"Croyez ceux qui cherchent la vérité, doutez de ceux qui la trouvent"

"Believe those who seek the truth, doubt those who find it"

André Gide, Ainsi soit-il, Journal 1939-1949, Souvenirs, Gallimard, Bibliothèque de la Pléiade, 1954, p. 1233

“Si je l'avais connu plus tôt, j'aurais placé ce genre en tête de la famille des Lépidoïdes,
tant il diffère de tous les poissons connus. Il comprend les animaux les plus curieux que j'aie jamais observés ; leurs caractères sont même si extraordinaires , qu’il
ma fallu l'examen le plus attentif et le plus scrupuleux, et les preuves les plus évidentes,
pour me convaincre que ces êtres mystérieux étaient réellement des poissons.”

“If I’d known earlier, I would have placed this genus at the base of the lepidoides family, for it differs from all known fish. It contains the strangest animals that I have ever observed; their characters are so extraordinary that I have required the attentive and scrupulous studies, and the most solid proof to convince myself that these mysterious beings were truly fish.”

Louis Agassiz regarding the genus *Cephalaspis*, 1935. p. 135 in Recherches sur les Poissons Fossiles. 2. Contenant l’histoire de l’ordre des Ganoïdes. Neuchâtel, 85–300 pp.

University of Alberta

DESCRIPTION OF NEW SPECIES OF OSTEOSTRACI FROM THE MAN ON THE HILL LOCALITY, NORTHWEST TERRITORIES, CANADA, WITH CONSIDERATION OF THE PHYLOGENETIC AND BIOGEOGRAPHIC SIGNIFICANCE OF THE NEW TAXA

by

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A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Master of Science
in
Systematics and Evolution

Department of Biological Sciences

Fall 2011
Edmonton, Alberta

ABSTRACT

The Lochkovian (Lower Devonian) Man on the Hill (MOTH) locality, Northwest Territories, Canada, is a Konservat-Lagerstätte, where articulated early vertebrate remains are found. Among the early vertebrates preserved at the MOTH locality are the Osteostraci. Many specimens of osteostracan have been recovered since the last descriptions of osteostracan material from MOTH. New species of osteostracan are described here, including five new genera. The new taxa are examined in a phylogenetic analysis that includes most of the genera of the Osteostraci. The topology recovered was then used to reconstruct the ancestral biogeographic distributions of osteostracans. Of particular interest among the new taxa is a new family that includes *Superciliaspis*, and a primitive non-cornuate osteostracan. The new osteostracans support dispersal from Spitsbergen, Norway into MOTH with a specimen of *Machairaspis*, and the presence of *Waengsjoeaspis* at both localities, but all of the species, including six genera, are endemic to MOTH.

ACKNOWLEDGEMENTS

I would like to thank the following people for help in accessing and examining collections at various institutions during my research. From the Canadian Museum of Nature, Margaret Currie, Kieran Shepard, and Stephen Cumbaa. From the Redpath Museum, Virginie Millien, Anthony Howell, Karen Samonds, and Robert Carrol. From the Royal Ontario Museum, Kevin Seymour, and Brian Iwama. From the University of Bristol, Elizabeth Loeffler. And from the British Museum of Natural History, Zerina Johanson.

I would like to thank my colleagues at the University of Alberta for their time and help over the course of my program, Aaron LeBlanc, Alessandro Palci, Andrew Wendruff, Derek Larson, Eric Snively, Erin Maxwell, Juan Liu, Julien Divay, Kelly Grieve, Lida Xing, Michael Burns, Michael James, Miriam Reichel, Phil Bell, Robin Sissons, Stephanie Blais, Victoria Arbour, and Scott Persons. I would like to extend my gratitude to Alan Lindoe for his expert preparation of the specimens used in this study. I would like to thank Robert Sansom, Jessica Hawthorn, and Lindsey Mackenzie for discussion on osteostracans and early vertebrates. I would like to thank Katherine Potapova for her translation of russian.

Funding for my research has been provided through a teaching assistantship from the Department of Biological Sciences, University of Alberta.

Finally, I would like to acknowledge the guidance of the members of my Committee, Alison Murray, and Brian Chatterton. And I would particularly like to thank my Supervisor Mark Wilson, for his patience and his guidance.

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UALVP, University of Alberta Laboratory for Vertebrate Paleontology, **NMC**, Canadian Museum of Nature. **BMNH**, British Museum of Natural History.

Anatomical Abbreviations are provided in Chapter 2. All other abbreviations are defined in-text, or in the appropriate captions.

CHAPTER 1:

GENERAL INTRODUCTION TO THE OSTEOSTRACI AND THE MAN ON THE HILL LOCALITY, NORTHWEST TERRITORIES, CANADA.

INTRODUCTION

The earliest vertebrates appear in the Late Cambrian (Young et al., 1996). These vertebrates were jawless and covered in an exoskeleton of dermal bone. Armoured jawless vertebrates survived until the Late Devonian, and came in a variety of forms, with complex phylogenetic relationships. Among the greatest examples of both diversity and disparity in these groups are the Osteostraci. Osteostracans are an extinct clade of jawless vertebrates that were present from the Wenlockian (Early Silurian); (Ritchie, 1967) through to the Frasnian (Late Devonian); (Arsenault and Janvier, 1995). The greatest diversity of osteostracans occured in the Early Devonian (e.g., Janvier, 1985, 1988; Afanassieva, 1991; Mark-Kurik and Janvier, 1995; Adrain and Wilson, 1994) and the diversity decreased sharply during the Middle and Late Devonian (e.g., Janvier and Newman, 2005; Arsenault and Janvier, 1995, though Otto and Laurin, 1999, offer an alternative consideration of Middle Devonian osteostracan diversity). The Osteostraci are limited in their geographic distribution to Euramerica (the Laurentia, Baltica and Avalonia terranes together) and the Altaids, as well as the Kara terrane (Blieck and Janvier, 1993; Sansom, 2009b).

The classification of the Osteostraci has been contentious as the two oldest groups, the Tremataspididae and the Ateleaspididae, vary greatly from each other. This has led to two separate hypotheses as to the phylogenetic relationships within osteostracans. The Tremataspididae-basal hypothesis, says that paired fins evolved within the Osteostraci and that separate lineages of cornuate osteostracans (those possessing cornual processes) were derived independently (Westoll, 1945; Denison, 1951a). The *Ateleaspis*/Ateleaspididae-basal model holds that the paired pectoral fins are primitive and that the cornua evolved once and were subsequently lost in some more derived taxa (Janvier, 1985; Sansom, 2009a). Recent cladistic analysis (Sansom, 2009a) has favoured the latter model. Based on the Ateleaspididae-basal model, the Osteostraci share a number of characteristics with jawed vertebrates to the exclusion of all other early vertebrate groups, including: an epicercal tail, paired pectoral fins, perichondral bone, a sclerotic ring, and endolymphatic openings (Sansom, 2009a, Forey, 1984; Sahney and Wilson, 2001). The perichondral ossification of cartilages inside the head allows the preservation of a great deal of the internal anatomy of osteostracans from many localities. Osteostracans therefore have one of the best known anatomies among the early vertebrates (Stensiö, 1927; Janvier, 1974, 1985).

General Features of Osteostracans

Nasohypophyseal Opening—Osteostracans share with lampreys a single, median nasohypophyseal opening (Stensiö, 1927). The nasohypophyseal opening is located just anterior to the pineal opening on the dorsal surface of the headshield. This feature may be a synapomorphy of lampreys and osteostracans (Stensiö, 1927), but it has also been suggested to be a primitive vertebrate character (Janvier, 1985; and see Forey, 1984 for discussion). In osteostracans the nasohypophyseal opening is clearly divided into a hypophyseal division ('h' in Fig. 1.1), and a posterior nasal division in the external dermoskeleton ('n' in Fig.

1.1).

Median and Lateral fields—The most obvious synapomorphy of the Osteostraci is the median field ('mf' in Fig. 1.1), located posterior to the pineal opening along the midline, and the lateral fields ('lf' in Fig. 1.1), paired on either side of the headshield and usually just medial to the lateral margin of the headshield. No homologous or analogous structure is known for any other agnathans and their function remains unclear. Once thought to be electric organs (Stensiö, 1927), they are more likely sensory organs, probably related to a pressure or acoustic sensory function (Westoll, 1945; Cory, 1955). The lateral fields are connected to the vestibular cavity via three to five thick canals, the 'sel' canals (Stensiö, 1927; Westoll, 1945; Denison, 1951a).

Median Dorsal Crest—On many forms of osteostracan there is a median dorsal crest, or spine, posterior to the median field. In the primitive Ateleaspididae there are two dorsal fins present, and no dorsal crest; however, in the other non-cornuate, *Hemicyclaspis*, there is no dorsal crest and only a single median scute anterior to the posteriormost dorsal fin (Janvier, 1996).

Cornual Processes—The most divisive feature among osteostracans is the presence of cornua ('cp' in Fig. 1.1), a pair of spines lateral to the pectoral fins. Primitive osteostracans, the non-cornuates, lack cornua (Janvier, 1985), while many of the more advanced forms, particularly those that lived during the Devonian, possess cornua in a variety of shapes and morphologies (e.g., Stensiö, 1927, 1932). The Tremataspididae and the Kiaeraspididae have secondarily lost these cornua (Janvier, 1985; Sansom, 2009a), and in the Benneviaspidida the cornua are sometimes reduced or vestigial. Sansom (2008) discussed the homology of cornua and endoskeletal extensions in the Thyestiida (inclusive of Tremataspididae and Kiaeraspididae).

Orbits—The orbits of osteostracans ('o' in Fig. 1.1) are located on the dorsal surface of the head and typically faced dorsally (e.g., *Benneviaspis*, *Boreaspis*, Janvier, 1985) or dorsolaterally (e.g., *Superciliaspis*, Dineley and Loeffler, 1976; Adrain and Wilson, 1994; Hawthorn et al., 2008; *Machairaspis*, Janvier, 1985). A dorsal projection anterior to the orbit is noted for some species and described here (Chapters 4 through 7). Sclerotic capsules, shared with the gnathostomes, are present in some, but not all, osteostracans (Heintz, 1939; Janvier, 1985).

Ventral Surface of the Headshield—The head of osteostracans is flat on the ventral surface and vaulted dorsally to varying degrees. The above-mentioned characters of osteostracans are all visible on the dorsal surface of the headshield, while the branchial openings and the mouth are located on the ventral surface of the headshield. The branchial openings are paired and run along the lateral edge of the oralobranchial fenestra, a circular gap in the ventral headshield covered by minute platelets, tesserae, or large plates (Heintz, 1939; Stensiö, 1932; and Robertson, 1938 respectively). The mouth is located at the anterior end of the oralobranchial fenestra, immediately posterior to the margin of the headshield. The shape of the mouth can vary greatly in osteostracans (Robertson, 1938; Heintz, 1939; White and Toombs, 1983, Adrain and Wilson, 1994).

General Histology of Osteostracan Dermoskeleton—Like many ostracoderms the histology of the dermoskeleton can vary greatly among taxa within the clade. Generally three layers are present with varying degrees of thickness and development. There is a basal layer of lamelar, cellular bone, a middle layer of porous vascular bone, and a superficial layer (Russell, 1954 in Belles-Isles, 1989; Janvier, 1996). The superficial layer is typically dentinous (Denison, 1951b); however, it can be heavily modified in various osteostracan taxa to include an enameloid layer (e.g., *Timanaspis*, Afanassieva and Karatajute-Talimaa, 2009) or lack the dentinous layer entirely (e.g., *Superciliaspis*, Dineley and Loeffler, 1976).

The MOTH Locality

The Man On The Hill (MOTH) locality, Northwest Territories, Canada, is located in the Mackenzie Mountains, north of Nahanni National Park Reserve. The vertebrate producing 'Fish Layer' is of Lochkovian (Early Devonian) age and is within the Delorme Group (Gabrielse et al., 1973; Blieck et al., 1987; Adrain and Wilson, 1994). This 'Fish Layer' is made up of alternating bands of varying thicknesses of light and dark argilaceous shale (Zorn et al., 2005).

MOTH is a 'Konservat Lagerstätte' for Early Devonian vertebrates. Articulated skeletal remains of acanthodians, putative and undoubted chondrichthyans, heterostracans, thelodonts, and osteostracans have all been described from the locality (Adrain and Wilson, 1994). The diversity preserved at MOTH from each of these groups of early vertebrates is remarkable, as is the quality of preservation. Of particular importance is the diversity of osteostracans, many of which have yet to be described and named. Osteostracans from MOTH are informative about the biostratigraphy of the MOTH locality and about the diversity, phylogeny and biogeography of the Osteostraci. Eight new species including five new genera are described here. Their phylogenetic relationships with previously described osteostracan taxa are examined, and the significance of new taxa to the biogeography of osteostracans is discussed.

LITERATURE CITED

Adrain, J. M., and M. V. H. Wilson. 1994. Early Devonian cephalaspids (Vertebrata: Osteostraci: Cornuata) from the southern Mackenzie Mountains, N.W.T., Canada. Journal of Vertebrate Paleontology 14:301–319.

Afanassieva, O. D., and V. K. Voichyshyn. 1991. Revision of the podolian osteostracans (Agnatha). Paleontologicheskiy zhurnal. 1991: 82–90. [Translated from Russian]

Afanassieva, O. B., and V. N. Karatajute-Talimaa. 2009. The histology of the Upper Silurian osteostracan Timanaspis kossovoii Obruchev (Agnatha) from North Timan, Russia. Acta Zoologica (Stockholm) 90 (Suppl. 1): 38–43.

Arsenault, M., and P. Janvier. 1995. Combien d'Ostéostracés a Miguashia. Geobios 19: 19–22.

Belles-Isles, M. 1989. *Yvonaspis*, nouveau genre d'Osteostraci (Vertebrata, Agnatha) du Dévonien (Emsien-Eifélien) des Grés de Gaspé (Québec, Canada). Canadian Journal of Earth Sciences 26: 2396-2401.

Blieck, A., and P. Janvier. 1993. Siluran-Devonian vertebrate biostratigraphy of Siberia and neighbouring terranes. 87–103. in Long, J. A. (ed.). Palaeozoic Vertebrate Biostratigraphy and Biogeography. Belhaven Press, London, 369 pp.

Blieck, A., D. Goujet, and P. Janvier. 1987. The vertebrate stratigraphy of the

Lower Devonian (Red Bay Group and Wood Bay Formation) of Spitsbergen. Modern Geology 2: 197–217.

Cory, L. 1955. The so-called electric organs of ostracoderms. The American Naturalist 89:177–178.

Denison, R. H. 1951a. Evolution and classification of the Osteostraci. Fieldiana, Geology 11:156–196.

Denison, R. H. 1951b. Exoskeleton of early Osteostraci. Fieldiana, Geology 11: 198–218

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

Forey, P. L. 1984. Yet more reflections on agnathan-gnathostome relationships. Journal of Vertebrate Paleontology 4:330–343.

Gabrielse, H., S. L. Blusson, and J. A. Roddick. 1973. Geology of Flat River, Glacier Lake and Wrigley Lake map areas, District of Mackenzie, Northwest Territories. Geological Survey of Canada, Memoir 366:1–268.

Hawthorn, J. R., M. V. H. Wilson, and A. B. Falkenberg. 2008. Development of the dermoskeleton in *Superciliaspis gabrielsei* (Agnatha: Osteostraci). Journal of Vertebrate Paleontology 28:951–960.

Heintz, A. 1939. Cephalaspida from the Downtonian of Norway. Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo. Matematisk-Naturvidenskapelig Klasse 5:1–119.

Janvier, P. 1974. The sensory line system and its innervation in Osteostraci (Agnatha, Cephalaspidomorphi). Zoologica Scripta 3: 91–99.

Janvier, P. 1985. Les Cephalaspides du Spitsberg. Cahiers de Paléontologie, Section Vertébrés. Éditions du Centre National de la Recherche Scientifique, Paris: 244 pp.

Janvier, P. 1988. Un nouveau Céphalaspide (Osteostraci) du Dévonien Inférieur de Podolie (R.S.S. d'Ukraine). Paleontologica 33: 353–358.

Janvier, P. 1996. Early Vertebrates. Clarendon Press, Oxford, 393 pp.

Janvier, P., and M. J. Newman. 2005. On *Cephalaspis magnifica* Traquair, 1893, from the Middle Devonian of Scotland, and the relationships of the last osteostracans. Transactions of the Royal Society of Edinburgh: Earth Sciences 95: 511–525.

Mark-Kurik, E., and P. Janvier. 1995. Early Devonian Osteostracans from Severnaya Zemlya, Russia. Journal of Vertebrate Paleontology 15: 449–462.

Otto, M., and M. Laurin. 1999. Osteostracan tesserae from the Baltic Middle Devonian: morphology and microanatomy. Neues Jahrbuch für Geologie und Paläontologie. Monatshefte 1999: 464–476.

Ritchie, A. 1967. *Ateleaspis tessellata* Traquair, a non-cornuate cephalaspid from the Upper Silurian of Scotland. Journal of the Linnean Society, Zoology 47:69–81.

Robertson, G. M. 1938. The Tremataspidae: part II. American Journal of Science 35:273–296.

Sahney, S. and Wilson, M. V. H. 2001. Extrinsic labyrinth infillings imply open endolympatic ducts in Lower Devonian osteostracans, acanthodians and putative chondricthyans. Journal of Vertebrate Paleontology 21:660-669.

Sansom, R. S. 2008. The origin and early evolution of the Osteostraci (Vertebrata): a phylogeny for the thyestiids. Journal of Systematic Palaeontology 6:317–332.

Sansom, R. S. 2009a. Phylogeny, classification and character polarity of the Osteostraci (Vertebrata). Journal of Systematic Palaeontology 7:95–115.

Sansom, R. S. 2009b. Endemicity and palaeobiogeography of the Osteostraci and Galeaspida: a test of scenarios of gnathostome evolution. Palaeontology 52:1257–1273.

Stensiö, E. A. 1927. The Devonian and Downtonian vertebrates of Spitzbergen. 1. Family Cephalaspidae. Skrifter om Svalbard or Nordishavet 12:1–391.

Stensiö, E. A. 1932. The cephalaspids of Great Britain. British Museum (Natural History), London, 220 pp.

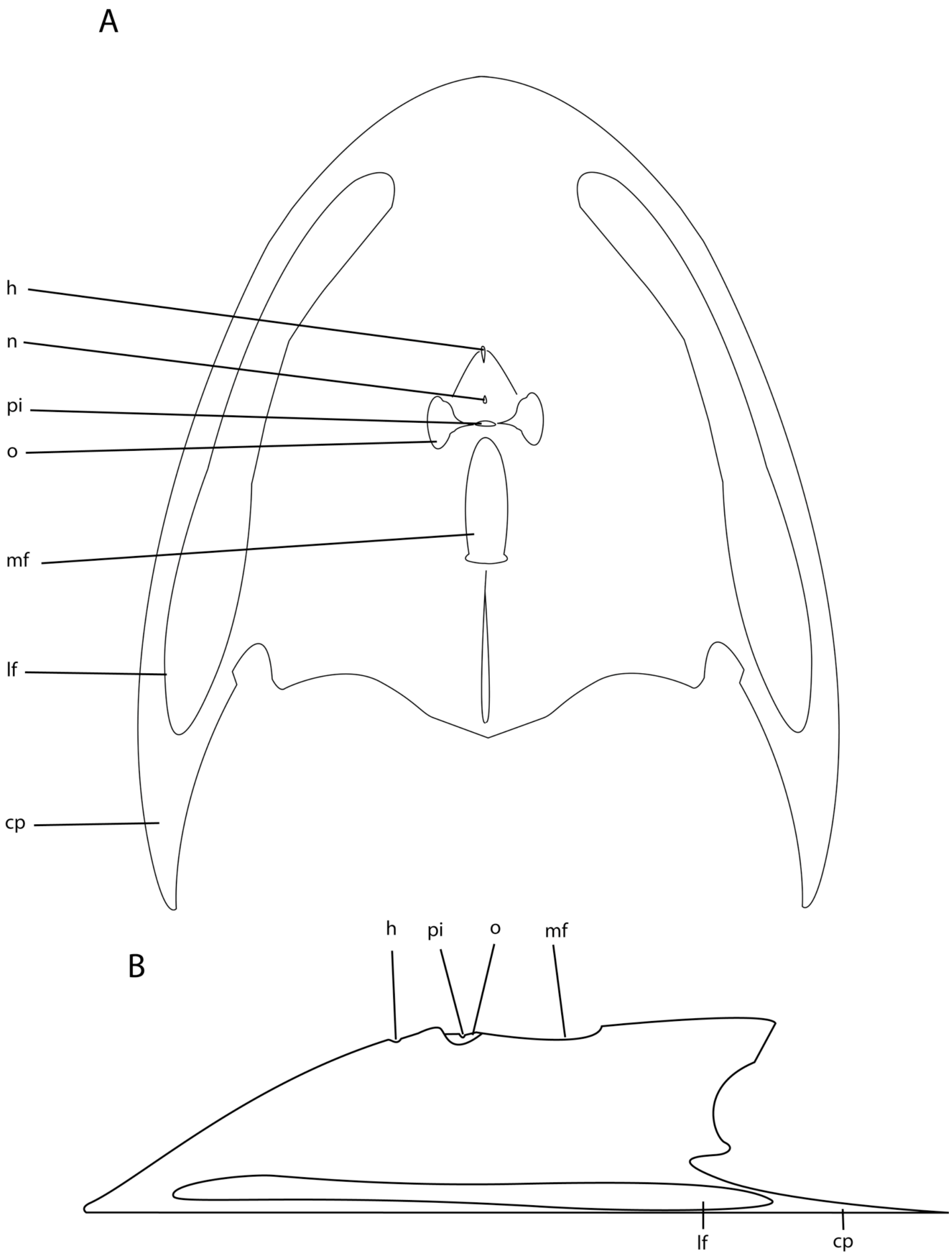
Westoll, T. S. 1945. A new cephalaspid fish from the Downtonian of Scotland, with notes on the structure and classification of ostracoderms. Transactions of the Royal Society, Edinburgh 61: 241–357.

White, E. I., and H. A. Toombs. 1983. The cephalaspids from the Dittonian section at Cwm Mill, near Abergavenny, Gwent. Bulletin of the British Museum of Natural History (Geology) 37:149–171.

Young, G. C., V. N. Karatajute-Talimaa, and M. M. Smith. 1996. A possible Late Cambrian Vertebrate from Australia. Nature 383: 310–312.

Zorn, M. E., M. W. Caldwell, and M. V. H. Wilson. 2005. Lithological analysis of the Lower Devonian vertebrate-bearing beds at the MOTH locality, N.W.T., Canada: insights to taphonomy and depositional setting. Canadian Journal of Earth Science 42:763–775.

FIGURE 1.1. Outline diagrams of a cornuate osteostracan (*Waengsjoeaspis nahanniensis*) in **A**, dorsal, anterior to the top of the page, and **B**, left lateral view, anterior to the left of the page. A list of abbreviations is available in the Materials and Methods chapter.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CHAPTER 2:

A DESCRIPTION OF THE MATERIALS AND METHODS USED IN THIS STUDY INCLUDING: LOCALITY, PREPARATION, MEASUREMENTS, ABBREVIATIONS, PHYLOGENETIC ANALYSIS, AND BIOGEOGRAPHIC RECONSTRUCTIONS

MATERIALS AND METHODS

Locality—All specimens listed were collected as talus from the 'Fish Layer' of the Man On The Hill (MOTH) section in the Mackenzie Mountains, Northwest Territories (NWT), Canada (Adrain and Wilson, 1994). The MOTH locality itself is the so-called 'Fish Layer' in the MOTH section and is equivalent to Geological Survey of Canada (GSC) locality 69014 (Wilson and Caldwell, 1998). The locality is composed of alternating dark grey and light grey laminae of argillaceous limestone, and is currently believed to have been deposited in an intra-shelf topographic low below storm-wave-base (Zorn et al., 2005). The 'Fish Layer' is situated within Section 43, unit 10 of Gabrielse et al. (1973). Gabrielse et al. (1973) considered this a transitional zone between the basinal shales of the Road River Formation and the shallower carbonates of the Delorme Formation. An Early Devonian age is estimated for this locality, based primarily on vertebrate biostratigraphy because of a lack of well-preserved invertebrate specimens (Adrain and Wilson, 1994). The specimens described here are from the University of Alberta Laboratory for Vertebrate Paleontology collections (UALVP) and Canadian Museum of Nature (NMC, formerly National Museums of Canada). Specimens from the British Museum of Natural History (BMNH) are included for discussion.

Preparation—Specimens were prepared by immersion in low concentration (5-15%) acetic acid, followed by gentle removal of loose matrix using soft brushes. Specimens were coated in ammonium chloride sublimate for photography, except where specified in the figure captions.

Measurements—For specimens with only one complete side preserved, the measurement for maximum width was taken as twice the maximum width of one side of the specimen, from the midline. The maximum width of the headshield (A in Fig. 2.1) was measured, and usually occurred just posterior to the base of the cornual processes in most osteostracans described here. The total length of the headshield (B in Fig. 2.1) was measured from the anterior-most point of the headshield to halfway between the posterior tips of the cornua. Measurements of the width of the median field (C in Fig. 2.1) are taken from immediately anterior to the external openings of the endolymphatic ducts. The length of the median field (D) is measured from the anterior end to the posterior end along the midline of the median field. Length of the cornua (E in Fig. 2.1) is measured from the posterior tip of the cornual process anteriorly to a point transverse to the anterior margin of the pectoral sinus. Width of the cornua (F in Fig. 2.1) is measured from the anterior end of the pectoral sinus transversely across the headshield to the lateral margin of the cornual process. Prepineal length (G in Fig. 2.1) is measure from the anterior end of the pineal opening to the anterior-most end of the headshield. Postpineal length (H in Fig. 2.1) is measured from the anterior end of the pineal opening to the posterior end of the abdominal division. Length of the lateral fields (I in Fig. 2.1) were measured from their anterior tip to their posterior tip, along the long axis midway between the lateral and medial margins of the lateral fields. Width of the lateral fields (J in Fig. 2.1) were measured at their greatest width, transverse to the long axis of the lateral field. Orbit width (K in Fig. 2.1) was measured at the span of geatest width of the orbit, perpendicular to the long axis of the headshield. Orbit length (L in Fig. 2.1) was measured at point of greatest length, parallel to the long axis of the headshield. Inter orbital distance (M) was measured from the medialmost margin of one orbit to the medialmost margin of the opposing orbit. Hypophyseal to pineal distance (N in Fig. 2.1) was measured from the anterior end of the hypophyseal division of the nasohypophyseal opening to the anterior end of the pineal opening. Hypophyseal to nasal distance (O in Fig. 2.1) was measured from the anterior end of the nasal opening to the anterior end of the hypophyseal opening.

Anatomical Abbreviations—**ah.l**, left antorbital horn **ah.r**, right antorbital horn, **a.lf**, anterior expansion of the lateral field **bo**, a branchial opening, **bo.1–5**, branchial openings 1–5 **bs.l**, left branchial series, **bs.r**, right branchial series, **cp**, cornual process, **dt**, dorsal tesserae of the headshield, **fa**, canal for the Facial Nerve, **g.1,** 1st groove in the ventral dermoskeleton of *Acerocephale*, **g.2**, second groove in the ventral dermoskeleton of *Acerocephale*, **h**, hypophyseal division, **li**, labyrinth infillings, **ls**, lateral scales, **lf**, lateral field, **m**, mouth, **mc**, the crest or ridge bordering the medial margin of the lateral field, **mf**, median field, **m.m.t.**, the canal for the maxillary and mandibular branch of the trigeminal nerve, **mr**, ridge medial to the lateral margin of the headshield, **n**, nasal division, **o**, orbit, **oc**, ostracod impression, **pf**, pectoral fin, **pi**, pineal opening, **pi.p**, pineal plate, **ps**, pectoral sinus, **p?.l**, plate of unknown affinity on specimen’s left side, **p?.r**, plate of unknown affinity on specimen’s right side, **sb**, base of a dorsal scale, **sc**, crown of a dorsal scale, **sel 1**, 1st canal connecting the labyrinth and the lateral field, **sel 2**, 2nd canal connecting the labyrinth and the lateral field, **sel 3**, 3rd canal connecting the labyrinth and the lateral field **sf**, supraoral field, **sp**, sclerotic plates, **t**, tubercles, **ul**, 'upper lip' of oral platelets, **vls**, ventrolateral scales.

Analyses

Phylogenetics—For the phylogenetic analysis, the character matrix of Sansom (2009a) was used with the addition of new genera from MOTH described in this study, and with the addition of the codings for '*Cephalaspis*' *novascotiae* from Sansom (2009b). Changes to Sansom's (2009a) codings and characters are summarized in the Analysis section of Chapter 8.

Because of the large number of taxa involved, and the uncertainty around the base of the Cornuata, the analysis could not be run to completion using PAUP 4.10b (Swofford, 2000) and the phylogenetic program TNT (Goloboff et. al, 2008) was used to determine the most parsimonious topologies. *Lampetra* was set as the outgroup. A Majority Rules consensus established the most frequently recovered clades, using TNT traditional search with 1000 replicates of random addition sequence, TBR Branch Swapping, and Hold 100 trees at each stepwise addition. Some 360 most-parsimonious trees were retained. A Majority Rules consensus tree was formed from the most-parsimonious trees (Fig. 8.1) and all clades with less than fifty percent frequency among the most-parsimonious trees were collapsed.

Reconstruction of Geographic Distributions—For the reconstruction of the geographic distributions of the osteostracans only the Osteostraci were used (see Sansom, 2009b). *Ateleaspis* was set as the outgroup, for the purposes of analysis in TNT; however, this did not permit a monophyletic Ateleaspididae, as was recovered in the more complete phylogenetic analysis described above. For the purpose of reconstructing the ancestral geographic distributions the resulting topology was rooted at the base of the Ateleaspididae. Ancestral geographic distributions, for each clade, were reconstructed at both the basin and the terrane levels based on the topology for the majority rules consensus of the 'osteostracan only' analysis. Terrane- and basin-level distributions were coded as characters, following phylogenetic analysis, and reconstructed using the parsimony ancestral character reconstruction in Mesquite (Maddison and Maddison, 2010).

Taxa—All osteostracans from Sansom's (2009a) analysis were used, and "*C.*" *novascotiae* was added from Sansom's (2009b) biogeographic analysis. *Acerocephale*, *Glabrapelta* (based on *Glabrapelta cristata*), *Dentapelta*, and *Ceramantyx* were also included from the chapters of this study.

LITERATURE CITED

Adrain, J. M., and M. V. H. Wilson. 1994. Early Devonian cephalaspids (Vertebrata: Osteostraci: Cornuata) from the southern Mackenzie Mountains, N.W.T., Canada. Journal of Vertebrate Paleontology 14:301–319.

Gabrielse, H., S. L. Blusson, and J. A. Roddick. 1973. Geology of Flat River, Glacier Lake and Wrigley Lake map areas, District of Mackenzie, Northwest Territories. Geological Survey of Canada, Memoir 366:1–268.

Goloboff, P. A., J. S. Farris, and K. C. Nixon. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.

Maddison, W.P., and D.R. Maddison. 2010. Mesquite: A modular system for evolutionary analysis. Version 2.74. http://mesquiteproject.org.

Sansom, R. S. 2009a. Phylogeny, classification and character polarity of the Osteostraci (Vertebrata). Journal of Systematic Palaeontology 7:95–115.

Sansom, R. S. 2009b. Endemicity and palaeobiogeography of the Osteostraci and Galeaspida: a test of scenarios of gnathostome evolution. Palaeontology 52:1257–1273.

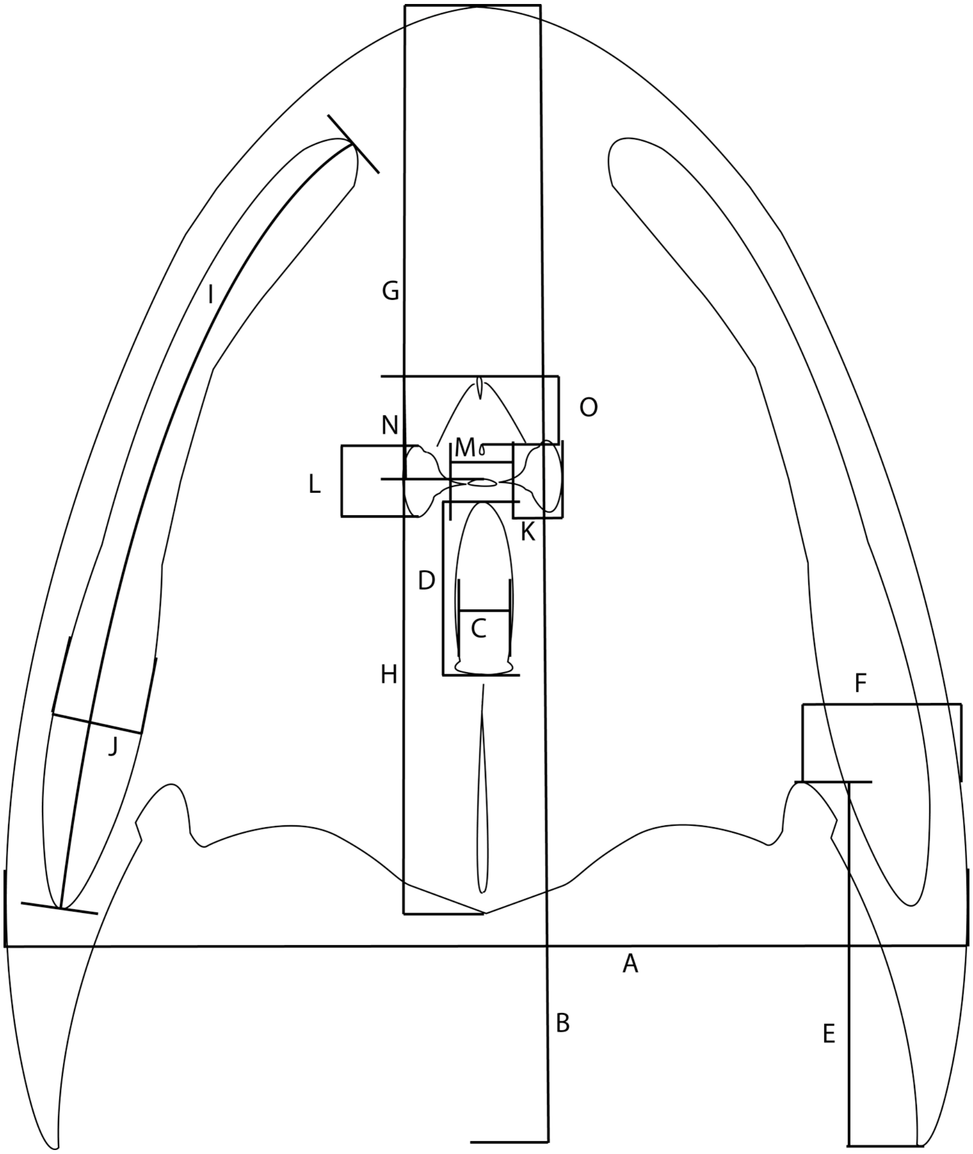
Swofford, D. L. 2000. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts

Wilson, M. V. H., and M. W. Caldwell. 1998. The Furcacaudiformes: a new Order of jawless vertebrates with thelodont scales, based on articulated

Silurian and Devonian fossils from northern Canada. Journal of Vertebrate Paleontology 18: 10–29.

Zorn, M. E., M. W. Caldwell, and M. V. H. Wilson. 2005. Lithological analysis of the Lower Devonian vertebrate-bearing beds at the MOTH locality, N.W.T., Canada: insights to taphonomy and depositional setting. Canadian Journal of Earth Science 42:763–775.

FIGURE 2.1. Outline diagram of a cornuate osteostracan (*Waengsjoeaspis nahanniensis*) demonstrating measurements taken during description of taxa in this study. Symbols are associated with measurements in text in the Measurements section of Chapter 2: Materials and Methods.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CHAPTER 3:

ACEROCEPHALE ACANTHOLEPIS, GEN. ET SP. NOV., A NEW GENUS AND SPECIES OF NON-CORNUATE OSTEOSTRACAN FROM THE MAN ON THE HILL LOCALITY, NORTHWEST TERRITORIES, CANADA

INTRODUCTION

The Osteostraci are the sister group to the Gnathostomata. This means that any shared condition between the Osteostraci and the Gnathostomata may represent a shared primitive characteristic, an ancestral character state for both groups. The earliest osteostracans are the Ateleaspididae from the Wenlock of Scotland (Ritchie, 1967) and the Ludlow of Ringerike, Norway (Heintz, 1939; Davies et al., 2005) and the Tremataspididae from the Ludlow of Ringerike, Norway (Heintz, 1967b) and the Wenlock of Oesel, Estonia (Robertson, 1938, 1945). Both of these groups lack the cornua that are prevalent in later osteostracans, but the two groups are not closely related to each other (Janvier, 1985). Both families have been proposed as basal members of the Osteostraci (Westoll, 1945 and Denison, 1951 suggested that the Tremataspididae are basal, while Stensiö, 1932, Sansom, 2009, and Janvier, 1985, proposed that the Ateleaspididae are basal); however, in recent studies (e.g., Sansom, 2009) the Ateleaspididae have been resolved as a basal group of osteostracans, while the Tremataspididae are resolved as a much more drived group. Janvier (1985) found the Ateleaspididae to be a paraphyletic assemblage at the base of the Osteostraci. Together with *Hemicyclaspis*, the ateleaspidids form a primitive grade of osteostracans referred to as the 'non-cornuates.' These are united by a lack of cornual processes, and an externally tessellate headshield and an absence of the derived characteristics of other taxa lacking cornua, namely the superfamilies Kiaeraspidoidea and Tremataspidoidea (e.g., Janvier, 1996; Sansom, 2009). Under the *Ateleaspis*-as-basal model, early osteostracans would have possessed paired pectoral fins, a headshield composed of small polygonal tesserae, and a trunk covered in small rhomboid lateral scales, rather than the long rectangular lateral scales of more advanced osteostracan taxa. It has also been suggested that the numerous small tubercles ornamenting the headshield and trunk of the Atealeaspididae are also primitive for osteostracans (Sansom, 2009).

Acerocephale acantholepis, gen. et sp. nov., a new non-cornuate osteostracan from the Man On The Hill (MOTH) locality, Northwest Territories, Canada, represents the only known non-cornuate taxon from MOTH. It is based on a single nearly complete specimen in ventral view and a fragment of trunk with scales in articulation. The Early Devonian (Lochkovian) age of the 'Fish Layer' at MOTH (Adrain and Wilson, 1994) makes this new species the youngest non-cornuate osteostracan ever described. The new non-cornuate osteostracan can be distinguished from other osteostracans based on its basally constricted pectoral fins and its dorsal trunk ornament. The trunk scales and their ornament are of particular interest as there are similarities between these scales and the scales of other early vertebrates, particularly early chondrichthyans. The sister-group relationship between osteostracans and gnathostomes (Forey, 1984; Sansom, 2009) and the primitive position of *A. acantholepis*, gen. et sp. nov., within the Osteostraci makes the state of the scales of *A. acantholepis*, gen. et sp. nov., significant because of the potential for homologous shared characteristics between *Acerocephale*, gen. nov., and gnathostomes. This could provide information on the primitive conditions of scale growth and formation for the Osteostraci and the

Gnathostomata.

SYSTEMATIC PALEONTOLOGY

Class OSTEOSTRACI Lankester, 1868

Order incertae sedis

Family ATELEASPIDIDAE Traquair, 1899

ACEROCEPHALE, gen. nov.

Etymology—*Acero*, derived from *Akeros*, Greek, “hornless” *cephale*, derived from *kephale*, Greek, “head,” in reference to the absence of cornual processes on the headshield. Gender feminine.

Type and Only Known Species—*Acerocephale acantholepis*, sp. nov.

Diagnosis—As for type and only known species.

ACEROCEPHALE ACANTHOLEPIS, sp. nov.

Fig. 3.1–3.3

Etymology—*Acantho*, derived from *akanthos*, Greek, “spiny” and *lepis*, Greek, “scale,” in reference to the scales of the trunk, which are ornamented with denticles. Gender feminine.

Holotype—UALVP 43641, a headshield and anterior portion of the trunk in ventral view, but missing the right pectoral fin and the caudal fin (Fig. 3.1, 3.2, 3.3A–C).

Paratypes—UALVP 42184, fragment of trunk including articulated scales with long narrow denticles (Fig. 3.3D).

Diagnosis—Osteostracan lacking cornual processes. Ventral tesserae of headshield grading into scales of pectoral fin. Pectoral fins constricted at base. Margin of headshield composed of tiny individual plates. Scales of ventrolateral ridge and dorsal trunk small and rhomboid with numerous denticles ornamenting external surface. Denticles of trunk posteriorly pointed and arranged in alternating transverse rows across each scale. Number of denticles in each row increasing across each scale. Numerous small pores visible in base of each trunk scale with one pore in center and layers of pores surrounding it.

Differs from all other Ateleaspididae by a constricted base of the pectoral fin, and from all osteostracans by the distinct, microsquamose trunk scales, ornamented with rows of denticles. Differs from *Aceraspis* and *Hirella*, whose margins are composed of a rim divided into three distinct sections, and ornamented with rows of long ridges (Heintz, 1939), while the margin of the headshield for both *Acerocephale* and *Ateleaspis* is composed of numerous small, separate plates. Differs from *Ateleaspis* in that the plates composing the margin of the headshield are arranged in groups of three, with one elongate plate and two smaller triangular plates.

Type Locality—The “Fish Layer”, at the Lower Devonian MOTH locality, Mackenzie Mountains, Northwest Territiories, Canada (Gabrielse et al., 1973), in the transitional beds between the Road River Formation and the

Delorme Formation.

Description

Cephalic Shield Measurements of the Holotype—The total length of the headshield, as estimated from the anterior end of the headshield to a point transverse to the base of the pectoral fins, is 51 mm. The maximum width is at least 57 mm as estimated from the maximum width of the left side of the headshield. The prepineal length of the headshield is 27 mm. The hypophyseal division of the nasohypophyseal opening is 14 mm from the pineal region. The nasal division of the nasohypophyseal opening is 4 mm from the hypophyseal division of the nasohypophyseal opening. The pectoral fin is 19 mm long and 14 mm wide at its maximum width, roughly 3 mm from the base of the pectoral fin; the base itself is 11 mm wide. Each of the large plates at the base of the trunk is 14 mm long and 10 mm wide at its longest and widest dimensions.

Headshield—In the holotype, a headshield articulated with the anterior of the trunk is preserved in ventral view (Fig. 3.1). The ventral shield is preserved across the headshield, except at the posterior end, where the dorsal dermoskeleton is exposed in visceral view. Impressions of two ostracods (oc, in Fig. 3.1) are visible posterior to the left orbit and an impression of one ostracod (Fig. 3.1) is visible posterior to the right orbit. Two large plates are present at the base of the trunk in mirror image of one another. Each plate has a flat end and an elongate, projecting curved end. Each of the two large plates has four to six grooves running parallel to the long axis of the plate. The plate on the left side of the specimen (p?.l in Fig. 3.1) is composed of a rough layer of bone. The plate on the right side (p?.r in Fig. 3.1) is covered in a layer of tuberculate bone with long denticles, very small, thin and close together, but the rough layer of bone is also visible under the tuberculate bone. The identity of these plates of bone is unknown as they are too broad and short to be the pectoral girdle, and it is possible that they are allochthonous. A single plate in visceral view is located at the proximal end of the pectoral fin; this plate does not resemble any plates in articulation in this specimen and so it is likely also allochthonous. The internal anatomy of UALVP 43641 (the holotype) is not preserved.

The headshield is parabolic, tapering posteriorly immediately anterolateral to the pectoral fin (Fig. 3.1). The length of the headshield is estimated to be equal to or slightly less than the width of the headshield. The posterior border of the headshield is unclear but the preorbital length is estimated to be equal to the postorbital length.

An external view of the dorsal dermoskeleton of the headshield is not available, but small, individual tesserae are distinguishable in visceral view proximal to the pectoral fin, and anterior to the right side of the trunk (Figs. 3.1 and 3.3A). The dorsal headshield tesserae are small compared to those of other tessellate osteostracans, but they are larger than the tesserae of the ventral shield in the holotype. Linear grooves in the ventral shield may represent sensory lines. The grooves are most obvious on the right side of the headshield where two lines are clearly visible. The first line (g.1 in Fig. 3.1) originates lateral to the nasal division, running straight anterolaterally. The second line (g.2 in Fig. 3.1) originates halfway along the first line and runs posterolaterally in a laterally convex curve. A groove posterior and medial to the labyrinth infillings runs posteriorly then posterolaterally along the underside of the dorsal headshield. This groove is present in a layer of bone visceral to the tesserae of the ventral shield rather than in the tesserae themselves. The groove is lined by parallel broken ridges of bone, morphology typical of sensory canals in other osteostracans. The abdominal division and posterior margin of the headshield are obscured by the pair of large plates at the base of the trunk. Anterior to these plates there is no embossment of a median dorsal crest; however, this crest typically begins at the posterior end of the median field, which is obscured by the ventral dermoskeleton.

Orbits, Pineal Region, and Nasohypophyseal Region—The borders of the orbits are obscured by the ventral dermoskeleton so an accurate reconstruction cannot be made; however, the lateral margin of the left orbit is visible as a thickened ridge of bone, which may be divided into separate plates. A large gap in the visceral skeleton covering the left orbit is visible at the posterior end of the orbit. Based on this visceral view, the orbits were small. The labyrinth infillings are preserved as mounds of white grains roughly midway along the length of the headshield. The pineal plate and opening are not visible; a depression is present anteromedial to the labyrinth infillings and could represent their location.

The nasohypophyseal opening is present in visceral view (Fig. 3.1). Based on this view there is a constriction between the nasal division and the hypophyseal division. The nasohypophyseal opening is located far anteriorly on the headshield, with the nasal division being located about halfway between the labyrinth infillings and the anterior margin of the headshield. The hypophyseal division is equal in size to the nasal division. The morphology of the nasohypophyseal depression cannot be discerned from a ventral view of the headshield.

Median Field—The anterior margin of the median field is unclear. An anteriorly convex transverse ridge between the labyrinth infillings may represent the anterior margin, but this is far posterior to the orbits. The anteriorly convex dip in the ventral dermoskeleton medial to the left orbit is a better candidate, since this is also the most probable location of the pineal region, which makes up the anterior margin of the median field in most osteostracans. The lateral and posterior margins are not preserved, being covered by the ventral dermoskeleton of the headshield. Therefore the length and shape of the median field cannot be determined.

Cornua—No cornua are present in the specimen. A ridge of bone that runs medial to the lateral margin of the headshield (Fig. 3.2B) along its preserved length curves medially at the posteriormost preserved section of the headshield. This ridge points towards the base of the pectoral fin. A V-shaped pair of ridges is present proximal to the base of the pectoral fin. A medial ridge runs anteriorly while a lateral ridge runs anterolaterally. The lateral ridge lines up with the posterior end of the ridge that is medial to the lateral margin of the headshield. Lateral fields are not visible.

Pectoral Fin—The left pectoral fin (Fig. 3.1, 3.3A) is in articulation with the headshield and is nearly complete. The pectoral fin is constricted where it connects with the headshield. The fin extends from the headshield at an oblique angle to the long axis of the headshield, rather than perpendicular to the long axis of the headshield as it is the condition in most osteostracans (e.g., *Superciliaspis* and *Waengsjoeaspis*, Adrain and Wilson, 1994: figs. 3C and 7B respectively). Immediately distal to its base, the pectoral fin broadens before tapering distally to a narrow, rounded tip. Both the ventral and the dorsal scales decrease in size distally along the pectoral fin. The lateral margin of the pectoral fin is only preserved at the proximal end. The scales of the lateral margin are smooth and are larger and more robust than the rest of the scales on the pectoral fin. The ventral scales are mainly preserved at the distal end of the pectoral fin. The ventral scales are tuberculated with narrow ridges that run proximodistally. The dorsal scales are only visible in visceral view but are clearly larger than the ventral scales for the same region of the pectoral fin. The dorsal scales of the pectoral fin are concave in the center with a central pore. The long axis of the base of a dorsal scale is perpendicular to the long axis of the pectoral fin. The bases of the dorsal scales abut one another.

Margin of the Headshield—The margin of the headshield is only preserved at the anterior end of the headshield (Fig. 3.1, 3.2A). It is composed of small, smooth plates similar to the tesserae of the ventral dermoskeleton. The arrangement of the plates of the margin changes from anterior to posterior. The anterior plates are arranged the same as the tesserae of the ventral dermoskeleton as rosettes (see below). This rosette arrangement is retained along the lateral rim of the headshield margin, but the arrangement changes medial to these rosettes, to units of three plates. Each three-plate unit is composed of a large central plate with a long axis parallel to the headshield margin and two smaller triangular plates. There is a lateral projection from the middle of the large plate and the two triangular plates are located on either side of this projection. The units follow in series laterally from the margin of the headshield. The margin of the headshield is not visible in dorsal view, but it is wide in ventral view.

Ventral Headshield—The ventral dermoskeleton shows little differentiation between the oralobranchial chamber and the rest of the headshield (Fig. 3.1). It is composed of small, circular platelets, which are arranged as a rosette, with a central platelet surrounded by six smaller, circular platelets. Each rosette is here considered be a tessera. Additional small, round platelets can join each tessera. The individual platelets are occasionally fused at the superficial layer. The tesserae between the branchial series and the margin of the headshield are smaller and ornamented with rows of posteriorly pointing denticles.

The oral region of the ventral headshield is covered by tesserae that are smaller and thinner than those of the rest of the ventral dermoskeleton. These oral tesserae are preserved in a variety of shapes and orientations. The outer surface of the oral tesserae can be smooth or ornamented with long, low, posteriorly pointing denticles. The denticles are arranged in a row of three to four, with some tesserae possessing a second row of three to four denticles. The typical tesserae of the ventral dermoskeleton are not present around the oral region, which extends from immediately posterior to the anterior margin of the headshield to the posterior end of the nasal division and laterally to a point anterior to the first branchial opening.

The size and shape of the mouth cannot be distinguished directly, but based on the width of the ‘upper lip’ (Fig. 3.2A) the mouth was wide relative to the size of the headshield. Anterior to the oral region and overlapping the headshield margin is a short, wide, crescentic strip of delicate scales in visceral view that represents the ‘upper lip’ (Adrain and Wilson, 1994). The bases of the ‘upper lip’ scales are rhomboid, with a thick rim relative to the size of the scale. The center of the base of the scale has a central pore surrounded by circles of smaller pores, and has grooves radiating from the center. The median scales of the ‘upper lip’ are smaller and more varied in shape than the more lateral scales of the ‘upper lip’.

Five branchial openings are visible on the left side of the headshield (Fig. 3.2D) and three branchial openings are visible on the right side of the headshield (Fig. 3.2C). The branchial series extends anteroposteriorly medial to the lateral margin of the ventral headshield. Each branchial opening is bordered anteriorly and posteriorly by a ridge, the branchial arch, extending medially to the center of the headshield. The medial border of each branchial opening is a medially convex, semicircular series of ventral dermoskeleton tesserae. The branchial openings are bordered laterally by tesserae that are slightly smaller than those of the medial ventral dermoskeleton. The branchial openings of the right branchial series are covered by scales smaller than the surrounding ventral tesserae. The scales are ornamented with a row of long, posteriorly pointing denticles. The branchial openings of the left branchial series are completely uncovered.

Trunk—The shape of the trunk cannot be determined as the right side and posterior end of the trunk are not preserved. The ventrolateral ridge is only preserved on the left side of the trunk. The scales lateral to the ventrolateral ridge are identical to those of the ventrolateral ridge. These are the dorsal scales and so the description of the dorsal scales also applies to the scales of the ventrolateral ridge. The trunk dorsal scales are visible in visceral view on the right side of the anterior of the trunk, lateral to the two large plates (Fig. 3.1). The bases of the trunk dorsal scales are a series of rhombic rims, each with a large pore in the center that is surrounded by smaller pores. An external view of the dorsal trunk scales is available lateral to the ventrolateral ridge (Fig. 3.3B, C) and along the ventrolateral ridge itself. The dorsal trunk scales have long denticles that are deeper and more robust than those on the ventral trunk scales. The dorsal trunk denticles point posteriorly and extend posteriorly beyond the base of the scale. The denticles directly overlie the base of the dorsal trunk scales (Fig. 3.3C); no neck is present on any scales. The denticles of the dorsal trunk scales (Fig. 3.3B) are numerous (between eight and eighteen denticles per scale, with at least one scale having twenty-five) and arranged as a semicircular cluster, the convex side pointing anteriorly. Denticles are consistent in size among dorsal trunk scales, for a given position on a scale. The denticles are shorter in the first two anterior rows and longer, narrower, and with a sharper posterior point in the posterior rows of each scale. Matrix, the removal of which could risk the loss of scales, still covers much of the bases of the dorsal trunk scales, making counts of pores and reconstruction of pore layout difficult and inexact. The pores in the base of the dorsal trunk scales vary in size but usually the central pore is the largest and is surrounded by smaller pores, with an additional ring of pores in some scales.

There are between nine and sixteen pores on each scale.

The ventral scales are visible on the left side of the trunk and the posterior right side of the trunk (Fig. 3.1). The ventral trunk scales near the anterior of the trunk are rectangular and arranged in anterolateral to posteromedial rows. The individual borders of these scales are undifferentiated posterior to the first two visible rows. The posterior margin of each row of ventral trunk scales can still be distinguished as a ridge except at the posteriormost preserved end of the trunk. The ventral trunk scales are ornamented with rows of numerous gracile, triangular denticles. The posteriormost denticles of each scale extend distally from the scale base at a greater angle than the anterior denticles of each scale. The ventral trunk scales near the posterior end of the trunk grade medially from those with an arrangement of denticles similar to those of the ventrolateral scales to rows of flat-lying, short, rounded denticles pointing posteriorly. The only possible candidate for a dorsal fin is a triangle of dorsal scales at the posterior end of the trunk. The squamation of the scales does not change across this section.

The scales of UALVP 42184 are similar to the scales found on the posterior end of the ventral surface of the trunk of the holotype of *Acerocephale acantholepis* (UALVP 43641), which is why it is designated as a paratype for the species. The bases of some scales are in visceral view and are identical to those of UALVP 43641. The base is rhomboid with a thickened rim. A central pore in the base is surrounded by several other pores. Several of the denticles on scales of the paratype, UALVP 42184 (Fig. 3.3D), have broken at their distal ends. In transverse section the denticles are solid bone (probably dentine, as there are no vacuities or vascular openings) throughout. Lines radiate from the center of the denticles that have been broken. These lines are probably the tubules of dentine in the crown. These tubules run from the external surface to the center of the denticle. If these lines are tubules it would be consistent with dentine as the superficial layer for the denticles, and the radiating morphology would be consistent with a gradual infilling of the pulp cavity. The bases of the denticles are not exposed in transverse or longitudinal section through denticle breakage anywhere on UALVP 42184, and so the association of pores with each denticle cannot be confirmed on this specimen either.

Remarks

Much of the ventral headshield and trunk are preserved on UALVP 43641 (Fig. 3.1). The lateral margin of the headshield, the opercular flaps of the left branchial openings and part of the ventral surface of the pectoral fin are not preserved. The scales and small plates covering these areas would have been susceptible to loss via erosion. The remainder of the specimen is intact and articulated, suggesting that any erosion was very low energy.

The grooves described on the ventral headshield of the holotype (UALVP 43641) do not correlate with any sensory lines described for the ventral shield of osteostracans (Janvier, 1974). This leaves the identification of these grooves as being uncertain. The groove near the median field, posteromedial to the labyrinth infillings, has many possible contributers: the longitudinal dorsal branch of the lateral nerve, the dorsal spino-occipital nerve, and a posterior branch of the vertebromedullary vessel are all located around this position (based on the reconstruction of the internal anatomy of *Scolenaspis*, Janvier, 1985: fig. 33), though none of them is directly associated with the median field, which would be located in this region of the dorsal headshield of *Acerocephale*.

There is no gap in the scales around the oral region to indicate the location and shape of the mouth. The 'upper lip' (Figs. 3.1, 3.2A) is taken as a proxy of the mediolateral extent of the mouth, but no such proxy can be provided for the anteroposterior extent of the mouth.

A triangular section of dorsal scales lateral to the trunk may represent a dorsal fin; however, unlike the dorsal fins of other non-cornuates (e.g., Heintz, 1967a; Ritchie, 1967) there would be no difference in squamation between the anterior part and the rest of the fin. It is therefore more probable that the dorsal fin is not visible in UALVP 43641 and the triangular section of dorsal trunk scales is simply an articulated fragment of the dorsal trunk. Because pulp cavities are not confirmed for individual denticles, reference to each denticle unit as an odontode is reserved for the discussion.

DISCUSSION

Absence of the Cornua

The cornual processes are not present in the two known specimens of *Acerocephale acantholepis*. Two possible reasons for this exist: either the cornual processes were never present, or the cornual processes were removed from the specimen as a result of taphonomic processes, in particular preburial ones. It is suggested here that based on the other non-cornuate characteristics of *Acerocephale* (discussed below) and the retention and articulation of much of the headshield, including many small tesserae and scales, the cornual processes were not present during life. The cornual processes of osteostracans are typically a continuous, fused unit (e.g., as in *Waengsjoeaspis*, see Wängsjø, 1952; Janvier, 1985; Adrain and Wilson, 1994) or are composed of a few large plates (e.g., as in *Superciliaspis*, see Dineley and Loeffler, 1976; Adrain and Wilson, 1994). The pectoral fin, the trunk scales, and the scales of the headshield are all preserved on the holotype of *A. acantholepis*. Only the posterior of the margin of the headshield, composed of small plates, is not preserved. Any forces that could have removed the cornual processes would also have been strong enough to remove the pectoral fin and trunk as well. It is therefore most likely that a cornual process was not present in *A. acantholepis*.

Affinities of *Acerocephale*

Acerocephale can be referred to the Ateleaspididae based on the small scales composing the ventral shield and the short, parallel ridges that form the margin of the headshield. The absence of cornua is also a key feature, though not exclusive, for the family. The ornament for all members of Ateleaspididae is composed of numerous small tubercles. *Acerocephale* may also represent a transitional form between the Ateleaspididae and *Hemicyclaspis* as the pectoral fin in the new genus is clearly separate from the trunk, unlike other members of the Ateleaspididae, but, based on the dorsal headshield that is visible in visceral view anterior to the pectoral fin, there is none of the differentiation between the pectoral fin and the headshield observed in *Hemicyclaspsis* (Stensiö, 1932; Janvier, 1985). The tiny individual plates that make up the margin of the headshield of UALVP 43641 are similar to those that compose the margin of the headshield of *Ateleaspis* (Ritchie, 1967), and both of these taxa have a margin different from the other members of the Ateleaspididae (*Aceraspis* and *Hirella*, Heintz, 1939). The nasohypophyseal opening is slit-shaped in *Aceraspis*, *Hirella*, and *Ateleaspis* (Heintz, 1939; Ritchie, 1967). The condition of the nasohypophyseal opening is not clear as it is poorly preserved in *Acerocephale* and the morphology of the visceral components is likely not representative of the exterior dorsal morphology of the opening itself.

The opening for the mouth of *Acerocephale* cannot be distinguished from the scales around the oral region. The only proxy available as to the shape of the mouth is the ‘upper lip’ visible at the anterior margin of the headshield. In *Waengsjoeaspis* and *Superciliaspis*, the width of the mouth is equal to the width of this ‘upper lip’ (Chapter 4 and Adrain and Wilson, 1994, respectively) and so, if the same relationship of ‘upper lip’ to mouth size applies to the new genus, the mouth of *Acerocephale* would have been very wide. This would have differed from the narrow mouth observed in *Aceraspis* (Heintz, 1939).

The nasohypophyseal opening is located farther anteriorly on the headshield, and constricted between the nasal and hypophyseal divisions. However, this is based only on the visceral view and does not included the dorsal dermoskeleton, which can greatly alter the shape of the opening (see Chapter 4 on *Waengsjoeaspis*).

Acerocephale is the only non-cornuate osteostracan described from the Lower Devonian. *Acerocephale* also possesses characteristics of the Ateleaspididae, *Hemicyclaspis*, and more derived osteostracans, and of early chondrichthyans. The chondrichthyan-like polyodontode morphology of *Acerocephale* is unique among osteostracans. Because the development of the microsquamose squamation not known for other osteostracan taxa it is not possible to determine whether the polyodontode scales present in *Acerocephale* are primitive for both osteostracans and gnathostomes, or whether they are instead convergent between the two groups.

Trunk Scales

The evolution of vertebrate dermal elements has been a subject of great interest. Given their phylogenetic position as sister group to gnathostomes, osteostracans have the potential to provide much information on this stage in vertebrate evolution. Unfortunately the mesosquamose condition of most osteostracans is considered a derived characteristic within the group and models for the primitive states of odontode arrangement and development are based on thelodonts and gnathostomes, especially chondrichthyans. *Arandaspis* and Ordovician vertebrate remains are generally microsquamose (except *Sacabambaspis*; Janvier, 1996). Even in primitive osteostracans (e.g., *Ateleaspis*, *Aceraspis*, and *Hirella*) the trunk scales, although further divided than in more advanced osteostracans, are composed of elongate rectangular lateral scales (Heintz, 1939; Ritchie, 1967) and are mesosquamose, rather than the microsquamose condition of early gnathostomes and thelodonts (Karatajute-Talimaa, 1998). The holotype of *Acerocephale*, described here, represents the only near-complete osteostracan specimen that differs considerably from the normal osteostracan, mesosquamose, arrangement of the trunk scales (the rectangular scales of *Ilemoraspis* are of a different morphology and, although much more divided than the lateral scales of other osteostracans, Sansom 2008, are probably still mesosquamose).

The difference between the scales of *A. acantholepis* and those scales typically referred to as chondrichthyan (Karatajute-Talimaa, 1998) is the absence of a neck and the associated neck canals, and the presence of a thick rim of basal bone around the base of the scale, rather than a laminar layer covering the visceral surface of the scale (present in both chondrichthyans and thelodonts, Karatajute-Talimaa, 1998) or an anterior basal projection of laminar bone (thelodonts, Karatajute-Talimaa, 1998). The scales of *A. acantholepis* resemble those of early chondrichthyans in that there are multiple denticles on each scale, arranged in rows transverse to the length of the scale. The number of denticles per scale roughly coincides with the number of pores visible in the base of each individual scale. If each pore coincides with a denticle it would be indicative of a pulp cavity for each denticle, and it would be consistent with a polyodontode morphology. Denticles on the paratype UALVP 42184 are broken and display a radiation of bone from a central point in the cross-section of the denticle. This central point is proposed to be the remains of a pulp cavity in the denticle, supporting the identification of these denticles as individual odontodes. The arrangement of denticles is such that the largest denticle is often in the second or third row, and the surrounding denticles are smaller—the smallest being at the anterior end of the scale—and the posterior end of the scale has large denticles. The largest pores are in the center and are surrounded by pores, arranged in concentric, or 'areal,' regions.

Ventrolateral trunk scales vary in size and number of denticles. The squamation of the ventral trunk scales is less clear as the boundaries between scales are not delineated. This is especially prevalent towards the posterior end of the trunk, and so a clear discussion of their characteristics is not possible, but the ventral trunk scales appear to be similar in morphology and arrangement to the dorsal trunk scales.

Scale Growth

Arrangement and size relation of the denticles on individual trunk scales is constant among scales. Also, no ridges or layers of bone are visible on individual denticles. This is inconsistent with growth of individual odontodes following scale formation. Growth of the scales of *Acerocephale acantholepis* occurred through addition of odontodes to each scale. No growth of individual odontodes seems to have occurred following the initial formation of the scales, and there is no sign of fusion between individual scales either.

Growth of Denticles—Variation in the size of denticles on a single scale, and between scales of the dorsal trunk and scales of the ventral trunk could be a result of growth of individual denticles; however, there are no layers of bone visible on the denticles, to indicate growth, and denticles are of similar size for their location between scales on the dorsal trunk and scales on the ventral trunk. Examination of transverse sections of the distal end of the denticles of UALVP 42184 reveals an absence of outward growth of the denticle. There are no cyclical layers within the denticle, and from an external view there is no addition of ornament or layers of bone on the outside of the denticle. Rather, the development of the denticle appears to be one of internal mineralization. The dentine in the denticle is not arranged as horizontal layers, but instead, the superficial dentine layer radiates from a central point in the denticle. The dentine was probably laid down from outside to inside in the denticle and therefore absence of a pulp cavity in the denticle is a result of infilling with dentine. This would be consistent with a polyodontode development where the odontode does not grow, and rejects the suggestion put forth by Gross (1972 in Otto and Laurin, 2001) that the hollow tubercles in osteostracans form from an expansion of vascular canals in the dermoskeleton, at least for the denticles of *A. acantholepis*.

Addition of Odontodes—Based on the arrangement of the pores, the largest denticle usually being in the center of the scale, and the areal adherence of odontodes onto the scale, a continuous growth model is considered the most likely scenario for scale growth in *A. acantholepis*. The base of the scale is concave, and the odontodes are clearly separate from one another (Fig. 3.3B). There is no incorporation of one scale into another scale, and the denticles vary in size. This would most closely resemble the B_2 subtype of the *Ctenacanthus* type of scale growth (Karatajute-Talimaa, 1992); however, if *Acerocephale* had *Ctenacanthus*-type scale growth, we should see a variation in the size of the scales. Also, the denticles fuse to one another in the crown of the scale in *Ctenacanthus* type scales, while in *Acerocephale* the denticles fuse at the base of the scale rather than in the crown. The smallest denticles of *Acerocephale* are at the anterior end of the scale; however, the largest denticles are not always at the posterior end, inconsistent with an anterior addition of denticles to the scale, making the addition of odontodes irregular, and probably occurring laterally and posteriorly on the scale. The denticles are typically similar in size among scales and scales are typically similar in size to one another in a given section of the trunk. Because earlier ontogenetic stages are not known for *Acerocephale* it is difficult to determine methods of growth for the scales of the trunk, and so in spite of superficial similarities with chondrichthyan scales, comparisons with chondrichthyan growth types must remain tentative.

Development of the osteostracan dermal elements has been speculated upon, but only the ontogenetic series of *Superciliaspis* is known (Hawthorne, 2008). Hawthorn et al. (2008) discussed the development of the squamation of the trunk but were unable to provide information on the development of individual units in the trunk. The scales of *Acerocephale* resemble those of some chondrichthyans in possessing numerous elongate odontodes, arranged in transverse rows (e.g., *Teslepis*, Karatajute-Talimaa and Novitskaya, 1992) and a rhomboid base. Unfortunately, as only a single almost complete specimen and a fragment of trunk with scales are known for this taxon, the development of the scales of *Acerocephale* is unknown at this time. While possession of individual odontode units appears to be shared with the chondrichthyans, and a micromeric polyodontode morphology may also be shared with chondrichthyans, and therefore, possibly gnathostomes, the development of polyodontode scales is too uncertain to ascertain homology between scale growth in *Acerocephale* and scale growth in the Chondrichthyes.

SUMMARY

A new non-cornuate osteostracan, *Acerocephale acantholepis*, is described from MOTH, it represents the youngest known non-cornuate osteostracan, as it is Lochkovian (Early Devonian) in age. *Acerocephale* is placed in the Ateleaspididae based on the absence of cornua, paired pectoral fins, a covering of minute platelets over the oralobranchial region of the ventral headshield, and a margin of the headshield which is composed of small elongate plates. The most unique characteristic of *Acerocephale* are the scales of the trunk. These scales are polyodontode and are ornamented with sharp, posteriorly pointed individual denticles. Each denticle is hypothesized to possess a pulp cavity, based on the numerous pores on the basal surface, and centrally radiating bone visible in transverse section of the distal end of the denticles.

LITERATURE CITED

Adrain, J. M., and M. V. H. Wilson. 1994. Early Devonian cephalaspids (Vertebrata: Osteostraci: Cornuata) from the southern Mackenzie Mountains, N.W.T., Canada. Journal of Vertebrate Paleontology 14:301–319.

Davies, N. S., P. Turner, and I. J. Sansom. 2005. A revised stratigraphy for the Ringerike Group (Upper Silurian, Oslo Region). Norwegian Journal of Geology 85: 193–201.

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

Denison, R. H. 1951. Evolution and classification of the Osteostraci. Fieldiana, Geology 11:156–196.

Forey, P. L. 1984. Yet more reflections on agnathan-gnathostome relationships. Journal of Vertebrate Paleontology 4:330–343.

Gabrielse, H., S. L. Blusson, and J. A. Roddick. 1973. Geology of Flat River, Glacier Lake and Wrigley Lake map areas, District of Mackenzie, Northwest Territories. Geological Survey of Canada, Memoir 366:1–268.

Heintz, A. 1939. Cephalaspida from the Downtonian of Norway. Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo. Matematisk-Naturvidenskapelig Klasse 5:1–119.

Heintz, A. 1967a. Some remarks about the structure of the tail in cephalaspids. Pp.

21-36 in Problemes Actuels de Paléontologie (Évolution de Vertébrés). Colloques Internationaux du Centre National de la Recherche Scientifique. Centre National de la Recherche Scientifique, Paris.

Heintz, A. 1967b. A new tremataspidid from Ringerike, South Norway. Journal of the Linnean Society (Zoology) 47: 55–68.

Janvier, P. 1974. The sensory line system and its innervation in Osteostraci (Agnatha, Cephalaspidomorphi). Zoologica Scripta 3: 91–99.

Janvier, P. 1985. Les Cephalaspides du Spitsberg. Cahiers de Paléontologie, Section Vertébrés. Éditions du Centre National de la Recherche Scientifique, Paris: 244 pp.

Janvier, P. 1996. Early Vertebrates. Clarendon Press, Oxford, 393 pp.

Karatajute-Talimaa, V. 1992. The early stages of dermal skeleton formation in chondrichthyans. 223–231. In Mark-Kurik, E. (ed.). Fossil fishes as living animals Academy of Sciences of Estonia, Tallin, 299 pp.

Karatajute-Talimaa, V. 1998. Determination methods for the exoskeleton of early vertebrates. Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe 1: 21–52.

Karatajute-Talimaa, V. and L. I. Novitskaya. 1992. *Teslepis* - A new genus of Mongolepid elasmobranch from the Lower Silurian of Mongolia. Paleontological Journal 4: 36-46. (In Russian)

Lankester, E. R. 1868. A Monograph of the Fishes of the Old Red Sandstone of Britain. Part I. The Cephalaspidae. Monograph of the Palaeontographical Society, London, 62 pp.

Otto. M., and M. Laurin. 2001. Microanatomy of the dermal skeleton of

Balticaspis latvica (Osteostraci, Middle Devonian). Journal of Vertebrate Paleontology 21: 186–189.

Ritchie, A. 1967. *Ateleaspis tessellata* Traquair, a non-cornuate cephalaspid from the Upper Silurian of Scotland. Journal of the Linnean Society, Zoology 47:69–81.

Robertson, G. M. 1938. The Tremataspidae: part I. American Journal of Science 35:172–206.

Robertson, G. M. 1945. Cephalaspids from the Upper Silurian of Oesel, with a discussion of cephalaspid genera. American Journal of Science 243: 169–191.

Sansom, R. S. 2009. Phylogeny, classification and character polarity of the Osteostraci (Vertebrata). Journal of Systematic Palaeontology 7:95–115.

Stensiö, E. A. 1932. The cephalaspids of Great Britain. British Museum (Natural History), London, 220 pp.

Traquair. R. H. 1899. Report on fossil fishes collected by the Geological Survey of Scotland in the Silurian rocks of the South of Scotland. Transactions of the Royal Society of Edinburgh 39: 827–864.

Wängsjø, G. 1952. The Downtonian and Devonian vertebrates of Spitsbergen. IX. Morphologic and systematic studies of the Spitsbergen cephalaspids. Results of Th. Vogt's Expedition 1928 and the English-Norwegian-Swedish Expedition in 1939. Norsk Polarinstitutt Skrifter 97:1–611.

Westoll, T. S. 1945. A new cephalaspid fish from the Downtonian of Scotland, with notes on the structure and classification of ostracoderms.

Transactions of the Royal Society, Edinburgh 61: 241–357.

FIGURE 3.1: Large composite image of *Acerocephale acantholepis*, gen. et sp. nov., UALVP 43641, holotype in ventral view. Scale bar is equal to 10 mm.

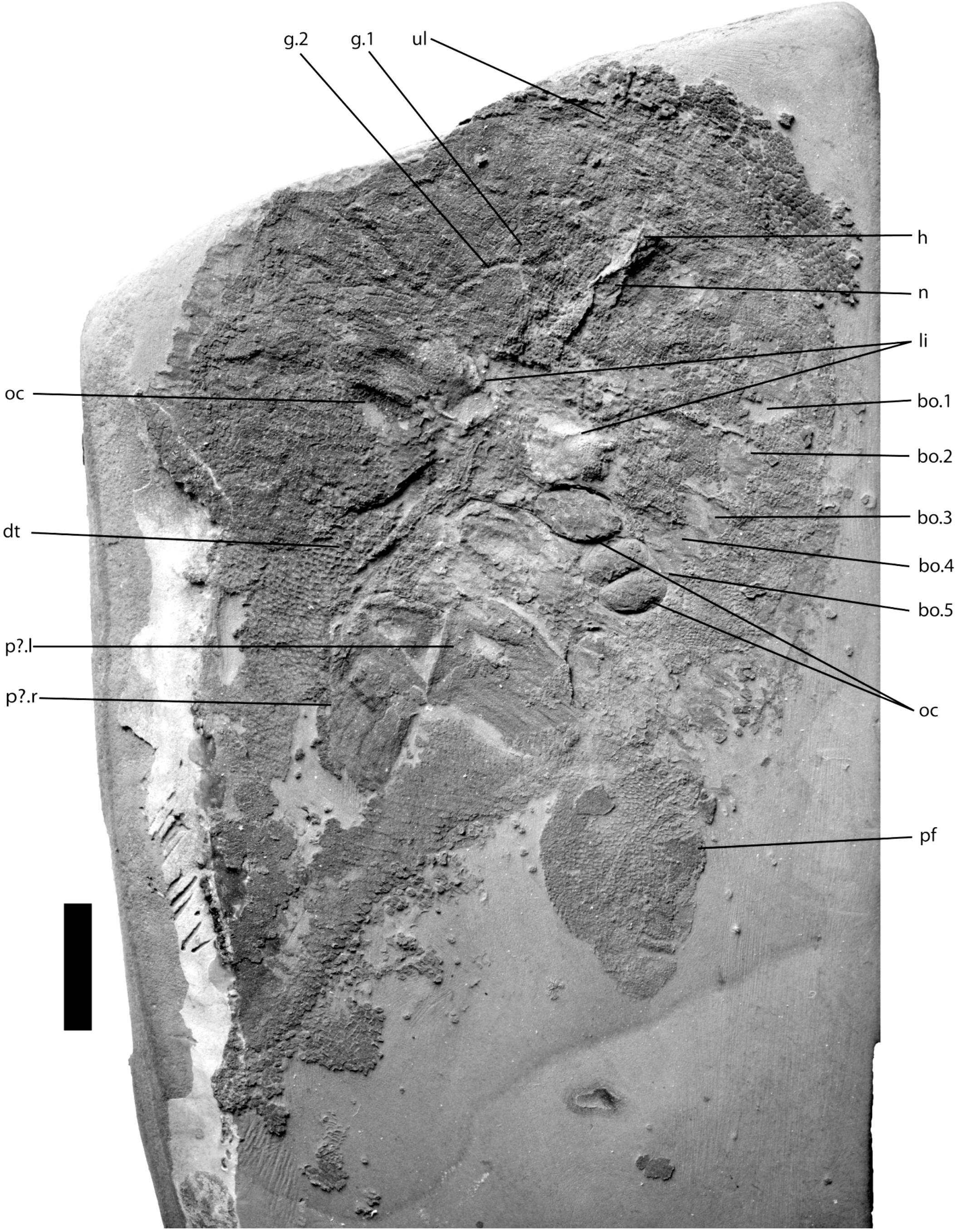
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FIGURE 3.2. Detailed images of *Acerocephale acantholepis*, gen. et sp. nov., UALVP 43641, the holotype. Each detailed image is a close-up of a boxed area in the whole specimen image below it. **A**, detail of the anterior margin of the headshield, in particular the three plate units composing much of the headshield margin should be noted. **B**, the posterolateral margin of the headshield, the ridge medial to the margin of the headshield labelled as **mr**. **C**, the right branchial series in detail, with the first three branchial openings labeled; the covering of the openings is preserved. **D**, the left branchial series in detail, with the first five branchial openings preserved, the opercular covering absent. Scale bars equal to 10 mm.

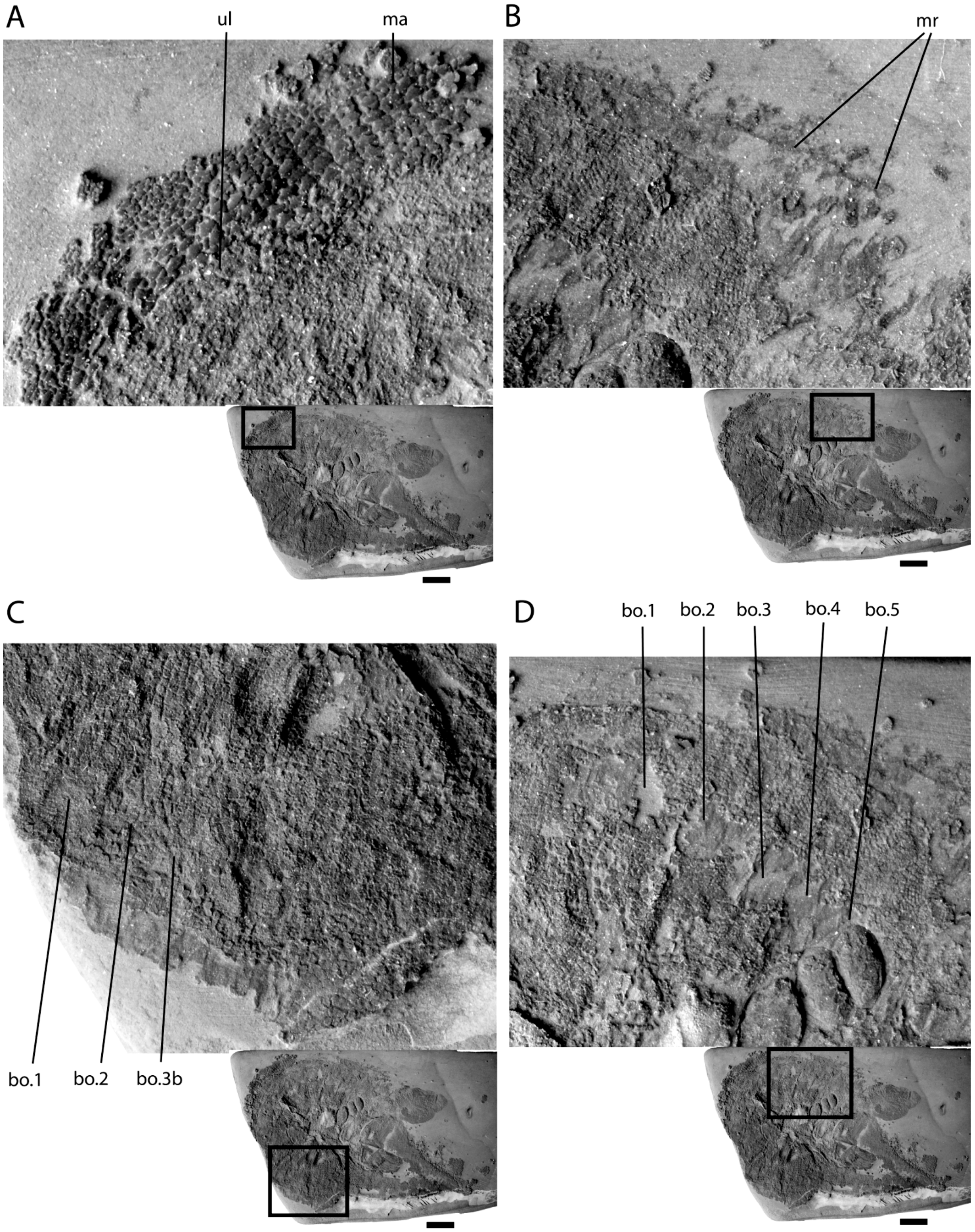
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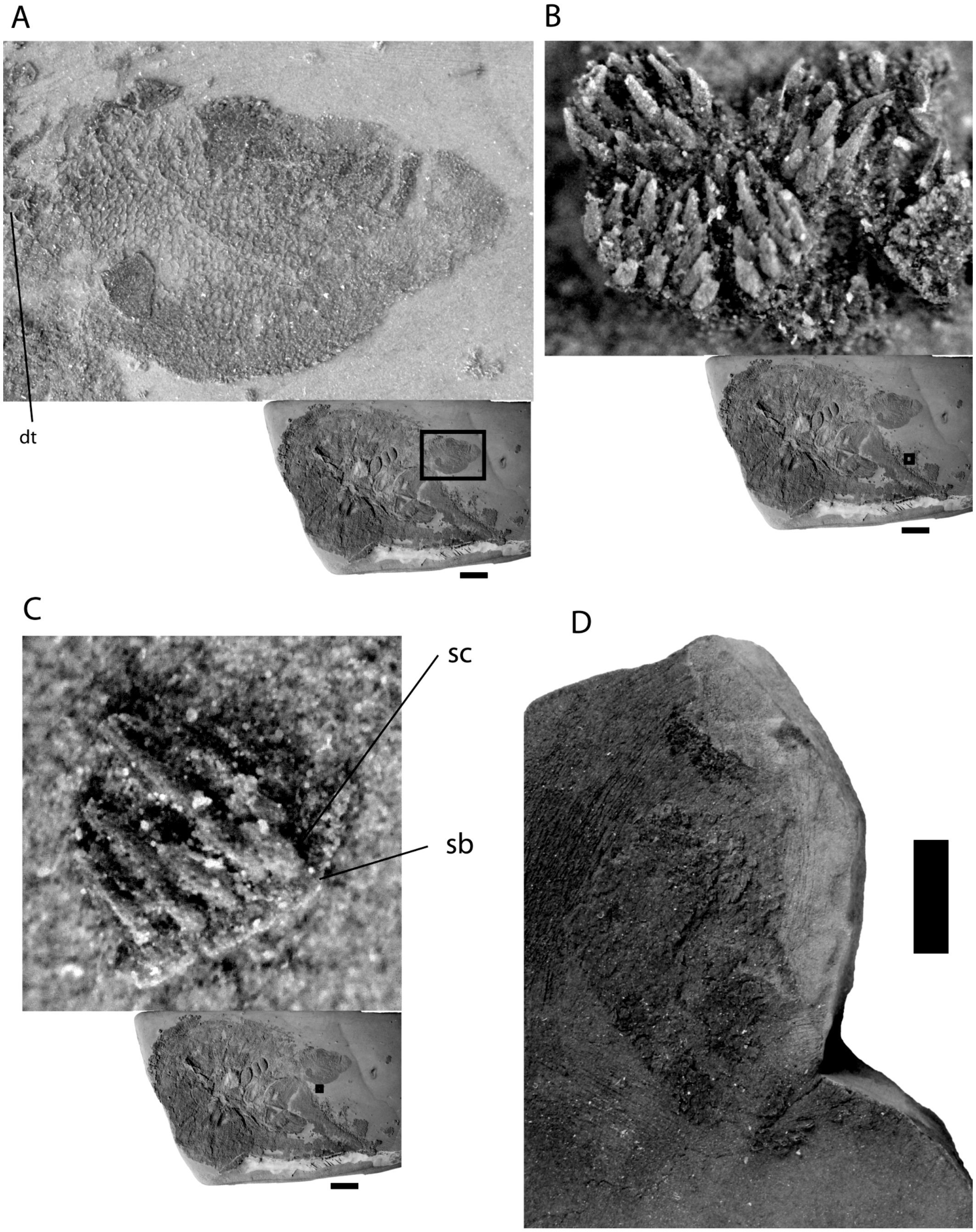
FIGURE 3.3. A–C *Acerocephale acantholepis*, gen. et sp. nov., detailed images of UALVP 43641, the location of each detailed image is shown as a box in the whole-specimen image below it. **A**, detail of the pectoral fin, not the constricted base and the dorsal scales proximal to the base of pectoral fin (to the left on the image), which resemble the proximal scales on the pectoral fin. **B**, detail image of dorsal trunk scales in oblique dorsal view, the denticles clearly arranged with the smallest at the anterior end. **C**, another detail image of a dorsal trunk scale, this one viewed from the anterior; the denticles connecting directly with the base of the scale. **D**, the paratype of *A. acantholepis*, gen. et sp. nov., UALVP 42184, an articulated fragment of trunk scales. Scale bars equal to 10 mm.


A
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CHAPTER 4:

WAENGSJOEASPIS PLATYCORNIS, SP. NOV., A NEW SPECIES OF CORNUATE OSTEOSTRACAN FROM THE MAN ON THE HILL LOCALITY, NORTHWEST TERRITORIES, CANADA, WITH A REDESCRIPTION OF *WAENGSJOEASPIS NAHANNIENSIS**

*This Chapter has been submitted for publication and authorship is shared with Mark V. H. Wilson. Each section of this chapter, along with the figures were written and assembled by myself; however, advice on organization, and edits to grammar were based on the suggestions and advice of the Mark V. H. Wilson.

INTRODUCTION

The Man On the Hill (MOTH) locality is a Lower Devonian (Lochkovian) Konservat-Lagerstätte from which a large diversity of early vertebrate remains have been recovered. Among the early vertebrates preserved at MOTH are numerous members of the class Osteostraci. *Waengsjoeaspis* is a genus of osteostracan known from both MOTH, in the Mackenzie Mountains of Canada, and Spitsbergen, Norway. Our recent review of the diversity of osteostracans at MOTH has identified a second species of *Waengsjoeaspis*. The first species of *Waengsjoeaspis* known from the locality, *W. nahanniensis* Adrain and Wilson, 1994, is redescribed herein and compared to the new species, which is described for the first time.

Osteostracans are an extinct group of jawless vertebrates, the first of which was described by Louis Agassiz (1835) as *Cephalaspis lyelli*. Among jawless vertebrates, osteostracans are easily recognized by their epicercal tail and the presence of pectoral fins in numerous species, both important characters that osteostracans share with primitive jawed vertebrates (Forey, 1984; Janvier, 1996; Sansom, 2009a). Osteostracans are also distinguished by peculiar sensory fields located on an armored head. No analog for these structures is available among any known extant or fossil taxa, making a more precise interpretation of their function difficult (Janvier, 1996). In the 175 years since Louis Agassiz's original description of *Cephalaspis lyelli*, the descriptions of numerous species from a range of localities in Europe, North America, and Siberia (e.g., Stensiö, 1927, 1932; Denison 1952, 1955; Obruchev, 1956; Janvier, 1985a) have provided a clearer understanding of osteostracan diversity and biogeography (Sansom, 2009a, b).

The Man On The Hill (MOTH) locality is a Lower Devonian vertebrate locality in the Mackenzie Mountains, Northwest Territories, Canada, known for its exquisite preservation of both jawed and jawless early vertebrates. MOTH has yielded a large variety of heterostracan, fork-tailed thelodont, osteostracan, acanthodian and putative chondrichthyan species (e.g., Dineley and Loeffler, 1976; Wilson and Caldwell, 1993; Hanke, 2002). "*Cephalaspis*" *gabrielsei* was the first osteostracan described from MOTH by Dineley and Loeffler (1976). Adrain and Wilson (1994) then erected the new genus *Superciliaspis* for "*Cephalaspis*" *gabrielsei* and described two new species of osteostracan from MOTH: *Diademaspis mackenziensis* and *Waengsjoeaspis nahanniensis*. Here we redescribe *Waengsjoeaspis nahanniensis* to reflect what is now seen as reduced variation in characters and we describe a second species of *Waengsjoeaspis* that provides new information on the trunk and ventral headshield.

The genus *Waengsjoeaspis* was erected by Janvier (1985a) to include "*Cephalaspis*" *excellens* Wängsjø, and "*Cephalaspis*" *vogti* Stensiö, both species known only from Spitsbergen, Norway. Janvier (1985a) based his diagnosis of the genus primarily on specimens of *Waengsjoeaspis excellens*. The characters of the genus included: the separation of the nasal and hypophyseal divisions, a median field that does not contact the pineal furrow, an 'sel' 1 canal, the canal which connects the lateral fields with the vestibular cavity (Westoll, 1945; Janvier, 1985), that bifurcates just medial to the lateral field, and a medial recess in the myodome. *Waengsjoeaspis nahanniensis* was described by Adrain and Wilson (1994). It differs from the two species of *Waengsjoeaspis* from Spitsbergen in having a narrower median field and a median edge of the cornua that is smooth, rather than armed with barbs.

In their description of *W. nahanniensis*, Adrain and Wilson (1994) noted a great deal of variation in the morphology of the headshield. The proportions of the cornua were observed as being particularly variable and this was explained as differences in the direction of compaction of the headshield during burial. Along with variation in the proportions of the cornua there is also variation in the median field. New specimens present a different explanation for the variation of *W. nahanniensis*: the presence of a second species of *Waengsjoeaspis* at MOTH. The preservation of bilaterally symmetrical specimens of both species show that these characters are not a result of distortion of specimens, but rather a result of real morphological variation. This variation is considered here to be evidence of speciation rather than sexual dimorphism, individual variation, or ontogenetic variation. Among extant agnathans, sexual dimorphism has been reported for lampreys (e.g., Lyons et al., 1996; Vladykov, 1955; Bond and Kan, 1973, Dendy and Scott, 1953) but is generally rather minor and primarily expressed as differences in body size. The morphological variation between *W. nahanniensis* and *W. platycornis*, sp. nov., is unlikely to be individual variation within the population as the characters separating the two species are both distinct and consistently correlated with each other.

At present, *Waengsjoeaspis* is only known from the island of Spitsbergen (the largest island in the Svalbard archipelago north of Norway) (Wängsjø, 1952; Janvier, 1985a) and from the MOTH locality in northwestern Canada (Adrain and Wilson, 1994), although possible fragments have been reported from the *Traquairaspis* conglomerates of Berlin, Germany, and the *Psammosteus* Limestone Group in Britain (Ørvig, 1969). These deposits are all considered to be of Early Devonian age (Janvier, 1985a; Adrain and Wilson, 1994).

In his original description of the genus, Janvier (1985a) noted that *Waengsjoeaspis* shares characters with the thyestidians, with *Nectaspis*, and with tremataspidians. Beyond these conclusions, Janvier was unable to discern the phylogenetic relationships of *Waengsjoeaspis* within the Osteostraci. Sansom (2009a) provided the first comprehensive cladistic analysis of osteostracan genera. In his analysis, *Waengsjoeaspis* is placed in a clade with *Camptaspis* and *Yvonaspis*. This clade is placed basal to the Benneviaspidida; however, according to Sansom the classification of these taxa is ambiguous given a lack of "reliable synapomorphies" (Sansom, 2009a:17). Although it is clear that *Waengsjoeaspis* bears cornual spines, and is therefore a cornuate osteostracan, a more precise classification of this genus remains uncertain.

SYSTEMATIC PALEONTOLOGY

Class OSTEOSTRACI Lankester, 1868

Subclass CORNUATA Janvier, 1985a

Order and Family incertae sedis

WAENGSJOEASPIS Janvier, 1985a

Type Species—*Cephalaspis excellens* Wängsjø (1952: 308); Early Devonian, Fraenkelryggen Formation, Spitsbergen.

Other Species—"*Cephalaspis*" *vogti*, *W. nahanniensis*, *W. platycornis*, sp. nov.

Diagnosis—The diagnosis for *Waengsjoeaspis* remains as described by Adrain and Wilson (1994): a cornuate with a short median field whose anterior end does not contact the posterior edge of the pineal plate, and separation of the nasal and hypophyseal openings.

Remarks

The genus was erected by Janvier (1985a) on the basis of both external and internal characters. When Adrain and Wilson (1994) assigned *Waengsjoeaspis nahanniensis* to this genus, no internal characters were known for this species and so the diagnosis was modified to only include external characters. The new species, *W. platycornis,* sp. nov., only preserves a single internal character. Because there is still no information on internal characters in *W. nahanniensis*, the diagnosis by Adrain and Wilson (1994) for the genus, using external characters only, is retained.

WAENGSJOEASPIS NAHANNIENSIS Adrain and Wilson, 1994

(Fig. 4.1)

Waengsjoeaspis nahanniensis Adrain and Wilson, 1994, p. 310, figs. 7A, 8A, C, non 7B, 8B (original description).

Holotype—UALVP 19140, the left side of a headshield with a cornual process, nasohypophyseal region, orbit, pineal plate, and partial median field preserved (Fig. 4.1A).

Paratypes—UALVP 19255, cornual process and pectoral sinus; UALVP 41643, visceral view of headshield with cornual processes (Fig. 4.1D); UALVP 41645, fragments of headshield including: partial margin, orbits, nasal opening, and median field; UALVP 41735, orbits and median field in visceral view; UALVP 41747, posterior three-quarters of headshield in dorsal view (Fig. 4.1C); UALVP 42213, nearly complete headshield with anterior of trunk, missing left cornual process (Fig. 4.1B); UALVP 52494, partial headshield in visceral view with fragment of margin; UALVP 52605, articulated specimen including headshield and anterior of trunk in dorsal view.

Revised Diagnosis—A species of *Waengsjoeaspis* with narrow cornual processes, but lacking barbs on the cornua. The length of the cornual processes is equal to two and a half times the basal width of the cornual process. The median field is long and narrow with the lateral borders of the median field running parallel, or nearly parallel, to the midline of the headshield.

Differs from *Waensjoeaspis excellens* by absence of barbs on medial margin of cornual processes, and by a longer, more narrow median field in relation to size of headshield. Differs from *Waengsjoeaspis platycornis*, sp. nov., by cornual processes longer relative to width of their base and by median field that is more narrow than that of *W. platycornis*, sp. nov., and does not widen posteriorly.

Revised Description

Unless otherwise mentioned, these observations are in agreement with Adrain and Wilson (1994); deviations from the earlier description are based on additional material, and on the reassignment of some previously referred specimens to *W. platycornis*, sp. nov., *Waengsjoeaspis* sp., or to cf. *Waengsjoeaspis* sp. Measurements of specimens of *W. nahanniensis* are recorded in Table 4.1.

General Morphology—The headshields of all specimens are clearly longer than their maximum width. The dorsal surface of the headshield is covered in numerous small tesserae (Fig. 4.1). These tesserae generally increase in size posteriorly. In addition to information in the original description, we note that these tesserae are typically hexagonal but that larger tesserae are more irregular in shape. Some tesserae have concentric growth rings bordering their margins; this is particularly common posteriorly. There is a large pre-pineal region of the headshield, with the pineal furrow located roughly halfway between the anterior end of the headshield and the posterior end of its abdominal division, where the shield extends over the trunk. A low median dorsal crest extends from the posterior border of the median field to the posterior end of the headshield. No dorsal spine is present (Fig. 4.1C).

Orbits, Nasohypophyseal Region, and Pineal Region—The orbits are longer than they are wide, having a raised lateral rim composed of fused tesserae and a median notch where the orbit contacts the pineal furrow. It is the pineal furrow itself, rather than the pineal plate as described by Adrain and Wilson (1994), that narrows medial to the orbits before widening around the pineal opening. The pineal plate is large and fills the pineal furrow. The nasal and hypophyseal divisions are separate openings found in a triangular depression bordered posteriorly by the orbits and pineal furrow (Fig. 4.1A, B). The teardrop-shaped hypophyseal opening is located at the anterior tip of the nasohypophyseal depression and tapers posteriorly. The nasal opening is located roughly a quarter of the distance from the pineal opening to the hypophyseal opening, on a raised mound (Fig. 4.1A, B). The nasal opening is also teardrop-shaped but tapers anteriorly. On either side of the nasal mound, fine furrows run from just lateral to the pineal opening to the anterior margin of the median field, broken by the pineal furrow (Adrain and Wilson, 1994:fig. 8A).

Median Field—The median field is long and narrow, its length relative to its width being between 2.4:1 and 3.5:1. The lateral edge of the median field runs roughly parallel to the midline of the headshield and is bordered by a robust rim of several thick polygonal plates. The anterior margin of the field is rounded in all specimens, except in UALVP 41747 where the anterior edge of the median field is straight instead (Fig. 4.1C). The posterior margin, where clearly preserved, is convex; however, it appears to be straight in the holotype. Small polygonal tesserae cover the median field (Fig. 4.1A).

Cornua and Lateral Fields—The cornual processes are long and narrow. They are approximately one-third the length of the entire headshield and two and a half times longer than wide. The medial surface is continuous and smooth, lacking barbs. The lateral fields are outlined most clearly by a slight separation between higher tesserae of the headshield and lower ones of the lateral fields. The lateral fields are long and narrow, but, contra Adrain and Wilson (1994), are observed here as having a rounded anterior tip and widening posteriorly before tapering into the cornual process (Fig. 4.1A, B). The length in relation to the width of the lateral fields is approximately 10:1. The lateral fields are covered in tesserae identical to those of the dorsal headshield except that they lack concentric growth rings.

Margin of the Headshield—The margin of the headshield is smooth, with closely spaced pores, and is composed of a fused set of polygonal plates, larger than tesserae. It is rather narrow in dorsal aspect (Fig. 4.1A, B), and broad in ventral view (Fig. 4.1D). The original description of the ventral shield of *W. nahanniensis* was based on UALVP 32915; this specimen can no longer be assigned to *W. nahanniensis* because it does not preserve the median field, cornua, or nasal opening and therefore a description of the ventral shield cannot be provided for this species.

Pectoral Fin and Trunk—Based on its wide median field, wide cornua, and circular nasal opening, UALVP 19145, the specimen for which the original description of the pectoral fin is provided, is here designated (see below) as the holotype of *W. platycornis*, sp. nov., instead of *W. nahanniensis*. UALVP 19257, the specimen on which the original description of the trunk and ventral trunk of *W. nahanniensis* is based, can no longer be assigned to this species because of the lack of preservation of the median field, and differences in the cornual process and pectoral fin. UALVP 42213, a specimen that is clearly referable to *W. nahanniensis*, provides a clear comparison of the pectoral fin (Fig. 4.1B). That of UALVP 42213 is morphologically virtually identical to that of UALVP 19145, even having similar dimensions; therefore, the description of the pectoral fin of *W. nahanniensis* based on UALVP 42213 applies also to the pectoral fin of *W. platycornis*, sp. nov., based on UALVP 19145.

The pectoral fin is approximately the same width as the pectoral sinus and extends posteriorly as far as the tip of the cornual process. The scales of the pectoral fin are large and irregularly-shaped immediately posterior to the anterior tip of the pectoral sinus. The scales grade into short, wide rectangular scales along the medial margin and diamond-shaped scales lateral to these. The scales towards the lateral and posterior edges of the pectoral fin are much smaller than those mentioned previously, irregular in shape and pebbly in texture, rather than smooth (these "pebbles" are sometimes connected). The scales along these margins are the smallest on the fin.

The description of the ventral surface of the trunk and pectoral fin can no longer be based upon UALVP 19257 because it is of uncertain species assignment. UALVP 42213 provides a dorsal view of the trunk including the anterior-most region of the median dorsal ridge. No median dorsal scales or scutes are present; instead the lateral scales extend dorsally, towards the midline, where they contact one another. The lateral scales are narrow and overlap slightly with the next more posterior scales. The ventrolateral ridge scales of UALVP 42213 are very similar to those of UALVP 19145 described by Adrain and Wilson (1994) but here designated (see below) as the holotype of *W. platycornis*, sp. nov. Each scale along the ventrolateral ridge can be considered as two parts that actually grade into one another: the part of the scale that is directly along the ridge and the portion of the scale that is dorsal to this. The dorsal part of the scale is similar to the lateral scales, but with its long axis directed anteriorly and medially rather than the anterior and lateral direction of the lateral scales (Fig. 4.1B). The portion of the ridge scale that caps the ventrolateral ridge is slightly more robust than the rest of the scale, although it is slightly less robust than that observed in UALVP 19145. The ventrolateral ridge portion tapers posteriorly and is covered with fewer, larger pores. No dorsal or caudal fins can be conclusively referred to this species.

Remarks

Some specimens originally referred to *W. nahanniensis* do not preserve the diagnostic characters of this species, and therefore the additional information they provided for the original description is excluded from this modified description.

Specimens of *W. nahanniensis* display a large variation in median field width, but the field is always narrower than that of *W. platycornis*, sp. nov. UALVP 19140, 41747, and 42213 in particular have exceptionally long, narrow median fields.

WAENGSJOEASPIS PLATYCORNIS, sp. nov.

(Figs. 4.2, 4.3)

Osteostraci indet.: Dineley and Loeffler, 1976:173, NMC 21561 only.

Waengsjoeaspis nahanniensis Adrain and Wilson, 1994 (in part): Adrain and Wilson, 1994:figs. 7B, 8B.

Etymology—*Platy*, derived from *platys*, Greek, "wide, broad" and *cornis*, Latin, "horn," in reference to the broad cornual processes. Gender masculine.

Holotype—UALVP 19145, preserving the headshield, pectoral fin, and partial trunk but missing the right pectoral fin and cornual process, the left orbit, and the left half of the median field (Fig. 4.2A) (Adrain and Wilson, 1994:fig. 7B).

Paratypes—UALVP 19141, right half of margin of headshield, orbits, and nasohypophyseal region; UALVP 32969, visceral view of mostly complete headshield (Fig. 4.2C) (Adrain and Wilson, 1994:fig. 8B); UALVP 41633, partial headshield with orbits, nasohypophyseal region, and pineal furrow preserved in dorsal view; UALVP 41477, complete dorsal headshield preserved in visceral view (Fig. 4.2B); UALVP 41883, small headshield with trunk preserved in dorsal view (Fig. 4.3B); UALVP 43086, nearly complete dorsal headshield preserved in visceral view (Fig. 4.3D); UALVP 44008, cornual processes and margin of headshield in ventral view; UALVP 52493, headshield in internal view, dermoskeleton not preserved (Fig. 4.3C); UALVP 52495, partial headshield with fracture along right side and spreading of headshield across left side (Fig. 4.3A); NMC 21561, median field and nasohypophyseal region preserved in visceral view.

Diagnosis—A species of *Waengsjoeaspis* lacking barbs along the medial edge of the cornual process, but with a median field that that is wide relative to its length and widens posteriorly. The base of each cornual process is wider in relation to its length than in *W. nahanniensis* or *W. excellens*. Cornual processes are no more than twice as long as wide.

Differs from *W. excellens* by absence of barbs along medial margin of cornual processes. Differs from *W. excellens* and *W. nahanniensis* by median field that widens posteriorly. Cornual processes length relative to width of base less than *W. nahanniensis*.

Type Locality—The Lower Devonian (Lochkovian) “Fish Layer” at MOTH, Mackenzie Mountains, Northwest Territories, Canada, in transitional beds between the Road River Formation and the Delorme Formation (Gabrielse et al., 1973).

Description

Measurements of specimens of *W. platycornis* are recorded in Table 4.2.

Headshield—In the holotype, the headshield forms a broad semicircle and, as with most osteostracans preserved at MOTH, is crushed dorsoventrally. The left orbit and left side of the median field are not preserved. The headshield is also missing the right pectoral sinus and the right cornual process (Fig. 4.2A).

The dorsal headshield is covered in small, polygonal tesserae. These are generally smaller towards the anterior of the headshield, and larger posteriorly. The tesserae are often hexagonal, but some have a more irregular shape and appear to be several tesserae fused together. Some tesserae show centrifugal growth lines, especially those positioned medially and posteriorly on the headshield. The tesserae are ornamented with numerous small pores across the surface, but lack denticles or tubercles. Gaps in the dermoskeleton of the dorsal headshield provide a visceral view of parts of the ventral shield. The ventral tesserae are generally smaller than the dorsal tesserae with multiple porous centers within a single tessera. Radiating canals are visible along the edge of each tessera and more shallow ones are visible between porous centers.

The infraorbital sensory line is preserved medially on the right side of the headshield and laterally on the left side of the headshield. The infraorbital sensory line runs medial to the lateral field; however, as detailed below, the precise extent of the lateral field is not always clear. The infraorbital sensory line is present as a shallow groove in the superficial layer of the tesserae.

The dorsal median crest is not preserved in the holotype and there is no evidence of a dorsal spine. In UALVP 41477 the median crest is seen in ventral view (Fig. 4.2B). It starts immediately posterior to the median field and extends to the posterior end of the headshield. The crest is shallow and no dorsal spine is present.

Orbits, Pineal Region, and Nasohypophyseal Region—The orbits and pineal furrow are located halfway between the anterior and posterior ends of the headshield. Only the right orbit is preserved (Fig. 4.2A). The orbit is circular and has a raised lateral rim composed of tesserae from the dorsal headshield. The pineal furrow runs between the orbits, perpendicular to the anteroposterior axis of the specimen (Fig. 4.2A, 4.3C). The furrow narrows medial to the orbits and then widens around the pineal opening. The pineal plate is short and wide (Fig. 4.2A) and fills the pineal furrow. It extends from the medial edge of the orbit to the pineal opening. The surface of the pineal plate is covered in small pores; this ornament is identical to that of the tesserae. The pineal opening itself is round on its right side; however, the left side is incomplete. The pineal opening of UALVP 41477 (Fig. 4.2B) is expanded laterally. The nasal and hypophyseal divisions of the nasohypophyseal are separated, with each division forming its own opening. The nasal opening appears circular on the holotype, but the superficial layer of the dermoskeleton has been eroded away making it likely that the shape is an artifact of preservation. The nasal opening is elongate and tapers anteriorly in visceral view in UALVP 32969 and UALVP 41477. The hypophyseal opening is teardrop-shaped, tapering posteriorly in all specimens. The region around the nasal and hypophyseal openings is only faintly depressed; however, the superficial layer of the dermoskeleton is poorly preserved here.

Median Field—The median field is long and wide, having a length to width of only 1.6:1. There are no tesserae preserved in the median field, although in UALVP 41477 polygonal ridges within the median field may represent casts of small tesserae (Fig. 4.2B. The shape of the median field is variable among specimens (Fig. 4.2). It is rounded anteriorly (Fig. 4.2A, B), though the anterior tip itself is not preserved in the holotype, and it widens posteriorly to a width equal to the external openings of the endolymphatic ducts, a width that is maintained (Fig. 4.2C) or increases slightly (Fig. 4.2A, B) for most of its length, then either tapers uniformly to a blunt point posteriorly (Fig. 4.2C) or is truncated posteriorly except for a median rounded lobe (Fig. 4.2B). The lateral edge of the median field in the holotype is bordered by at least three large plates that appear to be formed from fusion of tesserae, as shown by faint polygonal grooves (Fig. 4.2A).

Cornua and Lateral Fields—The cornua are directed posteriorly and broad, each one only twice as long as its maximum width at its base. The tip of the cornual process curves medially slightly. The length of each cornual process is nearly half the length of the headshield excluding the cornua, or nearly one-third the total length of the headshield. The medial margin of the cornual process lacks denticles or barbs and is uninterrupted and covered by a texture resembling that of tesserae. This continuous medial margin may extend around the pectoral sinus, but is fractured where the pectoral sinus is preserved (Figs. 4.2A, 4.3B). The lateral margin of the cornual process changes posteriorly from smooth plates to a series of flat, broad, and close-fitting tubercles. The dorsal surface of the cornua posterior to the lateral fields is continuous and smooth in UALVP 19145 and UALVP 41883, except for numerous small pores identical to those covering the tesserae of the headshield and except where fractures in the cornua dermoskeleton are present.

The lateral field is difficult to distinguish from the rest of the dermoskeleton, but appears to be long and narrow, though less narrow than that of *W. nahanniensis*, having a length to width of 7.4:1. The border of the lateral field is identified by a slight separation of tesserae in the dorsal headshield. The tesserae of the lateral fields are identical to those of the rest of the headshield except that there are no centrifugal growth rings. The rounded anterior ends of the lateral fields extend to the rostral region of the headshield as far medial as the orbits (Fig. 4.2A). The lateral field is poorly preserved at its posterior end on the holotype; it extends at least to the cornual process, but not to the tip of the cornual process. The lateral margin of the lateral field is very close to the margin of the headshield. The medial margin is equidistant from the lateral margin along the length of the lateral field.

Margin of the Headshield—The margin of the headshield is formed from fused or tightly joined rectangular plates. The posterior margin of the headshield extends well posterior to the pectoral sinus and tapers posteriorly into an abdominal division. It is lined by unfused tesserae. The margin is narrow in dorsal view (Fig. 4.2A). Based on UALVP 41477, the margin is much wider in ventral view (Fig. 4.2B, see also Fig. 4.2C). Despite the crushed condition of the headshield of the holotype, the margin maintains a vertical depth. The lining of the oral or pharyngeal cavity is not preserved on any specimen.

Pectoral Fin—The pectoral fin of the holotype appears identical to that of

UALVP 42213, a specimen of *W. nahanniensis*, even having similar dimensions, and so the description of the pectoral fin for *W. platycornis* is the same as the description of the pectoral fin for *W. nahanniensis*.

Trunk—The trunk tapers lateral to the abdominal division of the headshield, then maintains its width posteriorly (Fig. 4.2A). The lateral scales are transversely elongate, with a smooth, slightly convex anterior edge and a rough, slightly convex posterior edge (Fig. 4.2A). The surface ornament of these lateral scales is identical to that of the tesserae of the headshield. Shallow grooves forming polygonal shapes appear to denote the tesserae that have fused to form the lateral scales. Anterior lateral scales appear to be formed from hexagonal tesserae similar to those of the headshield, while posterior lateral scales appear to be formed from square scales or tesserae (Fig. 4.2A). Ventrolateral scales are imbricated and robust along the ventrolateral ridge, but dorsally these scales resemble lateral scales (Fig. 4.2A). The dorsal portion of each ventrolateral scale is directed anterodorsal to the ventrolateral ridge (Fig. 4.2A). Ventrolateral scales are not apparent until about 15 mm posterior to the anterior end of the pectoral sinus, as far posterior as the pectoral fin extends; anterior to the ventrolateral scales are lateral scales lacking any robust imbricated portions like those more posteriorly along the ventrolateral ridge. The ventral covering of the trunk, the dorsal fin, and the caudal fin are not known for any specimens referable to *W. platycornis*.

Internal Morphology—In UALVP 52493, the dermoskeleton is scarcely preserved or completely missing (Fig. 4.3C). This is fortuitous as it reveals a sensory field canal, ‘sel’ 1, (Stensiö, 1927; Janvier, 1985a) which has been infilled with grains from the labyrinth canals (Sahney and Wilson, 2001), creating a cast of the ‘sel’ 1 canal. In this specimen, ‘sel’ 1 originates from just anterior to the orbit and extends anterolaterally as a single canal until it bifurcates medial to the lateral field, a feature also seen in the species of *Waengsjoeaspis* from Spitsbergen.

Remarks

Adrain and Wilson (1994) assigned *Waengsjoeaspis nahanniensis* to the genus *Waengsjoeaspis* based on external characters alone, due to a lack of internal characters preserved for osteostracans from MOTH; however, a previously undescribed specimen of *Waengsjoeaspis* from MOTH, *W. platycornis*, sp. nov., has an ‘sel’1 canal that bifurcates just medial to the lateral field, a diagnostic internal character for *Waengsjoeaspis* from Janvier’s (1985a) original description. The description of *W. platycornis* does not provide any additional internal characters for the species of *Waengsjoeaspis* from MOTH, and as no specimen of *W. nahanniensis* clearly displays ‘sel’ 1 for its full length, this character is currently not definitely known to be diagnostic for the entire genus.

Differences between the two species from MOTH include the fact that the headshield of *W. platycornis* is generally wider than it is long. This is in contrast to what is observed in *W. nahanniensis*, for which complete specimens have a headshield that is longer than wide, as seen even in UALVP 41643, in which there are no fractures in the headshield.

Both UALVP 32969 and UALVP 41883 have cornua that are slightly more than twice as long as they are wide. The median field of UALVP 32969 is also narrower than the median fields of the holotype and UALVP 41477. This difference is not ontogenetic because UALVP 32969 is nearly the same size as the holotype, but rather may represent individual variation within the species. UALVP 32969 is nevertheless referred to *W. platycornis* based on having a median field that widens posteriorly.

The pectoral fin of *W. platycornis*, sp. nov., is as described by Adrain and Wilson (1994) for UALVP 19145, designated here as the holotype of the new species, but with additional details. A description of the pectoral fin of *W. nahanniensis* would be identical to that of *W. platycornis* based on the pectoral fin of UALVP 42213, referable to *W. nahanniensis* based on shape of the median field and shape of the cornual process.

The infraorbital sensory line is visible on the holotype of *W. platycornis* and on a specimen of *W. nahanniensis*, UALVP 52605. Although the infraorbital sensory line appears to pass medial to the lateral fields it is not nearly as far medially as has been observed in *Thyestes* (Janvier, 1974). The lateral line, reported by Sansom et al. (2008) as being located directly above the ventrolateral ridge in *Ilemoraspis kirkinskayae*, is not seen in either *W. platycornis* or *W. nahanniensis* despite very well-preserved sections of the ventrolateral ridge and the region dorsal to it in both species.

WAENGSJOEASPIS cf. *W. PLATYCORNIS*

(Fig. 4.4A)

Referred Specimen—UALVP 52501, a nearly complete ventral shield including oral and branchial platelets.

Identification—UALVP 52501 is described here as *Waengsjoeaspis* cf. *W. platycornis* based on having a median field that is greater than 8 mm wide. The dorsal headshield is obviously distorted: the posterior margin of the left orbit is lateral and anterior to the left labyrinth infilling and the median field is far posterior to both the pineal plate and the orbits. Therefore, the width of the median field of this specimen may be a result of distortion rather than morphology.

UALVP 52501 is preserved in ventral view with a nearly complete ventral shield and a ventral view of a partially preserved pectoral fin. The observations here are in agreement with those for the ventral aspect of the headshield described but not figured for UALVP 32915 by Adrain and Wilson (1994). UALVP 32915 does not preserve a nasal opening, median field, or cornual process and therefore, although assignable to *Waengsjoeaspis*, it is not assignable to either MOTH species of *Waengsjoeaspis*.

Ventral Shield—The ventral side of the headshield is covered in close-fitting polygonal tesserae, smooth except for a covering of fine pores. Unlike the hexagonal dorsal tesserae, the ventral tesserae are usually square to rectangular and are not as regularly arranged. Ventral tesserae are typically small, but can vary in size and are generally larger at the posterior end of the ventral shield, where some of them appear to be formed from fusion of smaller, hexagonal tesserae.

A nasal opening can be observed embossed on the ventral shield just anterior to the orbits. A separate hypophyseal opening is embossed on the ventral shield anterior to the nasal opening.

Branchial openings can each be distinguished by a row of tesserae anterior to the branchial opening, similar to those on the rest of the ventral shield, followed posteriorly by multiple rows of smaller rounded platelets (an example is labelled from the anterior row of tesserae as **bo** in Fig. 4.4A). The series of branchial openings extends from just anterior and lateral to the orbits, posteriorly and medially in an arc. The series ends medial to and anterior to the pectoral sinus. The number of branchial openings is unclear as the anterior end of the right series is not preserved, and the branchial openings on the left side have been greatly distorted so that the covering of only a few of the openings is discernable. UALVP 32915, briefly described but not figured by Adrain and Wilson (1994) but referred here to *Waengsjoeaspis* sp., has two openings anterior to the orbits while UALVP 52501 has at least four openings posterior to the orbits.

Mouth—The mouth of UALVP 52501 appears to be wider than long. Small, somewhat rhomboid platelets are visible along the posterior margin of the mouth. The pores on the platelets are larger than those on the surrounding tesserae. The anterior border of the mouth is poorly preserved, and mostly missing because beyond the edge of the rock slab along the specimen's right side. Where the anterior oral platelets are not preserved, there is a visceral view of the anterior region of the dorsal headshield. This permits a view of the supra-oral field, which is denticulated with a straight posterior margin, beginning 2 mm anterior to the posterior margin of the mouth. Where visible, the platelets along the anterior border of the mouth are irregular in shape, smaller than platelets along the posterior margin of the mouth, and have larger pores. The posterior platelets are bordered posteriorly by square tesserae with fine pores. Posterior to these tesserae are regularly arranged, elongate, rectangular tesserae that, together, form a chevron posterior to the mouth.

Pectoral Fin—The pectoral fin can be seen in ventral view (Fig. 4.4A). The lateral scales are small and thick with few, irregularly-shaped openings rather than the pores observed in other scales. These lateral pectoral fin scales resemble the marginal scales described in dorsal view for UALVP 42213 (*W. nahanniensis*), and observed also in UALVP 19145, the holotype of *W. platycornis*, sp. nov. Elsewhere on the pectoral fin, larger, thin, highly porous scales are present. A precise description of the squamation of the ventral side of the pectoral fin is difficult due to some disarticulation of the scales and some concealment of the fin by the cornual process. As with the holotype of *W. platycornis*, sp. nov., and UALVP 42213 (*W. nahanniensis*), the pectoral fin is nearly as long as the cornual process.

Remarks—The ventral side of UALVP 52501 gives a clear outline of the shape of the mouth (Fig. 4.4A). Despite the specimen being preserved asymmetrically, the posterior margin of the mouth appears to be more or less intact and symmetrical. Only a few specimens of Osteostraci have been preserved with intact oral platelets and a mouth. The mouth is wide and short, as observed in *C. cradleyensis* (White and Toombs, 1983), rather then the more narrow and rhomboid mouth of *Superciliaspis gabrielsei* Adrain and Wilson, 1994. Like those of *S. gabrielsei*, the anterior oral platelets of UALVP 52501 are much smaller and less polygonal than the platelets bordering the posterior margin of the mouth and are often resting on top of one another. Unlike the posterior oral platelets of *Superciliaspis* with smaller platelets medially, the posterior oral platelets of *Waengsjoeaspis* as seen in UALVP 52501 are arranged as a flat border with the next more posterior tesserae arranged as an anterior pointed chevron. The small size and absence of regular arrangement of the anterior platelets may indicate an 'upper lip' of flexible and possibly muscular tissue.

WAENGSJOEASPIS sp.

Cephalaspididae indet.: Dineley and Loeffler, 1976:173

Osteostraci indet.: Dineley and Loeffler, 1976:173

Waengsjoeaspis nahanniensis Adrain and Wilson, 1994: Adrain and Wilson, 1994:311–312 (in part).

Referred Specimens—The following specimens were originally referred to *Waengsjoeaspis nahanniensis* by Adrain and Wilson (1994) but lack the elements of the headshield diagnostic for either species currently known from MOTH: UALVP 19147, UALVP 19148, UALVP 19254, UALVP 19256, UALVP 23154, UALVP 23185, UALVP 32908, UALVP 32910, UALVP 32913, UALVP 32914, UALVP 32915, UALVP 32968, , UALVP 32982.

The following specimens lack elements of the headshield diagnostic for either species of *Waengsjoeaspis* from MOTH, and have not previously been referred to a taxon: UALVP 19144, UALVP 23268, UALVP 32905, UALVP 32976, UALVP 41454, UALVP 41475, UALVP 41480, UALVP 41628, UALVP 41716, UALVP 41732, UALVP 41741, UALVP 41745, UALVP 41750, UALVP 41866, UALVP 41933, UALVP 52503, NMC 21556, NMC 21557, NMC 21558, NMC 21562, NMC 21565, NMC 21567.

Remarks—UALVP 32915 consists of a partial headshield in ventral view. The right side of the mouth is preserved and the morphology and arrangement of oral platelets is the same as that observed for UALVP 52501, described above. More small platelets are preserved anterior to the mouth on UALVP 32915, but the supra-oral field is not preserved.

cf. *WAENGSJOEASPIS* sp.

(Fig. 4.4B, C)

Waengsjoeaspis nahanniensis Adrain and Wilson, 1994: Adrain and Wilson, 1994:311 (list of paratypes), 312-314 (description of pectoral fin and trunk).

Referred Specimens—UALVP 19257, posterior end of headshield and trunk in ventral view (Fig. 4.4B); and UALVP 41716, posterior end of headshield, including right pectoral sinus and right pectoral fin, and trunk, in ventral view (Fig. 4.4C).

Ventral Shield—UALVP 19257, listed as a paratype of *W. nahanniensis* by Adrain and Wilson (1994), is instead identified here as cf. *Waengsjoeaspis* sp. This species likely belongs in the genus based on tesserae on the headshield and ventrolateral trunk scales that are indistinguishable from those described for both species of *Waengsjoeaspis* from MOTH; however, it differs from other known species from MOTH in having a pectoral fin that does not extend the full length of the cornual process and the presence of a distinct knobby ornamentation along the median margin of the cornual process. There are also small barbs along the posteromedial edge of the cornual process. A few barbs are also visible on UALVP 41716, a smaller specimen of *Waengsjoeaspis* that also has a pectoral fin that does not extend the length of the cornual process and is therefore also referred to cf. *Waengsjoeaspis* sp. Unlike those of *W. excellens* and *W. vogti*, the barbs on UALVP 19257 and 41716 are only present at, and near, the posterior tip of the cornual process. The barbs on the cornual process of UALVP 41716 are larger in both relative and absolute size and are more distinct than those of UALVP 19257.

Trunk—The trunk of UALVP 19257 is as described by Adrain and Wilson (2004) in dorsal view with much of the ventral trunk scales exposed. The lateral scales are made up of rows of smaller, square scales. These lateral scales extend from near the median dorsal ridge (the median dorsal region is not preserved) to the ventrolateral ridge. The ventrolateral ridge is visible in both internal and, far to the posterior, in external view. The imbricated portion of the ventrolateral scales observed in other specimens of *Waengsjoeaspis* is far less robust in both UALVP 19257 and UALVP 41716. The ventral side of the trunk is present in visceral view. The ventral side of the trunk is composed of small square scales directed anteromedially.

Pectoral Fin—The pectoral fin of UALVP 19257 is clearly shorter than the cornual process. Larger rhomboid scales are present anteriorly and medially on the pectoral fin. The scales become smaller laterally and posteriorly. The smaller specimen of UALVP 41716 has a pectoral fin that is even smaller relative to the cornual process than in UALVP 19257. The marginal scales are the same as described above for UALVP 19145, the holotype of *W. platycornis*, sp. nov.

Remarks—Cf. *Waengsjoeaspis sp.* is represented by specimens that are tentatively referred to the genus *Waengsjoeaspis* based on a similarity of surface texture of the headshield and slight medial curve of the cornual process but cannot be assigned to a genus or species with certainty. None of the characters diagnostic of the genus are preserved, and the distinct barbs present at the posterior tip of the cornual processes along with the short pectoral fins relative to the cornual processes, observed for both specimens of cf. *Waengsjoeaspis* sp., are distinct from what has been observed in other species of *Waengsjoeaspis*. There remains a possibility that these differences could be a result of ontogeny rather than speciation as both specimens are from individuals smaller than those known for either species of *Waengsjoeaspis* from MOTH. In support of an ontogenetic interpretation of differences between these two specimens and the two species of *Waengsjoeaspis* from MOTH, the characters are more extreme in the smaller specimen, UALVP 41716, than they are in UALVP 19257.

DISCUSSION

The recognition of a second species of *Waengsjoeaspis* and identification of new or newly prepared specimens assignable to the genus *Waengsjoeaspis* have revealed new details on the relationships, morphology, growth, and variation within this group of osteostracans. The new species provides insight into the relationships between the MOTH and the Spitsbergen species of *Waengsjoeaspis*. Additional specimens have provided new details on the ventral shield and infraorbital sensory line in the genus. Detailed preservation of tesserae in both dorsal and visceral view demonstrates a growth pattern of the dermoskeleton similar to that postulated for *Superciliaspis* by Hawthorn et al. (2008). In addition, variation among specimens is here reinterpreted as reflecting taxonomic differences rather than mostly taphonomic effects.

Relationships Within *Waengsjoeaspis*

Both species from MOTH are represented by individuals that are larger than known specimens of *W. excellens* (Wängsjø, 1952) and *W. vogti* (Stensiö, 1927). The cornua of the Spitsbergen *Waengsjoeaspis* species are barbed along the medial margin, while *W. nahanniensis* and *W. platycornis* sp. nov. lack barbs along the median margin of the cornual processes.

“*Cephalaspis*” *vogti* (Stensiö, 1927) was originally described based on only a few fragments of headshield. Wängsjø (1952) only referred a few specimens to this species and these were fragmentary as well. The only features of “*Cephalaspis*” *vogti* that were considered to be diagnostic are a narrow cornual spine and pectoral sinus with a short, wide abdominal section (Stensiö, 1927), barbs along the median margin of the cornual spine, and a possible facial, or trigeminal nerve anterior to the sel 1 canal (Wängsjø, 1952). Janvier (1985a) refers this species to *Waengsjoeaspis*; however, specimens of *W. vogti* do not preserve any of the external characters considered diagnostic of *Waengsjoeaspis*. Although *W. vogti* does share some characters with other species of *Waengsjoeaspis*, such as narrow pectoral sinuses and a short, wide abdominal section, none of these characters is exclusive to *Waengsjoeaspis*. Therefore, the inclusion of this species within the genus remains somewhat dubious until more complete specimens can be found.

It is necessary to distinguish primitive features (seen in close outgroups) from derived features (preferably unique within the genus). Among the three undoubted species of the genus, it is likely that *Waengsjoeaspis platycornis* and *W. nahanniensis* share more characteristics with each other than either does with *W. excellens*. While *W. nahanniensis* shares a narrow cornual process with *W. excellens* and the median field is wide relative to its length in both *W. excellens* and *W. platycornis*, *W. platycornis* and *W. nahanniensis* share smooth medial margins of the cornua, as well as a rounded anterior edge of the median field. The median field of *W. platycornis* narrows anteriorly and seems to be of similar length, relative to headshield length, to that of *W. nahanniensis*, while the median field of *W. excellens* maintains a nearly uniform width and is short for the length of the headshield. *Waengsjoeaspis vogti* does share the presence of barbs along the medial edge of the cornua with *W. excellens* (Wängsjø, 1952; Janvier, 1985a) but the generic assignment of *W. vogti* is only tentative.

The plesiomorphic states of the above characters, used to discuss the relationships of species within *Waengsjoeaspis*, are difficult to determine given the lack of clarity concerning the classification of *Waengsjoeaspis*. If *Waengsjoeaspis* is considered to be a basal member of either the Thyestida (Janvier, 1985a) or a sister to the Benneviaspida (Sansom, 2009a), then it is likely that the plesiomorphic conditions of the characters differentiating species within *Waengsjoeaspis* would be shared with the non-cornuates, and with *Procephalaspis*, *Camptaspis* and *Yvonaspis*. The last three taxa mentioned are cornuates. Among all three, the cornual processes are smooth along the medial margin and on *Camptaspis* and *Yvonaspis* the cornua are long and narrow (Denison, 1951, 1952; Belles-Isles, 1989). The shape of the median field varies greatly among osteostracan genera; however, among the non-cornuate Osteostraci the median field is usually long and narrow, with the anterior margin resting flat against the pineal plate (Stensiö, 1932; Heintz, 1939 in Sansom, 2009a; Ritchie, 1967). It would be likely, therefore, that the primitive condition for

Waengsjoeaspis would be a combination of long, narrow cornua with a smooth medial margin and a long, narrow median field, the character states observed for *W. nahanniensis*. The wider median field and barbed cornual processes of *W. excellens* would therefore be more derived conditions. The rounded anterior border of the median field is the only derived character that *W. platycornis* sp. nov. shares with *W. nahanniensis*, but it is one more than either species shares with *W. excellens*. For this reason the MOTH *Waengsjoeaspis* species are considered here to be more closely related to each other than either is to *W. excellens*.

Additional Characters for ***Waengsjoeaspis***

Waengsjoeaspis platycornis preserves characters that were previously unknown for *Waengsjoeaspis*. These characters include: the shape and position of the mouth, the arrangement of the branchial openings, and the shape of the infraorbital sensory line.

Mouth—The mouth of *Waengsjoeaspis* is preserved in two specimens and is short and wide (Fig. 4.4A). However, the morphology of the mouth does not provide much support for one relationship or another in the Osteostraci, as the mouth is only known for a few species of osteostracan. The most similar oral region belongs to *Cephalaspis cradleyensis* (White and Toombs, 1983). The mouth of *C. cradleyensis* is also short and wide, but unfortunately the squamation of the region of the ventral shield anterior to the mouth is unknown. The oral openings of other osteostracans are typically narrower, such as for *Aceraspis* (Heintz, 1939), *Ateleaspis* (Ritchie, 1967), and *Tremataspis* (Robertson, 1938a&b). Stensiö (1932) reconstructed the mouth of *Hemicyclaspis murchisoni* as being short and wide; however, no specimen of *Hemicyclaspis* has been published that would support this reconstruction. The mouth of *Superciliaspis* is also narrower (Adrain and Wilson, 1994) than that of *Waengsjoeaspis*, but the platelets bordering the anterior of the mouth in *Waengsjoeaspis* are similar to many of those that border the anterior of the mouth in *Superciliaspis*, which has a distinct 'upper lip.' Given that this region of the ventral shield is almost never preserved in osteostracans (the possible exception being *Tremataspis* (Robertson, 1938b:pl. 2 fig. 9 and Text-fig. 2)) it is quite possible that an 'upper lip' composed of small platelets was present in other cornuate osteostracans as well. It is possible that a flexible 'upper lip' may have been useful for selectively feeding on detritus along the seafloor.

Branchial Openings—The branchial openings of *Waengsjoeaspis* are covered in opercular flaps (see Donoghue et al., 2000) a character that is likely primitive among Osteostraci (based on the cladistic analysis of Sansom, 2009a). Although a precise count of branchial openings is not possible for *Waengsjoeaspis*, there are at least 5 on each side and, given that the morphology for the branchial openings is similar to that seen in both *C. cradleyensis* (White and Toombs, 1983) and *Superciliaspis* (Adrain and Wilson, 1994), there are likely seven branchial openings (based on personal observation by the first author of specimens of both *S. gabrielsei* and *C. cradleyensis* and contrary to the count of eight by White and Toombs, 1983).

Infraorbital Sensory Line—The infraorbital sensory line passes just medial to the lateral field. This condition is also known for Thyestida, which includes Tremataspidae under Sansom's (2008, and 2009a) classification; however, the infraorbital sensory line of *Waengsjoeaspis* extends farther laterally than in thyestids.

Most of the additional characters for *Waengsjoeaspis* that have been described here based on new specimens from MOTH are shared with numerous, distantly related osteostracans and are most likely plesiomorphic. Unfortunately, this provides little clarity on the phylogenetic relationships of *Waengsjoeaspis*. In Sansom's (2009a) classification, *Waengsjoeaspis* is placed within the sister group to the Benneviaspida, but only shares a single character with the other taxa in unnamed group D and the Benneviaspida: a smooth ornamentation, or lack of ornamentation of the headshield. Smooth ornamentation is also seen in *Hemicyclaspis* and is likely a primitive character for all of the Osteostraci. *Waengsjoeaspis* does not share any characteristics with the Zenaspida that are not already known to be plesiomorphic for cornuate osteostracans. It should be noted that *Waengsjoeaspis* does share an infraorbital sensory line medial to the lateral fields with members of the Thyestida. This would support a relationship between *Waengsjoeaspis* and thyestids that was tentatively suggested by Janvier (1985a), and so perhaps *Waengsjoeaspis* could be a basal thyestid.

Growth in *Waengsjoeaspis*

Both species of *Waengsjoeaspis* from MOTH show signs of both synchronous and centrifugal growth of their dermoskeleton. Synchronous growth, as described by Hawthorn et al. (2008), is the simultaneous or independent formation of a tessera or dermal plate, which can be followed by addition and fusion of several small tesserae around the central tessera. This can be seen in a dorsal view of *Waengsjoeaspis*, by larger, irregularly-shaped tesserae that are clearly composed of smaller, polygonal tesserae that have fused. In visceral view of both the dorsal and ventral dermoskeleton there can be seen tesserae with multiple, small, porous centers, separated by small radiating canals. In *Waengsjoeaspis* these fused tesserae do not always contain the several tesserae as seen in *Superciliaspis* (Hawthorn et al., 2008), but often are composed of only two or three tesserae. In *Superciliaspis*, synchronous growth and fusion are followed by centrifugal growth through addition of bone around the margin of each tessera, most of which are compound units. This addition of dermal bone forms the rings of growth visible on the tesserae (Hawthorn et al., 2008). Similar rings are also present in *W. nahanniensis* and *W. platycornis*, primarily on tesserae around the orbits, median field and nasohypophyseal region and towards the posterior of the median shield.

Morphological Variation in MOTH *Waengsjoeaspis*

When morphological variation is observed in the fossil record there are usually several different explanations, including individual variation, sexual dimorphism, taphonomy, ontogeny, and speciation. In this study the majority of the morphological variation was attributed to speciation, because sets of character states were observed to correlate with one another more frequently than they did with opposing character states. Sexual dimorphism has previously been considered for fossil agnathans (Elliott, 1983), but is generally not considered an important source of shape variation given that the different shapes are seen in specimens of different sizes, and the majority of sexual dimorphism in extant jawless vertebrates is related to body size.

Taphonomy—Taphonomy was given as the original explanation for the variation in morphology observed in the specimens of *Waengsjoeaspis* from MOTH by Adrain and Wilson (1994). In the original description of *Waengsjoeaspis nahanniensis*, the paratype UALVP 19145 (herein, the holotype of *W. platycornis*, sp. nov.) was noted as being much wider than the holotype. It was concluded by Adrain and Wilson (1994) that this was because the specimen has been deformed differently from UALVP 19140. Adrain and Wilson (1994) described UALVP 19145 as spreading laterally, rather than fracturing and being crushed vertically as is observed for UALVP 19140. The "nearly complete exposure of the left 'pectoral' fin, and the relatively greater distance between the left fin and the trunk" (Adrain and Wilson, 1994:315) of UALVP 19145 was given as evidence that this region had been spread out during its burial; however, the cornual process and pectoral fin of UALVP 42213, a specimen with fractures along the headshield, are identical to those of UALVP 19145. This shows that the pectoral and cornual region is reasonably undistorted in UALVP 19145. The ventral surface of the cornual process (Figs. 4.1D, 4.2B, C), which was horizontal in life, has a similar length to width to the dorsal surface (Figs. 4.1A–C, 4.2A) in each of the two species. Therefore, the dorsal surface could not have been inclined much from the horizontal. Thus, cornual widths are not greatly affected by taphonomy, and are a reliable taxonomic character. Where distortion does appear is at the trunk. The lateral scales of UALVP 42213, a specimen of *W. nahanniensis*, cover the pectoral fin. This is because the headshield was crushed dorsoventrally, while the trunk was spread laterally, unlike UALVP 19145.

Differing angles of compaction were suggested as the cause of differences in distortion of specimens. This seems unlikely because in UALVP 42213 of *W. nahanniensis* and in UALVP 41477 of *W. platycornis*, the specimens are approximately bilaterally symmetrical and would therefore appear to have been compressed vertically. The exceptions to this are UALVP 52495, where the right side has fractured while the left side is spread (Fig. 4.3A), and UALVP 52501 where the left side is considerably narrower than the right side (Fig. 4.4A). The asymmetry of these specimens could have been caused by differing angles of compaction, but among the specimens with a considerable portion of both sides preserved only UALVP 52495 and 52501 demonstrate asymmetry clearly. As well, what is exposed of the cornual region of UALVP 52495 is undeformed, and the plates forming the cornual process of UALVP 52501 are undeformed and are merely disarticulated.

Ontogeny—Although there is a marked size difference between the holotypes of the two species, an ontogenetic relationship is also considered unlikely because other specimens of the two morphotypes overlap in size yet maintain their morphological disparity. Furthermore, the absolute width of the median fields of *W. nahanniensis*, typically the larger of the two species of

Waengsjoeaspis from MOTH, is actually smaller than that of specimens of *W. platycornis*. This is inconsistent with the proportionate growth described for *Superciliaspis* (Hawthorn et al., 2008) and, given the similarities in centrifugal and synchronous growth of the dermoskeleton in *Waengsjoeaspis*, *Superciliaspis* likely provides a reliable model for ontogeny of the dermoskeleton of *Waengsjoeaspis*.

SUMMARY

At least two species of *Waengsjoeaspis* are present at MOTH. Both species of *Waengsjoeaspis* are larger than species described from Spitsbergen (Wangsjø, 1952; Janvier, 1985a), and share characters that make them both more closely related to each other than either is to the Spitsbergen species. New characters provided for *Waengsjoeaspis* by new specimens from MOTH, although informative on the generalized anatomy of this osteostracan, provide little phylogenetic clarity for this enigmatic taxon, but similarities between *Waengsjoeaspis* and many members of the Thyestida make it likely that *Waengsjoeaspis* belongs to this order**.**

LITERATURE CITED

Adrain, J. M., and M. V. H. Wilson. 1994. Early Devonian cephalaspids (Vertebrata: Osteostraci: Cornuata) from the southern Mackenzie Mountains, N.W.T., Canada. Journal of Vertebrate Paleontology 14:301–319.

Agassiz, L. 1835. Recherches sur les Poissons Fossiles. 2. Contenant l’histoire de l’ordre des Ganoïdes. Neuchâtel, 85–300 pp.

Belles-Isles, M. 1989. *Yvonaspis*, nouveau genre d'Osteostraci (Vertebrata, Agnatha) du Dévonien (Emsien-Eifélien) des Grés de Gaspé (Québec, Canada). Canadian Journal of Earth Sciences 26: 2396-2401.

Bond, C. E., and T. T. Kan. 1973. *Lampetra* (*Entosphenus*) *minima* sp. nov., a dwarfed parasitic lamprey from Oregon. Copeia 1973:568–574.

Dendy, J. S., and D. C. Scott. 1953. Distribution, life history, and morphological variations of the Southern Brook Lamprey, *Ichthyomyzon gagei*. Copeia 1953:152–162.

Denison, R. H. 1951. Evolution and classification of the Osteostraci. Fieldiana, Geology 11:156–196.

Denison, R. H. 1952. Early Devonian fishes from Utah Part 1. Osteostraci. Fieldiana, Geology 11:265–287.

Denison, R. H. 1955. Early Devonian vertebrates from the Knoydart Formation of Nova Scotia. Fieldiana, Zoology 37:449–464.

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

Donoghue, P. C., P. L. Forey, and R. J. Aldridge. 2000. Conodont affinity and chordate phylogeny. Biological Reviews 75:191–251.

Elliot, D. K. 1983. New Pteraspididae (Agnatha, Heterostraci) from the Lower Devonian of Northwest Territories, Canada. Journal of Vertebrate Paleontology 2:389–406.

Forey, P. L. 1984. Yet more reflections on agnathan-gnathostome relationships. Journal of Vertebrate Paleontology 4:330–343.

Gabrielse, H., S. L. Blusson, and J. A. Roddick. 1973. Geology of Flat River, Glacier Lake and Wrigley Lake map areas, District of Mackenzie, Northwest Territories. Geological Survey of Canada, Memoir 366:1–268.

Hanke, G. 2002. *Paucicanthus vanelsti* gen. et sp. nov., an Early Devonian (Lochkovian) acanthodian that lacks paired fin-spines. Canadian Journal of Earth Science 39:1071–1083.

Hawthorn, J. R., M. V. H. Wilson, and A. B. Falkenberg. 2008. Development of the dermoskeleton in *Superciliaspis gabrielsei* (Agnatha: Osteostraci). Journal of Vertebrate Paleontology 28:951–960.

Heintz, A. 1939. Cephalaspida from the Downtonian of Norway. Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo. Matematisk-Naturvidenskapelig Klasse 5:1–119.

Janvier, P. 1996. Early Vertebrates. Clarendon Press, Oxford, 393 pp.

Janvier, P. 1985. Les Cephalaspides du Spitsberg. Cahiers de Paléontologie, Section Vertébrés. Éditions du Centre National de la Recherche Scientifique, Paris: 244 pp.

Lankester, E. R. 1868. A Monograph of the Fishes of the Old Red Sandstone of Britain. Part I. The Cephalaspidae. Monograph of the Palaeontographical Society, London, 62 pp.

Lyons, J., O. J. Polaco, and P. A. Cochran. 1996. Morphological variation among the Mexican lampreys (Petromyzontidae: *Lampetra*: subgenus *Tetrapleurodon*). The Southwestern Naturalist 41:365–374.

Obruchev, D. V. 1956. [Cephalaspids from the Lower Devonian of Tuva]. Doklady Akademii Nauk SSSR 106:917–919. [In Russian].

Ørvig, T. 1969. The vertebrate fauna of the Primaeva beds of the Frænkelryggen Formation of Vestspitsbergen and its biostratigraphic significance. Lethaia 2:219–239.

Ritchie, A. 1967. *Ateleaspis tessellata* Traquair, a non-cornuate cephalaspid from the Upper Silurian of Scotland. Journal of the Linnean Society, Zoology 47:69–81.

Robertson, G. M. 1938a. The Tremataspidae: part I. American Journal of Science 35:172–206.

Robertson, G. M. 1938b. The Tremataspidae: part II. American Journal of Science 35:273–296.

Sahney, S. and Wilson, M. V. H. 2001. Extrinsic labyrinth infillings imply open endolympatic ducts in Lower Devonian osteostracans, acanthodians and putative chondricthyans. Journal of Vertebrate Paleontology 21:660-669.

Sansom, R. S. 2008. The origin and early evolution of the Osteostraci (Vertebrata): a phylogeny for the thyestiids. Journal of Systematic Palaeontology 6:317–332.

Sansom, R. S. 2009a. Phylogeny, classification and character polarity of the Osteostraci (Vertebrata). Journal of Systematic Palaeontology 7:95–115.

Sansom, R. S. 2009b. Endemicity and palaeobiogeography of the Osteostraci and Galeaspida: a test of scenarios of gnathostome evolution. Palaeontology 52:1257–1273.

Stensiö, E. A. 1927. The Devonian and Downtonian vertebrates of Spitzbergen. 1. Family Cephalaspidae. Skrifter om Svalbard or Nordishavet 12:1–391.

Stensiö, E. A. 1932. The cephalaspids of Great Britain. British Museum (Natural History), London, 220 pp.

Vladykov, V. D. 1955. *Lampetra zanandreai*, a new species of lamprey from northern Italy. Copeia 1955:215–223.

Watson, D. M. S. 1954. A consideration of ostracoderms. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences 238:1–25.

Wängsjø, G. 1952. The Downtonian and Devonian vertebrates of Spitsbergen. IX. Morphologic and systematic studies of the Spitsbergen cephalaspids. Results of Th. Vogt's Expedition 1928 and the English-Norwegian-Swedish Expedition in 1939. Norsk Polarinstitutt Skrifter 97:1–611.

White, E. I., and H. A. Toombs. 1983. The cephalaspids from the Dittonian section at Cwm Mill, near Abergavenny, Gwent. Bulletin of the British Museum of Natural History (Geology) 37:149–171.

Wilson, M. V. H., and M. W. Caldwell. 1993. New Silurian and Devonian fork-tailed “thelodonts” are jawless vertebrates with stomachs and deep bodies. Nature 361:442–444.

Wilson, M. V. H., and M. W. Caldwell. 1998. The Furcacaudiformes: a new order of jawless vertebrates with thelodont scales based on articulated Silurian and Devonian fossils from northern Canada. Journal of Vertebrate Paleontology 18:10–29.

Zorn, M. E., M. W. Caldwell, and M. V. H. Wilson. 2005. Lithological analysis of the Lower Devonian vertebrate-bearing beds at the MOTH locality, N.W.T., Canada: insights to taphonomy and depositional setting. Canadian Journal of Earth Science 42:763–775.

FIGURE 4.1. Specimens of *Waengsjoeaspis nahanniensis* Adrain and Wilson, 1994. **A**, UALVP 19140, the holotype, left half of a headshield, dorsal view; **B**, UALVP 42213, a headshield with articulated trunk and complete pectoral fin, dorsal view; **C**, UALVP 41747, headshield with median dorsal ridge, dorsal view; **D**, UALVP 41643, partial headshield with cornual process, ventral view. Scale bars equal 10 mm.

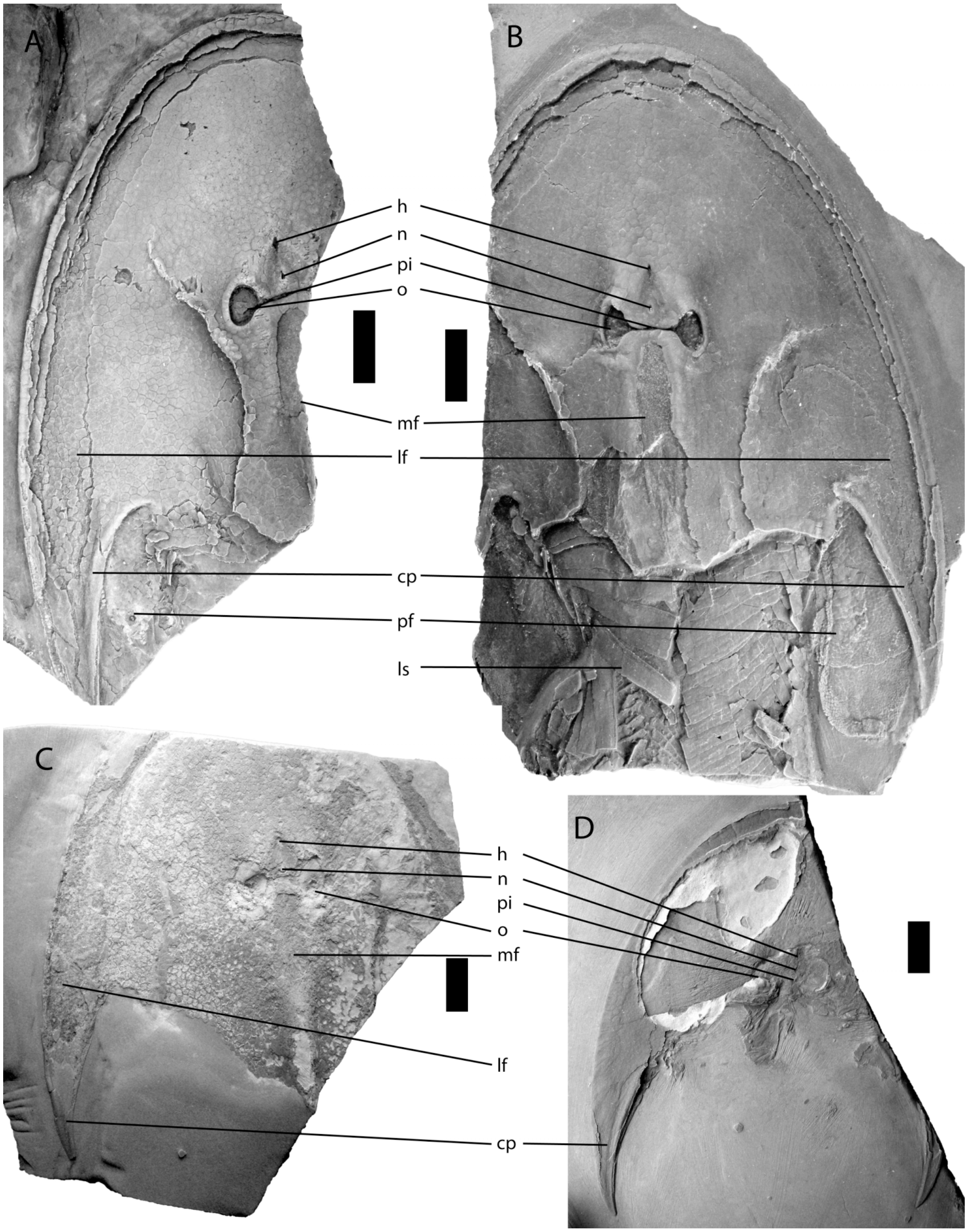
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FIGURE 4.2. Specimens of *Waengsjoeaspis platycornis*, sp. nov. **A**, UALVP 19145, the holotype, headshield with articulated trunk and complete pectoral fin, dorsal view; **B**, UALVP 41477, large headshield, ventral view; **C**, UALVP 32969, headshield with ventral surface of dorsal tesserae clearly visible. Ventral View. Scale bars equal 10 mm.

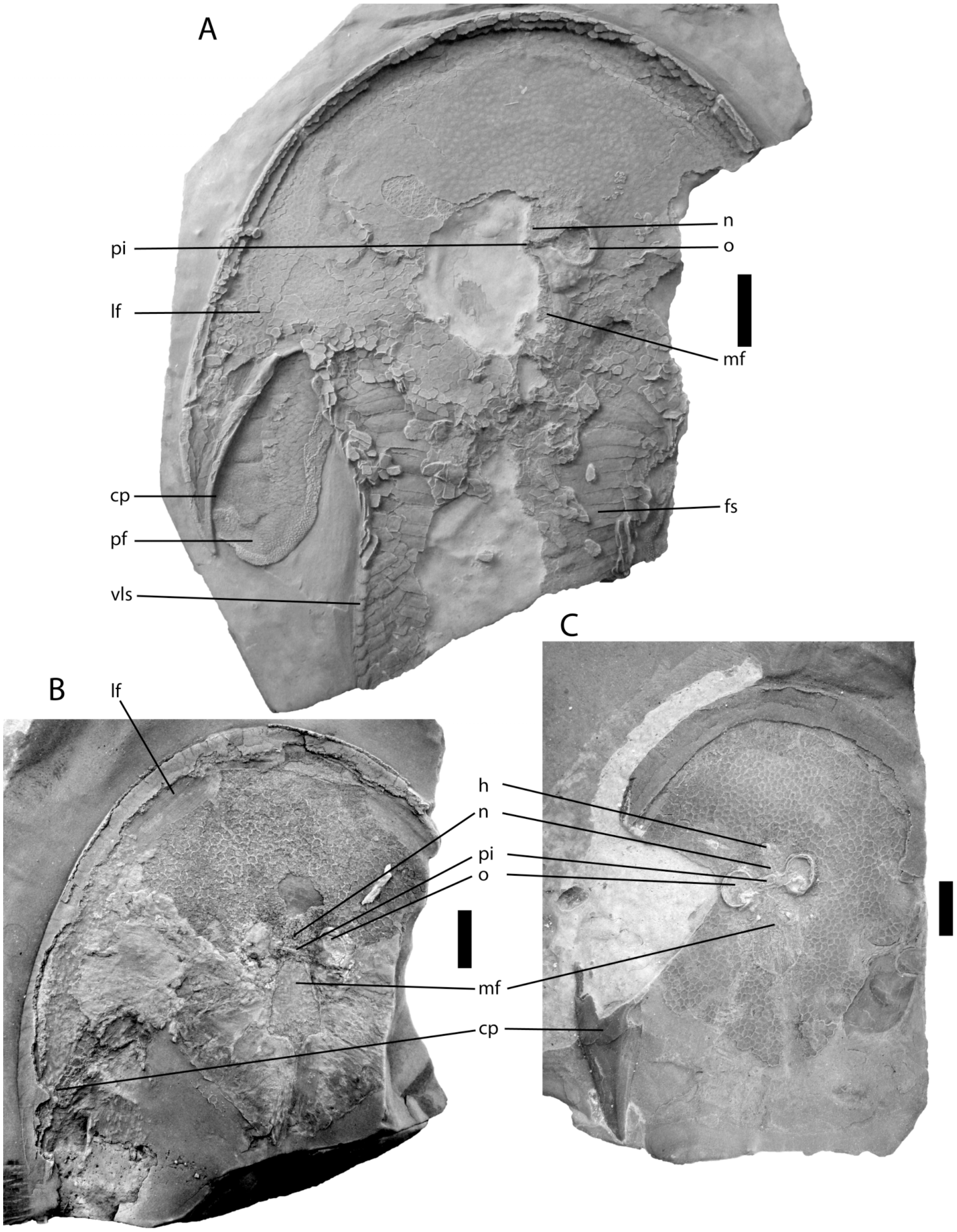
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FIGURE 4.3. Specimens of *Waengsjoeaspis platycornis*, sp. nov. **A**, UALVP 52495, partial headshield, right side showing fracturing where headshield overlaps, left side spread, dorsal view; **B**, UALVP 41883, small specimen including headshield and trunk, dorsal view; **C**, UALVP 52493, headshield with infilling of ‘sel’ 1 canal by white sand from labyrinth, dorsal view; **D**, UALVP 43086, headshield exposing ventral surface of dorsal tesserae, ventral view. Scale bars equal 10 mm.

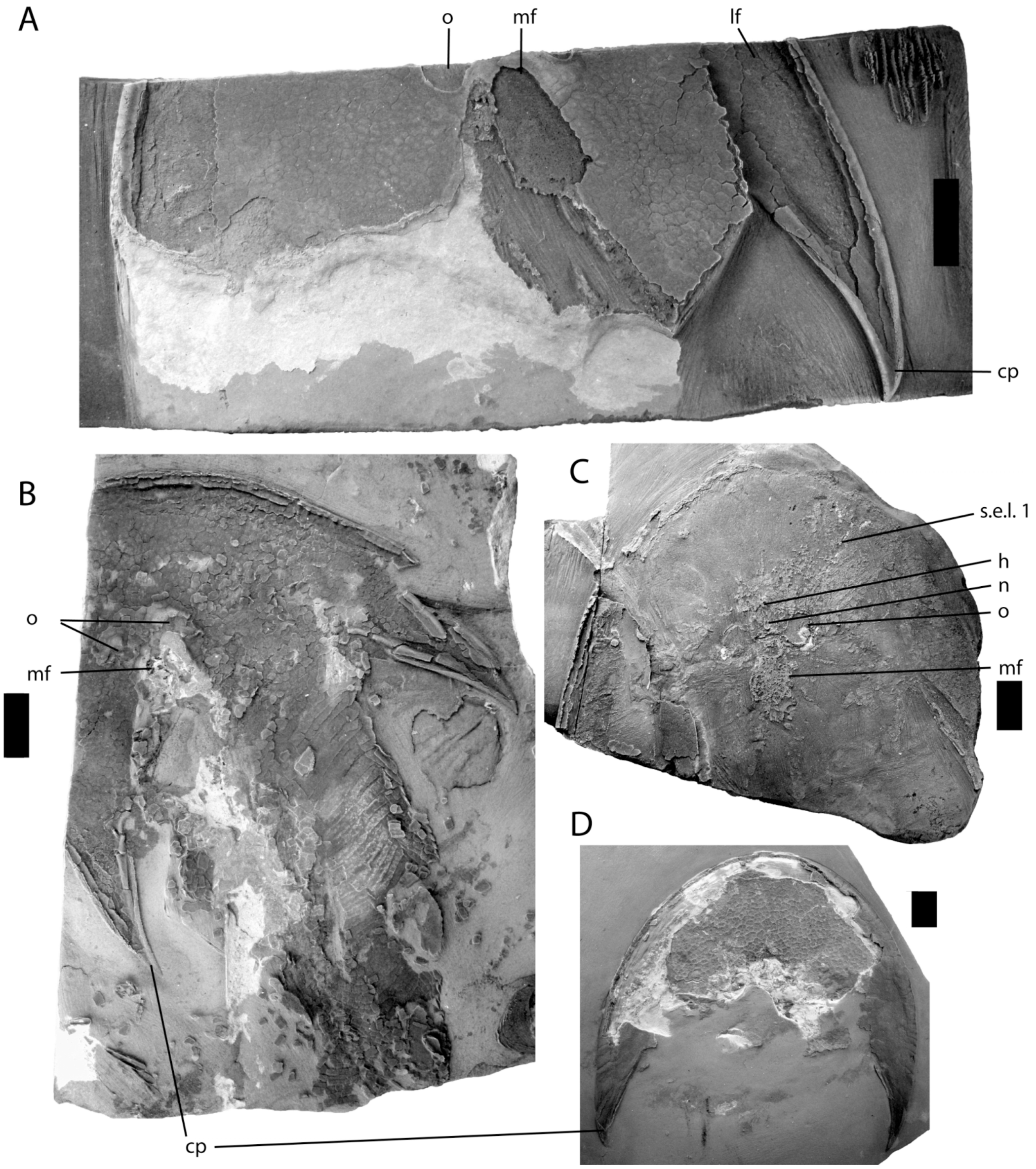
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FIGURE 4.4. **A**, UALVP 52501, *Waengsjoeaspis* cf. *W. platycornis*, headshield in ventral view with ventral tesserae and platelets preserved; **B**, UALVP 19257, cf. *Waengsjoeaspis* sp., posterior end of headshield including pectoral fin and barbed cornual process, with articulated trunk, ventral view; **C**, UALVP 41316, cf. *Waengsjoeaspis* sp. Trunk and posterior end of headshield including barbed cornual process and complete pectoral fin. Scale bars equal 10 mm.

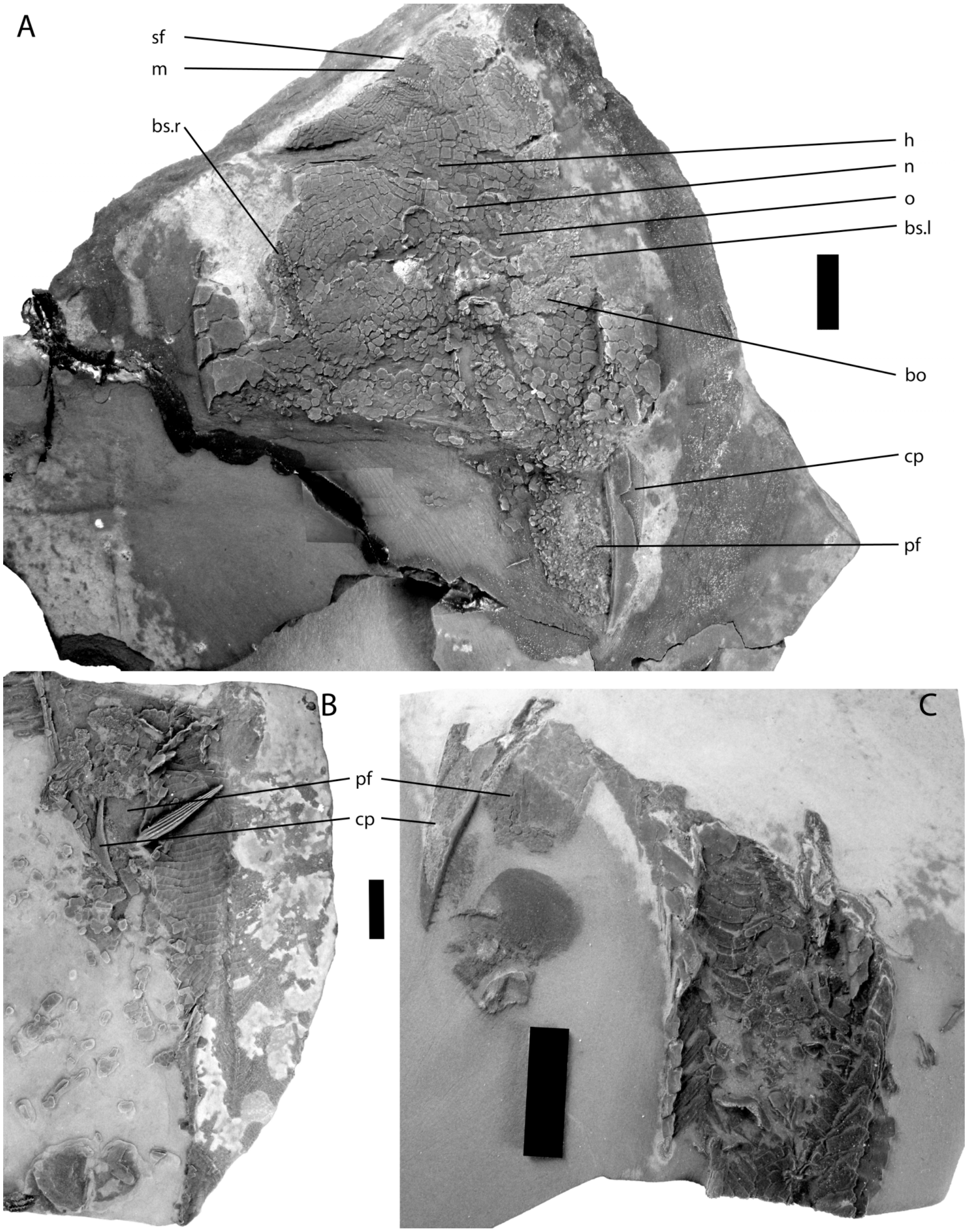
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TABLE 4.1. Table of measurements of the headshield for specimens of *Waengsjoeaspis nahanniensis*.

Holotype	T.L.	M.W.	Pr.L.	Po.L.	H.P.D.	M.F.L.	M.F.W.	C.L.	C.W.
UALVP19140	100	85*	41	—	7	15	6	—	16^{L}
Paratypes									
UALVP 41643	82	68*	—	—	—	—	—	28^{R}	13^{R}
UALVP 41747	—	88*	—	45	7	15	6	28^{L}	12^{L}
UALVP 42213	93	76*	40	—	8	16+	5	30^{R}	13^{R}
UALVP 52605	83	83	—	—	—	—	—	$30^{R}/29^{L}$	$14^{R}/13^{L}$

^{L}, Left; ^{R}, Right; *, measurement of width taken from midline and doubled; —, measurement not available; +, actual distance is greater than the measurement given. Abbreviations: **T.L.**, Total Headshield Length; **M.W.**, Maximum Headshield Width; **Pr.L.**, Prepineal Length; **Po.L.**, Postpineal Length; **H.P.D.**, Hypophyseal to Pineal Distance; **M.F.L.**, Median Field Length; **M.F.W.**, Median Field Width; **C.L.**, Cornual process Length; **C.W.**, Cornual process Width. All measurements are in mm.

TABLE 4.2. Table of measurements of the headshield for specimens of *Waengsjoeaspis platycornis* sp. nov.

Holotype	**T.L.**	**M.W.**	**Pr.L.**	**Po.L.**	**H.P.D.**	**M.F.L.**	**M.F.W.**	**C.L.**	**C.W.**
UALVP 19145	78	91*	33	—	6	—	9*	30^{L}	15^{L}
Paratypes									
UALVP 32969	76	70*	31	32	5	13	8	23^{R}	11^{R}
UALVP 41477	81	90*	36	33	—	14	9	29^{R}	15^{R}
UALVP 41883	—	69	—	—	—	—	—	24^{L}	12^{L}
UALVP 43086	74	79	32	—	6	—	—	26^{R}	13^{R}
UALVP 44008	65	73*	—	—	—	—	—	21^{R}	13^{R}
UALVP 52493	—	84*	35	—	6	13	8	—	—

^{L}, Left side of headshield; ^{R}, Right side of headshield; *, measurement of width taken from midline and doubled; —, measurement not available. Abbreviations: **T.L.**, Total Headshield Length; **M.W.**, Maximum Headshield Width; **Pr.L.**, Prepineal Length; **Po.L.**, Postpineal Length; **H.P.D.**, Hypophyseal to Pineal Distance; **M.F.L.**, Median Field Length; **M.F.W.**, Median Field Width; **C.L.**, Cornual process Length; **C.W.**, Cornual process Width. All measurements are in mm.

CHAPTER 5

FIRST REPORT OF *MACHAIRASPIS* FROM THE MOTH LOCALITY, NORTHWEST TERRITORIES, CANADA, WITH THE DESCRIPTION OF A NEW SPECIES, *MACHAIRASPIS SERRATA,* SP. NOV.

INTRODUCTION

A new species of *Machairaspis*, *M. serrata,* sp. nov., from the Man On The Hill (MOTH) locality, Northwest Territories, Canada is the first report of the genus *Machairaspis* from the MOTH locality, and the second from northern Canada (Dineley, 1994). The genus *Machairaspis* was first erected by Janvier (1985a) to include the type species '*Cephalaspis*' *corystis* originally described by Wängsjø (1952), as well as '*Cephalaspis*' *isascheni* and '*Cephalaspis*' *ibex*, '*Cephalaspis*' *hastata*, and *Machairaspis battaili* based on their shared similarities in ornament, and the tall dorsal spine at the posterior end of the headshield. '*Cephalaspis*' *doryphorus* also shares the prominent dorsal spine with the other species of *Machairaspis*, but differs in the smooth surface of the dermoskeleton of the headshield, the shape of its lateral fields, and the presence of barbs on the medial margin of the cornua (Wängsjø, 1952; Janvier, 1985a). Janvier (1985a) included *Machairaspis* within his "scolenaspidiens", defined by a hypophyseal division larger than the nasal division of the nasohypophyseal opening, large tubercles, prominent median dorsal spine, expanded lateral fields at the anterior and posterior ends, and thick but narrow cornua onto which the lateral fields extend.

The genus *Machairaspis* was only known from the Early Devonian beds of Spitsbergen, Norway (Stensiö, 1927; Wängsjø, 1952; Janvier, 1985a), and has more recently been described from the Early Devonian of Prince of Wales Island, Northwest Territories, Canada (Dineley, 1994) and of Podolia, Ukraine (Janvier, 1985b). *Machairaspis serrata*, sp. nov., now extends the geographic range of

Machairaspis to the MOTH locality, Northwest Territories, Canada. *M. serrata*, sp. nov., is also the smallest species of *Machairaspis* known and supports the strong biogeographic and biostratigraphic similarities between MOTH and the Fraenkelryggen and Ben Nevis formations of Spitsbergen that has been proposed by several authors (Dineley and Loeffler, 1976; Adrain and Wilson, 1994; Blieck et al., 1987).

SYSTEMATIC PALEONTOLOGY

Class OSTEOSTRACI Lankester, 1868

Subclass CORNUATA Janvier, 1981

Order ZENASPIDIDA Stensiö, 1958

Family ZENASPIDIDAE Stensiö, 1958

Subfamily SCOLENASPIDINAE Janvier, 1985a

MACHAIRASPIS Janvier, 1985a

Type Species—*'Cephalaspis' corystis* (Wängsjø 1952: 352)

Other Species—'*Cephalaspis' isascheni*, '*Cephalaspis' ibex*, '*Cephalaspis*' *hastata*, *Machairaspis battaili*, *Machairaspis serrata*, sp. nov.

Modified Diagnosis—The diagnosis is the same as Janvier (1985a) with only minor modification. The dorsal spine is taller than the headshield. The anterior margin of the dorsal spine is concave. The ornamentation is made up of small tubercles circular at the base, narrowly join and regularly set out again on the surface of the headshield. The hypophyseal division is definitely broader than the nasal division, but situated at the bottom of a deep pit. The cornual processes are short and narrow.

Remarks

Much of Janvier's original diagnosis is retained; however, diagnosis of the high dorsal spine is changed from occasionally being inclined forwards to a concave anterior margin so that the diagnosis of the dorsal spine applies to all members of the genus.

MACHAIRASPIS SERRATA, sp. nov.

Fig. 5.1, 5.2

Etymology—The specific epiphet is from the adjective *serratus*, Greek, "toothed like a saw" in reference to the row of barbs on the posterior margin of the dorsal spine. Gender feminine.

Holotype—UALVP 53224, a small headshield in left lateral view (Fig. 5.1, Fig. 5.2A, C).

Paratypes—UALVP 23154, a dorsal spine in lateral view (Fig. 5.2B).

Diagnosis—A species of *Machairaspis* ornamented on the dorsal dermoskeleton with numerous denticles, so-called because the tubercles are hollow and distally pointed.

Differs from other all *Machairaspis* species by a margin of the headshield that has large denticles ornamenting the distal surface and by barbs along the posterior margin of the dorsal spine curve to a dorsal point.

Type Locality—The MOTH locality, Mackenzie Mountains, Northwest Territories, Canada, in the transitional beds of the "Fish Layer" between the Road River and Delorme Formations (Gabrielse et al., 1973).

Description

Measurements of the Holotype—The total length of the headshield, including the cornua, is 22 mm; the total height of the headshield, including the dorsal spine, is 34 mm; the height of the headshield excluding the dorsal spine is 13 mm. The vertical height of the dorsal spine alone is 21 mm, and the length of the base of the dorsal spine is 7 mm. The barbs on the posterior margin of the dorsal spine are 0.5–0.8 mm long from the base to the tip of each barb. The prepineal length of the headshield is estimated to be 8 mm and the postpineal length of the headshield is estimated to be 10 mm, not including the cornua. The width of the left orbit is 4 mm as are the length of the left orbit and the length of the right orbit. The estimated length of the median field is 4 mm. The hypophyseal division is 1.3 mm from the pineal furrow. The lateral field is 2 mm from the lateral margin of the headshield. The lateral fields are 2–3 mm wide and 15 mm long.

Measurements for Paratype, UALVP 23154—The dorsal spine is 12.5 mm high and the length of the base of the dorsal spine is 5 mm. The barbs are 0.3–0.7 mm long.

Headshield—The headshield of the holotype is small and preserved in left lateral view (Fig. 5.1A). A prominent dorsal spine is visible, as are a cornual process, the lateral fields, the left orbit and a single large opening anterior to the orbit. The large opening is most likely the hypophyseal division of the nasohypophyseal opening. The headshield is tall for its size, being almost two-thirds as high as it is long, not including the dorsal spine. The prepineal region of the head shield is short and high, and inclined steeply from the rostral region of the headshield to the pineal plate.

The headshield is covered in a continuous dermoskeleton that is ornamented with numerous small denticles (Fig. 5.1A). These denticles are smaller and more closely spaced towards the anterior of the specimen and become larger and more widely separated posteriorly. The anterior denticles are also tri-radiate, sometimes fusing with other tri-radiate denticles at the ends. The denticles posterior to the orbits (Fig. 5.1B) and at the median regions of the headshield consist of irregular protrusions. The denticles along the posterior margin are close together, especially dorsally. The superficial layer of the dermoskeleton is absent medial to the anterior half of the lateral field. The denticles lateral to the lateral field (Fig. 5.1C) are close together, small and circular at the base; however, the distal ends are broken in such a way that an accurate description of entire denticles is not possible.

The dorsal spine is as tall as the headshield is long and is continuous with the headshield (Fig. 5.1A). The anterior margin of the dorsal spine is concave where it meets the headshield at the base of the dorsal spine. The posterior edge of the dorsal spine is straight along its entire length; together with its concave anterior edge this gives the dorsal spine a dorsally tapering, knife-like appearance. The dorsal spine is ornamented with three distinct types of denticle that grade from one to the other posteroventrally (Fig. 5.2A). The denticles along the anterior margin are large relative to other denticles on the headshield and dorsal spine and are triangular in longitudinal section with the highest point being at the dorsal end. The denticles are arranged in rows that run anteroposteriorly around the anterior margin of the dorsal spine. The denticles themselves are directed dorsoventrally. The dermoskeleton between denticles of this region is covered in dorsoventral furrows. These furrows are narrow and very small. The width of each furrow is roughly half the distance between the furrows. The rows of large denticles grade dorsally into a random placement of large, robust tubercles. Posterior to the large denticles are dense rows of smaller denticles. These denticles are the same length as those of the posterior region of the headshield, but narrower (Fig. 5.2A). The rows of denticles are arranged anteroventrally to posterodorsally, with the denticles themselves pointed dorsally. The denticles are triangular in longitudinal section with the tallest point being midway along the length of each denticle. The ventral and posterior-most area of the dorsal spine is covered in denticles identical to those of the posterior end of the headshield (Figs. 5.1A, 5.2A). The ventral one-third of the posterior margin of the dorsal spine is smooth. Dorsal to this the dorsal spine is ornamented with a median row of large, sharp dorsally pointed barbs (Fig. 5.2A). Lateral to these barbs along the posterior margin of the headshield is a second row of barbs that are smaller than those on the median row.

Orbits, Nasohypophyseal Region, and Pineal Region—The left orbit is preserved with a raised lateral rim. This orbit is circular in lateral view (Figs. 5.1A, 5.2C). A dense covering of denticles ornaments the area around the rim of the orbit (Fig. 5.2C). Large dorsal protrusions or antorbital horns are present anterior to the orbits. These antorbital horns (Figs. 5.1A, 5.2C) are robust at the tip and have an ornament of long, distally pointed denticles similar to those on the anterior margin of the dorsal spine. Thin, rough bone within the orbit is interpreted as ossification of the sclerotic capsule, though it is possible that this is an ossification of the orbital wall itself instead. The posterior end of the sclerotic capsule has several breaks, gaps, and openings. A single large opening with two anterior concavities and one dorsal concavity is present. A small anteroposteriorly elongate opening is ventral to the large opening. A deep groove posteroventral to the large opening runs dorsoventrally.

The pineal opening is not visible. The pineal plate itself is visible (Fig. 5.2C), primarily from the medial end of the orbit. The lateral end of the pineal plate (Fig. 5.2C) is broad and rounded; the medial end is covered by the prepineal dermoskeleton of the headshield but the pineal plate does shorten medially where it is exposed. The hypophyseal division of the nasohypophyseal opening (Figs. 5.1A, 5.2C) is visible as a large opening that has been compressed laterally so that it tapers ventrally. A small notch at the posterodorsal end of the hypophyseal division is the nasal division. The nasal division is considerably smaller than the hypophyseal division.

Median Field—The median field is not clearly preserved due to distortion and due to loss of the left lateral margin. The extent of the median field can be constrained from the pineal furrow to the anterior end of the dorsal spine and is therefore short; however, the width and shape of the median field remains unknown.

Cornua and Lateral Fields—The posterior end of the cornual process is not preserved. What is preserved of the cornual process is wide at the base, tapering sharply towards the posterior end, and posteriorly directed (Fig. 5.1A). The medial margin of the cornual process is smooth where it is preserved. The pectoral sinus is shallow and wide and has the same ornament as the posterior dermoskeleton of the headshield. The posterior margin of the headshield is broken dorsally/medially but present at the ventral/lateral end.

The lateral fields can be distinguished by an absence of denticulated dermoskeleton in their region. The fields are also more clearly defined anteriorly by a shallow groove and a change in texture in the exposed deeper layers of the dermoskeleton. The fields are broad, and long, extending onto the cornua posteriorly and nearly coming into contact with each other at the anterior end. The length to width of the lateral fields is 5:1. The lateral field tapers anteriorly and posteriorly. Denticles are present past the dermoskeleton lateral to the orbits. This indicates that the medial margin of the lateral field is missing along much of its length. The denticles border the ridges of highest relief in the visceral skeleton. It is at this point that the medial margin of the headshield was probably located and the medial margin of the lateral field would have been equidistant from the lateral margin of the lateral field along its posterior half. The right lateral field is visible on the rostral region of the specimen.

Margin of the Headshield—The margin of the headshield (Fig. 5.1A, and partially in Fig. 5.1C) consists of bone that is more robust than that of the rest of the headshield. The distal and ventral ornament of the margin consists of a series of small and large, posteriorly pointed denticles that become smaller and more uniform in size towards the cornua. The dorsal ornament of the margin changes from small, sparse denticles anteriorly to anteroposterior rows of denticles pointed along the rows at the cornual process. The number of rows increases posteriorly onto the cornual process until a maximum of five rows is visible. A second row of denticles also appears medial to the distal-most row at roughly the same region as the other rows of denticles appear. The margin is otherwise covered in small, sparse bumps dorsally and is narrow along the ventral margin (where it is visible at the anterior end of the specimen).

Remarks

The only specimen referrable to *M. serrata,* other than the holotype is a smaller dorsal spine (UALVP 23154, Fig. 5.2B) unassociated with any other vertebrate fossils. UALVP 23154 is referred to *M. serrata* on the basis of the concave anterior margin of the dorsal spine and the dorsally pointed barbs on the posterior margin of the dorsal spine (Fig. 5.2B). It differs from the holotype in that it is smaller (shown to the same scale as the holotype in Fig. 5.2A, B), and it is lower relative to its anteroposterior length than the dorsal spine of the holotype.

The ornament of the anterior and lateral surfaces of the dorsal spine of UALVP 23154 is noticeably absent or sparse compared to the dorsal spine of the holotype. The reduced height relative to the length of the base of the dorsal spine, and the reduced ornamentation and overall smaller size of UALVP 23154 are interpreted as characteristics of a juvenile specimen of *M. serrata*.

DISCUSSION

The new species of *Machairaspis*, *M. serrata*, differs from other species of *Machairaspis* by its small size, and by unique ornament of the dorsal spine. *Machairaspis serrata* is consistent at the generic level with previous biostratigraphic correlations of the MOTH locality and extends the geographic range of the genus.

Specimen Size

Machairaspis serrata is much smaller than other species of *Machairaspis* (*M. isachseni*, the next smallest species, has a headshield 5.4 mm long, Stensiö, 1927, compared to 2.2 cm for the holotype of *M. serrata*) and therefore the ontogenetic condition of the holotype must be considered before conclusions are drawn as to the specific relationships of this new species. The ornament of the dorsal spine is unique to this taxon. The relative height of the dorsal spine is also very large relative to that of the headshield, compared to other species of *Machairaspis*. Because a dorsal spine (UALVP 23154) that is slightly shorter along the base and much shorter in dorsoventral height (Fig. 5.2A, B), is known from MOTH and can be referred to *M. serrata* based on its ornament, the difference in proportions between the holotype and other species of *Machairaspis* is not a result of an early ontogenetic stage. In fact if the smaller referred specimen of UALVP 23154 is considered as an earlier ontogenetic stage than the holotype, it could be concluded that the dorsal spine actually increases in height relative to the size of the headshield later in ontogeny. This would be consistent with observations by Hawthorn et al. (2008) regarding the development of *Supercilaspis gabrielsei* where absolute size and relative proportions of the dorsal spine also increased through ontogeny.

Machairaspis serrata most closely resembles *M. ibex* based on the extension of the lateral fields onto the cornua and exceptional height of the dorsal spine (Wängsjø, 1952). The lateral fields of *M. battaili* are incompletely known but the posterior margin of the dorsal spine is concave rather than straight (Janvier, 1985a), while the lateral fields of *M. corystis* do not extend onto the cornual processes. The shape of the median field varies among species of *Machairaspis* and therefore the median field can provide information about the species-level relationships of *Machairaspis*. Unfortunately, the median field of *Machairaspis serrata* is not preserved well enough to determine its shape.

Affinities of *Machairaspis*

In his original description of *Machairaspis*, Janvier (1985a) included the genus in his "scolenaspidiens", which includes *Scolenaspis* and the family

Zenaspididae, composed of *Diademaspis*, *Tegaspis*, and *Zenaspis*. Sansom's (2009) classification refers to this clade as Zenaspididae, and divides it into two unnamed subfamilies, one consisting of *Scolenaspis*, *Machairaspis*, and *Superciliaspis*, with *Ukrainaspis* (formerly *Heraspis* of Afanassieva, 1991, changed by Sansom, 2009) as a sedis mutabilis, and the other subfamily consisting of *Tegaspis*, *Stensiopelta*, *Diademaspis*, and *Zenaspis*. In Sansom's (2009) phylogenetic analysis, *Machairaspis* is resolved in a sister relationship with *Superciliaspis*, while *Scolenaspis* is basal to both. The characters uniting *Machairaspis* and *Superciliaspis* are based exclusively around the tall dorsal spine; however, *Superciliaspis* differs from the Zenaspididae because of its narrow median field bordered by raised ridges and because of the absence of the pineal plate. *Superciliaspis* also differs from *Machairapis* as the former has a tesselate dermoskeleton of the headshield, while the latter has a continuous dermoskeleton across the headshield, and the two taxa differ from each other in the morphology of their dorsal spine.

Machairaspis and *Superciliaspis* are the only two known osteostracans with dorsal spines at least as tall as their headshields; however, there are numerous morphological differences between these spines. The dorsal spine of *Superciliaspis* is composed of numerous plates, with a single dorsal plate running in a linear incline from anterior to posterior along the headshield (Dineley and Loeffler, 1976). The dorsal spine of *Superciliaspis* points posteriorly from the headshield. The anterior margin of the dorsal spine is a dorsal incline and the posterior margin is straight until the point where the lateral plates of the dorsal spine meet the long dorsal plate of the dorsal spine. This is in contrast to the condition seen in *Machairaspis*. The dorsal spine of *Machairaspis* is continuous with the rest of the headshield, and it has a straight posterior margin and a concave anterior margin, making the dorsal spine extend straight dorsally from the headshield (Fig. 5.1A, 5.2A).

Superciliaspis is not only different from *Machairaspis*, but also from all of the Zenaspididae, sharing only an expanded hypophyseal opening (Janvier, 1985a). Based on the previously mentioned characteristics, *Supercilaspis* should be excluded from the Zenaspididae, or be placed basal to the two subfamilies within the Zenaspididae. *Machairaspis* on the other hand should be retained within the Zenaspididae, and referred to Sansom's (2009) unnamed subfamily B along with *Scolenaspis*. This unnamed subfamily B can be considered equivalent to the subfamily Scolenaspidinae, but would be based on the cladistic relationships of *Machairaspis*, *Scolenaspis*, and *Ukrainaspis*, a clade in Sansom (2009), rather than being defined by unique synapomorphies, because the characters that these three taxa share are present in other clades as well, either as plesiomorphies or homoplasies.

Stratigraphic Distribution of *Machairaspis*

Machairaspis is present in the '*Psammosteus'* horizon at the base of the vertebrate bearing beds at Spitsbergen and is common in the Ben Nevis Formation of the Red Bay Group of Spitsbergen; *M. isachseni* and *M. battaili* are both recorded in the Wood Bay Formation (Stensiö, 1927; Janvier, 1985a). This gives

Machairaspis a stratigraphic distribution throughout the Lower Devonian beds of Spitsbergen. Along with *Waengsjoeaspis*, at the upper part of the Fraenkelryggen Formation, the presence of *Machairaspis* is consistent with the Lochkovian age previously proposed for MOTH (Bieck et al., 1987, Adrain and Wilson, 1994).

Geographic Distribution of *Machairaspis*

The presence of *M. serrata* at MOTH extends the geographic range of *Machairaspis* from Spitsbergen, Norway (Janvier, 1985a), Podolia, Ukraine (Janvier, 1985b) and Prince of Wales Island, Nunavut, Canada (Dineley, 1994) to MOTH, Northwest Territories, Canada. At the generic level there is a strong similarity in the Early Devonian among the osteostracan faunas of Spitsbergen and of North America, with MOTH and Spitsbergen sharing *Machairaspis*, *Waengsjoeaspis*, and *Diademaspis* (Adrain and Wilson, 1994, although classification of *D. mackenziensis* is debated by Voichyshyn, 2006). *Machairaspis* and *Parameteoraspis* are found at both Prince of Wales Island (Dineley, 1994) and Spitsbergen (Janvier, 1985a). Many members of the Zenaspididae (*Tegaspis*, Belles-Isles and Janvier, 1984, *Zenaspis*, Janvier, 1985b; Voichyshyn, 2006; *Machairaspis*, Janvier, 1985b, *Diademaspis*, Afanassieva, 1989; Voichyshyn, 2006) are present at both Podolia and Spitsbergen, but have not been identified from MOTH. Conversely a large number of genera, *Supercilaspis* (Dineley and Loeffler, 1976; Adrain and Wilson, 1994) and five more described in this thesis, have not yet been identified from any other localities and are seemingly endemic to MOTH. This would seem to suggest that although there are a few widespread taxa of Zenaspidida found at MOTH and across the Laurentia terrane and at the Podolia locality, there is a clear endemism of osteostracan taxa at the MOTH locality.

SUMMARY

A new species of *Machairaspis*, *M. serrata*, was described based on a single headshield in lateral view and a small dorsal spine. This is the first documented occurrence of *Machairaspis*, a genus known from Spitsbergen, Norway (Janvier, 1985a), Podolia, Ukraine (Janvier, 1985b), and Prince of Wales Island, Canada (Dineley, 1994) at MOTH, Northwest Territories, Canada. The dorsally pointed barbs of the posterior margin of the dorsal spine are the most obvious diagnostic characteristic of the species. Discovery of a new species of *Machairaspis* from the MOTH locality supports previous proposals of a close biogeographic relationship between the Early Devonian faunas of MOTH and Spitsbergen, Norway (Blieck et al., 1987).

LITERATURE CITED

Adrain, J. M., and M. V. H. Wilson. 1994. Early Devonian cephalaspids (Vertebrata: Osteostraci: Cornuata) from the southern Mackenzie Mountains, N.W.T., Canada. Journal of Vertebrate Paleontology 14:301–319.

Afanassieva, O. B. 1989. New cephalaspids (Agnatha) from the Lower Devonian of Podolia. Paleontologicheskiy zhurnal. 1989: 51–59. [Translated from Russian]

Afanassieva, O. B. 1991. Tsephalaspidi Sovetskogo Soyuza (Agnatha) [Cephalaspids of the Soviet Union]. Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR 248: 1–144 [in Russian].

Belles-Isles, M., and P. Janvier. 1984. Nouveaux ostéostracés du Dévonien Inferieur de Podolie (RSS d'Ukraine). Acta Palaeontologica Polonica 29: 195–208.

Blieck, A., D. Goujet, and P. Janvier. 1987. The vertebrate stratigraphy of the Lower Devonian (Red Bay Group and Wood Bay Formation) of Spitsbergen. Modern Geology 2:197–217.

Dineley, D. L. 1994. Cephalaspids from the Lower Devonian of Prince of Wales Island, Canada. Palaeontology 37: 61–70.

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

214.

Gabrielse, H., S. L. Blusson, and J. A. Roddick. 1973. Geology of Flat River, Glacier Lake and Wrigley Lake map areas, District of Mackenzie, Northwest Territories. Geological Survey of Canada, Memoir 366:1–268.

Hawthorn, J. R., M. V. H. Wilson, and A. B. Falkenberg. 2008. Development of the dermoskeleton in *Superciliaspis gabrielsei* (Agnatha: Osteostraci). Journal of Vertebrate Paleontology 28:951–960.

Janvier, P. 1981. *Norselaspis glacialis* n.g., n.sp. et les rélations phylogénétiques entre les Kiaeraspidiens (Osteostraci) du Dévonien inférieur du Spitsberg. Palaeovertebrata 11: 19–131.

Janvier, P. 1985a. Les Cephalaspides du Spitsberg. Cahiers de Paléontologie, Section Vertébrés. Éditions du Centre National de la Recherche Scientifique, Paris: 244 pp.

Janvier, 1985b. Preliminary description of Lower Devonian Osteostraci from Podolia (Ukrainian S.S.R.). Bulletin of the British Museum (Natural History): Geology 38: 309–334.

Lankester, E. R. 1868. A Monograph of the Fishes of the Old Red Sandstone of Britain. Part I. The Cephalaspidae. Monograph of the Palaeontographical Society, London, 62 pp.

Sansom, R. S. 2009. Phylogeny, classification and character polarity of the Osteostraci (Vertebrata). Journal of Systematic Palaeontology 7:95–115.

Stensiö, E. A. 1927. The Devonian and Downtonian vertebrates of Spitzbergen. 1. Family Cephalaspidae. Skrifter om Svalbard or Nordishavet 12:1–391.

Stensiö, E. A. 1958. Les Cyclostomes fossiles ou Ostracodermes. Pp. 173–425 in P. P. Grass´e (ed.), Traité de Zoologie. Masson, Paris.

Voichyshyn, V. 2006. New osteostracans from the Lower Devonian terrigenous deposits of Podolia, Ukraine. Acta Palaeontologica Polonica 51: 131–142.

Wängsjø, G. 1952. The Downtonian and Devonian vertebrates of Spitsbergen. IX. Morphologic and systematic studies of the Spitsbergen cephalaspids. Results of Th. Vogt's Expedition 1928 and the English-Norwegian-Swedish Expedition in 1939. Norsk Polarinstitutt Skrifter 97:1–611.

FIGURE 5.1. *Machairaspis serrata*, sp. nov. holotype, UALVP 53224. **A**, the holotype, a small headshield with a tall dorsal spine in left lateral view. **B**, close-up image of the holotype showing the denticles ornamenting the dermoskeleton posterior to the orbits; many of the denticles are broken. **C**, detailed image of the dermoskeleton and margin of the headshield lateral to the lateral field.

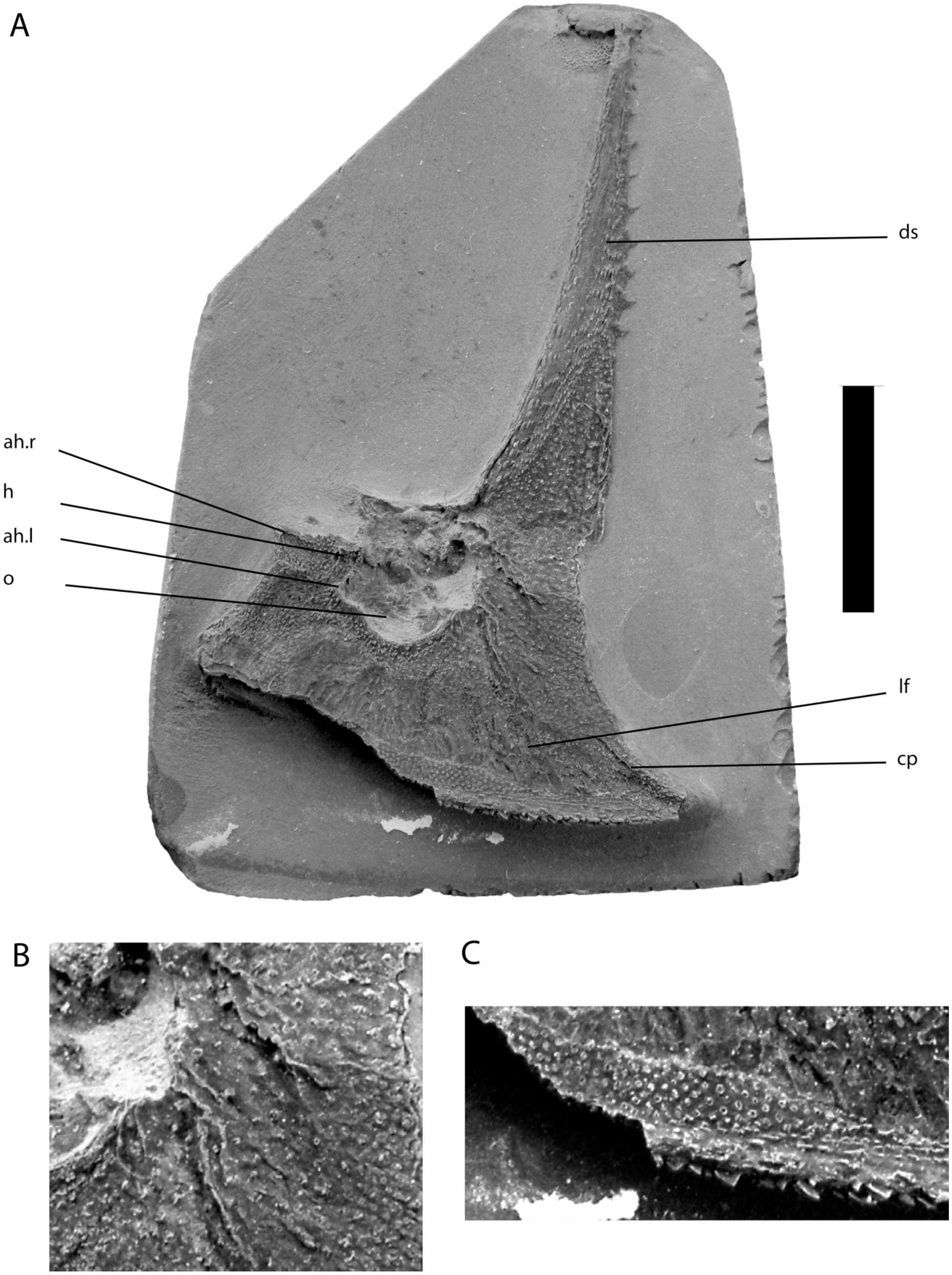
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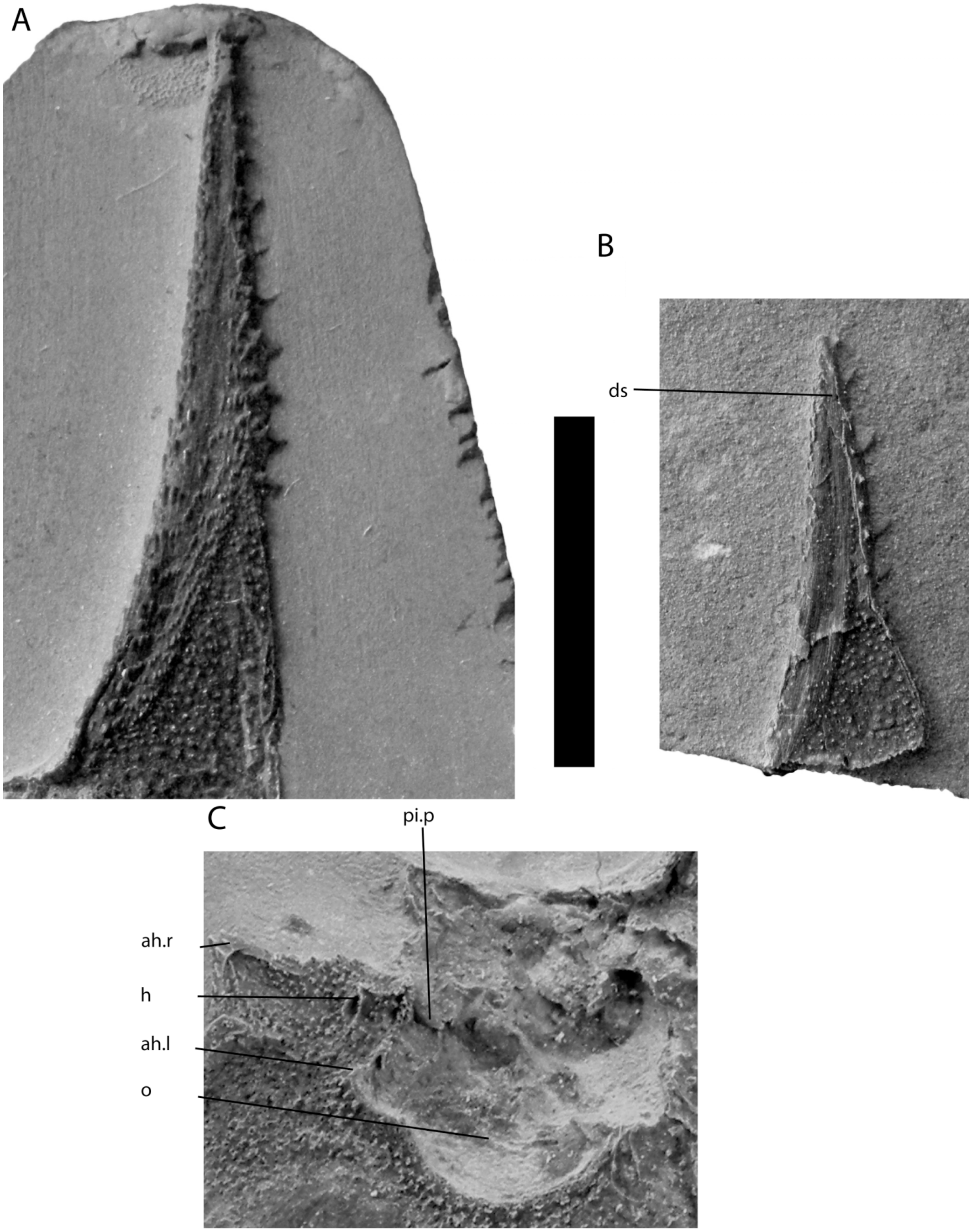
FIGURE 5.2. *Machairaspis serrata*, sp. nov. specimens, including the holotype, UALVP 53224 A, C and B, the paratype, UALVP 23154. **A**, a detailed image of the dorsal spine of the holotype, the dorsally directed barbs on the posterior margin are diagnostic of *M. serrata*, sp. nov., **B**, the paratype for *M. serrata*, sp. nov., a small dorsal spine, to scale with A. **C**, a detail image of the left orbit, hypophyseal opening and pineal plate.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CHAPTER 6:

THE SUPERCILIASPIDIDAE, A NEW FAMILY OF CORNUATE OSTEOSTRACANS FROM THE EARLY DEVONIAN (LOCHKOVIAN) MOTH LOCALITY, WITH THE DESCRIPTION OF TWO NEW GENERA AND THREE NEW SPECIES

INTRODUCTION

The Lochkovian (Early Devonian) Man on the Hill (MOTH) locality, Northwest Territories, Canada, has produced a vast diversity of early vertebrates (e.g., Dineley and Loeffler, 1976; Wilson and Caldwell, 1998), including several species of osteostracan (Adrain and Wilson, 1994). All of the osteostracan species from MOTH are endemic; however, three of the genera, *Waengsjoeaspis*, *Machairaspis*, and *Diademaspis*, are also known from Spitsbergen (Adrain and Wilson, 1994; Chapter 5). Previous to this study, *Superciliaspis* was the only genus of osteostracan endemic to MOTH to be described (Dineley and Loeffler, 1976; Adrain and Wilson, 1994).

The genus *Superciliaspis* was originally established by Adrain and Wilson (1994) to include the species '*Cephalaspis*' *gabrielsei* which was described by Dineley and Loeffler (1976). Sansom (2009) provided the first phylogenetic analysis to include *Superciliaspis*. He resolved *Superciliaspis* as a member of "Unnamed subfamily B" (Sansom, 2009: p. 112) within family Zenaspididae and order Zenaspidida. *Machairaspis*, *Scolenaspis*, and *Ukrainaspis* are also included in "Unnamed subfamily B" for which there were no clear synapomorphies. The absence of a pineal plate, and the raised ridges of plates that border the median field differentiate *Superciliaspis* from other Zenaspidids

Three new species are described here comprising two new genera of cornuate osteostracans that share several characteristics with *Superciliaspis gabrielsei*. *Glabrapelta cristata* gen. et sp. nov., *Glabrapelta minima,* gen. et sp.

nov., and *Dentapelta loefflerae*, gen. et sp. nov., are all described from MOTH. *Glabrapelta*, gen. nov., and its two new species are based on three previously undescribed specimens from the UALVP collections. *Dentapelta loefflerae*, gen. et sp. nov., is described based on a new specimen from MOTH in the UALVP collections, as well as NMC 21554, originally described by Dineley and Loeffler (1976) as Cephalaspidinae indet. Together with *Superciliaspis gabrielsei*, these new species are referred to a new family: Superciliaspididae. The Superciliaspididae are placed within the order Zenaspidida.

SYSTEMATIC PALEONTOLOGY

Class OSTEOSTRACI Lankester, 1868
Subclass CORNUATA Janvier, 1981
Order ZENASPIDIDA Stensiö, 1958
Family SUPERCILASPIDIDAE, fam. nov.

Diagnosis—Zenaspidida differing from all other Zenaspidida in having orbits close together, with a ratio of orbit width to interorbital distance of at least 0.7:1, by thickened ridges of large or fused plates bordering median field, and by a long and narrow median field.

Remarks

Variation exists in the orbit width to interorbital distance among specimens of the same species as well as among species. This variation is likely a result of taphonomy. Specimens of *Superciliaspis* preserved in lateral view (Dineley and Loeffler, 1976; Hawthorn et al., 2008), along with the holotype of *Dentapelta loefflerae*, gen. et sp. nov., and to a lesser extent UALVP 43214, a paratype of *Glabrapelta cristata*, gen. et sp. nov., all show orbits facing dorsolaterally, and in the case of the first two, an orbit that is nearly circular as preserved. This is important because specimens compressed vertically without lateral displacement or spreading (identifiable by longitudinal fractures in the dermoskeleton where it overlaps) would result in oval orbits in which the anteroposterior (horizontal) width is preserved, but the vertical distance is shortened. The anteroposterior width should be roughly equal to the actual width of the orbit.

This would mean that the specimens with a relatively low ratio of orbit width (measured transversely) to interorbital distance would underestimate their actual ratio. However, in other taxa of Zenaspidida for which the orbits are clearly preserved, and especially those for which measurements have previously been obtained, the orbits are typically circular and dorsal facing, and thus their orbit width to interorbital distance is not being underestimated.

GLABRAPELTA, gen. nov.

Figs. 6.1, 6.2, 6.3, 6.6A, B

Etymology—*Glabra*, Latin, “smooth,” and *pelta*, Latin, “shield.” In reference to the unornamented headshield. Gender feminine.

Type Species—*Glabrapelta cristata*, gen. et sp. nov.

Other Species—*Glabrapelta minima*, gen. et sp. nov.

Diagnosis—Cornuate osteostracans in which the pineal plate is anteroposteriorly expanded medially, pineal opening is large, wider than long, and rectangular, and the headshield is unornamented and the circumareal canals are external.

Differs from other Superciliaspididae in the presence of a pineal plate, and absence of any ornamentation on the dorsal surface of the headshield. Differs from *Superciliaspis* by absence of a cornual plate along medial margin of cornual process. Differs from *Dentapelta*, but not *Superciliaspis*, by externally visible tesselation of dermoskeleton of headshield.

GLABRAPELTA CRISTATA, sp. nov.

Figs. 6.1, 6.2, 6.6B

Etymology—*Cristata*, Latin, means "ridged," in reference to the ridge medial to the lateral fields. Gender feminine.

Holotype—UALVP 43639, a nearly complete headshield in dorsal view (Figs. 6.1A, 6.2, 6.6B).

Paratypes—UALVP 42731. a partial headshield including regions anterior to median dorsal crest (Fig. 6.1B), and UALVP 43214, a partial headshield with some depth (Fig. 6.1C).

Diagnosis—*Glabrapelta* with lateral field bordered medially by low ridge of bone. Maximum width of orbits equal to or slightly less than interorbital distance. Differs from *Glabrapelta minima*, sp. nov., by lateral fields expanded at their anterior ends, relative to their width along the rest of their length.

Type Locality—Same as for previously mentioned species. The Lower Devonian (Lochkovian) transitional beds between the Road River Formation and the Delorme formation. In particular the "Fish Layer" at the MOTH locality, Northwest Territories, Canada (Gabrielse et al., 1973).

Description

Headshield—Measurements of the headshields of *G. cristata* are provided in Table 6.1. The posterior margin of the dorsal shield (Fig. 6.1A) is broken. A fracture runs anteroposteriorly along the left side of the headshield, lateral to the median field. The fracture extends as far anteriorly as the orbits, and extends posterior to the broken posterior margin of the headshield. A similar fracture is also observed in UALVP 43214. The headshield is roughly as long as it is wide. The headshield is parabolic, with a rounded anterior end in UALVP 41731 (Fig. 6.1B) and UALVP 43214 (Fig. 6.1C).

The headshield is formed of small, polygonal tesserae covered in small pores, but lacking any tubercles or other form of superficial ornamentation. The tesserae are separated by external circumareal canals, but are fused at the basal layer. Between tesserae, pores regularly pass viscerally through the circumareal canal; these pores are consistent in position and size with the radiating canals observed in the dermoskeleton of *Waengsjoeaspis nahanniensis* and *W. platycornis*. The tesserae do not have centrifugal growth rings. The tesserae in some areas of the dorsal headshield are fused at the superficial layer. The tesserae are smaller medially and larger laterally. Those bordering the median field are mostly fused together. The infraorbital sensory line is a continuous shallow groove in the tesserae extending anterolateral to the orbits and passing through the lateral field before passing medially from the anterior ends of the lateral fields (can be observed in all three specimens but is most clearly in UALVP 43214). A sensory line, possibly the postorbital sensory line, is present posterior to the labyrinth infilling in UALVP 41731.

The dorsal median crest is present as a single ridge starting from the posterior end of the median field and extending posteriorly in a slight incline (Fig. 6.1A). The dorsal median crest is low and thick, with a dense superficial bone layer as seen in cross section in the holotype. The surface texture of the dorsal median crest is covered in small pores like the rest of the dorsal dermoskeleton. The dorsal median crest is continuous and composed of fused plates.

Orbits, Pineal Region, and Nasohypophyseal Region—The orbits are longitudinally oval and closely set (Figs. 6.1, 6.6B). The interorbital distance is nearly equal to the width of each orbit. Anterior to the orbits are dorsal projections. These antorbital horns are low and long, sloping anteriorly from a distal peak where the antorbital horn is adjacent to the orbit, for several millimeters. The pores of the antorbital horns are large and farther apart than those of the rest of the dorsal dermoskeleton. The lateral rim of the orbits is raised and thick, being composed of fused tesserae (Fig. 6.6B). The medial border of the orbit has a deep median notch where the pineal furrow contacts the orbit. The region posterior to the orbits is raised and rugose from the underlying labyrinth infillings. Long plates with the same texture as the dorsal dermoskeleton are visible in the posteromedial region of the left orbit. Based on their position and shape these are consistent with the sclerotic plates. A plate in the right orbit could be sclerotic or could be the broken distal tip of the right antorbital horn (Fig. 6.6B). The interior of the orbit of UALVP 43214 is covered in a rough layer of visceral bone that is part of the sclerotic capsule.

The pineal furrow is completely closed and covered on either side of the anterior border of the median field (Figs. 6.1, 6.6B). The pineal furrow is therefore only present lateral to the anterior margin of the median field as a narrow line that extends to the medial margin of the orbits. The pineal plate (Fig. 6.6B) is small and spindle-shaped where it is exposed at the anterior end of the median field. The lateral end of the pineal plate is visible at the median notch of the left orbit. The pineal plate tapers lateral to the pineal opening and expands to a flat surface at the median notch. The dermoskeleton of the pineal plate has the same surface texture as the headshield lateral to the pineal opening, but no dermoskeleton is present anterior or posterior to the pineal opening (Fig. 6.6B). The pineal opening is rectangular and one-and-a-half times wider than it is anteroposteriorly long. The pineal opening of UALVP 43214 is trapezoidal, rather than rectangular, with a short anterior side and a long posterior side. The pineal opening faces posterodorsally, the posterior margin being nearly level with the exposed inner surface of the median field.

The nasohypophyseal opening (Figs. 6.1, 6.6b) is constricted between the nasal and hypophyseal divisions. The nasal division is small, circular, and on a raised mound. The hypophyseal division is rhomboid and expanded relative to the nasal division. The nasohypophyseal depression is triangular, extending from the anterior end of the hypophyseal division to the medial side of the antorbital horns (Fig. 6.6B).

Median Field—The median field is long and narrow (Fig. 6.1A), but widens posteriorly to the external openings of the endolymphatic ducts. The lateral margin of the median field is gently scalloped, conforming to the shape of the fused plates lining the median field as a thick ridge. The anterior margin lies flat against the pineal plate. The posterior margin of the median field extends to the anterior end of the median dorsal crest; it tapers to a rounded tip beginning at the external openings of the endoymphatic ducts, which are located inside the median field, at three-quarters the length of the field. The external covering of the median field is not preserved. The visceral texture of the exposed surface of the median field is rough and pitted.

Cornua—The cornual process is narrow, with a smooth and continuous medial and lateral margin (Fig. 6.1A). The pectoral sinuses are shallow and narrow on both sides of the dorsal headshield. The medial surface of the cornual process is ornamented with pores identical to those of the dermoskeleton. The lateral margin of the process is thin and as porous as the medial margin. The dorsal surface of the process is broken near the lateral margin, but is otherwise continuous and covered in pores. The tesserae of the dermoskeleton of the cornua are fused.

Lateral Fields—Each lateral field extends from its anterior tip, which is longitudinally in line with the lateral margin of the orbit, posteriorly onto the cornual process. The field is narrow and even in width along most of its length (Fig. 6.1); however, the anterior end of the field is expanded in width (Fig. 6.2) and the posterior end tapers where it enters the cornual process.The field is bordered medially by a narrow, low, convex ridge (Fig. 6.2); this ridge is most obvious on the holotype and on UALVP 43214. The medial margin and lateral margins of the field are uneven, conforming to the shapes of the tesserae bordering it. The lateral margin of the lateral field is close (3 mm) to the margin of the headshield. Tesserae are preserved covering the anterior end of the left lateral field and at the region of the right lateral field that is opposite the external openings of the endolymphatic ducts.

Margin of the Headshield—The margin of the headshield is broken along its preserved length in the holotype but in UALVP 43214 and UALVP 41731 it forms a continuous rim. The rim is narrow dorsally and its dorsal surface is the same as as that of the dorsal dermoskeleton, except that the pores are farther apart. Unfortunately a ventral view of the rim of the headshield is not available.

Remarks

The presence of a fracture in the headshield of two of the three specimens is a result of compression of a deep headshield. The similarity in the placement of the fracture is consistent with a similarity in the depth and shape of the headshields in life.

The shape of the pineal opening varies slightly between specimens of *G. cristata*. In all specimens the pineal opening is longer than it is wide and has four sides. The pineal opening of the holotype is rectangular (Fig. 6.6B); both the anterior and posterior borders are of equal length. In UALVP 43214, the anterior border is slightly rounded and shorter than the posterior border. In UALVP 42731, the posterior border of the pineal opening is slightly rounded and the oblique angle of the right lateral border would necessitate an anterior border shorter than the posterior border in order for the margins to connect. The variation in the shape of the pineal opening is likely a result of variation in the amount of compression each specimen underwent during taphonomy. UALVP 42731 underwent the greatest compression, while UALVP 43214 underwent the least compression. The median field of UALVP 43214 also appears to be slightly wider than the median fields of UALVP 42731 and the holotype (UALVP 43639).

The ridge medial to the lateral fields (Fig. 6.2) is present on the holotype and UALVP 43214, and discontinuously on UALVP 41731 and on either side of the headshield. While an embossment of an underlying structure could have caused such a feature, the ridge is not present on any other species of osteostracan from MOTH, including *Waengsjoeaspis*, which also has a dermoskeleton covered in pores and tesserae similar to the dermoskeleton of *Glabrapelta cristata* and has undergone similar taphonomic processes. The dorsal surface of the plates bordering the lateral field of *Glabrapelta minima*, sp. nov., is also smooth and this ridge is not present. I conclude that, whether this ridge represents a dermoskeletal structure or an embossed underlying structure it represents a morphologically distinct feature of *Glabrapelta cristata*.

GLABRAPELTA MINIMA, sp. nov.

Figs. 6.3, 6.6A

Etymology—*Minima*, Latin, meaning "least" in reference to the small size of the holotype. Gender feminine.

Holotype and Only Specimen—UALVP 43083 right side of a small headshield in dorsal view (Fig. 6.3, 6.6B).

Diagnosis—Maximum orbital width much larger, between one-and-a-quarter and one-and-a-half times, than interorbital distance, and orbital width to interorbital distance larger than in *G. cristata* (1.4 compared to 0.7 in *G. cristata*). Distinct anteroposteriorly elongate tubercles lining anterior border of pectoral sinus.

Glabrapelta minima differs from *G. cristata* by its large orbits relative to its headshield, its tubercles lining the pectoral sinus, and its small size. It also lacks the ridge medial to the lateral field, as well as the anterior expansions of the lateral fields that are present in *G. cristata*. *Glabrapelta minima* resembles '*C.*' *pygmaea* (Wängsjø, 1952: pl. 9, figs. 1-3), with large orbits close together and a small headshield, but *G. minima* lacks barbs on the medial margin (Fig. 6.3B) and the cornua are narrower and more posteriorly directed (Fig. 6.3A) than those of

‘*C.*’ *pygmaea*.

Type Locality—MOTH locality, same as for *G. cristata*.

Description

Headshield—Measurements of the headshield of *G. minima* are provided in Table 6.1. The headshield lateral to the medial half of the right orbit and posterior to the left pectoral sinus and the median field is not preserved (Fig. 6.3A), but the preserved portion shows that the headshield is small and triangular. Standard proportions of the headshield, particularly the prepineal length and postpineal length, cannot be determined because the rostral region and abdominal division of the headshield are not preserved.

The headshield is covered in tesserae, the surface of which are smooth, except for numerous small pores. The pores of the dermoskeleton range in shape from circular to elliptical. The tesserae are fused across the dorsal headshield, separated by shallow grooves and often bordered on one or both sides by a narrow ridge. The separation of tesserae in the superficial layer is most obvious anterior to the nasohypophyseal opening. The infraorbital sensory line is visible as a shallow groove in the dorsal dermoskeleton, which passes from the lateral margin of the orbit, through the lateral field transverse to the anterior end of the orbit.

Orbits, Pineal Region, and Nasohypophyseal Region—The orbits are circular (Fig. 6.3A, C) and very large relative to the size of the headshield (Fig. 6.3A) and are close together; the ratio of orbit width to interorbital distance is 1.4:1. The antorbital region is not preserved, but based on the curvature of the dermoskeleton anterior to where the antorbital horns are on *Waengsjoeaspis* and *Glabrapelta cristata*, the antorbital horns were not present, or low in *G. minima*. The lateral border of the orbits is a continuous, raised rim of fused tesserae (Fig. 6.3A, C). The medial border is preserved on the right orbit but not on the left orbit. It is smooth and continuous, not raised, and broken where the orbit meets the pineal plate. The concentrations of white grains, visible visceral to the dermoskeleton and posteromedial to the orbits, as well as ventral to the posterior end of the orbits, are the labyrinth infillings. These white grains are also found under the posterior end of the orbits. The interior of the orbit is covered in a very thin layer of bone that is either the sclerotic capsule or the ossified orbit cavity. As discussed below, the evidence favors this being the sclerotic capsule. The capsule is strongly inclined at the anterior end of the orbit, and ridges, interpreted here as nerves, and 'sel' canals, are embossed on it (Fig. 6.3C, D). Because the facial and trigeminal nerves are embossed, it is most likely that the capsule has been compressed over these nerves and the 'sel' canals, because the facial and trigeminal nerves typically pass through the orbit cavity and therefore would not be embossed on the orbit cavity. Two ridges are embossed in the center of the orbit, running longitudinally, with a smaller ridge lateral and parallel to these and at least two more ridges extending transversely across the posterolateral end of the orbit. The medial-most ridge and the two lateral-most ridges originate from a wide, round, embossed structure at the posterior end of the orbit that overlies the anterior end of the labyrinth infillings (Fig. 6.3C, D). Despite being beneath the orbit, the wide, round structure at the posterior end of the orbit, is likely the vestibular division of the labyrinth cavity. The three more medial ridges are therefore considered to be, from medial to lateral, the canal for the maxillary and mandibular branch of the trigeminal nerve, the canal for the facial nerve, and the 'sel' 1 canal. The two most lateral ridges are therefore 'sel' 2 and 'sel' 3, respectively (Fig. 6.3C, D). A ridge runs across the previously mentioned ridges, transversely across the middle of the orbit. An identification of this ridge cannot readily be supplied given the current models for the preceding ridges.

The shape of the pineal furrow is unclear as the dermoskeleton bordering that region of the orbits is broken (Figs. 6.3C, 6.6A). The pineal plate extends to the medial margins of both orbits. The pineal plate is anteroposteriorly deeper medially, where the pineal plate meets the median field (Fig. 6.6A). The ornament of the pineal plate is the same as that of the dorsal dermoskeleton of the headshield, but the dermoskeleton is not present posterior to the pineal opening. The pineal plate is thicker anterior to the pineal opening than it is posterior to the opening. The opening is rectangular and is wider than long. The posterior margin of the opening is broken and at least as high as the exposed visceral layer of the median field.

The nasohypophyseal opening is constricted between the nasal division and the hypophyseal division (Fig. 6.6A). Of the nasal division, only the anterior right margin is preserved. Constrained by the dermoskeleton, the nasal division is smaller than the hypophyseal division. The hypophyseal division is rhomboid and the margin is determined by a border of superficial layer of the dermoskeleton. A layer of bone visceral to the superficial layer of the dermoskeleton is present within the hypophyseal division. The nasohypophyseal depression is triangular. The anterior end of the depression is at the anterior end of the hypophyseal division and the posterior margin is flanked by the orbits. The depression is deeper anteriorly than it is posteriorly as it widens towards the orbits.

Median Field—The median field is long and narrow and is constricted anteriorly, just posterior to the pineal opening (Fig. 6.3A, 6.6A). The anterior border of the median field extends to the pineal plate and is as wide as the pineal opening. The lateral margin of the median field widens posteriorly and is fused on either side. The right lateral border of the median field is continuous and a raised secton of dermoskeleton runs parallel to it; however, this region overlies the labyrinth infilling. The posterior margin of the median field and the external openings of the endolymphatic ducts are not preserved. No tesserae are preserved covering the median field.

Cornua—Only the base of the left cornual process is preserved (Fig. 6.3A), and it is very narrow. The preserved parts of the medial and lateral margins of the cornual process are smooth and continuous, with the same porous surface as seen on the tesserae of the dorsal headshield. The entirety of the preserved dorsal surface of the cornual process is taken up by the lateral field. The pectoral sinus is shallow, narrow, and the margin is continuous. Tubercles, pointed anteriorly and rounded posteriorly, ornament the anterior margin of the pectoral sinus (Fig. 6.3B).

Lateral Fields—Only the left lateral field is preserved and the anterolateral-most tip is not preserved (Fig. 6.3A). The remainder of the anterior end of the lateral field is rounded. The field is long and narrow and extends anteriorly until it is longitudinal to the lateral margin of the orbits, and posteriorly onto the cornual process. The dermoskeleton of the headshield, perhaps owing to compression, extends onto the lateral field where it meets the cornual process; posterior to this the lateral field tapers. The medial margin of the field is formed of tesserae and the border conforms to the margins of the tesserae. The lateral margin of the lateral field is close to the headshield margin, but the exact shape of the margin is unclear since it is broken along most of its length. The lateral and medial margins of the lateral field are equidistant from one another until the cornual process; no expansions of the lateral field are present at either the anterior end or the posterior end. No tesserae are preserved covering the lateral field.

Margin of the Headshield—The margin of the headshield (Fig. 6.3A) is broken at several points, but appears to form a continuous rim, with no furrows separating tesserae. The rim is unornamented and composed of smooth dermoskeleton like that of the rest of the headshield. The rim is very narrow in dorsal view and mostly appears as a thin vertical wall.

Remarks

An alternative interpretation of the ridges embossed in the orbit is that the three more medial ridges are, from medial to lateral, the canal for ‘sel’ 1, the canal for the facial nerve, and the canal for the glossopharyngeal nerve, and that the canals for ‘sel’ 2 and ‘sel’ 3 are the transverse ridges at the posterolateral end of the orbit. The interpretation given in the description (Fig. 6.3D) is preferred as it explains nearly all of the structures embossed and their spacial arrangement (Fig. 6.3C). However, the description does not account for the glossopharyngeal nerve, while the alternative interpretation offered here does not include the maxillary and mandibular branches of the trigeminal nerve. The white grains infilling the labyrinth cavity (Sahney and Wilson, 2001) are present under the posterior end of the orbit, supporting the interpretation of the embossment at the posterior end of the orbit that was provided in the description. Deformation of the headshield through compression is obvious and could have contributed to the orbit overlying the vestibular division of the labyrinth cavity.

Evidence of deformation of the headshield goes beyond the obvious compression of the specimen. The dermoskeleton cuts across the lateral field at the base of the cornual process, a condition not observed in any known species of osteostracan. The oblong pores of the dorsal dermoskeleton also suggest deformation from the circular pores noted on *G. cristata*.

DENTAPELTA, gen. nov.

Etymology—The generic name dentapelta is derived from *dentis*, Latin, meaning "tooth," *pelta*, Latin, meaning "shield," for the tooth-like denticles that ornament the headshield. Gender feminine.

Type and Only Known Species—*Dentapelta loefflerae*, sp. nov.

Diagnosis—Same as for the type and only known species.

DENTAPELTA LOEFFLERAE, sp. nov.

Figs. 6.4, 6.5, 6.6D

Cephalaspidinae indet. Dineley and Loeffler, 1976, p. 168, pl. 27, fig. 1; text-fig. 72B (original description).

Etymology—The specific epiphet *loefflerae* honors Elizabeth Loeffler, for her contributions to the study of the early vertebrate material from MOTH.

Holotype—NMC 21554, right side of a headshield in dorsal view (Fig. 6.4A, 6.5D).

Paratypes—UALVP 32408, a fragment of dermoskeleton from a headshield (Fig. 6.4B); UALVP 43640, right side of a headshield missing the lateral margin and the cornual process (Figs. 6.4C, 6.5A–C).

Diagnosis—A cornuate osteostracan in which the dermoskeleton is composed of numerous denticles. The denticles are circular at their base and increase in size posteriorly on the headshield. The posterior denticles are hollow in the center and point posteriorly. The median field is constricted at its anterior end where it passes between the labyrinth infillings. No pineal plate is present; instead, the median field meets directly with the anterior end of the pineal furrow. The orbits are close together and oblong in dorsal view, but nearly circular in lateral view.

Differs from other Superciliaspididae by continuous dermoskeleton covering headshield and by denticulate ornamentation of dermoskeleton. Differs from *Glabrapelta* by absence of pineal plate (a feature shared with *Superciliaspis*).

Differs from *Superciliaspis*, but not *Glabrapelta*, by absence of cornual plate.

Type Locality—The MOTH locality, same as for *G. cristata*.

Description

Headshield—Measurements of the headshields of *D. loefflerae* are provided in Table 6.1. The following descripton is primarily based on the holotype, NMC 21554 (Fig. 6.4A, also Dineley and Loeffler, 1976: pl. 27 fig.1, and text-fig. 72B) with details supplemented primarily by UALVP 43640 (Fig. 6.4C). A specimen of a thelodont overlies the right side of NMC 21554. The headshield is moderately large for an Early Devonian osteostracan at an estimated width of nearly 8 cm. The left side of the headshield is missing, with the exception of the median field. The anterior margin of the headshield, median dorsal crest or spine (see Remarks), and the posterior tip of the cornual process are also not preserved. The lateral regions of the headshield are crushed flat, while the median region of the headshield is still preserved in three dimensions. A fracture runs anterolaterally to posteromedially along the right side of the headshield. Based on UALVP 43640, it can be determined that the prepineal length of the headshield is equal to, or slightly shorter than, the postpineal length of the headshield.

The headshield is covered by a continuous, rather than tesselate, dermoskeleton that is ornamented with numerous small denticles (Fig. 6.5A). Where the denticles are broken, a large cavity is visible in the center of each. At the anterior end of the headshield, the denticles are closer together, smaller and more rounded, but with a short posterior point. The denticles of the anterior headshield of UALVP 43640 are smaller than those of the holotype and project dorsally, with no posterior points (Fig. 6.5B). Denticles at the anterior end of the headshield of both the holotype and UALVP 43640 also have small ridges radiating anteriorly from their bases. The ornament of the headshield grades posteriorly into larger, more widely spaced denticles (Fig. 6.5A). The posterior denticles have a circular base and a flat, triangular top pointing posteriorly. The surface of the dermoskeleton between denticles is pitted or consists of radiating canals. In the posterior regions of the dorsal dermoskeleton, polygonal external circumareal canals are visible. These canals represent the borders of tesserae (the interareal grooves of Stensiö, 1927); therefore, it can be determined that multiple denticles are found on each tessera.

Sensory lines are visible on the headshield as pairs of parallel broken ridges of bone on the external surface of the dermoskeleton. The infraorbital sensory line extends laterally from the orbit and then anteriorly towards the margin of the headshield. The infraorbital sensory line of the holotype is incomplete at its lateralmost point where it approaches the lateral field, making it difficult to determine whether the infraorbital sensory line passes through the lateral field; however, the infraorbital sensory line of UALVP 43640 is complete and does not pass through the lateral field, passing more medially on the headshield instead. Another sensory line, the postorbital sensory line (Janvier, 1974), extends laterally then posteriorly from the posterior end of the orbit. A sensory line of unknown identity is visible lateral to the orbit and the infraorbital sensory line on both the holotype and UALVP 43640. On UALVP 43640, a sensory line extends laterally from immediately anterior to the external openings of the endolymphatic ducts; the distal portion of this sensory line is also preserved on the holotype. This last sensory line is most likely the transverse zonal sensory line, only the proximal portion of which is preserved on UALVP 43640, but the lateral portion of which may be present on NMC 21554, the holotype.

Denticles around the median field, lateral rim of the orbit, nasohypophyseal opening, along the dorsal margin of the headshield, and on the cornua are similar to those ornamenting the posterior part of the headshield but are smaller and more numerous. The ornament of the antorbital horns grades dorsally from the denticles of the headshield into more robust and irregularly-shaped tubercles. Squamation of the proximal region of the median dorsal ridge is preserved on UALVP 43640. The denticles of the median dorsal ridge are larger than those of the posterior dermoskeleton and all point posteriorly. The denticles are also much closer together, with some denticles fused together.

The ventral dermoskeleton of the headshield is preserved in visceral view on the right side of UALVP 43640 (Fig. 6.5C), lateral to the preserved regions of the dorsal dermoskeleton. Large pores in the ventral dermoskeleton are inferred to represent the pulp cavities of individual denticles. The denticles of the ventral dermoskeleton are more closely spaced than those of adjacent regions of the dorsal dermoskeleton. Radiating canals are visible between denticles. There does not appear to be a distinct pattern in the distribution of the denticles, but at the lateral edge of the ventral dermoskeleton there is a change in morphology of the visceral layers to canals running medially to laterally. This change in morphology may mark the extent and position of the lateral field (Fig. 6.5C). The ventral dermoskeleton is continuous where it is preserved on UALVP 43640.

The median dorsal ridge of the holotype is only preserved at the anterior tip where it contacts the posterior margin of the median field. The crest is more complete in UALVP 43640, in which its base is preserved along most of its length. The posterior end of the crest is not preserved, but the crest extends as far posterior as what is preserved of the posterior margin of the headshield. The crest is at least half again as long as the median field is continuous with the headshield, and extends dorsally at least 3 mm above the rest of the headshield.

Orbits, Pineal Region, and Nasohypophyseal Region—The orbit of the holotype faces laterally more than dorsally. The orbit is nearly circular in lateral view, but elliptical in dorsal view. The lateral margin of the orbit is a thick, raised rim (Figs. 6.4A, 6.6D). A tall, dorsally projecting antorbital horn is present anterior to the orbit. The antorbital horn is small relative to the size of the headshield. A median notch is present where the orbit contacts the pineal furrow, which is narrow, being overlapped laterally by the posterior edge of the medial margin of the orbit. The furrow widens medially where it becomes the anterior margin of the median field. The median part of the pineal furrow is obscured by matrix, covering the pineal opening (Fig. 6.6D). A great deal of the pineal furrow and the anterior margin of the median field are exposed and no pineal plate is visible. The median notch of the orbits is also barren of any lateral extensions of the pineal plate. Based on the lack of a pineal plate at the median notch of the orbit and at the anterior end of the median field it is concluded that the pineal plate is not present in *Dentapelta*.

The nasohypophyseal opening is constricted between the nasal and the hypophyseal divisions. The nasal division is anteroposteriorly elongate. A foramen faces posteriorly from the anterior end of the nasal division. The nasal division posterior to the foramen consists of a layer of bone that shallows towards the posterior, tapering end of the nasal division. The nasal division is present on a raised mound one-quarter the distance from the pineal furrow to the anterior tip of the hypophyseal division. The hypophyseal division is incompletely preserved in both the holotype and UALVP 43640 but the shape and size can be determined from what has been preserved. The hypophyseal division is larger than the nasal division. A sulcus is visible in the rough visceral layer of bone within the hypophyseal division. The sulcus is rounded anteriorly and pointed posteriorly. A foramen is present at the anterior end of the sulcus. Posterior to this foramen, the sulcus shallows posteriorly. The hypophyseal division is bordered by a raised rim of dermoskeleton. The shape of the hypophyseal division of the holotype is uncertain but it does taper posteriorly. The hypophyseal division of UALVP 43640 is rhomboid, based on the right side, as the left side of the headshield is not preserved.

Median Field—The median field is long and narrow (Fig. 6.4A, C), with a length-to-width ratio between 2.7:1 and 3:1. The lateral margins are raised ridges parallel to each other along the posterior half of the median field, but constrict anteriorly, giving a bottle-neck shape to the median field. The anterior margin of the median field is flat where it contacts the pineal furrow. The posterior margin of the headshield of the holotype is bilobate where the anterior tip of the median dorsal ridge extends onto the median field. The posterior margin in UALVP 43640 is shallowly rounded; however, this region is not preserved in three dimensions on UALVP 43640 as it is on NMC 21554 (the holotype). The external openings of the endolymphatic ducts are only visible on UALVP 43640, where the lateral margin of the median field turns to form the posterior margin, 17 mm posterior to the pineal furrow. No covering for the median field has been preserved for either specimen.

Cornua—The cornual process points posteriorly for its known length and is narrow and long (Figs. 6.4A, 6.5D). The medial margin of the process is continuous and ornamented with sparse denticles that are smaller and more numerous anteriorly. No barbs are present along the medial margin (Fig. 6.5D), but visceral layers of dermoskeleton are exposed along it. These visceral layers of bone show clear linear grooves running anteroposteriorly that are closer together laterally. The lateral margin of the cornual process is ornamented with two rows of denticles: a dorsal and a ventral row. The dorsal row consists of posteriorly pointed denticles similar to those of the posterior dermoskeleton of the headshield, but more narrow and with a groove on the distal surface that runs the length of the denticle. The denticles at the base of the cornual process are the same as those at the posterior end of the cornual process, but the denticles in between are shorter and more rounded. The denticles of the ventral row also point posteriorly but are more robust than those of the dorsal row and lack a groove on the distal surface.

The denticles increase in length posteriorly along the ventral row.

Lateral Fields—The lateral field anterior to the orbits is not preserved. The field extends posteriorly onto the cornua (Fig. 6.5D) and is narrow and its margins are equidistant along its known length. The median margin is uneven, and for some sections minutely scalloped. The lateral margin is 4.5 mm from the margin of the headshield and is also uneven. The posterior margin tapers where the lateral field extends onto the cornual process.

Pectoral Fin—The pectoral sinus is as far anterior on the headshield as the posterior margin of the median field (Fig. 6.4A). The sinus is broken along its posterior margin but is clearly deep and narrow.

Remarks

As mentioned above, NMC 21554, the holotype, was previously referred to Cephalaspidinae indet. by Dineley and Loeffler (1976). This new taxon is distinct from the most recent diagnosis of *Cephalaspis* (Janvier and Newman, 2005) and the Cephalaspidinae. Janvier (1985) defined the Cephalaspidinae (his "cephalaspidiens") by cornua that are broad and flat, and by lateral fields that extend far onto the cornua, nearly touching the tip. However NMC 21554 has narrow cornua and although each lateral field extends onto the cornual process, it does not extend near the tip. Because NMC 21554 does not meet the criteria of Janvier (1985) it is removed from the Cephalaspidinae and a new genus and species are erected to recognize NMC 21554 and and the two other specimens as a unique taxon.

Differences between specimens of *Dentapelta* are due to the differences in compression of the headshield. The headshield of NMC 21554 (Fig. 6.4A) is preserved with full depth of the orbit, median field and nasohyphophyseal opening. The headshield of UALVP 43640 (Fig. 6.4C) has been flattened across its entire dorsal surface. This has led to differences in the shape of the median field and the orbit. Because the nasohypophyseal opening is relatively horizontal, its shape does not vary between the two specimens. The holotype has been prepared such that there is no matrix within the nasohypophyseal opening. This has revealed separate openings inside of the nasal division and the hypophyseal division of the nasohypophyseal opening. For comparison with the nasohypophyseal openings of other osteostracans, the boundaries of the nasal and hypophyseal divisions should be defined by the extent of the superficial layer of the dermoskeleton. Under this interpretation, the nasohypophyseal opening is constricted between the nasal and hypophyseal divisions, and the hypophyseal division is expanded relative to the nasal division. A fracture lateral to the median field, also present in specimens of *G. cristata*, is the result of vertical compression of the headshield of both specimens of *D. loefflerae*.

Posterior to the median field, a dorsal crest is present on many osteostracans; in a few taxa (‘*Cephalaspis’ novascotiae*, *Pattenaspis*, *Zenaspis*, *Diademaspis*, *Scolenaspis*, *Ukrainaspis*, *Machairaspis*, and *Superciliaspis*) this crest rises distinctly above the headshield and, where preserved in lateral view or in three dimensions, rises posteriorly (Janvier, 1985; Voichyshyn, 2006; Sansom, 2009). The median dorsal crest of *Dentapelta* is likely of the same condition as that of the previously mentioned taxa given that, compared to *W. nahanniensis* and *W. platycornis* (Chapter 4) and *Glabrapelta*, the minimum height of the crest over the headshield is higher and distinguishes itself from the rest of the posterior headshield by roughly 3 mm.

DISCUSSION

Placement of the Superciliaspididae

The family Superciliaspididae is retained within the order Zenaspidida based on the expansion of a raised rim around the orbits, and a laterally widened pineal foramen in *Superciliaspis* and *Glabrapelta*; the condition of the pineal opening is not known for *Dentapelta*. The Superciliaspididae are distinguished from other Zenaspidida by having orbits closer together relative to orbit width: interorbital distance divided by the orbit width is 2.5–3.3 in *Zenaspis* and about 4 in *Diademaspis* (Voichyshyn, 2006), and 1.2–1.5 in *G. cristata*, 0.7 in *G. minima*, and 0.7–1.2 in *Dentapelta*, 1.3 in *Superciliaspis* specimen UALVP 34170. other characters include a reduction or absence of the pineal plate, thickened ridges of large or fused plates bordering the median field, and a long and narrow median field. Maximum width of the headshield divided by the width of the median field is 19 in *Dentapelta*, 14 in *G. cristata*, and 14 in *Superciliaspis* based on specimen UALVP 34170, compared to 9–11 for *Zenaspis*, and about 7 for *Diademaspis* (Voichyshyn, 2006). The Superciliaspididae share with the Zenaspididae an expanded hypophyseal division of the nasohypophyseal opening relative to the nasal division (Sansom, 2009; Janvier, 1985), the homology of which is discussed below. All taxa within the Superciliaspididae have posteriorly pointing cornual processes and pectoral sinuses that are narrow and far lateral on the headshield. The hypophyseal division of the nasohypophyseal opening is also rhombic.

Internal Relationships of Superciliaspididae

Dentapelta is sister to *Supercilaspis* based on the absence of a pineal plate and by an infraorbital sensory line that passes just medial to the lateral field. Although a median dorsal crest is present in all three taxa, it is much more prominent in *Dentapelta* and *Supercilaspis*, even to the point of a full dorsal spine in *Superciliaspis* (Dineley and Loeffler, 1976). All of the genera in the Superciliaspididae are differentiated from one another by ornament, as well as by whether the superficial layer is continuous (*Glabrapelta*) or absent (*Superciliaspis*: Dineley and Loeffler, 1976). The only characteristic that *Glabrapelta* shares with *Superciliaspis* to the exclusion of *Dentapelta* is the external circumareal canals dividing the tesserae of the headshield. Like *Glabrapelta* and *Superciliaspis*, the dermoskeleton of the headshield of *Dentapelta* is divided into tesserae, but in *Dentapelta* a thin layer of bone overlies the circumareal canals. The condition of the superficial layer of *Dentapelta* is less certain as there is a continuous layer across the headshield (Fig. 6.5A, B), but it is unclear as to whether this superficial layer is composed of dentine, or is an exposure of the middle layer. The pectoral sinus of *Dentapelta* (Fig. 6.4A) is positioned much farther anteriorly than that of either *Superciliaspis* or *Glabrapelta* (Figs. 6.1A, 6.3A), and is aligned with the posterior end of the median field. In sum, *Superciliaspis* and *Dentapelta* share characters with one another that are not seen in *Glabrapelta*.

Comparison of the Ornament of *Dentapelta* With That of Other Osteostracans

The ornament of *Dentapelta* is unique among previously described osteostracans, with only *Balticaspis*, and isolated tesserae from the Middle Devonian showing similar ornament (Otto and Laurin, 2001; Otto and Laurin, 1999, respectively). It is a continuous dermoskeleton covered in recumbent denticles (Figs. 6.4, 6.5A, B). Each denticle is hollow in the center and circular at the base. The top of each denticle is smooth and flat and points posteriorly. Similar ornamentation is known from isolated Middle Devonian osteostracan tesserae from Tori Põrgu, Estonia (Otto and Laurin, 1999: fig. 2A–C) that share the posterior point and smooth flat top of the denticle, but the denticles described by Otto and Laurin (1999) are much larger and the dermoskeleton is separated into tesserae.

Otto and Laurin (1999) compared these isolated tesserae to *Balticaspis*, a partial, articulate osteostracan headshield from the Middle Devonian (Otto and Laurin, 2001), but later determined that the tubercles of *Balticaspis* could be differentiated by the presence of an internal cavity and a radial canal system (Otto and Laurin, 2001). The denticles of *Dentapelta* resemble the tubercles of *Balticaspis* in that they also possess an internal cavity and radiating canals. The differences between the ornament of *Balticaspis* and of *Dentapelta* are primarily in external differences in the shape of the denticles/tubercles. The tubercles of *Balticaspis* are smaller, and distally rounded compared to those of *Dentapelta*.

As *Balticaspis* is only preserved in ventral view, the only clear macroscopic character differentiating it from *Dentapelta* is the presence of a medial plate along the cornual process, a feature not observed in the holotype of *Dentapelta*. The ventral dermoskeleton is not known for *Dentapelta*, and therefore the external morphology of the ventral denticles cannot be reliably compared with that of *Balticaspis*; instead the ornament can more easily be distinguished from *Balticaspis* based on the visceral features of the ventral dermoskeleton, preserved in UALVP 43640, a paratype of *Dentapelta*. In *Balticaspis* a basal layer of bone covers the base of the tubercle in visceral view. The hollow cavity in the base of denticles of *Dentapelta* extends through the middle layer and is exposed in visceral view across what is preserved of the ventral dermoskeleton, clearly differing from the condition seen in *Balticaspis*.

Affinities of the Internal Anatomy of *Glabrapelta minima*

The internal anatomy of osteostracans is best preserved in Boreaspididae and the Kaieraspididae (Stensiö, 1927; Janvier, 1985). The reconstruction of *Scolenaspis* by Janvier (1985) did not include the facial and trigeminal nerves and so reconstruction of the nerve canals of *G. minima* (Fig. 6.3D) was based primarily on reconstructions of the internal anatomy of *Benneviaspis*, *Boreaspis*, *Belonaspis*, and *Kaieraspis* by Janvier (1985). The 'sel' 1 canal of *G. minima* is not visible anterior to the orbit and so the location of its bifurcation, an important character in defining orders (Janvier, 1985; Sansom, 2009), cannot be clearly compared with that of other osteostracan taxa. The model for the nerves and 'sel' canals of *G. minima* shows little deviation from the internal anatomy of *Benneviaspis* (Janvier. 1985: fig. 75, p. 157). The alternative model offered in the remarks section for *G. minima* would require the facial nerve to be lateral to 'sel' 1; in all other osteostracan taxa for which the internal anatomy is known this does not occur until farther anterior to the labyrinth cavity and lateral to the orbit (Stensiö, 1927; Janvier, 1985). The internal anatomy of *G. minima* does not differ from the conditions seen in other osteostracan taxa for which the nerves and 'sel' canals are known and suggests widespread conservation of spatial relationships of the facial and trigeminal nerves and the 'sel' canals in the Osteostraci, at least among cornuate taxa.

The Hypophyseal Division

Where the inside of the hypophyseal division of the nasohypophyseal opening is exposed in specimens of *Dentapelta* (NMC 21554), *G. minima* (UALVP 43083), and *Superciliaspis* (UALVP 32485), an opening more visceral than the superficial layer surrounding the hypophyseal division is present within a slit-shaped groove. This opening within the hypophyseal opening has not been reported for any other osteostracan taxa; however, the internal anatomy of the nasohypophyseal opening is rarely well preserved in osteostracans from localities other than MOTH, with matrix often infilling the opening. This opening is therefore a shared character within the Superciliaspididae, but without information on the presence or absence of this character for taxa outside the Superciliaspididae, the phylogenetic utility of this character is limited.

The hypophyseal division of the Superciliaspididae is expanded relative to the nasal division. This feature is shared with the Zenaspididae; however, the openings within the hypophyseal divisions of the Superciliaspididae are not known for the Zenaspididae, and the hypophyseal divisions of the Superciliaspididae differ in shape from the Zenaspididae, rhomboid compared to circular respectively. These features may indicate that the expansion of the hypophyseal division is homoplasic between the two families.

SUMMARY

A new family is recognized, for *Superciliaspis*, and two new genera comprising three new species: *Dentapelta loefflerae*, *Glabrapelta cristata*, and *G. minima*. This new family is referred to as the Superciliaspididae, and is, at present, endemic to MOTH. A long and narrow median field, narrow, posterior pointing cornua, a median field bordered by raised ridges of fused plates, and orbits close together characterize the Supercilaspididae. A laterally expanded pineal opening and raised orbital rims place the Superciliaspididae in the Order Zenaspidida.

LITERATURE CITED

Adrain, J. M., and M. V. H. Wilson. 1994. Early Devonian cephalaspids (Vertebrata: Osteostraci: Cornuata) from the southern Mackenzie Mountains, N.W.T., Canada. Journal of Vertebrate Paleontology 14:301–319.

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

Gabrielse, H., S. L. Blusson, and J. A. Roddick. 1973. Geology of Flat River, Glacier Lake and Wrigley Lake map areas, District of Mackenzie, Northwest Territories. Geological Survey of Canada, Memoir 366:1–268.

Janvier, P. 1974. The sensory line system and its innervation in Osteostraci (Agnatha, Cephalaspidomorphi). Zoologica Scripta 3: 91–99.

Janvier, P. 1981. *Norselaspis glacialis* n.g., n.sp. et les rélations phylogénétiques entre les Kiaeraspidiens (Osteostraci) du Dévonien inférieur du Spitsberg. Palaeovertebrata 11: 19–131.

Janvier, P. 1985. Les Cephalaspides du Spitsberg. Cahiers de Paléontologie, Section Vertébrés. Éditions du Centre National de la Recherche Scientifique, Paris: 244 pp.

Janvier, P., and M. J. Newman. 2005. On *Cephalaspis magnifica* Traquair, 1893, from the Middle Devonian of Scotland, and the relationships of the last osteostracans.

Lankester, E. R. 1868. A Monograph of the Fishes of the Old Red Sandstone of Britain. Part I. The Cephalaspidae. Monograph of the Palaeontographical Society, London, 62 pp.

Otto, M., and M. Laurin. 1999. Osteostracan tesserae from the Baltic Middle Devonian: morphology and microanatomy. Neues Jahrbuch für Geologie und Paläontologie. Monatshefte 1999: 464–476.

Otto. M., and M. Laurin. 2001. Microanatomy of the dermal skeleton of *Balticaspis latvica* (Osteostraci, Middle Devonian). Journal of Vertebrate Paleontology 21: 186–189.

Sahney, S. and Wilson, M. V. H. 2001. Extrinsic labyrinth infillings imply open endolympatic ducts in Lower Devonian osteostracans, acanthodians and putative chondricthyans. Journal of Vertebrate Paleontology 21:660-669.

Sansom, R. S. 2009. Phylogeny, classification and character polarity of the Osteostraci (Vertebrata). Journal of Systematic Palaeontology 7:95–115.

Stensiö, E. A. 1927. The Devonian and Downtonian vertebrates of Spitzbergen. 1. Family Cephalaspidae. Skrifter om Svalbard or Nordishavet 12:1–391.

Stensiö, E. A. 1958. Les Cyclostomes fossiles ou Ostracodermes. Pp. 173–425 in P. P. Grass´e (ed.), Traité de Zoologie. Masson, Paris.

Voichyshyn, V. 2006. New osteostracans from the Lower Devonian terrigenous deposits of Podolia, Ukraine. Acta Palaeontologica Polonica 51: 131–142.

Wängsjø, G. 1952. The Downtonian and Devonian vertebrates of Spitsbergen. IX. Morphologic and systematic studies of the Spitsbergen cephalaspids.

Results of Th. Vogt’s Expedition 1928 and the English-Norwegian-Swedish Expedition in 1939. Norsk Polarinstitutt Skrifter 97:1–611.

Wilson, M. V. H., and M. W. Caldwell. 1998. The Furcacaudiformes: a new Order of jawless vertebrates with thelodont scales, based on articulated Silurian and Devonian fossils from northern Canada. Journal of Vertebrate Paleontology 18: 10–29.

FIGURE 6.1. Specimens of *Glabrapelta cristata*, gen. et sp. nov. **A**, the holotype, UALVP 43639, in dorsal view, this is the most complete specimen of *G. cristata*. **B**, UALVP 42731, a paratype of *G. cristata*, anterior half of the headshield and most of the right side of the median field, in dorsal view. **C**, UALVP 43214, another paratype of G. cristata, anterior half of a headshield in dorsal view, it has greater depth than either UALVP 43639, the holotype, or UALVP 43214. Each scale bar is equal to 10 mm.

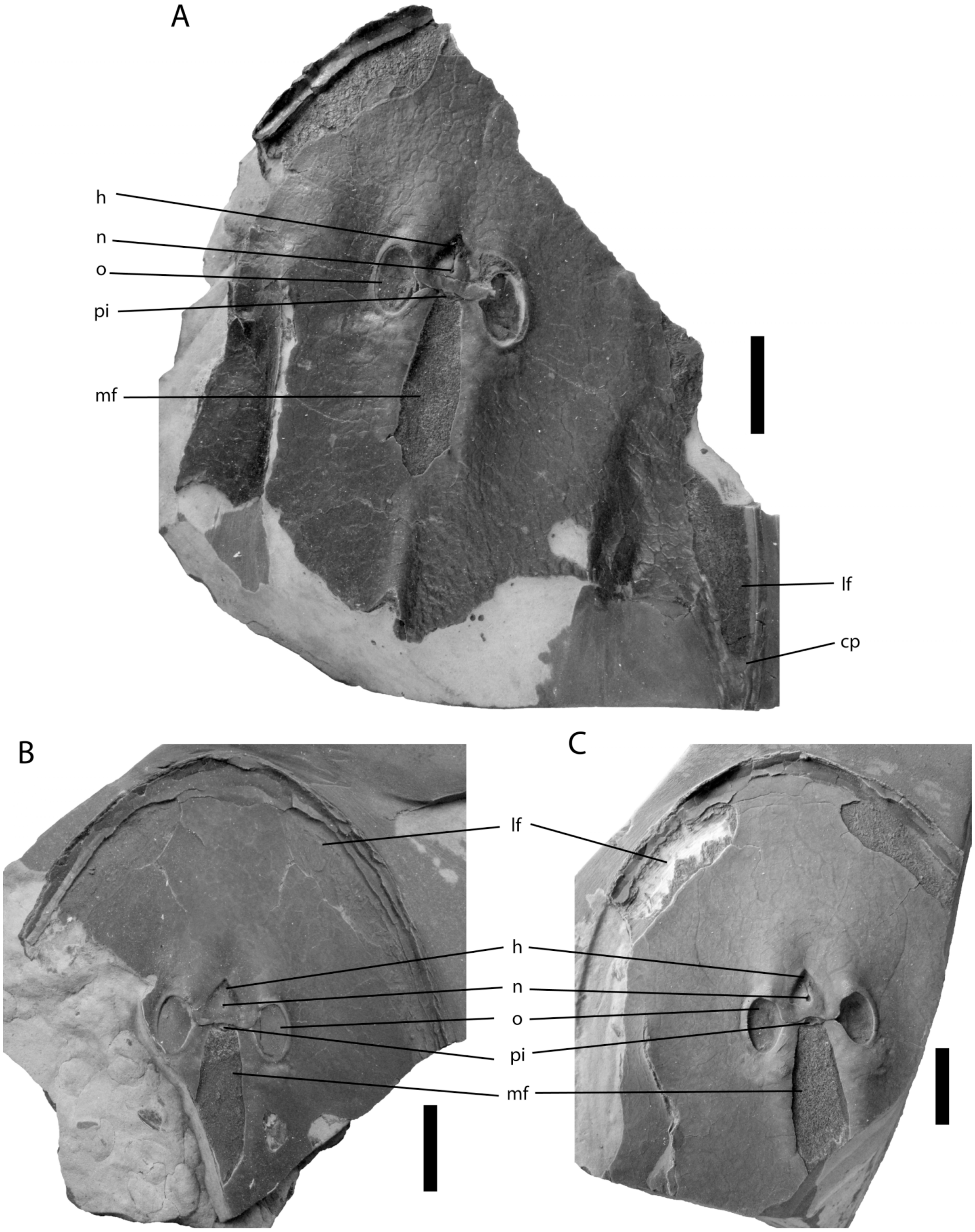
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FIGURE 6.2. Closeup of the anterior end of the lateral field of UALVP 43639, the holotype for *G. cristata*, sp. nov. The anterior expansion of the lateral field and the crest or ridge bordering the medial margin of the lateral field, two diagnostic characters of *G. cristata*, sp. nov., are labeled.

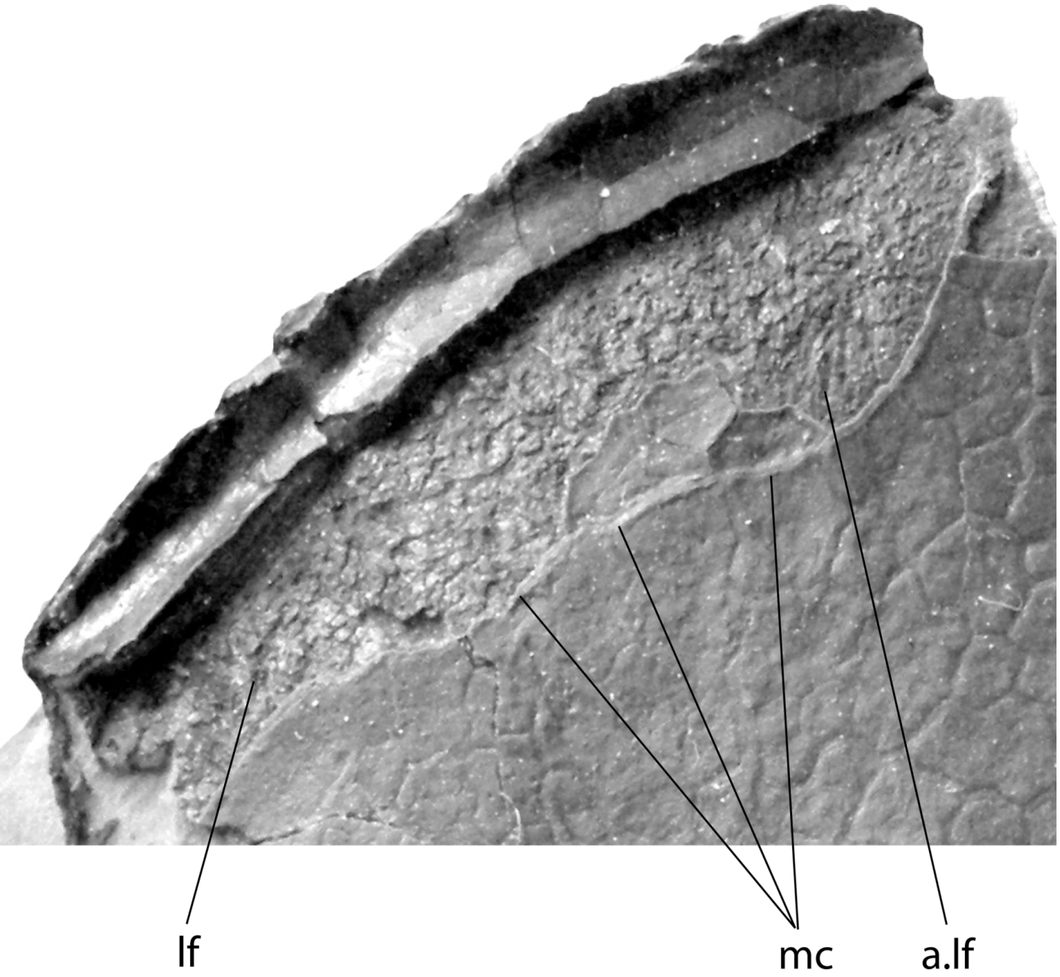
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FIGURE 6.3. The holotype of *Glabrapelta minima* gen. et sp. nov., UALVP 43083. **A**, whole specimen of holotype in dorsal view, consisting of the left anterior half of a headshield. **B**, a detailed image of the pectoral sinus of the holotype, note the tubercles lining the anterior margin. **C**, a detail image of the orbit of the holotype, with the nerves and ‘sel’ canals embossed on the sclerotic capsule of the orbit, diagrammed in **D**, ridge transverse to other canals denoted by arrow. The scale bar is equal to 10 mm.

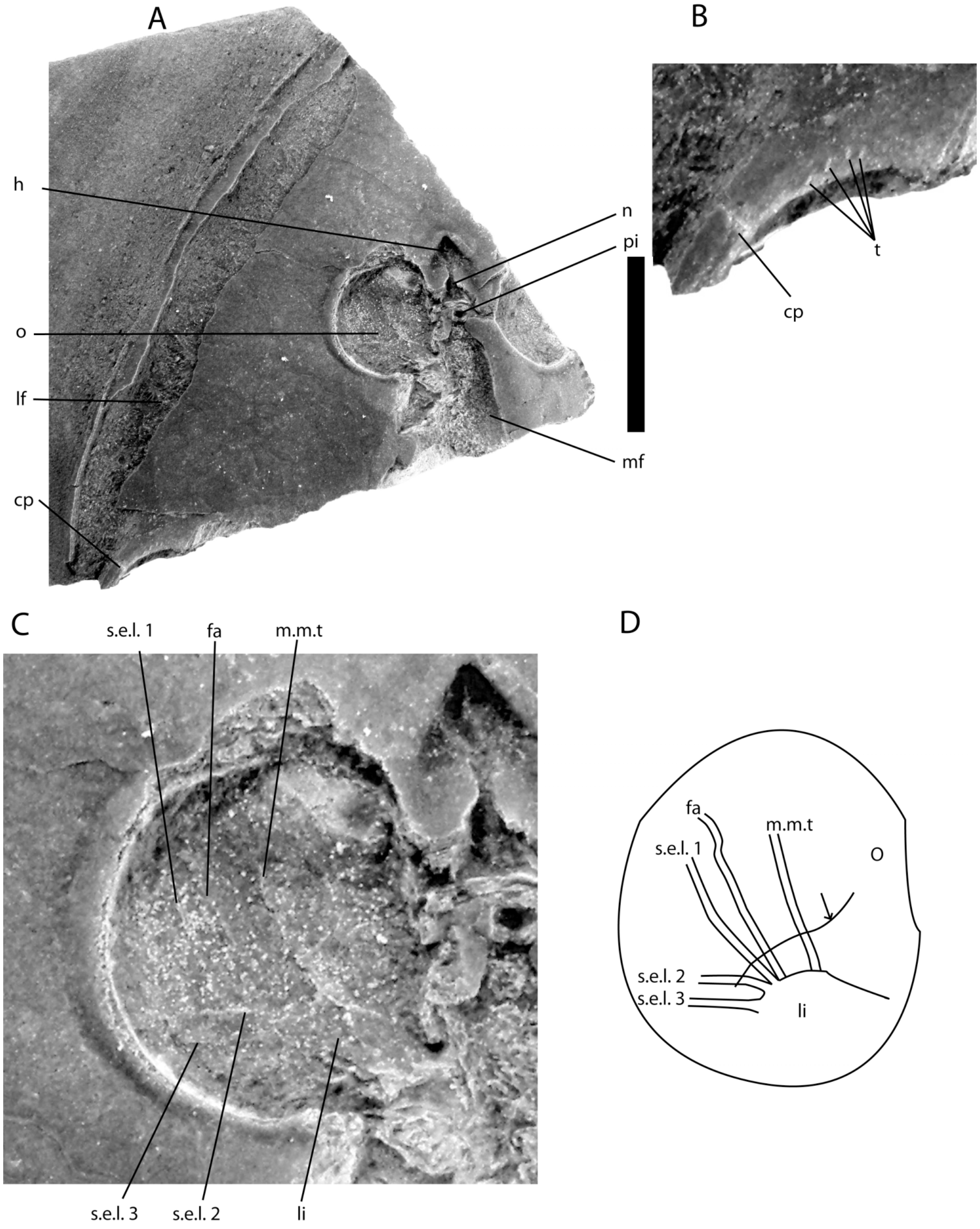
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FIGURE 6.4. Specimens of *Dentapelta loefflerae*, gen. et sp. nov. **A**, the holotype of *D. loefflerae*, gen. et sp. nov., NMC 21554, the right side of a headshield in dorsal view, a thelodont overlying the specimen highlighted in black, the specimen was not coated in ammonium chloride for this photograph. **B**, a paratype of *D. loefflerae*, gen. et sp. nov., UALVP 32408, a fragment of the headshield in dorsal view; the superficial layer is absent over much of the specimen. **C**, UALVP 43640, a paratype of *D. loefflerae*, gen. et sp. nov., the right side of a headshield in dorsal view; the ventral headshield is present in visceral view lateral to the dorsal dermoskeleton. Each scale bar is equal to 10 mm.

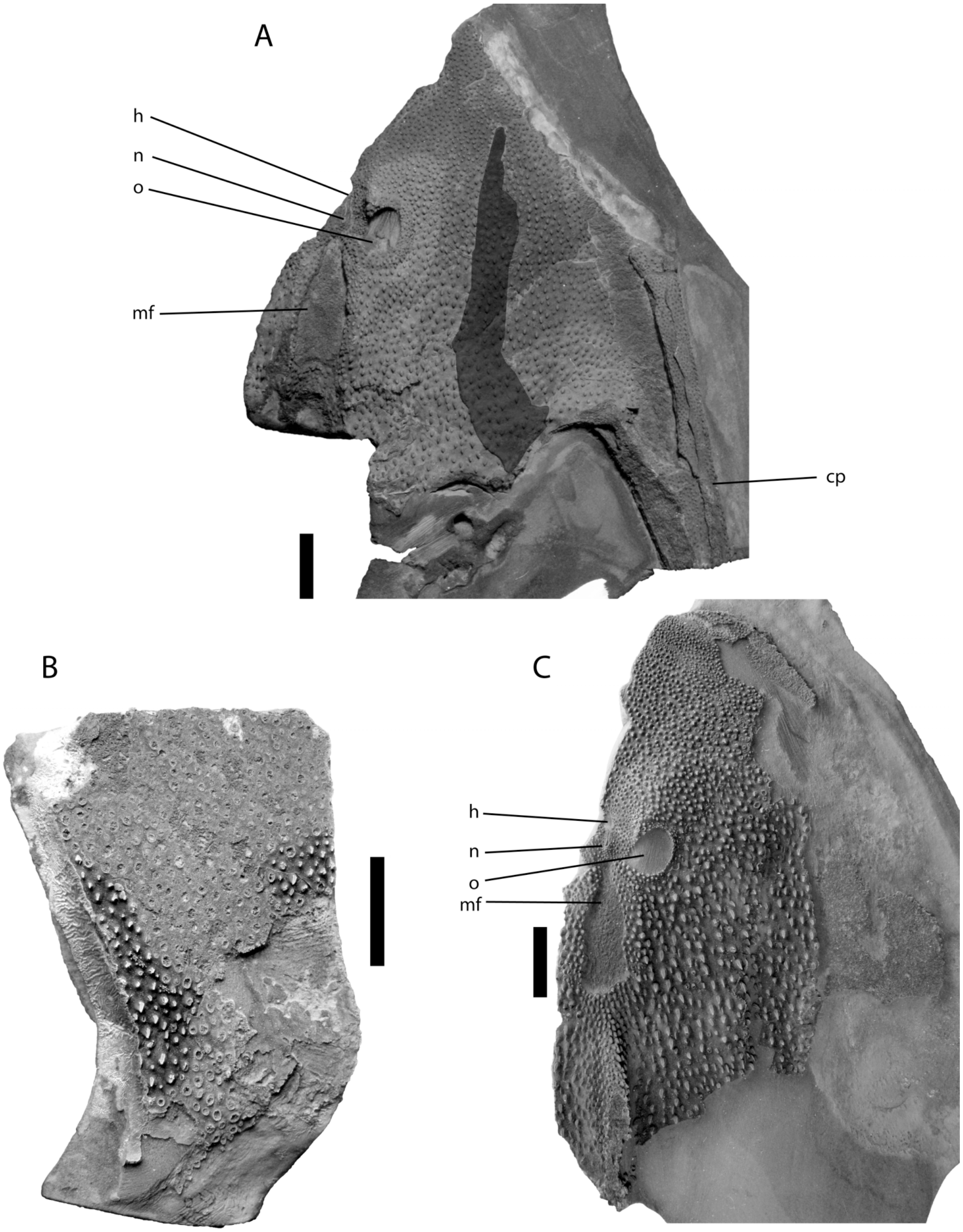
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FIGURE 6.5. Detailed images of specimens of *D. loefflerae*, gen. et sp. nov. **A**, dorsal dermoskeleton from UALVP 43640, a paratype of D. loefflerae gen. et sp. nov., from posterior and lateral to the right orbit. **B**, dorsal dermoskeleton, also from UALVP 43640, from the anterior end of the headshield. **C**, UALVP 43640 ventral dermoskeleton from lateral to the preserved extent of the dorsal dermoskeleton, in visceral view. **D**, the base of the cornual process from the holotype, NMC 21554, the base is continuous, with no plates, and lacks barbs, specimen was not coated in ammonium chloride when photograph was taken.

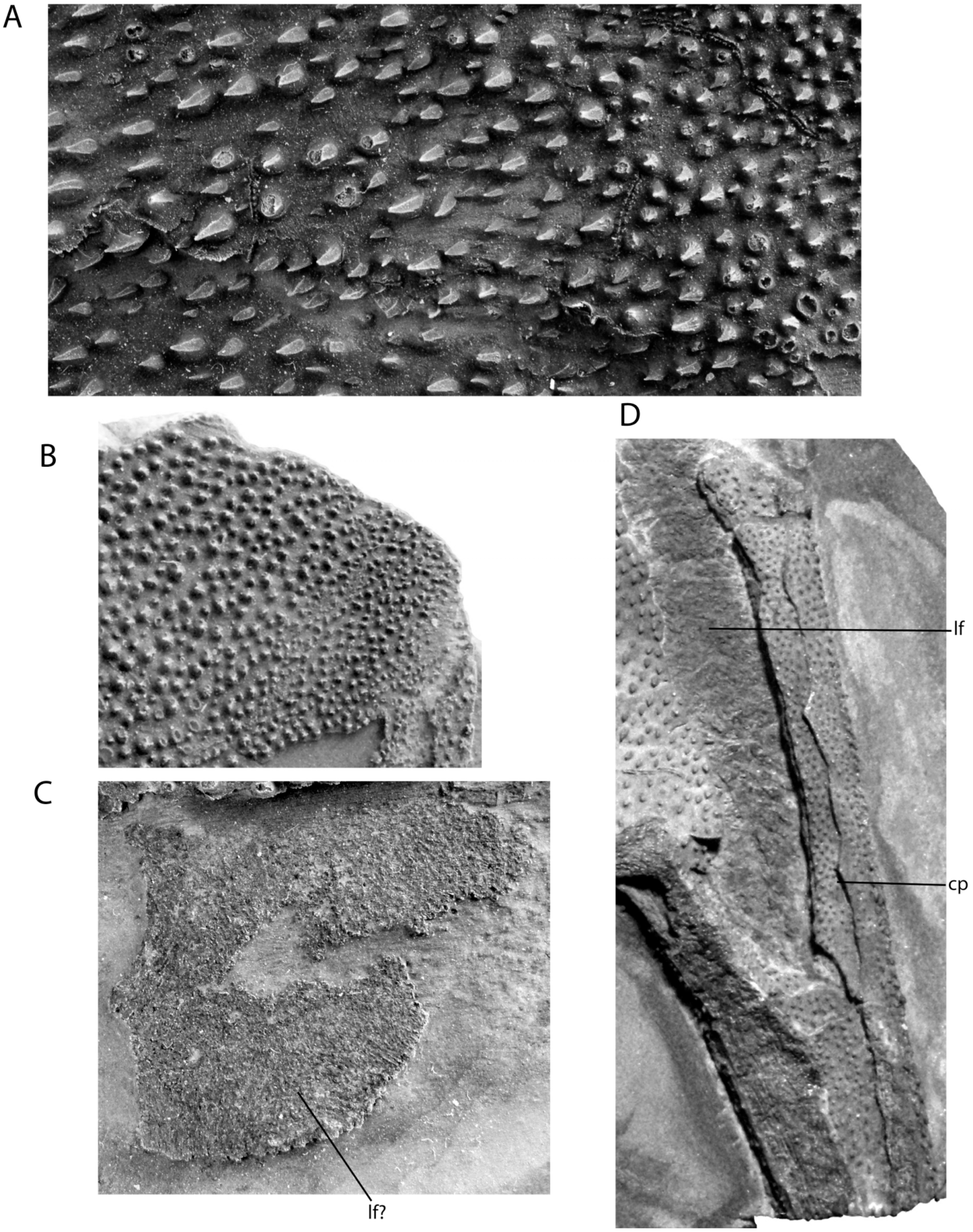
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FIGURE 6.6. Detailed images of the orbits, nasohypophyseal and pineal region of the headshield of: **A**, UALVP 43083, the holotype of *Glabrapelta minima*, gen. et sp. nov. **B**, UALVP 43639, the holotype of *Glabrapelta cristata*, gen. et sp. nov. **C**, UALVP 32485, a specimen referrable to *Supercilaspis gabrielsei*. **D**, UALVP 43640, a paratype of *Dentapelta loefflerae*, gen. et sp. nov.

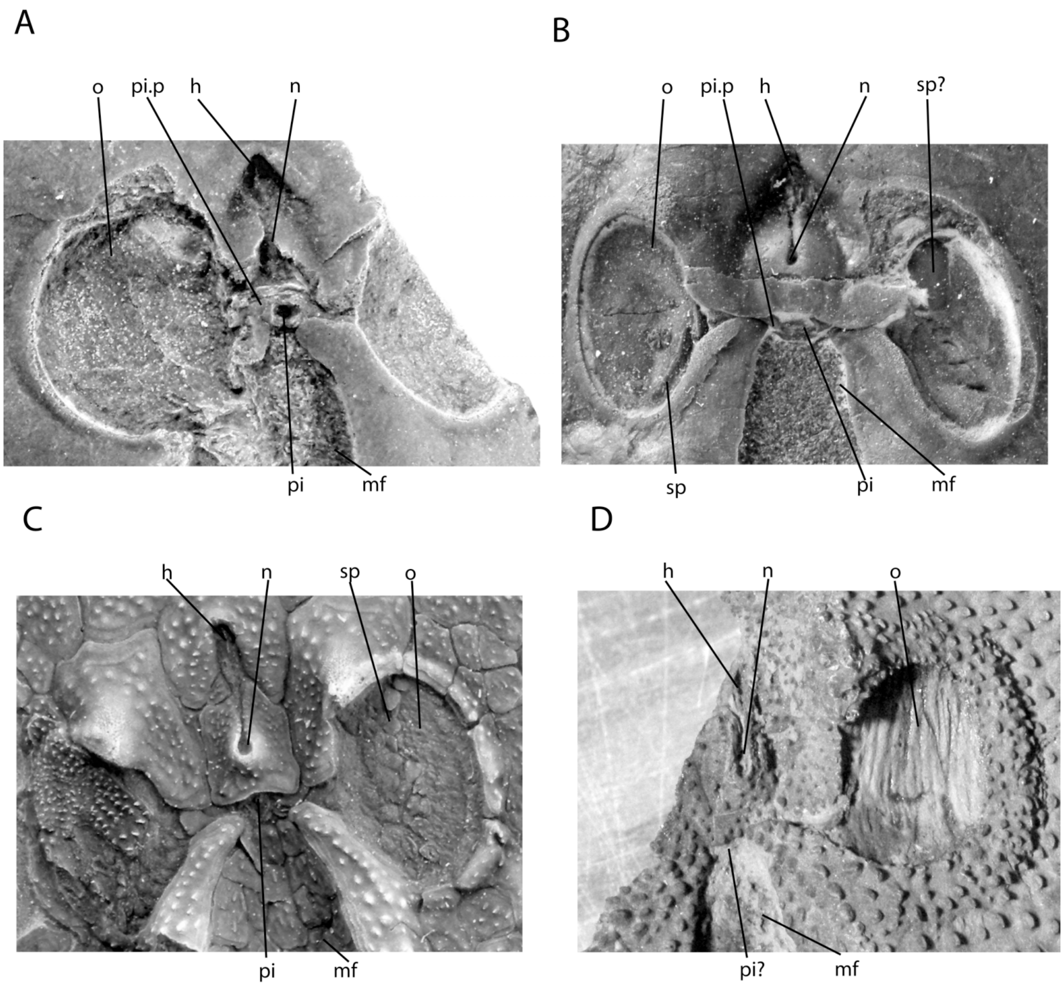
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TABLE 6.1. Table of measurements of specimens of *Glabrapelta* and *Dentapelta*.

Taxon	T.L.	M.W.	Pr.L.	Po.L.	I.O.D.	O.W.
G. cristata						
Holotype: UALVP 43639	—	78*	29+	34+	6.4	4.4^R/4.3^L
UALVP 41731	—	—	32	—	6.2	4.4^{RL}
UALVP 43214	—	—	35	—	6.2	5.2^R/5.1^L
G. minima						
Holotype: UALVP 43083	—	45.6*	16.2+	—	3.7	5.5^L
D. loefflerae						
Holotype: NMC 21554	79+	136	—	—	6+	5^R
UALVP 43640	—	97*+	15.5+	50.4	4.8	7^R

^{L}, Left; ^{R}, Right; ^{A}, Anterior expansion *, measurement of width taken from midline and doubled; —, measurement not available; +, actual distance is greater than the measurement given. Abbreviations: **T.L.**, Total Headshield Length; **M.W.**, Maximum Headshield Width; **Pr.L.**, Prepineal Length; **Po.L.**, Postpineal Length; **I.O.D.**, interorbital distance. **O.W.**, maximum transverse orbit width. All measurements are in mm.

TABLE 6.2. Table of additional measurements for specimens of *Glabrapelta* and *Dentapelta*.

Taxon	H.P.D.	M.F.L.	M.F.W.	L.F.L.	L.F.W	C.W.
G. cristata						
Holotype: UALVP 43639	6.2	18	6	—	4.7/5.8^{A}	9
UALVP 41731	5.2	18+	5.7+	—	4.8/5.8^{A}	—
UALVP 43214	6.2	19.5+	7.5	—	4/5^{A}	—
G. minima						
Holotype: UALVP 43083	4.4	—	5.0	32.7	3.0	—
D. loefflerae						
Holotype: NMC 21554	—	19	7.1	—	6.4	19
UALVP 43640	6.6	19.4	6.4	—	—	—

^{L}, Left; ^{R}, Right; ^{A}, Anterior expansion *, measurement of width taken from midline and doubled; —, measurement not available; +, actual distance is greater than the measurement given. **H.P.D.**, Hypophyseal to Pineal Distance; **M.F.L.**, Median Field Length; **M.F.W.**, Median Field Width; **C.L.**, Cornual process Length; **C.W.**, Cornual process. Width. All measurements are in mm.

CHAPTER 7:

TWO NEW MONOTYPIC GENERA OF OSTEOSTRACANS FROM THE EARLY DEVONIAN (LOCHKOVIAN) MOTH LOCALITY, NORTHWEST TERRITORIES, CANADA

INTRODUCTION

There are numerous species of osteostracan from the Man On The Hill (MOTH) locality, Mackenzie Mountains, Northwest Territories, Canada. MOTH contains a great diversity of early vertebrates of Early Devonian (Lochkovian) age (Dineley and Loeffler, 1976; Adrain and Wilson, 1994). Among the Osteostraci of MOTH are new taxa that display unique morphologies but for which specimens are incomplete, or whose combination of characters is inconsistent with known classifications of the families or orders of the Osteostraci.

Previous chapters of this study have focused on particular clades or species that can be referred to previously established genera or placed with some confidence in the current osteostracan phylogeny (Sansom, 2009). The descriptions of the new taxa provided here include those taxa that cannot be included in an order or family, but which represent morphologies and characteristics that distinguish them from other known osteostracan species. Taxonomy is here provided for two new monotypic genera, *Ceramantyx odontotos*, gen. et sp. nov., and *Ancyraspis enormis*, gen. et sp. nov. Preliminary descriptions are also provided for additional specimens that may represent new species of osteostracan, but are too incomplete for formal taxonomy.

SYSTEMATIC PALEONTOLOGY

Class OSTEOSTRACI Lankester, 1968

Subclass CORNUATA, Janvier, 1981

Order incertae sedis

Family incertae sedis

CERAMANTYX, gen. nov.

Etymology—*Ceram,* derived from *Keramic*, Greek, meaning "plate," and *antyx*, Greek, meaning "edge, or rim" referring to the imbricated plates that compose the margin of the headshield.

Type and Only Known Species—*Ceramantyx odontotos*, sp. nov.

Diagnosis—As for type and only known species.

CERAMANTYX ODONTOTOS, sp. nov.

Fig. 7.1–7.3

Etymology—The specific epiphet is from Greek *odontotos*, meaning "with teeth" in reference to the posterior pointing tubercles of the headshield margin. Gender masculine.

Type and Only Specimen—UALVP 42648, a complete headshield and the anterior part of the trunk in dorsal view.

Diagnosis—Cornuate osteostracan with rim of headshield divided into rectangular, imbricated plates. Anterior margin of headshield is parabolic and maximum width of headshield is reached anterior to orbits and maintained to tips of cornual processes. Trunk ornamented with small, longitudinal tubercles in clusters.

Differs from all other osteostracan taxa by a headshield margin composed of separate, imbricated plates. Shares with *Superciliaspis* prominent, ornamented antorbital horns and thick ornamented plates posterior to the orbits and lateral to the median field. But differs by small, clustered denticles ornamenting the dermoskeleton, and shape of margin of the headshield. Headshield shape similar to Diademaspis, but differs by dermoskeletal ornament, large separate plates posterior to the orbits, plates laterally bordering orbits.

Type Locality—Locality MOTH "Fish Layer" from the beds that transition between the Road River Formation and the Delorme Formation. The locality is from the Lochkovian (Lower Devonian) of the Mackenzie Mountains, Northwest Territories, Canada (Gabrielse et al., 1973).

Description

Headshield—The headshield and trunk are preserved in dorsal view (Fig. 7.1). The headshield is longer than wide including the cornua, although there is very poor separation between the trunk and headshield. An acanthodian overlies the left side of the trunk (Fig. 7.1). The prepineal length of the headshield is estimated to be equal to the post-pineal length of the headshield. The anterior one-third of the headshield is parabolic, while the posterior two-thirds of the headshield are of a nearly constant width with a gradual widening of the headshield towards the base of the cornual processes, though this could be taphonomic.

Clusters of small denticles ornament the dermoskeleton of the headshield. The clustering of the denticles would be consistent with tesselation; however, no external circumareal canals are visible. A continuous dermoskeleton is possible for the headshield, but there is no separation of scales on the trunk either (Fig. 7.2A); therefore, the continuous dermoskeleton is interpreted here as a taphonomic artifact rather than a biological character and a reliable interpretation of the state of the dermoskeleton cannot be provided here. Tesserae are visible around the base of the cornua (Fig. 7.2B) and plates are visible around the margin of the orbit (Fig. 7.2C).

The denticles of the dermoskeleton are extremely small and short and can be pointed posteriorly or pointed straight dorsally. The anterior end of each denticle varies from transverse and flat, to forked. Denticles anterior to the orbits on the dorsal surface of the headshield (visible posterior to the margin of the headshield in Fig. 7.2D) vary greatly in morphology from circular, distal protrusions, to triangles, to tri-radiate dorsal projections, to tall, narrow ridges. These ridges form between denticles that are close together. The ridges can vary in both height and length, incorporating multiple denticles. The denticles positioned farther posterior are triangular in dorsal view. Denticles between the orbits and over the labyrinth infillings are often broken (Fig. 7.2C), as are denticles in various clusters across the headshield. The center of each of these broken denticles is hollow; therefore, the term ‘denticles’ is preferred over ‘tubercles’ in describing these structures (Chapter 3). The dermoskeleton between denticles is rough and pitted and no canals are present. The pits are often grouped between clusters of denticles. Pits within each group are evenly spaced.

A cluster of four tesserae are visible lateral to the rim of the left orbit (Fig. 7.3A), with their visceral surfaces exposed dorsally. The base of each plate has a central pore surrounded by smaller pores. Polygonal tesserae are present anterior to the cornua (Fig. 7.2B). The bases of these tesserae are filled with canals and vacuities in visceral view. The external surface of the plates is smooth, except for numerous evenly spaced pores of uniform size. Tesserae are also visible near the median field and median dorsal crest. Where the tesserae are displaced, a thin basal layer is visible and tall, narrow denticles project directly from the base of the scale. No rims of thickened basal bone are present around the base of the tesserae (e.g., for rims of basal bone in Adrain and Wilson, 1994: fig. 8B, and Chapter 6: fig. 6.6). In visceral view, canals radiate from central pores in the dermoskeleton of tesserae on the headshield, except for those at the base of the cornual process where only numerous small pores are present. Three small polygonal tesserae are present at the anterior end of the headshield. Two of these plates are in visceral view and one is in lateral view. The plate in lateral view has a flat base, no neck, and distally pointing denticles. The three plates are separate from the dermoskeleton of UALVP 42648 and could be allochthonous to the specimen.

The infraorbital sensory line is visible on both sides of the headshield as a series of evenly separated, short, narrow grooves in the dermoskeleton. The infraorbital sensory line extends laterally and anteriorly from the orbits and then medially towards the rostrum. It is anterior to the 'sel' 1 canal on the right side of the headshield. Because the anterior end of the lateral field cannot be discerned from the dermoskeleton, it cannot be determined whether the infraorbital sensory line passes through the lateral field.

A groove in the dorsal dermoskeleton on the right side of the headshield extends nearly straight anterolaterally from the anterolateral edge of the orbit to the margin of the headshield. This groove bifurcates just medial to the headshield margin. The position, direction, and extension to the margin of the headshield are all consistent with the 'sel' 1 canal to the lateral field (Stensiö, 1927; Janvier, 1985a). Posterior to the groove for the 'sel' 1 canal is a second groove running more laterally and whose medial half is not preserved. This is most likely 'sel' 2.

A median dorsal crest is present (Fig. 7.3B). The posterior end of the median dorsal crest is covered by scales from the acanthodian specimen preserved on the block. The crest is convex in transverse section and has anteriorly rounded and posteriorly pointed denticles (Fig. 7.3B). The denticles are larger than the denticles of the dorsal dermoskeleton of the headshield and of the trunk.

Orbits, Pineal Region, and Nasohypophyseal Region—The orbits are oblong, small, and close together (Fig. 7.2C). Antorbital horns are present. The antorbital horns are ornamented with denticles larger than those of the dorsal dermoskeleton and the denticles of the antorbital horns increase in size grading posteriorly (Fig. 7.2C). Ridges connect the denticles that are dorsal- and posteriormost on the antorbital horns. The denticles along the antorbital horn point distally rather than posteriorly, as they do along the headshield. The distal surface of the anterior denticles is ridged on either side of the posterior point. The surface of the posterior denticles is smooth and either flat or with a single crest. Pitting is visible in the dermoskeleton anterior to the denticles of the right antorbital horn. The lateral margin of the orbits is composed of square, gently convex plates covered in small, round, and distally pointing denticles. The medial margin of the orbits is not differentiated into separate plates, but has denticles like those that ornament the lateral margin of the orbits. Labyrinth infillings are preserved posterior to the orbits (Figs. 7.1, 7.2C). The left labyrinth infilling is exposed as a mound of white grains. The right labyrinth infilling is covered by thick, convex plates ornamented with large, posteriorly pointing denticles. Inside the orbit, a layer of bone is present that is similar to the dorsal dermoskeleton, but with no ornament except for a rough texture. There are breaks in the bone layer, but none of these are consistent between both orbits and therefore are probably taphonomic rather than anatomical in origin.

The pineal region, including the pineal plate and the pineal opening, is covered by a plate of bone, possibly osteostracan, that is allochthonous to UALVP 42648 (Fig. 7.2C). An anteriorly rounded opening between the anterior ends of the antorbital horns is likely the nasal division of the nasohypophyseal opening. Only the anterior and right side of the nasal division (Fig. 7.2C) is preserved, the rest is covered by the same plate that covers the pineal region of the headshield. The nasal division tapers posteriorly, based on what is visible on the right side of the nasal division. The hypophyseal division is located at the anterior end of the nasohypophyseal depression. The shape of the hypophyseal division cannot be determined; the bordering dermoskeleton is broken. The depression is triangular and defined by a ridge of denticles taller than the surrounding dermoskeleton. The ridge extends anteromedially from the anterior ends of the antorbital horns. The dermoskeleton within the nasohypophyseal depression is flat, with typical ornamentation for the headshield.

Median Field—The border of the median field can be distinguished by a rim of tall, posteriorly pointing denticles along the anterior margin and distally pointing denticles along the lateral and posterior margins (Fig. 7.1). The median field is long and narrow. The lateral margin of the field is better preserved on the right side of the headshield than the left and is straight and longitudinal to the midline of the headshield. The denticles along either side of the lateral margin are smaller between the labyrinth infilling and the posterior margin of the median field than at the posterior margin of the field or covering the labyrinth infilling. The anterior border of the field is rounded (Fig 7.2C). The posterior margin of the median field is seen to end anterior to the median dorsal crest, but the shape is not preserved. The shape of the posterior margin of the field is more transverse on the left side of the median dorsal crest than the right side. The precise location of the external openings of the endolymphatic ducts is not known, but white grains visible under the dermoskeleton, at the posterior right end of the median field, provide an approximate location for the openings inside the median field. The dermoskeleton covering the median field is ornamented with small, evenly spaced denticles varying slightly in size.

Cornua—The cornua are short and triangular and the tips point posteriorly (Fig. 7.1, 7.3C). The medial surface of the cornual process is continuous and is ornamented with a row of barbs. The barbs are short and curve distally so that they point anteriorly. The lateral margin of the process is continuous from where the margin is transverse to the base of the pectoral fin, to the tip of the cornual process. Rows of denticles run anteroposteriorly along the lateral margin of the process. The denticles of the lateralmost row are larger than those of the more medial rows. All denticles along the lateral margin of the cornual process posteriorly, with lateral ridges running to the posterior tip of each denticle. The dorsal dermoskeleton of the processes is only preserved at the tips of the cornua where it is ornamented with large denticles in alternating rows. The areas of the cornual process where the dorsal dermoskeleton is absent could represent the posterior extent of the lateral field. The ventral dermoskeleton of the process is exposed in visceral view where the dorsal dermoskeleton is absent, and is covered in narrow, longitudinal grooves and ridges, each of which is evenly space from the adjacent grooves and ridges.

Lateral Fields—The lateral fields are long and narrow and the margins are equidistant along its length. A low, narrow groove in the dorsal dermoskeleton that is about 5 mm from the lateral margin of the headshield represents the medial border of the lateral field. This low groove is present on both the left and right sides of the headshield. The lateral fields are visible as far anteriorly as the anterior end of the nasohypophyseal depression, but the anterior end of the lateral fields cannot be differentiated from the dermoskeleton of the headshield. As the 'sel' 1 canal is visible anterolateral to the orbit, the lateral field must extend at least this far. The lateral border of the lateral field cannot be discerned from the dermoskeleton near the lateral margin of the headshield. The only visible difference between the dermoskeleton of the lateral field and the dermoskeleton of the headshield is tesselation of the lateral field at the base of the cornual processes (Fig. 7.2B). The lateral field extends posteriorly onto the cornual process, determined by both an absence of dorsal dermoskeleton on the cornual process and the extension of the medial border of the lateral field to the base of the cornual process.

Margin of the Headshield—The margin of the headshield is composed of numerous articulated plates. The plates are rectangular with a long axis perpendiclular to the length of the margin. The plates of the margin are small and convex and are visible in visceral view on the right side of the headshield and the anterior end of the left side of the headshield, and in external view on the left side of the headshield. Each plate is ornamented with two transverse rows of oakleaf-shaped tubercles (Fig. 7.3D). The anterior end of each plate is overlapped by the posterior row of tubercles of the preceding plate. The imbricated margin plates are not present at the anterior end of the headshield; instead, a pair of the anteriormost marginal plates tapers posteriorly on either side of a small anteriorly tapering medial plate.

Pectoral Fin—The pectoral fin on the left side of the headshield is clearly preserved, but the right pectoral fin is covered by the trunk (Fig. 7.1). The pectoral fin extends the length of the cornual process. The lateral margin of the left fin is covered by the cornual process, but the medial margin is visible (Fig. 7.3C). The separations between the scales of the pectoral fin are not visible. Short, delicate denticles cover the distal end of the dorsal surface of the fin and narrow ridges cover the medial end of the dorsal surface. The medial margin of the fin is ornamented with short, thick denticles.

Trunk—The trunk is preserved for a length equal to the length of the headshield. Because an acanthodian covers the left side of the trunk, the shape of the trunk cannot be determined. A ventrolateral ridge is not preserved on the right side, so determined because the squamation of the trunk does not change at the lateral margins. The denticles ornamenting the trunk (Fig. 7.2A) are similar to those of the headshield but are longer. The median dorsal ridge of the trunk can be distinguished by a line of posteriorly pointing denticles that are larger than the other denticles of the trunk. The ridge runs from the median dorsal crest posteriorly along the right side of the trunk. The denticles on the trunk typically point posteriorly, but clusters of denticles can point laterally or medially at various points along the trunk. The denticles are , for the most part, arranged in clusters of rows of closely spaced denticles. The first row of each cluster is short, usually with two or three denticles; the number of denticles in each row of a cluster increases posteriorly along that cluster. The clusters likely represent individual scales of the trunk, though their margins are indistinguishable from one another. The dermoskeleton of the trunk appears continuous, despite random fractures in the dermoskeleton. The dorsal fin and caudal fin are not preserved.

Remarks

The similarity in colour and texture between the dermoskeleton of UALVP 42648, the holotype, and the surrounding matrix makes it difficult to differentiate one from the other and obscures the separation between the tesserae. This creates the illusion of a continuous dermoskeleton. That this continuity of the dermoskeleton is not real is shown by the fact that the appearance extends onto the pectoral fin and the trunk. The trunk of osteostracans is typically composed of rhomboid or rectangular flank scales arranged oblique to the median dorsal ridge of the trunk (Stensiö, 1932; Heintz, 1967), allowing for flexure of the trunk when the animal was swimming. A continuous dermoskeleton of the trunk would not permit locomotion for *Ceramantyx*.

cf. *CERAMANTYX* sp. indet. Type 1

Fig. 7.4

Referred Specimen—UALVP 23194, a partial headshield preserved in ventral view.

Description

State of Preservation and the Headshield—Two to three individual osteostracan specimens are present on the same block (Fig. 7.4A). A specimen of *Superciliaspis*, consisting of disarticulated tesserae, trunk scales, and marginal plates, is present on the right hand side of UALVP 23194. The other possible specimen (Fig. 7.4B), posterior to UALVP 23194, may be a separate specimen of the same species as UALVP 23194, or a disarticulated section of UALVP 23194. The headshield of UALVP 23194 is about 4 cm wide The anterior third of the headshield is parabolic, and the posterior two thirds of the articulated headshield are straight from anterior to posterior (Fig. 7.4A).

The dorsal dermoskeleton is composed of numerous small, polygonal plates in visceral view on the right side of the headshield. The dorsal tesserae are also visible in both superficial and visceral view in a small excavation in the block on the right of the specimen. The bases of the dorsal tesserae have no rims. A central pore surrounded by radiating canals is present in the base of each dorsal tessera. Multiple pore and canal units can be present on one plate. The superficial layer of dorsal plates is unornamented except for numerous small pores. The superficial layer of the dorsal tesserae is thicker than the middle layer; the basal layer is not present and the pores and radiating canals at the base of the middle layer are visible. The bases of the tesserae are unfused. Ventral tesserae are visible across much of the headshield, but features such as the branchial openings and the mouth are indistinguishable from the rest of the ventral dermoskeleton. The tesserae adjacent to the headshield margin are larger than the rest of the tesserae, with pores larger and farther apart than elsewhere on the ventral dermoskeleton or margin, and the ventral tesserae medial to these are much smaller. Tesserae also become smaller medially along the headshield. The ventral tesserae are quadrangular and those posterior to the orbit are larger than those anterior to the orbit. The ventral tesserae anterior to the left orbit are the smallest on the headshield. The pores of the ventral tesserae are the same distance apart as those of the dorsal tesserae.

Orbits, Pineal Region, and Nasohypophyseal Region—Two concentrations of orange, weathered grains in the center of the headshield are the labyrinth infillings. A single plate with a keyhole-shaped opening is visible anteromedial to the labyrinth infilling on the left side of the specimen.

Cornua—The cornua are not present in articulation with the headshield, and no associated plates can be referred to UALVP 23194 with any certainty.

Margin of the Headshield—The margin of the headshield is thick. The lateral margin of the headshield is present far posterior to the labyrinth infillings. The headshield margin is composed of short, rectangular plates that are longest transverse to the direction of the margin (Fig. 7.4C). These plates are laterally convex and imbricated, with the posterior margin of each plate overlapping the anterior margin of the next plate (Fig. 7.4C). The anterior margin of the headshield retains the rectangular plates, though they are no longer imbricated. The lateral surface of the headshield margin is smooth except for rows of pores running anteriorly to posteriorly. A break in a marginal plate at the anterior left end of the headshield shows a thick middle layer and a thin basal layer below the superficial layer.

Trunk—No clear change in squamation separates trunk from headshield and so it is difficult to differentiate trunk scales from those of the head. Scales far posterior to labyrinth infillings are generally larger than those at the more anterior regions of the headshield and are typically rhomboid or hexagonal. A fragment of osteostracan posterior to UALVP 23194 may be a fragment of trunk from the same individual. The scales vary greatly in size and include two patches of small, porous scales on either side of the specimen (Fig. 7.4B). A continuous section of curved, highly porous vertebrate exoskeleton is present near one of the patches, and if it is tentatively considered a cornual process, would represent cornua composed of separate plates, similar to UALVP 41476 described below, but it is too far posterior to the main headshield plates to be referred to UALVP 23194 with any confidence. None of the scales of the posterior specimen are arranged in rows, as would be expected for the scales of the dorsal or ventral trunk.

Remarks

The keyhole-shaped opening anteromedial to the left labyrinth infilling could be the nasohypophyseal opening, but is placed too far posteriorly to be in life position. If this is the nasohypophyseal opening, the hypophyseal division is the same size as the nasal division and the opening is constricted between these divisions.

A complete taxonomy of this specimen is not provided, despite a unique combination of characters, as the specimen itself is both incomplete and, if the section on the posterior left hand side of UALVP 23194 is part of the same individual, disarticulated. This makes it impossible to accurately determine the spacial relationships of the margins, and to identify external characteristics of the headshield with confidence.

cf. *CERAMANTYX* sp. indet. Type 2

Fig. 7.5

Referred Specimen—UALVP 41476, the right half of a dorsal headshield in visceral view (Fig. 7.5).

Headshield—The cornual process, lateral half of the right orbit, and the margin of the headshield from the cornual process to the anterior end of the headshield, are preserved. For stability the specimen was coated in cyanoacrylate, obscuring some fine details of the headshield. The anterior half of the headshield is parabolic, while the lateral margin runs straight anteroposteriorly for the rest of the distance to the cornual processes. The headshield is probably about as long as it is wide, though the left half of the specimen is not preserved. The abdominal division is short and wide, making up most of the posterior width of the headshield. The dorsal dermoskeleton is composed of small polygonal tesserae, only preserved in visceral view on UALVP 41476. The bases of the tesserae of the dorsal headshield are unfused. The center of each tessera is porous, with canals radiating from the center to the margin of the tessera. The margin of the base of each tessera is thin and shallow. The preorbital region of the headshield is slightly longer than the postorbital region.

Orbits, Nasohypophyseal Region, and Pineal Region—The right orbit is preserved at the medial edge of the specimen. The lateral margin of the orbit extends dorsally; this would result in a raised rim around the orbit in dorsal view. The labyrinth infilling is preserved posterior to the orbit as a concentration of white grains (Fig. 7.5). The posterior margin of the orbit is a single plate with two anterior projections.

Median Field—The median field is not preserved. This may be because the lateral margins of the median field are medial to the lateral margins of the orbit. If so the median field was narrow, but the length and shape cannot be determined based on UALVP 41476.

Cornua—The cornual process is short and triangular, though the posterior tip is not preserved (Fig. 7.5). The cornual process is composed of three separate plates, grading from margin plates to cornual plates, the posteriormost plate being the largest. The cornual process points posteriorly. The superficial layer of the lateral margin of the cornual process is thick, with few pores across its surface. The medial margin of the cornual process is highly porous. The ventral surface of the cornual process, like the medial margin, is covered in numerous small pores. The lateral margin of the cornual process is straight anteroposteriorly, while the medial margin runs diagonally from anteromedial to posterolateral.

Margin of the Headshield—The margin of the headshield is composed of numerous plates. These plates are imbricated, with the posterior margin overlapping the anterior margin of the more posterior plate. The plates of the headshield margin are rectangular, laterally convex, longer than wide transverse to the margin of the headshield, and ornamented with oakleaf-shaped tubercles. The lateral margin of the plates of the headshield margin becomes longer than the medial margin of each of these plates, closer to the cornual process. The anterior end of the margin of the headshield is not divided into rectangular plates; instead, the plates are indistinguishable from one another and the margin is flat and longer than other regions. At the anterior margin, the oakleaf-shaped tubercles of the margin are mostly aligned transverse to the headshield and, like the rest of the margin tubercles, longitudinal to the margin of the headshield. The ornament at the anterior margin of the headshield grades posteriorly towards the oralobranchial cavity, to much more gracile oakleaf-shaped tubercles.

Pectoral Fin—The pectoral sinus is small and located far laterally on the headshield as well as shallow and far posterior to the orbit (Fig. 7.5). The margin of the pectoral sinus is also broken. The pectoral fin itself is not preserved.

Class OSTEOSTRACI Lankester, 1868

Subclass CORNUATA Janvier, 1985a

Order and Family incertae sedis

ANCYRASPIS, gen. nov.

Etymology—*Ancyr*, derived from *ankyra*, Greek for “anchor,” combined with *aspis*, Greek, meaning “shield” in reference to the cornual process resembling the hook on an anchor. Gender feminine.

Diagnosis—As for type and only known species

Type and Only Known Species—*Ancyraspis enormis*, sp. nov.

ANCYRASPIS ENORMIS, sp. nov.

Fig. 7.6

Etymology—The specific epiphet *enormis*, Latin, means "huge," in reference to the large size of the holotype.

Holotype—UALVP 43638, the posterior left quarter of a headshield, and the anterior end of the trunk, articulated in visceral view (Fig. 7.6A, C).

Paratype—UALVP 43962, numerous disarticulated but associated trunk scales, likely lateral scales (Fig. 7.6B).

Diagnosis—Long, narrow, medially curved cornual process; thick rectangular ventral and lateral trunk scales; thick, smooth basal layer on trunk scales that is either continuous or blocky; ventral headshield, ventral trunk scales, and ventrolateral ridge scales ornamented with elongate, posteriorly pointed denticles; and pectoral fin making oblique, rather than transverse, angle from the headshield.

Shares with *Dentapelta* posterior pointing, distally flat, denticles on continuous dermoskeleton, differs from *Dentapelta* by large, medially curved cornual process, denticles more elongate at their base. Medial curve to cornual process similar to *Zychaspis siemiradzkii*, *Spangenhelmaspis staxrudi*, and '*Cephalaspis*' *watsoni*, but differs from these taxa by greater size, and by ornamentation.

Type Locality—As for *Ceramantyx odontotos*. The MOTH locality.

Description

Measurements—Maximum width estimated to be 270 mm, based on the width from halfway across the trunk to the most lateral point of the cornual process, transverse to the longitudinal axis of the trunk.

General Morphology and Ornamentation—UALVP 43638 consists of a cornual process, pectoral fin, and anterior segments of the trunk in ventral view (Fig. 7.6A). The ventral dermoskeleton of the headshield is continuous. Numerous denticles of various sizes ornament the dermoskeleton. The small denticles point ventrally from a circular base. The base of the largest denticles is elliptical. The distal surface of the largest denticles points posteriorly with a wide groove running anteroposteriorly. The distal groove is absent from more medial denticles. Small denticles aree interspersed among the large denticles, but some large denticles are also adjacent to one another. The dermoskeleton between denticles is regularly pitted with circular pits. Medially, the dermoskeleton of the ventral headshield separates into polygonal tesserae. Multiple denticles are present on each tessera.

Cornua—The left cornual process is preserved except for the posterior tip and the anterior end of the lateral margin. The cornual process tapers posterior to the base, becoming long and narrow, and begins to curve medially almost immediately posterior to the base (Fig. 7.6A, C). The cornual process has a thick middle layer, like that of the trunk, where it is exposed in breaks in the dermoskeleton along the medial margin. The medial margin of the cornual process is not barbed (Fig. 7.6C); instead. it is ornamented with denticles like those of the ventral headshield. The lateral margin of the cornual process is raised and thick (Fig. 7.6C). Denticles that are larger than those of the ventral headshield border the lateral margin of the cornual process. The ventral dermoskeleton of the cornual process is continuous medially and divided into polygonal tesserae laterally (Fig. 7.6C). The ventral surface of the cornual process is ornamented with denticles, but the distal surfaces of these, particularly those denticles of the lateral margin, are smooth and rounded and lower than the denticles of the rest of the headshield.

Pectoral Fin—The distal and lateral margins of the pectoral fin are not preserved past the base of the fin and therefore the length and shape of the fin cannot be determined. The fin extends at an oblique lateral angle from the pectoral sinus (Fig. 7.6A). The ventral surface of the fin is covered with tesserae ornamented with denticles. The proximal denticles resemble those of the headshield. The denticles of the fin become smaller distally to resemble those of the small denticle morphology of the headshield except with more radiating ridges. The distalmost denticles of the pectoral fin are wider, more circular, and have shorter radiating ridges than the more proximal denticles. The distal surface of the distalmost denticles is flat and smooth. There is greater variation in the size of the tesserae of the fin distally, with more small tesserae appearing, than at the proximal end of the fin. The smallest tesserae may only possess a single denticle, while larger tesserae have multiple denticles. The dorsal tesserae are preserved in visceral view at the distal end of the fin, and they are polygonal or circular. The base of each tessera has a central pore with canals radiating from it. Multiple pore and canal units can be present on one tessera. The distalmost dorsal tesserae of the fin are small, with only one pore. The bases of the dorsal tesserae of the pectoral fin lack a rim.

Trunk—The ventral headshield margin grades from continuous dermoskeleton to long, rectangular scales. The ventrolateral ridge scales are slightly imbricated, the posterior overlapping the anterior (Fig. 7.6A). The dorsal halves of the ventrolateral scales are not visible because the ventrolateral scales are splayed so that the ventral half of each ventrolateral scale is extended laterally. The ornament of the ventrolateral ridge scales is the same as the ornament for the ventral trunk scales. Where the ventrolateral ridge approaches the base of the pectoral fin, the ventrolateral scales are no longer imbricated. Lateral scales of the dorsal surface of the trunk are in visceral view. These scales run anteromedially. The margin of the base of the lateral scales has a wide rim and the base is covered in a smooth layer of basal bone. The ventral and lateral scales of the trunk are divided into square to rectangular units. The superficial layer of the scales of the trunk is thin; the middle layer is very vascular and thick.

The ventral scales of the trunk become narrower posteriorly and run anterolaterally. They are 3mm long anteroposteriorly. The ornament of the ventral trunk scales is the same as that for the ventral dermoskeleton. The dermoskeleton between denticles on the trunk is regularly pitted in offset rows. The posterior margin of each ventral scale overlaps the anterior margin of the next, posterior scale.

Remarks

A specimen of *Ischnacanthus*, the trunk of a lepidaspidid, the scales of a putative chondrichthyan, and the scapulocoracoid of an acanthodian, tentatively referrable to *Ischnacanthus*, are associated with the specimen.

The lateral trunk scales of the paratype, UALVP 43962, are smaller than the trunk scales of the holotype, UALVP 43638, and the basal layer is blocky (Fig. 7.6B) rather than smooth and continuous for each scale (Fig. 7.6A). The ornament of UALVP 43962 is identical to that of the holotype, and the specimen is also very thick in cross-section.

The holotype, UALVP 43638, was determined to be in ventral view based on the anterolateral direction of the trunk scales, the absence of a lateral field around the cornual process, and the presence of tesserae only at the anteromedial end of the specimen, roughly where the oralobranchial region would be on other osteostracans (e.g., *Hirella*, Heintz, 1939; *Cephalaspis cradleyensis*, White and Toombs, 1983).

Class OSTEOSTRACI Lankester, 1868

Subclass Order and Family incertae sedis

OSTEOSTRACI indeterminate

Fig. 7.7

Referred Specimens—UALVP 33028, anterior left quarter of a dorsal headshield in ventral view.

Description

General Morphology—The anterior end of the headshield is almost flat, transverse to the rest of the headshield, while the lateral margin extends posterolaterally to the edge of the block. The visceral view of the dorsal dermoskeleton is blocked by a thin layer of bone, Which is most likely the perichondral bone based on the rough, pitted texture (Janvier, 1985a), median to the margins and anterior to the branchial openings. A partial dorsal view of the anterior end of the specimen is available on the other side of the block (Fig. 7.7B). The exposed dorsal dermoskeleton is inconsistent in texture across the headshield, making it unlikely that the most superficial layers are preserved on this specimen. Pores and canals cover the dorsal surface of the headshield. This is likely exposure of the basal layer and, towards the posterior end of the exposed area of the headshield, the middle layer of the dermoskeleton. The dermoskeleton is exposed in dorsal view along the right side of the specimen, where tall tubercles are set close together. These tubercles are larger than those on the ventral surface of the headshield margin and have ridges radiating from their anterior end. The tubercles appear to have been solid, but have not been broken to the base so the presence or absence of a cavity in the base of the tubercle cannot be determined. There are no external circumareal canals visible and therefore the dorsal dermoskeleton is likely continuous throughout the headshield. In cross-section the superficial layer at the base of the tubercles is very thin and the middle layer and the basal layer are of equal thickness to one another, with large vacuities being present in the latter. The canals of the margin of the headshield are arranged longitudinal to the margin itself, while the canals of the rest of the headshield do not share any pattern in the visceral layers. The more superficial layer of dermoskeleton has canals radiating from many highly porous centers. At the edges of the exposed area, ornament is visible in the form of either denticles or tubercles in cross–section.

Orbits, Nasohypophyseal Region, and Pineal Region—The margin of the orbit is preserved as a thick, curved ridge of bone anterior to the labyrinth infilling. The orbits are far posterior on the headshield relative to the rostral region, but not far posterior relative to the branchial sulci. The labyrinth infilling is visible under a thin layer of bone near the posterior end of the preserved portion of the specimen (Fig. 7.7A). The sclerotic capsule is ossified. An opening is present anterior and lateral to the center of the capsule. This is the only large opening in the sclerotic capsule. The nasohypophyseal opening is not visible.

Margin of the Headshield—The deep bone of the headshield margin is exposed at the margin's posterior end. The deeper layers of bone are permeated by canals and vacuities. The canals that are at the same depth as one another are arranged in a radiating pattern around pores. The margin of the headshield is continuous along its entire preserved length, except for a single, deep groove running across the margin. This groove is located transverse to the first branchial fossa. The ventral surface of the margin is thick and wide, as is the visible dorsal region. The ventral surface of the margin of the headshield is ornamented with stellate denticles at its anterior end (Fig. 7.7B). The ornament grades laterally from small distal projections to larger denticles with thick radiating ridges from the base of the denticle. The dermoskeleton between the denticles of the ventral headshield margin is regularly pitted, all pits of equal size.

Ventral Shield—The plates or tesserae of the ventral shield are not preserved. The mouth is unknown except for the supraoral field (Fig. 7.7A, C), a denticulated region that is present at the anterior end of the oralobranchial region. This denticulated region is short and wide, with a straight posterior margin and an anterior margin that follows the margin of the headshield.

The posterior margin of the prebranchial fossa is perpendicular to the long axis of the headshield. The first branchial fossa is much larger than the second and the second branchial fossa is larger than the third; this pattern repeats for each more posterior branchial fossa. Six branchial arches are preserved on the left side, starting from the anterior of the specimen. The branchial fossae are numbered anterior to posterior as bf.1-6 (Fig. 7.7A). The fossae are anteroposteriorly adjacent to one another, separated by the branchial arches. Each branchial fossa extends laterally to the headshield margin, radiating from the pineal and orbital region of the headshield, and is bordered by a thin ridge of bone where the branchial arch lies. The branchial fossa extends posteriorly for a short distance where it contacts the lateral margin; this would be consistent with the location of the branchial opening at the lateral margin of the oralobranchial region.

Internal Anatomy—An opening is located within the visceral skeleton, far anterior and on the midline of the headshield. This opening is oval, with a tapering posterior end. This opening is located at the posterior end of the prebranchial fossa, in the groove for the dorsal aorta. No such structure has been described for other osteostracans (Stensiö, 1927; Janvier, 1985a).

Remarks

The first branchial fossa is exceptionally large and indicates the presence of a large prepineal region relative to the rest of the headshield (Fig. 7.7A). The branchial arches are well known for the Benneviaspidida (Janvier, 1985a) where only *Boreaspis* has a large first branchial fossa and a large prebranchial fossa. The arrangement of the branchial arches in most of the Benneviaspidida is orthobranchiate, or arranged perpendicular to the long axis of the headshield, while in UALVP 33028 and most other osteostracans, the branchial arches are oligobranchiate (oblique to the long axis of the headshield) (Janvier, 1985a).

Class OSTEOSTRACI Lankester, 1886

Subclass CORNUATA, Janvier 1981

Family and Order incertae sedis

CORNUATA indeterminate

Fig. 7.8

Referred Specimen—UALVP 41453, the posterior half of a headshield and an articulate trunk in ventral view.

Description

General Description—The pectoral fins and the tip of the left cornual process are also preserved (Fig. 7.8). The ventral shield is composed of numerous small, polygonal tesserae that form most of the headshield. The tesserae of the ventral headshield and the scales at the anterior end of the trunk are disarticulated. Ventral tesserae are ornamented with many small tubercles between pores, often with the tubercles on ridges in concentric rings. Towards the posterior end of the headshield the tesserae are larger and ornamentation is more sparse. The dermoskeleton is thin where it is exposed in cross-section, through gaps in the ventral headshield. No laminar basal layer is visible, and the tessera is primarily composed of the middle layer and a thinner superficial layer.

The median dorsal crest is embossed on the ventral dermoskeleton as a low, narrow ridge. The anterior end of the median dorsal crest is far posterior to the labyrinth infillings; the posterior end is not preserved on the specimen.

Orbits, Pineal Region, and Nasohypophyseal Region— The labyrinth infillings are visible as a pair of concentrations of white grains near the anterior end of the preserved section of the headshield (Fig. 7.8); unfortunately, the margins of the orbits cannot be distinguished through the ventral dermoskeleton anterior to them. A single sulcus is visible anterior and medial to the labyrinth infillings that is most likely the nasal opening.

Median Field—In most osteostracans in which a median dorsal crest is present, the posterior margin of the median field extends to the anterior end of the median dorsal crest. The anterior end of the median field is usually in contact with the pineal plate, or opening (e.g., *Diademaspis*, Janvier, 1985a), or just posterior to the pineal plate (e.g., *Waengsjoeaspis*, Janvier, 1985a). Given that the anterior end of the median dorsal crest of UALVP 41453 is far posterior to the labyrinth infillings, which are posterolateral to the pineal opening in osteostracans (Sahney and Wilson, 2001), if this is the same for this taxon, then the median field of UALVP 41453 was exceptionally long. The margins of the median field are covered by the ventral dermoskeleton and so the shape cannot be determined.

Cornua—Based on the length of the pectoral fin, the cornual process is long and points posteriorly, the medial margin being longitudinal with the rest of the specimen (Fig. 7.8). The medial margin of the process is ornamented with small, medially pointed barbs, that are evenly spaced along its preserved length, except for the posterior tip. The dorsal surface of the process is highly porous. The pores are larger and sometimes elongate at the lateral side and at the posterior end of the cornual process.

Pectoral Fin—The shape of the pectoral fins is unclear, because both fins were folded prior to burial, though if they were unfolded they would probably be broad and rounded at the distal end, since the medial margin is rounded. It is clear that the pectoral fin is at least as long as the cornual process, as the tip of the left fin lies approximately as far posteriorly as the posterior tip of the process. Minute scales cover each pectoral fin; these scales are ornamented with oakleaf-shaped tubercles. The tubercles become more robust at the lateral margin of the pectoral fin. The ornamentation is much lower relief and less robust at the proximal and medial ends of the fin.

Trunk—The preserved portion of the trunk is two-and-a-half times the postorbital length of the headshield, but the caudal end of the trunk is not preserved. The trunk tapers gradually. The lateral trunk scales are rhomboid and anterodorsally elongate. Numerous small, elongate pores cover the lateral scales. The ventrolateral ridge is clearly differentiated from the rest of the trunk (Fig. 7.8). The ornament of the ventrolateral ridge scales at the anterior end of the trunk is elongate pores between ridges, grading posteriorly to posteriorly pointed tubercles at the posteroventral end of each scale; the ornament grades to posteriorly more robust tubercles at the posteroventral end of each scale. The dorsal half of each ventrolateral ridge scale resembles the lateral scales in ornament and direction of the long axis, and the ventral half is robust, convex, and imbricated with the adjacent scales. The external surface of the trunk scales anterior to the ventrolateral ridge is the same as the ventral and lateral trunk scales, not convex, or tuberculate.

Ventral Trunk—The ventral trunk is bordered laterally by the ventrolateral ridges. The scales of the ventral trunk are rhomboid and larger than the tesserae of the ventral headshield. At the anterior end of the trunk, the ventral scales are arranged in anterolateral rows, farther posteriorly on the trunk there is no clear arrangement of the scales. The ornament of the ventral scales adjacent to the ventrolateral ridge is comprised of rows of numerous small, posteriorly pointed tubercles. The ornament grades medially to longer, more slender ridges.

Remarks

UALVP 41453 is left in open taxonomy as not enough of the headshield is preserved to provide a clear diagnosis for this species. This taxon differs from other species known from MOTH based on its thin dermoskeleton, thinner than that of *Waengsjoeaspis*, *Glabrapelta*, and *Superciliaspis*, and its ornament of the ventral dermoskeleton, differing from that described for other osteostracan taxa. Unfortunately, without the cornual processes, median field, or nasohypophyseal opening, a comparison with other osteostracan taxa is difficult as for many other taxa the ventral shield and the trunk are not known.

DISCUSSION

The new taxa and specimens described in this chapter represent morphologies that do not readily allow them to be referred to known orders or families. Compared to taxa dealt wih in earlier chapters, the classification of these taxa is much less clear, and so a discussion of the affinities of *Ceramantyx*, *Ancyraspis*, and the indeterminate taxa described above will consider the possible relationships between these taxa and other Osteostraci.

Affinities of *Ceramantyx*

The margin of *Ceramantyx* represents a condition that has not been previously described for an osteostracan. The margin of the headshield of many osteostracans is smooth and continuous (e.g., *Waengsjoeaspis*, Janvier, 1985a;

Adrain and Wilson, 1994), but in *Ceramantyx* the plates are separate and imbricated (Fig. 7.3D). This is also distinct from the narrow ridges that compose the margin of the headshield of *Aceraspis* and *Hirella* (Heintz, 1939), and the numerous longitudinal plates of *Ateleaspis* (Ritchie, 1967) and *Acerocephale* (Chapter 3). Oakleaf-shaped tubercles ornament the marginal plates. This ornament is similar to the ornament of the dermoskeleton of *Lepidaspis* of the tesselate heterostracans (Dineley and Loeffler, 1976).

Homology of Ornament—The ornament of the Osteostraci is varied across numerous clades (Stensiö, 1932) making the homology of this character difficult to assess. The ornament of *Ceramantyx* varies over the headshield and across the trunk, but two features of the denticles are consistent: they are small, and, where visible because they are broken, they are hollow in the center. Hollow individual denticles would be consistent with a pulp cavity or an individual pore and would be similar to the condition observed in *Acerocephale*, *Dentapelta*, and *Balticaspis* (pers. Obs.; Otto and Laurin, 2001); however, these denticles very greatly in external morphology in *Ceramantyx* and are much smaller than those of the other taxa mentioned. The denticles of *Ceramantyx* are all small and are often clustered as are the tubercles of the Ateleaspididae, *Stensiopelta*, and *Superciliaspis* (Heintz, 1939; Janvier, 1985c; Adrain and Wilson, 1994). It is possible that the denticles of *Ceramantyx* are homologous with the tubercles of primitive osteostracans, but without detailed examination of the histology of the dermoskeleton of *Ceramantyx*, it is not possible to determine the development or source of these denticles.

Homology of Macroscopic Characteristics—The ornament of the antorbital horns and the plates bordering the median field in *Ceramantyx* resemble those features in *Supercilaspis*; however, the overall shape of the headshield differs considerably from the triangular headshield of *Superciliaspis* (Dineley and Loeffler, 1976). The overall shape of the headshield resembles that of *Diademaspis poplinae* (Janvier, 1985a); however, the ornament is distinct from that of this species, and the median field is narrower (width of headshield divided by width of median field is 15 in *Ceramantyx*, compared to 7 in *Diademaspis*, Voichyshyn, 2006), and the fused plates posterior to the orbits and antorbital horns also distinguish *Ceramantyx* from species of *Diademaspis* (Afanassieva, 1989; Janvier, 1985a; Voichyshyn, 2006). The plates posterior to the orbits are large and heavily ornamented, similar to those of *Superciliaspis* (Dineley and Loeffler, 1976; Adrain and Wilson, 1994), but the shape of the headshield and the short, triangular cornua and the ornament of the rest of the headshield of *Ceramantyx* clearly differentiate this taxon from *Superciliaspis*. *Ceramantyx odontotos* has a rim of plates around the orbit (Fig. 7.2C), but there is no relief that would indicate a raised orbital rim, such as that seen in Zenaspidida, *Camptaspis*, and *Yvonaspis*. It is possible that a raised rim was present in life, but was flattened along with the rest of the specimen during taphonomy, because the rim of the orbit of UALVP 41476 (*Ceramantyx* sp. indet. Type 2, Fig. 7.5) appears to be raised, so the condition of this character remains uncertain for the genus *Ceramantyx*. The ornamentation of the headshield of *Ceramantyx* odontotos is unique, the ‘sel’ canals bifurcate far distal to the orbits, like in the

Benneviaspidida and Thyestiida, while the overall shape of the headshield resembles *Diademaspis* within the Zenaspidida. *Ceramantyx* possesses a combination of characteristics that make it unique, but which also defy precise classification, as many of these characteristics are shared with various disparate osteostracan taxa.

Characters that Differentiate *Ceramantyx* sp. indet. Type 1 and Type 2

Unlike *C. odontotos* and UALVP 41476 (*Ceramantyx* sp. indet. Type 2), UALVP 23194 (*Ceramantyx* sp. indet. Type 1) maintains a rectangular shape to its marginal plates at the anterior end of the headshield. The ornament of the marginal plates differs between UALVP 23194 on the one hand, and UALVP 41476 and *C. odontotos* on the other. The marginal plates of *C. odontotos* and UALVP 41476 are ornamented with oakleaf-shaped tubercles (Fig. 7.3D), but the margin of UALVP 23194 is covered in rows of pores (Fig. 7.4C). Both UALVP 23194 and UALVP 41476 have a dermoskeleton composed of polygonal tesserae, while tessellation of the dermoskeleton of UALVP 43638, the holotype of *Ceramantyx odontotos* (Fig. 7.1), is not known.

UALVP 41476 is tentatively referred to *Ceramantyx* based on presence of individual imbricated plates along its headshield margin, and on its overall headshield shape. UALVP 41476 shares with *C. odontotos* oakleaf-shaped tubercles on the margin. But, unlike the condition observed in UALVP 41476, the lateral and medial margins of the marginal plates in *C. odontotos* are of equal length all the way to the cornual process. UALVP 41476 differs from *C.*

odontotos primarily because of the cornua. The cornua of *C. odontotos* are a single continuous unit at their margins (Fig. 7.3C). The cornua of UALVP 41476 are instead composed of three separate plates (Fig. 7.5). The shape of the cornual process is similar between UALVP 41476 and *C. odontotos*, but the composition is significantly different. The plates composing the cornual process of UALVP 41476 are more similar in arrangement to the cornual plates of *Superciliaspis* (Dineley and Loeffler, 1976; Adrain and Wilson, 1994) than to *C. odontotos*, but the plates along the margin of the headshield are imbricated and tuberculate, like those of *Ceramantyx odontotos*, rather than the continuous rim around the headshield that is present in *Superciliaspis*.

Affinities of *Ancyraspis enormis*

Ancyraspis enormis, at a maximum width 27 cm, represents the largest known osteostracan from MOTH and one of the largest osteostracans from any Early Devonian deposit, behind *Diademaspis poplinae* (35 cm maximum width, estimated from BMNH p.44727) and '*Meteoraspis' hoegi* (at least 23 cm, based on no. 12, Stensio, 1927 pl 9) (Janvier 1985a; plate 2, and plate 8 fig. 1 respectively). The denticles that ornament the ventral surface of the specimen are similar in superficial morphology to those found on *Dentapelta* and the denticles discussed by Otto and Laurin (1999). The most remarkable characteristics of this specimen are the long, medially curved cornual processes (Fig. 7.6A, C). The cornual processes of larger, later, Middle and Late Devonian osteostracans are short, often very broad, and point posteriorly (*Escuminaspis*, *Levesquaspis*, *Balticaspis*, *Ilemoraspis*, Janvier et al., 2004; Janvier and Arsenault, 2005; Otto and Laurin, 2001; Sansom, 2008 respectively) or posterolaterally (*Trewinia*, Janvier and Newman, 2005). The cornua of *Diademaspis* are short and triangular (Janvier, 1985a). *Zychaspis siemiradzkii*, *Spangenhelmaspis staxrudi*, and '*Cephalaspis*' *watsoni* share the strong medial curve in the cornual processes with the new taxon; however, the ornament and size of these taxa differs considerably from those features in *Ancyraspis*. The broad combination of characters preserved, and the absence of preservation of other characters, makes the classification of *Ancyraspis* limited to the Cornuata, with no clear affinities to other osteostracans.

Wear on the ventral headshield is consistent with the benthic interpretation of osteostracans (Afanassieva, 1992; Denison, 1956; Janvier, 1985b). The denticles are lowest in the areas of the headshield with the greatest relief, namely the lateral margin of the cornual process (Fig. 7.6C). The distal surface of the denticles on the cornua is always the same height from the dermoskeleton and very smooth.

Affinities of UALVP 33028

The affinities of this specimen are difficult to ascertain as the morphology of the median and lateral fields, the cornua, the nasohypophyseal opening and the pineal opening, and the postpineal region of the headshield as a whole, are all unknown. The antorbital region of the headshield is very long and the dorsal dermoskeleton of the headshield is continuous (Fig. 7.7A, B), both of which are characters shared with *Cephalaspis* (Janvier and Newman, 2005); however, the denticulate ornament and broad margin clearly differentiate this specimen from the holotype of *Cephalaspis lyelli* (Agassiz, 1935), the only species that can be referred to the genus *Cephalaspis* with confidence (Janvier and Newman, 2005). The specimen is orthobranchiate (Stensiö, 1927), similar to most osteostracans other than the benneviaspidids.

The only taxon with which UALVP 33028 bares distinctive similarity with is *Cephalaspis lyelli*, but there are obvious differences in the morphology and ornamentation of the margin of the headshield, and in the ornamentation of the dorsal dermoskeleton.

Affinities of UALVP 41453

A ventral headshield composed of tesserae, and posterior pointing cornual processes are common features among cornuate osteostracans (Janvier, 1985a; Sansom, 2009). Short, rhomboidal lateral trunk scales, such as those found in UALVP 41453, are known for *Ateleaspis* (Ritchie, 1967), *Aceraspis* and *Hirella* (Heintz, 1939), *Acerocephale* (Chapter 3), and *Ilemoraspis* (Sansom et al., 2008). All of those osteostracans, except *Ilemoraspis*, are considered to be primitive (Janvier, 1985a; Sansom, 2009; Chapter 3); however, Hawthorn et al. (2008) noted that juvenile specimens of *Superciliaspis* have numerous small lateral scales that eventually fuse into the elongate lateral scales common among cornuate osteostracans, and so this feature could be a juvenile character of UALVP 41453.

The features of UALVP 41453 (long median field, barbs on the medial margin of the cornual process, and an ornament of numerous small tubercles) are too common among osteostracans to provide a clear indication of the affinities of this specimen other than membership in Cornuata (Janvier, 1985a; Sansom, 2009).

SUMMARY

Several osteostracan specimens from MOTH represent unique morphologies, but do not readily fit into previously recognized clades. Although two specimens are referrable to a new genus, *Ceramantyx*, they are too incomplete and poorly preserved to provide a specific classification, while the new species, *Ceramantyx odontotos*, is the most complete of the new taxa, but has no clear affinities to the major groups of osteostracans. The new genus and species *Ancyraspis enormis*, and two specimens that likely represent new species, are too incomplete to provide taxonomic information, and so, while representing yet more diversity among the osteostracans from MOTH, cannot currently contribute to classification of the MOTH osteostracans.

LITERATURE CITED

Adrain, J. M., and M. V. H. Wilson. 1994. Early Devonian cephalaspids (Vertebrata: Osteostraci: Cornuata) from the southern Mackenzie Mountains, N.W.T., Canada. Journal of Vertebrate Paleontology 14:301–319.

Afanassieva, O. B. 1989. New cephalaspids (Agnatha) from the Lower Devonian of Podolia. Paleontologicheskiy zhurnal. 1989: 51–59. [Translated from Russian]

Afanassieva, O. B. 1992. Some peculiarities of osteostracan ecology. 61–70. In Mark-Kurik, E. (ed.). Fossil fishes as living animals Academy of Sciences of Estonia, Tallin, 299 pp.

Agassiz, L. 1835. Recherches sur les Poissons Fossiles. 2. Contenant l'histoire de l'ordre des Ganoïdes. Neuchâtel, 85–300 pp.

Denison, R. H. 1956. A review of the habitat of the earliest vertebrates. Fieldiana: Geology 11: 361–457.

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

Gabrielse, H., S. L. Blusson, and J. A. Roddick. 1973. Geology of Flat River, Glacier Lake and Wrigley Lake map areas, District of Mackenzie, Northwest Territories. Geological Survey of Canada, Memoir 366:1–268.

Hawthorn, J. R., M. V. H. Wilson, and A. B. Falkenberg. 2008. Development of the dermoskeleton in *Supericiliaspis gabrielsei* (Agnatha: Osteostraci). Journal of Vertebrate Paleontology 28:951–960.

Heintz, A. 1939. Cephalaspida from the Downtonian of Norway. Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo. Matematisk-Naturvidenskapelig Klasse 5:1–119.

Heintz, A. 1967. Some remarks about the structure of the tail in cephalaspids. pp. 21-36 in Problemes Actuels de Paléontologie (Évolution de Vertébrés). Colloques Internationaux du Centre National de la Recherche Scientifique. Centre National de la Recherche Scientifique, Paris.

Janvier, P. 1981. *Norselaspis glacialis* n.g., n.sp. et les rélations phylogénétiques entre les Kiaeraspidiens (Osteostraci) du Dévonien inférieur du Spitsberg. Palaeovertebrata 11: 19–131.

Janvier, P. 1985a. Les Cephalaspides du Spitsberg. Cahiers de Paléontologie, Section Vertébrés. Éditions du Centre National de la Recherche Scientifique, Paris: 244 pp.

Janvier, P. 1985b. Environmental framework of the diversification of the Osteostraci during the Silurian and Devonian. Philosophical Transactions of the Royal Society of London, series B 309: 259–272.

Janvier, P. 1985c. Preliminary description of Lower Devonian Osteostraci from Podolia (Ukrainian S.S.R.). Bulletin of the British Museum (Natural History): Geology 38: 309–334.

Janvier, P., and M. J. Newman. 2005. On *Cephalaspis magnifica* Traquair, 1893, from the Middle Devonian of Scotland, and the relationships of the last osteostracans. Transactions of the Royal Society of Edinburgh: Earth Sciences 95: 511–525.

Lankester, E. R. 1868. A Monograph of the Fishes of the Old Red Sandstone of Britain. Part I. The Cephalaspidae. Monograph of the Palaeontographical Society, London, 62 pp.

Otto, M., and M. Laurin. 1999. Osteostracan tesserae from the Baltic Middle Devonian: morphology and microanatomy. Neues Jahrbuch für Geologie und Paläontologie. Monatshefte 1999: 464–476.

Otto. M., and M. Laurin. 2001. Microanatomy of the dermal skeleton of *Balticaspis latvica* (Osteostraci, Middle Devonian). Journal of Vertebrate Paleontology 21: 186–189.

Ritchie, A. 1967. *Ateleaspis tessellata* Traquair, a non-cornuate cephalaspid from the Upper Silurian of Scotland. Journal of the Linnean Society, Zoology 47:69–81.

Sahney, S. and Wilson, M. V. H. 2001. Extrinsic labyrinth infillings imply open endolympatic ducts in Lower Devonian osteostracans, acanthodians and putative chondricthyans. Journal of Vertebrate Paleontology 21:660-669.

Sansom, R. S. 2008. The origin and early evolution of the Osteostraci (Vertebrata): a phylogeny for the thyestiids. Journal of Systematic Palaeontology 6:317–332.

Sansom, R. S. 2009. Phylogeny, classification and character polarity of the Osteostraci (Vertebrata). Journal of Systematic Palaeontology 7:95–115.

Sansom, R. S., S. A. Rodygin, and P. C. J. Donoghue. 2008. The anatomy, affinity and phylogenetic significance of *Ilemoraspis kirkinskayae* (Osteostraci) from the Devonian of Siberia. Journal of Vertebrate Paleontology 28: 613–625.

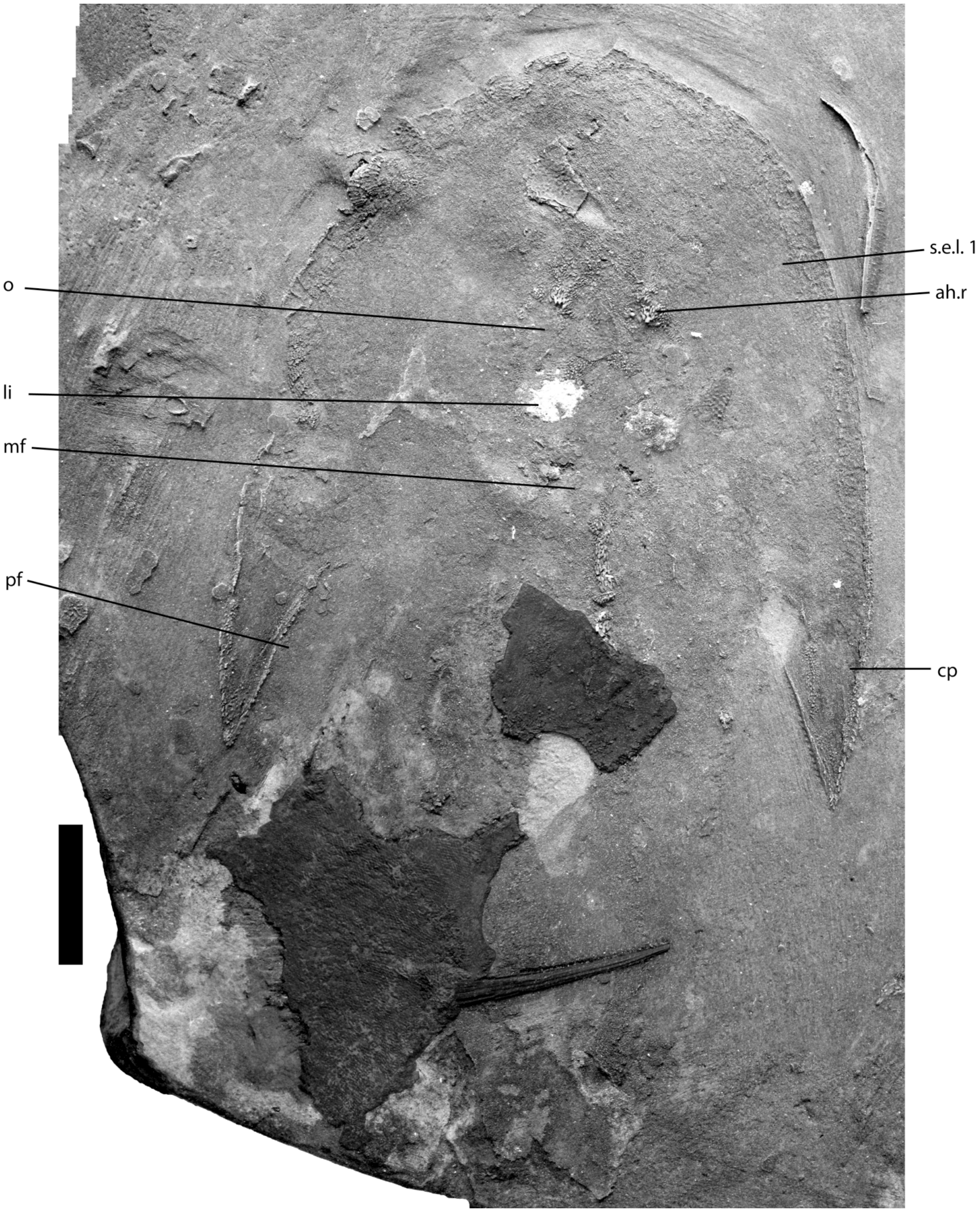
Stensiö, E. A. 1927. The Devonian and Downtonian vertebrates of Spitzbergen. 1. Family Cephalaspidae. Skrifter om Svalbard or Nordishavet 12:1–391.

Stensiö, E. A. 1932. The cephalaspids of Great Britain. British Museum (Natural History), London, 220 pp.

Voichyshyn, V. 2006. New osteostracans from the Lower Devonian terrigenous deposits of Podolia, Ukraine. Acta Palaeontologica Polonica 51: 131–142.

White, E. I., and H. A. Toombs. 1983. The cephalaspids from the Dittonian section at Cwm Mill, near Abergavenny, Gwent. Bulletin of the British Museum of Natural History (Geology) 37:149–171.

FIGURE 7.1. A composite image of UALVP 42648, the type and only specimen of *Ceramantyx odontotos* gen. et sp. nov., in dorsal view. A headshield and anterior portion of the trunk, with an acanthodian (highlighted in black) overlying the left side of the trunk. The scale bar is equal to 10 mm.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cp

FIGURE 7.2. Detailed images of the holotype of *Ceramantyx odontotos*, gen. et sp. nov. **A,** the dorsal scales of the anterior end of the trunk. **B,** tesserae at the base of the cornual process, possibly from the lateral field. **C**, the orbits, including the antorbital horns. **D**, margin of the headshield at the anterior end of the headshield. Boxes on composite images relate to the location of specific images. The scale bar is equal to 10 mm.

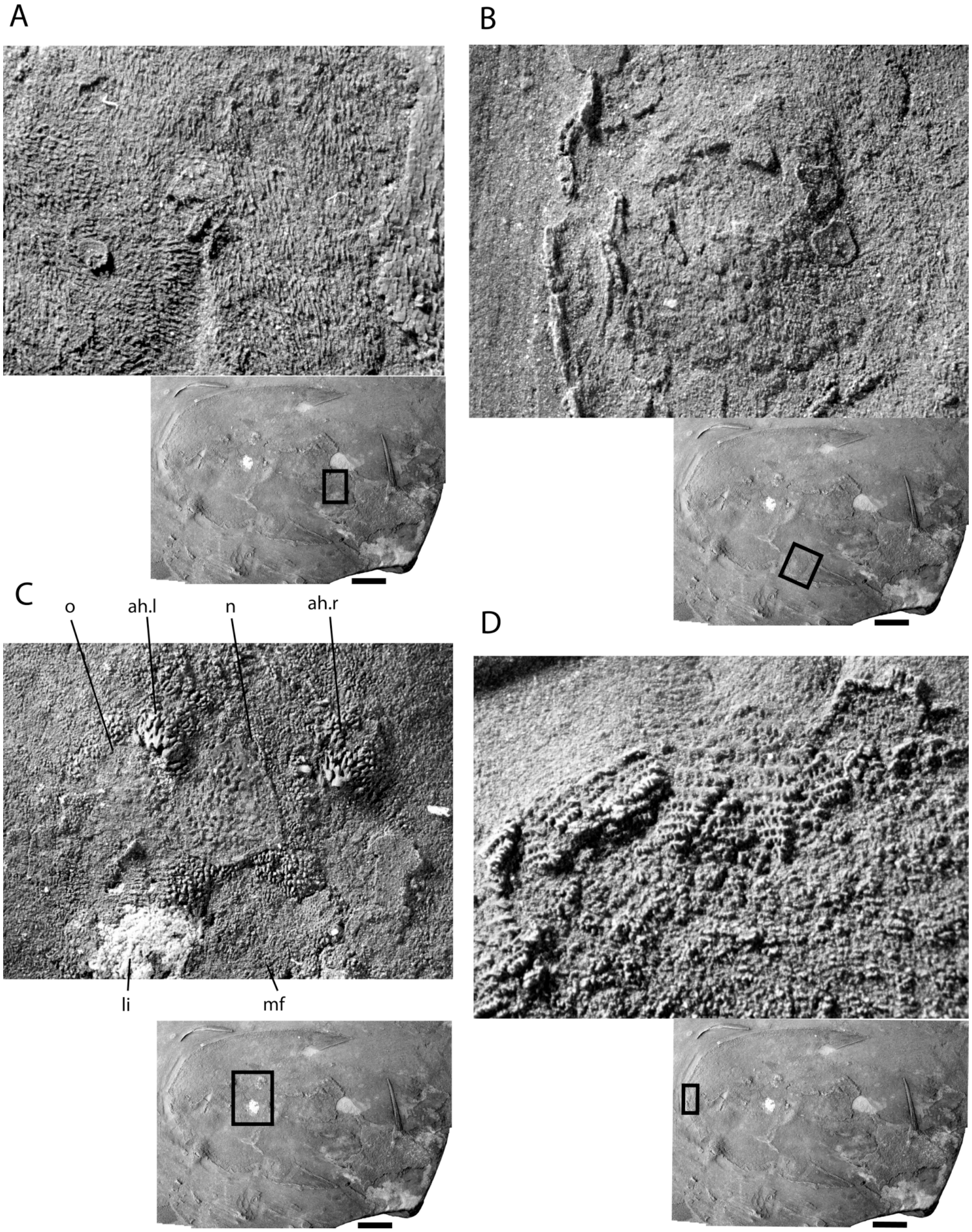

A
B
C
o
ah.l
n
ah.r
li
mf
D

FIGURE 7.3. More detailed images of the holotype of *Ceramantyx odontotos*, gen. et sp. nov. **A,** dermal tesserae in visceral view, note the radiating canals at the periphery of each plate. **B,** the median dorsal crest of the headshield, posterior to the median field. **C**, the cornual process and pectoral fin. D, detailed image of the plates forming the margin of the headshield. Boxes on composite images relate to the location of specific images. The scale bar is equal to 10 mm.

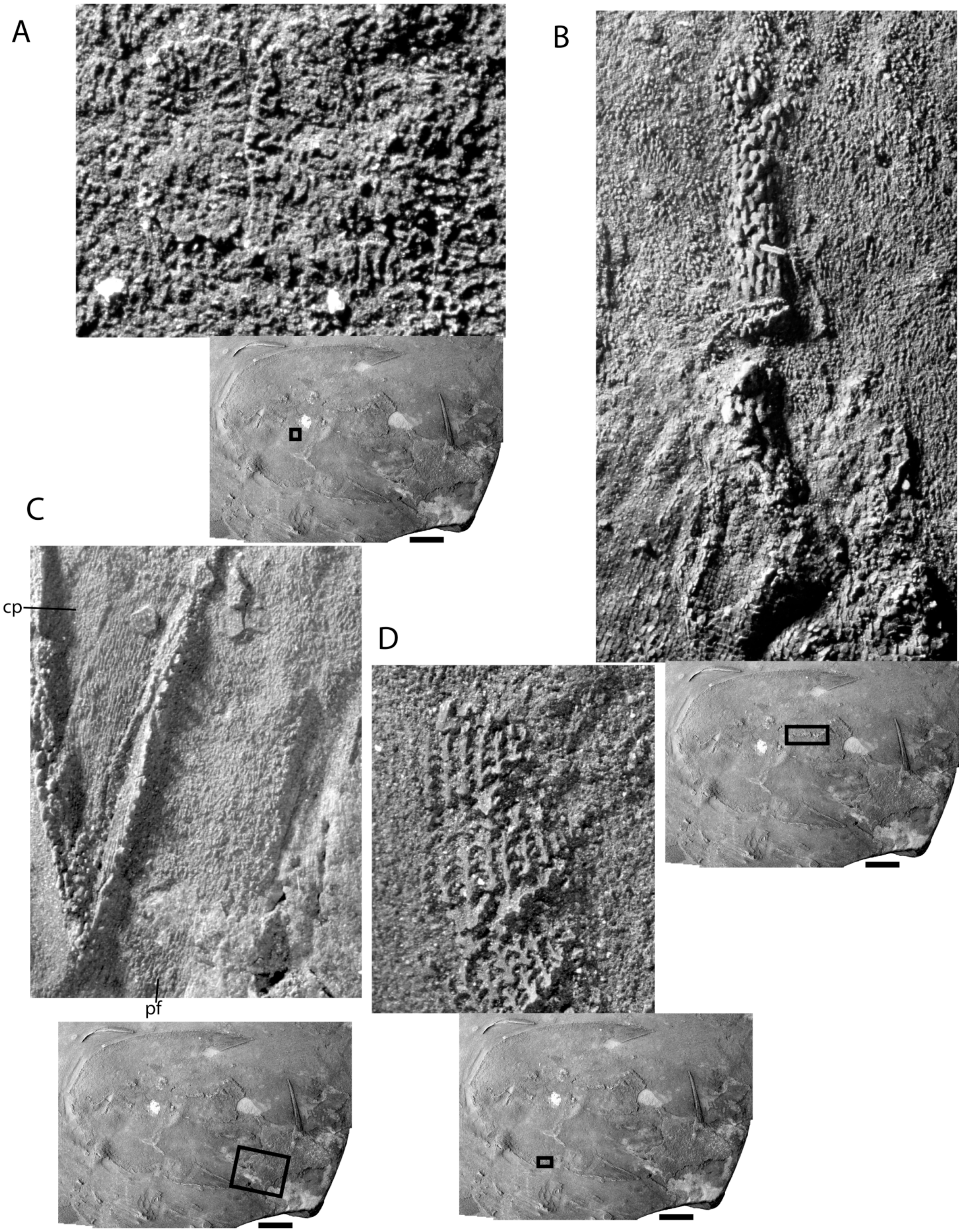

A
B
C
cp
pf
D

FIGURE 7.4. *Ceramantyx*, gen. nov., sp. indet. Type 1. **A**, a whole-specimen image of UALVP 23194, *Ceramantyx* sp. indet. Type 1. **B**, scales and tesserae from *Ceramantyx* sp. indet. Type 1, that may belong to UALVP 23194, or may represent a second individual. **C**, detailed image of the lateral margin of the headshield of *Ceramantyx* sp. indet. Type 1, UALVP 23194. Scale bars equal 10 mm.

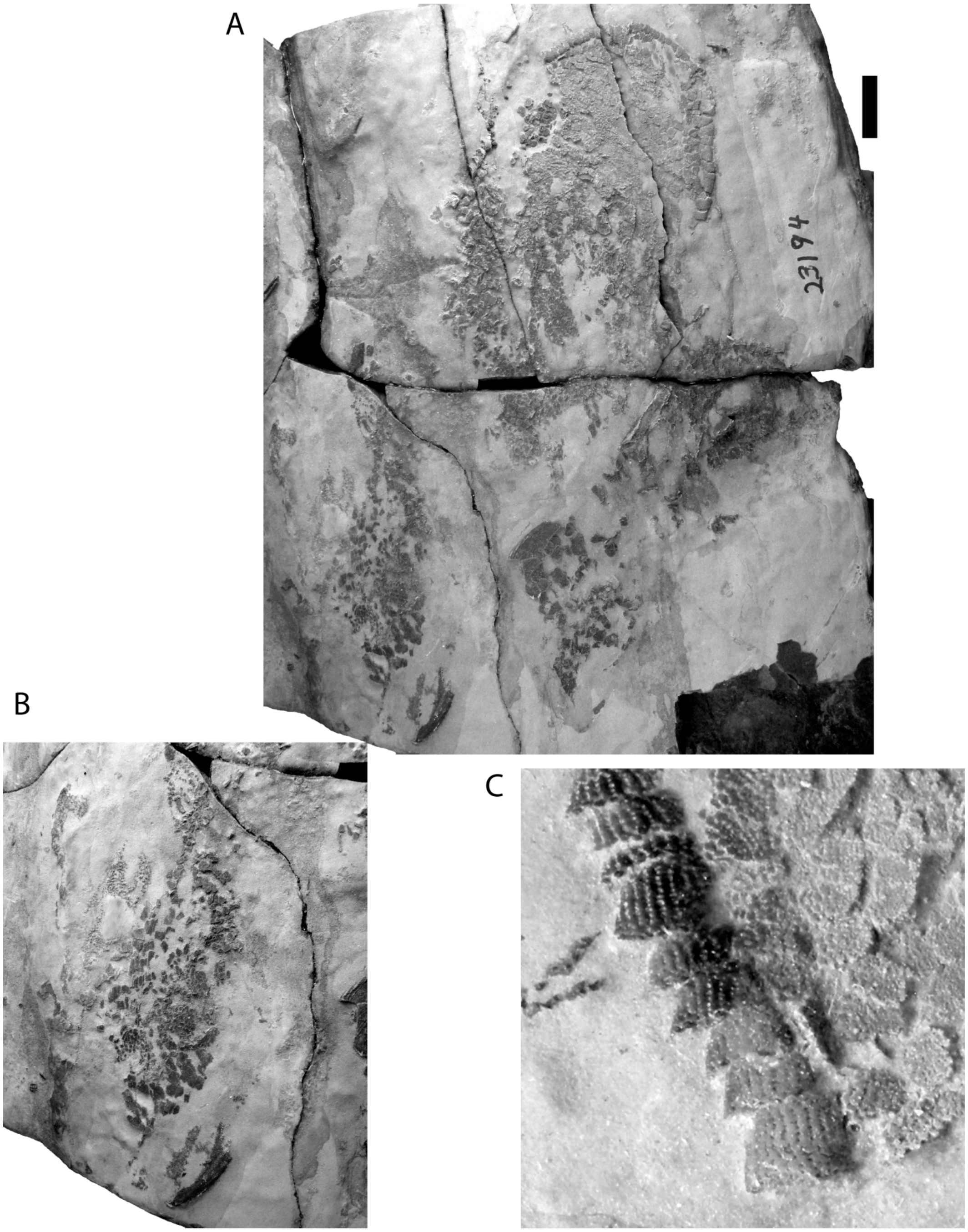

A
23194
B
C

FIGURE 7.5. *Ceramantyx* sp. indet. Type 2, UALVP 41476, the right half of a dorsal headshield in ventral view. Scale bars equal 10 mm.

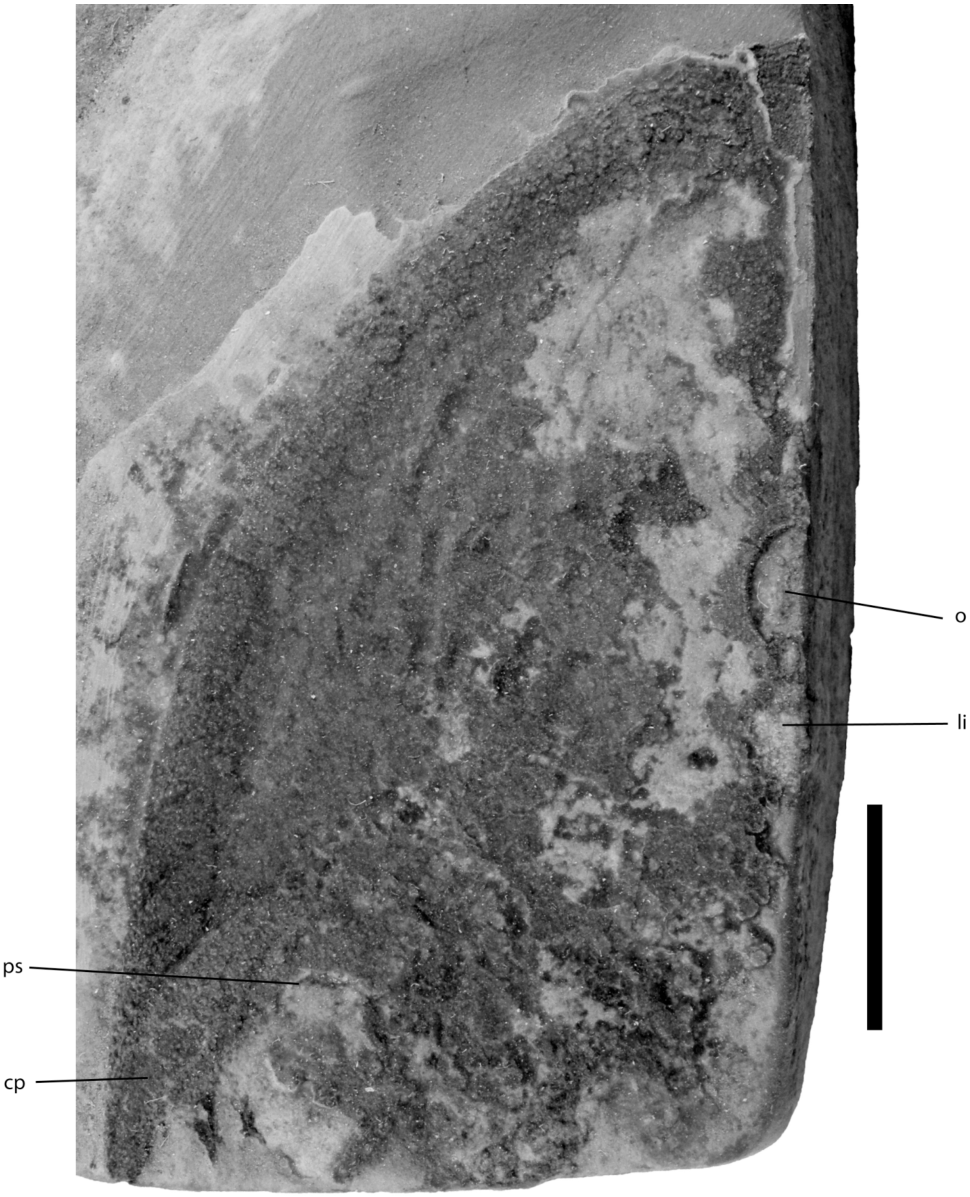

o
li
ps
cp

FIGURE 7.6. Specimens of *Ancyraspis enormis*, gen. et sp. nov., including **A**, a composite image of the holotype, UALVP 43638, a partial headshield and trunk in ventral view, and **B**, UALVP 43692, the paratype, a disarticulate concentration of trunk scales. **C**, a detailed image of the left cornual process, in particular the lateral margin of the cornual process. UALVP 43638 was not coated in ammonium chloride. Scale bars equal 10 mm.

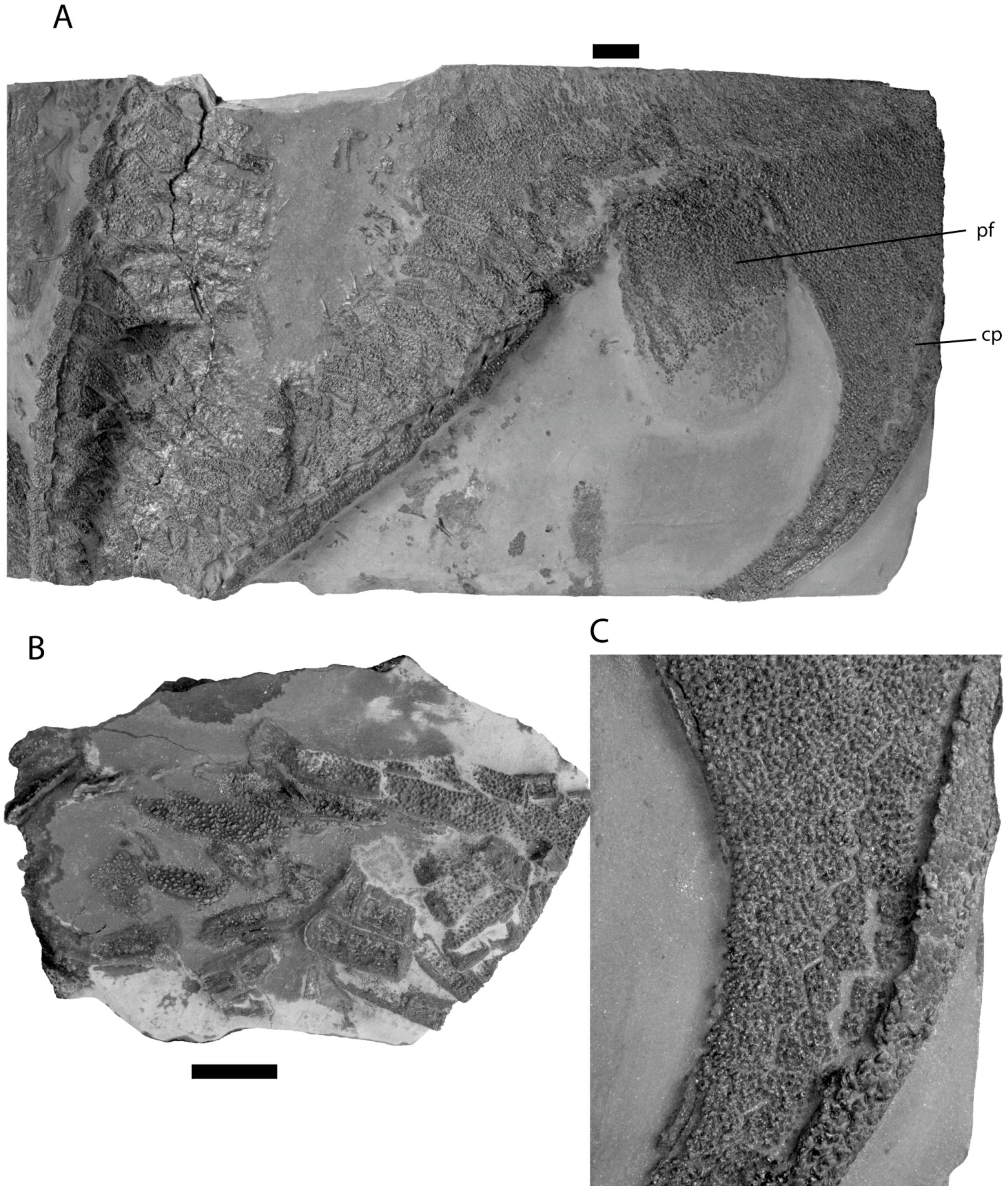

A
pf
cp
B
C

FIGURE 7.7. Indeterminate osteostracan taxon from the MOTH locality. Osteostraci indeterminate, UALVP 33028, a partial headshield in **A**,ventral view and, **B**, dorsal view. **C**, magnified image of boxed area in A showing headshield margin and supraoral field. Scale bars equal 10 mm

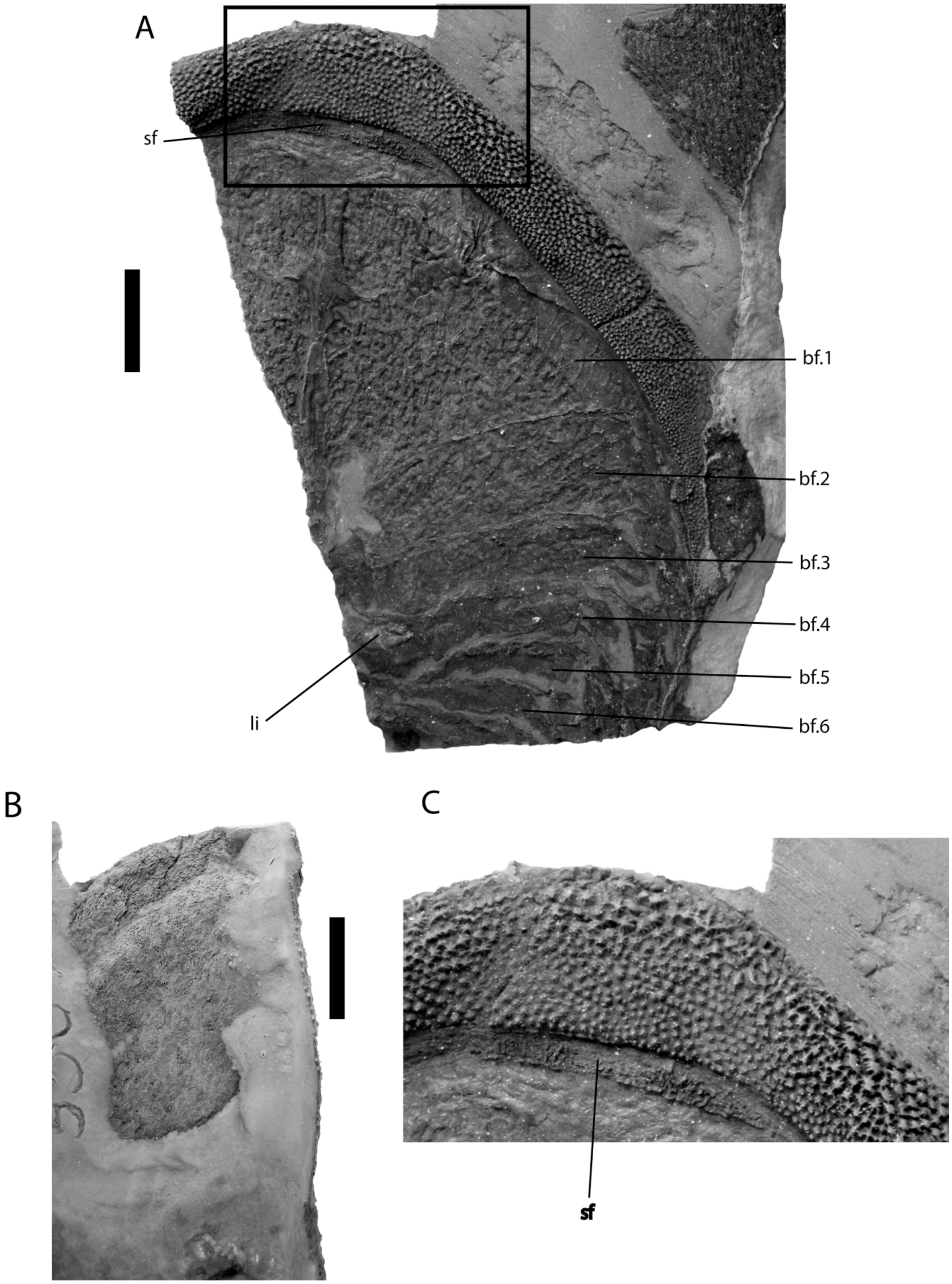
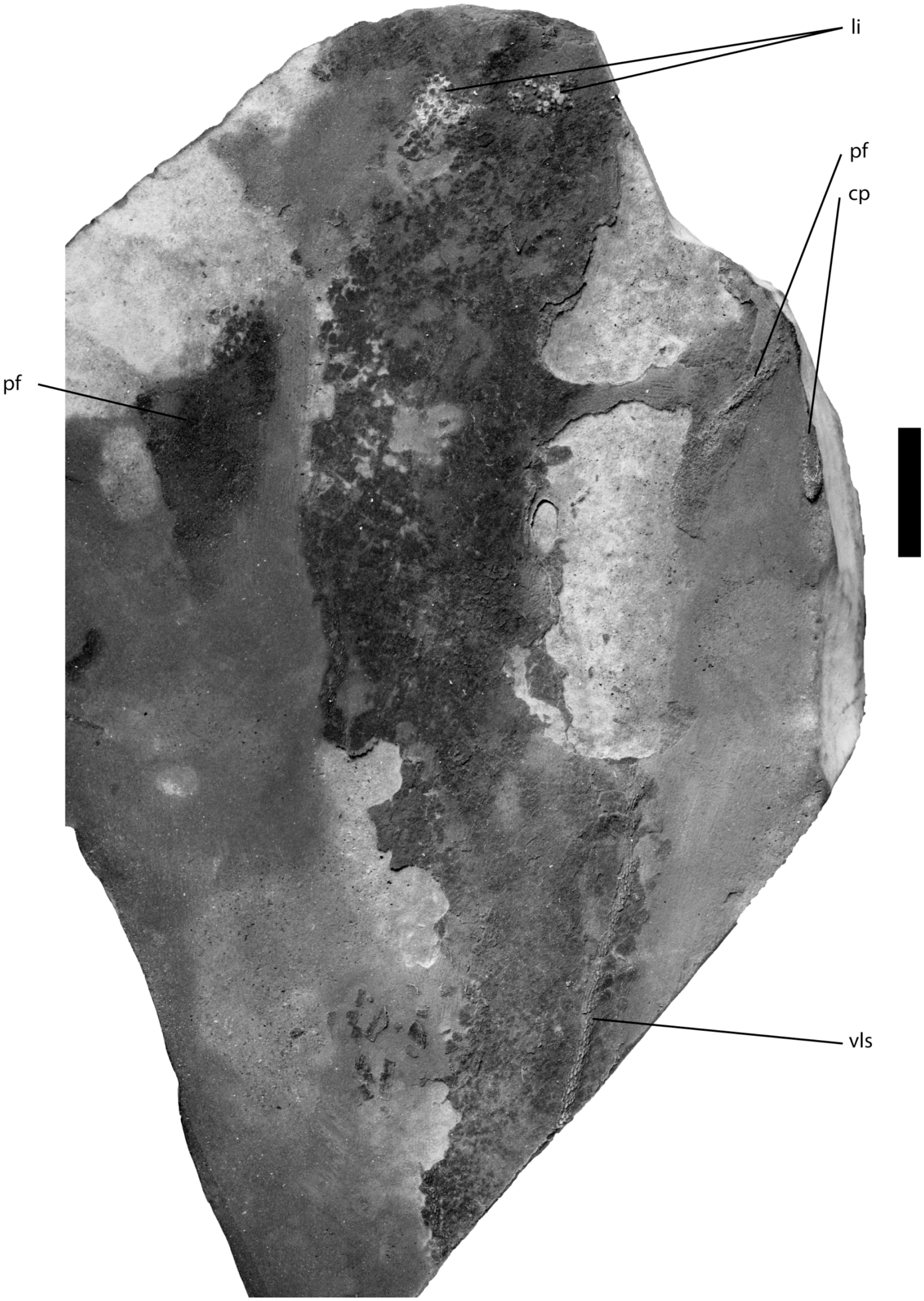

A
sf
bf.1
bf.2
bf.3
bf.4
bf.5
bf.6
li
B
C
sf

Fig. 7.8. Cornuata indet. A composite image of UALVP 41453, the posterior half of a headshield and articulated trunk in ventral view. Scale bar equals 10 mm


li
pf
cp
pf
vls

CHAPTER 8

THE PHYLOGENY AND BIOGEOGRAPHY OF THE OSTEOSTRACI WITH THE INCLUSION OF NEW TAXA FROM THE MOTH LOCALITY, NORTHERN CANADA

INTRODUCTION

Previous chapters (Chapters 3–7) of this study have briefly discussed the classification and relationships of the new osteostracan taxa described from the Man On The Hill (MOTH) locality, Northwest Territories, Canada, but have not examined the new taxa by means of a formal cladistic analysis. A phylogenetic analysis based on the data and results of Sansom (2009a) will herein include those new genera from MOTH for which specimens are sufficiently complete to provide a reliable placement within the Osteostraci. These genera are: *Acerocephale*, *Glabrapelta*, *Dentapelta*, and *Ceramantyx*. The hypotheses of previous chapters will be tested here, in particular the classification of *Acerocephale* within the Ateleaspididae, and the monophyly of the Superciliaspididae are of interest.

Because of the importance of osteostracans in the biostratigraphic correlations of vertebrate localities during the Late Silurian and the Early Devonian (Long, 1993), a reconstruction of the biogeographic distributions of the Osteostraci (as in Sansom, 2009b) is based on the new phylogeny produced here, primarily focusing on the geographic importance of the MOTH locality and its fauna. Previous examinations of the biogeographic distributions of osteostracans (Blieck et al., 1987; Sansom, 2009b) have found a close association between the osteostracan faunas of Spitsbergen and Podolia (Ukraine), as well as similarities between the faunas of Spitsbergen and those of northern Canada (Dineley, 1994; Adrain and Wilson, 1994). There does not appear to be any osteostracan taxon shared between MOTH and Avalonia, but it should be noted that many of the osteostracan taxa from Great Britain that were described by Stensiö (1932) have been attributed to *Cephalaspis* on the basis of generalized cornuate osteostracan characters (Janvier, 1985a; Sansom, 2009a), and many of the specimens are incomplete. Janvier and Blieck (1993) remarked that the Early Devonian osteostracan diversity of North America is limited to only a handful of taxa; however, previous chapters, and more recent studies (Adrain and Wilson, 1994; Dineley, 1994) show a vast diversity of North American osteostracans, primarily from the Zenaspidida. The MOTH locality is of particular interest because it represents a topographic low on the continental shelf, below storm wavebase (Zorn et al., 2005), representing a much deeper marine environment than either Spitsbergen (Blomeier et al., 2003) or Podolia (Voichyshyn, 2006). Overall, MOTH contains some examples of osteostracan diversity characteristic of Euramerica (Laurentia, Baltica, and Avalonia terranes) (Janvier and Blieck, 1993) in the presence of *Waengsjoaspis* and *Machairaspis*, as *Machairaspis* has been reported from Spitsbergen, Podolia, and Prince of Wales Island (Janvier, 1985a; Janvier, 1985b; Dineley, 1994), but much of the osteostracan diversity at MOTH is endemic.

ANALYSES

Phylogenetic Analysis

Limitations of Sansom's (2009a) Dataset—The phylogenetic analysis presented in this study is based on the characters and taxa of Sansom (2009a) as this is the most comprehensive cladistic analysis of osteostracans, including the greatest number of osteostracan taxa. Unfortunately, due to the breadth of Sansom's analysis, there are certain limitations that will be summarized here. There are more taxa than there are informative characters for the phylogeny of the Osteostraci (77 taxa, and only 64 informative characters for osteostracan inter-relationships, Sansom, 2009a); this leads to polytomies because it relies on combinations of characters to define lower level clades, including reversals, rather than individual diagnostic characters. Sansom (2009a) includes numerous taxa, however, as they are required to polarize the characters both for, and within, each osteostracan clade. Reducing the number of taxa will result in paraphyletic grades forming clades, the characters that support them would otherwise be plesiomorphic. The result of having more taxa than informative characters is that there are numerous possible most-parsimonious trees and the preferred topology only involves the most commonly established clades, rather than a single topology that requires fewer changes in character state than the others. Unfortunately the numerous taxa are necessary to establish character polarity.

Here the taxa from Sansom's (2009a) phylogenetic analysis are all included despite of the reduced support for the resulting topology, as they retain the character polarity from his analysis. This will ensure that any changes to topology or character polarity with the addition of the new osteostracan taxa from MOTH will only be the result of the addition of those taxa.

Alterations to Sansom's (2009a) Dataset—The coding of characters for

Superciliaspis varies from that of Sansom (2009a) based on specimens from the UALVP collections and re-examination of the originally described specimens from GSC locality 69014 (Dineley and Loeffler, 1976). In particular the following changes are made: the lateral fields extend onto the cornua, but not to the tips, the infraorbital sensory line passes medial to the lateral fields, and the raised rim of the headshield margin is questioned.

Several of the characters described by Sansom (2009a) do not include a state that represents the range of conditions observed among the Osteostraci, after inclusion of the new taxa from MOTH. Other characters do not accurately differentiate the conditions seen among osteostracans. The states and codings for some of the characters of Sansom (2009a) were altered for this analysis. A description of the changes to the characters of Sansom (2009a) is provided here, along with brief descriptions for the codings of the new taxa for characters of particular interest.

The data matrix of Sansom (2009a) is used for this analysis. The original character descriptions of Sansom's (2009a) analysis are provided here verbatim. Modifications or comments to Sansom's (2009a) characters, based on new taxa or examination of new specimens of *Superciliaspis*, are provided below individual characters.

External Headshield Morphology

Sansom (2009a: 101) character (Ch.) 1. "Median rostral extensions: (0) absent; (1) present. Rostral extensions in the form of processes and lobes are known in a number of disparate taxa. *Tauraspis rara* Mark-Kurik and Janvier, 1995, represents a unique case not possessing an anterior process of the shield in the median line, but two symmetrical anterolateral processes."

Sansom (2009a: 101) Ch. 2. "Rostral extension: (0) short and curved: (1) prolonged with near parallel lateral margins. *Rostral* extensions can be in the form of lobes (e.g. *Hoelaspis*, *Wladysagitta*) or straight thin processes (e.g. *Belonaspis*, *Dicranaspis*); no intermediate stages are known (Fig. 4)."

Sansom (2009a: 101) Ch. 3. "Terminal or dorsal oral notch: (0) absent; (1) present. Both *Acrotomaspis* and *Gustavaspis* have a terminally positioned oral notch as defined by Janvier (1981a: 113)."

Sansom (2009a: 101) Ch. 4. "Lateral fields: (0) absent; (1) present. Arsenault and Janvier (1995) and Janvier and Arsenault (1996) state that *Escuminaspis* (synonym of *Alaspis*) and *Levesquaspis* lack lateral fields and this is confirmed by observations. *Trewinia magnifica* Traquair, 1893, may also lack lateral fields; the gap between the lateral margin of the headshield and the larger central tesserae may represent a thin lateral field akin to that seen in *Parameteoraspis* or may be a preservational artefact (Janvier and Newman 2005). Observations of the material fail to inform upon this problem."

Sansom (2009a: 101) Ch. 5. "Lateral field division: (0) absent; (1) present."

Sansom (2009a: 101) Ch. 6. "Lateral field is divided: (0) once into two units; (1) divided twice, into three units; (2) divided three times, into four units. The lateral field is divided into two units in the tremataspidids *Trematapis* and

Oeselaspis as well as in *Axinaspis* (a kiaeraspidid). Certain other kiaeraspidids show further subdivision (i.e. three units in *Nectaspis* and four units in *Acrotomaspis* and *Gustavaspis*). Lateral field subdivision has also been observed in some *Dicranaspis* (a boreaspidid) species (Janvier 1985[a]; Wangsjø 1952). This, however, has not been observed to be the case for the type species, *D. gracilis*."

Sansom (2009a: 101) Ch. 7. "Lateral field posteriormost point: (0) posterior to the level of the external opening of the endolymphatic ducts; (1) anterior to this level. In cases of lateral field subdivision, the posterior-most point of the posterior division is used (Fig. 4)."

Sansom (2009a: 101) Ch. 8. "Lateral field anteriormost point: (0) anterior to the level of the nasal division of the hypophysial opening; (1) level or posterior to the nasal division (Fig. 4)."

Sansom (2009a: 102) Ch. 9. "Lateral fields shape: (0) narrow (maximum width between 7–30% of maximum length); (1) short and broad (maximum width over 30% of maximum length); (2) extremely narrow and confined to lateral margin of shield (maximum width less than 7% of maximum length). These first two character states were identified by Sansom (2008). An additional character state is identified here by expanding the quantitative investigation to non-thyestiid taxa. This new character state (extremely narrow) is known in only *Parameteoraspis* and *Hildenaspis* (Fig. 4)."

Sansom (2009a: 102) Ch. 10. "Lateral fields extending onto the abdominal division posterior to the pectoral sinus: (0) absent; (1) present. Lateral fields extending onto the abdominal division are known in disparate taxa, such as the kiaeraspidids, some boreaspidids and *Didymaspis* (Fig. 4).”

Sansom (2009a: 102–103) Ch. 11. “Lateral fields’ relation to cornua: (0) not reaching the cornua; (1) extends on to the cornua; (2) extends right to the tip of the cornua. Janvier (1981a, 1985[a]) defines the cephalaspidids as possessing a lateral field extending onto the cornual process. The condition is also observed to occur in a number of other taxa. In both *Hildenaspis* and *Parameteoraspis*, the lateral field is observed to extend to the very tip of the cornua (Fig. 4).”

Sansom (2009a: 103) Ch. 12. “Lateral field posterior widening: (0) absent; (1) present. Janvier (1985[a]) defines the Zenaspididae (*Zenaspis*, *Diademaspis* and *Tegaspis*) on the basis of a posteriorly enlarged lateral field. This condition is observed to occur in other taxa including *Wladysagitta*, *Ectinaspis* and some benneviaspidids (Fig. 4).”

Sansom (2009a: 103) Ch. 13. “*Median field: (0) absent; (1) present. The presence of a median field is an autapomorphy of the Osteostraci.”

Sansom (2009a: 103) Ch. 14. “Median field posterior: (0) a single point; (1) rounded; (2) flat; (3) bilobate; (4) trilobate (Fig. 4).”

Character (Ch.) 14: the posterior margin of the median field in *Dentapelta* is coded as bilobate based on the holotype, despite the paratype UALVP 43640 having a rounded posterior margin, as the depth of the median field and surrounding dermoskeleton is preserved in the holotype, NMC 21554, but not UALVP 43640.

Sansom (2009a: 103) Ch. 15. “Median field separation from the pineal plate or foramen: (0) absent; (1) present."

Sansom (2009a: 104) Ch. 16. "*External endolymphatic ducts: (0) absent; (1) present. Character 22 of Donoghue et al. (2000) and Donoghue and Smith (2001)."

Sansom (2009a: 104) Ch. 17. "External endolymphatic openings' location in relation to median field: (0) internal; (1) external."

Sansom (2009a: 104) Ch. 18. "Pineal plate: (0) absent; (1) present."

Sansom (2009a: 104) Ch. 19. "*External pineal opening: (0) covered; (1) uncovered. Character 4 of Donoghue et al. (2000) and Donoghue and Smith (2001)."

Sansom (2009a: 104) Ch. 20. "Pineal foramen lateral widening: (0) absent; (1) present. Variation is observed in the shape of the pineal foramen of Osteostraci – the plesiomorphic condition being circular whilst a derived condition being laterally widened, with width far exceeding length (Fig. 4)."

Sansom (2009a: 104) Ch. 21. "Interorbital distance: (0) less than or equal to one orbital breadth; (1) greater than one orbital breadth. This quantitative character was defined by Sansom (2008)."

Ch. 21: although there is variation in the orbit width in specimens of *Superciliaspis*, the least distorted specimens of *Superciliaspis* show a circular orbit with a width equal to or slightly larger than the interorbital distance. (e.g., UALVP 32485, in Chapter 6).

Sansom (2009a: 104) Ch. 22. "*Sclerotic ossicles: (0) absent; (1) present. Character 81 of Donoghue et al. (2000) and Donoghue and Smith (2001)."

Sansom (2009a: 104–105) Ch. 23. “Rim surrounding the orbits: (0) absent; (1) present. In some taxa, including both zenaspidids and cephalaspidids, the cephalic shield surrounding the orbits is dorsally raised, forming an orbital rim. The condition is typified by *Diademaspis* (Janvier 1985[a]: figs 100, 101).”

Sansom (2009a: 105) Ch. 24. “*Median dorsal opening: (0) absent; (1) present. The median dorsal opening is an autapomorphy of the Galeaspida.”

Sansom (2009a: 105) Ch. 25. “*External nasal opening: (0) single median; (1) paired. Character 14 of Donoghue et al. (2000) and Donoghue and Smith (2001).”

Sansom (2009a: 105) Ch. 26. “*Nostrils’ placement: (0) dorsal; (1) terminal/ventral. Adapted character 45 of Goujet and Young (1995).”

Sansom (2009a: 105) Ch. 27. “Circum-nasal depression: (0) absent; (1) present.”

Ch. 27: The compression of the headshield gives the impression of an absence of the circumnasal depression, but a triangular (Ch. 28) impression is noted in some specimens of *Superciliaspis* and the coding for *Superciliaspis* is here altered accordingly.

Sansom (2009a: 105) Ch. 28. “Circum-nasal depression shape: (0) triangular; (1) oval (Fig. 4).”

Sansom (2009a: 105) Ch. 29. “Nasohypophysial opening shape: (0) round; (1) slit shaped; (2) possesses a constriction between nasal and hypophysial divisions; (3) split into nasal and hypophysial divisions. The nasohypophysial opening demonstrates a large degree of variation within the Osteostraci (Janvier

1985[a]: 110). The plesiomorphic condition is a slit with a constriction between the nasal and hypophysial divisions. Derived conditions include the round shape of *Ilemoraspis* and *Tannuaspis*, a slit shape (i.e. without constriction) observed in *Parameteoraspis* and some thyestidiids. In some taxa (i.e.*Waengsjoeaspis* and *Nectaspis*), the constriction is such that the nasal and hypophysial divisions are separate (Fig. 4)."

Sansom (2009a: 105) Ch. 30. "Hypophysial division expansion (i.e. greater in size than nasal division): (0) absent; (1) present. In those taxa that possess a constriction between the nasal and hypophysial divisions, there is variation with regards to the proportions of the divisions. An expanded hypophysial division (i.e. the anterior division) is used by Janvier (1985[a]) to define the zenaspidids (i.e. 'scolenaspidians') (Fig. 4)."

Sansom (2009a: 105) Ch. 31. "Infra-orbital sensory line: (0) makes a loop over the lateral field; (1) passes more medially closer to the nasohypophysial opening, failing to cross the lateral field. See Sansom (2008) for a discussion."

Sansom (2009a: 105) Ch. 32. "*Festooned pattern of sensory canals on dorsal headshield: (0) absent; (1) present. Presence of this character is an autapomorphy of the Galeaspida."

Sansom (2009a: 105) Ch. 33. "*Median transverse canals: (0) two or more; (1) one. Character 30 of Zhu and Gai, (2006), uniting eugaleaspidiform and polybranchiaspidid galeaspids."

Sansom (2009a: 105) Ch. 34. "*Lateral transverse canal: (0) absent; (1) present. Adapted from character 32 of Zhu and Gai (2006)."

Sansom (2009a: 105) Ch. 35. "*Posterior supraorbital sensory canal: (0) absent; (1) present. Character 39 of Zhu and Gai (2006), uniting eugaleaspidiform and polybranchiaspidid galeaspids."

Sansom (2009a: 105) Ch. 36. "Cornual extensions: (0) absent; (1) present; (2) 'vestigial'. Cornual extensions of the headshield are absent in the non-cornuates, kiaeraspidids, *Didymaspis* and some species of *Benneviaspis*. Certain boreaspid taxa (*Belonaspis*, *Spatulaspis*, *Tauraspis* and possibly *Hapilaspis*) have extremely reduced cornua-like structures, similar to those of other Osteostraci, including kiaeraspidids. The tremataspidids pose a problem with regard to homology of endoskeletal extensions and cornua, discussed by Sansom (2008). Here, they are treated as lacking cornua, but possessing endoskeletal extensions (character 42)."

Ch. 36: *Acerocephale* is coded as excluding these cornual extensions, as supported in Chapter 3; however, a separate analysis was also run where *Acerocephale* was coded as missing this character; the resulting differences in topology, if any, are described below.

Sansom (2009a: 105) Ch. 37. "Cornua shape: (0) thin; (1) broad and flat. Janvier (1985[a]) considers a number of character states for the length and width of cornua for different groups. The majority of this variation is considered as continuous and homoplastic. Only one distinct character state is observed for cornual shape – the cornua of *Parameteoraspis*, *Escuminaspis*, *Levesquaspis*, *Balticaspis*, *Trewinia* and *Diademaspis*, which are all flat, extremely broad and nearly triangular (Fig. 4)."

Sansom (2009a: 105) Ch. 38. “Cornual plate: (0) absent; (1) present. *Trewinia*, *Balticaspis*, *Escuminaspis* and *Superciliaspis* are all observed here to possess a long thin plate on the postero-medial edge of the cornual process, occasionally disarticulated. This cornual plate is not seen in any other osteostracan taxa.”

Sansom (2009a: 105) Ch. 39. “Posterolateral margin of the shield curvature direction: (0) medial; (1) posterior; (2) straight; (3) lateral. This character concerns the curvature of the cornual process in relation to the lateral margin of the cephalic shield as demonstrated in Fig. 4.”

Sansom (2009a: 105) Ch. 40. “Pectoral sinus in relation to the level of orbits: (0) posterior; (1) level or anterior (Fig. 4).”

Sansom (2009a: 105) Ch. 41. “Abdominal division of the shield length: (0) less than twice the distance between the nasohypophysial opening and the level of the external openings of the endolymphatic ducts; (1) more than twice this distance. This quantitative character was defined by Sansom (2008).”

Sansom (2009a: 105) Ch. 42. “Posterolateral endoskeletal extensions lateral to abdominal division: (0) absent; (1) present. This character is discussed by Sansom (2008) in relation to homology with cornual processes. The extensions observed in *Dartmuthia*, *Saaremaaspis*, *Aestiaspis*, *Tyriaspis*, *Sclerodus* and *Tannuaspis* are not considered as homologous with cornua by reason of the absence of a pectoral sinus. The condition in *Didymaspis* is considered to be unique.”

Sansom (2009a: 105) Ch. 43. “Vertical impressions (‘fused scales’) on the posterior of abdominal division: (0) absent; (1) present.”

Sansom (2009a: 105) Ch. 44. “Dorsal spinal process: (0) absent; (1) present.

Sansom (2009a: 105) Ch. 45. Dorsal spinal process height: (0) less than height of the cephalic shield; (1) greater than height of cephalic shield. Where the dorsal spine is present, variation exists with respect to its height. In this regard, there are two taxa with a spinal process far exceeding the length of any other – *Machairaspis* (Janvier 1985[a]: fig. 105) and *Superciliaspis* (Dineley and Loeffler 1976: 166; Hawthorn et al. [2008]).”

Sansom (2009a: 105) Ch. 46. “*Dorsal armour in two parts (anterior and posterior): (0) absent; (1) present. Presence of this feature is considered as an autapomorphy of placoderms (Janvier 1996).”

Sansom (2009a: 105) Ch. 47. *Median dorsal plate: “(0) absent; (1) present. Presence of this feature is considered as an autapomorphy of placoderms (Janvier 1996).”

Sansom (2009a: 105) Ch. 48. “*Body armour forming a complete ring: (0) absent; (1) present. Presence of this feature is considered as an autapomorphy of placoderms (Janvier 1996).”

Sansom (2009a: 105) Ch. 49. “Cephalic shield dorso-ventral flattening: (0) absent; (1) present. The flattening of the shield was used by Janvier (1985[a]: figs 78, 97) to define *Benneviaspis* and allied taxa. This character is difficult to assess for taxa known from compressed material and in these cases is coded as unknown. ”

Sansom (2009a: 105) Ch. 50. “*Gill opening shape: (0) pores; (1) slits. Character 27 of Donoghue et al. (2000) and Donoghue and Smith (2001).”

Sansom (2009a: 106) Ch. 51. “*Gill opening position: (0) lateral; (1) ventral. Character 31 of Donoghue et al. (2000) and Donoghue and Smith (2001).”

Sansom (2009a: 106) Ch. 52. “*Lateral external branchial openings arranged in postero-ventral slit: (0) absent; (1) present. Used by Janvier (1996) to unite Anaspida and Hyperoartia.”

Sansom (2009a: 106) Ch. 53. “Opercular flaps: (0) absent; (1) present. Character 32 of Donoghue et al. (2000) and Donoghue and Smith (2001).”

Sansom (2009a: 106) Ch. 54. “*Long branchiostegals in the hyoidean gill cover: (0) absent; (1) present. Used by Janvier (1996) to unite acanthodians and osteichthyans.”

Sansom (2009a: 106) Ch. 55. “*Jaws: (0) absent; (1) present.”

Sansom (2009a: 106) Ch. 56. “*Palatoquadrate shape: (0) omega; (1) beta shaped. This character was used by Janvier (1996) to unite acanthodians with other gnathostomes following observations by Schaeffer (1975).”

Sansom (2009a: 106) Ch. 57. “*Jaw musculature’s attachment to the palatoquadrate: (0) medial; (1) external. This character was used by Janvier (1996) to unite acanthodians with other gnathostomes following observations by Schaeffer (1975).

Sansom (2009a: 106) Ch. 58. *Mouth position: (0) terminal; (1) ventral.

Adapted from character 35 of Donoghue et al. (2000) and Donoghue and Smith (2001)."

Sansom (2009a: 106) Ch. 59. "*Oral plates: (0) absent; (1) present. Character 76 of Donoghue et al. (2000) and Donoghue and Smith (2001)."

Sansom (2009a: 106) Ch. 60. "Oralobranchial covering: (0) minute scales; (1) tesserae; (2) dermal plates; (3) one or two massive dermal plates. The majority of osteostracans, where the feature is preserved, demonstrate an oralobranchial chamber covered in tesserae, comparable in size and composition to those of the cephalic shield. *Ateleaspis* and *Aceraspis* both possess a covering of micro-scales whilst tremataspidids such as *Dartmuthia*, Tremataspids, *Saaremaaspis* and *Tyriaspis*, all possess large plates. Galeaspids and most pteraspidomorphs possess just one or two massive plates."

Ch 60: as discussed regarding *Acerocephale* in Chapter 3, the oralobranchial covering consists of minute scales in *Acerocephale*, *Aceraspis*, and *Ateleaspis*, but not in *Hirella* or *Hemicyclaspis*.

Sansom (2009a: 106) Ch. 61. "*Visceral arches fused to the neurocranium: (0) absent; (1) present. Character 52 of Donoghue et al. (2000) and Donoghue and Smith (2001)."

Sansom (2009a: 106) Ch. 62. "Disposition of the interbranchial ridges of the oralobranchial chamber roof: (0) oligobranchiate; (1) orthobranchiate; (2) nectaspidiform. The conditions of oligobranchiate (the majority of osteostracans) and orthobranchiate (benneviaspidids and most kiaeraspidids) and nectaspidiform (*Nectaspis* only) were defined by Stensiö (1958, 1964), and relate to the angles of the branchial ridges of the oralobranchial chamber in relation to the perpendicular axis."

Fins and body

Sansom (2009a: 106) Ch. 63. "Paired fins: (0) absent; (1) present. In many cases the presence of paired fins is inferred on the basis of supporting structures such as pectoral fenestrae and areas of fin attachment, rather than direct observation."

Sansom (2009a: 106) Ch. 64. "Paired fin separation from the abdominal division: (0) absent; (1) present. *Ateleaspis* and *Aceraspis* are often reconstructed with paired fins attached in some degree to the abdominal division (Heintz 1939; Westoll 1945; Ritchie 1967; Janvier 1981b, 1985[a]), unlike other Osteostraci which display a marked separation (Fig. 4)."

Ch. 64: as discussed in Chapter 3 with regard to *Acerocephale*, the paired fins are separate, as in *Hirella* and *Hemicyclaspis*, while those of *Ateleaspis* and *Aceraspis* are connected to the trunk.

Sansom (2009a: 106) Ch. 65. "Paired fins relation to cephalic shield: (0) continuous; (1) delimited at pectoral sinus. In the non-cornuates *Ateleaspis*, *Aceraspis* and *Hirella*, the squamation of the head and trunk gradually grades into the squamation of the fin. In *Hemicyclaspis* and Cornuata, the headshield forms a fused unit, with the squamation between the head and paired fin clearly delimited (Fig. 4)."

Sansom (2009a: 106) Ch. 66. "*Fin spines: (0) absent; (1) present."

Sansom (2009a: 106) Ch. 67. “*Pelvic fins: (0) absent; (1) present.”

Sansom (2009a: 106) Ch. 68. “*Dorsal fins: (0) absent; (1) present.”

Sansom (2009a: 106) Ch. 69. “Dorsal fins’ condition: (0) a single scute; (1) a single fin; (2) two fins, anterior and posterior. The occurrence of both anterior and posterior dorsal fins is known only in the non-cornuates *Ateleaspis*, *Aceraspis* and *Hirella*. Other osteostracan taxa have either a single dorsal scute (i.e. certain thyestiid taxa such as *Auchenaspis*, *Tyriaspis* and *Tremataspis*) or, as in the majority of taxa for which the area is known, a single dorsomedian fin.”

Ch. 69: the state of the dorsal fin (a potentially informative character for non-cornuate osteostracans) is not known for *Acerocephale*.

Sansom (2009a: 106) Ch. 70. “Horizontal caudal lobe: (0) absent; (1) present. The horizontal caudal lobe is often used as an apomorphy to define the Osteostraci. It is not present, however, in the thyestiids *Saaremaaspis*, *Tyriaspis*, *Tremataspis* and *Ilemoraspis*.”

Sansom (2009a: 106) Ch. 71. “*Tail condition: (0) hypocercal; (1) epicercal; (2) isocercal. Character 49 of Donoghue et al. (2000) and Donoghue and Smith (2001).”

Histology and ornament

Sansom (2009a: 106) Ch. 72. “*Three layered exoskeleton: (0) absent; (1) present. Character 71 of Donoghue et al. (2000) and Donoghue and Smith (2001).”

Sansom (2009a: 106) Ch. 73. “*Cephalic dermoskeleton bone: (0) cellular;

(1) acellular. Character 67 of Donoghue et al. (2000) and Donoghue and Smith (2001). The majority of histologically characterised Osteostraci possess osteocyte lacunae. *Escuminaspis* (a.k.a. *Alaspis*) is noted, however, by Ørvig (1965, 1968) to have a 'reduced' exoskeleton and lacks cellular bone."

Sansom (2009a: 106) Ch. 74. "*Lamellar aspidin: (0) absent; (1) present. Character 66 of Donoghue et al. (2000) and Donoghue and Smith (2001)."

Sansom (2009a: 106) Ch. 75. "*Dental lamina: (0) absent; (1) present."

Sansom (2009a: 106) Ch. 76. "*Dentine: (0) absent; (1) present."

Sansom (2009a: 106) Ch. 77. "*Dentine condition: (0) mesodentine; (1) orthodentine; (2) semidentine. Character 69 of Donoghue et al. (2000) and Donoghue and Smith (2001)."

Sansom (2009a: 106) Ch. 78. "Superficial layer of the dermoskeleton: (0) absent; (1) present only in tubercle tips; (2) present in continuous areas. Variation (i.e. continuous in tremataspidids and some other taxa) in the development of the superficial layer of Osteostraci (also known as the dentinous layer, or mesodentine) was noted by Denison (1951b) and Janvier (1985[a]–d)."

Sansom (2009a: 106) Ch. 79. "*Enamel/oid: (0) absent; (1) present. Adapted from character 70 of Donoghue et al. (2000) and Donoghueand Smith (2001). *Sacabambaspis* as per Sansom et al. (2005)."

Sansom (2009a: 106–107) Ch. 80. "Superficial glassy layer of dermal armour: (0) absent; (1) present. In some thyestiid Osteostraci, a layer of 'enameloid' is noted (Denison 1951b; Janvier 1985c) to occur overlaying the superficial/dentinous layer (a continuous layer in *Tremataspis* and *Dartmuthia*'s ventral surface, or restricted to the tubercles in *Oeselaspis* and *Dartmuthia*'s dorsal surface). Donoghue et al. (2000: 214) distinguish enamel/oid tissues from the superficial layer of thyestiid Osteostraci by reason of an absence of an enameloid–dentine junction in the latter. They are, therefore, treated as two separate characters here."

Sansom (2009a: 107) Ch. 81. "*Tessellation of the dermoskeleton: (0) absent; (1) present."

Sansom (2009a: 107) Ch. 82. "Tessellation condition: (0) formed by external circumareal canals; (1) formed by internal circum-areal canals; (2) formed by invading vascular network. The plesiomorphic condition is for tessellation of the dermoskeleton to be external (in the case of Osteostraci, formed by external circum-areal canals). The mosaic pattern of tessellation is not observed on the external surface of Osteostraci such as the benneviaspidids, kiaeraspidids and most thyestidids where the inter-areal grooves are either not apparent or consist of pores. Galeaspids demonstrate a unique condition of tessellation as defined by Wang et al. (2005)."

Sansom (2009a: 107) Ch. 83. "Tesserae fusion: (0) fused to the basal (laminar) layer; (1) loosely connected. In the tessellate Osteostraci, a developed basal (laminar) layer usually connects the tesserae, thus forming a singled fused unit for the headshield. In certain taxa, however (i.e. *Ilemoraspis*, *Escuminaspis*, *Trewinia*, *Balticaspis*, *Superciliaspis*), a 'regression' of the dermoskeleton (sensu Ørvig, 1968) has taken place and as a result the tesserae are not fused and are often disarticulated. (e.g. Hawthorn et al. [2008])."

Sansom (2009a: 107) Ch. 84. “Vascular canals (i.e. intra-areal canals) of the middle (spongy bone) layer arrangement: (0) radial; (1) irregular; (2) in parallel bundles. The intra-areal canals of the middle layer are arranged radially (i.e. radiating from a point at the centra of tesserae) in the majority of Osteostraci. In some tremataspidids the intra-areal canals form an irregular fine-meshed network and in most Benneviaspidida, parallel bundles are formed. There is generally a strong correlation between the condition of the inter- and intra-areal canals but they are treated as separate characters here (Sansom, 2008).”

Sansom (2009a: 107) Ch. 85. “Perforated horizontal lamina in the sensory-line canals and vascular system: (0) absent; (1) present. See Sansom (2008) for discussion.”

Sansom (2009a: 107) Ch. 86. “Ornamentation of dorsal surface: (0) smooth; (1) closely set tubercles; (3) narrow parallel ridges; (4) fine granulation formed from the middle layer; (5) large widely spaced tubercles; (6) embossed elevations surrounding large tubercles. See Sansom (2008) for discussion.”

Sansom (2009a: 107) Ch. 87. “*Galeaspedin (previously, aspidine) tubercles: (0) absent; (1) present. Presence of this character is considered by Zhu and Gai (2006) and Wang et al. (2005) as an autapomorphy of Galeaspida.”

Sansom (2009a: 107) Ch. 88. “Tubercles’ shape: (0) rounded/smooth; (1) costulate/ ridged; (2) oak-leaf shaped (2).”

Ch. 88: *Ceramantyx* displays the oakleaf-shaped tubercles on the plates of the margin of the headshield, and an odd denticulate ornament on the dorsal dermoskeleton. Elongate tubercles are present on the trunk and the pectoral fins;

these are generally ridged, making *Ceramantyx* polymorphic 1/2 where the *Ceramantyx* dorsal ornament is an autapomorphy of the taxon and is therefore excluded as a state, since states that can be coded as equivalent in other taxa are present. *Dentapelta* presents an ornament unique among the genera represented (Chapter 6, in particular see discussion regarding Otto and Laurin, 1999) where large denticles ornament the headshield. These denticles are smooth on top, hollow in the center, and in the large specimens they point posteriorly. The tubercles described for *Balticaspis* may be homologous (*Dentapelta* chapter again); however, the codings by Sansom (2009a) will be retained for *Balticaspis*, and here *Dentapelta* is given a separate coding for tubercle shape (3, large posteriorly pointing denticles). Though referred to as denticles, based on their posterior point, and association with individual pores, the denticles of *Acerocephale* are more elongate than, and lack the circular base of, the denticles of *Dentapelta*, and are coded as 4: small elongate posteriorly pointing denticles.

Sansom (2009a: 107) Ch. 89. “Tubercles’ distribution: (0) scattered/continuous; (1) grouped.”

Sansom (2009a: 107) Ch. 90. “Tubercles’ local size variation: (0) homogenous; (1) heterogeneous. Within individuals, tubercle size can vary dramatically, either globally or locally. Local size variation is defined here as occurring within the approximate area of a ‘tessera’ as oppose to a global size variation (e.g. small tubercles at centre of headshield, larger marginal tubercles).”

Sansom (2009a: 107) Ch. 91. “Longitudinal rows of tubercles on the abdominal division: (0) absent; (1) present. See Sansom (2008) for discussion.”

Sansom (2009a: 107) Ch. 92. "Cavities in the base of large tubercles: (0) absent; (1) present. Large tubercle cavities are observed only in *Thyestes*, *Sclerodus* and *Balticaspis*."

Sansom (2009a: 107) Ch. 93. "Marginal rim large sharp tubercles: (0) absent; (1) present."

Sansom (2009a: 107) Ch. 94. "Marginal rim dorsal surface: (0) flat; (1) thin parallel ridges; (2) a raised rim. Non-cornuate Osteostraci such as *Ateleaspis*, *Aceraspis* and *Hirella* possess thin parallel ridges lining the marginal rim of the cephalic rim, whilst most osteostracan taxa lack this feature. *Superciliaspis* uniquely possesses a raised marginal rim of the cephalic shield."

Ch. 94: the raised rim of *Superciliaspis* is not considered a valid coding, as it is considered here as resulting from taphonomic forces, resulting from a different preservational environment than other osteostracan taxa, rather than a biological condition (see the *Waengsjoeaspis* chapter for an example of a raised rim in an osteostracan from MOTH). *Superciliaspis* is instead coded as having a flat margin, as is the condition observed for most other osteostracan taxa. The margin of *Ateleaspis* is coded by Sansom (2009a) as having multiple narrow, longitudinal ridges; however, neither Ritchie (1967), nor Heintz (1939) make note of this, and instead the margin of *Ateleaspis* is composed of numerous small, elongate plates. The margin of *Acerocephale* is considered here to also possess this condition, with numerous small plates, though the pattern is not identical to that in *Ateleaspis*. Here, only *Hirella* and *Aceraspis* possess longitudinal ridges on the margin of their headshield. A third character state is coded as 2 for Character

94: margin of the headshield being composed of numerous, longitudinally elliptical plates entirely separate from one another. *Ceramantyx* also presents a unique characters state (coded as 3): margin composed of imbricated, laterally convex, rectangular plates.

Sansom (2009a: 107) Ch. 95. "Large tubercles or fused tubercles forming a short ridge laterally flanking the median field: (0) absent; (1) present."

Sansom (2009a: 107) Ch. 96. "Denticulation of the supra-oral field: (0) confined to anterior rim; (1) extending far backward into a triangle shaped supra-oral field; (2) not denticulated but heavily vascularised (2). See Sansom (2008) for discussion."

Sansom (2009a: 107) Ch. 97. "*Calcified cartilage/mineralised endoskeleton: (0) absent; (1) present."

Sansom (2009a: 107) Ch. 98. "*Perichondral ossification: (0) absent; (1) present. (Wang et al. 2005)."

Sansom (2009a: 107) Ch. 99. "Perichondral ossification condition: (0) regular; (1) cancellous. The endoskeleton in most Osteostraci is composed of regular lamellae of perichondral bone. The Boreaspididae are defined by Janvier (1985[a]) by their spongy/cancellous perichondral bone, similar in nature to the endochondral bone of Osteichthyes."

Internal Anatomy

Sansom (2009a: 107) Ch. 100. "*Neurocranium shape: (0) broad; (1) narrow and deep. Janvier (1996: 242, fig. 5.2) considers a narrow and deep neurocranium to be a synapomorphy of osteichthyans and acanthodians."

Sansom (2009a: 107) Ch. 101. "*Extensive suborbital shelf of the braincase: (0) absent; (1) present. Presence of this character was considered by Young (1986) to be a synapomorphy of placoderms and chondrichthyans, but as Janvier (1996) states, it is also known in osteostracans and galeaspids."

Sansom (2009a: 107) Ch. 102. "*Braincase fissures (i.e. ventral, otico-occipital): (0) absent; (1) present. The absence of these fissures in placoderms is noted by Young (1986), presence being a synapomorphy of osteichthyans, chondrichthyans and acanthodians."

Sansom (2009a: 107) Ch. 103. "Medial recess of the postero-ventral myodome: (0) absent; (1) present. See Sansom (2008) for discussion."

Sansom (2009a: 107) Ch. 104. "*Fusion of the nasal capsule (rhinocapsular bone) to the rest of the braincase: (0) absent; (1) present. Fusion is considered by Young (1986) as a synapomorphy of osteichthyans and chondrichthyans."

Sansom (2009a: 107) Ch. 105. "*Ossified endoskeletal sclera encapsulating the eye: (0) absent; (1) present. Character 82 of Donoghue et al. (2000) and Donoghue and Smith (2001)."

Sansom (2009a: 107) Ch. 106. "*Superior oblique eye muscle inserting in the anterior part of the orbit: (0) absent; (1) present. Presence is considered by Young (1986) as a synapomorphy of osteichthyans and chondrichthyans."

Sansom (2009a: 107) Ch. 107. "*Internal rectus eye muscle inserting in the anterior part of the orbit: (0) absent; (1) present. Presence is considered by

Young (1986) as a synapomorphy of osteichthyans and chondrichthyans."

Sansom (2009a: 108) Ch. 108. "*Eye-stalk uniting eye and braincase: (0) absent; (1) present. Presence is considered by Janvier (1996) as a synapomorphy of placoderms, chondrichthyans and stem-osteichthyans."

Sansom (2009a: 108) Ch. 109. "The maximum number of 'sel' canals leading from the labyrinth to the lateral fields: (0) five; (1) less than five. In certain tremataspidids (e.g. *Tremataspis*, *Oeselaspis*), a reduction in the number of 'sel' canals leading to the lateral field is noted to have occurred (Denison 1951a; Janvier 1985c,d)."

Sansom (2009a: 108) Ch. 110. "The 'sel' 1 canal leading to the lateral field bifurcation point: (0) between the orbit and lateral field; (1) adjacent to the lateral field; (2) adjacent to orbit. The bifurcation point of 'sel' canal 1 was used to define different families by Stensiö (1927, 1932) and Janvier (1985[a]), i.e. the cephalaspidids have a bifurcation very close to the orbit in the form of an <elbow> whilst thyestiids, benneviaspidids, kiaeraspidids and *Waengsjoeaspis* have a bifurcation point close to the lateral field. Janvier (1985[a],d) considers a bifurcation occurring between these two points as plesiomorphic."

Sansom (2009a: 108) Ch. 111. "*Marginal vein (0) absent; (1) present. An autapomorphic feature of the Osteostraci (Janvier 1996: 111), yet the condition in Galeaspida is currently under review (Z. Gai, pers. comm., 2007)."

Sansom (2009a: 108) Ch. 112. "*Semicircular canal number: (0) two; (1) three. Character 20 of Donoghue et al. (2000) and Donoghue and Smith (2001)."

RESULTS

Phylogeny

Results of the present analysis are given in Figure 8.1 as a 50% majority-rule consensus of 360 most parsimonious trees of 358 steps each. Compared to Sansom's (2009a) phylogeny, there are no changes in previously established clades, except for the removal of *Superciliaspis* from its sister relationship with *Machairaspis*, and the formation of a clade recognized here as a family within the order Zenaspidida: the Superciliaspididae (Fig. 8.1). This change occurred despite the assumption of homology between the tall dorsal spines of both *Superciliaspis* and *Machairaspis*. Such separation of these two taxa would indicate that the extension of the dorsal spine is the result of convergence, rather than a shared ancestral condition, a conclusion supported by the differences between these taxa in the morphology of this feature, as was discussed in Chapter 5.

Acerocephale is resolved as sister to *Ateleaspis* within a monophyletic Ateleaspididae (Fig. 8.1). Synapomorphies of the Ateleaspididae are the presence of two dorsal fins, the state for which is not known for *Acerocephale* (Chapter 3); pectoral fins that are continuous in ornament and dermoskeleton with the headshield; and notably, absence of cornual processes. *Acerocephale* shares with *Ateleaspis* a margin of the headshield that is made up of numerous longitudinal plates, and tesserae of the headshield that are not fused at the basal layer. Like

Hirella, *Acerocephale* has pectoral fins that are differentiated from the trunk and abdominal division (Heintz, 1939), a characteristic not shared with *Aceraspis* or *Ateleaspis* (Heintz, 1939; Ritchie, 1967). In *Aceraspis*, *Ateleaspis*, and *Acerocephale* the oralobranchial region is covered in minute platelets (Heintz, 1939; Ritchie, 1967) rather than tesserae as in *Hirella*, and the other non-cornuate osteostracan, *Hemicyclaspis* (Heintz, 1939; Stensiö, 1932).

Ceramantyx is resolved within Zenaspidida (Fig. 8.1) on the basis of a few shared characteristics with *Stensiopelta* and the Zenaspididae, rather than for synapomorphies of the whole group. The placement of *Ceramantyx* with *Stensiopelta* (Fig. 8.1) is based exclusively on the small, clustered tubercles of each and on an 'sel' 1 canal that bifurcates adjacent to the lateral field. Removal of Characters 88 or 89 of Sansom (2009a), the two ornament characters that place *Ceramantyx* in the Zenaspididae, results in the collapse of the base of Zenaspidida and removal of *Stensiopelta* and *Ceramantyx* from the Zenaspididae. All other aspects of the osteostracan phylogeny remain the same. The reliance of *Ceramantyx* on characteristics of the ornament, a highly variable feature of osteostracans (Stensiö, 1932), leaves the phylogenetic placement of *Ceramantyx* uncertain and a more thorough summary of the characteristics of this taxon is provided below.

Removal of character 86, the gross ornament of the surface of the headshield, the only character that places *Waengsjoeaspis* and 'Unnamed group D' of Sansom (2009a) basal to the Benneviaspidida, collapses the nodes between the clade of *Hildenaspis*, *Mimetaspis*, *Pattenaspis*, and *Zychaspis*, and the

‘Unnamed group D’ and the Benneviaspididae into a polytomy with the Benneviaspidida and the Thyestiida. The frequency of resolution of Zenaspidida among the most parsimonious trees is also greatly reduced. Lastly, when the coding for the presence or absence of the cornual processes (character 36 in Sansom, 2009a) is changed to ‘unknown’ for *Acerocephale*, this genus is still retained in the Ateleaspididae.

In this phylogenetic analysis. the Superciliaspididae (Chapter 5) are resolved as a clade in 100% of the most-parsimonious trees. The characters that support this clade are the high orbit width relative to the interorbital distance, and a raised border of fused plates along the median field. *Superciliaspis* and *Dentapelta* form a clade based on the absence of a pineal opening, and a median dorsal spine, though the spine for *Dentapelta* is incomplete. The Supercilaspididae are not included in the Zenaspididae in the majority rules consensus, despite sharing an expanded hypophyseal division of the nasohypophyseal opening relative to the nasal division.

DISCUSSION

Characteristics of *Ceramantyx*

As stated in Chapter 7, the classification of *Ceramantyx* is rather difficult given that it possesses a combination of characters from a variety of groups.The lateral field of *Ceramantyx* extends onto the cornua, but not to the tip; this is a condition that is widespread among primitive cornuate osteostracans and is therefore primitive for osteostracans in the subclass Cornuata. Lateral widening of the pineal opening is a synapopmorphy of the Zenaspidida, the clade of the current phylogeny that includes *Ceramantyx*, but the condition of the pineal opening is not known for *Ceramantyx*.

Ceramantyx odontotos has a rim of plates around the orbit, but there is no relief that would indicate a raised orbital rim, such as that seen in Zenaspidida, *Camptaspis*, and *Yvonaspis* (Denison, 1952; Belles-Isles, 1989; Sansom, 2009a). It is possible that the raised rim was flattened along with the rest of the specimen during taphonomy or diagenesis, and the rim of the orbit of *Ceramantyx* sp. indet. Type 2, UALVP 41476, appears to be raised, so the condition of this character remains uncertain for *Ceramantyx*. The interorbital distance, an important character for the Superciliaspididae and the Thyestiida, in *Ceramantyx* is less than the orbit width, a common condition among the Zenaspidida and the clades basal to the Benneviaspididae (Sansom, 2009a). The nasohypophyseal opening is primarily covered by a large allochthonous plate; therefore, the shape and expansion of this opening, an important set of characters among osteostracans (Janvier, 1985a), cannot be used for comparison of *Ceramantyx*.

The posterolateral margin of the headshield of *Ceramantyx* points posteriorly (Character 39 of Sansom, 2009a), a primitive condition for osteostracans. The caudal region and dorsal fin, areas that preserve characters that can differentiate the Thyestiida and the basal osteostracans (Sansom, 2009a), are not preserved in *Ceramantyx*.

The intra-areal canals of *Ceramantyx* are arranged radiating from the center of the tesserae, a condition that is likely primitive, with only the Benneviaspididae and the Tremataspididae showing different conditions (Sansom, 2009a). The homology of the ornament of *Ceramantyx* with other osteostracans is doubtful and closely set tubercles are a primitive characteristic of osteostracans (Sansom, 2009a), though the oakleaf-shaped tubercles of the headshield margin resemble those of the tesselate heterostracan *Lepidaspis* (Dineley and Loeffler, 1976) and the ornament of some other primitive vertebrates (Janvier, 1996; Gagnier, 1993). The denticles of *Ceramantyx*, particularly those of the trunk, are clustered, as are those in *Acerocephale*, *Escuminaspis* (Arsenault and Janvier, 1995), the Zenaspididae, and *Tegaspis* (Stensiö, 1927).

Cavities are present in the denticles of *Ceramantyx*, similar to those of *Dentapelta* (Chapter 6) and the tubercles of *Balticaspis*, *Sclerodus*, and *Thyestes* (Otto and Laurin, 2001; Stensiö, 1927), but the denticles of *Ceramantyx* are much smaller than those of the other taxa.

As in Superciliaspididae, the median field of *Ceramantyx* is bordered by thick, fused ridges. The borders of the median fields of *Waengsjoeaspis* (Sansom, 2009a) and many members of the Thyestiida (Sansom, 2009a) are also formed from thickened ridges of dermoskeleton. The 'sel' 1 canal of *Ceramantyx* bifurcates adjacent to the lateral field, a condition shared with *Stensiopelta* (Janvier, 1985b), the Benneviaspidida and Thyestiida (Sansom, 2009). Primitively in osteostracans, the 'sel' 1 canal bifurcates between the orbit and the lateral field rather than adjacent to either one or the other (Janvier, 1985; Sansom, 2009a).

The above characteristics could indicate a variety of possible affinities for

Ceramantyx, including similarities to *Superciliaspis*, the Benneviaspidida or Thyestiida, or to *Diademaspis*; however, the current cladistic analysis places *Ceramantyx* as sister taxon to *Stensiopelta*, in spite of a lack of synapomorphies with the Zenaspididae or Zenaspidida, based primarily on the characteristics of its ornamentation. Ornamentation can be highly variable among the Osteostraci and so the position of *Ceramantyx*, based on such highly variable characteristics, is rather tentative, given the absence of other synapomorphies of the groups within which it is resolved.

Biogeography

Results of this analysis are given in Figure 8.2 based on an osteostracan-only maximum-parsimony analysis with 360 most-parsimonious trees and a length of 258 steps. The maximum-parsimony reconstruction of the ancestral distributions for the osteostracans is generally in agreement with the ideas of Sansom (2009b), as the Zenaspida are still widespread across Euramerica, while the new taxa included in this study do not provide information on the other groups. During the Late Silurian the non-cornuate osteostracans were distributed over a large area of Euramerica, while *Acerocephale*, the only known Early Devonian non-cornuate, was restricted to the MOTH locality of northern Canada.

A limitation of the computer analysis TNT is that it only permits the use of one taxon as the outgroup. For the ancestral distribution reconstructions this resulted in a topology where *Ateleaspis*, rather than the Ateleaspididae, was basal and the Ateleaspididae were a paraphyletic grade at the base of the Osteostraci.

For comparison of geographic distributions, the monophyly of the Ateleaspididae, as resolved in the more inclusive phylogenetic analysis, is constrained and the tree is rooted at the base of the family. Under this model the ancestral distribution of the Osteostraci is Østlandet. Under the *Ateleaspis*-basal model the ancestral distribution of the Osteostraci is more widespread, across Østlandet, MOTH, and Scotland. A terrane-level reconstruction of the biogeographic distributions of osteostracans differs from the basin-level reconstruction in that both Laurentia and Baltica are reconstructed as the ancestral distribution of osteostracans, rather than the Østlandet basin in the Baltica terrane. All other ancestral distributions at the basin level are consistent with the distributions reconstructed at the terrane level (i.e., the basins reconstructed at each node are from the terranes reconstructed for those same nodes).

Biogeography of Osteostracans from MOTH—At least 3 clades dispersed into MOTH (location denoted by a five-point star in Fig. 8.3) from the areas of Østlandet (location denoted by the circle in Fig. 8.3) (*Acerocephale*) and Spitsbergen (hexagon in Fig. 8.3) (Zenaspidida, or Superciliaspidae, *Ceramantyx* and *Machairaspis* separately), and *Waengsjoeaspis*. Two distinct dispersal events are probable with an early event from Østlandet and a later event from Spitsbergen. The dispersal from Østlandet may have occurred in the Late Silurian as there are no osteostracan remains yet reported from the nearby Early Wenlock (Early Silurian) Avalanche Lake locality (Wilson and Caldwell, 1998). Notably absent from MOTH are the Thyestiida. It is likely that there was little interchange between MOTH and Saaremaa (Oesel) in Estonia. Species clearly assignable to the Benneviaspidida are also absent from MOTH. The Benneviaspidida are only known from the Ben Nevis Formation of Spitsbergen (Janvier, 1985) and from the Early Devonian of Podolia (Afanassieva, 1989, 1990).

MOTH possesses agnathan taxa in common with both the Ben Nevis and the Wood Bay Formations (Blieck et al., 1987), making it difficult to reconcile the ancestral distribution reconstructed for the osteostracans with the stratigraphic ages of taxa from the locality. Blieck et al. (1987) concluded that there are two faunal assemblages, one correlated with the Frankelryggen Formation of Spitsbergen, the other correlated with the Ben Nevis Formation of Spitsbergen. Based on personal observations, *Lepidaspis*, a genus diagnostic of the Ben Nevis Formation (Blieck et al., 1987), is common as disarticulated remains associated with most of the species from MOTH. It is quite likely that the dispersal of osteotracans and other early vertebrates is much more complicated than the currently proposed relationships (e.g., Sansom, 2009b; and those proposed here).

It is clear that two or three genera are common to both MOTH and Spitsbergen, but all of the osteostracan species from MOTH are endemic to the locality, so far as is known. This strengthens the proposed biogeographic association of Spitsbergen with the Laurentia terrane (Blieck et al., 1987), while the osteostracans further strengthen the proposed endemism of the MOTH locality. This apparent endemism at MOTH may be the result of uniqueness of the environment preserved compared to other Early Devonian vertebrate localities.

MOTH is of particular significance given that it is interpreted as a marine topographic low in a continental shelf, below storm wavebase (Zorn et al., 2005).

This makes it possible that the osteostracans found at MOTH were living in deeper water than any other known osteostracans, with the possible exception of *Sclerodus* (Denison, 1956). As many of these osteostracans are from the Zenaspidida, the widespread distribution of Zenaspidida may be explained by their distribution in marine environments, and their more mobile *Cephalaspis* eco-morphological type (Afanassieva, 1992). An association with marine sediments, and a more mobile lifestyle than other osteostracan orders, may have allowed the Zenaspidida to disperse to regions that were unattainable to less mobile osteostracans, or those that were confined to a non-marine habitat.

SUMMARY

Acerocephale, *Glabrapelta*, *Dentapelta*, and *Ceramantyx* were included in a cladistic analysis. It was determined, based on this analysis, that *Acerocephale* belonged in the Ateleaspididae, *Glabrapelta* and *Dentapelta* formed a clade with *Superciliaspis* (the Superciliaspididae) and *Ceramantyx* was a member of the Zenaspididae, though only on the basis of characteristics of the ornament. The osteostracan diversity at MOTH includes a mixture of primitive non-cornuate osteostracans, as well as members of the Zenaspidida, and other cornuate osteostracans of uncertain affinities. There do not appear to be any members of the Thyestiida at MOTH. *Acerocephale* likely represents a dispersal into MOTH from Øslandet Norway, while *Ceramantyx*, *Machairaspis*, and the Supercilaspididae represent a separate dispersal from Spitsbergen, Norway.

Waengsjoeaspis, which forms a clade with *Yvonaspis* and *Camptaspis*, also appears to have dispersed into MOTH from Spitsbergen, though its position at the base of the Benneviaspidida is somewhat contentious (Janvier, 1985a; Sansom, 2009a).

LITERATURE CITED

Arsenault, M., and P. Janvier. 1995. Combien d’Ostéostracés a Miguashia. Geobios 19: 19–22.

Adrain, J. M., and M. V. H. Wilson. 1994. Early Devonian cephalaspids (Vertebrata: Osteostraci: Cornuata) from the southern Mackenzie Mountains, N.W.T., Canada. Journal of Vertebrate Paleontology 14:301–319.

Afanassieva, O. B. 1989. New cephalaspids (Agnatha) from the Lower Devonian of Podolia. Paleontologicheskiy zhurnal. 1989: 51–59. [Translated from Russian]

Afanassieva, O. B. 1990. New Lower Devonian *Benneviaspis* (Agnatha) from Podolia. . Paleontologicheskiy zhurnal. 1990: 129–132. [Translated from Russian]

Afanassieva, O. B. 1992. Some peculiarities of osteostracan ecology. 61–70. In Mark-Kurik, E. (ed.). Fossil fishes as living animals. Academy of Sciences of Estonia, Tallin, 299 pp.

Belles-Isles, M. 1989. *Yvonaspis*, nouveau genre d'Osteostraci (Vertebrata, Agnatha) du Dévonien (Emsien-Eifélien) des Grés de Gaspé (Québec, Canada). Canadian Journal of Earth Sciences 26: 2396-2401.

Blieck, A., D. Goujet, and P. Janvier. 1987. The vertebrate stratigraphy of the Lower Devonian (Red Bay Group and Wood Bay Formation) of Spitsbergen. Modern Geology 2:197–217.

Blomeier, D., M. Wisshak, W. Dallmann, E. Volohonsky, A. Freiwald. 2003. Facies analysis of the Old Red Sandstone of Spitsbergen (Wood Bay Formation): reconstruction of the depositional environments and implications of basin development. Facies 49: 151–174.

Denison, R. H. 1951a. Evolution and classification of the Osteostraci. Fieldiana, Geology 11:156–196.

Denison, R. H. 1951b. Exoskeleton of early Osteostraci. Fieldiana, Geology 11:198–218

Denison, R. H. 1952. Early Devonian fishes from Utah part 1: Osteostraci. Fieldiana: Geology 11: 265–287.

Denison, R. H. 1956. A review of the habitat of the earliest vertebrates. Fieldiana: Geology 11: 361–457.

Dineley, D. L. 1994. Cephalaspids from the Lower Devonian of Prince of Wales Island, Canada. Palaeontology 37: 61–70.

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

Donoghue, P. C., P. L. Forey, and R. J. Aldridge. 2000. Conodont affinity and chordate phylogeny. Biological Reviews 75:191–251.

Donoghue, P. C., and P. Smith. 2001. The anatomy of *Turinia pagei* (Powrie), and the phylogenetic status of the Thelodonti. Transactions of the Royal Society of Edinburgh: Earth Sciences 92: 15–37.

Gagnier, P.-Y. 1993 *Sacabambaspis janvieri*, vertébré Ordovicien de Bolivie. I. Analyse morphologique. Annales de Paléontology 79: 19–69.

Goloboff, P. A., J. S. Farris, and K. C. Nixon. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.

Goujet, D., and G. C. Young. 1995. Interrelationships of the placoderms revisited. Pp. 89–95 in H. Lelièvre, S. Wenz, A. R. M. Blieck & R. Cloutier (eds), Premiers Vertébrés et Vertébrés Inférieurs. Géobios, Mémoires Spécial 19. Paris.

Hawthorn, J. R., M. V. H. Wilson, and A. B. Falkenberg. 2008. Development of the dermoskeleton in *Superciliaspis gabrielsei* (Agnatha: Osteostraci). Journal of Vertebrate Paleontology 28:951–960.

Heintz, A. 1939. Cephalaspida from the Downtonian of Norway. Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo. Matematisk-Naturvidenskapelig Klasse 5:1–119.

Janvier, P. 1981a. *Norselaspis glacialis* n.g., n.sp. et les rélations phylogénétiques entre les Kiaeraspidiens (Osteostraci) du Dévonien inférieur du Spitsberg. Palaeovertebrata 11: 19–131.

Janvier, P. 1981b. The phylogeny of the Craniata, with particular reference to the significance of fossil ‘agnathans’. Journal of Vertebrate Paleontology 1: 121–159.

Janvier, P. 1985a. Les Cephalaspides du Spitsberg. Cahiers de Paléontologie, Section Vertébrés. Éditions du Centre National de la Recherche Scientifique, Paris: 244 pp.

Janvier, P. 1985b. Preliminary description of Lower Devonian Osteostraci from Podolia (Ukrainian S.S.R.). Bulletin of the British Museum (Natural History): Geology 38: 309–334.

Janvier, P. 1985c. Les Thyestidiens (Osteostraci) du Silurien de Saaremaa (Estonie). Première partie: morphologie et anatomie. Annales de Paléontologie 71: 83–147.

Janvier, P. 1985d. Les Thyestidiens (Osteostraci) du Silurien de Saaremaa (Estonie). Deuxième partie: Analyse phylogénétique, répartition stratigraphique, remarques sur les genres *Auchenaspis*, *Timanaspis*, *Tyriaspis*, *Didymaspis*, *Sclerodus* et *Tannuaspis*. Annales de Paléontologie 71: 187–216.

Janvier, P. 1996. Early Vertebrates. Clarendon Press, Oxford, 393 pp.

Janvier, P. and M. Arsenault. 1996. Osteostraci. Pp. 123–133 in H. P. Schultze and R. Cloutier (eds), Devonian Fishes and Plants of Miguasha, Quebec, Canada. Friedrich Pfeil, Munich.

Janvier, P., and A. Blieck. 1993. The Silurian-Devonian agnathan biostratigraphy of the Old Red Continent. 67–86. in Long, J. A. (ed.). Palaeozoic Vertebrate Biostratigraphy and Biogeography. Belhaven Press, London, 369 pp.

Janvier, P., and M. J. Newman. 2005. On *Cephalaspis magnifica* Traquair, 1893, from the Middle Devonian of Scotland, and the relationships of the last osteostracans. Transactions of the Royal Society of Edinburgh: Earth Sciences 95: 511–525.

Long, J. A. 1993. Morphological characteristics of Paleozoic vertebrates used in biostratigraphy. 3–24. in Long, J. A. (ed.). Palaeozoic Vertebrate Biostratigraphy and Biogeography. Belhaven Press, London, 369 pp.

Mark-Kurik, E., and P. Janvier. 1995. Early Devonian Osteostracans from Severnaya Zemlya, Russia. Journal of Vertebrate Paleontology 15: 449–462.

Ørvig, T. 1965. Palaeohistological notes 2. Certain comments on the phyletic significance of acellular bone tissue in early lower vertebrates. Arkiv för Zoologi 16: 551–556.

Ørvig, T. 1968. The dermal skeleton; general considerations. Pp. 374–397 in T. Ørvig (ed.), Current Problems of Lower Vertebrate Phylogeny. Proceedings of the 4th Nobel Symposium. Almqvist and Wiksell, Stockholm.

Otto, M., and M. Laurin. 1999. Osteostracan tesserae from the Baltic Middle Devonian: morphology and microanatomy. Neues Jahrbuch für Geologie und Paläontologie. Monatshefte 1999: 464–476.

Ritchie, A. 1967. *Ateleaspis tessellata* Traquair, a non-cornuate cephalaspid from the Upper Silurian of Scotland. Journal of the Linnean Society, Zoology 47:69–81.

Sansom, I. J., Donoghue, P. C. J., and G. Albanesi. 2005. Histology and affinity of the earliest armoured vertebrate. Biology Letters 1: 446–449.

Sansom, R. S. 2008. The origin and early evolution of the Osteostraci (Vertebrata): a phylogeny for the thyestiids. Journal of Systematic Palaeontology

6:317–332.

Sansom, R. S. 2009a. Phylogeny, classification and character polarity of the Osteostraci (Vertebrata). Journal of Systematic Palaeontology 7:95–115.

Sansom, R. S. 2009b. Endemicity and palaeobiogeography of the Osteostraci and Galeaspida: a test of scenarios of gnathostome evolution. Palaeontology 52:1257–1273.

Scotese, C. R., and W. S. McKerrow. 1990. Revised world maps and introduction. 1–21. in McKerrow, W. S. and Scotese, C. R. (eds). Palaeozoic Palaeogeography and Biogeography. Geological Society Memoirs 12, London, 435 pp.

Schaeffer, B. 1975. Comments on the origin and basic radiation of the gnathostome fishes with particular reference to the feeding mechanism. Pp. 101–109 in J. P. Lehman (ed.), Problèmes actuels de paléontologie. Évolution des vertébrés. Colloques Internationaux du Centre National de la Recherche Scientifique, Paris.

Stensiö, E. A. 1927. The Devonian and Downtonian vertebrates of Spitzbergen. 1. Family Cephalaspidae. Skrifter om Svalbard or Nordishavet 12:1–391.

Stensiö, E. A. 1932. The cephalaspids of Great Britain. British Museum (Natural History), London, 220 pp.

Traquair, R. H. 1893. On the discovery of *Cephalaspis* in the Caithness Flags. Report of the British Association for the Advancement of Science 54: 747.

Voichyshyn, V. 2006. New osteostracans from the Lower Devonian terrigenous deposits of Podolia, Ukraine. Acta Palaeontologica Polonica 51: 131–142.

Wang, N.-Z., Donoghue, P. C. J., Smith, M. M., and I. J. Sansom. 2005. Histology of the galeaspid dermoskeleton and endoskeleton, and the origin and early evolution of the vertebrate cranial endoskeleton. Journal of Vertebrate Paleontology 25: 745–756.

Wängsjø, G. 1952. The Downtonian and Devonian vertebrates of Spitsbergen. IX. Morphologic and systematic studies of the Spitsbergen cephalaspids. Results of Th. Vogt's Expedition 1928 and the English-Norwegian-Swedish Expedition in 1939. Norsk Polarinstitutt Skrifter 97:1–611.

Westoll, T. S. 1945. A new cephalaspid fish from the Downtonian of Scotland, with notes on the structure and classification of ostracoderms. Transactions of the Royal Society, Edinburgh 61: 241–357.

Wilson, M. V. H., and M. W. Caldwell. 1998. The Furcacaudiformes: a new Order of jawless vertebrates with thelodont scales, based on articulated Silurian and Devonian fossils from northern Canada. Journal of Vertebrate Paleontology 18: 10–29.

Young, G. C. 1986. The relationships of placoderm fishes. Zoological Journal of the Linnean Society 88: 1–55.

Zhu, M., and Z.-K. Gai, 2006. Phylogenetic relationships of galeaspids (Agnatha). Vertebrata PalAsiatica 44: 1–27.

Zorn, M. E., M. W. Caldwell, and M. V. H. Wilson. 2005. Lithological analysis of the Lower Devonian vertebrate-bearing beds at the MOTH locality, N.W.T., Canada: insights to taphonomy and depositional setting. Canadian Journal of Earth Science 42:763–775.

FIGURE 8.1. 50% Majority Rule consensus of 360 most-parsimonious trees of 358 steps, from a maximum-parsimony analysis of the Osteostraci and the major vertebrate clades using the traditional search algorithms in TNT. Numbers on branches represent percentage of most parsimonious trees in which a particular clade was recovered. Osteostracan taxa with representatives from MOTH are in bold. New taxa from preceding chapters that have been added to the data set are indicated with <. Families of importance to new taxa are labelled. Orders of the Osteostraci are labelled in all caps.

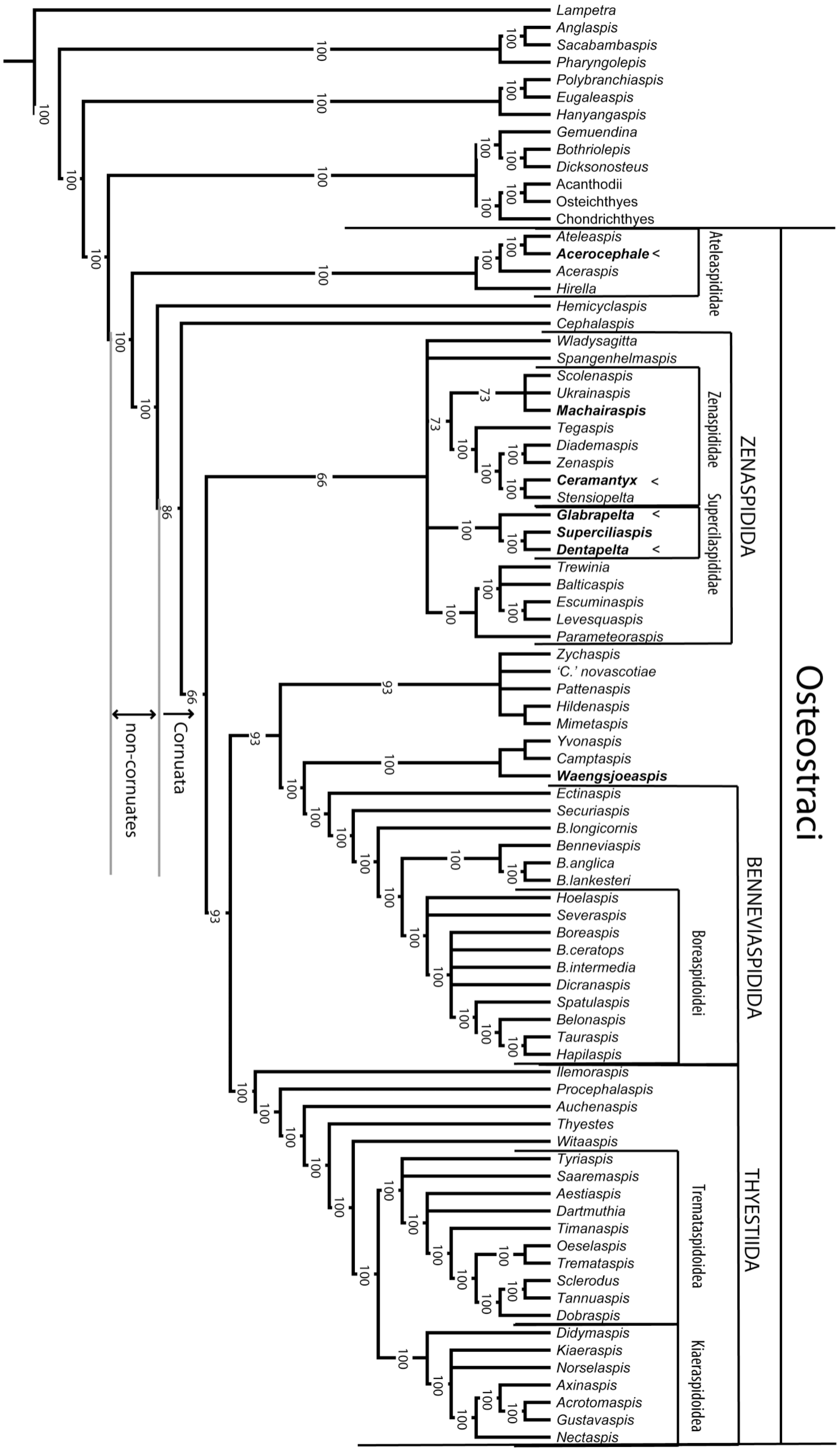

Lampetra
Anglaspis
Sacabambaspis
Pharyngolepis
Polybranchiaspis
Eugaleaspis
Hanyangaspis
Gemuendina
Bothriolepis
Dicksonosteus
Acanthodii
Osteichthyes
Chondrichthyes
Ateleaspis
Acerocephale <
Aceraspis
Hirella
Ateleaspididae
Hemicyclaspis
Cephalaspis
Wladysagitta
Spangenhelmaspis
Scolenaspis
Ukrainaspis
Machairaspis
Tegaspis
Diademaspis
Zenaspis
Ceramantyx <
Stensiopelta
Glabrapelta <
Superciliaspis
Dentapelta <
Zenaspididae
Supercilaspididae
ZENASPIDIDA
Trewinia
Balticaspis
Escuminaspis
Levesquaspis
Parameteoraspis
Zychaspis
'C.' novascotiae
Pattenaspis
Hildenaspis
Mimetaspis
Yvonaspis
Camptaspis
Waengsjoeaspis
Ectinaspis
Securiaspis
B.longicornis
Benneviaspis
B.anglica
B.lankesteri
Hoelaspis
Severaspis
Boreaspis
B.ceratops
B.intermedia
Dicranaspis
Spatulaspis
Belonaspis
Tauraspis
Hapilaspis
Boreaspidoidei
BENNEVIASPIDIDA
Ilemoraspis
Procephalaspis
Auchenaspis
Thyestes
Witaaspis
Tyriaspis
Saaremaspis
Aestiaspis
Dartmuthia
Timanaspis
Oeselaspis
Tremataspis
Sclerodus
Tannuaspis
Dobraspis
Trematapidoidea
Didymaspis
Kiaeraspis
Norselaspis
Axinaspis
Acrotomaspis
Gustavaspis
Nectaspis
Kiaeraspidoidea
THYESTIDA
Osteostraci
non-cornuates
Cornuata
100
73
66
93
86

FIGURE 8.2. Comparison of paleobiogeographic reconstructions of ancestral distributions using maximum-parsimony ancestral character reconstruction in Mesquite, for distributions of osteostracan taxa at both the basin (left) and terrane (right) levels. Ancestral distributions of each node are in the grey boxes.

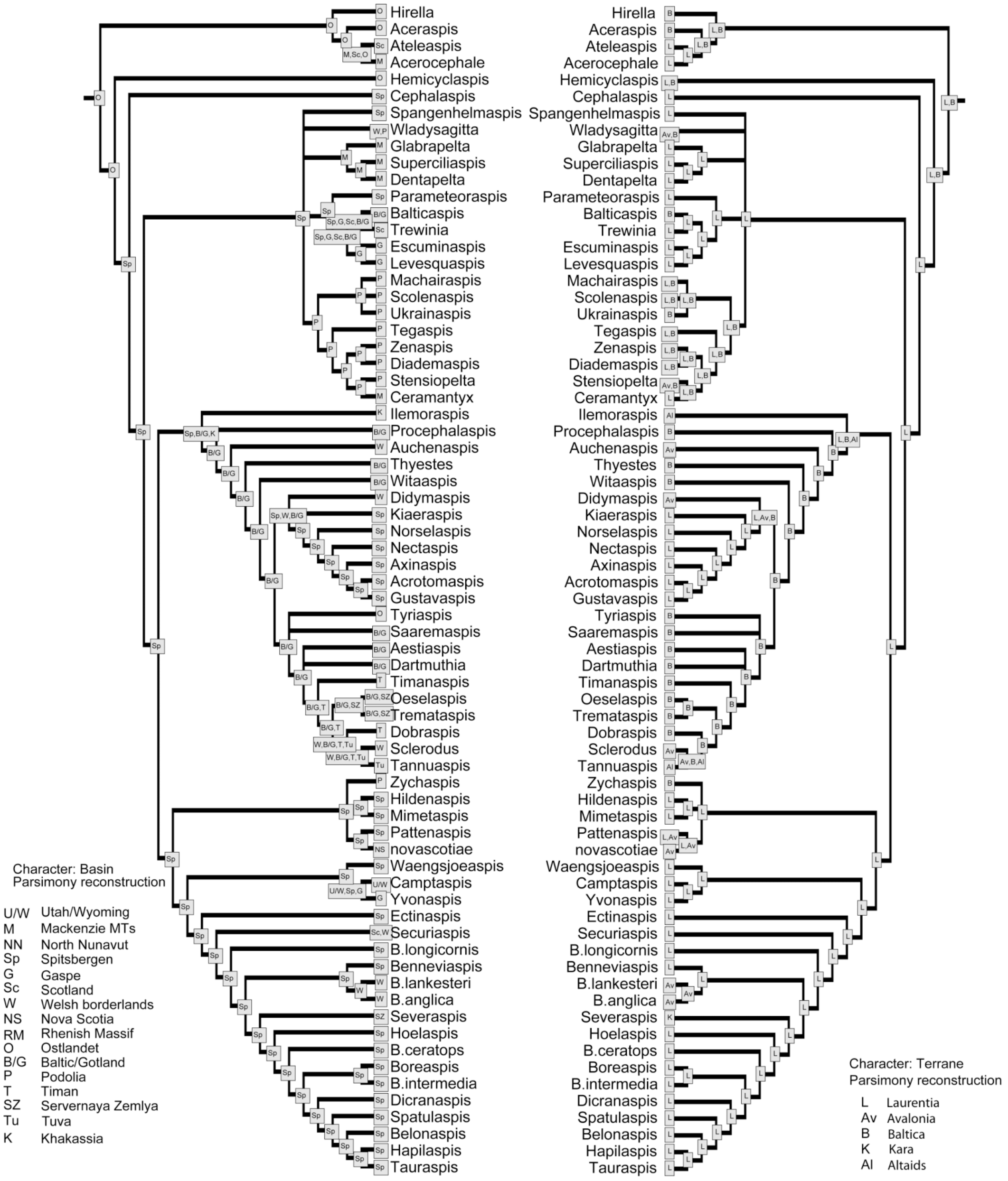

Hirella
Aceraspis
Ateleaspis
Acerocephale
Hemicyclaspis
Cephalaspis
Spangenhelmaspis
Wladysagitta
Glabrapelta
Superciliaspis
Dentapelta
Parameteoraspis
Balticaspis
Trewinia
Escuminaspis
Levesquaspis
Machairaspis
Scolenaspis
Ukrainaspis
Tegaspis
Zenaspis
Diademaspis
Stensiopelta
Ceramantyx
Ilemoraspis
Procephalaspis
Auchenaspis
Thyestes
Witaaspis
Didymaspis
Kiaeraspis
Norselaspis
Nectaspis
Axinaspis
Acrotomaspis
Gustavaspis
Tyriaspis
Saaremaspis
Aestiaspis
Dartmuthia
Timanaspis
Oeselaspis
Tremataspis
Dobraspis
Sclerodus
Tannuaspis
Zychaspis
Hildenaspis
Mimetaspis
Pattenaspis
novascotiae
Waengsjoeaspis
Camptaspis
Yvonaspis
Ectinaspis
Securiaspis
B.longicornis
Benneviaspis
B.lankesteri
B.anglica
Severaspis
Hoelaspis
B.ceratops
Boreaspis
B.intermedia
Dicranaspis
Spatulaspis
Belonaspis
Hapilaspis
Tauraspis
Character: Basin
Parsimony reconstruction
U/W Utah/Wyoming
M Mackenzie MTs
NN North Nunavut
Sp Spitsbergen
G Gaspe
Sc Scotland
W Welsh borderlands
NS Nova Scotia
RM Rhenish Massif
O Ostlandet
B/G Baltic/Gotland
P Podolia
T Timan
SZ Servernaya Zemlya
Tu Tuva
K Khakassia
Character: Terrane
Parsimony reconstruction
L Laurentia
Av Avalonia
B Baltica
K Kara
Al Altaids

FIGURE 8.3. Reconstruction of Early Devonian geography, centered on Euramerica. Map is modified from Scotese and McKerrow (1990). The MOTH locality (star), and Spitsbergen (hexagon), and Ostlandet (circle) basins are labelled.

APPENDIX 1. Characters 1–65. Character Matrix used for both the phylogenetic analysis, and for biogeographic reconstruction. Character codings have been modified from Sansom, 2009a. A, 0/1; B, 1/2 for characters 1–112. Characters 113 and 114 are the codings for Basin level distributions and Terrane level distributions respectively. For character 113, the codings are **1**, Utah/Wyoming, **2**, Mackenzie Mountains, **3** North Nunavut, **4**, Spitsbergen, **5**, Gaspe, **6**, Scotland, **7**, Welsh Borderlands, **8**, Nova Scotia, **9**, Rhenish Massif, **A**, Ostlandet, **B**, Baltic/Gotland, **C**, Podolia, **D**, Timan, **E**, Severnaya Zemlya, **F**, Tuva, **G**, Khakassia. For character 114 the codings are, **1**, Laurentia, **2**, Avalonia, **3**, Baltica, **4**, Kara, **5**, the Altaids. Characters 113 and 114 were not used for the cladistic analyses, only for most parsimonious reconstruction of the ancestral distributions.

Taxa	5	10	15	20	25	30	35	40	45	50	55	60	65
Lampetra	0-00-	-----	--0--	0--10	10-00	0--20	-0000	0----	---0-	00000	010-0	--00-	1-0--
Pharyngolepis	0-00-	-----	--0--	?-010	10000	0--2?	-0?00	0----	--10-	00000	010-0	--01-	?-0--
Sacabambaspis	0-00-	-----	--0--	0-0?0	1100?	1----	-0?00	0--1-	-?10-	00000	000-0	--013	?-0--
Anglaspis	0-00-	-----	--0--	0-000	1000?	?----	-0001	0--1-	-?00-	00001	000-0	--013	?-0--
Hanyangaspis	0-00-	-----	--0--	?-01?	10?11	0----	-1010	0--0-	0?00-	000?0	1-0-0	--013	1?0--
Polybranchiaspis	0-00-	-----	--0--	?-010	10111	0----	-1111	0--0-	0?00-	000?0	1-0-0	--013	1-0--
Eugaleaspis	0-00-	-----	--0--	?-010	10111	0----	-1111	11010	0000-	000?0	1-0-0	--01?	1-0--
Gemuendina	0-00-	-----	--0--	?-000	11001	0----	-0000	0--10	0010-	11111	00101	00-0-	0-100
Bothriolepis	0-00-	-----	--0--	1-100	01001	0----	-0000	0--10	1?00-	11101	00101	00-0-	0-111
Dicksonosteus	0-00-	-----	--0--	1-100	11001	1----	-0000	10000	0000-	11101	00101	00-0-	0-111
Acanthodii	0-00-	-----	--0--	?-??0	11001	1----	-0??1	0--10	0-10-	00001	00?11	1?-0-	0-110
Chondrichthyes	0-00-	-----	--0--	1-000	11001	1----	-0???	0--10	0-10-	00001	00?01	11-0-	0-110
Osteichthyes	0-00-	-----	--0--	1-?00	11001	1----	-0001	0--10	0-00-	00001	00111	11-0-	0-110
Ateleaspis	0-010	-1000	-0110	10110	11000	0??20	00000	0--10	0010-	00000	1-1-0	--110	??100
Aceraspis	0-010	-1000	-0100	10111	11000	01020	00000	0--10	0010-	00000	1-1-0	--110	10100
Hirella	0-010	-0000	-0110	10110	11000	01120	?0???	0--10	0010-	00000	1-1-0	--111	?0110
Hemicyclaspis	0-010	-0000	-0110	10110	11000	01020	00000	0--10	0010-	00000	1-1-0	--111	10111
Cephalaspis	0-010	-0000	10110	10110	11000	01020	?0000	10010	0010-	00000	1-1-0	--11?	10111
Parameteoraspis	0-010	-0020	20110	10111	1?100	0??1-	?0???	11010	0000-	000?0	1-?-0	--1?1	1?111
Hildenaspis	0-010	-0000	20100	10?10	0?000	01020	?0???	10000	0000-	0000?	1-?-0	--1??	???11
Pattenaspis	0-010	-0000	101?0	10110	1?000	01020	?0000	10000	00010	00000	1-?-0	--1??	10111
Mimetaspis	0-010	-0000	10100	10110	0?000	01020	00???	10000	0000-	0000?	1-?-0	--1??	?0111
Zenaspis	0-010	-0000	01100	10111	1?100	01021	00000	10010	00010	00000	1-1-0	--111	10111
Diademaspis	0-010	-0000	011?0	10111	1?100	01021	00000	10010	00010	00000	1-?-0	--1??	10111
Machairaspis	0-010	-0000	00120	10111	1?100	01121	?0000	10010	00011	00000	1-?-0	--1??	10111
Tegaspis	0-010	-0000	01120	10111	1?100	01121	?0???	10010	0000-	00000	1-?-0	--1??	10111
Scolenaspis	0-010	-0000	00120	10111	1?100	01021	?0000	10010	00010	00000	1-?-0	--1??	10111
Zychaspis	0-010	-0000	10100	1011?	1?000	01021	?0???	10000	0000-	00000	1-?-0	--1??	??111
Stensiopelta	0-010	-0000	10100	10111	1?100	01021	?0???	10020	0000-	00000	1-?-0	--1??	??111
Ukrainaspis	0-010	-0000	00120	10111	1?100	01?2?	?0???	10010	00010	0000?	1-?-0	--1??	?0111
Benneviaspis	0-010	-1000	11141	10010	0?000	01020	00000	10010	0000-	00010	1-?-0	--1??	11111
B.lankesteri	0-010	-0000	01141	10110	0?000	01020	??000	10020	0000-	0001?	1-?-0	--1??	??111
B.anglica	0-010	-0000	01141	10010	0?000	0101-	?0???	10020	0000-	0001?	1-?-0	--1??	??111
B.longicornis	0-010	-1000	11100	10110	0?000	01020	?0???	10020	0000-	0000?	1-?-0	--1??	??111
Hoelaspis	10010	-1000	01110	10010	0?000	01020	00000	10031	0000-	00000	1-?-0	--1??	11111
Severaspis	11010	-1000	111?0	??010	0?000	01?20	?????	10031	?0???	0000?	1-?-0	--1??	??111
Boreaspis	11010	-1001	00100	10010	0?000	01020	?0???	10021	0000-	00000	1-?-0	--1??	11111
B.ceratops	11010	-1001	00100	10010	0?000	01020	?0???	10031	0000-	00000	1-?-0	--1??	11111
B.intermedia	11010	-1001	00100	10010	0?000	01020	?0???	10021	0000-	00000	1-?-0	--1??	11111
Belonaspis	11010	-1001	00100	10010	0?000	01020	?0???	20010	0000-	00000	1-?-0	--1??	11111
Dicranaspis	11010	-0001	00100	10010	0?000	01020	?0???	10011	0000-	00000	1-?-0	--1??	11111
Spatulaspis	11010	-1001	00100	10010	0?000	01020	00000	20011	0000-	00000	1-?-0	--1??	11111
Kiaeraspis	0-010	-1001	-0111	11011	1?000	01020	?0???	0--10	0010-	00000	1-?-0	--111	11111
Norselaspis	0-010	-0001	-0111	10010	1?000	01020	?0???	0--10	0000-	00000	1-?-0	--111	11111
Axinaspis	0-011	00001	-0131	10010	1?000	01020	?0???	0--10	0000-	00000	1-?-0	--1??	11111
Nectaspis	0-011	10001	-0111	10010	1?000	01030	10000	0--10	0000-	00000	1-?-0	--1??	12111
Acrotomaspis	0-111	200?1	-0131	10010	1?000	01020	?0???	0--20	0000-	00000	1-?-0	--1??	1?111
Gustavaspis	0-111	20011	-013-	1000-	1?000	01020	?0???	0--20	0000-	00000	1-?-0	--1??	??111
Procephalaspis	0-010	-0000	00130	10110	1?000	01020	10000	10010	0010-	00000	1-1-0	--111	10111
Auchenaspis	0-010	-0000	00131	10110	0?000	01020	?0???	10010	0010-	00000	1-?-0	--111	10111
Thyestes	0-010	-1000	00111	11110	01000	0111-	10000	10010	0010-	00000	1-?-0	--11?	1?111
Witaaspis	0-010	-1000	-0111	11110	0?000	01120	10000	0--10	0010-	00000	1-?-0	--11?	10111
Tyriaspis	0-010	-0000	00101	1?110	01000	0111-	?0???	0--1-	0110-	000?0	1-0-0	--112	??0--
Aestiaspis	0-010	-0100	00111	11110	01000	0111-	10???	0--1-	?110-	00000	1-?-0	--11?	100--
Dartmuthia	0-010	-0000	00111	11110	01000	0111-	10000	0--1-	0110-	00000	1-0-0	--112	100--
Saaremaspis	0-010	-0000	00111	11110	0?000	0111-	10???	0--1-	?110-	00000	1-0-0	--112	100--
Timanaspis	0-010	-??00	?0100	11110	??000	01?A-	?0???	0--0-	1?00-	0000?	1-?-0	--1??	??0--
Sclerodus	0-010	-1110	001?1	1?110	01000	0111-	?0???	0--0-	?1?0-	0000?	1-?-0	--1??	1?0--
Dobraspis	0-010	-1110	-0111	11110	0?000	011B0	?????	0--0-	???0-	0000?	1-?-0	--1??	??0--
Oeselaspis	0-011	00110	-0111	11110	0?000	0111-	10000	0--0-	1000-	00000	1-?-0	--11?	??0--
Tremataspis	0-011	00110	-0111	11110	01000	0111-	10000	0--0-	1000-	00000	1-0-0	--112	100--
Balticaspis	?????	-????	??1??	?????	?????	?????	?????	11110	000??	000?0	1-0-0	--?11	??111
Camptaspis	10010	-?000	101?1	?0010	1?100	0??30	?0???	10000	000?-	0000?	1-?-0	--1??	??111
Didymaspis	0-010	-0001	-0131	10010	0?000	01120	10???	0--10	1000-	00000	1-?-0	--11?	10111
Ectinaspis	0-010	-0000	11120	10110	1?000	01020	?????	10020	0000-	0000?	1-?-0	--1??	??111
Escuminaspis	0-00-	-----	--130	?0011	1?100	0??20	?0000	11100	0000-	000??	1-?-0	--1?1	??111
Hapilaspis	0-010	-?001	001??	????0	0?000	01?20	?????	2--10	0??0-	0000?	1-?-0	--1??	??111
Ilemoraspis	0-010	-0110	00120	110?0	1?000	00-0-	10000	10010	0000-	000??	1-?-0	--111	??111
Levesquaspis	0-00-	-----	--12?	?????	1?100	0????	?0???	11?00	000??	000??	1-?-0	--1??	??111
Securiaspis	0-010	-1000	11120	10110	1?000	01020	00000	10020	0000-	0000?	1-?-0	--1??	?1111
Spangenhelmaspis	0-010	-1000	10120	10111	1?100	01020	00???	10000	0000-	00000	1-?-0	--1?1	??111
Superciliaspis	0-010	-0000	101?0	10011	0?100	01021	10???	10110	00111	00000	1-1-0	--111	??111
Tannuaspis	0-010	-?110	00121	??010	1?000	00-0-	?????	0--0-	?1?0-	0000?	1-?-0	--1??	??0--
Tauraspis	01010	-?001	001??	????0	0?000	01???	?????	20010	?0?0-	0000?	1-?-0	--1??	?1111
Trewinia	0-0?0	-0020	201?0	?01?1	1??00	0????	?0???	11110	0000-	000??	1-?-0	--11?	??111
Yvonaspis	10010	-0000	10130	10010	1?100	0101-	?0???	10?00	0000-	0000?	1-?-0	--1??	??111
Waengsjoeaspis	0-010	-0000	10121	10110	1?000	0103-	?0???	10000	0000-	00000	1-?-0	--1?1	10111
Wladysagitta	10010	-0000	10120	1011?	1?100	0102?	?0???	10010	000?-	0000?	1-?-0	--1??	??111
C.novascotiae	0-010	-0000	101A0	10111	1?000	01021	?0???	10000	00110	0000?	1-?-0	--1??	??111
Acerocephale	0-01?	????0	1?1??	?????	???00	0???0	???00	0--10	00?0-	000?0	1-1-0	--110	10110
Glabrapelta	0-010	-0000	1?110	10111	01100	01021	00000	10010	?0?0-	000??	1-??0	--1??	??111
Dentapelta	??01?	?0000	1?130	100??	0?100	01021	10000	10010	?0?1?	0000?	1-??0	--1??	??111
Ceramantyx	0-010	-0?00	101??	?0???	1??00	0????	?0?00	10010	00?0-	000??	1-??0	--1??	??111

APPENDIX 1 CONTINUED. Characters 66–114. Character Matrix used for both the phylogenetic analysis, and for biogeographic reconstruction. Character codings have been modified from Sansom, 2009a. A, 0/1; B, 1/2 for characters 1–112. Characters 113 and 114 are the codings for Basin level distributions and Terrane level distributions respectively. For character 113, the codings are **1**, Utah/Wyoming, **2**, Mackenzie Mountains, **3** North Nunavut, **4**, Spitsbergen, **5**, Gaspe, **6**, Scotland, **7**, Welsh Borderlands, **8**, Nova Scotia, **9**, Rhenish Massif, **A**, Ostlandet, **B**, Baltic/Gotland, **C**, Podolia, **D**, Timan, **E**, Severnaya Zemlya, **F**, Tuva, **G**, Khakassia. For character 114 the codings are, **1**, Laurentia, **2**, Avalonia, **3**, Baltica, **4**, Kara, **5**, the Altaids. Characters 113 and 114 were not used for the cladistic analyses, only for most parsimonious reconstruction of the ancestral distributions.

```
Taxa                  70    75    80    85    90    95   100   105   110
Lampetra           -0110 00100 0--00 ----- -0--- ----- -00-- 00-00 00?-- 00 ??
Pharyngolepis      -00-0 00110 0--00 10--- 10000 0000- -00-? ??-?0 ???-- 0? ??
Sacabambaspis      -00-0 20110 1?-10 00--- 10200 0000- -00-? ??-?0 ???-- 0? ??
Anglaspis          -00-0 20110 11-00 0---- 30200 0000- -00-? ??-?0 ???-- 00 ??
Hanyangaspis       -???? ?0100 0--00 12--0 11101 00?0- -10-? ??-?0 ??0-- 00 ??
Polybranchiaspis   -???? ?0100 0--00 12--0 11100 0000- -10-0 10-00 ??0-- 00 ??
Eugaleaspis        -???? ?0100 0--00 12--0 1110? 0000- -10-0 10-00 ??0-- 00 ??
Gemuendina         011?0 11000 12-00 10--- 10011 0000- -110? ??-?1 00?-- 01 ??
Bothriolepis       0?110 11000 12-00 0---- 10000 0000- -1100 ??-?1 00?-- 01 ??
Dicksonosteus      01110 1100? 1B-00 0---- 1000? 0000- -1100 10-01 001-- 01 ??
Acanthodii         11120 ?1001 1A-?0 0---- -0--- ----- -1101 01-?1 ???-- 01 ??
Chondrichthyes     11120 11001 11-10 0---- -0--- ----- -11-0 10-11 111-- 01 ??
Osteichthyes       01120 11001 11-10 0---- -0--- ----- -1101 01-11 111-- 01 ??
Ateleaspis         00121 11??0 ????0 101?? 10000 00020 ?1?0? ????? ????? ?? 61
Aceraspis          00121 11000 10200 10000 10000 00010 11100 10111 00000 10 A3
Hirella            0012? 11000 10?00 100?? 10000 00010 ?1?0? ????? ???00 ?0 A3
Hemicyclaspis      00111 11000 10200 1000? 10001 00001 01100 10?11 ??000 10 {3 6 7 A}{1 2 3}
Cephalaspis        00111 11000 10100 1000? ?00?? 00000 0110? ????1 ???02 ?0 {4 6 7}{1 2}
Parameteoraspis    0???? ??000 ??100 1000? 10??1 0000? 01?0? ????? ???0? ?? {3 4}1
Hildenaspis        0???? ??0?0 ????0 ?1-?? 10001 00000 ?110? ????? ????? ?? {4 9}{1 2}
Pattenaspis        0???? ?1000 10B00 1000? 100-? 0?000 ?1100 ?011? ???02 ?? {4 9 C}{1 2 3}
Mimetaspis         0???? ??000 ??100 1000? 10?-? 0?000 ?110? ??1?1 ???02 10 {4 C}{1 3}
Zenaspis           00111 11000 10100 10000 10111 00000 01100 10111 ??000 10 {4 6 7 C}{1 2 3}
Diademaspis        0???? ??000 10100 100?? 10111 00000 ?1?0? ????? ????? 10 {4 C}{1 3}
Machairaspis       0???? 1?000 10100 1000? 10?01 00000 ?110? ????? ????? 10 {2 4 C}{1 3}
Tegaspis           0???? ??0?0 ??100 1000? 10010 00000 ?1?0? ????? ????0 ?? {4 C}{1 3}
Scolenaspis        0???? 1?000 10100 100?? 100?1 00000 ?1100 1??11 ???00 10 {4 C}{1 3}
Zychaspis          0???? ??0?0 ????0 1000? 10000 00000 01?0? ????? ????? ?? C3
Stensiopelta       0???? ??0?0 ????0 100?? 10111 00000 01?0? ????? ???0A ?? {7 C}{2 3}
Ukrainaspis        0???? ????0 ????0 100?? 100?? 0?0?0 ?1??? ????? ???00 ?? C3
Benneviaspis       0???? ??000 10??0 11-2? 000-- 0-000 21100 10111 00001 10 {4 C E}{1 4}
B.lankesteri       0???? ??0?0 ????0 11-2? 000-- 0-000 ?110? ????? ???01 10 72
B.anglica          0???? ??0?0 ????0 11-2? 000-- 0-000 ?110? ????? ???01 10 72
B.longicornis      0???? ??0?0 ????0 1???? ?0??? 00000 ?110? ????? ????A ?? 41
Hoelaspis          0???? ??000 10??0 11-2? 000-- 0-000 ?1100 10111 00001 1? 41
Severaspis         0???? ??0?0 ????0 11-2? ?0??? ???00 ?110? ????? ????1 ?? E4
Boreaspis          0???? ??000 10??0 11-2? 000-? 0-000 ?1110 10111 00001 10 41
B.ceratops         0???? ??0?0 ????0 11-2? 000-- 0-000 ?111? ????? ???01 ?? 41
B.intermedia       0???? ??0?0 ????0 11-2? 000-- 0-000 ?1110 10111 00001 ?0 41
Belonaspis         0???? ??000 10??0 11-2? 000-- 0-000 ?1110 10111 00001 10 41
Dicranaspis        0???? ??000 10??0 11-2? 000-- 0-000 ?1110 10?11 ??001 10 41
Spatulaspis        0???? ??000 10??0 11-2? A00?? 0?000 01110 10111 00001 10 41
Kiaeraspis         0???? ??000 10200 11-0? ?01?? 0?001 21100 10011 00001 10 41
Norselaspis        0???? ?10?0 ????0 11-?? 1010? 00001 21100 10011 00001 10 41
Axinaspis          0???? ??000 10200 11-0? 101?? 0000? 2110? ????? ???01 1? 41
Nectaspis          0???? ??000 10200 11-0? 001-1 0-001 ?1100 1001? 00001 10 41
Acrotomaspis       0???? ??0?0 ??100 11-0? 10101 00001 ?110? ????? ???01 1? 41
Gustavaspis        0???? ??0?0 ??A00 11-0? 101?1 0000? ?110? ????? ???01 1? 41
Procephalaspis     0???? ?1000 10100 10001 10101 10100 01100 10011 ??001 1? B3
Auchenaspis        0010? ??0?0 ??100 11-0? 10101 1?101 01100 1001? ??001 10 72
Thyestes           0???? ?1000 10100 11-?1 10101 11101 11100 1001? ??001 1? B3
Witaaspis          0???? ??000 10000 1000? 400-- 1-101 ?1100 1??1? ??001 10 B3
Tyriaspis          -0100 1?0?0 ????0 11-?? 10000 0000? 11??? ????? ????? ?? A3
Aestiaspis         -???? ??000 10101 10011 300-- 1-001 11??? ????? ????? ?? B3
Dartmuthia         -0?A? 1100? 10201 10011 10000 10000 11100 10011 00001 10 B3
Saaremaspis        -???0 11000 10000 11-11 400-- 0-001 ?1??? ????? ????? ?? B3
Timanaspis         -???? ?1000 1000? 11-?0 300-- 1-000 ?1??? ????? ????? ?? D3
Sclerodus          -???? ??000 10001 11-1? 10000 ?1100 ?1?0? ????? 0001? ?? 72
Dobraspis          -???? ??0?0 ????? 1???? ?0??? ??00? ?110? ????? ????1 ?? D3
Oeselaspis         -???? ?1000 10101 11-11 600-- 0-000 21100 1001? ??011 10 {B E}{3 4}
Tremataspis        -0100 11000 10201 11-11 500-- 0-000 11100 10011 00011 10 {B E}{3 4}
Balticaspis        0???? ?1000 ????0 1010? 10000 ?100? ????? ????? ????? ?? B3
Camptaspis         0???? ??0?0 ??100 100?? 000-- 0-000 ?1??? ????? ????? ?? 11
Didymaspis         0???? ??000 10000 11-0? 10000 00001 21100 10011 ??0?1 1? 72
Ectinaspis         0???? ??0?? ????0 1000? 000-- 0-000 ?110? ????? ???01 ?0 41
Escuminaspis       00111 ??100 10??? 101?? 10010 00000 ?1??? ????? ????? ?? 51
Hapilaspis         0???? ??0?0 ????0 ?1-?? ?0??? 0000? ?11?? ????? ????0 ?? 41
Ilemoraspis        00?00 1??00 10??0 1010? 300-- 0-000 ?1??? ????? ????? ?? G5
Levesquaspis       0???? ????0 ????? 11-?? 1000? 00000 ?1??? ????? ????? ?? 51
Securiaspis        0???? ??0?0 ????0 1??0? 000-- 0-000 ?110? ????? ???00 ?? {6 7}{1 2}
Spangenhelmaspis   0???? ??0?0 ????0 1000? 1000? 00000 ?110? ????? ???00 1? 41
Superciliaspis     0?1B1 1?0?0 ??000 101?? 10001 00001 ?1??? ????? ????? ?? 21
Tannuaspis         -???? ??000 10??0 11-?? 10100 ?010? ?110? ????? ???11 ?? F5
Tauraspis          0???? ??0?0 ????0 ?1-2? 000-- ?-?00 ?11?0 1?11? ????1 ?? 41
Trewinia           0???? ????0 ????0 1010? 30?-- 0-000 ?1??? ????? ????? ?? 61
Yvonaspis          00??? 11000 10??? 1000? ?0??? ??000 ?110? ????? ???01 ?? 51
Waengsjoeaspis     0???? 11000 10200 1000? 000-- 0-001 ?1100 1?11? ???01 10 {2 4}1
Wladysagitta       0???? ??0?0 ????0 100?? 10??? 00000 ?110? ????? ????? ?? {7 C}{2 3}
C.novascotiae      0???? ?1?00 ?0100 100?? 100?? 0?000 ?1?0? ????? ????B ?? 82
Acerocephale       00??? ?1?0? ??100 101?? 10411 0?02? ?11?0 ????? ?00?? ?0 21
Glabrapelta        0???? ?1?00 ??200 1000? 000-- 0-001 ????0 ????? ?00?? ?0 21
Dentapelta         0???? ?1??? ??200 11-0? 10301 01001 ????0 ????? ?00?? ?0 21
Ceramantyx         00??? ?1??? ??200 ???0? 10B10 01031 ?11?0 ????? ?00?1 ?0 21
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CHAPTER 9:

GENERAL CONCLUSIONS

GENERAL CONCLUSIONS

The Lower Devonian (Lochkovian) MOTH locality, Northwest Territories, Canada (Gabrielse et al., 1973; Adrain and Wilson, 1994), preserves articulated osteostracan remains from a time of extreme diversity among the group (Janvier, 1996). Previously three species of osteostracan had been named from MOTH (Dineley and Loeffler, 1976; Adrain and Wilson, 1994). The current study describes five new genera, including eight new species of osteostracans, as well as a new family of Cornuata. The new taxa described include a new species of *Waengsjoeaspis*, a new species of *Machairaspis*, two new genera of uncertain affinities, and a new species of the primitive Ateleaspididae, the youngest member of the family yet known. These new species expand the known diversity of the MOTH locality about three-fold and clearly represent not only an expanded diversity at MOTH but an expanded disparity of forms as well. There is a wide variety of morphologies among the MOTH osteostracans, including differences in ornamentation, overall body form, and general morphology of the headshield.

Four of the new genera, *Acerocephale*, *Ceramantyx*, *Glabrapelta*, and *Dentapelta*, are considered complete enough that they were included in a phylogenetic analysis based on the cladistic analysis put forth by Sansom (2009a). The new family, Superciliaspididae, is a member of the Order Zenaspidida, while the enigmatic *Ceramantyx* is resolved as a member of the Zenaspididae through cladistic analysis. *Acerocephale* resolves as a member of the Ateleaspididae and is the sister taxon to *Ateleaspis*.

The dataset from Sansom's (2009b) analysis was used to determine the possible biogeographic relationships among MOTH and other osteostracan localities. The addition of the new taxa to previous reconstructions of the ancestral geographic distributions of osteostracans results in distributions and dispersal patterns similar to those proposed in a previous analysis by Sansom (2009b), differing with a dispersal into MOTH from Øslandet, but agreeing in that at least two groups dispersed from Spitsbergen into MOTH, the Zenaspidida and *Waengsjoeaspis*. These dispersals support a connection between the Laurentia and Baltica terranes, while the large number of species of osteostracan that are unique to MOTH suggest an endemism of MOTH taxa compared to those fom the Lower Devonian of Spitsbergen and Podolia, which share a number of genera with each other. Only one of the genera, *Machairaspis*, is shared among Podolia, Spitsbergen, and MOTH (Chapter 5 and Janvier, 1985a, 1985b). *Waengsjoeaspis* is shared between Spitsbergen and MOTH (Adrain and Wilson, 1994), while numerous genera (e.g., *Diademaspis*, *Benneviaspis*, *Tegaspis*, *Stensiopelta*, *Mimetaspis*, Belles-Isles and Janvier, 1984; Janvier, 1985b; Afanassieva, 1989) are shared between Spitsbergen and Podolia.

The osteostracans of the MOTH locality add significantly to the known diversity of Lower Devonian early vertebrates as well as reveal the presence of a new family of cornuate osteostracans, and a new non-cornuate osteostracan. The new non-cornuate osteostracan, *Acerocephale*, is the youngest member of the Ateleaspididae to be described, and represents the only member to be described from MOTH or the Lower Devonian. *Acerocephale* is particularly significant as it possesses a micromeric, polyodontode trunk scale morphology that was previously unknown among osteostracans, but a scale morphology that is similar to many early chondrichthyans (Karatajute-Talimaa, 1998). Although not the most parsimonious solution, given the derived state of *Acerocephale* within the Ateleaspididae, it bears consideration that this polyodontode, micromeric condition might in the future prove to be another synapomorphy of osteostracans and gnathostomes.

LITERATURE CITED

Adrain, J. M., and M. V. H. Wilson. 1994. Early Devonian cephalaspids (Vertebrata: Osteostraci: Cornuata) from the southern Mackenzie Mountains, N.W.T., Canada. Journal of Vertebrate Paleontology 14:301–319.

Afanassieva, O. B. 1989. New cephalaspids (Agnatha) from the Lower Devonian of Podolia. Paleontologicheskiy zhurnal. 1989: 51–59. [Translated from Russian]

Belles-Isles, M., and P. Janvier. 1984. Nouveaux ostéostracés du Dévonien Inferieur de Podolie (RSS d'Ukraine). Acta Palaeontologica Polonica 29: 195–208.

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

Gabrielse, H., S. L. Blusson, and J. A. Roddick. 1973. Geology of Flat River, Glacier Lake and Wrigley Lake map areas, District of Mackenzie, Northwest Territories. Geological Survey of Canada, Memoir 366:1–268.

Janvier, P. 1985a. Les Cephalaspides du Spitsberg. Cahiers de Paléontologie, Section Vertébrés. Éditions du Centre National de la Recherche Scientifique, Paris: 244 pp.

Janvier, P. 1985b. Preliminary description of Lower Devonian Osteostraci from

Podolia (Ukrainian S.S.R.). Bulletin of the British Museum (Natural History): Geology 38: 309–334.

Janvier, P. 1996. Early Vertebrates. Clarendon Press, Oxford, 393 pp.

Karatajute-Talimaa, V. 1998. Determination methods for the exoskeleton of early vertebrates. Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe 1: 21–52.

Sansom, R. S. 2009a. Phylogeny, classification and character polarity of the Osteostraci (Vertebrata). Journal of Systematic Palaeontology 7:95–115.

Sansom, R. S. 2009b. Endemicity and palaeobiogeography of the Osteostraci and Galeaspida: a test of scenarios of gnathostome evolution. Palaeontology 52:1257–1273.