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Contents

Part A. Geological and Taxonomic Background Information

1. Geological setting of the Essi Farm fossil site.

New *Microbrachius* material described herein comes from the Essi farm site in southern Estonia, from the Abava member of the Burtnieki Formation. The Abava Member is a stratigraphic unit in the Baltic area (NW of the East European Platform) that was previously thought to cross the Middle/Late Devonian boundary. Currently it is constrained to the Middle Devonian as the overlying Gauja Formation has yielded Middle Devonian miospores and higher plants, particularly *Svalbardia banksii* Matten (Jurina & Raskatova 2012, Mark-Kurik & Põldvere 2012). The Abava Member is about 20-30 m thick and consists of poorly cemented light coloured clastic rocks: fine-grained sandstone, siltstone and claystone, dominating in the upper part (Extended Data Figure 1; hereafter abbreviated as 'ED Fig.').

Fish fossils are fragmentary, characteristic for the Devonian of the Baltic area. The Abava Member exposures in the middle course of the Võhandu River have yielded a number of taxa which include: *Psammolepis abavica* Mark-Kurik, *Ganosteus stellatus* Rohon, *Psammosteus* sp., *Watsonosteus* sp., *Asterolepis essica* Lyarskaya, *Microbrachius* sp. cf. *M. dicki* Traquair, *Cheiracanthus* cf. *C. brevicostatus* Gross, *Cheiracanthus* sp., *Acanthoides*? sp., Chondrichthyes, *Glyptolepis* sp. *Laccognathus* sp., Dipnoi and *Cheirolepis gaugeri* Gross.

In the Essi farm section the uppermost white cross-bedded sandstone is exceptionally rich in fish microremains. There are a large number of isolated tubercles and small scale-like complex elements of *Psammosteus* sp. Tiny and delicate *Microbrachius* plates are common. Several *Microbrachius* plates showing better preservation came from the overlying red and violet claystone.

2. Identification of the Essi farm *Microbrachius* material.

Two of the authors (EMK, JAL) examined the complete collection of antiarch plates from Essi farm and agree that the assemblage belongs within the genus *Microbrachius* for the following reasons: plates are of typical *Microbrachius* shape and form closely resembling those of Microbrachius dicki, of very small size (for a Middle Devonian adult antiarch) and with characteristic sparse linear dermal ornamentation.. Hemmings (1978) defines the genus

as having a few key features that we also identify on the Essi specimens. These include the shape and proportions of the PMD plate (length/breadth index of 100, our specimen in ED Fig. 2C has l/br I of exactly 100; our PMD has 4-5 linear striae on each side of the dorsal lamina, whereas in *M. dicki* the PMD has similar number of lines (e.g. see Fig 2h, Eday Flags specimen). The Essi specimens show closer similarity to *M. sinensis* (Pan 1984) in having a longer posterior process on the PMD plate (Pan, 1984, pl.1 fig. 4). We are not confident of assigning the material to any species as the material is incomplete and has not been formally studied in detail, therefore we cannot compare complete head and trunk shield armours with the type species. We therefore assign the Essi farm material to *Microbrachius* sp. for the present. Some well-preserved examples of the plates are shown in ED Fig 1.

3. Geological setting of the Eday Flagstones *Microbrachius* material.

The Eday Flagstone Formation is an extensively studied series of rocks found throughout the Orkney Islands in northern Scotland (British Geological Survey 1999 and references therein). The formation is part of the Eday Group which is the uppermost unit of the Middle Old Red Sandstone (Givetian) of the Orkney Islands (ED Fig. 2). The Eday Flagstone Formation is a cyclic system with alternating bands of sandstones, siltstones and mudstones. The sedimentology is indicative of a fluvial-lacustrine environment (Trewin & Thirlwall 2002). The fish-bearing horizons are generally found in the flaggy mudstones which predominate in the lower part of the formation. The preservation of the fish is variable with the best preservation occurring in the more southern exposures, particularly in South Ronaldsay. The fish fauna consists of *Watsonosteus fletti*, *Pentlandia macroptera*, *Tristichopterus alatus*, *Microbrachius dicki* and rare *Asterolepis* remains. The fish are preserved in lacustrine deposits ranging from small oxbow lake-like deposits (generally devoid of *Microbrachius*) to large lakes that must have covered several kilometres. It is in one of these larger lake deposits in South Ronaldsay that the specimens of *Microbrachius* described here were collected. Further geological and palaeontological information on the Eday Flags can be found in Berry & Hilton (2006).

Part B. Further Discussion of antiarch reproductive structures

4. Structures possibly related to the pelvic girdle or reproduction in antiarch posterior ventrolateral (PVL) plates

During the course of this research we revisited the morphology of antiarch PVL plates to determine whether any structures that might be related to reproduction exist near the internal lamina of the subanal lamina of the PVL plate: the region where the *Microbrachius* claspers and *Microbrachius*, *Pterichthyodes* and *Bothriolepis* female genital plates elements have been found.

A specimen of *Yunnanolepis porifera* from the early Devonian Xitun Formation of China was newly prepared to show the internal features of the PVL plates for the first time in this basal group of antiarchs (ED Fig. 4a-c). *Parayunnanolepis*, a closely related genus, has a short PVL plate which is abutted posteriorly by the dermal pelvic girdle (Zhu *et al.* 2012).

In other antiarchs such as asterolepidoids and bothriolepidoids, dermal pelvic girdles are absent: the PVL plates extend posteriorly (as the subanal lamina) to occupy the same space as the pelvic girdles in yunanolepidoids (e.g., *Parayunnanolepis xitunensis*, Zhu *et al*. 2012). In sinolepidoids such as *Grenfellaspi*s and *Dayoushania* (Wang *et al.* 1992) the subanal lamina is also absent, so presumably separate pelvic bones might have been located posteriorly to the trunkshield as in *Yunnanolepis* and *Parayunnanolepis*. Either the dermal pelvic plates are fused to the PVL plates to form the subanal lamina in derived antiarchs, or the PVLs expanded posteriorly to form this lamina.

The dorsal surface of the posterior region of the PVL plates in *Yunnanolepis* show an unusual feature not seen in any other antiarch, the presence of a well-defined vertical ridge or lamina that borders the inner mesial area of the subanal lamina (ED Fig.4c, p.ri). In *Parayunnanolepis* the posterior margin of the PVL plates abuts a pair of small dermal plates interpreted as the dermal pelvic girdle bones, with the smaller triangular endogirdle sitting within. We suggest the possibility that these ridges could relate to either muscle attachments for pelvic or reproductive organ musculature, or to divide space within the trunk cavity for internal reproductive organs.

The subanal lamina on the specimens of *Bothriolepis* (ED Fig. 4 d-f) shows features not normally seen or preserved on other specimens. They suggest that there was a well-developed

platform (pl) in some specimens, possibly females, for resting the female genital plates as has been identified in *Bothriolepis* and illustrated in the paper (Fig. 2j-m). We also find possible muscle attachment scars (m.att?) and two well-defined ridges, inner (ri.i) and outer (ri.o) which could serve for partitioning or nesting of the reproductive structures (ED Fig 4e,f). This unusually complex posterior area of the ventral trunkshield suggests that there was some connection for musculature and positioning of cartilaginous elements that may have served in reproductive biology, especially so in view of the absence of the pelvic girdle and fin in this region.

5. Further support for internal fertilisation in antiarchs through growth series

Internal fertilisation in antiarchs is also supported from growth series. The minimum size of juvenile antiarchs can be deduced from presumed hatchery or nursery sites and from preserved antiarch embryonic armours. These are defined as small armours preserving yolk sac attachment spaces in the ventral armour, which lack a median ventral plate (Downs *et al.* 2011; other examples Upeniece & Upenieks 1992, Long *et al.* 1997, Young 1988). The smallest known *Bothriolepis* embryos have dermal armour of 11-18mm, implying juveniles of around 20-25mm total length: while there is no direct evidence of oviparity or viviparity, *Bothriolepis* embryos were thus approximately 18-25% of average adult body length, similar in size to those of confirmed viviparous placoderms, namely ptyctodontids (Long *et al.* 2008) and arthrodires (Long *et al.* 2009). The smallest recorded complete specimen of *Pterichthyodes* from the Middle Devonian of Scotland is 22 mm in armour length compared to estimated maximum adult armour size of 230mm (Hemmings 1978) which indicates a ratio of ~10% adult length in the presumed hatchling. This ratio also holds for *Asterolepis* from the Lode Quarry where juveniles have trunk armours 13-14mm long, indicating approximate total embryo length of ~20-22 mm (Upeniece & Upenieks 1992). In larval actinopterygians, the body is curled up to fit inside a small spherical egg, such that a 20mm salmon larva can fit inside a 5-6 mm diameter egg (Fleming & Gross 1990). Placoderms with developing long trunkshields could not necessarily curl up to sizes smaller than the minimum length of this dermal armour. This measurement therefore gives an estimated minimum egg length of around 13-15mm for most of the antiarch species discussed above. This is large, at least double the maximum known egg diameter for typical externally spawning fishes; forms with larger eggs typically have adaptations such as mouthbrooding for aerating these eggs

(Bonislawska *et al.* 2001). For the Atlantic salmon (*Salmo salar*) egg size can vary between 5.5-6.6mm in adult fishes which are on around 70-80 cm in average and 1.5m in maximum length (Aulstad & Gjedrem 1973). Thus in this typical spawning fish, where eggs are relatively large due to their aerobic environment, the ratio for egg diameter to adult length is less than 0.01, compared with an estimated ratio between 0.18-0.25 for antiarch placoderms. The large absolute and relative size of these antiarch hatchlings is inconsistent with reproduction via typical spawning and external fertilisation; it is more likely that young *Bothriolepis* emerged from larger eggs permitted by internal fertilisation and prolonged egg retention (or even viviparity), similar to those of modern chondrichthyans.

6. Copulatory Ability and Clasper Growth in *Microbrachius*

The large immobile L-shaped claspers of *Microbrachius* imply that the males must have copulated by laying side by side with the female and then moving back on an angle slightly to swing the clasper around into the female cloacal area. In this mating position only the distal end of the clasper would have interlocked with the tuberculated small dermal plates resting on or behind the subanal lamina of the PVL plates, presumably within the cloacal chamber. The coarsely spinose dermal ornamentation on the ventral surface of the larger claspers could have served to stabilise the clasper on the tuberculated plates during mating. We suggest that the well-developed hooks and spines along the mesial edge of the distal segment of the pectoral appendage might also have been used to hold the male and female together when jostling for the correct mating position (Fig. 3e, main paper). This could have been a prime function for the pectoral appendage of antiarchs, the use of which has long been debated. The hook-shaped claspers in ptyctodontid placoderms might have functioned in much the same way as in Microbrachius. If this hypothesis is correct then arthrodires, having straight claspers like chondrichthyans, would have been the first gnathostomes capable of mating in an inverted face to face position, as in some chondrichthyans.

Observation of the known sample of males with claspers suggests the claspers were in various stages of growth (ED Fig. 3). This suggests the possibility that the males grew the claspers rapidly with the onset of puberty prior to mating. The development and growth of the gonopodium in teleost fishes is regulated by increased levels of testosterone (Offen et al. 2013) and something similar could be predicted in antiarch males. We also note that as *Microbrachius* has been found from several localities throughout the Middle Old Red

Sandstone of Scotland (eg Exnabrae, Orkneys, John OGroats, Shetland etc), but only our specimens from the South Ronaldsay site in the Orkneys (Eday Flags) have claspers. This material possibly represents either a unique environmental setting or precise annual timing for mating when the carcasses were buried.

PART C. PHYLOGENETIC ANALYSIS

7. Data and methodology

To test the support for placoderm monophyly in the expanded dataset, searches were performed in PAUP* with placoderms constrained to be monophyletic. This resulted in 2391 trees of length 645, 5 steps longer than the most parsimonious tree. The difference was not significant under the Templeton nonparametric test (P >0.4), though it should be noted that this test has low power (Lee 2000), a problem exacerbated by missing data in fossils. In this tree, a monophyletic Placodermi is sister to all other gnathostomes, and antiarchs are the sister to all other placoderms.

7.1. Expanded Matrix

Phylogenetic Analysis. We expanded the most recent data matrix of gnathostomes (Dupret et al 2014) by adding 14 placoderm taxa (*Remigolepis, Sinolepis, Microbrachius, Eurycaraspis, Quasipetalichthys, Diandongpetalichthys, Wuttagoonaspis, Aethaspis, Holonema,, Groenlandaspis, Compagopiscis, Incisoscutum, Eastmanosteus* and *Dunkleosteus*).

Three additional characters (256-258) were also added, and one character (122) was split into two (122, 259) as discussed below. The expanded matrix thus included 259 characters and 91 taxa (85 taxa after deletion of poorly known placoderms; see below).

Character 256: Central dermal skull bone (nuchal) with converging posterior pit-line canals and supraorbital canals (absent 0; converging but not meeting 1; crossing as an X in bone, 2). This character is only applicable in taxa with a nuchal bone. This character is characteristic of ptyctodontids and petalichthyids where the main lateral line canals converge to form an X in the centre of the nuchal plate. In some cases they converge, but do not meet (as in *Brindabellaspis*, phyllolepids, and some petalichthyids like *Macropetalichthys*).

Character 257: Deep, high supragnathal bone with durophagous occlusal surface (absent 0; present 1). This character is only applicable in taxa with a supragnathal bone. This feature is found in all known ptyctodontids where the dentition is preserved. No other placoderm group shows similar robust morphology of the supragnathal plates.

Character 258: Intromittent organ (‘clasper’) includes one large J-shaped element (absent 0; present 1). This character is only applicable in taxa with claspers. Only ptyctodontids show multiple dermal bones comprising the claspers, with a single large J-shaped element and two additional distal denticles-bearing plates. The J-shaped element (Fig 1e) is the largest element of the three dermal units (Miles & Young, 1977). This character is coded based on a new review of placoderm pelvic girdles and claspers which shows the presence of bony claspers in a number of arthrodires including *Coccosteus*, *Millerosteus*, *Incisoscutum* and *Compagopiscis* (Trinajstic et al., 2014). Using this information we have coded certain placoderms as having claspers ‘present’ where previously they were unknown (hence our revised coding for character 122 as well). In addition we recoded characters for *Buchanosteus* relabelled as *Parabuchanosteus* following a major review of this group of arthrodires based on new material from the Early Devonian of Australia and the USSR (Long et al. 2014).

Given the extensive anatomical and topological differences between placoderm claspers and chondrichthyan claspers (Trinajstic *et al*. 2014), character 122 in Dupret *et al.* (2014: see also Brazeau 2009) - “claspers present/absent” - was split into two separate characters (122, 259 below). This coding assumes *a priori* that the claspers in placoderms and chondrichthyans are non-homologous. However, even if the very different placoderm and chondrichthyan structures were treated as potentially homologous (by coding them as the same derived condition in a single character, *sensu* Brazeau 2009; Dupret *et al.* 2014), this did not change tree topology or inferred optimisation (the derived states in placoderms and chondrichthyans still emerged as non-homologous).

Character 122 - modified: Intromittent organ (‘clasper’) containing bone, not associated with pelvic fins. Absent - 0, present - 1.

Character 259: Intromittent organ (‘clasper’) consisting entirely of cartilage, formed from distal part of pelvic fin. Absent - 0, present - 1.

All characters were treated as unordered, as in earlier versions of this matrix (e.g. Zhu et al. 2013). Parsimony analyses used PAUP* (Swofford, 2003), with most parsimonious trees (MPTs) found via heuristic searches involving 1000 random addition searches followed by a strict and a majority-rule consensus; bootstrapping was performed with 200 replicates followed by a majority-rule consensus. All compatible groupings were included in the

majority-rule consensus trees (LE50=YES); thus, all majority-rule clades were retrieved even if found in less than 50% of trees.

Two agnathan taxa (Galeaspida and Osteostraci) were included as outgroups, with Osteostraci set as the furthest outgroup as per Dupret *et al*. (2014). Bremer support was calculated using reverse constraint commands generated by Treerot (Sorenson & Franzosa 2007), with heuristic searches modified to use the above search strategies.

In order to prevent any search from being trapped on islands with large numbers of MPTs, NCHUCK was set to 1000 and CHUCKSCORE needs to be set to any number far shorter than the most parsimonious tree length (we set it to 1). These settings allow PAUP to more effectively find and sample the pool of most parsimonious trees: it will sample no more than 1000 trees from each tree "island", and thus will not fill all available memory by retaining millions of trees from a single island. An indication of the effectiveness of this strategy is that, in the re-analysis of the original dataset (Dupret et al. 2014), our searches found most-parsimonious trees that were shorter than, and quite different from, the trees found in their original analysis (see results).

Analyses with all 91 taxa resulted in weak resolution in many areas of the tree (especially among placoderms) due to the unstable position of rogue taxa; accordingly, placoderms with >75% missing data (unknown or inapplicable) were omitted from subsequent analyses: *Sinolepis, Gavinaspis, Sigaspis Parayunnanolepis, Quasipetalichthys,* and *Diandongpetalichthys.* These results (for a dataset of 259 characters) are consistent with simulated results using datasets of 100 and 500 characters, which showed a sharp drop in phylogenetic accuracy for taxa with between 60% and 80% missing data (Wiens 2003). Although *Microbrachius* has >75% missing data, it is a key taxon in this study and was thus retained. These 85-taxon analyses (83 gnathostomes and 2 agnathan outgroups) had much improved resolution.

Optimisation of claspers. Characters 122 and 259 above, relating to unequivocal evidence of internal fertilisation, were optimised on both the majority-rule and strict consensus trees for the 85-taxon dataset, under both acctran and deltran, using PAUP and Mesquite (Maddison & Maddison 2011). The majority-rule tree was fully resolved and happened to be one of the primary (ie most parsimonious) trees, so it could be considered to be the "most typical" of the pool of most parsimonious trees and the most suitable single tree on which to interpret character evolution. Although the strict consensus tree is usually a suboptimal tree,

and thus optimising characters on such trees can be inadvisable, the soft polytomies did not affect the character of interest; optimisation of this character on the strict consensus accordingly produced the same result.

We ran a further analysis changing the coding of character 259 to "unknown" rather than absent in *Cladoselache,* given the potential uncertainty in this taxon. The presence of claspers in *Cladoselache* was reviewed at a Society of Vertebrate Paleontology presentation (Maisey, 2008), which was attended by JAL, and discussed recently with Dr. J. Maisey (pers. comm. 2014). It was concluded that presence of claspers in this genus should be considered equivocal, based on an unpublished specimen in the Buffalo Museum plus a poorer, ambiguous earlier record (Hussakof & Bryant 1918).

The expanded data matrix can be found in Supplementary Information file 2, along with all PAUP search, Bremer and bootstrap commands, and exclusion taxon sets (for unstable taxa deleted in analyses of the expanded dataset).

7.2. Original Matrix (Dupret *et al*. 2014).

Because the analysis of the expanded data matrix yielded rather different tree topologies to those published in Dupret *et al.* (2014), we re-analysed the original dataset, to investigate whether the published trees were actually the correct trees for their dataset. Analysis of this matrix, using the same PAUP settings discussed above, yielded shorter trees which were quite different to those published in Dupret *et al.* (2014), and much more similar to those we retrieved in our expanded data matrix. However our analyses do not change the main phylogenetic conclusion from that paper, that 'posterior-nose' placoderms are basal.

The original data matrix (Dupret *et al.* 2014) can be found in Supplementary Information file 3, along with the PAUP search, Bremer and bootstrap commands used in the present analysis.

8. Results

8.1. Expanded Matrix

Phylogenetic analysis. The analysis of the expanded dataset (85 taxa after deletion of 6 wildcard taxa), found 7039 most-parsimonious trees of length 640 (because not all trees

are always sampled on large tree islands, re-running the analysis would sample a slightly different number of trees). The strict and majority-rule trees are shown in ED Figs. 5 and 6. Bremer and bootstrap support are shown for all clades in the strict consensus. The results support the paraphyly of placoderms with respect to crown gnathostomes (osteichthyans plus the acanthodian-chondrichthyan clade), and antiarchs as the sister to all other gnathostomes (i.e. the most basal clade on the gnathostome stem); both these results are consistent with most recent analyses (e.g. Brazeau 2009; Davis *et al*. 2012; Zhu *et al*. 2013; Dupret *et al.* 2014). Ptyctodontids are low on the gnathostome stem and thus not particularly closely related to crown gnathostomes, while arthrodirans (see Carr & Hlavin 2010) are the closest "typical" placoderm relatives of crown gnathostomes. The analysis finds the Silurian genus *Entelognathus*, which combines "typical placoderm" characters of the dermal skeleton and braincase with osteichthyan-like marginal jaw bones, within crown gnathostomes (as sister to osteichthyans), rather than the sister group of all crown gnathostomes (Zhu *et al.* 2013), or even below ptyctodontids on the gnathostome stem (Dupret *et al.* 2014). All sampled acanthodians are placed as stem chondrichthyans (*contra* Davis *et al.* 2012), but as a paraphyletic assemblage (Zhu *et al.* 2013), rather than a monophyletic group (Dupret *et al.* 2014). Phenetic similarities between acanthodians and chondrichthyans were documented by Davis *et al*. (2012), but that study dispersed acanthodians across the chondrichthyan, osteichthyan and gnathostome stems.

Optimisation of claspers (characters 122, 259). Bony claspers independent of the pelvic fin (122), and thus internal fertilisation, are acquired at the base of gnathostomes; they are most parsimoniously inferred to have been present in all stem gnathostomes (ie in placoderms), and are lost in the most recent common ancestor of crown gnathostomes (2 steps). Cartilaginous claspers consisting of modified pelvic fins (259) are acquired near the base of chondrichthyans but lost in *Cladoselache* (2 steps). If evolution of claspers and internal fertilisation is assumed to be irreversible (ie no losses permitted), there would be 7 implied changes: 3 acquisitions of body claspers (122) within placoderms (antiarchs, ptyctodonts, and arthrodires) as well as 4 separate acquisitions of cartilaginous claspers (259) within chondrichthyans (*Orthacanthus*, *Cobelodus*, *Akmonistion*, and the clade including *Tristychius*, *Chondrenchelys*, *Debeerius*, *Hamiltonichthys* and *Onychoselache*). However, the similarity of claspers across placoderms is more consistent with a single origin (with implied reversal); the same argument also applies to chondrichthyans. As all known living male chondrichthyans bear claspers it is likely that fossil chondrichthyans also had them,

even if the fossils of taxa do not show them preserved (likely due to lack of large numbers of specimens). Furthermore, the implied reversal in chondrichthyans might not be required, given that absence of claspers in *Cladoselache* is unresolved (i.e. questionable, see above). As expected, changing the coding of character 259 in *Cladoselache* to ? (rather than 0) did not change the retrieved tree topologies, but reduced tree length by 1 through removing the implied loss of cartilaginous claspers within chondrichthyans (*Cladoselache* when coded as ? is most parsimoniously reconstructed as retaining bony claspers).

8.2. Original Matrix

Reanalysis of the original matrix of Dupret *et al.* (2014) found 808 trees of 611 steps, and the strict and majority-rule consensus trees are shown in ED Figs. 7 and 8. Bremer and bootstrap support are shown for all clades in the strict consensus. The published trees (Fig. 1 and ED Figures 1 and 2 in Dupret *et al*., 2014) were 614 steps long and thus not the most parsimonious trees for this dataset; bootstrap and Bremer supports were not presented.

There are notable differences between the trees found here, and the (longer) trees presented in Dupret *et al.* (2014): thus, some unexpected clades proposed by them appear to be analytic artefacts. First, ptyctodontids are here placed in a much more conventional position deep amongst placoderms (Goujet & Young 1995; Brazeau 2009), rather than as sister-taxon to crown gnathostomes. *Entelognathus* is here placed within crown gnathostomes (as sister to osteichthyans) rather than below ptyctodontids on the gnathostome stem. We note that braincase and palatoquadrate morphology of this taxon clearly distinguish it from the Osteichthyes, and we suggest its position on the tree could be also be an artefact caused by the absence of dermal jaw bone characters for chondricthyans and acanthodians. Finally, acanthodians are broadly paraphyletic with respect to chondrichthyans, rather than their monophyletic sister group.

In all these topological relationships, the trees found here shown in ED Figures 5,6 closely resemble the trees found in the expanded dataset (see above), as would be expected given the minor modifications implemented.

Part D. References

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