

***Heddeichthys* – a new tristichopterid genus from the Dura Den Formation, Midland Valley, Scotland (Famennian, Late Devonian)**

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Abstract

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A new tristichopterid genus, *Heddeichthys*, from the Famennian of Scotland is described based on material previously assigned to a number of different genera, including *Glyptopomus*, *Gyroptychius* and *Eusthenopteron*. The validity of the new genus is established by a discussion of the reasons for the invalidity of the previous assignments. *Heddeichthys* is characterized by a combination of derived and primitive tristichopterid features. Derived features include the presence of symphyseal dentary fangs and premaxillary pseudofangs, a diamond-shaped symmetric caudal fin, a low posterodorsal expansion of the maxilla, and a posteriorly positioned kite-shaped pineal series. Primitive features include a postorbital and jugal contribution to the orbital margin and a parasphenoid with a ventral keel. External dermal bones are rather poorly preserved in the referred material, with few easily discernible sutures. The holotype specimen, a three-dimensionally preserved skull, was scanned by computed tomography to reveal well-preserved internal dermal bones, including entopterygoids, vomers and parasphenoid. There is no preserved endoskeletal material. As the first representative of derived tristichopterids described from Britain, *Heddeichthys* lends support to the idea that faunal dispersion between Gondwana and Laurussia in the Late Devonian was widespread. Derived tristichopterids have been described from all continents except South America. In contrast, the basal tristichopterids *Eusthenopteron* and *Tristichopterus* are still only described from Laurussia.

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Introduction

The Dura Den Formation consists of some 40 m of deposits at the transition between the Glenvale and Knox Pulpit Formations, in the Famennian of the northeastern part of Midland Valley, Scotland (Fig. 1A). A transition from mainly fluvial to mainly aeolian deposition took place in the succession when the Dura Den Formation was deposited, with widespread aeolian influences in the lower part of the overlying Knox Pulpit Formation (Fig. 1B) (Trewin and Thirlwall 2002). Preserved Dura Den fish are flat, or more or less

three-dimensional with a sand infilling. The latter has been interpreted as showing death from sub-aerial exposure, with sand subsequently filtering into the dried bodies. Mass deathbeds might represent shallow pools that were overcome by moving sand dunes, killing and entombing the fish. The main fish-yielding bed (yielding large numbers of the porolepiform *Holoptychius* Agassiz, 1839) shows fish preserved between two surfaces with desiccation cracks. Somewhat higher (around 15 m) in the Formation, an additional bed with a localized concentration of the placoderm *Bothriolepis* Eichwald, 1840, is present.

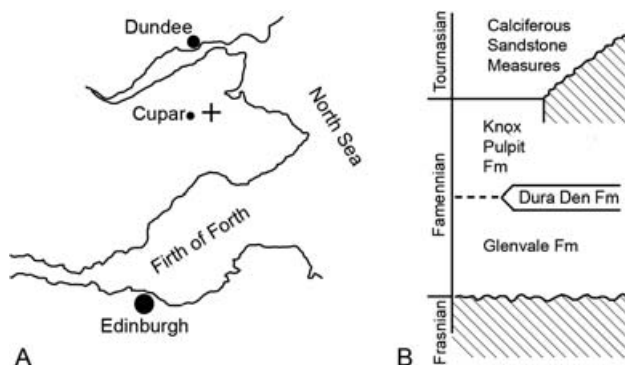


Fig. 1—**A.** Map of eastern Midland Valley, Fife, Scotland, with Dura Den locality marked by a cross. —**B.** Stratigraphical column of Upper Devonian of Northeast Midland Valley [modified from Dineley and Metcalf (1999)].

The fish fauna of Dura Den is dominated by *Holoptychius*, which accounts for around 90% of the specimens currently in museum collections (Andrews 1982). Placoderms are represented by *Bothriolepis* and *Phyllolepis* Agassiz, 1844. Rarer occurrences include *Glyptopomus* Agassiz, 1844, *Phaneropleuron* Huxley, 1861, and *Heddeleichthys*, the first two of these a cosmine-free ‘osteolepid’ tetrapodomorph and a lungfish, respectively, and the last the subject of this paper. It is noteworthy that the Dura Den fauna shows a rather unusual size range of preserved *Holoptychius* individuals, with all specimens being much smaller than the median size of those found at other localities.

Heddeleichthys belongs to the Tristichopteridae Cope, 1889, the sister taxon of the clade consisting of the elpistostegalian grade and the tetrapods (Ahlberg and Johanson 1998). Apart from *Heddeleichthys*, two tristichopterids have been reported from the British Isles. These are the Givetian genus *Tristichopterus* Egerton, 1861, and the Frasnian *Eusthenopteron traquairi* Westoll, 1937. Both represent the basalmost part of the tristichopterid group, which are small fish that retain many of the characters of more generalized ‘osteolepid’ members of the tetrapod stem group. Tristichopterids are described from other parts of Laurussia (*Eusthenodon* Jarvik, 1952, from the Famennian of Greenland, Pennsylvania, Russia and Belgium; *Platycephalichthys* Vorobyeva, 1959, and *Jarvikina* Vorobyeva, 1977, from the Frasnian of the Baltic region; *Eusthenopteron* Whiteaves 1881, from the Frasnian of Canada, Russia and the Baltic states; *Hynieria* Thomson, 1968, from the Famennian of Pennsylvania) and from Gondwana (Ahlberg and Johanson, 1997, and *Mandageria* Johanson and Ahlberg, 1997, from the Famennian of Australia; *Notorhizodon* Young *et al.*, 1992, from the late Middle or early Late Devonian of Antarctica; *Eusthenodon* from the Famennian of South Africa and Australia Johanson 2004).

The group is uniquely characterized by a posteriorly displaced, small extratemporal bone in the posterior part of

the skull roof (‘postspiracular’ bone) (Ahlberg and Johanson 1997). All tristichopterids except for *Tristichopterus* share the synapomorphy of having two fang positions on the posterior coronoid and ectopterygoid (Snitting, unpublished results). Other tristichopterid features with a wider distribution among the Tetrapodomorpha include the loss of cosmine, round scales with an internal boss, a small kite-shaped parasymphyseal dental plate, parallel supraorbital sensory canals, and short transverse crescent-shaped anterior pit lines (Jarvik 1980; Ahlberg and Johanson 1997).

Heddeleichthys was originally figured by Anderson (1859) as *Diplopterus Dalgleisiensis* [sic] in his monograph on the Dura Den sandstone and the fossils found there. The specimen illustrated by Anderson (1859) is in all probability the same specimen that Jarvik (1950) designated as holotype of *Eusthenopteron? dalgleisiensis* (BGS 53442), a provisional species of *Eusthenopteron*. Other synonyms of *Heddeleichthys* include *Glyptopomus kinnairdi* (Woodward 1891; Watson and Day 1916), *Gyropterychius Heddelei* [sic] (Traquair 1892) and *Eusthenopteron cf. traquairi* (Westoll 1940).

Materials and Methods

The examined specimens belong to the National Museum of Scotland, Edinburgh (NMS) and the British Geological Survey, Nottingham (BGS). All material comes from the Middle Famennian Dura Den Formation, Midland Valley, Scotland, and was collected in the 19th century by John Anderson (Anderson 1859; Andrews 1982). Specimen BGS 53442 was scanned using computed tomography at the University of Texas, Austin. The resulting scan series contains 735 slices, with an inter-slice distance of 91.76 µm (Fig. 2). Digital reconstructions based on the scan series were produced in the medical imaging software MIMICS (<http://www.materialise.com/mimics>; Leuven, the Netherlands).

Systematic palaeontology

Sarcopterygii Romer, 1955

Tetrapodomorpha Ahlberg, 1991

Tristichopteridae Cope, 1889

Heddeleichthys gen. nov.

Type species. *Diplopterus Dalgleisiensis* Anderson, 1859

Diagnosis. As for type and only species.

Etymology. The name *Heddeleichthys* was designated by the late Dr Mahala Andrews, but nothing written remains from her work on the genus (personal communication, P. E. Ahlberg). The genus name is in honour of Matthew Forster Hedde (1828–1897), who supervised the Dura Den excavations in 1853.

Heddeleichthys dalgleisiensis (Anderson, 1859)

1859 *Diplopterus Dalgleisiensis* (Anderson)

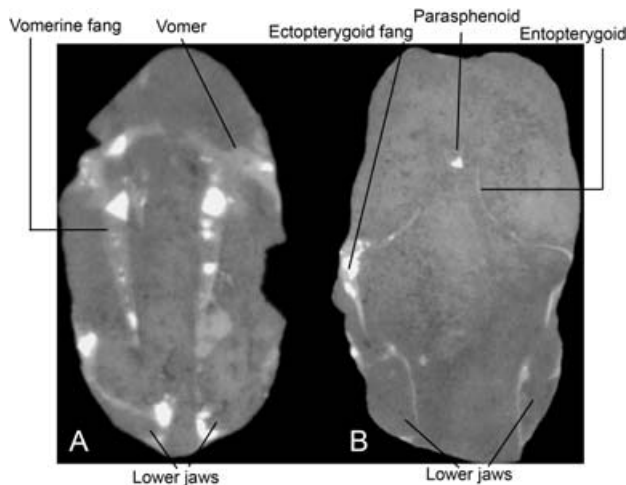


Fig. 2—**A.** Transverse section of holotype (scan image 71) at the level of the vomerine fangs. —**B.** Transverse section of holotype (scan image 281) at the level of the anterior ectopterygoid fang.

1862 *Glyptolaemus* (Powrie)

1890 ?*Glyptolaemus kinnairdi* Huxley (Woodward and Sherborn)

1890 *Glyptolaemus kinnairdi* Huxley (Traquair)

1891 *Glyptopomus kinnairdi* Huxley (Woodward)

1892 *Gyroptychius Heddelei* (Traquair)

1916 *Glyptopomus kinnairdi* Huxley (Watson and Day)

1940 *Eusthenopteron* cf. *traquairi* (Westoll)

1950 *Eusthenopteron?* *dalglesiensis* (Jarvik)

Referred specimens. NMS.G.1920.32A (imperfectly preserved cheek, snout and lower jaw); NMS.G.1966.39.1 (imperfectly preserved cheek, snout, shoulder girdle and lower jaw, with part of the body and fins); NMS.G.2007.22.1 (three-dimensionally preserved dorsal part of skull); NMS.G.1966.39.9 (part of body with fins); BGS 53442 (laterally flattened skull).

Holotype. BGS 53442.

Diagnosis. A tetrapodomorph of intermediate size (40–50 cm total body length), with a torpedo-shaped skull with a long portion of parietal shield (around 40%) anterior to the orbits, a drop-shaped pineal with a posterior corner in a position posterior to the orbits, jugal and postorbital contribution to the orbital margin, a weakly developed posterodorsal expansion of the maxilla, an anterior dentary fang, a premaxillary pseudofang accompanied by a posterior mesial extension of the premaxilla, anterior and middle coronoids with a marginal tooth row, a distinct lateral vertical lamina on the coronoids, long posterior processes of vomers, a small and

posteriorly displaced extratemporal ('postspiracular'), a rhombic caudal fin, and round cosmine-free scales.

Etymology. The species name designated by Anderson (1859) is in honour of Mr and Mrs Dalglish, who were the owners of the Dura Estate, and who were made honorary members of the Literary & Philosophical Society of St Andrews in 1861, on the recommendation of Heddele.

Comments. The generic name *Diplopterus* Agassiz, 1835, was invalidated by Jarvik (1948, p. 240) based on the fact that no species was described, and the name therefore does not conform to the rules of binary nomenclature. *Diplopterus* Traill, 1841, was invalidated by Sedgwick and McCoy (1854) because of homonymy (which also applies to *Diplopterus* Agassiz, 1835), and reassigned to the new genus *Diplopterax*. However, this genus immediately became a junior synonym of *Gyroptychius* McCoy, 1848, and is therefore also invalid (see also Woodward 1891, p. 375; Säve-Söderbergh 1933, p. 104 and plate 14:2).

Glyptolaemus (Huxley 1861) is a junior synonym of *Glyptopomus* Agassiz, 1844, (Powrie 1862). It is interesting to note that the reconstruction of *Glyptopomus kinnairdi* provided by Watson and Day (1916, fig. 2) clearly shows the presence of a posteriorly displaced extratemporal ('postspiracular') lateral to the extratemporal series, a tristichopterid synapomorphy (Ahlberg and Johanson 1997). *Glyptopomus sensu* Watson and Day (1916) is therefore different from the *Glyptopomus minor* Agassiz, 1844, figured by Anderson (1859, plate 2) and the *Glyptopomus* illustrated by Huxley (1861, fig. 4).

Traquair (1892) assigned a specimen of *Glyptolaemus* to *Gyroptychius Heddelei* based on the presence of a diamond-shaped symmetric tail (this specimen is part of the described *Heddeleithys* material, NMS.G.1966.39.1, Fig. 5A,B). The identification was at the same time regarded by Traquair as somewhat uncertain, since the scales of his *Glyptolaemus* specimen did not seem to match the scales of *Gyroptychius*.

Eusthenopteron cf. *traquairi*, described from a single incomplete parietal shield, was assigned to species based on the very posterior position of the pineal opening, which according to Westoll (1940) excluded the possibility of the specimen belonging to either *E. foordi* or *E. savesoderberghi* Jarvik, 1937. However, the *E. cf. traquairi* specimen does not match the holotype of *E. traquairi* either, because of the kite-shaped pineal series of the former compared to the round pineal series of the latter (Westoll 1937, fig. 1; Westoll 1940, fig. 3). *Eusthenopteron* cf. *traquairi* probably comes from the Famennian Rosebrae Beds, which are roughly contemporaneous with the Dura Den Formation (Trewin and Thirlwall 2002). *Eusthenopteron traquairi*, on the other hand, comes from the Frasnian Boghole, part of the Nairn Sandstone, Elgin, making that species broadly contemporaneous with *E. savesoderberghi* from the Frasnian of Latvia (Jarvik 1937).

Even though the feature is visible on the holotype specimen, there is no mention of the presence of symphyseal dentary

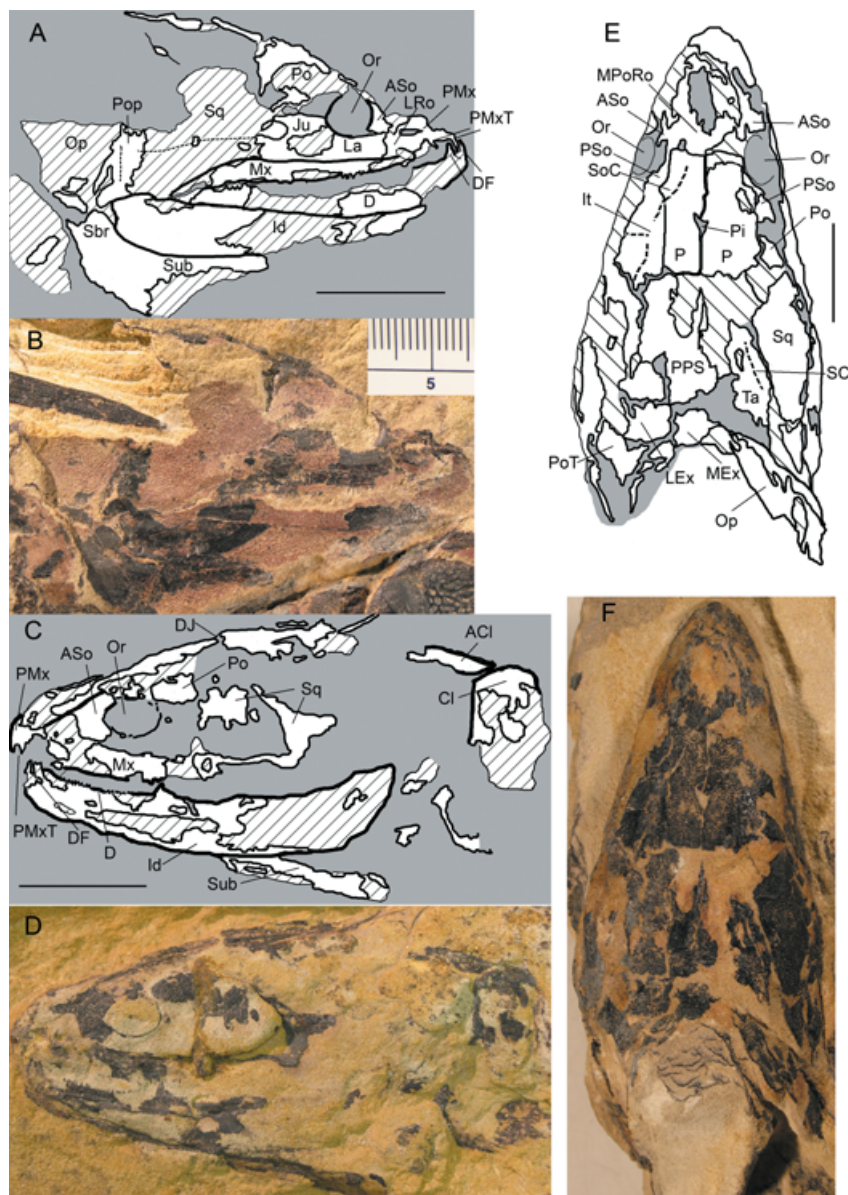


Fig. 3—*Heddeleithys dalgleysiensis* NMS.G.1920.32A (A,B), NMS.G.1966.39.1 (C,D), NMS.G.2007.22.1 (E,F). —**A, B.** Skull and lower jaw in lateral view. —**C, D.** Skull, lower jaw and part of pectoral girdle in lateral view. —**E, F.** Skull roof in dorsal view. Scale bars = 2 cm. Abbreviations: ACI, anocleithrum; ASo, anterior supraorbital; Cl, cleithrum; D, dentary; DF, dentary fang; DJ, dermal intracranial joint; Id, infradentaries; It, intertemporal; Ju, jugal; LEx, lateral extrascapular; LRo, lateral rostral; MEx, median extrascapular; MPoRo, median postrostral; Mx, maxilla; Op, opercular; Or, orbit; Pi, pineal opening; PMx, premaxilla; PMxT, premaxillary tooth; P, parietal; Po, postorbital; Pop, preopercular; PoT, posttemporal; PPS, postparietal shield; PSo, posterior supraorbital; Sbr, submandibulo-branchiostegal; SC, sensory canal; SoC, supraorbital sensory canal; Sq, squamosal; Sub, submandibulars; Ta, tabular.

fangs in the original description of *E. dalgleysiensis* (Jarvik 1950), something that clearly distinguishes *Heddeleithys* from *Eusthenopteron*.

Description

The Dura Den material provides no preserved endoskeletal ossification. The description of the external dermal bones of the skull is based on specimens BGS 53442, NMS.G.2007.22.1, NMS.G.1966.39.1 and NMS.G.1920.32A. The preservation of the external dermal bones is very patchy, and few sutures are traceable with confidence. NMS.G.1920.32A (Fig. 3A) is preserved in association with numerous *Bothriolepis* individuals, and probably comes from

the higher of the two fish-yielding beds present at Dura Den. Other specimens (except for the holotype, BGS 53442) are found in association with numerous *Holoptychius* individuals, probably showing the lower of the two beds. The mode of preservation differs between the two beds, with no sand-infill of the specimen (NMS.G.1920.32A) assigned to the upper bed. The other specimens, including the holotype, all show some degree of three-dimensional preservation.

Dermal bones of the cheek and opercular series

The largest cheekbone is the squamosal, surrounded by the preopercular and the quadratojugal posteriorly, the maxilla ventrally, and the postorbital and jugal anteriorly (Figs 3A,B,

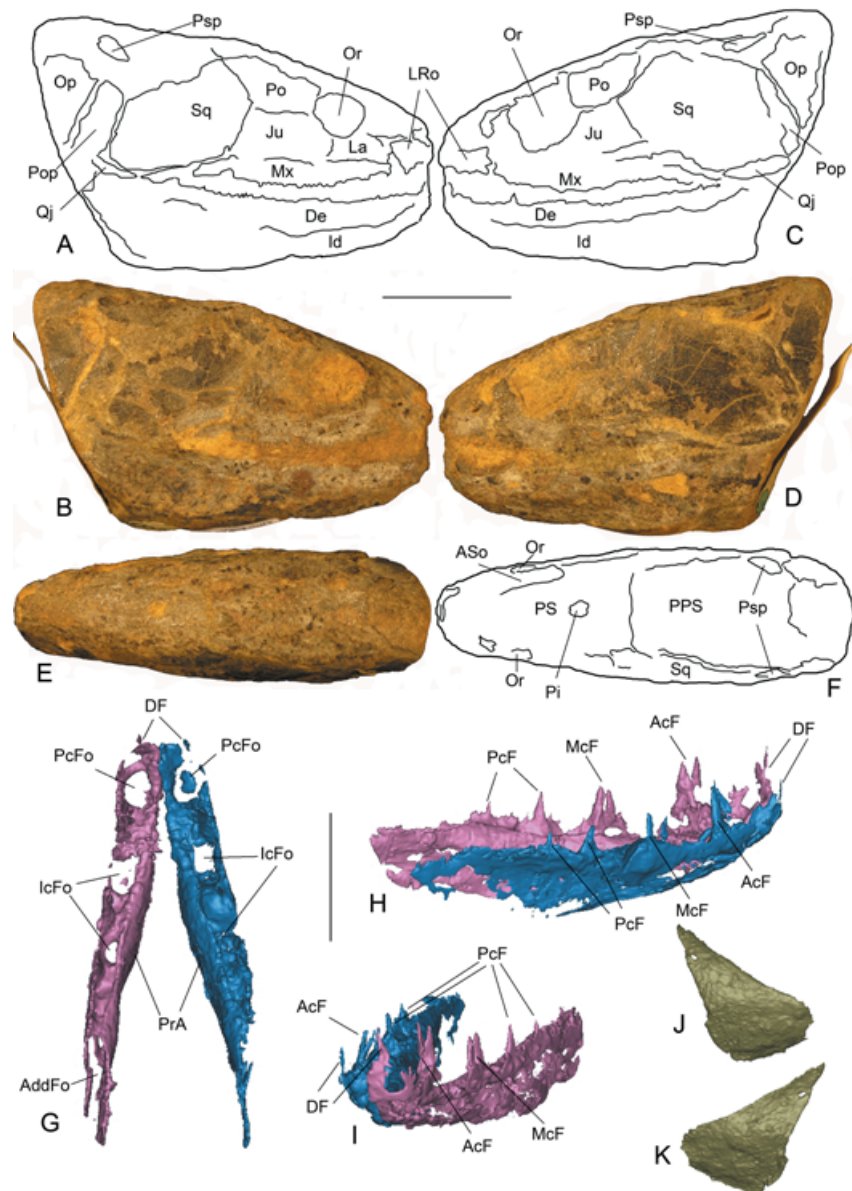


Fig. 4—*Heddeleithys dalglesiensis* BGS 53442. —**A, B**. Skull in right lateral view. —**C, D**. Skull in left lateral view. —**E, F**. Skull in dorsal view. —**G, I**. Mimics reconstructions of lower jaws in dorsal (G), right posterolateral (H), and left anterolateral (I) views. —**J, K**. Mimics reconstructions of right clavicle in external (J) and internal (K) views. Scale bar = 2 cm. Abbreviations: AcF, anterior coronoid fang; AddFo, adductor fossa; ASo, anterior supraorbital; De, dentary; DF, dentary fang; IcFo, intercoronoid fossa; Id, infradentaries; Ju, jugal; La, lachrymal; LRo, lateral rostral; McF, middle coronoid fang; Mx, maxilla; Op, opercular; Or, orbit; PcF, posterior coronoid fang; PcFo, precoronoid fossa; Pi, pineal opening; Po, postorbital; Pop, preopercular; PPS, postparietal shield; PrA, prearticular; PS, parietal shield; Psp, posteriorly displaced extratemporal ('postspiracular'); Qj, quadratojugal; Sq, squamosal.

4A–D and 5C,D). A large overlap area for the postorbital and jugal, larger than the corresponding area in *Eusthenopteron*, is present anteriorly on the squamosal (Fig. 5C,D). The maxilla is rather narrow throughout its entire length, with only a low posterodorsal process ventral to the approximate position of the suture between the jugal and the squamosal (Fig. 3A,B). Dorsal to the maxilla, the jugal and lacrimal provide the ventral part of the orbital margin (Figs 3A,B, 4A,B and 5C,D). The jugal contribution to the margin is larger than in *Cabonnichthys*, and is more similar to the condition in *Eusthenopteron* (Jarvik 1980; Ahlberg and Johanson 1997). The same is true for the postorbital, which is excluded from the orbital margin in *Cabonnichthys*, *Eusthenodon* and *Mandageria*, but contributes to the posterior part of the margin in *Eusthenopteron* and

Heddeleithys (Ahlberg and Johanson 1997; Jarvik 1980). Contrary to the interpretation by Jarvik (1950) the postorbital is not greatly extended posteriorly (Fig. 4A–D), unlike the postorbitals of *Cabonnichthys*, *Mandageria* and *Eusthenodon* (Ahlberg and Johanson 1997), but is more similar to *Eusthenopteron*. The rest of the orbital margin is provided by the two supraorbitals (Figs 3 and 4E,F). The poor preservation in this area means that the actual shapes of the supraorbitals are not known. The posterior supraorbital contacts the intertemporal (Fig. 3E,F). This is unlike the condition in *Mandageria* and *Eusthenodon*, where these bones are separated by the postorbital (Ahlberg and Johanson 1997).

The preopercular is bar-like and vertical, much like in *Eusthenopteron* (Jarvik 1980) (Figs 3A,B and 4A–D). The

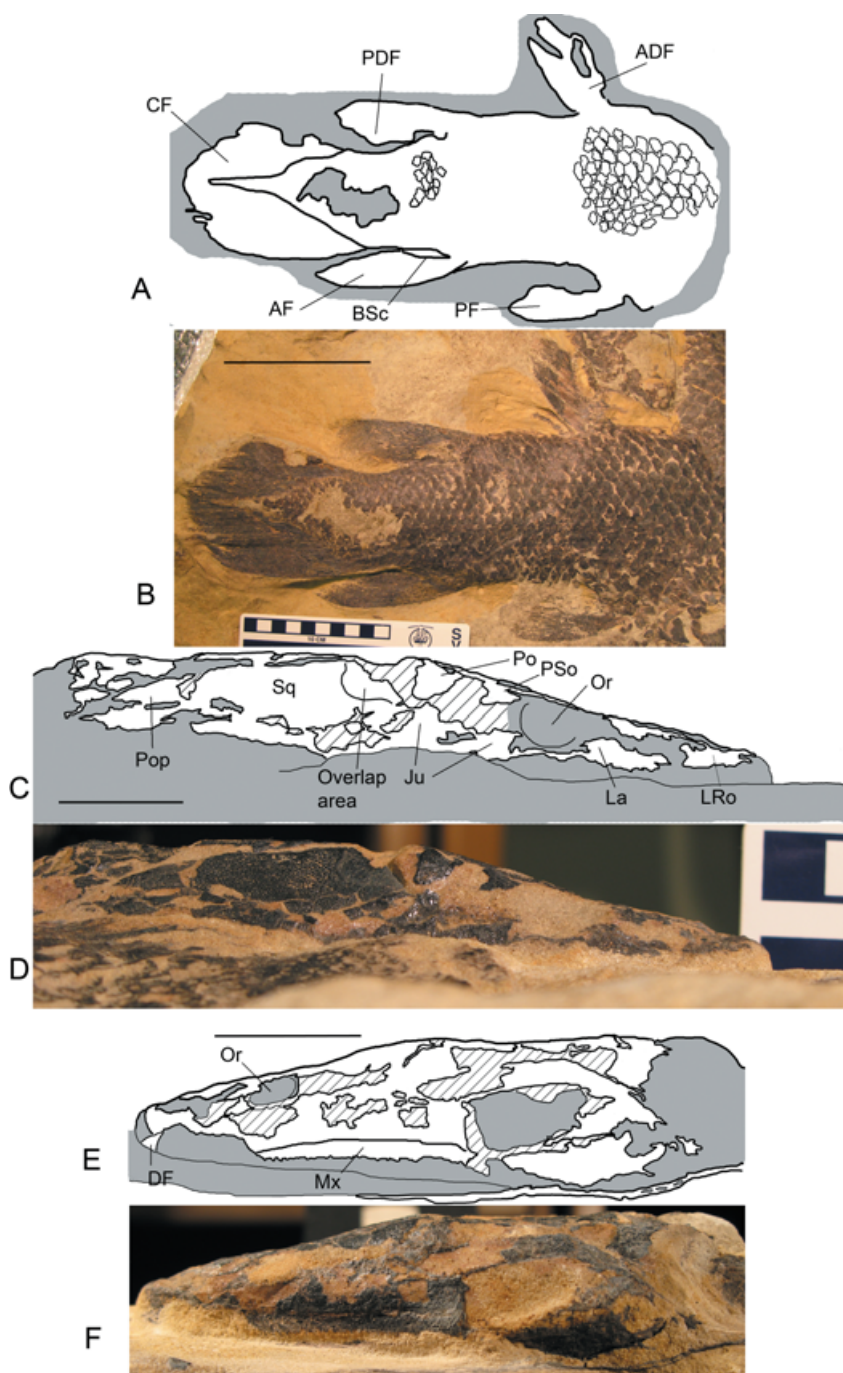


Fig. 5—*Heddleichthys dalgleisiensis* NMS.G.1966.39.9 (A,B), NMS.G.2007.22.1 (C–F).

—A, B. Posterior part of body in right lateral view; —C–F. Skull in right lateral (C, D) and left lateral (E, F) views. Scale bar = 10 cm for A, B, 2 cm for C–F.

Abbreviations: ADF, anterior dorsal fin; AF, anal fin; Bsc, basal scute; CF, caudal fin; DF, dentary fang; Ju, jugal; La, lachrymal; Mx, maxilla; Or, orbit; PDF, posterior dorsal fin; PF, pelvic fin; Po, postorbital; Pop, preopercular; Sq, squamosal.

opercular is not preserved in its entirety, but seems to be similar to the rather high one in *Eusthenopteron*. This feature is somewhat exaggerated in specimen BGS 53442 as the result of lateral compression of the skull.

Dermal bones of the anterior part of the skull roof and snout

The anteriormost part of the snout is not well enough preserved to enable a detailed description. A large median

postrostral is present, immediately anterior to the parietals (Fig. 3E,F). The ventral margin of the external nostril is provided by the lateral rostral (Figs 3A,B and 4A–D). The parietals surround a drop-shaped pineal opening with a posterior point. The pineal is positioned posterior to the orbits (Figs 3E,F and 4E,F). The drop- or kite-shape of the pineal series is clearly visible in specimen NMS.G.1961.21 (Fig. 3E,F), but not in specimen BGS 53442 (Fig. 4E,F). It is highly questionable, however, if the latter specimen

actually preserves the true shape of the pineal because the opening has clearly been manually prepared. Both the shape and the position of the pineal are comparable to the condition in *Cabonnichthys*, *Mandageria* and *Eusthenodon*. Basal tristichopterids such as *Eusthenopteron* and *Tristichopterus* instead show a round pineal opening situated at the level of the orbits, which is also seen in more basal tetrapodomorphs such as *Osteolepis* Agassiz, 1835 (Ahlberg and Johanson 1997). The parietals are rather long and narrow (approximately 1.7 times longer than broad), with ossification centres anterior to the pineal opening, and end anteriorly at the level of the centre of the orbits (Fig. 3E,F). Compared to other tristichopterids, this is most similar to *Mandageria*, while *Eusthenopteron* and *Cabonnichthys* both have parietals that end anterior to the orbits (Jarvik 1980; Ahlberg and Johanson 1997; Johanson and Ahlberg 1997). Part of the supraorbital sensory canal is visible on the left side of specimen NMS.G.1961.21, crossing from the parietal onto the intertemporal, where the canal divides into one vertical and one longitudinal component (Fig. 3E,F). The suture between the parietal and intertemporal is not visible. There is a considerable preorbital division of the anterior half of the skull roof (Figs 3E,F and 5C–F).

An enlarged premaxillary tooth (or pseudofang) is present anteriorly (Fig. 3A–D). The tooth is associated with a posteriorly directed flange ventrally on the premaxilla, similar to what can be observed in *Mandageria* (Johanson and Ahlberg 1997). Premaxillary pseudofangs, which are different from fangs on the dentary and coronoids in that they do not have a corresponding replacement pit and are part of the marginal tooth row, are also present in *Cabonnichthys*, *Mandageria* and *Eusthenodon* (Ahlberg and Johanson 1997).

Dermal bones of the posterior part of the skull roof and shoulder girdle

The sutures between the postparietals and the supratemporal and tabular are not clearly visible. A short portion of the sensory canal running through the tabular can be seen on the right side of specimen NMS.G.1961.21, indicating the position of the tabular–postparietal suture slightly mesial to this canal (Fig. 3E,F). The extrascapulars are not well enough preserved to allow any description of their overlap. The extent of the overlap of the lateral extrascapulars onto the median extrascapular varies among tristichopterids, with a large overlap present in *Mandageria*, resulting in a very short exposed anterior margin of the median extrascapular (Johanson and Ahlberg 1997). A small, posteriorly displaced extratemporal ('postspiracular') bone is present dorsal to the operculum (Fig. 4A–F). An anocleithrum and the dorsal part of a cleithrum are preserved on specimen NMS.G.1966.39.1, but they are not sufficiently well preserved to enable much comment (Fig. 3C,D). The exposed surface of the anocleithrum seems to be long, similar to *Eusthenopteron* but unlike *Mandageria* (Jarvik 1980; Johanson and Ahlberg 1997). An anteriorly directed overlap area for the next element in

the pectoral girdle is present protruding from the anterior margin of the anocleithrum. An isolated right clavicle is present in specimen BGS 53442 (Fig. 4J,K). It closely resembles the clavicle of *Eusthenopteron* (Andrews and Westoll 1970).

Palate

Both entopterygoids, along with dermopalatine and ectopterygoid, are well preserved in specimen BGS 53442 (Fig. 6). Posteriorly, the dorsal entopterygoid margin is almost vertical, before turning to an almost horizontal course. The margin then rises abruptly towards the dorsalmost point of the entopterygoid. Anterior to the dorsalmost point, the margin has a straight vertical course. The commissural lamina of the entopterygoid is very long, with an anterior termination far anterior to the ascending process. Being endoskeletal, the ascending process itself is not preserved. This is also true for the endoskeletal articulation area (anteriormost part of autopalatine) anterior to the commissural lamina, as well as for the quadrate. Holes are present in the horizontal lamina of the entopterygoid. These holes would have been filled by exposures of the (endoskeletal) autopalatine in life.

An anteroventrally directed ridge is present on the mesial face of the entopterygoid (Fig. 6C,D). This ridge marks the posterior limit of the space connecting the spiracular opening to the buccal cavity (Brazeau and Ahlberg 2006). The ridge is slightly more oblique in *Heddeleithys* than in *Eusthenopteron* (Jarvik 1980; Brazeau and Ahlberg 2006). No buccal denticles are preserved.

The dermopalatine has a prominent anterior process, which curves slightly dorsally and mesially. This process defines the lateral edge of the hole left by the unpreserved anteriormost tip of the autopalatine (Fig. 6G–J). It also defines the posterolateral margin of the choana. One fang position is present on the dermopalatine, in addition to a marginal row of smaller teeth. Two dermopalatine fangs are attached in position on specimen BGS 53442, because the replacement fang is fully developed. The ectopterygoid carries one large fang anteriorly, as well as marginal teeth. Posteriorly, there is a smaller fang, which is intermediate in size between the anterior ectopterygoid fang and the marginal teeth.

Each vomer is equipped with a very large fang, which carries a prominent cutting edge (Fig. 6). No marginal tooth row can be observed, but a transverse vertical lamina is preserved anterior to the fang. Each vomer has a long posterior process that runs along the parasphenoid laterally on each side (Fig. 6G–J). The posterior processes are firmly attached to the sides of the parasphenoid. This arrangement can also be seen in *Eusthenopteron* (Jarvik 1980) and *Panderichthys* Gross, 1941 (Per Ahlberg, personal communication), although the posterior processes are shorter in *Panderichthys*. The vomerine processes almost reach the anterior termination of the entopterygoid. The vomers are in medial contact

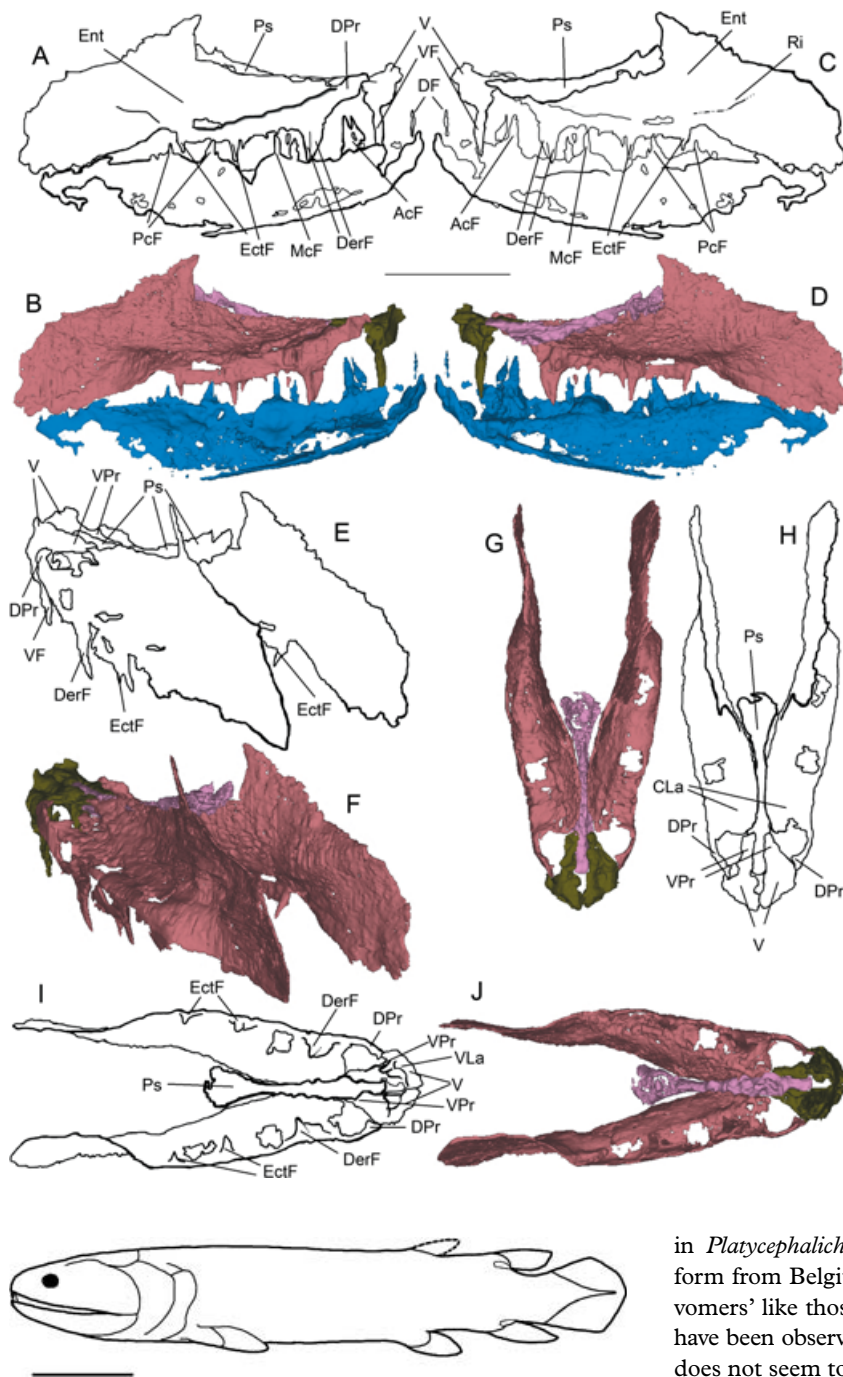


Fig. 6—*Heddeleichthys dalglesiensis* BGS 53442. —**A, B**. Palate and lower jaw in right lateral view. —**C, D**. Palate and lower jaw in left lateral view. —**E, F**. Palate in left posterolateral view; —**G, H**. Palate in dorsal view; —**I, J**. Palate in ventral view. Scale bar = 2 cm. Abbreviations: AcF, anterior coronoid fang; CLa, commissural lamina; DerF, dermopalatine fang; DF, dentary fang; DPr, anterior process of dermopalatine; EctF, ectopterygoid fang; Ent, entopterygoid; McF, middle coronoid fang; PcF, posterior coronoid fang; Ps, parasphenoid; V, vomer; VF, vomerine fang; VLa, vertical lamina of vomer; VPr, posterior process of vomer.

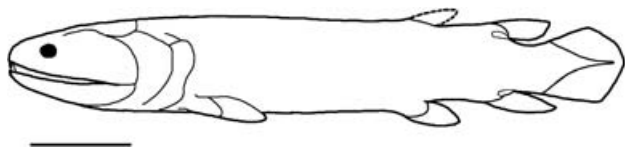


Fig. 7—*Heddeleichthys dalglesiensis*. Body reconstruction, mainly based on NMS.G.1966.39.1 (anterior part) and NMS.G.1966.39.9 (posterior part). Scale bar = 5 cm.

anteriorly, with an intervomerine canal between the anterior termination of the parasphenoid and the midline contact of the vomers. The lateral edge of the posterior process is developed into a large corner, for articulation with the anterior process of the dermopalatine (Fig. 6G–J). A similar condition is seen

in *Platycephalichthys*, *Hyneria* and a new *Eusthenodon*-like form from Belgium (Clément *et al.* in press). No ‘accessory vomers’ like those present in *Cabonnichthys* and *Mandageria* have been observed (Ahlberg and Johanson 1997), and there does not seem to be space for any considering the extension of the posterior processes of the vomers.

The parasphenoid is somewhat hourglass-shaped, with posterior and anterior lateral expansions. The anterior expansion of the parasphenoid partly supports the posterior processes of the vomers ventrally. Posteriorly, the parasphenoid is deflected slightly dorsally, unlike the anterior half, which is orientated horizontally. The anterior extremity of the parasphenoid is at the same level as the anteriormost point of the dermopalatine. A ventral keel or crest is present on the parasphenoid. This is similar to *Eusthenopteron*,

Cabonnichthys and *Mandageria*, where the crest supports a raised, flat denticulated area (Jarvik 1980; Ahlberg and Johanson 1997; Johanson and Ahlberg 1997). *Eusthenodon* instead displays a condition where the denticulated area is slightly concave and recessed into the main body of the parasphenoid. Outgroup comparison with less crownward tetrapodomorphs such as *Medoevia* Lebedev, 1995, *Gogonasus* Long *et al.*, 1997, and *Kenichthys* Chang & Zhu, 1993, suggests that the latter condition is derived (Lebedev 1995; Long *et al.* 1997; Zhu and Ahlberg 2004).

Lower jaw

The general shape of the lower jaw compares closely to that of *Eusthenopteron* (Jarvik 1980) (Figs 3A–D and 4G–I). The dentary is rather slender, and narrows in height posteriorly. A large dentary fang is present anteriorly. Both dentary fangs are preserved in vertical section, so the presence of a cutting edge cannot be confirmed (Fig. 4H). The dentary fang on each side is situated lateral to the corresponding premaxillary pseudofang in the upper jaw. Among tristichopterids, anterior dentary fangs are also present in *Platycephalichthys*, *Cabonnichthys*, *Mandageria*, *Hynieria* and *Eusthenodon*. Dentary fangs can also be found in some members of other sarcopterygian groups (rhizodonts, megalichthyids and tetrapods) (Ahlberg and Johanson 1997).

The coronoids show similar proportions to other tristichopterids [except for *Tristichopterus*, where the posterior coronoid is not quite as elongate (personal observation.)]: the middle and anterior coronoids are almost equal in length, and the posterior coronoid is twice the length of either of these (Fig. 4G,H). The anterior and middle coronoids have one fang position, with the anterior coronoid fang being the largest. As on the dermopalatine, two fangs are present in position on the anterior coronoid (fang and fully developed replacement fang). On the posterior coronoid, two fang positions are present. The posteriormost fang is the smallest of all coronoid fangs. All other tristichopterids except for *Tristichopterus* have the same fang setup, with two positions on the posterior coronoid. A marginal tooth row on a vertical lamina is present on the middle and posterior coronoids (Fig. 4H,I). A precoronoid fossa is present, probably floored by (unpreserved) Meckelian bone in life. The coronoids are separated by intercoronoid fossae (Fig. 4E).

General body shape and squamation

The posterior part of the body is preserved in specimen NMS.G.1966.39.9 (Fig. 5A,B). *Heddleichthys* has round, cosmine-free scales, which are poorly preserved. Traquair (1892) described the scales as thin and rounded with fine, concentric ridges. Round cosmine-free scales are typical for tristichopterids, but are also found in rhizodonts (Ahlberg and Johanson 1998). No internal view of a scale is presented in any specimen, so the presence of an internal boss cannot

be verified. The scales of the caudal peduncle are somewhat smaller than those of the more anterior parts of the body. The size and position of the dorsal fins is similar to that found in *Eusthenopteron*, with the first dorsal opposite the pelvic fins, but unlike *Cabonnichthys* and *Mandageria*, where the dorsal fins are reduced in size and the first dorsal is posteriorly displaced (Ahlberg and Johanson 1997; Johanson and Ahlberg 1997). Basal scutes are present. The caudal fin is symmetrically diamond-shaped, which is the same condition as in *Mandageria*, *Eusthenodon* and *Cabonnichthys*. A body reconstruction is provided in Fig. 7. The presence or absence of independent radials distal to the neural arches (present in *Mandageria* and *Cabonnichthys*), supporting the epichordal lobe of the caudal fin, is not possible to verify in *Heddleichthys*. Overall body length seems to have been around 50 cm, which is within the *Eusthenopteron* size range but smaller than the holotype of *Cabonnichthys*. *Heddleichthys* is the smallest member of the derived part of the Tristichopteridae, fitting in well with the size structure of the Dura Den fauna (with rather small individual fish) suggested in the introduction for *Holoptychius*.

Discussion

The interrelationships of tristichopterids were discussed by Long (1985). He included *Eusthenodon*, *Jarvikina*, *Eusthenopteron* and *Tristichopterus*, and concluded that tristichopterids were a monophyletic group within ‘Osteolepiformes’. The first computer-based analysis of tristichopterid interrelationships was performed by Ahlberg and Johanson (1997). Their resulting cladogram indicated several character transformations that took place within the group, from basal forms like *Tristichopterus* to the most derived members of the clade, such as *Eusthenodon* and *Mandageria*. The latter are characterized by greatly enlarged size, posteriorly displaced median fins, a symmetric diamond-shaped caudal fin, the presence of symphyseal dentary fangs and premaxillary pseudofangs, the presence of cutting edges on the dentary, vomerine and coronoid fangs and the premaxillary pseudofangs, a posteriorly positioned kite-shaped pineal opening, a low posterodorsal expansion of the maxilla, the absence of marginal teeth on the anterior and middle coronoids, and the presence of epichordal radials in the caudal fin. In addition to these features, the bone pattern in the skull roof also varies between basal and derived tristichopterids. This includes different compositions of the orbital margin, variable bone patterns in the snout region, and variable degrees of overlap of the lateral extrascapulars onto the median. Some of the characters just mentioned form the basis of the phylogenetic analysis performed by Ahlberg and Johanson (1997). Because of the small number of characters in this dataset, it is easy to track the character changes. A gradual acquisition of the characteristics of the most derived tristichopterids (*Mandageria* and *Eusthenodon*) is inferred, and serves to establish the various taxa in the group. *Heddleichthys* shares the following character states with *Mandageria* and *Eusthenodon*:

dentary fangs, premaxillary pseudofangs, diamond-shaped caudal fin, a posteriorly placed kite-shaped pineal opening, a low posterodorsal expansion of the maxilla, cutting edges of fangs present (at least on the vomerine fangs), and a median postrostral that ends anterior to the orbits. Retained primitive tristichopterid characteristics of *Heddeleithys* (absent in *Mandageria* and *Eusthenodon*) are: considerable jugal and postorbital contribution to the orbital margin, the presence of marginal teeth on a vertical lamina on the coronoids, small to moderate body size, and contact between the posterior supraorbital and the intertemporal and lachrymal. This unique character combination is what serves to define *Heddeleithys* as a separate tristichopterid genus.

A new phylogenetic analysis and extended discussion of the Tristichopteridae is forthcoming in a separate publication co-authored by the present author.

Heddeleithys is the first tristichopterid described from the British Isles showing the aforementioned derived characters. Previously, the British tristichopterid record was limited to *Tristichopterus* and *Eusthenopteron*, both basal members of the group. The biogeographical record of *Tristichopterus* and *Eusthenopteron* is limited to Laurussia, with occurrences in Scotland, Latvia, Russia and eastern Canada (Johanson 2004). Including new discoveries of *Eusthenodon*, which has been recognized as a widely distributed genus for some time, recent descriptions of tristichopterids belonging to the derived part of the clade (such as *Heddeleithys*, *Mandageria*, *Cabonnichthys* and *Hynieria*) has indicated a wide diversity and biogeographical distribution of moderately to highly derived tristichopterids (Ahlberg *et al.* 2001; Clément 2002; Johanson 2004). This increase in descriptions of widely distributed, closely related taxa lends support to the idea that Gondwana and Laurussia were in close proximity to each other during the Late Devonian, as suggested by Scotese and McKerrow (1990) and McKerrow *et al.* (2000). Other Late Devonian vertebrates also show similar patterns of distribution and migration, as discussed by Ahlberg *et al.* (2001).

An alternative scenario based on palaeomagnetic data places Gondwana further south, possibly at a south polar position, with Laurussia far removed from Gondwana's northern margin (Li *et al.* 1993). If these palaeomagnetic data are reliable, with a south polar position in Central Africa during the Late Devonian–Early Carboniferous, interpretation of the biogeographical data requires a more stretched pathway for taxa dispersing between the two continents, made up of some of the smaller, independent blocks available [via Kazakhstan and Siberia, Li *et al.* (1993)]. This scenario, however, requires a large degree of latitudinal migration, from a tropical to subtropical zone (Greenland, Great Britain, Pennsylvania, Baltica) via much higher latitudes (Siberia, Kazakhstan), and back to the close proximity of the equator again (Eastern Australia).

Given that representatives of all parts of the Tristichopteridae (basal forms: *Tristichopterus*, *Eusthenopteron*; moderately derived forms: *Heddeleithys*, *Jarvikina*; highly derived forms:

Eusthenodon and a *Eusthenodon*-like form from Belgium), as well as the sister taxon of the Tristichopteridae, *Spodichthys* Jarvik, 1985 (Snitting 2008), are now described from Laurussia, whereas only moderately derived and highly derived forms are described from Gondwana (*Cabonnichthys*, *Notorhizodon*, *Mandageria*, *Eusthenodon*) [with the possible exception of an occurrence in Northern Gondwana (present-day Morocco) of *Eusthenopteron* [*Eusthenopteridae* gen. et sp. indet., Lehman 1977; Lelièvre & Janvier 1986]], it seems likely that the emergence of tristichopterids took place somewhere in Laurussia, with a subsequent radiation and dispersal to Gondwana. Since *Eusthenodon*, (together with *Mandageria*) the most derived of all described tristichopterids is also the most cosmopolitan, a continuous migration–dispersal pattern between Laurussia and Gondwana during the Late Devonian is suggested.

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