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Actinopterygian and acanthodian fishes from the Viséan of East Kirkton, West Lothian, Scotland

M. I. Coates

ABSTRACT: Forty-one specimens of acanthodians and actinopterygians were examined from Units 26 to 38 of the Geikie Tuff, Little Cliff Shale and East Kirkton Limestone of the Viséan East Kirkton Limestone sequence. The results yielded six actinopterygian species including a platysomid and two probable juveniles of uncertain affinities, and three acanthodians including two acanthodidids and a climatiid-like denticle. Most specimens consist of isolated bones and scales, but articulated remains of an acanthodian and actinopterygians were found in Units 37 and 38 of the East Kirkton Limestone. The faunal composition is characteristically Oil-Shale in aspect and resembles that of Broxburn (Pumpherston). The presence of deep-bodied and juvenile fishes in the same strata combined with the mode of preservation indicate a palaeohabitat with limited current action and a soft substrate.

KEY WORDS: Acanthodian, actinopterygian, Carboniferous, Climatiiformes, *Eurynotus*, Platysomidae, Viséan, Scotland, East Kirkton.

This synoptic review of the actinopterygian and acanthodian fishes is one of a series of papers on the East Kirkton Viséan biota in this volume. The outstanding importance of the East Kirkton site derives from the unique snap-shot it provides of an early Carboniferous terrestrial community, as inferred partly from the preponderance of non-aquatic tetrapods and invertebrates. Rolfe *et al.* (1990) reported the presence of numerous fish fragments at the site, but these appeared to be restricted to the horizons above the tetrapod-bearing strata of the East Kirkton sequence (Giekie Tuff and Little Cliff Shale). However, the fish remains are now known to include isolated scales and articulated specimens, the distribution of which extends into Units 36–38 of the East Kirkton Limestone, overlapping the uppermost range of disarticulated and probably transported tetrapod bones. There is no evidence of coexistence between these fishes and the characteristic articulated tetrapods of the lower part of the East Kirkton Limestone (Clarkson *et al.*, this volume). Actinopterygian diversity includes small adults occurring in association with tiny juveniles and a moderately deep-bodied platysomid; an indeterminate number of acanthodian taxa are present, including an apparently juvenile form.

Details of the locality and stratigraphy of the East Kirkton sequence are given in Rolfe *et al.* (this volume). Material studied is held by the following institutions: University Museum of Zoology, Cambridge (UMZC), National Museums of Scotland, Edinburgh (NMS).

1. Descriptions and comments

Superclass GNATHOSTOMATA (sensu Forey, 1984)

plesion Acanthodii Woodward, 1891

Order ACANTHODIFORMES Miles, 1966

Family Acanthodidae Huxley, 1861

'tiny acanthodian' Rolfe *et al.* 1990

Material. Specimens NMS G 1993.6.1 (Fig. 1), NMS G 1993.6.2a&b and NMS G 1993.6.3.

Horizon. NMS G 1993.6.1 was collected from Unit 36 of the Little Cliff Shale. NMS G 1993.6.2 and NMS G 1993.6.3 were collected from Units 26 and 29 of the Geikie Tuff.

Description. NMS G 1993.6.1 (Fig. 1) consists of the fin spines, scales, pectoral girdle and jaws of a small individual of uncertain length. If this were a specimen of *Acanthodes wardi* (based upon Miles' composite reconstruction (Miles 1970)), then the pectoral spines would translate to a fish of ~30 mm. The severely disrupted head retains a pair of mandibular bones, one of which carries a large, ankylosed tooth (Fig. 1, at) (cf. *Acanthodopsis,* Hancock & Atthey 1868). The palatoquadrate is known only from a fragment spanning the quadrate and metapterygoidal region. The identity of a patch of ridged perichondral bone adjacent to one of the mandibles is uncertain; it may be part of the neurocranial periosteal layer. A pair of thin, arched bone slivers (Fig. 1, sc) appear to be vestiges of the sclerotic ring. Scattered, short branchiostegal rays surround the jaws. Black swellings and depressions of approximately equal size occupy the otic region. These are interpreted either as statoliths or as in-fillings of the utricular and saccular recesses, as preserved in *Acanthodes ovensi* (Forey & Young 1985) and *Utahacanthus guntheri* (Schultze 1990).

The endoskeletal shoulder girdle is preserved as an incomplete scapulocoracoid, with a natural mould of the articular region. It compares closely with the scapular of *Howittacanthus kentoni* (Long 1986a), having none of the additional ossifications found in *Acanthodes* (Miles 1973). The pattern of foramina in the articular region of the scapulocoracoid is unknown. The pectoral fin spines have become disarticulated from the girdle, but remain as a pair below the anterior end of the trunk. Each spine has a thickly keeled, convex leading edge and lateral surfaces incised with fine, posteroproximally directed grooves. The fin webs are unknown. The dorsal fin spine is just over half the length of the pectoral spines, and the pelvic spines are about one third of the pectoral fin spine length. The caudal region is unknown.

The scales are typically acanthodid and are very small, with an unornamented rhombic crown. A histological investigation of the scale morphology has not been undertaken. The lateral-line canals appear to be preserved as a pair of ridges running along both sides of the laterally flattened anterior trunk region, terminating in the vicinity of the otic capsules. These may simply be ridges in the matrix, and no specialised sensory scales have been observed.

NMS G 1993.6.2 consists of two sections of acanthodian fin spine. These total 10 mm in length and differ from those of NMS G 1993.6.1 in having smooth sides, although they are curved similarly and also have a prominent anterior keel.

NMS G 1993.6.3 may be a fragment of endoskeletal pectoral girdle, which resembles preservationally the spine of NMS G 1993.6.2.

Comments. The scale morphology, elaborate form of the fin spines, and the presence of an apparently ankylosed tooth, resemble those of *Acanthodopsis* (Ischanacanthidae Denison, 1979; Acanthodidae Long, 1986b).

Order CLIMATIFORMES Berg, 1940

Family Climatiidae Berg, 1940

Material. Specimen NMS G 1993.6.4a (Fig. 2).

Horizon. NMS G 1993.6.4a comes from Unit 31 of the Geikie Tuff.

Description. NMS G 1993.6.4a consists of a small laminar bony plate bearing a pair of tubercles, as shown in Figure 2. It closely resembles one of the mesondentinous ornamented tesserae of the climatiid *Climatius reticulatus*, as figured in Denison 1979 (fig. 16B). In both the tubercles are round or ovoid, with the surface drawn into ridges which converge towards a central apex.

Comments. This tiny specimen is the only recorded evidence of a climatiid acanthodian from the fish beds. It bears no resemblance to any part of the acanthodian material described above. If this specimen has been identified correctly as belonging to a climatiid, then it constitutes an unexpectedly late record of a group, which Denison describes as occurring between the Middle Silurian and the Upper Devonian (Frasnian). However, given the extremely poor preservation of much of the acanthodian material at East Kirkton, the possibility that this plate belongs to the species described earlier cannot be excluded.

Superclass GNATHOSTOMATA (sensu Forey, 1984)

Class ACTINOPTERYGII Woodward, 1891

Infraclass ACTINOPTERI (sensu Patterson, 1982)

Species A

Material. Specimens NMS G 1993.6.5a–c, NMS G 1993.6.6, NMS G 1993.6.7, G 1993.6.8, NMS G 1993.6.9, and NMS G 1993.6.10a and b (Fig. 3A).

Horizon. NMS G 1993.6.5a–c comes from Unit 26 or Unit 28 of the Geikie Tuff; NMS G 1993.6.6, G 1993.6.7 and NMS G 1993.6.8 come from Unit 34, NMS G 1993.6.9 from Unit 35, and NMS G 1993.6.10 from Unit 36, each of which originates from the Little Cliff Shale.

Description. All of this material consists of isolated scales except for NMS G. 1993.6.10, which comprises the near-complete posterior half of a small fusiform actinopteran (Fig. 3A). The scales bear a characteristic dermal ornament (Fig. 3B) consisting of a set of five, deeply incised grooves which are parallel with the anterior and ventral edges, together with posteriorly directed, occasionally bifurcating ridges occupying the remainder of the surface. The trunk and caudal fin of NMS G 1993.6.10a and b probably include 50% of the total body length (~60 mm). The dorsal, anal, caudal and fragments of the pelvic fins are preserved, including rows of fringing and caudal fulcra. Although the body outline is fairly clear, relatively few precise details are discernible.

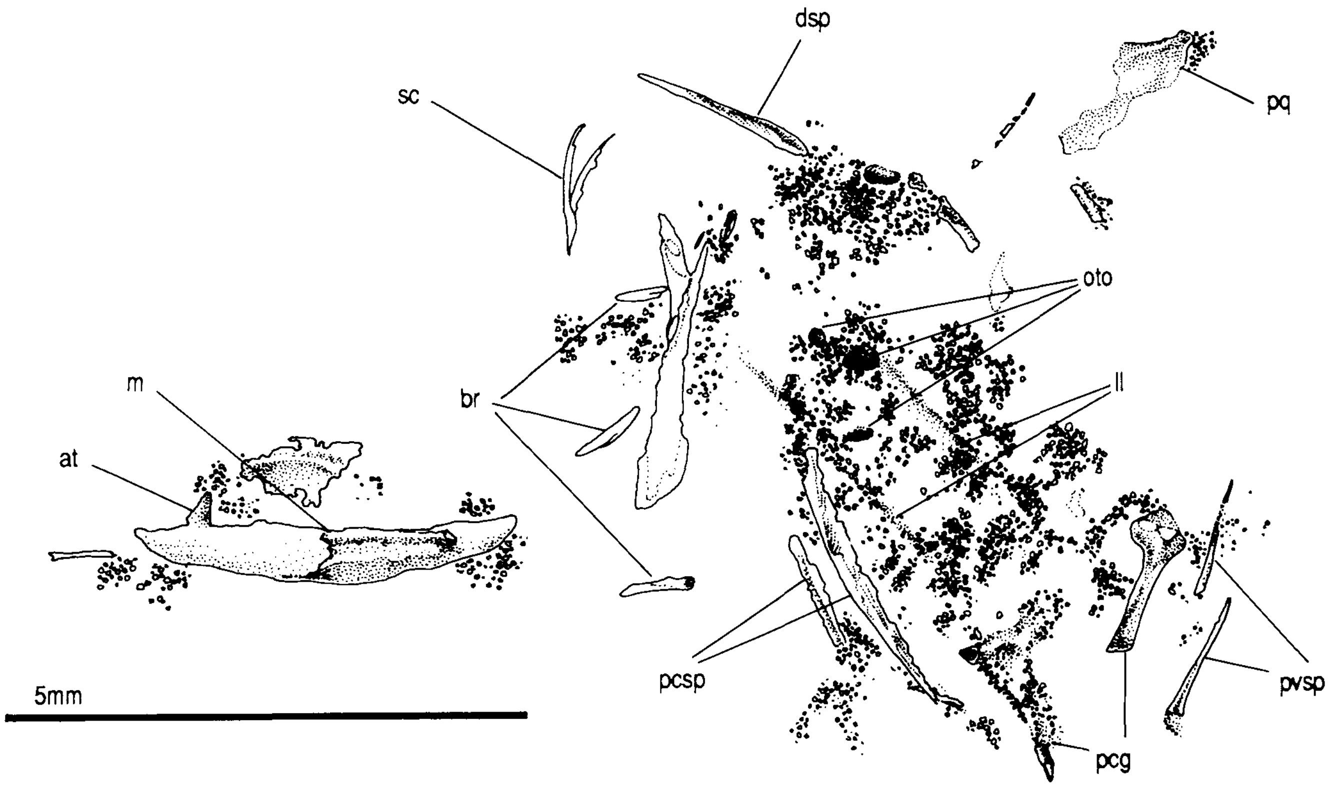


Figure 1 NMS G 1993.6.1, 'tiny acanthodian' (Rolfe *et al.* 1990), from the black shale and ironstone component of Unit 36 of the Little Cliff Shale. Abbreviations: br, branchiostegal rays; dsp, dorsal spine; 11, lateral line; m, mandible; oto, otoliths; pcg, pectoral girdle; pcsp, pectoral spine; pq, palatoquadrate; pvsp, pelvic spine.

Comments. Although not much larger than the specimens identified as juveniles (see below), the more clearly discernible scale ornament and shape, and the narrow-based fins of Species A (compare the lengthy insertion of the anal fin in Fig. 6A with that of Fig. 3A) resemble adult early-actinopteran morphology. The scale ornament consisting anteriorly of vertical ridges and posteriorly of posteroventrally directed ridges is found in many of the contemporaneous '*Rhadinichthys*'-grade fishes of the Scottish Lower Carboniferous. Although not identical, the strongly denticulated scales resemble most closely those of *R. carinatus*.

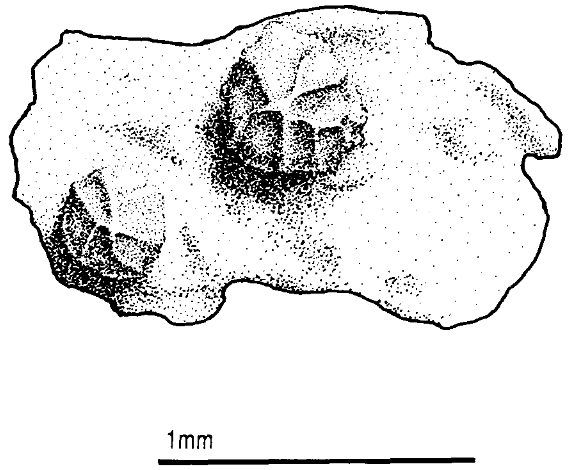


Figure 2 NMS G 1993.6.4a, the speculatively identified climatiid tessera from Unit 31 of the Geikie Tuff.

Species B

Material. Specimens NMS G 1993.6.11a and b, NMS G 1993.6.12a and b, NMS G 1993.6.13, NMS G 1993.6.14a and b, and NMS G 1993.6.15a and b (Fig. 4A).

Horizon. All specimens were collected from Unit 26 or Unit 28 of the Geikie Tuff, apart from NMS G 1993.6.15a and b, which comes from the Little Cliff Shale (assumed to originate from uppermost Unit 33).

Description. All of the Species B material consists of isolated scales. These are usually incomplete, but appear to be of the usual rhombic type, with an almost-smooth surface and posterior edge (Fig. 4A); each is about 1·5 mm wide. Because of its relatively small size and co-occurrence in the upper Units of the Geikie Tuff, an incomplete dentary on NMS G 1993.6.14a, of 14 mm length, may also belong to this species.

Species C

Material. Specimens NMS G 1993.6.16a–c, NMS G 1993.6.17, NMS G 1993.6.18, NMS G, 1993.6.19, NMS G

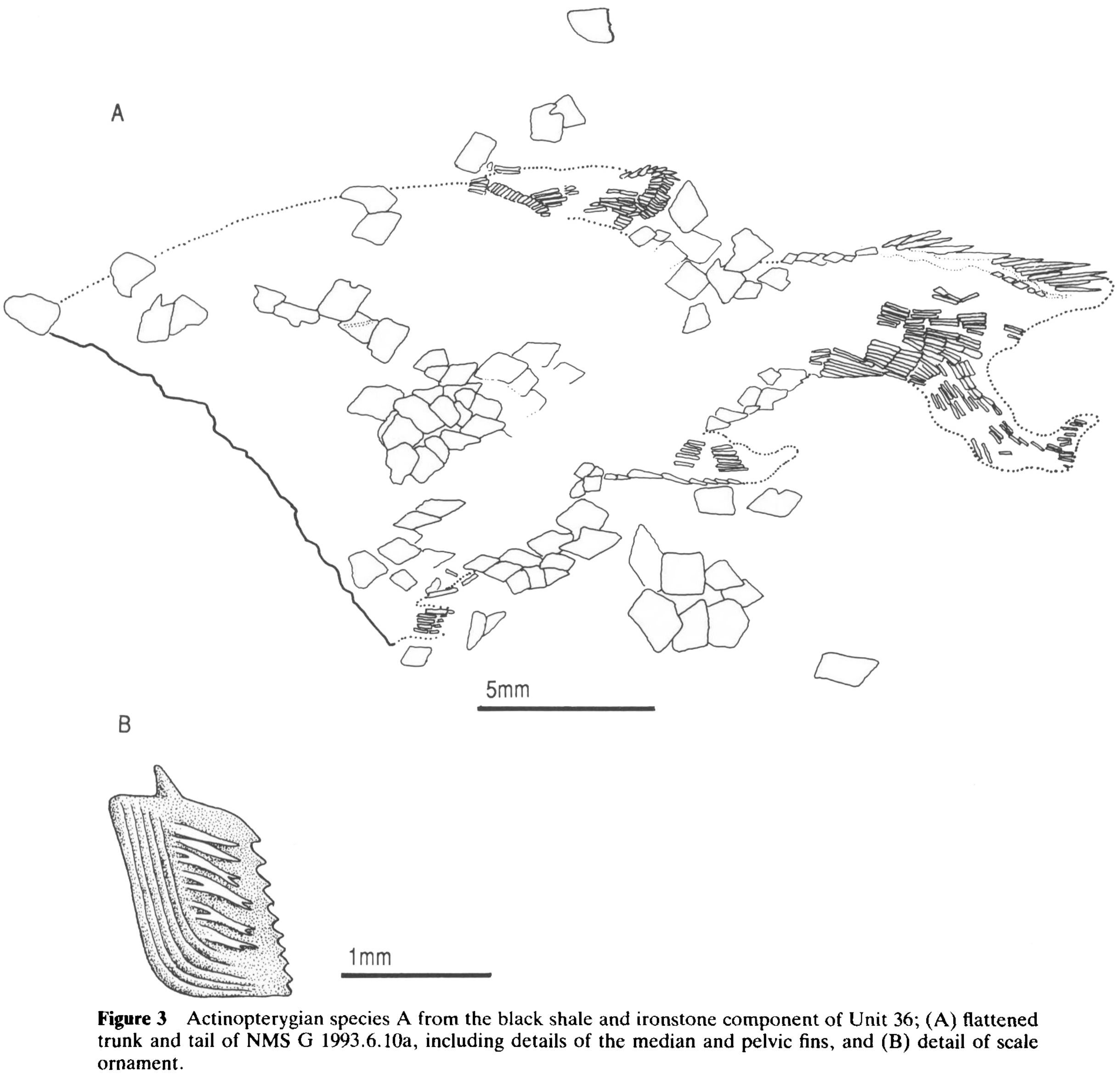


Figure 3 Actinopterygian species A from the black shale and ironstone component of Unit 36; (A) flattened trunk and tail of NMS G 1993.6.10a, including details of the median and pelvic fins, and (B) detail of scale ornament.

1993.6.20a and b, NMS G 1993.6.21 and NMS G 1993.6.22a–g (Figs 4B, C).

Horizon. NMS G 1993.6.16 was collected from Unit 27 and NMS G 1993.6.17 from Unit 29 of the Geikie Tuff; NMS G 1993.6.18 was collected from Unit 33 and NMS G 1993.6.19 from Unit 35 of the Little Cliff Shale; NMS G 1993.6.20 and NMS G 1993.6.21 were collected from Unit 36, and NMS G 1993.6.22 from Unit 37 of the East Kirkton Limestone.

Description. Most of the material consists of isolated scales, but NMS G 1993.6.20a and b contains the separated head and trunk of an individual of which the total length was approximately 120 mm. The scales are almost smooth, with a faint ridged ornament and a finely denticulated posterior edge (Fig. 4B). The shape and distribution of the squamation suggests that this, too, was a fusiform species. The cranial material is crushed dorsoventrally, and many bones are unidentifiable (Fig. 4C). A pair of long, slender dentaries each bear small, conical teeth. The maxillae have a long, posteriorly expanded region, the frontals are short and broad, and the premaxillae contain a substantial portion of the ethmoid commissure. The oral surface of the right palate is visible, still articulated with the internal surface of the maxilla, and bears an array of granular teeth. The parasphenoid dominates the center of the crushed skull and is indistinguishable anteriorly from the ventral portion of the ethmosphenoidal wall. The parasphenoid has a well-developed, laterally expanded posterior region (which overlies the remains of the rostral), and a pair of laterally directed lappets, which form a significant dermal component of the basipterygoid processes. Fractured sheets of dermal bones surrounding these remains may represent opercular material.

Comments. The closest comparable taxon to Species C recorded from other Viséan or Namurian fish faunas of the Scottish Midland Valley is *Elonichthys robisoni* Hibbert. Both have similar scale size and ornament, body-length, fin distribution, and proportions of known cranial bones. However, *E. robisoni,* like most other members of the genus *Elonichthys* Giebel, has been described only superficially in Traquair's (1877–1914) summary of the 'ganoid fishes'. Congeneric species which have been subjected to a more thorough examination have usually been found to require the erection of a new genus. From among these newly erected taxa, *Mansfieldiscus* Long (1988) from the Lower Carboniferous of Victoria, Australia, appears to be the most similar to Species C. However, once again the similarities are of a rather general nature: size, estimated shape, proportions of the maxilla, breadth of frontals. The presence of a posteriorly expansive parasphenoid with well-developed basipterygoid processes in both taxa provides tenuous evidence of their phylogenetic interrelationships, suggesting that both may lie, *incertae sedis,* within the stem-group of Gardiner and Schaeffer's (1989) '*Pteronisculus*' group, with other Scottish Lower Carboniferous genera such as *Nematoptychius* and *Acrolepis.*

Species D

Material. Specimen NMS G 1993.6.23.
Horizon. Unit 35 of the Little Cliff Shale.
Description. This is an isolated maxilla which has a

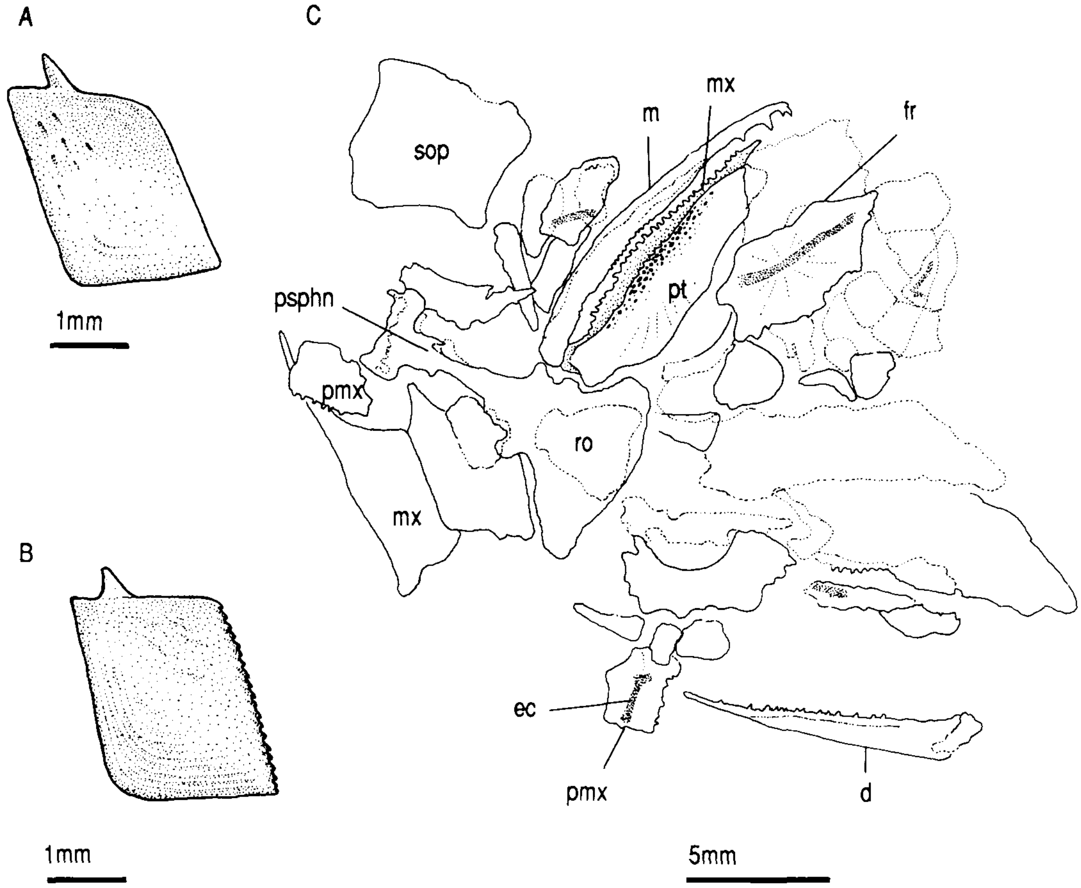


Figure 4 (A–C) Actinopterygian species B and C from the Geikie Tuff and the East Kirkton Limestone; (A) scale from species B, (B) scale from species C, and (C) disrupted head of almost complete specimen (NMS G 1993.6.20) of species C from laminated limestone component of Unit 36. Abbreviations: d, dentary; ec, ethinoid commissure; fr, frontal; m, mandible; mx, maxilla; pmx, premaxilla; psphn, parasphenoid; pt, pterygoid; ro, rostral; asop, sub operculum.

relatively short, subrectangular, posterior expanded region. Its total length is 5·5 mm. The dentition is barely discernible, but appears to consist of a single row of teeth. The dermal ornament is insufficiently clear to be of diagnostic value.

Comments. The shape of this maxilla suggests that it belongs to a species with a near-vertical jaw suspension. A close comparison may be made with *Mesopoma* Traquair (see reconstructions in Moy-Thomas & Bradley Dyne 1938). It is not of the more-rounded triangular form of common Oil-Shale taxa such as *Pseudogonatodus*.

Species E

Material. Specimen NMS 1993.6.21a–c (Fig. 5).

Horizon. Unit 36 of the East Kirkton Limestone.

Description. This specimen includes several large broken scales, the most complete of which (Fig. 5) is about 9 mm tall and 4 mm wide and ornamented with prominent ganoin ridges, which occasionally bifurcate or fuse. The ridges are oriented along an anterodorsal-posteroventral axis. The presence of an anterodorsal process and the location of the dorsal peg are unknown.

Comments. This scale closely resembles those of *Cosmoptychius striatus*, a large (up to 28 cm long) fusiform predator, which is relatively common within the Lower Carboniferous Scottish Oil-Shale faunas. This genus is known to have relatively deep flank scales with a similarly formed ganoine-ridge ornament with rounded apices (Traquair 1877–1914, plate III). However, the similarity of scale ornament cannot be conclusive and other likely candidates include *Watsonichthys*, or, given the deep proportions, a deep-bodied platysomid (although none are known to have this form of ornament, and their scales usually lack the anterodorsal process characteristic of most early actinopterygians). NMS G 1993.6.21 includes several different scale types, including species C, E and an array of unidentified scraps. This specimen may represent some form of gut-residue; the scales appear to be relatively undigested and the overall form of this aggregation is not coprolitic.

Juvenile specimens.

Material. Specimens NMS G 1993.6.24a and b and NMS G 1993.6.25 (Figs 6A and B).

Horizon. NMS G 1993.6.24 comes from Unit 36 and NMS G 1993.6.25 from Unit 38 of the East Kirkton Limestone.

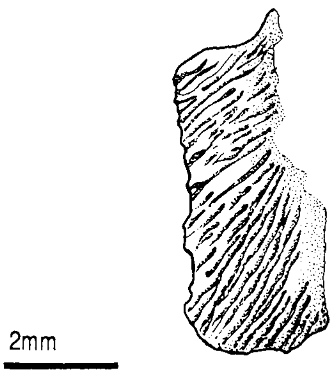


Figure 5. From NMS G 1993.6.21; large scale attributed to *Cosmoptychius*, from the laminated limestone component of Unit 36.

Description. This pair of juvenile actinopterygians (Figs 6A, B) cannot be assigned to any of the above taxa. Both have relatively well-ossified maxillae with large, expanded posterior regions. These indicate that the gape extended postorbitally, and that the suspensorium was angled obliquely. The frontals enclose an open pineal foramen in NMS G 1993.6.24a and b. Both juveniles have a single pair of large otoliths (statoliths), one in each otic capsule. NMS G 1993.6.25 retains evidence of the cleithrum and supracleithrum, but the squamation consists only of a body-shaped area of crushed scales. NMS G 1993.6.24 is flattened dorsoventrally and exposed from the ventral surface. The abdominal area is disrupted and evidence of the paired fins lost. The broad based, well-preserved anal fin precedes the tail, which retains a series of dorsal fulcral scales. Fragments of the dorsal fin are present. Both specimens appear to have been around 30 mm long.

Comments. Each of these specimens corresponds fairly closely to the general form of previously described, subadult early actinopterygians. Schultze and Bardack (1987) figure several similarly sized examples of '*Elonichthys hypsilepis*' from the Mazon Creek fauna. Like the East Kirkton specimens, these have broad-based fins, tails in which the posterior extremity is almost never preserved (cf. Figs 6A and B), squamation developed most clearly in the posterior region of the tail and trunk (NMS G 1993.6.24) and skulls in which the jaws are the most completely ossified structures. Lowney (1980) describes almost identical ontogenetic features among the juvenile actinopterygians of the Bear Gulch fauna, Montana. It is possible that these specimens may represent small adults, but without the evidence of a complete growth-series sustained argument concerning the ontogenetic status of these taxa would be inconclusive. Similarly, the different shapes of the maxillae in these two specimens may indicate the presence of separate taxa, or simply an artifact of taphonomic distortion.

Family PLATYSOMIDAE Traquair, 1879

Genus *Eurynotus* Agassiz, 1833

Eurynotus sp.

Material. Specimens NMS G 1993.6.26a and b, NMS G 1993.6.27a and b, NMS G 1993.6.28, NMS G 1993.6.29 and NMS G 1993.6.30a–h (Fig. 7A, B).

Horizon. NMS G 1993.6.24 comes from Unit 34 and NMS G 1993.6.27 from Unit 35 or Unit 36 of the Little Cliff Shale; NMS G 1993.6.28 and NMS G 1993.6.29 come from Unit 36, and NMS G 1993.6.30 from Unit 37 of the East Kirkton Limestone.

Description. NMS G 1993.6.30 (Fig. 7B) is the most complete actinopterygian fossil known from East Kirkton. Other eurynotid specimens include disarticulated skull and girdle bones. The cranial region of NMS G 1993.6.30 is in poor condition, but retains impressions of the lower jaw and triangular maxillae, both of which bear vestiges of the marginal crushing dentition. The dermal ornament of the maxillae resembles that of *Eurynotus crenatus* (Traquair 1879), except that the vertical striae pass dorsally into a narrow tuberculated strip parallel to the anterodorsal edge. The broad frontals contain a highly branched section of the supraorbital canal, exposed most clearly on NMS G 1993.6.29. Crushed remains of the palatal toothplates (described in detail by Watson 1928) lie anteriorly to one of the pair of characteristically tall cleithra preserved on specimens NMS G 1993.6.30 and NMS G 1993.6.28. Low-angle illumination of NMS G 1993.6.30 reveals the

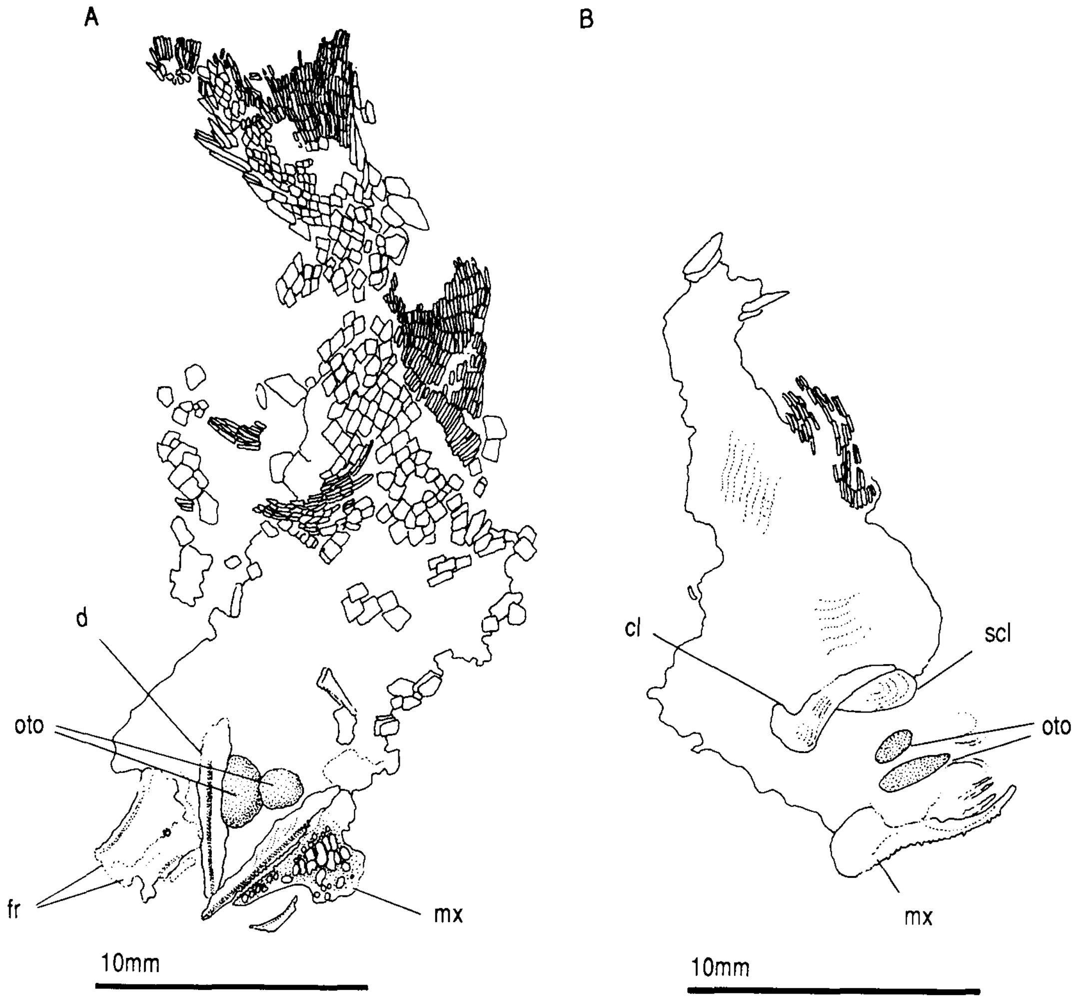


Figure 6 Articulated juvenile actinopterygians from the East Kirkton Limestone; (A) NMS G 1993.6.24 from Unit 36, and (B) NMS G 1993.6.25 from Unit 38. Abbreviations; cl, cleithrum; d, dentary; fr, frontal; m, mandible; oto, otolitho; scl, supracleithrum.

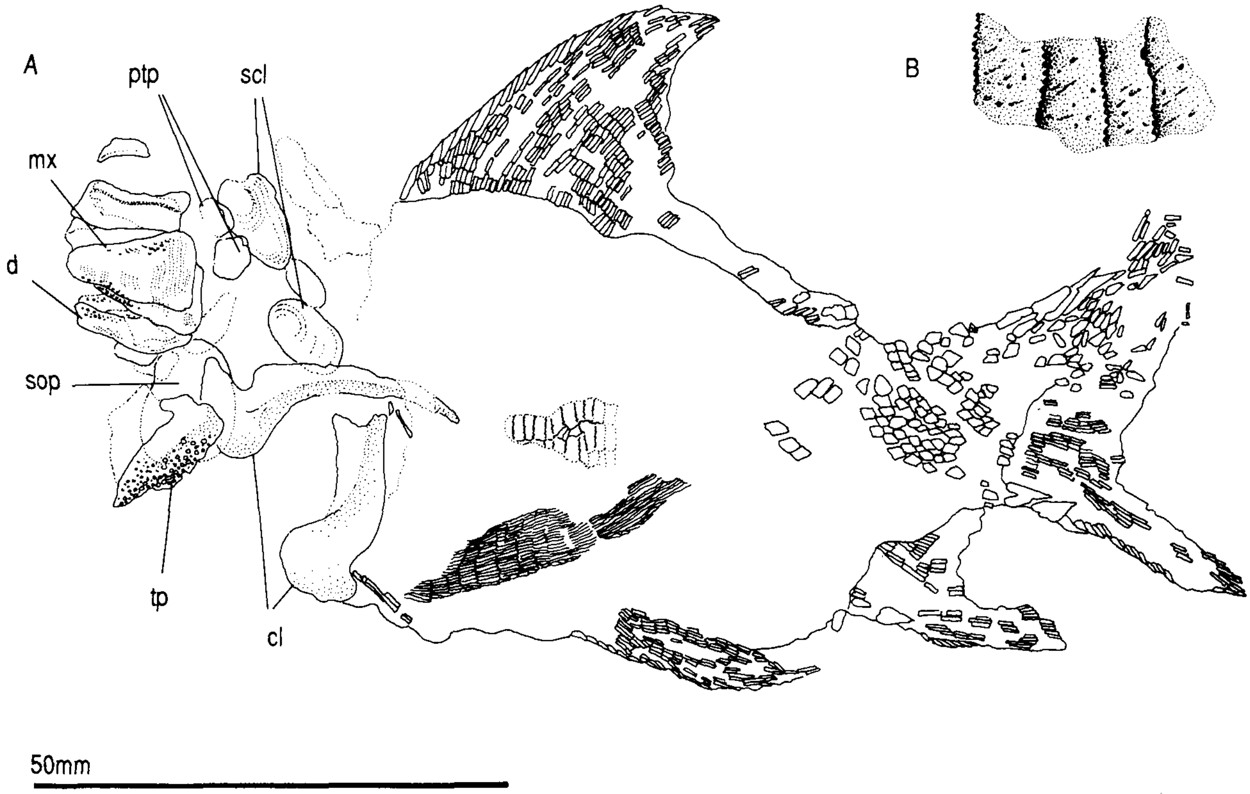


Figure 7 Articulated specimen (NMS G 1993.6.30) of *Eurynotus*; (A) patch of flank scales showing punctate surface and serrated posterior edges, and (B) almost entire body with dissociated cranial bones and toothplates. Abbreviations: cl, cleithrum; d, dentary; m, mandible; ptp, pterygoid; scl, supracleithrum; sop, suboperculum; tp, tooth plate.

presence of a large rounded subopercular, both supracleithra, a postcleithrum, and a pair of parietals/post-temporals.

The trunk and fins of NMS G 1993.6.30 are almost intact, and correspond fairly closely to Traquair's (1879, plate III) restoration of *Eurynotus crenatus*. The long-based dorsal fin is slightly larger, with a relatively taller apex to the leading edge and, similarly, the short-based anal fin is also deeper. The pelvic fin of the East Kirkton specimen is longer proximodistally, and although the distance from the anal to pelvic fins is the same as in *E. crenatus*, the pelvic-pectoral distance is reduced by 25%. The pectoral fin is known from the excavated natural impression in the counterpart; it appears to have been as extensive as that of *E. crenatus*. The scales are preserved as a body-shaped mat of crushed and fused fragments. Exposed natural casts of the exterior scale-surfaces (Fig. 7A) reveal the ornament to be restricted to sparse oblique grooves, occasional pores, and denticulated posterior edge. Trunk length, as measured from the most deeply indented region of the tail to the anterior edge of the pectoral girdle, is 96 mm; the greatest body depth is 54 mm. These proportions are shorter and deeper than those of Traquair's reconstruction.

Comments. At present it is not possible to establish whether the East Kirkton material represents a new species of *Eurynotus*. In comparison with a Wardie specimen catalogued as *E. crenatus* (UMZC GN 1020) the East Kirkton specimen is about 20% smaller and has a deeper gibbose trunk; the fin sizes and insertions, and the ornamentation of the maxillae are subtly different. A comparison of the body-profiles of restored eurynotids is illustrated in Fig. 8. Traquair (1879) records three species of *Eurynotus*: *E. crenatus*, from the Burdiehouse limestone (described and figured by Hibbert, 1836), and *E. fimbriatus* from Wardie harbour, north of Edinburgh, both of which are Viséan (the former from Asbian Strathclyde Group deposits, the latter from the earlier Holkerian Strathclyde Group, Smithson 1985), and *E. tenuiceps* from Triassic sediments of Sunderland, Massachusetts, although Redfield had already rediagnosed this as a species of *Ischypterus*. Traquair recommended that the taxonomy of the remaining two species (*E. crenatus* and *E. fimbriatus*) should be reviewed and suggested that *Platysomus*? *insignis* De Koninck 1878, from the Calcliferous limestone of Viesville, Belgium (Lower Carboniferous), might also be a species of *Eurynotus*. Agassiz (1833, pp. 153–60) distinguished *E. fimbriatus* from *E. crenatus* only by the possession of slightly smaller scales, and Traquair's 1867 discussion of eurynotid relationships provides no diagnostic features at the specific level. However, the fine lithographic plates in De Koninck's 1878 paper support Traquair's suggestion that *Platysomus*? *insignis* is a species of *Eurynotus*. In 1903 Traquair described *Eurynotus crenatus* and *E. fimbriatus* as synonymous, but recorded a further species, *E. microlepidotus* from the Boroughlee (Burghlee, Andrews and Carroll 1991) Ironstone of the basal Namurian (Smithson 1985). Watson (1928) supplied the most recent and detailed description of eurynotid material, concerning the structure of the palate and toothplates of a Wardie specimen (identified as *E. crenatus*). Figure 8 shows a close correspondence between the restored body-profile of the East Kirkton species, and an outline of the illustration of the Belgian taxon, although the strongly ridged scales of the latter deny conspecificity.

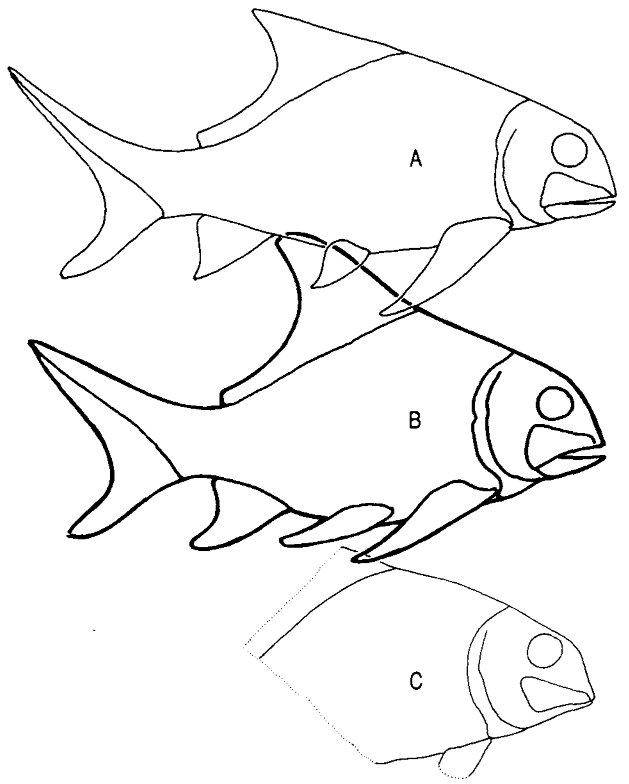
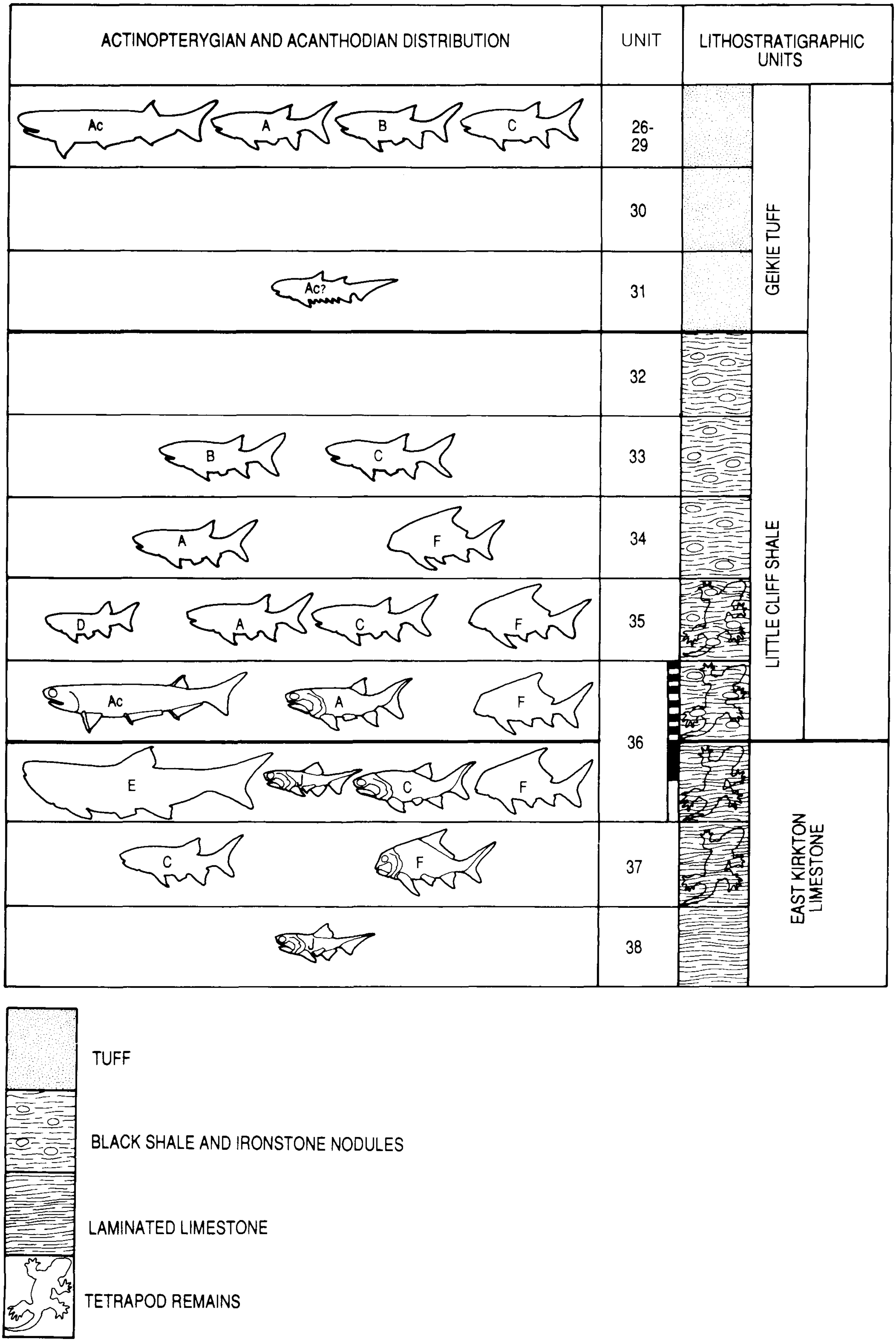


Figure 8 Body-profiles of eurynotids; (A) *Eurynotus crenatus* after Traquair 1879, (B) East Kirkton eurynotid and (C) *Platysomus insignis* after De Koninck 1878.

Traquair's recommended taxonomic review is beyond the scope of this paper. However, the discovery of the East Kirkton eurynotid provides fresh impetus to re-examine a genus which he described (1879, p. 349–50) as 'especially abundant in Edinburghshire and Fifeshire; indeed, in the Calciferous Sandstone series of the latter county it seems to form the great majority of all the smaller fishes which the collector meets with'. In fact, *Eurynotus* is found within all of the known Strathclyde Group (formerly Oil-Shale Group) fish faunas of Scotland (see Discussion). The Belgian species requires redescription, if it can be located (De Koninck published no catalogue numbers); the material remains, presumably, in the Musée Royal d'histoire Naturelle de Belgique, Brussells. Traquair notes a further eurynotid locality in the Possil ironstones of the west of Scotland. The spatial and temporal distribution of *Eurynotus* may be confused by the misspelling of this genus as *Eurynothus* in Romer (1966), Lehman (1966) and Carroll (1988). Romer's entry for *Eurynothus* (*sic*) (repeated in Carroll 1988) notes the distribution as extending from the Mississippian and Pennsylvanian of Europe and North America, and the Pennsylvanian of Northern Asia, to (surprisingly) the Middle Triassic of South America. Lehman includes the Lower Carboniferous of Scotland, the Carboniferous of Ireland, Belgium and Siberia. The origins of these additional records of *Eurynotus* are, at present, unknown to the author.

2. Discussion

The actinopterygian and acanthodian fishes of the limestones, shales, and tuffs above the tetrapod strata of East Kirkton are more diverse and occasionally more complete than their original description in Rolfe *et al.* (1990) suggests. However, most of the specimens, particularly those of the Geikie Tuff, consist of scattered, isolated bones and scales. This may indicate that the uppermost Units of


ACTINOPTERYGIAN AND ACANTHODIAN DISTRIBUTION
UNIT
LITHOSTRATIGRAPHIC UNITS
Ac
A
B
C
26-29
30
Ac?
31
32
33
34
D
F
35
E
J
36
37
38
GEIKIE TUFF
LITTLE CLIFF SHALE
EAST KIRKTON LIMESTONE
TUFF
BLACK SHALE AND IRONSTONE NODULES
LAMINATED LIMESTONE
TETRAPOD REMAINS

the East Kirkton sequence contain nothing more than a sample of accumulated organic detritus derived from a variety of distant habitats. Only the articulated specimens may represent an aquatic fauna in the general proximity of the eventual site of fossilisation. If these finds are plotted on a column of the East Kirkton Units, a distinct distributional pattern becomes apparent (Fig. 9). The greatest taxonomic diversity and the highest concentration of articulated specimens occurs in Units 35 and 36 at the base of the Little Cliff Shale and the top of the East Kirkton Limestone. These beds contain the articulated fusiform actinopterygians (species A, cf. *Rhadinichthys carinatus*, and C, cf. *Elonichthys robisoni*), an articulated juvenile actinopterygian and the 'tiny acanthodian'. NMS G 1993.6.21, identified tentatively as gut-residue, also originates from this basal fish assemblage. The gut residue was examined carefully for fragments of tetrapod bone and several slender spindle-shaped structures were found which resemble gastralia. However, these are more probably the narrow scales from the caudal lobe of an actinopterygian. No invertebrate material was found.

The East Kirkton actinopterygian and acanthodian assemblage resembles the fresh water/brackish Oil-Shale fish faunas of the Scottish Midland Valley. Traquair (1903) reviewed the fishes from most of these, including Wardie, Straiton and Pentland (Dunnet Shale), Burdiehouse, Broxburn (Pumpherston Oil Shale), Gilmerton, Niddrie, Loanhead and Boroughlee/Burghlee. In 1907 Traquair supplemented this list with a description of the Gullane (Cheese Bay) fish fauna, and most recently Briggs and Clarkson (1983) reported the presence of two actinopterygians from the contemporaneous Granton shrimp bed. Wood (1975) reworked the Wardie Shales (containing perhaps the best known of the Oil-Shale faunas) and confirmed the presence of some of the rarest actinopterygian members. Smithson's (1985) and Andrews and Carroll's (1991) reviews of Scottish Carboniferous tetrapod localities include most of the Oil-Shale faunas, with revised stratigraphical information and the location of many of these sites mapped relative to the mid-Carboniferous Lake Cadell. Details of the lacustrine depositional environment were discussed by Briggs and Clarkson (1985) with particular reference to the palaeoenvironment of Gullane.

The actinopterygians and acanthodians of East Kirkton resemble closely (if not exactly) the most widely distributed and characteristic members of the Oil-Shale fish faunas: *Eurynotus crenatus*, *Elonichthys robisoni*, *Cosmoptychius striatus* and *Rhadinichthys* sp., missing only *Nematoptychius greenocki*. Acanthodians are usually represented by the spines of *Acanthodes* sp. and gyracanthids, although the latter are conspicuously absent from East Kirkton. The Pumpherston Oil-Shale fauna (Viséan, Asbian) is the most similar to the East Kirton assemblage, including *Eurynotus crenatus*, *Elonichthys robisoni*, *Rhadinichthys carinatus*, *Mesopoma macrocephalum*, and *Acanthodes* sp., and mising *Nematoptychius* and gyracanthid material. The possible presence of *Cosmoptychius* (species E) distinguishes East Kirkton from the Pumpherston fauna, as does the presence of *Elonichthys*- (species B and C) and *Rhadinichthys*-like (species A), rather than conspectific taxa. If the isolated maxilla (species D, Unit 35) is interpreted correctly as belonging to a species of *Mesopoma*, then the presence of this genus is unique to East Kirkton and Pumpherston (Broxburn) among the Oil-Shale faunas. Why the East Kirkton fauna resembles one recorded from the Asbian, rather than Brigantian (e.g. Gilmerton), may result from its palaeogeographical location. Broxburn is the closest geographically of the Oil-Shale faunas and both are situated near the western edge of Lake Cadell. Gilmerton is relatively remote from these sites, and may contain a record of a different habitat and community within the inferred borders of the Oil-Shale lake.

The East Kirkton actinopterygians are not distributed widely within brackish or marine fish faunas such as Foulden (Clarkson 1985), Glencartholm (Schram 1983), or Bearsden (Wood 1982). Only *Mesopoma* is known principally from brackish waters (Glencartholm and Bearsden). *Eurynotus* and *Cosmoptychius* are known only from fresh/brackish conditions, and do not appear to have extended their range into the marine environment. The remaining pair of genera, *Rhadinichthys* and *Elonichthys*, are probably taxonomically polyphyletic, and, therefore, above the specific level are uninformative with respect to determining palaeoecological environments. *Acanthodes* is distributed widely, with attributed fragments occurring in most Carboniferous fish faunas.

The relative sizes and shapes of the actinopterygian and acanthodian genera are illustrated in Fig. 10. From these it is clear that they represent a number of differently specialised swimmers and feeders (Keast and Webb 1966). The deep-bodied taxa are suited for low energy environments and negotiating confined spaces. The dentitions of these fishes are often specialised, and in *Eurynotus* consist of durophagous toothplates (*contra* Lehman 1966). Such quiet conditions may also be suited for juveniles, as represented by the actinopterygian and acanthodian specimens. In contrast, fusiform taxa such as species C and E may also be found in open waters subjected to stronger currents. These fish are generalised predators, having long gapes and snapping jaws armed with short conical teeth. This interpretation of the aquatic environment is corroborated by the condition of the articulated fish carcasses. Huber's (1992) comments on the taphonomy of the fishes of the Upper Carboniferous Kinney Brick Quarry fauna (New Mexico) seem to be fairly applicable to the conditions of the black shale/ironstone. Huber refers to Elder and Smith's (1988) study of fish taphonomy, in which this preservational pattern is attributed to specimens lodging in the substrate, and bacterial invasion via the gill and cranial openings resulting in decomposition of the skull and anterior-trunk region before the remainder of the carcass. Scales scattered around the original body outline, rather than unidirectional dissociation of the carcass caused by current action, indicate the work of scavengers (Figs 1, 3A, 4C, 5). This suggests that the fish may have remained exposed on fine, silty substrate for several days and perhaps weeks. The presence of intact lepidotrichia does not necessarily indicate rapid burial; these remain coherent structures for rather longer

Figure 9 Stratigraphic diagram of East Kirkton actinopterygian and acanthodian distribution, preservation and diversity. Capital letters refer to species designations as given in text except for the following: Ac—acanthodian material; Ac?—possible climatiid tessera; F—eurynotid material; J—juvenile specimens. Empty profiles indicate disarticulated or isolated scales or bones; detailed profiles indicate articulated specimens. Black and white bars in Unit 36 box represent Sub-units 1–14: junction between Little Cliff Shale and East Kirkton Limestone is between sub-units 12 and 13. Distribution of isolated tetrapod remains included to emphasize known vertebrate faunal diversity from the upper part of the East Kirkton sequence.

than the remainder of the body. In contrast to this form of preservation, the more commonly found isolated bones and scales are the product of flotation and decomposition in the water column prior to deposition. This process results in a shower of dissociated bones and scales settling across a wide area of the benthic substrate.

The East Kirkton fishes, therefore, could be envisaged as the inhabitants of a meandering near-shore environment, with little current action, and slightly anoxic conditions near the silty lake bed limiting the action of scavengers. When compared to the actinopterygian and acanthodian complement of other Oil-Shale faunas, the mix of taxa and body-forms is remarkably consistent. Deep-bodied and fusiform fishes are present in all except for Granton. Each fauna except for Granton is known also to include the remains of tetrapods. Because *Eurynotus* occurs in at least eight out the ten remaining faunal assemblages, this suggests that material associated with the Belgian species (*Platysomus*? *insignis*) should be reinvestigated for evidence of further tetrapod remains.

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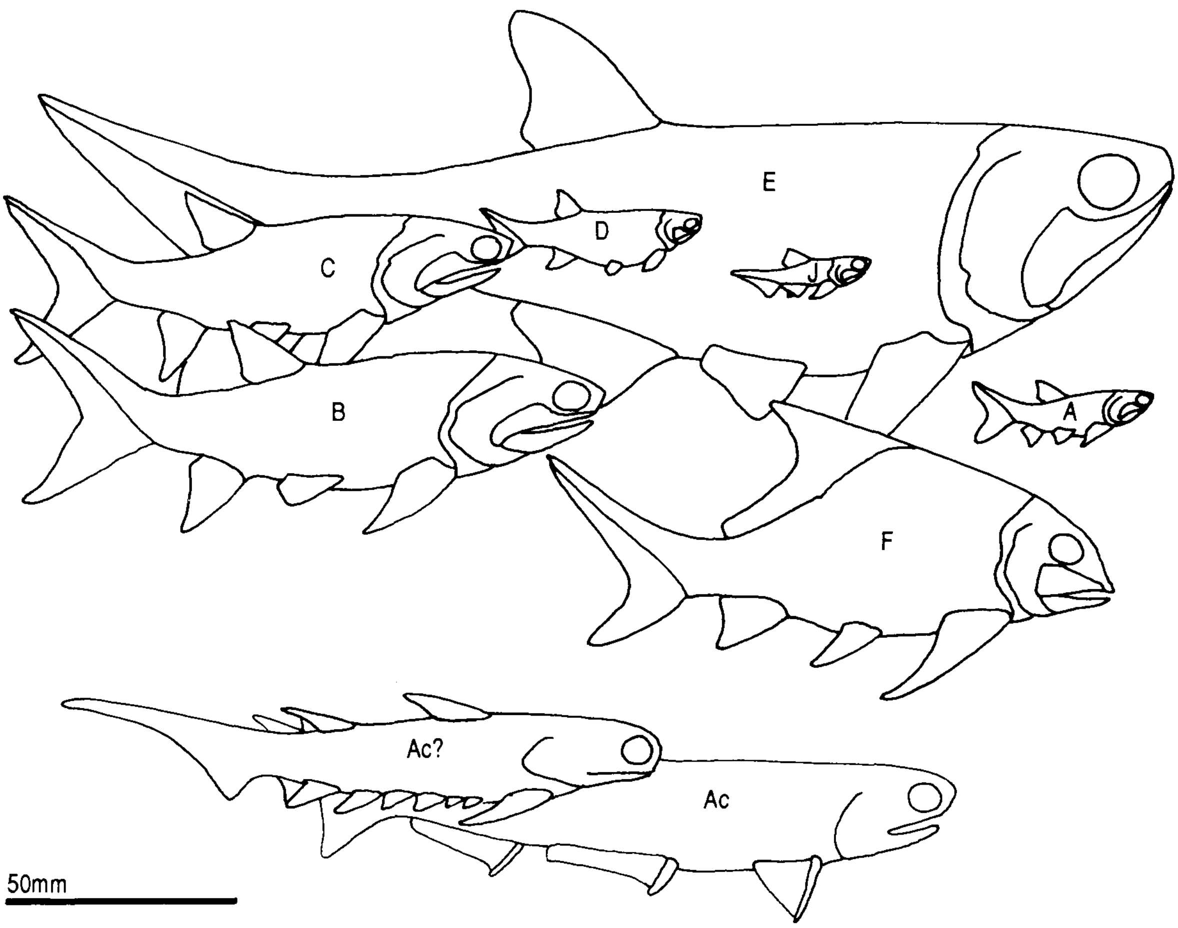

Figure 10 Diagrammatic representation of total East Kirkton actinopterygian and acanthodian fauna drawn to (estimated) proportional sizes. Key to lettering given in caption of Fig. 9.

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