

DISARTICULATED BIVALVE SHELLS  
AS SUBSTRATES FOR ENCRUSTATION BY THE  
BRYOZOAN *CRIBRILINA PUNCTURATA* IN THE  
PLIO-PLEISTOCENE RED CRAG OF  
EASTERN ENGLAND

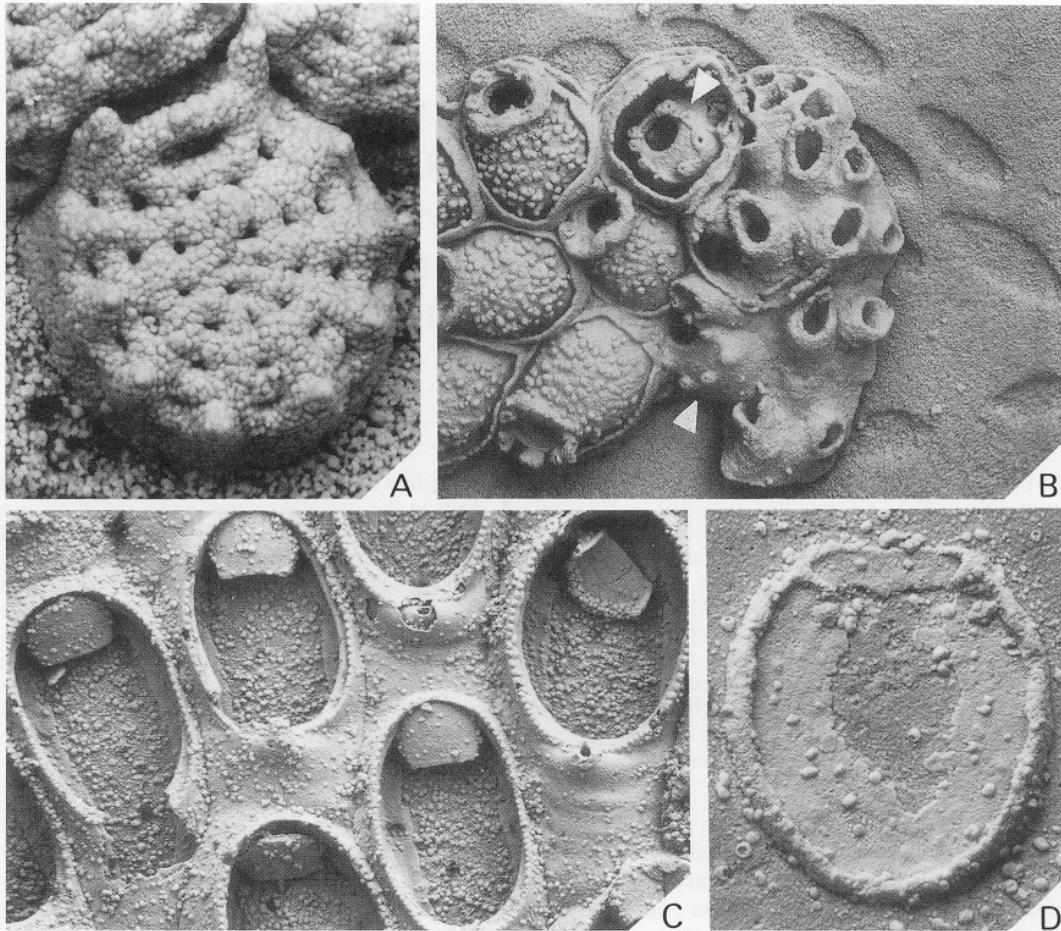
by J. D. D. BISHOP

**ABSTRACT.** *Cribrilina puncturata* (Wood, 1844) forms small, patch-like colonies encrusting the concave (almost invariably lower) surface of disarticulated bivalve mollusc shells in the Plio-Pleistocene Red Crag of eastern England. The species is restricted to the deeper central part of each shell, away from the margin. Peripheral abrasion of the shell's surface, which might have removed marginal settlement, is rejected as the major agent in producing the observed distribution. A number of larval behaviour mechanisms that might have been responsible are therefore considered. All are discounted except one: that the larva crept up the slope of the shell's inner surface towards the highest point (geonegative movement) before fixation. This hypothesis seems to explain many details of the settlement pattern. *C. puncturata* apparently exploited the shell's major concavity as a refuge from physical disturbance in a high-energy environment, and its larval settlement behaviour appears to have been specialized for concavo-convex (bivalve) substrates. A second category of refuge, minor local concavities anywhere on the shell's surface, was occupied during the vulnerable early astogenetic stages of two other bryozoan species, both with a runner-like colony morphology.

DISARTICULATED bivalve shells on an unconsolidated sea-bed offer a restricted area for potential encrustation, and are often isolated from other solid substrates (including other shells). Shells of the same species and size may be regarded as natural replicate settlement panels, and topographically equivalent areas can be defined on conspecific shells of different size. The bivalve assemblage as a whole may include a wide variety of sizes and shapes. Shells therefore present considerable scope for study as small, discrete, and sometimes short-lived substrates that have relevance to the ecological concepts of spatial refuges (Jackson 1977; Buss 1979) and habitat islands or isolated patches (Schoener 1974; Osman 1977; Keough 1984). This was recognized by Miller and Alvis (1986). In addition to their small size and potential isolation, most shells have another notable feature, bidirectional curvature, which has a strong influence on their hydrodynamic behaviour (Allen 1984). The significance of this concavo-convex shape for a potential encruster, particularly in relation to physical disturbance, is the underlying theme of the present paper.

The lower, sand-wave facies of the Plio-Pleistocene Red Crag is exposed on the coast and at numerous inland localities in a region of north-east Essex and south-east Suffolk approximately bounded by Walton-on-the-Naze, Ipswich, Woodbridge, and Chillesford. It consists of poorly consolidated, coarse (but often poorly sorted) shelly sands, showing large-scale tabular cross-bedding. The sand-waves had amplitudes of up to 5 m (commonly 2–3.5 m), and were the product of a flow regime that generated net sediment transport roughly towards the south-west in perhaps 15–25 m of water (Dixon 1979). Boatman (1973) and Bridges (1982) considered the local current regime to have been tidally dominated, while Dixon (1979) attributed only secondary sedimentary structures in this facies to tidal action.

The sand-wave facies often contains abundant disarticulated bivalve mollusc shells, which may be fairly evenly distributed within the deposit or may form more or less distinct bands (in which



TEXT-FIG. 1. A, *Cribrilina puncturata* (Wood, 1844), BMNH D56116, ancestrula (with proximal parts of periancestrular zooids); Red Crag, Brightwell, approx.  $\times 250$ . B, BMNH D56997, successive episodes of colonization of the same region of a shell by bryozoans; Red Crag, Newbourn (different exposure from that referred to as 'Newbourn' in text),  $\times 58$ . The oval pits were etched in the shell surface by a colony of *Electra* sp., subsequently detached; the etchings were then partially overgrown by a tubuliporine cyclostome; a cheilostome, *?Balantiostoma* sp. (ancestrula indicated by lower arrow), settled on the cyclostome, probably after its death since the ancestrula partially covered an already abraded peristome; finally, a second cheilostome, probably also *?Balantiostoma* sp. (ancestrula only, indicated by upper arrow), apparently settled within a damaged zooid of the first (although the established first colony may possibly have overgrown the ancestrula). C, *E. crustulenta* (Pallas, 1766), British Geological Survey ZK 2658; Red Crag, Butley Priory,  $\times 82$ . Calcified opercula, attached to the frontal membrane in life, are preserved *in situ* (or slightly displaced) at the distal (top) ends of the zooids. D, *C. puncturata*, BMNH D55856, basal remains of ancestrula after abrasion; Red Crag, Shottisham, approx.  $\times 210$ .

imbrication sometimes occurs). The shells are almost all in convex-up orientation. They are often encrusted by bryozoans on their concave (inner, almost invariably lower) surface; similar encrustation of the convex surface is much rarer. The Bryozoa are quite diverse, with at least thirty-five species recognized by the present author from the Red Crag as a whole. Preservation is often very good, although colonies may be extremely delicate and require careful cleaning. At most exposures, the

encrusters are dominated by inconspicuous species forming small, scattered colonies. Perhaps for this reason, the bryozoan fauna is poorly documented.

*Cribrilina puncturata* (Wood, 1844) is the most widespread and, at many localities, the most abundant cheilostome bryozoan encrusting Red Crag bivalves. It is the only cheilostome to encrust shells in any numbers in the relatively impoverished assemblage of the Red Crag of Butley. The colonies are generally small, rarely having more than fifty autozooids, but produced ovicells (skeletal chambers in which embryos were brooded) very early in colony development. As is typical for Bryozoa, the colony was founded by an ancestrula (text-fig. 1A), a single zooid arising in all known cases from the metamorphosis of a mobile larva. The ancestrula of *C. puncturata* is morphologically distinct from subsequent zooids, which were produced by a process of budding to yield a patch-like colony of contiguous zooids. *C. puncturata* is not known to occur outside the Red Crag. In this paper, the pattern of its settlement on the concave surface of bivalve shells is described, and possible explanations for this pattern discussed. The behavioural (or other) mechanism by which a settling larva came to be on the underside of a shell is not considered.

In the material studied, only about 25% of *C. puncturata* colonies are in contact with another bryozoan. The Bryozoa as a whole generally cover less than 5% of the area of the concave shell surface. It is furthermore apparent that the preserved colonies were not all alive at the same time—a particular shell may show several successive episodes of encrustation (text-fig. 1B). Other encrusting organisms are rare or absent (although serpulid worms and barnacles may be reasonably abundant at Red Crag sites other than those studied here). Whilst the presence of soft-bodied encrusters cannot be discounted, it seems unlikely that biological interactions in the form of competition for space were important on the shells studied. The settlement patterns observed are accordingly discussed primarily in terms of the rigorous physical conditions of the sand-wave environment.

#### MATERIAL AND METHODS

The encrusted fossil shells studied came from three Suffolk pits, at NGR TM 250430, TM 275434, and TM 318457, which are referred to below simply as Brightwell, Newbourn, and Shottisham, respectively. The material from Brightwell and Newbourn is referable to the lower, sand-wave facies of the Red Crag described above. The shells from Shottisham are from trough-bedded sands somewhat intermediate in character between the lower facies and the upper, nearshore/onshore facies of Dixon (1979). Shells from the channel deposits above the trough-bedded sands at Shottisham were not included in the study.

Four taxa of shells are considered: *Glycymeris glycymeris* (Linnaeus, 1758), *Macoma obliqua* (J. Sowerby, 1817), *M. praetenuis* (Leathes in Woodward, 1833), and *Spisula* sp(p). A range of shell shapes was present in the *Spisula* material available, representing a number of nominal species and subspecies that could not be confidently distinguished. To restrict the degree of variation (in order to ensure that comparison between shells was reasonably valid), the investigation was limited to relatively equilateral *Spisula* shells with oval (rather than markedly triangular) outlines; the shells were selected on this basis without a priori knowledge of the settlement of *C. puncturata* on them. *G. glycymeris* and *Spisula* sp(p). are referred to below by genus.

*Glycymeris* from Brightwell were collected by P. G. Cambridge and S. A. Clark and presented to the British Museum (Natural History) in 1964 and 1965. The material studied here was selected from a larger series to give a set of complete shells with undamaged inner surfaces, covering the desired size ranges. There was no a priori knowledge of the positions of *C. puncturata* settlement on the shells at the time of selection. *Spisula*, *Glycymeris*, *M. obliqua*, and *M. praetenuis* from Shottisham, and *Spisula* from Newbourn were collected during 1983 and 1984 by the author and colleagues. All suitable specimens of the relevant mollusc species from the Shottisham and Newbourn series were included in the analysis. Only 2–3% of shells at these two localities were preserved in concave-up orientation.

The encrusted shells on which settlement was studied are detailed below, with their registration numbers in the Department of Palaeontology, British Museum (Natural History):

*Spisula*: Newbourn, n = 49 (D55670, 55671, 55679, 55682, 55684–55687, 55693, 55694, 56912, 56913, 56915, 56921, 56923, 56934, 56949, 56950, 56978, 56981, 57437–57465), mean height = 16.7 mm (standard deviation,  $\sigma = 1.3$  mm); Shottisham, n = 27 (D55920, 55934, 55935, 55941, 55944, 55945, 55947–55949, 55953–55958, 56066, 56094, 56095, 56097, 56100, 56102, 56105–56108, 56110, 57730), mean ht. = 14.7 mm ( $\sigma = 1.5$  mm).

*Glycymeris*: Brightwell (D49145, 49208, 49209, 49356, 49358, 49360, 49372, 49389, 49399, 49406, 49411, 49423, 49425, 49429, 56117, 56122), small shells,  $n = 7$ , mean ht. = 28.9 mm ( $\sigma = 1.3$  mm); large shells,  $n = 9$ , mean ht. = 44.4 mm ( $\sigma = 1.3$  mm); both sets combined,  $n = 16$ , mean ht. = 37.6 mm ( $\sigma = 7.8$  mm); Shottisham,  $n = 13$  (D55900–55907, 56046–56049, 56053), mean ht. = 37.0 mm ( $\sigma = 8.0$  mm).

*M. obliqua*: Shottisham,  $n = 35$  (D55832, 55834, 55835, 55837, 55839, 55842, 55843, 55847, 55921, 55923–55925, 55927, 55928, 55930, 55931, 55963–55967, 56071–56076, 56079–56085, 56114), mean ht. = 27.4 mm ( $\sigma = 6.0$  mm).

*M. praetenuis*: Shottisham,  $n = 46$  (D55849, 55850, 55852–55854, 55856, 55860, 55862, 55863, 55865, 55867, 55868, 55870, 55871, 55875, 55970–55972, 55974, 55976–55989, 55992, 55993, 55995, 55997–56000, 56004, 56006, 56008, 57732–57734), mean ht. = 21.5 mm ( $\sigma = 2.8$  mm).

To hold a shell in the standard position for observation, it was placed concave-up on cotton wool that slightly over-filled a small rectangular-sided box. Putting a heavy glass lid on the box compressed the cotton wool, pressing the shell evenly upwards against the glass, through which observations could then be made; when viewed perpendicularly to the glass, the shell was therefore seen at or very near to its maximum projected area. The orientation of the concave-up shell with respect to the glass lid was taken to be similar to the positioning the shell would adopt when laying convex-up on a planar surface (except of course that the respective positions were inverted).

The term *shell depth contour* is used below for the line joining points on the inner surface of the shell at the same vertical distance from the surface of the glass against which the shell was pressed. For instance, the 0.6 depth contour joined points 0.6 of the vertical distance from the glass to the furthest (deepest) point on the inside of the shell. Contours were plotted using the plane of focus of a compound microscope, with the shell levelled (in its box) on the stage of the microscope. Vertical movement of the microscope stage was measured using a dial gauge. Horizontal movement, to map the shell's outline and contours, was plotted from the stage's Vernier scales on to graph paper. The generation of shell depth contours was in general carried out for a single left and a single right valve of each shell taxon; the same shells were used to provide the standard shell outlines (see below). However, the 0.6 depth contour was mapped for three right valves of different sizes for *Glycymeris* (text-fig. 4B).

The term *isoclinic line* is used below for the line joining points on the inside of the levelled shell at which the shell's surface formed a particular angle to the horizontal. A small metal ball (a sphere of diameter 1.0 mm) was placed inside the shell, with the shell in its box resting on a surface inclined at the relevant angle. When the box was turned slowly through 360° (so that successive portions of the shell's margin were brought to the lowest point), the isoclinic line could be traced from the successive positions of the ball. The movement of the ball was often somewhat unpredictable because the shells' surfaces were not perfectly smooth, and it was necessary to adopt the following procedure to obtain reasonably consistent results: after plotting the position of the ball at one point during the rotation of a shell, the observation box was lifted to the horizontal position so that the ball moved to the centre of the shell; the box was rotated a fraction of a turn and then lowered back on to the tilted surface; the lid of the box was tapped gently several times to ensure that the ball had rolled back to a new stable position, which was then plotted; this process was repeated until a full turn of the shell had been completed. Isoclinic lines were plotted for five left and five right valves of each shell taxon. The lines from the five shells could be reduced to a single summary line which passed through the mean position of the individual lines. The summary lines for left and right valves of the same shell taxon were combined by simply drawing midway between the two.

As a rough index of internal concavo-convexity, the ratio of a shell's greatest internal depth to the diameter of a circle equal in area to its maximum projected area was adopted. On this basis, the relative concavo-convexity of the taxa studied was: *Spisula*  $\approx$  *Glycymeris*  $\approx$  *M. obliqua*  $>$  *M. praetenuis*.

In *Glycymeris* and *Spisula*, the left and right valves are almost exact mirror images of one another, apart from details of the hinge line. However, in the two species of *Macoma* considered here, the curvature of the shells differ. The posterior portions of both valves, viewed dorsally, are deflected to the right (although the overall concavo-convexity and the outlines of the left and right valves in two dimensions are similar). When laid convex-up on a flat surface, the margin of the left valve is therefore raised at the umbo and along much of the ventral margin; that of the right valve is raised at the posterior corner and along the anterodorsal margin.

The ancestrula of each colony represents the position of larval fixation and metamorphosis ('settlement' below). In colonies where the origin was not preserved, settlement was mapped immediately proximal to the astogenetically youngest (most proximal) part of the remaining portion. For each species of shell, a standard outline was taken from one left valve and one right valve of typical shape near the middle of the size range of the

shells from which settlement was mapped. The position of settlement of *C. puncturata*, and the isoclinic lines, were plotted on to the standard outline of the appropriate species of shell of the correct handedness using a zoom binocular microscope fitted with drawing-tube attachment and with its optical axis perpendicular to the glass lid of the observation box. The standard shell outline and the image of an actual shell were aligned as follows: the umbos were superimposed, and the outlines placed so that any discrepancy between the respective dorsal margins was evenly shared between the anterior and posterior sides; the magnification was adjusted so that the ventral margins were congruent or, in the event of slight differences in ventral shape, so that the overlap of one outline by the other in one place was compensated elsewhere on the ventral margin. In this way, details of several shells could be mapped on to a common outline. Repeated mapping of the same shell indicated an acceptable level of precision. Shell depth contours were transferred from xerographic reductions of the graph paper plots (see above) on to the standard shell outlines by the same system.

Kuiper's two-sample test, as described by Batschelet (1981), was used to evaluate statistically the differences between the settlement patterns on contrasting categories of shell of the same species. (The test is a development of the Kolmogorov-Smirnov test for application to circular distributions, and gives results independent of the chosen zero direction.) The plane delimited by the standard shell outline was divided into seventy-two 5° sectors radiating from its centre of area. Settlement points were counted within each sector for both categories of shell, then Kuiper's test was applied to the counts. Two patterns were considered to be significantly different if the resulting value of the test statistic,  $V_{n,m}$  (where  $n$  and  $m$  were the respective numbers of points of the two categories), corresponded to a probability,  $p$ ,  $< 0.05$ .

### THE PATTERN OF SETTLEMENT

When the positions of *C. puncturata* ancestrulae were mapped from several shells on to a common outline, definite settlement patches were apparent for each of the four taxa of shell studied (text-fig. 2). Settlement was almost always away from the margin, within the deeper part of the shell. In *Spisula*, settlement was tightly packed within the 0.6 depth contour, and indeed mostly fell within the 0.8 depth contour; patterns of settlement on the left and right valves were not significantly different (Newbourn:  $V_{33,52} = 0.198$ ,  $p > 0.50$ . Shottisham:  $V_{22,32} = 0.362$ ,  $0.50 > p > 0.20$ ). In *Glycymeris*, settlement was mostly within the 0.6 depth contour, and distributions of ancestrulae were again similar on the left and right valves (Brightwell:  $V_{65,71} = 0.127$ ,  $p > 0.50$ . Shottisham:  $V_{18,56} = 0.161$ ,  $p > 0.50$ ). Settlement on *M. praetenuis* was also almost restricted to the area within the 0.6 depth contour, but in this case the spatial distribution differed between left and right valves (Shottisham:  $V_{88,99} = 0.314$ ,  $0.005 > p > 0.002$ ), with settlement on the right valve being generally slightly nearer to the anterior margin. *M. obliqua* showed a similar pattern, with dense settlement within the 0.6 depth contour but with the exact pattern differing between left and right valves (Shottisham:  $V_{57,112} = 0.306$ ,  $0.02 > p > 0.01$ ); the main settlement patch of the right valve was nearer to the anterior margin, and small secondary patches associated with the adductor muscle scars were also apparent on this valve.

### POSSIBLE EXPLANATIONS FOR THE OBSERVED PATTERN

#### *Abrasion*

It might be argued that settlement of *C. puncturata* is indiscriminate, and that the pattern described above is produced by abrasion of peripheral encrustation before fossilization, leaving only colonies on the deeper, more protected part of the shell. This pattern of peripheral abrasion was observed in the differential removal of Indian ink from *Glycymeris* shells abraded by Red Crag sediment during mechanical agitation under water in a jar. Furthermore, discrepancies between the settlement patches of *C. puncturata* on the differently curved left and right valves of *Macoma* spp. might be expected under this hypothesis. However, the following observations suggest that the hypothesis should be rejected:

a. The umbonal region of the inner surface of the shell is the most strongly concave (text-fig. 4C) and is thus relatively well protected from abrasion. It nevertheless has very sparse recorded settlement of *C. puncturata* (for instance, text-fig. 2).

b. On *Glycymeris* from Brightwell, colony portions of *Electra crustulenta* (Pallas, 1766) and *Phylactellipora* sp. are occasionally seen near the shell margin in positions unprotected from abrasion

by any local concavity. These species are considerably less common on the shells than *C. puncturata* (and no more robust than it), and the persistence of recognizable remains indicates that at least traces of *C. puncturata* would be expected in marginal regions of the shell if colonies had ever been present there.

c. The preservation of *C. puncturata* colonies is often very good, with no sign of abrasion. Other encrusting species on the shells have erect or semi-erect structures such as long peristomes (in tubuliporine cyclostomes) and oral spines (in *Hemicyclopora* sp.) which often remain intact. This suggests that the *most recent* encrustation of many Red Crag shells was not exposed to any wear, i.e. that many shells were not transported subsequent to their last colonization. Perhaps the best evidence of this is the preservation *in situ* of the calcified opercula of *E. crustulenta*, which are unsupported in the absence of soft tissue (text-fig. 1C). These are seen at many localities, including Brightwell and Shottisham. It therefore seems that at least some shells would reveal random settlement by *C. puncturata* if such a pattern existed before abrasion. This has not been observed.

#### *Avoidance of light*

Once under a shell, larvae might show a behavioural response (such as skototaxis, low photokinesis, or negative phototaxis) taking them away from any source of light. Since light could only filter into the space under a complete convex-up shell around its margins, settlement in the central part of the shell might result.

It is possible to test this idea using the fact that some of the shells studied have borings, presumably produced by naticid gastropods. The holes are in a characteristic place for a particular species of shell, and are relatively large (text-fig. 3A, C). The penetration of light through a hole in the shell would be expected to affect the settlement pattern of *C. puncturata* under the present hypothesis. *Spisula* shells are bored close to the umbo (text-fig. 3A). Displacement of the settlement patch towards the ventral margin of the shell might be predicted. In fact (text-fig. 3B) the position of settlement is not affected (Newbourn:  $V_{26, 59} = 0.246$ ,  $p > 0.50$ . Shottisham:  $V_{10, 44} = 0.350$ ,  $p > 0.50$ ). *M. praetenuis* shells are bored some distance ventral to the umbo (text-fig. 3C). Again (text-fig. 3D), no disruption of the pattern of settlement is apparent (Shottisham, left valves:  $V_{34, 65} = 0.221$ ,  $p > 0.50$ ; only one bored, encrusted right valve available). A behavioural response to light does not, therefore, seem to be important in determining the final position of settlement.

The possibility that the position of settlement is mediated by a behavioural response to current patterns under the shell (or to pressure differentials associated with the current) can similarly be discounted because the presence of borings in the shell might also be expected to modify or disrupt the resulting pattern.

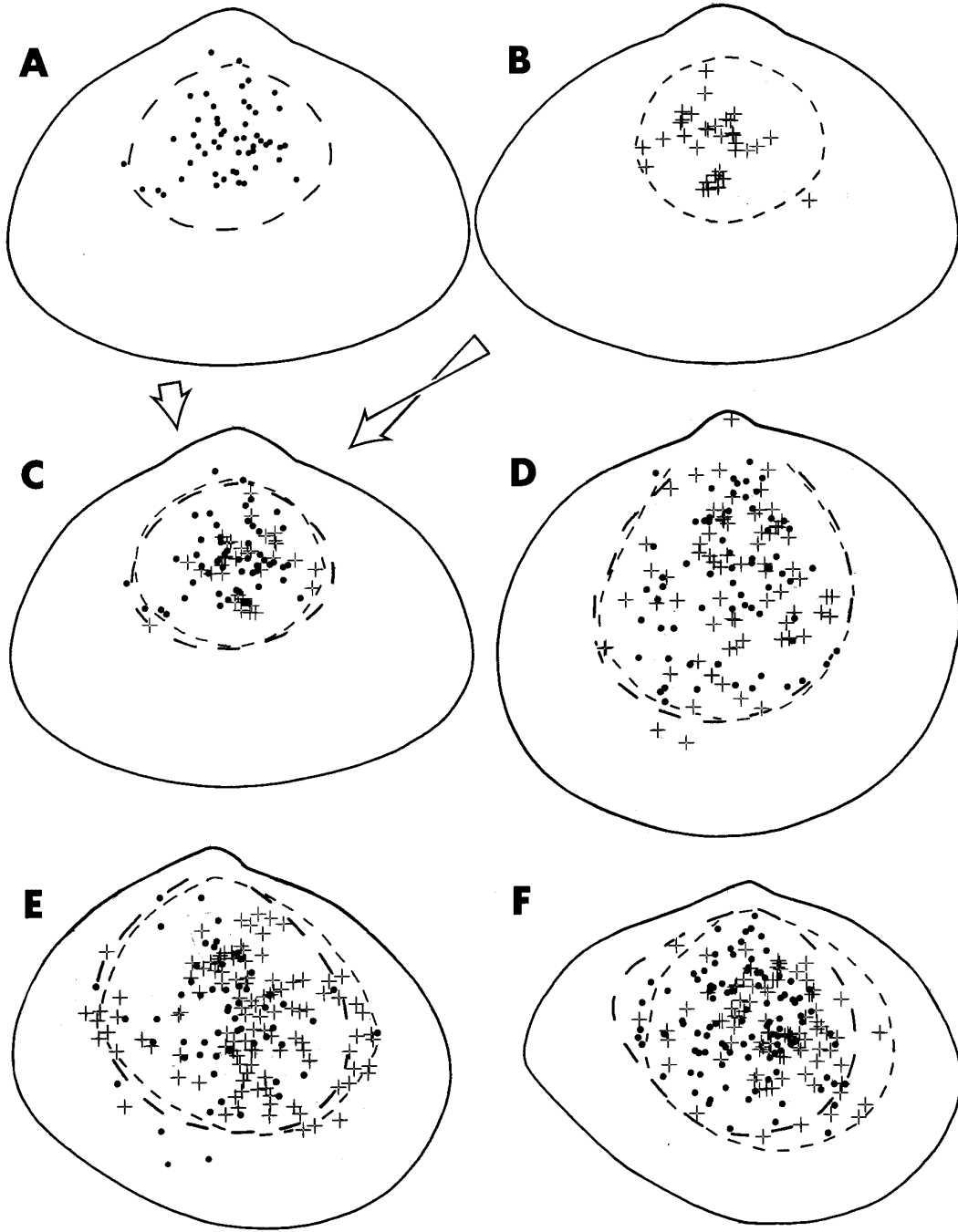
#### *Avoidance of sediment*

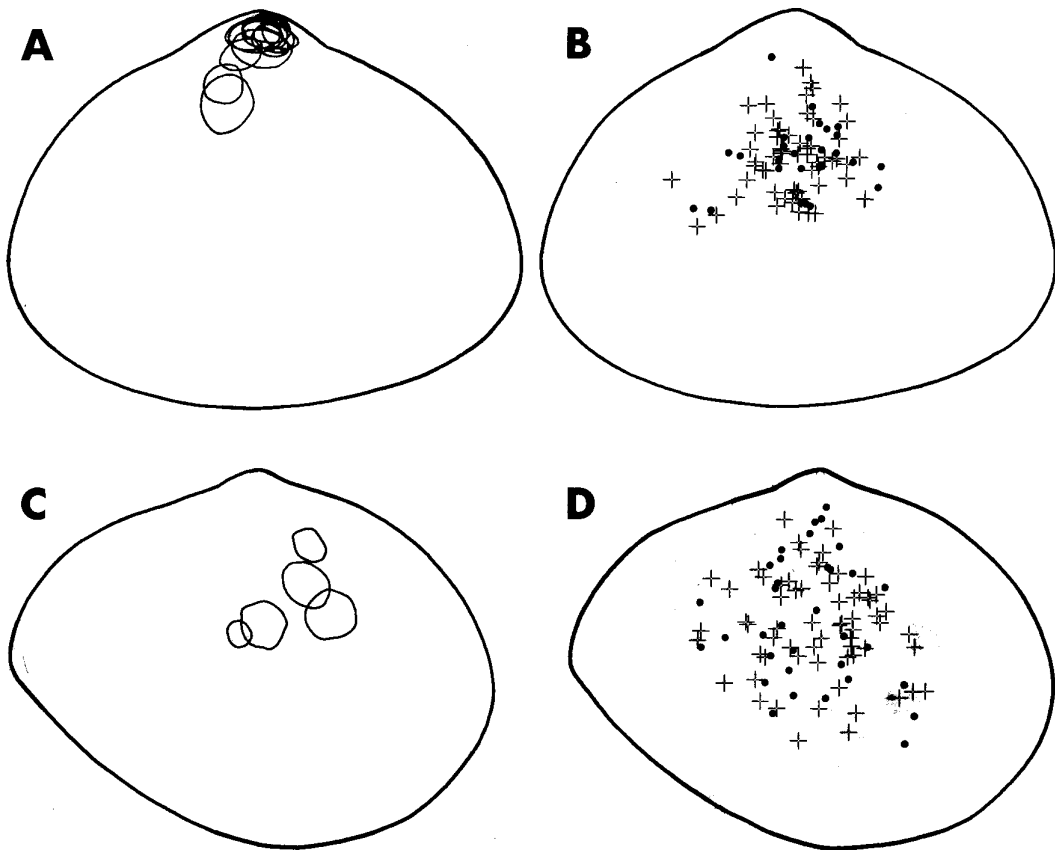
Settlement might occur only on regions of the undersurface of the shell free of sediment. Since contact with the sediment would be expected around the margin of a convex-up shell, a pattern of settlement broadly similar to that observed might result. However:

a. Under a hypothesis of simple sediment avoidance (i.e. without the requirement for a threshold distance above the sediment) settlement very close to the margin would occur on shells that did not

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TEXT-FIG. 2. Settlement of *Cribrilina puncturata* mapped on to standard outlines of four taxa of shell from the Red Crag, with shell depth contours; all outlines are of left valve (anterior margin to the right) except B, right valve; settlement on left valve shown as dots, on right valve as crosses; contours of left valve shown as large dashes, of right valve as small dashes. A-C, *Spisula* from Newbourn (30 left valves, 19 right), with 0.8 depth contours; in C the settlement and contour of the right valve have been transferred, after left-right reversal, on to the outline of the left valve. In D-F, the details of the right valve have similarly been transferred to the left valve. D, *Glycymeris* from Brightwell (7 left valves, 9 right), with 0.6 depth contours. E, *Macoma obliqua* from Shottisham (14 left valves, 21 right), with 0.6 depth contours. F, *M. praetenuis* from Shottisham (22 left valves, 24 right), with 0.6 depth contours.



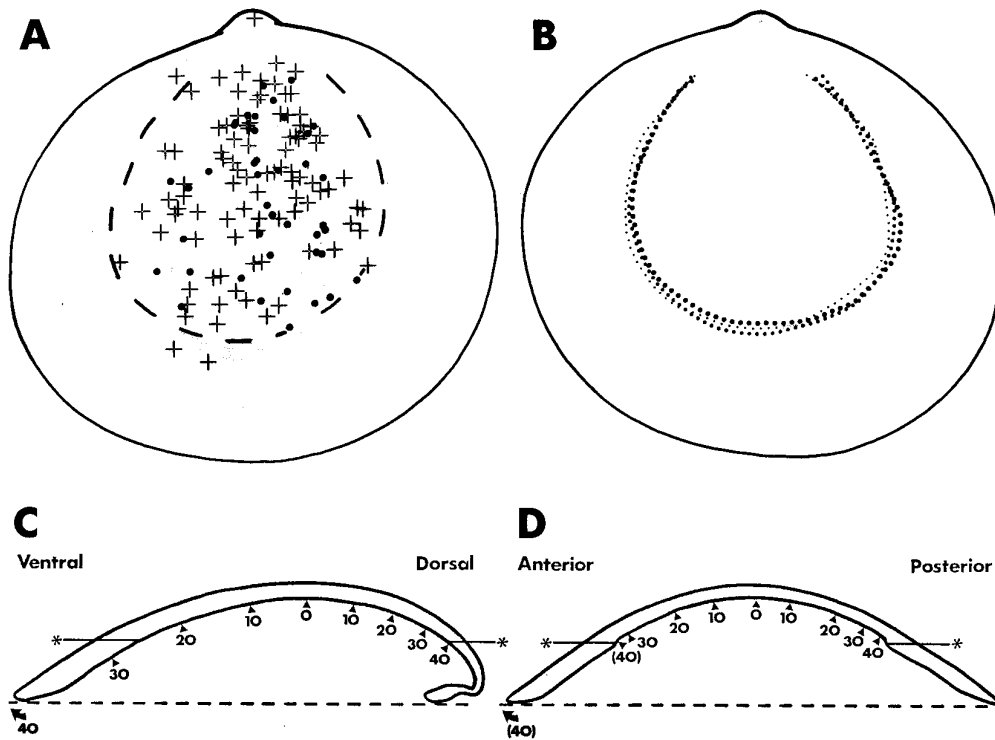


TEXT-FIG. 3. Settlement of *Cribrilina puncturata* on bored and unbored shells. A, B, *Spisula* from Newbourn, data from left and right valves shown together on outline of left valve (11 bored shells, 38 unbored). C, D, *Macoma praetenuis* from Shottisham, left valves only (5 bored shells, 17 unbored). A, C, outlines of borings, drawn to scale for individual shells. B, D, settlement (dots, bored shells; crosses, unbored).

sink into the sand at all, possibly because they were in contact with another shell or large sediment particle (such as a shell fragment). Such settlement in *C. puncturata* is not observed.

b. If a threshold distance above the sediment were required for settlement to occur, a greater proportion of the inner surface of large (deeper) shells would be encrusted than of small (shallower) shells. This is not observed. In text-fig. 4A, settlement on large and small *Glycymeris* shells from Brightwell is compared. (Medium sized shells were ignored.) The settlement patches are not significantly different ( $V_{41, 95} = 0.226$ ,  $0.50 > p > 0.20$ ), being almost completely restricted to the area within the 0.6 depth contour in both shell sizes. The position of the contour relative to the shell margin remains much the same as the shell grows (text-fig. 4B), reflecting the almost isometric growth in *Glycymeris* noted by Thomas (1975). However, the contour is at an absolute vertical distance of about 6.5–7 mm from the margin in large shells but about 4 mm in small shells. The greatest depth of the small shells is in fact only about 6.5–7 mm. It seems extremely unlikely, under the hypothesis of a threshold distance, that a compensatory factor, such as greater penetration of the sediment by larger shells, could produce the observed congruity of settlement patches. It appears instead that *the*



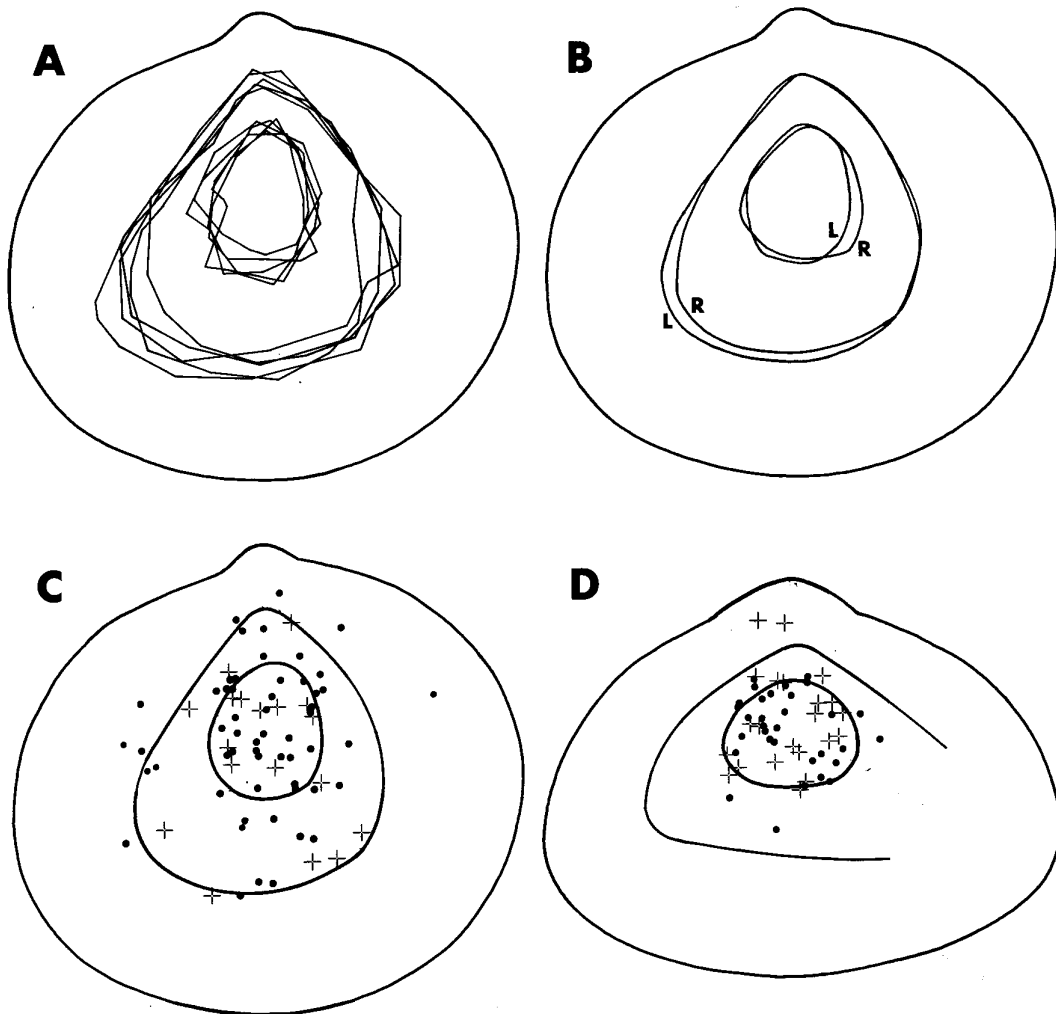


TEXT-FIG. 4. A, settlement of *Cribrilina puncturata* on small (height 27–31 mm) shells (dots) and large (height 43–47 mm) shells (crosses) of *Glycymeris* from Brightwell; data from left and right valves shown together on outline of left valve, with 0.6 shell depth contour. B, 0.6 depth contour for three right valves of *Glycymeris*, shown on common shell outline. Small dots, 29 mm high shell from Brightwell; medium dots, 39 mm high shell from Walton-on-the-Naze; large dots, 44 mm high shell from Brightwell. (Dots do not represent individual data points in B.) C, D, sections of relatively unworn *Glycymeris* shells from Walton-on-the-Naze. Approximate position of highest point on inside of shell at various angles of tilt indicated (figures in degrees); \*— indicates position of 0.6 depth contour.

*settlement pattern relates not to any absolute dimension of the shells but to their shape*, which remains relatively constant as they grow, giving an almost identical distribution of ancestrulae on shells of different size. Most convex-up shells *in situ* in the Red Crag are in any case full of sand, and recent observations indicate that at least some present-day bryozoans can live on surfaces that are in contact with or buried in sand (see Discussion).

#### *Settlement at highest point*

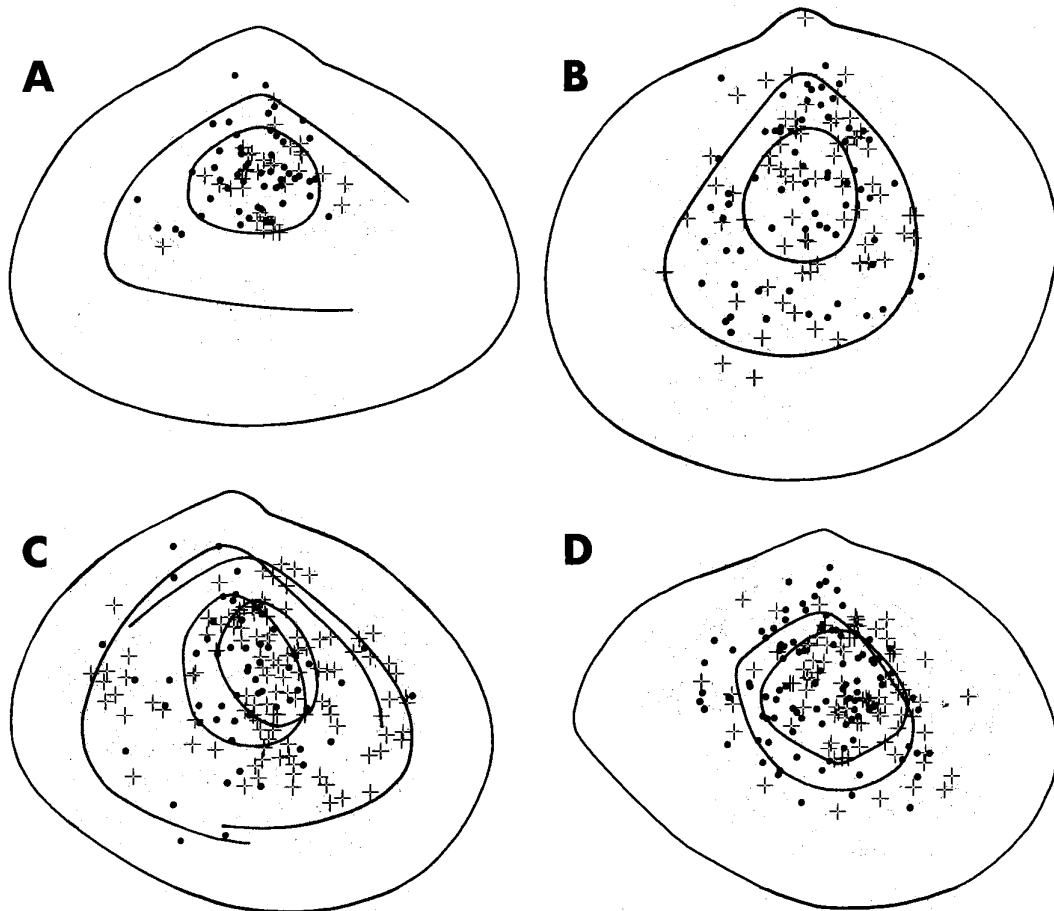
Larvae might settle at or near the highest part of the inside of the shell. If the shells were all laying on a horizontal surface, clumped settlement at the same place in each shell (the very deepest point) might be expected. However, little of the sea-bed in a sand-wave system is horizontal. Shells resting on a sloping sediment surface may be correspondingly inclined from the horizontal. Thus, Salazar-Jiménez *et al.* (1982, p. 580) observed shells inclined parallel to bedding in steeply dipping stoss laminae. Even on a horizontal surface, shells may be tilted by imbrication or local sediment scouring. It should also be borne in mind that several shells of each species were scored to produce the observed settlement patterns, and that each individual shell could show several different episodes of encrustation, possibly with movement of the shell between episodes as the sand-wave system migrated. To predict the



TEXT-FIG. 5. A,  $30^\circ$  (outer group) and  $15^\circ$  (inner) isoclinic lines for 5 left valves of *Glycymeris* from Brightwell (heights 27–46 mm), plotted on a common shell outline. B, summary  $30^\circ$  (outer) and  $15^\circ$  (inner) isoclinic lines for 5 left (L) and 5 right (R) valves of *Glycymeris* from Brightwell, shown on outline of left valve. C, D, settlement of *Cribrilina puncturata* at Shottisham, with  $30^\circ$  and  $15^\circ$  isoclinic lines averaged for both left and right valves; settlement on left (dots) and right valves (crosses) shown on outline of left valve. C, on *Glycymeris* (8 left valves, 5 right). D, on *Spisula* (15 left valves, 12 right);  $30^\circ$  isoclinic line incomplete anteriorly where it passed to the margin of a number of individual shells.

pattern of settlement that would be expected in these circumstances under a hypothesis of highest-point settlement, it is first necessary to consider the shape of the bivalve shell.

Sections through a *Glycymeris* valve are shown in text-fig. 4C, D. The section from the umbo to the ventral margin (text-fig. 4C) resembles part of a logarithmic spiral (as noted by Thomas 1975), with the curvature decreasing towards the ventral margin. As the shell is tilted, the highest point inside it will move. Very high angles of tilt are required to displace the highest point into the umbo, whereas tilting



TEXT-FIG. 6. Settlement of *Cribrilina puncturata* on four taxa of Red Crag shells (settlement data the same as in text-fig. 1), with isoclinic lines; settlement on left (dots) and right valves (crosses) shown on outline of left valve. A, *Spisula* from Newbourn, and B, *Glycymeris* from Brightwell; both with 30° (outer) and 15° (inner) isoclinic lines averaged for left and right valves. C, *Macoma obliqua* from Shottisham, with 30° (outer) and 15° (inner) isoclinic lines shown separately for left and right valves; lines for right valve are further to the right (more anterior); see text for explanation of incompleteness of 30° lines. D, *M. praetenuis* from Shottisham, with 15° isoclinic lines shown separately for left and right valves; line for right valve is further to the right (more anterior).

in the opposite direction rapidly moves it towards the ventral margin. The depth contours, used up till now to describe the settlement patterns, are not symmetrical with respect to these angles of tilt. For instance, the 0.6 depth contour in *Glycymeris* passes nearer to the umbo but further from the ventral margin than the 30° tilt points (text-fig. 4C). The anterior to posterior section (text-fig. 4D) is more symmetrical, but has steps at the edge of the buttressed anterior and posterior adductor muscle scars that block the movement of the highest point toward the margin of the shell as it is progressively tilted. (In the other shell taxa considered, the adductor muscle scars are not raised on low buttresses as in *Glycymeris*, but form more or less distinct depressions.)

An isoclinic line (see Methods section) describes the movement of the highest point on the inside of the convex-up shell as it is rotated at a particular angle of tilt. It follows that, under a hypothesis of

highest-point settlement, the isoclinic line for a particular angle will delimit the predicted settlement patch on shells that may be tilted in any direction by that angle or less at the time of settlement. Text-fig. 5A shows the 15° and 30° isoclinic lines for five left valves of *Glycymeris* from Brightwell plotted on to a common outline. The lines are similar for different sizes of shell. The position of the 30° line is relatively uniform between shells in the dorsal half of the shell, running close to the edges of the adductor muscle scars, but varies between shells somewhat towards the ventral margin, where curvature is relatively weak. In text-fig. 5B, single lines summarize those for individual left valves and individual right valves. The lines for left and right valves agree closely. In text-figs. 5C and 6B, the summary lines for left and right valves of *Glycymeris* have been combined. At both localities studied, the area delimited by the 30° isoclinic line agrees well with the observed settlement patch, but the region within the 15° isoclinic line does not seem to be associated with particularly dense settlement. In contrast, the densest settlement on *Spisula* (in which the isoclinic lines were again congruent between left and right valves) is restricted to the area within the 15° isoclinic line at both localities studied (text-figs. 5D and 6A). The proportion of settlement inside the 15° line is significantly lower for *Glycymeris* from Shottisham than for *Spisula* from the same locality (text-fig. 5C cf. D) (Fisher's  $2 \times 2$  exact test,  $Z = 2.54$ ,  $0.02 > p > 0.002$  in two-tailed test; settlement on right and left valves combined).

The 30° isoclinic lines of *M. obliqua* were interrupted in the shallowly curved posterior and posteroventral sectors of all five right valves, and in the anteroventral sector of three of the left valves (i.e. the ball rolled to the edge of the shell in these cases). The 30° summary lines shown in text-fig. 6C are therefore incomplete, but where both are plotted the line for the right valve is somewhat anterior to that for the left valve. A similar relative displacement is seen very clearly in the 15° isoclinic lines, which roughly delimit the non-coincident zones of densest settlement on left and right valves. Particularly in large examples, the adductor muscle scars of *M. obliqua* constitute significant secondary concavities within the shell. In the case of the right valve, there are recognizable patches of settlement associated with these regions, giving a large overall spread of settlement. However, little or no settlement is associated with the scars of the left valve.

When *M. praetenuis* shells were tilted at 30°, the ball moved to the edge of the shell in a high proportion of cases, particularly around the anterior and posterior margins. This obviously reflects the low concavo-convexity of *M. praetenuis* shells, and no 30° isoclinic lines are shown in text-fig. 6D. The 15° summary isoclinic lines for left and right valves are not concurrent (text-fig. 6D), the line for right valves showing a relative anterior displacement corresponding to the similar displacement of settlement noted previously.

It therefore appears that highest-point settlement could produce differences in settlement between right and left valves of *Macoma* spp. very similar to those observed.

## DISCUSSION

### *Settlement vs. recruitment*

Keough and Downes (1982) issued a strong caveat for those seeking to infer the larval settlement behaviour of sessile marine invertebrates from the observed spatial distribution of recruits to the attached juvenile phase. They argued that the initial settlement pattern could be subject to strong modification by differential mortality in the period between settlement and observation, even if that period were reasonably brief. In the present study, it was possible to recognize isolated ancestrulae of *C. puncturata* early in the second (histogenic) phase of metamorphosis (as defined by Zimmer and Woollacott 1977), at a stage in which only the most basal parts of the vertical zoecial walls were calcified. (An abraded condition superficially similar to this early stage is shown in text-fig. 1D.) Nielsen (1981) reported that calcification was underway 12 hours after settlement in two cheilostome species from California. Cook (1985) observed development of the ancestrula in a variety of Ghanaian cheilostomes, and reported that calcification could be observed as little as 2 hours after settlement; the ancestrula was complete after 24 to 48 hours. The possibility of significant mortality during the

brief first (morphogenetic) phase of metamorphosis cannot be discounted in the present study. Nevertheless, it is considered probable that the time period between larval fixation and the deposition of recognizable calcification by the developing ancestrula of *C. puncturata* was sufficiently short for the true settlement pattern to have remained substantially unaltered by differential mortality.

#### *Larval behaviour*

Having encountered an appropriate substrate and stopped swimming, gymnolaemate larvae generally creep or glide over its surface for some time by ciliary action. They eventually undergo fixation and metamorphosis at a chosen point or swim off, presumably in search of another potential settlement site (Cook 1985, and references therein). As stated in the Introduction, the mechanism by which the larvae of *C. puncturata* reached the underside of shells is not considered here. However, it may be noted in this context that some bryozoan larvae, after a swimming phase, are able to burrow in sand (Cook and Chimonides 1985). Once under a suitable convex-up bivalve shell, it is considered very probable that larvae of *C. puncturata* crept up the slope of the lower surface before metamorphosis. Settlement at or near the highest point on the undersurface of the shell appears to offer the best explanation of the observed distribution of ancestrulae. The following observations support this hypothesis: 1, settlement very close to the umbo of a shell would not be expected, and it is rarely observed; 2, the extent of the settlement patch is similar in small and large shells, in proportion to the total area of the shell, as would be predicted from the proposed behaviour; 3, no major disruption of the pattern is anticipated in bored shells, and none is seen; and 4, this behaviour could produce the observed difference in settlement patterns between the slightly asymmetrical left and right valves of *Macoma* spp.

Might a gravity response by the creeping larva be involved in the production of the observed pattern in *C. puncturata*? Research on larval behaviour of Recent encrusting marine cheilostome Bryozoa has almost exclusively involved swimming movements of littoral and shallow sublittoral species. Whilst phototactic responses in these have been reported frequently, geotaxis has rarely been mentioned. Negative geotaxis may be partly responsible for the observed settlement of *E. crustulenta* predominantly on the underside of hard substrates in the Baltic (Silén and Jansson 1972). Ryland (1974, 1977) suggested, on the basis of observations by earlier authors, that initial geonegativity was shown by two species of *Bugula*; he noted that the role of gravity responses in free-swimming bryozoan larvae remained little understood, and had rarely been distinguished from associated light responses. Nielsen (1981) considered that an initial geonegative response, as well as photopositivity, was present in swimming larvae of '*Hippodiplosia*' *insculpta* (Hincks, 1882). Pires and Woollacott (1983) demonstrated a true gravity response in larvae of *B. stolonifera* Ryland, 1960 and light-independent upward swimming in response to an unknown cue in *B. neritina* (Linnaeus, 1758). They pointed out that, in the context of free-swimming invertebrate larvae, the term geotaxis had sometimes been applied in a broad sense to any light-independent vertical movement, and that apparent geotaxis might arise as a response to temperature gradients, hydrostatic pressure, or geomagnetic fields, as well as directly to gravity.

Depth gradients of hydrostatic pressure or temperature seem very unlikely to have been involved in the orientation of creeping *C. puncturata* larvae since the vertical distance between the centre and margin of a shell is very small (several mm at most). The possibility of a response to the vertical component of the local geomagnetic field cannot be excluded, although a true gravity response seems more probable. Larvae creeping to the edge of a highly tilted shell presumably moved off in search of another shell, since settlement at the edge of a shell has not been observed.

It is perhaps worth noting that the location of the highest point on the concave surface of a shell by a larva moving according to any of the vertical stimuli suggested here would probably not be very accurate. This is because the component of the stimulus acting in the relevant direction for orientation (i.e. up and down the slope of the shell's surface) would decrease as the highest point was approached, being proportional to the sine of the angle of inclination of the local surface to the horizontal. Thus settlement was probably only *approximately* at the highest point. The observed spread of settlement

within an isoclinic line may have been partly caused by this inaccuracy in addition to any tilting of the shell at the time of colonization.

Under the hypothesis of highest-point settlement, two possible explanations may be put forward for the greater concentration of settlement within the 15° isoclinic line in *Spisula* compared with *Glycymeris* (text-fig. 5C cf. D). *Glycymeris* may, on average, have been more tilted than *Spisula* at the time of settlement. No evidence is available to confirm or disprove this suggestion. Alternatively, the larva of *C. puncturata* may have been able to locate the highest point more accurately in *Spisula* than in *Glycymeris*. Two factors suggest that this may have been the case. First, the *Spisula* shells studied are considerably smaller than those of *Glycymeris*, so that the distance to be travelled by the larva to the highest point would have been much shorter. Second, the inner surface of the shells studied is in general considerably smoother in *Spisula* than in *Glycymeris*. The upward movement of the larva in response to the true slope of the shell would therefore have been less disrupted by local surface microrelief in *Spisula*. (*Glycymeris* has very durable shells, and most Red Crag examples are considerably worn and pitted, except in the cliff exposure at Walton-on-the-Naze, Essex.) It should be mentioned that a similar difference between *Spisula* and *Glycymeris* might be predicted under a hypothesis of peripheral abrasion after random settlement, since abrasion would be expected to affect a greater proportion of the surface in smaller shells. Reasons for discounting abrasion as the major cause of the observed distribution of *C. puncturata* have been given above. In addition, the broad settlement patch on the relatively small shells of *M. praetenuis* (text-fig. 6D) is contrary to the pattern expected from peripheral abrasion. It is in agreement with the prediction for highest-point settlement, since the shells of this species are relatively weakly concavo-convex.

#### *Disarticulated bivalve shells as substrates for encrustation*

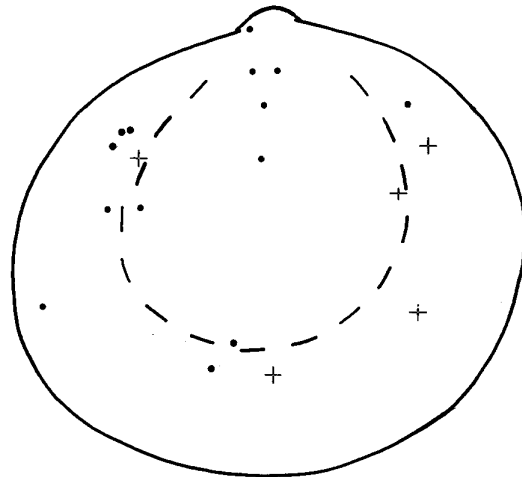
Potential problems for an organism encrusting a small solid substrate on a particulate sea-bed include: 1, abrasion by current-entrained sediment particles; 2, crushing when the substrate is transported or changes attitude; 3, clogging of feeding or respiratory structures by suspended or settling sediment, particularly fine particles; and 4, deep burial of the substrate, curtailing the supply of resources from the water column. It seems possible to make a number of general statements concerning the behaviour of single concavo-convex mollusc (or brachiopod) shell substrates on a sandy sea-bed that may relate to these dangers.

Shells in the convex-up position are much more hydrodynamically stable than when resting concave-up (Hall 1843, p. 52; Sorby 1908, p. 189; confirmed by numerous subsequent workers). Concave-up shells are relatively easily transported across sand by currents, but may readily invert to the convex-up position, stopping transport, if tripped by an obstacle or an irregularity of the sediment surface (Brenchley and Newall 1970). Conversely, convex-up shells may flip to the concave-up position at the crest of a passing sand ripple (Menard and Boucot 1951, p. 148). This occurs more easily with relatively small shells (Clifton and Boggs 1970). Stationary shells in either attitude may also topple into their own current scour marks and thus rest at high angles to the general sediment surface. This is often a prelude to burial (Johnson 1957; Brenchley and Newall 1970). Shells washed into sediment traps such as burrows may exhibit predominantly concave-up or near-vertical orientation (Salazar-Jiménez *et al.* 1982).

The convex surface of a shell in either the convex-up or concave-up position may be abraded by passing grains when there is a current capable of entraining sediment particles. Sediment scour may occur locally around the shell even in currents incapable of mobilizing the sediment elsewhere (Johnson 1957). The fate of the concave surface will depend on the position of the shell. Sediment winnowed from eddies in the lee of a concave-up shell may accumulate on its upper surface (Brenchley and Newall 1970). In contrast, when the shell is convex-up, the concave surface is unaffected by sediment falling from local eddies (or settling when the current slackens), and is also relatively protected from abrasion by current-entrained particles.

Settlement on the concave surface of a convex-up disarticulated shell would therefore seem to minimize the chances of mechanical damage or clogging for an encruster in an environment with significant sediment transport. Certain disadvantages appear to offset this protection: restricted water

TEXT-FIG. 7. Settlement of *Phylactellipora* sp. (dots) and *Electra crustulenta* (crosses) on *Glycymeris* from Brightwell, data from left and right valves shown together on outline of left valve, with 0.6 shell depth contour.



movement would be expected compared with the upper surface of the substrate, and there may be very limited space (if any) between the lower surface of the shell and the sediment. However, various observations strongly suggest that Recent marine bryozoans can sometimes grow and reproduce buried in the superficial layers of sand (Cook 1985; Håkansson and Winston 1985; Cook and Chimonides 1985). It must be presumed that they are able to feed successfully by extending their lophophores (delicate ciliated tentacle crowns by which Bryozoa suspension-feed) into the interstitial spaces of the sand immediately adjacent to the colony, provided that the sediment is sufficiently coarse. It seems probable that the supply of resources, such as food and oxygen, from the water column would be progressively reduced with increasing depth of burial, so that survival would no longer be possible below a certain level.

Geonegative movement during selection of the site of fixation seems particularly appropriate for a colonizer of the underside of markedly concavo-convex disarticulated bivalves in a current-swept sandy environment. It would result in settlement in the relatively protected central region away from the margins of the shell. Settlement on an excessively tilted shell (which might be in a sediment trap or in the process of burial by scouring) would be avoided if the shell's attitude were such that its highest point was somewhere on its ventral or lateral margins. If, however, the umbonal region of a highly tilted shell were uppermost, settlement on or near this very concave (and hence relatively protected) area of the undersurface would result. Settlement on shells in the unstable concave-up position would be precluded. It therefore seems that geonegative movement immediately prior to fixation could minimize a colony's subsequent exposure to shell substrate transport or deep burial within the sand-wave system, and reduce mechanical damage to the colony during those episodes of shell overturning and transport that did occur. This perhaps accounts in part for the relative success of *C. puncturata* in the harsh Red Crag environment. However, it should be noted that the expected resultant colonization is in precisely the area most likely to be affected by settling sediment on a shell that was subsequently overturned. The behaviour mechanism inferred here would therefore only be advantageous in environments where a colonized shell, having then been inverted to the concave-up position, would be unlikely to remain in that position for a significant period of time before reverting to the hydrodynamically stable convex-up configuration. The very clear preponderance of convex-up shells in Red Crag exposures suggests that this was the case in the Red Crag sea.

The small, patch-like colony of *C. puncturata* completed its life history in the area immediately adjacent to the point of larval settlement. Any mechanical damage or clogging was therefore likely to be colony-wide. It appears that the deepest central region of the undersurface of convex-up shells was

treated by *C. puncturata* as a temporally and spatially predictable refuge (in the sense of Buss 1979) from physically mediated disturbance in a high-energy environment, exploited by the bryozoan through specialized settlement behaviour.

The Recent pterobranch hemichordate *Rhabdopleura compacta* Hincks, 1880, which also forms minute encrusting colonies, was reported by Stebbing (1970) to be restricted to a microhabitat apparently very similar to that noted here for *C. puncturata*. Stebbing studied material dredged from a coarse to very coarse sand bottom at depths of c. 21–24 m off south Devon, England. *R. compacta*, and many other encrusting species of the associated fauna, was found only on the concave surface of disarticulated bivalve shells (mostly *Glycymeris*). (The precise distribution of settlement was not recorded.) Observations by SCUBA diving in the same area revealed that shells were scattered on an undulating sea-bed, and that all disarticulated valves were lying in the convex-up position.

In contrast to *C. puncturata*, colony growth in *Phylactellipora* sp. and *E. crustulenta* on Red Crag shells was strongly directional with periodic branching (runner-like morphology in the sense of Buss 1979). A large colony therefore reached various parts of the shell distant from the point of settlement. These two species commonly occurred as colony fragments dissociated from any recognizable colony origin. Survival after the early growth stages may have involved regrowth of undamaged fragments after partial colony mortality caused by episodes of physical disturbance. When most of the colony was covered by an accumulation of fine sediment, unaffected parts that were able to feed may have exported metabolites to neighbouring zooids. *Phylactellipora* sp. and *E. crustulenta* had rugophilic settlement behaviour that resulted in the ancestrula nestling in a local minor irregularity anywhere on the shell's (lower ?) surface (text-fig. 7). Such sites were found amongst the dentition of the cardinal plate, along the edges of adductor muscle scars, at the margin of pre-existing encrustation of the shell, and in any surface pitting caused by abrasion or bioerosion. Through their settlement behaviour, these two species therefore utilized local minor irregularities as predictable refuges for early astogeny, but they treated refuges for later colony growth as spatially unpredictable (in the sense of Buss 1979), each colony spreading out to minimize the probability of total colony mortality. This settlement and growth strategy is appropriate for colonization of a variety of hard substrates in addition to disarticulated shells, and is relevant to the survival of biological competition for space as well as of physically mediated disturbance (Buss 1979; Jackson 1979).

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