A new species of cyathaspid (Vertebrata: Pteraspidomorphi: Heterostraci) from the Lower Devonian Drake Bay Formation, Prince of Wales Island, Nunavut, Arctic Canada

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Abstract. A new genus and species of cyathaspid heterostracan, *Faberaspis elgae*, is described from the Early Devonian (Lochkovian, *Pedavis pesavis* conodont Zone) Drake Bay Formation of Prince of Wales Island, Nunavut, Arctic Canada, where it is associated with a rich shallow marine invertebrate fauna. *Faberaspis* is most closely related to *Poraspis*, but differs in details of the ornament and in possessing a more complete network of lateral line canals.

Key words: phylogeny, Cyathaspididae, Agnatha, Heterostraci, Lower Devonian, Drake Bay Formation, Arctic Canada.

INTRODUCTION

Vertebrate faunas from the Upper Silurian and Lower Devonian of Arctic Canada are well known and have been published in a series of papers since their discovery in 1955 (Thorsteinsson 1958). This is particularly true for the Heterostraci, a widespread group of armoured jawless vertebrates in which the head and forepart of the body are encased in a carapace consisting of a variable number of bony plates, and that are associated with possible non-marine and proximal environments of the Old Red Sandstone continent (see Elliott et al. 1998 and references therein; Elliott & Swift 2010; Elliott 2013, 2016). The Cyathaspididae constitute a family within the Heterostraci in which the carapace consists of a dorsal and ventral shield including branchial and suborbital plates. The dorsal shield consists of a dorsal median plate, the surface of which may be divided by sutures into subdivisions termed epitega that represent areas of independent growth, and the paired branchial and suborbital plates. The ventral shield contains the ventral median plate and the plates of the oral cover. The branchial plates are long and narrow, and the branchial notch on the dorsal margin encloses the branchial opening ventrally, a corresponding notch in the lateral margin of the dorsal plate encloses them dorsally. The paired branchial openings commonly occur along the lateral borders of the dorsal plate where their position ranges from far posteriorly to the mid-shield. The ornamentation consists of dentine ridges commonly arranged in a longitudinal pattern on the shields. However, in a few of the geologically oldest members of this taxon, the ornamentation is dominated by scale-like elements formed by short ridges. The presently known age range of this order is Wenlock to Emsian (Denison 1964; Elliott & Petriello 2011).

In 1975 a palaeontological expedition from Göttingen and Cologne universities (Germany) visited Arctic Canada (Langenstrassen & Schultze 1996) and *inter alia* collected agnathans and gnathostomes in Lower Devonian localities on the northern part of Prince of Wales Island (Fig. 1A). At Drake Bay, on the north-western coast of Prince of Wales Island, the group explored exposures along Drake Bay and Smith Bay further south and collected the cyathaspid described here at locality P11 at the northern end of Smith Bay (Langenstrassen & Schultze 1996: fig. 11; Elliott et al. 2015; Fig. 1B). This cyathaspid is a member of the sub-family Poraspidinae (*sensu* Denison 1964), members of which are already well known from the Arctic (Elliott et al. 1998). The type genus, *Poraspis*, has a wide geographic distribution having been reported from Spitsbergen, eastern and western Europe as well as Canada's District of Mackenzie and Arctic Archipelago, and the western United States (see Elliott & Petriello 2011 and references therein). The genus also has a wide

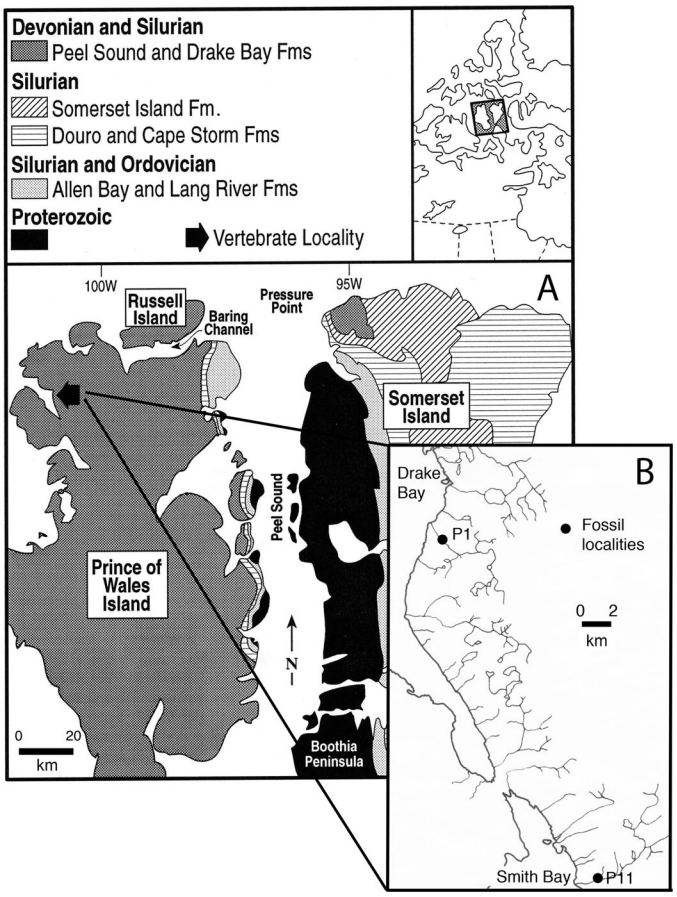

Fig. 1. Geologic map of Prince of Wales Island (**A**) with the location of the fossil locality P11 (**B**).

temporal range from the Pridoli of Arctic Canada, through the Lochkovian of western Europe, Spitsbergen and Arctic Canada, to the early or middle Pragian of Arctic Canada and the Emsian of the western United States.

MATERIAL AND METHODS

The specimen is preserved in a calcareous siltstone and was prepared mechanically using an engraving tool with a tungsten-carbide bit. The measurements and ratios employed follow those used by Denison (1964). The specimen is the property of the Geology–Palaeontology Institute and Museum of the University of Göttingen and bears its catalogue number (prefixed GZG.V.).

STRATIGRAPHY AND AGE

The cyathaspid described here was collected from the Drake Bay Formation (Mayr 1978), at Smith Bay on the western coast of Prince of Wales Island, in 1975 (Langenstrassen & Schultze 1996; Fig. 1). The Drake Bay Formation represents the most distal carbonate facies of the transition of sediments from fresh water to marine that grades westwards across Prince of Wales Island. To the east the Peel Sound Formation (Thorsteinsson & Tozer 1963) consists of red sandstones and siltstones grading upwards into oligomict conglomerates and pebbly sandstones, deposited over a large delta system as sub-aerial fans prograding from the rising Boothia Uplift. The formation was divided into lower and upper members on Prince of Wales Island (Miall 1970); the lower consisting of interbedded limestone, siltstone, sandstone and oligomict conglomerate is exposed only as a narrow band along the flank of the Boothia Uplift. The upper member is characterized by the disappearance of virtually all but conglomerate in the succession (Miall 1970). Westwards it grades through five distinct facies cropping out as north–south bands; conglomerate in the east is replaced laterally by conglomerate–sandstone, sandstone, sandstone–carbonate and carbonate. To the west the marine carbonate facies has been renamed the Drake Bay Formation (Mayr 1978), based on a section from a well on Russell Island, off the north coast of Prince of Wales Island, and is probably laterally equivalent to the entire Peel Sound Formation (Mayr 1978). The lower member consists of white to very light brown, crystalline

dolomite, while the upper member consists of grey carbonates interbedded with siltstones (Mayr 1978). The specimen described here comes from the upper member.

A geological section is not available for the locality that yielded the specimen described here (Fig. 1B). The sediments consist of grey, marly to sandy and dolomitic limestones. A continuous transition from fine-grained, limy sandstone, to limy siltstone, to micritic limestones and limy marlstones with dolomitic content changing from horizon to horizon was observed. The sediments are well sorted with thinly bedded layers changing to fissile layers. At more northerly localities at Drake Bay (Fig. 1B, P1) 50 cm to 2 m thick sandstones are intercalated in the marly limestones. These can be seen to thin out over short distances and are interpreted as tidal channels within a shallow coastal sea (Langenstrassen & Schultze 1996).

Smith (1976, 1980) and Mayr (1978) noted the presence of brachiopods of possible Early Devonian age from the lowest part of the upper member and suggested an age of Ludlow to earliest Devonian for the lower member and Gedinnian to early Siegenian (Lochkovian–early Pragian) for the upper member. Sampling for conodonts in the upper member (Smith 1976; Mayr et al. 1980) yielded *Ozarkodina remscheidensis* in the lower and middle parts, indicating a Pridoli–Lochkovian age, and *O. remscheidensis remscheidensis* and *Pedavis pesavis* (Langenstrassen & Schultze 1996) in the upper part, indicating a Lochkovian age (*pesavis* Zone). Surface outcrops near the well on Russell Island yielded a Pragian fauna from strata near the top of the section, so the upper member appears to be Lochkovian, extending into the Pragian at the top. This age determination is supported by identification of microvertebrates in the upper member (Vieth 1980; Märss et al. 2006).

Based on the scale fauna, Vieth (1980) noted an age range from late Lochkovian in the more northerly localities to early Lochkovian farther south. The locality yielding the new cyathaspid was dated as early Lochkovian (Vieth 1980).

SYSTEMATIC PALAEONTOLOGY

Class PTERASPIDOMORPHI Goodrich, 1909
Subclass HETEROSTRACI Lankester, 1868
Order CYATHASPIDIFORMES Berg, 1937
Family CYATHASPIDIDAE Zych, 1931
Subfamily PORASPIDINAE Kiaer, 1932
Genus *Faberaspis* new genus

Type species. *Faberaspis elgae* new species.

Diagnosis. As for the type and only known species.

Etymology. From Latin *faber*, a smith, after Smith Bay, and Greek *aspis*, a shield.

Remarks. The Poraspidinae are a cyathaspid subfamily in which the epitega are indicated faintly or not at all, and the dentine ridges are long and mainly longitudinal in orientation, although they may radiate on the anterior and diagonally on the lateral parts of the dorsal shield (Denison 1964). *Faberaspis* has no epitega and shows a particularly regular arrangement of longitudinal ridges that show only a slight radiation anteriorly.

Faberaspis elgae new species
Figure 2

Holotype. One dorsal shield, GZG.V.29511.

Diagnosis. Large poraspid, length 52.0 mm, width ratio 0.49, orbital ratio 0.21. Ridges flat-topped, 7 per mm at midline and 5 per mm at lateral margin; longitudinal on the dorsal shield, fanning slightly over rostrum; starting at the level of the branchial opening a band of two or three coarse round-topped ridges is present marginally, increasing to seven around the orbit and 12 at the anterior margin. Pineal macula present. Epitega not present. Sensory canal system as in *Poraspis* but with more complete connection of the transverse commissures.

Etymology. Named after our colleague Dr Elga Mark-Kurik in recognition of her many important contributions to the study of early vertebrates.

Occurrence. Twenty-eight kilometres south of the *Powichthys* locality, Smith Bay, western coast of Prince of Wales Island, Nunavut, Arctic Canada (Fig. 1). Locality P11 of Langenstrassen & Schultze (1996). Drake Bay Formation, upper member; early Lochkovian, *pesavis* conodont Zone.

Description. The material consists of one dorsal median plate missing part of the right anterior margin and with an incomplete posterior margin (Fig. 2A). The plate is elongated and moderately vaulted, although crushing may have flattened it. The plate is generally poraspid in shape with a broadly rounded rostrum and a convex lateral margin that becomes straight posterior to the branchial notch. There is no abrupt narrowing in front of the orbits as in *Poraspis*, and the orbital notch is not distinct. The branchial notch is fairly shallow and the postbranchial lobe is distinct and well developed. The posterior margin is mostly missing but the preserved posterolateral part is broadly rounded.

The ornamentation consists of fine, flat-topped ridges, 7 per mm in the midline (Fig. 2C), continuous and longitudinally oriented over much of the plate. Anteriorly the ridges fan slightly over the rostrum, additional

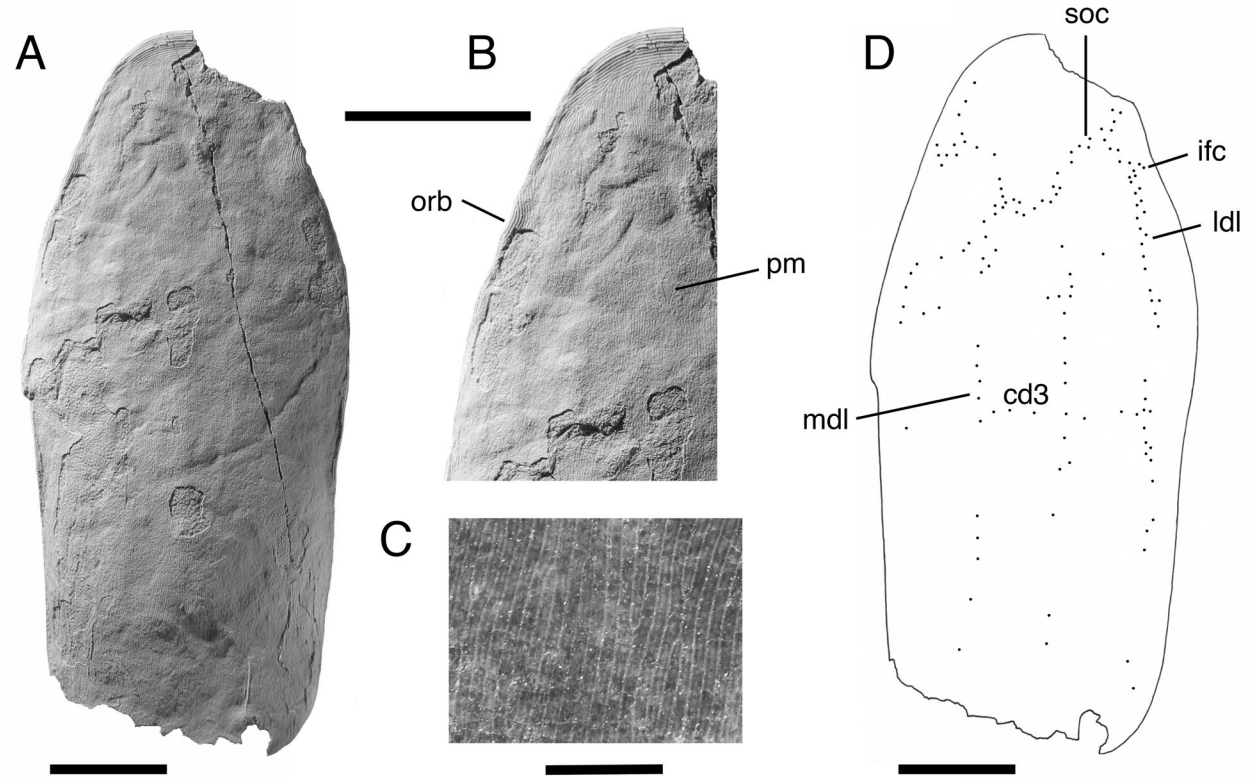

Fig. 2. *Faberaspis elgae* n. gen. et sp. holotype GZG.V.29511. **A**, dorsal shield in dorsal view. **B**, enlargement of the rostral area to show ornament detail and the pineal macula. **C**, detail of the ornamentation in the mid-line and just posterior to the pineal macula. **D**, sensory canal system of the dorsal shield. Abbreviations: cd3, third cross-commissure; ifc, infraorbital canal; ldl, lateral dorsal canal; mdl, medial dorsal canal; orb, orbit; pm, pineal macula; soc, supraorbital canal. Scale bar is 10 mm for A, B and D, 1 mm for C. (Fig. 2C is copyrighted by GZG Museum/ G. Hundertsmark).

ridges in the midline originating at a centre anterior to the position of the pineal organ. There is a small, tear-shaped pineal macula, a few millimetres behind the orbit level in the midline of the dorsal shield (Fig. 2B). Laterally 2–3 round-topped, coarser (5 per mm) ridges form a marginal band (Fig. 2B). At the level of the orbit these increase in number to 6–7, they then reduce to 2–3 anterior to the orbit before widening into a band of 10–12 ridges across the anterior margin of the rostrum.

The sensory pores of the canal system are distinct over the rostrum but less so posteriorly, and in some areas the canals themselves are visible due to the very thin bone of the plate. The general pattern (Fig. 2D) is distinctly poraspid with the lateral longitudinal canals connected to the infraorbital and supraorbital canals and the supraorbital canals meeting behind the pineal. Although the arrangement of the more posterior part of the system is unclear there is a complete connection between the transverse commissures and the longitudinal canals anteriorly.

Remarks. This species is clearly a poraspidinid as it has no epitega and shows the characteristic poraspid outline and continuous longitudinal dentine ridges. *Poraspis* is a widespread genus, both temporally and geographically, the oldest being the smallest described cyathaspids and occurring in the Late Silurian of Arctic Canada and the youngest being the largest members of the genus and occurring in the Lochkovian of the Welsh Borders and Arctic Canada (Elliott et al. 1998 and references therein). The genus was reviewed by Blieck & Heintz (1983) who rationalized the originally described species, showing that many overlapped in morphology, reducing the described species from eight to three. Elliott et al. (1998) added four new species from Arctic Canada and showed that *Poraspis sericea* is present in Arctic Canada as well as the Welsh Borders, a rare occurrence of a species common to the Arctic and European successions. Although clearly not a poraspid *Faberasis elgae* is most similar in outline to *Poraspis sturi* (Alth 1874; Voichyshyn 2011) but differs from it in being significantly smaller. *Faberaspis* also has a more regular arrangement of the ridges on the anterior part of the shield together with a band of ridges parallel to the anterior margin that are not found in *Poraspis* species.

Additionally, the sensory canal system in *Faberaspis* is similar to, but more complete, than that in any of the species of *Poraspis* (Denison, 1964).

DISCUSSION

The early history of discovery and description of cyathaspids has been covered in detail by Kiaer & Heintz (1935, pp. 31–39) and is not repeated here. The taxon was initially recognized as a suborder by Kiaer (1932), who named it the Cyathaspida and included it with the suborders Psammosteida and Pteraspida within the order Heterostraci. He included within this taxon heterostracans in which (1) the orbits are not surrounded by the dorsal shield but form semicircular notches in it, (2) the large oblong branchial plate situated between the dorsal and ventral plates is detached and (3) the dentine ridges forming the surface of the dermal skeleton are smooth and not crenulated as in the pteraspids. At that time Kiaer (1932) also recognized two tribes within the Cyathaspida: (1) the Poraspidei, in which the dorsal shield was not divided into epitega and (2) the Cyathaspidei, in which four epitega were present on the dorsal shield. The Poraspidei included the families Poraspidae, Palaeaspidae, Dinaspidae, Anglaspidae and Ctenaspidae, while the Cyathaspidei included the families Cyathaspidae, Tolypaspidae, Diplaspidae and Traquairaspidae (Kiaer 1932). This remained the most complete treatment of the taxon until 1964 when Denison published a comprehensive review defining the cyathaspids as a family, the Cyathaspididae. Within the family he recognized a series of sub-families that adhere fairly closely to the families recognized by Kiaer (1932) although several of them were amalgamated: Tolypelepidinae, Cyathaspidinae, Irregulareaspidinae, Poraspidinae and Ctenaspidinae. The sub-families were recognized by (1) the presence or absence of apparent scale components in the shield, (2) the presence or absence of distinct epitega and (3) the pattern, length and uniformity of the superficial dentine ridges.

In 1976 Dineley and Loeffler published a monograph on ostracoderms from the Delorme and associated formations in the Mackenzie Mountains, Canada. This study included cyathaspids and broadly supported the classification of Denison (1964) with slight modifications. The Tolypelepidinae were seen as the most primitive group and a new species of *Tolypelepis* was added together with the new genus *Asketaspis*. Cyathaspidinae was accepted with the addition of several new species, as was Poraspidinae. The Irregulareaspidinae was enlarged by the addition of *Nahanniaspis*, which is preserved as completely articulated individuals. The only disagreement with the classification of Denison (1964) is in the position of *Dikenaspis* as a member of the Irregulareaspidinae. In their view, *Irregulareaspis*, *Dinaspidella* and *Nahanniaspis* share a suite of characters that indicate their close relationship, while *Dikenaspis* is connected only by the presence of an anastomosing lateral line system. Dineley & Loeffler (1976) suggest that this is different in type from that of *Irregulareaspis* and suggest instead that *Dikenaspis* should be placed in the Cyathaspidinae and that the Irregulareaspidinae are more closely related to the Poraspidinae.

No further attempts to develop an understanding of the relationships of the Cyathaspididae were made until 1996. Janvier (1996: fig. 4.8) showed in cladistic form (although without a cladistic analysis) as part of a phylogeny of the Heterostraci a simple cyathaspid phylogeny in which *Nahanniaspis* represented basal forms and *Anglaspis* and *Torpedaspis* more advanced forms, while the ctenaspids and amphiaspids formed a sister-group.

Novitskaya (2004) reviewed fossil 'agnathans and early fishes' of the former USSR and treated the cyathaspids as an order, Cyathaspidiformes, as Obruchev (1964; order Cyathaspidida) had done previously. Novitskaya (2004) recognized the families Cyathaspididae, Tolypelepididae, Irregulareaspididae, Poraspididae, Anglaspididae (that is *Anglaspis* plus *Liliaspis* and *Paraliliaspis*) and Ctenaspididae. Voichyshyn (2011) reviewed Early Devonian 'armoured agnathans' of Podolia, Ukraine, and also treated the group, without cladistic analysis, as order Cyathaspidiformes with the following families: Cyathaspididae, Irregulareaspididae, Poraspididae and Ctenaspididae.

Within the Heterostraci only the Pteraspididae have been subjected to a cladistic analysis (Pernègre & Elliott 2008) until an analysis of the Cyathaspididae was published by Lundgren & Blom (2013). Randle & Sansom (2016) reanalysed the Pteraspididae, and then (2017) sought to provide an overview of the relationships of all the 'higher' heterostracans with a combined phylogenetic hypothesis, which does not present a clear phylogeny for the Cyathaspididae.

The analysis of Lundgren & Blom (2013) was based on Denison (1964) and did not attempt to address changes in the composition of the family used by later workers (e.g. the exclusion of the ctenaspids by Janvier 1996). It also implicitly accepted the definition of the family provided by Denison (1964, pp. 350–351) although this was not stated or discussed by them. They produced a repeatable, heuristic parsimony search for a consensus tree that has a few taxonomically explainable clades. In a review by these authors of the 61 characters, some have indirectly weighted traits by duplication, in other cases taphonomic alteration has not been recognized

when selecting characters. Also, many of the 37 included taxa from Denison (1964) no longer fit the taxonomic diagnosis of cyathaspids. One of the characters listed is the presence of paired branchial plates (Denison 1964, p. 350), and this was also one of the three characters used by Kiaer (1932) to identify his Cyathaspidida. We therefore consider that this feature is an important one in defining a cyathaspid. However, although present in almost all of the taxa Denison (1964) lists within the family, this character is not present in a number of them. *Allocryptaspis* was included by Denison (1964) who assumed the branchial plates had fused to the dorsal shield. However, Elliott et al. (2004) showed that such a process would have resulted in a branchial opening completely enclosed by the dorsal plate and suggested instead that that this taxon had never possessed branchial plates. In the ctenaspids (*Ctenaspis*, *Arctictenaspis* and *Zaphoctenaspis*) the branchial opening is posteriorly directed and there is no evidence for the presence of branchial plates. Elliott & Blieck (2010) removed them from the Cyathaspididae and included them within the Ctenaspididae. The same is true for *Ariaspis* for which Elliott & Swift (2010) showed the presence of a continuous lateral lamina with no notch for the branchial opening and a posterior opening for the branchial duct. A branchial plate was identified in *Listraspis* by Denison (1964), however, a review of the original and some additional material indicates that this is a lateral lamina not separated from the rest of the dorsal shield (DKE, pers. obs.). This taxon requires further study and description.

There is a considerable amount of disagreement between the classification presented by Denison (1964) and the hypothesized phylogeny of Lundgren & Blom (2013) as very few of the established subfamilies are recognized as clades in the consensus tree. *Asketaspis* is in a polytomy with the outgroup, *Athenaegis*. The tolypelepids are paraphyletic and form a basal group. The ctenaspids are shown as a monophyletic group in a clade that also includes *Allocryptaspis* and *Alainaspis*. Although the rest of the tree is well resolved, it shows little similarity to the subfamilies developed by Denison (1964). For example, *Dinaspidella* and *Pionaspis* species appear in different parts of the tree although there have been no previous indications that they are incorrectly attributed. By excluding the taxa not accepted as cyathaspids by us, and using the data as published by Lundgren & Blom (2013) the resulting phylogeny shows little resolution and produces a large polytomy of the ingroup outside of an *Asketaspis*/*Tolypelepis* cascade and three retained clades of *Dikenaspis* + *Irregulareaspis*, *Anglaspis* + *Liliaspis* and *Archegonaspis* + *Ptomaspis*.

Although we are not presenting a new phylogeny at this time, we will be publishing one elsewhere. Preliminary results indicate that *Faberaspis elgae* is part of a clade including *Poraspis* and *Homalaspidella*, which is therefore similar to the Poraspidinae of Denison (1964). This clade appears to be most closely related to the Boothiaspidinae, a new subfamily of cyathaspids (Elliott 2016) from the Early Devonian and late Silurian of Arctic Canada and western United States. These are the most derived of the Cyathaspididae and are united by the lack of epitega on the dorsal shield.

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REFERENCES

Alth, A. von. 1874. Ueber die palaeozoischen Gebilde Podoliens und deren Versteinerungen [About the Palaeozoic formations of Podolia and their fossils]. *Abhandlungen Geologischen Reichsanstalt Wien*, **7**(2) [1874–1882], 1–79 [in German].

Berg, L. S. 1937. A classification of fish-like vertebrates. *Bulletin of the Academy of Sciences of the USSR, Biology Series*, **4**, 1277–1280 [in English and Russian].

Blieck, A. & Heintz, N. 1983. The cyathaspids of the Red Bay Group (Lower Devonian) of Spitsbergen. *Polar Research*, **1**, 49–74.

Denison, R. H. 1964. The Cyathaspididae: a family of Silurian and Devonian jawless vertebrates. *Fieldiana: Geology*, **13**, 309–473.

Dineley, D. L. & Loeffler, E. J. 1976. Ostracoderm faunas of the Delorme and associated Siluro-Devonian formations, North West Territories, Canada. *Special Papers in Palaeontology*, **18**, 1–214.

Elliott, D. K. 2013. A new cyathaspid (Agnatha, Heterostraci) with an articulated oral cover from the Late Silurian of the Canadian Arctic. *Journal of Vertebrate Paleontology*, **33**, 29–34.

Elliott, D. K. 2016. The Boothiaspidinae, a new agnathan subfamily (Heterostraci, Cyathaspididae) from the Late Silurian and Early Devonian of the western United States and the Canadian Arctic. *Journal of Paleontology*, **90**, 1212–1224.

Elliott, D. K. & Blieck, A. 2010. A new ctenaspid (Agnatha, Heterostraci) from the Early Devonian of Nevada, with comments on taxonomy, paleobiology and paleobiogeography. In *Morphology, Phylogeny, and Paleobiogeography of Fossil Fishes* (Elliott, D. K., Maisey, J. G., Yu, X. & Miao, D., eds), pp. 25–38. Verlag Dr. F. Pfeil, Munich.

Elliott, D. K. & Petriello, M. A. 2011. New poraspids (Agnatha, Heterostraci) from the Early Devonian of the western

United States. *Journal of Vertebrate Paleontology*, **31**, 518–530.

Elliott, D. K. & Swift, S. 2010. A new species of *Ariaspis* (Agnatha: Heterostraci) from the Late Silurian of the Canadian Arctic. *Journal of Vertebrate Paleontology*, **30**, 1874–1878.

Elliott, D. K., Loeffler, E. J. & Liu, Y. 1998. New species of the cyathaspidid *Poraspis* (Agnatha: Heterostraci) from the late Silurian and Early Devonian of Northwest Territories, Canada. *Journal of Paleontology*, **72**, 360–370.

Elliott, D. K., Reed, R. C. & Loeffler, E. J. 2004 A new species of *Allocryptaspis* (Heterostraci) from the Early Devonian, with comments on the structure of the oral area in cyathaspidids. In *Recent Advances in the Origin and Early Radiation of Vertebrates* (Arratia, G., Wilson, M. V. H. & Cloutier, R., eds), pp. 455–472. Verlag Dr. F. Pfeil, Munich.

Elliott, D. K., Schultze, H.-P. & Blieck, A. 2015. A new pteraspid (Agnatha, Heterostraci) from the Early Devonian Drake Bay Formation, Prince of Wales Island, Nunavut, Arctic Canada, and comments on environmental preferences of pteraspids. *Journal of Vertebrate Paleontology*, **35**, DOI: 10.1080/02724634.2015.1005098.

Goodrich, E. S. 1909. *A Treatise on Zoology. Part IX. Vertebrata Craniata (First Fascicle: Cyclostomes and Fishes)* (Lankester, R., ed.). Adam and Charles Black, London, 518 pp.

Janvier, P. 1996. *Early Vertebrates*. Oxford Monographs on Geology and Geophysics, 33, Oxford Science Publications and Clarendon Press Oxford, 393 pp.

Kiaer, J. 1932. The Downtonian and Devonian vertebrates of Spitsbergen. IV. Suborder Cyathaspidida. *Skrifter om Svalbard og Ishavet*, **52**, 6–26.

Kiaer, J. & Heintz, A. 1935. The Downtonian and Devonian vertebrates of Spitsbergen. V. Suborder Cyathaspidida. Part I, Tribe Poraspidei, Family Poraspididae. *Skrifter om Svalbard og Ishavet*, **40**, 4–138.

Langenstrassen, F. & Schultze, H.-P. 1996. Unterdevonische Fischfunde aus Sedimenten des Flachmeerbereiches der kanadischen Arktis [Lower Devonian fish discoveries from the shallow marine sediments of the Canadian Arctic]. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **201**, 33–93 [in German, with English abstract].

Lankester, E. R. 1868. On some new cephalaspidean fishes. *Reports of the British Association for the Advancement of Science, London*, **37**, 63.

Lundgren, M. & Blom, H. 2013. Phylogenetic relationships of the cyathaspidids (Heterostraci). *GFF*, **135**, 74–84.

Märss, T., Wilson, M. V. H. & Thorsteinsson, R. 2006. Silurian and Lower Devonian thelodonts and putative chondrichthyans from the Canadian Arctic Archipelago. *Special Papers in Palaeontology*, **75**, 1–144.

Mayr, U. 1978. Stratigraphy and correlation of Lower Paleozoic formations subsurface of Cornwallis, Devon, Somerset and Russell islands, Canadian Arctic Archipelago. *Geological Survey of Canada Bulletin*, **276**, 1–39.

Mayr, U., Uyeno, T. T., Tipnis, R. S. & Barnes, C. R. 1980. Subsurface stratigraphy and conodont zonation of the lower Paleozoic succession, arctic platform, southern Arctic Archipelago. In *Current Research, Part A, Geological Survey of Canada Paper*, **80-1A**, 209–215.

Miall, A. D. 1970. Continental marine transition in the Devonian of Prince of Wales Island, Northwest Territories. *Canadian Journal of Earth Sciences*, **7**, 125–144.

Novitskaya, L. I. 2004. Podklass Heterostraci [Subclass Heterostraci]. In *Iskopaemye pozvonochnye Rossii i sopredel'nykh stran. Beschelyustnye i drevnie ryby* [*Fossil Vertebrates of Russia and Adjacent Countries. Agnathans and Early Fishes*] (Novitskaya, L. I. & Afanassieva, O. B., eds), pp. 69–207. Geos, Moscow [in Russian].

Obruchev, D. V. 1964. *Osnovy paleontologii. Beschelyustnye, Ryby* [*Fundamentals of Paleontology. Agnathans, Fishes*], *IA (11)* (Orlov, J. A., ed.). Nauka, Moskva, 522 pp. [in Russian; English translation, 1967. Israël Program for Scientific Translation, Jerusalem].

Pernègre, V. & Elliott, D. K. 2008. Phylogeny of the Pteraspidiformes (Heterostraci), Silurian–Devonian jawless vertebrates. *Zoological Scripta*, **37**, 391–403.

Randle, E. & Sansom, R. S. 2016. Exploring phylogenetic relationships of Pteraspidiformes heterostracans (stem-gnathostomes) using continuous and discrete characters. *Journal of Systematic Palaeontology*, **15**, 583–599.

Randle, E. & Sansom, R. S. 2017. Phylogenetic relationships of the 'higher heterostracans' (Heterostraci: Pteraspidiformes and Cyathaspididae), extinct jawless vertebrates. *Zoological Journal of the Linnean Society*, **XX**, 1–17.

Smith, R. E. 1976. *Lower Devonian (Lochkovian) Brachiopod Paleoecology, and Biostratigraphy of the Canadian Arctic Islands*. Ph.D. dissertation, Oregon State University, Corvallis, Oregon, 362 pp.

Smith, R. E. 1980. Lower Devonian (Lochkovian) biostratigraphy and brachiopod faunas, Canadian Arctic islands. *Geological Survey of Canada Bulletin*, **308**, 1–155.

Thorsteinsson, R. 1958. Cornwallis and Little Cornwallis islands, District of Franklin, Northwest Territories. *Memoirs of the Geological Survey of Canada*, **294**, 1–134.

Thorsteinsson, R. & Tozer, E. T. 1963. Geology of northern Prince of Wales Island and northwestern Somerset Island. In *Geology of the North Central Part of the Arctic Archipelago, Northwest Territories (Operation Franklin)* (Fortier, Y. O., Blackadar, R. G., Glenister, B. F., Greiner, H. R., McLaren, D. J., McMillan, N. J., Norris, A. W., Roots, E. F., Souther, J. G., Thorsteinsson, R. & Tozer, E. T., eds), *Geological Survey of Canada, Memoir*, **320**, 117–129.

Vieth, J. 1980. Thelodontier-, Acanthodier- und Elasmobranchier-Schuppen aus dem Unter-Devon der kanadischen Arktis (Agnatha, Pisces). *Göttinger Arbeiten zur Geologie und Paläontologie*, **23**, I–III, 1–69 [in German, with English abstract].

Voichyshyn, V. 2011. The Early Devonian armoured agnathans of Podolia, Ukraine. *Palaeontologia Polonica*, **66**, 1–211.

Zych, W. 1931. *Fauna ryb Dewonu I Downtonu Podola. Pteraspidomorphi: Heterostraci* [*The Fish Fauna of the Devonian and Downtonian of Podolia. Pteraspidomorphi: Heterostraci*]. Part **IA**. Słowo Polskie, Lwów, 91 pp. [in Polish].

Uus tsüataspiidi (Vertebrata: Pteraspidomorphi: Heterostraci) liik Alam-Devoni Drake Bay kihistust Walesi Printsi saarelt Kanada Arktikast

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On kirjeldatud tsüataspiidse erikilbilise üks uus perekond ja liik *Faberaspis elgae*. Selle üksik seljakilp leiti Kanada Arktikast Walesi Printsi saarelt Drake Bay kihistust Lochkovist Alam-Devonist. Koos selle selgroogse seljakilbiga esineb leiukohas rikkalikult madalmereliste selgrootute fossiile. *Faberaspis*'e vanus on määratud temaga samaaegse konodondi *Pedavis pesavis*'e järgi. *Faberaspis* sarnaneb perekonnale *Poraspis*, kuna neil mõlemal puudub kilbi jagunemine epitegumiteks (kilbi elementideks) ja mõlemal on ühesugune kilbi kuju ning piki kilpi kulgevad katkematud dentiiniribikesed. Erinevused ilmnevad skulptuuri detailides ja *Faberaspis*'e täielikumas küljejoonekanalite võrgus.