A Middle Devonian chasmataspid arthropod from Achanarras Quarry, Caithness, Scotland

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Synopsis

A new fossil of the rare and little known arthropod group Chasmataspida (Chelicerata), is described as *Achanarraspis reedi* gen. et sp. nov. from the Middle Devonian (late Eifelian) of Achanarras Quarry, Caithness, Scotland. This is the first known occurrence of arthropod remains from this locality. Chasmataspids appear to be closely related to eurypterids and fossils of these groups have been confused with each other in the past. *Achanarraspis* resembles Lower Devonian chasmataspids from Germany, the Midland Valley of Scotland and the Severnya Zemlya Archipeligo, Siberia, but is distinguished from these taxa in possessing a carapace which is distinctly longer than the preabdomen, sharp lateral epimera on all postabdominal tergites, and a distinctive telson morphology. The Middle Devonian age makes *Achanarraspis* the youngest chasmataspid yet known and significantly extends the known stratigraphical range of the group. Other occurrences of arthropods from the Caithness Flags are reviewed and include conchostracan crustaceans, incomplete eurypterids and a now lost xiphosuran specimen collected in the late 1800s.

Introduction

The Middle Devonian 'fish bed' sequences of the Orcadian Lake Basin exposed in Caithness and the Moray Firth coast of the north of Scotland are world-renowned for the diversity and preservational state of the fossil fish they contain (Trewin 1986). Drifted plant remains and rare arthropods have also been infrequently found preserved within these deposits. To date, the arthropods have received little scientific study or attention from collectors. We report here the discovery of a fossil from Achanarras Quarry SSSI (Site of Special Scientific Interest) which belongs to a little known group of unmineralized chelicerate arthropods, the chasmataspids.

The Chelicerata include spiders and scorpions (Arachnida), horseshoe crabs (Xiphosura) and the extinct sea scorpions (Eurypterida). Chasmataspids appear to represent an additional, distinct group of fossil chelicerates and until recently were known from only three species: *Chasmataspis laurencii* Caster and Brooks (1956) from the Ordovician of Tennessee, USA and *Diploaspis casteri* Størmer (1972) and *Heteroaspis novojilovi* Størmer (1972) both from the Early Devonian of Germany. Both Caster and Brooks (1956) and Størmer (1972) interpreted chasmataspids as an unusual order of Xiphosura, a group from which they have now been removed (Anderson and Selden 1997; Dunlop and Selden 1997) and re-interpreted as a distinct clade of the Chelicerata, closely related to eurypterids (Dunlop 1997; Dunlop *et al.* 1999).

During recent studies of the existing material, two new Early Devonian chasmataspid taxa were brought to light. *Forfarella mitchelli* Dunlop *et al.* (1999), from the Early Devonian Dundee Formation of the Midland Valley, Scotland was recognized as a chasmataspid by Charles Waterston in the 1960s, but was not formally described and was curated under an unpublished manuscript name in the eurypterid collection of the Natural History Museum, London. A second taxon represented by an assemblage of over sixty specimens from the Early Devonian Severnya Zemlya Formation of the Severnya Zemlya Archipeligo, north of Siberia which were provisionally assigned to Eurypterida (Novilskaya *et al.* 1983), are in fact the most complete chasmataspids yet found (Dunlop 1997), including some appendage details. A full description of this material is currently in progress by JAD. Two further specimens from the Early Devonian of Siberia were described as eurypterids by Novojilov (1959), but may also be chasmataspids (Størmer 1972) and would merit restudy. We are also aware of some Upper Cambrian trace fossils (Wahlman and Caster 1978) which we believe are the resting traces of a *Chasmataspis*-like animal, based on our present knowledge of chasmataspid ventral morphology. Chasmataspids were therefore more widespread than has previously been recognized.

In this paper, we describe a new, Middle Devonian (late Eifelian) chasmataspid collected from lacustrine sediments exposed in Achanarras Quarry, Caithness. This is the youngest chasmataspid yet recorded and only the fifth species of this group to be formally described. It also points to a more varied and extensive biota inhabiting the waters of this Middle Devonian lake.

Materials and methods

The chasmataspid fossil was collected by Mr John Reed of Rousay, Orkney, from tip material at Achanarras Quarry in August 1991 and provisionally identified and labelled as *Pterygotus anglicus*, a eurypterid. In early 1998, Mike Newman noticed the specimen in a fossil dealer's stock in southern England, and realizing the scarcity of Orcadian Basin arthropod material, successfully obtained the specimen for study. The specimen is deposited in the palaeontology collections of the Department of Geology and Petroleum Geology, University of Aberdeen, accession number 12242.

The fossil is preserved as a very low relief negative, and so a cast was made to facilitate study and photography. Siliastic E-RTV (a silicone rubber kit manufactured by Dow-Corning) was used to cover the surface. The resultant cast was then filled with Bueler epo-thin resin to form a mould from which multiple rubber casts could be produced without deterioration of the original fossil surface. One cast was gold coated and studied under a Scanning Electron Microscope in an attempt to identify details such as cuticle sculpture. However, although the casting medium produced a faithful reproduction, no good surface detail or cuticular structure was observed; the sediment grain size being too large to facilitate preservation of fine detail. Interpretative drawings of the specimen were produced using a *camera lucida*. Comparisons were made with chasmataspid material from the Smithsonian Institution, Washington, the Natural History Museum, London and the Lithuanian Institute of Geology, Vilnius; as well as preserved specimens of the extant xiphosuran *Limulus polyphemus*. Markus Poschmann (Waldesch) provided specimens and photographs of new *Diploaspis* material from Germany. A preserved section through the entire thickness of the Achanarras fish bed, housed at the Dept. of Geology & Petroleum Geology, University of Aberdeen, was examined in an attempt to match the distinctive lamination sequence observed on the cut and acid-etched edge of the slab containing the chasmataspid.

Stratigraphy and depositional environment

The strata in Achanarras Quarry [ND 150544]; see Trewin (1993*a*, fig. 3)) include the Achanarras Limestone Member at the top of the Lower Caithness Flagstone Group of the Middle Devonian fill of the Orcadian Basin (summary in Mykura 1991). The Achanarras Limestone Member is commonly referred to as the Achanarras fish bed on account of the rich fish fauna which is preserved in deep water lacustrine laminites (Trewin 1986). Fish bed localities bearing the Achanarras fauna are widespread in the Orcadian Basin (Hamilton and Trewin 1988; Mykura 1991) and represent a period of high lake level. The freshwater fauna is generally considered to be of late Eifelian age (Mykura 1991).

The Achanarras Limestone Member is overlain at Achanarras by 8 m of strata comprising dolomitic lacustrine laminites and beds of fine-grained sandstone interpreted as turbidites (Trewin 1986). The lithology in which the chasmataspid is preserved consists of laminites of micaceous siltstone and dolomicrite. Whilst the specimen cannot be exactly positioned in the section, the laminite type indicates that it comes from above the fish-bearing part of the section, either at the top of the Achanarras Limestone Member, or from laminites interbedded with turbidites. The chasmataspid described here was probably deposited as a drifted carcass in a deep water, poorly oxygenated lacustrine environment far away from its life habit in the shallower regions of the lake. It is preserved as a thin film of carbonaceous material, through which very fine sand grains project. The original cuticle does not appear to have been preserved in this fossil.

Morphological interpretation

Chasmataspids resemble eurypterids and xiphosurans, but can be distinguished from both groups by their unique, autapomorphic pattern of opisthosomal tagmosis (e.g. Dunlop and Selden 1997). Dorsally, the chasmataspid opisthosoma comprises a reduced first tergite, a preabdomen of three, probably fused, tergites (termed a buckler by Caster & Brooks (1956)) and a postabdomen of nine annulate freely articulating segments formed by fusion of corresponding tergites and sternites. This gives a total of 13 opisthosomal segments (Anderson and Selden 1997) and is followed posteriorly by a tapering telson or tail spine segment. Chasmataspids have both median and lateral eye tubercles, the latter situated anteriorly on the carapace and reduced genal spines at the posterior corners of the carapace. Study of the Severnya Zemlya material suggests that the lateral eyes in chasmataspids may have been located on ophthalmic ridges, though this character is not evident in the older *Chasmataspis*, or the less well preserved Devonian forms. All other Devonian chasmataspids possessed a pair of small swimming paddles which were probably the sixth prosomal appendage pair, although none of the paddle-bearing material shows a complete coxo-sternal region or a complete set of appendages which would confirm this interpretation. We therefore reconstruct *Achanarraspis* with reduced swimming paddles (appendage VI), in direct comparison with the well preserved Devonian form *Diploaspis*. The morphology of the telson, or tail spine structure as reconstructed here for *Achanarraspis* also requires some explanation. Due to the low surface relief of the structure, it does not show up well on the whitened photograph (Fig. 1). However, photographed immersed under 70% alcohol, the telson is seen to be spatulate in outline rather than styliform (Fig. 3). We are confident that this is the actual outline rather than one which formed as a result of damage or fragmentation of the structure as this is of a similar morphology to the telson of *Diploaspis*.

Affinities

Chasmataspids were initially interpreted as an order of the Xiphosura (see introduction). Eldredge (1974) suggested that Chasmataspida were a sister group to Eurypterida as both groups have paddles. However, this

FIG. 1. *Achanarraspis reedi* gen. et sp. nov. A new chasmataspid arthropod from the Middle Devonian of Achanarras Quarry, Caithness, Scotland. Scale bar equals 0.9 cm. Photograph of specimen whitened with ammonium chloride.

character is absent in superfamily Stylonuroidea and is not preserved in the Ordovician *Chasmataspis*, and so is likely to be a convergent character developed independently in both. Bergström (1975) retained *Chasmataspis* in Xiphosura, but regarded *Heteroaspis* as Chasmataspida *incertae sedis*, and excluded *Diploaspis* from Xiphosura on the grounds of non-chelate prosomal appendages in this taxon. Subsequently, Bergström (1979) retained this polyphyletic interpretation and drew a phylogeny in which *Diploaspis* was close to the origins of arachnids. More recently, Anderson and Selden (1997) removed all chasmataspids from Xiphosura, noting chasmataspid characters not seen in xiphosurans such as a 13-segmented opisthosoma with its unique pattern of tergal fusion. Dunlop and Selden (1997) recognized Chasmataspida as a distinct, monophyletic taxon on the autapomorphy of the opisthosomal tagmosis pattern, and suggested a relationship of the form (Chasmataspida (Eurypterida + Arachnida)).

Subsequent work on the original *Chasmataspis* material has shown that some of the characters taken from the literature and used in the analysis of Dunlop and Selden (1997) were incorrect. Furthermore the new Severnya Zemlya material is especially significant as it shows that chasmataspids had both a metastoma and a median abdominal appendage (Dunlop 1997; Dunlop *et al.* 1999), characters previously thought to be autapomorphic for eurypterids. These characters strongly support a Chasmataspida + Eurypterida relationship. Chasmataspids have short, stubby, epimera on the carapace (genal spines) and may also show development of ophthalmic ridges. Both of these characters are absent in eurypterids, but are characteristic of xiphosurans. However, these characters could be symplesiomorphic and the chasmataspid opisthosomal segment number and tagmosis pattern is substantially different to that of xiphosurans. The position of Chasmataspida therefore remains to be tested against other chelicerates using the new character database derived from ongoing studies of this group.

Systematic palaeontology

Chelicerata (Heymons 1901)

Chasmataspida (Caster and Brooks 1956)

Remarks. See Dunlop *et al.* (1999) for a discussion of the status of Chasmataspida.

Family Diploaspididae (Størmer 1972)

Diagnosis. Small chasmataspids with semicircular or subrectangular carapace and with a distinctly tapering postabdomen and a short telson; postabdomen in Chasmataspididae elongate and not strongly tapering. No division of preabdominal tergites into medial and lateral plates (Dunlop *et al.* 1999, emended from Størmer 1972).

Type genus. Diploaspis (Størmer 1972)

Remarks. Our new fossil resembles both published and unpublished descriptions of other Devonian chasmataspids (Størmer 1972; Dunlop 1997). All other Devonian forms are placed in Diploaspididae. We question the validity of Heteroaspididae Størmer 1972 which might be a synonym of Diploaspididae (see Dunlop *et al.* 1999). The use of the form and proportion of the carapace as a taxonomic character is well established in the closely related eurypterids, and we feel justified in using the same criteria here.

Achanarraspis gen. nov.

Diagnosis. Diploaspidids with a carapace which is distinctly longer than the preabdomen. Postabdominal tergites all possess paired lateral epimera. Telson spatulate.

Type and only species. Achanarraspis reedi gen. et sp. nov. By monotypy.

Etymology. The generic name is based on, and includes, the locality name, Achanarras, a quarry near the village of Spital, Caithness and recognizes previously named chasmataspids with the ending – *aspis*. We are aware that the name *Achanarrella* which could have been used for this fossil for its phonetic similarity to the chasmataspid taxon *Forfarella*, described recently by Dunlop *et al.* (1999). However, there is already a small, problematic agnathan organism recorded from Achanarras informally named *Achanarella* (with one 'r') and the similarity in names would undoubtably cause future confusion.

Remarks. While there may be grounds for referring our new specimen to an existing genus of Devonian chasmataspid we note that most importantly, there is a distinct morphological difference in terms of the proportions of the carapace and postabdomen between this and other genera, and secondly, our fossil is stratigraphically the youngest yet discovered. In addition, no other Devonian forms have postabdominal epimera. We accept that this fossil has been substantially compressed and flattened, but consider this has not drastically changed the relative proportions of the prosoma and opisthosoma. In other diploaspidids the carapace is approximately the same length as the preabdomen, and epimera are restricted to certain postabdominal segments only.

Achanarraspis reedi gen. et sp. nov.
(Figs 1–4.)

Diagnosis. As for genus.

Holotype. Aberdeen University Dept. of Geology & Petroleum Geology Palaeontology Collection. No. 12242.

Type stratum and locality. Lower Caithness Flagstone Group, Achanarras Limestone Member, Middle Devonian, late Eifelian from Achanarras Quarry [ND 150544], near Spital, Caithness, Scotland.

Etymology. The specific epithet is in honour of the original collector, Mr John Reed of Lowerhammerfield, Rousay, Orkney.

Additional material. None.

Description. The holotype and only specimen is preserved in dorsal view and in very low relief. As such, morphological details are faint. Though provisionally labelled by the collector as a pterygotid eurypterid, this new fossil clearly shows the characteristic chasmataspid pattern of opisthosomal tagmosis (Figs 1 and 2): a reduced first segment, a broad, 3-segmented preabdomen and a narrow, 9-segmented postabdomen plus a short spatulate telson (Fig. 3). The carapace is subtrapezoidal with small genal spines. Two faint, approximately circular markings near the anterior corners of the carapace probably represent the lateral eye tubercles, while a tiny pair of circular structures in the center of the carapace are almost certainly the median eyes (Figs 1 and 2). Very faint traces of structures which may be appendages are preserved within the confines of the carapace, but they are of such low surface relief and poor contrast against the background that they are difficult to interpret with any degree of certainty. Their apparent presence on the dorsal surface of the carapace must be either due to breakage of the surface or more likely compaction of these robust structures up through the thin cuticle. The preabdomen is broad with rounded lateral margins. Preabdominal segmentation is difficult to determine, but faint, curving transverse lineations are likely tergite boundaries (Figs 1 and 2). The postabdomen is long and tapers posteriorly, ending in a short spatulate telson. All nine postabdominal segments can be distinguished (Figs 1 and 2), the first five bear laterally positioned paired pits, perhaps indicating the location of apodemes (ventral muscle attachment sites). The

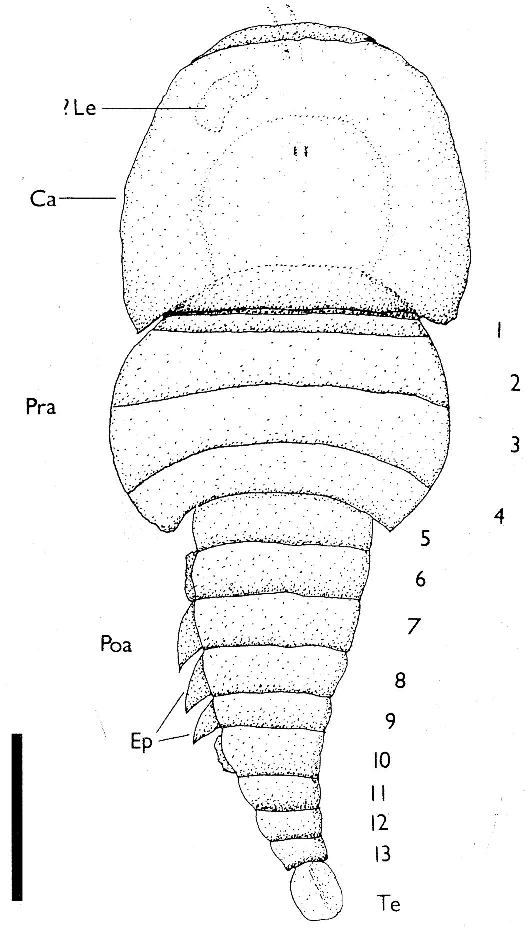

FIG. 2. Interpretative *camera lucida* drawing of the chasmataspid. Abbreviations as follows: 1–13, Opisthosomal segment number; Ca, Carapace; Ep. Epimeron; ?Le ?Lateral eye; Poa Postabdomen; Pra Preabdomen. Scale bar equals 0.5 cm.

following measurements are given in mm: Total length approx. 30, carapace length 9, basal width 12, preabdomen length 7, maximum preabdomen width 12, telson length 2.1, telson width 2.

Remarks. The spatulate telson of *Achanarraspis* is an important morphological character which may have implications regarding the inter-relationship of the various chasmataspid taxa. Of the presently described taxa, the majority have styliform telsons, the shape in *Forfarella* is unknown and only *Diploaspis* has a similarly spatulate telson. A morphological reconstruction of *Achanarraspis reedi* gen. et sp. nov. is presented in Fig. 4.

Occurrence. A. reedi gen. et sp. nov. is known only from the type locality.

Other Orcadian Lake arthropods

To date, there has been little investigation of the other faunal elements associated with the fish from the Middle Devonian Orcadian Lake Basin. Trewin (1976) identified various small trace fossils from the Middle Devonian of Stromness including *Isopodichnus* of probable arthropod origin. An early Devonian ichnofauna from the Ousdale

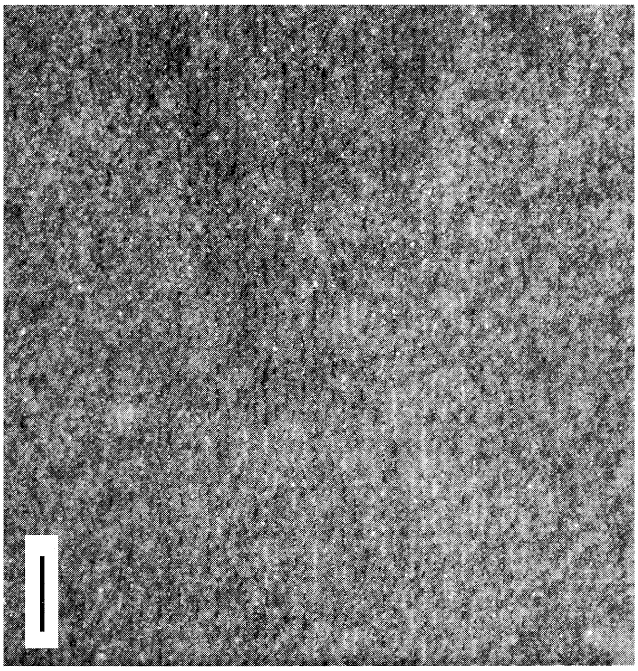

FIG. 3. Detail of the postabdominal region and spatulate telson of *Achanarraspis reedi* gen. et sp. nov. Scale bar equals 1 mm. Specimen photographed under 70% alcohol.

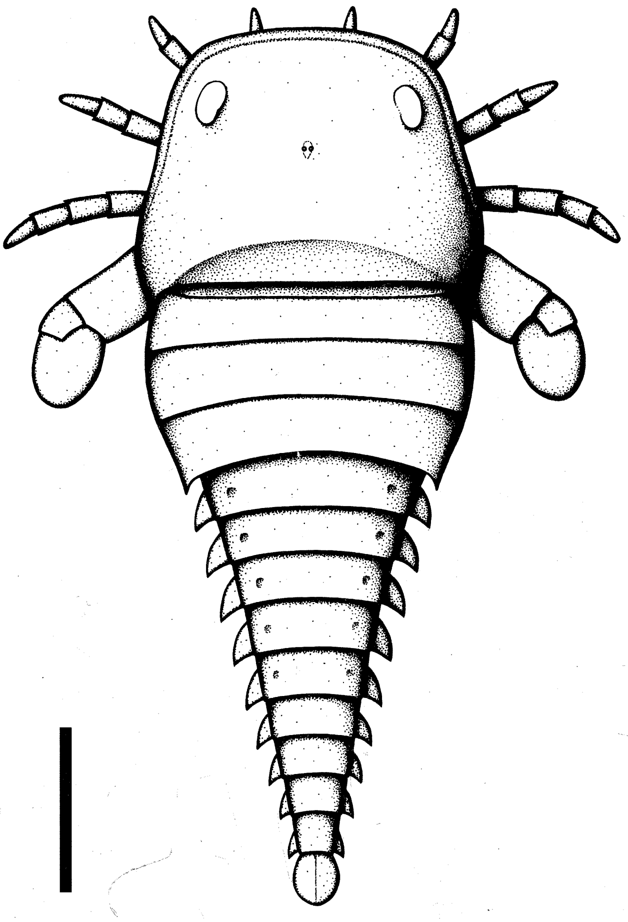

FIG. 4. Reconstruction of *Achanarraspis reedi* gen. et sp. nov. in dorsal view. Appendages and some carapace details based on comparisons with other Devonian chasmataspids. Scale bar equals 0.5 cm.

Mudstones includes seven genera probably produced by arthropods (Trewin 1993*b*), and other arthropod-related traces are known from the Moray Firth Coast (Trewin and Kneller 1987; Carroll 1990). Three groups of arthropod body fossils have previously been recorded from the Orcadian Basin: branchiopod crustaceans, eurypterids and a xiphosuran; the chasmataspid described here brings the total number to four. The occurrence and identity of these arthropod fossils are described below.

Asmussia membranacea (Pacht 1849)

The conchostracan crustacean, *Asmussia membranacea* is recorded from a restricted number of stratigraphic levels within the Orcadian lake basin (Crampton and Carruthers 1914; Wilson *et al.* 1935; Donovan *et al.* 1974; Astin 1990). Conchostracans are small branchiopod crustaceans whose body is partially enclosed in a bivalved shell. Extant taxa are largely restricted to freshwater environments where they are semi-infaunal suspension feeders, and their fossil relatives are likewise interpreted (Webb 1979). *Asmussia membranacea* has also been recorded from the Upper Devonian strata of Miguasha, Canada (Martens 1996). Carroll (1990) examined the sedimentology of five sites with *Asmussia*-bearing lithologies within the Orcadian Lake Basin, and concluded that horizons containing *Asmussia* appeared to be restricted to the transgressive phase of lacustrine transgression/regression cycles. In these, *Asmussia* was likely to be a washed-in faunal element associated with disarticulated fish scales and coprolites. This would appear to agree with the general assumption that *Asmussia* occupied a shallow water niche on the lake margins of the basin, well away from potential preservation within the deep water fish-bearing laminites so characteristic of the Caithness fossil localities.

Pterygotus dicki (Peach 1883)

This species of eurypterid was formally described by Peach (1883) from an array of disarticulated and incomplete postabdominal segments and is apparently restricted to the Middle Devonian Orcadian Lake, although this may be a taxonomic problem rather than an actual distribution. The taxonomy of pterygotid eurypterids in general needs extensive revision, as it currently includes large numbers of probably synonymous taxa based on similarly incomplete material. Cheliceral dentition and the shape of the telson and metastoma appear to be the most valid morphological characters to use, thus the naming of these few scattered segments as a distinct species is taxonomically unsound. A pertinent example of this, is the report of Geikie (1879) of fragments of cuticle 'probably of *Pterygotus*' from the Sandwick fish bed in Orkney. However, Kjellesvig-Waering (1964) accepted the original assignment by Peach (1883) as valid and suggested that the Orcadian material should be named *Pterygotus (Pterygotus?) dicki*. This seems burdensome and a re-examination of the type material is required to establish whether it is a valid taxon or not. However, an important point to note from the original description of Peach (1883) is the presence of an unusual cuticular ornament forming a posterior marginal fringe to the segments absent from all known examples of *Pterygotus*. This ornament, which Peach figured in detail, bears striking similarities to that seen on the Lower Carboniferous eurypterid genus *Cyrtoctenus* (Størmer and Waterston 1968). The type material of *Pterygotus dicki* (Peach 1883) resides in the Type and Figured collections of the National Museum of Scotland, Edinburgh registered as NMS G1878.5.540.

The disarticulated state of all of the eurypterid material discovered to date from the Orcadian Lake Basin strongly suggests a similarly transported origin to that of the conchostracan crustaceans and indeed, Peach (1883) commented upon the likelihood of this. Although these large (up to 1.5 m in length) arthropods possessed small paddles on the distal pair of prosomal appendages, they may not have been strong enough swimmers to venture out into the open waters of the lake, instead remaining close to the shallows where smaller arthropod and fish prey could be captured. Indeed, it may be that the curious structures consisting of attached tergites and sternites forming compacted ellipses of cuticle perpendicular to bedding which Peach (1883) described as 'Adam's plates' formed as the result of floating, disarticulating eurypterid exoskeletons which fell through the water column to the lake floor where they were fortuitously preserved.

The 'Limuloid'

Peach (1883), in the same article describing *Pterygotus dicki*, noted an arthropod fossil from flagstones near John o' Groats House, Caithness, which he identified as a 'limuloid' or xiphosuran. The specimen was collected by his father, C. W. Peach. The line drawing of the specimen (which is reproduced here in Fig. 5), strongly suggests the presence of genal spines, a median opisthosomal axis and posteriorly directed tergal epimera. The opisthosoma comprises of nine segments, each with lateral tergal epimera which are of approximately the same size and shape. Tergites 7–9 appear to be uncoalesced and retain separate lateral boundaries. The tail spine is short and styliform with a median ridge running down the entire axial length. Although extensive searches of collections were made in Caithness (Eila MacQueen, pers. comm.) and in all other major Scottish museum collections, the specimen could not be located and as a result must be considered lost. Unusually, it was not accessioned with the type material of *P. dicki* in the NMS, although figured in the same article. This is unfortunate as it is the first and only record of a Middle Devonian xiphosuran.

As to the identity of this fossil, Peach (1883) suggested that 'the affinities of the creature are more with *Belinurus* than any other known limuloid' which was a fair statement at the time, as only a handful of fossil xiphosuran taxa had been formally described. However, the uncoalesced nature of the last three opisthosomal segments and the presence of lateral tergal epimera strongly suggests that it is more closely related to the Upper Devonian *Kasibelinurus* (Pickett 1993), described originally from Australia and subsequently found in strata of similar age in Pennsylvania and New York State, USA (Babcock *et al.* 1995). In the

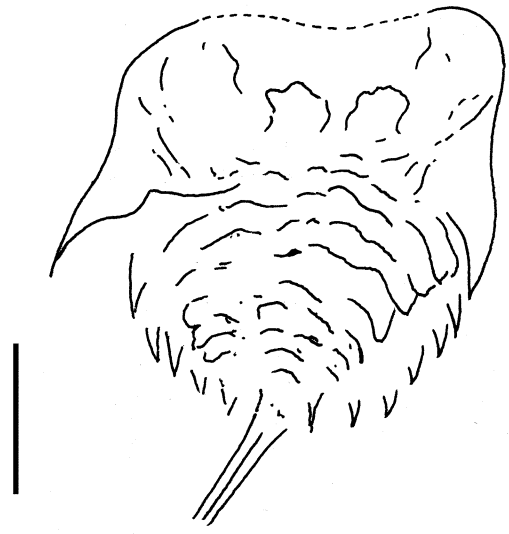

FIG. 5. Reproduction of the original sketch diagram of the Orcadian Lake limuloid by Peach (1883). Scale bar equals 1 cm.

former locality, *Kasibelinurus* is in an undoubtably freshwater setting, whilst in the latter, it appears to be a faunal element mixed with a nearshore marine biota including echinoderms and giant conularids (Babcock *et al.* 1995). *Kasibelinurus* was recognized in a recent study by Anderson and Selden (1997) as being a sister taxon to all other xiphosurids, which include the 'limuloids' or more correctly, members of the Suborder Limulina which includes all extant species.

Controls on preservation

Arthropods, and eurypterids in particular are a relatively common faunal element of many fish-bearing lithologies in the Early Devonian of the Midland Valley of Scotland (Trewin and Davidson 1996) as well as quarries in fluvial sandstones such as Carmyllie (Armstrong and Patterson 1970). Amongst these, the genus *Pterygotus* is probably by far the most commonly cited example, although other taxa are known. This may be because it is truly distinctive enough to identify from isolated fragments, or what is more likely, any large arthropod cuticles from these beds are consigned to the bucket taxon *Pterygotus*.

Two main questions are raised by this occurrence. Firstly, why do the Early Devonian fish-bearing beds contain many more abundant arthropod genera and specimens than the Middle Devonian Orcadian beds? Secondly, what does this tell us, if anything, about the habitats of the arthropods which have been discovered in the Orcadian Lake Basin sediments so far?

In answer, it seems likely that the lateral extent of Lake Forfar (see Trewin and Davidson 1996) was far smaller than the lake in which the Caithness fish beds formed. Consequently, floated or washed-in plant and animal material had a higher likelihood of being incorporated into fish bed laminite sequences due to the factor of proximity to source. The discovery of rare arthropod and plant fossils within the strata at Achanarras appears to back the suggestion that, for the most part, the marginal environments of the lake supported a thriving ecosystem on which the fish fed (Trewin 1986). It was only when elements of this biota were swept out into the open water over the deepest parts of the lake and sank to the lake floor, that they stood a chance of preservation within the laminite fish beds. All previous reports of chasmataspid fossils have been associated with shallow lagoonal or freshwater lacustrine palaeoenvironmental settings. Although this is likely to be in part due to a preservational bias, it would appear to be the typical habitat of these arthropods.

An alternative explanation for the absence of arthropods from within the fish bearing unit at Achanarras could be that conditions were not amenable for their preservation, and it is only with the establishment of different physiochemical conditions, suggested by the faint ghostly outlines of poorly preserved *Dipterus* towards the top of the sequence, that arthropods stood a chance of being preserved. Sites of exceptional preservation of Upper Carboniferous age where both arthropod and vertebrate fossils co-occur were studied in some detail by Schultze and Maples (1992) who noted that, in most cases, localities with vertebrates preserved often lacked unmineralized arthropod fossils and *vice versa*. The differing preservational requirements of each of the groups often meant that exclusion from fossilization was due to different sediment conditions rather than actual absence from the fauna.

Acknowledgements

We are especially grateful to Mike Newman who noticed the specimen in a dealer's stock, negotiated its 'release' and traced the original collector. We thank Simon J. Braddy for helpful discussions on eurypterid relations. Andrew Ross and Claire Mellish (British Museum (Natural History)), Jann Thompson (Smithsonian Institution), Valentina Talimma (Lithuanian Institute of Geology) and Markus Poschmann (Waldesch, Germany) allowed access to comparative material and photographs. LIA and NHT acknowledge a Leverhulme Trust grant to the University of Aberdeen.

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MS. accepted for publication 24*th April* 2000