

A NEW AGNATHAN FROM THE LOWER DEVONIAN OF ARCTIC CANADA, AND A REVIEW OF THE TESSELLATED HETEROSTRACANS

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ABSTRACT. A new tessellated heterostracan, *Aporemaspis pholidata* gen. et sp. nov., is described from the Snowblind Bay Formation of Cornwallis Island in the Canadian Arctic Archipelago. Its age is late Lochkovian, and it is thought to be related to other tessellated forms from the Delorme Formation, District of Mackenzie, NWT. Two fragments of armour from the Delorme Formation are tentatively assigned to *Aporemaspis* gen. nov. The known genera of tessellated heterostracans are reviewed, and it is concluded that at present our knowledge of the group is insufficient to support a meaningful classification, although it is clear that the Ordovician genera should not be considered to be heterostracans.

THE rich ostracoderm localities on Prince of Wales, Somerset and Cornwallis Islands in the Canadian Arctic were discovered by the Geological Survey of Canada in 1955 (Thorsteinsson 1958). Further discoveries have since been made and some of the faunas described (Elliott and Dineley 1985, and references therein). Although much of the material remains undescribed, it has already been shown to be of considerable importance to the study of heterostracan relationships, as the area seems to have formed both a centre of origin and a locus of adaptive radiation for several heterostracan groups (Thorsteinsson 1967; Elliott 1984). The specimen described here has been selected because, although incomplete and difficult to assign taxonomically, it is one of the few known examples of an articulated tessellated heterostracan.

The specimen (Pl. 107, text-fig. 2) was collected in 1976 from scree below cliffs of the basal Snowblind Bay Formation on the north shore of Read Bay, Cornwallis Island (text-fig. 1). The locality was originally described by Thorsteinsson (1958) who noted the presence of '*Ctenaspis* n.sp. cf. *C. dentatus*, *Anglaspis* n.sp., *Cyathaspidinae* indet., *Pteraspis* sp. indet. cf. *P. podolica*, shagreen-like scales resembling *Kallostrakon podura*, and indeterminate bones and spines probably of acanthodians'. More recent work on this, and stratigraphically equivalent, localities (Miles 1973; Dineley 1976; Elliott 1983) has resulted in the following faunal list: *Stegobrachiaspis baringensis*, *Unarkaspis schultzei*, *Ctenaspis* cf. *C. russelli*, *Anglaspis* sp., *Weigeltaspis* sp., *Cephalaspis* sp., *Arthrodira* indet., *porolepid* indet., and *Ischnacanthus* sp. The shagreen-like scales reported by Thorsteinsson (1958) are now unfortunately lost; however, Thorsteinsson (pers. comm. 1984) reports that they did not show any resemblance to the specimen described here.

The Snowblind Bay Formation was erected by Thorsteinsson and Fortier (1954) for a body of conglomerate at Read Bay on the east-central coast of Cornwallis Island (text-fig. 1). It grades into the Sophia Lake Formation and forms the top of the thick, conformable succession of Ordovician to Devonian rocks on Cornwallis Island (Thorsteinsson 1980). The vertebrate fauna is dated as Late Lochkovian (Elliott 1984), based on faunal similarities with the upper member of the Peel Sound Formation at Baring Channel on Prince of Wales Island. There, vertebrates were associated with *Pelekysgnathus serratus serratus* (determined by O. H. Walliser; H. P. Schultze, pers. comm. 1976) and other conodonts closely resembling forms found in Upper Lochkovian and Lower to Middle Pragian (Upper Gedinian-Siegenian) strata elsewhere in the Canadian Arctic (Uyeno in Gibling and Narbonne 1977). Although no date is available for the base of the Snowblind Bay Formation, the maximum age for the fauna is limited by the determination of an Early to possibly Middle Lochkovian age for the strata directly below it (Thorsteinsson 1980).

SYSTEMATIC PALAEONTOLOGY

The heterostracans described in this paper are the property of the National Museum of Canada, Ottawa (NMC).

Order HETEROSTRACI Lankester, 1868

Family uncertain

Genus APOREMASPIS gen. nov.

Etymology. Greek *aporema*, meaning doubt or perplexity, and *aspis* meaning shield.

Diagnosis. As for the only species, *Aporemaspis pholidata*.

Aporemaspis pholidata sp. nov.

Plate 107, text-fig. 2

Etymology. Greek *pholis*, meaning scale.

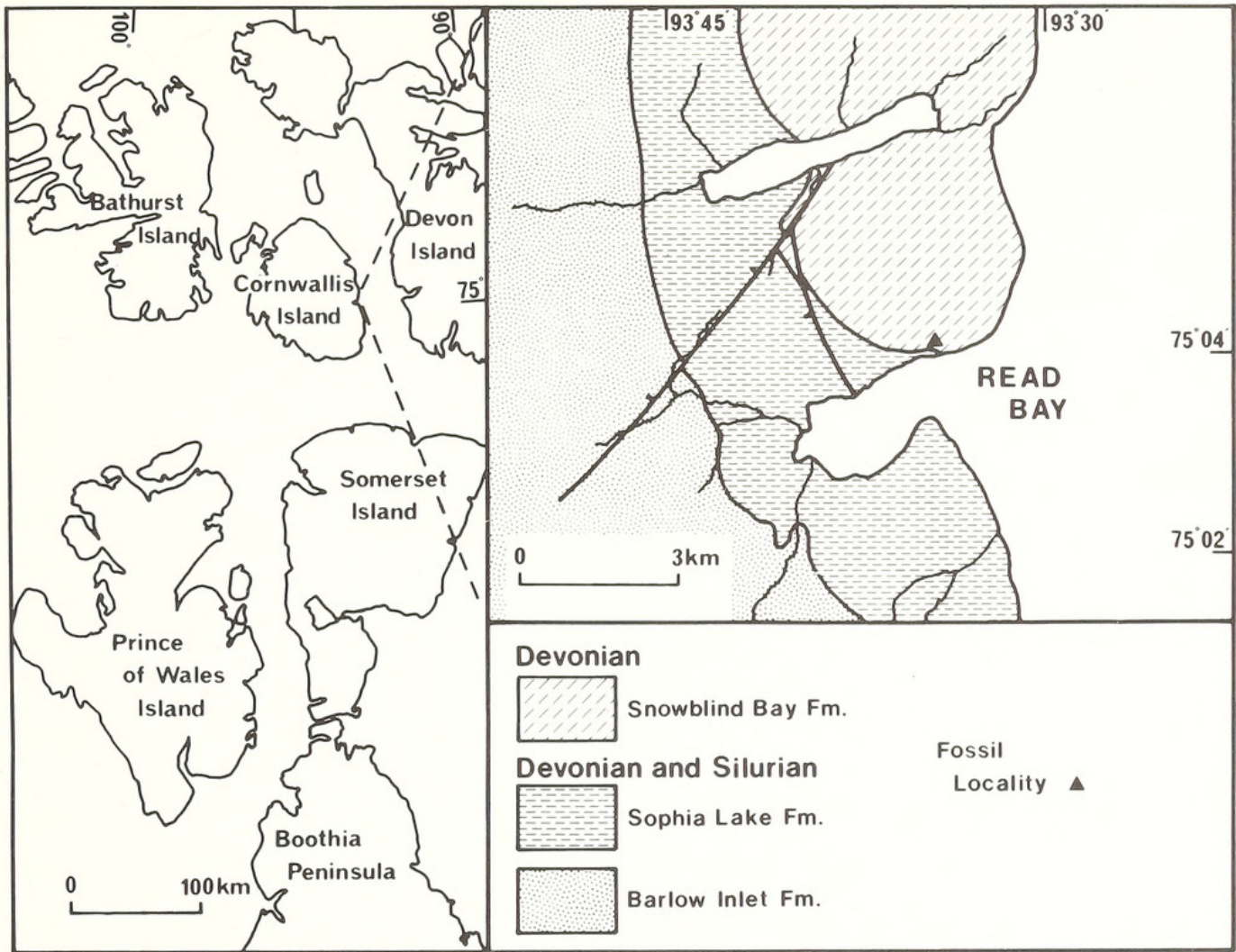
Holotype. NMC 34010, articulated specimen.

Locality. Basal part of the Snowblind Bay Formation on the north shore of Read Bay, Cornwallis Island. 93° 34' W 75° 04' N (text-fig. 1). Locality 42 of Thorsteinsson (1958).

Diagnosis. Cephalothorax elongated and dorsoventrally compressed; tail narrow. Armour composed of discrete elements, 0.5–1.5 mm long and 0.5–1.0 mm wide, the bases of which are normally not fused. Each element typically bears a single ridge of almost equivalent area, the shape of the ridge varying according to the position of the element on the body. Anteroventrally, the ridges are broad, ovoid and flat-topped; laterally, they are more elongated. Posteriorly, on the caudal fragment, elements are associated into lozenge-shaped groups of two or three ridges. This pattern of ridges becomes more regular and symmetrical towards the posterior.

Description. The gross morphology of this unique specimen is difficult to reconstruct as it was separated into two pieces, possibly by the action of predators, prior to burial (Pl. 107, fig. 1). Much of the dorsal surface, all of the left side, and the caudal termination are also missing. The two segments have been rotated slightly in relation to each other; however, the similarity of ornamentation on the broken margins indicates that these come from the same individual. The cephalothoracic segment was at least 70 mm long as shown by the dorsal surface (Pl. 107, fig. 2). Although the left side is missing, the width of the animal anteriorly appears to have been about 40 mm. The posterior segment of the animal has been bent approximately at the point where a change in ornamentation can be seen. This segment is approximately 49 mm long, its maximum width of 20 mm occurs at the anterior end, posteriorly a width of 12 mm is maintained from the bend. It seems, therefore, that in overall dimensions this animal would have been at least 110 mm long with an anterior width of about 40 mm tapering posteriorly to about 12 mm. The specimen is somewhat dorso-ventrally flattened; the distinct dorsal and ventral laminae of the rigid lateral margins suggest that this is a reflection of the original shape of the animal, although it has been accentuated by post-mortem crushing.

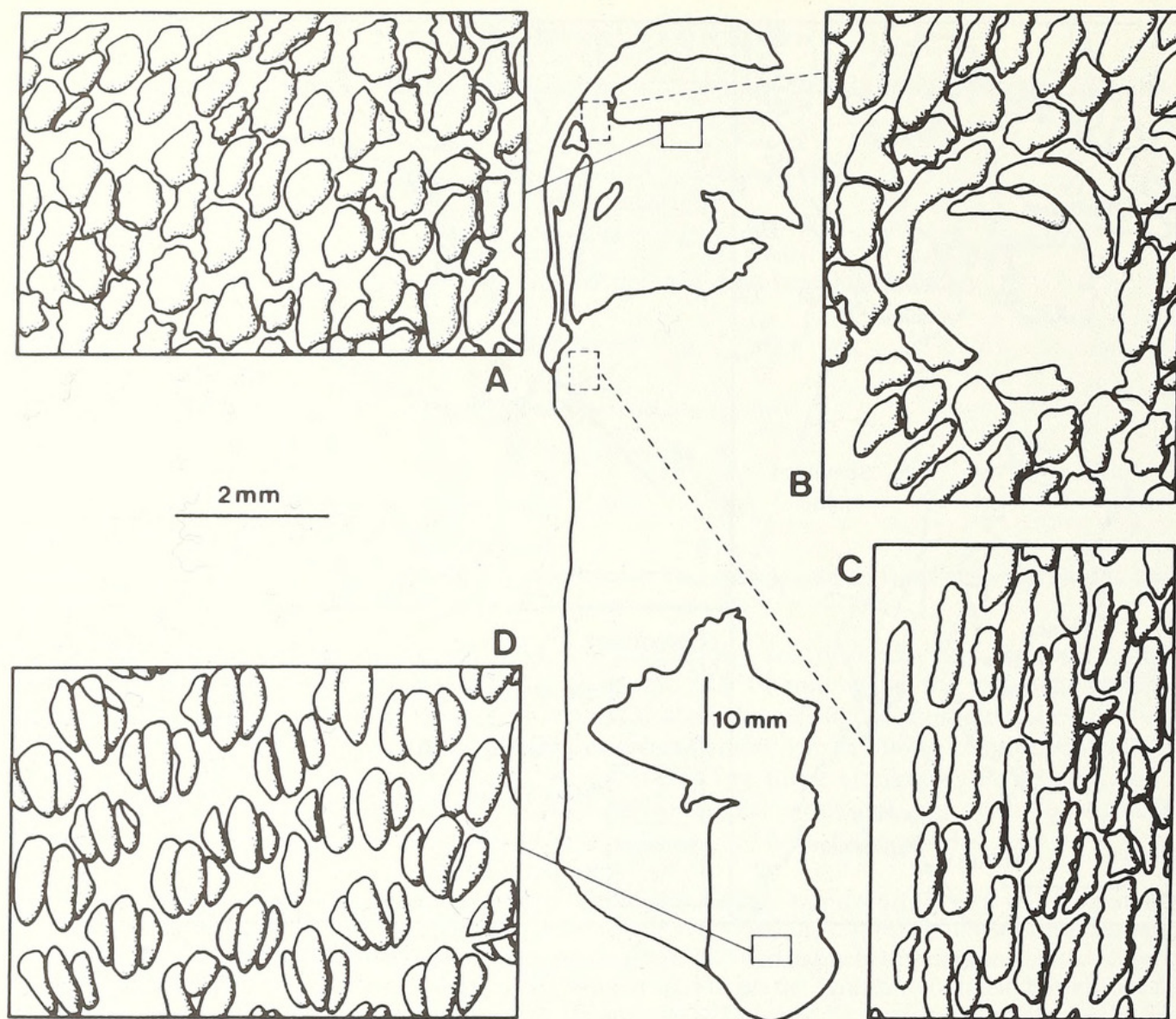
Cephalothorax. The dorsal surface (Pl. 107, fig. 2) is preserved only as a marginal band 5 mm deep that appears to have been structurally more coherent than other portions of the dermal armour. Anteriorly, it includes the right orbit (text-fig. 2B) which has a diameter of 2 mm and appears to have been dorsolaterally directed in life. The coherence of the lateral margin of the dorsal surface appears to be due to the fact that in this area the elements are joined together at the base, as can be seen on broken edges, as they are also in the rostral area. Laterally, each element is oriented parallel to the margin and bears an elongated ridge (text-fig. 2C), smooth-topped and with denticulate margins. This ornamentation becomes more ovoid and irregular ventrally (Pl. 107, fig. 3; text-fig. 2A) where the elements are often overturned and isolated showing that they were not joined and, therefore, presumably provided a more flexible covering. Each ventral element is about 0.5–0.75 mm thick and is composed of a basal plate surmounted by a broad flat crown of almost the same areal extent. On the most anterior ventral elements, the superficial crowns are very closely spaced. This differs from the lateral margin of the dorsal surface where the elongate ridges are quite widely spaced though the bases are joined.



TEXT-FIG. 1. Locality map and geology of Read Bay collecting site.

The rostral area is present mostly as an external mould of the dorsal surface visible in the ventral aspect of the specimen and, though indistinct, suggests that the rostral margin may have been somewhat rounded in life. The large anterior ventral area which is devoid of armour is assumed to indicate the position of the oral region. However, no particular orientation of ornament can be seen at the margins of this gap, and it is probable that the mouth was somewhat smaller than is suggested by this opening. There is no evidence of a branchial opening or openings as the relevant area is missing from the specimen. Two small pores anterior to the orbit may represent part of the sensory canal system, but the system may have opened through the bases of the elements or in soft tissue between them.

Caudal region. The armour of the caudal fragment shows a gradual change throughout its length; anteriorly, the skeletal elements are similar in size and shape to those of the ventral part of the cephalothorax. Passing gradually posteriorly, they assume a rather more regular arrangement, with elements associated in groups of two or three and with ridges having smooth rather than denticulate margins. The typical grouping of elements involves a longer central ridge flanked on either side by a short curved ridge, producing a lozenge shape. Broken and displaced elements indicate that, in the central part of the caudal region, the individual elements within each lozenge remain as discrete entities. At the posterior end of the caudal fragment, however, elements within the majority of the lozenges are united by their basal layers. The arrangement of the lozenges becomes increasingly regular and symmetrical towards the posterior, but nowhere do they appear to be imbricated (Pl. 107, fig. 4, text-fig. 2d). No dorsal or ventral median rows of elements are visible and, as it seems reasonable to suppose that the caudal fin was laterally compressed, it is probable that the caudal region as preserved presents a lateral aspect. It is not possible to determine the extent or shape of the caudal fin.



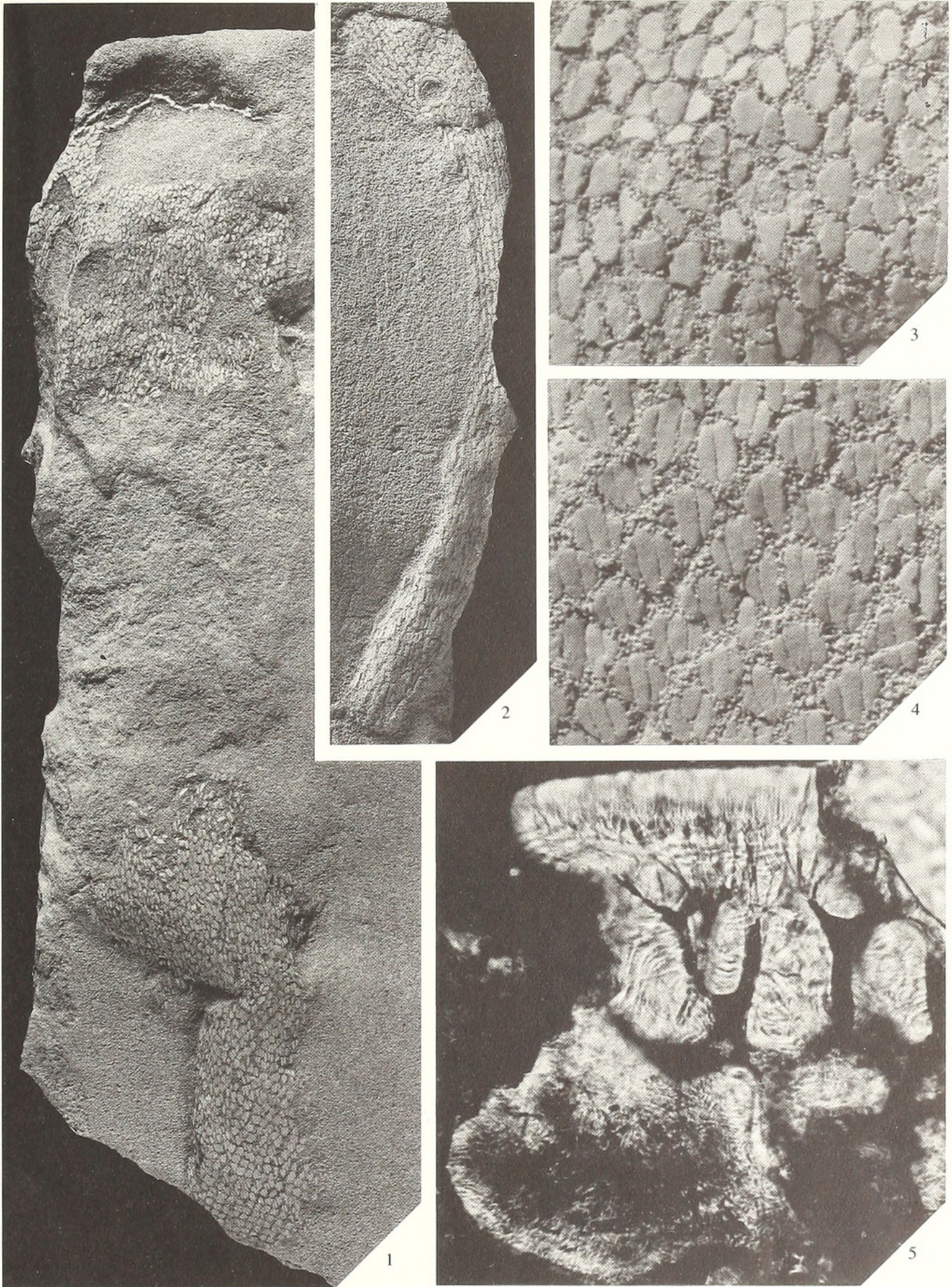
TEXT-FIG. 2. *Aporemaspis pholidata* gen. et sp. nov., NMC 34010, showing details of ornamentation on ventral (A, D) and dorsal (B, C) surfaces.

Histology. The preservation of the bone is not ideal but, in thin section (Pl. 107, fig. 5), each element can be seen to consist of four main layers. The basal layer is variable in thickness and appears dense and fibrous with slight indications of laminations parallel to the base. It typically forms an expanded base to the element and it is this layer that forms a continuous sheet in the lateral and anterior parts of the shield. Occasional canals run through the basal layer and open at the base and into the median layer above.

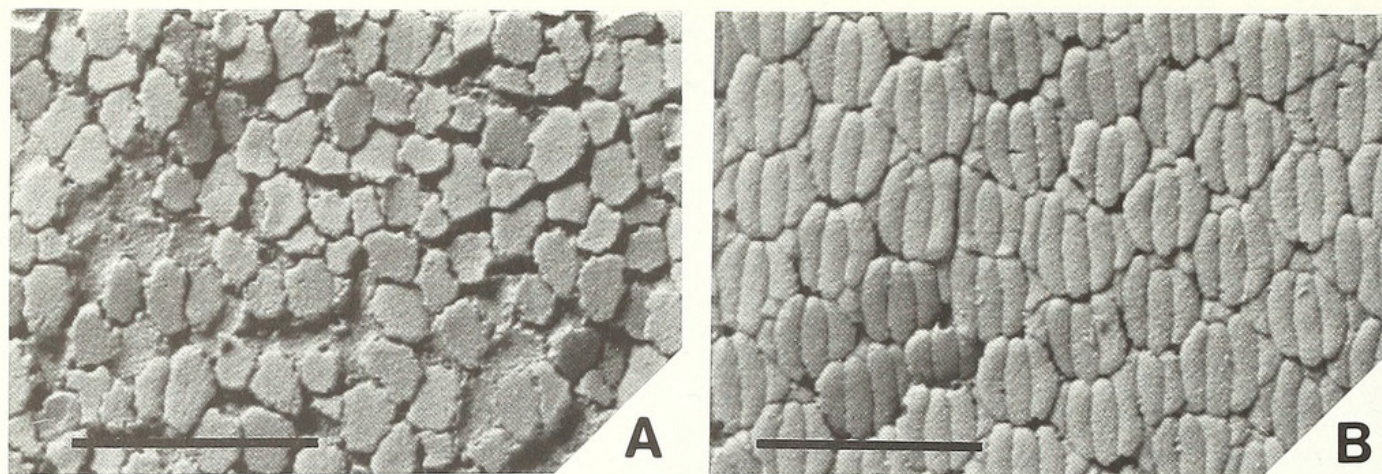
The median layer is not cancellous, as in the Pteraspidae and Cyathaspidae, but consists of a regular system of vertical canals rising from a horizontal basal canal (Pl. 107, fig. 5). These canals are surrounded by thick aspidin which shows strong laminations that sometimes cut and sometimes parallel the margins of the main canals. Above the median layer is an upper layer in which horizontally-laminated aspidin is penetrated

EXPLANATION OF PLATE 107

Figs. 1–5. *Aporemaspis pholidata* gen. et sp. nov. from the Snowblind Bay Formation, Cornwallis Island. Holotype, NMC 34010. 1, Ventral view showing oral area, $\times 1.3$. 2, Dorsal view showing orbit, $\times 1.3$. 3, Detail of ornamentation in antero-ventral area, $\times 10$. 4, Detail of ornamentation in caudal area, $\times 10$. 5, Thin section of isolated element, $\times 100$.



ELLIOTT and LOEFFLER, *Aporemaspis*



TEXT-FIG. 3. *Aporemaspis* sp. gen. nov. from the Delorme Formation, Northwest Territories. Details of ornamentation from shield fragments from the antero-ventral region (A, NMC 40611) and the caudal region (B, NMC 40610). Scale bars, 2.5 mm.

by many fine canals rising from the apices of the vertical canals in the median layer. These fine canals branch close to the surface of the element forming a zone of fine tubules. This outer zone is not laminated and appears to be formed of dentine.

DISCUSSION

Heterostracans typically have armour which consists of a number of large plates covering the anterior part of the body, and imbricate scales covering the tail. The large plates tend to be regular in shape and symmetrical (or symmetrically arranged, in the case of paired plates); they may be in direct contact with one another, or separated by a mosaic of small plates, as in some psammosteids. The arrangement and number of the large plates is sufficiently constant that these characters are of taxonomic value at higher levels. However, included amongst the Heterostraci in the majority of classification schemes, there are a small number of forms with dermal armour consisting of numerous small plates or tesserae, which may be fused loosely or locally into irregular sheets and strips. These areas of fused tesserae do not appear to be constant in size, shape or number of constituent units; in one genus, *Lepidaspis*, the basal plates of the skeletal elements show varying degrees of fusion in different specimens. This was interpreted by Dineley and Loeffler (1976) as evidence that progressive fusion of the basal plates took place during the growth of the individual. Examples of these 'tessellated' forms include the Ordovician *Astraspis* and the Devonian *Tesseraspis*, which are known both as isolated tesserae, and as coherent sheets of tesserae. *Lepidaspis* and *Aserotaspis*, from the Delorme Formation of northern Canada (Dineley and Loeffler 1976) are also known from articulated material. Other heterostracans which are preserved only as isolated polygonal tesserae, or small groups of tesserae, may have had a similar level of organization of their hard tissues; examples include *Kallostrakon*, *Oniscolepis*, and *Strosipherus*.

The morphology and affinities of these tessellated forms are poorly understood, largely because the dermal armour tends to disintegrate into its component elements unless exceptional conditions favour its preservation. Nevertheless, tessellated heterostracans have been used as examples to support various evolutionary schemes for the early vertebrates, notably those proposed by Tarlo (1967) and Halstead (1973). However, it remains to be demonstrated that the tessellated heterostracans are a monophyletic group; the tesserae may be primitive in some, and derived in others. Elliott's (1987) recent re-examination of *Astraspis* has revealed that it had multiple pairs of branchial openings, a feature previously unknown in early vertebrates which have acellular bone of heterostracan type, though anaspids do have multiple branchial openings and scales composed of lamellar bone only. As branchial openings have not been described for any other of the tessellated forms, we do not know if they had single or multiple pairs. Improved knowledge of these forms is

probably crucial to our understanding of the evolution of the early vertebrates. While the new genus *Aporemaspis* provides no immediate solutions, its description contributes to the growing store of information on these tessellated forms, and its comparison with other members of the group may give clues to its relationships.

Two genera from the Delorme Formation, *Aserotaspis* and *Lepidaspis*, provide unusually good examples of articulated tessellated heterostracans (Dineley and Loeffler 1976). *Aserotaspis canadensis* is a large form, apparently with a dorso-ventrally flattened cephalothorax. The anterior dorsal surface only is preserved, showing tesserae interlocking to form a continuous sheet. Over most of the surface, they are large and polygonal, and bear an ornament of numerous flat-topped twig-like ridges (Dineley and Loeffler 1976, pl. 18); these tesserae appear to be rather loosely associated with one another and, even when closely adpressed, their borders are clearly visible. Around the lateral margin of the holotype, and in the region of the orbit, the ornament is coarser and the tesserae are not clearly delimited. This coarser type of ornamentation, particularly that developed on the left side of the holotype of *Aserotaspis canadensis*, is very similar to that seen in the same position in *Aporemaspis pholidata*. Although Dineley and Loeffler (1976, p. 138) originally described this as 'a coarsely ornamented fragment of indeterminate origin', it is possible to recognize a gradation from the tesserae of the central area of *Aserotaspis* to the more rigid and coarsely ornamented marginal part where the basal part of the armour seems to be continuous. Similar coarse ornament is present around the orbit, but there is no evidence of branchial openings in this rigid marginal area of *Aserotaspis*. Unfortunately, comparison of *Aserotaspis* with *Aporemaspis* is rendered all the more difficult because the former is known only from the dorsal surface of the cephalothorax, the latter from the ventral. However, there are numerous points of similarity. Both taxa appear to have been rather dorsoventrally compressed, with a broadly rounded anterior margin and small marginally situated orbits, and the lateral margins of the cephalothoracic region, around and behind the orbits has dermal armour which is more rigid than that of the adjacent tesserate parts, and appears to be united by a continuity of the basal, spongy part of the armour. Furthermore, the ornamentation of the margins of the cephalothoracic region is very similar in *Aserotaspis* and *Aporemaspis*. It is possible that the two taxa merely represent dorsal and ventral aspects of closely similar forms, but in the absence of more complete material, this cannot be proven.

Lepidaspis serrata, also from the Delorme Formation, is known from a larger number of specimens. It has a broad, dorsal-ventrally flattened body with a rounded anterior margin and a narrow tail (the overall shape was likened to a table-tennis bat by Dineley and Loeffler 1976). The armour is largely composed of isolated scale-like elements. On the cephalothorax, the elements consist of an oval basal plate surmounted by a single barbed ridge. Individual animals show varying degrees of contact between these elements; they may be completely separate from one another, or the basal plates may be fused together to form a solid carapace. The lateral margins of the cephalothorax and the borders of the small dorso-laterally situated orbits are rather different in structure: the barbed ridges are rather broader and flatter, and rather more closely-spaced than the rest of the ornament, and the basal plates form a continuous layer. On the tail of *Lepidaspis*, the dermal elements are rather shorter and broader than on the cephalothorax, each basal plate bearing two or three short, barbed ridges. A median row of ridge scales, ornamented with numerous barbed ridges, extends along the length of the tail on both dorsal and ventral surfaces.

Although the ornamentation of *Lepidaspis* is quite distinct from that of *Aporemaspis*, there are notable similarities between the two forms in that the lateral and orbital parts of the cephalothorax are more solidly constructed than the central parts, with continuity of basal layers, and the caudal elements are composite, consisting of more than one ridge per basal plate.

Other fragments of armour bearing ornamentation similar to that seen in *Aporemaspis pholidata* are present in the Delorme Formation, however. Two specimens (text-fig. 3) show associated elements similar to those present in the antero-ventral and caudal regions of *Aporemaspis pholidata*. NMC 40610 (text-fig. 3B) shows a series of lozenge-shaped groups of ridges of a similar size and shape to those seen in the caudal region of *A. pholidata*. The ornament is extremely regular and,

as the fragment has a maximum width of 20 mm, it would appear to have come from a larger animal than the type of *A. pholidata*. The second fragment (NMC 40611, text-fig. 3A) consists of elements similar to those found in the antero-ventral region of *A. pholidata*, but also seems to have come from a much larger animal. In both specimens, the extreme regularity of the ornamentation and lack of gradation into other element types suggests that these fragments cannot be attributed with certainty to that species. For the moment, therefore, we are placing them in the genus *Aporemaspis* with no attribution to species.

Dineley and Loeffler (1976) were unsure of the affinities of *Lepidaspis* and *Aserotaspis*. They included *Aserotaspis* in the Heterostraci, *incertae sedis*, but felt that the histology of *Lepidaspis* was too poorly-known even for that ascription. Halstead has since examined thin sections of the bone of *Lepidaspis*, and confirmed that it is aspidin. Unfortunately, in neither of these genera is the number or the position of the branchial openings known.

Astraspis, and its contemporary *Eriptychius*, from the Ordovician Harding Sandstone of North America are also forms with dermal armour made up of tesserae. Although more commonly known from isolated tesserae of various types, three articulated specimens are known. The single articulated specimen of *Eriptychius* reveals little, but the two of *Astraspis* are sufficiently complete to provide the basis for a reconstruction (Elliott 1987).

The dorsal armour of the cephalothoracic region of *Astraspis* is composed of a number of polygonal tesserae, each ornamented with numerous tiny tubercles. Distinctive ridge plates, each strongly keeled, are aligned to form a median and two pairs of lateral crests. Short grooves which cross the dorsal surface of some of the tesserae have been interpreted as lateral line canals (Ørvig, in Stensiö 1958). Most of the polygonal tesserae have a distinctly conical shape, with a single apical tubercle around which the smaller tubercles are grouped. Denison (1967) referred to this as a 'primordial cluster' and described how the tesserae grew in area by marginal addition, and in thickness by apposition of successive generations of tubercles on the surface. Such growth apparently continued throughout life and was accompanied by a limited amount of resorption and reformation of the bone. It is noteworthy that the simple structure with a single 'primordial cluster' is not shared by the ridge plates or the lateral line plates. In the former, there may be a single longitudinal ridge, or a row of tubercle clusters; the lateral line plates are similarly composite, having as many as seven of the prominent tubercles. These patterns are particularly clear in the first of the articulated specimens to have been described, USNM 8121, which is regarded by Denison (1967) as a young individual. Some of the tesserae are more closely associated than others but, since neither specimen preserves any actual bone, it is impossible to determine the extent of the fusion. Presumably, if marginal growth of the tesserae occurred throughout life, and if the articulated specimens both represent young individuals, the tesserae would not have been permanently fused, if at all.

Elliott's (1987) recent redescription of one of the articulated specimens of *Astraspis* has revealed that the dorsal tesserae grade posteriorly into imbricated polygonal scales, and that there was a ventro-lateral series of tesserae notched by a row of at least 8 branchial openings. The reconstruction shows an animal which is quite clearly different in overall morphology from the Canadian genera *Aporemaspis*, *Aserotaspis* and *Lepidaspis*; it also contrasts with the other Ordovician genera, the rather anaspid-like *Arandaspis* from Australia (Ritchie and Gilbert-Tomlinson 1977) and *Sacabambaspis*, from Bolivia (Gagnier *et al.* 1986). The systematic position of *Astraspis* clearly must be reassessed. The relationship between *Astraspis* and the tessellated 'heterostracans' also remains uncertain; and in the absence of evidence to the contrary, we must assume that they had a single pair of branchial openings. Although the shape and ornamentation of the tesserae of *Lepidaspis*, *Aserotaspis*, and *Aporemaspis* are quite distinct, there are broad similarities in overall shape and organization which suggest a possible relationship between the three Canadian genera. *Tesseraspis*, *Kallostrakon*, and *Oniscolepis* are too incompletely known for even the most tentative suggestion to be made about their affinities, although there is probably sufficient material available in museum collections to permit a more detailed study of *Tesseraspis*.

In conclusion, we would suggest that *Astraspis* be excluded from the Heterostraci on the basis of

its multiple branchial openings and that the other Ordovician genera should likewise be excluded, though they are less well known at present. The Lower Devonian genera *Lepidaspis*, *Aserotaspis*, and *Aporemaspis* are retained within the Heterostraci but, though they probably represent a separate family, we do not feel that it can be adequately characterized at present. *Tesseraspis*, *Kallostrakon*, and *Oniscolepis* should remain within the Heterostraci, but retained as *incertae familiae* pending more detailed study.

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