
Foulden

[NS 921 552]

Highlights

Foulden in Borders is one of the few sites in the Dinantian of Scotland to yield a significant fish fauna of 12 or more species, six of them being actinopterygians. The fish bed represents a semi-permanent lake within an alluvial coastal plain.

Introduction

The fossil fishes from Foulden have been recognized as internationally important since their discovery in 1910–1912 by T.M. Ovens, who died in 1912 at the age of only 19. His collection of fishes was described by White (1927), who named five new species. Excavations in 1980 and 1981, funded jointly by S.P. Wood, the Nature Conservancy Council, the Hunterian Museum and the Royal Scottish Museum, yielded many new specimens, as well as contextual information determined from careful bed-by-bed collecting. The fishes from Foulden, their taphonomy and palaeoecology were described in a thematic series of papers published in 1985 in the *Transactions of the Royal Society of Edinburgh: Earth Sciences* (Anderton, 1985; S.M. Andrews, 1985; Clarkson, 1985; Forey and Young, 1985; Gardiner, 1985; Wood and Rolfe, 1985).

Description

The Fish Bed at Foulden consists of 3.9 m in the base of Bed 16 (Wood and Rolfe, 1985), which is set in a unit of 1.1 m of finely laminated siltstone, becoming more shaly upwards (Figure 9.9). The Fish Bed is further divided into an upper 3.1 m portion, separated from a basal bio-turbated part where fossil fishes are less well preserved. It lies within the lower part of the Lower Carboniferous Cementstone Group of Berwickshire and is probably of Tournaisian (Courseyan) age. The fish bed is c. 100 m above the base of the Cementstones, which are sparsely fossiliferous, with the exception of Foulden, and its fauna is mainly of ostracods, bivalves and fish fragments, plus some plant material.

The field and laboratory methodology used at Foulden was based on that used in Illinois by Zangerl and Richardson (1963). A large slab was lifted and removed to the laboratory, having been marked up with a grid and north arrows. The Fish Bed is rubbly, which made reassembly difficult. A polished vertical section was cut as a basis for the detailed log, and the beds were stripped off, one by one, their contents being plotted with reference to two marker horizons. The fossils could then be coded for three-dimensional burial position and orientation.

The careful plotting of the fossil content lamina by lamina showed that actinopterygian fishes and malacostracan crustaceans always occur at separate horizons. One level was crowded with small acanthodian fishes, showing a preferred orientation, and plant fragments. Other remarkable horizons were a rhipidistian-rich layer, a coprolite horizon and a bivalve–malacostracan horizon (Figure 9.9).

Fauna

Acanthodii: Acanthodiformes: Acanthodidae

Acanthodes ovensi White, 1927

Type and only locality

Gyracanthus sp.

Osteichthyes: Sarcopterygii: (Actinistia)

Coelacanthiformes cf. *Rhabdoderma* sp.

Osteichthyes: Sarcopterygii: Osteolepiformes: Rhizodonta

?*Strepsodus aulacnamensis* Andrews, 1985

Type and only locality

?*Strepsodus* n. sp.

Osteichthyes: Sarcopterygii: Dipnoi

?lungfish scale

Osteichthyes: Actinopterygii: Carbovelidae

Phanerosteon ovensi (White, 1927)

Type and only locality

Osteichthyes: Actinopterygii: Styracopteridae

Styracopterus fulcratus (Traquair, 1881)

Osteichthyes: Actinopterygii: Strepheoschemidae

Strepheoschema fouldenensis White, 1927

Type locality

Aetheretmon valentiacum White, 1927

Type locality

Osteichthyes: Actinopterygii: Cosmoptychidae

Cosmoptychius striatus (Agassiz, 1835)

cf. *Rhadinichthys* sp.

Chondrichthyes: Elasmobranchi: Bradyodonta

cf. *Lopbodus* sp.

TETRAPODA:

?acanthrosaur *incertae sedis*

Foulden is the type locality for seven species of fishes, and unique locality for three of these (Figure 9.10). White (1927) noted that the fish assemblage consists of small forms of new actinopterygian (palaeoniscid) genera that are complete, plus larger forms of fishes which are represented by teeth, scales and other isolated fragments which belong to predatory fishes. These latter forms are well known in the Carboniferous, and widely distributed, whereas the small complete forms are rarer, or restricted to Foulden.

All the acanthodians are imperfectly preserved. The swarm of small acanthodians on Bed A had poorly ossified cranial structures, and they were compressed, so that accurate measurements could not be made. The specimens collected by earlier workers, mainly Ovens, are larger, but are also poorly preserved (Forey and Young, 1985). The larger individuals which occur outside this layer are more ossified anteriorly (Wood and Rolfe, 1985). Also, the small specimens only had scale cover on the posterior half of the body. *Gyracanthus* sp. is based on poorly preserved fragments of spines which were found at several horizons in Bed 16, and from Beds 13 and 14 (Forey and Young, 1985).

The coelacanth cf. *Rhabdoderma* sp. has been described by Forey and Young (1985) from an almost complete fish discovered in Bed 16 (no accurate horizon given), but preservation is poor.

Rhizodonts were large, and they are normally preserved only as scattered remains. The head of the complete (holotype) specimen of ?*Strepsodus aulacnamensis* in the Foulden assemblage has been crushed dorsoventrally and does not allow a detailed study.

Acanthodes ovensi White, 1927 is one of the earliest acanthodid acanthodians. White (1927) described it from seven specimens, of which only the holotype was a full-grown individual, 90–100 mm long. The other specimens were very small, being c. 30–50 mm long. Acanthodian material collected from the 1980–1981 dig consists mainly of a crowd of 173 specimens in Bed A. Forey and Young (1985) re-evaluated the species from the type specimens and the new material. *Acanthodes ovensi* is distinguished from Upper Carboniferous and Permian *Acanthodes* by the shape of the tail, the shorter gill chamber, the continuation of the scale cover over the head, and the posterior position of the pelvic fin spine (Figure 9.10).

Gyracanthus sp. is based on fragments of spines found at several horizons in Bed 16 and from Beds 13 and 14 (Forey and Young, 1985). White (1927) also reported *Gyracanthus* sp. indet. from two fragments collected by Ovens.

The coelacanth fishes are a small element in the Foulden fauna. The ornament of the Foulden coelacanth, cf. *Rhabdoderma*, is distinctive (Figure 9.11)C. *Rhabdoderma* sp. has been described by Forey and Young from an almost complete fish found in Bed 16, but the preservation is poor. Head bones are ornamented with long ridges parallel to the long axes of the bones or with slightly elongate tubercles, which radiate out from the centre of ossification, or with small rounded tubercles. Forey and Young (1985) described this as an intermediate pattern compared with other Carboniferous and Devonian coelacanths. The Foulden coelacanth is similar to *R. ardrrossense* (see below) in the ornament of the skull roof, but is unique in the fine tubercular ornament on the angular and gular.

Archibald Geikie (1864) reported rhizodont scales from Foulden, and White (1927) described the material collected by Ovens as scales of *Rhizodus hibberti* and *Strepsodus* sp., plus teeth of *S. sulcidens* and *S. striatulus*. These are form species for different shapes of scale and tooth. The first complete rhizodont discovered at Foulden during the 1980 excavations offered the opportunity to understand rhizodonts as a whole; elements that had previously only been found in isolation could now be linked to their associated parts (S.M. Andrews, 1985).

The rhizodont material from Foulden falls into two size ranges with no intermediates. The small specimens include the first complete rhizodont, and they are by far the smallest rhizodonts so far known (S.M. Andrews, 1985), being from 0.13 to 0.5 m long. The large ones are 1.3–3.5 m in total length.

S.M. Andrews (1985) gave the name ?*Strepsodus aulacnamensis* to the small fossils and this species is known only from Foulden (Figure 9.11)A,B. The larger specimens may belong to the same species, which would imply that the small fishes are juveniles. This idea is supported by the small number of growth lines on the scales of the small specimens, and the large size of the orbit. There are four associated individuals, and several isolated elements of the small specimens, including the complete specimen, which is 345 mm long. A striking feature is a large sclerotic ring formed of numerous plates around the large orbit. The teeth are slender; sigmoidal and conical types occur. The mandibular ramus bears a large symphyseal sigmoid tusk, followed by a row of smaller recurved conical marginal teeth (Figure 9.11)B. The maxilla has marginal teeth like those of the mandibular. The dermal bones are smooth and ornamented by pits which may be rounded, irregular, or elongated into wavy ridges.

There are ossified fin spines present in the tail, and median fin supports also are present. The notochord is unrestricted by ossified centra. The fins differ from other sarcopterygians in that the scale-covered lobe makes up the bulk of the fin, with the fin-webs merely narrow marginal fringes. The pectoral fins are enlarged into stiff paddles, and the other fins are very small. The pelvic girdle and fin supports are not ossified, which may well be a juvenile feature. The bones of the shoulder girdle, in as far as can be seen, extend ventrally to form a broad and long shield of thick bone (Andrews and Westoll, 1970b).

The scales are cycloid and thin and apparently lack cosmine. They are ornamented by fairly straight fine sub-parallel ridges. Up to two growth lines are seen, but on the internal surface of the scale there is another series of up to ten lines. The internal side of the scale is also ornamented, unlike any other rhizodont, including the scales of the large specimen from Foulden. The overlapping area of the scale is covered by granular denticles arranged in concentric and radiating lines. The main lateral line canal shows as a well-marked groove or fold in the scales. There are at least six subsidiary canals along the flanks.

?*Strepsodus* sp. is the large form from Foulden, based on two associated specimens and numerous isolated bones and teeth. It is probably the same species as the small form, ?*S. ancylonamensis* Andrews, 1985, but has some significant differences (S.M. Andrews, 1985). The teeth of the large form are all proportionally stouter than those of the small form.

Actinopterygian fishes are the commonest vertebrate fossils at Foulden and include four rare palaeoniscid species. Foulden is the type and only locality for *Phanerosteon ovensi*. White's original material consisted of eight specimens, and ten new specimens were collected in 1980–1981. White (1927) claimed that the only differences between *P. mirabile* (from Glencartholm, q.v.) and *Carboveles ovensi* were the degree of squamation and the shape of the tail. Gardiner (1985) showed that the tail was the same in the two species, and also that White (1927) had been in error to describe the trunk of *C. ovensi* as being covered by small round scales; in fact the scales only occurred ventrally behind the pectoral girdle. *Phanerosteon ovensi* is also distinguished from *P. mirabile* (Figure 9.12) by the ornamentation on the skull roof and by the extent of scaling on the tail.

The type locality for *Styracopterus fulcratus* is Tarras Waterfoot. Gardiner (1985) included the species *Fouldenia ottadinica* as a synonym of this species. *Fouldenia ottadinica* was originally described by White (1927) from nine specimens from Foulden collected by Ovens. A further 15 specimens were discovered during the 1980–1981 excavations. *Fouldenia ottadinica* had been said (Moy-Thomas, 1937b) to differ from *S. fulcratus* by different-sized opercular and scales with bilobed posterior margins, but Gardiner (1985) showed that bilobed scales only occur on restricted areas of *F. ottadinica*.

Strepheoschema fouldenensis is a deep-bodied fish described originally from six specimens (White, 1927) and emended by Gardiner (1985) after the collection of a further 23 specimens from the 1980–1981 excavations. The line of the body (Figure 9.12) is marked by enlarged paired median ridge scales, which is a feature unique to *Strepheoschema* and *Aetheretmon*. Gardiner (1985) designated a new family, the Strepheoschemidae, to include this genus and *Aetheretmon*, which had originally been included in the Rhadinichthidae (Gardiner, 1967a).

Aetheretmon valentiacum is the most common early actinopterygian at Foulden, represented by many juveniles ((Figure 9.12)A). White (1927) described it from six specimens. Gardiner (1985), using the type material, plus 44 new specimens and material from Crooked Burn, showed that there was a continuous series of skull and scale ornamentation types, and concluded that only one species was represented by the two species originally described from Foulden, plus two from Coomsden Burn (White, 1927; Moy-Thomas, 1938a). *Aetheretmon valentiacum* was a fusiform fish which had unarticulated pectoral fin rays, a feature of many stem-group neopterygians (Gardiner, 1985). The fulcra (ridge scales above the tail) are long and pointed, and there is a pair of large ventral ridge scales in front of the anal fin (presumably around the vent), similar to those of *Strepheoschema*.

Three fragments of *Cosmoptychius striatus* were recognized by Gardiner (1985) from the distinctive size, shape and ornamentation of a maxilla. This species is characteristic of the Lower Oil Shale Group of the Forth region and 'its occurrence at Foulden is unexpected' (Gardiner, 1985, p. 65). The remainder of the material consists of palaeoniscid scales, cf. *Rhadinichthys*.

Wood and Rolfe (1985, p. 6) reported a single ?tetrapod scute, possibly an acanthracosaur from Bed 16.

Interpretation

The setting is interpreted as fresh- to brackish-water, with a hint of marine influence. The Cementstones environment was an 'extensive, low relief monotonous, silty to muddy floodplain crossed by occasional small sluggish meandering rivers. The floodplain passed imperceptibly seawards into coastal mudflats. The rivers frequently flooded onto the floodplain depositing silt and mud' (Anderton, 1985, p. 9). The floodplain was the scene of numerous crevasse splays from breached channel banks, and was subject to occasional marine inundations. Shallow, ephemeral and probably brackish lakes could have supported restricted faunas, but they would have low preservation potential on a drying floodplain. The Foulden Fish Bed represents a semi-permanent, relatively deep and relatively freshwater lake (Anderton, 1985). The lake was established where sedimentation did not keep pace with tectonic subsidence, and the area became increasingly submerged, becoming first a swamp, then becoming totally submerged as a shallow lake, some 5 m deep, which gradually silted up. As suggested by S.M. Andrews (1985), if this was a shallow area which could seasonally flood, it would provide a safe environment for small fishes, into which large predators could gain access at times of higher levels of water, in order to breed, or possibly to seek prey.

In discussing the possible causes for the mass mortalities in the fish bed, Anderton (1985) compared the lacustrine environment with that of Achanarras (q.v.). Unlike that Middle Devonian lake, the shallow lake at Foulden shows no evidence of a permanently stratified and eutrophic environment: there is little evidence of varved sediments, and the lake was very shallow. However, temporary stratification could have occurred during hot calm weather and, when followed by storms and deposition of sediment, would have provided a mechanism for the preservation of the fauna (Anderton, 1985). It may be assumed that the many fossils represent a school of young individuals killed off by local environmental changes (Wood and Rolfe, 1985).

Otoliths, possibly of acanthodians, are known from Foulden.

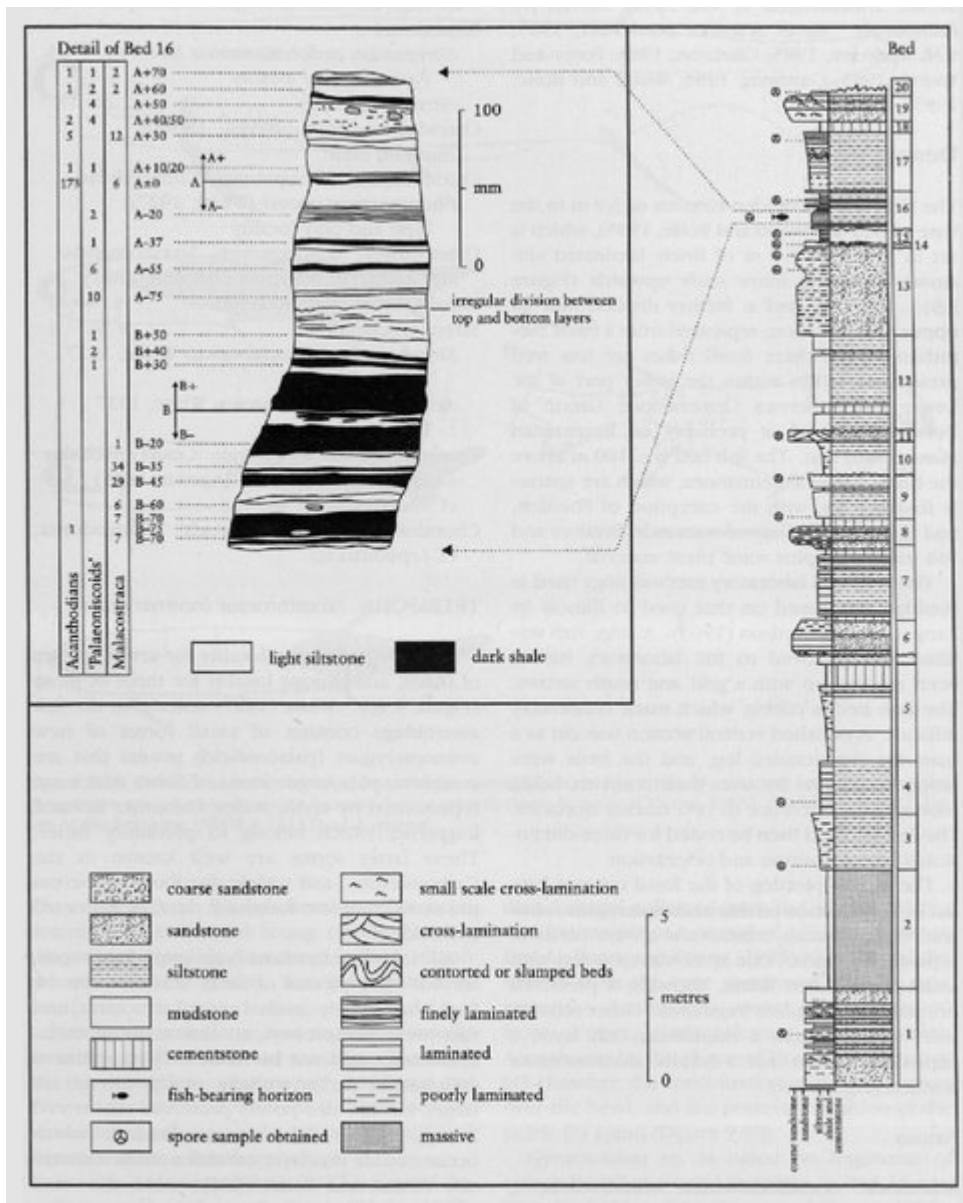
The complete specimens of rhizodonts from Foulden offer new opportunities for functional interpretation. S.M. Andrews (1985) compared the pectoral fin of rhizodonts with the paddles of plesiosaurs and ichthyosaurs. Rhizodont teeth are deeply rooted, superficially similar to crocodiles, to help retain struggling prey.

The ornamentation on the internal side of the scale of the rhizodont ?*Strepsodus aulaconamensis* may be a juvenile feature. The bosses at the centre of each scute were previously thought to be for attachment, or insertion of muscle. The articulating scales of the Foulden material led S.M. Andrews (1985) to suggest that the boss was merely to thicken up this area of body cover. The differences in stoutness of the teeth between the small and large forms of ?*Strepsodus* may be the result of growth (and possible associated change of diet) or may simply represent different regions of the mouth. The small and large forms were found at different horizons, and their distribution may represent a partial separation in the population, perhaps by depth or by seasonal floods. In the latter case, it could mean that the large fishes moved into previously inaccessible areas to breed, so that on return to normal conditions the young fishes could live in safer shallow waters.

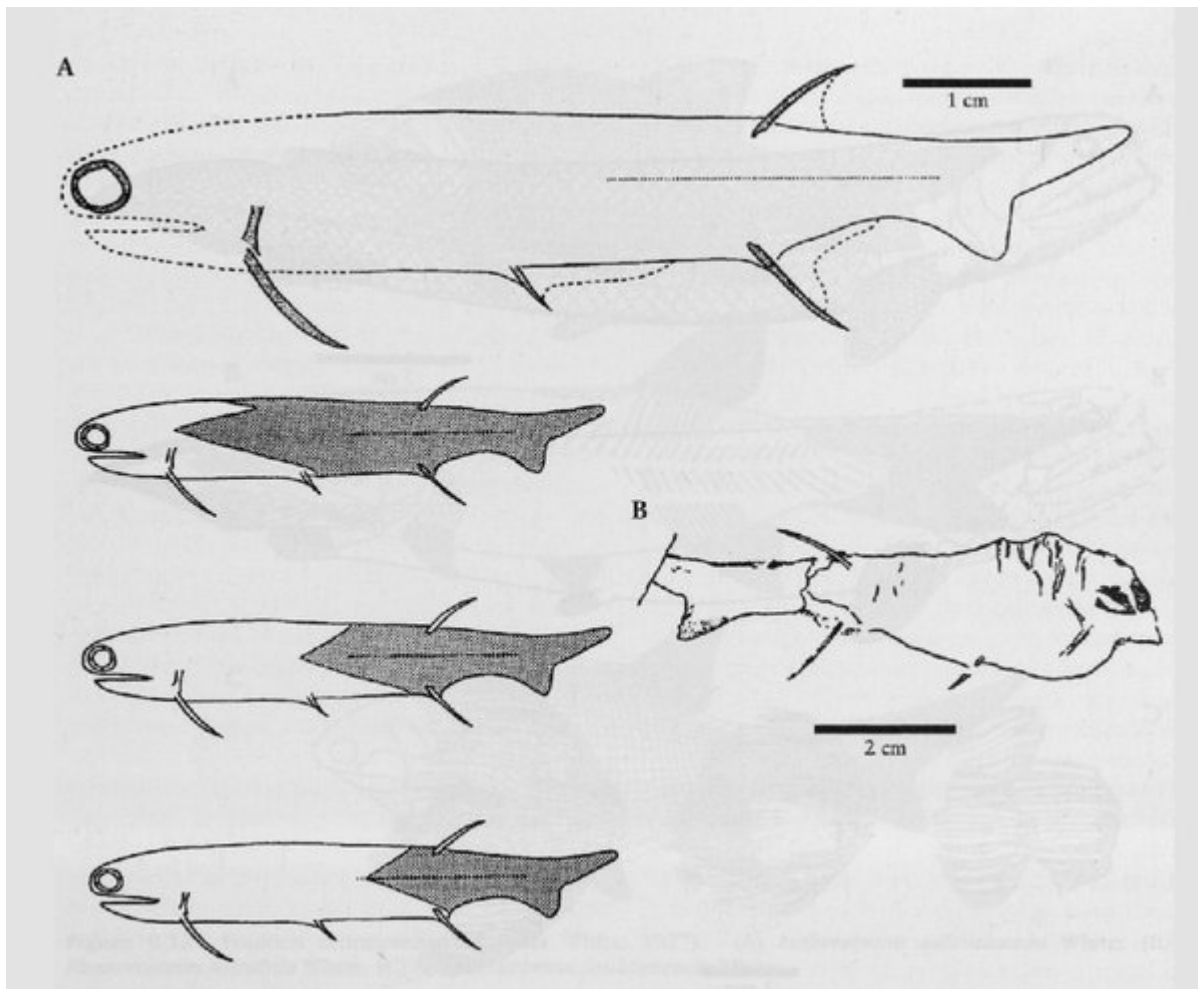
Conclusion

Although the fish assemblage (12 spp. or more) from Foulden is relatively small, the fact that several species appear to be unique to the site suggests a somewhat special, perhaps confined lake and gives the site its conservation value. Small complete individuals and small juveniles dominate the assemblage, but sometimes much larger fishes had access to the area. ?*Strepsodus aulaconamensis* and *Acanthodes ovensi* are represented by juveniles, and there is evidence of larger members of what are, or are most probably that same species. Excavations in 1980–1981 proved the richness of the site, and its potential for the future.

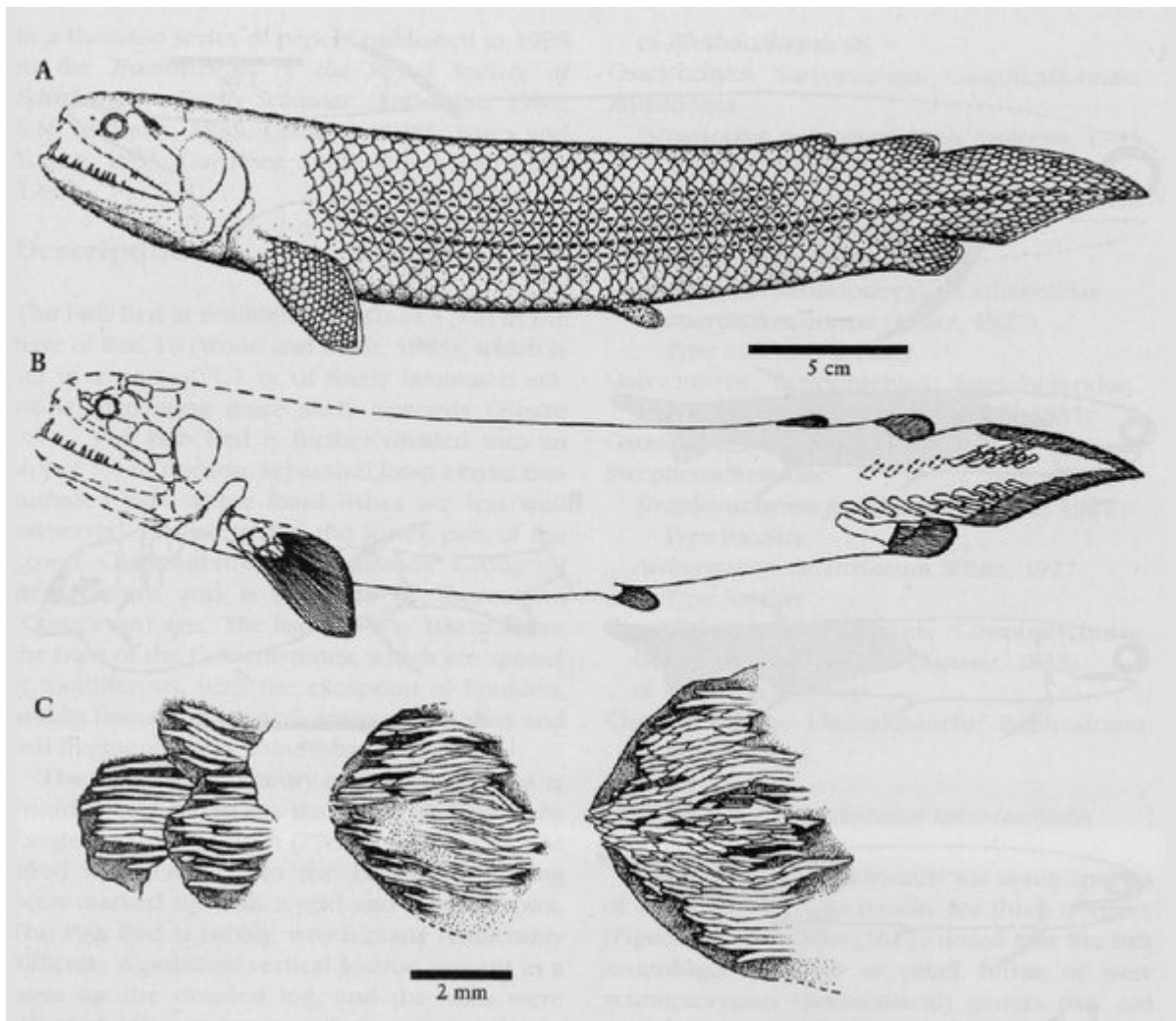
References



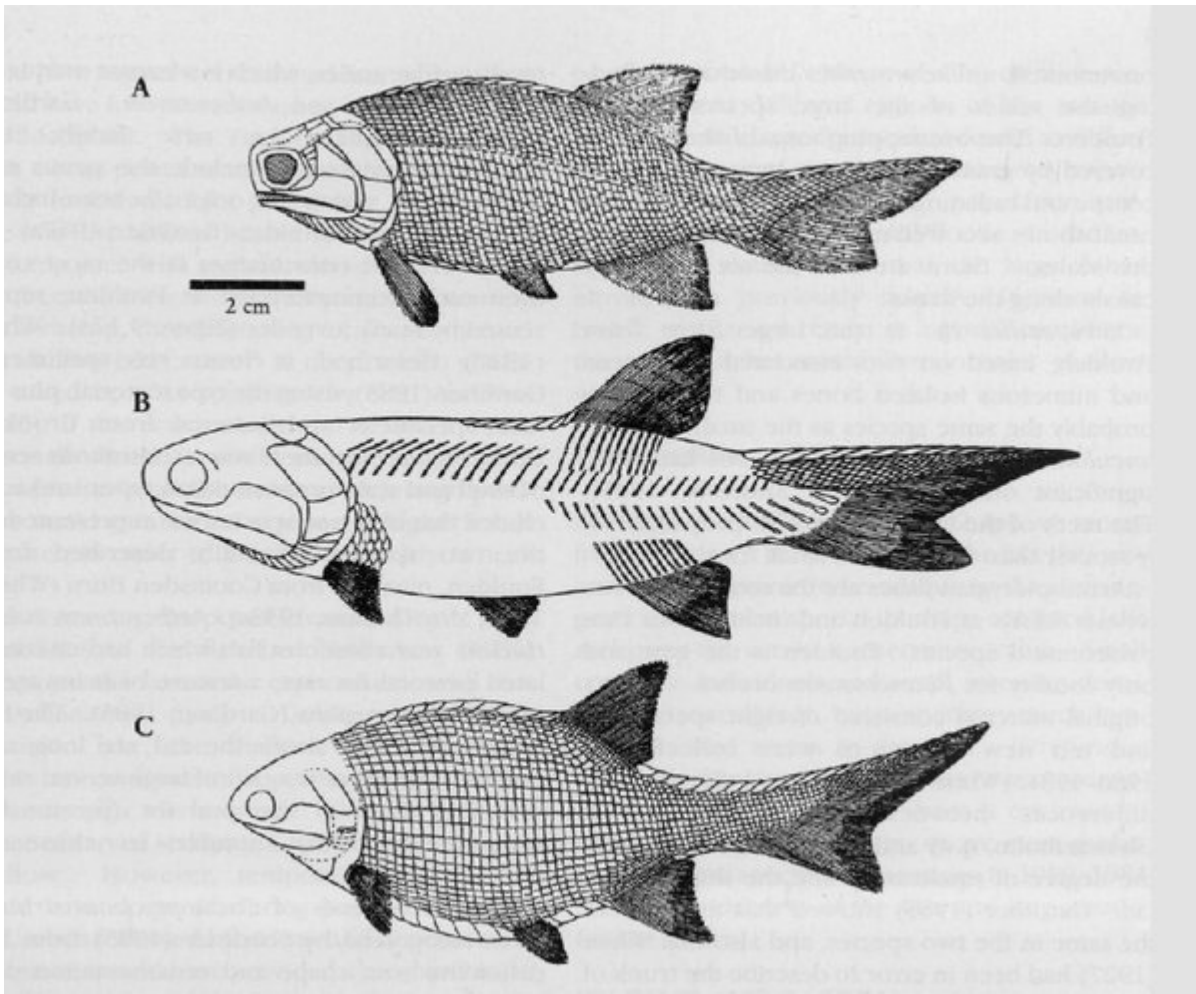
(Figure 9.9) Stratigraphical section at the Foulden site with the fish bed detailed (after Wood and Rolfe, 1985).



(Figure 9.10) Foulden acanthodians: (A) *Acanthodes ovensi* White, with a series of immature forms showing the progressive spread of squamation forward during growth (from Forey and Young, 1985): (B) White's (1927) figure of the holotype (NHM P 13137) of *A. ovensi*.



(Figure 9.11) Foulden sarcopterygians: (A) preliminary reconstruction of *?Strepsodus aulaconamensis* sp. with scale cover; (B) *?Strepsodus aulaconamensis* Andrews, with scales omitted to show lepidotrichia and axial skeleton (after S.M. Andrews, 1985) Many of the head and axial skeleton bones are largely conjectural. (C) Coelacanth flank scales (from Forey and Young, 1985).



(Figure 9.12) Foulden actinopterygians (after White, 1927). (A) *Aetheretmon valenticum* White; (B) *Phanerosteon mirabile* White; (C) *Strepheoschema fouldenensis* White.