A preliminary account of the fishes of the Lower Cretaceous Wessex Formation (Wealden Group, Barremian) of the Isle of Wight, southern England

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Abstract

Bulk screening of Lower Cretaceous Wessex Formation (Wealden Group, Barremian) plant debris beds exposed on the south-east and south-west coasts of the Isle of Wight, southern England, has resulted in the recovery of large quantities of isolated chondrichthyan and osteichthyan fish remains. Among these are teeth representing five species of hybodontoid sharks: *Egertonodus basanus*, *Lonchidion breve*, *Lonchidion crenulatum*, *Vectiselachos ornatus*, and *Parvodus heterodon*. Six additional hybodontoid tooth morphs have also been identified. Three are assigned to *Hybodus* sp. and three to *Lonchidion* sp. At least two of the latter may represent new species. Three neoselachian teeth were also recovered, two of which represent a protospinacid shark and the third a rhinobatid ray. Osteichthyan remains pertaining to four orders, Pycnodontiformes, Lepisosteiformes, Amiiformes and Aspidorhynchiformes, and the genera *Coelodus*, ?*Scheenstia*, *Caturus*, and *Belonostomus* have also been recorded. A further pycnodont represented by isolated teeth is also present in the assemblage together with other bony fish remains possibly representing additional taxa. Scanning electron micrographs were obtained of specimens representative of each taxon and these, together with a taxonomic list of the fish assemblages recovered from each of the two plant debris beds considered here, are presented. These assemblages are discussed in terms of community structure and the palaeoenvironments they represent.

Introduction

Despite much recent work, particularly in China, Spain, and the USA, continental biodiversity during the Early Cretaceous remains poorly understood, reflecting the scarcity of continental deposits for this period of time. However, the non-marine Wealden Supergroup of southern Britain (late Berriasian to earliest Aptian) has yielded a great diversity of plant and animal fossils (Batten, 2011) and is therefore of paramount importance when considering palaeobiodiversity at this time. Among these fossils, chondrichthyan and osteichthyan remains are common, particularly in the bone beds of mainland Britain (Allen, 1949) and in the plant debris beds (Sweetman & Insole, 2010) of the Isle of Wight. The latter have yielded the second-most diverse non-avian dinosaur assemblage yet recorded for the Lower Cretaceous, the most diverse being that comprising part of the Jehol Biota of East Asia (Zhou & Wang, 2010). They have also yielded abundant microvertebrate remains (Sweetman, 2011a), including the teeth, dermal denticles, and fine spines of chondrichthyans, and the teeth, scales, and bones of osteichthyans. Despite this abundance, and until this pilot study, little had been done to investigate Wessex Formation fish assemblages. Furthermore, only one recent study of the Wealden Group chondrichthyans of mainland Britain has been undertaken (Patterson, 1966), with other studies dating from the early part of the

20th century (e.g. Woodward, 1916–1919). Similarly, the osteichthyan fauna has also received little attention since Woodward's (1916–1919) account. Although macroscopic fish remains have been recorded from the Isle of Wight (e.g. Egerton, 1845), the remainder of the fauna represented by microremains has only recently been described in outline (Duffin & Sweetman, 2011; Forey & Sweetman, 2011). Other accounts, apart from that of Sweetman & Underwood (2006), who document a scyliorhinid neoselachian from the Wessex Formation, amount to generally incomplete species lists based on small-scale studies and lack figures (e.g. Freeman, 1975; Evans, Barrett & Ward, 2004). In order to gain some understanding of Wessex Formation fish assemblages as a whole within the very limited time constraints applicable to this study, microvertebrate remains from just two of almost 30 horizons sampled by one of us (S. C. Sweetman) were examined. These are plant debris bed 38 (Radley, 1994), occurring near the top of the Wessex Formation at Yaverland on the south-east coast of the Isle of Wight, and bed L9 (Stewart, 1978), placed some 65 m lower in the succession exposed north-west of Grange Chine in Brighstone Bay on the south-west coast (Fig. 1, 2). Although substantially more matrix has been processed from bed 38 than from bed L9 (see below), samples from these beds were chosen for examination, being particularly rich in microvertebrate remains as a whole. Amongst the large amount of fish material recovered, 3944 chondrichthyan and osteichthyan specimens were isolated and identified (Fig. 14), of which 112 are presented in figures in this article. Some of this material undoubtedly represents new taxa but detailed comparative descriptions and diagnoses are not provided in this preliminary account. They will be provided elsewhere when material from all of the sampled horizons has been examined.

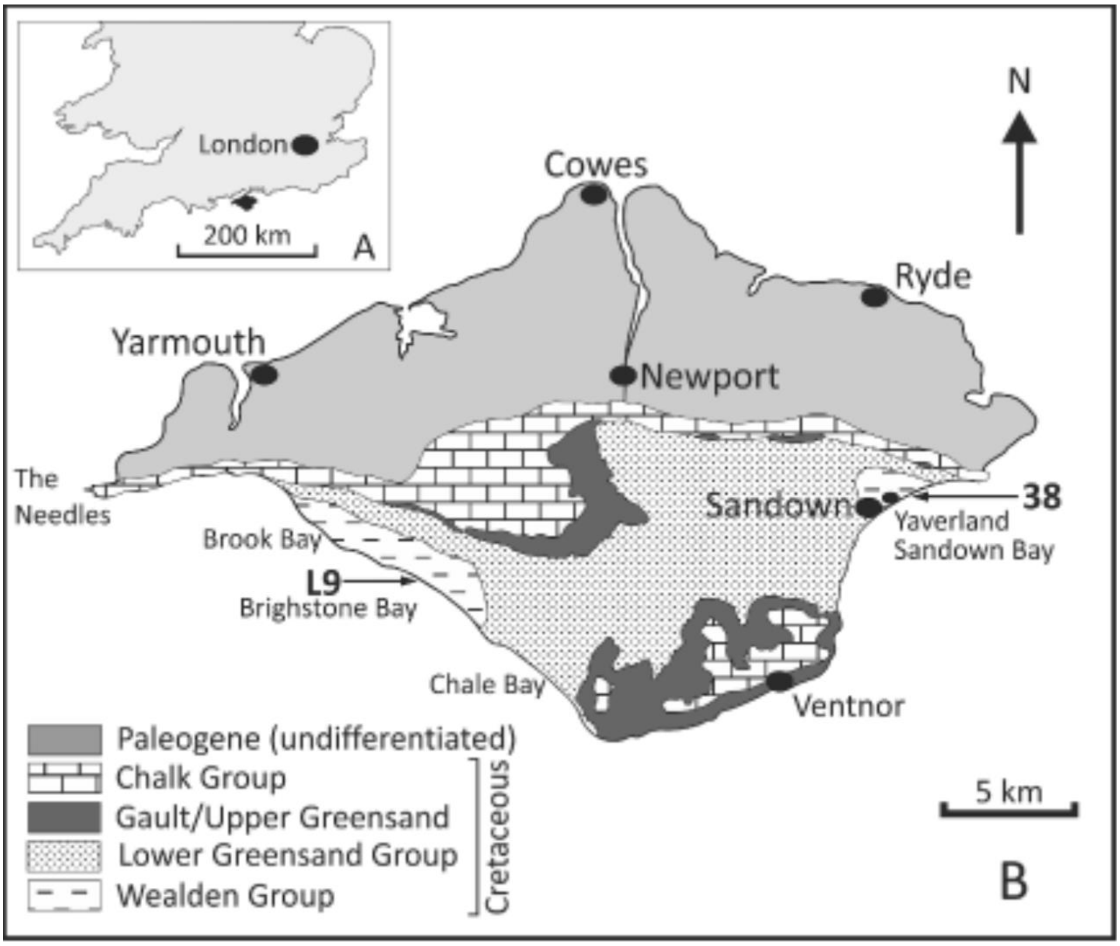


Figure 1: Outline map of southern Britain showing the location of the Isle of Wight (A). Outline geological map of the Isle of Wight showing outcrop localities for beds 38 and L9 (B).

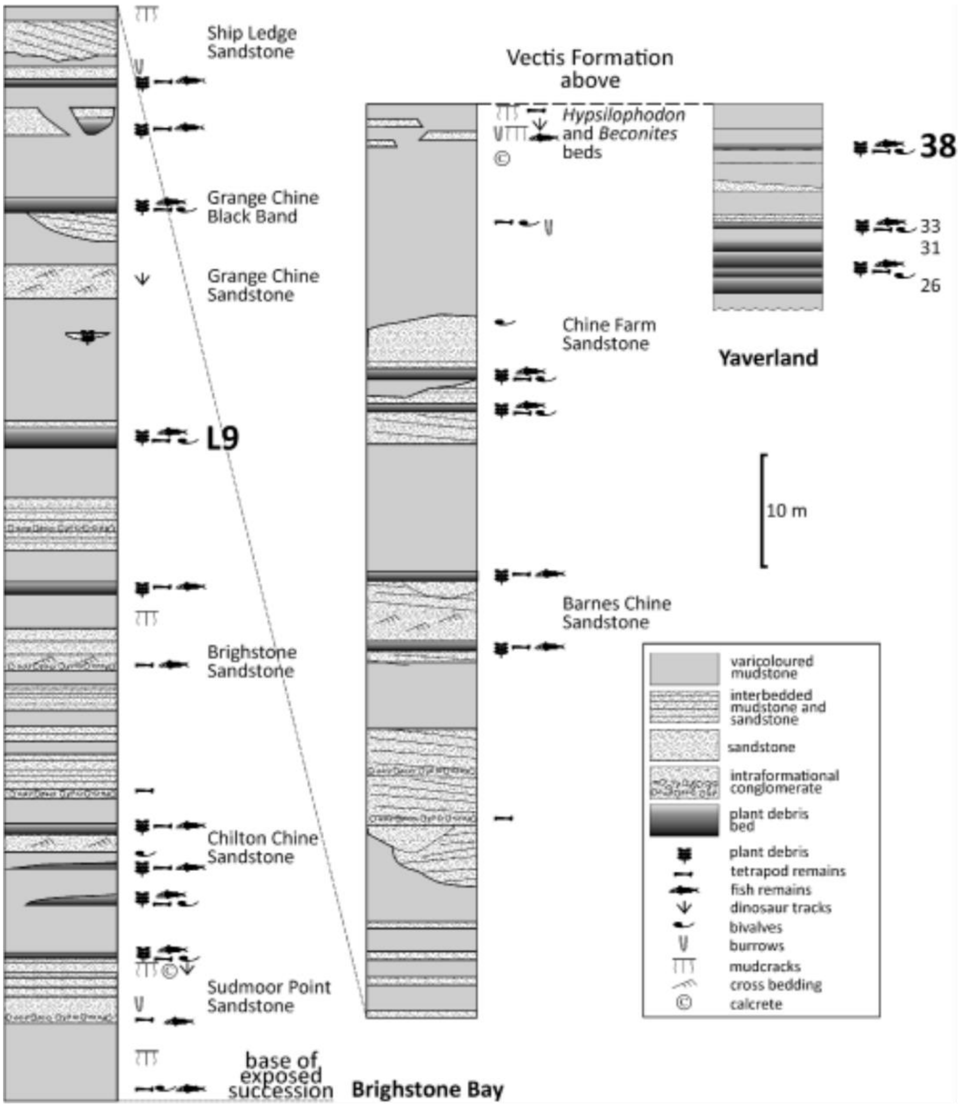


Figure 2: Schematic lithological logs of the Wessex Formation exposed in Brighstone Bay on the south-west coast of the Isle of Wight and the upper part exposed in Sandown Bay on the south-east coast in the vicinity of Yaverland. Brighstone Bay section based on Stewart (1978, Fig. 15, p. 35) with modifications based on Radley and Allen 2012 and personal observations (S. C. Sweetman, 2013). Sandown Bay section modified from Radley (1994).

Geological Setting

The Wealden Supergroup of southern England was deposited in two sub-basins (the eastern Weald Sub-basin and the western Wessex Sub-basin), separated by a structurally elevated area known as the Portsdown High (for a general account see Batten and Austen, 2011 and Sweetman, 2011b). In the latter sub-basin, the Wealden Group comprises the primarily fluvial Wessex Formation overlain in the east by the lagoonal Vectis Formation (Stewart, 1978). Both are well exposed in coastal sections (Fig. 1), the exposures being constantly refreshed by erosion. Consistent evidence from a number of studies indicates that the exposed Wessex Formation was deposited during the Barremian, with the Hauterivian–Barremian boundary lying close to the level of the Pine Raft (White, 1921), seen at low tide at Hanover Point on the south-west coast. The overlying Vectis Formation is late Barremian to earliest Aptian (Kerth & Hailwood, 1988; Allen & Wimbledon, 1991; Robinson & Hesselbo, 2004). The Wessex Formation mainly comprises varicoloured, oxidized, overbank mudstones that have been subject to prolonged periods of paedogenesis, with subordinate alluvial sandstones, and highly subordinate, but distinctive, thin lenticular beds, basally conglomeratic, rapidly fining upwards, and containing abundant plant debris (Fig. 2). The latter were originally termed lignite beds (White, 1921) but are now referred to as plant debris beds *sensu* Oldham (1976). Sweetman & Insole (2010) interpret this facies as representing the product of an exceptional combination of otherwise common events: wildfires triggered by lightning strike and torrential rainfall. Wildfires produced areas denuded of ground cover and opened forest canopies. In the event of heavy rainfall immediately thereafter, these areas were particularly vulnerable to runoff and erosion. Progressive entrainment of sediment and organic matter transformed sheet-floods in these settings into debris flows capable of transporting the trunks of trees and bones of the largest animals living on the floodplain. They were also powerful enough to traverse areas crossed by streams and occupied by ponds. As a result, the remains of the largest and smallest animals present in the Wessex Formation ecosystem were mixed together and transported in these flows, as were those of animals occupying both aquatic and terrestrial habitats. Similar deposits with their unique palaeontological content have so far only been recorded from the Wessex Formation of southern England (Sweetman & Insole, 2010).

Material and Methods

Samples totalling about 750 kg dry weight were taken from bed 38, in the vicinity of Ordnance Survey national grid reference (NGR SZ) 61693 85223, and about 150 kg dry weight from bed L9 at NGR SZ 41781 81880. These samples were processed to recover microvertebrate remains using a bulk screening machine modified from the design of Ward (1981) incorporating a sieve with a 330 µm mesh (Sweetman, 2011a). Coarse material (> 2.8 mm) was removed and sorted by eye. Plant debris from the remaining fraction was removed hydromechanically and the remaining residue was graded using a nest of sieves. Each fraction was then picked using a binocular microscope. Fish remains were separated by the second author into morphotypes pending identification. Digital images were obtained for representative specimens of each morphotype using a scanning electron microscope (JSM-6100) and associated software (SemAfore version 4.00; Insiööritoimisto J.Rimppi Oy). All specimens were coated with gold-palladium using an E500 Sputter Coater to prevent charging by the electron beam. Specimens shown in the figures in this article, all of which were recovered from residues obtained from bed 38 at Yaverland, and unfigured material, are accessioned in the collections of the Natural History Museum, London under accession numbers NHMUK PV P 73421 - P 73609.

Institutional and other abbreviations

NHMUK, the Natural History Museum, London; NGR SZ, UK Ordnance Survey national grid reference; c, centre; l, left; lr, lower; m, middle; r, rig=ht; u, upper.

Results

Sharks and rays

Systematic palaeontology

Superclass CHONDRICHTHYES Huxley, 1880

Class ELASMOBRANCHII Bonaparte, 1838

Cohort EUSELACHII Hay, 1902

Superfamily HYBODONTOIDEA Owen, 1846

Family HYBODONTIDAE Owen, 1846

***Hybodus* sp. 1**

Figure 3A–D

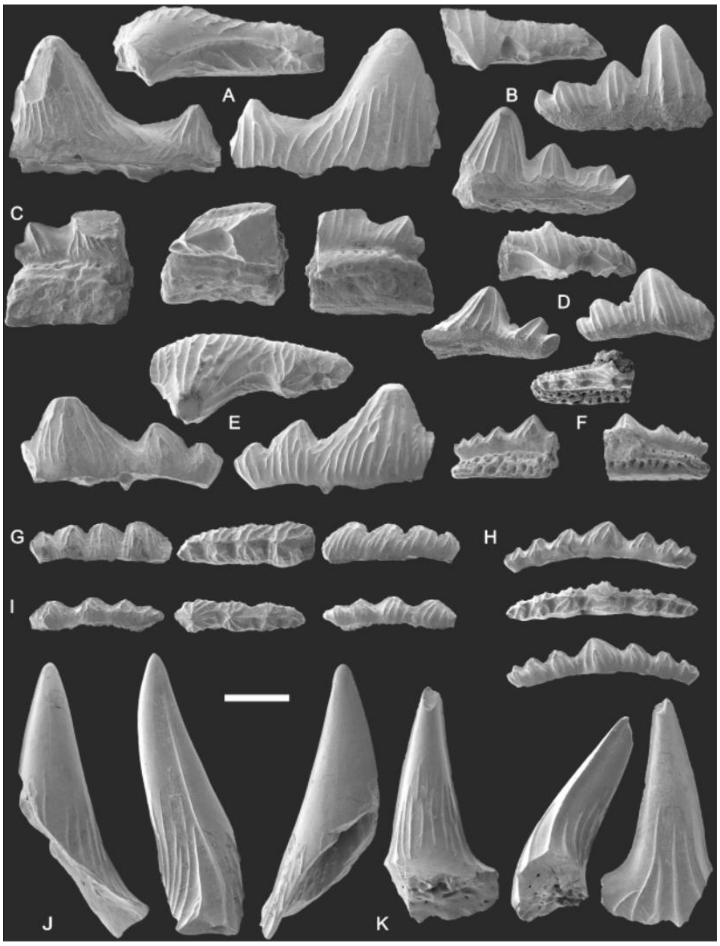


Figure 3: Scanning electron micrographs of chondrichthyan teeth from the Barremian Wessex Formation of the Isle of Wight. *Hybodus* sp. 1 (Woodward, 1916–1919): NHMUK PV P 73412 fragmentary anterior tooth (A) in l. lingual, u. occlusal, and r. labial views; NHMUK PV P 73413 fragmentary anterolateral tooth (B) in lr. lingual, u. occlusal, and r. labial views; NHMUK PV P 73414 fragmentary anterior tooth with part of the root (C) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73415 fragmentary lateral tooth (D) in lr. lingual, u. occlusal, and r. labial views. *Hybodus* sp. 2: NHMUK PV P 73417 fragmentary anterior tooth (E) in l. lingual, u. occlusal, and r. labial views; NHMUK PV P 73418 fragmentary anterolateral tooth with part of the root (F) in l. lingual, u. occlusal, and r. labial views; NHMUK PV P 73419 fragmentary lateral tooth (G) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73420 complete anterolateral tooth crown (H) in u. lingual, m. occlusal, and lr. labial views. NHMUK PV P 73425 fragmentary posterior tooth (I) in l. lingual, m. occlusal, and r. labial views. *Egertonodus basanus* (Egerton, 1845): NHMUK PV P 73425 central cusp (J) in l. lingual, m. lateral, and r. labial views; NHMUK PV P 73426 central cusp (K) in l. lingual, m. lateral, and r. labial views. Scale bar represents 1 mm.

Material

Eleven fragmentary teeth represented by NHMUK PV P 73412 - P 73415.

Description

Teeth are up to 3 mm high with an estimated length of 5–6 mm, all teeth recovered being broken. They have a moderately high and slender central cusp with well-developed cutting edges, which slightly curve lingually. The central cusp is flanked on both sides by up to three lateral cusplets. Ornamentation consists of vertical ridges ascending the crown from just above the crown–root junction both labially and lingually, often bifurcating basally, especially on the lingual side. The root is tabular with a concave labial face and bears few foramina.

Remark

This tooth morphology is similar to that of *Hybodus parvidens* (Woodward, 1916–1919). However, it is distinct in that the central cusp is significantly lower and bears more numerous and finer ridges than the teeth of *H. parvidens*.

Hybodus sp. 2

Figure 3E–I

Material

Two-hundred and fifty-one mostly fragmentary teeth represented by NHMUK PV P 73417 - P 73421.

Description

Teeth are up to 2.5 mm high with an estimated length of 5 mm, all teeth recovered being broken. The central cusp is low, squat, and flanked on both sides by up to four lateral cusplets. These are very low, decreasing in height away from the central cusp, but are well demarcated from each other. A long occlusal crest extends from one extremity of the crown to the other, passing through the apices of the central cusp and lateral cusplets. The crown is strongly ornamented on both labial and lingual sides. Strong vertical ridges arising from the crown–root junction ascend the crown to the occlusal crest and cusp apices. The ridges commonly bifurcate basally and are often interspersed with finer, shorter ridges. The root is tabular, with a concave labial face.

Remark

This tooth morphology is somewhat similar to that of *Hybodus brevicostatus*Patterson, 1966. However, it is distinct in that the central cusp is significantly lower, more heavily ornamented, and lacks labial bosses.

Hybodus ?sp. 3

Not figured

Material

Twenty-two fragmentary teeth comprising NHMUK PV P 73423 - P 73424.

Description

Teeth are very similar in size, shape and ornamentation to those of *Hybodus* sp. 2; however, they differ in having a higher and more conical central cusp and lateral cusplets. Of the two beds studied, this tooth morph was only recorded from bed L9 and examination of teeth referable to *Hybodus* recovered from the numerous other horizons sampled is required in order to ascertain whether or not the L9 material does indeed represent an additional species.

Genus *EGERTONODUS*Maisey, 1987

Egertonodus basanus (Egerton, 1845)

Figure 3J, K

Material

Seven fragmentary teeth represented by NHMUK PV P 73425 and NHMUK PV P 73426.

Description

Only central cusps have been identified with confidence. These are high (up to 4.5 mm), inclined lingually, and sharply pointed with well-defined cutting edges. Both faces of the crown are ornamented by numerous fine, vertical ridges arising just above the crown–root junction. The lingual face of the crown has apicobasally longer ridges than the labial face. Complete specimens recovered from contemporaneous strata in the Weald Sub-basin have a central cusp flanked on both sides by up to three low cusplets (Patterson, 1966).

Family LONCHIDIIDAE Herman, 1977

Genus *LONCHIDION*Estes, 1964

Lonchidion breve Patterson, 1966

Figure 4A–C

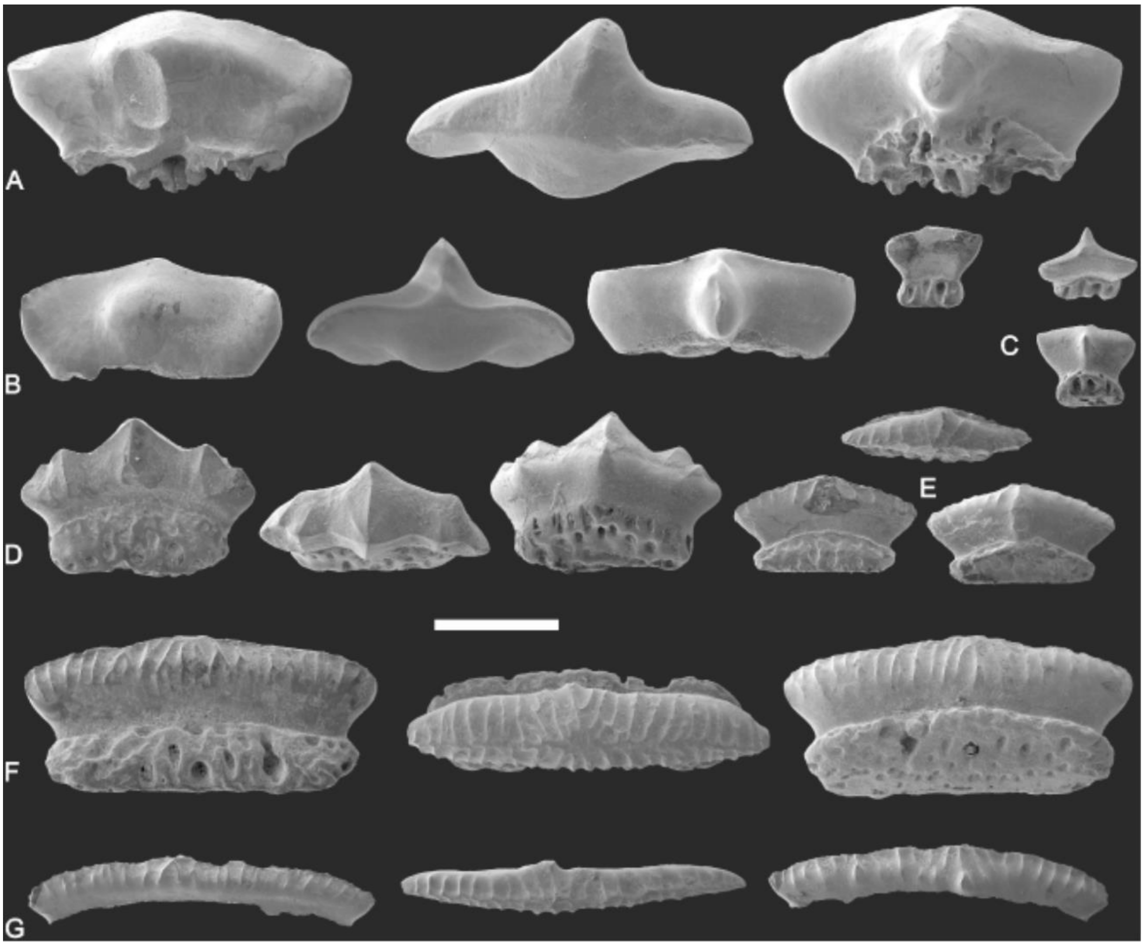


Figure 4: Scanning electron micrographs of chondrichthyan teeth from the Barremian Wessex Formation of the Isle of Wight. *Lonchidion breve*Patterson, 1966: NHMUK PV P 73428 lateral tooth (A) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73429 anterolateral tooth (B) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73430 complete anterior tooth (C) in l. lingual, r. occlusal, and lr. labial views. *Lonchidion* sp. indet.: NHMUK PV P 73433 almost complete (one lateral cusplet is missing)?symphyseal tooth (D) in l. lingual, m. occlusal, and r. labial views. *Lonchidion striatum*Patterson, 1966: NHMUK PV P 73434 complete anterior tooth (E) in l. lingual, u. occlusal, and r. labial views; NHMUK PV P 73435 complete lateral tooth (F) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73436 posterior tooth (G) in l. lingual, m. occlusal, and r. labial views. Scale bar represents 1 mm.

Material

Two-hundred and sixty-four teeth, some fragmentary, represented by NHMUK PV P 73428 - P 73430.

Description

Teeth are up to 2.5 mm long and 1 mm high. There is a low central cusp, but lateral or accessory cusplets are absent. The crown is smooth, devoid of any ornament. The labial process is moderate to strong. Some teeth bear a spherical cavity on the lingual face that accommodates the tip of the labial process of the succeeding tooth. Some teeth have a well-developed wear facet on the occlusal surface.

Lonchidion sp. indet.

Figure 4D

Material

One tooth, NHMUK PV P 73433.

Description

The tooth is 2 mm long and 1 mm high. There is a clearly marked, but low, central cusp and two pairs of minute lateral cusplets. The labial process is weak. Ornamentation is limited to weak vertical folds descending from each face of the central cusp and those of the cusplets. These terminate before the crown–root junction. The root is typical for this genus, with large foramina on the lower parts of the root and a few, irregularly placed, smaller foramina close to the crown–root junction.

Remark

The tooth is very similar to, but not as gracile as, a specimen figured by Underwood & Rees (2002, Plate 2, figs 4, 5, 9) and referred by them to *Lonchidion crenulatum*Patterson, 1966. However, only one tooth of this morphology was recovered during this study and this, together with cusp symmetry, suggests that it may be an undiagnostic symphyseal tooth.

Lonchidion striatum Patterson, 1966

Figure 4E–G

Material

Five-hundred and three teeth, some fragmentary, represented by NHMUK PV P 73434 - P 73436.

Description

The teeth are larger than those of *L. breve* and *L. crenulatum* (up to 4.5 mm long). The elongated crown bears a strong occlusal crest. The central cusp is very low and flanked by very weak, irregular lateral cusplets. The crown is ornamented both labially and lingually by strongly developed vertical ridges. These arise just above the crown–root junction, ascending the crown to the occlusal crest, and occasionally bifurcating basally. The labial process is weak and surmounted by a strong vertical ridge. The root is typical for the genus, with large foramina on the lower parts of the root and a few, irregularly placed, smaller, circular foramina close to the crown–root junction.

Lonchidion sp. 1

Figure 5A–D

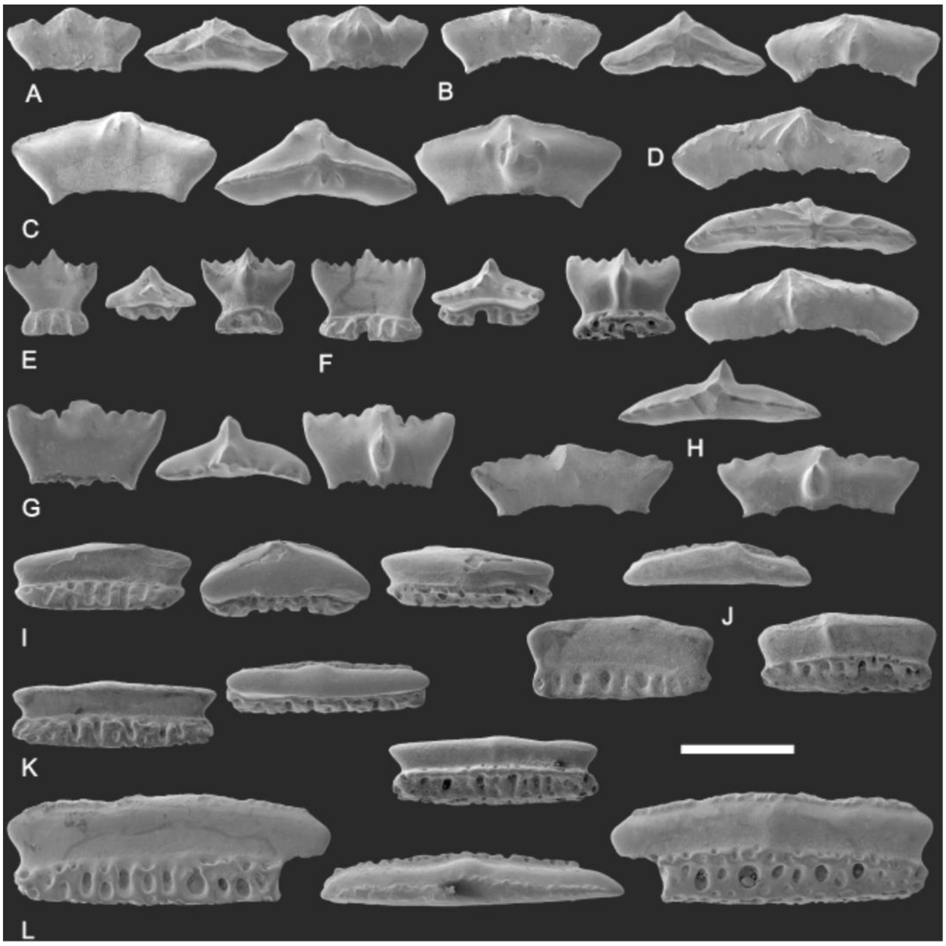


Figure 5: Scanning electron micrographs of chondrichthyan teeth from the Barremian Wessex Formation of the Isle of Wight. *Lonchidion* sp. 1: NHMUK PV P 73439 anterior tooth (A) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73440 anterolateral tooth (B) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73441 lateral tooth (C) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73442 posterolateral tooth (D) in u. lingual, m. occlusal, and lr. labial views. *Lonchidion* sp.2: NHMUK PV P 73445 anterior tooth (E) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73446 anterolateral tooth (F) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73447 posterior tooth (G) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73448 posterolateral tooth (H) in l. lingual, u. occlusal, and r. labial views. *Lonchidion* sp. 3: NHMUK PV P 73451 complete tooth of uncertain location (I) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73452 complete tooth of uncertain location (J) in l. lingual, u. occlusal, and r. labial views. NHMUK PV P 73453 complete tooth of uncertain location (K) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73454 substantially complete tooth of uncertain location (L) in l. lingual, m. occlusal, and r. labial views. Scale bar represents 1 mm.

Material

Two-hundred and four teeth, some fragmentary, represented by NHMUK PV P 73439 - P 73442.

Description

The teeth are up to 2.5 mm long. They have a low central cusp but lateral cusplets are absent. A small number of ridges ascend the crown both labially and lingually, terminating at the apex of the central cusp. The labial process is poorly developed.

Remark

Teeth in the range of morphology assigned to this species have been recorded from both beds 38 and L9. These teeth are somewhat similar to those of *Vectiselachos ornatus* (Woodward, 1889) but this taxon has only been recorded from bed 38. The unequivocal occurrence of this morphotype in both beds 38 and L9 suggests that it cannot be confused with anterior teeth of *V*. *ornatus* (see Fig. 14). Furthermore, although these teeth conform to the description and drawings of those of *L. crenulatum* provided by Patterson (1966), they do not conform to the tooth morphology attributed to this taxon by Underwood & Rees (2002, Plate 2, figs 9). This tooth morphology may therefore represent a new species.

Lonchidion sp. 2

Figure 5E–H

Material

Seven-hundred and thirty-eight teeth, some fragmentary, represented by NHMUK PV P 73445 - P 73448.

Description

The teeth are up to 2 mm long. They have a low central cusp and several irregularly placed lateral cusplets that descend a crenulated occlusal crest. The crown is not ornamented. The labial process is well developed in smaller and higher teeth. The root is typical for this genus, but the smaller and higher teeth in the sample possess a very characteristic central sulcus unique among teeth referable to *Lonchidion*.

Remark

This tooth morphology has not previously been reported and may represent a new species.

Lonchidion sp. 3

Figure 5I–L

Material

Thirteen teeth, some fragmentary, represented by NHMUK PV P 73451 - P 73454.

Description

The teeth are up to 3 mm long, very gracile, and lack a central cusp. The crown is smooth and devoid of ornament. The labial process is either absent or only very weakly defined. The root is typical for the genus, with large foramina apically and a few, irregularly placed, smaller, circular foramina close to the crown–root junction.

Remark

It has been suggested that this morphotype may represent indeterminate worn, abraded or autodigested (e.g. Fig. 5L) lonchidiid teeth (C. Underwood, pers. comm.). However, no characteristic striations as a result of trituration are visible (as is commonly observed in teeth of *L. breve*), and all or part of the root is preserved in all specimens assigned to this morphotype. This strongly suggests that this morphotype is distinct and may therefore represent an additional new species. However, this assessment is tentative pending the recovery of additional material.

Genus VECTISELACHOS**Rees & Underwood, 2002**

V. ornatus (Woodward, 1889)

Figure 6A–D

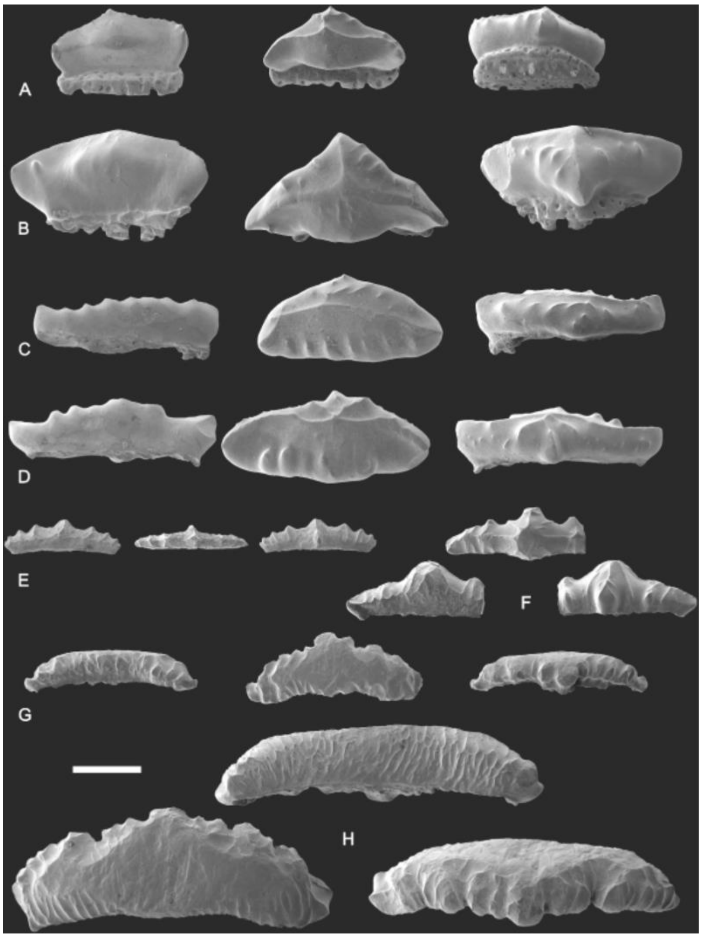


Figure 6: Scanning electron micrographs of chondrichthyan teeth from the Barremian Wessex Formation of the Isle of Wight. *Vectiselachos ornatus* (Woodward, 1889): NHMUK PV P 73457 anterior tooth (A) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73458 anterolateral tooth (B) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73459 lateral tooth (C) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73460 lateral tooth (D) in l. lingual, m. occlusal, and r. labial views. *Parvodus heterodon* (Patterson, 1966): NHMUK PV P 73462 anterior tooth (E) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73463 anterolateral tooth (F) in l. lingual, u. occlusal, and r. labial views; NHMUK PV P 73464 posterior tooth (G) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73465 posterior tooth (H) in r. lingual, u. occlusal, and r. labial views. Scale bar represents 1 mm.

Material

Two-hundred and eighty-four teeth, some fragmentary, represented by NHMUK PV P 73457 - P 73460.

Description

The teeth are up to 4 mm long. Anterior teeth are bulkier, with a well-demarcated central cusp and labial process. They are weakly ornamented, primarily with striations and rarely with granulae. Lateral teeth are lower, more heavily ornamented, and invariably bear granulae. The labial process in lateral teeth is poorly developed or absent. The root is apicobasally lower than the crown and at the crown–root junction it is not as wide as the crown. It bears large apical foramina and a few, irregularly placed, smaller circular foramina close to the crown–root junction.

Genus *PARVODUS*Rees & Underwood, 2002

Parvodus heterodon (Patterson, 1966)

Figure 6E–H

Material

Ten teeth, some fragmentary, represented by NHMUK PV P 73462 - P 73465.

Description

Teeth are up to 4 mm long. When unworn, the elongated crown possesses a strong occlusal crest. The moderate central cusp is flanked by up to three pairs of low lateral cusplets. The labial process is strong in anterior teeth but weaker in laterals. Lateral teeth have numerous strong, vertical ridges, the density of which is greater than that of anterior and posterior teeth.

Infraclass NEOSELACHII Compagno, 1977

Remarks

Other than teeth of *Palaeoscyllium* aff. *formosum*, previously isolated and described by Sweetman & Underwood (2006), only three teeth referable to neoselachians were recovered during this study, all from residue obtained from bed 38 at Yaverland. Of these, two (Fig. 7A, B) most closely resemble the teeth of *Protospinax* reported from the Bathonian of England (Underwood & Ward, 2004, plate 11–13). The other (Fig. 7C) falls within the range of morphological variation recorded by Underwood & Rees (2002) for teeth of *Belemnobatis variabilis* from the Berriasian Purbeck Limestone Group. Apart from *Protospinax*, which has now been recorded from Cretaceous strata (Guinot *et al.*, 2013), these taxa are usually encountered in deposits considerably older than the Wessex Formation and more specimens are required in order to draw firm conclusions with regard to their affinities. Specimens NHMUK PV P 73467. and NHMUK PV P 73468. (Fig. 7A, B) are therefore referred to *Protospinax* indet. sp. and NHMUK PV P 73469. (Fig. 7C) to *Belemnobatis* aff. *variabilis*.

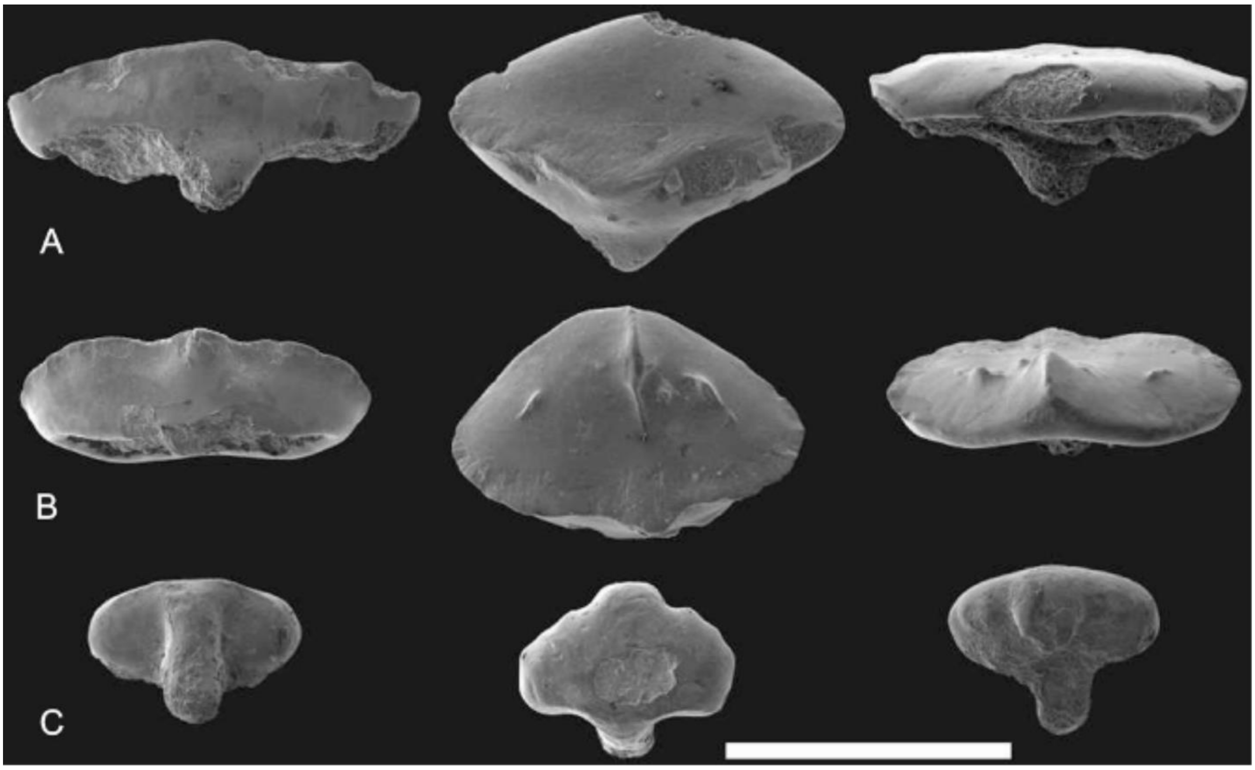


Figure 7: Scanning electron micrographs of neoselachian teeth from bed 38 of the Barremian Wessex Formation at Yaverland, Isle of Wight. *Protospinax* sp.: NHMUK PV P 73467 (A) in l. lingual, m. occlusal, and r. labial views; NHMUK PV P 73468 (B) in l. lingual, m. occlusal, and r. labial views. *Belemnobathis*aff. *variabilis*: NHMUK PV P 73469 (C) in l. lingual, m. occlusal, and r. labial views. Scale bar represents 1 mm.

Superorder HYPNOSQUALEA de Carvalho & Maisey, 1996

Family PROTOSPINACIDEA Woodward,1916–1919

Genus *PROTOSPINAX*Woodward, 1916–1919

Protospinax sp. indet.

Figure 7A, B

Material

Two teeth, NHMUK PV P 73467 and NHMUK PV P 73468.

Description

The teeth are respectively 1.3 mm (Fig. 7A) and 1.2 mm (Fig. 7B) long. The crown is flat and bears no cusps. That of NHMUK PV P 73467. (Fig. 7A) is devoid of ornamentation and bears a wear facet on the lingual side. NHMUK PV P 73468. (Fig. 7B) is ornamented with fine labio-lingually oriented ridges, which, mesially and distally, are confined to the centre of the crown. That at the midline of the crown extends to the labial side. In both specimens the labial process is very poorly defined. The median lingual uvula is relatively short and triangular.

Order RAJIFORMES Berg, 1940

Suborder RHINOBATOIDEI Fowler, 1941

Family incertae sedis

Belemnobatis aff. Variabilis

Figure 7C

Material

One tooth, NHMUK PV P 73469.

Description

The tooth is approximately 0.7 mm long. The crown is rounded, bears no cusps and is devoid of ornamentation. There is a weak and rounded labial process. The median lingual uvula is well developed and narrow.

Other chondrichthyan remains

Figures 8 and 9

Figure 8: Scanning electron micrographs of chondrichthyan cephalic and dorsal fin spines from the Barremian Wessex Formation of the Isle of Wight: NHMUK PV P 73470 a partial cephalic spine missing the apex and part of the basal area of attachment on the right side (A) in l. dorsal, u. Lateral, and r. ventral views; NHMUK PV P 73471 striated cephalic spine fragment (B) in l. anterior, m. lateral, and r. posterior views; NHMUK PV P 73472 unstriated cephalic spine fragment (C) possibly referable to the taxon represented by NHMUK PV P 73470 (Figure 8A); NHMUK PV P 73473 apical part of a dorsal fin spine (D) with blunt posterior denticles not extending to the apex in l. anterior, m. lateral, and r. posterior views; NHMUK PV P 73474 apical part of a dorsal fin spine (E) with basally elongated posterior denticles extending to the apex in l. anterior, m. lateral, and r. posterior views. Scale bar represents 1 mm.

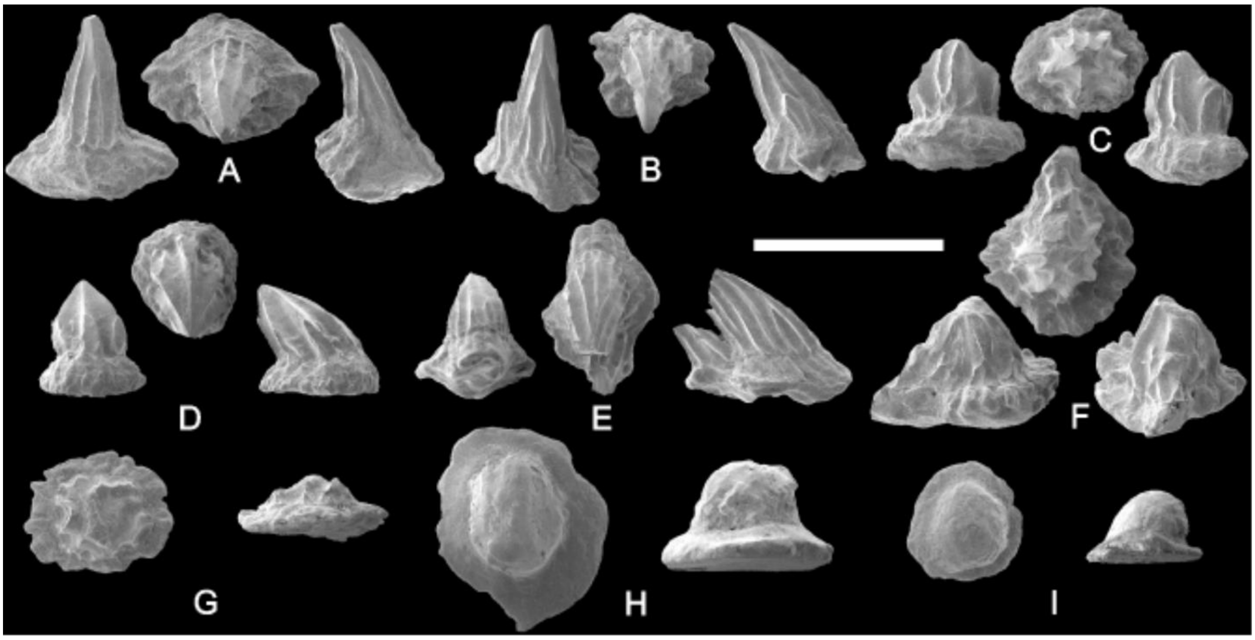


Figure 9: Scanning electron micrographs of chondrichthyan dermal denticles from the Barremian Wessex Formation of the Isle of Wight: NHMUK PV P 73475 (A) in l. anterior, r. apical, and r. lateral views; NHMUK PV P 73476 (B) in l. anterior, r. apical, and r. lateral views; NHMUK PV P 73477 (C) in l. anterior, r. apical, and r. lateral views; NHMUK PV P 73478 (D) in l. anterior, r. apical, and r. lateral views; NHMUK PV P 73479 (E) in l. anterior, r. apical, and r. lateral views; NHMUK PV P 73480 (F) in l. anterior, u. apical, and r. lateral views; NHMUK PV P 73481 (G) in l. apical, r. lateral, views; NHMUK PV P 73482 (H) in l. apical, and r. lateral views; NHMUK PV P 73483 (I) in l. apical and r. lateral views. Scale bar represents 1 mm.

Material

Fragmentary cephalic and dorsal fin spines represented by NHMUK PV P 73470 - P 73474 and dermal denticles represented by eight specimens of varying morphology, NHMUK PV P 73475 - P 73483.

Although teeth are the most readily identified chondrichthyan remains occurring in beds 38 and L9, other remains are also present. These include fragmentary cephalic (Fig. 8A–C) and dorsal fin (Fig. 8D, E) spines, and dermal denticles (Fig. 9). None of these remains can be identified with confidence to generic or specific levels.

Bony fishes

Systematic palaeontology

Class OSTEICHTHYES Huxley, 1880

Subclass ACTINOPTERYGII Klein, 1885

Order PYCNODONTIFORMES Berg, 1937

Family PYCNODONTIDAE Agassiz, 1833 [1833–1844]

A pycnodont fish was first reported from Wealden strata by Mantell (1827) who showed figures of two ‘palates’ from the Tilgate Forest but the figures were of insufficient quality for generic identification. The lack of symmetry of his figure 26 suggests a splenial dentition, and a slight decrease in the size of the teeth hints at it being the right splenial. Later, Agassiz (1833–1844) referred the specimens to *Pycnodus microdon* (Agassiz, 1833–1844; p.17) and later still (Agassiz, 1833–1844, p. 196, plate 72, figs 6–14) referred them to a new species of *Pycnodus*, *Pycnodus mantellii*. Agassiz's illustrations are much better than those of Mantell, and it is clear that the assemblage of material represents splenial and vomerine dentitions. It is also clear that more than one genus is represented just from the splenials. For example, the splenial of plate 72 (fig. 8) has smooth teeth with a medial row of ‘bean’-shaped teeth paralleled by oval teeth with their long axis orthogonal to that of the medial row. In contrast, the splenial of plate 72, (fig. 9) has rugose or tuberculate teeth and the medial row is bordered by oval teeth that are directed antero-laterally. It is not clear which of the figures of Agassiz is the type specimen, and thus *P*. *mantelli* requires serious reappraisal to determine its validity.

A little later still, but in the same volume, Agassiz (1833–1844, p.234) referred *P*. *mantellii* to the genus *Gyrodus*. His figure is similar to that of Mantell's (1827)figure 26, but the tooth crowns appear to be somewhat ornamented. Costa (1853) referred the species to the genus *Glossodus*, as *Glossodus mantelli*, but this genus was already used for an albuloid teleost. Therefore, in his review of Austrian fishes, Heckel (1856) referred *G*. *mantelli* to the pycnodont genus *Ceolodus*. Woodward (1896) briefly mentioned *Ceolodus mantelli*, but did not refigure it or challenge its referral to *Coelodus*.

Apart from listings by Woodward (1895) and a description of isolated dentitions referred to *Coelodus* sp. by Forey & Sweetman (2011) there have been no serious studies of Wealden Group pycnodonts. Furthermore, it seems that none has been reported previously from the Wessex Formation of the Isle of Wight.

Genus COELODUS *Heckel,* 1854

Coelodus sp.

Figure 10A–F, 13N–P (but see the remarks above and those below concerning isolated branchial teeth, Fig. 10I–K).

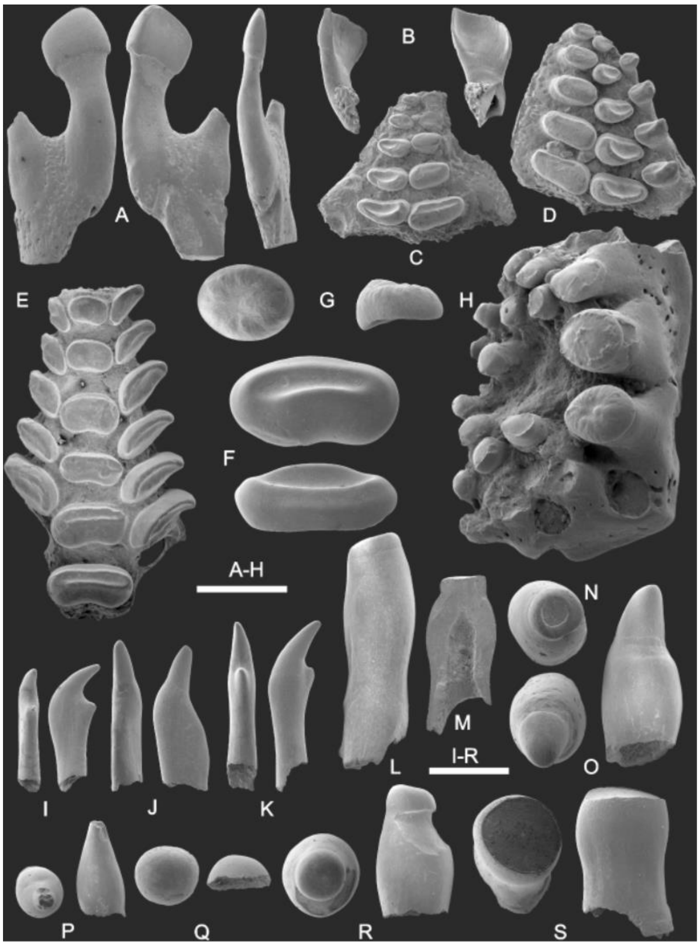


Figure 10: Scanning electron micrographs of osteichthyan remains from the Barremian Wessex Formation of the Isle of Wight. *Coelodus* sp.: NHMUK PV P 73485 a premaxillary or dentary tooth (A) in l. labial, m, lingual and r. anterior views; NHMUK PV P 73486 a premaxillary or dentary tooth (B) in l. oblique anterior and r. lingual views; NHMUK PV P 73487 a left splenial fragment (C) in occlusal view; NHMUK PV P 73488 a right splenial fragment (D) in occlusal view; NHMUK PV P 73489 a vomer fragment (E) in occlusal view; NHMUK PV P 73490 an isolated vomer or splenial tooth (F) in u. apical and lr. anterior or posterior views. Pycnodontiformes indet.: NHMUK PV P 73497 an isolated tooth (G) in l, apical and r. lateral views; NHMUK PV P 73498 a ?left splenial fragment (H) in oblique occlusal view. Neopterygii indet.: NHMUK PV P 73503 branchial tooth (I) in l. posterior and r. lateral views; NHMUK PV P 73504 a branchial tooth (J) in l. posterior and r. lateral views; NHMUK PV P 73505 a branchial tooth (K) in l. posterior and r. lateral views *?Scheenstia* sp.: NHMUK P. a premaxillary, maxillary, or dentary tooth (L) in lateral view; NHMUK P. a premaxillary, maxillary, or dentary tooth (M) in longitudinal cross-section; NHMUK P. a premaxillary, maxillary, or dentary tooth (N) in apical view; NHMUK P. a premaxillary, maxillary, or dentary tooth (O) in l. apical and r. lateral views; NHMUK P. a premaxillary, maxillary, or dentary tooth (P) in l. apical and r. lateral views; NHMUK P. a pterygo-palatine or vomer tooth (Q) in l. occlusal and r. lateral views; NHMUK P. a premaxillary, maxillary, or dentary tooth (R) in l. apical and r. lateral views; NHMUK P. a premaxillary, maxillary, or dentary tooth (S) in l. apical and r. lateral views. Scale bars represent 1 mm.

Material

Three-hundred and sixty-nine specimens, mostly comprising isolated teeth but also including fragmentary tooth-bearing bones. These are represented by NHMUK PV P 73485 - P 73493.

Description

The dentition comprises marginal cutting or nipping teeth on the premaxilla and dentary, the crowns often being borne on a stem or neck (Fig. 10A, B) and crushing teeth on three main tooth-bearing bones, the unpaired, medially located vomer in the upper jaw and the paired splenials on the inside of the lower jaw. Crushing teeth of the splenials and vomer are often bean-shaped and sometimes have a central depression (Fig. 10C–F).

Pycnodontiformes indet

Figure 10G, H (but see remarks concerning isolated branchial teeth, Fig. 10I–K, below).

Material

Fifty-five specimens, mostly comprising isolated teeth but also including very fragmentary splenial and/or vomer fragments. These are represented by NHMUK PV P 73497 and NHMUK PV P 73498, respectively.

Description

Teeth from the crushing dentition are generally small (≤ 1 mm maximum dimension) and can be readily distinguished from those of *Coelodus* by their consistent sub-oval outline and distinctive pustulate or wrinkled surface ornamentation. Most also bear a shallow, but distinct, central pit flanked laterally by a low acuminate or mediolaterally extended cuspule.

Remark

Similar teeth have also been recorded from the Barremian of Spain (Estes & Sanchíz, 1982).

Order LEPISOSTEIFORMES Hay, 1929

***Genus SCHEENSTIA*López-Arbarello & Sferco, 2011**

?*Scheenstia sp.*

Figure 10L–S, Figure 13A–M

(but see remarks concerning isolated branchial teeth, Fig. 10I–K, below).

Material

Eight-hundred and seven specimens comprising isolated teeth and scales represented by NHMUK PV P 73507 - P 73514 and NHMUK PV P 73515 - P 73527, respectively. Also NHMUK PV P 73528, an isolated tooth from bed L9 (not shown in a figure).

Description

As in pycnodontiforms, some lepisosteiforms, including *Scheenstia*, possess a nipping and crushing dentition. However, in the latter, all teeth are spherical or styliform and never leaf- or bean-shaped. Those occurring on the splenials, pterygo-palatines, and vomers are circular in occlusal outline, domed, and often bear a central, conical cusp when unworn. Teeth of the premaxilla, maxilla, and dentary are also circular in outline but usually of smaller diameter and generally taller than those occurring elsewhere in the dentition. Some crowns, particularly those of the premaxilla and anterior part of the dentary, are, as in pycnodontiforms, borne on a stem or a neck (e.g. Fig. 10L–R).

Remarks

No substantially complete specimens of large lepiosteiforms have been recovered from the Wealden Group of the Isle of Wight. However, partially articulated specimens, and isolated tooth-bearing and other skull bones in the collections of the Isle of Wight County Museum Service, closely resemble similar material from the Wealden Supergroup of mainland Britain attributed to *Scheenstia mantelli*, for which almost complete specimens are known. In view of this, the Isle of Wight material has been placed with this taxon in the past (e.g. Radley, 1994: 202; Forey & Sweetman, 2011, both as *Lepidotes mantelli*). Specimens in private collections, including an almost complete, but small and as-yet-undetermined lepisosteiform (or ?semionotiform), suggest that other lepisosteiform genera may be present the Wealden Group (S. C. Sweetman pers. observ.). Referral of all fragmentary material to *Scheenstia*, and in particular to *S. mantelli*, should therefore be considered with caution as most of it lacks characters sufficient to diagnose it to genus and species.

Lepisosteiforms, semionotiforms, and pycnodontiforms have highly similar claw- and hook-shaped branchial teeth and these are abundant in residues from the plant debris beds (e.g. that comprising NHMUK PV P 73572, which includes a large collection of such teeth from bed 38). As noted by Kriwet (2005: 174), if *Scheenstia* (*Lepidotes* in his account) and pycnodonts co-occur, as they do in the plant debris beds of the Wessex Formation, it is only possible to attribute isolated branchial teeth to Neopterygii indet.

Order AMIIFORMES Hay, 1930

Family CATURIDAE Owen, 1860

Genus *CATURUS*Agassiz, 1834 [1833–1834]

Caturus sp.

Figure 11A–E

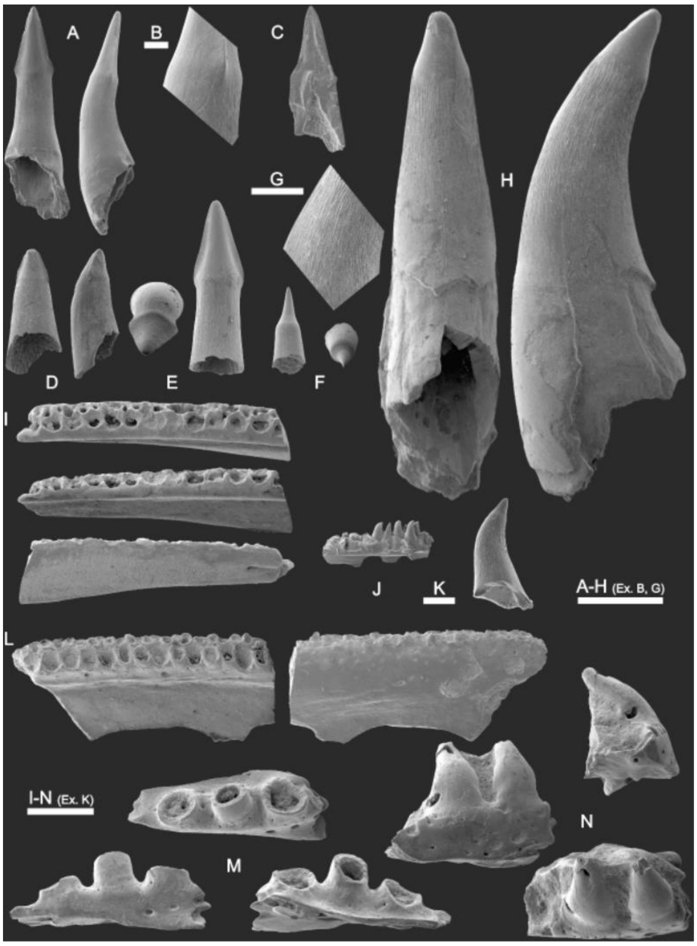


Figure 11: Scanning electron micrographs of osteichthyan remains from the Barremian Wessex Formation of the Isle of Wight. *Caturus* sp.: NHMUK PV P 73531 an isolated tooth (A) in l. lingual and r. mesial or distal views, detail of ornamentation at the base of the crown (B); NHMUK PV P 73532 an isolated tooth in cross-section (C); NHMUK PV P 73533 an isolated tooth (D) in l. lingual and r. mesial or distal views; NHMUK PV P 73534 an isolated tooth (E) in l. oblique apical and r. lingual views. *Belonostomus* sp.: NHMUK PV P 73540 an isolated tooth (F) in l. lingual and r. oblique apical views; NHMUK PV P 73541 an isolated tooth (G, H), detail of ornamentation at the base of the crown (G), l. lingual and r. mesial or distal views (H). NHMUK PV P 73543 an indeterminate jaw fragment (I) in u. occlusal, m. lingual, and lr. labial views. NHMUK PV P 73544 an indeterminate jaw fragment (J), orientation uncertain and enlargement of a tooth detached from it (K). NHMUK PV P 73545 an indeterminate jaw fragment (L) in l. oblique occlusal and r. labial views. NHMUK PV P 73546 an ?amiid jaw fragment (M) in l. labial, u. occlusal, and r. lingual views. NHMUK PV P 73547 an indeterminate ?amiid jaw fragment (N) in l. labial, u. mesial or distal and lr. occlusal views. Scale bars represent 1 mm, except: B, 100 µm; E, 500 µm; and K, 100 µm.

Material

Three-hundred and sixty-one isolated teeth (some broken) represented by NHMUK PV P 73531 - P 73534.

Description

Most teeth of this genus have a long basal neck ornamented with longitudinal striations that disappear at the base of very distinctive spearhead- or arrowhead-shaped crowns. However, the length of the neck and crown morphology are variable, depending upon the position in the dental arcade, and it is possible that some of the teeth referred here to *Caturus* may pertain to other amiiforms for which diagnostic material are currently unavailable (see discussion below).

Order ASPIDORHYNCHIFORMES Berg, 1937

Family ASPIDORHYNCHIDAE Nicholson & Lydekker, 1889

Genus *BELONOSTOMUS*Agassiz, 1834 [1833–1834]

Belonostomus sp.

Figure 11F–H

Material

Thirty-two isolated teeth represented by NHMUK PV P 73540 - P 73541.

Description

Teeth assigned to this species can be of very different sizes. The largest teeth are located on the premaxilla, palatine, and presymphysial bones, whereas the supramaxilla bears smaller teeth. They are ornamented with longitudinal striations along the shaft that unite basally. These ridges ascend the neck to the base of the apex of the crown, which comprises a light-coloured acrodin cap.

Other osteichthyan remains

Figures 11I–N, 12 and 13

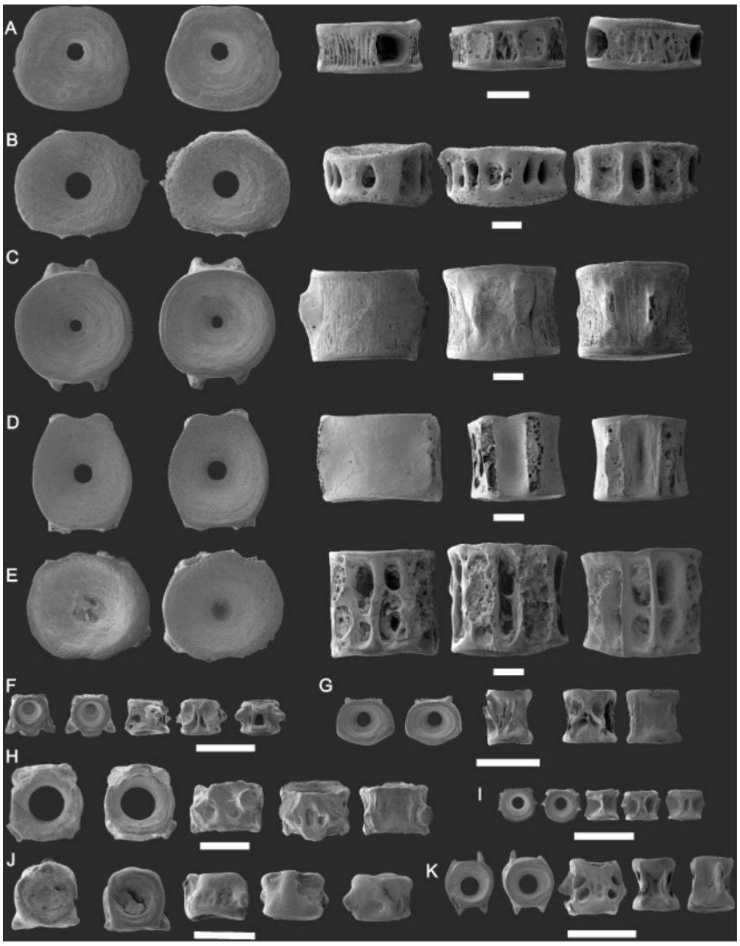


Figure 12: Currently undetermined osteichthyan vertebrae from the Barremian Wessex Formation of the Isle of Wight. Orientation of specimens is uncertain: NHMUK PV P 73548 (A); NHMUK PV P 73549 (B); NHMUK PV P 73550 (C); NHMUK PV P 73551 (D); NHMUK PV P 73552 (E); NHMUK PV P 73553 (F); NHMUK PV P 73554 (G); NHMUK PV P 73555 (H); NHMUK PV P 73556 (I); NHMUK PV P 73557 (J); NHMUK PV P 73558 (K). Scale bars represent 1 mm.

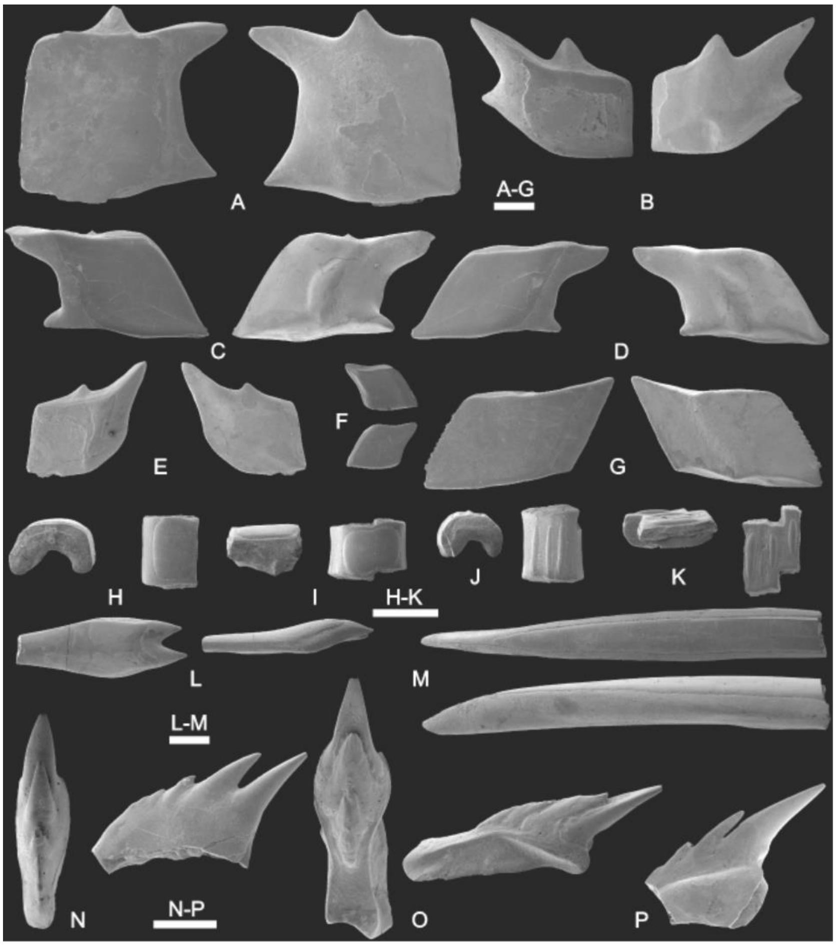
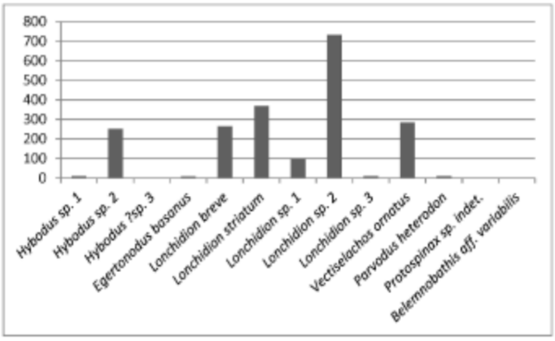


Figure 13: Osteichthyan scales from the Barremian Wessex Formation of the Isle of Wight. *Scheenstia* sp. (A–M). A–G excluding F, l. external and r. internal views. F, u. external and lr. internal views. Lateral scales: NHMUK PV P 73515 (A); NHMUK PV P 73516 (B); NHMUK PV P 73517 (C); NHMUK PV P 73518 (D); NHMUK PV P 73519 (E); NHMUK PV P 73520 (F); NHMUK PV P 73521 (G); NHMUK PV P 73522 (H). Fin scales: I–K, l. cross-section and r. external views. NHMUK PV P 73523 (I); NHMUK PV P 73524 (J); NHMUK PV P 73525 (K); NHMUK PV P 73526 (L) position uncertain., l. external and r. lateral views; NHMUK PV P 73527 (M) position uncertain, u. external and lr. lateral views. *Coelodus* sp.: NHMUK PV P 73491 (N) dorsal or ventral median scale in l. dorsal or ventral and r. lateral views; NHMUK PV P 73492 (O) dorsal or ventral median scale in l. dorsal or ventral and r. lateral views; NHMUK PV P 73493 (P) dorsal or ventral median scale in lateral view. Scale bars represent 1 mm.

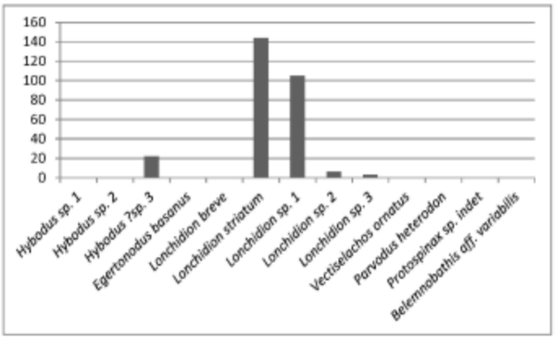
Hybodus sp. 1	11	0.54 %
Hybodus sp. 2	251	12.30%
Hybodus sp. 3	0	—
Egertonodus basanus	7	0.34 %
Lonchidion breve	264	12.93%
Lonchidion striatum	369	18.08%
Lonchidion sp. 1	99	4.85 %
Lonchidion sp. 2	732	35.86%
Lonchidion sp. 3	10	0.49 %
Vectiselachos ornatus	284	13.91%
Parvodus heterodon	10	0.49 %
Protospinax sp. indet.	1	—
Belemnobathis aff. *variabilis*	2	—

A 38



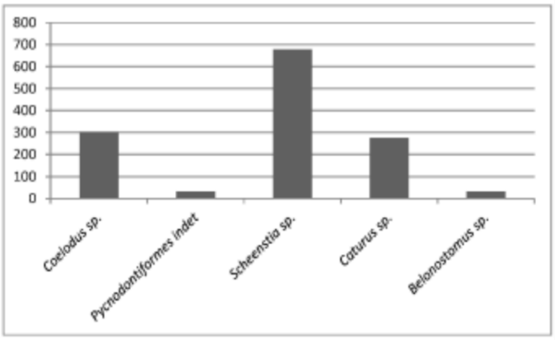
Hybodus sp. 1	0	—
Hybodus sp. 2	0	—
Hybodus sp. 3	22	7.86 %
Egertonodus basanus	0	—
Lonchidion breve	0	—
Lonchidion striatum	144	51.43%
Lonchidion sp. 1	105	37.50%
Lonchidion sp. 2	6	2.14 %
Lonchidion sp. 3	3	1.07 %
Vectiselachos ornatus	0	—
Parvodus heterodon	0	—
Protospinax sp. indet.	0	—
Belemnobathis aff. *variabilis*	0	—

B L9



Coelodus sp.	303	22.94%
Pycnodontiformes indet.	33	2.50 %
Scheenstia sp.	677	51.25%
Caturus sp.	189	20.89%
Belonostomus sp.	32	2.42 %

C 38



Coelodus sp.	66	16.92%
Pycnodontiformes indet.	22	5.64 %
Scheenstia sp.	130	33.33%
Caturus sp.	172	44.10%
Belonostomus sp.	0	—

D L9

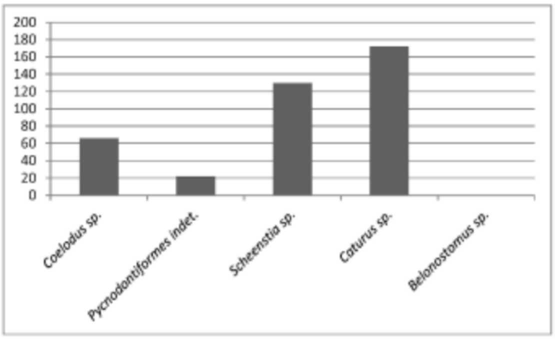


Figure 14: A list of chondrichthyan taxa recovered from bed 38 of the Barremian Wessex Formation exposed at Yaverland on the south-east coast of the Isle of Wight showing the number of specimens for each taxon, the percentage of the total represented by each, and a bar graph providing a graphical representation of the relative abundance of specimens for each taxon (A). A list of chondrichthyan taxa recovered from bed L9 of the Barremian Wessex Formation exposed north-west of Grange Chine on the south-west coast of the Isle of Wight showing the number of specimens for each taxon, the percentage of the total represented by each, and a bar graph providing a graphical representation of the relative abundance of specimens for each taxon (B). A list of osteichthyan taxa recovered from bed 38 of the Barremian Wessex Formation exposed at Yaverland on the south-east coast of the Isle of Wight showing the number of specimens for each taxon, the percentage of the total represented by each, and a bar graph providing a graphical representation of the relative abundance of specimens for each taxon (C). A list of osteichthyan taxa recovered from bed L9 of the Barremian Wessex Formation exposed north-west of Grange Chine on the south-west coast of the Isle of Wight showing the number of specimens for each taxon, the percentage of the total represented by each, and a bar graph providing a graphical representation of the relative abundance of specimens for each taxon (D). Note. Broken teeth were counted, each part being counted separately. This may have resulted in an over-count of taxa with teeth susceptible to postmortem breakage.

Material

Abundant bones, including vertebrae and scales, the majority of which are fragmentary. These are represented here by NHMUK PV P 73473 & P 73474, NHMUK PV P 73548 - P 73558, and NHMUK PV P 73559 - P 73571 and P 73491 - P 73493.

Isolated bones, including vertebrae, and scales are common among microvertebrate remains recovered from the Wessex Formation, but this material awaits further study. Representative jaw fragments are shown in Figure 11I–N, vertebrae in Figure 12 and scales in Figure 13.

Discussion and Conclusions

Based on tooth morphology, five species of hybodontoid shark have been identified, *E. basanus*, *L. breve*, *L. striatum*, *P. heterodon*, and *V. ornatus*. The assemblages also appear to contain two, or possibly three, species belonging to the genus *Hybodus* and at least two, or possibly three, additional species belonging to the genus *Lonchidion*, but determination of these is beyond the scope of this study. Three teeth attributable to neoselachian sharks assigned to the families Protospinacidae Woodward, 1916–1919 and Rhinobatidae Müller & Henle, 1838–1841 have also been identified. Osteichthyans are represented by four genera, *Coelodus*, ?*Scheenstia*, *Caturus*, and *Belonostomus* belonging to the orders Pycnodontiformes, Lepisosteiformes, Amiiformes, and Aspidorhynchiformes, respectively. However, it is possible that some of the isolated teeth and partial dentitions referred here to *Coelodus* sp. may, in fact, represent one or more additional pycnodontiform genera with similar dentitions. Unfortunately, the fragmentary material currently available precludes further analysis. Furthermore, some of the amiiform teeth recovered from both beds (e.g. Fig. 8D) are similar to those described for other amiiform fishes, including those of the genus *Ionoscopus*Costa, 1853. Again, more substantial remains are required in order to draw firm conclusions.

Bed 38 contains a molluscan assemblage, dominated by unionid bivalves with rarer viviparid and very rare physid gastropods. This assemblage is considered to represent 'the best-developed freshwater equilibrium fauna in the non-marine Lower Cretaceous of the Weald-Wessex basin' (Radley & Barker, 2000). In addition, the presence of an abundant and diverse lissamphibian fauna strongly supports the conclusion that the floodwaters and resulting debris flow leading to deposition of bed 38 only sampled terrestrial and freshwater environments (Sweetman & Insole, 2010). Molluscs are uncommon in bed L9 but unionid bivalves have been recorded (S. C. Sweetman, pers. observ.) and it also contains abundant and diverse lissamphibian remains. This suggests that this bed also contains only organisms inhabiting terrestrial and freshwater environments. However, random sampling of these environments by the floodwaters responsible for deposition of each bed has inevitably led to differences in their palaeontological content. This renders any attempt to define the freshwater environments (e.g. lakes, streams, or rivers) inhabited by individual fish taxa and groups of taxa somewhat problematic. However, the model proposed by Sweetman

& Insole (2010) for the generation of the plant debris beds suggests minimal time averaging for taxa contained in each bed. The assemblages described here therefore represent what these authors call a 'snapshot' of the fish assemblages present in the area sampled by flood events occurring immediately before deposition of each. In view of this, some conclusions with regard to palaeoecology can be drawn.

Direct evidence of diet, such as preserved gut contents, is extremely rare in the fossil record and unknown for non-marine chondrichthyans. For these, diet has to be inferred from dental morphology. The bed 38 and bed L9 chondrichthyan assemblages represent taxa adapted to the exploitation of a diverse range of trophic resources. High-crowned species, such as *E. basanus* and *H. parvidens*, and, to a lesser extent, *H. brevicostatus*, have a typical cutting and tearing dentition, suggesting that they may have preyed primarily on small bony fishes (Underwood & Rees, 2002). The neoselachian *Palaeoscyllium* aff. *formosum* also has teeth of similar morphology (Sweetman & Underwood, 2006, Text-fig. 3, p. 461), suggesting a similar diet but their very small size perhaps precludes this, and the high-cusped teeth of this taxon may have been used to secure slippery wriggling prey, such as annelids. Within the Lonchidiidae, the more low-crowned tooth morphology of *Lonchidion* and *Parvodus* reflects cutting and crushing of prey items for these genera, whereas the bulkier, lower-crowned tooth morphology of *Vectiselachos* suggests a more exclusively crushing feeding strategy adapted to exploitation of molluscs, crustaceans (although with the possible exception of burrows evidence for them is scant), and small bony fishes (Underwood & Rees, 2002), the remains of which are abundant in both bed 38 and bed L9. Despite the fact that each species undoubtedly had a different number of teeth in its dentition and probably replaced them at different rates, the high proportion of low-crowned lonchidiid teeth compared with high-crowned teeth (Fig. 14) suggests a greater abundance and diversity of small, relatively immobile, and possibly hard-shelled food items in Wessex Formation aquatic palaeoenvironments.

Within the bony fish assemblages, a similar diversity of feeding strategies is suggested by tooth morphology. Both *Coelodus* and *Scheenstia* have a well-developed crushing dentition, with *Coelodus* also possessing marginal cutting or nipping teeth. Both may have fed, at least in part in the case of *Coelodus*, which may have been omnivorous, on shelly molluscs, thus sharing the same ecological niche as lonchidiid hybodonts but generally utilizing larger prey items. Unpublished studies indicate that quantitative microtextural analysis of tooth surfaces in these taxa may shed further light on their feeding strategies. The typical spearhead-shaped tooth crown morphology of *Caturus* indicates that it was a predatory fish. The needle-shaped teeth of *Belonostomus* located on an elongated rostrum (see Woodward, 1916–1919) indicate equally that it was a predatory fish but probably exploiting trophic resources different to those of *Caturus*.

During early Mesozoic times, hybodonts lived in marine environments and were the principal representative of chondrichthyan faunas. When the diversity of actinopterygians and neoselachians increased from the Middle Jurassic onwards, their diversity declined in parallel, until, by the Early Cretaceous, they represented only a minor component of marine assemblages. However, by that time hybodont lineages were flourishing in non-marine environments where neoselachians were largely absent. A freshwater shark assemblage, very similar to that of the Wessex Formation, has been reported from bone beds of the Wealden Supergroup of mainland Britain by Patterson (1966). He also listed a number of taxa as occurring in Lower Cretaceous deposits on the Isle of Wight. However, these records appear to relate to the Vectis Formation, either directly or as being derived from it in the overlying marine Atherfield Clay. Underwood & Rees (2002), reported a similar freshwater assemblage from the earliest Cretaceous Purbeck Group of Dorset. They sampled different horizons within the Lulworth and Durlston formations and identified six species representing four genera, *Hybodus*, *Egertonodus*, *Lonchidion*, and *Polyacrodus* (the latter now considered to be a nomen dubium with the species *P. parvidens* and *P. brevicostatus* referred to *Hybodus*). In addition, these samples yielded many rhinobatoid ray teeth, always associated with mollusc remains and interpreted as being indicative of more saline intervals. The unusual association of hybodonts and batoids in the near or complete absence of other neoselachian sharks is known from the Jurassic of Germany (Duffin & Thies, 1997) and the Cretaceous of Brazil (e.g. Martill, 1993) and Texas (Thurmond, 1971). Thus, the recovery of protospinacid and rhinobatid teeth from bed 38 further supports the conclusion of Underwood & Rees (2002) that some rays may have been able to tolerate lower salinities (freshwater in the case of those occurring in bed 38) than almost all other neoselachians. A further notable example of a neoselachian capable of tolerating freshwater conditions is *Palaeoscyllium* aff. *formosum* (Sweetman & Underwood, 2006), which co-occurs in bed 38 with the protospinacid and rhinobatid reported here.

The Lower Cretaceous of the Basque-Cantabrian Basin in the north of Spain has recently yielded a fish fauna similar to that presented in this study (Bermúdez-Rochas, 2009). There, six hybodontoid genera have been recorded from the freshwater Vega de Pas Formation: *Hybodus*, *Egertonodus*, *Planohybodus*, *Lonchidion*, *Parvodus*, and *Lissodus*. Actinopterygian remains have also been recovered and assigned to three orders: Pycnodontiformes, Semionitiformes (now Lepisosteiformes, see López-Arbarello & Sferco, 2011), and Ammiiformes. This fish assemblage appears to resemble more closely that of the English Wealden than assemblages from other sites of similar age in Europe (e.g. Belgium and Germany). It appears likely that the capability of hybodonts to colonize and exploit freshwater environments allowed them to evade competition from the majority of neoselachians adapted to the marine realm and unable to spend even short periods of time in waters of reduced salinity.

Isolation of specimens, scanning electron microscopy, and identification of specimens described here was undertaken during a 3-month internship by the second author. Time for a preliminary assessment of fish assemblages from the Wessex Formation was therefore limited and large quantities of unsorted fish material obtained from the remainder of plant debris beds sampled by the first author awaits study.

However, with one exception, cursory examination of this indicates that fish assemblages occurring in these beds are similar to those recorded from beds 38 and L9. The exception is the occurrence of neoselachians in bed 38. Neoselachian remains have not been recorded from any other horizon and are very uncommon in bed 38. The river system occupying the Wessex Sub-basin floodplain flowed from west to east (Stewart, 1978; Allen, 1998) and bed 38 occurs at the eastern-most exposure of and in the uppermost part of the Wessex Formation, immediately below the overlying lagoonal Vectis Formation (+ Fig. 2). It seems possible therefore that neoselachians entering the Wessex Formation river system were euryhaline (Sweetman & Underwood, 2006) and that those present in bed 38 may represent taxa more commonly residing in waters of higher salinity. Such waters may have been present only a short distance to the east at the time of deposition of this bed, but further to the east lower in the succession. Comparison of assemblages from the remainder of the succession may shed further light on this and on faunal and palaeoenvironmental diversity during the time of deposition of the Wessex Formation, as exposed on the Isle of Wight.

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