

THE LIFE OF ACHATINIDAE IN LONDON

Presidential Address

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INTRODUCTION

My last address to this Society dealt with aspects of functional morphology in the buccal mass of the trochid (Nisbet, 1973). Attempts to analyse the neural control of buccal mass activity were unsuccessful owing to the small size of the animal. It also became clear that, at the time of the earlier work on *Monodonta* (Nisbet, 1953), little was known about the functional characteristics.

For these reasons I decided, in 1951, to examine the nervous system of a large snail, and was fortunate in obtaining help from Dr H. G. Caswell, who was working as an agricultural entomologist at the, then, University College of Ibadan, Nigeria.

MATERIAL AND METHODS

(a) *Material*

Each year, from 1952 to 1956, twenty-four to thirty-six living snails were sent to me from Nigeria. The life of Achatinidae in London therefore started in July 1952 but, although these imported snails laid many eggs, mortality was very high and it was not until the summer of 1955 that I managed to rear fifteen babies through to maturity and reproduction the following year.

In 1966 Dr Sandison (of Westfield College, London) sent me six snails from Ibadan and 1969, eighteen adult Nigerian snails were purchased in this country. Of the latter, one died within 3 days, a second died in January 1974, several have been used for dissection and eight are still living and breathing (4½ years in the College).

Nearly all the specimens from Nigeria were *Archachatina (Calachatina) marginata* (Swainson) subspecies *ovum* (or *A. marginata ovum* (Pfeiffer); see Bequaert, 1950). The exceptions were a few specimens of *A. marginata suturalis* Philippi and one specimen of *Achatina (Achatina) achatina* Linne. The last (*Achatina*) was received in July 1955, and lived until 23 March 1960, but laid no eggs.

In 1958, eighteen snails were sent to me from Limbe, Malawi. These consisted of equal numbers of *Achatina fulica hamillei* Petit and *A. panthera lamarckiana* Pfeiffer.

A. fulica survived and bred for 5 years, but is now extinct in the College. *A. panthera* is still surviving and breeding.

Nine specimens of *Burtoa nilotica obliqua* (von Martens) were brought back from Jinja, Uganda, by a member of the College staff. These animals bred for 3 years before dying out.

Also in 1960, a French student, Pierre Andre, returned from Mali bringing with him one large specimen of *A. (Achatina) achatina* L. (from Mamou) and a smaller specimen of *A. achatina monochromatica* Pilsbry (from Konakry). *A. (Achatina) achatina* like its predecessor, lived for 4 years but laid no eggs. *A. a. monochromatica* on the other hand, started to lay eggs after 2-3 months that gave rise to a colony of about fifty snails (cf. Mohr, 1949). Although this colony has almost become extinct, two specimens are living today.

We have at present about 200 adult and young *Archachatina*, a somewhat smaller number of *Achatina panthera* and two surviving *A. a. monochromatica*. Keeping these animals healthy is a necessary condition for our research. The observations on their growth and behaviour are incidental to the need for living material. Our records, therefore, lack the completeness and continuity that is desirable.

(b) *Methods of culture*

These have changed over the years, particularly in respect of the culture of young animals. The changes result in part from the fact that during the last 10 years Dr Plummer has taken care of the young animals giving them special attention and doing the considerable amount of work involved. Current practice is as follows.

(i) *Vivaria for adults*. These consist of either rectangular, zinc-lined wooden or insulation board structures 4 x 2 x 2 ft, with sloping glass doors (Fig. 1) or cubical 2 x 2 x 2 ft structures of the same materials. Each contains a 200W heater element enclosed in perforated zinc. The heater is connected via a thermostat to a mains stepdown transformer, through which supply voltages can be varied with seasonal temperature changes. A layer of steam sterilized soil 9 in. deep covers the bottom of each tank and pieces of natural chalk are placed on the surface.

The aim is to maintain a temperature of *c.* 26°C and a relative humidity of *c.* 80% in each tank (Caswell, 1956). The humidity was originally assisted by the inclusion of large bowls of water but, when many animals are present, it is better to avoid excessive wetness by reliance on the food and the animals themselves. On temperature, we have to accept the inevitable swing of 2-3°C above and below the mean. We therefore set the thermostats at 25°C and check that the maximum does not much exceed 28°C nor the minimum fall below 23°C. A swing in either direction beyond these points results in a rising rate of snail aestivation and if the temperature change is prolonged snail deaths follow.

(ii) *Vivaria for growing snails*. These were formerly small (10 x 8 in.) fish tanks, standing on shelves in the main vivaria, where they occupied valuable space and tended to become overheated. Dr Plummer has substituted plant propagators, containing an inch or two of soil. These are kept in groups (a) in a large (*c.* 5 x 2½ x 1½ ft) wooden container with removable perspex fronts. The container has two heaters and a thermostat and may hold up to eighteen

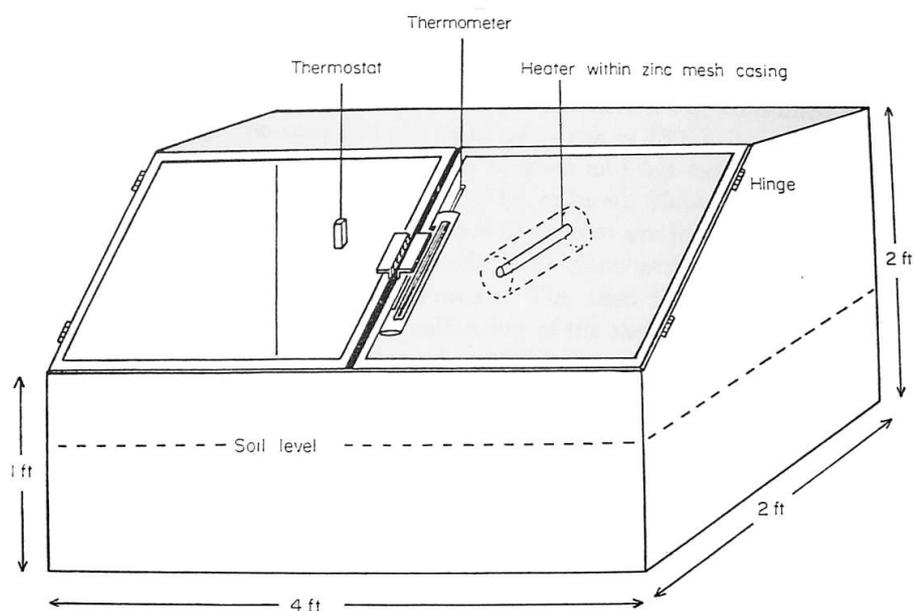


Fig 1. Diagram of one of the larger vivaria providing accommodation for twenty to forty snails according to their size. Humidity is maintained partly by means of a water bowl (if needed), partly by occasional spraying and also by the food and the snails themselves.

large propagators, (b) two smaller, similar containers each containing about five large propagators. The sizes of the propagator used are small ones ($8\frac{1}{2} \times 6$ in.) for recently hatched snails and large ones ($13 \times 8\frac{1}{2}$ in.) for the larger, growing babies.

(iii) Number of snails maintained. This has varied from an impossible peak that approached 500 adults and a similar number of young snails in the late 1950s, to a few tens of snails when heavy inroads on numbers have occurred due to coincidence of research use and unwanted deaths through neglect. If these animals are to be maintained it is necessary for those using them to pay constant attention to their conditions and not to rely on technical assistance.

We now stabilize our populations at about 200 adult *Archachatina* plus a similar number of growing animals and corresponding numbers of *A. panthera* which are small and take up less room. Both these genera have been useful for our researches on the nervous system (*Archachatina*) and on muscle - particularly cardiac fine structure and pharmacology (*Archachatina* and *A. panthera*).

(iv) Feeding and cleaning. When I first received *Archachatina* I talked to W. J. Rees, who had kept some *A. fulica* for a time (Rees, 1951). He recommended cabbage as a staple diet. However, *Archachatina* refused to eat it and seemed prepared to die rather than try! Lettuce was substituted for cabbage and this was readily eaten, together with apples, potatoes and a little carrot.

An estimate of average consumption per snail (*Archachatina*) in a population of fifty snails

ranging from 70-170 mm shell length was made in October 1956. Fresh food weighed 8.6 kg (lettuce, 1.4 kg; apple, 2.7 kg; potato 2.7 kg; carrot 1.8 kg). Waste food (potato and carrot) weighed 1.2 kg; consumed food weighed 7.4 kg. Average consumption per snail per week = 150g.

The animals were formerly cleaned and fed twice a week but the heavy cost in labour, time and food had to be reduced. Nowadays, the snails are cleaned and fed once a week and the food quantities are just adequate.

Cleaning and feeding needs to be done with care in the handling of the snails, especially the growing animals. The shell lip is easily damaged and when this happens, distortion and callousing of the shell frequently leads to loss of the animal.

Cleaning should remove only the excessively polluted soil and food debris. Hygienically clean tanks lead to cessation of feeding and reproduction, and ultimately to death of the snails (see p. 177). A tendency towards slum conditions has to be aimed at, especially in the case of *A. panthera*.

ASPECTS OF BEHAVIOUR

A number of behavioural aspects were briefly described in an earlier paper (Nisbet, 1961).

(a) *Aestivation*

Under culture conditions, that aim at a fairly uniform environment, the normal conditions aestivation might be presumed to be absent. However, all these Achatinidae burrow extensively, particularly when they have recently arrived in the country. *Archachatina* tend to adapt more readily (3-4 months) than other genera, and most individuals appear to be active each night. Nevertheless, a few may be found below soil level at any time, although not usually in true aestivation. It is, therefore, necessary to define aestivation as a condition of dormancy in which the snail has formed an epiphragm and remains entirely quiescent. This happens occasionally with *Archachatina*, more extensively with *Achatina achatina*, *A. fulica*, *A. panthera* but less with *Burtoa*. The snails also burrow in order to oviposit, when they construct a smooth-walled oval cavity within which the eggs are laid, the snail usually returning to the surface the following evening.

The third condition, of dormancy without forming an epiphragm, may arise casually in individuals of a group of active snails. It has happened with each of the two *Achatina* (*Achatina*) *achatina*, possibly because they did not like the company they were forced to keep (*Archachatina*). It also happens extensively when conditions in the vivarium become too hot (above 28°C), too cold (below 23°C) or too dry, but not when conditions become excessively wet. This kind of dormancy may lead into normal aestivation but it may be significant in other ways. One *A. (Achatina) achatina* received in July 1955, spent only 6 weeks of the following 20 months above ground. Yet, during this period (to 18 March 1957) it had increased its shell length by 8.2 mm (120.5-128.7mm) and its breadth by 5.0 mm (65.0-70.0 mm). The addition of new shell to the body whorl at its greatest width was 28.5 mm. Most of this additional shell growth occurred while the snail was below ground and

might be related to the need for a balance of development between such parameters as shell size, shell thickness and body size.

Lastly, in adverse conditions, some snails may aestivate without burrowing. This enables observation of the process of epiphragm formation. The animal retracts within its shell, leaving about 2-5 mm of the internal surface of the lip exposed. The collar is extended to enclose the retracted foot and secretes a yellowish mucous layer. The latter slowly whitens, finally becoming a thin, tough, shiny and slightly flexible structure with a fine slit that follows the line of the pneumostome.

Aestivation withdrawal differs from defensive withdrawal in that, although in both cases the left posterior half of the folded foot blocks the shell aperture, in the former case the mantle collar is extended as a thin layer over the foot, leaving a very small aperture through which the foot can be seen and over which the epiphragm is thinner than elsewhere (Fig. 2).

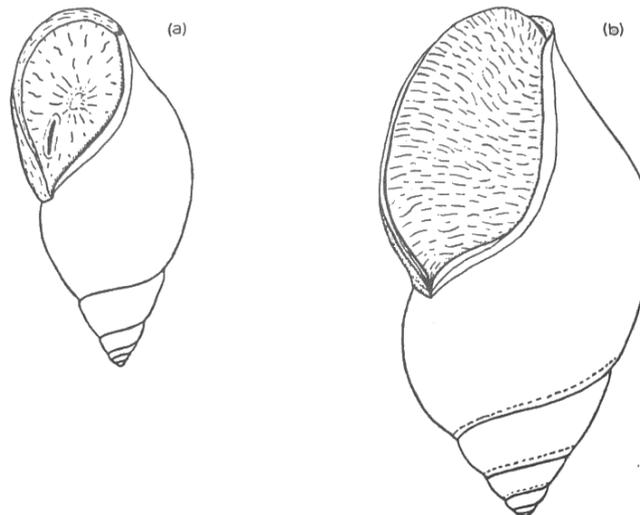


Fig. 2. (a) *A. panthera lamarckiana* in aestivation. Note the slit-like aperture in the epiphragm, over the closed pneumostome: and the central thin depression where the mantle collar leaves a small area of foot exposed. (b) *Archachatina marginata*, showing defensive withdrawal. In this case the foot covers and protects the collar.

(b) *Sleeping and defecation*

Unlike *H. pomatia* in captivity (Howes and Wells, 1934) most *Archachatina* become active every night. With the morning light they retire to the darker corners of the vivarium, seeking to attach themselves, head upwards, to a vertical wall. Each animal adheres to the surface by the posterior half of its foot, the anterior portion - with the head - being withdrawn in the shell.

Frequently, during the period of daytime quiescence, snails defecate. This may also happen during the night time activity when the snail, if moving, stops and withdraws its head. From this point the process is the same by day or night. The pneumostome is widely opened, the anterior part of the foot is raised and folded longitudinally except for its anterior limit, then turned back on the right side of the body until it reached the pneumostome (Fig. 3a).

The faeces pass out of the anus and move slowly across the outer anterior border of the pneumostome, following the line of the groove into which the valve-like fold fits on closure of the aperture (Fig 3b). The faecal rod or string passes slowly into the funnel formed by the anterior limit of the foot and disappears between the closed ventral halves of the latter. The rod moves down a tube formed in the mid-line of the foot by the close apposition of the more lateral regions. Reaching the substratum at about the middle of the length of the foot, the faeces pile up and remain at this point when the snail moves away.

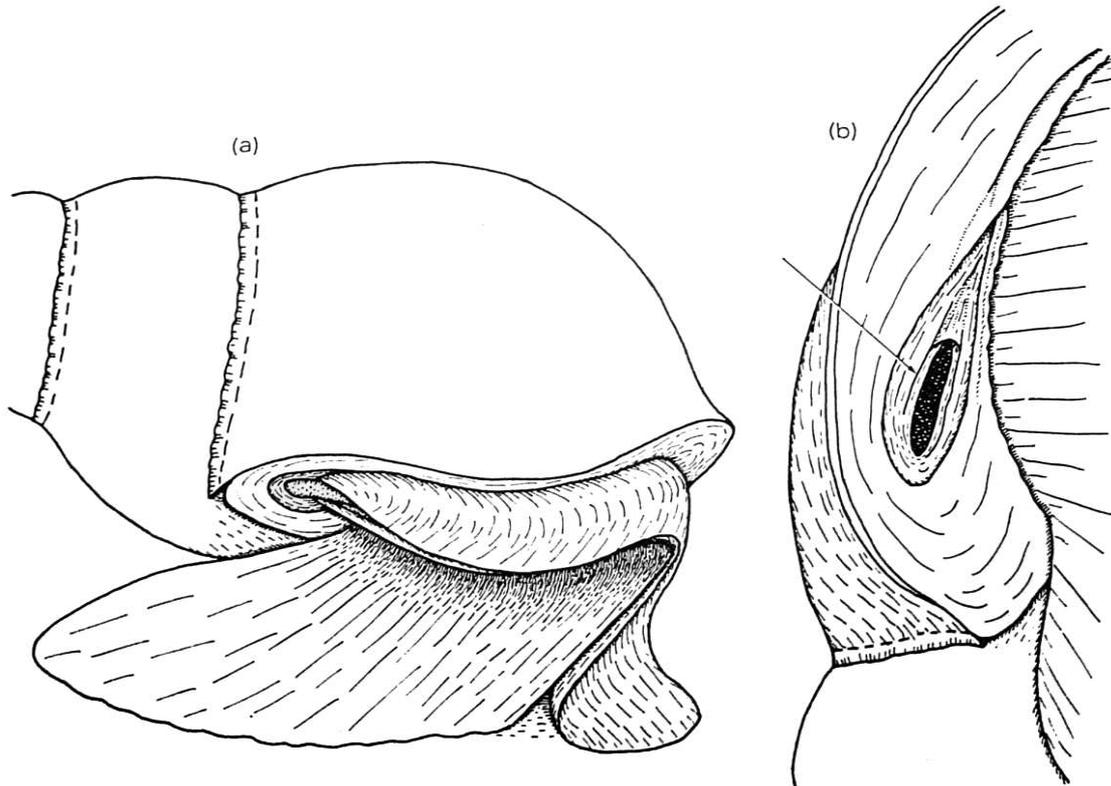


Fig 3. *Archachatina marginata* (a) defecating: the faecal rod (shown stippled) passes along the lateral border of the pneumostome, into a funnel formed by the anterior border of the foot and thence to the surface to which the posterior half of the foot is attached. When the animal moves away the faecal mass is left adhering to the surface. (b) View of the pneumostome showing the lateral groove (arrowed) along which the faeces pass

Movement of the faeces appears to be assisted in three ways: (i) by lubrication from the massive rectal mucous glands; (ii) by powerful ciliary action outwards from the pneumostome along the valve groove; (iii) by gentle, rhythmic pedal waves passing from the anterior limit of the foot backwards in the same sense as the movement of the rod.

The faecal rod may be of three kinds. (i) A thick, firm, rather dry structure, about 3.5 mm in diameter, consisting of compacted soil particles with little evidence of food material.

(ii) A similar, rather dry structure, containing compacted soil particles, but consisting of comminuted food and clearly coloured by the latter. Carrot, lettuce and potato are easily identified and appear to be quite undigested. (iii) A slimy, glutinous, dark greenish-brown string, about half the diameter of the former rods, apparently largely or wholly material from the digestive glands.

(c) *Waking and cleaning*

As night falls the snails show signs of movement. There is a slow extension of the head and partial eversion of tentacles. The anterior foot spreads a little on to the substratum. Although little further movement may be seen for the next 30-60 min the animal is, nevertheless, becoming active. Dorsal body waves (see p. 178) pass over the upper surface of the foot, the collar, and the shell lip, before extending the collar to enfold the lip. There is frequent slow fidgeting - withdrawal of the collar, and further cleaning of the shell lip - before the latter is finally settles in the collar groove. The behaviour is strongly reminiscent of a cat cleaning itself although the movements are much slower.

(d) *Movement and feeding*

When the animal has finished cleaning itself, it extends its head and foot and ambulation commences, the dorsal body waves now being more powerful. Shortly after this a snail may cease ambulation, its head being slowly lowered to the soil and then raised again. The process is repeated a number of times and the soil below the head is ingested, leaving a shallow depression that is wet from the snail's activities - apparently due to secretion that accompanies the dorsal body waves. Ambulation may then recommence, the snail may delicately examine a piece of apple with its anterior tentacles, its down-turned optic tentacles and with its lips. It may now commence to feed, its activity being accompanied by powerful and rapid dorsal body waves that bring a watery secretion from the external surface of the head and cervical region into the feeding area. There is some evidence for suggesting that each snail may have a cycle of feeding activities, viz. the ingestion and comminution of food that is then defecated without, or with very little digestion; the ingestion of soil - and some food - followed by digestion and defecation; and, finally a period (?one night) of little intake of food followed by a day when the faecal string consists of material from the digestive gland. There may be a 3-day cycle, that raises problems in the feeding of these animals. It also raises the question of the animal's possible need for regular ingestion of soil flora and fauna together with rotting food material. In one useful but hazardous experiment a vivarium was provided with double-sterilized soil, all surface soil and faeces were removed 3 times weekly and the loss replaced with more sterilized soil. The first sign of trouble was a cessation of oviposition in a formerly actively reproducing population of mixed ages. In 3 weeks the snails then ceased to feed and became lethargic and, in the following month, 13 out of 24 snails died. At this point the experiment was terminated!

Although availability of calcium is known to be important for health and for egg production (Crowell, 1973) this mineral was present in the form of pieces of natural chalk, in addition to what might have been present in the soil.

The dorsal body waves (Nisbet, 1961) are not known to have been described in any other pulmonates. They are prominent in all achatinids that have been examined, when they snails are active. They consist of superficial waves of contraction that arise at some level within the mantle cavity, spread down the 'pillar' of the body and outwards on to the dorsal surface of the head and foot, one part of each wave moving forward to the head and disappearing at the level of the oral surface, the other part flowing backwards to disappear at the posterior limit of the foot. Coincident with the wave there is the expression of fluid from the surface of the body and foot, apparently glandular secretion expelled by muscular contraction. Much of the expressed fluid sinks back into the corrugations of the surface as the wave passes.

The dorsal body waves are not directly related to the pedal locomotory waves. The former are present as weak waves of low frequency (6-8 per min) in a stationary or slowly crawling animal: they become more vigorous, at higher frequency (15 per min) in a stationary feeding animal, with a more copious secretion that is carried into the feeding area. Particularly powerful waves, with frequencies of 60 per min, can be seen in animals feeding on succulent material (apple) or when examining another snail. The velocity of these waves varies between 9 and 17 mm sec⁻¹ and their wavelength varies from 25 to 30 mm. They appear to be generated independently on the two sides of the animal, often at slightly different frequencies. Thus, they move into and out of phase during a period of observation. Their function, unless it be external salivation, is unknown but, in the context of their behaviour, might best be described as indicating the level of the 'central excitatory state'.

The pedal locomotory waves are similar to those described in other pulmonate snails (e.g. Lissmann, 1945, 1946; Jones, 1973). They have been described in *Archachatina* (Nisbet, 1961) but there are comparative aspects that are of interest here.

There are usually nine pedal waves and their frequency is about 20 per min in a wide range of snail sizes. Their wavelength is proportional to the length of the foot: in a snail of 125-130 mm shell length, with a foot 170-180 mm in length, the wave length is 20 mm (contraction waves being 4-5 mm wide and fixation bands 15 mm wide). The velocities of the waves vary between 6.0 and 10.0 mm sec⁻¹; the corresponding forward velocities of the animals range from 0.5 to 1.0 mm sec⁻¹. Thus, the pedal waves have a velocity of about ten times that of the animal. The waves span the full width of the foot (c. 60 mm); in the slowly moving animal (0.5 mm sec⁻¹), however, only the middle 30 mm may be in contact with the substratum but, in the faster moving snail (1.0 mm sec⁻¹) the whole of the foot may be used.

It is enlightening to compare the velocities of different snails, for example, an adult (130 mm) and baby (20 mm) *Archachatina*, and an *Helix aspersa*. Although the small snails appear to travel faster than the large animal, this is illusory. When their rates are measured

they, also, lie in the range 0.5-1.0 mm sec⁻¹. A long series of observations on some marine snails by one of my students gave the following figures for animals climbing a sea-water filled glass jar: *Nuccella lapillus*, 0.5 mm sec⁻¹; *Littorina saxatilis*, 0.3-1.0 mm sec⁻¹; *L. littoralis*, 0.3-1.0 mm sec⁻¹; *Gibbula cineraria*, 0.3-1.0 mm sec⁻¹ (most at 0.5 mm sec⁻¹ but one high velocity of 3.0 mm sec⁻¹); and *Monodonta lineata*, 1.0-2.7 mm sec⁻¹ (most observations giving 2.0 mm sec⁻¹). The two questions that might be asked, on these figures, are (a) is the relative uniformity of velocities in different snails a simple reflection of the characteristics (e.g. maximum contraction velocity) of this type of smooth muscle? (b) Are the pedal muscles of *Monodonta* (and perhaps *Gibbula*) different from those of other snails?

(e) *Responses to peripheral stimulation*

(i) *Retraction*. The responses of these snails to experimental stimulation (touch, a tap or pressure of a stylus) are of interest in three respects, viz. cephalic and columellar muscle retraction, cardiac inhibition and glandular secretion from the collar.

In an extended and ambulating animals, a light touch to a tentacle or the head causes momentary inversion of these structures. A powerful tap to the head is followed by retraction of the whole head and cervicum. This is the fastest response that we have seen in the animal, being completed in about 250 msec. The response of the heart can also be seen if a portion of the body whorl is first broken away to expose the pericardium.

The 'normal' cardiac cycle in the crawling animal shows a frequency difference between auricular and ventricular systoles. The auricle contracts about four times per min, the ventricle about fifteen times per minute. Thus, although it is known that in the isolated heart the auricle can drive the ventricle (Nisbet and Plummer, 1968), the the normal animal it appears to behave as a conduit for much of the time.

During normal ambulation the snail allows its shell to lag behind the moving body, periodically shortening the columellar muscle to bring the shell back into place, each contraction being accompanied by a cessation of cardiac systole. The sharp, tap on its head produces a powerful contraction of the columellar muscle and a sustained inhibition of the heart. If the stimulus is a damaging one, there is also a massive orange-green secretion from the glands of the collar. The secretion appears to be not so much repugnatorial as entangling and distracting to small predators (see Durrell, 1958).

We believe that we know the pattern of this defensive reflex and the giant neurons that give rise to it.

(ii) Attempts to prevent retraction. It is possible to experiment with these large snail in ways that would be difficult or impossible in our smaller species. For instance, a snail of 165-mm shell length may extend its head 126 mm (5 in.) in front of its shell. The breadth of its head is about 23mm (1 in.), the total length of the foot 250-270 mm (10-11 in.) and its breadth 90 mm (3½-4 in.).

On a number of occasions such a snail was firmly gripped between finger and thumb just in

front of the shell lip and an attempt made to fix the thumb and finger and not to relax or tighten during the snail's movements. The measured separation of finger and thumb averaged 8 mm (3/10 in.) (Fig. 4).

On each trial the same sequence of events followed. (1) An immediate, powerful retraction of the head and foot. (2) Retraction of the head stops at the obstruction although sustained contraction of the columellar muscle can be felt (painfully!) by the experimenter and continues throughout the following sequence. (3) A long pause ($\frac{1}{2}$ -1 min.) is followed by partial protraction of the head and by trial (partial) protractions of the tentacles, usually one at a time. Incomplete eversion seems to be due to the experimenter's pressure on the retractor muscles. With lighter pressure the tentacles may be fully everted and many be turned backwards towards the obstruction. The trial period may last for another $\frac{1}{2}$ -1 min. (4) Another long pause follows (*c.* 1 min). (5) Finally a slow, sustained retraction develops and continues until the head is pulled back behind the obstruction (what happens to the buccal mass?) (6) The head is immediately protracted again, the snail's lips and tentacles then exploring the obstruction.

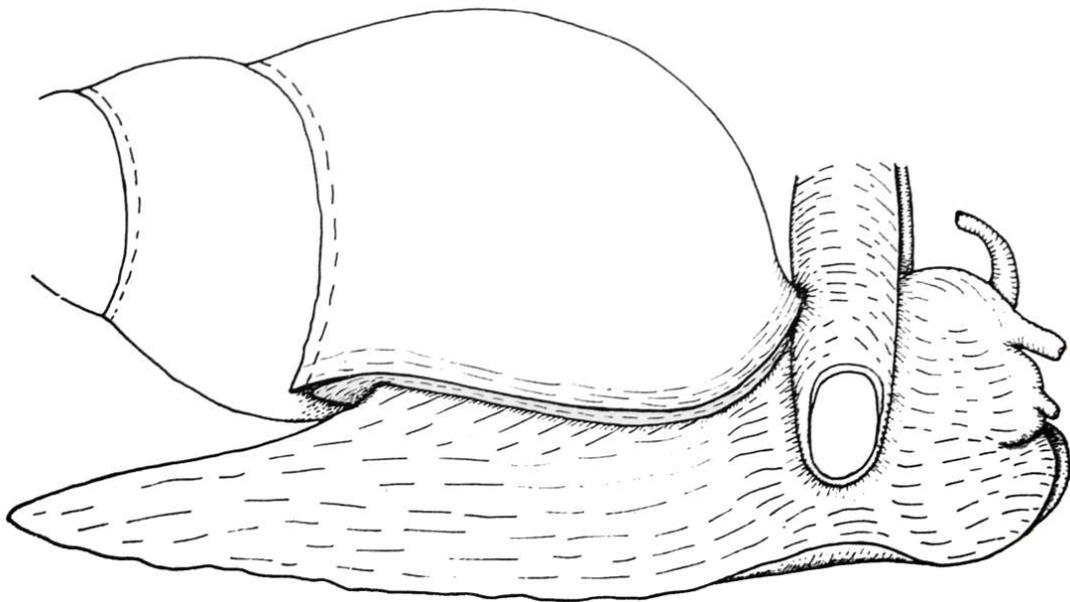


Fig. 4. *Archachatina marginata*. Response of the snail to presence of the experimenter's finger and thumb that are preventing further retraction of the head. Note that at this stage the columellar muscle is in sustained contraction, the head muscles are partially relaxed and one everted posterior tentacle is recurved over the head, apparently in an attempt to examine the obstruction. For further explanation see p. 179.

The sequence of events gives the impression of a very slow trial of the alternatives of forward and backward escape from the obstruction and the final selection of sustained retraction. The immediate protraction of the head (6, above) is quite different from the animal's reaction to other forms of peripheral stimulation, suggesting curiosity rather than the more usual purely defensive recoil.

ASPECTS OF OVIPOSITION AND DEVELOPMENT

In the present account I shall confine my remarks to the general features of those achatinids that have been kept in the College. The specific and detailed analysis of development in *Archachatina* is dealt with elsewhere (Plummer, 1975).

(a) *The numbers and sizes of eggs in the Achatinidae*

It is known that the genus *Achatina* lays small eggs. Bequaert (1950, p. 19) remarks of *A. (Achatina) achatina* that 'the eggs are surprisingly small for the size of the snail', giving the figures 8.0-8.7 mm for the length and 6.5-7.0 mm for the width in the nominate race. Our two specimens of this subspecies laid no eggs, but a single specimen of *A. a. monochromatica* Pilsbry did, as have its offspring to the present time. Although the latter subspecies is considerably smaller than the former, the average lengths and widths of its eggs are 60% greater. The clutch sizes and the sizes of eggs in this and other species kept, including *Archachatina*, are shown in Table 1.

TABLE 1

	Size of clutch	Size of eggs (mm)			
		Average Length	Range	Average Width	Range
<i>Achatina achatina monochromatica</i>	20-40	10.2	8.5-11.3	8.0	6.6-8.6
<i>Achatina fulica</i>	50-200	6.3	5.3-7.8	5.6	3.2-5.4
<i>Achatina panthera</i>	20-120	5.9	4.1-6.8	4.5	3.2-5.1
<i>Archachatina marginata</i>	3-16	20.1	10.6-25.1	15.7	9.3-19.2
<i>Burtoa nilotica</i>	40-50	4.7	4.5-5.3	3.9	3.6-4.4

The single individual of *A. a. monochromatica* received in 1960 (shell length 82.6 mm and width 61.4 mm) - and its offspring - have laid eggs with the following dimensions. In fifty-three eggs measured from four clutches the average length was 10.2 mm (range 8.5-11.3 mm) and the average width 8.0 mm (range 6.6-8.6 mm). The number of eggs in a clutch varies between twenty and forty.

Achatina fulica hamillei Petit (shell size 104 mm and by 61 mm) was more prolific. Two-thirds of a clutch (forty-seven eggs) were measured, giving an average length of 6.3 mm (range 5.3-7.8 mm) and the average width 5.6 mm (range 3.2-5.4 mm). The number of eggs laid as a clutch varied from about fifty to two hundred. Smaller clutches did not start to hatch for a week or more, but in the large clutches, young snails were hatching within 24 hr and continued to hatch for a further week. The daily increase in eggs in the oviduct could be seen through tpneumostomeome, increments continuing for about 8 days before oviposition occurred. The maximum size to which the offspring grew was 84 mm shell length by 44 mm shell width.

A. panthera lamarckiana Pfeiffer (shell size 112 mm by 58 mm) laid eggs in a size range similar to those of *A. fulica*. As with the latter, the offspring are smaller than their parents, growing to maximum dimensions of 80 mm shell length by 43 mm in width. A clutch of forty-eight eggs from one of these animals had an average length of 5.9 mm (range 4.1-6.8 mm) and an average width of 4.5 mm (range 3.2-5.1 mm).

The clutch numbers are, however, smaller (twenty to one hundred and twenty egg and the incubation time 4 to 10 days).

Burtoa nilotica obliqua (von Martens) also reproduced well for several years, laying clutches of forty to fifty eggs. Seven eggs from a clutch of an individual with the shell dimensions of 75 mm by 53 mm gave an average length of 4.7 mm (range 4.5-5.3 mm) and width of 3.9 mm (range 3.6-4.4 mm).

The information for *Archachatina marginata ovum* is more complete than for other species because it has been kept continuously for 22 years and has provided our main research animals. Unlike *Achatina fulica* and *A. panthera*, the offspring appear to maintain their growth and to reach the average sizes characteristic of African adult snails (shell length 130 mm and width of 80 mm, see Plummer, 1975, and also Bequaert, 1950).

The average clutch size, taken from 123 clutches (see Plummer, 1975) is 8.6 with a range of from three to sixteen eggs. The average length of the eggs is 20.1 mm (range 10.6-25.1 mm) and average width is 15.7 mm (range 9.3-19.3 mm).

(b) *The colours of snails and their shells*

In Achatinidae, as in other gastropods, the colour and pattern of the shell provides information of taxonomic value. The body colour of the snail, occasionally referred to, has a lesser significance. Yet, in both our African and home-bred snails colour change occurs in the shell and the body.

(i) Colour changes in the shell. With cultured animals there is a trend to a darker shell, particularly noticeable in *A. a. monochromatica* (which is 'fulvous yellow' during growth and becomes chestnut-brown with age: this change was also noted for some African shells by Bequaert, 1950). Similarly, the shell of *A. panthera* also darkens to a chestnut-brown. With African *Achatina achatina* and *Archachatina* there is frequently a more abrupt change. The normal colour pattern ceases on their arrival in this country, further growth of the shell showing uniform pale yellow coloration. This does not appear to be due to temperature changes during their transport, since home-bred animals have suffered such changes without effect. Nor does it appear to be caused by diet as such: home-grown animals show normal shell colours. What may be significant is the change of diet and possibly soil flora suffered by imported animals.

(ii) *Colour changes in the body.* There is a general trend towards a paler body colour in our cultured snails, except in *A. panthera* which has a naturally pale body. These changes appear to be environmental in origin since they are not noticeable in imported animals.

In *Archachatina*, however, there has arisen a sudden change to a uniformly pale body coloration that appears to be genetic in origin. This apparent mutation is reported in Dr Plummer's paper. Even in these animals, however, the pale cream body becomes tinged with brown as they age.

The culture of these Achatinidae has involved us in much labour for many years. Their large

size and high environmental temperature, with correspondingly high metabolic levels mean that feeding and cleaning operations are both expensive and time-consuming. The rewards are an ability to study in some detail the varied behavioural activities of these animals and the opportunity to use experimental techniques that would be difficult or impossible with smaller gastropods.

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