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Middle Devonian acanthodians from Belarus – new data and interregional biostratigraphy

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ABSTRACT:

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The Lower Devonian (Emsian) and Middle Devonian of Belarus contain assemblages of biostratigraphically useful faunal and floral microremains. Surface deposits are few, with most material being derived from borehole cores. Acanthodian scales are particularly numerous and comparison with scales from other regions of the Old Red Sandstone continent (Laurussia), specifically the Orcadian Basin of Scotland, the Baltic Region, Spitsbergen, and Severnaya Zemlya have demonstrated a lot of synonymy of acanthodian species between these areas. This is especially the case between Belarus, the Orcadian Basin and the Baltic Region, which has allowed us to produce an interregional biostratigraphic scheme, as well as to postulate marine connection routes between these areas. The acanthodian biostratigraphy of Belarus is particularly important as it is associated with spores and marine invertebrates, so giving the potential of more detailed correlations across not only the Old Red Sandstone continent, but elsewhere in the Devonian world. We also demonstrate that differences in preservation (e.g., wear and how articulated a specimen is) is one of the main reasons for synonymy.

Key words: Acanthodian; Belarus; Baltic; Scotland; Stratigraphy; Scales.

INTRODUCTION

A number of authors in the middle of the last century (e.g., Westoll 1951) started to comment on the similarity of the Middle Devonian vertebrate genera across the Old Red Sandstone continent (Laurussia). However, it was Mark-Kurik (1991, 2000) who first identified conspecific fish in different regions (the Baltic Region and the Orcadian Basin of Scotland). Specifically, she noted that certain placoderm species from the Baltic Region had been erected based on disarticulated, often three-dimensional bones, which were the same species as flattened, articulated specimens from the Orcadian Basin. Hence, differences in preservation caused synonymy in placoderm species. Into the 21st century, more detailed work based on acanthodians had identified conspecific forms not only in the Baltic Region and the Orcadian Basin, but also Belarus, Spitsbergen, and Severnaya Zemlya (Burrow *et al*. 2016, 2020, 2021; den Blaauwen *et al*. 2019; Newman *et al*. 2019, 2021b). The reason for acanthodian synonymy is discussed later in this article. In this work we bring together the published information on the Belarus Middle Devonian biostratigraphy, which up until now has often been published in obscure and difficult to find publications. Also, presented here is new information not published before. This is important as the Belarus acanthodians are associated with spore and marine invertebrate species, so giving the potential of more detailed cor-

Text-fig. 1. Borehole location map in Belarus. Boreholes: 1 – Pinsk 26; 2 – Pinsk 10; 3 – Korma 1; 4 – Lepel 1; 5 – Chashniki 53; 6 – Rudnya 14; 7 – North-Polotsk 1.

relations across not only Laurussia, but elsewhere in the Devonian world.

Belarusian Middle Devonian material is mostly derived from borehole cores. These boreholes are located in the Pripyat Trough, the North Pripyat Shoulder, the Gomel Structural Dam, the Bragin-Loev, Zhlobin and Latvian Saddles, on the northern, eastern and south-eastern slopes of the Belarusian Anteclise, in the Orsha Depression, and the north-western slope of the Voronezh Anteclise (Text-fig. 1). The geological structure of these areas was discussed by Kruchek *et al.* (2001) and Obukhovskaya T.G. *et al.* (2010).

The Eifelian deposits of Belarus consist mostly of terrigenous and carbonate-terrigenous rocks. There are no surface outcrops of this age, with all the material being derived from borehole cores. The strata vary in thickness from around 10 m on the slopes of the Belarusian Anteclise, to around 100 m in the Orsha Depression and the Pripyat Trough. Three sedimentological units that were deposited during three phases of marine transgression can be distinguished (Obukhovskaya T.G. *et al.* 2010, 2013). The depositional environment was a shallow marine basin that in the middle of the Eifelian became highly saline and lagoonal in nature. Towards the end of the Eifelian the salinity decreased and reached more normal marine levels (Plax 2013a). The geology and stratigraphy of these deposits is discussed in more detail below.

The Givetian of Belarus consists of terrigenous deposits, but there are few fossiliferous surface outcrops. Therefore, most of the material has been derived from borehole cores (Text-fig. 1). The Givetian strata ranges in thickness from around 185 m in north-eastern Belarus decreasing from east to west. In the northern part of the Pripyat Trough, the succession is up to 230 m thick, but diminishes to 120 to 154 m in the central regions and is less than 100 m in the marginal areas (Obukhovskaya T.G. *et al*. 2010). The Givetian can be subdivided into three substages (lower, middle and upper Givetian) on the basis of palaeontological and sedimentological data (Obukhovskaya T.G. *et al*. 2010, 2014). The depositional environment is referred to a low salinity, shallow marine basin, either deltaic or lagoonal in nature, with a high fluvial input (Kruchek *et al*. 2001; Plax 2013a). The geology and stratigraphy of these deposits is discussed in more detail below.

In this article we discuss and figure material (much of it new or reinterpreted) from the upper Eifelian (Kostyukovichi Regional Stage) through to the lower and middle Givetian (Polotsk Regional Stage) of Belarus. This includes new acanthodian material recently collected by one of the authors (DPP) from the Polotsk Regional Stage. To provide geological context we also summarise the complete succession of the Eifelian and Givetian in Belarus and briefly discuss the Emsian deposits as this is the horizon where some of the acanthodians discussed in this article first appear.

MATERIAL AND METHODS

Individual acanthodian scales were collected from several cores retrieved from boreholes that penetrated Middle Devonian strata in Belarus (Text-fig. 1). Upper Eifelian (Kostyukovichi Regional Stage) scales were retrieved from the Chashniki 53, Korma 1, Lepel 1 and Rudnya 14 boreholes. Givetian scales were retrieved from the Pinsk 10, Pinsk 26 and North-Polotsk 1 boreholes. The scales were separated from the rock matrix using the standard rock dissolution technique with formic 5% and acetic 9% acids. The resulting sediment was then washed and dried, with the scales retrieved manually using an MBS-1 binocular microscope. Electron microphotographs of the scales were made with a JSM-5610 LV (JEOL, Japan) scanning electron microscope housed at the Centre for Physical and Chemical Investigations at the Belarusian State Technological University, Minsk, Belarus. The photographs were processed with Adobe Photoshop CC 2019, the figures were created with CorelDRAW Graphics Suite 2019. All specimens are housed in the palaeontological collection at the Department of Mining, Belarusian National Technical University (BNTU).

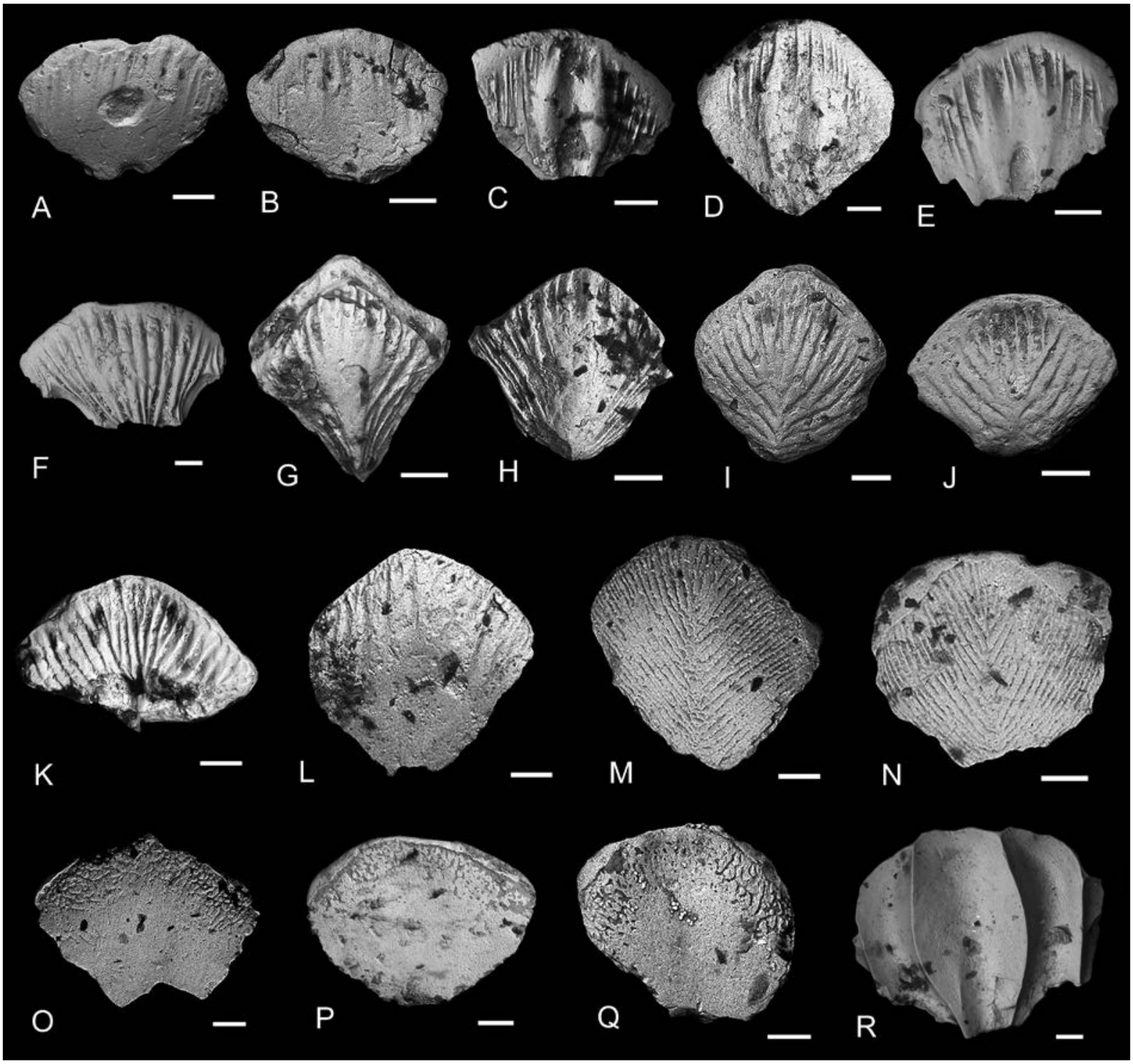
NEW AND REVISED RECORDS OF MIDDLE DEVONIAN ACANTHODIANS IN BELARUS

Kostyukovichi Regional Stage

This stage (upper Eifelian) yields the following acanthodian scales: *Cheiracanthus brevicostatus* Gross, 1973 (Text-fig. 2A, B), *Cheiracanthus latus* Egerton, 1861 (Text-fig. 2C–E), *Markacanthus costulatus* Valiukevičius, 1985 (Text-fig. 2F), *Ginkgolepis talimae* (Valiukevičius, 1985) (Text-fig. 2G, H), *Diplacanthus tenuistriatus* Traquair, 1894 (Text-fig. 2I–K), *Rhadinacanthus longispinus* (Agassiz, 1844) (Text-fig. 2L), *Ptychodictyon sulcatum* Gross, 1973 (Text-fig. 2M, N), *Ptychodictyon rimosum* Gross, 1973 (Text-fig. 2O–Q), and *Nostolepis kernavensis* Valiukevičius, 1985 (Text-fig. 2R).

Valiukevičius (1981) was the first author to list *Cheiracanthus brevicostatus* in the Kostyukovichi Regional Stage and later figured one specimen (as a line drawing; Valiukevičius 1985, pl. 11, fig. 1). This article is the first to figure photographs of specimens (Text-fig. 2A, B) from this stage. The crown morphology of the scales of *C. brevicostatus* is very similar to *Cheiracanthus murchisoni* Agassiz, 1835, but as pointed out by Gross (1973), the crown ridges are of unequal width in the former, being more uniform in the latter. Both BNTU 47/19-50p (Text-fig. 2A) and BNTU 47/19-34g (Text-fig. 2B) show this *C. brevicostatus* character and fall into the morphological range of scale crown ornamentation described by Burrow *et al*. (2021) based on articulated specimens from Scotland.

Cheiracanthus latus has not been previously been listed as occurring in Belarus. This is because Burrow *et al*. (2020) recognised that *Cheiracanthus longicostatus* Gross, 1973 was a subjective junior synonym of *C. latus*. Specimens of *C. latus* were first figured from the Kostyukovichi Regional Stage by Plax (2016a, pl. 6, figs 4–9, 11). However, it seems prudent to figure some well-preserved examples,



Text-fig. 2. Eifelian (Kostyukovichi Regional Stage) acanthodian scales from Belarus, crown views. The anterior edge of the scales faces the top of the page. **A**, **B** – *Cheiracanthus brevicostatus* Gross, 1973; A – BNTU 47/19-50p, B – BNTU 47/19-34g. **C**–**E** – *Cheiracanthus latus* Egerton. 1861; C – BNTU 47/19-50d, D – BNTU 47/19-39d, E – BNTU 43/5-2b. **F** – *Markacanthus costulatus* Valiukevičius, 1985; BNTU 121/2-1. **G**, **H** – *Ginkgolepis talimae* (Valiukevičius, 1985); G – BNTU 47/19-7b, H – BNTU 47/19-39e. **I**–**K** – *Diplacanthus tenuistriatus* Traquair, 1894; I – BNTU 47/19-39b, J – BNTU 47/19-50g, K – BNTU 47/19-39h. **L** – *Rhadinacanthus longispinus* (Agassiz, 1844); BNTU 47/19-39a. **M**, **N** – *Ptychodictyon sulcatum* Gross, 1973; M – BNTU 47/19-7a, N – BNTU 47/19-7g. **O**–**Q** – *Ptychodictyon rimosum* Gross, 1973; O – BNTU 47/19-39r, P – BNTU 47/20-3a, Q – BNTU 102/6-5. **R** – *Nostolepis kernavensis* Valiukevičius, 1985; BNTU 47/10-18. A-D, G-P are from the Lepel 1 borehole; E is from the Chashniki 53 borehole, F is from the Korma 1 borehole, Q is from the Rudnya 14 borehole. Scale bars equal to 100 µm.

with the correct species name to avoid future confusion. BNTU 47/19-50d (Text-fig. 2C), BNTU 47/19-39d (Text-fig. 2D) and BNTU 43/5-2b (Text-fig. 2E) have the two characteristic, broad, median ridges on the scale crown. BNTU 47/19-50d and BNTU 47/19-39d also have the characteristic median oval pit near the posterior edge of the scale crown. All three scales fall into the morphological range of scale crown ornamentation described by Burrow *et al*. (2020) based on articulated specimens from Scotland.

The holotype of *Markacanthus costulatus* is from the Kostyukovichi Regional Stage and was figured by Valiukevičius (1985, pl. 2, fig. 18). BNTU 121/2-1 is a better-preserved specimen of *M. costulatus* than the holotype and provides details at higher resolution (Text-fig. 2F) than the original description. BNTU 121/2-1 has a smooth anterior rim, with deep grooves and ridges on the scale crown typical for the species. The specimen falls into the morphological range of scale crown ornamentation described by Newman *et al*. (2021b) based on an articulated specimen from Scotland. In Belarus, *M. costulatus* is only known from the Kostyukovichi Regional Stage.

Ginkgolepis talimae was originally placed in the genus *Cheiracanthus* Agassiz, 1835 when the species was erected by Valiukevičius (1985) for scales from the Eifelian Narva Regional Stage of the Baltic Region. The species was later placed in the newly erected genus *Gingkolepis* by Pinakhina and Märss (2018). Whilst *G. talimae* has been listed as present in the Kostyukovichi Regional Stage (e.g., Valiukevičius and Kruchek 2000), this article is the first in which specimens from this stage have been figured. BNTU 47/19-7b (Text-fig. 2G) is a relatively well-preserved scale showing a thick, wide median ridge with well-defined smaller ridges. BNTU 47/19-39e (Text-fig. 2H) is a more worn scale, but still falls into the morphological range of scale crown ornamentation described by Valiukevičius (1985). In Belarus, *G. talimae* is only known from the Kostyukovichi Regional Stage.

Diplacanthus tenuistriatus scale crown morphology was first figured by Burrow *et al*. (2016), although Gross (1973) and Valiukevičius (1985) did figure scale crowns under the synonym (in part) *Diplacanthus carinatus* Gross, 1973 (Burrow *et al*. 2016). However, these specimens were from the Baltic Region. Here we show the species presence in Belarus deposits for the first time, first appearing in the Kostyukovichi Regional Stage. BNTU 47/19-39b (Text-fig. 2I) is well preserved and has the typical fanning out ridges from the posteromedian ridge. BNTU 47/19-50g (Text-fig. 2J) and BNTU 47/19-39h (Text-fig. 2K) are less well preserved but still fall into the morphological range of scale crown ornamentation described by Burrow *et al*. (2016) based on articulated specimens from Scotland. The differences in preservation of scale crowns of this species is discussed below.

Gross (1947) was the first author to publish anatomically accurate figures of the scale crown ornamentation of *Rhadinacanthus longispinus*. More recently, Burrow *et al*. (2016) published a detailed account of the species including the scale crown ornamentation. Plax (2016a) was the first author to list *R. longispinus* in the Kostyukovichi Regional Stage, but this article figures a specimen from this stage for the first time. BNTU 47/19-39a (Text-fig. 2L), whilst not particularly well-preserved, has the typical sharp, parallel ridges extending back from the anterior crown. These ridges bifurcate at the anterior rim, typically for the species. The scale falls into the morphological range of scale crown ornamentation described by Burrow *et al*. (2016) based on articulated specimens from Scotland.

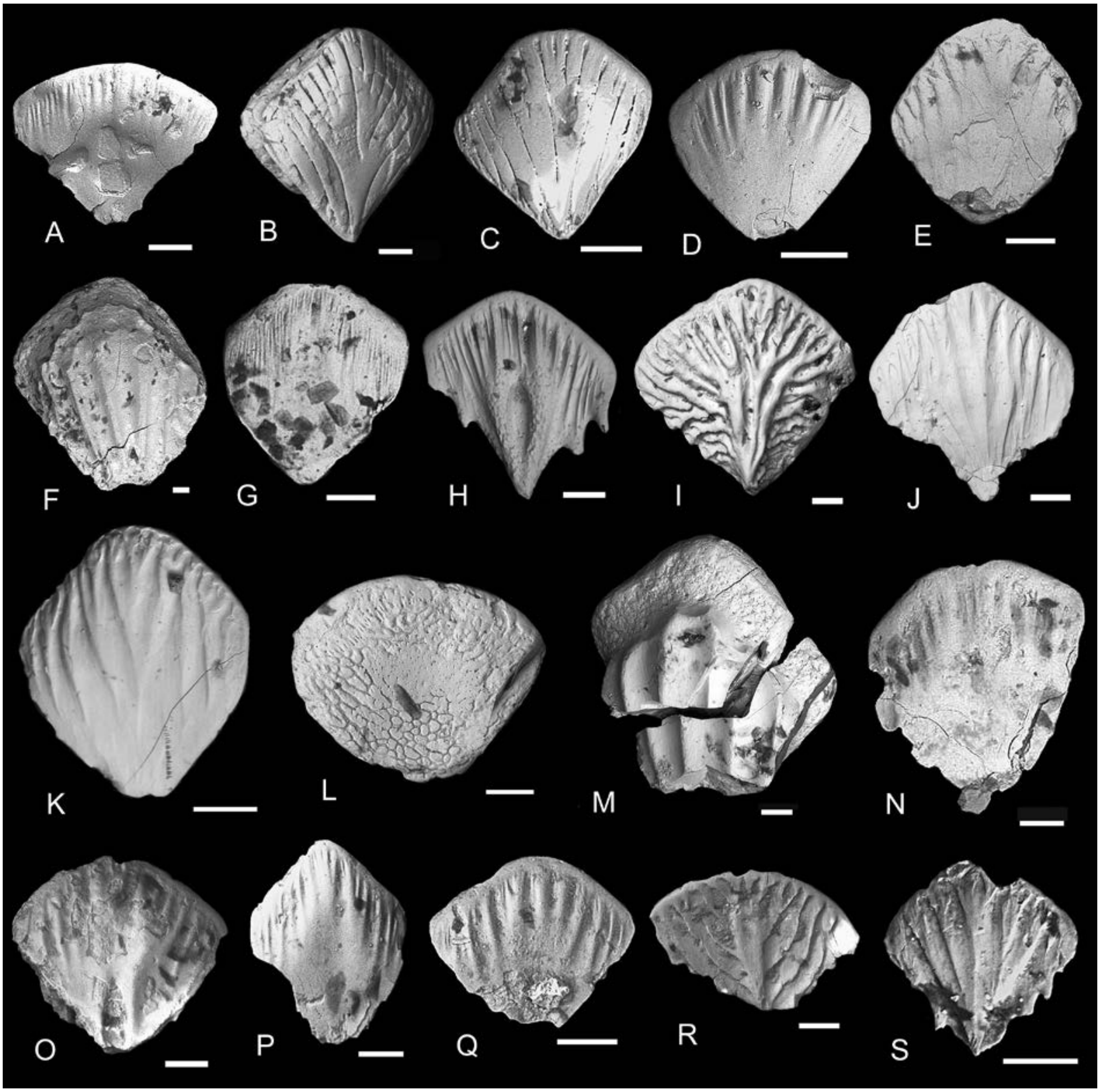
Ptychodictyon sulcatum was first listed as present in the Kostyukovichi Regional Stage by Valiukevičius and Kruchek (2000). However, it was Plax (2016a, pl. 5, figs 11–13) who first figured specimens of *P. sulcatum* from this stage. In this article we figure two of the specimens from Plax (2016a), BNTU 47/19-7a (Text-fig. 2M) and BNTU 47/19-7g (Text-fig. 2N), but as larger images and in higher resolution. Both scales have a crown ornamentation of narrow, fanning out grooves typical for the species and compare well with the original description by Gross (1973).

Ptychodictyon rimosum was first listed as present in the Kostyukovichi Regional Stage by Valiukevičius and Kruchek (2000). However, it was Plax (2016a, pl. 5, figs 3–7, 10) who first figured specimens from this stage. In this article we figure three of the specimens from Plax (2016a), BNTU 47/19-39r (Text-fig. 2O), BNTU 47/20-3a (Text-fig. 2P) and BNTU 102/6-5 (Text-fig. 2Q), but as larger images and in higher resolution. All three scales have a crown ornamentation of cell-like structures typical of the species and compare well with the original description by Gross (1973).

Nostolepis kernavensis was first listed as present in the Kostyukovichi Regional Stage by Valiukevičius and Kruchek (2000). However, it was Plax (2015, pl. 4, figs 7, 8) who first figured specimens from this stage. In this article we figure one of the specimens from Plax (2015), BNTU 47/10-18 (Text-fig. 2R), but as a larger image and in higher resolution. BNTU 47/10-18 is a well-preserved scale showing the sharp parallel ridges separated by a shallow, wide trough characteristic for the species and compares well to the original description by Valiukevičius (1985). *Nostolepis kernavensis* is only known from the Kostyukovichi Regional Stage in Belarus.

Polotsk Regional Stage

In the Polotsk Regional Stage we confirm the presence of *Cheiracanthus brevicostatus* (Text-fig. 3A), *Cheiracanthus peachi* den Blaauwen, Newman and Burrow, 2019 (Text-fig. 3B, C), *Cheira-*



Text-fig. 3. Givetian acanthodian scales, crown views, from the Goryn (A-F), Stolin (G-M) and Moroch beds (N-S) in Belarus. The anterior edge of the scales faces the top of the page. **A**, **G**, **N** – *Cheiracanthus brevicostatus* Gross, 1973; A – BNTU 41/6a-1a; G – BNTU 85/16-10k; N – BNTU 85/21-2c. **B**, **C** – *Cheiracanthus peachi* den Blaauwen, Newman and Burrow, 2019; B – BNTU 41/76-2; C – BNTU 41/6a-2b. **D**, **P**, **Q** – *Cheiracanthus intricatus* Valiukevičius, 1985; D – BNTU 41/6a-2g; P – BNTU 85/21-1a; Q – BNTU 85/21-1n. **E**, **J**, **K, S** – *Rhadinacanthus longispinus* (Agassiz, 1844); E – BNTU 41/6a-2e; J – BNTU 126/1-42; K – BNTU 126/1-47; S – BNTU 85/21-2n. **F**, **M** – *Nostolepis gaujensis* Valiukevičius, 1998; F – BNTU 41/6a-2a; M – BNTU 126/1-15. **H**, **O** – *Cheiracanthus latus* Egerton, 1861; H – BNTU 126/1-51; O – BNTU 85/21-1p. **I**, **R** – *Diplacanthus tenuistriatus* Traquair, 1894; I – BNTU 126/1-17; R – BNTU 85/23-5e. **L** – *Ptychodictyon rimosum* Gross, 1973; BNTU 126/1-79. A-F are from the Pinsk 26 borehole; G and N-S are from the Pinsk 10 borehole; H-M are from the North-Polotsk 1 borehole. Scale bars equal to 100 μm.

canthus intricatus Valiukevičius, 1985 (Text-fig. 3D), *Rhadinacanthus longispinus* (Text-fig. 3E) and *Nostolepis gaujensis* Valiukevičius, 1998 (Text-fig. 3F) from the Goryn Beds; *C. brevicostatus* (Text-fig. 3G), *Cheiracanthus latus* (Text-fig. 3H), *Diplacanthus tenuistriatus* (Text-fig. 3I), *R. longispinus* (Text-fig. 3J, K), *Ptychodictyon rimosum* (Text-fig. 3L) and *N. gaujensis* (Text-fig. 3M) from the Stolin Beds; *C. brevicostatus* (Text-fig. 3N), *C. latus* (Text-fig. 3O), *C. intricatus* (Text-fig. 3P, Q), *D. te-*

nuistriatus (Text-fig. 3R) and *R. longispinus* (Text-fig. 3S) from the Moroch Beds.

Whilst Valiukevičius and Kruchek (2000) listed *C. brevicostatus* as present throughout the Polotsk Regional Stage, this article is the first to figure and correctly identify specimens from this stage. Plax and Kruchek (2014, pl. 4, fig. 4) figured BNTU 85/16-10k, a scale from the Stolin Beds, as *Cheiracanthus longicostatus* which we identify here as *C. brevicostatus*. Higher resolution images of BNTU 85/16-10k (Text-fig. 3G) show that it falls into the morphological range of scale crown ornamentation of *C. brevicostatus* described by Burrow *et al*. (2021). We have also identified BNTU 41/6a-1a (Text-fig. 3A), a scale from the Goryn Beds, and BNTU 85/21-2c (Text-fig. 3N), a scale from the Moroch Beds, as belonging to this species. Therefore, this article provides proof that *C. brevicostatus* is present throughout the Polotsk Regional Stage.

Valiukevičius and Kruchek (2000) listed *C. latus* (under its synonym *C. longicostatus*) as present throughout the Polotsk Regional Stage. Poorly preserved scale BNTU 85/15-10a from the Stolin Beds, identified by Plax and Kruchek (2014, pl. 4, fig. 6) as *Diplacanthus gravis* Valiukevičius, 1988, is hereby assigned to *C. latus*. BNTU 126/1-51 (Text-fig. 3H) is a better-preserved scale of *C. latus* from the Stolin Beds. From the stratigraphically younger Moroch Beds, Plax and Kruchek (2014, pl. 4, fig. 3) figured scale BNTU 85/21-2d of *C. latus* (as *C. longicostatus*). Another scale BNTU 85/21-1p from the Moroch Beds (Plax and Kruchek 2014, pl. 4, fig. 7, as "*D. gravis*") we also identify as a scale of *C. latus* (Text-fig. 3O). All the scales above fall into the morphological range of scale ornamentation described by Burrow *et al*. (2020). Whilst *C. latus* (as *C. longicostatus*) is listed from the Goryn Beds in various articles (e.g., Valiukevičius 1988; Valiukevičius *et al*. 1995; Valiukevičius and Kruchek 2000), no author has figured any specimen from this horizon and we have not identified any such specimens. However, as the species is present in strata both above and below the Goryn Beds, its absence is most likely a result of collecting bias. Below we discuss variation in scale preservation causing the misidentification of the species *C. latus*.

Cheiracanthus peachi was only recently recognised as a new species based on articulated specimens from the Givetian of the Orcadian Basin of Scotland (den Blaauwen *et al*. 2019). In that same article it was noted that a scale figured by Valiukevičius (1985, pl. 13, fig. 8) identified as possibly *Diplacanthus carinatus* was in fact a scale of *C. peachi*. This specimen was noted by Valiukevičius (1985) as being in the upper Narva Regional Substage, now known as the Kostyukovichi Regional Stage (Obukhovskaya T.G. *et al*. 2010). Similarly, den Blaauwen *et al*. (2019) also noted that a scale figured by Plax and Kruchek (2014, pl. 3, fig. 16), identified as *D. carinatus* from the Goryn Beds, belonged in *C. peachi*. This scale, BNTU 41/76-2, is refigured here in a larger format and at higher resolution (Text-fig. 3B). We have also identified another scale of this species, BNTU 41/6a-2b (Text-fig. 3C), also from the Goryn Beds. Both scales show the characteristic narrow grooves fanning out towards the anterior and fall into the morphological range of scale crown ornamentation described by den Blaauwen *et al*. (2019) based on articulated specimens.

Valiukevičius (1985) erected the species *Cheiracanthus intricatus* based on isolated scales from the Eifelian of the Baltic Region. It was quite a surprise when Newman *et al*. (2019) discovered articulated specimens of this species in the upper Givetian of Spitsbergen (Svalbard). This clarified the morphological range of scale crown ornamentation for the species. Valiukevičius and Kruchek (2000) listed *C. intricatus* as present in just the Kostyukovichi Regional Stage, although no specimens have been figured from any regional stage of Belarus. Plax and Kruchek (2014, pl. 4, fig. 2) figured a scale, BNTU 85/21-1a, from the Moroch Beds as *Cheiracanthus* sp. In this article we identify BNTU 85/21-1a as *C. intricatus* (Text-fig. 3P). Another two scales, BNTU 85/21-1n (Text-fig. 3Q) from the Moroch Beds and BNTU 41/6a-2g (Text-fig. 3D) from the Goryn Beds are identified here as *C. intricatus*. All the above scales show the characteristic grooves and ridges fanning out to the anterior, with short grooves and ridges between these longer ridges at the anterior edge. All the scales fall into the morphological range of scale crown ornamentation described by Newman *et al*. (2019). The lack of identifiable specimens in the Stolin Beds is probably due to collecting bias, as the species is present in strata above and below.

As mentioned above, the scale crown ornamentation of *Diplacanthus tenuistriatus* has only been described recently by Burrow *et al*. (2016). Plax and Kruchek (2014, pl. 3, fig. 15) figured a scale, BNTU 41/6a-1c, from the Goryn Beds as *Diplacanthus carinatus*. Burrow *et al*. (2016) identified BNTU 41/6a-1c as *Diplacanthus crassisimus* (Duff, 1842), but for reasons discussed below regarding scale preservation we determine the specimen as *D. tenuistriatus*. We have also identified BNTU 126/1-17 (Text-fig. 3I) from the Stolin Beds as an excellent example of a scale of the species. Only a very worn scale, BNTU 85/23-5e (Text-fig. 3R) of the species has been identified by us from the Moroch Beds. All these scales fall in the morphological range of scale crown ornamentation described by Burrow *et al*. (2016). From the above it is clear that *D. tenuistriatus* is present throughout the Polotsk Regional Stage.

Rhadinacanthus multisulcatus Valiukevičius, 1988 was considered by Burrow *et al*. (2016) to be a subjective junior synonym of *Rhadinacanthus longispinus* and all articles on Belarus prior to this work use this subjective junior synonym. Valiukevičius and Kruchek (2000) listed *R. longispinus* as present throughout the Polotsk Regional Stage but did not provide any figures. Plax and Kruchek (2014, pl. 3, fig. 17) figured a scale BNTU 41/6a-2e from the Goryn Beds here reproduced in a larger format and in higher resolution. We have also identified two scales of the species from the Stolin Beds, BNTU 126/1-42 (Text-fig. 3J) and BNTU 126/1-47 (Text-fig. 3K). Finally, we have identified a scale from the Moroch Beds, BNTU 85/21-2n (Text-fig. 3S). All four scales fall into the morphological range of scale crown ornamentation described by Burrow *et al*. (2016). The above proves *R. longispinus* is present throughout the Polotsk Regional Stage.

Valiukevičius and Kruchek (2000) listed *Ptychodictyon rimosum* as present throughout the Polotsk Regional Stage but provided no figures. However, we have only identified one scale, BNTU 126/1-79 (Text-fig. 3L) from the Stolin Beds. BNTU 126/1-79 is well preserved and compares well with the original description by Gross (1973). It seems likely the species is also present in the Goryn Beds due to its presence in overlying and underlying strata. The species' absence in the Goryn Beds is probably due to collecting bias. We have no evidence for the species' presence in the Moroch Beds.

Nostolepis gaujensis has not been recorded in Belarus deposits before this article. We have identified one scale, BNTU 41/6a-2a (Text-fig. 3F) from the Goryn Beds and another scale, BNTU 126/1-15 (Text-fig. 3M) from the Stolin Beds. The species is morphologically similar to *Nostolepis kernavensis* with *N. gaujensis* having slightly lower and blunter ridges, and wider and shallower troughs between the ridges (Pinakhina and Märss 2018). In the original description by Valiukevičius (1998) the figures are small and indistinct. In turn, Pinakhina and Märss (2018) provided clearer figures and both BNTU41/6a-2a and BNTU 126/1-15 compare well to their figures. We have no evidence for the species' presence in the Moroch Beds.

SEDIMENTOLOGY, DEPOSITIONAL ENVIRONMENT AND INTER-REGIONAL BIOSTRATIGRAPHY, UPPER EMSIAN–GIVETIAN

Vitebsk Regional Stage: As some of the Middle Devonian acanthodians first appear in the late Emsian it seems prudent to list the acanthodian fauna from this horizon in Belarus. The upper Emsian in Belarus is subdivided into the Obol and Lepel Beds of the Vitebsk Regional Stage (Obukhovskaya T.G. *et al*. 2010). The acanthodians present in this stage mostly consist of isolated scales and include *Cheiracanthus brevicostatus*, *C. crassus* Valiukevičius, 1985, *C. gibbosus* Valiukevičius in Valiukevičius and Karatajūtė-Talimaa, 1986, *C. krucheki* Valiukevičius in Valiukevičius and Karatajūtė-Talimaa, 1986, *C. latus*, *Diplacanthus kleesmentae* Valiukevičius in Valiukevičius and Karatajūtė-Talimaa, 1986, *Ectopacanthus flabellatus* Valiukevičius in Valiukevičius and Karatajūtė-Talimaa, 1986, *Laliacanthus singularis* Karatajūtė-Talimaa in Valiukevičius and Karatajūtė-Talimaa, 1986, *Markacanthus parallelus* Valiukevičius in Valiukevičius and Karatajūtė-Talimaa, 1986, *Nostolepis gracilis* Gross, 1947, *Ptychodictyon ancestralis* Valiukevičius in Valiukevičius and Karatajūtė-Talimaa, 1986 and *Rhadinacanthus primaris* Valiukevičius in Valiukevičius and Karatajūtė-Talimaa, 1986. As well as the scale-based species listed above, undeterminable fin spines are also present. For a full faunal list see Valiukevičius and Karatajūtė-Talimaa (1986), Valiukevičius and Kruchek (2000), Plaksa (2007, 2008) and Plax (2008, 2015, 2016a, 2017a).

As with the later deposits discussed below, the deposits of the Vitebsk Regional Stage were laid down in a marine environment, consisting of a shallow coastal basin (Plax 2013a).

The Vitebsk Regional Stage has been correlated based on the palaeontology with the Rezēkne Regional Stage (Formation) of the Baltic States (Lyarskaya 1978; Sorokin *et al*. 1981; Valiukevičius and Kruchek 2000) and the lower part of the Ryazhsk Regional Stage (Novobasovo Beds) of the central part of the East European Platform (Rodionova *et al*. 1995).

Adrov and Osveya Regional Stages: The Eifelian deposits (Text-fig. 4) start with the Adrov and Osveya Regional Stages (lower Eifelian) which conformably overlie the upper Emsian Vitebsk Regional Stage. These two stages were deposited during an initial marine transgression phase. The Adrov Regional Stage consists of dolomites and sandstones with oolites

Eifelian					Givetian					
lower		middle		upper	lower	middle		upper		
Polygnathus c. partitus	*Polygnathus c. costatus*	*Tortodus k. australis*	*Tortodus k. kockelianus*	*Polygnathus x. ensensis*	*Polygnathus hemiansatus*	*Polygnathus varcus*		1.	2.	Conodont zone
Adrov	Osveya	Gorodok		Kostyukovichi	Polotsk			Ubort		Regional Stage
					Goryn	Stolin	Moroch			Beds
Periplecotriletes tortus		*Grandispora naumovae*		*Rhabdosporites langii - Chelinospora timanica*	*Geminospora vugata - Retispora archaeolepidophyta*		*Cristatisporites triangulatus - Corystisporites serratus*	*Ancyraspora incisa - Geminospora micromanifesta*		Miospore zone

Text-fig. 4. Stratigraphic scheme for the Middle Devonian of Belarus. 1 stands for the *Schmidtognathus hermanni–Polygnathus cristatus* Zone, 2 stands for the *Klapperina disparilis* Zone.

at the base. The lower part of the Osveya Regional Stage consists of predominantly sulphate mudstones with the upper part consisting of mudstones, marls and sandstones. The Adrov and Osveya Regional Stages correspond to the *Periplecotriletes tortus–Elenisporis biformis* miospore zone (Obukhovskaya T.G. *et al*. 2010; Obukhovskaya V.Y. 2011).

The Adrov Regional Stage is characterised by the presence of the psammosteid *Guerichosteus heterolepis* (Preobrazhensky, 1911) (Glinskiy and Pinakhina 2018). This species has already been used to characterise this zone under its synonym *Schizosteus heterolepis* (Preobrazhensky, 1911) (Plaksa 2007, 2008; Plax 2008). The Adrov Regional Stage is equivalent to the Pärnu Regional Stage in the Baltic region (Sorokin *et al*. 1981; Valiukevičius and Golubtsov 1986; Mark-Kurik 2000) and the upper part of the Ryazhsk Regional Stage (Osetrov Beds) of the Central Devonian Field in Russia (Rodionova *et al*. 1995).

The acanthodians present in the Adrov Regional Stage consist of individual scales of *Cheiracanthus brevicostatus*, *C. crassus*, *C. gibbosus*, *C. latus*, *Ectopacanthus flabellatus*, *Laliacanthus singularis*, *Markacanthus parallelus* and *Rhadinacanthus primaris*. Also present are acanthodian fin spines of *Archaeacanthus quadrisulcatus* Kade, 1858 and *Haplacanthus marginalis* Agassiz, 1844. For a full faunal list see Valiukevičius and Kruchek (2000), Plaksa (2007, 2008) and Plax (2008, 2012, 2015, 2016a, 2017a).

The Osveya Regional Stage is characterised by the presence of the acanthodian *Cheiracanthoides estonicus* Valiukevičius, 1998 (Valiukevičius *et al*. 1995; Plaksa 2007, 2008; Plax 2008). The Osveya Regional Stage is equivalent to the Vadja Regional Substage of the Narva Regional Stage in the Baltic region (Valiukevičius 1985, 1994; Mark-Kurik 2000). It is also equivalent to the Dorogobuzh Regional Stage of the central part of the East European Platform of Russia (Rodionova *et al.* 1995).

The acanthodians present in the Osveya Regional Stage consist of individual scales of *Cheiracanthoides estonicus*, *Cheiracanthus brevicostatus*, *C. crassus* and *C. latus*. Also present are *Haplacanthus marginalis* acanthodian fin spines. For a full faunal list see Valiukevičius and Kruchek (2000), Plaksa (2007, 2008) and Plax (2008, 2015, 2016a, b, 2017a).

Gorodok Regional Stage: The middle Eifelian Gorodok Regional Stage conformably overlies the Osveya Regional Stage and was deposited during a second marine transgression. This stage consists of mudstones, marls and sandstones at the base, predominant dolomites in the middle, and mudstones and marls at the top. The Gorodok Regional Stage corresponds to the *Grandispora naumovii* miospore zone (Obukhovskaya T.G. *et al*. 2010; Obukhovskaya V.Y. 2011). Regarding the ichthyofauna, the Gorodok Regional Stage is characterised by the presence of the acanthodian *Ptychodictyon rimosum* (Valiukevičius *et al*. 1995; Plaksa 2007, 2008; Plax 2008).

The Gorodok Regional Stage is equivalent to the Leivu Regional Substage of the Narva Regional Stage in the Baltic region and the Klintsov and Mosolovo regional stages of the central part of the East European Platform in Russia (Valiukevičius and Golubtsov 1986; Valiukevičius 1994; Valiukevičius *et al*. 1995; Mark-Kurik 2000).

The acanthodians present in the Gorodok Regional Stage consist of individual scales of *Cheiracanthus brevicostatus*, *C. crassus*, *C. latus*, *Ptychodictyon distinctum*, *P. rimosum*, *P. sulcatum*, and *Rhadinacanthus longispinus*. Also present are *Haplacanthus marginalis* fin spines. For a full faunal list see Valiukevičius and Kruchek (2000), Plaksa (2007, 2008) and Plax (2008, 2015, 2016a, 2017a, b).

Kostyukovichi Regional Stage: The upper Eifelian Kostyukovichi Regional Stage conformably overlies the Gorodok Regional Stage and was deposited during a third and most clearly expressed marine transgression. The base of this stage consists of silty mudstones with occasional sandier layers. Above these mudstones are dolomite limestones with interlayers of marls and mudstones. The upper part of this stage consists of thin-layered mudstones with occasional thin siltstone layers. This stage corresponds to the *Rhabdosporites langii–Chelinospora timanica* miospore zone (Obukhovskaya V.Y. 1998). Regarding the ichthyofauna, the stage is characterised by the presence of the psammosteid *Schizosteus striatus* (Gross, 1933) (Plaksa 2007, 2008; Plax 2008) and the acanthodian *Nostolepis kernavensis* (Valiukevičius *et al*. 1995; Valiukevičius and Kruchek 2000; Plaksa 2007, 2008; Plax 2008). Perhaps of more importance is the presence of the conodont *Polygnathus xylus ensensis* Ziegler, Klapper and Johnson, 1976 (Ziegler and Sandberg 1990; Narkiewicz and Kruchek 2008), an unequivocal marine datable fossil.

The Kostyukovichi Regional Stage correlates with the Kernavè Regional Substage of the Narva Regional Stage in the Baltic region (Sorokin *et al*. 1981; Valiukevičius and Golubtsov 1986; Valiukevičius 1994; Mark-Kurik 2000), the Chernyi Yar Stage of the Central Devonian Field of Russia (Rodionova *et al*. 1995; Valiukevičius and Kruchek 2000), the Kolva Regional Stage of the Timan-Pechora Region (Valiukevičius and Kruchek 2000; Valiukevičius 2003), and the Veliky Most Subformation of the lower part of the Lopushany Formation in the Volhynia-Podolia Region of Ukraine (Plax 2011). Based on the study of the conodonts and miospores, the Kostyukovichi Regional Stage corresponds to the global biotic Kačák Event (Marshall *et al*. 2007; Obukhovskaya T.G. *et al*. 2012; Narkiewicz *et al*. 2015).

Acanthodian scales figured in this article come from several boreholes (described below) that have penetrated the Kostyukovichi Regional Stage. From the Lepel 1 borehole located within the Vileyka Buried Ridge of the Belarusian Anteclise, several species were identified at depths levels 195.0 m, 194.0 m and 182.0 m. These include individual scales of the acanthodians *Cheiracanthus brevicostatus*, *C. latus*, *Ginkgolepis talimae*, *Nostolepis kernavensis*, *Ptychodictyon rimosum*, *P. sulcatum* and *Rhadinacanthus longispinus*. Also identified were acanthodian fin spines of *Haplacanthus marginalis* and *Archaeacanthus quadrisulcatus*. From other fish groups were found disarticulated remains of the psammosteids *Schizosteus striatus* and *Pycnolepis splendens* (Eichwald, 1844), the antiarch *Asterolepis estonica* Gross, 1940, teeth of the shark *Karksiodus mirus* Ivanov, Märss and Kleesement, 2011, scales of the shark *Karksilepis* cf. *parva* Märss in Märss *et al*., 2008, scales of the actinopterygians *Cheirolepis gaugeri* Gross, 1973 and *Orvikuina vardiaensis* Gross, 1953. For a full faunal list see Plax (2016a).

From the Chashniki 53 borehole located within the Orsha Depression, a few species have been identified at depth level of 214.0 m. These included individual scales of the acanthodians *Cheiracanthus brevicostatus* and *C. latus*, and fin spines of *Haplacanthus marginalis*. Also identified were shell fragments of inarticulate brachiopods and fragmentary indeterminable remains of other fish groups. For a full faunal list see Plax (2017a).

From the Korma 1 borehole located within the Zhlobin Saddle, individual scales of the acanthodians *Nostolepis kernavensis* and *Markacanthus costulatus* and undeterminable acanthodian fin spines have been identified at depth level 193.5 m. Also identified were undeterminable fragments of psammosteid heterostracans, tetrapodamorphs, sarcopterygians and actinopterygian scales. Rare ostracods have also been identified. For a full faunal list see Plax and Murashko (2021).

From the Rudnya 14 borehole located within the Vileyka Buried Ridge of the Belarusian Anteclise, individual scales of the acanthodian *Ptychodictyon rimosum* as well as undeterminable tetrapodamorph remains have been identified at depth level 208.6 m. For a full faunal list see Plax (2008, 2016a).

For a full list of all the fauna collected from the numerous boreholes that have penetrated the Kostyukovichi Regional Stage in Belarus see Valiukevičius and Kruchek (2000), Plaksa (2007, 2008) and Plax (2008, 2013b, 2015, 2016a, 2017a, b, 2019).

Polotsk Regional Stage: The Polotsk Regional Stage (lower to middle Givetian) usually unconformably overlies the Eifelian Kostyukovichi Regional Stage (Text-fig. 4). It is equivalent to the lower and middle Givetian and corresponds to the *Geminospora extensa* miospore zone (Obukhovskaya T.G. *et al*. 2010, 2014). This stage is subdivided into the Goryn, Stolin and Moroch beds.

The Goryn Beds and the lower part of the Stolin Beds are early Givetian in age and correspond to the *Geminospora vulgata–Retispora archaeolepidophyta* miospore zone (Obukhovskaya T.G. *et al*. 2010, 2014). The upper part of the Stolin Beds and the Moroch Beds are middle Givetian in age and correspond to the *Cristatisporites triangulatus–Corystisporites serratus* miospore zone (Obukhovskaya T.G. *et al.* 2002, 2010, 2014).

The lower Givetian Belarus strata are equivalent to the Aruküla Regional Stage of the Baltic region (Mark-Kurik 2000; Plax 2008), the lower part of the Givetian deposits of Poland (Turnau and Racki 1999; Turnau and Narkiewicz 2011), the Vorob'ev Regional Stage and the lower part of the Ardatov Regional Stage of the Central Regions of the Russian Plate (Rodionova *et al.* 1995; Obukhovskaya T.G. *et al.* 2010). In addition, according to Obukhovskaya T.G. *et al.* (2014), the base of the aforementioned *Geminospora vulgata–Retispora archaeolepidophyta* miospore zone, the morphon *Geminospora lemurata* (Balme) Playford, 1983 also allows its correlation with the *Geminospora lemurata* miospore zone of Western Europe (Streel and Loboziak 1996).

During the deposition of the upper part of the Stolin and Moroch Beds (middle Givetian), the first appearance of acritarchs indicates a marine environment (Obukhovskaya T.G. *et al.* 2014). This horizon is equivalent to the Pelcha Regional Stage of the Lviv-Lublin Trough (Miłaczewski and Kruchek 2002) in which the conodonts of the middle *Polygnathus varcus* Zone characterising the global biotic Taghanic Event were determined in south-eastern Poland (Narkiewicz and Narkiewicz 1998). According to the ichthyofauna, the upper part of the Stolin Beds (*Asterolepis dellei* placoderm faunal zone and *Pycnosteus tuberculatus* psammosteid heterostracan faunal zone; Mark-Kurik 2000, figs 3, 4) and the Moroch Beds (*Microbrachius* placoderm faunal zone; Mark-Kurik 2000, figs 3, 4) can be correlated with the Burtnieki Regional Stage of the Baltic Region (Plaksa 2007, 2008; Plax 2008). Recently, the presence of *Microbrachius* Traquair, 1888 (*M. kedoae* Mark-Kurik, Newman, Toom and den Blaauwen, 2018) has been confirmed in Belarus. A *Microbrachius* species is also present in the Baltic Region, but it has not been diagnosed to species level (Long *et al.* 2016; Mark-Kurik *et al.* 2018).

The Goryn Beds are composed of cyclic series of mudstones, siltstones and sandstones. The Stolin Beds consist of sandy mudstones with occasional marls, dolomites and dolomitic marls. The Moroch Beds consist of a cyclic series of mudstones, marls, siltstones and sandstones. The sedimentology of these beds was discussed in detail by Kruchek *et al.* (2001), Obukhovskaya T.G. *et al.* (2010) and Plax (2014a). These three beds contain various organic remains including foraminifers, scolecodonts, ostracods, conchostracans, bivalves, gastropods, inarticulate brachiopods, crinoids, ichthyofauna, plant fragments and miospores (see above). The invertebrates are poorly studied and are not well preserved, so have little use for biostratigraphy. Therefore, the ichthyofauna and miospores are most useful for determining the age, division, and correlation of the three beds. The stratigraphically important groups of fishes for the three beds are the heterostracans, placoderms and acanthodians. The acanthodians were discussed by various authors (Valiukevičius 1985, 1988, 1998; Valiukevičius *et al.* 1995; Valiukevičius and Kruchek 2000; Plaksa 2007, 2008; Plax 2008, 2014a, 2015, 2016a, 2017a; Plax and Kruchek 2014). The placoderms were also discussed by several authors (Mark-Kurik 2000; Plaksa 2007, 2008; Plax 2008, 2014a, 2015; Plax and Kruchek 2010). Only a few articles discuss the heterostracans (Plaksa 2007; Plax 2008, 2014a; Plax and Kruchek 2010, 2014). The chondrichthyans, sarcopterygians and actinopterygians are also found in these beds, but no significant biostratigraphic importance has been discerned by any authors so far (Golubtsov *et al.* 1978; Mark-Kurik 2000; Plaksa 2007, 2008; Plax 2008, 2014a, 2015; Plax and Kruchek 2010). The fauna for each of the beds is discussed in more detail below.

Goryn Beds. From the Pinsk 26 borehole located in the western part of the Pripyat Trough within the Turov Centricline, several species have been identified at depth levels 385.2 m and 384.5 m. These include individual scales of the acanthodians *Cheiracanthus brevicostatus*, *C. intricatus*, *C. peachi*, *Markacanthus alius* Valiukevičius, 1988 (DPP pers. obs.), *Diplacanthus tenuistriatus* and *Rhadinacanthus longispinus*. Also identified were fin spines of *Haplacanthus marginalis*. From other fish groups disarticulated remains of indeterminable psammosteids, sarcopterygians and actinopterygians were also recovered. Invertebrates were also recovered from the borehole including undetermined ostracods and lingulids shell fragments. For a full faunal list see Plax and Kruchek (2014) and Plax *et al.* (2016).

Stolin Beds. From the Pinsk 10 borehole located in the western part of the Pripyat Trough within the Starobin Centricline, several species have been identified at depth levels 146.0 m, 142.9 m and 141.0 m. These include individual scales of the acanthodians *Cheiracanthus brevicostatus*, *C. latus* and *Diplacanthus tenuistriatus*. Also identified were fin spines of *Haplacanthus marginalis*. From other fish groups disarticulated remains of indeterminable psammosteids, sarcopterygians and actinopterygians have been recovered. Invertebrates were also recovered from the borehole, including a lingulid shell fragment. For a full faunal list see Plax and Kruchek (2014).

From the North-Polotsk 1 borehole located within the Latvian Saddle, several species have been identified at depth level 231 m. These include individual scales of the acanthodians *Cheiracanthus latus*, *Rhadinacanthus longispinus*, *Ptychodictyon rimosum* and *Diplacanthus tenuistriatus*. From other fish groups were recovered disarticulated remains of the psammosteid *Tartuosteus* cf. *maximus* Mark-Kurik in Obruchev and Mark-Kurik, 1965, scales of the chondrichthyan *Karksilepis parva*, as well as disarticulated indeterminable remains of placoderms and actinopterygians. Invertebrates were also recovered from the borehole including lingulid shell fragments, as well as plant remains. Data on the fossils from this borehole has not been published previously.

Moroch Beds. From the Pinsk 10 borehole, several species have been identified at depths levels 122.0 m, 113.0 m, 103.7 m and 99.0 m. These include individual scales of the acanthodians *Cheiracanthus latus*, *C. intricatus*, *Rhadinacanthus longispinus* and *Diplacanthus tenuistriatus.* From other fish groups were recovered scales of *Orvikuina vardiaensis* and disarticulated, indeterminable remains of psammosteids, placoderms and sarcopterygians. Invertebrates were also recovered from the borehole including scolecodonts and lingulids shell fragments, and plant remains. For a full faunal list see Plax and Kruchek (2014).

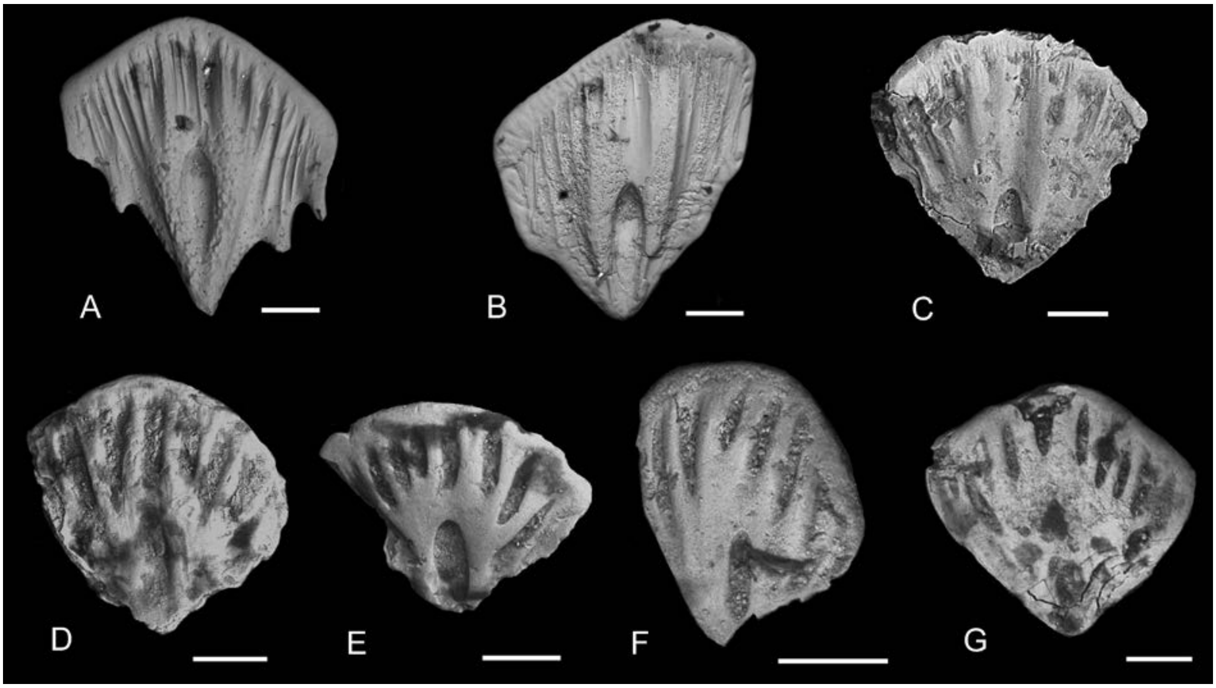
Ubort Regional Stage: The upper Givetian Ubort Regional Stage conformably overlies the Polotsk Regional Stage and is late Givetian in age. It is the lowest stage of the Lan Superstage (Text-fig. 4). The stage is composed of fine-grained mudstones, siltstones and sandstones in no clear cyclic pattern. The deposits have been interpreted as being laid down in a low salinity, shallow sea (Plax 2013a).

The Ubort Regional Stage corresponds to the *Ancyrospora incisa–Geminospora micromanifesta* miospore zone (Obukhovskaya T.G. *et al.* 2010, 2014). Disarticulated heterostracans, placoderms and to a lesser extent, acanthodians, are important for biostratigraphy. Fin spines of the acanthodians *Devononchus concinnus* (Gross, 1930) and *Diplacanthus laevis* (Gross, 1933) have been identified from this horizon, but individual acanthodian scales are indeterminable at species level (Valiukevičius *et al.* 1995; Valiukevičius and Kruchek 2000; Plax 2014b). Heterostracans and placoderms have been described by several authors (Golubtsov *et al.* 1990; Mark-Kurik 2000; Plaksa 2007, 2008; Plax 2008, 2014b). Other ichthyofauna has been identified (sarcopterygians and actinopterygians) but is less useful for biostratigraphy (Mark-Kurik 2000; Plaksa 2007, 2008; Plax 2008, 2014b).

The Ubort Regional Stage corresponds to the *Psammolepis paradoxa* psammosteid heterostracan faunal zone and the *Asterolepis ornata* antiarch placoderm faunal zone (Mark-Kurik 2000, figs 2, 3). This has allowed Plaksa (2007, 2008) and Plax (2008) to correlate the stage with the Gauja Regional Stage of the Main Devonian Field in the Baltic Region (Sorokin *et al.* 1981). The Ubort Regional Stage also correlates to the Yastrebovka Formation of the Central Devonian Field and the Pashija Regional Stage of the eastern regions of the East European Platform (Rodionova *et al.* 1995).

ERRONEOUS SPECIES IDENTIFICATIONS DUE TO DIFFERENCES IN PRESERVATION

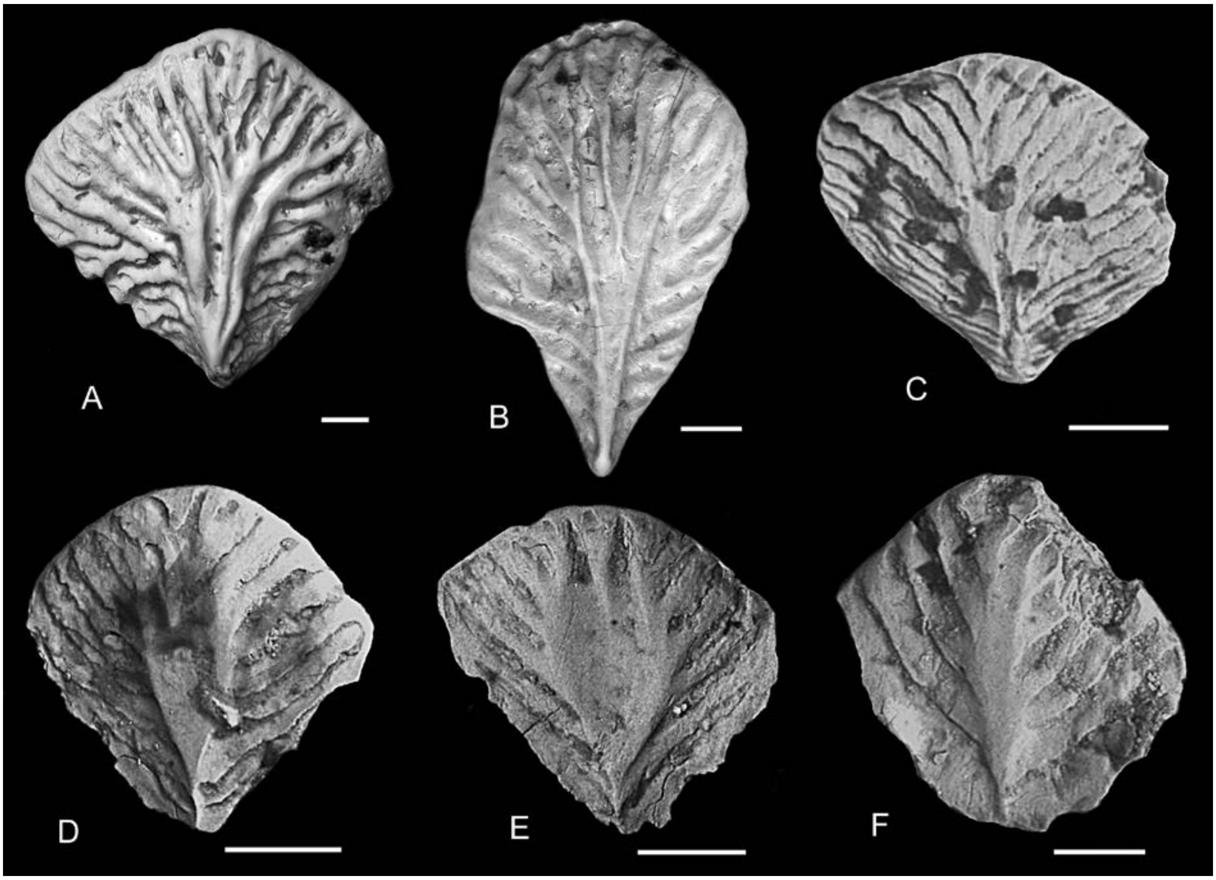
In several recent articles (Burrow *et al.* 2016, 2020, 2021; den Blaauwen *et al.* 2019; Newman *et al.* 2021b) it has been shown that several Middle Devonian acanthodian species from the Baltic Region and Belarus are subjective junior synonyms of species from the Orcadian Basin of Scotland. The main reason for the erection of new taxa was that the Scottish species were created for articulated fish in which the squamation was poorly known, whereas the Baltic species were based on isolated scales. Another reason for the erection of these new species in the Baltic Region and Belarus was that prior to the pioneering work of Elga Mark-Kurik (e.g., Mark-Kurik 1991, 2000), the Orcadian Basin was considered a separate realm with regard to the rest of the Old Red Sandstone continent and therefore, the species there were endemic. This caused authors to find minor, insignificant differences between the scales of the Baltic Region and Belarus species and similar Orcadian Basin species. For example, Burrow *et al.* (2020) demonstrated that the scale-based Baltic Region species, *Cheiracanthus longicostatus* is a subjective junior synonym of *C. latus*. The differences between these two species were very minor and disappeared when a greater suite of specimens of *C. latus* was examined by Burrow *et al.* (2020). Another reason for the lack of recognition of synonymy of species between these areas was due to differences in preservation. Orcadian Basin specimens are generally better preserved as they are often articulated



Text-fig. 5. Differences in preservation of Givetian *Cheiracanthus latus* Egerton, 1861 acanthodian scales from Belarus, crown views. The top of the scales is the anterior edge. A – BNTU 126/1-51, Stolin Beds; B – BNTU 126/1-46, Stolin Beds; C – BNTU 85/21-1k, Moroch Beds; D – BNTU 85/16-10a, Stolin Beds; E – BNTU 85/16-10g, Stolin Beds; F – BNTU 85/16-10n, Stolin Beds; G – BNTU 85/16-10l, Stolin Beds. A and B are from the North Polotsk 1 borehole, C-G are from the Pinsk 10 borehole. Scale bars equal to 100 µm.

individuals. The Baltic Region and Belarus specimens are usually preserved as individual scales, often worn due to abrasion and weathering. Text-fig. 5 illustrates a range of Belarus scales of *C. latus* from the best preserved to the poorest identifiable scale. BNTU 126/1-51 is an unworn, well preserved scale (Text-fig. 5A) and compares well with the Orcadian Basin examples (Burrow *et al*. 2020). Even moderately worn scales such as BNTU 126/1-46 (Text-fig. 5B) and BNTU 85/21-1k (Text-fig. 5C) compare well with the Orcadian Basin examples. However, with very worn scales (Text-fig. 5D–G), the comparison is less clear, and it is only because we have a range of preservation in the Belarus examples that we know they belong in the same species.

Another species, *Diplacanthus tenuistriatus* is also often confused with other species. This situation was not helped by the scale crown morphology not being described until Burrow *et al*. (2016, fig. 23). This led Gross (1973), for example, to erect a new scale-based species *Diplacanthus carinatus* (only tentatively placed by him in the genus *Diplacanthus* Agassiz, 1843). Burrow *et al*. (2016) demonstrated that *D. carinatus* is a subjective junior synonym of *D. tenuistriatus*. Another problem is that differences in preservation of individual scales of *D. tenuistriatus* can make them look morphologically distinct. In the case of scales of *D. tenuistriatus* from the Baltic Region and Belarus, virtually all the scales have some wear, whereas the specimens figured by Burrow *et al*. (2016) from the Orcadian Basin of Scotland were mostly from articulated individuals. However, BNTU 126/1-17 (Text-fig. 6A) has only minimal wear of the scale crown ridges and is a fine example of the species showing the scale crown ornamentation. As long as these ridges are not too worn, such as in BNTU 126/1-45 (Text-fig. 6B), *D. tenuistriatus* is relatively easy to identify. The difficulty arises when these ridges are very worn, such as BNTU 41/6a-1c (Text-fig. 6C) where species identification can be difficult, especially when relying on published figures for identifications. BNTU 41/6a-1c was originally figured by Plax and Kruchek (2014, pl. 3, fig. 15) as *D. carinatus*, but in a low resolution and as a small figure. This led Burrow *et al*. (2016) to mistakenly list the specimen in a synonymy list under *Diplacanthus crassisimus*. When BNTU 41/6a-1c is figured in higher resolution (Text-fig. 6C)



Text-fig. 6. Differences in preservation of Givetian *Diplacanthus tenuistriatus* Traquair, 1894 acanthodian scales from Belarus, crown views. The top of the scales is the anterior edge. A – BNTU 126/1-17, Stolin Beds; B – BNTU 126/1-45, Stolin Beds; C – BNTU 41/6a-1c, Goryn Beds; D – BNTU 85/16-10d, Stolin Beds; E – BNTU 85/16-10c, Stolin Beds; F – BNTU 85/23-7c, Stolin Beds. A and B are from the North-Polotsk 1 borehole, C is from the Pinsk 26 borehole, D-F are from the Pinsk 10 borehole. Scale bars equal to 100 µm.

and comparison is made with a range of worn scales (Text-fig. 6) it becomes clear that the scale belongs in *D. tenuistriatus*. As the scale crowns of *D. tenuistriatus* (Text-fig. 6D–F) become more progressively more worn they can begin to look more like the worn *D. crassisimus* scales. It is, therefore, useful to look at a range of scale crown wear to make a species determination as we have here.

As can be seen from the two examples above, great care is required in assessing an acanthodian species based on worn, individual scales. It is better to have as many scales as possible from a given locality or core to assess a species. However, where this is not possible, it is reasonable to make use of scales from other localities where they are more numerous to get a range of preservation. When dealing with biostratigraphy it is better to err on the side of caution as we think we have done in this article.

INTERREGIONAL BIOSTRATIGRAPHIC CORRELATION OF MIDDLE DEVONIAN ACANTHODIANS (ORCADIAN BASIN, THE BALTIC REGION AND BELARUS)

It has been known since the 20th century that there was a faunal connection in the Middle Devonian between the Baltic Region and the Orcadian Basin in Scotland (Mark-Kurik 1991). This was assumed to be due to river overflow from the fluvio-lacustrine Orcadian Basin to the marine areas of the Baltic Region (Newman and Trewin 2008). Mark-Kurik (1991, 2000) listed several congeneric and possibly conspecific fish taxa that occurred in both areas. Evidence for co-specific placoderms and tetrapodamorphs has only recently been published (Newman *et al*. 2015, 2017). Of particular interest for this article is the presence of conspecific acanthodians in

<table>
<tr><th colspan="3">Belarus</th><th colspan="3">Baltic (Estonian members)</th><th colspan="2">Scotland (Caithness units)</th></tr>
<tr><th>Regional Stage</th><th>Beds</th><th>Acanthodians</th><th>Regional Stage</th><th>Member</th><th>Acanthodians</th><th>Stratigraphical unit</th><th>Acanthodians</th></tr>
<tr><td rowspan="6">Polotsk</td><td>Moroch</td><td>Cb, Ci, Cl, Dt, Rl</td><td rowspan="3">Burtnieki</td><td>Abava</td><td rowspan="3">Cb, Cl, Dc, Dt, Pr, Ps Rl, Ng</td><td rowspan="3">John o’Groats Sandstone Group</td><td rowspan="3">No acanthodians</td></tr>
<tr><td rowspan="3">Stolin</td><td rowspan="3">Cb, Ci, Cl, Dt, Rl, Ng</td><td>Koorküla</td></tr>
<tr><td>Härma</td></tr>
<tr><td rowspan="3">Aruküla</td><td>Tarvastu</td><td rowspan="3">Cb, Cl, Ci, Dc, Dt, Pr, Ps, Rl, Mc</td><td>Mey Flagstone Formation</td><td>Cp, Mc, Dt, Rl</td></tr>
<tr><td rowspan="2">Goryn</td><td rowspan="2">Cb, Ci, Cp, Rl, Ng</td><td>Kureküla</td><td rowspan="2">Spital Flagstone Formation</td><td rowspan="2">Cg, Dc, Dt, Rl</td></tr>
<tr><td>Vijandi</td></tr>
<tr><td>Kostyukovichi</td><td rowspan="5"></td><td>Cb, Cl, Cp, Mc, Gt, Dt, Rl, Ps, Pr, Nk</td><td rowspan="3">Narva</td><td>Kernavé</td><td>Cm, Cb, Cl, Ci, Cg, Dc, Dt, Rl, Pr, Ps, Mc, Nk</td><td>Achanarras Fish Bed Member</td><td>Cl, Cg, Cm, Dc, Dt, Rl</td></tr>
<tr><td>Gorodok</td><td>Cb, Cl, Rl, Ps, Pr,</td><td>Leivu</td><td>Cm, Cl, Ci, Dc, Dt, Rl, Pr, Ps</td><td rowspan="2">Lybster Flagstone Formation</td><td rowspan="2">Cb, Dc</td></tr>
<tr><td>Osveya</td><td>Cb, Cl</td><td>Vadja</td><td>Cm, Cl, Dc, Dt, Rl, Pr</td></tr>
<tr><td>Adrov</td><td>Cb, Cl</td><td>Pärnu</td><td></td><td>Cb, Cl</td><td colspan="2" rowspan="2">No acanthodians</td></tr>
<tr><td>Vitebsk</td><td>Cb, Cl</td><td>Rēzekne</td><td></td><td>Cb, Cl</td></tr>
</table>

Text-fig. 7. Middle Devonian acanthodian biostratigraphic column of the Baltic Region, Belarus and the Orcadian Basin of Scotland. Acanthodian species: *Cb – Cheiracanthus brevicostatus*; *Cg – Cheiracanthus grandispinus*; *Ci – Cheiracanthus intricatus*; *Cl – Cheiracanthus latus*; *Cm – Cheiracanthus murchisoni*; *Cp – Cheiracanthus peachi*; *Dt – Diplacanthus tenuistriatus*; *Gt – Ginkgolepis talimae*; *Mc – Markacanthus costulatus*; *Ng – Nostolepis gaujensis*; *Nk – Nostolepis kernavensis*; *Pr – Ptychodictyon rimosum*; *Ps – Ptychodictyon sulcatum*; *Rl – Rhadinacanthus longispinus*.

both regions, but also in Belarus and Spitsbergen (Svalbard) (Burrow *et al*. 2016, 2020, 2021; den Blaauwen *et al*. 2019; Newman *et al*. 2019, 2021b). In this article we have expanded the information on what acanthodian interregional species are present in the Middle Devonian of Belarus. Below, we discuss the individual species and their biostratigraphic distribution across the various regions.

In the Baltic Region, *Cheiracanthus brevicostatus* has a long range from the Rēzekne (upper Emsian) to Burtnieki (middle Givetian) regional stages (Valiukevičius and Kruchek 2000). In Belarus there is a similar range starting in the Vitebsk Regional Stage and ending in the Moroch Beds at the top of the Polotsk Regional Stage (Text-fig. 7). Specimens from these two areas consist of isolated scales. Burrow *et al*. (2021) described the first articulated specimens of *C. brevicostatus* (from the Orcadian Basin of Scotland). The species has a narrow range in the Orcadian Basin being confined to the upper part of the middle Eifelian Lybster Flagstone Formation. It is worth noting that the Emsian deposits of the Orcadian Basin are poor in vertebrate fossils with only scales of the sarcopterygian *Porolepis* sp. known (Collins and Donovan 1977). However, it seems likely that the presence of *C. brevicostatus* in the Orcadian Basin was a chance introduction from the Baltic Region or Belarus in the middle Eifelian, with the species being extinct in the basin by the time the Achanarras Fish Bed Member was laid down. The species long range makes it of little use for biostratigraphy across the Old Red Sandstone continent.

Burrow *et al*. (2020) described in detail the three *Cheiracanthus* species (*C. grandispinus* McCoy, 1848, *C. latus*, and *C. murchisoni*) described in the 19th century from the Orcadian Basin of Scotland. *Cheiracanthus murchisoni* has a narrow range in the Orcadian Basin being mostly confined to the Achanarras Fish Bed Member (perhaps a little higher but not by much; Burrow *et al*. 2020; Text-fig. 7) and equivalent strata in the Orcadian Basin. The species is quite rare outside the Orcadian Basin with Burrow *et al*. (2020) only confirming its presence in the Narva Regional Stage of the Baltic Region, so appearing a little earlier than in the Orcadian Basin. The species is unknown from Belarus.

Cheiracanthus grandispinus has a longer range than *Cheiracanthus murchisoni* first appearing in the Achanarras Fish Bed Member and continuing to quite high in the Spital Flagstone Formation (Burrow *et al*. 2020). The species is rare outside the Orcadian Basin with Burrow *et al*. (2020) only confirming its presence in the Kernavė Member of the Narva Regional Stage of the Baltic Region. Therefore, the species appears at about the same time in both areas, although it occurs a little higher up in the Orcadian Basin (Text-fig. 7). This narrow biostratigraphic range could be quite useful, but the species is very rare and unknown in Belarus.

Cheiracanthus latus was the last species to be erected in the 19th century from the Orcadian Basin. The species has a very narrow range in the Orcadian Basin being confined to equivalents of the Achanarras Fish Bed Member in the Moray Firth area (Burrow *et al*. 2020). Burrow *et al*. (2020) demonstrated it had a wide distribution outside the Orcadian Basin, being present in the Rēzekne Regional Stage to the top of the Burtnieki Regional Stage in the Baltic Region. In this article we show that *C. latus* has a similar range in Belarus, first appearing in the Vitebsk Regional Stage and ending at the top of the Polotsk Regional Stage in the Moroch Beds (Text-fig. 7). Newman *et al*. (2019) also comment on Valiukevičius' (1979) statement on the presence of *Cheiracanthus longicostatus* in the Eifelian of Spitsbergen. Burrow *et al*. (2020) showed that this species is a subjective junior synonym of *C. latus*. However, Valiukevičius (1979) did not figure any specimens of the species, so Newman *et al*. (2019) could not confirm its presence in Spitsbergen.

Cheiracanthus peachi was first identified in the Orcadian Basin where it has a narrow range, in the Mey Flagstone Formation and its Orkney equivalent (den Blaauwen *et al*. 2019). The species has not been identified in the Baltic Region (den Blaauwen *et al*. 2019). In this article we identify the species in the Kostyukovichi Regional Stage up to the Goryn Beds at the base of the Polotsk Regional Stage. In both areas the biostratigraphical range is quite narrow, with the earlier occurrence in Belarus (Text-fig. 7). This narrow range in both areas makes the species potentially useful for biostratigraphy.

In the Baltic Region, *Cheiracanthus intricatus* first appears in the middle of the Leivu Member in the Narva Regional Stage and disappears in the Kureküla Member in the Aruküla Regional Stage (Valiukevičius and Kruchek 2000). In this article we show that the species was present throughout the Polotsk Regional Stage, so first appearing a little later but lingering longer than the Baltic Region (Text-fig. 7). The species is unknown from the Orcadian Basin. Its youngest known occurrence is very high up in the upper Givetian of Spitsbergen (Newman *et al.* 2019).

In the Baltic Region, *Markacanthus costulatus* has a relatively short biostratigraphic range starting at the top of the Narva Regional Stage in the Kernavé Member and ending in the Vijandi Member of the Aruküla Regional Stage (Valiukevičius and Kruchek 2000). In this article we show the species is confined to the Kostyukovichi Regional Stage in Belarus. Newman *et al*. (2021b) described the first articulated specimen of *M. costulatus* (in this case from the Orcadian Basin). In the Orcadian Basin the species is present in a very narrow zone at the top of the Mey Flagstone Formation. As only one specimen is known in the Orcadian Basin it must have been a chance introduction, probably from the Baltic Region via river overflow to the marine environment. This narrow range in both areas makes the species potentially useful in biostratigraphy.

In the Baltic Region *Ginkgolepis talimae* has a relatively short biostratigraphic range first appearing at the top of the Narva Regional Stage in the Kernavé Member and ending in the Vijandi Member of the Aruküla Regional Stage (Valiukevičius and Kruchek 2000). In this article we show the species only occurs in the Kostyukovichi Regional Stage in Belarus. The species is not present in the Orcadian Basin (Text-fig. 7). This narrow range in both areas makes the species potentially useful for biostratigraphy.

Burrow *et al*. (2016) described in detail the three diplacanthid species *Diplacanthus crassisimus*, *D. tenuistriatus* and *Rhadinacanthus longispinus* from the Orcadian Basin. *Diplacanthus crassisimus* has a long range in the Orcadian Basin, first appearing in the top of the Lybster Flagstone Formation and disappearing in the top of the Spital Flagstone Formation (Burrow *et al*. 2016). They also demonstrated that *D. crassisimus* has a long range in the Baltic Region being present in the Narva, Aruküla, and Burtnieki regional stages (Text-fig. 7). This means the species appeared earlier and disappeared later in the Baltic Region. This species is unknown from Belarus. As discussed above, the one scale of *D. crassisimus* identified by Burrow *et al*. (2016) from Belarus is now identified as *D. tenuistriatus*. Of interest is that Burrow *et al*. (2016) identified the two scales from the Eifelian? Vstrechnaya Formation of Severnaya Zemlya, figured by Valiukevičius (2003, fig. 20K, L) as *Diplacanthus carinatus*, as *D. crassisimus* scales. Due to the long range of the species it is unlikely to be useful biostratigraphically.

Diplacanthus tenuistriatus is quite a rare species in the Orcadian Basin, but has a long range, first appearing in the Achanarras Fish Bed Member and disappearing in the middle of the Mey Flagstone Formation and its equivalent in Orkney. Burrow *et al*. (2016) demonstrated that *D. tenuistriatus* had a long range in the Baltic Region, being present in the Narva, Aruküla, and Burtnieki regional stages, so showing the species appeared earlier and ended later in the Baltic Region (Text-fig. 7). In this article we show that in Belarus *D. tenuistriatus* first appeared in the Kostyukovichi Regional Stage and disappeared at the top of the Moroch Beds at the top of the Polotsk Regional Stage. Due to the long range of the species it probably has little use in biostratigraphy.

The final diplacanthid species from the Orcadian Basin described by Burrow *et al*. (2016) was *Rhadinacanthus longispinus* which has the same biostratigraphic range in the Orcadian Basin as *Diplacanthus tenuistriatus*. Also, the species has the same biostratigraphical range as *D. tenuistriatus* in the Baltic Region (Burrow *et al*. 2016). In this article we show *D. tenuistriatus* also had a long range in Belarus first appearing a little later than the Baltic Region in the Gorodok Regional Stage and disappearing at the top of the Polotsk Regional Stage in the Moroch Beds. Due to the long range of the species it probably has little use in biostratigraphy.

In the Baltic Region, *Ptychodictyon sulcatum* first appears in the upper part of the Leivu Member in the Narva Regional Stage and disappears in the Kureküla Member of the Aruküla Regional Stage (Valiukevičius and Kruchek 2000). In this article we show the species first appears in Belarus at the same time in the Gorodok Regional Stage. *Ptychodictyon sulcatus* is also present in the Kostyukovichi Regional Stage but then disappears in Belarus, earlier than in the Baltic Region. This species is not present in the Orcadian Basin (Text-fig. 7). The fairly narrow range may make the species useful for biostratigraphy.

Ptychodictyon rimosum has quite a long biostratigraphic range in the Baltic Region, first appearing in the Leivu Member in the Narva Regional Stage and disappearing in the top of the Burtnieki Regional Stage (Valiukevičius and Kruchek 2000). In this article we show the species starts at the same time in Belarus in the Gorodok Regional Stage but disappears earlier in the Stolin Beds of the Polontsk Regional Stage. The species is not present in the Orcadian Basin (Text-fig. 7). Due to the long range the species is not very useful for biostratigraphy.

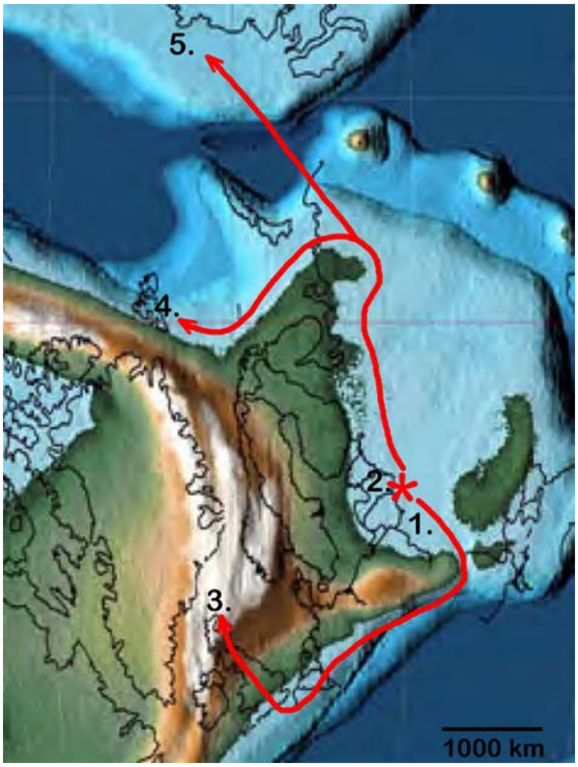
In the Baltic Region *Nostolepis kernavensis* is only known from the Kernavé Member of the Narva Regional Stage. As we have shown in this article, in Belarus the species is only known from the equivalent Kostyukovichi Regional Stage. It is therefore an excellent zonal fossil. Unfortunately, the species is not present in the Orcadian Basin (Text-fig. 7).

In the Baltic Region, Valiukevičius and Kruchek (2000) recorded *Nostolepis gaujensis* from the uppermost Givetian Gauja Regional Stage and the Upper Devonian Amata Regional Stage. Later, Märss *et al*. (2008) identified the species in the Härma Member of the Burtnieki Regional Stage in the Baltic Region (Text-fig. 7). The species appears earlier in Belarus in the Goryn Bed of the Polotsk Regional Stage. However, the species disappears quite quickly in Belarus in the Stolin Beds of the Polotsk Regional Stage. This species is not present in the Orcadian Basin (Text-fig. 7). The long range of the species is not very useful for biostratigraphy.

Ptychodictyon distinctum Valiukevičius, 1979 was erected based on isolated scales from the Eifelian of Spitsbergen. Valiukevičius and Kruchek (2000) listed the species in the Leivu Member of the Narva Regional Stage to the Vijandi Member of the Aruküla Regional Stage in the Baltic Region. Valiukevičius and Kruchek (2000) also report the species in the Gorodok and Kostyukovichi regional stages of Belarus. However, we know of no specimens of *P. distinctum* and no specimens have been figured from Belarus.

CONCLUSIONS

In Middle Devonian strata, various acanthodian species are widely distributed across the Baltic Region, Belarus and the Orcadian Basin of Scotland, with a more limited distribution in Spitsbergen. There must also have been a connection, probably in the Eifelian, between the Baltic Region and Severnaya Zemlya as both areas have the species *Diplacanthus crassisimus* present. Text-fig. 7 shows the biostratigraphic distribution of various acanthodian species found in the Baltic Region, Belarus and the Orcadian Basin. Whilst we can be sure that these areas with co-specific acanthodians were connected at one time or another, care must be taking in assuming the earliest occurrence when a given species evolved. However, considering the number of different species appearing in certain regions, several conclusions can be made. It seems clear that the Orcadian Basin, Spitsbergen and Severnaya Zemlya were peripheral areas. The main speciation seems to have occurred in the Baltic Region and Belarus. Both these regions were nearshore environments in the Middle Devonian. The Baltic Region strata were deposited in a very large estuary (e.g., Tanavsuu-Milkeviciene and Plink-Bjorklund 2009; Tanavsuu-Milkeviciene *et al*. 2009). In this article we show that the Belarus deposits were laid down in nearshore environments. The Spitsbergen upper Givetian deposits were accumulated in a marginal marine lagoon (Newman *et al*. 2019), probably as part of an estuarine environment (Newman *et al*. 2021a).



Text-fig. 8. Middle Devonian (Givetian) dispersal routes around Laurussia. Localities: 1 – Belarus, 2 – Baltic Region (Estonia and Latvia), 3 – Orcadian Basin, Scotland, 4 – Spitsbergen (Svalbard), 5 – Severnaya Zemlya. Red arrows show hypothetical dispersal routes from the Belarus/Baltic Region (marked *) to other areas.

The latest palaeomap of the Middle Devonian (Givetian) shows the relative positions of the areas mentioned above in Laurussia (Text-fig. 8 modified slightly from Scotese 2014, map 68). The red arrows indicate the dispersal routes from the shallow seas which covered modern day Belarus and the Baltic Region to more peripheral areas. Other regions mentioned in this article were along these dispersal routes. Most of these routes were via the sea, but as the Orcadian Basin was around 1000 km inland, in an upland area, the connection had to be via rivers. The fish arrived with waves in the Orcadian Basin when there was basin overflow to the marine environment via rivers. Connection with the marine environment must have been strong at times as the Orcadian Basin shares at least nine co-specific forms with the Baltic Region. As well as the acanthodians described in this article, these co-specific forms include tetrapodamorphs and arthrodires (Newman *et al*. 2015, 2017). Newman and Trewin (2008) suggested that the Orcadian Basin fish were able to tolerate various salinities for the reasons outlined above. Furthermore, there is also a growing body of evidence that Palaeozoic fish in general could tolerate a range of salinities (e.g., Carpenter *et al*. 2015).

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