X—The Ostracoderm *Pteraspis* Kner and the Relationships of the Agnathous Vertebrates

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I—Introduction

Ever since the attention of geologists turned to the Old Red Sandstone more than one hundred years ago, the shields and isolated plates of the Ostracoderm now known as *Pteraspis* have been familiar fossils to all who have collected from the lower beds of that formation in the West of England ; indeed, not only are they the commonest fossils in the Lower Old Red Sandstone, but often they are the sole identifiable organic remains present, and are locally abundant.

At the first it was realized that these isolated shields covered only the anterior half of the animal, but the nature of the covering of the posterior region was unknown for many years, and its form is as yet undescribed. Even now, when the genus has been recorded from widespread areas abroad and hundreds, possibly thousands, of specimens have been collected in England alone, less than a dozen examples of the squamation from behind the carapace have been figured or described, and all of these consist of either isolated scales or at the most fragments, generally from immediately behind the shields ; and none gives any indication of the shape of the caudal region. The published restorations of the genus therefore have been entirely hypothetical in regard to the form of the hinder part of the animal (LANKESTER, 1868, p. 18, text-fig. 8 ; WOODWARD, 1891, p. 161, text-fig. 15 ; TRAQUAIR, 1899, p. 851, text-fig. 7 ; LERICHE, 1903, p. 169, text-fig. 1 ; GROSS, 1933, p. 107, text-fig. 6). Except the last, these restorations agree in showing a long heterocercal tail, which for mechanical reasons would have made it extremely difficult for the creature to have raised itself from off the bottom, since the effect of the thrust of such a tail would have been to depress the snout,* and *Pteraspis* had no paired limbs to counteract this movement ; while the arrow-shaped diphycercal tail given by GROSS to *P. dunensis* is scarcely more practical. The discovery by KIAER (1924) of the reversed heterocercal, or hypocercal, tail in the *Anaspida* gave the first clue as to the type of propelling organ that the Pteraspids must have had, and in restoration-models made for the Geological Department of the British Museum four or five years ago *Pteraspis* was given a lower caudal lobe much longer than the upper. A little later KIAER's restoration of *Anglaspis* showed that a hypocercal tail was present in the allied Cyathaspids (KIAER, 1932, p. 19, text-fig. 11) ; and finally, while collecting Lower Old Red fossils in Herefordshire with Mr. H. A. TOOMBS, I obtained specimens of *Pteraspis rostrata* complete with caudal region, and these show clearly that the forecast of a hypocercal tail was correct (figs. 1–2, 61–65, and 98–99, Plate 25).

The history of the genus *Pteraspis* until 1891 has been summarized by WOODWARD (1891, p. 161) and need not be repeated. Since that date there have been published a few short papers by LERICHE (1903–26), chiefly on *P. crouchi* and *P. dunensis*, one on the latter species by DREVERMANN (1904), a description of the sensory canal system and a critical discussion of the organization of the genus by STENSIÖ (1926, 1927, p. 315), and a remarkable paper on some new species from Spitsbergen by KIAER (1928). In this last work KIAER described and figured the complete dorsal armour of one species and the ventral armour, including the mouth-plates, of a second. Subsequently STENSIÖ (1932, pp. 183–194) described a hypothetical reconstruction of part of the internal anatomy of the anterior region of *Pteraspis* based on KIAER's material and made the suggestion that the so-called external ornamentation of the plates of the carapace was formed by the grooves of the mucous system. On this point, light is thrown by some of the specimens described below and will be referred to again later. Lastly, important papers on the Pteraspids have been published by ZYCH (1927, 1931), GROSS (1933, 1933*a*), and BROTZEN (1933*b*).†

* *See* BREDER, 1926, p. 225.

† Dr. BROTZEN has done me the favour of allowing me to read the MS. of a further contribution to this subject, which will be published shortly. This deals particularly with the broad forms originally described from the U.S.A. by BRYANT (1932, 1933, 1934) as *Protaspis*.

II—Material and Methods*

The principal specimens are the more or less complete animals mentioned above. There are six of these specimens (figs. 1 and 2, and figs. 98, 99, Plate 25), each of which preserves almost the whole of the external anatomy, including the mouth-plates and the caudal fin. In addition, there are a number of important fragmentary specimens, including two fine tails (figs. 51, 55) and a caudal region that shows the dorsal lateral lines (fig. 64). All the specimens are flattened, the carapaces generally dorso-ventrally, the tails laterally, and in every instance both sides are preserved, one on one slab, the other on its counterpart. Originally, all the bone was present; but this was so crushed that it masked all the details, and, since the matrix was fortunately free from calcareous matter, this was etched away with dilute HCl, leaving exquisite external moulds that show the very finest details.

The matrix of these fossils is a very fine, green silt-stone which formed a thin, restricted lenticular band in a rock of normal coarse grey sandstone. The first specimen (figs. 98, 99, Plate 25) was found in pieces among the debris on the floor of the quarry known as Wayne Herbert, near Newton, S.W. Herefordshire, and it is a remarkable fact that the caudal region was found by Mr. H. A. Toombs two months before the rest of the specimen, and that neither fragment was collected on account of the *Pteraspis*, which at the time showed merely as a black streak across the fractured ends of the two slabs, on one of which there was a fine *Cephalaspis* and on the other the remains of an Acanthodian. Although several other fragmentary remains were obtained later, the band itself was not located for nearly a year, chiefly owing to obscuring of the face of the quarry by vegetation after it had fallen into disuse, but it was finally found to be a thin bed at the bottom of the quarry-face, about 2 in. thick, and covering an area of approximately 9 ft. by 4 ft. On three sides it either passed into the coarser, non-productive rock or just thinned out; but how much had already been quarried away is not known, probably not a great deal. The form of this bed is important, for it seems to me that it represented a single, dried-up pool, and that therefore the animals it contained were strictly contemporaneous. From this it follows that the extraordinary variations to be found in the score of specimens of *Pteraspis* (apparently no two specimens are identical) are individual, for it is most unlikely that numerous species of a single genus should be found in so restricted an area and each represented by only one or two specimens. With the *Pteraspis* were a similar number of *Cephalaspis*, both large and small, and about a dozen Acanthodians, some of them complete and representing at least two genera, one of them being about 1 ft. in length. *Pterygotus* was also represented by large fragments, apparently of *P. anglicus*, but no determinable plant-remains were found. All beds in this quarry are considered by Mr. Wickham King to belong to his Dittonian zone II. 2 (*see* King, 1925, p. 383; 1934).

* Unless otherwise stated, all the specimens described and figured in this paper are in the Department of Geology of the British Museum (Natural History).

Other new specimens described below comprise a fair number of well-preserved dorsal shields, but the great majority are isolated dorsal and ventral discs. Some were found in the beds above the silt-stone lenticle in Wayne Herbert quarry, while many others came from Castle Mattock, Pool, and Gwyn Genni quarries a few miles away. The quarries are apparently all in the same horizon except the last, which

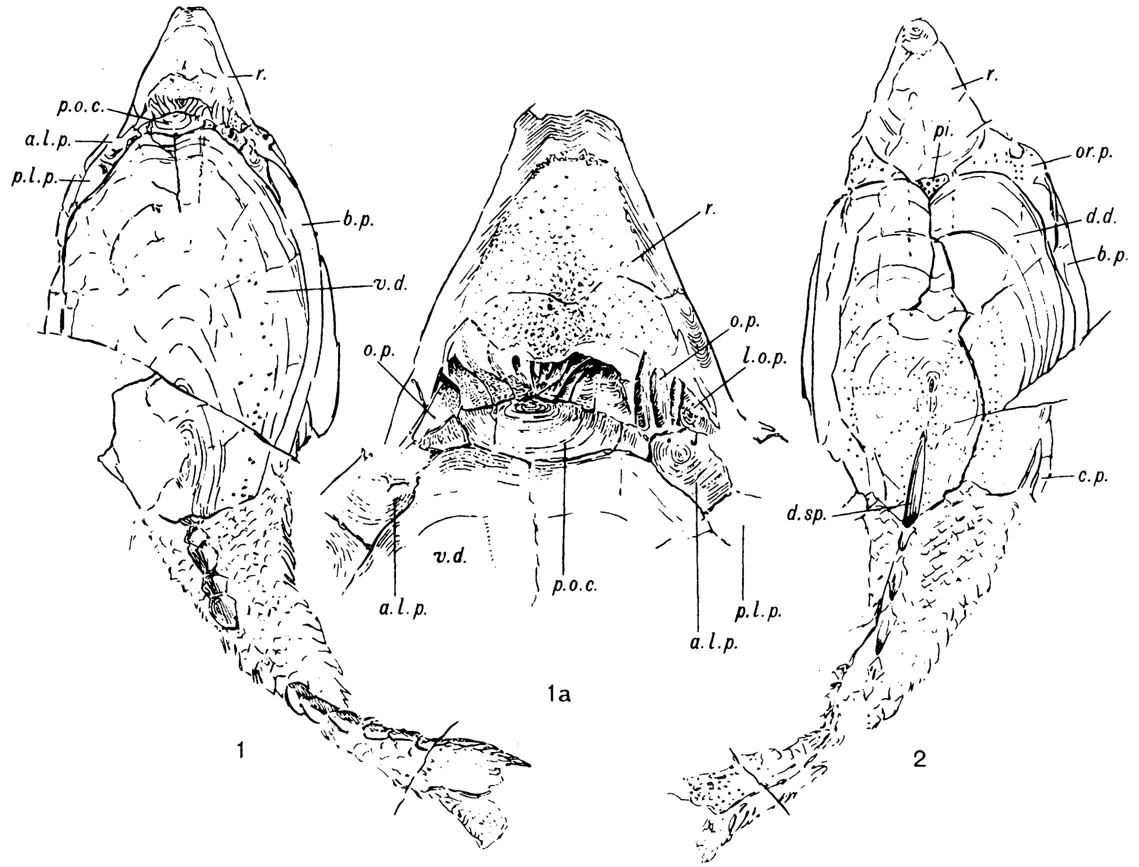


FIG. 1—*Pteraspis rostrata* (AGASSIZ), var. *toombsi* nov. Ventral side of almost complete individual preserved as external mould. Lower Old Red Sandstone (zone II. 2) ; Wayne Herbert Quarry, Herefordshire. (P. 16789—× $\frac{3}{4}$ approx.) 1A. Oral region of same. (× 3 approx.)
FIG. 2—Dorsal side of same specimen. (P. 16790—× $\frac{3}{4}$ approx.)
a.l.p., anterior lateral plate ; *b.p.*, branchial plate ; *c.p.*, cornual plate ; *d.d.*, dorsal disc ; *d.sp.*, dorsal spine ; *l.o.p.*, lateral oral plate ; *o.p.*, oral plates ; *or.p.*, orbital plate ; *pi.*, pineal plate ; *p.l.p.*, posterior lateral plate ; *p.o.c.*, post-oral cover ; *r.*, rostrum ; *v.d.*, ventral disc.

Unless otherwise stated, the lettering in all figures follows that given in figs. 1 and 2.

seems to be in zone II. 3, and all the rocks, although varying in colour from green to deep red, are poor in calcareous matter, so that the treatment of the fossils with acid has produced equally good results ; indeed, in some specimens not only are the external details finely preserved, but the infillings of matrix of the sensory canals are left standing in bold relief. In these quarries several species of Cephalaspids are commonly found with the Pteraspids, while spines on *Onchus* and indeterminable plant-remains occur here and there. The only other fossils in these beds (other than the silt-stone layer at Wayne Herbert) are a fragment of the Arthropod, *Prearcturus gigas*, from the uppermost beds at Wayne Herbert, and broken plates of the Arthrodire *Weigeltaspis*, a new genus recently described from Poland (BROTZEN, 1933*a*, p. 648).

The remaining specimens have been developed by hand, except for a few internal casts, and show the actual plates. While most of these were collected many years ago, the best examples are from a magnificent series of dorsal and ventral shields and isolated scales collected by Mr. WICKHAM KING from the Guildings Brook section, also in zone II. 2, at Trimpley, Worcestershire, while of equal interest are the less perfect specimens, also collected by Mr. KING, from Downtonian beds, zones I. 8–9, in Corvedale, Shropshire.

The specimens from the Dittonian of Herefordshire are chiefly referable to forms of *Pteraspis rostrata* (AGASSIZ) and *P. crouchi* LANKESTER, but Castle Mattock and Gwyn Genni quarries have each yielded a few specimens of a new species, both of which are remarkable in that they resemble some of the Podolian Pteraspids in having high, vertical dorsal spines and large, arcuate cornua. The Trimpley fossils are all of *P. rostrata*, but those from Corvedale belong to an undescribed species which has been recorded as "*Cyathaspis leathensis*" by KING (1925, p. 387; 1934, p. 530). Lastly, one fragmentary specimen of the Scottish *P. mitchelli* Powrie is described, so that all the known British species are included except *P. cornubica* (M'COY), of which no satisfactory material is available.

The numerous specimens of *P. crouchi* and *P. rostrata* show that there is a remarkable degree of variation among individuals of the same species. Often the characters are constant for the individuals from one locality or area, and are considered to be of varietal value, but in one instance certain features are inconstant even within the variety. Moreover it seems, by comparison with material from other countries, that the value of a character varies from area to area, or from species to species. These points have become clear only as the result of the wealth and, more especially, the completeness of the material now available, for it is often difficult to determine even the species of isolated plates satisfactorily, particularly the dorsal and ventral discs so commonly found, since, apart from individual variations, they change in shape with age, and at certain stages the disc of one species closely resembles that of another at a different stage. In extreme cases, even a nearly complete animal can be identified only after careful scrutiny (*cf.* figs. 18, 42, and fig. 104, Plate 26).

* * * * *

The genus *Pteraspis*, as we now know, had a complex armoured carapace covering the anterior half of the body, and a caudal region completely invested in overlapping rhomboid scales (*see* restorations, figs. 83–85). The carapace is longer than broad and more or less rectangular, with a triangular rostrum that generally varies in length according to the species, while laterally, at the hinder end of the shield, there is on each side a cornu, behind and slightly above the single branchial opening. The carapace is flattened dorso-ventrally in front, but it becomes gradually deeper towards the hinder end, where there is a median dorsal spine.

The orbits are lateral or slightly dorsal in position, and are placed far forwards, at the level of the hinder margin of the rostrum.

Apart from the dorsal spine,* which, as BRYANT (1933, p. 291) has suggested, is probably not a part of the carapace at all but an enlarged ridge-scale, there are nine plates visible in dorsal view,† and these, since they are frequently found in association, are known as the dorsal shield ; they are the dorsal disc, forming the greater part of the shield, the minute pineal plate,* the rostrum, and the paired orbital, branchial and cornual plates ; all but the first two are visible from below. So far, no external nares have been discovered.

The ventral shield is largely composed of the ventral disc, and this is usually the only plate found, for the others are all small and very rarely preserved, being known only in the specimens of *P. rostrata* from the silt-stone lenticle at Wayne Herbert and in one foreign species. In the English fossils these plates consist of two pairs of laterals and a variable number, from one to three, of hitherto undescribed elements, the post-oral covers ; but in the foreign species, *P. vogti* KIAER (1928, text-figs. 2, 3) from the Downtonian of Spitsbergen, there is apparently only one pair of lateral plates and no post-oral covers at all.

The oral region, between lower posterior margin of the rostrum and the anterior border of the ventral disc, is partly filled in by the post-oral covers, on the inner side of which is a series of about sixteen strangely shaped oral plates.

The scales region behind the carapace is deep and broad anteriorly, but it tapers gradually behind to form a rounded caudal peduncle, which supports a deep, strongly hypocercal tail. There are no other fins, median or paired.

The growth-stages of the individual plates can often be determined with some degree of precision, for they are frequently marked by local thickenings of the bone, and when this is absent they can generally be estimated by the " ornamentation," which consists of very fine ridges running approximately parallel with the margins of the plate.

III—DESCRIPTIONS OF THE SPECIMENS

(*a*) Size and Proportions

The size of individuals naturally varies with age and species. In the best-known English form, *P. rostrata*, the dorsal shield without the dorsal spine measures on an average about 80 mm out of a total length of 165 mm and has a maximum breadth of a little under 50 mm, but the largest specimens greatly exceed these figures, for

* It is difficult to believe that the dorsal spine and the pineal plate are really absent from *P. gosseleti* LERICHE (1906, p. 26, Plate 1, figs. 6–9) ; if so, then this species must be referred to a new genus.

† These plates, as remarked by ZYCH (1931, p. 23) and BROTZEN (1933*b*, p. 436, etc.), are fused together in the adult by their basal layer.

they attain a length from the tip of the rostrum to the hinder margin of the dorsal shield of not less than 133 mm, and would therefore have had a total length of about 270 mm. But these very large specimens are exceptional, at any rate in collected material, and for other reasons are considered to belong to a separate variety.

The dorsal shields of the other common English species, *P. crouchi*, do not, so far as we are aware, attain so large a size, but the biggest examples are a little longer than the average shields of *P. rostrata*, about 100 mm, but of this the rostrum takes up a larger proportion, so that the dorsal discs have approximately the same dimensions.

The dorsal shield of the new species from Castle Mattock Quarry, *P. jackana*,* is also about as long as the average specimens of *P. rostrata*, but as the rostrum is short the dorsal disc is actually longer and also very much wider measured over the curve.

The shields of the second new species, *P. stensiöi*,† are both rather smaller than that of *P. jackana*, the larger measuring a little over 70 mm in length.

The specimen of *P. mitchelli* was probably larger than the foregoing, but *P. leathensis* was easily the smallest of the British species, for the dorsal disc has only about two-thirds of the length of that of our standard *P. rostrata*, while the ventral discs are relatively smaller.

(*b*) The Plates Forming the Carapace

(i) *The Dorsal Shield*

The dorsal disc—In its general form the dorsal disc of a fully grown specimen of each of the six British species of *Pteraspis* described in this paper is oblong and longer than broad, with more or less parallel sides when the specimens are flattened ; but in nature the hinder part of the plate was strongly arched transversely, so that the breadth appears to diminish gradually towards the rear (figs. 3*b*–*d*). The anterior margin is always indented medially to receive the pineal plate, and the antero-lateral corners are more or less rounded off, so that the plate has roughly the form of a truncated heart. Posteriorly the disc is abruptly bevelled by the two hinder margins, which meet at the centre to form a median posterior angle. These posterior margins may be straight or slightly concave, and the angle they form is deeply excavated for the insertion of the dorsal spine. Although in general form the dorsal disc of the adult is similar in four of the species, it varies considerably in detail, not only according to the species but with age, so that isolated specimens are often extremely difficult to determine even specifically.

The dorsal disc of *P. rostrata* is found in five forms so different that, in conjunction with differences in other plates, it seems proper to consider them as belonging to distinct varieties.

* This new species is named in honour of Mr. G. H. Jack, *F.G.S.*, formerly County Surveyor of Herefordshire, to whom I am indebted directly for many of the fine new Ostracoderms from Herefordshire, now in the British Museum (Natural History), and indirectly for all.

† Named in honour of Professor Erik Stensiö, whose researches have done so much to establish the systematic position of the " Ostracoderms."

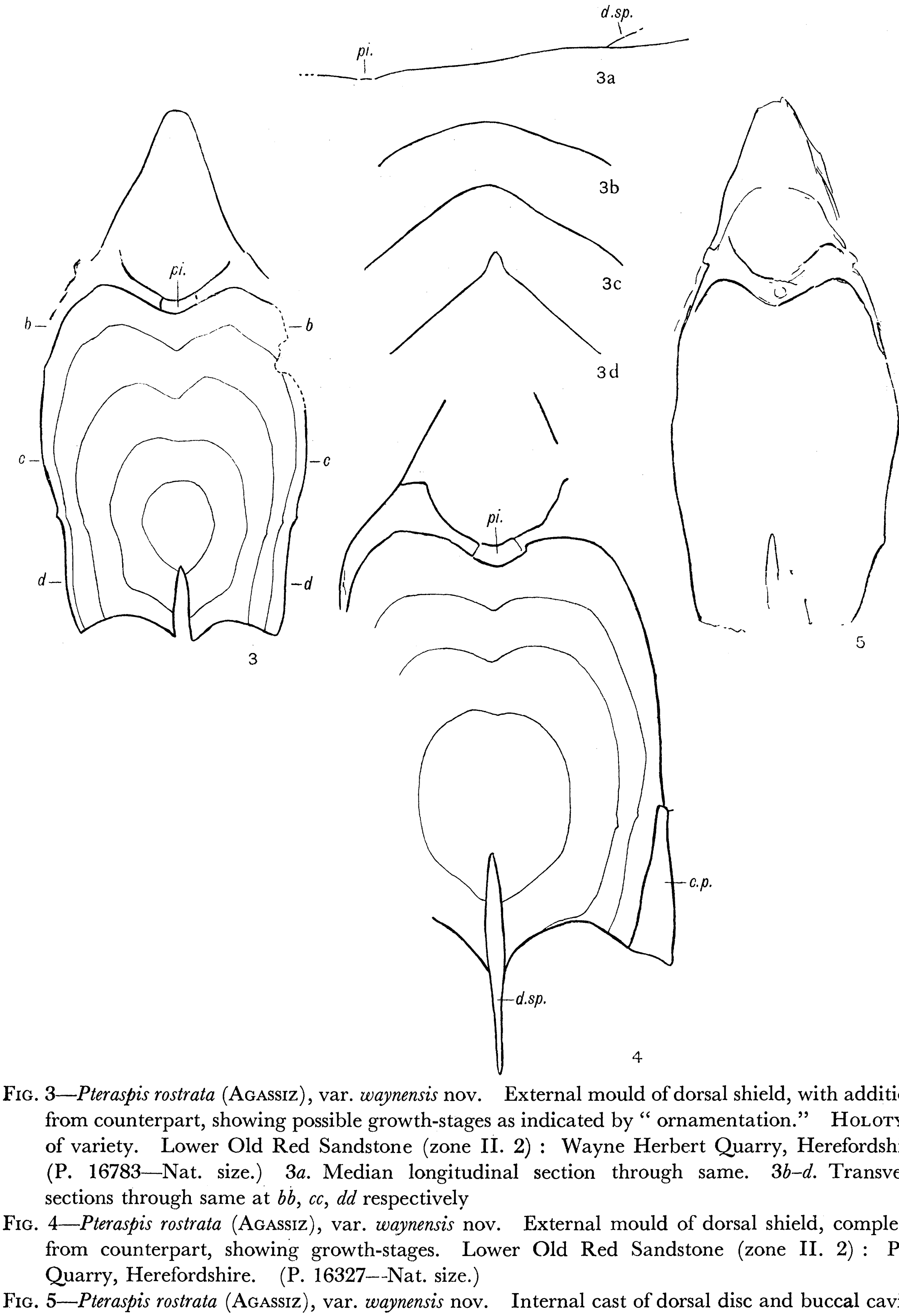


FIG. 3—*Pteraspis rostrata* (AGASSIZ), var. *waynensis* nov. External mould of dorsal shield, with additions from counterpart, showing possible growth-stages as indicated by " ornamentation." HOLOTYPE of variety. Lower Old Red Sandstone (zone II. 2) : Wayne Herbert Quarry, Herefordshire. (P. 16783—Nat. size.) *3a*. Median longitudinal section through same. *3b–d*. Transverse sections through same at *bb*, *cc*, *dd* respectively

FIG. 4—*Pteraspis rostrata* (AGASSIZ), var. *waynensis* nov. External mould of dorsal shield, completed from counterpart, showing growth-stages. Lower Old Red Sandstone (zone II. 2) : Pool Quarry, Herefordshire. (P. 16327—Nat. size.)

FIG. 5—*Pteraspis rostrata* (AGASSIZ), var. *waynensis* nov. Internal cast of dorsal disc and buccal cavity, with outline of rostrum. Lower Old Red Sandstone (zone II. 2) : Wayne Herbert Quarry, Herefordshire. (P. 16522—Nat. size.)

AGASSIZ's type-specimen of *Cephalaspis rostratus* (*see* LANKESTER, 1868, Pl. IV, fig. 2), now in the Museum of the Geological Survey (No. 21444), is largely an internal cast from beds of the Dittonian zone II. 1 at Whitbach, Shropshire, and is very immature. It is therefore difficult to be certain as to what is the typical form of the species until more material has been collected from the type-locality and horizon, and this, for the time being, is impossible owing to the state of the quarry ; I have therefore ventured to name all five varieties, although it is possible that one may later be considered to be of the typical form.

The first variety, *P. rostrata waynensis*, occurs principally at Wayne Herbert Quarry, Herefordshire, where, with a single exception, all the specimens found above the silt-stone lenticle are of this type. One dorsal shield from Pool Quarry, a few miles distant from Wayne Herbert (fig. 4), seems to be of the same form, as is also, though with less certainty, a fragment from Cradley (P. 8867). A typical specimen of this variety, of average size and quite uncrushed, is No. P. 16783 (figs. 3, 66, and fig. 101, Plate 25; counterpart No. P. 16784, fig. 67). The disc measures about 55 mm in length* and 43 mm at its broadest, somewhat in front of the middle of its length. The anterior emargination is wide and somewhat angular, the antero-lateral corners rounded. The lateral margins are slightly sinuous, and run so that the uncrushed shield appears to narrow towards the hinder end. At about one-third of their length from the posterior margins their curvature is interrupted by a slight angular projection, which in the complete animal forms the point where the branchial plate separates from the dorsal disc to form the branchial opening (*see* restoration, fig. 79). The hinder margins of the disc are almost directly transverse and decidedly concave, while the socket of the median dorsal spine is short and rather narrow. In median longitudinal section the disc is nearly straight, but rises gently towards the rear (fig. 3*a*). In cross-sections (figs. 3*b*–*d*) the disc is gently arched anteriorly, but this arching increases and becomes more angular backwards, until on each side of the dorsal spine the surfaces are flat and nearly at right-angles to one another.

The approximate growth-stages, as indicated by the "ornamentation," are interesting, fig. 3. At first, the lines are oval without an anterior emargination and with only a notch for the reception of the dorsal spine. Growth in the early stages seems to have taken place more or less evenly around the periphery of the immature plate, although the shape became more quadrangular and the insertion of the median dorsal spine deeper. When the length was about 35 mm, the anterior emargination became noticeable and growth along the posterior margins ceased ; thereafter the plate gradually assumed its adult shape. This marked change in shape with age makes it difficult to understand how the various plates forming the dorsal shield (and this applies equally to those on the ventral surface) fitted together in the very young animals, if they were fully armoured ; it is, of course, possible that they were not, but that there were considerable spaces between the individual plates. ZYCH (1931,

* The length of the dorsal disc, as used in this paper, is measured along the median line, from the centre of the pineal emargination to the level of the hinder margin on each side of the socket of the dorsal spine.

pp. 69–72), in discussing the distribution of the sensory canal system, makes some pertinent remarks on this point ; he suggests that the young Pteraspids had no carapace, and that it was not until they had attained almost adult dimensions that it commenced to form. The gradual ossification of the carapace, he remarks, extended from the primitive centre of growth over the anterior surface of the animal. He bases his theory on three small specimens of the dorsal disc of an unidentified species of *Pteraspis* (*ibid.*, figs. 42–44), which, while they have the adult form, lack the outer lateral sensory canals ; and argues that these canals must have been present but in the soft, unossified tissues between the plates ; moreover, small discs are always found isolated and never with the other plates of the dorsal shield attached to them. I think that he is right ; but it is curious that very small shields of the rounded form seen in the earliest growth-stages are never, in my experience of the English species, found, as they should have been if the growth had been gradual from the start, although their smallness and shapelessness may be reasons for their absence from collectors' bags.

The discs of the specimens with caudal regions from Wayne Herbert (fig. 2 ; fig. 99, Plate 25 ; and figs. 104–106, Plate 26) have similar proportions to the foregoing, but they differ in the form of the anterior margin, which is decidedly narrower owing to the bevelling of the antero-lateral corners, and the pineal emargination is very much narrower and more definite. This form I have named *P. r. toombsi*, in honour of Mr. H. A. Toombs, to whom the discovery of the fine specimens from the silt-stone lenticle is entirely due.

A third variety, *P. r. virgoi*,* is represented by a single dorsal shield in counterpart (fig. 15), one side of which shows the greater part of the external mould, the other the internal cast. This disc has similar proportions to those of the two preceding forms, but the anterior margin is wide and, except for the narrow and deeply incised pineal emargination, almost straight, while the antero-lateral corners are angular. The socket of the dorsal spine is long and narrow.

Another variety, to be known as *P. r. trimpleyensis*, is represented by the fine specimens from the Guildings Brook section (II. 2) at Trimpley, Worcestershire, collected by Mr. Wickham King. The dorsal disc (fig. 7 ; fig. 100, Plate 25) is readily distinguished from those of the other forms by its extremely narrow pineal emargination and its broad, rounded antero-lateral corners. All the specimens from this locality are of this kind (*cf.* the broad, distorted specimen, fig. 8), which seems nearest to the typical form and to numerous, rather ill-preserved specimens from Cradley (fig. 6—*see* Lankester, 1868, Pls. V–VII), except that the disc is decidedly broader. The early stages are similar to those of *P. r. waynensis*.

The opposite tendencies are seen in certain large specimens from Monmouthshire, which I consider to form a fifth variety, *P. rostrata monmouthensis*. In these (fig. 9) the anterior emargination is very wide and angular, and the antero-lateral corners are

* This form is named in honour of Mr. R. G. Virgo, District Surveyor of the South-Western area of Herefordshire, in appreciation of the very great help he has always given me in collecting material from the quarries in his charge.

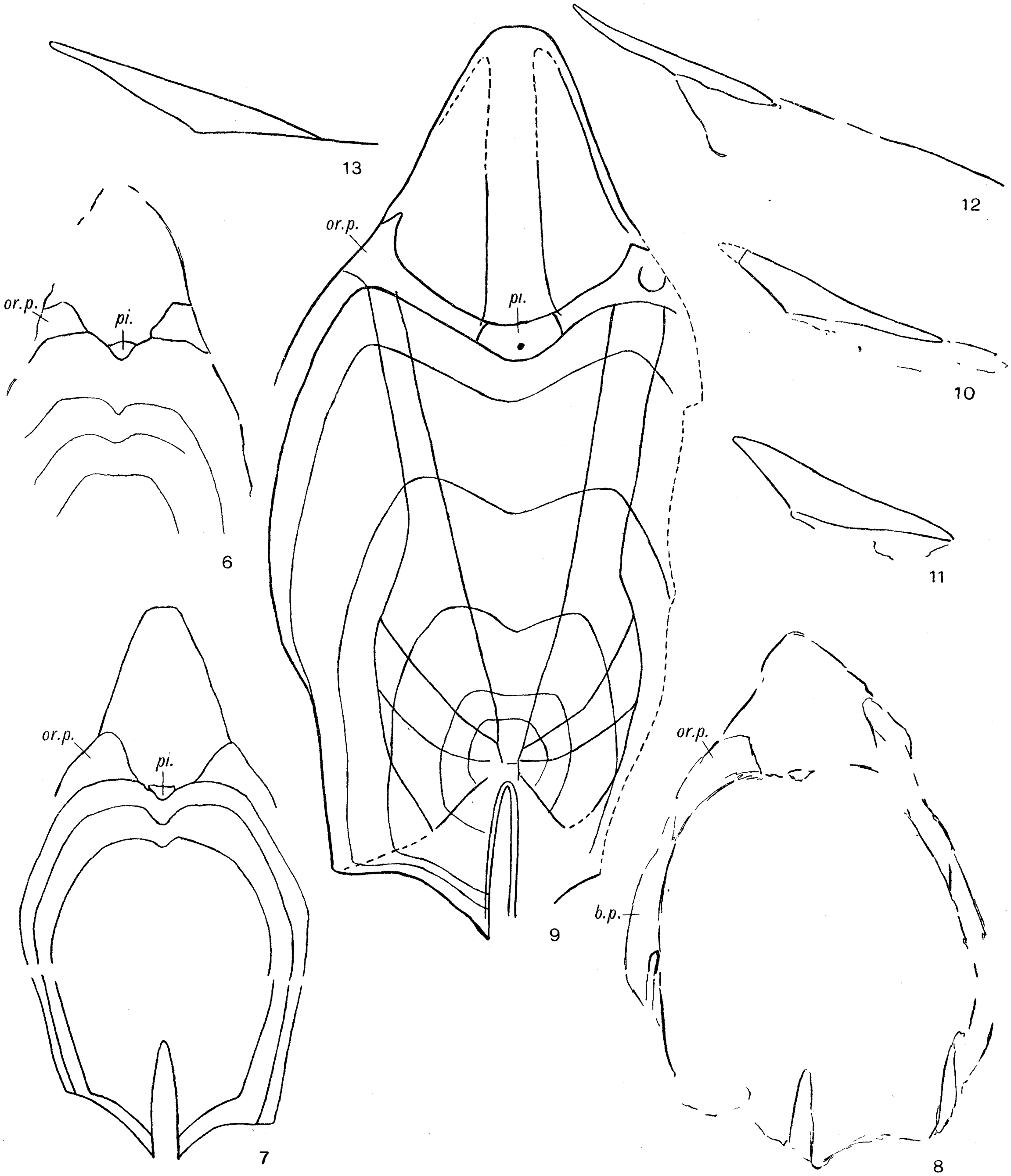


FIG. 6—*Pteraspis rostrata* (AGASSIZ), var. *trimpleyensis* nov. Anterior part of dorsal shield preserved as external mould. Lower Old Red Sandstone (zone II. 1) : Cradley, Herefordshire. (P. 3242*a*—Nat. size.)

FIG. 7—*Pteraspis rostrata* (AGASSIZ), var. *trimpleyensis* nov. Complete dorsal shield showing growth-stages ; branchial and cornual plates and median dorsal spine omitted. HOLOTYPE of variety. Lower Old Red Sandstone (zone II. 2) : Guildings Brook, Trimpley, Worcestershire. (P. 16478.I—slightly reduced.)

FIG. 8—*Pteraspis rostrata* (AGASSIZ), var. *trimpleyensis* nov. Broad and much distorted specimen. Lower Old Red Sandstone (zone II. 2) : Guildings Brook, Trimpley, Worcestershire. (P. 16481.I—Nat. size.)

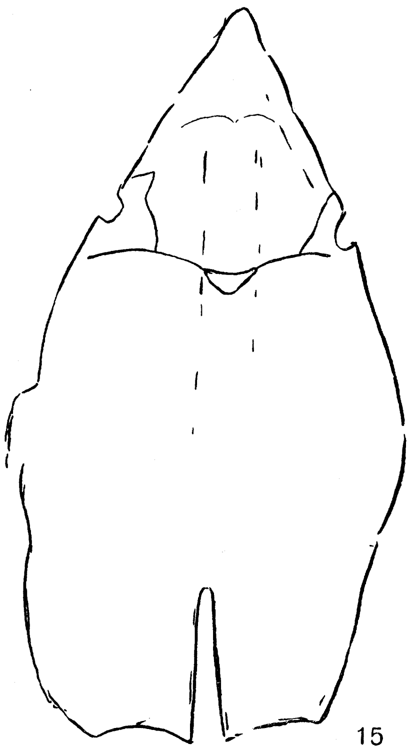
FIG. 9—*Pteraspis rostrata* (AGASSIZ), var. *monmouthensis* nov. Dorsal shield preserved as external mould and showing approximate growth-stages based on " ornamentation " and distribution of sensory canal system. HOLOTYPE of variety. Lower Old Red Sandstone (zone II. 1) : Goldtops, Monmouthshire. (P. 5034—Nat. size.)

FIGS. 10–11—*Pteraspis rostrata* (AGASSIZ), var. *trimpleyensis* nov. Dorsal spines in side view. Lower Old Red Sandstone (zone II. 2) : Guildings Brook, Trimpley, Worcestershire. (P. 16474, P. 16475—$\times 1\frac{1}{4}$.)

FIG. 12—*Pteraspis crouchi* LANKESTER, var. *mattockensis* nov. Dorsal spine in side view. Lower Old Red Sandstone (zone II. 2) : Castle Mattock Quarry, Herefordshire. (P. 16846—$\times 1\frac{1}{4}$.)

FIG. 13—*Pteraspis rostrata* (AGASSIZ), var. *toombsi* nov. Dorsal spine in side view. Lower Old Red Sandstone (zone II. 2) : Wayne Herbert Quarry, Herefordshire. (P. 17477—$\times 1\frac{1}{4}$.)

almost right-angles, while the early growth-stages are nearly square. In the specimen figured, P. 5034, the dorsal disc is not less than 88 mm long in the median line, and thus it is the largest example of *P. rostrata* recorded. This form has not been found beyond Monmouthshire and the adjacent borders of Herefordshire.



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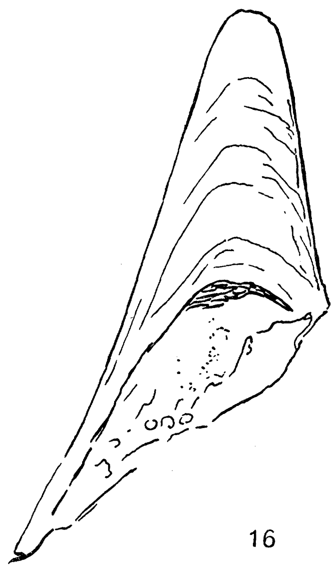

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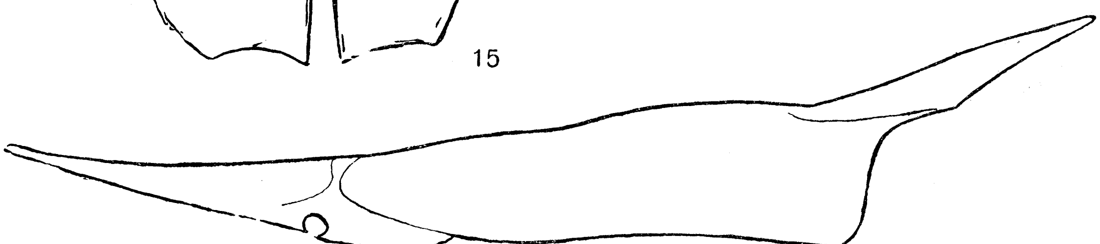

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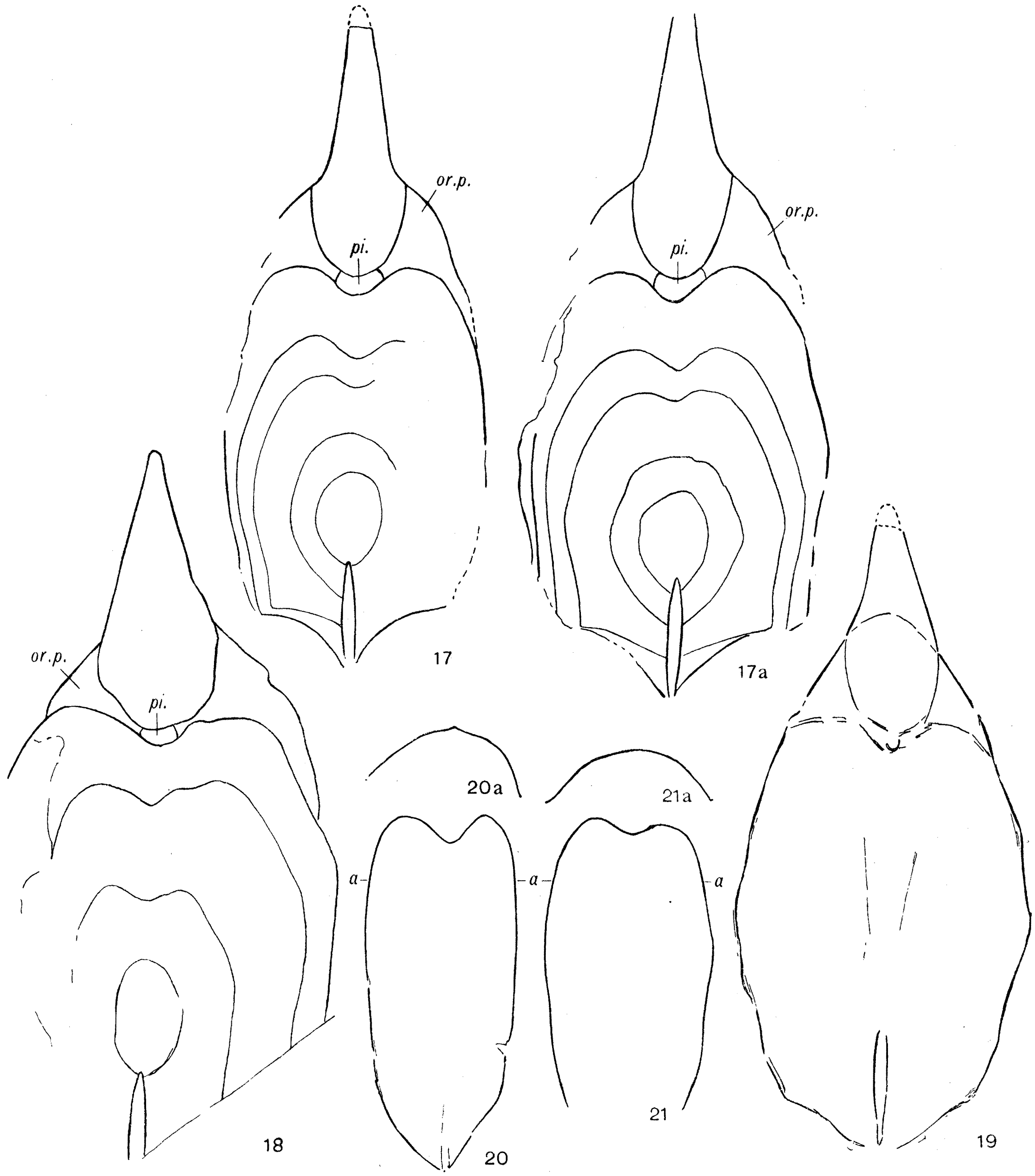
FIG. 14—*Pteraspis crouchi* LANKESTER, *forma typica*. External mould of specimen split longitudinally. Lower Old Red Sandstone (zone II. 2) : Pool Quarry, Herefordshire. (P. 17633—× $1\frac{1}{2}$.)

FIG. 15—*Pteraspis rostrata* (AGASSIZ) var. *virgoi* nov. Internal cast of dorsal shield with additions from counterpart. HOLOTYPE of variety. Lower Old Red Sandstone (zone II. 2) : Wayne Herbert Quarry, Herefordshire. (P. 17490-1—slightly enlarged.)

FIG. 16—*Pteraspis rostrata* (AGASSIZ), var. *toombsi* nov. External mould of rostrum with imperfect cast of buccal cavity. Lower Old Red Sandstone (zone II. 2) : Wayne Herbert Quarry, Herefordshire. (P. 17492—× 3.)

In the dorsal discs of adult specimens of the typical *P. crouchi* (figs. 14, 17–19 and 63—*see also* LERICHE, 1903, Pl. V; 1924, Pl. III, figs. 4, 5), the pineal emargination is generally deeper and the disc narrower across the anterior end than in most forms of *P. rostrata*, but resembling in these respects the discs of *P. r. toombsi*, so that it is some-



Pteraspis crouchi LANKESTER, forma typica

Lower Old Red Sandstone (zone II. 2) : Pool Quarry, Herefordshire

FIG. 17—Dorsal shield preserved as external mould. (*a*) Sketch of same specimen flattened out to show real proportions of dorsal disc and approximate growth-stages based on " ornamentation." (P. 16325—Nat. size.)

FIG. 18—Dorsal shield preserved as external mould with additions from counterpart. (P. 16456 ; counterpart, P. 16455—Nat. size.)

FIG. 19—Dorsal shield preserved as internal cast, except rostrum which is an external mould of lowre surface. (P. 16313—Nat. size.)

Pteraspis crouchi LANKESTER, var. *heightingtonensis* nov.

Lower Old Red Sandstone (zone II. 3) : Heightington, Worcestershire

FIGS. 20–21—Internal casts of dorsal discs. The first is the HOLOTYPE of the variety. 20*a*, 21*a*, cross-sections of same at *a–a*. (42150, 38035—Nat. size.)

times extremely difficult to determine with certainty to which species an isolated disc belongs.

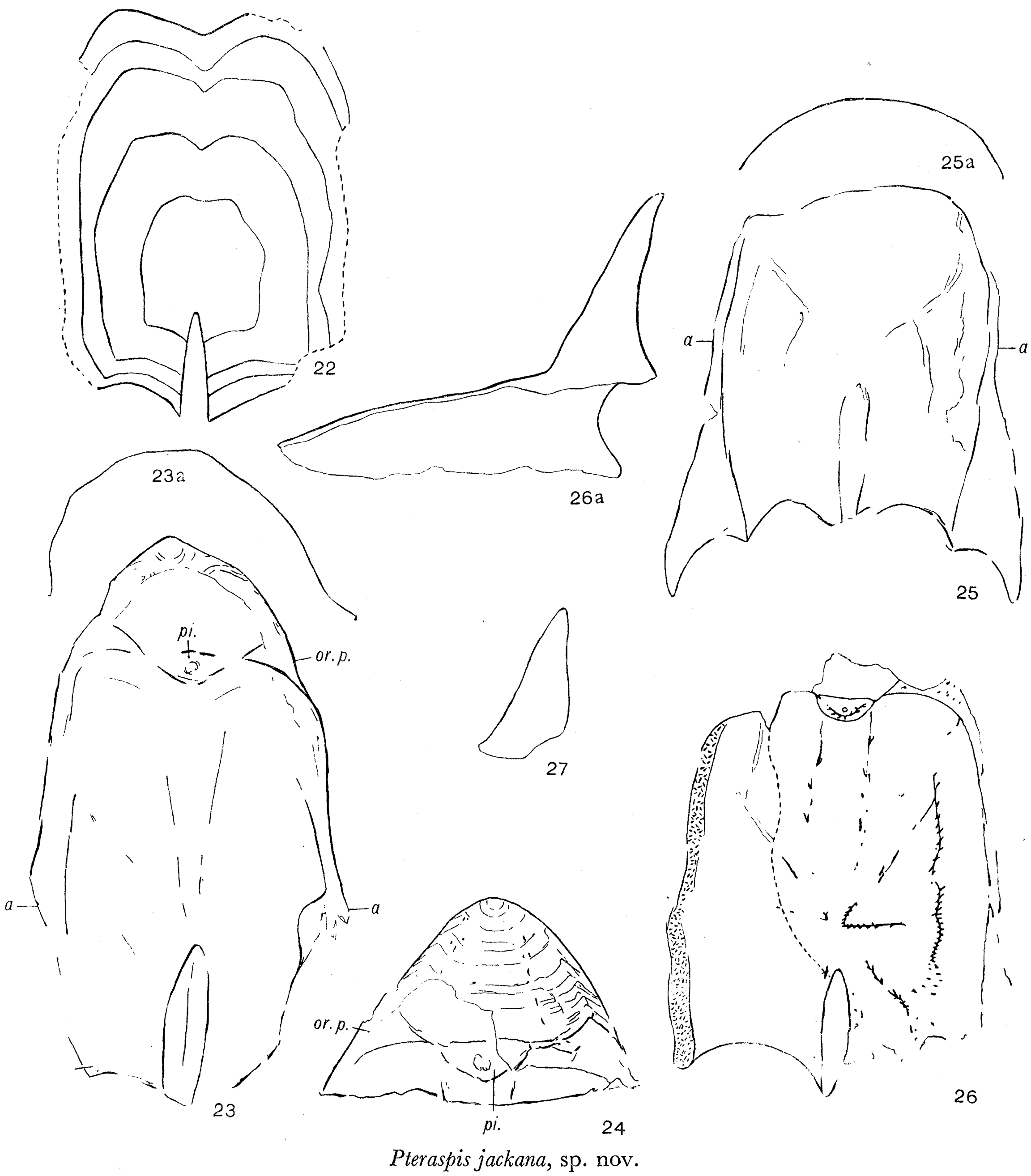
The specimens noted above are all from Pool Quarry (figs. 14, 16, 34). They agree very well with the most complete of LANKESTER's original specimens (1868, Pl. III, fig. 8), which is from Acton Beauchamp (zone II. 3), Worcestershire, and is hereby selected as the LECTOTYPE of the species ; but there seem to be two distinct varieties.

In the first variety, *P. crouchi heightingtonensis*, the dorsal disc (figs. 20–21) is most distinctive by reason of its very obvious narrowness, the maximum breadth over the curve being less than two-thirds of the maximum (not median) length. This form has been recorded only from Heightington, Worcestershire.

In the second variety, *P. crouchi mattockensis*, the distinctive features are in the rostrum and orbital plates (fig. 69), the dorsal disc, especially of the smaller individuals, figs. 71–72, being similar to those of the typical form. This variety has been found only at Castle Mattock Quarry, Herefordshire.

P. jackana is represented by two fairly complete dorsal shields (one in counterpart), a rostral extremity, and an isolated dorsal spine (figs. 23–27). The length of the dorsal disc is very little greater than the maximum breadth measured over the curve, which is considerable in the holotype (fig. 23), although not entirely natural, being partly due to distortion ; in dorsal view the squareness of the disc is naturally not shown, owing to its convexity. The pineal emargination seems somewhat variable in form ; in the holotype it is shallow and broad, but in the second shield (fig. 26) it is rather narrower and deeper. The insertion of the dorsal spine is long and wide, while the hinder margin on each side of the dorsal spine is markedly concave and forms a very short posterior angle, which scarcely reaches behind the level of the lateral margins. The latter have their usual somewhat sinuous form anteriorly, but just behind the middle of their length they suddenly narrow, doubtless to allow an increase in size of the base of the cornual plates to give added support for the large cornua. The growth-stages resemble the adult shape of the disc in being very broad, almost squarish, and are very similar to those seen in an isolated disc from Wayne Herbert Quarry (fig. 22), which is probably of this species, although it is not quite so broad relatively as the specimen from Castle Mattock ; but this is partly due to the imperfection of the lateral margins. In the earliest growth-stages the pineal emargination is very slightly marked, but it soon becomes narrow and well defined and then widens out again, so that the whole anterior margin is concave at its final stage of development. Growth along the posterior border continues until an unusually late stage.

The dorsal disc of *P. stensiöi* is also very broad when flattened, for the median length is about 50 mm and the breadth over the curve 45 mm in the smaller and more complete of the two specimens, both of which are from Gwyn Genni, a quarry in an apparently higher horizon (II. 3) than the others. The anterior emargination is wide and shallow, and the lateral margins, as in *P. jackana*, suddenly narrow at a point a little in front of the level of the dorsal spine and somewhat behind the middle of their length. The posterior margin of the dorsal disc is unique in the genus, for the insertion of the dorsal spine is entirely occluded in the disc, and the median posterior



Pteraspis jackana, sp. nov.
Lower Old Red Sandstone (zone II. 2)

FIG. 22—External mould of imperfect dorsal disc probably of this species, showing growth-stages. Wayne Herbert Quarry, Herefordshire. (P. 16829—Nat. size.)

FIG. 23—Imperfect dorsal shield preserved largely as internal cast. HOLOTYPE. (*a*) Cross-section at *a–a*. Castle Mattock Quarry, Herefordshire. (P. 16776—Nat. size.)

FIG. 24—Rostral region of dorsal shield. Near Pandy, Monmouthshire. (P. 16463—Nat. size).

FIG. 25—Imperfect dorsal shield, the disc being preserved as internal cast. (*a*) Cross-section at *a–a*. Castle Mattock Quarry, Herefordshire. (P. 17627—Nat. size.)

FIG. 26—Counterpart of same specimen—to right of dotted line it is preserved as external mould and shows sensory canals; remainder shows inner surface of disc with cross-section stippled. (*a*) Lateral view of same, taken along dotted line. (P. 17628—Nat. size.)

FIG. 27—External mould of isolated dorsal spine. Castle Mattock Quarry, Herefordshire. (P. 17636—Nat. size.)

angle is scarcely noticeable, the whole margin being generally concave. In the occlusion of the socket of the dorsal spine in the disc *P. stensiöi* resembles *P. primaeva* KIAER. The growth-stages have similar shape and proportions to the adult disc, although the insertions of the cornua are very much less definite. Whether the socket of the spine was always entirely enclosed is not clear.

The dorsal disc of *Pteraspis leathensis*,* sp. nov. (fig. 30), from the Downtonian of Corvedale, Shropshire, and elsewhere, is most distinctive in form. As in *P. jackana*, it is nearly square when flattened, the maximum breadth being about 32 mm and the length along the median line 38 mm. In spite of its small size, the holotype seems to be mature, and this is supported by the diminutive proportions of the other plates of this species. The most remarkable feature is the form of the anterior margin, which resembles that of the Spitsbergen species, *P. primaeva* KIAER. The emargination is well defined but extremely narrow and angular, and the maximum length of the disc on each side is close to the median line. From there the margin runs diagonally backwards and then transversely to the antero-lateral corners, which are therefore considerably behind the foremost parts of the disc. From the corners the lateral margins of the shield run almost straight to the posterior borders, which are markedly concave and form a pronounced posterior angle deeply excavated for the broad median dorsal spine. Although in its present condition this unique specimen is absolutely flat, in life it must have been very strongly arched, for the ventral plates are relatively much narrower.

In *P. leathensis* the early growth-stages, as indicated by the " ornamentation," are long and narrow ; but the disc increased in size more rapidly along the sides than elsewhere, so that the flattened adult shield is almost square. Two features in the growth of this plate are noteworthy ; firstly, the anterior emargination appears very late, and secondly, growth along the posterior margin is almost as great as along the anterior, even more than in the disc referred to *P. jackana* above (fig. 22).

The form of the dorsal disc of the Scottish *P. mitchelli* is rather uncertain. The only specimen in the British Museum (fig. 32) is very imperfect, but it shows a deep, narrow anterior emargination and very wide, rounded antero-lateral corners, so that the anterior margin of the shield is extremely narrow. In the specimens figured by LANKESTER (1868, Pl. V, figs. 2, 6, 10, 11) similar features are shown ; except in the last, the disc seems to be short and broad, and has a wide, pronounced posterior angle. In one also, fig. 2, the socket for the dorsal median spine is wide, but in a second, fig. 10, it is narrow.

The pineal plate—Fitting into the anterior median emargination is the very small pineal plate.

In *P. rostrata* it is always broader than long, but there are two very distinct types of plate in that species. In *P. rostrata wayensis*, *P. r. toombsi*, and *P. r. monmouthensis* it is four-sided and bowed towards the disc, so that the anterior margin is concave

* This species has been recorded by WICKHAM KING (1925, p. 357 ; 1934, p. 530) without description under the name of " *Cyathaspis leathensis*."

and the posterior correspondingly convex, while there are distinct lateral borders in contact with the orbitals (figs. 2–4, 9). In *P. r. trimpleyensis* and *P. r. virgoi* this plate is triangular, the posterior margin forming the apex and the anterior being straight or slightly convex (figs. 6–8, 15); in these specimens there are no lateral margins, for the plate is cut off from the orbitals by the rostrum. It is interesting to note that in his restoration of the species, Lankester (1870, Pl. VII, fig. 9) figures the pineal plate in this way.

In *P. crouchi* the same two forms are to be found. In the typical specimens of the species (figs. 17–19) the bowed, four-sided type of pineal plate is present, but in *P. c. mattockensis* (fig. 69) it seems to have been triangular in shape and cut off from the orbitals. In *P. c. heightingtonensis* it is unknown. In Lankester's restoration of *P. crouchi* (1870, Pl. VII, fig. 8) there is no pineal plate.

In *P. jackana* (figs. 23, 24, 26) the pineal plate, although very wide, is triangular and just separated from the orbitals by the rostrum, but in *P. stensiöi* (figs. 28, 29), although equally wide, it is four-sided and in contact with the orbitals.

The shape of the pineal plate in *P. leathensis* (fig. 30) is distinctive, for it is rhombic and widely separated from the orbitals.

In *P. mitchelli* the pineal plate (fig. 32) is roughly in the form of an equilateral triangle with the apex towards the rear and the base gently curved forwards.

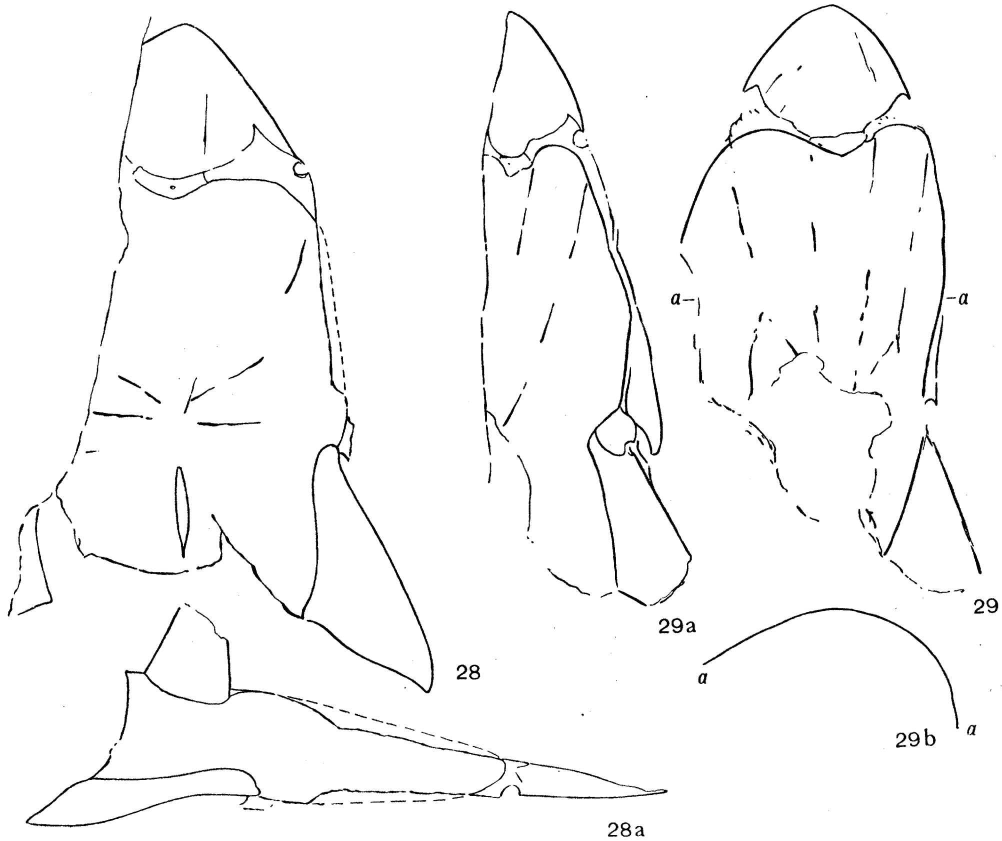
The orbital plates—These plates are rarely found complete in the British material, and in most species only the antero-dorsal portion is preserved.

The orbital plates are principally lateral in position and of irregular shape. They form the sides of the carapace around the orbits and are consequently bowed dorso-ventrally. In *Pteraspis rostrata toombsi*, the only form here described in which they are completely known (*Or. P.*, figs. 2, 83–85), their anterior margin on the dorsal surface is very oblique and gently concave where it is in contact with the rostrum, which they completely separate from the dorsal disc by a process running inwardly and backwards to the pineal plate, with which each plate has a short longitudinal line of contact. In front of the orbit the margin turns sharply downwards and backwards, bordering in its course the lateral oral plate, the two lateral plates, and for a short distance the anterior end of the branchial plate. The posterior inner margin of an orbital plate is strongly concave and borders the dorsal disc throughout, running backwards to meet the outer margin at a very acute angle, and thus forms a wedge separating for a short distance the dorsal disc and the branchial plate.

The orbital plates in *P. r. waynensis* differ from those just described in that the medial process which meets the pineal plate is longer, narrower, and less obliquely directed (figs. 3–5), while the angle formed by the anterior inner and outer margins seems to be less acute, or even slightly rounded.

In *P. r. monmouthensis* (fig. 9) the circum-orbital part is relatively smaller and the medial process even longer than in *P. r. waynensis*.

In the other two forms of *P. rostrata*, *P. r. trimpleyensis* (figs. 7, 8; fig. 100, Plate 25) and *P. r. virgoi* (fig. 15), the shape of the orbital plates is very different, for there is no medial process to meet the pineal plate. In the former, the part around the orbit is large and the anterior inner margin slopes obliquely inwards to form a very acute angle with the hinder margin at some little distance from the pineal ; whereas in the second variety the anterior inner, although sinuous, runs almost directly backwards and meets the posterior almost at right-angles ; its anterior angle, that formed with the outer border, is also more acute with that in *P. r. trimpleyensis*.



Pteraspis stensiöi, sp. nov.

FIG. 28—External mould of imperfect dorsal shield. HOLOTYPE. (*a*) Lateral view of same. Lower Old Red Sandstone (zone II. ?3) : Gwyn Genni Quarry, Herefordshire. (P. 17629—Nat. size.)

FIG. 29—External mould of imperfect dorsal shield showing remains of sensory canals. (*a*) Half lateral view of same specimen showing branchial region hidden by curvature of dorsal disc in previous figure. (*b*) Cross-section of same at *a–a*. Lower Old Red Sandstone (zone II. ?3) : Gwyn Genni Quarry, Herefordshire. (P. 17630—Nat. size.)

In *P. crouchi* the orbital plates are extended further forwards than in most varieties of *P. rostrata*, the anterior inner margin being more nearly longitudinal in direction owing to the form of the rostrum, but here again there are two types ; in the typical form (figs. 14, 17, 19, 68) the plates are in contact with the pineal by means of a medial extension separating the rostrum from the dorsal disc, as in *P. r. waynensis*, etc., but in *P. c. mattockensis* (fig. 69), as in *P. r. trimpleyensis* and *P. r. virgoi*, the orbital plates are separated from the pineal by the rostrum. The same feature is to be seen in all but one of the other four species ; in *P. jackana* (figs. 23, 24) the plates are very short and the medial extension is long and very acute, just failing to touch the pineal plate, in this last feature differing from those of *P. stensiöi* (figs. 28, 29) ; in *P. leathensis* (fig. 30) the orbital plates probably extended forwards as in *P. crouchi*, but the anterior inner margin meets the posterior, which is very sinuous owing to the form of the dorsal disc, almost at right-angles ; while in *P. mitchelli* (fig. 32) the plates are short and the antero-posterior contact is acute.

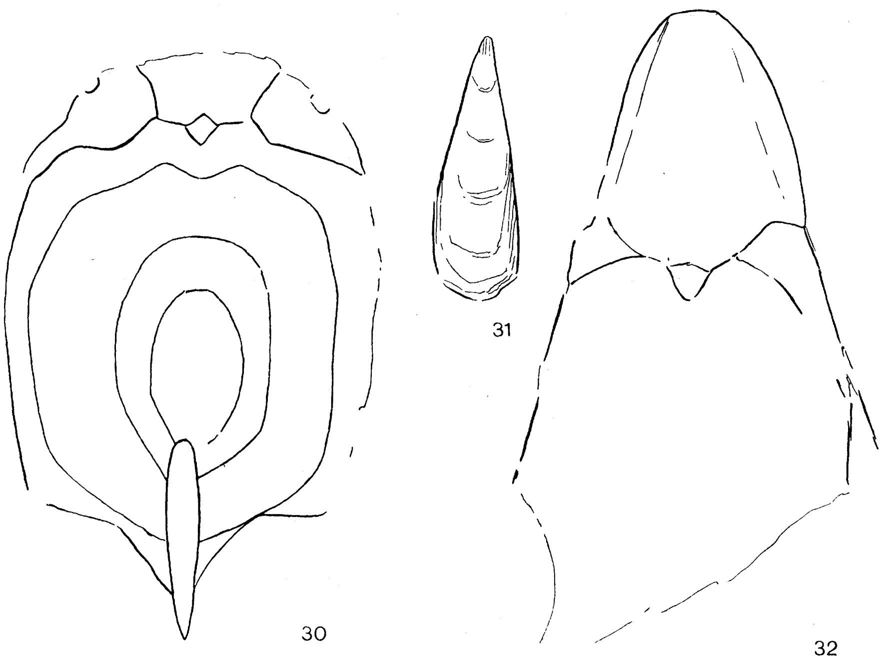


FIG. 30—*Pteraspis leathensis*, sp. nov. External mould of imperfect dorsal shield without rostrum, showing approximate growth-stages based on " ornamentation." HOLOTYPE. Downtonian (zone I. 8) : Leath Stream, Corvedale, Shropshire. (P. 14521—× $1\frac{1}{2}$.)

FIG. 31—*Pteraspis leathensis*, sp. nov. External mould of rostrum. Downtonian (zone I. 9) : Stream by Oldfield, Shropshire. (P. 16851—× $1\frac{1}{2}$.)

FIG. 32—*Pteraspis mitchelli* POWRIE. External mould of imperfect dorsal shield. Lower Old Red Sandstone (zone uncertain) : Bridge of Allan, Stirlingshire. (P. 16808—Nat. size.)

The rostrum—The rostrum is generally considered to be one of the most typical plates of the carapace, and in the species considered here it is the one most easily identified specifically when isolated ; yet, in the species *P. rostrata*, it shows a remarkable range of variation in form within a single variety. In general the rostrum is roughly triangular in dorsal view and, except in the most elongated forms, flattened. It is most likely that the under-surface always sloped somewhat upwards (in *P. crouchi* the whole rostrum was apparently curved upwards), as in the snouts of living sharks, so as to facilitate the rising of the animal from off the bottom, or to a higher level when swimming.

In *P. rostrata* the rostrum is depressed and has the form of an isosceles triangle with the apex rounded off, and typically the two sides are at an angle of about 45° to one another, continuing the line of the orbital plates in dorsal view ; the most striking exception to this is the extreme forms of *P. r. toombsi* (figs. 16, 42 ; fig. 104, Plate 26), in which this plate is much elongated and more pointed. The posterior margin is very convex on the dorsal surface and equally concave on the lower (figs. 1, 2 : in this specimen the rostrum is shortened and widened by crushing), where it forms the upper margin of the mouth (figs. 41–47) and then slopes inwards and upwards to act as the " maxillary tooth-plate." In the new specimens there is little evidence of the median projection on the oral margin which KIAER (1925, p. 124, text-fig. 3) has termed the " Rostral Beak." In front of the oral margin there is a median, slightly depressed area, which, as described below, bears an " ornamentation " of fine tubercles.

In three of the five varieties of *P. rostrata* the proportions seem fairly constant within the variety, although differing from one to another ; in the fourth only one specimen is known, but in the fifth, *P. r. toombsi*, there is a quite wide range of variation. Table I shows the approximate relative proportions of the rostrum in the different forms of *P. rostrata.*

TABLE I

Variety	Length of rostrum / Length of dorsal shield	Length of rostrum / Max. breadth of rostrum	Form of tip of rostrum
toombsi	> 1 : 3—2 : 5	3: 2—2 : 1	Very narrow
waynensis	> 1 : 3	3 : 2	Narrow
trimpleyensis	< 1 : 3	4 : 3	Blunt
virgoi	1 : 3	< 4 : 3	Very acute
monmouthensis	< 1 : 3	8 : 7	Very blunt

The proportions given are, of course, only approximate, for this plate is very liable to distortion, and these variations may be due partly to that cause, which certainly accounts for the longitudinal grooves on the upper surface of the rostrum described by some authors (*e.g.*, WOODWARD, 1891, p. 162) as being characteristic of the species, for it is absent in all the new specimens.

In *Pteraspis crouchi* the rostrum is very long and attenuated, and sharply separated from the rest of the dorsal shield when seen from above, at least in the typical form (figs. 17–19, 68); in cross-section it was more or less rounded towards the extremity and was thus very easily distorted (fig. 18), although the upward curvature of the distal end, noted by several authors, seems to have been natural (fig. 14). In the adult its length was about two-fifths that of the dorsal shield without the spine, but in the younger specimens (fig. 68) it was seemingly less. In *P. c. mattockensis* (fig. 69) the rostrum was apparently broader. Growth, as in all species, apparently took place along the hinder margin only.

The rostrum of *P. jackana* (figs. 23, 24) is very short and broad, its length being only about two-thirds of its maximum breadth and only slightly exceeding one-fifth of the total length of the dorsal shield without the spine. The tip is more or less rounded and the two sides are very nearly at right-angles to one another. In its form it closely resembles that of the earlier and much smaller *P. gosseleti* (LERICHE, 1906, p. 26, Pl. I, figs. 6–9), but apart from the differences in size that species is distinguished from *P. jackana* by characters of the dorsal disc, namely, the supposed absence of the anterior emargination and of the socket for the dorsal median spine.

The rostrum of *P. stensiöi* (figs. 28, 29) is very like that of *P. jackana* in shape, but its length is greater relatively to the median length of the dorsal disc, although this apparent difference is solely due to the curious form of the hinder margin of the disc, of which the median angle is very slightly developed.

In the Downtonian *P. leathensis* (fig. 31) the rostrum is long and attenuated, rather like that of *P. crouchi* but perhaps a little stouter and more triangular in form. Its length is three times its maximum breadth, but its size relative to the dorsal shield is unknown, as it has never been found attached.

The rostrum of *P. mitchelli* (fig. 32) is somewhat like that of *P. rostrata monmouthensis*, but tapers less and is more rounded distally. Its length is contained between three and three and a half times in the total length of the dorsal shield without the spine, and it exceeds its maximum breadth by about one-sixth. In the specimens figured by LANKESTER (1868, Pl. V, figs. 2, 6, 10), the rostra are even broader and blunter, but just how much of their massiveness is due to distortion is not clear.

The dorsal spine—The dorsal spine is rarely preserved and usually the empty socket is the only evidence that it was present.

In *P. rostrata* the spine is depressed. It is sometimes described as being large, but in our specimens of *P. r. waynensis* (fig. 4) its exserted portion is shorter than the socket and slender, being low and laterally compressed. In both this form and in *P. r. toombsi* the length of the inserted portion varies with the individual, being contained from about three and a half to four and a quarter times in the median length of the dorsal disc (figs. 2–5,) but in *P. r. toombsi* the exserted portion is longer than in the other (fig. 13). In *P. r. monmouthensis* (fig. 9) the length of the socket is little more than one-quarter that of the disc, but in *P. r. virgoi* (fig. 15) and *P. r. trimpleyensis* (fig. 7) it attains one-third. In the last variety the spine is very short and triangular in side view, for the exserted portion forms only two-fifths of the total length of the spine (figs. 10, 11).

The dorsal spine of *P. crouchi* is also depressed. It is long and slender in *P. c. mattockensis* (fig. 12) but in the typical form it is of moderate length, laterally compressed and triangular in side view (fig. 14). The socket in the variety is markedly shorter than the exserted portion and is less than one-quarter the median length of the disc (fig. 69) ; but in typical specimens it is relatively longer, being contained only three and a half times in the length of the disc in external moulds (figs. 14, 17–19, 68), and, owing to the thickness of the disc and the slope of the spine, even fewer in internal casts (LANKESTER, 1868, Pl. III, fig. 2).

The spine of *P. leathensis* (fig. 30) is remarkably short and stout, for the exserted portion forms only one-quarter of the total length, although the socket is one-third as long as the dorsal disc. The angle which this spine made with the shield must have been very small, and the spine itself flattened.

To judge from the specimens of *P. mitchelli* figured by LANKESTER (1868, Pl. V, figs. 2, 10), the dorsal spine was much depressed in this species also ; it is inserted for about one-third of the median length of the dorsal disc, but in the first figure it is broad and in the second narrow, with a slender exserted portion equal in length to the socket.

The dorsal spines of *P. jackana* and *P. stensiöi* differ from those of the other British species in being erect (figs. 26*a*, 28*a*). In the former, the base in the external mould fig. 26) is about one-third as long as the dorsal disc and about two-thirds as long as the spine is high, and separates the two concave sides of the posterior margin, forming the apex of the posterior angle, as in the species previously described. The spine is laterally compressed and tapers distally, for the anterior margin is more or less straight and slopes backwards towards the pointed apex, while the posterior is vertical and slightly concave or straight (fig. 27). In *P. stensiöi* the base of the spine is unique in that it does not reach the posterior margin and is therefore set relatively far forward (fig. 28*a*). The length of the socket is only one-quarter that of the dorsal disc, which itself is relatively short in the median line, and the base is very much more compressed laterally than that in the preceding form. Only the proximal part of the spine is preserved in outline, but this shows that both the margins were straight, the anterior being vertical and the posterior inclined forwards.

The plates forming the sides of the carapace, especially the branchial plates, are seldom well preserved, for only in three varieties of *P. rostrata* are they known in detail.

The branchial plates—The branchial plates are well preserved in *P. rostrata toombsi* (figs. 1, 2 ; figs. 104, 105, Plate 26), *P. r. waynensis* (figs. 66, 67 ; fig. 101, Plate 25), and *P. r. trimpleyensis* (fig. 8 ; fig. 100, Plate 25). In all three forms the branchial plate of each side is narrow, elongated, and curved dorso-ventrally to form the lateral margin of the carapace. Anteriorly, this plate is pointed and separates the dorsal disc from the hinder half of the posterior lateral plate (figs. 1, 2 ; fig. 100, Plate 25). It borders the disc for about half the length of the latter, and then curves outwards and downwards to form the outer margin of the branchial opening, under which in *P. r. waynensis* it continues to form a narrow strip below the cornual plate to within a short distance of the hinder end of the carapace (fig. 66) ; in *P. r. trimpleyensis* (fig. 100, Plate 25) and *P. r. toombsi* (fig. 105, Plate 26) this strip seems tohave been absent. The whole of its inferior border is in contact with the ventral disc (fig. 1; *see* restoration, figs. 83–85). In *P. r. trimpleyensis*, the branchial plate seems to have been relatively shorter than in the other forms, for its length in front of the opening is scarcely longer than the cornual plate (fig. 100, Plate 25), whereas in *P. r. waynensis* and *P. r. toombsi* it is considerably so (fig. 66 ; fig. 105, Plate 26), and consequently the branchial opening is further to the rear.

The cornual plates—From the branchial opening backwards to the hinder border a cornual plate forms the lateral margin of the dorsal shield. In *P. rostrata* it is expanded dorso-laterally to form a small triangular cornu, which is widest behind and narrows forwards until it disappears above the branchial opening (fig. 66; fig. 100, Plate 25; figs. 105, 106, Plate 26). Below the cornu the plate is flatter than the branchial plate and thus its obliquely truncated anterior margin forms the inner boundary of the branchial opening. Dorsally it only just touches the branchial plate, but below the two plates are in contact for some distance. BROTZEN (1933*b*, text-fig. 3), figures an ideal restoration of the branchial region of a *Pteraspis*, which differs in detail from that described above.

No plate that can be identified as a cornu has been found associated with the English material of *P. crouchi*, which is curious, for several of the dorsal shields are quite well preserved (*e.g.*, figs. 17–19) and LERICHE (1924, p. 148, text-figs. 2, 3; Pl. III, fig. 8) has figured as such a large, backwardly curved plate found associated with his Belgian specimens.

In both *P. jackana* and *P. stensiöi* the cornua are very large. In the former (fig. 25) they are widest at the level of the posterior margin of the dorsal disc, the width of each being about two-fifths of the distance between them. In form each cornu is arcuate, the outer margin being long and gently convex, while the posterior is short and concave, so that the plate curves backwards for some distance behind the level of the posterior margin, about equal to one-sixth of the length of the dorsal disc. The base is deep, as is shown by the cutting-away of the posterior lateral margin of the disc. In *P. stensiöi* the cornua are even broader, for the width of each at the level of its inner posterior angle equals about one-half of its distance from its fellow. The plate is very nearly triangular, for the long anterior margin curves only slightly and at the hinder end, while the posterior margin is merely sinuous and moderately long; as in *P. jackana*, the cornu projects backwards far beyond the disc, and the base is unusually deep (fig. 28).

The cornua of *P. leathensis* and *P. mitchelli* are not known to me.

(ii) *The Ventral Shield and Oral Apparatus*

Isolated ventral discs are plentiful in British material, but the complete undersurface is shown only in the specimens of *P. rostrata toombsi* (fig. 1; fig. 98, Plate 25). In these one may see the large ventral disc, the lateral plates, of which there are two pairs in this form, the oral plates, and the hitherto undescribed post-oral covers.

The ventral disc—The ventral disc forms by far the great part of the ventral surface. This plate has been identified only in three of the British species here described, *P. rostrata*, *P. crouchi*, and *P. leathensis*, and, owing to their similarity in form at certain stages, the plates of the first two species are generally very difficult to identify and have been frequently confused, especially as they often occur in the same beds; the growth-stages are, however, different, and when these are shown the species may be separated with ease, but certain of the varieties can seldom be determined without knowledge of the origin of the specimens.

In the youngest " ornamentation " stages of *P. rostrata* the ventral shield has the shape of an ellipse with the anterior end slightly flattened and the posterior bevelled to form an obtuse posterior angle, the plate being twice as long as broad (fig. 35). Growth at first, if one may judge by the " ornamentation," takes place far more rapidly in front and antero-laterally than along the posterior half of the sides, and is

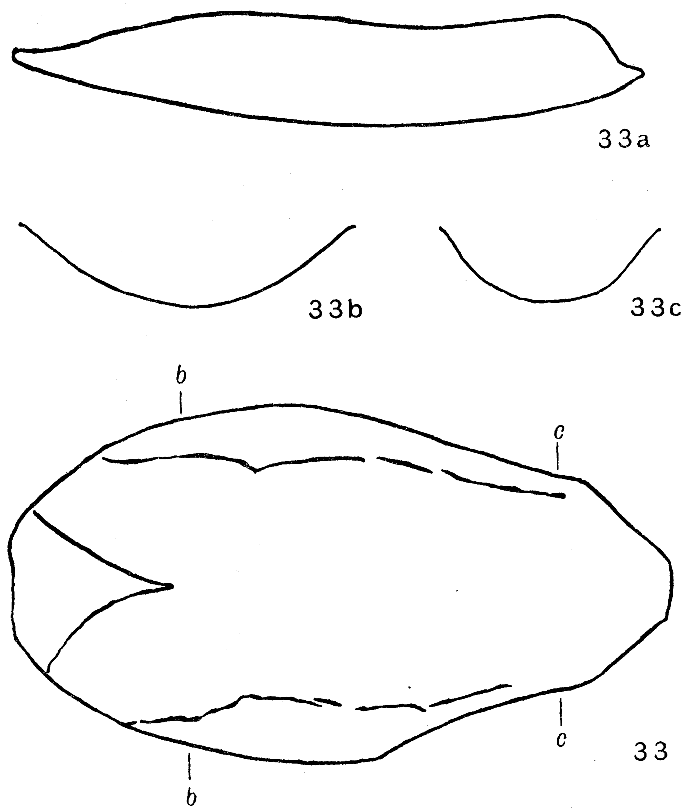


FIG. 33—*Pteraspis rostrata* (AGASSIZ), var. *waynensis* nov. Ventral disc preserved as internal mould and showing grooves due to main sensory canals (the oblique branches of the lateral canals have left no impressions). (*a*) Side view. (*b*) Cross-section at *b–b*. (*c*) Cross-section at *c–c*. Lower Old Red Sandstone (zone II. 2) : Wayne Herbert Quarry, Herefordshire. (P. 16524—slightly reduced.)

entirely absent along the hinder margin, so that the plate becomes more ovoid in form until the adult outline is assumed.

In *P. r. toombsi* (fig. 35), *P. r. waynensis* (fig. 33), and *P. r. trimpleyensis* (figs. 36, 39) the outlines are similar, but in the large specimens referred to *P. r. monmouthensis* (fig. 34) it is considerably more elongated, partly by reason of its size. In life, the ventral disc was considerably inflated, being strongly arched transversely, especially in the posterior half, so that this region appears pinched in, making well-preserved specimens appear more pear-shaped than the commonly flattened examples (compare figs. 33, 34, with 35, 36). In specimens of *P. r. waynensis* (fig. 33*a*) and probably also in *P. r. trimpleyensis* and *P. r. toombsi*, the disc is gently bowed from front to rear, but in the large specimen identified with *P. r. monmouthensis* (fig. 34*a*) this curve is flattened out.

The young stages of the ventral disc of *Pteraspis crouchi* are very distinctive, being of the form described by LANKESTER (1868, p. 23, Pl. II, figs. 5–8, 12, 13 ; 1870, Pl. VII,

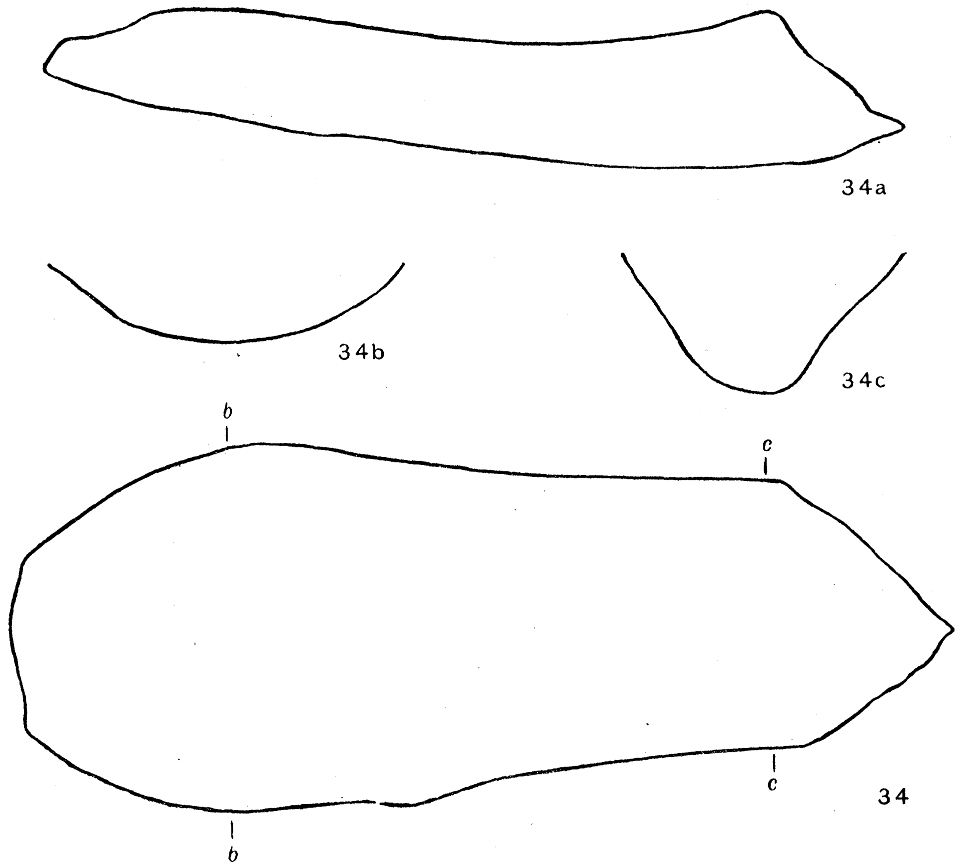
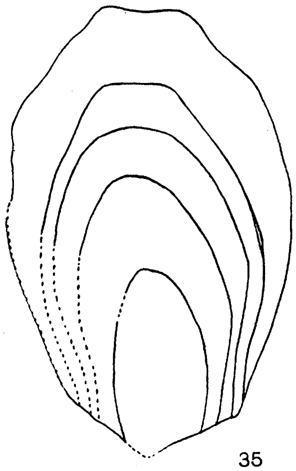


FIG. 34—*Pteraspis rostrata* (AGASSIZ), (?) var. *monmouthensis*. Ventral disc preserved as internal mould. (*a*) Side view. (*b*) Cross-section at *b–b*. (*c*) Cross-section at *c–c*. Lower Old Red Sandstone (zone II. 3) : Kentchurch Hill, Herefordshire. (P. 5861—slightly reduced. N.B.—This is the specimen figured by Woodward (1891, Pl. IX, fig. 2)

fig. 2) as *Scaphaspis rectus*. The plate is more than twice as long as broad, with the lateral margins roughly parallel, and the posterior margins forming an obtuse median angle and the anterior an acute angle, which may be truncated (fig. 37). Growth, as in *P. rostrata*, takes place chiefly in front and not at all behind, and for a considerable period the original shape is preserved (figs. 37, 75) ; later, however, the antero-lateral borders swell out and the plate comes to resemble in outline the adult discs of *P. rostrata* of average size, so that if the growth-lines are not preserved it is impossible to identify an isolated disc with certainty (*cf.* figs. 33, 37, 74). At present, there is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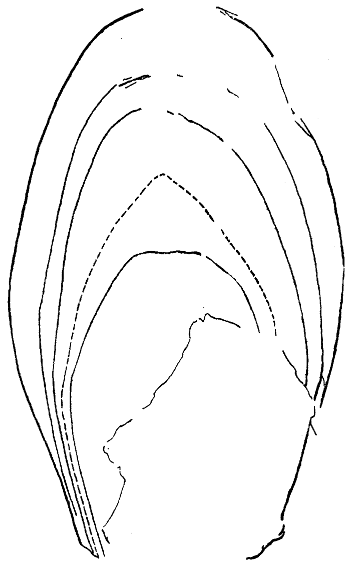
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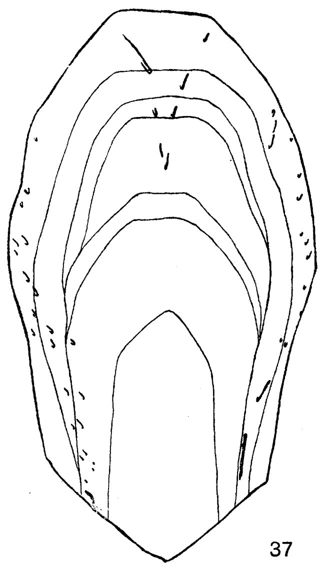
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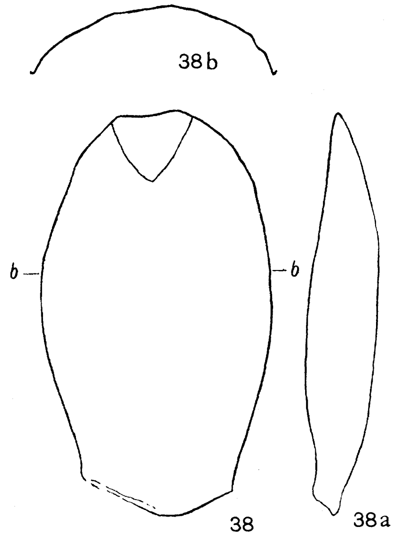


FIG. 35—*Pteraspis rostrata* (AGASSIZ), var. *toombsi* nov. Ventral disc preserved as external mould and showing growth-stages. Same specimen as in fig. 1. (Approx. Nat. size.)

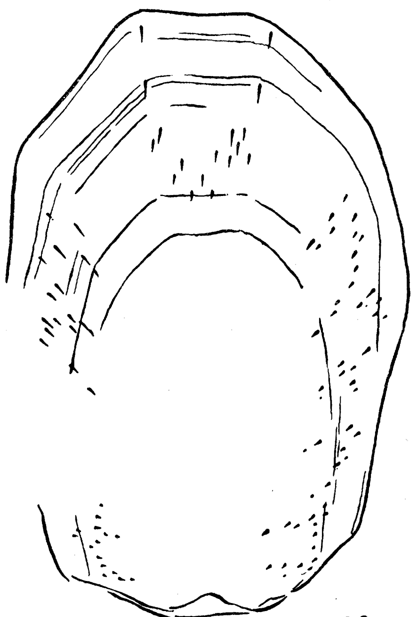
FIG. 36—*Pteraspis rostrata* (AGASSIZ), var. *trimpleyensis* nov. Ventral disc showing growth-lines and one (broken) line of " ornamentation." Lower Old Red Sandstone (zone II. 2) : Guildings Brook, Trimpley, Worcestershire. (P. 16481.IV—Nat. size.)

FIG. 37—*Pteraspis crouchi* LANKESTER, forma typica. External mould of ventral disc showing growth-stages and partial distribution of pores of sensory canals. The plate appears narrow posteriorly owing to increased convexity of cross-section. This specimen was associated with the dorsal disc shown in fig. 68. Lower Old Red Sandstone (zone II. 2) : Pool Quarry, Herefordshire. (P. 16520.II—slightly enlarged.)

FIG. 38—*Pteraspis leathensis*, sp. nov. Ventral disc preserved as internal cast. (*a*) Side view. (*b*) Cross-section at *b*–*b*. Downtonian (zone I. ?) : near Trimpley, Worcestershire. (42160—$\times 1\frac{1}{2}$.)

insufficient material to establish whether there are differences between the ventral discs of the typical form and those of the varieties, but one specimen of the ventral disc of *P. c. mattockensis* (fig. 75) seems to have preserved the rectangular form to a later stage than the typical specimens ; and this is true to an even greater extent of the discs of *P. c. heightingtonensis* (figs. 78, 79).

The ventral discs of *P. leathensis* (figs. 38, 77) resemble small editions of the adult plates of *P. rostrata* of average size (*cf.* fig. 33) except that they are rather more oval and the posterior margins are more nearly transverse, forming a continuous bow-shaped curve without a distinct median angle. The growth-stages are difficult to determine, for the " ornamentation " is arranged about a median longitudinal axis



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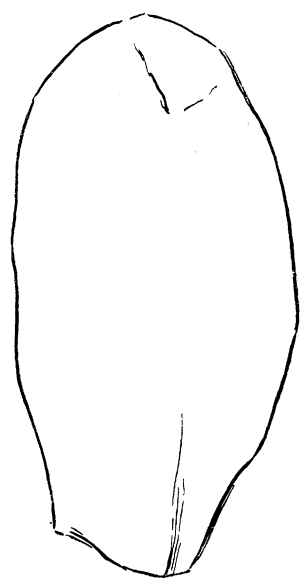

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FIG. 39—*Pteraspis rostrata* (AGASSIZ), var. *trimpleyensis* nov. External mould of ventral shield showing growth-lines and distribution of sensory pores. Lower Old Red Sandstone (zone II. 2) : Guildings Brook, Trimpley, Worcestershire. (P. 17364—× $1\frac{1}{3}$.)

FIG. 40—*Pteraspis novae-scotiae*, sp. nov. Internal cast of ventral shield. HOLOTYPE. Knoydart Formation : McArras Brook, near Knoydart, N. Nova Scotia. (P. 9117 *a*—× 2.)

which extends from the hinder margin forwards for about two-thirds of the length of the disc, so that the earliest " ornamentation " stages are extremely long and narrow ellipses (specimens Nos. P. 14523–4), an impossible shape for the young animal. This suggests either that the " ornamentation " is independent of the growth-stages, which is certainly not altogether true in the middle and later stages, or that the disc was not formed until an unusually late stage in this species, the young animals being soft-bodied without an ossified carapace (*see* p. 390 *supra*).

No specimens of the ventral discs of *Pteraspis jackana*, *P. stensiöi*, or *P. mitchelli* are known to me.

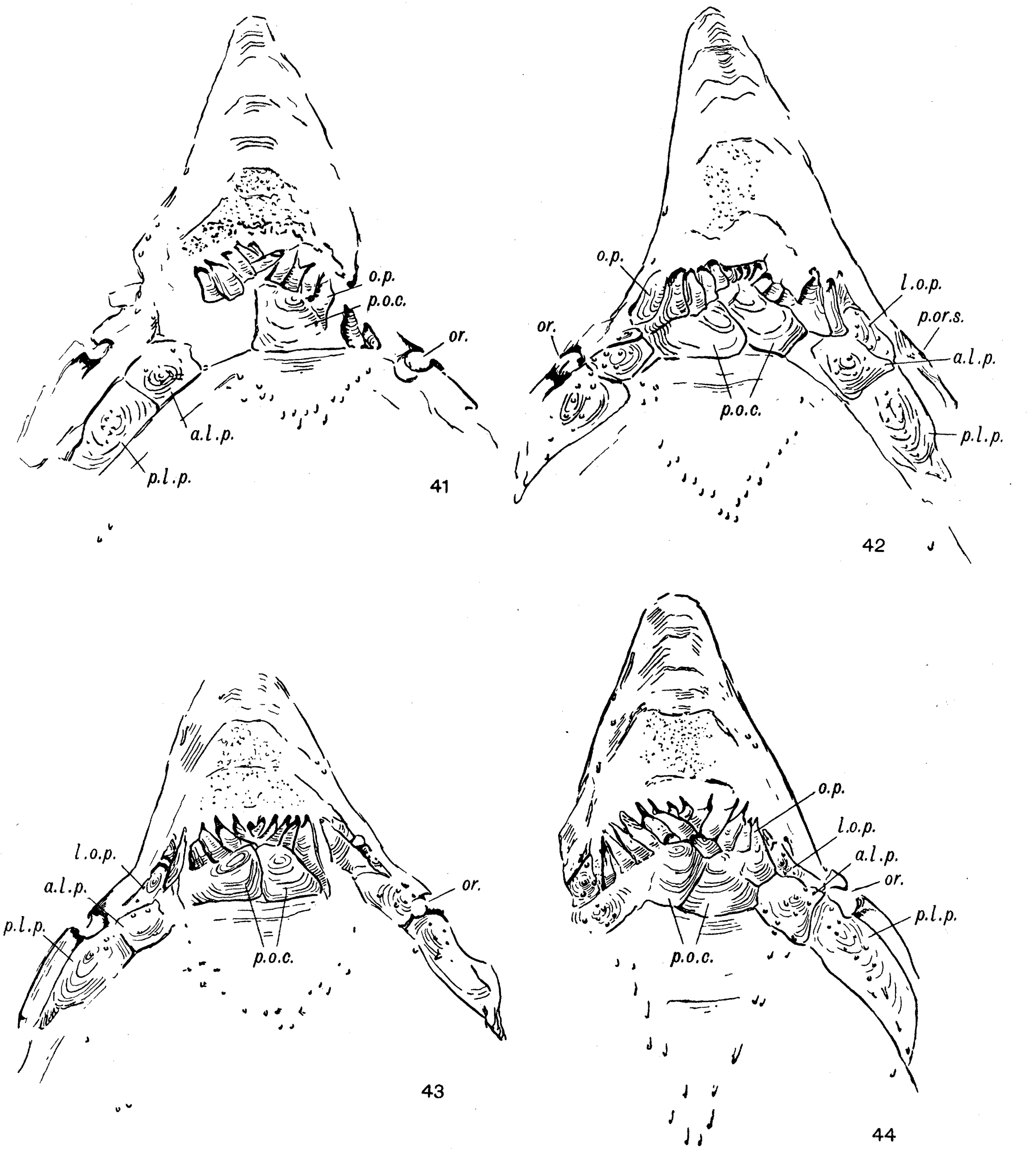
The plates bounding the sides of the ventral discs are the lower vertical flanges of the cornual plates for a short distance behind, and the branchial plates for the greater part of its length (*see* restorations, figs. 84, 85) ; this is exactly as is shown in the previous restorations of *Pteraspis rostrata* and in KIAER's restoration of *P. vogti* from the Downtonian of Spitsbergen (1928, p. 121, text-fig. 2) ; but the plates bounding the antero-lateral and anterior margins of the ventral disc in our specimens of *P. rostrata toombsi* (figs. 1, 1*a*, 41–47, 82, 85 ; fig. 98, Plate 25), the only British form in which they are known, differ considerably in detail from those figured by KIAER, for there are two instead of one pair of lateral plates between the disc and the orbitals, and the disc is separated from the oral series by a variable number of post-oral covers, which are absent in *P. vogti*.

The lateral plates—As noted above, there are two pairs of plates separating the orbitals and the ventral disc in *P. rostrata toombsi* (figs. 1, 1*a*, 41–47 ; fig. 98, Plate 25). Each of the posterior pair is about thrice as long as broad ; it tapers behind where it separates the angular anterior end of the branchial plate from the ventral disc, and is truncated in front where it is in contact with the anterior plate. The latter is about as broad as the posterior plate, but somewhat shorter ; it is pentagonal, for beside the margins in contact with the orbital, ventral, and posterior lateral plates, it has two short anterior margins, one in contact with the post-oral cover, and at right-angles to it another bordering the oral series.

One specimen (fig. 46) has three lateral plates on the left side.

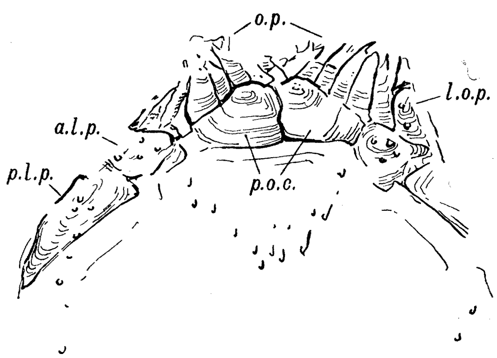
The oral plates and post-oral covers—The oral plates are very well preserved in at least eight specimens of *P. rostrata toombsi* (figs. 1*a*, 41–47), chiefly as moulds showing all surfaces. This system of plates is remarkable in many respects, and differs somewhat from that of *P. vogti* as described by KIAER (1928, p. 121, text-figs. 2, 3). The oral plates vary in number according to the individual, some specimens having only twelve (fig. 43) in addition to the pair of lateral oral plates, others thirteen (figs. 44, 47), but most have fourteen (figs. 1*a*, 42, 45). They are long plates, narrow and deep at the anterior end, but becoming gradually flat and wide to the rear. The gradation is not even on both sides of the plate, as in a double wedge, for the outer side diminishes in height less rapidly than the inner, so that the oral surface is asymmetrically concave (fig. 48). In addition the plate is generally slightly curved medially in dorsal view. The length of most of the plates is much greater than their breadth at the hinder end, but one or two at the centre are short and appear to be normally overlapped by their neighbours. To some extent all the plates seem to have been overlapped along their inner margin, although I can detect no smooth area of overlap on the underside of the overlying plates. Each is " ornamented " on all four sides of the deep and narrow anterior ends with fine tubercles or broken-up ridges, which pass behind into fine ridges of the same type as elsewhere on the external surface of the body-armour, being arranged longitudinally along the sides and transversely across the broadening undersurface ; but the upper surface becomes smooth, being apparently the area of attachment (P. 17525). On each side of this series, filling in the triangular space between the anterior lateral plate and the rostral margin, are two plates (*l.o.p.*, figs. 42–46), of which the anterior is small and triangular, forming the apex of the area, while the posterior is quadrangular and very much larger. These two plates together obviously correspond to KIAER's " lateral oral plate," yet, apart from there being two, they differ in that the larger bears that part of the sensory canal which connects the lateral ventral canal with the lower rostral, and this was probably fixed and formed the real corner of the mouth. The oral plates do not reach backwards to the anterior margin of the ventral disc, as in KIAER's specimens, but are covered to a large extent by one or more new elements, the " post-oral covers." These plates are remarkable for their variation in shape and number, both being apparently individual characters ; in two specimens (figs. 1*a*, 47) there is only one very wide plate between the two anterior laterals, although the second specimen has another very small plate immediately in front ; but the common number is two (figs. 41–43, 45, 46), which are more or less triangular and always unequal in size, that on the left side generally being the larger. In one example only (fig. 44) there is a small third plate between the apices of the two principals.

It is not easy to understand how this complicated system of oral and cover-plates functioned in life. KIAER (1928, p. 123), in his description of the mouth-parts of *P. vogti*, describes the oral plates as being provided with " tooth-plates " ; these were not plates in the strict sense of the word, but merely roughened areas on the anterior oral sides of the plates which, in his specimens, are expanded inwards, and formed by the breaking-up of the " ornamentation." These, he thought, bit against a " maxillary tooth-plate," again just a roughened area on the pre-oral margin of the rostrum. In *P. r. toombsi* this roughened area is extensive, sometimes occupying half the underside of the rostrum, and is slightly depressed. The oral plates could have bitten only along the hinder margin where the rostrum turned inwards and projected into the buccal cavity. These plates are always arranged in the same way and seldom lie so far forwards as the roughened area, there being only one instance of their doing so (fig. 47). Actually they must have been arranged in life very much as they are in the fossils, for the least disturbance would scatter such delicate objects. Thus arranged, it is difficult to see how they could have functioned as KIAER suggested, forming a " sort of biting or crushing mouth," for their grasping and holding powers must have been extremely feeble and, moreover, considerably hampered by the post-oral covers, although these seem to have been absent in his Downtonian species. STENSIÖ (1932, p. 184) has pointed out that these plates could not have worked directly against each other with their tuberculated surfaces, nor could the plates have moved up and down like a lower jaw, and compares them and the " maxillary plate " with the epidermal teeth on the rasping-organ and " ethmoidal plate " of *Myxine*. This seems to me to be a wholly fictitious comparison ; there is no evidence whatever of a powerful structure corresponding to the Hag-fish's tongue, as GOODRICH (1929, p. 46) has already pointed out, and the form of the plates seems to militate against their use in this manner. Only the posterior dorsal half of each plate was attached, the remainder being covered with epidermis, like the rest of the " ornamented " exoskeleton, the " ornamentation " of which STENSIÖ has plausibly correlated with the sensory or mucous system. The denticles on the anterior ends of the plates and on the underside of the rostrum show no signs of wear, as they must have done if they



FIGS. 41–44—*Pteraspis rostrata* (AGASSIZ), var. *toombsi* nov. External moulds of ventral surface of rostrum and of oral apparatus. P. 17479, fig. 42, is the HOLOTYPE of the variety. Lower Old Red Sandstone (zone II. 2) : Wayne Herbert Quarry, Herefordshire. (P. 17482, P. 17479, P. 17486, and P. 17488 respectively—all approx. × 2.)
p.or.s., post-orbital sensory canal.

had formed part of a tritoral surface, but seem more likely to have formed the bases of fine sensory papillae, which, like the feelers in front of the sturgeon's mouth, would be of immense value to an animal feeding on the bottom of muddy waters. Moreover, the absence of external nares in these animals would have made feeding by rasping difficult, if not impossible. KIAER (1928, p. 130) has definitely decided against the



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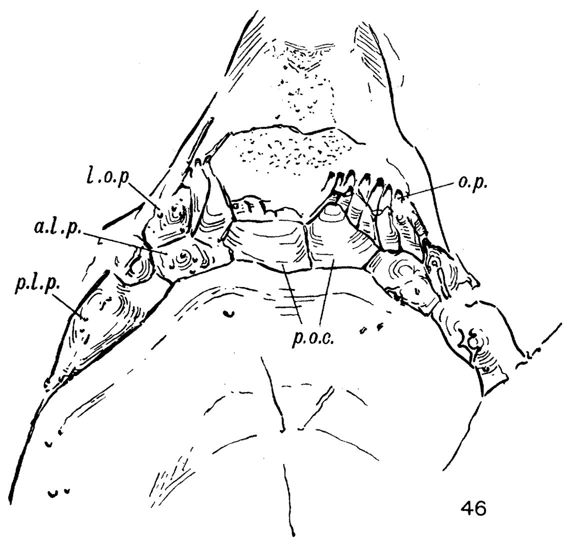

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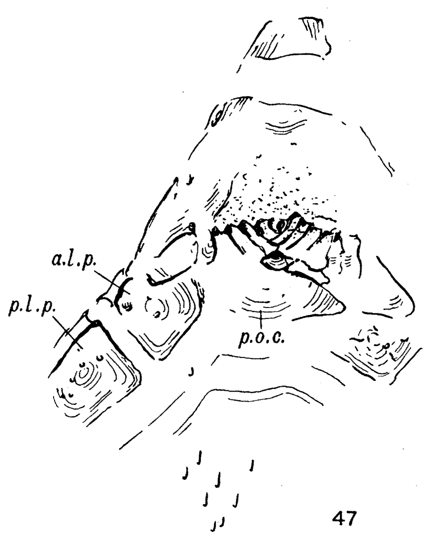

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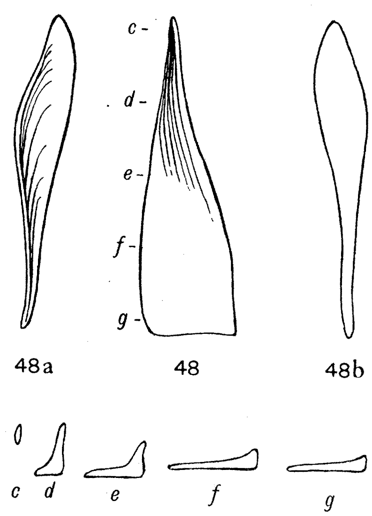
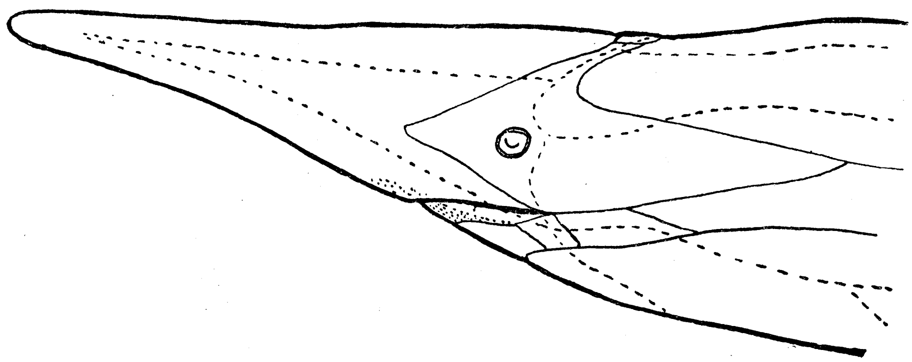


FIGS. 45–47—*Pteraspis rostrata* (AGASSIZ), var. *toombsi* nov. External moulds of ventral surface of rostrum (except in fig. 45) and of oral apparatus. Lower Old Red Sandstone (zone II. 2) : Wayne Herbert Quarry, Herefordshire. (P. 17478, P. 17487, and P. 17484 respectively—all approx. × 2.)

FIG. 48—Oral plate of right side restored, dorsal view. (*a*) Left lateral view. (*b*) Right lateral view. (*c–g*) Cross-sections from front to rear (× 6)

possibility of the mouth of Pteraspids being protrusible, but I consider to some extent it must have been so. The presence of "ornamentation" on all four surfaces of the oral plates except the hinder part of the upper side, shows clearly that they were free of one another and, as their form suggests, could move one on another, at the same time being connected in series by the epidermis. They could only move forwards



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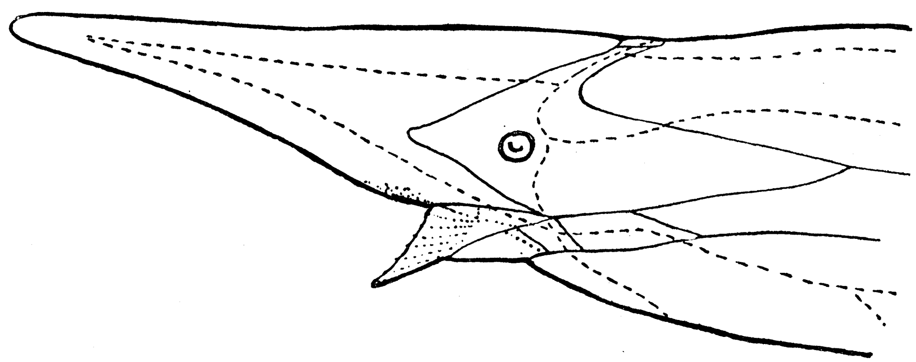

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FIG. 49—*Pteraspis rostrata* (AGASSIZ), var. *toombsi* nov. Restoration of head with mouth closed. Sensory canals shown by broken lines. (Approx. × $2\frac{1}{2}$.)
FIG. 50—Same with mouth protruded

and downwards, at the same time splaying to form a kind of scoop or shovel (*see* restorations, figs. 49, 50) whereby mud and decaying refuse could have been taken off the bottom, for it seems most likely that such were their food and habitat.

(*c*) The Body behind the Carapace

Hitherto, the covering of the body behind the carapace of a Pteraspid has been known from published descriptions of five or six fragments of squamation and a few isolated scales (LANKESTER, 1864, p. 195, Pl. XII, figs. 3, 4; 1868, p. 18, Pl. V, figs. 1, 3, 5, 7, 8. LERICHE, 1924, p. 154, text-fig. 6, Pl. III, fig. 12 ; 1926, p. 25, Pl. I, figs 1, 2; Pl. III, fig. 3; Pl. IV, figs. 1, 1*a*. ZYCH, 1931, figs. 41, 49, 51, phots. 26, 28–31), although two almost complete but badly crushed specimens of the allied genus *Protaspis* with both carapace and caudal region have recently been described from Wyoming (BRYANT, 1934, pp. 152, 153, Pls. XXI, XXIII, XXIV, fig. 1). Of the European Pteraspids the only specimen comprising fragments of both carapace and squamation that has been described in detail is the well-known fossil obtained by LANKESTER from Cradley, Herefordshire. This specimen LANKESTER (*loc. cit.*) interpreted as part of the dorsal shield showing the insertion of the dorsal spine followed by the scales of the back, and he tentatively referred it to *Pteraspis crouchi* ; later WOODWARD (1891, p. 163) re-described the fossil and demonstrated that it belonged to *P. rostrata* and that LANKESTER's orientation of it was incorrect, the supposed socket of the dorsal spine being the division between the dorsal and ventral shields (actually it is a groove made by the breaking away of the cornu) and the squamation that on the anterior region of the left flank. The specimens of *Protaspis* figured by BRYANT (*loc. cit.*) show that this form had " a slender and attenuated whiplike body covered with large scales " and " apparently there was a median series of long, pointed scales both dorsal and ventral. Towards the posterior end of the trunk the scales remain comparatively large, and only two or three scales are contained in the depth of the body." Of a specimen belonging to a second species of this genus the author remarks that " the body behind the armor is slender and defended by median dorsal and ventral series of large, pointed scales with a few lateral scales intervening. Approaching the tail, the lateral scales become smaller and more numerous, extending into the tail itself. The tail was either truly heterocercal, or of the reversed heterocercal type known as hypocercal. The fulcral scales rapidly diminish in size on the tail portion." As we shall see from the new specimens of *Pteraspis rostrata*, the squamation of the caudal region in the European form was similar to that described in the American, and that the tail was truly hypocercal, so that the tail of *Protaspis* was most likely of the same type.

The scaly region behind the carapace is very well shown in the new specimens of *Pteraspis rostrata toombsi*, in some of which it is complete to the tip of the tail (figs. 1 and 2, 51–55, 63–65, and 83–85 ; and figs. 98, 99, Plate 25). Most of the fossils are flattened dorso-ventrally, but seldom symmetrically, for the anterior dorsal and ventral ridge-scales usually lie nearer one side than the other, suggesting that in this part the animal was more or less round-bodied. The tail itself is, of course, turned on one side and lies in the bedding-plane. The squamation is usually well preserved, except occasionally for a slight telescoping just behind the carapace and some confusion of the scales where the dorsal surface passes into the ventral. The scale-covered region is slightly overlapped by the hinder end of the carapace, and from there it tapers to the root of the tail, which is strongly hypocercal, for the lower lobe is narrow and very much longer than the upper, from which it is separated by a shallow emargination, figs. 51–54 ; fig. 103, Plate 26. The caudal fin is about as deep as the body immediately behind the carapace and about twice as deep as the pedicle. The proportions of the scaly region seem to vary somewhat, as Table II shows, but these differences are most likely due to longitudinal distortion, a process to which this part is obviously more liable than the rigid carapace.

TABLE II

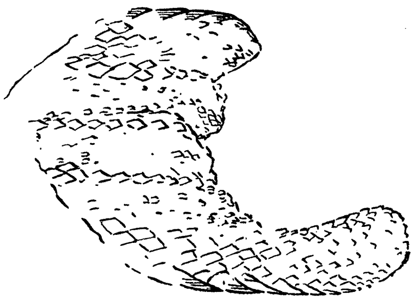
Specimen	Length of dorsal shield	Length of dorsal disc	Dorsal disc* to tip to upper caudal lobe	Ventral disc to tip of lower caudal lobe
	cm	cm	cm	cm
P. 16790	7·8	5·0	7·3	—
P. 17477	—	5·1	7·3	8·5
P. 17480	8·0	4·6	8·0†	—
P. 17485	7·5	4·5	7·8	10·2
P. 17521	7·4	4·1†	7·0	7·8†
P. 17525	—	—	6·9	7·8

* Measured from middle point between dorsal spine and cornu.
† Imperfect.

Thus the squamous region to the tip of the upper caudal lobe is approximately as long as the dorsal shield, but more than one-third of this represents the caudal fin (figs. 105, 106, Plate 26), while the finger-like lower lobe may be nearly one-quarter as long.

From the hinder margin of the carapace to the caudal fin, the body is covered with thick imbricating scales arranged in oblique dorso-ventral rows, with dorsal and ventral series of median ridge-scales. The surface of the flank-scales normally exposed is rhombic in shape, but when the squamation has been so stretched as to show the complete scales (fig. 107, Plate 27), the anterior angle is seen to be somewhat rounded, and what is most striking is that the whole is ornamented with ridges and grooves like the external surface of the plates of the carapace. Now since the outermost layer of the ridges seems to be of a form of enamel of ectodermal origin and the overlap is quite extensive, the pockets formed by the epidermis must have been unusually deep—unless the whole scale was of dermal origin. The arrangement of the squamation generally was regular, the scales becoming slightly smaller dorsally, ventrally, and caudally, except that those in contact with the dorsal ridge-scales are less uniform in shape and very much deeper than long (figs. 63, 64), and that here and there on the flanks occur odd double scales. These are most curious, for they occupy the areas of two ordinary scales, and the areas so occupied may be both in one dorso-ventral row or one in each of two adjacent rows. An example of each kind actually in contact with one another is shown in fig. 107, Plate 27. Such double scales are plentiful in association with the Trimpley shields, to which they and the ridge-scales with them are disproportionately large, for while all the shields are of about the same size as the Wayne Herbert fossils, the scales are sometimes twice as big (figs. 56–60). However, all these scales are isolated and so one cannot be absolutely certain that they belonged to the same specimens as the shields, but if not, then there are no shields for the scales, and reversely.

Both the number of the scales in a row and the number of rows from the carapace to the caudal pedicle seem to vary widely from one individual to another ; for instance, in P. 17522, the only specimen which is completely compressed laterally, there appears to be only about nine or ten scales in an anterior row, and about fifteen rows to the base of the caudal pedicle ; whereas in others the numbers are as high as



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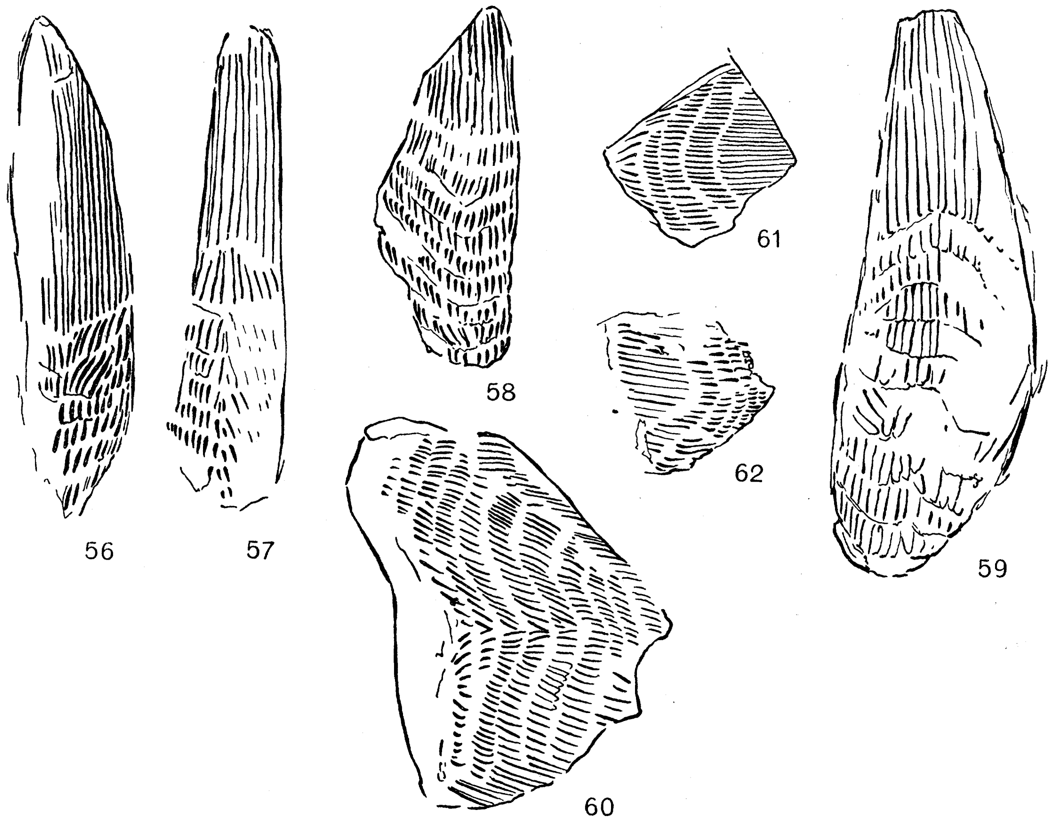
FIGS. 51–55—*Pteraspis rostrata* (AGASSIZ), var. *toombsi* nov. External moulds of caudal fins showing variation in length of lower lobe. Lower Old Red Sandstone (zone II. 2) : Wayne Herbert Quarry, Herefordshire. In fig. 55, the upper lobe is incomplete and folded under the lower. (P. 17488. II, P. 17521, P. 17477, P. 17485, and P. 17488. III, respectively—all approx. × 2.)

fifteen and twenty-five respectively ; this is surely a remarkable range, which, however, cannot be correlated with any other differences.

Behind the caudal pedicle the scales decrease in size rapidly, except for several rows which continue along the ventral margin to the tip of the lower lobe, presumably covering the body axis, and a smaller number along the dorsal (figs. 51–55). In addition, there are three series, each comprising two or more rows of scales much larger than the small lancet-shaped scales that form the groundwork of the fin, and

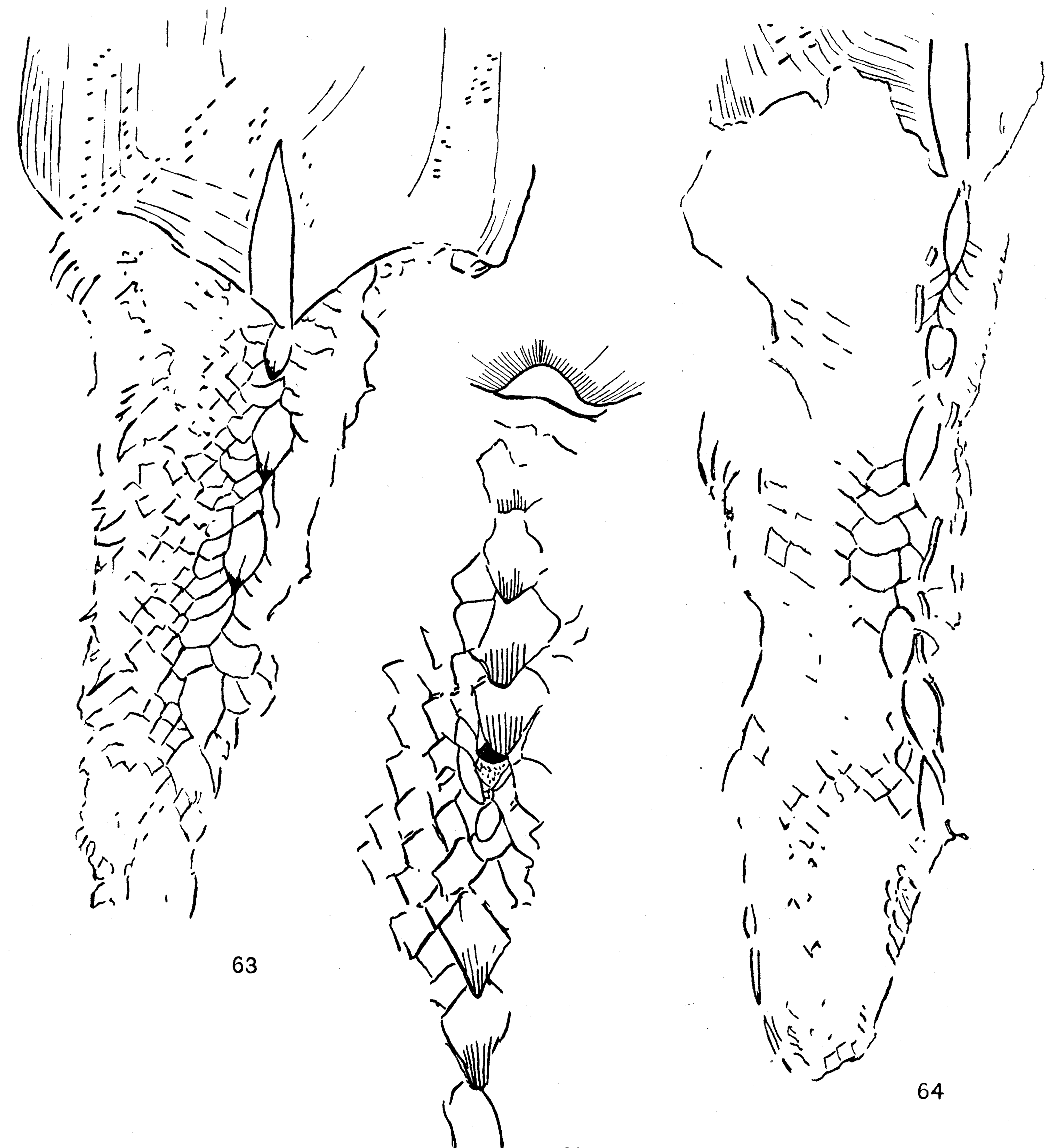


Pteraspis rostrata (Agassiz), var. *trimpleyensis* nov.
Lower Old Red Sandstone (zone II. 2) : Trimpley, Worcestershire

Figs. 56–59—Ridge-scales, presumably from the anterior part of the dorsal series. (P. 16479. III, P. 16480. I, P. 16476. II, P. 16479. II—× approx. 6, 7, 8, 4½ respectively.)
Fig. 60—Large irregular scale of uncertain position. (P. 16572—× 7.)
Fig. 61—Flank-scale. (P. 16478. XVI—× 7.)
Fig. 62—Imperfect flank-scale. (P. 16476. I—× 7.)

these run longitudinally at about equal distances from one another and from the dorsal and ventral series, from the caudal pedicles to the hinder margin of the fin, forming rays to support the web. At first, these " rays " give one the impression that the fins are much folded or puckered, but I am satisfied that this is not the explanation of this unusual feature, although it certainly does emphasize them in some specimens.

The dorsal series of median ridge-scales starts with four large, well-separated oval scutes bearing low, backwardly-directed spines (figs. 2, 63, 64) ; of these, the first was completely hidden by the overhanging dorsal disc and is seldom seen, while the second and third must have been covered by the dorsal spine when seen from above. Each of these scutes is in length equal to three or four rows of body-scales and is



Pteraspis rostrata (Agassiz), var. *toombsi* nov.

Lower Old Red Sandstone (zone II. 2) : Wayne Herbert Quarry, Herefordshire

Figs. 63, 64—External moulds of dorsal surface of scaly region of trunk, the second showing portions of dorsal lateral lines of both sides. (P. 17481 and P. 17523—both × $1\frac{2}{3}$.)

Fig. 65—External mould of anterior part of ventral series of ridge-scales, showing supposed anus. (P. 17482—× $2\frac{1}{3}$.)

separated from its neighbours in front and behind by about two rows, which meet those of the opposite side in mid-line. The fourth scute is followed after an interval of three or four rows of flank-scales by a continuous series of deeply overlapping fulcra, of which the first are long and fairly wide; but they decrease in size as they pass on to the upper margin of the tail, reaching to the very tip (figs. 51–54). The number in this series is about a dozen.

The ventral series of ridge-scales is also discontinuous, but is divided apparently by the anus into a short anterior and a long posterior section reaching to the tip of the tail. In both sections every scale overlaps the one behind it (fig. 65), and those behind the supposed anus are rather larger than the corresponding scales of the dorsal series. The row starts with five moderately large oval scales, ridged down the middle and pointed behind (fig. 1, and restoration, fig. 85). Immediately after the fifth scale the squamation is somewhat indistinct, but it seems most probable that here was the anal opening,* and this is followed by an interval of about 11 or 12 mm, equal to five or six oblique rows of lateral scales, in which the surface is covered by flat scales of varying shapes belonging to the lateral series. Thereafter the row of ridge-scales recommences with somewhat flatter scales than before, and these decrease in size and grade caudally into ordinary fulcral scales. This posterior portion of the ventral ridge-scales comprises about fifteen scales, not including the smallest at the extremity. There are also very minute fulcra-like scales along the upper margin of the elongated lower lobe (fig. 51).

Isolated ridge-scales are not uncommon on the Trimpley slabs (figs. 56–59), and although all are of the usual lanceolate type yet none shows the posterior spine noted in the anterior scutes of the dorsal series of *P. r. toombsi*. All are large, but not so disproportionately as the irregular double scales.

Zych (1931, figs. 41, 49, 51) has restored some of the Podolian species with prominent lateral ridge-scales along the flanks, but I think that he has misinterpreted as such the upturned edges of the ordinary flank-scales.

(*d*) "Ornamentation," Growth-Stages and Sensory Canal System

The ornamentation of the carapace, as is well known, consists of very numerous fine parallel ridges, each plate having its own independent series which serves to define its limits. On the more elongated plates, such as the branchial and cornual, they run along the major axis, but on the more equilateral plates they are roughly concentric, although the focus is not necessarily a point at the middle of the length of the plate; for instance, in the two discs it is much elongated, sometimes double, and situated considerably nearer the hinder margin than the anterior. The ridges on the anterior part of the orbital plates are centred about the orbits, so that they run parallel with the length of the shield on the medial processes, and thus at right-angles

* It is, however, also possible that the anal opening was situated at the anterior end of the scaly region and is obscured by the overhanging of the ventral disc. This position would be more in keeping with the arrangement in *Drepanaspis*.

to the ridges on the rostrum and dorsal disc, clearly defining their limits ; but on the elongated posterior portions they are longitudinal. On the lateral plates they are concentric, allowing the margins to be easily determined.

The pattern on the oral plates has been described already (p. 408) and need not be repeated.

The pattern on the dorsal surface of the snout in *P. rostrata* varies somewhat and within a variety ; in the Herefordshire specimens (and in most others) the " ornamentation " is concentric about a point near the tip of the rostrum, forming a series of backwardly directed arcs ; but in some of the Trimpley fossils the ridges are more in the form of chevrons of which the acuteness of the median angle increases towards the tip, where the series is almost longitudinal. However, this variation is not even of varietal significance, for in other examples from the same locality all gradations between the two patterns may be seen. On the sides of the rostrum, well shown in a Worcestershire specimen (P. 16477), they form a series of double chevrons, and on the underside a marginal series runs forwards and slightly inwards, joining with those of the opposite side across the front of the snout (fig. 1*a*). On the central part of the underside, which seems to have been slightly depressed, the ridges are broken up into minute irregular pieces, and this roughness increases as the mouth is approached.* Towards the posterior part of this area, the rostrum turns sharply inwards and upwards to form the anterior margin of the mouth. The inner area, as we have already mentioned, corresponds to the " maxillary tooth-plate " of *P. vogti* KIAER (1928, p. 123), for there is no sign of a separate plate ; we may also note from the description of the " tooth-plate " in *P. vogti* that these on the oral plates appear to be merely projections of the latter and were armed with denticles " which probably represent dentine ridges which have been divided into separate points," while the maxillary tooth-plate is " a projecting edge which is slightly convex " separated from the rostral area, which " bends down a trifle in the shape of a beak," by a marked groove, and that this plate is armed in a manner similar to the oral tooth-plates. Except that the " tooth-plates " do not project inwards and are thus not so well marked off from the plates that bear them, this description roughly corresponds to what is found in our specimens of *P. rostrata toombsi*, in which the maxillary " dentition " is formed by denticles on the inflected oral area of the rostrum, and the lower by those on the oral side of the anterior parts of the oral plates.

The scales on the posterior half of the body are thick and apparently consist of the same layers as the plates of the carapace, and their " ornamentation " (figs. 56–62, is formed by similar ridges of dentine arranged in various patterns. On the flank-scales (fig. 107, Plate 27) there are six or more ridges forming anteriorly directed chevrons parallel with the dorsal and ventral front margins, and these are succeeded behind by longitudinal ridges divided into lengths by chevron-shaped grooves parallel with the anterior ridges, the distance between them, at first very small, increasing

* I can find no trace of the lateral grooves which ZYCH (1931, p. 42) finds bounding the sides of this area from the corner of the mouth, and which he considers to be connected with the external nares.

towards the hinder end of the scale, where they are sometimes altogether absent. Occasionally there is a small confused area between the two series of ridges in the middle of the scale. As shown in fig. 107, Plate 27, the whole of the outer surface of the flank-scales is ornamented and there is no smooth area of overlap. The pattern on the ridge-scales is, on the whole, similar to that on the flank-scales, but the anterior chevrons are generally much more numerous and are prolonged postero-laterally to cover most of the sides of these $\wedge$-shaped scales, while their apices are in some instances inverted, especially on the larger ventral ridge-scales.

The " ornamentation " of the Trimpley scales consists largely of the broken longitudinal ridges (figs. 56–62), and lacks the anterior chevrons so conspicuous in *P. r. toombsi*.

The nature of the " ornamentation " of the carapace has been described in detail by Stensiö (1932, pp. 191–2). The ridges are of dentine covered with some form of enamel, and are separated by grooves that are very narrow distally but wider basally, a section of a dentine-ridge being T-shaped. These grooves were so richly supplied by branches from the radiating canals that Stensiö considered them to correspond to the so-called mucous canal system of the Cephalaspids ; that is to say, the " ornamentation " of fine dentine-ridges was incidental to the mucous system.

The dentine-ridges are extremely fine, numbering from about fifty to eighty in a centimetre in all the species here described, the number varying according to their position on the carapace, being fewest, and therefore widest, near the anterior margin of the dorsal disc, and most numerous and narrowest near the posterior lateral margin of both dorsal and ventral discs ; their size and number is governed by the rate of growth of the portion of the plate on which they are situated. They are closely appressed distally, and when well preserved are very finely denticulated. I can find little evidence of variation in number according to species, as has been suggested by some authors, but, as noted by Lankester (1868, pp. 31, 33), the form of the ridges in very well-preserved specimens seems to be of some specific value ; they are flat in *P. crouchi*, more or less rounded in *P. rostrata* and *P. jackana*, and rather $\wedge$-shaped in fresh specimens of *P. leathensis*.

The external " ornamentation " of the plates of the carapace is modified by two other features, the lines of growth and the sensory canal system. The lines of growth generally coincide with the dentine-ridges, but owing to interpolations between the latter and other small irregularities this is not invariably so (*see* fig. 36). As Leriche has pointed out more than once, the rate of growth around the discs especially is very unequal, for it takes place to a much greater extent along the anterior and antero-lateral margins than along the posterior parts of the sides, while it stops at an early stage along the hinder margin of the dorsal disc, except in *P. leathensis* and *P. jackana*, and is altogether absent along that margin in the ventral, thus accounting for the posterior position of the focus of the ornamentation in these plates. The growth-lines, which are local thickenings of the carapace, occur at irregular intervals,* and are

* Bryant (1934, p. 154) has suggested that the lines of growth are annual and that one may thereby determine the age of the animal at the time of its death ; but their irregularity does not support this interesting suggestion.

very much more marked in some specimens than in others, as in the Trimpley fossils; indeed, in the latter the whole substance of the shields shows signs of hypertrophy.

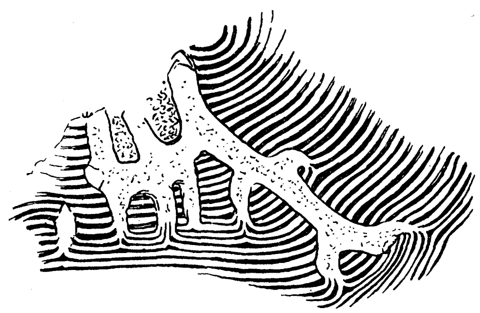
The greater part of the sensory canal system of the carapace is beautifully shown in a number of specimens, in most of which the substance of the carapace has been removed with acid, leaving the infillings of the canals standing in bold relief (figs. 9, 26, 66, 68–77). The canals lay in the cancellous layer beneath the mucous grooves, with which they are seen to communicate by short lateral processes given off on both sides, these processes splitting distally into fine canals which pass into the grooves (fig. 66*a*). Above each junction of the two systems is a minute slit or pore by which the sensory canals apparently opened directly on to the surface; these slits are well figured by ZYCH (1931, phots. 16, 21), who, however, does not mention any connection between the sensory canals and the grooves. It is by these pores that the course of the sensory canals can be traced in specimens in which the ornamentation is preserved (some may be seen in fig. 100, Plate 25). Moreover, the canals themselves frequently cause a swelling on the underside of the plate which leaves a series of grooves, so puzzling to LANKESTER (1868, p. 29), on internal casts.

The arrangement of the sensory canals has been figured and described in several species (WOODWARD, 1887, p. 478, text-fig.; 1891, p. 168, text-fig. 16; LERICHE, 1906, p. 30, text-fig. 12, etc.; STENSIÖ, 1926; JAEKEL, 1927, p. 884, text-fig. 32; KIAER, 1928, p. 120, text-figs. 1, 2; ZYCH, 1931, p. 48, figs. 41–44, 49–51, phots. 19, 23; BROILI, 1933, p. 2, text-fig. 1; GROSS, 1933*a*, p. 50, text-figs. 3A, 4). STENSIÖ's paper is of primary importance from the point of view of the homologies of the various canals, and in it he figures the distribution, somewhat incomplete owing to the imperfection of the material, of both dorsal and ventral discs of *P. rostrata* and *P. crouchi*. KIAER gave a restoration of the canal system of the dorsal surface of the carapace of *P. primaeva* and of the ventral of *P. vogti*, both species being from the Downtonian of Spitsbergen; while ZYCH shows the distribution in several interesting species from Podolia, which he refers to a new genus, *Podolaspis*. Lastly, BRYANT (1933, p. 295, text-fig. 2*c*, Pl. I) has described and figured the distribution of this system in a new allied genus, *Protaspis*, from the Lower Devonian of Wyoming. The specimens of *P. rostrata* and *P. crouchi* described below, considerably supplement STENSIÖ's description as to detail, for in many the most minute features are to be observed, while the less perfect shields of *P. jackana* and *P. stensiöi* show the general distribution of the system in these species. The course of the various canals in these English forms is so similar that they will be described together; indeed, I have discovered no features by which the species may be distinguished by the canal system alone.

It will be seen that the sensory canal system on the carapace of these species varies considerably in detail in the individuals, and occasionally striking discrepancies may be seen between the two sides of the same specimen.

On the dorsal disc (fig. 81) are two pairs of longitudinal sensory canals, of which the inner and outer on each side are connected in the posterior half of the plate by three transverse canals radially directed, the two hindmost continuing medially to join the inner pair. In all the known specimens of *P. rostrata* from Wayne Herbert and

Trimpley, the inner longitudinal canals start at the anterior margin of the disc close to the median line and continue directly backwards until near the focus of the " ornamentation," that is, for about two-thirds the length of the plate, where they



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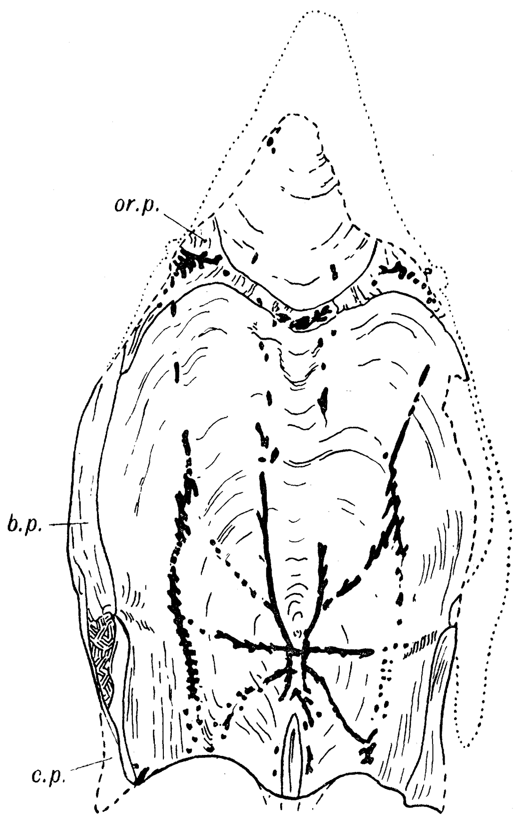

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Pteraspis rostrata (Agassiz), var. *waynensis* nov.

Fig. 66—Imperfect dorsal disc preserved as external mould and showing parts of the sensory canals infilled with matrix. (Same specimen as in fig. 3 and fig. 101, Plate 25. Slightly enlarged.)

Fig. 66*a*—Cast of sensory canals of right (left of figure) post-orbital region of same specimen showing connection with external " ornamentation." (Greatly enlarged.)

Fig. 67—Counterpart of same specimen preserved as internal cast and showing external mould of lower surface of rostrum. (Slightly enlarged.)

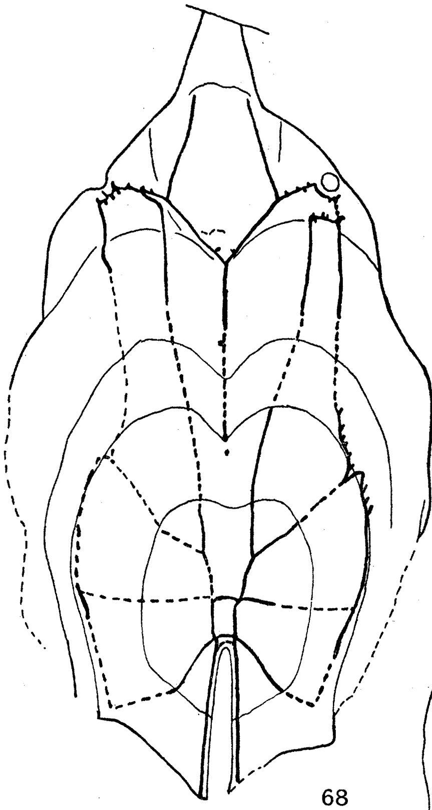
turn obliquely inwards and run close to one another for a short distance before slightly diverging in front of the socket of the dorsal spine, where they immediately run into, or, by a double cross-commissure, are connected with a $\wedge$-shaped canal that borders the socket and passes out of the disc on each side (figs. 2, 66 ; fig. 101, Plate 25). In all specimens of *P. r. monmouthensis* (fig. 9) and of *P. crouchi* whatsoever (figs. 68–72), the inner longitudinal canals are widely separated at the anterior border of the disc and run obliquely backwards and inwards towards the focus of the " ornamentation," thereafter continuing as in the other forms ; there is, however, some individual variation, for in some specimens the separation anteriorly is less marked than in others, while among the specimens of *P. rostrata* from Cradley both forms may be seen (*cf.* Stensiö, 1926, p. 5, text-fig. 2—this is a specimen from Cradley showing widely separated inner longitudinal canals). It is possible that this feature is of no systematic importance, but, on the other hand, most of the fossils from Cradley are not sufficiently well preserved to determine the variety of *P. rostrata* to which they belong, and while some of them, *e.g.*, fig. 6, seem to be referable to *P. r. trimpleyensis*, other varieties may also be present. The distance between the inner canals at the anterior border is also very much affected by the size of the specimen, for the canals, as we shall note again later, are constant in size and position in the individual and do not grow with the shield, and therefore it is clear that canals will be closer together anteriorly in small specimens (fig. 71) than in large. We may notice here one remarkable specimen of *P. crouchi* of the typical form (fig. 68) in which the left (right of figure) longitudinal canal is most irregular, for instead of entering the disc directly from the transverse inter-orbital canal, it is given off from the outer longitudinal canal along the margin of the disc.

The outer lateral longitudinal canals start at the anterior margin of the disc just behind the orbits, in all well grown specimens of both species, and run backwards and generally slightly inwards (this part is not, of course, present in small discs) and then just before, or at, their junction with the anterior transverse canal (figs. 2, 66, 68–70) they start to diverge. They then continue backwards parallel with the convex margins of the disc as far as their junction with the posterior transverse canal close to the posterior border of the disc, thereafter turning outwards to leave the plate near the postero-lateral corner (figs. 66, 70–72).

The sensory canals of the dorsal shield of *P. jackana* (figs. 23, 24, 26) are very similar to those of the two species described above, the only feature to be specially noted being the course of the inner longitudinal canals, which joined the inter-orbital canal close to the median line in all three specimens ; in *P. stensiöi* (figs. 28, 29) the canals are moderately close together at this point.

No sensory canals have as yet been traced in *P. leathensis* or in *P. mitchelli.*

That both the outer and inner longitudinal canals pass into the squamation behind the shield there is no doubt; but this can be seen in only one specimen (fig. 64) and then only for the inner canals, which can be traced intermittently on both sides, running immediately below the dorsal ridge-scales as far as the level of the second scale of the posterior series, above the caudal pedicle. How far they continued one cannot



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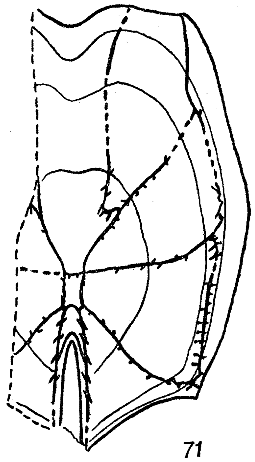

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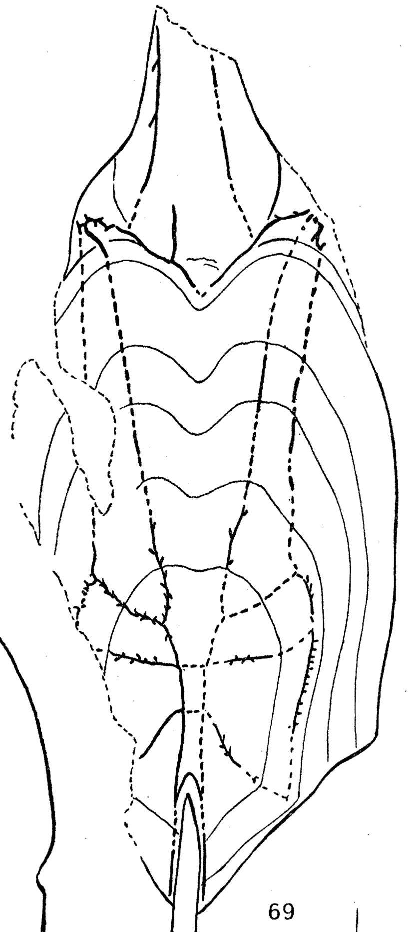

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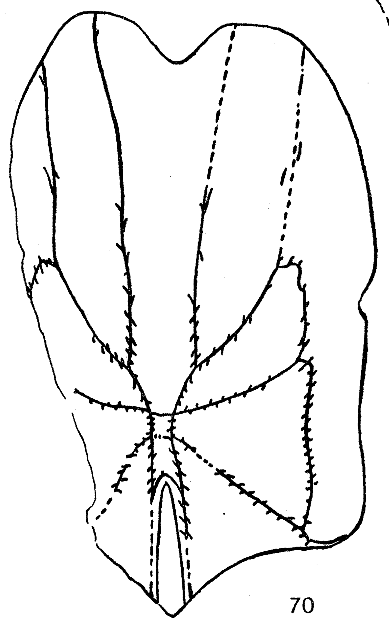

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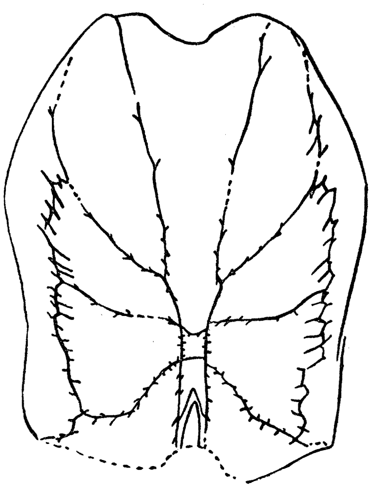

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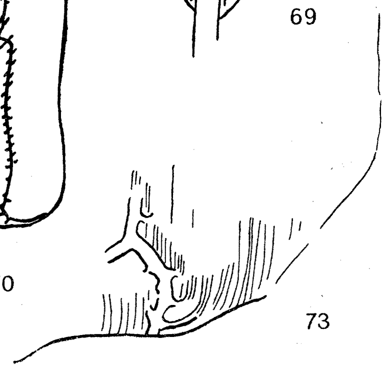

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FIG. 68—*Pteraspis crouchi* LANKESTER, *forma typica*. Dorsal shield of young specimen preserved as external mould and showing growth-stages of disc and irregular distribution of sensory canals. Lower Old Red Sandstone (zone II. 2) : Pool Quarry, Herefordshire. (P. 16520.I—$\times 1\frac{1}{3}$.)

FIG. 69—*Pteraspis crouchi* LANKESTER, var. *mattockensis* nov. External mould of dorsal shield showing growth-stages of disc and distribution of sensory canals. HOLOTYPE of variety. Lower Old Red Sandstone (zone II. 2) : Castle Mattock Quarry, Herefordshire. (P. 16490.I—$\times$ $1\frac{1}{3}$.)

FIG. 70—*Pteraspis* cf. *crouchi* LANKESTER, *forma typica*. External mould of dorsal disc showing sensory canals. Lower Old Red Sandstone (zone II. 2) : Wayne Herbert Quarry, Herefordshire. (P. 16848.I—$\times$ $1\frac{1}{3}$.)

FIG. 71—*Pteraspis* ? *crouchi* LANKESTER, var. *mattockensis* nov. External mould of fragmentary dorsal disc of young individual showing growth-stages and sensory canals. Lower Old Red Sandstone (zone II. 2) : Castle Mattock Quarry, Herefordshire. (P. 16487—$\times$ $1\frac{1}{3}$.)

FIG. 72—*Pteraspis* ? *crouchi* LANKESTER, var. *mattockensis* nov. External mould of dorsal disc of young specimen showing unusually elongated tubuli. Lower Old Red Sandstone (zone II. 2) : Castle Mattock Quarry, Herefordshire. (P. 16832—$\times$ $1\frac{1}{3}$.)

FIG. 73—*Peteraspis rostrata* (AGASSIZ), ? var. *waynensis* nov. Left (right of figure) postero-lateral corner of external mould of ventral disc showing passage of lateral longitudinal canal from disc into scaly region of trunk. Lower Old Red Sandstone (zone II. 2) : Wayne Herbert Quarry, Herefordshire. (P. 16838—$\times$ 5.)

say, nor is it possible to be certain how they opened on to the surface of the scales. In one scale a minute branch can be seen, but this is almost at the end of the canal ; possibly one such branch opens to the surface in each scale, but if so they must have been exceedingly small, for their openings cannot be detected on the surface of the other scales ; it is, perhaps, more likely that they opened on to the surface through tubuli running between the scales.

Tubuli connecting the sensory canals with the grooves of the superficial " ornamentation " are given off on both sides of all canals at varying intervals (fig. 66, 68–72). On the transverse canals and on those parts of the longitudinal canals behind their junction with the anterior transverse canals the tubuli are short, crowded, and arranged obliquely on alternate sides, those on the outer or anterior side being directed forwards, and those on the inner or posterior side backwards. In front of this junction, however, the tubuli become longer and are set at rapidly increasing intervals, so that they become very rare and widely spaced in the anterior region of the larger discs, and all those on the inner longitudinal canals are directed forwards. The disc figured in fig. 72 is exceptional on account of the unusual length and spacing of the tubuli along the posterior portion of the outer longitudinal canals.

A large pore lies immediately over the pineal pit, and immediately behind this a transverse inter-orbital canal runs outwards on each side through the medial branch of the orbital plate towards the orbit, behind which it curves slightly backwards and downwards, and is there joined by the outer longitudinal canal from the dorsal disc. Below this point it continues downwards to pass on to the ventral disc by way of the posterior corner of the lateral oral plate and by the anterior lateral plates (fig. 42 ; *see* restorations, figs. 81, 82). As on the dorsal disc, the tubuli occur on both sides of the canal ; they are concentrated near the pineal sensory organ, three or four on each side and one or two behind and communicating with it, and behind the orbits, where there are nine or ten, three directed towards the eyes being particularly long (figs. 66*a*, 67, 68). The inner longitudinal canals join the inter-orbital canal either near the pineal sensory organ, as in *P. r. toombsi*, *P. r. waynensis*, and *P. r. trimpleyensis* (figs. 2, 66 ; figs. 100, 101, Plate 25 ; *see* restoration, fig. 81), or close to the outer longitudinal canals, as in *P. r. monmouthensis* and *P. crouchi* of the typical form and *P. c. mattockensis* (figs. 9, 68, 69). The specimen of the typical *P. crouchi* shown in fig. 68, as noted above, is remarkable in that the inner longitudinal canal of the left (right of figure) side does not join the inter-orbital canal at all, but is connected to the outer canal of its side by a transverse branch, and also that a median longitudinal canal reaching to the centre of the dorsal disc is given off from the inter-orbital canal behind the pineal organ.

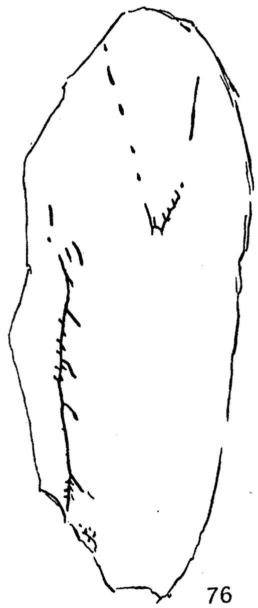
The paired rostral canals leave the inter-orbital canal at various points between the pineal plate and the orbits ; close to the pineal plate in *P. r. monmouthensis*, *P. jackana*, and *P. stensiöi* (figs. 9, 24, 28, 29), a little further out in *P. r. waynensis* and *P. r. trimpleyensis* (figs. 66, 81 ; figs. 100, 101, Plate 25), and about midway between in *P. crouchi* (figs. 68, 69), while in *P. r. toombsi* and the specimen of *P. rostrata* from Cradley, figured by Stensiö (1926, p. 5, text-fig. 2), they arise near the orbits.

The canal on each side runs in a slightly curved line to a point on the rostrum just behind the tip, the length of its course naturally varying according to the species, and then makes a sharp bend, turning backwards and gradually downwards along the side of the rostrum on to the under-surface, where it leaves the plate. (This return branch is particularly well shown in a specimen of *P. r. trimpleyensis*, No. P. 16477.) The tubules of the rostral canals are very few in number and accordingly widely spaced. In *P. r. waynensis* all are directed forwards on alternate sides of the canal (*see* fig. 81), but the only examples known in specimens of other species (*P. crouchi mattockensis*, fig. 69) are two directed backwards and, although apparently consecutive, are on the same side.

After leaving the rostrum the lower branch of the rostral canals in *P. r. toombsi* (this is shown in no other form) traversed the lateral oral plate, as is shown by the pores, and so entered the anterior lateral plate (figs. 1, 41–47) ; it then crossed the posterior lateral plate into the ventral disc to form the lateral longitudinal canal on each side (*see* restoration, fig. 82). In the crossing of the lateral oral plate by this canal the arrangement in this form differs from that in *P. vogti* as restored by KIAER (1928, p. 121, text-fig. 2), in which it runs directly from the rostrum into the single lateral plate, and thence to the ventral disc.

In no specimens are the canals of the ventral disc as well preserved as those of the dorsal shield, but sufficient remains to indicate their general distribution. These specimens represent all but one variety of *P. rostrata* (figs. 1, 33, 39, 74), all forms of *P. crouchi* (figs. 37, 76, 78, 79), and *P. leathensis* (figs. 38, 77), and it will be seen that in all the distribution is essentially the same ; indeed, the arrangement varies as much between individuals as between different species (*cf.* figs. 75 and 76). There is on each side a lateral longitudinal canal, which entered the disc from the posterior lateral plate at the antero-lateral corner of the disc, and then ran backwards at a short distance from, and more or less parallel with, the sides of the disc as far as the hinder margin, from which it passed out on to the body (fig. 73), giving off in its course six or more short postero-medially directed branches, the number of which seems to have depended on the size of the plate rather than on the species. Its course on the scaly region has not yet been traced. The post-orbital part of the inter-orbital canal, after traversing the orbital plate and the anterior lateral plate, entered the ventral disc at some little distance in front of the lateral longitudinal canal (fig. 42), and ran from the anterior border of the disc obliquely backwards to meet its fellow of the opposite side at the middle of the plate. The course of these two canals is very variable within a species—in some specimens they form a wide V, with either straight (figs. 38, 42, 74, 77), or concave (fig. 33) sides, sometimes a long, narrow V (figs. 37, 76, 78, 79) sometimes a short loop (figs. 41, 45, 75), and very occasionally there is a joint posterior continuation, so that they are in the form of a Y ; in any case they leave a prominent scar on internal casts of the ventral disc, even when no other marking is to be seen.

The tubules of the canals of the ventral disc are not well displayed in any specimen, but so far as one may judge, they occur at short intervals on alternate sides of the canals.



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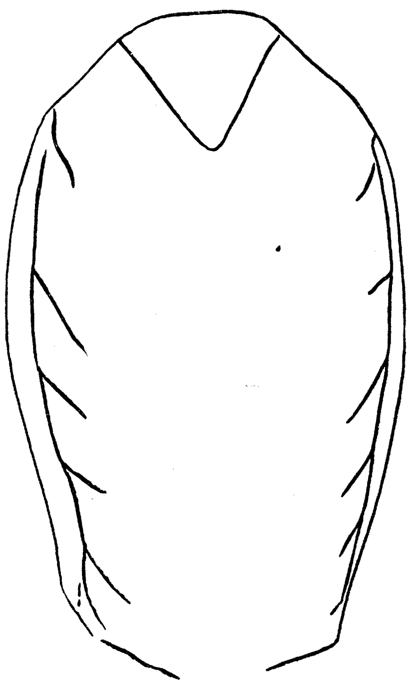

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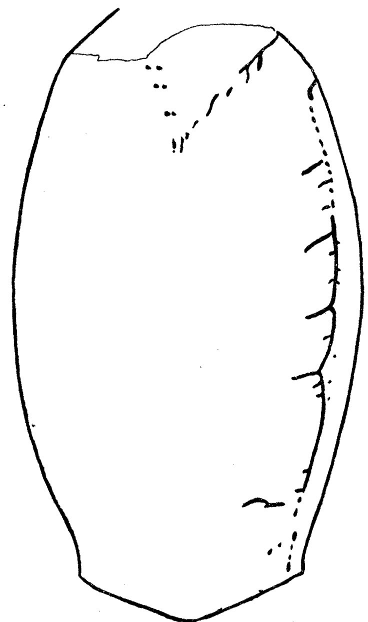

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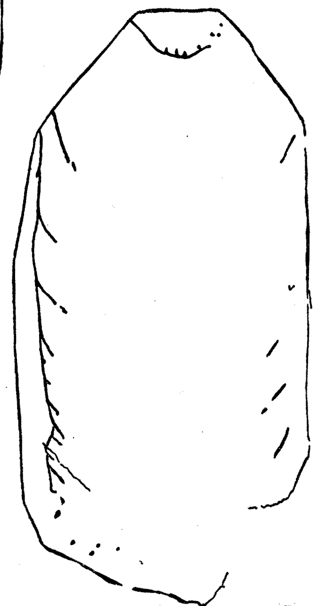

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FIG. 74—*Pteraspis cf. rostrata* (AGASSIZ), var. *waynensis* nov. Internal cast of ventral disc showing grooves of sensory canals. Lower Old Red Sandstone (zone II. 2) : Pool Quarry, Herefordshire. (P. 16836—× $1\frac{1}{3}$.)

FIG. 75—*Pteraspis crouchi* LANKESTER, var. *mattockensis* nov. Internal cast of ventral disc showing sensory canals. Lower Old Red Sandstone (zone II. 2) : Castle Mattock Quarry, Herefordshire. (P. 16834—× $1\frac{1}{3}$.)

FIG. 76—*Pteraspis crouchi* LANKESTER, var. *mattockensis* nov. Internal cast of imperfect ventral disc showing sensory canals. Lower Old Red Sandstone (zone II. 2) : Castle Mattock Quarry, Herefordshire. (P. 16843—× $1\frac{1}{3}$.)

FIG. 77—*Pteraspis leathensis*, sp. nov. Internal cast of ventral disc showing sensory canals. Downtonian (zone I. ?) : near Trimpley, Worcestershire. (42159*a*—× 2 approx.)

IV—Systematic Position of the Pteraspids and Relationships of the Ostracoderms

The question of the relationships of the Pteraspids and the other " Ostracoderms " has been much to the fore in recent years, thanks to the classical work of Kiaer (1924, 1932) on the Anaspids, and of Stensiö (1926, 1927, 1932) on the Cephalaspids. Both these authors have recently published classifications of the group, but these are fundamentally different. Kiaer's (1932) arrangement is as follows—

AGNATHA

Group 1—Monorhina
- Order 1—Osteostraci
- 2—Cyclostoma

Group 2—Diplorhina
- Order 1—Thelodonti
- 2—Heterostraci
  - Sub-order i—Psammosteida
  - ii—Cyathaspida
  - iii—Pteraspida

That of Stensiö (1927, p. 379, etc.)—

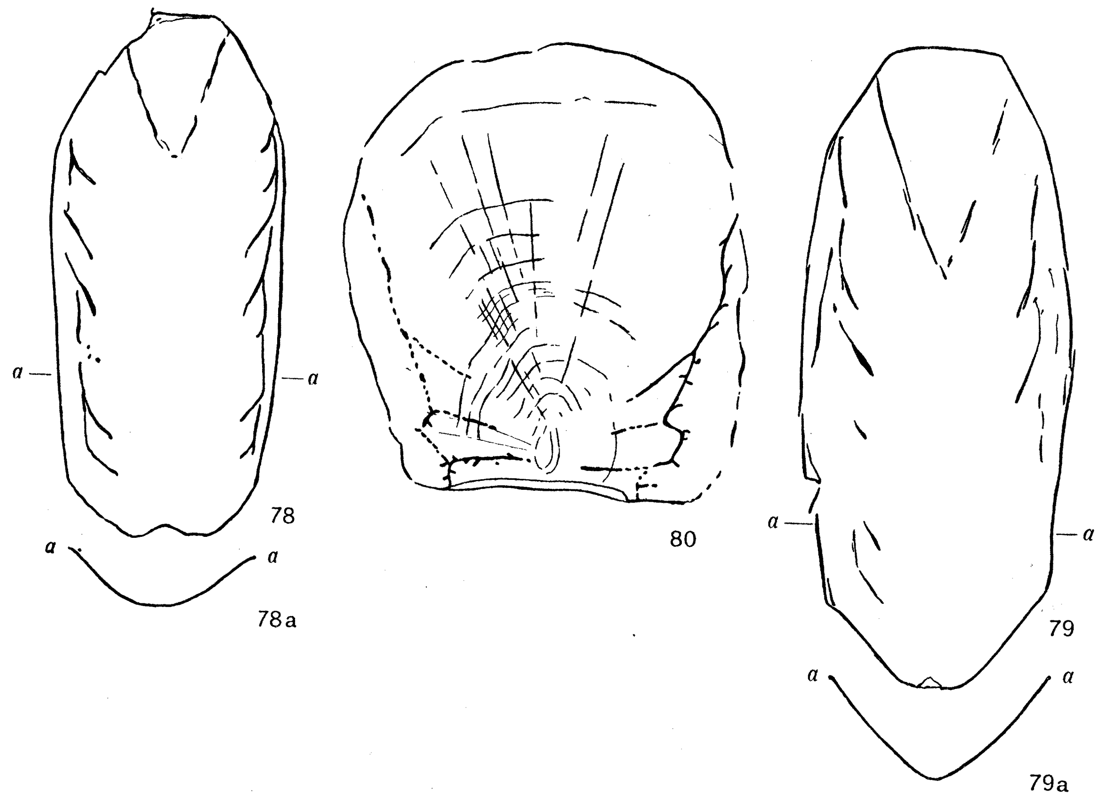
AGNATHA

Class—Ostracodermi (Cyclostomata)
- Sub-class A—Pteraspidomorphi
  - Order 1—Heterostraci
    - Family—Coelolepidae
    - Pteraspidae
    - Drepanaspidae
  - 2—Palaeospondyloidea
  - 3—Myxinoidea
- Sub-class B—Cephalaspidomorphi
  - Order 1—Osteostraci
  - 2—Anaspida
  - 3—Petromyzontia

Both, we may note, associate the Ostracoderms with the living Cyclostomes in the Group Agnatha. Kiaer divides the various members into two groups according as they were monorhine (Osteostraci and Cyclostomes) or diplorhine (Thelodonts, or Coelolepids, and Heterostraci). Stensiö, however, while preserving the name Ostracodermi for the whole and making it synonymous with Cyclostomata, forms two main divisions, the Pteraspidomorphi (Heterostraci, including Coelolepids, *Palaeospondylus* and the living Myxinoids) and the CEPHALASPIDOMORPHI (OSTEOSTRACI, ANASPIDA, and the living Petromyzontids). This association of the Ostracoderms with the living Cyclostomes is not a new idea, for it was mooted long ago by COPE (1889, pp. 852–3), WOODWARD (1897, p. 379 ; 1898, p. 1), and others (*see* the excellent summary of the history of the Cephalaspids by STENSIÖ, 1927, pp. 1–16), and seems now to be generally accepted (REGAN, 1929, p. 923 ; WOODWARD, 1932, p. 22 ; and others) ; but although some authors accept STENSIÖ's classification in detail (SÄVE-SÖDERBERGH, 1934, p. 3), others have strongly criticized his division of the living Cyclostomes into two branches derived from different Ostracoderm stocks (GROSS, 1932, p. 109 ; REGAN, 1929, p. 923 ; GOODRICH, 1931)—REGAN considers this arrangement to be " rather speculative," while GOODRICH makes some very damaging criticisms, none of which has been satisfactorily answered by STENSIÖ in his later work (1932, pp. 183–194). The chief objection to this classification is based on the relationship of the Petromyzontids to the Myxinoids, GOODRICH and others considering that the possession by both of the rasping organ armed with horny teeth, closely similar branchial apparatus, and other common anatomical features militates against their having a diphyletic origin. This objection seems to be valid, especially in view of the very great differences between the Pteraspids and the Cephalaspids. But GOODRICH goes farther and questions the derivation of any of the Cyclostomes from the Cephalaspids, which, if any, seem to be the more nearly related. He points out that the Cyclostomes have lost all trace of denticles, " those very persistent structures," besides the bony skeleton and paired limbs, and even queries the recognition of the dorsal median opening as a naso-hypophyseal pore, and suggests the possibility of its being a second pineal eye. For this, there seems to be less evidence than for STENSIÖ's suggestion, which has the advantage in that the pore closely resembles, superficially at any rate, a known structure in form and position. The real evidence that Cyclostomes were actually derived from the Cephalaspids does not seem very strong, but that they had a remote common ancestry is much more clearly indicated, for they possess important features in common, as, for example, the agnathous mouth, the sub-epidermal vascular plexus, in general the arrangement of the sensory canals, and the naso-hypophyseal opening. Except the last, these features are apparently possessed also by the Pteraspids, and the absence of the naso-hypophyseal opening may be deemed to be due to a more primitive condition.

We may now compare in detail the features of the Pteraspids and the Cephalaspids. Generally speaking, the close association of these two groups has been accepted from very early times (*see* STENSIÖ, 1927, pp. 1–16), although the reasons for this were at first superficial. On this point LANKESTER made characteristic comment (1870, p. 62) : " The HETEROSTRACI are at present associated with the OSTEOSTRACI because they are found in the same beds, because they have, like *Cephalaspis*, a large head-shield and because there is nothing else with which to associate them. There is at present no evidence that the body and fins of *Pteraspis* and its allies were like those of *Cephalaspis*, and the shields are not closely similar in plan, much less in histological structure, as to warrant any inference of similarity in other parts . . ." Later (1897, pp. 45–47) he became more convinced of their dissimilarity and remarked that

" There is absolutely no reason for regarding *Cephalaspis* as related to *Pteraspis* beyond that the two genera occur in the same rocks " (and, incidentally, even more hotly denied any relationship between either genus and the Cyclostomes). GOODRICH (1909, p. 194) cautiously described the OSTRACODERMI, in which were included Pteraspids, Cephalaspids, Anaspids and Pterichthyids, as a " merely provisional group " of Gnathostomes and seemed to have difficulty in finding characters to justify the association of these heterogeneous groups, and some of those he quoted, as the heterocercal tail and single dorsal fin, we now know to be untrue ; and there matters stood until KIAER and STENSIÖ brought forward their classifications, rejecting the



FIGS. 78, 79—*Pteraspis crouchi* LANKESTER, var. *heightingtonensis* nov. Internal casts of ventral discs showing grooves of sensory canals. (78*a*, 79*a*). Cross-sections at *a–a*. Lower Old Red Sandstone (zones II. 3 and II. ?) : Heightington and ? Trimpley, Worcestershire. (42149*a* and 38034*a* respectively—× $1\frac{1}{3}$.)

FIG. 80—*Doryaspis nathorsti* (LANKESTER). External mould of ventral disc showing sensory canals. Lower Devonian : Dickson Bay, Spitsbergen. (P. 6492—× $1\frac{1}{3}$.)

Pterichthyids entirely, and once more associating the Cephalaspids, Pteraspids, and Anaspids with the Cyclostomes. The chief characters common to the first two groups have already been noted ; in addition, STENSIÖ (1932, pp. 183–194) notes also the backward extent of the carapace and the development of the posterior parts thereof, the coherence of the endocranium, visceral endoskeleton, and endoskeletal shoulder-girdle, and the distribution of the sensory canal system, but more especially the supposed similarity between the mouth-parts and the micro-structures of the exoskeleton. With regard to the last, one may emphasize the supposed similarities or the more obvious differences according to one's prejudices, and the other likenesses seem to be either insufficiently established or of less certain systematic importance. However, taken as a whole, the similarities do indicate a remote common ancestry at least, but that it is remote may be seen from the following table of differences—

Cephalaspids	Pteraspids
Nasal sac single	Nasal sac probably double
Naso-hypophyseal opening dorsal	No external nasal opening and hypophysis ventral
Well-developed pectoral fins	No paired fins or vestiges thereof
Tail strongly heterocercal	Tail strongly hypocercal
Dorsal fin or fins present	No dorsal fins
Orbits dorsal and close together	Orbits lateral and widely separated
External branchial openings separate	External branchial opening single
Oral plates apparently immoveable, continuous with ventral visceral exoskeleton	Oral plates free
Exoskeleton with bone-cells	Exoskeleton without bone-cells
Strongly innervated "electric fields"	No "electric fields"
Body-scales with well-differentiated area of overlap	Body-scales imbricating, but without differentiated area of overlap

These features are obviously of varying systematic importance, but, taken as a whole, the differences make a formidable argument against any but the most distant relationship. Most significant to me seems the difference of structure of the caudal fins ; for the hypocercal tail is not one that has alone any mechanical advantage over other types, as perhaps the heterocercal has (*see* BREDER, 1926, p. 227), and is therefore unlikely to have been developed except in response to some mechanical need ; it certainly could not have been developed from the heterocercal, or reversely, but both must have been derived from a diphycercal ancestor. The mechanical necessity that would make such a tail as the hypocercal useful could only be the loss of ability to keep an even keel due to the degeneration of the pectoral fins in an animal with a diphycercal tail overweighted anteriorly by the unequal development of armour, as are the Pteraspids and Cephalaspids ; or to the development of armour anteriorly in a diphycercal animal already without pectoral fins. Of these alternatives the former is the less likely, for such a creature would have every stimulus to preserve its pectoral fins, whereas an unarmoured animal, being of more or less even density throughout its length, would have no especial need for the corrective action of pectoral fins so long as its tail was equilobate, for the thrust from such a fin is directly forwards, and any desired alteration in level could be achieved by simply flexing the axial skeleton, as in such living "fishes" as the Cyclostomes and the African and South American Lung-fishes, all of which have degenerate or no paired limbs and squamation, and equilobate tails. A creature with a heterocercal tail could not lose its pectoral fins and survive, for the effect of such a tail is to depress the snout, and without the anterior paired fins it could never rise from the bottom, even if unarmoured.* It seems most probable, therefore, that the Pteraspids were derived from a naked, diphycercal ancestor which had already lost its paired fins, or, more likely, which had never developed them, and the acquisition of the hypocercal tail followed immediately as the result of the unequal growth of an armoured covering. If the ancestral Pteraspids never developed paired fins from the primitive fin-fold, then they must have branched off from the main Agnathous stem considerably before the other members of the group, a suggestion which is supported by the more primitive condition of the nasal and hypophyseal elements ; later they became specialized in

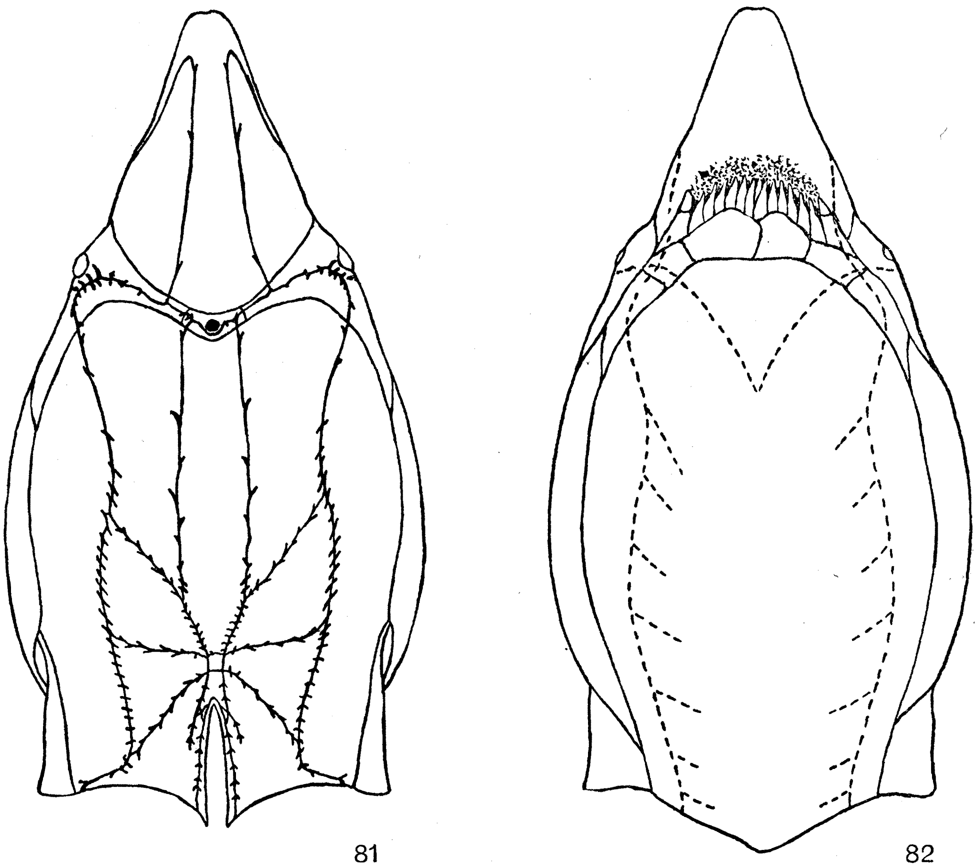


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FIG. 81—*Pteraspis rostrata* (AGASSIZ), var. *waynensis* nov. Restoration of dorsal surface of carapace (dorsal shield) showing distribution of sensory canals and tubuli. (Approx. nat. size.)

FIG. 82—*Pteraspis rostrata* (AGASSIZ), var. *waynensis* nov. Restoration of ventral surface of carapace, showing approximate distribution of sensory canals. (Approx. nat. size.)

their own way in the development of the exoskeleton, oral apparatus, and the formation of a single branchial opening.

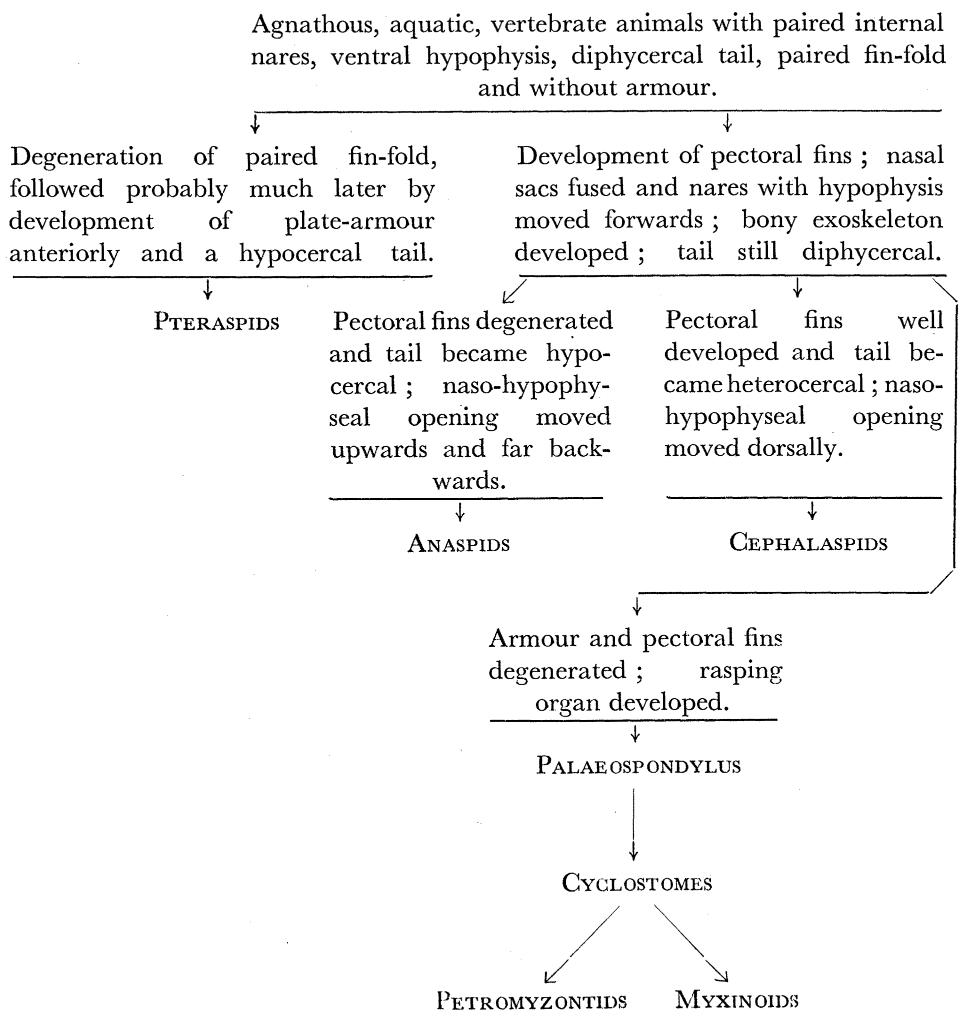
The position of the Anaspids is intermediate between the Pteraspids and Cephalaspids, for the presence in them of pectoral spines suggests that they had pectoral fins and lost them, and this and the fact that the movement forwards

* The action of the heterocercal tail in modern sharks is also counterbalanced to some extent by the upward tilting of the snout, but the presence of pectoral fins is the major factor in the control of direction.

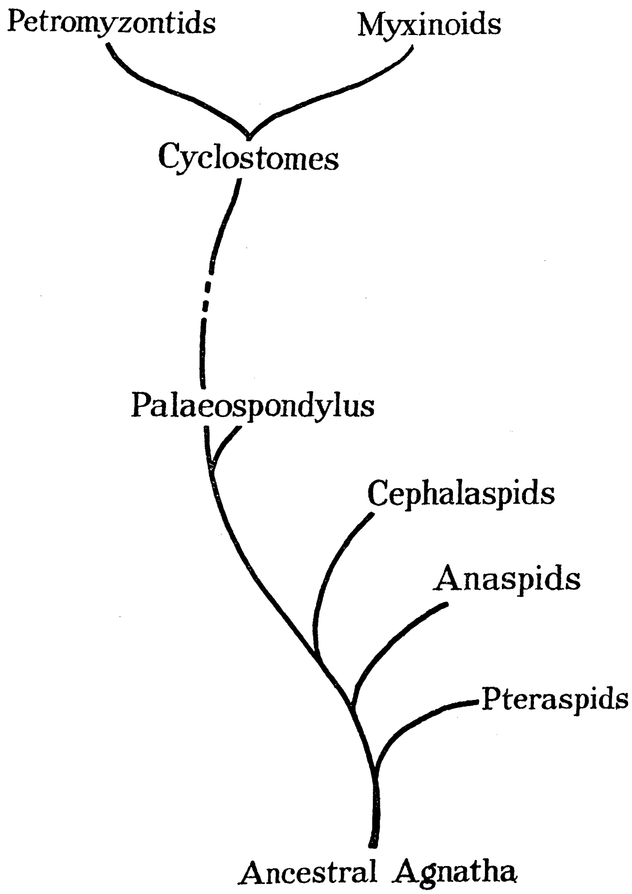
and upwards of the naso-hypophyseal pore had probably already started before they branched from the main stem, indicates that their common ancestry with the Cephalaspids was longer than that of the Pteraspids. If so, we may expect to find their exoskeletal micro-structure more nearly resembling that of the OSTEOSTRACI. Their acquisition of a hypocercal caudal fin was probably later than that of the Pteraspids, possibly after they had developed their armour, for this is evenly distributed, and the gradual loss of the pectoral fins would not be so immediately disastrous as in other AGNATHA.

The Cephalaspids seem to have been the last of the aberrant AGNATHA to diverge from the main stem leading to the modern Cyclostomes, a stem which might perhaps include the remarkable genus *Palaeospondylus*, for this seems already to have developed the rasping tongue so characteristic of the living Hag-fishes and Lampreys (BULMAN, 1931), a feature which obviously strengthens the view that the Cyclostomes are monophyletic and which militates against the possibility of their direct derivation from the already specialized Cephalaspids, some of which are even younger than *Palaeospondylus* itself.

One may imagine the AGNATHA to have developed in something like the following manner :—



Diagrammatically the relationships of the AGNATHA may be shown as follows—



There seems little point in creating a complicated series of divisions in an endeavour to express the exact relationship of the various members of the group, when they may be generally shown by placing them in four classes of roughly equal importance—

Group AGNATHA

Class and Order 1—HETEROSTRACI

Family—Palaeaspidae
Cyathaspidae
Pteraspidae
Drepanaspidae

2—ANASPIDA

3—OSTEOSTRACI

4—CYCLOSTOMA

Sub-Order—Palaeospondyloidea
Hyperartii (Petromyzontida)
Hyperotreti (Myxinoidea)

On the whole, this classification resembles KIAER's (1932) rather than STENSIÖ's (1927, p. 379), but differs very considerably in detail. No emphasis is put on the double or single state of the nasal sacs, as the latter condition is held to be secondary. The Anaspids are rated as a separate class and the Coelolepids are altogether omitted, while the arrangement of families within the HETEROSTRACI is considerably altered. KIAER, we may observe, excluded the Coelolepids (THELODONTI) from the HETEROSTRACI and treated the Psammosteids (Drepanaspids), Cyathaspids and Pteraspids as separate sub-orders, sub-dividing the Cyathaspids into two tribes and nine families, six of which comprise but one genus. STENSIÖ, and also WOODWARD (1932, p. 30), classifies the Coelolepids as one of the three families composing the HETEROSTRACI, of which the other two are the DREPANASPIDAE and the PTERASPIDAE, the latter containing not only the Pteraspids proper but all KIAER's CYATHASPIDAE. In my opinion the position of the Coelolepids as Heterostracans is certainly not yet proven. STETSON (1928) discussed this matter at some length, pointing out that the earlier authors down to TRAQUAIR believed the Coelolepids to have Elasmobranch affinities on the evidence of their scale-structure, but TRAQUAIR left them in the HETEROSTRACI, as he believed the whole of that group to be so related. STENSIÖ's later work (1927, p. 330) had made this position apparently untenable and denied completely any relationship between the Elasmobranchs and Coelolepids. But nevertheless STETSON pointed out that really little was known of the members of this family except the external shape and the scale-structure, and considered that on the whole the evidence favoured their affinities being with the Elasmobranchs, and suggested that they formed an order of that class, at the same time supposing some distant connection between the ancestral sharks and Ostracoderms. Later (1931, p. 147) he described a specimen of *Thelodus* showing some rather obscure visceral structures which he considered to resemble the gill-arches of the Elasmobranch embryo rather than gill-chambers of Ostracoderms, differing thereby from STENSIÖ's (1927, p. 331) interpretation of another specimen, and further gave details of the mouth, which was apparently represented by a dark carbonaceous ring armed with " numerous, fine, closely set, thornlike scales similar in every way to the larger scales of the head and trunk." If, as STETSON suggests, the carbonaceous ring indicates a cartilaginous support, the mouth presents a suspicious resemblance to that of an Elasmobranch. GOODRICH (1907, p. 755), in his classical paper on the structure of scales in fish, denies the resemblance in structure between the Coelolepids and the Placoid scales and remarks that " the superficial tubercles and the plate (of the HETEROSTRACI) should not be compared to the pointed tip and expanded basal plate of an ordinary Selachian placoid scale." But if we omit the base in each case (and that in the placoid scale is merely a downgrowth of the denticle, which need not necessarily have taken place, while that of the HETEROSTRACI is apparently an entirely different structure) the resemblance is striking enough. The precise systematic position of the Coelolepids therefore must still be considered uncertain in view of our meagre knowledge of the group and the conflicting evidence, but the balance of evidence, however slight, seems to favour Elasmobranch affinities ; in any case, they had much better be removed from the

Heterostraci altogether. Without the Coelolepids the Heterostraci form a very homogeneous group composed of animals which are obviously closely related and separated into families according to the complexity of the armour of the head and trunk. I consider that there are four such families, for I would separate the " Cyathaspida " of Kiaer from the Pteraspidae, making two distinct families therefrom, the Palaeaspidae (Poraspidei of Kiaer) and the Cyathaspidae (Cyathaspidei of Kiaer). Thus restricted, the Heterostraci comprise the Palaeaspidae, Cyathaspidae, Pteraspidae, and the Drepanaspidae, which show in this order progressive potential flexibility of the carapace, a tendency which was almost certainly advantageous, and which one might therefore have anticipated. This does not, of course, imply that they were derived from one another in that order by a continuous process of breaking up of the plates of the exoskeleton, for the earliest known members of three of the families at least are roughly contemporaneous ; but they do represent a series of animals of common origin which have developed along similar lines, but which have reached different stages in their development.

V.—Classification of the Heterostraci

We may order and define our groups as follows—

Order HETEROSTRACI

Diagnosis—Benthonic AGNATHA, probably all diplorhine, with broad, depressed head and trunk protected by carapace of exoskeletal plates, varying in number and composed of three layers without true bone-cells, namely, a basal laminar layer, a middle layer, generally thick and cancellous, and a superficial layer of some form of dentine ; orbits widely separated and lateral in position. Upper margin of mouth formed by posterior border of rostrum, the lower by a series of narrow longitudinal plates, both bearing roughened areas of the same nature as external " ornamentation." Branchial pouches with common exit placed more or less postero-laterally in respect to the trunk. Paired and median fins, except tail, absent ; caudal region behind carapace long and tapering, protected by regularly arranged, overlapping scales and dorsal and ventral series of fulcra, all of same structure as plates of trunk-armour ; tail laterally compressed and hypocercal. Dermal sense-organs well developed.

Families—Palaeaspidae, Cyathaspidae, Pteraspidae (type-family, as restricted below), Drepanaspidae

Family—Palaeaspidae (Poraspidei of Kiaer)

Diagnosis—Heterostracans with principal dermal armour of head and trunk consisting of undivided dorsal shield notched anteriorly for orbits, single pair of large, free branchial plates, small sub-orbital plates, and simple ventral shield ; no median dorsal spine ; micro-structure typical ; ridges of external " ornamentation " fine and smooth ; (*in Anglaspis*), scales of region behind carapace few and large, one row on flank being especially deep ; main canals of dermal sense-organs of dorsal disc comprising two pairs running longitudinally connected by four or more transverse commissures : (in *Anglaspis*) lower lobe of tail considerably longer than upper.

Genera—Palaeaspis CLAYPOLE (type-genus—? includes *Poraspis* KIAER), *Homolaspis* KIAER, *Dinaspis* KIAER, *Dictyaspis* KIAER, *Anglaspis* JAEKEL, *Ctenaspis* KIAER.

Family CYATHASPIDAE (CYATHASPIDEI of KIAER)

Diagnosis—Heterostracans with carapace consisting of dorsal shield divided superficially into four plates, rostral, dorsal disc, and paired elongated orbitals notched anteriorly for orbits ; paired large, free branchial plates (sub-orbital plates unrecorded) ; no median dorsal spine, and ventral shield simple (squamation of region behind carapace imperfectly known) ; ridges of external " ornamentation " fine and smooth, and micro-structure typical. (Sensory canal system imperfectly known.)

Genera—Cyathaspis LANKESTER (type-genus), *Archegonaspis* JAEKEL, *Eoarchegonaspis* KIAER, *Tolypelepis* PANDER, *Diplaspis* MATTHEW, *Traquairaspis* KIAER.

Family PTERASPIDAE

Diagnosis—Heterostracans with carapace consisting of dorsal shield divided into nine plates superficially—rostrum, pineal, dorsal disc, and paired orbitals enclosing orbits, branchials and cornuals ; and ventral disc bounded antero-laterally by one or two pairs of lateral plates ; median dorsal spine inserted in hinder margin of dorsal disc ; oral plates narrow and numerous. Micro-structure either typical or thin and dense. Ridges of " ornamentation " fine and crimped or sub-divided. Scales of region behind carapace small, numerous, and rhomboid. Main canals of dermal sense-organs of dorsal disc arranged in two pairs longitudinally connected on each side by three commissures radially arranged. Tail (in *P. rostrata*) deep, very inequilobate, and slightly emarginate.

Genera—Pteraspis KNER (type-genus), *Cyrtaspis* BRYANT, *Doryaspis* KIAER MS.

Family DREPANASPIDAE (PSAMMOSTEIDAE)

Diagnosis—Heterostracans with carapace divided dorsally into twelve principal plates—rostrum, dorsal disc and paired orbital plates enclosing orbits, post-orbitals, branchials and cornuals—and simple ventral disc, the paired plates being separated from the unpaired by a mosaic of numerous small plates ; median dorsal spine inserted in hinder margin of dorsal disc, and ventral disc similarly notched for anal opening. External " ornamentation " tubercular ; dermal sense organs apparently lying superficially to bone-tissue, of which middle layer is without regular cancellae, and superficial layer discontinuous. Scales of region behind carapace small, numerous, and rhomboid ; tail deep, almost equilobate, and slightly emarginate.

Genera—Drepanaspis SCHLÜTER, *Psammosteus* AGASSIZ, (?) *Pycnosteus* PREOBRAJENSKY, *Dyptychosteus* PREOBRAJENSKY, *Ganosteus* ROHON.

Family PTERASPIDAE*

Genus *Cyrtaspis* BRYANT 1932

Diagnosis—Pteraspids with broad shield, strongly vaulted ; rostrum short and broad ; branchial plates extremely long and openings posteriorly placed, near hinder margin of dorsal disc ; cornual plates small or rudimentary. Median dorsal spine small and scale-like. Ridges of superficial " ornamentation " either entire or interrupted. Plates extremely thin and dense, with reduced cancellae in middle layer. (Outer longitudinal and posterior transverse sensory canals of dorsal disc apparently absent, the anterior and middle transverse commissures passing out at front margin of plate.)†

Sub-genera—*Cyrtaspis* BRYANT typicum, *Protaspis* BRYANT.

Sub-genus *Cyrtaspis* BRYANT 1932, typicum

Diagnosis—Species of *Cyrtaspis* with broad branchial plates and branchial openings behind level of posterior margin of dorsal disc (cornual plates unknown but probably rudimentary). Ridges of superficial " ornamentation " in the form of rows of beads or papillae.

Genotype—*C. ovatus* BRYANT, Lower Devonian : Wyoming, U.S.A.

Species—*C. ovatus*, *papillatus*, *sculptus*, *falcatus* BRYANT. Lower Devonian : Wyoming U.S.A.

Sub-genus *Protaspis* BRYANT 1933

Diagnosis—Species of *Cyrtaspis* with narrow branchial plates and branchial openings slightly in front, or at level, of posterior margin of dorsal disc ; cornual plates small. Ridges of superficial " ornamentation " crenulated or divided into short lengths.

Lectogenotype—*P. bucheri* BRYANT, hereby chosen. Lower Devonian ; Wyoming, U.S.A.

Species—*P. bucheri*, *dorfi*, *brevirostris*, *nanus*, *amplus*, *perlatus*, *perryi*, *cingulus*, *constrictus*, BRYANT. Lower Devonian : Wyoming, U.S.A.

Genus *Pteraspis* KNER 1847

Synonyms—*Palaeoteuthis* ROEMER, 1855. *Archaeoteuthis* ROEMER, 1855. ‡*Scaphaspis* LANKESTER, 1864—in part. *Rhinopteraspis* JAEKEL, 1919. *Podolaspis* ZYCH, 1931. *Althaspis* ZYCH, 1931. *Lericheaspis* ZYCH, 1931. *Belgicaspis* ZYCH, 1931. *Glossoidaspis* BRANSON and MEHL, 1931.

Diagnosis—Pteraspids with dorsal shields moderately broad, depressed anteriorly but arched behind ; rostrum variable in form ; distance of branchial openings from

* For remarks on the family, *see* under the genus *Pteraspis* below.

† BROTZEN in his unpublished paper denies that the distribution of the sensory canals in *Protaspis* is different from that in *Pteraspis*.

‡ I hereby choose *C. lewisii* as the genotype of *Scaphaspis*, thus making it an absolute synonym of *Pteraspis*.

hinder margin of dorsal disc equal approximately to one-third length of disc ; cornual plates well developed, forming cornua of various shapes and sizes. Dorsal spine prominent and usually large. Ridges of superficial " ornamentation " entire and crenulated. All three layers of plates and scales well developed. Outer and inner longitudinal sensory canals of dorsal disc complete, traversing length of plate and connected by three transverse canals radiating from focus of " ornamentation."

Genolectotype—Cephalaspis lewisii Agassiz (*C. rostratus* Agassiz), hereby selected.

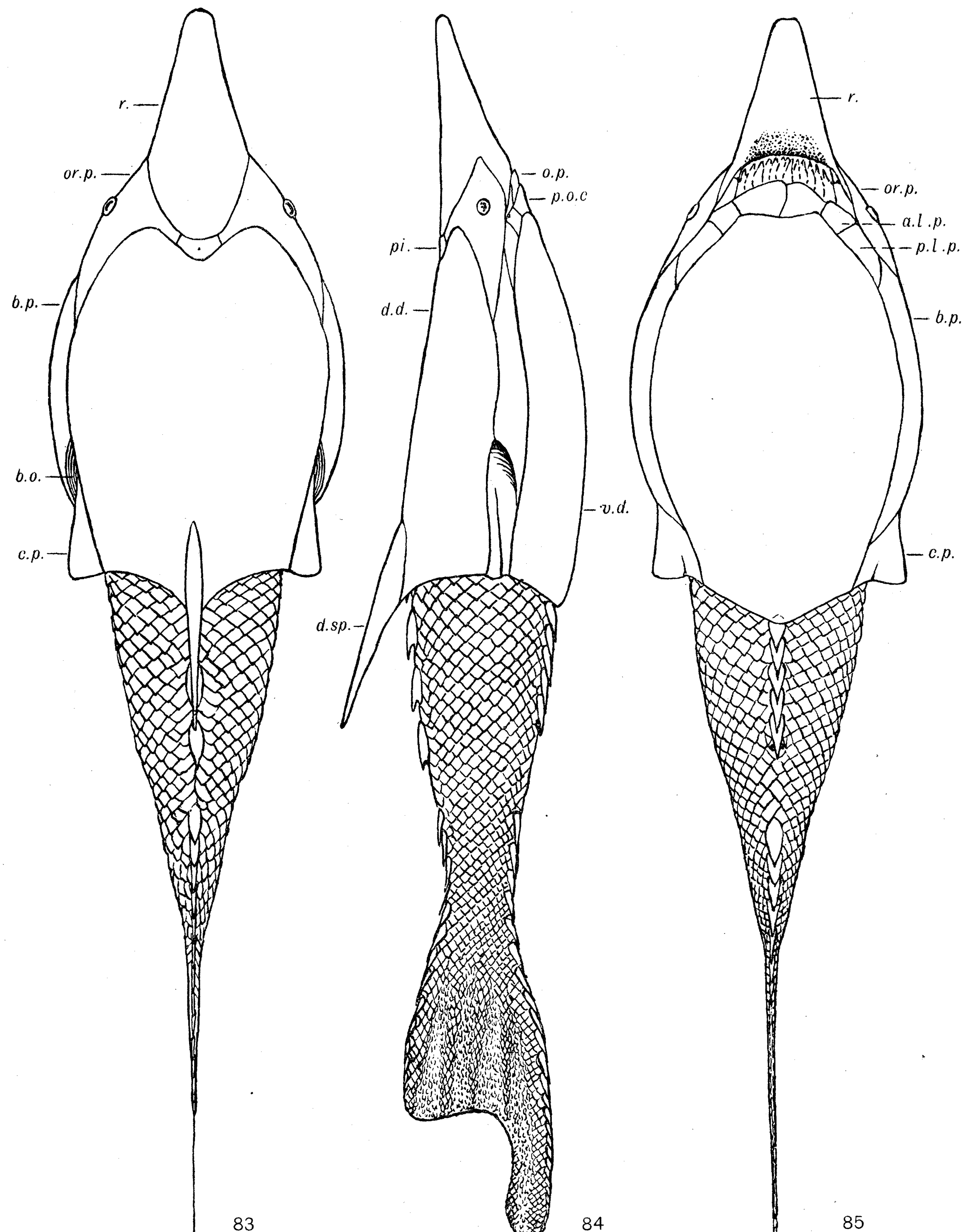
Remarks—Recently several papers have been published on the Pteraspids and *Pteraspis* in particular, and in view of the opinions expressed as to the status and scope of this important genus I propose to discuss these matters again here.

The genus *Pteraspis* was based by Kner (1847, pp. 159–165) on two of Agassiz's species, *Cephalaspis lewisii* and *C. lloydii* (Agassiz, 1835, pp. 149, 150), and on some Polish specimens which he left unnamed. Brotzen (1933*b*, p. 435) seems to consider that the Polish material is the type of the genus, but this clearly cannot be so, for these fossils remained specifically indeterminate until Lankester (1868, p. 2, foot-note) gave the name " *Scaphaspis knerii* " to one form and Alth (1874) redescribed the fauna. One of the two named species quoted by Kner must be selected as the genotype, but actually this is not necessary, for they are synonyms, and since *Cephalaspis lewisii** (and not *C. lloydii*, as Lankester (1868, p. 20) has it) has page-priority in Agassiz's original descriptions, this is *de facto* the genotype ; since, however, *Cephalaspis lewisii* is itself a synonym of *C. rostratus*, to which in its turn it must yield page-priority in Agassiz " Poissons fossiles," *Cephalaspis rostratus* is unquestionably the genotype *de jure* of *Pteraspis*. This species was chosen as such by Huxley many years ago (1858, p. 861), but his choice was arbitrary and unorthodox, for he selected this species simply because it was the best known, and without being aware of its full significance, or even that it was congeneric with *C. lewisii* ; indeed, Lankester (1868, p. 20) decided that it was not, and, accepting Huxley's choice of *C. rostratus* as the type of *Pteraspis*, put *C. lloydii*, in which he included *C. lewisii*, with two other " species " in a new genus, *Scaphaspis*.

Since Lankester's time, the true nature of the plates included in *Scaphaspis* as the ventral discs of the species of *Pteraspis* and *Cyathaspis* has, of course, been established (Alth, 1886, p. 61) ; and Woodward (1891, p. 162), while recognizing the specimens of *Cephalaspis lewisii* and *C. lloydii* as probably belonging to *Pteraspis rostrata*, maintained the position of the last-named species as the genotype of *Pteraspis*, thus putting the matter beyond dispute.

Many species of *Pteraspis* have now been described, some with long snouts and others with short ; and, as usual when a genus is much increased in size, authors have endeavoured to subdivide it. The first to do so was Jaekel (1919, p. 74, foot-note, text-fig. 1*d*), who separated the long-snouted form *P. dunensis* as the type of a new

* I select the original of Agassiz's fig. 9 (1935, Pl. 1*b*) as the lectotype of *C. lewisii*, for the specimen shown in his fig. 10 is apparently the ventral disc of the species *P. crouchi*, described later by Lankester.



Restoration of *Pteraspis rostrata* (Agassiz), var. *toombsi* nov.

Fig. 83—Dorsal view Fig. 84—Right lateral view Fig. 85—Ventral view

All figures approximately of the natural size. (Lettering as in figs. 1, 2) genus *Rhinopteraspis*, characterized by the extreme length of the rostrum and dorsal spine and the supposedly small size of the scales covering the body behind the carapace. The first two of these characters are not, in my opinion, of generic value, for all sizes in these plates may be found among the various species, while the third is not true, the scales differing little in their relative dimensions from those of *P. rostrata* (*see* LERICHE, 1924, p. 154, text-fig. 6 ; and above).

Another supposed genus, *Glossoidaspis*, has been put forward by BRANSON and MEHL (1931, p. 523) for some discs found in the Jefferson Formation of Utah, but, as BRYANT (1932, p. 228) has already pointed out, there is nothing in the description to distinguish *Glossoidaspis* from *Pteraspis*.

ZYCH (1931, p. 86, expl. figs. and photographs) has gone further and divided the PTERASPIDAE proper into three sub-families, the distinguishing features of which are the breadth of the pre-orbital part of the rostrum, the direction of the orbits, and the presence or absence of the pineal plate. The first and second of these characters are interdependent, and until it can be proved that they mark definite strains or trends, which is not altogether impossible, they may be regarded as trivial distinctions only ; the third character, based on the supposed absence of the pineal plate in *P. crouchi* as restored by LANKESTER (1868, Pl. VII, fig. 8), is wholly fallacious, for it is present in that species and almost certainly in all, in spite of LERICHE's assertion to the contrary in respect to *P. gosseleti* (1906, p. 27). In any circumstances the genotype, *P. rostrata*, upon which ZYCH has based his ROSTRASPINAE, could only be the type of the typical sub-family. A second sub-family, the BELGICASPINAE, is based on the long and narrow-snouted *P. crouchi*, which, however, is only the type of a new sub-genus, *Belgicaspis* ; while the third family, the PODALASPINAE, comprises the long but broad-snouted Podolian species forming the new genus *Podolaspis*, with two sub-genera, *Althaspis* and *Lericheaspis*. For none of these new sub-divisions can I see at the moment any justification, and I regard all these forms as species of *Pteraspis* KNER, as indeed BROTZEN (1933*b*) has already properly so treated them.

BRYANT's genera *Cyrtaspis* (1932, p. 232) and *Protaspis* (1933, p. 294), however, are more firmly established, the posterior position of the branchial openings with the consequent diminution in size of the cornua (these plates are certainly present in all species, even as the author himself suggests, although he does not figure them in his restorations of *P. bucheri* and *P. dorfi*), the characteristic distribution of the sensory canals* and the remarkable thinness of the plates of the dorsal shield surely distinguish these forms from *Pteraspis* ; yet they do not seem sufficient to justify the creation of a new family—after all, genera must have some outstanding distinctions, and *Cyrtaspis* and *Protaspis*, which apparently differ from one another only in their external " ornamentation," are typical Pteraspids, comprising, so far as we know, the same plates as the type-genus and having very similar caudal regions ; to my mind, putting them into a separate family only obscures their obvious relationships. The rather

* BROTZEN in his unpublished paper denies that the distribution of the sensory canals in *Protaspis* is different from that in *Pteraspis*.

striking structure of their plates is interesting, for it is thin and dense, apparently without the usual numerous cancellae in the middle layer ; but nevertheless this remarkable feature should not be allowed to outweigh the similarities between the genera, and I am not prepared to consider it of more value than a distinction between sub-families. The distinctions between *Cyrtaspis* and *Protaspis* themselves seem to me over-rated, these being matters of " ornamentation " and the breadth of the branchial plates, so that if *Protaspis* is not completely synonymous with *Cyrtaspis*, it must be regarded as not more than a sub-genus of it.

The family PTERASPIDAE, as I see it, thus comprises only two genera, *Pteraspis* KNER and *Cyrtaspis* BRYANT, at the moment, but certainly others will soon be described.

The PTERASPIDAE are most nearly related to the DREPANASPIDAE (or PSAMMOSTEIDAE as some authors prefer to call the family), as TRAQUAIR (1899, p. 851), although he reversed the surfaces of *Drepanaspis*, and STENSIÖ (1927, p. 328) have pointed out ; indeed, the plates of the armour in the two types may easily be correlated, the obvious differences being that in *Drepanaspis* the orbital plates were sub-divided, the pineal plate was not developed as a separate entity, and the branchial and cornual plates were separated from the dorsal and ventral discs by a mosaic of small plates. Moreover, we now know that the caudal regions were similar in that they were scale-covered with dorsal and ventral series of ridge-scales, and had a deep, hypocercal tail. It is also possible that the plates behind the mouth in *Drepanaspis* may be correlated with the oral plates of *Pteraspis* (*see* STETSON, 1931, p. 149, text-figs. 5–7 ; KIAER, 1928, p. 121, text-fig. 4) ; but this is less certain, and, in view of their apparent rigidity, it seems more likely that their homologies are rather with the post-oral covers,* the oral plates being reduced or simply not preserved. The form of the mouth was very different, and it is still undecided whether the mouth itself was wholly dorsal or terminal in position, PATTEN (1932, p. 518, fig. 6) and STETSON favouring the former view and KIAER the latter. But in general *Drepanaspis* is just a large, broad, and flattened Pteraspid.

Species—Numerous " species " of *Pteraspis* and *Scaphaspis* have been described, but nearly all are based on isolated dorsal and ventral discs, so that many of these names have afterwards been found to be synonymous. There seem to be about thirty good species of this genus, one-half of which are based on Polish material, and of the rest all but two North American and two Spitsbergen species are from North-Western Europe. The range of the genus in time was short, for no specimens have been recorded from strata earlier than the Upper Silurian or younger than the Lower Devonian.

Upper Silurian and Downtonian :—

P. leathensis, sp. nov., West of England.
P. gosseleti LERICHE, Pas-de-Calais.
P. primaeva KIAER, Spitsbergen.
P. vogti KIAER, Spitsbergen.

* *See* the restorations by PATTEN, 1932, p. 518, fig. 6.

P. kneri (LANKESTER), Podolia — *P. major* ALTH (1874, Pl. I, figs. 3, 4) in part.
P. podolica ALTH, Podolia — *Scaphaspis haueri* Alth : the lectotype of this species is the original of ALTH's Pl. I, fig. 5 (BROTZEN, 1934, p. 439).
P. radiata (ALTH), Podolia.
P. obovata (ALTH), Podolia.
P. brevirostra ZYCH, Podolia — *P. sturi* mut. *brevirostra* ZYCH (1927, p. 15, Pl. II, fig. 3).
P. zychi BROTZEN, Podolia.
P. iwaniensis BROTZEN, Podolia — *P. sturi* mut. *major* ZYCH 1927.

Lower Old Red Sandstone and Lower Devonian :—

P. rostrata (AGASSIZ), West of England, ? N. France and Belgium — *Cephalaspis lewisii* AGASSIZ and *C. lloydii* AGASSIZ.
P. crouchi LANKESTER, West of England and Pas-de-Calais — *Scaphaspis rectus* LANKESTER.
P. jackana, sp. nov., West of England.
P. stensiöi, sp. nov., West of England.
P. mitchelli POWRIE, Scotland.
P. cornubica (M'COY), Cornwall.
P. dunensis (ROEMER), Eifel, Belgium, and Luxemburg — *Scaphaspis bonnensis* SCHLÜTER, *P. rhenana* SCHLÜTER, *P. dewalquei* FRAIPONT.
P. traquairi LERICHE, Pas-de-Calais.
P. rotunda GROSS, Rhenish Prussia.
P. smith-woodwardi BROILI, Eifel.
P. augustatus ALTH, Podolia — *P. sturi* mut. *rostrata* ZYCH 1927, *Podolaspis rostrata* ZYCH 1931.
P. major ALTH, Podolia — *P. lerichei* mut. *rostrata* ZYCH 1927, *P. lerichei* BROTZEN. (Lectotype, original of ALTH, 1874, Pl. III, figs. 3–5, hereby chosen.)
P. brotzeni, nom. nov., Podolia — *P. lerichei* mut. *major* ZYCH 1927, *P.* (*Althaspis*) *major* ZYCH 1931, *P. major* BROTZEN *nec* ALTH.
P. elongata (ALTH), Podolia — *P. sturi* mut. *elongata* ZYCH 1927, *P. lerichei* mut. *elongata* ZYCH 1927, *P.* (*Althaspis*) *elongata* ZYCH 1931, *P. elongata* ZYCH of BROTZEN.
P. concinna BROTZEN, Podolia.
P. magnipinealis BROTZEN, Podolia.
P. lata ZYCH, Podolia — *P. sturi* mut. *lata* ZYCH 1927, *P. lerichei* mut. *lata* ZYCH 1927, *P. lerichei* mut. *latissima* ZYCH 1927, *P. latissima* BROTZEN.*
P. longirostra ZYCH, Podolia — *P. lerichei* mut. *longirostra* ZYCH 1927, *P.* (*Lericheaspis*) *longirostra* ZYCH 1931, *P. longirostrata* BROTZEN.
P. gigantea (BRANSON and MEHL), Utah.

* BROTZEN proposes to refer this species to a new genus.

P. novae-scotiae, sp. nov., Nova Scotia — *P. cf. crouchi*, AMI 1901, p. 309. The small isolated ventral discs from the Knoydart Formation noted by AMI are certainly not referable to the English species. They are of similar size and shape to the ventral discs of *P. leathensis* (figs. 30, 45), but are decidedly narrower. Although imperfectly known, it is better that this form, the first *Pteraspis* recorded from the New World, should have a distinctive name than be referred to by one from which unwarranted conclusions could be drawn. The holotype (P. 9117) is shown in fig. 40.

Scaphaspis nathorsti LANKESTER (1884, p. 5, Pl. I, figs. 1–3) from the Lower Devonian of Spitsbergen is clearly not a species of *Pteraspis*, although a Pteraspid. The ventral discs, the only parts described as yet, are extremely broad, and the concentric grooves of the " ornamentation " are coarser than in species of *Pteraspis* and modified by numerous fine grooves radiating from the focus, which is at some distance from the hinder margin. The lateral sensory canals have a similar course to those in the type-genus, but the medial oblique branches are unusually long, and there is apparently no anterior V-shaped canal (fig. 75; fig. 102, Plate 25). KIAER, in an unpublished MS, has named the genus *Doryaspis*.

The synonymies of the Podolian species given above are purely tentative, for I have not had the opportunity of examining the type-material; they are largely based on BROTZEN'S work (1933*b*).

On the whole, with our present information the genus *Pteraspis* KNER presents in its numerous species remarkably uniform structure, not only in the form and number of the plates composing the carapace and the course of the canals of the sensory system, but, so far as we know, in the details of the caudal region,* the species differing from one another solely in the proportions of the various plates and the inclination of the dorsal spine, the most obvious of these differences being in the form of the rostrum and dorsal spine. I therefore entirely reject the division of the genus proposed by JAEKEL, BRANSON, and MEHL, and particularly ZYCH. Three departures from the standard form are, however, to be noted—all in Downtonian species: firstly, the French *P. gosseleti* LERICHE (1906, p. 26, text-fig. 8, Pl. I, figs. 6–9) is said to lack both pineal plate and dorsal spine, which is hardly credible, and three of the figures, especially fig. 9, seem to show a socket for the dorsal spine; therefore I regard both these supposed characters as being extremely doubtful. Secondly, the restoration *P. primaeva* KIAER (1928, text-fig. 1), the inner pair of longitudinal canals of the dorsal disc are represented as stopping short of the anterior border of the disc; this also needs confirmation. Lastly, in the second species from Spitsbergen, *P. vogti* KIAER (1928, text-fig. 2, Pl. XII, fig. 1), there is only one pair of lateral plates and no post-oral covers, so that this species shows marked differences from the English *P.*

* BRYANT'S reproduction (1933, text-fig. 2*e*) of the sensory canals of the dorsal disc of *P. longirostra* ZYCH is incorrectly copied, and there is nothing in ZYCH'S figure (1931, fig. 49) to suggest that they were abnormal; and the lateral rows of ridge-scales in ZYCH'S restorations (1931, figs. 41, 49, 51) are based, I feel sure, on the misinterpretation of flank-scales seen on edge.

rostrata. Here, possibly, there may be true generic distinctions; but as these features are known as yet in these two species alone, the matter may be left for future discussion.

Both Zych (1927) and Brotzen (1933*b*) have endeavoured to establish among the numerous Downtonian and Lower Devonian species from Podolia two lineages showing progressive lengthening of the rostrum and diminution in size of the cornua. Of Brontzen's lineages the first is characterized by short, posteriorly arched dorsal discs, upright dorsal spines, and the pineal plate free from the orbitals; the second by long, flat dorsal discs, slightly inclined dorsal spines, and the pineal plate in contact with the orbitals. These series appear to be well founded, but whether similar lines of evolution can be found outside Podolia is much less certain. In North-Western Europe, we have no series of species from one area comparable with those in Poland, and the linking up of the Spitsbergen forms with *P. rostrata* and *P. dunensis* to form a comparable lineage, as Brotzen indicates, is entirely speculative.

The six British species do not seem nearly related to one another, except, perhaps, *P. jackana* and *P. stensiöi*, which stand apart from the others by reason of their short, blunt snouts, large cornua, and erect dorsal spines. Of the others *P. leathensis* and *P. crouchi* have very different dorsal discs and spines, although their rostra are long, narrow, and sharply marked off from the rest of the shield, therein differing from the later continental species, *P. dunensis*. Lastly, *P. rostrata* and *P. mitchelli* seem in their form to be isolated from their neighbours.

We may note one feature which both Zych and Brotzen have insisted on as being of at least specific value, the presence or absence of contact between the pineal plate and the orbitals. It may be of importance in the Podolian forms, and Brotzen, as we have noted above, makes it one of the characters of his lineages, but it certainly is not in the two English species, *P. rostrata* and *P. crouchi*, for although I have used it as a secondary varietal character, I am not sure that it has even that small value.

The British species of *Pteraspis*

Pteraspis leathensis, sp. nov. (Figs. 30, 31, 38, 77, 94)

1925. *Cyathaspis leathensis*, W. W. King, p. 357 (name only)

Diagnosis—A *Pteraspis* of small size, length of dorsal disc not exceeding 38 mm along the median line and approximately equal to its maximum width (shield with rostrum about 60 mm long); anterior emargination of dorsal disc narrow and angular, the anterior margin on each side being straight and short, then passing outwards and slightly backwards in a wide sigmoid curve to form rounded antero-lateral corner with almost straight and parallel sides. Dorsal spine short and relatively broad, depressed, with inserted portion three and one-half times as long as the exserted and equal to one-third length of disc. Rostrum narrow, sharply divided from disc and tapering evenly and acutely, about three times as long as maximum width. Pineal plate rhomboid, widely separated from orbitals, which do not extend far in front of orbits, being strongly convex in dorsal view, and meeting sides of rostrum approximately at right angles. Ventral disc ovoid with short, flattened anterior margin and convex posterior margin lacking distinct median angle. Ridges of " ornamentation " numbering from 50 to 80 per cm and A-shaped in section.

Holotype—Flattened dorsal shield with imperfect rostrum, in the British Museum (No. P. 14521, text-fig. 30).

Distribution—Upper Downtonian and possibly base of Dittonian (zones I. 8–9 ; ? II. 1) : Shropshire and Worcestershire.

Pteraspis rostrata (AGASSIZ). (For figures, *see* varieties)

1835–1906 *See* LERICHE, 1906, p. 32. 1926 *Pteraspis rostrata,* STENSIÖ, p. 4, text-figs. 2, 3. 1927 *Pteraspis rostrata,* JAEKEL, text-figs. 15, 32. 1931 *Pteraspis rostrata,* ZYCH, p. 86, figs. 19, 25.

Diagnosis—A *Pteraspis* attaining a total maximum length of about 270 mm but usually smaller. Dorsal disc of adult oblong, with length along median line equal to $1\frac{1}{16}$–$1\frac{1}{4}$ maximum breadth, which is slightly in front of centre of plate ; disc depressed anteriorly but strongly vaulted posteriorly ; indentation of anterior margin variable and antero-lateral corners either rounded or angular. Dorsal spine depressed, laterally compressed, and triangular in side-view, the inserted portion being about one-half total length, and one-quarter to one-third length of disc. Cornua very small and triangular. Rostrum depressed, of moderate length and triangular with blunt extremity, varying in length from one and one-sixteenth to one and one-half maximum breadth at base, and equal to one-third total length of dorsal shield.* Pineal plate broader than long, either three- or four-sided, and may or may not be in contact with orbital plates, which do not extend far in front of orbits, being only slightly convex outwards in dorsal view and continuing line of rostrum. Ventral disc in young specimens more or less elliptical with posterior angle and flattened anterior margin, becoming more ovoid or elongated in adult, the length being from one and a half to three times the maximum breadth. Ridges of "ornamentation" numbering from 50 to 80 per cm and rounded in section.

Holotype—Internal cast of small dorsal shield with imperfect rostrum, in the Museum of the Geological Survey (No. 21444).

Distribution—Dittonian (zones II. 1–3) : West of England ; ? Northern France and Belgium.

Remark—The identity of the typical form is uncertain owing to the imperfect condition of the Holotype.

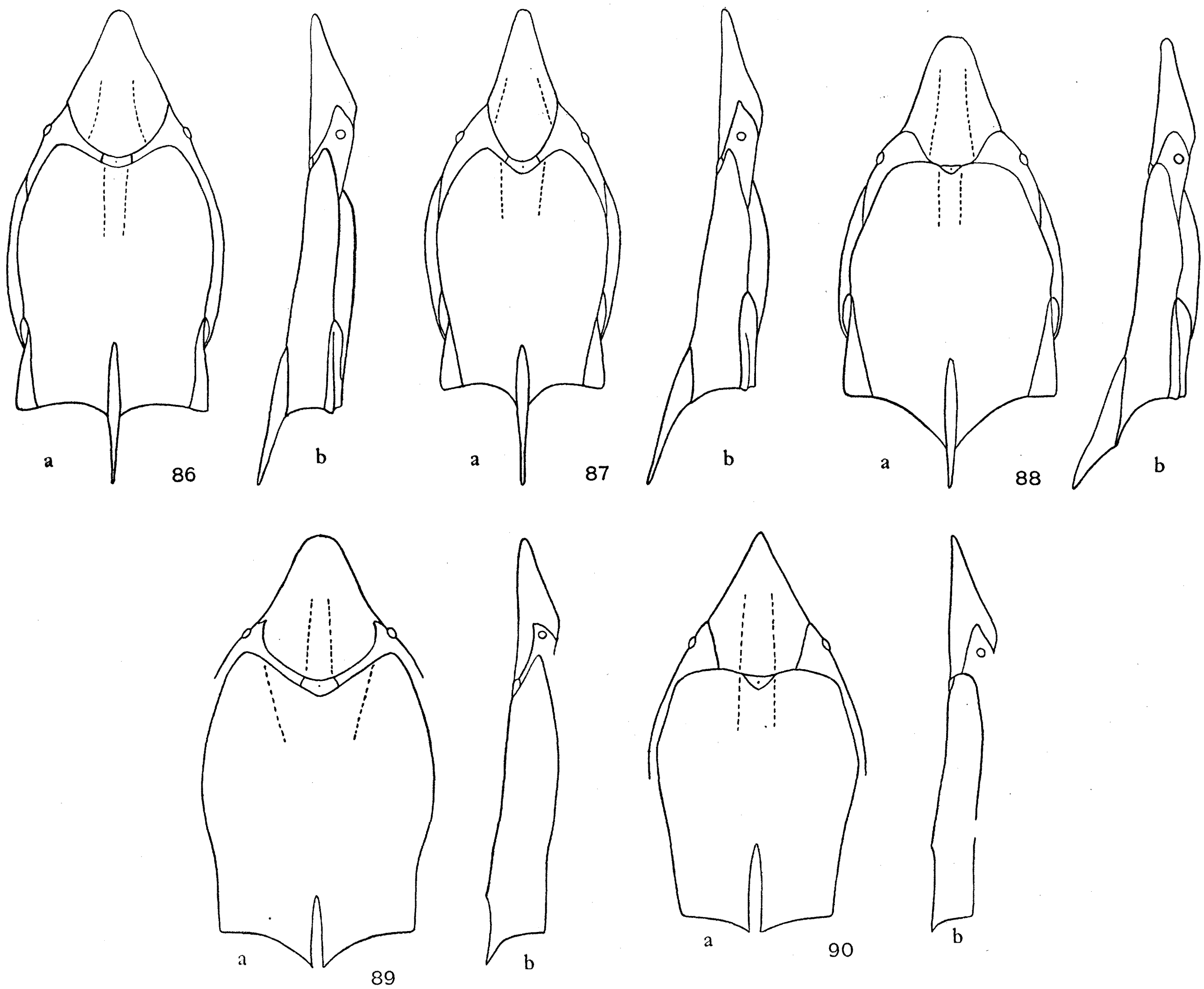
Pteraspis rostrata (AGASSIZ), var. *waynensis* nov.

(Figs. 3–5, 33, 66, 67, ?73, ?74, 81, 82, 86 ; fig. 101, Plate 25)

Diagnosis—A variety of *P. rostrata* of moderate size, the length of dorsal shield without spine not exceeding 90 mm. Dorsal disc with wide anterior emargination and more or less rounded antero-lateral corners. Rostrum with slightly concave sides and rather narrow tip, the length being somewhat less than one and a half times

* This is always measured along the median line without the dorsal spine but including the sockets.

the maximum breadth and rather more than one-third of length of shield. Pineal plate from two to two and a half times as broad as long, four-sided with concave anterior and convex posterior margins, and short, straight, lateral borders in contact with long medial extensions of orbital plates. Dorsal spine slender, with exserted portion rather shorter than socket. Ventral disc of adult roughly oval.



FIGS. 86–90—Restorations in outline of the dorsal shields of the varieties of *Pteraspis rostrata* (AGASSIZ). *a* in dorsal view ; *b* in lateral view. The anterior part of the inner longitudinal sensory canal of the dorsal disc and the posterior part of the superior rostral canal are indicated by broken lines. 86. *P. r. waynensis* ($\times \frac{2}{3}$). 87. *P. r. toombsi* ($\times \frac{2}{3}$). 88. *P. r. trimpleyensis* ($\times \frac{2}{3}$). 89. *P. r. monmouthensis* ($\times \frac{4}{9}$). 90. *P. r. virgoi* ($\times \frac{2}{3}$).

Holotype—External mould and internal cast of dorsal shield, in the British Museum (Nos. P. 16789–90 ; figs. 3, 66, 67 ; fig. 102, Plate 25).

Distribution—Lower Old Red Sandstone (Dittonian, zone II. 2) : Wayne Herbert and Pool Quarries, Herefordshire.

Pteraspis rostrata (Agassiz), var. *toombsi* nov.

(Figs. 1, 2, 13, 16, 35, 41–55, 63–65, 83–85, 87 ; figs. 98, 99, Plates 25)

Diagnosis—A variety of *P. rostrata* of moderate size, length of dorsal shield not exceeding 90 mm and total length about 180 mm. Dorsal disc with narrow anterior emargination and margin, and antero-lateral corners well rounded. Form of rostrum variable, generally rather pointed with slightly concave sides, and length varying between one and a half times to twice its maximum breadth, and from rather more than one-third to two-fifths of length of dorsal shield. Dorsal spine long and slender, with exserted portion somewhat longer than socket. Other plates as in *P. r. waynensis*. Superficial " ornamentation " of scales comprising six or more fine ridges forming anteriorly directed chevrons followed by longitudinal ridges divided into lengths by chevron-shaped grooves parallel with the anterior ridges, at first close together but at increasing intervals towards the hinder end, where they are sometimes absent.

Holotype—External mould of both surfaces of animal and lacking only extension of lower caudal lobe, in the British Museum (Nos. P. 17479–90; fig. 42; fig. 104, Plate 26).

Distribution—Lower Old Red Sandstone (Dittonian, zone II. 2) : Only in siltstone lenticle at base of Wayne Herbert Quarry, Herefordshire.

Pteraspis rostrata (Agassiz), var. *virgoi* nov. (Figs. 15, 90)

Diagnosis—A variety of *P. rostrata* of moderate size, length of dorsal shield being about 85 mm. Dorsal disc with narrow anterior emargination but otherwise straight anterior margin and angular antero-lateral corners. Rostrum with straight sides and acute tip, the length being rather less than one and one-third times maximum breadth and one-third length of dorsal shield. Pineal plate roughly triangular, about two and a half times as broad as long and widely separated from orbitals. Dorsal spine and ventral disc unknown.

Holotype—Internal cast and imperfect external mould of dorsal shield, in the British Museum (Nos. P. 17490–1 ; fig. 15).

Distribution—Lower Old Red Sandstone (Dittonian, zone II. 2) : Wayne Herbert Quarry, Herefordshire.

Pteraspis rostrata (Agassiz), var. *monmouthensis* nov. (Figs. 9, ?34, 89)

Diagnosis—A variety of *P. rostrata* of a great size, the length of dorsal shield attaining 133 mm. Dorsal disc with extremely wide anterior emargination, occupying whole of anterior margin, and angular antero-lateral corners. Rostrum with more or less straight sides and broad tip, length being only one and one-eight times maximum breadth and slightly less than one-third of length of shield. Pineal plate rather more than twice as broad as long, four-sided with concave anterior and convex posterior margins, and short, straight, lateral borders in contact with very long and narrow medial extensions of orbital plates (dorsal spine unknown). Ventral disc of adult elongated.

Holotype—External mould of dorsal disc without spine, in the British Museum (No. P. 5034; fig. 9).

Distribution—Lower Old Red Sandstone (Dittonian, zone II. 1); Monmouthshire and ? (zone II. 2), S.W. Herefordshire.

Pteraspis rostrata (Agassiz), var. *trimpleyensis* nov.

(Figs. 6, 7, 8, 10, 11, 36, 39, 56–62, 88; fig. 100, Plate 25)

Diagnosis—A variety of *P. rostrata* of moderate size, length of dorsal shield not exceeding 95 mm. Dorsal disc with extremely narrow anterior emargination and wide, rounded, antero-lateral corners. Rostrum with straight sides and broad tip, length being about one and one-third times the maximum breadth and rather less than one-third the length of shield without spine. Pineal plate triangular and widely separated from orbitals, of which medial extensions are short and pointed. Dorsal spine very short and triangular in side view, with exserted portion much shorter than socket. Ventral disc of adult roughly oval.

Holotype—Complete dorsal shield in the British Museum (No. P. 16478. I; fig. 7; Pl. I, fig. 100, Plate 25).

Distribution—Lower Old Red Sandstone (Dittonian, zone II. 2): Trimpley, Worcestershire and ? E. Herefordshire.

Pteraspis crouchi Lankester (For figures, *see* varieties)

1835–1906. *See* Leriche, 1906, p. 27.
1924. *Pteraspis crouchi*, Leriche, p. 147, text-figs. 2, 3; Pl. IV.
1926. *Pteraspis crouchi*, Stensiö, p. 3, text-figs. 1, 4.
1927. *Pteraspis crouchi*, Jaekel, text-fig. 53.
1931. *Pteraspis crouchi* and *Belgicaspis*, Zych, p. 86, figs. 16, 17, 22, 26, 40.

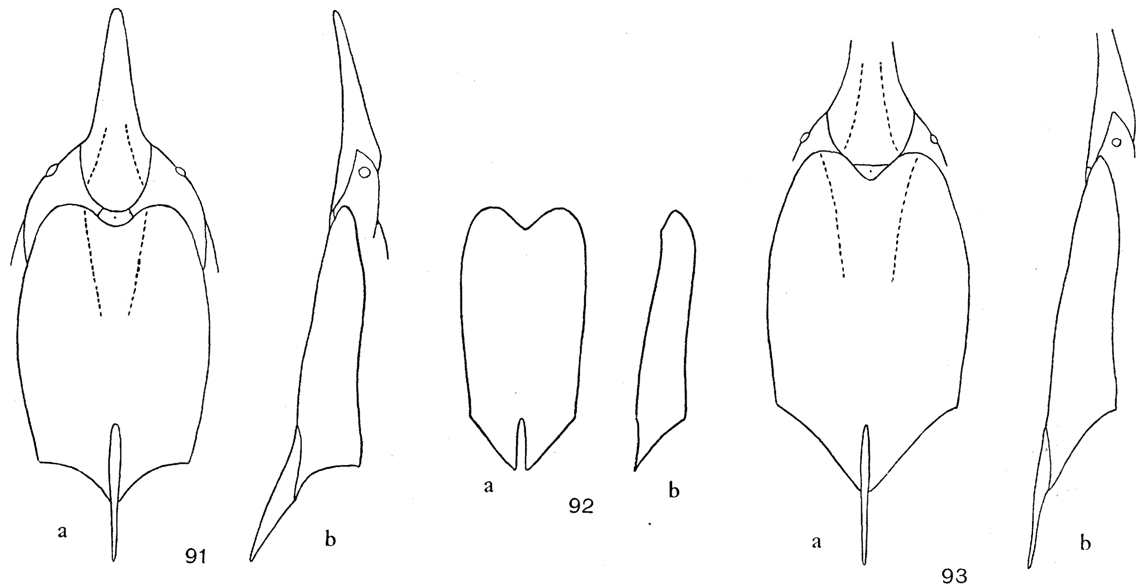
Diagnosis—A *Pteraspis* with dorsal shield attaining length of about 100 mm. Dorsal disc of adult oblong, with length along median line equal to one and a quarter to one and a half times maximum breadth, which is rather narrow across front end and apparently vaulted throughout, but especially posteriorly; anterior emargination rather deep and wide. Dorsal spine depressed and moderately long, narrow in side-view, with inserted portion narrow and moderately deep, but less than half total length of spine, and one-fifth to two-sevenths length of disc. Cornua moderately large, narrow, and arcuate, reaching some distance behind dorsal disc. Rostrum oval in section, long and attenuated, narrowing rapidly immediately in front of orbitals and forming two-fifths of total length of dorsal shield, and two and a half to three times maximum breadth. Pineal plate broader than long, either three- or four-sided, and may or may not be in contact with orbital plates, which extend for some distance in front of orbits on each side of rostrum, being strongly convex outwards in dorsal view but continuing line of expanded base of rostrum. Ventral disc in young stages more than twice as long as broad, with almost straight and parallel sides, becoming more or less ovoid in adult with flattened anterior margin, length being rather less than twice as great as maximum breadth. Ridges of "ornamentation" numbering from 50 to 80 per cm and flattened in section.

Lectotype—Internal cast of dorsal shield with imperfect rostrum, the original of LANKESTER's (1868), fig. 8, Plate 3, in Ludlow Museum, hereby selected.

Distribution—Lower Old Red Sandstone (Dittonian, zones II. 1–3): West of England and Pas-de-Calais.

Pteraspis crouchi LANKESTER, *forma typica* (Figs. 14, 17–19, 37, 68, ? 70, 91)

Diagnosis—The typical form of *P. crouchi*, with rostrum rapidly decreasing in width immediately in front of orbital plates and free portion extremely attenuated; pineal



FIGS. 91–93—Restorations in outline of the dorsal shields of the varieties of *Pteraspis crouchi* LANKESTER. (*a*) Dorsal view. (*b*) Lateral view. The anterior part of the inner longitudinal sensory canal of the dorsal disc and the posterior part of the superior rostral canal are indicated by broken lines. 91. *P. c.* typica (× ⅔). 92. *P. c. heightingtonensis*—dorsal disc only (× ⅔). 93. *P. c. mattockensis* (× ⅔).

plate four-sided with concave anterior and convex posterior margins, and lateral margins straight, short, and in contact with medial extensions of orbital plates. Insertion of dorsal spine about one-third median length of dorsal disc, which equals about one and a quarter to one and one-third maximum breadth.

Lectotype—As for species.

Distribution—As for species.

Pteraspis crouchi LANKESTER, var. *mattockensis* nov. (Figs. 12, 69, ? 71, ? 72, 75, 76, 93)

Diagnosis—A variety of *P. crouchi* with rostrum broader at base and narrowing less rapidly than in typical form; pineal plate triangular and separated from medial extensions of orbital plates. Insertion of dorsal spine one-fifth medial length of dorsal disc, which is about one and one-third times its maximum breadth.

Holotype—External mould of dorsal disc with imperfect rostrum, in the British Museum (No. P. 16490. I ; fig. 69).

Distribution—Lower Old Red Sandstone (Dittonian, zone II. 2) : S.W. Herefordshire.

Pteraspis crouchi LANKESTER, var. *heightingtonensis* nov. (Figs. 20, 21, 78, 79, 92)

Diagnosis—A variety of *P. crouchi* known only by extremely narrow and small dorsal and ventral discs ; median length of dorsal disc not exceeding 50 mm and equal to one and a half times maximum breadth ; that of ventral disc somewhat exceeding twice its maximum breadth.

Holotype—Internal cast of dorsal disc, in the British Museum (No. 42150; fig. 20).

Distribution—Lower Old Red Sandstone (Dittonian, zone II, 3) : N.W. Worcestershire.

Pteraspis jackana, sp. nov. (Figs. 22–27, 96)

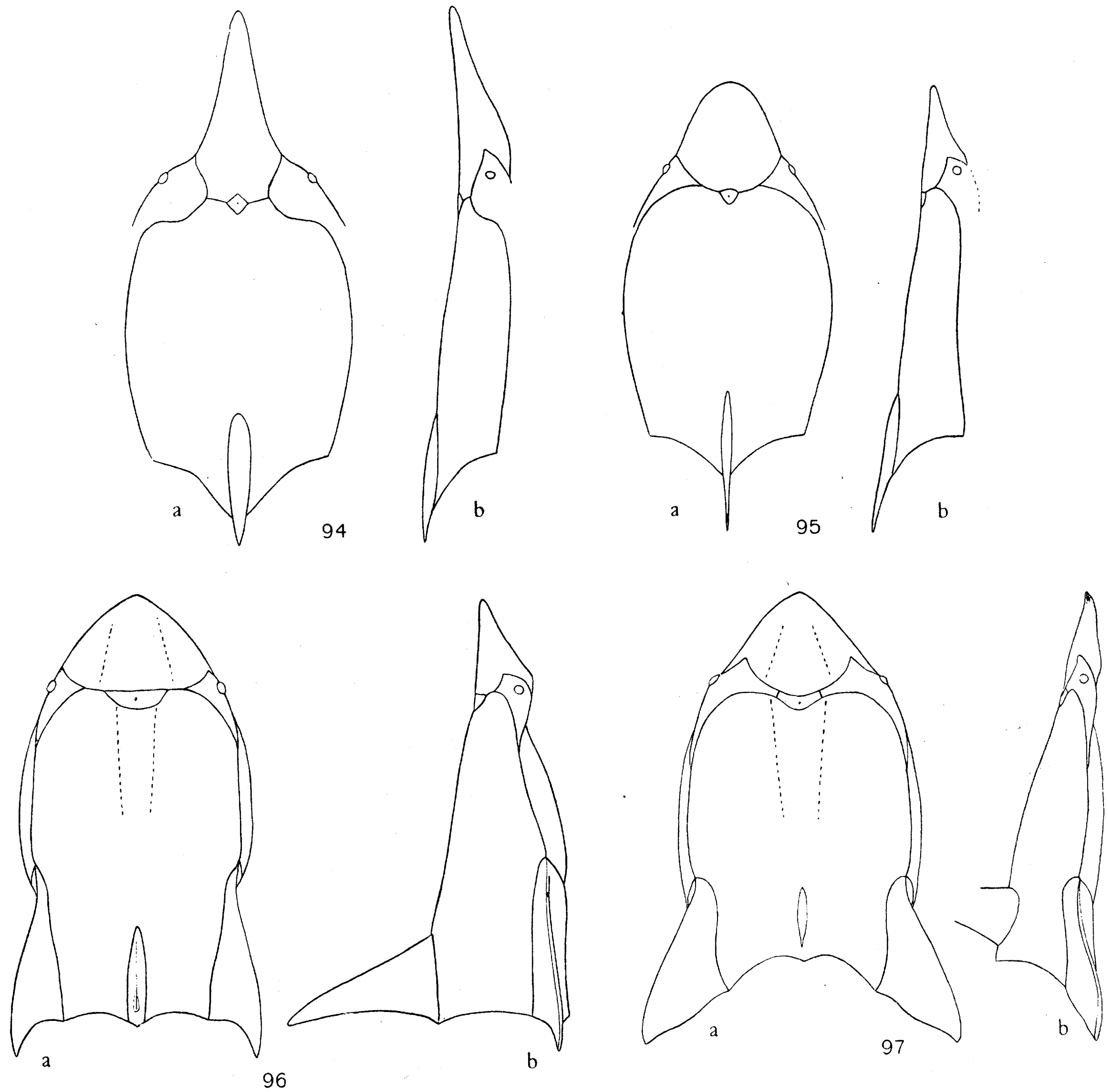
Diagnosis—A *Pteraspis* with dorsal shield attaining length of 90 mm. Dorsal disc very nearly as broad as long and apparently strongly arched throughout ; indentation of anterior margin generally wide and shallow, antero-lateral corners rounded, and posterior margins concave, forming very short posterior angle. Dorsal spine erect, pointed, and laterally compressed with straight or concave posterior margin and sloping anterior margin ; base of spine wide and long, forming posterior median angle of shield, with length equal to two-fifths of median length of dorsal disc and two-thirds height of spine. Cornua large, broad, and arcuate, reaching some distance behind dorsal disc. Rostrum broad and depressed, bluntly pointed and extremely short, its length being only two-thirds of its maximum breadth and one-quarter of total length of dorsal shield. Pineal plate triangular but very much wider than long, apparently just in contact with narrow, pointed, medial extensions of orbitals, which do not extend far in front of orbits but continue line of rostrum. (Ventral disc unknown.)

Holotype—Internal cast of dorsal shield, in the British Museum (No. P. 16776 ; fig. 23).

Distribution—Lower Old Red Sandstone (Dittonian, zone II. 2) : S.W. Herefordshire and N. Monmouthshire.

Pteraspis stensiöi, sp. nov. (Figs. 28, 29, 97)

Diagnosis—A *Pteraspis* with dorsal shield attaining a length of 90 mm. Dorsal disc nearly as broad as long and apparently strongly arched throughout ; indentation of anterior margin wide and shallow, antero-lateral corners rounded, and posterior margin concave and entire, with inconspicuous posterior angle. Dorsal spine erect, much laterally compressed, with forwardly sloping posterior margin (at base) and vertical anterior margin ; base of spine very narrow and short, not reaching posterior margin of disc, with length equal to one-quarter of median length of dorsal disc. Cornua very large, broad, and roughly triangular, reaching some distance behind disc. Rostrum broad, depressed, bluntly pointed, and extremely short, its length being



FIGS. 94–97—Restoration in outline of the dorsal shield of British species of *Pteraspis*. (*a*) Dorsal view. (*b*) Lateral view. The anterior part of the inner longitudinal sensory canal of the dorsal disc and the posterior part of the superior rostral canal are indicated by broken lines. 94. *P. leathensis*, sp. nov. (Nat. size). 95. *P. mitchelli* POWRIE ($\times \frac{2}{3}$). 96. *P. jackana*, sp. nov. ($\times \frac{2}{3}$). 97. *P. stensiöi*, sp. nov. $\times \frac{2}{3}$)

about two-thirds of its maximum breadth and rather greater than one-quarter of total length of dorsal shield. Pineal plate from three to three and a half times as broad as long, four-sided, with slightly concave anterior and convex posterior margins, and short, straight, lateral borders in contact with very long and narrow medial extensions of orbital plates, which do not extend far in front of orbits, but continue line of rostrum. (Ventral disc unknown.)

Holotype—External mould of imperfect dorsal shield, in the British Museum (No. P. 17629; fig. 28).

Distribution—Lower Old Red Sandstone (Dittonian, zone II. ? 3) : S.W. Herefordshire.

Pteraspis mitchelli POWRIE (Figs. 32, 95)

Diagnosis—A *Pteraspis* with dorsal shield attaining a length of about 100 mm, but generally smaller. Dorsal disc nearly as broad as long, apparently arched throughout; anterior emargination very narrow and deep, and antero-lateral corners wide and rounded. Dorsal spine depressed with insertion deep, equal to about one-third of median length of dorsal disc. Rostrum depressed, broad, and of moderate length, tapering gradually to a blunt extremity, the length being slightly greater than its maximum breadth and contained about three and a half times total length of dorsal shield. Pineal plate triangular, about as broad as long, and widely separated from medial extensions of orbital plates, which do not continue far in front of orbits and are straight in dorsal profile, continuing line of rostrum. (Ventral disc unknown.)

Holotype—Dorsal shield in counterpart, whereabouts unknown.

Distribution—Lower Old Red Sandstone (zone uncertain) : Angus and Stirlingshire.

In conclusion, it is my pleasant duty to express my thanks to those who have given me much willing help, both in field and study. To Mr. G. H. JACK, formerly County Surveyor of Herefordshire, I owe not only the first specimens (among them some of the most important) from what were to me then new localities, but facilities to collect myself; facilities which were readily continued after Mr. JACK's retirement by his successor, Mr. R. G. GURNEY. Mr. R. G. VIRGO, the Surveyor of the South-Western district of Herefordshire, has helped in every possible way, and without his ready assistance it would have been impossible to have obtained all the material that has been collected during the last two years.

Mr. H. A. TOOMBS, of the Department of Geology of the British Museum (Natural History), was my companion during many pleasant weeks in the field, and to his keenness and flair for collecting is due the discovery of most of the important specimens, particularly those from the silt-stone lenticle at Wayne Herbert.

Mr. M. BURTON, of the Department of Zoology, and Commander VERNON EDWARDS also gave me valuable assistance in collecting; while to Mr. W. H. T. TAMS, of the Department of Entomology, I am indebted for some of the photographs which form the plates.

Through Mr. M. A. C. HINTON, F.R.S., I have had from the Trustees of the GODMAN EXPLORATION FUND much valuable financial support, enabling me to work on a far more ambitious scale than would otherwise have been possible.

To Mr. W. WICKHAM KING a special tribute is due ; not only has he shown me the best of his Worcestershire localities, but he has presented the pick of his own rich collection to the British Museum (Natural History).

Sir ARTHUR SMITH WOODWARD, F.R.S., who has communicated this paper, and Dr. C. TATE REGAN, F.R.S., Director of the British Museum (Natural History), have both given me much assistance and valuable criticism, while Professor ERIK STENSIÖ, of the State Museum of Stockholm, Dr. ANATOL HEINTZ, of the Palaeontological Museum at Oslo, and Dr. C. J. STUBBLEFIELD, of H.M. Geological Survey, have afforded me every facility to study the rich collections in their charge. Moreover, while in Stockholm, I had the advantage of discussing the Podolian Pteraspids with Dr. W. ZYCH and Dr. F. BROTZEN and of examining the material which they have recently collected, and in Oslo I was privileged to examine the remarkable series of sections which the late Professor J. KIAER had prepared from his Spitsbergen Pteraspids ; for this courtesy I am indebted to Dr. HEINTZ.

To all these gentlemen I wish to tender my warmest thanks.

VI—SUMMARY

The material described above adds very largely to our knowledge of the important genus, *Pteraspis*, so that the whole of its external morphology is now tolerably well known ; and, moreover, it throws light on the relationships between the various groups forming the Ostracoderms. The following are the chief points.

The tail in the genus *Pteraspis* is strongly hypocercal, the lower lobe being considerably longer than the upper and produced into a long, narrow process.

The whole of the caudal region behind the carapace is invested with thick, rhomboid imbricating scales of the same composition as the plates, which diminish in size caudally, but which have a complete covering of " enamel " on the outer surface, there being no differentiated area of overlap. Both dorsally and ventrally there is a median series of enlarged ridge-scales divided into two parts by an interval after about the fifth scale from the front ; all overlap the scale behind except those of the anterior part of the dorsal series, which are well separated from one another and are produced into a conspicuous thorn-like spine (*P. rostrata* AGASSIZ sp.). The median dorsal spine, which is inserted in the dorsal disc, is evidently the most anterior member of this series much enlarged.

Pteraspis has no paired fins whatever, and it is probable that these were never developed ; nor are there any median fins other than the caudal fin.

The sensory canal system is uniform in all the species in which it is known, and is intimately connected by numerous tubuli with the supposed mucous grooves, which were probably sensory, forming the external " ornamentation " of the plates and scales, and to these grooves it seems to have acted as a collecting system.

The system of mouth-plates in *P. rostrata* is generally similar to that of the Downtonian *P. vogti*, except that the lateral oral plates bear part of the sensory canal

connecting the lateral canal of the ventral disc and the inferior rostral canal. The oral plates apparently formed the expanding frame-work of a protusible lower lip that was scoop-like and probably partly suctorial in function, the whole being invested with soft tissues. The " ornamentation " of the distal ends of these plates is much broken up, almost granular, and, like the roughened area in front of the mouth, was highly sensitive to aid in the detection of suitable material for food, which must have consisted of animal or vegetable detritus in or on the muddy bottom, the animal being benthonic in habit. There were no external nares.

As suggested by ZYCH, the plates of the carapace were not formed until a relatively late stage, and at first were not in contact with one another.

The English species, *Pteraspis rostrata* and *P. crouchi*, are divisible into local, possibly stratal, varieties, remarkable for the differences in form of the orbital and pineal plates, differences which are considered elsewhere to be of specific value. It is clear that the taxonomic value of certain characters varies much, not only according to the area but according to the form, one variety of *P. rostrata* showing a wide range in the proportions of the rostrum, usually one of the best characters for identifying a specimen.

The genus *Pteraspis* is in general uniform in external characters, the most striking exception to this being the possession by *P. rostrata* of post-oral covers, which are lacking in the earlier *P. vogti*. Apart from this character, which is too rarely seen to be of immediate systematic value, there seems little reason for sub-dividing the genus.

The genus *Pteraspis*, the American *Cyrtaspis*, and the undescribed Spitsbergen forms (*Doryaspis*, etc.) compose the family PTERASPIDAE, which with the closely allied DREPANASPIDAE, CYATHASPIDAE, and PALAESPIDAE forms the HETEROSTRACI.

The HETEROSTRACI, ANASPIDA, OSTEOSTRACI, and CYCOLSTOMATA are related to one another inasmuch as they are classes of the same group AGNATHA, but none is ancestral to another, the classes branching off from the main stem at successive periods in the order named.

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Description of Plates

Plate 25

Fig. 98—*Pteraspis rostrata* (Agassiz), var. *toombsi* nov. External mould of ventral surface of a specimen complete save for lower caudal lobe. Lower Old Red Sandstone, Wayne Herbert Quarry, Herefordshire. (P. 16789—Nat. size.)

Fig. 99—Mould of dorsal surface of same specimen. (P. 16790—Nat. size.)

Fig. 100—*P. rostrata* (Agassiz), var. *trimpleyensis* nov. Dorsal shield collected by Mr. Wickham King. Lower Old Red Sandstone, Trimpley, Worcestershire. (P. 16478. I—Nat. size.)

Fig. 101—*P. rostrata* (Agassiz), var. *waynensis* nov. Imperfect external mould of dorsal shield, showing sensory canals. Lower Old Red Sandstone, Wayne Herbert Quarry, Herefordshire. (P. 16783—Nat. size.)

Fig. 102—*Doryaspis nathorsti* (Lankester). External mould of ventral disc. Lower Devonian, Dickson Bay, Spitsbergen. (P. 6492—Nat. size.)

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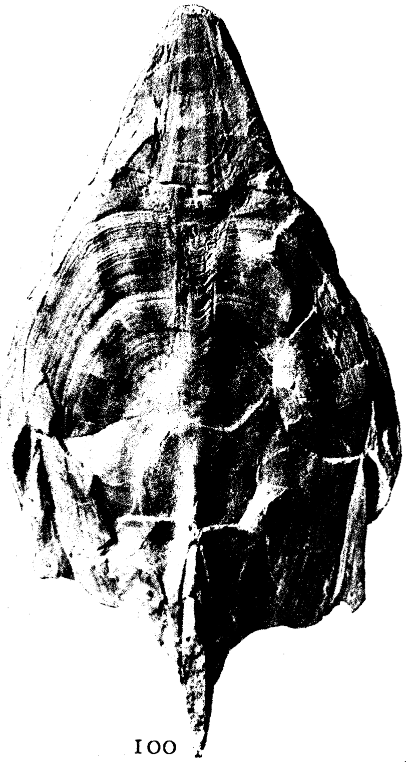

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Pteraspis and Doryaspis

Plate 26

Pteraspis rostrata (Agassiz), var. *toombsi* nov.

Lower Old Red Sandstone, Wayne Herbert Quarry, Herefordshire.

Fig. 103—External mould of isolated tail. (P. 17488. II—× 3.)

Fig. 104—External mould of dorsal surface of an almost complete specimen. Holotype of variety. (P. 17480—Nat. size.)

Fig. 105—A similar specimen without rostrum, but with complete tail. (P. 17477—Nat. size.)

Fig. 106—A similar specimen. (P. 17485—Nat. size.)

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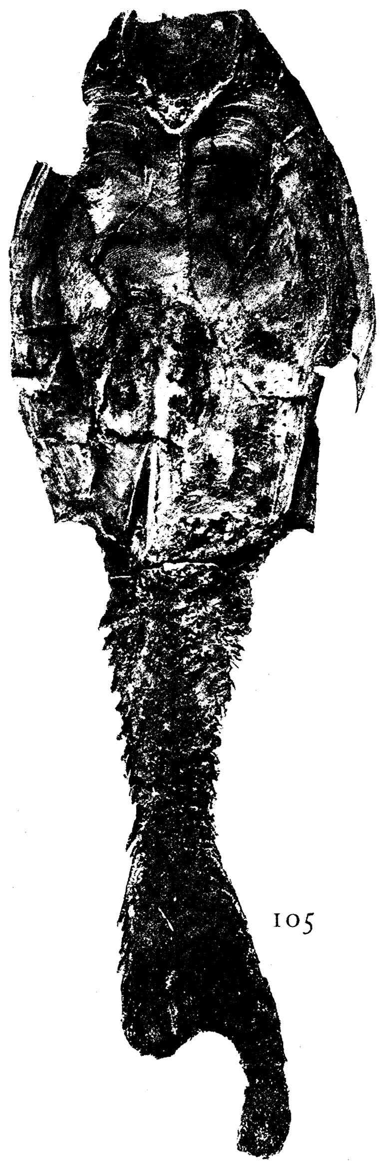

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Pteraspis rostrata var. TOOMBSI

PLATE 27

Pteraspis rostrata (AGASSIZ), var. *toombsi* nov.

Lower Old Red Sandstone, Wayne Herbert Quarry, Herefordshire.

FIG. 107—Squamation of the flank slightly distorted and showing the complete scales. The specimen is an external cast, but the lighting has been reversed so as to give the effect of a positive. (P. 17522—× 5.)

FIG. 108—External mould of squamation. (P. 16790—× 14.)

FIG. 109—External mould of the anterior squamation of the upper left flank. (P. 16790—× 5.)

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The squamation of Pteraspis

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Pteraspis and Doryaspis

PLATE 25

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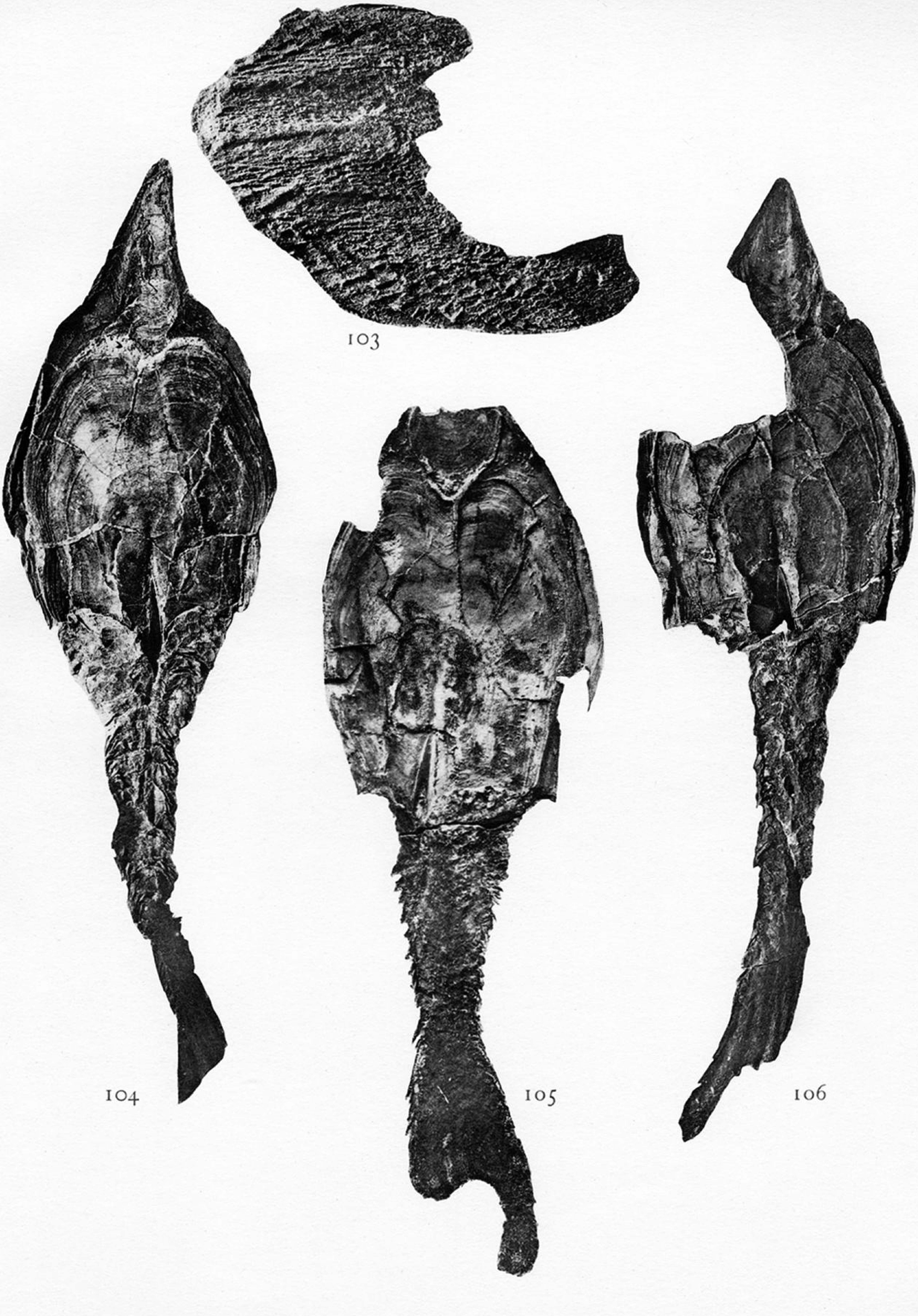

Pteraspis rostrata var. Toombsi

PLATE 26

Pteraspis rostrata (AGASSIZ), var. *toombsi* nov.

Lower Old Red Sandstone, Wayne Herbert Quarry, Herefordshire.

FIG. 103—External mould of isolated tail. (P. 17488. II—× 3.)

FIG. 104—External mould of dorsal surface of an almost complete specimen. HOLOTYPE of variety. (P. 17480—Nat. size.)

FIG. 105—A similar specimen without rostrum, but with complete tail. (P. 17477—Nat. size.)

FIG. 106—A similar specimen. (P. 17485—Nat. size.)

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The squamation of Pteraspis

PLATE 27

Pteraspis rostrata (AGASSIZ), var. *toombsi* nov.

Lower Old Red Sandstone, Wayne Herbert Quarry, Herefordshire.

FIG. 107—Squamation of the flank slightly distorted and showing the complete scales. The specimen is an external cast, but the lighting has been reversed so as to give the effect of a positive. (P. 17522—× 5.)

FIG. 108—External mould of squamation. (P. 16790—× 14.)

FIG. 109—External mould of the anterior squamation of the upper left flank. (P. 16790—× 5.)