THE RESPONSES AND ORIENTATION OF THE BIVALVE *LASAEA RUBRA* MONTAGU

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(Text-figs. 1–7)

Lasaea rubra, like other small Erycinacea, is unusual among eulamellibranchs in its relatively great mobility on the surface of the substrate. It can crawl about as freely as a small gastropod and lays down a mucous trail for the attachment of its progressing foot, drawing the shell and body rhythmically forward after each advance thrust of the foot. Unlike some other Erycinacea, *L. rubra* has no well-defined sole; it attaches by the sharp lower edge and part of the side of the foot, which is strongly ciliated and well supplied with mucous glands. In most burrowing eulamellibranchs, the site of communication with the surrounding water has shifted to the paired siphons at the posterior end. The Erycinacea, however, have an anterior inhalant siphon; and—as in forward moving prosobranch gastropods (Morton, 1958)—there is an obvious adaptive advantage in receiving the ingoing current from the water into which the animal is moving.

L. rubra lives normally attached by temporary byssus threads, nestling in small crevices between slate laminae, in irregularities of the rock surface, and especially in *Pygmaea* lichen tufts and inside the empty shells of the barnacle *Chthamalus stellatus* (Morton, Boney & Corner, 1957). It shows a marked thigmotaxis or preference for lateral contact. When removed from its site it appears at once very restless. Placed in a glass bowl in room light it shows three very obvious responses: it will crawl away from a source of light, it will take any opportunity to climb a sloping or vertical surface, and if enough specimens are close together they will ultimately aggregate in small clusters and attach to each other by byssus threads.

Lamellibranchs without eyes or exploratory tentacles are not usually thought of as direction-finding animals, and there appears to be as yet no account of migration by an adult eulamellibranch in response to external stimuli. This paper will present the results of some experiments to elucidate the responses of *Lasaea rubra* to the stimuli of light, gravity and lateral contact, and will attempt to show the relevance of these to its orientation and maintenance of position on the shore.

Material was obtained in the *Chthamalus stellatus* zone of the upper inter-area tidal at Tinside, Plymouth, being brought to the Laboratory in chips of rock or barnacle shells, and kept cool in the dark until used for experiments

within, at the most, 2 or 3 h of collecting. The shell being closed when out of water, the animals received no immediately previous light stimulus, and were left attached *in situ* until a few minutes before the experiment. They were then immersed in watch-glasses of sea water only for so long as was necessary to moisten the shell and allow the very rapid emergence of the foot and siphon.

All experiments were performed in a dark box, a metre each dimension, with non-reflecting blackened sides. This was closed in front by a black curtain and kept in a dark room at a cool room temperature of 15° C. The experimental substratum was a glass sheet of 13 cm square, marked out with a working field 11 cm square, gridded with centimetre squares (Fig. 1 B). The animals crawled readily on this glass, providing a record of their own trails by the secreted mucous track. After an experiment such trails could be made easily visible by gently agitating the glass sheet in a suspension of talcum powder in water, and could then be dried and varnished; in practice it was found much more convenient and equally accurate to redraw them at once at the same scale on squared graph paper.

The apparatus for light-response experiments is shown in Fig. 1 A. It consisted of a galvanized iron photographic dish (*t*) 5 cm deep painted with black marine varnish and lined with non-reflecting black 'Cobex' plastic sheeting, with vertical sides and a 2 cm. margin turned inwards horizontally at the top to absorb small amounts of light reflected from the glass. The lamp-box (*b*) held a 12 V tungsten filament lamp with a luminous intensity in the direction of the experimental plate of 9·2 candelas. The colour temperature of the lamp was 2900° K. The filament (*l*) was 8 cm behind the aperture of the box. *p–p*1 represents the glass plate on the floor of the dish, and *s* the beginning of the experimental field, 7 cm inside the lighted area. *s–s*1 is the length of the light gradient used in the experiments. Illumination fell off laterally along the transverse line of *s* by 1 % at 2 cm from the centre of the light path, and by 4 % at the extreme edge of the experimental field. For the conditions of the experiment, and with the steepness of the *s–s*1 gradient, transverse illumination at a given level was considered as being approximately uniform. Refraction and reflexion of light at the water surface were calculated as for an average angle of incidence of 20°; and the intensity of light incident at *s–s*1 was taken to be approximately 40 % of the corresponding value at the water surface. The animal having no apparatus for light concentration or image formation, the illumination *I*, received at *s*, at a distance of 20 cm from the light source may be calculated

$$I = \frac{c}{(ls)^2} \times 0\cdot4 = \frac{9\cdot2}{0\cdot2^2} \times 0\cdot4 = 9\cdot2 \text{ lux,}$$

where *c* is the luminous intensity of the source in candelas and *ls* the distance from the source in metres. Illumination at the far edge of the experimental field, *s*1 30 cm from the source, will be 4·1 lux.

A series of neutral filters of optical densities 0·1–4·8 were in separate experiments placed in the light path at the aperture of the lamp-box at f. The greatest care was taken to avoid leakage of light around the filters.

For experiments involving gravity a rectangular glass trough was used, 20 cm deep, and the experimental glass plate was raised to the angle of inclination required by varying the length of a suspending wire. In experiments at a high angle of slope animals were given 3–5 min to attach by the foot to the glass plate, while at a lower slope; after this the plate was raised, any progress already made by the animals being noted and the resultant length of trail disregarded.
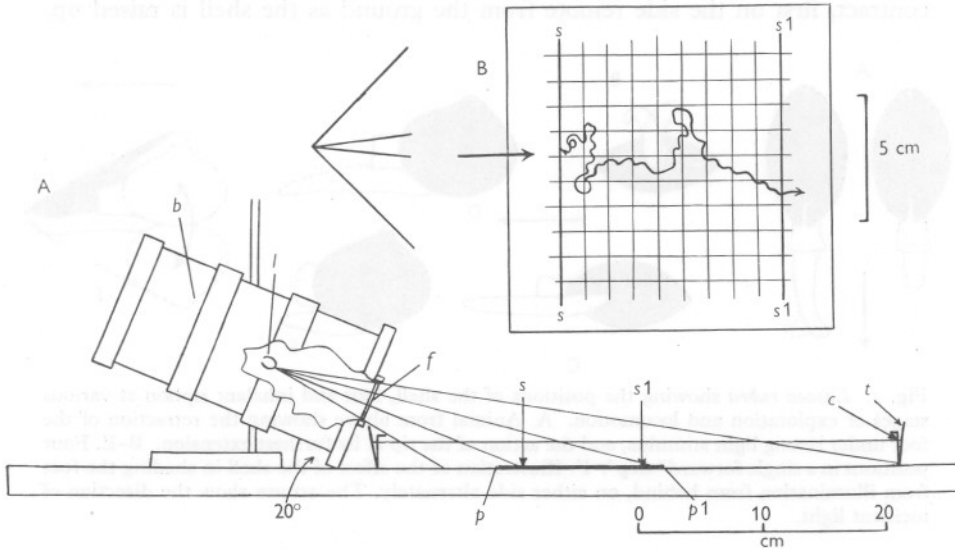

Fig. 1. A. (*a*) Apparatus used in experiments on photo-orientation; (*b*) lamp-box; (*c*) 'Cobex' dull surface lining sheet; (*f*) filter; *l*, light source of lamp; *p–p*1, experimental glass plate; *s–s*1, limits of experimental field; *t*, experimental trough. B. Experimental glass sheet showing the course of a trail, running across the gridded area. The arrow shows the direction of the light gradient falling off from *s* to *s*1, and approximately uniform transversely. Also shown are the angles +45 to −45, and +5 to −5 used in the presentation of data.

MOVEMENTS

The method of locomotion is illustrated in Fig. 2. The foot forms a slender tongue, perfectly colourless and translucent, that can be thrust out a distance equal to the length of the shell. From the anterior end, above the foot, also emerges the inhalant siphon, a short stout tube, somewhat laterally compressed; its margin is plain or sometimes very slightly crenate, and the opening can be narrowed by the margin drawing in. The tip of the fully extended foot is slightly flattened against the substrate and narrowly spatulate; but this is the only suggestion of a 'sole' and when lifted free the whole

lower margin of the foot is sharp-edged and very narrow. A forward 'step' takes place in several stages (Figs. 2 B–E). From the resting position with the shell lying on one side or the other, the foot is put out and freely moved about, being thrust from side to side and curved beneath the shell as its pointed tip appears to feel for purchase. It attaches to the ground by the keel-like ventral edge and the lower part of one side, which is almost opaque and possesses mucous glands and cilia (see Popham, 1940). As it becomes fully extended the main site of attachment seems to be the sharp ventral edge. With the foot so extended the heavy shell is drawn forward upon it and hauled into an upright position, ventral margin lowermost, as the retractor muscles of the foot contract, first on the side remote from the ground as the shell is raised up,
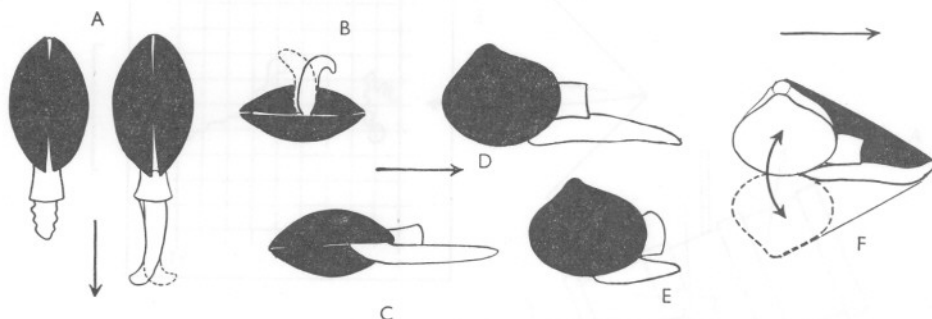

Fig. 2. *Lasaea rubra* showing the positions of the shell, foot and inhalant siphon at various stages of exploration and locomotion. A. Animal from above showing the retraction of the foot under strong light stimulus, and the action of the tip at its furthest extension. B–E. Four positions in a single forward 'step'. F. Illustration of the effect of the shell in shading the foot from illumination from behind, on either side alternately. The arrows show the direction of incident light.

and then on both sides as it is drawn sharply forward. On completion of each step the foot is very short, with an angled 'heel' behind and projects in front little more than the length of the siphon. The foot is almost immediately extended again for the next step and the shell slumps to one side or the other, being raised vertically once more at the ensuing foot contraction.

Lasaea rubra has no macroscopically differentiated light receptors, but either of the two parts of the body (foot or siphon) exposed in front could—it was suspected—be responsible for the light sense and for detecting bilateral differences in light intensity at successive points of time—that is, to serve as receptors suitable for the type of reaction called a 'klinotaxis' by Fraenkel & Gunn (1940). In *Mya* and *Cardium* the posterior siphon tips, being alone exposed at the surface, are photosensitive and bear rudimentary 'eyes'. In Pectinidae the whole mantle margin bears tentacles and eyes forming the sensory outstations of the body. In *Lasaea rubra* the siphon is short and relatively immobile. Though it is probably diffusely photosensitive, the main

exploratory role has passed to the tip of the foot, the anteriormost point of the body, which can, moreover, be freely moved about. During extension its tip can be slightly raised and curved tentatively to one side, then—after a momentary contraction—to the other. Rather more frequently after a movement to one side, the foot is partly or wholly withdrawn into the shell before emerging to make a new exploratory movement upon the other side.

By such side to side movements *L. rubra* can employ the foot as a direction receptor. The shell shades the sensitive region from light directly behind, so that relative intensity of light incidence at either side must be detected by lateral movements of the foot. With a strong light source in front of the animal, the exploratory activity of the foot is greatly intensified and on first emerging there is no attempt to grip the substrate; instead the tip of the foot is raised well clear of the ground and very freely moved about, the tip now extending narrowly, now being pulled back and contracted. Such movements may continue some time before the foot is planted and sustained forward progress is usually not attempted till the animal has swung away from the directly anterior light source.

A behavioural comparison can best be found in a very different animal, the dipteran maggot, which Fraenkel & Gunn (1940) would regard as the classic case of orientation by klinotaxis, 'a directed orientation made possible by means of regular deviations and involving comparisons of intensities at successive points in time'. The tiny pointed anterior end of the maggot has no well-defined photoreceptor. Variation in stimulation must occur as it is drawn in and covered by succeeding segments and then put out again. Thus, just as with the momentary contraction or withdrawal of the foot in *L. rubra* the 'photoreceptive region does not pass straight from one side position to the next, but goes through a series of light intensities which includes the comparative darkness of the contracted position'.

As the shell falls to one side or the other during extension of the foot, a wide shadowed zone is cast around the foot on that side (Fig. 2 F). It was at first suspected that regular recumbence of the shell on one side and the other, with alternate steps, would in itself give a rough power of comparison of light intensities, making possible—as it were—a klinotaxis without lateral deviation by the foot. In Fig. 5 is shown a 20 min record of the movements of an animal away from a light source; it will be seen that there is no strictly regular alternation of the shell to right and left sides and that after slumping in one position, there is a tendency to return there for several steps. In addition, the time frequency of light comparison by the shading of the shell would be very low and much more sensitive comparison is in fact possible by the deviations of the foot. A shadowed zone on a particular side must, however, afford the animal a wider sector in which it can move transversely to the light path while still effectively shaded from direct light.

BEHAVIOUR IN DARKNESS: ORIENTATION BY LIGHT

When removed from its site and placed in the dark on a smooth flat surface, *L. rubra* is unable to orient, and crawls about to produce trails of three kinds: (i) about a third of the animals tested in the dark made a short trail of a few millimetres in length, after which they attached by the byssus thread and made no further movements; (ii) a smaller number produced trails that were difficult to follow exactly or to measure, since they were tightly convoluted with continual changes of direction; (iii) the majority produced a strongly convoluted and frequently looped trail, crawling over distances of up to 200 mm in the half-hour period of the experiment. These undirected movements have much in common with the dark behaviour described by Ullyott (1936) in the flatworm *Dendrocoelum*. They show under uniform conditions a certain basal frequency of turning, random in direction. The character of such trails can best be quantitatively represented by expressing against time the rate of change of direction (r.c.d.) in angular degrees per minute. When *Dendrocoelum* were placed in uniform non-graded light, the r.c.d. was found to increase with the intensity of light stimulation. With *Lasaea rubra* in the dark on a smooth surface, we must regard the deprivation of lateral contact as constituting in itself, as illustrated by trails of type (iii), a stimulus of intensity sufficiently high as to produce a r.c.d. equivalent to that shown by animals in light. The character of type (iii) trails and the amount of turning they show do not appreciably alter from the dark condition after the provision of uniform non-direction light (Fig. 3). Ullyott found that *Dendrocoelum* became 'adapted' to the stimulus of light, i.e. the r.c.d. at a given level of illumination fell off with time. With *Lasaea rubra* in the dark, though the stimulus of deprivation of lateral contact appears as high as that provided by light, adaptation was seldom seen: the r.c.d. was not in general lower after 30 min than at the beginning of an experiment. (The high peaks shown in Fig. 3 (1), for a trail made in directional light, fall well within the range shown by many dark trails.)

With uniform ungraded lighting, from the light source of 9·2 candelas, 20 cm vertically above, diffused by a sheet of opal glass, *L. rubra* showed few

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Legend to Fig. 3.

Fig. 3. A. Rose diagrams showing the relative extent of trails produced at various angles: (*a*) aggregated results of experiments on flat surface in the dark; (*b*) results of experiments with a non-directional light gradient, illumination falling from right to left, showing klinokinesis with adaptation. B. Traced records of representative trails produced: (left) on a level surface in the dark, with examples of types (ii) and (iii) referred to above; (right) in experiments using a non-directional light gradient, illumination falling from right to left. C. Histograms showing the characteristics of various types of trail over a 30 min period: (1) in a gradient of lateral light, falling from 9·2 lux; (2) on a level surface in the dark; (3) with uniform light incident from above; (4) climbing a slope of 30° from the horizontal in the dark. Ordinate: degrees angular change of direction; abscissa: time in minutes.
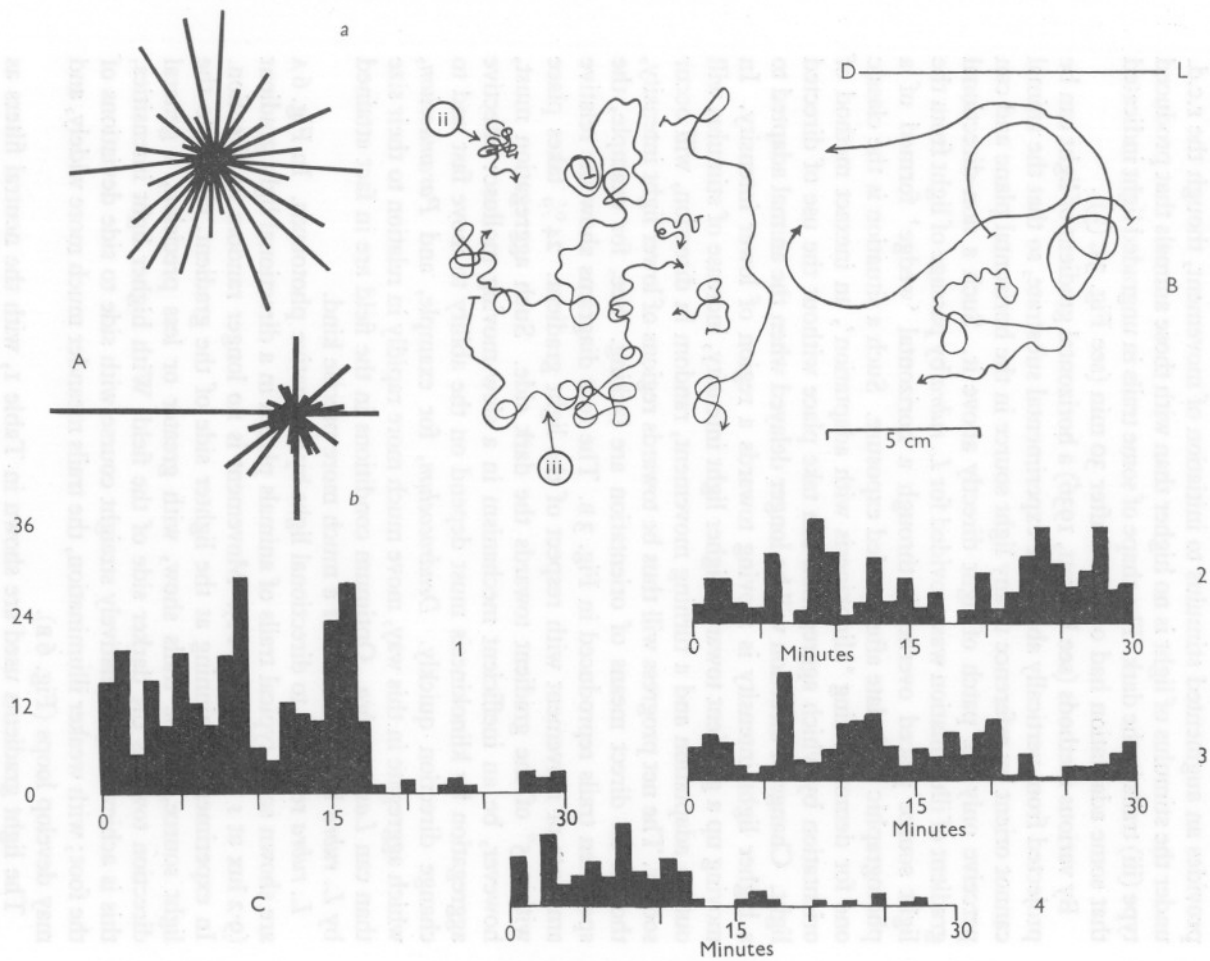
Fig. 3. For legend see opposite page.

or none of the trails of types (i) and (ii); all the animals used were highly active and made long, meandering and looping trails of type (iii). Light provides an augmented stimulus to initiation of movement, though the r.c.d. under the stimulus of light is no higher than with those animals that produced type (iii) trails in the dark. The shape of some trails in ungraded light indicated that some adaptation had occurred after 30 min (see Fig. 3 c (3)).

By various methods (see Ullyott, 1936) a horizontal gradient of light can be projected from vertically above the experimental substrate, so that the animal cannot orient by reference to any light source in the horizontal plane and can perceive only the patch of light directly above it. Such a non-directional gradient of illumination was provided for *L. rubra* by passage of light from the light source placed overhead, through a horizontal 'wedge' formed of a photographic half-plate after graded exposure. Such a situation is the classic one for demonstrating 'klinokinesis with adaptation', an inexact method of orientation by which aggregation can take place without the use of directed light. Change of direction will be longer delayed when the animal adapted to a higher light intensity is moving towards a region of lower intensity. In moving up a gradient towards higher light intensity, increase of stimulus will outrun adaptation and a turning movement, random in direction, will occur sooner. The net progress will thus be towards regions of lower light intensity, though all direct means of orientation are lacking. See, for example, the specimen trails reproduced in Fig. 3 b. The rose diagrams show the relative amounts of movement with respect of the light gradient. 24% takes place within 5° of the gradient towards the dark side. Such aggregation must, however, be an inefficient mechanism in a slow-moving mollusc: effective aggregation by klinokinesis must depend on the ability to move fast and to change direction quickly. *Dendrocoelum*, for example, and *Paramaecium*, which aggregate in this way, move much more rapidly in relation to their size than can *Lasaea rubra*. Optimum conditions in the field are in fact attained by *L. rubra* by orientation of a much more precise kind.

L. rubra responds to directional light by a negative phototaxis. In Fig. 6 A are shown some typical trails of animals placed in a directional light gradient (9·2 lux at *s* to 4·1 lux at *s*1). Movement is no longer random in direction. In experiments beginning at the lighter side of the gradient, closest to the light source, all the trails show, with greater or less precision, a general direction towards the darker side of the field. With higher light intensities, this is achieved by a relatively straight course with side to side deviations of the foot; with weaker illumination, the trails meander much more widely, and may develop loops (Fig. 6 b).

The light gradients used are shown in Table 1, with the neutral filters as shown. Efficiency of orientation was determined by totalling for each experiment the distances crawled by all the animals used, at various angles to the direction of the light gradient. The results are expressed in the rose diagrams

(Fig. 4) from which the data shown graphically could be further calculated. In the graphs, two sets of values are plotted; for each light intensity the percentage of the total linear movement represented by parts of the trails between $+5°$ and $-5°$ with the line of the light gradient, and similarly the percentage of trails formed at angles of between $+45°$ and $-45°$ with the line of the gradient. With similar rose diagrams (Fig. 3) the randomness of movement in the dark, and movement in a non-directional gradient have already been shown. In these calculations initial or intermediate parts of the trails showing small loops or continued alteration of direction, without sustained directional movement for a length of 1 cm, were disregarded.

TABLE 1. ILLUMINATION WITH THE RANGE
OF NEUTRAL FILTERS USED

Density of filter*	Transmission	Illumination at *s* (lux)	Illumination at *s* 1 (lux)
0·1	0·79	7·26	3·23
0·2	0·63	5·79	2·58
0·3	0·50	4·60	2·05
0·59	0·26	2·40	1·02
0·98	0·10	0·92	0·41
2·06	0·0087	0·08004	0·03567
3·0	0·001	0·0092	0·004
4·02	0·000095	0·00087	0·00038
4·8	0·000016	0·000138	0·000060

Illumination of full moon on a clear night   0·2 lux   } (le Grand, 1948)
Illumination of a moonless night   0·0003 lux }

* All densities referred to here are optical densities $\left(\log_{10} \dfrac{\text{light incident}}{\text{light transmitted}}\right)$.

The trails made at higher light intensities undoubtedly represent klinotactic orientation; but it is not easy to mark an arbitrary distinction between these and the trails at lower intensities, some of which are better regarded as klinokinetic, with random changes of direction achieving orientation by adaptation. The loss of randomness is with increasing stimulation obviously gradual, and it is this power to make regulated deviations in relation to the direction of the gradient, followed by appropriate response, that marks the attainment of klinotaxis. A further calculation reveals what may be described as the 'inefficiency ratios' in such klinotactic and klinokinetic orientation: the total length of the trail crawled was divided by the progress achieved, i.e. the length of the straight line joining the initial and end points of the trail, regardless of its angular direction, and the result expressed logarithmically. With improving orientation at the higher light intensities this will approach zero, though such a value is never attained with photo-orientation alone.

Some measure of the amount of activity of the animals at the various light intensities was obtained by averaging the total length of all the trails obtained with each illumination level, reduced to unit time of 30 min. Too great precision should probably not be assigned to values so derived. They fall
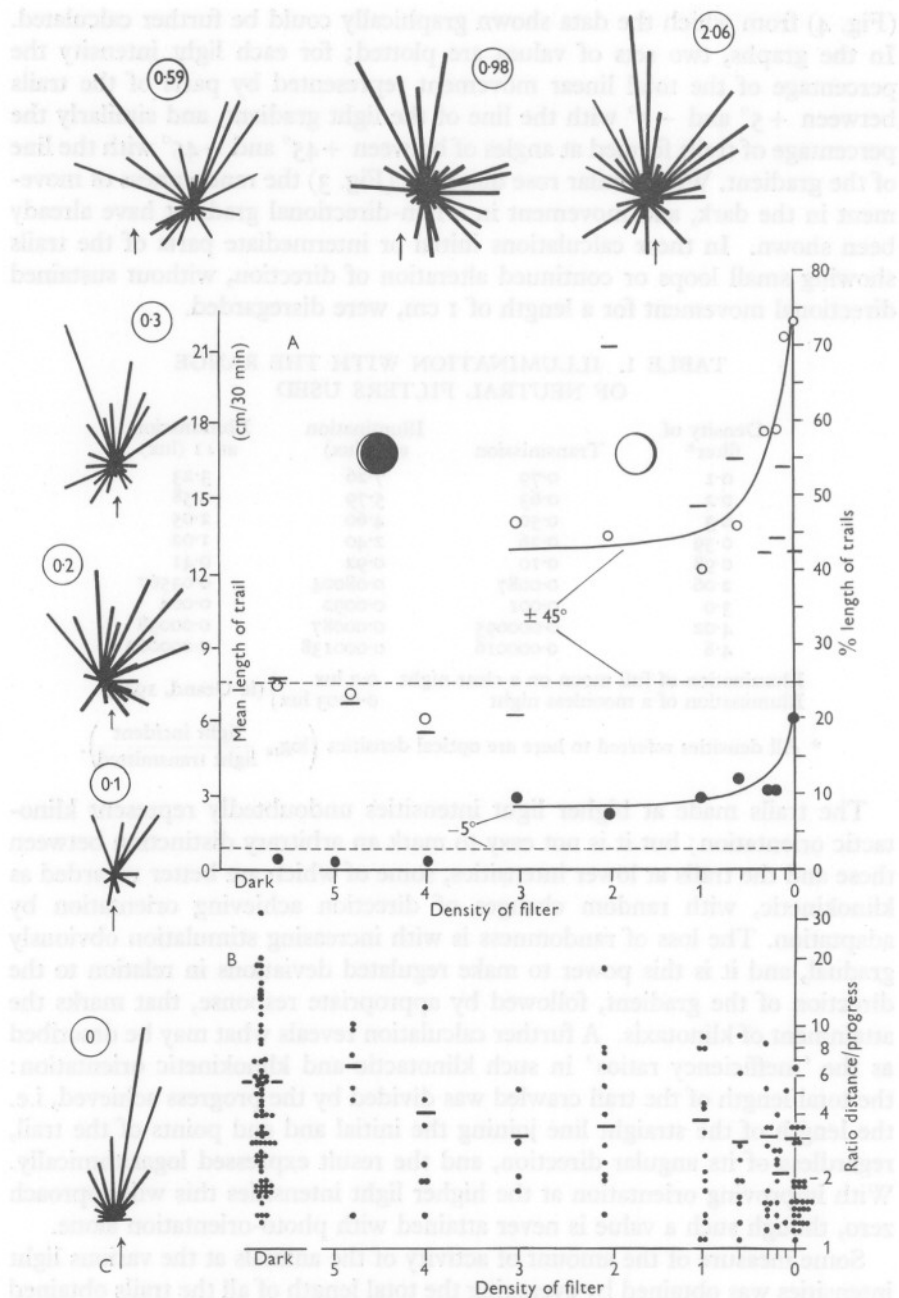
Fig 4 For legend see opposite page.

into two groups. The lower group, at light intensities below 0·01 lux, have a lower total activity, not much greater than that in the dark. Activity strongly increases with illumination from 0·1 lux upwards, with, however, a tendency to fall back at the highest levels of illumination; this last finding is an expression of the greater directness of the trail and the smaller expenditure of wide meanders and loops, at higher light intensities.

Efficiency of orientation, as assessed by the results in Fig. 4, shows three levels. First, using a 9·2 lux illumination, with transmission reduced to one ten-thousandth and below, there is no orientation. Movement at angles within 45° of the light gradients is no better than the random value to be expected with animals in the dark (in one experiment involving only a small number of trails the value falls somewhat below the theoretic random). Above this level of illumination there is a threshold where the values for orientation with the 45° and 5° angles show a strong improvement upon the random level. Orientation is now possible away from the light source and down the gradient; but as shown by their high inefficiency factor, and their form in Fig. 6 B, the trails are of the meandering and looping sort characteristic of a klinokinesis. With an illumination of above 2 lux, orientation finally achieves the character of klinotaxis; trails are much more direct or with smaller meanders (see Fig. 6 A). The curves for orientation both within angles of 45° and 5° show a steep upward trend, towards the values obtained with 9·2 lux. On the graph of Fig. 4 are inserted the values for the illumination of a moonless night and a fine night with full moon (see le Grand, 1948). Photo-orientation is clearly impossible on a moonless night; the threshold for klinokinetic orientation lies at roughly half the illumination of full moon, while the characteristics of the more precise klinotactic orientation are revealed only at illuminations of a twilight order and above.

Legend to Fig. 4

Fig. 4. Results of experiments on photo-orientation. A. Graphs showing the percentages of the total lengths of trails formed between angles of $+5°$ and $-5°$ with the line of the light gradient [●—●]; and between angles of $+45$ and $-45°$ to the gradient [○—○]. On the abscissa are represented the values for log light transmission, used in the various experiments, 0 corresponding to an illumination of 9·2 lux. The broken horizontal lines show the theoretical values for random movement as on a level surface in the dark, without orientation. The intensity of illumination on a moonless night and on a clear night with full moon is indicated by symbols on the graph (see le Grand, 1948). The short horizontal lines for each illumination represent the mean length of trail formed in 30 min in the aggregated experiments (see left ordinate), and thus give a measure of the level of activity. B. Scatter diagram showing for individual trails at various illuminations the value for the 'inefficiency factor' of distance crawled/progress achieved. Small cross-bars represent mean values. C. Rose diagrams (at the left and upper margins) showing the relative extent of the trails produced at the varying angles from the direction of the light gradient, for different levels of illumination. The illumination is represented by the values in small circles for the filter density (= minus log transmission). The light gradient falls off in the direction of the arrows.

GRAVITY RESPONSES

Efficiency of orientation greatly improves if the substrate is inclined. *Lasaea rubra* is strongly negatively geotactic, and as the angle of the experimental glass sheet was inclined more steeply from the horizontal, the trails (i) became more direct and meandered less and (ii) increasingly took the steepest path.[1]

In moving up a sloping surface, *L. rubra* attaches itself securely by two means: the viscid mucus of the foot is generally sufficient to give it a hold as effective as that of a snail on a steep surface; while at the steepest inclinations, 50° or more from the horizontal the byssal gland secretes a 'safety-line' which is fastened to the substrate at intervals of about 1·5 cm. This is thin and strong, looking like a strand of spider web, laid down parallel to the mucous trail of the foot, and crossing it occasionally if the latter should slightly meander. If the mollusc should then fall off from a steep surface, it will swing freely, still attached by the short available length of free byssus line, instead of falling the considerable distance to the bottom of the slope. By taking contact with the substrate it can at once resume crawling a centimetre or two below the point it had last reached. Such accidents are clearly recorded on the trails as short parallel lengths of double track (see Fig. 5). This safety device must be responsible for the animal's surprising freedom to wander out of crevices and to exist as a freely mobile lamellibranch on rock faces strongly exposed to wave action. Several sorts of bivalve can crawl along the surface; but few can be so apparently defenceless against wave battering and dislodgement as *L. rubra*. The safety line may also be secreted on a flat surface, though it is here much less distinct and, especially where the trails meander considerably, it is not often seen.

In experiments on inclined surfaces in the dark the experimental glass plate was sloped at 10° intervals, at angles of 10°–90° from the horizontal. The efficiency of orienting at 90° to the horizontal edge of the plate was estimated with two curves, as for the light response. The curves of Fig. 5 agree well with the curve of Hovey (1928), expressing the mean angle of upward orientation against the angle of inclination of the substrate. Even at the lowest angle of inclination, *L. rubra* has an orienting efficiency equivalent to that obtained with the highest light intensity used on the flat; and as the angle is increased this efficiency improves greatly. The trails run more directly up the slope; the meanderings are altogether eliminated, so that with slopes of 50° and above, undeviating straight trails were generally obtained, running straight up from the lower edge of the glass plate. Full efficiency is attained at 50°–60° inclination of the slope and thereafter little improvement

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[1] See Fraenkel & Gunn (1940) for discussion of the view that efficiency of orientation on sloped surfaces in many animals is due to postural reflexes, with the use of the statocysts, avoiding the tendency to roll if the angle of ascent of 90° with the horizontal is too far departed from.
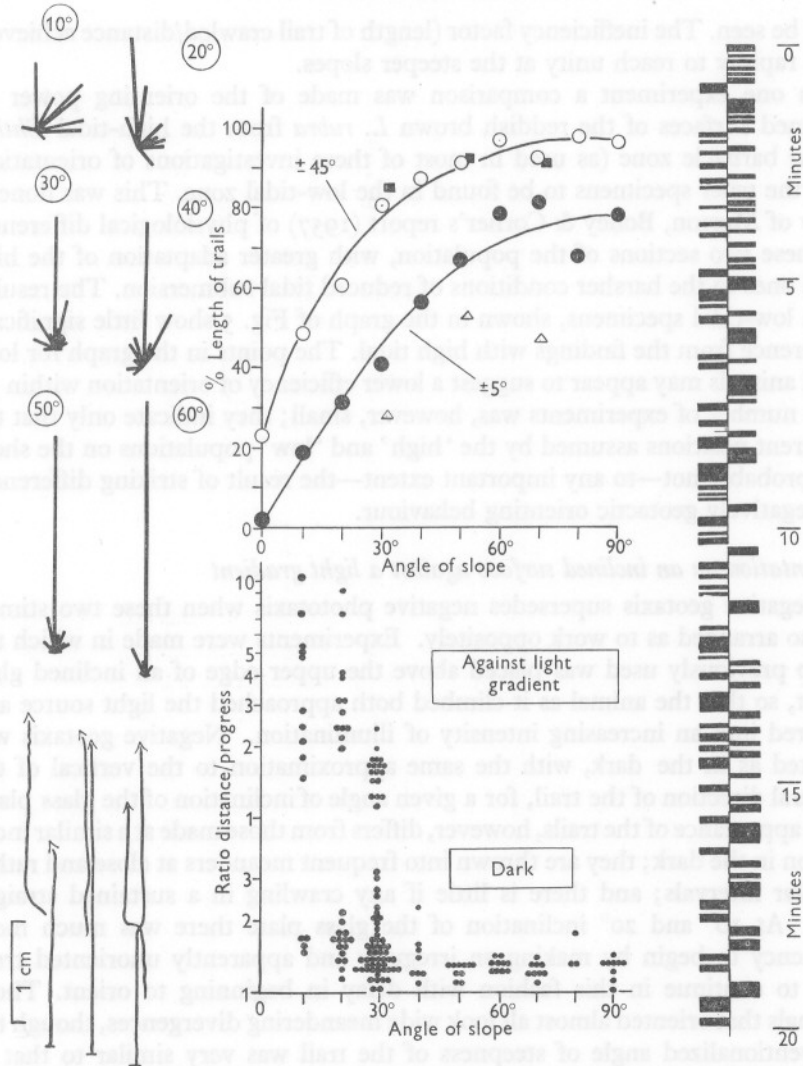
Fig. 5. Graphs showing results of experiments on orientation upon inclined surfaces. Above. Percentages of the total lengths of trails formed between angles of $+5°$ and $-5°$ to a line running directly up the slope [●—●], and between angles of $+45°$ and $-45°$ to such a line. [○—○]. The circles represent experiments with high-tidal animals which were used for most of the work; the triangles and squares show values for the few experiments with animals from low tide. Below. Scatter diagram showing for individual trails in various experiments the values for the 'inefficiency factor' of distance crawled/progress achieved. The lower points are for inclined surfaces in the dark; the upper points are for trails made on inclined surfaces by animals crawling against a light gradient. *Left*. Rose diagrams showing for various angles of inclination of the surface the relative amounts of trail produced at angles to a line running directly up the slope. *Left below*. Portions of trail produced on inclined surfaces after the animal had fallen from the glass plate and—retained by its byssal mooring line—had commenced a fresh trail. *Right*. A record of 20 min movement by a single *Lasaea rubra*, showing the periods of subsidence of the shell alternately to left and right, between 'steps' (see p. 9).

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is to be seen. The inefficiency factor (length of trail crawled/distance achieved) falls rapidly to reach unity at the steeper slopes.

In one experiment a comparison was made of the orienting power on inclined surfaces of the reddish brown *L. rubra* from the high-tidal *Chthamalus* barnacle zone (as used in most of these investigations of orientation) and the paler specimens to be found in the low-tidal zone. This was done in view of Morton, Boney & Corner's report (1957) of physiological differences in these two sections of the population, with greater adaptation of the high tidal ones to the harsher conditions of reduced tidal submersion. The results, with low-tidal specimens, shown in the graph of Fig. 5 show little significant difference from the findings with high tidal. The points in the graph for low-tidal animals may appear to suggest a lower efficiency of orientation within 5°. The number of experiments was, however, small; they indicate only that the different positions assumed by the 'high' and 'low' populations on the shore are probably not—to any important extent—the result of striking differences in negatively geotactic orienting behaviour.

Orientation on an inclined surface against a light gradient

Negative geotaxis supersedes negative phototaxis when these two stimuli are so arranged as to work oppositely. Experiments were made in which the lamp previously used was placed above the upper edge of an inclined glass sheet, so that the animal as it climbed both approached the light source and entered into an increasing intensity of illumination. Negative geotaxis was elicited as in the dark, with the same approximation to the vertical of the general direction of the trail, for a given angle of inclination of the glass plate. The appearance of the trails, however, differs from those made at a similar inclination in the dark; they are thrown into frequent meanders at close and rather regular intervals; and there is little if any crawling in a sustained straight line. At 10° and 20° inclination of the glass plate there was much more tendency to begin by making an irregular and apparently unoriented trail, and to continue in this fashion with delay in beginning to orient. Those animals that oriented almost all took wide meandering divergences, though the conventionalized angle of steepness of the trail was very similar to that of trails on correspondingly steep surfaces in the dark. The inefficiency factor of length of trail crawled/distance achieved was, however, considerably increased. With animals climbing a 30° slope against the light, a few trails were relatively straight and unconvoluted; the majority meandered continuously, though with shorter and more regular divergences than at 10° and 20°. The path followed by these trails shows that the animal never crawled for long directly towards the light source, nor was either of its sides continually exposed for more than a short time to the full incidence of lateral light. The frequent changes of direction enabled the previously exposed side to be regularly shaded. The side for the time being uppermost, i.e. exposed to full lateral illumination could

not, however, be shaded from light by the shell as is possible on the flat. The heavy weight of the shell and body in climbing will always tend to slump downwards over the side already away from the light.
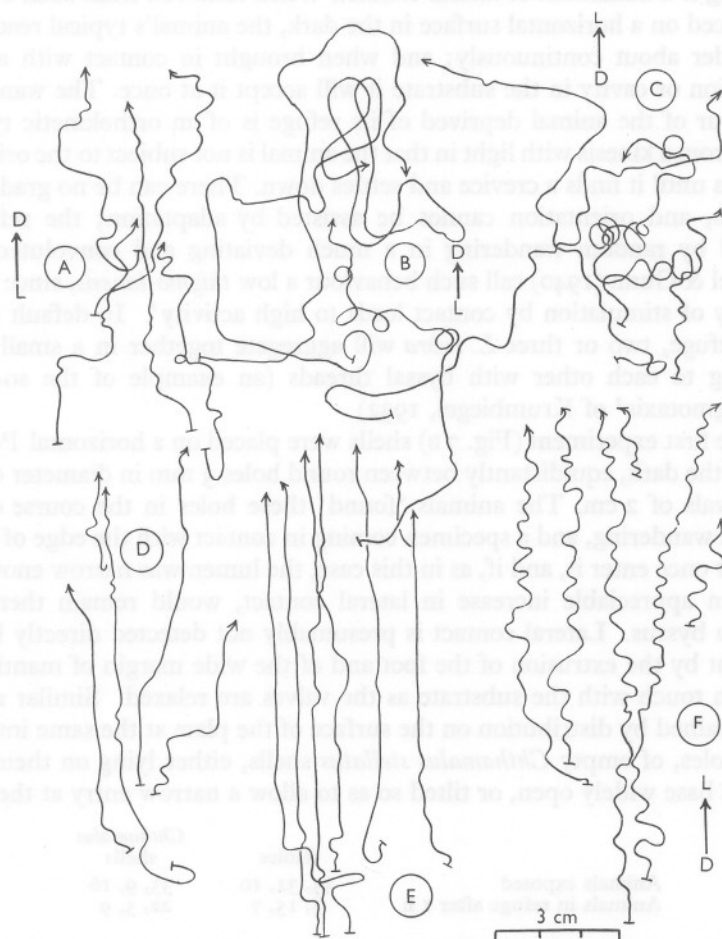

Fig. 6. Representative specimen trails with various orienting stimuli. For each group the direction of the stimulus producing orientation would be represented by a line running directly up the page. (Rather more than half natural size). A. Photoklinotactic trails in a gradient of illumination falling from 9·2 to 4·1 lux over 9 cm. B. Photoklinokinetic trails in a gradient of illumination falling from 0·080 to 0·036 lux over 9 cm. C. Trails produced in climbing a surface inclined at 30° to the horizontal, *towards* an illumination of 9·2 lux at the end-point. D. Trails produced in climbing a surface inclined at 30° to the horizontal, in the *dark*. E. Trails produced in climbing a surface at 60° to the horizontal in the *dark*. F. Trails produced in climbing a surface inclined at 30° to the horizontal, *towards* an illumination of 9·2 lux at the end-point.

RESPONSES TO LATERAL CONTACT

The normal habit of *Lasaea rubra* is to nestle in a narrow crevice or depression affording it a maximum of lateral contact. When removed from such contact, and placed on a horizontal surface in the dark, the animal's typical reaction is to wander about continuously; and when brought in contact with a small depression or cavity in the substrate it will accept it at once. The wandering behaviour of the animal deprived of its refuge is of an orthokinetic type; it differs from a kinesis with light in that the animal is not subject to the orienting stimulus until it finds a crevice and settles down. There can be no gradient of stimulus, and orientation cannot be assisted by adaptation; the refuge is attained by random wandering in a much deviating and convoluted trail. Fraenkel & Gunn (1940) call such behaviour a low *thigmo-kinesis*, since 'a low intensity of stimulation by contact leads to high activity'. In default of any other refuge, two or three *L. rubra* will aggregate together in a small heap, attaching to each other with byssal threads (an example of the so-called 'idiothigmotaxis' of Krumbiegel, 1932).

In the first experiment (Fig. 7 B) shells were placed on a horizontal Perspex plate in the dark, equidistantly between round holes 3 mm in diameter drilled at intervals of 2 cm. The animals 'found' these holes in the course of un-oriented wandering, and a specimen coming in contact with the edge of a hole would at once enter it, and if, as in this case, the lumen was narrow enough to afford an appreciable increase in lateral contact, would remain there and secrete a byssus. Lateral contact is presumably not detected directly by the shell, but by the extrusion of the foot and of the wide margin of mantle that comes in touch with the substrate as the valves are relaxed. Similar results were obtained by distribution on the surface of the plate at the same intervals as the holes, of empty *Chthamalus stellatus* shells, either lying on their sides with the base widely open, or tilted so as to allow a narrow entry at the base.

	Holes	*Chthamalus* shells
Animals exposed	33, 32, 10	33, 9, 16
Animals in refuge after 1 h	8, 15, 7	22, 5, 9

From Fig. 7 B, showing the trails laid down in a typical experiment, it is clear that of those animals in refuges, all had reached their shell or hole without previously touching any other; every animal once within a refuge had stayed there, and that those remaining without refuge had never in the course of the experiment made contact with a shell or a hole.

At the point of entry into a randomly found hole, a short vertical descent is necessary from the flat surface. This would appear to be of a thigmotactic nature (as distinct from random thigmokinesis): contact with the concave interior of the hole guides the animal during its deeper entry into the refuge. Such a thigmotaxis will reverse the normal negative geotactic response.

A similar change of the general behaviour pattern in response to irregularities in the substrate has already been described by Fraenkel (1927) for the high-tidal periwinkle *Melaraphe neritoides*. This snail passes through transverse crevices on its upward climb, crawling into the bottom of a crevice and emerging by crawling out upside-down along its roof. The normally negative phototaxis is here reversed.
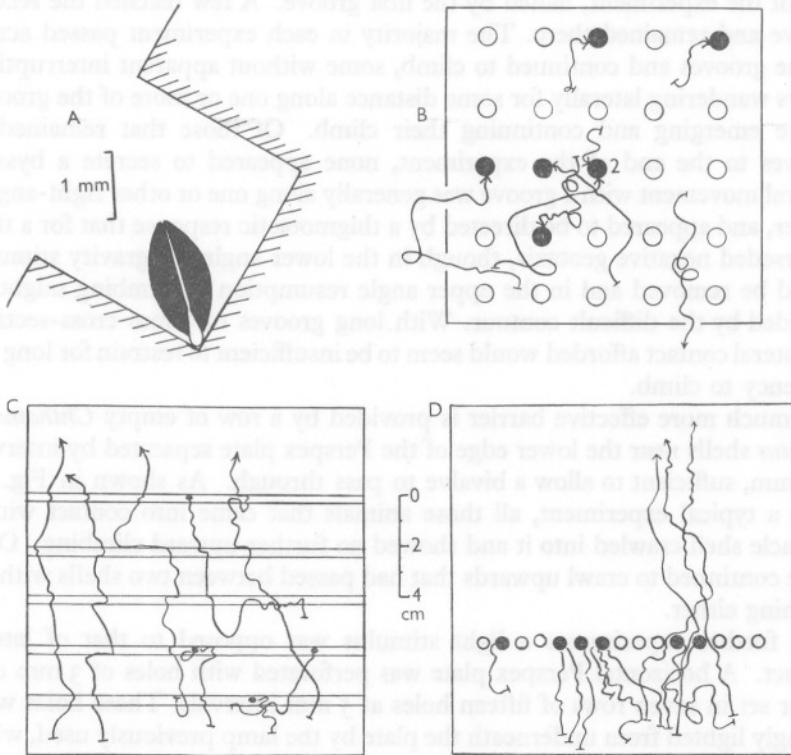

Fig. 7. A. Diagram showing typical position assumed by *Lasaea rubra* crawling along a groove cut in a Perspex sheet, with the maximum thigmotactic stimulus afforded by either of the angles. B. Diagram showing the trails of six *L. rubra* that have arrived at a refuge, crawling in the dark, with random change of direction over a smooth, level surface studded at regular intervals with holes. Black circles represent occupied holes. C. Representative trails of *L. rubra* climbing up a Perspex sheet inclined at an angle of 30° and with its surface interrupted at intervals by transverse grooves. D. Representative trails of *L. rubra* climbing a glass sheet inclined at an angle of 30°, with a barrier of a line of *Chthamalus* barnacle shells. Those animals that made contact with a barnacle were arrested and took refuge in the shells shown as black circles. Those that continued to the top of the sheet had made no contact with barnacle shells.

Thigmotaxis opposed to the stimuli of light and gravity

The lateral contact provided by a crevice or a depression will normally in *Lasaea rubra* supersede the usual responses to both light and gravity.

Experiments were made with Perspex sheets, inclined in the dark at an angle of 30° to the horizontal. The upward path of the negatively geotactic animals was interrupted at intervals of 2 cm by four transversely cut horizontal grooves, of square cross-section and measuring 3 mm along the side. Animals were placed in a row at the lower edge of the plate and allowed to climb. In each of the six experiments, a small proportion of animals were, for the 1 h duration of the experiment, halted by the first groove. A few reached the second groove and remained there. The majority in each experiment passed across all the grooves and continued to climb, some without apparent interruption, others wandering laterally for some distance along one or more of the grooves before emerging and continuing their climb. Of those that remained in grooves to the end of the experiment, none appeared to secrete a byssus. Lateral movement with a groove was generally along one or other right-angled corner, and appeared to be directed by a thigmotactic response that for a time superseded negative geotaxis, though in the lower angle the gravity stimulus would be removed and in the upper angle resumption of climbing might be impeded by the difficult contour. With long grooves of 3 mm cross-section, the lateral contact afforded would seem to be insufficient to restrain for long the tendency to climb.

A much more effective barrier is provided by a row of empty *Chthamalus stellatus* shells near the lower edge of the Perspex plate separated by intervals of 3 mm, sufficient to allow a bivalve to pass through. As shown in Fig. 7 D from a typical experiment, all those animals that came into contact with a barnacle shell crawled into it and showed no further upward climbing. Only those continued to crawl upwards that had passed between two shells without touching either.

In further experiments a light stimulus was opposed to that of lateral contact. A horizontal Perspex plate was perforated with holes of 3 mm diameter set in seven rows of fifteen holes at 5 mm intervals. These holes were strongly lighted from underneath the plate by the lamp previously used, while the rest of the plate was painted underneath with black marine-varnish, so that the experimental surface on top of the plate was kept dark. A thin glass plate was placed beneath, to provide a transparent floor for the holes. Forty-five animals were randomly distributed on the lower half of the plate and a low stimulus of directional light was provided, much weaker than light in the holes. Under this stimulus the animals moved with wide meandering trails across the plate towards the area of the holes. After 8 h, out of a total of forty-five animals, thirty-four were within holes, a proportion very comparable to those that found refuge in unlighted holes or barnacle shells. Contact with the edge of a hole would appear to release a thigmotactic behaviour resulting in entry to the hole regardless of the opposing stimuli of light or gravity.

In another experiment a horizontal Perspex sheet was set up in the dark,

varnished black underneath, and pierced with forty holes 3 mm across. Two *L. rubra* were placed in each. The plate was inspected after an hour in the dark and the animals that had emerged from holes were counted and replaced. The holes were then brightly illuminated from beneath and the plate inspected again after a further hour.

Number of animals originally in holes	80
Number emerged after first hour dark and then replaced	15
Number emerged after second hour lighted	9

Of the dominance of thigmotaxis over phototaxis we have already an example in the literature, the short study of the responses of newly settled *Hiatella arctica* spat by Hunter (1949); here the animals settled in crevices provided by glass slides fixed together at an angle, even though these crevices were the most brightly lighted spots.

DISCUSSION: MAINTENANCE OF POSITION ON THE SHORE

The movements and orientation of *Lasaea rubra* from the *Chthamalus stellatus* zone, as studied here, appear to be directed to securing and maintaining the position of the population on the upper shore, and within that level to acquiring crevices, empty barnacle shells or other lodgements protecting the animals from detachment by waves and currents and from desiccation and the actions of direct light. As a dimyarian eulamellibranch of 'normal'-looking ovoid shape, *Lasaea rubra* would at first appear to be strikingly little adapted for life on wave-exposed rock faces. It has made none of the sacrifices to semi-permanent byssal attachment with alteration of symmetry undergone, for example, by the Mytilidae. Its first advantage is its minute size (see Morton, Boney & Corner, 1957). Its shell, moreover, when viewed edgewise is lentiform and well streamlined against impact of moving water.

Lasaea lacks the frail shell and obese appearance of its relative *Kellya suborbicularis*, which is much more confined to low-tidal crevices and much less peripatetic; and there is no suggestion of the wedge-shaped shell found in the burrowing Erycinacea such as *Montacuta ferruginosa*. The *Lasaea* shell is indeed of an ideal construction for lying submerged in, and filtering from the merest film of splash. There are three other important adaptive features, an extensible foot that can provide viscous attachment to the substrate, a byssal gland that can secrete an attachment line where needed, and a forward facing inhalant siphon, serving as an anteroceptor.

L. rubra may from time to time creep about on open rock surfaces and can readily alter its fixed position. In spite of the precaution of a safety line, the result of movements of disturbed water would tend to carry dislodged shells downshore. The dominant orientation reaction shown by *L. rubra* when removed from a crevice is that of negative geotaxis, by which it will climb even against a gradient of light to which at other times it would respond

negatively. Gravity must be the most continuously sustained stimulus to which *L. rubra* is exposed when out of its lodgement; and it is the stimulus most efficiently responded to, forming, so to speak, the 'coarse adjustment' mechanism, for large-scale maintenance of position. Negative phototaxis is effective only on relatively level surfaces in the absence of a strong gravity stimulus. It serves as an alternative coarse adjustment mechanism, not with the same precision as the gravity response, but nevertheless with the efficiency of a klinotaxis at the illumination of a moonlit night. Such a reaction should produce aggregation in the darkest places which will be crevices or barnacle shells or depressions suitable for nestling. The lowest threshold for photo-orientation is somewhat higher than the illumination level of a night without moonlight; and at the lower levels of detectable light, orientation is chiefly by the inefficient mechanism of klinokinesis. A low level thigmokinesis produces random wandering with very convoluted trails in the absence of a light or gravity stimulus; and once the edge of a narrow depression or crevice is randomly located, a thigmotactic response carries the animal into its narrow confines, even in opposition to the normal responses to gravity and light. Thigmotaxis is a very strong response in *L. rubra* and provides the 'fine adjustment' mechanism by which a suitable crevice is ultimately secured. Preference for lateral contact, and perhaps in part avoidance of light, may constitute a 'token stimulus' leading the animal to a place of shelter whose real advantages are, however, protection from dislodgement by waves or currents, from desiccation in a dry atmosphere and perhaps from predation.

L. rubra is seldom found singly but usually in clusters of two or three large shells with many half grown or newly born beside them. This aggregation may represent a special case of thigmotaxis; but another mechanism must be considered in the Erycinacea, that of chemotaxis. The anterior position of the inhalant siphon offers a preadaptation for direction finding by chemotaxis, and orientation towards other animals may be a rather regular faculty of the commensal Erycinidae and Galeommatidae. In *Montacuta ferruginosa* with *Echinocardium cordatum* there is a well-developed chemotaxis towards the host. I shall describe this elsewhere. In the non-commensal *Lasaea rubra* there is another possibility of chemo-orientation, an 'homoio-chemotaxis' assisting the animals to find their near neighbours at the final stage of aggregation. A hundred or so animals scattered in a Petri dish of sea water overnight will usually resolve themselves in up to a dozen heaps attached together by the byssus. In the investigation of light and gravity orientation, it was first necessary to know to what extent, if at all, the movements of *L. rubra* were influenced by the detection of others of their kind at close range. From a study of all the recorded trails, with animals distributed at 2 cm apart or more, there was no significant evidence of influence of one animal on another. Trails on a dark, a lighted, or an inclined surface, presented the same apparent randomness with respect to any other animal as they did with respect to a

given compass direction when a single animal was studied alone. In the light and gravity experiments reported here any effect of the animals upon each other appeared to be quite subdued by the stronger orienting stimulus. Yet with animals spaced as closely as 1 cm apart, there appeared instances of aggregation that seem anomalous on any theory of complete randomness. For example, in one experiment with a perforated Perspex sheet, animals were found to aggregate in one hole in a group of as many as seven, in others in fours and threes. Statistical investigation of the randomness of aggregation at very short distances must, with the general subject of chemotaxis in Erycinacea, be reserved to a later paper.

L. rubra of the low tidal zone appeared to show an essential similarity in their orienting behaviour, including that of negative geotaxis, with the high tidal ones. Low tidal *L. rubra* are less well adapted to withstand the inter-mittence of submersion of the upper shore, and it may be these physiological disabilities that set an upper limit to the distribution of the pale forms. Whether there may be genetical differences in the two sections of the population is not known. The lower limit of the upper shore population would tend to be maintained by their upward crawling tendency. The upper limit, about that of the upper barnacle line, must be imposed by the short duration of submersion there, with the low humidity of the atmosphere and the diffi-culty of crawling for any great distance on a dry substratum. *L. rubra* in the laboratory will sometimes crawl out of water on to a damp surface but never out of a saturated atmosphere. Its upper limit is quite sharply marked with no gradual falling off either in numbers or in mean size. Morton *et al.* (1957) have already mentioned the ecological advantages of a high level shore habitat to a mollusc of warm temperate distribution, reaching the northern limit of its range in Great Britain, and breeding in summer. It appears to prefer the maximum warmth of the sun on the substrate, consistent with the avoidance of desiccation; to both these requirements, the pattern of its orienting be-haviour effectively contributes.

SUMMARY

The responses of the small bivalve *L. rubra* to light, gravity and lateral contact have been studied in relation to its orientation and maintenance of position on the shore. In the dark, on a flat surface, or in uniform light, *Lasaea* crawls freely about with meandering unoriented trails. At about half the illumi-nation of full moon, orientation by klinokinesis with adaptation becomes

possible, rising by twilight to a negative photoklinotaxis by which darker crevices and refuges are found fairly directly. On a sloping surface *Lasaea* will crawl upwards, more directly as the slope is increased, and its negative geotactic behaviour will supersede negative phototaxis, so that it will crawl upwards even against a light gradient. As soon as chance contact is made with a small hole or crevice, an empty barnacle shell, or a groove affording lateral contact, both the light and gravity reactions are superseded: the animal will crawl downwards into a hole or enter it against a gradient of bright light from a dark surface. It is suggested that in the natural habitat negative geotaxis provides a coarse adjustment to the securing and maintenance of position, while the reactions to light and lateral contact give an increasing precision in the securing of shelter with protection from wave action, light and desiccation.

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