

Eurypterids from the Viséan of East Kirkton, West Lothian, Scotland

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ABSTRACT: The hibbertopteroid eurypterid genera *Hibbertopterus*, *Dunsotopus*, and *Cyrtotenus* occur in the East Kirkton Limestone of Bathgate, West Lothian. Most specimens are fragmentary and appear to have been washed into the depositional area with plant debris and tuffaceous sediment. Nearly all of the identifiable material can be attributed to *Hibbertopterus scouleri* (Hibbert), but two isolated *Cyrtotenus* combs, and a femur comparable with *Dunsotopus* have also been recognised.

New material of *Hibbertopterus scouleri* (Hibbert) reveals that the posterior legs and telson resemble those of the cyrtotenusids more closely than was previously thought. It is possible that *Hibbertopterus*, *Dunsotopus*, and *Cyrtotenus* are indistinguishable except by relatively minor characteristics, and that all of the material from East Kirkton Quarry might be derived from a single eurypterid species. However, associations of the diagnostic sclerites which would demonstrate that these taxa are either cogenetic or distinct have not yet been found.

KEY WORDS: Cuticle, functional morphology, appendages, systematics, feeding, locomotion, Palaeozoic, Viséan, East Kirkton, Scotland.



Hibbertopteroids are an enigmatic group of Upper Palaeozoic eurypterids which have been recorded from Europe, Russia, South America and South Africa (Waterston 1957; Waterston *et al.* 1985). Specimens are usually fragmentary, so that relationships between hibbertopteroid taxa have proved obscure. Of the twelve nominal species included in this group, only two are known from reasonably complete specimens, *Hibbertopterus scouleri* (Hibbert, 1836) and *Cyrtotenus wittebergensis* Waterston, Oelofsen and Oosthuizen, 1985. Hibbertopteroids are short-bodied eurypterids characterised by a large, domed, prosomal shield (carapace) and specialised food-gathering structures on the second, third and fourth pairs of prosomal appendages.

Lower Carboniferous eurypterids are rare, and much of our knowledge of these forms is derived from Scottish material. Waterston (1957, 1968) reviewed the Scottish Lower Carboniferous eurypterids, including the unusual species *Hibbertopterus scouleri* (Hibbert, 1836). Several three-dimensionally preserved specimens of this eurypterid were found at East Kirkton Quarry, West Lothian, in the early years of the last century. In spite of the fine preservation of these specimens, a number of important questions relating to the prosomal appendage structures, the nature of the telson, and the mode of life of *Hibbertopterus* remain outstanding. Subsequent to S. P. Wood's re-examination of this locality in 1984 a large collection of eurypterid material has been amassed, and this paper summarises preliminary findings based on that material. Details of the locality and stratigraphy can be found in Rolfe *et al.* (this volume).

1. Preservation and taphonomy

Organic cuticle is preserved in all specimens. Those which are three-dimensionally preserved are invariably coated with accretionary carbonate and it is also found on some

flattened material. Cuticle scraps ranging from a few millimetres to tens of centimetres in diameter are relatively common, but recognisable isolated sclerites or articulated specimens are rare.

Preserved cuticle is thinner than would be expected for very large arthropods, and it is likely that only an outer exocuticular region is preserved. Dalingwater (1986) suggested that a region analogous to the hyaline exocuticle of scorpions may also occur in eurypterids, which could explain why eurypterid cuticle has been preserved whilst that of arthropod groups that lack hyaline exocuticle is absent. The taphonomy of scorpions from East Kirkton Quarry is discussed by Jeram (this volume), and since eurypterid taphonomy is similar, no further discussion is given here.

2. Systematic descriptions

Specimens described below are located in the collections of the National Museums of Scotland, Edinburgh (NMS), the British Museum (Natural History), London (BMNH), and the Hunterian Museum, University of Glasgow (GLAHM)

Superfamily HIBBERTOPTEROIDEA Kjellesvig-Waering, 1959

Family Hibbertopteridae Kjellesvig-Waering, 1959

Genus *Hibbertopterus* Kjellesvig-Waering, 1959

Emended diagnosis. Hibbertopterid eurypterids in which the walking-legs have basal extensions ('Laden') but do not have a longitudinal posterior groove in any of the podomeres. Telson hastate, with median keel composed of two lateral shoulders separated by a median indentation.

Type species. *Hibbertopterus scouleri* (Hibbert, 1836)

Hibbertopterus scouleri (Hibbert, 1836)

(Figs 1, 2b–d, 3a–c–f, 4A)

Synonymy. See Waterston (1957)

Emended diagnosis. As for genus.

Lectotype. Three-dimensionally preserved prosoma with anterior portion of mesosoma, G55/76, in the collections of Glasgow Art Gallery and Museum. From the Lower Carboniferous (Brigantian) East Kirkton Limestone, Bathgate, West Lothian.

Additional material. Three syntypes listed by Waterston (1957) and NMS G 1955.15. Also new material collected from the type locality between 1984 and 1992. The most significant specimens are figured or cited below.

Description. A single relatively complete specimen preserved in a tuffaceous matrix (BMNH In. 62181) from spoil heaps at the entrance to the quarry. The cuticle collapsed and distorted considerably prior to the deposition of accretionary carbonate over exterior surfaces. The attitude of preservation is unusual, with the opisthosoma

curled under the prosoma. Portions of two metasomal segments are visible projecting out from under the carapace on the right side of the specimen (Fig. 1A, left). Ventral prosomal structures have been shunted anteriorly and to the left. This resulted in the anterior appendages becoming trapped under the overhanging margin of the carapace, whilst the two posterior pairs of legs project laterally from beneath the carapace. The slab on which the carapace was originally exposed was split during collection, the plane of splitting passing slightly dorsal to the ventral prosomal surface. This has revealed structures not seen previously since, when intact, the ventral prosomal surface is shielded by the large metastoma and plate-like projections of the trochanters, the 'Laden' (see reconstruction in Waterston 1957, text-fig. 3). Distortion of the specimen has resulted in the anterior coxae bending upwards under the carapace and out of the plane of splitting, so they are not visible. However, the coxae of the posterior walking-legs are visible,

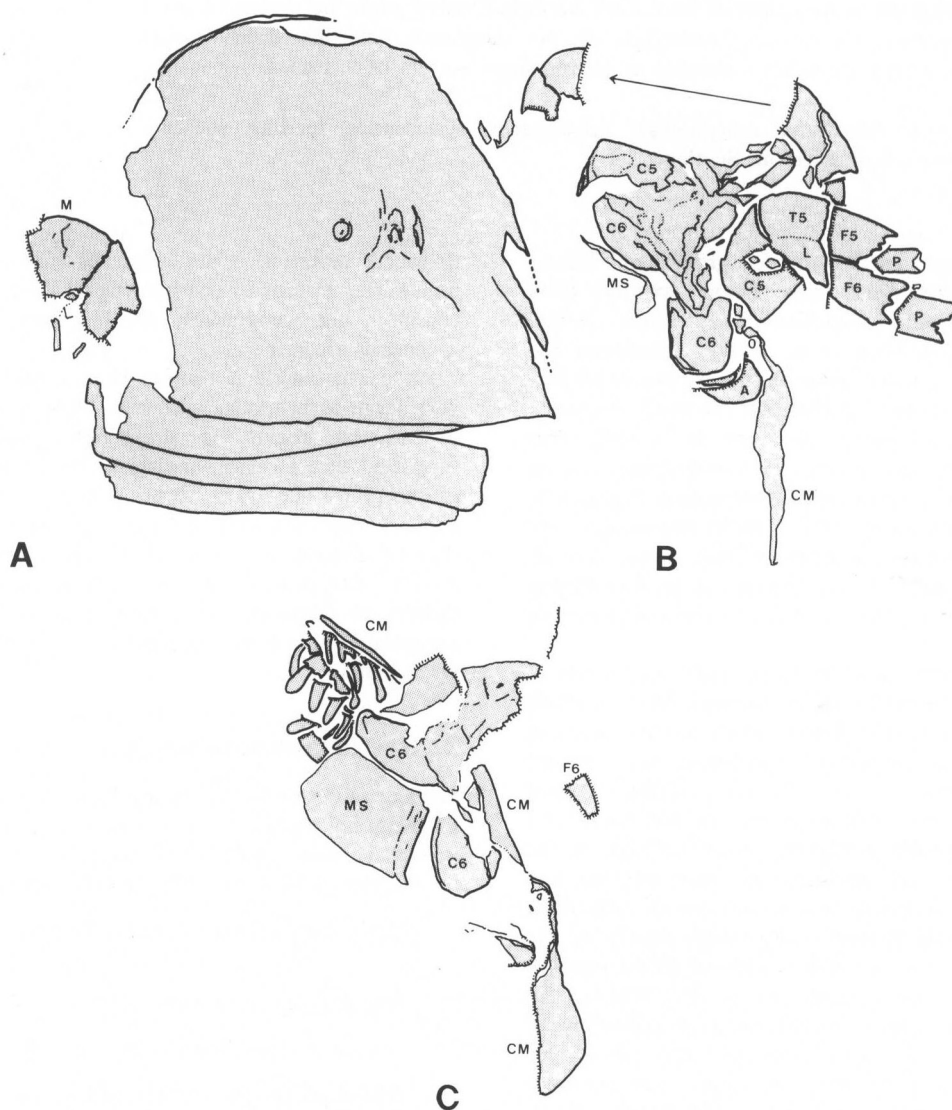


Figure 1 *Hibbertopterus scouleri* (Hibbert), BMNH In. 62181, pt & cpt slabs, from the East Kirkton Limestone, $\times 0.5$. (A) and (B) have been reversed, left to right, to reveal the relationship of the sclerites more clearly. The carapace is exposed dorsal side uppermost on the pt slab (A), with ventral prosomal structures exposed on the underside of the slab (C). These have been mechanically prepared and acid etched to reveal as much cuticle as possible, so that structures do not all lie in a single plane and are viewed from the ventral side. (B) shows features which lie ventrally to those in (C) and are viewed from the dorsal side. Note the distal ends of at least three anterior legs with long flanges projecting from under the carapace in (C). Abbreviations: coxa (C), trochanter (T), femur (F), patella (P), Laden (L), metasoma (M), metastoma (MS), carapace margin (CM), abdominal plate (A).

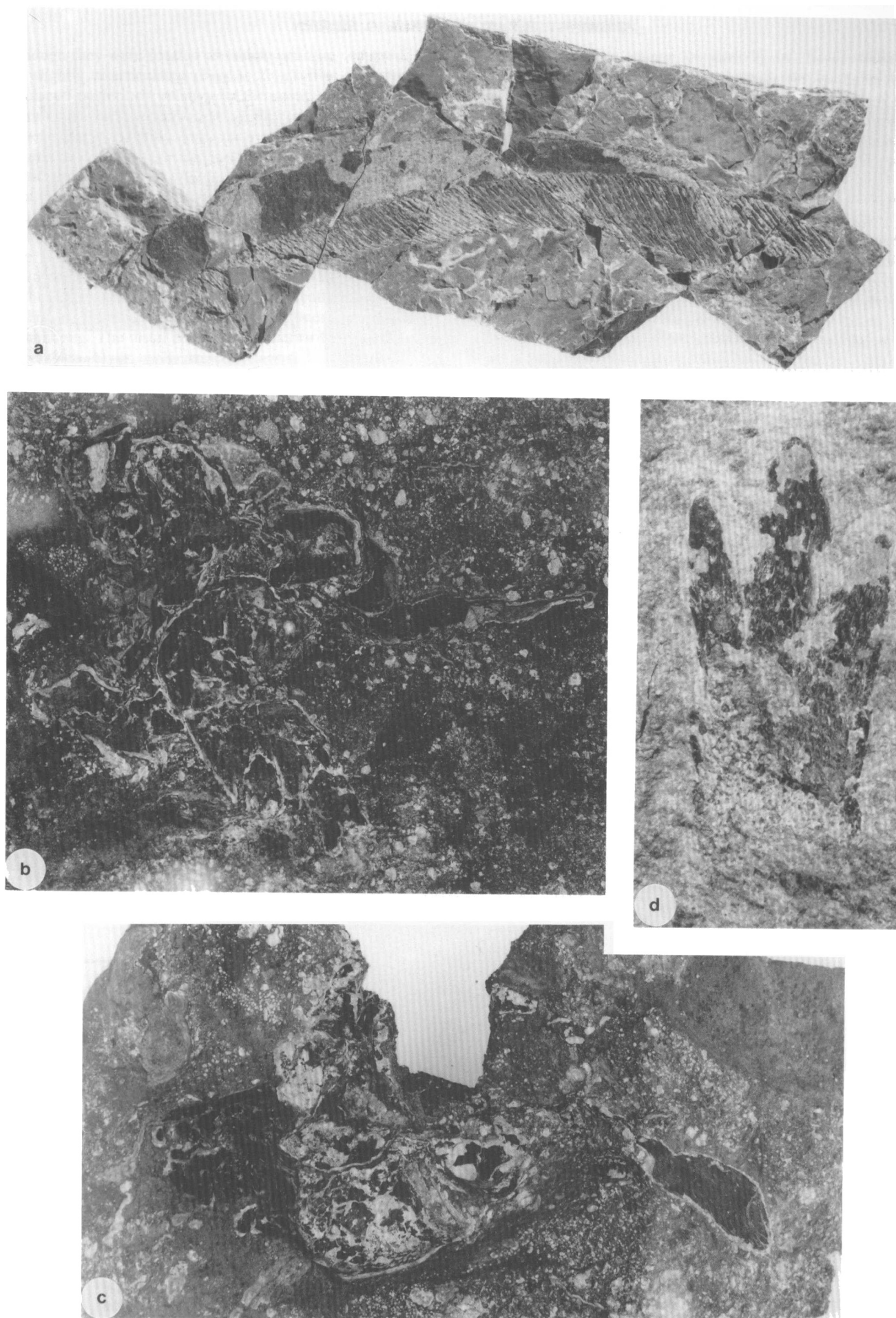


Figure 2 (a) *Cyrtoctenus* sp., NMS G 1986.2.4 (pt), comb from the East Kirkton Limestone, $\times 0.75$. (b–d) *Hibbertopterus scouleri* (Hibbert), from the East Kirkton Limestone; (b) BMNH In. 62181, prosomal appendages viewed from dorsal side, see Fig. 1B for explanation, $\times 0.85$; (c) BMNH In. 62181, prosomal appendages viewed from ventral side, see Fig. 1C for explanation, $\times 0.85$; (d) NMS G 1987.7.10. (pt), probable tibia of posterior leg, $\times 2$.

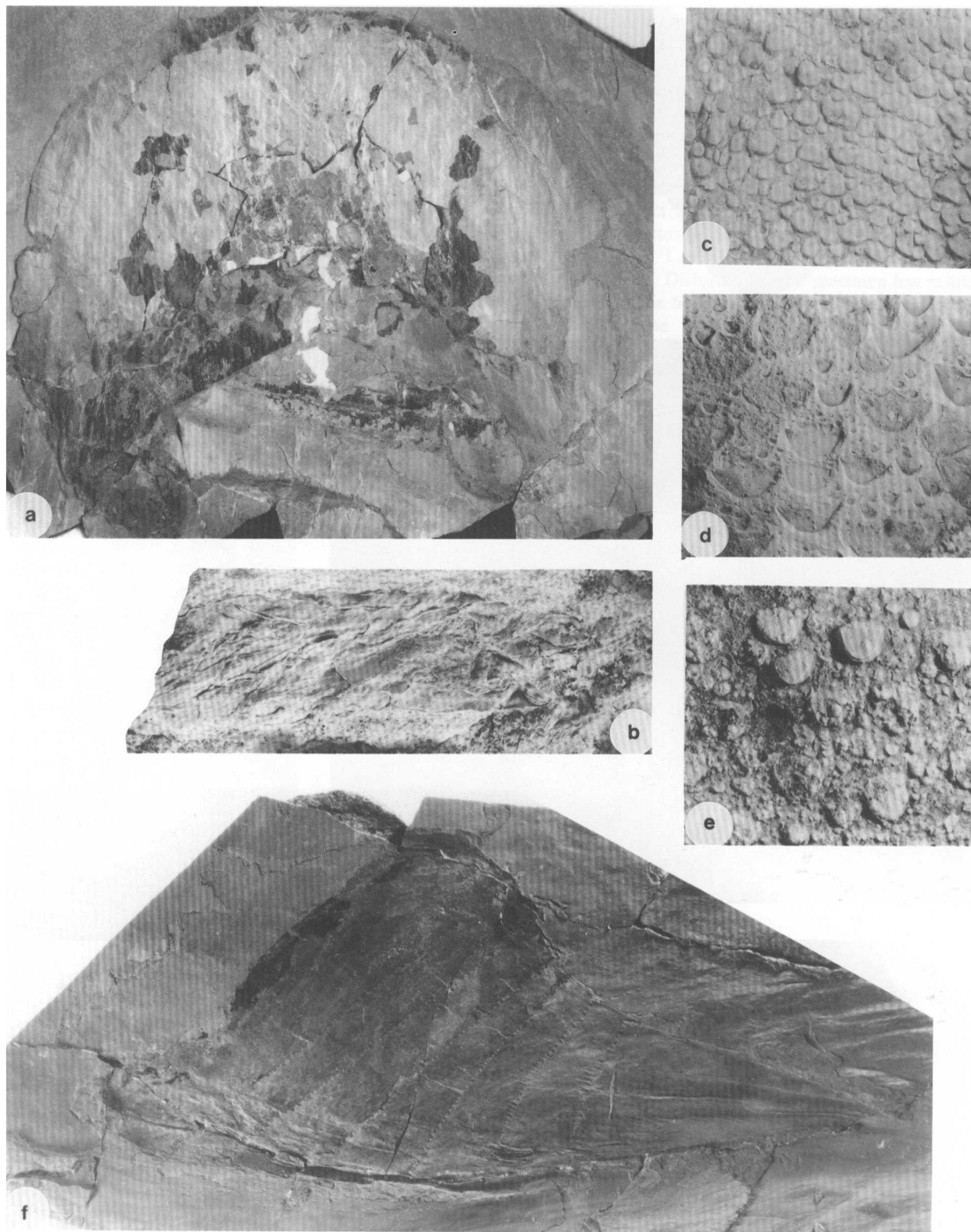


Figure 3 Eurypterids from the East Kirkton Limestone. (a) *Hibbertopterus scouleri* (Hibbert), very large carapace with tergite fragments, NMS G 1990.1.1b, $\times 0.17$. (b) cf. *Dunsotopus* sp., femur of posterior leg, distal end to right, NMS G 1992.43.2, whitened specimen, $\times 1.25$, see Fig. 4B for explanation. (c–e) Isolated cuticle fragments with ornament resembling parts of *Hibbertopterus*, see text for explanation, whitened specimens, $\times 2$: (c) NMS G 1992.43.4; (d) NMS G 1992.43.1, natural mould of cuticle surface in accretionary calcite; (e) NMS G 1992.43.5. (f) *Hibbertopterus scouleri* (Hibbert), metasoma with telson, viewed from ventral side. NMS G 1992.14.6, $\times 0.66$.

although they were rotated as cuticle collapse occurred, and are slightly disarticulated (Figs 1, 2b, c). The metastoma is displaced posteriorly relative to the coxae and its posterior margin is folded dorsally. The structure of prosomal appendage 5 is particularly interesting. The coxa, which originally would have been oriented with its long-axis vertically, now lies on its side (Fig. 1B). Articulated with it is a single, very large, trochanter. This may be a fused double trochanter, or it is possible that a small annulus-like second trochanter remains obscured by overlapping cuticle. The trochanter bears a broad dorsal 'Lade' (Fig. 1B), but the distal end is not seen as it is truncated by a shear plane in the matrix. The succeeding femur is greatly foreshortened in Figure 1B, and in life would have been approximately 30 mm long. The distal end of the posterior femur (prosomal appendage 6) is well preserved and fragments of the proximal end are preserved overlying the coxa of appendage 5, and on the counterpart slab (Fig. 1C). Its estimated minimum length based on these is 40 mm. Unfortunately the distal podomeres of the posterior legs are not preserved. A large isolated podomere (NMS G 1987.7.10, Fig. 2d) has a *Hibbertopterus*-like cuticle ornament and probably represents the tibia of prosomal appendage 5 or 6.

Only the sensory spines of appendages 2, 3 and possibly 4, are exposed in BMNH In. 62181 (Fig. 1C; see also Waterston 1957, text-figs. 3, 4). Waterston (1957, p. 275, pl. 2, fig. 7) described the sensory structures and suggested that a 'small cylindrical chitinous ring' preserved within the socket of each structure is the remains of a sensory hair. Controlled etching of accretionary carbonate which

encrusted sensory spines of BMNH In. 62181 failed to provide any evidence of setae, although fine hairs and setae were revealed by this process on other parts of the integument. Indeed, the sensory structures bear a resemblance to scorpion peg organs and, although the structures in question are larger than Recent scorpion peg organs, a similar chemosensory function is possible.

The lateral margins of two abdominal plates are visible on the counterpart of the complete specimen (BMNH In. 62181, Fig. 1B). These have been pushed anteriorly beneath the posterior leg coxae and are largely obscured. However, the cuticle ornament can be matched with other known *Hibbertopterus* abdominal plates (see Waterston 1957) and with isolated abdominal plates collected recently. One incomplete example, NMS G 1992.43.3, has an estimated breadth of 55 mm, and represents one of the smallest individuals of *H. scouleri* known.

Specimen NMS G 1992.14.6 (Fig. 3f) consists of the posterior end of an opisthosoma. The fifth abdominal plate, entire metasoma, and the telson are present, preserved with the ventral side exposed. The cuticle ornament is similar to that of the abdominal plates and metasomal segments of *H. scouleri* (e.g. BMNH In. 62181, NMS G 1891.92.479), so that there is little doubt that the specimen should be attributed to *H. scouleri*. The telson is very like that of *Cyrtotenus wittebergensis*, the prominent ventral keel having raised lateral shoulders and a median furrow (see reconstruction in Waterston *et al.* 1985), although the anterior margin is not seen because it is slightly telescoped into the posterior metasomal segment. The cuticle ornament

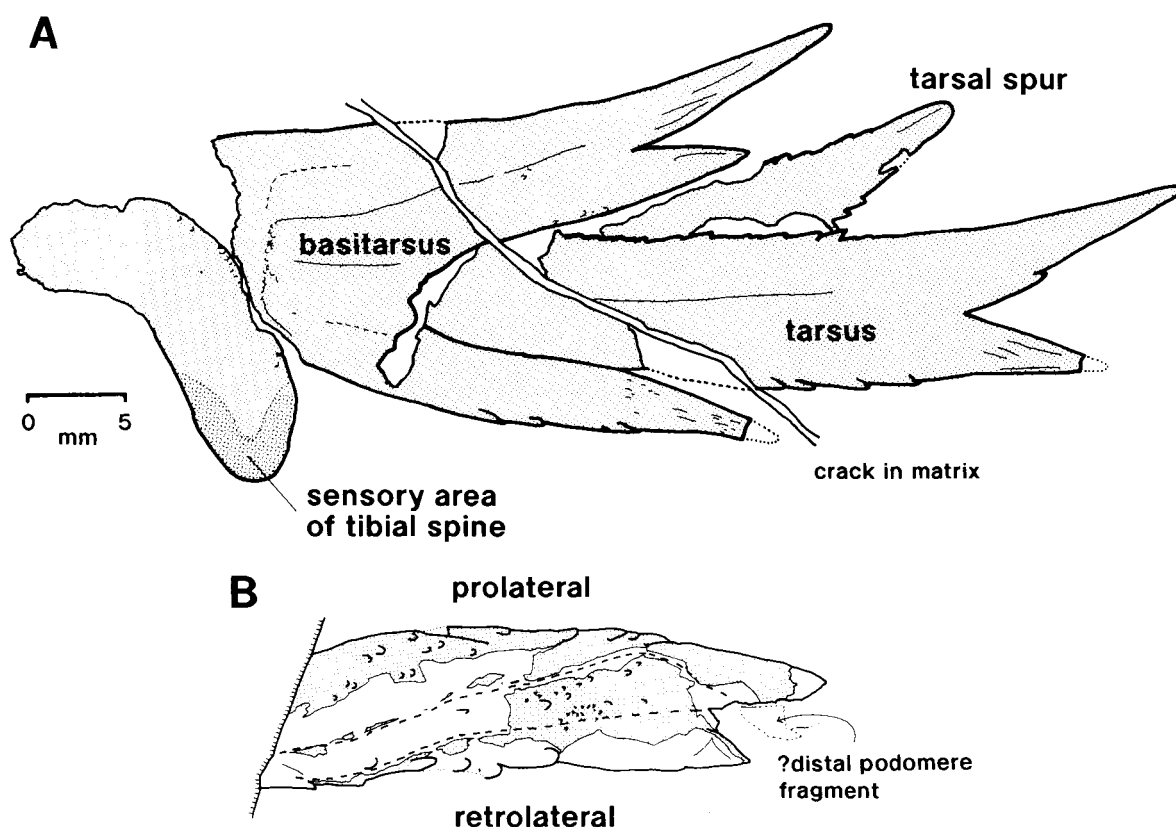


Figure 4 Eurypterids from the East Kirkton Limestone. (A) *Hibbertopterus scouleri* (Hibbert), GLAHM A23078, distal podomeres of prosomal appendage 4, dorsal view. Cuticle is indicated by stipple, and sensory area of tibial spine is indicated by heavy stipple. (B) cf. *Dunsotpterus* sp., NMS G 1992.43.2, femur viewed from dorsal (superior) side, explanatory diagram for Fig. 3b. Cuticle indicated by stipple. Where cuticle is absent, ventral features are seen as a mould of the cuticle surface in accretionary carbonate. Dashed lines indicate the location of deep compression folds in the ventral cuticle. These folds mark the boundary of the posterior groove. Note that this podomere is flattened and slightly twisted. See Fig. 3b for scale.

of the telson ventral surface, particularly at the anterior end, resembles that of tergite cuticle from the holotype of *Mycterops blairi* Waterston 1968. Isolated scraps of similar cuticle occurring in the East Kirkton Limestone (e.g. NMS G 1992.43.4, Fig. 3c), which were at first thought to be derived from *Mycterops*, can probably be attributed, therefore, to large specimens of *H. scouleri*. Other cuticle scraps (e.g. NMS G 1992.43.1, NMS G 1992.43.5, Figs. 3d, e) have lunules of two discrete size classes and also resemble *Mycterops* fragments (Waterston 1957, pl. 4, fig. 1; Waterston 1968, pl. 1, fig. 3), but these fragments can be matched perfectly with cuticle from near the tergite lateral margins of *H. scouleri* (e.g. BMNH In. 62181).

The largest recognisable specimen of *H. scouleri* is a flattened prosoma articulated with portions of two tergites (NMS G 1990.1.1, Fig. 3a) from Unit 82 equivalent (Rolfe *et al.*, this volume). The carapace is approximately 650 mm in diameter. Because the carapace was originally strongly domed, flattening has caused some distortion. The posterior-lateral lobes, for example, are folded in under the carapace, and there is a deep, transverse fold behind the eyes which has brought the posterior margin far further forward than it would have been in life. In other respects, such as the position of the lateral and median eyes, and the nature and distribution of cuticle ornament, this appears to be a typical, although large, specimen of *H. scouleri*. However, the cuticle is complexly folded and the specimen requires further study.

Specimen GLAHM A23078 (Fig. 4A) is the distal end of a posterior prosomal appendage, consisting of a partial tibial spine, the basitarsus, moveable tarsal spur, and the tarsus. These are orientated dorsal (superior) side uppermost. The cuticle is well preserved, and is densely ornamented with small lunules typical of *H. scouleri*. At the distal ends of fixed spines, the lunules become elongated to form cuticular striations. The tibial spine has a distal sensory area covered with sense organs identical to those present on *Hibbertopterus* prosomal appendages 2 and 3. Both of these appendages have sensory spines on all of the distal podomeres, including the telotarsus (Waterston 1957, test-figs 3, 4). The combination of a sensory tibial spine with non-sensory distal podomeres in GLAHM A23078 suggests that it represents the previously unknown fourth prosomal appendage of *H. scouleri*.

Family Cyrtoctenidae Waterston *et al.*, 1985

Type genus. *Cyrtoctenus* Størmer & Waterston, 1968

Genus *Cyrtoctenus* Størmer & Waterston, 1968.

Diagnosis. As Waterston *et al.* 1985

Type species. *Cyrtoctenus peachi* Størmer & Waterston, 1968.

Cyrtoctenus sp.

(Fig. 2a)

Material. Two isolated *Cyrtoctenus* combs, NMS G 1986.2.4 and NMS G 1987.7.24, from the Lower Carboniferous (Brigantian) East Kirkton Limestone, at East Kirkton Quarry, Bathgate, West Lothian.

Description. The larger of the two specimens, NMS G 1986.2.4 (Fig. 2a), is 220 mm long. It bears two rows of filaments. Part of the proximal end is obscured by matrix, so that it is not possible to estimate the total number of filaments present, although 86 were counted. Conical fulcra at the bases of filaments are absent and the rachis is ornamented with lunules. Both specimens are typical type-A combs (see Waterston *et al.* 1985, p. 346). These are most

completely known in the type species, *C. peachi*, with which the East Kirkton specimens are compared most appropriately, but the comb structure is less well known in other species, and so detailed comparisons are not possible. In addition to *C. peachi*, *C. caledonicus* (Salter) also occurs in the Lower Carboniferous of Scotland, although this species (known from a unique specimen) has large conical fulcra at the bases of filaments.

Genus *Dunsopterus* Waterston, 1968

Diagnosis. As Waterston 1968, p. 9.

Type species. *Dunsopterus stevensoni* (R. Etheridge Jr, 1877).

cf. *Dunsopterus* sp.

(Figs 3b, 4B)

Material. A single femur, NMS G 1992.43.2, from the Lower Carboniferous (Brigantian) East Kirkton Limestone, Bathgate, West Lothian.

Description. The femur measures 53 mm in length, although the proximal end is missing. It is almost certainly derived from the posterior walking-leg (prosomal appendage 6) of a large eurypterid. The distal end bears two large spurs and, by analogy with *Hibbertopterus*, the larger of these marks the anterior (prolateral) side of the podomere. A complex set of cuticular folds runs along the axis of the podomere, and these mark the position of a longitudinal posterior groove like that of *Dunsopterus* or *Cyrtoctenus* (Waterston *et al.* 1985, p. 345). The cuticle ornament consists of relatively sparse, but large, lunules arranged in discrete rows, particularly on the prolateral and retrolateral sides. This is closer to the arrangement of lunules in *D. stevensoni* than that in podomeres associated with combs of *C. peachi*, in which lunules are more abundant and less concentrated into rows (Waterston *et al.* 1985, fig. 9b). However, as Waterston *et al.* (1985, p. 345) point out, the posterior groove is probably a specialisation to increase the strength of long podomeres in very large eurypterids, and it may not occur in smaller individuals of the same species. If this is the case, then the podomere could be derived from *Hibbertopterus*. A posterior groove has not been observed in any podomeres associated with articulated specimens of *Hibbertopterus*, but those specimens with podomeres preserved are all <50 cm long and may be too young to show this feature.

3. Discussion

Waterston *et al.* (1985) acknowledged the possibility that *Cyrtoctenus* and *Dunsopterus* are cogenetic, because the fragmentary material of *Dunsopterus* recognised to date represents sclerites which are either poorly known in *Cyrtoctenus*, or have little diagnostic potential. It is striking that both genera are known only from remains of very large individuals. Waterston (1957, text-fig. 8) compared a small carapace from the Calciferous Sandstone Series of Kimmerghame Quarry with *Hibbertopterus* (= *Campylocephalus*). This is the type locality of *Dunsopterus stevensoni* and Waterston (1957, p. 282) considered that the carapace might be from a juvenile *Dunsopterus*. Moulded integuments of juveniles would ordinarily be expected to dominate unbiased arthropod assemblages (e.g. Sheldon 1988). Preservational bias may be one reason for the dominance of large eurypterid fragments in some assemblages (see Jeram, this volume), but as *Hibbertopterus* specimens from the East Kirkton Limestone

have even sclerites with very thin cuticle preserved (e.g. Waterston 1957, pl. 2, fig. 5), it seems unlikely that differential preservation is a significant factor in this case. All of the smaller specimens from East Kirkton Quarry, both complete and isolated sclerites, can be attributed to *Hibbertopterus scouleri*; so, is it possible that as *H. scouleri* grew it developed a specialised morphology similar to that of *Cyrtoctenus* and *Dunsopterus*?

Anterior appendages of *Hibbertopterus* are certainly specialised for food gathering. Distal podomeres of the first three pairs of walking-legs bear long spine-like flanges. Each of these is densely covered with sense organs at its distal end (Waterston 1957, text-fig. 4; pl. 2, fig. 7). Since these appendages could hardly be employed for grasping, and both the chelicerae and coxal gnathobases are weakly developed, predation on relatively large animals can probably be discounted. The lack of specialisations for swimming or trap feeding support this conclusion. It is far more likely that the anterior appendages were used to rake through soft sediment for shallow infauna, such as small crustaceans, which when detected could be swept into the oral region.

Waterston *et al.* (1985) advanced some strong arguments for a sweep-feeding mechanism in *Cyrtoctenus*. The feeding method proposed by these authors differs slightly from that suggested here for *Hibbertopterus*, since it was envisaged that food material was collected by the filtering action of the comb structures. Shallow infauna tends to be dominated by animals of small body size and as *Hibbertopterus* grew the 'raking' method may have become less efficient, because an increasingly large proportion of the infauna would be small enough to pass between the flanges. For *Hibbertopterus* to have reached lengths of a metre or more, and yet still feed on tiny invertebrates, some modification of the food-gathering appendages and/or feeding method would have been necessary. Although the above is largely speculative, it is not inconceivable that the late post-embryonic development of *Hibbertopterus* included the development of *Cyrtoctenus*-like food-gathering structures and grooved podomeres as responses to the demands of feeding and locomotion at large body sizes.

Rolfe (1986) suggested that *H. scouleri* showed some terrestrial adaptations, and terrestrial activity in other eurypterids has also been discussed (Selden 1984, 1985). Waterston *et al.* (1985) considered that *Cyrtoctenus* was aquatic because of its mode of feeding, and also, because the posterior prosomal appendages show no adaptations for swimming (see Briggs *et al.* 1991), locomotion was primarily by walking. Prosomal appendages 2 and 3 of hibbertopteroids were apparently not involved in locomotion. Appendage 4 of *Hibbertopterus* (e.g. GLAHM A23078) and *Cyrtoctenus* (Waterston *et al.* 1985, fig. 6) combined feeding and locomotory functions, whilst the posterior two pairs of legs were entirely locomotory, so hexapody is inferred. The elongated fixed spines on the basitarsus and telotarsus of *Hibbertopterus* appendage 4 may be an adaptation for spreading the load of locomotory appendages on soft muddy substrates.

Indirect evidence for at least limited terrestrial activity is provided by the East Kirkton assemblage. The smallest eurypterid sclerites are derived from individuals approximately 200 mm long. Assuming that early stadia were significantly smaller than this, and that taphonomic factors have not removed juvenile cuticle, it can only be concluded that eurypterids were not breeding in the East Kirkton lake. The rarity of complete specimens in the East Kirkton Limestone, and the relative abundance of cuticle fragments

in horizons rich in comminuted plant debris (Jeram, this volume), suggests that eurypterids were not permanent inhabitants of the lake, but of the area immediately around it. It may be that large hibbertopteroids were feeding on small invertebrates such as brine shrimps in seasonal pools adjacent to the lake, and perhaps in the lake shallows at times when the water could support a restricted temporary fauna. The absence of juveniles suggests that the nearest nursery pools were outside the East Kirkton lake catchment area and that larger individuals capable of terrestrial activity dispersed from them into the catchment area. Clearly, there is a great deal more evidence needed before such speculation can be objectively tested. It is hoped that further study of the East Kirkton eurypterid fossils will ultimately answer some of the questions raised in this discussion.

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