

ON BRAZILIAN SUPRALITTORAL AND BRACKISH
WATER SNAILS

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(With figures 1-9)

On their way from an ancestral marine, probably intertidal, habitat to land and therewith to rich sources of oxygen and vegetable food the Ellobiidae (Pulmonata, Basommatophora) have been favoured by their mode of reproduction. Most of them hatch as young snails, and their velum and operculum are embryonal. Semper (1880; quoted from Pelseneer 1894, p. 114-15) was the first to observe this. Mörch's earlier statement (1867, p. 2) of free-swimming larvae evidently refers to Melampodinae, a sub-family of the Ellobiidae. The vast geographic distribution of *Melampus* over the Indopacific islands led Fischer & Crosse (1880, p. 21) to suppose free larvae for the species of this genus. The first egg masses of *Melampus bidentatus* Say were recorded by Hausman (1932), the veligers of several Melampodinae discovered by Morrison (1953; 1958b). One of these is *M. coffeus* (L.), as Dr. Joseph P. E. Morrison kindly informed by letter (November 7, 1962).

Our observations on ellobiids with free larvae refer to *M. coffeus* (Linné, 1758) and *Detracia parana* Morrison, 1951, both common on the beach of Cananéia (25°S), where we could work thanks to Dr. Ingvar Emilsson, Director of the Oceanographic Institute, São Paulo, and Dr. Victor Sadowsky, Head of the Research Station. There, in front of the garden, we found egg masses on dead leaves, stones, and pieces of wood in winter (June 1962) and summer (January 1963). Seven to 15 mm long snails of *M. coffeus* were spawning; the exceptional maximum length of our *Detracia parana* was 7 mm, but already 4.5 mm long snails are mature. In nature the spawns occur principally at the level

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of neap tide high water-line. In our dishes set up with material from the shore they were found also on the nearly dry uppermost leaves, whose level corresponds to about spring tide high water-line. Generally two spawns were laid close together, and two snails of *M. coffeus* or *D. parana* sat near them, as if they had mated recently.

According to the different size of mature snails the size of the egg masses varies widely. The roundish, jelly-like clusters of *M. coffeus* are 1 mm high, 3-4 mm across, and contain 500-2,000 eggs, each around 80-90 μ in diameter, and enclosed in a capsule about 130 μ long and 92 μ in diameter. In conformity with the smaller size of the snails the egg masses of *D. parana* often contain only about 5-600 eggs, but there were also some larger ones. The capsules are about 110 μ long, 75 μ broad, the eggs 74 μ long and 67 μ in diameter.

At about 30°C (January 1963) the veligers of *M. coffeus* hatch after 10-11 days if the spawn is attained by water, if not, they remain in the jelly for some more days. They are colourless, with an average length of 95 μ and breadth of 87 μ , have statocysts but neither tentacles nor eyes. The surface of the shell is somewhat rough, especially on the sides; 3 days later the shell had grown to 114 μ . The velum is as in the 12 days old embryo of *Ovatella myosotis* (Meyer 1955, fig. 27). As the smallest crawling snails of *M. coffeus* found had 1.1 mm long shells, the planktonic life of the veliger is evidently rather long.

Two species which develop to the crawling stage within the egg capsule occur together with the mentioned Melampodinae. These are *Blauneria heteroclita* (Montagu, 1808) and *Ellobium pellucens* (Menke, 1830), both of the subfamily Ellobiinae as defined by Morton (1955a, p. 158). With Morrison (1958a, p. 123) we use the name *Ellobium*, not *Auriculastra*, for *pellucens*, and justify this in a forthcoming paper.

Blauneria has a sinistral, up to 7 mm long shell. Spawns of 2, 3, 4, and up to 10 eggs fastened to dead leaves were found in June 1963. They resemble those of *Ovatella myosotis* (Meyer 1955, fig. 24; Morton 1955b, fig. 21). The largest spawn was 1.6 mm long, 1 mm broad; the capsules, each with one egg, as in the other species, measured 0.5-0.56 mm. The diameter of the eggs begins with 0.1 mm and increased about 10 μ a day (temperature 18-20°C). On the 12th day the embryo was 0.24 mm long. The small number of big egg capsules containing a large supply of albumen contrasts with the great number of small capsules in the Melampodinae.

On the third day the stage of 64 cells was attained, on the 6th day the embryos rotated, and on the 7th day they had a bilobed velum. First the velum increases in size and is reduced later

on. After 3-4 weeks the crawling snails hatch. This is a rapid development. It lasts, it is true, twice as long as that of the Melampodinae which leave the capsules as larvae, but this difference of time corresponds to the 10°C lower temperature. Evidently the supply of albumen speeds metamorphosis efficiently.

The hatching snail has a lenticular shell, 0.31-0.36 mm in greater diameter, and consists of one and a quarter of a whorl (Fig. 1). The shell is dextral and reverses its direction to the left with 0.4-0.5 mm (Fig. 2). The larval operculum persists in snails up to 0.68 mm shell length and is shed with 0.7 mm. The operculum has a process for the attachment of the columellar muscle which does not occur in the larval operculum of the Melampodinae.

The eggs of *Ellobium pellucens* were not found in nature, but in covered dishes, some containing muddy sand on the bottom, all a great quantity of the blackish undermost parts of the grass mat that shelters the soil at the finding place, pieces of banana stalks and of old wood, and some oyster shells. Moisture was provided with brackish water.

The snails were brought into the dishes at the end of June 1963 and began to lay eggs on September, 12. The spawn is an irregularly wound or partially straight, up to 30 cm long string of jelly (Figs. 3-4). It contains about 1,000 eggs in a single row. The glittering jelly stuck to grass, banana stalks, and wood. The string is 0.4-0.5 mm thick, the capsules, whose position is generally oblique, are 0.48-0.5 mm long and 0.33 mm in diameter. The eggs measure 0.27×0.19 mm. The capsules are smaller than in *Blauneria heteroclita*, the eggs bigger, hence the amount of albumen is smaller in *E. pellucens*. This difference becomes even more striking if the size of spawning *Blauneria*, around 4 mm, is compared with that of *Ellobium*, 14 mm. The glitter of the egg string disappears after some days, the string becomes discontinuous after 17 days. Then the single capsules lie over one another, no longer in rows.

The embryos gastrulate 24 hours after egg laying, at an average temperature of 23°C, and on the third day rotate in their capsules. Those of 5 days have a distinct shell, whose great distance from the body is remarkable. On the 7th day the body is 0.2 mm long, the shell 0.27 mm. From this age to the 16th day the daily growth of the shell is about 10 μ . The velum begins inconspicuous and becomes rather large after 18-20 days. From then on it decreases. The embryonic period lasts 4 weeks at the above mentioned temperature.

The size of the emerging snail is about the same as that of *Blauneria heteroclita*, and development takes about the same time. But the temperature during the observation of *Ellobium pellucens*

was higher than that recorded for *Blauneria*. Hence the rate of development of *Ellobium* is slower. We do not know the cause of this difference, the bigger eggs, the smaller amount of albumen, or a slower specific rhythm of cell division. The hatched snail (Fig. 6) stands on its short foot, its about 0.35 mm long shell raised upright. The latter has one and a quarter to one and a half whorl, is sinistral (Fig. 5), and has few distinct narrow growth lines. The swollen top of the tentacle in the adult is preceded by a limited ciliated thickening. Sole and anterior border of the foot are strongly ciliate. A 0.15 mm long, 0.12 mm broad operculum (Fig. 7) with a concentric mark bears an about 25 μ long process for the retractor as in *Blauneria*.

The radula (Fig. 8) is 58 μ long, 46 μ broad, and consists of 17 rows with up to 5.1.5 teeth. These numbers as well as the shape of the teeth differ widely from the adult radula. The form of the rhachidian tooth is similar in several other adult species of the family, but the lateral teeth of the juvenile *Ellobium pellucens* are peculiar.

Animals of 3 mm shell length found in nature in June indicate that the observed spring breeding of *E. pellucens* is not the only time of reproduction which occurs in the course of a year. *Blauneria heteroclita* spawned frequently in our dishes, every time with a maximum of 10 descendants. The reproduction of *Melampus* and *Detracia* is the most intense of our 4 species and, as little as that of *Blauneria*, restricted to a determinate period. Certainly only few larvae of a melampodinian spawn attain the age of metamorphosis and a suitable shore to settle on. *Ellobium pellucens*, whose numerous eggs produce crawling snails, should be expected to colonize our observed beach intensely. It is, however, rare at all seasons and in nearly all micro-niches. A patchy occurrence in their specific environment is known of many Ellobiidae, and *Ellobium pellucens* shows this in an extremely high degree. Also the records of its range, W and SW Florida, Guadeloupe, and British Guiana, are scarce for a rather big species known since 1830 and impossible to be confounded with others.

On the place, that we studied, the rarity of *Ellobium pellucens* might be tentatively explained by a high rate of annihilation of young snails, whose shells up to 10 mm are much thinner than those of young Melampodinae. Possibly such young snails of *E. pellucens* are often eaten by crabs (*Sesarma miersi iheringi* Mary J. Rathbun, 1918), very common at the beach of Cananéia. We have only a single observation in favour of this hypothesis, because crabs and snails are nocturnal and hide when illuminated. An 8 mm shell was found broken as by pincers and still containing rests of the body. Malaysian *Sesarma* are called omnivorous, chiefly herbivorous (Verwey 1930, p. 182), southeastern African

species are recorded to prey on the juveniles of other mangrove animals (Macnae & Kalk 1962, p. 31).

As frequently in the supralittoral fringe of lagoons and estuaries (Morton 1955a, p. 131; Abbott 1958, p. 229), also at Cananéia an *Assimineia* (Prosobranchia, Rissoacea) is associated with the Ellobiidae. We consider as a subspecies of *A. succinea* (Pfeiffer 1840, p. 253), to be described elsewhere. Its egg capsules, up to 0.4 mm in diameter, are fastened singly to dead leaves with a sticky belt. They develop without a planktonic larval phase. At 20-23°C young snails hatch in 4-5 weeks. They measure 0.35-0.36 mm in antero-posterior direction and 0.3 mm from back to foot. This development contrasts with the hatching veligers (Sander, 1950) of *A. grayana* Fleming, whose development, it is true, was not studied under natural conditions (ibid., p. 149; Fretter & Graham 1962, p. 401). The European species is more than twice as long (up to 7 mm) as ours (2.9 mm), but its egg capsules have only half the diameter (0.2 mm) of the Brazilian form. These measurements perhaps suggest free larvae as normal stage in the development of *A. grayana*. On the other hand we obtained prematurely freed swimming veligers of *Ellobium pellucens*. Their capsules had been accidentally washed into the water in our dish, were taken out and damaged by handling.

Fusiform juvenile nematodes of the order Rhabditoidea are frequent between mantle epithelium and shell of our *Assimineia*. Such a location is not recorded by Mengert (1953) and Turner & Pini (1960). The worms are free, neither encysted nor ensheathed, and evidently harmless inquilines.

Our *Assimineia* lives at levels which are under water only at spring high tides, like *A. grayana*, whereas the species of *Littoridina* (Prosobranchia, Hydrobiidae) are water snails and occur, as those of *Hydrobia*, in marine, brackish and fresh water (Fretter & Graham 1962, p. 577-83). When their environmental water recedes, e.g., in the upper course of a "mangrove-priel" (= channel, Emery & Stevenson 1957, p. 678) in the dry season, or at ebb tide on an insolated flat, they burrow into the soft soil and become dormant. We know 3 species of *Littoridina* from the mangrove region of São Paulo, all eurythermic and euryhaline, as other animals of this habitat. They live in water of different salinity and endure rapid changes of temperature and salt. As not many species tolerate the wide environmental fluctuations in estuaries and lagoons, interspecific competition there is moderate, and the population density of the *Littoridina*-species is very high (Haderlie & Clark 1959, p. 465).

The most marine of them, *L. australis* (d'Orbigny, 1835), has the widest range, from 40°35' S to 22°55' S. We recently described the subspecies *L. australis nana* Marcus (1963, p. 33 ff.) from

São Paulo and Rio, and mention only some biological facts here. We have it from coastal sea and brackish water and from a locality where, at least for hours, the water is fresh. It lives on the bottom and among plants. It attaches its single egg capsules ($120 \times 80 \mu$), each with one egg, with their largest side principally to living shells and opercula of its own species, like *Hydrobia ulvae* (Henking 1894, p. 91-92). After about 5 days (25°C) veligers of 120μ shell length hatch, still without tentacles in contrast with the following species.

Within the range of *L. australis* occurs *L. charruana* (d'Orbigny, 1840), recorded from Montevideo to Santos. Its shell is broader than that of *australis*, its osphradium of wavy outlines, not a simple C-shaped band, the communication of the prostate with the mantle cavity is a long duct, not a pore, and a gonopericardial duct, distinct in the female of *australis*, was not found in *charruana*. Whilst *L. australis australis* has up to 7, *australis nana* up to 4 penial warts, *charruana* has up to 16.

We received some preserved snails of *L. charruana* from the outlet of a lagoon at 30°S , where the variations of salinity from 34.5‰ to 4.5‰ , exceptionally even 1.5‰ may occur within 10 hours in correspondence with tides and winds, as the collector, Mr. Jorge Petersen, kindly informed. In June 1963 masses of *Eichhornia* and *Salvinia* drifted along the lagoon Mar Pequeno in front of Cananéia, where some of them stranded. To judge from the nearest beds of these plants they came from the 70 km distant region of Iguape (for maps see Besnard 1950, p. 9 or Gerlach 1958, fig. 1). Among their roots hundreds of living *L. charruana* were found. In the course of at least 5 days they had passed from oligohaline to polyhaline brackish surface water. Already Ihering (1895, p. 123, 128) has recorded *L. charruana* from Iguape found among the rootlike fibres of *Salvinia*. Our snails had 1-2 eggs with capsules ready to be spawned in the nidamental duct. Young crawling stages with 0.4 mm shell length and 0.2 mm long tentacles were found among the roots. The free-swimming larvae evidently remain among the plants, possibly orientated by their tentacles already developed in hatching veligers.

On the sandy seashore that extends over 200 km between Santos and Cananéia with short interruptions consistent pads of *Eichhornia* are frequent. If these are driven into the mouth of a coastal creek, its vegetation can be occupied by snails and veligers of *L. charruana*. Thus the range of this euryhaline hydrobiid may be extended by tidal and longshore currents, though it has no true pelagic phase. Where a river valley expands into a coastal plain, and stagnant side waters are formed, wind or flood tides might drive floating plants and the snails and larvae between them upstream and deposit them in such sheltered niches.

Eggs and swimming veligers were obtained in the laboratory. The measurements of the capsules vary from 125×110 to $135 \times 85 \mu$. Each contains one egg, 75μ in diameter. In the standing water of our dishes the capsules were often fastened with their small side to the rootlike fibres of *Salvinia*, near their base. These fibres also serve as food for the snails. At an average temperature of 20°C the veligers hatched in 10 days. They have 2 reddish brown patches on the velum and short primordial tentacles (Fig. 9). The granulated shell is 110μ long and 90μ broad.

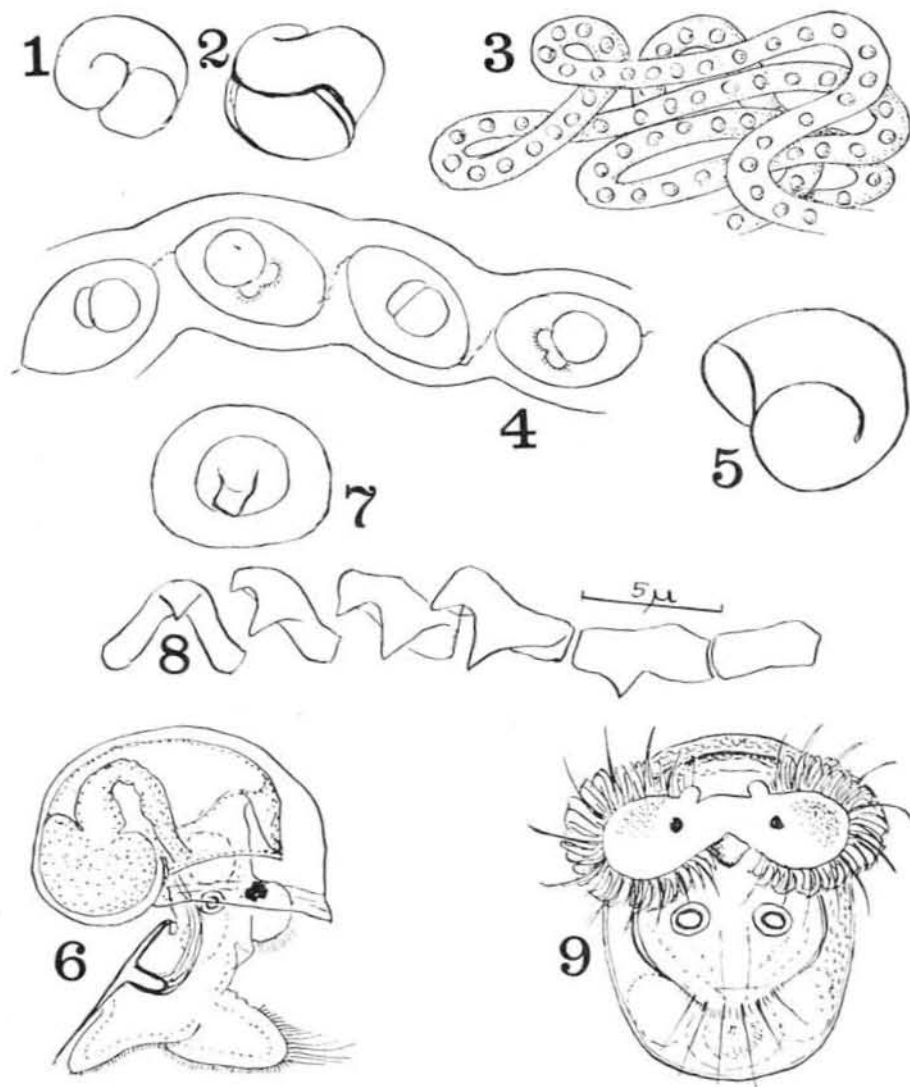
The river Cubatão, 15 km landwards from the Bay of Santos, is mentioned among the finding places of *L. charruana* (Pilsbry 1911, p. 558). From there came soil and plants for an artificial mangrove swamp of 12 sq. meters in the botanical garden of the Faculty of Philosophy, São Paulo. Among algae in its slightly brackish shallow water we found a large population of a *Littoridina*, called *L* 3 here, because its name and morphology will be published elsewhere. Its shell is like that of *australis*, narrower than that of *charruana*. The male copulatory organ has a densely ciliated tip which bears a papilla on the convex and a broad hump on the concave side.

The chief vegetation of the alluvial plain north of Santos, where *L* 3 lives, is mangrove; salinity and temperature of its ponds, creeks and rivers vary widely in correspondence with rainfalls, tides, and seasons. In our jars the snails endured slightly brackish as well as coastal sea water ($31\text{-}34 \text{‰}$), tolerated 41°C for some hours in dishes with black mud exposed to the sun, and withstood foul water and falling dry for several hours. In fresh water taken from an old aquarium they became rigid rapidly. In the artificial swamp outdoors the snails had laid eggs from August to the beginning of November. After a period of much rain, when their water became nearly fresh, multiplication ceased, and the population regressed. Brought into brackish water in the laboratory, their reproductive activity started again in the course of 48 hours. As in *Potamolithus lapidum* (d'Orb.) (Ihering 1885, p. 98) and *Littoridina tenuipes* Pilsbry (1952, p. 52) females outnumber males in *L* 3 ($2/3$ females, $1/3$ males). Copulation is accomplished head to head as in *L. australis nana*, or side by side. Often, though less frequently than in *Littorina* (Ankel 1936, p. 158-59), males try to join with other males. The egg capsules are generally attached as in *L. a. nana*, but in the stagnant water of the swamp and in our dishes they are also fastened to light, movable substrata, empty shells, dead leaves, and algae. The capsules are $0.35\text{-}0.38$ mm in greater diameter, hence more than twice the size of those in *nana* and *charruana*. The difference of the shell length of the 3 species is much less pronounced, and moreover *L* 3 is intermediate between the bigger *charruana* and the

Figs. 1-2 — *Blauneria heteroclita*. 1. Shell of newly hatched snail. 2. Young shell reversing direction.

Figs. 3-8 — *Ellobium pellucens*. 3. Part of egg string. 4. Same with higher power. 5. Shell of hatching snail. 6. Crawling young snail. 7. Operculum of same. 8. Half row of radula of same.

Fig. 9 — Veliger of *Littoridina charruana*.



smaller *nana*. The developmental type of *L 3* is correlated with its big egg capsule. It contains one egg, 0.18 mm in diameter, which grows to the size of the capsule, e.g., 0.36×0.3 mm. Crawling snails hatch *L 3*, the veliger stage is passed through within the capsule. This development takes longer: *nana* hatches in 5 days (25°C), *charruana* in 10 (20°), and *L 3* in 3 weeks ($22-25^{\circ}$). The hatching snail has an osphradium, but no gill. The epithelium of the mantle skirt forms seven 15μ long projections over the vein in 0.4 mm long snails; in a 0.6 mm long animal these gill filaments are 60μ long.

RESUMO

Na faixa supralitoral de Cananéia (25°S) as Ellobiidae (Pulmonata, Basommatophora) *Melampus coffeus*, *Detracia parana* e *Blauneria heteroclitata* são comuns; *Ellobium pellucens* é raro. Dos ovos das duas primeiras espécies saem larvas; dos das outras, caracóis. A direção das voltas é sinistral nas conchas dos veligeres e em *Ellobium* saído do ovo; dextral em *Blauneria*, cuja concha é sinistral no caracol adulto. Depois da eclosão, opérculo ainda existe nos jovens caracóis de *Blauneria* e *Ellobium*. Associada às Ellobiidae vive uma subespécie do prosobrânquio *Assiminea succinea*; desenvolve-se diretamente, com véliger apenas embrionário. Dá-se o mesmo com uma das 3 espécies de *Littoridina* (Prosobranchia, Hydrobiidae) encontradas nas águas dos manguezais; as 2 outras, *L. australis nana* e *L. charruana*, têm larvas que nadam livremente.

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