Research article

SJG
*Scottish Journal of Geology*

Published online August 14, 2015

doi:10.1144/sjg2014-006 | Vol. 51 | 2015 | pp. 141–147

# Scottish Middle Devonian fishes in Estonia

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**Abstract:** A number of Estonian Devonian fishes are shown to be junior synonyms of Scottish species. The Estonian sarcopterygian osteolepid *Gyroptychius pauli* was originally thought to be closely related to the Scottish species *Gyroptychius milleri* being differentiated by minor morphological differences of the skull roof. However, here we show that the only skull roof available of *G. pauli* to the original description (the holotype) was badly damaged in places. This and the fact that skull roofs of osteolepid fishes are morphologically highly variable has allowed us to compare the Estonian and Scottish species and show that *G. pauli* is a junior synonym of *G. milleri*. It has also been known for some time that Estonian coccosteid arthrodire *Coccosteus orvikui* was a junior synonym of the Scottish species *Coccosteus cuspidatus*. Here we present the evidence for this assumption and also show that the Scottish coccosteid arthrodire *Millerosteus minor* is almost certainly present in Estonia. Finally, it is shown that the three species have the same stratigraphical distribution in the two regions, strongly indicating a close faunal connection between the Middle Devonian of Estonia and the Middle Devonian Orcadian Basin of Scotland.

**Received** 21 February 2014; **accepted** 6 May 2015

## Introduction and geological setting

The Middle Devonian Orcadian Basin consists of a series of cyclic lacustrine deposits with fluvial sediments becoming more common as you go up sequence (Trewin & Thirlwall 2002). The fossil fishes are found within these lacustrine deposits being particularly well preserved in the well-varved flagstones. The Estonian Middle Devonian fishes described in this study were found in marine cross-bedded sandstones and siltstones. A synopsis of the Middle Devonian geology of Estonia is found in Kleesment & Mark-Kurik (1997). The character of sedimentary basin and environment during the Middle Devonian in the Baltic is described by Kuršs (1992).

The publication commonly called the 'Caithness Memoir' (Crampton & Carruthers 1914) was the first time that the geology of the Orcadian Basin was described in detail. At that time it was thought that there was no connection between the Orcadian Basin and the marine Devonian. This was because there was little faunal evidence for a connection, the Orcadian Basin being mostly devoid of invertebrates except for a few, mostly endemic arthropods (Anderson *et al*. 2000). The overwhelming faunal content of the Orcadian Basin is the fossil fishes but these were considered endemic until Mark-Kurik (2000) recognized *Coccosteus cuspidatus* Miller (1841) *ex* Agassiz MS as being present in both areas. Newman & Trewin (2008) were also able to demonstrate that the arthrodire *Actinolepis* occurred in both areas, but were unable to determine the species for the Scottish specimen. One palaeontological area that has been studied extensively is the palynology (e.g. Marshall *et al.* 1996, 2007, 2011) which has provided the best correlative tool between the two areas in recent times.

The only Middle Devonian marine incursion into the Orcadian Basin was recognized by Marshall *et al.* (1996). They described a single, unique marine incursion in the Eday Marls (mid–late Givetian) in Orkney during the highest late Middle Devonian sea stand. The fossil fauna in this incursion is scarce, consisting of only scolecodonts and acritarchs. Younger Frasnian (Upper Devonian) incursions occurred further east in the North Sea. However, all these incursions occurred above the Middle Devonian fish-bearing horizons; the Eday Flags being the highest strata to contain fish (Trewin & Thirlwall 2002, fig. 8.17). Further down in the Orcadian Basin sequences marine incursions have not been documented, with Trewin & Thirlwall (2002) concluding that there was a fluvial connection at least during the Eifelian between the Orcadian Basin and the marine environment. It is still too early at this stage to comment further on the nature of these faunal connections. However, in this study we provide further evidence of this faunal connection by demonstrating that as well as the arthrodire *Coccosteus cuspidatus* mentioned above, the osteolepid *Gyroptychius milleri* Jarvik (1948) is also present in both areas. Furthermore, the small arthrodire *Millerosteus minor* (Miller 1858) is probably also present in both areas.

The specimens described below are housed in the British Geological Survey in Edinburgh, Scotland (prefixed BGSE); the National Museums of Scotland in Edinburgh, Scotland (prefixed NMS); the Institute of Geology at Tallinn Technical University, Estonia (prefixed GIT) and

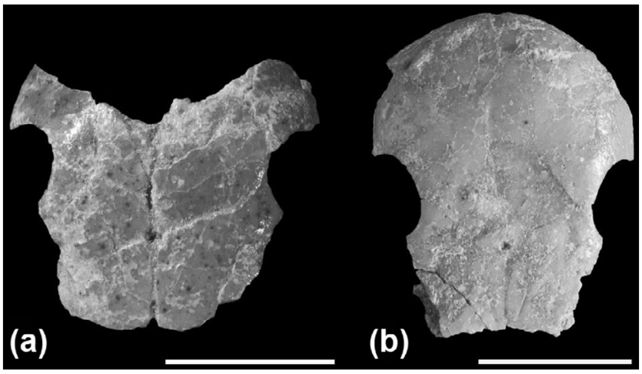


**Fig. 1.** *Gyroptychius milleri* from the Devonian of Estonia: (**a**) GIT 365-165 from Tamme Cliffs in the Kureküla Member; (**b**) GIT 365-203 from Aruküla Caves in the Viljandi Member. All scale bars 10 mm.

Tamme Cliffs: Givetian

the Geological Museum of the University of Tartu, Estonia (prefixed TUG).

## Estonian and Scottish *Gyroptychius* species

In 1977 Vorobyeva raised the osteolepid sarcopterygian species *Gyroptychius pauli*. Vorobyeva's (1977) description was based only on the skull. She had three specimens at her disposal including the holotype GIT 365-151 (old number Pi 1063), consisting of a near-complete skull in dorsal aspect with the visceral surface visible on the other side. The other two specimens were GIT 365-168 (old number Pi 1619), a part of a lower jaw, and GIT 365-152 (old number Pi 1558), a squamosal plate. Another specimen, GIT 365-157 (old number Pi 1603), a lower jaw missing the posterior end, has also been placed in this species in recent times by the museum staff. This is a very limited amount of material on which to base an osteolepid species. The most obvious character of *G. pauli* is the deep orbital notches. This obvious character has enabled the authors to identify two more specimens of *G. pauli*, being GIT 365-165 (old number Pi 1615) and GIT 365-203 (Fig. 1). Both specimens are parietal shields of very small or juvenile individuals. Vorobyeva (1977) also noted this obvious character and drew comparison with the Scottish species *Gyroptychius milleri* which shared the same character. She considered that the two forms were very closely related with only a small number of characters separating them. However, Vorobyeva (1977) relied on Jarvik's (1948) description of *G. milleri* and the figures he provided. Even Jarvik (1948) had only cranial material available and that was in limited number. In the last few decades many new specimens of *G. milleri* have been collected, including many fully articulated with the postcranial bodies. As discussed in Newman & den Blaauwen (2007), the individual bones of osteolepid skulls are very variable in both shape and size. A large suite of skulls is generally required to take into account the variability of any given osteolepid species otherwise there is a risk of creating synonymies.

Considering the close morphological similarity between *Gyroptychius milleri* and *Gyroptychius pauli*, it is prudent to look at the character differences used by Vorobyeva (1977) to distinguish between the two species.

Vorobyeva (1977) firstly considered *Gyroptychius pauli* to have a narrower skull roof than *Gyroptychius milleri*. In this regard she had only the holotype (GIT 365-151) at her disposal. If the holotype is compared to Vorobyeva's (1977, fig. 29B) line drawing of the specimen (Fig. 2), it can be seen that she was mistaken in her placing of the left orbit, making it too close to the right orbit. This had the effect of making the skull roof too narrow in *G. pauli*. Also, *G. milleri* specimens are crushed flat whereas *G. pauli* specimens are much less deformed. This means that *G. milleri* specimens are flattened out particularly at the anterior orbital notches. This makes the orbits look almost like they are dorsally placed whereas in reality they would be more laterally placed in the living animal. Therefore, the preservation of *G. milleri* is the reason why some specimens appear slightly wider than the corresponding unflattened *G. pauli* specimens notwithstanding the error made by Vorobyeva (1977) in the left eye placement in the holotype.

Secondly, Vorobyeva (1977) considered that the orbits were placed more anteriorly in *Gyroptychius pauli* than *Gyroptychius milleri*. This is difficult to ascertain in GIT 365-151 as the left and right orbits are in different positions. The left side orbit is much smaller than the right and it is placed more posteriorly. It seems that the edges of the right

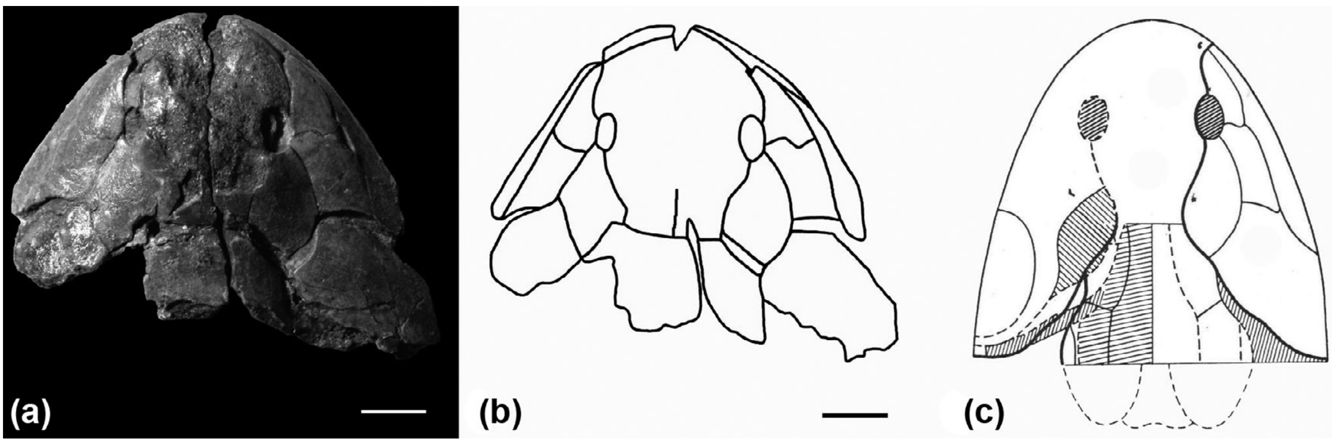


**Fig. 2.** *Gyroptychius milleri* from the Tamme Cliffs of Estonia: (**a**) photograph of GIT 365-151; (**c**) line drawing of GIT 365-151; (**b**) reproduction of the same specimen by Vorobyeva (1977, fig. 29B). Scale bars 10 mm.

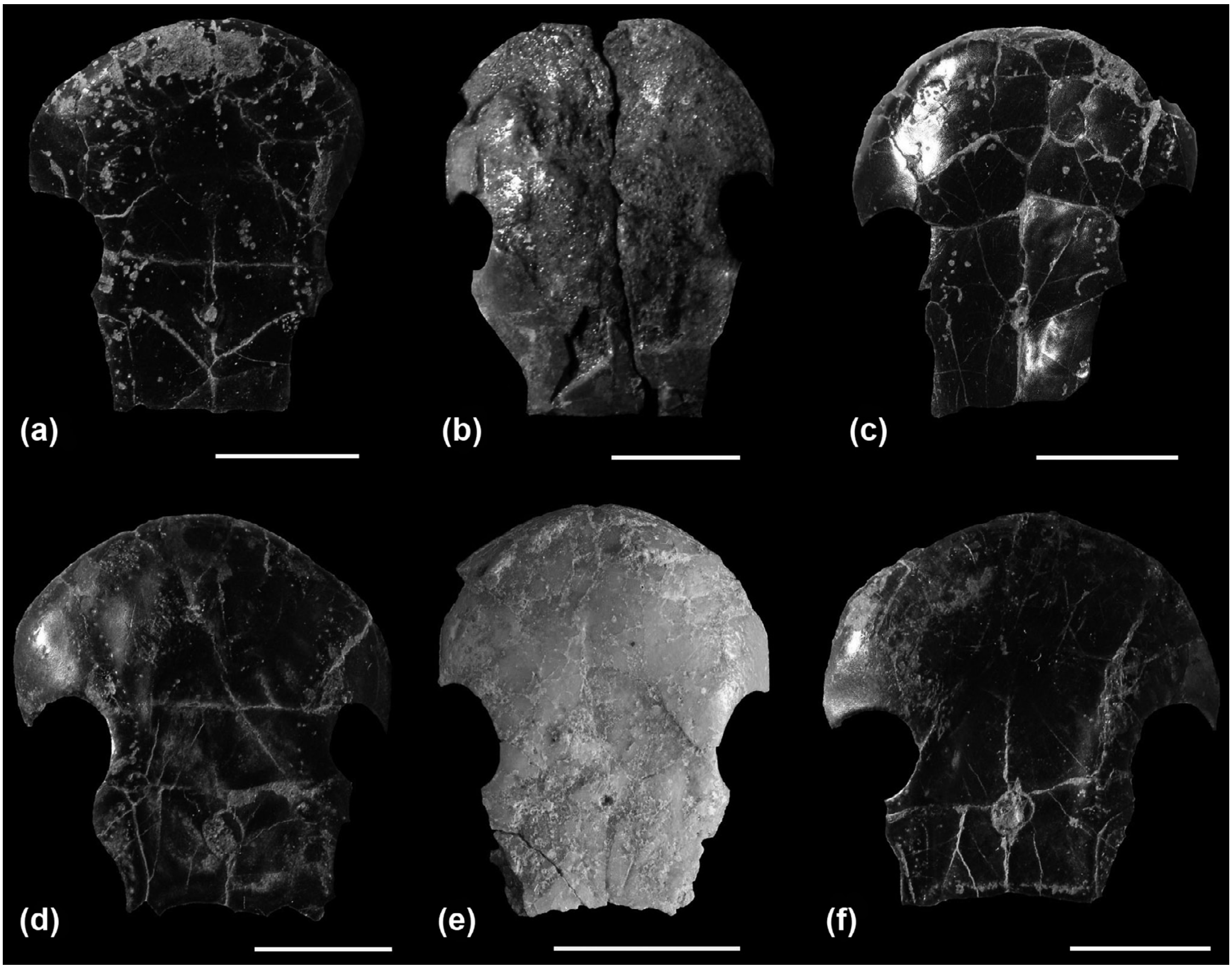


**Fig. 3.** *Gyroptychius milleri* from the Devonian of Scotland and Estonia: (**a**) BGSE 1224 from Scrabster Hill, Caithness, Scotland; (**b**) GIT 365-151 from Tamme Cliffs, Estonia; (**c**) NMS G.2014.4.1 from Point of Buckquoy, Orkney, Scotland; (**d**) BGSE 10444 from Samuel Geo, Caithness, Scotland; (**e**) GIT 365-203 from Aruküla Caves, Estonia; (**f**) BGSE 10445 from Samuels Geo, Caithness, Scotland. All scale bars 10 mm.

side orbit have been damaged at the left-hand and anterior edge, so making it appear not only larger than the left side orbit but also placing it too far anteriorly. The left side orbit is surrounded by well-defined bones and, when compared with Scottish *G. milleri* specimens (Fig. 3), there is no difference in orbit positions between *G. milleri* and *G. pauli* in relation to the front of the skull.

The third character that Vorobyeva (1977) used to distinguish between *Gyroptychius milleri* and *Gyroptychius pauli* was the postorbital section of the parietal bone being longer in *G. pauli*. The ratio between anterior and posterior parts of the skull either side of the postorbital notch is a good way to rationalize the length of the postorbital section. In *G. milleri* this ratio falls between about 1.72 and 3.92 – quite a large range. In the holotype of *G. pauli* the ratio is about 1.70 (using the undamaged left orbit). However, the front of the skull is damaged and so this ratio is an underestimate. Certainly the true figure falls within the variation of *G. milleri*. The other measurable specimen of *G. pauli* GIT 365-203 has a ratio of about 2.16, which falls in the middle of the *G. milleri* ratio.

From the above it is clear that there are no specific differences between *Gyroptychius milleri* and *Gyroptychius pauli* from the material currently available and that *G. pauli* must be considered a junior synonym of *G. milleri*.

## Estonian and Scottish coccosteids

Obruchev ([1930] 1931) identified a small coccosteid from the NW of Russia as *Coccosteus* cf. *decipiens* (a common synonym of *Coccosteus cuspidatus*). Later, this arthrodire was named as either *Coccosteus* cf. *minor* (Gross 1933), a probable species of *Millerosteus* (Miles & Westoll 1968; Denison 1978), or as *Coccosteus orvikui* (Gross 1940; Obrucheva 1962, 1966). Various exoskeletal plates of larger size in the Tallinn collection (GIT) enabled Mark-Kurik (2000) to determine that *C. orvikui* was a junior synonym of *C. cuspidatus*. The previous species identifications were based on rare plates of mainly juvenile individuals, particularly the nuchal plate TUG 1554-6 (previously known as Pi 0046), the holotype of *C. orvikui*, and the posterior ventrolateral plate GIT 117-5 (previously known as Pi 0068). Our study compares the Estonian *C. cuspidatus* specimens (Fig. 4) with the Scottish specimens as described in great detail by Miles & Westoll (1968).

Estonian collections of *Coccosteus cuspidatus* consist of isolated plates: three from the skull and nine from the body

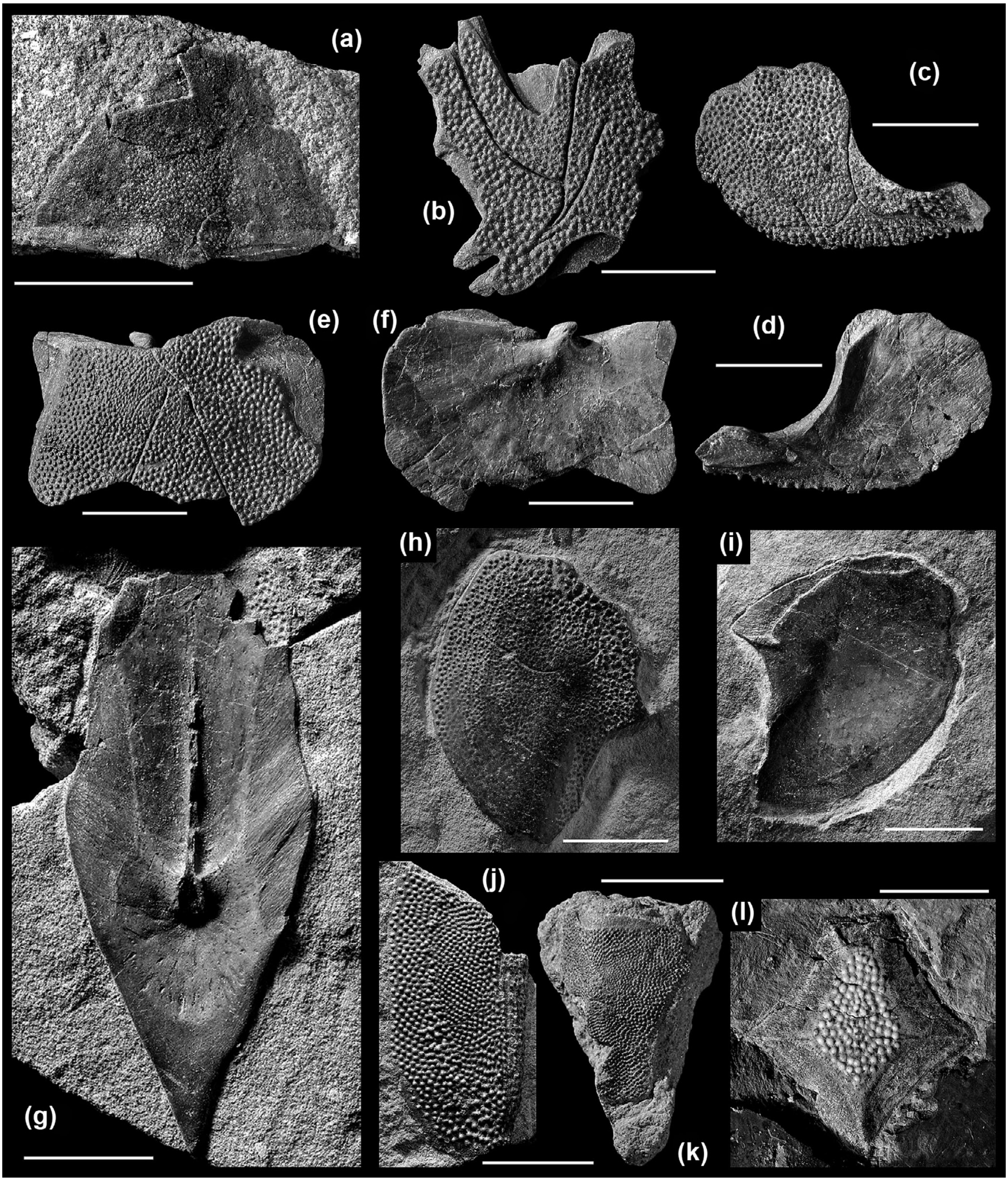


**Fig. 4.** *Coccosteus cuspidatus* from the Devonian of Estonia: (**a**) TUG 1554-6 nuchal plate; (**b**) GIT 689-1 right central plate; (**c–d**) GIT 689-2 right suborbital plate with (d) in visceral aspect; (**e**, **f**) GIT 689-3 right anterior dorsolateral plate with (f) in visceral aspect; (**g**) GIT 689-5 median dorsal plate in visceral aspect; (**h**) GIT 689-7 left anterior ventolateral plate; (**i**) GIT 689-8 left anterior ventrolateral plate in visceral aspect; (**j**) GIT 689-9 left posterior ventrolateral plate; (a–j) all from the Gorodenka Brook locality; (**k**) GIT 117-5 right posterior ventrolateral plate from the Poruni River locality; (**l**) GIT 689-10 posterior median ventral plate from Värska drill core (at a depth of 220 m). All scale bars 10 mm.

armour. Two plates are from juveniles, a nuchal and a posterior ventrolateral, whilst the rest are from adult specimens.

TUG 1554-6 (Fig. 4a) is a nuchal plate of a juvenile *Coccosteus cuspidatus* (the nuchal plate is one of the most diagnostic plates in coccosteids). Miles & Westoll (1968) provided an in-depth description of various nuchal plates as they did for all the plates of the complete species. In comparison with Miles & Westoll's figures (1968, figs 3a–d and 4c, e, f), TUG 1554-6 has a blunt posteromedian cusp hardly protruding from the posterior margin (e.g. Miles & Westoll

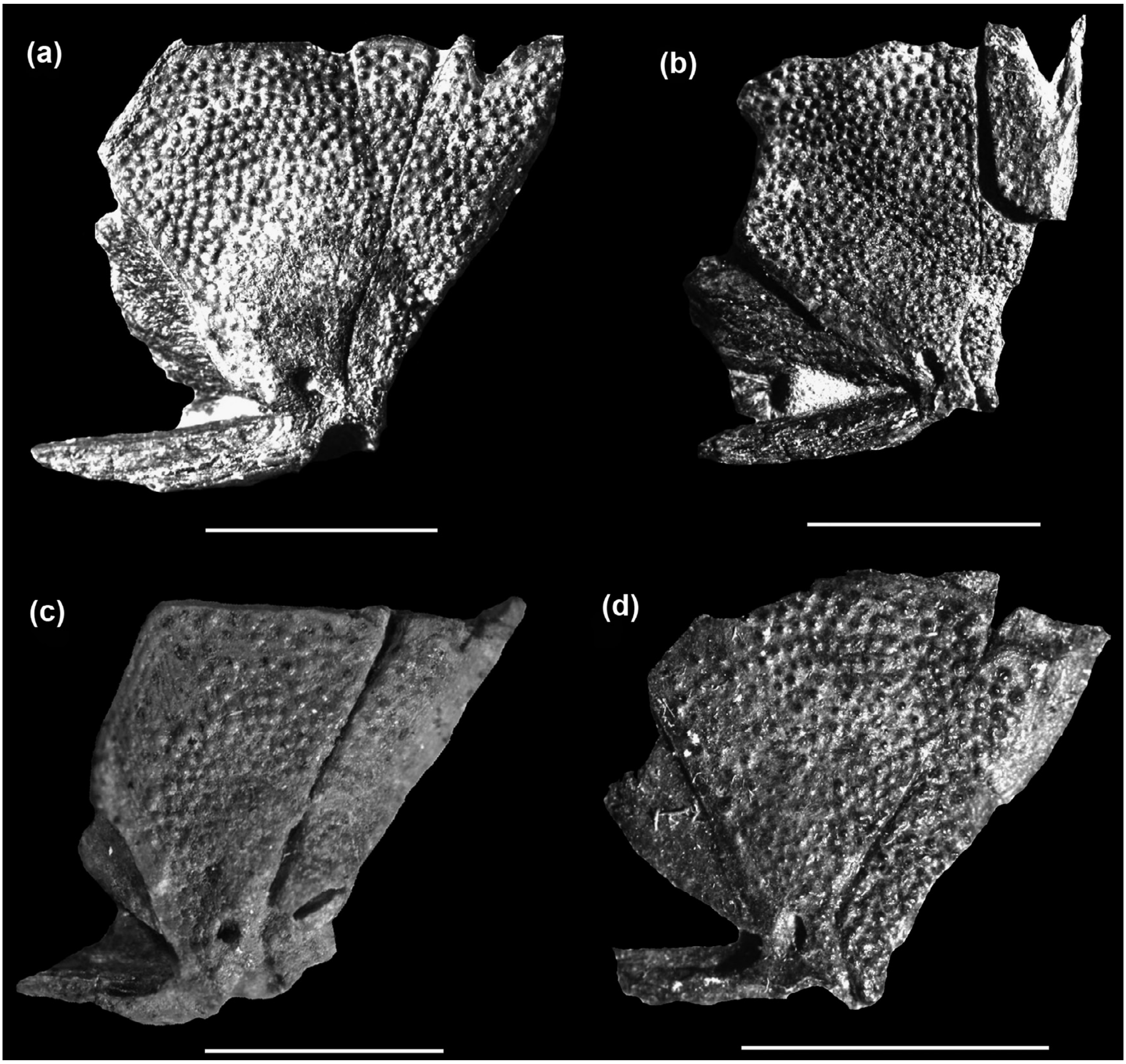


**Fig. 5.** *Millerosteus* paranuchal plates from Caithness, Scotland and Estonia: (**a**) NMS G.2014.4.4 *Millerosteus minor* from Pennyland, Caithness; (**b**) NMS G.2014.4.3 *Millerosteus minor* from Pennyland, Caithness; (**c**) GIT 561-1 *Millerosteus* cf. *minor* from Tarvastu, Estonia; (**d**) NMS G.2014.4.2 *Millerosteus minor* from Pennyland, Caithness. All scale bars 5 mm.

1968, fig. 4b). There are closely packed tubercles in the centre of TUG 1554-6 but very few on the lateral sides of the plate. Miles & Westoll (1968, fig. 4a) also state that the anterior margin of the nuchal plate of juveniles is convex rather than concave as seen in the adults. As well as being small, TUG 1554-6 has a convex anterior margin.

GIT 689-1 (Fig. 4b) represents a right central plate. In *Coccosteus cuspidatus*, central plates are highly variable (Miles & Westoll 1968, fig. 7). Although the anterior edge is slightly incomplete and posterolateral part is broken off in GIT 689-1, the overall morphology is very similar to *C. cuspidatus* plates from Scotland. GIT 689-1 has a long middle pit-line which is shorter than that shown in Miles & Westoll's (1968) figure 7g and the posterior pit line is probably as long as in figure 7c.

The suborbital plate GIT 689-2 (Fig. 4c, d) comes from the right side of the head. The plate in *Coccosteus cuspidatus* has only minor variation in outline shape (Miles & Westoll 1968, fig. 14). Comparison with Miles & Westoll's figure (1968, fig. 13a–d) show no differences to GIT 689-2, even to the position of the pit for cutaneous sensory cells on the outer surface.

The right anterior dorsolateral plate GIT 689-3 (Fig. 4e, f) is morphologically very similar to the reconstruction of the anterior dorsolateral plate of *Coccosteus cuspidatus* figured by Miles & Westoll (1968, fig. 30). There is a small degree of variation in this plate (Miles & Westoll 1968, fig. 31). Note the similarity of the lateral line system of GIT 689-3 compared with Miles & Westoll's (1968) figure 31h, showing in addition a supernumerary lateral line groove.

The median dorsal plate GIT 689-5 (Fig. 4g) is exposed from its visceral surface. The outline shape of this plate in *Coccosteus cuspidatus* is quite characteristic. GIT 689-5, when compared with Miles & Westoll's figure (1968, fig. 28a) of the visceral surface of *C. cuspidatus*, shows no discernible difference, despite the broken off carinal process.

The anterior ventrolateral plates GIT 689-7 (Fig. 4h) and GIT 689-8 (Fig. 4i, exposed in visceral aspect) both come from the left side. These specimens are very similar to the restorations of the anterior ventrolateral of *Coccosteus cuspidatus* figured by Miles & Westoll (1968, fig. 40). Still, the ventral sensory line groove is shorter in GIT 689-7 and does not reach the margins of the plate.

Two different posterior ventrolateral plates have been found. A larger left plate, GIT 689-9 (Fig. 4j), is incomplete at its anterior end and with the short spine at the posterolateral corner broken off. The mesial curved edge overlapped the right plate as was the common case in *C. cuspidatus* (Miles & Westoll 1968, fig. 41a). A band of larger tubercles runs parallel to the mesial margin. GIT 117-5 (Fig. 4k) is a slightly incomplete right posterior ventrolateral plate which is much smaller and with finer ornament than GIT 689-9. It is clearly a juvenile plate. When compared with Miles & Westoll's (1968, fig. 41a) restoration of a *C. cuspidatus* right posterior ventrolateral plate, it is virtually identical in morphology.

The posterior median ventral plate GIT 689-10 (Fig. 4l) shows no morphological differences to the specimens of *Coccosteus cuspidatus* figured by Miles & Westoll (1968, fig. 39d–f), except that the plate is a bit more rectangular.

Mark-Kurik (2000) also suggested that the coccosteid arthrodire genus *Millerosteus* was probably present in Estonia. This identification was confirmed by Mark-Kurik & Põldvere (2012). It is unfortunate that only a solitary paranuchal plate, GIT 561-1 (Fig. 5c), of *Millerosteus* is known from Estonia. Desmond (1974) provided the most recent detailed description of the Scottish species *Millerosteus minor*. However, he provided only one drawing of a paranuchal plate (fig. 1E) and so did not describe its variability. Figure 5a, b, d demonstrates the variability of this plate in the Scottish form, which, when compared with GIT 561-1, shows it is morphologically very similar to *M. minor*. However, without more Estonian material and a comprehensive study on the variability of *M. minor* in the Scottish material (something like Miles & Westoll's 1968 description of *Coccosteus cuspidatus*), we are unwilling to go above stating that GIT 561-1 probably belongs in *M. minor*. So, for the moment, GIT 561-1 must be considered *Millerosteus* cf. *minor* until new material is collected and a fuller description is made of the Scottish specimens of *M. minor*, particularly the variability of the individual plates.

## Stratigraphical conclusions

All the *Gyroptychius milleri* specimens from Estonia come from the Tamme Cliffs in the Kureküla Member, except GIT 365-203 which comes from the Aruküla Caves in the underlying Viljandi Member. Both these members are in the Aruküla Formation. The underlying Kernavė and Leivu formations have the coccosteid *Coccosteus cuspidatus*. The uppermost member of the Aruküla Formation, the Tarvastu Member, contains the coccosteid *Millerosteus* cf. *minor* (see Mark-Kurik & Põldvere 2012, fig. 3). This exactly mirrors the situation in Scotland where *G. milleri* is found between *C. cuspidatus* in the Achanarras Fish Bed Member and *Millerosteus minor* in the Mey Flagstone Formation (see Newman & Dean 2005, table 1). This is strong evidence for the direct faunal correlation between Scotland and Estonia. Other genera (rather than species) are also found in both regions, e.g. the arthrodires *Actinolepis, Homostius* and *Watsonosteus* (Newman & Trewin 2008; Newman 2010; Mark-Kurik & Põldvere 2012). Recently, the antiarch *Microbrachius* has also positively been shown to occur in both areas (Long *et al.* 2015). Finally, Scottish acanthodian genera (e.g. *Cheiracanthus* and *Diplacanthus*) have also been described from Estonia based on their scales (e.g. Valiukevičius 1998). Further detailed investigation of the fish fauna of Scotland and Estonia (plus closely related regions) is currently in progress by the authors and is likely to refine further the species correlation between the two regions.

## Acknowledgements and Funding

We would like to thank Uisdean Michie (Nottingham) for useful discussion on the Scottish stratigraphy and Gennadi Baranov (Institute of Geology, Tallinn) for photographing the specimens used in Figure 4. We would also like to thank Mark Dean (formerly of the British Geological Survey, Edinburgh) and Stig Walsh (National Museums of Scotland) for access to specimens in their care. We would also like to thank two anonymous reviewers and the handling editor Breandán MacGabhann for help in producing the final version of this article. This is a contribution to IGCP596: Climate change and biodiversity patterns in the mid-Palaeozoic (Early Devonian to Late Carboniferous).

*Scientific editing by Breandán Anraoi MacGabhann*

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# Geological Photo Feature

## Folding in Dalradian rocks, Portsoy, Aberdeen

An F3 asymmetrical fold in striped and laminated quartzose and micaceous psammites of the Dalradian 'Portsoy Group' (Easdale Subgroup), on the rocky headland to seaward of the swimming pool by Portsoy. The folds limbs are strongly attenuated and there is a weak axial planar cleavage developed. Possible early fold closures may be due to originally lenticular bedding.

Photo Tom Bain, BGS Photo P008615.


## Wave ripples, Stoer Group, Bay of Stoer

These wave ripples were developed in mudstones of the Stoer group.
The sediments were deposited in a rift environment, some 1180 Ma ago, and represent the oldest undeformed sedimentary rocks in Britain.

BGS photo P518652. 