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# On the habits of *Pandora inaequivalvis* (Linné)



BY

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# ON THE HABITS OF *PANDORA INAEQUIVALVIS* (LINNÉ)

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## Introduction

The probable habits of *Pandora inaequivalvis* were discussed recently by Allen (1954), but, due to the lack of time available, no experiments were carried out to verify the conclusions reached, i.e. that this animal is adapted for life on the surface of the substratum on *very* sheltered beaches at low tide level. Whilst visiting the Station Biologique, Roscoff, during the months July to September 1954, opportunity was taken to carry out a few experiments to determine the general habits of this animal, particularly in regard to its possible burrowing habits.

*Pandora inaequivalvis* can be found lying unattached on the surface of the sand on very sheltered shores on the Brittany coast at L.W.S.T. level and below. No buried specimens were found either in 1952 or 1954, although algal growth confined to the extreme posterior end of the shell suggested that they are buried at times. The siphons are very short and are not capable of extending more than two or three millimetres. *Pandora* was never seen to burrow on the shore, although there is a moderately developed foot and the pedal gape is sufficiently wide for the foot to be extended. It was thought likely (Allen, 1954) that the foot is used to uncover the animal if it becomes silted over. It is unusual to find a lamellibranch lying on the surface of the substratum and not using a byssus unless, unlike *Pandora*, it moves actively, e.g. species of *Pecten* and *Chlamys*. An exception is found in *Placenta* (*Placuna*) *placenta* which lies at the surface of stiff mud in shallow bays from the Arabian Sea to the coasts of China (Hornell, 1909). It is even more unusual to find such an animal in the littoral zone and it could only be expected on extremely sheltered shores.

Like *Pecten*, *Pandora* has a markedly inequivalve shell. Yonge (1946) states that *Pandora* and *Corbula* are the only species of lamellibranchs where the inequivalve state is *not* associated with horizontal disposition. Field observations do not bear this out, for *Pandora* was found to lie horizontally on either side. These observations together with those discussed by Allen (1954) suggested that the normal position for *Pandora* is lying at the surface of the sand horizontally on its curved side.

## Experimental Results

*Pandora* was collected from a very sheltered and slightly shelving sandy-mud beach at Penpoull, near Roscoff. The experiments were carried out in a series of small tanks with a continuous flow of water running through them. Observations in 1952, confirmed in 1954, showed that if specimens were placed on the glass bottom of tanks, they did not move from the position in which they were placed. Whether the animal lay on the right (curved) valve or the left (flat) valve made no difference to the result.

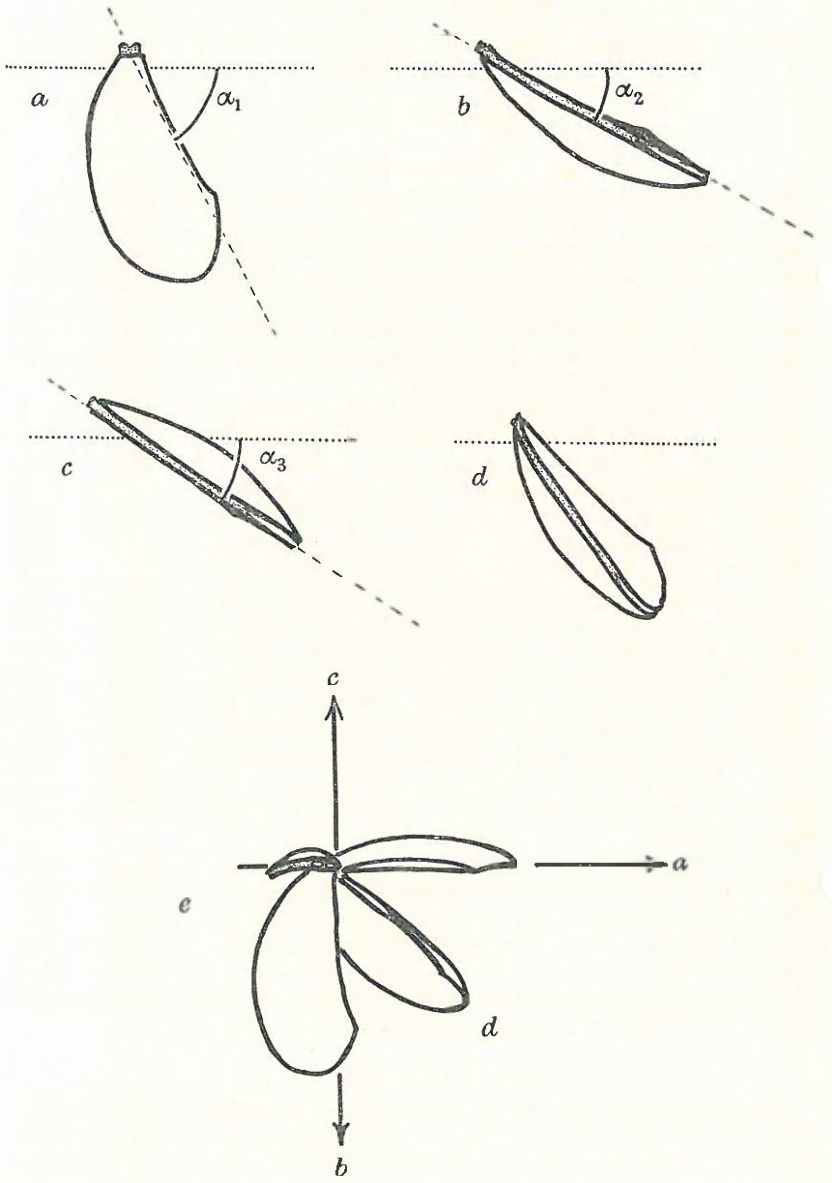


FIG. 1.—Positions of buried shells. a, b, c and d viewed from the side ; e viewed from above. $\alpha_1$, $\alpha_2$ and $\alpha_3$, angles between the buried shell and the substratum. For further details see the text.

Occasionally the foot was extended and touched the bottom, but no attempted digging was observed.

A number of experiments were carried out to determine ; (1) whether animals at the surface of their normal substratum will bury and orientate themselves, and if so, whether variation of their position at the surface has any effect on their subsequent movements and, (2) the effect of burying *Pandora* at varying depths and in varying positions.

(1) *Observations on animals placed upon the substratum.*

Specimens of *Pandora* were laid horizontally on the surface of their normal substratum of sandy-mud and comparisons of the subsequent activities were made between animals that were placed horizontally with the curved valve uppermost and those similarly placed but with the flat valve uppermost. Observations were taken over periods varying from three to eighteen days according to the experiment. Information was recorded on the manner of and time taken for burrowing and the final position of the shells was noted. Of the animals that burrowed 201 out of 213 had less than three millimetres of shell showing at the end of the experiment and many of these were placed so that the tip of the siphons was level with the surface of the substratum.

Classification of the final position taken up by the animals was attempted and observations on the buried *Pandora* showed that they were found in three positions (see Fig. 1). These positions were : (*a*) where the flat valve was vertical (Fig. 1*a*), (*b*) where the flat valve was uppermost (Fig. 1*b*) and (*c*) where the curved valve was uppermost (Fig. 1*c*). The angles $\alpha_1$, $\alpha_2$ and $\alpha_3$ (Fig. 1) varied for different specimens ; $\alpha_1$ varied from 90° to approximately 15° and was never found to be more than 90°. The minimum reading for angle $\alpha_1$ appears to depend on the clearance of the inhalant aperture above the substratum. Thus the lower the readings for the angle $\alpha_1$ the greater will be the area of shell above the level of the substratum. $\alpha_2$ was found to vary from 80° to 10°, any shell with angle $\alpha_2$ greater than 80° being classified among group (*a*). Few shells were found with angle $\alpha_2$ greater than 45°. A similar range of values to angle $\alpha_2$ was shown by angle $\alpha_3$. Positions (*a*) and (*b*) are therefore in planes at right-angles to one another (Fig. 1*e*). Occasionally shells were to be found in positions intermediate to (*a*) or (*b*) (Fig. 1*d*). Such shells were classified (*a*) or (*b*) according to which was the more suitable.

The results from the first two experiments are summarized in Fig. 2 and Table 1. These results indicate that the time taken to burrow in those animals placed with the curved valve uppermost is less than in those with the flat valve uppermost. The phrase ' time taken to burrow ' does not refer to the speed at which individual animals move into the substratum but to the length of time between placing the animals on the surface of the substratum and the time when fixed numbers of them have become buried. The final numbers of animals buried were approximately the same for the two initial positions. In experiment 2, where the time taken to burrow was approximately the same for the two positions, it should be noted that the animals used in this experiment were the same as those used in experiment 1.

The most common position was found to be (*b*) in both experiments.

Only a small percentage (8·3%) in experiment 2 were found in position (*c*). These animals had been originally placed with the curved side uppermost and, possibly due to the short duration of the experiment (72 hrs.), had not reached their final position of (*a*) or (*b*) (see p. 183). No animal that burrowed died, but in experiment 1 a fairly high percentage (see Table 1) of those that remained at the surface died.

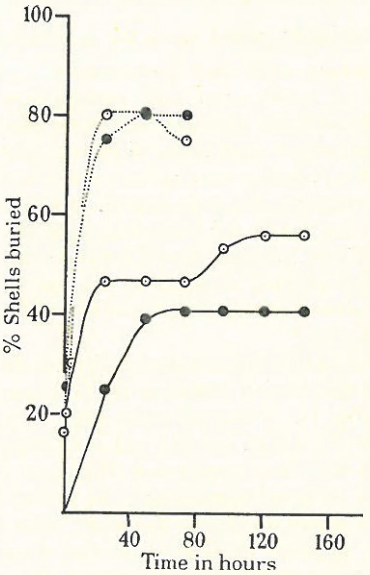


FIG. 2.—To show rate of burrowing (see text).—Expt. 1; - - - Expt. 2 (the same animals as used in Expt. 1). Black circles, shells placed with the flat valve uppermost; open ring and dot, shells placed with curved side uppermost.

TABLE 1

| No. of Experiment | 1 | | 2 | |
|---|---|---|---|---|
| Duration of Experiment | 144 hrs. | | 72 hrs. | |
| Original shell position | cvu | fvu | cvu | fvu |
| Number used | 30 | 36 | 24 | 20 |
| Final position | | | | |
| (*a*) | 20·0 | 13·9 | 25·0 | 10·0 |
| % Buried (*b*) | 36·7 | 30·6 | 41·7 | 70·0 |
| (*c*) | — | — | 8·3 | — |
| % Alive but not buried | 26·7 | 44·4 | 25·0 | 20·0 |
| % Dead at the surface | 16·7 | 11·1 | — | — |

All percentages given are percentages of the total number of animals used. cvu, curved valve uppermost; fvu, flat valve uppermost.

These two experiments showed that *Pandora* will burrow and that it will do so not only from a horizontal position with the curved side up but also when the flat valve is uppermost, the position thought to be normal for the species. As many as 80% of the specimens placed in these positions buried themselves, but these and later experiments showed that some animals

(approximately 25%) remained at the surface of the substratum for considerable lengths of time and were never observed attempting to burrow.

The orientation of the animal on the surface is not necessarily the only stimulus to burrowing and it is natural to believe that the movement of the animal is concerned with the raising of the siphons above the bottom deposits. This is a major problem for short-siphoned species (Yonge, 1946, 1948). Thus burrowing may also be correlated with the touch of the mantle or foot with the substratum. Although it is highly probable that in the above experiments the animals placed with the flat valve uppermost did not lie

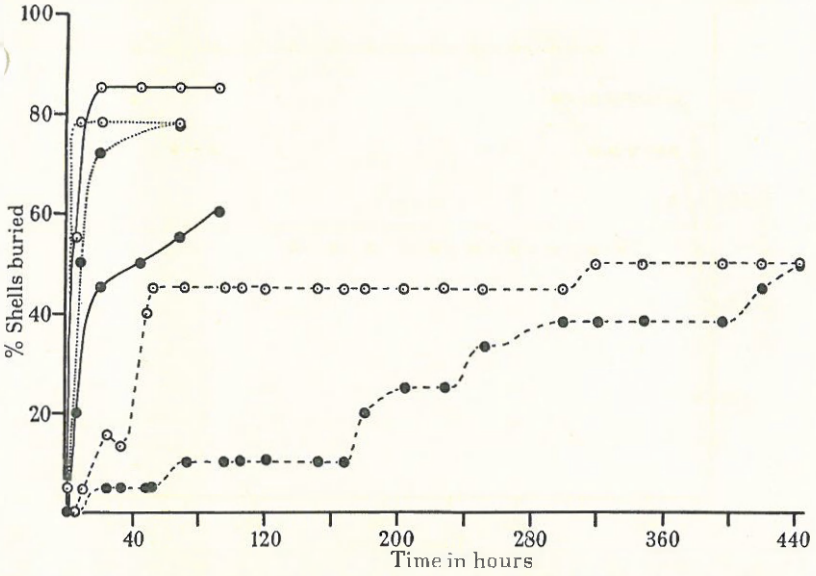


FIG. 3.—To show the rate of burrowing (see text).—Expt. 3 (the same animals used as in Expt. 1); - - - Expt. 4 (the same animals as used in Expt. 3); —Expt. 5 (newly collected animals). Black circles, mantle not in contact with the sand; open ring and dot, mantle in contact with the sand.

so that the mantle, when expanded, would not touch the substratum, no special precautions were taken to see that it did not touch. It must be noted that some specimens of *Pandora* placed with the curved valve uppermost so that the mantle, and particularly the siphons, would be in contact with the substratum when they were expanded, were able to remain in the same position yet extend their siphons sufficiently to clear the surface of the substratum. Therefore three experiments were carried out to discover whether there was any effect on the time taken to burrow when the mantle touched the substratum.

Two groups of *Pandora*, in equal numbers, were placed on the surface of the substratum with the flat valve uppermost. One group (P.1) was so placed that the mantle would touch the substratum when it was expanded and the other group (P.2) was placed so that the mantle could not touch the substratum.

The results (Fig. 3 and Table 2) show that those animals so placed that the mantle could not touch the substratum when expanded still burrowed, but the time taken to burrow was much longer than in the case of those the mantle of which could touch the substratum. As in experiments 1 and 2 the final percentages of buried specimens were approximately the same for both groups. Similar results to those obtained in experiments 1 and 2 were obtained in experiments 3 and 4 where, when the same specimens had been used in both experiments, the time taken to burrow for groups P.1 and P.2 was approximately the same in the second experiment.

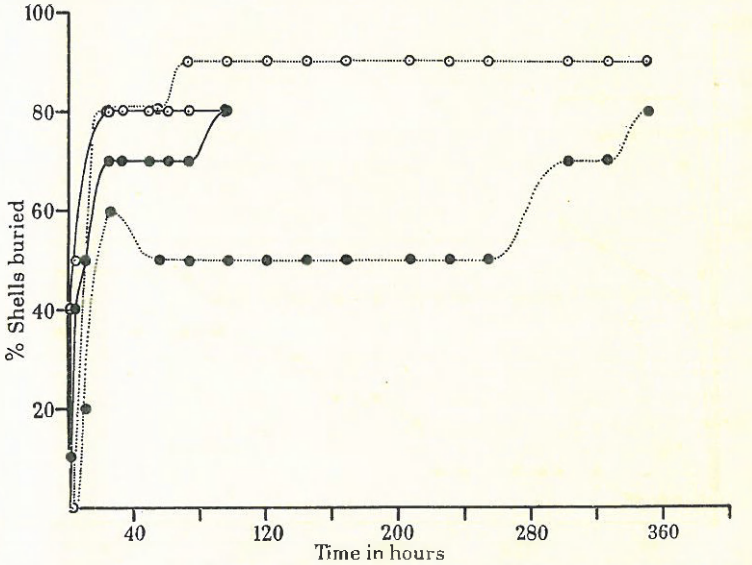


FIG. 4.—To show rate of burrowing (see text).—Expt. 6 (the same animals used in Expt. 5); - - - Expt. 7 (newly collected animals). Black circles, shells placed with the flat valve uppermost; open circle and dot, shells placed with curved valve uppermost.

Experiment 5 was carried out with animals freshly brought in from the beach. Here the time taken to burrow was not only different in the two groups but longer than in the two previous experiments (see Fig. 3).

TABLE 2

| No. of Experiment | | 3[a] | | 4[a] | | 5[b] | | |
|---|---|---|---|---|---|---|---|---|
| Duration of Experiment | | 92 hrs. | | 68 hrs. | | 444 hrs. | | |
| Original shell position | | P.1 | P.2 | P.1 | P.2 | P.1 | P.2 | |
| Number used | | 20 | 20 | 14 | 14 | 20 | 20 | |
| Final position | | | | | | | | |
| % Buried | (*a*) | 15·0 | 25·0 | 50·0 | 64·3 | 30·0 | 25·0 | 5·0[c] |
| | (*b*) | 70·0 | 35·0 | 28·6 | 14·3 | 15·0 | 20·0 | |
| | (*c*) | — | — | — | — | — | — | |
| % Alive but not buried | | 15·0 | 40·0 | 14·3 | 21·4 | 25·0 | 30·0 | |
| % Dead at surface | | — | — | 7·1 | — | 25·0[d] | 20·0 | |
| % Dead buried | | — | — | — | — | 5·0 | — | |

a, Used specimens—the same specimens used in experiments 3 and 4; b, Fresh specimens; c, Final position of the shell not certain; d, Three specimens with less than one-third of the shell buried.

Analysis of the positions of the buried animals shows that only in experiment 3 were there more shells in position (*b*) than in position (*a*). It is possible that the large numbers found in position (*a*) in experiment 4 were due to the shortness of the duration of this experiment. As was found in experiments 1 and 2, approximately 25% of the animals remained at the surface alive. The greatest death rate was among those animals that had just been collected from the beach. This is also similar to the results of experiments 1 and 2. Although none of the shells was found in position (*c*) one shell after burrowing reappeared at the surface and remained there with the curved valve uppermost.

It must be concluded that although the stimulus of touch on the mantle shortens the time taken to burrow, the animals will burrow without this stimulus and the final numbers of animals buried are approximately the same.

Experiments 1 and 2 were repeated making sure that the mantle of those animals placed with the flat valve uppermost did not touch the substratum when extended, and the results obtained (Fig. 4 and Table 3) were similar to the first two experiments. The time taken to burrow was less in those animals laid with the curved valve uppermost yet the final numbers buried were approximately the same. Approximately 20% of the animals remained at the surface. Those specimens which were newly brought in from the shore were again much slower starting to burrow than those that had been used in previous experiments and the death rate in those animals used for the first time was high. The final positions of the buried specimens show that there was none in position (*c*). Of animals that had been placed with the curved valve uppermost more were found to be in position (*a*) than in position (*b*) at the end of the experiment, and more shells were found in position (*b*) than in position (*a*) in animals that had originally been placed with the flat side uppermost.

TABLE 3

| No. of Experiment | | 6 | | 7[a] | |
|---|---|---|---|---|---|
| Duration of Experiment | | 96 hrs. | | 350 hrs. | |
| Original shell position | | cvu | fvu | cvu | fvu |
| Number used | | 10 | 10 | 10 | 10 |
| Final position | | | | | |
| % Buried | (*a*) | 60·0 | 30·0 | 70·0 | 20·0 |
| | (*b*) | 20·0 | 50·0 | 20·0 | 40·0 |
| | (*c*) | — | — | — | — |
| % Alive but not buried | | 20·0 | 20·0 | — | 20·0 |
| % Dead at the surface | | — | — | 10·0 | 20·0[b] |

a, Fresh animals from the shore; b, One specimen with the curved valve uppermost, it attempted to dig and turned over.

(2) *Experiments with buried animals.*

Three experiments were carried out to determine the effect of burying *Pandora*.

In experiment 8 specimens were buried horizontally with the flat valve uppermost under one inch of substratum. The animals were divided into two size groups, the smaller 2·3 cm. or less in length and the larger 3·0 cm. or more in length. The rate at which the siphons of the buried animals appeared at the surface and the position of the shells at the end of the

experiments were noted. The results are shown in Fig. 5 and Table 4. The mortality rate in experiment 8 was very high. In both size groups 50% of the animals died. More large specimens than small were able to move to the surface and some specimens, particularly the smaller, were able to survive buried for at least ten days. No distinction was made between positions (*a*) and (*b*) in experiment 8 but no shells were found in position (*c*).

Experiment 8 was repeated, except that the animals were placed under a quarter to a half inch of substratum instead of one inch. Over 90% of the animals in this experiment (9) reached the surface of the substratum and at a far quicker rate than in experiment 8 (see Fig. 5). One animal unburied

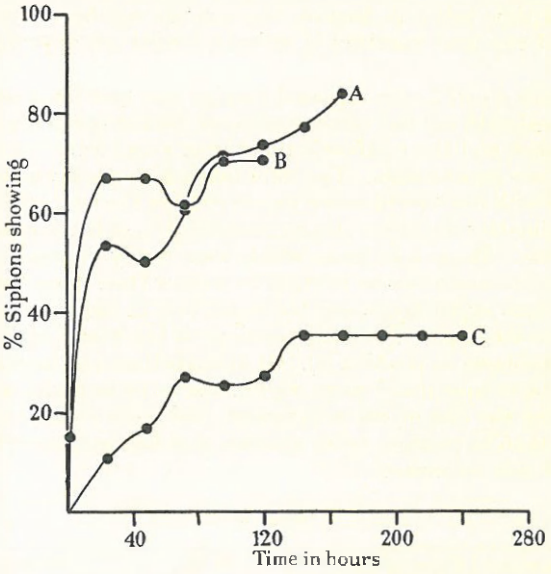


FIG. 5.—To show the rate at which siphons appear at the surface. A, Expt. 10; B, Expt. 9; C, Expt. 8.

itself completely. The smaller specimens, again, were less able to reach the surface than the larger. Only 57·1% of the former were at the surface but another 28·6% were buried but alive. The majority of the animals at the surface were found in position (*b*) and the small specimens that were still under the surface of the substratum had moved to position (*b*).

Finally, in experiment 10, experiment 9 was repeated, i.e. animals were placed under a quarter to a half inch of substratum, though here the specimens were inverted and placed with the curved valve uppermost instead of the flat valve uppermost. Large specimens only were used. The rate of emergence was quick (see Fig. 5) and 88·4% successfully protruded their siphons above the level of the substratum. Only 26·9% were in position (*c*); most of the shells were in position (*a*) (46·1%), and only 11·6% were found in position (*b*). Two animals were observed to unbury themselves completely and one of these later reburied.

TABLE 4

| No. of Experiment | | 8 | | 9 | | 10 |
|---|---|---|---|---|---|---|
| Duration of Experiment | | 240 hrs. | | 120 hrs. | | 168 hrs. |
| Depth and position of animals | | 1″ fvu | | ¼–½″ ovu | | ¼–½″ ovu |
| Size of animal | | small | large | small | large | large |
| Number used | | 14 | 14 | 14 | 12 | 26 |
| Final position | | | | | | |
| % Siphons showing | (*a*) | 7·2 | 21·4 | 7·1 | — | 46·1[b] |
| | (*b*) | | | 50·0 | 83·4 | 11·6 |
| | (*c*) | — | — | — | — | 26·9 |
| % Alive, siphons not showing[a] | | 42·8 | 28·6 | 28·6 | — | — |
| % Uncovered completely fvu | | — | — | — | 8·3 | — |
| ovu | | — | — | — | — | 3·9[c] |
| % Dead in original position | | 50·0 | 50·0 | 14·3 | 8·3 | 11·6 |

a, All animals in position (*b*) ; b, One animal unburied completely for 24 hours and then reburied ; c, Dead.

## DISCUSSION AND CONCLUSIONS

It was unfortunate that there was not sufficient time to repeat experiments, but the results obtained enable some conclusions to be reached about the habits of *Pandora inaequivalvis*.

Approximately 70% of a total of 258 animals used in experiments 1–7 buried themselves. The time taken to burrow varied from experiment to experiment. Shells placed on the surface of the substratum with the curved side uppermost burrowed sooner than those placed with the flat valve uppermost, even when the latter were so placed that the expanded mantle touched the substratum. Also, shells placed horizontally at the surface of the substratum with the flat valve uppermost so that the mantle when expanded would touch the substratum burrowed sooner than those similarly placed but with the mantle unable to touch the substratum. The final percentage of shells buried was approximately the same for all experiments. Animals used in previous experiments burrowed sooner than those freshly brought in from the beach.

The time taken from the commencement of burrowing to a position where the siphons were just showing varied from fifteen minutes to as much as three days. Digging movements were of the typical lamellibranch type (Stoll, 1938, and Quayle, 1949). *Pandora* was never observed to move over the surface of the substratum and always burrowed from the position in which it was placed. The animal is levered by the extruded foot until it lies on the free shell margins. It lies on the anterior part of the free margins opposite the pedal gape and typical seesaw movements carry the shell vertically downwards, the angle $\alpha_1$ varying according to the specimen but always tending to increase to 90°. At the same time there is a tendency for the animal to move to position (*b*). This latter movement takes place gradually. The most noticeable feature of the majority of the movements of *Pandora* is the slowness at which they are carried out. It appears that position (*b*) is the most frequent position taken up by *Pandora* under experimental conditions, the angle $\alpha_2$ being not more than 40°. Apart from an occasional shell reappearing at the surface, *Pandora* was never observed to move from its buried position, this being different from *Venerupis* as reported by Quayle (1949).

Although these experiments show that *Pandora* will reappear at the

surface, this does not occur frequently enough to explain why so many shells are present at the surface of the substratum of the beaches. If buried they will move so that the siphons are at or above the surface of the substratum, but if they have been buried to a depth of one inch or more the mortality rate is very high and probably more than 50% of the animals will die. It was shown that some animals are able to live below the surface of the substratum for at least ten days.

It is necessary to correlate the observations in the field with those from the experiments as set out above. No buried animals were found on the shore but many had tufts of algae confined to the siphonal end of the shell. In 1952 most of the animals collected were lying with the flat valve uppermost (no count was taken). In 1954 counts were made, and of 80 animals collected on 19th July, two were lying with the curved valve uppermost to every one with the flat valve uppermost. On the day preceding this collection there had been a strong gale. On 1st August, of 120 *Pandora* collected half were lying with the curved side uppermost and half with the flat valve uppermost, and on 16th August, when over 200 shells were collected, the proportions for the two positions were the same as for the first collection on the 19th July. In the latter case, again, there had been bad weather previous to the collection. At neap tides when *Pandora* was not uncovered, animals could be seen and collected from under one to two feet of water at the surface of the substratum.

The experimental animals were kept at a similar temperature to those in the field (18° C) but were not subjected to anything comparable to tidal conditions. The water in the tanks was siphoned slowly but the current produced little or no sand movements. The experiments show that the majority of the *Pandora* that do burrow are covered by less than half an inch of sand. It is reasonable to suppose that the scour on the beach, although slight, will be sufficient to uncover the shells and, particularly in rough weather, even to turn them over so that the curved valve is uppermost. This is supported by the high numbers of shells found in this position after rough weather. A shell lying with the curved valve uppermost is less likely to be moved by the water movements than a shell lying curved side down and resting on a fraction of the valve surface. Those animals lying with the curved valve uppermost will be the first to burrow.

It must be concluded that in still conditions the most frequent position for *Pandora* will be position (*b*) where the shell is tending to the horizontal with the curved valve down and with all but the siphonal region below the surface of the substratum. It is highly probable that tidal movements constantly unbury the animals and may turn them so that they lie with the curved valve uppermost. Those lying in the latter position and those where the mantle touches the substratum will be the quickest to bury and orientate themselves again. Movements are slow and animals can tolerate lying both with the curved valve uppermost or the flat valve uppermost for long periods. Few will survive if buried more than one inch under the substratum, but at depths of half an inch or less *Pandora* can re-orientate itself.

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## Summary

Observations and experiments show that *Pandora inaequivalvis* is adapted for life at the surface of a sandy substratum on very sheltered shores at E.L.W.S.T. level. Burrowing movements are very slow and no horizontal movements were observed. In still water animals most frequently lie just below the substratum in a horizontal plane with the siphons showing and with the flat valve uppermost at an angle of less than 40° to the surface. They will tolerate lying at the surface of the substratum on either valve for periods up to twenty days at the least. In the field water movements appear to keep the animals uncovered for considerable periods of time, in fact no buried specimens were found.

The times taken to burrow under experimental conditions are given, also details of the position taken up by the animal and of its habits.

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