Larval shells of four Jurassic bivalve molluscs

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SYNOPSIS. Well-preserved bivalve larval shells of Jurassic age are described for the first time, from four species of Pteriomorpha from the south of England, *Liostrea plastica, L. irregularis, Oxytoma* sp. and *Meleagrinella* sp. They are compared with modern counterparts and inferences concerning larval development are tentatively drawn.

INTRODUCTION

Between 1982 and 1984 four attempts were made, by staff of the British Museum (Natural History) Department of Palaeontology, to recover the remains of a plesiosaur from the Upper Kimmeridge Clay Formation, at NGR SY 706722, the foot of Grove Cliff on the east side of the Isle of Portland, Dorset, U.K. (Fig. 1). This successful enterprise resulted in the unification of material, previously collected and in the Dorset County Museum, with that collected by BM(NH) staff. A report on the plesiosaur was made by Brown (1984), and on the associated fauna and stratigraphical position by Palmer (1988). This account deals with juvenile shells which have larval shells, 'prodissoconchs', still preserved in place at the umbones of the valves.

Stratigraphical position of material

The oldest horizon present on the Isle of Portland is a 25·4 cm bituminous indurated shale, the Blackstone in the Upper Kimmeridge Clay, which crops out on the shore north of Castletown at the extreme north end of the island. With a southerly dip and little or no major faulting, it follows that all the Kimmeridge Clay down to Mean High Water is above the Blackstone and equivalent to shales with *Pectinatites, Pavlovia* and *Virgatopavlovia* of the main outcrops at Chapman's Pool.

The fauna contained two species of ammonite, *Pavlovia rotunda* and *P. concinna*, which, together with the associated fauna, allowed an exact correlation to be made with bed 2 'hard bituminous shales' of Cope (1978) in the Rotunda Zone in Chapman's Pool. This shelly horizon has a wide distribution in southern England, from Hartwell in Buckinghamshire to the Bristol Channel (Palmer 1988).

Method of treatment

It was evident at the excavation site, even with a c 10 hand lens, that some bedding planes were covered with juvenile oysters up to 2 mm long, while some had prodissoconchs well preserved on the umbones. Slabs of shale were broken up and repeatedly boiled in a strong solution of Sainsbury's Liquid Cleaner, which proved effective and yielded a rich microfauna. Foraminiferans, ostracods, juvenile molluscs, together with arm hooks of a coleoid cephalopod, brachiopods, echinoderms, cirripedes and numerous skeletal fragments and teeth of fish were present, and were hand-picked from insoluble mineral residue under low-power stereo magnification. Spat of *Liostrea, Oxytoma* and *Meleagrinella* were isolated and mounted on 100-cell microslides, and were measured using a light microscope fitted with a graticule eyepiece. Figs 6–8 summarize these measurements and show that ultimate size of the prodissoconchs was rather variable. The measurements are probably accurate within the limits f 0·003 mm.

Some of the better-preserved spat were selected for photography under the scanning electron microscope (SEM) of the BM(NH) EM Unit, using low magnification of uncoated specimens as recommended by Taylor (1986). The SEM micrographs form the basis of Plates 1–5 of this report, except Plate 2, figs 9–11. The latter were made with normal light photography since the shell of *Plagiostoma gigantea* was too large to fit into the 'environmental chamber' of the SEM, while the prodissoconchs were not sufficiently well preserved to allow accurate measurements to be made.

All the material is deposited in the BM(NH) Dept. of Palaeontology.

DEFINITION OF TERMS

The following terms are used in describing bivalve larval development, and are listed in order of development.

1. Non-incubatory: release of gametes into sea where fertilization and larval development takes place.
2. Incubatory: retention of fertilized eggs within the mantle cavity by female and released at veliger stage.
3. Trochophore: non-feeding invertebrate larval stage with biconical outline, and with a ciliated equatorial band and an apical tuft.
4. Planktotrophic: feeding in the plankton.
5. Lecithotrophic: obtaining nourishment for development from the yolk of an egg.
6. Veliger: feeding molluscan larval type following on from trochophore stage. Veligers develop a shell, have a through gut and a ciliated swimming velum in an antero-ventral position.
7. Velum: bi- to multi-lobed ciliated tissue developed from either side of the head in gastropods, or anterior to the foot in bivalves.
8. Prodissoconch: complete larval shell of bivalve mollusc up to metamorphosis.
9. Prod. I: initial area of prodissoconch laid down as a single sheet of shell by the shell gland, but lacking co-marginal growth.
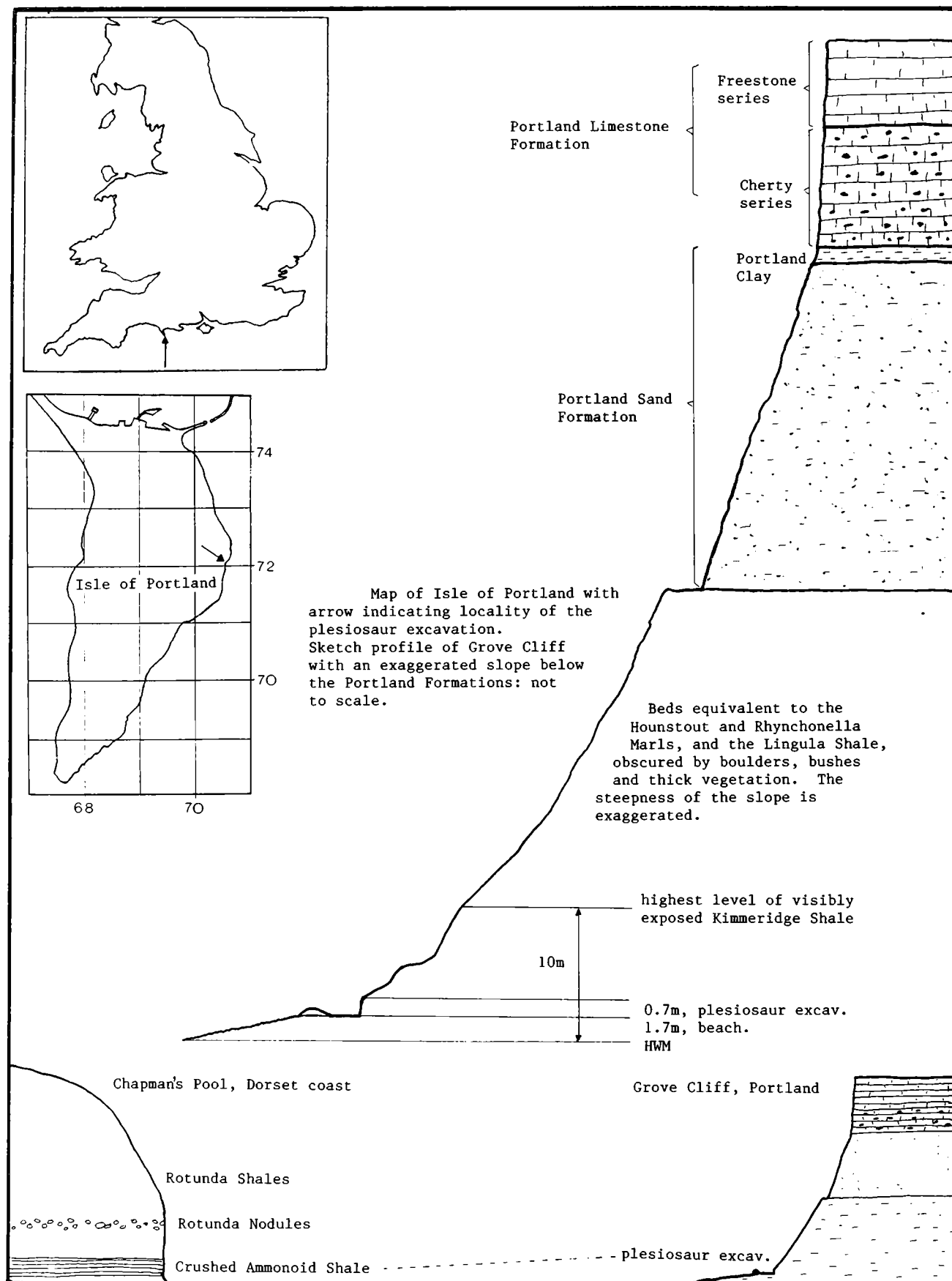10. Prod. II: region of prodissoconch with co-marginal growth increments.

Fig. 1 Diagram of section and maps showing occurrences of material described.
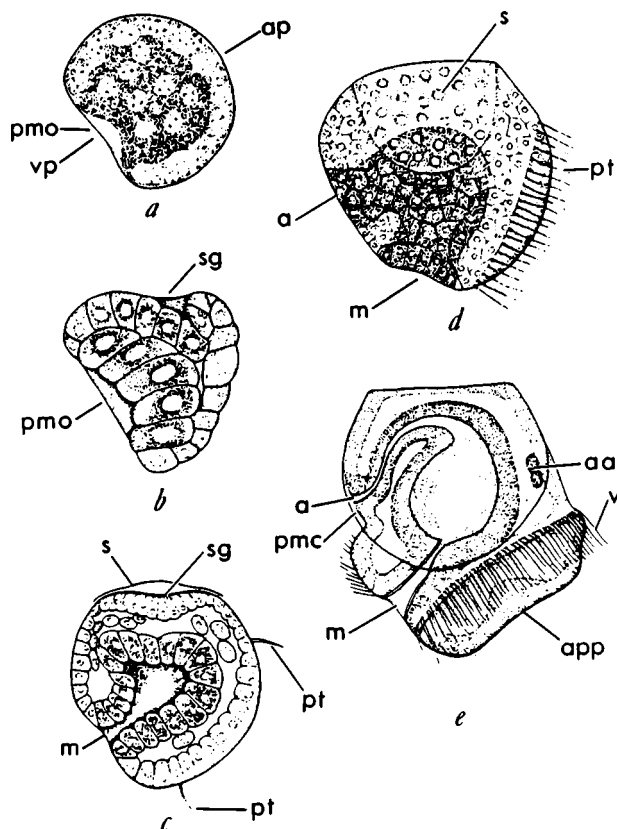
Fig. 2 Early development of *Ostrea edulis*, redrawn from Horst (1882), with presumptive dorsal region (shell gland and later the hinge) at top and anterior to right: *a*, gastrula; *b*, early trochophore; *c*, middle trochophore; *d*, late trochophore; *e*, early veliger. (a = anus, aa = anterior adductor, ap = animal pole, app = apical pit, m = mouth, pmc = presumptive mantle cavity, pmo = presumptive mouth opening, pt = prototroch, s = shell, sg = shell gland, v = velum, vp = vegetal pole.)
(Fig. 1 of Waller, 1981.)

11. Pediveliger: terminal phase of Prod. II when larva briefly develops a foot for crawling and searching for a suitable substrate for cementation.
12. Metamorphosis: loss of velum, foot and change of shell growth direction, accompanying settlement of veliger, cementation and beginning of benthic mode of life.
13. Dissoconch: co-marginal shell growth after metamorphosis, together with internal shell thickening.

DESCRIPTION OF MATERIAL

Liostrea plastica (Trautschold 1860)   Fig. 4; Plates 1, 2
See Kelly (1984) for synonymy, which includes *Liostrea bononia* (Sauvage & Rigaux, 1871).

MATERIAL. 56 juveniles with prodissoconchs well preserved, 51 RV and 5 LV; together with 60 pediveliger prodissoconchs, with no dissoconch growth, which are all more or less crushed and distorted. Figured specimens LL41326–32, BM(NH).

DESCRIPTION. More or less equivalve, strongly opisthogyrous, longer than high, demarcation between Prod. I and Prod. II
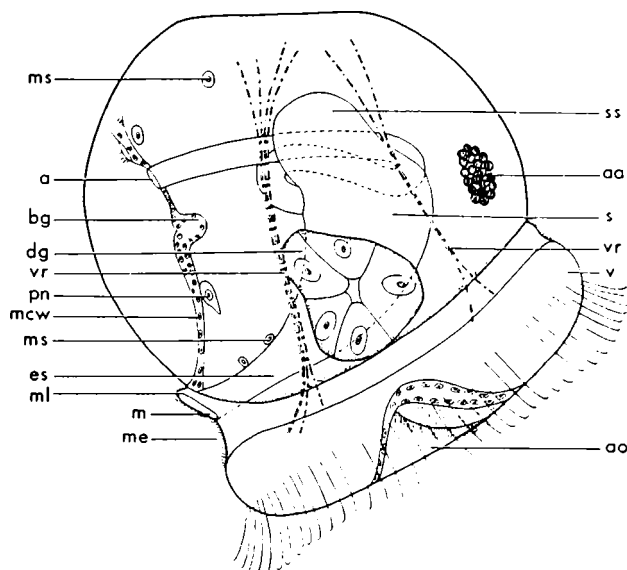

Fig. 3 Anatomy of a young, newly released, six-day-old veliger larva of *Ostrea edulis*, redrawn from Erdmann (1935). (a = anus, aa = anterior adductor, ao = apical organ, bg = primordial byssal gland, dg = digestive gland, es = esophagus, m = mouth, mcw = mantle cavity wall, me = mouth embayment, ml = mouth lobe, ms = free mesenchymal cell, pn = protonephridium, s = stomach, ss = style sac, v = velum, vr = velar retractor.)
(Fig. 2 of Waller, 1981.)

not sharply defined, Prod. II with around 30 concentric ridges covering about 0·8 of the height; junction between prodissoconch and dissoconch at metamorphosis very sharply defined with a tendency for final four or five concentric ridges to become crowded. The colour of the prodissoconch in daylight is a pale bluish grey; that of the dissoconch a dark brownish grey.

DIMENSIONS. 50 prodissoconchs on the umbones of juveniles were measured for height (h) and length (l); then h/l was calculated as a percentage, together with mean, maximum, minimum and standard deviation for height, length and h/l(%). This is summarized in Table 1, with standard deviation, SD, based on n–1.

Table 1 Dimensions of prodissoconchs of *Liostrea plastica* (Trautschold).

	Mean	Max.	Min.	SD
height μm	368·8	480	310	33·73
length μm	435·6	520	360	38·9
h/l %	85·2	110·5	75·0	7·59

A histogram showing the frequency distribution of height and length is given in Fig. 6.

DISCUSSION. Comparison of larval shell of *Liostrea* and *Ostrea* (Waller 1981: figs 33, 66, 67, 137, 141, 142; and Plates 1 and 2 herein) show that, though both are undoubtedly oysters, the larval shells are very different. The shell of *Liostrea* has the overall appearance of a heterodont bivalve while the ribs remind one of *Astarte* or a venerid bivalve; *Ostrea edulis*, by contrast, has a smooth and rounded subspherical outline with
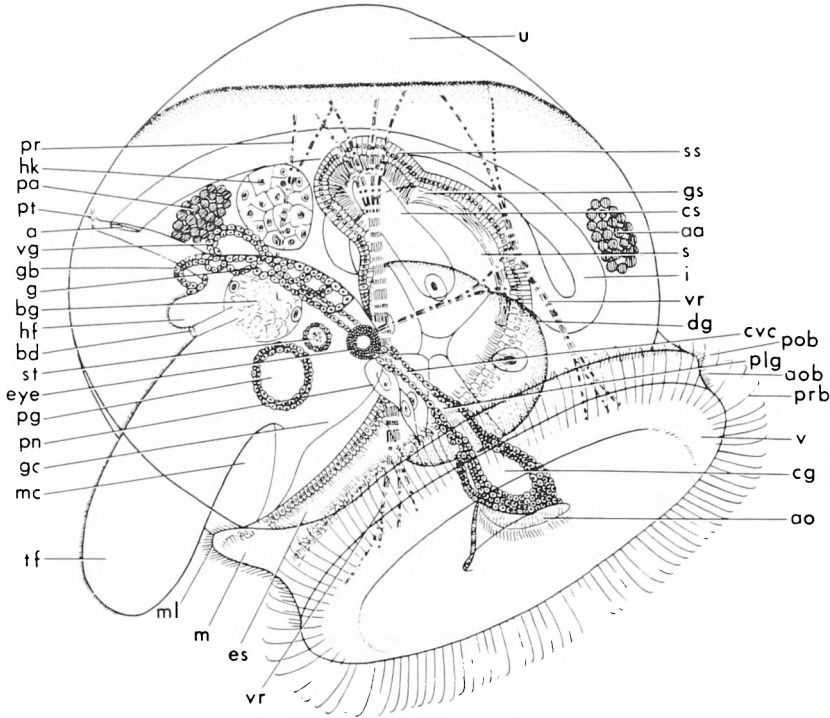
Fig. 4 Anatomy of a pediveliger larva of *Ostrea edulis*, redrawn from Erdmann (1935). (a = anus, aa = anterior adductor, ao = apical organ, acb = adoral ciliary band, bd = byssal gland duct, bg = byssal gland, cg = cerebral ganglion, cs = crystalline style, cvc = cerebropleural–visceral connective, dg = digestive gland, es = esophagus, eye = eye, g = gill primordium, gb = gill bridge, gc = gill cavity, gs = gastric shield, hf = heel of foot, hk = primordium of heart and kidney, i = intestine, m = mouth, mc = mantle cavity, ml = mouth lobe, pa = posterior adductor, pg = pedal ganglion, plg = pleural ganglion, pn = protonephridium, pob = postoral ciliary band, pr = pedal retractor, prb = preoral ciliary band, pt = postanal ciliary tuft, s = stomach, ss = style sac, st = statocyst, tf = toe of foot, u = umbo, v = velum, vg = visceral ganglion, vr = velar retractor.) (Fig. 3 of Waller, 1981.)
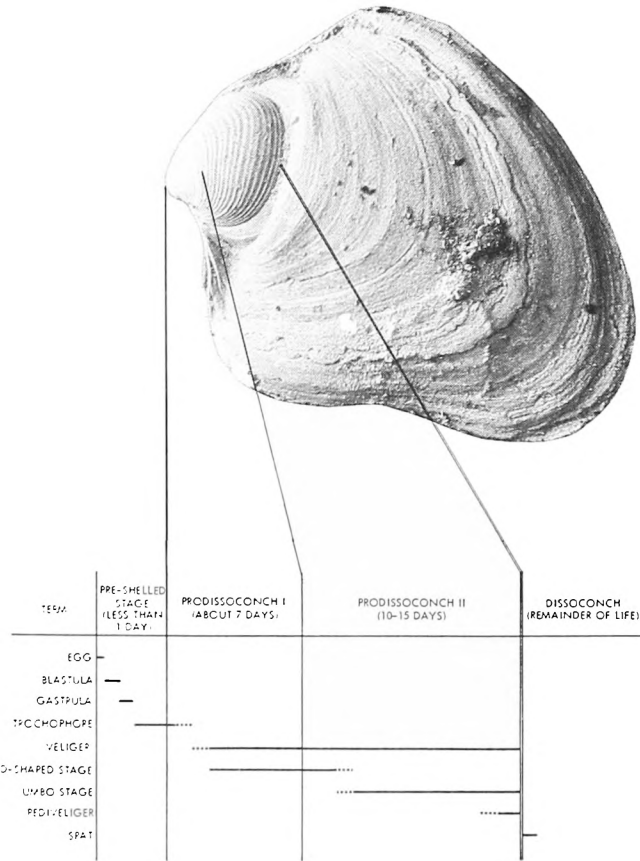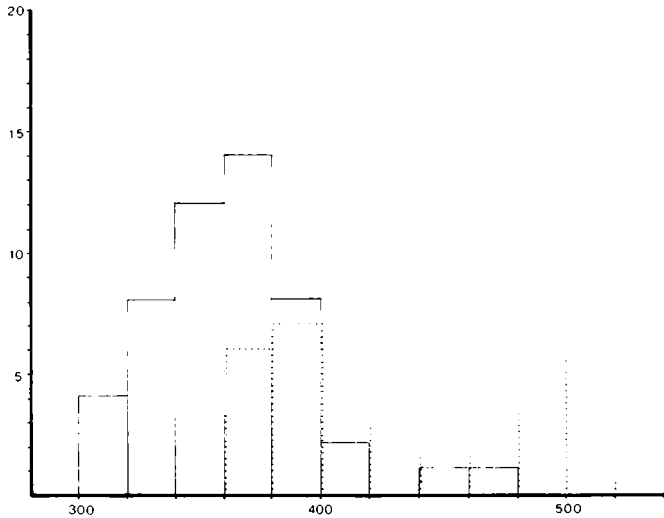

Fig. 6 Frequency distribution of height and length of pediveliger of *Liostrea plastica* at metamorphosis. The *x* axis represents dimensions in microns μ; *y* axis represents frequency; solid lines = height; dotted lines = length.

a relatively large Prod. I development (Waller 1981: figs 90–96) compared with Prod. II.

Ostrea edulis does not release gametes into the sea where external fertilization can take place, but employs a more advanced reproductive strategy. Instead, nearby males release sperm into the sea which is drawn into the female mantle cavity by feeding currents, where it fertilizes eggs contained in a 'brood pouch'. Zygotes then undergo development through blastula, gastrula and trochophore stages within the egg (Fig. 2), at which stage they are released as free swimming veliger larvae (Fig. 3).

Fig. 5 is an adaptation of Waller's (1981: 11, fig. 4) diagram correlating the development stages of the living *Ostrea edulis*
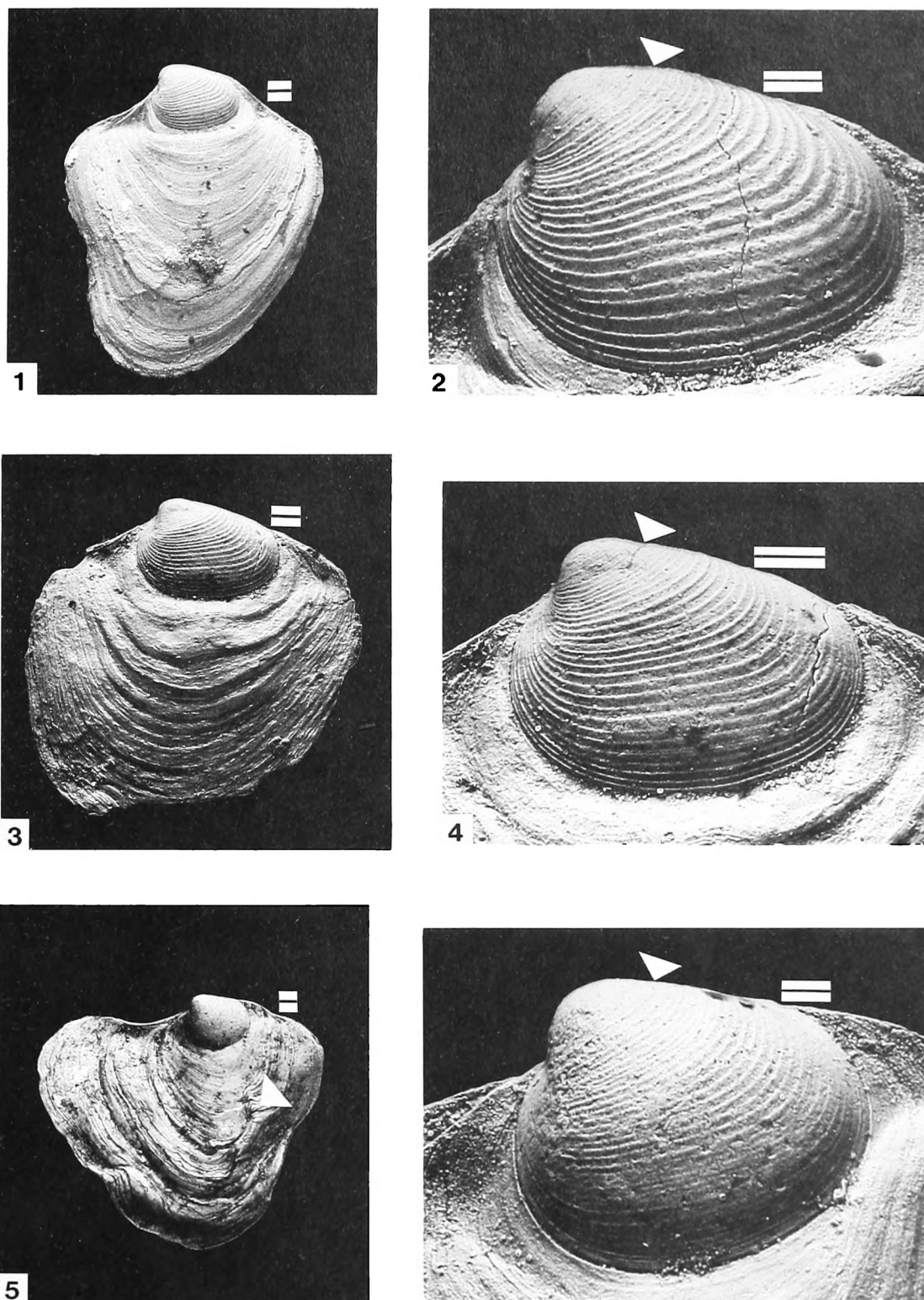

Fig. 5 Correlation of development stages of *Ostrea edulis* with *Liostrea plastica*. (Modified after fig. 4 of Waller, 1981.)

PLATE 1 *Liostrea plastica.*

Fig. 1   Complete right valve of juvenile with prodissoconch, LL41326; scale bar = 100 μ.

Fig. 2   Enlarged view of prodissoconch in fig. 1; arrow indicates inferred Prod. I/Prod. II boundary; scale bar = 50 μ.

Fig. 3   Right valve, broken ventrally, with prodissoconch, LL41327; scale bar = 100 μ.

Fig. 4   Enlarged view of prodissoconch in fig. 3; arrow indicates inferred Prod. I/Prod. II boundary; scale bar – 50 μ.

Fig. 5   Right valve of juvenile with prodissoconch, showing shell repair in dissoconch (arrow) and pronounced development of posterior margin, LL41328; see also Pl. 2, fig. 3 for enlarged view of repair; scale bar = 100 μ.

Fig. 6   Enlarged view of prodissoconch in fig. 5; arrow indicates inferred Prod. I/Prod. II boundary; scale bar – 50 μ
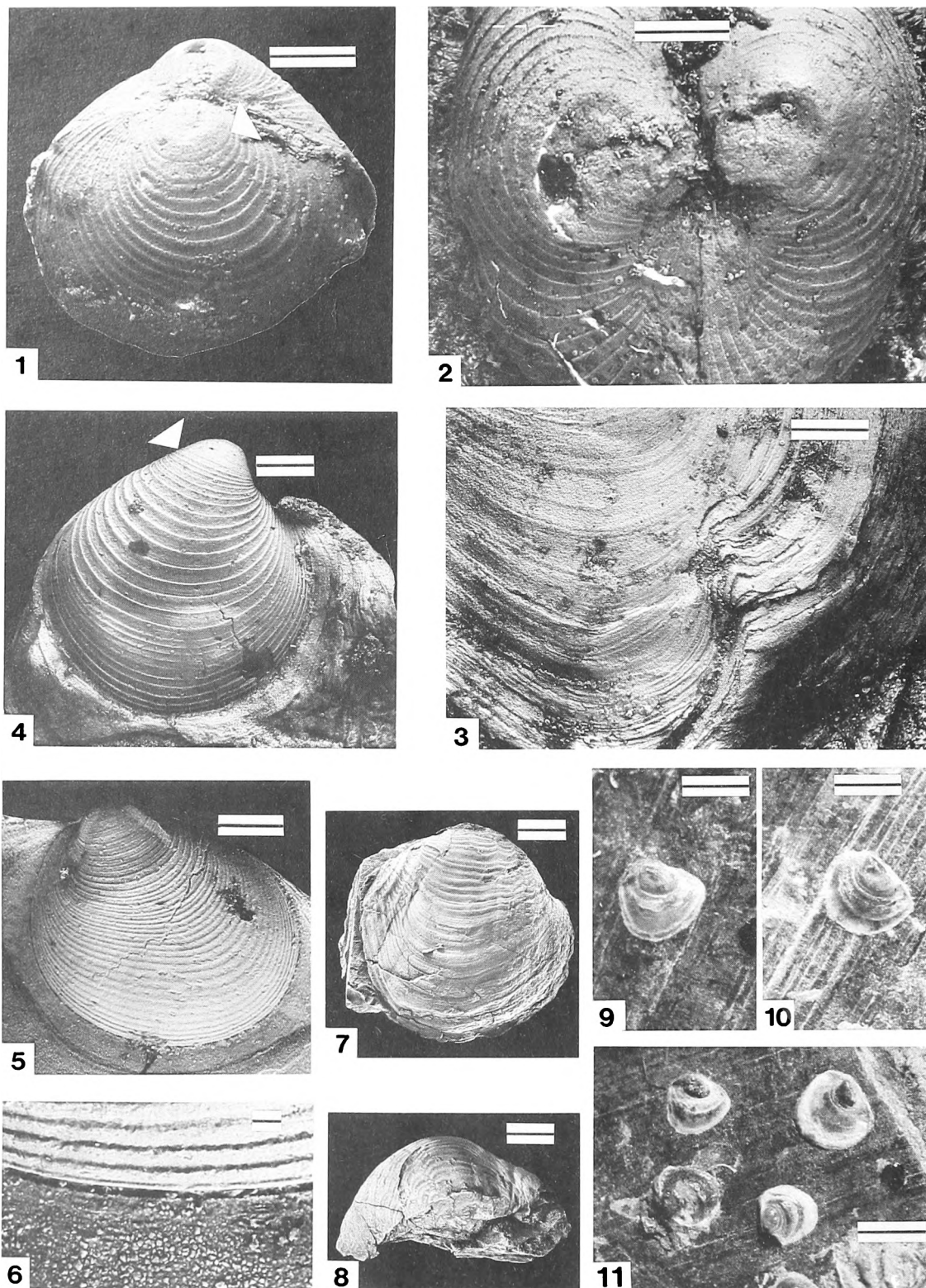
PLATE 2   *Liostrea plastica*, figs 1–8; *Liostrea irregularis*, figs 9–11.

Fig. 1   Uncrushed complete pediveliger viewed from right valve, LL41329; arrow indicates inferred Prod. I/Prod. II boundary; scale bar = 100 μ.

Fig. 2   Enlarged posterodorsal view of fig. 1, right valve on the right; no evidence of posterodorsal notch; scale bar = 50 μ.

Fig. 3   Enlarged view of the shell repair shown in Pl. 1, fig. 5, LL41328; scale bar = 100 μ.

Fig. 4   Left valve of juvenile with prodissoconch showing very high h/l % ratio and clear Prod. I/Prod. II boundary (arrow), LL41330; scale bar = 100 μ.

Fig. 5   Prodissoconch with well-defined boundary with dissoconch at metamorphosis, LL41331; scale bar = 100 μ.

Fig. 6   Enlarged view of prodissoconch/dissoconch boundary shown in fig. 5; scale bar = 10 μ.

Fig. 7   Complete right valve of adult *Liostrea plastica* showing xenomorphic 'ornament' on posterior surface, LL41332; scale bar = 10 mm.

Fig. 8   Dorsal view of fig. 7; scale bar = 10 mm.

Figs 9–11   Right valves of juvenile *Liostrea irregularis* attached to *Plagiostoma gigantea*, from the Lower Jurassic, Hettangian, Angulata Zone of Southam, Warwick, LL41333; scale bars = 1 mm.
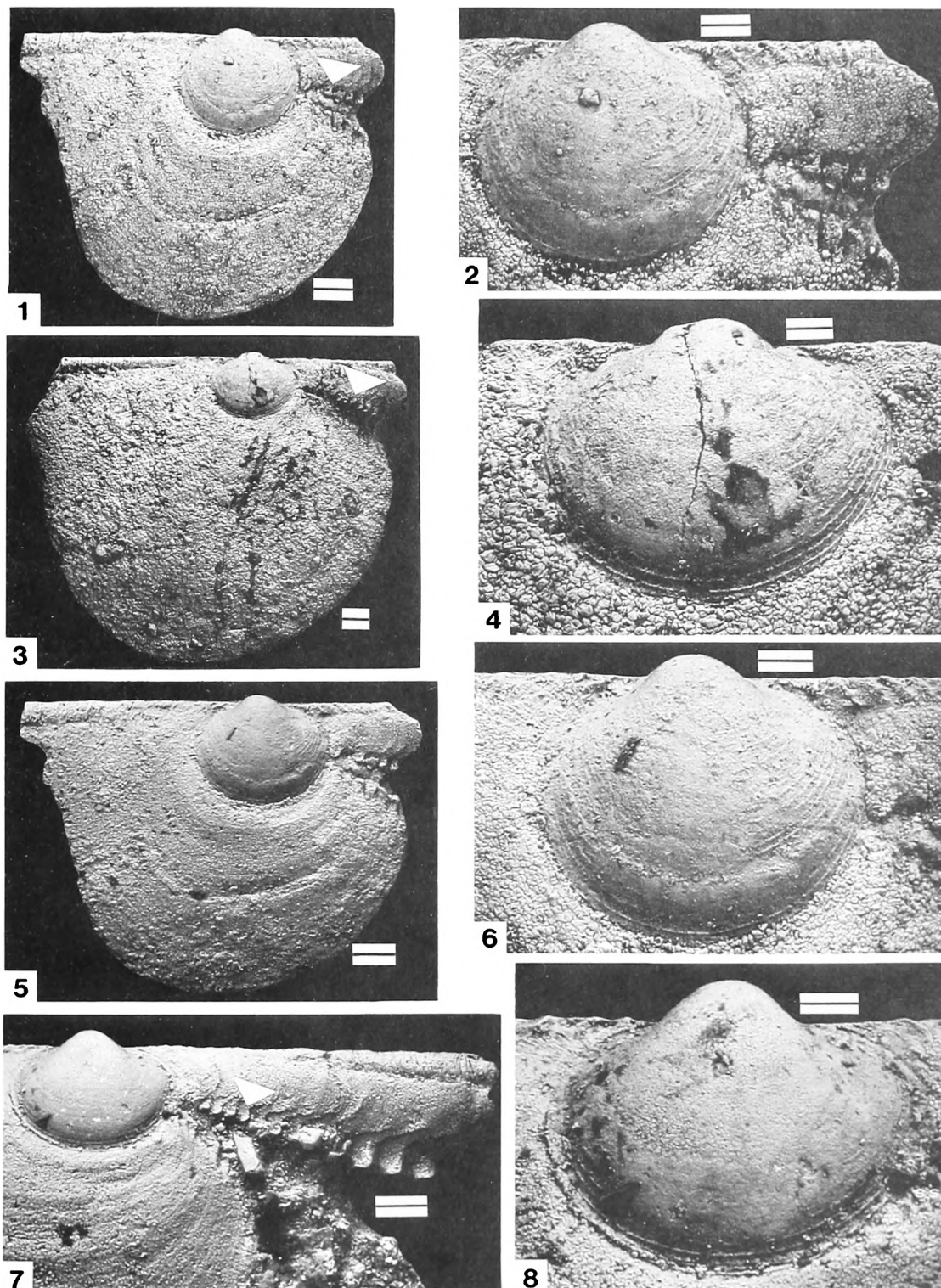
PLATE 3 *Oxytoma* sp., right valves only.

Fig. 1 Complete juvenile with prodissoconch and early development of ctenolium (arrow), LL41334; scale bar = 100 μ.
Fig. 2 Enlarged view of prodissoconch shown in fig. 1; scale bar = 50 μ.
Fig. 3 Juvenile with prodissoconch and well-developed ctenolium (arrow), LL41335; scale bar = 100 μ.
Fig. 4 Enlarged view of prodissoconch shown in fig. 3; scale bar = 50 μ.
Fig. 5 Complete juvenile with prodissoconch, LL41336; scale bar = 100 μ.
Fig. 6 Enlarged view of prodissoconch shown in fig. 5; scale bar = 50 μ.
Fig. 7 Enlarged section of anterodorsal region of juvenile showing ctenolium (arrow) and prodissoconch, LL41337; scale bar = 100 μ.
Fig. 8 Enlarged view of prodissoconch shown in fig. 7; scale bar = 50 μ.

with *Liostrea* from the Kimmeridge Clay. The duration of stages given at the head of the column are for *Ostrea edulis* only. Stages from egg to trochophore are short, less than a day: the change from trochophore to veliger larva marks the initiation of primary shell, laid down in one sheet by the shell gland and lasting about seven days – Prod. I. Co-marginal growth produces the concentric ridges and the development of an umbo during 10–15 days – Prod. II. Though the number of concentric ridges formed by *Liostrea* during Prod. II is variable, the mean of seven specimens was 29 ridges, almost twice the maximum number of days, 15, taken by *Ostrea edulis* to pass through Prod. II phase. On the assumption, therefore, that each concentric ridge represents 1 day's growth, this implies that the larval planktotrophic Prod. II phase of *Liostrea* would be roughly twice as long as in *O. edulis*. Since *O. edulis* incubates its eggs it can be expected to have a short planktotrophic veliger phase, which is normal for incubatory molluscs. If *Liostrea* did not incubate its eggs then a longer larval stage might be expected, so the implied discrepancy between the Prod. II phases of *O. edulis* and *Liostrea* may not be inconsistent with known larval durations.

At the end of Prod. II the veliger sinks to the sea floor to begin its benthic existence, and develops a foot (pediveliger phase), with which it crawls about searching for a suitable substrate upon which to cement itself by the left valve. During this phase the velum atrophies, while the shell retains the form of the prodissoconch. Upon cementation the foot also begins to atrophy, and the shell changes colour and growth direction, forming the familiar oyster-shape of the dissoconch. The junction between prodissoconch and dissoconch shell growth is sharply demarcated on all spat examined.

Clearly, the brief pediveliger phase is critical in the life of an oyster. If no suitable substrate is found then the oyster cannot cement itself and will almost certainly die. Similarly, high mortality at this phase is evident in the large number of crushed and distorted prodissoconchs of *Liostrea*, easily identified by their pale bluey-grey colour, with no dissoconch growth.

Liostrea irregularis (Münster, 1833)   Pl. 2, figs 9–11
    See Stenzel 1971 for synonymy.

MATERIAL. A *Plagiostoma gigantea* J. Sowerby 1814, 115 mm in length, with numerous adherent juvenile oysters most of which are under 1·3 mm in length with prodissoconchs in place. Associated with these is an adult *Liostrea irregularis* 49 mm in height, on the evidence of which the juvenile oysters are assigned to Münster's species. LL41333, BM(NH).

DESCRIPTIONS AND DIMENSIONS. Shells apparently smooth with strongly opisthogyrous umbones coinciding with the posterior edge, resembling in outline the nuculoid *Nuculoma*. The demarcation between Prod. I and Prod. II is far from clear in most specimens, but Plate 2, fig. 9 shows a prodissoconch RV with a shining hemispherical dome which is one eighth of the length of the prodissoconch. Rough measurements, made on a scaled photograph, indicate the length of prodissoconch at c. 0·5 mm; the Prod. I stage is thus of the order of c. 60 μm across. These measurements are the best the author could achieve.

Oxytoma sp.   Plates 3, 4

MATERIAL. 52 juvenile shells with prodissoconchs well preserved, 16 RV and 36 LV. Figured specimens LL41334–41, BM(NH).
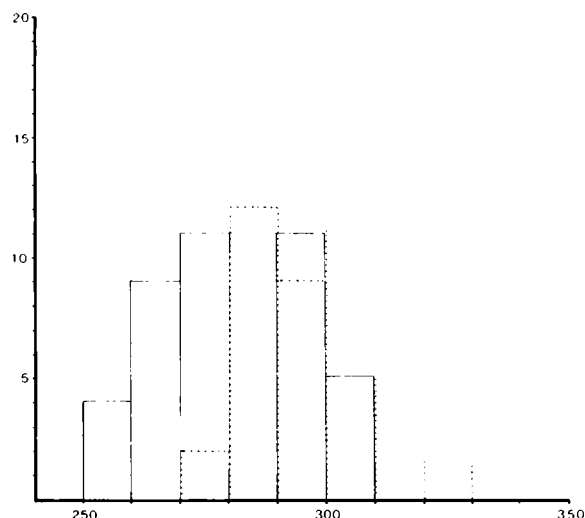

Fig. 7 Frequency distribution of height and length of prodissoconch of *Oxytoma* sp. at metamorphosis. The *x* axis represents dimensions in microns μ; *y* axis represents frequency; solid lines = height; dotted lines = length.

DESCRIPTION. Equivalve, almost ovate in outline with a prominent and centrally placed, rounded umbo interrupting the dorsal outline; slightly longer than tall, shell almost smooth but with fewer than 14 faint concentric ridges at the anterior and posterior surfaces, and fewer than 3 along the ventral margin. The junction between Prod. I and Prod. II is obscure and the faint concentric ridges give no clear indication where it is. No pediveliger two-valved specimens, lacking dissoconch growth, were seen in the picked sample, though there would have been no difficulty in recognizing them if present. Colour of prodissoconch in daylight not distinguishable from the dark brownish grey of the dissoconch.

DIMENSIONS. Though left and right valves were measured separately, no significant difference was observed so that, for purposes of calculation, left and right valves were taken together in Table 2; n = 52.

Table 2 Dimensions of prodissoconchs of *Oxytoma* sp.

	Mean	Max.	Min.	SD
height μm	276·5	300	250	14·8
length μm	295·9	320	270	13·7
h/l %	93·68	103·57	84·97	3·76

A histogram showing the frequency distribution of height and length is given in Fig. 7.

DISCUSSION. An unresolved difficulty lies in assigning these juvenile *Oxytoma* to an adult named form. L. R. Cox held the view that *O. inequivalvis* ranged almost throughout the Jurassic: W. J. Arkell held that it was confined to the Lower Jurassic. Until the stratigraphical taxonomics of this group are worked out the species name of these prodissoconchs is best left open.

Waller (1984) reminds us of three forms of ctenolium structures to be distinguished. A true ctenolium is formed by the mantle along the margin of the disc beneath the auricular notch. It is composed of lathic calcite, part of the internal structure of the shell. He compares this with the callus, or
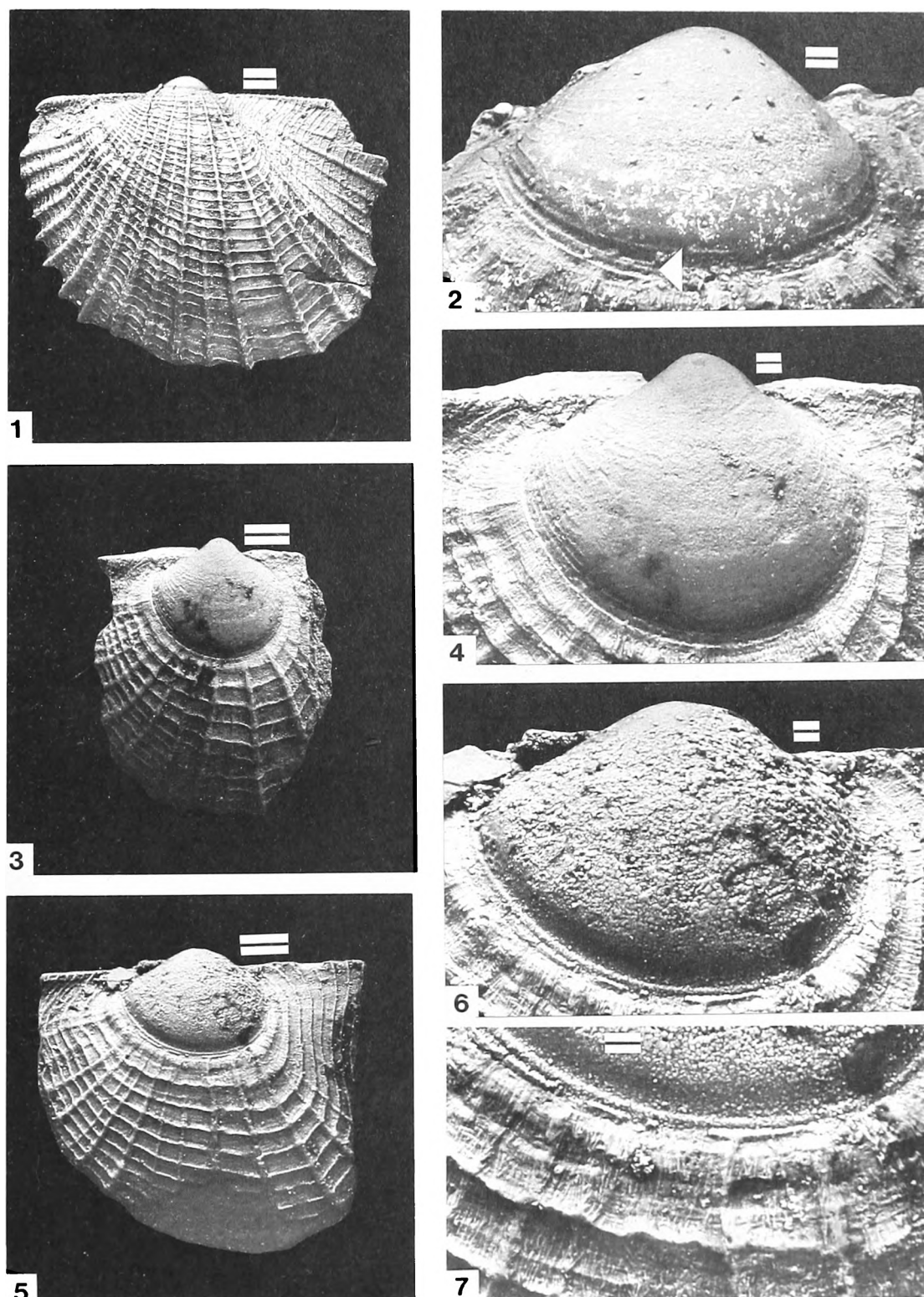
PLATE 4 *Oxytoma* sp., left valves only.

Fig. 1 Advanced juvenile with prodissoconch showing scalariform 'ornament', LL41338; scale bar = 200 μ.

Fig. 2 Enlarged view of prodissoconch of another specimen, LL41339, showing four strong growth halts at prodissoconch/dissoconch boundary (arrow); scale bar = 20 μ.

Fig. 3 Broken juvenile with prodissoconch, LL41340; scale bar = 100 μ.

Fig. 4 Enlarged view of prodissoconch in fig. 3, showing growth halts at prodissoconch/dissoconch boundary and immediate fine divaricate 'ornament' ventral to the boundary; scale bar = 20 μ.

Fig. 5 Juvenile with prodissoconch, LL41341; scale bar = 100 μ.

Fig. 6 Enlarged view of prodissoconch of fig. 5, showing two pronounced growth halts at prodissoconch/dissoconch boundary; scale bar = 20 μ

Fig. 7 Enlarged view of fig. 5 showing immediate formation of radial ribs and divaricate 'ornament' ventral to prodissoconch/dissoconch boundary; scale bar = 20 μ.
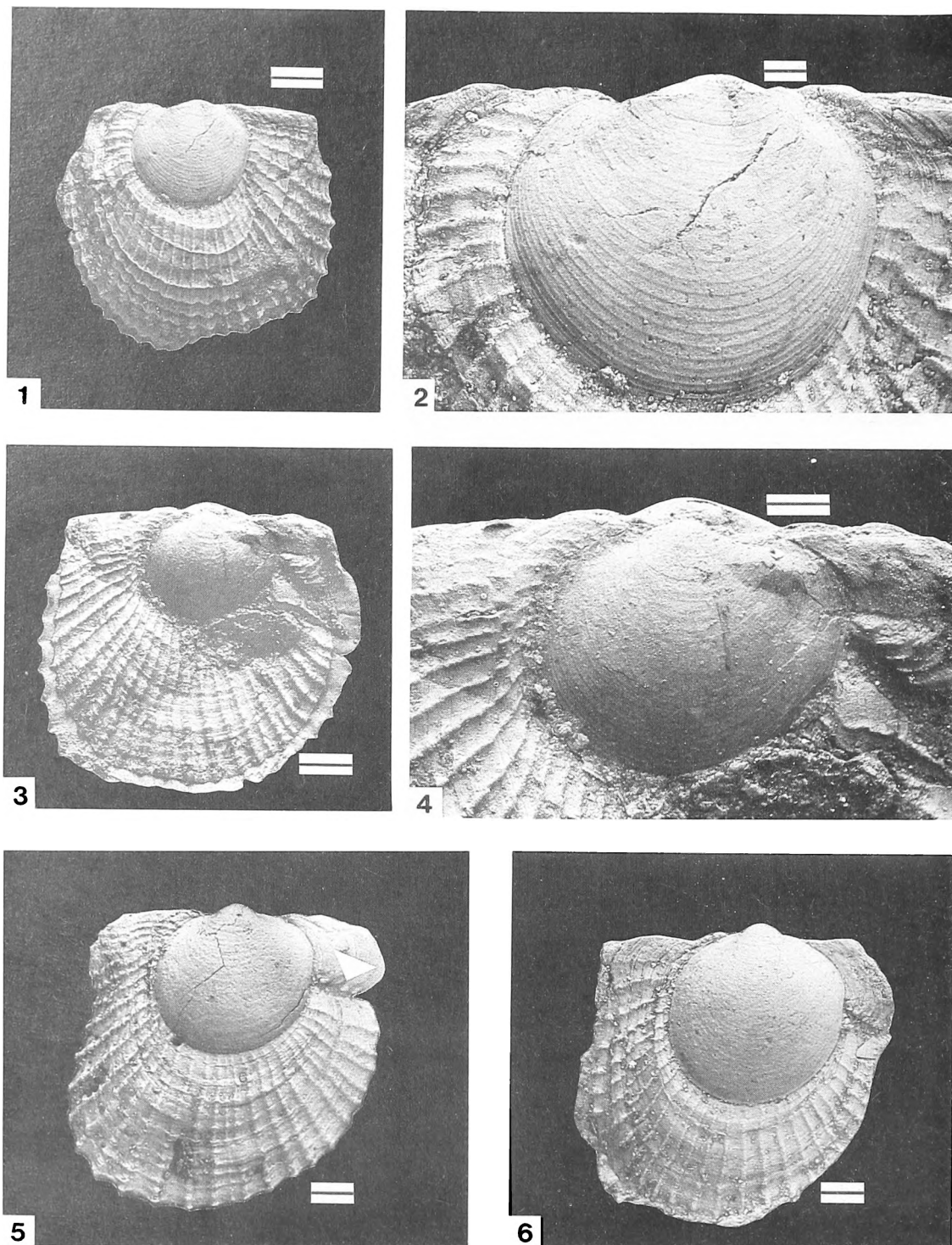
PLATE 5 *Meleagrinella* sp.

Fig. 1 Complete left valve with prodissoconch, LL41342; scale bar = 200 μ.

Fig. 2 Enlarged view of prodissoconch of fig. 1, showing approximation of growth halts before prodissoconch/dissoconch boundary, and immediate formation of radial ribs after boundary; scale bar = 50 μ.

Fig. 3 Complete two-valved juvenile viewed from right valve, LL41343; scale bar = 200 μ.

Fig. 4 Enlarged view of prodissoconch in fig. 3, slightly crushed anteriorly, showing ctenolium formed immediately after metamorphosis; scale bar = 50 μ.

Fig. 5 Complete right valve with prodissoconch and well-developed anterior auricle, showing three teeth of ctenolium (arrow), LL41344; scale bar = 100 μ.

Fig. 6 Complete right valve with larger than average prodissoconch and obscurely developed anterior auricle (arrow), LL41345; scale bar = 100 μ.

inductura, of gastropods. A pseudoctenolium is a similar line of denticles in the same position, but composed of the primary shell layer, prismatic calcite. A third category is a line of denticles on the ventral side of the right anterior auricle (Pl. 3, fig. 7). The juveniles illustrated in Plate 3 show clearly that auricular spines and a pseudoctenolium are present, since the latter is composed of prismatic calcite which is continuous with the disc (Pl. 3, fig. 2). This simply confirms Waller's earlier observation and is illustrated in his (1984) figure 3c

Waller succinctly summarizes the function of the ctenolium as follows. 'The function of the ctenolium is to separate the threads of the byssus by hooking the threads and preventing their accumulation in the apex of the byssal notch. The flat band of byssal threads passing over the disk flank when the foot is retracted is more resistant to rotational forces on the shell than would be a cord-like narrow strand of threads. The byssal attachment is thereby strengthened' (1984: 217).

Pl. 3, figs 1–6 and Pl. 4. fig. 7 confirm that prismatic calcite is confined to the right valve only in *Oxytoma*.

Meleagrinella sp.   Plate 5

MATERIAL. 57 juvenile shells with prodissoconchs well preserved, 42 RV and 15 LV. Figures specimens LL41342–5, BM(NH).

DESCRIPTION. Almost equivalve, outline subcircular, with small, centrally placed umbones interrupting the dorsal outline; shell surface with faint concentric growth ridges apparently terminating at the base of rounded hemispherical umbones. The junction between Prod. I and Prod. II is assumed to be at the position where faint concentric ridges terminate at the base of the umbones. No pediveligers were seen, though, again, they would have been clearly apparent if present, these prodissoconchs being noticeably larger and rounder than those of either *Liostrea* or *Oxytoma*. About 26–30 concentric ridges were counted from the base of the umbones to the prodissoconch/dissoconch boundary. The anterior edge shows a faint inflection at the point where the anterior auricular notch will be developed in the dissoconch (Pl. 5, fig. 6). The colour of the prodissoconch and dissoconch is not noticeably different.

DIMENSIONS. Since left and right valves were not significantly different in height and length dimensions, they were calculated together; but note that 57 lengths were measured, but only 54 heights and 54 h/l% calculations.

Table 3 Dimensions of prodissoconchs of *Meleagrinella* sp.

	Mean	Max.	Min.	SD
height μm	398·2	440	360	21·44
length μm	403·9	440	340	20·94
h/l %	98·95	105·88	90	3·76

A histogram showing the frequency distribution of height and length is given in Fig. 8.

DISCUSSION. Since no adult specimens of *Meleagrinella* were seen in the macrofauna it is not possible to assign these prodissoconchs and juveniles to a species. The relatively large size of these compared with *Oxytoma*, together with the count of approximately 24–30 concentric ridges, suggests, if
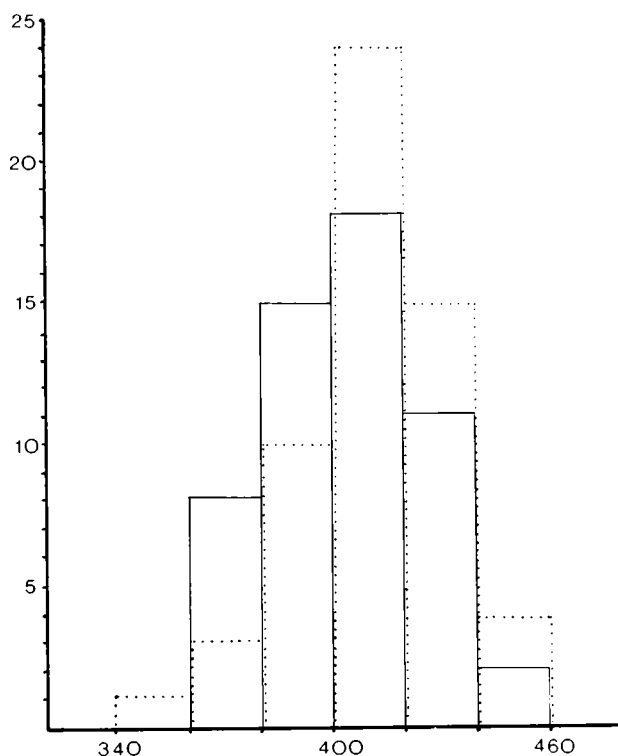

Fig. 8 Frequency distribution of height and length of prodissoconch of *Meleagrinella* sp. at metamorphosis. The *x* axis represents dimensions in microns μ; *y* axis represents frequency; solid lines = height; dotted lines = length.

each ridge represents a day's growth, that these veligers had a long larval life. In view of their absence in the macrofauna it is evident that the benthic conditions were not suitable for their development. This reminds us of Thorson's (1950: 17) observation that veligers, and other invertebrate larvae, can prolong their larval life until a suitable substrate is found.

The auricular notch indicates a functioning byssus, but no trace of a ctenolium or pseudoctenolium was seen. The ventral edge of the right anterior auricle does, however, display a series of rounded knobs each of which coincides with a growth line (Pl. 5, fig. 5). These, though functioning as a ctenolium, are analogous with Waller's (1984) 'auricular spines', seen also in *Oxytoma*.

DISCUSSION

Literature on the larval development of Jurassic bivalves is almost non-existent; though Jablonski & Lutz (1983) have assembled a vast literature dealing with the subject of larval ecology, the greater part is, not surprisingly, concentrated on living animals.

A great deal of work has been carried out on the larval development, from fertilized egg to metamorphosis, of the European oyster *Ostrea edulis* Linne 1758. Virtually all this work was brought together and amplified in a superbly illustrated synthesis by T. Waller (1981), which was used (pp. 59–64) as a basis for interpreting *Liostrea plastica* Figs 2–5 here are modified reproductions of Waller's originals, and they alone tell the outline story of the larval development

with the minimum of words, while Waller's figs 9–150 provide an abundance of detail concerning the development of the veliger larva through Prod. II to metamorphosis.

In the absence of descriptions of larval development of Pectinacea the larval shells of *Oxytoma* and *Meleagrinella* can only be described. Cope (1968) discussed the well-known oyster infestation of Upper Kimmeridgian ammonites; and figured (1968: pl. 2, fig. 2) a *Pectinatites* plastered with *Liostrea multiformis* (Koch & Dunker). He concluded that their presence as adults was 'dependent entirely on the presence of vacated ammonite shells on the sea floor'.

Palmer (1988) has argued an alternative hypothesis, since some ammonites are 'infested' on both sides, that the idea of delicate hydrostatic adjustments in ammonites implies the presence of shell-cleaning behaviour in all ammonites as being close to a biological necessity. Therefore some of the ammonites were 'infested' after the animal was dead but while the shell was still floating. The evidence seems to indicate that examples to fit both hypotheses could be present.

Thorson (1950) stressed the significance of limiting ecological factors controlling the distribution of marine invertebrates; and he isolated three which act upon the weakest link in the chain of development, the larval stage. First, it was found that the temperatures required to induce spawning are considerably higher than the normal temperature requirements of adults; second, that gamete production takes place at the top end of the salinity range tolerated by adult animals; third, the food requirements of larval marine invertebrates is between 5 and 10 times higher than for adults. In order to achieve a coincidence of these critical and very definite factors, some marine animals migrate from places that the adults can tolerate, to a place where the larvae can survive (Thorson 1950).

If the weakest link lies in the larval life where mortality is highest, then another stage of high mortality for *Liostrea* lies in the dissoconch stage, from metamorphosis to around 2 mm length. The number of pediveligers and juvenile dissoconchs up to 2 mm far exceeds the number of adult oysters collected.

No pediveligers of *Oxytoma* or *Meleagrinella* were seen, though adults of the former do occur, but not the latter; while juvenile dissoconchs, up to 2 mm, of both genera were about equally common. This again indicates a critical stage.

Clearly, then, the limiting factor is the substrate: the shales of the Kimmeridge Clay were once a soft muddy bottom which was suitable for neither cementing oysters not byssally attached pectinaceans. The lucky ones found an empty ammonite shell to grow on (Cope 1968) or a floating one (Palmer 1988). The rest did not survive growth beyond 2 mm. Several authors, including Thorson (1946, 1950), have suggested that early post settlement is the time of greatest mortality. Quantitative tests, though difficult with living animals, are virtually impossible with fossil bivalves.

If the Prod. I/Prod. II boundaries in the three genera described here have been correctly identified, then it is evident that Prod. I is an order of size smaller than Prod. II. This would rule out incubation of eggs: it therefore appears that all three genera had wholly planktotrophic development from relatively small eggs. At the same time the relatively large Prod. II phase of *Meleagrinella* may indicate a prolonged larva phase necessitated by the lack of suitable substrate for byssal attachment. It is known that larvae of molluscs can delay settlement and metamorphosis until a sutiable substrate is encountered (Thorson 1946).

PALAEOECOLOGICAL REMARKS

Palmer (1988) has argued that the plesiosaur excavation at Portland is stratigraphically equivalent to Cope's (1978) bed 2, hard bituminous shale, at Chapman's Pool on the coast of Dorset. This correlation is founded on ammonites, *Pavlovia* spp., and supported by the presence of shell beds with the same benthic and pelagic faunal elements at both localities.

Casey (1967) showed that the Upper Lydite Bed at Hartwell, Bucks, is equivalent to beds, at Chapman's Pool, from the Rotunda Nodule Bed up to the base of the Portland Sands. The Hartwell Clay below the Upper Lydite Bed is therefore equivalent to shales below the Rotunda Nodule Bed at Chapman's Pool; that is, bed 2. The correlation is supported by the arcticid bivalve *Venericyprina argillacea* Casey, present in the Hartwell Clay and also at Chapman's Pool, and in the plesiosaur excavation at Portland.

Lloyd *et al.* (1973) reported pavloviid ammonites in Kimmeridge Clay, 10 km north of Combe Martin in the Bristol Channel. The ammonites correlate with either bed 1 or 2 at Chapman's Pool; but the author has argued, on the evidence of cirripeds at both localities and at Portland, a correlation with bed 2 at Chapman's Pool and the plesiosaur excavation at Portland.

If these correlations are correct then it is evident that benthic shelly beds occur, at the same stratigraphical level, at Portland, Chapman's Pool and Hartwell in one direction and in the Bristol Channel in another direction. These rich benthic horizons are unlikely to be purely local events and fortuitously at the same stratigraphical level, but part of a widespread ecological event resulting in rich living for benthic communities. An abundant microfauna of ostracods and foraminiferans, together with numerous filter-feeding bivalves, fish and plesiosaurs, are all elements of an elaborate food chain founded on a widespread plankton field which was stable for several thousand years.

CONCLUSIONS

Liostrea, Oxytoma and *Meleagrinella* all had planktotrophic larvae with a prolonged veliger Prod. II stage which may have been related to a lack of suitable habitats for cementing oysters and bysally attached pectinaceans. A period of 30 days veliger Prod. II phase is suggested on the evidence of rib counts on larval shells of *Liostrea*. A high mortality characterized the phase from pediveliger to dissoconch development up to 2 mm.

Those oysters that attached themselves to empty ammonite shells, either on the sea floor or while still floating, were able to grow to maturity; but the greater majority settled on a muddy sea floor and died at 2 mm of dissoconch growth. All this took place in the context of a postulated widespread plankton field, extending, at least, from Portland to the Bristol Channel and Buckinghamshire.

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REFERENCES

Brown, D. S. 1984. Discovery of a specimen of the plesiosaur *Colymbosaurus trochanterius* (Owen) on the Island of Portland. *Proceedings of the Dorset Natural History and Archaeological Society*, Dorchester, **100**: 170.

Casey, R. 1967. The position of the Middle Volgian in the English Jurassic. *Proceedings of the Geological Society of London*, **1640**: 128–133.

Cope, J. C. W. 1968. Epizoic oysters on Kimmeridgian ammonites. *Palaeontology*, London, **11** (1): 19–20.

—— 1978. The ammonite faunas and stratigraphy of the upper part of the Upper Kimmeridge Clay of Dorset. *Palaeontology*, London, **21** (3): 469–533.

Erdmann, W. 1935. Untersuchungen über die Lebensgeschichte der Auster, 5. Über die Entwicklung und die Anatomie der 'ansatzreifen' Larve von *Ostrea edulis* mit Bemerkungen über die Lebensgeschichte der Auster. *Wissenschaftliche Meeresuntersuchungen der Kommission zur Wissenschaften Untersuchung der Deutschen Meere (Helgoland)*, Kiel & Leipzig, n.s. **19** (6), 25 pp., 5 figs, 8 pls.

Horst, R. 1882. Bijdrage tot de kennis van de ontwikkelingsgeschiedenis van der oester (*Ostrea edulis*). *Tijdschrift der Nederlandsche Dierkundige Vereeniging*, Leiden, **6**: 25–34, pl. 3. (Engl. transl. Jacobson, H. 1886, *Report United States Commissioner of Fisheries*, Washington, **1884** (34): 891–910, 2 pls.)

Jablonski, D. & Lutz, R. A. 1983. Larval ecology of marine benthic invertebrates: palaeobiological implications. *Biological Review of the Cambridge Philosophical Society*, **58** (1): 21–89.

Kelly, A. R. A. 1984. Bivalvia of the Spilsby Sandstone and Sandringham Sands (Late Jurassic–Early Cretaceous) of Eastern England. Part I: 1–94, 20 pls. *Monograph of the Palaeontographical Society*, London.

Lloyd, A. J., Savage, R. J. G., Stride, A. H. & Donovan, D. T. 1973. The geology of the Bristol Channel floor. *Philosophical Transactions of the Royal Society of London*, (A) **274** (1244): 595–626.

Palmer, C. P. 1988. The Kimmeridgian fauna associated with the Portland plesiosaur. *Proceedings of the Dorset Natural History and Archaeological Society*, Dorchester, **109** (1987): 109–112.

Stenzel, H. B. 1971. Oysters. *In* Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology*, N (Mollusca 6, Bivalvia 3): N953–N1224. Geol. Soc. Amer. and Univ. Kansas Press.

Taylor, P. D. 1986. Scanning electron microscopy of uncoated fossils. *Palaeontology*, London, **29** (4): 685–690.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates. *Meddelelser fra Kommissionen for Danmarks Fiskeri og Havundersøgelser*, Copenhagen, (Plankton) **4** (1). 523 pp.

—— 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Review of the Cambridge Philosophical Society*, **25**: 1–45.

Waller, T. R. 1981. Functional morphology and development of veliger larvae of the European oyster *Ostrea edulis* Linné. *Smithsonian Contributions to Zoology*, Washington, **328**. 70 pp.

—— 1984. The ctenolium of scallop shells: functional morphology and evolution of a key family-level character in the Pectinacea (Mollusca: Bivalvia). *Malacologia*, Ann Arbor, **25** (1): 203–219.