

UC Berkeley

PaleoBios

Title

Late Silurian to earliest Devonian vertebrate biostratigraphy of the Birch Creek II section, Roberts Mountains, Nevada, U.S.A.

Permalink

<https://escholarship.org/uc/item/6bb3q574>

Journal

PaleoBios, 40(4)

ISSN

0031-0298

Authors

Burrow, Carole Jan
Murphy, Michael
Turner, Susan

Publication Date

2023

DOI

10.5070/P940454153

Supplemental Material

<https://escholarship.org/uc/item/6bb3q574#supplemental>

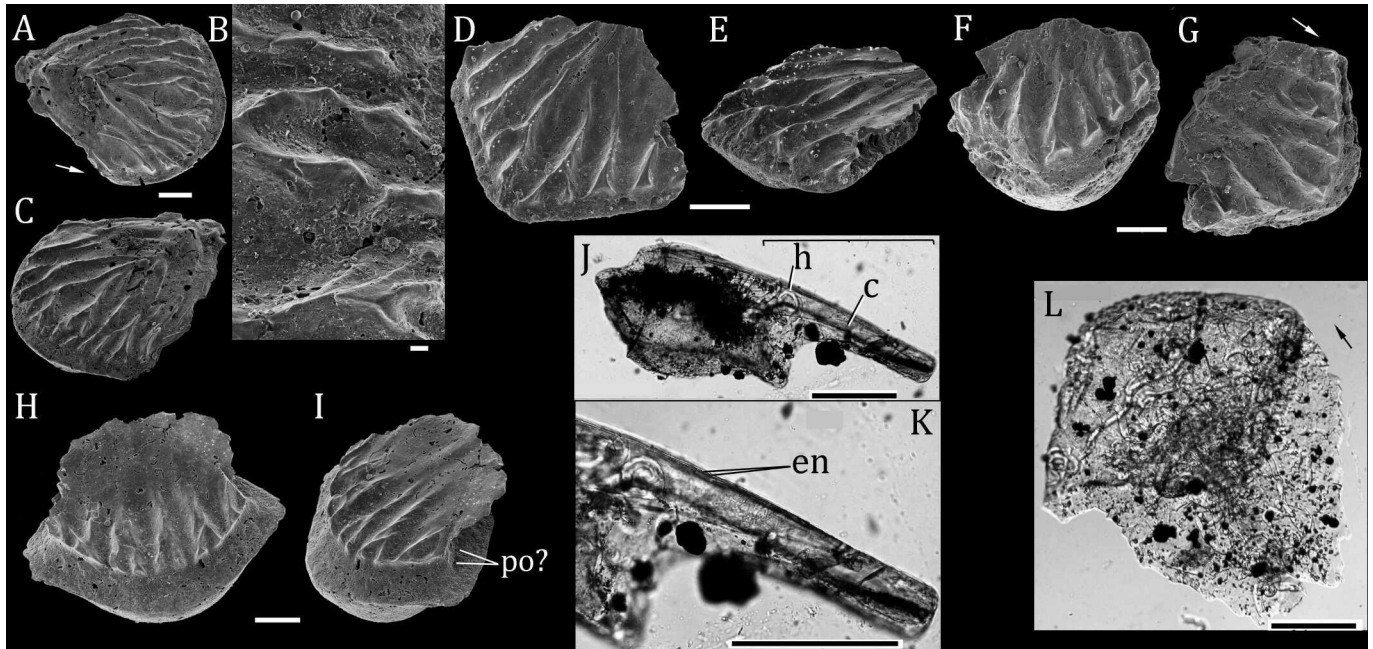
Copyright Information

Copyright 2023 by the author(s). This work is made available under the terms of a Creative Commons Attribution-NonCommercial-ShareAlike License, available at <https://creativecommons.org/licenses/by-nc-sa/4.0/>

Peer reviewed

PaleoBios

OFFICIAL PUBLICATION OF THE UNIVERSITY OF CALIFORNIA MUSEUM OF PALEONTOLOGY



**Carole J. BURROW, Michael A. MURPHY, and Susan TURNER (2023).
Late Silurian to earliest Devonian vertebrate biostratigraphy of the
Birch Creek II section, Roberts Mountains, Nevada, U.S.A.**

Cover: Scales of a new genus and species of acanthodian. See Figure 5 for details.

Citation: Burrow, C.J., Murphy, M.A., and Turner, S. 2023. Late Silurian to earliest Devonian vertebrate biostratigraphy of the Birch Creek II section, Roberts Mountains, Nevada, U.S.A. *PaleoBios* 40(4): 1-32.

DOI: <https://doi.org/10.5070/P940454153>

LSID: urn:lsid:zoobank.org:pub:58312615-0833-432E-BF5D-3DFFBF361AAA

Copyright: Published under Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International (CC-BY-NC-SA) license.

Late Silurian to earliest Devonian vertebrate biostratigraphy of the Birch Creek II section, Roberts Mountains, Nevada, U.S.A.

Carole J. Burrow¹, Michael A. Murphy², and Susan Turner¹

¹Geosciences, Queensland Museum

122 Gerler Road, Hendra, Queensland 4011, Australia, carole.burrow@gmail.com

²Department of Earth Sciences, University of California, Riverside,
900 University Avenue, Riverside, CA 92521

Intensive sampling of uppermost Silurian to lowermost Devonian levels of the marine sequence of the Roberts Mountains Formation exposed in the Birch Creek II section, Nevada has yielded assemblages of vertebrate microremains dominated by acanthodian scales. Taxonomic assessment of the vertebrates represented shows a suite and succession of taxa most similar to those recorded from contemporary circum-Arctic assemblages, with scales of the poracanthoid acanthodians *Poracanthodes punctatus*, *P. canadensis*, *Radioporacanthodes porosus* and ischnacanthid *Gomphonchus sandelensis* most abundant below the Silurian–Devonian (S–D) boundary (as previously determined by conodont and graptolite occurrences), and stem chondrichthyan ‘acanthodians’ *Nostovicina laticristata* and other *Nostovicina* spp. (order, family indet.) the most abundant above the boundary. Just one endemic acanthodian taxon, *Funicristata nevadaensis* nov. gen. nov. sp., was found, in the uppermost Silurian. Agnathan vertebrate remains are rare relative to acanthodian scales, with dermal fragments of heterostracans at fewer than 10 levels and scales of thelodonts from 12 levels scattered throughout the whole section. Scales of thelodonts *Apalolepis*, *Barlowodus* spp., *?Boreania*, *Gonioporus alatus*, *?Lanarkia*, *Loganellia*, *Nikolivia*, *Talivalia*, *Thelodus*, *?Turinia* sp., and *Trimerolepis* spp. are found below the purported S–D boundary. Rarer thelodont scales including *Barlowodus* sp., *Boreania* sp. cf. *minima*, and *N. gutta* are found above that level. The only identifiable gnathostome remains of groups other than acanthodians are from the putative osteichthyan *Lophosteus* sp. and chondrichthyans *Ellesmereia schultzei* and *Polymerolepis* sp., in the uppermost horizons below this level.

Keywords: paleobiogeography, ‘Acanthodii’, *Funicristata*, Thelodonti, Heterostraci, Chondrichthyes, stem Osteichthyes

INTRODUCTION

The Birch Creek II (BC II) section of the Roberts Mountains Formation in the northern Roberts Mountains of central Nevada, U.S.A. (Fig. 1A, B) is one of the primary sequences from which the data regarding the middle Silurian–Lower Devonian integrated brachiopod–graptolite–conodont biostratigraphy was derived for the Cordilleran region of western North America (e.g., [Murphy 1977](#)). The section shows generally a shoaling-upward sequence that began in the early Wenlock and terminated by the middle Lochkovian. The Siluro-Devonian boundary was estimated at the 567 foot level (= 172.8 m) by [Berry and Murphy \(1975\)](#), but it could be lower as there is no record

of *Monograptus angustidens* (an indicator of late Přidolí age) in the section (MAM, personal observation). The BC II is one of the few sections in the region where the Silurian–Devonian (S/D) boundary is exposed in facies where coarse detrital limestones are present with a background sedimentation of shaly carbonates, and therefore is important for integrating the graptolitic and shelly facies biostratigraphies. The invertebrate biostratigraphy of the section was intensively studied and discussed nearly five decades ago ([Johnson et al. 1973, 1976](#), [Berry and Murphy 1975](#), [Klapper and Murphy 1975](#), [Murphy and Edwards 1977](#)). Since then, acanthodian and thelodont scales (e.g., [Turner and Murphy 1988](#)), ostracodes, and

Citation: Burrow, C.J., Murphy, M.A., and Turner, S. 2023. Late Silurian to earliest Devonian vertebrate biostratigraphy of the Birch Creek II section, Roberts Mountains, Nevada, U.S.A. *PaleoBios* 40(4): 1-32.

DOI: <https://doi.org/10.5070/P940454153>

LSID: urn:lsid:zoobank.org:pub:58312615-0833-432E-BF5D-3DFFBF361AAA

corals have been added to the list of faunal components, conodont taxonomy has evolved considerably, and sampling methods and spacing have been improved so that a much more detailed picture of this short segment of earth history is now available.

Considering the conodont fauna, all of the conodonts thought to be cosmopolitan in 1975 have been reclassified. Neither *Walliserodina eosteinhornensis* (Walliser 1964) nor *Zieglerodina remscheidensis* (Ziegler 1960) is present in the section and the range given for *Wurmiella excavata* (Branson and Mehl 1933) is greatly restricted. Murphy (2016) revised the taxonomy for the conodont fauna above the S/D boundary in the section, erecting new genera *Cypricriodus*, *Praeicriodus*, *Cuspi-grandiosa*, and *Eurekadonta*. Along with the recognition that *Cypricriodus hesperius* (Klapper and Murphy 1975; formerly *Icriodus woschmidti hesperius*) is not closely related to *C. woschmidti* (Ziegler 1960) and that *C. woschmidti* occupies a higher stratigraphic position than

formerly supposed (Fig. 1B), the correlation of the S/D boundary at Birch Creek has lost some of the precision earlier attributed to it. However, the occurrence of graptolites *Monograptus uniformis* Pribyl (1940), the index fossil for the base of the Devonian, at the 571' (174 m) level, and the last occurrence of the upper Přídolí Biozone taxon *Monograptus transgrediens* Perner (1899) at the 477' (145.4 m) level, serve to give some constraints to the boundary. In addition, the coral faunas of the section are now better known and patches of the boundstone facies of the reefs, for which presence was inferred by Winterer and Murphy (1960) on the basis of the rapid facies changes along the north face of the Roberts Mountains, have been mapped but not yet published. Some levels have also produced ostracodes in abundance (Stone and Berdan 1984).

Regarding vertebrates, acanthodian scales are found at many levels, thus the section is especially important in the case of acanthodian history because the segment

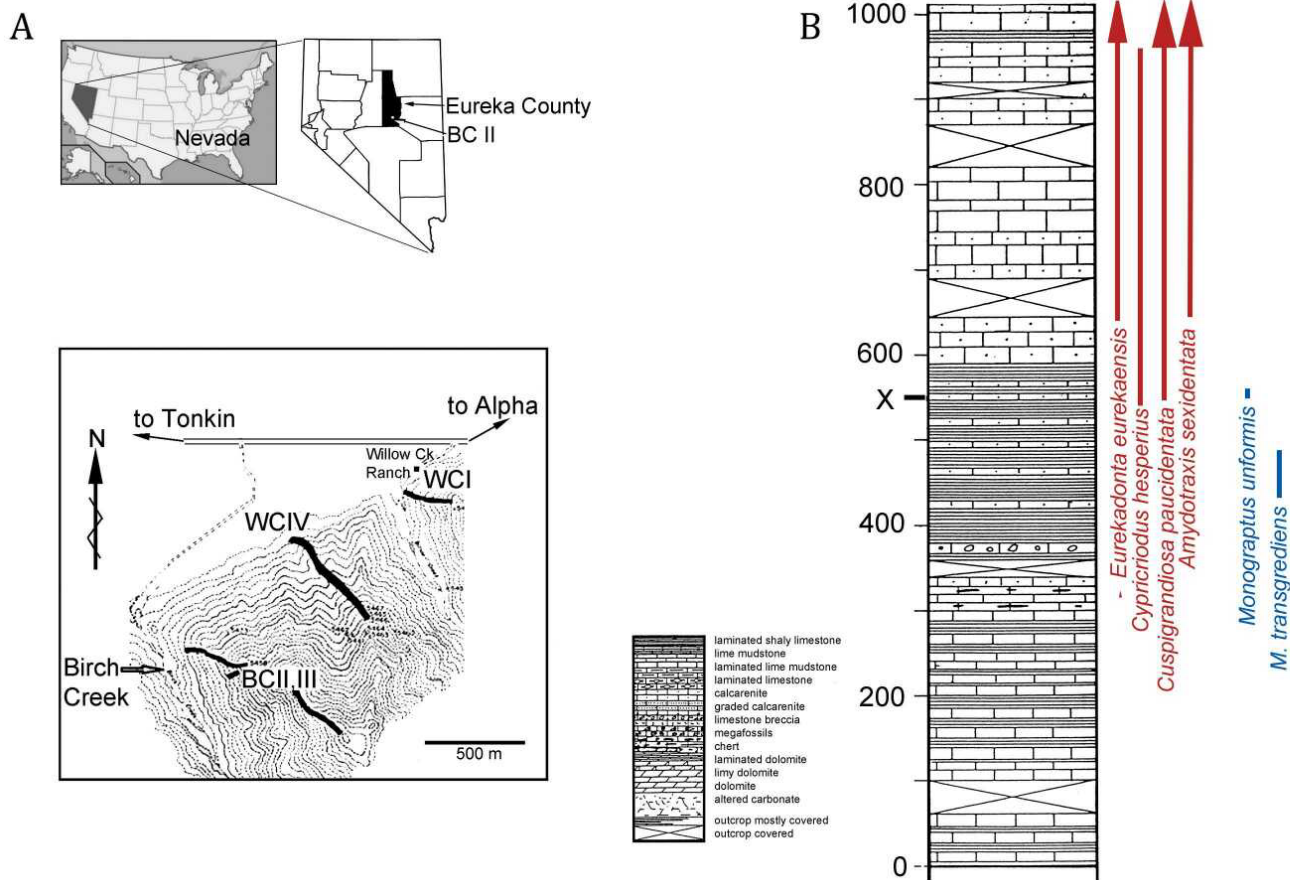


Figure 1. Birch Creek II section, central Roberts Mountains, Nevada. A. locality map, topographic map showing locations of sections BC II, BC III, WC I, WC IV after Murphy (2016, appendix 1). B. stratigraphic column through the uppermost Silurian–lowermost Devonian (after Klapper and Murphy 1975, fig. 5; scale on left is in feet; X denotes their proposed Silurian–Devonian boundary at approx. 567' = 172.8 m level); to the right, stratigraphically significant conodont ranges in red, graptolites in blue (see Murphy 2016, fig. 2).

of time around the S/D boundary is poorly represented in many areas of the world. Although other vertebrates are much rarer in the section, they are significant in being taxa that are also found in the circum-Arctic region. Some vertebrate microremains from Nevada were discussed by Turner and Murphy (1988) and Turner (1999) and a selection, including from BC II, were described by Parkes (1995) in his B.Sc. Honours thesis; his identifications are reassessed below. Much more detailed sampling yielding larger assemblages now provides a better picture of the thelodont, acanthodian, and chondrichthyan scale sequence across the S/D boundary.

This paper summarizes the data on the BC II section that have become available since the earlier work and reinterprets some of the biostratigraphic conclusions in the light of the more complete data available today.

CONODONT BIOSTRATIGRAPHY

The range of *Cypricriodus hesperius* in the Birch Creek II section in Nevada, given by Klapper and Murphy (1975, table 2: *Icriodus hesperius*: see Murphy (2016) for revised nomenclature) as 561–868 feet (i.e. 171–264.6 m), did not overlap the 1012–1086 feet (308.5–331 m) range of *Eurekadonta eurekaensis* (formerly *Ozarkodina eurekaensis*). Klapper (1977) established a biostratigraphic scheme based on the *hesperius*–*eurekaensis* sequence at Birch Creek that has been used throughout the world.

However, recent collections from this section have extended the ranges of both taxa so that *Eurekadonta eurekaensis* now extends down to 638.5 feet (194.6 m) and *C. hesperius* extends up to 959 feet (292.3 m); their distribution is apparently strongly facies dependent. This suggests that the Cordilleran biostratigraphic zones established by Klapper in 1977 need modification and should no longer be used as a standard of reference. *C. hesperius* was regarded by Murphy (2016) as the taxon long misidentified as "*Icriodus woschmidti* Ziegler", possibly with a global distribution beginning a short time before the appearance of *Monograptus uniformis* near the base of the Devonian in the Cordilleran region. Whereas *Cypricriodus hesperius* is widespread and useful for the recognition of the latest Silurian and earliest Devonian, the geographic distribution of *Eurekadonta eurekaensis* is restricted.

MATERIAL AND METHODS

Measurements of stratigraphic levels in the section were originally measured in feet; these measurements are given here but with the metric equivalent in brackets after the imperial measurement. The vertebrate scales

from all levels through the section are relatively poorly preserved, being riddled with hyphal (fungal) borings (e.g., Bystrow 1956, Goujet and Locquin 1979). Many of the scales collected from the acid residues over the last couple of decades were whitened with ammonium chloride and photographed by MAM using a light binocular microscope, and the images are included here in Supplementary File 1. Selected scales from relatively vertebrate-rich levels were coated with platinum and imaged using a JEOL-8300 scanning electron microscope (SEM) at the University of Queensland, or imaged uncoated using a Hitachi Tabletop TM-1000 environmental scanning electron microscope (ESEM) at the Queensland Museum by CJB. Other scales were embedded on glass slides using Crystalbond, thin sectioned using 1500 and 2000 grit wet and dry sandpaper, covered with Entellan and a coverslip, and photographed using an Olympus BX-50 microscope and DP-12 imaging system by CJB. Figured specimens are in the University of California Riverside (UCR) Museum Collection, Earth Sciences Department. Specimens originally figured by Parkes (1995) are catalogued in the Australian Museum Fossil Collection, Sydney (AMF), but we have been unable to locate them. CJB is responsible for the detailed gnathostome taxonomy and ST for the thelodont taxonomy; all authors have contributed to the manuscript.

Other institutional abbreviations—CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; GSC, Geological Survey of Canada collection, Ottawa; IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing; LIGG, Institute of Geology and Geography, Vilnius, Lithuania; MB.f, Museum für Naturkunde, Berlin, Germany; MMMC, Geological Survey of New South Wales Microfossil Collection, Londonderry, New South Wales, Australia; NNM, Nationaal Natuurhistorisch Museum, Leiden, the Netherlands; Tü Pi, Museum für Geologie und Paläontologie der Universität, Tübingen, Germany.

SYSTEMATIC PALEONTOLOGY

Remarks—As acanthodians are by far the most abundant and speciose of the vertebrate fauna, in this instance acanthodians and other gnathostomes are described before the agnathans.

GNATHOSTOMATA GEGENBAUR, 1874

CHONDRICHTHYES HUXLEY, 1880

ACANTHODII OWEN, 1846

Remarks—Based on recent phylogenetic analyses including Burrow et al. (2016) and Coates et al. (2018), the Acanthodii are now recognised as a paraphyletic

group of stem chondrichthyans. Some of the cladograms generated by these analyses (e.g., Burrow et al. 2016, fig. 41, Coates et al. 2018, fig. 3, Dearden et al. 2019, suppl. fig. 4b) retrieve the Ischnacanthiformes, (most) Diplacanthiformes, and Acanthodiformes as a clade. Coates et al. (2018) suggested that the term Acanthodii should be restricted to defining this group. A consensus has by no means been achieved for this approach, in which the analyses use taxa based on articulated fish. Here we follow the taxonomy of Burrow (2021), which includes other taxa based on scales with superposed crown growth in the Acanthodii sensu novo.

ISCHNACANTHIFORMES BERG, 1940

PORACANTHODIDAE VERGOOSSEN, 1997

PORACANTHODES BROTZEN, 1934

Type species—*Poracanthodes punctatus* Brotzen, 1934

PORACANTHODES PUNCTATUS BROTZEN, 1934

(FIG. 2A–2G; TABLE 1; SUPPL. 1, FIGS. 1?, 2–18)

Poracanthodes punctatus Brotzen 1934, 43, pl. 3 figs. 1, 8.

“scales ... were assigned by Parkes (1995) to *P. punctatus*” in part; Burrow et al. 1999, 355, 358.

“*P. punctatus* ... scales ... figured ... are from *P. canadensis*” in part; Burrow 2003a, 490.

Type material—The syntype scales MB.f.11979a and b figured by Brotzen (1934, pl. 3 figs. 1, 8), were from an erratic limestone boulder Bey. 36 in northern Germany. Gross (1947, 1971) used Brotzen’s material in his redescription of *P. punctatus* and other taxa, and captioned scale MB.f.11979b (Gross 1947, text-fig. 11A) as the holotype, now designated as the lectotype by Burrow & Märss (2022).

Referred specimens—*Poracanthodes punctatus* scales are found at most levels from 395’–513’ (120.4–156.4 m) in the BC II section (Table 1), and include UCR 930-1, -2, -5, -6 (all level 395’=120.4 m), and AMF 97948, 97950 (level 402’=122.5 m), figured by Parkes (1995, fig. 32.5, 32.6, 32.9, 32.10): Roberts Mountains Formation.

Description—These scales are the most common form in the lower levels of the section. They have a relatively smooth crown with a shallow sulcus leading back from the anteromedian corner, and close-set evenly spaced pores along the margin between growth zones paralleling the posterolateral edges of the crown (Fig. 2A, 2D–2F). Ridges are absent or only very weakly developed along

the anterior margin of the crown (Fig. 2A). Each side of the undersurface of the posterior crown on most scales has three large openings to the pore canal system at the crown–neck junction (Fig. 2A–2C, 2F, 2G). The area of the neck below the openings has strong buttresses aligned with the openings, separated by deep grooves. A strong rim separates the neck and base, which is convex and of a similar height to the neck, with the deepest area usually forward of the centre of the scale and with the front of the base protruding in front of the anterior edge of the crown.

Despite the poor preservation and extensive hyphal borings through the scales, the scale crowns are observed to have the pore canal layout typical of *Poracanthodes punctatus*, with c. six radial pore canals interconnected by arcade canals, from which short canals rise up to the pore openings aligned along the growth zones on the crown.

Comparison—These scales conform to the morphology of the lectotype scale (Brotzen 1934, pl. 3.1; see Burrow and Märss 2022) from an earliest Devonian (Lochkovian) erratic boulder (Bey. 36) of the north German lowlands. Gross (1971) noted that the scales from this level were morphologically the same as those from the Beyrichienkalk and the Kaugatuma and Ohesaare Beds (Přidolí, Upper Silurian) of the Baltic countries, but the latter differed in having many more radial canals (4–10) in their internal pore canal system, and should probably be assigned to a new species – to date, this has not been done. The BC II scales resemble the older forms, but with no morphological features to distinguish them (other than the number of large canal openings under the posterior crown), we prefer to keep the present nomenclature, whilst recognizing that the number of radial canals decreases between the upper Přidolí and the lowermost Devonian. *Poracanthodes punctatus* is a zonal vertebrate for the Baltic in the upper Přidolí (Märss et al. 1995; Märss and Mannik 2013), although its range is greater in shallow shelf than in deep shelf environments (Märss 1997, fig. 6). As well as the Baltic region and the north German lowlands, *P. punctatus* is recorded from the Přidolí of the Barlow Inlet Formation (Märss et al. 1998) and Cape Phillips Formation (Burrow et al. 1999) in the Arctic Canadian Archipelago, upper Přidolí erratics of the northern Netherlands (Vergoossen 1999a), uppermost Přidolí and lowermost Lochkovian of the Welsh Borderlands (Vergoossen 2000, table 1, Turner et al. 2017), Ludlow–Přidolí of October Revolution Island and Komsomolets Island and Lochkovian–Pragian of Severnaya Zemlya (Valiukevičius 2003a), and the S–D boundary beds in the Eastport Formation, Maine (Turner and Burrow 2018). It has also been recorded from another

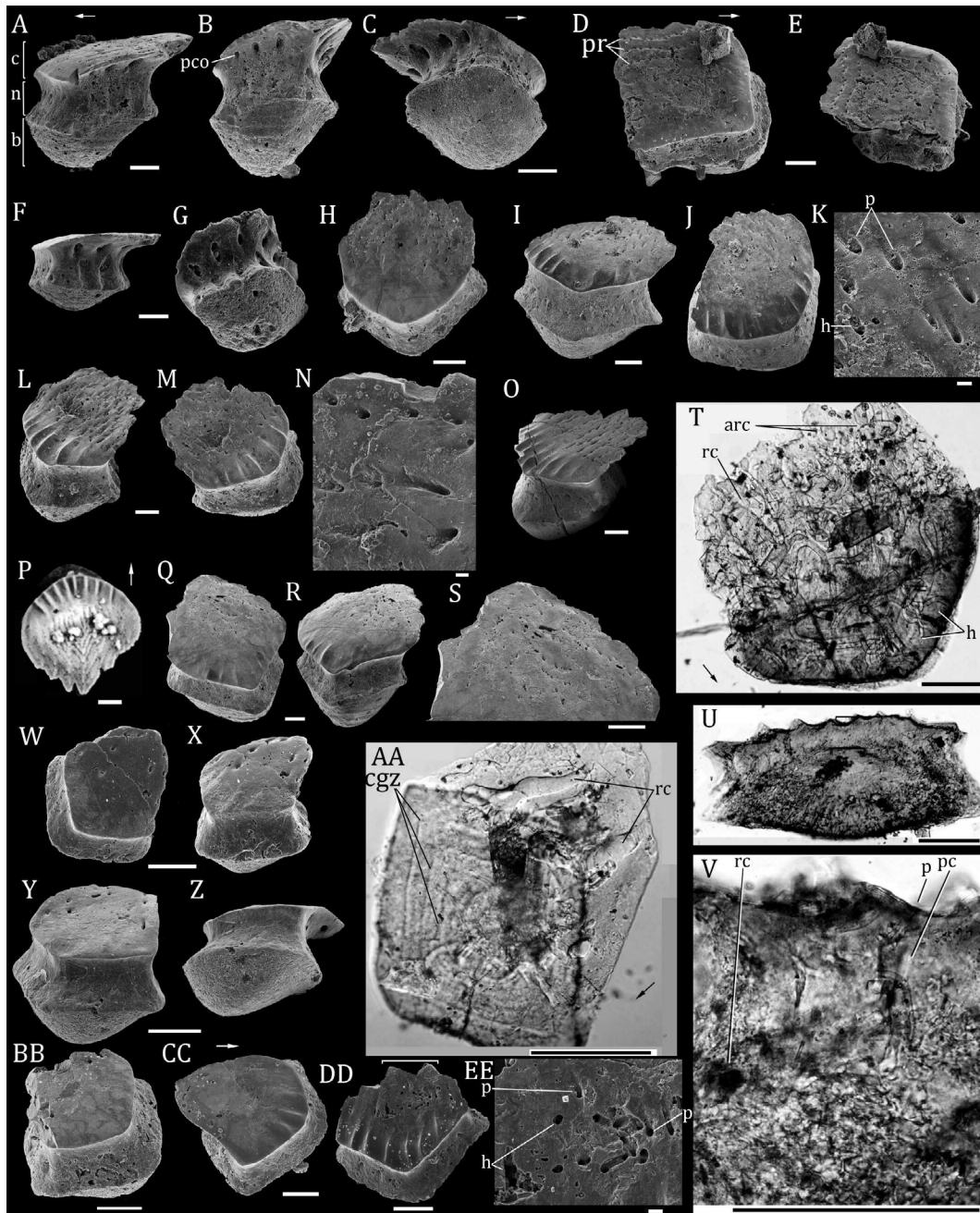


Figure 2. Poracanthodid acanthodian scales from Upper Silurian levels of the Birch Creek II section, SEM images. **A–G.** *Poracanthodes punctatus*: **A, B.** UCR 930-2 (level 395') in lateral and posterobasal views; **C.** UCR 930-6 (level 395') in posterobasal view; **D, E.** UCR 930-5 (level 395') in crown and posterocrown views; **F, G.** UCR 930-1 (level 395') in lateral and basal views. **H–P, ?Q–V.** *Poracanthodes canadensis*: **H, I.** UCR 930-4 (level 395') in crown view; **J, K.** UCR 10746-6 (level 430.5') in crown view plus closeup of crown pores; **L–N.** UCR 10750-6 (level 456.5') in anterior and crown views, and closeup of pores near hyphal borings; **O.** UCR10746-5 (level 430.5') in laterocrown view; **P.** UCR 540-1 (level 510') in crown view (from Supplement 1, fig. 17); **Q–S.** UCR 10768-3 (level 518.3') in crown, anterocrown views, and closeup of posterior crown surface; **T.** UCR 930-8 (level 395'), horizontal thin section through crown; **U, V.** UCR 10746-12 (level 430.5'), vertical thin section through anterior half of crown; **W–BB.** *Radioporacanthodes porosus*: **W, X.** UCR 10750-7 (level 456.5') in crown and anterocrown views; **Y, Z.** UCR 10746-4 (level 430.5') in anterocrown and lateral views; **AA.** UCR 10746-9 (level 430.5') in crown view; **BB.** UCR 10750-11 (level 456.5'), horizontal thin section through crown, showing two radial pore canals, viewed with Nomarski optics. **CC–EE.** *Radioporacanthodes scheiei*: **CC.** UCR 10750-5 (level 456.5') in crown view; **DD, EE.** UCR 10750-1 (level 456.5') in crown view plus closeup of pores and hyphal borings. Abbreviations: arc=arcade canals; b=scale base; c=scale crown; h=hyphal borings; n=neck; p=pore; pc=pore canal; pco=pore canal opening under posterior crown; pr=pore canal opening row on crown surface; rc=radial canal. Scale bars=0.1 mm, anterior of scale is to left or down, otherwise arrows point to anterior. See Table 1 for meterage.

area in the Roberts Mountains Formation, in the Přidolí of Pete Hanson Creek (Burrow 2003a).

PORACANTHODES CANADENSIS BURROW & VERGOOSSEN, 1999

(FIG. 2H–2P, T–V ?2Q–S; TABLE 1; SUPPL. 1, FIGS. 2–19)

Poracanthodes canadensis Burrow et al. 1999, 353–356, figs. 3A–C, 3F, 3G, 4A–F, 5A, 5B, ?3D, ?3E, ?4G, ?7A–D. “scales ... were assigned by Parkes (1995) to *P. punctatus*” in part; Burrow et al. 1999, 355, 358.

“*P. punctatus* ... scales ... figured ... are from *P. canadensis*” in part; Burrow 2003a, 490.

Diagnosis—see Burrow et al. (1999).

Type material—Holotype scale GSC 116340; Paratype scales: flank scale GSC 116339, transitional scale GSC 116343; Locality C-11460, Marshall Peninsula, Cornwallis Island, arctic Canada; Cape Phillips Formation (Late Silurian, Ludlow or Přidolí).

Referred specimens—*Poracanthodes canadensis* scales are found at most levels from 395'–518.3' (120.4–156.8 m) in the BC II section (Table 1), and include UCR 10750-6 (456.5'=139.1 m), UCR 10746-5, -6 (430.5'=131.2 m), UCR 930-4 (395'=120.4 m), possibly UCR 10768-3 (518.3'=158 m), and thin sections UCR 930-8 and -9 (395'=120.4 m); also AMF 97947 (level 513'=156.4 m) and AMF 97951 (level 402'=122.5 m), figured by Parkes (1995, fig. 32.1, 32.2, 32.9, 32.10): Roberts Mountains Formation.

Description—The scales have 6–16 short, sharp, mostly even-spaced ridges running back from the anterior edge of the crown. The rest of the crown is relatively smooth, with close-set evenly spaced pores along the margin between growth zones paralleling the zig-zagging posterolateral edges of the crown (Fig. 2H–2P). Unfortunately, the posterior area of most scale crowns has broken off, and the zig-zag orientation of the outer rows of pores, characteristic of *P. canadensis*, is only rarely preserved (Fig. 2P). Each side of the undersurface of the posterior crown on most scales has three or four large openings to the pore canal system at the crown-neck junction. The neck and base morphology is comparable with that of *P. punctatus*. One of the scales figured (Fig. 2Q–S) could possibly be from *P. punctatus*, as the anterior crown ridges are only weakly developed (or alternatively, worn down) and there is a slight anterior median sulcus.

Despite the poor preservation and extensive borings through the scales, thin sectioning shows that the scales have the pore canal layout typical of *Poracanthodes*

canadensis, with six or eight radial pore system canals interconnected by v-shaped arcade canals, from which short canals rise up to the pore openings aligned along the growth zones on the crown (Fig. 2T–V).

Comparison—Scales of *P. canadensis* can be distinguished from other poracanthodid taxa by their multiple short sharp ridges along the anterior rim of the crown and the alignment of pore openings parallel with the posterolateral edges of the crown, forming a zigzag pattern paralleling the jagged denticulations in younger zones. The taxon is only recorded elsewhere from the Přidolí of the Barlow Inlet Formation (Märss et al. 1998) and Cape Phillips Formation, Arctic Canadian Archipelago (Burrow et al. 1999), and now from Nevada.

RADIOPORACANTHODES VERGOOSSEN, 1999A

Type species—*Poracanthodes porosus* Brotzen, 1934.

RADIOPORACANTHODES POROSUS (BROTZEN, 1934)

(Fig. 2W–AA, ?2BB; Table 1; Suppl. 1, figs. 3–13)

Poracanthodes porosus Brotzen 1934, 44, pl. 3 fig. 2.

Diagnosis—see Vergoossen (1999a).

Type material—The holotype scale MB.f.11989a (Brotzen 1934, pl. 3 fig. 2, Gross 1947, text-fig. 11M) is from an erratic limestone boulder in northern Germany (Early Devonian, Lochkovian).

Referred specimens—Scales probably occur at most levels from 395.01'–491.3'=M48A (120.4–149.7 m), and possibly up to 510.90' (155.7 m) in the BC II section (Table 1), and include UCR 10750-7 (456.5'=139.1 m), UCR 10746-3, -4, -9 (430.5'=131.2 m) and thin section UCR 10750-11 (456.5'=139.1 m): Roberts Mountains Formation.

Description—The most common scale form of this species in the BC II section has a flat relatively smooth crown with a shallow median sulcus and up to six low weak ridges on the anterior margin (Fig. 2W–Y). These scales are smaller on average than those of *Poracanthodes*, being less than 0.3 mm wide and long. Pore openings in the posterior half of the crown surface are round, or short slits, and arranged in two or four subparallel rows leading back from the widest area of the crown to its posterolateral edges, although on most scales the posterior end of the crown has broken off (Fig. 2Y, BB). A horizontal thin section of the crown of one of the smaller scales (Fig. 2AA) shows two radial canals of the pore canal system, without any interconnecting arcade canals. The posterior

crown is missing on one scale (Fig. 2BB), but the anterior crown and exposed canals in the posterior fracture surface indicate that this is also probably *R. porosus*.

Comparison—Scales of *Radioporacanthodes porosus* sensu stricto (i.e. conforming to the type illustrated by Brotzen 1934, pl. 3.2) can be distinguished morphologically from other poracanthodid taxa by their median sulcus on the anterior rim of the crown, their lack of, or only weakly developed, anterior crown ridges, and the subparallel to radial alignment of large pores or small slits on the posterior half of the crown. The taxon is widely distributed, being recorded in the Lower Devonian erratic boulders of the north German lowlands, Pridolí–Emasian of the Baltic countries (Valiukevičius 2000), upper Pridolí–lowermost Lochkovian of the Welsh Borderlands (Vergoossen 2000, pl. 3.28, 3.29, Turner et al. 2017), Lochkovian Cookeys Plains Formation, New South Wales, Australia (Burrow 2003b), Lochkovian Borschchov and Ivane Regional Stages, Ukraine (Plax 2011) and possibly the lowermost Devonian of Tewo and Zoige counties, West Qinling Mountains, China (Wang et al. 1998: *Poracanthodes* cf. *P. porosus* and *Poracanthodes zoigensis*). The scale varieties with much more ornate crowns from the Baltic and central Urals that Märss (1986, 1997) and Valiukevičius (1998) assigned to *Poracanthodes porosus* have subsequently been reassigned to *Poracanthodes? lehmani* Vergoossen (1999b), and *Radioporacanthodes biblicus* (Lehman 1937) by Vergoossen (2002a); neither of these species are found in the BC II section.

RADIOPORACANTHODES SCHEII (SPJELDNAES, 1967)
(FIG. 2CC–EE; TABLE 1; SUPPL. 1, FIGS. 2, 3, 5, 9–13)

Ischnacanthus? Scheii Spjeldnaes 1967, 807, figs. 1–3, pl. 1.

Radioporacanthodes scheii; Burrow 2013, 947, figs. 2–6.

Diagnosis—see Burrow (2013).

Type material—The holotype is fin spine CMN55213, in a block with other fin spines, jaw fragments and scales considered to be conspecific; from the northwest side of Irene Bay, Ellesmere Island, arctic Canada, Devon Island Formation (Pridolí? or early Lochkovian).

Referred specimens—Rare scales recognized at levels 395' (120.4 m), 424.9' (129.5 m), 430.5' (131.2 m), 456.5'–471' (139.1–143.6 m) in the BC II section, including UCR 10750-1, -5 (level 456.5'=139.1 m): Roberts Mountains Formation.

Description—These scales are characterised by

regularly spaced short sharp ridges along the anterior edge of the crown, without a median sulcus. Pore openings are relatively small, with a maximum of six subparallel rows running back along the posterior half of the crown (Fig. 2CC–EE). The undersurface of the posterior crown has the large canal openings characteristic of this family (not illustrated). The small pores on the crown surface are not always visible with a light microscope, and some scale varieties lack pores.

Comparison—Burrow (2013) reassigned this species from “*Ischnacanthus?*” to *Radioporacanthodes* based on presence of a pore canal system in the crown of most scales, while also recognising that some variants lack a pore canal system. The BC II scales show some similarity with those of *Poracanthodes canadensis* in having many short ridges along the anterior edge of the crown, but differ in having a few small pores in subparallel rows on the posterior crown, rather than rows of many pores paralleling the posterolateral crown edges. As noted above, some scales also lack a pore canal system, making it difficult to distinguish these from scales of *Gomphonchus volborthi* (Rohon, 1893), a species resurrected by Vergoossen (1999c), and *Gomphonchus sandelensis* scales with weakly developed anterior crown ridges. *G. volborthi* usually has rounded weak anterior ridges, and is probably restricted to older strata (Vergoossen 1999c). The scales differ from the *Gomphonchopus hoppei* variants, which lack a pore canal system in having a smoothly curving anterior crown margin rather than a relatively sharp mid-margin angle (Vergoossen 1999a, figs. 41–45, 55, 56).

GOMPHONCHOPORUS VERGOOSSEN, 1999A

Type species—*Gomphodus hoppei* GROSS, 1947.

GOMPHONCHOPORUS HOPPEI (GROSS, 1947)

(FIG. 3A–3E, ?3F, ?3G; TABLE 1; SUPPL. 1, FIGS. 12?, 18–25)

Gomphonchus hoppei Gross 1971, 56–58, figs. 21C, 21D, 22E, 23, 24A–D, pl. 1.28–1.30, 2.1–2.3, 3.36, 9.4–9.9.

Gomphonchopus hoppei Vergoossen 1999a, 242–244, figs. 40–57.

Diagnosis—see Vergoossen (1999a).

Type material—Holotype: scale MB.f.449 (Gross 1947, pl. 24 fig. 7); from the Beyrichienkalk, northern Germany; exact collection locality unknown (Late Silurian, Pridolí?).

Referred specimens—Scales at most levels from

513'–591.5' (156.4–180.3 m), and possibly level 468' (142.6 m) in the BC II section, including UCR 944-11 (527.25'=160.7 m), UCR 5439-2, 3, UCR 5439-1, 7? (level 549'=167.3 m); and AMF 97959, 97960 (level 513'=156.4 m), figured by Parkes (1995, fig. 33.5–33.8, captioned as Acanthodian 1 and *Poracanthodes* sp.): Roberts Mountains Formation.

Remarks—As discussed by Vergoossen (1999a), the type scales described and figured by Gross (1947, 1971) were abraded, with delicate structures missing, in particular, the lateral areas of the posterior crown. For this reason, Vergoossen (1999a) nominated well-preserved scales from a northern Netherlands erratic as neotype and paratypes. However, the type specimen is still repositioned in the MB.f collection so those allocations are not valid. Being better preserved than the type scales, those from the Netherlands erratic are more useful for comparative purposes.

Description—Scales from BC II are comparable with the scale nominated by Vergoossen as a neotype (1999a, pl. 4.42–4.44) and have numerous ridges leading back from the anterior margin (Fig. 3A), whereas others have a shallow median sulcus running back from the anterior edge of the crown to the level of the lateral corners, and only a few short low ridges running back from the anterior margin (Figs. 3A–3D, ?3F, ?3G). The straight anterior edges of the crown meet at an acute angle. The posterior crown is formed of appositional growth zones, expressed on the surface as long slits paralleling the straight posterolateral edges of the crown, or with more anterior growth zones appearing to overlap the growth zone behind (Fig. 3A). Few of the BC II scales have the posterolateral edges preserved, but at least one scale (Parkes 1995, fig. 33.5, 33.6) has the close-set denticulations that are visible on the well-preserved scales figured by Vergoossen (1999a). The scale neck is concave all round, and of comparable height to the base, with a marked rim separating neck and base. A strong median ridge rises from the posterior base towards the lower surface of the crown (Fig. 3A, B), and the undersurface of the posterior crown (Fig. 3E) shows the wide canal openings that typify poracanthodid scales. Some scales with relatively long aligned slits on the posterior crown surface (Fig. 3F, G) are tentatively assigned to the species.

Comparison—Some scales approach the morphology of small (fin?) scales from *Zemlyacanthus menneri* (Valiukevičius 1992, pl. 10.6–10.8), but only have straight slits and pore openings in the posterior area of the crown, rather than zigzag slits extending close to the anterior margin that characterize *Z. menneri*, and so are assigned

on this basis to *G. hoppei*.

ZEMLYACANTHUS VERGOOSSEN, 1997

Type species—*Poracanthodes menneri* Valiukevičius, 1992.

Remarks—The pore canal system in *Z. menneri* scales is of the punctatiform type *sensu* Vergoossen (1997), with both arcade and radial pore canals (Valiukevičius 1992), but the scales differ from those of *Poracanthodes* and *Radioporacanthodes* in having only appositional growth zones forming the posterior crown, and canals opening out on the surface in long slits parallel to the denticulated posterolateral edges. In scales of *Poracanthodes* the canals open out through rows of small pores with the same alignment, and in *Radioporacanthodes* through slits or large pores in radiating rows above the radial canals. *Gomphonchoporus* scales with pore canal systems are porosiform. For these reasons, and because it is the only poracanthodid species known from articulated fish, Vergoossen (1997) erected the new genus *Zemlyacanthus*. Here we recognise the validity of this genus, based on the features listed here.

ZEMLYACANTHUS MENNERI (VALIUKEVIČIUS, 1992)

(Fig. 3H–J; Table 1; Suppl. 1, figs. 18, 22)

Poracanthodes menneri Valiukevičius, 1992, 195, pl. 1–10, text-figs. 1–12.

Zemlyacanthus menneri; Vergoossen 1997, 45, 46.

Type material—Holotype scale LGMTI 35-360; paratypes LGMTI 35-358, 35-355, 35-354, 35-340, 35-341, 35-342, 35-350; Pod'emnaya River, outcrop 67, bed 12, October Revolution Island, Severnaya Zemlya Archipelago, Russia, Severnaya Zemlya Formation (Lower Devonian, Lochkovian).

Referred specimens—Scales at levels 513' (156.4 m), 549' (167.3 m), 554.5' (169.0 m), and 556.5' (169.6 m) in the BC II section, including three scales at 556.5' (Suppl. 1, fig. 22), and AMF 97961, 97962 (both level 513'=156.4 m), figured by Parkes (1995, fig. 33.9–33.12): Roberts Mountains Formation.

Description—Scales from level 556.3' (169.6 m) strongly resemble flank scales from the type, articulated specimens of *Zemlyacanthus menneri*, showing overlapping apposed crown growth zones extending back from close to the anterior margin of the scale crown (Fig. 3H–J). This anterior margin lacks well-formed ridges, with just a few short low rounded ridges occasionally present near the middle of the margin. The apposed growth zones

forming the crown are denticulated, particularly in the larger more posterior zones, and sometimes comprise lines of slits/overlaps, rather than having uninterrupted overlaps. There is a sharp rim between the neck and base of the scale, with the latter protruding slightly in front of the crown. The convex base and concave neck are of similar heights.

Comparison—Some scales represented in the BC II samples closely resemble those from the type, articulated fishes (Valiukevičius 1992, pl. 10) from the Lochkovian of October Revolution Island. Those BC II scales (Fig. 3F, G), tentatively assigned to *Gomphonchoporus hoppei* (Gross 1947), are similar to some of the smaller scales on the type *Z. menneri* fish (Valiukevičius 1992, pl. 10.8), and they are found at the same level as the scales readily assigned to *Z. menneri*. Overlap of scale morphotypes between different taxa is a common problem in taxonomy based on isolated scales, particularly when samples are rich in taxa but poor in numbers. Also, recognition that both scales with and without a pore canal system can belong to a poracanthodid species (e.g., Vergoossen 1999a, Burrow 2013) further complicates taxonomic assignments.

TRUNDLELEPIS BURROW, 1997

Type species—*Trundlelepis cervicostulata* Burrow, 1997.

TRUNDLELEPIS CERVICOSTULATA BURROW, 1997
(Fig. 3K–3P; Table 1; Suppl. 1, figs. 18–21)

Trundlelepis cervicostulata Burrow 1997, 57, fig. 4A–E, pl. 3 figs. 7–11.

Diagnosis—see Burrow (2002).

Type material—Holotype scale MMMC02239; paratypes scales MMMC02236, 02234; GSNSW locality C607, near Trundle, central New South Wales, Australia, Connemarra Formation (Lower Devonian, Lochkovian).

Referred specimens—Scales were recovered from most levels from 513'–532' (156.4–162.2 m), including UCR 944-3, -12, -17 (level 527.25'=160.7 m), UCR 10768-4 (level 518.3'=158 m), and thin sections UCR 944-22, -23 (level 527.25'=160.7 m): Roberts Mountains Formation.

Description—Scales have a flat crown, longer than wide, with 6–8 strong ridges leading back from the anterior margin and tapering out before the central area of the crown (Fig. 3K, M, N). The median ridges are often slightly asymmetrical in cross section, being steeper on

the outer face, but the area between these ridges is at the same level as the rest of the crown, without a median sulcus. Some scales have one or two round pores opening out through the outer growth zone in the posterior half of the scale. The neck is deep all round, with 'buttressing' posteriorly. The large, convex base usually protrudes in front of the anterior margin of the crown, sometimes to the extent that the bulk of the base is forward of the crown (Fig. 3O). As with other scales from the section, hyphal borings penetrate densely, but the tissues forming the crown (Fig. 3O, P) are recognisable as syncitial mesodentine (*sensu* Valiukevičius and Burrow 2005) and orthodentine. Unlike poracanthodids with extensive pore canal systems, growth zones are discernible in the whole crown. Wide-calibre pore canals form a simple system comprising a few vertical canals from the undersurface to the upper surface of the crown, near the lateral edges (Fig. 3P).

Comparison—The scales show a range of profiles and crown ornament, comparable with that in the type material from the Lochkovian of southeastern Australia (Burrow 1997, 2002, figs. 21A–21F, 23A–23D, 32A–32G). This taxon represents perhaps the last stage in the loss of a pore canal system in the scale crown for poracanthodids – a progression noted by Vergoossen (e.g., 1999a) – with only some scales having vertical, unconnected canals penetrating the outermost crown growth zones. Several other latest Silurian or earliest Devonian scales with comparable morphology from other regions could also be from *Trundlelepis cervicostulata*, including ones from the Přídolí of the Klouk Beds, Czechia (Märss 1997, pl. 7.3–7.10: captioned *Gomphonchus* sp. 3, *Gomphonchus* sp.) and Sweden (Vergoossen 2002b, fig. 45: captioned *Acanthodii* gen. et sp. indet.). The lack of distinctive crown features can make identification of scales from this species difficult when based only on morphology, as several latest Silurian–earliest Devonian taxa also have scales with a deep neck, convex anteriorly protruding base, and a flat crown with subparallel or radial ridges along the anterior margin. For example, *Arenaceacanthus arcuatacanalis* Valiukevičius (2004a) and *Bracteacanthus assiduus* Valiukevičius (2004a) from the Přídolí of Lithuania, *Nostovicina paravolborthi* (Valiukevičius 2003b) from the Přídolí of Timan–Pechora, and *Nostolepis tcherkesovae* Valiukevičius (1994) from the Lochkovian of Taimyr and Timan–Pechora have a similar morphology, but none of these taxa have morphotypes with the simple vertical canals penetrating the posterior crown growth zones exhibited in some scales of *Trundlelepis* from the type locality as well as the BC II section.

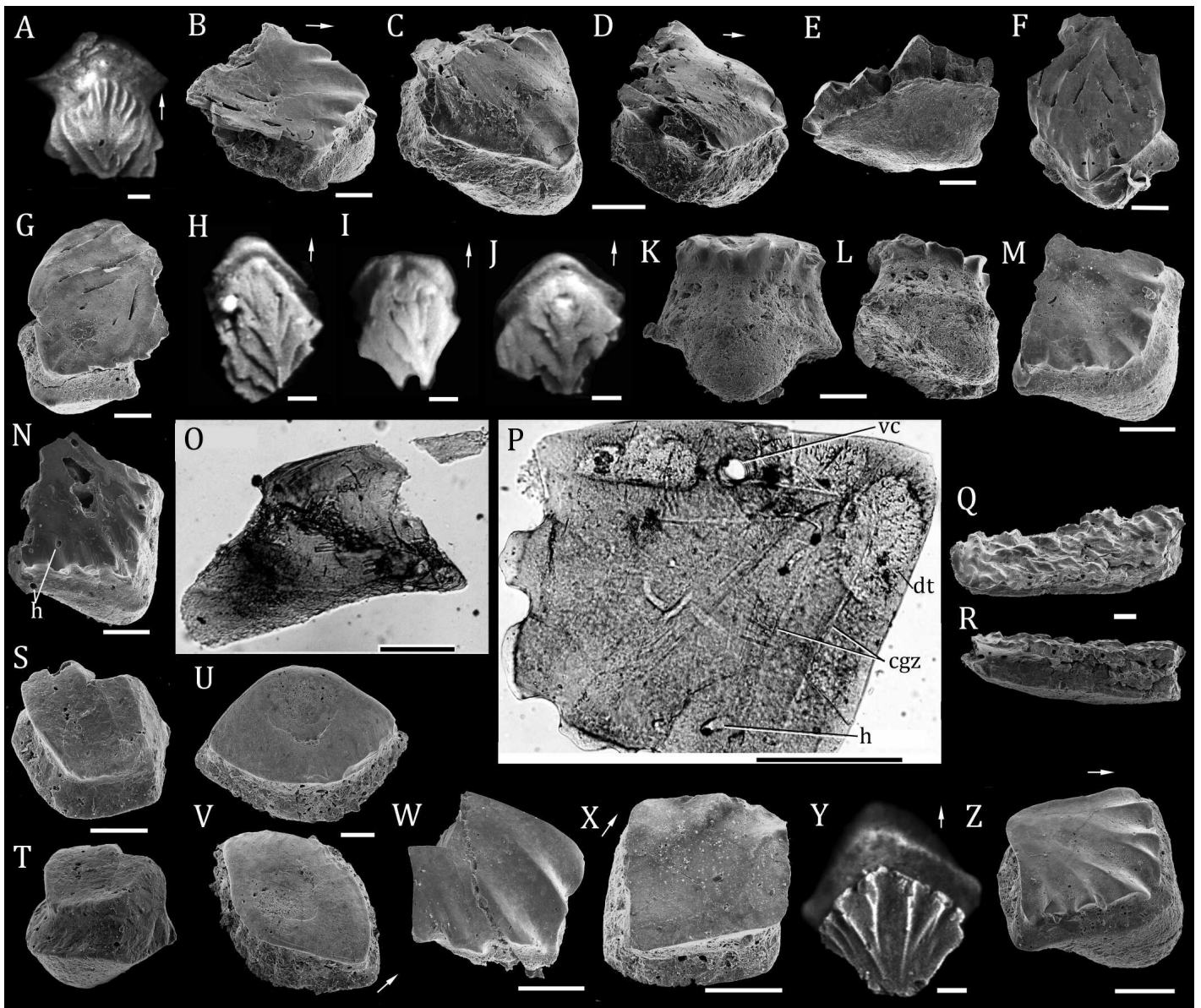


Figure 3. Poracanthodid and ischnacanthid acanthodian scales from Upper Silurian levels of the Birch Creek II section. **A–E, ?F, ?G.** *Gomphonchoporus hoppei*: **A.** UCR 949-1 (level 567.3') in crown view (from Supplement 1, fig. 24); **B.** UCR 944-11 (level 527.25') in laterocrown view; **C, D.** UCR 5439-2 (level 549') in anterocrown and laterocrown views; **E.** UCR 5439-3 (level 549') in basal view; **F.** UCR 5439-7 (level 549') in crown view; **G.** UCR 5439-1 (level 549') in anterocrown view. **H–J.** *Zemlyacanthus menneri*: UCR 10815-1, 2, 3 (level 556.5'), in crown views (from Supplement 1, fig. 22). **M–P.** *Trundlelepis cervicostulata*: **K, L.** UCR 10768-4 (level 518.3') in anterior and lateral views; **M.** UCR 944-17 (level 527.25') in crown view; **N.** UCR 944-3 (level 527.25') in crown view; **O.** UCR 944-23 (level 527.25'), vertical longitudinal thin section; **P.** UCR 944-22 (level 527.25'), horizontal thin section through crown. **Q, R.** Poracanthodidae gen., sp. indet. sensory line scale UCR 930-3 (level 395') in crown and posterior views. **S–V.** *Gomphonchus sandelensis*: **S, T.** UCR 10746-11 (level 430.5') in crown and lateral views; **U, V.** UCR 930-7 (level 395') in antero- and posterocrown views. **W–Z.** *Gomphonchus mediocostatus*: **W.** UCR 944-6 (level 527.25') in crown view; **X.** UCR 944-16 (level 527.25') in crown view; **Y.** UCR 942-1 (level 526') in crown view (from Supplement 1, fig. 20); **Z.** UCR 944-19 (level 527.25') in laterocrown view. Abbreviations: cgz=crown growth zones; dt=dentine tubules; h=hyphal borings; vc=vertical canals. Scale bars=0.1 mm, anterior of scale is to left or down, otherwise arrows point to anterior. See Table 1 for meterage.

PORACANTHODIDAE GEN. ET SP. INDET.
(FIG. 3Q, R ; TABLE 1 ; SUPPL. 1, FIGS. 2)

Referred specimens—A few sensory line scales were recovered from levels 395'–492.3' (120.4–150.1 m) in the BC II section, including UCR 10750-9 (level 456.5'=139.1 m) and UCR 930-3 (level 395'=120.4 m), AMF 97928 (level 503'=153.3 m), AMF 97929 (level 446.5'=136.1 m) figured by Parkes (1995, fig. 29.9–29.12: captioned *Chondrichthyan* 1, 2), AMF 97949, 97952–97954 (all level 402'=122.5 m), AMF 97955 (level 395'=120.4 m) figured by Parkes (1995, fig. 32.5, 32.6, 32.11–32.16: captioned *Poracanthodes punctatus*); fragments of dentigerous jaw bone are from levels 424.9' (129.5 m), M48B=491.8' (149.9 m), and M48C=492.3' (150.1 m): Roberts Mountains Formation.

Description—Short, wide scales are identified as ones that edged the sensory lines on the head, by comparison with squamation of articulated poracanthodid *Zemlyacanthus menneri* (Valiukevičius 1992, pl. 9.6a, 6b). These scales have a similar structure in all known poracanthodids, with multiple short sharp ridges and tubercles along the straight anterior margin overlapping similar ridges which cover the crown, or at least the anterior half of the crown with the posterior half showing rows or lines of pores. The posterior edge has often fractured off, revealing the posteriorly directed canals of the pore system. Pores open out on the crown between the ridges and tubercles. The neck is short and concave, and the base is low and slightly convex.

Other elements include jaw fragments that are probably poracanthodid, because no other ischnacanthiform elements are found at the same levels.

ISCHNACANTHIDAE WOODWARD, 1891
GOMPHONCHUS GROSS, 1971

Type species—*Gomphodus sandelensis* Pander, 1856.

GOMPHONCHUS SANDELENSIS (PANDER, 1856)
(FIG. 3S-V; TABLE 1; SUPPL. 1, FIGS. 1–3, 11, 12, 13)

Gomphodus sandelensis Pander 1856, 76, pl. 6 figs. 15–17.

Gomphonchus sandelensis Gross 1971, 53, figs. 19E–G, 20, 21A, 21B, 22A–D, pl. 5.11, 9.15–9.17.

Diagnosis—Relatively large *Gomphonchus* scales with a smooth crown that extends beyond the base all round, and a high neck with vertical ribbing posteriorly. Scales

have durodentine superficially in some of the youngest crown growth lamellae; they lack radial vascular canals.

Type material—The syntype scales from the Ohesaare Beds, Ohesaare Cliffs (Pander 1856, pl. 6 figs. 15, 16; Ohesaare Formation) and Sandla (Pander 1856, pl. 6 fig. 17; lower Kaugatuma or upper Kuressaare Stage), Saaremaa Island, Estonia (Late Silurian, Pridolf) have been long lost.

Referred specimens—Scales assigned to this species are rare compared to the number of poracanthodid scales, occurring at various levels from 395'–545' (120.4–166.1 m), including UCR 930-7 (level 395'=120.4 m) and UCR 10746-11 (level 430.5'=131.2 m); AMF 97957, 97958 (level 513'=156.4 m), figured by Parkes (1995, fig. 33.1–33.4) and thin sections AMF 97994, 97995 (level 513'=156.4 m), figured by Parkes (1995, fig. 42.1, 42.2): Roberts Mountains Formation.

Description—Scales have a smooth flat crown, sometimes with a shallow median sulcus (Fig. 3S, T) or very weak short ridges along the anterior margin (Fig. 3U, V); the crown is usually wider and longer than the base. The scales can be difficult to distinguish from those *Poracanthodes punctatus* scales, which also have a smooth flat crown, with pore openings often only detectable in SEM images.

GOMPHONCHUS MEDIOCOSTATUS VERGOOSSEN, 1999A

Type material—Holotype NNM 423013; paratypes NNM 423014–423023, NNM 423044, NNM 423045; East Baltic derived erratic limestone boulder 62, Oosterhaule, northern Netherlands, Late Silurian (Pridolf).

GOMPHONCHUS SP. AFF. *G. MEDIOCOSTATUS*
(Fig. 3W–3Z; Table 1; Suppl. 1, figs. 20, 21)

Referred specimens—Rare scales assigned to this species occur in a very restricted range, at levels 526' (160.3 m), 527.25' (160.7 m), and possibly 527' (160.6 m), and include UCR 944-6, -8, -17, -19 (level 527.25'=160.7 m): Roberts Mountains Formation.

Description—Scales from BC II with crowns resembling the type scales of this species have a marked median sulcus extending over half the length of the crown, usually edged by sharp ridges. Smaller scales have only these two ridges (Fig. 3W, X), larger scales have oblique lateral ridges directed towards the median ridges (Fig. 3Y, Z). Most scales have a short- to medium-height neck. The base is strongly convex. Histological structure was not investigated, due to the lack of material.

Comparison—The type scales of *Gomphonchus*

mediocostatus are from an upper Přidolí East Baltic-derived erratic limestone; the species is also recorded from Lithuania, Timan–Pechora (Valiukevičius 2005), Latvia (Valiukevičius 2004b), the Welsh Borderlands (Vergoossen 1999a) and Novaya Zemlya (Burrow et al. 2018). In Latvia, Valiukevičius (2004b) nominated *G. medicostatus* as the acanthodian index species for his second highest fine-scale biostratigraphic interval in the Přidolí. A crown ornament similar to that of *G. medicostatus* has been illustrated in a number of other taxa, including *Pechoralepis zinaidae* (Valiukevičius 2003b, fig. 3K) from the Lochkovian of Timan–Pechora, and one of the morphotypes of the older taxon *Gomphonchus? turnerae* from the Ludlow of north Queensland, Australia (Burrow and Simpson 1995, fig. 2A–C). The type scales of *G. medicostatus* all have deep necks with relatively shallow bases, thus differing from the BC II scales with their short necks and deeply convex bases.

ACANTHODII

ORDER, FAMILY INDET.

NOSTOVICINA VALIUKEVIČIUS & BURROW, 2005

Type species—*Nostolepis fragilis* Valiukevičius, 2003a.

Remarks—All identifiable scales of the *Nostolepis*-type *sensu lato* (e.g., Gross 1947, 1971) recovered from the BC II section, except those assigned to *Nostolepis matukhini*, correspond to species that have been reassigned to *Nostovicina* Valiukevičius and Burrow (2005), which all lack Stranggewebe (short parallel-oriented mesodentine tubules) in the crown.

NOSTOVICINA ELEGANS (BROTZEN, 1934)

Diplacanthoides elegans Brotzen, 1934, p. 26, pl. 1.11a–c.

Nostolepis elegans Valiukevičius 2004b, 130, fig. 5A–M.

Type material—Holotype scale MB.f.11937 (Brotzen 1934, pl. 1.11a–c) is from erratic limestone boulder Bey. 36 or 37, northern Germany (Lower Devonian, Lochkovian).

NOSTOVICINA SP. CF. *N. ELEGANS*
(FIG. 4A; TABLE 1; SUPPL. 1, FIG. 13)

Referred specimens—One scale from level 470.2' (143.3 m): Roberts Mountains Formation.

Description—The solitary medium-sized scale assigned to this species is characterized by having an elevated central area in the elongate crown, with just one or two short ridges leading back from the anterior edge. Narrow lower ledges run along each side of the central crown plane. The base is moderately convex, a neck is lacking, and the crown is inclined anteroposteriorly.

Comparison—The type material of *N. elegans* was found in Lower Devonian erratics of the Baltic basin, and the species has been reported from Ludlow to Lochkovian deposits, including from the Přidolí of southern Sweden (Vergoossen 1999b, pl. 2.16, 2.17), Lithuania (Valiukevičius 2005, figs. 2I, 2J, 7, 8) and Latvia (Valiukevičius 2004b, table, fig. 5A–M). The work by those authors indicates that *Nostovicina elegans* is a valid species, countering Gross' (1947) dismissal of *Diplacanthoides elegans* as a junior synonym of *Nostolepis striata*. Certainly, in the BC II section, this is amongst the few *Nostolepis*-type scales *sensu* Gross (1947) found in the upper Silurian below the 513' level, with no scales comparable with the holotype of *N. striata* found at any level. The scale is only tentatively assigned to *N. elegans* based on its morphology, because the histological structure was not investigated.

NOSTOVICINA LATICRISTATA (VALIUKEVIČIUS, 1994)
(FIG. 4B–D, 4J; TABLE 1; SUPPL. 1, FIGS. 19)

Nostolepis laticristata Valiukevičius, 1994, 149, 150, fig. 70.1, pl. 18.9, 19.1–19.3.

Nostovicina laticristata Valiukevičius and Burrow 2005, 646.

Type material—Holotype LIGG 30-1569; Uryum Beds, Tareya River, Taimyr, Russia (Lower Devonian, Lochkovian).

Referred specimens—Scales assigned to this species occur at levels 517–613' (157.6–186.8 m), and include UCR 10768-6, -10 and thin section UCR 10768-11 (level 518.3'=158 m): Roberts Mountains Formation.

Description—Small scales up to 0.4 mm wide, with crowns mostly conforming to two morphotypes, both of which have a smooth flat subtriangular surface with five or six short, usually smoothly rounded and nonbranching, ridges leading back from the anterior crown margin. Posterolateral edges of the crown are straight or slightly convex and lack denticulations, converging at a slightly obtuse angle. One morphotype has several oblique ridges leading back from the posterior corner along the lateral faces of the crown (Fig. 4B), and the other morphotype

lacks ridges on the posterolateral sides of the crown (Fig. 4C, D). All scales have a short or no neck. The base is convex and about the same height as the crown plus neck, lacking a marked rim between the neck and base. As usual for BC II scales, histology is poorly preserved with scales having extensive hyphal borings. Four wide growth zones form the crown (Fig. 4J).

Comparison—This taxon was erected for *circa* 5000 isolated scales from the Lochkovian of Taimyr by Valiukevičius (1994), who originally assigned the species to *Nostolepis*; it was subsequently reassigned to *Nostovicina* Valiukevičius and Burrow (2005), based on histological structure. Some scales from Timan–Pechora that Valiukevičius (1994) assigned to this species were reassigned to *Nostolepis adzvensis* Valiukevičius (2003b) and subsequently by Valiukevičius and Burrow (2005) to *Pechoralepis adzvensis*, based once again on histological differences. The two species *Nostovicina laticristata* and *Pechoralepis adzvensis* are virtually impossible to differentiate on morphology alone, but histological study of scales confirmed that those from BC II are *N. laticristata*. The latter show a similar range in size and morphology to scales from the Lochkovian of the Arctic Canadian Archipelago, which Vieth (1980) assigned to *Gomphonchus* sp. cf. *G. hoppei*, and which have since also been assigned to *N. laticristata* (Valiukevičius 1994, Turner and Burrow 1997: CJB, personal observation of scales from GSC localities C-8771, C-67653, C-76085). A partial articulated fish from the Lochkovian MOTH locality of Northwest Territories, Canada (Hanke 2001, figs. 82–85: captioned as *Nostolepis tewonensis*?) is here considered to be *Nostovicina laticristata*. Lochkovian–Pragian scales from southeastern Australia that are now assigned to *Nostovicina guangxiensis* (Wang, 1992) have a very similar or greater range of crown morphotypes (Burrow 2002, figs. 4E–I, 5J–M, 12A, C, D), but these scales are on average much larger than those of *N. laticristata*. One of the type scales of *Nostolepis tewonensis* (Wang et al. 1998, pl. 1H) from the lower Lochkovian of the Xiaputonggou Formation, Tewo county, China, resembles the simplest variants of *Nostovicina laticristata*, and it seems possible that the Chinese scales from that level should be reassigned to the latter species. The holotype and other paratype scales of *N. tewonensis* were from the much older, upper Wenlockian Miaogou Formation. *N. laticristata* is now recorded from the Lochkovian of arctic Canada, Northwest Territories Canada, Nevada, Taimyr, Podolia, and east Baltic countries (Valiukevičius 1994, 2000, Turner and Burrow 1997).

NOSTOVICINA GUANGXIENSIS (WANG, 1992)

Nostolepis guangxiensis Wang 1992, 282, 283, pl. 1.3–1.5.

Gomphonchus? guangxiensis Burrow 1997, 64, figs. 6A–C, pl. 1.4–8, pl. 4.1–6.

Nostovicina guangxiensis Valiukevičius & Burrow 2005, 646.

Type material—Holotype IVPP V9745.1; Paratypes IVPP V9745.2–4 and thin section IVPP V9745.5; Ertang Formation, Guangxi, China (Lower Devonian, Emsian).

NOSTOVICINA SP. CF. *N. GUANGXIENSIS*

(FIG. 4E–I, K, L; TABLE 1; SUPPL. 1, FIGS. 23, 25–29)

Referred specimens—Scales assigned to this species occur at levels 527.25' (160.7 m), 562–564' (171.3–171.9 m), 591.5–600' (180.3–182.9 m), 674' (205.4 m), 712' (217 m), and include UCR 5443-1, UCR 5443-3, UCR 5443-4, UCR 5443-6 and thin section UCR 5443-7 (level 562.6'=171.5 m); also AMF 97963, 97967 (level 562.6'=171.5 m), figured by Parkes (1995, fig. 33.13, 33.20, 33.21, captioned as *Nostolepis* sp.): Roberts Mountains Formation.

Description—Scales are medium-sized, about 0.5 mm wide, with crown morphologies similar to those in *N. laticristata*, but with up to nine short ridges along the anterior crown margin (Fig. 4E–H). A few scales have an almost circular crown outline (Fig. 4I), approaching the morphology of *Nostovicina multangula* (Valiukevičius 1994). Scale bases are strongly convex and deep (Fig. 4K), usually lacking a marked rim between the neck and base. Odontocytic mesodentine with tubules directed upwards are just visible in the four crown growth zones, bone cell lacunae are rare or absent in the scale base, and the bases are filled with bundles of Sharpey's fibers (Fig. 4K, L).

Comparison—The oldest occurrence of Palaeozoic scales with this range of morphotypes is on the unique partial articulated holotype of *Yealepis douglasi* Burrow & Young (1999) from the Ludlow of Victoria, Australia; the youngest occurrence is the type material (scales) of *Nostovicina guangxiensis* from the early Emsian of Guangxi, China. Scales of *N. guangxiensis* are the most common acanthodian remains in the earliest Lochkovian section at Utopolu, Czechia (CJB, personal observation), and one of the two most common species in the Lochkovian Connemarra Formation, central New South Wales, Australia (Burrow 2002). As noted, scales of *N.*

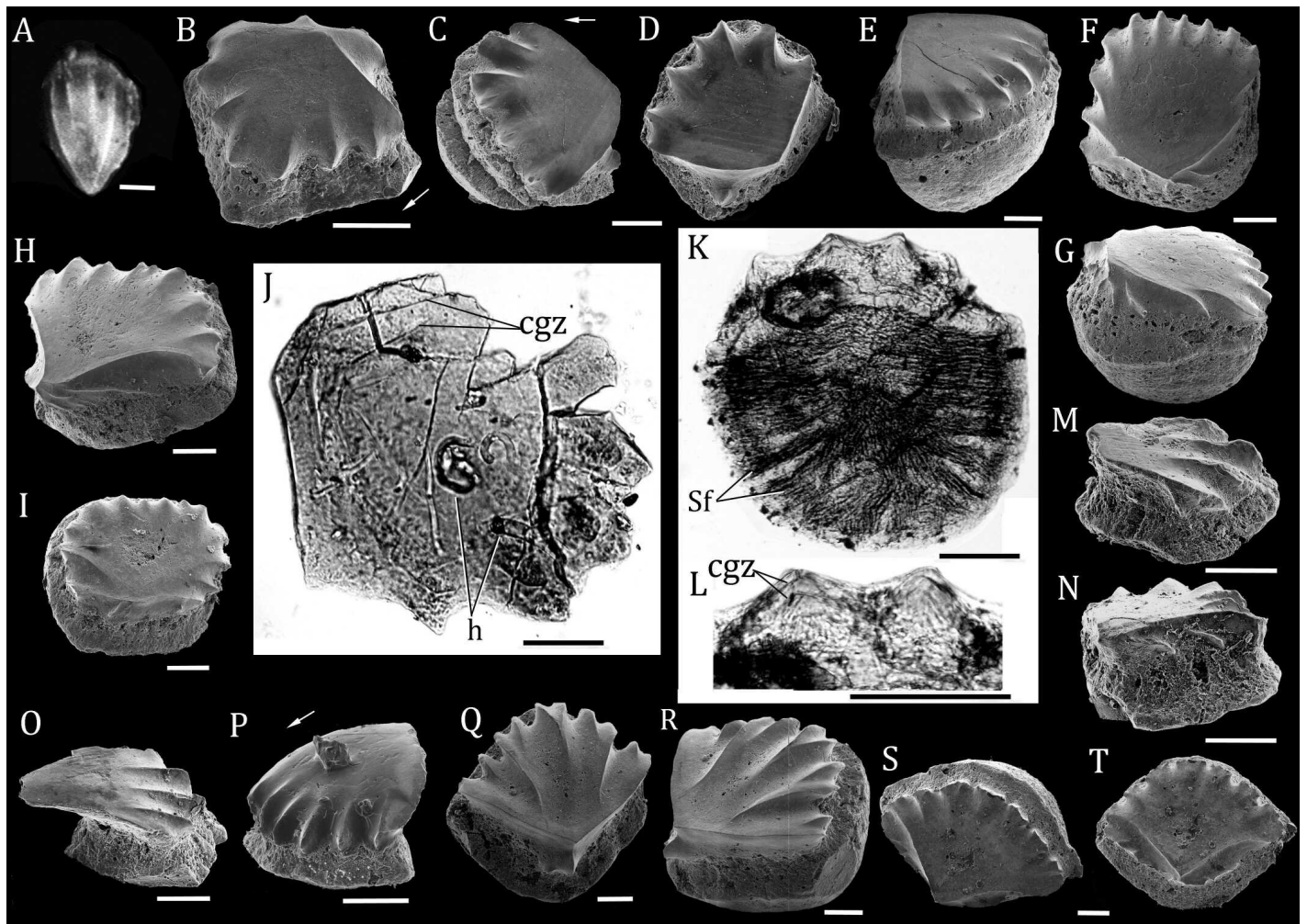


Figure 4. *Nostovicina* and *Nostolepis* sp. acanthodian scales from the Siluro-Devonian boundary levels of the Birch Creek II section. **A.** *Nostovicina* sp. cf. *N. elegans*: UCR 10755-1 (level 470.2') in crown view (from Supplement 1, fig. 13). **B–D, J.** *Nostovicina laticristata*: **B.** UCR 10768-10 (level 518.3') in crown view; **C, D.** UCR 10768-6 (level 518.3') in anterocrown and crown views; **J.** UCR 10768-11 (level 518.3') horizontal thin section through crown. **E–I, K, L.** *Nostovicina* sp. cf. *N. guangxiensis*: **E.** UCR 5443-1 (level 562.6') in anterocrown view; **F, G.** UCR 5443-3 (level 562.6') in crown and lateral views; **H.** UCR 5443-4 (level 562.6') in posterocrown view; **I.** UCR 5443-6 (level 562.6') in crown view; **K, L.** UCR 5443-7 (level 562.6') vertical transverse section, magnified view of crown structure in **L.** **M–P.** *Nostovicina* sp. cf. *N. lacrima*: **M.** UCR 5439-8 in lateral view; **N.** UCR 5439-6 in posterior view; **O.** UCR 5439-4 (level 549') in lateral view; **P.** UCR 10768-1 (level 518.3') in anterior view. **Q–T.** *Nostolepis matukhini*: **Q, R.** UCR 5443-2 (level 562.6') in crown and laterocrown views; **S, T.** UCR 5443-5 (level 562.6') in crown and anterocrown views. Abbreviations: cgz=crown growth zones; h=hyphal borings; Sf=Sharpey's fiber bundles. Scale bars=0.1 mm, anterior of scale is to right or up, otherwise arrows point to anterior. See Table 1 for meterage.

laticristata show the same range of crown morphotypes, but the scales are always smaller than those attributed to *N. guangxiensis*. The same crown morphotypes are also found on scales of the recent Gulper shark *Centrophorus granulosus* (Reif 1985, pl. 5.B1), a demersal deep-water fish. This crown morphology undoubtedly is related to the lifestyle of the fish (see Ferron et al. 2018).

NOSTOVICINA LACRIMA (VALIUKEVIČIUS, 1994)

Nostolepis lacrima Valiukevičius 1994, 153, 154, pl. 19.8–19.11.

Nostovicina lacrima Valiukevičius and Burrow 2005, 646.

Type material—Holotype scale LIGG 30-1604; Uryum beds, Tareya River, Taimyr, Russia (Lower Devonian, Lochkovian).

NOSTOVICINA SP. CF. *N. LACRIMA*

(Figure 4M–P; Table 1; Suppl. 1, figs. 19–21, 25–27, 29)

Referred specimens—Scales from levels 518.3' (158 m), 526' (160.3 m), 527' (160.6 m), 527.25' (160.7 m), 549' (167.3 m), 562' (171.3 m), 562.6' (171.5 m), 591.5'

(182.6 m), 599.5' (182.7 m), 600' (182.9 m), 712' (217 m), including UCR 5439-8, -6, -4 (level 549'=167.3 m), UCR 10768-1 (level 518.3'=158 m): Roberts Mountains Formation.

Description—These scales from the BC II section have a range of morphotypes, within the range shown by the type material of *N. lacrima*, but are relatively rare in the samples. Scales are less than 0.3 mm wide with a shallow base, 4–6 sharp, single smooth ridges running back from the rounded anterior crown margin to mid-crown (Fig. 4M–P), and occasionally short weak ridges running down towards the base from the middle of the side of the crown (Fig. 4M, N). The crown is narrower than the base, but usually extends behind the posterior corner of the base.

Comparison—Some of the scales with short ridges on the side of the crown resemble the body scales of *Nostolepis? tewonensis* (Wang et al. 1998), from the late Wenlockian of Zoige county and early Lochkovian of Tewo county, China. Unfortunately, no histological description or illustrations were given for *N? tewonensis*, so it is unknown to which of the new histology-based genera, which Valiukevičius and Burrow (2005) separated off from *Nostolepis sensu lato*, this species conforms. *Nostovicina lacrima* type material comprises 100 scales, and so, like *Nostolepis matukhini* (see below), is relatively rare even in the type locality, and, given the number of nostolepid-type species erected by Valiukevičius (1994) from those type localities in Taimyr plus variation within species, we only tentatively assign the relatively rare scales in BC II section to *N. lacrima*.

NOSTOLEPIS PANDER, 1856

Type species—*Nostolepis striata* Pander, 1856.

NOSTOLEPIS MATUKHINI VALIUKEVIČIUS, 1994 (FIG. 4Q–T; TABLE 1)

Nostolepis matukhini Valiukevičius 1994, 157, 158, figs. 68.2–68.5, 69.1, 69.2, pl. 20.9, 20.10.

Type material—Holotype LIGG 30-1627; Uryum beds, Taimyr, Russia (Lower Devonian, Lochkovian).

Referred specimens—Scales assigned to this species occur at levels 527.25' (160.7 m) and 562.6' (170.1 m) and include UCR 5443-2, -5 (level 562.6'=170.1 m): Roberts Mountains Formation.

Description—Scales with a distinctively ornamented crown, with 5–7 strong, smooth subparallel or radial ridges that bifurcate towards the anterior margin.

Posterolateral edges of the crown are straight and smooth, converging at a slightly obtuse angle at the posterior corner (Fig. 4Q–T). The base is moderately convex, and the neck has only small pore openings. Scarcity of material precluded thin sectioning to examine histology.

Comparison—The crown ornament on *N. matukhini* scales is very distinctive, with all ridges bifurcating along the anterior margin, a feature not shown in any other nostolepid-type scales.

FUNICRISTATA N. GEN. BURROW, 2023

Type species—*Funicristata nevadaensis* n. sp., by monotypy.

Zoobank LSID—urn:lsid:zoobank.org:act:FD6D940A-FAFF-4FFE-9E35-042B7EBC2315

Diagnosis—as for the species.

Occurrence—Roberts Mountains Formation, central Nevada (Late Silurian, Přidolí).

Etymology—Funis, Latin for rope or cord, referring to the appearance of the crown ridges, and crista, Latin for crest or ridge.

Remarks—These scales have a highly distinctive crown ornament, not observed in any known scale taxa. The poor preservation of histological structure of scales from this level in the section, with dense hyphal borings through the base and crown, obscures details that could help assign them to a family or order.

FUNICRISTATA NEVADAENSIS N. GEN, N. SP. BURROW, 2023 (FIG. 5; TABLE 1; SUPPL. 1, FIGS. 2, 5–7, 9–11, 14)

Zoobank LSID—urn:lsid:zoobank.org:act:1BB5B9FC-3E9B-4F4B-B238-A25CA0E9A8D8

Diagnosis—Acanthodian with small scales up to 0.5 mm wide and 0.6 mm long; crown with strong branched ridges with a 'twisted' appearance leading back from anterior edge and converging towards posterior corner of crown, or at least extending past lateral corners of crown; neck low or absent anteriorly on most scales, with only small pore openings; base only slightly convex and deepest below anterior margin of crown; crown extends up to a base-length beyond posterior corner of base; four or five superposed crown growth zones with a thin enameloid top; wide-calibre canal extends from primordial crown growth zone to posterior corner of crown, its presence usually marked by longitudinal ridge on crown.

Holotype—Holotype scale UCR 10750-3 (Fig. 5A–C); 456.5' (=139.1 m) level, BC II section, Roberts Mountains, Eureka county, central Nevada, U.S.A.: Roberts Mountains

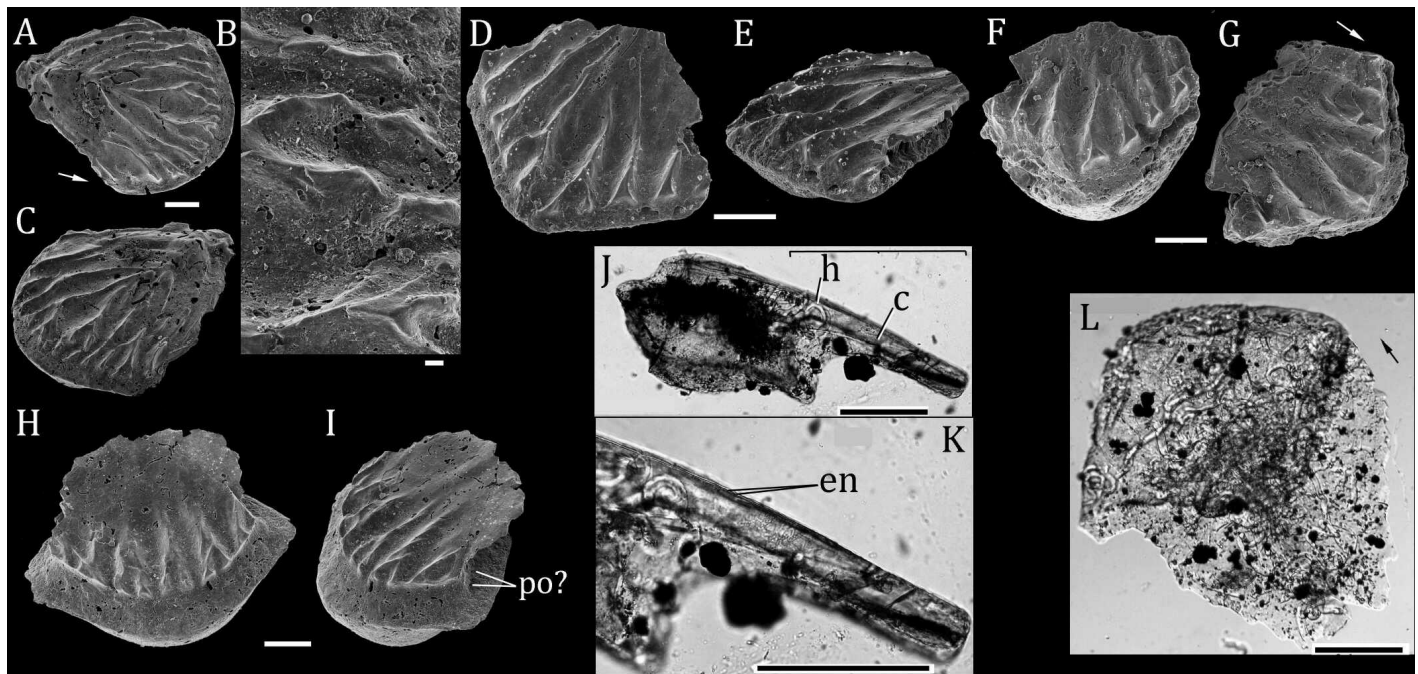


Figure 5. *Funicristata nevadaensis* n. gen. n. sp. from the uppermost Silurian of the Birch Creek II section. **A–C.** UCR 10750-3 (level 456.5') in crown views and magnified view of the crown ridges; **D, E.** UCR 10750-2 (level 456.5') in crown and lateral views; **F, G.** UCR 10746-10 (level 430.5') in anterocrown and crown views; **H, I.** UCR 10746-8 (level 430.5') in anterocrown and laterocrown views; **J, K.** UCR 10750-10 (level 456.5') vertical longitudinal section; **L.** UCR 10750-12 (level 456.5') horizontal section through crown. Abbreviations: c=canal; en=enameloid; h=hyphal boring; po=pore openings. Scale bars=0.1 mm in **A, B, D–L**, 0.01 mm in **C**; anterior is to left or down, otherwise arrows point to anterior. See Table 1 for meterage.

Formation (Late Silurian, Přidolí).

Paratypes—Paratypes scales UCR 10750-2, UCR 10746-8, -10, thin sections UCR 10750-10, 12.

Referred specimens—Forty-three scales including the type specimens.

Occurrence—Only known from the type locality at levels 395–492.3' (120.4–150.1 m).

Etymology—Nevada, for the U.S. state where the type material was found, and ensis, Latin suffix denoting place.

Description—Scales are small, up to 0.5 mm wide, 0.6 mm long and 0.3 mm high. Most scales appear dorsoventrally compressed, with a low or absent neck anteriorly on most scales (Fig. 5A–E). The crowns have a distinctive ornament comprising branching ridges with a 'twisted' or rope-like appearance leading back from the anterior edge, extending towards the posterior corner of crown (Fig. 5A–G), or at least extending past the lateral corners of the crown (Fig. 5H, I). The crown extends up to a base-length beyond the posterior corner of the base, with most scales having a marked median ridge running back from the middle of the scale to the posterior tip (Fig. 5A, E, I). In many scales, particularly the more 'flattened' examples, the crown ornament resembles a branching tree, with the

posterior median ridge being the trunk with the radiating, branching ridges extending out towards the anterior edges. The neck has only small pore openings (Fig. 5I). The base on all scales is only slightly convex and deepest below the anterior margin of the crown, with a marked rim between the base and neck.

Histological preservation is poor at these levels, with extensive hyphal borings, so that only general features can be discerned. The crown has four or five growth zones with all except the embryonic zone being extremely thin under the crown surface, comprising only enameloid posterior to the apex of the base (Fig. 5J, L). A wide calibre canal runs from the embryonic zone up and back through the middle of the posterior crown, aligned with the median ridge on the crown surface, to the posterior corner (Fig. 5J, K). Fine branching dentine tubules rise up in the anterior parts of the crown. No bone cell lacunae are detectable in the base.

Comparison—These scales differ from all known taxa, based on their distinctive crown ornament resembling a tree with successively branching ridges. The single large canal extending from the primordial zone back to the posterior corner could indicate that the taxon is a highly

derived poracanthodid, but no poracanthodids resemble this species in morphology or position of pore canals.

CHONDRICHTHYES HUXLEY, 1880

ELEGESTOLEPIDIDAE ANDREEV, COATES, KARATAJÛTÈ-TALIMAA, SHELTON, COOPER AND SANSOM, 2017

ELLESMEREIA VIETH, 1980

Type species—*Ellesmereia schultzei* Vieth, 1980.

ELLESMEREIA SCHULTZEI VIETH, 1980

(FIG. 6A–C; TABLE 1; SUPPL. 1, FIGS. 4, 5, ?20)

Ellesmereia schultzei Vieth 1980, 54, figs. 26, 27, pl. 9.

Type material—Holotype GSC 2, Member A, Red Canyon River Formation, Ellesmere Island, Canada (Lower Devonian, Lochkovian).

Referred specimens—Rare scales in BCII at level 430.5' (131.2 m) and possibly another very large scale at level 525' (160 m): Roberts Mountains Formation.

Description and comparison—The scales at the lower levels have a broad central longitudinal ridge flanked by narrow ridges paralleling the central ridge. All ridges extend the length of the crown. The base is concave

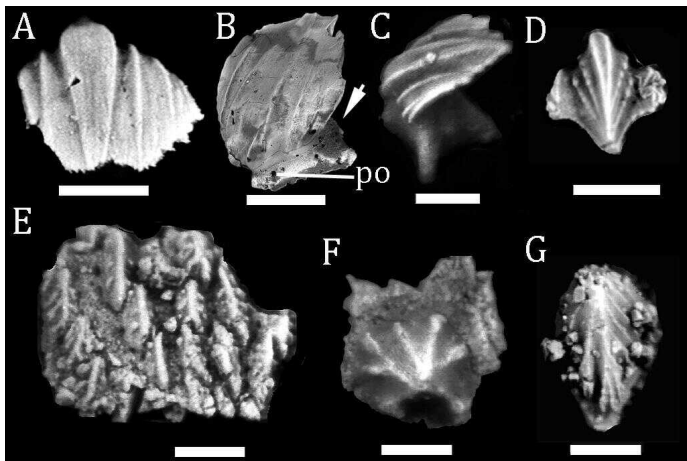


Figure 6. Chondrichthyan and stem osteichthyan scales from the uppermost Silurian of the Birch Creek II section; A, C–G, light microscope images of whitened specimens; B, ESEM image. A–C. *Ellesmereia schultzei*. A, scale UCR 10746-44 (level 430.5') in crown view (from Suppl. 1, fig. 5); B, UCR 10746-28 (level 430.5') in anterolateral-crown view; C, scale UCR10746-45 (level 430.5' in crown and lateral views (from Suppl. 1, fig. 4). D. *Polymerolepis* sp. scale UCR 10752-1 (level 458.67') in crown view (from Suppl. 1, fig. 11). E–G. *Lophosteus* sp. cf. *L. superbus*. E, dermal bone fragment 10754-1 (level 468') in external view (from Suppl. 1, fig. 12); F, G, tubercles UCR951-1, 2 (level 457') in crown views (from Suppl. 1, fig. 10). Scale bars=0.25 mm, anterior of scale is up or to left, otherwise arrow points to anterior. See Table 1 for meterage.

with a sub-diamond outline. The morphology conforms to that of the type scales from the Lochkovian Member A, Red Canyon River Formation, Ellesmere Island, Arctic Canada, figured by Vieth (1980, pl. 9).

POLYMEROLEPIDIFORMES KARATAJÛTÈ-TALIMAA, 1968

POLYMEROLEPIDIDAE KARATAJÛTÈ-TALIMAA, 1968

POLYMEROLEPIS KARATAJÛTÈ-TALIMAA, 1968

Type species—*Polymerolepis whitei* Karatajûtè-Talimaa, 1968.

POLYMEROLEPIS SP.

(FIG. 6D; TABLE 1; SUPPL. 1, FIGS. 5, 7, 11, 14)

Referred specimens—Very rare, one scale at level 458.67' (139.8 m) and possible scale fragments from 430.5' (131.2 m), 453' (138.1 m), 492.3' (150.1 m): Roberts Mountains Formation.

Description and comparison—The scales and scale fragments have finely noded ridges. The scale base is always flat or concave. The type material of *P. whitei* from the Lochkovian of Podolia shows a wide range of scale morphotypes (e.g., Obruchev and Karatajûtè-Talimaa 1967, pl. 2 figs. 1–4, Karatajûtè-Talimaa 1998, figs. 6, 7). Hanke et al. (2013, figs. 1–5) demonstrated in their description of a partial articulated specimen from the Lochkovian MOTH locality in the Northwest Territories, Canada assigned to *P. whitei*, comprising an anal fin and part of the caudal fin and peduncle, that the scale variation over the body is even greater than seen in the type scales. Specimens referred to *P. whitei* from the younger Lochkovian (*delta* conodont Zone) Windmill Limestone, Simpson Park Range, Nevada include head, fin, and body scales (Turner and Murphy 1988, table 1, figs. 2.14, 15, 20, 22–26). The Nevadan scales are the first record in the Silurian for this taxon. Given the morphological variation in scales from the known localities, it seems possible that more than one species is represented, so we only refer the BC II specimens to an open taxon within the genus rather than to the type species.

OSTEICHTHYES HUXLEY, 1880

LOPHOSTEIFORMES GROSS, 1969

LOPHOSTEIDAE GROSS, 1969

LOPHOSTEUS PANDER, 1856

Type species—*Lophosteus superbus* Pander, 1856.

LOPHOSTEUS SUPERBUS PANDER, 1856

Type material—Pander's specimens have long been lost, so Gross (1969) erected a neotype, scale Tü Pi 1359/1 (Gross 1969, fig. 1A, B, 2H₁₋₃); Ohesaare Regional Stage, Ohesaare Cliff, Saaremaa, Estonia (Upper Silurian, upper Pridolí).

LOPHOSTEUS SP. CF. *L. SUPERBUS*
(FIG. 6E–G; TABLE 1; SUPPL. 1, FIGS. 1, 10, 12)

Referred specimens—Scales assigned to this species occur at levels 318' (96.9 m), 457' (139.3 m), 468' (142.6 m), and possibly 527.25' (160.7 m): Roberts Mountains Formation.

Description—The rare remains comprise scale and dermal bone fragments (Fig. 6E–G), the former ornamented with inclined, elongate ridged tubercles (Fig. 6E) with the best example being a broken scale from level 318' having parallel elongate tubercles extending the length of the rhombic scale. The dermal bone fragments mostly have more stellate tubercles (Fig. 6F).

Comparison—The best-preserved scale fragment compares closely with scales of the type species *L. superbis* from the upper Pridolí Ohesaare Beds, Saaremaa Island, Estonia rather than with scales of other species. (See Schultze and Märss 2004, for examples of *Lophosteus* spp. From the Baltic, Canada, and Russia).

OSTEICHTHYES?
SARCOPTERYGII?

FAMILY, GENUS, SP. INDET.
(TABLE 1; SUPPL. 1, FIGS. 12, 14, 21, 25, 29, 30, 31)

Referred specimens—Teeth from ten levels between 395' (120.4 m) and 711' (216.7 m) including one tooth in level 468' (142.6 m; Suppl. 1, fig. 12), three in level 527' (160.6 m; Suppl. 1, fig. 21) and level 623' (189.9 m; Suppl. 1, fig. 29).

Description and remarks—These isolated smooth conical teeth mostly appear broken off a base. Some of the teeth (levels 527' and 623') appear socketed and thus could be onychodont teeth, which might suggest that the Lochkovian is reached, as the oldest known onychodont, a toothed lower jaw from China (Zhu and Janvier 1994), bears this type of teeth. Turner and Murphy (1988) noted the presence of similar teeth in the Lochkovian Windmill Limestone of Nevada.

PTERASPIDOMORPHI GOODRICH, 1909
HETEROSTRACI LANKESTER, 1868

HETEROSTRACI INDET. GEN. ET SP.
(TABLE 1; SUPPL. 1, FIGS. 7, 11, 12, 14, 18)

Referred specimens—Scale fragments were collected from BC II section at six levels from 430.5' to 513' (131.2–156.4 m): Roberts Mountains Formation.

Remarks—Most remains are conjoined tesseræ such as the three small irregular tesseræ from level 458.67' (Suppl. 1, fig. 11). Some (Suppl. 1, figs. 7, 14, 18) resemble traquairaspid remains with slender oak-leaf pattern tubercles: traquairaspids typically range from Pridolí to early Lochkovian. One plate from level 468' (Suppl. 1, fig. 12) is pteraspid- or poraspid-like, typical of early Lochkovian elsewhere (e.g., Turner et al. 2017). Turner and Murphy (1988, fig. 1.1–6, 8–15, 24) described heterostracan microremains from the Lochkovian Simpson Park section, Nevada. Parkes (1995) also identified heterostracan remains in two levels of BC II (402', 446').

As yet, there is no major review of heterostracan dermal scales; a handbook and major description of Cornwallis Island fauna are awaited (D.K. Elliott pers. comm. 2021, Thorsteinsson and Elliott 2022).

THELODONTI JAEKEL, 1911

Remarks—Thelodont scales are found throughout the section but mostly as single or a few specimens. In all there are only around 100 scales throughout the section from 19 levels, far fewer than the acanthodian scales except at one level, 430.5' (see below and Table 1, Suppl. 1). Hence most identifications are tentative because of the lack of a full range of morphotypes. Scales at most levels are poorly preserved with (fungal or algal) borings (see e.g., Goujet and Locquin 1979).

LOGANELLIFORMES TURNER, 1991
LOGANELLIA FREDHOLM, 1990

Type species—*Thelodus scoticus* Traquair, 1898.

LOGANELLIA SP. CF. *L. CUNEATA*
(TABLE 1; SUPPL. 1, FIGS. 1, 4)

Referred specimens—One scale from BCII level 27' (8.2 m); two scales from level 430.5' (131.2 m): Roberts Mountains Formation.

Description and comparison—Elongate teardrop-shaped scales with two sharp crown ridges. The base is oval and extends about two-thirds crown length. There is no anterior basal spur.

This scale resembles those described as *Loganellia cuneata* (Gross 1947, pl. 3; 1967, pl. 3) from the Přidolí of Britain, Europe, and Russia (Märss et al. 2007) but also is similar to the much older *L. sulcata* and *L. prolata* (Märss et al. 2002) from the Lower Silurian of arctic Canada. Without more material, the designation can only be tentative.

PHLEBOLEPIFORMES BERG 1937

KATOPORODIDAE MÄRSS ET AL., 2002

TRIMEROLEPIS OBRUCHEV & KARATAJŪTĒ-TALIMAA, 1967

Type species—*Trimerolepis lithuanica* KARATAJŪTĒ-TALIMAA in OBRUCHEV & KARATAJŪTĒ-TALIMAA, 1967.

Remarks—The scales of this genus type are rare and found in the lower part of the BC II section, hence our identifications are tentative. *Trimerolepis* species occur mostly in the Přidolí to lower Lochkovian (Märss et al. 2007).

TRIMEROLEPIS TRICAVA (GROSS, 1967)

Type material—Holotype scale MB.f. 903 (Gross 1967, pl. 2.23), *Thelodus parvidens* Zone, Beyrichienkalk 1 (upper Ludlow to lower Přidolí, Silurian), northern German plain.

TRIMEROLEPIS SP. CF. *T. TRICAVA*

(FIG. 7A; TABLE 1; SUPPL. 1, FIGS. 3, 5, 10)

Referred specimens—Rare, four specimens: two possible from level BCII 424.9' (129.5 m); one from 430.5' (131.2 m); one from level 457' (139.3 m): Roberts Mountains Formation.

Description and comparison—These scales are all head or transitional cephalopectoral. They are tripartite scales with smooth crowns rising slightly to a posterior point. The central section has a shallow anterior groove and is separated from the postero-lateral flanges by a concave groove. The postero-lateral crown rim has slight crenulation.

These scales are most like those of *Trimerolepis tricava* (Gross 1967). Gross (1967) first identified this taxon as 'Katoporus tricavus' in the late Silurian *Thelodus parvidens* Zone of Beyrichienkalk 1 (upper Ludlow to lower Přidolí) from the North German erratics. Märss et al. (2002, 2006) discovered scales referred to *Trimerolepis tricava* from the lowest measured beds (0.0 m–51.0 m, and on up to 87 m) in the southern Read Bay section

on eastern Cornwallis Island, arctic Canada, which is the stratotype for the Přidolí part of the Barlow Inlet Formation. Otherwise this taxon is known in the Přidolí of Britain, Europe, and the Baltics (Märss et al. 2007).

TRIMEROLEPIS SP.

(FIG. 7B; TABLE 1; SUPPL. 1, FIG. 9)

Referred material—two specimens from BC II: one scale from level 456.5' (139.1 m); one scale, AMF97876, figured by Parkes (1995, fig. 22.19, 20) from level 503' (153.3 m) (Fig. 7B) – this specimen is missing: Roberts Mountains Formation.

Description and comparison—The small tripartite possible trunk or cephalopectoral scale from level 456.5' has deeply serrated lateral flanges flanking a higher flat-topped median section. The elongate arrowhead-shaped transitional scale from level 503' assigned by Parkes (1995, p. 52-54, fig. 19, 20) to *Katoporus* sp. cf. *K. tricavus* is also *Trimerolepis* sp. It has a smooth anteriorly tripartite crown, slightly broken to one side. There is a shallow anterior groove to the central section and is separated from the laterally expanded parts by grooves, to one side with a much deeper embayment, which might be a sensory pore canal opening. The crown slopes gently and tapers to the rounded posterior point. The neck is a shallow groove separating crown and base. The latter is narrow and follows the shape of the crown and is broadly rhomboidal with the posterior and one lateral rim broken. The pulp cavity is open and also roughly diamond-shaped and the many pore canal openings typical of *Trimerolepis* dentine ('Katoporus type' of Gross 1967) can be seen (Fig. 7B). The specimen from 456.5' resembles some from *Tr. gemmelus* Märss et al., 2002. On the complete side of the crown in AMF97876, there are four 'serrations' resembling those of *Tr. serrata* rather than the slightly older-occurring *Tr. tricava*; however, all head to transitional scales of this genus (e.g., the type and other species, Märss et al. 2007) are very similar. *Tr. serrata* and *Tr. gemmelus* were described by Märss et al. (2002) from the Lochkovian Barlow Inlet Formation, south of Read Bay, Cornwallis Island.

GONIPORUS GROSS, 1967

Type species—*Thelodus alatus* Gross, 1947.

GONIPORUS ALATUS (GROSS, 1947)

(TABLE 1; SUPPL. 1, FIG. 5)

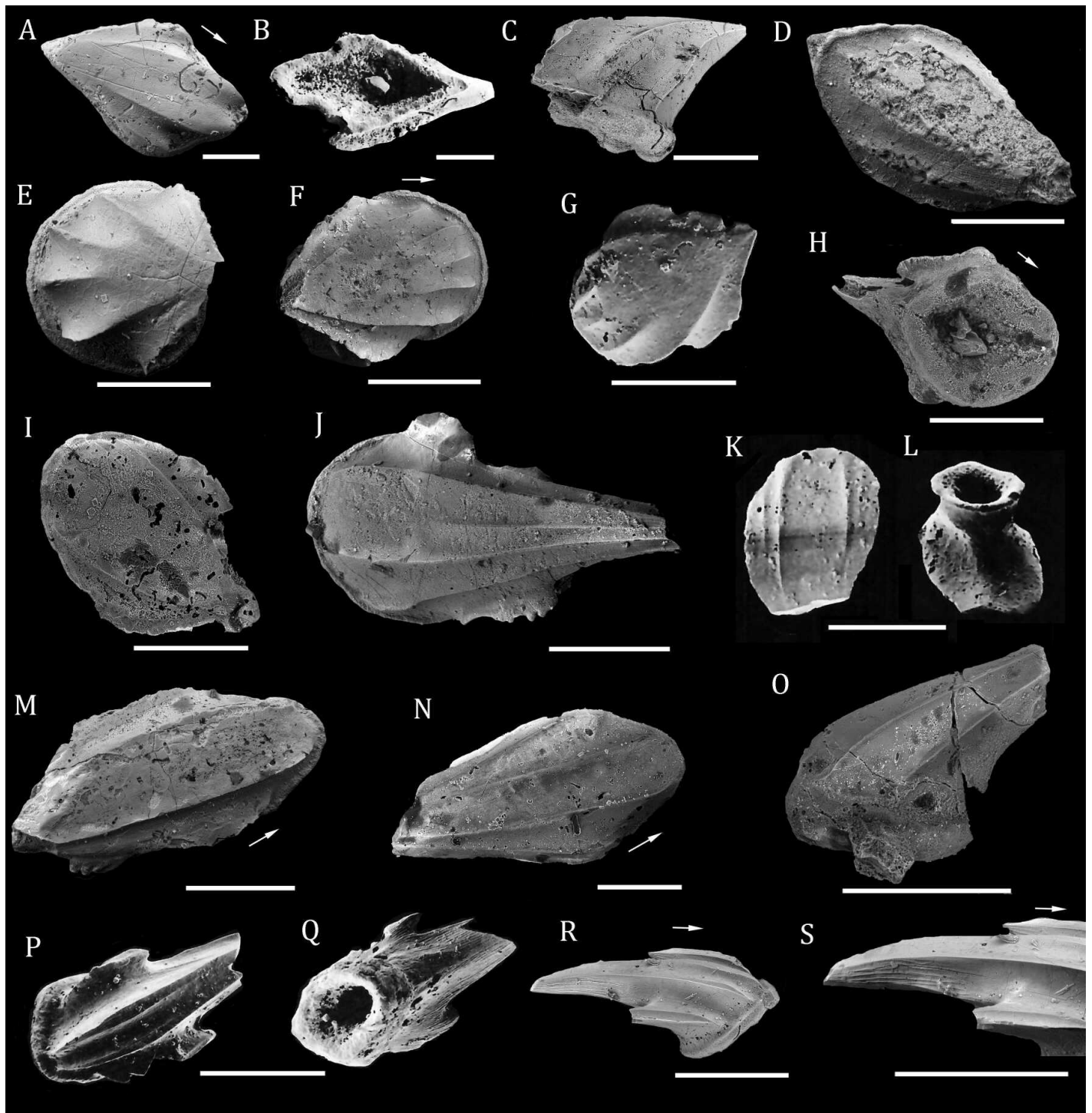


Figure 7. Thelodont scales from the uppermost Silurian of the Birch Creek II section, all level 430.5' except B, C, G, K, L, P, Q. **A.** *Trimerolepis* sp. cf. *T. tricava*. UCR 10746-43 in crown view. **B.** *Trimerolepis* sp. AMF97876 (Parkes 1995, fig. 22.19, 20) from level 503', base view. **C.** ?*Lanarkia* sp. UCR 944-20 (level 527.25') in lateral view. **D.** ?*Turinia* sp. UCR10746-19, showing taphonomic effects and ultrasculpture, in crown view. **E-J.** *Nikolivia* spp. **E.** UCR 10746-13 with cell pattern on surface in crown view; **F.** UCR 10746-20 in crown view; **G.** AMF97875 (Parkes 1995, fig. 22.17, 18) from level 402' with possible bite marks, in crown view; **H.** UCR 10746-27 in ventral basal view; **I.** UCR 10746-25 showing taphonomic effects in crown view; **J.** *Nikolivia* sp. cf. *N. auriculata*, UCR 10746-18 in crown view. **K, L.** *Apalolepis* sp. AMF97872 (level 503') (Parkes 2005, fig. 22.11, 12), crown and basal views. **M-O.** *Talivalia* sp. cf. *T. elongata*. **M.** UCR 10746-17 in crown view; **N.** UCR 10746-37 in crown view; **O.** UCR 10746-21 in lateral view. **P-S.** *Barlowodus* sp. cf. *B. tridens*. **P, Q.** AMF97874 (level 875') in crown and basal views (Parkes 2005, fig. 22.15, 16). **R, S.** UCR 944-21 (level 527.25') in laterocrown view, closeup in S showing striated ultrasculpture. Scale bars=0.2 mm; anterior to left or top, otherwise arrow points to anterior. See Table 1 for meterage.

Type material—Holotype scale MB.f.410 (Gross 1947, pl. 1 fig. 5a, b), Beyrichienkalk, Danzig (now Poland) (uppermost Silurian, Přidolí).

Referred material—Three scales from BCII level 430.5' (131.2 m): Roberts Mountains Formation.

Description and Remarks—These specimens are typical of the taxon, with one transitional cephalo-pectoral and two trunk scales (see e.g., Gross 1947, 1967). Distribution is in the Přidolí of Europe, Britain, and Russia and possibly into lowermost Lochkovian (Märss et al. 2007).

THELODONTIFORMES KIAER, 1932

Remarks—Several of the thelodontiform scales are rounded head scales (see Suppl. 1, e.g., figs. 4, 8, 12: levels 430.5', 456.5', 468') with simple crenulated rims and a rounded base with a large pulp cavity opening. These scales are also typical of many thelodont taxa of different families. These scales resemble *Thelodus* sp. cf. *T. admirabilis* Märss, 1982 found in the late Přidolí of Europe (Märss et al. 2007). For now, they are left in open nomenclature until further material is found.

LANARKIIDAE OBRUCHEV, 1949 LANARKIA TRAUQUAIR, 1898

Type species—*Lanarkia horrida* Traquair, 1898.

?LANARKIA SP.

(FIG. 7C; TABLE 1; SUPPL. 1, FIG. 11)

Referred specimens and Remarks—At least two possible scales from BC II section: one from level 458.67' (139.8 m), one from level 527.25' (160.7 m) (Fig. 7C). *Lanarkia* species are known mainly from earlier Silurian rocks in Scotland, mainland Europe, and arctic Russia, as well as in arctic Canada (Märss et al. 2007). The scale from 527.25' is most like those called *Thelodus traquairi* by Gross (1967), originally "*Lanarkia costata*" of Gross, 1947, from the north German Beyrichienkalk (Bey. 1, early Přidolí) and ones from Poland (late Přidolí; Gross 1947, Märss 1997), which have been referred to *Lanarkia* (Märss et al. 2007).

TURINIIDAE OBRUCHEV, 1964 TURINIA TRAUQUAIR, 1895

Type species—*Cephalopterus pagei* Powrie, 1870.

?TURINIA SP.

(FIG. 7D; TABLE 1; SUPPL. 1, FIGS. 5, 9)

Referred specimens—Possibly three scales in BCII section: two at level 430.5' (131.2 m) and one at 456.5' (139.1 m): Roberts Mountains Formation.

Description—One scale in 430.5' is a robust trunk scale with the posterior tip broken off, by which the central large pulp canal can be seen. The base is extended anteriorly into a wide spur. A further possible trunk scale is boat-shaped with a poorly preserved crown with prominent ridges and a median narrow platform, a wide shallow neck and a small anterior prong on the large ellipsoid base (Fig. 7D). A broken trunk scale from level 456.5' has a posteriorly expanding and possibly high crown. The undersurface of the posterior crown in a trunk scale has a strong median rib and three to four lateral ones (Suppl. 1, fig. 9). There is a broken anterior rounded base with a large pulp opening.

Remarks—These few scales resemble those of the type species and might be *Turinia pagei* but their preservation is poor and/or they are broken and this taxon does not usually occur below the Siluro-Devonian boundary. Turiniid scales with several ventral crown ribs are also seen in *Turinia borentsia* from the Lower Devonian Red Bay Group of Spitsbergen (Blom and Goujet 2002, e.g., pl. 1.6, 8). *Turinia*-like scales have been recorded in some localities such as the Welsh Borders and Irian Jaya (Märss et al. 2007, Turner et al. 2017).

BOREANIA KARATAJÜTÈ-TALIMAA, 1985

Type species—*Boreania minima* Karatajütè-Talimaa, 1985.

BOREANIA MINIMA KARATAJÜTÈ-TALIMAA, 1985

Type material—Holotype scale LitNIGRI no. 35-456 (Karatajütè-Talimaa 1985, fig. 1.24); obn. 4, sl. 3, Matusevich R., October Revolution Island, Severnaya Zemlya, Russia: Pod'yemnaya Formation (early Lochkovian, Lower Devonian) (NB. might be lost).

BOREANIA SP. CF. B. MINIMA

(TABLE 1; SUPPL. 1, FIGS. 10?, 11, 12, 22?, 25?)

Referred specimens—Rare; 5 specimens in BCII: possibly one scale at level 457' (139.3 m); one at level 458.67' (139.8 m); one at level 468' (142.6 m); possibly one scale at level 556.5' (169.6 m); possibly one scale at

level 591.5' (180.3 m): Roberts Mountains Formation.

Description—Small rounded, presumed head or oral scales where the crown is only slightly larger than the base. The crown has numerous ridges and the rim is wavy. One head or special (lateral line?) scale from level 458.67' has a high rounded crown with a distinct embayment at one place in the crown/neck interface and below on the deep base there is a large foramen, which might be related to a pore canal (Suppl. 1, fig. 11).

Remarks—The scales in Nevada most probably belong to *B. minima* but their rarity does not allow a definite assessment. One tripartite scale in 430.5' could be *B. minima* or might be *Trimerolepis tricava* (see remarks above). Because of its earlier location in the section, an alternative identification for the scale at level 457' might be *Thelodus admirabilis* Märss, 1982 but based on one poor scale, this is uncertain; these taxa are known from early to late Přidolí, respectively (Märss et al. 2007). Karatajūtė-Talimaa (1985) defined the genus *Boreania* based on Turner's (1984) assessment of a separate species that she called '*Turinia*' *minima* and similarities to southern Baltic specimens that Karatajūtė-Talimaa (1964) had referred to *Turinia pagei*. This taxon is typical of the latest Přidolí to lower Lochkovian of the Baltic states, the Welsh Borders, Spitsbergen and October Revolution Island (Märss et al. 2007). Usually, *B. minima* is associated with the key Lochkovian taxon *Turinia pagei*. Interestingly, the latter taxon is noticeable by its absence, except for one or two possible broken turiniid-like scales (see above).

NIKOLIVIIDAE KARATAJŪTĖ-TALIMAA, 1978

NIKOLIVIA KARATAJŪTĖ-TALIMAA, 1978

Type species—*Nikolivia balabayi* Karatajūtė-Talimaa, 1978.

NIKOLIVIA SPP.

(FIG. 7E–J; TABLE 1; SUPPL. 1, FIGS. 5, 9, 20, 25)

Referred material—Rare except for one level; c. 15 specimens from section BC II: one scale AMF97875 from 402' (122.5 m)– this specimen is missing; c. 11 from 430.5' (131.2 m), 456.5' (139.1 m); level 527.25' (160.7 m); one specimen from level 591.5' (180.3 m): Roberts Mountains Formation.

Description and comparison—AMF97875 and the other *Nikolivia* scales from BC II, notably from 430.5', resemble scales of *N. gutta*, *N. aligera* Karatajūtė-Talimaa, 2002 (Fig. 7A–E), and *N. auriculata* Märss et al., 2002 (Fig. 7F). These nikoliid taxa are found in the early Lochkovian

elsewhere (Märss et al. 2007). The specimen that Parkes (2005, fig. 22.17, 18; Fig. 7G) captioned as *Amaltheolepis* sp. cf. *A. winsnesi* from 402' is a typical nikoliviid scale, bilaterally symmetrical, small (0.4 mm long x 0.3 mm wide) and rounded. The central squat teardrop-shaped crown section is smooth and rounded anteriorly and raised slightly, curving to a posterior point with three short anterior ridges that extend less than a quarter scale length. There is a pair of lateral flattened lappets with a simple but slightly imperfect (damaged?) rim with small scallop-shaped concavities, two on one side and one on the other. The central surface of the crown is smooth with a broad middle raised ridge extending from the midpoint near the base to the posterior point. The neck is smooth and low. The anteriorly placed base is a rounded torus: relatively smooth, deep, and mature with a smaller central rounded pulp opening. One possible thelodont specimen (Suppl. 1, fig. 25:?) from level 591.5' just above the S–D boundary appears typical of *Nikolivia gutta* Karatajūtė-Talimaa, 1978 with its smooth heart-shaped crown.

Remarks—Parkes (1995) interestingly misidentified scale AMF97875 (Fig. 7G) as an amaltheolepid. Here we refer it to *Nikolivia* sp. But there are not enough scales in the Nevadan material to judge the variation. Nikoliviid scales are typical of the Early Devonian (Lochkovian) in Europe, and elsewhere in North America (Märss et al. 2007). The small regular concavities on the rim of the lateral lappets of the specimen might be damage made in handling the specimen or a pathological feature as they resemble bite-marks, but this has not been seen elsewhere. Lepidophagy is common in modern bony fishes and it is feasible that the scale was attacked in life or alternatively post-mortem by another fish or even by an unknown invertebrate.

APALOLEPIDIDAE TURNER, 1976

APALOLEPIS KARATAJŪTĖ-TALIMAA, 1968

Type species—*Apalolepis obruchevi* Karatajūtė-Talimaa, 1968

APALOLEPIS SP.

(FIG. 7K, L; TABLE 1)

Referred specimens—One scale, AMF97872 from BCII level 503' (153.3 m) – this specimen is missing: Roberts Mountains Formation.

Description—Parkes (1995, p. 55, fig. 22.11, 12) correctly identified and described this broken scale. The

crown is flattened and smooth, the upper surface divided by simple ridges into a central part and two lateral fields, the ventral surface smooth. The crown rises gently to the posterior edge at about 20 degrees from the anterior edge. The neck is high and smooth. The base is typical for the genus, being anteriorly placed, small and rounded with a shallow torus and slightly anterior point.

Remarks—Vieth (1980) tentatively assigned one scale (not figured) from the Lochkovian Member A, Red Canyon River Formation to *?Apalolepis*. Elsewhere, *Apalolepis* taxa are only found in the Lochkovian (Märss et al. 2007).

TALIVALIIDAE MÄRSS, WILSON AND THORSTEINSSON, 2002

TALIVALIA MÄRSS, WILSON AND THORSTEINSSON, 2002

Type species—*Nikolivia elongata* Karatajūtė-Talimaa, 1978.

TALIVALIA ELONGATA (KARATAJŪTĖ-TALIMAA, 1978)

Type material—Holotype scale LitNIGRI no 15-494 (Karatajūtė-Talimaa 1978, pl. XLII.6a, b), Zalyeshchiki, Podolia, Ukraine (Lower Devonian, Lochkovian, Ivanov horizon). [might be missing]

TALIVALIA SP. CF. *T. ELONGATA*

(FIG. 7M–O; TABLE 1; SUPPL. 1, FIGS. 4, 5, 7, 30)

Referred specimens—Six scales from BC II; three from level 430.5' (131.2 m); two broken scales from level 453' (138.1 m); one scale from 722.5' (220.2 m): Roberts Mountains Formation.

Description and comparison—Most scales closely resemble the elongate teardrop-shaped trunk scales of *Talivalia elongata* sensu stricto (Karatajūtė-Talimaa 1968, 1978). One scale in 430.5', seen in ventral view has small papillae on the thickened basal torus placed anteriorly (Suppl. 1, fig. 5). *Talivalia elongata* is well known from many circum-Arctic sites spanning late Přidolí to Lochkovian (Märss et al. 2007). Turner and Burrow (2018) referred one scale from the late Přidolí Eastport Formation of Moose Island, Maine uncertainly to the genus *Talivalia*.

“BARLOWODIDAE” MÄRSS, WILSON AND THORSTEINSSON, 2002

BARLOWODUS MÄRSS, WILSON AND THORSTEINSSON, 2002

Type species—*Barlowodus excelsus* Märss et al., 2002.

BARLOWODUS TRIDENS MÄRSS, WILSON AND THORSTEINSSON, 2002

Type material—Holotype scale UALVP 44700 (Märss et al. 2002, pl. 1, fig. 18), upper Barlow Inlet Formation, southern Read Bay section, Cornwallis Island, Canadian Arctic Archipelago (lowermost Devonian, lower Lochkovian).

BARLOWODUS SP. CF. *B. TRIDENS*

(FIG. 7P–S; TABLE 1; SUPPL. 1, FIG. 4)

Referred specimens—one scale from BC II level 430.5' (131.2 m); one from level 527.25' (160.7 m); one scale AMF 97874 from BC II level 875' (266.7 m); this last specimen is missing: Roberts Mountains Formation.

Description and comparison—A scale figured by Parkes (1995, fig. 22.15, 16, captioned as *?nikoliviid* gen. et sp. indet.; Fig. 7P, Q) is c. 0.4 mm long with a broken posterior crown, which rises quite steeply posteriad. The dorsal crown is elongated and subdivided into three with a raised central section with two high flat-topped ridges with a deep central groove anteriorly that flattens posteriad. Laterally there are expanding lappets, one anteriorly seen to the left, also with a bifurcate dorsal ridge that extends about one-third of the crown, and on the left a series of two broken and one complete ridge that extends about two-thirds of crown length. The posterior points of the lappets tend to be rounded but are also broken. A flattened lateral ridge then extends from the base of the lappets towards the broken posterior tip. The ventral crown is covered with an ultrasculpture of fine parallel striae extending from the anterior crown/neck interface to the posterior tips of the lateral lappets and posterior section of the broken crown. The neck itself is relatively shallow and unornamented. The base is oval, extending about one-quarter of the estimated length of the scale. It is relatively mature with a thick torus surrounding the large central oval pulp opening and with a slight anterior thickening. One small, rounded scale has a strong tripartite crown with deep grooves between the high flat ridges. It is most like the simpler cephalopectoral or trunk of *B. tridens* (e.g., Märss et al. 2006, text-fig. 65) from the Přidolí Barlow Inlet Formation of Cornwallis Island. The scale from level 527.25' is tricuspid with clear striated

ridges on the sides of the cusps (Fig. 7R, S).

Remarks—Märss et al. (2002, 2006) discovered the thelodont genus *Barlowodus* in the southern section eastern Cornwallis Island at Read Bay (RBBI and RBBI*), which became the stratotype for the Přidolí Barlow Inlet Formation that is formed from argillaceous carbonate marine rocks. At 59.0 m from only one sample, Märss et al. (2002) identified three taxa, *Barlowodus tridens*, *B. excelsus*, and *B. floralis*, the latter doubtfully. *Barlowodus tridens* sensu stricto is only known elsewhere from Cornwallis Island. However, scales possibly from this, as well as the other two species of this genus, were recorded from the late Přidolí Barlow Inlet Formation by Märss et al. (2006, pp. 124-126).

The fine microornament on the scale figured by Parkes (1995, fig. 22.15,16; Fig. 7P, Q) is similar to that in other Devonian taxa such as *Neoturinia* spp., *Barlowodus floralis* and even *Boothialepis thorsteinssoni* (Märss et al. 2006, pl. 16). Such fine ridging on the scales might have contributed to drag reduction (e.g., Reif 1985). It is unusual in the Nevadan case being on the ventral surface of the crown; we tentatively refer it to *B. sp. cf. tridens*. However, it is at a level much higher than the other thelodont scales, in the lower to middle Lochkovian.

BARLOWODUS FLORALIS MÄRSS, WILSON AND THORSTEINSSON, 2002

Type material—Holotype scale UALVP 44955 (Märss et al. 2002, pl. 1, fig. 17), upper Barlow Inlet Formation, southern Read Bay section, Cornwallis Island, Canadian Arctic Archipelago (lowermost Devonian, lower Lochkovian).

BARLOWODUS SP. CF. B. FLORALIS
(FIG. 8A–K; TABLE 1; SUPPL. 1, FIGS. 4, 5, 7)

Referred specimens—Circa 20 specimens from BC II level 430.5' (131.2 m); two from level 453' (138.1 m): Roberts Mountains Formation.

Description and comparison—Small scales with complex crown sculpture, all with fine ribbed ultrasculpture (Fig. 8A–K). One possible head or oral scale has a high multi-ridged crown and high neck with a rounded base and large central pulp opening (Fig. 8A). One possible cephalopectoral scale has a flattened rhombic crown which rises only slightly to a posterior point; fine ultrasculpture as well as borings can be seen on the surface (Fig. 8B). Most scales are trunk scales. The crowns rise gently posteriad with three flat ridges or a system of bifurcating ridges separated by deep or wide

grooves. The posterior or posterolateral crown margin is multi-pointed (Fig. 8A, C–F, H–K).

Most scales in level 430.5' seem affected by fungal damage (as noted for other specimens above). Histology was attempted using anise oil but the structure is disrupted and so we cannot verify the apparent “criss-cross aspidine ‘pegs’” noted as characteristic for the genus and separate family by Märss et al. (2006, p. 121). However, a similar criss-cross pattern of Sharpey’s fiber bundle spaces is found in other deep and swollen old bases of other thelodont scale taxa such as *Thelodus laevis* (e.g., Bystrow 1957, Gross 1967).

Remarks—Most of the scales from Nevada seem closest to *B. floralis*. The type locality for the latter is at 34.5* m in the same section where it co-occurs with the other two *Barlowodus* species (Märss et al. 2006).

?*BARLOWODUS SP.*
(TABLE 1; SUPPL. 1, FIG. 7)

Referred specimens—two scales from BCII section level 453' (138.1 m); two scales from BC II section level 527.25' (160.7 m): Roberts Mountains Formation.

Description—These specimens are not well preserved but might be trunk scales of a species of this genus.

DISCUSSION

The vertebrates found in the S–D boundary beds in the Birch Creek II section comprise many taxa that are the same or similar to those from the circum-Arctic region. Generally, acanthodian scales greatly outnumber thelodont scales suggesting relatively deeper water, except for level 430.5' where thelodonts *Nikolivia*, *Talivalia*, and *Barlowodus* predominate. Horizons around this level are predominantly laminated shaly limestones, perhaps indicative of lagoonal deposition. Märss and Einasto (1978) noted that in the north Baltic Silurian sequences, thelodonts were more characteristic of lagoonal belt deposits, with acanthodians becoming dominant in shoal/shelf belt deposits during the Přidolí. The relative abundance of acanthodians over thelodonts at this time also coincides with high global sea levels (Melchin et al. 2012, fig. 21.11) and presumably deeper water on the continental shelves.

The acanthodian faunal assemblages show a general succession similar to that found in stratigraphic sequences in the Baltic, northern Russia, the Welsh Borderlands, Canada, China, and eastern Australia, with ischnacanthiform acanthodians being the dominant taxa through the Přidolí and an influx of *Nostolepis* sensu

lato species just below the S–D boundary. Distributions listed here for previously known taxa are based on Burrow (2021). Most of the acanthodian taxa represented in the BC II section are also found in circum-Arctic regions, with only one new endemic species *Funicristata nevadaensis*, recognized in upper Přídolí levels of the section. *Poracanthodes punctatus* is the vertebrate zone fossil for the upper Přídolí (Märss et al. 1995), up to the FAD of thelodont *Trimerolepis timanica* (Märss and Mannik 2013). Although found in circum-Arctic localities as well as Nevada (BC II, and also Pete Hanson Creek, see Burrow 2003a), *P. punctatus* is not known from any Gondwanan localities, nor are any other punctatiform

poracanthodids (*sensu* Vergoossen 1997). Punctatiform *Poracanthodes canadensis* is only recorded from arctic Canada and Nevada. Porosiform poracanthodid *Radioporacanthodes scheii* shows a similar distribution to *P. canadensis*, whereas *Radioporacanthodes porosus* occurs more widely, possibly being found in eastern Australia (Burrow 2002) and China as well as the circum-Arctic region, Welsh Borderland, and Nevada. *Gomphonchoporus hoppei* and *Zemlyacanthus menneri* are only found in the latter three regions (Burrow 2003b). *Trundlelepis cervicostulata* is possibly quite widely distributed worldwide in the uppermost Silurian and lowermost Devonian. Although it has not previously been certainly identified

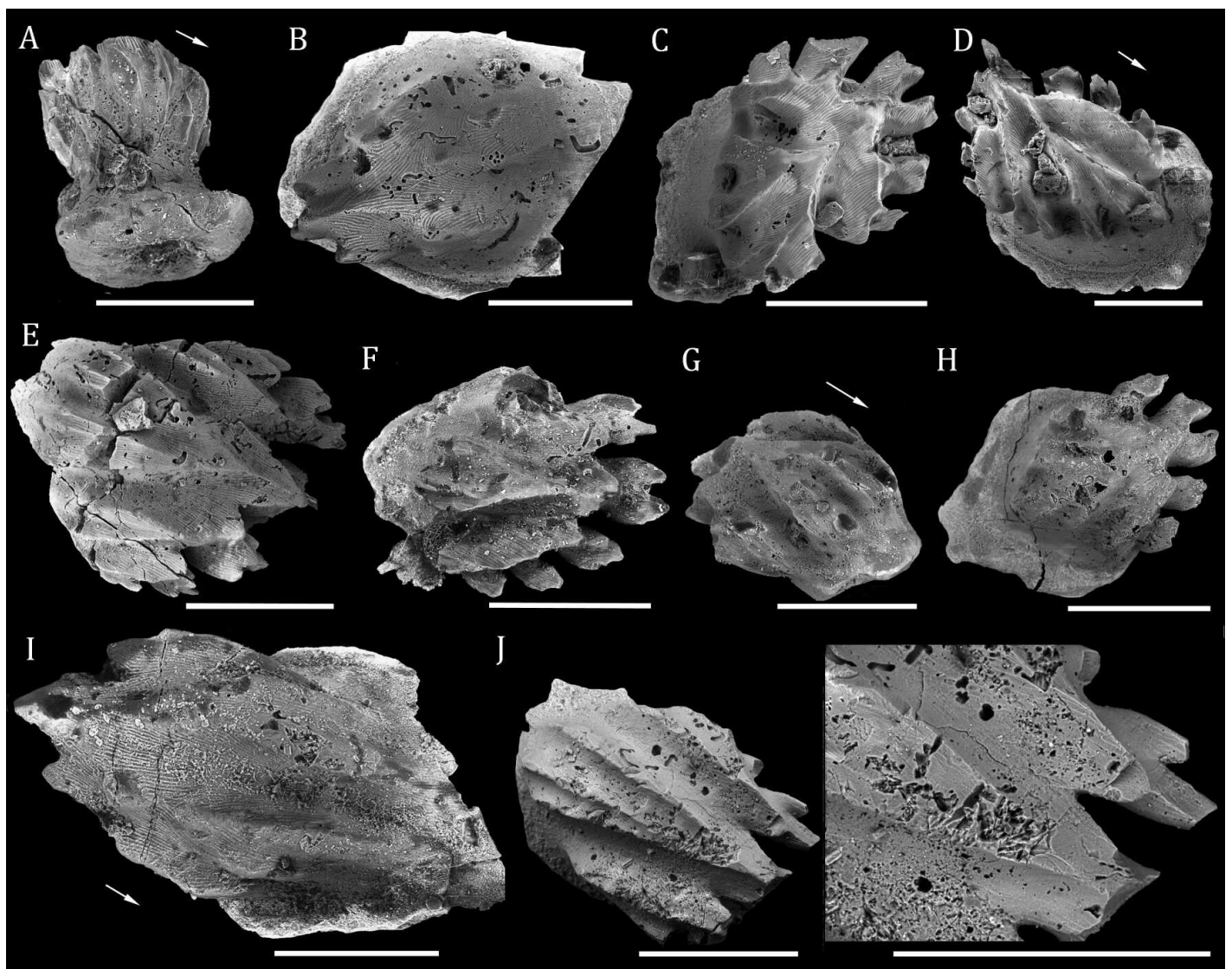


Figure 8. A–K. Scales of thelodont *Barlowodus* sp. cf. *B. floralis* from the uppermost Silurian of the Birch Creek II section, all level 430.5'. A, UCR 10746-31 in baso-lateral view; B, UCR 10746-35 in crown view; C, UCR 10746-36 in crown view; D, UCR 10746-34 in crown view; E, UCR 10746-42 in crown view; F, UCR 10746-29 in crown view; G, UCR 10746-24 in crown view; H, UCR 10746-38 in crown view; I, UCR 10746-23 in crown view; J, K, UCR 10746-14, in crown view, and close up of dorsal mid-crown showing ultrasculpture and taphonomic effects. Scale bars=0.2 mm; anterior to left except A, D, G, I. See Table 1 for meterage.

outside Australia in the Lochkovian, we tentatively report it from the Přidolí of Czechia and Sweden (CJB personal observation), and possibly the Emsian of China (Burrow 2021), a distribution suggesting it could have dispersed from Laurussia to Gondwana. *Gomphonchus sandelensis* has a relatively wide stratigraphic range through the Přidolí and Lochkovian in the Baltic and throughout Eurasia, the Welsh Borderland, and North American eastern maritime states, but occurs only at Přidolí levels in the Birch Creek II section. *Gomphonchus mediocostatus* is only known from the uppermost Přidolí, in the Welsh Borderlands across the Baltic to Novaya Zemlya as well as Nevada. *Nostolepis striata*, one of the commonest acanthodians of the Přidolí and Lochkovian in the Baltic, is absent from the BC II section.

The most marked change in fauna is not at the level previously considered as the S–D boundary (567' level), but at the 513' level, with *Nostovicina* spp. dominating the assemblages above this. The only *Nostolepis* species represented is *N. matukhini* at the 562.6' level, which is otherwise only known from Taimyr, Russia. *Nostovicina laticristata*, which is distributed widely in the circum-Arctic region, appears at the 513' level and is the most abundant acanthodian up to the 545' level; poracanthodid *Zemlyacanthus menneri*, only previously known from arctic Russia, is the most abundant for the next couple of levels, then *Nostovicina* sp. cf. *N. guangxiensis* is most abundant through the rest of the section. *N. guangxiensis* is found in the Early Devonian of China, eastern Australia, and Chukotka, Russia.

The only identifiable non-acanthodian gnathostomes found in the section are the chondrichthyans *Ellesmereia schultzei* and *Polymerolepis* sp., and the stem osteichthyan *Lophosteus* sp. cf. *L. superbus*, with scattered rare occurrences from 395' (120.4 m) up through the Přidolí. *Ellesmereia* is only known elsewhere from the Lochkovian of Arctic Canada, and *Polymerolepis* is known from the Lochkovian of Podolia, the Welsh Borderlands (Turner et al. 2017), Northwest Territories, Canada, and the Simpson Park Range, Nevada. *Lophosteus* spp. have been described from the Baltic, arctic Canada, Russia (Schultze and Märss 2004), and eastern Australia (Burrow 1995, Burrow and Turner 2000).

Thelodont scales are much rarer than acanthodian scales; the taxa represented are all found elsewhere from localities across Laurussia, notably in arctic Canada. Interestingly, some of the taxa, *Turinia?* sp., *Apalolepis* sp., *Talivalia elongata*, occur earlier in the Birch Creek II section than is known elsewhere (Märss et al. 2007). Scales of the *Barlowodus* taxa also occur in the late Silurian in

Nevada but there are scales referred to this genus in the late Přidolí from Cornwallis Island in arctic Canada (Märss et al. 2006).

CONCLUSIONS

The BC II section of Nevada provides a good continuous late Silurian to earliest Devonian section ranging from the Přidolí into the Lochkovian. Based on the current assessment of the invertebrate distributions, the Silurian–Devonian boundary is somewhere between levels 477 to 567 feet (145.4 to 172.8 m).

Overall, the vertebrate taxa in the BC II section, described here, indicate that Nevada had connections to the circum-Arctic region, and also to eastern Gondwana, during the latest Silurian to earliest Devonian. All these regions were subtropical or tropical at the time; distribution of the vertebrates described here supports a dispersal route from the Baltic region around the northern shores of the Old Red Sandstone continent (Laurussia) and down the western shore to the Nevada region. This area could have been the source region for some eastern Gondwanan taxa, given their earlier appearance in the BC II sequence (Fig. 9). As might be expected from the biogeographic distribution of invertebrates including conodont taxa, the closest faunal similarity for the Nevada vertebrate assemblage is with northwestern and arctic Canada. Stone and Berdan (1984) noted that the Nevada ostracodes include both North American and Eurasian elements, with closest similarities to northwestern Canadian and eastern Alaskan faunas, the basis for the western North American Cordilleran Ostracode Province of Berdan (1990). The distribution of corals (Pedder and Murphy 1997) also accords with that shown

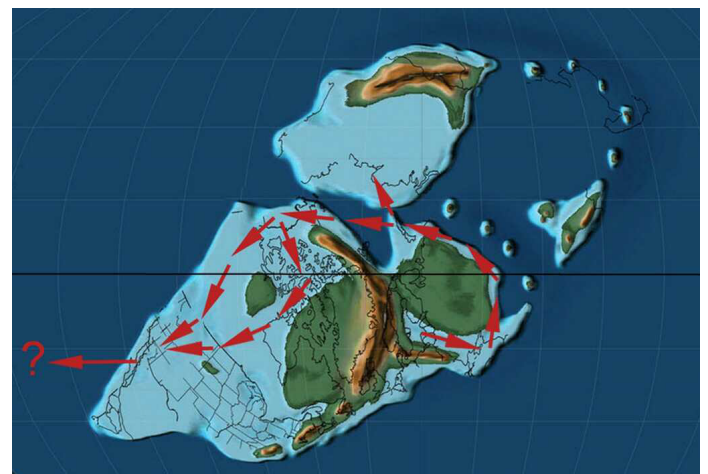


Figure 9. Paleogeographic reconstruction for the late Silurian, base map from Scotese (2014, map 73), showing possible vertebrate dispersal route from the Baltic to the circum-Arctic and thence south to western Laurentia.

by the vertebrates.

The completeness of the BC II section, combined with intensive collecting from closely spaced levels, reveal transitional forms between the well-represented poracanthodid taxa. For example, some scales assigned to *Gomphonchoporus hoppei* (Fig. 3.6, 3.7) approach the *Zemlyacanthus menneri* morphotype, and *Trundlelepis cervicostulata* shows perhaps the last stage in the reduction of the pore canal system in the scale crown for poracanthodids. The occurrence of *Nostovicina* spp. increases dramatically from about the 517' [157.6 m] level, below the previously estimated level of the S–D boundary, whereas the poracanthodids decrease dramatically. This change could indicate that the boundary is lower than the 567' level estimated by Berry and Murphy (1975), or alternatively, could be related to a regression at this time associated with a drop in sea level, as postulated by some workers (Melchin et al. 2012, fig. 21.11).

Based on their occurrences at relatively low levels in the BC II section, several thelodont taxa, notably *Turinia*, *Apalolepis* and *Nikolivia* spp., and the chondrichthyans *Ellesmereia schultzei* and *Polymerolepis*, thought previously to be restricted to the Devonian, first appear in the late Silurian in Nevada, even if the S/D boundary is lower than 567'. Based on these occurrences and of the rarer remains such as the heterostracan and possible onychodont, the S/D boundary could be close to the lowest level (477' = 145.4 m) supported by the graptolite and conodont ranges.

The relative abundance of acanthodian taxa in the section, associated with the low numbers of specimens for each taxon compared with contemporary assemblages in the Baltic (for example), have hampered our investigation to some degree. Nevertheless, the results of our study show the potential for adapting biostratigraphic schemes based on acanthodian taxa from the Baltic region to inter-regional and possibly worldwide correlations.

ACKNOWLEDGEMENTS

We thank the two anonymous reviewers for their comments and suggested improvements to the manuscript, and acknowledge the support and facilities provided to CJB and ST by the Queensland Museum.

LITERATURE CITED

- Andreev, P.S., M.I. Coates, V. Karatajūtė-Talimaa, R.M. Shelton, P.R. Cooper, and I.J. Sansom. 2017. *Elegestolepis* and its kin, the earliest monodontode chondrichthyans. *Journal of Vertebrate Paleontology* 37(1):e1245664.
- Berdan, J.M. 1990. The Silurian and Early Devonian biogeography of ostracodes in North America. *Geological Society, London, Memoirs* 12(1):223–231.
- Berg, L.S. 1937. A classification of fish-like vertebrates. *Izvestiya Akademii Nauk USSR*, 1193 Seriya Biologicheskaya 4:1277–1280.
- Berg, L.S. 1940. Classification of fishes, both recent and fossil. *Trudy Instituta Zoologicheskikh Akademiia Nauk* 5(2):85–517.
- Berry, W.B.N., and M.A. Murphy. 1975. Silurian and Devonian graptolites of central Nevada. *University of California Publications in Geological Sciences* 110:1–109.
- Blom, H. 1999. Vertebrate remains from Upper Silurian–Lower Devonian beds of Hall Land, North Greenland. *Geology of Greenland Survey Bulletin* 182:1–80.
- Blom, H., and D. Goujet, 2002. Thelodont scales from the Lower Devonian Red Bay Group, Spitsbergen. *Palaeontology* 45(4):795–820.
- Botella, H., C. Martínez-Pérez, and R. Soler-Gijón. 2012. *Machaeracanthus goujeti* n. sp. (Acanthodii) from the Lower Devonian of Spain and northwest France, with special reference to spine histology. *Geodiversitas* 34:761–783.
- Branson, E.B., and M.G. Mehl. 1933. Conodonts from the Bainbridge Formation (Silurian) of Missouri. *University of Missouri Studies* 8:39–52.
- Brotzen, F. 1934. Erster Nachweis von Unterdevon im Ostseegebiete durch Konglomeratgeschiebe mit Fischresten. Zweiter Teil (Paläontologie). *Zeitschrift für Geschiebeforschung* 10:1–65.
- Burrow, C.J. 1995. A new lophosteiform (Osteichthyes) from the Lower Devonian of Australia. *Geobios, Mémoire Spécial* 19:327–333.
- Burrow, C.J. 1997. Microvertebrate assemblages from the Lower Devonian (pesavis/sulcatus zones) of central New South Wales, Australia. *Modern Geology* 21:43–77.
- Burrow, C.J. 2002. Lower Devonian acanthodian faunas and biostratigraphy of south-eastern Australia. *Memoirs of the Association of Australasian Palaeontologists* 27:75–137.
- Burrow, C.J. 2003a. Poracanthodid acanthodian from the Upper Silurian (Pridoli) of Nevada. *Journal of Vertebrate Paleontology* 23(3):489–493.
- Burrow, C.J. 2003b. Earliest Devonian gnathostome microremains from central New South Wales (Australia). *Geodiversitas* 25(2):273–288.
- Burrow, C.J. 2011. A partial articulated acanthodian from the Silurian of New Brunswick, Canada. *Canadian Journal of Earth Sciences* 48(9):1329–1341.
- Burrow, C.J. 2013. Reassessment of *Ischnacanthus? scheii* Spjeldnaes (Acanthodii, Ischnacanthiformes) from the latest Silurian or earliest Devonian of Ellesmere Island, arctic Canada. *Canadian Journal of Earth Sciences* 50(8):945–954.
- Burrow, C.J. 2021. Handbook of Paleichthyology. Vol. 5. Acanthodii, Stem Chondrichthyes. Verlag Dr Friedrich Pfeil, Munich. 166 pp.
- Burrow, C.J., and T. Märss. 2022. Neotypes for some upper Silurian acanthodian taxa from the Baltic Sea Region and the Welsh Borderland. *Estonian Journal of Earth Sciences* 71:17–24.
- Burrow, C.J., and A.J. Simpson. 1995. A new ischnacanthid

- acanthodian from the Late Silurian (Ludlow, *ploecken-sis* Zone) Jack Formation, north Queensland. *Memoirs of the Queensland Museum* 38(2):383–395.
- Burrow, C.J., and S. Turner. 2000. Silurian vertebrates from Australia. *Courier Forschungsinstitut Senckenberg* 223:169–174.
- Burrow, C.J., and G.C. Young. 1999. An articulated teleostome fish from the Late Silurian (Ludlow) of Victoria, Australia. *Records of the Western Australian Museum Suppl.* 57:1–14.
- Burrow, C.J., J. den Blaauwen, M. Newman, and R. Davidson. 2016. The diplacanthid fishes (Acanthodii, Diplacanthiformes, Diplacanthidae) from the Middle Devonian of Scotland. *Palaeontologia Electronica* 19.1.10A:1–83.
- Burrow, C.J., A.O. Ivanov, and V.B. Ershova. 2018. Acanthodians from the Silurian–Devonian boundary beds of Novaya Zemlya Archipelago, Russia. *GFF* 140(3):241–248.
- Burrow, C.J., H. Lelièvre, and D. Janjou. 2006. Gnathostome microremains from the Lower Devonian Jawf Formation, Saudi Arabia. *Journal of Paleontology* 80:537–560.
- Burrow, C.J., J.M.J. Vergoossen, S. Turner, T. Uyeno, and R. Thorsteinsson. 1999. Microvertebrate assemblages from the Upper Silurian of Cornwallis Island, Arctic Canada. *Canadian Journal of Earth Sciences* 36:349–361.
- Bystrow, A.P. 1956. On the damage caused by fungi in the skeletal elements of fossil animals. *Leningrad University Vestnik Seria Geologo-Geographich* 11:30–46 (in Russian).
- Bystrow, A.P. 1957. *Proshloye, nastoyashchii, boodooshchii chyelovyeka. [The past, present, and the future of man]*. Medgiz, Leningrad. (in Russian).
- Coates, M.I., J.A. Finarelli, I.J. Sansom, P.S. Andreev, K.E. Criswell, K. Tietjen, M.L. Rivers, and P.J. La Riviere. 2018. An early chondrichthyan and the evolutionary assembly of a shark body plan. *Proceedings of the Royal Society B: Biological Sciences* 285:20172418.
- Dearden, R.P., C. Stockey, and M.D. Brazeau. 2019. The pharynx of the stem-chondrichthyan *Ptomacanthus* and the early evolution of the gnathostome gill skeleton. *Nature Communications* 10:2050.
- Dineley, D.L., and E.J. Loeffler. 1976. Ostracoderm fauna of the Delorme and associated Siluro-Devonian formations, North West Territories, Canada. *Special Papers in Palaeontology* 18:1–218.
- Ferron, H.G., C. Martínez-Pérez, S. Turner, E. Manzanares, and H. Botella. 2018. Patterns of ecological diversification of thelodonts. *Palaeontology* 61:303–315.
- Fredholm, D. 1990. Agnathan vertebrates in the Lower Silurian of Gotland, Sweden. *Geologiska Föreningens i Stockholm Förhandlingar* 112:61–84.
- Gegenbaur, C. 1874. *Manuel d'anatomie comparée*. Simon Raçon et Comp., Paris. 844 pp.
- Goodrich, E.S. 1909. Cyclostomes & Fishes. Pp. xvi + 1–518 in E.R. Lankester (ed.). *A Treatise on Zoology*, Pt. 9. Vertebrata Craniata (1st fasc.). Macmillan, London.
- Goujet, D., and M.V. Locquin. 1979. Découverte de spores fongiques dans les écailles de poissons et d'agnathes Paléozoïques: *Mycobistrovia lepidophaga* gen. et sp. nov. *Comptes Rendus du 104th Congrès National des Sociétés Savantes, Bordeaux, Section des Sciences* 1:87–99.
- Gross, W. 1947. Die Agnathen und Acanthodier des obersilurischen Beyrichienkalks. *Palaeontographica Abt. A* 96:91–161.
- Gross, W. 1967. Über Thelodontier-Schuppen. *Palaeontographica Abt. A* 127:1–67.
- Gross, W. 1969. *Lophosteus superbus* Pander, ein Teleostome aus dem Silur Oesels. *Lethaia* 2:15–47.
- Gross, W. 1971. Downtonische und Dittonische Acanthodier-Reste des Ostseegebietes. *Palaeontographica Abt. A* 136:1–82.
- Hanke, G.F. 2001. Comparison of an early Devonian acanthodian and putative chondrichthyan assemblage using both isolated and articulated remains from the Mackenzie Mountains, with a cladistic analysis of early gnathostomes. Unpublished PhD thesis, University of Alberta, Edmonton, Canada.
- Hanke, G.F., M.V.H. Wilson, and F.J. Saurette. 2013. Partial articulated specimen of the Early Devonian putative chondrichthyan *Polymerolepis whitei* Karatajūtė-Talimaa, 1968, with an anal fin spine. *Geodiversitas* 35:529–543.
- Huxley, T.H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly the Mammalia. *Proceedings of the Zoological Society of London* 43:649–662.
- Jaekel, O.M.J. 1911. *Die Wirbeltiere; eine Übersicht über die Fossilien und lebenden Formen*. viii+252 pp. Gebrüder Borntraeger, Berlin.
- Johnson, J.G., A.J. Boucot, and M.A. Murphy. 1973. Pridolian and early Gedinnian age brachiopods from the Roberts Mountains Formation of central Nevada. *University of California Publications in Geological Sciences* 100:75 pp.
- Johnson, J.G., A.J. Boucot, and M.A. Murphy. 1976. Wenlockian and Ludlovian age brachiopods from the Roberts Mountains Formation of central Nevada. *University of California Publications in Geological Sciences* 115:213 pp.
- Karatajūtė-Talimaa, V.N. 1964. Danyye k stratigrafii nijnego devona ujnnoi Pribaltiki. [Data on the stratigraphy of the Lower Devonian of the southern Baltic States]. Pp. 21–39 in V.N. Karatajūtė-Talimaa and V. Narbutas (eds). *Voprosy Stratigrafii i Paleogeografii Devona Pribaltiki* [Questions of stratigraphy and paleogeography of the Devonian Baltics]. Mintis, Vilnius (in Russian).
- Karatajūtė-Talimaa, V.N. 1968. Novye Telodonti, Heterostraki i Artrodiry iz Chortlovskogo Horizonta Podolii [New Thelodonti, Heterostraci and Arthrodira from the Choztkovian Horizon of Podolia]. Pp. 33–42, 168, in D.V. Obruchev (ed.). *Ocherki po Filogenii i Sistematike iskopaemykh Ryb i Bescheliustnykh* [Sketches on phylogeny and taxonomy of fossil fishes and Agnatha]. Nauka, Moscow (in Russian with English summary).
- Karatajūtė-Talimaa, V.N. 1978. *Telodonty Silura i*

- Devona SSSR i Shpitsbergena [Silurian and Devonian thelodonts of the USSR and Spitsbergen]. 334 pp., Mokslas, Vilnius. (in Russian).
- Karatajūtė-Talimaa, V.N. 1985. Telodinti Pod'yemnyenskoj Sviti (Nizhniy Devon, Zhedin) Severnoy Zemli I ikh korrelyatsionnoye znacheniye [Thelodonts of the Podyomnaya [sic] Formation (Lower Devonian, Gedinnian) of Severnaya Zemlya and their correlative importance]. *Nauchniye Trudi Visshikh Uchyebnikh Zavedeniy Litovskoy SSR, Geologija* 6:50–60. (in Russian with English summary).
- Karatajūtė-Talimaa, V.N. 1998. Determination methods for the exoskeletal remains of early vertebrates. *Mitteilungen aus dem Museum für Naturkunde Berlin, Geowissenschaftliche Reihe* 1:21–51.
- Karatajūtė-Talimaa, V.N. 2002. Lower Devonian (Lochkovian) thelodonts from October Revolution Island (Severnaya Zemlya Archipelago). *Geodiversitas* 24, 4:791–804.
- Kiaer, J., and A. Heintz. 1932. New coelolepids from Upper Silurian on Oesel (Esthonia). *Eesti Loodusteaduse Arhiiv* 1 v 10, no. 3, 3/4:1–8.
- Klapper, G. 1977. Lower and Middle Devonian conodont sequence in central Nevada, with contributions by D. B. Johnson. In M.A. Murphy, W.B.N. Berry and C.A. Sandberg (eds.). *Western North America: Devonian. University California, Riverside Campus Museum, Contribution* 4:33–54.
- Klapper, G., and M.A. Murphy. 1975. Silurian–Lower Devonian conodont sequence in the Roberts Mountains Formation of central Nevada. *University of California Publications in Geological Sciences* 111:68 pp.
- Lankester, E.R. 1868. The Fishes of the Old Red Sandstone of Britain. Part I. The Cephalaspidae. *Monographs of the Palaeontographical Society* 21(92):1–33.
- Lehman, J.P. 1937. Les Poissons du Downtonien de la Scanie (Suède). Thèse, Université de Paris 664, Rennes. 98 pp.
- Märss, T. 1982. *Thelodus admirabilis* n. sp. (Agnatha) from the Upper Silurian of the East Baltic. *Eesti NSV Teaduste Akade Toimetised* 31, K. Geol. 3, 112–116.
- Märss, T. 1986. Silurian vertebrates of Estonia and West Latvia. Valgus, Tallinn. 104 pp. (In Russian).
- Märss, T. 1997. Vertebrates of the Pridoli and Silurian-Devonian boundary beds in Europe. *Modern Geology* 21:17–41.
- Märss, T., and R. Einasto. 1978. Distribution of the vertebrates in the sediments of the various facies of the Silurian in northern Baltic countries. *Eesti NSV teaduste Akadeemia Toimetised, Keemia, Geoloogia* 1:16–22 (in Russian with English summary).
- Märss, T., and P. Mannik. 2013. Revision of Silurian vertebrate biozones and their correlation with the conodont succession. *Estonian Journal of Earth Sciences* 62:181–204.
- Märss, T., D. Fredholm, V. Karatajūtė-Talimaa, S. Turner, L. Jeppsson, and G. Nowlan. 1995. Silurian vertebrate biozonal scheme. *Geobios Mémoire Spécial* No. 19:369–372.
- Märss, T., K.L. Soehn, and M.V.H. Wilson. 1998. Microvertebrate-based correlations of the Llandovery–Wenlock boundary in some sections of the Selwyn and Franklinian sedimentary basins, northern Canada. *Ichthyolith Issues, Special Publication* 4:37–39.
- Märss, T., M.V.H. Wilson, and R. Thorsteinsson. 2002. New thelodont (Agnatha) and possible chondrichthyan (Gnathostomata) taxa established in the Silurian and Lower Devonian of Arctic Canada. *Proceedings of the Estonian Academy of Sciences, Geology* 51:88–120.
- Märss, T., M.V.H. Wilson, and R. Thorsteinsson. 2006. Silurian and Lower Devonian thelodonts and putative chondrichthyans from the Canadian Arctic Archipelago. *Special Papers in Palaeontology* 75:1–44.
- Märss, T., S. Turner, and V. Karatajūtė-Talimaa. 2007. Agnatha II-Thelodonti. Volume 1B. 143 pp. Verlag Dr Friedrich Pfeil, Munich.
- Melchin, M.J., P.M. Sadler, B.D. Cramer, R.A. Cooper, F.M. Gradstein, and O. Hammer. 2012. Chapter 21 - The Silurian Period. Pp. 525–558 in F. M. Gradstein, J. G. O. D. Schmitz, and G. M. Ogg (eds.) *The Geologic Time Scale*. Elsevier, Boston.
- Murphy, M.A. 1977. The Silurian – Devonian of Nevada. Pp. 264–271 in A. Martinsson (ed.) *The Silurian-Devonian boundary: final report of the Committee on the Silurian-Devonian Boundary within IUGS Commission on Stratigraphy and a state of the art report for Project Ecostratigraphy*. I.U.G.S. Series A, No. 5, Schweizerbart'sche, Stuttgart.
- Murphy, M.A. 2016. *Cypricriodus hesperius* (Klapper and Murphy, 1975) – taxonomy and biostratigraphy. *University of California, Riverside Campus Museum Contribution* 8:1–20.
- Murphy, M.A., and L.E. Edwards. 1977. The Silurian-Devonian Boundary in Central Nevada. In Murphy, M.A., W.B. Berry, and C.A. Sandberg (eds.) *Western North America: Devonian. University of California, Riverside Campus Museum Contribution* 4:183–189.
- Obruchev, D.V. 1949. [Type Vertebrata]. Pp 316–328 in Luppov, N.P. (ed.) *Atlas of index fossils of the fossil faunas of the USSR*. Vol. 2, Silurian System. Nauka, Moscow. (In Russian)
- Obruchev, D.V. 1964. *Osnovy Paleontologi*. v. 11. Ryby i Byescheliustnikh. [Fundamentals of Palaeontology: Fishes and Agnatha: A manual for paleontologists and geologists of the USSR]. 522 pp. Nauka, Moscow. (in Russian).
- Obruchev, D.V., and V.N. Karatajūtė-Talimaa. 1967. Vertebrate faunas and correlation of Ludlovian–Lower Devonian in eastern Europe. Pp. 5–14 in Patterson, C. and P.H. Greenwood (eds.) *Fossil Vertebrates*. Linnean Society of London and Academic Press, London.
- Owen, R. 1846. *Lectures on the comparative anatomy and physiology of the vertebrate animals*. Pt. I, Fishes, i–xi+304 pp. Longman, Brown, Green and Longmans, London.
- Pander, C.H. 1856. *Monographie der fossilen Fische des silurischen Systems der Russisch-Baltischen Gouvernements*. Obersilurische Fische. 91 pp. Buchdruckerei der Kaiserlichen Akademie der Wissenschaften, St. Petersburg.

- Parkes, R. 1995. Late Silurian–Early Devonian vertebrate microremains from Nevada and southeastern Australia: biochronology, biogeography and application of novel histological techniques. Unpublished B.Sc. (Hons) thesis, Macquarie University, Sydney, NSW.
- Pedder, A.E.H., and Murphy, M.A. 1997. Lochkovian Rugosa of Nevada. *Geological Society of America Special Publication* 321:341–386.
- Perner, J. 1899. Études sur les graptolites de Bohème. 3-ième partie, section b. Bellman, Prague. 24 pp.
- Plax, D.P. 2011. Devonian ichthyofauna of the Volyn Monocline. *Lithosphaera* 35(2):12–21.
- Powrie, J. 1870. On the earliest vestiges of vertebrate life; being a description of the fish remains of the Old Red Sandstone of Forfarshire. *Transactions of the Geological Society of Edinburgh* 111:284–301.
- Příbýl, A. 1940. On Czech representatives of monograptids of the *Pristiograptus nudus* group. *České Akademie Ved a Umení Trida* 2(16):1–14.
- Reif, W. 1985. Squamation and ecology of sharks. *Courier Forschungsinstitut Senckenberg* 78:1–255.
- Rohon, J.V. 1893. Die obersilurischen Fische von Oesel. Teil II. *Memoires de l'Académie Impériale des Sciences de St Petersburg, VIIe série*, vol. 41, 38 Mr.(Nr. 5):1–124.
- Schultze, H.P., and T. Märss. 2004. Revisiting *Lophosteus*, a primitive osteichthyan. *Acta Universitatis Latviensis* 679:57–78.
- Scotese, C.R. 2014. Atlas of Silurian and Middle-Late Ordovician paleogeographic maps (Mollweide Projection), Maps 73 – 80, Volumes 5, The Early Paleozoic, PALEOMAP Atlas for ArcGIS, PALEOMAP Project, Evanston, IL.
- Spjeldnaes, N. 1967. Acanthodians from the Siluro-Devonian of Ellesmere Island. Pp. 807–813 in D. H. Oswald (ed.). International Symposium on the Devonian System, II. Alberta Society of Petroleum Geologists, Calgary.
- Stone, S.M., and J.M. Berdan. 1984. Some Late Silurian (Pridolian) ostracodes from the Roberts Mountains, central Nevada. *Journal of Paleontology* 58:977–1009.
- Thorsteinsson R., and D.K. Elliott. 2022. Silurian and Devonian Heterostraci (Vertebrata) of the Canadian Arctic Archipelago. *Palaeontographica Canadiana* 40:1–348.
- Traquair, R.H. 1895. The extinct vertebrate animals of the Moray Perth area. Pp. 235–285 in J.A. Harvie Brown and T.E. Buckley (eds.). A Fauna of the Moray Basin, Vol. II. David Douglas, Edinburgh.
- Traquair, R.H. 1898. [Report on fossil fishes]. Summary of Progress, Geological Survey of Great Britain, 1897, p. 72–76.
- Turner, S. 1976. Thelodonti (Agnatha). *Fossilium Catalogus* pars 122. W. Junk, 's-Gravenshage, 35 pp.
- Turner, S. 1984. Studies of Palaeozoic Thelodonti (Craniata : Agnatha). Unpublished PhD thesis, University of Newcastle upon Tyne, England, 2 vols.
- Turner, S. 1991. Monophyly and interrelationships of the Thelodonti. Pp. 87–119 in Chang, M.-M., Y-H. Liu, and G-R. Zhang (eds.). Early vertebrates and related studies of evolution. Science Press, Beijing.
- Turner, S. 1999. Early Silurian to Early Devonian thelodont assemblages and their possible ecological significance. Pp. 42–78 in Boucot, A. J., and J. Lawson (eds.). Palaeocommunities: a case study from the Silurian and Lower Devonian. IGCP 53, Project Ecostratigraphy, Final Report. Cambridge University Press, Cambridge.
- Turner, S., and C.J. Burrow. 1997. Lower to Middle Devonian microvertebrate assemblages from Arctic Canada. Pp. 43–44 in A. Ivanov, M.V.H. Wilson, and A. Zhuravlev (eds.). Circum-Arctic Palaeozoic Vertebrates Symposium. *Ichthyolith Issues* Special Publication 4, St Petersburg, 23–26 September 1997.
- Turner, S., and C.J. Burrow. 2018. Microvertebrates from the Silurian–Devonian boundary beds of the Eastport Formation, Maine, eastern USA. *Atlantic Geology* 54:171–187. doi:10.4138/atlgol.2018.006
- Turner, S., and M.A. Murphy. 1988. Early Devonian vertebrate microfossils from the Simpson Park Range, Eureka County, Nevada. *Journal of Paleontology* 62:959–964.
- Turner, S., C.J. Burrow, R.B. Williams, and P. Tarrant. 2017. Welsh Borderland bouillabaisse: Lower Old Red Sandstone fish microfossils and their significance. *Proceedings of the Geologists' Association* 128(3):460–479. doi:10.1016/j.pgeola.2017.04.006
- Valiukevičius, J.J. 1992. First articulated *Poracanthodes* from the Lower Devonian of Severnaya Zemlya. Pp. 193–214 in E. Mark-Kurik (ed.). Fossil Fishes as Living Animals. Academia 1, Academy of Sciences of Estonia, Tallinn.
- Valiukevičius, J.J. 1994. Acanthodians and their stratigraphic significance. Pp. 131–197, 236–243 in S. Cherkasova, V. Karatajūtė-Talimaa and R. Matukhin (eds.), Stratigraphy and Fauna of the Lower Devonian of the Tareya Key Section (Taimyr). Nedra, Leningrad. (in Russian).
- Valiukevičius, J.J. 1998. Acanthodians and zonal stratigraphy of Lower and Middle Devonian in East Baltic and Byelorussia. *Palaeontographica* Abt. A 248:1–53.
- Valiukevičius, J.J. 2000. Acanthodian biostratigraphy and interregional correlations of the Devonian of the Baltic States, Belarus, Ukraine and Russia. *Courier Forschungsinstitut Senckenberg* 223:271–289.
- Valiukevičius, J.J. 2003a. New late Silurian to Middle Devonian acanthodians of the Timan-Pechora region. *Acta Geologica Polonica* 53:209–245.
- Valiukevičius, J.J. 2003b. Devonian acanthodians from Severnaya Zemlya Archipelago (Russia). *Geodiversitas* 25:131–204.
- Valiukevičius, J. 2004a. New Wenlock–Pridoli (Silurian) acanthodian fishes from Lithuania. *Acta Palaeontologica Polonica* 49(1):147–160.
- Valiukevičius, J. 2004b. Silurian succession of the Luzni-4 borehole (Latvia). *Acta Universitatis Latviensis* 679:120–147.
- Valiukevičius, J. 2005. Silurian acanthodian biostratigraphy of Lithuania. *Geodiversitas* 27(3):349–380.
- Valiukevičius, J., and C.J. Burrow. 2005. Diversity of tissues in acanthodians with "*Nostolepis*"-type histological structure. *Acta Palaeontologica Polonica* 50:635–649.

- Vergoossen, J.M.J. 1995. Remarks on microremains of acanthodians (Gnathostomata) from the late Pridoli of Manbrook (upper Silurian, Great Britain). *Geobios Mémoire Spécial* 19:399–401.
- Vergoossen, J.M.J. 1997. Revision of poracanthodid acanthodians. In A. Ivanov, M.V.H. Wilson, and A. Zhuravlev (eds.). *Circum-Arctic Palaeozoic Vertebrates: Biological and Geological Significance*. St Petersburg, 23–26 September 1997. *Ichthyolith Issues Special Publication* 4:44–46.
- Vergoossen, J.M.J. 1999a. Late Silurian fish microfossils from an East Baltic-derived erratic from Oosterhaule, with a description of new acanthodian taxa. *Geologie en Mijnbouw* 78:231–251.
- Vergoossen, J.M.J. 1999b. Late Silurian fish microfossils from Helvetsgraven, Skåne, Sweden. *Geologie and Mijnbouw* 78:267–280.
- Vergoossen, J.M.J. 1999c. Siluro–Devonian microfossils of Acanthodii and Chondrichthyes (Pisces) from the Welsh Borderland/South Wales. *Modern Geology* 24:23–90.
- Vergoossen, J.M.J. 2000. Acanthodian and chondrichthyan microremains in the Siluro–Devonian of the Welsh Borderland, Great Britain, and their biostratigraphical potential. *Courier Forschungsinstitut Senckenberg* 223:175–199.
- Vergoossen, J.M.J. 2002a. Late Silurian fish microfossils from Ramsåsa, Locality H, Scania, south Sweden, with some remarks on the body zonation scheme used in thelodont studies. *Scripta Geologica* 123:41–69.
- Vergoossen, J.M.J. 2002b. Late Silurian fish microfossils from Ramsåsa (sites D and ‘south of church’), Skåne, south Sweden. *Scripta Geologica* 123:93–158.
- Vieth, J. 1980. Thelodontier-, Acanthodier- und Elasmobranchier-Schuppen aus dem Unter-Devon der Kanadischen Arktis (Agnatha, Pisces). *Göttinger Arbeiten Geologie und Paläontologie* 23:1–69.
- Walliser, O.H. 1964. Conodonten des silurs. *Abhandlungen des Hessisches Landesamt für Bodenforschung zu Wiesbaden* 41:1–106.
- Wang, N.-Z. 1992. Microremains of agnathans and fishes from Lower Devonian of Central Guangxi with correlation of Lower Devonian between Central Guangxi and Eastern Yunnan, South China. *Acta Palaeontologica Sinica* 31(3):298–307.
- Wang, N.Z., J.Q. Wang, G.R. Zhang, and S.T. Wang. 1998. The first discovery of Silurian and Early Devonian acanthodians from Zoige and Tewo counties, West Qinling Mountains. *Vertebrata Palasiatica* 36:268–281.
- Wilson, M.V.H., and Caldwell, M.W. 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(1):10–29.
- Winterer, E.L., and M.A. Murphy. 1960. Silurian reef complex and associated facies, central Nevada. *Journal of Geology* 68(2):117–139.
- Woodward, A.S. 1891. Catalogue of the fossil fishes in the British Museum (Natural History). Part II. British Museum (Natural History), London, 567 pp.
- Zhu, M., and Janvier, P. 1994. Un Onychodontide (Vertebrata, Sarcopterygii) du Dévonien Inférieur de Chine. *Comptes Rendues de l’Academie des Sciences Paris* 319:951–956.
- Ziegler, W. 1960. Conodonten aus dem Rheinischen Unterdevon (Gedinnium) des Remscheider Sattels (Rheinisches Schiefergebirge). *Paläontologische Zeitschrift* 34:169–201.