Silurian ostracoderms from Washington Land (North Greenland), with comments on cyathaspid structure, systematics and phyletic position

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The few detached dermal elements recorded here document a new ostracoderm fauna comprising undeterminable species of one anaspid, two cyathaspids and a heterostracan which might have its closest relatives among the pteraspids. This fauna is derived from marine deposits of ultimate Wenlock or possibly Early Ludlow age at the top of the Lafayette Bugt Formation in its type section, in Washington Land, western North Greenland. It is probably equivalent to one of the undescribed faunas known from the *Monograptus testis – M. nilssoni* sequence of the Cape Phillips Formation in the Canadian Arctic Archipelago. Comparative material from Norway and Spitsbergen is considered in this study which prompted general comments on cyathaspid squamation, vestigial fin structure, cyathaspid systematics, their phyletic position relative to the pteraspids, system of stability control in swimming, their habitats and diets.

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The ostracoderm material considered here includes a few detached scutes and a single dermal element referable to the *Heterostraci* and the *Anaspida*, respectively. The specimens were collected by Dr. John M. Hurst during field work carried out in 1976 and 1977 by the Geological Survey of Greenland (GGU) which was aimed at clarifying the distribution, stratigraphy and facies development of the Silurian marine deposits known from previous investigations to occur throughout western Washington Land and Hall Land (see review in Hurst, 1980a, pp. 5–11). Results directly related to this primary aim were published by Hurst (1980a), but observations and collected material have subsequently been discussed in a variety of contexts in other papers by that writer and colleagues (Hurst, 1980b, 1981; Hurst & Kerr, 1982; Hurst & Surlyk, 1982, 1983; Hurst *et al.*, 1983; Surlyk *et al.*, 1980; Surlyk & Hurst, 1984). The collected graptolites were dealt with separately by Bjerreskov (1981) who also reconsidered similar material commented upon by Koch (1920, 1925) and by Poulsen (1934).

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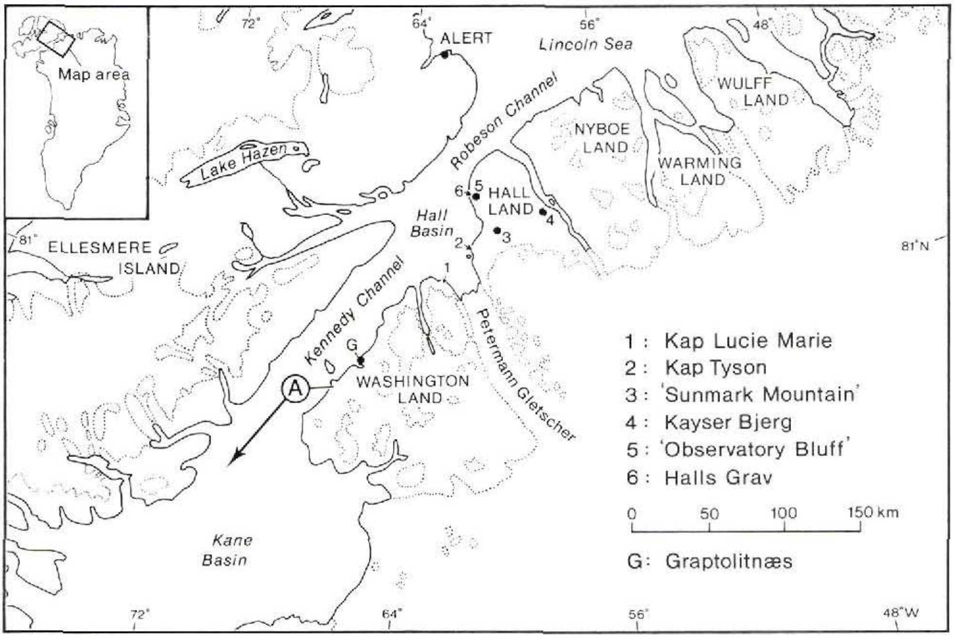
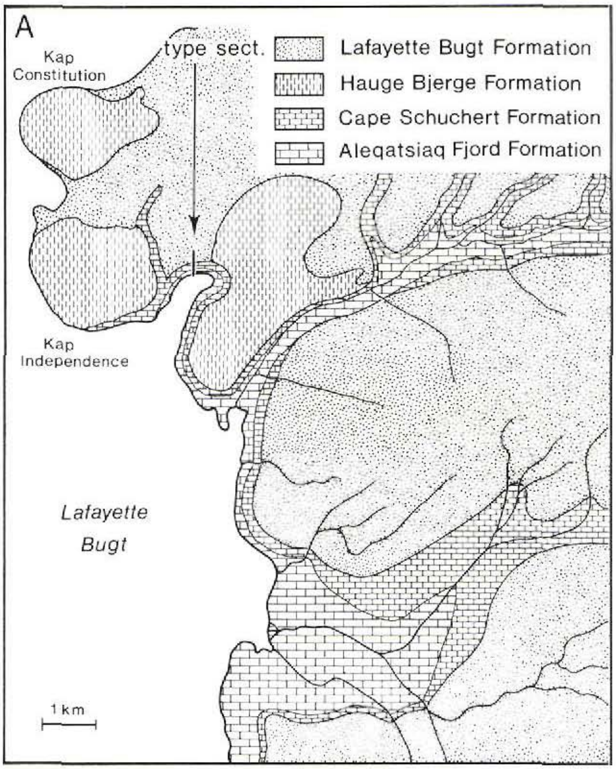




LITHOLOGY: Fig. B →

- ▨ Conglomerate
- ▨ Interbedded calcarenite (50%) and mudstone (50%)
- ▨ Mudstone (Shale)
- ▨ Cherty mudstone
- ▨ Limestone (Lime mudstone)
- ▨ Cherty limestone (nodular)

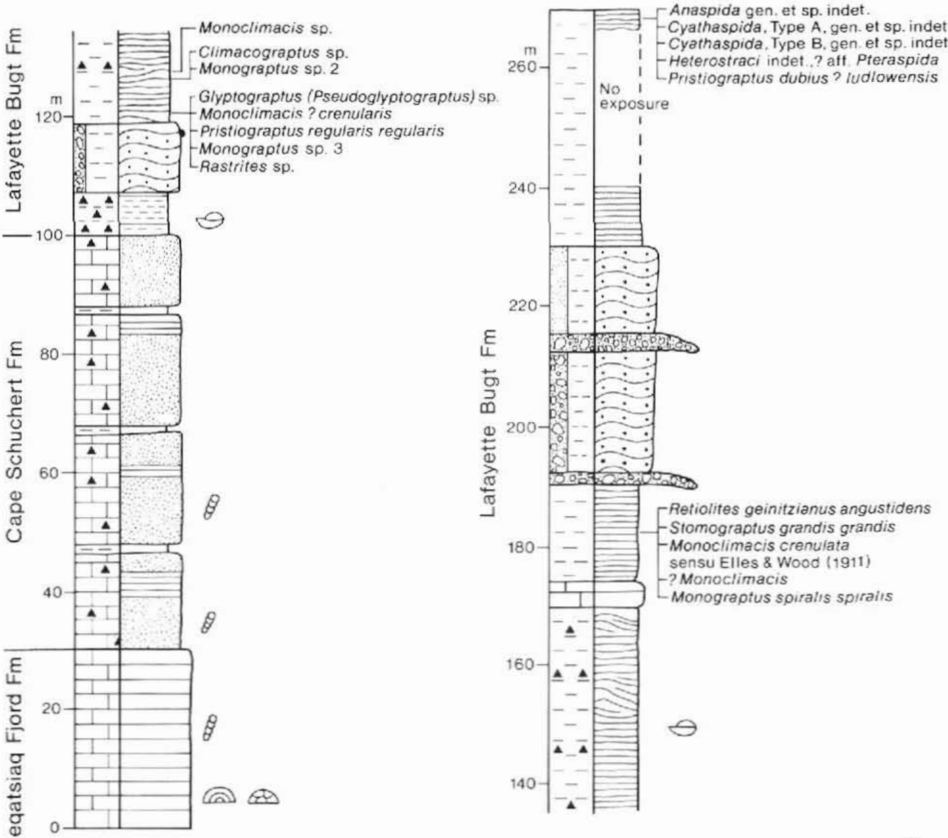
STRUCTURE: Fig. B →

- ▨ Structureless *massive*
- ▨ Structureless massive
- ▨ Even parallel lamination
- ▨ Laminated graded calcarenites alternating with laminated mud
- ▨ Skeletal sand streaks
- ▨ Thin bedded
- ▨ Indistinct parallel lamination
- Stromatoporoids
- Tabulate corals
- Brachiopods
- Echinoderms

Fig. 1. Localities for Silurian and Siluro-Devonian vertebrate fossils in western North Greenland. The anaspid and heterostracans dealt with in this paper were collected in Washington Land from mudstone beds at the top of the type section of the Lafayette Bugt Formation (A); the sedimentary log (B) also shows occurrences of age diagnostic graptolites.

Detached thelodont scales and anaspid remains of Llandovery–Wenlock age are known from deposits at localities 1–4 (see Turner & Peel, this volume). Locality 5, situated about 2 km east of Halls Grav, has yielded considerable assemblages of vertebrate microfossils, probably of Pridoli age. These include thelodonts, cyathaspids, anaspids and acanthodians.

Figs A and B are adapted from Hurst (1980a) and Bjerreskov (1981).



The specimens under consideration occur in the dark grey, but yellowish weathering, fine-grained and finely laminated mudstone constituting the top part of the Lafayette Bugt Formation in its type section, just east of Kap Independence (fig. 1A), and described in Hurst (1980a, pp. 80–82, figs 55, 57, 61 & pl. 2). The approximate position of the fossiliferous beds containing the present ostracoderm specimens and associated graptolites is indicated in fig. 1B.

Freshly exposed specimens have the hard tissue constituents stained deep brown to black whereas in those that have been subjected to weathering, the hard tissues have acquired a whitish colour. External morphological details are generally well preserved (figs 6A–B, 7A–D, 8A–B, 9A). In the cyathaspid scutes even delicate internal structures such as the roughly vertical septae of the cancellous layer are preserved uncollapsed. These can be observed where the calcium carbonate infillings have been removed by the acetic acid digestion used in the preparation of the specimens (figs 7A, D). The high clay and silt content of the surrounding rock made it necessary to adopt a procedure of alternating chemical and mechanical preparation following the principles outlined in Bang (1976, pp. 28–34).

In its 300 m thick type section, graptolites indicate that the Lafayette Bugt Formation ranges from the Middle through Late Llandovery (*Monograptus spiralis* zone), upwards towards the Wenlock–Ludlow boundary and perhaps beyond this into the basal Ludlow (fig. 1B). The stratigraphically youngest graptolites occur at about the same level at the top of the type section as the ostracoderms described in this paper, and apparently represent the Early Ludlow subspecies *Pristiograptus dubius ludlowensis*. Bjerreskov (1981, pp. 6, 31–32, fig. 2D) considered, however, the alternative possibility that the youngest material could be *P. dubius dubius* suggesting a Wenlock age for the host deposits. Whichever of these possibilities proves to be correct, it would appear that the top of the Lafayette Bugt Formation as developed in the type section is chronostratigraphically equivalent to part of the *Monograptus testis – M. nilssoni* sequence of the Cape Phillips Formation of the Arctic Canadian Archipelago (Thorsteinsson, 1958; Thorsteinsson *in* Fortier *et al.*, 1963; Thorsteinsson & Kerr, 1968; Berry & Boucot, 1970) where vertebrate assemblages comprising a variety of ostracoderms have been discovered. Comparison with this and other Canadian material is attempted in a later section.

Four of the available ostracoderm specimens are scutes referable to the Cyathaspida (figs 7A–D, 8A–B). Examination of these, and comparison with other material including articulated specimens from the Palaeontological Museum (Oslo) collections, has stimulated general comments concerning the trunk-tail squamation of the Cyathaspida and several topics significant for vertebrate palaeozoology in general. These are presented below as a prelude to the description of the Washington Land faunal assemblage.

The cyathaspid trunk-tail squamation

According to known articulated material, two largely different trunk squamation categories may be recognised within the Cyathaspida. Each of these categories, referred to in the sequel as the *Anglaspis* and the *Nahanniaspis* categories, respectively, is distinguished by its particular development and arrangement of the constituent scutes.

The first of the categories is typified by the well-known, almost complete and three-dimensionally preserved *Anglaspis heintzi* specimens from the Lower Devonian Red Bay Group of west Spitsbergen on which Kiær (1932) based the now classical restoration, recently slightly amended with respect to features of the tail by Blieck & Heintz (1983, figs 15D–E, 16D). In addition to the median dorsal and ventral series of symmetrical scutes, the trunk squamation in this material consists of very large and high, roughly rectangular dorso-lateral scutes which cover most of the body side, and are joined below by small, roughly rhomboid ventro-lateral scutes (*Sc. d-l, Sc. v-l,* fig. 2A). This material also provided the basis for the likewise classical reconstructions which were published by Kiær & Heintz (1935, figs 50, 53) of the trunk squamation in the other Red Bay Group cyathaspid, *Poraspis* (fig. 3A). These reconstructions, however, remain unconfirmed by articulated material. A squamation essentially of this category is present in the Early Devonian *Allocrytaspis*, according to Denison (1953, pp. 302–304, fig. 61; 1960; 1964, p. 323). It also appears in the Late Silurian – ?Early Devonian *Torpedaspis*, though here minute scutes (termed dorso-laterals by Broad & Dineley, 1973, figs 21, 30, pl. 9, fig. 1) occur inserted between the median dorsal scutes and the very large, high scutes forming the main cover of the trunk side.

Turning to the *Nahanniaspis* category (figs 2B–C) one finds a trunk squamation which, in addition to the dorsal and ventral median series of symmetrical scutes, is mainly composed of two longitudinal series of nearly equally large and high, roughly rectangular scutes: one dorso-lateral and one ventro-lateral series covering the body sides (*Sc. d-l, Sc. v-l,* figs 2B–C). However, between the ventro-laterals and the series of median ventral scutes, small rhombic scutes may in some instances be found, constituting a third longitudinal series (the sub-ventro-lateral: *Sc. sv–l,* fig. 2B) which is occasionally supplemented by even smaller 'extra' scutes of varying number and position (see fig. 2B). These two sorts of scutes are referred to collectively as 'additionals' by Dineley & Loeffler (1976). Finally, in squamations belonging to this category, a rhombically shaped scute (called the paracornual scute in the following: *Sc. pcorn,* figs 2B–C) occurs on both sides of the body, adjacent to and just behind the dorsal shield cornual lobe and other plates here bounding the branchial opening posteriorly.

Squamations of this category are known from articulated material of several genera and species including, besides the Early Dittonian *Nahanniaspis mackenziei* from western North Canada, the likewise Early Dittonian *Dinaspidella* sp. and the Late Silurian *Homalaspidella* cf. *H. borealis,* both from western North Canada (Dineley & Loeffler, 1976), and also *Irregulareaspis hoeli* from the Spitsbergen Red Bay Group (fig. 2C; see also Kiær, 1932; Blieck & Heintz, 1983). It may be added that an incomplete specimen of another Spitsbergen Red Bay Group species, *Homalaspidella nitida,* shows features (*Sc. v-l, Sc. mv,* fig. 7E) indicating that its trunk squamation is also of this category.

With respect to the question of which one of the two categories may possibly be the most specialised, it deserves mentioning that squamations of the *Nahanniaspis* category show peculiarities probably related to, and representing remnants of, vestigial ventrolateral finfolds. In view of this, and a number of other points of difference considered more fully below, it seems reasonable to assume that squamations of the *Anglaspis* category are the more advanced in terms of degree of specialisation.

Remarks on the subfamily Irregulareaspidinae

The fact that the genus *Homalaspidella,* according to the evidence noted above, is now known to have a trunk squamation essentially similar to that of *Irregulareaspis, Dinaspidella* and *Nahanniaspis*, renders untenable the suggestion made by Dineley & Loeffler (1976, pp. 103–104) that a "squamation of this type is possibly restricted to the Irregulareaspidinae".

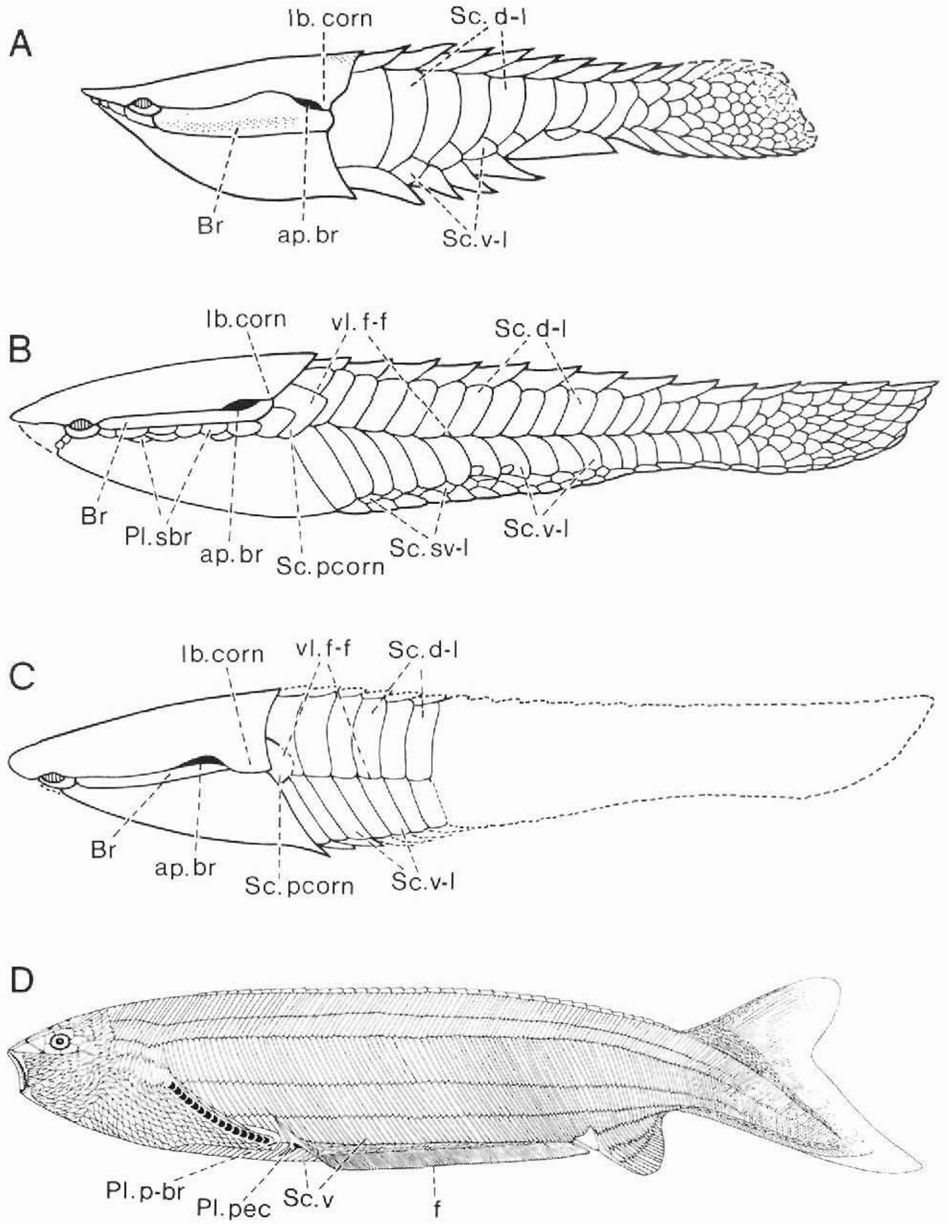


Fig. 2. Squamation patterns of the *Anglaspis* (A) and *Nahanniaspis* (B, C) categories. A, *Anglaspis heintzi*, approx. × 1.3; B, *Nahanniaspis mackenziei*, approx. × 1.7; C, *Irregulareaspis hoeli*, approx. × 0.9. In the *Nahanniaspis* category, vestiges of the ventrolateral fin-folds (*vl. f-f*) appear to be retained in the postcarapacial exoskeleton, as indicated by the conspicuous arrangement of the main constituents, including the paracornual scute (*Sc. pcorn*), and the dorso-lateral and ventro-lateral scutes (*Sc. d-l, Sc. v-l*). These show essentially the same arrangement and relationships as are displayed in the anaspids (here exemplified by D, *Pharyngolepis oblongus*, approx. × 0.7) by the post-branchial plate (*Pl. p-br*), →

This particular subfamily, erected by Denison (1964) and amended by Dineley & Loeffler (1976) to include *Irregulareaspis, Dinaspidella* and *Nahanniaspis*, may perhaps still be accepted as a valid systematic unit. However, evidence for this is narrowing as it is now known that *Nahanniaspis mackenziei* and *Irregulareaspis hoeli* differ fundamentally from each other with respect to features of the branchial plate, as commented upon by Blieck & Heintz (1983, pp. 52–53; see also figs 2B–C of the present paper).

Another significant difference is that the series of small scute-like plates, which in *Dinaspidella* and *Nahanniaspis* (*Pl. sbr,* fig. 2B) occupy positions between the branchial plate and the ventral shield, has no equivalent whatsoever in *Irregulareaspis*, as represented by the articulated specimen of *I. hoeli* (fig. 2C). This is contrary to the assumption made by Dineley & Loeffler (1976, pp. 93, 101).

Cyathaspid squamations and the origin of the Pteraspida

A question still vigorously debated is whether or not the Cyathaspida could possibly include the phylogenetic predecessors of the Pteraspida, as has been maintained by several writers (see Elliott, 1984a, also for references). These writers discussed a broad variety of features, but generally left virtually untouched those related to the squamation as developed in the two groups now under consideration.

Actually known cyathaspid squamations, which particularly with respect to their trunk parts may be considered as highly specialised, have morphologically little in common with the squamation known from a number of representatives of the Pteraspida, including the Early Devonian *Protopteraspis (Simopteraspis) vogti* (figs 9D–E), *Pteraspis rostrata* (White, 1935), *Protaspis dorfi* (Denison, 1953), *P. (Cosmaspis) transversa* (Denison, 1973) and *Lyktaspis nathorsti* (Heintz, 1968). Incidentally, according to the writer's observations on the material, the squamation pattern of *Lyktaspis* differs in certain respects from that shown by the reconstruction made by N. Heintz and subsequently published by Obruchev (1967, fig. 44) and Stensiö (1968, fig. 18A). Regardless of this, in the writer's opinion, it is hardly possible to imagine in which way and by which processes any cyathaspid squamation of the known categories could have been transformed during phylogeny into the squamation pattern of the Pteraspida, as represented by the species just referred to.

There is, of course, no good reason to suppose that the two main categories reviewed above should represent the entire range of variation regarding shape and arrangement of the scutes that may occur within the Cyathaspida. However, as demonstrated by Märss (1977), large and high flank scutes are evidently distinctive parts even of the squamation of *Tolypelepis*, which, according to most writers, is generally regarded as occupying a key position within, and exhibiting characters common to, the ancestral stock of the Cyathaspida. According to this evidence it seems reasonable to assume that, irrespective of in whatever form

the prepectoral plate (*Pl. pec*) and the following series of body scales (*Sc. v*) which extend backwards along the dorsal and the ventral margin of the base of the long ventrolateral fin (*f*).
Figs A and C redrawn from Blieck & Heintz (1983), although C is shown reversed and amended with respect to trunk squamation features, according to the writer's analysis of specimen PMO D 474 (holotype of *I. hoeli*). Figs B and D redrawn from Dineley & Loeffler (1976) and Ritchie (1964), respectively. Other abbreviations: *Br,* branchial plate; *Pl. sbr,* subbranchial plates; *Sc. sv–l,* scutes of subventro-lateral series; *ap. br,* branchial opening; *lb. corn,* cornual lobe of dorsal shield.

the variation might otherwise appear, specialised large and high flank scutes are basic characteristics which are present in cyathaspid squamation as a general feature. If this really reflects the true situation, as the writer tends to believe, then it implies that the Cyathaspida as a whole is entirely disqualified as a potential phylogenetic ancestral group for the Pteraspida.

Finally, it deserves mentioning that the Traquairaspida, judging from what little is known with regard to their squamation (White, 1946; Dineley, 1964), seem to be that group which is likely to contain the most probable candidates for the origin of the Pteraspida. This opinion has also been maintained by Dineley & Loeffler (1976) and others on the basis of other evidence.

Ventrolateral fin-fold vestiges in the cyathaspid exoskeleton

Paired fins have so far never been observed in any heterostracan, but certain parts of the exoskeleton such as the cornual lobes (*lb. corn,* figs 2A–C, 3A) and the cornual plates in cyathaspids and pteraspids, respectively, have been interpreted as remnant structures originating from vestigial ventrolateral fin-folds (Stensiö, 1958, pp. 244, 411–413; 1964, pp. 176, 355–357; see also Jarvik, 1980a, pp. 484, 493–494). Although this interpretation has been considered doubtful by many writers (e.g. Denison, 1964, pp. 325, 349; Miles *in* Moy-Thomas & Miles, 1971, pp. 51–52) it seems, with respect to the cyathaspids, to be perfectly consistent with a variety of features of the *Nahanniaspis* category squamation (see also below) as this is known from *Irregulareaspis, Nahanniaspis* (figs 2B–C) and *Dinaspidella* (Dineley & Loeffler, 1976, fig. 29, pl. 12, figs 1–4). In these cyathaspids, the paracornual scute and the following juxtaposed series of nearly equally large and high dorso-lateral and ventro-lateral scutes (*Sc. pcorn, Sc. d-l, Sc. v-l,* figs 2B–C) mark off a distinct structural line which extends backwards from a position adjacent to and just behind the dorsal shield cornual lobe and other plates that bound off the branchial opening posteriorly, following a more or less zigzag course along the side of the body to reach the tail (*vl. f-f,* figs 2B–C). This peculiar arrangement of the principal constituents of the squamation corresponds in all essentiall respects to that of those plates and scales in anaspids (e.g. *Pterygolepis nitidus* and *Pharyngolepis oblongus*, figs 2D, 6C–E) which form the exoskeleton adjacent to the posterior branchial openings, and in front of and along the entire base of the greatly extended ventrolateral fin (*Pl. p-br, Pl. pec, Sc. v,* figs 2D, 6C–E). Mention may be made also of the resemblance in principle between the features of the cyathaspid squamations under consideration and those of the paired ventrolateral crests developed in various parts of the exoskeleton of the cephalaspids, where these crests extend far back on the body (Stensiö, 1958, 1964; Heintz, 1967). Likewise, they resemble the paired ventrolateral crests present in the adults of many extant and extinct fishes, as demonstrated by Jarvik (1965, 1980a, b).

The paired fins in adult extant fishes, as well as any ventrolateral crests here, are derivatives of paired continuous ventrolateral fin-folds, as is well documented by ontogenetic series (see Jarvik, 1965, 1980a, b; also for extensive references). The corresponding paired appendages structures present in adult extinct fishes no doubt had a similar ontogenetic origin. Thus, there is every reason to assume that the paired fins and/or ventrolateral crests where present in adult extinct agnathans, like the anaspids referred to above and the cephalaspids, were also derived ontogenetically from longitudinal continuous ventrolateral fin-folds (see also Janvier, 1975).

By comparison, the structural peculiarities of the *Nahanniaspis* category squamations considered above, strongly suggest the original presence, course and extension of longitudinal continuous ventrolateral fin-fold rudiments even in the embryos of these cyathaspids. This conclusion tallies with, and provides additional support for, Stensiö's (1958, 1964) interpretation of the cornual lobes as ventrolateral fin-fold derivatives. It is insignificant that the vestiges of the ventrolateral fin-folds in the cyathaspid squamations occupy almost a median position along each side of the body, in contrast to the position in compared extinct agnathans and fossil and recent fishes. The cyathaspid condition probably represents modifications acquired in conjunction with the development of the bulky endoskeleton of the head; these include the formation of a particularly capacious ventral portion and the location of the external branchial opening far up on each side of the carapace.

The apparent absence of vestiges of ventrolateral fin-folds in squamations of the *Anglaspis* category is hardly indicative of a primitive condition. On the contrary, the very high dorsoventral scutes, which in these cyathaspids dominate the adult squamation and cover most of the side of the trunk and part of the tail (fig. 2A), probably result from specialisations related to specific modifications of internal body structures, possibly including rearrangement of the body musculature. Accordingly, squamations of the *Anglaspis* category may be regarded as in some respects more specialised than those of the *Nahanniaspis* category. Regardless of this, the development of the huge dorso-lateral scutes would inevitably have affected other structures, including ventrolateral fin-fold rudiments. The postcarapacial portions of these may have been effectively obscured or entirely suppressed, so as to leave no discernible vestiges in adult squamations of the *Anglaspis* category.

In conclusion, there seems to be good evidence that the cyathaspids, like other lower vertebrates, also had ventrolateral fin-folds as part of their structural inventory (in this context, see also the general discussion by Bjerring, 1984, pp. 23, 26–27). These were obviously vestigial, and like the corresponding structures in extant *Neomyxine biniplicata* (see Jarvik, 1980a, figs 377A–B), apparently lacked the potential to develop into true paired fin structures (see also below). However, structural vestiges in the adult body squamations of *Irregulareaspis, Nahanniaspis* (figs 2B–C), *Dinaspidella* and *Homalaspidella*, suggest that the vestigial ventrolateral fin-folds in cyathaspids also extended far back on the side of the tail, obviously well beyond the position of the anal opening. This pattern is exactly similar to what is known in some other fossil agnathans (see Heintz, 1967) and in many extant and extinct fishes (cf. Jarvik, 1965; 1980b, pp. 116–118).

Stability and swimming in cyathaspids

Cyathaspid squamations of the *Nahanniaspis* category and, to a lesser extent, those of the *Anglaspis* category are reminiscent in several respects of the squamations of such phylogenetically distant forms as recent catfishes of the family Callichthidae (e.g. *Callichthys callichthys, Brochis coeruleus* and *Hoplosternum littorale*). The analogous specialisations could suggest that the relevant cyathaspids had a basically similar swimming pattern and were adapted to living conditions in roughly the same sort of environments as those characteristic of the recent catfishes. The latter also seems to be in accord with the broad similarity in mouth position and other features considered below.

With respect to similarity in swimming pattern, it is evident that this would require the existence of some sort of mechanism in the cyathaspids which could perform the same general functions of stabilising and balancing of the body, both during active swimming and inactive hovering in the water, as carried out by the well-developed paired fins and the dorsal and anal fins occurring in the callichthid species mentioned above. The cyathaspids under consideration apparently lacked the potential to develop true paired fins from their embryonic ventrolateral fin-folds (see above). However, the suggestion made by some writers (e.g. Romer, 1966; Miles *in* Moy-Thomas & Miles, 1971), that cyathaspids were reduced to entirely erratic swimming appears quite unlikely, considering the success with which these agnathans persisted and diversified during the considerable span of time of their existence. The improbability of erratic swimming is also stressed by the well differentiated sensory line system occurring on the carapace, and the nature of the membraneous labyrinth. In cyathaspids, as is well-known, this organ was sufficiently well-developed for the anterior and the posterior semicircular ducts practically always to have left clearly defined impressions upon the internal surface of the dorsal exoskeletal shield.

Poraspis seems to be the only cyathaspid where the minute morphology of the plates forming the boundary of the left and the right branchial openings has been precisely recorded, thanks to the meticulous study made by Kiær & Heintz (1935, pp. 123–125, figs 51–54). The morphology suggests that the left and the right external (efferent) branchial ducts, outside the carapace, extended slightly backwards and outwards as apparently short, tube-like soft tissue structures which opened through apertures in the dermis (*ap.br.ex, d.br.ex,* fig. 3). Such conditions may have been present in cyathaspids in general, and the two tube-like extensions may have served other functions than just that of expelling the exhaled water slightly further backwards on both sides of the body. In the writer's opinion, they were integral parts of the stabilisation and balancing system by which cyathaspids achieved control of pitch, yaw and roll during active swimming and under inactive hovering. Such control was accomplished by intimate and finely balanced interaction between the thrust produced by the tail fin and the largely sideways directed thrusts produced by the controlled expulsion of water from both sides of the branchial apparatus (figs 3B–D).

In addition to the powerful muscular pump necessary for all heterostracans to maintain an adequate water flow through the branchial chambers (e.g. Watson, 1954; Stensiö, 1958, 1964, 1968; Denison, 1964), the suggested system also requires that the external aperture of the tube-like extensions could be adjusted by expansion or contraction to provide the appropriate control of the thrust force of the expelled water stream flowing through the efferent branchial duct. This also means that some sort of simple non-return valve was situated at the outlet of each branchial chamber. Finally, to effectively stabilise and balance the body in the water, appropriate deflection of the left and the right side thrust relative to each other had to be achieved. This means that each external branchial aperture also required a directional control capability (figs 3B–D). These functions could be achieved, for example, in a somewhat similar way to the control of the projecting nasal tubes in many recent fishes, including representatives of the loricarids.

It is appropriate to mention, however, that the soft tissue extensions of the left and the right efferent branchial ducts occupy locations along the anterior margin of the cornual lobes (*lb.corn,* fig. 3A). These cornual lobes are parts of the anterior trunk division of the exoskeleton and may in part correspond to derivatives of the paired ventrolateral fin-folds incorporated in the zonal divisions of the cranio-thoracic shield in various cephalaspids (Stensiö, 1958). Consequently, in *Poraspis* and other cyathaspids, the cornual lobes and the adjacent

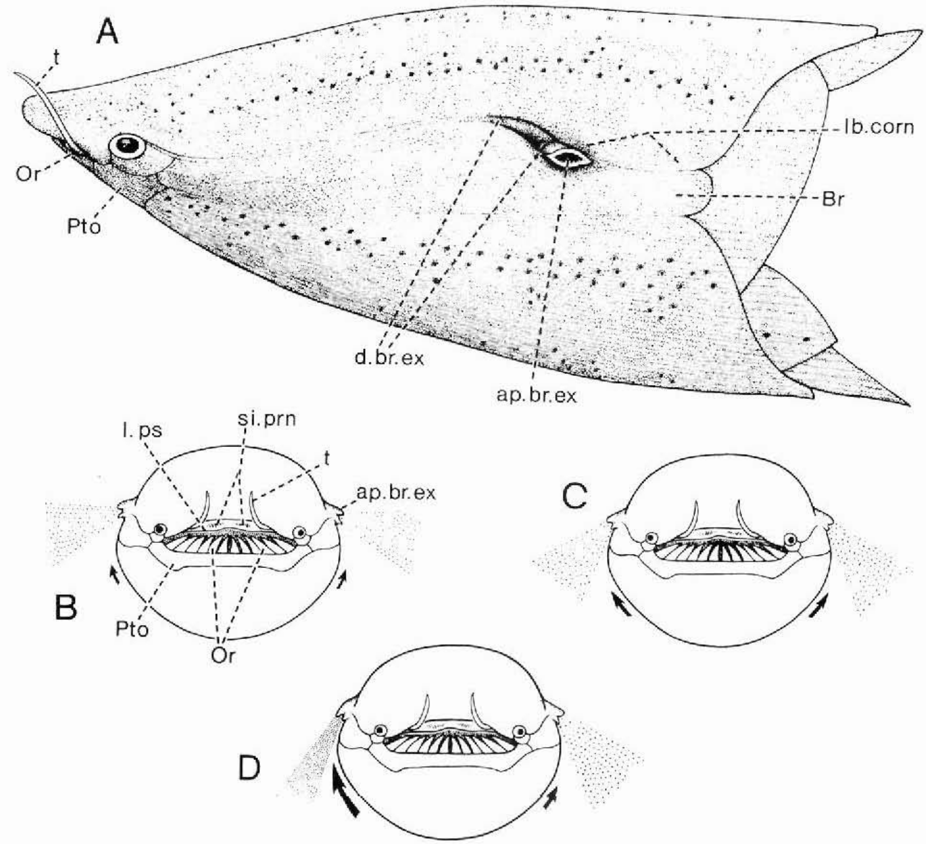


Fig. 3. A, reconstruction of *Poraspis* cf. *P. polaris*, approx. × 3. Features of the exoskeleton surrounding the branchial opening on each side of the carapace, suggest that the left and right efferent branchial ducts were extended externally by a soft tissue, tube-like structure (*d.br.ex*). Each tube may have terminated in a nozzle (*ap.br.ex*) capable of regulating the pressure and directing the thrust of the exhalant water stream. B–D illustrate this schematically showing the specimen in anterior view. Interaction between the left and the right side thrusts could thus have achieved stabilising and balancing functions (indicated by arrows) similar to those provided by the pectoral fins in fishes. Drawings based on figures in Kiær & Heintz (1935) and Blieck & Heintz (1983).

Other abbreviations: *Or*, oral plates; *Pto*, post-oral plate; *l.ps*, palato-subnasal lamina; *si. prn*, prenasal sinus; *t*, barbels.

parts of the branchial plates (*Br*, fig. 3A), as well as related endoskeletal and soft tissue structures (including the extensions of the efferent branchial ducts), were also served by basically the same components of the nerve and circulatory systems as those known in the cephalaspids. Thus, the tube-like extensions of the efferent branchial ducts in cyathaspids could be specialised sections of the paired ventrolateral fin-folds. This, in its turn, would explain the derivation of the muscular material that would of necessity be associated with these soft tissue tubes, and which would also be in accord with their assumed role as integral functional parts of the stabilisation and balancing system in these agnathans.

Judging from figured pteraspid material showing features such as the position, shape and size of the branchial opening in the carapace (e.g. White, 1935, 1950, 1961; Stensiö, 1958, 1964, 1968), a similar stabilisation and balancing system, as now suggested for the cyathaspids, could have been present in the pteraspids. In this latter group, the adjustable external soft tissue branchial apertures may have had a different shape and the system was perhaps refined by intimate interactions between the thrust from the expelled water stream and the sweptback, wing-like, lateral protrusions of the cornual plate situated on each side of the carapace, just posterior to the branchial opening.

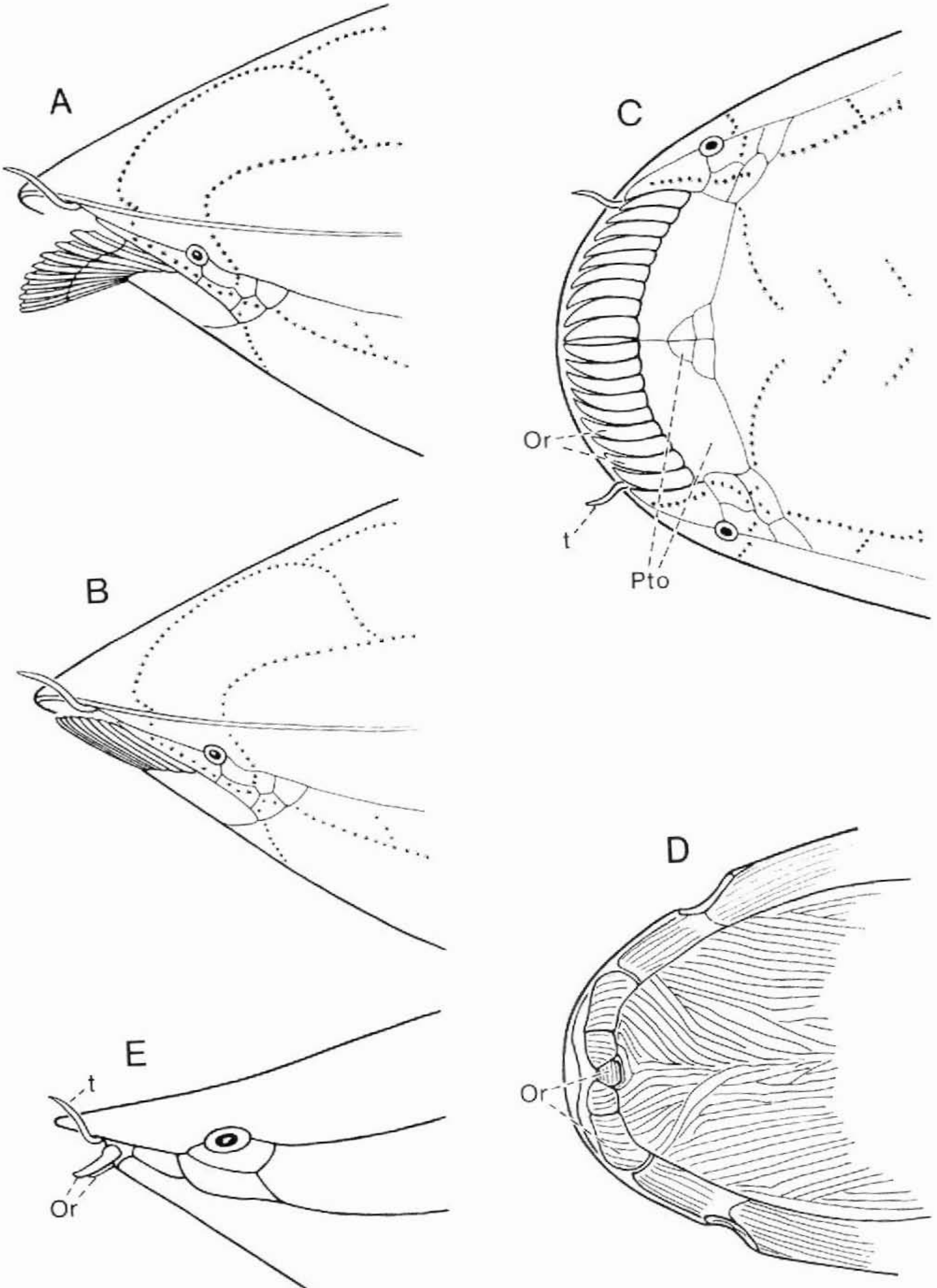
It is possible that systems similar to those considered for the cyathaspids and the pteraspids occurred commonly among the heterostracans as a whole. This possibility is clearly worth consideration since existing alternative explanations (e.g. Denison, 1971) fail to adequately explain how the representatives of this large group of agnathans, existing from the Ordovician and into the Devonian, mastered some of the most crucial problems related to their obviously successful life in the aquatic medium.

Cyathaspid habitats and diets

Cyathaspids were probably a well differentiated group with respect to both mode of life and choice of habitat (Denison, 1964; Dineley & Loeffler, 1976), although the majority of them probably preferred shallow water environments. Some may have been adapted to a benthonic life in shallow water, as has been assumed, for example, for the ctenaspids, where the club-like body-shape suggests partial burial in the bottom sediment, with their terminal, transverse, slit-like mouth acting as a trap for small organisms (Dineley, 1976). In contrast to such comparatively inactive forms, fusiform cyathaspids with a trunk-tail squamation of the *Nahanniaspis* or *Anglaspis* categories, were probably fairly active and perhaps adapted to similar life conditions as those of the recent Callichthidae, as suggested above. If so, the cyathaspids now under consideration lived in environments with abundant vegetation of algae. The cyathaspids make their first known occurrence at the Llandovery–Wenlock boundary in marine environments where algae are known to have been in existence and well diversified from the Early Palaeozoic (Wray, 1977). In such circumstances, it is reasonable to assume that a significant part of the feeding activity of some cyathaspids could have been browsing upon algal vegetation, in similar fashion to the omnivorous recent catfishes referred to above. Such algal vegetation with its associated semi-microscopic epifauna and adhering animal detritus would have provided these cyathaspids with a rich and balanced diet.

The assumed mode of feeding and choice of food for cyathaspids of this type seem to be in perfect accord with the subterminal mouth and the general character of their jaw apparatus, as known from *Allocrytaspis laticostata* and *Anglaspis heintzi*, respectively (fig. 4). These

Fig. 4. The cyathaspid oral apparatus in *Allocrytaspis laticostata* (A–C) and *Anglaspis heintzi* (D–E). The multiple, slender and elongated oral plates in *Allocrytaspis* are shown in extended (A) and in retracted positions (B, C, lateral and ventral views, respectively). Scissor-like movements between the oral plates served to cut the supposed food of algal vegetation and transmit it into the mouth cavity. In *Anglaspis*, the oral apparatus consists of a few larger plates shown tentatively restored in a much flattened specimen, viewed ventrally (D). When extended (E) these plates may have acted as a scraping device. Figs A–C based on Denison (1960, 1964); D–E on Heintz (1962) and Blieck & Heintz (1983). *Or,* oral plates; *Pto,* post-oral plates; *t,* barbels.


A
C
Or
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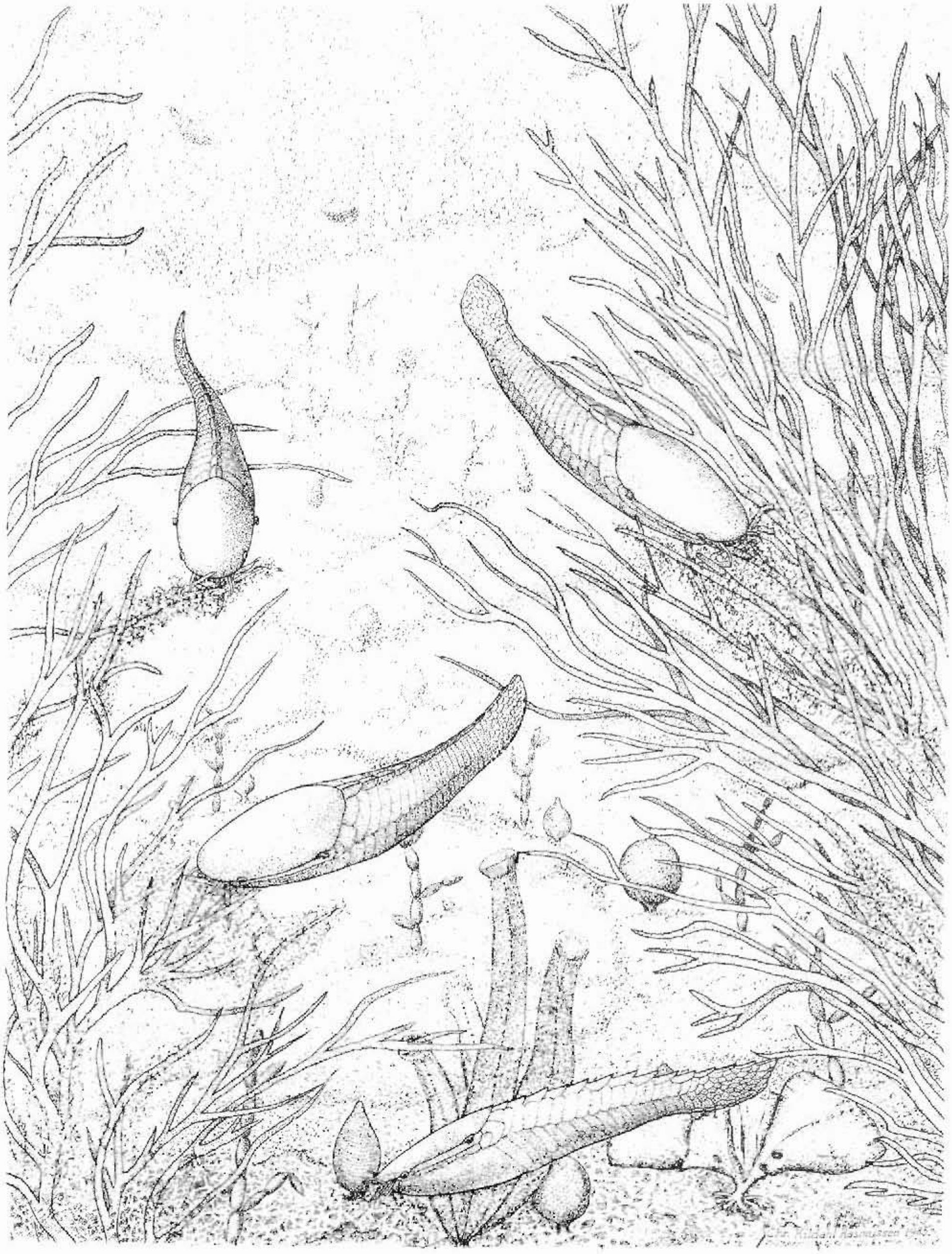


Fig. 5. Feeding cyathaspids, represented by *Nahanniaspis mackenziei*. The reconstruction assumes that the oral apparatus in this species was largely similar to that of *Allocrytaspis*.

two forms differ from each other with respect to number, size and shape of the constituent oral plates (figs 4A–E), but essentially similar jaw constructions are known from certain pteraspids (Kiær, 1928; White, 1938, 1968; Heintz, 1962; Stensiö, 1958, 1964, 1968). The mode of seizing and transmitting the food into the mouth in the cyathspids may also have been largely like that of these pteraspids, whose jaw apparatus presumably acted in much the same general way as that of the recent myxinoids (Janvier, 1974; Jarvik, 1980a). According to Janvier, these particular pteraspids may have been necrophagous, instead of having subsisted mainly on scooped-up detritus or on food particles filtered from the water (White, 1961, 1968; Heintz, 1962). This necrophagous diet could, however, hardly have been coped with by the evidently much weaker jaw apparatus in the cyathaspids; there is, moreover, no evidence to suggest that cyathaspid oral plates could retract far backwards into the mouth as interpreted in the pteraspids (Janvier, 1974, figs $2B_{1\text{-}2}$, D; see also comments in Jarvik, 1980a, p. 502). Cyathaspids may have been able to pick up selected food particles from the bottom, as suggested by Denison (1961). However, such particles would probably have been merely additions to their main diet of algae, for the browsing of which their jaw apparatus seems particularly well suited. The likely workings of the constituent oral plates are briefly outlined and illustrated in figs 4 & 5.

The parallels in terms of environment and diet postulated above may suggest that the cyathaspids under discussion also resembled recent catfishes in possessing some sort of sensory barbels situated in the immediate proximity of the prenasal sinus and the mouth, as has been assumed in other contexts by various writers, including Stensiö (1958, 1964, 1968), Janvier (1974) and Dineley (1976).

Description of the fossil material

The Washington Land ostracoderm specimens now under consideration are all from GGU sample 216789 (Lafayette Bugt Formation type section, Kap Independence, Washington Land; figs 1A–B) and have been given MGUH. VP. numbers referring to the catalogue of the vertebrate palaeontological collection in the Geologisk Museum (University of Copenhagen) where the figured specimens are deposited. Material figured in this paper includes also articulated anaspid, cyathaspid and pteraspid specimens (prefix PMO) belonging to the Paleontologisk Museum, Oslo. The classification adopted in the following description and discussion is essentially that outlined by Jarvik (1980a, pp. 443–446).

Cyclostomata

Cephalaspidomorphi

Anaspida gen. et sp. indet.

This single detached dermal element (MGUH. VP. 3233; figs 6A–B) demonstrates the presence of a representative of an ostracoderm group previously reported from somewhat older marine Silurian deposits (uppermost Llandovery – lowermost Wenlock; fig. 1, locality 2) in western North Greenland by Norford (1972, pp. 21, 31; see also Bendix-Almgreen, 1976, p. 538) and now recognised in samples from the younger Silurian deposits in Hall Land

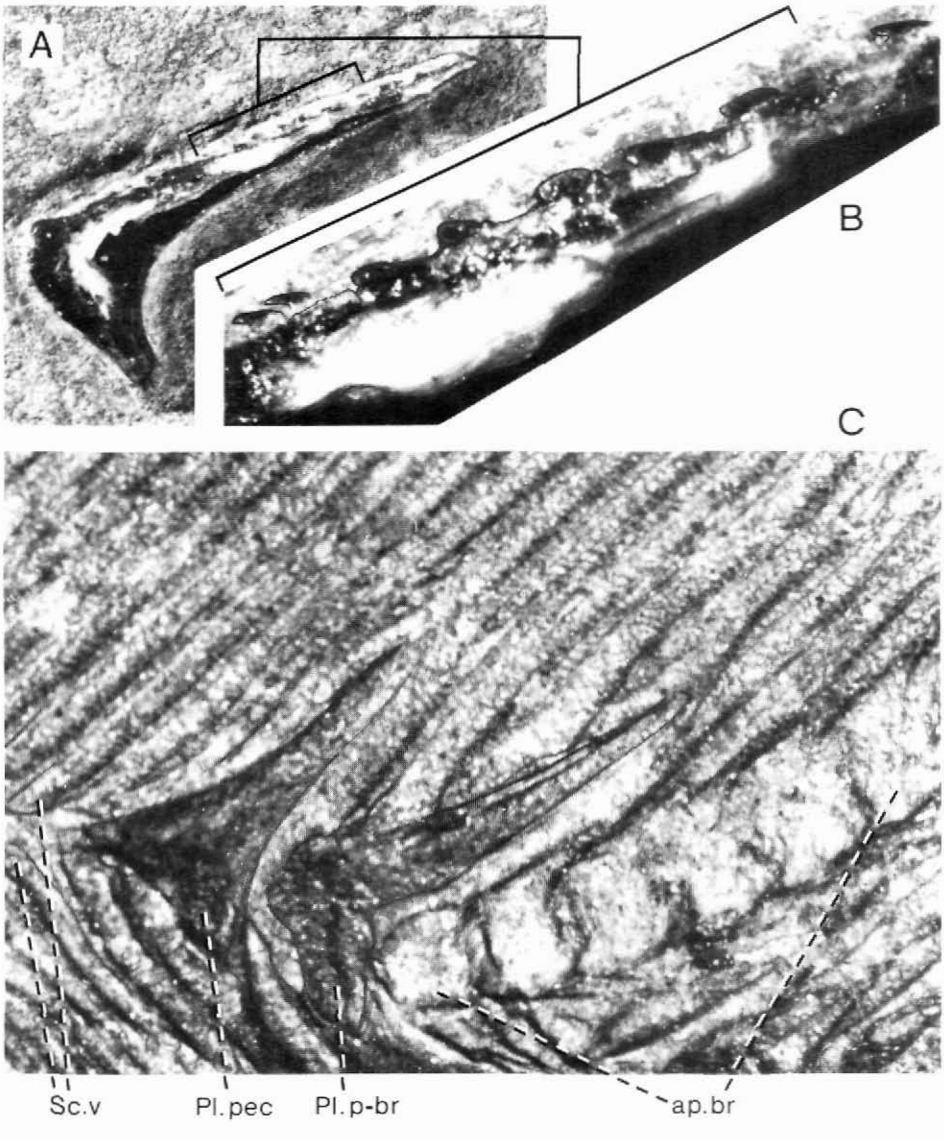
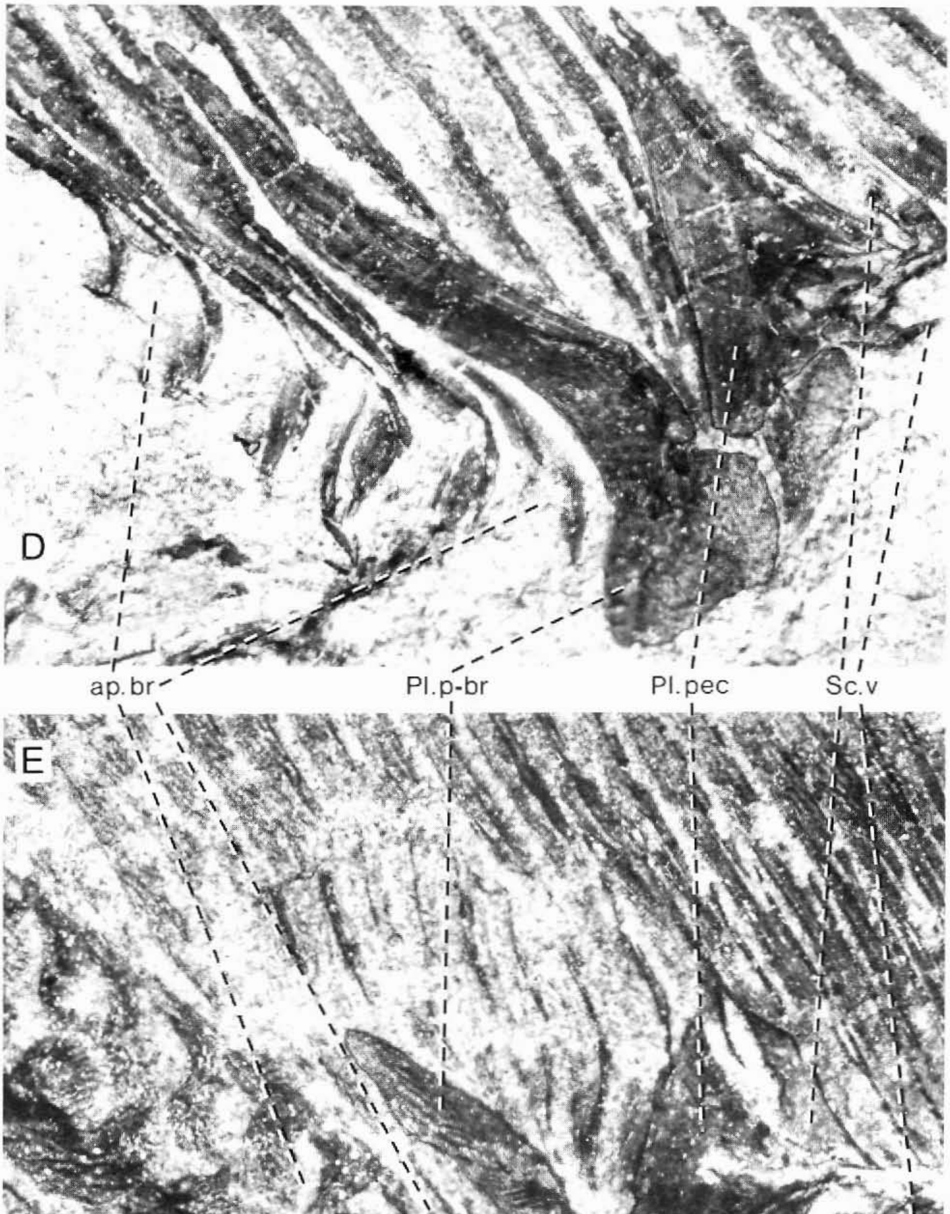


Fig. 6. A–B, *Anaspida* gen. et sp. indet., MGUH. VP. 3233, post-branchial plate of the left side seen in medial view (A, approx. × 9.6) and detail (B, approx. × 38.5) to show blunt to pointed dentine crest protruding from the posterior edge of the largely unexposed external surface. C–E, parts of articulated anaspids showing the post-branchial plate (*Pl. p-br*), as positioned relative to the posterior branchial apertures (*ap. br*), and to the prepectoral plate (*Pl. pec*). This latter is situated in front of the long ventrolateral fin (not preserved in these specimens) and the series of body scales (*Sc. v*) extending along the dorsal and ventral margin of the fin base. C, D, *Pterygolepis nitidus* (Kiær), PMO E 1149 (paratype) & E 0394; E, *Pharyngolepis oblongus* Kiær, PMO E 1038 (paratype); all from Rudstangen, Ringerike, Norway. Specimens photographed in alcohol, approx. × 9.6.


D
ap. br
Pl. p-br
Pl. pec
Sc. v
E

(fig. 1, locality 5; Bendix-Almgreen, unpublished observations; see also Bendix-Almgreen & Peel, 1974; Bendix-Almgreen, 1976; Turner & Peel, this report).

The specimen under consideration is shaped almost like a hockey-stick (fig. 6A) and is to some extent reminiscent of the so-called post-cephalic rods of *Lasanius problematicus* (Traquair, 1899; Parrington, 1958, fig. 3) from Ludlow deposits of South Scotland (principally in the Lesmahagow region; for stratigraphy see Westoll, 1958, p. 239). This similarity does not, however, extend to detailed features which indicate that the small dermal bone mainly displays its smooth medial side, though part of its originally exposed and ornamented surface can be observed along one margin. The ornamentation seems to consist of oval to elongate, strongly convex and entirely smooth tubercles, some apparently tapering to a point at one end (fig. 6B). On the medial side, a distinct but narrow groove-shaped concavity extends from the expanded area of the bone along the entire length to the tip of its major rod-like portion (fig. 6A).

Judging from its shape, proportions and other features there can be little doubt that this particular exoskeletal element corresponds to the post-branchial plate (= prepectoral plate: Stensiö, 1958, 1964) of the well-developed exoskeleton occurring in the few anaspid species known from articulated material. These include *Pterygolepis nitidus* (figs 6C–D), *Pharyngolepis oblongus* (figs 2D, 6E), *Rhyncholepis parvulus* (Kiær, 1924; Stensiö, 1958, 1964; Ritchie, 1964) and *Birkenia elegans* (Heintz, 1958). At least the three former of these species are derived from deposits which, according to Bockelie (1973; see also Märss, 1982), may be placed in the Late Wenlock and Early Ludlow and, consequently, are largely contemporaneous with those yielding the specimen under discussion. This post-branchial plate occupied a position on the left side of the body. It is with respect to its general proportion and its long, slender, rod-like portion, developed more like the post-branchial plate in *Rhyncholepis parvulus* and *Birkenia elegans* (Kiær, 1924, fig. 36; Heintz, 1958, fig. 4c) than that of *Pterygolepis nitidus* or *Pharyngolepis oblongus (Pl. p-br,* figs 6C–E). However, it appears to differ from the four species just referred to (see Gross, 1938 and figs 6C–E) and also, perhaps, from *Saarolepis oeseliensis* (Gross, 1958, 1968; Martinsson, 1966; Mark-Kurik, 1969; Märss, 1982) of the Wenlock to Ludlow, in terms of its exposed surface ornamentation, as far as this can be discerned. Its ornamentation might be more reminiscent of that carried by the scutes of the undetermined anaspid described and figured by Gross (1958) from the *Beyrichienkalk* erratics of North Germany. However, the degree of the similarity and its significance, for example, in terms of relationships, is perhaps not determinable even after direct comparison between the German material and the present specimen. Incidentally, such comparison would require considerable additional preparation of the post-branchial plate from Greenland.

Pteraspidomorphi
Heterostraci

Leaving aside the still poorly known but probable astraspid representative *Palaeodus* from the Lower Ordovician Glauconitic Sand of Estonia (Ørvig, 1958), this major group of ostracoderms makes its first well documented occurrence in the early Middle Ordovician (Ritchie & Gilbert-Tomlinson, 1977; Ritchie, 1985). In the writer's opinion, it cannot possibly include the form *Anatolepis*, known from Late Cambrian and Early Ordovician material and considered by various writers to be a vertebrate (for alternative interpretation and full references see Peel, 1979; Peel & Larsen, 1984; Turner & Peel, this report).

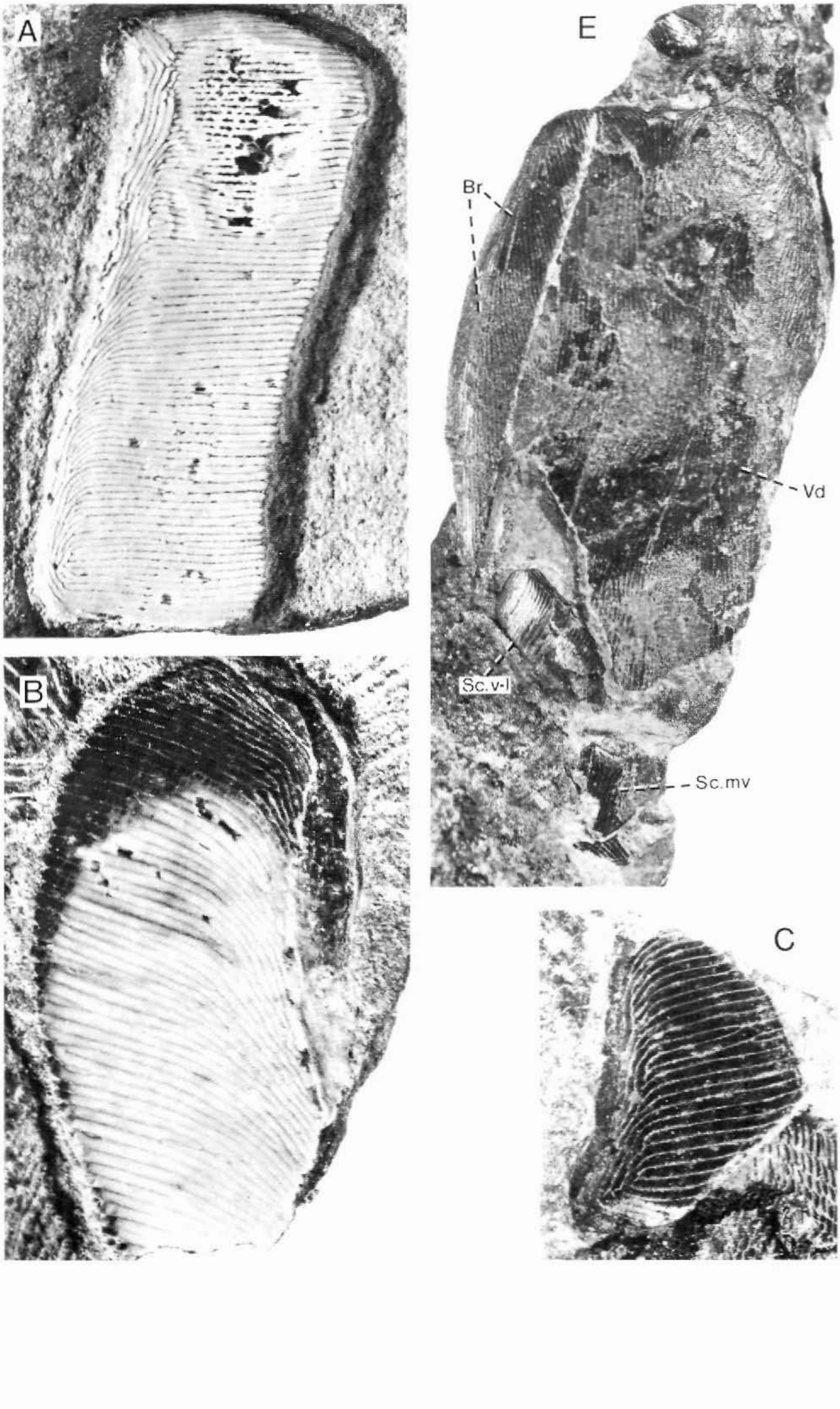
Heterostracans are represented by a mere five detached scutes in the Lafayette Bugt Formation material. However, by virtue of their ornamentation, one can recognise no less than three distinct types among these few scutes; each type probably representing a distinct though not determinable genus and species. Two of these types can be classified clearly enough among the Cyathaspida. The third type is reminiscent of scutes of the Pteraspida, and perhaps could pertain to an early representative of this group.

Cyathaspida, Type A, gen. et sp. indet.

The three scutes (MGUH. VP. 3229–3231; figs 7A–D) dealt with here can hardly have been derived from the trunk-tail squamation of a single specimen, and present no definite evidence indicating the nature of the squamation in its entirety in this indeterminable cyathaspid. Thus, it is not possible to determine, if the squamation was anything like one of the two main categories so far recognised within the cyathaspid group (see above). However, comparison in terms of their general shape (figs 7A–B) shows that two of the scutes under consideration may have belonged to the series of dorso-laterals in a squamation of the *Anglaspis* category or, alternatively, to the series of dorso-laterals and/or ventro-laterals in one of the *Nahanniaspis* category. The third scute (fig. 7C), judging from its shape, could be part of either the series of ventro-laterals as developed in a squamation of the former of the two categories, or it could have occupied a position in the caudal part of either of them.

The three scutes are fairly thin structures. The areas once overlapped by adjacent scutes are narrow, corresponding to conditions generally shown by laterally situated scutes in cyathaspid squamations including those of *Homalaspidella nitida* (fig. 7E), *Poraspis* sp. (Kiær & Heintz, 1935, pp. 108–118, figs 45–49), *Allocrytaspis utahensis, A. laticostata* (Denison, 1953, figs 61, 65B; 1960, fig. 123; 1964, fig. 96), *Torpedaspis elongata* (Broad & Dineley, 1973, fig. 23, pl. 10, fig. 1), *Pionaspis amplissima, Dinaspidella* sp. and *Nahanniaspis mackenziei* (Dineley & Loeffler, 1976, figs 28, 35, pl. 9, fig. 5; pl. 12, fig. 4).

The ornamentation in all three scutes is composed of fine (5–7 per mm), smooth and slightly convex to flat dentine ridges (figs 7A–D) which mainly extend antero-posteriorly and protrude to form the serrated posterior scute edge. Close to the anterior edge of the exposed portion, however, the ridges show a general tendency to coalesce into groups as they change direction; each group comprises several dentine ridges which coalesce to form a single ridge extending for a short distance roughly parallel with the anterior scute margin (figs 7A–C). In these features of ornamentation, the scutes under consideration are most similar to, though still distinguishable from, scutes of *Nahanniaspis mackenziei*, whereas they show nothing resembling the tuberculation occurring on the dentine ridges of scutes of *Allocrytaspis laticostata*. Neither is there anything similar to the numerous separate and minute denticles clustered along the anterior border in scutes of *Pionaspis amplissima* (and apparently similarly in scutes of *Torpedaspis elongata*) or the generally distinctly separate dentine ridges extending dorso-ventrally along the entire anterior border of the exposed portion in scutes of *Poraspis* sp., species of *Anglaspis* (Gross, 1961, pp. 90–93, figs 5G–H), *Homalaspidella nitida* (fig. 7E), *Tolypelepis undulata* (Märss, 1977) and in the scute considered below as *Cyathaspida*, Type B, gen. et sp. indet. (figs 8A–B).


A
E
Br
Vd
Sc.v-l
Sc.mv
B
C

Sensory line pores were detected in one of the present scutes (*p.s*, fig. 7D). The same specimen, lacking some of the exposed surface with its ornamentation and hard tissues below, has been prepared by acetic acid digestion. This disclosed certain semi-microscopic features showing that the internal structure is like that generally met with in the cyathaspid exoskeleton (e.g. Gross, 1961, fig. 6; Denison, 1964, figs 100–102). To be more explicit, the apparently thin basal layer supports the roughly vertical walls of the well-developed (and here uncollapsed) cancellous layer (*cav*, fig. 7D) which is followed upwards by a comparatively thick layer of hard tissue that possibly represents the so-called reticular layer, but everywhere is seen to be intimately contiguous with the hard tissue constituting the superjacent dentine ridges (fig. 7D). The scalloped edges of these later ridges are reminiscent, for example, of those shown by the dentine ridges of *Anglaspis* (Gross, 1961, figs 5G–K) and leave only a narrow slit for the opening outwards of the intercostal grooves (*i.g*, fig. 7D) which appear oval in transverse section.

In the absence of thin sections of the present material, no definitive histological comparison can be made with the exoskeleton of other cyathaspids. However, it may be mentioned

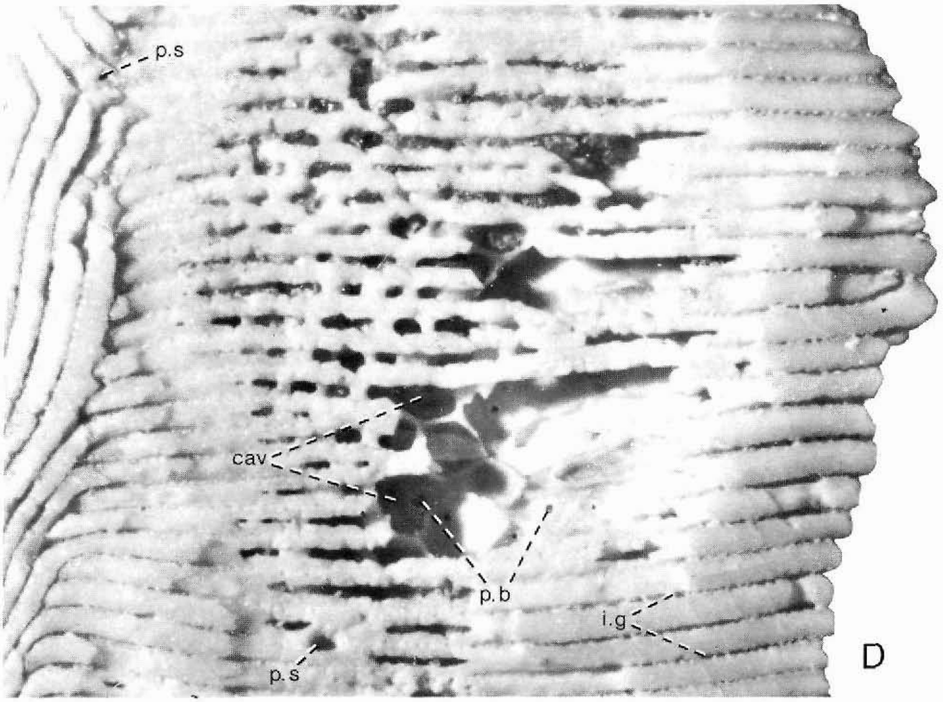


Fig. 7. A–D, *Cyathaspida* gen. et sp. indet., Type A. Three scutes all shown in superficial view. A, D, MGUH. VP. 3229, approx. × 8 and × 32 respectively; B, MGUH. VP. 3230, approx. × 8; C, MGUH. VP. 3231, approx. × 8. E. *Homalaspidella nitida* (Kiær), PMO D 148, paratype, approx. × 5.3, Ben Nevis Formation, *Ctenaspis* horizon, Ben Nevis, south-west slope, Spitsbergen.

Br, branchial plate; *Sc. mv*, scute of median ventral series; *Sc. v-l*, scute of ventro-lateral series; *Vd*, ventral shield; *cav*, cancellous layer cavities; *i.g*, intercostal grooves; *p.b*, apertures in basal layer; *p.s*, pores of sensory canal system.

that, with the exception of the apparently thin basal layer, the dimensions shown by the various layers relative to each other in the present material, are particularly reminiscent of those known from *Vernonaspis sekwiae* as figured by Denison (1964, fig. 100C). The similarity might not be entirely fortuitous; other evidence suggesting derivation of the scutes from a representative of this genus is considered below.

Cyathaspida, Type B, gen. et sp. indet.

The single scute (MGUH. VP. 3232, figs 8A–B) now under consideration, to judge from its general shape in comparison with scutes of the articulated material reviewed above, may once have occupied a position in the series of dorso-laterals as developed in a squamation of the *Anglaspis* category. Alternatively, it could have belonged to either the series of dorsolaterals or of ventro-laterals in a squamation of the *Nahanniaspis* category.

This thin, high and short scute has narrow overlapped areas, similar to the Type A scutes described above and those that occupy lateral positions in the large majority of known cyathaspid squamations. Above all, it is distinguished by features of its ornamentation.

As shown by figs 8A–B, the ornamentation is composed of smooth, flat to slightly convex dentine ridges and flat, polygonal dentine patches all combining into a distinctive ornamental pattern. Several dorso-ventrally extending dentine ridges, located anteriorly, occupy about one third of the entire exposed portion. These ridges are joined towards one end along a zigzag line by the strongly incurving proximal parts of the dentine ridges of the horizontally directed series. Presumably somewhat similar conditions occurred at the other end of the imperfectly preserved scute. The majority of the horizontally directed dentine ridges (3.5–4 per mm) are slightly curved or entirely straight in their course, but all ridges of this kind extend to, and partake in the formation of, the coarse, but poorly defined serration along the posterior edge of the scute. A zone of dentine patches which show considerable variation in both shape and size (figs 8A–B) is conspicuously intercalated between the series of dorso-ventrally extending dentine ridges, and the horizontally directed ridges.

Sensory line pores occur on the scute (*p.s*, fig. 8B) which, from features discernible on fracture surfaces examined under the binocular microscope, appears to have a comparatively deep, well-developed cancellous structured layer and, external to this, a thin layer apparently formed largely of the hard tissues of the dentine ridges. The sharp, almost contiguous edges of the latter leave the intercostal grooves to open outwards through extremely narrow slits (fig. 8B).

The scute under consideration differs entirely in all essential features of its ornamentation from the broadly similarly shaped Type A scutes of the present material (figs 7A–B) as well as from the ornamentation shown by similarly shaped scutes of *Poraspis* sp., *Allocrytaspis laticostata, A. utahensis, Torpedaspis elongata, Pionaspis amplissima, Dinaspidella* sp., *Nahanniaspis mackenziei*, species of *Anglaspis* (for references, see above) and *Homalaspidella nitida* (fig. 7E). It also appears to be entirely different with respect to both shape and ornamentation from the single, detached scute known of *Tolypelepis leopoldensis* (Loeffler & Jones, 1977, pl. 80, fig. 4). On the other hand, its ornamentation resembles that shown by scutes of *Tolypelepis undulata* which, according to Märss (1977, figs 9A–D), belong to the series of dorso-laterals. It is difficult to decide from the information published by Märss whether the scutes just referred to, in contrast to other scutes of *T. undulata* and the tessera-

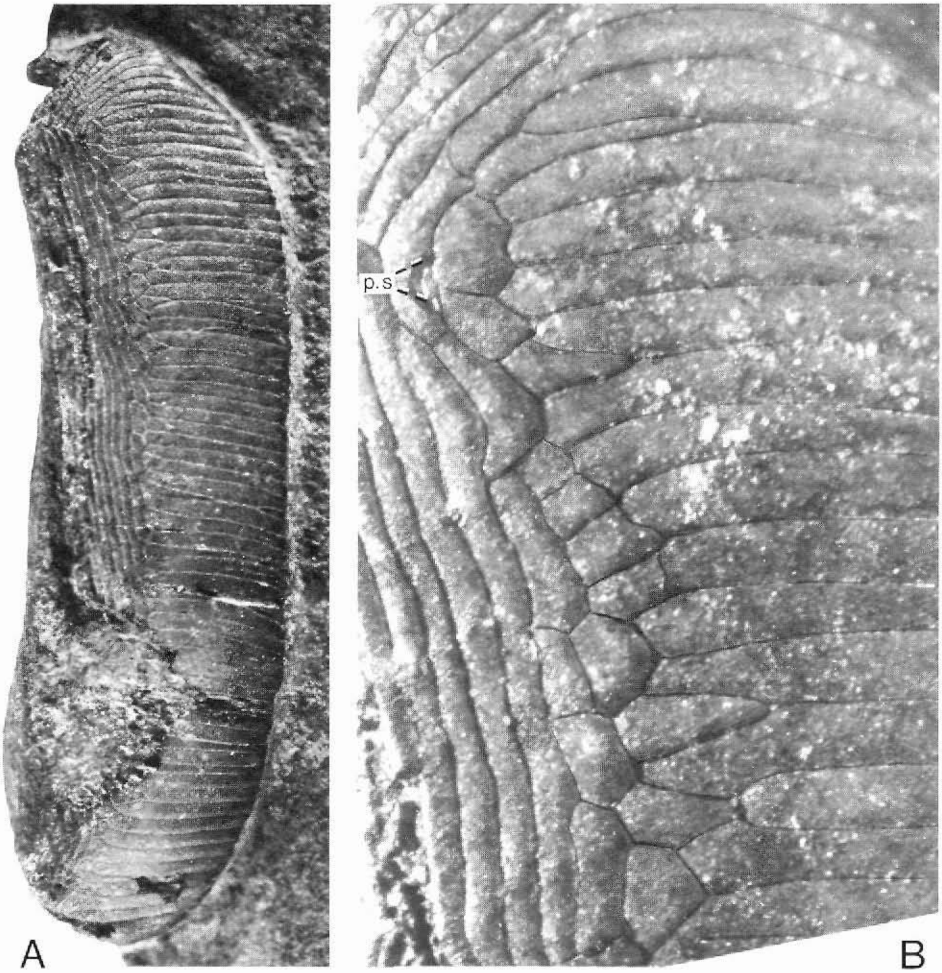


Fig. 8. *Cyathaspida* gen. et sp. indet., Type B. MGUH. VP. 3232. A, scute in superficial view, approx. × 8; B, detail of same to show variation in shape of dentine patches intercalated between the series of vertically and horizontally directed dentine ridges, approx. × 32. *p.s,* pores of sensory canal system.

like units constituting the shields and the plates of its carapace, have flat or merely moderately convex dentine ridges and patches which are of equal height. This seems to be the case, judging from the published figures, and may imply a high degree of similarity between the two forms. It is not known if such similarities in ornamentation have much significance in terms of cyathaspid generic and specific interrelationships. It may be, however, that the present scute was derived from a genus and species closely related to *T. undulata,* which occur in younger Silurian deposits in the Baltic area (see Märss, 1982, p. 101).

It deserves mention that the present scute is also reminiscent of *T. undulata* as figured by Märss (1977, figs 4, 12) in such other features as the well-developed, deep cancellous layer, and the thin superficial layer apparently mainly formed of hard tissues of the dentine ridges.

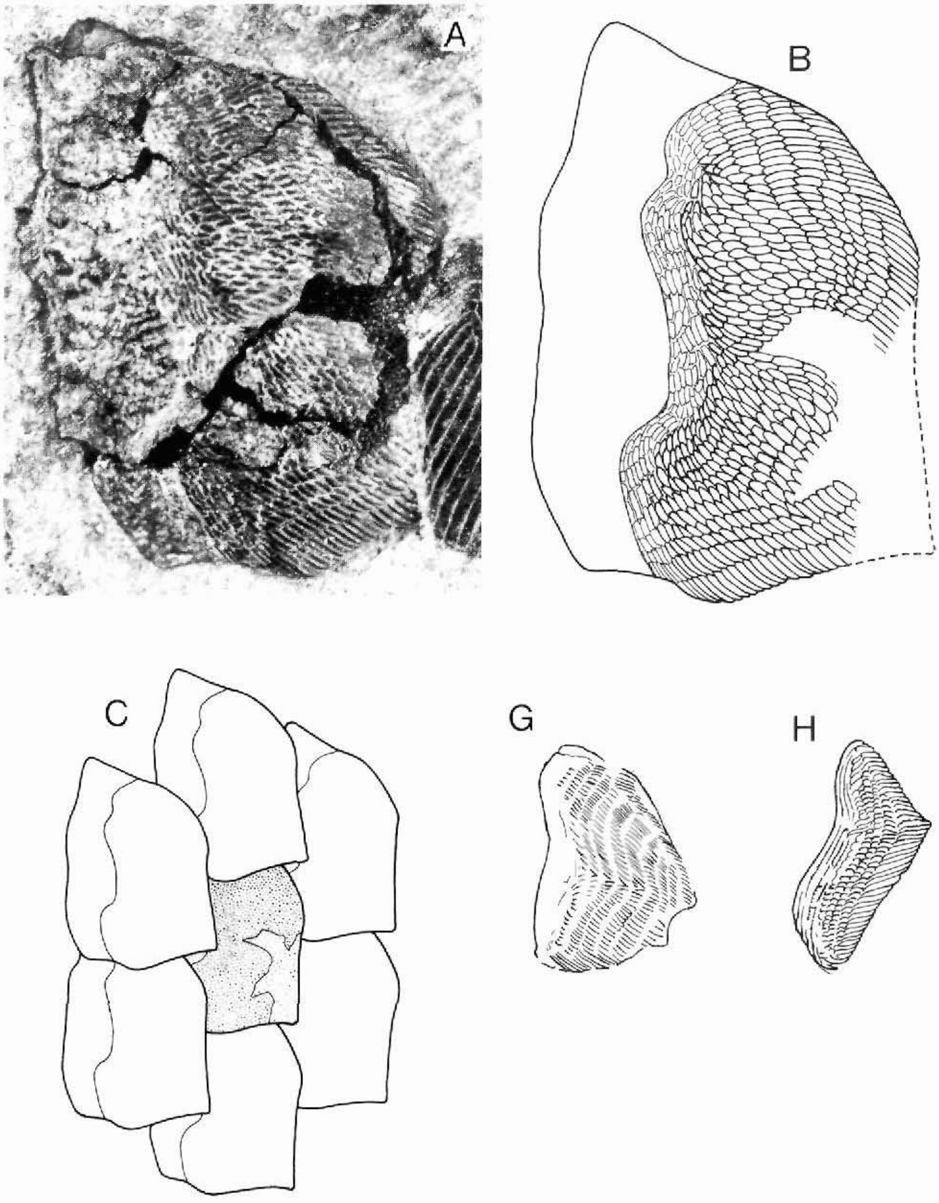
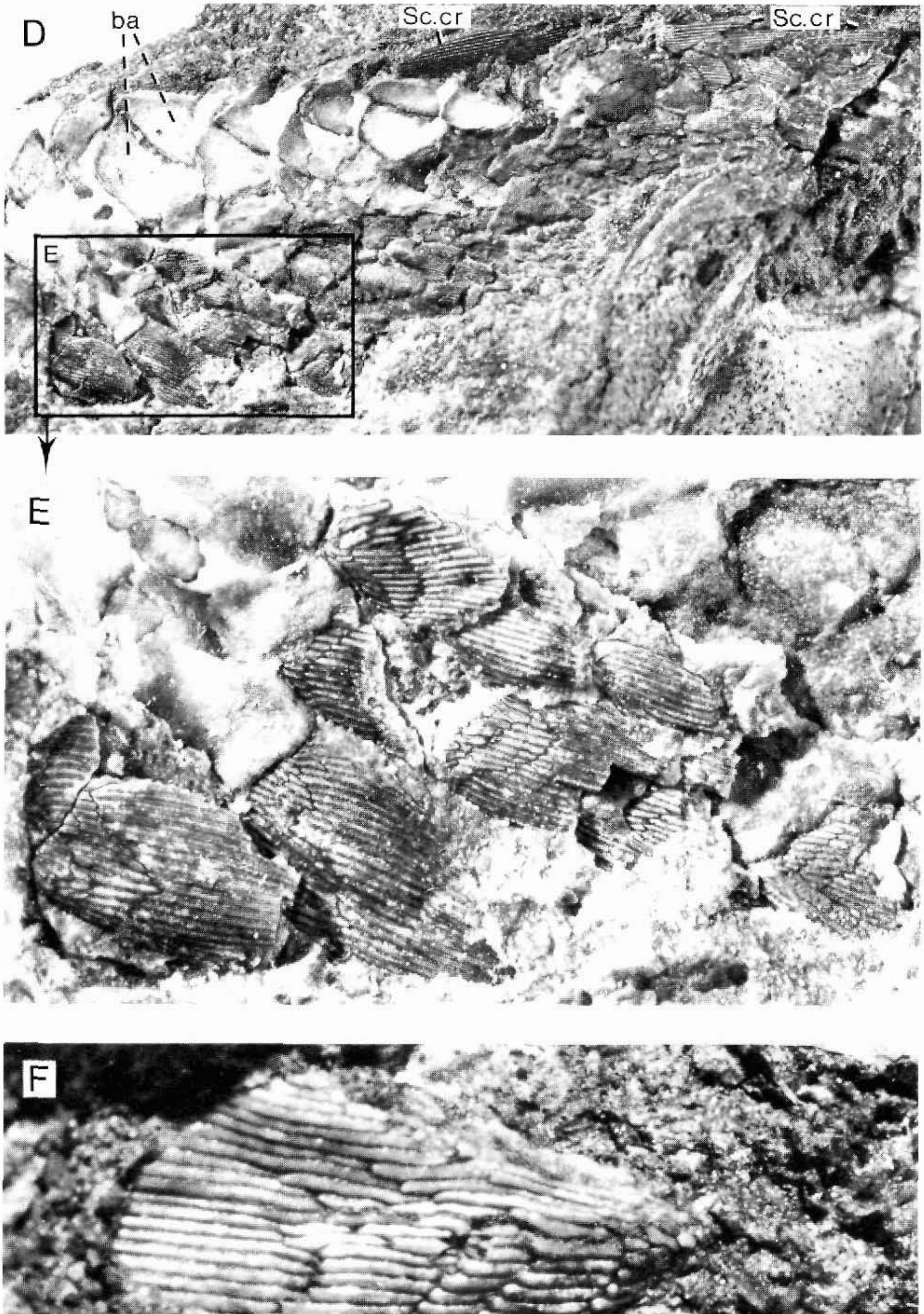


Fig. 9. A–C, *Heterostraci* indet., ? aff. *Pteraspida*, MGUH. VP. 3234. Detached imperfectly preserved scute shown in superficial view as exposed (A) and restored (B), approx. × 8. The scute occupied a lateral position probably in the left side squamation, part of which is tentatively restored in C, approx. × 3. D–E, *Protopteraspis (Simopteraspis) vogti*, articulated trunk-tail squamation (approx. × 3.2) showing median crest scutes and impressions of same (*Sc. cr*) and flank scutes, some displaying their concave, smooth basal face (*ba*), others their superficial ornamental dentine ridge patterns seen enlarged in E, approx. × 9.6; PMO D 4853, Red Bay Group, Ben Nevis, north side, 400 m, Spitsbergen. F, ? *Protopteraspis (Simopteraspis)* sp., detached median crest scute in superficial view, approx. × 19.2. PMO D 437, Red Bay Group, Ben Nevis, north plateau, 600 m, Spitsbergen; same sample containing scute of *Poraspis* sp. figured by Kiær & Heintz (1935). G, *Pteraspis rostrata*, large flank scute, superficial view, approx. × 4. Redrawn from White (1935). H, *Protopteraspis (Simopteraspis) leathensis*, so-called 'double flank-scale', probably from the right side squamation, but lacking the entire overlapped area, superficial view, approx. × 5. Redrawn from White (1950).


D
ba
Sc.cr
Sc.cr
E
E
F

Heterostraci indet., ? aff. *Pteraspida*

The scute (MGUH. VP. 3234, figs 9A–B) now to be dealt with suffered damage when the embedding rock was split in the field. Subsequently it could neither be entirely restored nor fully exposed; its posteriormost portion remains concealed underneath a scute assigned to *Cyathaspida*, Type A, gen. et sp. indet.

The present scute is asymmetrical and roughly pentagonal in shape. It has a slightly concave basal face while, in superficial view, it shows a comparatively broad and thin overlapped area and a moderately convex exposed portion covered by ornamental dentine ridges. These short and keel-like structures are for the main part orientated longitudinally and arranged in concentric chevron-like zones extending parallel to the posterior scute margin (figs 9A–B). However, those dentine ridges which occupy locations just adjacent to the overlapped area tend to form transversally directed series extending parallel to the anterior border of the exposed portion (figs 9A–B). Here, the ornamentation shows distinct abrasion marks which, judging from the otherwise unabraded appearance displayed by the dentine ridges elsewhere, are no doubt primary features formed during life from intimate contact with the protruding edges of scutes lying immediately in front of the present one. Analysis of the abrasion marks suggests an arrangement of the scutes surrounding the present one somewhat like that shown in fig. 9C.

Comparisons show that there is little resemblance between the scute now under discussion and those known from cyathaspid squamations. Neither is there any particular similarity between its ornamentation and that of the median spine-like scute incorporated posteriorly in the dorsal shield of the species *Ariaspis ornata* (Denison *et al.*, 1963, figs 68–69; Denison, 1964, fig. 148) from the Silurian of Canada, or that comparatively much coarser ornamentation shown by the scute referred by Obruchev (1967, pl. 3, fig. 2) to *Putoranaspis dentata* from the Lower Devonian.

The present specimen shows some resemblance to the scute-like units constituting the posterior part of the detached shield considered by Dineley & Loeffler (1976, pp. 146–148, fig. 63) under the designation of *Heterostraci* indet., Type 2. However, the features in question are hardly indicative of any close relationship between them; nor is there any evidence which warrants reference of this scute to the Traquairaspida. Even considering the conditions pointed out by Ørvig (1969, pp. 224–225), it appears that the ornamental dentine ridge patterns exhibited by carapace plates of the traquairaspids (e.g. Dineley & Loeffler, 1976) and by the few scutes known from them (White, 1946; Dineley, 1964) differ in essential respects from that of the scute under discussion.

The scute does show similarity in both shape and ornamentation with scutes from various representatives of the *Pteraspida*, including *Protopteraspis (Simopteraspis) vogti*, and ?*P. (S.)* sp. (figs 9D–F), *Pteraspis rostrata* (fig. 9G; White, 1935, figs 56–62, pl. 27, figs 107–109), *P. (Pteraspis) dairydinglensis* (White, 1961, pl. 39, figs 9–10, 12, 14, 16–18; pl. 40, figs 15, 18–19, 24–25, 27; pl. 41), *P. (Cymripteraspis) leachi* (White, 1961, pl. 45, figs 1–2), *P. (Rhinopteraspis) dunensis* (White, 1938, figs 6–7), *Protopteraspis leathensis* (fig. 9H; White, 1950, figs 10–13, pl. 5, figs 3–5), *Zascinaspis carmani* (Denison, 1960, fig. 141), *Protaspis (Europrotaspis) crenulata* (White, 1961, figs 22–25, pl. 43, fig. 5; pl. 44, fig. 3), *P. (Cosmaspis) transversa* (Denison, 1973, figs 1, 3; concerning the generic affiliation of the various species just referred to, see Stensiö, 1958, 1964; Tarlo, 1961; Denison, 1970; Novitskaya, 1975; Dineley & Loeffler, 1976). It is to some extent even reminiscent of those of *Drepana-*

spis gemuendenensis as described and figured by Gross (1963, figs 7B, 7L, pl. 6, fig. 5; pl. 7, figs 4–5: pl. 9, figs 1, 4) and Lehman (1967, pl. 1; pl. 3, fig. D) inasmuch as scutes of this species also have short, longitudinally directed dentine ridges arranged in concentric chevron-like zones extending parallel to the posterior border. They show, however, nothing like the anterior zone of transversally directed dentine ridge series seen in the present scute. Moreover, the dentine ridges are quite differently shaped in the scutes of *D. gemuendenensis* which, according to Gross (1963, p. 145), have comparatively narrow overlapped areas. Judging from the perfectly preserved scutes of *Psammolepis paradoxa* (Ørvig, 1968, figs 5B–C) and other forms, it seems that narrow overlapped areas are common for scutes of the Drepanaspida which, accordingly, also in this respect are distinguishable from the present scute.

Returning to the Pteraspida, one finds that the scutes of such species as *Pteraspis (Rhinopteraspis) dunensis* and *Protopteraspis leathensis* (White, 1938, 1950) have overlapped areas which in both shape and size are fairly similar to that of the present scute. The ornamental dentine ridge pattern in the Greenland scute is, moreover, particularly similar in several respects to that of scutes of *Pteraspis rostrata, Protopteraspis leathensis* (White, 1935, pl. 27, figs 107–108; 1950, figs 10–14, pl. 5, figs 3–4) and of some of *Zascinaspis carmani* (Denison, 1960, figs 141B,D,G) in which a distinctly delimited zone of transversally directed series of dentine ridges extending parallel to the anterior border of the exposed portion also occurs.

Considered in its entirety, the ornamental dentine ridge pattern displayed by the scute under discussion presents merely a slight variation on the ridge pattern theme which is not only characteristic for the squamation of many pteraspids, but is also encountered in other parts of the dermal skeleton in various pteraspids. The latter include *Zascinaspis carmani, Protaspis (Europrotaspis) crenulata, P. (Protaspis) mcgrewi, P. (Cosmaspis) transversa, P. (Cosmaspis)* sp. and *Lampraspis tuberculata* (Denison, 1953, fig. 84A; 1960, figs 129, 135; 1970, figs 5, 7E–F, 14, 26; 1973, pl. 1, figs 2, 4; White, 1961, pl. 44, fig. 7). Finally, although not entirely exposed, the scute under discussion seems to be shaped, by and large, like the so-called 'double flank-scales' known from some pteraspid squamations (figs 9G–H).

The histology of the present scute remains unknown. However, judging from fracture surfaces inspected at high magnification under the binocular microscope, its internal structure is reminiscent of, for example, *Lampraspis tuberculata* (Denison, 1973, fig. 2C), though the basal layer in this species appears to be thicker than in the present specimen.

It is evident that the present scute is in many respects very similar to scutes of the Pteraspida, and even shows features in common with other parts of the exoskeleton as developed in a variety of representatives of this group. It is quite another matter, however, as to what extent such similarities may justify the inclusion, however provisional, of detached material like this single scute among the Pteraspida. If this is its true systematic association, it means that the scute is perhaps the earliest indication yet known for the occurrence of that heterostracan group.

The Washington Land ostracoderm assemblage and its relationship to Silurian faunas from North Western and Arctic Canada

As noted above, it is particularly appropriate to compare the present Lafayette Bugt Formation assemblage with faunas yielding ostracoderms from deposits at various localities in the Canadian Arctic Archipelago. These include: (1) beds of the *Monograptus testis – M. nilssoni* sequence of the Cape Phillips Formation on Cornwallis and Little Cornwallis Islands (Thorsteinsson, 1958, 1967, 1973; see also Thorsteinsson *in* Fortier *et al.*, 1963; Thorsteinsson & Kerr, 1968); and (2) beds of the Allen Bay Formation on Prince of Wales Island (Turner & Dixon, 1971; Dixon *et al.*, 1972; Thorsteinsson, 1980) and equivalent strata on Somerset Island (Dineley & Loeffler, 1976).

Although these Canadian Silurian vertebrate faunas still await full publication, it has been reported that their cyathaspids include species referable to the genera *Vernonaspis, Archegonaspis, Homalaspidella* and *Anglaspis*, together with other forms said to resemble certain of these genera and others, including *Ptomaspis, Pionaspis, Ariaspis* and *Corvaspis* (Thorsteinsson, 1967, 1973; Turner & Dixon, 1971; Dineley & Loeffler, 1976). With respect to their cyathaspids, these faunas are clearly generically similar to the fauna of the perhaps slightly younger deposits at Beaver River, south-east Yukon (Denison *et al.*, 1963; Denison, 1964; see also Broad & Lenz, 1972; Dineley & Loeffler, 1976, pp. 196–197). With regard to the faunas from the Cape Phillips Formation, this similarity is further emphasised by the presence of a form which Thorsteinsson (1967) considered to be reminiscent of *Tesseraspis denisoni* (Tarlo, 1964) which is also known from the Beaver River fauna. The latter fauna, as well as those referred to above, also shows some similarity to faunas recorded from strata dated as late Silurian or Siluro-Devonian on Somerset Island and Prince of Wales Island (the Cape Storm and the Douro Formations and the lower member of the Peel Sound Formation; Broad, 1973; Broad & Dineley, 1973; Loeffler & Jones, 1976, 1977; Miall *et al.*, 1978; Thorsteinsson, 1980; Elliott & Dineley, 1983; Elliott, 1984a, b), and in Western Yukon (the Gossage Formation) and District of Mackenzie (the Delorme Formation; Broad & Lenz, 1972; Dineley & Loeffler, 1976).

In the context of these Canadian faunas, it is significant to note that the two distinct types of cyathaspid scutes present in the Lafayette Bugt Formation assemblage are clearly distinguishable from species of *Homalaspidella, Pionaspis* and *Anglaspis*, as presently known. These, as well as species of *Corvaspis* and the traquairaspids, likewise known to occur in certain of the Canadian faunas, obviously need no further consideration in the following evaluation:

Cyathaspida, Type A, gen. et sp. indet.

The fact that this type of scute is represented by three of the six specimens from Washington Land possibly suggests that the Type A scutes pertain to the most common element in the original Lafayette Bugt Formation fauna. Thus, it may be proposed that Type A scutes may belong to the most common cyathaspid in Wenlock–Ludlow and younger Silurian faunas in the general area of western North Greenland and northern and Arctic Canada. Such arguments point towards an association of the Type A scutes with the genus *Vernonaspis*, which is represented by several species in all the relevant Canadian faunas and which is also the most widespread and common cyathaspid genus in the Late Silurian rocks of North America in general (see Denison, 1964, p. 368; Dineley & Loeffler, 1976, tab. 1 and fig. 41).

The association of the Type A scutes with *Vernonaspis* is to some extent supported by the fact that several features of the ornamental dentine ridge pattern of the scutes (including the shape and range of size of the dentine ridges, their mode of coalescing and dichotomous branching) are similar to ornamentation on the post-pineal portion of the dorsal shield of, for example, *Vernonaspis major* and *V. epitegosa* (Denison, 1964, fig. 122; Broad & Lenz, 1972, fig. 4). Both these species are also present in the Beaver River cyathaspid fauna where a large proportion of the entire identified and recorded material actually belongs to *Vernonaspis*. Many of the apparently abundant, but detached cyathaspid scutes known from this locality, may also belong to *Vernonaspis*. The entire scute material was, however, dealt with summarily and left totally unfigured by Denison *et al.* (1963, p. 132). The same seems to be the case with respect to all other scute material known of *Vernonaspis* (see Denison, 1964, p. 324).

It is thus concluded here that the *Cyathaspida*, Type A, gen. et sp. indet. should possibly, if not probably, be assigned to *Vernonaspis*. Verification of this, however, requires direct comparison with scute material from species of this genus, and this has not been available to the writer. On account of the wide stratigraphic range of *Vernonaspis* (Late Wenlock to Pridoli) the mere presence of an unidentified species only tentatively assigned to the genus cannot refine available evidence concerning the age of the top part of the Lafayette Bugt Formation in its type section.

Cyathaspida, Type B, gen. et sp. indet.

As discussed above, the single Type B scute might be derived from the squamation of a genus and species closely related to *Tolypelepis*. A close relative of this genus has been reported from the fauna of Late Llandovery or Early Wenlock age from the Cape Phillips Formation (Thorsteinsson, 1967). Species of *Tolypelepis* are also known from Late Silurian deposits elsewhere in North Western and Arctic Canada where the Late Silurian or Early Devonian *Asketaspis interstincta,* believed to be related to *Tolypelepis*, also occurs (Dineley & Loeffler, 1976; Loeffler & Jones, 1977). Species of the genus *Ptomaspis* are also widespread here, and are generally assumed to occupy a position close to *Tolypelepis* in cyathaspid phylogeny. One form reported from the Cape Phillips Formation fauna which is apparently of ultimate Wenlock rather than Early Ludlow age (see below), is said to resemble *Ptomaspis* (Thorsteinsson, 1967, 1973). However, as there is no information available as to the precise affinity of the Type B scute, it cannot contribute any evidence regarding the age determination of the Lafayette Bugt Formation vertebrate bearing beds under discussion.

Heterostraci indet., ? aff. *Pteraspida*

The scute considered here belongs to a heterostracan which might possibly be classified among the Pteraspida. This suggestion may appear more than sanguine, but it is a possibility worth consideration – not least because evidence has been presented by Elliott & Dineley (1983) and Elliott (1984a) that the Canadian Arctic during Late Silurian times may have been an evolutionary centre for the Pteraspida, whose origin and closer relationships to other heterostracan groups remain unclarified as noted above.

This aspect aside, the present scute cannot reasonably be associated with material in any of the faunas reported from the relevant parts of the Cape Phillips Formation and the transition beds between the Allen Bay and Read Bay Formations. Nor is there anything recorded from younger Silurian faunas elsewhere in North Western and Arctic Canada to support or weaken the suggested association of this scute with the Pteraspida. In such circumstances it cannot contribute a more precise age determination of the top of the Lafayette Bugt Formation type section than that available from the graptolites (fig. 1B).

Anaspida gen. et sp. indet.

The detached post-branchial plate proving the presence of an anaspid in the Lafayette Bugt Formation ostracoderm assemblage seems at the moment to be its only element which might have significance in the context of biostratigraphical evaluation.

Within the geographical entity comprising the present-day Canadian Arctic Archipelago and western North Greenland, anaspids are known to occur in the Late Llandovery – Early Wenlock and to persist into the Pridoli (Thorsteinsson, 1967, 1973; Norford, 1972; Bendix-Almgreen, 1976 and unpublished observations). It is, however, remarkable that among the various heterostracan faunas reported from the Canadian Arctic Archipelago, and which are direct relevant in the present context, only one fauna has been reported to include anaspids. This particular fauna is derived from the Cape Phillips Formation and may, judging from the sparse information so far published, be the one which Thorsteinsson (1967) first referred to the Early Ludlow, but subsequently reconsidered as being more likely of latest Wenlock age (Thorsteinsson, 1973, pp. 53–54). In this case, the vertebrate part of this fauna includes, in addition to an anaspid, a variety of cyathaspids (some provisionally referred to *Vernonaspis* or *Archegonaspis,* others said to resemble *Homalaspidella* and *Ptomaspis*), a *Tesseraspis denisoni*-like heterostracan, thelodonts and the form *Pilolepis margaritifera,* supposed to be an early elasmobranch possibly related to the menaspid bradyodonts (Thorsteinsson, 1973).

Even considering the present undetermined status of the anaspid material from both this Cape Phillips Formation fauna and from the present Lafayette Bugt Formation assemblage, the occurrence of these particular ostracoderms might imply that the two vertebrate assemblages are stratigraphically equivalent.

Concluding comments on correlation and age

The evidence of age considered above is admittedly far from conclusive. Neither the cyathaspid scutes nor the scute of the *Heterostraci* indet., ? aff. *Pteraspida* provide any precise information concerning the age of the vertebrate yielding beds of the Lafayette Bugt Formation type section. The occurrences, however, are not out of harmony with the suggested correlation offered by the anaspid. If this suggestion can be accepted, it will place the top of the Lafayette Bugt Formation type section in the ultimate Wenlock rather than in the Early Ludlow. It remains, accordingly, doubtful as to whether or not this type section at all reaches beyond the Wenlock–Ludlow boundary, as Bjerreskov (1981) was inclined to believe.

It deserves notice, however, that the upper age limit of the type section has no consequence with respect to the range in age of the Lafayette Bugt Formation in its entirety. Elsewhere, such as in the reference section at Graptolitnæs located to the north of the type section (fig. 1, locality G), the occurrence of *Bohemograptus bohemicus bohemicus* at a higher stratigraphic level in the formation indicates clearly enough that here it reaches up into the Early Ludlow (Hurst, 1980a, pp. 82–83; Bjerreskov, 1981, pp. 9, 12, 33–34, figs 1, 3).

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