Mesozoic Res.	2(3)	97-149	9 Plates, 11 Text-figs	Leiden 1990

Early Kimmeridgian bivalves of southern England

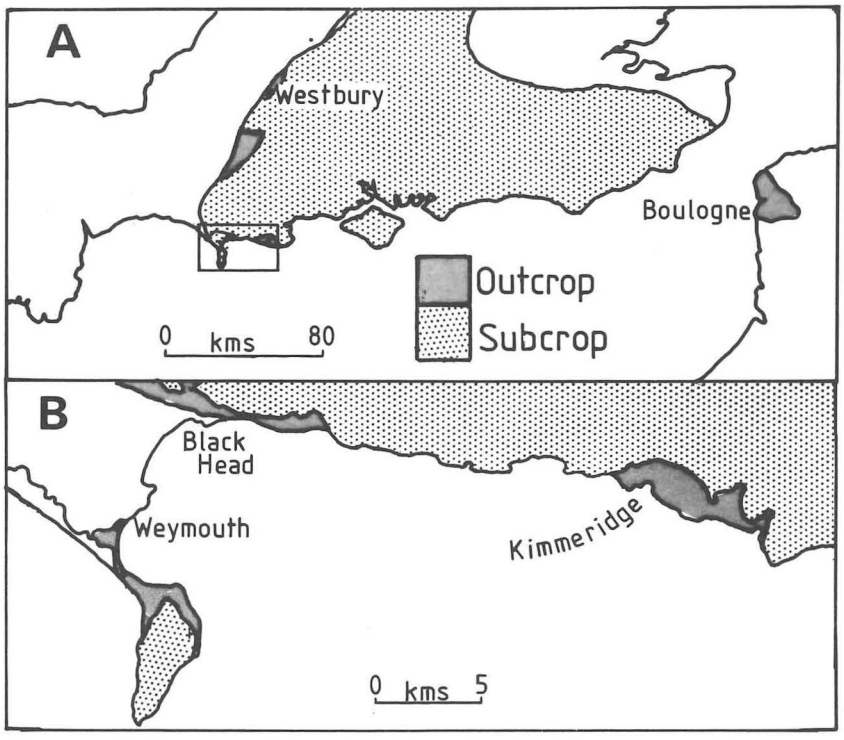
CLAUS KOCH CLAUSEN & PAUL B. WIGNALL

Abstract: The bivalves from the Late Jurassic, Lower Kimmeridge Clay, Westbury, Wiltshire, are monographed and the bivalves from other Kimmeridgian localities in southern England and equivalent strata from Boulogne, France, are recorded, with the distribution shown in range charts.
42 bivalves are described of which four are new and two probably new, together with comments on their stratigraphical range and autecology.

C. K. CLAUSEN, Institute of Historical Geology and Palaeontology, Copenhagen University, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark.
P. B. WIGNALL, Department of Earth Sciences, University of Leeds, Leeds LS2 9JT, England.
Accepted: 15 April 1989

INTRODUCTION

It is the aim of this work to monograph the bivalves of the Lower Kimmeridge Clay from Westbury, Wiltshire and to discuss their distribution in the Kimmeridgian of England and northern France (Text-fig. 1). Apart from occasional described species the only previous work on Kimmeridge bivalves is contained in Blake (1875) although there is a list of Kimmeridgian bivalves in Hallam (1976). Other British Late Jurassic bivalve faunas have been described more recently by Arkell (1929-37) from the Corallian; Cox (1925, 1929) on the Portland Beds and Kelly (1984) on the Spilsby Sandstone.



Text-fig. 1. Principal localities at which Kimmeridge Clay bivalves were collected during this study. Kimmeridge Clay outcrop and subcrop is shaded.

However these refer to bivalves from relatively coarse grained, shallow-water deposits which are distinctly different from the fine grained facies of the Kimmeridge Clay. As a consequence thay contain very few species in common with the Kimmeridge Clay faunas. The only comparable study of Late Jurassic mud-dwelling bivalves is by Duff (1978) on the Lower Oxford Clay although this fauna is significantly older and only 12 of the 46 species described by Duff (1978) were still extant in the Kimmeridgian. A composite range chart of the Kimmeridge Clay bivalves is given in Text-fig. 2.

Elsewhere important contributions have been made to Kimmeridgian bivalves in the works of Gerasimov (1955) on the Russian Platform; Chavan (1945, 1952) on northern France and Fürsich (1982) on East Greenland. The present work attempts to document the bivalve taxa from the Lower Kimmeridge Clay exposed in the Westbury clay-pit (Birklund *et al.* 1983) where detailed bed-by-bed collections has been undertaken; specimens were identified directly in the field or studied more closely in the laboratory. Species distribution within the entire Kimmeridgian of England and northern France are also summarized in the form of range charts, in order to illustrate the effects of faunal turnover and environmental change.

Most of the bivalves are crushed, although they are otherwise well preserved. The degree of crushing is mainly dependent upon the degree of inflation and the orientation of the shell within the sediment. Thus, vertically embedded shells (e.g. preserved in life position) are often badly cushed. Preparation was done with a scalpel as no other methods were found useful. Nearly all the bivalves are preserved in their original shell mineralogy; either aragonite or calcite. The aragonite shells usually show no obvious signs of dissolution. Calcite shells are usually preserved uncrushed.

The specimens were coated with ammonium chloride before photographing. Figured specimens are deposited in the Natural History Museum, London (prefix NHM).
A representative sample of the bivalves have also been deposited as the Natural History Museum, and their reference number is given (eg: LL41137) with the species description. A collection of bivalves can also be found in Copenhagen at the Institute of Historical Geology and Paleontology.

LOCALITIES

1. **Westbury,** Wiltshire (Nat. Grid. Ref. ST 882528).

The clay-pit at this locality was dug for cement-making by the Blue Portland Cement Company. The pit currently exposes some 40 m of Kimmeridge Clay ranging from the middle-lower Mutabilis Zone (20 m) to the upper part of the Eudoxus Zone (20 m).

The ammonites have been documented in Birkelund *et al.* (1983), and the dinoflagellate stratigraphy by Nøhr-Hansen (1986). An unpublished study of the geochemistry was undertaken by I. Salinas and B. Buchart (University of Copenhagen). A preliminary account of the palaeoecology of the bivalves was given by Clausen (1985).

The bivalve fauna is very rich at nearly all horizons. Gastropods occur throughout, but are not a diverse element of the fauna.

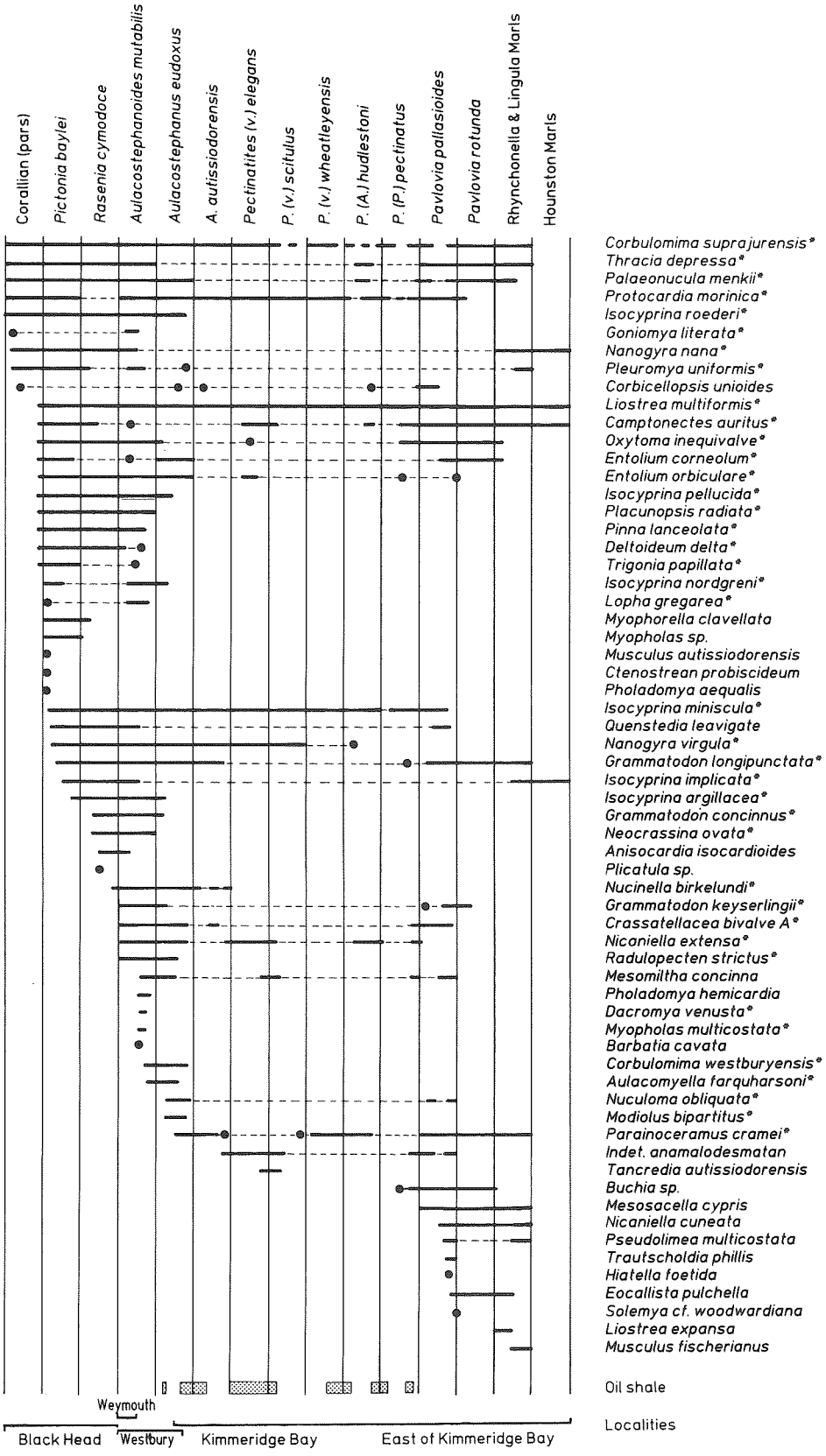
About 16400 bivalve specimens have been recorded.

2. **Black Head,** Osmington Mills, Dorset (SY723819).

The Black Head exposures represent the only currently exposed section in the basal Kimmeridgian beds of southern England (Cox and Gallois 1981), although it is rather badly weathered. The faunas in the uppermost Corallian and the Baylei and Cymodoce Zones have been collected as part of a palaeoecological analysis (Wignall 1988, 1990). Similar horizons can be examined, in the equally badly weathered outcrops, in Ringstead Bay 2 km to the east.

3. **Wyke Regis,** Weymouth, Dorset (SY668763).

At the southwestern end of the badly degraded exposures in Portland Harbour a relatively well exposed, 5 m thick section in the Lower Mutabilis Zone can be examined. This strata conviently fills the gap between the Black Head and Westbury localities.



Text-fig. 2. Composite range chart of the Kimmeridge Clay bivalves arranged after first appearance. The specimens marked with an asterisk are described in the text.

4. Kimmeridge Bay, Dorset (SY889795 to SY955771).

Exposures of Kimmeridge Clay stretch for 7 km on either side of the type-locality at Kimmeridge Bay. A complete succession is exposed from the upper Eudoxus Zone to the Kimmeridge-Portlandian boundary. Bed-by-bed collecting has been undertaken throughout this sequence. Only the topmost Fittoni Zone is poorly exposed at the present time and it was only possible to sample at a limited number of short sections in this zone.

5. Boulogne, France.

The 16 km of cliffs north of Boulogne exposure 122 m of relatively near-shore Kimmeridgian facies. De Loriol (1874-75) monographed the fauna from this sequence, whilst Ager and Wallace (1967a, b) have described the sedimentary environments. A virtually complete sequence has been logged and collected in the cliffs between Boulogne and Wimereux although the upper half of the Schistes de Chatillion was examined to the east of Cap Gris Nez, as it is inaccessible in the Boulogne section. It should be noted that the Late Kimmeridgian of this study equates to the Early Portlandian of French workers.

TAXONOMY

In the main, the synonymies only refer to the type specimen and the latest author to give a comprehensive synonymy list. In the descriptions, the terms small, medium and large are defined by the following size ranges: small, up to 1.00 cm long; medium 1.01 to 3.00 cm; large 3.01 cm and over.

Class	*Bivalvia* Linne 1758
Subclass	*Palaeotaxodonta* Korobkov 1954
Order	*Nuculoida* Dall 1889
Superfamily	*Nuculacea* Grey 1824
Family	*Nuculidae* Grey 1824

Genus ***Nuculoma*** Cossmann 1907

Type species: *Nucula castor* d'Orbigny 1850: 339, no. 178. Figured in Cottreau 1925: 21, pl. 39, fig. 23, 24.

Nuculoma obliquata (Blake 1875)
Plate 1 A, B.

1875 *Nucula obliquata* sp. nov.; Blake, p. 228, pl. 12, fig. 5.

Material. 2 specimens from Westbury (LL41355-6), 1 specimen from Chapmans Pool east of Kimmeridge Bay (LL41130).

Description. A very small form, not exceeding 5 mm in length. Umbones only weakly ophisthogyrate for the genus; they occur a quarter of the distance from the posterior end. Ornament consist of fairly prominent growth lines. Moderate to highly inflated.

Remarks. Although Blake's original figure is not clear and the holotype has been lost the description appears to indicate a *Nuculoma*. As this is the only species of *Nuculoma* known from the Kimmeridge Clay it is probable that they are attributable to *N. obliquata*.
N. oxfordiana (Roeder 1882) is a similar form from the Corallian (Arkell, 1929) although it is more inflated and posseses more ophisthogyrate umbones. *N. nuxavellana* Kelly 1984 is of very similar outline but has a more prominent hinge plate than *N. obliquata*.

Range. A very rare form occurring sporadically in the Mutabilis and Eudoxus Zones of Westbury and in the Pallasioides Zone of Chapmans Pool, east of Kimmeridge.

Autecology. A mobile deposit-feeder.

Genus ***Palaeonucula*** Quensted 1930

Type species. Original description; Quensted, 1930, p. 110, pl. 12, fig. 9: *Nucula hammeri* Defrance, 1825, p. 217. Upper Lias of France.

Palaeonucula menkii (Roemer, 1836)
Plate 1 C, D.

1836 *Nucula menkii* sp. nov.; Roemer, p. 98, pl. 6, fig. 10.
1929 *Nucula menkii* Roemer; Arkell, p. 33, pl. 1, figs. 1, 1a.

Material. 1 specimen from Westbury (LL41357).

Description. Medium-sized to large *Palaeonucula*, subtrigonal to elliptical in outline, inequilateral. The umbo occur approximately one third of the distance from the posterior end. Posterior margin straight to gently convex, anterior margin straight. Ornament of irregularly spaced commarginal growth lines. Dentition taxodont, teeth chevron shaped, points of chevron directed towards the umbo; Chondrophore socket in right valve. Adductor muscle scars deeply impressed, subequal to equal. Pallial line simple and complete.

Remarks. The variation in this species is not great, the degree of elongation is the most variable feature. The shell is normally very thick and readily breaks off in flakes.

Specimens of this species occasionally show colour-banding of alternating light and dark brown bands.
This species differs from *P. calliope* (d'Orbigny 1850) in having a much smaller umbonal cavity.

Range. This species ranges throughout the Kimmeridge sections in England, although it is rare in the most organic-rich facies that constitute the central part of the formation. Not recorded above the Schistes de Chatillon in the Boulogne section. Bajocian—Tithonian according to Hallam (1976).

Autecology. A mobile deposit-feeder that probably lived just below the sediment-water interface (Yonge, 1939). Morris (1979) has suggested nuculids are indicative of oxygen-restricted environments, however the Kimmeridge forms are typically found in well oxygenated aerobic mudstone facies and not in the more organic-rich and presumably more oxygen-poor shale facies.

Superfamily *Nuculanacea* Adams & Adams 1858
Family *Nuculanidae* Adams & Adams 1858
Genus *Dacromya* Agassiz 1840

Type species. Original designation Agassiz, 1840: 500; *Nucula lacryma* J. de C. Sowerby 1824.

Dacromya venusta (Sauvage, 1871)
Plate 1 E, F.

1871 *Leda venusta* sp. nov.; Sauvage, p. 356.
1872 *Leda venusta* Sauvage; Sauvage, p. 180, pl. 11, fig. 7.
1875 *Leda lineata* sp. nov; Blake, p. 228, pl. 12, fig. 12.

Holotype. Figured by Sauvage 1872, pl. 11, fig. 7, from Kimmeridgian of Delahodde at Brequerecques.

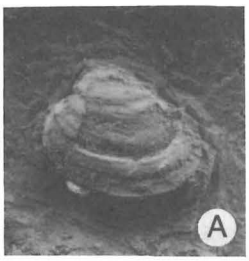
Material. 3 specimens from Westbury (LL41358, LL41131).

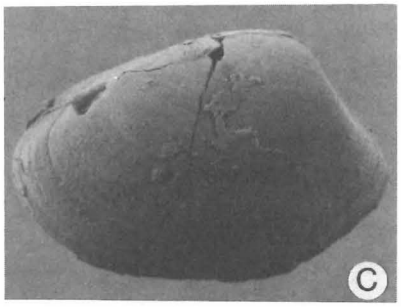
Description. Small-sized species, equivalve, triangular to slightly rostrate in outline. Well inflated, maximum near center of shell. Umbones places around centre of shell, depressed, ophisthogyrate. Escutcheon broad lanceolate to pseudocordate, bounded by a sharp carina; lunule very weakly defined, lanceolate and broad centrally. Ornament consisting of regularly commarginal and radial ribs, resulting in a reticulate pattern which, in the outer part of the lunule, are very irregular. Ligament internal.
Hinge line occupies 2/3 of the dorsal margin, anterior row of teeth gently concave with up to 10 teeth, chondrophore not seen.

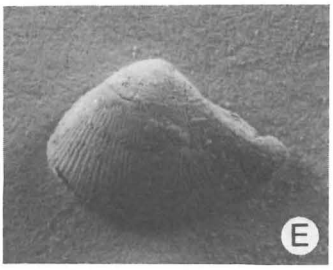
Adductor muscle scar sub-equal, posterior scar very deep, circular to trigonal, anterior scar less deep, circular to ovate, pallial line weakly developed and complete. Shell margin crenulated.

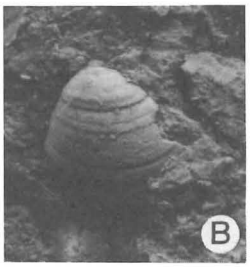
Remarks. In one specimen the posterior end was truncated—rostrate. The shell often shows intense algal-fungal borings.

Range. Mutabilis Zone of Westbury, particularly in the Pentacrinus bed. Kimmeridgian according to Hallam (1976).



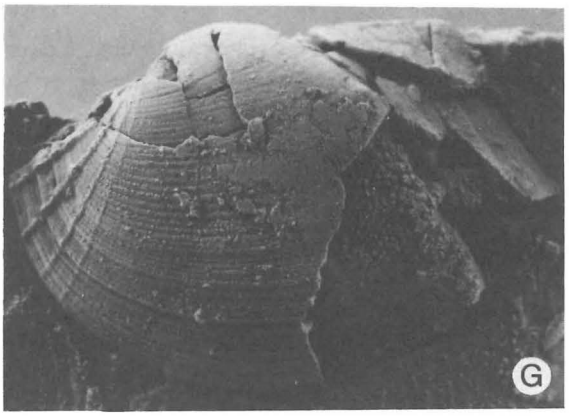


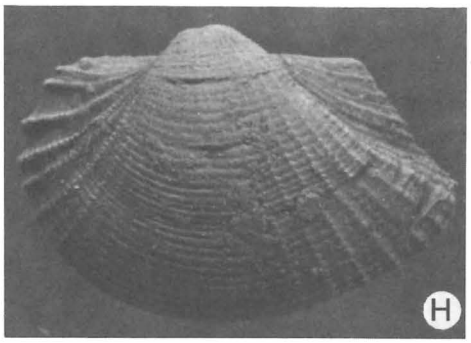




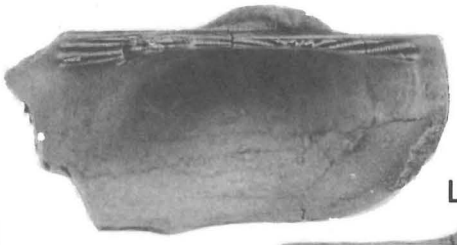

D

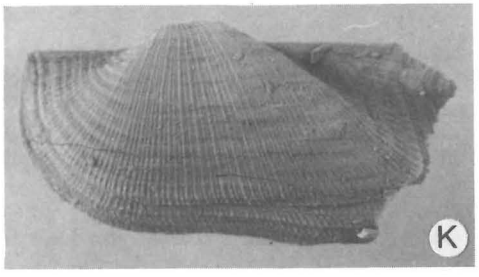

F






I


L




M

Autecology. A mobile deposit-feeder that presumably fed via its palp proboscides as it does not appear to have possessed a siphon as evidenced by the complete pallial line.

Subclass	*Pteriomorphia* Beurlen 1944
Order	*Arcoida* Stoliczkia 1871
Superfamily	*Arcacea* Lamarck 1809
Family	*Parallelodontidae* Dall 1898
Subfamily	*Grammatodontinae* Branson 1942

Genus ***Grammatodon*** Meek & Hayden 1860

Type species. Original designation Meek & Hayden, 1860: 419: *Arca (Cullaea) inornata* Meek & Hayden, 1858: 51, from the Lower Jurassic, Black Hills, Dakota, U.S.A..

Subgenus ***Grammatodon*** s.s.

Grammatodon (Grammatodon) concinnus (Phillips, 1829)
Plate 1 G-I.

1829 *Cucullaea concinna* sp. nov.; Phillips, pl. 5, figs. 9, 31.
1978 *Grammatodon (G.) concinnus* Phillips; Duff, p. 36, pl. 2, figs. 7, 11-17, 19.

Holotype. Yorkshire Museum 941, figured Phillips 1829, pl. 5, fig. 9, pl. 2, fig. 7; Oxford Clay, Yorkshire.

Material. 7 specimens from Westbury (LL41114-8, LL41359-60).

Description. Medium-sized to large shell. Outline obliquely subrectangular, with long straight hinge line occupying whole length of shell. Sharply defined posterior umbonal carina marking off radially ribbed posterior area with 12-15 ribs. 5-7 coarse, widely-spaced radial riblets diverge from the anterior side of umbones, separated by intercalatory fine radial striae. Umbones small. Inflation moderate.

Ligament duplivincular, cardinal area broad. Dentition taxodont, teeth radiating upwards from a point immediately below umbones. Anterior series short and oblique, posterior series flex over and run subparallel to hinge margin. Pallial line entire.

PLATE 1

Nuculoma obliguata (Blake, 1875).
A. LL41355; right valve; × 5. Eudoxus Zone, Westbury.
B. LL41356; right valve; × 5. Eudoxus Zone, Westbury.

Palaeonucula menkii (Roemer, 1836).
C, D. LL41357; left valve, interior and exterior of the same valve; × 3.5. Mutabilis Zone, Westbury.

Dacromya venusta (Sauvage, 1871).
E, F. LL41358; left valve, interior and exterior of the same specimen; × 3.5. Mutabilis Zone, Westbury.

Grammatodon (G.) concinnus (Phillips, 1829).
G. LL41359; left valve; × 3.5. Mutabilis Zone, Westbury.
H, I. LL41360; left valve, interior and exterior of the same specimen; × 7.4. Mutabilis Zone, Westbury.

Grammatodon (G.) longipunctata (Blake, 1875).
J. LL41361; left valve; × 5.5. Mutabilis Zone, Westbury.

Grammatodon (C.) keyserlingii (d'Orbigny, 1850).
K, L. LL41362; left valve, interior and exterior of the same specimen; × 3.5. Mutabilis Zone, Westbury.
M. LL41363; left valve, showing variation in dentition; × 3.5. Mutabilis Zone, Westbury.

Remarks. Duff (1978, p. 37) discussed the variation in this species. In the Westbury specimens it is mainly the number of riblets in the anterior part and the posterodorsal angle which varies. In contrast to the specimens from the Oxford Clay there are no radial striae in between the riblets.

Range. This is the first record of this species above the Oxfordian. Cymodoce Zone of Black Head, Mutabilis and Eudoxus Zones in Westbury. Callovian to Oxfordian in France, Germany, Switzerland and Poland (Duff, 1978).

Autecology. Probably a shallow burrowing filter feeder, although it may have been a semi-infaunal nestler (Duff, 1978).

Grammatodon (Grammatodon) longipunctata (Blake, 1875)
Plate 1 J.

1875 *Arca longipunctata* sp. nov.; Blake, p. 228, pl. 12, fig. 4.

Holotype. NHM L19932, figured Blake 1875, pl. 12, fig. 4. Syntypes NHM L70482/3 and L84625-32.

Material. 6 specimens from Black Head (LL41128-9), 7 specimens from Westbury (LL41119-22, LL41361) and 5 specimens from Chapmans Pool (LL41123-7).

Description. Small to medium-sized shell, outline subrectangular, with long straight hinge-line occupying nearly the whole length of shell. Sharply defined umbonal carina running from posterior side of umbones to posteroventral angle, marking off radially ribbed posterior area with 3-5 riblets. Umbones small, prosogyrate, slightly salient to hinge margin and not contiguous. Inflation moderate. Central and anterior part of shell ornamented by final radial striae, giving a finely cancellate pattern where they cross growth lines. Ligament duplivincular, cardinal area broad, widening with age, well-defined, not ornamented.

Dentition taxodont, teeth radiating upwards from a point immediately beneath umbones. Anterior series short and oblique, flex over outermost anterior and runs subparallel to hinge margin, posterior series longer, flex over and runs parallel to subparallel to hinge line. Dorsal and ventral sides of all teeth are very finely crenulated. Adductors scars ovate to irregular, pallial line entire.

Remarks. This species illustrates a moderate range of variation; in particular the sharpness of the umbonal carina, the degree of elongation, and the presence or absence of the posterior riblets are the most variable features. Specimens of *G. longipunctata* from the Upper Kimmeridge Clay show much weaker radial striae.

Blake (1875, p. 228) notes that *G. longipunctata* has the same general shape as *G. rhomboidalis* (Contejean). However, de Loriol & Pellat (1875-76) have figured the hinge of *G. rhomboidalis* and it is distinctly different from *G. longipunctata*. *G. concinnus* has a sharper posterdorsal angle, the riblets in the posterior part are larger, more prominent and in greater number. Furthermore *G. longipunctata* has much longer and parallel posterior teeth. *G. spilbiense* Kelly 1984 is a similar form although it is slightly less elongate and possesses different posterior dentition.

Range. *G. longipunctata* appears in the base of the Baylei Zone at Black Head and ranges throughout the Kimmeridge Clay of England to the mid-Fittoni Zone, although it is absent between the upper Autissiodorensis Zone and the mid Pectinatus Zone as seen at Kimmeridge. It appears sporadically throughout the Kimmeridgian of Boulogne in the finer-grained facies.

Autecology. Juvenile specimens up to 5 mm in length posses a distinct ventral byssal sinus and strong reticulate ornament. Larger specimens are more finely ornamented and lack a byssal sinus suggesting a major change in mode of life during ontogeny. Juvenile forms were probably epibyssate whilst more mature individuals seem to have lost their byssus and may have become infaunal filter feeders. *G. longipunctata* is, however, rather elongate for an infaunal arcid (Stanley, 1970) although the centre of inflation lies dorsally of the mid line and the posterior region is broadly truncated both indicating an infaunal life position (Duff, 1978).

Subgenus ***Cosmetodon*** Branson 1942

Type species. Original designation Branson 1942: 248: *Arca keyserlingii* d'Orbigny, 1850: 369; genotype figured by Arkell as *Beushausenia keyserlingii* (d'Orbigny) from Borissjak (Arkell 1930, pl. 14, figs. 9, 9a, 10).

Grammatodon (Cosmetodon) keyserlingii (d'Orbigny 1850)
Plate 1 K-M.

1850 *Arca keyserlingii* d'Orbigny; d'Orbigny, p. 369, No. 357.
1875 *Arca reticulata* sp. nov.; Blake, p. 229, pl. 12, fig. 11.
1929 *Parallelodon keyserlingii* d'Orbigny; Arkell, p. 38, pl. 1, figs. 6, 6a.
1930 *Parallelodon reticularum* Blake; Arkell, p. 337.
1930 *Beushausenia keyserlingii* d'Orbigny; Arkell, pl. 14, figs. 9, 9a, 10.
1982 *Grammatodon (C.) keyserlingii* d'Orbigny; Fürsich, p. 16, figs. 4 F-G, I-M, Q, S.

Material. 2 specimens from Weymouth (LL41112-3), 2 specimens from Westbury (LL41362-3).

Description. Medium- to large-sized shell, rectangular in outline, with long straight hinge line occupying the whole length of shell. Conspicious sulcus extending radially from the umbo, broadening ventrally; posterodorsal margin concave forming a wing. Broad umbonal carina running to posteroventral margin. Inflation moderate. Umbones situated about one-third of shell length from anterior, borad, prosogyrate. Ornament of fine radial striae, resulting in an elongate cancellate pattern where they cross growth lines. Dentition taxodont, teeth radiating upwards from a point below umbones, short teeth below umbo forming z-like pattern; anterior part of hinge with 4-5 short and oblique teeth, the anterior ones longer and subparallel to hinge margin. Dorsal and ventral margin of all teeth finely crenulated.

Ligamen duplivincular, adductor muscle scars unequal (coloured). Pallial line entire.

Remarks. As noticed by Fürsich (1982) *G. (C.) keyserlingii* is a highly variable species, the main variations being the position of umbones, length/height ratio, shape of posterior and anterior margins and degrees of downward curvature of ventral margin. This variation has caused a great number of names assigned to this species; there can be little doubt that *G. reticulata* as described by Blake (1875) and perhaps also *Parallelodon simile* Bigot MSS as described by Chavan (1952) are junior synonyms.

Range. *G. keyserlingii* ranges from Callovian to latest Jurassic (Fürsich, 1982), although it is relatively rare in Britain (Arkell, 1929).

Autecology. Epibyssate filter feeder.

Superfamily *Limopsacea* Dall 1895
Family *Manzanellidae* Chronic 1952

Genus ***Nucinella*** Wood 1851

(The classification of the *Treatise* is used here although it should be noted that Allen and Sanders (1969) have suggested a closer affinity with the protobranchs)

Type genus. Description by Wood, 1851, *Pleurodon ovalis* Wood, 1840; subsequent designation by Stoliczka.

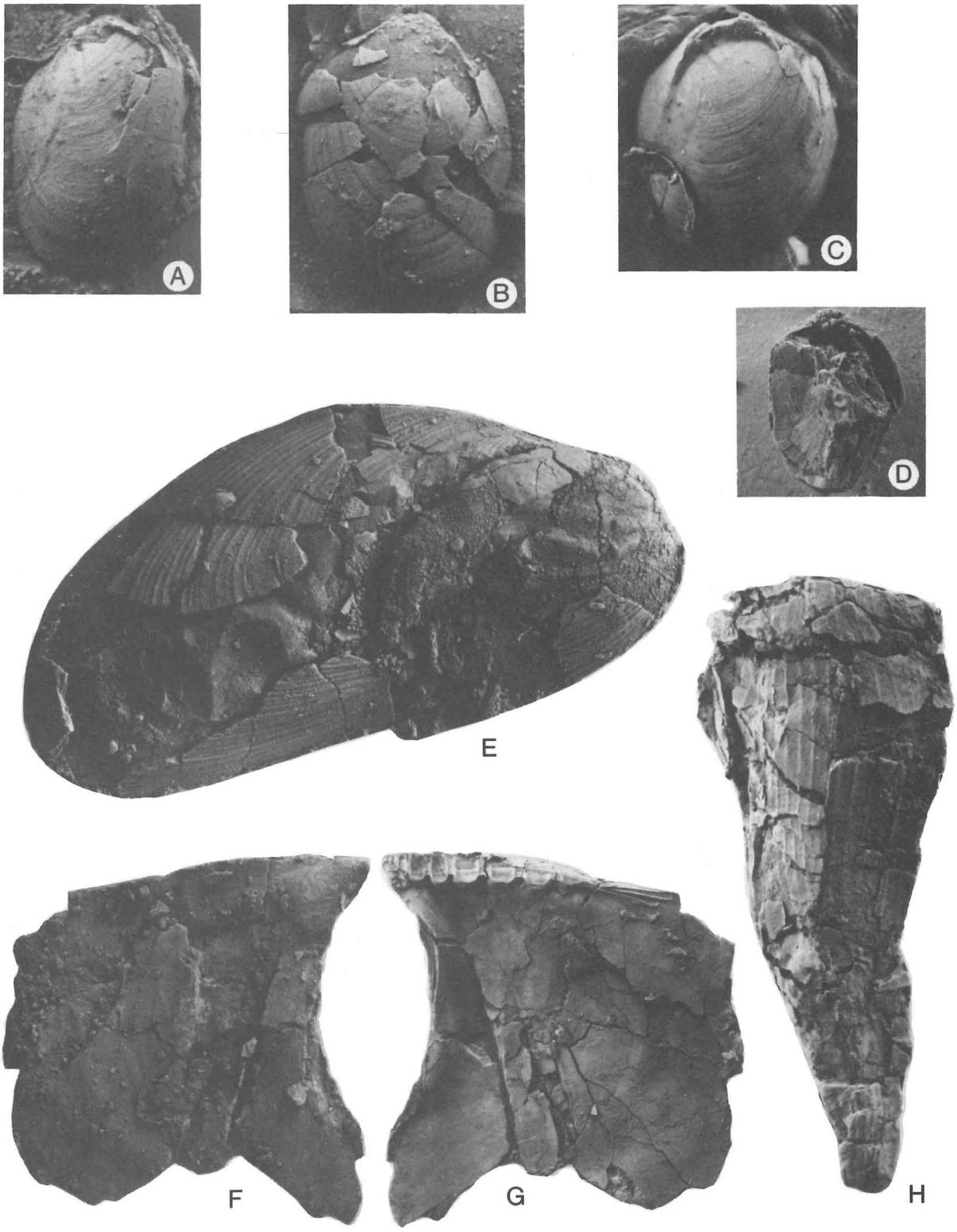
Nucinella birkelundi sp. nov.
Plate 2 A-D, text-fig. 3.

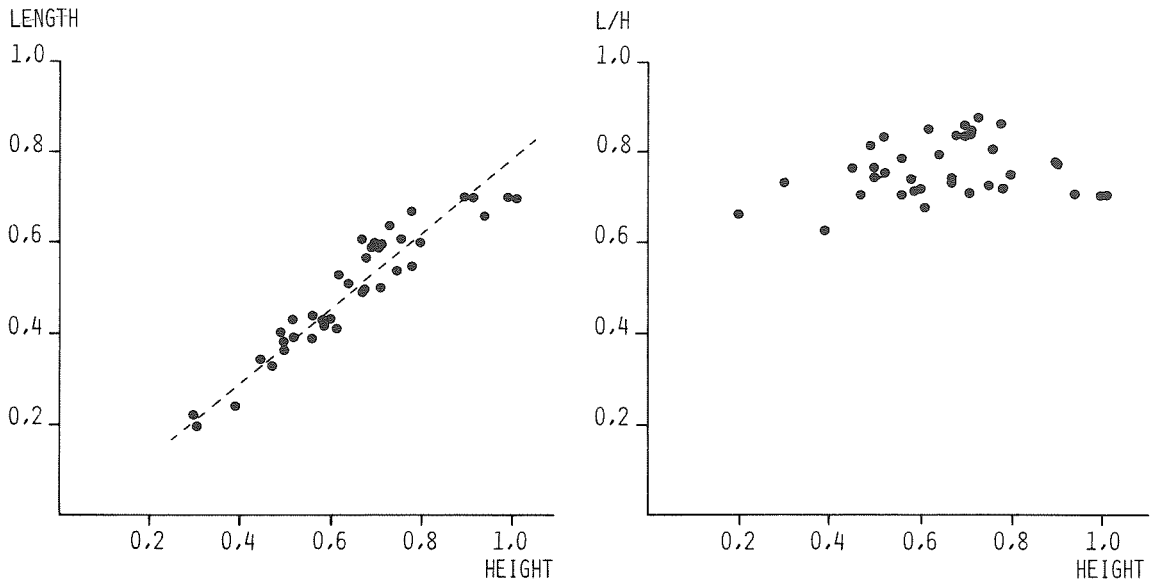
Derivatio nominis. In honour of the late professor Tove Birkelund.

Holotype. NHM41364 from the Mutabilis Zone in Westbury. Paratypes. NHM41365 and NHM41366 from the Mutabilis Zone of Westbury. Furthermore 6 specimens from Westbury (LL41132-6) and 2 specimens from Weymouth, LL41137.

Diagnosis. Medium-sized to large *Nucinella*, ovate in outline. The exterior is smooth. Dentition of at least 7 taxodont cardinals, which are elongate to circular in outline.

Description. Shell small, ovate in outline, height about 1.5 times length, equivalve, inequilateral. Dorsal margin straight to gently convex, anterodorsal angle sharp to rounded, around 100°; anterior margin long, straight to gently convex, ventral margin evenly rounded, smaller than dorsal part of the shell; posterior margin gently convex, subparallel to anterior margin; posterodorsal margin straight to gently convex with no, or only weakly defined, posterodorsal angle. Inflation moderate, with maximum near centre of shell. Umbones small, ophistogyrate, not prominent, only very slightly salient to the hinge margin, not contiguous.


A
B
C
D
E
F
G
H



Text-fig. 3. A Length/height ratio of *Nucinella birkelundi* nov. sp. and B. Length/height ratio plotted against height showing the small variation during growth.

Ornament consists only of irregularly spaced faint commarginal growth lines; no radial elements are present. Sometimes weak colour-banding can be observed. Dentition consists of at least 7 taxodont cardinals, the central ones elongate, the outer ones rounded to complete circular or pointed. One strong buttressed anterior lateral in each valve, sometimes a small ridge within the lateral socket is seen. Only one muscle scar near the anteroventral margin is seen. Margin entire.

Remarks. Vokes (1956) discussed at length the occurrence and evolution of *Nucinella* from Lower Jurassic to Recent and showed that the Permian genus *Manzanella* is to be considered as ancestral to *Nucinella*.

Allen and Sanders (1969) described the soft parts of a Recent species and showed that it is the posterior adductor muscle that is absent and not the anterior one, and suggested that *Nucinella* may be derived from the actinodont bivalves of the Lower Ordovician.

Nucinella birkelundi sp. nov. differs from *Nucinella liasinas* (Bistram in Vokes 1959) from the Hettangian near Lake Lugano (Swiss-Italian border) in being larger, the difference between height and length are greater and

---

PLATE 2

Nucinella birkelundi sp. nov.
A. Holotype NHM41364; left valve; × 5.5. Mutabilis Zone, Westbury.
B. Paratype NHM41365; right valve; × 5.5. Mutabilis Zone, Westbury.
C. Paratype LL41366; left valve; × 5. Mutabilis Zone, Westbury.
D. interior of left valve; × 3.5. not preserved.

Modoilus (M.) bipartitus J. Sowerby, 1818.
E. LL41367; right valve; × 2.3. Mutabilis Zone, Westbury.

Auquilerella sp.
F, G. LL41368; right valve, interior and exterior of the same valve; × 1.2. Mutabilis Zone, Westbury.

Pinna (P.) lanceolata J. Sowerby, 1821.
H. LL41369; complete specimen; × 1.7, Mutabilis Zone, Westbury.

by having more than five transverse teeth in the cardinal series. *N. birkelundi* sp. nov. seems to be more like *N. glabrata* Stoliczka, 1871 from the Cenomanian (?) of India but again differs in being larger and by having only one strong lateral in each valve, not two in the left valve (Vokes, 1956).

Range. First appears immediately above the Black Head Siltstone, in the lower Cymodoce Zone of Black Head; it is especially common in the Mutabilis Zone of Westbury. Final appearance is in the upper Autissiodorensis Zone of Kimmeridge Bay.

Autecology. Recent *Nucinella* have no siphons, a simple gut and draw inhalent water into the shell anteriorly (Allen & Sanders 1969). The shell morphology and the large foot are similar to *Nucula* and it appears probable that this species, and other *Nucinella*, were mobile deposit feeders.

Order *Mytiloida* Ferussac 1822
Superfamily *Mytilacea* Rafinesque 1815
Family *Mytilidae* Rafinesque 1815
Subfamily *Modioœinae* Keen 1958

Genus ***Modiolus*** Lamarck 1799

(nom. conserv. pro *Volsella* Scapoli, 1777 (ICZN opinion 325, 1955)).

Type species. By absolute tautonomy: *Mytilus modiolus* Linnaeus, 1758, p. 706. Recent.

Subgenus ***Modiolus*** s.s.

Modiolus (Modiolus) cf. ***bipartitus*** J. Sowerby 1818
Plate 2 E.

1818 *Modiola bipartita* sp. nov.; J. Sowerby, p. 17, pl. 210, fig. 4 (*non* fig. 3).
1982 *Modiolus (M.) bipartitus* J. Sowerby; Fürsich, p. 21, fig. 7 C-D.

Material. 3 specimens from Westbury (LL41367, LL41109), 1 specimen from Equihen, S. of Boulogne (LL41108).

Description. Large *Modiolus*, elongate elliptical to subtrapezoidal in outline with short obliquely truncate anterior margin. Umbones small, pointed. Well inflated. Ornament of irregularly spaced concentric growth lines. Interior not seen.

Remarks. The Westbury specimens agree well with the *M. bipartitus* figured by Fürsich (1982) but are much less indented in the ventral margin than the true *M. bipartitus*.

Range. In England *M. bipartitus* range from Late Bathonian to Kimmeridgian, but it is rare in sediments younger than the Oxfordian (Cox, 1965).

Autecology. A semi-infaunal filter feeder (Stanley 1972); Fürsich 1982).

Superfamily *Pinnacea* Leach 1819
Family *Pinnidae* Leach 1819

Genus ***Pinna*** Linne 1758

Type species. Subsequent designation Children 1823, p. 34: *Pinna rudis* Linne: 1758; figured Lamarck 1819: 60, pl. 2, fig. 80; Recent, West Indies.

Subgenus ***Pinna*** s.s.

Pinna (Pinna) lanceolata J. Sowerby 1821
Plate 2 H.

1821 *Pinna lanceolate* sp. nov.; J. Sowerby, p. 145, pl. 281.
1978 *Pinna (P.) lanceolata* J. Sowerby; Duff, p. 45, pl. 3, figs. 14, 16, 19, 29, text-fig. 12a.
1982 *Pinna (P.) lanceolate* J. Sowerby; Fürsich, p. 30, figs. 6A, 11 A, D.

Neotype. Arkell (1933: 222) states 'Topotype here made neotype', but he figured two topotypes whilst the one accepted by Duff (1978) as neotype (Arkell pl. 28, fig. 5) is stated to be a 'chorotype: ?topotype'. The one in pl. 29, fig. 3 is stated as topotype, from the Lower Calcareous Grit, Scarborough, England.

Material. 1 specimen from Black Head (LL41110), 2 specimens from Westbury (LL41369, LL41111).

Description. Long, narrow *Pinna* with dorsal and ventral margins diverging regularly. Valves with median carina well-developed. Dorsal part of valve with 8-10 wire-like radial ribs, fading posteriorly; ventral part with 3-5 radial ribs on part of valve nearest to median carina and subconcentric growth rugae.

Remarks. This well-known Corallian species has been described by Arkell (1933: 219) and needs no further extensive description, the difference between it and *Pinna mitis* are outlined by Duff (1978: 44, text-fig. 12). The specimens found in Westbury are considerably smaller than the typical Oxfordian specimens.

Range. Callovian to Tithonian in Europe (Hallam 1976), Mid Volgian to Late Valangian of Greenland (Fürsich 1982).

Autecology. A semi-infaunal filter-feeder, lying with its posterior portion above the substrate (Fürsich 1980, 1982). They are fairly commonly found in life position in the Black Head Siltstone and also at Westbury. They are also found strewn on ammonite-covered bedding planes in the lowest sub-bituminous shales of the Mutabilis Zone at the latter locality. *Entolium orbiculare* is also associated with these ammonite plasters. The occurrence of a dense covering of ammonites may have stabilized the substrate sufficiently to encourage the colonization of *Pinna*.

Order	*Pterioida* Newell 1965
Suborder	*Pteriina* Newell 1965
Superfamily	*Pteriacea* Grey 1847 (1820)
Family	*Bakevelliidae* King 1850

Genus ***Aquilerella*** Chavan 1951

Type species. Original designation Chavan, 1951, p. 211: *Perna kobyi* de Loriol, 1901, p. 99.

Aquilerella sp.
Plate 2 F, G.

Material. 1 specimen from Westbury (LL41368).

Description. Specimen large, rhombic in outline, higher than long. Beak slightly subterminal. Dentition of right valve consists of two short, oblique teeth below beak and two elongate posterior teeth which are parallel to dorsal margin. There are two small ligament pits dorsal to anterior teeth, followed by 6 larger oval pits, diminishing in height posteriorly. Adductor scar large, ovate to circular. Inflation low, surface smooth. Umbonal angle 60°.

Remarks. The only specimen is incomplete, but differs in dentition and probably also in outline from *A. kobyi* (de Loriol, 1901), *A. aldingeri* Fürsich (1982) and *A. pseudoperna* Chavan (1952).

Autecology. An adpressed epibyssate or semi-infaunal form.

Genus ***Gervillella*** Waagen, 1907

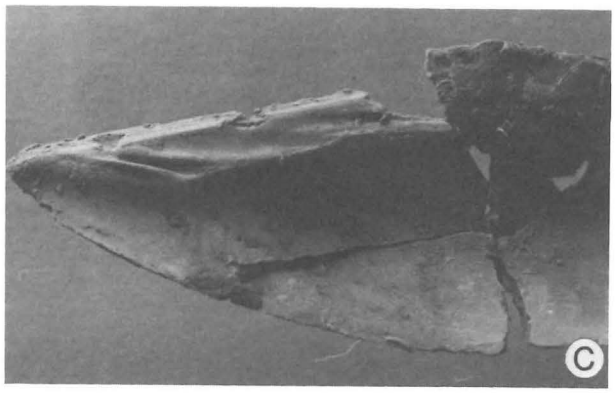
Type species. Original designation by Waagen 1907: 98: *Perna aviculoides* J. Sowerby 1814: 147; subsequent designation Cox 1940: 112.

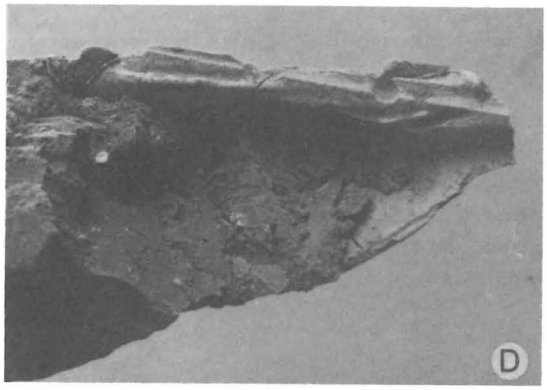
Gervillella aviculoides (J. Sowerby 1814).
Plate 3 A-F.

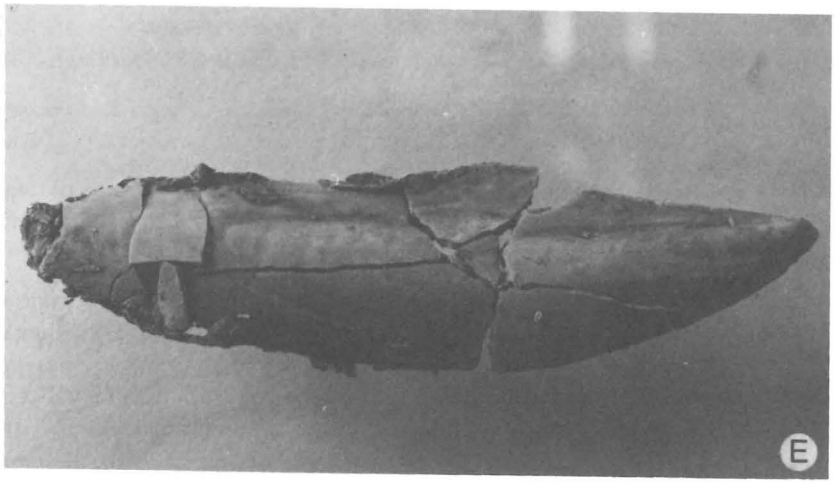
Type species. Arkell (1933: 204) designated the largest specimen in his fig. 7 as lectotype, figured by Sowerby, 1814 pl. 66, fig. 1-4 as the holotype is lost.


A


B


C


D


E


F


G


H


I

1814 *Perna aviculoides,* sp. nov.; J. Sowerby: 147, pl. 66, figs. 1-4.
1836 *Gervillia tetragona* sp. nov.; Roemer: 85, pl. 4, fig. 111.
1901 *Gervillia roederi* sp. nov.;de Loriol, p. 95, pl. 7, figs. 2-4.
1933 *Gervillia aviculoides* (J. Sowerby); Arkell, p. 203, pl. 26, figs. 1-5.
1965 *Gervillella aviculoides* (J. Sowerby); Cox, p. 44.

Material. 5 specimens from Westbury (LL41370-3).

Description. Large-sized *Gervillella*, shell thick around umbones, getting thinner posteriorly. Anterior auricle small, pointed, posterior auricle large and long, well defined. Juvenile specimens are longitudinally elongate and slightly curved, narrow, with anterior and posterior margin parallel.

Hinge line with thick but narrow ligament-area, bearing 5-8 nearly quadrate ligament pits, all of which cross the whole width of the area. In the juvenile specimens there are 5 widely separated ligament pits, central one largest, the most anterior one elongated and oblique to hinge line.

Dentition taxodont with 3 oblique lateral teeth, just posterior of umbones and 1-2 lateral teeth subparallel to hinge line, situated further posteriorly. In the juveniles there are 2-3 short anterior teeth and 3 well-defined elongate posterior teeth, the most dorsal of which is interrupted by ligament pits. These posterior teeth change position with growth of the ligament area.

Surface smooth with irregularly spaced commarginal growth lines.

Remarks. The well preserved material from Westbury clearly show the change in position of the teeth.

Autecology. A semi-infaunal form often occurring in clusters.

Family *Posidoniidae* Frech 1909

Genus ***Aulacomyella*** Furlani 1910

Type genus. Original designation Furlani 1910: *Aulacomyella problematica* Furlani 1910.

Aulacomyella aff. ***farquharsoni*** Cox 1935
Plate 3 G-I.

1935 *Aulacomyella farquharsoni* n. sp., Cox, p. 167, pl. 15, fig. 9.

Holotype. NHM, L.61135, figured in Cox 1935, from the Kimmeridge of Somalia.

Material. 7 specimens from Westbury (LL41374, LL40931-34).

PLATE 3

Gervillella aviculoides (J. Sowerby, 1814).
All specimens are from bed M8 and M9 of Mutabilis Zone, Westbury.
A, B. LL41370; group of juvenile specimens; × 1.6. B.
Interior of one of the juvenile, left valve; × 3.5.
C. Right valve; × 2.4, not preserved.
D. LL41373; left valve; × 3.3.
E. LL41371; right valve; × 3.3.
F. LL41374; bivalved specimen; × 2.3.

Aulacomyella aff. *farquharsoni* Cox 1935.
All specimens occur on the same sample; LL41375, from an organic-rich shale in the Lower Eudoxus Zone.

G. Right valve; × 3.3.
H. Right valve; × 5.
I. Left valve; × 1.

Description. Large-sized species, thin-shelled, equivalve, slightly asymmetric. Circular to oval in outline, hinge line is short, typically less than 40% of the maximum width. Umbones small, not salient, slightly anteriorly placed. Anterodorsal margin gently convex, posterodorsal margin angled at about 150°. Maximum shell length is in a posterodorsal line from the umbone. Valves flat, hardly inflated.

Ornament of numerous radial riblets, these are radial on the posterior flank and curve gently on the anterior flank, being convex in a posterior direction. The riblets are cross cut by comarginal growth wrinkles, giving reticulate ornament virtually all over the shell.

Remarks. *A. farquharsoni* show some variation in the strength of the ribbing but the curvature of the anterior riblets is not nearly so well developed as in the Kimmeridge Clay forms. *Avicula nummulina* described by Blake (1875, p. 230) appears similar although the hinge line is longer.

Range. Occur from bed M18 (upper Mutabilis Zone) to be base of bed E7 (Lower Eudoxus Zone) at Westbury. The occurrences of Somalia appear to be of similarly restricted stratigraphic range, in the middle Early Kimmeridgian.

Autecology. At Westbury, as in Somalia, *Aulacomyella* aff. *farquharsoni* tends to occur in huge numbers in discrete beds, forming lumachelles. This suggest opportunistic colonization in a harsh environment and/or the competitive exclusion of other forms. However, a number of other factors suggest a pseudoplanktonic mode of life, possibly living attached pendently to driftwood. The factors include its widespread, virtually global occurrence, its facies crossing distribution (it is found in sandstones, siltstones, calcareous clays and moderately organic-rich mudstones), and its very thin shell. The problems of autecologic interpretation are very similar to those for the earlier Jurassic posidoniid, *Bositra*. In the Westbury sediments the sporadic occurrence of large numbers of *A.* aff. *farquharson* has no effect upon the remainder of the benthic association. This suggests that normal benthic factors were not controlling its distribution. The suggestion of Duff (1978) for Oxford Clay posidoniids, that these forms lived attached to floating benthic algae appears reasonable as this accounts for their appearance in huge numbers and yet their occurrence is not reflected by the remainder of the benthos.

Family *Inoceramidae* Zittel 1881 (ICZN 473)

Genus ***Parainoceramus*** Voronetz 1936

Type species. Original designation Voronetz, 1936, p. 23 (P. *bulkurensis*), subsequent designation Cox, 1964, p. 47.

Parainoceramus cramei sp. nov.
Plate 4 A-D, text-fig. 4.

Derivatio nominis. After Dr. J. A. Crame.

Material. Holotype NHM41377, Plate 4 D, from the Eudoxus Zone, Westbury. 8 paratypes from Westbury (NHM41375-6, LL41096-41101) and 6 specimens from around Kimmeridge Bay (LL41102-7).

Diagnosis. Small to medium-sized *Parainoceramus*, subrhomboidal in outline with very weakly defined anterior auricle.

Description. Small to medium-sized *Parainoceramus*, probably equivalve, inequilateral, subrhomboidal to subovate in outline.

Anterior auricle weakly defined with anterior margin straight to gently concave, sometimes an anteroventral angle is developed, around 150°, ventral margin evenly rounded continuing into posterior margin which is long, gently convex. Posterodorsal angle weakly defined, around 90°, dorsal margin straight. Inflation low.

Umbones small, pointed, with well developed protoconch, prosogyrate. Hinge line long, about half length of shell, with broad ligament area. Ligament multivincular, with at least 8 ligament pits, broadening posteriorly.

Dentition. In right valve there are two small teeth below the beak joined dorsally and making an asymmetrical chevron, with a "socket" below. These teeth mark the anterior extremity of hinge line. There are no posterior teeth. The left valve contains one prominent spoonlike cardinal tooth, situated just below umbo (Text-fig. 4).

Ornament of irregular commarginal growth-lines, sometimes also irregular concentric ridges, fading distally. On the internal posterior-layer there are faint radial ribs. Outer ostracum of prismatic calcite. Musculature not seen.

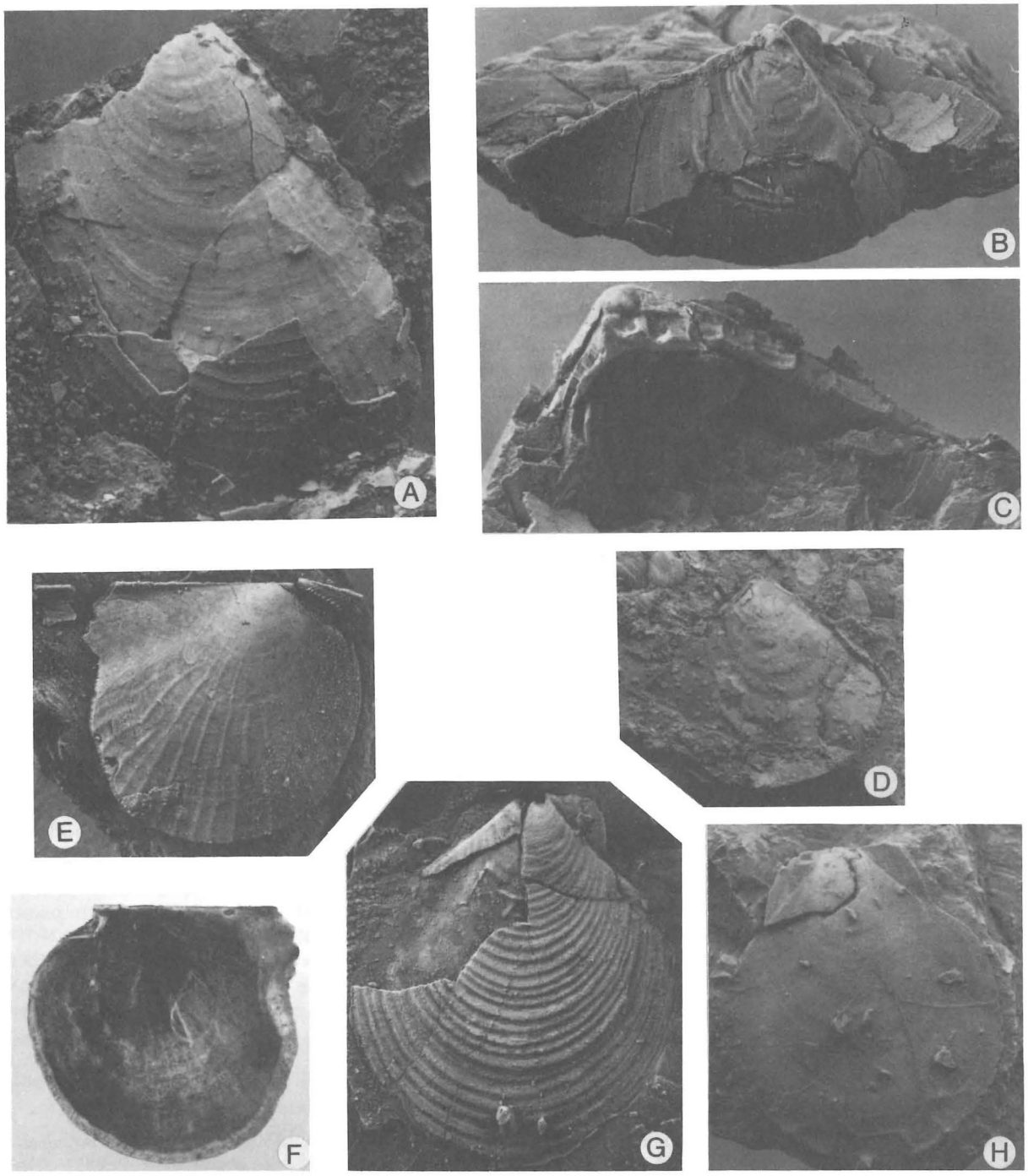
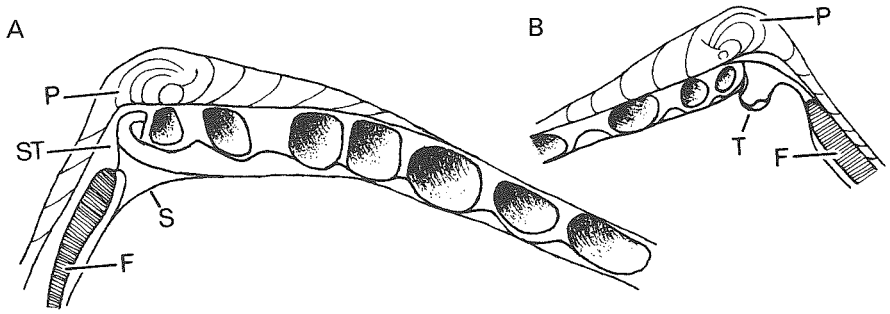


PLATE 4

Parainoceramus cramei sp. nov.
A. NHM41375; paratype; right valve; × 2.2. Eudoxus Zone, Westbury.
B, C. NHM41376; paratype; interior and exterior of right valve; × 10. Eudoxus Zone, Westbury.
D. NHM41377; holotype; right valve; × 3.3. Eudoxus Zone, Westbury.

Oxytoma (O.) inequivalve (J. Sowerby, 1819).
E, F. LL41378; exterior and interior of the same specimen, right valve; × 3.6. Mutabilis Zone, Westbury.

Entolium (E.) orbuculare (J. Sowerby, 1817).
G. LL41379; right valve; × 3.6. Mutabilis Zone, Westbury.
H. LL41380; left valve; × 3.6. Mutabilis Zone, Westbury.



Text-fig. 4. Hinge line of *Parainoceramus cramei* sp. nov., app. × 10. A. Right valve, NHM LL41376, with clearly developed protoconch (P), secondary dentition (ST) and inner fibrous calcite (F). S is the most probable "socket" for the tooth in left valve, possibly only functioning in juvenile stages. B. Left valve, with prominent tooth (T), the outer margin of shell partly reconstructed.

Remarks. *Parainoceramus* is the only inoceramid genus to have hinge teeth, although they are not always present (Duff 1978). Small rudimentary teeth in the right valve are common, but there are no records of a larger tooth in the left valve. The only left valve in which the hinge is visible is a small one and it is possible that it is a juvenile feature as no distinct socket is found in any of the right valve hinges.

Blake (1875, 1880) described *Inoceramus rasenensis* from the Lower Kimmeridge of Market Rasen. However, this is a much larger form with a trigonal outline and sharper, more prominent beaks. *P. socialis* (Goldfuss) ia another coeval form from the Solnhofen Limestone, but it is more rounded than the quadrate *P. cramei*. *P. golberti* (Zakharov and Turbina 1979), a Lower Volgian form from the Central Russian Platform (Kelly 1984) is similarly quadrate but possesses a much shorter hinge line.

Range. First appears in the lower Eudoxus Zone in some numbers and then occurs sporadically in higher beds until the Pectinatus/Pallasioides Zones, where it is fairly abundant. Last occurrence is in the mid Fittoni Zone.

Autecology. The range of *P. cramei* almost exactly coincides with the distribution of organic-rich facies in the Kimmeridge Clay suggesting that this form was tolerant of reduced oxygen levels. The presence of a low broad umbonal ridge running parallel to the straight anterior border is suggestive of an epibyssate form with the saggital plane vertical. However there is no byssal sulcus and so byssal attachment was possibly only weak, although this may have been all that was required in low energy, oxygen-deficient mudstone environments. There is no evidence of this species clustering together in nests (cf. Duff 1978: 16).

Superfamily *Pectinacea* Rafinesque 1815
Family *Oxytomidae* Ichikawa 1958

Genus ***Oxytoma*** Meek 1864

Type species. Original designation Meek 1864: 3339: *Avicula muensteri* Bronn 1830: 164 (= *Avicula inequivalvis* J. Sowerby 1819: 78) from Braunjura δ of Thunan, Germany

Subgenus ***Oxytoma*** *s.s.*

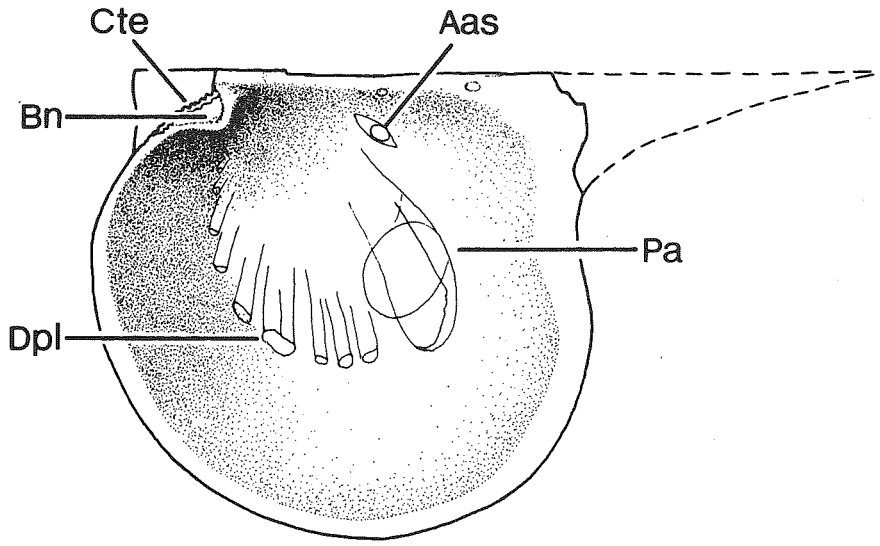
Oxytoma (Oxytoma) inequivalve (J. Sowerby, 1819)
Plate 4 E, F, text-fig. 5.

1819 *Avicula inequivalvis* sp. nov. J. Sowerby, p. 78, pl. 244, figs. 2, 3.
1978 *Oxytoma (O.) inequivalve* (J. Sowerby); Duff, p. 54, pl. 4, figs. 7, 9, 11, 13, 15-19, 21-23.
1982 *Oxytoma (O.) inequivalve* (J. Sowerby); Fürsich, p. 34, figs. 6 B-F.

Lectotype. Designated by Arkell 1933: 194. British Museum 43259a, J. Sowerby 1819, pl. 244, fig. 2, LV, pl. 4, fig. 16.

Material. 4 specimens from the Kimmeridge Bay (LL41077-80), 1 specimen from Westbury (LL41378).

Description. Medium-sized *Oxytoma*. Right valve suborbicular to subovate, thin, more or less flat, with small umbones placed one third of shell length behind anterior margin. Hinge line long giving maximum shell length. Posterior auricle large, flattened, very elongate, sharply pointed, anterior auricle small, pointed, with deep byssal notch. Ornament of widely interspaced, shallow primary radial riblets with growth halts, radial striae between and upon primary riblets intersect with fine commarginal growth-lines to give a minute net pattern upon the entire surface. Ligament (RV) elongate parallel to hinge margin. Ctenolium consisting of about 12 parallel ridges terminated by a tooth, just anterior of umbo. Running anterodorsally from ventral margin of adductor muscle scar is a disjunct pallial line consisting of 10 round to elongate pallial muscle scars. All muscle scars show traces of being moved ventrally during growth (Text-fig. 5).



Text-fig. 5. Interior of *Oxytoma (O.) inequivalve*, LL41378, showing details of the musculature and the cardinal area, app. × 13. Note the small anterior adductor scar (Aas), the large posterior adductor (Pa), the ctenolium (Cte), the deep byssal notch (Bn) and the disjunct pallial line (Dpl).

Remarks. The status and variation of this species has been discussed at length by Arkell (1933: 192), Cox (1940: 48) and Duff (1978: 56) who all came to different conclusions (see also Fürsich 1982: 36). Duff also discussed the apparent lack of a ctenolium in the Oxford Clay specimens, but on a single well-preserved specimen from the Lower Kimmeridge Clay this is present on the outside of the right valve. There is thus no reason to assume that there were very few byssal threads.

Range. Lias to late Volgian of Europe. Occurs sporadically throughout the Kimmeridgian of England and France; only found in significant numbers in the Pectinatus to Rotunda Zone interval of Dorset. According to S. Kelly (pers. comm. 1984) *O. inequivalve* includes *O. octavia* (d'Orbigny) which extends the range from Lias to late Volgian of Europe.

Autecology. An epifaunal filter feeder. The well developed byssal notch indicates byssal attachment. Duff (1975, 1978) suggests that they may have attached pendently to floating algae. However, there is no reason why the sporadic specimens in the Kimmeridge Clay could not have lived attached to shell fragments on the sea floor.

Family *Entoliidae* Korobkov 1960

Genus ***Entolium*** Meek 1865

Type species. Original designation Meek, 1865: *Pecten demissum* Phillips as illustrated by Quensted 1858.

Subgenus ***Entolium*** s.s.

Entolium (Entolium) orbiculare (J. Sowerby 1817)
Plate 4 G, H.

1817 *Pecten orbicularis* sp. nov. Sowerby, p. 193, pl. 86.
1982 *Entolium orbiculare* (J. Sowerby); Fürsich, p. 38, fig. 15 A-B, D.E.
1984 *Entolium (E.) orbiculare* (J. Sowerby); Johnson, p. 35, pl. 1, fig. 19.

Material. 4 specimens from Westbury (LL41379-80, LL41089-90).

Description. Medium-sized, suborbicular, subequilateral, subequivalve; left valve slightly more inflated than right valve. Umbonal angle varying between 115° and 120° in adult specimens. Auricles rather small, triangular in outline, subequal on right valve, slightly projecting above hinge line; auricles of left valve equal, anterior auricle of right valve forming a less obtuse angle with flank than posterior auricle. Auricles distinctly set off from flank by thin groove.

Surface of left valve smooth, including auricles, with very faint commarginal growth lines, on the right valve these growth lines are accompanied by grooves on the entire surface; the spaces between the grooves are about three times the width of the elevated grooves themselves. Interior not seen.

Range. Johnson (1984: 59) notes that *E. (E.) orbiculare* first appears in the Oxfordian and ranges to the Ryazanian of E. England. Occurs in the basal zones of the Kimmeridge, and also in the upper 3 zones east of Kimmeridge Bay. It occurs more commonly, although it is never abundant, in the Early Kimmeridgian of Boulogne.

Autecology. The symmetrical auricles indicate that this was a free-lying rather than a bysally attached form (Stanley 1972). The prominent concentric grooves on the right valve may have helped to anchor the posterior in the sediment. Johnson (1984) describes this as a fairly eurytopic form with a preference for high energy nearshore environments. This is supported by the distribution within the Kimmeridge Clay where *E. (E.) orbiculare* tends to occur in the less organic-rich mudstones at the top and bottom of the formation whilst it is absent from the organic-rich shales in the central part of the formation.

Entolium (Entolium) corneolum (Young & Bird 1828)
Plate 5 D, F.

1828 *Pecten corneolus* sp. nov. Young & Bird, p. 234, pl. 9, fig. 5.
1978 *Entolium (E.) corneolum* (Young & Bird); Duff, p. 62, pl. 4, figs. 25, 29, 30, pl. 5, figs. 3-5, text-fig. 20.
1984 *Entolium (E.) corneolum* (Young & Bird); Johnson, p. 45, pl. 1, figs. 20, 22, 24-27.

Neotype. Designated by Duff 1978: 62, Oxford University Museum J 8151, figured by Arkell, 1930, pl. 7, fig. 4.

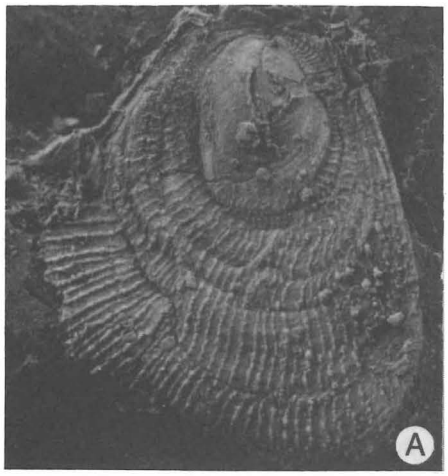
PLATE 5

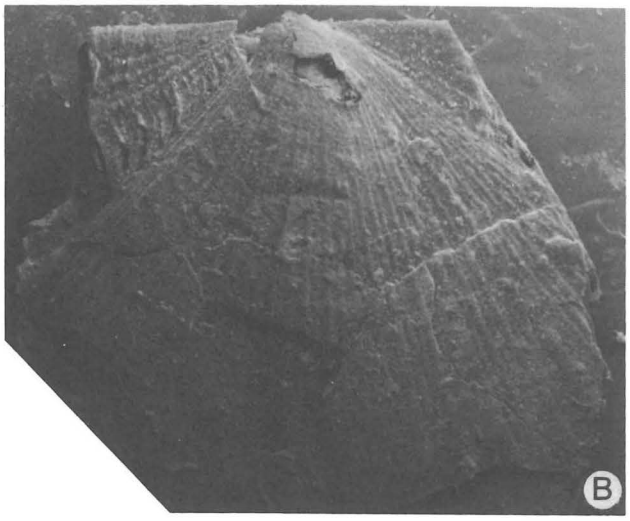
Entolium (E.) corneolum (Young & Bird, 1828).
D. LL41385; bivalved specimen; × 1.7. Mutabilis Zone, Westbury.
F. LL41386; internal of right valve; × 1.2. Mutabilis Zone, Westbury.

Placunopsis radiata (Phillips, 1929).
A. LL41381; left valve; × 3.6. Mutabilis Zone, Westbury.
C. LL41382; right valve; × 2.5. Mutabilis Zone, Westbury.

Radulopecten strictus (Münster in Goldfuss, 1836).
B. LL41383; left valve; × 13. Mutabilis Zone, Westbury.
E. LL41384; internal of right valve; × 1.5. Mutabilis Zone, Westbury.

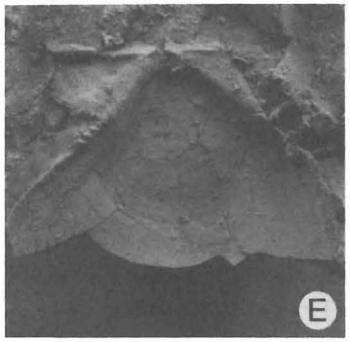
Camptonectes (C.) auritus (Schlotheim, 1813).
G. LL41387; internal of right valve; × 2.7. Mutabilis Zone, Westbury.

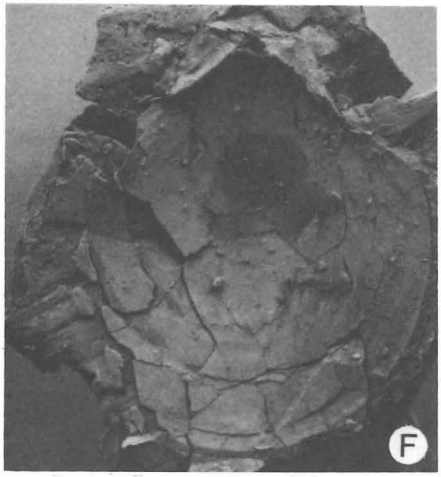

A

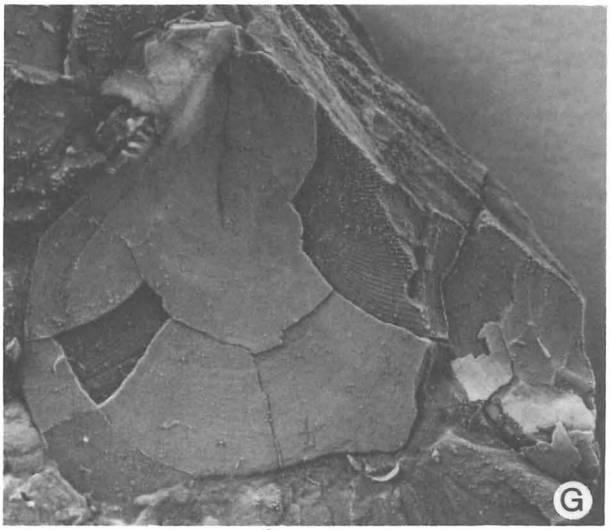

B


C


D


E


F


G

Material. 5 specimens from Westbury (LL41385-6, LL41086-8).

Description. Large shell, equivalve or subequivalve, inequilateral, suborbicular in outline. Umbonal angle around 110°. Auricles relatively small, triangular in outline, auricles of left valve projecting above hinge line. Auricles distinctly set off from flank by thin groove. Surface smooth on both valves but the growth lines seen as light coloured layers in the nearly transparent shell are crossed by very irregular radiating lines. The large posterior adductor placed dorsally of median of shell can only be seen due to colouring.

Remarks. This well-known species has been described by Arkell (1930), Duff (1978) and Johnson (1984).

Range. Toarcian to ?basal Cretaceous (Johnson 1984: 52). Same distribution as *E. (E.) orbiculare* in the Kimmeridge Clay of England. Occurs sporadically in the Late Kimmeridgian of Boulogne.

Autecology. Very similar to *E. (E.) orbiculare*, a free-lying low-level suspension feeder occurring in a wide range of facies (Johnson 1984).

Camptonectes Group

Genus ***Camptonectes*** Agassiz in Meek 1864.

Type Species. Subsequent designation, Stoloczka 1871: 425: *Pecten lens* J. Sowerby 1818: 3, pl. 205, fig. 2, 3, from the Corallian beds of England.

Subgenus ***Camptonectes*** s.s.

Camptonectes (Camptonectes) auritus (Schlotheim 1813)
Plate 5 G.

1813 *Chamites auritus* sp. nov. Schlotheim: 103.
1978 *Camptonectes (C.) auritus* (Schlotheim); Duff, p. 66, pl. 5, figs. 22, 25.
1984 *Camptonectes (C.) auritus* (Schlotheim); Johnson, p. 115, pl. 3, figs. 25-40.

Neotype. Designated by Duff 1978: 66: British Museum L80525, figured by J. Sowerby 1818, pl. 205, fig. 2. Type species from Oxfordian, Headington, near Oxford.

Material. 4 specimens from Kimmeridge Bay (LL41091-3, 41095), 1 specimen from Boulogne (LL41094) and 1 specimen from Westbury (LL41387).

Description. Medium to large species, inequivalve, planoconvex, right valve almost flat. Inequilateral, auricles small, anterior auricles larger than posterior, with large byssal sinus beneath it. Outline suborbicular to subovate, umbonal angle around 105°. Anterior auricles of right valve elongate.

Ornament consisting of fine, divaricate striae, densely punctate where they cross the fine commarginal growth lines. Resilifer not seen.

Ctenolium well-developed, with 4 teeth, placed along dorsal margin of right valve, immediately anterior to byssal notch. Pallial line entire. One circular adductor muscle scar seen slightly posterior and slightly dorsal to centre of body of shell as a yellow spot.

Remarks. Arkell (1930: 95) and more recently Johnson (1984) have gone to some lengths to unravel the confused taxonomy of this species.

Range. Basal Lias to the Ryazanian stage (Cretaceous) (Johnson 1984). Occurs throughout the Kimmeridgian of southern England and Boulogne although only in limited numbers.

Autecology. A reclining epibyssate form, as evidenced by the well developed byssal notch. A highly eurytopic species able to withstand all but the most soupy substrates (Johnson 1984: 123). It is the most common pectinid in the Kimmeridge Clay and was evidently able to withstand reduced oxygen levels as it occurs sporadically in some highly organic-rich shales. Johnson (1984) notes that Lower Toarcian specimens were equally oxygen tolerant.

Genus ***Radulopecten*** Rollier 1911

Type Species. Original designation by Morris & Lycett 1853: 10, pl. 1, fig. 16: *Pecten hemicostatus*. Subsequent designation by Rollier 1911: 158.

Radulopecten strictus (Münster in Goldfuss 1836)
Plate 5 B, E.

1833 *Pecten strictus* sp. nov. Münster in Goldfuss, p. 49, pl. 91, fig. 4a-c.
1875 *Pecten strictus* Münster; de Loriol et Pellat, p. 190, pl. 22, figs. 10-15.
1984 *Radulopecten strictus* Münster; Johnson, p. 201, pl. 10, figs. 4-6.

Material. 3 specimens from Weymouth (LL41081-3), 3 specimens from Westbury (LL41383-4, LL41084).

Description. Shell medium to small, suborbicular in outline, subequilateral. Hinge line straight, about two-thirds of overall length of shell; auricles of left valve unequal, with left anterior auricle large than posterior. Angle of posterior auricle about 120°, that of anterior auricle about 90°. Umbo situated slightly dorsally of auricles. Hinge line forming a slight angle outwards with the umbo at the center. Fairly well developed byssal notch.

Left valve with densely-packed fine radial riblets, continuing on both auricles, where they become subhorizontal to dorsal margin. These riblets are crossed by regularly spaced fine concentric lamellae, which are present over the whole shell, but are most clearly seen around umbones and on the anterior auricle giving rise to a very faint reticulate pattern.

Resilifer not seen. Internal structures not seen.

Range. Johnson (1984: 201) records this species from the Late Oxfordian to the Late Kimmeridgian. During this survey *R. strictus* was only recorded from the Mutabilis Zone of Weymouth and Westbury and in the Argiles and Calcaires du Moulin Wibert of Boulogne, although it is never common.

Autecology. A reclining epibyssate, low level filter feeder.

Family Terquemiidae Cox 1964

Genus ***Placunopsis*** Morris & Lycett 1853

Type species. Original description by Morris & Lycett 1853: 5: *Placunopsis fibrosa* Laube 1867: 16 (= *jurensis* (non Roemer sp.) Morris & Lycett: ICZN pend.)

Placunopsis radiata (Phillips 1829)
Plate 5 A, C.

1829 *Orbicula radiata* sp. nov. Phillips, p. 130, pl. 4, fig. 12.
1929 *Placunopsis radiata* Phillips; Arkell, p. 49, pl. 3, figs. 4, 5.
1982 *Placunopsis radiata* Phillips; Fürsich, p. 56. fig. 24 K, M.

Material. 1 specimen from Weymouth (LL41073), 4 specimens from Westbury (LL41381-2, ll41074), 1 specimen from Boulogne (LL41076).

Description. Small to medium sized shell, suborbicular or ovate to elliptical in outline, subequilateral, not auriculate. Sometimes a nearly straight hinge line occurs, but often no hinge line is seen. Umbone is placed just dorsally of the hinge line. Ornament of radial riblets or ribs, more or less irregularly spaced, spreading out from umbonal region, itself being smooth, sometimes interrupted by irregular growth-lines, which are imperfectly concentric.

Remarks. This species is moderately variably in outline and sculpture as also seen from the variaty of names given to it.

Range. Corallian to basal Portlandian of Europe. A very rare form in the Kimmeridgian occurring principally in the more shelly condensed intervals.

Autecology. A cemented low-level suspension feeder.

Suborder *Ostreina* Ferussac 1822
Superfamily *Ostreacea* Rafinesque 1815
Family *Gryphaeidae* Vyalow 1936

Genus ***Deltoideum*** Rollier 1917

Type species. Original designation Rollier 1917: 556: *Ostrea sowerbyana* Bronn, 1836: 316 (nom. subst. pro *O. deltoida* J. Sowerby 1816, non Lamarck, = *O. delta* Smith, 1817: 18: SD Arkell, 1932: 149).

Deltoideum delta (Smith 1817)
Plate 6 F, G.

1816 *Ostrea deltoidea* Lamarck; Sowerby, p. 111, pl. 98 (non Lamarck).
1817 *Ostrea delta* sp. nov. Smith, p. 18, Oak Tree Plate fig. 6.
1931 *Ostrea (Liostrea) delta* Smith; Arkell, p. 149, pl. 16, figs. 2-4, pl. 15, fig. 6, pl. 14, fig. 6.

Lectotype. Designated by Cox (1930): British Museum no 43357, figured by Sowerby (1816, pl. 98), Smith (1817, fig. 6).

Material. 2 specimens from Black Head (LL41040-1), 2 specimens from Westbury (LL41393, LL41042), 2 specimens from Ringstead Bay (LL41038-9).

Description. Very large flat shell, equivalve to subequivalve, very inequilateral, triangular to sickle-shaped. Left valve as flat as right valve, with low broad smooth irregular concentric undulations and few poorly adpressed growth squamae.

Attachment area ranges from small to very large, including the entire left valve. Right valve without radial elements. Ligamental area flat, rather high, pointed in posterior direction, resilifers of right and left valve very shallow excavated, in one specimen filled with ligamental residue; anterior burrelet slightly flatter and much longer than posterior one. A marginal ridge is running from the ligamental area along the posterodorsal margin of both right and left valve. Adductor muscle scar shallow, situated close to the posterodorsal margin, circular to slightly elongate or quadrate

Remarks. Arkell (1931:151 et seq.) has given a very good description and discussion of the species so that no further remarks are necessary.

PLATE 6

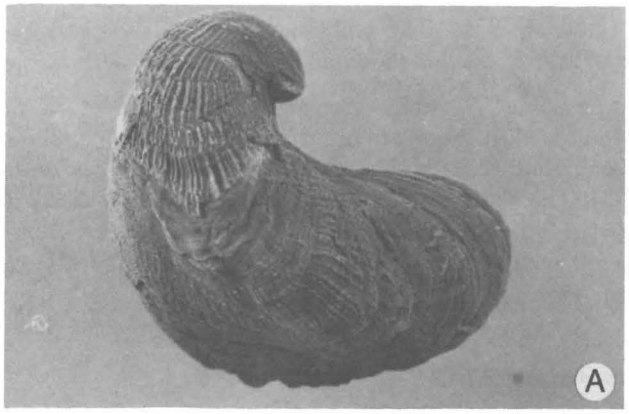
Nanogyra virgula Deshayes, 1831.
A. LL41388; left valve; × 2.5. Eudoxus Zone, Westbury.

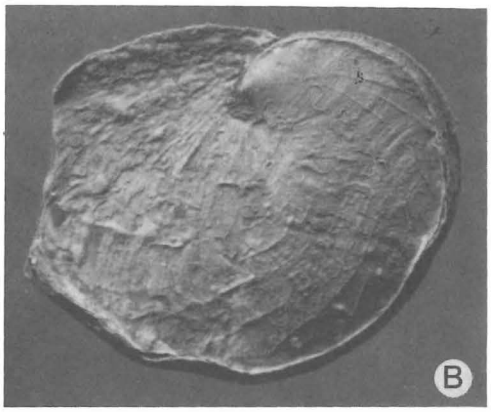
Nanogyra nana (J. Sowerby, 1822).
B. LL41389; right valve; × 4. Mutabilis Zone, Westbury.

Lopha (A.) gregarea (J. Sowerby, 1816).
C. LL41390; internal of left valve; × 1.6. Mutabilis Zone, Westbury.

Liostrea multiformis (Koch, 1837).
D. LL41391; right valve with xenomorphic ornament; × 0.7. Mutabilis Zone, Westbury.
E. LL41392; right valve; × 2.6. Mutabilis Zone, Westbury.

Deltoideum delta (Smith, 1817).
F, G. LL41393; right and left valve of bivalved specimen, left valve with *Nanogyra nana*; × 0.5. Mutabilis Zone, Westbury.

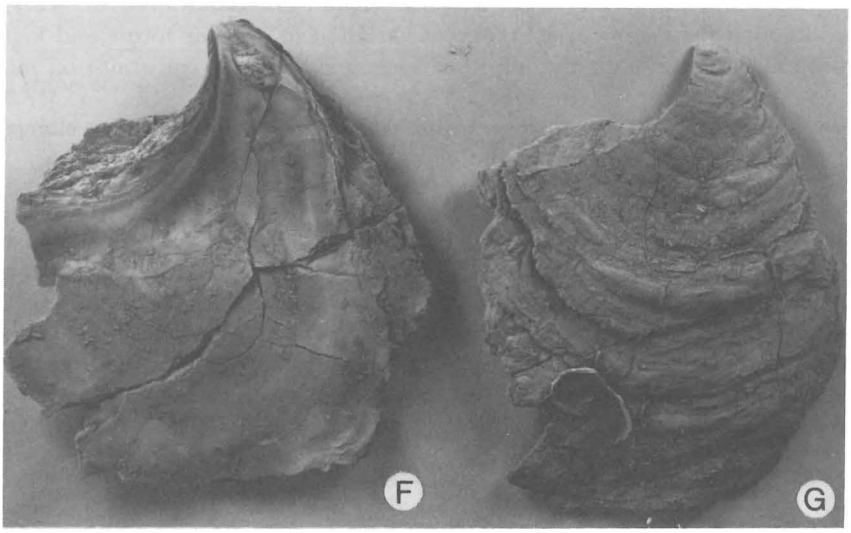

A


B


C


E


D


F
G

Range. Late Bajocian to Kimmeridgian of Europe (Hallam 1976). The highest occurrence is in bed M12 (Birkelund *et al.* 1983) of the mid-Mutabilis Zone.

Autecology. Seilacher *et al.* (1985) have suggested that *Deltoideum* is a mud-sticker based upon its spoon-shaped or sickle-shaped morphology. However this is not substantiated by their field occurrence where they commonly form pavements with specimens cemented on top of one another. It is thus more likely that they lay on the sediment as illustrated by Fürsich (1977, figs. 20 & 25). The sickle-shaped morphology probably reflects the internal morphology of a large pair of gills, with the broad form representing a "snow-shoe" strategy. *D. delta* is most abundant in offshore condensed mudstone facies, such as the base of the Baylei Zone at Black Head. It is a very rare form in the more nearshore Boulogne strata.

Genus *Liostrea* Douville 1904

Type species. Original designation Douville, 1904: 546: *Ostrea sublamellosa* Dunker 1846.

Liostrea multiformis (Koch 1837)
Plate 6 D, E.

1837 *Ostrea multiformis* sp. nov.; Koch et Dunker, p. 45, pl. 5, fig. 11 (*non* 116, g, i, l).
1860 *Ostrea plastica* sp. nov.; Trautschold, p. 339.
1871 *Ostrea bononiae* sp. nov.; Sauvage et Rigaux, p. 354.
1872 *Ostrea bononiae* Sauvage et Rigaux; p. 175, pl. 10, fig. 8.
1872 *Ostrea matronensis* sp. nov.; de Loriol *et al.*, pl. 23, figs. 5-7.
1872 *Ostrea multiformis* Koch: de Loriol *et al.*, pl. 23, figs. 16-20.
1875 *Ostrea bononiae* Sauvage; de Loriol & Pellat, pl. 23, fig. 9, pl. 24, fig. 16a, b.
1875 *Ostrea lineolata* sp. nov., de Loriol & Pellat, pl. 22, figs. 10a, b.
1875 *Ostrea multiformis* Koch, de Loriol & Pellat, pl. 24, figs. 6a, b, 7-10.
1936 *Ostrea bononiae* Sauvage; Spath p. 102, pl. 39, figs. 10-12, pl. 49, fig. 6a, b.
1968 *Ostrea bononiae* Sauvage and *O. multiformis* Koch; Cope, pl. 2, figs. 1, 2a.
1982 *Liostrea plastica* (Trautschold); Fürsich, p. 62, figs. 26 A, B, D.
1984 *Liostrea plastica* (Trautschold); Kelly, p. 52, pl. 7, figs. 17, 18, 20.
1987 *Liostrea* sp., Cox *et al.*, figs. 46, 47.

Material. 9 specimens from Westbury (LL41391-2, LL41061-66, LL41072), 5 specimens from Kimmeridge Bay (LL41067-71).

Description. Medium-sized to large *Liostrea*, very thin-shelled for the genus. Left valve is cemented for at least part of ontogeny and is nearly always shallow, right valve ranges from very flat to highly convex, almost bowl-shaped, xenomorphic ornament is commonly developed when attached to ammonites. Umbo well developed with maximum inflation occurring immediately dorsally of it. Ornament consists of irregular concentric folds of varying strength and very occasionally weak irregular thread-like radial grooves. Valves are commonly highly asymmetric although they show every range of variation to circular forms and highly elongate oval forms. When growing in nests the proximity of other oysters is the main constraint on morphology.

Internally the sub-umbonal cavity is weak to absent whilst the adductor muscle scar is elongate and feebly impressed. Ligament and hinge area are narrow and elongate anterodorsally.

Remarks. Oysters are notoriously variable in morphology and the specimens from the Kimmeridge Clay are no exception. Brannan (1983) has studied the pre-Kimmeridge oysters of the Jurassic and recognized only 2 species, *L. moreana* (Buvignier 1852) and *L. hisingeri* (Nilsson 1832), from the plethora of names available. Only *L. hisingeri* illustrates a similar range of morphologies to the Kimmeridge forms, however the left valve is typically deeper in these earlier forms. Two species names are currently recognized for thin-shelled oysters of the Kimmeridge Clay, *L. plastica* and *L. multiformis*. Cope (1968) has even assigned oysters in the same nest to both these species. Every range of morphology between these two forms can be found and there is no reason to suppose that they are distinct species, therefore the senior synonym, *L. multiformis*, is used.

Range. Found throughout the Kimmeridge Clay. Cox (1925, 1929) did not record this form from the Portlandian, although Kelly (1984) records similar forms from the ?Ryazanian (basal Cretaceous).

Autecology. Principally a cemented low-level filter-feeder. The wide range of morphologies indicates a great degree of variation on this theme. Broad flat forms may have been adapting the "show-shoe" principal for life on soft muddy substrates. The bowl-shaped forms may similarly have been recliners in soft muds. Nests are commonly formed, presumably nucleted on a shell fragment. Ammonites are also commonly encrusted by oysters. Cope (1968) has suggested that many ammonites, in the Kimmeridge Clay, are encrusted on their undersurface only, probably reflecting a rheophobic tendency of the settling larvae. In this survey a total of 17 oyster-encrusted ammonites were collected of which 12 were encrusted on both sides, 4 were encrusted on the upper surface and only 1 specimen was found with oysters on the lower side only. Fürsich (1984: 62) also noted that most encrusted ammonites from Greenland had oysters on both sides. It is therefore seems probable that most encrusted ammonites were colonized whilst they were still floating in the water column.

Tribe ***Exogyrina*** Vyalov 1936

Genus ***Nanogyra*** Beurlen 1958

Type Genus. Designated by Beurlen, 1958: 206: *Gryphaea nana* J. Sowerby 1822, v. 4, p. 114.

Nanogyra nana (J. Sowerby 1822)

1822 *Gryphaea nana* sp. nov. J. Sowerby, vol. 4, p. 114, pl. 383.
1932 *Exogyra nana* (J. Sowerby), Arkell, p. 175, pl. 17, figs. 2-21, pl. 18, figs. 3-11, pl. 19, figs. 4, 4a.
1978 *Nanogyra nana* J. Sowerby; Duff, p. 84, pl. 9, figs. 2-5.
1982 *Nanogyra nana* J. Sowerby; Fürsich, p. 65.

Lectotype. Designated Arkell 1932: 180: J. Sowerby 1822, pl. 383 (left figure): British Museum 43340c. Kimmeridge Clay, Dorset, England.

Material. 7 specimens from Black Head (LL41044-50), 1 specimen from Westbury (LL41389).

Description. Right valve flat, left valve globular to moderately convex. Outline suborbicular or subtrigonal, elliptical, ovate to comma-shaped, all specimens spirally twisted. Left valve bilobate in some individuals; spiral groove ending in sinus at valve margin located dorsally of branchitellum. Spiral beak of left valve coils tightly over ligamental area. Muscle scar located about halfway between anterior and posterior margin. Quensted muscle scar not visible.

Remarks. This species has been studied in great detail, the best description of the type species and excellent synonymy were given by Arkell (1932: 175-180).

Range. Bajocian to Portlandian (Arkell 1932). Only common in the Baylei to lower Mutabilis Zones of the Kimmeridge Clay of England. More common in the Boulogne section, particularly in the Argiles du Wimereux.

Autecology. Most exemplers of *N. nana* have a large attachment area and so were presumably cemented throughout their life, however, some specimens have a very small attachment area and so were probably reclining forms (Fürsich and Oschmann 1986: 72). The abundance of *N. nana* tends to correlate inversely with *N. virgula* suggesting some competitive exclusion.

Nanogyra virgula Deshayes 1831
Plate 6 A.

(nom conserv. pro *striata* Smith, 1817 and *angusta* Lamarck, 1819 by ICZN opinion 310, 1954).

1817 *Chama striata* sp. nov.: Smith, p. 45.
1819 *Gryphaea angusta* sp. nov.; Lamarck, p. 200.
1821 *Gryphaea virgula* sp. nov.; Defrance, p. 26 (nomen nudum)
1831 *Gryphaea virgula* sp. nov.; Deshayes, p. 90, pl. 5, figs. 12, 13.
1986 *Nanogyra virgula* (Defrance), Fürsich and Oschmann, figs. 2 & 6.

Material. 1 specimen from Weymouth (LL41056), 4 specimens from Kimmeridge Bay (LL41052-5), 4 specimens from Boulogne (LL41057-9), 2 specimens from Westbury (LL41388, LL41060), 1 specimen from Ringstead Bay (LL41051).

Description. Shell small, greatly variable in outline, inequivalve. The main difference from *Nanogyra nana* are the radial ribs on the left valve, the right valve, the right valve often shows short, marginal "riblets". Also, the attachment area of *N. virgula* is smaller (Fürsich and Oschmann 1986).

Remarks. The name *Nanogyra virgula* was given priority to *N. striata* by the ICZN Opinion 310 (Hemming 1954). *Gryphaea angusta* was not illustrated and so is considered a *nomen nudum*.

Ziegler (1969) records both *N. nana* and *N. virgula* from the Upper Baylei Zone. However these transitional forms appear to be true *N. virgula*.

Range. First appears in the upper Baylei Zone, it becomes exceedingly abundant in the Mutabilis and Eudoxus Zones. The last recorded example is found in the basal Hudlestoni Zone of Kimmeridge, it disappears at a similar level in the Boulogne section. It would appear that this represents the true extinction of the species as suitable facies, higher up the succession, are devoid of this form.

Family *Ostreida* Rafinesque 1815
Subfamily *Lophinae* Vyalov 1936

Genus ***Lopha*** Röding 1978

Type species. Original designation Röding 1978: 168:*Mytilus crtistagalli* Linne 1758: 704, SD Dall, 1898: 672.

Subgenus ***Actinostreon*** Bayle 1878

Type species. Original designation Bayle 1878, explanation to pls 132, 143: *Ostrea solitaria* J. Sowerby, 1824, v. 5, p. 105, pl. 468, rit. 1. 1. SD Douville, 1879.

Lopha (Actinostreon) gregarea (J. Sowerby 1816)
Plate 6 C.

1816 *Ostrea gregarea* sp. nov. Sowerby, p. 19, pl. 61, figs. 1, 3.
1933 *Lopha gregarea* J. Sowerby; Arkill, p. 183, pl. 22, figs. 5, 6, pl. 23, figs. 1-4.

Material. 1 specimen from Black Head (LL41043), 1 specimen from Westbury (LL41390).

Description. Medium-sized *Lopha*, subequivalve except for attachment surface near the umbo of left valve. Triangular-cresentic in outline but very variable. Attachment area mostly large. The ribs or plicae smooth, without hyote spines, with 30-40 interlocking zigzags, the tip of which are mostly acute-angled. Adductor muscle scar large, ovate in outline.

Remarks. Arkell (1933) has given a comprehensive discussion of the synonymy and no further description is needed.

Range. Aalenian to Tithonian according to Hallam (1976). A very rare form in the Kimmeridge Clay only occurring in the Baylei Zone at Black Head and the Pentacrinus bed at Westbury

Autecology. Occurs in nests, cemented together.

Subclass *Palaeoheterodonta* Newell 1965
Order *Trigonioida* Dall 1889
Superfamily *Trigonacea* Lamarck 1819
Family *Trigoniidae* Lamarck 1819

Type species. By ICZN Opinion 327 (1955) *Venus sulcata* Hermann, 1781, pl. 4, fig. 9.

Subgenus ***Trigonia*** s.s.

Trigonia (Trigonia) papillata Agassiz 1840
Plate 7 C.

1840 *Trigonia papillata* sp. nov. Agassiz, p. 39, pl. 5, figs. 10-14.
1872 *Trigonia papillata* Agassiz; de Loriol, p. 304, pl. 6, fig. 27.

1872 *Trigonia papillata* Agassiz; Lennier, p. 94.
1874 *Trigonia papillata* Agassiz; Brauns, p. 315.

Material. 1 specimen from Westbury (LL41394).

Holotype. Designated by Arkell 1928: 28: figured by Agassiz 1840, pl. 5, figs. 10-12.

Description. Small rostrate *Trigonia*, triangular in outline, well inflated, equivalve, inequilateral; umbones situated within anterior third of shell. Flanks of shell with around 17 rows of strong commarginal, very regular ribs, bending sinuously in the anterior part of shell. Marginal carina strong, ridge-like, topped at regular intervals by rib-like varices, much denser than ribbing on flanks of shell. Median carina and escutcheon carina ornamented by rows of small tubercles in growth direction, space in between with 6 small radial rows of tubercles. Dentition and muscle scars not seen.

Remarks. This may be a junior synonym of *T. recticulata* Agassiz 1840 (see Arkell 1928: 81 2et seg.) although the trigonids in general still require further work, in order to determine their phylogeny.

Range. Corallian to Early Kimmeridgian. Fairly common in the Boulogne section. Only found in the Pentacrinus bed (mid Mutabilis Zone) at Westbury.

Subclass	*Heterodonta* Neumayer 1884
Order	*Veneroida* H. Adams & A. Adams 1856
Superfamily	*Crassatellacea* Ferussac 1822
Family	*Astartidae* d'Orbigny 1844
Subfamily	*Astartinae* d'Orbigny 1844

Genus ***Neocrassina*** Fischer, 1866

(nom. subst. pro *Crassinella* Bayle 1878, *non* Guppy 1874).

Type species. Subsequent designation Dall 1903: 1487: *Astarte oblique* Deshayes, 1830: 80 (= *Cypricardia obliqua* Lamarck 1819).

Subgenus ***Neocrassina*** s.s.

Neocrassina (Neocrassina) ovata (Smith 1816)
Plate 7 A, B.

1816 *Venus* sp.: Smith, fig. 8.
1817 *Astarte ovata* sp. nov.; Smith, p. 44, 52, 205.
1932 *Astarte ovata* Smith; Arkell, p. 231, pl. 32, figs. 1-12.
1945 *Astarte (Neocrassina) ovata* Smith; Chavan, p. 56, text-figs. 6, 7.

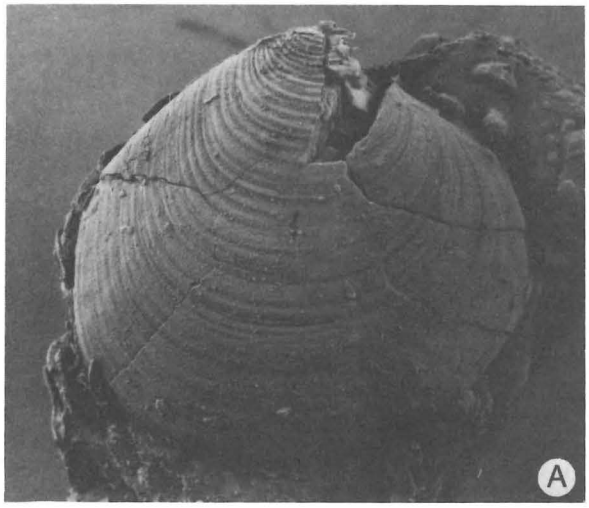
Lectotype. Designated by Cox 1930: 298: figured by W. Smith, Oak tree plate, fig. 8.

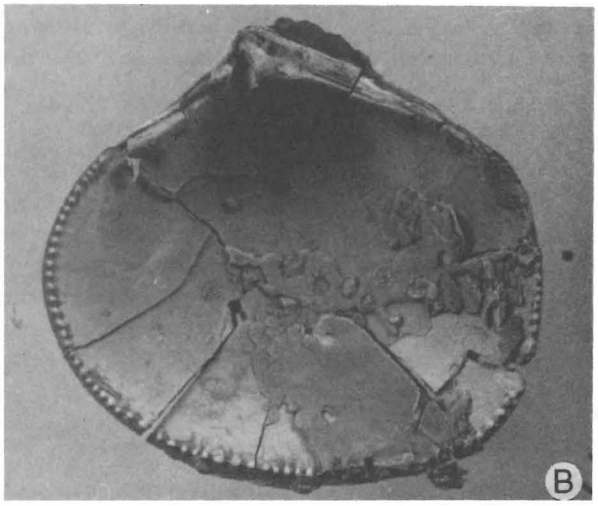
Material. 2 specimens from Westbury (LL41028, 41395).

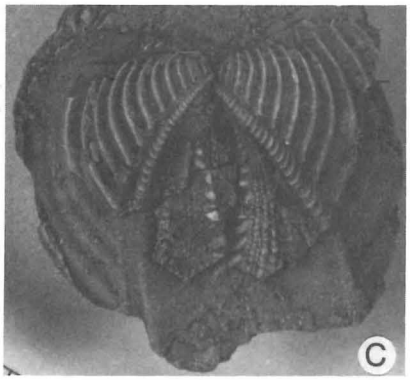
Description. Medium-sized species, inequilateral, ovate to subquadrate in outline, with length greater than height. Anterodorsal margin almost straight to slightly concave, curving smoothly into continuously rounded anterior and ventral margins; posterodorsal margin gently convex. Umbones small, prosogyrate, variably produced, placed anterior about one third of shell length. Inflation low. Lunule elongate, small and shallow, lanceolate in outline; escutcheon elongate, lanceolate, reaching almost to posterodorsal angle, obliquely flattened and external. Cardinal plate heavy and wide, cardinal teeth elongate and subtrigonal, not parallel. Adductor scars placed immediately beneath ends of cardinal plate, subequal. Margin denticulate.

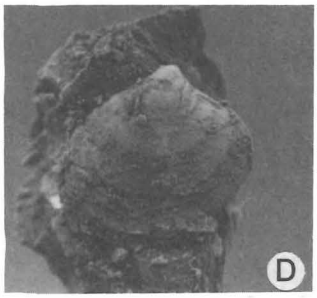
Remarks. Arkell (1934) gives a complete synonymy list and notes that this species shows a wide range of variation in tumidity and shape, and in prominence of the umbo. It seems to be a subquadrate form which dominates in the Kimmeridge Clay.

Range. Corallian to Early Kimmeridgian (Arkell 1932: 235). Last recorded in the lower Eudoxus Zone at Westbury. Not recorded from the nearshore deposits of Boulogne.

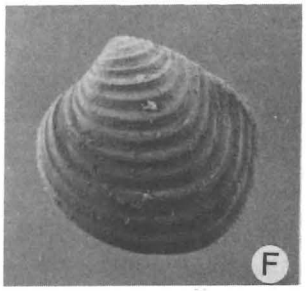

A


B

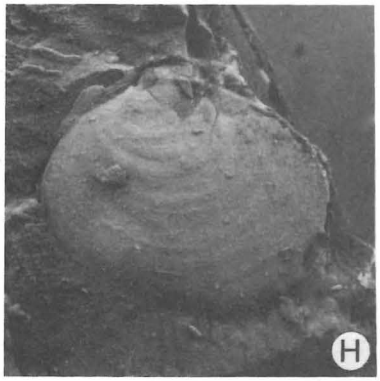

C

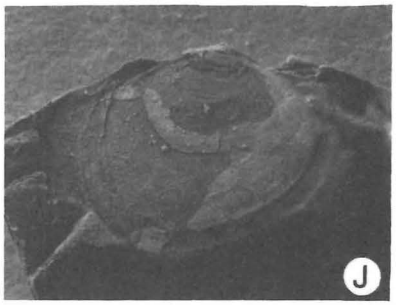

D

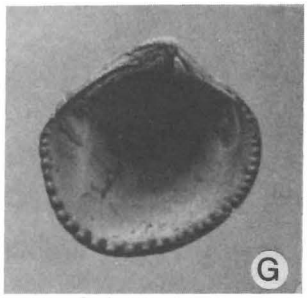

E

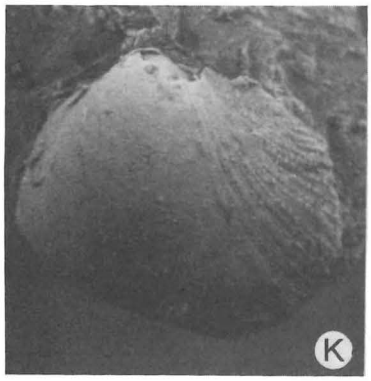

F

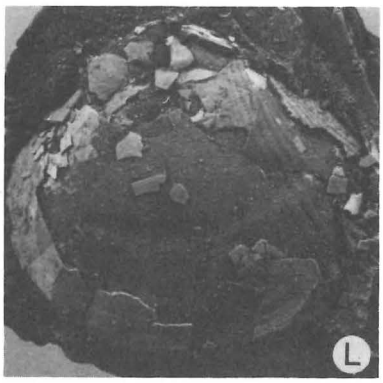

I

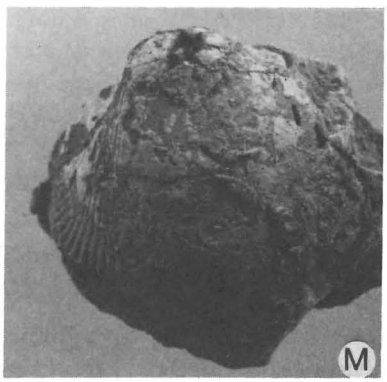

H


J


G


K


L


M

Autecology. A shallow infaunal filter feeder. Fürsich (1982: 73) has suggested a semi-infaunal mode of life for some astartids based on the occurrence of encrustation of the posterior portion of the shell. However, it is possible that the encrustation occurred after death with the winning and partial exhumation of the shell. It is a common form in coarse and medium grained facies in the Corallian (Arkell 1932: 235), however by the Early Kimmeridgian it appears to have been ousted from this habitat as it is only found in offshore mudstones and not in the nearshore Boulogne section.

Genus ***Nicaniella*** Chavan 1945

Type species. Original designation Chavan 1945: 43: *Astarte communis* Zittel & Goubert, 1861.

Subgenus ***Nicaniella*** s.s.

Nicaniella (Nicaniella) extensa Phillips 1829

Plate 7 D-G.

1829 *Crassina extensa* sp. nov.: Phillips, pl. 3, fig. 21.
1837 *Astarte minima* Phillips; Goldfuss, p. 192, pl. 134, fig. 15 (*non* Phillips).
1847 *Astarte supracorallina* sp. nov.: d'Orbigny.
1850 *Astarte supracorallina* d'Orbigny; d'Orbigny, p. 15.
1850 *Astarte mysis* sp. nov.: d'Orbigny, vol. 2, p. 50 (fig. d 1932 Boule, pl. 65, figs. 13, 14, 21).
1852 *Astarte supracorallina* d'Orbigny; Buvignier, pl. 20, figs. 47, 48.
1875 *Astarte supracorallina* d'Orbigny; de Loriol & Pellat, p. 87, pl. 15, fig. 15.
1875 *Astarte mysis* d'Orbigny; de Loriol & Pellat, p. 98, pl. 15, fig. 36a, b.
1932 *Astarte extensa* (Phillips); Arkell, p. 237, pl. 34, figs. 21-30.
1985 *Nicaniella extensa* (Phillips); Oschmann, pl. 3, fig. 5.

Neotype. In the Sedgwick Museum, Cambridge (Arkell 1932: 240).

Material. 17 specimens from Westbury (LL41029-37, 41396, 41398), 4 specimens from Kimmeridge Bay (LL41025-7, 41397).

PLATE 7

Trigonia (T.) papillata Agassiz, 1840.
C. LL41394; bivalved specimen; × 1.7. Mutabilis Zone, Westbury.

Neocrassina (N,) ovata (Smith, 1816).
A, B. LL41395; external and internal of the same specimen, right valve; × 3.6. Mutabilis Zone, Westbury.

Nicaniella (N.) extensa Phillips, 1829.
D. LL41396; poorly ornamentet right valve;; × 10. Mutabilis Zone, Westbury.
E. LL41397; right valve; × 5.5. Scitulus Zone, Kimmeridge Bay, Dorset.
F, G. LL41398; external and internal of the same specimen, left valve; × 3.6. Mutabilis Zone, Westbury.

Crassatellacea bivalve A.
H. LL41399; bivalved specimen; × 5.5. Mutabilis Zone, Westbury.
I. LL41400; internal of left valve; × 9. Mutabilis Zone, Westbury.
J. LL41401; right valve; × 3.4. Mutabilis Zone, Westbury.

Protocardia (P.) morinica (J. de C. Sowerby, 1929).
K. LL41402; left valve; × 7.5. Mutabilis Zone, Westbury.
L. LL41403; left valve; × 2.3. Eudoxus Zone, Westbury.
M. LL41404; right valve; × 2.3. Eudoxus Zone, Westbury.

Description. Shell small to medium-sized, moderately inflated, inequilateral, suborbicular to subquadrate in outline, with length slightly greater than height. A broad but weak umbonal ridge tends to develope between umbone and posteroventral angle. Umbones placed slightly anterior of median, prominent, prosogyrate, slightly salient. Ligamental nymph short but well defined. Lunule well developed, concave; escutcheon smaller and lanceolate, bounded by a sharp carina, extending to posterodorsal angle; lunule and escutcheon with fine growth striae.

Ornament of shell consisting of 12-15 regularly spaced commarginal ribs, with faint concentric intercostal threads, space between ribs is usually about three times as wide as the ribs themselves. Margin denticulate, denticulation extending to ends of lateral teeth. Adductor muscle scars subequal; pallial line entire.

Remarks. This is a highly variable astartid and as a consequence the taxonomy has become particularly complex (Blake 1875, Birkelund *et al.* 1983: 303). *N. (N.) extensa* is a common form from the Corallian (Arkell 1932) and from the Upper Kimmeridge Clay (Oschmann 1985), however the abundant Lower Kimmeridge *Nicaniella* have been attributed to *N. (N.) supracorallina*. The Supracorallina bed has been named for a horizon in the upper Mutabilis Zone where the species is particularly common (Bed 22 of Gallois & Cox, 1976). The disjunct distribution of *N. (N.) extensa* has more to do with the taxonomy of the species than any interspecific competition.

Goldfuss (1837) illustrated this species under the name *Astarte minima* Phillips 1829, however this is a different species from the Great Oolite. d'Orbigny (1847) described *A. supracorallina* from the Lower Kimmeridge and included the specimen incorrectly called *A. minima* by Goldfuss (1837) in the type collection. However, it would appear that the specimen described as *Crassina extensa* by Phillips (1829) is the same species as the forms found throughout much of the Lower Kimmeridge Clay, although it was poorly figured.

Arkell (1932) also thought that the astartids of the the Lower Kimmeridge were attributable to *N. (N.) extensa* (although in Arkell (1947) he still uses the name *A. supracorallina*). Some Lower Kimmeridge forms from Cambridgeshire and Lincolnshire were thought to be *A. mysis* (Arkell 1932), however this is probably also a junior synonym of *N. (N.) extensa*. *A. multiformis* Roeder may also be a synonym (see Arkell 1932: 239).

Range. Corallian to Late Kimmeridgian. It is particularly common in the upper Mutabilis Zone but is also found in great numbers in the upper Elegans and lower Scitulus Zones. Last appearance is in the upper Pectinatus Zone, above this it appears to be replaced by *N. (N.) cuneata* (J. Sowerby 1816), a form with more broadly spaced ribs. In the shallow-water Boulogne sediments *N. (N.) extensa* appears to be replaced earlier as it is absent from the Argilles de la Crèche, in which *N. (N.) cuneata* is abundant.

Autecology. A shallow infaunal filter-feeder, the truncated posterior margin indicating a close proximity to the sediment surface. The ribs are markedly asymmetrical and so were probably an aid in burrowing (Stanley 1975). A highly eurytopic form able to survive the low oxygen regimes of the Upper Kimmeridge Clay. In bed E5 of the lower Eudoxus Zone (Birkelund *et al.* 1983) a virtually smooth variant occurs (still recognizable by its dentition, denticulate margin and outline). This loss of ornament may reflect an adaptation to lowered salinities (Sanders *et al.* 1965, Remane 1971), however this is not indicated by the isotopic evidence (Salinas pers. comm. 1985).

Crassatellacea bivalve A.
Plate 7 H-J.

Material. 5 specimens from Weymouth (LL41015-19), 4 specimens from Kimmeridge (LL41021-4), 3 specimens from Westbury (LL41399-401).

Description. Shell small, equivalve, inequilateral, suboval to oval in outline, very thin-shelled. Anterior margin evenly rounded, ventral margin straight to gently convex; posteroventral angle rounded, posterior margin longer than anterior margin, straight to gently convex; dorsal margin straight to gently convex. Inflation very low. Umbones very small, prosogyrate. Ornament of faint commarginal growth lines, occasionally fairly prominent during early stages of ontogeny.

Dentition heterodont. In left valve a large socket is seen, corresponding to a trigonal cardinal in right valve, there is a prominent posterior lateral, above which the shell margin of right valve may have fitted, and a prominent shell ridge just anterior of umbo.

Remarks. We have not been able to assign this species to any genus or family but it seems reasonable to assume that it belongs to the superfamily Crassatellacea. *Astarte salfeldi* Cox 1925 is a similar form, although it is not conspecific. The possibility exists that this is an, as yet undescribed, taxon of Upper Jurassic astartids, although more material needs to be examined to test this hypothesis.

Range. Throughout the Kimmeridge Clay.

Autecology. A moderately shallow infaunal filter-feeder. Although this form is never common it occurs most frequently in the more normally oxygenated mudstone facies at the base and top of the Kimmeridge Clay. Not found in the coarser grained facies of the Boulogne sections.

Superfamily *Cardiacea* Lamarck 1809
Family *Cardiidae* Lamarck 1809
Subfamily Cardiinae Keen 1951

Genus ***Protocardua*** von Beyrich, 1845

Type species. Subsequent designation by Herrmansen 1847: 336: *Cardium hillanum* J. Sowerby 1813: 41, pl. 14, upper fig.

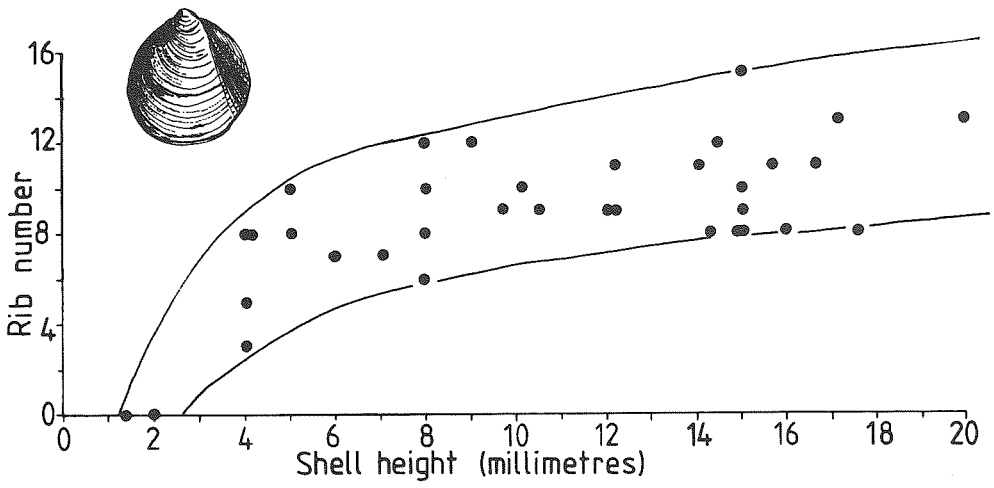
Subgenus ***Protocardia*** s.s.

Protocardia (Protocardia) morinica (J. de C. Sowerby 1829)
Plate 7 K-M, text-fig. 6.

1872 *Cardium morinicum* sp. nov.; de Loriol *et al.*, pl. 14, figs. 9, 9a, 10, 10a.

Material. 1 specimens from Weymouth (LL41007), 4 specimens from Westbury (LL41008, 41402-4), 2 specimens from Kimmeridge Bay (LL41009-10), 4 specimens from the Boulonnais (LL41011-4).

Description. Shell medium-sized (the largest specimen being 2.5 cm tall) equivalve, subcircular in outline, nearly as high as long. Hinge margin slightly reflexed. No umbonal carina, posterior area being delimited solely by ornament pattern. Umbones large, slightly prosogyrate. Ligament external, parivincular, very short, no lunule or escutcheon. Ornament of up to 15 radial riblets on posterior part of shell. occupying the area between posterior margin and posterior part of umbo. Riblet addition is independent of shell size above 4 mm in height (Text-fig. 6). Remainder of shell solely with fine commarginal growth lines. Inflation low to high. Margin entire except for crenulation where radial riblets reach shell margin. Posterior adductor muscle scar subcircular, anterior not seen, pallial line seemingly entire.



Text-fig. 6. Rate of rib addition in *Protocardia morinica*. Above 4 mm height, rib addition is shown.

Remarks. A large number of names are available for Upper Jurassic protocardids. This is a reflection of a moderate degree of evolutionary turnover, a high degree of provincialism and some degree of synonymysing. This last factor is particularly the case for the Callovian-Oxfordian form, *P. (P.) striatula* (J. de C. Sowerby 1829), see Duff (1978: 102). This form differs from *P. (P.) morinica* in being more quadrate in outline and possessing fine radial striae posterior of the radial riblets, a feature clearly seen in the holotype (NHM, LL43154). Apparently *P. (P.) striatula* persisted in the northern Boreal Kimmeridge of Greenland (Fürsich 1982) whilst new forms took its place further south. *P. (P.) intexta* (Munster 1837) is a coeval Kimmeridge form from the Haute Marne, which posesses more numerous but finer radial ribs than *P. (P.) morinica.*

Range. First appears in the marly clay immediately below the Baylei Zone at Black Head and ranges through to the upper Rotunda Zone. It similarly ranges throughout the Kimmeridge section at Boulogne. It is particularly common as phosphatic steinkerns in the phosphatic nodule horizons in this section. As noted by Pruvust (pers. comm. in Dutertre 1926: 400) these steinkerns are readily mistaken for examples of *Buchia.*

Autecology. A shallow infaunal filter-feeder. Between the Mutabilis and Hudlestoni Zones this is consistently one of the most abundant bivalves. It was clearly able to tolerate very low oxygen-levels as it commonly occurs in highly organic-rich shales totally devoid of other forms of benthic life. Its occurrence in swarm abundances on many bedding planes forming shell pavements indicates an opportunistic life strategy (Myers & Wignall 1987).

Specimens in mudstones tend to show much lower inflation than those in coarser-grained sediments; to some extent this reflects different amounts of compaction, however it may also reflect a genuine ecophenotypic response to different environmental conditions.

Superfamily *Articacea* Newton 1891
Family *Arcticidae* Newton 1891

Genus ***Isocyprina*** Roeder 1882

Type species. Subsequent designation Cossmann, 1921: *Cardium cyreniforme* Buvignier 1852.

Genus ***Isocyprina*** s.s.

Isocyprina (Isocyprina) cf. ***roederi*** Arkell 1932
Plate 8 A.

non *Cuprina cyreniformis* (Buvignier 1852); Roeder 1882, p. 92, pl. 2, fig. 5 a & b, pl. 4, figs. 1 a & b.
?1897 *Isocyprina cyreniformis* Buvignier; de Loriol p. 83, pl. 12, fig. 17.
?1901 *Isocyprina cyreniformis* Buvignier; de Loriol p. 59, pl. 4, figs. 7-9.
?1932 *Isocyprina roederi* nom. nov.; Arkell, p. 263; pl. 35, fig. 21.

Holotype. Refigured by Arkell, 1932: 35, fig. 21. Figured by Roeder 1882 Pl. 2, fig. 5b from Chailles, Pfirt, France.

Material. 1 specimen from Weymouth (LL40987), 5 specimens from Westbury (LL40988-91, 41405).

Description. Shell small, equivalve, suborbicular to ovate in outline. Inflation very low. Umbones placed slightly anterior of median of shell, small, prosogyrate, no salient. Ornament consisting of very fine commarginal growth lines. Ligament interval.

Dentition of left valve. All long, prominent, terminating near 2b, which is chevron-shaped with $2b_1$ longer than $2b_2$. 4a is rather long and slender. PII as a ridge, only weakly developed. 2a not seen. Dentition of right valve not seen. Margin entire, musculature not seen.

Remarks. This species has not been recorded from the Kimmeridge Clay previously. The dentition of *I. roederi* has been discussed by Casey (1952).

Range. Oxfordian to Early Kimmeridgian of England and France.

Last appearance in the Lower *Eudoxus* Zone of Westbury.

Subgenus ***Venericyprina*** Casey 1952

Type species. *Isocyprina (Venericyprina) argillacea* Casey 1952, pl. 8, figs, 8, 9, pl. 9, figs. 5, 6, text-fig. 14, 27, 28, 63, 64 (Kimmeridgian).

Remarks. It seems, from the material found in Westbury, that the rostrate shell should not be included as a subgeneric character.

Isocyprina (Venericyprina) argillacea Casey 1952
Plate 8 B-D.

1952 *Isocyprina (V.) argillacea* sp. nov.: Casey, p. 137, pl. 8, figs, 8, 9, pl. 9, figs. 5, 6, text-figs. 14, 27, 28, 63, 64.

Holotype. Geological Survey Museum, London, no. 27841.

Material. 5 specimens from Westbury (LL40990, 41406-8), 2 specimens from the Boulonnais (LL40991-2).

Description. Shell medium-sized to large, equivalve, inequilateral, ovate in outline. Inflation moderate. Umbones prosogyrate, broadly rounded with a small ridge running to posteroventral angle. Beaks small, placed anteriorly about one-third of shell length. Shell smooth with commarginal growth-lines.

Dentition of left valve: AII fairly short, with striations, getting parallel with 2a, which is wedge-shaped and ends dorsally of $2b_1$. 2b chevron-shaped, $2b_1$ twice as long as $2b_2$. 4b strongly ophisthocline. PII as thickening of hinge plate.

Dentition of right valve: AI fairly short, colaminar with 1; 1 is longer than 2a, AIII parallel to AI but smaller, continuing into 3a which is thin, wedge-shaped, high. 3b with a slight groove, strongly ophisthocline, slender, rectangular. PI very long but with overgrowth from dorsal margin about one-third from umbo. Muscle scars triangular to ovate, subequal. Pallial line with short, angular sinus.

Remarks. This species is fairly common in the English Kimmeridgian as also noted by Casey (1952). This species differs externally from *I. (V.) implicata* by being less inflated in the umbonal region and by its straighter anterodorsal margin.

Range. The Early Kimmeridgian of England and France, particularly in the Schiste de Chatillon at Cap Gris Nez.

Autecology. A moderately-deep infaunal filter-feeder.

Isocyprina (Venericyprina) implicata (de Loriol 1875)
Plate 8 E-G.

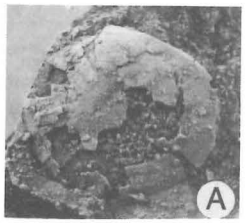
1875 *Cyprina implicata* sp. nov.; de Loriol, p. 43, pl. 13, figs. 10, 11.
1880 *Cyprina elongata* sp. nov.; Blake, p. 232, pl. 9, figs 14, 14a.
1925 *Venilicardia subquadrata* sp. nov.; Cox, p. 145, pl. 4, figs. 1a, 1b.
1929 *Eocallista implicata* (de Loriol); Cox, p. 186.
1929 *Eocallista implicata* var. *elongata* (Blake); Cox, p. 187.

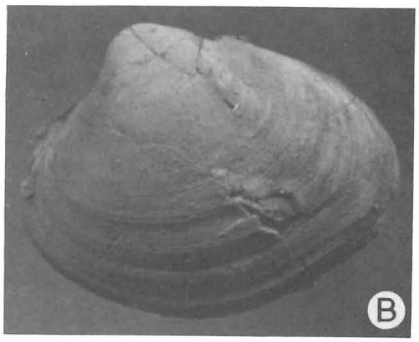
Material. 2 specimens from Chapmans Pool, East of Kimmeridge (LL40995-6), 2 specimens from Wimereux, north of Boulogne (LL40993-4), 3 specimens from Westbury (LL41409-11).

Description. Shell medium-sized to large, equivalve, inequilateral, rectangular-ovate in outline, not prostrate, moderately inflated height, slightly smaller than length. Umbones prominent, broadly rounded, prosogyrate, mesial or slightly anterior to median. Beaks minute, not salient.

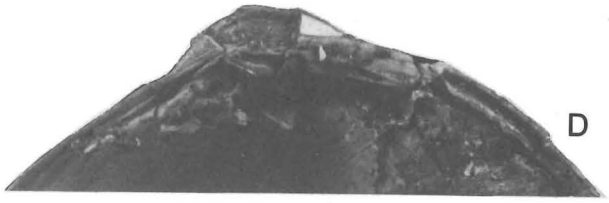
Dentition of left valve: AII fairly short, with striations, colaminar with 2a, which is weakly defined. 2b chevron-shaped, $2b_1$ around three times as long as $2b_2$, 4b strongly ophisthocline. PII as thickening of hinge plate.

Dentition of right valve: AI fairly short, 1 rather long, prominent. AIII smaller than AI, continuating into 3a with a z-structure, 3b triangular, with groove. PII long, with striations. Muscle scars ovate, subequal, pallial line entire.

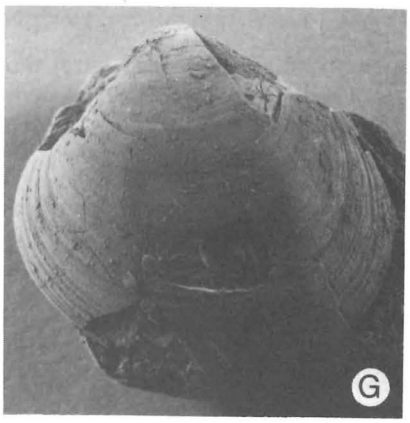

A


B

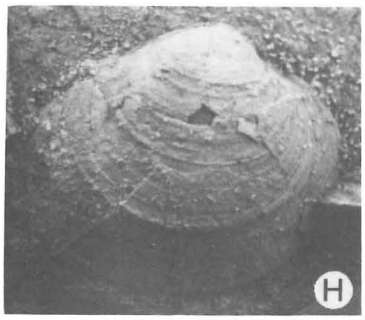

C


D

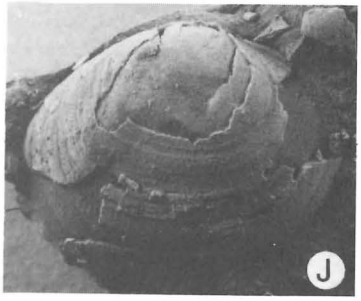

E


G

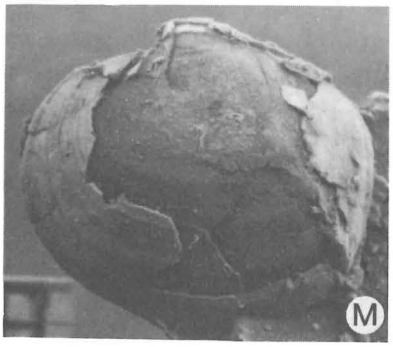

F

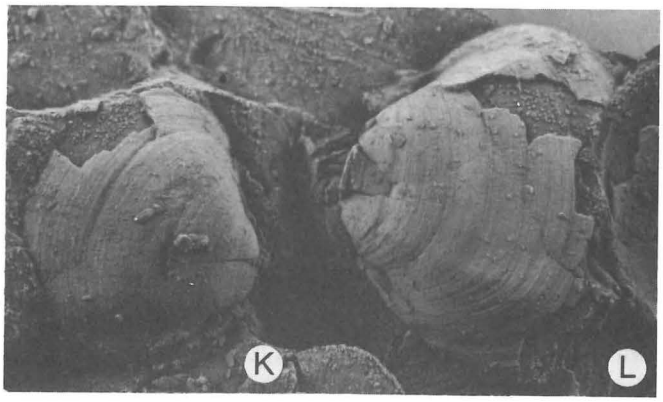

H


I


J


N


M


K
L

Remarks. This species is a very close ally of *I. (V.) argillacea* but differs in being more rectangular in outline, not rostrate. In left valve 2a is colaminar with $2b_1$ (in *argillacea* 2a ends dorsally of $2b_1$), in right valve there is a z-structure between AIII and 3a, and 3b being broader, more triangular. Furthermore there is no pallial sinus.

This species shows a great degree of external variation particularly with regard to elongation (see Cox 1925, 1929), the shape of the anterior margin which may be quite pointed and in the shape of the posterior margin which may be quite elongate.

Range. First appears in the Baylei Zone of Black Head and ranges throughout the Kimmeridge Clay into the Portlandian although it is absent from the organic-rich facies in the center of the formation. Found in the Calcaire du Moulin Wibert and the Argilles de Wimereux of Boulogne.

Autecology. A shallow infaunal filter-feeder, the fairly pointed anterior margin presumably helped in penetrating during burrowing (Stanley 1975). Appears to have preferred siltstones rather than mudstones as it reaches the peak of its abundance in the silty Fittoni Zone at the top of the Kimmeridge Clay.

Isocyprina (Venericyprina) minuscula (Blake 1875)
Plate 8 H-J, text-fig. 7.

1875 *Lucina minuscula* sp. nov.; Blake, p. 227, pl. 12, fig. 8.
1960 *Lucina minuscula* Blake; Chatwin, fig. 10.9
1985 *"Lucina" minuscula* Blake; Oschmann, pl. 3, fig. 6.
1987 *"Lucina" minuscula* Blake; Cox *et al.*, fig. 4C.

Type specimen. The holotype was not presented to the NHM; along with the rest of Blake's collection in January 1907 and must therefore be considered lost. Neotype designated here Plate 8 H (LL41412).

Material. 12 specimens from Westbury (LL40972-82, 41413), 5 specimens from Kimmeridge (LL40983-6, 41412).

PLATE 8

Isocyprina (I.) cf. *roederi* Arkell, 1932.
A. LL41405; left valve; × 3.4; Mutabilis Zone, Westbury.

Isocyprina (V.) argillacea Casey, 1952.
B. LL41406; left valve; × 2.6. Mutabilis Zone, Westbury.
C. LL41407; hinge of left valve; × 5.3. Mutabilis Zone, Westbury.
D. LL41408; hinge of right valve; × 5.3. Mutabilis Zone, Westbury.

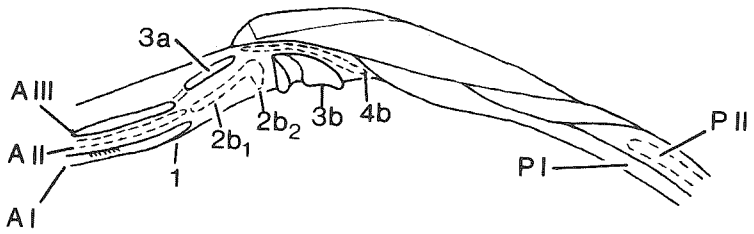
Isocyprina (V.) implicata (de Loriol, 1875).
E. LL41409; hinge of right valve; × 5.3. Mutabilis Zone, Westbury.
F. LL41410; hinge of left valve; × 5.3. Mutabilis Zone, Westbury.
G. LL41411; left valve; × 2.7. Mutabilis Zone, Westbury.

Isocyprina (V.) minuscula (Blake, 1875).
H. NHM41412; neotype; right valve; × 6. Autissiodorensis Zone, W. of Kimmeridge Bay.
I. LL41413; hinge of right valve; × 5.3. Mutabilis Zone, Westbury.
J. More ovated right valve; × 3.1. Mutabilis Zone, Westbury not preserved.

Isocyprina (V.) nordgreni nov. sp.
K. NHM41414; holotype; right valve; × 3.5. Mutabilis Zone, Westbury.
L. NHM41415; paratype; left valve; × 3.5. Mutabilis Zone, Westbury.

Isocyprina (V.) pellucida Casey, 1952.
M. LL41416; hinge of right valve; × 3.5. Mutabilis Zone, Westbury.
N. LL41417; left valve; × 5. Mutabilis Zone, Westbury.

Description. Medium-sized shell, ovate-elliptical in outline, low inflation. Anterior margin well rounded, slightly pointed, ventral margin evenly rounded, lowest point posterior of median, posterior of margin evenly rounded to very slightly truncated, posterodorsal margin straight to very gently convex, sloping. Ornament consists of numerous fine commarginal growth-lines.



Text-fig. 7. Dentition of *Isocyprina (V.) miniscula* (Blake, 1875). Note the strongly bifid 3b and the striations on AI. × 10.

Dentition of left valve: AII fairly short, 2a not clearly developed, 2b chevron-shaped, $2b_1$ about three times as long as $2b_2$, broad socket between $2b_2$ and 4b, which is strongly ophisthocline, long, with the dorsal end immediately below umbo in continuation with dorsal margin. PII as thickening of hinge plate (Text-fig. 7).

Dentition of right valve: AI shorter than AIII, being equally strongly developed, 1 columinar with AI, the thin 3a columinar with AIII, 3b chevron-shaped, divided in two, broad, triangular, PI long, prominent, but overgrown by hinge margin about one-third from umbo. AI and PI with striations in the middle of the teeth.

Pallial line entire. Muscle scars ovate, semiequal.

Remarks. This species shows a wide range of variation particularly in the length of the anterodorsal side and thus the position of the umbones and the degree of elongation. Blake (1875: 227) clearly wanted to attribute this species names to the ubiquitous shells which occur in the organic-rich shales of the middle part of the formation as he state that they occur, "in the Upper Kimmeridge in millions everywhere". However, curiously he figured a highly atypical form from the Lower Kimmeridge of Market Rasen which has umbones placed more anteriorly than usual and consequently has a longer posterodorsal margin.

This species is very close to *I. (V.) birkelundi* Fürsich (1982), but differs in being more elongate-ovate and in its dentition by having a bifid and very prominent 3b and by having striations on AI and PI. The possibility still exists, however, that *I. (V.) birkelundi* is a northern Boreal variant.

Autecology. A shallow infaunal filter feeder tolerant of low oxygen levels.

Isocyprina (Venericyprina) nordgreni sp. nov.
Plate 8 M, N, text-fig. 8.

Derivatio nominis. After Maria Nordgren.

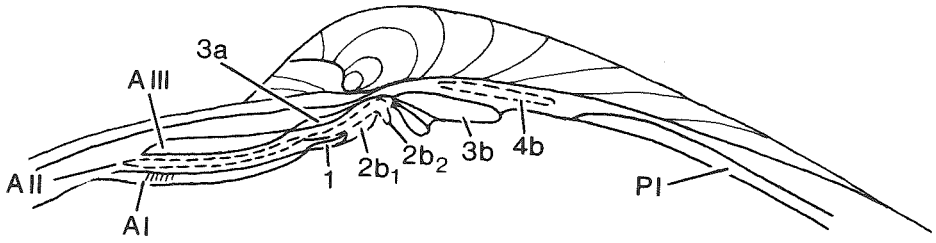
Diagnosis. Medium-sized *Isocyprina*, subquadrate to subrectangular in outline; detention with a long 3a coherent with 3b.

Holotype. Figured in Plate 8 M (LL41414), from the Mutabilis Zone in Westbury and paratype from the same horizon (LL41415).

Material. 3 specimens from Black Head (LL41004-6), 3 specimens from Westbury (LL41003, 41414-5).

Description. Medium-sized shell, inequilateral, subrectangular in outline. Anterior and ventral margins well rounded, posteroventral angle weakly defined, posterior margin straight to gently convex, posterodorsal margin straight, sloping. One obtuse ridge runs from umbo to anterior margin, another runs from umbo to posteroventral angle. Ornament of fine commarginal growth-lines.

Dentition of left valve (Text-fig. 8): AII fairly short, cross-striated, clearly separated from 2b, which is chevron-shaped. $2b_1$ is about 4-5 times as long as $2b_2$. 4b strongly ophisthocline, lying very close to hinge margin. PII not seen.



Text-fig. 8. Dentition of *Isocyprina (V.) nordgreni* nov. sp. Note the large 3b. × 10.

Dentition of right valve: AI striated, twice as long as AIII, 2a not developed, 3a very long, grown together with 3b, which is very large, clearly separated in two. PII not seen. Muscle scars not seen.

Remarks. This species differs from the other *Isocyprina* in being subquadrate in outline and in dentition by the long 3a grown together with 3b leaving a socket for the very small $2b_2$.

Range. Topmost Corallian of Black Head to the Virgula Limestone of the Lower Eudoxus Zone, Westbury.

Autecology. A shallow infaunal filter-feeder found only in offshore mudstones.

Isocyprina (Venericyprina) pellucida Casey 1952
Plate 8 K, L, text-fig. 9.

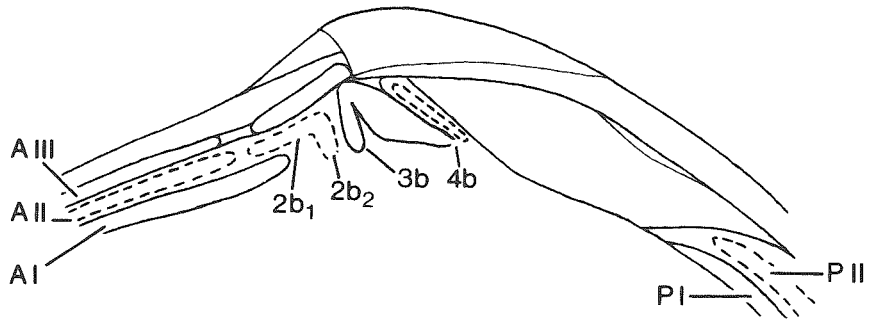
1875 *Cyprina cyreniformis* sp. nov. Blake, p. 227, pl. 12, fig. 6.
1907 *Cyprina cyreniformis* (?) Blake; Davies, p. 54, 44.
1952 *Isocyprina (V,) pellucida* nom. nov. Casey, p. 137.

Lectotype. British Museum (Nat.Hist.) LL20366, figured by Blake, pl. 112, fig. 6.

Material. 8 specimens from Westbury (LL40997-41002, 41416-7).

Description. Medium-sized shell, equivalve, inequilateral, subquadrate to subrectangular in outline. Anterodorsal and anterior margins rounded, ventral margin evenly convex, posteroventral angle obtuse, posterior margin straight to gently convex, posterodorsal angle rounded, posterodorsal margin gently convex. A well-defined carina runs from umbo to posteroventral angle. Umbones prominent, beaks small, not salient, placed anterior about one-third of shell length. Ornament solely of fine commarginal growth lines. Inflation moderate.

Dentition (Text-fig. 9) of right valve consisting of AI and AIII subparallel, of nearly equal length, 3a short, prominent, 3b consisting of one short tooth directed posteroventrally and one longer tooth subposteroventral to hinge margin, together chevron-shaped, PI long, parallel to margin. Dentition of left valve: AII long, thin, $2b_1$ as a continuation, with only a slight separation-groove, $2b_2$ nearly at a right angle to $2b_1$, shorter, 4b straight, clearly defined. PII long, not well defined. Muscle scars not seen.



Text-fig. 9. Dentition of *Isocyprina (V.) pellucida* Casey, 1952. × 10.

Remarks. Although Casey (1952) gave this species a new name he did not in any way figure or describe the hinge, but just stated that Blake's figure was unsatisfactory, and it is a junior homonym of *Cardium cyreniforme* Buvignier 1852. The variation in *I. (V.) pellucida* is mainly on the curvature of the posterior margin, some are nearly straight while others are more evenly convex.

I. pulchella (de Loriol 1875) is a closely related form from the Portlandian although it differs in having a convex posterior margin.

Range. Blake (1875) recorded this form abundantly in the basal Kimmeridge Clay. During this survey it was first recorded in the topmost Corallian, with its final occurrence in the middle Eudoxus Zone at the top of the Westbury pit. A possible example of *I. (V.) pellucida* was found in the Argiles du Wimereaux at the top of the Kimmeridge in Boulogne.

Autecology. A shallow infaunal filter-feeder, the flat posterior margin indicating its close proximity to the surface.

Order	*Myoida* Staliczka 1870
Suborder	*Myina* Stoliczka 1870
Superfamily	*Myacea* Lamarck 1809
Family	*Corbulidea* Lamarck 1818
Subfamily	*Corbulinae* Lamarck 1818

Genus ***Corbulomina*** Vokes 1945

Type species. Original designation: *Corbulomima nuciformis* Vokes, 1945: 10, pl. 2, figs. 5-8. Cretaceous.

Corbulomima suprajurensis (d'Orbigny 1850)
Plate 9 A, B, E, text-fig. 10.

1850 *Corbula suprajurensis* sp. nov. d'Orbigny, p. 50, no. 107.
1932 *Corbula suprajurensis* d'Orbigny; Cottreau, p. 190, pl. 65, fig. 9.
1952 *Corbulomima suprajurensis* d'Orbigny; Chavan, p. 122, pl. 4, figs. 72-75.
1985 *Corbulomima suprajurensis* (d'Orbigny); Oschmann, pl. 4, fig. 1.

PLATE 9

Corbulomima suprajurensis (d'Orbigny, 1850).
A, B. LL41418; exterior and interior of right valve; × 3.6. Mutabilis Zone, Westbury.
E; LL41419; bivalved specimen; × 5.5. Mutabilis Zone, Westbury.

Corbulomima westburyensis nov. sp.
C. NHM41420; holotype; right valve; × 5. Mutabilis Zone, Westbury.
D. NHM41421; paratype; left valve; × 5. Mutabilis Zone, Westbury.

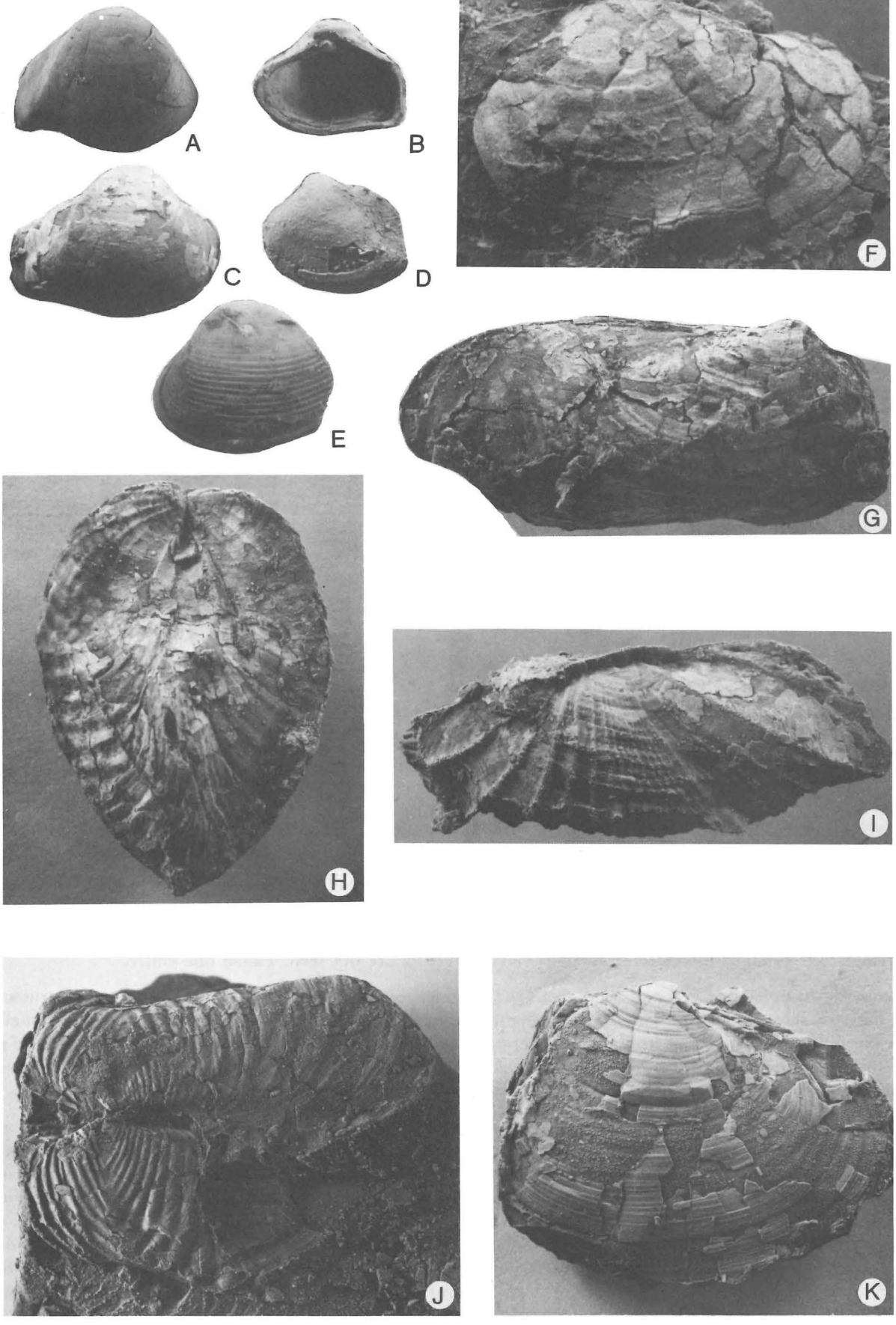
Pholadomya (P.) hemicardia Roemer, 1836.
H. LL41422; bivalved specimen; × 1.7. Mutabilis Zone, Westbury.

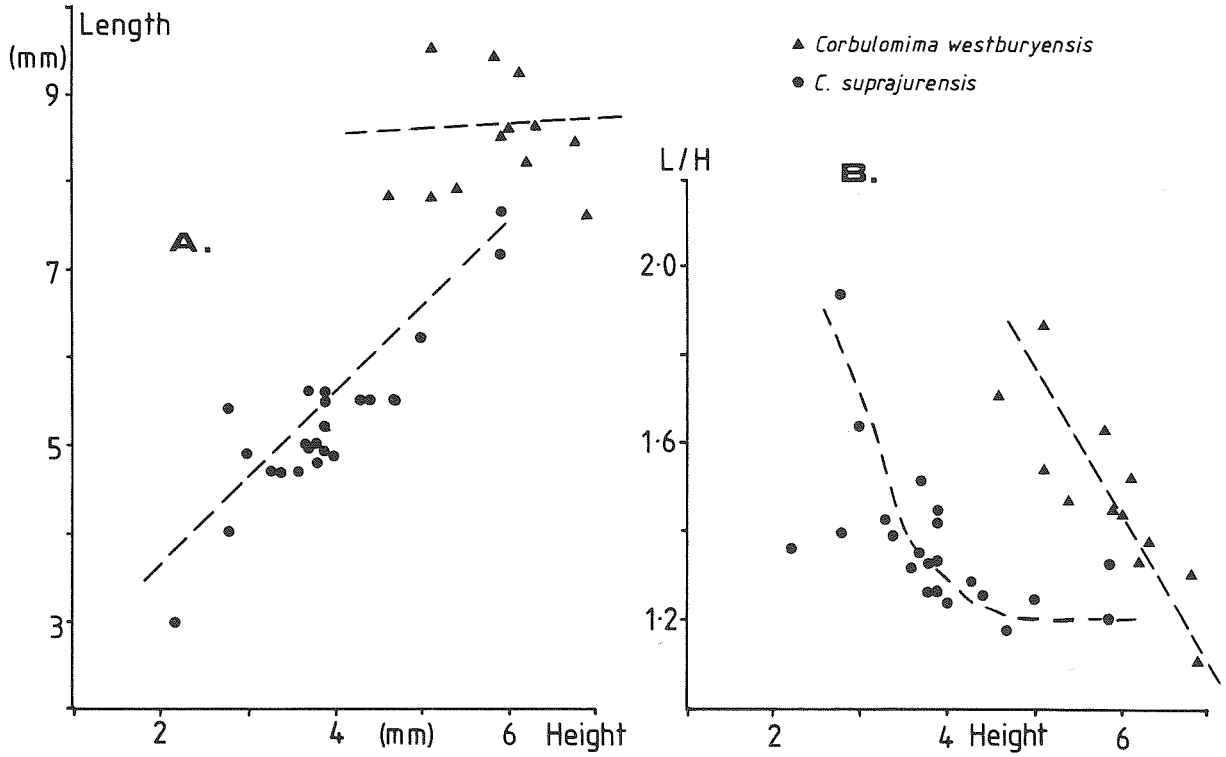
Goniomya (G.) literata (J. Sowerby, 1819).
J. LL41423; bivalved specimen; × 2. Mutabilis Zone, Westbury.

Myopholas multicostata (Agassiz, 1842).
I. LL41424; compressed, bivalved specimen; × 2.8. Mutabilis Zone, Westbury.

Pleuromya uniformis (J. Sowerby, 1813).
F. LL41425; right valve; × 3.3. Eudoxus Zone, Westbury.
G. LL41426; elongate left valve; × 1.7. Mutabilis Zone, Westbury.

Thracia (T.) depressa (J. de C. Sowerby, 1823).
K. LL41427; bivalved specimen; × 1.7. Mutabilis Zone, Westbury.


A
B
C
D
E
F
G
H
I
J
K



Text-fig. 10. A. Plot of length v.s. height for the two *Corbulomima* species from Westbury showing little difference between the species. B. Plot showing the slightly greater length/height ratio of *C. westburyensis*. Measurements in millimetres.

Holotype. Figured in Cottreau 1932. Paris Museum, d'Orbigny collection 4666, from the Corallian of Villerveux, Calvados, Normandy.

Material. 6 specimens from Black Head (LL40951-55, LL40957) 4 specimens from Westbury (LL40958-59, 41418-9), 10 specimens from Kimmeridge (LL40960-69), 4 specimens from Boulogne (LL40948-50, LL40956).

Description. Shell small, inequivalve, right valve larger than left, subtrigonal to truncate in outline. Highly inflated with maximum in region near umbo. Umbones large, with a small beak, prosogyrate, placed slightly anterior of median. Slight inflexion of ventral border immediately anterior of the truncate rostrum.

Ornament consists of fine to medium commarginal ribs or only faint growth lines, probably depending on flaking off the outer shell-layer. Shell very thick, with internal nacerous layer. Lunule very broad. Single large circular to trigonal cardional tooth in right valve. Musculature not seen. Pallial line entire.

Remarks. As noted by Lewy and Samtleben (1979) the conchiolin layer in the shell weakens the shell structure in the early stages of fossilization, often causing the valves to split apart into two quite different-looking shells. In Westbury there are complete transitions between smooth shells and ribbed ones, and there seems to be no justification for splitting them into different species. The L/H-H curve (text-fig. 11) shows that *Corbulomima suprajurensis* is more elongate as juvenile, getting primarily higher during growth.

Upper Jurassic *Corbulomima* is in urgent need of revision as noted by Duff (1978), a wealth of names are available and the development-lineages between the postulated different species have never been established, although they are important faunal elements during the whole U. Jurassic. *C. obscura* (J. de C. Sowerby) from the Lower Oxfordian (Duff, 1978) has an identical L/H ratio but lacks a ventral inflexion whilst *C. macnellii* (Morris 1850) does posses a weak inflexion but is less elongate. Both species are also considerable smaller. *C. carinata* (Buvignier 1852), and its junior synonym *C. autissiodorensis* (Cotteau 1868) is strongly inflexed and is clearly closely related to *C. suprajurensis*. *C. dammariensis* (Bubignier 1852) is another closely related species that becomes common in the Portlandian; its taxonomy is confusing in that the original figure lacks a posterior ridge whilst subsequent figures possess this feature (eg. Cox 1929).

Range. Late Oxfordian to topmost Kimmeridge. Abundant in the Black Head Siltstone and at many horizons above this.

Autecology. A shallow infaunal filter-feeder. Stanley (1970: 189) noted that Recent corbulids are sluggish burrowers and utilise a few byssal threads to stabilize themselves in the sediment.

C. supracorallina commonly forms monospecific plasters in the organic-rich shales in the central part of the formation, particularly the Autissiodorensis and Elegans Zones. They are typically less inflated however, indicating a possible ecologic control on morphology. It appears likely that this form was therefore an oxygen-tolerant opportunist. Corbulids are able to keep their valves tightly closed during periods of excessively reduced oxygen (Lewy & Samtleben 1979), thus giving them an advantage in dysaerobic environments.

Corbulomima westburyensis sp. nov.
Plate 9 C, D.

Derivatio nominis. From Westbury where it was first discovered.

Diagnosis. Small to medium-sized *Corbulomima*, elongate-oval in outline with moderate inflation.

Holotype. Plate 9 C from the Mutabilis Zone of Westbury.

Material. Holotype Plate 9 C from the Mutabilis Zone of Westbury (LL41420). Paratype from the same horizon (LL41421). Also, 2 specimens from Westbury (LL40970, 41085), 1 specimen from Boulogne (LL40971).

Description. Shell small to medium-sized, inequilateral, inequivalve, right valve slightly larger than left valve, elongate oval in outline. Anterodorsal margin concave, anterior margin rounded, passing smoothly into convex ventral margin, posteroventral angle clearly defined, around 90°, marked by a weak ridge from umbo. Posterior margin straight, posterodorsal angle clearly defined, around 140°, posterodorsal margin straight. Inflation moderate. Umbones medium-sized to large, prosogyrate. Ornament of commarginal ribs or only faint growth lines.

Dentition of a large cardinal tooth in right valve and a weakly developed posterior lateral tooth. Musculature not seen.

Remarks. This species is different from *suprajurensis* (see Text-fig. 10) by being less inflated and more elongate (Text-fig. 10A). The umbo is smaller and the posterior areas is more prominent, perhaps because it is less globose. It also lacks a ventral inflexion. *C. dammariensis* is a very similar species although it has more prosogyrate umbones.

Range. A short-ranged form, upper Mutabilis to mid Eudoxus Zone of Westbury. Also found in the lower Schiste de Chatillion at Boulogne.

Autecology. As for *C. suprajurensis* although it appears to have been less tolerant of reduced oxygen levels. The 2 species of corbulid are rarely common in the same bed suggesting some degree of interspecific competition.

Subclass	*Anomalodesmata* Dall 1889
Order	*Pholadomyoida* Newell 1965
Superfamily	*Pholadomyacea* Gray 1847
Family	*Pholadomyidae* Gray 1847

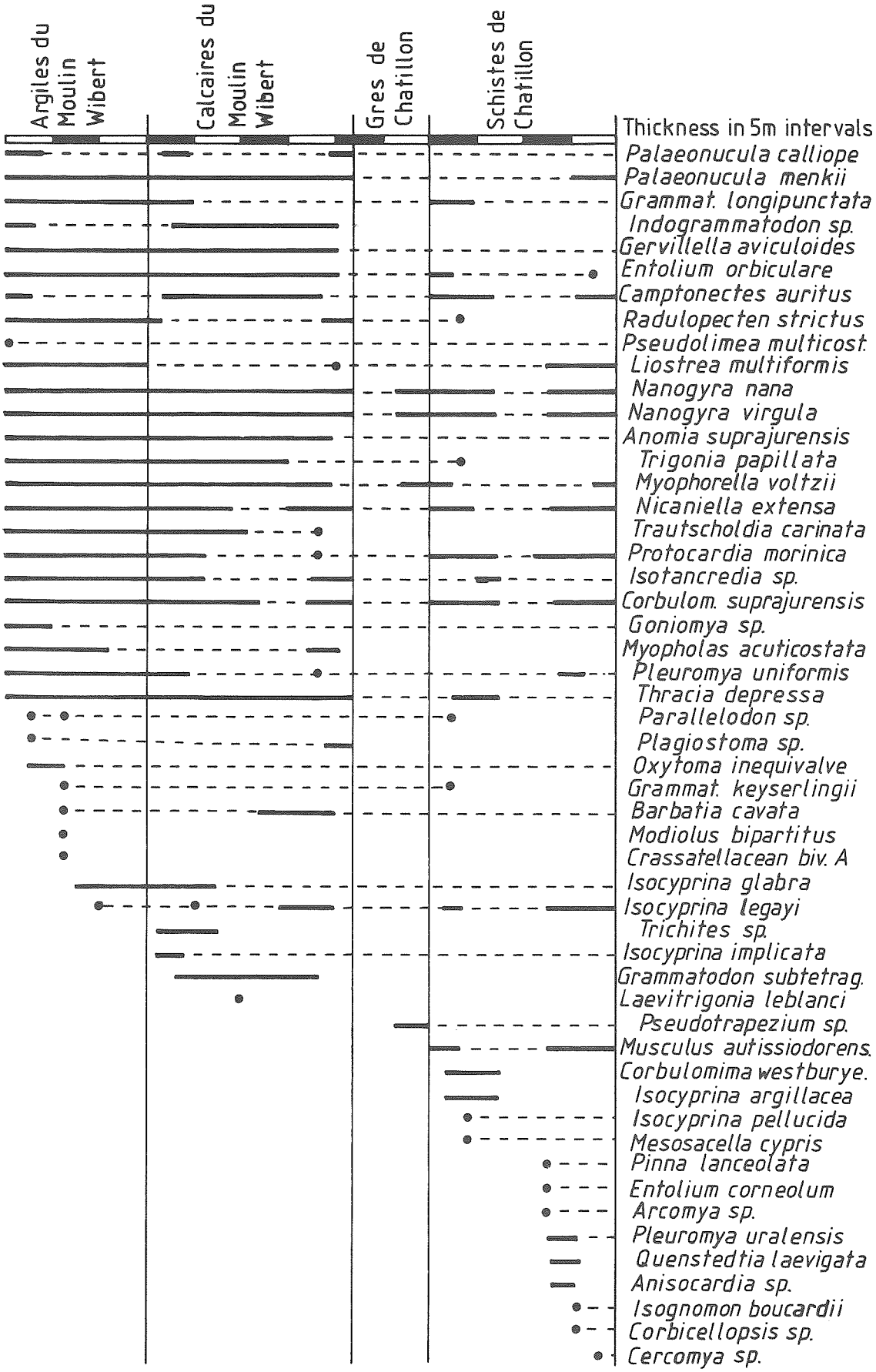
Genus ***Pholadomya*** G. B. Sowerby 1, 1825

Type species. Subsequent designation Gray 1847: 194: *Pholadomya candida* G. B. Sowerby 1, 1825.

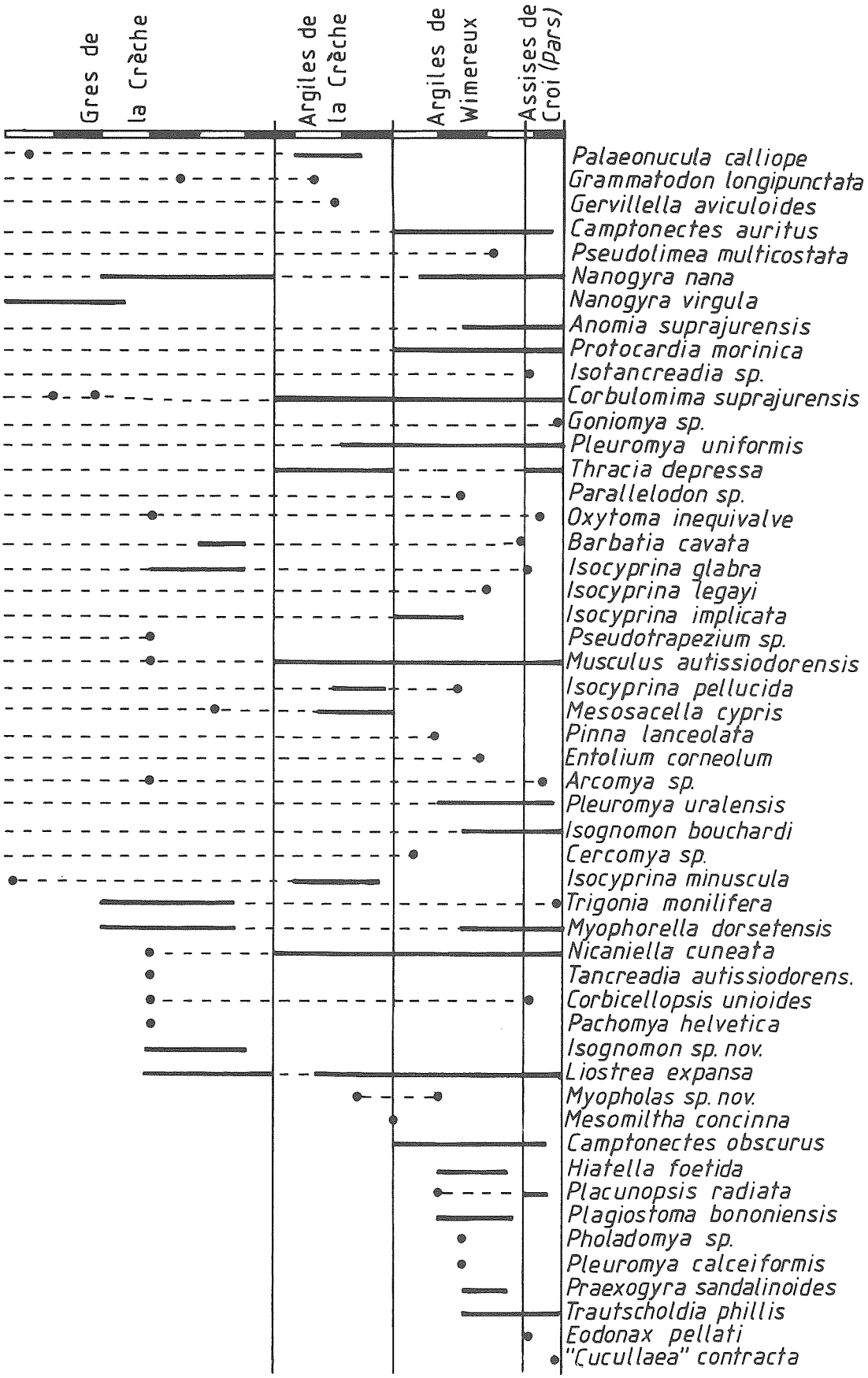
Subgenus ***Pholadomya*** s.s.

Pholadomya (Pholadomya) hemicardia Roemer 1836
Plate 9 H.

1836 *Pholadomya hemicardia* sp. nov.: Roemer, p. 131, pl. 9, fig. 18.
1982 *Pholadomya (P.) hemicardia* Roemer: Fürsich, p. 96, fig. 35 A-D.



Text-fig. 11. Range chart of bivalves from the Early Kimmeridgian formations of Boulogne, northern France, arranged in order of first appearance (see Ager and Wallace 1967a, b for locality details).



Text-fig. 11 cont'd. Range chart for the Late Kimmeridgian formations of Boulogne.

Material. One specimen from Westbury (LL41422).

Description. Shell medium-sized to large, elongate, inequilateral, equivalve, gaping posteriorly. Anterior end short, truncated, ventral margin moderately convex, posterior elongate, more produced, well rounded. Inflation moderate, largest in the anterior part of shell. Umbones well rounded, prosogyrate, salient, situated about one-quarter to one-fifth of shell length from the anterior. Ornament consisting of 8-14 radial ribs which are distributed over the whole surface except the posterodorsal and the anterodorsal regions, with well developed growth lines. Between the second and third rib from the anterior a faint shallow sulcus is usually developed. Dentition and internal structures not seen.

Remarks. This species is fairly common in layer M 8 in Westbury, where it occurs in life position.

Range. Kimmeridgian to Volgian.

Autecology. A deep infaunal form with siphons permanently extended (Fürsich 1982).

Genus ***Goniomya*** Agassiz 1841

Type species. Subsequent designation Herrmannsen, 1847:486: *Mya angulifera* J. Sowerby 1819: 46 (= *Mya intersectans* Smith 1817: 92).

Subgenus ***Goniomya*** s.s.

Goniomya (Goniomya) literata (J. Sowerby 1819)
Plate 9 J.

1819 *Mya? literata* sp. nov. J. Sowerby, p. 45, pl. 224, fig. 1.
1935 *Goniomya literata* J. Sowerby; Arkell, p. 344, pl. 48, figs. 1-7.
1982 *Goniomya literata* J. Sowerby; Fürsich, p. 98, figs. 35 E, 36 C-D.

Type species. Holotype NHM l43031, from the ?Lower Calcaceous Grit of Scarborough (Arkell 1935: 345).

Material. One specimen from Westbury (LL41423).

Description. Shell medium-sized to large, subequivalve, inequilateral, elongate-oval in outline, thin shelled. Posterior gape moderately wide, anterior gape narrow. Inflation moderate. Umbones broad, placed anterior one-third of shell-length, beaks prosogyrate to almost orthogyrate. Ornament consisting of V-shaped ribs which intersect faint commarginal growth-lines, the V-shaped ribs die out towards the ventral margin, which is commonly smooth. An imaginary line bisecting the angle of V's runs from the umbones to the ventral margin in a slightly posterior direction. Pallial sinus present.

Remarks. *G. (G.) literata* is the commonest *Goniomya* in the Upper Jurassic as demonstrated by Arkell (1935) and Fürsich (1982). Only two specimens were found in Westbury and these distorted specimens are longer than normal, in some way resembling *G. (G.) bicarinata* Fürsich in shape, but without the important ridge from umbo to posteroventral margin.

Range. Only found in the Mutabilis Zone at Westbury. Aalenian to Tithonian (Hallam 1976).

Autecology. A deep infaunal filter-feeder.

Family *Myopholadidae* Cox 1964

Genus ***Myopholas*** Douville 1907

Type species. Original designation Douville, 1907: 107: *Pholadomya multicostata* Agassiz, 1842: 52.

Myopholas multicostata (Agassiz 1842)
Plate 9 I.

1842 *Pholadomya multicostata* sp. nov. Agassiz, p. 52, pl. 2^3, figs. 1-12, pl. 1, figs. 3, 4, pl. 3^1, fig. 10.
1907 *Myopholas multicostata* (Agassiz); Douville, pl. 2, figs. 6, 7.

Type species. As for genus.

Material. 2 specimens from Black Head (LL40946-47), one specimen from Westbury (LL41424).

Description. Medium-sized to large shell, inequivalve, right valve slightly larger than left valve, inequilateral, elongate-ovate in outline. Anterior margin sharply rounded, ventral margin evenly convex, posterior margin straight, sloping, posterodorsal angle broadly rounded, dorsal margin straight. Valve margins with rather wide posterior and narrow anterior gape. Inflation high, at maximum beneath the umbones, diminishing regularly in posterior direction. Umbones broadly rounded, prosogyrate, situated anterior to midlength and strongly incurved. Ornament of prominent, narrow radial ribs which are widely separated on anterior and posterior part of shell and closely arranged and weaker on median parts. Commarginal growth lines are fairly prominent in the median area giving a reticulate pattern. Ligament subinternal. Internal structure not seen.

Remarks. The variation of this species has been discussed by Agassiz (1842) and de Loriol (1872). The Kimmeridge Clay forms differ from the forms recorded from France in the median reticulate ornament, they resemble *M. percostata* Douvillé in this respect. It might thus be regarded as intermediate between these two species or perhaps as a new species.

Range. It is well-known from the Early Kimmeridgian of Europe. Common in the Wyke Siltstone at Black Head and the Calcaire du Moulin Wibert, Boulogne

Autecology. A deep burrowing form, may have actively bored into stiff mudstones. Anterior and posterior gapes indicates permanent dwelling in borings/burrows. *M. multicostata* is found in life position in shell gravels of the Calcaire du Moulin Wibert where they may have nestled.

Family *Pleuromyidae* Dall 1900

Genus ***Pleuromya*** Agassiz 1842

Type species. Subsequent designation Herrmannsen, 1847: 297: *Mya gibbosa* J. de C. Sowerby, 1823:19, pl. 419.

Pleuromya uniformis (J. Sowerby 1813)
Plate 9 F, G.

1813 *Unio uniformis* sp. nov. J. Sowerby, p. 83, pl. 33, fig. 4.
1935 *Pleuromya uniformis* J. Sowerby; Arkell, p. 325, pl. 45, figs. 1-13.
1978 *Pleuromya uniformis* J. Sowerby; Duff, p. 116, pl. 13, figs. 11, 14, 18, 21.
1982 *Pleuromya uniformis* J. Sowerby; Fürsich, p. 106, fig. 39 A-D.

Holotype. British Museum 43224, figured by J. Sowerby, 1813 pl. 33, fig. 4.

Material. 3 specimens from Westbury (LL40935, 41425-6), 5 specimens from the Boulonnais (LL40936-40).

Description. Elongate-elliptical in shape, anterodorsal margin concave, anterior margin truncated, forming an obtuse angle with the slightly convex ventral margin. Lowermost, most ventrally situated point of shell usually in posterior half, posterior margin slightly tapering, well-rounded, posterodorsal, margin subparallel to ventral margin. Obtuse ridge running from the umbo to the anteroventral margin, commonly followed posteriorly by a shallow sulcus, which finds its expression at the ventral margin in a slight sinuosity. Inflation small to moderate, umbones inflated, prominent, situated about one-third of shell length from the anterior, beaks orthogyrate. Ornament of fine commarginal growth lines and irregular, conspicuous, commarginal folds.

Remarks. The synonymy of *P. uniformis* has been discussed fully by Arkell (1935), Cox & Arkell (1948) and Duff (1978). *P. uniformis* is one of the most variable and long ranging species of Jurassic bivalves. Fürsich (1982) noted within one sample transitional stages between *P. uralensis* (d'Orbigny 1845) and *P. uniformis* and concludes that most likely these two species are separate but exhibit some overlap in morphology. The specimens from Westbury are very elongate examples of *P. uniformis* and so resemble *P. alduini.*

Range. Bathonian to Portlandiana of England, France, Germany, Switzerland and Poland, Late Callovian to Mid Volgian of Greenland, Late Jurassic of India.

Autecology. A deep infaunal filter-feeder. It is absent from organic-rich shales due to anoxic conditions existing too close to or above the sediment surface but it is otherwise common in the mudstones and siltstones

of the Kimmeridgian particularly in the nearshore sections of the Boulogne area. It is noteworth that less elongate variants of *Pleuromya* tend to inhabit coarser grained facies such as the Corallian (Arkell 1934) and Kimmeridge of Boulogne. The occurrence of elongate forms may therefore indicate ecological control on their morphology.

Superfamily *Pandorecea* Rafinesque 1815
Family *Thraciidae* Stoliczka 1870

Genus ***Thracia*** Leach, in J. de C. Sowerby 1823

Type species. Subsequent designation Anton 1839: 2: *Thracia pubescens* Lamarck, 1819: 83.

Subgenus ***Thracia*** s.s.

Thracia (Thracia) depressa (J. de C. Sowerby 1823)
Plate 9 K.

1823 *Mya depressa* sp. nov. J. de C. Sowerby, p. 19, pl. 418.
1936 *Thracia depressa* (J. de C. Sowerby); Arkell, p. 354, pl. 50, figs. 7-10.
1978 *Thracia (T.) depressa* J. de C. Sowerby; Duff, p. 118, pl. 13, figs. 13, 19, 20, 22, 23, 28.
1982 *Thracia (T.) depressa* J. de C. Sowerby; Fürsich, p. 113, figs. 42 A-F.

Type. Holotype is lost (Arkell 1936: 355).

Material. 2 specimens from Weymouth (LL40943-44), 1 specimen from Black Head (LL40941), 1 specimen from the Boulonais (LL40945), 1 specimen from Westbury (LL41427).

Description. Large thin-shelled *Thracia*, subrectangular to elongate-elliptical in outline, rather variable. Anterodorsal margin gently convex, anterior margin evenly rounded, passing into the gently convex ventral margin, posterior margin slightly rostrate, posterodorsal margin straight to gently concave.

Umbones prominent, ophisthogyrate, placed posterior to median. Surface with fine commarginal striae.

Internal structures not seen.

Remarks. *Thracia incerta* (Thurman in Roemer) has been accepted as a distinct Kimmeridgian and Portlandian species by many authors (for references see Duff 1978: 119-20). The species supposedly differs from *T. depressa* in being more elongate and having anteriorly placed umbones. Duff (1978) recently studied *Thracia* from the Oxford Clay and showed that these species intergrade, but noted that very elongate specimens from the Kimmeridgian and Portlandian may, in fact, constitute a separate species.

The Westbury specimens are not elongate and may thus safely be considered as *T. depressa.*

Range. Aalenian to Tithonian (Hallam 1976). Found throughout the Kimmeridgian of England and northern France althougth it is absent from the more organic-rich facies.

Autecology. *T. depressa* has the morphology of a deep infaunal form. Yonge (1937) has described the Recent species *T. pubescens* which is able to produce mucus-lined tubes which act as extensions of the siphons enabling it to burrow even deeper. It is therefore surprising that of 304 specimens of *Thracia* identified from the lower Multabilis Zone at Westbury, 27% were fragmented, 17% were isolated but complete valves, 56% were articulated specimens lying on the bedding plane whilst only one complete example was found in the supposed life position with the antero-posterior line vertical.

It is therefore suggested that the life position of *T. depressa* was horizontal. The specimen found in vertical position may have died whilst it was burrowing upwards. This horizontal position may represent a behavioural response to low oxygen levels a few centimetres below the sediment surface; this would have prevented *Thracia* from burrowing to its maximum depth.

Other Bivalves from the Lower Kimmeridge Clay, Westbury.

Apart from the bivalves described above a number of other species occur, which have not been described due to their extreme rarity and/or their bad state of preservation.

Mesomiltha concinna (Damon 1860) A number of examples have been found, always preserved in life position with the commissural plane vertical and the antero-posterior line horizontal. As a consequence they have been badly distorted by compaction.

Quenstedia laevigata (Phillips 1829). Specimens are much smaller than is typical for the Corallian examples of this species (Arkell 1934: 296), rarely exceeding 1 cm in length. Anomalodesmatan sp. A of Duff (1978) closely resembles these Kimmeridge forms of *Q. laevigata* and may be attributable to it.

BIVALVE SPECIES DISTRIBUTION

Southern England. The bivalve fauna in the basal Kimmeridge Clay is dominated by oysters, *Deltiodeum delta* and *Nanogyra nana* (Text-fig. 2) indicating prolonged periods of sediment starvation. The associated fauna includes deep burrowing forms, *Pleuromya* and *Myopholas*, more akin to the underlying Corallian. Above the Cymodoce Zone Black Head Siltstone the typical Lower Kimmeridge Clay aerobic mudstone facies appears. This contains a diverse bivalve assemblage dominated by various species of *Isocyprina, Corbulomima* and *Grammatodon longipunctata.* Periods of sediment starvation are reflected by accumulations of *Nanogyra virgula* at Westbury (Text-fig. 2). More rigorous benthic current activity is probably indicated by beds with abundant *Nicaniella extensa.*

The first major organic-rich shales appear in the lower Eudoxus Zone at Westbury and these continue to be important until the Pectinatus Zone. The bivalve assemblage is much reduced by the onset of reduced oxygen levels (Text-fig. 2) and only *Protocardia, Corbulomima* and *Isocyprina minuscula* appear to have been able to thrive under such conditions. The return of more normal aerobic mudstone conditions in the Pallasioides Zone introduces a series of bivalve assemblages reminiscent of the Oxford Clay (Duff 1975). Deposit feeders (*Mesosaccella, Paleonucula*) and epibyssate filter feeders (*Pseudolimea, Parainoceramus*) are dominant (Text-fig. 2). The topmost Fittoni Zone is developed as a siltstone facies and contains an epifaunal assemblage consisting of *Camptonectes, Nanogyra* and *Liostrea.*

Boulogne, Northern France

The marly siltstone and sandy limestones which constitute the basal 2 formations of the Boulogne section contain a very diverse and yet highly variable bivalve assemblage (Text-fig. 11). Large infaunal filter-feeders tend to dominate eg.: *Myophorella, Indogrammatodon, Pleuromya* and *Isotancredia* although oysters are locally common, especially *Nanogyra virgula.*

The central part of the Schiste de Chatillon is the only organic-rich unit to be developed in the Boulogne section and it contains a similar fauna to the English equivalents. The nearshore Gres de la Crèche sandstone contains a primarily allochthonous fauna characterized by *Isognomon*. The overlying Argiles de la Crèche contain a uniform and fairly low diversity bivalve assemblage of *Nicaniella cuneata, Mesosaccella, Corbulomima* and Limids (Text-fig. 11).

The phosphatic nodule beds in the uppermost part of the succession show a prolonged history. Infaunal forms such as *Protocardia* and *Pleuromya* are commonly phosphatised whilst epifaunal oysters and pectinids commonly dominate the assemblages.

ACKNOWLEDGEMENTS

This paper is compiled from two seperate theses and numerous people who have helped in different ways to make the work possible.

C.K.C. would like first of all to dedicate this work to the late professor T. Birkelund who supervised me and gave much good advice; H. Nøhr Hansen and I. Salinas for valuable discussions on different aspects of the Kimmeridge Clay at Westbury on which we worked together; F. Fürsich (informal supervisor), M. Vilhjalmsson, and C. Heinberg for valuable discussions on taxonomic problems; S. Kelly and F. Fürsich for critically reading earlier drafts of the manuscript; J. Aagaard for the fine photographic work, E. Møller Hansen for technical assistance and M. Nordgren for her support and technical assistance with the plates, where Henrik Engelund likewise helped.

P.B.W. would like to thank his former supervisors Tony Hallam of Birmingham University and Noel Morris at the Natural History Museum, London. Funding was provided by a joint NERC/CASE award with the NHM which is gratefully acknowledged.

REFERENCES

AGASSIZ, L. 1840 *Etudes critique sur les Mollusques fossiles.* Mémoires sur les trigones. 58 pp., 11 pls. Neuchâtel.

AGASSIZ, L. 1842-1845 *Etudes critiques sur les Mollusques fossiles.* Monographie des Myes. 287 pp., 93 pls. Neuchâtel.

AGER, D.V. and WALLACE, P. 1967a The environmental history of the Boulonnais, France. *Proceedings of the Geologists' Association* 77: pp. 385-418.

AGER, D.V. and WALLACE, P. 1967b Easter field meeting in the Boulonnais, France. *Proceedings of the Geologists' Association* 77: pp. 415-435.

ALLEN, J.A. and SANDERS, H.L. 1969 *Nucinella serrei* Lamy (Bivalvia: Protobranchia), a monomyarian solemyid and possible living actinodont. *Malacologia* 7: pp. 381-396.

ARKELL, W.J. 1929-1937 A monograph of British Corallian Lamellibranchia. *Palaeontographical Society (Monograph).*

ARKELL, W.J. 1930 The generic position and phylogeny of some Jurassic Arcidae. *Geological Magazine* 67: pp. 297-310, 337-352, pls. 14-16.

ARKELL, W.J. 1947 *The geology of the country around Weymouth, Swanage, Corfe and Lulworth.* Memoirs of the Geological Survey of Great Britain, 386 pp.

BEYRICH, H.E. 1845 *Protocardia*, eine neue Gattung fossiler Muscheln. *Zeitschrift für Malakozoologie* 2: pp. 17-20.

BIKEKUND, T., CALLOMON, J.H., CLAUSEN, C.K., NØHR HANSEN, H. and SALINAS, I. 1983 The Lower Kimmeridge Clay at Westbury, Wiltshire, England. *Proceedings of the Geologists' Association* 94: pp. 289-309

BLAKE, J.F. 1875 On the Kimmeridge Clay of England. *Quarterly Journal of the Geological Society of London* 31: pp. 196-233.

BLAKE, J.F. 1880 On the Portland Rocks of England. *Quarterly Journal of the Geological Society of London* 36: pp. 189-236.

BLAKE, J.F. 1905-1907 A monograph on the fauna of the Cornbrash. *Palaeontographical Society (Monograph)*, 102 pp.

BORISSJAK, A. 1904 Die Pelecypoden der Jura-Ablagerungen im europaeischen Russland. 11. Arcidae. *Mem. Com. Geol.* newseries 19: 63 pp.

BRANNAN, J. 1983 *Taxonomy and evolution of Triassic and Jurassic non-lophate oysters.* Unpublished PhD thesis, Oxford University.

BRANSON, C.C. 1942 *Parallelodon, Grammatodon* and *Beushausenia* (= *Cosmetodon* new name). *Journal of Palaeontology* 16: pp. 247-249.

BRAUNS, D. 1874 *Der obere Jura im nordwestlichen Deutschland.* 434 pp., Braunschweig.

BUVIGNIER, A. 1852 *Statistique géologique, minéralogique, minérallugique et paléontologique du département de la Meuse,* Paris.

CASEY, R. 1952 Some genera and subgenera, mainly new, of Mesozoic heterodont lamellibranchs. *Proceedings of the Malacological Society of London* 29: pp. 121-176, pls. 7-9.

CHATWIN, C.P. 1960 *The Hampshire basis and adjoining areas.* British Regional Geology Series, 3rd ed. HMSO.

CHAVAN, A. 1945 Les lamellibranches hétérodontes des Sables Astartiens de Cordebugle (Calvados). *Journal of Conchology* 86 (2): pp. 41-86, pl. 1.

CHAVAN, A. 1952 Les pélécypodes des Sables Astartiens de Cordebugle (Calvados). *Abhandlungen schweizer Paläontologie Gesellschaft.* 69: pp. 1-132, pls. 1-4.

CLAUSEN, C.K. 1984 *Lower Kimmeridgian bivalves from Westbury, Wiltshire, England. Systematics and palaeoecology.* Unpublished PhD thesis, Copenhagen University [In Danish].

CLAUSEN, C.K. 1985 Bivalve-ecology in the Lower Kimmeridge Clay (Upper Jurassic, England). *Dansk geologische Forenschrift*, Arskrift for 1984, pp. 123-126.

CONTEJEAN, C. 1860 Etude de l'étage Kimméridgien dans les environs de Montbéliard et dans le Jura. *Mémoire Société Emul. Doubs.* 4: pp. 1-352, pls. 1-27.

COPE, J.C.W. 1968 Epizoic oysters on Kimmeridgian ammonites. *Palaeontology* 11: pp. 19-20.

COTTREAU, J. 1925-1932 Types du Prodrome de Paléontologie stratigraphique universelle d'Alcide d'Orbigny. 2, Callovien-Portlandian. *Annales Paléontologie* 14-21: pp. 1-222, pls. 37-68.

COX, B.M. and GALLOIS, R.W. 1981 The stratigraphy of the Kimmeridge Clay of the Dorset type area and its correlation with some other Kimmeridgian sequences. *Report of the Institute of Geological Sciences* 80/4.

COX, B.M., LOTT, G.K., THOMAS, J.E. and WILKINSON, I.P. 1987 Upper Jurassic stratigraphy of four shallow cored boreholes in the UK sector of the southern North Sea. *Proceedings of the Yorkshire Geological Society* 46: pp. 97-110.

COX, L.R. 1925 The fauna of the basal shell bed of the Portland Stone, Isle of Portland. *Proceedings of the Dorset Natural History and Antiquarian Field Club* 46: pp. 113-172.

COX, L.R. 1929 A synopsis of the lamellibranchia of the Portland Beds of England. *Proceedings of the Dorset Natural History and Antiquarian Field Club* 50: pp. 131-202.

COX, L.R. 1930 On British fossils names by William Smith. *Annals and Magazine of Natural History* (10), 6: pp. 287-304, pl. 12.

COX, L.R. 1935 Jurassic Gastropoda and Lamellibranchia. In: *The Mesozoic Palaeontology of British Somaliland*. London, pp. 148-197, pls. 14-21.

COX, L.R. 1940 The Jurassic lamellibranch fauna of Kachh (Cutch). *Memoir of the Geological Survey of India, palaeontologica indica* (9) 3: pp. 1-157, pls. 1-10.

COX, L.R. 1964 Notes concerning the taxonomy and nomenclature of fossil Bivalvia (mainly Mesozoic). *Proceedings of the Malacological Society of London* 36: pp. 39-48, pl. 1.

COX, L.R. 1965 Jurassic Bivalvia and Gastropoda from Tanganyika and Kenya. *Bulletins of the British Museum of Natural History (Geology) Supplement*, 213 pp., 30 pls.

COX, L.R. and ARKELL, W.J. 1948-1950 A survey of the Mollusca of the British Great Oolite Series, primarily a nomenclatorial revision of the monographs by Morris & Lycett (1851-55), Lycett (1863) and Blake (1905-07). *Palaeontological Society*. part 1 (1948) 48 pp., part 2 (1949) pp. 49-105.

CRAME, J.A. 1982 Late Jurassic inoceramid bivalves from the Antarctic peninsula and their stratigraphic use. *Palaeontology* 25: pp. 555-603.

DEFRANCE, A. 1821 Huitres. *Dict. Science nat.* Paris 22: pp. 20-33.

DESHAYES, G.P. 1831 *Coquilles caract. des Terrains.*

DOLLFUSS, A. 1863 *La fauna kimméridgienne du Cap de la Heve.* Paris 102 pp, 18 pls.

DOUVILLE, M. 1907 Les lamellibranches cavicoles on desmodontes. *Bulletin de la Société Géologie de France.* 4th serie, 7: pp. 96-114, pl. 2.

DUFF, K.L. 1975 Palaeoecology of a bituminous shale: the Lower Oxford Clay of central England. *Palaeontology* 18: pp. 443-482.

DUFF, K.L. 1978 Bivalvia from the English Lower Oxford Clay (Middle Jurassic). *Palaeontographical Society (Monograph).*

DUTERTRE, A.-P. 1926 Les Aucelles des terrains Jurassiques supérieurs du Boulogne. *Bulletin de la Société Géologie de France.* 4th series, 26, pp. 395-422.

FÜRSICH, F.T. 1977 Corallian (Upper Jurassic) marine benthic associations from England and Normandy. *Palaeontology* 20: pp. 337-385.

FÜRSICH, F.T. 1980 Preserved life position of some Jurassic bivalves. *Paläontologische Zeitschrift* 54: pp. 289-300.

FÜRSICH, F.T. 1982 Upper Jurassic bivalves from Milne Land, East Greenland. *Grønlands Geologische Undersøgelse Bulletin* 114.

FÜRSICH, F.T. & OSCHMANN, W. 1986 Autecology of the Upper Jurassic oyster *Nanogyra virgula* (Defrance). *Paläontologische Zeitschrift* 60: pp. 65-74.

GALLOIS, R.W. & COX, B.M. 1976 The stratigraphy of the Lower Kimmeridge Clay of eastern England. *Proceedings of the Yorkshire Geological Society* 41: pp. 13-26.

GOLDFUSS, G.A. 1833-1840 *Petrefacta Germaniae.* Dusseldorf.

HALLAM, A. 1976 Stratigraphic distribution and ecology of European Jurassic bivalves. *Lethaia* 9: pp. 245-259.

HEMMING, F. 1954 Opinion 310. Opinions and declarations rendered by the *International Commission on Zoological Nomenclature* 8/27: pp. 355-364.

JEFFRIES, R.P.S. & MINTON, P. 1965 The mode of life of two Jurassic species of "*Posidonia*". *Palaeontology* 8: pp. 156-185.

JOHNSON, A.L.A. 1984 The palaeobiology of the bivalve families Pectinidae and Propeamussiidae in the Jurassic of Europe. *Zitteliana* 11.

KAUFFMAN, E.G. 1978 Benthic environments and paleoecology of the Posidonienschiefer (Toarcian). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 157: pp. 18-36.

KELLY, S.R.A. 1984 Bivalvia of the Spilsby Sandstone and Sandringham Sands (Late Jurassic-Early Cretaceous) of eastern England. Part 1. *Palaeontographical Society (Monograph).*

KOCH, C.L. & DUNKER, W. 1837 *Beiträge zur Kenntnis des Norddeutschen Oolithgebirges und dessen Versteinungen.* Braunschweig.

LAMARCK, J.B.P.A. de M. de 1819 *Histoire naturelle des animaux sans vertébres* 6/1.

LENNIER, G. 1872 Etudes géologiques et paléontologiques sur l'embouchure de la Seine et les falaises de Haute-Normandie. Le Havre.

LEWY, Z. and SAMTLEBEN, C. 1979 Functional morphology and palaeontological significance of the conchiolin layers in corbulid pelecypods. *Lethaia* 12: pp. 341-351.

LORIOL. P. de 1872 Description des fossiles. In: LORIOL, P. de, ROYER, E. and TOMBECK, H. Monographie paléontologique et géologique des étages supérieurs de la formation jurassique du département de la Haute-Marne. *Mémoire de la Société Linnéenne* 16. Caen, Normandie.

LORIOL. P. de 1874-1875 Descriptions des fossiles. In: LORIOL, P. de and PELLAT, E. Monographie paléontologique et géologique des étages supérieurs de la formation jurassique des environs de Boulogne-sur-Mer. *Mémoires de la Société Phys. Genève* 24.

LORIOL. P. de 1896-1901 Etude sur les mollusques et brachipodes de l'Oxfordien supérieur et moyen du Jura vernois. *Abhandlungen schweizer Paläontologie Gesellschaft* 23: pp. 1-77 (1896), 24: pp. 78-158 (1897), supplement to 28: pp. 1-119 (1901).

LORIOL. P. de & COTTEAU, G. 1868 Monographie paléontologique et géologique de l'étage Portlandien du département de l'Yonne. *Bulletin de la Société des Sciences de l'Yonne* 1: pp. 1-260, pls. 1-15.

LYCETT, J. 1863 Supplementary monograph on the Mollusca from the Stonesfield Slate, Great Oolite, Forest Marble and Cornbrash. *Palaeontographical Society (Monograph).*

MEEK, F.B. & HAYDEN, F.V. 1860 Systematic catalogue of Jurassic, Cretaceous and Tertiary fossils collected in Nebraska. *Proceedings of the Academy of Natural Sciences of Philadelphia.*

MOORE, R.C. (ed.) 1969 *Treatise on invertebrate palaeontology.* Part N. Mollusca 6, Bivalvia, 1224 pp.

MORRIS, J. & LYCETT, J. 1851-1855 A monograph of the Mollusca from the Great Oolite. *Palaeontographical Society (Monograph)* 1. Univalves, pp. I-VIII, 1-130, (1851). 2. Bivalves, pp. 1-80, (1853). 3. Bivalves, pp. 81-147, (1855).

MORRIS, K.A. 1979 A classification of Jurassic marine shale sequences: an example from the Toarcian (Lower Jurassic) of Great Britain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 26, pp. 117--126.

MYERS, K.J. & WIGNALL, P.B. 1987 Understanding Jurassic organic-rich mudrocks new concepts using gamma ray spectromety and palaeoecology: examples from the Kimmeridge Clay of Dorset and the Jet Rock of Yorkshire. In: LEGGET, J.K. and ZUFFA, G.G., eds. *Marine classic environments: concepts and case studies*, pp. 175-192. Graham and Trotam Ltd, London.

NØEHR-HANSEN, H. 1986 Dinocyst stratigraphy of the Lower Kimmeridge Clay, Westbury, England. *Bulletin of the Geological Society of Denmark* 35, pp. 31-51.

ORBIGNY, A. d' 1847 *Paléontologie français.* Description des mollusques et rayonnes fossiles. Terrains crétacés. 3. Lamellibranches. pp. 501-807, pls. 414-489.

ORBIGNY, A. d' 1850 *Prodrome de paléontologie stratigraphique universelle des animaux et mollusques et rayonnes.* Part 1, 394 pp. Part 2, 428 pp. Paris

OSCHMANN, W. 1985 Faziensentwicklung und Provinzialismus in Nordfrankreich und Sudetenland zur Zeit des obersten Jura (Oberkimmeridge-Portland). *Müncher Geowissenschaftliche Abhandlungen* 2.

PHILLIPS, J. 1829 *Illustrations of the geology of Yorkshire.* York, 192 pp.

QUENSTED, W. 1930 Die Anpassung an die grabende Lebensweisse in der Geschichte der Solenomyiden und Nuculacean. *Geologische und Paläontologische Abhandlungen*, Neue Serie 18, pp. 1-119, pls. 1-3.

REMANE, A. 1971 Ecology of brackish water. In: REMANE, A. and SCHLIEPER, C., eds. Biology of brackish waters. *Binnengewässer* 25, pp. 1-120.

ROEDER, H.A. 1882 *Beitrag zur kentniss des Terrain a Chailles und seiner Zweischaler in der Umgegend von Pfirt im Oberelsass.* Strasbourg, 110 pp.

ROEMER, F.A. 1836 *Die Versteinerungen der Norddeutschen Oolithen-Gebirges.* Hannover, 218 pp.

ROEMER, F.A. 1839 *Die Versteinerungen der Norddeutschen Oolithen-Gebirges.* Ein Nachtrag. Hannover 65 pp.

SANDERS, H.L., MANGELSDORF, P.C. Jr, & HAMPSON, G.R. 1965 Salinity and faunal distribution in the Pocasset River, Massachusetts. *Limnology and Oceanography* 10, pp. 216-229.

SAUVAGE, H.E. and RIGAUX, E. 1871 Diagnoses d'espèces nouvelles des Terrains jurassiques supérieurs de Boulogne-sur-Mer (Pas-de-Calais). *Journal de Conchology* 20, pp. 165-187, pls. 8-12.

SCHLOTHEIM, E.F. VON 1813 Beiträge zur Natur-geschichte der Versteinerungen in geognostischer Hinsicht. *Miner. Taschenbuch* 7, pp. 3-134, pls. 1-4.

SEILACHER, A. 1982 Posidonia Shales (Toarcian, S. Germany) stagnant basin model revalidated. In: GALLITELLI, E.M., ed. *Paleontology, essential of historical geology.* pp. 25-55. STEM, Modena Press.

SEILACHER, A., MATYJA, B.A. & WIERBOWSKI, A. 1985 Oyster beds: morphological response to changing substrate conditions. In: BAYER, U. and SEILACHER, A., eds. *Sedimentary and evolutionary cycles.* pp. 421-435. Springer-Verlag, Berlin.

SMITH, W. 1816-1819 *Strata identified by organised fossils.* London.
SMITH, W. 1817 *Stratigraphical system of organised fossils.* London, 113 pp.
SOWERBY, J. 1812-1822 *The mineral conchology of Great Britain.* 1. pp. 1-236 (1812-15) 2. pp. 1-239 (1815-18) 3. pp. 1-186 (1818-21) 4. pp. 1-104 (1821-22).
SOWERBY, J. de C. 1822-1846 *The mineral conchology of Great Britain.* 4. pp. 105-151 (1822-23) 5. pp. 1-171 (1823-25) 6. pp. 1-235 (1826-29). Index (1840-1846).
SPATH, L.F. 1936 The Upper Jurassic invertebrate faunas of Cape Leslie, Milne Land. II. Upper Kimmeridgian and Portlandian. *Meddelser om Grønland* 99/3, pp. 1-180.
STAESCHE, K. 1926 Die Pectiniden des schwabischen Jura. *Geologische und Paläontologische Abhandlungen* Jena (N.F.) 15, 136 pp., 6 pls.
STANLEY, S.M. 1970 Relation of shell form to life habits of the Bivalvia (Mollusca). *Memoir of the Geological Society of America* 125.
STANLEY, S.M. 1972 Functional morphology and evolution of byssally attached bivalve mollusks. *Journal of Paleontology* 46: pp. 165-212.
STANLEY, S.M. 1975 Adaptive themes in the evolution of the Bivalvia (Mollusca). *Annual Review of the Earth and Planetary Sciences* 3, pp. 361-385.
TRAUTSCHOLD, H. 1860 Recherches géologiques aux environs de Moscou. Couche Jurassique de Galiowa. *Bull. Soc. Imp. Nat. Moscou* 33, 338-361.
VOKES, H.E. 1956 Notes on the Nucinellidae (Pelecypoda) with description of a new species from the Eocene of Oregon. *Oregon Journal of Paleontology* 30, pp. 652-671.
WIGNALL, P.B. 1988 *The palaeoecology and sedimentology of the Kimmeridgian of England and northern France.* Unpublished PhD thesis, Birmingham University.
WIGNALL, P.B. 1990 Benthic palaeoecology of the Late Jurassic Kimmeridge Clay of England. *Special papers in Paleontology* 43.
YOUNG, G. & BIRD, J. 1828 *A geological review of the Yorkshire coast: describing the strata and fossils occurring between the Humber and the Tees, from the German Ocean to the plains of York.* 2nd edition, Whitby. 366 pp., 17 pls.
YONGE, C.M. 1937 The formation of siphonal openings by *Thracia pubescens. Proceedings of the Malacological Society of London* 22, pp. 337-338.
YONGE, C.M. 1939 The protobranchiate mollusca: a functional interpretation of their structure and evolution. *Philosophical Transactions of the Royal Society of London B230,* pp. 79-147.
ZAKHAROV, V.A. & TURBINA, A.C. 1979 Early Neocomian inoceramids of northern Siberia. In: SAKS, V.N. and ZAKHAROV, V.A. Conditions of life in Mesozoic seas with Boreal faunas. *Trudy, Institute Geol. Geofiz. Siberia Otd.* 411, pp. 23-36, pls. 1-13, [In Russian].
ZIEGLER, B. 1969 Uber *Exogyra virgula* (Lamellibranchiata, Oberjura). *Eclogae Geologische Helvetia* 62: pp. 685-696.