Palaeoecology of Portlandian Gastropods from the South Midlands

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Abstract. The Portlandian strata of Buckinghamshire were deposited in sheltered shallow-marine to nonmarine settings during the Late Jurassic regression. Distal environments were characterised by a low diversity gastropod fauna. Proximal marine settings supported micromorphic gastropod faunas, possibly associated with putative algal meadows. Coarser-grained bioclastic substrates were intermittently colonised by the nerineoid *Aptyxiella portlandica*. Low-salinity lacustrine facies are characterised by low diversity faunas dominated by small provalvatids.

This report is founded upon investigations undertaken by the author nearly twenty years ago, whilst researching aspects of the palaeontology and palaeoecology of Portlandian (Late Jurassic) gastropods. The author's interest in Portlandian palaeontology had been initiated through investigation of the poorly exposed succession in the Vale of Aylesbury and Thame Valley of Buckinghamshire, in the southern Midlands of England, during the late 1970s. There, the richly fossiliferous strata (Fig. 1) are stratigraphically condensed and generally poorly cemented relative to the expanded successions in the Dorset type-area of southwest England (Townson, 1975; Wimbledon, 1980). Thus, small exposures were a rich source of invertebrate fossils including many gastropods.

The Portlandian Stage is represented in the Vale of Aylesbury and Thame Valley by siltstones, sandstones (often glauconitic) and sandy, micritic and shell-fragmental limestones (Portland Sand and Portland Stone members of the Portland Formation; Glaucolithus up to Kerberus Zone, up to *c*. 13 m thick), overlain by the fine-grained limestones, mudstones and calcareous mudstones of the Purbeck Formation (Kerberus Zone; up to *c*. 10 m thick; Wimbledon, 1980; Horton, Sumbler, Cox & Ambrose, 1995; Fig. 1). The Portland Sand and Portland Stone are further subdivided into named units (Bristow, 1968; Wimbledon, 1980; Horton *et al*., 1995; Fig. 1; Table 1). Horton *et al*. (1995) took developments of the Upper Shell Marl (Table 1) to mark the base of the Purbeck Formation. It is included within the Creamy Limestone in this account on palaeontological grounds, following Bristow (1968) and Radley (1991).

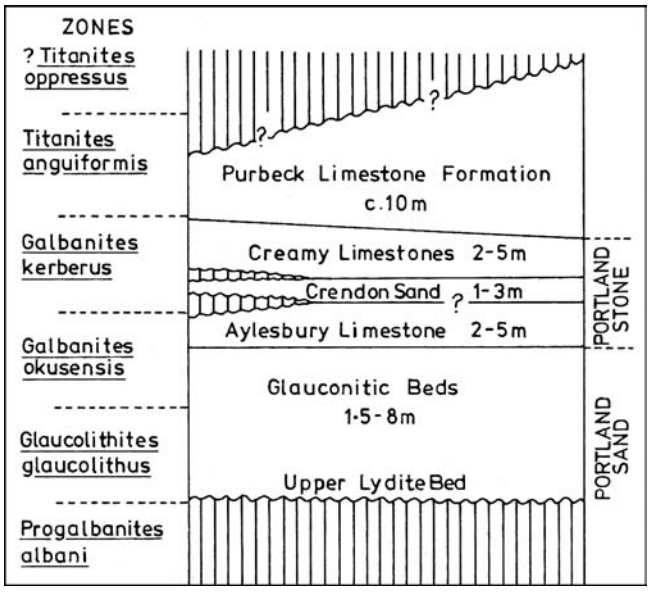

***Figure 1**. Outline of Portlandian stratigraphy in Buckinghamshire; vertical ornament indicates beds locally absent (adapted from Wimbledon, 1980).*

The Portlandian succession represents the last phase of marine deposition in a northeastern embayment of the southern English Wessex Basin adjacent to the London Platform, during the terminal Jurassic regression (Cope, Rawson & Wimbledon, 1992). The Portland Sand and Portland Stone are taken to represent shallow-water nearshore marine environments, influenced by sea-level fluctuations of regional magnitude (Wimbledon, 1987; Cope *et al*., 1992; Horton *et al*., 1995). Above, the Purbeck Formation yields molluscs and ostracods that confirm a marginal-marine to nonmarine setting influenced by fluctuating salinity (Barker, 1966; Radley, 1991; Horton *et al*., 1995).

Gastropod distribution

Gastropod faunas had been previously recorded from the Buckinghamshire Portlandian by numerous authors, notably Fitton (1836), Blake (1880), Hudleston (1881, 1887) and Davies (1899). The author's study of Buckinghamshire material was based upon a combination of newly collected material and specimens preserved in recognised collections, notably that of the Buckinghamshire County Museum, Aylesbury. Among the available fossil localities during the late 1970s and 1980s, there were a small number of disused quarries that included a geological Site of Special Scientific Interest (SSSI) (Warren Farm, Stewkley; SP 852243; Barker, 1966; Bristow, 1968), as well as a freshly dug SSSI excavation on the site of a former quarry (Bugle Pit, Hartwell, SP 79321205; Radley, 1991; Horton *et al*., 1995) and several partly overgrown sections in roadside ditches and road embankments. Temporary exposures were noted in Aylesbury town centre (Radley, 1990, 1993a).

Upper Shell Marl	0.15 - 0.23m
'Last' Portland Limestone	0.30m
Lower Shell Marl	0.15 - 0.23m
'Main' Portland Limestone	>1.8m

***Table 1**. Lithostratigraphic terminology for the Creamy Limestone subdivision of the Portland Stone in Buckinghamshire(after Bristow, 1968).*

Portland Sand and Portland Stone

The investigations confirm a low-diversity gastropod fauna throughout much of the Portland Sand and Portland Stone, ranging from the Upper Lydite Bed (basal Portland Sand, Glaucolithus Zone) up into Bristow's (1968) 'Main' Portland Limestone division of the Creamy Limestone (upper Portland Stone, Kerberus Zone; Fig. 1, Table 1). The fauna is dominated by two large taxa: the pleurotomariid *Bathrotomaria rugata* (Benett) (Fig. 2), and the whelk-like *Natica elegans* J. de C. Sowerby (Radley, 1990, 1993b). Additionally, the small, turbiniform *Ooliticia cunningtoni* Cox (Cox, 1925) was recorded from the Upper Lydite Bed in a ditch section north of Whitchurch (SP 80872271). A poorly preserved small cerithioid was noted in the Aylesbury Limestone (temporary sections in Buckingham Street, Aylesbury; SP 819139). The small *Natica*-like *Ampullospira ceres* (de Loriol) occurs rarely in the 'Main' Portland Limestone at Warren Farm, Stewkley.

Blake (1880) and Hudleston (1887) had noted a fauna of small gastropods within the upper part of the 'Main' Portland Limestone. The author's investigations, initially at Warren Farm, confirmed the widespread presence of a micromorphic fauna of gastropods, bivalves and other fossils at this level. Amongst these were large numbers of *A. ceres*, small cerithioids, the inferred rissoid *Rissoa acuticarina*

***Figure 2**.* Bathrotomaria rugata *(Benett); internal mould; Portland Stone Member (Portlandian, Upper Jurassic); Buckinghamshire, locality unknown. Buckinghamshire County Museum specimen AYBCM: 1880.190.101. Diameter of specimen is 108 mm.*

***Figure 3**. Shelly limestone enclosing moulds of high-spired* Aptyxiella portlandica *(J. de C. Sowerby); 'Last' Portland Limestone (Creamy Limestone, Portland Stone Member, Portlandian, Upper Jurassic); Haddenham Station quarry, Buckinghamshire. The upper internal mould is 45 mm long. Bucks. County Museum specimen AYBCM: 1923.52.1.*

Blake, the aporrhaid *Chenopus* (*Quadrinervus*) *beaugrandi* (de Loriol) and the actaeonellid *Actaeonina* (*Ovactaeonina*) *insularis* Cox (Cox, 1925). *A. ceres* was especially abundant in the now overgrown road cutting at Whitchurch (SP 800211; Bristow & Kirkaldy, 1962).

During early 1991, temporary sections in fields adjacent to Dinton Castle, near Stone (SP 765115), exposed various levels of the Portland Sand and Portland Stone (Radley, Shipp & Wimbledon, 1997). There, the highest part of the 'Main' Portland Limestone was developed as poorly indurated chalky micrite. Micropalaeontological residues yielded large numbers of micromorphic gastropods preserved mainly as micritic casts. The fauna is overwhelmingly dominated by minute cerithioideans, generally poorly preserved. Initial investigations also revealed taxa identified earlier from Stewkley and Whitchurch, namely *A. ceres* and *C. (Q.). beaugrandi*. The remaining shells await detailed documentation but include taxa resembling *Actaeonina* (*Ovactaeonina*) *hypermeces* Cossmann, *Hydrobia chopardiana* (de Loriol), *Nerita minima* Credner, *Odostomia jurassica* de Loriol, *Provalvata sabaudiensis* (Maillard), ?*Pseudomelania pupoides* Arkell and *Tornatella leblanci* de Loriol (de Loriol & Pellat, 1866, 1874; Arkell, 1941).

Above the 'Main' Portland Limestone, the uppermost 0.6-0.75 m of the Creamy Limestone comprises a bivalve-rich bioclastic limestone bed interbedded with oyster-rich shelly mudstones ('Last' Portland Limestone and Lower and Upper Shell Marl of Bristow, 1968; Table 1). Sieved residues from the Lower Shell Marl at Warren Farm (bed WH3 of

Barker, 1966) yielded a number of badly preserved micromorphic gastropods including shells resembling *Provalvata* cf. *helicoides* de Loriol, *H.* cf. *chopardiana* and *Orthostoma granum* de Loriol. The 'Last' Portland Limestone was exposed at a number of sites, notably Dinton Castle, the Bugle Pit, Whitchurch, and Warren Farm. It was confirmed as the sole source of the high-spired nerineoid *Aptyxiella portlandica* (J. de C. Sowerby) in Buckinghamshire (Fig. 3), together with *A. ceres*, a few minute *Hydrobia*-like shells and probable cerithioids including *Uchauxia quadrigranosa* Cox (Cox, 1925), poorly preserved as moulds or calcite replacements.

Purbeck Formation

The basal beds of the Purbeck Formation were sampled at the Bugle Pit, Whitchurch, Warren Farm (see above) and temporary exposures on Whaddon Hill, near Stone (SP 787133). Thinly-bedded ostracodal limestones yielded a few small gastropods including probable hydrobiids and cerithioids, the provalvatid *P. helicoides* and a possible neritoid (details provided by Radley, 1990). Clements (1973) recorded a number of taxa including *Hydrobia* sp. and *P. helicoides* from various levels of the Purbeck Formation at the Bugle Pit (Figs. 4, 5). Higher in the

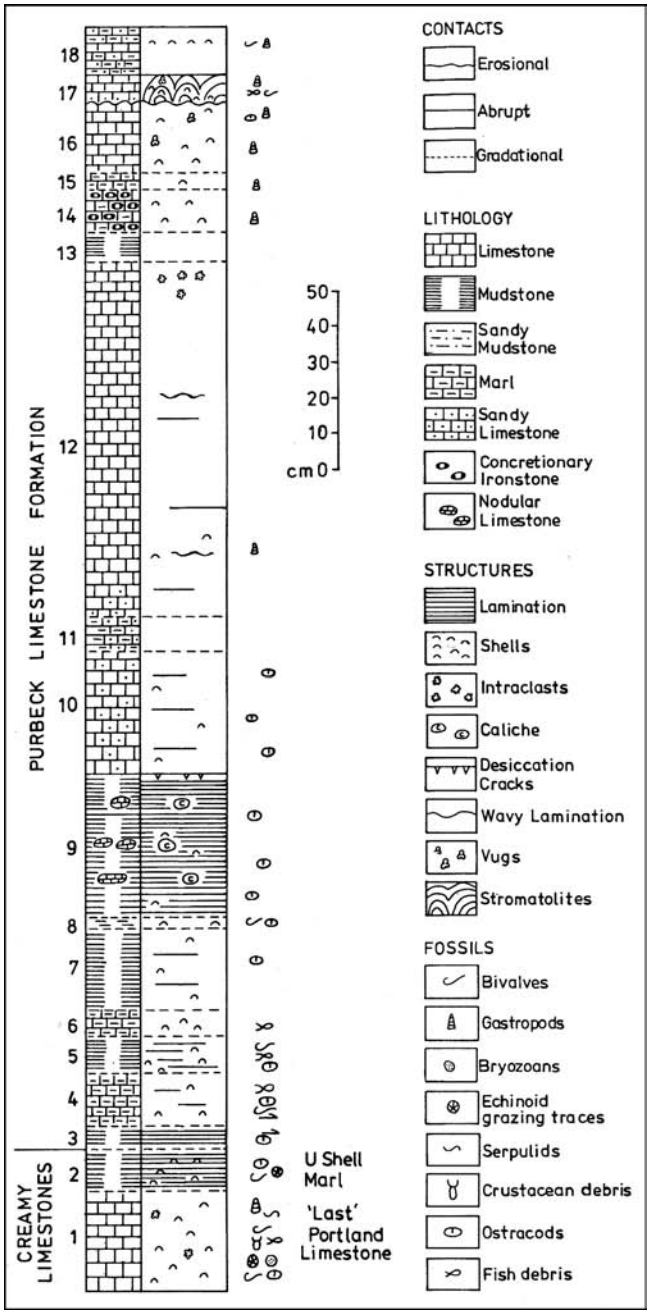

***Figure 4**. Succession of Portlandian strata at the Bugle Pit, Hartwell, Bucks. (SP79321205) (from Radley, 1991).*

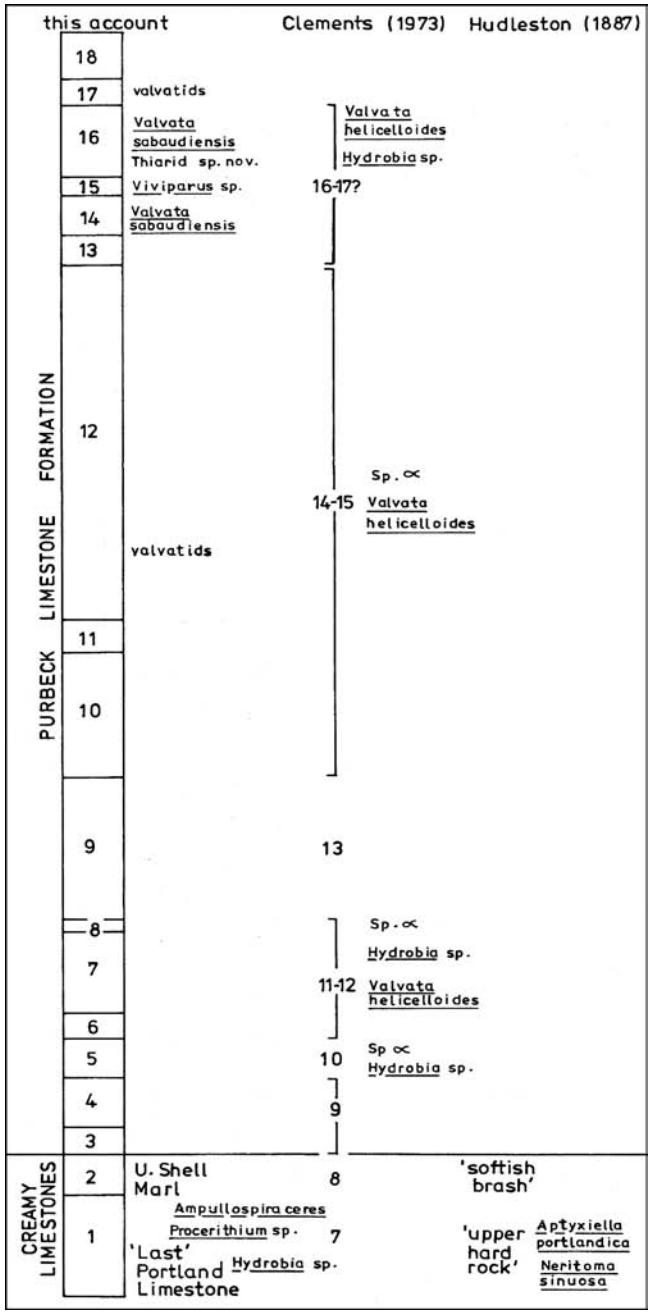

***Figure 5**. Distribution of gastropods in Portlandian strata at the Bugle Pit, Hartwell, Bucks. (from Radley, 1991).*

Purbeck Formation, relatively massive micrites locally enclose dense concentrations of shell debris including *P. sabaudiensis*, preserved mainly as casts and moulds (Radley, 1991). Fossil sites include the Bugle Pit, Whaddon Hill and Warren Farm. Other, rarer taxa at the Bugle Pit include a small viviparid and a possible thiarid (Fig. 5). Additionally, *Hydrobia* sp. was recorded at Warren Farm (Radley, 1990).

Palaeoecology

Most of the gastropod taxa encountered have been previously recorded from the Portland Sand, Portland Stone and Purbeck Formation of Dorset, by Blake (1880), Cox (1925), Clements (1973) and others. Several are new records for Buckinghamshire (Radley, 1990, 1991), where the Portland Sand and Portland Stone are also rich in large bivalves, ammonites, serpulids, bryozoans, echinoderms, foraminifera and ostracods (Blake, 1880; Arkell, 1947; Barker, 1966; Radley *et al*., 1997). Normal or near-normal marine conditions undoubtedly prevailed, notwithstanding the scarcity or absence of other marine groups such as corals, nautiloids and brachiopods.

Extant pleurotomariids are unspecialised epibenthic grazers on sponges, gorgonians and other invertebrates, generally below the level of primary photic plant production (Hickman, 1984; Harasewych, Pomponi & Askew, 1988; Anseeuw & Goto, 1996; Harasewych, 2002). In Dorset, southwest England, the pleurotomariid *B. rugata* ranges from the deep-water sandstones of the West Weare Sandstones (Portland Sand Formation; Glaucolithus up to Okusensis Zone) through to the shallow-water carbonates of the Portland Stone (Radley, 1993b, Fig. 2). Radley (1993b) took the wide bathymetric distribution as evidence for an algal grazing mode, though Harasewych, Pomponi & Askew (1988) had earlier suggested that pleurotomariids had become spongivorous by the Late Jurassic. Perhaps significantly, sponge remains are widely distributed in the Portland Stone (Townson, 1975), adding weight to this hypothesis. Naticoid predatory drill-holes (Kowalewski, 1993) have not been identified in potential Portlandian prey (bivalves; other gastropods). It has been suggested that possible Portlandian naticoids such as *N. elegans* and *A. ceres* were unspecialised opportunistic scavengers and/or predators of soft-bodied organisms (Radley, 1991).

By analogy with the molluscan faunas of extant marine seagrass ecosystems (Brasier, 1975), and the shallow-water setting envisaged for the Creamy Limestone (Radley, 1991), the micromorphic fauna at the top of the 'Main' Portland Limestone (Table 1) was taken to indicate a sheltered algal 'meadow' environment (comprising areas of mud-grade sediment colonised and stabilised by rooted algae), inhabited by a phytal microfauna (Radley, 1990; Radley *et al*., 1997). Algal environments of this nature may have been widespread in Mesozoic shallow-marine settings, before the radiation of true seagrasses (Fürsich & Wendt, 1977). Recent analogues may occur along the Trucial Coast of the southeastern Persian Gulf, where gastropod-rich lime muds are accumulating in protected shallow coastal embayments colonised by seagrasses (Purser & Evans, 1973). Like Recent counterparts in tropical and subtropical vegetation-rich marginal marine environments, the abundant cerithiids may have fed upon algae as well as organic-rich sediment (Warmke & Almodovar, 1963; Houbrick, 1974; Taylor & Reid, 1984).

Nerineoid gastropods such as *A. portlandica* (Fig. 3) are interpreted as herbivorous deposit feeders. High-spired *A. portlandica* was probably at least semi-infaunal (M.J. Barker, 1990). In Buckinghamshire and elsewhere, the association of *A. portlandica* with coarse-grained shelly carbonates rich in micritised bioclasts and/or ooids (Radley, 1990, 1991; Townson, 1975; Fürsich, Palmer & Goodyear, 1994) suggests that this taxon was a deposit feeder amongst algoid-infested grains, within temporarily stabilised bioclast-rich sediment (Radley, 1991).

Among the low-diversity, essentially micromorphic fauna of the Purbeck Limestone, the provalvatid *P. helicoides* characterises high salinity facies within southern English basal Purbeck beds. Conversely, *P. sabaudiensis* appears to typify low-salinity settings in these strata (Clements, 1973; Radley, 2002). Recent valvatoids commonly occur in shallow, sheltered fresh water rich in vegetation (Yen, 1951). Such a setting is envisaged for the Purbeck fauna (Radley, 1991).

The Portlandian strata of southern England illustrate Walther's 'law' of facies (Hallam, 1975), whereby in regressive situations, successions of strata lacking major stratigraphic breaks can equate to the former offshore-onshore arrangement of facies belts. Thus, within the context of the semi-enclosed south midlands embayment (Bristow, 1968; Cope *et al*., 1992), the essentially fine-grained strata that dominate the Portland Sand and Portland Stone are taken to represent low-energy shallow marine environments influenced by minor sea-level fluctuation, passing up into the marginal-marine to non-marine Purbeck Formation (Wimbledon, 1987; Horton *et al*., 1995). Tidal effects were probably negligible, given the restricted epicontinental setting and absence of tidal sedimentary structures. A simple pattern of gastropod distribution emerges within this palaeoenvironmental framework, dominated by *B. rugata* and *N. elegans* within the mixed clastic-carbonate strata that comprise the marine succession. Algal meadows are thought to have existed close to the shoreline, inhabited by the micromorphic fauna noted herein. The 'shell marls' and 'Last' Portland Limestone (Table 1) are attributed to very shallow muddy nearshore settings, influenced by periodic current and/or wave agitation that generated molluscan bioclasts. Micritisation of this shell debris, and colonisation of the coarsest substrates by *A. portlandica* was widespread (Radley, 1991).

The Purbeck Formation represents a mosaic of coastal lagoonal, lacustrine and carbonate mudflat environments, fringing the retreating sea (Radley, 1991; Horton *et al*., 1995). Low diversity gastropod faunas, dominated by provalvatids, characterised the more permanent low-salinity water bodies (Radley, 1991). Inferred nonmarine gastropods of 'Purbeck' aspect may have been reworked into shallow-marine 'Portland' settings through alluvial runoff.

Acknowledgements

Mike Barker (School of Earth and Environmental Sciences, University of Portsmouth) is thanked for providing constructive comments on an early draft of this paper. Mike Palmer (Buckinghamshire County Museum) kindly supplied photographs of Portlandian gastropods.

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