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A new Early Devonian (Emsian) arthrodire from the Northwest Territories, Canada, and its significance for paleogeographic reconstruction

Hans-Peter Schultze and Stephen L. Cumbaa

Draft

H.-P. Schultze, Natural History Museum, University of Kansas, 1345 Jayhawk Blvd.,
Lawrence, Kansas 66045-7561, USA E-mail: hp1937@ku.edu

S.L. Cumbaa (corresponding author), Canadian Museum of Nature, P.O. Box 3443,
Station D, Ottawa, ON K1P 6P4, Canada E-mail: scumbaa@mus-nature.ca

Abstract:

An heterostiid arthrodire, *Herasmusius dayi* sp. nov., is described from upper Lower Devonian marine deposits of the Bear Rock Formation along the Anderson River, Northwest Territories, Canada. New elements described for the genus for the first time include the suborbital, submarginal (also new for the family Heterostiidae), the lateral shoulder girdle with posterior lateral, anterior dorso-lateral, and posterior dorso-lateral plates and possible infragnathal plate. We present a new reconstruction of the cranial region of *Herasmusius*, previously known only from supposedly freshwater-shallow marine deposits of roughly the same age in the Wood Bay Group of Spitsbergen.

The late Early Devonian fishes that are common to the Arctic region of northwestern Canada and the island of Spitsbergen in the Svalbard archipelago of Norway, the porolepiform *Heimenia* and the arthrodire *Herasmusius* described here, demonstrate the existence of a barrier-free paleogeographic connection between those continental blocks by the late Early Devonian. Comparison of the entire Anderson River vertebrate fauna with other boreal faunas of similar age indicates additional paleogeographic connections north of and around the Old Red Sandstone Continent to the Baltic region, central Europe, and even to the New Siberian Islands and South China, in contrast to most current published paleogeographical reconstructions.

Résumé:

Un arthrodire hétérostiidé, *Herasmius dayi* sp. nov., est décrit à partir de dépôts marins de la partie supérieure du Dévonien inférieur provenant de la formation de Bear Rock, sur les berges de la rivière Anderson, Territoires-du-Nord-Ouest (Canada). De nouveaux éléments du squelette de ce genre sont décrits pour la première fois: les plaques suborbitaire et submarginale (une nouveauté également pour la famille Heterostiidae), la ceinture scapulaire latérale avec la plaque postéro-latérale, la plaque dorso-latérale antérieure, la plaque dorso-latérale postérieure et ce qui pourrait être la plaque infragnathale. Nous présentons une nouvelle reconstitution de la région crânienne de *Herasmius*, qu'on connaissait précédemment uniquement à partir de dépôts supposés d'eau douce ou marins peu profonds du groupe de Wood Bay au Spitsberg daté approximativement de la même période.

Les poissons de la fin du Dévonien inférieur qui sont communs à la région arctique du Nord-Ouest canadien et à l'île de Spitsberg dans l'archipel du Svalbard, en Norvège, c'est-à-dire le porolépiforme *Heimenia* et l'arthrodire *Herasmius* décrit-ici, démontrent l'existence d'une connexion paléogéographique ouverte entre ces blocs continentaux vers la fin du Dévonien inférieur. Une comparaison de l'ensemble de la faune de vertébrés fossiles de la rivière Anderson avec les autres faunes boréales d'âge similaire indique la présence d'autres connections paléogéographiques situées au nord et aux alentours du continent des Vieux Grès Rouges et menant à la région baltique, à l'Europe centrale et même aux îles de la Nouvelle-Sibérie et au sud de la Chine, contrairement à la plupart des reconstructions paléogéographiques publiées récemment.

Key words: Lower Devonian, paleogeographic connections, Arctic Canada, arthrodire, Heterostiidae

Introduction

In 1995 and 1997, two joint expeditions of personnel from the Museum für Naturkunde, Berlin, Germany, and the Canadian Museum of Nature, Ottawa, Canada, excavated a fossil fish locality discovered in 1958 by Standard Oil geologists in the Lower Devonian Bear Rock Formation, along the Anderson River of the western Canadian Arctic about 330 km east of Inuvik (Fig. 1). The 1997 expedition included J. Chorn and J. Harrison, formerly of the Natural History Museum, University of Kansas. The museum expeditions recovered many vertebrates, including complete specimens of the actinopterygian *Dialipina* (Schultze and Cumbaa 2001) and the small acanthodian, *Melanoacanthus* (Cumbaa and Schultze 2002). Porolepiforms, principally of the genus *Heimenia* (Ørvig 1969; Schultze 2000) are the most common vertebrate remains, especially the ubiquitous scales; the porolepiform *Nasogaluakus* is known by only one specimen (Schultze 2000). The dipnoan *Melanognathus* (Schultze 2001), represented by one skull roof and many lower jaws, is not as common. Only two small, isolated arthrodire fragments were recovered during the first two expeditions, from a locality about five kilometers downriver.

In 2008, a third joint expedition to the Anderson River locality included Stephen Cumbaa and Richard Day (Canadian Museum of Nature), Hans-Peter Schultze (Natural History Museum, University of Kansas) and John Chorn (Johnston County Community

College, Overland Park, Kansas). Substantial arthrodire remains were discovered. These most recently discovered arthrodire specimens are described here.

Geology and Stratigraphy

In 2001, Cumbaa and Schultze (2002, p. 1457) described the locality on Anderson River as “two 150 m long lenses about 1 km apart that are bisected by the river”. In 2008, we realized that the two lenses belong to the same horizon of limestones and dolomites, which occurs along the river with considerable variation in the number of fish fossils along the exposure. The “two lenses” (AND–3/3A and AND–4/4A, Fig. 1) represent two concentrations of fossil fishes within the same horizon. There are differences in concentration and content even from one side of the river to the other. Complete specimens of *Dialipina*, the acanthodian *Melanoacanthus*, and the head of the porolepiform *Nasoga-luakus*, as well as remains of the porolepiform *Heimenia* were discovered at locality AND–3A on the right bank of the river. Numerous remains of *Heimenia* were found on the left bank at locality AND-3 and on a small rocky islet in the river a few meters offshore from the locality in 1995. *Dialipina* scales and *Melanognathus* jaws were found in the shoreline deposits at locality AND–3. The arthrodires described here were discovered in 2008 in one deeper *in situ* layer at locality AND–3, except for one bone recovered from a loose block at the downstream end of AND-3A. The arthrodire layer is approximately half a meter below the AND-3 layers containing *Dialipina* scales, *Melanognathus* jaws and *Heimenia* remains.

The second concentration or “lens” (AND–4) lies 1 km upriver from locality AND–3 near our 2008 campsite. The locality AND–4 on the right side of the river produced

parts of the porolepiform *Heimenia*, the head and jaws of the dipnoan *Melanognathus* and scales of *Dialipina*. Sarcopterygian scales were found on the left bank (locality AND-4A).

Two additional localities (AND-1 and -5) were discovered in 1995, about 7 km down the river. These localities, small limestone outcroppings, produced only a few fragments of bone. Two isolated fragments of ornamented placoderm bone were found at AND-5, and represent one or more indeterminate arthrodire species.

All the fish remains occur in the lower to lower-middle part of the Bear Rock Formation, which bridges the Lower/Middle Devonian boundary (Balkwill and Yorath 1970). The large ostracode *Moelleritia canadensis*, indicative of an Emsian age (Norris 1997), is ubiquitous in the vertebrate-bearing strata; thus we estimate late Early Devonian (Emsian) in age (for detailed discussion of the age see Cumbaa and Schultze 2002) for the fish remains.

Material and Methods

The arthrodire remains described here were collected in 2008 and are deposited in the Canadian Museum of Nature, Ottawa, Ontario, Canada (CMN) except for one specimen collected in 1995 at locality AND-5, now in the collection of the Museum für Naturkunde, Berlin, Germany (MB).

The specimens were taken in plaster jackets from the field, and were prepared at the Canadian Museum of Nature in Ottawa by Alan McDonald using a pin vise and needle and a PaleoTools Micro Jack. He also prepared Figure 1 (locality map) and Figure 13 (paleogeographic map). The specimens were drawn with a camera lucida on Wild M4

and Leitz M8 microscopes by H.-P. Schultze. The drawings comprising Figures 3B-8B and 12B were transferred in ink by the late Jörg-Peter Mendau, Berlin, and those for Figures 2A, 2B, 9, 10A and 10B were digitally inked by Susan Laurie-Bourque, Ottawa. Photographs for figures 3A, 4A, 5A, 7A, 8A and 13A were taken by S. L. Cumbaa using a Canon EOS 7D digital SLR and EF 24-105 F/4L IS USM lens; those for figures 6A and 11 were taken by O. Sanisidro, Museum of Natural History, Lawrence, Kansas. The photo used as Figure 4C was taken in the field by John Chorn using a Nikon D-90 with AF-S Micro Nikkor 60mm f/2.8G ED lens.

We follow Denison (1978, p. 123-124) in the terminology and the abbreviations of bones and sensory lines.

Systematic paleontology

Most of the collected arthrodire remains belong to one species, *Herasmius dayi* n. sp. At least two other arthrodire species are represented by single bones.

Class Placodermi M'Coy, 1848

Order Arthrodira Woodward, 1891

Suborder Brachythoraci Gross, 1932

Family Heterostiidae Jaekel, 1903

DIAGNOSIS (Zhu et al. 2016, p. 4, emended): Moderately to very large arthrodires with the cranial and trunk shields broad and dorso-ventrally compressed. Skull roof narrows anteriad, and the postero-lateral corners of the skull roof are in line with the foremost

point of the nuchal gap. Small orbits antero-dorsally positioned. Rostral plate comparatively short rostro-caudad, pineal plate narrow. The condyles of the cranio-thoracic articulation are strongly developed, but not transversely elongated. The lateral wall of the thoracic armor is much reduced; the anterior lateral plate is fused with the anterior dorso-lateral plate and forms an elongated, rod-like far anterior reaching process. There is a prominent posterior carinal process of the ventral keel on the median dorsal plate.

REMARKS: Three genera, *Heterostius* Asmuß, 1856, *Herasmius* Ørvig, 1969 and *Yinostius* Wang et Wang, 1984, comprise the family Heterostiidae. The Heterostiidae are placed at the base of the brachythoracan arthrodires by Young (1981) and Denison (1984), whereas *Heterostius* appears within derived Brachythoraci, the Eubrachythoraci, in cladograms of arthrodires published by Zhu and Zhu (2013: *Heterostius* sister of the three included *Dunkleosteus* species) and Zhu et al. (2015: (((*Heterostius* + *Yinostius*) *Dunkleosteus amblyodoratus*) *Dunkleosteus terrelli* + *raveri*)). The main characters for the placement within higher brachythoracans are the pronounced postero-lateral corner of the skull roof, and the posterior carinal process of the median dorsal plate. Zhu and Zhu (2013) cited six synapomorphies of *Dunkleosteus* and *Heterostius*. Zhu et al. (2016) placed one species of *Dunkleosteus*, *D. amblyodoratus*, as sister of *Heterostius* + *Yinostius* based on fusion of the anterior lateral plate and the anterior dorso-lateral plate, a character of Heterostiidae; nevertheless, these plates are unknown in *Dunkleosteus amblyodoratus* (Carr and Hlavin 2010). The latter species is known only by nuchal and paranuchal plates and the parasphenoid. There is a time gap between the first appearance

of the Early/early Middle Devonian Heterostiidae and the Late Devonian Dunkleosteidae; *Yinostius* is of Emsian age, as is *Herasmius*. We will return to this placement later.

Genus *Herasmius* Ørvig, 1969

DIAGNOSIS (Ørvig 1969, p. 278 emended): A brachythoracid arthrodire genus belonging to the family Heterostiidae, reaching moderate size (for that family). Preorbital plates short rostro-caudad and broad compared to the other two genera. Central plate proportionally large, extending backwards laterally to the nuchal plate for about half the rostro-caudal length of that plate. Parannuchal plate proportionally short and wide. Nuchal plate with tripartite anterior portion comprising a broad middle extension bordered by two short lateral processes.

REMARKS: The length/width relationship of the head shield (Ørvig 1969, p. 278) is not accepted here as a character because the middle part of the skull is missing. In addition the specimen is distorted, so that the width of the nuchal is a tectonic feature (Fig. 2A). Tectonic deformation may also be the reason that the bones in the holotype appear thin. *Herasmius* is distinct from the other two genera in the family by the shape of the central plate and their posterocaudal extension along the nuchal plate, and the anterior broad process of the nuchal plate.

TYPE SPECIES: *Herasmius granulatus* Ørvig, 1969

DIAGNOSIS (Ørvig 1969, p. 278/279 emended): Dermal bones showing an ornamentation of very fine, closely-set tubercles. Wide middle part of the tripartite anterior nuchal plate (about 2 times as wide as long rostrocaudad); preorbital plates squarish and a little wider than long; anterior part of central plates squarish.

REMARKS: As part of our comparison, we tried to eliminate the tectonic distortion and to restore the skull roof of *Herasmius granulatus* on the basis of the new species from Anderson River, which was recovered largely complete and relatively undistorted. The nuchal plate of *H. dayi* n. sp. is taken as the focal point. In addition the length of the central plates is equalized with the length of the central plate of *H. dayi* n. sp.. The result is a longer and less wide skull roof (Fig. 2B) with a width/length ratio of about 1.5 similar to *Heterostius*. *Yinostius* and *H. dayi* n. sp. are a little less wide (width/length ratio 1.3 to 1.4).

TYPE LOCALITY: Valley Jakobsendalen, NW part of Andrée Land, Spitsbergen.

GEOLOGICAL AGE: Verdalen member of Stjørdalen Formation, Wood Bay Series, Lower/Middle Devonian (after Birkenmajer 1964 and Piepjohn 1997: Emsian; after Ørvig 1969 and Blicek et al. 1987: at the Lower/Middle Devonian boundary).

Herasmius dayi sp. nov. (Figs. 3-9)

ZooBank No: urn:lsid:zoobank.org:pub:887766C5-5AEB-491E-B866-35CF84BA7C42

HOLOTYPE: CMN FV 54694 (posterior head shield + anterior shoulder girdle = field number AND-3 – 34) (Fig. 3).

REFERRED SPECIMENS: CMN FV 54663a, b (three bones: left suborbital plate, infragnathal + postorbital plate with tubercles and infraorbital sensory line = AND-3 – 3, Fig. 7); CMN FV 54664 (nuchal plate = AND-3 – 4); CMN FV 54665 (left suborbital plate = AND-3 – 5; Fig. 6); CMN FV 54683 (part of median dorsal plate = AND-3 – 23); CMN FV 54697a, b (piece of anterior lateral plate = AND-3 – 37); CMN FV 54699 (median dorsal, right anterior dorso-lateral + anterior lateral, and left central plates = AND-3 – 39; Fig. 4); CMN FV 54700a (left submarginal plate and piece of unidentified bone [probably the right margin of a median dorsal plate] = AND-3 – 40a; Fig. 5); CMN FV 54700b (left anterior lateral and posterior lateral plates = AND-3 – 40b; Fig. 8); CMN FV 54720 (part of median dorsal plate = AND-3 – 60); CMN FV 54737a, b (median dorsal plate broken in different pieces preserved in one block = AND-3 – 77).

LOCALITY: Standard Oil Company locality AR.25.58 at 68°11'06" N Latitude, 125°49'72" W Longitude, Anderson River in the western Canadian Arctic, about 330 km east of Inuvik, N.W.T., Canada.

AGE AND GEOLOGICAL FORMATION: Early Devonian (Emsian); lower part of Bear Rock Formation.

ETYMOLOGY: Named to honor the special efforts by Richard Day toward the excavation of the arthrodires at locality AND-3, as well as his roles as camp manager, chief cook, logistics specialist and expedition member in 1995, 1997, and 2008.

DIAGNOSIS: Ornamentation of tubercles variable in size, from large to small tubercles changing on the same bone. Wide middle part of the tripartite anterior nuchal plate (width 1.5 times its length, thus narrower than in *H. granulatus*). Central plates with anterior and posterior digitate sutures.

DESCRIPTION: The anterior part of the holotype (Fig. 3) is weathered away, and the posterior border represents a saw cut in front of the outcrop wall. It is the skull of a brachythoracid arthrodire with nuchal, paranuchal, central, marginal, postmarginal, and submarginal plates, and remains of the left postorbital plate. The shoulder girdle shows the anterior half of the median dorsal plate, the anterior dorso-lateral plate with anterior lateral plate, the left posterior dorso-lateral and the left posterior lateral plate.

The nuchal plate has a width/length ratio of 1.4, and the median part of the tripartite anterior portion a width/length ratio of about 1.3. The anteriad-directed lateral processes of the tripartite anterior portion are short; the median anterior portion is broad with a digitate anterior suture. The posterior halves of the central plates are preserved; they reach postero-laterad over half the length along the nuchal plate and connect in a zigzag suture with the paranuchal plates. Both central plates have a posteriad-directed medial process, which forms the lateral margin of the tripartite anterior portion of the nuchal plate.

The rounded paranuchal plates are broad and short. The groove of the main lateral

line passes over the paranuchal from the marginal plate to the articulation with the shoulder girdle. On the left paranuchal plate the main lateral line is split; the anterior groove stops in the posterior third of the bone where it approaches the groove of the posterior part of the main lateral line, which continues as the groove of the posterior pit line towards the center of the paranuchal bypassing the anterior part of the main lateral line.

The marginal plates are long and narrow, about 3 times longer than wide. On the marginal plates, the groove of the otic branch of the infraorbital line splits in to the continuing main lateral line and the postero-ventrad directed postmarginal sensory line. The suture of the marginal plate with the paranuchal plate forms a "tongue" towards the paranuchal on the left side, but not on the right side. The right postmarginal plate is displaced from the contact with the marginal plate, whereas on the left side the suture between both plates is difficult to follow. A submarginal plate lies lateral to the marginal and postmarginal plates. The right one is preserved turned in to the skull plane, whereas the left one is pushed against the skull so that its shape is not visible. The right submarginal plate has a long anteriad directed shaft and a posterior short part oblique to it, the foot. The boot-like shape of the submarginal plate is unusual within arthrodires.

Single plates were collected in addition to the holotype. These are the nuchal, central, suborbital and submarginal plates. Specimen CMN FV 54664 represents a large (1.6 times the size of the nuchal plate of the holotype) nuchal plate lacking the posterior margin. It shows the broad median part with its anterior digitate margin and the small anteriad-directed lateral processes of the tripartite anterior portion. Large and small tubercles cover the surface. A broad band of small tubercles runs antero-posteriad in the middle of the nuchal.

A nearly complete left central plate (Fig. 4) appeared when the right part of the median dorsal plate was lifted on specimen CMN FV 54699. In addition the right antero-lateral and the anterior dorso-lateral plates became visible. The central plate has the posterior zigzag suture like the central plates of the holotype and shows the medial process, which borders laterally the tripartite anterior portion of the nuchal; in addition the anterior part of the central is preserved with a digitate anterior border and the grooves of two sensory lines, the supraorbital and the central lateral line. A weak groove runs of the posterior pit line runs postero-laterad on the postero-lateral extension of the central plate towards the paranuchal plate. The suture with the postorbital plate is straight.

A separate left submarginal plate (Fig. 5) appears on specimen CMN FV 54700a. It shows the same boot-like shape as the right submarginal plate on the holotype; it is more arched towards the marginal and postmarginal plates than the submarginal on the holotype. We did not find any submarginal plate of similar shape in the literature, and the submarginal plate is not known for any of the three heterostiid genera. Nevertheless an identically- shaped bone exists in the Estonian material of *Heterostius ingens* (personal communication by E. Mark-Kurik). Thus the boot-like shape of the submarginal plate seems to be unique for heterostiids.

There are two bones seen only from their inside surfaces. We interpret them as left suborbital plates (Figs. 6, 7) by comparison with the suborbital plate of *Heterostius* (Heintz 1930, fig. 2). The isolated one (CMN FV 54665, Fig. 6) has a posterior part with irregular margins; it narrows anteriorly and arches antero-dorsad so that it surrounds partially the orbit (see reconstruction, Fig. 9). The second left suborbital plate is associated with two plates on specimen CMN FV 54663 (Fig. 7); it is 1.5 times larger

than CMN FV 54665 and has a rounded posterior dorsal margin compared to the bayed posterior dorsal margin of the smaller suborbital plate.

The elongated straight and flat bone (Fig. 7) may represent an infragnathal. The reason for such an interpretation is the ridge parallel to the straight margin of the bone. The bone looks quite different from other infragnathals in arthrodires. Infragnathals are not known in heterostiids. The tuberculated plate with the groove of a sensory line may be part of the postorbital plate judging from the arched course of the sensory line groove. This is the postorbital part of the infraorbital sensory line, if the interpretation of the bone as the postorbital plate is correct. The tuberculated process could be compared with the process on the right postorbital in the reconstruction of *Heterostius ingens* (Heintz 1930, fig. 2). In front of the process lies a long area overlapped by the preorbital. That would mean that the postorbital plate does not reach the orbit, and the preorbital plate is broader than in both reconstructions of *Herasmius*, that by Ørvig (1969) and the one presented here (Fig. 9), and forms the posterior margin of the orbit. Nevertheless, we are not certain of the identification.

In the holotype, the partially preserved shoulder girdle with median dorsal plate, anterior dorso-lateral that extends as far forward as the anterior lateral plate, with posterior dorso-lateral and posterior lateral plates follows behind the skull roof (Fig. 3). The anterior part of the median dorsal is preserved in the holotype only. A short antero-median process reaches in to the nuchal gap. The median dorsal possesses laterally an invagination, into which the anterior dorso-lateral plate fits. The anterior dorso-lateral plate reaches around the antero-lateral extension of the median dorsal plate forming a short pre-median dorsal process. The median dorsal plate possesses a median keel on its

inner side that extends posteriad reaching the cranial process (Fig. 3). The image of the median dorsal plate of specimen CMN FV 54699 (Fig. 4C) taken in the field shows the median dorsal plate best, as it suffered somewhat during removal and transport (Figs. 4A, B). The short antero-median process is not known from *Heterostius*. The invagination of the lateral side and posteriad reaching cranial process can be clearly seen.

Two anterior dorso-lateral plates (Figs. 4, 8) were discovered in addition to the ones on the holotype. The right anterior dorso-lateral on CMN FV 54699 (Fig. 4) is preserved together with its fused anterior lateral plate. In contrast the isolated left anterior dorso-lateral plate (CMN FV 54700b) is associated with the posterior dorso-lateral plate, but it lacks the anterior lateral plate (Fig. 8); the latter is broken off at the antero-ventral corner of the anterior dorso-lateral plate. The middle tuberculated portion of the external surface of the anterior dorso-lateral plate is bordered dorsally by the area overlapped by the antero-lateral corner of the median dorsal plate and ventrally by the area overlapped by the posterior lateral plate. The anterior dorso-lateral plate extends as a triangular shape on to the posterior dorso-lateral plate. The posterior border of the posterior dorso-lateral plate is broken; nevertheless the plate should not reach much further caudad. The posterior dorso-lateral plate has only a small exposed area; most of the plate is covered by the median dorsal and the anterior dorso-lateral plates, and some of the ventral part by the posterior lateral plate. The groove of the main lateral line runs along the lower part of the anterior dorso-lateral and posterior dorso-lateral plates; it continues from the anterior dorso-lateral plate to the posterior dorso-lateral plate at the point where the suture between the plates reaches anteriorly. A narrow strip, the pre-median dorsal process, borders anteriorly the area overlapped by the median dorsal plate; it surrounds the antero-lateral

extension of the median dorsal plate. In front the short and strong condyle, which articulates with the paranuchal plate, points upwards. Deep depressions border the condyle posteriorly and antero-ventrally. The narrow antero-ventral groove separates the condyle from the subglenoid fossa. The subglenoid fossa has a grooved (fan shaped) lateral surface and a small dorsal area.

A large overlapped area lies below the tuberculated area of the anterior dorso-lateral plate; that could be the overlap area of the posterior lateral plate, which would reach forward past the area of articulation. Gross (1933, fig. 9 A, F) figured and described a groove in the same area in *Heterostius*; Abel (1927, figs. 1, 2A) reproduced unpublished figures of *Heterostius* by Jaekel, where the deepened region is interpreted as attachment for muscles. On the holotype of *Herasmius dayi* n. sp., an elongated bone, the posterior lateral plate, lies in this area on the left side of the specimen (Fig. 3).

The second isolated bone, a right anterior dorso-lateral plate together with its anterior lateral plate, appeared when parts of the median dorsal plate were removed on specimen CMN FV 54699 (Fig. 4A, B). The area overlapped by the median dorsal plate is preserved with the narrow strip surrounding the antero-lateral extension of the median dorsal plate, the pre-median dorsal process. In front of the narrow strip, the condyle of the exoskeletal articulation is visible. A rounded narrow anterior lateral plate extends in front of the anterior dorso-lateral plate.

RECONSTRUCTION: The reconstruction of *Herasmius dayi* n. sp. (Fig. 9) is based mainly on the holotype. The isolated central plate (Fig. 4) allowed the extension of the skull roof further anteriad. Pre- and postorbital plates are adapted from the reconstruction

of *Herasmius granulatus* by Ørvig (1969), with the addition of the suborbital plates after the *Heterostius* reconstruction by Heintz (1930). The anterior shape of the central plate leaves a wider space for the pineal plate than in *Herasmius granulatus* and *Heterostius ingens*. The position of the submarginal corresponds to its appearance in the holotype. It is not certain that it covered the antero-lateral plate in dorsal view. Placing a submarginal in Heintz's reconstruction of *Heterostius ingens* would cover the antero-lateral plate partly. The shoulder girdle is well preserved in the holotype; the posterior part of the median dorsal plate is added from specimen CMN FV 54699 (Fig. 4).

COMPARISON: Ørvig (1969) described the new heterostiid genus, *Herasmius*, from the Verdalen member of Stjørdalen Formation, at the boundary of Lower to Middle Devonian of Spitsbergen and compared it with *Heterostius* from the Middle Devonian (Eifelian) Aruküla beds of Estonia. Both genera have in common the anterior position of small orbits and the arrangement and shape of the preorbital, postorbital, marginal and paranuchal plates and their sensory line system in the cranial roof, as well as a long antero-lateral fused to the anterior dorso-lateral plate and a pronounced posterior cranial process on the median dorsal plate in the shoulder girdle. The shape of the suborbital plate is also very similar. After Ørvig (1969), the main difference between both genera is the width/length ratio of the skull roof. In *Herasmius* the skull length is supposedly 70% of skull width whereas in *Heterostius* it is 54%. Nevertheless there are problems with these ratios as shown above. The type and only specimen of *Herasmius granulatus* is tectonically deformed in lateral direction, so that the length/width ratios are misleading. The nuchal is not as broad as in Ørvig's 1969 reconstruction (fig. 3A; here Fig. 2A). In addition, the

anterior portion of the skull roof is separated from the left posterior part, so that the length of the skull roof is not measurable. Proportions given by Ørvig (1969) are therefore not verifiable and not usable to argue that the specimens of Vestspitsbergen belong to a different genus than *Heterostius*. Our reconstruction of Ørvig's form from Vestspitsbergen, *Herasmius granulatus* (Fig. 2B), results in a length/width ratio of the skull roof of 67%, the same as that of *Heterostius ingens*. *Herasmius dayi* n. sp. gives a length/width ratio of 74%, similar to that of *Yinostius major* (75%). Thus the length/width ratio cannot be used to distinguish the three genera.

Comparing *Heterostius ingens* Asmuß, 1856, with our new reconstruction of *Herasmius granulatus* shows that the length/width proportions of the skull roof are similar; even the nuchal plate has a similar length/width ratio. The difference between the two species is the configuration of the anterior portion of the nuchal plate. The median process reaches rostrad with digitate sutures with the central plates left and right of a median narrow anterior spike (Fig. 10A) in *Heterostius ingens*, whereas the median process is tripartite in *Herasmius granulatus* and *H. dayi* n. sp., with a broad median portion accompanied by two short lateral processes. The second difference between both genera is the length and relation to the nuchal plate of the central plates. The central plates reach farther posteriad along the nuchal plate in *Herasmius* than in *Heterostius*. In contrast the distance is short in *Heterostius*, thus the paranuchal is shorter and broader in *Herasmius*.

The shapes of the triangular nuchal plate and of the central plates of the third genus, *Yinostius* (Fig. 10B), of the Heterostiidae are very distinct from those of the same bones of the two other genera of the family. We use here the reconstruction of *Yinostius*

by Wang and Wang (1984, fig. 1C; here Fig. 10B) with the postero-lateral corners not as far back as in Zhu et al. (2015, figs. 6D, 7C, 8A), as the photographs and figure 5 in Zhu et al. (2015) show a position as in Wang and Wang (1984, fig. 1C). The triangular nuchal plate of *Yinostius* is very distinct from that of the other two genera; it lacks a tripartite anterior portion. The central plates reach only a little back from the tip of the nuchal plate so that the paranuchal plates are very long antero-medial to postero-lateral. The central plates are very short and the preorbitals narrow in comparison to the other two genera.

The median dorsal plate of *Herasmius* (Ørvig 1969, fig. 4D; here Figs. 3, 9) possesses a short anterior process extending to the space between the nuchal and median dorsal plates. Such a process does not occur in *Heterostius* and *Yinostius*. The posterior cranial process is known in all three genera; the reconstruction of the median dorsal of *H. granulatus* (Ørvig 1969, fig. 4C) does not show the process, as this part of median dorsal is not preserved.

We place the arthrodire from Anderson River in Ørvig's genus *Herasmius* based on the shape of the anterior portion of the nuchal plate and the posterior extension of the central plates. The new species, *Herasmius dayi*, is distinct from *H. granulatus* in the anterior shape of the central plates, which are squarish in *H. granulatus* but narrower and with a digitate suture with the preorbital plate in *H. dayi* n. sp.. The pineal plate appears to be wider in *H. dayi* n. sp.. It separates the anterior parts of the central plates judging from their shape; that is not the case in *H. granulatus*, *Heterostius* and *Yinostius*. The middle part of the anterior tripartite portion of the nuchal plate is wider in *H. granulatus* (two times wider than long) than in *H. dayi* n. sp. (1.5 times wider than long).

The description of *Herasmius dayi* n. sp. adds to our knowledge of the heterostiids in the following ways:

1. Neither a description nor the presence of a submarginal has been published from heterostiids. The boot shaped submarginal occurs in position in the holotype of *H. dayi* n. sp.. This is a shape quite different from the elongate submarginal in other arthrodires; however, a submarginal of *Heterostius* in Estonian material is said to have the same shape (E. Mark-Kurik, personal communication).
2. Infragnathals are not known in heterostiids. The bone interpreted as such here for *H. dayi* n. sp. is different from those of other arthrodires, which are not flat like this bone. There may be some similarities to *Angarichthys* (Heintz 1934, fig. 28I), an homosteid.
3. A small posterior lateral plate is known in *Heterostius* (Fig. 10A), but is lacking in *Homostius* after Heintz (1934). In contrast to *Heterostius*, the posterior lateral plate in *Herasmius* is elongated.
4. The suborbital is new for the genus *Herasmius*. It has a shape similar to that in *Heterostius*.

OTHER ARTHRODIRE MATERIAL:

Two placoderm bones from locality AND-3 do not belong to the genus *Herasmius*, a plate with small tubercles CMN FV 54691 (AND-3 – 31; Fig. 11) and a right suborbital plate CMN FV 54827 (AND-3A – 47; Fig. 12). The plate with small tubercles represents a central plate cf. *Bryantolepis*, a sister taxon to Phlyctaenoidei (included in the paraphyletic “Actinolepidoidei” by Dupret et al. 2009 and Elliott and Carr 2010). The groove for the central lateral line and pit lines are missing. The anterior me-

dial corner of the plate is broken off. Bryantolepids are known from Lower Devonian rocks.

The right suborbital plate CMN FV 54827 (Fig. 12) has a dorsal margin invaginated slightly for the postorbital plate; the posterior margin is straight with a narrow overlap area for the postsuborbital plate; its ventro-posterior corner is broken off (or cut during field collection). The ventral margin shows a broad ventral extension. The anterior process is massive with a dorsal extension as in *Dunkleosteus*. The anterior margin above the anterior process is slightly bowed towards anteriad. The vertical part of the infraorbital sensory canal is preserved, but neither its anterior extension nor the supraoral canal. The squarish shape of the suborbital plate is otherwise found only in *Dunkleosteus* within arthrodires (Heintz 1932, fig. 21); it lacks the ventral tongue-shape extension of the anterior process of *Dunkleosteus*, but possesses the dorsal protuberance of the anterior process (labeled “a” in Heintz 1932, fig. 21). The ventral margin is not straight as in *Dunkleosteus* but has a similar broad ventral extension. We place the specimen within the dunkleosteids. That placement would extend the temporal extent of the dunkleosteids to the Early Devonian and close the time gap between Early Devonian Heterostiidae and Late Devonian Dunkleosteidae see above).

We collected scrappy arthrodiran material (MB f.19149) in 1995 at locality AND-5. These are two unidentifiable pieces of bone with large tubercles.

Paleogeography

Genera shared with other Emsian localities

The arthrodire *Herasmius dayi* n.sp. is the most recent addition to the small but relatively diverse Early Devonian (Emsian) fauna of Anderson River, NWT, Canada. The new species shows closest similarities to *Herasmius granulatus* Ørvig (1969) from Vestspitsbergen (Verdalen Member, Stjørdalen Formation, Wood Bay Group) in the Svalbard archipelago, also of Emsian age (Ørvig 1969; Clément 2001*a, b*). The two localities also share a second genus, the porolepiform *Heimenia* (Ørvig 1969; Clément 2001*b*; Mondéjar-Fernández and Clément 2012).

Herasmius is so far restricted to the Anderson River and to Spitsbergen, whereas *Heimenia* has a wider distribution in the Lower Devonian, from Spitsbergen to the Baltic region (Lyarskaya 1981, Clément 2001*a*), central Europe (Holy Cross Mountains, Poland [Ørvig 1969], and the Klerf Beds of the Eifel, Rhenish Slate Massif, Germany [Jessen 1989: early Emsian]), as well as to China (Wang 1986: Givetian; Zhu 2000; Zhao and Zhu 2010: late Emsian). Thanh and Janvier (1987) list *Heimenia*-like sarcopterygian scales from the Lower Devonian (Lochkovian) of Vietnam.

A third Anderson River vertebrate genus is found not in Spitsbergen but in Lower Devonian strata elsewhere. The actinopterygian *Dialipina salgueiroensis* was first described from Anderson River (Schultze 1968; Schultze and Cumbaa 2001); the genus *Dialipina* has also been reported from Lower Devonian deposits (Lochkovian) on Kotelnny Island, New Siberian Islands, Russia (Mark-Kurik 1974; Schultze 1977), and from South China (lower Emsian; Zhao and Zhu 2010). Schultze (1992) also reported *Dialipina* from the Kotui Basin, Siberia (Lochkovian and Pragian). The Lochkovian Kotui Basin fossil skulls have since been re-described by Giles et al. (2015) as a new genus and species, *Janusiscus schultzei*, which is interpreted as a basal gnathostome.

Table 1 lists Lower Devonian localities that share vertebrate genera with the Anderson River localities.

Paleogeographic connections and possible dispersal routes

The shared presence of two genera of large, active fish (*Herasmius* and *Heimenia*) at Anderson River, NWT, Canada, and on Spitsbergen in the Svalbard archipelago indicates a viable open-water connection between the two areas by late Early Devonian. The presence of *Heimenia* in the Lower Devonian of the Baltic region, central Europe, south China and possibly Vietnam suggests widespread distribution of *Heimenia* by the Early Devonian. Similarly, occurrences of a third Anderson River fish genus, the much smaller *Dialipina*, indicate a very lengthy marine connection by the late Early Devonian between the Canadian Arctic, Siberia, and South China.

Paleoenvironment

In discussing paleogeographic connections between the three genera and the localities in Table 1, we focus on marine links. The Anderson River fauna is unquestionably shallow water marine, with ostracodes, eurypterids, other invertebrates and fishes together in a limestone and dolomite matrix consistent with its mapped description within the marine Bear Rock Formation (Balkwill and Yorath, 1970; Cumbaa and Schultze 2002).

The *Herasmius* and *Heimenia* locality in Spitsbergen (Wood Bay Formation, Verdalen Member) has traditionally been considered to be of continental origin (Pernègre and Blieck 2016). The Verdalen Member is primarily composed of carbonate sediments but many of the fossils have been found in terrigenous material. However, the occur-

rence of lingulids and other usually marine fossils lead Goujet (1984) and others (Blieck 1984; Goujet and Emig 1985; Blieck and Janvier 1999) to the conclusion that the paleoenvironment was semi-continental – fjords and estuaries fed by rivers (Pernègre and Blieck 2016). Blomeier et al. (2003) examined the sedimentation of the Wood Bay Formation and concluded that in the upper part of the Verdal Member, the late Early Devonian environment was a broad lake plain which developed into a marginal marine coastal plain with open connections to the sea, influenced by recurrent sea-level highstands. These studies, while differing in specific interpretation, indicate that the depositional environment of the late Early Devonian *Herasmius* and *Heimenia* fauna in northern Spitsbergen was intermittently or more permanently marginal marine.

Similarly, the source of deposition at localities in the Baltic region has been interpreted as continental, based in part on the clastic sedimentation. Others (Mark-Kurik 1991a; Kuršs 1986, 1992) considered them as shallow marine. Kuršs (1992) noted that near the end of the Early Devonian there was a shift from marine carbonate to siliciclastic deposition, most likely from the Baltic Shield and/or the Caledonian foreland.

The paleoenvironment of *Heimenia* from the Klerf Beds of the Eifel, Rhenish Slate Massif of Germany is not entirely clear, but a recent study indicates that the area in the Early Devonian included marine, brackish, and terrestrial settings (Wehrmann et al. 2005). Porolepidid porolepiforms are considered as fully marine or near shore inhabitants (Clément 2001a; Mondéjar-Fernández and Clément 2012). The fish-bearing sequences in the Alken quarry are interpreted as representing a nearshore marine environment. Intertidal, shallow water habitat with reduced salinity persisted over a lengthy pe-

riod in the Early Devonian, with the basin characterized by balanced subsidence, rapid sedimentation and fluctuating sea levels (Wehrmann et al. 2005).

Localities 5 and 6 in Table 1, Kotelny Island (Siberia/New Siberian terrane) and southwest China (South China block), are clearly of marine origin. Schultze (1977, 1982) cited a marine environment for the Kotelny Island, Siberia *Dialipina* locality. The Yujiang Assemblage from Sichuan, China, which includes *Dialipina*, is associated with conodonts, corals, brachiopods and bivalves indicating a neritic shelf facies (Zhao and Zhu 2010). The Chuandong Assemblage from Yunnan, China, which includes *Heimenia*, had a shelf facies depositional environment (Zhao and Zhu 2010).

In conclusion, the paleoenvironmental interpretations of the localities where *He-rasmusius*, *Heimenia* and *Dialipina* occur place the genera in marine to lagoonal biota but always with a connection to the marine realm.

Dispersal routes

Plotting possible dispersal routes for these genera can be seen as a work in progress. The early occurrences of ?*Heimenia* in the Lochkovian of Vietnam and of *Dialipina* in the Lochkovian and Pragian of Siberia could indicate a migration route from the east and northeast to Spitsbergen and Anderson River. A connection between the Canadian Arctic north of and around the Old Red continent to Spitsbergen, Siberia, the Baltic region (as in Blieck and Cloutier 2000, fig. 2A; Mark-Kurik et al. 2013 for the Lochkovian; Pernègre and Blieck 2016 for Pragian and Emsian) and to central Europe is necessary to explain the faunal similarities. Lukševičs et al. (2010) discussed paleozoogeographical connections of the Devonian vertebrates of Baltica. Blieck and Janvier (1999), building on Young (1990), linked the occurrences in the Canadian Arctic, Spitsbergen and Siberia

within an Arctic faunal province and the occurrences in the Baltic region, Poland and the Old Red continent to a North Atlantic faunal province (see also Blieck 2009, fig. 10).

Zhao and Zhu (2010) discussed possible dispersal routes within the context of five major vertebrate faunal provinces for the Early Devonian, highlighting three possible routes to accommodate the evidence from China, based on two different paleogeographic reconstructions.

There have been significant changes in the understanding of Paleozoic paleogeography since the late 1980s, particularly the movement of individual blocks and terranes, the timing of collisions as larger continental masses were formed, and their geographic positions. For example, the latitudinal position of the locality at Anderson River, NWT (~68°N currently) would have an estimated latitudinal position in the Early Devonian near 30°N (Ziegler 1981), approximately 5°-10°N (Scotese and McKerrow 1990; Kent and Van der Loo 1990), or as roughly 5°-8°S latitude in the current decade (Lawver et al. 2011; Golonka and Gaweda 2012; Torsvik and Cocks 2013; Domeier and Torsvik 2014). Witzke (1990) was an exception to the conclusions in the majority of earlier papers in estimating more southerly positions for Laurentia + Baltica (now Laurussia). Here we use the more recent paleogeographic and plate tectonic papers (Lawver et al. 2011; Golonka and Gaweda 2012; Torsvik and Cocks 2013; Domeier and Torsvik 2014) to estimate the paleolatitude for the Anderson River locality in the Emsian as roughly 5°-8° S latitude.

Figure 13 indicates the position of the Lower Devonian localities that share genera with the Anderson River locality on a paleogeographic reconstruction that approximates the position of paleocontinents and terranes in the Early Devonian. Young (1990) plotted many Devonian vertebrate occurrences, including most of those listed here in Ta-

ble 1, on a base map by Scotese (1986). He did not include the Anderson River locality. Young's base map is an Early Devonian (Lochkovian) projection, but the localities include those from the entire Devonian.

Many published maps of Early Devonian paleogeography and paleobiogeography show that potential faunal dispersal routes between some of the localities in Table 1 could have been blocked by the coalescence of land masses in the late Early Devonian. However, most show more open marine connections in the Late Silurian and earliest Devonian (e.g., Johnson et al. 2000; Golonka et al. 2003; Lawver et al 2011; Torsvik and Cocks 2013), and it seems likely that the presence of at least some of the genera recognized from the late Early Devonian localities in Table 1 is the result of earlier connections.

No landmass barriers are apparent in the late Early Devonian reconstructions (Figs. 13) between the New Siberian Islands terrane and the South China block, and the Anderson River and other Laurussian localities presented in Table 1. Distance and water depth could well have presented obstacles, but not barriers, to slow swimmers dependent on shallow water environments.

Figure 13, based on Colpron and Nelson (2009; fig. 12), although placing the paleocontinents and terranes 15 degrees or more farther north than the 5°-8° S latitude of more recent studies, presents a view of the northern margin of Laurussia in the Early Devonian (Emsian, 401 Ma) showing shallow marine and shelf connections between the Laurussian localities of Anderson River and Spitsbergen, (W-E) and the Siberia/New Siberian Islands terrane locality of Kotelny Island (SW-NE), as well as open water at or adjacent to the Baltic states, central Poland and Rhenish Slate localities to the southeast.

Open marine connections between the more northern localities and those that were near the central and southern parts of Baltica at the time it collided with Laurentia to form Laurussia, are less straightforward than they would have been in the Late Silurian and Lochkovian (Mark-Kurik et al. 2013). An Emsian connection could have been possible from the western Canadian Arctic north of and around the Old Red Sandstone Continent, through a shallow shelf separating it from Siberia (Arctic Province of Blieck and Janvier 1999). A lengthy journey through the shrinking Ural Ocean and around the northeast part of Baltica and down the Rheic Ocean coast (North Atlantic Province of Blieck and Janvier 1999) would have been required to complete the journey. While possible, this lengthy route seems unlikely. If most of the paleogeographic base maps are correct and the contact between Laurentia and Baltica was complete by the late Early Devonian, it seems probable that *Heimenia*, the single genus linking the Anderson River Emsian fauna with the Baltic and central Europe localities, had dispersed before the closing of open marine links. *Heimenia* is considered to be a marine species (Mondéjar-Fernández and Clément 2012).

Of the genera not shared between Spitsbergen and the Anderson River, NWT, the Spitsbergen thelodont *Amaltheolepis* is known from the Emsian of Lithuania and the Severnaya Zemlya archipelago (Karatajuté-Talimaa 1978; Märss et al. 2007), and the Eifelian of Vestspitsbergen (Ørvig 1969; Karatajuté-Talimaa 1978), requiring a connection between Vestspitsbergen, the Baltic and Russia. *Dialipina*, first described from Anderson River, is known also throughout the Lower Devonian of Siberia (Gedinnian, Kotelný Island; Lochkovian and Pragian, Kotui Basin (Schultze 1977, 1992), but not from areas between Siberia and Spitsbergen. The early occurrences of *Dialipina*

indicate an Early Devonian connection from Siberia to the Canadian Arctic; the same direction from Russia to the Baltic and Spitsbergen is shown by the occurrences of *Amaltheolepis*. *Heimenia* shows an even wider distribution, including China and possibly Vietnam (Fig. 13).

Discussion

A connection between the Canadian Arctic north of and around the Old Red Sandstone continent to Spitsbergen, Siberia and the Baltic region (as in Dineley and Loeffler 1993, fig. 6.1; Blicek and Janvier 1999, fig. 9.17 [*Turinia* fauna connecting the Arctic and North Atlantic provinces] and Blicek and Cloutier 2000, fig. 2A) and to central Europe is necessary to explain the faunal similarities. Mark-Kurik (1991) used the communality of placoderm fishes (and partly the co-occurring fish fauna) to correlate Emsian deposits over the mentioned area. The placement of continental blocks and terranes in most recent paleogeographical reconstructions of the late Early Devonian does not accommodate such connections.

Johnson et al. (2000, fig. 10a,b), for example, using paleogeographic reconstructions by Ziegler (1988), showed that an open marine connection existed in the Silurian/earliest Early Devonian between the Baltic basin on the east of the Old Red continent south to the Rhineland, and west to western and northern North America. However, their late Early Devonian reconstruction shows the marine Baltic basin as completely enclosed. The paleogeographic reconstructions of Golonka et al. (2003, fig. 9) and Golonka and Gaweda (2012, fig. 10) reflect the facies and occurrences of the taxa discussed here (Table 1) reasonably well, but also include a closed Baltic basin. These

localities in Table 1 are all coastal and connected by sea in the Colpron and Nelson (2009) reconstruction (see also Blieck and Cloutier 2000, fig. 2A after McKerrow et al 1991 fig. 6). The Colpron and Nelson (2009)-based reconstruction (Fig. 13), although positioning the continental blocks and terranes farther north than most recent sources, best accommodates the evidence for paleogeographic connections provided by the occurrence of the Early/Middle Devonian fish fauna at Anderson River and the other localities in Table 1, particularly by showing an open Baltic basin and a more open “northwest passage” around the northern edge of Laurussia.

Until such time as they are found elsewhere, the mesacanthid acanthodian *Melanoacanthus minutus* (Cumbaa and Schultze 2002), the holoptychiid porolepiform *Nasogaluakus chorni* (Schultze 2000), and the early lungfish, *Melanognathus canadensis* (Jarvik 1967; Schultze 2001), are unique to the Lower Devonian (Emsian) shallow marine fauna of the Anderson River.

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vored widespread marine connections among Early Devonian fish faunas.

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Table 1. Lower Devonian localities, shared genera, and paleogeographic units.

Lower Devonian Locality	Shared Genera	Paleocontinent or Terrane	
		Mid-Late Silurian	Early Devonian
Anderson River, NWT, Canada (this paper; Schultze 2000; Schultze 1968; Schultze & Cumbaa 2001)	Arthrodira - <i>Herasmius</i> Actinopterygii - <i>Dialipina</i> Porolepiformes - <i>Heimenia</i>	Laurentia	Laurussia
Vestspitsbergen, Svalbard, Norway (Ørvig 1969; Clément 2001b; Mondéjar- Fernández & Clément 2012)	Arthrodira - <i>Herasmius</i> Porolepiformes - <i>Heimenia</i>	Svalbard	Laurussia
Lithuania, Poland, Belarus (Lyarskaya 1981; Clément 2001a; Ørvig 1969)	Porolepiformes - <i>Heimenia</i>	Baltica	Laurussia
Rhenish Slate Massif, Germany (Jessen 1989)	Porolepiformes - <i>Heimenia</i>	Baltica	Laurussia
Kotelny Island, Siberia, Russia (Schultze 1977, 1992)	Actinopterygii - <i>Dialipina</i>	New Siberian Islands terrane	Siberia + New Siberian Islands
Yunnan and Sichuan, China; ?NE Vietnam (Zhao & Zhu 2010; Wang 1986; Zhu 2000; Trinh & Janvier 1987)	Actinopterygii - <i>Dialipina</i> Porolepiformes - <i>Heimenia</i>	South China	South China

Figure captions

Figure 1.

Localities along Anderson River: AND-3 and -3A, and AND-4 and -4A are localities on the opposite sides of the river; these localities belong to same horizon. AND-5 lies about 7 km down the river from locality AND-3. Db, Lower Devonian; Ks, Upper Cretaceous. Geological mapping based on Balkwill and Yorath (1970).

Figure 2.

Herasmius granulatus Ørvig, 1969. A. Reconstruction of skull roof of holotype by Ørvig (1969, fig. 3A); B. Reconstruction of skull roof of holotype based on nuchal and central plates of *H. dayi* without tectonic distortion. Verdalen Member, Stjørdalen Formation, Wood Bay Group, Emsian/Eifelian; Vestspitsbergen. Ce, central plate; Nu, nuchal plate.

Figure 3.

Herasmius dayi n. sp., holotype CMN FV 54694, posterior skull roof + anterior shoulder girdle in dorsal view; Bear Rock Formation, upper Emsian; Anderson River, N.W.T., Canada. A. photograph; B. interpretative drawing. Adl, anterior dorso-lateral plate; Al, antero-lateral plate; Ce, central plate; ioc.ot, otic branch of the infraorbital line; lc, main lateral line; Mg, marginal plate; Md, median dorsal plate; Nu, nuchal plate; Pnu, paranuchal plate; Pdl, posterior dorso-lateral plate; pmc, postmarginal sensory line; Pmg, postmarginal plate; ppl, posterior pit line; Sm, submarginal plate. Scale bar = 1 cm.

Figure 4.

Herasmius dayi n. sp., CMN FV 54699, median dorsal, right anterior dorso-lateral with antero-lateral, and left central plates; Bear Rock Formation, upper Emsian; Anderson River, N.W.T., Canada. A. photograph; B. drawing; C. specimen in the field. Adl, anterior dorso-lateral plate; Al, antero-lateral plate; cc, central lateral line; Ce, central plate; Md, median dorsal plate; o.Md, area of Adl overlapped by Md; ppl, posterior pit line; soc, supraorbital lateral line. Scale bar in drawing = 1 cm.

Figure 5.

Herasmius dayi n. sp., CMN FV 54700a, left submarginal plate in lateral view; Bear Rock Formation, upper Emsian; Anderson River, N.W.T., Canada. A. photograph; B. drawing. Scale bar in drawing = 1 cm. *Dialipina* scale visible above center of submarginal.

Figure 6.

Herasmius dayi n. sp., CMN FV 54665 left suborbital plate from the inside; Bear Rock Formation, upper Emsian; Anderson River, N.W.T., Canada. A. photograph; B. drawing. Scale bar = 1 cm.

Figure 7.

Herasmius dayi n. sp., CMN FV 54697, left suborbital from the inside, infragnathal from the inside, and unidentified bone. A. photograph; B. drawing. ioc.pt, postorbital part of

infraorbital sensory line; Ig, ?infragnathal; Pto, postorbital plate; So, suborbital plate.

Scale in drawing = 1cm.

Figure 8.

Herasmius dayi n. sp., CMN FV 54700b, left anterior dorso-lateral (antero-lateral broken off) and posterior dorso-lateral plates in lateral view; Bear Rock Formation, upper Emsian; Anderson River, N.W.T., Canada. A. photograph; B. drawing. Adl, anterior dorso-lateral plate; gp, glenoid process; lc, main lateral line; o.Md, area of Adl overlapped by median dorsal plate; o. Pl, area of Adl overlapped by median dorsal plate; Pdl, posterior dorso-lateral plate; sgp, subglenoid process. Scale bar in drawing = 1cm.

Figure 9.

Herasmius dayi n. sp., reconstruction of skull roof and shoulder girdle in dorsal view based on holotype CMN FV 54694, 54699 (central, antero-lateral and median dorsal plates), 54665 (suborbital plate) and 54700a (submarginal plate); Adl, anterior dorso-lateral plate; Al, antero-lateral plate; cc, central lateral line; Ce, central plate; ioc.ot, otic portion of the infraorbital sensory line; lc, main lateral line; Md, median dorsal plate; Mg, marginal plate; Nu, nuchal plate; Pdl, posterior dorso-lateral plate; Pmg, postmarginal plate; Pi, pineal plate; Pl, postero-lateral plate; pmc, postmarginal sensory line; Pn, paranuchal plate; Pro, preorbital plate; Pto, postorbital plate; Ro, rostral plate; Sm, submarginal plate; So, suborbital plate; soc, Supraorbital sensory line. Bear Rock Formation, upper Emsian; Anderson River, N.W.T., Canada.

Figure 10.

A. *Heterostius ingens* Asmuß, 1856, reconstruction of skull and shoulder girdle in dorsal view after Heintz (1930, fig. 2). Aruküla beds, Eifelian, Middle Devonian; Estonia. B. *Yinostius major* Wang and Wang, 1984; reconstruction of skull and shoulder girdle in dorsal view after Wang and Wang (1984, fig. 2). Jiucheng Formation, upper Emsian, Lower Devonian; near Wuding, Yunnan Province, south-western China.

Adl, anterior dorso-lateral plate; Al, antero-lateral plate; cc, central lateral line; Ce, central plate; ioc, infraorbital sensory line; ioc.ot, otic portion of the infraorbital sensory line; lc, main lateral line; Md, median dorsal plate; Mg, marginal plate; Nu, nuchal plate; orb, orbit; Pdl, posterior dorso-lateral plate; Pmg, postmarginal plate; Pi, pineal plate; Pl, postero-lateral plate; pmc, postmarginal sensory line; Pn, paranuchal plate; Pro, preorbital plate; Pto, postorbital plate; Ro, rostral plate; Sm, submarginal plate; So, suborbital plate; soc, supraorbital sensory line.

Figure 11.

‘Bryantolepis,’ unidentified plate, CMN FV 54691B; Bear Rock Formation, upper Emsian; Anderson River, N.W.T., Canada. Scale bar = 1 cm.

Figure 12.

‘Dunkleosteus’; suborbital plate, CMN FV 54827, in lateral view. ioc.so, suborbital portion of infraorbital sensory canal. A. photograph; B. drawing; scale in drawing = 1 cm. Bear Rock Formation, upper Emsian; Anderson River, N.W.T., Canada.

Figure 13.

Early Devonian (late Emsian, c. 395 Ma) paleogeographic reconstruction, based on Colpron and Nelson (2009, fig. 12). Localities shown as in Table 1: 1- Anderson River, NWT, Canada; 2 – Vestspitsbergen, Svalbard, Norway; 3- Baltic (Lithuania, Poland, Belarus); 4 – Rhenish Slate Massif, Germany; 5 – Kotelny Island, Siberia, Russia; 6 – Beichuan, Sichuan, China and Ludian, Yunnan, China. The possible *Heimenia* occurrence in northeastern Vietnam is included here with the localities from China.

AFR=Africa, ARB=Arabia, AVL=Avalonia, BAL=Baltica, IND=India, KAZ=Kazakhstan, LAU=Laurentia, MEX=Mexico, SCH=South China, SEU=Southern Europe, SIB=Siberia. Shaded areas indicate orogenies, including the Appalachians and Caledonides along the medial margins of Laurentia and Baltica. Dashed outline represents possible crustal fragment now submerged in the Arctic Ocean. More recent paleogeographic reconstructions (e.g., Golonka and Gaweda 2012; Domeier and Torsvik 2014) shift the plates farther south, by roughly 15-18°. This suggests a paleolatitude of 5°-8°S for Locality 1.

Table 1. Lower Devonian localities, shared genera, and paleogeographic units.

Lower Devonian Locality	Shared Genera	Paleocontinent or Terrane	
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Vestspitsbergen, Svalbard, Norway (Ørvig 1969; Clément 2001b; Mondéjar- Fernández & Clément 2012)	Arthrodira - <i>Herasmius</i> Porolepiformes - <i>Heimenia</i>	Svalbard	Laurussia
Lithuania, Poland, Belarus (Lyarskaya 1981; Clément 2001a; Ørvig 1969)	Porolepiformes - <i>Heimenia</i>	Baltica	Laurussia
Rhenish Slate Massif, Germany (Jessen 1989)	Porolepiformes - <i>Heimenia</i>	Baltica	Laurussia
Kotelny Island, Siberia, Russia (Schultze 1977, 1992)	Actinopterygii - <i>Dialipina</i>	New Siberian Islands terrane	Siberia + New Siberian Islands
Yunnan and Sichuan, China; ?NE Vietnam (Zhao & Zhu 2010; Wang 1986; Zhu 2000; Trinh & Janvier 1987)	Actinopterygii - <i>Dialipina</i> Porolepiformes - <i>Heimenia</i>	South China	South China

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Localities along Anderson River: AND-3 and -3A, and AND-4 and -4A are localities on the opposite sides of the river; these localities belong to same horizon. AND-5 lies about 7 km down the river from locality AND-3. Db, Lower Devonian; Ks, Upper Cretaceous. Geological mapping based on Balkwill and Yorath (1970).

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Figure 2.
Herasmius granulatus Ørvig, 1969. A. Reconstruction of skull roof of holotype by Ørvig (1969, fig. 3A); B. Reconstruction of skull roof of holotype based on nuchal and central plates of H. dayi without tectonic distortion. Verdalen Member, Stjørdalen Formation, Wood Bay Group, Emsian/Eifelian; Vestspitsbergen. Ce, central plate; Nu, nuchal plate.

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Figure 3.

Herasmius dayi n. sp., holotype CMN FV 54694, posterior skull roof + anterior shoulder girdle in dorsal view; Bear Rock Formation, upper Emsian; Anderson River, N.W.T., Canada. A. photograph; B. interpretative drawing. Adl, anterior dorso-lateral plate; Al, antero-lateral plate; Ce, central plate; ioc.ot, otic branch of the infraorbital line; lc, main lateral line; Mg, marginal plate; Md, median dorsal plate; Nu, nuchal plate; Pnu, para-nuchal plate; Pdl, posterior dorso-lateral plate; pmc, postmarginal sensory line; Pmg, postmarginal plate; ppl, posterior pit line; Sm, submarginal plate. Scale bar = 1cm.

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Figure 4.
Herasmius dayi n. sp., CMN FV 54699, median dorsal, right anterior dorso-lateral with antero-lateral, and left central plates; Bear Rock Formation, upper Emsian; Anderson River, N.W.T., Canada. A. photograph; B. drawing; C. specimen in the field. Adl, anterior dorso-lateral plate; Al, antero-lateral plate; cc, central lateral line; Ce, central plate; Md, median dorsal plate; o.Md, area of Adl overlapped by Md; ppl, posterior pit line; soc, supraorbital lateral line. Scale bar in drawing = 1cm.
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Figure 5.

Herasmius dayi n. sp., CMN FV 54700a, left submarginal plate in lateral view; Bear Rock Formation, upper Emsian; Anderson River, N.W.T., Canada. A. photograph; B. drawing. Scale bar in drawing = 1cm. Dialipina scale visible above center of submarginal.

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Figure 6.
Herasmius dayi n. sp., CMN FV 54665 left suborbital plate from the inside; Bear Rock Formation, upper Emsian; Anderson River, N.W.T., Canada. A. photograph; B. drawing. Scale bar = 1cm.

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Herasmius dayi n. sp., CMN FV 54697, left suborbital from the inside, infragnathal from the inside, and unidentified bone. A. photograph; B. drawing. ioc.pt, postorbital part of infraorbital sensory line; Ig, ?infragnathal; Pto, postorbital plate; So, suborbital plate. Scale in drawing = 1cm.

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Herasmius dayi n. sp., CMN FV 54700b, left anterior dorso-lateral (antero-lateral broken off) and posterior dorso-lateral plates in lateral view; Bear Rock Formation, upper Emsian; Anderson River, N.W.T., Canada. A. photograph; B. drawing. Adl, anterior dorso-lateral plate; gp, glenoid process; lc, main lateral line; o.Md, area of Adl overlapped by median dorsal plate; o. Pl, area of Adl overlapped by median dorsal plate; Pdl, posterior dorso-lateral plate; sgp, subglenoid process. Scale bar in drawing = 1cm.

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Adl, anterior dorso-lateral plate; Al, antero-lateral plate; cc, central lateral line; Ce, central plate; ioc, infraorbital sensory line; ioc.ot, otic portion of the infraorbital sensory line; Ic, main lateral line; Md, median dorsal plate; Mg, marginal plate; Nu, nuchal plate; orb, orbit; Pdl, posterior dorso-lateral plate; Pmg, postmarginal plate; Pi, pineal plate; Pl, postero-lateral plate; pmc, postmarginal sensory line; Pn; paranuchal plate; Pro, preorbital plate; Pto, postorbital plate; Ro, rostral plate; Sm, submarginal plate; So, suborbital plate; soc, supraorbital sensory line.

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Figure 11.
'Bryantolepis;' unidentified plate, CMN FV 54691B; Bear Rock Formation, upper Emsian; Anderson River, N.W.T., Canada. Scale bar = 1 cm.

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'Dunkleosteus'; suborbital plate, CMN FV 54827, in lateral view. ioc.so, suborbital portion of infraorbital sensory canal. A. photograph; B. drawing; scale in drawing = 1 cm. Bear Rock Formation, upper Emsian; Anderson River, N.W.T., Canada.

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Figure 13.
 Early Devonian (late Emsian, c. 395 Ma) paleogeographic reconstruction, based on Colpron and Nelson (2009, fig. 12). Localities shown as in Table 1: 1- Anderson River, NWT, Canada; 2 – Vestspitsbergen, Svalbard, Norway; 3- Baltic (Lithuania, Poland, Belarus); 4 – Rhenish Slate Massif, Germany; 5 – Kotelnny Island, Siberia, Russia; 6 – Beichuan, Sichuan, China and Ludian, Yunnan, China. The possible Heimenia occurrence in northeastern Vietnam is included here with the localities from China. AFR=Africa, ARB=Arabia, AVL=Avalonia, BAL=Baltica, IND=India, KAZ=Kazakhstan, LAU=Laurentia, MEX=Mexico, SCH=South China, SEU=Southern Europe, SIB=Siberia. Shaded areas indicate orogenies, including the Appalachians and Caledonides along the medial margins of Laurentia and Baltica. Dashed outline represents possible crustal fragment now submerged in the Arctic Ocean. More recent paleogeographic reconstructions (e.g., Golonka and Gaweda 2012; Domeier and Torsvik 2014) shift the plates farther south, by roughly 15-18°. This suggests a paleolatitude of 5°-8°S for Locality 1.

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