HIBERNATION AND AESTIVATION IN GASTROPOD MOLLUSCS.

On the habits of a Slug from Dalhousie (Western Himalayas), with remarks on certain other species of Gastropod Molluscs.

By Sunder Lal Hora, *D.Sc., F.L.S., F.Z.S., Zoological Survey of India*, Calcutta.

CONTENTS.

Habits of the Dalhousie Slug.

I was spending the summer of 1927 at Dalhousie, altitude about 7,000 feet above sea level, in the Western Himalayas and in the course of my daily walks I noticed the peculiar habits of the common slug, *Anadenus dalhousiensis* Bhatia.[1] The months of May and June are generally very hot and dry in this part of the country, but fortunately during my stay the weather remained pleasant on account of occasional rain storms. These storms are rather unusual for this time of the year. There was a regular alternation of hot and dry weather for a fortnight or so followed by cloudy weather with rain for three or four days. During these wet days a number of slugs were always noticed crawling about on the roads and rocks at the side, but on the approach of the dry weather they gradually became scarce and ultimately disappeared altogether even from shady places. After observing this behaviour of the slug on three or four occasions I became interested to learn what happened to these animals during the dry weather. During the rains a few individuals were collected and kept under observation in an insect-breeding cage. A thick layer of loose earth was placed at the bottom of the cage and a few stones were also kept inside in the corners. Some fresh vegetation was also put inside to provide nourishment. The animals confined in the cage were quite active for the first few hours and crawled about on the glass sides of the cage, but as the sun became bright and the weather dry, the animals retreated one by one from the exposed surfaces and sought shelter under the shady sides of the stones (away from the window) and began to prepare themselves for aestivation. It was noticed that out of half a dozen specimens five went to the stone farthest away from the light and only one sought shelter under a different stone. The method of aestivation is as follows. When a slug finds a suitable place for rest,

[1] Bhatia, *Proc. Zool. Soc. London*, p. 876 (1926).

it applies the foot firmly to the rock and contracts considerably in length; a sticky secretion is poured out from the surface which, after a time, hardens into a thin film. The animal now contracts a little more so that it appears to be enclosed in a membranous sheath. It lies in this condition till the return of favourable weather. The animals were found to lie in this condition in large masses, each enclosed at the exposed end in its own sheath. When it rained again the cage was put outside, and the animals revived in a very short time and again became active. The cage was now brought inside the room and so long as the surfaces inside the cage remained wet the slugs remained active. After a couple of days, however, the animals showed a tendency to aestivate and some of them were actually buried in the loose earth to see how they would behave, but after a few hours all of them were found resting under stones. Those that were buried in the earth had come out and were as clean as their fellow individuals.

Professor Jai Chand Luthra of the Agricultural College at Lyalpur was staying with me when I was experimenting with these slugs. He informed me that he had seen large masses of slugs hibernating in this way on the under sides of stones in a dry stream-bed[1] at Dehra Dun. On making enquiries among the people at Dalhousie I was informed that they had also observed masses of hibernating slugs.

It is generally known that "the Slugs burrow into the earth and form a small chamber which they line with mucus."[2] Oldham[3] thus describes the habits of *Testacella scutulum* in Hertfordshire: "During hot, dry weather, and in the cold of winter, *Testacella* is inactive. It then constructs a cocoon-like cell of earth agglutinated with its mucus, in which it remains until the return of more genial conditions. Heavy rains incommode it, flooding its under ground retreats and driving it and the earthworms on which it feeds to the surface." The common slugs of Dalhousie and of Dehra Dun, probably belonging to different genera, and probably also of other hilly places in India, do not form under-ground burrows but secrete a house of mucus while sticking to the sheltered sides of rocks. I believe that this difference of habit is due to the fact that in these mountains there is very little loose soil (on account of the torrential rains) and the surface is very hard so that the slugs find it difficult to burrow. This might also account for the fact that these animals retire into dry stream-beds for the purpose of aestivating, for in these places they would find sheltered positions under loose rocks, whereas in the neighbouring country the soil is too hard for them to excavate.

---

[1] The bed of an intermittent rapid-flowing stream provides shelter for quite a number of animals during drought, firstly, because the bed perhaps contains more moisture than the surrounding country, and secondly, because the narrow crevices among loose stones provide shelter both from the sun and from enemies. Baker (*Science, N. Y.* XLIX, p. 519, 1919) found that certain species of Lymnaeidae always hibernated in the bed of an intermittent stream. He says that "Such species as *Galba caperata* (Say), *G. cubensis* (Pfr.) and *G. bulimoides* and its varieties are typical of these habitats. *Galba palustris* and some other species normally living in marshes may at times be compelled to adopt this hibernating type of habitat during annual periods of drought."

[2] Woodward, *The Life of the Mollusca*, p. 72 (London; 1913).

[3] Oldham, *Trans. Hertfordshire Nat. Hist. Soc.* XV, p. 194 (1913).

Pearl [1] has recorded some curious observations on the habits of the slug *Agriolimax*. According to this author the slug retires to water for the purpose of hibernation. "This hibernation" he says, "was induced by low temperature, and while in the hibernating state the respiratory exchange became extremely low, so that the slug could exist practically as well in water as in air." He found that in a warm room the animal revived and crawled out of the water. From these observations he concludes that, "There seems to be some biological significance in this sort of behaviour of an hibernating animal with reference to water. During the winter months the temperature of the water at the bottom of a river or pond is considerably higher than that of the surface layer of the soil. Hence an organism runs much less risk of being frozen to death when at the bottom of a body of water then when simply beneath a stone or the upper layers of the soil." Indeed, this phenomenon is remarkable. So far as I am aware no air-breathing animal can stand submersion in water for any length of time without dangerous consequences. I shall show later how these terrestrial molluscs avoid excess of water to save themselves from "drowning." By a variety of peculiar devices all hibernating or aestivating molluscs are capable of "excluding cold and retaining their own moisture." Pearl's observations can perhaps be interpreted differently in the light of the following account.

I have always found it convenient in the course of my field work to kill slugs and snails for museum purposes[2] by drowning them in water. Immediately these animals are placed in water they begin to crawl about actively. This rapidity of movement gradually slows down and finally ceases and the animals sink to the bottom in a contracted condition. Before long, however, the molluscs become active again and make further efforts to obtain atmospheric air and it is during these efforts that they ultimately die in a fully expanded condition due to asphyxiation. Slugs are hardier than snails and are more difficult to "drown." I found it useful to leave the snails in water overnight, but for slugs this period was insufficient. It must, however, be remembered that the time taken in "drowning" these animals depends on the temperature of the water in which they are kept. In warm water they move about briskly and are soon exhausted, whereas in cold water they become benumbed and will rest quietly at the bottom for a considerable time before death overtakes them. At Dalhousie it was noticed that the slugs were perfectly stupefied after two days in cold water, but when transferred to spirit they contracted suddenly and still showed signs of life. Pearl left a slug in the cold sticking to the inner side of the dish above water-level and after a time he found that the amimal was lying in a comatose condition under water. "It is not certain," he says, "whether the animal crawled down into the water or simply fell in, having loosened its hold on the glass. It seems probable that the former action is what occurred, for the slug was found some distance

[1] Pearl, *Rep. Mich. Acad. Sci.* III, pp. 75, 76 (1902).

[2] Mr. B. B. Woodward informs me that slugs can be prepared for the purpose of exhibition and study by killing them in a solution (not strong) of Epsom Salts. It works better than simple drowning and kills the animal extended.

from where it would have been had it simply fallen into the water." I suggest that the position of the slug shows that it had probably struggled for a short time on dropping into the water before it became quiet and benumbed by the cold. This author subjected his specimen of *Agriolimax* to changing conditions of heat and cold at short intervals and it seems more probable that when subjected to cold the animal contracted and lost its hold on the glass and fell into the water. Pearl's observations can be repeated with any slug with the same results, though the slug may be known to hibernate in burrows or under stones. I have already shown that the actual contact of water with the animal is an essential cause of its awakening from slumber (see also p. 363 below). To me it seems highly improbable that terrestrial molluscs retire to water for the purpose of hibernation, and the observations of Pearl only show that the cold has a benumbing effect on the slug just as it would have on any other animal.

There is a further point in the habits of the Dalhousie slug which requires consideration. It has been pointed out that these animals aestivate in masses. This can be explained by the fact that the slugs living in a particular area would seek shelter under rocks providing them with certain optimum conditions of safety on the approach of danger. Naturally there being few such places in the neighbourhood the hibernating individuals would come together. In the case of these slugs I believe the concerted action has some other biological significance also. The rigorous conditions under which these animals live demand that soon after the return of favourable conditions they should copulate so that the eggs can be laid as early as possible in good weather. This provision naturally gives the progeny a better chance to survive during the first unfavourable weather. This habit appears to be quite common to almost all the hibernating and aestivating species of Gastropod molluscs. Certain snails, like *Helix aspersa*, form large masses[1] by applying their mouths to one another, while others, like *H. pomatia*, hibernate singly, but several of them are found together in one place usually among the roots of trees.[2] The snails that I have studied so far hibernate or aestivate singly, but quite a number of them were always found in one place. Stephens[3] found a large number of individuals of *Cochlicopa lubrica* in the same position sticking to the outer surface of the door and frame of the dark-room at the Iowa Lakeside Laboratory after a cold rain at night and a cold wind in the morning. The rain had probably driven these snails up to the door frame from their retreats.

In my previous work[4] on this subject I confined my attention to the behaviour of Indian snails and for want of leisure was unable to consult literature on the non-Indian species. During my stay at Edinburgh I have been able to study the mode of life of the common garden-snail, *Helix aspersa*, and have examined the literature, and I

---

[1] Allman, *Journ. Linn. Soc. London* (Zool.) XXV, pp. 517-520 (1894-5); Swanton, *Zoologist*, pp. 312-314 (1915).

[2] Beetson, *Journ. Conch. Leeds* XVI, pp. 31-36 (1919).

[3] Stephens, *Science, N. Y.* LXVIII, p. 271 (1918).

[4] Hora, *Rec. Ind. Mus.* XXVII, pp. 401-403 (1925); *Journ. Bombay Nat. Hist. Soc.* XXXI, pp. 447-449 (1926); Hora and Rao, *Rec. Ind. Mus.*, XXIX, pp. 49-62 (1927).

am now in a position to discuss certain aspects of my observations on Indian species in greater detail. I have here to express my thanks to Mr. A. D. Hobson for supplying me with material of *H. aspersa*.

TREE-CLIMBING HABITS OF CERTAIN SNAILS AND THEIR BIOLOGICAL SIGNIFICANCE.

I have already recorded the occurrence of *Succinea arboricola* Rao in large numbers on the bark of mango trees at Lonavla, Western Ghats. The individuals were found in a comatose condition in August, 1924 during a period of heavy rainfall. In December 1925 only a few individuals were found in similar situations. I searched for the molluscs in all likely places on both these occasions, but the aestivating or hibernating individuals were found only on the mango trees in the compound of the Hamilton Hotel at Lonavla which during the rainy season is marshy. A few active individuals of the species were collected from among moss at the base of a mango tree on the Lonavla-Khandhala road, but I was not able to find any aestivating individuals on its lower branches. Another point about this species is worthy of record. Out of hundreds of specimens collected by me, Dr. H. S. Rao was able to find only two adult examples, while all the others were young specimens. Alkins [1] has recently contributed some interesting observations on the habits of "*Hygromia fusca* (Montagu)"[2] and he found that in certain districts there is a regular seasonal migration of these snails from the ground to the tops of trees. He remarks that, "It is evident too that the shell is in general to be found most abundantly and reliably on the ground in late autumn and winter, say from October to March. In summer the species is scarce and sometimes not to be found on the ground in woodland habitats where it is known to live, and this appears to be due to a habit of ascending trees and shrubs and living amongst the leaves; it is quite evident, however, that the tree-climbing habit is not invariably followed even where suitable trees abound." His explanation of this peculiar behaviour is as follows: "It seems unlikely that the shells find in the trees some food that is not available on the ground below; and the likeliest explanation of their seasonal climbing would appear to be that they avoid by this expedient the attention of some enemy which cannot or at any rate does not itself climb. It may be significant that at the season when tree climbing is the rule the snails are immature: full-grown shells may be able to withstand the attacks of the hypothetical enemy. The seasonal prevalence of the habit would, however, be equally well explained if the enemy itself were active in spring and early summer. If it were in addition wide spread but not ubiquitous in its distribution, the ascertained distribution and habits of the snail would follow at once." I have noticed several species that climb trees for purposes of aestivation. A large number of individuals of *Pupisoma evezardi* Blandford were collected from crevices in the bark

---

[1] Alkins, *Journ. Conch. Leeds* XVII, pp. 243-247 (1925).

[2] Mr. B. B. Woodward informs me that *Hygromia fusca* (Montagu) is a synonym of *Zenobiella subrufescens* (Miller).

of trees at Lonavla along with snails of *Succinea arboricola*, and *Buliminus* (*Subzebrinus*) *dextrosinister* Annandale and Rao was observed by me aestivating singly on trunks of trees in hot and dry months; Dr. H. S. Rao has also informed me that he has on several occasions noticed snails of *Ariophanta* sp. in South India attached to Cactus plants in a state of aestivation during drought. Among Succineid molluscs, " There are species like *Indosuccinea semiserica* and allied forms which are found living on shrubs and trees in the rainy season. They never seem to require large areas of water as a necessary condition for their existence or sustenance. During the drier months they apparently hibernate in concealed positions on the plants on which they live, and with the approach of the rainy season they rouse themselves to activity and feed chiefly on fresh vegetable matter such as leaves and shoots of plants."[1] The peculiar slug-shaped molluscs of the family Janellidae, confined to New Zealand, the Australian region and probably to the Andaman and Nicobar Islands, are found living on trees and shrubs. The common garden-snails are known to ascend wet walls and climb trees after a heavy downpour. Taylor, in his account of the land and freshwater molluscs of the British Isles, describes several instances of the tree-climbing habits of the snails. *Helix nemoralis* prefers drier and more open situations and its habit of ascending trees during heavy rain is well known (Taylor, p. 280); *H. hortensis* is at times quite arboreal in its habits (p. 331); *H. pisana* hiberantes and aestivates on trees (p. 374) and *Helicigona lapicida* either climbs on trees or lives on rocks. Stephens [2] observed specimens of *Cochlicopa lubrica* after a cold rain at night sticking to the door and frame of the ' dark-room ' at the Iowa Lakeside Laboratory and it seems probable, as mentioned above, that though it was cold and the animals were hibernating, the cold rain had flooded their underground retreats and had driven them out.

In the case of the marine air-breathing molluscs of the family Neritidae Littorinidae, etc., the same tree-climbing habit can be observed, at any rate, in certain species. Tattersall [3] has pointed out that there is a distinct gradation in the habitat of certain species of *Littorina;* thus *L. littorea* lives in the *Laminaria* and *fucus* zones, *L. obtusata* lives in the zone where it is exposed at every low tide, and *L. rudis* and *L. neritoides* live practically actually out of water. Sewell [4] records finding *L. scabra* and *L. obesa* living on the trunks and branches of trees above the water-level in the Nicobar Islands, and I have on several occasions noticed the shrubs near brackish pools literally covered with these snails, both in the Gangetic Delta and in the deltaic region of the Irrawadi. The piers below the Pamban Bridge in South India were similarly covered with these amphibious molluscs, and, as a matter of fact, this phenomenon can be observed along the solid supports of any harbour constructions in India. I have not studied the marine air-breathing molluscs in detail and am, therefore, not in a position to say much about their habits.

---

[1] Rao, *Rec. Ind. Mus.*, XXVII, p. 386 (1925).
[2] Stephens, *Science, N. Y.* LXVIII, p. 271 (1918).
[3] Tattersall, *Fisheries Ireland Sci. Invest.* I, pp. 6, 7 (1920).
[4] Sewell, *Rec. Ind. Mus.* XXVI, pp. 535, 540 (1924).

From the above instances it is clear that the tree-climbing habit has been acquired by several totally different types of molluscs living in very widely separated countries. Alkin's explanation about the behaviour of "*Hygromia fusca*" does not appear to me quite feasible. I give below what seems to me to be the probable reason for this peculiar behaviour.

I need not consider here the causes which have induced aquatic organisms at different periods to seek atmospheric air for the purpose of respiration. Prashad [1] has shown that certain Gastropod molluscs have taken to breathing air in comparatively recent times and a study of the respiratory organs of these snails shows the varying degree of modification which they have undergone for this purpose. The degree of adaptability of these air-breathing snails to their changed environment can be measured by the time that is taken in "drowning" these animals. Water that was hitherto absolutely essential for their life gradually becomes a source of danger. The more a species becomes adapted for a terrestrial life the more it becomes independent of water and actually begins to avoid it. In the tree-climbing habits of the different snails we may find an explanation of this fact. During heavy rainfall the ground in places may become soaked with water and this would interfere with the aerial respiration of the snails. Possibly it is to avoid this that most of the snails climb up walls and trees. It is obvious that on hard ground, where no such danger would exist, the molluscs would not need to climb trees and might continue to live on the ground. This may explain the peculiar distribution of "*Hygromia fusca*" and *Succinea arboricola* in different places. In the case of those snails that burrow in earth for hibernation or aestivation it is known that heavy rain incommodes them and by flooding their underground retreats drives them out of their burrows. It is probably to obviate this difficulty that snails like *Ariophanta*, *Bulliminus*,[2] *Indosuccinea semiserica*, *Succinea arboricola* and others have devised the method of hibernating on trees and spending most of their lives in these arboreal surroundings.

The behaviour of "*Hygromia fusca*" tallies in most respects with that of *Succinea arboricola*. Both the molluscs climb trees in summer, in both the tree-climbing individuals are young and in both "the tree-climbing habit is not invariably followed even where suitable trees abound." In the preceding account I have given an explanation of this behaviour, but it remains for me to indicate why young individuals only are found on the trees. It seems to me probable that under natural conditions these molluscs live for one year only and that each brood on the approach of unfavourable weather climbs up trees, descending only when conditions are favourable. It is possible that in their young stages these molluscs are more liable to be drowned after a downpour than mature individuals and the tree-climbing habit is only a device to get over it.

So far as I know, all the species of molluscs in India are active during the rainy season, but it is remarkable that *Succinea arboricola* aestivates

---

[1] Prashad, *Proc. Twelfth Ind. Sci. Congress*, pp. 126-143 (1925).

[2] Mr. B. B. Woodward informs me that *Buliminus* is preoccupied by *Bulimina* Ehrenberg, but I leave this point for the attention of abler hands.

during this period. I thought at first that this was due to the fact that the animal protects itself from being swept away by torrential rains, but it now seems to me more probable that at Lonavla even the surface of the leaves and branches of trees are so wet in the rainy season that the animal cannot properly exercise its respiratory functions. So it tides over this period of heavy rainfall by aestivating. That there must be some difficulty in breathing under such conditions is shown by the change in the position of the pulmonary opening in some of these terrestrial or amphibious molluscs. I have already referred to the peculiar slug-like molluscs of the family Janellidae which live on trees. In them " the pulmonary cavity is very peculiar. It consists of a rounded or oval cavity deeply sunk into the body on the dorsal side and opening to the exterior on the dorsal or lateral surfaces."[1] In the case of the slugs even the shell has been sacrificed in order to place the pulmonary opening in such a position that the animal could breathe when partly submerged in water. Here is a remarkable instance of adaptation for breathing air even when the animal is partly submerged in water. Among the air-breathing vertebrates such as Crocodiles and Cetaceans we find a similar adaptation for breathing air even when the animal is submerged in water. In a way these two types of animal provide a fine illustration of the phenomenon of convergence in evolution.

There are certain species of air-breathing Gastropod molluscs which do not climb trees during heavy rainfall but live on rocks either on the sides of rushing streams or on rocks kept moist by the spray of a water-fall. *Turbinicola saxea*, *Neritina perotettiana* and a small species of *Paludomus* common at Lonavla belong to the former category, while *Lithotis rupicola* and *Cremnochonchus syhadrensis* may be cited as instances of the second type. I have here referred only to those species of molluscs on which I have made personal observations. In *Turbinicola saxea*, which lives on wet rocks at the sides of streams at Khandhalla, the pulmonary " opening is more anteriorly situated and is much larger than in the genus *Pila*," (Prashad, *op. cit.*, p. 13). Probably a similar change of position and modification of the pulmonary opening takes place in *Neritina* and *Cremnochonchus* both of which are operculate snails. In the case of *Lithotis rupicola*, a Succineid mollusc, an interesting type of modification takes place. Very little is known regarding the habits of this peculiar snail. I found them common on rocks below the falls at Khandhalla in the rainy season along with *Cremnochonchus syhadrensis ;* but all attempts to discover its retreats in the dry weather have resulted in failure. This species lies flat on the rocks with its massive foot fully extended ; it has solved the problem of breathing in such situations by developing a groove-like siphon on the inner side of the shell. About the function of this groove Dr. H. S. Rao states : " The function of the groove must for the present remain obscure as the habits of this species are still imperfectly known. It may perhaps be suggested that the groove serves to increase the quantity of air in the pulmonary chamber when needed."[2] Similar tubes are devoloped in Cyclophoridae, and

[1] Prashad, *Proc. Twelfth Ind. Sci. Congr.* pp. 129, 130 (1925).
[2] Rao, *Rec. Ind. Mus.* XXVII, p. 390 (1925).

Woodward[1] remarks about them as follows: "Certain land operculates, belonging to the Cyclophoridae, dwelling in Further India, Malaysia, have a peculiar provision for admission of air during aestivation. In some species this consists of a simple notch in the peristome close to the suture, but in others the notch becomes converted into a short-necked aperture placed a little way back from the mouth, while in yet others a distinct tube is developed, either attached to the body whorl or standing free from it." I have not observed any of these peculiar molluscs in a state of aestivation, but it appears to me very likely that these respiratory tubes have been developed to enable the animal to breathe when it lives on very wet rocks. The various members of the Cyclophoridae show all possible gradations in the evolution of this structure and it would be highly interesting to correlate the development of this structure in the various forms with their mode of life. There is no doubt, however, that this structure has been independently evolved in *Lithotis* and in the Cyclophoridae probably in response to a similar stimulus. Here we have another instance of parallel evolution or convergence.

THE "HIBERNACULUM" OF CREMNOCHONCHUS SYHADRENSIS.

Cremnochonchus syhadrensis has been observed to aestivate or hibernate on rocks projecting out of the water at the edge of the pool below the falls at Khandhalla. The individuals were found in small pits well protected from the mid-day sun. These pits were fairly deep and in some cases it was not possible to take the animal out even with the help of a pair of forceps. These pits have probably been formed by the snails in the way described by Woodward[2] as follows: "The most remarkable hibernacula, or winter abodes, are, however, those formed in sheltered positions in limestone rocks, when by frequent resort the snails in course of years erode burrows in the stone, which in places becomes honeycombed by them." In these narrow and deep pits *Cremnochonchus syhadrensis* tides over the unfavourable weather in a state of torpor well protected from the adverse climatic conditions as well as the ravages of its enemies. Taylor (1914, pp. 244-246) has described and figured the pits of *Helix aspersa.*

THE EPIPHRAGM: ITS FORM AND FUNCTION.

It is a well known fact that snails react to the extremes of seasonal changes more or less passively. They hide themselves in a variety of ways on the approach of unfavourable weather. "In all these resting-places they either fasten the mouth of the shell with mucus to some object or to a fellow-snail's shell; or, when isolated, close the aperture of the shell with a film of dried mucus to exclude the cold and retain their own moisture. This film is known as the "epiphragm," or "hybernaculum," and has usually a small aperture left near the centre as an air-passage. In very cold weather, as the animal retreats farther into its shell, it will form a second or even a third epiphragm, with

[1] Woodward, *The Life of Mollusca*, pp. 73, 74 (London; 1913).
[2] Woodward, *The Life of Mollusca*, pp. 72, 73 (London; 1913).

a space between each. In some cases, such as the Roman Snail (*Helix prmatia*), this epiphragm is impregnated with lime salts to such an extent as to make it quite a solid lid (hence the name, from *pomum*, a lid)." (Woodward, *op. cit.* pp. 72, 73). Considerable literature has grown up round the structure and formation of the epiphragm in the common garden snails of Europe. In 1915, Flössner gave an excellent account of the epiphragm of *H. pomatia*. His article is entitled " Zur Biologie, Struktur und Bildungsweise des Winterdeckels von *Helix pomatia* " ; it is beautifully illustrated and contains a complete bibliography at the end.[1] A few general observations on the form of the epiphragm with special reference to the presence or absence of the aperture during the period of sleep and to the succession of epiphragms that is formed in certain individuals may be made at this point.

Fischer [2] found that a complete epiphragm is formed when a snail hibernates singly, but when in contact with some hard object only the borders are soldered. Taylor [3] found that a complete epiphragm is always formed in *Helix aspersa*, but my own observations confirm those of Fischer. When an individual of *Helix aspersa* is watched against a glass surface at the beginning of the process of hibernation, it is observed that the very much contracted foot is applied to the substratum the glandular mantle forming a border on all sides of it. In the region of the pulmonary opening this continuous border is partly interrupted by the aperture which lies fairly close to the hard shell. In this way the cementing fluid is secreted along the borders only. When the shell is properly fixed to the object by the secretion, the animal withdraws its foot over the whole of which the mantle spreads. Before the animal finally withdraws into the shell it closes the aperture in the region of the pulmonary opening with secretion from the calcareous glands in the adjoining mantle region. So far as I have been able to observe no aperture is left in the cementing substance for the purpose of respiration.

I have examined several specimens of *H. aspersa* with a complete epiphragm, which is very thin except in the position of the pulmonary opening, where a white calcareous plate is formed. This calcareous plate is liable to damage and in most of the individuals it was found to be cracked. No other aperture was found in the epiphragm. It may, however, be remarked that those snails that normally hibernate by applying their mouths to some hard object when made to hibernate without any support secrete a thin epiphragm. The reason of this is obvious, for in their natural mode of sleep a great deal of the opening is closed by the substratum and they have acquired the habit of secreting just enough material to cement their mouths to the object. When forced to hibernate without a substratum the same amount of fluid is used in forming the entire epiphragm. On the other hand, the snails that normally hibernate or aestivate without a solid substratum usually secrete a very thick epiphragm, such as is found in *H. pomatia* and

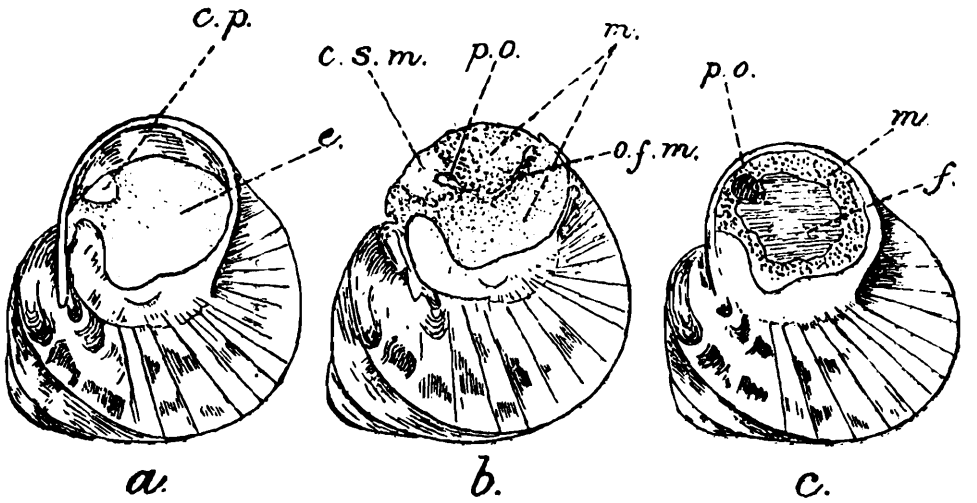
---

[1] Flössner, *Zool. Anz.* XLV, pp. 337-346 (1915).

[2] Fischer, *Journ. Conchyliol.* IV, p. 397-403 (1853).

[3] Taylor, *Monograph of the Land and Freshwater Mollusca of the British Isles*, I, p. 310 (1894).

Macrochlamys glauca. Mr. B. B. Woodward informs me that the south European *Helix aperta* and the Syrian species of *Albea* do the same.



TEST-FIG. 1.—Hibernating individuals of *Helix aspersa.*

a. Hibernating animal showing epiphragm *in situ.*

b. Comatose animal after removal of the epiphragm and a part of the outer whorl.

c. Animal in the process of cementing its edge to the substratum before hibernation.

c. p. = calcareous plate of epiphragm ; *c. s. m.* = chalk-secreting area of mantle ; *e* = epiphragm ; *f* = foot ; *m* = mantle ; *p. o.* = pulmonary opening ; *o.f.m.* = overlapping folds of mantle.

In the snails with this habit a thick epiphragm is a necessity and a solid structure is formed. Generally there is no aperture but sometimes by the breaking down of the highly calcareous region of the epiphragm of *H. pomatia* a hole is formed (Flossner, *op. cit.*). I did not observe an aperture in the epiphragm of *M. glauca.* Allman[1] found that in the epiphragm of *H. aspersa* " Immediately over the site of the respiratory orifice the epiphragm is perforated by a small aperture which affords access from without to the atmospheric air," and in a foot-note he adds : " I have never met with *Helix aspersa* in a state of hibernation in which the perforation of the epiphragm was not present ; and yet I can find no published account of it." Smith[2] on the other hand remarked that, " The epiphragm of *Helix pomatia* and *H. aspersa* does not apear to be perforated." I have examined about a hundred specimens of *H. pomatia* and did not find one with a perforated epiphragm. I have indicated above what appears to me to be the case in these garden snails. If a hibernating individual is examined after removing the epiphragm, the region of the mantle surrounding the pulmonary opening appears to be quite distinct. That region secretes the calcareous plate, which breaks down and leaves a hole in the epiphragm. So long as the animal is secreting the substance for the epiphragm it is active, as is evidenced by the rhythmical opening and closing of the pulmonary aperture. But when the epiphragm is formed and the animal is about to retire to sleep, the aperture is closed hastily by the calcareous glands. The breathing movements of the animal leave an impress on the solidifying epiphragm

[1] Allman, *Journ. Linn. Soc. London* (Zool.) XXV, pp. 517-520 (1894-95).
[2] Smith, *Proc. Malac. Soc. London* III, p. 309, foot-note (1899).

and usually a ridge is seen in the centre corresponding with the mantle fold below. In the epiphragm of *Achatina immaculata* Lam. from Nyasaland Smith[1] has described a slit-like structure which is closed, so that the epiphragm does not permit evaporation during periods of great heat and dryness. The ridge on the epiphragm corresponds in position to the slit-like opening between the two lobes of the mantle. The same author[2] has described the following structure of the epiphragm of *Thaumastus sangoae:* " The outer or curved margin exhibits from end to end a series of minute perforations. They look as if they have been pricked through from the inner surface, each being on a little prominence. On the under surface each perforation is more or less surrounded by a raised short ridge-like loop, the ends of which are open on the inner side. The outer surface is rather uneven, but, with the exception of the outer perforated edge, is generally rather smooth." The epiphragm of *T. bitaeniatus* is more or less similar to *T sangoae.* From the very nature of these apertures it seems to me clear that they have been formed by forcing out air through them from inside. This must have resulted from the respiratory movements of the animal when the epiphragm was being secreted. The snail does not close these apertures as *Helix aspersa* does when it finally retires to sleep, and it would be interesting to see whether they possess any special area of the mantle for secreting calcareous matter.

In the epiphragms of *Glessula hastula* and *Zootecus insularis* I have shown that apertures of a definite nature are present. In these two snails the animal is capable of maintaining its connection with the atmospheric air. (I am not aware of the conditions under which the snails of *Zootecus insularis* secrete this perforated type of epiphragm). In both the species there is a series of epiphragms and the aperture enables the animal to breathe when it is engaged in manufacturing the inner epiphragm. In this case the aperture is not the result of the breaking down of a portion of the epiphragm but is a definite structure made for a definite purpose. The structure of the canal leading to the aperture is different in these two snails, that of *Z. insularis* being more elaborate than that of *G. hastula.*

The conditions under which a series of epiphragms is formed in *Helix pomatia* and *H. aspersa* are probably different from those of *G. hastula* and *Z. insularis.* In all the specimens of *H. aspersa* that I have examined there is only one epiphragm. These individuals had hibernated in cardboard boxes in the laboratory and, as I have pointed out above, their epiphragms were more or less complete. In nature, however, the calcareous portion of the epiphragm breaks down very often as is clear from Flössner's account and from Allman's observations. Under such conditions the animal becomes exposed to the rigours of the weather again. It probably reacts to this change by receding farther into the shell and secreting a new epiphragm. If by chance this second epiphragm is damaged, it secretes a third one and so on.

In *Helix pomatia* the succession of epiphragms is of a different nature. The outermost epiphragm is thick and solid and the inner ones corres-

[1] Smith, *Proc. Malac. Soc. London* III, pp. 309, 310 (1899).
[2] Smith, *Ibid,* IV, pp. 3, 4 (1904).

pond to those of *H. aspersa.* Flössner found that out of a hundred specimens of *H. pomatia* one snail had 1 epiphragm, 15 had 2, 33 had 3, 27 had 4, 20 had 5, 3 had 6 and one had 7. If the above results be represented graphically they show a regular curve of frequency, but I am unable to explain how the animal goes on secreting epiphragms when it has ceased to have any access to atmospheric air for respiration owing to the formation of the imperforate outermost epiphragm. In the case of certain Indian snails such as *Macrochlamys glauca* that aestivate in summer a uniformly thick epiphragm is secreted. By damaging this epiphragm I have induced the animal to secrete another below it, though in nature I did not find a single individual with more than one epiphragm. The succeeding epiphragms are always much thinner than the outer ones, but sometimes it happens that the animal is unable to secrete a complete epiphragm and under these circumstances it desiccates completely after 5 or 6 hours.

AWAKENING AFTER TORPIDITY.

Fischer [1] has recently recorded some observations on the awakening of snails and summarizes his results as follows: " Quatre faits sont donc acquis par mes expériences :—

1. L'humidité de l'air n'est pas une condition nécessaire au réveil.
2. La lumière accélère le réveil dans de grandes proportions.
3. Le réveil par la combinaison des facteurs lumière et remouvellement de l'air s'obtient plus rapidement que par la lumière seule.
4. Le renouvellement de l'air, en dehors des autres facteurs, est capable de provoquer le réveil."

In the case of the aestivating species, except *Succinea arboricola,* that I have studied in nature and in the laboratory, it has been found that actual contact with water is more or less necessary to revive them from slumber. Johnston [2] gives a series of instances where " Snails become torpid when the atmosphere is hot and dry;. ....and, as often as they are unbound by the application of a warm moisture, they come forth from the shell strong and vigorous." Rao [3] found that in the case of *Macrochlamys glausa* " actual contact with moisture helps it to throw off its epiphragm, and that a cool atmosphere alone is not enough to arouse it from its seasonal slumber." The case of *Succinea arboricola* is somewhat different. It aestivates both during the rainy season and in the extremely dry season. It was observed that in the case of *Glessula hastula* actual contact with water was not necessary for its awakening, but a certain degree of warmth was required. It was found that " direct sunlight does not of itself stimulate the activities of these animals and, secondly, that warmth in moderation along with a high degree of humidity suits them very well."[4] The case of *Helix*

[1] Fischer, *C. R. Acad. Sci. Paris* CLXXXI, pp. 1186-1188 (1925).
[2] Johnston, *An Introduction to Conchology,* p. 261 (1850).
[3] Rao, *Rec. Ind. Mus.* XXIX, p. 54 (1927).
[4] Hora, *Rec. Ind. Mus.* XXIX, p. 57 (1927).

pomatia is similar to that of *Glessula hastula* and it is probable that both the species at the time of hibernation respond to a dry and cold temperature. Recently, (February, 1928), a large number of hibernating individuals were received by the Zoology Department from France. To awaken them from slumber the box containing the specimens was kept in a warm place for two days but only 6 per cent of the individuals revived in this way. The others were revived in a short time in contact with warm water. A few individuals were kept in cold water for two days, a couple of specimens were kept near an electric radiator in a box for 6 hours, a few others were left in a glass window for days and some were actually kept in strong light for hours and in all these cases there was no apparent effect on the state of their torpor. In every case it was possible to revive them in a short time in contact with warm water. This indicates that for the activity of these snails both warmth and moisture are essential. I have studied the behaviour of *Helix aspersa* with the following results.

Two specimens of equal size were selected and their membranous epiphragms were removed. One was left in a dry dish and the other was placed in a dish with a small quantity of water. After a couple of hours it was seen that the former animal had shown no sign of activity, while the latter had come out of the shell and was crawling about. Both the dishes were left near an anthracite stove overnight and bits of cabbage leaf were supplied as food for the animals in case they needed it. In the morning it was found that the snail in the dry dish was without any change, while its fellow had fed and had passed some faecal matter. The second snail was crawling about on the sides of the dish. Through an oversight it escaped afterwards. The other specimen was left under an electric light and a gas-light for quite a long time, but showed no signs of activity. When placed in a card-board box in the laboratory overnight, it stuck to the side of the box and was found in this condition next morning. The animal was forcibly detached and revived in contact with cold water. At night it was provided with food and left in the cold. In the morning it was found sticking to the side of the dish with its massive foot, but it had not touched food nor was there any other evidence of its activity during the night. For the next two days it was left in a dish with a small quantity of water and in spite of the cold the animal crawled a little on the wet surface of the dish. It did not feed but passed a certain quantity of faecal matter. It was then transferred to a card-board box and after a couple of hours it was found in a hibernating condition sticking to the side of the box.

The above observations show that (1) the animal can be revived in contact with water; (2) a certain amount of warmth is necessary for the activity of the animal, and (3) it reacts to a dry surface in a very short time and goes into a state of torpor. The last point deserves some consideration. It is known that slugs and snails progress with the help of heir slimy foot, and if they are allowed to crawl on a smooth surface a tract of slime is left behind. On a dry surface this slime appears to retard the movements of the animal, which reacts to this condition by hibernating or aestivating. It is in the mode of locomotion of these animals that one can trace their preference for wet surfaces.

They require a wet surface but not water in excess; the latter is distinctly harmful as has been shown above.

In nature it is found that species like *Macrochlamys glauca* seek shelter under stones from the glare and the heat of the sun in the hot months of May and June in Northern India. The dryness of the weather makes them retire into a state of torpor. In the rainy season (July, August and September) these moisture-loving creatures come out from their retreats and in spite of the heat, are quite active. The European garden-snails hibernate in winter, but lead an active life in the bright, warm and wet summer. From the above discussion it appears probable that Indian snails are capable of enduring extremes of temperature without apparent discomfort, provided moisture is given to them. In the case of *Helix pomatia* it has recently been demonstrated[1] by the test of molecular concentration of the blood that a close correlation exists between the presence or absence of moisture in the air and the activity of the snail.

Allman (*op. cit.*) has observed in the case of *Helix aspersa* that "On the approach of spring, and when the conditions rendering necessary the presence of an epiphragm no longer exist, the snail once more awakens from its sleep, and the central opening in the phragmatogenic disc again makes its appearance, and gives exit to the foot and head of the snail, which then, pressing on the membranous epiphragm, ruptures it and thus allows the animal to enter freely into all its relations with the surrounding medium." T is is in all probability the method adopted by all the snails that secrete a thin membranous epiphragm to release themselves from their confinement; but in the case of the species that secrete a thick epiphragm I suppose a method exists similar to that described by me for *Macrochlamys glauca* and *Glessula hastula*. The margin of the epiphragm is softened by a secretion from the foot and the whole structure is lifted as a lid and carried for sometime as a false operculum. In the case of *Helix pomatia* I have observed that the animal ruptures the thin membranous epiphragms, but with regard to the outermost thicker epiphragm its behavior is the same as that of *M. glauca* and *G. hastula.*

Conclusions.

In the preceding pages I have attempted to discuss the phenomena of hibernation and aestivation from several points of view as shown by the study of the Gastropod molluscs of India and other countries. It seems to me probable that this habit has been independently acquired by the various groups of snails under very diverse conditions. From a study of the respiratory organs of the Pulmonates Prashad, *op. cit.*, p. 129, was led to conclude that, "The origin of a pulmonary chamber for direct aerial respiration is polyphyletic, and the so-colled lung or lung-sac seems to have been evolved at different times in various classes." The habit of hibernation and aestivation appears to be the direct outcome of the terrestrial habits of these snails and its evolution has to be explained along similar lines to those suggested by Prashad for the pulmonary

[1] Marcel Duval, *Nature* CXXI, p. 194 (1928).

chamber. The great diversity shown by the snails recalls the oft-repeated saying of my late chief, Dr. N. Annandale—" No one formula can express, much less explain, evolution." Pearse in his recent book on Ecology, after discussing this phenomenon in the entire animal kingdom concludes that " dormant states in animals are usually associated with (in certain cases apparently caused directly by, or a preparation for) periods during which there is lack of food, cold, heat, drought, accumulation of waste products, lack of oxygen or other unfavourable conditions. Metabolism is reduced and an animal perhaps survives until the environment again reaches a condition that is favourable for renewed activity. The stimuli that bring about dormancy are apparently not the same for all animals, or in some cases even for all individuals of a single species."

My sincere thanks are due to Lt.-Col. R. B. S. Sewell, Mr. A. S. Kennard and Mr. B. B. Woodward for going through the paper and for making valuable suggestions. I am also indebted to Dr. B. Prashad for the identification of the Dalhousie slug and to Mr. M. Sayeeduddin for the delineations of the snail.

Literature.

Alkins, W E. Note on the Habits of *Hygromia fusca* (Montagu). *Journ. Conch. Leeds* XVII, pp. 243-247 (1925).

Barker, F. C. The Ecology of North American Lymnaeidae. *Science, N Y* XLIX, pp. 519-521 (1919).

Beetson, H. Field Notes on *Helicodonta obvoluta* Müller. *Journ. Conch. Leeds* XVI, pp. 31-36 ; 45-50 (1919).

Clementi, A. Sulla pressione osmotica dell'emolinfae dei tessuti di Helix A. durante il letargo. *Atti. Acc. Lincei* (*Rendiconti*) (6), II, pp. 284, 285 (1925).

Fischer, P. H. Influence de la Lumiére et du renouvellement de l'air sur le revéil des Escargots. *C. R. Acad. Sci. Paris* CLXXXI, pp. 1186-1188 (1925).

Flössner, W Zur Biologie, Struktur und Bildungsweise des Winterdeckels von *Helix pomatia. Zool. Anz. Leipzig* XLV, pp. 337-346 10 figs. (1915). (See bibliography for ealier references).

Hadden, N. G. Hibernation of *Succinea elegans* Risso. *Journ. Conch. Leeds* XV, p. 216 (1917).

Hora, S. L. On the Habits of a Succineid Mollusc from the Western Ghats. *Rec. Ind. Mus.* XXVII, pp. 401-403 (1925).

Hora, S. L. On some interesting features of the fauna of the Western Ghats. *Journ. Bombay Nat. Hist. Soc.* XXXI, pp. 447-449 (1926).

Hora, S. L. Hibernation and Aestivation in Gastropod Molluscs. Introduction, pp. 49, 50. On the Habits of a Hibernating Species of Gastropod Mollusc from Pashok (Eastern Himalayas), with remarks on certain other species. *Rec. Ind. Mus.* XXIX, pp. 56-62 (1927).

Johnston, G. *An Introduction to Chonchology*, pp. 252-268. (London : 1850).

Lawson, A. K. Aestivation of *H. hortensis. Journ. Conch. Leeds* XVIII, p. 10 (1926).

Longstaff, J. Observations on the habits of *Cochlitoma zebra* var. *fulgurata* (Pfeiffer), and *Cochlitoma zebra* var. *obesa* (Pfeiffer), in confinement. *Proc. Zool. Soc. London*, pp. 379-387, 3 pls. (1921).

Oldham, C. *Testacella scutulum* in Hertfordshire. *Trans. Hertfordshire Nat. Hist. Soc.* XV, pp. 193, 194 (1913).

Pearl, R. A curious habit of the slug *Agriolimax*. *Rep. Mich. Acad. Sci.* III, pp. 75, 76 (1902).

Pearse, A. S. *Animal Ecology*, pp. 114-120 (1926) (May be consulted for references dealing with the subject in general).

Prashad, B. Respiration of Gastropod Molluscs. *Proc. Twelfth Indian Sci. Congr.*, pp. 126-143 (1925).

Quick, H. E. Notes on the Anatomy and Reproduction of *Paludestrina stagnalis*. *Journ. Conch. Leeds* XVI, pp. 96, 97 (1920).

Rao, H. S. On Certain Succineid Molluscs from the Western Ghats, Bombay Presidency. *Rec. Ind. Mus.* XXVII, pp. 385-400 (1925).

Rao, H. S. Note on two species of Aestivating Gastropod Molluscs from the Kangra Valley. *Ibid.* pp. 50-56 (1927).

Rasmussen, A. T. Theories of Hibernation. *Amer. Naturalist*, L, pp. 609-625 (1916).

Robson, G. C. Note on *Glyptorhagada silveri* (Angas.) *Proc. Malac. Soc. London* X, p. 265 (1913).

Sewell, R. B. S. Observations on growth in certain Molluscs and on changes correlated with growth in the radula of *Pyrazus palustris* (with a note on the radula by the late N. Annandale). *Rec. Ind. Mus.* XXVI, pp. 535, 540 (1924).

Shelford, V. E. Modifications of the behaviour of land animals by contact with air of high evaporating power. *Journ. Animal Behav. Boston* IV, pp. 31-49 (1914).

Smith, E. A. Note on the Epiphragm of *Achatina immaculata*, Lam. *Proc. Malac. Soc. London* III, pp. 309, 310 (1899).

Smith, E. A. Notes on the Epiphragms of *Thaumastus sangoae* and *T. bitaeniatus*. *Ibid.* VI, pp. 3, 4 (1904).

Spence, G. C. Note on *Helix pomatia*. *Journ. Conch. Leeds* XIII, p. 178 (1911).

Stelfox, A. W. A cross between typical *Helix aspersa* and var. *exalbida* : its results and lessons. *Journ. Conch. Leeds* XIV, pp. 293-295 (1915).

Stephens, T. C. Concerted behaviour of Terrestrial Mollusks. *Science, N. Y* LXVIII, p. 271 (1918).

Tattersall, W. M. Notes on the breeding habits and life-history of the Periwinkle. *Fisheries Ireland Sci. Invest.* I, pp. 6, 7 (1920).

Taylor, J. W. *Monograph of the Land and Freshwater Mollusca of the British Isles*. (Leeds : 1894-1914).

Swanton, E. W. A Catalogue of the Land and Freshwater Mollusca of Sussex. *Zoologist*, (4) XIX, pp. 312-314 (1915).

Woodward, B. B. *The Life of the Mollusca*. (London : 1913).

Zoological Department,
University of Edinburgh,
March, 1928.