



CARBONIFEROUS (TOURNAISIAN) FISH ASSEMBLAGES FROM THE ISLE OF BUTE, SCOTLAND: SYSTEMATICS AND PALAEOECOLOGY

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Abstract: We describe fish assemblages from the Carboniferous (mid- to late Tournaisian) Ballagan Formation at two localities, Hawk's Nib and Mill Hole, on the Isle of Bute, Scotland. Fossil material occurs in thin, locally reworked dolomitic limestone beds, interpreted as the deposits of very shallow lakes or lagoons, developed on, or adjacent to, a seasonally dry coastal plain. The mostly disarticulated fossils comprise isolated teeth, mandibles, scales, tesseræ, dermal bones, lepidotrichia and vertebrae. The fauna includes rhizodonts (cf. *Archichthys portlocki*, cf. *Strepsodus sauroides*), lungfish (*Sagenodus* sp.), other sarcopterygians (*Megalichthys* sp.), one shark (*Ageleodus pectinatus*), climatiiform acanthodians and indeterminate actinopterygians. The Mill Hole

assemblage is especially noteworthy because it includes some putative juvenile forms (*Archichthys* and *Sagenodus*). A critical review of the habitat preferences of the documented taxa suggests that most were either euryhaline or, in the case of *Archichthys*, probably endemic to brackish or freshwater settings. The Bute fish beds fall within a crucial evolutionary period during which many fish and other animal groups were infiltrating nonmarine environments, either passively or actively. It may be that lakes and lagoons may have functioned as protected nurseries for juveniles during this wave of colonization.

Key words: Tournaisian, vertebrate, rhizodont, Britain, nonmarine, nursery.

THE radiation of animals into freshwater ecosystems (rivers and lakes) was a major event in the history of life (Gray 1988; Bennett *et al.* 2012). The first convincing evidence for freshwater communities comes from rocks of Silurian age (Boucot and Janis 1983), and by the early Devonian, freshwater ecosystems were becoming widespread (Halstead 1985; Buatois *et al.* 1998; Morrissey *et al.* 2004). This wave of colonization was likely triggered by the rise of vascular plants (Edwards and Wellman 2001), which provided a rich source of detrital organic matter in aquatic environments for the first time (Buatois *et al.* 1998), and it was further facilitated through the evolution of osmoregulatory systems (Miller and Labandeira 2002). The ongoing collision of Laurussia and Gondwana (Hercynian Orogeny) led to increased clastic input into the Rheic Ocean during the early Carboniferous, and existing carbonate-dominated facies were supplanted by extensive deltaic systems (Ford and Golonka 2003). By the end of the Carboniferous, freshwater

ecosystems were diverse, trophically complex and present in almost every conceivable aquatic setting (Park and Gierlowski-Kordesch 2007).

This invasion of freshwater is not understood as thoroughly as it could be because fossil assemblages have often been recorded without an adequate facies context. Traditionally, strata have merely been subdivided into marine facies (containing stenohaline taxa) and nonmarine facies (lacking stenohaline taxa), the latter representing a broad spectrum of environments ranging from freshwater to brackish to near-marine salinities (Calder 1998). Recognition of specifically freshwater settings is challenging (Gray 1988; Schultze 2009) because assessment is based, in large part, on negative evidence or on microfossils that may be hard to detect, identify correctly and interpret properly (e.g. ostracods, Bennett 2008; 'Spirorbis', Taylor and Vinn 2006).

Inferences concerning the palaeosalinity tolerances of many Carboniferous fishes are particularly poorly

constrained (Schultze 2009). Despite having been reported from hundreds of localities worldwide over more than 175 years (Agassiz 1843*a, b*; Calder 1998; Warren *et al.* 2000; Turner *et al.* 2005; Ginter *et al.* 2010), freshwater, marine and brackish communities have not yet been reliably circumscribed (Carpenter *et al.* 2011). This has led to much debate over the habitat preference of taxa that historically have been interpreted as freshwater organisms (see e.g. Masson and Rust 1984; Calder 1998; Dick 1998), based on their occurrence in nonmarine strata (Schultze 2009); in many cases, the facies context of such fossils has been subsequently re-evaluated as brackish or near-marine (Falcon-Lang *et al.* 2006; Grey *et al.* 2011).

In this paper, we describe two assemblages of Carboniferous (Mississippian; mid- to late Tournaisian) fishes in facies context from the Isle of Bute, Scotland. Our findings further highlight the difficulty of inferring palaeosalinity with precision because, although the facies context of our fossils would appear to be exclusively terrestrial or freshwater, the fossil assemblages themselves mostly comprise purported euryhaline or brackish-adapted taxa, including some putative juvenile forms. This apparent infiltration of euryhaline or brackish-adapted taxa into terrestrial and freshwater settings is of evolutionary significance, supporting the hypothesis that marine-based organisms were either actively or passively colonizing nonmarine settings during this time and that coastal and inland waterways may have served as protected nurseries for juveniles (Schultze *et al.* 1994; Williams *et al.* 2006; Bennett *et al.* 2012). It is also worth noting that these assemblages fall within 'Romer's Gap', the 15–20 million year period following the Devonian–Carboniferous boundary during which tetrapods are extremely scarce (Coates and Clack 1995).

GEOLOGICAL CONTEXT

Background

The fossil fish assemblages reported here come from two localities on the Isle of Bute, Scotland: Mill Hole near Ascog (55°49'57.48"N; 5°01'30.93"W) and Hawk's Nib near Kilchattan Bay (55°44'09.58"N; 5°00'2.69"W) (Fig. 1A). The earliest reference to fossil vertebrates on the Isle of Bute is Bryce (1872); included in a list of fossil fauna discovered in the island's 'fossiliferous clays', the entry in its entirety reads: 'Fishes: a few vertebrae'. Bryce did not specify where on the island these were discovered, merely listing several coastal locations where fossiliferous clays were common, including Rothesay Bay.

There the matter rested until numerous fossiliferous horizons were discovered at the Hawk's Nib locality by G. D. Matheson, while investigating the geology of the

southern end of the island as part of an undergraduate thesis project (Matheson 1962). While chiefly a geological study, his unpublished thesis included a brief description of some fragmentary fish remains, most notably including a left mandibular ramus (see below), accompanied by five hand-drawn illustrations. This thesis was the basis for a more comprehensive contribution (Matheson 1963) which included a description of additional material from a second site near Montford (Grid Ref. OS 362: 106640) discovered by local geologist E. McGuinness, as well as noting the existence of a third locality at Ascog containing a thin plant-bearing horizon associated with a coal seam. Nevertheless, Matheson (1963) reported only scattered actinopterygian 'ganoid' scales and fragments of dermal bones, which he attributed to the family Palaeoniscidae, and he did not undertake a detailed study of the sedimentary succession in which they occur. Although the fossils of Hawk's Nib were of slightly better quality (most notably a left mandibular ramus complete with two rows of teeth; Matheson 1963, fig. 1), these were also attributed to Palaeoniscidae.

Stratigraphical placement of fossil sites

The fossil sites occur in two small Mississippian basins developed during the extensional reactivation of Caledonian lineaments (Leeder 1987, 1988; Waters and Davies 2006) associated with the Highland Boundary Fault, which runs through the Isle of Bute (Tanner 2008; Fig. 1A). The Mississippian strata either conformably overlie, or occur in normal fault contact with, the Devonian Bute Conglomerate Formation (Upper Old Red Sandstone; Young and Caldwell 2011*a, b*). The most complete record of the Mississippian fill of these basins is seen in a British Geological Survey (BGS) borehole drilled at Ascog Hill (IGS Ascog Borehole NS 06/SE 8; Grid Reference NS 0986 6302), about 1 km south-west of the Mill Hole site (Armstrong 1978; Fig. 1B). This proves a 296-m-thick Mississippian succession comprising, from base to top, the Tournaisian to, possibly, earliest Viséan Kinnesswood, Ballagan, Clyde Sandstone and Birgidale formations (Paterson and Hall 1986; Browne *et al.* 1999; Read *et al.* 2002), capped by the mid-Viséan Clyde Plateau Volcanic Formation (Fig. 2), whose lower part has yielded radiometric ages of 334.7 ± 1.7 Ma and 335.2 ± 0.8 Ma in mainland outcrops (Monaghan and Pringle 2004; Monaghan and Parrish 2006; Young 2008, 2009).

The exact stratigraphical placement of the rocks at Mill Hole is uncertain, and unequivocal age interpretation is problematic because strata in the Ascog area are poorly exposed and highly faulted (Fig. 2). Based on the assumption that basaltic agglomerates and tuffs containing fossil

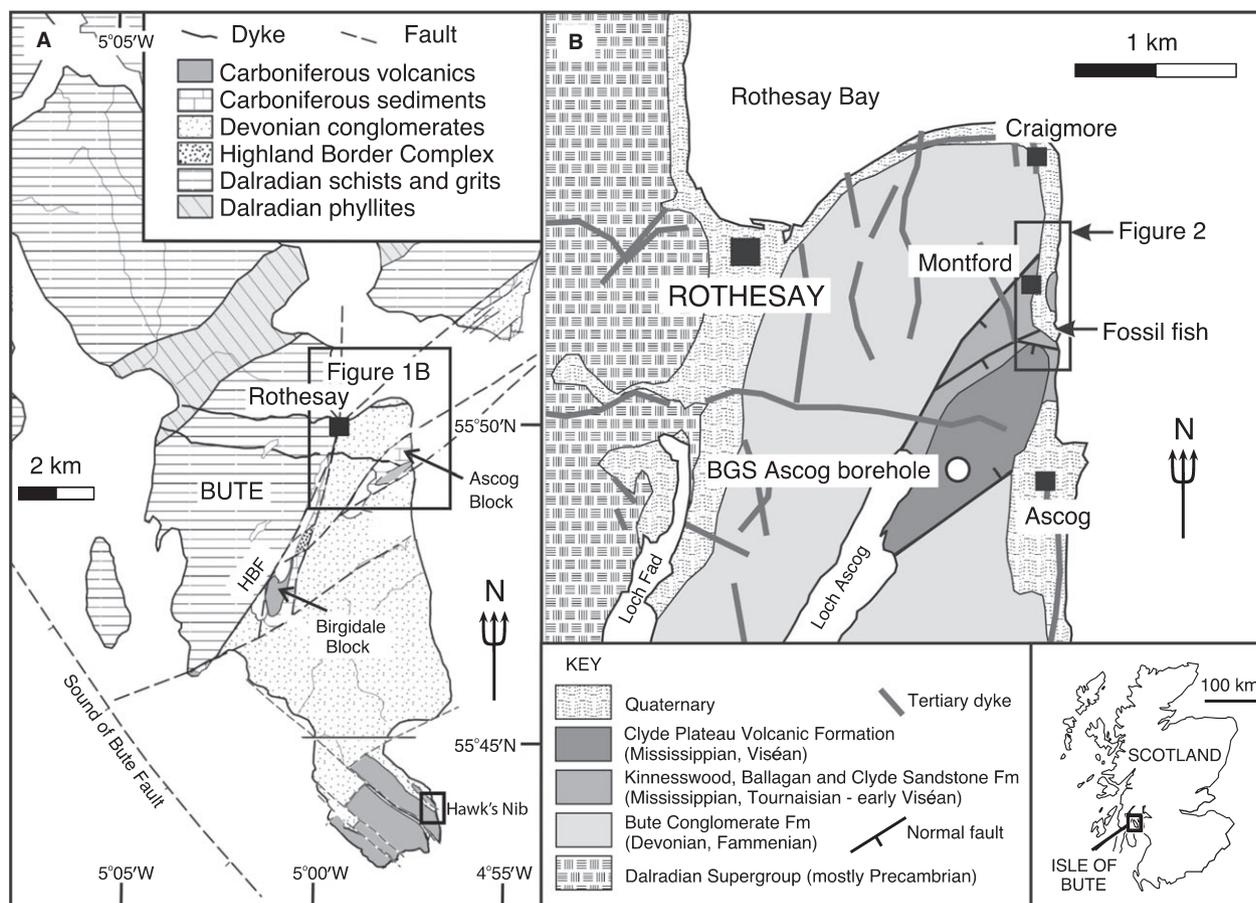


FIG. 1. Geological setting. A, summary geological map of the Isle of Bute (reproduced from Young and Caldwell 2011b) showing the general location of the fossil sites at Mill Hole and Hawk's Nib. B, general map of the Ascog Block (inset map location of the Isle of Bute in Scotland).

trees (*Pitus primaeva*, *P. antiqua*, *P. withamii*) within fluvial floodplain facies (Falcon-Lang *et al.* 2010; Henderson and Falcon-Lang 2011), located *c.* 200 m north of Mill Hole at Montford, are an eruptive precursor to the Clyde Plateau Volcanic Formation, BGS geologists mapped the entire Ascog section as belonging to the late Tournaisian Clyde Sandstone Formation and younger strata (BGS 1:50 000 map, Dunoon 029E). Young and Caldwell (2011a) described similar basaltic tuffs from the lowermost Clyde Sandstone Formation on adjacent Great Cumbrae, broadly supporting the BGS age determination for the Montford tuffs. In their detailed map of the Ascog section, Young and Caldwell (2011b, fig. 11) assigned the Montford strata to the Clyde Sandstone Formation, but placed the Mill Hole strata in the earliest Viséan Birgidale Formation, based on the similarity of brick-red mudstone facies with those of that formation seen in the Ascog borehole. However, a fault block of early Tournaisian Kinnesswood Formation separates the Montford and Mill Hole sites, and facies at the latter site more closely resemble those of the Ballagan Formation. Thus, following Hill

and Buist (1995), we assign the Mill Hole strata, with uncertainty, to the mid- to late Tournaisian Ballagan Formation.

The stratigraphical placement of the second site at Hawk's Nib is somewhat better constrained (Fig. 1A). Here, a much more substantial fault-bounded succession is present in which Devonian Bute Conglomerate Formation (Upper Old Red Sandstone) is conformably overlain by strata whose lithology is consistent with the Kinnesswood and Ballagan formations (Young and Caldwell 2011b, fig. 6). South of another fault, a thin succession of sandstone and red/purple mudstone beds is conformably overlain by the basal basaltic lavas of the Clyde Plateau Volcanic Formation, which are up to 340 m thick in this area (Young and Caldwell 2011c). Based on its position below the volcanics, this thin sedimentary deposit is interpreted as part of the Clyde Sandstone and Birgidale formations. The fish-bearing beds studied by Matheson (1963), and in this current paper, occur in the middle part of the Ballagan Formation (Young and Caldwell 2011b). We note that neither ostracods nor palynomorphs

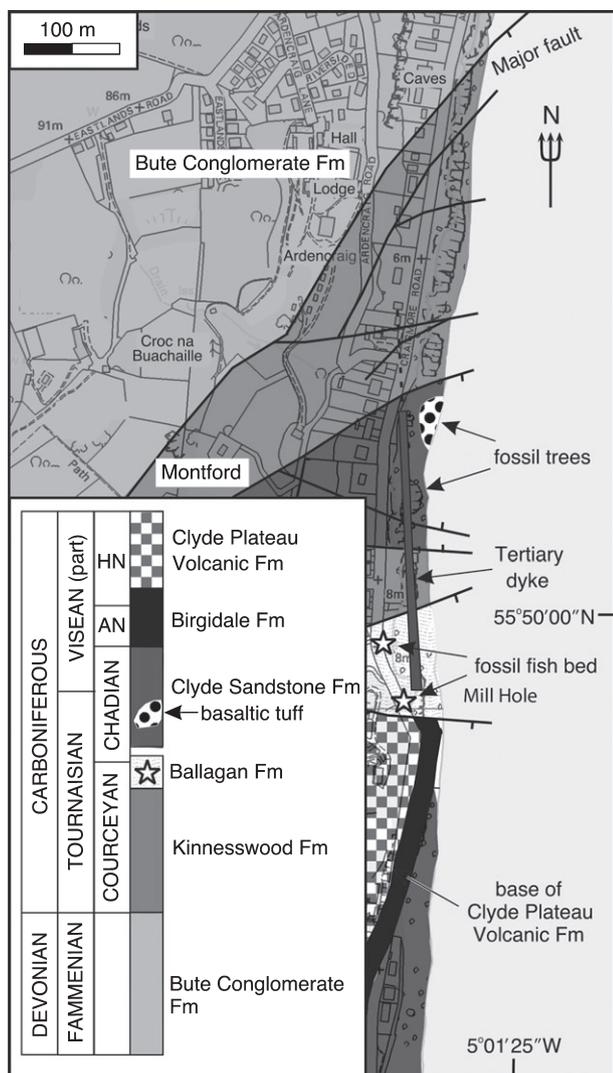


FIG. 2. Detailed geological map for Mill Hole fossil assemblage described herein (after British Geological Survey map, Young and Caldwell 2011b, and own mapping). See Figure 1 for overall context. *Abbreviations:* AN, Arundian; HN, Holkerian.

have yet been recovered from the fish beds, either at Mill Hole or at Hawk's Nib, and consequently, strata cannot be tied to regional biozonation (Stephenson *et al.* 2002, 2004), which would facilitate more precise correlation.

Mill Hole facies

The Mill Hole site comprises several small, scattered outcrops on the foreshore. The fish-bearing unit crops out at the base of a vegetated coastal bank, just above the high tide mark, on the south side of a small stream called the Millburn (Fig. 2). With difficulty, a vertical section, approximately 2 m × 2 m in area, was cleared of soil to investigate the sedimentary facies, and fish fossils were

collected. Another outcrop of these beds occurs on the north side of the burn, c. 20 m distant along strike, but is similarly poorly exposed. The original site investigated by Matheson (1963) is probably a further 25 m to the north, but is now covered by riprap (protective boulders) emplaced as a coastal sea defence; it is almost certain that he collected material from the same bed as currently crops out either side of the burn. A few other exposures occur on the beach below high water mark.

The total thickness of the Mill Hole composite succession is only about 6.5 m (Fig. 3). Near the base of the succession is 1-m-thick red/purple-mottled palaeosol, with abundant caliche nodules amalgamating to form a petrocalcic layer. This is overlain by several metres of red mudstone, thickly bedded and locally containing scattered caliche nodules. Above this is a sharp-based, orange-red dolomitic limestone, 0.12 m thick, somewhat nodular, containing fragmentary fish skeletal remains (mandibles, teeth, scales, tesseræ, bone, etc. locally articulated) and rare lepidodendroid impressions. On the south side of the burn, a poorly laminated dark grey shale, <0.6 m thick, overlies the dolomitic limestone and contains charcoal, lepidodendroid axes and some stigmarian roots in its upper part; rare, fragmentary fish skeletal remains are also found towards its base. To the north of the burn, the orange-red dolomitic limestone is also found, but here it is overlain by an intensively rooted medium grey shale that grades up into a poorly laminated medium grey shale; again, rare and fragmentary fish remains occur in the lower part of this unit. The succession is capped by a second red/purple-mottled palaeosol overlain by further beds of red mudstone containing caliche nodules.

Hawk's Nib facies

The Hawk's Nib site is well exposed along the rocky foreshore about 150 m south of Hawk's Nib. Here, the entire Ballagan Formation, which is c. 60 m in thick in this area, was examined, but only 11.5 m of strata bracketing the fish bed was logged in detail (Fig. 3). The logged section begins with a distinctive red/green-mottled mudstone showing caliche nodules and pseudoanticlines. This is sharply overlain by a 1.7-m-thick succession comprising several, small upward-coarsening bodies capped by fine- to medium-grained sandstone showing symmetrical ripples, cross-lamination or planar bedding and, possibly, invertebrate burrows of *Skolithos* type. The upper surfaces of some sandstone units contain small caliche nodules.

Above this is a c. 6-m-thick succession comprising massive beds of mostly red mudstone, up to 1.2 m thick, showing pseudoanticlines and, locally, red/green-mottling and caliche nodules. At a few horizons, these red mudrocks contain 0.1-m-thick layer of red dolomitic

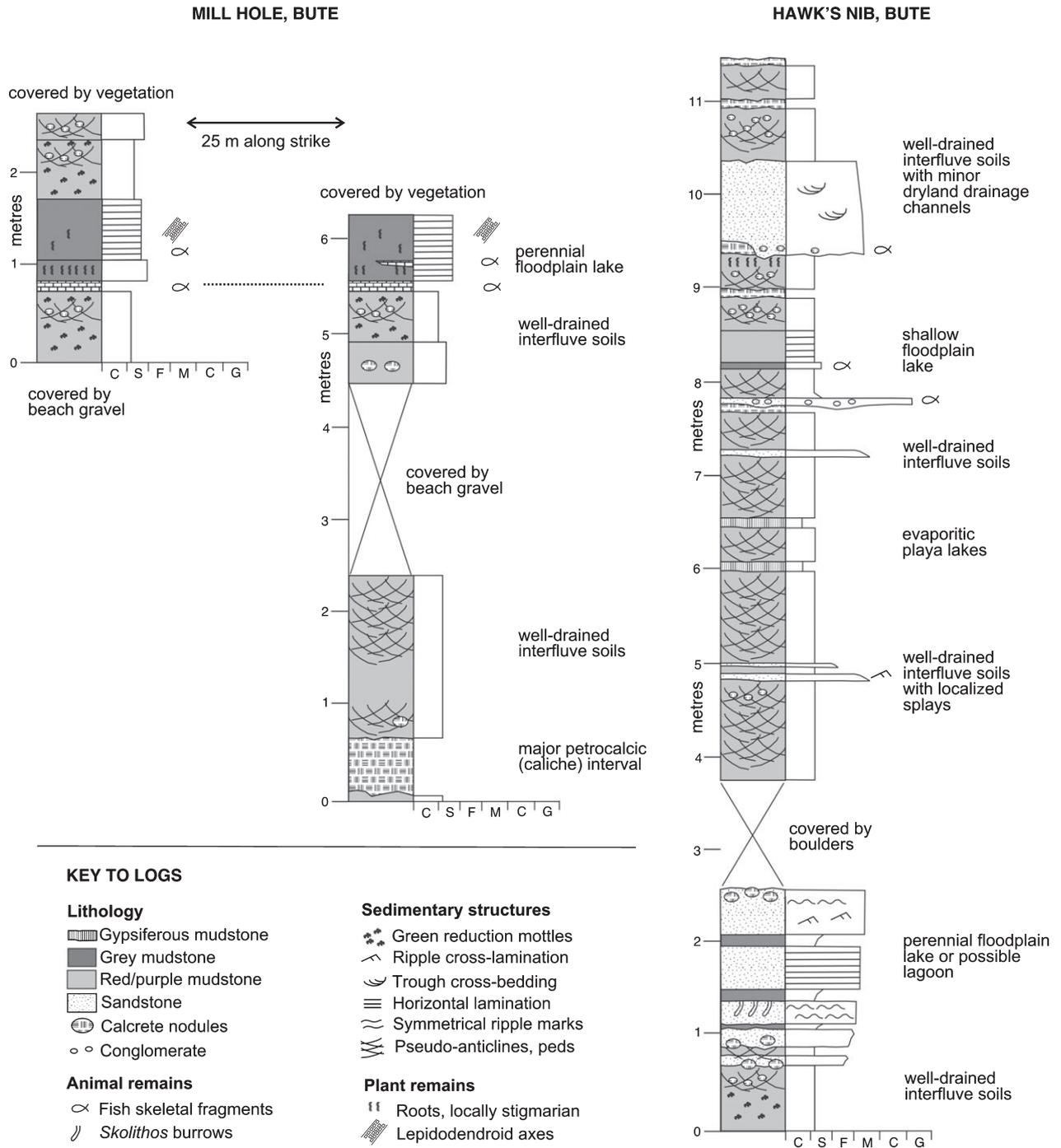


FIG. 3. Sedimentary logs for Mill Hole and Hawk's Nib (see Figs 1–2 for location details).

limestone containing veins of gypsum. At one additional level (7.8 m above the base of the log in Fig. 3), there is an 80-mm-thick intraformational conglomerate, the base of which gently cuts down into one of the red dolomitic limestone and comprises red mud and dolomite intraclasts. The conglomerate contains abundant fish skeletal remains (mandibles, teeth, scales, etc. mostly to entirely disarticulated), a few of which show attached *Spirorbis*.

Based on his field descriptions, we infer that this is the bed from which Matheson (1963) collected his fauna. Another 0.1-m-thick layer within the red mudrock succession (8.5 m above the base of the log in Fig. 3) is a weakly laminated grey mudstone and contains rare fish skeletal fragments.

Near the top of the logged succession is a medium-grained, trough cross-bedded sandstone, 1.2 m thick, with

an erosive base that cuts down into an amalgamated caliche nodular interval (a major petrocalcic bed) and also contains very rare fish skeletal material (9.4 m above the base of the log in Fig. 3). This is overlain by purple/green-mottled mudstone beds and additional amalgamated caliche nodular intervals.

Palaeoenvironment

The mid- to late Tournaisian Ballagan Formation has been interpreted as the deposits of a low-lying coastal plain subject to episodic and restricted marine influence (Read *et al.* 2002). Positioned just south of the equator, within the monsoonal belt, climate was seasonally dry as indicated by regional studies of schizohaline lagoonal deposits (Leeder 1974), palaeosols (Wright 1990; Andrews and Nabi 1998) and tree-rings in fossil woods (Falcon-Lang 1999*a, b*). This interpretation is confirmed for Mill Hole and Hawk's Nib, which both show widespread development of caliche nodules, indicative of a strong rainfall seasonality under subhumid to more arid tropical climates (Tandon and Gibling 1994).

A study of over 700 invertebrate samples from the Ballagan Formation, at sites further to the east in the Midland Valley of Scotland, has revealed evidence (nautiloids) for only four stenohaline marine transgressions in the entire succession (Stephenson *et al.* 2004). Marine transgressions apparently came from the east; their influence decreased to the north and west (Read *et al.* 2002), with the Isle of Bute basins studied here lying near the western inland edge of the depositional complex (Young and Caldwell 2011*b*). Stable isotopic studies ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) of bulk carbonate, ostracods and molluscs (Stephenson *et al.* 2004; Williams *et al.* 2006) indicate that the chemistry of open water facies (cementstones), commonly developed in the Ballagan Formation in its central and eastern deposition areas, either reflects a mixture of fresh and marine water (brackish conditions), or evaporated freshwater under the seasonal climate (hypersaline conditions).

However, in the far western depositional belt of the Ballagan Formation, on the Isle of Bute, open water facies are relatively uncommon. Here, the dominant sedimentary motif, both at Mill Hole and especially at Hawk's Nib, is of red mudrock beds showing pseudoanticlines, green reduction mottles and caliche nodules indicative of seasonally dry palaeosols with vertic properties (Tandon and Gibling 1994). In addition, at both sites, there are some very thick (*c.* 1 m) amalgamated petrocalcic palaeosols, which suggest stable interfluvial areas where sedimentation rate was minimal, and mature soils could develop over tens of thousands of years (Mack and Leeder 1999). Overall, these features point to a wholly terrestrial environment.

Nonetheless, a few water bodies did temporarily exist in this landscape. At Mill Hole, the sharp-based dolomitic limestone containing fish is interpreted as the deposit of a very shallow, but fairly extensive, body of standing water. There is no faunal indication (e.g. *Lingula*, ostracods) that this is a brackish deposit (lagoon), as in some other aquatic facies in the Ballagan Formation (Stephenson *et al.* 2002, 2004; Williams *et al.* 2006); instead, the association with palaeosols tends to indicate a freshwater lake setting. Although negative evidence is difficult to interpret, the absence of ostracods also suggests a freshwater interpretation because true freshwater ostracods did not evolve until later in the Carboniferous (Bennett 2008; Bennett *et al.* 2012). The presence of dolomite further suggests that the lake was hydrologically closed and therefore likely prone to fluctuations in water level, dissolved oxygen and salinity (Platt and Wright 1991). Such environmental fluctuations may have contributed to the fish kills represented by the dense skeletal accumulation, as observed in the modern wet/dry tropics (Townsend *et al.* 1992). The partial articulation of some of the fish remains further suggests quiet bottom-water conditions. Rooted, dark grey shales with charcoal overlying the limestone are interpreted as the deposits of the muddy lake shoreline, which supported fire-prone stands of lepidodendroid trees (Scott and Jones 1994).

Numerous thin horizons of dolomitic limestone, within a succession of well-drained cumulative palaeosols in the middle of the Hawk's Nib section, point to the development of similar, although possibly smaller and more short-lived, open water bodies. Some of these units show small gypsum veins, suggesting that they periodically evaporated towards hypersalinity, or even complete desiccation. Other more substantial, but still shallow, bodies of standing water are represented by upward-coarsening profiles in the lower part of the logged Hawk's Nib section. These former beds show *Spirorbis*, while the latter beds show *Skolithos* burrows, which together provide limited evidence for brackish water influence (Buatois *et al.* 2005; Schultze 2009; Carpenter *et al.* 2011). Nonetheless, palaeosols bracketing all these open water associations at Hawk's Nib suggest a dominantly terrestrial or freshwater setting; however, it is impossible to completely rule out that some, or all, of these water bodies were connected to the sea as brackish lagoons, at least for short intervals. The fish-bearing intraformational conglomerate, which erodes one of these lacustrine or lagoonal beds, probably represents the deposit of a wet season flood. We infer that such a flood reworked fish skeletal material from dry lakebeds or a silted-up lagoon, and re-deposited it in a concentrated lag in a floodplain hollow (Behrensmeier 1991). Trough cross-bedded sandstone bodies in the

upper part of the section are interpreted as the deposits of small alluvial drainages that dissected the seasonally dry coastal plain.

MATERIAL AND METHODS

Approximately 15 kg of the orange-red dolomitic limestone was obtained from the Mill Hole site and transported to the School of Earth Sciences, University of Bristol, for processing. Although lithologically similar, the hardness of the matrix was quite variable and, as the material had been collected over several years, some specimens had become quite desiccated and friable. Extraction of fossil elements therefore followed up to three stages, as appropriate, based on their size and the nature of the matrix: (1) where possible, obscuring matrix was removed mechanically, using a pin-vice, fine-haired brush and tweezers; (2) where this was not initially possible, specimens were softened by immersion in water for 3 days, and a second attempt was made; (3) where the matrix proved resistant to both approaches (or where there were no visible elements >5 mm in size), specimens were disaggregated by repeated immersion in a 5 per cent acetic acid solution, buffered using tricalcium diorthophosphate and sodium acetate (spent acid, generated by adding a small quantity of sodium carbonate to each freshly prepared batch of acid solution). Each cycle comprised a 3-day immersion in the acid solution, followed by a 6-day 'rinse' (to neutralize any residual acid) in a mixture of water, detergent and sodium carbonate. During each cycle, specimens were suspended in a plastic sieve to aid acid circulation. Residue from the acid digestion process was passed through a series of sieves (aperture sizes: 1.0, 0.5, 0.25 mm) and decanted onto filter paper. After approximately 2 days of drying, fossils were manually picked from the residue under a standard reflected light microscope. To prevent breakage during extraction, fossil elements deemed vulnerable to damage were coated in a weak, ethanol-based contact adhesive (Mowital).

Specimens too small for conventional photography were gold-coated using a Bio-Rad SC650 sputter-coater and subsequently imaged using a Hitachi S-3500N scanning electron microscope. Material is accessioned in the Hunterian Museum, Glasgow (GLAHM), and described in the following systematic section. Insufficient new material could be extracted from the intraformational conglomerate at Hawk's Nib site, so we restricted study to the existing collection (Matheson 1963) at GLAHM and present a critical redetermination of those specimens following the main systematic section dealing with the Mill Hole material.

SYSTEMATIC PALAEOLOGY OF MILL HOLE ASSEMBLAGE

Subphylum VERTEBRATA Linnaeus, 1758
Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Incerti ordinis
Incertae familiae

Genus AGELEODUS Owen, 1867a

Type species. Ageleodus pectinatus Agassiz, 1843b

Remarks. *Ageleodus* has been described only from isolated teeth, and this means that it has been impossible to determine its higher taxonomic status; although morphologically similar to some petalodontiform genera, most notably *Ctenoptychius*, Hansen (1985) removed it from this order on the basis of its conical cusps, lack of imbricated basal ridges and lack of tubular dentine, which is a feature of all other petalodontiform teeth that have been subjected to histological analysis (Ginter *et al.* 2010). It has even been proposed (Lebedev 1996) that *Ageleodus* 'teeth' are actually the branchial denticles of a xenacanthid shark, *Diplodoselache antiqua*, as they are often associated with the teeth of this genus (e.g. Turner 1993; Turner and Burrow 2011) and, furthermore, the specimens examined in that study, from the Andreyevka-1 locality, central Russia, were found to lack enameloid. However, they differ from the denticles in other xenacanthids (Ginter *et al.* 2010) and the co-occurrence of *Diplodoselache* and *Ageleodus* is certainly not universal; further investigations have also identified enameloid in *Ageleodus* (Garvey and Turner 2006), leading to the suggestion that the Andreyevka specimens are embryonic (which would explain both their lack of enameloid and small size).



FIG. 4. Photomicrograph of *Ageleodus pectinatus* from Mill Hole. GLAHM 152112 *Ageleodus pectinatus* tooth, labio-lingual view. Abbreviations: x, mesio-distal axis; y, labio-lingual axis. Scale bar represents 5 mm.

Terminology used to describe the specimens described here follows Downs and Daeschler (2001); mesio-distal refers to the long axis of the tooth, while labio-lingual is perpendicular to this axis (Fig. 4).

Ageleodus pectinatus Agassiz, 1843b

Figures 4, 5A

- 1843b *Ctenoptychius pectinatus* Agassiz, p. 100.
 1843b *Ctenoptychius denticulatus* Agassiz, p. 101.
 1867b *Ageleodus diadema* Owen, p. 234.
 1888 *Callopristodus pectinatus* Traquair, p. 85.
 1996? *Diplodoselache antiqua* Lebedev, p. 401,
 fig. 13a–c.

Material. Ten isolated teeth (GLAHM 152112, GLAHM 152119/2, GLAHM 152247).

Diagnosis. Mesio-distally elongated teeth, crown possessing multiple conical cusps approximately equal in length, pectinate or digitate in their arrangement. Crown mesio-distally wider than base, which contains numerous nutritive foramina.

Description. Teeth with denticulated crowns possessing 5–19 conical cusps, the tips of which are frequently missing. Mesio-distal length of crown, 1–5 mm. Base (where present) contains numerous nutritive foramina (c. 15–50 depending on the size of the tooth) and may also exhibit longitudinal furrows that broadly correspond with the cusps in location and number.

Remarks. The presence of basal longitudinal furrows is a diagnostic feature of the only other currently known *Ageleodus* species, *A. altus*, first described by Garvey and Turner (2006) based on a single specimen from the earliest Tournaisian of the Mansfield Basin, Victoria, Australia; the authors also cite small cusp size (2.5 mm), the number of cusps (seven) and shape of cusps (stepped, rather than smooth) as unique attributes of this species. Interestingly, the authors noted that the presence of longitudinal furrows may be, in fact, an ontogenetic feature; as the size, number and shape of cusps of the *A. altus* holotype all fall within the range of variation established by Downs and Daeschler (2001) for *A. pectinatus*, we consider *A. altus* to be a *nomen dubium* and retain the Bute specimens within *A. pectinatus*.

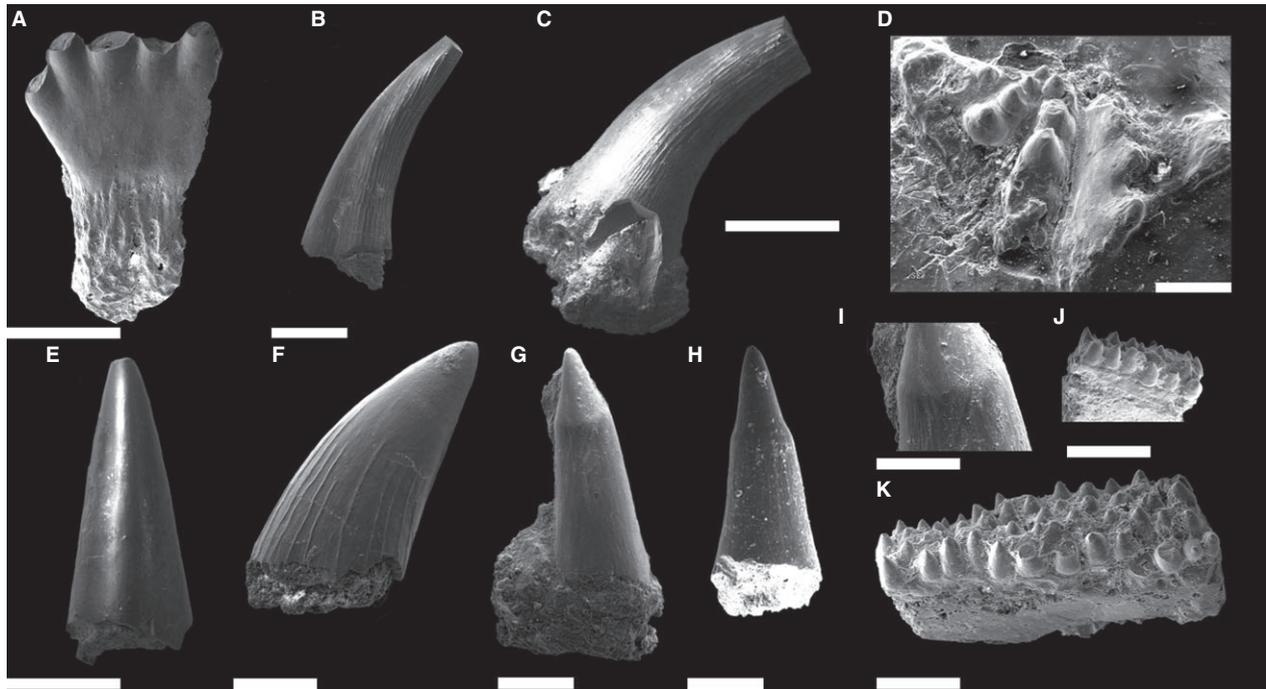


FIG. 5. SEM micrographs of microvertebrate remains from Mill Hole. A, GLAHM 152119/2 *Ageleodus pectinatus* tooth, labio-lingual view. B, GLAHM 152120/1 Rhizodontida indet. cf. *Strepsodus sauroides* tooth, mesio-distal view. C, GLAHM 152121 Rhizodontida indet. cf. *Archichthys portlocki* tooth, mesio-distal view. D, GLAHM 152124 Dipnoi indet. cf. *Sagenodus* tooth plate, oblique occlusal view. E, GLAHM 152120/4 Vertebrata indet. tooth, morphotype A, lateral view. F, GLAHM 152120/5 Vertebrata indet. tooth, morphotype B, lateral view. G–K, Actinopterygii indet.; G–H, GLAHM 152123/2, GLAHM 152123/4 teeth in lateral view; I, magnified view of G, showing dentine–acrodin boundary; J–K, GLAHM 152123/1, GLAHM 152123/3 jaw fragments in oblique occlusal view. Scale bars represent 1 mm (A, C, E), 1 mm (B, D), 0.5 mm (F, I, J, K), 200 μ m (G) and 250 μ m (H).

Class ACANTHODII Owen, 1846
 Order CLIMATIIFORMES Berg, 1940.
 CLIMATIIFORMES indet.

Figure 6A

Material. Thirty fragmented dermal tesserae (GLAHM 152118/3, GLAHM 152118/2, GLAHM 152263).

Diagnosis. Tesserae possessing stellate tubercles.

Description. Basal plates with distinctive vermiform sculpture, supporting irregularly spaced tubercles, ranging in size from 0.2 to 1.0 mm.

Remarks. Dermal tesserae (modified dermal bones of the cranial and cheek regions) of this type are common amongst the climatiids, occurring in at least the families Climatiidae (*Climatius reticulus*; Denison 1979, fig. 16b), Kathemacanthidae (*Kathemacanthus rosulentus*; Gagnier and Wilson 1996, fig. 4a₃) and in the currently unassigned climatiid *Acritolepis ushakovi* (Valiukevičius 2003, fig. 7h). The most commonly occurring Carboniferous acanthodian taxon in northern Britain, Gyraacanthidae (Turner *et al.* 2005), has also traditionally been considered part of this order (Denison 1979; Warren *et al.* 2000), although recent work on Lower Devonian acantho-

dian faunas (Hanke and Wilson 2002; Valiukevičius 2003; Burrow 2007) suggests that the order Climatiiformes may be paraphyletic (Turner *et al.* 2005). The specimens are extremely similar to an isolated element described by Coates (1994, fig. 2) from Unit 31 of the Viséan Geikie Tuff (East Kirkton Limestone sequence, West Lothian, Scotland); although lacking the ornament of the basal plate, the tubercles appear identical. Coates assigned this element, albeit tentatively, to the family Climatiidae, also noting the resemblance to the illustration of Denison (1979, fig. 16b).

Class OSTEICHTHYES Huxley, 1880
 OSTEICHTHYES indet.

Figures 6D, H; 7

Material. Three blocks bearing 21 proximal lepidotrichia (GLAHM 152109, GLAHM 152231, GLAHM 152240, GLAHM 152237), one neural/haemal vertebral element (GLAHM 152109) and 22 isolated distal lepidotrichia (GLAHM 152118/5, GLAHM 152118/4, GLAHM 152254).

Description. Proximal lepidotrichia: long, tubular, gently recurved elements, gradually tapering along their length and hollow where seen in cross-section. Approximately 15 of these are

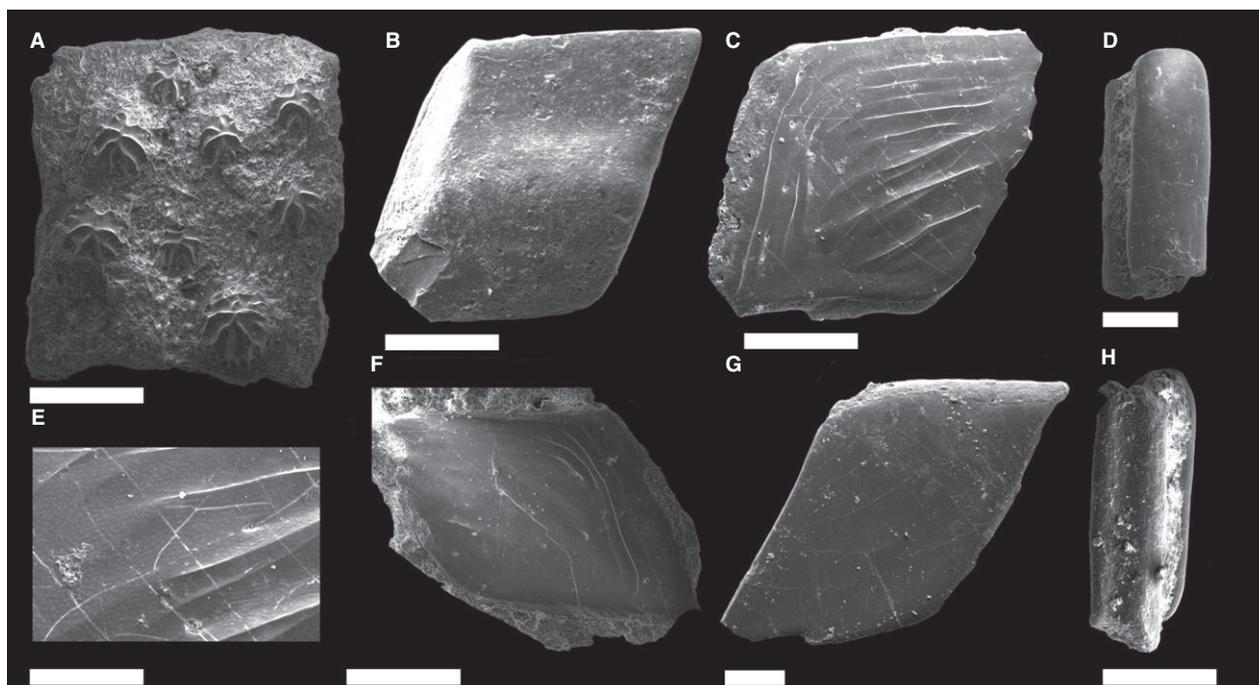


FIG. 6. SEM micrographs of acanthodian and actinopterygian remains from Mill Hole. A, GLAHM 152118/3 Climatiida indet. dermal tesserae. B–C, E–G, Actinopterygii indet. rhombic scales; B, GLAHM 152122/6 interior surface showing keel; C, GLAHM 152122/2 exterior surface showing transverse ridges; E, expanded view of C, showing ganoine surface with ‘gridded’ pores; F, GLAHM 152122/3 scale showing denticulated posterior margin; G, GLAHM 152122/5, exterior surface lacking ornament; D, H, Osteichthyes indet. distal lepidotrichium; D, GLAHM 152118/5 exterior view; H, GLAHM 152118/4 interior view. Scale bars represent 0.5 mm (A–C, E–H) and 100 μ m (D).

clustered together (GLAHM 152109; Fig. 7), partly fragmented and in a state of disarray, such that the proximal and distal tips are not preserved. Neural/haemal vertebral element: associated with the cluster of proximal lepidotrichia is a single element consisting of a partial neural/haemal arch and spine. The arch is equipped with anterior process; the spine is laterally compressed, narrows at its mid-section and is rotated through *c.* 45 degrees along its length. Distal lepidotrichia: U-shaped to cylindrical segments with a rhombic to ovoid scale-like structure affixed to one face, ranging in length from 0.75 to 3.0 mm.

Remarks. The terminology for the dermal fin rays of osteichthyans is complex, with camptotrichia (lungfishes), lepidotrichia (all other osteichthyans), actinotrichia (fine collagenous fibrils extending from the tips of lepidotrichia at the distal-most margins of the fins) and dermatotrichia (a general term encompassing all of the above, and also the ceratotrichia of chondrichthyans) all in current use. There has also been disagreement over whether the term ‘lepidotrichium’ should refer to both jointed and unjointed portions (e.g. Arratia 2009) or only to the distal segmented portion (e.g. Johanson *et al.* 2005) of the fin rays, as Goodrich (1904) did not explicitly distinguish between the two when he proposed the term. Arratia (2009) addressed the problem by referring to the jointed and unjointed portions as distal and proximal lepidotrichia, respectively, and we follow this terminology here.

Subclass ACTINOPTERYGII Cope, 1887

ACTINOPTERYGII indet.

Figures 5G–K; 6B–C, E–G; 8

Material. Thirteen isolated teeth, three jaw fragments bearing multiple teeth (GLAHM 152123/2, GLAHM 152123/4, GLAHM 152123/1, GLAHM 152123/3, GLAHM 152255), 280 isolated rhombic scales (GLAHM 152122/6, GLAHM 152122/2, GLAHM

152122/3, GLAHM 152122/5, GLAHM 152256, GLAHM152126) and one basal fulcrum (GLAHM 152127).

Diagnosis. Teeth equipped with apical caps of acrodin; rhombic scales bearing a superficial covering of ganoine.

Description. Teeth: straight or gently recurved conical teeth, ranging from 0.25 to 1.60 mm in length, with distinct translucent apical caps. Jaw fragments may possess a single tooth row, or a homogenous field of up to 50 teeth, closely packed but arranged in no particular pattern.

Scales: moderately elongated rhombic scales ranging in size from 0.25 to 1.5 mm (long axis), with smooth, slightly curved ventral, dorsal and anterior margins; the posterior margin may be smooth, or possess asymmetrical serrations. Peg-and-socket articulation typically absent, but is observed in a small number of cases (e.g. GLAHM 152126; Fig. 8A). The external surface may be equipped with 5–10 ridges parallel to the long axis of the scale, which when present vary between specimens from highly prominent to barely visible; whether ridged or smooth, the outer surface is gridded with pores of approximately 5 µm diameter, spaced 10 µm apart. Where peg-and-socket articulation is absent, the interior surface is featureless except for the keel, which runs the length of the scale from the dorsal to ventral margin. The single basal fulcrum (GLAHM 152127; Fig. 8B) is arrowhead-shaped and approximately 3 mm in length.

Remarks. An apical cap of the hypermineralized tissue acrodin is a unique derived feature of the Actinopterygii, not seen in any other group (Ørving 1978). There are, however, several cases in which it is absent, for example *Cheirolepis* (Patterson 1982), *Severnichthys* (pers. obs.), the pachycormids and some teleosts (Gardiner *et al.* 2005). Gridded pores of the type observed here are characteristic of ganoine, a hypermineralized tissue that forms the outer surface of ganoid scales and is plesiomorphic for Actinopterygii (Schultze 1966, 1977a). Furthermore, the gross morphology is similar to that of the idealized actinopterygian

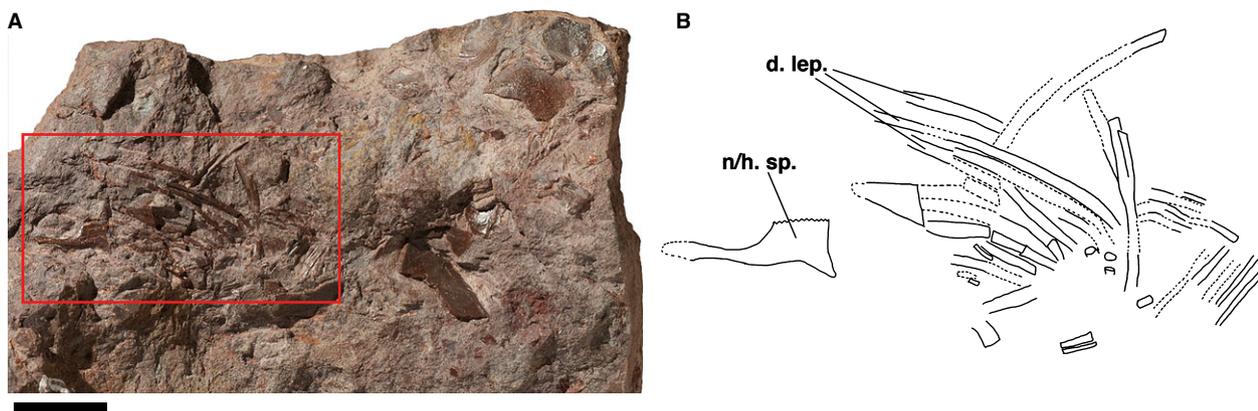


FIG. 7. Light photograph and interpretive drawing of osteichthyan remains from Mill Hole. GLAHM 152109 Osteichthyes indet. A, disarticulated proximal lepidotrichia and partial vertebral arch and spine. B, interpretive line drawing of A. **Abbreviations:** d. lep., distal lepidotrichia; n/h. sp., neural/haemal spine. Scale bar represents 10 mm (A) and 2.5 mm (B).

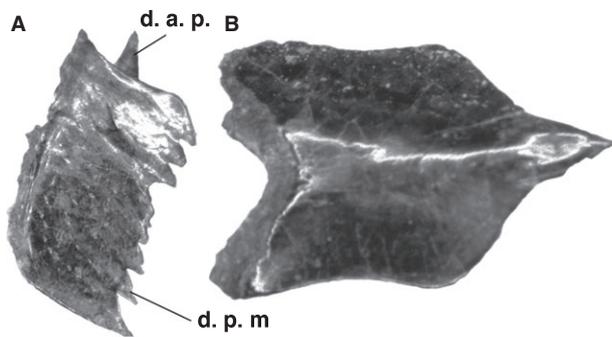


FIG. 8. Photomicrographs of actinopterygian remains from Mill Hole. A, GLAHM 152126 Actinopterygii indet. rhombic scale, external view, showing dorsal articulating peg (d. a. p.) and denticulated posterior margin (d. p. m.). B, GLAHM 152127 Actinopterygii indet. basal fulcrum, external view. Scale bar represents 0.5 mm.

rhombic scale illustrated by Schultze (1966, fig. 1a–b), although most of the Bute specimens lack peg-and-socket articulation; this is typical of the less derived palaeoniscoid-type ganoid scales of more basal actinopterygians (Gambella and Bartsch 2002). The morphological variation possible between scales from different parts of the body has been described in detail for Mesozoic actinopterygians by Schultze (1966), who showed that the sculpture of the ganoin surface, form of the posterior margin and height/width ratio of the scales all vary depending on their location. In his idealized example, the level of ornamentation showed a clear gradient, from robust sculpture in the opercular region to completely smooth near the caudal region; the variation seen in the Bute specimens therefore need not necessarily represent multiple actinopterygian taxa. Conversely, although the scales of many British Carboniferous basal actinopterygian fishes have been described in some detail (e.g. Traquair 1877–1914), this variability results in considerable overlap of characters between genera. In the context of a complete individual where the higher taxonomy is certain, scales may indeed help in generic- and species-level identification; in the case of isolated scales with relatively simple ornamentation such as those described here, this is unfortunately not the case.

Basal fulcra are defined as large, laterally expanded paired or unpaired scale-like structures that precede the bases of the median fins (and sometimes also the paired fins) of actinopterygians; these may be lanceolate, leaf- or arrowhead-shaped and are arranged in overlapping rows (Arratia 2008). As yet, their presence has not been confirmed in any nonactinopterygian fishes (Arratia 2009); variation in the number and form of basal fulcra of the caudal fin has been demonstrated amongst actinopterygian groups, falling into two distinct patterns that may be taxonomically informative (Arratia 2009), but this is obviously not applicable to isolated elements.

Subclass SARCOPTERYGII Romer, 1955
 Infraclass TETRAPODAMORPHA Ahlberg, 1991
 Order RHIZODONTIDA Andrews and Westoll, 1970
 Family RHIZODONTIDAE Traquair, 1881 *sensu* Andrews and Westoll, 1970

Genus ARCHICHTHYS Hancock and Atthey 1870

Type species. *A. portlocki* (Portlock, 1843 ex Agassiz MS).

Remarks. The genus *Archichthys* has only quite recently been revived as a valid taxon (Jeffery 2006), having long been considered a junior synonym of *Strepsodus* (e.g. Woodward and Sherborn 1890). Recent examination of well-preserved *Rhizodus* material suggests, however, that *Archichthys* may in fact be a juvenile ontogenetic variant of *Rhizodus* (J. Jeffery, pers. comm. 2011 to DC). The ongoing uncertainty surrounding this genus will only be resolved by the discovery of more complete specimens; at present, it is known almost exclusively from isolated teeth, with the exception of a single isolated left dentary, a partial right mandibular ramus and several tentatively assigned scales (Jeffery 2006). Terminology used to describe the specimens follows that of Jeffery (2003) for generalized rhizodontid teeth, whereby the faces of the tooth are designated labial (convex face), lingual (concave face) and mesio-distal (both lateral faces; as the tooth is isolated, there is no way to distinguish the two).

cf. Archichthys portlocki (Portlock, 1843 ex Agassiz MS)
 Figures 5C; 9A–C

- 1843 *Holoptychius portlocki* Portlock, p. 463, pl. 13, figs 1–13.
- 1843a *Holoptychius portlockii* Portlock, 1843; Agassiz, p. 180.
- 1861 *Rhizodus portlockii* Portlock, 1843; Salter, p. 223.
- 1870 *Archichthys sulcidens* Hancock and Atthey, p. 266.
- 1891 *Strepsodus sulcidens* Hancock and Atthey, 1870; Woodward, p. 352.
- 1891 *Strepsodus portlocki* Portlock, 1843; Woodward, p. 353.
- 1903 *Strepsodus sulcatus* Traquair, p. 700.
- 1927 *Strepsodus cf. sulcidens* Hancock and Atthey, 1870; White, p. 259.
- 1985 *Large form*; Andrews, fig. 12a.

Material. Four isolated teeth (GLAHM 152115, GLAHM 152121, GLAHM 152252).

Diagnosis. Robust, recurved teeth, oval in cross-section and with up to 17 prominent basal plications. Fine longitudinal striae visible on the tooth surface, regularly spaced

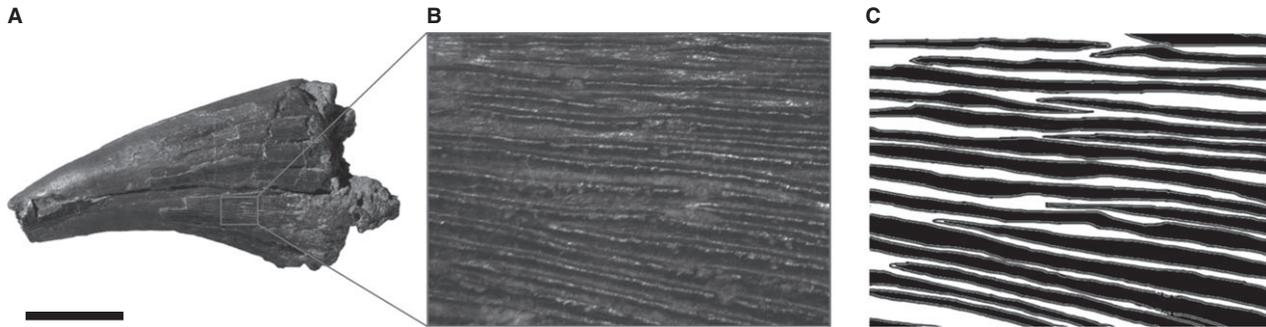


FIG. 9. Light photographs and interpretive drawing of cf. *Archichthys portlocki* from Mill Hole. GLAHM 152115 Rhizodontida indet. cf. *Archichthys portlocki*. A, tooth, mesio-distal view. B, expanded view of A showing surface striae. C, interpretive line drawing of B. Scale bar represents 5 mm (A) and 0.5 mm (B–C).

and closely packed (approximately ten per mm), periodically branching or merging and following the curve of the tooth as seen in mesio-distal view.

Description. The largest, most complete specimen is 20 mm long and 6–9 mm in diameter; including the missing tip, the total length would have likely reached 25 mm. All surfaces bear fine longitudinal striae; those of the lingual face are more prominent and diverge less often than those of the labial face, and a gradation between the two states is observed on the mesio-distal faces. Close inspection reveals that the striae do not in fact merge or diverge, but disappear before reaching adjacent striae (or appear in close proximity to them, when ‘diverging’; Fig. 9B–C). The striae of the labial face in particular exhibit the ‘woven’ texture described by Jeffery (2006) for *Archichthys portlocki*.

Remarks. The specimens described above differ noticeably in one respect from those examined by Jeffery (2006), in that the striae on which their identification rests cover the entire tooth surface, whereas in the *A. portlocki* type series they are invariably absent from the labial face. This pattern is seen in one other rhizodontid, namely *Letognathus hardingi* Brazeau from the Tournaisian Horton Bluff Formation of Nova Scotia, Canada; there is, however, an important difference in form between the two genera, as the teeth of the latter are long and slender (Brazeau 2005), while those of the former are short and robust.

Genus **STREPSODUS** Huxley in Huxley and Etheridge, 1865
cf. *Strepsodus sauroides* Binney, 1841
Figure 5B

Material. Thirty isolated teeth (GLAHM 152120/1, GLAHM 152253).

Description. Recurved or sigmoid teeth 0.75–2.25 mm in length, oval in cross-section, slender, with longitudinal striae 10–20 μ m in width covering the entire tooth surface, more prominently on the lingual and mesio-distal faces. Striae do not follow the curve of the tooth as seen in lateral view, and are straight and regu-

larly spaced basally, with increasing branching and converging towards the apex. Base generally missing, but shows signs of plications where partially present (e.g. GLAHM 152120/1; Fig. 5B).

Remarks. The striae of this morphotype are similar in appearance to those of *Strepsodus sauroides* (compare Fig. 5B with Jeffery 2003, fig. 11c–d), which also possess a regular, straight arrangement basally and ignore the curve of the tooth. Unlike *Strepsodus*, however, the striae are present on all surfaces, rather than just the lingual and mesio-distal faces, and are narrower than is typical for the genus; Jeffery (2003) reported a consistent width of 40–50 μ m, regardless of the size of the tooth.

SARCOPTERYGII *incerti ordinis*
Family ?MEGALICHTHYIDAE Hay, 1902

Genus ?MEGALICHTHYS Agassiz, 1843a

Type species. *Megalichthys hibberti* Agassiz, 1843a.

?*Megalichthys* sp.
Figures 10, 11A–B, D–E

Material. Thirteen scales (GLAHM 152108, GLAHM 152113, GLAHM 152114, GLAHM 152116, GLAHM 152230, GLAHM 152233, GLAHM 152234, GLAHM 152235, GLAHM 152236, GLAHM 152248, GLAHM 152257) and one indeterminate dermoskeletal element (GLAHM 152108).

Diagnosis. Rounded scales featuring on their external surface a prominent, diamond-shaped, cosmine-covered region; dermal bone with superficial covering of cosmine.

Description. Scales: round to teardrop-shaped, 6–12 mm in diameter, with a diamond-shaped, cosmine-covered exposed region; the remaining overlap surface bears a complex sculpture. Cosmine is absent from one specimen (GLAHM 152116, Fig. 11D–E), revealing the underlying ornament of robust

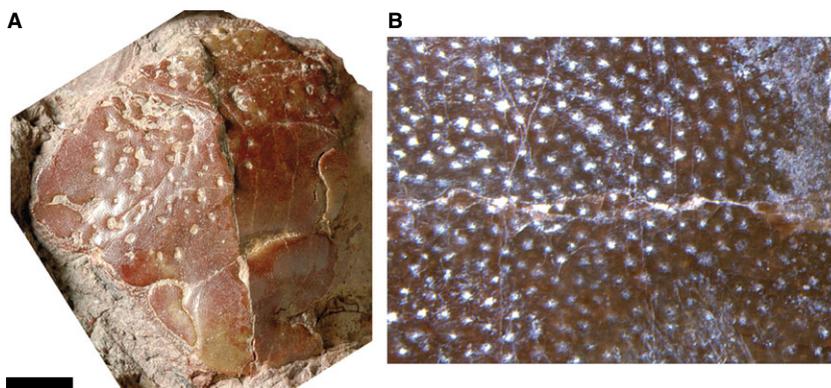


FIG. 10. Light photograph of sarcopterygian dermoskeletal element from Mill Hole. GLAHM 152108 ?*Megalichthys* sp. A, indeterminate dermatocranial element. B, expanded view of A showing flask-shaped pore cavities visible through translucent enameloid layer. Scale bar represents 80 mm (A) and 285 μm (B).

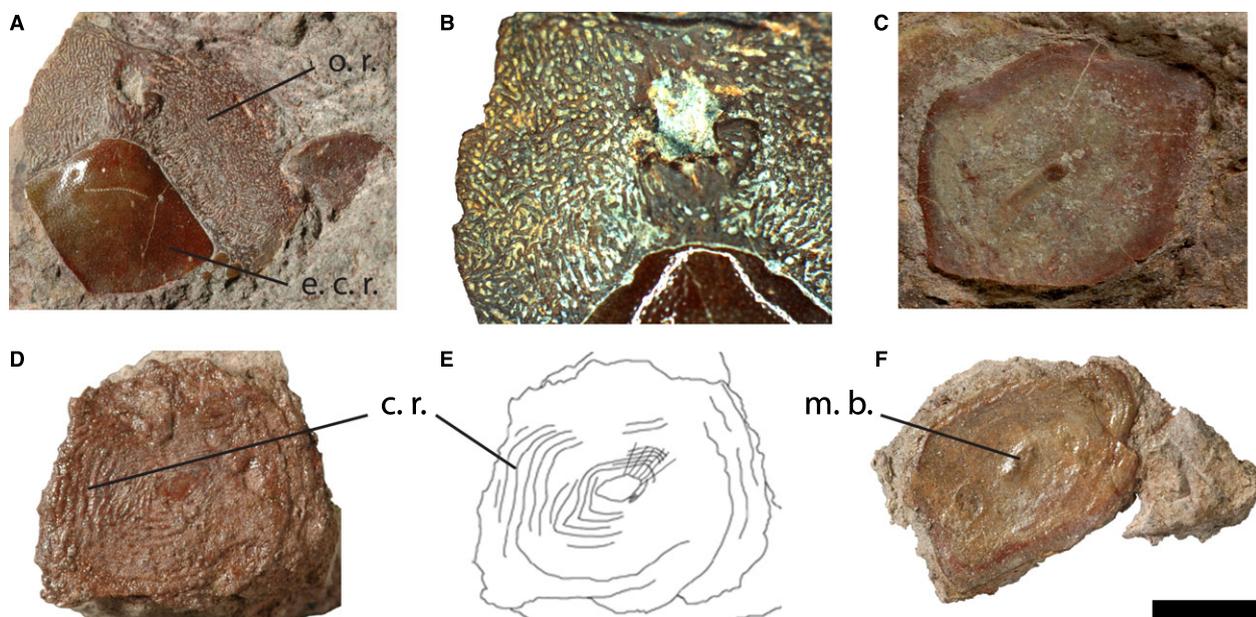


FIG. 11. Light photographs and interpretive line drawing of sarcopterygian dermal elements from Mill Hole. A–B, D–E ?*Megalichthys* sp.; A, GLAHM 152113 ?*Megalichthys* sp. scale in external view; B, expanded view of A showing complex sculpture of ornamented region; D, GLAHM 152116 cosmine-absent scale of ?*Megalichthys* sp., external view; E, interpretive line drawing of D. C, F, Tetrapodomorpha indet. scales in external view; C, GLAHM 152125; F, GLAHM 152114. *Abbreviations:* e. c. r., exposed cosmine-covered region; c. r., concentric ridges; m. b., median boss; o. r., overlapped region. Scale bar represents 500 μm (A), 200 μm (B), 165 μm (C), 250 μm (D–E), 425 μm (F).

concentric ridges and fine, closely packed radial striae typical of cosmine-absent scales of this genus (see Holland *et al.* 2010, fig. 6 g). Dermoskeletal element: unidentified dermal bone, the surface of which bears small, regularly spaced pores approximately 50 μm in diameter, spaced 200 μm apart; each pore connects to an underlying flask-shaped cavity, visible through the translucent, enamel-like surface layer. About 50 per cent of the surface bears irregularly shaped regions lacking the surface layer, and these have invariably been infilled by matrix.

Remarks. Scales: Andrews (1985, p. 69) remarked that ‘it would be hopeless to attempt to classify osteolepids on

teeth and scales’, a statement that reflects our lack of understanding of the systematics of the group as much as the difficulties inherent in identifying isolated scales. Nonetheless, the cosmine overlap region closely resembles that of the scales of *Megalichthys* as originally illustrated by Agassiz (1843a, pl. 64, fig. 3). In addition, according to Thomson (1977, p. 255): ‘A striking feature of many osteolepids is the consistent pattern of sculpturing that exists on the upper surface of the underlying spongiosa ... in *Megalichthys* it seems to exist on all dermal elements, even (in the case of material usually described as

M. intermedius) under the cosmine of the scales'. Stratigraphical considerations also support our identification, as *Megalichthys* is the only confirmed cosmine-bearing taxon known from the Carboniferous of Britain.

Dermoskeletal element: cosmine, as currently defined, is a composite material comprising basal cellular bone, a dentine layer that incorporates a complex pore-canal network and a superficial enamel layer (Friedman and Brazeau 2010); it is the unique configuration of the pore-canal network, in particular the flask-shaped pore cavities and superficial pores in the enamel surface (Fig. 10B), which distinguish cosmine from other, similarly composed integumentary hard tissues (Sire *et al.* 2009). Cosmine is a derived sarcopterygian feature, synapomorphic for Rhipidistia (*sensu* Cloutier and Ahlberg 1996) but, as noted above, amongst British Carboniferous taxa it has only been confirmed in *Megalichthys*. Regions in which cosmine is absent are frequently observed in the dermal skeleton of cosmoid taxa and are generally assumed to arise from resorption of this material on either a seasonal (possibly during migration between marine and freshwater environments) or ontogenetic basis (Thomson 1975, 1977). The level of resorption observed in GLAHM 152108 is similar to that of the 'mixed cosmine' of Thomson (1975, fig. 38).

TETRAPODAMORPHA indet.
Figure 11C, F

Material. Fourteen isolated scales (GLAHM 152125, GLAHM 152114, GLAHM 152128, GLAHM 152232, GLAHM 152241).

Diagnosis. Rounded to subrhombic scales lacking cosmine, with concentric growth lines and a prominent median boss.

Description. Rounded to subrhombic scales 5–12 mm in diameter and approximately 0.75 mm thick, with concentric growth lines and a median boss which may be circular, ovate or tear-drop-shaped; this is interpreted as the inner surface of the scale.

Remarks. Scales with an inner surface of this type are known from numerous Carboniferous tetrapodomorphs, including the rhizodopsids, rhizodontids and tristichopterids, as well as certain unassigned genera such as *Medoevia* and *Canowindra* (Holland *et al.* 2010); they are similar to the scales illustrated by Portlock (1843; reproduced in Jeffery 2006, fig. 1), which were included as part of the type series for *Archichthys portlocki*, although they lack the faint tubercles seen in those specimens. The basic configuration of the outer surface is also consistent with that of a typical rhizodontid (e.g. Andrews 1985; Holland *et al.* 2007, fig. 3; Holland *et al.* 2010, fig. 6e), but poor preservation precludes detailed identification.

Infraclass DIPNOMORPHA Ahlberg, 1991
Order DIPNOI Müller, 1845

Remarks. The identification of isolated dipnoan tooth plates, especially where these are incomplete, is hampered by the considerable intraspecific variability arising from wear, resorption and ontogenetic change (Thomson 1964; Reed 1985; Kemp 1997; Smith and Krupina 2001; Friedman 2007). Although it is possible in at least some cases to clearly differentiate the dental plates of closely related species (e.g. Schultze and Chorn 1997), it is generally agreed that positive identification should not rest on tooth plates alone and that taxa erected solely on such isolated elements should be regarded as *nomina dubia* (Schultze and Chorn 1997; Clément 2009). Thus, our assignment of the specimens to the family Sagenodontidae, although supported by geographical and stratigraphical considerations (*Sagenodus* was widespread in the Carboniferous of Euramerica; Schultze and Chorn 1997; Olive *et al.* 2012), should be treated with caution. In the following description, 'width' is measured labio-lingually and 'length' is perpendicular to this.

Family SAGENODONTIDAE Woodward, 1891

Genus ?SAGENODUS Owen, 1867a
?Sagenodus sp.
Figures 5D, 12A–B

Material. Two incomplete prearticular tooth plates (GLAHM 152117, GLAHM 152258), three incomplete, isolated tooth plates (GLAHM 152124/1–2, GLAHM 152244).

Diagnosis. Tooth plates with radiating, straight tooth ridges, bearing distinct teeth with confluent bases.

Description. Subtriangular tooth plates up to 9 mm long, bearing up to five tooth ridges comprising between one and five distinct cusps, laterally compressed (lingual ridge) to conical in shape. Cusps rounded for all specimens except GLAHM 152124, in which they are more pointed. Length/width ratio is 4.5 and 1.75 for the two specimens in which it can be accurately measured (GLAHM 152244 and GLAHM 152124/1, respectively). Damage to the occlusal surface is common, and thus, the true number of cusps and ridges would likely have been higher than reported here. Specimens GLAHM 152117 and GLAHM 152258 retain attached portions of the prearticular; the most complete specimen (GLAHM 152117) is identified as a left prearticular, of total length 17 mm.

Remarks. To date, only four lungfish genera, namely *Ctenodus*, *Sagenodus*, *Straitonia* and *Uronemus*, have been confirmed in the Carboniferous of Europe. *Uronemus* features highly specialized tooth plates and can be discounted (Smith *et al.* 1987). The distinction between

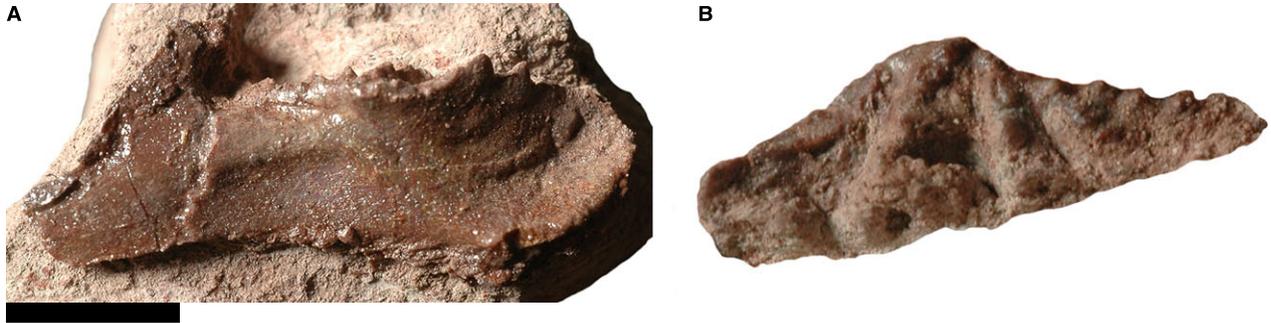


FIG. 12. Light photographs of dipnoan jaw element from Mill Hole. GLAHM 152117 ?Sagenodontidae cf. *Sagenodus* sp. A, partial left prearticular and attached tooth plate, lingual view. B, occlusal view. Scale bar represents 10 mm (A) and 5 mm (B).

Sagenodus and *Ctenodus* can be somewhat blurred (see for example the debate surrounding ‘*Sagenodus*’ *plicatus*: Dawson 1868; Romer and Smith 1934; Sternberg 1941; Baird 1978; Schultze and Chorn 1997), but in general the two are differentiated by radiation being weak or absent in the tooth ridges of the former (Schultze and Chorn 1997). *Sagenodus* is only distinguishable from the closely related *Straitonia* (Upper Carboniferous of Midlothian, Scotland) by the arrangement of the dermal bones of the skull (Thomson 1964); the dentition of *Straitonia* is unknown, but generally assumed to be similar to that of *Sagenodus* (Thomson 1964; Campbell and Barwick 1986, 1990), so it cannot be excluded that the specimens described here belong to *Straitonia*. Therefore, we assign the Bute specimens with caution to *Sagenodus*. When mature, *Sagenodus* is known to have attained a length in excess of 1 m, with tooth plates typically between 30 and 50 mm long (Schultze and Chorn 1997); this implies that the very small tooth plates described here represent individuals at an early ontogenetic stage. Furthermore, tooth-plated dipnoans such as *Sagenodus* typically undergo a progressive change from isolated cusps to combined tooth ridges during ontogeny (Kemp 1995, 2000); in all specimens described here, the cusps are still separate, providing a further indication of juvenility.

VERTEBRATA indet

Remarks. Most of the remaining isolated teeth recovered fall into one of two morphotypes, which lack any diagnostic features to permit clear identification: they could be fish or tetrapod.

Morphotype A
Figure 5E

Material. Four isolated teeth (GLAHM 152120/4, GLAHM 152246).

Description. Straight conical teeth, 0.5–1.5 mm in length, with a smooth surface and no other distinguishing features.

Morphotype B
Figure 5F

Material. Four isolated teeth (GLAHM 152120/5, GLAHM 152249).

Description. Recurved, striated teeth, 0.5–1.25 mm in length, circular in cross-section, with a low width/length ratio. Striae present on all faces but generally restricted to proximal portion of the tooth; rarely, a single striation may run the entire length of the tooth along each of the mesio-distal faces, giving the impression of a ‘cutting edge’.

HAWK’S NIB MATERIAL

Material described by Matheson (1963) from the Hawk’s Nib locality, accessioned in the Hunterian Museum, Glasgow, comprising 47 specimens (GLAHM V3695–V3706, V3708–V3719, V3722–V3746, V3749), was also examined and compared with the Mill Hole assemblage (above).

Description and identification

The Hawk’s Nib material comprises isolated scales and dermatocranial fragments, as well as GLAHM V3706, a dentary bearing a double row of teeth (Matheson 1963, fig. 1), GLAHM V3710, a putative maxillary jaw fragment, and GLAHM V3702, a fragmented osteichthyan proximal lepidotrichium. Aside from GLAHM V3702, Matheson (1963) referred all of these specimens to the family Palaeoniscidae, noting that while the shape of the anterior portion of GLAHM V3706 (which he identified as a left mandibular ramus) was typical of *Fouldenia*

White, 1927 (= *Styracopterus* Traquair, 1890; Moy-Thomas 1937), *Carbovels* White, 1927 (= *Phanerosteon ovensi* Gardiner, 1985) and *Elonichthys* Giebel, 1848, the type specimens of these genera were not sufficiently well preserved for comparison with that specimen. None of these genera are currently placed within Palaeoniscidae, but instead in three separate families: Styracopteridae Moy-Thomas, 1937, Carbovelidae Romer, 1945 and Elonichthyidae Aldinger, 1937. The order 'Palaeonisciformes' is now understood to be a paraphyletic assortment of basal actinopterygians (Carroll 1988; Gardiner *et al.* 2005). Therefore, following current taxonomy, Matheson's identification would be Actinopterygii indet. cf. *Styracopterus* Traquair, 1890, *Phanerosteon ovensi* Gardiner, 1985 or *Elonichthys* Giebel, 1848. On the second jaw fragment (GLAHM V3710; identified by him as a maxillary extension), Matheson (1962) was equally cautious; although he considered it 'practically identical in shape and character' (Matheson 1962, caption for fig. 35) to that of *Carbovels ovensi* as illustrated by White (1927, fig. 15), he felt this was insufficient evidence for identification. Finally, he identified GLAHM V3702 as an acanthodian spine without evidence. In assigning the scales to the family Palaeoniscidae, Matheson (1963, p. 41) did not cite any specific diagnostic features, instead merely remarking that: '...their shape and ornamentation resembles that of known Lower Carboniferous Palaeoniscids'.

The character of GLAHM V3706 highlighted by Matheson, the 'quickly tapering anterior end of the lower jaw', is not diagnostic for *Styracopterus*, *Phanerosteon* or *Elonichthys* (Traquair 1914; Gardiner 1985), nor for that matter any other Carboniferous actinopterygian of which we are aware; the literature is replete with examples of mandibles apparently similar in shape to that depicted by Matheson (1963, fig. 1) belonging to a variety of basal actinopterygian taxa with no close relation, including the Haplolepididae (Westoll 1944, fig. 7b, 8c), the Elonichthyidae (Traquair 1914, fig. 2), *Mesopoma* (Coates 1993, fig. 1, 2a), Carbovelidae and Styracopteridae (Gardiner 1985, fig. 1a). The arrangement of the teeth into separate rows based on size, with an inner row of larger teeth and an outer row of smaller teeth, has long been recognized as a common 'palaeoniscoid' feature, with similarly wide distribution amongst basal actinopterygians (see e.g. Traquair 1914) although it is worth noting that the distinctive teeth of *Styracopterus* allow us to rule out that particular genus (Gardiner 1985). Examination of GLAHM V3710 (accessioned in the museum catalogue as '*Phanerosteon ovensi* scale') reveals that, although similar in outline, there is only a general resemblance in 'character' (i.e. external ornament) to the relevant figure in White (1927, fig. 15). The ornamentation is complex and reticulated, once again in a manner common to many 'palaeoniscoid' fishes. Regarding the scales, the characters displayed (rhombic shape, superficial ridges, peg-and-socket articulation, e.g. Schultze 1966, fig. 1) are

not diagnostic for the family Palaeoniscidae, nor any other particular 'palaeoniscoid' family. Thus, with the exception of GLAHM V3702, we refer all of the above material to indeterminate Actinopterygii.

Only one specimen in the collection, GLAHM V3702 (the 'acanthodian spine'), cannot be confidently referred to the Actinopterygii and is here identified as an osteichthyan proximal lepidotrichium. Three other specimens (GLAHM V3735, V3738 and V3741) are noteworthy in bearing single examples of the polychaete annelid genus *Spirorbis* (or, possibly, *Microconchus* (Tentaculita, Microconchida); see Taylor and Vinn 2006 for uncertainties surrounding this genus).

Comparison with Mill Hole assemblage

The Hawk's Nib assemblage is relatively poorly preserved and depauperate compared to the Mill Hole assemblage, probably reflecting the fact that it has been reworked by floods and redeposited, resulting in fragmentation, abrasion and sorting. Nonetheless, both assemblages are generally similar, with actinopterygian scales the most common elements. As with those collected from Mill Hole, the scales from Hawk's Nib vary in their level of ornamentation; the posterior margin may be smooth or serrated and the outer surface of the scale may possess ridges of varying prominence. The pattern of ridges, where present, is more variable; in addition to a transverse pattern as seen in some of the Mill Hole specimens (e.g. Fig. 6C), a more complex configuration (Matheson 1963, fig. 2) is also often observed.

Other comparisons with the Mill Hole assemblage are as follows: (1) isolated teeth are not found in the Hawk's Nib assemblage and, furthermore, the *in situ* teeth of the actinopterygian dentary (Matheson 1963, fig. 1) do not closely resemble the isolated actinopterygian teeth recovered from Mill Hole; (2) none of the dermal bone fragments of the Hawk's Nib material possesses cosmine; (3) the single proximal lepidotrichium from Hawk's Nib is indistinguishable from those described from Mill Hole (Fig. 7).

DISCUSSION

In summary, the two fish skeletal assemblages (Mill Hole and Hawk's Nib) from the Ballagan Formation of the Isle of Bute, Scotland, contain elasmobranch chondrichthyans (*Ageleodus pectinatus*), acanthodians (Climatiiformes), actinopterygians, rhizodonts (cf. *Archichthys portlocki*, cf. *Strepsodus sauroides*), dipnoans (?*Sagenodus* sp.) and other sarcopterygians (?*Megalichthys* sp.). These collections are too small and fragmentary to make any meaningful inferences about the relative proportions of taxa in the communities; however, the individual taxa allow some

detailed palaeoecological inferences. Here, we review evidence for the salinity tolerances of these taxa and consider wider implications for the mid-Palaeozoic colonization of freshwater environments in the light of our recognition that some specimens appear to be juveniles.

Juvenility of Bute dipnoans

Most dipnoans, both fossil and extant, possessed permanent dentitions that increased in size as the individual matured (Kemp 2002, 2005) and, as discussed previously, we infer from their very small size in comparison with those of adult *Sagenodus* that the tooth plates described here belonged to juveniles. Although isolated teeth of juveniles are not uncommon (Kemp 2000), complete growth series for fossil dipnoans are rare (Campbell and Barwick 1998; Kemp 1998) and much of our understanding of lungfish ontogeny is based on studies of extant genera. It has been shown, at least for *Neoceratodus forsteri*, that growth rate is strongly affected by environmental conditions (Kemp 1986) and size can therefore only provide a rough guide to the age of an individual (Kemp 2005). Because the dentition is permanent, characteristic patterns of wear accrue over the life of the fish and these wear patterns may provide additional evidence for age determinations. This has been described in detail for several living and extinct Cenozoic genera (*Protopterus*, *Neoceratodus*, *Mesoceratodus* and *Archaeoceratodus*; Bemis 1984; Kemp 2005) and appears to be common to most extinct tooth-plated groups (Kemp 2003).

A generalized developmental sequence for tooth-plated lungfish, described in detail by Kemp (2005), can be summarized as follows:

1. Separate tooth cusps, arranged in a pattern of rows characteristic for the taxon in question, erupt, forming a dentition of sharp teeth suitable for feeding on small, fairly soft invertebrates.
2. The bases of the cusps fuse but remain covered by epithelium. The cusps begin to lose their sharp points.
3. The basal plate is exposed and the cusps begin to occlude, increasing the rate of abrasion/attrition; cusps become increasingly rounded. The diet begins to include more resistant plant material.
4. The distinct cusps are lost, being reduced to tooth ridges. The tooth plates are now suitable for crushing tough invertebrate and plant material.
5. Normal grinding and crushing of food produces wear on the tooth plates; the inter-ridge furrows become increasingly rounded and the ridges themselves may become rounded or multifaceted. Impact pits may also form in the furrows if crushing was the dominant action (this depends on available food type).

All of the Bute specimens exhibit separate cusps rather than ridges and the furrows between tooth rows are sharply incised; in the case of specimen GLAHM 152124, the cusps are particularly distinct, retaining a more pointed form and more distinct bases, but in all other cases tips of the cusps are well rounded. It is expected that the dentition of recently hatched individuals would be too poorly mineralized to be preserved (Kemp 2000), but the Bute tooth plates are clearly at a fairly early stage of development. An estimate based on the rate of development in *Neoceratodus forsteri* (see Kemp 1995) suggests the Bute lungfishes were less than one year old.

Inferred salinity tolerance of taxa

The sedimentary facies of the two collection sites, comprising predominantly cumulative palaeosols, suggest a terrestrial context, with thin fish-bearing units deposited in standing water bodies associated with either a freshwater floodplain lake (Mill Hole) or a brackish lagoon (Hawk's Nib). In contrast, the inferred salinity tolerance of the fossil assemblages suggests that most fishes were seasonal visitors from open marine waters, as described in the following sections.

Ageleodus. The facies distribution of *Ageleodus*, which occurs widely in the latest Devonian and Carboniferous, strongly suggests that this shark had a broad salinity tolerance. Specimens from sites with well-documented sedimentary facies occur in settings ranging from normal marine in the Pennsylvanian of central Montana, USA (Alaska Bench limestone; Hansen 1985), restricted marine in the Pennsylvanian of Nova Scotia, Canada (Falcon-Lang *et al.* 2006; Grey *et al.* 2011), brackish embayments in the Mississippian of Tula region, Russia (Lebedev 1996), brackish estuarine/deltaic in the early Mississippian (Tournaisian) of Central Queensland, Australia (Turner 1993), and in putatively freshwater fluvial channels in the latest Devonian (Famennian) of Pennsylvania, USA (Downs and Daeschler 2001; Daeschler *et al.* 2003). Today, only a small proportion (<5%) of elasmobranch taxa are able to tolerate nonmarine salinities owing to osmoregulatory barriers (Ballantyne and Robinson 2010), and of these, only 36 species are obligate freshwater fishes (Martin 2005). Similarly, most nonmarine Palaeozoic sharks, rather than being obligate 'freshwater' sharks, as once suggested (e.g. Zangerl 1981; Gray 1988), were probably either diadromous, capable of migrating between marine and nonmarine settings, or adapted to fresh to brackish embayments (see Carpenter *et al.* 2011 for a review). In the case of *Ageleodus*, facies occurrences point to euryhaline tolerance, with a probably dominant marine mode of life indicated by the fact that it is known from

both Euramerica and Gondwana (Turner 1993; Garvey and Turner 2006), suggesting that it was well capable of migrating across open marine waters. Elsewhere in Scotland, *Ageleodus pectinatus* is known from several Mississippian localities further east in the Midland Valley where it is locally associated with marine dasycladalean algae (Anderson 2009).

Dipnoans, acanthodians and Megalichthys. Other taxa in the Bute assemblages that were probably euryhaline include the lungfish, *Sagenodus*, the climatiid acanthodian(s?) and the sarcopterygian, *Megalichthys*. Schultze and Chorn (1997) argued against the traditional interpretation of *Sagenodus* as a strictly freshwater organism, citing numerous examples of its occurrence in marginal to shallow marine environments (e.g. Schultze and Maples 1992) and concluding that it was euryhaline. Denison (1979, p. 17) showed that acanthodians were tolerant of a range of salinity levels and highlighted that climatiids, in the form of *Gyracanthus*, are known from brackish to near-marine facies (e.g. Falcon-Lang *et al.* 2006; Grey *et al.* 2011; see also Turner *et al.* 2005 for a review of the family Gyracanthidae), while other members of the order are also known from fully marine (Lower Devonian marine limestones of Sichuan, China; Turner and Wang 2000) and marginal or nonmarine (e.g. Ducabrook Formation, central Queensland, Australia; Turner *et al.* 2005) deposits. A diadromous mode of life, seasonally migrating between fresh and marine water bodies, has also been proposed for the sarcopterygians *Ectosteorhachis* and *Megalichthys* to explain cosmine resorption seen in these taxa, although this phenomenon could also be an ontogenetic effect (Thomson 1975, 1977). Subsequent work (Borgen 1989) ruled out the suggestion that resorption was a mechanism to allow for the growth of dermal bones, but beyond this the matter remains unresolved. Regardless, the occurrence of *Megalichthys* in both nonmarine (Central Bohemian region, Stephanian of the Czech Republic; Zajíc 2008) and marine settings (Robinson, Hamilton and Garnett localities, Pennsylvanian of Kansas, USA; Schultze 1995) supports a euryhaline capability.

Archichthys and Strepsodus. The salinity tolerance of rhizodonts in the Bute assemblages is harder to assess. The type series of *Archichthys portlocki* is from the upper Tournaisian of Londonderry, Northern Ireland (Portlock 1843). The locality is uncertain, but the fossils were probably collected from calcareous shale beds exposed along the banks of the Altogowan and Moyola rivers, in the vicinity of Maghera, possibly from the Tournaisian Altogowan Formation, part of the Calcareous Sandstone Series (Portlock 1843; Clack and Ahlberg 2004). Recent work suggests the Altogowan Formation comprises open marine, lagoonal, peritidal and evaporitic sabkha facies (Greensmith 1965;

Mitchell and Somerville 2011). At the main locality, Portlock (1843) reported that *Archichthys* was associated with *Gyracanthus*, *Bellinurus* and *Calamites* (with attached *Spirorbis*). *Gyracanthus* is commonly associated with brackish settings (Turner *et al.* 2005; Falcon-Lang *et al.* 2006); as noted above, *Bellinurus* is considered a brackish to near-marine taxon, based on its occurrences in offshore facies at Mazon Creek, Illinois, USA (Falcon-Lang *et al.* 2006), and while our understanding of the palaeoecology of *Spirorbis* remains in flux (Taylor and Vinn 2006), it is probably a brackish indicator as well (Carpenter *et al.* 2011). A second important *Archichthys* locality occurs above the early Pennsylvanian Low Main Coal at Newsham, Northumberland, UK (Jeffery 2006). This deposit was interpreted as a freshwater oxbow lake deposit formed within a coal swamp (Boyd 1984), but the black shale facies and ostracod (*Geisina*) and bivalve (*Naiadites*) fauna suggest at least some brackish influence (cf. Falcon-Lang *et al.* 2006). *Strepsodus* is similarly reported from a number of sites interpreted as brackish-influenced water bodies in North America (e.g. the Tournaisian Blue Beach site of Nova Scotia; Dawson 1868; Tibert and Scott 1999), Australia (mid-Viséan Middle Paddock site of the Drummond Basin, Queensland; Parker *et al.* 2005) and Europe, particularly the UK (e.g. Foulden, Berwickshire, Scotland; Andrews 1985; Dineley and Metcalf 1999); see Jeffery (2006) for a full checklist of published species. While *Archichthys* shows a high degree of endemism (which implies limited ability to migrate, as expected for oligohaline fishes), *Strepsodus* is globally distributed; nonetheless, unlike *Ageleodus*, both taxa are unknown from normal marine facies. This suggests that, although these rhizodonts were inhabitants of fresh to brackish coastal environments rather than the open sea, they may have occupied different ecological niches, with *Archichthys* (if indeed the genus does prove to be valid) preferring the fresher end of the spectrum.

Actinopterygians. The identity of the abundant actinopterygian material in the Isle of Bute assemblages is too poorly resolved to make general inferences about the probable life habits of these fish. Carboniferous actinopterygians are found in facies ranging from freshwater to marine (Falcon-Lang *et al.* 2006; Štamberg 2006; Carpenter *et al.* 2011). However, this does not necessarily suggest euryhaline tolerance because individual species may show a narrower range of habitat preferences.

Evolutionary and ecological models of freshwater colonization

The invasion of freshwater environments by marine groups was a recurring theme over the course of the Palaeozoic; following the earliest reliable record of nonmarine fishes in

the Silurian, repeated waves of colonization and radiation are seen in the fossil record (Halstead 1985; Gray 1988). The Carboniferous saw the appearance of many new freshwater vertebrate and invertebrate groups, possibly exploiting niches made available by the late or end Devonian Kellwasser and Hangenberg extinction events (Sallan and Coates 2010). Despite the importance of these radiations, they generally remain poorly understood (Bennett *et al.* 2012). Two models, termed passive and active, have been proposed to explain how this wave of colonization might have occurred (Hutchinson 1967). In the active model, animals invaded freshwater settings to exploit underutilized niches, while in the passive model, they became stranded in freshwater settings following marine regression and adapted to survive in their new context. As Bennett *et al.* (2012) noted, the Mississippian strata of the Midland Valley of Scotland contain an important archive for investigating the factors that influenced nonmarine colonization. Being a narrow, long, fault-bounded embayment, facing the open ocean to the east, the Midland Valley was subject to periodic, but ephemeral, marine transgressions (Read *et al.* 2002) and for most of its depositional history comprised a complex of freshwater, brackish and hypersaline water bodies, at times connected, and at times, isolated. The infiltration and survival of marine-adapted animals in these environments was likely improved by the seasonally dry climate (Wright 1990; Falcon-Lang 1999a), which elevated the salinity of nonmarine water bodies towards marine levels (Williams *et al.* 2006).

Evidence that the site was a nursery

All of the dipnoan remains found at Mill Hole represent juveniles at a fairly early stage of development, and depending on the status of *Archichthys*, immature sarcopterygians may have been represented also. This raises the question of whether juveniles were a particularly common component of the fauna and, if so, what this might signify. Taken at face value, the proportion of juvenile material is low, only two per cent. However, because isolated teeth and scales make up the bulk of the recovered specimens, estimating the actual number of individuals represented is problematic; replacement rates differ between taxa (e.g. continuous tooth replacement in chondrichthyans versus no replacement at all in dipnoans), as do the absolute numbers of teeth and scales. The possibility of preservation bias must also be considered.

Nonetheless, the fact remains that 100 per cent of the confirmed dipnoan remains recovered from Mill Hole are juveniles; although the sample size is small, this implies a preponderance of immature lungfishes at this locality. Several upper Palaeozoic localities dominated by juveniles of various groups have been described, for example

Acanthodes, various 'palaeoniscid' actinopterygians and the hybodont *Hamiltonichthys* from the Hamilton quarry lagerstätte, Kansas (Zidek 1985; Gottfried 1988; Maisey 1988, 1989), *Coelacanthus* and *Palaeoniscum* at Hüger Mountain, Hasbergen (Diedrich 2009), and *Rhabdoderma exiguum* from the Mazon Creek lagerstätte (Schultze 1984); in the case of Hamilton Quarry, the associated occurrence of *Palaeoxyris* (chondrichthyan egg cases) confirms this was a spawning site, leading to speculation that the locality functioned as a nursery (Schultze *et al.* 1994; Maisey 1988, 1989). This is in accord with the behaviour of modern marine fishes, which often spawn close to shore, especially in estuaries (Schultze *et al.* 1994), and indeed, this appears also to have frequently been the case amongst fossil groups (Schultze 1999). The term 'nursery' as used here refers to an environment employed specifically for spawning and as a home for juveniles, in which the adult organisms do not normally reside. Thus, if a restricted water body provides a permanent habitat for an entire population, this does not qualify as a nursery, even though spawning takes place there. Therefore, the presence of eggs or egg cases does not, in itself, confirm that a particular site was used in this way; confirmation requires the co-occurrence of juvenile individuals as the dominant component of the fauna. A further complication is that it may be difficult to identify the parent taxon of fossilized eggs; *Palaeoxyris*, with its extensive taxonomic history, is an excellent example of this problem (Fischer and Kogan 2008; Mamay 1994; Godfrey 1995).

Modern dipnoans are exclusively freshwater fishes inhabiting rivers, streams, shallow lakes, swamps and marshes in Africa, South America and Australia (Goudswaard *et al.* 2002; Mlewa *et al.* 2005; Nelson 2006); in the case of *Neoceratodus*, eggs are normally attached to submerged aquatic plants near the banks of rivers, and it is amongst dense patches of these plants that hatchlings and juveniles shelter, while *Protopterus* and *Lepidosiren* construct burrows for their young in the banks of shallow lakes and rivers (Allen *et al.* 2002; Goudswaard *et al.* 2002). During the Palaeozoic, dipnoans were far more taxonomically diverse and occupied a wider range of environments than today (see Inferred salinity tolerance of taxa, above). Juvenile dipnoan material including tooth plates has been reported from several localities, including the North American Mazon Creek and Australian Gogo Formation fossil lagerstätten (*Megapleuron zangerli* Schultze, 1977b; *Palaeophichthys parvulus* Eastman, 1908; *Adololopas moyasmithae* Campbell and Barwick, 1998), Catombal Range and Gap Creek in New South Wales (*Chirodipterus potteri* Kemp, 1998) and Severnaya Zemlya, Siberia (*Tarachomyx oepiki* Barwick, Campbell and Mark-Kurik, 1997); however, assemblages dominated by juveniles are rare (see Lund 1970, 1973; Schultze 1977b). With the exception of Severnaya Zemlya, which is normal

marine (Barwick *et al.* 1997), these sites all appear to represent near-shore marine or estuarine environments (Schultze 2009; Long and Trinajstić 2010; Kemp 2000).

The fact that, unlike other localities from which juvenile dipnoan material has been described, Mill Hole represents a fully freshwater environment is significant because it suggests one possible mechanism for active infiltration of euryhaline fishes into nonmarine settings: the use of these extensive connected inland water bodies as protected nurseries where young could be reared more safely. This would represent a logical extension of the tendency already seen in such fishes to rear young in marginal, near-shore habitats and provide a link to the subsequent extensive freshwater radiations of the Carboniferous. In the absence of definitive proof, however, this remains purely speculative; the question of whether *Sagenodus* used the Mill Hole site as a protected nursery remains open until further material can be found.

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