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Copulation in antiarch placoderms and the origin of gnathostome internal fertilization

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Reproduction in jawed vertebrates (gnathostomes) involves either external or internal fertilization[1]. It is commonly argued that internal fertilization can evolve from external, but not the reverse. Male copulatory claspers are present in certain placoderms[2–4], fossil jawed vertebrates retrieved as a paraphyletic segment of the gnathostome stem group in recent studies[5–8]. This suggests that internal fertilization could be primitive for gnathostomes, but such a conclusion depends on demonstrating that copulation was not just a specialized feature of certain placoderm subgroups. The reproductive biology of antiarchs, consistently identified as the least crownward placoderms[5–8] and thus of great interest in this context, has until now remained unknown. Here we show that certain antiarchs possessed dermal claspers in the males, while females bore paired dermal plates inferred to have facilitated copulation. These structures are not associated with pelvic fins. The clasper morphology resembles that of ptyctodonts, a more crownward placoderm group[7,8], suggesting that all placoderm claspers are homologous and that internal fertilization characterized all placoderms. This implies that external fertilization and spawning, which characterize most extant aquatic gnathostomes, must be derived from internal fertilization, even though this transformation has been thought implausible. Alternatively, the substantial morphological evidence for placoderm paraphyly must be rejected.

Among living fish (non-tetrapod vertebrates) internal fertilization is mostly effected by copulatory structures representing modifications of the pelvic fins (chondrichthyans[9]) or anal fins (the gonopodium of some teleost fishes[10,11]). The discovery in arthrodiran[3] and ptyctodont placoderms[2,4] of copulatory structures (claspers) originally[3,12] but incorrectly[4] interpreted as modified pelvic fins implied that any placoderms lacking pelvic appendages would have also lacked claspers, and therefore reproduced externally by spawning. This was thought to be the case with the antiarchs, recently considered the sister group of all other jawed vertebrates[5–8]. Deposits where small antiarch juveniles suffered mass mortality have been interpreted as nurseries associated with mass spawning events[13].

Microbrachius, a small bothriolepidoid antiarch, is known from complete articulated specimens from the Middle Devonian (Givetian) period of Scotland[14], the Early–Middle Devonian of China[15,16] and by isolated plates from the Essi Farm site in Estonia (Extended Data Figs 1 and 2 provide geological background for sites of specimens described herein). Numerous new articulated specimens from the Eday Flags, Orkney Islands, Scotland, UK, show either male dermal claspers or female genital plates in life position (Figs 1 and 2 and Extended Data Fig. 3), and one specimen from Estonia shows an isolated right posterior ventrolateral (PVL) plate with an attached dermal clasper (Fig. 1a–c) (Supplementary Information A1 and A2 and Extended Data Figs 1 and 2).

The clasper of *Microbrachius* is a deeply grooved dermal bone (Fig. 1a–c, h–m) that curves laterally, similar to the main hooked dermal clasper element of ptyctodontid placoderms[2,4]. The groove (gr, Fig. 1l, m) may have served to transfer sperm, or encased a structure that carried the sperm canal. The articulated specimens show some of the claspers in mesial contact, sutured in the midline (Fig. 1i, k) indicating they were not mobile. The extended wing of the clasper extends laterally as far as the width of the trunkshield (Fig. 1h, j, k), potentially enabling a male *Microbrachius* clasper to reach the cloaca of a female if the two individuals were side by side (Fig. 3). Ventrally the claspers have well defined dermal ornamentation of small posteriorly directed spines, and have a series of larger spines along the distal margin (Fig. 1i, m). Variation in clasper size probably reflects individual sexual maturity (Extended Data Fig. 3).

Female *Microbrachius dicki* (Figs 2e–g and 3a, b) show paired blade-like structures in the same region corresponding to the male clasper (Fig. 2g). These blades carry a distinctive ornament of curving ridges and marginal tubercles on their dorsal (that is, internal) surfaces: the only internally facing ornament in their dermal skeleton. Identical internal ornament is seen in *Pterichthyodes*[14], where it occurs on separate dermal plates preserved atop the dorsal (internal) side of the subanal lamina of the PVL plates (Fig. 2a–d) in similar position as the male claspers. Within other placoderms, where separate male and female dermal elements are known, they are similarly positioned[2,4]. These dermal plates are flat and taper to meet the lateral ends of the transverse ventral ridge inside the lateral lamina of the PVL plate (Fig. 2f–h). We interpret these structures in *Microbrachius* and *Pterichthyodes* as female genital plates, similar to the post-pelvic plates found in some female ptyctodonts[4], and suggest that the claspers attached to them during mating by gripping the internal ornament which faced into the cloacal chamber (Fig. 3e and Extended data Fig. 9).

Two specimens of the Late Devonian antiarch *Bothriolepis* also show small semicircular plates sitting on the distal area of the subanal lamina of the PVL plates (Fig. 2h–j). They are only visible in dorsal view, and show a slight thickening anteriorly with a line of roughened pits for ligamentous or muscle attachment near the anterior margin. We interpret these as female genital plates as they do not resemble male claspers in *Microbrachius*, and occupy the same topology as the paired genital plates in female *Pterichthyodes*. We also identify new features on the subanal lamina of the PVL plates in other antiarchs, which probably relate to their reproductive anatomy (Extended Data Fig. 4 and Supplementary Information B4).

We thus have compelling evidence for a clasper-based system of internal fertilization in *Microbrachius*, strong circumstantial evidence for the same system in *Pterichthyodes* and plausible evidence for the

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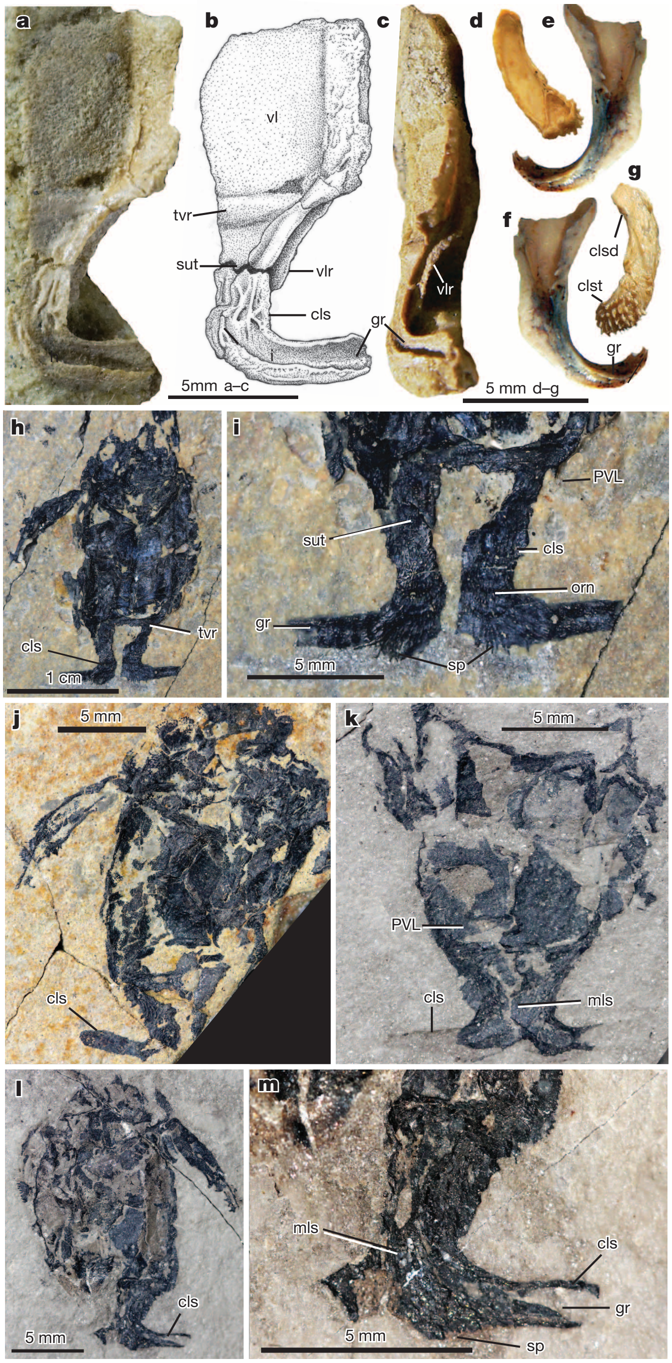

Figure 1 | Male reproductive structures in antiarchs and ptyctodontids. **a**–**c**, *Microbrachius* sp. right PVL plate, GIT 628-24 in (**a**) dorsal view, (**b**) interpretive drawing and (**c**) lateral view. **d**–**g**, Dermal clasping elements of ptyctodont *Austroptyctodus gardineri*, NHMUK PV P57665; **d**, dermal hooked elements in dorsal and ventral (**g**) views; **e**, large hooked dermal element in ventral view; **f**, reversed image. **h**–**m**, Male *M. dicki* specimens showing claspers with close-up views of some specimens. **h**, **i**, NHMUK PV P73397; **j**, NHMUK PV P77402; **k**, NHMUK PV P77401; **l**, **m**, NHMUK PV P77405. Abbreviations: cls, dermal clasping elements; clsd, distal clasping element; clst, terminal hooked clasping element; gr, groove; mls, midline suture; orn, ornament; PVL, posterior ventrolateral plate; ri, ridge; sp., spines; sut, suture between clasper and PVL; tvr, transverse lateral ridge; vl, ventral lamina; vlr, ventrolateral ridge.

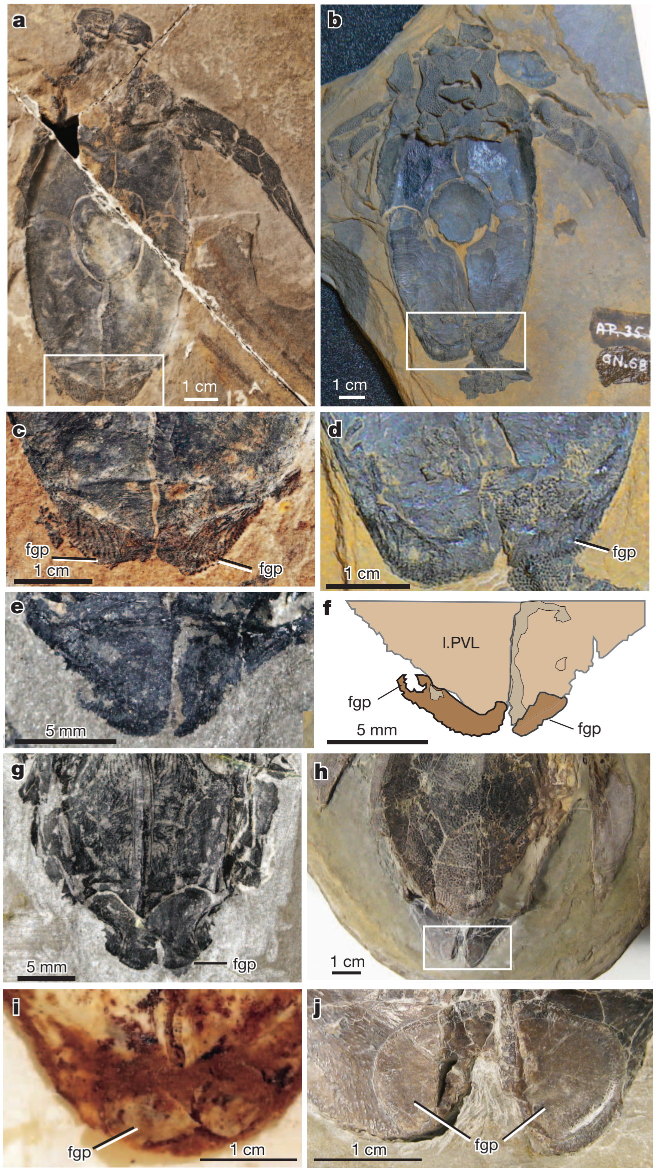

Figure 2 | Female reproductive structures in Middle–Late Devonian antiarchs. **a**, **c**, *Pterichthyodes milleri*; NHMUK PV P32544; **b**, **d**, UMZC 687. **e**–**g**, *M. dicki*; **e**, **f**, NHMUK PV P73398; **g**, NHMUK PV P73399. **h**, **i**, *Bothriolepis canadensis*, V11127 (Smithsonian), showing armour (**h**) and female genital plates (**i**). **j**, *Bothriolepis* sp. ANU V1040, close up of paired female genital plates. Abbreviations: fgp, female genital plates; l.PVL, left posterior ventrolateral plate.

same in *Bothriolepis*. Although male claspers have not been described in antiarchs other than *Microbrachius*, even from taxa such as *Bothriolepis*[17,18], *Asterolepis*[19] and *Remigolepis*[20] known from hundreds of articulated specimens with tails preserved, we suggest that internal fertilization is general for the Antiarchi. As the dermal skeleton is quite reduced in advanced antiarchs, we propose that the claspers in some forms might have also been cartilaginous and thus not well preserved. Further evidence for internal fertilization in antiarchs comes from their large hatchlings[13] (Supplementary Information B4).

The clasper in *Microbrachius* is clearly different from the pelvic girdle and fin, known only in one antiarch: *Parayunnanolepis* from the Early Devonian of China[21]. More derived asterolepidoid and bothriolepioid antiarchs lack pelvic girdles and fins, which are thus assumed to be lost (secondarily absent) in these groups[19]. In chondrichthyans, the clasper is attached to the posterior extremity of the pelvic fin metaptyerygium[9,22,23]. In ptyctodont and arthrodire placoderms, the clasper is immediately posterior to the pelvic fin[4], and has previously been interpreted as an elaboration of the pelvic fin skeleton[2,3]. However, new evidence shows that the clasper of arthrodires does not articulate directly with the pelvic girdle or fin[4]. In ptyctodonts the endoskeleton of the clasper (if present)

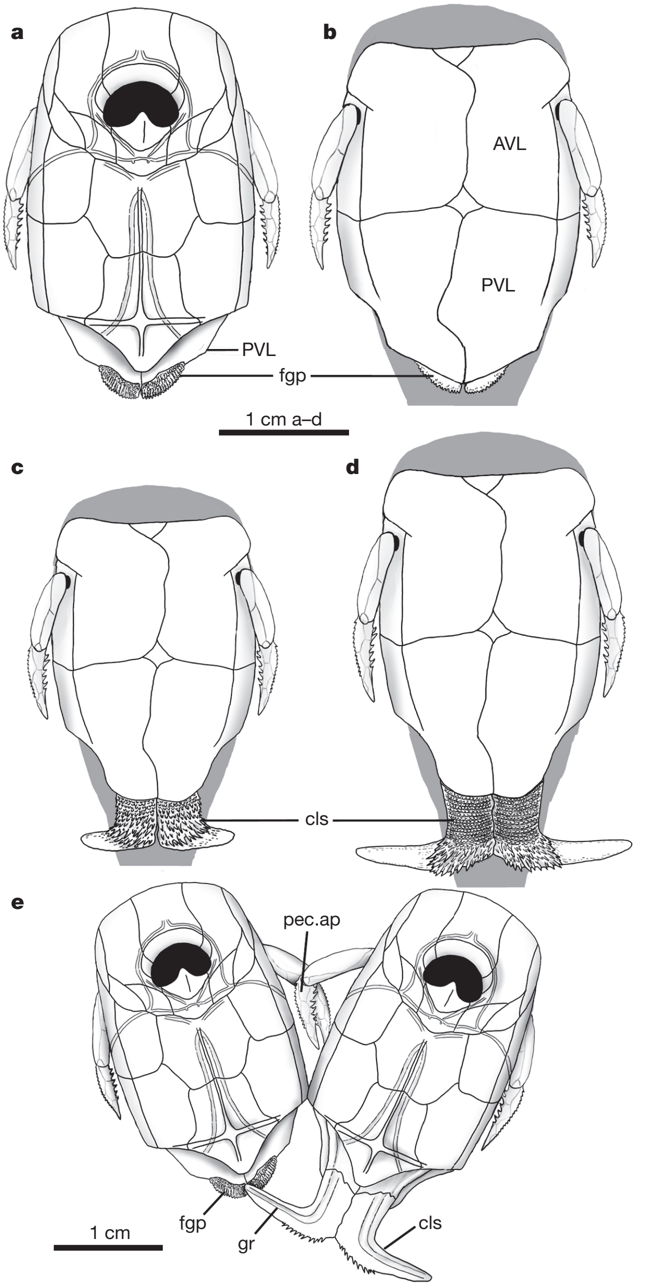

Figure 3 | Male and female sexual dimorphism in *M. dicki*. Reconstruction of female *M. dicki* in (**a**) dorsal and (**b**) ventral views; **c**, **d**, male *M. dicki* ventral views showing variations in clasper development; **e**, hypothetical mating position for *Microbrachius*. Abbreviations as for Figs 1 and 2 plus pec.ap, pectoral appendage.

was unossified[12], making it more difficult to determine its precise relationship to neighbouring structures, but the dermal components of the claspers are consistently preserved some distance posterior to the pelvis[2,4,12]. All known placoderm claspers thus differ from chondrichthyan claspers in being independent from the pelvis and pelvic fin. The principle dermal element of the ptyctodont clasper is a large curved, grooved plate (Fig. 1e, f) that distinctly resembles and is thus probably homologous to the dermal clasper of *Microbrachius*, whereas arthrodire claspers have a much smaller but plausibly homologous dermal bone tip[3,4]. Based on similarities in position (behind and independent of pelvic region), and materials (dermal bone), the claspers of antiarchs, ptyctodonts and arthrodires are most probably homologous with each other, but not homologous with the claspers of chondrichthyans.

To evaluate the evolution of claspers and reproductive biology across gnathostomes, we expanded upon a recently published phylogenetic analysis[8] with the addition of 14 placoderm taxa, three new characters (256–258), and one character (122) split into two (122, 159) (Supplementary Information C7, 8). Our analyses of both expanded and original data sets yielded very similar trees, which supported placoderm paraphyly and placed antiarchs as the sister group to all other gnathostomes (Extended Data Figs 5 and 6 and Supplementary Information C7, 8). Our analyses found shorter trees for the original data set[8], supporting a more orthodox position for ptyctodonts lower on the gnathostome stem (Extended Data Figs 7 and 8 and Supplementary Information C8). The shortest tree indicates that bony claspers separate from the pelvic fin arose in the most recent common ancestor of jawed vertebrates and were lost in the most recent common ancestor of crown gnathostomes (Fig. 4 and Extended Data Figs 5 and 6).

These results have intriguing biological implications. The implied loss of bony claspers and implied reversion to external fertilization in crown gnathostomes appears heterodox: loss of internal fertilization and acquisition of external fertilization is not widely accepted, at least

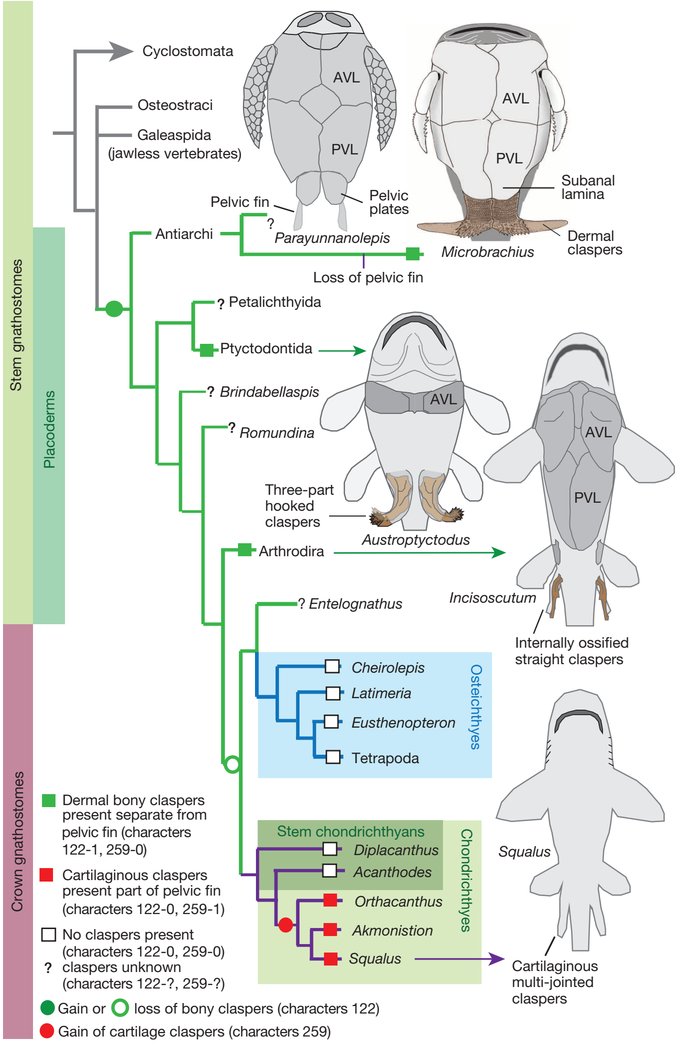

Figure 4 | Phylogeny of major lineages of gnathostomes, based on analysis of an expanded version of the data set from ref. 8. Distribution and morphology of two kinds of clasper are mapped on the phylogeny. Claspers are most parsimoniously inferred to have evolved in the most recent common ancestor of all gnathostomes, then lost before or at the node of crown group gnathostomes. Claspers developed as a modified part of the pelvic fin skeleton appear as a synapomorphy of all chondrichthyans. The full tree with branch supports and states for all terminal taxa is shown in Extended Data Figs 5 and 6. See Supplementary Information for further details of the analysis.

in vertebrates[1,11] although it could have happened multiple times in invertebrates[24]. The shared, unique morphology and post-pelvic position of claspers in all placoderms is more consistent with a single origin, and thus represents a potential synapomorphy supporting placoderm monophyly[25].

If all placoderm claspers are homologous, as we suggest, this gives rise to alternative implications with equally startling significance for early vertebrate evolution. If placoderm paraphyly is accepted, on the basis of the optimal trees here (and consistent with the majority of recent analyses[5–8]), then external fertilization and spawning employed by the majority of recent bony fishes and many lissamphibians must have evolved from clasper-mediated internal fertilization. If claspers are accepted as *prima facie* evidence of placoderm monophyly[25], the transformation of cranial architecture within the Placodermi documented by several recent analyses[5–8] must be entirely convergent on crown gnathostomes, as the antiarchs belong to the cluster of primitive placoderms with posteriorly placed rostronasal capsules and a trabecular 'upper lip'[8]. Placoderm monophyly is also inconsistent with the co-occurrence of placoderm and osteichthyan characteristics in Silurian taxa such as *Entelognathus*[7]. Resolution of the status of placoderms, which will require data both from fossil anatomy and the reproductive physiology of extant fishes, is one of the most pressing tasks currently facing early gnathostome palaeontology.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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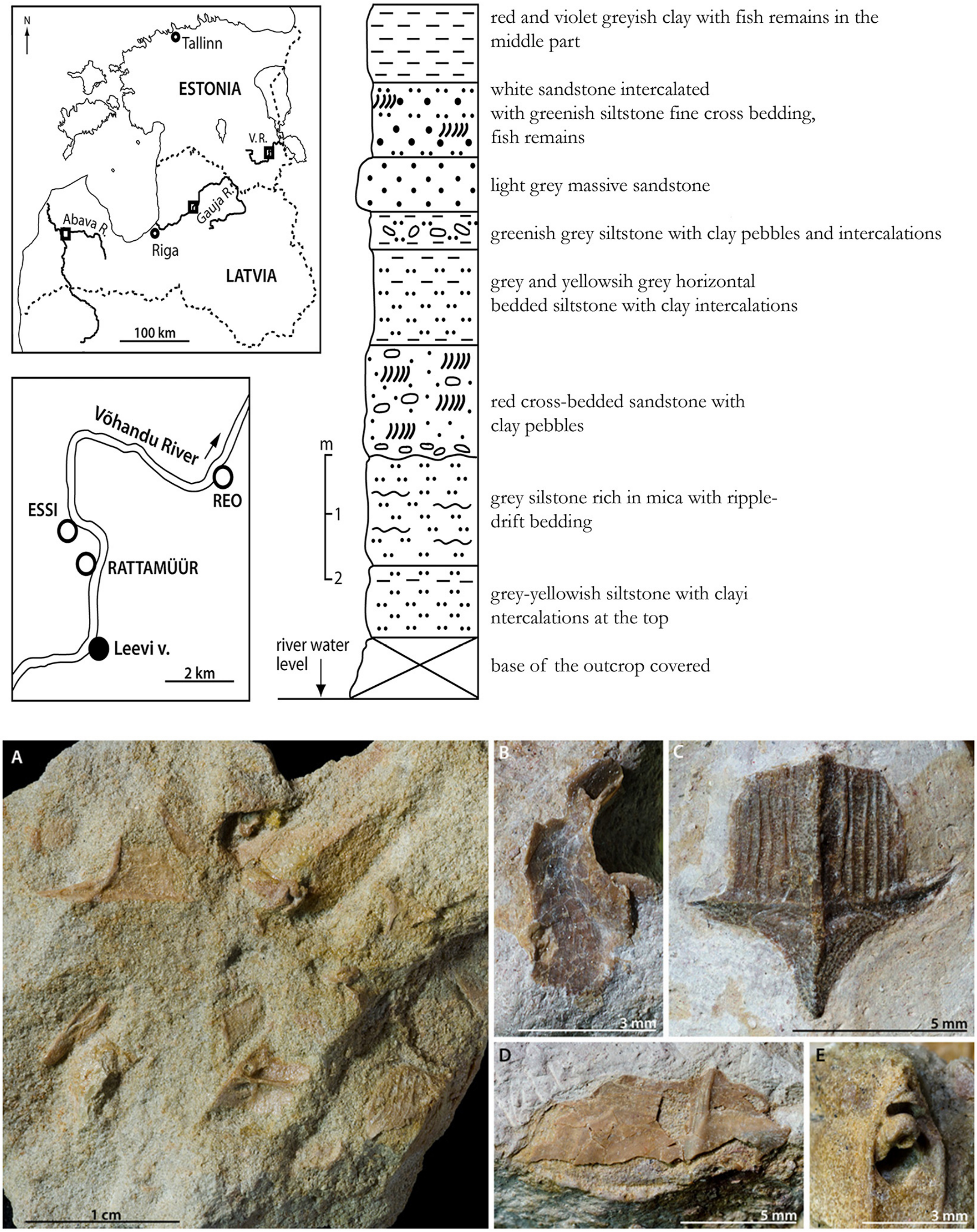
Author Contributions The project was designed by J.A.L., with material examined and described by J.A.L., E.M.K., Z.J., K.T., B.C. and P.E.A. M.S.Y.L. performed phylogenetic analyses with input from J.A.L., G.C.Y. and B.C. M.N., J.D.B. and R.J. collected and prepared material, provided site information and input to the discussion. Illustrations were made by J.A.L. and B.C. with photography supplied for some specimens by the Natural History Museum, London, and by the Institute of Geology at Tallinn University of Technology. All authors contributed to data interpretation, figures and writing of the paper.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to J.A.L. (john.long@flinders.edu.au).



Extended Data Figure 1 | Location and stratigraphic position of Estonian specimens of *Microbrachius*. Top, map showing locality of the Essi Farm site, Estonia, and stratigraphical section where the fossils were found. Modified from ref. 26. Below, *Microbrachius* sp. plates from Essi Farm, Estonia. **a**, GIT 628-37, sample showing several small plates and fragments; **b**, GIT 628-9, right lateral plate, visceral view; **c**, 628-3, posterior median dorsal plate, dorsal view; **d**, GIT 628-25, right posterior ventrolateral plate, visceral view; **e**, GIT 628-18, anterior section of anterior ventrolateral plate, lateral view showing brachial process. All specimens held within the Institute of Geology at Tallinn University of Technology, Estonia, collection GIT 628.

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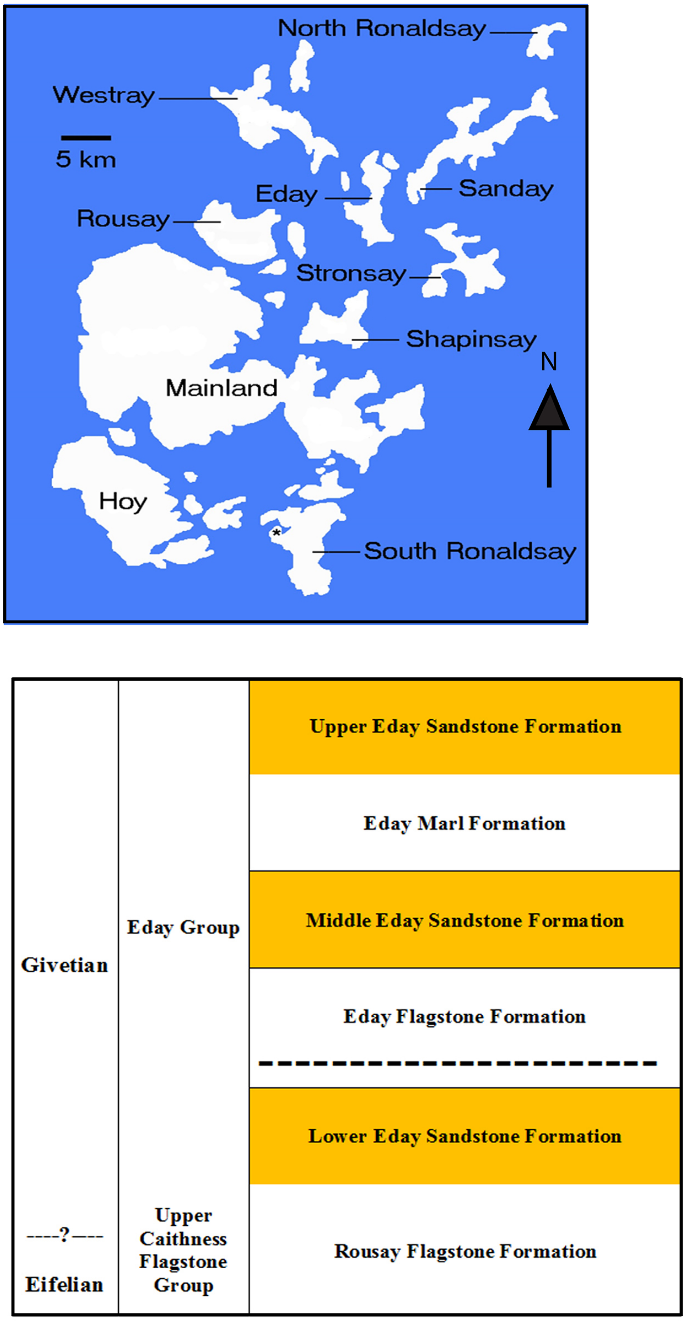
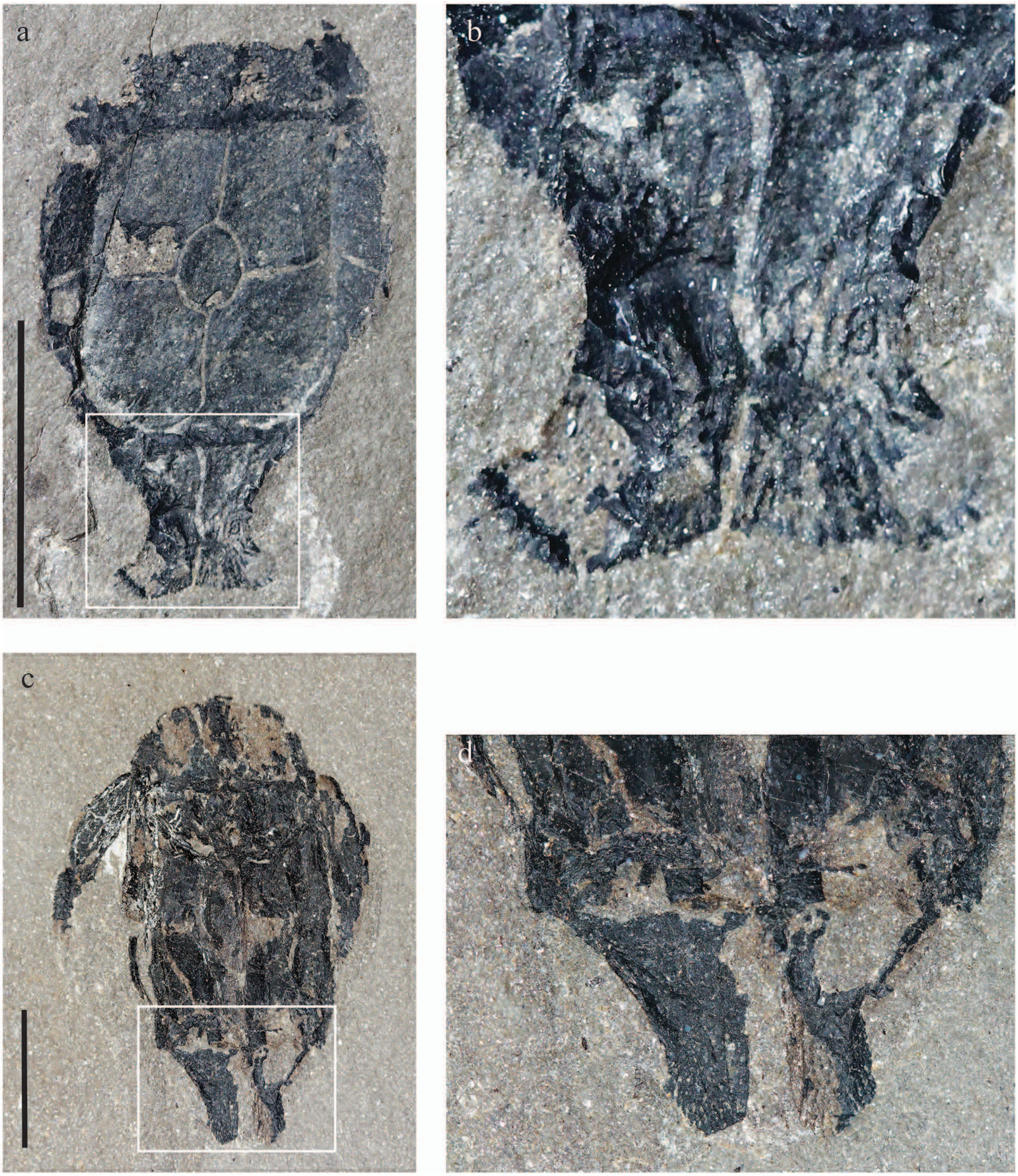
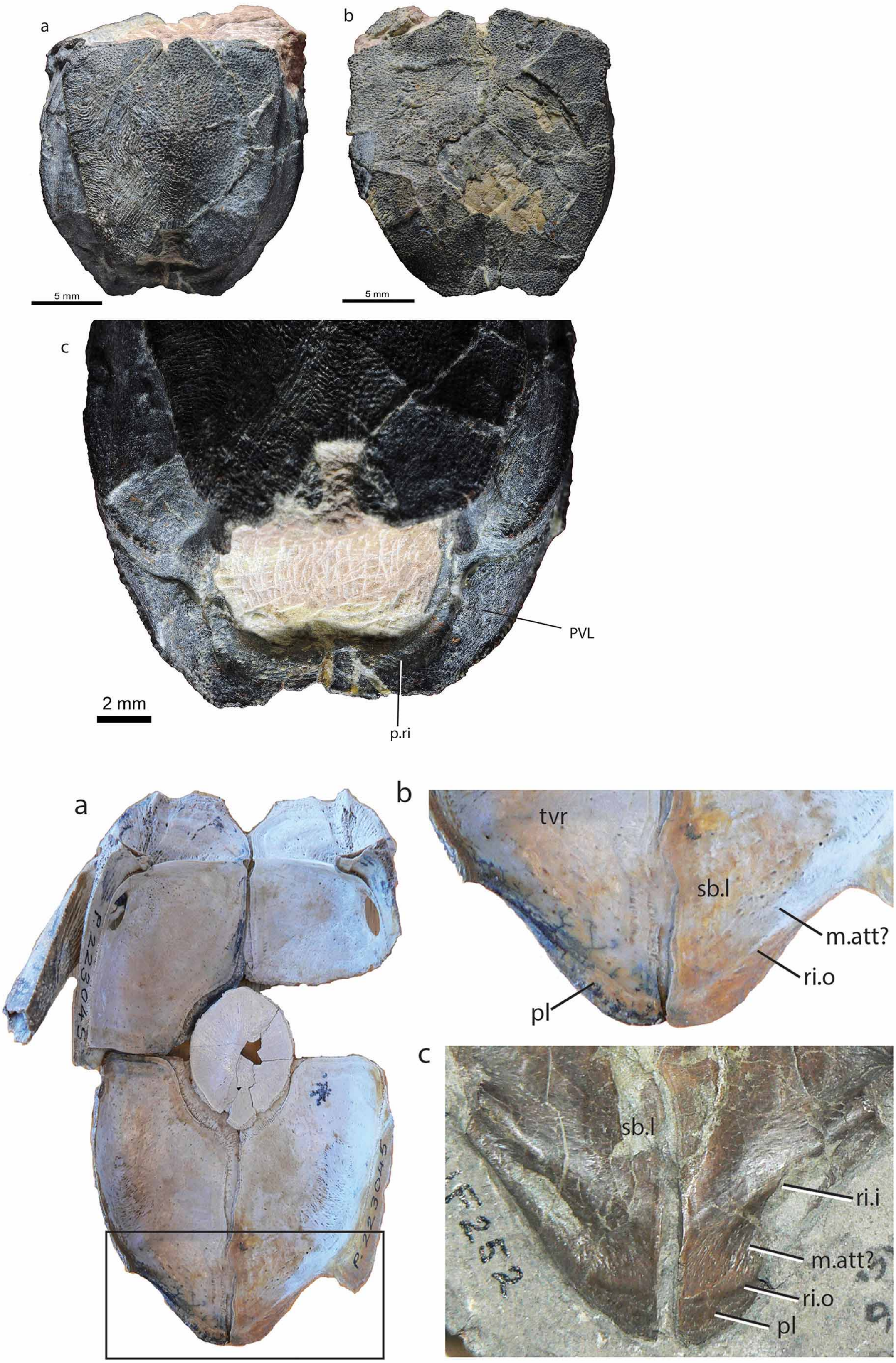


Givetian	Eday Group	Upper Eday Sandstone Formation
		Eday Marl Formation
		Middle Eday Sandstone Formation
		Eday Flagstone Formation -
		Lower Eday Sandstone Formation
----?---- Eifelian	Upper Caithness Flagstone Group	Rousay Flagstone Formation

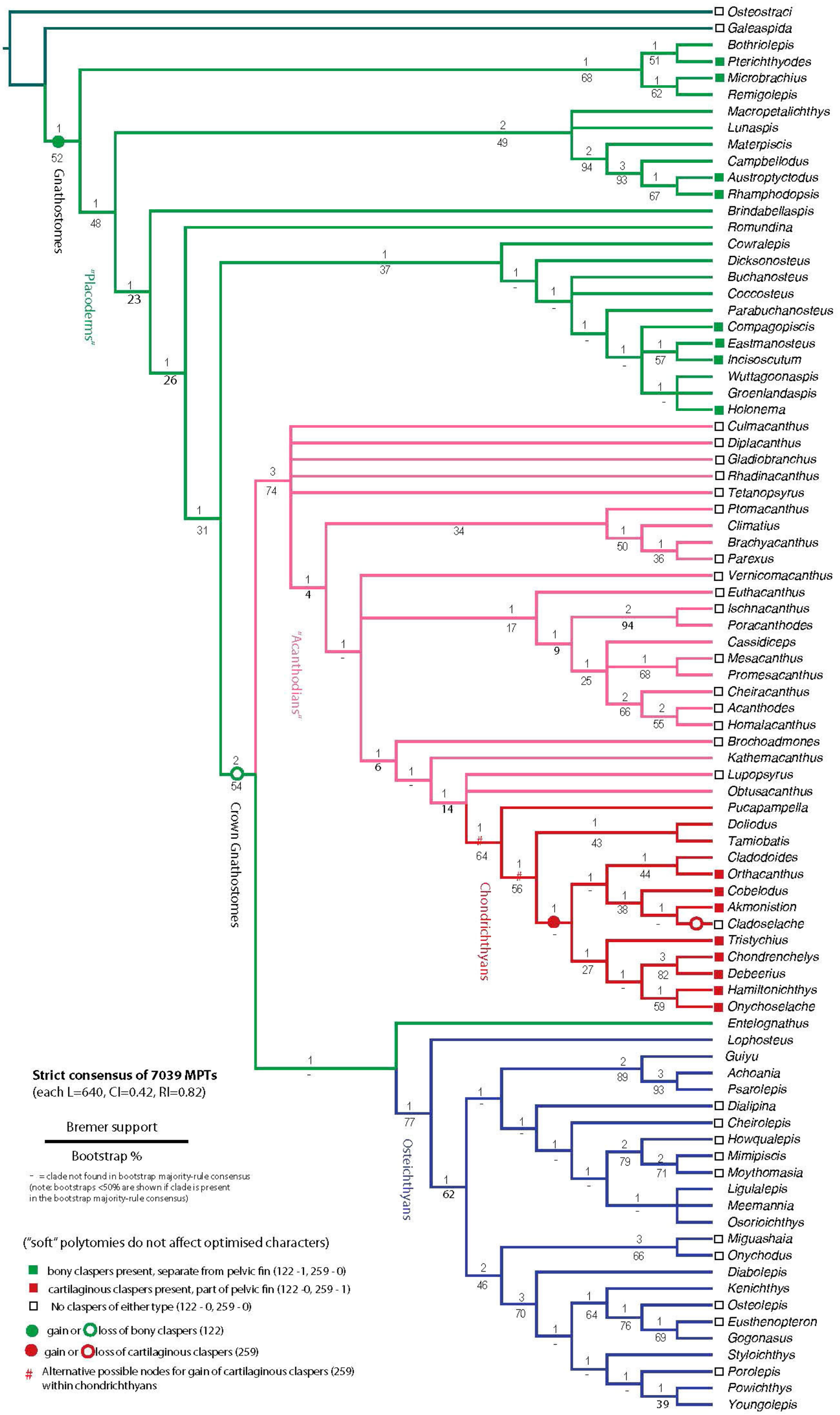
Extended Data Figure 2 | Location and stratigraphic position of new Scottish specimens of *M. dicki* described herein. Top, map of the Orkney Islands with an asterisk marking the location where the specimens of *M. dicki* described in this paper were collected. Below, stratigraphical column of the upper part of the Middle Devonian in the Orkney Islands with the position of the Eday Flagstone Formation fish beds marked by a dotted line.



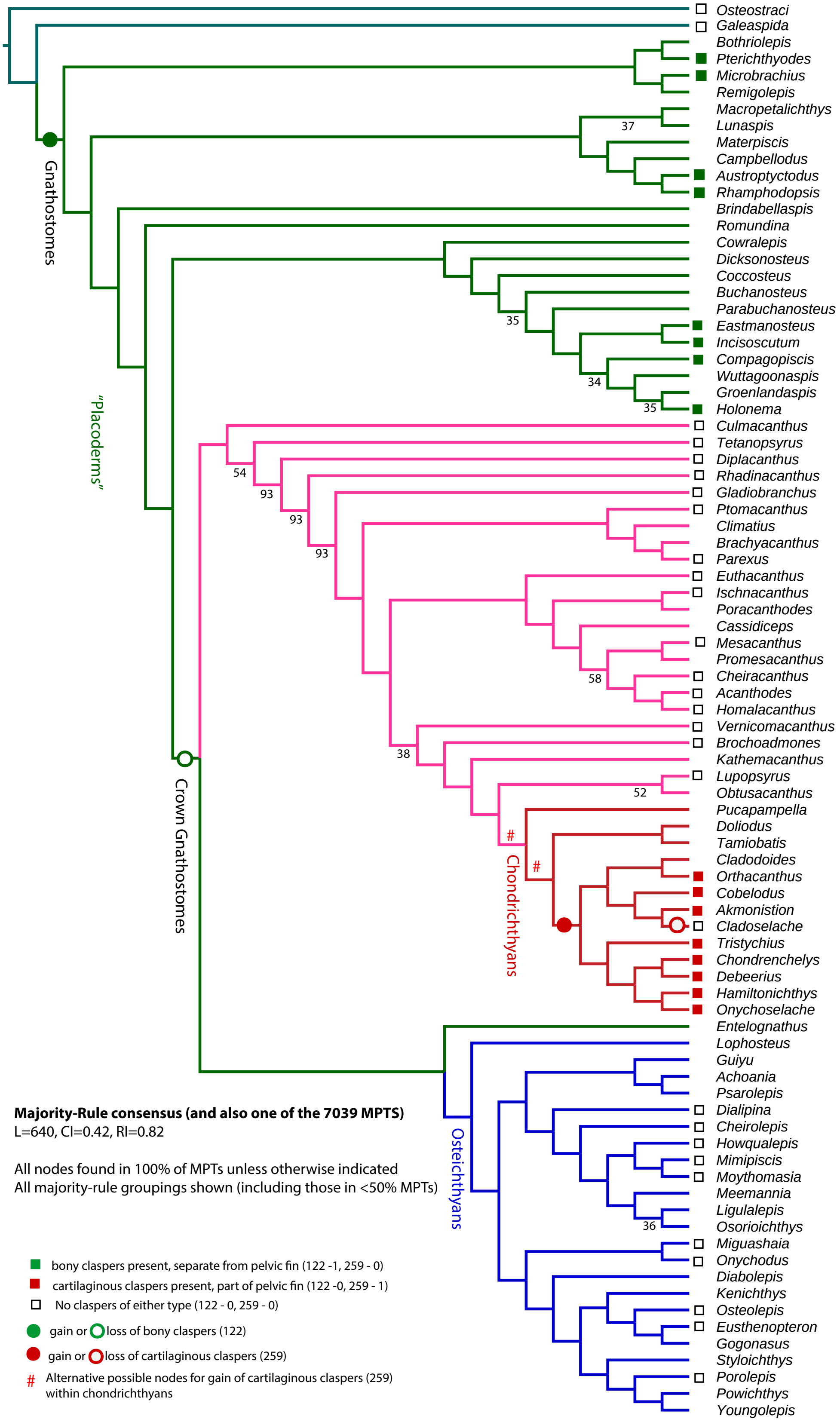
Extended Data Figure 3 | Growth of claspers in *M. dicki* males. **a**, **b**, NHMUKVP P 77400, claspers only weakly developed, no lateral wing; close up of claspers in **b**; **c**, **d**, NHMUK VP P 77403 showing further caudally directed growth of claspers; **d**, close up of claspers showing fusion in midline. Scale bars, 1 cm.



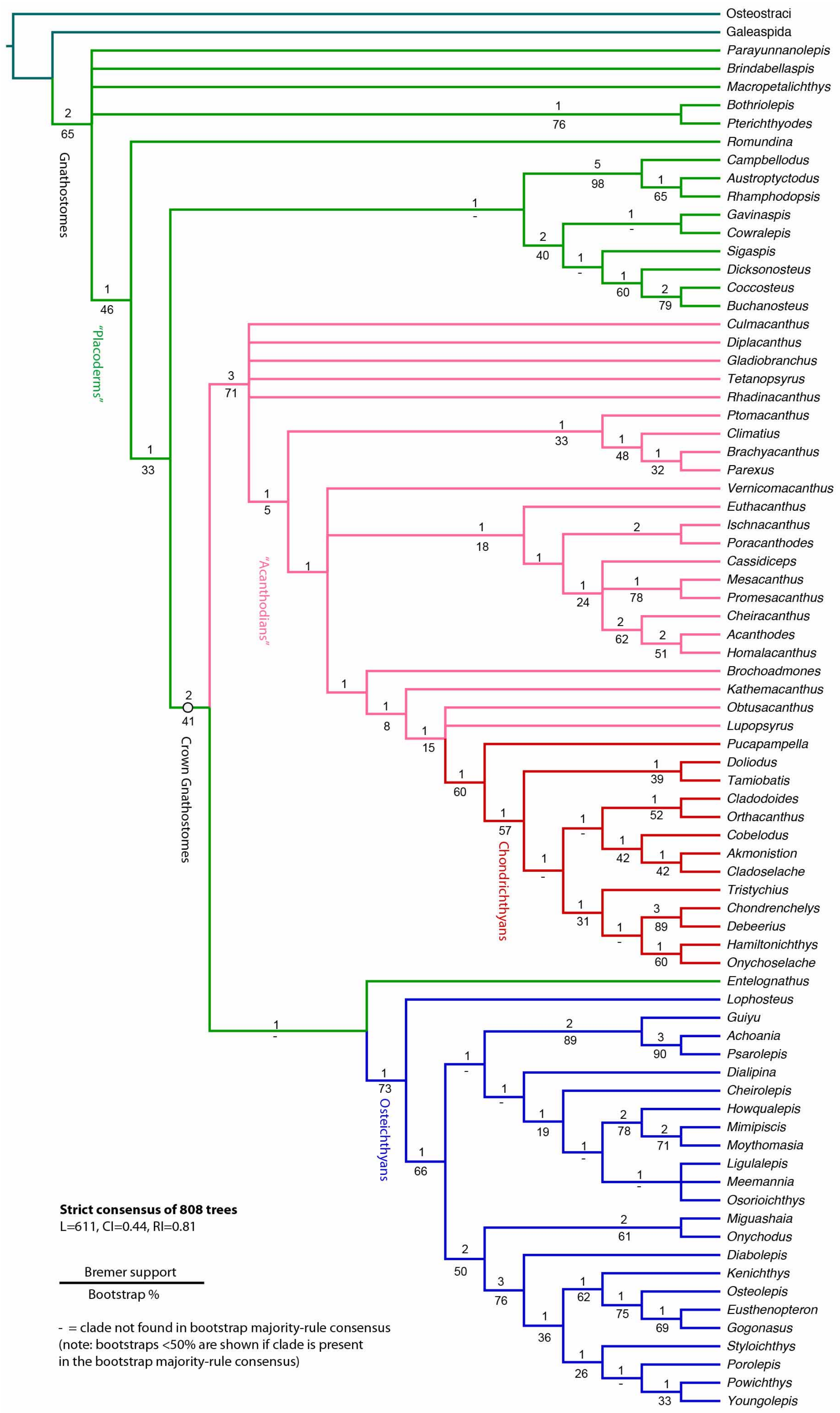
Extended Data Figure 4 | New information on pelvic region anatomy in antiarchs. Top, *Yunnanolepis porifera,* Xitun Formation, Yunnan, China. Specimen IVPP V19359) in (**a**) dorsal view, (**b**) ventral view and (**c**) showing posterior region of trunkshield prepared to show internal side of the PVL plates. p.ri, strong ridge on the dorsal surface of the posterior region of the PVL plates. Below, **a**, **b**, *Bothriolepis* sp., Gogo Formation, Western Australia (P223045, Museum Victoria, Melbourne); **c**, *B. canadensis*, Escuminac Formation, Quebec, Canada (UF 252, Field Museum, Chicago). Abbreviations: m.att?, muscle attachment area; ri.i, internal ridge, ri.o, outer ridge; pl, platform; sb.l, subanal lamina; tvr, transverse ridge (= crista transversalis interna posterior, Stensiö 1948).



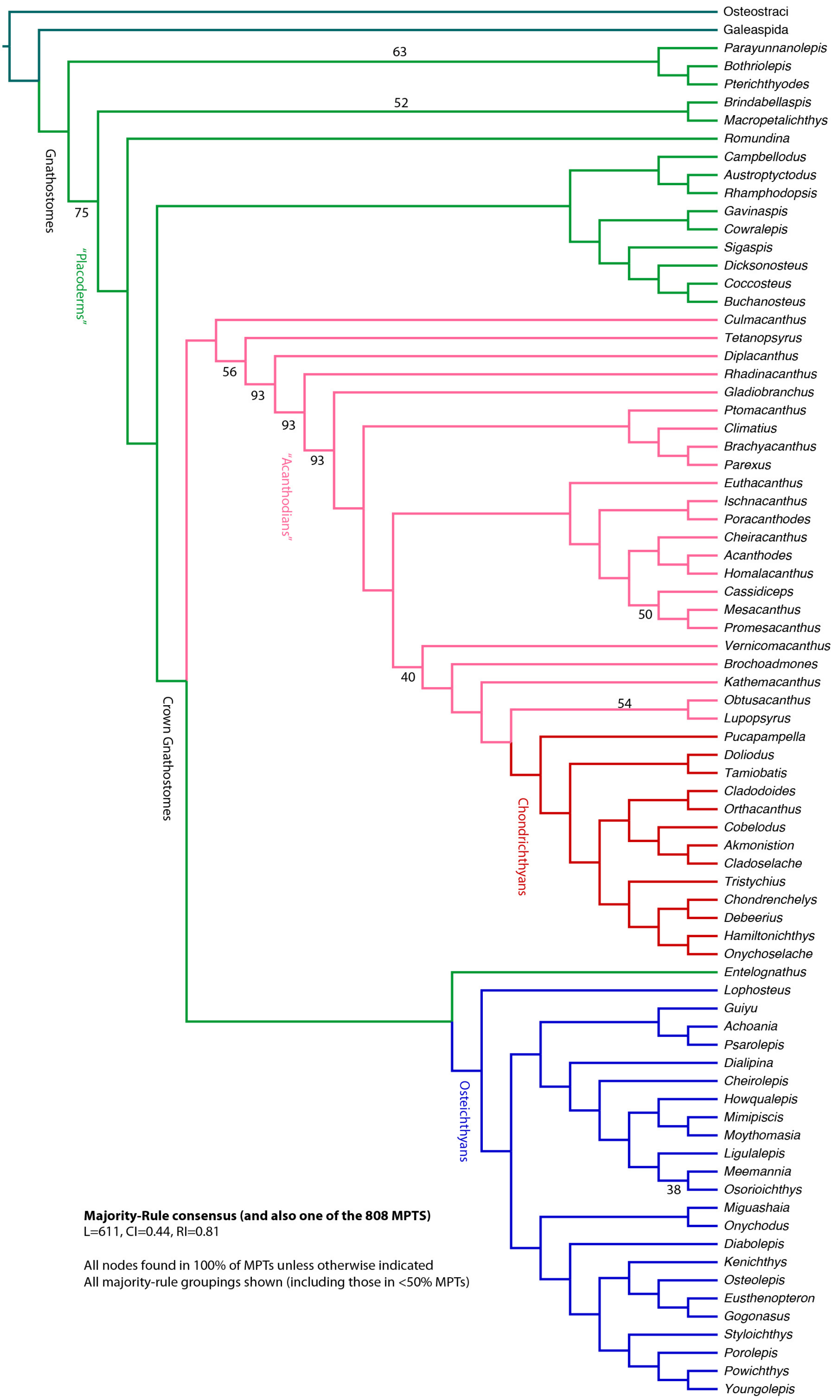
Extended Data Figure 5 | Strict consensus tree from 7,039 trees ($L = 640$) from analysis of the expanded data set (85 taxa, 259 characters). Numbers on branches denote Bremer and bootstrap support. Green squares denote presence of bony claspers (character 122), red squares denote presence of cartilaginous claspers (character 259) and white squares denote absence of both types of clasper. Circles denote gain/loss of the two types of clasper under the most-parsimonious optimization.



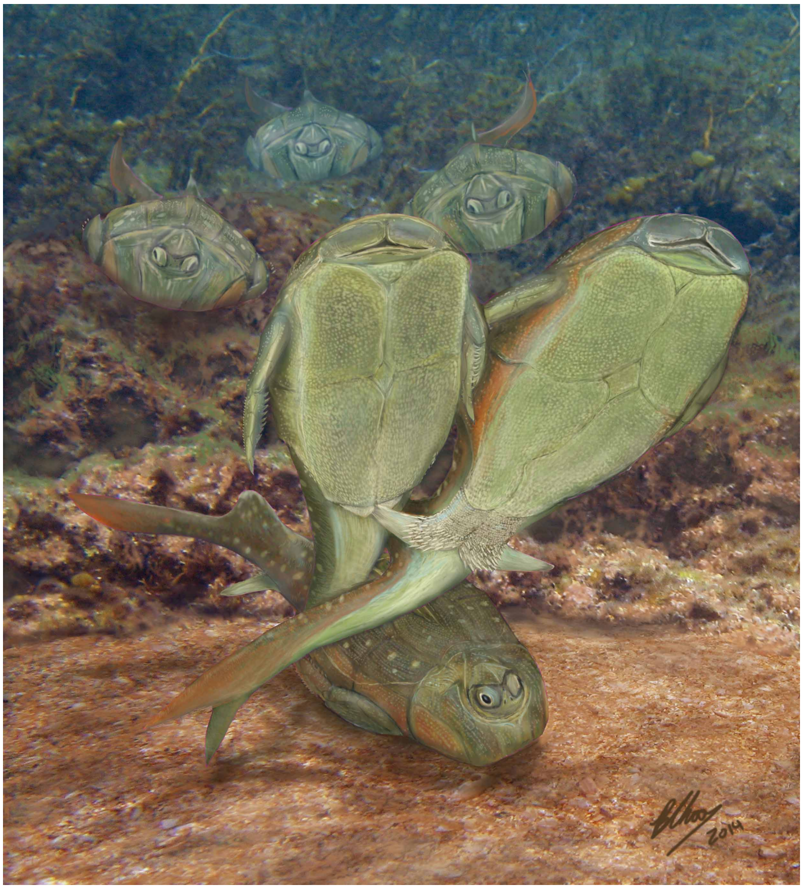
Extended Data Figure 6 | Majority-rule consensus tree, and one of the most-parsimonious trees (length 640) from analysis of the expanded data set (85 taxa, 259 characters). Numbers on branches indicate the percentage of most-parsimonious trees that contain a particular clade (100% unless otherwise indicated). Green squares denote presence of bony claspers (character 122), red squares denote presence of cartilaginous claspers (character 259) and white squares denote absence of both types of clasper. Circles denote gain/loss of the two types of clasper under the most-parsimonious optimization.



Extended Data Figure 7 | Strict consensus tree from 808 trees ($L = 611$) from re-analysis of the data set in ref. 8. Numbers on branches denote Bremer and bootstrap support.



Extended Data Figure 8 | Majority-rule consensus tree, and one of the most-parsimonious trees (length 611) from analysis of the data in ref. 8. Numbers on branches indicate percentage of MPTs that contain a particular clade (100% unless otherwise indicated).



Extended Data Figure 9 | Reconstruction showing hypothetical mating *Microbrachius*, with male to the right, female on left. Artwork by B. Choo.