

PREVIOUSLY UNREPORTED SPINY LIMID BIVALVES FROM THE BLUE LIAS FORMATION (EARLY JURASSIC: HETTANGIAN) OF LYME REGIS, DORSET, UK

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We report the first records of the epifaunal, limid bivalves, *Ctenostreon philocles* (d'Orbigny), *C?* sp. and *Antiquilima* sp. nov. from the Blue Lias Formation at Lyme Regis, Dorset. All three occur as well-preserved, complete shells or individual valves and one or more are reported from at least four horizons in the Hettangian. *Ctenostreon philocles* has previously been recorded from an even lower horizon in the Blue Lias Formation at Sedbury Cliffs on the Bristol Channel. *Antiquilima* sp. nov. may previously have been confused with *A. succincta* (Schlotheim). Specimens of *C?* sp. and *Antiquilima* sp. nov. were first collected in the mid-late 19th Century, but not previously reported in the scientific literature. All three species were byssally-attached, epifaunal recliners and occur at restricted horizons together with a diverse benthonic fauna.

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INTRODUCTION

The Blue Lias Formation on the south coast of England crops out east and west of Lyme Regis and must be one of the most intensely collected stratigraphic units in all of British geology. It has been famous for its fossils since the time of Mary Anning (1799-1847) and is currently exploited by amateur and professional collectors as well as academic palaeontologists. Records of fossils from the Blue Lias Formation in the scientific literature go back at least to de la Beche (1822, p. 46) who listed four species of bivalves and commented that *Gryphaea incurva* was not common at Lyme Regis. Later, de la Beche expanded his description of the geology and fossils around Lyme Regis and listed about a dozen species of bivalves (1826, p. 28). Wright (1860) gave a general account of the Lower Lias of southern England, in which he briefly mentioned the occurrence of four species of sea urchins in the Lower Lias at Pinhay Bay, to the west of Lyme Regis (1860, p. 397). Wright also listed fossils from the "Ammonites planorbis beds" (1860, pp. 397-398), including five species of bivalves, but he did not specify exact localities for these fossils. Later, in the same publication (1860, pp. 401-403) Wright listed the occurrences of common fossils bed by bed and gave a summary table of the species found in his "Ammonites Bucklandi or Lima beds", which included eleven species of bivalves. Between them these lists cover the entire Blue Lias Formation as exposed on the Devon-Dorset border. Woodward (1893, pp. 60-62) recorded the names local quarry men gave to individual beds in the Blue Lias around Lyme Regis, as well as the fossils they contained. The list was repeated in Woodward and Ussher (1906, pp. 35-37). Both papers record only the most common fossils, or those, usually ammonites, that are most useful in correlation. Lang (1914, pp. 310-311) recorded the fossils in the upper part of the Blue Lias Formation as exposed in Church Bay, east of Lyme Regis, again mainly listing the most common species and including records from the Survey Memoir (Woodward and Ussher, 1906). Later, Lang (1924) refined the

bed terminology and added bed numbers for the individual beds of the entire Blue Lias Formation. His bed numbering system is still in use today. Lang also recorded bed-by-bed occurrences of the fossils he found personally in this survey. Hallam (1960, table 4, pp. 28-29) recorded a more extensive list of fossils, zone by zone through the Blue Lias Formation, including 31 species of bivalves. Most recently, Hodges (2000) has started a monograph of Liassic bivalves, though he has not yet covered the limids. Finally, Lord and Davis (2010) have described and illustrated the fossils of the Lower Lias of the Dorset Coast. In that work, Palmer (2010, p. 125) updated Lang's taxonomy and illustrated several species from the Hettangian part of the Blue Lias Formation. None of these published papers listed the names of, or described or illustrated the bivalves that form the subject of this paper.

Although not as popular with collectors as ammonites and vertebrates, the bivalves of the Blue Lias Formation around Lyme Regis have been well documented in the palaeontological literature. Thus, it was surprising to discover several large, well-preserved specimens of bivalves that have apparently not been recorded previously from the Blue Lias of Devon and Dorset. The spiny limid bivalve genus *Ctenostreon* was initially discovered by us in May 2006 during a bed-by-bed examination of the Blue Lias Formation in Pinhay Bay, west of Lyme Regis, (Figure 1) originally aimed at recording the precise horizons in which ammonites were preserved (see Paul *et al.*, 2008). The original search discovered similar spiny limid bivalves in at least four different beds within the Hettangian part of the Blue Lias Formation (Figure 2). The significance of these bivalves was not appreciated at that time nor was it thought that more than one species might be involved, so the only evidence of their occurrence consists of two photographs of the first specimen encountered and notebook records. Subsequently, additional specimens have been found loose at Seven Rock Point (Figure 1).

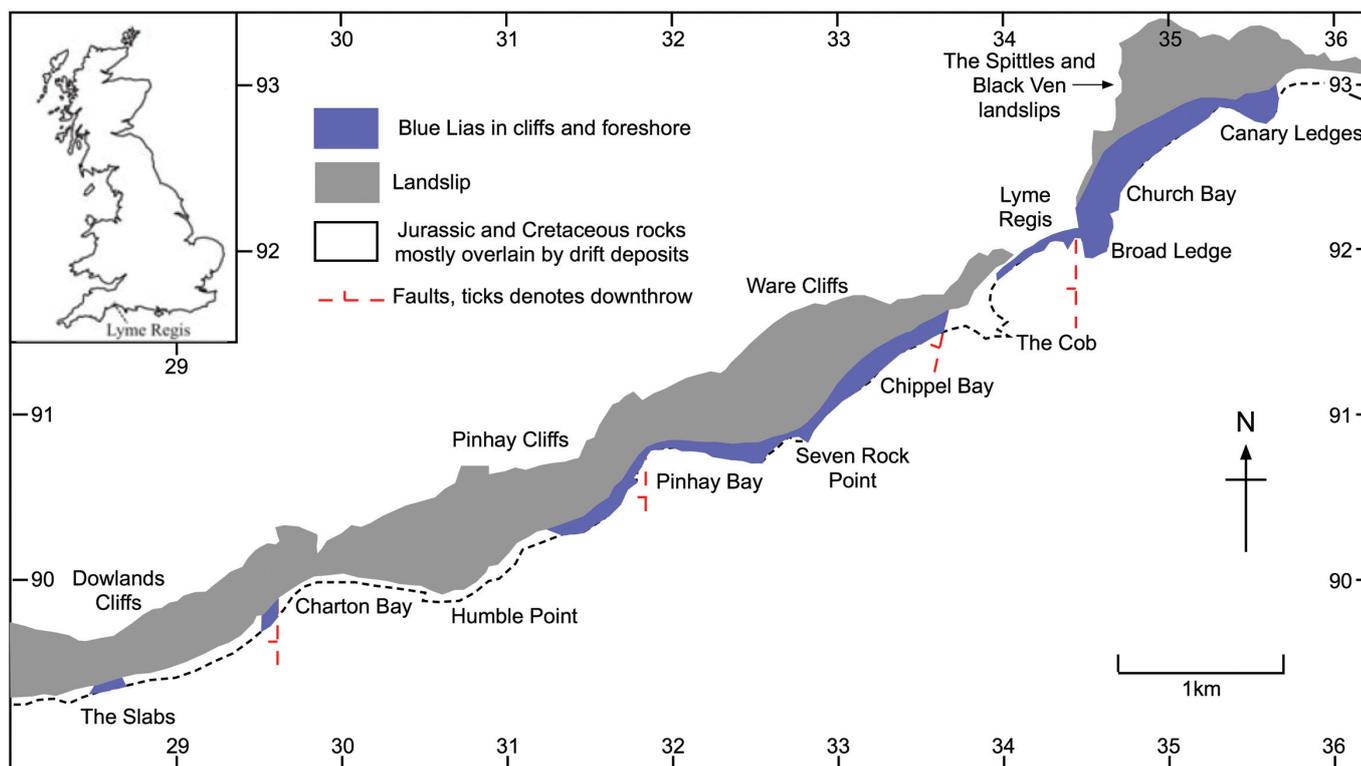


Figure 1. Exposures of the Blue Lias Formation to the east and west of Lyme Regis, Dorset. Numbers refer to 1 km squares of the National Grid. Redrawn from Gallois and Paul (2010, fig. 1).

In addition, on a visit to the British Geological Survey (BGS) collections at Keyworth, Nottinghamshire in November 2014, one of us (CRCP) came across two well-preserved spiny bivalves, labelled ‘*Ctenostreon* sp. Lower Lias (angulata zone), Lyme Regis, Dorsetshire’ (GSM 38789) and ‘*Ctenostreon tuberculatus* (Terquem) Lower Lias, Lyme Regis, Dorsetshire’ (GSM 91697). These were purchased as part of the E. H. Day collection in 1864-1866 and the Norris collection in 1878, respectively. The latter specimen had a note added by Peter Hodges suggesting that it might be a species of *Antiquilima*, not *Ctenostreon*. It differs in several respects from the common *A. succincta* (Schlotheim), which has been recorded in the Blue Lias of the ‘Jurassic Coast’ since at least Wright (1860, pp. 401-2, as *Lima antiquata* Sowerby, from Church Cliffs, East of Lyme Regis). Indeed, Peter Hodges (National Museum of Wales) has confirmed that this BGS specimen is a new species of *Antiquilima*, which he intends to describe in the second part of his monograph (Hodges *in lit.* 18/3/15). Certainly, the two BGS specimens differ in several respects and represent two different species. On cleaning the specimens collected by one of us (C. Andrew) near Seven Rock Point, it became clear that these represent a third species, which Hodges has identified as *Ctenostreon philocles* (d’Orbigny).

Arkel (1933, p. 602, pl. 29, fig. 3) illustrated a species of *Ctenostreon* as “*Lima terquemi*” from the “*pre planorbis beds*” of the Blue Lias of Somerset. In addition, Hodges (1994, p. 843) recorded *Ctenostreon philocles* (d’Orbigny) from his bed 19 of the Blue Lias, at Sedbury Cliff, on the Severn Estuary. Hodges regarded this level as equivalent to Lang’s bed H24 (Lang, 1924) in Pinhay Bay, Devon. Assuming Hodges’ correlation is correct, the Sedbury Cliff horizon is lower than any from which we have recorded spiny limid bivalves as our lowest known occurrence is in Lang’s bed H44. *Ctenostreon philocles* has also been recorded from the British Hettangian by Hodges and Simms (2004, p. 36) where it is said to range from the “*Pre-Planorbis Beds to the Complanata Subzone (Rhaetian to Upper Hettangian)*”. According to Peter Hodges (*in lit.* 1/7/15) the specimens came from the Lias of Somerset and Avon (Bristol

City Museum and Bristol University collections) and South Wales (National Museum of Wales). The purposes of this paper are to illustrate the specimens from Devon and Dorset, to record their precise horizons and to discuss their palaeoecology. Specimens discussed and illustrated here are in the collections of the British Geological Survey (GSM) and the Lyme Regis Philpot Museum (LYMPH).

STRATIGRAPHIC OCCURRENCE

Bed-by-bed recording in 2006 identified single, well-preserved valves of *Ctenostreon* sp. and/or *Antiquilima* sp.nov. from Lang’s beds H44, 6 (Lower Skulls Shales), 9 (Under White), and 15 (Upper Skulls). There was also a doubtful occurrence in bed H56. All of these are either nodular limestone beds or shales associated with nodular limestones. All *in situ* specimens were preserved on the upper surfaces of the limestones or shales and were essentially complete. None was collected, so we do not know if those examples had both valves preserved nor which species they represent. However, preservation of spines up to 8-9 mm long (Figure 3) suggests that in either case the shells cannot have been transported very far before final burial. Further examples have since been collected from loose blocks near Seven Rock Point. These apparently came from Upper or Lower Skulls, to judge by the lithology of the enclosing limestone. Known stratigraphic distribution (at least bed H24 to 15, Upper Skulls; Pre-Planorbis Beds to Complanata Subzone of the Angulata Zone according to Hodges and Simms 2004, p. 36) suggests that these bivalves are long ranging species, but local in their occurrence.

The Blue Lias Formation typically consists of pale grey limestone beds separated by marl and/or shale beds. The limestone beds are typically impure micrite mudstones to wackestones, whereas the more siliciclastic-rich beds in between may include one or more horizons of pale grey calcareous marl, dark grey marl, or laminated black shale. Fossils are generally more common in the limestones than in

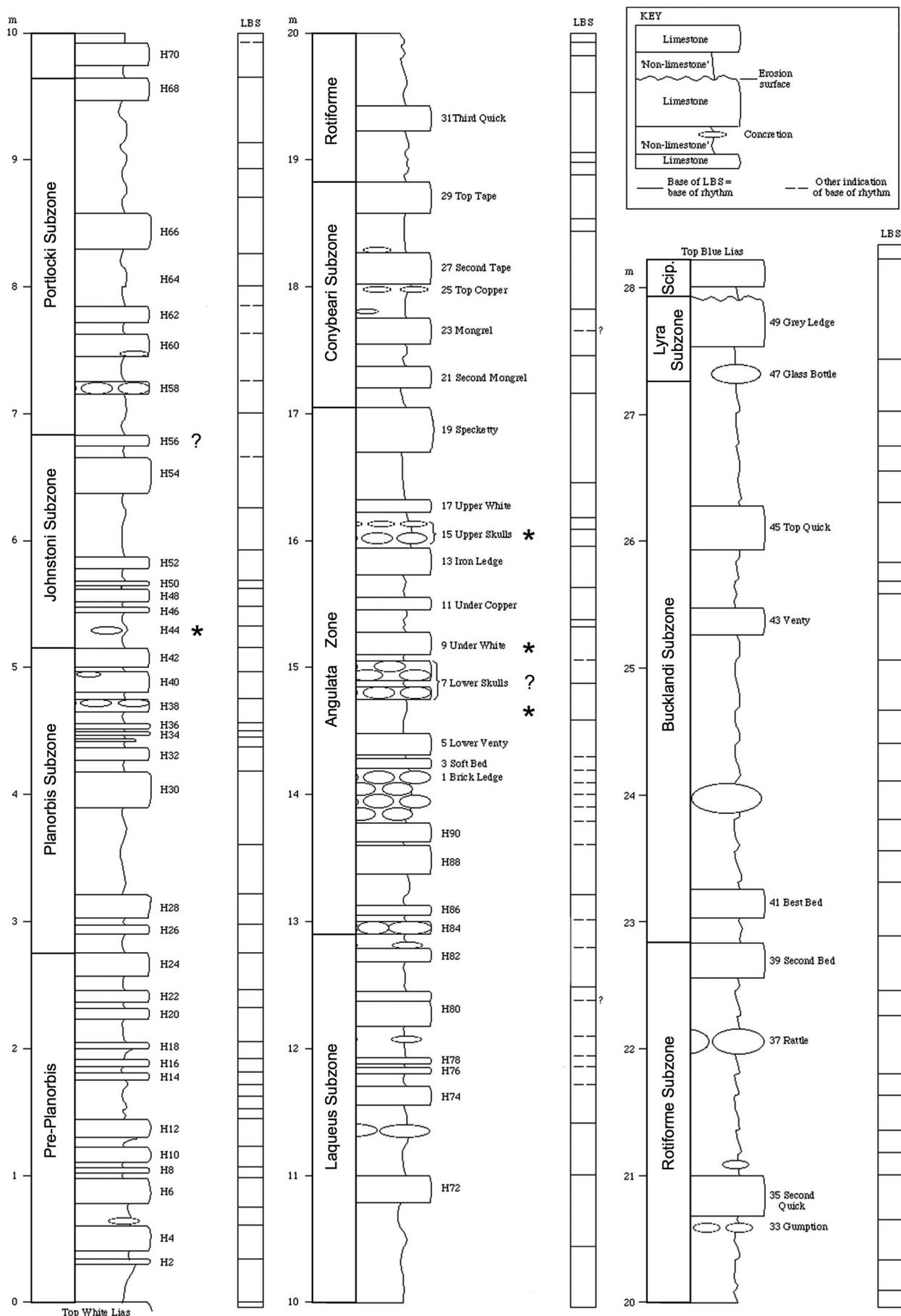


Figure 2. Lithological log of the Blue Lias Formation in the vicinity of Lyme Regis, Dorset, to show occurrences of newly recorded limid bivalves. Redrawn from Paul et al. (2008, fig. 4). Bed numbers and names after Lang (1924). Asterisks indicate known stratigraphic positions of spiny limid bivalves. 'Non-limestone' refers to any or all of laminated black shale (LBS), dark marl or pale marl.

the more siliciclastic units, especially the laminated black shales. The succession is rhythmic, with each rhythm having a sharp base overlain by laminated black shale, which usually grades up into dark grey marl, then pale grey marl, commonly with concretionary to tabular micritic limestone, and typically back into dark grey marl before the base of the next rhythm. The rhythms are not always symmetrical and in many cases the only evidence for the upper dark marl is the fill of trace fossils, especially *Rhizocorallium* in the tops of the limestone beds. In such cases the laminated black shale rests directly on pale grey marl or limestone. The pale marls may be bioturbated and fossiliferous. In some, but not all, rhythms they are cemented into hard limestone beds, so that the number of limestone beds is significantly lower than the number of sedimentary rhythms (Figure 2).

Moghadam and Paul (2001, fig. 3, p. 287) and Martin (2004, fig. 10, p. 152) used trace fossil assemblages to infer palaeo-oxygenation curves and concluded that oxygen levels fluctuated from anoxic to well-oxygenated throughout most of the sedimentary rhythms. Usually oxygenation levels correlate well with lithology; laminated black shales were anoxic, pale marls and limestones well-oxygenated. Nevertheless, laminated limestones occur at several levels, indicating that oxygen levels could be low even when carbonate-rich sediment was accumulating. Certainly, unfossiliferous, laminated limestone beds occur in the sequence both above and below Lang's bed H44 where we have recorded the first occurrence of spiny limid bivalves (Paul *et al.*, 2008, fig. 6, p. 263). Robust, benthic fossils, such as bysally-attached, limid bivalves, only occur in the most well oxygenated levels of the Blue Lias.

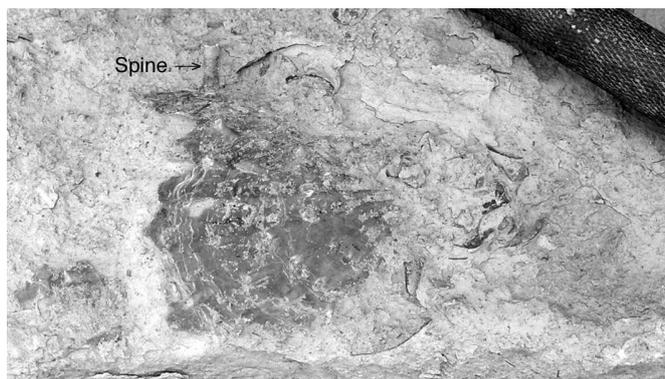


Figure 3. *Ctenostreon* ? sp. in situ in Lang's bed H44 (Lang, 1924). Note the well-preserved spine. Chisel baft is 13 mm in diameter.

DESCRIPTIONS

All the specimens described herein share the following characteristics. They have gently to strongly convex shells with very obvious radiating ribs and strong growth lines. Periodically at major growth lines the ribs give rise to hollow spines that extended up to about 10 mm from the surface of the shells. These hollow spines were sealed internally by the next growth increment. The radiating ribs are significantly narrower than the intervening grooves, which reach up to four times as wide as the ribs. The ribs themselves may be squamate or rounded and vary in number. The shells have lateral auricles, or ears, developed either side of the umbo, but these are only well preserved in some of the available specimens. As limid bivalves, the shells would originally have had byssal gapes anteriorly, shared equally by both valves, but again this part of the shell is poorly preserved or exposed in our material. It seems wisest to describe the individual examples as with such limited material it is difficult to get a sense of the variation in each purported taxon.

Ctenostreon philocles (d'Orbigny) Figure 4

LYMPH 2015/29 is a complete pair of valves, but only one can be seen clearly (Figure 4a). It is 60 mm long by 50 mm wide, moderately tumid and the pair of valves was at least 18 mm thick. The shell is almost symmetrical with a small part of one auricle preserved, but the other worn away by recent erosion. It has eight obvious ribs radiating from the umbo, which bear spines periodically at stronger growth lines. At least six or seven spines occur on each rib, but wear and preparation may have removed some. We estimate some nine or ten spines occurred on each rib during growth. The ribs reach 3 mm wide at their widest, whereas the grooves in between are up to 7-8 mm across. The hollow spines reach at least 5 mm long, but none is complete. The grooves show very obvious growth lines, but also up to six extremely fine radiating incised lines, which are not easy to see. The growth lines are much more prominent and at least nine major growth lines occur. These control the development of the spines, although occasionally the odd individual spine occurs between the major growth lines. Where the spines are damaged the underlying shell material with fine growth lines can be seen. Thus, most of the spines were sealed internally in life. Externally, the spines are arcs of a circle towards the hinge line and, where undamaged, were closed towards the ventral margin of the shell. Thus, they formed short tubes when first secreted. If they were open to the seawater in life, this only occurred in spines at the growing edge of the shell. Spines in this specimen arose at a steep angle to the underlying ridges and were sometimes perpendicular to the general shell surface (Figure 4d right).

LYMPH 2015/28 is a block of limestone containing two separate, almost complete valves. The larger (Figure 4c) is now 45 mm long (umbo to ventral margin) by 43 mm wide, apparently without the auricles preserved, but distinctly asymmetrical and with at least 13 radiating ribs that bear short spines. The ridges are not strongly raised, reach 2, rarely 3 mm across ventrally and are separated by wider grooves that reach 3, rarely 4 mm across ventrally. Spines appear to have been more frequent and more strongly developed on the anterior and posterior three or four ribs and weaker on the central ribs. This does not seem to be due to wear or preparation damage. Furthermore, the spines on the anterior ribs are slightly oblique to the rib and directed anteriorly, whereas those on the posterior ribs are oblique but directed posteriorly. Twenty to thirty extremely fine striae occur in the grooves between the ribs. Spines are narrow, about 1 mm across and lie at a low angle to the ridges (Figure 4e). They were sealed internally by the next growth increment of the shell. The growth lines are obvious, but vary less in their strength than in *Ctenostreon* sp. (see below). Nevertheless, major growth lines can be recognized, especially in the early growth stages. Spines are much less regularly associated with major growth lines than in *Ctenostreon* sp.

The smaller example (Figure 4b) is an incomplete valve, about 30 mm (hinge to ventral margin) by at least 25 mm wide. It bears at least 10 radiating ridges with spines that are about half the width of the grooves in between. Part of one auricle is preserved (Figure 4b upper right) and makes the hinge line appear to be perpendicular to the dorso-ventral axis so the shell appears to be much less asymmetrical. However, the full outline cannot be seen. Spines are regularly developed on all ridges, including the central ones. There are nine or ten spines on each ridge, which are definitely hollow. As in the larger specimen, the spines on anterior ridges are offset slightly to the anterior; those on posterior ridges are offset slightly to the posterior. Numerous, extremely fine striae occur in the grooves between the ridges.

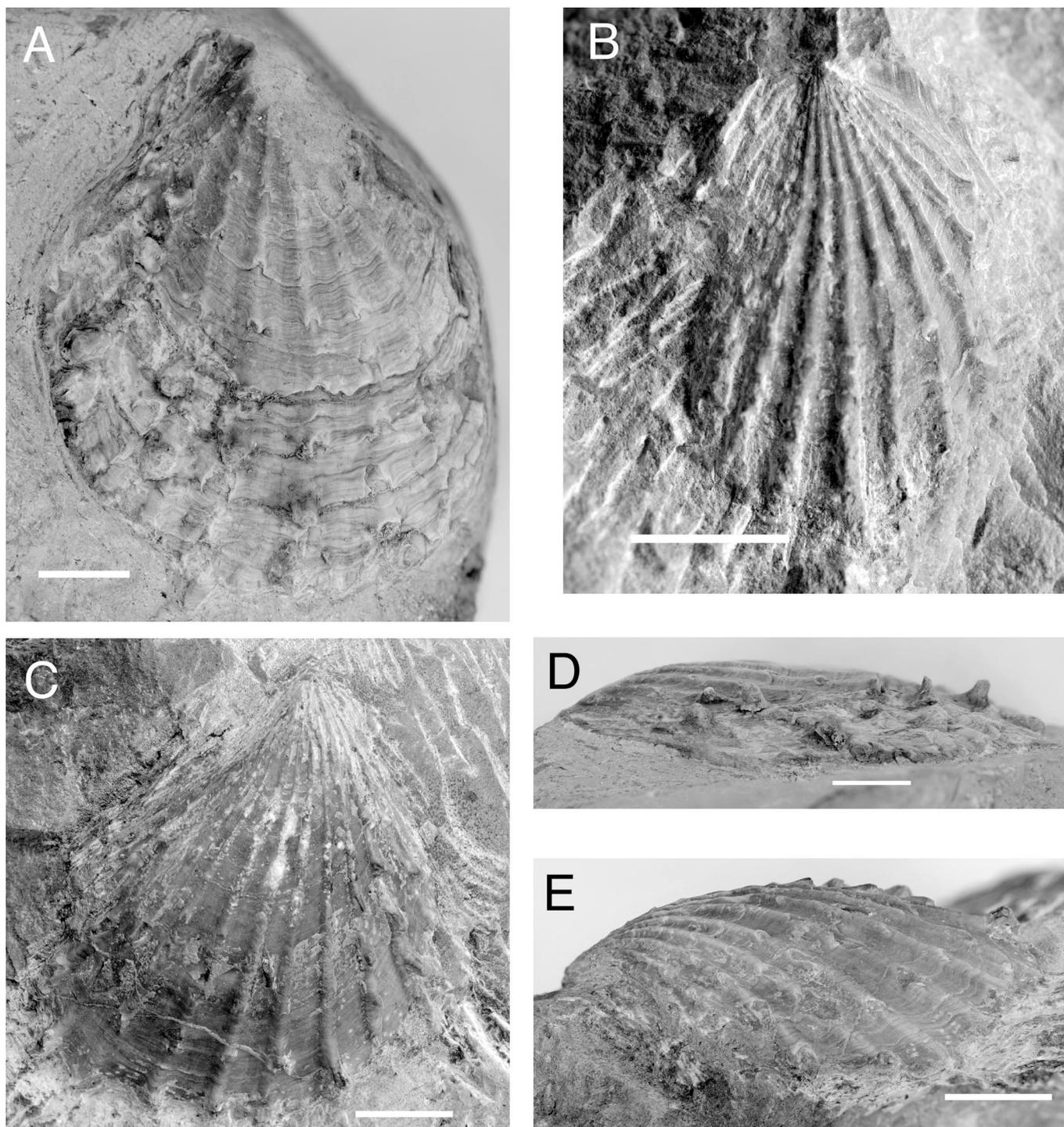


Figure 4. *Ctenostreon philocles* (d’Orbigny) loose from the Blue Lias Formation of Devon (probably from Upper Skulls, Seven Rock Point). (a) LYMPH 2015/29 to show valve outline, prominent ridges and spines on major growth lines. (b) LYMPH 2015/28a another partially exposed example with more ribs and less obvious spines. (c) LYMPH 2015/28b a second example showing ribbing and spines. (d) LYMPH 2015/29 lateral view of (a) to show convexity and erect spines. (e) LYMPH 2015/28a lateral view of (c) to show convexity and oblique spines. (a) whitened with ammonium chloride. Scale bars = 10 mm.

***Ctenostreon ? sp.* Figure 5**

The Day collection specimen (GSM 38789, Figure 5) is a strongly convex single valve 61 mm long (hinge to ventral margin) by 63 mm wide and with eight obvious, narrow, radiating ridges from which short spines extend periodically. The ridges reach about 3 mm wide, whereas the grooves in between are much wider and reach 9 mm across. The spines are the same width as the ridges and reach up to 11.5 mm long. The grooves show numerous, obvious growth lines, but no sign of radiating ornament. The specimen is still partially buried in the sediment and the ears adjacent to the umbo cannot be seen.

***Antiquilima sp. nov.* Figure 6**

The Norris collection specimen (GSM 91697, Figure 6) is an almost complete, obviously asymmetrical valve with part of one auricle preserved and shows that the hinge line was oblique to the longest dimension of the shell. The valve is 60 mm long (hinge line to ventral margin) by 60 mm wide at its widest and only very weakly convex. Twelve strong ribs radiate from the umbo and bear spines periodically. The ribs increase in width regularly as the shell grew and are almost as wide as the grooves between them. Growth lines are prominent, but numerous fine radiating striae occur in the grooves as well. The



Figure 5. *Ctenostreon* ? sp. BGS GSM 38789, Day collection, “angulata zone, Lyme Regis”. Scale bar = 10 mm.

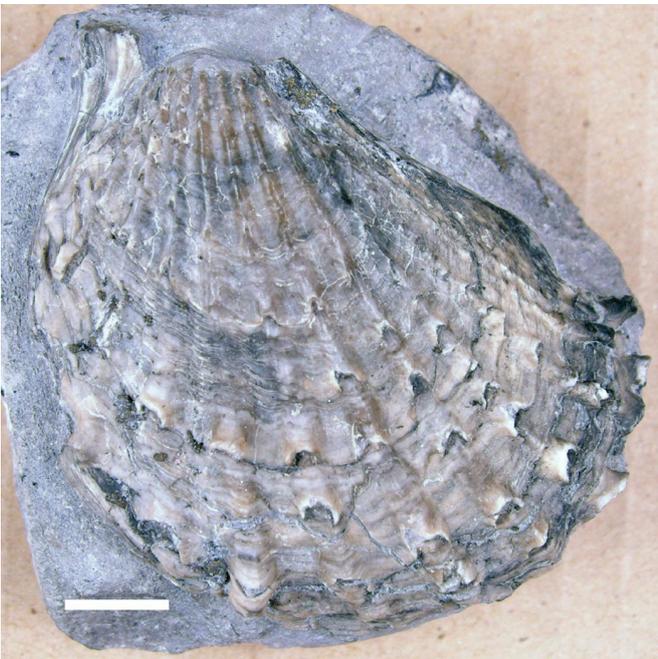


Figure 6. *Antiquilima* sp. nov. BGS GSM 91697, Norris collection, “Lower Lias, Lyme Regis”. Scale bar = 10 mm.

spines are more quadrate in outline towards the hinge line and were sealed internally. None is complete so their precise orientation and length are unknown.

Discussion

These specimens show considerable variation. *Ctenostreon* ? sp. (GSM 38789, Figure 5) is more strongly convex than all the other specimens, has fewer radiating ribs (eight) and the widest

grooves compared to the width of the ridges. No fine radiating striae occur in the grooves. Specimens of *Ctenostreon philocles* (Figure 4) are moderately convex, have from 8-13 radiating ribs and the grooves in between vary from a little wider to over twice as wide as the ribs. The variation correlates inversely with the number of ribs; the more ribs there are the narrower the intervening grooves are. The orientation of the spines is also variable, both in the angle the spines bear to the radiating ribs and whether or not they align with the growth direction of the ribs. In some specimens the grooves appear to lack fine radiating striae, whereas in others they are common and obvious. Finally, *Antiquilima* sp. nov. has the least convex shell, which is obviously oblique to the hinge line, twelve strong radiating ribs which are more rectangular in section and only slightly narrower than the grooves in between, which bear obvious radiating striae.

The original field photograph (Figure 3) shows a specimen with seven, possibly eight radiating ribs, which appear to be rounded in section and have relatively wide grooves in between. It does not appear to be strongly convex, but otherwise resembles *Ctenostreon* ? sp. (BGS 38789). The specimen was not fully exposed, so the number of ribs may originally have been higher, but the width of the grooves suggests not much higher. Since we now know that more than one species is involved, it remains uncertain to which of these taxa the other specimens localized to individual beds belonged.

PALAEOECOLOGY

In bed H44 *Ctenostreon* ? sp. occurs with a relatively diverse fauna of other bivalves, including *Liostrea hisingeri* (Nilsson), *Modiolus* (*Cyranus*) *billanus* J. Sowerby, *Plagiostoma giganteum* J. Sowerby, *Gresslya striatula* Agassiz, *Gryphaea*-like oysters, *Entolium* sp., *Chlamys* (*Chlamys*) *valoniensis* (Defrance), plus other unidentified limids and inoceramids? Bed H44 also yields the ammonite *Caloceras*. Spiny limids are accompanied by a similarly diverse bivalve fauna in the higher beds, which includes *Antiquilima succincta* (Schlotheim), *P. giganteum*, *Gresslya galathea*, *Modiolus* sp., *Entolium* sp., limids, pectinids and *Gryphaea*. Schlotheimiid ammonites also accompany the spiny limids in these higher beds in Pinhay Bay. Hodges (1994, p. 843) stated that at Sedbury Cliffs *C. philocles* was accompanied by numerous *P. giganteum*, *Pseudolimea* sp. and *Pinna semistriata* (Terquem), but ammonites (*Psiloceras*) first appear about a metre higher in his bed 23.

Hallam (1976) recognized four principal associations of bivalves in the European Jurassic. His “marine basinal association” in “non-bituminous bioturbated clay or marl” included such genera as *Gresslya*, *Modiolus*, *Chlamys*, *Plagiostoma*, *Pseudolimea*, *Gryphaea* and *Liostrea*. Although the only species of *Ctenostreon* he listed was *C. pectiniforme* (Hallam, 1976, p. 257), which ranges from the Upper Toarcian to Tithonian, it seems likely that *C. philocles* also occurs in this rather basinal facies association. We suspect that the ‘basin’ was not very deep in the early Hettangian, but probably had a basinal fauna due to restricted circulation. For example, Moghadam and Paul (2001, pp. 299-301) undertook an ichnofacies analysis and concluded that the trace fossil assemblages of the Blue Lias in Devon and Dorset represented a modified *Arenicolites* facies, developed in clay-grade not more typical sand-grade sediments. This ichnofacies usually occurs in sands deposited by an increased energy event. The Blue Lias environment was not normally high energy, although veneers of dark marl rich in shell chips do suggest periodic storm deposition. Martin (2004, p. 152) referred to erosive bases of shale units that again suggest higher energy events. In addition, the succession in Devon-Dorset is condensed (less than 28 m to the top of the Lyra Subzone, Figure 2, herein) with respect to that in Somerset (c. 155 m to the same level, Warrington and Ivimey-Cook, 1995, fig. 5, p. 12). The significant erosion level within Lang’s bed 49 (Gallois and Paul, 2010, fig. 5, p. 130) also suggests the thin local succession arises

at least as much from lack of accommodation space as from sediment starvation. Although traditionally regarded as offshore facies, there is little to confirm that the Blue Lias of the Devon and Dorset coast was deposited in even deeper shelf waters, let alone a fully basinal environment.

Lymph 2015/29 has another spiny limid within it largely covered by epifaunal oysters (Figure 7). Limids are byssally-attached, epifaunal bivalves and the associated oysters suggest that bottom conditions were suitable for epifauna at least for long enough for more than one generation of epifaunal bivalves to develop. Similarly, specimens of *A. succincta* also commonly have epifaunal oysters cemented to them (see Palmer, 2010, pl. 19, fig. 4).



Figure 7. LYMPH 2015/29 loose from the Blue Lias Formation of Devon (probably from Upper Skulls, Seven Rock Point). Two oysters growing on another spiny limid bivalve, a small part of the external surface of which shows (arrowed). Both oysters have impressions of the limid spines as well as additional small juvenile oysters growing on their inner surfaces. Whitened with ammonium chloride. Scale bar = 10 mm.

FUNCTIONAL MORPHOLOGY

Bivalves grow by accretion, commonly adding daily or tidal increments to the shell. Nevertheless, periodically slower growth often results in major growth lines, sometimes referred to as 'winter rings'. Hyote spines develop because the mantle extends locally, where ribs occur in the species discussed herein, and the extensions curve around to meet themselves on the side facing the commissure, thus forming a hollow tube. Solid spines result from the lumen of this tube being occluded as the mantle extensions retract. Hyote spines are usually sealed internally as soon as the next growth increment of the bivalve shell commences. In *Ctenostreon*, *Antiquilima* and *Oxytoma* hyote spines are strongly associated with 'winter rings'. Thus, if hyote spines function to convey seawater into or out of the shell, they can only do so briefly while the internal opening still exists. This does not prevent the spines having other functions by modifying the external surface of the valve, or valves.

Hyote spines are found in several Lower Jurassic bivalves, including *Ctenostreon philocles*, *Antiquilima* sp. nov., *Oxytoma* (*Palmoxytoma*) *cygnipes*, *Chlamys pollux* and *Plicatula spinosa*. Comparisons between these species are instructive, but each example needs separate analysis and more than one function may be involved. For the purposes of this discussion, it is convenient to concentrate on *P. spinosa*, *C. philocles* and *O. (P.) cygnipes* as they cover a range of morphological variation. *Plicatula* was directly cemented to hard substrates so most spines occur on the upper valve. They are not confined to

radiating ridges, nor concentrated on major growth lines. Thus, they tend to be randomly distributed over the surface and some may have been functional as open tubes more or less continuously, but allowing a reduced circulation capacity when the valves were closed. In contrast, *O. (P.) cygnipes* was byssally attached, with a lower and upper valve. The spines were confined to six very narrow ridges on the upper valve and only occur on major growth lines. Thus the spines could only have functioned seasonally and with a significantly reduced capacity (10% or less). *Ctenostreon* is intermediate between these extremes. It was also byssally attached but with the plane of the commissure perpendicular to the substrate. The valves are more or less symmetrical with spines on both, but confined to radiating ribs (8-13) and concentrated on major growth lines. Thus, like *O. (P.) cygnipes*, the spines were only functional seasonally, when the shell was growing at its slowest rate and with a reduced circulation capacity, but greater than that of *O. cygnipes*.

While the hyote spines are open possible functions include early warning of unfavourable seawater conditions, more efficient orientation of currents over the gills, and a compromise between the requirements of protection by closing the shell versus those of feeding and respiration by maintaining a connection to the seawater outside the shell (Paul, 1975). After the spines were sealed, possible functions include mechanical protection and production of an anti-predatory or anti-fouling surface.

Rudwick (1965) argued that the delicate hyote spines of the brachiopod *Acanthothiris* functioned as an early warning system. The spines extend beyond the shell margin and curve towards the plane of the commissure. They remain open internally long after they first start growing. Thus several spines have their distal tips in a position to test the seawater approaching the brachiopod shell. An essential part of his argument was that functional, open spines curved in towards the plane of the commissure. The hyote spines of the bivalves discussed here meet neither condition. They tend to curve away from the plane of the commissure and only those at the shell edge remain open. It also seems unlikely that these hyote spines functioned to orientate currents more efficiently over the gills, as Carter (1968) suggested for the Cretaceous oyster *Arctostrea*. Hyote spines in *Arctostrea* lie at the crests of the zigzag commissure, which itself is the principal means of current orientation. All the bivalves discussed here lack zigzag commissures and all would have had reduced circulation when the valves were closed. Whatever the function of the hyote spines, *Ctenostreon* and *O. cygnipes* could only have benefited seasonally.

The concentration of hyote spines on major growth lines (sometimes called 'winter rings') when the shells were growing at their slowest rate may be significant. If the spines functioned as water conduits when the valves were closed this only occurred when conditions were unsuitable for shell growth. The fact that the circulation capacity would have been reduced to an estimated 50% maximum in *Ctenostreon*, but perhaps less than 10% in *O. cygnipes*, suggests that the more vital function was respiratory gas exchange rather than food gathering. The estimates are based on the assumption that the shells would gape to a maximum equivalent to the internal diameter of the hyote spines. It is also reasonable to assume that the bivalves were not feeding actively when they were not growing their shells.

The spines are not mechanically defensive as suggested for the spines of the bivalves *Hysteroconcha* and *Hecuba* by Carter (1967), as they are neither sharp nor solid, nor directed towards any approaching predator (see Paul, 1975). The ribs in the valves of *Ctenostreon* and *O. cygnipes* added strength and stiffness to the shells, but do not result from an undulose or zigzag commissure (Rudwick, 1964). With undulose commissures a rib on one valve corresponds to a groove on the opposite valve, which results in ridges and grooves being of almost equal width. In the spiny limids discussed herein the ribs increase in width during growth more slowly than the grooves in between,

suggesting there was an optimal width for the ribs for some reason. Furthermore, the ribs do not bifurcate, nor were additional ribs intercalated between existing ones as the shells grew. Thus, both the relative and absolute widths of the intervening grooves continued to increase during growth. The spines formed because the mantle edges on either side of the ribs met ventrally (towards the commissure) and secreted a common suture.

Since the spines are as wide as the ribs, this suggests that it was the diameter of the spines (which were effectively inlet canals) that controlled the width of the ribs. Rudwick (1964) showed that inhalent structures can be protected from penetration by parasites, predators or even inert particles that might clog them, by being narrowest at the entrance. This could explain why the ribs in *Ctenostreon* and especially *O. cynipis* did not increase in size as rapidly as the grooves in between during growth as this would have resulted in larger inhalent canals (hollow spines). Indeed, it is also possible that the ribs themselves may have allowed ingress of food and oxygen-bearing currents even when the shells were closed. Internal views of *Ctenostreon* (see Cox *et al.* 1969, fig. C105.6b) show little indication that the shells were ribbed externally and confirm that the commissure was essentially planar. The external ribs correspond to shallow grooves on the internal surface only at the shell margins. Currents may have been able to enter these shallow grooves when the shells were closed. For a byssally attached epifaunal bivalve this is an ideal solution to the conflicting requirements of protection versus those of other vital functions such as feeding, respiration and reproduction. Closing the valves to complete the protection offered by the shells need not have caused cessation of circulating currents bringing oxygen and food into the shell, or voiding waste products.

Finally, the presence of the spines produces a much more uneven surface to the valves, which may have deterred predators or epifauna. For example, Harper (in Harper and Skelton, 1993, p. 141) recorded an experiment in which she offered the modern oyster *Saccostrea cucullata* with hyote spines and others from which the spines had been removed to the predatory gastropod *Morula musiva*, which naturally preys on this oyster in the wild. Of 23 oysters that were bored only four were spiny. This suggests the hyote spines act as an anti-predatory defence. Observations that when *S. cucullata* is bored in the wild the borings are often sited on worn parts of the shells tend to confirm this interpretation. Harper and Skelton suggested that the dense spine cover limited the space available for the predatory gastropods to apply both the radula and the accessory boring organ. Unfortunately, this explanation does not apply to hyote spines in Lower Jurassic bivalves. Both main groups of modern predatory boring snails leave characteristic boreholes (e.g. Taylor, 1970, pl. 46), but such boreholes are unknown below the Lower Cretaceous (Sohl, 1969; Taylor *et al.* 1983). Nevertheless, Harper and Skelton (1993, p. 141) noted that hyote forms of *Saccostrea cucullata* are rarely encrusted by other epibionts, so it is possible that the spines somehow act to prevent attachment of epibionts. The hyote spines only occur on the upper valve and Zuschin and Baal (2007) have recorded how dramatic the difference in diversity and concentration of sclerobionts is between the upper and lower valves of another large Recent oyster, *Hyotissa hyotis*. Such a function is consistent with abundant spines distributed over most of the valve surface and so could apply to shells of the Lower Jurassic, hyote bivalve *Plicatula spinosa*. This explanation seems unlikely to apply to *Ctenostreon* or *Antiquilima*. One of our examples of the former is largely covered by epifaunal oysters (Figure 7) and most examples of *A. succincta* have epifaunal bivalves attached despite having a decidedly prickly surface. We conclude that the most likely functional explanation of the hyote spines in *Ctenostreon* and *O. cynipis* is that they allowed respiration to continue seasonally when the bivalves closed their shells and were growing at the slowest rate.

STRATIGRAPHIC DISTRIBUTION

Jeans (1968) coined the term 'pulse faunas' for long ranging, calcitic fossils found in the Chalk of the Anglo-Paris Basin, but only at a few restricted horizons. Their restricted occurrence was not due to special diagenetic conditions such as those that allow the preservation of aragonitic fossils. We now know that these pulse faunas occurred when cooler boreal waters penetrated the Anglo-Paris Basin, bringing with them, for example, belemnites. Tethyan belemnite lineages became extinct at the base of the Cenomanian, whereas Boreal belemnites survived to the latest Cretaceous (e.g. Paul *et al.*, 1994; Mitchell and Carr, 1998). The Lower Lias of southern Britain appears to have experienced similar pulse faunas, exemplified particularly by the calcitic brachiopod *Spiriferina*. In the Blue Lias Formation this brachiopod only occurs in Upper Skulls (Lang's bed 15) and Best Bed (41). It reappears at similarly restricted horizons several times higher in the Lower Lias. We speculate that spiny limids may also have been part of Blue Lias pulse faunas, although possibly indicating incursions of southern, Tethyan waters. The original survey, which first detected them recorded them in Upper Skulls, among other horizons.

Finally, recording the precise stratigraphic levels at which fossils occurs is important for several reasons, not least in that it allows recognition of patchy stratigraphic distributions exemplified by Jeans' pulse faunas. Furthermore, Paul (1985) has shown that recording fossils by zones almost always increases their apparent stratigraphic ranges since few fossils appear and disappear exactly at zonal boundaries. In addition, the latter effect tends to produce a false pattern of substantial faunal change concentrated at zonal boundaries. Finally, everyone acknowledges that the fossil record is incomplete, although the significance of this fact is often misinterpreted. Nevertheless, we feel it incumbent on palaeontologists to record the occurrences of fossils, and so not contributing to this apparent incompleteness. Thus, we think it is significant that only now are we recording the occurrence of two taxa (*Ctenostreon*? sp. and *Antiquilima* sp. nov.) in the Blue Lias of Lyme Regis when the specimens were originally collected over 135 years ago.

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