THE DOWNTONIAN OSTRACODERM *CORVASPIS KINGI* WOODWARD, WITH NOTES ON THE DEVELOPMENT OF DERMAL PLATES IN THE HETEROSTRACI

by L. B. TARLO

ABSTRACT. Further specimens of the Downtonian Ostracoderm *Corvaspis kingi* Woodward are described, and the genus is shown to belong to the family Psammosteidae. The variation of ornamentation seen in *Corvaspis* is used to demonstrate the relationship between the three main types of growth of dermal plates known in the Heterostraci.

INTRODUCTION

THE affinities of the ostracoderm *Corvaspis kingi* have been the subject of much debate, but the discovery of new material and a reinterpretation of that already known now make it possible to place the genus in the family Psammosteidae, so that the family Corvaspidae becomes redundant.

A fragment of this ostracoderm, which had been collected by Professor J. Kiaer from the Downtonian of Spitsbergen, was figured although not described, by Jaeckel (1927, p. 925) as a new Palaeaspid (Cyathaspid). Woodward (1934, pp. 566–7) erected *Corvaspis kingi* for similar material from the Downtonian of Corvedale (Shropshire) collected by Mr. W. W. King, and placed the genus in the Cyathaspidae. Stensiö (1944, p. 4) recorded *Corvaspis* from the Czortkow Series of Podolia.

Denison (1953, pp. 304–18) redescribed the unusual ostracoderm *Cardipeltis* and noted that its histological structure and ornamentation closely resembled those of *Corvaspis*, but as little was then known of *Corvaspis* he was unable to suggest the possible relationship between these two genera. A few months after Denison's paper appeared, Dineley (1953) described further remains of *Corvaspis* including median plates, ridge plates, and orbital plates, as well as small irregular plates and scales.

Corvaspis, like most Heterostracans, has a complex carapace of bony plates covering its head and the anterior part of its trunk, the posterior part being covered by small scales. The carapace is made up of a number of different plates, the presence or absence of which is of diagnostic value. Dineley showed that *Corvaspis* must be excluded from the Cyathaspidae since it possesses orbital plates; he also regarded it as having ridge plates, and although he considered that the genus might be 'akin to the Drepanaspidae' (Psammosteidae), an animal having ridge plates clearly did not belong to any known family (1953, p. 166). In consequence, he felt justified in proposing a new family—the Corvaspidae—to receive *Corvaspis kingi* and his new species *C. graticulata*. As is shown below, however, Dineley's so-called 'ridge plates' can better be interpreted as branchial plates, thus equating *Corvaspis* with most other Heterostracans, and removing the necessity for a separate family.

Bystrow (1955, pp. 472–523) figured the microstructure of *Corvaspis kingi* which appears Cyathaspid in nature, but he showed that it was similar in certain respects to

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Kallostrakon podura which in turn could be compared with the Psammosteid *Psammolepis paradoxa*. Recently Stensiö (1958, pp. 321–6) reviewed previous work on *Corvaspis*, retaining it in the order Corvaspida (= Corvaspidae of Dineley). At the same time he suggested that the Ludlovian *Strosipherus* and the Dittonian *Penygaspis* might be included in this order. Further specimens of *Corvaspis kingi* collected during 1953–5 by Mr. J. R. L. Allen, Dr. L. G. Love, Dr. T. Orvig, Mr. H. A. Toombs, and myself are described below, and these help to establish the Psammosteid affinities of the genus. The new material comes from the Earnstrey Hall locality in Shropshire, details of which can be found in Wills (1935, p. 427). Most of the specimens come from the '4-foot band of very tough calcareous pellet rock and conglomerate', a large block of which has fallen into the bed of the stream.

DESCRIPTION OF PLATES

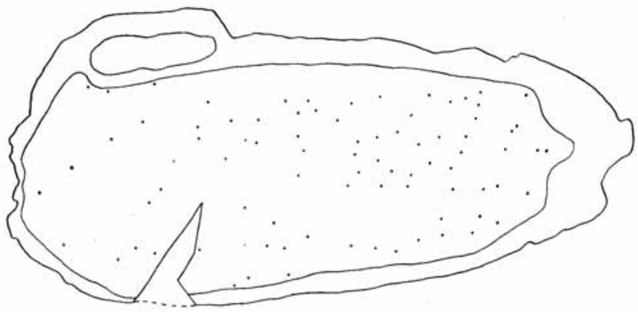
Median plates. Dineley (1953, p. 171) described an almost complete median plate, which Stensiö (1958, p. 324) suggests was on the ventral surface of the body. This plate is somewhat oval in outline, its anterior border being gently curved while the lateral borders are more or less straight. Unfortunately the posterior border is missing. The new material contains a complete median plate which has a similar anterior border, and a posterior border which is almost straight transversely. Its lateral edges are also fairly straight, but they tend to diverge posteriorly, so that, as can be seen from text-fig. 1, the plate is narrower anteriorly. A small plate is incorporated within the median plate on one side of the posterior part, making it asymmetrical.

There are other ventral median plates which seem to be variations on the simple oval one already described. In these the central part of the anterior border is produced, as is shown in text-fig. 2*b*.

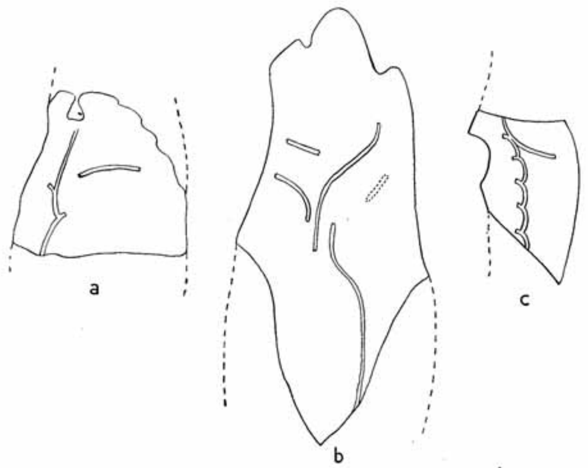
The type specimen described by Woodward is the anterior part of a median plate, the anterior border of which is deeply excavated at the midline. Stensiö interprets this plate as forming part of the dorsal surface of the animal, and the new collection also includes a similar bilobed median plate (see Pl. 38, fig. 3). In the Psammosteids, the Pteraspids, and also the Traquairaspids, the dorsal median plate has an excavated anterior border while the border of the ventral plate is generally convex, thus *Corvaspis* may well be related to one of these groups.

Both Woodward and Dineley noted that the sensory pores were in two irregular lines running longitudinally on either side of the median plates, and in text-fig. 1 the complete median plate is shown with the pores plotted. Though this gives some indication of the pattern of the sensory canal system itself, it can only be fully ascertained by grinding the specimen through to just below the dentine layer where the canal system proper occurs. This has recently been attempted, and from the specimens figured below (text-fig. 2) it appears that the canal system found is roughly comparable to those known in other Heterostracans, although the pattern is not a clear-cut one and cannot be used with any certainty. When more specimens are available to allow the necessary sacrifice, it may be possible to obtain a complete picture of the canal system in *Corvaspis*.

The ornamentation of the dermal plates is quite distinctive and can readily be used to identify the genus. Generally it consists of flat-topped dentine ridges with a faintly crenulate base; these ridges are usually disposed longitudinally and, as noted by Woodward (1934), in the median plates 'an irregular network of fine grooves divides this ridge ornament into small areas which have the false appearance of separate plates'. Woodward also described an ornamentation in which these small polygonal areas were separated by rows of small rounded tubercles instead of faint grooves and, as noted by Dineley, both types of ornament can appear in one plate. Stensiö (1958, p. 324) suggested



TEXT-FIG. 1. *Corvaspis kingi* Woodward. Ventral median plate with sensory pores plotted, wide border of rounded tubercles indicated; isolated area in upper left portion of figure represents incorporated tesserae. ×1, B.M. P.40575.

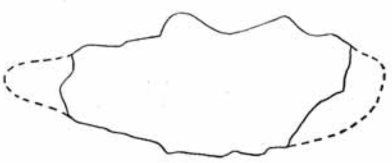


TEXT-FIG. 2. *Corvaspis kingi.* Fragments of median plates showing sensory canals; all horizontal sections taken at junction of cancellor layer and outer dentine layer. *a*, ×1, A–T 225; *b*, Anterior part of ventral median plate. ×1, A–T 238; *c*, ×1, A–T 309.

that the polygonal areas separated by tubercles belonged to the posterior part of the plate, the others being anterior. Some of the median plates recently found show that in *Corvaspis* there is a much greater variety of ornament than was formerly realized. It is in fact possible to trace a gradation from an ornamentation of polygonal areas separated by tubercles to one in which the longitudinal dentine ridges continue almost the whole length of the plate without a break. The significance of this variation is discussed below. In addition all median plates, whatever their form of ornamentation, have a wide border of rounded tubercles.

A specimen is also figured (Pl. 38, fig. 6) which shows the healing of damage in the carapace, the area of new growth consisting of dentine ridges arranged in random fashion.

Branchial plates. Some arched, elongate, asymmetrical plates were termed 'ridge plates' by Dineley (1953, p. 174), since he believed that they might correspond to the 'ridge scales' (fulcral scales) of other Heterostracans. He suggested that their degree of arching indicated that they were placed in the median line of the trunk or tail region rather than in a lateral position. The plate he figured is incomplete along one border, but luckily one of the new specimens is complete in this region and shows that the plate is even more asymmetrical than Dineley suspected; one border, probably the dorsal, having a very distinctive broad notch (see text-fig. 3). The arching and general shape of the plate is similar to that seen in the branchial plates of the Cyathaspids, Pteraspids, and Traquairaspids, and this, coupled with the strong asymmetry, suggests that the plate is in fact a branchial. Moreover, the specimen figured by Dineley shows a sensory canal running obliquely across one corner, which is consistent with its being a branchial plate rather than a ridge plate.



TEXT-FIG. 3. *Corvaspis kingi.* Left branchial plate, showing asymmetry and flange with broad notch on upper part of figure. $\times 1\frac{1}{2}$, A–T 233.

Along the crest of the branchial plate is a line of small tubercles, around which the adjacent dentine ridges curve, giving a very characteristic pattern. The remainder of the plate is covered with short ridges aligned longitudinally, except where they curve round sensory pores.

Orbital plates. Dineley (1953, p. 173) described and figured orbital plates for the first time, although all his specimens were small with irregular margins. Subsequently a specimen was discovered which shows that the orbitals are large rectangular plates with a circum-orbital sensory canal (Pl. 37, fig. 2). The specimens figured previously would thus seem to have been merely the central portions of the orbital plates, and this new find is of some significance since such a large orbital plate can only be envisaged as belonging to the carapace of a dorso-ventrally compressed animal like a Psammosteid. Previously the orbitals were taken to be small plates, which might well have belonged to any Heterostracan family outside the Cyathaspids.

In the central portion of the orbital plate, the dentine ridges are arranged in concentric rows around the orbital cavity, the rest of the plate being composed of a wide border of small tubercles. In one sector, however, the dentine ridges form a series of concentric rings around sensory pores.

Lateral plates. Dineley's small irregular plates are of two kinds: first those similar to the plate incorporated in the median plate described above, which are here termed tesserae, and second those here regarded as lateral plates. The latter, unlike the tesserae, have their dentine ridges arranged in a haphazard manner; some have a rather intricate outline, whereas others with a more simple outline are traversed by sensory canals (Pl. 37, figs. 5, 6). These lateral plates probably occur in the pre-orbital region of the ventral surface, situated behind and to the side of the mouth.

Tesserae. It was suggested by Dineley that the median plate was surrounded by a mosaic of small plates, and this is confirmed by the fact that they may become incorporated into the median plate around its margin (Pl. 37, fig. 1). Such fields of tesserae between the major plates are characteristic of the Psammosteidae. Unlike the lateral plates the tesserae are fairly simple in outline and in some the ornamentation consists of small tubercles arranged concentrically; others have a pattern of longitudinal ridges with only a narrow border of tubercles (Pl. 37, figs. 3, 4).

Post-orbital plate. A single asymmetrical and somewhat arcuate plate is included in the new collection (Pl. 37, fig. 7). It seems unlikely that this plate could have occupied a median position in the body and it is tentatively suggested that it represents a post-orbital plate, such as is present in the Psammosteids.

Microstructure. The histological structure of the plates and scales of *Corvaspis kingi* has been described and figured by Bystrow (1955, pp. 492–4). However, under high magnification it can be seen that the normal dentine tubules rebranch into innumerable and much finer tubules which continue through the seemingly structureless outermost layer to the exterior, as is shown in Pl. 37, fig. 8*b*.

AFFINITIES OF *CORVASPIS*

As has been demonstrated the possession of orbital plates excludes *Corvaspis* from the Cyathaspidae despite the fact that its plates have a similar histological structure, the cancellar layer possessing large spaces which reach from the basal lamellar layer to the outer dentine one. Moreover, it possesses fields of tesserae which are known only in the Ordovician Astraspids and the Psammosteids, but it is excluded from the former by its histological structure. This suggests Psammosteid affinities for *Corvaspis* but in the Psammosteids the cancellar layer has a spongy appearance. However, a transition from the typical Psammosteid condition to that in *Corvaspis* can be seen in *Kallostrakon podura* Lankester (a form related to *Corvaspis*) where both spongy tissue and large spaces are present.

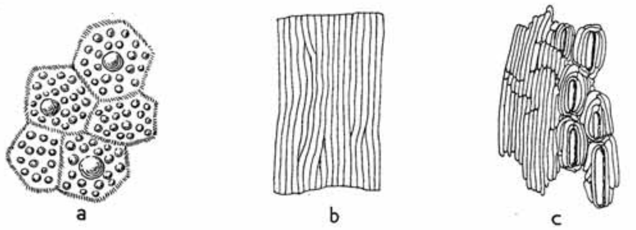
The large flat orbital plates fit best into the structure of a dorso-ventrally compressed animal such as the Psammosteid *Drepanaspis* (Obruchev 1943, pp. 268–71), and the plate interpreted as a post-orbital, if correctly diagnosed, would mean that *Corvaspis* must belong to this family since only in the Psammosteids is such a plate known.

The evidence thus points to the Psammosteid affinities of *Corvaspis* and for this reason it is here included within the family Psammosteidae, making it no longer necessary to retain the family Corvaspidae.

As noted above, the Dittonian *Cardipeltis* is similar to *Corvaspis* in both its histology and ornamentation, and in the possession of tesserae, branchials, and median plates. However, in *Cardipeltis* the median plate extends laterally as far as the branchial openings, whilst *Corvaspis* has a field of tesserae on either side of the median plate. If, in *Corvaspis*, the fields of tesserae around the median plate were to be completely incorporated into it, then a median plate similar to that in *Cardipeltis* could be produced. From the pattern of the sensory canal system in *Cardipeltis* it is clear that the known median plates extend only as far as the pineal region, and it seems reasonable to assume, as Stensiö has done (1958, p. 328), that there were small plates and orbitals anterior to the median plates. If this were so and further fusion of plates took place, one would have the condition where an entire carapace could arise as a single unit. This occurs in the Emsian Amphiaspids described by Obruchev (1938; 1958) from north-west Siberia, and *Cardipeltis* could thus be interpreted as an early offshoot from the Psammosteid stock leading to the Amphiaspids.

DEVELOPMENT OF DERMAL PLATES IN THE HETEROSTRACI

After the discovery by Woodward and White (1938) that primitive Elasmobranch scales are composite in nature, Orvig (1951) and Stensiö (1958) developed a new theory on the growth of scales and dermal bone in the lower vertebrates. Their recognition of



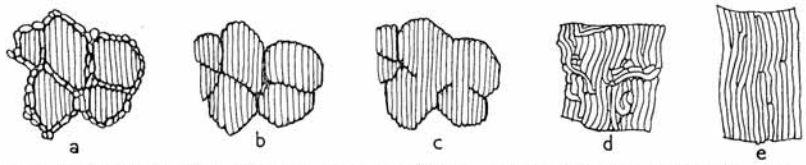
TEXT-FIG. 4. Ornamentation of dermal plates. *a*, *Astraspis sp.*, showing independent polygonal tesserae and zones of tubercles produced by cyclomorial growth. *b*, *Poraspis sp.*, showing longitudinal dentine ridges produced synchronomorially. *c*, *Tolepelepis sp.*, showing individual units produced by cyclomorial growth, with adjacent synchronomorial area.

the fact that two types of growth occur in dermal plates is here used to assess the significance of the variation in ornamentation within the Heterostraci.

The most primitive Heterostraci known are the Ordovician Astraspidae, which have a carapace composed of isolated polygonal tesserae. These small plates have an ornamentation consisting of one large tubercle surrounded by concentric rows of smaller tubercles. It is evident that during the early stages of ontogeny, single isolated tubercles were present in the skin which formed primordia around which successive zones of tubercles appeared, until the animal reached its definitive size, when the borders of the small plates thus formed would meet. The growth of these individual units by addition of zones of tubercles is termed cyclomorial growth by Orvig (1951, p. 367) (see text-fig. 4*a*).

In Silurian times the Heterostraci were represented by the Cyathaspids which had a carapace composed of two median plates and two branchials. These plates are ornamented by longitudinal dentine ridges, and in general appeared only when the animal was fully grown. There are no signs of cyclomorial growth, each plate being formed as a complete unit, with the dentine ridges all appearing simultaneously. This type of growth Orvig (1951, p. 367) termed synchronomorial (see text-fig. 4*b*).

A number of Cyathaspids are known from the Ludlovian of Oesel which do not possess this general type of ornamentation, but instead have one which can easily be derived from that seen in the Astraspids. The dorsal plate in *Tolepelepis*, for example, is made up of many cyclomorial elements, in each of which there is a longitudinal primordium, with smaller longitudinal ridges on either side. In the posterior part of the plate these elements take on the appearance of imbricating scales. The lateral region of the dorsal plate of *Tolepelepis*, however, has a similar ornamentation to that of the more normal Cyathaspids, showing synchronomorial growth, the only vestige of the individual elements being the faint grooves which break up the longitudinal dentine ridges (see text-fig. 4*c*). *Corvaspis* from the Downtonian shows further stages in the growth of the dermal plates, its median plates being more advanced than those of *Tolepelepis*. In *Corvaspis* the plates also appear to be formed of numerous polygonal units fused together, but each unit is formed synchronomorially in contrast to the cyclomorial formation in *Tolepelepis*. In the posterior part of the median plates of *Corvaspis*, the synchronomorial units are separated from one another by narrow zones of tubercles



TEXT-FIG. 5. Variation of ornament in *Corvaspis kingi*. *a*, Polygonal synchronomorial units with margins of tubercles produced by cyclomorial growth. *b*, Polygonal synchronomorial units separated by grooves. *c*, Partial fusion of adjoining synchronomorial units. *d*, Complete fusion of original polygonal units giving single large synchronomorial area with occasional random ornamentation. *e*, Final stage showing longitudinal dentine ridges running almost without a break (cf. *Poraspis* fig. 4*b*).

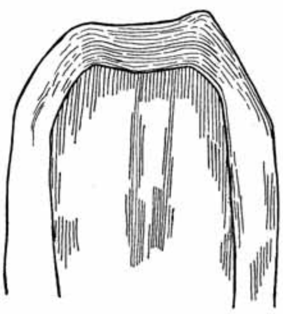
formed cyclomorially, giving the units the appearance of scales (Pl. 38, fig. 1; text-fig. 5*a*). It seems likely that, as suggested by Stensiö, the median plates gradually became continuous in this way with the squamation of the scales.

Normally the polygonal units are marked off from one another by faint grooves (Pl. 38, fig. 2; text-fig. 5*b*), but in some cases this division into individual units is incomplete, the dentine ridges of two or three synchronomorial units being continuous, probably due to the units fusing before calcification (Pl. 38, fig. 3; text-fig. 5*c*). A further stage is well seen in Pl. 38, fig. 4, and text-fig. 5*d*, where the only trace of the original polygonal unit is an occasional faint transverse groove and an irregularity in the arrangement of the dentine ridges. This type of ornament is also seen in the Dittonian *Cardipeltis* which seems to suggest that this genus is a direct descendant of *Corvaspis*. The final stage in the trend of ornamentation is seen in a specimen of *Corvaspis* in the collection of Birmingham University (B.U. 717) which shows a median plate ornamented by straight longitudinal ridges, which extend almost the whole length of the plate without interruption (Pl. 38, fig. 5; text-fig. 5*e*).

A similar trend is seen in *Traquairaspis* (Pl. 38, fig. 7) where the primitive Downtonian *T. campbelli* has, in the centre of the ventral median plate, a large synchronomorial unit in which the ornamentation is random as in *Corvaspis* (text-fig. 5*d*), suggesting that it was derived from a number of small individual units. The later Downtonian *Traquairaspis symondsi* possesses a large central synchronomorial unit completely devoid of ornamentation (White 1946). In both cases the central unit has around it concentric zones of cyclomorial growth.

In *Corvaspis* also, whatever the form of ornamentation of the median plates, they are bordered by rows of small rounded tubercles forming a zone of cyclomorial growth. This type of median plate in which there is a large central synchronomorial unit around which there is an area of cyclomorial growth is also seen in the primitive Dittonian Pteraspid *Penygaspis dixoni* (White), although in this case the ornamentation is typically Pteraspid (White 1938; Stensiö 1958) (text-fig. 6).

If the synchronomorial unit were acquired early in the ontogeny instead of when the animal was approaching its definitive size, and the area of its median plates continued to increase by concentric growth, this would give the normal type of growth seen in the Pteraspids, which are an advanced group of the Heterostraci. That this is more likely than the evolution of the Pteraspid type of growth direct from the Astraspid condition is borne out by vestiges of the primitive condition found in some Pteraspids. *Pteraspis althi* Stensiö, for example, has a pre-oral region composed of small polygonal synchronomorial units rather like those seen in *Corvaspis* (Stensiö 1958, p. 277), while in *Rhinopteraspis dunensis* (Roemer) this same region is composed of a single synchronomorial unit in which the dentine ridges run longitudinally without a break (Tarlo 1958). These contrast with *Pseudopteraspis elongata* (Zych), which has the normal Pteraspid cyclomorial growth in its pre-oral region, and as figured below (text-fig. 7) these examples of fundamentally different Pteraspids demonstrate the three main types of ornamentation found in the Heterostraci.



TEXT-FIG. 6. *Penygaspis dixoni* (White), showing large central synchronomorial unit around which concentric growth occurs cyclomorially (after White 1938).

EXPLANATION OF PLATE 37

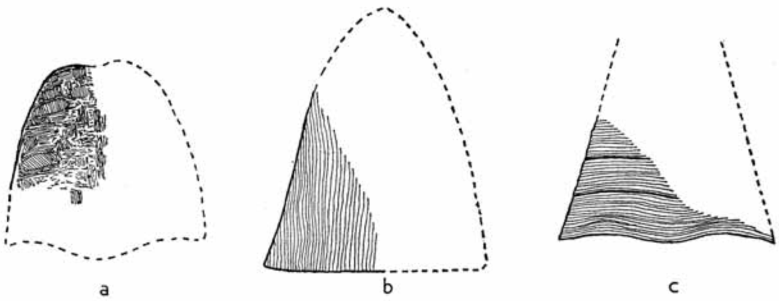
Figs. 1–8. *Corvaspis kingi* Woodward, Downtonian, Earnstrey Hall, Shropshire. 1, Anterior part of ventral median plate, showing the incorporation of tesserae on one side. ×2, B.M. P.40573. 2, Orbital plate. ×3, A–T 231. 3, Tessera, showing cyclomorial growth. ×3, A–T 308. 4, Tessera, showing synchronomorial growth. ×3, A–T 235. 5, Lateral plate, showing haphazard arrangement of ornament. ×3, A–T 234. 6, Lateral plate, traversed by line of sensory pores. ×3, A–T 226. 7, ? Post-orbital plate. ×2, B.M. P.40574. 8*a–b*, vertical section of scale. A–T 206. 8*a*. Complete scale. ×40. 8*b*. Part of scale, showing fine dentine tubules in outermost layer. ×220.

EXPLANATION OF PLATE 38

Figs. 1–6. *Corvaspis kingi* Woodward, Downtonian, Earnstrey Hall, Shropshire. 1, Fragment of median plate, showing polygonal areas separated by tubercles. ×2, B.U. 718. 2, Ventral median plate, showing polygonal areas separated by faint grooves. ×2, A–T 236. 3, Dorsal median plate, showing fusion of polygonal areas. ×2, A–T 237. 4, Ventral median plate, showing areas of random ornamentation. ×2, A–T 201. 5, Fragment of median plate with little trace of polygonal areas. ×2, B.U. 717. 6, Fragment of median plate showing healed area with random ornamentation. ×3, B.M. P.17038.

Fig. 7. *Traquairaspis campbelli* (Traquair), Downtonian. Natural mould of ventral median plate, showing central synchronomorial unit with random ornamentation, with outer zone of cyclomorial growth. ×2, B.M. P.27380.

Thus it can be seen that what were formerly considered to be three distinct types of growth of dermal plates in the Heterostraci are all related. The most primitive type is that in which independent cyclomorial plates increase in size until they form a complete carapace; the next major stage is where the complete median plate is a single synchronomorial unit, and finally if this unit is acquired at an early stage of life it can become a primordium around which cyclomorial growth can occur until the animal is fully developed.



TEXT-FIG. 7. Ornamentation of pre-oral regions in the pteraspids. *a*, *Pteraspis althi* Stensiö, showing individual synchronomorial units. *b*, *Rhinopteraspis dunensis* (Roemer), showing large single synchronomorial unit. *c*, *Pseudopteraspis elongata* (Zych), showing zones of cyclomorial growth.

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Repositories. A-T., Allen-Tarlo Collection, Reading University; B.U., Geological Department, Birmingham University; B.M., British Museum (Natural History), London.

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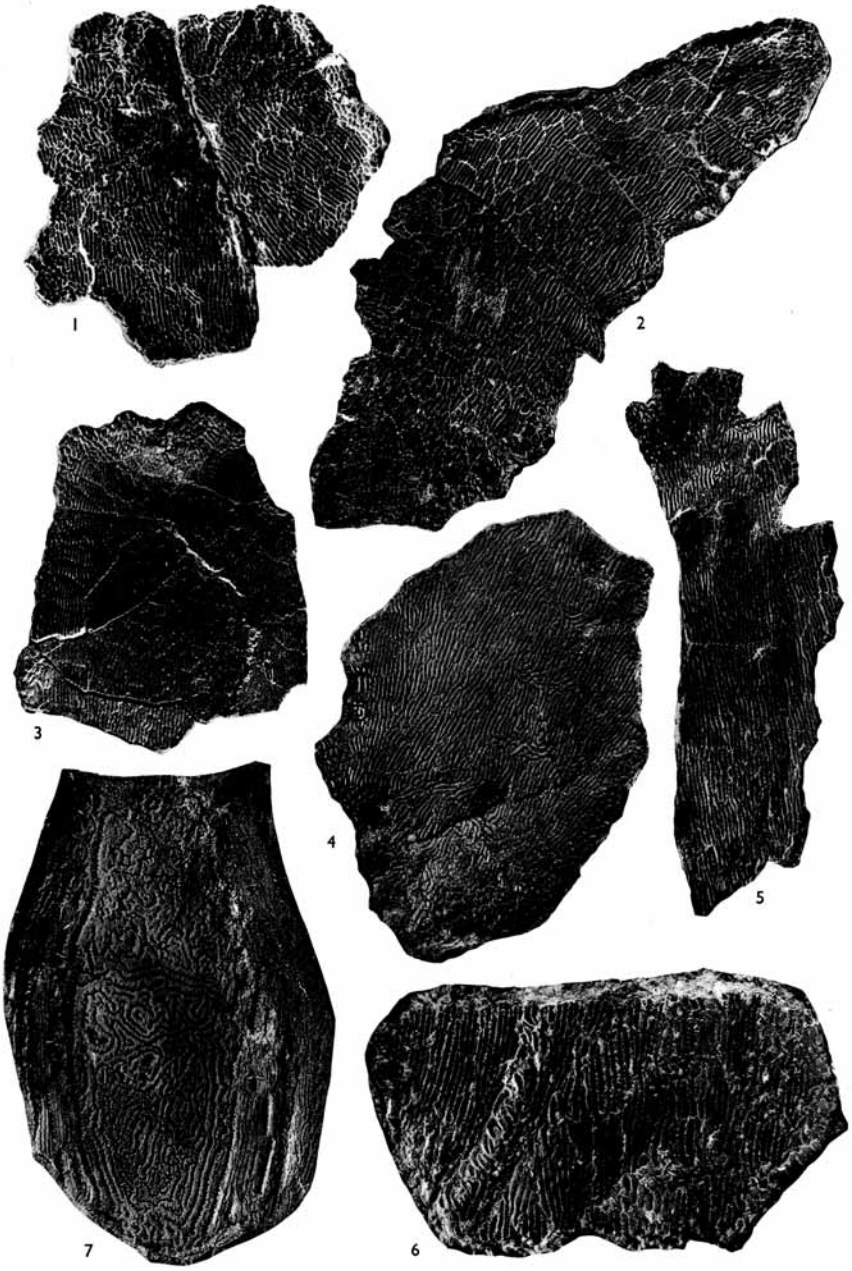

TARLO, *Corvaspis* and *Traquairaspis*