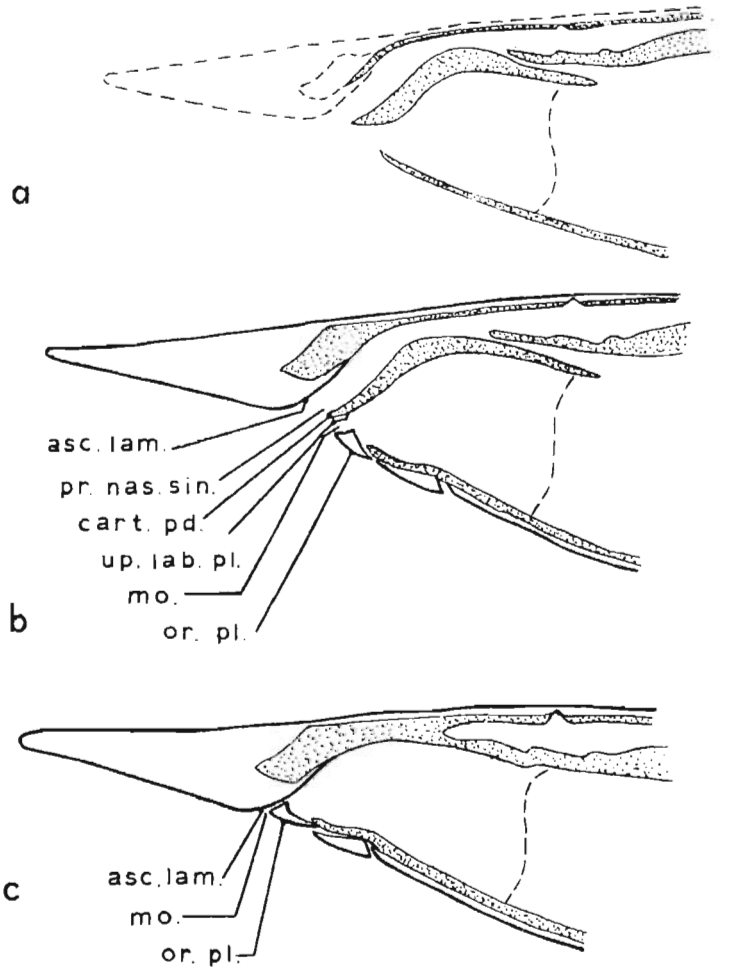

Fig. 13. — Sagittal sections of the snout region of pteraspids: *a* the arrangement of *Myxine* with pteraspid condition superimposed, *b* a pteraspid with the naso-oral region reconstructed according to Stensiö's (1958) hypothesis, showing similarity to *Myxine* and various hypothetical structures postulated by Stensiö; *c* a pteraspid reconstructed according to the evidence of the snout of *Rhinopteraspis cornubica*, showing the occlusion of the oral plates directly against the ascending lamella.

asc. lam. ascending lamella, *cart pd.* cartilaginous pad, *mo.* mouth, *or. pl.* oral plate, *pr nas. sin.* pre-nasal sinus, *up. lab. pl.* upper labial plate; cartilage stippled.

pre-oral field on either side of the ventral surface of the snout. These can best be interpreted as olfactory, and it is of interest to note that Stensiö figured similar grooves in his Podolian material (figs. 150, 154, 156) although he offered no explanation for them. Further confirmation that the heterostracans possessed paired nasal sacs is to be found in the cyathaspids, where small notches occur anterior to the orbital notches on the downturned lateral margins of the dorsal plate. These were interpreted by Kiaer and Heintz (1935) and Watson (1954) as marking the position of the opening to the olfactory organ, but Stensiö (1958, text-fig. 193) considered that they marked the position of hypothetical sensory tentacles.

Thus there can be little doubt that the heterostracans had double nasal sacs, and by virtue of this they are precluded from the ancestry of the myxinoid cyclostomes. This means that two fundamentally different groups together make up the Agnatha. One includes the cephalaspids and all modern cycloctomes, both lampreys and myxinoids, and the other the heterostracans which may perhaps include the ancestors of all higher vertebrates.

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L. BEVERLY TARLO

RHINOPTERASPIS CORNUBICA (McCOY) ORAZ UWAGI O KLASYFIKACJI I EWOLUCJI PTERASPIDÓW

Streszczenie

Praca zawiera pierwszy opis rostrum i części gębowych *Rhinopteraspis cornubica* (McCoy) na podstawie okazu, znalezionego ostatnio w piaskowcu plakodermowym Daleszyc koło Kielc (Tarlo, 1958).

Część tylna powierzchni wentralnej rostrum zajęta jest przez trójkątne pole preoralne, od którego odchyla się ścianka wstępująca tworząc przednią część sklepienia otworu ustnego i jamy gębowej. Z każdej strony wymienionej ścianki widać wydłużoną trójkątną płytkę paraoralną oraz głęboki rowek biegnący między tą płytką a brzegiem bocznym ścianki. Wydaje się, że jest to rowek węchowy, którym woda kierowała się do organów węchowych, położonych z boków gęby. Ornamentacja pola preoralnego składa się z podłużnych prążków dentyny, czego dotychczas nie obserwowano u pteraspidów.

Płytki oralne są zachowane w naturalnej pozycji artykulacyjnej. Jest ich siedem, przy czym środkowa jest największa. Widziana od przodu płytka ta jest trójkątna, zwrócona wierzchołkiem ku stronie wentralnej. Wielkość pozostałych płytek, o przekrojach również nieco trójkątnych, zmniejsza się ku bokom otworu ustnego.

Cechy okolicy rostralnej mają zasadnicze znaczenie dla klasyfikacji pteraspidów i na ich podstawie wyróżniane są tu rodzaje. Autor podaje zarys klasyfikacji pteraspidów, w którym uwzględnia propozycje zarówno White'a (1935—60), jak i Stensiö'ego (1958).

Poniżej podane są diagnozy rodzajów, uznawanych przez autora niniejszej pracy.

Genus *Penygaspis* Stensiö, 1958
Gatunek typowy: *P. dixoni* (White, 1938)
(fig. 4)

Diagnoza. — Mały pteraspid o długości płytki medialnej poniżej 4 cm; płytki medialne dorsalna i wentralna złożone z synchromorialnej jednostki centralnej, ornamentowanej podłużnymi prążkami dentyny.

Genus *Protopteraspis* Leriche, 1924
Gatunek typowy: *P. gosseleti* Leriche, 1906
(fig. 5)

Diagnoza. — Mały pteraspid o tępym, zaokrąglonym rostrum; mała płytka pinealna oddzielona szeroko od orbitalnych; pole preoralne nie rozwinięte; ścianka wstępująca wąska; płytki oralne zestawiające się z wentralną płytką środkową.

Genus *Zascinaspis* Stensiö, 1958
Gatunek typowy: *Z. heintzi* (Brotzen, 1936)
(fig. 6)

Diagnoza. — Pteraspid średniej wielkości, szeroki, płytka pinealna pentagonalna, przyległa do środkowego występu oralnej; pole preoralne nie rozwinięte; ścianka wstępująca szeroka i głęboka.

Genus *Althaspis* Zych, 1931
Gatunek typowy: *A. samsonowiczi* n. nom.
(fig. 7)

Diagnoza. — Pteraspid o długim rostrum; szeroka płytka pinealna, przylegająca do wąskiego występu środkowego orbitalnej; płytka paraoralna; powierzchnia wentralna rostrum ornamentowana poprzecznymi prążkami dentyny o przyroście cyklomorialnym; ścianka wstępująca rozwinięta.

Genus *Podolaspis* Zych, 1931
Gatunek typowy: *P. lerichei* (Zych, 1927)
(fig. 8)

Diagnoza. — Pteraspid szeroki; płytka pinealna szeroka, o zarysie półkolistym, nie przyległa do orbitalnych; pole preoralne występuje, lecz nie jest wyraźnie wyodrębnione od ścianki wstępującej.

Genus *Loricopteraspis* nov.
Gatunek typowy: *L. althi* (Stensiö, 1958)
(fig. 9)

Diagnoza. — Pteraspid o tępym rostrum; pole preoralne, złożone z małych jednostek synchronomorialnych, niektóre z nich ornamentowane podłużnymi prążkami dentyny, a inne — prążkami poprzecznymi.

Genus *Pteraspis* Kner, 1847
Gatunek typowy: *P. rostrata* (Agassiz, 1835)
(fig. 10)

Diagnoza. — Pteraspid typowy o trójkątnym rostrum, które może się przedłużać ku przodowi do pola preoralnego; pole preoralne dobrze rozwinięte, ornamentowane małymi brodawkami; ścianka wstępująca rozwinięta; płytki oralne smukłe, zestawiające się z postoralnymi pokrywami.

Genus *Mylopteraspis* Stensiö, 1958
Gatunek typowy: *M. robusta* Stensiö, 1958
(fig. 11)

Diagnoza. — Pteraspid o trójkątnym rostrum, płytka pinealna osiągająca lateralnie płytki orbitalne; pole preoralne dobrze rozwinięte; ścianka wstępująca istnieje; tylne rogi powierzchni wentralnej rostrum wystające ku środkowi; płytki oralne masywne.

Genus *Rhinopteraspis* Jaekel, 1919
Gatunek typowy: *R.cornubica* (McCoy, 1851)
(pl. I, II)

Diagnoza. — Pteraspid o rostrum wydłużonym w kształcie ostrza; pole preoralne utworzone przez pojedynczą jednostkę synchronomorialną; ścianka wstępująca dobrze rozwinięta; płytki oralne masywne; istnieją rowki węchowe; gruba ornamentacja, złożona z prążków dentyny (3—6 mm).

Cechy części rostralnej mają wartość taksonomiczną oraz wskazują na stosunki filogenetyczne. Z drugiej strony, proporcje różnych płytek pancerza zdają się tylko zmieniać z wiekiem geologicznym i — co za tym idzie — mają wartość jedynie

przy rozpatrywaniu ogólnych kierunków ewolucyjnych. Opierając się na cechach części rostralnej można stwierdzić, że formy o długim rostrum i szeroko opancerzonej przedniej części ciała zostały zrealizowane na dwóch niezależnych drogach i autor usiłuje wyłuszczyć sposób, w jaki się to odbyło.

Wreszcie, układ części gębowych *R.cornubica* jest ważny dla rozważań nad teorią Stensiö'ego, dotyczącą budowy wewnętrznej rostrum pteraspidów, przy czym autor dochodzi do wniosku, że pteraspidomorfy (Heterostraci), z uwagi na posiadanie podwójnych torebek węchowych, winny być wyłączone z linii przodków Cyclostomata typu śluzicowatych (Myxinoidea).

OBJAŚNIENIA DO ILUSTRACJI

Fig. 1 (p. 372)

Rhinopteraspis cornubica (McCoy), okaz D. 1145, z piaskowca plakodermowego Daleszyc. Oryginalny okaz zachowany jako odlew naturalny. Rysunek z odlewu lateksowego, wykonanego przez Dra J. Kulczyckiego; *asc. lam.* ścianka wstępująca, *olf. gr.* rowek węchowy z kanałem czuciowym na dnie rowka, *or.pls.* płytki oralne, *par.or.pl.* płytka paraoralna, *pre-or.fld.* pole preoralne.

Fig. 2 (p. 373)

a,b Płytki oralne *Mylopteraspis robusta* Stensiö: *a* od strony dorsalnej, b podłużny przekrój pionowy; × 3 (wg Stensiö, 1958, p. 263, fig. 142 C, D).

c,d Płytki oralne *Rhinopteraspis cornubica* (McCoy): *c* z przodu, płytka graniczy z podłużnymi prążkami dentyny pola preoralnego, *d* od strony wentralnej; × 3.

Fig. 3 (p. 375)

Ornamentacja powierzchni wentralnej rostrum u *Rhinopteraspis cornubica* (McCoy): *a* niedojrzałe rostrum G-P.M.B. 133, tworzące pojedynczą jednostkę synchronomorialną o wyodrębnionym polu preoralnym, × 0,5; b młode rostrum, B. M., P 22043, ukazujące ułożenie prążków dentyny w kształcie szewronów (wg White'a, 1956, p. 7, fig. 4), × 0,6; c dorosłe rostrum, G-P.M.B. 110, ukazujące trzy wyraźnie wyodrębnione strefy wzrostu: pierwsza, przednia — strefa synchronomorialnego wzrostu, o prążkach dentyny ułożonych podłużnie (jak na fig. 3*a*); środkowa strefa — prążki dentyny ułożone w charakterystyczne szewrony (jak na fig. 3b); tylna strefa — prążki dentyny ułożone łukowato (jak na fig. 1); × 0,5. *Uwaga*: Na dorosłym okazie pole preoralne zostało zniszczone.

Fig. 4 (p. 377)

Penygaspis dixoni (White), wentralne płytki medialne, ukazujące centralną synchronomorialną jednostkę z otaczającą strefą cyklomorialnego wzrostu (wg White'a, 1938, p. 106, fig. 18, 19).

Fig. 5 (p. 378)

Protopteraspis primaeva (Kiaer), część rostralna, widoczna od strony wentralnej, ukazująca wąską ściankę wstępującą (wg Stensiö, 1958, p. 262, fig. 141A).

Fig. 6 (p. 378)

Zascinaspis heintzi (Brotzen), część rostralna, od strony wentralnej, ukazująca dobrze rozwiniętą ściankę wstępującą (wg Stensiö, 1958, p. 339, fig. 189A).

Fig. 7 (p. 380)

Althaspis samsonowiczi n. nom., część rostralna, od strony wentralnej, ukazująca ściankę wstępującą i poprzeczne prążki dentyny (wg Stensiö, 1958, p. 282, fig. 157A).

Fig. 8 (p. 381)

Podolaspis lerichei (Zych), część rostralna, od strony wentralnej, ukazująca rozwój pola preoralnego od ścianki wstępującej (wg Stensiö, 1958, p. 282, fig. 157A)

Fig. 9 (p. 382)

Loricopteraspis althi (Stensiö), część rostralna, od strony wentralnej, ukazująca preoralne pole, złożone z małych, łuskowatych jednostek synchronomorialnych (schematycznie, wg Stensiö, 1958, p. 277, fig. 152A).

Fig. 10 (p. 383)

Pteraspis rostrata (Agassiz), rostrum od strony wentralnej, ukazujące pole preoralne z granulowaną ornamentacją, ściankę wstępującą, płytki oralne i pokrywę postoralną (wg White'a, 1935, p. 384, fig. 1a).

Fig. 11 (p. 384)

Mylopteraspis gracilis Stensiö, rostrum od strony wentralnej, ukazujące w rzucie środkowym postero-lateralne brzegi wentralnej powierzchni płytki rostralnej i dobrze zaznaczone pole preoralne (wg Stensiö, 1958, p. 259, fig. 139A).

Fig. 12 (p. 385)

Szkic filogenezy pteraspidów.

Fig. 13 (p. 388)

Sagitalne przekroje rostralnej części pteraspidów: *a* układ u *Myxine* z naniesionym typem pteraspidowym; *b* pteraspid ze zrekonstruowaną częścią nosowo-oralną, zgodnie z hipotezą Stensiö (1958), ukazujący podobieństwo do *Myxine* i różne hipotetyczne elementy postulowane przez Stensiö; *c* pteraspid zrekonstruowany opierając się na budowie rostrum *Rhinopteraspis cornubica*, ukazujący okluzję płytek oralnych bezpośrednio naprzeciw ścianki wstępującej; *asc.lam.* ścianka wstępująca, *cart.pd.* poduszeczka chrząstkowa, *mo.* otwór ustny, *or.pl.* płytka oralna, *pr.nas.sin.* zatoka prenazalna, *ip.lab.pl.* górna płytka wargowa; chrząstka oznaczona linią przerywaną.

Pl. I

Rhinopteraspis cornubica (McCoy), dorsalna płytka medialna, ukazująca chropowatą ornamentację prążków dentyny. Lektotyp. A 6955 *a*; łupki z Dartmouth. Lantic i Lantwit, Kornwalia (okaz w Sedgwick Museum, Cambridge).

Pl. II

Rhinopteraspis cornubica (McCoy), wentralna powierzchnia rostrum, ukazująca pole preoralne, płytki oralne, ściankę wstępującą i rowki węchowe. Okaz D.1145, z wapieni plakodermowych w Daleszycach, znajduje się w Zakł. Paleozool. PAN w Warszawie. (Szczegółowe objaśnienia — *vide* fig. 1 w tekście).

Л. БЕВЕРЛИ ТАРЛО

RHINOPTERASPIS CORNUBICA (McCOY) И ЗАМЕЧАНИЯ О КЛАССИФИКАЦИИ И ЭВОЛЮЦИИ ПТЕРАСПИД

Резюме

Работа содержит первое описание рыла и ротовых частей *Rhinopteraspis cornubica* (McCoy) на основании образца найденного в последнее время в плакодермовом песчанике Далешиц около Кельц (Тарло, 1958).

Задняя часть вентральной поверхности рыла занята треугольным оральным полем, за которым находится наклонная восходящая стенка образующая переднюю часть свода ротового отверстия и ротовой полости. С каждой стороны этой стенки видна треугольная параоральная пластинка и глубокий желобок, проходящий между этой пластинкой и боковым краем восходящей стенки. Представляется, что это обонятельный желобок, по которому вода направлялась к органам обоняния расположенным по бокам рта. Скульптура преорального поля состояла из продольных полосок дентина, что до сих пор не наблюдалось у птераспид.

Оральные пластинки сохранены в естественном положении. Их имеется семь, причем срединная является наибольшей. Смотря спереди она треугольной формы, обращенная вершиной к вентральной стороне. Величина остальных пластинок, тоже несколько треугольных в разрезах, уменьшается по направлению к бокам ротового отверстия.

Особенности области рыла имеют основное значение для классификации птераспид и на их основании разграничены здесь роды. Автор приводит набросок классификации птераспид, в котором учитывает предложения Уайта и Стенше (White, 1935—60; Stensiö, 1958). Ниже приведены диагнозы родов, признаваемых автором настоящей работы.

Род *Penygaspis* Stensiö, 1958
Типичный вид: *P. dixoni* (White, 1938)

Диагноз. Небольшой птераспид с медиальной пластинкой длиною менее 4 см; вентральная и дорсальная пластинка составленные синхрономориальной центральной единицей, украшенной продольными полосками дентина.

Род *Protopteraspis* Leriche, 1924
Типичный вид: *P. gosseleti* Leriche, 1906

Диагноз. Небольшой птераспид с тупым округленным рылом; небольшая пинеальная пластинка широко отделенная от орбитальных; преоральное поле неразвитое; восходящая стенка узкая: оральные пластинки соединяются с срединным вентральным щитком.

Род *Zascinaspis* Stensiö, 1958
Типичный вид: *Z. heintzi* (Brotzen, 1936)

Диагноз. Птераспид средней величины, широкий; пинеальная пластинка пентагональная, соприкасающаяся со срединным выступом оральной; преоральное поле не развито; восходящая стенка широкая и глубокая.

Род *Althaspis* Zych, 1951
Типичный вид: *A. samsonowiczi* n. nom.

Диагноз. Птераспид длиннорылый; широкая пинеальная пластинка, прилегающая к узкому срединному отростку орбитальной; параоральная пластинка; вентральная поверхность рыла украшена поперечными полосками дентина с цикломориальным приростом; восходящая стенка развита.

Род *Podolaspis* Zych, 1931
Типичный вид: *P. lerichei* (Zych, 1927)

Диагноз. Птераспид широкий; пинеальная пластинка широкая, полукруглого очертания, не соприкасается с орбитальными; преоральное поле имеется, но не выделено отчетливо от восходящей стенки.

Род *Loricopteraspis* nov.
Типичный вид: *L. althi* (Stensiö, 1958)

Диагноз. Птераспид тупорылый; преоральное поле состоит из небольших синхрономориальных единиц, некоторые из них покрыты продольными полосками дентина, другие-же поперечными.

Род *Pteraspis* Kner, 1847
Типичный вид: *P. rostrata* (Agassiz, 1835)

Диагноз. Типичный птераспид с треугольным рылом, которое может удлиняться спереди преорального поля; преоральное поле хорошо развито, украшено маленькими бородавочками; восходящая стенка развита; тонкие оральные пластинки соединяются с посторальными.

Род *Mylopteraspis* Stensiö, 1958
Типичный вид: *M. robusta* Stensiö, 1958

Диагноз. Птераспид с треугольным рылом; пинеальная пластинка достигает латерально орбитальную; преоральное поле хорошо развито; имеется восходящая стенка; задние рога вентральной поверхности рыла выступают к середине; оральные пластинки массивные.

Род *Rhinopteraspis* Jaekel, 1919
Типичный вид: *R. cornubica* (McCoy, 1851)

Диагноз. Птераспид с удлиненным рылом в виде острия; преоральное поле образованное единичной синхрономориальной единицей; восходящая стенка хорошо развита; оральные пластинки массивные; имеются обонятельные желобки; грубая орнаментировка из полосок дентина (3—6 мм).

Особенности области рыла имеют таксономическое значение и указывают филогенетические соотношения. С другой стороны, пропорции разных пластинок панцыря изменяются повидимому с геологическим возрастом и, что из этого следует — ценны единственно при рассмотрении общих эволюционных направлений. Основываясь на признаках области рыла можно установить, что длиннорылые формы и с широким панцырем были осуществлены двумя независимыми путями и автор старается наметить способ, как это произошло.

Наконец расположение ротовых частей *R. cornubica* имеет большое значение для суждения о теории Стенше, касающейся внутреннего строения рыла птераспид. Автор приходит к выводу, что птераспидоморфы (Heterostraci), обладая двойными обонятельными мешками, должны быть исключены из линии предков круглоротых типа миксин.

PLATES

EXPLANATION OF PLATES

Pl. I

Rhinopteraspis cornubica (McCoy)

Dorsal median plate showing coarse ornamentation of dentine ridges. Lectotype, A 6955a, form Dartmouth Slates, Lantic and Lantwit Bays, Cornwall, housed in Sedgwick Museum, Cambridge.

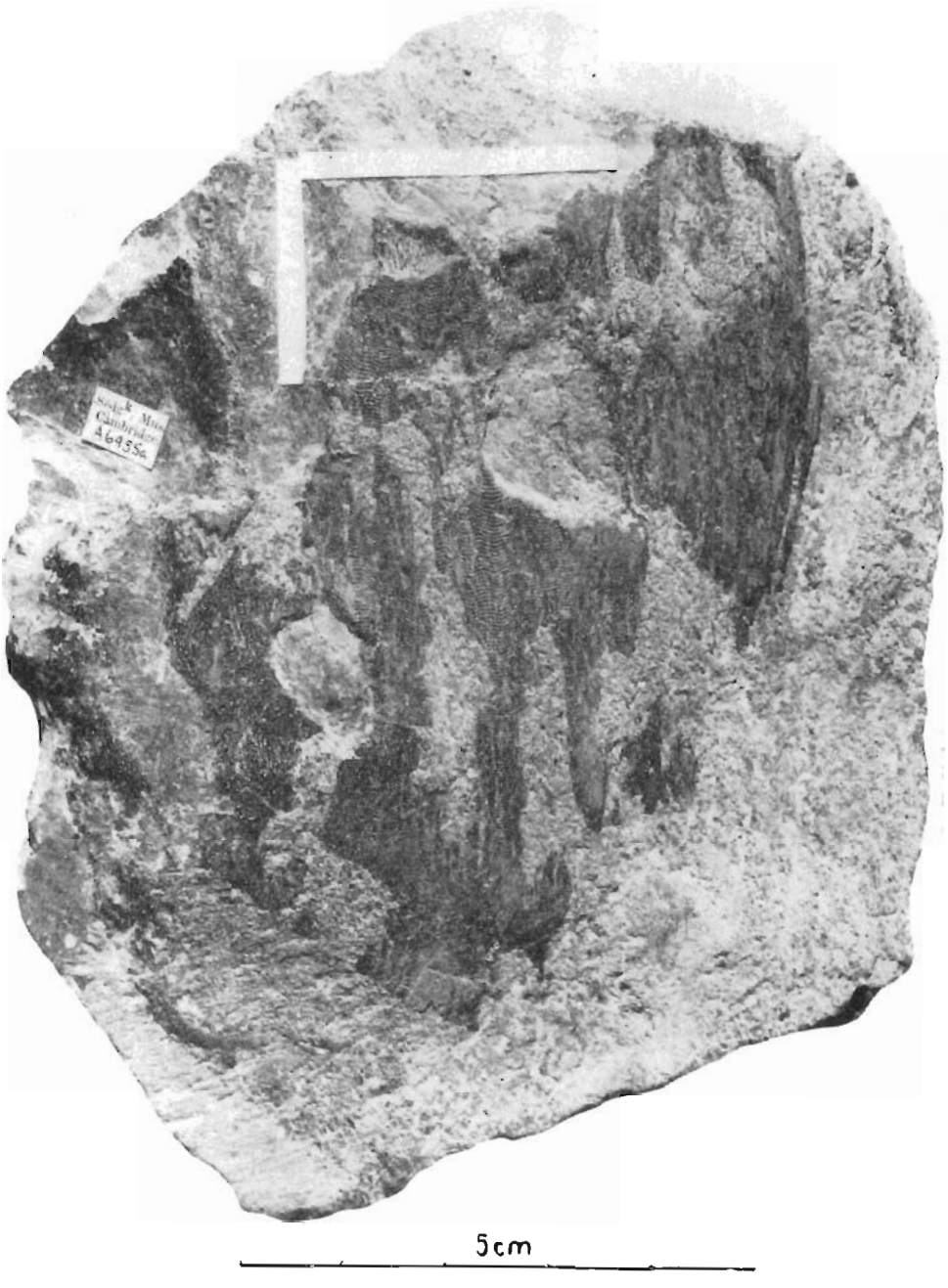
Photograph by A. Barlow

Pl. II

Rhinopteraspis cornubica (McCoy)

Ventral surface of snout showing pre-oral field, oral plates, ascending lamella, and olfactory grooves. Specimen D. 1145 from Placoderm Sandstone, Daleszyce, near Kielce, Holy Cross Mountains, housed in Palaeozoological Institute, Warsaw (for explanation see also text-fig. 1).

Photograph by W. Brackenbury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Cambridge
A6455a
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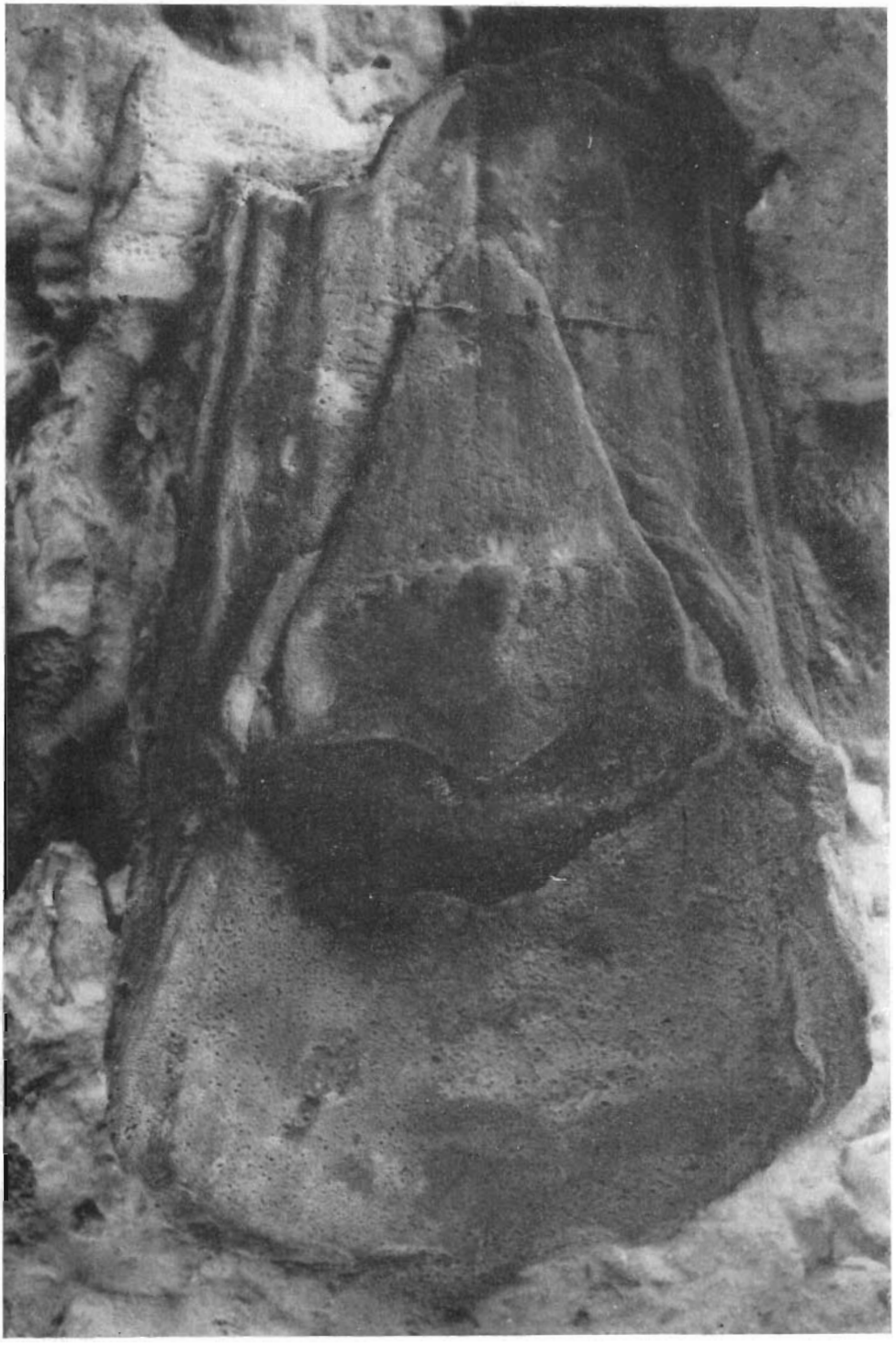
5 cm