

On *Cephalaspis magnifica* Traquair, 1893, from the Middle Devonian of Scotland, and the relationships of the last osteostracans

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ABSTRACT: The large Middle Devonian osteostracan *Cephalaspis magnifica* Traquair, 1893a, from the Late Eifelian Upper Caithness Flagstone Group of Caithness, Scotland, is redescribed on the basis of the holotype and a second, hitherto undescribed specimen. This species is assigned to a new genus, *Trewinia* gen. nov. and, on account of its probable lack of lateral cephalic fields, is regarded as a possible member of the Escuminaspididae, which are hitherto only known from the Late Devonian of Quebec, Canada. Other characters of the head shield of *T. magnifica* also accord with the structure of the largest known escuminaspidid *Escuminaspis*. The morphology, relationships and biogeography of the few other Middle and Late Devonian osteostracans are discussed. North American osteostracans are generally quite distinctive from European ones throughout the Devonian, and only few taxa seem common to the two areas. The Escuminaspididae could be one of these, and this would agree with similar distributions met with in other Middle and Late Devonian vertebrates from similar environments. The question of the possible causes of the decline and extinction of the various ‘ostracoderm’ groups after the end of the Early Devonian is briefly discussed, and environmental factors are favoured to account for their decline in abundance and diversity.

KEY WORDS: Canada, Escuminaspididae, Middle–Upper Devonian, morphology, Osteostraci, *Parameteoraspis*, systematics.

The large osteostracan *Cephalaspis magnifica* Traquair, 1893a, currently regarded as the largest representative of this group, is only known from Spittal Quarry in Caithness, Scotland, where it occurs in the lower part of the Upper Caithness Flagstone Group. Only two specimens are known at present, these being the holotype [National Museums of Scotland, Edinburgh (NMS.G) 1893.107.40; Fig. 1] and a second specimen donated in 1967 to the Natural History Museum, London (BMNH P60738a,b; Figs 2–7), which is undescribed. This specimen was discovered some time before it was donated, as indicated by Saxon (1967). This large osteostracan is dated as Late Eifelian and is thus one of the youngest representatives of this group (see Table 1). Other Eifelian osteostracans include, *Balticaspis latvica* Lyarskaya, 1981 (Otto & Laurin 2001a) and *Afanasiaspis porata* Otto & Laurin, 2001b (Otto & Laurin 1999, 2001b), from the Eifelian of Latvia and Estonia, respectively. *Corollaspis walteri* Solcher, 1999 (*nomen nudum*) is from supposedly Eifelian erratic boulders in Germany. The two latest osteostracans come from the Early Frasnian Escuminac Formation of Miguasha (Quebec, Canada) being, *Escuminaspis laticeps* (Traquair, 1890) [synonyms: *Cephalaspis rosamundae* Robertson, 1937, *Alaspis macrotuberculata* Ørvig, 1957; see discussion in Arsenault & Janvier (1995)] and *Levesquaspis patteni* (Robertson, 1936) (Arsenault & Janvier 1995).

The holotype of *C. magnifica* has only been illustrated in the form of a poorly informative drawing (Traquair 1894, pl. 7) and is redescribed here. In his monograph on the cephalaspids of Great Britain, Stensiö (1932, p. 142) stated that he never examined the holotype as it ‘could not be sent to Stockholm on account of its fragility’ and thus relied on Traquair’s description. The specimen BMNH P60738, which is represented by its part and counterpart, is far better preserved than the holotype, and provides some additional information as to the possible



relationships of this enigmatic form. There is little doubt that the two specimens belong to the same species, as they share the same size and proportions, the same characters of the ornamentation, and come from the same locality and horizon. In the 1980s, a redescription of this species was undertaken by M. Rowlands, under the supervision of Professor T. S. Westoll at the University of Newcastle-upon-Tyne, but was unfortunately never published and has thus not been used in this present work. The goal of the present article is to briefly redescribe the holotype and the referred specimen of *C. magnifica*, discuss its affinities, and provide some remarks on the Middle–Late Devonian osteostracans in general.

1. Geographical and geological setting

The Middle Devonian stratigraphy of Caithness is presently under a major review by the British Geological Survey and one of the authors (MJN), but the position of Spittal Quarry is fairly well known. The holotype of *C. magnifica* and specimen BMNH P60738 both come from Spittal Quarry in central Caithness, Scotland. Spittal Quarry is in the lower part of the Upper Caithness Flagstone Group (recently relegated to a subgroup by Auton (2003)), more precisely in the lower part of the Latheron Subgroup (Trewin & Thirlwall 2002). The new name, the Spittal Flagstone Formation, which includes Spittal Quarry and is equivalent to the Latheron Subgroup (Auton 2003), has been adopted by the British Geological Survey. The Spittal Flagstone Formation lies immediately above the Achanarras Fish Bed Member (also a new name, Auton 2003). A handwritten note (probably by T. S. Westoll) on the Natural History Museum specimen indicates a height of 200 ft (60 m) for Spittal Quarry’s stratigraphical height above the Achanarras Fish Bed Member and it may even be less than this. The Achanarras Fish Bed Member (also referred to as the

Table 1 List of the Middle and Upper Devonian osteostracans

Taxon	Locality	Formation	Age	References
<i>Escuminaspis laticeps</i> (Traquair, 1890)	Miguasha, Quebec, Canada	Escuminac Formation	Lower Frasnian	Arsenault & Janvier 1995; Janvier & Arsenault 1996, and references therein
<i>Levesquaspis patteni</i> (Robertson, 1936)	Miguasha, Quebec, Canada	Escuminac Formation	Lower Frasnian	Arsenault & Janvier 1995; and references therein
<i>Ilemoraspis kirkinskayae</i> Obruchev, 1961	Tchazykoiza area, autonomous region of Khakass, Russia	Ilemorovskaya Group	? Givetian (but now possibly Emsian or Eifelian)	Obruchev 1961; Afanasieva & Janvier 1985; Afanasieva 1991; A. Ivanov, pers. com. 2004
<i>Trewinia magnifica</i> (Traquair, 1893a)	Spittal Quarry Caithness	Lower part of the Upper Caithness Flagstone Group	Lower part of the Upper Eifelian	This article and references herein
<i>Balticaspis larvica</i> Lyarskaya, 1981	Talsi, Latvia (borehole core)	Pärnu Formation, Tori Member	Lowermost Eifelian	Otto & Laurin 2001a
<i>Afanassiaspis porata</i> Otto & Laurin, 2001	Tori Porgu, Estonia	Pärnu Formation, Tori Member	Lowermost Eifelian	Otto & Laurin 1999, 2001b
<i>Corollaspis walteri</i> , <i>nomen nudum</i>	Northern Germany	Erratic boulder	Middle Devonian	Solcher 1999

Achanarras-Niandt Limestone Member) is dated as Eifelian, more precisely the lower part of the Upper Eifelian (Trewin & Thirlwall 2002, fig. 8.17, p. 232). However, on the basis of the Devonian vertebrate faunas (in particular the occurrence of the arthrodire *Coccosteus cuspidatus*), Mark-Kurik (2000) correlates it with the Kernave horizon of Estonia, which is regarded as slightly younger, and uppermost Eifelian in age. However, there will be certain time drags of certain species. Recent investigations by the British Geological Survey and one of the authors (MJN), have shown that *Dipterus valenciennesi* occurs in older rocks in eastern Caithness than western Caithness, the findings of which will be published shortly in the new geological map of the Dounreay area (and there is no reason why *C. cuspidatus* might not be the other way round). To have a species appear at the same time everywhere should be considered with some reservations, especially in continental or marginal marine situations, as in the case of the Orcadian Basin and the Baltic region, where there are significant barriers between areas. Whatever the dating, *C. magnifica* is thus Late Eifelian in age; that is, the next youngest known osteostracan.

2. Systematic study

Like many other osteostracan species, *C. magnifica* has been referred to the genus *Cephalaspis*, because of its overall, horseshoe-shaped head shield. Any discussion about the status of the numerous *Cephalaspis* species requires a brief historical and nomenclatural review of this classical taxon, as already accounted for by White (1958).

The genus *Cephalaspis* was erected by Agassiz in 1835 (p. 135) for three species, *Cephalaspis lyelli* Agassiz, 1835, *Cephalaspis lloydi* Agassiz, 1835, *Cephalaspis lewisi* Agassiz, 1835, only one of which, *C. lyelli*, is an osteostracan, the other two species being heterostracans [the plates 1a, b in Agassiz (1835), with the illustration of the specimens, were in fact published in 1837].

C. lewisi and *C. lloydi* were then referred to the genus *Pteraspis* by Kner (1847), who thought they were the shells of cuttlefish. Huxley (1858) made thin sections through the plates of these two species, and demonstrated that they were actually vertebrate fragments, as they show evidence of a dentine layer (a hard tissue unique to vertebrates). He retained the name *Pteraspis* for them though, as their acellular histological structure was clearly different from that of the other specimens referred to *Cephalaspis*. *C. lyelli* remained thus the only species referred to *Cephalaspis*, but Agassiz's description of this species was based on a number of specimens from various localities of Scotland and England, only five of which were figured [Agassiz, 1835, pl.1a, figs1, 2; pl. 1b, figs1, 3, 5 (the specimen illustrated in the latter figure has been lost since at least 1870)]. Lankester (1870) erected two new species for three of the four remaining figured specimens: *Cephalaspis powriei* for the specimens figured by Agassiz (1835) in plate 1a, figure1 and plate 1b, figure1, and *Cephalaspis agassizi* for the specimen figured by Agassiz (1935) in plate 1b, figure 3. This left only one, relatively complete, specimen (BMNH 20087), figured by Agassiz (1835, pl.1a, fig. 2), which could bear the name *C. lyelli*, and was selected as the lectotype of this species by Lankester (1870). The counterpart of the latter specimen, which belonged to the collection of the Earl of Enniskillen, was reunited with its part in the collection of the British Museum (Natural History) in 1882 (BMNH P. 3233). White (1958) provided a detailed description of this specimen, based on both its part and counterpart, which now serves as a basis for defining the characters of the genus *Cephalaspis*.

Unfortunately, because of the lack of detailed information on the morphology of the lectotype of the type species of

Cephalaspis until 1958, many osteostracan species of this genus have been erected since Agassiz's monograph, generally on the basis of the vague resemblance of their head shield to that of *C. lyelli*, which is merely a general cornuate osteostracan morphology (Janvier 1981b, 1984, 1985a–c). Since 1835, 125 species have at one time or another been referred to *Cephalaspis* in publications (not to mention unpublished species names written on collection labels). Out of these species, four are *nomina nuda*, four have been synonymised with other osteostracan species, 67 have been referred to other genera, 19 are still provisionally referred to as '*Cephalaspis*', but show no character of the genus *Cephalaspis* or even the Cephalaspididae, although possibly belonging to the Cephalaspidida, and 30 are also provisionally referred to as '*Cephalaspis*', although they are of uncertain affinity and certainly do not belong to the Cephalaspidida. Finally, three species, *Cephalaspis producta* Wängsjö, 1952, *Cephalaspis cradleyensis* Stensiö, 1932, and *Cephalaspis sollasi* Stensiö, 1932, are regarded by Janvier (1985a, b) as possibly more closely related to *C. lyelli* than to any other osteostracan species, and are thus retained in the genus *Cephalaspis* proper. The latter four species share, in addition to characters of the Cephalaspidida and Cephalaspididae (Janvier 1985a, b), a small number of admittedly vague but apparently unique characters, such as a rather long preorbital portion of the head shield, a narrow median cephalic field, and an anterior shield margin that is roughly parabolic in shape. In fact, the genus *Cephalaspis* may well turn out to become restricted to its type species when a thorough revision of the British osteostracans is made, with consideration of the dermal ornamentation and other characters in all type specimens of the various species once referred to as *Cephalaspis*.

Cephalaspis magnifica is one of these numerous species which have been referred to *Cephalaspis* because of their rather generalised cornuate osteostracan morphology (horseshoe-shaped head shield and posteriorly or posterolaterally directed cornual processes), and because no other conspicuous characters suggest any relationships with another particular osteostracan genus. Its large size, broad cornual processes and broad median dorsal field vaguely suggested affinities with other, similarly-shaped osteostracans now referred to the genus *Parameteoraspis* Blicek, Goujet & Janvier, 1987 (Stensiö 1932, Wängsjö 1952, Janvier 1985a), yet with much reservation. Interestingly, Stensiö (1932, p. 144) considered that, in addition to various *Parameteoraspis* species, *C. magnifica* also bore some resemblance to *Escuminaspis* ('*Cephalaspis*') *laticeps*. In fact, the present study of the holotype of *C. magnifica* (NMS.G 1893.107.40) and the specimen BMNH P60738 shows that it probably lacks lateral cephalic fields. Although this character is merely an absence of a feature, it is only known in two other osteostracans, *E. laticeps* and *Levesquaspis patteni*, referred to a particular family, the Escuminaspididae (Arsenault & Janvier 1995), which is only characterised by this particular lack of lateral cephalic fields. This is regarded as a derived condition, since lateral fields are present in all other cornuate and non-cornuate osteostracans [the 'non-cornuate' osteostracans are a paraphyletic ensemble, which includes notably *Ateleaspis*, *Aceraspis*, *Hirella*, and *Hemicyclaspis*, the latter being the sister-group to the cornuates (Heintz 1939, Janvier 1981a,b, 1984, 1985a–c, 1996)].

The overall shape and size of the head shield of *C. magnifica* agrees best with that of *E. laticeps* (Janvier & Arsenault 1996, fig. 9) among the Escuminaspididae, but the two species differ somewhat in their ornamentation, which consist of thin, parallel or radiating rows of minute tubercles, sometimes forming thin ridges, in *C. magnifica* (Fig. 3C), and large,

rounded, mushroom-shaped tubercles in *E. laticeps* (Ørving 1968, Janvier & Arsenault, 1996, fig. 1C). However, the ornamentation of *C. magnifica* could be derived from a more simple, tuberculate ornamentation, which is widespread in osteostracans. Because of the uncertainty as to its lack of lateral cephalic fields, and because of its almost unique type of ornamentation, we prefer here to refer *C. magnifica* to a new genus, yet probably to be either referable to, or closely related to the Escuminaspididae.

Class Osteostraci Lankester, 1870

Subclass Cornuata Janvier, 1985b

Order indet.

Family ? Escuminaspididae Arsenault & Janvier, 1995

Genus *Trewinia* gen. nov.

Diagnosis. As for the type species (by monotypy).

Type species. *Cephalaspis magnifica* Traquair, 1893a

Origin of name. In honour of Professor Nigel Trewin (University of Aberdeen), a leading specialist of the Devonian of Scotland.

Trewinia magnifica (Traquair, 1893a)
(Figures 1–8)

v*1893a *Cephalaspis magnifica*; Traquair, p. 747.

1893b *C. magnifica*; Traquair, p. 206.

1894 *Cephalaspis magnifica* Traquair; Traquair, p. 269, pl. 7.

1932 *Cephalaspis magnifica* Traquair; Stensiö, p. 142, fig. 51.

1937 *Cephalaspis magnifica*; Westoll, p. 15.

1967 *Cephalaspis magnifica*; Saxon, p. 9.

1971 *Cephalaspis magnifica* Traquair; Henrichsen, p. 2.

1975 *Cephalaspis magnifica*; Saxon, p. 13.

1993 *Cephalaspis magnifica*; Trewin, p. 139.

1999 *Cephalaspis magnifica*; Dineley, p. 207.

Emended diagnosis. A large cornuate osteostracan with an almost semicircular head-shield margin, and probably lacking lateral cephalic fields. The tesserae of the exoskeleton are loosely connected (by lack of underlying endoskeletal ossification), proportionally small, and externally ornamented with parallel rows of very small, elongated tubercles, sometimes arranged in radiating rows on the larger tesserae. The tesserae of the orbital margins are ornamented with larger, rounded tubercles. The median cephalic field is broad, with parallel lateral margins, and covered with tesserae that are significantly smaller than those of the rest of the dorsal exoskeleton. The medial margin of the cornual processes is strengthened by a broad medial marginal plate that only bears slight indications of widely spaced and blunt mesial spiniform processes.

Holotype. NMS.G.1893.107.40 (Fig. 1), Edinburgh: an almost complete but slightly distorted head shield, preserved in dorsal aspect, associated with possible patches of the body squamation.

Referred material. BMNH P60738a,b, London (Figs 2–7): a complete but slightly distorted head shield preserved as part and counterpart, with associated patches of the right pectoral fin.

Horizon and locality. The two specimens known to date come from the same horizon and locality: the lower part of the Latheron Subgroup in the lower part of the Upper Caithness Flagstone Group, about 60 m above the Achanarras Fish Bed Member, lower part of the Upper Eifelian (Middle Devonian); Spittal Quarry (grid reference [ND173540]), Caithness, Scotland.

Remarks. The first mention of the name *Cephalaspis magnifica* occurs in a brief communication by Traquair (1893a). This author did not designate a holotype, but since the specimen referred to in the publication was unique, it can implicitly and unambiguously be regarded as the holotype. In this article, Traquair does not illustrate the specimen but mentions enough characters (shape, size, ornamentation) to regard the name as available and valid in 1893. His subsequent, more detailed description is accompanied by the first and only illustration of the holotype published to date (drawings of the entire specimen, of the ornamentation of two tesseræ and of an ensemble of tesseræ; Traquair 1894, pl. 7, figs 1–4).

2.1. Description

Specimen NMS.G 1893.107.40 (holotype). This specimen consists almost entirely of an impression with very little bone left (Fig. 1A). Perhaps it has deteriorated over the years, but little of what Traquair (1893a,b, 1894; repeated by Stensiö 1932) described is now visible. Small patches of bone exist, but would probably yield no histological information, as they are poorly preserved and do not include the full thickness of the bone. The only place where the bone is better preserved and shows the ornamentation is by the right orbit (Fig. 1C). The organisation of the exoskeleton can be seen as an impression of its basal surface (though it is fairly poor) and consists of fairly small polygonal tesseræ. The smaller scale ornamentation can only be seen by the right orbit, but consists of reasonably large tubercles (Fig. 1C). The presence of ornamentation on the circumorbital tesseræ indicates that the specimen is exposed in dorsal aspect.

Only the gross morphology can be discerned from this specimen. The orbits are fairly large (as is the whole headshield compared to most cephalaspids for that matter). Of note is the fact that the internal impression of the dermal bone of the medial orbital margin, seems interrupted in the middle of its medial margin (arrowhead, Fig. 1C); that is, at the level where the pineal plate meets the orbital margin in many other osteostracans (Janvier 1985a, fig 98). This is certainly a highly conserved landmark in the osteostracan exoskeleton, even when no independent pineal plate is present. The pineal (if any) and nasohypophysial openings could not be located with any degree of confidence due to the lack of bone in those areas, though vague impressions indicate the rough area between the orbits where they might have been. No lateral fields are visible, though the impression of a fairly large median field appears to be present. Vague impressions of probable, marginal spiniform processes can be seen along the medial margin of the medial marginal plate of the left-hand cornual process.

Although this head shield is certainly preserved in dorsal aspect, the impression of the roughly rectangular tesseræ, which form the rim of the oralbranchial fenestra, are underprinted below the dorsal surface (Fig. 1A, B). The fact that they appear as concave indicates that their external surface faces down. The actual outline of the oralbranchial fenestra is only known in this specimen, and shows a vague impression of a relatively broad oral notch.

Specimen BMNH P. 60738. This specimen consists of the part and counterpart of the same individual (Fig. 2). BMNH P. 60738b (Fig. 2B) shows patches of the actual dorsal surface of the exoskeleton and, more generally, either the impression of the internal (basal) surface of the exoskeleton, or patches of its basal layer. It is referred to below as the ‘part’. BMNH P. 60738a (Fig. 2A) shows essentially the impression of the external surface of the dorsal exoskeleton, with some patches of its superficial layer. It is referred to below as the ‘counter-

part’. Both also show some underprinted parts of the ventral exoskeleton, in particular the larger tesseræ surrounding the oralbranchial fenestra, which have been scattered into several, displaced portions (vr, Fig. 2A). A patch of small tesseræ situated in the right pectoral sinus of BMNH P. 60738b probably belongs to the squamation of the pectoral fin (pfs, Fig. 7). No body scale can be identified with certainty, although small fragments of exoskeleton that extend posteriorly to the head shield may be remnants of the anterior-most dorsal body squamation. The posterior margin of the interzonal division of the head shield is indistinct and formed by loose tesseræ, which progressively turned into the body squamation, as in *Escuminaspis laticeps*.

As in the holotype, the overall shape of the head shield is somewhat difficult to reconstruct, because of the dorsoventral compression of the specimen and foldings of its margins, which has distorted its outline. The outline of the reconstruction in Figure 8 is, however, essentially based on this specimen, which seems to have been less distorted in this respect. The slightly lobate anterior margin of the holotype is, we suspect, a consequence of a more extensive distortion. The same uncertainty also occurs in the shape of the head shield in *E. laticeps*, because of the loose connection between the tesseræ and the virtual lack of endoskeletal ossification (Janvier & Arsenaault 1996).

Cephalic fields. The median cephalic field is clearly visible on both the part and counterpart (Fig. 3A, B). Its lateral limits are well defined and formed by a series of slightly enlarged tesseræ of the main shield exoskeleton (hst, Fig. 4). In contrast, its anterior and posterior limits are less distinct. In the counterpart, it looks as if it is bounded posteriorly by a transverse series of large tesseræ, but these are in fact underprinted tesseræ of the posterior part of the margin of the oralbranchial fenestra (vr, Fig. 2A). The actual posterior limit of the field seems to be situated slightly behind this transverse series of tesseræ. Anteriorly, the median field seems to end at the level of the pineal region (pi, Fig. 3B), but shows a slight decrease in breadth just behind its anterior limit. As a whole, it was roughly rectangular in shape. The tesseræ which cover the median field (mft, Fig. 4) are significantly smaller than those of the surrounding exoskeleton (hst, Fig. 4), and seem to slightly decrease in size anteriorly (Fig. 3D).

The question of the presence or absence of lateral cephalic fields is not conclusively settled, but there is a strong probability for the lack of these fields. On the left side of this specimen, there seems to be a gap between the tesseræ of the dorsal exoskeleton and those of the shield margin (Fig. 2), and this vaguely suggests the presence of a relatively narrow lateral field that would lie close to the shield margin, more or less similar to that in *Parameteoraspis* (Janvier 1985a). There are three lines of argument for considering that this gap is an artefact of preservation. Firstly, this gap shows no evidence for tesseræ, be they smaller, as in the median field, or of similar size to those in the rest of the shield exoskeleton (the fact that the tesseræ covering the median field are still present and undisturbed makes it unlikely that all the lateral field tesseræ would be lost). Second, the few traces of exoskeleton seen in this gap show no trace of ornamentation and seem to be exposed in basal view, and they extend beneath the tesseræ of the dorsal surface of the shield. They are thus likely to be remnants of the ventral exoskeleton that extends between the oralbranchial fenestra and the shield margin. Third, the lateral limit of the dorsal shield tesseræ shows no evidence for a straight boundary, as seen in the case of the median field (Figs 3A, B, D, 4). This, admittedly, may not be a good argument, because the limit between the dorsal shield tesseræ and the lateral field tesseræ may be rather irregular in shape in



Figure 1 *Trewinia magnifica* (Traquair 1893a), Lower part of the Upper Caithness Flagstone Group, Eifelian (Devonian); Spittal Pavement Quarry, Caithness, Scotland. Holotype (National Museums of Scotland, Edinburgh, Geology; NMS.G 1893.107.40). Imperfect head shield in dorsal aspect. (A) general view of the specimen; arrowhead points towards the right-hand side of the head shield; (B) detailed view of the impression of the tesseræ, which form the rim of the oralbranchial fenestra; (C) detailed view of the right orbit and the remnants of the circumorbital tesseræ, showing traces of the tuberculate ornamentation; arrowhead points towards the interruption in the circumorbital margin, corresponding to the position of the pineal plate component. Scale bars = 10 mm.

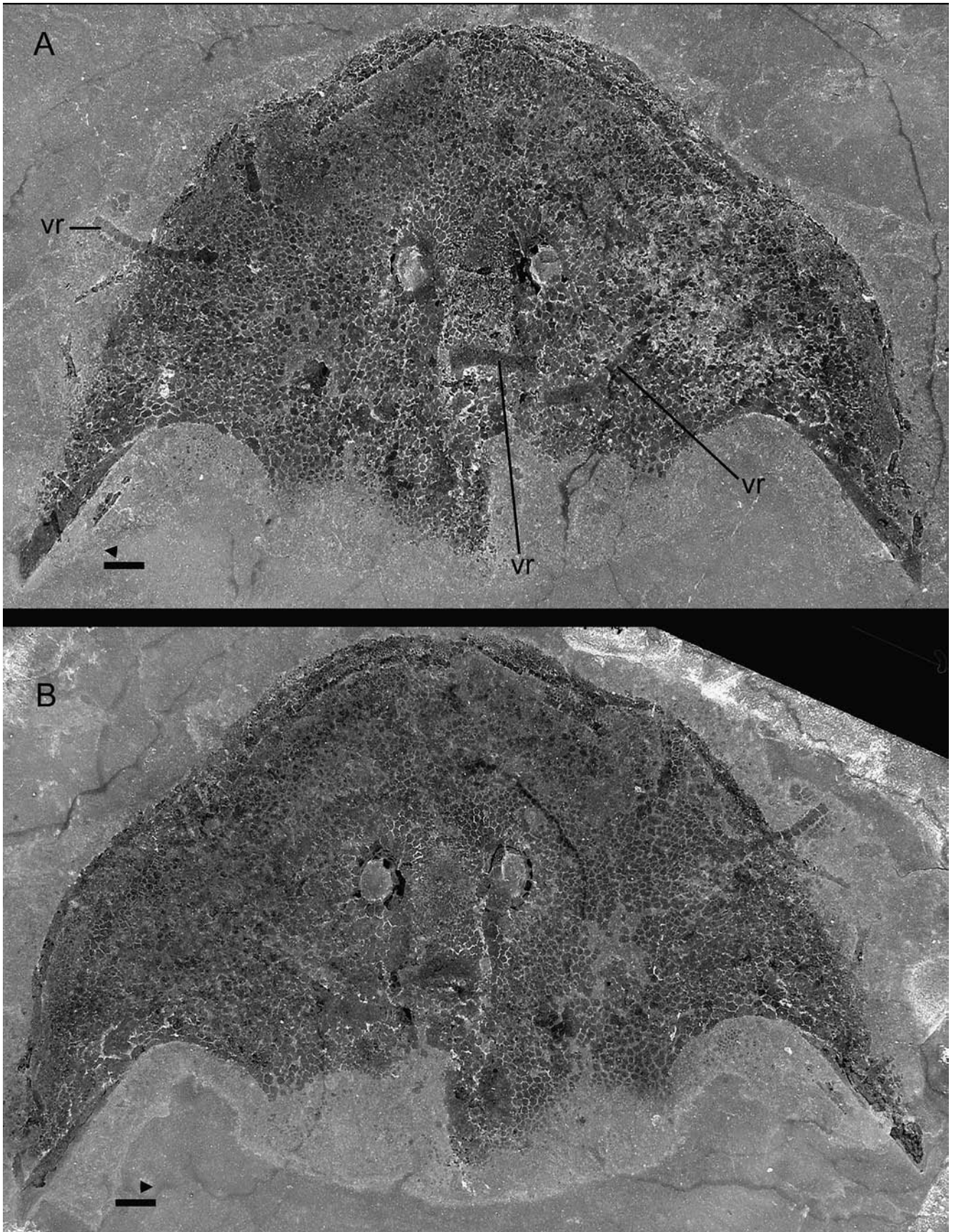


Figure 2 *Trewinia magnifica* (Traquair 1893a), Lower part of the Upper Caithness Flagstone Group, Eifelian (Middle Devonian); Spittal Pavement Quarry, Caithness, Scotland. Specimen BMNH P. 60738, Natural History Museum, London. (A) Counterpart of the head shield in dorsal aspect (P. 60738a); (B) part of the head shield in dorsal aspect (P. 60738b). Scale bars = 15 mm. Arrowheads point towards the right-hand side of the head shield. Abbreviation: (vr) underprinted portions of the ventral rim of the oralbranchial fenestra.

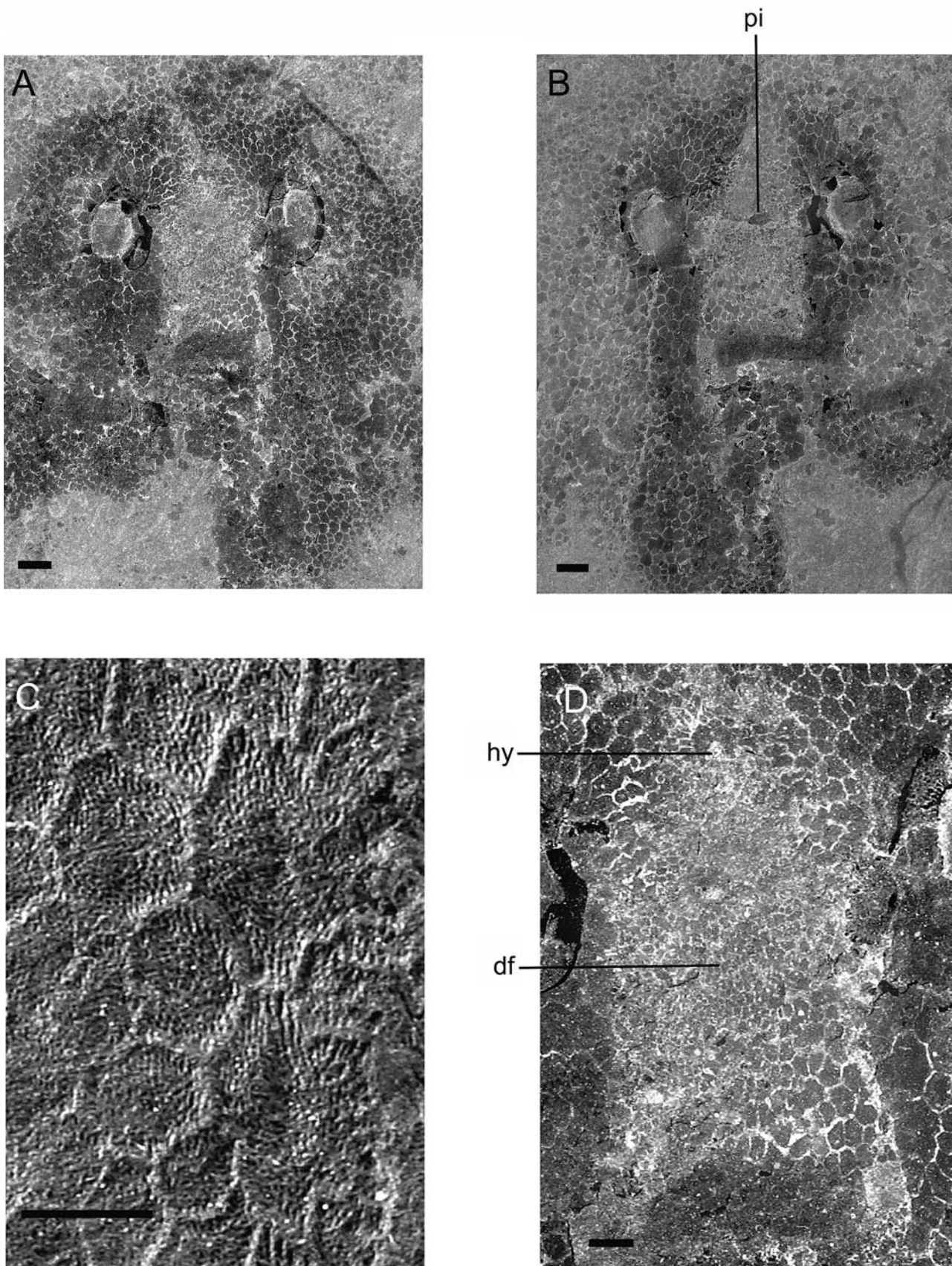


Figure 3 *Trewinia magnifica* (Traquair 1893a), Lower part of the Upper Caithness Flagstone Group, Eifelian (Middle Devonian); Spittal Pavement Quarry, Caithness, Scotland. Specimen BMNH P. 60738, Natural History Museum, London. (A, B), detail view of the central part of the head shield, comprising the median cephalic field, the orbitopineal and circum-nasohypophysial regions (A) part, P. 60738b; (B) counterpart, P. 60738a). (C) Detail view of the impression of the head shield tesserae which border the right margin of the median cephalic field (counterpart, P. 60738a); (D) enlarged view of the median dorsal cephalic field tesserae and circum-nasohypophysial regions (part, P. 60738b). Scale bars=10 mm for (A, B); 5 mm for (C, D). Abbreviations: (df) median dorsal cephalic field; (hy) hypophysial division of the nasohypophysial opening; (pi) fragment of unperforated exoskeleton covering the pineal region.

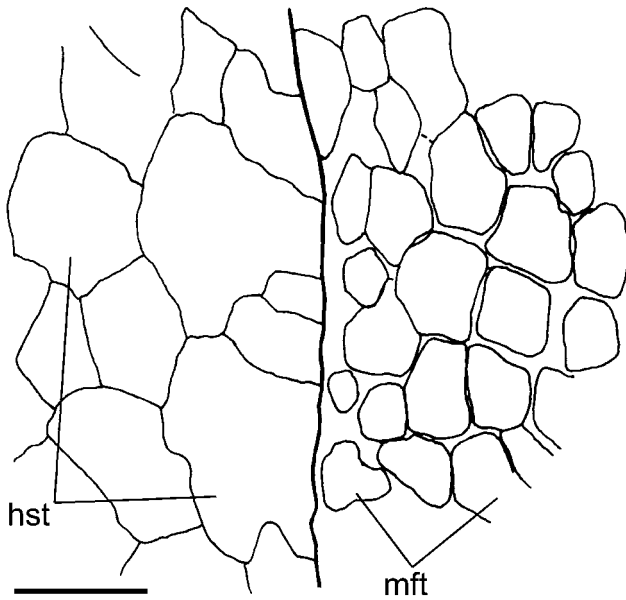


Figure 4 *Trewinia magnifica* (Traquair 1893a), Lower part of the Upper Caithness Flagstone Group, Eifelian (Middle Devonian); Spittal Pavement Quarry, Caithness, Scotland. Specimen BMNH P. 60738, Natural History Museum, London. Camera lucida drawing of the tesserae on either sides of the right-hand side margin of the middle part of the median dorsal cephalic field (based on P. 60738a; detail of Figure 3A). Scale bar=5 mm. Abbreviations: (hst) main head shield tesserae; (mft) median field tesserae.

the Zenaspida (e.g., Janvier 1985a, pl.2:1), which, however, display well-delineated median field margins [in contrast to the Cephalaspida (e.g. *Cephalaspis*, *Parameteoraspis*), which generally display well-delineated both lateral and median field margins]. We assume here that this gap in the exoskeleton of *T. magnifica* is not a lateral field, but rather results from a preservational artefact between the dorsal shield tesserae and those of the shield margin, due to the dorsoventral compression of the shield during fossilisation. More anteriorly on the left side of the same part, this disruption does not seem to have occurred and the dorsal shield tesserae seem to extend to the shield margin without any notable change in size and aspect. Still in the same part, a similar disruption seems to have occurred over a short distance anterolaterally on the left side, and the shield margin is totally lacking in the right lateral and posterolateral part of the shield (Fig. 2).

Orbits. The orbits are relatively large and oval in shape (Figs 2, 3, 5A). They are bordered medially and anteriorly by large, circumorbital tesserae (cort, Fig. 5B), and smaller ones laterally (Fig. 5A). These tesserae are ornamented with series of elongated tubercles, as on the rest of the dorsal surface of the head shield, but these abruptly turn into rather large, rounded tubercles near the orbital margin proper, as also seen in the holotype (Figs 1C, 5).

Nasohypophysial opening. The hypophysial division is the only part of the nasohypophysial opening that can be observed, and is best seen on the part of the specimen (Fig. 3A; hy, Fig. 6A). It is a small embayment in a single, horseshoe-shaped tessera (hyt, Fig. 6A), which, in turn, is surrounded anteriorly and laterally by several concentric series of smaller, sub-rectangular tesserae (Fig. 6A). Such a relatively large tessera, or hypophysial tessera, bordering the nasohypophysial opening anteriorly occurs in some other osteostracans, notably *Superciliaspis* (Dineley & Loeffler 1976, pl. 26; Adrain & Wilson 1994, fig. 5A) and *Ilemoraspis* (Afanassieva & Janvier 1985, fig. 6). The condition in *Escuminaspis* is unclear in this respect, but some specimens seem to show such a larger dermal bone unit anteriorly bordering the hypophysial division

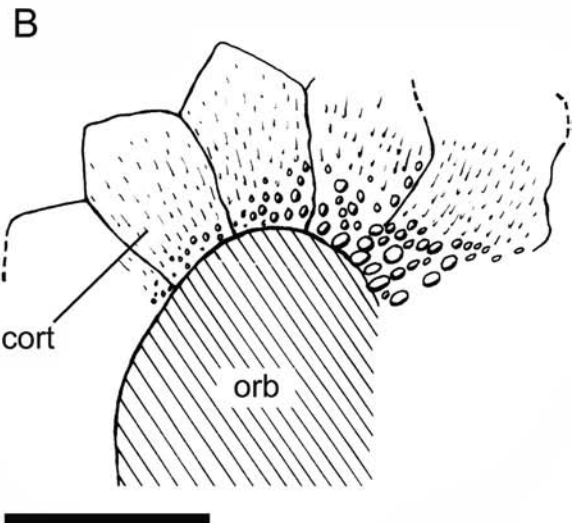
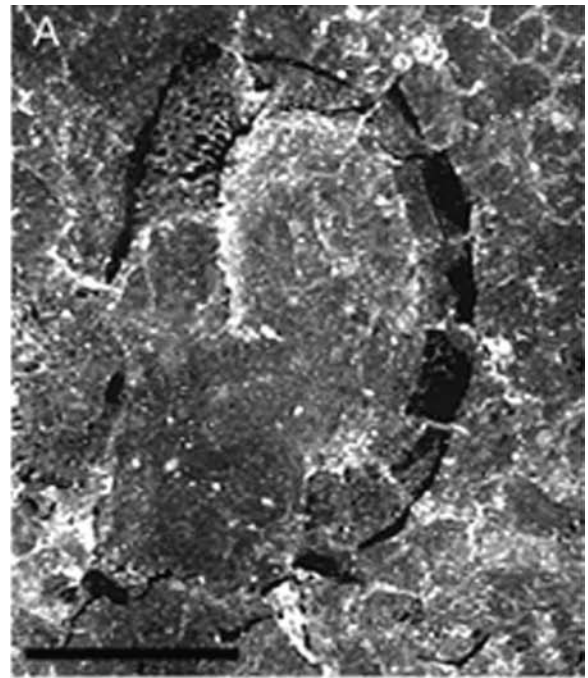


Figure 5 *Trewinia magnifica* (Traquair 1893a), Lower part of the Upper Caithness Flagstone Group, Eifelian (Middle Devonian); Spittal Pavement Quarry, Caithness, Scotland. Specimen BMNH P. 60738, Natural History Museum, London. (A) Orbit of the right-hand side of the part (P. 60738b); (B) camera lucida drawing of the tesserae surrounding the left-hand side orbit of the counterpart (P. 60738a; detail of Figure 2A). Scale bars=10 mm. Abbreviations: (cort) circum-orbital tesserae; (orb) orbit.

(Janvier & Arsenaault 1996, fig. 1B, C). This is particularly clear in an as yet undescribed specimen in the Miguasha Museum of Natural History (MHN 1–12–01A), in which the nasohypophysial opening straddles two large median tesserae: an anterior one, which includes the hypophysial division, and a posterior one, which includes the nasal division, as in *Superciliaspis*. Certain Early Devonian zenaspids (e.g., *Zenaspis powriei*, Stensiö 1932, pls 28:3, 30:3, *Zenaspis pagei*, Stensiö 1932, pl. 38:3) also display a similar hypophysial tessera. In large zenaspids (e.g. *Diademaspis*, Janvier 1985a, pl. 3:1a, 3b) however, the hypophysial division is surrounded by minute tesserae. The condition in the large species of *Parameteoraspis* is unclear, because of the continuous superficial layer of the exoskeleton, but some specimens show faint traces of the tesserae in this region, and their nasohypophysial opening is

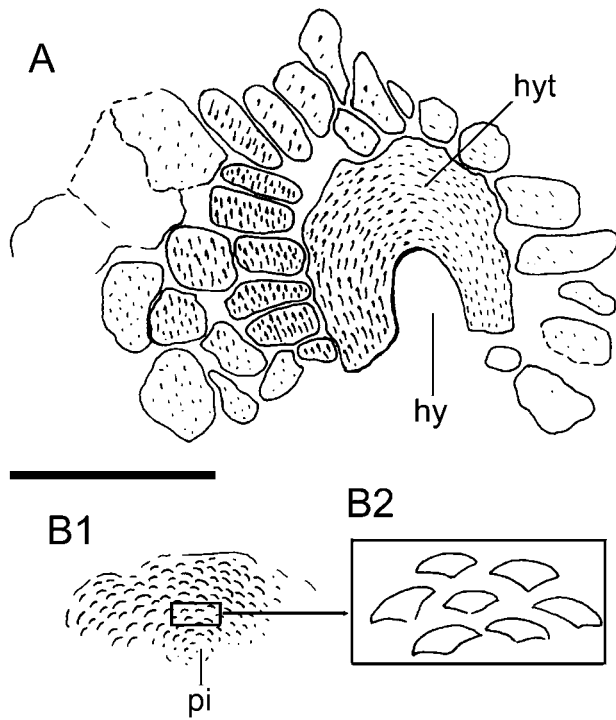


Figure 6 *Trewinia magnifica* (Traquair 1893a), Lower part of the Upper Caithness Flagstone Group, Eifelian (Middle Devonian); Spittal Pavement Quarry, Caithness, Scotland. Specimen BMNH P. 60738, Natural History Museum, London. (A) Camera lucida drawing of the anterior part of the circum-nasohypophysial region, based on the part (P. 60738b); (B) camera lucida drawing of the pineal region, based on the counterpart (P. 60738a; B1) and detail drawing showing the shape of the tubercles immediately in front of the centre of the pineal region (B2). Scale bar=5 mm for (A) and (B1). Abbreviations: (hy) hypophysial division of the nasohypophysial opening; (hyt) circum-hypophysial tessera; (pi) presumed centre of the pineal region, as indicated by the concentric rows of tubercles.

bounded by minute tesserae, but a large hypophysial tessera seems to be present anteriorly (Janvier 1985a, pl. 6:2b). The size and rounded shape of the hypophysial division of the nasohypophysial opening of *Trewinia magnifica*, however, recalls the condition in most generalised zenaspids (Janvier 1985a, fig. 59D), but also in *Escuminaspis* (Janvier & Arsenault 1996, fig. 4A). Although this may be a rather general morphology for osteostracans, it suggests that the shape of the naso-hypophysial opening was quite different from the slit-shaped one in *Parameteoraspis*, *Yvonaspis*, the *Benneviaspida* and *Kiaeraspida* (Janvier 1981b, 1985a; Belles-Isles 1989). The nasal division of this opening is unknown, and is hypothetically reconstructed in Figure 8.

Pineal region. There is no clear evidence for a pineal foramen, but the interorbital region shows traces of a thicker, transverse exoskeletal bar (Fig. 3B), which may include remnants of the pineal plate, as found in other large osteostracans, such as *Diademaspis* and *Parameteoraspis* (Janvier, 1985a). The place where the pineal opening should have been situated is clearly visible in imprint in the counterpart (pi, Figs 3B, 6B1), but shows no evidence for an opening. Instead, it is covered with closely-set, minute lozenge-shaped tubercles arranged into concentric rows (Fig. 6B2), centered on an area where the pineal opening should normally be located (pi, Fig. 6B1). At this level, however, there is no clear distinction in size between the foremost tesserae of the median field and the tesserae which cover the pineal and circum-nasohypophysial area.

Sensory-line grooves. Virtually no sensory-line grooves or canals can be observed on this specimen, essentially because the external surface of the exoskeleton, when preserved, is still much covered with matrix in the part, and because good impressions of the external surface in the counterpart are limited to a few areas, where no such groove occurs. Only a very short, transverse sensory-line groove may be visible, passing through the centre of two adjacent tesserae of the median field margin (Fig. 3C). If this slight groove actually is a sensory line, it would correspond to the proximal portion of the transverse postorbital sensory line (Janvier 1974, fig. 1). The only way to possibly observe a large part of the sensory-line pattern would be to remove entirely what is left of the exoskeleton in the counterpart.

Cornual processes. The cornual processes are broad and posterolaterally directed, and compare with those of some species of *Parameteoraspis* [e.g., *Parameteoraspis hoegi* (Stensiö, 1927), *Parameteoraspis gigas* (Wängsjö, 1952), or *Parameteoraspis lanternaria* (Wängsjö, 1952); see Janvier 1985a, figs. 107A, 112A, 114], but also *Escuminaspis* (Janvier & Arsenault, 1996, fig. 5). They are bordered medially with a single, large exoskeletal unit, referred to as the medial marginal plate. The surface of this plate is ornamented with series of small, elongated tubercles and bears a few, smooth and widely spaced spiniform processes along its medial edge, as also observed in the holotype (see above). These medial cornual ‘spines’ occur in a wide range of cornuate osteostracans and generally tend to become much reduced and even disappear in species with broad and flat cornual processes. The medial marginal plates form the entire tip of the cornual process, and, on the left-hand side, their dorsal surface shows a very small, anterolateral triangular embayment (Fig. 2). A similar embayment occurs in the same way in the medial marginal plate of *Parameteraspis* (Janvier 1985a, pls. 8: 3, 4; 9: 1a, 2a), where it accommodates the posterior tip of the lateral cephalic field, and its presence in *T. magnifica* could support the hypothesis that lateral fields were actually present. However this must be considered with great reservation, since such a triangular embayment also occurs in *Escuminaspis* and *Levesquaspis*, which clearly have no lateral fields (Arsenault & Janvier 1995, pl. 1: 2a; Janvier & Arsenault 1996, figs. 3B). In the latter, this embayment only accommodates the posteriormost tesserae of the dorsal surface of the cornual process.

Oralbranchial fenestra. The series of large tesserae that forms the rim of the oralbranchial fenestra is much disarticulated and some portions of it have been displaced to the side of the shield (vr, Fig. 2A).

Pectoral fin. Small, polygonal scales are preserved in the pectoral sinus of the right-hand side in BMNH P. 60738b and are likely to be scales of the pectoral fin (pfs, Fig. 7). They are much smaller than the tesserae of the head shield and their shape and relative size compare with that of the pectoral fin scales of *E. laticeps* (Janvier & Arsenault, 1996, fig.6; Janvier *et al.* 2004, fig. 2).

Body squamation. There is no clear evidence for the body squamation but, like in the holotype, the rearmost tesserae of the head shield become smaller and smaller, and may have passed progressively to the body squamation.

Histology. Like in the holotype, the exoskeleton is made up by a black, tarry matter, which shows no trace of a particular structure. When immersed in alcohol, the tesserae sometimes show only faint traces of the radiating vascular canals of the middle layer, but it is likely that no histological information (e.g., whether the exoskeleton is made up by acellular bone, as in *Escuminaspis*) can be obtained from such material.

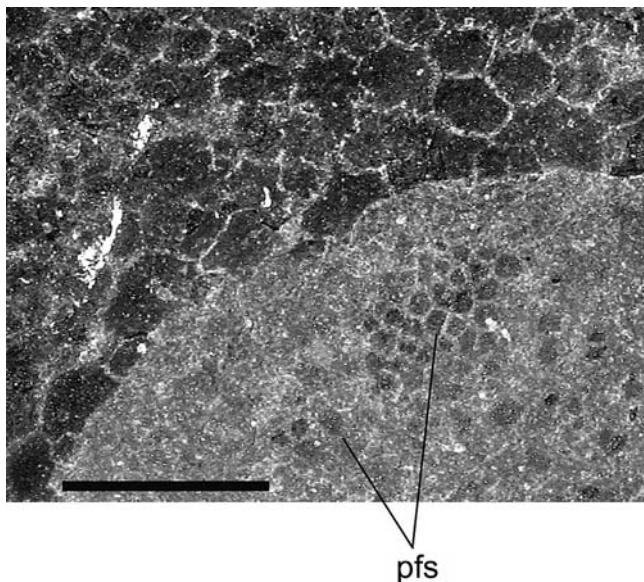


Figure 7 *Trewinia magnifica* (Traquair 1893a), Lower part of the Upper Caithness Flagstone Group, Eifelian (Middle Devonian); Spittal Pavement Quarry, Caithness, Scotland. Specimen BMNH P. 60738, Natural History Museum, London. Scales, probably of the dorsal surface of the pectoral fin of the right-hand side (P. 60738a; detail of Figure 2B). Scale bar=15 mm. Abbreviation: (pfs) pectoral fin scales.

2.2. Comparisons

Trewinia magnifica is remarkable by its very large size and broadly expanded head shield. Yet the outline of the latter is extremely difficult to reconstruct precisely, owing to the displacement of the tesserae, in particular along the shield margin. Both the holotype and BMNH P. 60738 show a slight angulation of the lateral shield margin in the anterior part of the cornual process. Such an angulation is known only elsewhere in ‘*Cephalaspis*’ *fracticornis* Wängsjö, 1952, which is in fact a large zenaspidid, probably belonging to the genus *Tegaspis*, and otherwise quite different from *T. magnifica*. However, we think that this angulation is an artefact of preservation, as is also the apparent anterior lobe of the holotype (Fig. 1A; Traquair 1894), and is a consequence of the lateral displacement of the marginal tesserae when the head shield has been dorsoventrally compressed. In fact, the anterior and lateral outline of the shield was probably either almost perfectly semicircular or slightly parabolic in shape (Fig. 8), as in, e.g., *Parameteoraspis laticornis*, *P. gigas*, or *P. hoegi* (Wängsjö 1952, figs 68, 70; Janvier 1985a, fig. 114). The presumed ‘anterior lobe’, which can be merely guessed on the holotype, was compared by Traquair (1894, p. 272) to the actual anterior lobe of ‘*Cephalaspis Campbelltownensis*’ (*sic*), now *Yvonaspis campbelltonensis* (Whiteaves, 1881), from the Lower Devonian (?Emsian), La Garde Formation of New Brunswick, Canada.

As demonstrated above, the presence or absence of lateral fields in *T. magnifica* is still a matter of debate. If these lateral fields are actually lacking, as we suspect (Fig. 8), then this considerably restricts the range of comparable osteostracans. In fact, lateral fields are clearly lacking in the two Late Devonian taxa, *Escuminaspis laticeps* and *Levesquaspis patteni*. Out of these two species, *T. magnifica* most closely resembles *E. laticeps* by its overall shape and the shape and breadth of its median cephalic field, as already suggested by Stensiö (1932). However, it is clearly distinct from the latter by its ornamentation. In *E. laticeps*, the entire head shield is ornamented with large, sparse, mushroom-shaped rounded tubercles, whereas the ornamentation of *T. magnifica* consists of very small,

elongated tubercles aligned into ridges, except on the margin of the orbits, where they approach the shape of those of *E. laticeps*. The ornamentation of *T. magnifica* also clearly differs from that of *Levesquaspis patteni*, which consists of scattered, pointed tubercles. Moreover, *T. magnifica* resembles *E. laticeps* in the structure of the posterior margin of the oralobranchial fenestra, which is made up by a series of roughly square or trapezoid tesserae (Fig. 1B; Janvier & Arsenaault 1996, fig. 1B2), whereas it consists of a single, transverse dermal bone unit in *Levesquaspis* (Arsenaault & Janvier 1995, pl. 1: 3b), as in most other cornuate osteostracans. However, it should be pointed out that a structure quite similar to that of *Trewinia* and *Escuminaspis* also occurs in the margin of the oralobranchial fenestra of some of the very large species of *Parameteoraspis* [e.g., *P. lata* (Stensiö, 1927); Janvier 1985a, fig. 113A], whereas smaller species retain a thick exoskeletal bar at this level [e.g., *Parameteoraspis oblonga* (Wängsjö, 1952); Janvier 1985a, fig. 106A]. This character may thus be quite variable, and possibly size-related.

The lack of a pineal foramen in osteostracans is relatively rare and hitherto known only in the kiaeraspidids *Gustavaspis* and *Acrotomaspis* (Wängsjö 1952, Janvier 1981b), which are otherwise entirely different from *T. magnifica*. At any rate, *E. laticeps* clearly displays a pineal foramen (Janvier & Arsenaault 1996, fig. 4B).

When compared to other Middle or Upper Devonian osteostracans, *Trewinia magnifica* clearly differs from the Eifelian *Balticaspis latvica*, ‘*Corollaspis walteri*’ and *Afanassiaspis porata* (Lyarskaya 1981, Otto & Laurin 1999, 2001a, b, Solcher 1999) by its ornamentation. The latter two species are only known from isolated tesserae and provide little information, apart from being evidence for an osteostracan with a poorly developed basal layer of the exoskeleton, whilst *B. latvica* is only known in ventral aspect. It is not known whether *B. latvica* had lateral cephalic fields or not, but the posterior margin of its oralobranchial fenestra seems to be composed of distinct tesserae (Lyarskaya 1981, Otto & Laurin 2001a), like in *Trewinia*, *Escuminaspis* and some species of *Parameteoraspis*. The odd-shaped *Ilemoraspis kirkinskayae* Obruchev, 1961 is supposedly from the Middle Devonian (?Givetian; yet recent, unpublished studies of the Ilemorovskaya Group now suggest it is either Emsian or Eifelian in age; A. Ivanov, pers. comm. 2004) of the Autonomous Region of Khakass, Russia, but neither its ornamentation and head shield morphology compares to that of *T. magnifica*, and it clearly possesses small lateral cephalic fields (Afanassieva & Janvier 1985).

There is thus no clear answer to the question of the affinity of *T. magnifica*, yet the choice may rather be between the Escuminaspididae (and particularly *Escuminaspis*) and the large *Parameteoraspis* species. Considering the probable lack of lateral fields in *T. magnifica*, as well as the shape of its hypophysial division of the nasohypophysial opening and locally tuberculate ornamentation, we are inclined toward favouring the former hypothesis, which would also agree with the relatively close age of *T. magnifica* and *E. laticeps* (yet this should not be regarded as an argument).

Currently, it is virtually impossible to carry out a phylogenetic analysis of osteostracans at the generic level, because the quality of the characters available from the material is too unbalanced (in part due to the lack of a detailed revision of the British taxa). The few taxa for which characters of the cranial internal anatomy are extensively known (e.g., the cephalaspidids *Mimetaspis* and *Pattenaspis*, the zenaspidid *Scolenaspis*, the kiaeraspidids *Kiaeraspis*, *Norselaspis* and *Nectaspis*, the thyestiids *Procephalaspis* and *Tremataspis*, and the benneviapidids *Benneviaspis*, *Boreaspis* and *Belonaspis*; Stensiö 1927,

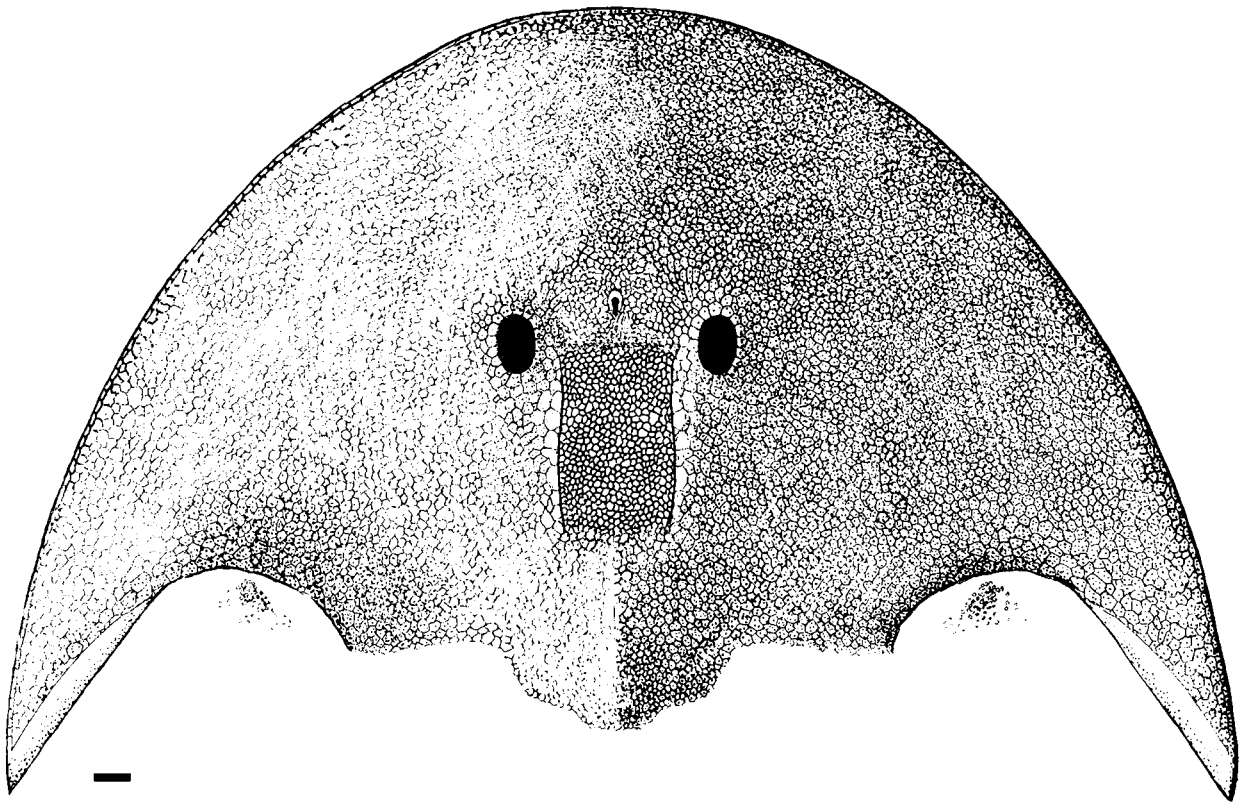


Figure 8 *Trewinia magnifica* (Traquair 1893a), Lower part of the Upper Caithness Flagstone Group, Eifelian (Middle Devonian); Spittal Pavement Quarry, Caithness, Scotland. Attempted reconstruction of the head shield in dorsal aspect. It is assumed here that this species did not possess lateral cephalic fields and that the nasophypophysial opening was very short. Scale bar=10 mm.

1964, Wängsjö 1952, Janvier 1981b, 1985a, c, 1996) show that most phylogenetic signals lie in such internal characters, which are unknown in the vast majority of osteostracans. A limited number of characters of the general morphology and exoskeleton (e.g., shape of the nasohypophysial opening or of the cephalic fields) can sometimes provide acceptable hints in assessing the systematic position of a particular species, but these are almost always subject to some homoplasy. In the particular case of *Trewinia magnifica*, for which there is little hope of ever obtaining data from the internal anatomy, these hints rather suggest closest relationships to *Escuminaspis*, pending the confirmation of its lack of lateral cephalic fields. This would, however, provide no answer to the question of the affinities of the Escuminaspididae.

Janvier (1985a, p. 131) considered that *Escuminaspis laticeps* shares at least three characters with the Zenaspidida: the ornamentation of large, rounded tubercles, with series of small tubercles bordering well-marked sensory-line grooves, the bilobate posterior margin of the median cephalic field, and the shield margin made up by series of small tesserae, not fused into larger dermal bone units. Later, Janvier & Arsenaux (1996) were still inclined toward considering this species as more closely related to the Zenaspidida than to any other major cornuate osteostracan taxon, but regarded the tessellate structure of the shield margin and the tubercle-bordered sensory-lines as possibly general osteostracan characters. However, some characters may not agree with such a position for the Escuminaspididae. In particular, the presence of a well-developed medial marginal plate of the cornual processes is rarely met with in the Zenaspidida [except for some generalised forms of the group, which have a very narrow medial marginal plate that fuses distally with the lateral margin of the cornual process (e.g. *Z. pagei*; Stensiö 1932, pl. 37:3)]. In fact the morphology of the cornual processes in *Escuminaspis* and

Trewinia, with a large medial marginal plate, is much closer to that in the cephalaspidid genus *Parameteoraspis* and probably also *Balticaspis*. Notwithstanding the difference in ornamentation, which is nevertheless known to be sometimes tuberculate in *Parameteoraspis* (Janvier 1985a, pls. 7: 1, 3, 8: 49: 2, 10: 1, 2; Bardenheuer & Janvier 1990, fig. 2), and shape of the nasohypophysial opening, the overall shield morphology of both *Escuminaspis* and *Trewinia* is strikingly similar to that of the large, Late Pragian species of *Parameteoraspis*, and a hypothesis of relationship between these taxa is probably the most sensible suggestion one can make at the moment. In addition, when compared to most other Early Devonian osteostracans, *Parameteoraspis* displays remarkably narrow lateral cephalic fields, whereas its median cephalic field remains very broad. This could possibly suggest a trend toward the reduction of the lateral fields, and their ultimate loss in the Escuminaspididae.

3. Remarks on osteostracan systematics and biogeography

Osteostracans display remarkable patterns of endemism throughout the Silurian and Devonian (Janvier 1985d, Blicek & Janvier 1999). Some taxa have a wider distribution than others, but there seems to be a clearer demarcation between North American and European taxa after the Lochkovian. Very few osteostracan genera are shared by North America and Europe, if one leaves aside the species still assigned to *Cephalaspis* for lack of revision (e.g., '*Cephalaspis wyomingensis* Denison, 1952). There are, however, a few possible exceptions. The non-cornuate genus *Hemicyclaspis* has been recorded from the Late Silurian and earliest Devonian of Wales, Gotland and Somerset Island (Arctic Canada) (Stensiö 1932, Spjeldnaes 1950, Dineley 1968).

Possible representatives of the genus *Parameteoraspis* [previously known from the Pragian of Spitsbergen and the Emsian of Rhineland; Stensjö 1927, Wängsjö 1952, Janvier 1985a, Friman & Janvier 1986, Bardenheuer & Janvier 1990; the record from Ukraine (Afanassieva 1991) remains doubtful] may occur also in the Lochkovian Peel Sound Formation of Prince of Wales Island, Northwestern Territories, Canada (Dineley 1994). '*Cephalaspis novascotiae* Denison, 1955, though of uncertain affinity, displays an overall morphology that is not too different from that of certain Lochkovian taxa from Britain and Spitsbergen. Finally, the genera *Waengsjoeaspis*, and possibly *Diademaspis*, previously known from the Lochkovian of Spitsbergen and the Pragian of Spitsbergen and Ukraine, respectively (Wängsjö 1952, Janvier 1985a,b, Afanasieva 1991), have been reported from the Lochkovian of northwestern Canada (Adrain & Wilson 1994). Other Lochkovian osteostracans from North America, such as *Superciliaspis gabrielsei* (Dineley & Loeffler 1976), cannot be readily referred to any of the major osteostracan taxa described from Europe, Spitsbergen and Ukraine. Similarly, the quite distinctive thyestiids, kiaeraspidids and benneviapidids, which are widespread in the Silurian and Lower Devonian of Europe, Spitsbergen, western Russia and Severnaya Zemlya, have never been recorded from North America. This strongly endemic pattern of distribution may be explained by the fact that practically all osteostracan species known to date, except for a few exceptions in Canada and the Baltic region, occur in marginal marine facies, and sometimes in facies that are regarded as fresh water deposits, because of either their sedimentological characteristics, or their lack of marine invertebrates. Such environments are generally regarded as favourable to endemism.

The composition of the younger osteostracan faunas of Europe and North America is also markedly different and none of the species described from the Emsian or Eifelian of Campbellton (New Brunswick, Canada), the Gaspé Sandstones (Quebec, Canada) [Pageau 1969; now all referred to *Yvonaspis* by Belles-Isles (1989)], or from Utah and Wyoming (USA; Bryant 1933, Denison 1952) share any uniquely derived characters with any particular European taxon, be they Lochkovian–Pragian or Emsian. Belles-Isles (1989) suggested that *Yvonaspis* could be more closely related to *Parameteoraspis*, due to its overall head shield shape and elongated, slit-shaped nasohypophysial opening, but other characters (distinct pineal plate, ornamentation, relative size of the tesserae) do not agree with this interpretation. It may also be pointed out that a number of North American, Lochkovian–Emsian taxa are distinctive in sharing large, loosely attached tesserae, and their head shield margin is often strengthened by large, rostral and lateral dermal units (e.g., *Camptaspis utahensis* Branson & Mehl, 1931, *Superciliaspis gabrielsei*, and possibly the *Yvonaspis* species; Denison 1952, Adrain & Wilson 1994, Belles-Isles 1989), and this might suggest that there is a clade of North American osteostracans, which would include these particular forms. The youngest known osteostracans, *Escuminaspis* and *Levesquaspis*, are equally difficult to relate to any other major taxon. As we have seen above, their lack of lateral cephalic fields suggests that they form a clade, to which could be added *Trewinia magnifica*, if this character can be definitely confirmed in this species. Such a North America and European distribution of the Escuminaspididae would be unusual among post-Lochkovian osteostracans, yet not too surprising since, notwithstanding a difference in age (Late Eifelian and Early Frasnian, respectively), the vertebrate faunas of the Escuminac Formation and Caithness Flagstone Group share many vertebrate taxa at the generic or familial level (Schultze & Cloutier 1996, Newman

& Trewin 2001). Now, the question remains as to whether this clade is rooted among European taxa, such as *Parameteoraspis*, or North American ones, such as *Yvonaspis*.

4. The decline and fall of osteostracans

The unexpected discoveries of *Escuminaspis laticeps* in the Upper Devonian, and then *Trewinia magnifica* in the Middle Devonian, at a time when osteostracans were supposed to have become extinct by the end of the Early Devonian, led Traquair (1894, p. 273) to raise once again the question of the imperfection of the geological record 'which a few writers seem even yet to be desirous of minimising'. To Traquair, these exceptional occurrences are a riddle. As he said of *Trewinia magnifica*: '... it must have had parents, and relatives, and ancestors. Where are they?' More than a century later, the situation is no better, and the last osteostracans still remain desperately scarce. Here the fossil record perhaps reflects the actual decrease in osteostracan diversity. The decline and finally extinction of the various 'ostracoderm' groups during the Silurian and Devonian is one of the leitmotifs of evolutionary palaeobiology. It is traditionally depicted as a consequence of the competition between them and the supposedly more efficient jawed vertebrates, or gnathostomes. Yet there are only two instances of predation by gnathostomes on 'ostracoderms': one is a small cephalaspid in the stomach contents of the Lochkovian acanthodian *Ptomacanthus* (Miles 1973, pl. 1:2; Denison 1979) and the other is a trace of bite, supposedly made by a sarcopterygian, on the cornual plate of a Late Devonian psammosteid heterostracan (Mark-Kurik 1966). This is rather meagre evidence for a supposedly fierce competition that has lasted for at least most of the Devonian, and perhaps part of the Silurian; that is about 50 million years.

Curiously, four of the major Devonian 'ostracoderm' groups that had diverged by at least the Early Silurian began to decline in abundance and diversity in the Eifelian: the heterostracans, thelodonts, galeaspids, and osteostracans. The anaspids (in the strict sense) are unknown after the Early Lochkovian, but are sometimes regarded as having survived until the Late Devonian, in the form of the so-called 'naked anaspids' *Euphanerops*, *Endeiolepis* and possibly *Achanarella*, and *Cornovichthys*. However, the relationships between these taxa and anaspids are now seriously questioned.

The youngest heterostracans (psammosteids) are Late Frasnian in age (Blieck 1984, Mark-Kurik *et al.* 1989, Janvier & Blieck 1993), the youngest thelodonts are Middle Frasnian (Young & Turner 2000; and possibly Famennian, V. Hairapetian, pers. com. 2004), the youngest galeaspids, from the Ningxia red beds of China are generally regarded as Late Famennian (Pan 1987; yet recent palynomorph-based datings suggest they could be older, and possibly Frasnian; Ritchie *et al.* 1992, p. 364), and the youngest osteostracans Early Frasnian (this article). Janvier (1985d, 1996) suggested that this important turnover in the shallow water Devonian vertebrate faunas may be due to environmental changes linked to the Middle Devonian marine transgression (although the marine transgression in the Orcadian Basin does not occur until long after the disappearance of *Trewinia* (Trewin & Thirlwall 2002), which have considerably reduced the extent of the marginal, tidal flat environments favoured by most 'ostracoderms'. Thelodonts, which are more often found in marine facies, seem to have been less sensitive to this change and remain comparatively abundant in the Middle and Late Devonian, where they occur essentially in marine platform sediments, alongside numerous gnathostomes that were supposed to outcompete them.

Apart from *Ilemoraspis kirkinskayae*, whose alleged Givetian age needs to be confirmed, all other Middle or Late Devonian osteostracans have a rather generalised cornuate morphology, and this may suggest that they have been restricted to a particular benthic ecological niche. None of the Middle and Late Devonian osteostracans display the highly derived morphologies of e.g., acrotomaspidids, boreaspidids, *Tauraspis*, or tremataspidids (Janvier 1981b, 1985a, c; Mark-Kurik & Janvier 1995). The same applies to the Middle and Late Devonian galeaspidids, which, albeit poorly known, seem to display a rather generalised ‘polybranchiaspidid’ morphology (Pan 1987, Pan & Ji 1993), and not the much derived morphologies of, e.g., the Early Devonian huananaspidiforms (Janvier 1996). In contrast, the youngest heterostracans belong to a single group, the psammosteids, which is amongst the most derived of the group (Blicek 1984, Janvier & Blicek 1993), yet their derived morphology appeared as early as the Pragian. The case of the thelodonts is more difficult to assess, as the systematics of the groups is mainly based on scale histology, but the youngest thelodonts all possess a thelodontid scale structure, which is known since the Silurian (Turner 1991). Whatever this may mean, it seems that the youngest known representatives of the major ‘ostracoderm’ taxa retain either a rather generalised overall morphology, or a derived but rather panchronic one. This suggests survival in a stable and restricted environment, which offers little opportunity for diverse ecological niches.

Janvier (1996) also suggested that the increasing abundance of certain benthic placoderm taxa (e.g., rhenanid, antiarchs, phyllolepidids) may have out-competed ‘ostracoderms’, which were essentially bottom-dwellers. This may hold for Euramerican osteostracans and heterostracans to some extent, which were confronted with the sudden abundance of antiarchs by the Eifelian or Givetian. However, there are counter-examples, such as the Lochkovian–Pragian of Southeast Asia, where many different bottom-dwelling galeaspid species lived alongside an amazing diversity of early antiarchs, or the Frasnian Escuminac Formation, where *Escuminaspis* and *Levesquaspis* lived in the same environment as the very abundant antiarch *Bothriolepis canadensis*. In the same way, Janvier’s (1996) hypothesis of a decline of ‘ostracoderms’ being linked to the decrease of shallow water, marginal sandy environments is contradicted by the condition in eastern Gondwana (essentially Australia and Antarctica), where such facies abound in the Middle and Late Devonian, although the only ‘ostracoderm’ taxon met with here, the pituriaspidids (Young 1991), is restricted to a single locality and horizon (the Emsian–Eifelian Cravens Peak Beds).

Finally, it should be noted that the decline of ‘ostracoderms’ in general coincides with the expansion of vascular plants on the continents and, consequently, the formation of extensive soil anchored on land by the vegetation. This may be a mere coincidence, but one may also hypothesise that the amount of organic particles shed into rivers and proximal marine environments may thus have become reduced and, considering that all ‘ostracoderms’ were probably either microphagous bottom-feeders, or suspension-feeders, their food resource may have become progressively lessened, whereas this had little impact on the essentially carnivorous gnathostomes.

Imagining such scenarios of evolutionary palaeobiology can lead to endless debates and many untestable theories, involving group competition and changes in the physical environment. In the particular case of the progressive extinction of the higher ‘ostracoderm’ taxa, the only hint is their relatively similar pattern of diversity decrease, at any rate for the morphologically quite similar osteostracans and galeaspidids.

5. Conclusions

The detailed redescription of the only two known specimens of *Trewinia* (*Cephalaspis*) *magnifica*, from the Late Eifelian Upper Caithness Flagstone Group of Scotland, confirms Stensiö’s (1927) hypothesis that this species resembles in many respects *E. laticeps*, from the Early Frasnian Escuminac Formation of Quebec, Canada, one of the youngest two osteostracans. *E. laticeps* and *L. patteni*, both from the same locality and level, are the only osteostracans that lack lateral cephalic fields and are therefore referred to a particular family, the Escuminaspididae. However, the present study has failed to provide conclusive evidence for or against the presence of lateral cephalic fields in *T. magnifica*, and thus its assignment to this family. A number of details observed in one of the specimens of *T. magnifica* (BMNH P. 60738) are nevertheless more consistent with an absence than with a presence of these cephalic fields. If *T. magnifica* turns out to be an escuminaspidid, this would represent the first post-Pragian evidence for the distribution of an osteostracan family in both North America and Europe. The affinities of escuminaspidids and *Trewinia* still remain in debate, yet certain characters, such as the large medial marginal plate of the cornual processes, as well as the overall head shield morphology, may suggest closer relationships to the European cephalaspidid genus *Parameteoraspis*.

A survey of the few Middle and Late Devonian osteostracans shows that all of them, except possibly *Ilemoraspis*, share the same, rather generalised cornuate overall morphology. The pattern of diversity decrease in Middle and Late Devonian osteostracans and galeaspidids appears quite similar and may reflect global changes in marginal marine or fresh water environments, namely the reduction of the extent of the areas favoured by Early Devonian ‘ostracoderms’, or changes in their food resources, rather than ecological competition with the gnathostomes.

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