

ON BRAZILIAN SUPRATIDAL AND ESTUARINE SNAILS

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with 10 plates

The following study comprises two Ellobiidae (Pulmonata) of the subfamily Melampodinae and three Rissoacea (Prosobranchia): one species of *Assiminea* Fleming, 1828, and two of *Littoridina* Souleyet, 1852. The association of ellobiids and *Assiminea* is frequent in the supralittoral fringe of lagoons and estuaries (Morton 1955b, p. 131; Abbott 1958, p. 229) For these thalassogenous snails and also for the Hydrobiidae and others the brackish water is a migratory route from an originally marine intertidal habitat to the land conquered by *Fythia*, *Carychium*, *Paludinella*, *Truncatella* and others. This emigration from the sea is especially evident in lower latitudes, where marginal backwaters of lagoons and estuaries dry out during the dry season (Moore 1958, p. 205) Also tolerance for low salinities is greater at higher than at lower temperatures (ibid., p. 43; Fretter & Graham 1962, p. 580)

Our thanks are due to the Directors of the Oceanographic Institute Dr. Ingvar Emilsson and Dra. D. Marta Vannucci, who granted us the permission to study at the Research Base of Cananéia, where our Friends, the Head of the Base, Dr. Victor and Mrs. Nanna Sadowsky, made our sojourns extremely agreeable.

As Linné's material of *Melampus coffeus* came from the Antilles, we wanted to compare snails from this region with ours and are grateful to our Friend, Prof. Dra. Diva Diniz Corrêa, who gathered many specimens during her stay at Curaçao, where she could work owing to a fellowship from the Royal Government of the Netherlands.

We are very much obliged to Dr. Joseph P. E. Morrison-Washington for informative letters and reprints on Ellobiidae. Thanks to the amiability of Prof. R. Tucker Abbott and Dr. Robert Robertson — Philadelphia we received Bahamian *Assiminea succinea* (Pfeiffer 1840) for comparison with our snails.

Thanks to our Colleagues Drs. Roger Lavallard, Sérgio Rodrigues, and Jorge Petersen we obtained *Melampodinae* from São Sebastião; Dr. Walter Narchi kindly collected *Melampus coffeus* at São Vicente near Santos. An artificial mangrove swamp installed by Prof. Dr. Aylthon Brandão Joly in the garden of the Department of Botany (Dir.: Prof. Dr. Mário Guimarães Ferri) furnished us a new species of *Littoridina*, which later on Dr. Walter Narchi also found in freshwater; another species of this genus we owe to Lic. Jorge Petersen.

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Melampus coffeus (Linné, 1758) (Figs. 1-18, 22)

By free swimming larvae and highly concentrated central nervous system the genus *Melampus* Montfort, 1810, stands apart from the remaining genera of the Ellobiidae, as far as the mentioned characters of the other genera are known. As Morton could not include living snails of *Melampus* in his thoroughgoing researches (1955 b, c) of the family, we took the opportunity of an ample living material for a study of the type-species, *M. coffeus* (L.)

Occurrence and habits

In Brazil (Lange de Morretes 1949, p. 122) *M. coffeus* is known to occur on the coasts of Bahia, Rio de Janeiro, São Paulo, and Paraná; the Museum (Dept. Zool. Secretary Agricult., São Paulo) has material also from the mangrove region of Itajahy, Northern Sta. Catharina. French Guiana (Dall 1886, p. 281), the West Indies (Warmke & Abbott 1961, p. 153) and Florida (Dall, l. c.) belong to the further range of *coffeus*. All records westward of the Cedar Keys, Florida, e. g. Louisiana (Behre 1950, p. 37), Texas (Hedgpeth 1950, p. 118), and Mexico (Dall, l. c.) refer, according to Morrison (1958a, p. 124), to *M. bidentatus* Say, frequently called *lineatus* (Johnson 1934, p. 159; Coomans 1962, p. 90)

On the coast of São Paulo *Melampus coffeus* was reported from Itanhaen, 50 km SW of Santos (Luederwaldt 1919, p. 367) and from Cananéia, 25° S (Gerlach 1958, p. 667), in both cases from the mangrove formation. The species was found on the ground, on the lower parts of the trunks, and under loose bark. We collected *M. coffeus* at such places too and can summarize: at day-time the species occurs under stones, wood, and leaves, about 30 cm above mean high tide-level (M. H. W.)

In São Sebastião (23° 50' S, 45° 20' W) the species was found under stones on the rather dry grassy border of a drainage ditch in July and August 1962. Only at high spring tides the fringe is covered by the sea.

In 1962 (June) and 1963 (January and June) we studied a gentle slope ("Gleithang"), an about 20 m long and 3 m broad area in front of the garden of the Oceanographic Station, at Cananéia (25° 01' S, 47° 50' W), where hundreds of 1-15 mm long snails lived. This locality in front of the laboratory allows for a more detailed description than could be given of any farther distant place observed only occasionally. Certainly the complex conditions upon which the life of these snails depends, cannot be fully analyzed, but a concrete image of a place where the snails thrive and spawn can be given. The first and fundamental question, why larvae repeatedly have reached our area, cannot be answered.

The mean salinity of the lagoon ("mar pequeno") in front of the Station is 20 per mill, wave action is generally slight. The soil is made up of coarse sand, marine sediments, and a great quantity of humus. The latter comes from decaying leaves swept together in the garden, from a bush of *Hibiscus tiliaceus*, and grasses and rushes which cover the area with a 30-50 cm high mat. These are so dense that the soil is always moist and protected against wind and sun. As *M. bidentatus* (Hausman 1932, p. 543) also *M. coffeus* is a chiefly nocturnal feeder. At day-time the snails hide under stones, empty oyster shells, between the leaves, or are buried into the surface of the soil. They are pronouncedly gregarious, forming nests of all possible sizes of animals. Our locality is separated from the garden by a wall of stones and cement, whose top is 80 cm above the soil. So the area is not quite natural, but on the whole it seems to be comparable with Gerlach's upper mangrove zone (1958, p. 644), where the terrestrial vegetation begins to landward.

The mean high tides (M. H. W.) reach their upper limit 10-30 cm under the level where the snails are most abundant. By onshore winds and spring tides, however, the whole strip of land is flooded. When such winds coincide with high tides, the water reaches the top of the wall. As Dr. Sadovsky kindly informed us, this happened e. g. four times in May 1962, and thrice during our stay in June 1962. Under these conditions the snails are covered with water for three hours or more. After such floods they are accumulated on the wall, where they climb as far as they are shadowed by grasses and bush. Evidently they had tried to get away from the rising water.

This reaction is understandable by the following experiment. When snails collected between leaves on land are thrown into a dish with water, they climb upwards, but do not close their narrow pneumostome permanently. At first the presence of air within the mantle cavity hinders the entrance of water, and it lasts some time till the air escapes in a row of small bubbles. Once this is accomplished the snails breathe water. Presumably the same happens when the flood rises. Only exceptionally the snails creep beyond the limit of the highest tides, or if they do more frequently than we found them between the crab grass in the garden, they return to their zone later on, or are eaten by birds.

Our *M. coffeus* likes shadow better than intense light. Snails were kept in São Paulo for a year in a vivarium in dim light with moist soil, rotten leaves and hiding places. The dish was 25 cm in diameter and covered with an inverted plastics salad-bowl. At night they crawled about on this cover, as their trails of mucus and faeces showed. At day-time only few snails remained exposed to the diffuse light, many of them hid under the leaves or oyster shells. In a glass dish of 15 cm diameter 10 snails were put into the darkened and 10 into the sunlit half. At 23°C. all 20 animals gathered in the dark in the course of 5 minutes. When dark and light side were exchanged, the same animals collected in the dark only after 30 minutes, except one snail that remained in the light area. After moving about nearly always on the same spot this snail withdrew into its shell.

Except for reproduction discussed in the following, active life does not seem to depend of temperature in our *Melampus*, *Detracia*, and *Assimineia*. All were lively in June 1962, when the temperature lowered to 6°C. or less, and in January 1963 with up to 37°C. To judge from the slow rate of growth in our vivarium, where the snails ate great quantities of lettuce, *M. coffeus* certainly attains an age of 3-4 years or more.

We found several snails with only one eye. Such were delayed in arriving in the dark, but they did not execute manege-movements. The many snails seen with defective tentacles probably had them pinched off by crabs. Grapsids of the species *Sesarma miersi iheringi* Mary J. Rathbun, 1918 (Dr. Michel Pedro Sawaya det.) were the only animals in our biotope which could have injured the snails. The other members of the accompanying fauna were: many *Littorina flava*, which occur between the leaves and on the wall, few *L. angulifera*, numerous specimens of the *Assimineia*-species described in the following, *Detracia parana*, *Ellobium pellucens*, *Blauneria heteroclita*, *Gastrocopta*-spec., mites, larvae of flies, harpacticids, enchytraeids, and nematodes. *Littorina* was already mentioned as associated with *Melampus* by Fischer & Crosse (1880, p. 2) Seaward from our grassy strip the intertidal zone, which is flooded even by neap high tides, is inhabited by *Neritina virginea*, *Littoridina australis nana*, and a *Nassarius*-spec.

The stomach contents of our *Melampus* consist of a closely compacted mass of plant material, coarser and mixed with more particles of soil in older than in younger individuals. Like the species studied by Morton (1955c, p. 134) *M. coffeus* is a rather unselective feeder. Decayed woody tissues, pieces of a root containing vessels, fungal mycelia, and fragments of leaves fill the stomach. In the vivarium in São Paulo hard leaves were gradually skeletonized by the snails, and fresh lettuce was eaten eagerly. Fresh *Ulva* was not accepted. Wet filter paper was ingested when no other food was available. A snail with a 9 mm long shell produced a 7 mm long and 0,6 mm thick faecal rod. The colour of the mucous faeces is brown to black, but if lettuce was ingested, green.

Among our gastropods which invade the land from the sea and breathe air as well as water, we distinguish four degrees of terrestrial adaptation. The Melampodinae occurring in the supralittoral fringe, over mean high water-level, are the most terrestrial. The new subspecies of *Assimineia succinea* described in the following belongs to the same group. For its reproduction the prosobranch is even less bound to the aquatic environment than our ellobiids.

The species of *Littorina* come under the next degree which is less terrestrial. Even *L. angulifera* whose locomotion and respiration are independent from water feeds only in wet habitats and releases its larvae into the water. *Littorina* is followed by *Siphonaria hispida* which also breathes air, but moves and feeds only in the wet. The opisthobranch *Onchidella indolens* is the least terrestrial degree, though it browses and breathes in air. But it spends only a short time in the aerial environment.

Species closely related with the mentioned ones are known to have widely different habits, so that the listed sequence from land to sea does not apply to all members of the corresponding genera. Even one and the same species may in other regions occur in different biotopes. Perry & Schwengel (1955, p. 198) e. g. record *M. coffeus* on the western coast of Florida as common in mud or tidal flats, often climbing bushes and grasses. At Piscadera Bay, Curaçao, Dr. Diva Diniz Corrêa found *M. coffeus* on the roots of mangrove trees and on various substrata lying on the mud. The habitats

studied by Morrison (1958b) in the Miami area, where *M. coffeus* is abundant, are intertidal, hence flooded with every high tide.

Shell (Figs. 1, 3, 4, 17, 18)

The proportion between length and width of the shell varies from 1,4 to 1,6:1. Our biggest shells from Cananéia are 15 mm long and 10 mm broad. The biggest snail from Curaçao is 16,5 mm long. The outer lip of the Antillean material bears up to 15, ours 10-13, small white riblets on the inner side. These sometimes go out from the edge and sometimes are separated from it by a smooth interspace. The smallest of our shells with this sculpture was 6,5 mm long, in younger ones the outer lip is smooth. A 13 mm long shell from Cananéia had no riblets on the inner side of the outer lip. A white fold on the columella is constant; on the parietal wall 1-2 folds occur. Sometimes the parietal region bears a thin callus, a glaze of irregular outlines.

The ground colour of living snails from the coast of São Paulo, Cananéia, and São Sebastião, varies from grey to dark brown and black. Occasionally there are light axial growth lines. Generally the body whorl bears three spiral light or yellowish bands which may be absent or vary from 1 to 4. The shells from Curaçao preserved in alcohol are less intensely pigmented, yellowish to greyish brown, with or without the lighter spiral bands.

The resorption of the internal partition of the visceral whorls in the Ellobiidae, discovered by Crosse & Fischer (1879; 1882), has proceeded far in *M. coffeus* (Figs. 3, 4, 22). In a similar way as in *Ovatella* (*Myosotella*) *myosotis* (Meyer 1955, p. 32) the columella is reduced already in a shell 1,2 mm long, that has 3-4 whorls separated externally by a sutural line. The columella only forms a thin calcareous lamina separating the body whorl from the rest of the compact visceral mass. Of the earlier windings of the columella no trace remains, and the inner surface of the spire is perfectly smooth. The resorption of the columella leads to the displacement of the columellar muscle (Fig. 6, cn) which is attached to the foremost suture (en) in two bundles. In the present species a small posterior liver (zo) is present in spite of the concentration of the visceral mass due to the extensive

dissolution of the inner whorls. Where the inner wall of the body whorl ends, a crumpled mass of conchiolin (Fig. 22, ci) lies along the free end of the calcareous lamina. This shows that the inner resorption does not comprise the organic matter of the shell. Similar conchinous material was seen in *Olivella*. It seems that the resorbed lime is stored in big transparent inclusions by the vesicular cells of the connective tissue and in glittering opaque white ones which powder the walls of the vessels. Cells of the connective tissue around the organs and especially the vessels are known to store lime in prosobranchs (Ankel 1936, p. 129; Fretter & Graham 1962, p. 281) and pulmonates (Simroth & Hoffmann 1927, p. 1040; Boettger 1944, p. 345)

As in many cephalaspideans (Lemche 1948, p. 8) the larval shell is covered by a very hard layer of secondarily deposited lime, and the apex is generally somewhat eroded. In our smallest, best preserved, 1,1 mm long shell a nucleus, 0,1 mm high and 0,2 mm across, sits transversely over the spire (see Fig. 1), hence is heterostrophic (Fischer & Crosse 1880, p. 12)

For the demonstration of a phyletic relation between the basal families of pulmonates and opisthobranchs Fischer & Crosse (l. c.), Harry (1951, p. 13) and Morton (1955b, p. 161) stressed the importance of a heterostrophic apex.

Head (Fig. 17), foot (Figs. 2, 6) and locomotion (Fig. 5)

The pointed tentacles are nearly cylindrical without bulbs at the bases. They are not retractile, only contractile by longitudinal muscles in their walls. Besides, strong fibres which belong to the columnar muscle system insert basally on the upper and lower wall of the tentacles. These retractors of the anterior border of the head are much stronger on the left than on the right side. The same asymmetry, explained as brought about by the right-hand male copulatory organ, has already been recorded for other pulmonates (see Simroth 1909, p. 208) Generally the tentacles diverge at an angle of 120° , but sometimes still more to the sides, or so much less as to become almost parallel. The eye lies axially in the base of the tentacle; the lens is directed towards the tip. When the tentacles are directed for-

wards, the eyes appear to lie in their axes; when the tentacles are spread, the eyes are nearer to the middle and to the skin of the tentacles. The light reaches the eyes through the epidermis whose pigmentation is slightly diminished in the ocular region. The anterior border of the head is extended into a pair of rounded, highly sensory oral lappets (Fig. 6, ro) These are light, without pigment, and so are mantle border and sole. From the likewise unpigmented borders of the foot the ascending hyponotal sides darken gradually to the general blackish body colour. The intensity of the colours of the inner organs varies individually from bright to pale.

As in other species of *Melampus* the anterior border of the foot (Figs. 2, 6) has a deep transverse groove (vv), and the hind end is split longitudinally. The groove receives the ciliated duct of the anterior pedal gland (vo) in its centre; the gland touches the pedal ganglia (ea). At the end of the first third of the sole a second groove (q) extends over its whole breadth, dividing the sole into a forefoot (oo) and a hindfoot (io). The columnar epithelium of the sole bears weak cilia and is underlain by the insunk cells of the sole glands (so). These cells are absent along the flat-celled anterior wall of the second pedal groove as in *M. boholensis* (Koslowsky 1933, p. 183).

The foot consists of a network of fine, single muscle fibres running in all directions, connective strands, and gland cells (so), separated by blood spaces (oa) and some large blood lacunae (si) parallel to the sole. While the animal is extended, all these spaces are turgid with blood; they counteract the muscular contractions. In the withdrawn snail they are emptied, and all the tissues of the foot lie tightly packed together. The fibres of the columellar muscles (cn) supply chiefly the hind part of the foot.

Otina otis moves by steps (Vlès 1913): the forefoot is lifted from the substratum and set down farther in front; then the process is repeated by the hindfoot. Koslowsky who studied only preserved snails supposed (1933, p. 181) that *M. boholensis* creeps in the same manner. *M. coffeus*, however, crawls as *Leucophytia bidentata* (Morton 1955c, p. 95). The whole ventral surface, from the oral lappets to the posterior end of the foot, is kept on the substratum continuously, and forefoot and hindfoot are not lifted from the ground.

The act of locomotion is well to be observed with the dissecting microscope when a snail glides on the underside of a glass plate. There is only one wave of contraction at a time, and only when that has passed out in front, a new one arises at the hind end. The same holds for *Ovatella myosotis* (Meyer 1955, p. 13-14) Moreover the process is uniform along the whole sole, so that the movement of the forefoot alone serves to understand the mechanics of the entire foot.

Ciliary action does not take part in locomotion; particles of carborundum brought onto the stretched sole remained on the spot in air as well as in water. Movement is effected by the muscles of the foot, including the columellar muscle, and by the swelling of the blood lacunae, which also brings about firm adhesion. The sole glides with changes from stretching forward its anterior part, fastening it and drawing the hind end after. The shape of the adhering surface shifts continuously. The part that is contracted transversely becomes longer and is thrust forward. Then it adheres in the new position, and by this contraction draws the following part behind it. Such a wave of forward movement begins at the tip of the tail and runs forward along the whole sole followed by a phase of broadening. The forward movement of the hind sole presses the fore end of the hindfoot into the second transverse groove (q). Figure 5 is a diagram of this process. When the fore end of the hindfoot is flattened out again, it forces the forefoot forward against the oral lappets (ro), so that its fore end is impelled into the anterior groove (vv). Advancing further the wave stretches the fore end of the forefoot and moves the oral lappets forward. Then a new wave of forward movement begins on the tail.

On moist filter paper or glass as well as on a leaf of lettuce the snail advances evenly, without the jerks of the head observed in *M. semisulcatus* (Knipper & Meyer 1956, p. 105)

When the fore end of the forefoot is pushed up into the anterior groove it comes into contact with the broad opening of the anterior pedal gland (Fig. 2, vo). When it rolls out again, it lays a mucous carpet onto the substratum.

At 22°C. snails crawled 60 mm per minute on glass, but generally the duration of their straight course is shorter. Another time at 25°C. they attained 120 mm per minute.

When the snail retracts, it pulls its head and forefoot far inwards and then withdraws the hindfoot without folding it forwards. Finally the aperture is closed by the mantle whose thickened margin protects the sole. The mantle edge lodges a wide vein (mn), so that an exchange of gases is possible even in withdrawn state.

The righting reaction of the snails is rapid and efficient. The projected foot can reach the substratum over the outer or over the inner lip. Also the tentacles and the oral lappets search for the ground, and when they touch it, direct the movements of the foot towards it. Adherence of the oral lappets is even essential for turning over the body and the shell. If the snails are laid on their back under water in a smooth glass dish, they take a longer time to right, but if the dish is lined with filter paper, they reacquire their normal position rapidly.

Mantle and pallial organs (Figs. 6, 22)

The mantle skirt overhangs the anterior region of the snail as a broad fold. The resulting spacious cavity lodges the retracted head and forefoot. A glandular groove (mv) accompanies the whole mantle edge on the outer side, and the inner side is profusely provided with big goblet cells (mu). Their secretion may be specially important when the mantle protects the retracted body. The circular vein (mn) swells the mantle edge; it pulsates in extended and retracted snails. The right and left mantle margin are confluent behind and form a pointed lappet (sr) lying along the posterior canal of the shell aperture. Evidently this lappet occurs in several ellobiids; it appears in Küster's figure of *Ellobium aurismidae* (1844, pl. A, f. 1), in *Marinula juanensis* (Odhner 1925, p. 4), in *Leucophytia bidentata* (Morton 1955c, f. 1, sp. 1.), in *Ellobium pellucens* and *Blauneria heteroclita* which we are beginning to study. On the left side a smooth furrow marks the limit between mantle skirt and hyponotum. In front and on the right side a septum (se) unites the mantle skirt with the back. This septum forms the hind wall of

the anterior cavity and confines the mantle cavity, which communicates with the exterior only near the posterior angle of the shell aperture.

The pallial opening is semicircular, convex dorsally and concave ventrally. In front its muscular borders surround the respiratory opening, the pneumostome (us). Behind, where the folds of the anal groove reach the slit (ar), the faecal rods are released. In air and in water the pneumostome opens and closes at irregular intervals. In front a high ridge (ri) separates the pneumostome from the deepening that corresponds to the furrow on the left side, and like it represents the lateral continuation of the anterior cavity. In front of and a small distance from the ridge the female aperture (y) is located, and forwardly the efferent duct (e) shows under the epidermis due to its pigment.

The mantle cavity is deep but does not extend along the whole body whorl (Fig. 22). Besides the small tubular anal glands (an) which are described together with the gut, two conspicuous separate glandular pads (ac) lie opposite to one another on the roof and floor in front of the anal groove (ve). Their secretion is emptied into the pallial cavity. The thick sleeve of gland cells that lines the tubular pallial opening in *Otina otis* (Morton 1955a, p. 116) is comparable with these pneumostomatal glands of *Melampus coffeus* and the following species. They are covered with ciliated epithelium and composed of large subepithelial gland cells of two different types. One contains homogeneous acidophilous, the other reticulate, pale blue secretion. The pads are underlain by vesicular cells with lime crystals.

Another gland discharging into the mantle cavity is the hypobranchial gland (h) developed in many, not all (Morton 1955c, p. 95) Ellobiidae. When present, it is situated to the left of the intestine (i) on the roof of the cavity. As in *Marinula juanensis* (Odhner 1925, p. 4, pl. 1, f. 5, d) it is weakly developed in both our species of Melampodinae.

In the opened mantle cavity of *Melampus coffeus* the hypobranchial gland is generally evident and appears as thickened epithelium thrown into transverse folds along the rectum. In sections it was not always distinct.

Hubendick (1945, p. 155) was right to separate the "Mantel-organ" of *Melampus boholensis* (Koslowsky 1933, p. 178) from the hypobranchial gland. This black organ (mo) exists in our species too. It lies in the roof of the pallial cavity, in front of the pericardium (c). It is not epithelial and not a gland at all, but an accumulation of connective tissue cells stuffed with dark pigment granules. Amoebocytes occur between these cells. An anterior vessel coming from the visceral sinus sends ramifications into the mantle organ. These emerge behind and unite to form a vessel which enters the pulmonary vein just at its entrance into the auricle. We did not find any organ in the Basommatophora comparable to this evidently lymphatic or excretory structure in *Melampus*. The tubular pallial glands of *Pythia* (Plate 1897, p. 121; Morton 1955b, p. 153), *Ovatella* (Pelseneer 1894, p. 73; Meyer 1955, p. 11-12) and *Carychium* (Morton 1955c, p. 133) are homologous with one another, but quite different from the present mantle organ.

Kidney (k), auricle and ventricle follow from right to left and from the pneumostome to the fundus of the mantle cavity. The kidney extends along the roof of the cavity, but is narrow in antero-posterior direction. The renal aperture (no) lies at its right end, the reno-pericardial, about 0,1 mm long duct on the left side. This duct opens into the atrial part of the pericardium. According to the degree of filling with liquid, breadth and transparency of the kidney vary. In all preparations and sections it is subdivided by antero-posterior lamellae into short chambers. In *Melampus boholensis* the lamellae leave a 0,45 mm long chamber free, while they occupy the entire extension of the kidney in both our *Melampodinae*.

At 18,5°C. the heart of *M. coffeus* pulsates 49 times per minute. A similar frequency was observed in *Ovatella* (Meyer 1955, p. 9). The aorta bifurcates into an anterior or cerebro-genital and a posterior branch near its origin from the ventricle. The former courses ventrally and supplies head, foot and the parts of the gut and reproductive organs that lie in these regions. The posterior aorta enters the visceral sac and ramifies to intestine, stomach, intestinal glands, inner genital ducts, and ovotestis, where it subdivides radially. Two recurrent vessels run from the gonad to the anterior digestive glands. From anterior and visceral venous lacunae the

blood is collected in the wide vein (mn) of the mantle edge. Also the intestinal-rectal sinus (si) communicates with this circular vein, whose contractions impel the blood into the afferent pulmonary vessels in the roof of the pallial cavity. These vessels are not much ramified and appear as light lines in the black-pigmented mantle roof. The efferent vessels converge to the pulmonary vein which runs along the anterior border of the kidney. Not the whole quantity of venous blood passes through the pulmonary vessels. From the rectal sinus afferent renal vessels lead blood to the kidney (k), whence efferent ones enter the pulmonary vein. In a similar way an already mentioned vessel leaves the visceral venous sinus, passes through the mantle organ (mo), and goes to the pulmonary vein at its entrance into the auricle.

Central nervous system (Fig. 7)

The nerve ring lies around the mouth cavity in front of the buccal mass or pharynx (uu) in contracted snails, in extended ones behind. The cerebral ganglia (ce) are connected by a thick supra-cerebral and a fine subcerebral (su) commissure; the first is a little shorter than the diameter of one of the ganglia. The right ganglion emits eight, the left seven nerves. The innermost is the thick tentacular nerve (ne). Next to it the thin optic nerve (on) runs to the eye. Its fibres were only traced into a subtentacular cerebral centre (xo), though they originate farther behind (Hanström 1928, p. 186). This centre, the lateral lobe, globulus or procerebrum (Simroth 1910, p. 284; Hanström 1928, p. 170), consists of small nerve cells as in other basommatophores (Hanström, p. 184). In two series of sections of 1,1 and 2,2 mm long *M. coffeus* the cerebral tubes were seen in their entire extension from the epidermis to the lateral lobe. In *Melampus fasciatus* the tentacular and optic nerve have a long common root (Meyer 1955, f. 14); probably their fibres are separate and only united by a common sheath. To judge from Knipper & Meyer's figure (1956, f. 8) the tentacle and optic nerves of *M. semisulcatus* have a common root too.

Outward to the optic nerve there are three nerves in *M. coffeus* whose course to skin and muscles was not followed. On the right

cerebral ganglion the sixth is the penial nerve (ie) The following nerve is the thick labial nerve (ni), which trifurcates at some distance from the ganglion and ramifies further, where it enters the oral lappet (ro) Between the labial nerve and the cerebro-pedal connective the thin sub-cerebral commissure (su) comes forth, and between cerebro-pedal (cc) and cerebro-pleural (nu) connective, the static nerve (ns) The cerebro-pleural connective is slightly thicker than the cerebro-pedal one. Both the left ones are nearly twice as long as the right ones, so that the nerve ring becomes asymmetric.

The long cerebro-buccal connectives originate ventrally. The light brown flecks in the connective tissue around the ganglia are represented by a layer of black pigment granules in the neurilemma of the buccal connectives. The buccal commissure (cv) is twice as long as the diameter of one of the ganglia. These lie under the beginning of the oesophagus as in the other ellobiids.

The pedal ganglia (ea) which touch one another are as big as the cerebral ganglia. Each ganglion emits six nerves. Two are directed obliquely forwards and sideways, they run towards the corresponding lateral regions of the foot, while four posterior nerves pass through the anterior pedal gland and enter the sole. The statocyst (ao) contains a great number of minute statocones. A parapedal commissure was not seen.

The visceral loop is so short that it lies in front of the pedal ganglia. Between the small pleural ganglia (eu, wu) it contains three larger ganglia as in most ellobiids (Ihering 1877, p. 22; Pelseneer 1894, f. 205; Simroth 1910, p. 255; Odhner 1925, pl. 1, f. 9; Morton 1955c, f. 31; Meyer 1955, p. 13, 14; Knipper & Meyer 1956, f. 6-8) There are only two in *Melampus boholensis* (Koslowsky 1933, p. 180) and *M. liberianus* (Hubendick 1945, p. 141) The last two species have the most specialized nervous system among the anatomically known ellobiids.

In *M. coffeus* all the visceral ganglia are almost contiguous but distinctly set off from one another. As generally in Basommatophora (Boettger 1944, p. 357) the pleural ganglia have no nerves in *M. coffeus*. The following right (supra-intestinal, zr) and left (pa-

rietal, zi) ganglia emit two nerves each. Those from the supra-intestinal ganglion are the inner and outer pallial nerves.

In contrast with *Ovatella myosotis* (Pelseneer 1894, f. 205, IV; Meyer 1955, f. 13, p), *Auriculodes gaziensis* (Knipper & Meyer 1956, f. 6), *Cassidula labrella* (ibid., f. 7), and possibly *Melampus fasciatus* (Meyer 1955, f. 14, ?p) there is no peripheral nor a central osphradial ganglion in *M. coffeus*. From the left (parietal) ganglion one nerve, the left pallial nerve, runs forward, the other side-ward, probably to the columellar muscle. The central ganglion of the visceral loop, the visceral or abdominal ganglion (as), emits three nerves, in a dozen dissected snails. The same was observed in *M. fasciatus* (Meyer, f. 14, o) These nerves were not followed to the internal organs.

The central nervous system of our two species suits to the general opinion that the Melampodinae are specialized Ellobiidae. The results obtained from an examination of the stomach diminish the value of this generalization and show that "each genus is a mosaic or blend of basal and more advanced characters" (Morton 1955b, p. 154)

Alimentary canal (Figs. 8-10)

The mouth (Fig. 2, m) is double T-shaped. When the snail feeds, the buccal opening is widened, the folds of the buccal cavity are flattened out, and jaw (j) and radula (ra) come forth. Clusters of subepithelial glands (iz) lying in the side walls of the buccal cavity as in other Basommatophora (Morton 1955c, p. 97) produce a lubricating mucus which is mixed with the food. The grasping action of the jaw is seen when the snail feeds on soft food, e. g., fungal mycelia. The jaw (Fig. 8) consists of about 35μ high, fine brown conchinous rods which form a 0,42 mm broad ribbon in the middle of the roof of the mouth cavity and a narrow continuation along the sides. The radula of an 8 mm long snail is 2,75 mm long and 0,6 mm broad. There are about 100 definitively developed straight rows, each 28μ high.

The narrow central tooth (Fig. 9, R) has an emarginate base. Its cusp bears a single straight denticle with a recess on either side.

These recesses give a tricuspid appearance to the central tooth, so that we cannot agree with Powell (1933, p. 148), that all traces of a tricuspid central tooth have vanished in *Melampus*. The 55 teeth of each half-row are not uniform. Lateral and marginal teeth can be distinguished by one or more ectocones on the latter. The limit between the two types of teeth is inconstant (Odhner 1925, p. 9). The 15-19 inner or lateral teeth have cusps with only one denticle, the mesocone. From the 16-20th tooth outwards an ectocone appears. The number of ectocones increases outwards to maximally seven, in other radulae only to four. Contrary to *M. luteus* (Odhner 1925, p. 10) the bases of the pectinate marginal teeth are not striped, so that vestiges of a coalescence are not evident. In the outer part of the row, from approximately the 40th tooth outwards, a single tiny endocone occurs. On the whole the lateral teeth are a little stronger than the marginal ones, and the latter decrease in height towards the end of the half-row.

The formula of a 12 mm long snail from Cananéia is 31.23.1 23.31, that of an animal from Curaçao, also 12 mm in length, 35.34.1.34.35. In these radulae of full-grown specimens the endocone of the marginal teeth is minute too and recognizable only in a favourable position of the cutting edge.

Except for its more prominent mesocone on the marginal teeth the radula of *Melampus coffeus* is similar to that of *M. bidentatus* (Morton 1955b, f. 7); the shells of *coffeus* and *bidentatus* are difficult to be distinguished (Holle & Dineen 1959).

Under the radula pouch the yellowish buccal mass is provided with a pair of powerful retractors. These originate united, together with the much thinner retractor of the penis, between the two halves of the columellar muscle in the apical suture. The white salivary glands (Fig. 2, sa) open into the pharynx to the sides of the dorsal food channel. In contracted snails their ducts pass through the nerve ring, in extended ones the latter lies far in front of them. Near its opening each salivary duct forms an ampulla; the glands themselves are long and broad tubes with irregular outlines. The salivary glands are evidently different in several Ellobiacea: tubular in *Leucophytia* (Morton 1955c, p. 98), *Carychium* (ibid., p. 135), and *Otina* (id. 1955a, p. 123); pinnate in *Pythia* (Plate 1897, p. 124), and

Melampus fasciatus (Meyer 1955, p. 5) In *Ovatella* they are lobate, intermediate between tubular and pinnate (Pelseneer 1894, p. 75, 114; Meyer l. c.) Those of *Melampus coffeus* are simple tubes. The fundi of both glands meet on the ventral wall of the oesophagus to which they are attached separately

The anterior oesophagus is unpigmented, nearly smooth, and richly ciliated. It is followed by the distensible posterior oesophagus (Fig. 10, o) or crop. The black longitudinal stripes of this section correspond to high longitudinal folds of its epithelium which is ciliated and contains some glands. The hind end of the posterior oesophagus is marked by a black strand (ui) which runs to the ventral wall of the stomach. Folds and pigment disappear gradually in the narrow gastric chamber (or) which receives the aperture (va) of the voluminous anterior digestive gland (za) on its dorsal side. In the Ellobiidae this chamber is called oesophageal atrium (Morton 1955c, p. 100), in the Onchidiacea initial chamber of the stomach (Fretter 1943, p. 689)

The globular stomach (Fig. 6, es) lies in the apex under the gonad (w) When it does not contain food, it is filled with a brownish clear jelly, evidently come from the digestive diverticula. The oesophagus and the pylorus lie on the anterior side, the oesophagus to the left, the pylorus to the right. The stomach, pylorus, and intestine (i) are colourless.

The anterior digestive gland (za) is subdivided immediately from its opening. The small posterior digestive gland (zo) enters through the ventral wall of the stomach, between cardia and pylorus but nearer to the latter. The follicles of this gland have a 0,2 mm long common duct. Beside the posterior hepatic aperture (x) the above-mentioned strand (ui) is attached, which connects the stomach with the hind oesophagus. This strand consists of muscle fibres coated with black connective tissue. The lobes of the intestinal glands are light brown, generally with darker contents in their cells.

A soft muscular pocket (ca) lined with cilia lies apically to the posterior hepatic aperture. It can be tucked into the gastric lumen and is then difficult to be seen, because it is much smaller than in *Leucophytia bidentata* (Morton 1955c, p. 100) Nevertheless it

is the same posterior caecum as in that species and in *Ovatella myosotis* (ibid., f. 18, cm) Two high folds go out from the aperture of the hind liver accompanying a deep groove whose cilia produce a forward directed current. Another current leads particles from the opening of the anterior digestive gland to the pylorus, where it unites with the first, and enters the intestinal groove (u) A third, weakly ciliated strip transports material from the oesophageal atrium to the region of the caecum and posterior liver opening.

The cilia of the pylorus rotate food particles (f), so that a string of stomach contents, a protostyle, originates which is continuous with the faecal string in the intestine.

On the whole the stomach is more a churning and triturating organ than one whose cilia move the food. The stomach, pylorus, and digestive glands show peristaltic movements. A considerable power of peristalsis was also observed in the digestive diverticula of *Ovatella myosotis* (Morton 1955c, p. 124) The coarse and hard food of *Melampus* is correlated with the predominantly muscular action of its stomach.

The gastric epithelium bears a rather fine, wrinkled cuticle in all parts not occupied by ciliated cells. The whole wall is coated with inner circular (rm) and outer longitudinal muscle fibres. By the varying contraction of these muscles thick belts are brought about in different gastric regions. Temporarily a kind of gizzard appears behind the pylorus, but a little later peristalsis shifts this thickening to the fundus. Also inconstant sacs and pouches of the stomach appear and disappear in quite different regions.

The stomach of *Melampus coffeus* can be compared with that of *M. boholensis*, as far as Koslowsky's brief account (1933, p. 171) of four preserved animals allows. Anterior and posterior digestive diverticula, posterior caecum, and non-constricted gizzard are similar. In *M. boholensis* the long distance between caecum and entrance of the posterior diverticulum, and the two cushions formed by the belt of muscles are probably no constant features but the state assumed in the moment of fixation.

Also Morton (1955b, p. 141) dissected only preserved snails, but these belonged to four different species of *Melampus*. In all of

them he stated the absence of a posterior digestive gland and caecum. An anterior, thin-walled oesophageo-intestinal chamber is almost completely separated from the posterior gizzard (f. 3 D). These differences are evidently morphological and cannot be explained as different states of contraction. *M. gundlachi* Pfeiffer, 1853, which belongs to Morton's material (p. 129) and is sometimes considered as a subspecies or variety of *coffeus* (e. g., Johnson 1934, p. 159; Coomans 1958, p. 103), should be separated specifically from *coffeus* by reason of its widely different stomach. On the other hand, *Melampus gundlachi* is conchologically still problematical (Holle & Dineen 1959, p. 51).

With the highly specialized stomachs of Morton's species contrasts the primitive one of *M. coffeus*. It is similar to that of *Ovatella myosotis*, which retains a generalized pattern (Morton 1955b, p. 138), and "perhaps represents an original or basic type in the Ellobiidae" (Morton 1955c, p. 90). So Morton's statement (1955b, p. 143) is corroborated: "it would appear that within the single genus *Melampus* the stomach may vary a good deal in specialization".

The course of the intestine of *M. coffeus* agrees with that in *Otina* (Morton 1955a, p. 129). The pylorus corresponds to a style sac, containing an intestinal groove between two typhlosoles with long cilia. The same features continue along the first bend of the intestine. Farther in front the groove and its folds disappear, the cilia become fewer, and the epithelial cells lower. Between the latter occur some glands. Frequently the faecal rods preserve the mark originated by their passage along the intestinal groove. As in *Ovatella myosotis* (Pelseneer 1894, p. 73, 75; Meyer 1955, p. 7), *Marinula juanensis* (Odhner 1925, p. 4) and *Melampus bohollensis* (Koslowky 1933, p. 173) the anus lies in the roof of the mantle cavity, and as in these species a ciliated groove (Fig. 6, ve) covered by folds leads the faeces outwards. An anal gland (an) as described for *M. bohollensis* (Koslowky 1933, p. 174-76) opens on either side of the anus. These sacculi consist of strongly ciliated epithelial cells and subepithelial flask-shaped secretory ones. Possibly their secretion reinforces that of the not numerous intestinal intra-epithelial glands gluing the faecal pellets together and lubricating their evacuation groove.

Reproductive organs (Figs. 11, 12)

The gonad (w), the most apical organ (Fig. 6), is a plate made up of ramified tubules with occasional anastomoses. On the left of its anterior or underside the gonadial artery enters the plate, and opposite to it, on the right side, the spermoviduct (s) leaves it. In most dissected snails the germinative epithelium contains dark brown pigment, as long as it is inactive, but exceptionally also pale specimens were seen. The cells of the connective tissue around the hermaphrodite gland have big transparent calcareous inclusions. A snail with 1,2 mm long shell had no gonad; in a 2,2 mm long one there was a primordium of a gonad lying farther in front between the lobes of the digestive gland. That is the definitive position in *Fythia* and *Carychium* (Morton 1955b, f. 4, 5), both with primitive genitalia. Also the hermaphrodite duct was in the primordial condition of a groove running along the columellar muscle but disappearing farther in front. A 4,3 mm long snail had a rather well developed genital tract, but no ripe spermatozoa. Towards the end of July 1962 the gonadial tubules were distended by masses of growing spermatocytes; in August ovocytes appeared. Small but numerous ovocytes were also seen in sectioned gonads of November 1961. In the reproductive period there is no relation between size and maturation of sperms. Big snails from Curaçao preserved in spring had their inner hermaphrodite duct filled with ripe sperm.

In living spermatozoa the conical head with a short acrosome, together 6μ long, can be distinguished from a 0,5 mm long middle piece whose anterior third is slightly spiral, and a 0,4 mm long tail. *Melampus coffeus* and *Detracia parana* are protandrous hermaphrodites like the other Ellobiidae (Morton 1955a, p. 133)

The brown spermoviduct (s) or little hermaphrodite duct runs forwards winding and accompanied by the posterior aorta. The ciliated duct forms a wide ampulla distended by sperm and opens into a narrower, also ciliated section (r) with peripheral recesses. This curved chamber seems to be the site of fertilization. Absorption of sperm in the niches was not seen. The following duct is the inner section of the large hermaphrodite duct (he) It lodges a fold which separates a seminal groove from the female tract. The large her-

maphrodite duct communicates with the albumen gland (a) From this dark yellow organ a broad winding duct goes out at its anterior end. This winding duct connects the albumen gland with the mucus-secreting part of the female way, the lighter yellow mucus or nidamental gland (g) As the mucus gland lies on the opposite side, the winding duct has to cross the large hermaphrodite duct. The mucus gland is a turreted spiral in which the female way begins at the base, rises to its apex and descends to the base again. Its secreting cells lie in clusters on the outer, convex side, while the inner, concave side is lined by high ciliated cells which probably transport the eggs through the spiral. The mucus gland communicates with the outer section of the hermaphrodite duct (z) This is continuous with the oviduct or vagina (v), a muscular, colourless tube with folded epithelium which runs forwards under the floor of the mantle cavity and opens (y) in a deep fold near the pneumostome. In our material from Cananéia and Curaçao the vagina describes some loops and then runs straight.

The outer section of the hermaphrodite duct receives the rather long canal of a bursa copulatrix (b) on its anterior wall. Opposite to it lies the departure of the efferent duct (e) Here the seminal groove of the hermaphrodite duct becomes a thin, closed tube. Alongside the vagina the male duct runs forwards under the floor of the mantle cavity to the level of the female opening (y) and farther to the level of the male pore (mi) Then it courses transversely to the left and turns backwards to the fundus of the salivary glands. Here the efferent duct opens with a tiny papilla (d) into a wider muscular tube, the penial sheath (p), which is thickened by strong annular muscle fibres and comprises $1/6$ to $1/4$ of the total length of the penis. It seems to function as a support for the small papilla and terminates with an end piece marked by a pigment collar This sheath, not the tiny papilla (Fig. 11, d), corresponds to the "penial papilla" (Koslowsky 1933, p. 127, f. 4, 7, pe. pa.) in *M. boholen-sis*. Outwards the male organ consists of a tube with glandular epithelium, the preputium (qi) The penis forms a hairpin bend with the male duct (e) and opens (mi) under the right tentacle. At its fundus a retractor (re) inserts, which originates between the two halves of the columellar muscle in the apical suture. By eversion of

the preputium and sheath the penial papilla comes to lie on the tip of the sheath.

The reproductive organs of *Melampus coffeus* are similar to those of *M. bidentatus* (Morton 1955b, f. 7), but in that species the mucus-secreting region, a separate outgrowth from the genital tract, is not traversed by sex products (p. 146) Though we did not see eggs passing through the corresponding voluminous spiral of *M. coffeus*, we presume that this rising and descending duct really is the way of the eggs. The reproductive organs of *M. luteus* (Odhner 1925, p. 5-6, pl. 1, f. 8 A) agree with those of *M. coffeus* and *M. bidentatus*. By its special glands annexed to the central region *M. bohokensis* (Koslowsky 1933, f. 4) differs from the other species, while the inner and outer organs are similar. The male intromittent organ has the same structure in all the mentioned species.

Eggs and larvae (Figs. 13-16)

Mörch's statement (1867, p. 236), that the larvae of the Ellobiidae, at that time Auriculidae, swim in the sea, is not specified. The velum and operculum of the embryo of ellobiids were observed by Semper (1880; see Pelsener 1894, p. 115; 1935, p. 539) Therefore and due to the geographic distribution of *Melampus* (Fischer & Crosse 1880, p. 21) the occurrence of free-swimming larvae became probable. Egg masses of *M. bidentatus* Say, *Detracia floridana* (Pfeiffer), and *Melampus olivaceus* Carpenter were found by Hausman (1932) and Morrison (1953; 1958b) Morrison was the first to observe the veligers of several Melampodinae, also of *M. coffeus* at Vero Beach, Florida (letter from Dr. Joseph P. E. Morrison of November 7, 1962) From the same letter we quote that *Pira*, by most workers still included in *Melampus* (sensu lato), has the same type of eggs as *Melampus* (s. str.), and its swimming stage must be the same. In the systematically widely distant genera *Cassidula* and *Laemodonta* Dr. Morrison found the eggs laid in a spiral string of jelly, and he thinks that the larvae are pelagic too.

On and between the black rotten leaves of the above-mentioned locality we found about six developing spawns on June 4, 1962. The next day the temperature decreased considerably, and no more egg

masses were obtained. The roundish, jelly-like clusters (Fig. 13) were 1 mm high, 2-5 mm across, and contained about 500-2000 eggs, each around 80-90 μ in diameter and enclosed in a capsule about 130 μ long and 92 μ in diameter

In our vivarium the gonads began to produce germ cells towards the end of July 1962 with rising temperature, but a week later it decreased again, and the snails' hermaphrodite gland diminished. At Cananéia in January 1963, after a fortnight of warm weather, snails from 7 to 15 mm length began to lay hundreds of egg masses on leaves, in nature principally at the level of neap high water-line, but in our dishes also on the nearly dry uppermost leaves. Stones and pieces of wood contained spawns too. Of *Melampus coffeus* and *Detracia parana* we generally found two spawns close together and two snails near them, as if they had mated recently. According to the different sizes of the mature snails the size of the egg masses varies widely

At about 30°C. the veligers hatch within 10-11 days, if the jelly is reached by water; if not, they remain in the jelly longer. 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 whole shell (Fig. 16) is somewhat rough, especially on the sides; three days later the shell had grown to 114 μ . The velum and operculum are as in the ellobiids which complete their development within the egg capsule (e. g., Meyer 1955, f. 27)

The smallest creeping snails had 1,2 mm long shells, so the planktonic life of the veliger is evidently rather long.

Detracia parana Morrison, 1951 (Figs. 19-21, 23-25)

Occurrence and classification

In the above-mentioned supra-littoral fringe at Cananéia in front of the garden of the Research Base, Oceanographic Institute São Paulo, we found a second melampodine, *Detracia parana*, together with *M. coffeus*. This species has the same transverse division in the anterior third, and the same bifid hind end of the foot as *M. coffeus*. Among the 4-5 mm long snails it was even more common than *M. c.* *Detracia parana* was not as resistant as *Melampus coffeus* in our vivarium, where it lived no longer than 4 months.

At the similar locality of São Sebastião *Detracia parana* and *Melampus coffeus* were found together too. Both species have a wide tolerance range for different salinities, as is shown by this occurrence on the supratidal fringe of the Canal of São Sebastião. When the surf of high water floods the biotope, the two Melampodinae are covered with normal sea water. A succeeding period of dry days may render food and substratum of the snails hypersaline.

As in the Miami region, where Morrison (1958a, p. 119) found *M. coffeus* together with *Detracia clarki*, we gathered the snails of our two species mingled, and only later on found out that we had, besides the true *Melampus coffeus* with its conoid shell, collected another, whose shell "is rounded to a point at both ends" as Dall (1886, p. 285) characterized *Detracia* Gray, 1840.

Morrison (1951, p. 19) had only four shells available, collected previous to 1885 at Pará, to-day generally Belém, State of Pará. A comparison of that small number of shells with the hundreds of our collection makes some annotations to the first description necessary. While the columellar lamella may be directed horizontally or anteriorly in ours as in the original material, the inside of the outer lip, Morrison's parietal wall, is not always smooth in our shells. Among 174 examined, 3,3-7,0 mm long shells of *parana* 107 had transverse riblets, 67 none. Both groups contain the measured maximum and minimum lengths, hence there is no correlation between size and riblets. The occurrence of more than one riblet is extremely rare, and three riblets were found only in one of the shells of this count. There is no callosity between columellar and parietal (Warmke & Abbott 1961, p. 151) or palatal (Morrison, l. c.) fold in our specimens as in the original ones, and the columellar wall of this region is rather flat. The parietal region shows a thin callus, a glaze of irregular outlines, not set off by colour from the neighbouring surface.

We think that the minute difference between Morrison's and our shells is no more than an intraspecific variation. Holle & Dieneen's studies (1959) of about 6 thousand shells from an area extended over 30 degrees of latitude make the conchological differences even between so well established species as *M. coffeus* and *M. bidentatus* questionable.

Detracia parana can be shortly characterized as follows:

Shell up to 7 mm long, thickest near the middle, comprising about 6-10 whorls: Outline of body whorl convex. Spire dark, body whorl brown, with lighter and darker spiral bands. Up to 3 riblets on inside of outer lip; 1 strong columellar and 1 parietal fold. Tentacles with bulbous bases and light ocular areas. All lateral teeth with 1 conspicuous ectocone, marginal teeth with 2-5 ectocones, 1 mesocone, and 1 distinct endocone. Number of ectocones increases outwards.

As the apex is eroded in all the larger specimens, the determination of the number of whorls is unsatisfactory, as Morrison (1951, p. 20, note 3) indicated.

Detracia globulus (d'Orbigny, 1835) from Ecuador to Panama (Reeve 1878, spec. 43; Morrison 1946, p. 33; Keen 1958, p. 506) is rather similar to *D. parana*, but the extensive columellar fold which reaches the anterior border is different.

Besides *M. coffeus* Lange de Morretes (1949, p. 121-122) mentioned *Melampus edentulus* v. Martens, 1865, and *M. olivula* Moricand, 1838, from Brazil. The former is not Brazilian, the locality "Ilha das Flores" does not refer to the small island in the Bay of Rio de Janeiro, but to Flores in the Sunda Sea. *M. olivula* (Küster 1844, p. 33) looks like a reddish *M. coffeus*. Anyhow, the Museum here has material labeled *M. olivula* from Bahia and Rio; the former is classified by v. Martens. According to Pfeiffer's key (1876, p. 301) *olivula* (n.º 16) has a single parietal fold against 2 in *coffeus* (n.º 24) The anterior one of these folds, i. e., that lying between columellar and posterior parietal fold, is small in our Antillean and Brazilian material. In the shells from Curaçao this fold is generally present, in those from Cananéia not always. Pfeiffer (p. 304) indicated *olivula* also from Colombia.

Shell (Figs. 19-21)

Maximum length 7 mm (*M. coffeus* in our material 15 mm) Proportion of length to breadth 3:2, as in *coffeus*; thickest near the middle (*coffeus* in posterior third) Outline of body whorl convex

(in *coffeus* nearly straight) Apical angle 90-100° (*coffeus* 100-110°)

Spire dark with a somewhat lighter band accompanying apical suture. Body whorl brownish with a lighter band along the posterior suture followed by a darker indistinctly delimited one and farther in front two lighter and two darker alternate bands, the last occupying nearly the whole anterior half of the body whorl. Surface colours translucent on inside of aperture; columellar fold and ribs on inside of outer lip white.

Apex eroded; in one shell (Fig. 21) partially ground away by wear, so that protoconch and surrounding larval shell appear. Long axis of latter forms an angle of 70-80° with that of definitive shell. Spire extends farther forwards than in *coffeus* (Fig. 18). Aperture shorter, hardly 3/4 of total length against more than 4/5 in *coffeus*.

Whole outer lip thin, with 0-3 riblets inside (*coffeus* 10-15 riblets). Columella with strong fold quite in front (in *coffeus* weaker and a little farther behind); parietal wall with one fold (*coffeus* 1-2), sometimes with a thin, glazy callus.

Shell resorption less intense than in *coffeus*, because remnant of internal partition extends beyond body whorl (in *coffeus* not quite to its inner end). Remainder of columella bowl-shaped, in *coffeus* funnel-shaped.

Characters of soft parts

In the following we describe the features that in *D. parana* are different from those in *M. coffeus*.

The tentacles (Fig. 19) are shorter than in *coffeus* (Fig. 17) their bases are bulbous and the eyes surrounded by an unpigmented area. One snail had 6 eyes on the base of one tentacle, of different sizes and position, probably a regenerative multiplication. The other tentacle had one normal eye.

As the columellar resorption goes less far in *parana* than in *coffeus*, the entire body whorl remains separated from the rest, the sac-shaped common visceral mass. Correspondingly the mantle cavity (mc) extends farther inwards in *parana* (Fig. 23) than in *coffeus* (Fig. 22). A hallmark for the free end of the inner wall of the

body whorl is the crumpled mass of conchiolin. Figs. 23 and 22 show this mass (ci) lying much farther behind in *parana* than in *coffeus*, where only part of the body whorl preserves its quality of a whorl. As the kidney (k) accompanies the roof of the pallial cavity, it is longer in *parana* than in *coffeus*. The glandular pads (ac) on roof and floor of the mantle cavity in the region of the pneumostome are smaller than in *coffeus*. Their connective tissue contains the same dark pigment granules as the mantle organ.

The black mantle organ (Fig. 24, mo) forms a funnel-shaped pouch between pallial roof and shell. This flap is 0,7 mm long in a 5,0 mm long snail, against 0,2 mm in a 6,1 mm long animal of *coffeus*. As in *Melampus* the renal pore is separated from the pneumostome by the length of the dorsal glandular cushion.

The central nervous system agrees with that of *M. coffeus* having three ganglia between the pleural ones in the short visceral loop.

The radula (Fig. 25) of a 6 mm long snail is 1,55 mm long and 0,4 mm broad. About 100 straight rows, each 14μ high, are full-developed, several more are still incomplete. The central tooth is broader than in *coffeus*; the denticle of the cusp is rounded, does not end with a point, the lateral recesses are less pronounced, so that a tricuspidate appearance is not suggested; the base is slightly concave, not emarginate. Already the first lateral tooth has a conspicuous ectocone. There is a total of 16 such teeth in the half-row which deserve the name of lateral teeth. The 16 following teeth bear one endocone, the mesocone, and 2-5 ectocones. The number of ectocones increases outwards, while the height of the teeth decreases. The endocone is distinct from its first appearance on the 17th tooth outwards.

The oesophagus is less intensely pigmented than in *coffeus*. The muscle strand between posterior oesophagus and stomach, the posterior digestive gland, and the caecum are the same as in *coffeus*; also the ciliated anal glands (Fig. 23, an) are present.

The ovotestis contains less numerous tubules than that of *coffeus*. The vagina of *parana* is less muscular and runs straight, without the loops between its beginning and forward course; the penis agrees with that of *coffeus*.

The first sign of maturity was seen on July 30, 1962, when the spermoviduct of a 4.5 mm long snail was filled with sperm. On August 7 ovocytes appeared in the hermaphrodite gland besides spermatozoa in the spermoviduct. In January 1963 after the temperature had begun to rise, egg masses were found on the beach together with those of *M. coffeus* in great numbers on leaves. In order to compare the spawn with that of *M. coffeus* many snails were kept in a dish with several layers of leaves, and here they began to lay eggs abundantly too. As in *M. coffeus* the size of the spawns varies according to that of the egg-laying snails. The specific difference between the spawns of *M. coffeus* and *D. parana* concerns only the size of the egg capsules. Masses of about 5-600 eggs were rather numerous, but there were also some larger ones. The capsules were about 110μ long, 75μ broad, the embryos 67μ in diameter and 74μ long.

General remarks

In this chapter we try to evaluate the characters of *Melampus coffeus* and *Detracia parana* for the system of the Ellobiidae and use the terms "primitive" and "advanced" These can be understood only if the ancestors of the ellobiids are defined; their descendants, frequently presumed among primitive Stylommatophora (Thiele 1935, p. 1102 and others), are only loosely connected with them in the present state of knowledge.

The Opisthobranchia, whose euthyneury has been achieved by detorsion, and the Pulmonata, which have retained torsion and re-arranged their nervous system by shortening or by zygotis (see Hubendick 1945, p. 180 ff.), have many important characters in common. Both subclasses are therefore considered to be connected at their roots (Hubendick 1945, p. 172 ff.; Morton 1955b, p. 160 ff.; Fretter & Graham 1962, p. 640)

The coordination is often substituted by the idea of an evolution; the Pulmonata are considered to be descendants of the Acteonidae (Pelseneer 1894, p. 117; Plate 1895, p. 204; Boettger 1955, p. 263) This opinion is supported by the streptoneury, the prosobranch position of the auricle and ventricle, the osphradium, the operculum, and the uninvaginable penis of *Acteon* which unites more

striking prosobranch features than any pulmonate. However the reproductive system of *Acteon* contains advanced characters (Fretter & Graham 1954, p. 582), and its gut, with exception of the position of the anus, is secondarily simplified. The cerebro-pleural ganglia are united, that is a secondary feature. Therefore the idea of a common root of the two euthyneurous subclasses should, in our opinion, not be substituted by a derivation of the pulmonates from the acteonids.

It is certainly desirable to have the root of the Euthyneura among the Prosobranchia Monotocardia, snails with pallial gonoducts and without a right gill, auricle, and kidney. Therefore microphagous or phytophagous lower Mesogastropoda, Rissoacea-Cerithiacea, are held for ancestors of the euthyneurous subclasses (Boettger 1955, p. 253-54; Fretter & Graham 1962, p. 638-40). Acteonidae, Pyramidellidae, and Omalogyridae are families with mixed prosobranch and opisthobranch characters. But most of the living mesogastropods are Taenioglossa, hence with regard to their radulae much more specialized than Cephalaspidea and Basommatophora. Also the stomachs of several ellobiids (Morton 1955b, p. 160), among them also *Melampus cofjeus* and *Detracia parana*, and that of *Siphonaria hispida* (Marcus 1960, p. 119-20) contain pre-mesogastropodan traits. A further difficulty for the idea of mesogastropodan origin of the euthyneurous subclasses, especially for the Lower Carboniferous opisthobranchs, comes from their age, because the oldest, not even quite safe, mesogastropods appear in the Upper Carboniferous. Wenz & Zilch (1959, p. 63), it is true, assigned the Anthracopupinae from the Upper Carboniferous to the Ellobiidae. Anywise we suppose that the discussion of the origin of the Euthyneura will reconsider a diotocardian (Hübendick 1945, p. 201), possibly trochonematacean or trochacean (Pelseneer 1894, p. 125; Fretter & Graham 1954, p. 583; Morton 1955c, p. 146-47) origin.

According to Pelseneer (1894, p. 114) and Morton (1955b, p. 158) the Ellobiidae are the most archaic Pulmonata from which the others descend. "If we were to reconstruct a type embodying the ancestral features needed in any ideal forerunner of both the Basommatophora and the Stylommatophora, it would be an ellobiid that this mollusc would most resemble" (Morton 1955c, p. 146). So a mari-

time and terrestrial group would be the ancestor of Amphibolacea, Siphonariacea (terminology of Wenz & Zilch 1959) and Chiliniidae, the latter with a primitive nervous system. This is quite improbable (Hubendick 1945, p. 159 ff.) The mentioned groups (Thalassophila + Chiliniidae) have a cephalaspidean gill, pallial ridges, pallial caecum, osphradium and an operculum in adult snails as primitive characters absent in the Actophila or Ellobiacea (Ellobiidae + Otinidae). In the latter the hypobranchial gland, gastric caecum, and open seminal groove are archaic characters absent in the former group. The spermatophores, frequent in the Siphonariacea, were considered as a remnant of terrestrial origin, but these are known of *Haminoea*, the Microhedylidae, and *Polycera quadrilineata* among the Opisthobranchia and of the cerithiacean Prosobranchia *Bittium* and *Triphora*, where we found them recently. The best phyletic arrangement of the basommatophores mentioned in this paragraph is the order Archaeopulmonata Morton (1955b, p. 163) and its subdivision into two suborders. These may continue with the names Thalassophila and Actophila, though the terms are rather inadequate.

As many other ellobiids *Melampus coffeus* and *Detracia parana* live in the supratidal fringe, in humid places sheltered from wind and intense light. In such "primitive habitats" (Morton 1955b, p. 130) occur also snails of the genera *Ophicardelus* and *Cassidula*. These resorb the internal walls of the shell in a much lower degree than *Melampus*. Hence the metabolism of the snails of *Melampus* and not an environmental condition must be responsible for this process. In the same biotope lives *Ovatella myosotis*, in other features primitive, which resorbs its shell nearly as far (Meyer 1955, p. 12-13) as *M. coffeus*.

An ancestral trait of *Melampus* is the heterostrophic apex, correlated with another primitive character, the free-swimming larval stage. *Pythia*, anatomically primitive, advances into terrestrial habitats farther than *Melampus*. Its embryos develop within the egg-capsules. Other genera however, whose retention of the embryo would enable them to accompany *Pythia*, remain maritime like *Melampus* which is tied to the neighbourhood of the sea.

Morton (1955b, p. 151) called the division of the foot "adaptive" to progression over a firm rock surface. It may be a pre-re-

quisite for life in this environment, not inhabited by *M. coffeus* and *D. parana*. Our species have such a foot, but use it on hard and soft substrata, wood and mud, as if it was a simple undivided sole.

Our Melampodinae breathe by the lung, i. e., the roof of the pallial cavity, and the mantle edge. As cutaneous respiration occurs also in the Onchidiacea, an early offshoot of the opisthobranchs, it evidently constitutes a heritage from the common root of both subclasses. An archaic character of *Melampus* and *Detracia* is the anal opening within the mantle cavity. The mantle organ of *Melampus* and *Detracia* is topographically comparable to the vascular knob, the "organe creux" in *Theodoxus* (see Fretter & Graham 1962, p. 94, f. 52, ho) considered as a vestigial right gill. Of course we do not think of a homology between so far distant animals.

The central nervous system of the Melampodinae is advanced. The cerebral commissure is short, the pedal one externally suppressed. On the other hand, the cerebro-pedal connectives are longer than in *Leucophytia* (Morton 1955c, f. 31) which Morton (1955b, p. 157) allots to a neighbouring subfamily. Principally the shortness of the visceral loop gives the central nervous system of the Melampodinae its advanced character, and as it was found in the species examined by all authors (Koslowsky 1933, f. 25; Hubendick 1945, p. 141; Morton 1955b, p. 152; Meyer 1955, f. 14; Knipper & Meyer 1956, f. 8), it is generical. The especially high concentration of the visceral ganglia in *M. boholensis* and *M. liberianus* does not occur in *M. bidentatus*, *M. fasciatus*, *M. semisulcatus*, *M. coffeus* and *D. parana*.

Odhner (1925, p. 13) called the jaw of the Melampodinae primitive. Knipper & Meyer (1956, p. 109) found a compact mandible in *Auriculodes gaziensis* whose nervous system and open seminal groove define it as a primitive form. Therefore they consider the jaw of *Melampus* to be secondarily simplified. The same contradictory judgement, simple or reduced, concerns the loose jaw of the Acroloxidae and Ancyliidae (Simroth 1910, p. 296; Hubendick 1962, p. 59); hence the mandible seems to be of little phylogenetic value (Simroth & Hoffmann 1917-1926, p. 869)

According to the weighty opinion of Odhner (1925, p. 12; Powell 1933, p. 148) the radula of the Melampodinae is specialized, because it is heterodont. It is however more polyodont than the

rather homodont radula of *Ellobium* which we, together with Odhner (l. c.) consider to be secondarily simplified and, on the whole, more advanced than that of *Melampus* and *Detracia*.

The stomach of *Melampus coffeus* and *Detracia parana* is advanced, pulmonate, in its predominantly muscular action, but contains archaic features too, viz. the ciliary currents, protostyle with typhlosole and food string, and a posterior caecum behind the entrance of the posterior liver diverticulum.

A mixture of specialized and primitive features exists in the reproductive system. The first preponderate, because the male and female ducts separate proximally. The male copulatory organ is simple. As the four examined species of *Melampus* mentioned in our preceding description are of regular size, not as small as *Otina otis* and *Carychium bidentatum* whose penes may possibly be understood to be secondarily reduced, the simple penis in *Melampus* and *Detracia* must be held for primitive. The ental departure of the bursa in the Melampodinae is advanced, when it is compared with the primitive *Pythia* and *Auriculodes gaziensis* (Knipper & Meyer 1956, f. 12, e). Such a comparison between different members of one family is less risky than that between the genital organs of remotely or doubtfully related systematic groups (Hubendick 1945, p. 127, 131, 171). If, for instance, the comparison is extended to rather primitive prosobranch families (Hydrobiidae, Rissoidae) and opisthobranchs with prosobranch characters (Acteonidae, Pyramidellidae) a proximal bursa would be primitive (Johansson 1954, p. 227 ff.)

Summing up these facts we find a mosaic of primitive and advanced characters in our Melampodinae. The same holds for most species of the Ellobiidae, a "rather unprogressive" family (Morton 1958, p. 163)

Assimineae succinea vina, subsp. nov. (Figs. 26-35, 37-40)

As mentioned above we found a species of *Assimineae* associated with our two Melampodinae at Cananéia (25° 01' S, 47° 50' W). The general aspect of our shells is similar to those of the *A. nitida*-complex (Abbott 1958, p. 231), the typical subspecies of which, *A.*

nitida nitida (Pease, 1865) is Polynesian. Nevertheless Abbott thinks (p. 255) that *nitida* has a very wide distribution as other inhabitants of estuaries and lagoons have, and that even shells determined as *A. modesta* (H. C. Lea, 1847) from the southeast coast of the United States might well be considered a subspecies of *nitida*. A cotype of Pease's material from the Society Islands was described and drawn by Abbott (1949, p. 272, f. 7a-c) It is similar to our shells, but its spire is higher. In *nitida* and its subspecies the length of the spire is slightly less than 2/3 that of the entire shell, hence that of the body whorl a little more than 1/3. In our material the body whorl occupies from slightly less than 2/3 to 6/7. Therefore we think that we cannot include our material in the *A. nitida*-complex.

From Abbott's catalogue of names connected with *Assimineia* (1958, p. 264-275) we learned that no Brazilian representative of the genus was described yet. It is true that Paladilhe's (1877, p. 11) survey of the geographic distribution of *Assimineia* includes "Brésil septentrional" This is evidently due to Frauenfeld (1864, p. 575, 664) who allotted *Paludina atomaria* Philippi to *Assimineia* and gave Pará, northern Brazil, as original locality. But that is really Rapa, also called Opara, Oparo, and Oparu (27° 36' S, 146° 31' W), SE of the Tubuai or Austral Islands (Abbott 1958, p. 265)

We compared our shells with the descriptions of species from the West Indies and considered also *A. eliae* Paladilhe (1875, p. 6; 1877, p. 15) found in Portugal, because Brazil has been colonized from that country, and small amphibious snails are easily transported by man with plants. *A. eliae* is larger (3,25-3,5 mm) than our shells, and the subsutural thread is neither mentioned nor illustrated.

Among the West Indian species *A. succinea* (Pfeiffer, 1840, p. 253) is very near to ours. The original description referring to material from Cuba is not sufficiently detailed for such a statement. But fortunately we received, as mentioned above, 38 shells collected in the mangrove of Bimini, Bahamas (Robertson 1960, p. 22) In agreement with Pfeiffer's diagnosis, the Bahamian shells are up to 2 mm in length, while ours reach 2,9 mm. This is uncommon, as gastropods of southern Brazilian and West Indian range are generally larger in the West Indies, e. g., *Melampus coffeus*.

The following measurements refer to our 6 largest specimens of *succinea* from Bimini: length 1,8-2 mm, width 1,33-1,4, height of aperture 0,94-1,0, body whorl 1,4-1,47 mm or 2/3-4/5 of total length, or as proportion to total length 0,7-0,79:1. The apical angle varies from 50 to 64°. Characters of the material from Bimini which differ from that from Cananéia: number of whorls 5, shells frequently, not always, heavier; apical whorl sometimes filled by secondary calcification; subsutural thread not recognizable in about 1/3 of shells; umbilical thread only sometimes developed.

Some peculiarities of the material from Bimini concerning the tentacular pigment and the radula will be mentioned together with the description of the corresponding parts of the snails from Cananéia. Possibly these differences, if revealed as constant by a more ample West Indian material, together with the larger size of the Brazilian shells would justify future specific separation. Under the present circumstance of the insufficiently known *succinea* from the type locality, Cuba, we prefer to consider the snails from Cananéia to be a subspecies, *succinea vina*, named for our Friends Dr. Victor and Mrs. Nanna Sadovsky.

Shell of *Assiminea succinea vina* (Fig. 26)

In 20 shells selected casually from a great number the length varies from 1,7 to 2,9 mm, the width from 1,4 to 2,0 mm, the height of the aperture from 1,08 to 1,40 mm, the length of the last whorl from 1,45 to 1,9 mm. So the body whorl measures 2/3 to 6/7 of the total length, or as proportion to the latter, 0,7-0,85:1. The apical angle varies from 50 to 67°. As in the material of *succinea* from Bimini also in that from Cananéia the apical whorl is wide; the larval shell comprises one-and-a-half whorls and is 0,35 mm in diameter.

The form of the shell is conical, its 5-6 whorls are moderately convex; their translucent walls are rather thin but firm. The colour is uniformly amber-yellow to light brown.

The impressed suture is smooth, not indented; a short distance below it runs a fine, but distinct and slightly raised spiral thread. Axial growth lines are more or less high. A columellar callus reaches

the deepened umbilicus and sometimes closes it. About 70% of the examined shells have a fine umbilical thread. The columella is strong, sometimes lighter than the rest of the shell. The passage from the inner to the outer lip is evenly rounded or slightly angled.

The operculum is corneous, paucispiral, colourless and smooth, without reinforcement for the attachment of the muscle fibres.

As in the *A. nitida*-complex (Abbott 1958, p. 218, n.º 6) some snails had an albinic shell, though the characteristic black tentacular spot was present.

The average size of the females is larger than that of the males, as in *A. grayana* (Bentham Jutting 1922 a, p. 410; Fretter & Graham 1962, p. 583) As not every male is smaller than every female, Krull's indication (1935, p. 404) of an inexistent sexual dimorphism can be understood, but his quotation of Bentham Jutting's statement repeats a misprint (Bentham Jutting 1922b) There is no relation between sex and a more or less acute apical angle of the shell.

The material of the present description is kept in the Department of Zoology, Faculty of Philosophy, University of São Paulo.

Head, foot and locomotion (Figs. 27-31)

As in other species of the genus the snout is broad and bilobed (ro) The tentacles (t) are short eye stalks, only little longer than broad and slightly broader than high. They are semiglobular; the black eye lies in the centre. Sometimes there are two or three eyes in one tentacle, probably originated as superregenerations (Ankel 1936, p. 199) The outer side of the tentacle bears a horizontal and longish black spot beneath the eye. According to the angle of view the spot assumes different position and shape.

In a dry specimen of *succinea* from Bimini, Bahamas, that was softened, there is a ring-shaped pigmented mark around the ocular peduncle.

The tentacular spot of the specimens from Cananéia is a constant character, while black pigment on the back of the head is not present in all snails. It is especially frequent in the nuchal region, but sometimes extends to the muzzle. The amount of this pigment is not correlated with age or sex.

The eye stalks of males and females have a specially high epidermis containing granular secretion on their underside. The right tentacle bears in both sexes a ciliated knob (na) at its base. On either side of the head a groove flanked by two unciliated ridges extends backwards from the point where the head and upper lip of the foot meet. The left groove ends under the mantle skirt. The right one forms the upper margin of a ciliated band. This band begins in the right suture between the mantle skirt and the back in the male, and farther behind, on the back under the genital aperture, in the female.

Head and foot are white; the skin of the visceral hump and the mantle skirt are often black. Also the skin of the back, that is the floor of the mantle cavity, contains dark pigment.

The foot is broad and short, though it may be lengthened in front and then projects beyond the head. A transverse groove (vv) of the anterior pedal border separates a shorter upper lip, Abbott's suprapodium (1958, p. 219), from a longer and thicker ventral portion (oo). In the middle of the groove opens the ciliated duct of a large anterior pedal gland (vo). The inner end of the duct collecting the secretion of the clustered gland cells is bent ventrally forwards. The sole is ciliated and richly provided with diffuse, subepithelial mucus glands. The hind end of the foot is rounded. The corners of the upper lip are continued into slight folds which run backwards and downwards towards the sole of the foot.

Locomotion begins with a contraction of the hind part of the sole which takes hold farther in front. Then the anterior part is loosed, lengthened and attached to the substratum again. Then the hind end is drawn forwards. Paladilhe (1877, p. 16) observed the similar locomotion of *A. eliae* and compared it with that of a looper caterpillar. The rapid locomotion of this type is especially distinct in the young snails of little weight. Generally one large wave begins behind and produces a deep transverse fold in the anterior region, but inconstant in its distance from the fore end. When the wave has arrived in front, a new wave starts behind. Irregularities occur, but 5 or 6 simultaneous waves (Abbott 1958, p. 219) were not observed. A broad carpet of mucus is produced by the snails when they glide on the surface film. They can, however, not spin due to the absence of a posterior pedal gland.

In their dish the snails creep away from the light, even from a not insulated window

Snails fallen onto the back righten easily When the snails move in water, their shell is supported by the water and stands over the creeping animal. Only its tentacles and the tip of the snout appear in front (Fig. 30) as in Fretter & Graham's figure of *A. grayana* (1962, f. 307 B) In the air the whole neck and anterior part of the foot are extended in front (Fig. 31) as in Ankel's figure (1936, f. 66), and the shell is dragged behind.

Pallial cavity and adjacent organs (Figs. 32, 33)

The pallial cavity is deep; it takes in water as well as air By use of carborundum we could observe an inhalant current entering the cavity over the left suture. An exhalant current runs along the neck and flows down on both sides. In the description of the head two lateral grooves without cilia were mentioned; they are evidently not implied in these currents. Also the areae of pallial and nuchal cilia cannot be coordinated easily with the currents. On the right side a band of ciliated cells extends from the right suture on the floor of the cavity and forwards to the angle between upper and lower pedal lip. As already mentioned, the right groove constitutes its dorsal border along the side of the head. Faecal pellets and mucus threads blackened by carborundum are expelled from the pallial cavity on this band, and the same transport can be assumed for the eggs.

On the left side there are two ciliated streaks, a weaker ventral and a stronger dorsal one. The former begins close behind the free edge of the mantle and does not extend far in front of it, where it is dorsal to the left cephalic groove. Compared with the disposition in exclusively aquatic snails these cilia would be the carriers of large particles fallen onto the floor out of the inhalant stream (Fretter & Graham 1962, p. 90), but this expellent function was not seen in our amphibious species. Opposite to these cilia there are longer ones on the roof of the pallial cavity which may be responsible for the incoming current. They go inwards, towards the left suture reaching osphradium and gill.

The inner part of the mantle cavity where these organs lie can be separated from the foremost part (Figs. 28, 29) Contraction of muscles in the mantle skirt can distend the dorsal pallial blood lacunae in such a manner that they become turgid and touch the floor. The broad band of high goblet cells (μ) with differently staining secretion along the inner side of the anterior mantle edge may be specially important, when only this part of the cavity is exposed to the air, maintaining a respiratory surface moist. The blood in the vessel (ν) running along the free edge of the mantle skirt can be oxygenated even when the greater part of the pallial cavity is closed off from the air. On the left side the marginal vessel bends inwards as osphradial and branchial vessel, so that a supply of oxygenated blood flows to the heart (Fig. 32)

Certainly the respiration is more generalized when the whole roof of the mantle cavity is exposed to water or damp air. The spacious blood lacunae of the roof receive blood from several parallel lacunae (ξ) lying under epithelial folds of the right side. These drain the anterior half of an ample intestinal sinus (σ) whose origin can be traced to the kidney and so functions as an efferent renal vein (Fretter & Graham 1962, f. 147 C, *erv.*)

A true ctenidium is not developed, but far backwards in the left suture the mantle epithelium over the vessel rises into 4 or 5 blunt ciliated projections (α) They are supplied with blood only at their bases. As this organ increases the respiratory surface, it may be considered as an auxiliary gill. In front of the gill there is a well developed osphradium (ω) It is crescent-shaped, open to the left side and lies a little dorsal to the left suture. The crescent is formed by a band of ciliated cells covered from both sides by folds of the mantle epithelium. The fold on the concave side lodges a short ganglion (γ), that on the convex side the vessel that comes from the mantle edge. The osphradium corresponds to that of Thiele's figure of *Pseudocyclotus* (1927, pl. 1, f. 17)

A large hypobranchial gland (η) consisting of high goblet cells whose secretion stains in different tones is developed on the intestinal sinus accompanying its loops. On its right side and in front the area of the hypobranchial gland is connected with that of the glands (μ) on the inner side of the free mantle edge. A rich supply with glands

and the intake of air into the pallial cavity are evidently correlated. In the fundus of the cavity the hypobranchial gland is contiguous with small blue-staining goblet cells (oe) on the floor. Possibly their secretion sticks particles entered with the inhalant current together for elimination.

Cells of this type surround also the slit-shaped ciliated renal aperture (no), which lies behind the gill and has a sphincter. The kidney (k) is a thin-walled sac about 1/3 the length of the snail, hence very large as in *A. grayana* (Fretter & Graham 1962, p. 296, 583). It spreads amongst the viscera surrounding oviduct and bursa copulatrix and reaches the columellar muscle. In *A. grayana* it extends also forwards alongside the rectum and pallial genital duct (ibid., p. 292), but such an extension is not developed in the much smaller *A. succinea vna*. A low vacuolated epithelium lines the major part of the renal sac, only a circular area apposed to the mantle is folded (oc) and has excretory character. The renal blood lacunae of this region communicate with the efferent branchial vein. The discoid central area of the kidney lying near the S-shaped turn of the intestine might perhaps be the bean-shaped glandular organ of Abbott's description (1958, p. 220). A reno-pericardial communication is established between the thin-walled renal sac and the hind end of the pericardium. There is no nephridial gland.

Central nervous system (Fig. 34)

In its general traces the central nervous system agrees with that of *A. grayana* (Krull 1935, p. 424 ff), but some details are different. This refers principally to the subintestinal or left branch of the visceral loop. The left pleural ganglion (wu) is ventrally apposed to but not coalesced with the left cerebral ganglion (cc). The subintestinal ganglion (un) lies under the oesophagus which curves to the right, and so the subintestinal ganglion lies to the right of the middle. Its connexion with the left pleural ganglion is much longer than that between the right pleural and the supra-intestinal ganglion. This topography agrees with Fretter & Graham's description of *A. grayana* (1962, p. 313). A pallial nerve goes out from the left pleural ganglion. A left connexion between this pleural and the supra-intestinal

ganglion could not be found; if it occurs it must be a peripheral left dialyneury. The right zygois (ec) is established by a zygoconnective (Simroth 1899, p. 355) between the subintestinal (un) and the right pleural (eu) ganglion. The abdominal ganglion (Fig. 33, as) lies between the pericardium (c) and the style sac (cr) as in *Pseudocyclotus* (Thiele 1927, p. 141)

The further differences between *A. grayana* (Krull 1935, f. 12) and *A. succinea vina* are minor. The pedal-metapodial connectives are shorter and the cerebral commissure is longer in our species. In both the right cerebro-pleural and the right pleural-supra-intestinal connectives are mere constrictions between the corresponding ganglia. The statoliths are somewhat flattened.

The central nervous system of *Assiminea succinea vina* is approached to Fretter & Graham's fourth group (1962, p. 310, f. 162 B), with exception of a left zygoconnective. The visceral loop remains long, about 1/5 of the length of the animal, and twisted.

Alimentary canal (Figs. 32, 35-36)

The roof of the ingesting gut is rich in goblet cells which continue through the cavity of the buccal bulb and along the oesophagus (o) beyond the level of the nerve ring. The bulbar buccal mass is haemoglobin-red, and its muscles are distinctly striated. The short salivary glands (sa) enter it to the sides of the dorsal food channel. The radular cushions are united in front, V-shaped.

The radula (Fig. 35) contains 60-75 rows. The central or rhachidian tooth has a denticulate cusp. On each side of the large median denticle there are 2, sometimes 3 smaller ones. Below these denticles of the cusp there are two rows of three basal denticles each, whose size decreases from the middle towards the sides. A broad peg-shaped process in the middle of the hind border of the rhachidian tooth fits into a hollow of the following central tooth. The large lateral or intermediate tooth has 2-3 lateral denticles flanking the largest one in the middle. A long basal piece connects the lateral with the inner marginal tooth. As in many other species (Abbott 1958, p. 222) the inner marginal tooth is longest and has the largest denticles. These amount to eight, two inner, one largest and five

outer ones. The outer marginal tooth is wide and spoon-shaped and has 10-12 fine denticles on the cusp. Even more than the denticles of the other teeth those of the outer marginal tooth have very different aspects in different views.

In the *succinea*-material from Bimini (Fig. 36) the rhachidian tooth has four basal denticles on either side, the cusp of the lateral tooth bears 3 pairs of denticles flanking the largest central one, the inner marginal tooth has a total of 6 denticles, 1 inner, 1 largest and 4 outer ones, and the outer marginal tooth has 14-16 denticles.

Behind the separation of the radular sac from the gut the lateral walls of the oesophagus are drawn out into capacious pouches. They communicate broadly with one another and with the lumen of the oesophagus. The wall of these pouches contains mucus-secreting goblet cells, but the term "Vorderdarmdrüse" (Thiele 1927, p. 141) is not appropriate to these dilatations which "presumably provide a certain amount of loose wall and space for accommodation of food during feeding" (Fretter & Graham 1962, p. 207). Behind the lateral pouches the oesophagus bends to the right. The following course is straight and contains longitudinal folds without goblet cells or other glands.

The wide stomach receives the oesophagus on the columellar side. Farther in front lies the opening of the ducts of the yellow digestive gland and a small ciliated evagination, evidently a sorting area. The anterior wall of the stomach bears a voluminous style sac (Fig. 32, cr) containing an ovoid style which is preserved in sections. For about 1/3 to 1/2 of its length the wall of the style sac is in slit-like communication with the intestine which leaves the stomach on the columellar side, between the entrance of the oesophagus and style sac. Opposite to the gastric opening of the style sac the epithelium of the fundus is cuticularized forming a medium-sized gastric shield. In *Assimineia* the occurrence of a style sac in restricted communication with the intestine (Yonge 1932, p. 275) has first been observed by Seshaiya (1932, p. 172) and later by Krull (1935, p. 414) and by Graham (1939, p. 90).

Snails preserved immediately after collection had plant cells and amorphous masses of vegetable substance in their stomach. Probably they feed on decaying animal material too (Abbott 1958, p.

225), and may also consume the big amoebae which live on the rotten leaves. As in other prosobranchs the connective tissue contains many amoebocytes around the stomach. In the digestive gland the secretory dark-staining cells in the angles of the hepatic tubules (Fretter & Graham 1962, p. 229) occur with great regularity.

The intestine (Fig. 32, i) runs forwards on the columellar side, and then curves back around the style sac. The intestinal wall apposed to the style sac bears a typhlosole. This ends in the following forward section which loops around the kidney. Already in this section the excrements appear as single pellets separated from one another. Then the intestine describes some more loops in the pallial roof and opens on the right side (ar) near the anterior border of the mantle skirt (mr). The position of the copulatory organ conditions a certain difference in the arrangement of these loops in males and females, but a straight course in the male and a strong loop in the female as in *A. grayana* (Krull 1935, p. 416) could not be confirmed. In the mantle skirt the intestine courses within the previously mentioned ample blood sinus.

Reproductive organs (Figs. 37-39)

The testis lies in the second whorl of the visceral mass behind the digestive gland. It produces only one type of sperms with lancet-shaped heads. The male duct descends winding on the columellar (cn) side. The inner section is thin-walled and narrow, the outer, sperm-storing part, wider and more muscular. Its narrow end piece (ev) enters the anterior half of the prostate (Fig. 38) which is a longish, curved organ in the penultimate whorl with lobular outer and smooth inner surface. Its high epithelium whose nuclei are partly basal and in part apical is glandular as in *A. grayana* (Fretter & Graham 1962, p. 345), containing principally red-staining spherules of secretion. By their secretory activity the prostatic cells may become so high that they nearly fill up the lumen of the organ. We have not seen any communication of the prostate with the mantle cavity. The outlet of the male duct (eo) is quite near to its entrance, while it lies at the anterior end of the prostate in *A. grayana* (Krull 1935, f. 15).

The ciliated efferent duct, whose wall is muscular, runs forwards under the skin of the back without communication with the overly-

ing pallial cavity, and enters the big penis with a loop (Fig. 37) The dorso-ventrally flattened male copulatory organ arises in the middle of the neck (Fig. 28), bends first backwards on the left and then forwards on the right side. It is smooth, 1,4 mm long, 0,18 mm broad, and 0,14 mm high. Beside the ejaculatory duct a thick nerve covered with a continuous layer of cells and nearly without ramifications courses to the tip of the penis. Generally the outer penial epithelium is about 13μ high; its nuclei are intra-epithelial. Once we found a cushion of 50μ high nonciliate epithelial cells in a 0,14 mm long, 0,12 mm broad area on the underside of the penis near the tip.

The ovary has a similar position as the testis on the columellar side of the second visceral whorl. It lies embedded in the digestive gland. The ovarian oviduct (oi) whose epithelium continues that of the ovary runs forward on the columellar side and is longer and wider than the following short ciliated renal oviduct (rn) The latter gives off a thin gonopericardial duct (uc) to the inner end of the pericardium (c)

The inner pallial oviduct forms a circle. It begins with an outwards directed part, then bends inwards and finally passes forwards to the albumen gland (a) Its first section has valvular folds, the next receives the duct of the receptaculum seminis (cs) and contains sperm in its lumen which evidently is the site of fertilization (r) Beside the entrance of the oviduct into the albumen gland the latter is connected with the bursa copulatrix (b) by a rather long canal.

The albumen gland occupies about half the length of the glandular pallial oviduct. Its high ciliated epithelium and the surrounding circular musculayer is pierced by the subepithelial gland cells which form a layer thrice as high as the epithelium. The outer half of the glandular oviduct is occupied by the shell glands (sn) and a terminal section without glands. Also the clusters of shell glands lie peripheral to the epithelium and its muscles. These are thicker in the terminal gland-less portion of the oviduct. The genital aperture (y) lies dorsal to the right suture and a little farther inwards than the anus.

Development (Fig. 40)

In January 1963 eggs were found at Cananéia on rotten leaves in the zone flooded at high spring tides, and with onshore winds also at mean tides. From July to December 1962 snails were kept in the laboratory in an inclined dish with moist earth, dead leaves and shell fragments on the higher, and brackish water on the lower side. Decaying leaves and fresh lettuce were given as food. In the beginning of spring, in October, four months after installation of the vivarium, they laid eggs. These were single and attached to leaves, not "lost" during creeping (Sander 1950, p. 148) nor clustered together with faeces in up to 5 mm long conglomerates (id. 1952, f. 1) as in *A. grayana*. Sometimes a faecal pellet stuck to the capsules of our species, but generally the thin-walled, conchinous capsule became only gradually incrustated with bacteria, algae and soil particles. A sticky belt fastens the eggs to the substratum, but they fall off easily. The capsules measure 0,38-0,4 x 0,32-0,34 mm. Newly laid eggs are 0,18 mm in diameter.

The development is direct, non-pelagic, and lasts 4-5 weeks at 20°-23°C. The embryo shows little movement within its capsule, probably because the ciliated lobes of the veliger are small and transitory. The snails hatch with a shell 0,35-0,36 mm long (antero-posterior axis) and 0,3 mm high (dorso-ventral axis); it has one-and-a-half whorls. Measurements and whorls correspond to those of the protoconch in adult shells collected in their natural environment. The surface of the larval shell is a little rough. The heart of newly hatched animals beats 27 times per minute at 20°C. The black spot on the outer side of the tentacle, characteristic of *A. succinea vina*, appears in 0,5 mm long snails.

The direct development of our species agrees with that of many other inhabitants of brackish water. It contrasts, however, with the pelagic development of *A. grayana* (Sander 1950). Eggs of that species found in terrestrial environment were brought into freshwater aquaria where many veligers hatched. Their colour marks would make it possible to identify them in the plankton, but Sander did not try that yet. According to Abbott (1958, p. 225) free-swimming larvae have been caught in plankton nets. This evidently refers

to Philippine species. For *A. grayana* Sander (1950, p. 149) leaves the question open whether snails instead of larvae would have come forth from the eggs, if these had remained in the terrestrial environment. Also Fretter & Graham (1962, p. 401) do not consider a pelagic development of *A. grayana* as natural. As however large individual egg capsules with direct development and small ones with pelagic larvae in one and the same genus occur in *Lacuna pallidula* and *L. vincta* (Hertling 1928) and in *Littorina obtusata* and *L. littorea*, we suppose that the small egg capsules (0,2 mm) of *A. grayana* normally give rise to free-swimming veligers.

Nematoda

Fusiform juvenile nematodes, about 0,35 mm in length and 15μ in diameter, occur frequently between the mantle and the shell, mainly in the region of the penultimate whorl, where they often form coherent layers. The worms belong to the Order Rhabditoidea. They are neither encysted nor ensheathed but free, straight or somewhat bent. Their cuticle has a very fine transverse and a little coarser longitudinal striation; the hind end is pointed. The pigment of the mantle epithelium is pressed to the sides by the worms which flatten the cells. Between the nematodes the epithelium remains high and here the pigment accumulates, so that the shape of the worm appears as a light area with black borders. The nematodes are probably "Dauerlarven" (Mengert 1953, p. 316) which do not eat and therefore do no harm to the snails. So they are inquilines, not parasites.

The scarce literature dealing with the occurrence of nematodes in snails and slugs summarized by Mengert (1953) and Turner & Pini (1960) shows that mainly the foot, gut, body cavity, and exceptionally the pulmonary cavity are inhabited. A habitat as the present one, between the shell and the mantle epithelium, does not seem to have been reported yet.

Littoridina Souleyet, 1852

The genus comprises Hydrobiidae occurring in South and Central America, Florida and Texas, which have penetrated from the sea into

brackish and fresh water. We recently described (Marcus 1963a) a subspecies of *L. australis* (d'Orbigny, 1835) from marine and brackish localities on the coast of São Paulo. Now we found another species in slightly brackish and fresh water. While veligers hatched from the small eggs of our coastal form, the development of the second is non-pelagic as in *Assimineia succinea vina*.

Littoridina miaulis, spec. nov. (Figs. 41-44)

Shell (Fig. 41) and operculum

The length of adult shells is generally 3-4 mm; the maximum found was 4,7 mm. The breadth which reaches 2,0 mm is a little less than half the length in adult shells or distinctly less in the largest ones. In smaller, 2,2 mm long shells the breadth is a little more than half (e. g., 1,15 mm) the length. In a group containing equal numbers of males and females the larger shells of females are more numerous than those of males. The largest female was 4,7 mm long, 2,0 mm broad; the largest male 4,0 mm long, 1,9 mm broad.

The shape of the shell is longish conical, but varies widely also among adults. The apical angle ranges from 30-50°. There is no relation between sex and the more or less acute apical angle. The proportion of length to breadth varies from 2,05:1 to 2,35:1 in females, and from 1,71:1 to 2,25:1 in males. Smaller animals are a little broader than larger ones, because the whorls increase more in length than in width.

Alive the shells are olivaceous; dry empty shells are transparent horny yellow to light brown, those containing the animal are pitch-brown.

There are 6-7 whorls, the first of which is quite flat. In correspondence with the above-mentioned different development of *L. australis nana* (*a n*) and *L. miaulis* (*m*) the apices have different measurements. The innermost semicircle is 0,06 (*a n*) and 0,12 mm (*m*), the diameter of the first whorl 0,12 (*a n*) and 0,18 mm (*m*). The one-and-a-half whorls which are formed within the egg capsule are finely granulated, not filled with secondary calcification in contrast with *L. australis nana*, but as thin and delicate as the following ones which generally have holes when they are dead.

The body whorl has about $3/5$ of the total length. The suture is distinct; the periphery of the whorls is evenly arched or more or less straight. In some shells the body whorl is nearly straight behind and angulate in front. Axial growth lines are visible; the periostracum is shining. The height of the aperture varies from 40,8% to 44% of the total length. The peristome is sharply angulated behind, continuous in front, the inner lip is slightly thickened, the outer lip thin and fragile; an umbilical chink may be present or not.

The paucispiral, colourless, thin and hyaline operculum is apertural in shape and nearly so in size. When the snail retracts completely, the soft rim of the operculum is bent and closes the aperture tightly. The nucleus lies in the anterior third of the operculum, a little nearer to its columellar margin. The retractor fibres insert on a ridge of the inner side of the operculum which surrounds the nucleus and extends backwards approximately in the mid-line of the operculum.

Most of the shells are beset with eggs of the own species and overgrown with gibbous crusts of Cyanophyceae. These algae grow only on the surface and do not erode the shell. Large colonies of a *Zoothamnium*-spec. grow on the shells.

Occurrence

We found the snails thriving in the slightly brackish stagnant water of the artificial mangrove swamp in the garden of the Department of Botany of the Faculty of Philosophy, University São Paulo. The "swamp" is installed in a cement basin of about 12 sq. m., open to sun and rain, and receives sea water from time to time. Soil and plants come from Cubatão, about 15 km landwards from the Bay of Santos. The chief vegetation of the alluvial plain north of Santos is mangrove; the salinity of its ponds, creeks and rivers varies widely in correspondence with tides and rainfalls. In March 1964 Dr. Walter Narchi found *L. miaulis* also in a freshwater aquarium.

The material on which the description is based is kept in the Department of Zoology, Faculty of Philosophy, University of São Paulo.

Morphology of soft parts (Figs. 42-44)

For the species of *Hydrobia* the pigmentation of the soft parts is systematically important (Seifert 1935). In *Littoridina australis nana* and *L. miaulis* these differences are less accentuated. Peculiar colour marks of the new species are a quite black snout with white labial discs; an often black mantle epithelium under the shell, especially in the apical region; and a brick-red testis. The absence of pigment in the osphradium and the ctenidium is a specific contrast with *L. a. nana*. The roof of the mantle cavity between the branchial leaflets may contain some dark pigment.

The snout is thick, not as long as that of *L. australis nana*, and therefore only the muzzle and the tentacles are seen during locomotion. The dark tentacles have white tips and bases as in *L. a. nana*, and the right and left one have a different equipment with cilia. The right tentacle has a dorsal and a ventral pigment-free mid-line with cilia, the left one further 12-18 ciliated stripes vertical to the axis of the tentacle, strong on the outer and weaker on the inner side. Transverse lines with cilia, or scattered tufts occur on the muzzle. The inhalant and exhalant currents are produced by a broad band of ciliated cells under the left and right tentacle respectively. Both bands continue onto the floor of the pallial cavity, but do not attain the fundus. The osphradium is covered by an epithelial fold as in *L. australis nana*. The number of gill leaflets is 29-33 in males, 33-42 in females. Following a suggestion of Hubendick (1955, p. 322-323) we compared the gills of *L. miaulis* with those of *L. australis nana*. Examining the leaflets in the central region of the ctenidium in both species we did not find any specific difference in their shape. There is a wide intraspecific variation of the top angle of the leaflets and of their straight or folded free side. This variation is evidently due to contraction and to the pressure of underlying organs in preserved specimens.

The central nervous system (Fig. 43) is similar to that of *Littoridina australis nana*. The cerebral ganglia (ce) are nearly as voluminous as the pedal ganglia (ea). The tentacular nerve (ne) forms a secondary ganglion, as in the mentioned *Littoridina*, in *Hydrobia ulvae* (Krull 1935, f. 10) and in *Bythinella scholtzi*, Krull's (p. 424)

Paludestrina steini. The cerebral commissure is shorter than half the breadth of one of the ganglia. The cerebro-buccal connectives are rather short, the buccal commissure (cv) is longer than the diameter of a buccal ganglion. Propodial (od) and metapodial (me) ganglia are developed, and the latter are connected by a commissure as in other hydrobiids. Both pleural ganglia are near to the corresponding cerebral ganglia, though the right one (eu) is a little less apposed to the right cerebral ganglion than the left one (wu) to the left. In *Littoridina australis nana* we did not find (Marcus 1963) the subintestinal ganglion (un) so close to the left pleural ganglion as in the present species. The connexion of the right pleural to the supra-intestinal ganglion is long, like in *Hydrobia ulvae* (Krull, l. c.) There are two ganglia in the visceral loop (vs) which lie at the fundus of the mantle cavity. The ganglion of the supra-intestinal branch lies farther backwards than that of the subintestinal branch. To this last ganglion a third visceral ganglion is apposed. The penial nerve (ie) originates from the right pleuro-pedal connective. A left zygosis is developed between a secondary ganglion of the osphradio-branchial nerve and the left pallial nerve.

In contrast to *Assimineia succinea vina* with a right zygoconnective (Fig. 34, ec) the central nervous system of *Littoridina* agrees with that of the lower Rissoacea (Fretter & Graham 1962, p. 310)

The radula (Fig. 44) has about 50 rows. The rhachidian tooth has a very broad base, a broadly curved low process in the middle of the base, and on the edge 3-5 denticles on either side of the median cusp. There are 1-2 denticles basally to the edge. The lateral tooth agrees with that of *L. australis nana* in the laterally elongated base, the edge with 2 medial, one larger, and 4 lateral denticles, and a blunt process projecting basally to the edge. Also the serrate marginal teeth are very similar; about 25 denticles occur on the inner and numerous minute ones on the outer marginal tooth.

The inner reproductive organs of male and female agree with those of *L. australis nana*, but the male copulatory organ (Fig. 42) is different. The brown lappet on the concave side, characteristic of *australis*, is constantly absent in *miaulis*. The penial tip is more complicated in *miaulis*. It is densely ciliated and bears a small papilla on the convex and a broad hump on the concave side. The ejaculatory

duct which passes winding through the shaft of the penis opens on the papilla. The shaft bears 1-5 round warts on the convex side; in 40% of the snails there was one wart, in 48% two, in 8% three, and in 4% five of them. The connective tissue of the warts contains pigment, and so do vesicular cells beside the male duct. The epithelial pigment is scattered and leaves the nuclei free.

Systematic discussion of *Littoridina miaulis*

As Hubendick's figures of the radulae of *Littoridina* species from Lake Titicaca (1955, f. 68-78) show, the range of variation is wide in this genus. Moreover different degrees of wear as well as the angle of view used for the drawing may produce different aspects. Therefore we do not stress the diversities between the radulae of *miaulis* and *australis nana*. In both the rhachidian tooth is broader behind than in *australis australis* (Thiele 1928, f. 27) Larger shells and eggs, and colourless osphradium and ctenidium are characters of *miaulis* which differ from *australis nana*. The most striking peculiarity of *miaulis* is the tip of the male copulatory organ with its small papilla and the large hump on its concave side (Fig. 42) *L. australis* is specifically characterized by the brown lappet on the concave side of the penial shaft (Marcus 1963a, f. 46), absent in *miaulis*.

In our copy of Ihering's paper on *Lithoglyphus* (1885) the drawings of the verge of *Potamolithus lapidum* (d'Orbigny, 1835) are wanting, but Pilsbry (1911, p. 566, f. 13) has copied them. The tip of the organ, "glans", in Ihering's terminology, surrounded by a "prepuce" is similar in *lapidum* and *miaulis*, but the former has no adhesive warts. The roundish, strong-walled shell with thick periostracum of *lapidum* shows that the species belongs to *Potamolithus*, while *miaulis* has a longish conical shell with thin walls and thin periostracum like the other species of *Littoridina*.

From southern Brazil also *L. piscium* (d'Orbigny 1835, p. 30) has been reported (Ihering 1895, p. 128), but need not be discussed, as penis and basal denticles of the rhachidian tooth (ibid., p. 123) differ from those in *miaulis*.

Pilsbry's excellent illustrations of the shells of *Littoridina* (1911) were compared with those of the present species.

Behaviour and development

The snails feed on detritus and lettuce; they creep with exploratory movements of the muzzle. The locomotion may be gliding or stepping.

When the snails from slightly brackish water were brought into sea water of 31-34 per mill, they continued alive without signs of difficulty, while they became rigid rapidly in fresh water taken from an old aquarium with *Elodea*. In August 1962 we found the snails laying eggs in the artificial swamp, and they continued to do so in our dishes with water of about 10 per mill salinity. During the time from August to the middle of November the temperature was uncommonly low, but the reproduction was not interrupted in our aquaria. In the last week of November the temperature rose abruptly. The snails tolerated 41°C. for some hours in the laboratory dishes with black mud exposed to the sun and are also resistant against foul water and becoming dry for some hours.

In the artificial swamp outdoors the animals were laying eggs from August to October. In the second half of November, after a period of much rain, the snails lived in nearly fresh water, but were not as numerous as before. At that time 180 examined specimens did not bear any eggs. Brought into the brackish water in the laboratory their reproductive activity started again in the course of 48 hours (Marcus 1963b, p. 47). Speaking about the species of *Hydrobia* that tolerate oligohaline brackish water, but not freshwater, Fretter & Graham (1962, p. 296) say: "There may be some other factor, perhaps concerned with reproduction, which prevents their final entry to freshwater" Moore (1958, p. 44) mentions species of *Littorina* and *Nucella* whose eggs do not survive in subnormal salinities tolerated by the adult snails.

Though the population of *L. mialuis* in the mangrove endures considerable changes of salinity, it evidently does not thrive in quite fresh water. The species *mialuis*, however, is not restricted to brackish water; the snails obtained in a freshwater aquarium in March 1964 were healthy and bore eggs with embryos.

The proportion of 2 females to 1 male corresponds to the most common type of numerical relations between the sexes in prosobranchs

(Ankel 1936, p. 150) Also in *Potamolithus lapidum* (d'Orb.) and *Littoridina tenuipes* Pilsbry more females than males were recorded by Ihering (1855, p. 98) and Pilsbry (1952, p. 52) respectively

The copula is accomplished head to head as in *L. australis nana*, or side by side. In both positions the male sits on the female and curves its much lengthened penis into the mantle cavity of its mate. Though not as often as in *Littorina* (Ankel 1936, p. 158-159) males try to join with other males; possibly they recognize females only by trial and error

The eggs are fastened principally to the shells and opercula of living snails: males or females of their own species as in *Hydrobia ulvae* (Henking 1894, p. 91-92) and *Littoridina australis nana*. They are also found on dead shells, stones, leaves, algae and roots. The capsules of *L. a. nana* are 0,12 mm in greatest diameter, and in *L. miaulis* 0,35-0,38 mm. At first the single egg of the latter has a diameter of 0,18 mm, and the embryo grows gradually to the dimensions of the capsule with a length of 0,36 mm and a breadth of 0,3 mm. The same measurements were found in newly hatched snails. The stage of the veliger is passed through within the capsule. The small velar lobes and a slow rotation can be seen through the wall of the capsule which is not incrustated. The development takes about 3 weeks at 22-25°C., against 5 days for the veliger of *L. australis nana*.

One hatching snail, 0,32 mm long, had tentacles of 70 μ , in another of 0,4 mm the tentacles were 0,15 mm, and when the shell is 0,6 mm long, the tentacles are 0,6 mm in length. The snail freed from the capsule has an osphradium but no ctenidium. Seven epithelial projections, 15 μ in length, appeared in the roof of the mantle cavity over the vein, when the snails were 0,4 mm long. When the snails had grown to 0,6 mm, the projections were 60 μ long.

Littoridina charruana (d'Orbigny, 1840) (Figs. 45-46)

The literature about *Littoridina* indicates the River Cubatão near Santos (Pilsbry 1911, p. 558) as occurrence of *L. charruana* (d'Orbigny 1840, p. 384; Ihering 1895, p. 123) Further localities of this species are: Iguape, State of São Paulo (24° 40' S, 47° 34' W), Rio Grande do Sul, and north of Montevideo (original locality)

We received eight snails from the mouth of the River Tramandai, an outlet of one of the numerous lagoons along the sea coast of Rio Grande do Sul. Lic. Jorge Petersen who collected them observed that the salinity of this biotope varies from 34,5 to 4,5, exceptionally even 1,5 per mill, within 10 hours, in correspondence with the tides and winds blowing from north or south.

The shells are up to 5,5 mm long, 3-3,3 mm broad and have 7 rather convex whorls. The proportion of length to breadth varies from 1,46-1,71:1. The colour is brown with a white and thickened inner lip and porcellaneous inside of the body whorl. The operculum is light yellow.

The radula (Fig. 45) contains about 50 rows. The rhachidian tooth is not very broad behind, and its tongue-shaped process is not prominent. The edge bears 4-6 denticles on either side of the central one. There is one stout, so-called basal denticle under the edge on either side. The base of the lateral or intermediate tooth is long. The slender cusp of the edge is flanked by one medial and 4-6 lateral smaller denticles. Basally to the edge projects a broad conical process. The two marginal teeth have serrate edges; the inner tooth bears about 25 coarse denticles, the outer one a great number of fine ones, of which those near the tip are a little larger.

The penis (Fig. 46) bears a great number of warts on the convex side. We saw 12-16 of them, Ihering (1895, p. 123) 11-12 in snails from Iguape. Some of these warts sit on the contour, others dorsal and ventral to it. One wart lies on the concave side in the bend between the broad basal and the narrower terminal part of the organ. The ejaculatory duct opens on a pointed papilla.

In June 1963 masses of *Eichhornia* and *Salvinia* drifted from fresh water near Iguape about 70 km along the lagoon called "mar pequeno" into the brackish water of Cananéia. Among their roots great numbers of *L. charruana* up to 6 mm were found alive. The species has veligers (Marcus 1963b, p. 47). In oligohaline brackish water *L. charruana* was still reproducing in May 1964.

Resumo

No litoral de São Paulo, *Melampus coffeus* (L.) vive acima da linha das marés regulares, debaixo de pedras e pedaços de madeira,

entre folhas caídas no solo, assim como sobre as raízes e troncos e debaixo da casca das árvores dos manguezais. Os caracóis necessitam de humidade e de proteção contra luz intensa. Suportam submersão por preamar alto, respirando dentro d'água. Alimentam-se de material vegetal mole, no cativo também de alface. As voltas internas da concha são reabsorvidas, sendo o cálcio armazenado no tecido conjuntivo. A locomoção realiza-se por músculos e por enchimento e esvaziamento de lacunas sanguíneas do pé. O caracol retraído pode respirar por meio do bordo do manto cuja veia pulsa. Caído no dorso, o animal recupera a posição normal, desde que os lóbulos orais atinjam o solo. O manto forma uma cavidade anterior que abriga, na retração, cabeça e parte anterior do pé. O ânus situa-se dentro da cavidade palial, mas, um sulco protegido por dobras conduz as fezes para fora, onde são evacuadas atrás da abertura respiratória. O sistema nervoso é concentrado; a alça visceral é curta e contém 3 gânglios, além dos pleurais. A rádula permite distinguir entre dentes laterais e marginais. O estômago muito musculoso conserva ainda glândula intestinal posterior, pequeno ceco atrás da entrada desta, sulcos ciliados, protóstilo e tiflosole. Os músculos gástricos e hepáticos são, principalmente, responsáveis pela movimentação do material ingerido. As vias masculina e feminina separam-se internamente. Aí encontra-se também a bôlsa copuladora. O ducto eferente termina com pequena papila que sai, por eversão, da comprida bainha penial. *M. coffeus* tem pequenos ovos em grande número e véliger de natação livre.

Detracia parana Morrison ocorre juntamente com *coffeus*. É menor que este, até 7 mm, tem voltas posteriores (espira) mais altas, grossura máxima no meio da concha, até 3 costelas no lado interno do lábio externo, 1 forte dobra bem na frente da columela e 1 parietal. O contôrno da volta anterior é convexo. Os tentáculos são mais curtos que em *coffeus*, as suas bases são bulbosas e os olhos circundados por áreas claras. O órgão do manto é muito mais extenso que em *coffeus*. As rádulas são diferentes (Figs. 9, 25) Na vagina que é menos musculosa faltam as alças entre o trecho inicial e o dirigido para a frente. Oviposturas e larvas correspondem às de *coffeus*.

Consideramos Pulmonata e Opisthobranchia como 2 subclasses de origem comum dos Prosobranchia. As Ellobiidae e Otinidae devem ser justapostas aos Thalassophila e às Chilinidae formando, juntamente com êstes, a ordem Archaeopulmonata. Nesta base, as Melampodinae apresentam-se como reunindo caracteres primitivos e especializados.

Assimineia succinea vina, subsp. nov., vive associada às Melampodinae mencionadas. *A. succinea* (Pfeiffer, 1840) da localidade original, Cuba, é menor. Material das Ilhas Bahamas determinado por R. T. Abbott como *succinea* e visto por nós apresenta diferenças na concha, radula e no pigmento do tentáculo, sistematicamente importante em *Assimineia*. Os animais respiram água e ar e possuem pequena brânquia quase no fundo da cavidade do manto e lacunas sanguíneas no teto desta. Pela turgescência das lacunas a parte posterior, maior, pode ser separada da pequena, anterior. O sistema nervoso é concentrado. O estômago possui grande estilo cristalino. O penis é liso; receptáculo seminal e bursa copulatrix situam-se muito para dentro, no início do oviduto palial. O rim é grande como em várias espécies da água salôbra. O desenvolvimento é direto, sem véliger livre. Nemátodes jovens, da Ordem Rhabditoidea, são freqüentes entre concha e epitélio do manto.

Littoridina miaulis, sp. nov., foi encontrada nágua fracamente salôbra do manguesal artificial do Departamento de Botânica da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo e num aquário de água doce. O manguesal tinha sido instalado com plantas e terra de Cubatão, ao norte de Santos. A espécie caracteriza-se, principalmente, pelo órgão copulador masculino. A fase larval é percorrida no casulo ovular. Dêste sai o gastrópodo definitivo, cuja brânquia, porém, se desenvolve somente depois da eclosão. *L. charruana* (d'Orb.) foi coletada pelo Lic. Jorge Petersen no "rio" Tramandaí (30° S), à saída de uma das lagoas na costa do Rio Grande do Sul. Aí, o colecionador observou variação da salinidade de 34,5 a 4,5 por mil, dentro de 10 horas. De massas flutuantes, compostas por *Eichhornia* e *Salvinia*, vindas da região de Iguape, obtivemos muitos exemplares vivos de *L. charruana*. Esta espécie tem velígeres.

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Explanation of letters

a — albumen gland	iz — oral glands
ac — pneumostomatal glands	j — jaw
ai — parapodial commissure	k — kidney
an — anal glands	m — mouth
ao — statocyst	mc — pallial cavity
ar — anus or opening of anal groove	me — metapodial ganglion
as — abdominal ganglion	mi — male aperture
au — auxiliary gill	mn — mantle vein
b — bursa copulatrix	mo — mantle organ
c — pericardium	mr — mantle edge
ca — caecum	mu — glands of mantle skirt
cc — cerebro-pedal connective	mv — mantle groove
ce — cerebral ganglion	na — ciliated knob of right tentacle
ci — mass of conchiolin	ne — tentacle nerve
cn — columellar muscle	ni — labial nerve
cr — style sac	no — renal aperture
cs — receptaculum seminis	ns — static nerve
cv — buccal commissure	nu — cerebro-pleural connective
d — penial papilla	o — oesophagus
e — efferent duct	oa — minute pedal blood lacunae
ea — pedal ganglion	oc — folded part of kidney
ec — right zygoconnective	od — propodial ganglion
ei — eye	oe — goblet cells of neck
en — end of suture	oi — oviduct
eo — male duct leaving prostate	on — optic nerve
es — stomach	oo — forefoot
eu — right pleural ganglion	or — oesophageal atrium
ev — male duct entering prostate	os — osphradium
f — food string	oz — osphradial ganglion
g — mucus gland	p — penis sheath
h — hypobranchial gland	q — second pedal groove
he — inner section of hermaphrodite duct	qi — preputium
i — intestine	r — fertilization chamber
ie — penial nerve	ra — radula
io — hindfoot	

re — penial retractor	uu — buccal bulb
ri — ridge in front of pneumostome	v — vagina, oviduct
rm — circular muscle layer	va — aperture of anterior liver
rn — renal oviduct	ve — anal groove
ro — oral lappets	vi — ventricle
s — spermooviduct	vo — anterior pedal gland
sa — salivary glands	vs — visceral loop and ganglia
se — septum	vv — anterior pedal groove
si — blood sinus	w — gonad
sn — shell glands	wu — left pleural ganglion
so — sole glands	x — aperture of posterior liver
sr — suture, in Fig. 6 posterior lappet	xi — parallel lacunae
su — subcerebral commissure	xo — lateral lobe
t — tentacle	y — female aperture
u — intestinal groove	z — outer section of hermaphrodite duct
uc — gonopericardial duct	za — anterior digestive gland
ui — muscular strand	zi — parietal ganglion
un — subintestinal ganglion	zo — posterior digestive gland
us — pneumostome	zr — supra-intestinal ganglion

PLATES

PLATE 1

Melampus coffeus

- Fig. 1 — Apex of 3 mm long shell.
Fig. 2 — Combined sagittal section of head and foot.
Fig. 3 — Shell 10 mm in length; half of body whorl thought to
be removed.
Fig. 4 — Transverse section of same; removed part stippled.
Fig. 5 — Five phases of locomotion.

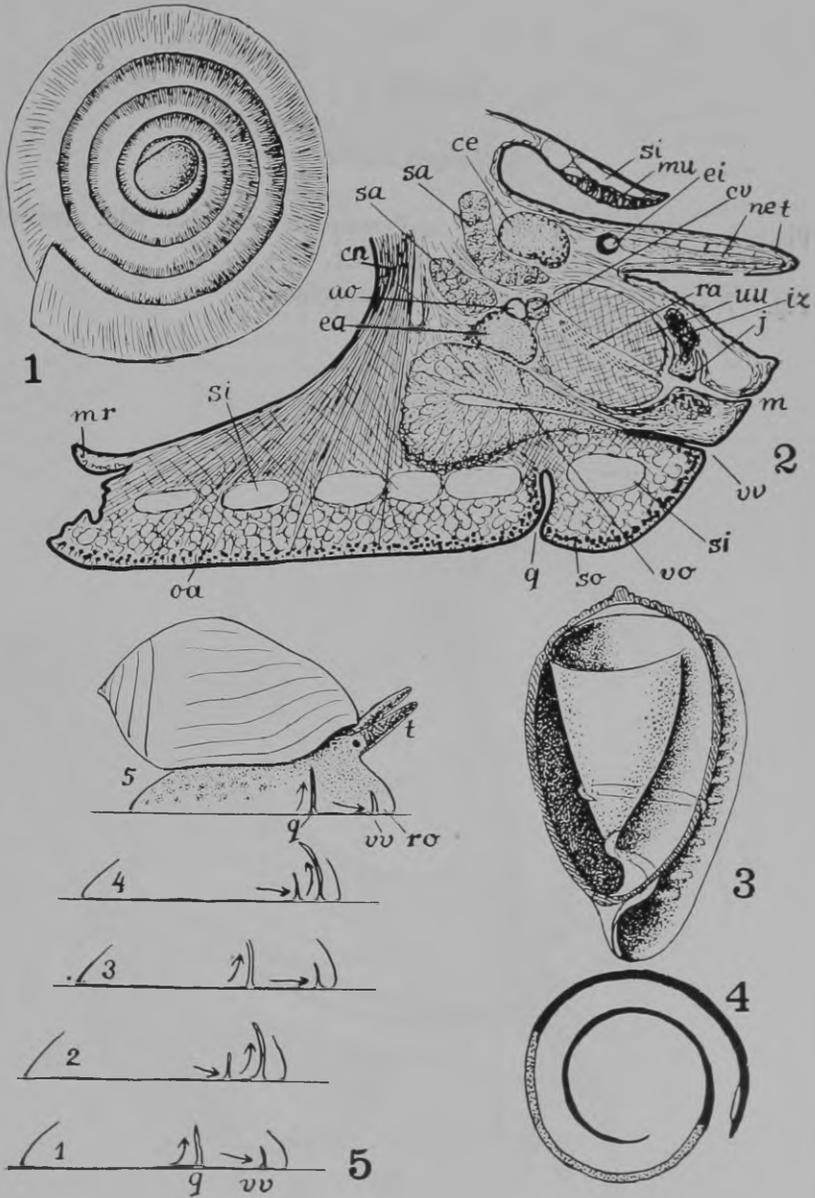


PLATE 2

Melampus coffeus

- Fig. 6 — Right side view of snail removed from shell with mantle partly unrolled; vessels black.
- Fig. 7 — Diagram of central nervous system.

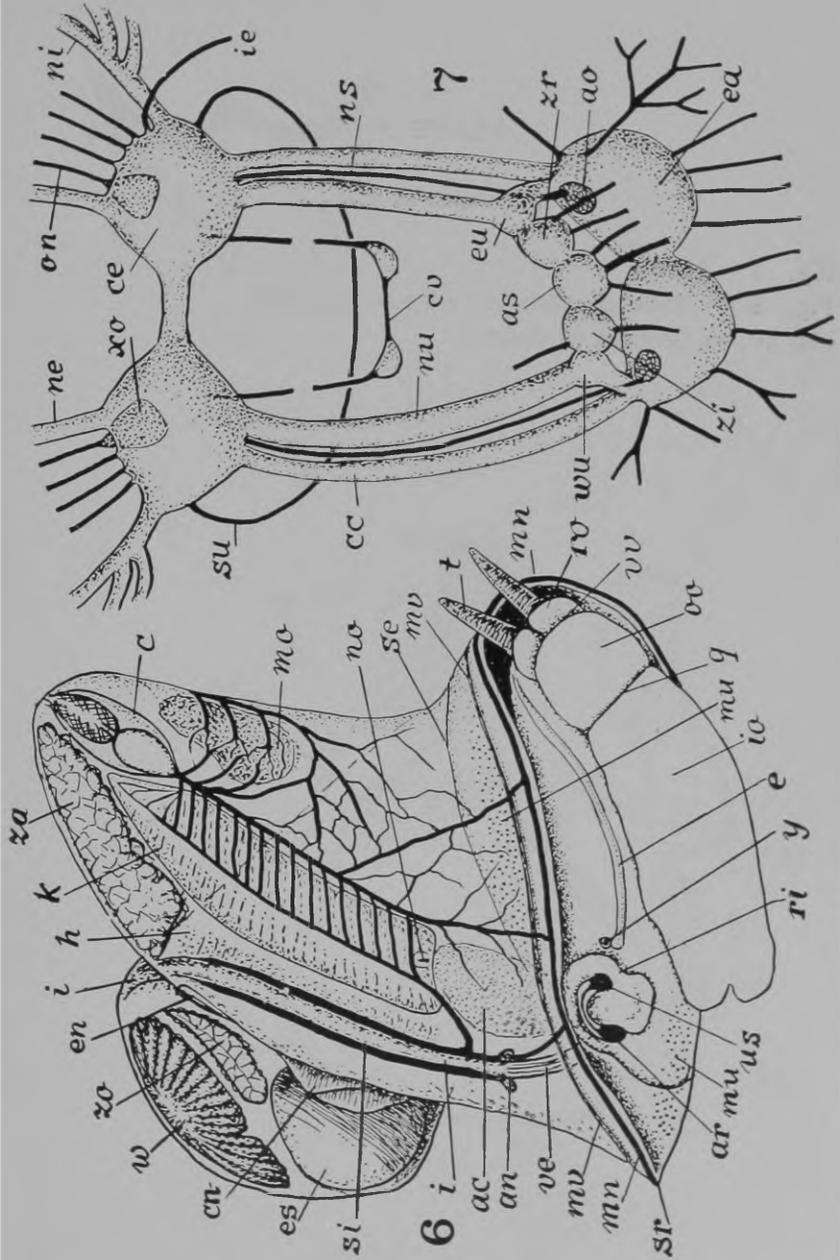


PLATE 3

Melampus coffeus

Fig. 8 — Jaw.

Fig. 9 — Teeth of radula of an 8 mm long snail.

Fig. 10 — Diagram of stomach.

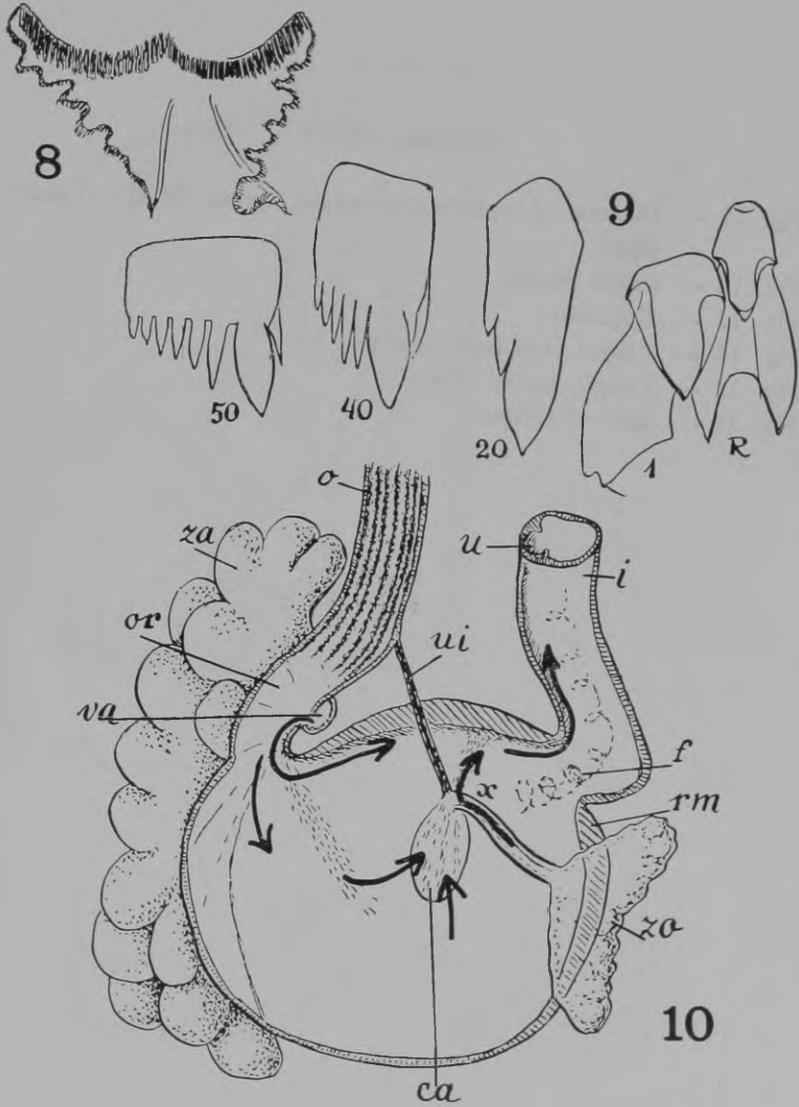


PLATE 4

Melampus coffeus

- Fig. 11 — Diagram of reproductive organs, spermooviduct (s) shortened.
- Fig. 12 — Penial papilla.
- Fig. 13 — Egg mass.
- Fig. 14 — Veliger seen from above.
- Fig. 15 — Veliger, lateral view.
- Fig. 16 — Shell of veliger.

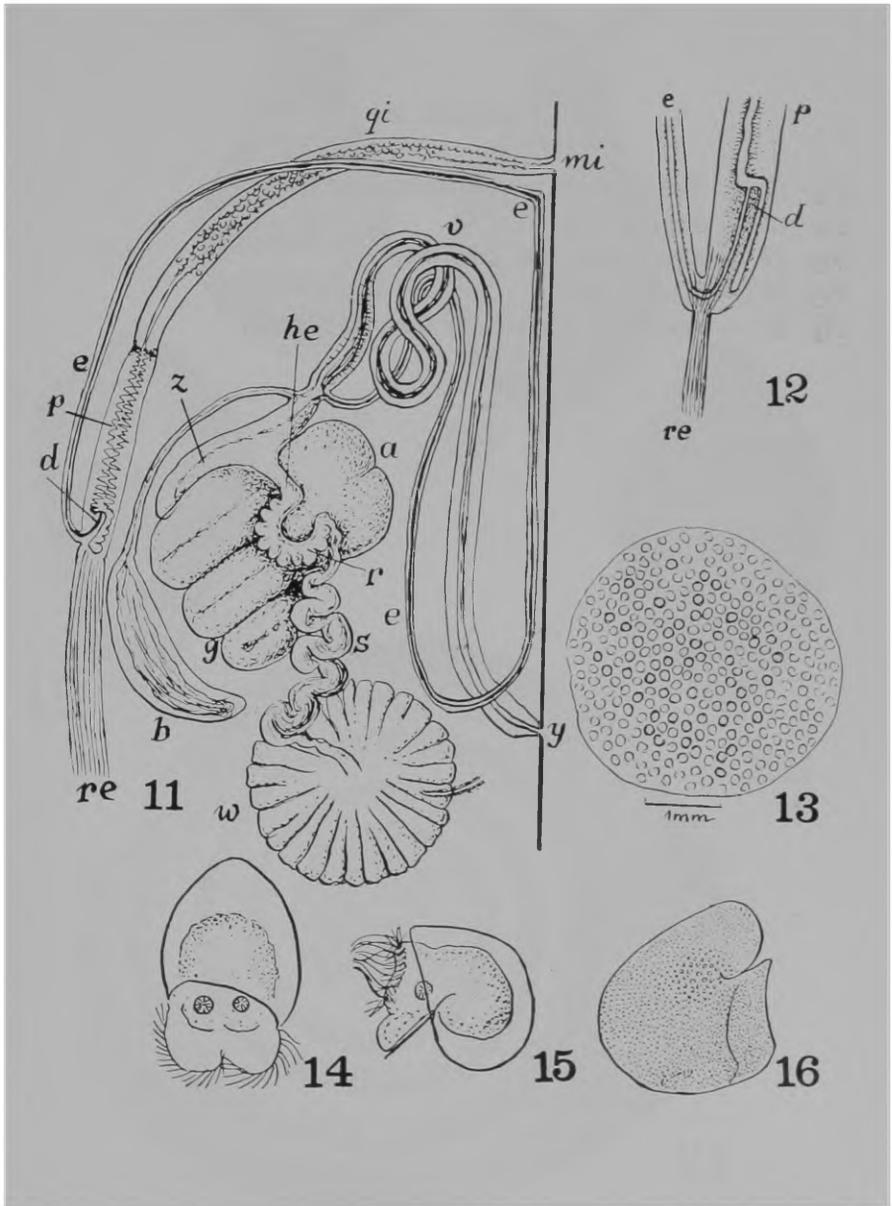


PLATE 5

Fig. 17 — *Melampus coffeus*, creeping.

Fig. 18 — Shell of same.

Fig. 19 — *Detracia parana*, creeping.

Fig. 20 — Shell of same.

Fig. 21 — Apex of a 4 mm long *Detracia parana*.

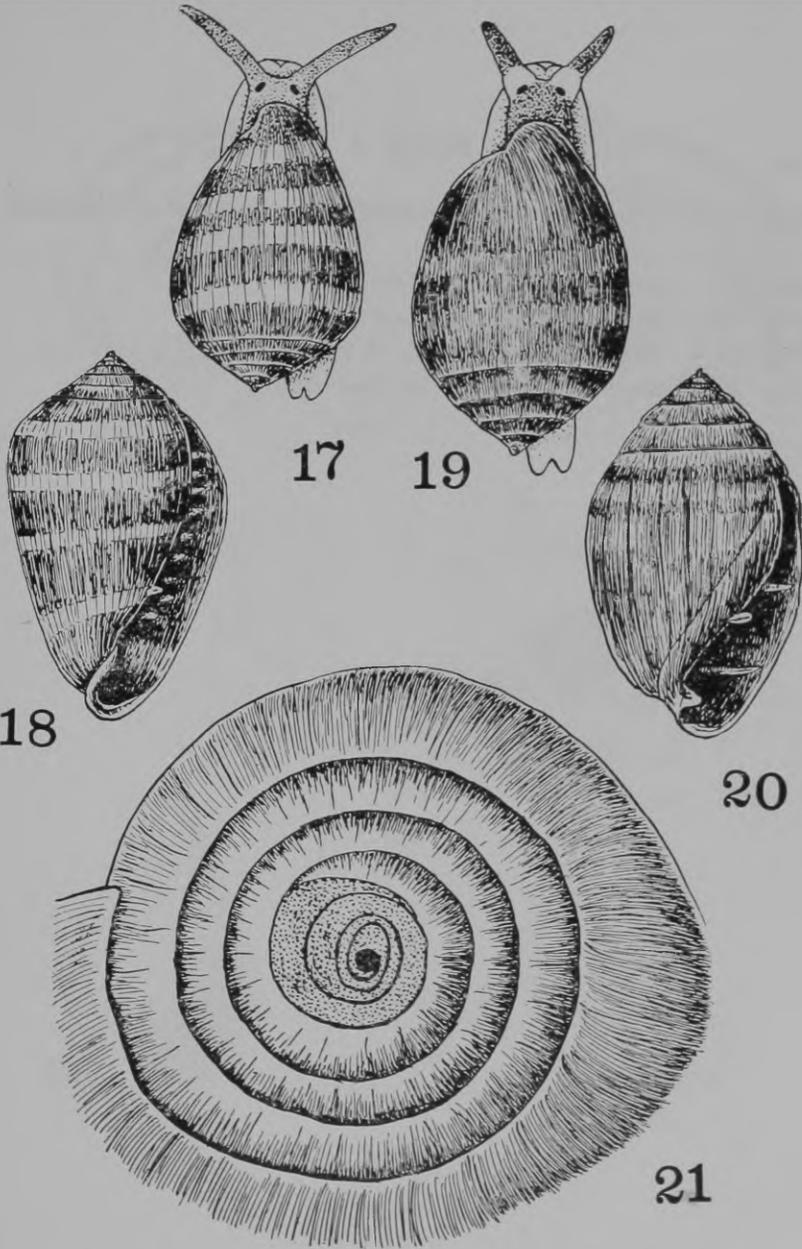


PLATE 6

- Fig. 22 — Transverse section on level of pneumostome of *Melampus coffeus*.
- Fig. 23 — Same of *Detracia parana*.
- Fig. 24 — *Detracia parana* removed from shell.
- Fig. 25 — *Detracia parana*, teeth of radula.
- Fig. 26 — Shell of *Assiminea succinea vina*.

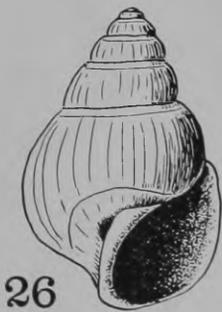
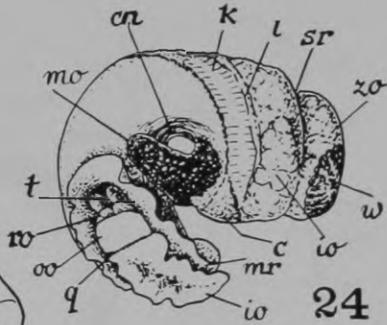
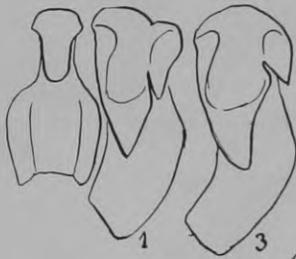
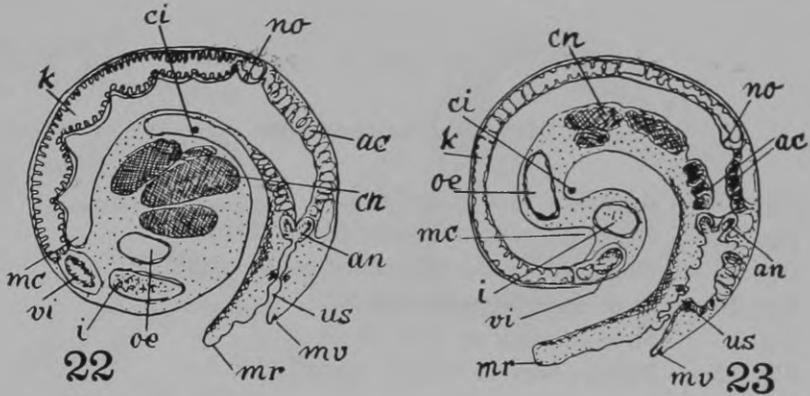


PLATE 7

Assiminea succinea vina

- Fig. 27 — Right side view of fore end.
Fig. 28 — Distended male with open pallial cavity.
Fig. 29 — Distended female with closed pallial cavity.
Fig. 30 — Snail crawling under water.
Fig. 31 — Snail crawling on glass in air.
Fig. 32 — Pallial cavity of female, opened.

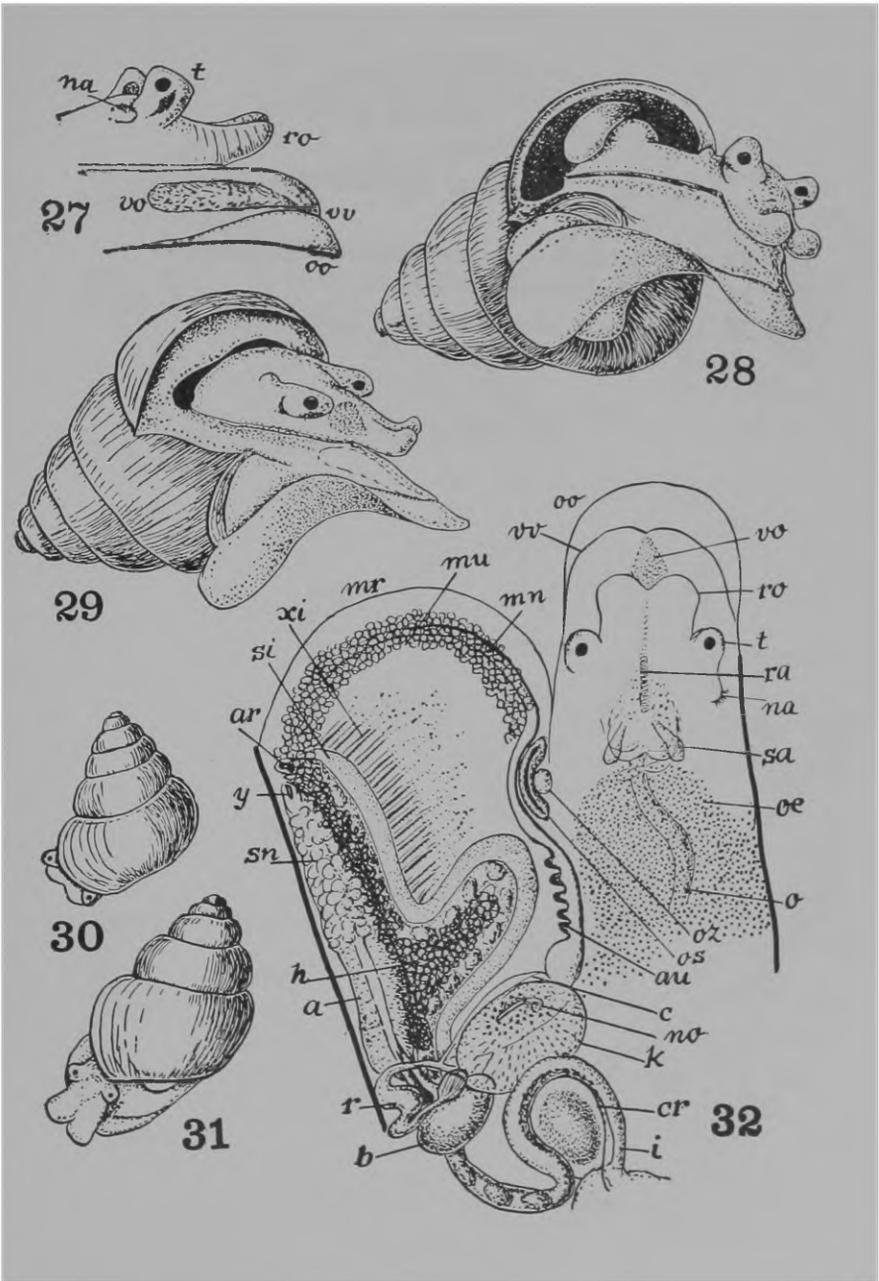


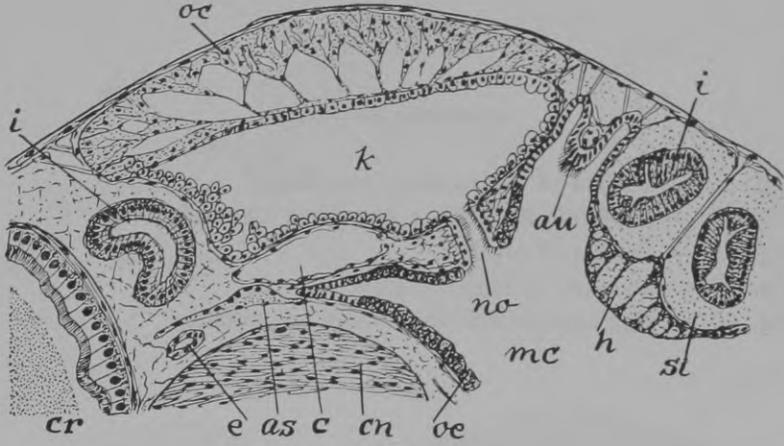
PLATE 8

Assiminea succinea vina

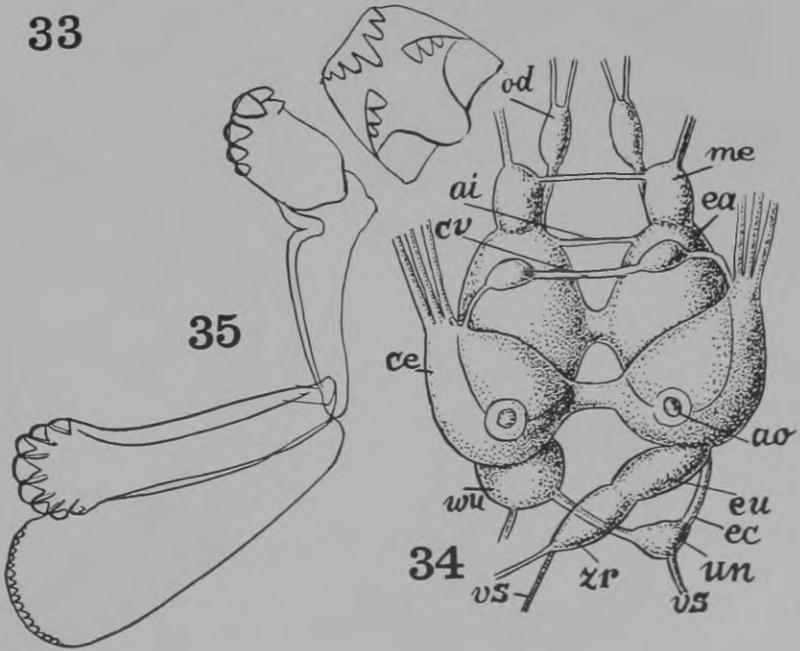
Fig. 33 — Combined transverse section of pallial roof.

Fig. 34 — Central nervous system.

Fig. 35 — Half-row of radula from Cananéia.



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PLATE 9

Assiminea succinea

- Fig. 36 — Radula of *A. succinea* from Bimini.
Fig. 37 — Penis of *A. succinea vina* from Cananéia.
Fig. 38 — Section of prostate.
Fig. 39 — Diagram of female organs.
Fig. 40 — Egg capsule with snail ready for hatching.

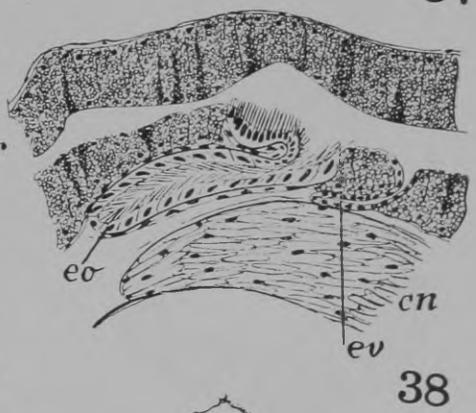
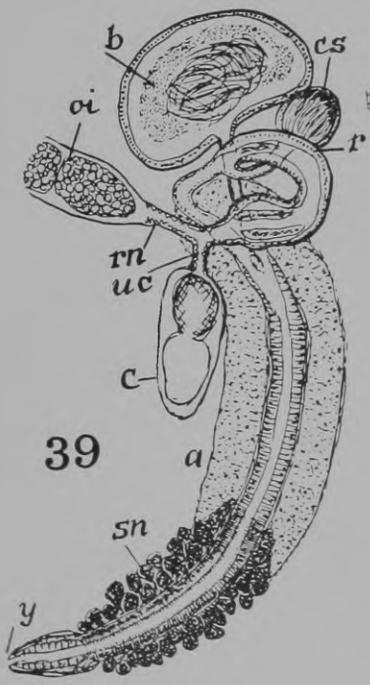
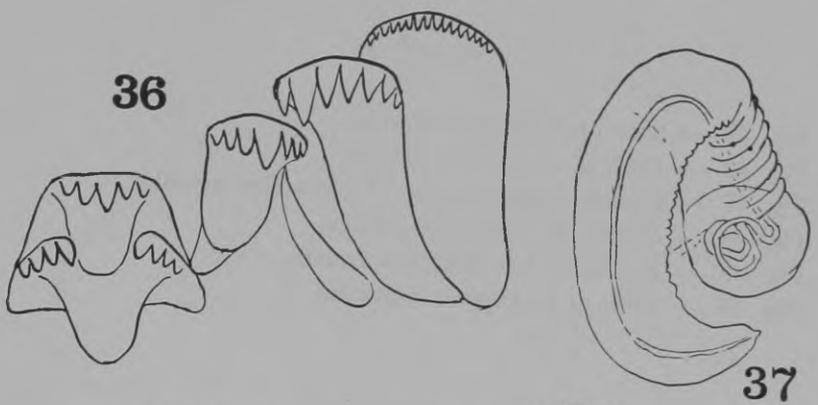


PLATE 10

- Fig. 41 — Shell of *Littoridina miaulis*.
Fig. 42 — Penis of *Littoridina miaulis*.
Fig. 43 — Central nervous system of *Littoridina miaulis*.
Fig. 44 — Radula of *Littoridina miaulis*.
Fig. 45 — Radula of *Littoridina charruana*.
Fig. 46 — Penis of *Littoridina charruana*.

