J.N.C.C.

Fossil Fishes of Great Britain

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Chapter 12

British Jurassic fossil fishes sites

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INTRODUCTION: PALAEOGEOGRAPHY AND STRATIGRAPHY

In Britain, rocks of Jurassic age occur in a long, almost continuous outcrop running from Dorset to Yorkshire, and in scattered patches in the islands off north-west Scotland, and in north-east Scotland (Figure 12.1). Following the onset of North Atlantic rifting and the fragmentation of the Late Palaeozoic supercontinent 'Pangaea' in the late Triassic and early Jurassic (Pitman and Talwani, 1972), marine conditions spread over much of the low-lying marginal alluvial plains during the Rhaetian transgression (latest Triassic). By the early Jurassic, a marine trans-

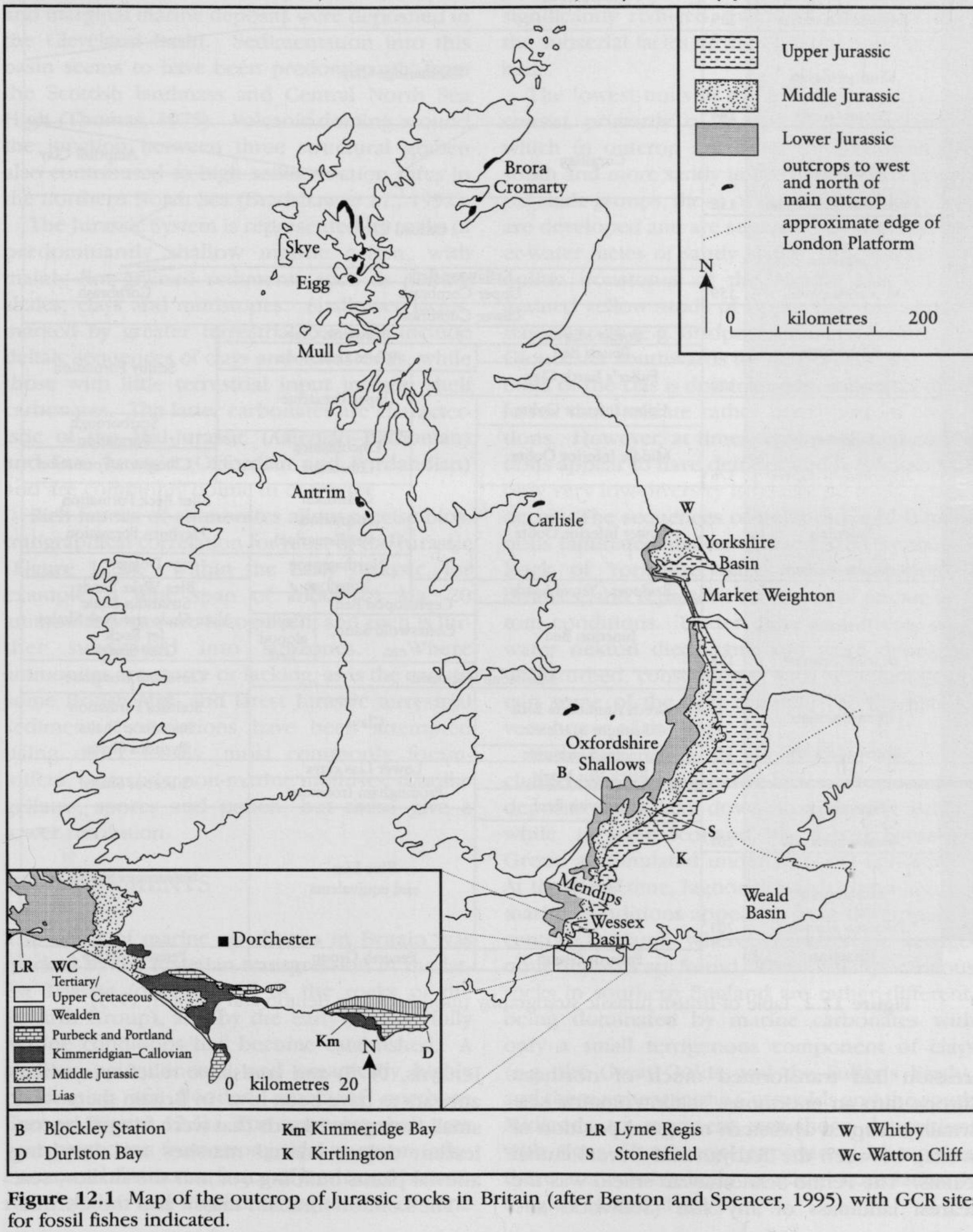


Figure 12.1 Map of the outcrop of Jurassic rocks in Britain (after Benton and Spencer, 1995) with GCR sites for fossil fishes indicated.

	Chronostratigraphy	Ma	Dorset	Midlands	Lincolnshire and Yorkshire
	Berriasian *Berriasella grandis*	135	Purbeck Beds		? Spilsby Sandstone ? ? Speeton Clay ?
Jurassic	**Portlandian** *Progalbanites albani*	139	Portland Beds	?	?
	Kimmeridgian *Pictonia baylei*	144	Kimmeridge Clay	Kimmeridge Clay	Kimmeridge Clay
	Oxfordian *Quenstedtoceras mariae*	152	Corallian		Ampthill Clay
	Callovian *M. macrocephalus*	159	Oxford Clay Kellaways Beds Upper Cornbrash	Oxford Clay Kellaways Beds Upper Cornbrash	Oxford Clay Kellaways Beds Cornbrash
	Bathonian *Zigzagiceras zigzag*	170	Lower Cornbrash Forest Marble *Boueti* Bed Fuller's Earth Clay	Lower Cornbrash Blisworth Clay White Limestone Upper Estuarine	Scalby Formation
	Bajocian *Hyperlioceras discites*	176	Upper Inferior Oolite Middle Inferior Oolite	Lincolnshire Limestone	Scarborough Formation Cloughton Formation
	Aalenian *Leioceras opalinum*	180	Lower Inferior Oolite	Grantham Formation (Lower Estuarine) Northampton Ironstone	Eller Beck Formation Hayburn Formation Dogger
	Toarcian *D. tenuicostatum*	188	Bridport / Yeovil Sands Junction Bed	Cephalopod Bed Cotteswold Sand, etc. Ceph-alopod Bed	Blea Wyke Sands Striatulus Shale Alum Shale and Peak Shales Jet Rock Grey Shales
	Pliensbachian *Uptonia jamesoni*	195	Marlstone Rock Bed Green Ammonite Beds Belemnite Marls etc. Armatus Limestone	Marlstone Rock Bed Clays	Cleveland Ironstone Staithes Formation Ironstone Shales Pyritous Shales
	Sinemurian *Arietites bucklandi*	201	Black Ven Marls Shales with Beef	Lower Lias clays Frodingham Ironstone	Siliceous Shales
	Hettangian *Psiloceras planorbis*	205	Blue Lias	Blue Lias and equivalents	Calcareous Shales
	Rhaetian		Penarth Group	Penarth Group	Penarth Group

Figure 12.2 Table of British Jurassic stratigraphy (modified from Benton and Spencer, 1995).

gression had transformed much of northern Europe into an enormous, shallow epeiric sea. Britain occupied a western marginal position of overlap between the Tethyan and Boreal faunal realms. The Fenno-Scandinavian shield was the nearest landmass of any size (Sellwood and Jenkyns, 1975) and landscape relief everywhere appears to have been low. In Britain there were small emergent islands that were fringed by coalescent deltas, coastal marshes and low-lying alluvial plains building out into the shallow sea.

The London–Brabant massif and the Cornubian island formed the major landmasses in the south of England; to the south lay the open sea of the Weald, Channel and Paris basins (Mégnien and Mégnien, 1980). Between the Welsh, Pennine and London–Brabant landmasses the fairly shallow-water marginal-marine conditions of the Midland or Cotswold–Weald Shelf prevailed. To the north of the London–Brabant land, alluvial and marginal marine deposits were deposited in the Cleveland Basin. Sedimentation into this basin seems to have been predominantly from the Scottish landmass and Central North Sea High (Thomas, 1975). Volcanic doming around the junction between three structural graben also contributed to high sedimentation rates in the northern North Sea (Bradshaw *et al.*, 1992).

The Jurassic System is represented by rocks of predominantly shallow marine origin, with mainly fine-grained sediments such as marine shales, clays and mudstones. Shallower facies, marked by greater terrestrial content, include deltaic sequences of clays and sandstones, while those with little terrestrial input include shelf carbonates. The latter carbonates are characteristic of the Mid-Jurassic (Aalenian–Bathonian) and Late Jurassic (Oxfordian and Portlandian) and are commonly oolitic in character.

Rich faunas of ammonites allow precise biostratigraphical correlation for most of the Jurassic (Figure 12.2). Within the Early Jurassic, for example, a time span of about 25 Ma, 20 ammonite zones are recognized, and each is further subdivided into subzones. Where ammonites are scarce or lacking, as is the case in some British Mid- and latest Jurassic terrestrial sediments, correlations have been attempted using other fossils, most commonly foraminifera, ostracods, non-marine molluscs, dinoflagellates, spores and pollen, but these give a lower resolution.

ENVIRONMENTS

The onset of marine conditions in Britain was marked by the Rhaetian transgression in the latest Triassic (documented in the rocks of the Penarth Group), and by the Early Jurassic fully marine conditions had become established. A shallow, epicontinental and organically highly productive sea flooded much of northern Europe (Figure 12.3). The extensive shelf area gave protection from strong tidal or storm influences, and distinctive facies of laminated bituminous shales and rhythmic sequences of lime mud and marl accumulated. Over shallow regions (swells), oolitic ironstones and condensed cephalopod limestones developed in the relative absence of terrigenous input.

Marine conditions continued through much of Jurassic time with major regressive intervals, during the Middle Jurassic and at the close of the Jurassic, when the area of epeiric seas became significantly reduced, eventually giving way to the subaerial facies of the Portland and Purbeck beds.

The lowest units of the British Jurassic (Lias) consist primarily of marine clay–shale facies, which in outcrop are more calcareous in the south and more sandy in the north. Two principal shale groups, those of the early and later Lias are developed and are separated by the shallower-water facies of sandy shales, sandstones and oolitic ironstones of the Middle Lias. Fine-grained yellow sands of Upper Lias and earliest Bajocian age (e.g. Bridport sands) crop out from Gloucester southwards to the Dorset coast. The biota of the Lias is dominated by marine benthic forms that indicate rather harsh bottom conditions. However, at times, environmental conditions appear to have deteriorated further so that only very low-diversity invertebrate fossil faunas occur. The sequences of unbioturbated bituminous laminated shales, characterized by the Jet Rock of Yorkshire, lack even protobranch bivalves, and represent the onset of anoxic bottom conditions. Under these conditions, mid-water nekton died, sank and were deposited undisturbed; consequently such sequences contain some of the best examples of the marine vertebrates of the time.

Bathonian times in the Mid-Jurassic were characterized by regressive facies. Fluvio-deltaic deposits were laid down in southern Britain while, in west Scotland, the Great Estuarine Group accumulated under lagoonal conditions. At the same time, lagoonal-marsh and marginal-marine conditions appear to have developed in central England, where characteristic terrigenous deposits are found. The contemporaneous rocks in southern England are rather different, being dominated by marine carbonates with only a small terrigenous component of clays (e.g. the Great Oolite and the Fuller's Earth), and these appear in the Cotswolds and the south Midlands to represent nearshore deposition, with signs of subaerial exposure. Ammonites there are consequently rare and correlation is difficult (Arkell, 1931).

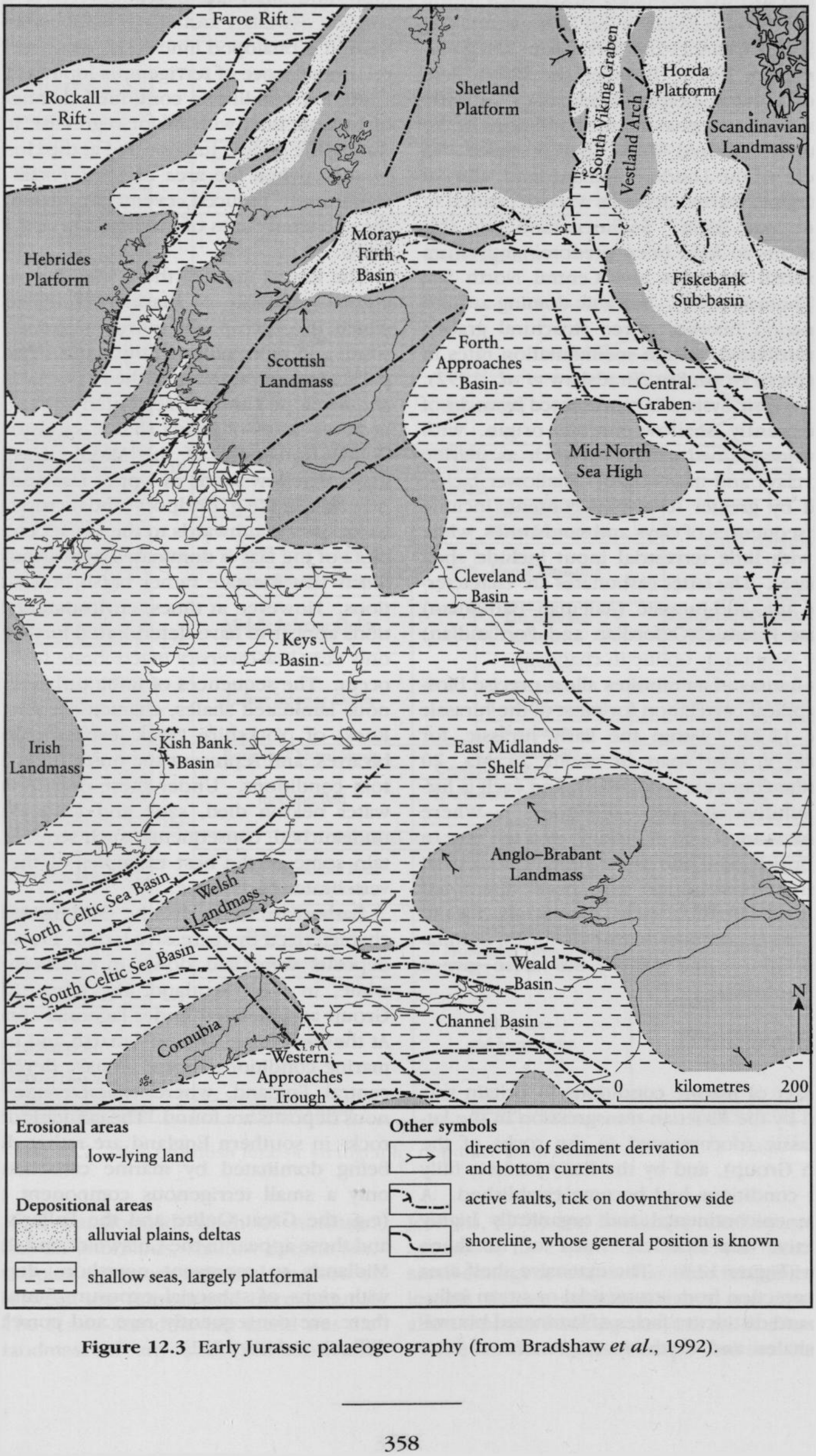


Figure 12.3 Early Jurassic palaeogeography (from Bradshaw *et al.*, 1992).

The succeeding rocks demonstrate a resumption of marine clastic sedimentation following commencement of the second major transgressive phase during the Callovian. The facies are predominantly monotonous, laterally extensive, dark bituminous clays which, in essence, mark a return to restricted muddy marine environments like those of the Early Jurassic (Duff, 1975). In southern Britain, these beds are represented by the Lower Oxford Clay. The deeper-water Kimmeridge Clay (clays, mudstones and shales) is comparable, being rich in preserved organic material (including kerogen) and containing a restricted marine benthos.

The Portland Group shows evidence of shallowing and renewed regression, and preserves a range of facies. The Cherty Beds are rich in sponge spicules and seem to have been deposited in calm deep marine water. The upper parts of the succession include oolites, micrites, and eventually evaporites (represented by halite and anhydrite) and soils, which document the progress of the regression. Marine incursions, including the Cinder Bed 'event', occur in the mid- to late Purbeck beds, which are otherwise predominantly non-marine and which span the Jurassic–Cretaceous boundary.

FISH FAUNAS

The trends in evolution set in the Triassic period were continued in the Jurassic. The most conspicuous feature of the fish assemblages is the dominance of more advanced actinopterygians, a grade of evolution to which only the gar-pikes and *Amia* (the bowfin) belong today. Chondrosteans (today's sturgeons, paddlefishes etc.) were then in decline; the coelacanths and the lungfishes, too, are both universally rare as Jurassic fossils, although some remains have been found in the British Jurassic succession. Meanwhile, the two great groups of Chondrichthyes, the Elasmobranchii and the Holocephali, are relatively common in marine strata.

A few palaeoniscoid-grade actinopterygians of relatively conservative structure lingered well into the Jurassic period. Actinopterygian evolution during this time is marked by progressive changes in the jaws and hyoid apparatus to increase the size and speed of opening of the oropharyngeal chamber. In the axial skeleton the vertebral centra became ossified and the scales became thinner and lighter, both tendencies assisting speedier swimming.

Many Jurassic neopterygians have rather deep bodies and superficially symmetrical tails; nearly all were active predators. Others developed an elongate shape. Most, though not all, were less than 1 m in length.

Mesozoic chondrichthyans show a diminished diversity of shape and structure compared with those of the Late Palaeozoic. Nevertheless the number of genera rose from seven or so in the Triassic to 41 in the Jurassic (McCune and Schaeffer, 1986). Few of the older conservative types survived. The neoselachians became the dominant forms with new developments in jaw kinetics and tooth shape. The cladodont teeth and jaws of the Palaeozoic elasmobranchs, designed for snatching and gulping, were replaced by mechanisms for cutting and gouging. As a result, prey size was no longer so critical. The anterior teeth were used to seize prey, the posterior to crush it. Fin spines were no longer so widely adopted, but claspers were retained. Hybodont sharks were common forms with simple cuspate teeth, two dorsal fin spines and claspers in the males. The ctenacanth group began a new but final radiation in the Early Jurassic and may have given rise to all modern sharks, skates and rays. The skates and rays make their appearance in the Middle Jurassic, while the Holocephali – the ratfishes and chimaeras – are well represented in the Jurassic by groups that resemble modern forms.

The Jurassic was thus a time when the extensive epeiric seas became populated by an increasingly diverse fauna of fishes. The first of the teleosts (higher bony fishes) were already present, but the 'Holostei' were declining.

Most fossil fishes obtained from the Jurassic of Britain are marine, but these are supplemented by important non-marine forms and the freshwater aquatic amphibians collected from the subaerial facies of the Middle Jurassic (e.g. Forest Marble, Stonesfield Slate). The most spectacular fish remains, and important collections, have come from the Early and Late Lias (Hettangian–Sinemurian), the Oxford Clay (Callovian) and the Kimmeridge Clay (Kimmeridgian). These fossils are commonly complete, or nearly complete, articulated skeletons, the result of undisturbed stagnant bottom waters unique to the northern European Jurassic shelf sea. The fish fauna from the Oxford Clay (Callovian) is very well preserved forming a centre-point of all international taxonomic studies.

EARLY JURASSIC OR LIAS

The Early Jurassic (Lias) of Britain is famous for its marine fish faunas. Hundreds of good specimens have been obtained from localities along the entire length of the outcrop, which stretches in a continuous belt between Dorset and the Yorkshire coast. Material is housed in collections in BATM, NHM, BRSMG, CAMSM, LEICSM, OUM, SM, YORMS. Authors include Egerton (1871, 1872a, 1872b, 1873), A.S. Woodward (1886, 1889a, 1889b, 1891a,1895a, 1906), Woodward and Sherborn (1890), Fox-Strangways (1892), H.B. Woodward (1893, 1894, 1895), Arkell (1933), Gardiner (1960), Macfadyen (1970), Thies (1983), Duffin (1981, 1993b), Duffin and Ward (1983b, 1993) and Evans and Milner (1994).

The British Lower Lias has yielded abundant fish material from dozens of localities from Dorset to Yorkshire and there are at least 40 sites in the Lower Lias that have yielded scattered vertebrate material. Many of these finds are only isolated teeth and scales, so that the majority of sites may be regarded as not significant. Abundant remains have come from the quarries around Street, Somerset (ST 4836) and Barrow-upon-Soar, Leicestershire (SK 5818), but there is very little chance of more finds unless excavations are resumed. Apart from the Lyme Regis sea-cliffs, all other sites have produced only sparse remains and those that still offer exposure seem to have low potential for future finds.

The Middle Lias of England has never produced as many fossil fishes as the Lower Lias and remains are so poor that the sites are not worth tracing. A few sites in the Upper Lias of Somerset, Gloucestershire, Northamptonshire and North Yorkshire have yielded good fish specimens. In particular the 'Fish and Saurian Bed' (*exaratum* Zone, *falciferum* Subzone) exposed at Strawberry Bank, Ilminster, Somerset (ST 361148), yielded abundant vertebrate material in the 19th century (Moore, 1852, 1856, 1866). This included fine specimens of *Caturus*, *Lepidotus* (=*Lepidotes*), *Leptolepis*, *Dapedium*, *Pachycormus* and *Pholidophorus*, in the Moore collection, BATM (Woodward, 1896), NHM and local museums. The quarry is now infilled (Duffin, 1978).

FISH SITES

Three Lias localities are selected as GCR sites for their unusually prolific faunas of marine fishes:

1. Lyme Regis coast (Pinhay Bay–Charmouth), Devon–Dorset (SY 325908–SY3793). Early Jurassic (Hettangian–Pliensbachian), Lower Lias (*Ostrea* Beds–Green Ammonite Beds).
2. Blockley Station Quarry, Gloucestershire (SP 181370). Early Jurassic (Pleinsbachian), Lower Lias (?*davoi* Zone–*ibex* Zone).
3. Whitby Coast (East Pier–Whitestone Point), North Yorkshire (NZ 901115–NZ 928104). Early Jurassic (Toarcian), Upper Lias (Grey Shales Formation, Jet Rock Formation, Alum Shale Formation: Toarcian).

LYME REGIS COAST (PINHAY BAY–CHARMOUTH) (SY 3291–SY 3793)

Highlights

Lyme Regis is the most famous British Early Jurassic fish site, and is one of the best in the world. For over 200 years abundant, articulated and well-preserved specimens of bony and cartilaginous fish have been found in the cliffs near the town. Lyme Regis is the type locality for 50 or more species of fish.

Introduction

The Lias exposures on the coast around Lyme Regis, Dorset (Figures 12.4), are world-famous for their fossil remains. Lyme Regis is historically important as the place where specimens have been collected since at least 1790 (Delair, 1969), and from 1810 to 1840 Mary Anning and her family (Tickell, 1996) found and sold many fine specimens to museums throughout the country. Around the same time, the 3rd Earl of Enniskillen (W.W. Cole) and Sir Philip Egerton made exceptional collections of fossil fishes. However, little stratigraphical information was provided with these early discoveries. Since then, many hundreds of specimens have been collected, and important finds are still being made.

Over 50 species of fish are recognized from here, and because of the long history of fossil collecting at this site, Lyme Regis is the type locality for many of these. Many of the remains are extremely well preserved, and beautifully articulated three-dimensional specimens have been recovered. Several complete specimens of

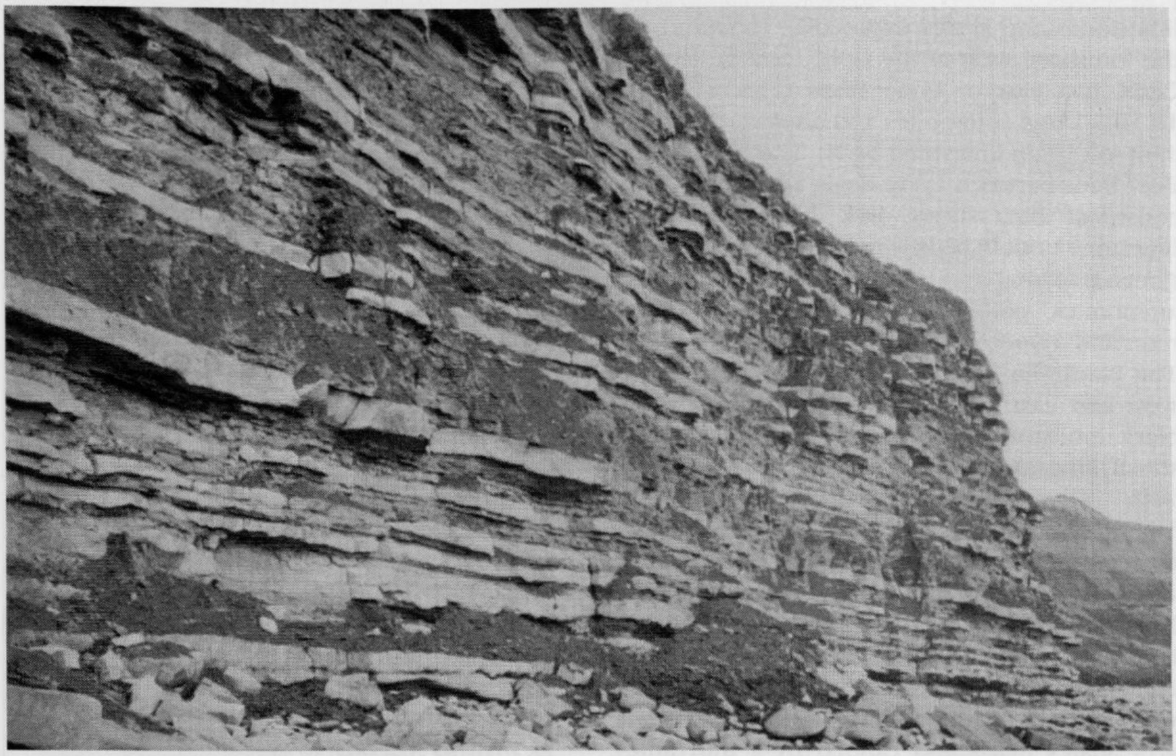


Figure 12.4 The Lower Liassic shales and cementstones in Ware Cliffs, north-west of Lyme Regis harbour (photo: G.W. Storrs).

the euselachians *Acrodus* and *Hybodus* from Lyme Regis have proved invaluable in determining the palaeobiology of hybodont sharks and in phylogenetic study of the group (Duffin, 1993b). Early neoselachians ('modern sharks', both the active predators and the skates and rays) are also present in the shark fauna (Duffin and Ward, 1993b). Chimaeroid taxa, including many articulated specimens, are also well represented in the assemblage and Lyme Regis is the type locality for two species of squalorajoid and three species of myriacanthid holocephalians (Patterson, 1965). Lyme Regis is also the type and only locality for the coelacanth *Holophagus gulo* and many species of actinopterygians. The fish faunas have been described in detail by Egerton (1871, 1872a, 1872b, 1873), A.S. Woodward (1886, 1889a, 1889b; 1891a, 1906) and Woodward and Sherborn (1890), and more recently reviewed by Gardiner (1960), Patterson (1965) Thies (1983), Duffin (1993b) and Duffin and Ward (1993b) amongst others.

Description

In the earliest description of the Lower Lias section at Lyme Regis, the major lithological divisions and the fossils they contained were noted (Egerton 1839). The abundance of ammonites meant that as early as the late 1850s, Oppel (1856) could adapt the zonal scheme for ammonites from the German sections to that in the Lyme Regis region. Numerous stratigraphers have provided detailed accounts of the Liassic succession at Lyme Regis (e.g. H.B. Woodward and Ussher, 1906; Lang 1914, 1924, 1932; Lang *et al.* 1923, 1928; Lang and Spath 1926; Palmer 1972). The general succession (Getty, 1980) is:

	Thickness (m)	Lang's bed numbers
– – – – – – – unconformity – – – – – – –		
Green Ammonite Beds	32	122–130
Belemnite Stone	0.15	121
Belemnite Marls	23	106–120
Armatus Limestone	0.4	105
Black Ven Marls	43	76–104
Shales with Beef Beds	23	54–75
Blue Lias	27	25–53
Ostrea Beds (= Pre-*planorbis* Beds)	2.5	1–24

The Blue Lias is a sequence of laterally extensive, alternating thin-bedded (and nodular) limestones and shales exposed in cliffs and on the foreshore west of the Cobb, and in Church Cliffs, just east of Lyme Regis (Figure 12.5A, 12.5B). Large ammonites and bivalves are abundant in certain limestone beds. The Shales with Beef Beds between Lyme Regis and Charmouth consist of thin, papery, dark shales, marls and limestone nodule beds with much fibrous calcite ('beef'), pyrite and selenite. Fossils include ammonites, poorly preserved bivalves, belemnites and numerous fishes, commonly complete. The Black Ven Marls, in the cliff and foreshore west and east of Charmouth, consist of blue-black mudstones and paper shales with occasional limestones. Many species of fish along with ammonites, bivalves, brachiopods, foraminifers and insects occur in these beds. Deposition of all sediments was marine and, although not marginal or intertidal, was probably close to shore because of the presence of insect, plant and dinosaur remains. The overlying Belemnite Marls consist of light grey marls with abundant lignite interbedded with dark grey shaley marls and capped by a thin limestone, the Belemnite Stone. These beds contain an abundant mollusc fauna and in particular exceptionally well-preserved belemnites and pyritous ammonites. The Green Ammonite Beds are composed of a bluish grey micaceous marly clay, with occasional nodules and bands of a hard grey limestone and ferruginous layers. The beds derive their name from the exquisite 'Green Ammonites' which are infilled with a green sparry calcite cement.

Although the provenance of many of the earlier fossil fish finds was inadequately documented (e.g. Egerton, *in* De la Beche, 1839), fishes have been collected from the 'Saurian Shales' at the top of the Blue Lias (equivalent to Lang's Bed 52: *scipionianum* Subzone, *semicostatum* Zone, Early Sinemurian), from the Shales with Beef Beds (*semicostatum–turneri* Zones, Early Sinemurian; MacFadyen, 1970, p. 97), and from the '*Obtusum* Shale' of the Black Ven Marls (*obtusum* Zone, Late Sinemurian) (Woodward, 1886, 1889a, 1889b, 1891a, 1906; Rayner, 1958; Figure 12.5B)

The importance of Lyme Regis as a fossil fish locality is that the material is extremely well preserved (e.g. Figure 12.6A, I). Although scattered fish remains occur throughout the succession, the better-preserved material from the shale and marl units includes many whole, but laterally compressed specimens of bony fish, and importantly a number of articulated partial chondrichthyan skeletons. It is for this reason that Lyme Regis is an essential reference for fish taxonomy.

Fauna

Based upon collections in the NHM, BRSMG and OUM and from references including Woodward (1886, 1889a, 1889b, 1891a, 1906), Duffin (1993b) and Duffin and Ward (1993b):

Chondrichthyes: Elasmobranchii: Euselachii: Hybodontoidea

- *Acrodus nobilis* Agassiz, 1837 (includes material designated *A. latus* Agassiz, 1839, *A. gibberulus* Agassiz, 1839 and *A. arietus* Quenstedt, 1858: Woodward, 1889)
- *A. anningae* Agassiz, 1839
- *Lissodus* sp.
- ?*Hybodus cloacinus* Quenstedt, 1858
- *H. raricostatus* Agassiz, 1843
- *H. medius* Agassiz, 1843

Chondrichthyes: Elasmobranchii: Neoselachii: Squalomorphii

- '*Palaeospinax*' *priscus* (Agassiz, 1843) *nomen dubium*
- *Synechodus occultidens* Duffin and Ward, 1993
- *S. enniskilleni* Duffin and Ward, 1993

Chondrichthyes: Elasmobranchii: Neoselachii: Galeomorphii

- *Agaleus dorsetensis* Duffin and Ward, 1983

Chondrichthyes: Holocephali: Chimaeriformes

- *Myriacanthus paradoxus* Agassiz, 1836
- *Metopacanthus granulatus* (Agassiz, 1837)
- *Recurvacanthus uniserialis* Duffin, 1981
- *Squaloraja polyspondyla* (Agassiz, 1836)
- *S. tenuispina* Woodward, 1886

Osteichthyes: Actinopterygii

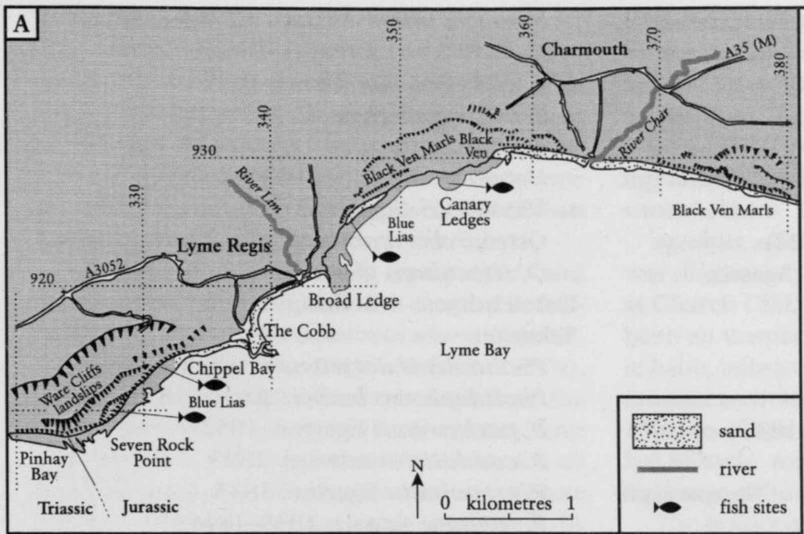
- *Centrolepis aspera* Egerton, 1844
- *Coccolepis liassica* A.S. Woodward, 1890
- *Cosmolepis ornatus* Egerton, 1854
- *Platysiagum sclerocephalum* Egerton, 1872

Osteichthyes: Actinopterygii: Saurichthyiformes

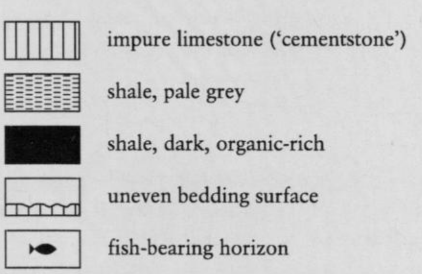
- *Saurorhynchus (Belonorhynchus) acutus* (Agassiz, 1844)
- *Belonorhynchus brevirostris* (Woodward, 1895)

Osteichthyes: Actinopterygii: Chondrostei: Acipenseriformes

- *Chondrosteus acipenseroides* Egerton, 1858
- *C. pachyurus* Egerton, 1858



Formation	Lang Bed numbers	Stage	System
Black Ven Marls	90–104 gap 76–89	Sinemurian	Jurassic
Shales with Beef	54–75		
Blue Lias	1–53		
	H25–84	Hettangian	
Ostrea Beds	H1–24	Rhaetian	Triassic
Penarth Group			



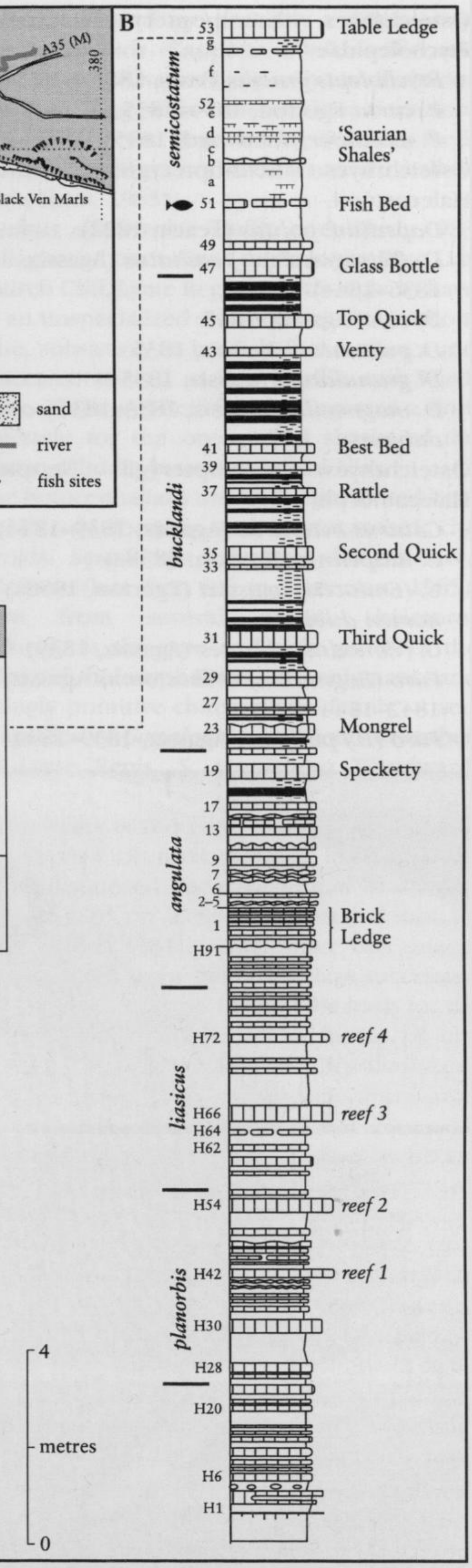


Figure 12.5 (A) Map of the coastal outcrop of the Lower Lias, Charmouth to Lyme Regis (after Benton and Spencer, 1995); (B) rock succession (after House, 1993).

Osteichthyes: Actinopterygii: Holostei: Ptycholepidae
Ptycholepis gracilis Davis, 1884
P. curta Egerton, 1854–1855
P. monilifer Woodward, 1895
Osteichthyes: Actinopterygii: Neopterygii: Halecostomi
Dapedium politus (Leach, 1822)
D. (Tetragonolepis) radiatus (Agassiz, 1836–1844)
D. colei Agassiz, 1835
D. punctatum Agassiz, 1835
D. granulatum Agassiz, 1835
D. magnevillei Agassiz, 1833–1836 *nomen dubium*
Osteichthyes: Actinopterygii: Neopterygii: Halecomorphi
Caturus heterurus (Agassiz, 1839–1844)
C. latipennis (Egerton, 1858a)
C. (Endactis) agassizi (Egerton, 1858a) *nomen dubium*
C. (Conodus) chirotes (Agassiz, 1839)
Furo (Eugnathus) orthostomus Agassiz, 1842–1844
Furo (E.) philpotæ Agassiz, 1839–1844
Furo (E.) minor Agassiz, 1839
F. (Lissolepis) serratus (Davies, 1884)
F. altus A.S. Woodward, 1895
F. latimanus (Agassiz, 1838–1844)
Furo sp.
Heterolepidotus rhombiter Egerton, 1834–1835 (Agassiz, 1837)
Osteoarchis macrocephalus Egerton, 1868
O. (Isoculum) granulatus (Egerton, 1868)
Osteichthyes: Actinopterygii: Neopterygii: Teleostei
Pholidolepis dorsetensis Nybelin, 1966
Pholidophorus bechei Agassiz, 1844
P. pachysomus Egerton, 1852
P. caudalis Woodward, 1895
P. crenaluata Egerton, 1843
P. limbata Agassiz, 1833–1844
Pholidophoraspis maculata Nybelin, 1966
Pholidophoropsis sp.
Pholidophoroides sp.
Proleptolepis elongata Nybelin, 1974
P. furcata Nybelin, 1974
P. megalops Nybelin, 1974
Osteichthyes: Sarcopterygii: Actinistia
Holophagus (Undina) gulo Egerton, 1861

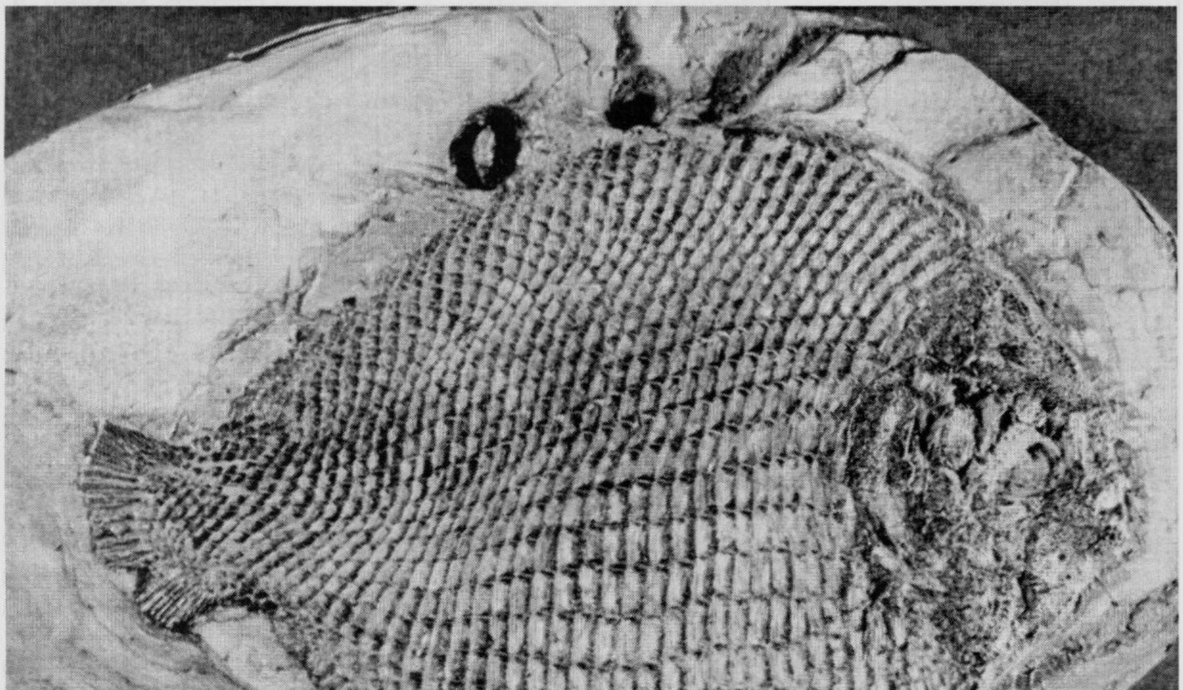


Figure 12.6 Liassic fishes from Lyme Regis: (A) , *Dapedium politus* (Leach), × 0.5 (Photo: courtesy The Natural History Museum, London, T00144/A). (Continued on p. 367).

Interpretation

About 100 'new species' were described from Lyme Regis in the 19th century, when almost every new specimen was given a name. (According to our present taxonomic list, Lyme Regis has yielded type specimens of more than 50 species.)

Hybodont sharks are well represented, and specimens recovered in the 19th century included the lectotype of *Hybodus reticularis* (Agassiz, 1833–45; Woodward, 1916; Maisey, 1987a), which was regarded as the type species of the genus *Hybodus*. Five Lyme Regis species have been referred to this genus and these are all based upon good articulated material (Figure 12.6H). These species were reviewed by Woodward (1889a) and Duffin (1993b), who described the difficulties involved in trying to ascribe isolated *Hybodus* teeth from the Lower Lias succession of Britain and mainland Europe to their type species. Great difficulties have become apparent in distinguishing between four of the Lyme species, *H. reticularis*, *H. raricostatus*, *H. delabechii* and *H. cloacinus*, even though represented by articulated material (Woodward, 1889a). Heterodonty exists in these species, especially with respect to overall tooth dimensions, morphology and patterns of ornamentation. Duffin (1993b) considered it probable that there is some synonymy amongst the species. However, he considered the five Lyme *Hybodus* species valid and he provided means of distinguishing their isolated teeth. The five species of *Hybodus* all possess a heterodont dentition, with the predominantly 'clutching-type' teeth (Cappetta, 1987) of a piscivorous animal.

Acrodus and *Lissodus* are also represented in the Lower Lias hybodont shark fauna at Lyme Regis (Figure 12.6I). Woodward (1889a) assigned two valid species, *A. anningae* and *A. nobilis* to the bottom-dwelling heterodont shark *Acrodus*. *Acrodus* is considered to have eaten fish, hard-shelled molluscs and crustacea (Cappetta, 1987).

Neoselachian sharks are also fairly well represented in the Lower Lias sequence of Lyme Regis (Thies, 1983). Duffin and Ward (1993b) have revised the taxonomy of the rather poorly known palaeospinacid sharks from Lyme Regis, and grouped the material into two species of a single genus, *Synechodus*. The palaeospinacids are considered to belong to the squalomorph neoselachians, and are probably a sister-group to the hexanchids (Cappetta, 1987; Duffin and Ward, 1993b). They are typically small sharks, up to 1 m long with a heterodont dentition. They possibly were slow-moving benthos, feeding on fish, molluscs and crustaceans in shallow waters (Thies, 1985).

Agaleus dorsetensis Duffin and Ward, 1983 was diagnosed on isolated teeth in the Blue Lias at Church Cliff, Lyme Regis. It is thought to have been an unspecialized swimmer with a benthonic habit, subsisting on hard-shelled molluscs and crustaceans, as well as fish (Duffin and Ward, 1983b). Thies and Reif (1985) suggested a similar lifestyle for the orectolobid sharks of the Callovian (Middle Jurassic) Oxford Clay.

The holocephalians are well-represented here by both squalorajids and myriacanthid chimaeroids. *Squaloraja polyspondyla* Agassiz is a small form (less than 0.6 m; Patterson, 1965), known from several partial skeletons. *Squaloraja* is the type and only genus of the squalorajid holocephalians, an enigmatic and seemingly primitive chimaeriform family. A second species of *Squaloraja* has been described from Lyme Regis, *S. tenuispina* Woodward, based upon a single front clasper.

Lyme Regis is the type and only locality for three species of myriacanthid, including the recently diagnosed *Recurvacanthus uniserialis* Duffin, named on a single isolated dorsal fin spine (Duffin, 1981). The other two genera were recovered from the Lower Lias succession in the 19th century and formed the basis for the diagnosis of the myriacanthid family of chimaeroids (Patterson, 1965). *Myriacanthus paradoxus* Agassiz is a large chimaeriform (over 1 m in length; Woodward, 1906; Patterson, 1965) described from articulated skull fragments and partial post-cranial remains (Woodward, 1891a). In contrast, the specimens of *Metopacanthus granulatus* (also known from partial skeletal remains) only reach 1 m, and the head is much less broad and flattened (Patterson, 1965). The type specimen of *Metopacanthus granulatus* was originally designated *Ischyodus orthorhinus* by Egerton (1871), but this was later corrected by Woodward (1889a, 1891a). Lower Lias myriacanthid chimaeroids are also known from France (Terquem, 1855), Holzmaden, Germany (Fraas, 1910), Hombois, Belgium (Duffin, 1980a), and Ostenso, Italy. Both sexes possessed a large frontal clasper. Squalorajids and myriacanthids are thought to have been largely bottom-dwellers with a durophagous diet.

Lyme Regis has yielded a fish fauna that seems to retain a rich contingent of primitive actinopterygians, including four type species plus a stem neopterygian (a saurichthyid), two species of chondrosteid acipenseriforms and a stem chondrostean. The primitive actinopterygians include the type and only species, *Centrolepis aspera* Egerton, known from three specimens collected at Lyme Regis. *Centrolepis* is a small form with a robust, somewhat elongated fusiform body covered in thick and highly ornamented scales (Woodward, 1890). *Coccolepis liassica* Woodward is also known only from Lyme Regis. It, too, is a small fish (up to 0.14 m long; Figure 12.6F) but clad in thin scales ornamented with irregularly arranged tubercles. This species has a large head and typical dentition of inner large conical teeth, flanked externally by minute slender teeth (Woodward, 1891a). *Oxygnathus* (also known as *Cosmolepis*) and *Platysiagum* complete the list of these rather similar primitive taxa from Lyme Regis.

The Lyme Regis chondrostean assemblage also includes the type specimen of the large saurichthyid species *Saurorhynchus (Belonorhynchus) brevirostris* (Woodward), also known from the Upper Lias of Whitby (q.v.) and Holzmaden, Germany (Reis, 1892; Woodward, 1895a). The species possessed a typically long, slender, tubular body and small head with pointed elongated mandible lined with sharp, well-spaced conical teeth (Gardiner, 1967). The acipenseriform chondrosteans *Chondrosteus acipenseroides* Egerton (Figure 12.6C) and *C. pachyurus* were also described from the Lower Lias of Lyme Regis. *Chondrosteus acipenseroides* is the type species and is known from several complete specimens collected from Dorset and Barrow-on-Soar, Leicestershire, in the 19th century (Woodward, 1895a), whilst *C. pachyurus* is only known from three imperfect specimens from Lyme Regis (Egerton, 1858b). *Chondrosteus* is large robust chondrosteid with a strongly heterocercal tail. The specimens commonly do not exceed a length of 1 m and both species possessed a well-developed headshield, weakly ornamented with ganoine-coated granulations. The jaws unusually lack a dentition and ribs are absent (Woodward, 1895a). *Chondrosteus* is also known from Upper Lias of Holzmaden, Germany (Frickhinger, 1991).

Halecostomid actinopterygians are represented in the Lower Lias of Lyme Regis by the deep-bodied semionotid genus *Dapedium*. Six species of *Dapedium* are known from this locality including the type species, *D. politus* (Leach, 1822; Figure 12.6A, A'). *Dapedium* is a moderately large fish, ranging from 0.3 to 0.6 m in length and with a rounded laterally flattened trunk, with tiny paired fins and dorsal and anal fins that extend from the mid part of the body to the base of the tail (Woodward, 1895a). The head was comparatively small with a highly differentiated dentition of robust, styliform teeth, some bicuspate. The bones of the head were usually ornamented with bumps coated in ganoine and the trunk scales were often ornamented with fine tubercles (Woodward, 1895a). *Dapedium* is a widespread genus, which extends from the Upper Triassic to Upper Lias in Europe (Frickhinger, 1991). Several more species (e.g. *D. orbis*, *D. dorsalis* and *D. angulifer*) have been described from Lower Lias successions in England, and many of the Lyme Regis species have been found in the Upper Lias of Europe (Woodward, 1895a; Wenz, 1967).

Caturids are most abundant at Lyme Regis and five genera (*Caturus*, *Furo*, *Heterolepidotus*, *Ptycholepis* and *Osteorachis*) have been described from the site. Different species and genera of caturids are essentially subdivided on the morphology and ornamentation of the head bones, and slight differences in the postcranial skeleton (Woodward, 1895a). The type genus, *Caturus*, possesses the general form, size and osteology typical of most of the genera listed here.

In the British Lower Liassic actinopterygian fish faunas two distinct levels of development were discernible: the halecostomid as exemplified by the semionotids such as *Dapedium*, and the halecomorphs such as *Caturus*. Both were predaceous fish, and in *Dapedium* the old conservative structure of the mouth and jaw mechanism persists. Here the cranial parts of the head were rigid, fully ossified, and there was a limited extent to the expansion of the mouth cavity. The fish could not make a sudden large intake of water. To catch prey speed was essential, yet the ability for fast acceleration was limited by the shape and position of the fins. In the caturids the new structure of the mouth parts and the mobility of the braincase increased suction power to the point where it aided seizure of prey, and improvements in body and fin kinetics

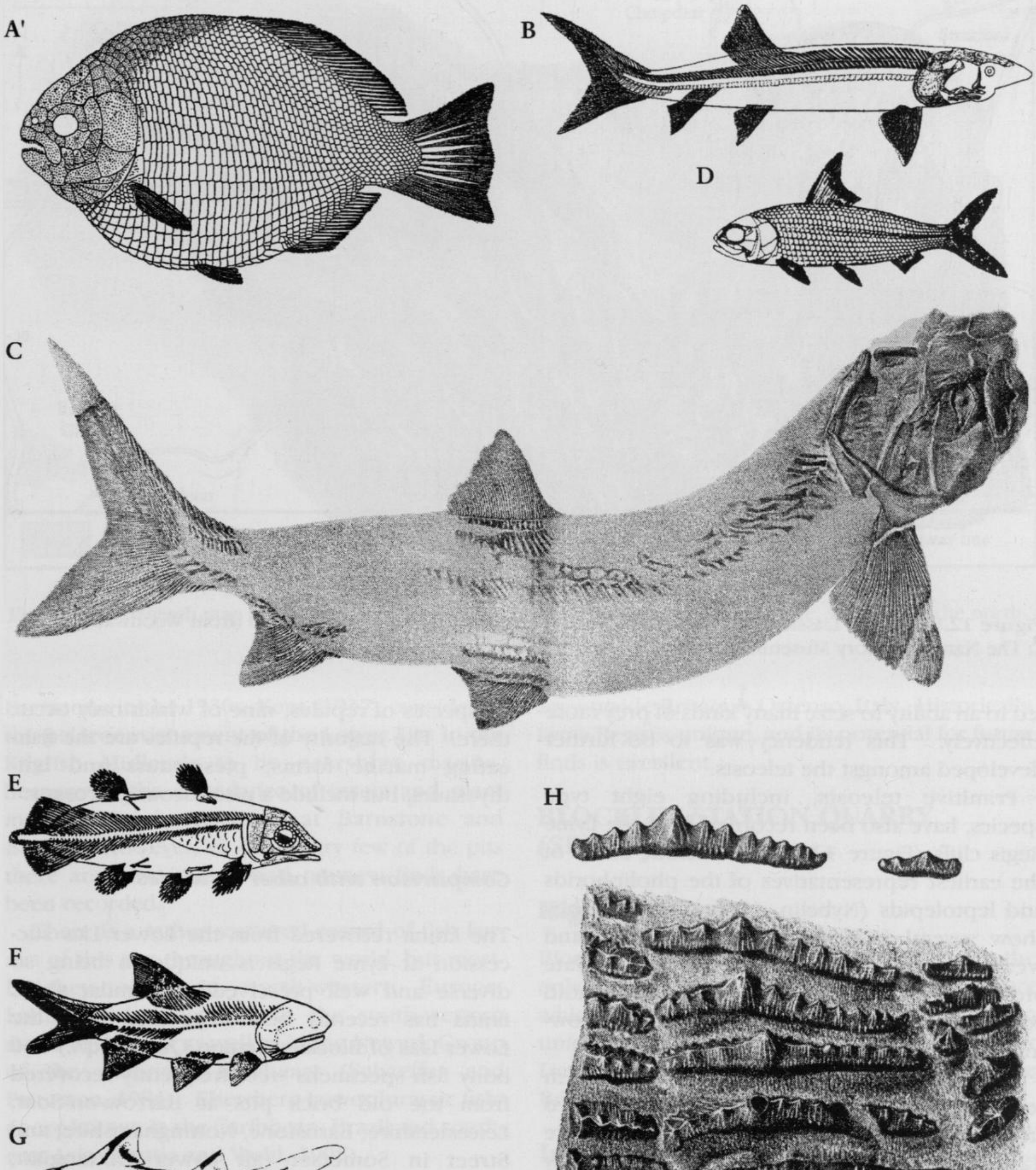


Figure 12.6 – *contd*. Liassic fishes from Lyme Regis: (A') (restoration), *Dapedium politus* × 0.2; (B) *Chondrosteus acipenseriodes* Egerton, × 0.1, restoration by Woodward (1895); (C) *Chondrosteus aeipenseroides* (Egerton) skeleton and body outline preserved, × 0.2; (D) the teleost *Pholidophorus* sp., × 0.1, restoration by Woodward (1895); (E) the coelacanth *Holophagus gulo* Egerton, × 0.25, restoration by Woodward (1895); (F) the palaeoniscoid *Coccolepis bucklandi* Agassiz, × 0.5; (G) the elasmobranch *Hybodus*, × 0.1, restoration by Maisey (1982); (H) teeth of the elasmobranch *Hybodus*, isolated individual teeth and part of the dental array, × 1.0. Figures from Woodward (1889–1901) © The Natural History Museum, London. (Continued on p. 368.)

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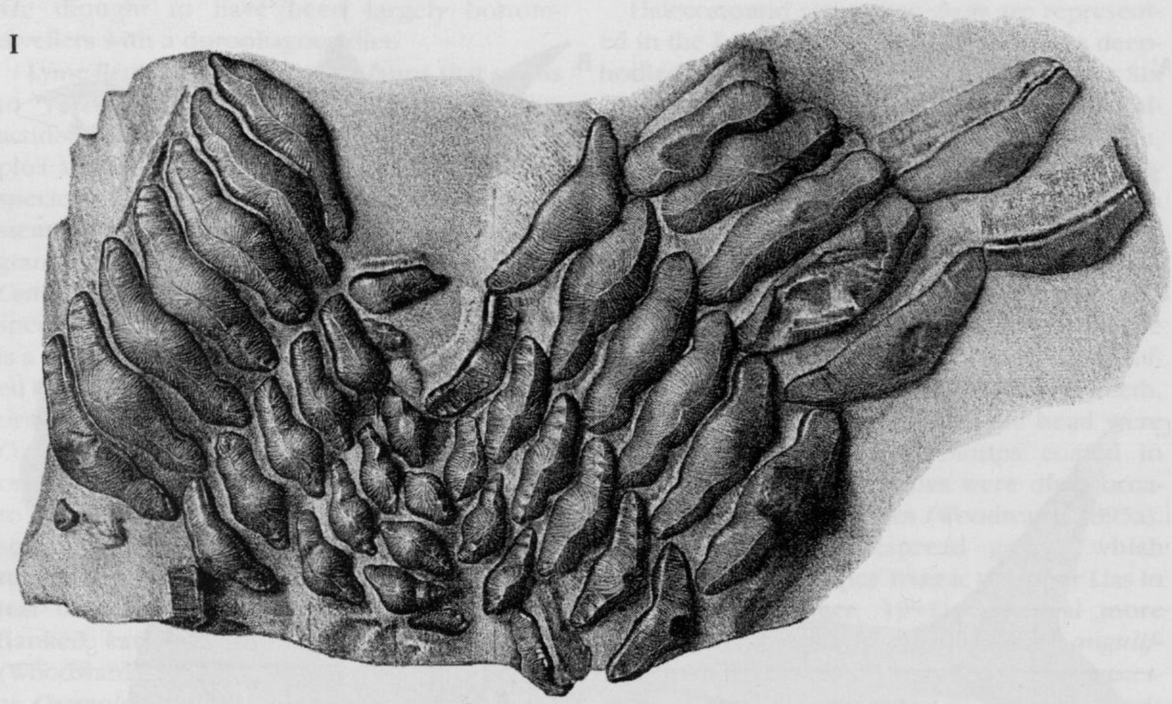


Figure 12.6 – *contd.* Liassic fishes from Lyme Regis: (I) array of *Acrodus* teeth, × 1.0 (from Woodward, 1895, © The Natural History Museum, London).

led to an ability to seize many kinds of prey more effectively. This tendency was to be further developed amongst the teleosts.

Primitive teleosts, including eight type species, have also been recorded from the Lyme Regis cliffs (Figure 12.6), and include some of the earliest representatives of the pholiphorids and leptolepids (Nybelin, 1966, 1974b). They show several features of the skull, jaws and weakly ossified vertebrae seen in all late Mesozoic teleosts, despite retaining ganoid scales. They were large voracious feeders growing to 60 cm in length.

Holophagus gulo Egerton, a large (0.7 m length) coelacanth genus, has been described from the Lower Lias at Lyme Regis (Figure 12.6E). Indeed, Lyme Regis is the type and only locality for this rare Jurassic actinistian fish, although isolated coelacanth material has been recorded from the Lower Lias at Barrow-on-Soar, Leicestershire (Woodward, 1891a) and a second species (*H. penicillata*) is known from the Upper Kimmeridgian of Germany. *Holophagus* is a stout-bodied, robust form, with a large, externally ornamented headshield and scales (Woodward, 1891a).

Lyme Regis has also yielded type specimens of 14 species of reptiles, nine of which only occur there. The majority of the reptiles are the fish-eating marine forms, plesiosaurs and ichthyosaurs, but include a piscivorous pterosaur.

Comparison with other localities

The fauna recovered from the Lower Lias succession at Lyme Regis is unique in being so diverse and well preserved. A similar shark fauna has recently been recovered from the Lower Lias of Blockley Station Quarry (q.v.) and bony fish specimens were frequently recovered from the old brick pits at Barrow-on-Soar, Leicestershire; Barnstone, Nottinghamshire; and Street in Somerset (all Lower Hettangian; Hallam, 1968). Like those of Lyme Regis, their fossil fishes are similarly well preserved and have yielded some type material (Woodward, 1891a, 1901). The assemblages from Barrow-on-Soar have been particularly well studied (Brodie, 1857a, 1857b; Browne, 1889a; Fox-Strangways, 1903; Gardiner, 1960) and many species of fish and reptile show evidence of soft tissue preservation (Martin *et al.*, 1986, and references therein). The same faunas were recovered from

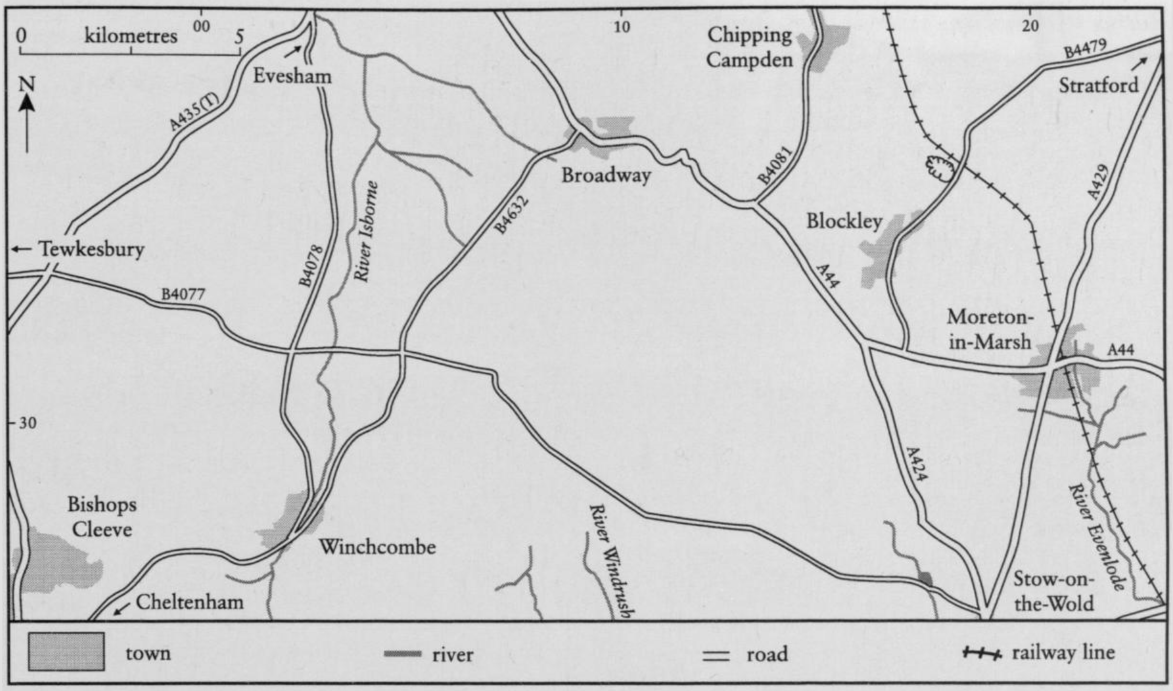


Figure 12.7 Sketch map of the area around the Blockley Old Station Quarry GCR site, which is to the north-east of Blockley.

Barnstone in the 1930s: Kent (1937) considered the palaeoenvironment of the Lower Lias in the English Midlands to be nearshore marine, because of the abundance of insect and plant material in the sections at Barnstone and Barrow. However, all but a very few of the pits there are now infilled and no new finds have been recorded.

There is a rather scattered record of fish faunas of this age throughout the world, but mostly they occur in north-western Europe, Lombardy in Italy and in the south-western states of the USA as well as in the Newark Group of the American northeast (Schaeffer and Patterson, 1984). Elsewhere Lower Jurassic fishes are known in the Caribbean, Brazil and south-east Asia (Arratia and Viohl, 1995).

Conclusion

The Lyme Regis coast section of Lower Lias is one of the most important fish-bearing sites in Britain and has an internationally recognized status, hence its conservation value. It has yielded many type specimens, the remains of which are extremely well preserved, it still yields whole fish, and the only comparable site of the same age outside Britain is Ostenso, Italy. Historically, Lyme Regis is unique, and its potential for future finds is excellent.

BLOCKLEY STATION QUARRY (SP 181370)

Highlights

Blockley Station Quarry in Gloucestershire is the only extant inland British Lower Lias exposure which has yielded fish material. It displays an unique section of the Upper Clays of the Lower Lias that are not exposed elsewhere in the British Isles.

Introduction

Blockley Station Quarry, a large brickpit in the northern Cotswolds (Figure 12.7), is well known to British Jurassic stratigraphers in displaying an unrivalled section through much of the Upper Clays of the Lower Lias (Pliensbachian). In recent years the workings have been extended both upwards and downwards and fish remains have been collected from a crinoidal horizon near the base of the quarry (Figure 12.8A, B).

Figure 12.8A Blockley Station Quarry, close-up of north-west faces of the Upper Clays in the Lower Lias, with basal limestones (photo: K. Page).

The fish-bearing unit, the Crinoid–Belemnite Bed, is composed of soft clay with abundant macroinvertebrate material, making bulk processing by wet sieving an excellent means of sampling large amounts of sediment for microvertebrate remains. Much of the material collected from Blockley comprises tiny shark teeth and denticles, fossils that would be missed by other means of field collecting.

The pit continues to be worked and there is much potential for future finds as the workings expand. The succession of the Upper Clays at Blockley is the most complete and fossiliferous (in terms of macro-invertebrates and, in particular, zonal ammonites) in the British Isles and provides missing information on a number of key Lower Lias stratigraphical issues, as beds of equivalent age elsewhere are unfossiliferous (e.g. the Midlands) or absent (e.g. Dorset; Callomon, 1963, 1968; Callomon *et al.*, 1993). Hence the new fish material can be precisely dated within the Pliensbachian zonation scheme, providing much-needed stratigraphical evidence for studies in macro-evolution of Lower Jurassic selachian groups.

Description

Although brickmaking began at Blockley in the early part of the 20th century, it appears that the section was fairly small and by all contemporary accounts unfossiliferous (e.g. Richardson, 1929). The first serious attempts to log the section came in the early 1950s when brickmaking resumed after a lull during the war years (e.g. Cox, 1950, p. 263; Channon, 1950, p. 260). The section recorded here is based upon the classic stratigraphical logs made during the latter part of the 1960s by J. Callomon (1968) and subsequently improved by him (*in* Callomon *et al.*, 1993), following extension of the workings in the 1980s:

	Thickness (m)
Lower Lias: Pliensbachian	
?davoei Zone, *maculatum* Subzone	
8. Clay, weathered	seen 1.0–2.0
7. Siltstone, buff, lenticular, bioturbated, sparsely fossiliferous, ammonites	0.0–0.2

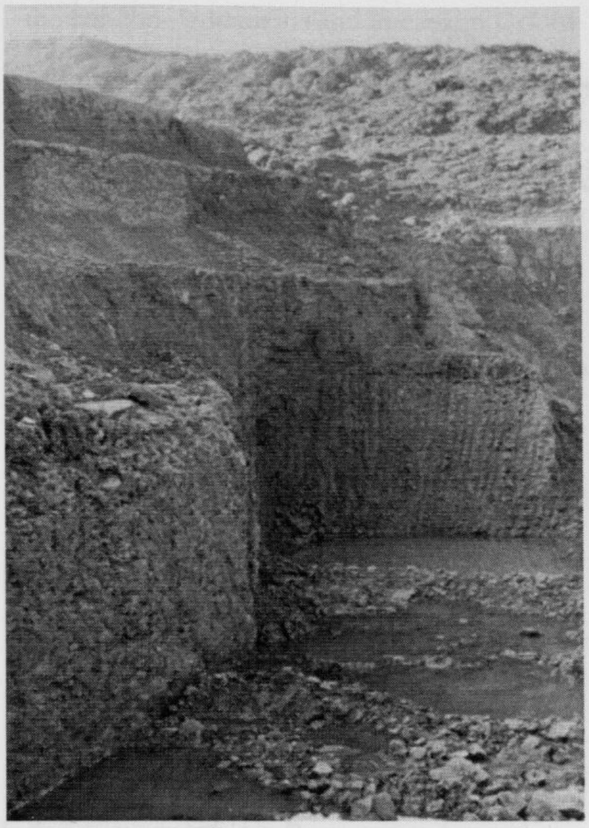


Figure 12.8B Blockley Station Quarry, north-west faces of the Upper Clays in the Lower Lias, with basal limestones (photo: S. Metcalf).

ibex Zone, *luridum* Subzone	
6. Clays, grey and brown, limonitic nodules abundant; sparsely fossiliferous	6.0
5. Clays, as above, with scattered small concretions and crushed fossils	4.0
4. Mudstone, impersistent, light brown or layer of calcareous concretions; Fauna IV	0.0–0.15
3. Clay, grey, fairly common ammonites	0.3
2. Pecten Bed. Mudstone, grey to light brown, fossils, many well preserved; highly diverse bivalve fauna, belemnites; Fauna III	0.15–0.45
1. Clay, grey very fossiliferous throughout, ammonite fauna; Fauna II	8.5
Z. Crinoid–Belemnite Bed coarse calcite shell and ossicles of *Belanocrinus* forming hard quarry floor; Fauna I	seen 0.15

Fish remains have so far only been recovered from Bed Z, which forms a hard base to the quarry. This bed is only exposed during most prolific quarrying activity, and was not recorded on the earlier logs of the section. The section has a rich invertebrate fauna, dominated by ammonites, belemnites and bivalves, with rarer brachiopods, gastropods and echinoderm material (Channon, 1950, p. 260). The ammonite succession at Blockley has provided a base for extensive studies into the phylogeny and evolution of liparoceratids (e.g. Callomon, 1968). This has meant that the units can be precisely correlated to the *ibex* and *davoi* Zones of the Lower Pliensbachian. The excellent biostratigraphical information for the Blockley section has meant that the fish-bearing unit and the overlying beds can be correlated with the Lower Lias of Dorset. The beds exposed at Blockley have provided much missing stratigraphical information on part of the Lower Lias, which is frequently unfossiliferous or not exposed elsewhere, as in Dorset (Callomon *et al.*, 1993).

The section was sketched by Phelps (1985) in a review of the ammonite bio- and chronostratigraphy of the Lower Pliensbachian. He subdivided many of the beds on Callomon's log and provided a tripartite division of the *luridum* Subzone, based upon liparoceratid ammonite zonule biostratigraphy. The section contains four distinct and clearly distinguishable ammonite faunas, which are labelled I–IV on Callomon's log. These can be correlated with equivalent faunas of the Dorset coast to illustrate the considerable non-sequence in the southern region (Callomon *et al.*, 1993). Bed Z (Crinoid–Belemnite Bed of Callomon *et al.*, 1993) correlates with one of the components, the Crumbly Bed, at the top of Lang's bed 120, the Belemnite Marls in Dorset (Lang *et al.*,1928) and bed 2, the Pecten Bed, is equivalent to the Belemnite Stone, or Lang's bed 121 of that region. All of the succeeding strata in the Blockley section (beds 3–8) are missing from the Dorset coast succession (Callomon *et al.*, 1993).

Fauna

Fish remains have been recovered from the lower shelly units (bed Z on Callomon's log) in the section at Blockley Station Quarry by bulk sampling (Ward, pers. comm., 1994). The fauna consists mostly of abundant microshark teeth, denticles, and semionotid scales and teeth (Ward, pers. comm.; Figure 12.9):

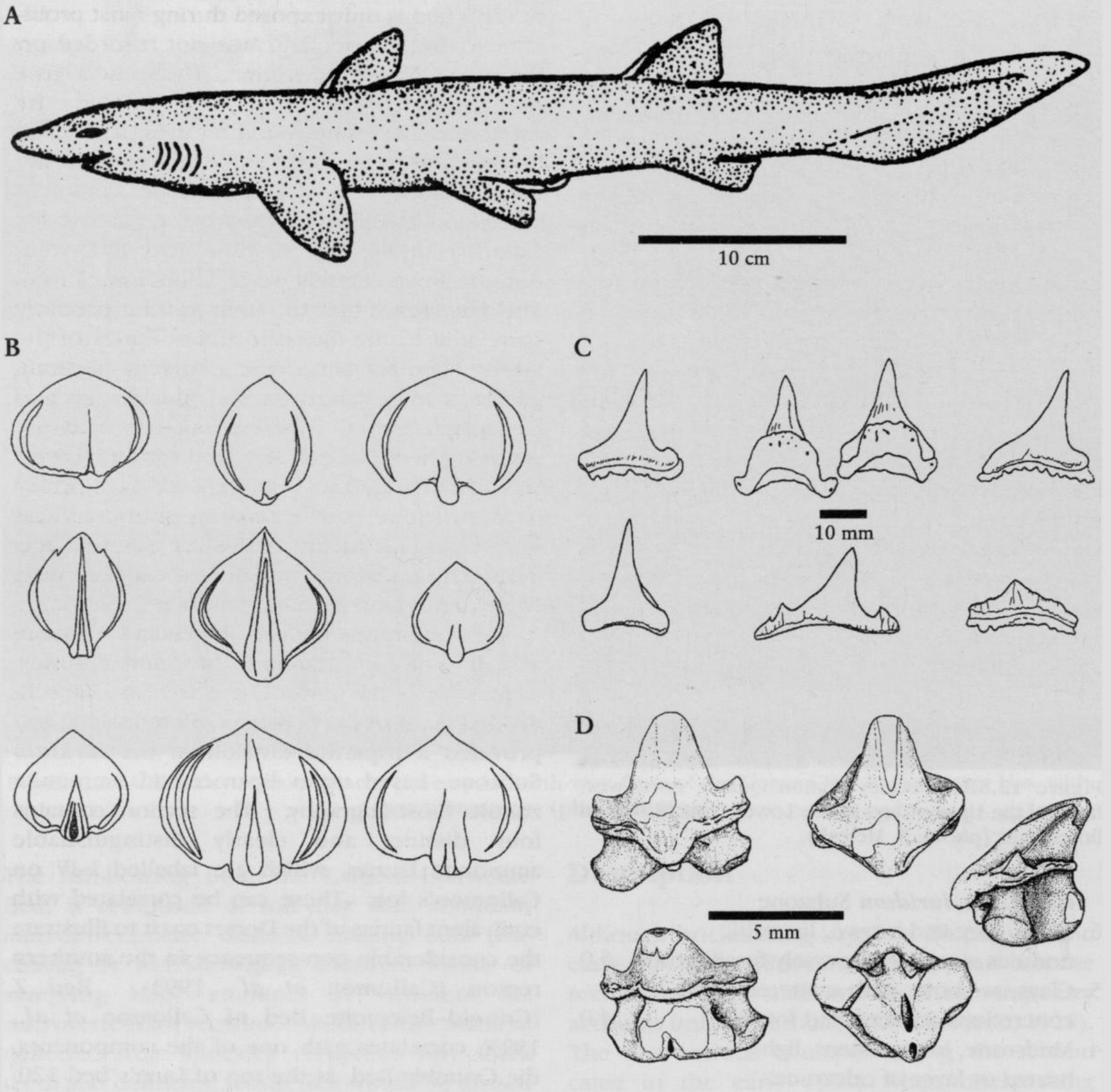


Figure 12.9 The elasmobranch fishes from Blockley Old Station Quarry: (A) restoration of *Synechodus* by Duffin and Ward (1983b); (B) denticles (× 30) and (C) teeth of *Synechodus* from Duffin and Ward (1983b); (D) views of tooth (holotype NHM P 60788) of *Agaleus dorsetensis* Duffin and Ward (1983b).

Chondrichthyes: Elasmobranchii: Neoselachii: Squalomorphii
Synechodus occultidens Duffin and Ward, 1993
S. enniskillenii Duffin and Ward, 1993.
Chondrichthyes: Elasmobranchii: Neoselachii: Galeomorphii
Agaleus dorsetensis Duffin and Ward, 1983
Osteichthyes: Actinopterygii: Neopterygii: Halecostomi
'*Lepidotes*' sp.

Interpretation

During the early Lias Epoch, central England formed part of a large depositional basin, which was gradually deepening towards the end of Upper Clay sedimentation. The clays of the Lower Lias represent deposition in normal offshore marine facies, although the basin tended to become periodically stagnant. Late Lower Lias subsidence probably was at its azimuth in Gloucestershire, although the Upper Clays thin toward the London–Ardennes island in eastern Oxfordshire and Northamptonshire (Hallam, 1968).

Scattered microvertebrate remains are recovered from the basal Crinoid–Belemnite Bed (bed Z) by bulk sampling and acid preparation of the calcareous cemented shelly clays. The residues are rich in an impoverished microshark fauna, which includes teeth and dermal denticles of the neoselachians, *Agaleus dorsetensis* Duffin and Ward, 1983, *Synechodus occultidens* Duffin and Ward, 1993 and *S. enniskillenii* Duffin and Ward, 1993, also known from the Lower Lias of Lyme Regis (Figure 12.9). The assemblage has poor diversity and little else except the ganoid scales and button-like teeth of semionotids (?*'Lepidotes'* sp.), which have been recovered from the washings. The prevalence of the small benthonic palaeo-spinacid and orectolobid sharks with unspecialized diets, and the bony fish with teeth, which suggest a durophagous habit, supports sedimentological evidence that the biodebris of the Crinoid–Belemnite Bed represents a locally stable shelly substrate or shell bank within the basin.

Comparison with other localities

The fish fauna recovered from the Upper Clays of the Lower Lias at Blockley complements the rather sporadic, but much better preserved, finds made at Lyme Regis during the 19th and 20th centuries. However, the fossiliferous sediments at Blockley Station can be bulk-processed for microscopic remains.

Conclusion

Blockley Station Quarry is important and has a conservation value as the only extant fish-bearing section of the Upper Clays (Pliensbachian) of the Lower Lias in the British Isles. The fish-bearing units yield a typical Liassic neoselachian fauna and are readily accessible for further bulk sampling which will undoubtedly continue to produce more specimens.

WHITBY COAST (EAST PIER–WHITESTONE POINT; NZ 901115–NZ 928104) (POTENTIAL GCR SITE)

Highlights

Historically, Whitby on the North Yorkshire coast is the most important Upper Lias fish-bearing locality in the country, yielding exceptionally preserved material, which includes eight type specimens. The sea cliffs along the coast are continuously eroded, enabling new material to be recovered each year.

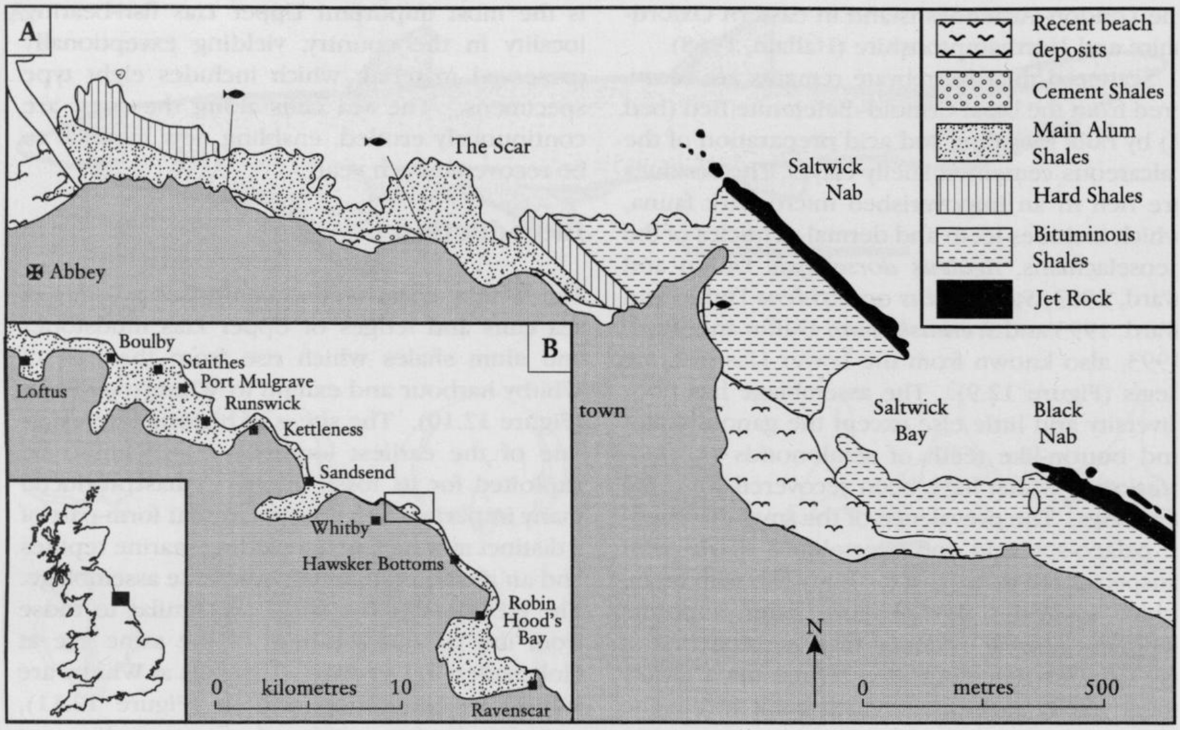
Introduction

The Whitby coast section comprises a series of sea cliffs and ledges of Upper Lias mudstones and alum shales which rise from the east of Whitby harbour and extend to Whitestone Point (Figure 12.10). The site is of historic interest as one of the earliest localities in Britain to be exploited for its fossil fishes. It has produced many important fish specimens that form part of a distinct marine fauna including marine reptiles and an abundant macroinvertebrate assemblage. The elements of the fauna are similar to those from the famous localities of the same age at Holzmaden in Germany. The cliffs at Whitby are subject to continuing erosion (Figure 12.11), and the site has produced many good recent finds and has the potential for more.

The wave-cut platform and cliffs east of Whitby harbour have been famous for their fossil fishes since the early part of the 19th century. In 1828 Young and Bird identified 'petrified pikes' (*Lepidotes semiserratus*) in the Jet Rock succession (1828, p. 261). Five species of fossil fish from the Lias of Whitby were briefly described and several others named in the classic monographic works of Louis Agassiz (1833–1845). Simpson (1855) and Egerton (1852) both recognized additional species and in 1876 a comprehensive faunal list was provided by J.F. Blake (*in* Tate and Blake, 1876, pp. 155–60). In a series of papers between 1886 and 1899, A.S. Woodward described and figured all the Whitby fish specimens deposited in the NHM from the large collections made by Egerton and the Earl of Enniskillen (Woodward, 1886, 1896, 1897, 1898, 1899c). In what was a truly modern examination of the late Liassic fish fauna, Woodward also examined other Natural History Museum specimens and attempted a comparative study with the Upper Liassic fish assemblages from Germany and France.

Description

The Upper Lias (Toarcian, Early Jurassic) of the Yorkshire coast consists of dark shales, with



C Zones	Subzones	Lithostratigraphy			Howarth's Bed Numbers	Thickness	Tate & Blake (1876)	Buckman (1910, 1915)
Hildoceras bifrons	*Catacoeloceras crassum*	Whitby Mudstone Formation	Alum Shale Member	Cement Shales	65–72	5.8 m		*braunianum* Zone
	Peronoceras fibulatum			Main Alum Shales	51–64	15.2 m	*communis* Zone	*fibulatum* Zone
	Dactylioceras commune							*subcarinatum* Z.
				Hard Shales	49, 50	6.3 m		*pseudovatum* Zone
Harpoceras falciferum	*Harpoceras falciferum*		Jet Rock Member	*Ovatum* Band	48	0.25 m		
				Bituminous Shales	41–47	23.0 m	*serpentinus* Zone	*exaratum* Zone
	Harpoceras exaratum			Jet Rock	33–40	7.1 m		
Dactylioceras tenuicostatum	*D. semicelatum*, *D. tenuicostatum*, *D. clevelandicum*, *Protogrammoceras paltum*		Grey Shales Member		1–32	13.3 m	*annulatus* Zone	*tenuicostatum* Zone
		Cleveland Ironstone Formation (part) 0.65 m						

Figure 12.10 (A), (B) Sketch map of the geology near Whitby with (C), rock succession in the local Upper Liassic (after Benton and Spencer, 1995). Fish bearing localities are marked on (A).

intermittent limestone, siltstone and sandy bands, and has been described in local detail (Tate and Blake, 1876; Dean, 1954; Howarth, 1955, 1962, 1973; Hemingway and Wright, 1992). The general succession at Whitby, summarized by Howarth (*in* Cope *et al.*, 1980a), and with revised nomenclature from Powell (1984), is:

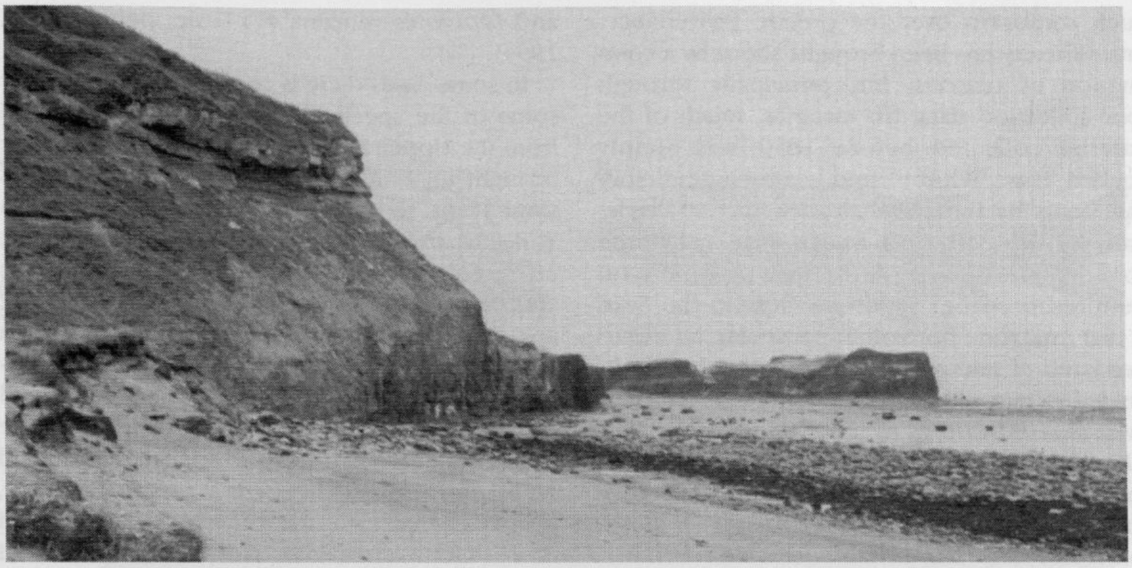


Figure 12.11 Saltwick Bay, Whitby: the cliff at the left is of the Alum Shale, topped by Dogger Sandstone and boulder clay. The distant Nab headland is also of Alum Shale; the Jet Shale crops out on the lower tidal area of the beach beyond the Nab. Both formations have yielded fossil fishes. (Photo: BGS no. A5519, Crown Copyright reserved.)

	Thickness(m)
– – – – – – – unconformity – – – – – – –	
Whitby Mudstone Formation	
Alum Shale Member (lower part of *Hildoceras bifrons* Zone)	
Cement Shales	5.8
Main Alum Shales	15.2
Hard Shales	6.3
Jet Rock Member (*Harpoceras falciferum* Zone)	
Ovatum Band	0.25
Bituminous Shales	23.0
Jet Rock	7.1
Grey Shales Member (upper and middle parts of *Dactylioceras tenuicostatum* Zone	13.3
Cleveland Ironstone Formation (upper part)	0.6

The beds are nearly flat-lying in the sections to the east of Whitby (Figure 12.11). The Jet Rock Member occurs in the seaward portions of the wave-cut platforms at Saltwick Nab and Black Nab just to the east of Saltwick Bay. The Main Alum Shales and Cement Shales occur mainly in the lower part of the cliff, and the upper part consists of the Middle Jurassic rocks above the unconformity. Most of the beds in the Whitby Upper Lias sequence have yielded sporadic fish remains.

The Jet Rock Member comprises well-cemented, finely laminated, grey or brown shales, locally bituminous with bands of small to large calcareous concretions known as 'doggers', up to 5 m in diameter. The unit is 1–3 m thick and the concretion-bearing horizons vary between 0.1 and 1.0 m in thickness. Fossil fishes are common in the Jet Rock Member and rarer remains also occur within the calcareous doggers (see below).

The Bituminous Shales are less well laminated than the Jet Rock and contain less bitumen. The shale units are 3–8 m thick, and there are three or four 0.15 m bands of pyrite-coated concretions. Fossils, including abundant fish remains, are often pyritized in these rocks (Woodward, 1899c; Howarth 1962; Hemingway, 1974).

The Hard Shales are a non-bituminous grey shale unit characterized by scattered calcareous concretions. Small, whole fish remains are typically found in the Hard Shales.

The Main Alum Shales are a sequence of alternating soft, grey, flaggy shales (0.25–5.00 m thick) and irregular bands containing scattered calcareous concretions and sideritic mudstone horizons. The shales typically weather to distinctive brittle flakes (Hemingway, 1974, p. 176).

Fish fossils appear to have been obtained from various horizons throughout the Jet Rock Member and Alum Shales Member, but there is much confusion over the precise provenance. This difficulty has been brought about by a combination of reasons, but principally through poor collection data; for instance, much of the material collected before 1850 was simply labelled 'Lias: Whitby', and bears contradictory statements by the early authors. For example, many of the early fish fossils were recovered from the mining of jet to the west of Whitby, on the foreshore from Sandsend Ness to the Scar. At that time, one horizon in particular, an indurated band of calcareous concretions ('doggers'), yielded so many large bones of the chondrosteid *Gyrosteus mirabilis*, in association with other fish remains, that the miners called it the 'animal dogger' (Tate and Blake, 1876). However, since Tate and Blake's description of the bed, much confusion has surrounded the exact location and position of the horizon in the series.

Recent changes in the nomenclature of ammonite zones have created further problems. Although Benton and Taylor (1984) reviewed the provenance of specimens on the basis of early collectors' reports and on a study of the matrix and ammonites associated with specimens, they focused exclusively on reptile remains. A similar study has not been attempted for the Whitby fishes. They do provide a good reference correlation of the different stratigraphical units and nomenclature used by previous authors, and this is outlined in Figure 12.10. Most of the type specimens and the most abundant specimens of Whitby fish were labelled '*serpentinus*' Zone (Tate and Blake, 1876; Fox-Strangways, 1892). The '*serpentinus*' Zone *sensu* Tate and Blake includes the Jet Rock and the lower portion of the Bituminous Shales, which probably incorporated the fish-bearing 'animal dogger' (bed 43; Howarth 1962). However, Fox-Strangways (1892, pp. 127, 137) moved the upper boundary of the '*serpentinus*' Zone to above the *Ovatum* Bed (bed 48; Howarth, 1962), which is the position currently accepted (Figure 12.10), although the zonal nomenclature has been changed (*falciferum* Zone; Howarth, 1962).

Although it now seems that most of the early specimens were recovered from the Bituminous Shales of the Jet Rock Member, in later Victorian times fish fossils were also collected from the Alum Shale Member during excavations for the alum industry along the coast between Saltwick and Whitby (Fox-Strangways and Barrow, 1915). The Hard Shales still yield abundant *Leptolepis* and *Lepidotes* remains (C. Little, pers. comm., 1994).

In some cases there is confusion over whether some of the specimens were actually collected from the Upper Lias sequence at Whitby or were brought to Whitby from other sources, such as Lyme Regis, to fuel the flourishing fossil trade in Yorkshire in late Victorian times (Tate and Blake, 1876; Fox-Strangways, 1892). In particular the specimens labelled as *Dapedius micans* Agassiz are considered to have been recovered from a Lower Lias locality, either Lyme Regis or Barrow-on-Soar, Leicestershire (Woodward, 1899c), and similar proposals were put forward for the species of *Belonostomus* and specimens labelled as '*Aspidorhynchus anglicus*' Agassiz. However, in his detailed investigation and descriptions of the Whitby fishes, Woodward (1896–1899) could find no clear evidence that this was the case (see Interpretation).

Many of the Whitby fishes, particularly those in doggers, are beautifully preserved in a state of part or complete articulation. Scavenging was presumably minimised by the prevailing anoxic conditions in the bottom sediment, as suggested by the bituminous nature of the rock. Tate and Blake (1876, p. 179) reported that many fossils in the Jet Rock were preserved in jet and these included 'ganoid' scales. Other incomplete skeletons may have been broken up prior to burial or by recent wave action before the specimens were collected from the foreshore. Much of the material of the large chondrosteid *Gyrosteus mirabilis* is disarticulated and, in some cases, fragmentary. Many of the specimens in the NHM recorded by Woodward (1899c) have suffered pyrite decay (1899c, p. 462). However, a taphonomic study of the fish remains has also been hampered by the lack of suitable collection data and in addition by the incompleteness of some specimens, the result of collection failure and artificial 'improvements' made to certain specimens.

Fauna

Large numbers of fish specimens from the Upper Lias of Whitby occur in Victorian collections in many of the provincial museums, but notable collections occur in the NHM, CAMSM, WHIMS and YORMS:

Osteichthyes: Actinopterygii: Chondrostei

Gyrosteus mirabilis A.S. Woodward, 1899

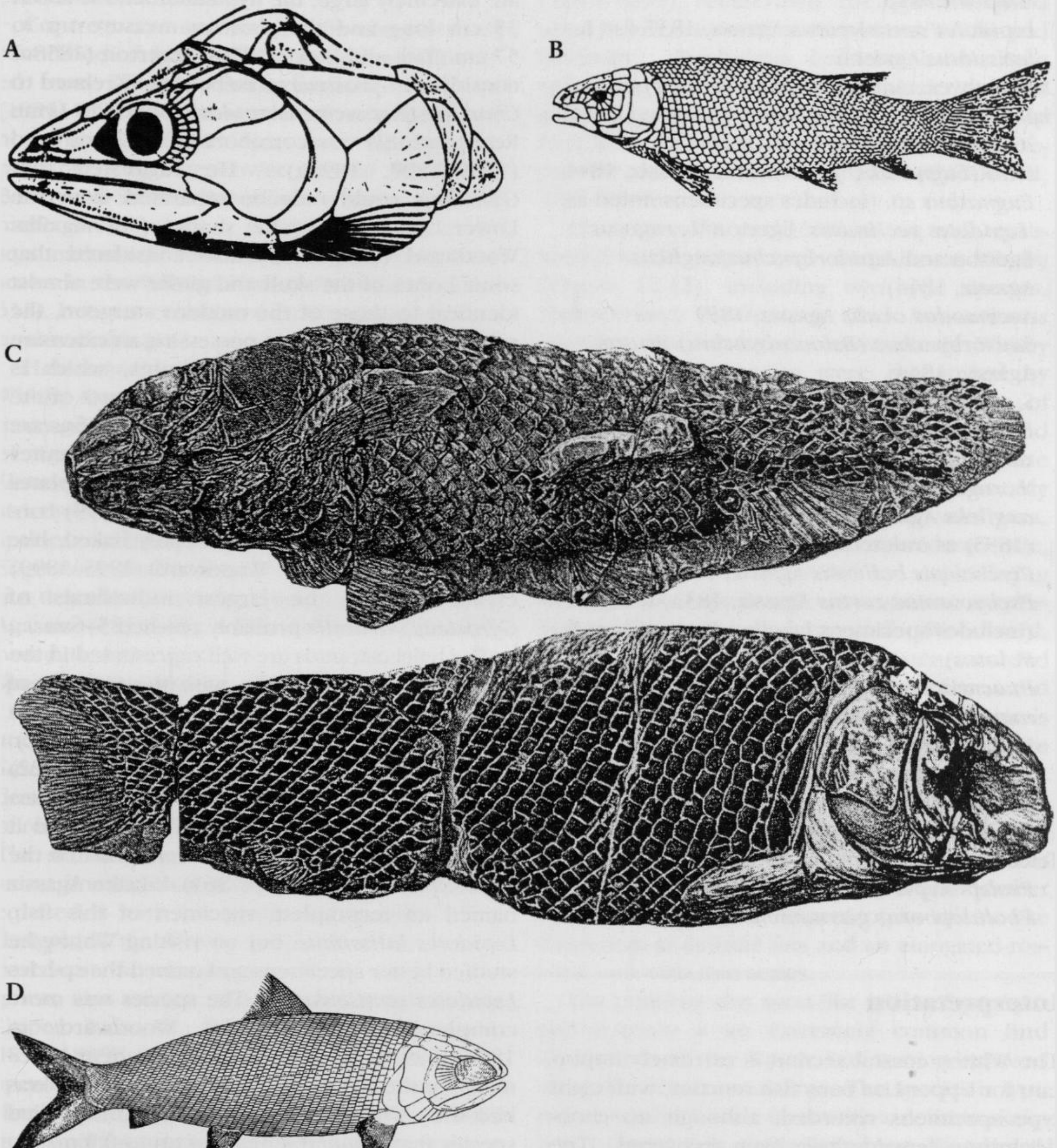


Figure 12.12 Upper Liassic osteichthyan fishes from the coast at Whitby: (A) *Pachycormus curtus* Agassiz, × 0.4, restoration of the head in lateral view by Lehman 1966; (B) *Lepidotes semiserratus* Agassiz, × 0.6, restoration by Jaekel 1929; (C) lateral views of *Lepidotes semiserratus* after Woodward 1895a; 1901, × 0.7; (D) *Ptycholepis* sp. × 0.25.

Osteichthyes: Actinopterygii: Neopterygii: Halecostomi

?Dapedium micans Agassiz, 1844

?Dapedium sp.

Lepidotes semiserratus Agassiz, 1837 (= *L. latissimus* Agassiz)

Osteichthyes: Actinopterygii: Neopterygii: Halecomorphi

?Caturus sp.

Furo (Eugnathus) fasciculatus Agassiz, 1844

Eugnathus sp. (includes specimens noted as '*Lepidotes pectinatus*' Egerton '*L. rugosus*' Egerton and *Aspidorhynchus anglicus* Agassiz, 1844)

Aechmodus ovalis Agassiz, 1839

Saurorhynchus (Belonorhynchus) acutus Agassiz, 1844

S. (B.) brevirostris (Woodward, 1895)

Heterolepidotes sp. includes specimens noted as '*Lepidotes pectinatus*' Egerton, '*L. rugosus*' Egerton and *Aspidorhynchus anglicus* Agassiz (but regarded by Woodward (1895) as indeterminable)

Ptycholepis bollensis Agassiz, 1832

Pachycormus curtus Agassiz, 1833–1844 (includes specimens labelled *P. gracilis* and *P. latus*)

P. acutirostris Agassiz, 1844 (= P. *macropterus* (Blainville))

?P. latipennis Agassiz, 1844

Saurostomus esocinus Agassiz, 1833–1844 (= P. *latirostris*)

Osteichthyes: Actinopterygii: Neopterygii: Teleostei

Proleptolepis saltviciensis Simpson, 1855

Pholidophorus germanicus Quenstedt, 1858

Interpretation

The Whitby coastal section is extremely important for Upper Lias bony fish remains, with eight type specimens recorded, although no chondrichthyan remains have been recovered. The bony fish type material includes the huge bones of the chondrosteid *Gyrosteus mirabilis*, recovered from the so-called 'animal dogger' in the Bituminous Shales. The fossilized remains of the sturgeon-like fish comprise mostly isolated bones, without head or trunk (Woodward, 1895–1899).

The osteology of *Gyrosteus mirabilis* was described in detail by A.S. Woodward in a series of articles on the fossil fishes of Whitby and other Lias localities (Woodward, 1889–1890, 1895–1899). The bones are usually ornamented with tubercles, ridges and striations, and many are extremely large; the hyomandibular is about 35 cm long and the clavicles measure up to 57 cm (Tate and Blake, 1876). Egerton (1858a) considered *Gyrosteus* to be be closely related to *Chondrosteus acipenseroides*, found at Lyme Regis and this was corroborated by Woodward (1889–1890, 1895a). He suggested that *Gyrosteus* could only be separated from the Lower Lias genus by the shape of its maxilla. Woodward (1895–1899) also considered that some bones of the skull and girdle were almost identical to those of the modern sturgeon, the remains differing only in possessing an extensive branchiostegal opercular apparatus, which is also present in *Chondrosteus*. Few parts of the postcranial skeleton are preserved. The fins are imperfectly known, and except for the scutes over the caudal fin, no scales or dermal plates have been found. Woodward (1895–1899) concluded that the body was probably naked, like that of *Chondrosteus*. Woodward (1895–1899) estimated that the largest individuals of *Gyrosteus mirabilis* probably reached 5–6 m.

The halecostomids are well represented in the fish collections of Whitby, with the remains of *Lepidotes semiserratus* being the most common find in the Upper Lias sections (Figure 12.12). These were first noted by Young and Bird (1822) as the remains of the 'genus *Esox* [the pike], several species of which have bony scales; and it seems most akin to the *Esox levivianus* or the *Esox chilensis*' (1822, p. 261). Later Agassiz named an incomplete specimen of this fish, *Lepidotes latissimus*, but on visiting Whitby he studied better specimens and named the species *Lepidotes semiserratus*. The species was more completely described by Woodward in 1895–1899 based upon several excellent specimens, in the NHM. *Lepidotes semiserratus* was hailed by Woodward as a robust, round-bodied species that attained lengths of up to 0.5 m.

The name *Lepidotus rugosus* was given by Agassiz (1844) for specifically indeterminate fragments, which included a portion of squamation referred to either of the halecomorphid genera *Heterolepidotus* or *Eugnathus* by Woodward (1895–1899). This is also the case for the imperfect jaw fragment described as *Aspidorhynchus anglicus* by Agassiz (1833–45) and the incomplete specimen named by Egerton (1843–1852), *Lepidotes pectinatus*. The latter specimen probably represented an unknown, and large species of *Heterolepidotes*, but is too poorly preserved for specific determination (Woodward, 1895–1899).

Controversy surrounds the fragmentary round-bodied halecostome *Dapedium*, recorded from Whitby. According to Woodward (1895–1899) some specimens of *Dapedium* noted by Agassiz (1844) as from Whitby, were probably from the Lower Lias of Whitby or Barrow-on-Soar. *Dapedium micans* was the name given by Agassiz (1844) to a specimen of squamation and some specifically indeterminate scales in the Natural History Museum (NHM P. 515), but was considered by Woodward to be a *nomen dubium*.

Halecomorphids are also abundant in the Whitby fossil fish assemblages, which includes many genera also recorded from the Lower Lias of Lyme Regis (e.g. *Caturus*, *Eugnathus*, *Heterolepidotus* and *Ptycholepis*), several are strictly Upper Lias taxa, and there are five type species. The type specimen of the caturid *Eugnathus fasciculatus* was first recorded but not described from the Upper Lias of Whitby by Agassiz (1833–45). Woodward (1895–1899) noted that the material was too imperfect for specific diagnosis.

Controversy also surrounds the specimens and diagnoses of the two Whitby species of *Saurorhynchus*. The first, *S. acutus*, was described from an imperfect skull and fragment of rostrum from Whitby by Louis Agassiz in 1844. The skull had a low roof and extremely long snout lined with a powerful dentition, and he equated it with his genus *Belonostomus*, but designated the Whitby specimen a new species based on the slenderness of the snout. The genus also occurs at Lyme Regis and in the Upper Lias of Württemberg (Woodward, 1895–1899). However, in a redescription of the specimens Woodward (1895–1899) suggested that they belonged to the Triassic long-snouted genus, *Belonorhynchus*. The second species, *Belonorhynchus brevirostris*, is a typical Lyme Regis form and has also been recovered from the Upper Lias of Germany. The specimen recorded from the Alum Shales of Whitby was once thought to have been from Lyme Regis, but Woodward (1895–1899) concluded that it was probably correctly labelled.

The caturid *Ptycholepis bollensis* was first described by Agassiz (1832) from a fragmentary specimen recovered from the Upper Lias of Whitby, but was originally named by him on material from the German Upper Lias succession of Boll, in Württemberg. Woodward (1895–1899) redescribed the species based upon better preserved material from Whitby and Germany. *Ptycholepis bollensis* is the type species of the fusiform, large-headed caturid genus (Figure 12.12) and reached lengths of up to 0.35 m, of which the skull made up to one-quarter of the total length (Woodward, 1895–1899).

The teleost-like pachycormids are well represented in the Upper Lias succession at Whitby (Figure 12.12), including two type species, *Pachycormus macropterus* and *Saurostomus esocinus*. The former are common in the Whitby Lias, and four species were recognized by Agassiz (1832–1844). However, only one of these species was described at the time, and Woodward (1895–1899) undertook a complete overhaul of the genus. He concluded that only *P. curtus* and *P. acutirostris* were valid taxa. The former is a stout species, of moderate size, reaching lengths of up to 0.5 m, and differing from the type species, *P. macropterus*, in possessing a much shorter skull (Woodward, 1895–1899). *P. curtus* has also been recorded from Upper Lias deposits in France and Germany. The second species, *P. acutirostris*, is based upon an imperfect skull specimen from Whitby, which may in fact belong to *P. macropterus* (Woodward, 1895–1899). A third species, *P. latirostris*, was synonymized by Woodward (1895–1899) with *Saurostomus esocinus*. *Pachycormus* is an important member of the fauna also in respect of its teleost-like characters of delicate fins and an elongated rostrum and with thin scales.

The primitive tiny sprat-like teleost *Leptolepis saltviciensis* is an extremely common find throughout all the Upper Lias section exposed along the Whitby coastline. The species is typically a small, slender form with a delicate skeleton no more than about 7 cm long (Woodward, 1895–1899). A second early teleost represented in the Whitby fossil fish assemblages is the Upper Lias species *Pholidophorus germanicus*, described from material recovered from Württemberg localities in southern Germany (Woodward, 1891b, 1895a).

Comparison with other localities

Other comparable Upper Lias localities occurring along the Yorkshire coast that have yielded a similar marine fauna include Saltwick and the old alum quarries at Kettleness (NZ 8316) and Loftus (NZ 7420). Further Yorkshire coast localities, including Runswick Bay, Robin Hood's Bay, Port Mulgrave, Staithes, Sandsend, Hawsker Bottoms, Boulby and Ravenscar (Old Peak–Blea Wyke Point) have also produced a comparable fauna. The Upper Lias of southern and central England is not so rich in fish fossils as the Lower Lias, but various localities in Somerset, Gloucestershire, Northamptonshire, Leicestershire, Lincolnshire and North Yorkshire have yielded a similar, but less impressive, fauna to that at Whitby. The localities at Blisworth (SP 7354) and Wellingborough (SP 9868) are still accessible but most of the others are inaccessible and have little potential for future finds. The undescribed collections of Upper Lias fossil fish made by Charles Moore from the 'Fish and Saurian Bed' (*falcifer* Zone, Toarcian) around Ilminster, Somerset (ST 3514), and now held in the Bath Geological Museum are comparable to those of Whitby, containing specimens of *Lepidotes*, *Dapedium*, *Caturus* and *Pachycormus* (Moore, 1852, 1856, 1866; Duffin, 1978). They exhibit exceptional three-dimensional preservation (Rayner, 1948), but the localities have now been infilled.

The Upper Lias caps the summits of Alderton (SP 101345) and Dumbleton (SP 008355) Hills in the northern Cotswolds and has yielded from the so-called 'Fish and Insect Beds' (*falcifer* Zone, Toarcian) pale limestone nodules which contain abundant fish and insect specimens. Wright recorded (1865, p. 156) *Sauropsis*, *Pachycormus*, *Pholidophorus*, *Lepidotes* and *Leptolepis*. The 'Fish Bed' at Dumbleton Hill has produced the only British specimens of the Upper Lias pachycormid which is *Euthynotus*, known from northern France and southern Germany (Woodward, 1895a, p. 377–9; Woodward, 1911). The semionotid *Tetragonolepis discus* Egerton 1853 was described from a partial fish from the Dumbleton 'Fish Beds' (Woodward, 1895a, pp. 160–1). Some of these specimens are located in GCM, NHM and other museums.

The fish faunas most similar to those from Yorkshire are from localities in the Upper Lias of south-west Germany (e.g. Holzmaden, Ohmden, Boll, Banz and Altdorf) and France (e.g. Normandy, Franche-Comté). Most of these sites cannot be compared readily with the Whitby section since the recorded finds are too sparse to constitute a 'fauna'. The exception is Holzmaden, Baden-Württemberg, where the bituminous laminated shales and grey mudstones of the Posidonienschiefer, a subdivision of the Schwarzjura ϵ (*tenuicostatum* to *bifrons* zones, Early Toarcian; Urlichs, 1977), have produced hundreds of specimens. These include *Hybodus* and *Paleospinax*, *Lepidotes* and *Dapedium*, *Ptycholepis*, *Tetragonolepis*, *Saurorhynchus*, etc. (Wild, 1990). Hauff (1921) noted that the bulk of these came from his subdivisions II 2 to II 13 (middle ϵ, upper *tenuicostatum* Zone to upper *falciferum* Zone), thus rather older on average than the Yorkshire coast finds.

Conclusion

The Yorkshire coast sites are clearly the best for British Upper Lias fishes, hence their conservation value. The coast between Whitby and Whitestone Point has yielded more specimens, and type specimens, than any other Upper Lias marine site in Britain, and many of them are articulated.

MID-JURASSIC OR DOGGER

The Mid-Jurassic epoch opened with a development of regressive facies across the British Isles (Figure 12.13). Fluvio-deltaic environments spread southwards into northern Britain and the North Sea, whilst central England and (at times) western Scotland (Hudson, 1964, 1983) became sites of shallow lagoonal sedimentation. Southern England was generally an area of marine shallows where extensive successions of shallow-water carbonates were laid down in the absence of terrigenous clastic detritus. In south-west England and farther to the south across Europe, fully marine Tethyan conditions prevailed. Periodic transgressions spread these marine conditions northwards. To the north of the Scottish landmass, boreal marine assemblages occasionally spread southwards into the region.

Fossil fishes have been found in numerous localities in the Mid-Jurassic (Aalenian–Callovian) of southern England and western Scotland, but the most productive sources for fishes are mainly in rocks of Bathonian and Callovian age. The typically shallow-water lagoonal and littoral marine facies of the

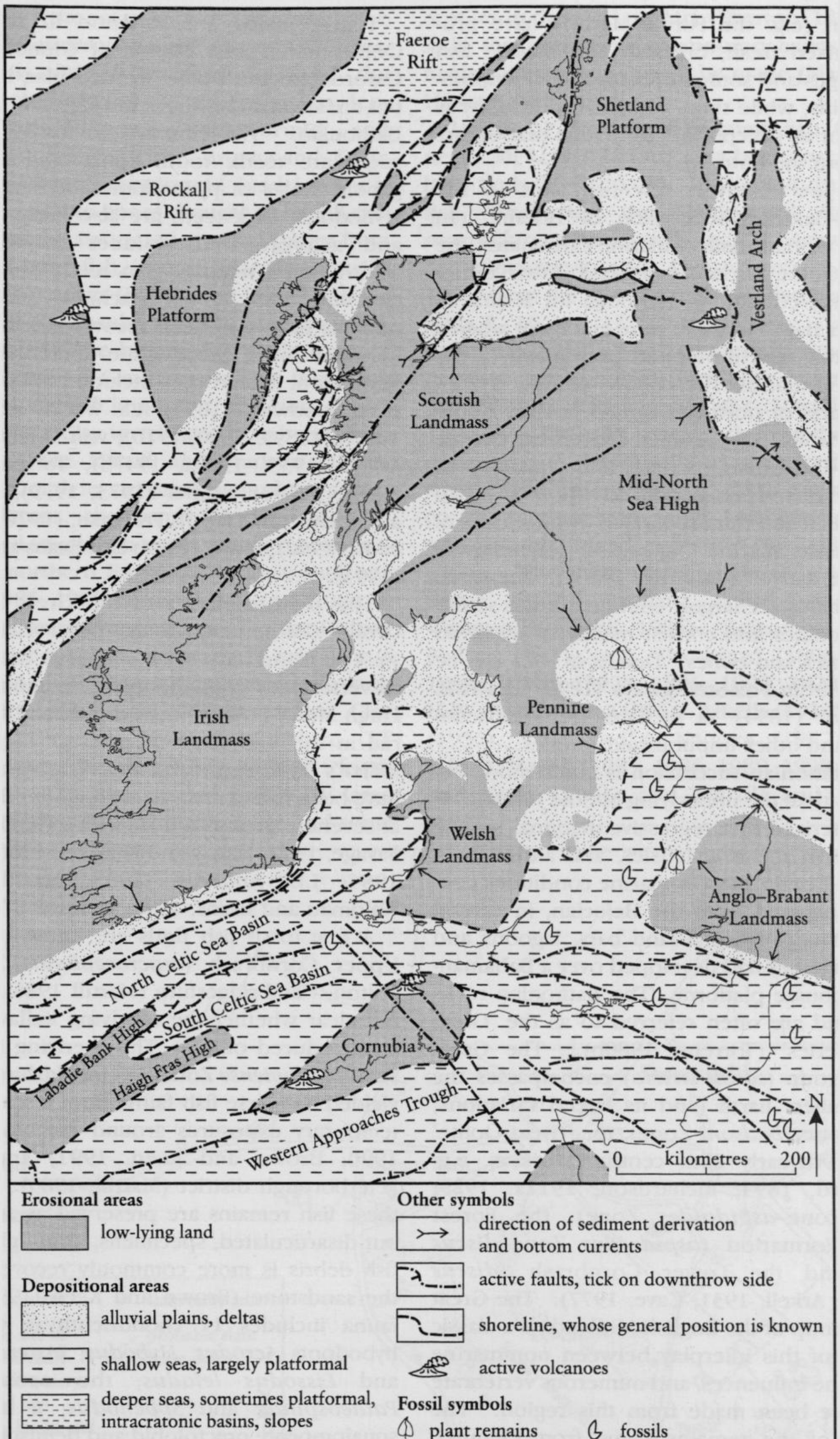


Figure 12.13 Palaeogeography of the Middle Jurassic (after Bradshaw *et al.*, 1992).

Bathonian (e.g. the Forest Marble) have produced mixed fresh, brackish and marine fish assemblages and some important small amphibian remains, while the Callovian Oxford Clay is famous for its exceptional fish fauna that occurs throughout the outcrop.

There are relatively few fish sites in the Aalenian–Bajocian succession of Britain. In southern Britain shallow-marine carbonates, the Inferior Oolite Group, were laid down under high-energy conditions, although for a time in the Lower Bajocian these were emergent when a karstic landscape developed over much of the English Midlands (Bradshaw *et al.*, 1992). Across parts of northern Britain, a river floodplain environment prevailed (Ravenscar Group, Aalenian–Bathonian), where four episodes of alluvial facies were deposited upon a broad coastal plain and were separated by interludes of transgressive marine deposition (Hemingway and Knox, 1973; Cope *et al.*, 1980a). The vertebrate remains are largely confined to the southern carbonates and consist mainly of scattered teeth, scales and bones. Details of sites can be obtained from Fox-Strangways (1892) and H.B. Woodward (1894) as well as from museum records and other unpublished sources.

The Bathonian succession is much more fossiliferous than the underlying Middle Jurassic. It is characterized by a regressive marginal marine sequence in the British Isles, and although in southern Britain shallow marine conditions continued unabated from the Bajocian, in central regions a network of island bars, lagoons and coastal marshes had developed over a Bahaman-type carbonate platform. The Bathonian rocks of England are often referred to as the 'Great Oolite Series' (Torrens, 1980b). The Great Oolite Group (*sensu stricto*) encompasses the Lower Fullers Earth (and its lateral variations; *zigzag* Zone–?*hodsoni* Zone), the 'Great Oolite' (*sensu* 19th–early 20th century workers, e.g. Woodward, 1894; Richardson, 1911a, 1929; *zigzag* Zone–*aspidoides* Zone), the Forest Marble Formation (*aspidoides* Zone–*discus* Zone) and the Lower Cornbrash (*discus* Subzone; Arkell, 1931; Cave, 1977). The Great Oolite Group of the English Midlands is a classic example of this interplay between non-marine and marine influences, and numerous vertebrate finds have been made from this region. The majority of the remains come from channel, lagoonal and lacustrine deposits, and these document a number of major faunal changes.

Fish remains are common in the 'Great Oolite' and Forest Marble of Gloucestershire, Oxfordshire and Dorset in particular, but localities are known elsewhere throughout the British Bathonian. The commonest fossils in these rocks are teeth, tooth plates and the thick ganoid scales of pycnodonts and semionotids. Hybodont shark teeth are also fairly common, and acid-prepared residues include many 'caturid'-type neopterygian teeth, shark denticles and teeth of neoselachians. Amphibian remains have also been recovered from several localities in the 'Great Oolite' and Forest Marble Formation. References include Phillips (1871), H.B. Woodward (1894), A.S. Woodward (1887a, 1887b, 1889a, 1890, 1910), von Huene (1926), Arkell (1933, 1947a, 1947b), Torrens (1968, 1969a, 1969b), Palmer (1973, 1979), Sellwood and McKerrow (1974), Freeman, (1976), Metcalf *et al.* (1992), Evans (1992) and Evans and Milner (1994).

The lagoonal facies of the Great Estuarine Group (Bathonian) of the Inner Hebrides in west Scotland have been known as sites for fossil vertebrates since the mid-19th century when Hugh Miller (1858) noted reptile and fish material in the Kildonnan Member of Eigg ('Hugh Miller's Bone Bed'). Further vertebrate remains have been found recently throughout the Group at several places in the Hebrides (Waldman and Savage, 1972; Harris and Hudson, 1980; Savage, 1984; J.E. Andrews, 1985; Martill, 1985; Waldman and Evans, 1994; Taylor *et al.*, 1995).

A few fossil fish finds are known from the Upper Cornbrash (*macrocephalus* Zone) of Stilton, Cambridgeshire (Martill 1986), but it is not clear whether the overlying Kellaways Clay has produced others. The overlying Kellaways Sand (*calloviense* Zone) of Lincolnshire recently yielded a diverse fish fauna from a scattering of temporary exposures around Lincoln (Brown, 1990; Brown and Keen, 1991) and in the Peterborough district (Martill, 1985). Some of these fish remains are preserved as associated, but disarticulated, specimens, although isolated fish debris is more commonly recovered from the sandstone (Brown and Keen, 1991). The fauna includes 11 chondrichthyan taxa (the hybodonts *Acrodus*, *Hybodus*, ?*Asteracanthus*, and *Lissodus leiodus*; the neoselachians *Palaeospinax* and *Sphenodus*; a hexanchid squalomorph; orectolobid and hemiscylliid galeomorphs; and the chimaeroids *Ganodus semistriatus* and *Ischodus egertoni*) and nine taxa of bony fishes (the semionotid *Lepidotes*; the dapediid *Heterostrophus*; the caturids *Caturus*, *Osteorachis* and *Heterolepidotus*; and the teleosts *Aspidorhynchus*, an unknown leptolepid, an unknown pachycormid and *Leedsichthys*; Brown, 1990; Brown and Keen, 1991). The huge pachycormid *Leedsichthys* is represented by two bones thought to be gill-rakers. Much of the associated material comes from the smaller bony fish, in particular the caturids and *Aspidorhynchus* (Brown and Keen, 1991).

The most spectacular remains of marine faunas derive from the bituminous shale units of the Lower Oxford Clay (particularly the *jason* Zone), and several important museum collections of Oxford Clay vertebrates have been made (for review, see Martill and Hudson, 1991). Many are complete, or nearly complete, articulated skeletons, the result of deposition in undisturbed stagnant bottom waters characteristic of the northern European Jurassic shelf sea (Martill, 1985, 1986, 1988; Martill and Hudson, 1991). The marine vertebrates from the Oxford Clay are particularly well preserved and form a centre-point of all international taxonomic studies. Indeed, the Lower–?Middle Oxford Clay locality at Christian Malford, Wiltshire (ST 957774), may be the only British fossil Lagerstätte. This site yielded extremely large numbers of beautifully articulated fish and some reptiles in the 19th century (Egerton, 1843), but sadly they were from a temporary exposure and further collections cannot be made (Martill and Hudson, 1991).

Martill (1986) noted isolated fish finds in nearly all Lower Oxford Clay horizons, particularly Beds 7, 8, 10, 11, 13–17 and articulated fish, (including the semionotid *Lepidotes macrochireus* Woodward, and the pachycormids *Asthenocormus* and *Hypsocormus*; Martill, 1986) from the more bituminous fissile shales of Beds 8, 10 and 12 (all *jason* Zone, Callovian; Callomon, 1968). Some of these fish specimens preserve gut contents, including fragments of the sprat-like teleost *Leptolepis* (Martill, 1986). The Lower Oxford Clay extends from the Dorset coast around Weymouth to the Scarborough coast, Yorkshire. However, there are no good coastal sections and active brickpits form the only sizeable inland exposures for field investigation. The main vertebrate-bearing localities occur around Bedford, Peterborough and Weymouth (Martill, 1986). References include Phillips (1871), A.S. Woodward (1886, 1888c, 1889a, 1890, 1892b, 1896, 1897, 1928, 1929); H.B. Woodward (1895), Arkell (1933), Leeds (1956), Ward and McNamara (1977), Thies (1983), Martill (1985, 1986, 1989, 1990), Brown and Keen (1991) and Martill and Hudson (1991).

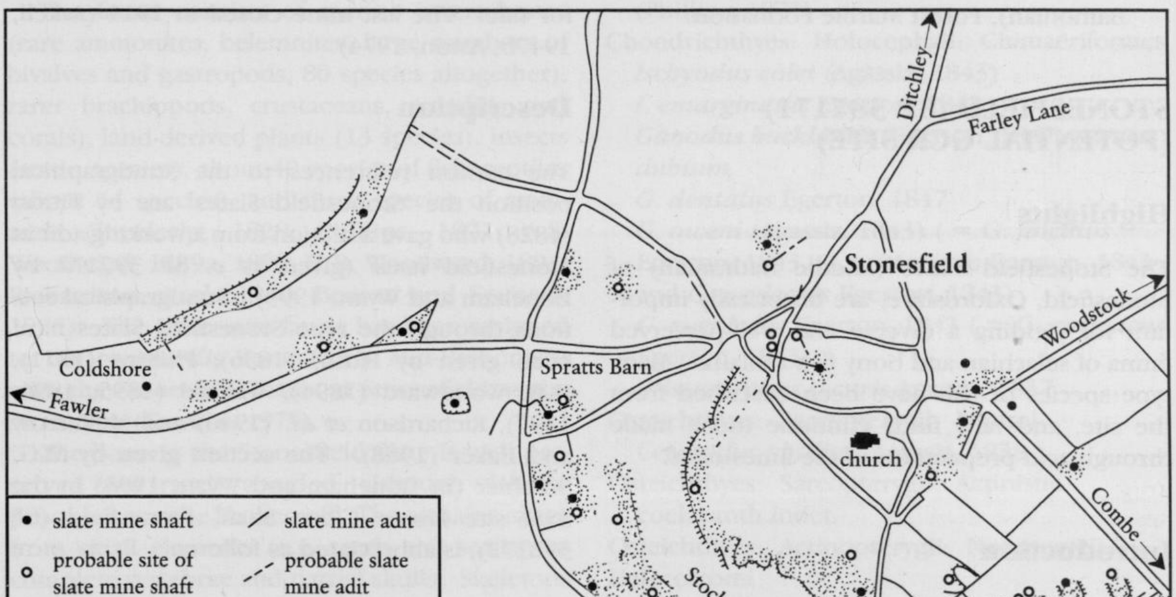


Figure 12.14 Map of the mines and workings in the Stonesfield Slate around Stonesfield (after Aston, 1974).

FISH AND TETRAPOD SITES

Three fish and tetrapod sites have been selected as GCR sites from the huge numbers that have been noted in the literature, as those representing the greatest range of faunas and preservation types, and as having the greatest potential for future collecting. These are all Bathonian in age; none of the Aalenian or Bajocian sites were reasonably accessible or have yielded material of good preservation, taxonomic interest or quantity. In addition, none of the important Callovian localities could be selected because they have either been lost to infill or degradation, or they are currently worked in a way that prevents the conservation of fossiliferous horizons. In addition, it is not possible to say that any one or two Oxford Clay sites are likely to be more or less productive than any other. The Mid Jurassic sites selected as GCR sites are:

1. Stonesfield, Oxfordshire (SP 387171). Mid-Jurassic (Middle Bathonian), Taynton Limestone Formation.
2. Kirtlington Old Cement Works, Kirtlington, Oxfordshire (SP 494199). Mid-Jurassic (Upper Bathonian), White Limestone Formation to Lower Cornbrash.
3. Watton Cliff, West Bay, Dorset (SY 451908–453907). Mid-Jurassic (Upper Bathonian), Forest Marble Formation.

STONESFIELD (SP 387171) (POTENTIAL GCR SITE)

Highlights

The Stonesfield Slates (Middle Bathonian) of Stonesfield, Oxfordshire, are historically important for yielding a diverse and well-preserved fauna of selachian and bony fish remains. Many type species of fish have been described from the site, and new finds continue to be made through acid preparation of the limestones.

Introduction

The series of quarries and mines that formerly worked the Stonesfield Slate at Stonesfield (Figure 12.14) are famous for yielding one of the most diverse vertebrate faunas of the Middle Jurassic. The Stonesfield 'slates', or 'tilestones' (Richardson *et al.*, 1946, p. 33) of Stonesfield contain an unusual mixture of marine, freshwater and terrestrial forms (Arkell, 1947a, pp. 40–1). The remains are all isolated elements, but include those of terrestrial animals such as mammals, tritylodont 'mammal-like reptiles', dinosaur, and pterosaurs, as well as marine reptiles and an abundant fish fauna (Phillips, 1871; Platt, 1758). The site has also been designated an SSSI for fossil reptiles and fossil mammals, and is included in the recent GCR review of British fossil reptile sites by Benton and Spencer (1995). Although the quarrying industry at Stonesfield is now extinct, re-excavation could produce many more finds.

In Roman times, local country houses were roofed with squared slabs of limestone 'slate'. In the 16th or 17th century it was discovered that when the freshly dug stone was exposed to the frost, it would split into thinner sheets. The quarries expanded production, providing roofing materials for local houses and building material for more important buildings farther afield (Arkell, 1947b). They remained productive until the late 19th century. The stone was reached by vertical shafts, usually about 6 m deep, and horizontal galleries were driven through the bed. During the 18th and 19th centuries, slate-digging employed numerous craftsman. The slate-makers examined each slab, and put aside fossils for sale. The last mine closed in 1911 (Arkell, 1947b; Aston, 1974).

Description

The earliest references to the stratigraphical position the 'Stonesfield Slates' are by Fitton (1828) who gave a section from a working adit in Stonesfield itself (given as *c.* SP 397172 by Boneham and Wyatt, 1993). Stratigraphical sections through the type Stonesfield Slates have been given by Fitton (1836), Phillips (1871), H.B. Woodward (1894), Walford (1895, 1896, 1897), Richardson *et al.* (1946) and McKerrow and Baker (1988). The section given by M.G. Sumbler (*in* Boneham and Wyatt, 1993) in the SSSI site Home Close Shaft, Stonesfield (SP 392172), is abbreviated as follows:

	Thickness (m)
Hampen Marly Formation	7.75
Taynton Limestone Formation	
Limestone, oolitic, shell-fragmental, sparry, cross-bedded	1.13

Marl, oolitic, shell-fragmental, shelly;pebbles of limestone and sandstone in lower part 0.31
Limestone, oolitic, shell-fragmental, sparry 0.27
Stonesfield Slate
Sandstone, fine-grained, calcareous, hard, with scattered ooliths; soft, cross-laminated and fissile at 12.78–13.13 m [depth in adit]; continuing below in hard, laminated, fissile sandstone with strings of ooliths; variably oolitic from 13.30 m with oyster shells 1.06
Limestone, coarse-grained oolitic, shell-fragmental, sparry 0.28

The Stonesfield Slate occurs low down within the Great Oolite sequence and in sedimentary character is typical of the succession as a whole, being composed mostly of shallow-marine carbonate facies (Figure 12.15). The Stonesfield Slate tilestone facies consists of quartz sands and siltstones with fine laminae (0.1–0.3 m apart) of ooliths. The unit is no more than 1.8 m thick at its type locality and it is confined to an elliptical area within 1.5 km around Stonesfield (Figure 12.14, based upon work by Aston, 1974, and Boneham and Wyatt, 1993).

The fauna consists of marine invertebrates (rare ammonites, belemnites, large numbers of bivalves and gastropods, 80 species altogether), rarer brachiopods, crustaceans, annelids and corals), land-derived plants (13 species), insects (seven species), about 40 species of fish, reptiles (about 14 species), and three species of mammals (Broderip, 1828; Phillips, 1871; A.S. Woodward, 1889a, 1890; H.B. Woodward, 1894; Richardson *et al.*, 1946; Benton and Spencer, 1995). The ammonite fauna has been assigned to the *progracilis* Zone (early Mid-Bathonian) with the Stonesfield Slates at Stonesfield as the stratotype (Torrens, 1974).

The bone in the Stonesfield Slate is well preserved and rarely abraded, although delicate processes may be broken off. The remains range from small elements (e.g. teeth and scales) to complete vertebrae and partial skulls. Skeletons are disarticulated. Thus there is evidence of short-term transport and sometimes violent breakage, and the bones may be associated with other coarse clasts (pebbles, shells, etc.).

Fauna

Major collections may be seen in the NHM, BGS(GSM), CAMSM, OUM. Most older university, city and private fossil collections in Britain have some teeth or bone scraps from Stonesfield, but are not recorded here.

Chondrichthyes: Elasmobranchii: Euselachii: Hybodontoidea
Asteracanthus semisulcatus Agassiz, 1837
A. acutus Agassiz, 1937
(*A. (Strophodus) favosus* (Agassiz, 1843) = A. *magnus*)
A. (Strophodus) lingualis (Phillips, 1871)
A. (Strophodus) magnus (Agassiz, 1838)
A. (Strophodus) tenuis (Agassiz, 1838)
Hybodus apicalis Agassiz, 1843 (fin spine)
H. dorsalis Agassiz, 1843
H. grossiconus Agassiz, 1843
H. levis A.S. Woodward, 1889
H. marginalus Agassiz, 1843
H. polyprion Agassiz, 1843
Leptacanthus serratus Agassiz (fin spine), 1837
L. semisulcatus Agassiz (fin spine), 1839
Lissodus leiodus (A.S. Woodward, 1887)
Chondrichthyes: Elasmobranchii: Neoselachii: Batoidea
Breviacanthus (Nemacanthus) brevis (Phillips, 1871)
Chondrichthyes: Holocephali: Chimaeriformes
Ischyodus colei (Agassiz, 1843)
I. emarginatus Egerton, 1843
Ganodus bucklandi (Egerton, 1847) *nomen dubium*
G. dentatus Egerton, 1847
G. oweni (Agassiz, 1843) (= G. *falcatus* Egerton, 1843, *G. psittacinus* Egerton, 1843 and *G. neglectus* Egerton, 1843)
G. rugulosus Egerton, 1843 (= G. *curvidens* Egerton, 1843)
Pristacanthus securis Agassiz, 1837
Osteichthyes: Sarcopterygii: Dipnoi
Ceratodus phillipsi Agassiz, 1838
Osteichthyes: Sarcopterygii: Actinistia
coelacanth indet.
Osteichthyes: Actinopterygii: Neopterygii: Halecostomi
Gyrodus perlatus Agassiz, 1844
Gyronchus (Mesodon) rugulosus (Agassiz, 1839–1844) (= *Gyrodus trigonus* Agassiz, 1837, *Pycnodus latirostris* Agassiz, 1844, *Pycnodus parvus* Agassiz, 1844)

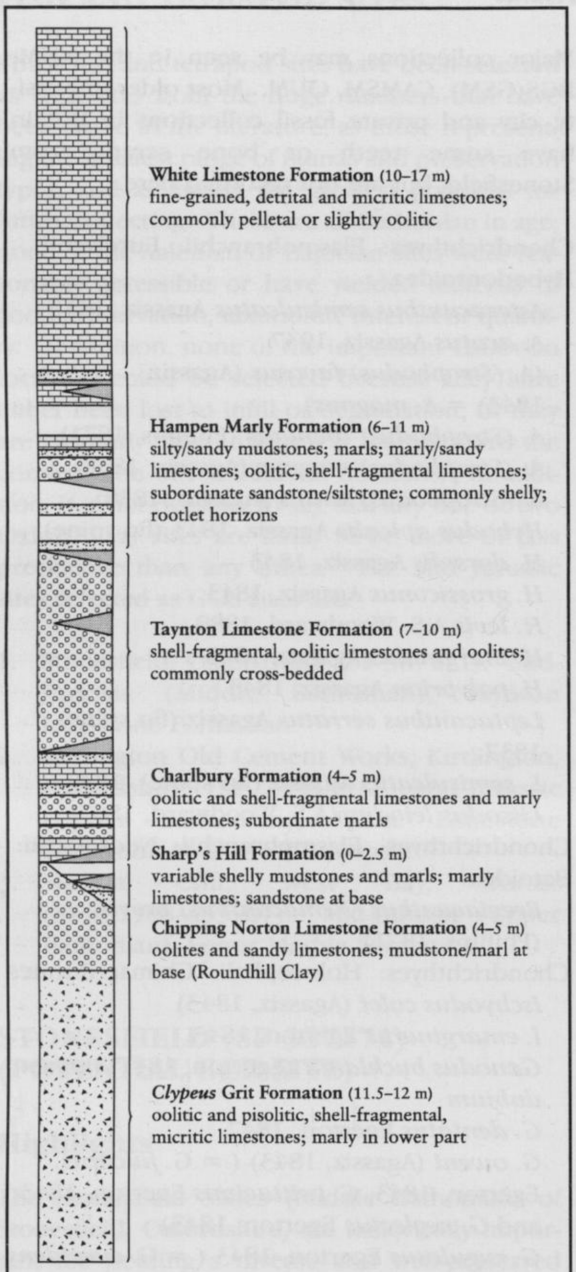


Figure 12.15 The Bathonian succession at Stonesfield, where the 'slate' occurs within the Taynton Limestone Formation (after Boneham and Wyatt, 1993).

G. (Mesodon) tenuidens (A.S. Woodward, 1895)
G. (Scaphodus) heteromorphus (A.S. Woodward, 1890) (= *Gyronchus ?oblongus* Agassiz, 1843)
Mesodon biserialis A.S. Woodward, 1889
M. bucklandi (Agassiz, 1833–1844) (= *Pycnodus hughii* Agassiz, 1844, *Pycnodus didymus* Agassiz, 1839–1844, *Pycnodus ovalis* Agassiz, 1839–1844 and *P.* Agassiz 1844)
?Lepidotes unguiculatus Agassiz, 1837
Lepidotes tuberculatus Agassiz, 1837
Macrosemius brevirostris Agassiz, 1844 *nomen dubium*

Osteichthyes: Actinopterygii: Neopterygii: Halecomorphi
Aspidorhynchus crassus A.S. Woodward, 1890 (= *Belonostomus flexuous* Philips, 1871 and *Sauropsis mordax* Agassiz, 1844)
Belonostomus leptosteus Agassiz, 1844
Caturus pleiodus Agassiz, 1844 *nomen dubium*

Osteichthyes: Actinopterygii: Neopterygii: Teleostei
'Allothrissops' disjectus A.S. Woodward, 1890
Leptolepis woodwardi Nybelin, 1974
Pholidophorus minor Agassiz, 1843–1844 *nomen dubium*
Ctenolepis cyclus Agassiz, 1843 *nomen dubium*

Interpretation

Sellwood and McKerrow (1974, pp. 204–5) noted sedimentary structures in the Stonesfield Slates that are indicative of deposition in upper flow regime conditions. Storm-produced scours occur filled with shell lags. The fossils point to a shallow-marine environment with a large input of terrestrial material. The bones, plants and insects may have been concentrated by rapid burial in sands brought offshore by storm-induced rip-currents. The features of bone preservation in a disarticulated state, and in coarse clastic units, point to sorting and rapid deposition, possibly during storms.

As in much of the Great Oolite Group of Oxfordshire, the clastic sediments and the land-derived plants and animals reflect the influence of the nearby London–Ardennes and Pennine–Welsh landmasses (Cope *et al.*, 1992), but the ammonites indicate that the Stonesfield Member is one of the few beds in the Bathonian

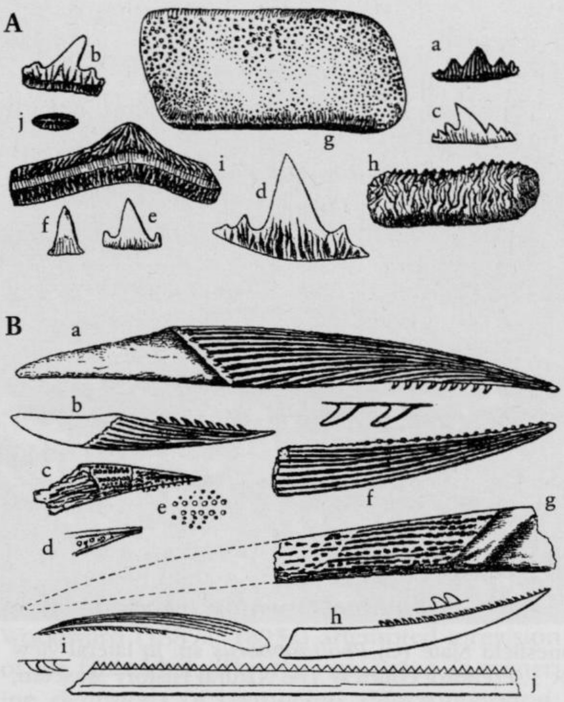


Figure 12.16 Vertebrate remains from the Stonesfield Slate were well known when Phillips published this plate in his Geology of Oxford and Thames Valley (1871): (A) all at × 1; a and b, *Hybodus jugosus* Phillips; c, *H. polyprion* Agassiz; d–f, *H. grossiconus* Agassiz; g, *Strophodus magnus* Agassiz; h, *S. lingualis* Phillips; i, *S. tenuis* Agassiz; j, *Acrodus* sp. (B) all at × 0.5; a, *Hybodus dorsalis* Agassiz; b, *H. apicalis* Agassiz; c, *Nemacanthus brevis* Phillips; d, *Ischyodus* sp.; e, granulated surface; f, *H. marginatus* Agassiz; g, *Asteracanthus tenuistriatus* Agassiz; h, *Leptacanthus striatus* Agassiz; i, *L. semi-striatus* Agassiz; j, *Pristacanthus securis* Agassiz. Several of these names are now invalid – the specimens belong to pre-established taxa. (Continued on p. 388.)

of Oxfordshire to be deposited in proximity to open marine conditions.

The dating and precise stratigraphical position of the Stonesfield Slate have been problematic because of its limited exposure and outcrop (Figure 12.14), and because of the scarcity of ammonites. Most authors have assumed that the Stonesfield Slate was laterally equivalent to the 'Stonesfield Slate' of Eyford, Gloucestershire (the Cotswold Slate or Eyford Member), and even to units near Bath and in Northamptonshire, and it was once regarded as a useful marker bed for the base of the Great Oolite (Fitton, 1836; Hull, 1859; H.B. Woodward, 1894; Walford, 1895, 1896).

Following the pioneering work of the 19th century and most importantly after the extinction of the mining industry at Stonesfield, recent stratigraphical positioning of the tilestones at Stonesfield has retained a degree of uncertainty. The most recent stratigraphical work on the tilestones (Wyatt, 1981; Boneham and Wyatt, 1993) was based upon a re-evaluation of the early sections at Stonesfield and boreholes in both the Stonesfield (Boneham and Wyatt, 1993) and Cheltenham (Wyatt, 1981) districts, and confirms the early sections. The 'slates' at Stonesfield were worked at several different horizons from within the Taynton Limestone Formation: to the west and in the village they occur at the top and in the middle of the formation, whilst in the east they occur at a much lower level towards the base of the formation (Figure 12.15, after Boneham and Wyatt, 1993).

The lithostratigraphical term 'Stonesfield Member' of the Sharps Hill Formation has been abandoned (see review in Boneham and Wyatt, 1993), whilst the 'Cotswolds Slates' (formalized as the Eyford Member) were reassigned to the newly defined Charlbury Formation (Boneham and Wyatt, 1993, p. 134), based on work in the Cheltenham and Cirencester districts (Wyatt, 1981).

Selachian remains, both hybodonts and neoselachians, are an important element of vertebrate faunas (Figure 12.16). (Many hybodont shark taxa were described from scattered teeth and fin spines from Stonesfield in the 19th century (Agassiz, 1833–1845; Phillips, 1871; Woodward, 1889a, 1890) and some of the species are probably synonyms). *Hybodus* teeth are particularly common in most facies, and are dominated by *H. grossiconus* and *H. polyprion*, species common in the Great Oolite Group (Woodward, 1890). Young (1984) has suggested that the teeth of *H. grossiconus* from Stonesfield are structurally similar to those of the primitive neoselachian shark *Palaeospinax egertoni* from the Toarcian of Holzmaden. Rarer multicuspid teeth may represent at least one other species. Other hybodont remains are the large crushing teeth of *Asteracanthus (Strophodus) magnus* and of the smaller *A. (S) tenuis* and rare *A. (S.) lingualis*, which are present within most facies at Stonesfield (Woodward, 1890). *Asteracanthus* has a heterodont dentition of large lateral crushing teeth and smaller cuspate anterior teeth (Cappetta, 1987) and is considered to be a large marine form (possibly attaining lengths of up to 4 m) that fed on crustaceans and molluscs.

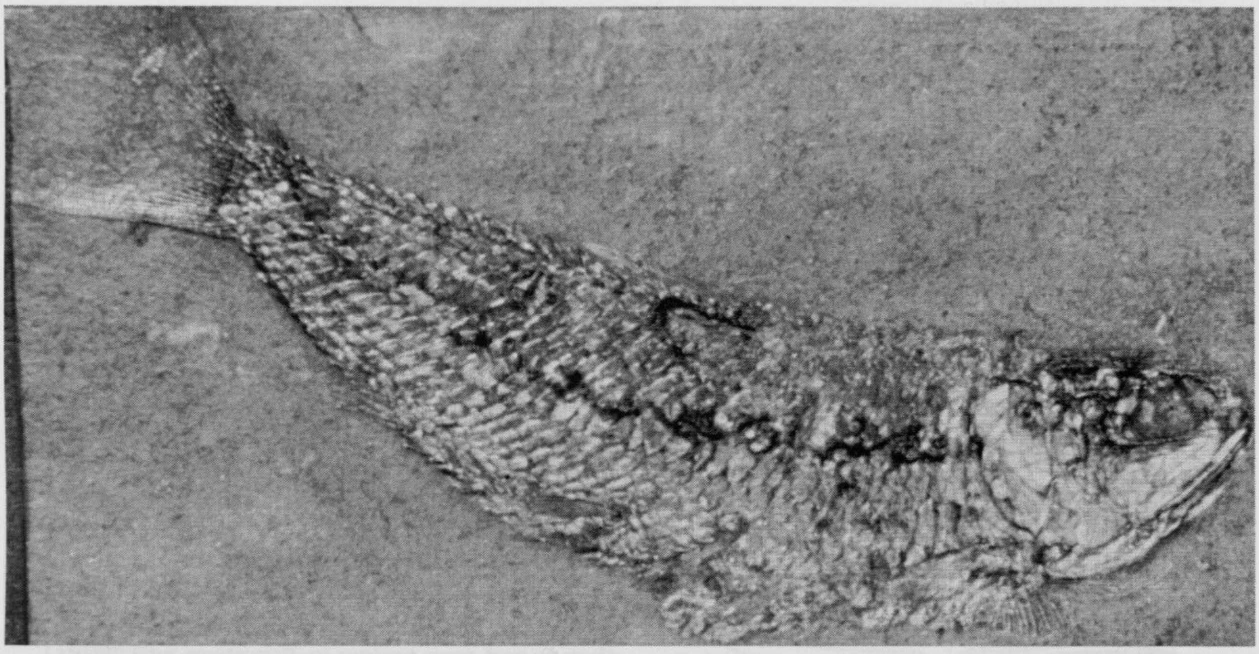


Figure 12.16 – *contd.* Vertebrate remains from the Stonesfield Slate (C) *Pholidophorus* sp. in lateral view showing rare excellent preservation of fish in this facies, × 1.0 (Photo: courtesy The Natural History Museum, London, T00848/A).

Previous authors working on Bathonian specimens (e.g. Phillips, 1871; Woodward, 1890, 1892b) classified these different tooth forms (Figure 12.16) as several species, including *A. (S.) lingualis* and *A. (S.) magnus* for the lateral teeth and *A. (S.) tenuis* for the anterior dentition, which are synonomous according to some authors (e.g. S. Metcalf and C. Underwood, pers. comm.). The fin spine taxon *A. semisulcatus* from Stonesfield was said by Woodward (1889a, p. 312) to be synonymous with the common tooth taxon, *A. magnus*.

Rarer hybodont teeth are represented by *Acrodus* sp., possibly synonymous with the small *Lissodus leiodus*, a species known from the Stonesfield Slates of Stonesfield, the Eyford Member of Minchinhampton and Severnhampton, Gloucestershire, the Forest Marble of Atford, near Bath, Somerset, and Bajocian material from Brora, Scotland (Woodward, 1887b, 1889a, 1890; Savage, 1963; Duffin, 1985; S. Metcalf and C. Underwood, pers. comm.). Hybodont spines are uncommon, but are represented by *Hybodus apicalis* and *H. dorsalis* (probably synonymous with the most common tooth species, *H. grossiconus* and *H. polyprion*; Metcalf and Underwood, pers. comm.). The fin spine genus *Leptacanthus* represents a very rare element and is considered by some (e.g. Cappetta, 1987) to be congeneric with *Hybodus* or *Acrodus*, although earlier references (e.g. Woodward, 1890, p. 290) suggested a chimaeroid affinity.

No teeth of neoselachian sharks have been recorded from the Stonesfield Slates, but sampling may not truly reflect their absence.

Beak-shaped and triangular mandibular and palatine dental plates (Figure 12.16) are fairly abundant in both tilestone facies of the 'Stonesfield Slates' and Eyford Member and represent several species of the chimaeroids *Ischyodus* (Figure 12.17) and *Ganodus*. Two species of *Ischyodus*, *I. colei* and *I. emarginatus*, three well-defined species of *Ganodus*, *G. oweni*, *G. dentatus* and *G. rugulosus*, and one poorly defined form, *G. bucklandi*, have been described from Stonesfield. Many more forms of *Ganodus* mandibular teeth were given specific names by Egerton (1843, 1847), but these were synonymized with the species listed above by Woodward (1889a).

The long list of bony fish remains from Stonesfield includes the type specimen of the lungfish *Ceratodus phillipsi* and several bones, including gular plates and a pterygo-quadrate in the NHM and OUM of an undetermined coelacanth (Woodward, 1890). The taxonomy of the pycnodonts from Stonesfield is a mess as numerous fragmentary dentitions and scales were given specific names by early workers (Prevost,

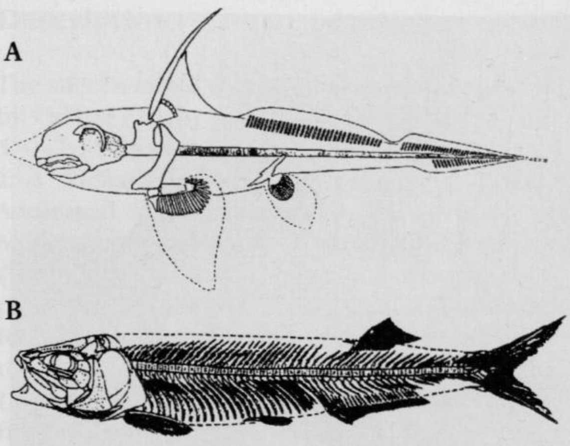


Figure 12.17 Fishes from the Stonesfield Slate. (A) The chimaeroid *Ischyodus* sp. in lateral view, × 0.5; (B) *Allothrissops*, × 0.3, restoration in lateral view (after Taverne, 1977).

1825; Agassiz, 1833–1845; Phillips, 1871). Woodward (1889a, 1895a) attempted a revision of the faunal list. The type specimen (a vomerine dentition) of *Gyronchus (Macromesodon) rugulosus* was described from Stonesfield; this species also includes the species *Gyrodus trigonus*, named by Agassiz (1833–45) on an unabraded example (NHM) of the upper dentition, and *Pycnodus latirostris* and *P. parvus*, based respectively upon large and small splenial dentitions by Agassiz (1833–45; Woodward, 1895a). Other species described from Stonesfield are *Procinates biserialis* based upon lower dentition (Woodward, 1889a) and *Gyronchus (Mesodon) tenuidens*, a small species known only from its splenial dentition (Woodward, 1895a, p. 207). The scale taxon '*Gyrodus perlatus*' is probably referable to *Macromesodon* (Woodward, 1889a, 1895a).

The semionotid *Lepidotes tuberculatus* Agassiz, 1837 is a dubious species described from scattered skeletal remains and scales in the Stonesfield Slates and other Bathonian deposits (Woodward, 1895a, pp. 88–9). *Macrosemius brevirostris* was named by Agassiz (1833–45) from material (a possible maxilla and left dentary bone) recovered from the 'Stonesfield Slates', but Woodward (1895a, pp. 180–1) found them insufficient for taxonomic determination and the species should be regarded as a *nomen dubium*.

The aspidorhynchid *Aspidorhynchus crassus* is a small species known only from isolated jaws and skulls in the Stonesfield Slates of Stonesfield. Agassiz (1833–45) gave the name *Sauropsis mordax*, but did not figure or describe the remains, which A.S. Woodward later referred to this halecostome genus not previously recorded from the Middle Jurassic (Woodward, 1889a, p. 296). Agassiz (1833–45) recorded by name only the presence of *Belonostomus leptosteus* in the tilestones at Stonesfield, which Phillips (1871) later figured. Although this genus is easily confused with *Aspidorhynchus*, it may be a valid taxon (Woodward, 1889a, p. 296), as fragmentary skulls in the NHM suggested the presence of *Belonostomus* in the 'Slates'.

The teleosts are represented by *Leptolepis* and *Pholidophorus*, '*Allothrissops*' (Figure 12.17B) and a dubious form based on rounded flank scales of an unknown actinopterygian, called *Ctenolepis cyclus* (Woodward, 1890). '*Allothrissops*' *disjectus* and '*L.*' *woodwardi* Nybelin are valid species based on abundant and well-defined fragmentary specimens, but *Pholidophorus minor* is based on a poorly preserved cranial roof and is a pholidophorid.

The reptile fauna of Stonesfield includes several aquatic piscivorous forms, such as the long-snouted crocodilians *Teleosaurus* and *Steneosaurus* (Steel, 1973). The remains of plesiosaurs and ichthyosaurs from Stonesfield have been mentioned by Phillips (1871, p. 183) and Lydekker (1889a, p. 245), and the pterosaur *Rhamphocephalus* is known from the Stonesfield Slate. These also are considered to have subsisted on fish.

Comparison with other localities

The fossil fauna of the Stonesfield Slate is unique. However, comparisons may be made with other Early and Mid-Bathonian faunas which contain some of the same species, and in particular with the Cotswold Slate (Eyford Member) to the west of Stow-on-the-Wold (*progracilis* Zone, Mid-Bathonian). Localities such as Huntsmans Quarry (SP 125254), Eyford Quarries (SP 135255, etc.) and Kyneton Thorns Quarry (SP 122264) have yielded a similar, but less diverse, fish fauna including a range of neoselachian and hybodont sharks, chimaeroids, halecostomes and a few possible teleost genera. However, the specimens are not nearly as well preserved as those from Stonesfield. The poor record of neoselachians in the Stonesfield Slates compared with that from the Eyford tilestones at Huntsmans Quarry is due to collection bias, as

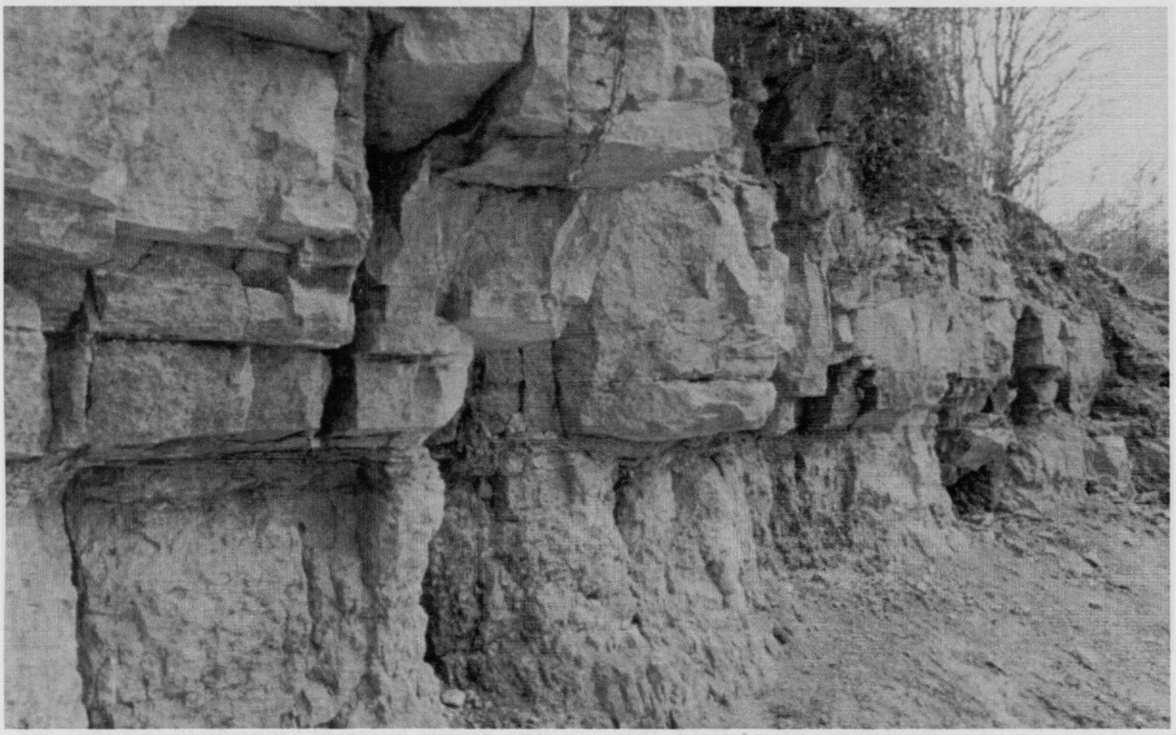


Figure 12.18 Photograph of the Kirtlington section, north face (photo: R Cottle).

many neoselachian teeth are less than 1–2 mm across and may have been overlooked by the early collectors. The conditions of deposition and faunal composition of the Cotswold Slate are very like those of the Stonesfield Slate, and the two units were formerly regarded as identical.

Conclusion

The conservation value of Stonesfield results from it being arguably the most important Middle Jurassic fossil fish site in the world, and its fauna is diverse and abundant, though consisting mainly of dispersed skeletal elements. It is important for the study of fossil fishes because its fauna is abundant, diverse and well preserved. There is much potential for further investigation of old collections held by museums in Britain and elsewhere, and possibly for reopening of quarry sections.

KIRTLINGTON OLD CEMENT WORKS QUARRY (SP 494199)

Highlights

The Forest Marble Formation (Upper Bathonian) at Kirtlington Old Cement Works in Oxfordshire has yielded a rich and diverse fauna of fishes based on teeth, including a microshark assemblage. This unique freshwater assemblage within an otherwise marine succession also includes an important amphibian component.

Introduction

Kirtlington Old Cement Works Quarry in the village of Kirtlington, Oxfordshire, has produced good faunas of fossil fishes and amphibians from the Forest Marble (Late Bathonian). The quarry was formerly worked for the manufacture of cement, and it closed about 1930 (Figure 12.18). Although exposures were excellent (Odling, 1913; Arkell, 1931), some of the faces became obscured more recently (McKerrow *et al.*, 1969; Palmer, 1973; Freeman, 1979). Fossil fishes, amphibians, reptiles, and mammals have been collected in recent years from the *fimbriatus–waltoni* Beds and from the Kirtlington Mammal Bed, a microvertebrate locality near the base of the Forest Marble (Freeman, 1976, 1979; Evans, 1989, 1990, 1991, 1992; Evans *et al.*, 1988, 1990; Evans and Milner, 1991, 1994).

Description

The succession in the quarry has been described by Odling (1913, pp. 493–4), Arkell (1931, pp. 570–2), Douglas and Arkell (1932, pp. 123–4), and Richardson (1946, pp. 69–71, 78–9). Additional information has been provided by McKerrow *et al.* (1969), McKerrow and Kennedy (1973) and Freeman (1979). The following composite section is based on these authors, and Richardson *et al.* (1946), in particular, with additions from Palmer (1973, 1979) and Torrens (1980, p. 36; numbering of individual beds is from the top down):

	Thickness (m)
Lower Cornbrash	
5. Limestone, rubbly and marly	1.07
4. Limestone, tough	0.76
3. Marl and rubbly limestone, in places nodular	0.23
2. *Astarte–Trigonia* Bed. Limestone, very hard, grey	0.61
1. Clay, brown, marly	0.30
Forest Marble Formation	
13. Clay, grey and buff, with some thin, irregular hard bands	1.53
12. Clay, dark grey (= Beds 3w–z of Freeman, 1979)	0.69
11. Limestone, yellowish, flaggy, locally marly and 'shaly', oolitic, with some inclusions of white lithographic limestone; ripple marks, rain pits (? = Bed 3v of McKerrow *et al.*,1969; Freeman, 1979)	0.61–0.92
(White Limestone Formation)	
10. Clay, grey-blue, with three pale mudstone layers, one at the bottom (= Beds 3p–u of McKerrow *et al.*, 1969; Freeman, 1979; = 'Unfossiliferous Cream Cheese Bed' of Odling, 1913, and Arkell, 1931). The basal unconsolidated 0.04–0.25 m brown marl unit (Bed 3p) is the Kirtlington Mammal Bed of Freeman (1979)	2.00
(White Limestone Formation)	
9. Coral–*Epithyris* Limestone (Upper *Epithyris* Bed or 'Fossiliferous Cream Cheese Bed' of Odling, 1913, and Arkell, 1931; ? Beds 3n–o of McKerrow, 1969). Limestone; at northern end an extremely hard, white, blue-hearted lithographic rock. Passes locally into unfossiliferous oolite	1.22–2.21
8. *fimbriatus–waltoni* Beds (= Bed 10 of Arkell, 1931; Beds 3k, l of McKerrow *et al.*, 1969). Clay, grey-green to greenish black, with some white pellets at top; bed largely made up of bivalves; when Bed 7 is absent, there is a lignite at the base	1.07
7. Oyster–*Epithyris* Marl (= Bed 9; Middle *Epithyris* Bed of Arkell, 1931; Bed 3k of McKerrow *et al.*, 1969). Marl, brown. Locally, a thin layer of corals occurs below	0–0.75
6. Limestone, hard, blue-hearted (? = Beds 3i, j of McKerrow *et al.* 1969)	0.92
5. Marl (? = Bed 3h of McKerrow *et al.*, 1969)	0.23
4 Limestone, similar to 8 (? = Bed 3g of McKerrow *et al.*, 1969)	0.84–0.92
3. *Epithyris* Limestone (= Lower *Epithyris* Bed of Arkell, 1931; ? = Beds 3a–f, Bed 1e of McKerrow *et al.*, 1969). Limestones, white, at west end of pit a mass of the brachiopod *Epithyris*. Thins out eastwards and replaced from beneath by lenticular limestones	2.44
2. *Aphanoptyxis ardleyensis* Bed. Limestones, well bedded	0.46–0.61
1. *Nerinea eudesii* Beds. Limestones in three courses	1.68

This section was recorded by Arkell (1931) in various parts of the quarry, which means that it is not a true log because of the large amount of lateral facies variation. The lower parts (Beds 8–13 in particular) are hard to match with the logs given by McKerrow *et al.* (1969, p. 58) because certain units, such as the *Epithyris* Limestone (Bed 11; Bed 1e of McKerrow *et al.*, 1969), are laterally impersistent.

There are problems in correlating the lithostratigraphy of the units in this quarry with those elsewhere in the northern Cotswolds, particularly the boundary between the White Limestone and the Forest Marble (e.g. Odling, 1913; Arkell, 1931, 1947a; Richardson *et al.*, 1946).

McKerrow *et al.* (1969) attempted a definition based largely on the oysters, and took the base of the Forest Marble to be at the base of the

Oyster–*Epithyris* Marl (Bed 7), as had Arkell (1931) initially. Palmer (1973, p. 61) pointed out that at Kirtlington the Coral–*Epithyris* Limestone (Bed 5) has a typical White Limestone fauna and lithology, and lowered the Forest Marble–White Limestone boundary to between Beds 4 and 5. Palmer (1979) further argued this point and divided the White Limestone Formation into three members, of which the Ardley Member (Beds 8–13) and the Bladon Member (Beds 5–7) are seen at Kirtlington. Palmer (1979, p. 208, fig. 5) made it clear that his Bladon Member is intended to include both the *fimbriatus–waltoni* and Upper *Epithyris* Beds of the Cherwell valley which rest on the *A. bladonensis* Bed. Torrens (1980, p. 36) recommended that the base of the Forest Marble be taken as 'the base of the clay overlying the Coral–*Epithyris* bed, or of the bed above at Kirtlington' (i.e. the base of Bed 3 or 4).

Vertebrates occur in the *fimbriatus–waltoni* Beds (Beds 2o, 3i, 4e, 6f of McKerrow *et al.*, 1969; base of the Bladon Member; Palmer 1979), and the Kirtlington Mammal Bed. The *fimbriatus–waltoni* Beds are greenish grey or black clay, which is often lignitic toward the base. Phillips (1871) recorded fish remains in association with the large bones of the sauropod dinosaur *Cetiosaurus oxoniensis*, within lignite resting upon the eroded surface of the underlying limestone. Since then other authors have reported large reptilian bones from the same beds (Richardson *et al.*, 1946; Arkell, 1931) and these are outlined in the GCR volume on fossil reptiles (Benton and Spencer, 1995).

The Kirtlington Mammal Bed (Bed 3p of McKerrow *et al.* 1969) is an impersistent lens, 21.5 m long and 0.04–0.25 m thick, in the north-eastern corner of the quarry (Figure 12.18; Freeman 1979, p. 136). The fish fauna within this unit occurs as dissociated remains of a variety of bony fishes and sharks. Associated fossils include microscopic freshwater charophytes, indeterminate plant fragments, and ostracods (Evans and Milner, 1994). The tetrapod remains include amphibians, reptiles and mammals (Evans and Milner, 1991, 1994). Most of the vertebrate material occurs as isolated elements, and some specimens show signs of abrasion and transport. However, delicate bones are also preserved in the accumulation. Some remains of marine fish in this horizon are regarded as being derived from the underlying White Limestone, along with marine invertebrates such as corals, brachiopods and echinoderm material (E. Freeman, pers. comm. to Evans and Milner, 1994). By contrast, a few genera (including much of the amphibian material) have most of their skeletal elements preserved, these are possibly those which have been transported least.

Fauna

It is assumed that older fish specimens labelled 'Kirtlington' in collections came from the *fimbriatus–waltoni* Beds, where there were extensive excavations for large reptilian remains (e.g. Phillips, 1871), since the microvertebrate remains of the Mammal Bed were not exploited before bulk preparation by Freeman (1976, 1979) and the University College, London, team (Kermack *et al.*, 1987).

(1) *fimbriatus–waltoni* Beds (data from Phillips, 1871)

Chondrichthyes: Elasmobranchii: Euselachii: Hybodontoidea

Asteracanthus sp.
Hybodus sp.

Osteichthyes: Actinopterygii: Neopterygii: Halecostomi

Pycnodonts *indet.*
Eomesodon bucklandi Woodward, 1918
Proscinates (Microdon) sp.
Lepidotes sp.

(2) Kirtlington Mammal Bed (data from Freeman, 1979; Evans and Milner, 1991, 1994; Evans *et al.*, 1988, 1990).

Chondrichthyes: Elasmobranchii: Euselachii: Hybodontoidea

Asteracanthus sp.
Hybodus polyprion Agassiz, 1843
Hybodus sp.
Lissodus pattersoni Duffin, 1985
L. wardi Duffin, 1985

Chondrichthyes: Elasmobranchii: Neoselachii: Batomorphii

Spathobatis sp.
'batoid'

Osteichthyes: Actinopterygii: Neopterygii: Halecostomi

Eomesodon sp.
Lepidotes sp.
pycnodont indet.

Osteichthyes: Actinopterygii: Neopterygii: Holostei: Halecomorphi

?amioid

TETRAPODA
Amphibia: Lissamphibia: Anura
Eodiscoglossus oxoniensis Evans, Milner and Mussett, 1990
Amphibia: Lissamphibia: Caudata
Marmorerpeton freemani Evans, Milner and Mussett, 1988
M. kermacki Evans, Milner and Mussett, 1988
Salamander A
Salamander B
Amphibia: Lissamphibia: Albanerpetontidae
Celtedens sp.

Interpretation

The biostratigraphy of the Bathonian at Kirtlington is difficult since no ammonites have been found locally, and very few elsewhere in comparable rocks (Torrens, 1969a, 1980). Finds of ammonites in the White Limestone of the Oxford area have permitted correlation of this unit with the *subcontractus* and *morrisi* Zones (Mid-Bathonian), and the *hodsoni* and lower *aspidoides* Zones (Late Bathonian), while the Forest Marble Formation is largely *aspidoides* and basal *discus* Zones (Late Bathonian) on the basis of correlation of beds above and below.

The approximate zonal assignments of the three members of the White Limestone Formation are: Shipton Member, ?*subcontractus* and *morrisi* Zones, Ardley Member, ?lower *hodsoni* Zone, and Bladon Member, ?upper *hodsoni*–lower *aspidoides* Zones (Palmer 1979; Torrens, 1980). However, the evidence for zonation of these members is 'not compelling' (Torrens, 1980, p. 37), and ostracod zonation (Bate, 1978) places the White Limestone of the Oxford area in ostracod zones 5–8, the Forest Marble and Cornbrash resolving to the top of zone 8 and above (= upper *discus* Zone).

The vertebrate-bearing *fimbriatus–waltoni* Beds (base of the Bladon Member) are thus dated as upper *hodsoni* Zone (basal Late Bathonian; Torrens, 1980, p. 36). However, the occurrence of the ostracod *Glyptocythere penni* in the *fimbriatus–waltoni* Beds led Bate (1978) to suggest that this unit belongs to the *discus* Zone. The Kirtlington Mammal Bed falls within the *aspidoides* or *discus* Zone (Freeman, 1979, p. 136).

Environmental interpretations have been made on the basis of the sedimentology of the *fimbriatus–waltoni* Beds. McKerrow *et al.* (1969, pp. 61–4, 80) interpreted the abundance of lignite and occasional caliche-like nodules as indicating shallow water with occasional subaerial exposure. Palmer (1979, pp. 210–11) noted the complex channelled interdigitations of this unit at Shipton (SP 4717), and suggested that deposition of some of the clays was local and catastrophic, and that the nodules were derived from elsewhere. He also (1979) supposed a quiet-water lagoonal environment subject to periodic current activity and influx of new sediment, perhaps during storms.

The marl sediment of the Kirtlington Mammal Bed contains subangular pebbles of oolitic limestones, comminuted shell debris, individual ooliths and rare silica sand grains, all of which suggest a temporary freshwater pool that received periodic influxes of poorly sorted sediment derived from local erosion of earlier Mid-Jurassic limestones (Freeman, 1979, p. 139). The ostracods, charophytes and fishes lived in the pool, and the plants and tetrapods presumably lived nearby.

As outlined by Evans (1990, p. 234), in Bathonian times Kirtlington lay on or near the south-west shore of a small island barrier some 30 km from the coast of the Anglo-Belgian landmass at a subtropical latitude of about 30°N (Palmer, 1979). Lignite, charophytes and freshwater ostracods and gastropods in the marly sediments suggests a coastal environment, which had low relief, with creeks, lagoons and freshwater lakes, rather like the Florida Everglades (Palmer, 1979). The vertebrate fauna of the Kirtlington Mammal Bed, with its fishes, amphibians and aquatic reptiles (choristoderes, crocodilians and turtles), agrees well with such a palaeoenvironmental scenario. Terrestrial elements, including the albanerpetonid amphibian, lizards, archosaurs and mammals, are much rarer (Evans and Milner, 1994); they may have been transported into the lagoon from inland.

The faunas of the two vertebrate-bearing beds at Kirtlington are rather different, which probably relates to preservational and environmental conditions rather than to the slight age difference. They will be discussed separately.

The only early reference to the fish fauna of Kirtlington is a brief mention of 'teeth of *Hybodus*, *Pycnodus* and *Strophodus*, and scales of *Lepidotus*' (Phillips, 1871, p. 244). *Hybodus* is a ubiqitous element in the classic Great Oolite sequences and the presence of this genus in the *fimbriatus–waltoni* Beds is not remarkable.

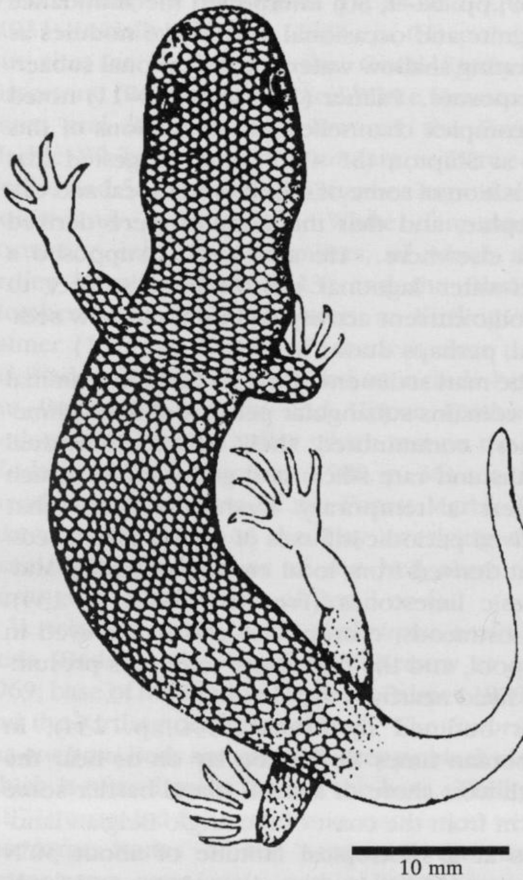


Figure 12.19 Amphibian remains from Kirtlington; the albanerpetonid *Celtedens*, restoration (after McGowan and Evans, 1995).

The reference to both pycnodont teeth and semionotid scales (Phillips, 1871) is also consistent with a shallow-marine fauna similar composition to other Great Oolite fish-bearing localities (cf. Rayner, 1958). The tetrapod fauna is dominated by long-snouted piscivorous crocodilians.

The fish, amphibians, reptiles and mammals from the Kirtlington Mammal Bed have been summarized by Freeman (1979), Duffin (1985) and Evans and Milner (1991, 1994). Details of the collecting and preparation techniques are given in Freeman (1976, 1979), Kermack *et al.* (1987) and Evans (1989). The reptiles have been described in the GCR fossil reptile sites volume (Benton and Spencer, 1995) and the mammals will be detailed in the GCR fossil mammal sites volume.

The fish fauna from the Mammal Bed is unremarkable; it contains the typical hybodont shark and halecostome bony fish components found in most Great Oolite Group assemblages. The microvertebrate fauna includes neoselachian teeth (Evans and Milner, 1994), and several may be attributable to the primitive ray *Spathobatis*, a genus present throughout the British marine Bathonian (D. Ward, pers. comm., 1993; S. Metcalf and C. Underwood, pers. comm.).

The bony fish component consists of disassociated teeth, and scales of various holosteans are the most abundant fossils within both meso- and microfossil fractions. The commonest is the pycnodont *Eomesodon bucklandi*, although *Proscinates* (*Microdon*) and at least one semionotid are also present. Microvertebrate samples contain gular plate and mandible fragments of far smaller fish; some of these, with closely spaced crushing teeth, may be a pycnodont. The vast majority of material is generically indeterminate. In many old collections it has been assigned to 'bucket genera' (e.g. Phillips, 1871; Woodward, 1890, 1892, Savage, 1963), especially *Eomesodon*, *Lepidotes* (ornamented bones and heavy scales) and *Pholidophorus* (light bones). Evans and Milner (1994) also record the presence of possible amioid teeth and jaws in the acid residues, which Freeman (1976) referred to *Caturus*. As with other Bathonian fish assemblages, there is some indication of durophagy (e.g. the hybodonts *Asteracanthus* and *Lissodus*, the 'batoid' neoselachian and the semionotid and pycnodont osteichthyans).

The amphibians include the dissociated and fragmentary remains of a frog referrable to the family Discoglossidae (*Eodiscoglossus oxoniensis*), four species of salamander (*Marmorerpeton kermacki*, *M. freemani* and two unnamed forms) and the small salamander-like *Celtedens* (Figure 12.19). *Eodiscoglossus oxoniensis* is the earliest identifiable discoglossid frog known, and one of the oldest frogs of modern aspect (Evans *et al.*, 1990). The specimens of *E. oxoniensis* from Kirtlington are comparable with *E. santonjae* from the Early Cretaceous of Montsech, Lérida Province, Spain, but they may be clearly distinguished by characters of the ilium and premaxilla. The only older frogs are the primitive *Triadobatrachus* from the Early Triassic of Madagascar, *Vieraella* from the Early Jurassic of Argentina and *Prosalirus bitis* from the Kayenta Formation (Pliensbachian, Early Jurassic) of Arizona (Shubin and Jenkins, 1995).

The record of the albanerpetontid is one of the oldest of this enigmatic tetrapod family, the oldest being from the Bajocian of Aveyron, France (Evans and Milner 1994). The ?amphibious albanerpetontids are also known from a range of localities including those in the Jurassic of Portugal, the Cretaceous of North America and Spain and the Miocene of France (McGowan, 1994; McGowan and Evans, 1995). Albanerpetonids were slender little animals, superficially not unlike newts.

Marmorerpeton kermacki and *M. freemani* are the earliest known salamanders (i.e. true Caudata; Evans *et al.*, 1988), more primitive than any other known forms, as shown by the absence of intravertebral spinal nerve foramina in the atlantal centrum. In other features these taxa resemble members of the family Scapherpetonidae, which comprises neotenous forms otherwise known only from the Late Cretaceous and Palaeocene. At present *Marmorerpeton* is under revision and its tentative attribution to the Scapherpetonidae, is unlikely to stand (S. Evans, pers. comms., 1994). Salamanders A and B are yet to be described.

Comparison with other localities

The fish and amphibian remains from Kirtlington Cement Works compare best with Mid- and Late Bathonian faunas nearby. The *fimbriatus–waltoni* Bed at Shipton-on-Cherwell quarry (SP 477175) has yielded abundant fish remains (Evans and Milner, 1994) and a diverse fauna with *Lissodus* has been recovered from the 'Monster Bed' (Palmer, 1979) at Woodeaton Quarry, Oxfordshire (SP 534122; Freeman, 1979, F. Mussett, pers. comm. to Evans and Milner, 1994). The Forest Marble at Tarlton Clay Pit, near Cirencester (SO 970001), has yielded a similar but fragmentary fauna to that from the Mammal Bed at Kirtlington, including albanerpetontids and the enigmatic caudates *Marmorerpeton*, and Kirtlington salamanders A and B (Evans and Milner, 1994). The palaeoenvironment of the Tarlton site is similar to that of the Mammal Bed (Ware and Windle, 1980; Ware and Whatley, 1983). Sections of Forest Marble at both Swyre (SY 525868) and Watton Cliff, Dorset (q.v.), yield a similar microvertebrate assemblage (Freeman, 1976; Evans and Milner, 1994). Marine elements, such as selachian teeth, are much better preserved there, whilst the tetrapod material is generally abraded and water-worn, indicating transport (Evans and Milner, 1994) into a more high-energy offshore environment (Holloway, 1983). Finally, the small section of offshore Forest Marble at the Leigh Delamere

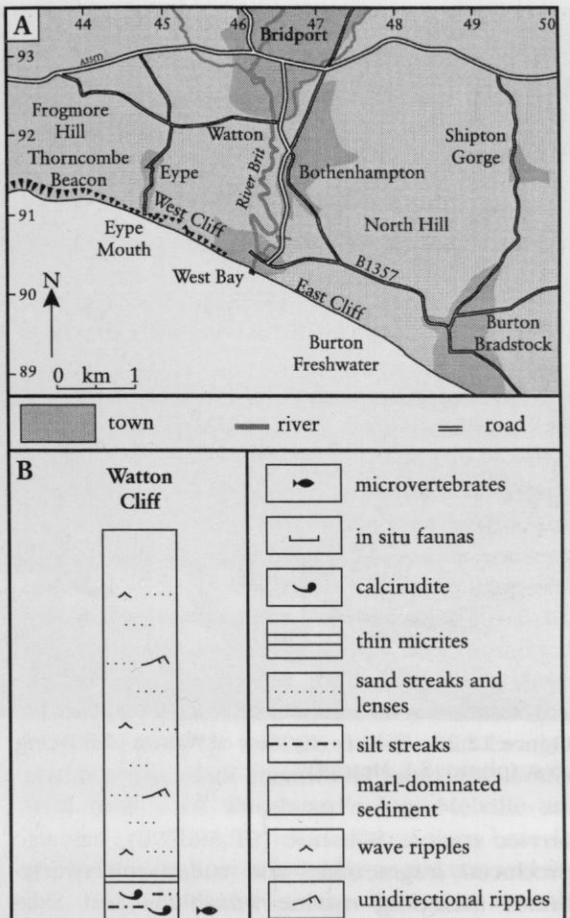


Figure 12.20 (A) Sketch map of the vicinity of the Watton Cliff (West Cliff) GCR site, Upper Bathonian of Dorset; (B) stratigraphical section through the Forest Marble (after Holloway, 1985). (Continued on p. 396).

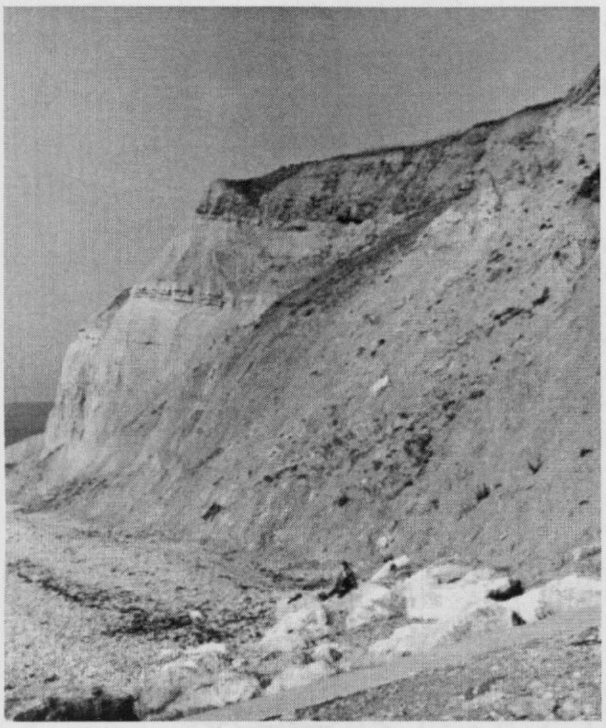


Figure 12.20 – *contd.* (C) View of Watton Cliff facing west (photo: S.J. Metcalf).

service station, Wiltshire (ST 890790), has also produced fragmentary and rolled microvertebrates including marine selachians and Salamander A (Evans and Milner, 1994; pers. obs., 1993).

Some older localities in the British Bathonian have yielded rich freshwater faunas; for example, Hornsleasow Quarry (SP 132323; earliest Bathonian) has yielded a similar, but less diverse, fish fauna and comparable amphibian remains (Metcalf *et al.*, 1992). At Stonesfield (q.v.; early Mid-Bathonian), and Huntsmans Quarry (SP 125254; early Mid-Bathonian) elements of the Kirtlington fauna, (although no amphibian material) have been recovered. *Marmorerpeton* also occurs in the Kilmalaug Formation on Skye (Waldman and Evans, 1994).

The Kirtlington Mammal Bed fauna resembles later rather than earlier Mesozoic freshwater assemblages (Evans *et al.*, 1988; Evans and Milner, 1994; pers. comm., 1993). Elements of the tetrapods are found in later assemblages, such as those at Guimarota (Oxfordian) and Solnhöfen (Portlandian), the Late Jurassic–Early Cretaceous Purbeck in Dorset (q.v.), the Early Cretaceous at Uña and Las Hoyas, Spain, and the Late Cretaceous of the Lance Formation of North America.

Conclusion

Kirtlington Quarry represents the best late Bathonian site for a variety of amphibian groups, and it is the source of numerous new forms. Marine fishes from the *fimbriatus–waltoni* Beds are comparable with those from the same unit at several other sites in Oxfordshire, but the variety of material is greater than elsewhere, and the site is still readily accessible for further excavation. The Mammal Bed fauna includes a unique freshwater assemblage of small fishes and amphibians, several of which are the earliest known occurrences of their respective groups (the first discoglossid frog and salamanders). Altogether the diversity of these faunas from different depositional environments gives the site its conservation value.

WATTON CLIFF (SY 451908– SY 453907)

Highlights

The Upper Bathonian assemblage at Watton Cliff in Dorset represents mixed marine and freshwater influences, including abundant microshark elements and amphibian remains. Two species of the hybodont shark *Lissodus* have been described from material collected in recent years from Watton Cliff.

Introduction

The Forest Marble (Upper Bathonian) at Watton Cliff (also known as Ware or West Cliff), West Bay (Figure 12.20A; Clements, 1989b), contains channel deposits within a thick shelly horizon (Figure 12.20B), which have yielded abundant microvertebrate material including a reworked terrestrial component (Evans, 1992; Evans and Milner, 1994). The site was excavated in the late 1970s by a team from University College, London, as part of a project on Middle Jurassic tetrapod assemblages (Kermack, 1988; Evans, 1992). The fauna consists of selachians, including microshark remains, bony fish and amphibian material comparable to that from the Forest Marble at Kirtlington Cement Works (q.v.; Evans, 1992; Evans and Milner, 1994; D. Ward, pers. comm., 1993). The site has also yielded abundant small reptilian remains (Evans, 1992), along with much rarer tritylodont mammal-like reptile and mammalian teeth (Freeman, 1976;

Ensom, 1977; Kermack *et al.*, 1987). The vertebrate-bearing channel-like deposits are rich in carbonaceous plant material and are thought to represent storm breaches through an offshore shell bank complex (Holloway, 1983).

Description

The cliff section at Watton Cliff has been described by H.B. Woodward (*in* Strahan, 1898, p. 8) and by Torrens (1969a, pp. 37–8). The succession here is the most complete sequence of Forest Marble in west Dorset (Figure 12.20B) and additional information on the geology has been provided by Melville and Freshney (1982, pp. 26–7), House (1989, pp. 57–9) and Holloway (1985, p. 260). The section given here is based on the work of H.B. Woodward with modern terminology and measurements applied where appropriate.

	Thickness (m)
(Cornbrash)	
Forest Marble Formation	
10. Flaggy blue limestone, showing ripple marks, and clays or shales, with 'race'; the limestone preponderant	3.04
9. Clays with 'race', shaley limestone, thin shelly limestone and thin leaves of sandy limestone, ferruginous in places; the clay preponderant	6.10
8. (= 'calcirudite' of Holloway = ?*Digona* Bed of Torrens = 'Mammal Bed' of Freeman). False-bedded shelly limestones, sandy and oolitic in places,with irregular clay seams, many ochreous galls, lignite; and with the bivalves *Camptonectes*, *Plagiostoma*, *Praeexogyra* and fragments of the crinoid *Apiocrinus*	3.00–4.60
7. Grey clay (impersistent)	0–0.90
6. Hard, white or grey marl, with thin seams of bluish shelly limestone	0.15
5. Blue, flaggy, argillaceous limestones, and blue and yellow clays, with thin layers of calcareous grit	9.15
4. (= *Boueti* Bed). Hard, sandy marl stained reddish brown; brachiopods '*Rhynconella*'-bed, with *Chamlys vagans*, *Goniorhynchia boueti*, *Avonothyris langtonensis*, *Ornithella digona*, and crinoid (*Apiocrinus*) ossicles and serpulids	0.36
Fuller's Earth	
3. Bluish yellow marl, with impersistent band of hard white marl	2.74
2. Hard, fissile white marl	0.84
1. Grey marls	seen 25.00

The section of Forest Marble at Watton Cliff is considered to be complete as the overlying Cornbrash was formerly exposed on the cliff top (Cope *et al.*, 1980b). The formation consists of three lithological units of roughly equal thicknesses (Arkell, 1947a). The lowest unit consists of a thick greeny brown marly clay interbedded with thin impersistent shelly limestones, silts and sandstone bands (Holloway, 1982). Similarly, the top horizon is dominated by laminated marly clays interbedded with very fine sandstones and silts. These two units are separated by 3–5 m of coarsely bioclastic limestone (bed 8 of Woodward's log), known as the 'calcirudite' bed (Holloway, 1982) and thought to be laterally equivalent to the brachiopod-rich bioclastic *Digona* Bed of the Weymouth region (Torrens, 1969a). At Watton Cliff a rich brachiopod-bearing, shell fragmental band, the *Boueti* Bed (bed 4 of Woodward's log; Melville and Freshney, 1982) provides a convenient base for the formation as it is laterally persistent and can be traced northwards into Somerset and the southern Mendips. This allows correlation with the succession in the southern Cotswolds (Arkell, 1947a; Cope *et al.*, 1980b).

Microvertebrates were recovered from the thick calcirudite horizon (Figure 12.20B), known since as the 'Mammal Bed', in the middle of the section (bed 8) by bulk sampling (Freeman, 1976; Kermack *et al.*, 1987; Kermack, 1988). This unit consists of individually impersistent sheets and lenses of planar or cross-bedded shell-fragmental and oolitic limestones, interbedded with thin marl drapes. The invertebrate macrofauna of the calcirudite units is largely made up of broken valves of *Praeexogyra hebridica* and whole large pectinids. Carbonized plant matter occurs as fine disseminated fragments and as large log material. The microvertebrate fauna has two well-defined components, the first consisting of well-preserved and clearly marine fish remains, and the second being comprised of a derived terrestrial tetrapod fauna. The tetrapod material is generally water worn, indicating considerable transport (Evans and Milner, 1994) into the high-energy offshore depostional environment.

Fauna

The vertebrate remains at Watton Cliff were recovered by bulk sieving and acid preparation techniques upon the shelly limestones and marls known as the 'Mammal Bed' (Freeman, 1976; Kermack, 1988; Evans 1992; D. Ward, pers. comm., 1995). Some of the material is now housed in the UCL (Evans, 1992, and pers. comm., 1993) but most is in NHM collections (Duffin, 1985; F. Mussett, 1996, pers. comm.).

Chondrichthyes: Elasmobranchii: Euselachii: Hybodontoidea
Asteracanthus sp.
Hybodus spp.
Polyacrodus sp.
Lissodus wardi Duffin, 1985
L. pattersoni Duffin, 1985
Chondrichthyes: Elasmobranchii: Neoselachii: Batomorphii
Spathobatis sp.
Chondrichthyes: Elasmobranchii: Neoselachii: Squalomorphii
Protospinax sp.
Chondrichthyes: Elasmobranchii: Neoselachii: Galeomorphii
Heterodontus sp.
orectolobid
?*Palaeocarcharias* sp.
Scyliorhinus spp.
Chondrichthyes: Holocephali: Chimaeriformes
chimaerid
Osteichthyes: Actinopterygii: Neopterygii: Halecostomi
Lepidotes sp.
pycnodontid
Amphibia: Lissamphibia: Anura
Eodiscoglossus oxoniensis Evans, Milner and Mussett, 1990
Amphibia: Lissamphibia: Caudata
Marmorerpeton sp.
'Kirtlington Salamander A'
Amphibia: Lissamphibia: Albenerpetontidae
albanerpetontid indet.

Interpretation

Detailed biostratigraphical correlation of the Forest Marble sequence in west Dorset with the standard Upper Bathonian zonation is not easy as no diagnostic ammonites have been recorded in these beds. Correlation can, however, be demonstrated based upon the prevalence of the lithostratigraphical marker beds, the *Boueti* and *Digona* Beds, and their characteristic faunas, as ammonites occur in the east Dorset succession and have been recovered from the two brachiopod-rich units. Arkell (1959) figured a specimen of *Clydoniceras (Delecticeras)* cf. *ptychophorum* Neumayr from the base of the *Boueti* Bed at Langton Herring (SY 608822) and *Clydoniceras hollandi* Buckman has been recovered from loose material beneath the outcrop of the

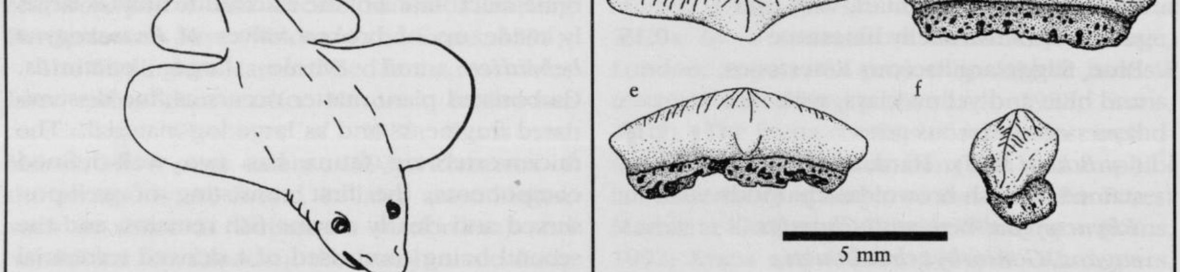


Figure 12.21 Elasmobranchs from the Bathonian: (A) *Protospinax*, × 0.1 restoration after Woodward 1919b. (B) *Lissodus pattersoni* Duffin (NHM P60706); a, occlusal view; b, labial view. *L. wardi* Duffin (holotype NHM P58701): c, occlusal view; d, lingual view; e, labial view; f, lateral view (from Duffin, 1985).

Digona Bed at Herbury (SY 613807; Cope *et al.*, 1980b). The former specimen does not allow precise correlation, but similar forms have been recorded from a succession in north-west Germany interpreted as indicating the *aspidoides* Zone. If Torrens' (1969a, pp. 37–8) assertion that the microvertebrate-bearing calcirudites (bed 8) are the lateral equivalent of the *Digona* Bed is correct, then the appearance of the subzonal ammonite *Clydoniceras hollandi* within this unit suggests a precise age for the Watton Cliff assemblage.

The calcirudite bed is thought to represent an offshore bank of unstable shell detritus. Holloway (1982) considered the shell debris forming the calcirudite to be derived from the underlying Forest Marble and that the only organisms living in the subtidal shoals and channels were the boring bryozoans and encrusting organisms. The remains of the small tetrapods and the large pieces of wood were deposited within the cross-cutting channels during the waning stages of storms, and suggest a close proximity to land (?Cornubia).

The fish fauna recorded from Watton Cliff is largely made up of microshark material such as teeth and dermal denticles (Figure 12.21), associated with a small bony fish component of teeth and scales (D. Ward, pers. comm., 1995). The ubiquitous Jurassic hybodont genera are present in the assemblage and include *Hybodus*, *Polyacrodus*, *Asteracanthus* and *Lissodus*. There may be more than one species of *Hybodus*, but these have yet to be fully described (D. Ward, pers. comm., 1995). Two species of *Lissodus* have been described by Duffin (1985) from the Mammal Bed calcirudites. These are *L. pattersoni* and *L. wardi* (Figure 12.21) which are also present in the Kirtlington Mammal Bed (Duffin, 1985).

Neoselachians are also a common component of the microshark fauna. These include *Spathobatis* and the ?ancestral squalid shark *Protospinax* (Figure 12.21), both forms adapted to a specialized benthic mode of life as their crushing-type dentition indicates (Cappetta, 1987). *Protospinax* is a rather enigmatic genus known from an almost complete skeleton from the Lower Tithonian (Portlandian: Upper Jurassic) of Solnhöfen, Germany. Teeth referred to this genus have a high, wide oval crown with a crest which rises to a prominent cusp and a low, bilobed root (Figure 12.21; Cappetta, 1987). In several localities these have been assigned to the squalid shark *Squalogaleus* (e.g. Thies, 1983). Maisey (1976) considered that *Protospinax* was synonymous with the batoid genus *Belemnobatis*, but on review of the type specimens, Cappetta (1987) decided that *Protospinax* was valid and most probably was a primitive squalomorph.

Galeomorph sharks are well represented in the Forest Marble fauna of Watton Cliff. A species of the extant heterodontid genus *Heterodontus* (D. Ward, pers. comm., 1995) represents one of the earliest occurrences of the genus and of the Heterodontidae (Cappetta, 1987). Several species of *Heterodontus* have been recorded from the Upper Jurassic of southern Germany (Schweizer, 1961, 1964) and undifferentiated heterodontid teeth and denticles have been described from the Forest Marble of Cirencester, Gloucestershire (Young, 1984). Modern *Heterodontus* is a small benthonic shark which lives in shallow, warm waters and possesses a differentiated clutching–grinding dentition that has undergone little modification from the earliest occurrence of the family (Cappetta, 1987). An orectolobid shark (Order Orectolobiformes) is also present in the acid residues, but generic diagnosis is uncertain (D. Ward, pers. comm., 1995). Orectolobids are a common neoselachian component of many Bathonian faunas, and have been recovered from the Middle and Upper Bathonian of the Cotswolds (Young, 1984; S. Metcalf and C. Underwood, pers. comm.). *Palaeocarcharias* is a genus described from three partial specimens from the Lithographic Stone (Upper Kimmeridgian) of Eichstätt, Germany (de Beaumont, 1960). According to its dentition, *Palaeocarcharias* probably is related to the Lamniformes, and the presence of its teeth in the Watton Cliff assemblage is the earliest occurrence of the genus and possibly the order (Cappetta, 1987). Scyliorhinid teeth (Order Carcharhiniformes) have also been recognized in earlier Bathonian deposits at Huntsmans Quarry, Gloucestershire (S. Metcalf and C. Underwood, pers. comm.) and in Africa, and teeth of the scyliorhinid *Scyliorhinus* are recorded from the Forest Marble at Watton.

The amphibians from the Forest Marble at Watton Cliff have yet to be fully described (Evans, 1992; Evans and Milner, 1994), but the composition of the fauna seems to be typical of late Bathonian tetrapod assemblages (cf. Evans *et al.*, 1988, 1990). The fauna includes all the major components of the Kirtlington Mammal Bed (see Kirtlington report) except for the undescribed caudate, 'Kirtlington Salamander B' (Evans, 1992). The affinities of these taxa are discussed in the site report for the Kirtlington Cement Works (q.v.).

Comparison with other localities

The microvertebrate assemblage from Watton Cliff is clearly similar to faunas from the Forest Marble and White Limestone successions of Oxfordshire and Gloucestershire. In particular the amphibian remains are directly comparable to those from Kirtlington (q.v.) and a detailed account of this and other late Bathonian freshwater faunas is given in the Kirtlington site report. The mid-Bathonian assemblages at Stonesfield (q.v.) and Huntsmans Quarry contain similar marine elements.

Conclusion

Watton Cliff presents the best exposure of the Forest Marble Formation (Upper Bathonian) in southern Britain and has been well dated. The 'Mammal Bed' fauna includes a unique mixed freshwater–marine assemblage of fishes and amphibians thus giving the site its conservation value. The cliff-top exposure is easily accessible and has great potential for future research collections to be made.

LATE JURASSIC OR MALM

Late Jurassic fish have come from many localities within the English outcrop between the Dorset coast and Yorkshire, and are represented in rocks ranging in age from Late Oxfordian to Portlandian. The sites are detailed below stage by stage and these listings are based on sources as noted, together with examinations of major museum collections.

Fish remains are rare in the Middle–Upper Oxford Clay (Callovian and Lower Oxfordian) and Corallian Beds (Mid–Late Oxfordian) (however see Martill *et al.*, 1994). The Middle–Upper Oxford Clay is a slightly calcareous, non-bituminous clay and is generally not quarried for brickmaking, consequently exposures and vertebrate finds are rare. A few sites (brickpits and coastal exposures around Weymouth, Dorset; Eye pit, Cambridgeshire (TF 231034); Warboys Brick Pit, Cambridgeshire (ST 308818); and Woodham brickpit, Buckinghamshire (SP 708185; Martill, 1986; Martill and Hudson, 1991) have yielded teeth, fin spines, bones and scales, mainly attributed to hybodont sharks, rare chimaeroid remains and some bony fishes. Micropalaeontological residues rarely yield neoselachian teeth and denticles (Martill and Hudson, 1991). The rarity of vertebrate faunas from British Early Oxfordian rocks is also matched abroad. References include Fox-Strangways (1892), H.B. Woodward (1895), Strahan (1898), Martill (1986) and Martill and Hudson (1991).

British Mid- and Late Oxfordian localities have produced fish remains. The Coral Rag (Mid-Oxfordian) of various sites in Wiltshire, Berkshire, Oxfordshire and Yorkshire has yielded scattered fish material. Comparable Mid- and Late Oxfordian sites abroad include Vaches Noires, near Dives; Normandy, Calvados, Bourgogne and La Vendée, and Boulogne-sur-Mer, France; the La Turbie–Cap d'Aggio region, Monaco; and Baden-Württemberg, Germany.

The Kimmeridge Clay (Kimmeridgian) has yielded abundant vertebrates and includes some of the best Late Jurassic marine fish faunas in the world. There are many localities, and abundant remains have been found in Dorset, Wiltshire, Oxfordshire, Cambridgeshire and Yorkshire. Specific localities include Ringstead Bay (SY 751813), Kimmeridge Bay (the coastal section between Gaulter Gap and Broad Bench; SY 898789–SY 908787), Smallmouth Sands harbour (SY 670768) and the Isle of Portland coast (SY 6871–SY 7072), Dorset; Westbury Clay Pit (ST 880527) and Swindon Brick and Tile Pits (SU 156834), Wiltshire; Headington Pits, Oxford (SP 555072), and Oday Hill landfill site, Abingdon (SP 492948), Oxfordshire. Most inland Kimmeridge sites are clay pits and in many cases these have been infilled. The landfill site at Oday Hill gravel pit is particularly rich in fossil fish remains which can be collected from shelly seams within the grey sandy facies of the Upper Kimmeridge Clay. References include Phillips (1871), Egerton (1872b), H.B. Woodward (1895), Strahan (1898), Arkell (1933, 1947a, 1947c), Brookfield (1978), Cope (1967, 1978) and Palmer (1988).

The term 'Portlandian' is used here to refer to the last stratigraphical stage of the Jurassic, in preference to 'Tithonian', the primary international reference standard. This is because a basal boundary stratotype for the Tithonian has not been selected, and because the Kimmeridgian stage as used by British workers is much longer than that used elsewhere. Stratigraphical equivalents are:

UK and northern France	Tethys	Russia, Poland
Portlandian Upper Kimmeridgian	Tithonian	Volgian
Lower Kimmeridgian	Kimmeridgian	Kimmeridgian

Cope (1993) attempted to resolve this problem by reintroducing the Bolonian Stage for the Upper Kimmeridgian *sensu anglico*, thus allowing the standard use of the Portlandian and Volgian stage names. For the present work the traditional British 'long' Kimmeridgian stage name is used.

In the Portland Beds (Lower Portlandian) fish have been found on the Isle of Portland, Dorset, and isolated specimens have been collected in Wiltshire, Oxfordshire and Buckinghamshire. References include Phillips (1871), H.B. Woodward (1895), Strahan (1898) and Arkell (1933, 1947a, 1947c).

The Purbeck Limestone Formation (Late Portlandian to Early Berriasian) is split between the Jurassic and Cretaceous. Extremely abundant remains have been obtained from Durlston Bay and quarries west of Swanage, Dorset, and the smaller freshwater and terrestrial animals are of particular importance (including important amphibian remains). Apart from their taxonomic significance, many of the faunas are interesting from the viewpoint of their palaeoecology, in that they occur in a variety of facies ranging from lacustrine and lagoonal to shallow marine, which in addition cross the Jurassic–Cretaceous (Portlandian–Berriasian) boundary. Specific localities include the old Swanage Quarries (SZ 021781, etc.; many forms found at Durlston Bay – exact information not available), Sunnydown Farm Quarry, Langton Matravers (SY 98227880; microvertebrate remains; Ensom, 1987, 1988, 1990; West, 1988; Ensom *et al.*, 1991), Dorset. References include H.B. Woodward (1895), Anderson and Bazley (1971), Ensom (1987, 1988, 1990), Ensom *et al.* (1991), Allen and Wimbledon (1991) and Clements (1993).

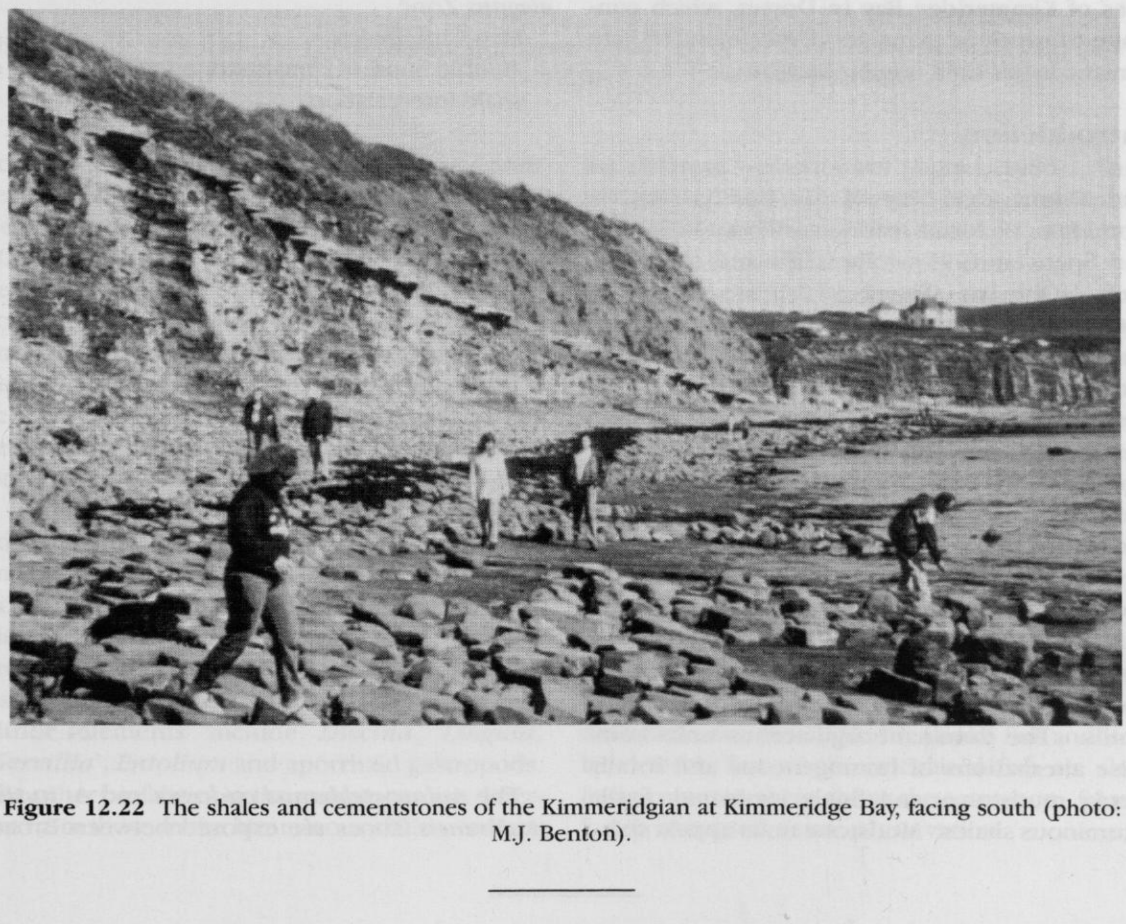


Figure 12.22 The shales and cementstones of the Kimmeridgian at Kimmeridge Bay, facing south (photo: M.J. Benton).

FISH AND AMPHIBIAN SITES

Most of the listed sites cannot serve as candidates for the GCR since they have been lost to landfill and building. For the most part, only coastal sites could be considered, and the richness and accessibility of the Dorset coast is reflected in the choice of the following two GCR sites:

1. Kimmeridge Bay (Gaulter Gap–Broad Bench; SY 898789–SY 908787). Late Jurassic (Early Kimmeridgian), Kimmeridge Clay.
2. Durlston Bay, Dorset (SZ 034780). Late Jurassic–Early Cretaceous (Portlandian –Berriasian), Portland Stone–Upper Purbeck Beds.

KIMMERIDGE BAY (GAULTER GAP–BROAD BENCH; SY 898789–SY 908787) (POTENTIAL GCR SITE)

Highlights

The cliff sections between Gaulter Gap and Broad Bench include the most famous fossil fish sites of Kimmeridge Bay in Dorset, which continue to produce many good specimens of Late Jurassic fishes on a regular basis.

Introduction

The Kimmeridge Clay of Kimmeridge Bay, is world famous for its marine vertebrates (Benton and Spencer, 1995). The cliffs and foreshore reefs of the bay (Figure 12.22) are subject to continuing erosion, and several finds have been made in recent years. They have potential for future discoveries. The geology of the site has been recorded by many authors, but in most detail by Cope (1967; *in* Torrens, 1969a; *in* Cope *et al.*, 1980b).

Description

The Kimmeridge Clay in Kimmeridge Bay is a 138 m sequence of grey to dark grey-blue ammonite-bearing mudstones and shales with sporadic cementstone (limestone/dolostone) bands. The dominant argillaceous units comprise alternations of homogeneous and locally blocky mudstones and finely laminated, fissile bituminous shales. Mudstone units appear to be structureless, but after weathering some mottling may be seen. The base of the mudstone units weathers out more sharply than the upper sections and the upper boundaries appear to be transitional to the bituminous shales. These are rather thinner than the mudstone units, from between 0.1 and 0.4 m thick, the mudstones measuring 0.1 m to about 1 m. Erosion of the mudstones and shales is rapid, but the cementstone bands stand out.

At Kimmeridge Bay, the beds dip south-east (Figure 12.22) and there are several faults. The general sequence, based on Cope (1967; *in* Torrens, 1969a; *in* Cope *et al.*, 1980b) is:

	Thickness (m)
Late Kimmeridgian (formerly Mid-Kimmeridgian)	
wheatleyensis Zone	
Grey Ledge Stone Band	0.7
scitulus Zone	
Upper Cattle Ledge Shales	10.8
Cattle Ledge Stone Band	0.5
Lower Cattle Ledge Shales	15.0
Yellow Ledge Stone Band	0.4
	27.4
elegans Zone	
Hen Cliff Shales	21.5
Double band of cementstone with shale intercalation	1.1
	22.6
Lower Kimmeridgian	
autissiodorensis Zone	
Maple Ledge Shales	22.5
Maple Ledge Stone Band	0.3
Gaulter's Gap Shales	32.0
Washing Ledge Stone Band	0.35
Washing Ledge Shales (upper part)	8.0
	63.15
eudoxus Zone	
Washing Ledge Shales (lower part)	5.0
The Flats Stone Band	0.5
Shales	3.0
Nannocardioceras Bed	0.02
Shales	1.0
Shales	seen to 15.0
	24.52

The *Aulacostephanus eudoxus* and *A. autissiodorensis* Zones are exposed between Broad

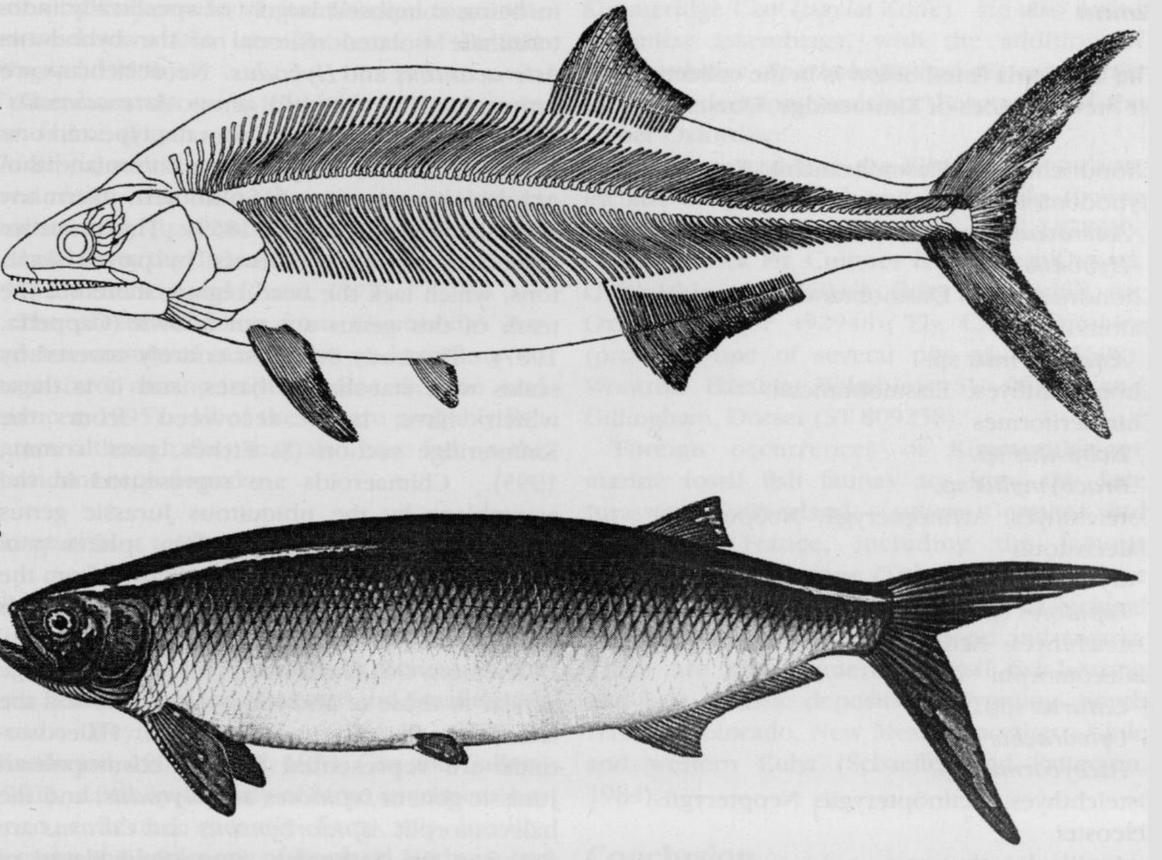


Figure 12.23 Fish from the Kimmeridgian: (A) *Hypsocormus*, sp. × 0.25 restoration by Woodward (1891, © The Natural History Museum, London); (B) *Thrissops* sp. × 0.5 restoration after Cox *et al.*, 1988.

Ledge and Maple Ledge. Named stone bands reach shore level as follows: The Flats at Broad Bench (SY 897787) and at The Flats (SY 905792); Washing Ledge (SY 907791); Maple Ledge (SY 909789). Hen Cliff, between Clavell Tower and Cuddle, exposes the *elegans*, *scitulus* and *wheatleyensis* Zones (the *Pectinatites* Zones). The stone marker bands include the Yellow Ledge, which reaches the shore at Yellow Ledge (SY 912782), and the Cattle Ledge and the Grey Ledge higher in the cliff.

The fauna of the Kimmeridge Clay is restricted to the mudstones and bituminous shale units and in both units is essentially the same, being dominated by infaunal bivalves, including *Lucina* and *Protocardia*. There is also an encrusting epifauna, but this is restricted, consisting only of oysters (*Liostrea* and *Nanogyra*). Minor elements include *Discina*, *Lingula*, '*Gervillia*', *Entolium* and aporrhaid gastropods. The other biofabrics in the mudstones are different from those in the bituminous shales, indicating different taphonomies (Aigner, 1980). This limited biota indicates somewhat oxygen-depleted bottom conditions, and that the vertebrates must have occupied a midwater zone.

In the past most specimens collected in the Kimmeridge area were ascribed to Kimmeridge Bay, although many are thought to have come from the cliffs further to the east, in an area known as the 'Kimmeridge Ledges', at Encombe Bay (SY 927776–SY 955771). Throughout the sequence scattered fish remains are common, and complete specimens are also found in the organic rich shales and coccolith limestone bands in the Bay. Fish material has been collected recently from the *hudlestoni* and *pectinatus* Zones at Rope Lake Head (SY 927776) and to the east at Freshwater Point (SY 943773). The remains mostly occur as incomplete specimens, detached jaws, partial skulls, caudal fins and isolated teeth, but whole articulated fish are also fairly common throughout the sequence. Some fossils show soft tissue preservation.

Fauna

The fish fauna listed below is in the collection of Mr Steven Etches of Kimmeridge, Dorset.

Chondrichthyes: Elasmobranchii: Euselachii: Hybodontoidea
Asteracanthus spp.
Hybodus spp.
Chondrichthyes: Elasmobranchii: Neoselachii: Batomorphii
Asterodermus sp.
Chondrichthyes: Elasmobranchii: Chimaeriformes
Ischyodus sp.
Brachymylus sp.
Osteichthyes: Actinopterygii: Neopterygii: Halecostomi
Gyrodus spp.
Lepidotes sp.
Osteichthyes: Actinopterygii: Neopterygii: Halecomorphi
Caturus spp.
Osteorachis sp.
Pachycormus sp.
Osteichthyes: Actinopterygii: Neopterygii: Teleostei
Aspidorhynchus sp.
Hypsocormus sp.
Allothrissops sp.
Eurycormus sp.
Leptolepis spp.
Pachythrissops sp.
Pholidophorus spp.
Thrissops sp.

Interpretation

The Kimmeridge Clay marks a period of widespread argillaceous sedimentation in north-west Europe in environments that were fully marine. The resulting thick series of clays and bituminous shales are considered to have been deposited in calm bottom waters, and anaerobic conditions may have prevailed in a stratified water column (Aigner, 1980), an environment similar to the present-day Black Sea. The sediments are essentially terrigenous in origin, indicating considerable erosion from a nearby landmass (? the London–Ardennes island and Cornubia), although there are no obvious plant macrofossils.

The shark fauna of the Kimmeridge Clay is similar to other Jurassic selachian assemblages in being composed largely of specifically indeterminate isolated material of the hybodonts *Asteracanthus* and *Hybodus*. Neoselachians are represented by a batoid genus '*Asterodermus*' sp. otherwise only known from the type and one other specimen from the Lower Tithonian lithographic limestones of Solnhöfen, Germany (Agassiz, 1833–45; Meyer, 1859). This primitive rhinobatid ray is represented by partial skeletons, which lack the head region, therefore the teeth of this genus are not known (Cappetta, 1987). The body is almost entirely covered by scales with star-shaped bases, and it is these which have been recovered from the Kimmeridge section (S. Etches, pers. comm., 1995). Chimaeroids are represented in the assemblage by the ubiquitous Jurassic genus *Ischyodus* and mandibular plates of *Brachymylus*, a form otherwise known from the Lower Oxford Clay of the English Midlands (Martill and Hudson, 1991).

The bony fish fauna comprises an assemblage similar to those of Mid-Jurassic sections and the later Purbeck Limestone Formation. Halecostomids are represented by the cosmopolitan Jurassic genera *Lepidotes* and *Gyrodus*, and the halecomorphs *Aspidorhynchus* and *Caturus* are found in the Bathonian 'Stonesfield Slates' of Stonesfield (q.v.) and the Purbeck fish faunas of Durlston Bay (q.v.). Recently discovered is a *Caturus* sp. specimen with a coleoid lodged in the gullet, strongly suggesting that the fish could feed on relatively large prey (Etches and Clarke, 1993). A further caturid, *Osteorachis*, is also recorded from the Kimmeridge Clay succession. This fairly large caturid is also known from the Lias of southern Britain, and the Oxford Clay (Callovian–Oxfordian) of the English Midlands (Martill and Hudson, 1991). The stout-bodied pachycormids are well represented in the Kimmeridgian of Kimmeridge Bay, including two genera, *Pachycormus* and *Hypsocormus*, which are long-ranging forms found in rocks of Early through to Late Jurassic age (Figure 12.23).

The Kimmeridge teleost assemblage contains species of the cosmopolitan Jurassic genera *Leptolepis* and *Pholidophorus*, and although the material is in excellent state of preservation (S. Etches, pers. comm., 1995), no specific determination has been made. However, it is fairly certain that the fauna will include the typical Upper Jurassic species diagnosed from the Purbeck Limestone Formation of Durlston Bay (q.v.). Pholidophorids are also represented in the fauna by *Eurycormus*, a stout-bodied form otherwise known from the Tithonian of Bavaria (Wagner, 1859b).

There are also two ichthyodectid genera in the fauna (Figure 12.23), *Pachythrissops* and *Thrissops*, which are similar to specimens recovered from the Late Jurassic succession at Durlston Bay (q.v.) and *Allothrissops*, an ichthyodectid from the Tithonian of Bavaria (Nybelin, 1974a; Patterson and Rosen, 1977).

The preserved fauna from Kimmeridge Bay consists mainly of marine fish and medium- to large-sized marine reptiles (see Benton and Spencer, 1995). All of these were probably fish eaters, although they may also have fed on the abundant cephalopods.

Comparison with other localities

Kimmeridge Clay fish sites comparable to Kimmeridge Bay include the Lower Kimmeridge Clay outcrop (*baylei–mutabilis* Zones) in the area around Portland Harbour and Smallmouth Sands, Weymouth (SY 669764–SY 672771; Woodward, 1901; Arkell, 1933; Cox and Gallois, 1981). Little in the way of large specimens has been collected recently from this locality, because the enclosure of Portland Harbour has reduced erosion. However, the relevant beds (*cymodoce* Zone) have been re-excavated and finds, including teeth, jaws, vertebrae and fin spines, continue to be made by bulk sampling the oyster-rich clay beds, which are exposed behind the rapidly eroding sea defences (A. Brokenshire, pers. comm., 1995; S. Etches, pers. comm., 1995). The faunal list given by A. Brokenshire (pers. comm., 1995) for this site includes hybodont sharks (*Hybodus*, *Sphenodus*, and *Asteracanthus*), neoselachians (*Synechodus*, squatinomorphs, squalomorphs, galeomorphs and batomorphs), chimaeroids (*Bractymylus*, *Ischyodus* and ?*Elasmodectes*), halecostomes (*Lepidotes*, *Macromesodon* and *Gyrodus*), halecomorphs (*Belonostomus*, *Hypsocormus*, *Aspidorhynchus* and *Caturus*) and teleosts (pholidophorid material, *Sphaeronchus* otoliths and *Eurycormus*). In addition, specimens are occasionally found offshore from this site, and in the degraded Kimmeridge Clay beds west of the classic site. C. Underwood (pers. comm., 1997) has recently found a diverse microshark fauna, including *Hybodus*, *Synechodus*, *Protospinax*, '*Squatina*' and possibly *Oroctoloboides*, within the basal Kimmeridge Clay (*baylei* Zone). He also noted a similar assemblage, with the addition of *Parasymbolus*, *Spathobatis* and *Heterodontus*, in the underlying Sandsfoot Formation of the Upper Oxfordian.

Sites comparable to the Kimmeridge section, include Swindon Brick and Tile Works (Lower Kimmeridge Clay), Wiltshire (SU 142838); Chawley Brick Pit, Cumnor Hurst, near Oxford, Oxfordshire (SP 475043); Oday Hill landfill site, Oxfordshire (SP 492948); Ely, Cambridgeshire (probably one of several pits at TL 55508); Wootton Bassett, Wiltshire (SU 0638), and Gillingham, Dorset (ST 809258).

Foreign occurrences of Kimmeridge-age marine fossil fish faunas are from the Late Jurassic of Switzerland, southern Germany, and Normandy, France, including the famous Lithographic Limestone (Tithonian) assemblage of Bavaria, as well as the Late Jurassic of Portugal and the Portlandian of Switzerland and Austria. There are also numerous fossil fish-bearing Mid–Late Jurassic deposits in Wyoming, South Dakota, Colorado, New Mexico, northern Chile and western Cuba (Schaeffer and Patterson, 1984).

Conclusion

The cliffs and foreshore exposures of the Kimmeridge Clay at Kimmeridge Bay yield a Late Jurassic fauna of exceptionally preserved fossil fish which rival the famous Tithonian age assemblages of southern Germany and give the site its conservation value. The cliffs are subject to continuing erosion, and fresh finds continue to be made every year.

DURLSTON BAY (SZ 035772–SZ 039786)

Highlights

The fish fauna from the Purbeck Limestone Group of Durlston Bay, Swanage is of special interest as it represents the latest occurrence in Britain of typical Jurassic fish assemblages. The fish remains are mostly fairly well preserved and 32 species have been described from this locality.

Introduction

The 2 km stretch of coastal sea cliffs between

Figure 12.24 The uppermost Jurassic and Lower Cretaceous shales and limestones in the northern part of cliff section at Durlston Bay (photo: J.L. Wright).

Peveril Point and Durlston Head near Swanage, Dorset, displays the finest sections of the Purbeck Limestone Group in Britain and comprise the type locality for the Formation (Figures 12.24 and 12.25). The strata of the Purbeck Limestone Formation here are famous for their exceptionally diverse fauna, which includes mammal remains unique to the early Cretaceous of Britain, and important reptilian material. The remarkable fish fauna has been known since 1816 (Webster, 1816). Museum collections made in the mid- and late 19th century formed part of A.S. Woodward's monograph upon the fossil fishes of the late Jurassic and early Cretaceous succession of the south coast of England (Woodward, 1915–1919). Both freshwater and marine forms occur, including abundant holostean material and teleost fishes. Durlston Bay is the type and only locality for two species of early teleost, *Thrissops molossus* and *Pachythrissops laevis*. It is also the type location for the coelacanth *Holophagus purbeckensis*.

Most of the vertebrates from Durlston have been obtained from the natural cliff exposures, but some of the more complete fish remains came from underground workings for the Purbeck 'Building Stones'. Although the latter source for fish material is no longer available, the extensive cliff exposures continue to yield new specimens. Many finds were made in the early 19th century by S.H. Beckles, in the course of his excavation of the cliff in an area, just north of the 'Zigzag path', that is, well south of the outcrop of the mammal bed at beach level.

The Purbeck section at Durlston Bay (Figure 12.26) has been described with varying degrees of accuracy by many authors (Austen, 1852, pp. 9–16; Bristow and Fisher, 1857, pp. 245–54; Strahan, 1898, pp. 91–6; Arkell, 1933, pp. 521–9; Clements, *in* Torrens, 1969a, figs A35–37, 1993). Cope and Clements (*in* Torrens, 1969a, pp. A57–A64), and MacFadyen (1970, pp. 134–52) gave a history of research on the stratigraphy and palaeontology of the Durlston section.

Description

The section of the Purbeck Limestone Group at Durlston Bay is based on the annotated stratigraphical logs of Clements (*in* Torrens, 1969a; 1993), where bed numbers are prefixed DB

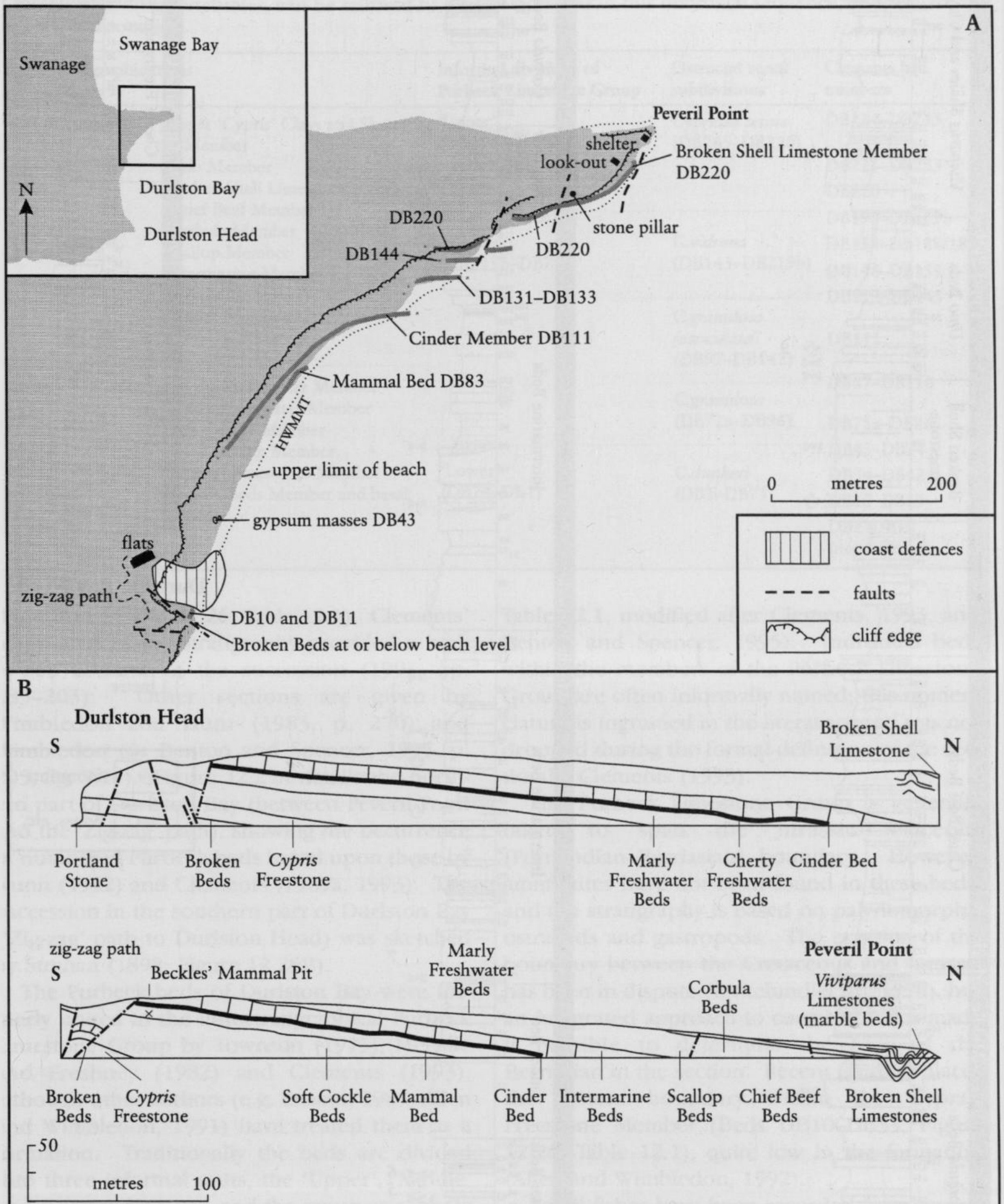


Figure 12.25 (A) Sketch map of the northern part of Durlston Bay (after Clements, 1993); letters and numbers refer to Clements' labelling of the beds. (B) Cliff profile at Durlston Bay (after Clements, 1993; Benton and Spencer, 1995).

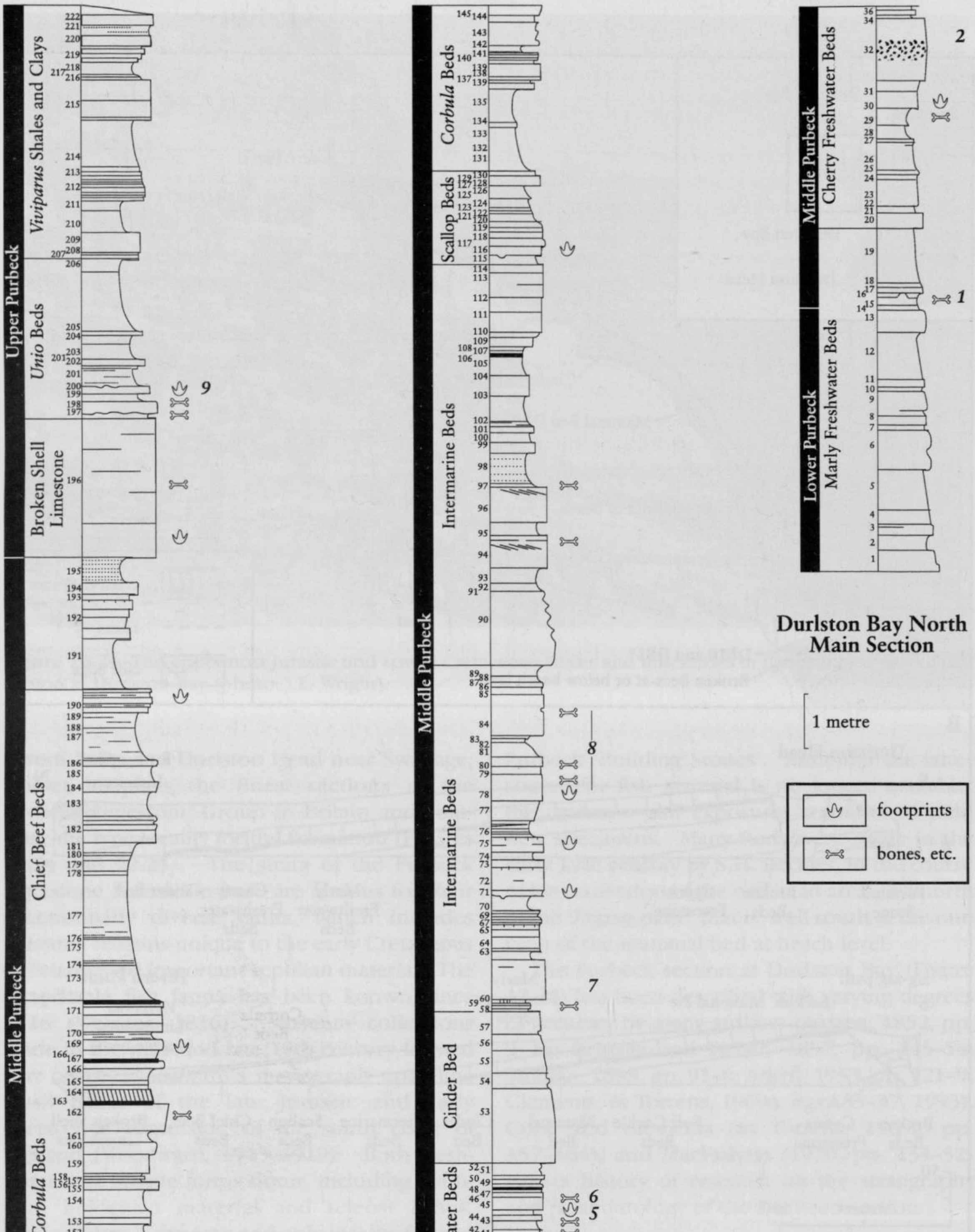


Figure 12.26 Stratigraphical section through the Purbeckian at Durlston Bay (after Benton and Spencer, 1995, and based on Wimbledon and Hunt, 1993). Numbers are those of Clements (*in* Torrens, 1969a).

Table 12.1 Designated stratal units in the Purbeck Limestone Group of the Durlston Bay section. Discoveries of fossils, including vertebrates, can be referred to precise horizons in this unbroken sequence, and related to the ostracod zonation.

Formal stratigraphic terms		Informal divisions of Purbeck Limestone Group	Ostracod zonal subdivisions	Clements bed numbers
Durlston Formation	Upper '*Cypris*' Clays and Shales Member	'Upper' (DB246–DB220)	*Cypridea setina* (DB245–DB220)	DB224–DB245
	Unio Member			DB221–DB223
	Broken Shell Limestone Member			DB220
	Chief Beef Member			DB190–DB219b
	Corbula Member	'Middle' (DB219b–DB75a)	*C.vidrana* (DB143–DB219b)	DB154–DB188/189
	Scallop Member			DB146–DB153
	Intermarine Member (or Upper Building Stones)			DB112–DB145
	Cinder Member		*C.granulosa fasciculata* (DB97–DB142)	DB111
Lulworth Formation	Cherty Freshwater Member			DB87–DB110
	Marly Freshwater Member		*C.granulosa* (DB72a–DB96)	DB75a–DB86
	Soft Cockle Member			DB43–DB74
	Hard Cockle Member			DB34–DB42
	'*Cypris*' Freestones Member	'Lower' (DB74–DB1)	*C.dunkeri* (DB1–DB71)	DB10–DB33
	Broken Beds Member and basal beds			DB1–DB10 (not exposed)

(Figure 12.25 and 12.26, Table 12.1). Clements' reappraisal of the stratigraphy provided a bed-by-bed account of the succession (1993, pp. 183–203). Other sections are given by Wimbledon and Hunt (1983, p. 270) and Wimbledon (*in* Benton and Spencer, 1995, p. 205, fig. 7.14). Figure 12.25A details the northern part of Durlston Bay (between Peveril Point and the 'Zig-zag' path), showing the occurrence of numbered Purbeck beds based upon those by Nunn (1992) and Clements (1989a, 1993). The succession in the southern part of Durlston Bay ('Zig-zag' path to Durlston Head) was sketched by Strahan (1898; Figure 12.25B).

The Purbeck beds of Durlston Bay were formerly united in the lithostratigraphical Purbeck Limestone Group by Townson (1975), Melville and Freshney (1982) and Clements (1993), although other authors (e.g. Ensom, 1985; Allen and Wimbledon, 1991) have treated them as a formation. Traditionally the beds are divided into three informal units, the 'Upper', 'Middle' and 'Lower' divisions, and the group as a whole has been split into two formal lithostratigraphical formations, the Durlston Formation above, and the lower, Lulworth Formation (Townson, 1975; Clements, 1993). Ensom (1985) formalized the minor lithostratigraphical divisions of Bristow (Bristow and Fisher, 1857, and *in* Damon, 1884) as members (Figure 12.26 and Table 12.1, modified after Clements, 1993, and Benton and Spencer, 1995). Individual beds within the members of the Purbeck Limestone Group are often informally named; this nomenclature is ingrained in the literature and was not dropped during the formal definition of the section by Clements (1993).

The Purbeck Limestone Group is generally taken to span the Jurassic–Cretaceous (Portlandian–Berriasian) boundary. However, ammonites have not been found in these beds, and the stratigraphy is based on palynomorphs, ostracods and gastropods. The position of the boundary between the Cretaceous and Jurassic has been in dispute (Birkelund *et al*., 1978), but an integrated approach to correlation has made it possible to determine the base of the Berriasian in the section. Recent opinion places the system boundary within the '*Cypris*' Freestone Member (Beds DB10–DB33; Figure 12.26; Table 12.1), quite low in the formation (Allen and Wimbledon, 1992).

Fossil fishes have been recorded from several levels in the sequence, between the Mammal Bed (Bed DB83 of the Marly Freshwater Member) at the base of the 'Middle Purbeck Beds' and the Upper '*Cypris*' Clays and Shales Member (Beds DB224–DB245), found in the highest part of the 'Upper Purbeck Beds' succession:

	Thickness (m)
DB221. Crocodile Bed (Bed 6 of Austen; Bed 81 of Bristow; Bed 200 of Allen and Wimbledon): plants, coprolites, fish, turtles, crocodiles	0.15
DB220. Broken Shell Limestone Member (Soft Burr) (Bed 9 of Austen; Bed 78 of Bristow; Bed 196 of Allen and Wimbledon): fishes and turtles	0.15
DB154–DB188/189. *Corbula* Member (Beds 22–44 (in part) of Austen; Beds 59–70 of Bristow; Beds 131–174 of Allen and Wimbledon): insects, fishes, turtles and footprints (West and El-Shahat, 1985)	7.6
DB112–DB145. Intermarine Member or Upper Building Stones (Beds 45–70, Turtle Beds of Austen; Beds 45–57, Intermarine Beds of Bristow; Beds 58–114 of Allen and Wimbledon):	
DB133, Red Rag (Bed 52 of Austen; Bed 54 of Bristow) yields fishes, turtles and coprolites	0.1
DB113 (Bed 69 of Austen; Bed 45d of Bristow; Bed 61 of Allen and Wimbledon) contains the remains of fishes and reptiles	0.5
DB87–DB110. Cherty Freshwater Member (Beds 72–88 of Austen; Beds 25–42 of Bristow; Beds 20–52 of Allen and Wimbledon):	
DB102 has yielded a diverse microvertebrate assemblage including fish (Ensom, 1988), amphibians, reptiles (Ensom *et al.*, 1991) and mammals (Ensom, 1987, 1988)	0.05
DB83. The Mammal Bed ('Dirt Bed') of Beckles excavations (Bed 93 of Austen; Bed 22 of Bristow; Beds 14–16 of Allen and Wimbledon): has yielded plant remains, ostracods, gastropods, bivalves, fish, reptiles (Benton and Spencer, 1995) and mammals	0.1

Although fish remains are found throughout the sequence, the best specimens are concentrated within the Intermarine Member or Upper Building Stones (DB112–DB145) of the 'Middle Purbeck Beds' (Woodward, 1915–1919). Many of the bony fishes in these limestone units are represented by whole or partial skeletons. However, many specimens have been crushed during lithification and details are lost (Woodward, 1915–1919).

Fauna

Thirty-two species of fish have been recorded here (Figure 12.27). Many specimens, however, are labelled merely 'Middle Purbeck Beds: Swanage' (e.g. Woodward, 1915–1919), and they could have come from some of the inland quarries. Fish collections in the following institutions were examined: NHM, BGS(GSM), CAMMZ, CAMSM, DORCM and OUM. References include Davies (1887) and A.S. Woodward (1890, 1895a, 1915–1919).

Chondrichthyes: Elasmobranchii: Euselachii: Hybodontoidea
- *Asteracanthus verrucosus* Egerton, 1854
- *A. semiverrucosus* Egerton, 1854
- *Hybodus ensis* Woodward, 1915–1919
- *H. strictus* Woodward, 1915–1919
- Hybodont cephalic spines

Osteichthyes: Actinopterygii: Neopterygii: Halecostomi
- *Lepidotes minor* Agassiz, 1833–1837
- *L. notopterus Agassiz*, 1835–1837
- *Lepidotes* sp.
- *Macromesodon daviesi* Woodward, 1890
- *Macromesodon* sp.
- *Eomesodon barnesi* Woodward, 1906
- *E. depressus* Woodward, 1915–1919
- *Eomesodon* sp.
- *Proscinates (Microdon) radiatus* Agassiz, 1839–1844
- *Ophiopsis dorsalis* Agassiz, 1844
- *Histionotus angularis* Egerton, 1855

Osteichthyes: Actinopterygii: Neopterygii: Halecomorphi
- *Caturus (Strobilodus) purbeckensis* (A.S. Woodward, 1890)
- *C. tenuidens* A.S. Woodward, 1895
- *Amiopsis (Megalurus) austeni* (Egerton, 1858a)
- *A. damoni* Egerton, 1858
- *Aspidorhynchus fisheri* Egerton, 1854

Osteichthyes: Actinopterygii: Neopterygii: Teleostei
- *Pholidophoristion ornatus* Agassiz, 1843–1844
- *Pholidophorus granulatus* Egerton, 1855
- *Ichthyokentema purbeckensis* Davies, 1887
- *Pleuropholis crassicauda* (Egerton, 1858a)
- *P. longicauda* (Egerton, 1858a)
- *Leptolepis* sp.
- *Pachythrissops laevis* Woodward, 1915–1919
- *Thrissops molossus* Woodward, 1915–1919

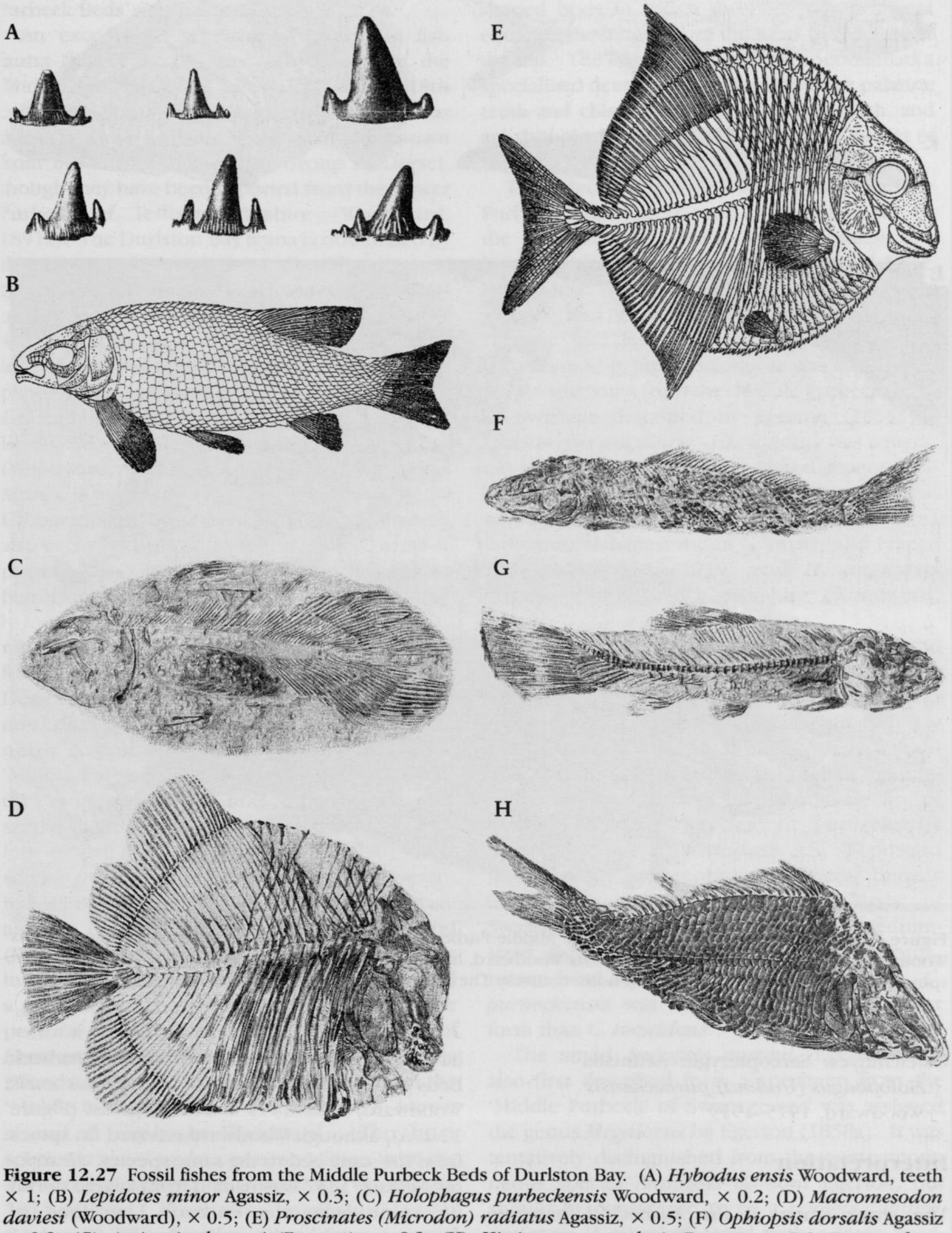


Figure 12.27 Fossil fishes from the Middle Purbeck Beds of Durlston Bay. (A) *Hybodus ensis* Woodward, teeth × 1; (B) *Lepidotes minor* Agassiz, × 0.3; (C) *Holophagus purbeckensis* Woodward, × 0.2; (D) *Macromesodon daviesi* (Woodward), × 0.5; (E) *Proscinates (Microdon) radiatus* Agassiz, × 0.5; (F) *Ophiopsis dorsalis* Agassiz × 0.3; (G) *Amiopsis damoni* (Egerton), × 0.3; (H) *Histionotus angularis* Egerton × 0.5. Figures from Woodward (1889–1901) © The Natural History Museum, London. (Continued on p. 412.)

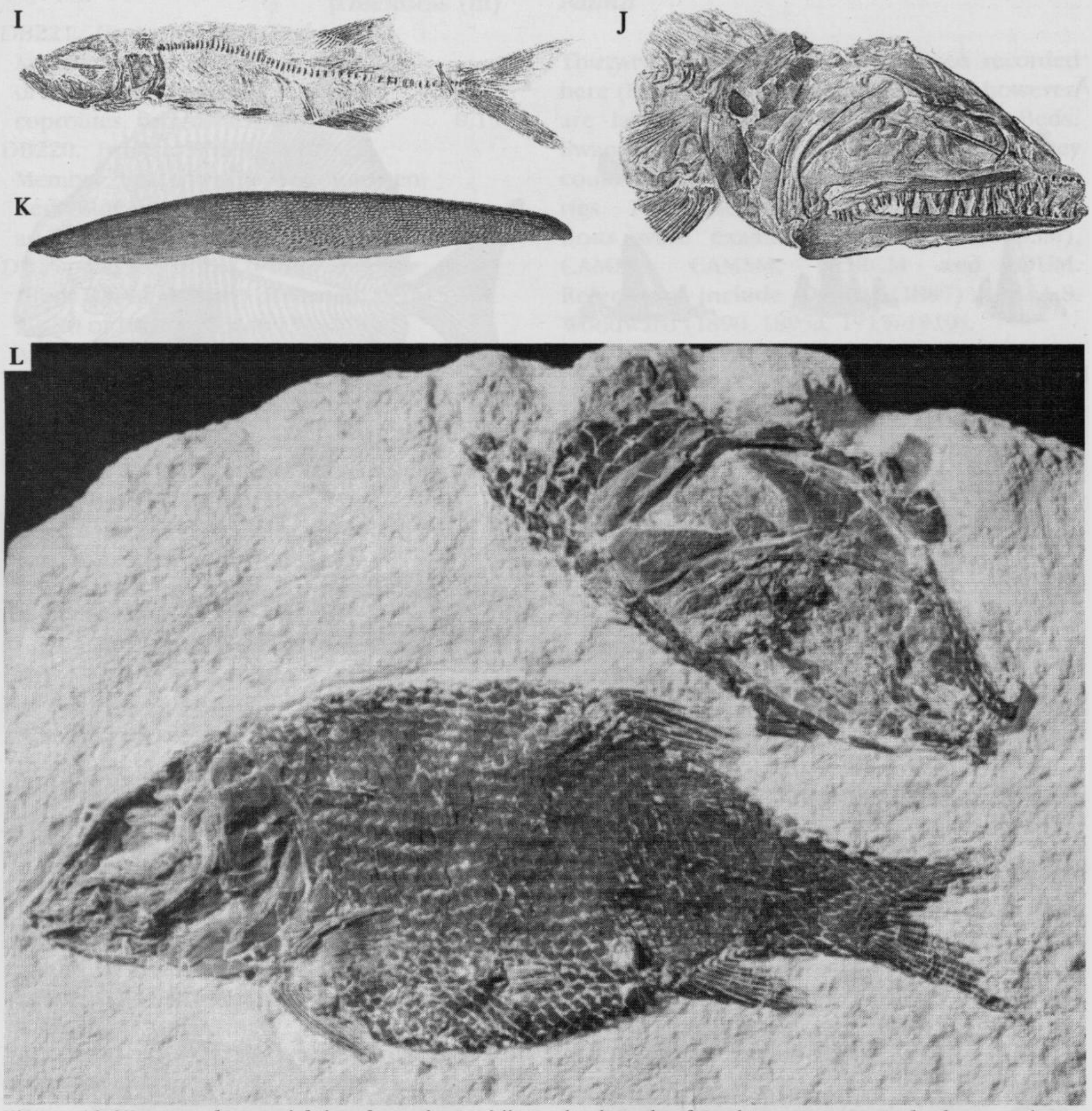


Figure 12.27 – *contd.* Fossil fishes from the Middle Purbeck Beds of Durlston Bay. (I) *Pachythrissops laevis* Woodward, × 0.25; (J) *Caturus purbeckensis* Woodward, head × 0.5; (K) *Asteracanthus verrucosus* Egerton fin spine × 0.5; (L) *Lepidotes* sp. × 0.5 (Photo: courtesy The Natural History Museum, London, T00562/A).

Osteichthyes: Sarcopterygii: Actinistia
Holophagus (Undina) purbeckensis Woodward, 1915–1919

Interpretation

The shark fauna of the Purbeck Limestone Group at Durlston Bay is similar to other Jurassic selachian assemblages, being composed largely of the isolated teeth, fin and cephalic spines of hybodonts. Four hybodont species have been described from the 'Middle Purbeck Beds' of the Swanage region. *Hybodus ensis* Woodward, 1915–1919 is a tooth genus (Figure 12.27A), although Woodward referred fin spines from the same bed to the same species. *H. strictus* Agassiz, 1837 was named from a large dorsal fin spine from the Purbeck Limestone of Swanage. Spines have also been referred to *Asteracanthus* (Egerton, 1854; Woodward, 1915–1919). Both *A. verrucosus* Egerton (Figure 12.27K) and *A. semiverrucosus* Egerton were named from distinctive large ornamented dorsal fin spines recovered from the 'Middle Purbeck Beds' and housed in the DORCM.

An exceptional primitive neopterygian fish fauna (Figure 12.27) was recovered from the 'Middle Purbeck Beds' of Swanage in the 19th century. Primitive actinopterygians such as those at Lyme Regis or Whitby are not known from the Purbeck Limestone Group of Dorset, though they have been reported from the Lower Purbeck of Teffont, Wiltshire (Woodward, 1891a). The Durlston Bay fauna is dominated by the semionotids and pycnodontid neopterygians. Two species of the semionotid *Lepidotes* occur at Swanage, including the type of *L. minor* Agassiz. This large species (up to 0.4 m in length), represented by numerous near complete specimens (Figure 12.27B), varies between a deep-bodied form with a rounded back (e.g. BGS(GSM) 27975) and a slim-bodied fish (Woodward, 1915–1919). *Lepidotes notopterus* Agassiz, a more delicate species known from the Lithographic Limestone of Solnhöfen, Germany, also occurs. Jaws and common isolated teeth of pycnodonts in the Purbeck Limestone Formation of Durlston Bay are mostly specifically indeterminate. However, more complete and rare specifically diagnostic specimens have been found at this and other Purbeck localities in Dorset and Wilstshire. *Macromesodon (Mesodon) daviesi* (Woodward, 1890), named upon a nearly complete fish (Figure 12.27D) from the 'Middle Purbeck' of Swanage, is a small (up to 0.25 m in length) deep-bodied pycnodont, with saddle-shaped scales ornamented with a row of four or five denticles (Woodward, 1890). The similar pycnodont, *Eomesodon*, is also present in the Purbeck Limestone Formation of Swanage and the Portland Stone of the Isle of Portland (Woodward, 1915–1919). *Eomesodon* had a much deeper body than *Mesodon* and possessed a prominant dorsal 'hump' which overhung the pectoral girdle and head. The head of *Eomesodon* is also more triangular in profile (Woodward, 1915–1919). Two species from the 'Middle Purbeck Beds' of Swanage are *E. barnesi* and *E. depressus* Woodward. The latter species is based upon a poor specimen from the Purbeck Formation of Durlston (Woodward, 1915–1919). *Proscinates radiatus* Agassiz (Figure 12.27E) was also named from a partial skeleton recovered from the 'Middle Purbeck' of the Swanage area. The species is represented by several specimens better preserved of features than the type (Woodward, 1915–1919). *Proscinates* possessed a deep and almost disc-shaped body in which the body depth almost equalled the length from the head to the base of the tail. The semionotid and pycnodonts had a specialized dentition of strong, stud-like palatine teeth and chisel-shaped premaxillary teeth, and are thought to have eaten a durophagous diet of molluscs and crustaceans.

The halecostomids are also represented in the Purbeck Limestone Group of Durlston Bay by the macrosemiids, which usually possessed a large and elegant dorsal fin (Bartram, 1977; Frickhinger, 1991) such as *Ophiopsis dorsalis* Agassiz and *Histionotus angularis* Egerton (Figure 12.27H). The type species of the macrosemiid genus *Histionotus* was based on a partial specimen from the 'Middle Purbeck Beds' of Swanage described by Egerton (1855) as *Histionotus angularis*. *Histionotus* was a medium-sized fish with a large head and pronounced dorsal hump, known from the Swanage species, two or three other species from the (Solnhöfen) Lithographic Limestone of Germany and France (Woodward, 1915–1919) and *H. angularis* Egerton from Tisbury, Wiltshire (Woodward, 1915–1919).

The halecomorphs are represented in the Purbeckian fish fauna by several species of the order Amiiformes, with caturids, amiids and aspidorhynchids present in the Durlston Bay sections (Woodward, 1915–1919). The ubiquitous Jurassic genus *Caturus* is known from fragments in the Purbeck Limestone Group of Dorset, with two species, *C. purbeckensis* Woodward and *C. tenuidens* A.S. Woodward named from fragmentary specimens (mostly jaws) from the 'Middle Purbeck Beds' of Swanage (Figure 12.27J). *Caturus* is a medium-sized fish with an elongate, fusiform trunk, robust head and deeply incised forked tail. *C. purbeckensis* was a much stouter and larger form than *C. tenuidens*.

The amiid *Amiopsis austeni* (Egerton) was also first described from a specimen from the 'Middle Purbeck' of Swanage and was assigned the genus *Megalurus* by Egerton (1858a). It was tentatively distinguished from the contemporaneous species *Amiopsis damoni* Egerton, but should be considered to be a *nomen dubium*. *Amiopsis* is a typical amiid with a large head, small, stout, styliform teeth and powerful jaws. It had an elongate, laterally compressed body covered in large oval scales, and a convex border to the caudal fin; it is known widely from the Lower Cretaceous of Europe (Figure 12.27G).

Ophiopsis dorsalis Agassiz is a robust (up to 0.2 m) form which possesses a fusiform body and deeply forked caudal fin (Figure 12.27F; Woodward, 1915–1919). The genus is represented by *O. penicillata* Agassiz in the 'Lower Purbeck' of Weymouth, Dorset, and the Purbeck Beds of the Isle of Portland and the Purbeck of Wockley, near Tisbury, Wiltshire (represented by *O. breviceps* Egerton). Species are diagnosed on their scale types, cranial anatomy and fin morphology (Woodward, 1915–1919).

The aspidorhynchids had a long, thin, fusiform body with robust, smooth rectangular scales and an elongated, slender rostrum, which projected out in front and overhung the mandible. They are also characterized by their symmetrically forked tail and relatively tiny paired and unpaired fins. The aspidorhynchids are represented in the Purbeck Limestone of Dorset by *Aspidorhynchus fisheri* Egerton. This is a species attaining a length of approximately 0.4 m, the head tapering to an acute rostrum, which projected a total of one-third of the length of the cranium (Woodward, 1915–1919). *Aspidorhynchus fisheri* is the last representative of this important Jurassic genus.

Primitive teleosts are fairly abundant in the rocks of the Purbeck Limestone Group of Dorset and include representatives of the orders Pholidophoriformes, Leptolepiformes and Ichthyodectiformes. Both pectinate-scaled and smooth-scaled forms of *Pholidophorous* occur in the Purbeck Limestone, and *P. ornatus* Agassiz and *P. granulatus* Egerton have been described from the 'Middle Purbeck' of Swanage (Woodward, 1915–1919). *Pholidophorus* is also known from the Purbeck Group of Weymouth, Isle of Portland, and Teffont, Wiltshire. The pholidophorids of the Purbeck Group are the last occurrence of this primitive teleost group. The Pleuropholidae are only known from one genus, *Pleuropholis*, which was originally described by Egerton (1854) for a small (<0.1 m) sprat-like form with a tiny mouth, from the 'Middle Purbeck' of Sutton Mandeville, Wiltshire. Other species were later named from the Purbeck Limestone Group of Wiltshire and Dorset. The small and rare *Ichthyokentema* has been described by Griffith and Patterson (1963). The leptolepids are only represented at Durlston Bay by undiagnostic fragments of the form genus *Leptolepis*, but there are two species of ichthyodectids and Durlston Bay is the type and only locality for both (Figure 12.26). The first, *Pachythrissops laevis* Woodward, is a large (0.5 m in length) species with a fusiform body, deeply forked tail and small head. The second, *Thrissops molosus* Woodward, is similarly a large form, attaining lengths up to 0.35 m, with a short, deep head and stout body. It also had a strongly incised forked caudal fin, with very delicate lobes. Both genera were covered in very thin and delicate cycloidal scales that are not often preserved as fossils, and had large bony gill-rakers (Woodward, 1915–1919). *Thrissops curtus* Woodward is distinguished from *T. molosus* on the basis of smaller size. Nybelin (1966, 1974a) and Forey (1973a) have suggested that *Pachythrissops* may be an early megalopid elopiform, as it shares osteological characters with Cretaceous forms and the modern-day tarpon *Megalops*.

The coelacanth *Holophagus purbeckensis* Woodward is only known from a single incomplete specimen from the 'Middle Purbeck Beds' of Swanage. The specimen lacks a head, but sufficient of the posterior portion of the body and the dorsal and caudal fins was preserved (Figure 12.27C) for Woodward (1915–1919) to erect the species. *Holophagus purbeckensis* is a stout fish which may have reached lengths of up to 0.4 m, and it possessed scales ornamented with coarse elongated tubercles (Woodward, 1915–1919).

Fossil amphibians have been recovered from bulk sampling two microvertebrate-rich clay horizons in the Cherty Freshwater Member (?Lower Cretaceous) at several localities on the Isle of Purbeck, Dorset (Ensom, 1987, 1988; Ensom *et al.*, 1991). The material includes abundant albanerpetontid salamander remains, and some discoglossid frog material which represent families known from the Middle and Upper Jurassic of Europe. However, more significant are the (as yet) undescribed jaw fragments representing the earliest record of a bactrachosauroidid salamander (Ensom *et al.*, 1991). The initial discoveries were made at Sunnydown Farm, near Langton Matravers (SY 982788), in two horizons correlated with DB102 and DB101 in Durlston Bay (Clements, 1993). DB102 has also been sampled at three other localties along a 6 km outcrop, including Durlston Bay, and at all these sites microvertebrates were recovered (Ensom *et al.*, 1991).

However, so far, no amphibian material has been recovered from the Durlston Bay section, although P.C. Ensom (pers. comm., 1995) considers this to be partly due to collection failure.

Comparison with other localities

Similar Purbeck Limestone Formation faunas have been recovered from many localities in Dorset and Wiltshire, and these have been documented above. Specifically, these include the microvertebrate-rich beds at Sunnydown Farm (SY 982788), Suttle's Quarry (SZ 020777) and Lovell's Quarry (SY 980790), Dorset (Ensom *et al.*, 1991), and an unconfirmed report of a fossil frog from the Purbeck of Swindon, Wiltshire (Hudleston, 1876). Purbeck fish faunas have been recovered from the 'Lower' and 'Middle Purbeck Beds' in the Vale of Wardour, Wiltshire, the Isle of Portland and Weymouth, Dorset, and from localities in Buckinghamshire (Woodward, 1915–1919).

Farther afield, elements of the Purbeck fish faunas are known in the Late Jurassic of Germany and France (Woodward, 1915–1919). The English Wealden (Early Cretaceous) fish assemblages and those from other parts of western and central Europe also contain remnants of the late Jurassic fauna.

Conclusion

The Purbeck beds of Durlston Bay have yielded one of the most important Late Jurassic fossil fish faunas in the world from which the site derives its conservation value. The Durlston fauna occurs in marine and non-marine rocks that occupy a unique position at the Jurassic–Cretaceous boundary; it includes amphibians and a diverse fish assemblage, including exceptionally preserved early teleosts.