FACULDADE DE FILOSOFIA, CIÊNCIAS E LETRAS DA UNIVERSIDADE DE SÃO PAULO

BOLETIM N.o 261
SÃO PAULO
BRASIL
1962

ZOOLOGIA N.º 24

Tôda correspondência deverá ser dirigida ao Departamento respectivo da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo — Caixa Postal 8 105, S. Paulo, Brasil.
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Impresso na Secção Gráfica da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo em 1962

SÃO PAULO — BRASIL
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COMPOSTO E IMPRESSO NA SECÇÃO GRÁFICA DA
FACULDADE DE FILOSOFIA, CIÊNCIAS E LETRAS
DA UNIVERSIDADE DE SÃO PAULO
1963

ON A BIOASSAY FOR ACETYLCHOLINE AND ON SOME PROPERTIES OF THE LONGITUDINAL MUSCLES OF HOLOTHURIA GRISEA (*ECHINODERMATA*)

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(4 figs.)

Smooth muscles of some Invertebrate animals are recommended for determination of the amount of Ach in extract of tissues. The body wall muscles of Sea Cucumber (*Holothuria grisea*) one of the most common Echinoderm found along the Brazilian coast, have been preferred for a bioassay and used in a very successful way.

The longitudinal muscles of that Echinoderm contract in the presence of as little as 1×10^{-14} g Ach/ml. The technique is very simple and inexpensive. As perfusion fluid filtered sea water is very convenient. The preparation of fresh animals does not have spontaneous movements, gives regular responses and has the great advantage of rapid relaxation. In average the muscles have a latent period of contraction of 10-15 seconds and relax 2-3 minutes after washing. These conditions permit a great number of assays in a short time. Eserinization is not necessary. Several experiments indicate regular proportion between the amount of Ach and the contraction (fig. 1).

Some precaution must be observed during the bioassay. Fresh recently captured animals give better results. The longitudinal muscles can be dissected easily and free from connective tissues. Ordinary atmospheric air or pure oxygen is used to oxygenate and stirr the bath. The bubbles must be fine and not much rapid in order not to disturb the muscle mechanically. The sensitivity to Ach is so high that small drops of the esther attached to the suspension thread must be avoided.

This method is largely used not only in the marine laboratories (Marine Biological Laboratory of São Sebastião and Aquario of Santos) but also in São Paulo where the Holothurians were kept in the laboratory in running filtered sea water.

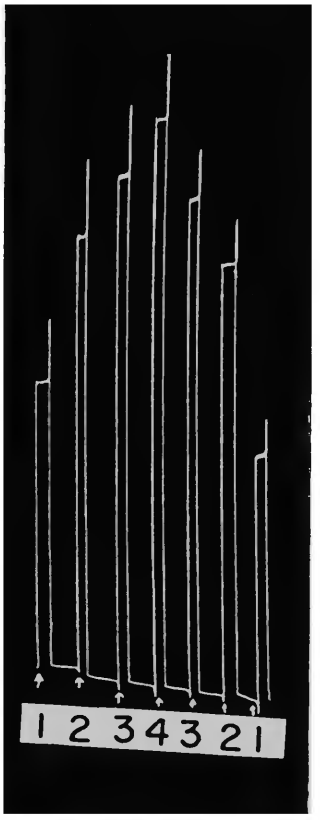

Fig. 1 — Contractions of the longitudinal muscle of the body wall of *Holothuria grisea* after excitation by Acetylcholine. 1 = 10^{-10}; 2 = 10^{-8}; 3 = 10^{-6}; 4 = 10^{-4}.

The uneserinized longitudinal body wall muscles of *H. grisea* was adopted as a bioassay for Ach by Ambache & Sawaya (1953) and the method is one of the most sensitive (Welsh & Tawarog 1960, p. 195). These authors refer that "the isolated longitudinal wall muscle of Holothuria is a method of Ach assay of great potential value in laboratories located near a source of marine animals". And add: "it would appear to be a specific assay, but this aspect requires further study".

In order to verify the specificity of the method for Ach, several experiments were performed in different conditions.

The body wall muscles of *H. grisea* is insensitive to many drugs as histamine, curare, adrenaline, nor-adrenaline, as Sawaya & Ancona Lopez (1950) have pointed out, and to the salts barium chloride and potassium chloride. Those authors have also verified that atropine does not antagonize the effect of Ach.

All those drugs were brought into action at physiological concentration, about 10^{-6} (1 μg). Some of them (histamine, adrenaline and nor-adrenaline) at higher doses (1×10^{-3} or 1×10^{-4}) provoke relaxation of the muscles. von Euler, Chaves & Theodosio (1952, p. 104) refers to the effect of histamine on the relaxation of the muscles and mention that adrenaline and dl-noradrenaline has no influence on those structures. In several experiments with histamine the relaxation effect was observed as concentration of 20 μg. At this doses adrenaline and nor-adrenaline have no effect at all.

Former studies of Sawaya & Ancona Lopez (1959) show that only nicotine induces strong contraction in doses of 1 μg. The influence of that alcaloid differs from that of Ach chiefly because the relaxation of the muscle after nicotine does not take place before 20-30 minutes and with Ach this period is regularly 20 sec. and never more than 3 minutes. In the case of nicotine there is an actual contracture from which the muscle recovers very slowly.

Another point to be mentioned is the behaviour of the muscle under eserine, physostigmine and other allied drugs. For the bioassay the uneserinized muscle is used. Eserine has no effect on the contraction but potentializes Ach. However, the after effect of eserine is a contracture of the muscle in the same way as the mentioned nicotine effect. The relaxation time is here about 20-30 minutes. This delay in relaxation and the strong sensitivity of the muscle to Ach indicate the use of uneserinized muscle in the bioassay.

The reactions of the longitudinal muscle to different concentrations of Ach are very constant. Fig. 2 and 3 shows the effect of small doses of Ach. These records could be obtained several times with the same muscle during more than 12 hours of working. In some cases, the same muscle after that period of work was kept in an ice-box at 2° or 3°C and on the next day experimented again with good results.

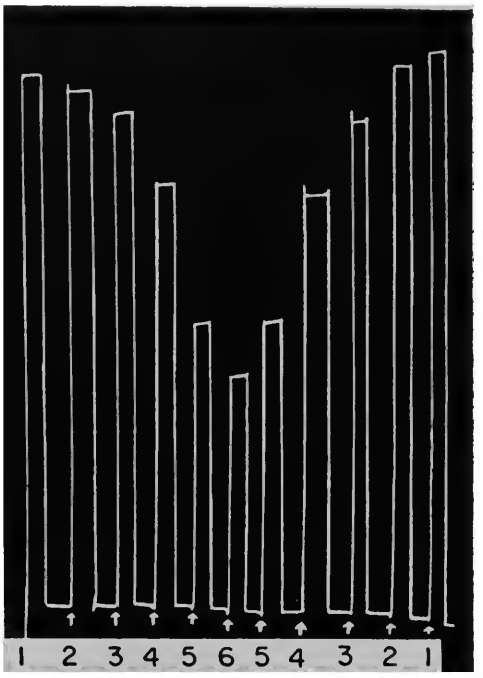

Fig. 2 — Contractions of the longitudinal muscle of the bod wall of *Holothuria grisea* after excitation by Acetylcholine. 1 = 10^{-4}; 2 = 10^{-5}; 3 = 10^{6-}; 4 = 10^{-7}; 5 = 10^{-8}; 6 = 10^{-10}.

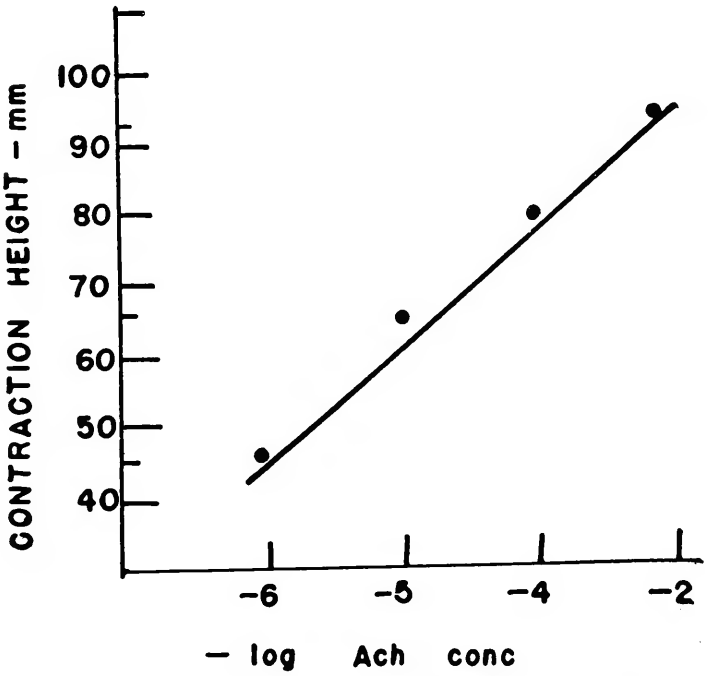

Fig. 3 — Contractions of the longitudinal muscle of the body wall of *Holothuria grisea*.

The perfusion fluid used was always filtered sea water. von Euler, Chaves & Teodosio (1952, p. 101) have employed sea water diluted with distilled water to 80% Such a dilution has no effect in our preparations.

In order to see if the dilution of sea water with distilled water has some influence on the contraction, the longitudinal muscles have been submitted to different concentration of sea water and after 5 to 15 minutes of contact of the perfusion diluted fluids the same doses of Ach were injected into the bath.

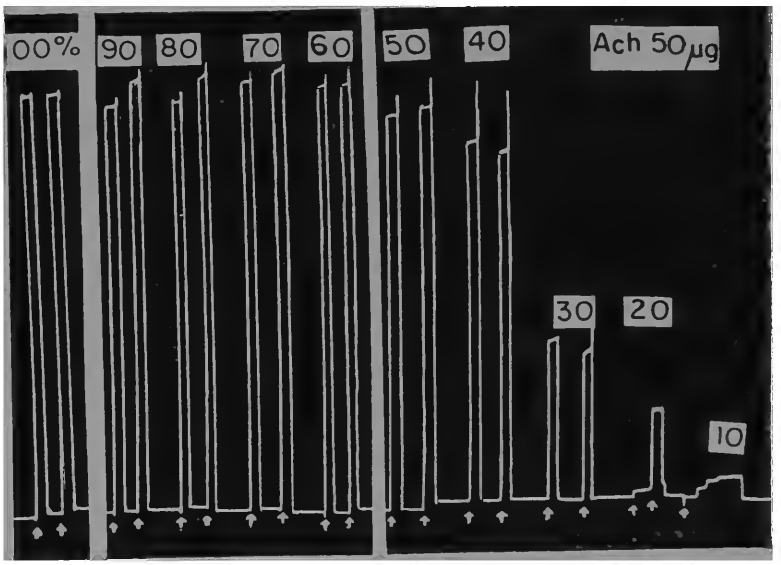

Fig. 4 — Contractions of the longitudinal muscle of the body wall of *Holothuria grisea* after excitation by 50µg of Acetylcholine diluted in different concentration of filtered sea-water.

Fig. 4 shows that the dilution of sea water with distilled water can be made to 60% without influence on the reaction of the muscle to Ach. After 60% the contraction is less and decreases when the perfusion fluid is diluted down to 20%. Dilution of sea water below 10% causes inhibition of the influence of Ach.

DISCUSSION

According to the results of several experiments the body wall muscles of *Holothuria grisea* can be used for Ach bioassay. Prati-

cally the contraction of those muscles are specific for Ach and nicotine. The contracture determined by the latter indicate the difference of those muscles' reactions.

As have been said the muscles are insensitive to several drugs of common use in pharmacology.

The physiology of the muscles of Echinoderms is very little known. Hanson & Lowy (1960, p. 265) in their study on muscles of Invertebrate animals do not give information on the muscles of Echinoderms.

SUMMARY

1. The body wall muscles of Sea Cucumber (*Holothuria grisea*) are very sensitive to acetylcholine and nicotine.
2. Reaction of the muscles under Ach is very characteristic, that is, the muscle reacts to as little as 1×10^{-14}, the latent periods is of 10-20 sec. and the relaxation occurs on 2-3 minutes after working.
3. Nicotine at physiological doses (1 μg) provokes contracture of the muscles.
4. The body wall muscles of *Holothuria grisea* can be recommended as very useful material for Ach bioassay.

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ON LEUCOZONIA NASSA

by EVELINE and ERNST MARCUS

(with 2 plates)

Four families of stenoglossan prosobranchs were studied in our Department, thaisids and buccinids by Edmund H. Smith, M. A., columbellids and olivids by ourselves. The present paper contains the description of a fasciolariid, *Leucozonia nassa* (Gmelin, 1791), frequent at the Base of Research, Bay of the Flamengo, which belongs to the Oceanographic Institute of the University of São Paulo. There we could work thanks to the Director of the Institute, Dr. Ingvar Emilsson, and the Head of the Base, Dr. Edmundo Nonato, to whom we are very much indebted.

NAME, RANGE, OCCURRENCE

Leucozonia cingulifera (Lamarck, 1816) is a synonym of *Voluta nassa* Gmelin, 1791 (Abbott 1955, p. 241). *Turbinella brasiliana* d'Orbigny (1841, p. 449) was described as different from *nassa* by absence of keel, weak nodules, wanting whitish band, 3 columellar folds, and yellowish aperture. These characters are variable and do not justify specific separation. The nodules, up to 11 in number on the body whorl, are distinct in our specimens, and so they are in d'Orbigny's figure 17 on plate 77. The keel is weak in our shells, and the whitish band often absent or indistinct. The folds are frequently 4, as in typical *nassa*. The aperture is either whitish or yellowish. At first sight it seems that *brasiliana* can be maintained as a subspecific name, because d'Orbigny's and our material have no spine or dentiform tubercle (Fischer 1887, p. 617) on the outer lip. But a Brazilian, hence geographically segregated, subspecies is not characterized by the absence of this spine, as is shown by Perry and Schwengel's figure (1955, pl. 35, f. 239) of a snail from Western Florida without

any spine. Also Keen (1958, p. 416) calls the tooth on the outer lip "weak to almost wanting in the type of *Leucozonia*", i. e., *nassa*.

The range of *Leucozonia nassa* extends from Florida through the West Indies and along the coasts of the Gulf of Mexico (Texas, Bank of Campeche) and the Caribbean Sea (Curaçao) to Brazil, southwards to the Bay of Guaratuba, Paraná (Gofferjé, 1950, p. 245). Perhaps the species attains its southern limit here, because it is not common in the littoral of Paraná (l. c.), contrary to the farther northern coast of Brazil (Souza Lopes & Alvarenga 1955, p. 174).

On the coast of São Paulo the snails live on boulders and rocks in the intertidal zone. During low tide they often hide in caves on the underside of the boulders or in the wet sand around their foot. The snails feed by means of the long proboscis on vermetids (*Petaloconchus*), barnacles, and polychaetes. The intestine of many snails contained great numbers of setae, e. g. of terebellids and sabellariids (ailerons of *Phragmatopoma*). Compared with *Thais haemastoma* they are very sluggish in movement; at night however, they are more active, as Mr. Edmund H. Smith observed in October 1960 near São Sebastião.

Among the several hundreds of snails which we have handled two snails had a shell of 49 mm length, generally the biggest were 40 mm.

EXTERNAL CHARACTERS AND MANTLE CAVITY

The soft parts are red, only the fore end of the foot is orange. The operculum is black; it is oval and acute at the apical nucleus. The eyes lie in the middle of the outer side of the tentacles. In one snail the left tentacle bore 3 eyes of almost equal size with the single right eye, one beside the other. Possibly this multiplication occurred during regeneration (Simroth 1907, p. 960). The siphon is short, bears a broad band of cilia on its borders and is supplied by nerves emerging from a big ganglion which lies at the base of the siphon among the fibres of the siphonal retractor.

The foot is short and rounded behind. Its anterior border is bilabiate and notched in the middle. The furrow is deep; the anterior pedal glands (Graham 1957, p. 141) arranged in packets discharge

to this groove on its whole breadth without a special duct. Behind the furrow lie conspicuous secondary ganglia formed by pedal nerves. The ventral pedal gland (l. c., p. 142) or female moulding gland is located in the anterior third of the sole as a rather smooth-walled sac. The pedal sucker of muricacean Stenoglossa (Fretter, 1946), also present in *Drupa* (Edmund H. Smith), does not occur in *Leucozonia nassa,* nor in other Buccinacea, as *Buccinum, Cantharus* (Edmund H. Smith), *Pisania* (id.), and the Columbellidae that we examined.

As the apical angle of the shell is 55-60°, the mantle cavity is intermediate between narrow and wide. Clusters of gland cells lie under the ciliated epithelium of the upper mantle edge in the connective tissue. The inferior mantle border is much less differentiated, also its nerves are thinner. The anterior region of the upper edge contains a blood lacuna and another is situated inwards to the glands. The principal blood-supply of the mantle is provided by a sinus on the outer, the shell-side, of the mantle. Hence a respiratory function of the ceiling of the pallial cavity is not suggested by the distribution of blood spaces in *L. nassa,* contrary to some columbellids examined by us and the phasianellid *Tricolia affinis*.

The hypobranchial gland consists of high cells. On the roof of the mantle cavity it extends on the right side, from the tip of the ctenidium to the fundus, where ceiling and floor coalesce. The gland occupies also part of the floor leaving free the vestibule and the rectum.

Under the genital aperture and the anus a ventral band of cilia runs to the mantle edge. Cilia occur also in front of the ventral hypobranchial lobe, but cease before they attain the anterior border. Another ventral ciliated strip leads the excretion from the renal slit forwards to the region underlain by the visceral ganglia. As this streak lies under the left side of the gill the particles transported by it can be taken over by the cilia that carry the sediments dropped from osphradium and gill to the right side. These cilia form a broad band under osphradium and ctenidium; they begin on the left side of the pallial floor and end under the female aperture where the current they produce merges into the principal outgoing one. The inhalant current is brought about by the cilia of the borders of the siphon and the branchial ones.

The ctenidium contains 285 leaflets and is 2,7 mm broad. The osphradium has 84 left and 108 right leaflets; it is 1,9 mm broad, viz. the left filaments 0,7, the right 0,9, and the axial ganglion 0,3 mm broad. Compared with the columbellids that we examined the osphradium is relatively small.

CENTRAL NERVOUS SYSTEM (Fig. 1)

The ganglia which are reddish in living snails lie all very near together as in the fasciolariid studied by Bouvier (1887, p. 254). Compared with *Buccinum* (ibid., p. 256 ff.) the nerve ring of *Leucozonia nassa* is even more concentrated, as the cerebro-pedal and pedal-pleural connectives are shorter, and the buccal ganglia (cc) not only in close contact with the cerebral ganglia as in *Buccinum* but also touching one another.

The pedal ganglia (ea) are long and are the biggest elements. Their anterior margins are subdivided into several cones as in the columbellids, and as in these the right ganglion is more dorsal than the left one. The anterior border of the foot is richly supplied with nerves. The cephalic aorta (ao) rises in front of the buccal ganglia and runs forwards over the pedal commissure.

The cerebral commissure is twice as high as broad. The pleural ganglia (eu) lie under the cerebral ones (er), the left pleural ganglion is considerably farther ventral. The siphonal branch of its thick pallio-siphonal nerve (sn) forms a secondary ganglion as in columbellids.

The left pleural ganglion is broadly connected with the subintestinal ganglion (iu) which lies under the right pleural ganglion. As in other Buccinacea the right zygoneury established by the union of the subintestinal with the right pleural ganglion is highly developed. A strong pallio-parietal nerve (wi) runs to the right side. It comes from the limit between right pleural and subintestinal ganglion. The supraintestinal ganglion (ai) is apposed to the right pleural ganglion without an external connective. Two visceral ganglia, a big bilobed and a smaller simple one, lie quite near to one another at the hind end of the anterior body cavity (Fig. 5, va). A third accessory ganglion is a little in front of these ganglia.

ALIMENTARY TRACT

The radula (Fig. 2) begins with colourless teeth in the oldest rows, while those of the newest series are brownish. The rhachidian tooth has 3 denticles. The lateral teeth have up to 7 denticles, the innermost of which is biggest, bears a minute point and ends with an inward curve.

The entrance of the proboscis sheath is fixed by muscles, but a great part of it follows the base of the proboscis when the proboscis is extruded. About 4 pairs of protractors of the proboscis sheath originate on the floor of the mantle cavity, and two thick bundles of retractors originating laterally on the wall insert behind them. The highly contractile proboscis is pinkish and attains, when fully extended, nearly twice the length of the shell. The buccal artery is thick.

The two pink salivary glands are completely separate. Their ducts are tucked into the lateral folds of the oesophagus which they join ectally from the nerve ring, between the fore end of the pharynx of Leiblein and the base of the proboscis. The salivary ducts open from both sides into the buccal cavity at the level of the fore end of the radula.

As in muricids, columbellids and the buccinid *Pisania* (Edmund H. Smith) the pharynx of Leiblein of *Leucozonia nassa* is pyriform. The effect of torsion, however, as known of muricids (Graham 1941, p. 17), is not recognizable in *L. nassa,* nor in the other mentioned Buccinacea. An orange ring around the anterior end of the pharynx of Leiblein is the mucous pad of other Stenoglossa (Graham 1941, p. 6, 12; Marcus 1959, p. 125-26), and as in these, the oesophagus enters the organ with a conical strongly ciliate valve. According to Amaudrut (1898, p. 237) there is no pyriform pharynx of Leiblein in certain fasciolariids (Fusininae). Also in the Buccinidae, *Pisania* has this pyriform organ, while *Buccinum* (Dakin 1912) and *Cantharus* (Edmund H. Smith) have not. In the Olividae, it is present in *Oliva* and *Lintricula,* not in *Olivella*. The nerve ring surrounds the oesophagus behind the pharynx of Leiblein.

The brown gland of Leiblein emits its duct from the anterior end. The duct is lined with high gland cells all around, while the gland itself is, as in other Buccinacea (Graham 1941, p. 17) less

secretory than in the Muricacea. In young snails (12 mm) the gland of Leiblein is tubular, in full-grown specimens its anterior part is wide and folded. The long and slender posterior end (Fig. 5, ei) enters the cephalic blood sinus (si), whence it extends into the afferent vessel of the accessory renal system (vi). Here it ends with a thinwalled ampulla under the renal epithelium. In our descriptions of columbellids whose elongated gland of Leiblein also attains the kidney we mention some similar long glands of Leiblein in the Stenoglossa; also in *Pisania* it extends into the kidney (Edmund H. Smith).

A reduced vestige of torsion occurs in the part of the mid-oesophagus that lies between the nerve ring and the entrance of the duct of the gland of Leiblein. The mid-oesophagus is theoretically (Graham 1941, p. 13) the expanded dorsal food channel, while the gland of Leiblein is the glandular ventral part of the oesophagus. It was stripped off from the dorsal part (ibid., p. 16), when the development of the long proboscis elongated the anterior oesophagus and pulled the mid-oesophagus through the nerve ring. The site of the attachment of the glandular ventral part is marked by a small group of unciliate cells. These appear at the level of the entrance of the gland of Leiblein, mid-dorsally in consequence of torsion. In transverse sections of this level the scar-like mark forms a shallow groove between the longitudinal folds of the mid-oesophagus, and this groove can be traced in the forwards following sections descending to a more ventral position. In *Leucozonia nassa* it cannot be followed to its mid-ventral place in front, because the shape of the oesophagus becomes irregular, where it is compressed by the nerve ring.

The wall of the posterior oesophagus is folded longitudinally. The organ is brown and fastened to the bottom of the body cavity by a muscle ring as in *Oliva* and *Olivancillaria* (Marcus, 1959, p. 126, 129). Behind this point the oesophagus widens, and the number of folds increases. Their height is irregular, but one of them, situated to the right of the middle, may be a little higher. Short behind the entrance of the oesophagus (Fig. 3, e) into the stomach lies the aperture (l) of the right duct of the digestive gland. The food string (oo) is transported over 6 high transverse folds which characterize the fundus of the stomach. To the left of the fundus extends the intestinal groove

(ir) accompanied on the inner side by the major typhlosole (rm). In the pyloric region the groove is bordered by the major and the minor typhlosole (mi). The beginning of this region approximately coincides with the aperture (l) of the left duct of the digestive gland. An elaborate transverse folding on the right side of the stomach may perhaps represent a posterior sorting area (sa) as in *Nassarius* (Graham 1949, p. 749, f. 22). The food string which is gradually transformed into a faecal string is passed to the pyloric region, where mucus produced by gland cells of the typhlosoles cements it to a faecal rod. No caecum nor a gastric shield are developed in the tubular stomach of this evidently purely carnivorous stenoglossan.

The typhlosoles continue beyond the pyloric region into the intestine (Fig. 8, i) which runs rather straight (Fig. 7, i). It contains bristles and teeth of polychaetes in the examined snails. If it is empty, its lumen may be star-shaped in transverse section, due to longitudinal folds, or more or less distinctly crescent-shaped.

RENAL ORGAN (Figs. 4, 5)

The dark reddish brown kidney belongs to the type that Perrier (1889, p. 250) found in his Sténoglosses Pycnonephridiens. The renal cavity communicates with that of the pericardium (ca) by a short ciliated duct (Fig. 8, re). Farther in front the renal wall and the pericardium are separated by the intervening nephridial and blood gland (oa). At this level the urinary chamber (ui) opens into the mantle cavity (p) by a wide slit-like aperture (ni).

The inner wall or floor of the kidney is a delicate, simple epithelium without glands. The roof or outer wall is extended into folds, the bigger of which, the principal system (f), hide the smaller folds of the accessory system (vi). From the renal sinus under the floor of the kidney muscular afferent renal vessels rise, pass through the floor and the renal cavity and attain the ridges of the principal folds. The epithelium of these folds consists of glandular renal cells and ciliated cells at the summits. Connective tissue containing some muscle fibres supports the epithelium and surrounds the narrow blood spaces supplied by the branches of the afferent vessels. From these internal blood spaces the blood is collected on the outer surface of the kidney in efferent vessels. These run towards the right renal border, then

along the hypobranchial gland (y) and through this to the afferent branchial vessel.

The afferent vessel of the accessory system originates from the cephalic sinus which contains the prolonged posterior end of the gland of Leiblein (ei). The vessel has thin walls and runs through the renal cavity near the wall, where it branches into the accessory folds (vi). These contain a net of connective tissue, minute blood lacunae, plentiful amoebocytes, and acidophilous crystalloids (Cuénot 1914, p. 281). Evidently the efferent vessels lead the blood from the accessory system chiefly through the nephridial and blood gland (oa) to the auricle (au).

MALE REPRODUCTIVE ORGANS

The dark red testis lies apically over the greenish digestive gland. The silky white efferent duct coils on the columellar side of the visceral mass. This testicular part of the male duct stores sperm, hence functions as seminal vesicle. Its epithelium is rather high, without cilia, and contains yellowish concretions; sperm absorption, as was verified in *Littorina* and several Stenoglossa (Fretter 1941, p. 175 ff.), was not observed in the sectioned 2 males. The following part of the male duct, the renal efferent duct, is straightened, ciliate, and its muscular coat is thick. A little in front of the fundus of the pallial cavity, in the region of the visceral ganglia and the extension of the hind end of the gland of Leiblein into the secondary afferent vessel of the kidney, muscular strands and vessels connect the renal efferent duct with diverticula of pericardium and kidney. Pervious ducts or pores are not developed.

The following pallial spermiduct (Fig. 6) runs in a bulge of loose connective tissue without any communication with the mantle cavity. The epithelium of this prostatic part is ciliate, thrown into folds and pierced by the ducts of glands. These penetrate the parietal muscles of the prostatic spermiduct, and the long orange clusters of the glands lie embedded into the richly developed vesicular connective tissue which surrounds the pallial male duct. The latter begins dorsally to the suture of the pallial cavity, beside the intestine. From the level of the anus forwards the spermiduct runs along the floor of the pallial cavity, near to its right border and shines orange-yellow

through the mantle. Under the mantle edge the duct curves to the left and enters the penis.

At rest, the penis is turned backwards. Sometimes its thread-like white tip extends far into the pallial cavity, sometimes it is completely retracted into the red base of the copulatory organ.

FEMALE REPRODUCTIVE ORGANS (Figs. 7, 8)

The dark red ovary supplied by white spotted vessels covers the apical halves of the whorls; full-grown ovocytes contain up to 30μ long yolk granules. The thin oviduct is lined with a low, simple epithelium in its ovarian section and runs between kidney (k) and intestine (i). Farther outwards the renal section (io) is characterized by a folded epithelium whose high cells have basal nuclei. This renal part begins at the level of the origin of the aorta from the ventricle. Still farther ectally the typical cilia of the renal oviduct appear, and there are more longitudinal folds. This section is connected with the pericardium (ca) by a broad and folded duct (no) which ends with a ciliated knob beside the outlet of the renopericardial communication (re). The gonopericardial duct has a layer of strong circular muscles near the pericardium. Also the buccinid *Pisania janeirensis* has a wide gono-pericardial duct (Edmund H. Smith).

Ectally to the gonopericardial duct the ciliated renal oviduct enters the albumen gland (az). This red organ has the form of a backwards turned U. Its lumen is compressed and slightly folded; the epithelium is ciliated as in the muricids and buccinids studied by Fretter (1941, p. 184, 190-92); the underlying gland cells are grouped in clusters and stain blue. The lumen of the albumen gland opens broadly into that of the capsule gland (cn). Where these two sections of the pallial oviduct communicate with one another, the ventral sperm channel of the capsule gland merges into the ciliated duct of the seminal receptacle (zs). This consists of many tubular pouches which lie on the inner or columellar side of the visceral coil, around the anterior end of the albumen gland. In the pouches the sperms lie in parallel bundles; no sign of sperm ingestion was seen.

The salmon coloured capsule gland (cn) is rather long and shows its differently staining regions already in the living snail. In

sections the ventral channel contained sperms. Between the capsule gland and the hypobranchial gland runs the intestine. Beside the rectum courses the most ectal part of the female duct, the vestibule (v). This winding organ, almost as long as the capsule gland, but contracted in Fig. 7, has a folded lumen lined with a rather low epithelium which bears long cilia and does not contain glands. The folds are highest in the innermost region of the vestibule, farther outwards the lumen becomes narrower, duct-like, and the muscular coat still thicker. A little in front of the anus (ar) the vestibular duct curves and forms a small papilla on whose tip (u) it opens.

A bursa copulatrix (ur) is dorsally annexed to the distal part of the vestibular duct. It projects from the muscle mantle of the vestibule. The bursal epithelium is high (60-180μ), not ciliated, but stuffed with granules. In many dissected snails and some sections the bursa contains brown amorphous masses, no recognizable sperms.

EGGS

On January 1, 1961 we found a snail whose shell was 35 mm in length laying egg capsules in a concavity of a rock, possibly an empty sea urchin hole, just emerging from low tide level. There were already 16 capsules attached to the ceiling of the hole laid in 4 rows of 4 capsules each. These are flattened bottles (Fig. 9), 7 mm high, 3,5 mm broad with a basal 1 mm long stalk. The blunt distal end of the capsule is plane and has a circular thinned area near one side. Each transparent capsule contained 40-50 dark pink eggs, about 0,4 mm in diameter. In our laboratory where *Leucozonia nassa* always behaves extremely inactive, the female did not lay further capsules; also the previously produced eggs did not develop over the stage of 4 blastomeres over night at a temperature of 30° C., so they were preserved. As in many gastropods the polocytes are big. The question whether the species has nurse-eggs must be left open; in each capsule a number of eggs did not cleave at all, but this may have been due to the warmth.

More or less similar egg capsules of Fasciolariidae were figured by Risbec (1932, p. 369), Habe (1944, p. 196, f. 5), and Perry and Schwengel (1955, figs. 352-354).

CONCLUSIONS

Leucozonia nassa is a typical stenoglossan snail. Its radula with richly dentate lateral plates whose size by far surpasses that of the rhachidian tooth assigns the species to the Buccinacea. The indications of Thiele's diagnosis of the family Fasciolariidae (1931, p. 326) were, for the most part, verified by the preceding study .The eyes, however, do not lie at the base of the tentacles, but higher upwards, and the ducts of the salivary glands do not pass through the nerve ring, but attain the anterior oesophagus farther in front.

There are many more fossil fasciolariids than recent ones. The range of the family is restricted principally to warm waters. Many species live below the intertidal zone, in which competition among animals is most intense. These facts suggest that the family on the whole recedes. Of course, this general impression cannot be confirmed by every single species, e. g., the present one which is frequent in the intertidal zone of our coast.

As many Stenoglossa *Leucozonia nassa* combines specialized and primitive traces, but the former overweigh the latter. The nervous system is highly concentrated; the stomach is of an advanced type without caecum and gastric shield; the kidney is compact; and the spermiduct is completely closed without any communication with the mantle cavity. Primitive features are the pyriform pharynx of Leiblein and the broad gono-pericardial duct of the female. The mixture of primary and secondary characters in many Stenoglossa explains Thiele's statement (1935, p. 1095): "the families belonging to the Stenoglossa are all more or less intimately related with one another".

Compared with *Thais haemastoma* the present species is more frequent in somewhat sheltered niches. Its shell is strong and thick, so that it might also withstand the surf which sweeps over the mentioned muricacean with great force. Possibly the foot of *Leucozonia nassa* is too small to warrant the snail an unfailing holdfast on fully exposed boulders. On the other hand, *L. nassa* hides in the wet sand around the rocky outcrops at low tide and lives also where the worms of *Phragmatopoma* build their tubes of the sand carried by the waves. Under both conditions the inhalant current of *Leucozonia nassa* will contain many sand grains, but the richly developed cilia of the floor of the pallial cavity evidently provide perfect sanitation.

RESUMO

Leucozonia nassa (Gmelin 1791) é o nome válido de *L. cingulifera* (Lamarck, 1816). O nome de *Turbinella brasiliana* d'Orbigny, 1841, não se justifica, nem subespecìficamente, pois foi introduzido baseado em caracteres variáveis da concha.

Leucozonia nassa é freqüente nas rochas próximas da Base de Pesquisas do Instituto Oceanográfico de São Paulo, 14 quilômetros a oeste de Ubatuba. Ocorre na zona das marés, principalmente em nichos ecológicos algo abrigados da ressaca, talvez devido à pequenez do pé, o órgão de aderência. O caramujo alimenta-se de poliquetos, p. e. *Phragmatopoma,* cracas, e *Petaloconchus* (Prosobranchia, Vermetidae) por meio da sua tromba muito comprida, distensível e contractil. Locomove-se durante a noite mais que de dia e se esconde, nas horas da baixa-mar, freqüentemente, na areia molhada ao pé das rochas.

Da anatomia do sistema nervoso, estômago, rim, e duto masculino infere-se alta especialização de *L. nassa* dentro da superfamília Buccinacea, ao passo que a faringe de Leiblein, de configuração piriforme, e o largo duto gonopericardial na fêmea são caracteres primitivos. O efeito da torção vê-se no trecho do esôfago médio delimitado pela desembocadura do duto da glândula de Leiblein e o anel nervoso. Na diagnose da família Fasciolariidae (Thiele, 1931, p. 326), à qual *Leucozonia* pertence, duas passagens devem ser alteradas, a relativa à posição dos olhos, situados distalmente à base da espécie presente, e a que se refere aos dutos salivares que atingem o esôfago anteriormente ao anel nervoso e, destarte, não o atravessam.

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EXPLANATION OF LETTERS

ai — supra-intestinal ganglion.
ao — aorta.
ar — anus.
au — auricle.
az — albumen gland.
b — ctenidium.
ca — pericardium.
cc — buccal ganglia.
cn — capsule gland.
e — oesophagus.
ea — pedal ganglia.
ei — gland of Leiblein.
er — cerebral ganglia.
oa — nephridial and blood gland.
on — osphradial-branchial nerve.
oo — food string.
p — pallial cavity.
re — renopericardial duct.
rm — major typhlosole.
sa — sorting area.
si — blood space.
sn — pallio-siphonal nerve.
u — female aperture.
ea — pleural ganglia.
f — principal folds of kidney.
i — intestine.
io — oviduct.
ir — intestinal groove.
iu — subintestinal ganglion.
k — kidney.
l — apertures of digestive gland.
me — mantle.
mi — minor typhlosole.
ni — renal aperture.
nn — tentacle nerve.
no — gonopericardial duct.
ui — urinary chamber.
ur — bursa copulatrix.
v — vestibule.
va — visceral ganglia.
ve — ventricle.
vi — acessory renal folds.
wi — right pallio-parietal nerve.
xn — penial nerve.
y — hypobranchial gland.
zs — seminal receptacle.

PLATES

PLATE 1

Fig. 1 — Central nervous system.

Fig. 2 — Two rows of radula.

Fig. 3 — Stomach opened on dorsal side.

Fig. 4 — Heart and kidney.

Fig. 5 — Combined transverse section of renal region.

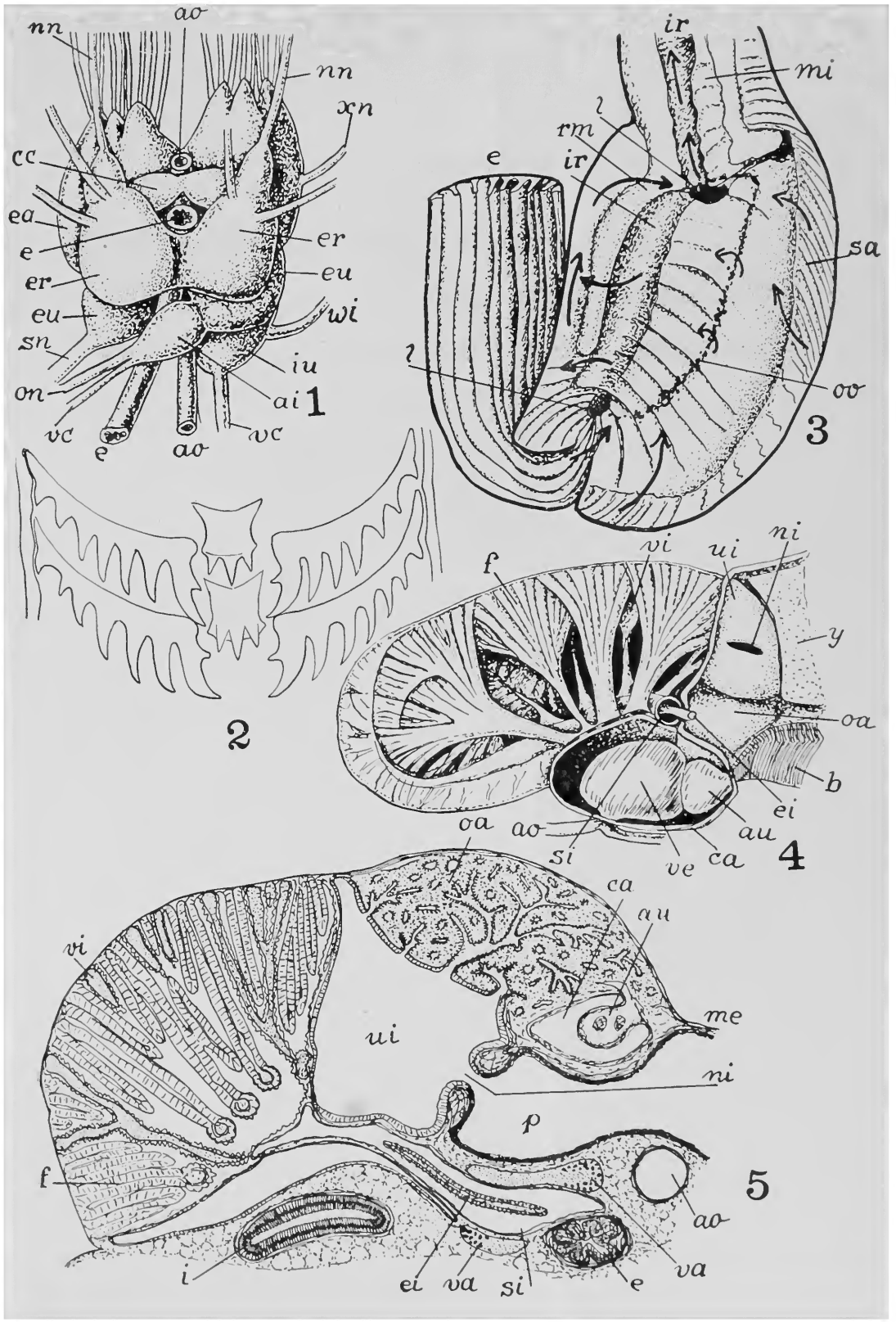
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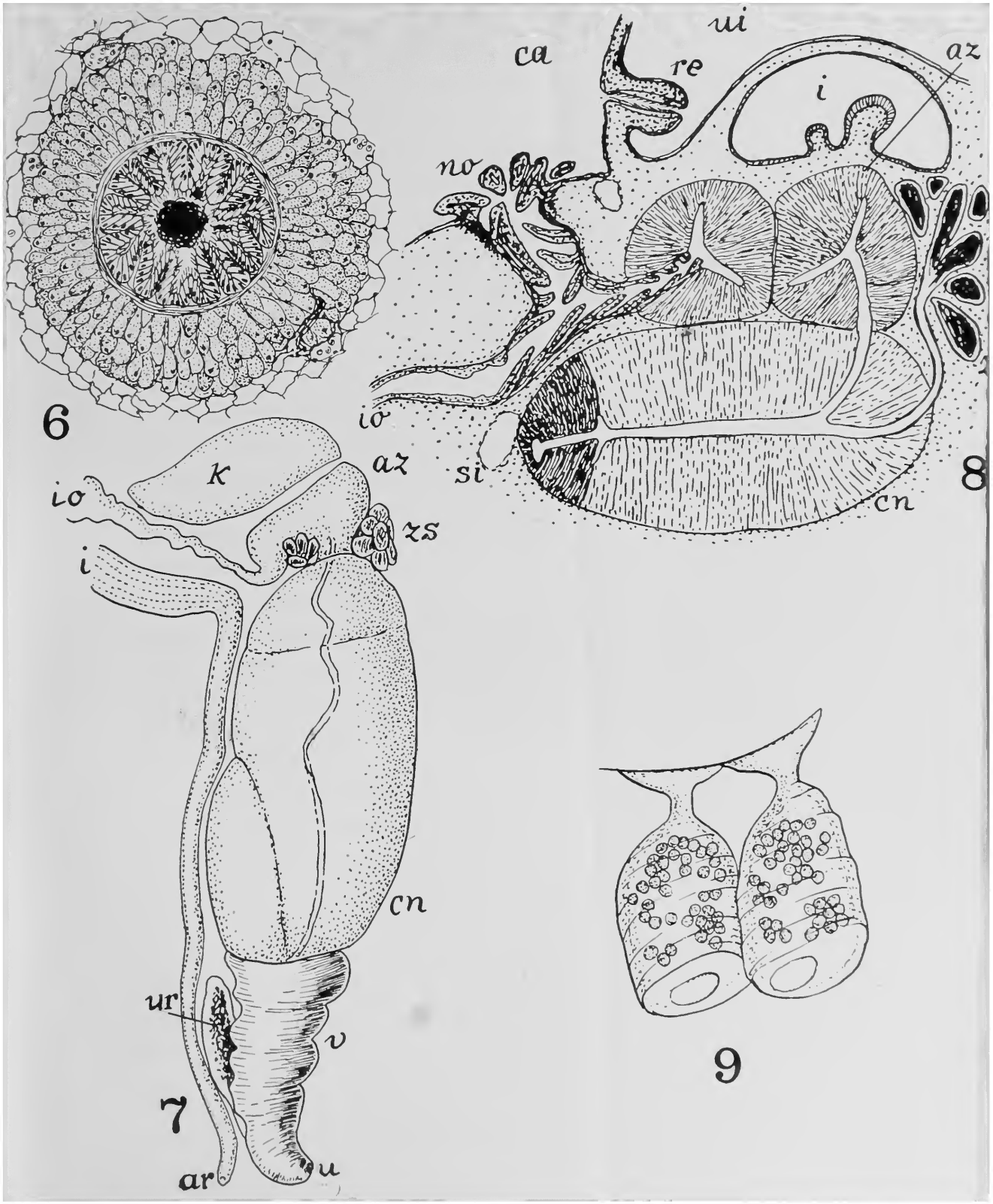
PLATE 2

Fig. 6 — Transverse section of prostatic part of sperm duct.

Fig. 7 — Female efferent organs.

Fig. 8 — Combined section of central region of female duct.

Fig. 9 — Egg capsules.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SÔBRE A OCORRÊNCIA DE STROPHOCHEILIDAE (*MOLUSCO GASTRÓPODE*) *NO RIO GRANDE DO SUL*

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(Com 1 Est.)

O presente trabalho teve por origem a necessidade de determinar a espécie dos caracóis coletados para execícios práticos de fisiologia comparada. Os caracteres dos animais do nosso material coincidem em grande parte com os de *Strophocheilus oblongus musculus* Becquaert, 1948, subespécie até agora sòmente citada para a Argentina e Paraguai.

Para o nosso estudo seguimos a monografia elaborada por Becquaert (1948) sôbre a revisão da família *Strophocheilidae*. Dela nos servimos também para a discussão e comentários. Grande auxílio nos prestou a excelente coleção malacológica existente no Departamento de Zoologia da Secretaria de Agricultura de São Paulo, estudada pelo próprio Becquaert.

Agradecemos ao Dr. Celso Paulo Jaeger o fornecimento de vários caracóis; ao Dr. Lindolpho Guimarães e ao Lic. José Luiz Moraes Leme também agradecemos pelas facilidades proporcionadas para a consulta da coleção malacológica do Departamento de Zoologia da Secretaria de Agricultura do Estado de São Paulo.

Daremos a seguir a diagnose do gênero, do subgênero e os elementos de que nos valemos para a determinação da subespécie, e após a discussão, apresentaremos alguns comentários sôbre as *Strophocheilidae*.

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GÊNERO *STROPHOCHEILUS* SPIX, 1827

Caracteres da concha: tamanho médio a muito grande (20 a 160 mm de comprimento), grande capacidade, oblonga-ovalada, elíptica ou em forma de fuso, relativamente larga em relação ao comprimento, sendo porém êste sempre maior do que a largura, com uma volta do corpo bastante desenvolvida, e com um ápice obtuso arredondado. O perióstraco pode ser fino ou moderadamente espêsso, colorido uniformemente ou com faixas verticais claras e escuras, às vêzes com zonas mais claras em forma de espiral, logo abaixo da sutura. A abertura é geralmente grande, mais alta do que larga, de forma oval alongada, podendo ser vertical ou mais ou menos oblíqua. Umbílico em forma de fenda ou completamente fechado; raramente perfurado ou aberto. Lábio externo geralmente bem expandido, com uma borda larga, mais ou menos acrescida de material calcáreo nos indivíduos velhos. Concha nepiônica excepcionalmente grande, com três a três e meia voltas, em geral coberta por uma escultura de costelas verticais, ou por estrias em espiral, às vêzes mesmo com granulações. As espirais pós-nepiônicas podem ou não ter granulações, ou esculturas verticais onduladas.

Becquaert (l. c. pág. 26) indica para *Strophocheilus* cinco subgêneros, a saber: *Strophocheilus* prop. dito, *Megalobulimus, Speironepion, Microborus,* e *Chiliborus,* dos quais nos interessa apenas o subgênero Megalobulimus.

SUBGÊNERO *MEGALOBULIMUS*

Espirais nepiônicas em sua maior parte com esculturas verticais completas ou incompletas, costelas ou dobras mais ou menos espaçadas, às vêzes com granulações diminutas; as outras espirais podem ser lisas, granulosas ou com estriações verticais. Concha geralmente grande (50 a 160 mm de comprimento) ovalada e alargada, geralmente achatada da frente para trás. Columela com ou sem vestígio de dobra; o lábio externo pode ou não ser refletido, sendo às vêzes acrescente em indivíduos velhos.

Becquaert (l. c., pág. 55) considera as "esculturas nepiônicas" como o caráter mais seguro para a distinção dos caracteres específicos, podendo elas diferir em tamanho, espaçamento, forma e extensão.

Segundo o autor, as conchas com esculturas nepiônicas concordantes devem considerar-se como ìntimamente relacionadas.

Os caracteres de forma e tamanho não são tão seguros, servindo entretanto para o reconhecimento de subespécies.

Cumpre notar que Morretes (1955, pág. 111) eleva o subgênero *Megalobulimus* Miller, 1878, para a categoria de gênero, e além de outros, cria o gênero *Psiloicus,* do qual *Psiloicus oblongus* Müller, 1774, é o tipo.

E' ausente a necessária justificativa do autor para estas novas introduções. Além do mais, alega não conhecer todos os representantes da família *Strophocheillidae* do Brasil, e os que conhece, nem todos estão em perfeito estado de conservação. Realmente, o novo gênero Megalobulimus foi criado com fundamento nos caracteres de três conchas mal conservadas (Morretes, l. c., p. 124).

A falta de uma tabela de dimensões e a comparação da diagnose do novo gênero (l. c., p. 112) com a de *Strophocheillus* (l. c., p. 110) não nos convenceu ainda da validade do novo gênero. Por isso, até que material mais abundante e estudos mais pormenorizados se façam, preferimos seguir Becquaert (1948) que apresenta dados baseados em material de tôda a América do Sul.

SINOPSE DAS SUBESPÉCIES DE *STROPHOCHEILUS* (*MEGALOBULIMUS OBLONGUS*)

Costelas nepiônicas numerosas, estreitas, quase retas, separadas por intervalos aproximadamente duplos da largura da costela. Concha em geral com uma espira cônica e estreitada, com um ápice obtuso. Abertura estreita e semi-elíptica, com uma columela quase reta. Peristômio rosa escuro, exceto na subespécie *albus*.

Esta descrição geral é válida para *S. oblongus,* bem como para as subespécies *albus, albescens, haemastomus, perelongatus, musculus, elongatus, lorentzianus* e *conicus*.

STROPHOCHEILUS (*MEGALOBULIMUS*) *OBLONGUS MUSCULUS* BECQUAERT 1948 (Figs. 1-4)

Concha de tamanho médio (mm 65,5 a 81,5 de comprimento e mm 37,5 a 45,0 de largura), de forma oblonga ovoidal (Fig. 1),

costelas de desenho grosseiro, côr pardo-clara, com columela, lábio externo e parede parietal róseo-clara ou róseo-avermelhada; abertura do peristômio de forma oval alongada, sendo mais alta do que larga (Figs. 3 e 4). Concha nepiônica volumosa, geralmente com uma acentuada escultura das costelas verticais (Fig. 2).

O material estudado consta de 15 conchas de adultos, tôdas provenientes de Pôrto Alegre.

As medidas destas conchas são as seguintes:

Comprimento mm	Largura vista frontal	Largura perfil	Comprimento abertura	Largura abertura
81,5	45,5	41,0	44,0	21,0
81,0	40,0	36,0	41,5	20,0
78,5	40,0	37,5	41,0	19,5
76,5	40,0	36,0	42,0	18,5
76,0	41,0	36,5	41,5	19,0
75,5	41,5	37,5	42,5	19,5
75,0	41,0	37,0	42,0	19,0
74,5	42,0	37,0	41,5	19,0
73,0	41,0	36,5	42,0	19,0
71,0	41,0	37,5	42,0	19,0
71,0	39,5	36,5	41,0	17,5
68,5	37,0	34,0	38,0	19,5
66,0	37,0	35,0	38,0	17,5
65,5	37,5	35,5	38,5	18,0
62,5	37,5	33,0	36,5	17,5

Comprimento: eixo maior vertical da concha, medido da ponta de espira ao lado basilar do lábio externo.

Largura em vista frontal: é o maior diâmetro transversal, medido em ângulo reto ao eixo vertical, da margem esquerda da espira do corpo ao ponto mais externo do lábio.

Largura em perfil: é a espessura dorso ventral da espira do corpo, medida em ângulo reto ao eixo vertical.

Comprimento da abertura: é o maior diâmetro, medido da junção superior do lábio externo e parede parietal até a parte basilar do lábio externo.

Largura da abertura: é o maior diâmetro transversal, medido em ângulo reto com o comprimento dentro do peristômio, da margem interna da columela à margem interna do bordo do lábio.

Ocorrência: Nas matas dos arredores de Pôrto Alegre, Estado do Rio Grande do Sul.

DISCUSSÃO

Dentro da espécie *Strophocheilus oblongus,* Becquaert (1948) reconhece nove formas distintas, já citadas, às quais atribui a hierarquia de subespécie para determinação sistemática.

A subespécie aqui descrita difere das outras principalmente pelo tamanho da concha e as proporções relativas, como se poderá ver pelas medidas mencionadas, além de outros caracteres que vêm mencionados por Becquaert (1948, pp. 59 e 61).

Seja dito que a forma geral se assemelha à de *S.o.haemastomus,* mas neste, o lábio externo é caracterìsticamente acrescente nas conchas adultas, servindo mesmo tal caráter para um cálculo aproximado da idade do animal.

Além disso, pela forma *S.o. musculus* distingue-se de *proclivis, auritus, santacrusi, carrikeri, capillaceus, terrestris, indigens, lichtensteini*. Pela forma e tamanho diferencia-se de: *granulosus, bronni, leucostoma, valenciennensis, maximus, intertextus, ovatus*. Pela espiral nepiônica pode-se separá-la de *globosus* e *sanctipauli*. O tamanho de *S. yporanganus* não permite confusão com *S.o. musculus,* e o número de espiras serve de caráter diferencial com *S. hauthali*.

COMENTÁRIOS

As Strophocheilidae foram estudadas no Brasil entre outros por Morretes (1937, 1949, 1953, 1955) e Buckup (1957). Não obstante, a literatura é relativamente confusa, e pareceria mesmo de interêsse um rápido comentário sôbre o estado atual da bibliografia com base no material de que dispusemos. Além disso, *S.o. musculus* é um gastrópode bastante comum nas matas circunjacentes a Pôrto Alegre, e pode constituir material de eleição para exercícios práticos de Zoologia e de Fisiologia Comparada, os quais, como se sabe, em outros países se fazem com *Helix pomatia,* que parece não foi assinalado entre nós. Além disso, não deixa de ser de importância o fato da ocorrência desta subespécie ser agora pela primeira vez mencionada para o Brasil.

A diagnose de moluscos, baseada ùnicamente nos caracteres da concha é relativamente precária, e principalmente daí decorrem as di-

ficuldades e divergências na taxonomia dêstes animais. Acontece que a anatomia interna das *Strophocheilidae* só é conhecida de quatro espécies do subgênero *Megalobulimus,* a saber: *Strophocheilus oblongus* (Guppy, 1866; Semper, 1874; Semper e Simroth, 1894; H. v. Ihering, 1884 e 1891; e Baker, 1926); *Strophocheilus oblongus lorentzianus* (Scott, 1939); *Strophocheilus ovatus* (Crosse e Fischer, 1875; Plate, 1896); *Strophocheilus terrestris* (Plate, 1896); e *Strophocheilus maximus* (Semper e Simroth, 1894). Os trabalhos mais completos são os de Scott (1939) e de Baker (1926). Acha-se também descrita a morfologia interna de *Gonyostomus* (*Anthinus*) *multicolor* Rang (1831).

As 41 espécies de *Strophocheilus* e as 4 de *Gonyostomus* reconhecidas até agora são indígenas da América do Sul, desde o norte de 40° de latitude Sul, até a Ilha de Trinidad, nas Antilhas.

A ocorrência de *S. oblongus* em algumas localidades das Antilhas parece ter sido devido à introdução pelo homem. Até agora não se encontrou nenhuma espécie ao norte do Canal do Panamá.

Admitem-se quatro centros principais de densidade de espécies. Dêstes, o mais importante é a metade oriental do Brasil, do Maranhão ao Rio Grande do Sul, onde se encontram tôdas as quatro espécies de *Gonyostomus,* duas de *Speironepion,* sete de *Strophocheilus* pròpriamente dito, bem como dez espécies de *Megalobulimus*. Um segundo centro é a região andina, desde a Bolívia até a Colômbia, na qual se encontram oito espécies exclusivas de *Megalobulimus*. O subgênero *Microborus,* com três espécies é restrito ao Uruguai e norte da Argentina, não se levando então em consideração material subfóssil encontrado no RGS por v. Ihering (Becquaert, p. 170). O subgênero *Chiliborus,* com quatro espécies, acha-se limitado à região central do Chile.

A família *Strophocheilidae* compreende ainda alguns dos maiores gastrópodes terrestres atualmente existentes, sendo excedida em tamanho entretanto por algumas espécies africanas da família *Achatinidae*. E' interessante notar que estas duas famílias parecem equivaler-se em seus respectivos continentes, onde ocupam aproximadamente os mesmos nichos ecológicos, isto apesar de serem as *Achatinidae* mais prolíficas em número de gêneros e espécies, tendo desenvolvido tipos arborícolas.

Em *Strophocheilidae,* o ôvo, de forma elíptica alongada, possui casca relativamente grossa; os lados são achatados, sendo as extremidades semelhantes. O tamanho do ôvo é proporcional ao do animal, sendo maior em *S. popelairianus* (mais ou menos 5 cm) o que vem a ser o máximo tamanho de ovos de moluscos terrestres.

Todos os caracóis são estritamente terrestres, com preferência por lugares protegidos, úmidos e sombrios, densamente cobertos por vegetação, tais como as encostas das florestas virgens. São geralmente de hábitos noturnos, escondendo-se em solo fôfo durante o dia. Podem ser encontrados em atividade durante o dia por ocasião de fortes chuvas, especialmente com temperatura elevada.

Durante épocas de sêca normalmente se enterram até 5 ou 10 cm de profundidade, o mesmo acontecendo na região sul durante o inverno, por ocasião de tempo frio e sêco.

Strophocheilus oblongus parece estar especialmente associado ao regime doméstico, pois é muito comum em jardins, terrenos cultivados e matas secundárias.

Na literatura especializada disponível, verificamos a indicação das seguintes espécies de *Strophocheilidae* no Rio Grande do Sul:

Strophocheilus (*Megalobulimus*) *oblongus* O. F. Müller, 1774
S. (*Megalobulimus*) *oblongus haemastomus* Scopoli, 1786
S. (*Megalobulimus*) *globosus* v. Martens, 1876
S. (*Megalobulimus*) *proclivis* v. Martens, 1888
S. (*Megalobulimus*) *granulosus abbreviatus* Becquaert, 1948
S. (*Strophocheilus*) *planidens fusoides* Becquaert, 1948
S. (*Strophocheilus*) *erythrosoma* Pilsbry, 1895
S. (*Microborus*) *lutescens* King e Broderip, 1832
Gonyostomus (*Anthinus*) *turnix albolabiatus* Jaeckel, 1927

Na localidade de Taquara do Mundo Novo coletaram-se: *S. oblongus, S. planidens fusoides, S. erythrosoma* e *S. proclivis.* De Santa Rosa, próximo ao Rio Uruguai, obtiveram-se *S. oblongus* e *Gonyostomus turnix albolabiatus.* De Santa Maria provem *S. oblongus haemastomus.* De Viamão é citado *S. oblongus haemastomus,* enquanto que em Pôrto Alegre foi encontrado *S. globosus.* Há também citação da ocorrência de *S. felipponei* para Pôrto Alegre (Buckup,

1957) mas esta espécie foi incluída por Becquaert na sinonímia de *S. globosus*.

Citam-se ainda coletas nas localidades de Bolassa e Rodersberg, supostamente no RGS, as quais entretanto não puderam ser localizadas. Para muitos outros exemplares colhidos não há indicação precisa de localidade, mas apenas Rio Grande do Sul.

Apesar de *S. oblongus musculus* nunca ter sido encontrado fora da Argentina e do Paraguai, devemos atentar entretanto para a semelhança de biótopos existentes na região da Depressão Central e Campanha do Rio Grande do Sul e na região norte da Argentina.

Becquaert menciona ainda uma possibilidade de intercruzamento entre *musculus* e *lorentzianus* na região norte da Argentina. Segundo êle, *lorentzianus* seria uma forma típica de regiões montanhosas, enquanto *musculus* estaria restrito a regiões planas e de mata rala, correspondentes estas últimas aos biótopos encontrados nos arredores de Pôrto Alegre.

SUMMARY

Specimens of land gastropods collected at Pôrto Alegre, Rio Grande do Sul, were identified by the authors as *Strophocheilus* (*Megalobulimus*) *oblongus musculus,* a subespecies up to now restricted to Argentina and Paraguay.

A revision has been made on the available litterature concerning the ocurrence of the *Strophocheilidae* at Rio Grande do Sul.

A diagnosis of the genus *Strophocheilus* and of the subgenus *Megalobulimus* is presented, as well as the necessary data for the identification of the subespecies *musculus*.

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ESTAMPAS

Strophocheilus oblongus musculus Bequaert 1948

Fig. 1 — Concha nepiônica.
Fig. 2 — Vista dorsal da concha.
Fig. 3 — Vista ventral da concha.

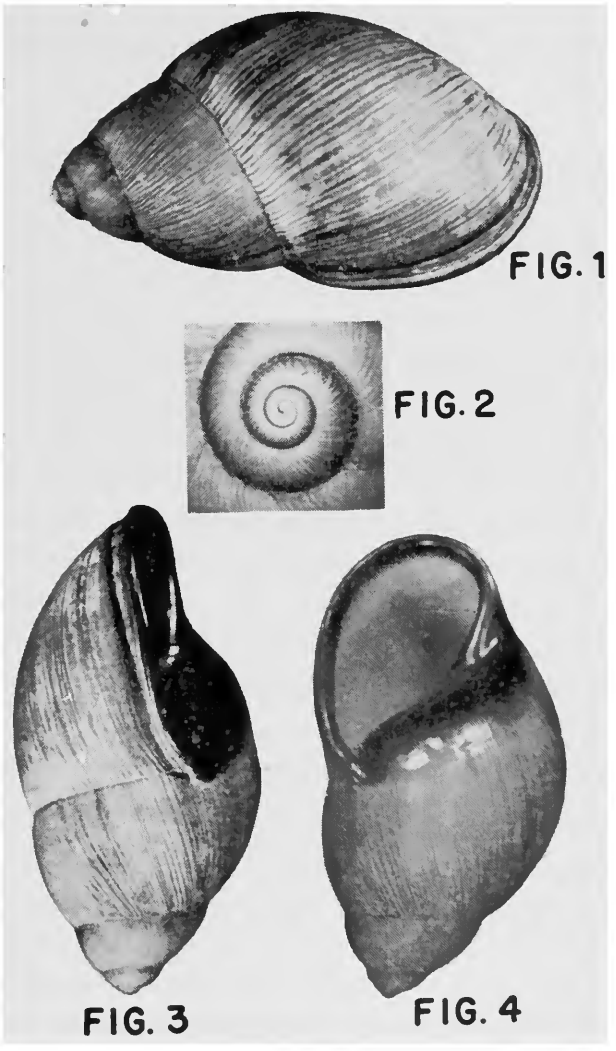
FIG. 1
FIG. 2
FIG. 3
FIG. 4

THE RESPIRATORY METABOLISM OF TROPICAL EARTHWORMS

III. *The influence of oxygen tension and temperature*

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In the two previous paper of this series we have focused (a) the normal respiratory rate, the role of haemoglobin and the relation between size and respiratory rate (MENDES & VALENTE, 1953) and (b) the intraepidermal capillaries and the action of externally applied adrenaline and acetylcholine on the respiratory rate (MENDES & NONATO, 1957) of some Brazilian earthworms (*Pheretima hawayana, Pontoscolex sp.* and *Glossoscolex sp.*). We now present the results of experiments performed to determine in what extent the variations of oxygen tension and temperature affect respiration.

In the present work only *Pheretima hawayana* has been used because its wide geographical distribution makes it the ittest earthworm in Brazil for a research aiming at the detection of climatic adaptations.

In fact, *Pontoscolex* and *Glossoscolex* can be regarded as typical genera of Equatorial and Tropical America, whereas *Pheretima* has been transported all over the world. In Japan it forms the largest number of endemic worms, it is characteristic of Burma and of the Indo-Malayan division, it occurs in Australia and Tasmania, being almost the only genus in the intervening islands between Australia and India. This "mighty genus", according to STEPHENSON (1930), relatively young and highly specialized, is by far the largest genus of Terricolae and appears to have power of conquering large territories and holding them itself alone, crushing all competitors. STEPHENSON (l. c.) also states that a number of species, including *P. hawaya-*

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na, are highly peregrine and have established themselves widely in the warmer regions of the globe, but he did not mention species of the genus when he discussed the Neotropical region nor included South America in its geographical distribution.

Pheretima, however, is known to occur in South America at least since the publication of the treatise of *MICHAELSEN* (1900), in which *P. barbadensis* is mentioned to exist in Chile (Santiago) and Brazil (Porto Alegre and Manaus) and *P. hawayana* in Brazil (Porto Alegre, Santos and S. Paulo).

STEPHENSON (l. c.) also informs that attempts to introduce *Pheretima* in temperate and cold climates have failed and that in England it has been maintained only in botanical gardens, not spreading outside.

Now, the fact that members of the genus can reach in the Southern hemisphere as far as Santiago (winter temperatures down to -4°C, occasional snowfalls) and in the Northern hemisphere up to Hakodate (*P. hilgendorfi*), Japan, where winters can be severe, does raise questions as to the inability of species of *Pheretima* to endure colder climates and fully justifies the choice of *P. hawayana* for our study. São Paulo, on the eastern edge (Serra do Mar) of the great Brazilian plateau, has a subtropical climate, with winter temperatures occasionally going within a day from almost zero (before sunrise) to 20°C (ca. 2 PM). This is partly due to the relatively high altitude of the city (ca. 800 m.). A study, therefore, of the respiratory responses to temperature variation of such a cosmopolitan earthworm exposed to such a climate may prove valuable for intra-and-interspecific comparisons with members of definitely temperate (such as Santiago) or warm (such as India) regions. As a matter of fact, in what concerns the relationship between respiration and temperature in earthworms, the literature is very scarse, as we shall see later in the discussion of this paper.

The respiratory responses of *P. hawayana* to varying oxygen tensions were studied because, to our knowledge, no such a type of work exists concerning tropical earthworms. Besides, the question of the interrelation between oxygen consumption and oxygen tension in earthworms is still open to discussion, since despite of recent evi-

dence (JOHNSON 1942, for instances) pointing to at least a relative dependence of the consumption on tension, this oligochete continues to be considered as good regulator of respiration (see BISHOP 1953) on basis of less accurate work.

METHODS

The animals came from the Faculty garden and stayed, before use, 24 hours in the dark, in moist chambers made of Petri dishes lined with moistened filter paper. The experimental procedure adopted was already described in detail in the first work of this series (MENDES & VALENTE, l. c.).

In the "oxygen tension" section of the present work, the oxygen uptake was measured at 25°C and 36 complete oscilations of the Warburg flasks per minute, during one hour and then compared with that of a second hour run at air tension or at a certain lowered oxygen tension. Gas mixtures were prepared using oxygen and nitrogen (twice washed in alkaline pyrogallol) in the desired percentages. The perfusion of the flasks took place usually during 10 minutes, while they were under shaking.

In the "temperature" section, different temperatures were obtained either heating the bath up to 45°C or cooling it with cooling unit, whose coil was kept completely immersed in the water. In either case it was possible to keep a chosen temperature within a maximum of 0.5°C variation, even when extremes temperatures were used. Before "zero readings", the flasks containing the animals stayed in the bath at least 15 minutes in order to get equilibration of the temperatures inside and outside.

One animal per flask was used throughout the experiments, which, of course, were performed in the dark. More details of the methods will be given below.

EXPERIMENTS

Oxygen consumption and oxygen tension in Pheretima. As stated above, the effects of varying oxygen uptake of *Pheretima* were studied by measuring a first hour uptake for each animal and then a second hour rate at air or at a certain lowered oxygen tension for

the same animal. This procedure allowed (a) to check the effect of the second hour stay in the flasks, by simply renewing the air inside the flasks instead of perfusing with a gas mixture of a lesser oxygen content: (b) to compare, for a same animal, the immediate effect of lowering the oxygen tension.

Table I and graph 1 show the results obtained. Whether considered *per se* or in percents of the 1st. hour rates, the values of the

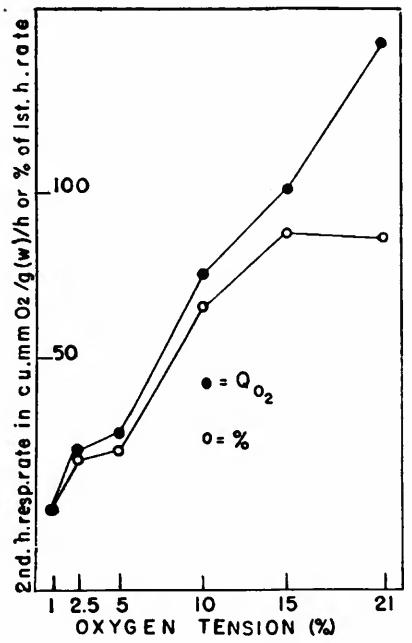

Fig. 1 — The relation between oxygen consumption and oxygen tension in *Pheretima hawayana*

2nd. hour rates clearly show that *P. hawayana* cannot regulate respiration from 10% 0_2 downwards. At 15% the respiratory rate is still insignificantly lower than at air, but from 10% downwards the decrease in the oxygen consumption is highly significant. The data also show that at air tension, a 2nd. hour stay in the flasks did not significantly alter the respiratory rate. The same holds for the 2nd. hour rate at 15% 0_2, which, as a matter of fact, in percents of the 1st. hour rate is higher than at air tension, although not significantly. In terms of $Q0_2$, in the graph of fig. 1, this cannot be seen on account of the higher values obtained both at 1st. and 2nd. hour (lighter animals were used) in the first series as compared with corresponding ones

in the second. The fact also explains why the curves in figure 1 do not agree between 21 and 10% 0_2 and emphasizes the advantage of expressing the rate at the different oxygen tensions in percents of the first hour rate rather than in absolute values measured.

TABLE I

The respiratory rates of the earthworm *Pheretima hawayana* at different oxygen tensions. 24 hour starving animals, in the dark, at 25°C and 36 strokes per minute. Mean local atmospheric pressure = 702 mm. Hg.

Exp. Ser.	N.° of Exps.	Gas phase in the flasks		Rates of oxygen consumption cu.mm. at N.T.P. per g per h. Means & std. devs.		P_1	2nd. hour mean rate as % of 1st. hour	P_2
		1st. h.	2nd. h.	1st. h.	2nd. h.			
1	10	air	air	169 49	139 35	0.8	85 05	
2	10	air	15%0_2	118 20	101 14	0.8	87 12	0.7
3	10	air	10%0_2	116 07	75 07	0.01	65 07	0.01
4	10	air	5%0_2	112 34	46 24	0.01	42 17	0.01
5	10	air	2.5%0_2	98 14	37 10	0.01	38 10	0.01
6	10	air	1%0_2	105 13	24 07	0.01	24 09	0.01

At the end of the experiments, in all series, the animals crawled out of the flasks by themselves, indicating that even the extremely low oxygen tensions used did not affect them.

Oxygen consumption and temperature. Table II and the graphs of figures 2 and 3 show the results obtained when the respiratory rate of *P. hawayana* was measured at different temperatures. In all experiments the animals passed directly from room temperature (ca. 25°C) to the temperature of the water bath and time was only given to equilibrate the temperatures in and outside the flasks. The results therefore express the immediate effects of transferring the earthworms from room to experimental temperatures.

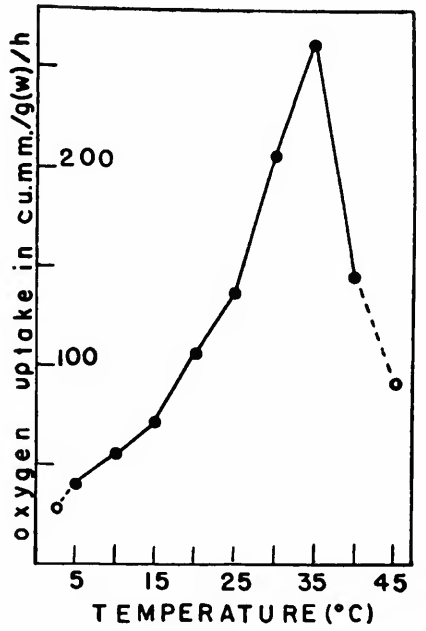

Fig. 2 — Graph relating the oxygen consumption to temperature in *Pheretima hawayana*.

In table II, for each temperature, the weight range is given in order to show that, due its relative narrowness, size effect little interfered with the results. We considered dangerous, in this section, to

TABLE II

The effects of temperature variation on the respiration of the earthworm *Pheretima hawayana*. Animals taken from room temperature (ca. 25°C). In the dark. Shaking rate = 36/min. Gas phase = air. $Q0_2$ = cu.mm.02/g(w.)/h.

Exper. Series	Temper. (°C)	N.° of cases	Weight range in g.	Mean $Q0_2$ & std. dev.	P
1	40	10	0.623-0.863	142 34	0,7
2	35	10	0.622-0.882	261 47	0,01
3	30	10	0.627-0.905	206 50	0,01
4	25	10	0.693-0.863	137 30	—
5	20	10	0.627-0.900	106 28	0,05
6	15	10	0.604-0.839	70 11	0,01
7	10	10	0.606-0.892	54 10	0,01
8	5	10	0.622-0.891	40 08	0,01
9	45	6	0.242-0.445	90 26	0,01
10	2	5	0.732-1.118	28 03	0,01

measure the respiratory rate of a same animal first at room temperature and then, in a second hour at a higher temperature. For the sake of uniformity, the same criterion was used when temperatures below 25°C were used. We think, however, that the ten experiments of each series afforded enough data to face the inconveniences of individual variations.

Taking 25°C as a starting point, a rise in temperature significantly increased the oxygen consumption up to 35°C. A Q_{10} of almost 2 is obtained when the rates at 25°C and 35°C are related. At 40°C the respiratory rate almost returned to the 25°C level and at 45°C the six data of table II show that respiration, expressed in QO_2, is significantly reduced as compared with the 25°C rate. These results, however, do not exactly express the situation of the animals above 35°C. In fact, as shown in the graph of figure 3, at

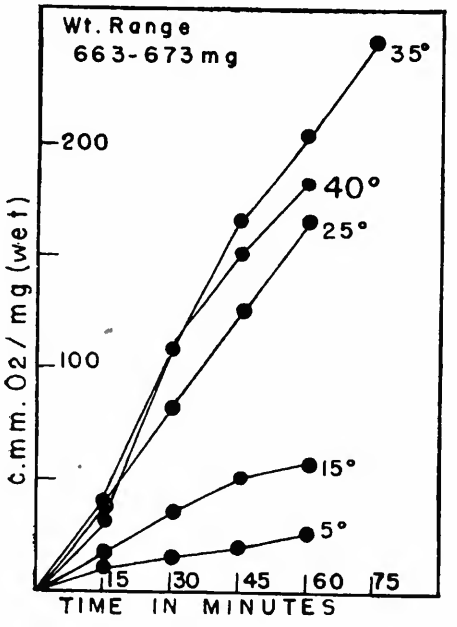

Fig. 3 — Time course of the oxygen consumption of *Pheretima hawayana* at different temperatures (°C.

40°C, respiration is at first greatly increased, to decrease after 30 minutes, leading to an hourly rate nearer the 25°C level. This decrease, after an initial increase, is still stronger and earlier at 45°C. Fig. 3 also shows that, at 35°C, the respiratory increase tends to decline after 45 minutes, when a slight inflection in the curve is ob-

served. Thus, the hourly rates determined at 40°C and 45°C really reflect a sudden increase in metabolism due to temperature rise, followed by a decrease due to temperature damage. In fact, from 35°C upwards, at the end of the experiments the animals were taken out of the flasks motionless and hemorrhagic. After one hour stay at 45°C, the animals were apparently dead, disrupt and dit not recover. At 40°C, body disruption was not observed, but the animals seldom recovered. Recovery was often observed after the hourly stay at 35°C.

A decrease in temperature also affected respiration since, from 20°C downwards, the respiratory rate was significantly lower as compared with the 25°C level. A Q_{10} of almost 2 is obtained when the rates at 25° and 20° are related respectively with those at 15° and 10°C. The graph of fig. 3 shows that the decrease can be detected after 15 minutes. The animals, however, were not apparently affected by the lowered temperatures used, since even after a 75 minutes stay at temperatures as low as 2°C, they emerged from the flasks in good condition. At 5°C they got out by themselves after a while at room temperature; at 2°C they seemed in a state of cold narcosis from which they generally recovered after a few hours. No external injury was observed in the animals submited to temperatures down to 2°C.

P. hawayana and Rapid Compensation for Temperature — Although it was not the purpose of this work to investigate *P. hawayana*'s ability to restore the normal respiratory rate after a prolonged stay at low temperatures, thus compensating for different temperatures, a preliminary study was made as to rapid compensation.

In this series, the respiratory rates of two lots of animals were measured in a first hour at 25°C and, then, one lot remained at this temperature and the other was transferred, within the Warburg flasks, to a bath at 5°C. Afterwards, the respiration of both lots was measured again for a certain length of time, with periodical renewal of the air inside the flasks to prevent oxygen debts. Unfortunately, due to the experimental conditions used, both lots, after ca. 24 hours, showed signs of being limp (they had been previously submitted to a 24 hour period of starvation in Petri dishes) and the experiment could not go on. Nevertheless, it provided at least some evidence which suggest

that in *P. hawayana* there is no rapid compensation for temperature. In fact, as shown in table III, after being transferred to 5°C the earthworms respired significantly less than those maintained at 25°C during all the duration of the experiment. A slight increase in oxygen consumption is observed when the rates at 9-10 PM (April 26) and those of the following day are compared. This increase, however, is not significant in terms of the rate at 25°C. As a matter of fact, the values determined in this series for 5°C never attained the level of those determined immediately after placing the animals at 5°C (see table II). The extremely low values registered after ca. 5 hours at 5°C (April 26, 9-10 PM) and the slightly higher ones of the following day indicate that, at least for this low temperature, the decrease in oxygen consumption immediately observed in the animals transferred from 25°C (table II) is not followed by a rapid compensatory increase.

It is interesting to mention that in this series, during the experiments, occasionally the animals put at 5°C failed to exhibit any

TABLE III

A test for rapid temperature compensation in *P. hawayana*
Gas phase: air $Q0_2$ = cu.mm.0_2/mg.(w.)/h. 36 strokes/min.

		LOT I				LOT II				
Day	Hours	N.° of animals	Temp. (°C)	Mean $Q0_2$	Std. dev.	N.° of animals	Temp. (°C)	Mean $Q0_2$	Std. dev.	P
April 26	4-5 PM	3	25	128	19	4	25	131	11	—
" "	6 PM		(lot kept at 25°)				(Lot transferred to 5°C)			
" "	9-10 PM	3	25	98	42	4	5	2	—	0.01
April 27	10-11 PM	3	25	110	34	4	5	18	4	0.01
" "	12AM-1 PM	2+	25	105	—	4	5	13++	9	0.01

+ one animal died ++ one animal did not practically respire.

oxygen consumption between two readings and in some cases gas was produced inside the flasks instead of being absorbed. Although in the control lot one of the animals died, the results show that no respiratory depression was due to the prolonged stay in the flasks.

DISCUSSION

1. Modern work on the *interrelation between oxygen consumption and the oxygen tension* in earthworms starts with JORDAN & SCHWARZ (1920), who, using specimens of *Lumbricus terrestris* narcotized with 10% alcohol, reported that, at 25°C, above 7% 0_2 the consumption independs of the tension. From these results and also from those obtained when hemoglobin was put out of action by carbon monoxide, they concluded that in the earthworm the oxygen normally used is that dissolved in the plasma and that the pigment serves for the subterranean life where the oxygen tension is low. The AA. used the gas pipette to measure respiration and drew conclusions from the respiratory rates of different animals submitted to different oxygen tensions.

DOLK & VAN DE PAAUW (1929) repeated JORDAN & SCHWARZ' work because they thought it was precarious to compare the rates of different animals on account of the unequal earth content of the gut, which might have influenced on the weight used as basis to express the oxygen consumption. They used single animals in a Krogh's microrespirometer, anesthetized with 8-9% alcohol, but made no reference as to whether the experiments were performed in the dark or not. In order to know the effect of the brief (6-8 minutes) immersion of the animals in alcohol, a procedure which aimed at obtaining "standard conditions", they previously followed the respiration of worms so narcotized for 48 hours and reported that after 20 hours the animals were quietly respiring at a constant rate, with the dorsal blood vessel normally pulsating. Consequently, they used in the experiments worms which were put in the respirometer chamber soon after a brief immersion in alcohol and there stayed overnight, with periodical renewal of the internal air, to keep the oxygen tension normal till just before the initial readings. Oxygen tensions below normal were obtained by letting the animals exhaust the gas inside the chamber and they were roughly calculated from the initial air volume at the animal's disposal and the subsequent oxygen consumption. The 0_2 uptake was not expressed in function of body weight, but in cu.mm./30 min. or in % of the first reading. With this procedure the

AA. believed to have avoided the inconveniences of individual weight variations.

Despite of using such a different procedure, DOLK & VAN DE PAAUW did not essentially obtain results different from JORDAN & SCHWARZ'. In fact, down to 2,5% 0_2 the oxygen consumption of the worms independed of the tension. This led the AA. to admit that earthworms are animals in which the metabolic rate is governed by the tissues over a wide range of oxygen tensions. Above 2,5% 0_2, a positive oxygen pressure would exist in the tissues, the combustion process being regulated by other limiting factor than oxygen transport. Recalling the conflicting views of Pflüger & Pfeffer and Thunberg on the subject, they went on to state that only in animals with tissue oxygen pressure constantly tending to zero the metabolic rate increases with the external 0_2 tension. In those with a positive pressure, even when the external tension is very low, the limiting factor is not tension, but enzymes and foodstuf. Earthworms, however, are not to be compared with Vertebrates, where oxygen uptake also does not very with oxygen tension over a wide range. In redblooded Invertebrates such as the earthworms, according to DOLK & VAN DER PAAUW'S results, it is the plasma not the blood pigment that is in charge of the oxygen transport down to very low external 0_2 tension; down to 7.5% 0_2 their curves for normal and CO-treated animals are the same. Thus, despite the fact that with increasing oxygen tensions more oxygen can dissolve in the plasma, the animals do not necessarily make use of it.

THOMAS (1935) criticized both JORDAN & SCHWARZ' and DOLK & VAN DER PAAU's works on the grounds that the alcohol concentrations used for narcosis were too strong. This *plus* individual variation towards alcoholic anaesthesia were likely to lead to false results. He therefore reinvestigated the matter, using more or less the same technical procedure as DOLK & VAN DER PAAUW and also not taking into account the body weight to express the oxygen consumption. He observed a great variation in the respiratory responses of the worms submitted to a brief immersion in 8-9% alcohol and reported that the respiration of worms treated with 6% alcohol dit not differ from that of normal ones kept quiet inside a long glass tube.

In either case, letting the animals exhaust the environmental oxygen to get low 0_2 tensions, THOMAS observed that from 20.9% to 15% 0_2 the oxygen uptake decreased and thereafter remained constant down to 3%, to decline again. The fact that above 15% 0_2, the consumption increasead with tension was considered by THOMAS as indicating that DOLK & VAN DER PAAUW's view regarding the interrelation between consumption and tension in earthworms is incorrect. He suggested that by some unknown mechanism (acting probably on the capillaries) more oxygen is admitted to the tissues above 15%, leading to a higher 0_2 uptake. Finally, he did not attribute to hemoglobin the constancy observed between 15 and 3%, because it occurred also in the CO-treated animals.

In 1942, JOHNSON, in a study of the function of hemoglobin in *Lumbricus herculeus,* measured parallelly the oxygen consumption of normal and CO-treated animals at different oxygen tensions. This work was undertaken on account of the faulty technique of the previous studies, which included (a) the narcosis of the animals, (b) the lack of reference to the light condition during the experiments, (c) a poor process of obtaining low 0_2 tensions by letting the animals exhaust the gas during a too long stay in the respiratory chamber and, finally (d) conclusions based on too little (sometimes only 2 cases!) number of experiments. JOHNSON's technique is in many respects comparable to that of the present work. The animals were kept at least 3 days in damp soil (earth or filter paper?) and darkness before the experiments. The oxygen consumption was measured in a Barcroft differential respirometer, in the dark and at 10°C, and expressed in function of the body weight. Oxygen tensions lower than normal were obtained by perfusing the flasks with proper $N_2/0_2$ mixtures. For each oxygen tension tested a large number of animals was employed and the data were treated statistically. All this procedure intended to minimize the effects of individual variation and made undoubtly JOHNSON's work the first sound experimental study dealing with respiration in earthworms. It is worth while therefore, to compare its results with ours.

JOHNSON's *Lumbricus,* at 10°C, regulated respiration down to 76 mm. Hg (ca. 10% 0_2), below this value respiration fell sharply.

Pheretima, at 25°C, already respired significantly less at 10% 0_2 than at air tension; thereafter respiration continued to regularly decline with decreasing tension. JOHNSON's results differ from all previous studies essentially in that already after 10% 0_2 there occurred (at 10°C) a loss in regulation, whereas in JORDAN & SCHWARZ; DOLK & VAN DER PAAUW's and THOMAS' works this happened at respectively 7, 2.5 and 3% 0_2 (at 25°C).

An attempt to explain why in our experiments the loss of regulation occurred already at 10% 0_2 involves necessarily the consideration of the temperatures used in JOHNSON's and our works. At air saturation, *Pheretima* exhibited a $Q0_2$ of 139 (table I) at 25°C and 54 (table II) at 10°C; JOHNSON's *Lumbricus* showed at 10°C a $Q0_2$ of about 38 (heavier animals were used!). It is probable then that the higher temperature used was responsible for the lesser ability of *Pheretima* to regulate respiration. In fact, one would expect a higher metabolism at 25°C than at 10°C, hence a greater dependence on the oxygen tension (BISHOP, l. c.).

This kind of reasoning leads to the consideration of whether DOLK & VAN DER PAAUW's view on earthworm respiration is correct or not; namely, that metabolism in this oligochete is solely regulated by enzymes and food-stuff and not by oxygen transport, the 0_2 pressure in the tissues being positive even when the external 0_2 tension is extremely low. BISHOP (l. c.), reviewing the question of the interrelations between oxygen consumption and oxygen tension in animals, emphasized the fact the different responses to decreased 0_2 tensions, in some cases, can be attributed to "different activity adjustments", sluggish animals being far more independent on tension than active ones. Lack of dependence of the oxygen consumption on tension, on the other hand, can be due to "sheer efficiency of respiratory mechanisms at low tensions, such as plasma hemoglobin which enables many aquatic animals to extract oxygen at very low 0_2 tensions".

Now, earthworms (at least *Pheretima* at 25°C!), although moving when undisturbed by slow peristaltic waves, can hardly be considered as sluggish animals. Their prompt reaction to peripheral stimulation by the "Zuckreflex" or quickly jumping, indicate a high

muscular tonus, which can only be maintained at the expense of a considerable degree of metabolic activity. It is difficult, therefore, to admit that in earthworms the tissular 0_2 pressure is kept positive, especially at extremely low 0_2 tensions. Neither can the presence of hemoglobin in earthworms blood be used as indicating independence of the 0_2 uptake on tension, in the sense of BISHOP's words. Whether one considers earthworms' haemoglobin as an oxygen storer (JORDAN & SCHWARZ, DOLK & VAN DER PAAUW) or an oxygen carrier (JOHNSON; MENDES & VALENTE) it is always difficult to understand how the pigment would serve to help regulation at the intermediate 0_2 tensions between air saturation and the tensions at which respiration begins to depend on the available oxygen. In this respect, it is important to emphasize the parallelism of the curves for normal and CO-treated animals observed either in the works of DOLK & VAN DER PAAUW and THOMAS or JOHNSON's, despite the diverging results regarding the function of hemoglobin. It is a pity that BISHOP, although knowing about JOHNSON's work (the critical tension, 76 mm. $Hg0_2$, obtained for *L. herculeus* at 10°C is mentioned at table 43 of his review), preferred to base his admission of earthworms as good regulators entirely on the less accurate work of DOLK & VAN DER PAAUW (pages 246-248).

Using the degree of activity as a criterion for, at least partially, explaining the interrelations between 0_2 consumption and 0_2 tension, one is tempted to analyse why earthworms under alcoholic anaesthesia should independ on tension over such a wide range. This could be understood in terms of a general metabolic depression due to narcosis, so that one would get, even at air saturation, a low respiratory rate for comparison with the rates at the decreased 0_2 tensions. Besides, the low degree of activity of the narcotized animals would really contribute to lessen the 0_2 depletion in the tissues, enabling them to apparently regulate respiration.

It is difficult, however, to compare JOHNSON's or our data with those obtained with narcotized animals, since neither DOLK & VAN DER PAAUW nor THOMAS expressed their results in terms of body weight, reporting only the volumes of the animals. Nevertheless, admitting roughly a volume / weight ratio ca. 1, probable

respiratory rates ($Q0_2$) can be calculated from their data expressed in cu.mm. 0_2/30 min., obtained at the beginning of the experiments (air saturation). Table IV includes all DOLK & VAN DER PAAUW's data and 3 of the 4 results presented by THOMAS, for a comparison with the $Q0_2$ of *Pheretima* of comparable volumes obtained by MENDES & VALENTE.

This rough calculation of $Q0_2$ for *Lumbricus* does not indicate that in DOLK & VAN DER PAAUW's experiments there was a respiratory depression (one out of 3 data is lower than those of *Pheretima* of comparable volumes); from THOMAS's calculated $Q0_2$, however,

TABLE IV

A comparison of the respiratory rates of *Lumbricus terrestris* and *Pheretima hawayana* to show the possible effects of alcoholic anaesthesia. Temperature = 25°C. Air saturation.

Experimental conditions	Light conditions	Volume (ml)	$Q0_2$	AUTHOR
narcotized	?	1.43	160	DOLK & VAN DER PAAUW
normal	dark	1.40	131	MENDES & VALENTE
narcotized	?	1.30	99	DOLK & VAN DER PAAUW
narcotized	?	1.08	156	DOLK & VAN DER PAAUW
normal	dark	1.00	143	MENDES & VALENTE
normal	dark	0.90	174	MENDES & VALENTE
normal	dark	0.60	271	MENDES & VALENTE
narcotized	?	0.43	168	THOMAS
narcotized	?	0.42	162	THOMAS
narcotized	?	0.18	208	THOMAS

there seems to be reason to admit depression since, despite the decreasing volumes, the rates do not proportionally increase as expected on basis of the value obtained for the 0.60 ml. *Pheretima*.

Narcosis was used in order to get "standard conditions", that is, quietness inside the respiratory chamber. THOMAS himself demonstrated that this is an useless procedure. Earthworms, due to thigmotaxis, can stay quiet and motionless inside glass flasks, especially in the dark.

2. Taking room temperature (25°C) as a starting point, a rise or a decrease in temperature by 5° intervals significantly altered the

respiratory rate of *Pheretima*. Up to 35°C, there occurred a respiratory increase. At 40°C, however, temperature definitely injured the animals, leading to a mean $Q0_2$ near the 25°C level, which only express an initial increase in respiration followed by a decrease due to temperature injury. Below 25°C respiration regularly decreased with temperature, but the animals were not apparently affected even by temperatures as low as 2°C.

Except for the work of KIRBERGER (1953), we do not know of any other particular paper dealing with the effect of temperature on the respiration of earthworms. The previous information on the subject seems to amount to the following: VERNON (1897, apud BULLOCK 1955), in his classical work, mentioned that in *Lumbricus* there exists a plateau extending over ca. 12°C when carbon dioxide output is plotted against temperature.

KIRBERGER is a member of the Kiel group led by PRECHT (see, for instances, PRECHT 1949) to which we owe in the last ten years important works on the relation between vital processes and temperature both at the organism and the cellular level. In 1953, she studied the problem in some Invertebrates, including the Oligochetes *Lumbriculus variegatus* (limnic) and *Eisenia foetida* (terrestrial). As to the earthworms, she previously found that a sudden increase of temperature from 15 to 25°C remarkably enhanced the respiratory rate, that is, the rate at 25°C in animals adapted to this temperature is lower than the rate at the same temperature of animals freshly transferred from 15°C. This temperature shock can be avoided by slowly (degree by degree) transferring the animals from 15°C to 25°C. The oxygen consumption of starving animals was about 70% of the fed ones. Whether starving or fed, *Eisenia* adapted to 15°C and 25°C exhibited at the experimental temperatures used (15, 20 and 25°C) the same respiratory rates. That is, the rates at 15, 20 and 25°C regularly increased whether the animals were transferred from a 15° or a 25° environment. No seasonal influence was also observed. The return point ("Umkehrpunkt") of the respiratory curve with increasing temperatures was located between 36°C and was found to be independent of the adaptation temperature. *Lumbriculus* behaved differently, in the sense that it showed respiratory adaptation;

the 0_2 uptake at the same experimental temperatures diminished with increasing adaptation temperatures. This different behaviour was attributed to the different biotopes of the two worms, terrestrial *Eisenia* being in nature less exposed to temperature variations than aquatic *Lumbriculus*. The succinodehydrogenase activity of the earthworm *Eisenia* was also found to be independent of the adaptation temperatures. Finally, KIRBERGER exposed *Eisenia* to a 30 minute immersion in bathes at different high temperatures in order to determine its heat resistance expressed as percents of survival. The resistance rose with increasing adaptation temperatures, seasonal influences being observed. No clear adaptation, however, was observed in the cellular level as juged by the succinodehydrogenase activity. Trying to explain why the "Umkehrpunkt" of the heat resistence depends of the adaptation temperature and that of the respiratory curve not, KIRBERGER emphasized that in the former case one has to consider the irreversible injury of the proteins because here the "Umkehrpunkt" coincides with the extreme limit temperature of life. This would also explain the lack of influence of the adaptation temperature on the "Umkehrpunkt" of the respiratory curve.

The data of table IV of this paper indicate that *Lumbricus* and *Pheretima* of comparable sizes have more or less equivalent respiratory rates when our results are confronted with DOLK & VAN DER PAAW'S, but that THOMAS' *Lumbricus,* although smaller, respired less than *Pheretima*. Had these authors not worked with narcotized animals, their results would serve to compare at a same temperature (25°C), the respiratory rates of a temperate and a tropical earthworm. JOHNSON's results interest in the sense that they were obtained with an accurate technique. Unfortunately, however JOHNSON neither added to the paper a table relating the animals weights to the respiratory rates nor had in mind determining a $Q0_2$ x temperature curve. Nevertheless, we can assume that 2.5-5.0 g. *L. herculeus* showed a mean respiratory rate of 38.8 at 10°C and air 0_2 tension. At the same conditions, 0.606-0.892 g. *Pheretima* exhibited an average $Q0_2$ of 54. Size effects, of course, render render difficult the comparison of both results. Based on the size rule, however, one might infer from JOHNSON's data that 0.6-0.8 g. *L. herculeus* would respire at 10°C more

than *Pheretima*. This could be taken as an indication of compensation for low temperature by the temperate form as opposed to the tropical form, provided that the latter would not return to the 25°C level (137) after acclimation at 10°C (see below). Reciprocally, tropical forms comparable in size to *L. herculeus* might be expected to exhibit at 25°C more or less the same respiratory rates as those of the temperate form at 10°C. Table V, which includes data of the first paper of this series (MENDES & VALENTE), shows that this may not be the case, since *Glossoscolex* with a similar weight range respired significantly more at 25°C than *L. herculeus* at 10°C.

TABLE V

A comparison of the respiratory rates of *L. herculeus, P. hawayana* and *Glossoscolex sp.* to check possible latitude effects and compensation for temperature. $Q0_2$ = cu.mm.0_2/g(w.)/h.

Animal	Wt. range (g)	Temper. (°C)	N.° of cases	Mean $Q0_2$	AUTHOR
P. hawayana	2.0-2.7	25°C	3	84.6	MENDES & VALENTE
L. herculeus	2.5-5.0	10°C	9	38.7	JOHNSON
Glossoscolex	2.5-5.5	25°C	3	64.6	MENDES & VALENTE

KIRBERGER's starving earthworms adapted to 25°C respired at 25, 20 and 15°C respectively 137, 87 and 68 cu. mm. 0_2/g/h. Our 0.6-0.9 g. *Pheretima* in practically the same conditions respired 137, 106 and 70. Here again the lack of information about the weights of the animals used in KIRBERGER's experiments ("Exemplare von annähernd gleicher mittlerer Grösse") renders difficult the detection of possible latitude effects. In both cases, however, the decline in temperature significantly lowered the $Q0_2$ and in neither case plateaus have been found to suggest compensation for temperature.

All these speculations, of course, do not make unnecessary a more detailed study of the interrelations between respiration and temperature in temperate earthworms for comparison with our data. Temperate forms, exposed and adjusted to large seasonal variations of temperature must be able to react to sudden changes in a manner different from that of tropical species. This aspect of the problem leads to the consideration of the question of a probable rapid compensation form temperature in earthworms.

3. It is generally admitted that poikilotherms operate at lower rates in colder habitats and seasons. In an exhausting review of the subject, BULLOCK (l. c.) reminds that the evidences that many coldblooded animals, on the contrary, are relatively independent of temperature, go back to at least 1899, when KREHL & SOETBEER concluded that in respect to temperature poikilotherms are not simply "die Spielbälle der Umgebung", but show metabolic adaptation of their protoplasm. That is, given time or even rapidly, "these species tend to maintain a certain level of metabolism or other characters measured as rates, compensating for different temperatures by homoeostatic mechanisms of various kinds".

Compensation for temperature has been studied mainly in the cases of aquatic animals, the bulk of information concerning temperate forms. According to EDWARDS & NUTTING (1950), SCHOLANDER, FLAGG, WALTERS & IRVING (1953) and others, a relative poverty of compensatory adaptation may be the rule for insects and possible other terrestrial groups.

VERNON's studies included earthworms, at least the temperate forms, among those terrestrial animals able to compensate (and rapidly) for temperature. KIRBERGER, however, working on a better base, did not confirm this finding. In her experiments, *Eisenia,* whether adapted to 25 or to 15°C, was unable to restore the normal respiratory rate, regularly following rise and decline in temperature with corresponding increase and decrease of the 0_2 uptake. At the cellular level, however, catalase activity and dehydrogenase activity showed some dependence on the adaptation temperature.

The results obtained with *Pheretima* also do not extend to this tropical earthworm the ability to rapidly compensate for temperature. Neither did *Pheretima* remain temperature insentive over the wide temperature range used (2-45°C), nor was it able to restore the 25°C respiratory level after a 24 hour stay at 5°C. Besides, *Pheretima* and KIRBERGER's *Eisenia* exhibited more or less the same "Umkehrpunkt", the former's situated between 35 and 40°C and the latter's located between 36-38°C (independent of the adaptation temperature).

Whether or not *Pheretima,* given time, would be able to compensate for temperature will be investigated in the near future in a

general study of the behaviour of terrestrial tropical poikilotherms towards temperature variation.

CONCLUSIONS

1. The oxygen consumption of 24 hours starving specimens of the earthworm *Pheretima hawayana* has been measured in the dark, in a Warburg apparatus, at 36 strokes per minute, under varying conditions of 0_2 tension and temperature.

2. Down to 15% 0_2, *P. hawayana* regulates respiration. At 10% 0_2, its respiratory rate is already significantly lower than at air tension. Thereafter, it continues to decline with decreasing 0_2 tensions.

3. The data of the literature on the interrelations between 0_2 uptake and 0_2 tension in earthworms are critically reviewed, especially those obtained with narcotized animals.

4. *P. hawayana* increases its respiratory rate when temperature rises up to 35°C. This temperature can be considered as critical on the upper side of the temperature range. At 40°C, the $Q0_2$ almost returns to the 25° level, but this only expresses a sudden great increase due to temperature rise, followed by a strong decrease due to temperature damage. At 45°C, this sudden increase is followed by an earlier and stronger decrease, leading to a $Q0_2$ lower than normal. At the end of the experiments at 40 and 45°C, the animals were motionless, hemorrhagic and disrupt.

5. *P. hawayana* regularly diminishes its 0_2 uptake, when temperature decreases from 25°C down to 2°C. The animals, however, are not apparently affected even by the extremely low temperatures used; after a 90 minute stay at 2°C they seemed to be in a state of cold narcosis, from which they emerged after a few hours at room temperature.

6. The scarcity accurate studies of the relations between temperature and respiration for temperate earthworms renders difficult the analysis of the behaviour of tropical *Pheretima* towards temperature variation. An attempt, however, was made to correlate the results with the few data of the literature in order to check probable latitude effects and compensation for temperature. A slight indica-

tion of compensation in the European *Lumbricus herculeus* is suggested in view of the results obtained with *Pheretima,* although this findings is not supported by data obtained with *Glossoscolex*.

7. Old evidence (VERNON 1895, apud BULLOCK 1955) points to *Lumbricu's* ability to rapidly compensate for temperature variations. The work of KIRBERGER (1953) with *Eisenia* did not confirm this finding. *Pheretima* neither remained temperature-insensitive over the wide temperature range used (2°C-45°C) nor was able to restore the 25°C level after a 24 hour stay at 5°C. Thus, it does not seem to rapidly compensate for temperature variation. Whether or not it slowly compensates will be the object of a future rerearch, which will include the responses of other tropical terrestrial Invertebrates to temperature variation.

CONCLUSÕES

1. O consumo de oxigênio de espécimes, jejunas de 24 horas, da minhoca *Pheretima hawayana* foi medido no escuro, em um aparelho de Warburg, a 36 agitações por minuto, sob condições variadas de tensão de 0_2 e temperatura.

2. Até 15% de 0_2, *P. hawayana* regula a respiração. A 10% de 0_2, sua taxa respiratória já é significativamente inferior à do ar. Depois, ela continua a declinar com a tensão de 0_2 decrescente.

3. Os dados da literatura acêrca das interrelações entre o consumo de oxigênio e a tensão de 0_2 nos oligoquetos terrestres foram revistos crìticamente, especialmente os obtidos com animais narcotizados, ressaltando-se o perigo dessa técnica.

4. *P. hawayana* aumenta sua taxa respiratória com o aumento de temperatura até 35°C. Essa temperatura pode ser considerada crítica no lado superior da gama de temperatura. A 40°C, o $Q0_2$ quase retorna ao nível de 25°C, mas isso apenas traduz um súbito grande aumento de metabolismo devido ao aumento de temperatura, seguido de um forte decréscimo devido ao dano térmico. A 45°C, êsse súbito aumento é seguido por um mais precoce e mais forte decréscimo, levando a um $Q0_2$ inferior ao normal. No fim dos experimentos a 40 e 45°C, os animais ficaram imóveis, hemorrágicos e superficialmente rompidos.

5. *P. hawayana* diminui regularmente o consumo de oxigênio quando a temperatura decresce de 25°C a 2°C. Os animais, porém, não pareceram afetados mesmo pelas temperaturas extremamente baixas usadas; após 90 minutos a 2°C, os animais pareciam em um estado de "narcose pelo frio" (cold narcosis), do qual emergiram ao cabo de algumas horas à temperatura ambiente.

6. A escassez de estudos cuidadosos das relações entre temperatura e respiração para as minhocas de clima temperado torna difícil uma análise do comportamento de *Pheretima* em face da variação de temperatura. Tentativa, todavia, foi feita no sentido de se correlacionar os resultados com os poucos dados da literatura, a fim de descobrir prováveis efeitos de latitude ou compensações. Leve indicação de compensação, isto é, retôrno respiratório ao normal ao cabo de prolongada permanência a baixa temperatura, foi sugerida para a espécie européia *Lumbricus herculeus,* em face dos dados obtidos para *Pheretima*.

7. Velho indício (VERNON 1895, apud BULLOCK 1955) sugere que *Lumbricus* ràpidamente compensa o metabolismo quando a temperatura varia. O trabalho de KIRBERGER (1953) não confirmou em *Eisenia* êsse resultado. *Pheretima* nem permanece insensível às variações de temperatura na ampla gama usada (2°-45°C), nem restaura o nível de 25°C respiratório após 24 horas a 5°C. Assim, não parece capaz de compensação rápida. Se compensa, porém, lentamente, será objeto de uma pesquisa futura, que incluirá também as respostas de outros invertebrados terrestres tropicais à variação de temperatura.

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QUELQUES DONNÉES NOUVELLES SUR LA STRUCTURE DE TONOFIBRILLES D'INSERTION MUSCULAIRE CHEZ CARCINUS MAENAS L.

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(4 Planches)

INTRODUCTION

Les modalités d'attache des muscles au squelette au cuticulaire des Crustacés ont donné lieu à de nombreuses observations, portant principalement sur les structures rencontrées au niveau de l'épithélium tégumentaire. Une revue de ces travaux est incluse dans la monographie de RICHARDS (1) sur le tégument des Arthropodes.

Un point commun à la majorité des descriptions d'insertions musculaires chez les Crustacés, concerne l'existence, dans l'épithélium, de fibrilles non striées transversalement, les tonofibrilles, qui joignent les myofibrilles à la cuticule. Étant donnée leur situation intermédiaire, ces tonofibrilles sont depuis longtemps le sujet de certaines controverses, notamment à propos de leur origine et de leurs relations avec les cellules épithéliales (cf. 1). Considérant la diversité des types d'attaches musculaires chez les Crustacés (cf. 2), le présent travail ne prétend pas apporter de réponses définitives et générales à ces vieilles questions. Il se limite à relater quelques observations préliminaires effectuées, chez un Crustacé Décapode, sur un type particulier de tonofibrilles d'insertion musculaire, relativement favorable à l'utilisation du microscope électronique. Il tente aussi d'établir dans quelle mesure ces observations peuvent être situées dans le cadre des résultats et des discussions de la cytologie classique.

Chez les Crustacés Décapodes, la principale difficulté de l'étude des tonofibrilles d'insertion musculaire, en microscopie électronique, réside dans la grande proximité d'un tégument dur, souvent fortement calcifié, qui s'oppose à la réalisation de coupes ultrafines par destruction irrémédiable du fragile couteau de verre. Le matériel utilisé ici est favorable en ce sens qu'il comporte un ensemble de cellules épithéliales et de tonofibrilles très allongées, en contact avec des apodèmes peu développés et relativement mous. Ces derniers ne sont pas un obstacle à un passage convenable du couteau de verre, si l'on prend la prend la précaution d'en éliminer la plus grande partie de la surface de coupe. Il a ainsi été possible d'obtenir un certain nombre d'électromicrographies, dont les principaux caractères sont indiqués dans les planches illustrant ce texte.

MATÉRIEL ET MÉTHODES

Le matériel étudié provient des troisièmes maxillipèdes du Crabe enragé, *Carcinus maenas L.* Chaque maxillipède comporte un exopodite terminé par un fouet animé de battements rapides. Deux apodèmes antagonistes partent de la base du fouet, sur lesquels viennent s'attacher les muscles moteurs des battements. Ce sont les tonofibrilles intermédiaires entre les muscles et les apodèmes qui font l'objet des observations suivantes.

En ce qui concerne la microscopie optique, les pièces sont fixées par les liquides de BOUIN, de HELLY ou de HALMI (3) et décalcifiées, soit par le propre fixateur (Halmi), soit par une solution à 5% d'acide trichloracétique. Afin d'obtenir un certain ramollissement du tégument décalcifié, après déshydratation jusqu'à l'alcool à 95°, les pièces sont maintenues quelques jours dans l'alcool butylique renouvelé. Les inclusions sont faites selon le procédé mixte à la celloidine-paraffine de PETERFI et les blocs obtenus sont débités en coupes de 5μ d'épaisseur. Les coupes sont ensuite traitées, soit par des colorations au bleu d'aniline (trichrome de MASSON ou Azan), soit par l'hémalun-picro-indigocarmin (4), soit par la réaction de MAC MANUS (5).

Pour la microscopie électronique, les fixations ont lieu pendant une heure à température ambiante, dans une solution de tétroxyde

d'osmium à 3%, tamponnée à pH 7,4-7,6 d'après la méthode de PALADE (6). Après déshydratation par la série des alcools, l'inclusion des pièces est faite dans un mélange de 9 parties de méthacrylate de n-butyle avec une partie de méthacrylate de n-méthyle, dont la polymérisation est assurée par 1% de Luperco C D B, à 60°C. Les coupes sont effectuées au microtome PORTER-BLUM, et observées aux grandissements originaux de 2.000 à 15.000, avec un microscope R C A, modèle E M U.

RÉSULTATS

Généralités

Les micrographies optiques des Figs. 1 et 2 donnent une vue d'ensemble, en coupe longitudinale, de l'attache de muscles sur un apodème du fouet de l'exopodite. Les principaux constituants d'une zone d'insertion musculaire quelconque de Crustacé s'y trouvent représentés: le squelette tégumentaire, qui est ici un apodème (Ap.), les muscles formés par les fibres musculaires (F.m.) renfermant les faisceaux de myofibrilles (Mf.), l'épithélium (Ep.) et les tonofibrilles (Tf.).

Les plus souvent chez les Crustacés, par exemple dans le cas de nombreux muscles des appendices locomoteurs, chaque fibre musculaire, possèdant un diamètre constant sur toute sa longueur, offre une surface d'insertion sensiblement égale à sa surface de section transversale. Les myofibrilles arrivent parallèlement les unes aux autres au contact de l'épithélium. Une particularité apparaît donc ici avec le phénomène de convergence des faisceaux de myofibrilles à proximité de l'épithélium, de telle sorte que les fibres musculaires présentent une extrêmité fusiforme (F.m., Fig. 2). Cette disposition peut s'interpréter en replaçant les muscles dans l'article qui les contient. En raison du profil triangulaire de ce dernier, l'ensemble des deux muscles antagonistes a la forme d'un cône allongé, dont le sommet correspond à l'attache distale des fibres musculaires sur les apodèmes très courts du fouet. Comme chaque muscle comprend le même nombre de fibres musculaires sur toute sa longueur, la surface disponible pour l'insertion de ces fibres sera bien moindre au sommet qu'à la base du cône musculaire. Il en résulte, au niveau de l'insertion distale,

cet aspect de concentration du matériel myofibrillaire sur la faible surface offerte par les apodèmes.

La partie de l'insertion musculaire examinée au microscope électronique comprend seulement les tonofibrilles, l'épithélium et la zone la plus interne de la cuticule. L'ultrastructure des fibres musculaires à déjà été rapportée dans un travail précédent (7); la région importante de jonction des myofibrilles avec les tonofibrilles est en cours d'étude. Les micrographies optiques des trois premières figures, de grandissements croissants, sont destinées à localiser, à l'échelle de l'histologie classique, les zones où sont observées les ultrastructures des autres planches. A cet effet, la Fig. 4, électromicrographie de faible grandissement, permet de faire la relation, en particulier par les noyaux allongés et les tonofibrilles, entre la Fig. 3 et les autres micrographies électroniques. Il faut remarquer que, dans cette Fig. 4, apparaît un nouveau constituant, le complexe des membranes plasmiques (m.p.) qui peut être un facteur important d'interprétation pour les relations entre les différentes parties de l'insertion.

Cuticule

La partie cuticulaire de l'insertion musculaire ici considérée, comporte les deux apodèmes qui partent de la base du fouet de l'exopodite. L'étude de coupes longitudinales sériées montre que ce sont bien des apodèmes, selon les termes de la définition (1), car ils apparaissent comme des replis tégumentaires invaginés, avec cavité centrale et épicuticule acidophile bordant la procuticule basophile. Chaque apodème présente un élargissement terminal déprimé dans sa partie centrale, l'ensemble évoquant le profil d'une ventouse pédiculée en coupe longitudinale. Dans le pédicule, la cavité de l'invagination est virtuelle et les épicuticules sont appliquées l'une contre l'autre; l'épaisseur de l'ensemble de la cuticule est faible: 4 à 6μ; la structure classique de la procuticule, en lamelles superposées, y est parfaitement conservée. Au contraire, dans la partie terminale élargie, la cavité centrale est bien développée; la cuticule de la dépression médiane, où viennent s'insérer les fibres musculaires, est beaucoup plus épaisse: 30 à 40μ et la lamellation de la procuticule n'y est plus discernable. L'apodème Ap. de la Fig. 1 montre cette zone cuticulaire épaisse sans lamellation; par contre, la cavité de l'invagination n'y

est pas visible parce que le plan de coupe est passé très latéralement, sur le bord de la dilatation terminale de l'apodème.

L'attache des fibres musculaires par l'intermédiaire de tonofibrilles sur les apodèmes du fouet de l'exopodite semble donc corrélative d'un épaississement du tégument et d'une disparition de la structure en lamelles de la procuticule. Dans cette dernière, on ne distingue plus que des faisceaux de fibrilles (F.c., Figs. 1 et 2), plus ou moins bien individualisés parce qu'empatés dans une substance fondamentale; ils sont orientés de façon prédominante dans le prolongement des tonofibrilles, c'est-à-dire selon la direction des forces de traction des fibres musculaires. En effet, étant donnée la forme des apodèmes, les fibres musculaires et les tonofibrilles qui les prolongent ne peuvent toutes entrer en contact avec le tégument selon le même angle d'incidence; certaines sont disposées perpendiculairement à la surface de l'apodème, d'autres au contraire très obliquement (Fig. 1). Il est ainsi possible de constater que l'orientation des faisceaux de fibrilles de la procuticule des apodèmes est en relation avec l'incidence des tonofibrilles.

Toutes les observations précédentes sont faites en microscopie optique, car avec le microscope électronique, la plus grande partie de l'apodème étant éliminée de la surface de coupe, on examine seulement la zone la plus interne de la cuticule, c'est-à-dire celle qui correspond à la couche membraneuse non calcifiée. Au microscope électronique, la zone de cuticule située à proximité de l'épithélium (Ap., Figs. 5, 9 et 10) apparaît comme formée de filaments fins (F.c. 1), beaucoup moins osmiophiles que les tonofilaments voisins et aussi moins individualisés, probablement parce que noyés dans la substance fondamentale cuticulaire. Leur diamètre se situe entre 150 et 250 A., cette mesure étant approximative en raison du manque de précision dans les contours. Les filaments sont disposés par faisceaux suivant un parcours légèrement ondulé, mais qui reste parallèle à la surface tégumentaire. Les groupes de filaments sont interrompus à intervalles irréguliers par des taches de forte densité (Figs. 9 et 10, F.c. 2); d'un développement inégal selon les cas, certaines sont très allongées et l'on peut y distinguer alors un autre type de filaments encore moins nettement délimité, mais d'une osmiophilie plus forte. L'orientation de ces filaments denses est dif-

férente, de telle sorte qu'ils forment avec le premier système de filaments, un angle sensiblement voisin de celui formé par les tonofibrilles avec la surface cuticulaire.

Il faut encore signaler, dans la cuticule proximale de l'apodème, des accumulations très denses d'osmium (O., Figs. 5 et 9), de contour subcirculaire, d'un diamètre variant de 0,3 à 0,4μ. Certaines zones de la cuticule proximale en sont complètement dépourvues; quand elles apparaissent, elles se trouvent alors à une distance les unes des autres allant de 2 à 5μ. Ces formations sont sans doute en relation avec les structures verticales de la cuticule.

L'épithélium

DRACH (8) a montré qu'il fallait distinguer, sur la face interne du tégument, des zones musculaires, correspondant aux zones d'insertion des muscles, et des surfaces cuticulaires banales, correspondant au tégument localisé entre les zones d'insertion de deux muscles voisins. Cette distinction est valable pour tous les articles des appendices et pour les sternites thoraciques.

Une subdivision analogue a été établie (9), non plus au niveau du muscle, mais à celui des fibres musculaires: à l'intérieur d'une même zone musculaire, il existe toujours, entre les zones d'insertion de fibres musculaires voisines, une surface cuticulaire banale. A ces deux types de surface tégumentaire interne correspondent deux types de cellules épithéliales: les cellules épithéliales d'insertion musculaire, comprises à l'intérieur de la surface d'insertion d'une fibre musculaire, à contenu obscurci par le passage des tonofibrilles, et les cellules épithéliales banales, à cytoplasme clair, sans tonofibrilles, localisées entre les surfaces d'insertion des fibres musculaires.

Dans le type d'insertion musculaire ici considéré, en dépit de la grande densité des myofibrilles et de la surface réduite des apodèmes, les cellules épithéliales banales sont présentes entre les groupes de cellules épithéliales à tonofibrilles situées en face de l'insertion des fibres musculaires (Ep. 1, Fig. 2). Elles se distinguent de leurs voisines, au microscope optique, par leur cytoplasme clair, leur noyau arrondi ou ovoïde et leurs dimensions: 40 à 60μ de long, 6 à 8μ de large. Les largeurs des cellules épithéliales sont toujours mesurées au niveau de leur contact avec la cuticule; le plus souvent, en effet,

le profil de l'empreinte de la cellule dans le tégument est perceptible, ce qui offre l'avantage de mesurer sur des limites rigides, non susceptibles de variation en fonction de la fixation ou de l'étirement provoqué par les muscles, dans le cas des cellules à tonofibrilles. La membrane basale, (m.b., Fig. 2), occupe la position habituelle, le long de la face interne des cellules épithéliales.

La longueur des cellules à tonofibrilles (Ep. 2, Fig. 2) est plus grande et également plus variable: de 100 à 500μ, parfois davantage. Il est remarquable que les cellules à tonofibrilles les plus courtes soient orientées perpendiculairement à la surface de l'apodème. D'une façon générale, elles sont d'autant plus longues qu'elles arrivent plus obliquement au contact de la cuticule (Fig. 1), et cette particularité a pour résultat d'établir une certaine compensation aux différences éventuelles de longueur des fibres musculaires en relation avec la forme de l'apodème. Leur largeur au niveau de la cuticule est du même ordre de grandeur que celle des cellules épithéliales banales, mais à une certaine distance du support rigide tégumentaire, elles paraissent d'autant plus étroites qu'elles sont plus allongées, comme si l'augmentation de leur plus grande dimension provenait, dans une certaine mesure, d'un phénomène d'étirement. Elles dépassent donc de beaucoup, du côté interne, la couche des cellules épithéliales banales. Or la membrane basale épithéliale est ici aussi en continuité avec le revêtement conjonctif du sarcolemme des fibres musculaires, comme cela a été observé pour beaucoup d'Arthropodes (cf. 1). En conséquence, à la périphérie de l'insertion d'une fibre musculaire, la membrane basale sous-jacente aux cellules épithéliales banales, s'infléchit et se dispose le long des faces latérales externes des cellules épithéliales à tonofibrilles, avant de se continuer par le sarcolemme.

Le contenu des cellules épithéliales à tonofibrilles est principalement caractérisé par une abondance très grande de tonofibrilles, organisées en faisceaux denses qui laissent peu de place pour le cytoplasme et les autres organites cellulaires. L'étirement de ces cellules, ajouté au faible volume cytoplasmique, se traduit par un allongement des noyaux qui se disposent parallèlement aux tonofibrilles. La micrographie optique de la Fig. 3 met en évidence deux cellules épithéliales voisines avec leur faisceau dense de tonofibrilles et leur noyau allongé, dans un cytoplasme réduit à une fine couche, le long des mem-

branes intercellulaires. Les noyaux des cellules épithéliales à tonofibrilles sont en général localisés à proximité de la cuticule.

L'influence de l'abondance et de l'étirement des tonofibrilles sur l'organisation des cellules épithéliales de l'insertion musculaire se retrouve en microscopie électronique. Très souvent, les structures sont serrées les unes contre les autres, comprimées entre les tonofibrilles et il devient difficile d'analyser les aspects obtenus sur les micrographies électroniques. La Fig. 8 montre une coupe longitudinale ultramince dans l'épithélium à tonofibrilles; trois noyaux allongés indiquent l'existence de trois cellules voisines qui sont donc particulièrement étroites à ce niveau et dont il est difficile de distinguer les limites et les ultrastructures. Il est quelquefois plus avantageux d'utiliser des préparations mal fixées, en condition d'hypotonie, comme c'est le cas dans la Fig. 4, parce qu'il se produit alors un certain gonflement de la cellule et une dispersion corrélative des structures qui les rend plus facilement reconnaissables.

Avec le microscope électronique, on rencontre donc de nouveau les noyaux allongés, orientés parallèlement aux tonofibrilles et localisés à proximité de la cuticule. Ces noyaux montrent l'ultrastructure habituelle (10) avec une chromatine diffuse, plus densément distribuée à la périphérie, une double membrane nucléaire et un ou plusieurs nucléoles très osmiophiles (Figs. 5, 6, 8 et 9).

Les mitochondries présentent également une dimension prédominante orientée selon les tonofibrilles. Elles sont de proportion nettement inférieures à celles des mitochondries rencontrées dans les fibres musculaires de l'exopodite (7); leur diamètre atteint au maximum 0,25μ et leur longueur dépasse rarement 2μ. Elles montrent une ultrastructure classique (11) avec des invaginations plus ou moins en forme de lamelles à partir de la membrane mitochondriale interne.

Un caractère nouveau et important des cellules épithéliales à tonofibrilles est mis en évidence par le microscope électronique. Il concerne l'existence de doubles membranes plasmiques continues qui traversent, plus ou moins parallèlement entre elles, le cytoplasme des cellules épithéliales entre les tonofibrilles (m.p., Figs. 4 à 13). Ce système de membranes plasmiques sera décrit dans un paragraphe particulier et commenté dans la discussion.

Tonofibrilles

Les relations entre les myofibrilles et les tonofibrilles ont donné lieu anciennement (cf. 1), surtout chez les Insectes, à deux séries d'observations bien différentes. Certains auteurs décrivaient une prolongation des myofibrilles par les tonofibrilles, d'autres affirmaient une solution de continuité entre les deux types de fibrilles, au niveau de la membrane basale. Il semble maintenant, que la notion d'une liaison fibrillaire continue, entre la cuticule et les myofibrilles, soit généralement admise. Il ne sera pas traité en détail ici, de la jonction entre myofibrilles et tonofibrilles ni du contact entre fibres musculaires et cellules épithéliales, car l'étude des ultrastructures de cette zone est en cours et fera l'objet d'une note ultérieure. Cependant, il est déjà possible d'affirmer, uniquement par les micrographies optiques, que dans les insertions musculaires du fouet de l'exopodite, les faisceaux de tonofibrilles se montrent bien en continuité avec les faisceaux de myofibrilles. L'observation est aisée dans le cas présent, car le sarcoplasme périphérique abondant de la fibre musculaire maintient la membrane basale à distance de l'extrêmité des myofibrilles, ce qui laisse apparaître clairement la zone de transition entre myofibrilles et tonofibrilles, (Fig. 2). Les faisceaux de tonofibrilles sont d'autant plus longs et plus denses qu'ils arrivent plus obliquement au contact de la surface de l'apodème.

Il est possible d'évaluer approximativement la concentration du matériel fibrillaire au niveau de l'épithélium, en comparant le diamètre d'un faisceau de myofibrilles parallèles, à une certaine distance de l'apodème, avec le diamètre du faisceau de tonofibrilles correspondant. Quand l'insertion est très oblique, il est fréquent de constater que le diamètre du faisceau de tonofibrilles atteint seulement le quart de celui du faisceau de myofibrilles. La concentration du matériel fibrillaire est telle qu'il n'est pas possible ici, de discerner les tonofibrilles les une des autres au microscope optique, au contraire du cas des insertions larges comme celles des fibres musculaires sur le tégument des appendices locomoteurs. L'existence des tonofibrilles se traduit seulement par une fine striation longitudinale du matériel dense qui relie les myofibrilles à la cuticule (Tf., Fig. 3); seules les coupes ultrafines, examinées au microscope électronique, permettent de les individualiser.

Le microscope électronique permet non seulement la mise en évidence de tonofibrilles isolées, mais encore il révèle que chaque tonofibrille est elle-même un faisceau de filaments submicroscopiques de 100 A. de diamètre, avec des intervalles de 100 à 200 A. (tf., Figs. 5 à 13). En considération du terme adopté par SELBY (12) pour les constituants submicroscopiques des tonofibrilles de cellules épidermiques chez l'Homme, ces filaments sont également désignés ici sous le nom de tonofilaments. Toutefois les observations de la microscopie électronique semblent montrer que tonofibrilles d'insertion musculaire des Arthropodes et tonofibrilles de cellules épidermiques des Mammifères sont des structures complètement différentes.

La subdivision des tonofibrilles en tonofilaments rappelle l'organisation des myofibrilles en faisceaux de myofilaments (13). Comme dans le cas de ces dernières, le diamètre des tonofibrilles est très variable et est surtout fonction du nombre de tonofilaments qui entrent dans leur constitution. Cependant, tandis que les myofibrilles des muscles de l'exopodite restent isolées et de même épaisseur sur toute leur longueur (7), il est fréquent d'observer la fusion de faisceaux voisins de tonofilaments en une seule tonofibrille plus volumineuse. Par ailleurs, dans les muscles de l'exopodite les myofilaments demeurent équidistants les uns des autres sur toute la longueur de la myofibrille. Au contraire, dans les tonofibrilles, il y a de façon irrégulière, des espaces internes produits par écartement des tonofilaments, occupés par du cytoplasme et même des mitochondries allongées (Cp., Fig. 8). La surface d'insertion d'une tonofibrille est beaucoup plus grande que sa surface de coupe transversale (Figs. 9 et 10). Ceci est attribuable à deux raisons principales: d'une part l'orientation oblique de la tonofibrille par rapport à la surface cuticulaire, d'autre part l'élargissement du faisceau des tonofilaments qui s'écartent légèrement les uns des autres avant de se joindre à la cuticule.

L'absence de striation transversale des tonofibrilles signalée depuis longtemps chez tous les Arthropodes (cf. 1) se remarque bien sur la Fig. 2, qui montre le passage d'un faisceau de myofibrilles typiquement striées (zones isotrope I et anisotrope A, ligne Z, disque de Hansen H) à un faisceau de tonofibrilles dépourvu de toute zo-

ration transversale. Ce caractère est confirmé par le microscope électronique (Figs. 6 à 13), tant à l'échelle de la tonofibrille que du tonofilament.

Membranes plasmiques longitudinales

Sur toutes les coupes ultrafines passant par les cellules épithéliales à tonofibrilles, le microscope électronique met en évidence un système de membranes plasmiques doubles qui traversent longitudinalement l'épithélium. Quand les tonofibrilles sont densément distribuées (Fig. 8), il est nécessaire d'utiliser de forts grandissements pour distinguer ces membranes, serrées et plus ou moins dissimulées par les tonofilaments. Ces doubles membranes ne sont pas toujours rectilignes; elles décrivent souvent de légères ondulations et parfois, de fortes sinuosités (Fig. 5). Cependant par leur orientation générale, elles sont parallèles entre elles selon la grande dimension des cellules, donc parallèles aux tonofibrilles. L'épaisseur de chaque membrane se situe aux environs de 50 A.; elles sont séparées l'une de l'autre par une distance assez peu variable, de l'ordre de 100 à 150 A.

Ces membranes plasmiques doubles sont continues sur toute leur longueur. Il a été observé la bifurcation d'une double membrane, indiquée par la flèche sur la Fig. 13, mais vis-à-vis du nombre d'électromicrographies considérées, ce phénomène n'est pas fréquent. A aucun des niveaux observés, les doubles membranes ne montrent de solution de continuité ni de fenestration multiple en un réseau du type réticulum endoplasmique. On peut le constater par la régularité des lignes denses qui figurent les membranes plasmiques, lorsqu'elles sont coupées transversalement; ceci se vérifie encore par la disparition quasi totale des membranes lorsqu'elles sont orientées tangentiellement au plan de coupe (Fig. 7). S'il s'agissait d'un réseau, ses mailles devraient alors apparaître de face.

Dans les zones cytoplasmiques comprises entre les doubles membranes, de nombreux profils d'endomembranes correspondent au réticulum endoplasmique. Ce sont surtout des vésicules de formes et de dimensions variables, distribuées irrégulièrement, sans apparence d'organisation déterminée. Elles sont très souvent appuyées contre les membranes plasmiques doubles, mais les préparations obtenues

jusqu'alors ne permettent pas d'affirmer de relation de continuité entre les deux formations.

Avec les seules micrographies électroniques de coupes longitudinales, il est possible de déduire que les membranes plasmiques doubles situées au voisinage d'une tonofibrille, forment autour de cette dernière, une enveloppe subcylindrique. — Il y a toujours une double membrane de chaque côté d'une tonofibrille, soit deux doubles membranes entre deux tonofibrilles voisines (Figs. 4, 6. 7, 10, 12 et 13). — Les doubles membranes sont situées à une distance relativement constante de la périphérie de la tonofibrille, comme si elles accompagnaient régulièrement son contour. En effet, plus le plan de coupe est latéral dans la tonofibrille plus celle-ci semble fine et plus les doubles membranes sont rapprochées l'une de l'autre (Figs. 10 et 11). Il arrive qu'il ne reste plus que quelques tonofilaments (x1, Fig. 10), et même dans certains cas limites, le plan de coupe n'intéresse plus que les deux doubles membranes qui sont alors très voisines (x2, Fig. 7). — Enfin, sur coupe oblique, en avant de l'extrêmité de la tonofibrille, les doubles membranes latérales se rejoignent (x3, Fig. 4); ceci indique qu'elles appartiennent à une même formation continue enveloppant la tonofibrille.

Il faut considérer un autre type de membranes plasmiques doubles longitudinales, sans relations directes avec les tonofibrilles, puisqu'il correspond à la juxtaposition des membranes cytoplasmiques de deux cellules épithéliales mitoyennes. On peut le reconnaître, sur coupe longitudinale, car il n'est pas en général à grande proximité d'une tonofibrille, mais c'est seulement par son passage entre deux noyaux voisins qu'on peut le distinguer avec certitude des membranes qui entourent les tonofibrilles. La Fig. 6 met en évidence les deux catégories de membranes plasmiques doubles: d'une part, les membranes plasmiques cellulaires (m.p. 1) passant entre les deux noyaux, d'autre part, l'enveloppe plasmique double d'une tonofibrille (m.p. 2). Il faut encore remarquer que les régions entre deux doubles membranes voisines, comme celles situées entre une double membrane et une tonofibrille, sont des zones cellulaires avec cytoplasme et réticulum endoplasmique. Seul le très faible espace localisé entre les deux membranes plasmiques correspond à l'espace extracellulaire.

Les deux catégories de membranes plasmiques doubles longitudinales se prolongent jusqu'au tégument. A proximité des premières couches cuticulaires, elles modifient leur parcours et commencent à décrire un système de sinuosités profondes, formant en coupe, des séries de boucles allongées plus ou moins mélangées les une aux autres (Figs. 9, 10 et 11). Le cytoplasme renferme alors des profils d'endomembranes plus nombreux et plus développés que dans les zones éloignées du tégument. Cette partie très contournée des doubles membranes sépare de la cuticule, la fraction cytoplasmique qui contient les noyaux allongés et qui appartient donc aux cellules épithéliales. Au contraire, les tonofibrilles entrent librement en contact avec la cuticule (Figs. 9 et 10), c'est-à-dire que le cytoplasme qui les contient vient s'appliquer directement contre la cuticule sans qu'il soit possible, dans la mesure des préparations, d'en discerner une limite figurée.

DISCUSSION

Chez divers Arthropodes, de nombreuses observations avec le microscope optique (cf. 1) on montré que les tonofibrilles se continuent dans la procuticule. Cette donnée se constate principalement dans le cas de surfaces d'insertions larges, où les myofibrilles et les tonofibrilles sont relativement en petit nombre. De ce fait, l'individualité des tonofibrilles est perceptible dans l'épithélium, de même que leur prolongement dans la procuticule. Dans le cas présent, il n'est pas possible d'individualiser des structures analogues aux tonofibrilles dans la procuticule de l'apodème. Mais il est également impossible d'individualiser les tonofibrilles dans les cellules épithéliales, tellement elles y sont nombreuses et densément réparties, cela en conséquence de la concentration des myofibrilles sur la surface réduite des apodèmes. De même que l'on constante seulement la présence de faisceaux de tonofibrilles dans l'épithélium, de même dans l'apodème, on voit seulement des faisceaux de fibrilles qui, orientés selon la direction des tonofibrilles, représentent probablement leur continuation dans la procuticule.

Un argument supplémentaire est apporté par l'épaississement du tégument au niveau de l'insertion musculaire, là où précisément apparaissent dans la procuticule ces faisceaux de fibrilles orientés dans le prolongement des faisceaux de tonofibrilles. Cette augmentation

peut multiplier jusqu'à sept ou huit fois l'épaisseur habituelle des zones de l'apodème où n'arrive pas de tonofibrille. On peut donc considérer que cette augmentation d'épaisseur serait en relation avec un apport important de matériel fibrillaire, constitué en l'occurence par le prolongement des faisceaux de tonofibrilles qui vient se mêler et s'ajouter au matériel cuticulaire banal. Ceci paraît d'autant plus vraissemblable que l'épaississement de la cuticule ne correspond en rien à un renforcement de l'apodème. En effet, la partie proximale de l'apodème qui transmet au fouet de l'exopodite la somme de toutes les forces de traction du muscle, présente la cuticule la plus fine avec une lamellation typique.

La disparition de la structure typique en lamelles de la cuticule, en face de l'insertion des faisceaux de tonofibrilles, peut s'interpréter de la même façon, comme la conséquence d'un apport considérable de matériel fibrillaire qui va se mêler aux fibrilles cuticulaires des lamelles. Il en résulte que ces dernières sont comme camouflées par les prolongements des tonofibrilles, plus nombreux et surtout d'une orientation bien différente. Il est remarquable que dans les zones où, en relation avec les irrégularités de contour de l'apodème, il n'y a pas d'insertion de tonofibrilles, la lamellation de la cuticule réapparaît et son épaisseur diminue.

L'interprétation précédente est établie d'après les observations de la microscopie optique. Les données de la microscopie électronique ne sont pas en contradiction avec cette hypothèse de la sommation de deux systèmes de fibrilles: l'un, universel, qui correspond aux fibrilles des lamelles cuticulaires, l'autre, au niveau des insertions, provenant du prolongement des tonofibrilles dans la cuticule. Il faut rappeler que le microscope électronique n'a permis d'observer ici que les premières couches de la partie non calcifiée de la cuticule (= couche membraneuse) pour laquelle le schéma de la structure lamellaire donné par DRACH (14) n'est pas valable. Pourtant, il est probable que les filaments peu osmiophiles, parallèles à la surface de l'apodème, soient des formations très voisines des fibrilles horizontales des lamelles. Les zones à filaments osmiophiles, allongées selon la direction des tonofibrilles, pourraient être considérées comme le prolongement des tonofilaments entre les fibrilles de la couche membraneuse. Leur orientation et leur densité correspondent bien à celles des tonofilaments; sur

la Fig. 9, qui montre le contact d'une tonofibrille avec la cuticule, cette correspondance est particulièrement nette. Le développement inégal de ces zones osmiophiles ne peut être attribué qu'à une orientation variable de leurs faisceaux de filaments denses par rapport au plan de la coupe (ces zones sont d'autant plus allongées que le grand axe des filaments se rapproche du plan de coupe et vice-versa), ce qui traduit une certaine ondulation du parcours des filaments denses dans la cuticule.

Avec le microscope optique, chaque faisceau de tonofibrilles semble être contenu dans une cellule épithéliale dont il occuperait la majeure partie du volume; au niveau de l'apodème, son insertion se localise à l'intérieur de la surface de contact de la face externe de la cellule épithéliale avec la cuticule. Le microscope électronique met en évidence les membranes plasmiques qui permettent d'établir des limites cellulaires nouvelles. C'est le cas de la zone de cytoplasme qui enveloppe chaque tonofibrille et qui est séparée du cytoplasme de la cellule épithéliale par une double membrane plasmique. Cette zone cytoplasmique à tonofibrille pourrait s'interpréter comme de nature épithéliale en considérant que, du fait d'un contour irrégulier et interpénétré des faces latérales des cellules épithéliales, elle représente chaque fois la coupe d'une expansion latérale de la cellule épithéliale voisine. Mais cette hypothèse est difficilement acceptable, d'une part à cause de la présence constante des doubles membranes autour de chaque tonofibrille, d'autre part en raison de l'accès direct des tonofibrilles à la cuticule. Au contraire, les zones de cytoplasme contenant les noyaux, considérées comme appartenant aux cellules épithéliales, sont séparées de la cuticule par le complexe sinueux des membranes plasmiques. Cela conduit alors au concept d'une cellule épithéliale criblée par des prolongements d'un cytoplasme d'une autre nature, renfermant chacun une tonofibrille et des mitochondries. Il reste à prouver si ces prolongements traversent effectivement les cellules épithéliales ou bien s'ils se localisent entre les cellules épithéliales. Dans ce dernier cas, il faut revenir encore à la notion de faces latérales des cellules épithéliales à profil très contourné, avec des dépressions longitudinales dans lesquelles pourraient être localisés les prolongements à tonofibrilles, donc en position intercellulaire. Une autre question se pose également sur la nature des membranes plasmiques qui entourent les

tonofibrilles. La membrane externe, par rapport à la tonofibrille, représente certainement la limite plasmique de la cellule épithéliale. Par contre, la membrane plasmique délimitant le prolongement cytoplasmique de la tonofibrille ne peut être identifiée qu'en mettant en évidence son origine. Naturellement, l'hypothèse la plus offerte rejoint les vues des cytologistes (cf. 1) qui regardaient les tonofibrilles comme des prolongements des myofibrilles à travers l'épithélium, et l'on est tenté de penser que la fibre musculaire accompagne les tonofibrilles jusqu'à la cuticule par des prolongements de sarcoplasme. Une étude plus avancée, avec des coupes longitudinales et transversales de la région de transition entre le muscle et l'épithélium, permettra sans doute d'obtenir des conclusions pour ces diverses suggestions. Quant à la grande abondance de replis dans les membranes plasmiques au contact de l'apodème, comme il s'agit d'un phénomène d'augmentation considérable des surfaces juxtaposées, il faudrait considérer ces aspects aux différentes phases du cycle d'intermue pour voir s'il y a des variations en relation avec la sécrétion de la cuticule, ou s'il s'agit de caractères structuraux permanents.

Quelles que soient leurs relations avec l'épithélium, les tonofibrilles exercent, par leur passage ou leur proximité, une grande influence sur la constitution de la cellule épithéliale d'insertion musculaire: allongement et orientation générale de la cellule, adaptation de la forme cellulaire au passage des tonofibrilles, réduction de l'espace disponible dans la cellule et déformation des organites (noyaux et mitochondries) dans le sens d'un allongement parallèle aux tonofibrilles. Cette influence est finalement en relation avec la traction que les fibres musculaires exercent sur les tonofibrilles, et il est possible qu'un certain nombre de caractères d'orientation des structures selon les forces de traction des muscles, soit déterminée au cours de la mue pendant la phase non calcifiée des téguments. En effet, il a été montré par WOLFE (15), chez les Insectes, que les tonofibrilles ne sont pas attaquées par le liquide de mue au cours de la résorption de l'ancien tégument, c'est-à-dire qu'elles sont présentes dès la formation des premières strates de la procuticule. Par leur intermédiaire, les muscles peuvent exercer des forces de traction orientées très tôt sur les éléments d'un ensemble tégumentaire en formation, le phénomène se continuant et s'augmentant à mesure de l'ac-

croissement tranversal des fibres musculaires, impliquant selon MUNSCHEID (16), la formation de nouvelles tonofibrilles dans l'épithélium et la procuticule. Au sujet de cette croissance transversale des muscles, il faut encore mentionner que l'augmentation de taille du faisceau de tonofibrilles, par la formation de nouvelles tonofibrilles dans l'épithélium, peut se faire selon plusieurs processus: par formation de nouveaux tonofilaments qui viennent grossir les tonofibrilles déjà existantes, par formation de nouvelles tonofibrilles dans les cellules épithéliales qui en contenaient déjà, par formation de nouvelles cellules épithéliales qui viendraient augmenter la surface de l'épithélium d'insertion musculaire, par apparition de tonofibrilles dans les cellules épithéliales banales, transformant celles-ci en cellules épithéliales à tonofibrilles annexées par l'insertion de la fibre musculaire. Ce problème apparaît donc comme assez complexe et ne pourra vraiment se résoudre qu'avec la confirmation des relations exactes entre les tonofibrilles et les cellules épithéliales.

Les tonofibrilles ne présentent pas les mêmes caractères d'individualité que les myofibrilles, en ce sens que les tonofilaments ne forment pas un seul faisceau continu et régulier sur toute leur longueur. Il a été signalé, en effet, que des regroupements de petits faisceaux en tonofibrilles plus grosses pouvaient se produire, de même qu'il pouvait apparaître, par endroits, à l'intérieur d'une même tonofibrille, une large zone de cytoplasme avec des mitochondries, subdivisant le faisceau de tonofilaments. Les tonofilaments semblent donc pouvoir se séparer les uns des autres ou se regrouper à n'importe quel niveau de leur longueur. Ceci est peut-être en relation avec l'absence de striation transversale et surtout de liaisons latérales à intervalle régulier entre les myofilaments, comme celles décrites par HODGE (17) dans un muscle d'insecte. Cependant, le nombre de tonofilaments est limité par l'enveloppe des doubles membranes plasmiques; c'est seulement à l'intérieur de cette limite qu'ils peuvent se grouper en un ou plusieurs faisceaux. On pourrait donc considérer cette quantité de tonofilaments, comprise à l'intérieur d'un prolongement cytoplasmique à travers l'épithélium, comme représentant l'unité tonofibrille. Quant à la continuation d'une myofibrille par une tonofibrille, la correspondance semble peu probable dans le type d'insertion étudiée ici, étant donnée l'irrégularité même des faisceaux de tonofilaments. Pour rencontrer

une équivalence entre les deux formations, il faudra sans doute considérer la continuation au niveau de l'unité filament: myofilament continué par tonofilament.

Un aspect controversé des insertions musculaires de Crustacés reste celui de l'existence de tendons entre certains muscles et le tégument. Cette notion même de tendon est assez variable selon les auteurs. RICHARDS (1) estime, pour l'ensemble des Arthropodes, qu'il y a un passage graduel des tonofibrilles aux tendons et des tendons aux apodèmes et aux apophyses. Au contraire DEBAISIEUX (2) oppose nettement tendons et apodèmes; pour cet auteur, les tendons sont des condensations de "substance interstitielle", principalement d'origine mésenchymateuse, sans chitine, donc complètement différents des apodèmes du squelette épidermique chitineux. MAYRAT (18) décrit un cas d'insertion musculaire par l'intermédiaire d'un long tendon n'ayant rien à voir avec une invagination de la cuticule, puisque ne participant jamais à l'exuviation et ne présentant pas d'épithélium sur son pourtour. WOLFE (15) a également montré que les tonofibrilles ne sont pas altérées par le liquide de mue. Il semble donc justifié de distinguer, d'une part, tonofibrilles et tendons non affectés par l'exuviation, d'autre part, apodèmes et apophyses renouvelés à chaque mue. Dans le cas de l'insertion musculaire du fouet de l'exopodite, on peut se demander si l'allongement important des cellules épithéliales et des tonofibrilles, la concentration des myofibrilles sur des faisceaux denses de tonofibrilles, la réduction de l'espace disponible pour les organites dans la cellule épithéliale, ne représentent pas une étape vers la formation de tendons. L'absence d'épithélium sur le pourtour, généralement observée, pourrait correspondre au fait que le tendon comporte dans sa constitution, des cellules épithéliales, mais tellement déformées, allongées et remplies de matériel tonofibrillaire, qu'il devient difficile d'en discerner les limites et les organites, sur toute sa longueur, avec le microscope optique.

RÉSUMÉ

Ce travail rapporte quelques observations nouvelles d'histologie et de microscopie électronique sur un type particulier d'attache musculaire chez un Crustacé Décapode, Carcinus maenas L. De nombreux faisceaux de myofibrilles viennent s'insérer, de façon convergente, sur

un apodème de surface réduite, par l'intermédiaire de faisceaux denses de tonofibrilles très allongées. La jonction des tonofibrilles avec le tégument semble corrélative d'un épaississement de la procuticule et d'une disparition de la structure en lamelles de cette dernière. On observe alors dans la procuticule, des faisceaux de fibrilles mal délimités, qui sont orientés suivant le prolongement des tonofibrilles. Au microscope électronique est examinée seulement la zone la plus interne non calcifiée de la cuticule, où des groupes de filaments denses, orientés suivant le prolongement des tonofilaments, recoupent une autre catégorie de filaments, moins osmiophiles, sensiblement parallèles à la surface tégumentaire. Dans les cellules épithéliales d'insertion musculaire, beaucoup plus longues que les cellules épithéliales banales, les tonofibrilles laissent peu d'espace pour le cytoplasme et les organites cellulaires; les noyaux et les mitochondries sont ainsi déformés et allongés selon la direction des forces de traction musculaire. Les tonofibrilles apparaissent, au microscope électronique, comme formées par des faisceaux de tonofilaments dépourvus de toute striation transversale. Traversant longitudinalement l'épithélium, une membrane plasmique double semble isoler une zone de cytoplasme autour de chaque tonofibrille. Quelques hypothèses émises dans la discussion tentent d'interpréter ces observations dans le cadre des problèmes soulevés par la cytologie classique, concernant d'une part, les relations des tonofibrilles avec la procuticule et les cellules épithéliales d'insertion musculaire, d'autre part, l'existence des tendons chez les Crustacés.

RESUMO

Êste trabalho relata algumas observações novas sôbre a histologia e a microscopia eletrônica de um tipo particular de inserção muscular em um Crustáceo Decápodo, *Carcinus maenas* L. Numerosos feixes de miofibrilas chegam de modo convergente até um apodema de superfície reduzida, a que se ligam por meio de feixes densos de tonofibrilas muito alongadas. A junção das tonofibrilas com o tegumento parece correlacionar-se com um aumento da espessura da procutícula e com um desaparecimento da estrutura lamelar desta última. Observam-se então, na procutícula, feixes de fibrilas mal individualizadas e orientadas segundo o prolongamento das tonofibrilas.

Com o microscópio eletrônico, examinou-se sòmente a zona mais interna não calcificada da cutícula, onde grupos de filamentos densos, orientados segundo o prolongamento dos tonofilamentos, cruzam outra categoria de filamentos, menos osmiofílicos, sensìvelmente paralelos à superfície tegumentar. Nas células epiteliais de inserção muscular, bem mais compridas do que as células epiteliais comuns, as tonofibrilas deixam pouco espaço para o citoplasma e os orgânulos celulares; os núcleos e as mitocôndrias são assim deformados e alongados paralelamente à direção das fôrças de tração muscular. Ao microscópio eletrônico, as tonofibrilas aparecem constituídas por feixes de tonofilamentos sem qualquer estriação transversal. Uma membrana plásmica dupla atravessa longitudinalmente o epitélio e parece isolar uma zona de citoplasma ao redor de cada tonofibrila. Algumas hipóteses emitidas na discussão, tentam interpretar essas observações em função dos problemas suscitados pela citologia clássica sôbre, de um lado, as relações das tonofibrilas com a procutícula e as células epiteliais de inserção muscular e, do outro, a existência de tendões nos Crustáceos.

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Pour toutes les facilités qui nous sont constamment offertes, nous exprimons nos remerciements au Docteur Helena de SOUZA SANTOS, au Docteur Persio de SOUZA SANTOS, au Professeur Paulo SAWAYA et au Professeur Paulo RIBEIRO de ARRUDA. Ce travail a pu être réalisé grâce à l'aide du Conseil National de Recherches du Brésil et de l'Université de São Paulo.

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LÉGENDES

A: zone anisotrope; Ap.: apodème; Cp.: zones cytoplasmiques situées à l'intérieur des tonofibrilles, pouvant contenir des mitochondries allongées; Ep.: épithélium; Ep. 1: cellules épithéliales banales; Ep. 2: cellules épithéliales à tonofibriles d'insertion musculaire; ex.: espaces extracellulaires; F.c.: fibrilles cuticulaires; f.c. 1: filaments cuticulaires parallèles à la surface tégumentaire; f.c. 2: filaments cuticulaires denses, orientés dans le prolongement des tonofilaments; F.m.: fibre musculaire; H: disque de Hansen; I: zone isotrope; m.b.: membrane basale; m.c.: membrane cellulaire; Mf.: myofibrilles; m.n.: membrane nucléaire double; m.p.: membrane plasmique longitudinale; m.p. 1: membrane plasmique double provenant de la juxtaposition des membranes cytoplasmiques de deux cellules épithéliales mitoyennes; m.p. 2: membrane plasmique double entourant une tonofibrille; Mt.: mitochondrie; N.e. 1: noyau des cellules épithéliales banales; N.e. 2: noyau des cellules épithéliales à tonofibrilles; nu.: nucléole; O.: dépôts d'Osmium de contour subcirculaire, peut-être en relation avec les pores cuticulaires; Sl.: sarcolemme; Sp.: sarcoplasme; Tf.: tonofibrilles; tf.: tonofilaments; xl.: coupe très latérale dans une tonofibrille, avec seulement quelques tonofilaments entre les deux membranes plasmiques doubles; x2: coupe longitudinale passant entre la tonofibrille et son enveloppe plasmique double qui, seule, est alors intéressée par la section; x3: les doubles membranes plasmiques latérales se rejoignent en avant d'une tonofibrille coupée obliquement; Z: ligne Z.

EXPLICATION DES PLANCHES

Fig. 1 — Micrographie optique de l'ensemble des insertions musculaires sur un apodème du fouet, en coupe longitudinale, dans l'exopodite du troisième maxillipède — x 170.

Fig. 2 — Micrographie optique de l'insertion de fibres musculaires sur la cuticule d'un apodème, en coupe longitudinale, même matériel — x 450.

Fig. 3 — Micrographie optique des cellules épithéliales d'insertions avec les faisceaux de tonofibrilles, en coupe longitudinale — x 1000.

Fig. 4 — Électromicrographie à faible grandissement d'une coupe oblique dans la région de l'épithélium à tonofibrilles d'insertion musculaire — x 5000.

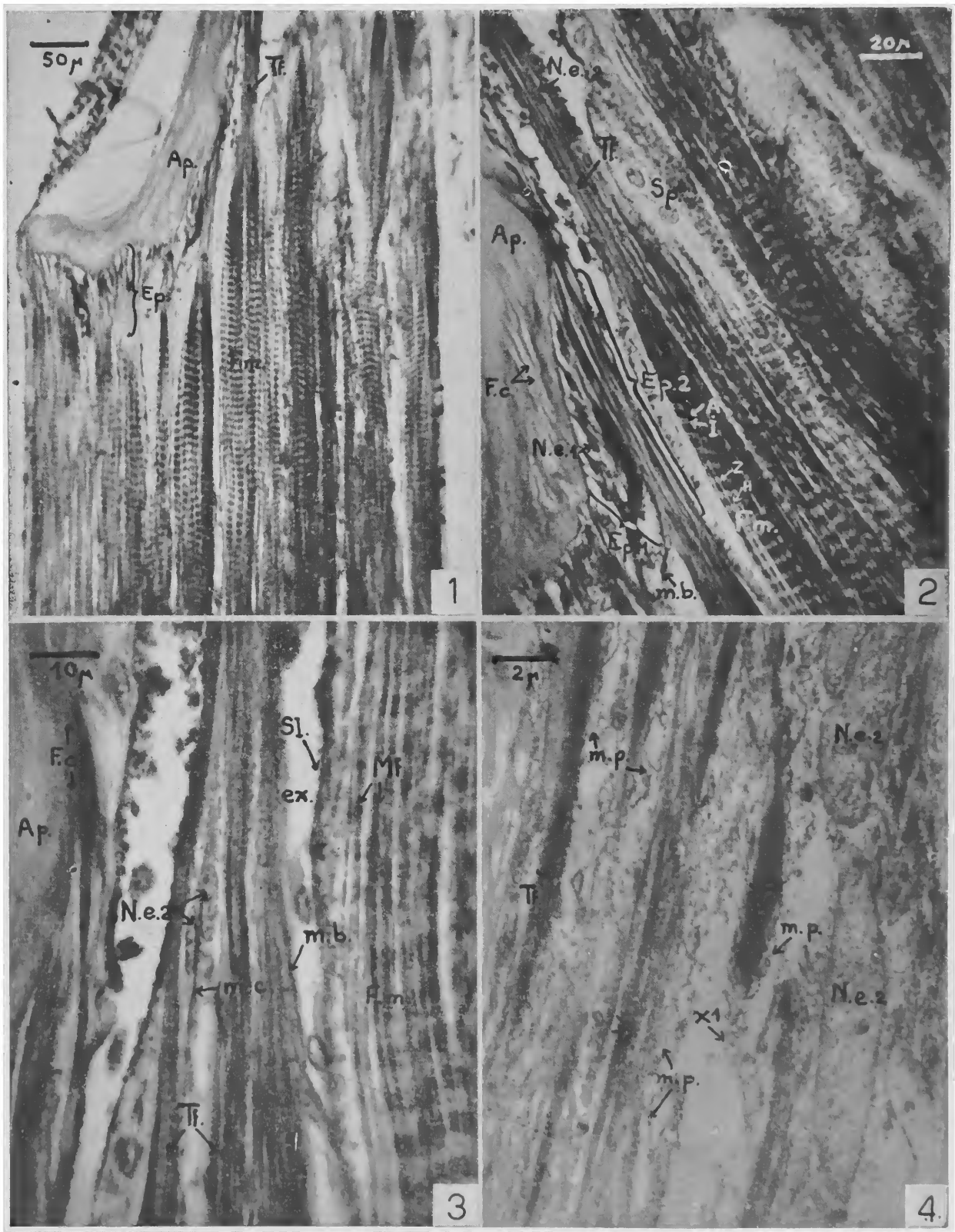
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Fig. 5 — Micrographie électronique d'une coupe oblique dans des cellules épithéliales à tonofibrilles au voisinage de l'apodème — x 12.500.

Fig. 6 — Électromicrographie d'une coupe sublongitudinale qui permet la distinction entre les membranes plasmiques de deux cellules épithéliales voisines et l'enveloppe plasmique double d'une tonofibrille — x 16.500.

Fig. 7 — Détails des membranes plasmiques doubles longitudinales et du réticulum endoplasmique au voisinage d'une tonofibrille — x 58.000.

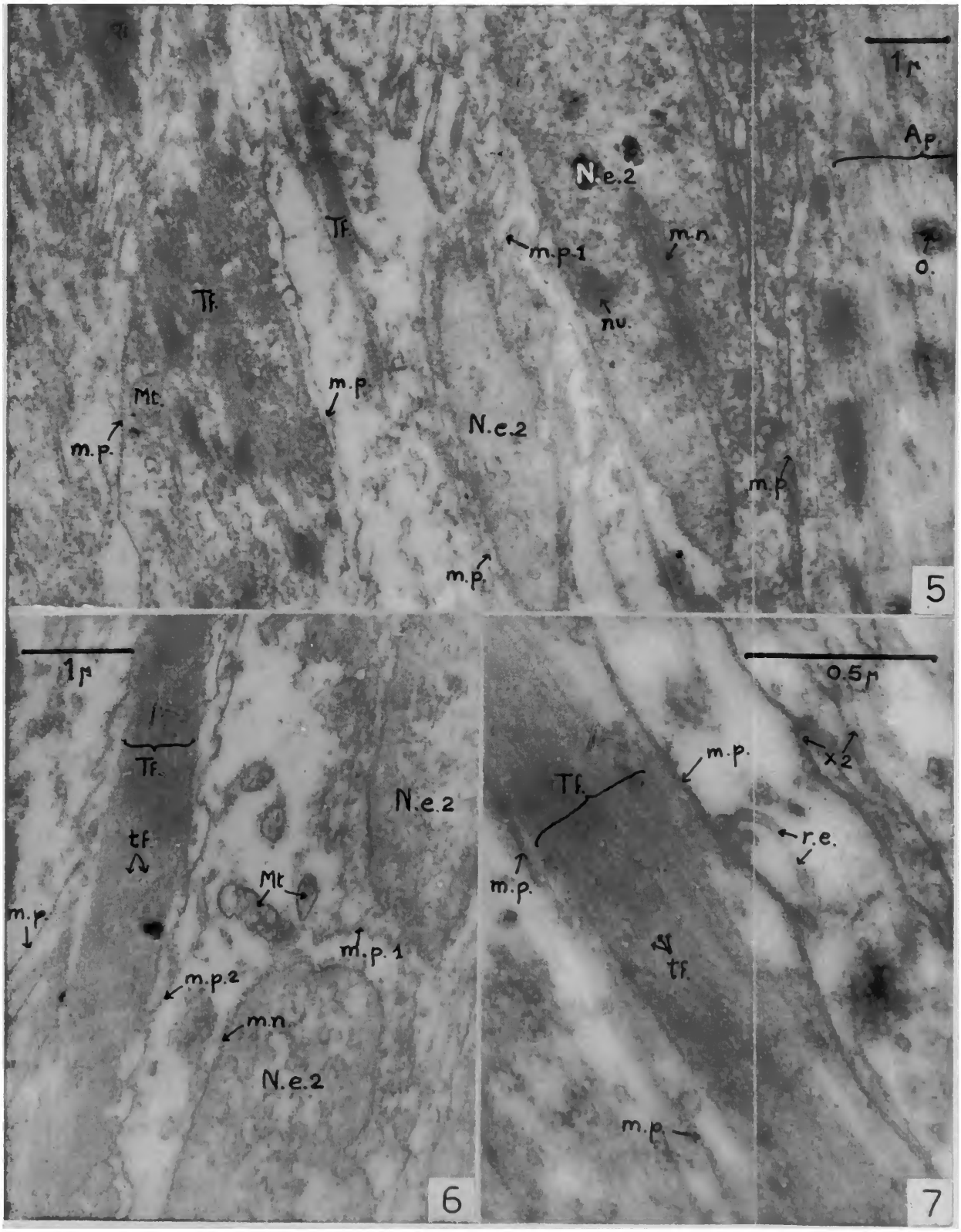
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Fig. 8 — Micrographie électronique d'une coupe longitudinale dans trois cellules voisines de l'épithélium à tonofibrilles — x 8.500.

Fig. 9 — Électromicrographie d'une coupe longitudinale dans la zone de jonction d'une tonofibrille avec la cuticule — 12.000.

Fig. 10 — Micrographie électronique montrant les boucles profondes formés par une membrane plasmique double longitudinale à proximité de la cuticule — x 25.000.

R. LAVALLARD — Structure de Tonofibrilles chez *Carcinus maenas* L.

EST. III — Figs. 8-10

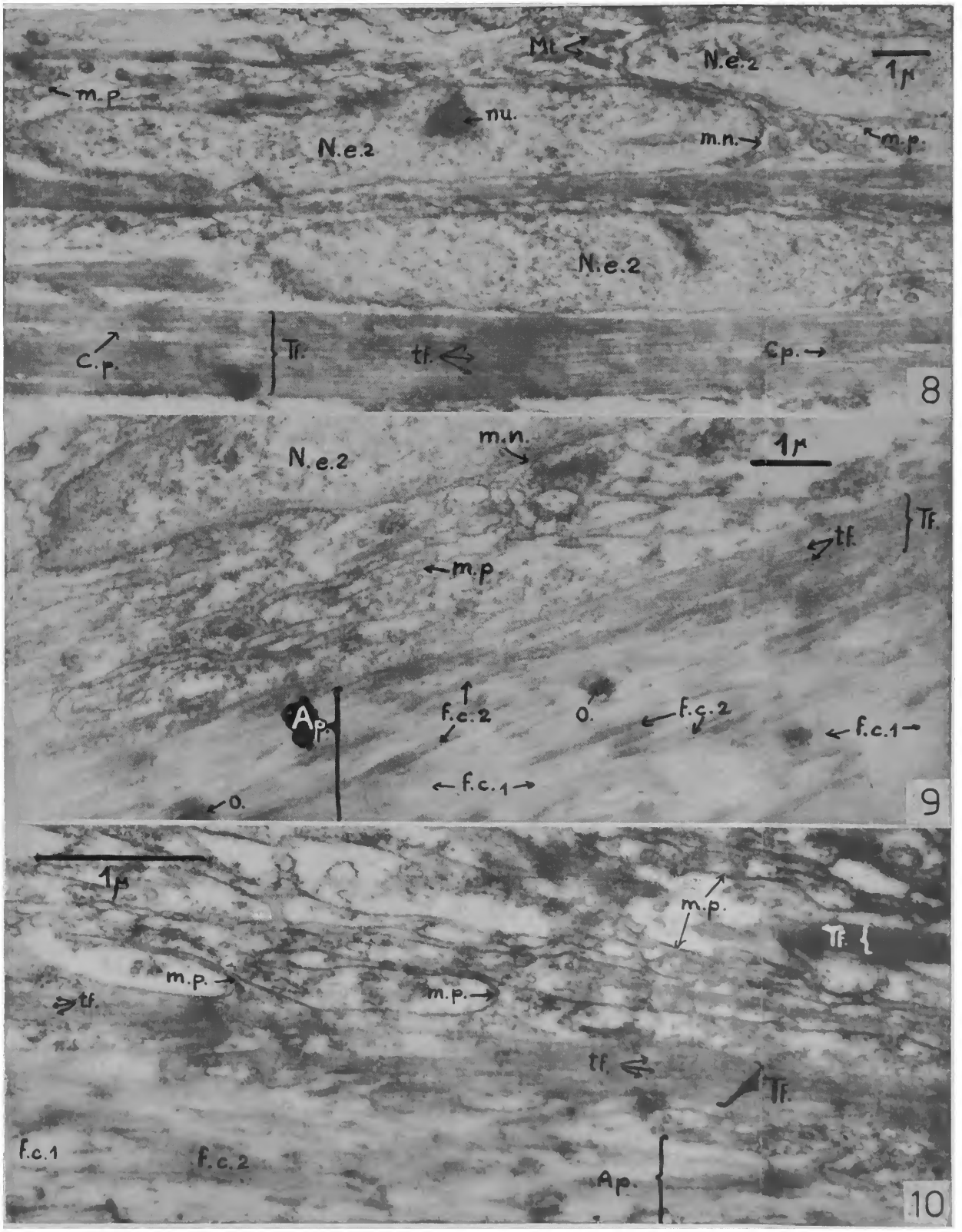
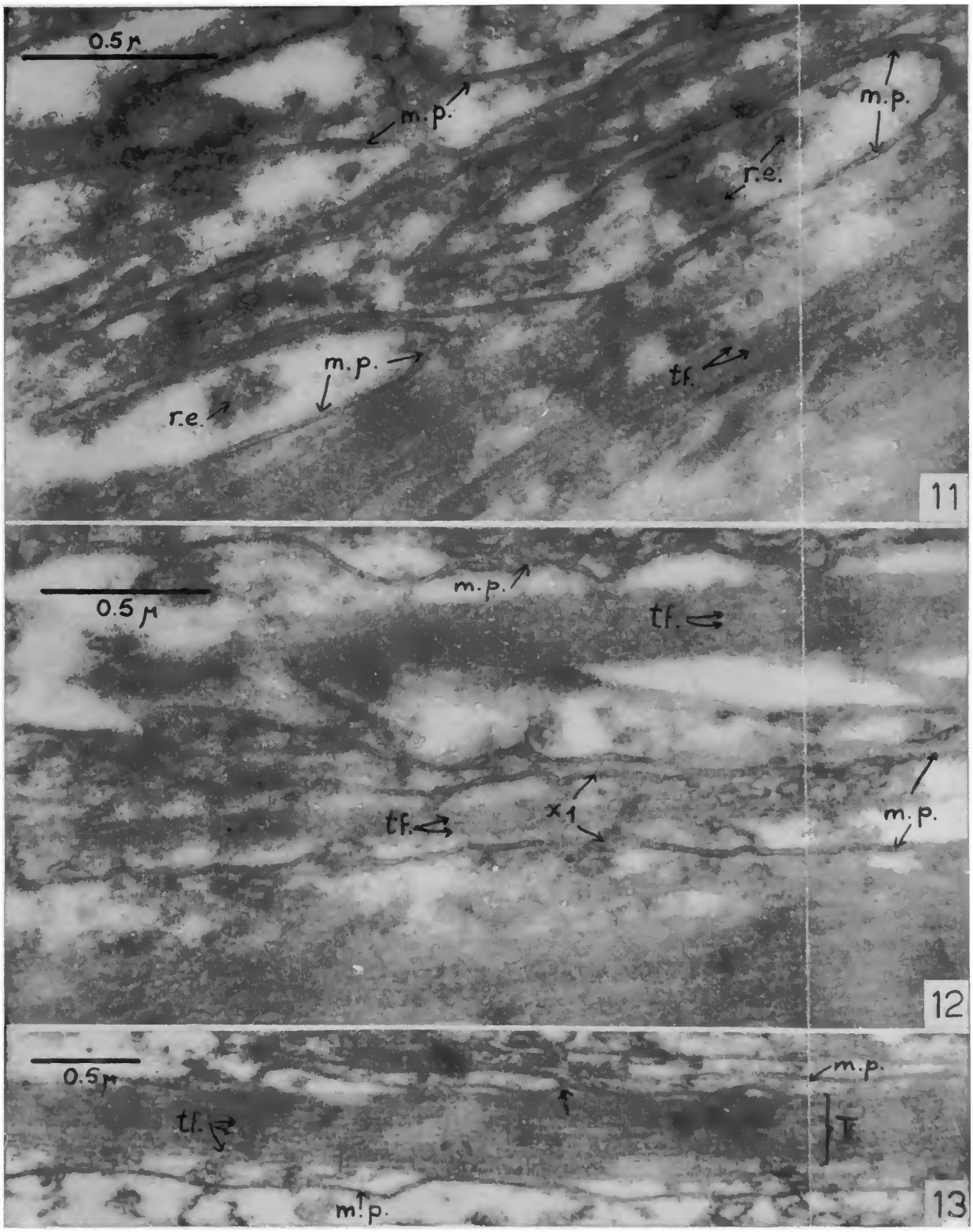


Fig. 11 — Même coupe longitudinale que dans la Fig. précédente, avec un grandissement plus fort pour la région des boucles de la membrane plasmique double au voisinage de la cuticle — x 57.000.

Fig. 12 — Micrographie électronique d'une coupe sublongitudinale dans un faisceau dense de tonofibrilles — x 54.000.

Fig. 13 — Électromicrographie d'une tonofibrille avec son enveloppe plasmique double, en coupe longitudinale — x 31.000.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SÔBRE LAGENIDAE E NODOSARIIDAE RECENTES DO BRASIL (FORAMINIFERA)

WALTER NARCHI

(com 10 pranchas)

ÍNDICE

INTRODUÇÃO

Muito pouco conhecemos da fauna do litoral Atlântico sul-americano, principalmente na costa do Brasil. Os foraminíferos são quase desconhecidos, sendo poucos os trabalhos publicados a respeito dêsses animais, nas águas brasileiras.

D'ORBIGNY (1839) nos resultados do seu "Voyage dans l'Amérique Méridionale", demonstrou a existência de foraminíferos no Brasil, em areia recolhida no Rio de Janeiro, aliás sem fornecer uma lista das espécies.

Em 1857 o "Plumper" coletou material na costa leste brasileira, do trecho entre Pôrto Seguro e Cabo Frio. Foram feitas oito sondagens cujas profundidades variaram de 57 a 1.700 m., sendo o ma-

terial encaminhado a PARKER, BRADY & JONES. No trabalho dêstes (1.888), "Foraminifera from Abrolhos Bank", várias espécies foram descritas e novas ocorrências assinaladas, constituindo o trabalho, a base para os estudos dos foraminíferos brasileiros. Cêrca de cem espécies ilustram o texto que é apenas um inventário faunístico.

Em 1873, a expedição "Challenger", após tocar nos rochedos da Ilha de São Paulo, dirigiu-se para os Estados de Pernambuco e Bahia onde coletou material de duas estações em águas profundas (1.240 e 4.500).

Em 1909 apareceu o trabalho de RHUMBLER que estudou os foraminíferos da "Plankton-Expedition", provenientes do Norte do Brasil, em profundidades além de 1.000 m.

Em 1925 e 1927 o "Meteor" coletou sedimentos na região equatorial entre a América do Sul e África. Na plataforma continental brasileira foram feitas algumas estações.

Em 1931 CUSHMAN & PARKER estudando as coleções feitas por WALDO L. SCHMITT, tiveram em mãos material de três estações do Rio de Janeiro e concluiram ser a fauna aí semelhante à das Índias Ocidentais.

Em 1952 CARVALHO & CHERMONT fizeram um levantamento dos foraminíferos da areia das praias do Estado de São Paulo, desde Ubatuba até Cananéia.

Em 1955, TINOCO, estudando material de Cabo Frio, descreveu algumas espécies novas e assinalou a ocorrência de *Oolina melo* d'Orbigny.

Em 1956 iniciei o estudo dos foraminíferos brasileiros, analisando amostras a mim confiadas pelo meu orientador, o Chefe de Secção no Instituto Oceanográfico da Universidade de São Paulo, Sr. JOÃO DE PAIVA CARVALHO. Nesse trabalho estudei as: Miliolidae, Peneroplidae e Alveolinellidae. Baseado em material de proveniências muito diversas, cheguei a reconhecer duas zonas do litoral do Brasil. Dentre os foraminíferos coletados do paralelo de 23° para o Norte, muitos são conhecidos das Índias Ocidentais. Estas espécies são próprias de águas tropicais. Da zona do paralelo indicado, para o Sul, a fauna de foraminíferos é diferente.

Em 1959 BOLTOVSKOY propôs-se a estudar os foraminíferos recentes da plataforma continental brasileira e descreveu espécimens encontrados entre as latitudes de 23° a 34° S, tentando relacioná-los com os da Argentina e os das Índias Ocidentais.

MÉTODOS DE ESTUDO

O material dado a mim pela direção do Instituto Oceanográfico, tinha sido coletado com o aparelho Van der Veen, Snaper e com um apetrecho especialmente adaptado a coletas de fundo. Explica-se a disparidade de métodos de coleta uma vez que esta foi feita em diferentes viagens, com diversos tipos de embarcações e equipamentos.

O material foi lavado e secado, após o que foi tamisado numa série de peneiras com diferentes tamanhos de malhas. Recebi o material já sêco; tratei-o por tetracloreto de carbono, de acôrdo com o método usado por OSAWA no laboratório de CUSHMAN. Como notei que muitos exemplares não flutuavam, foi necessário também o estudo do restante das amostras.

Preparei lâminas de fundo escuro e nelas fixei os foraminíferos, por meio de gôma adragante. Para facilitar o estudo confeccionei lâminas de exemplares provenientes das diferentes estações, separando-os por Famílias e posteriormente por Espécie, sendo estas conservadas na coleção da Secção de Oceanografia Biológica do Instituto Oceanográfico (I. O.).

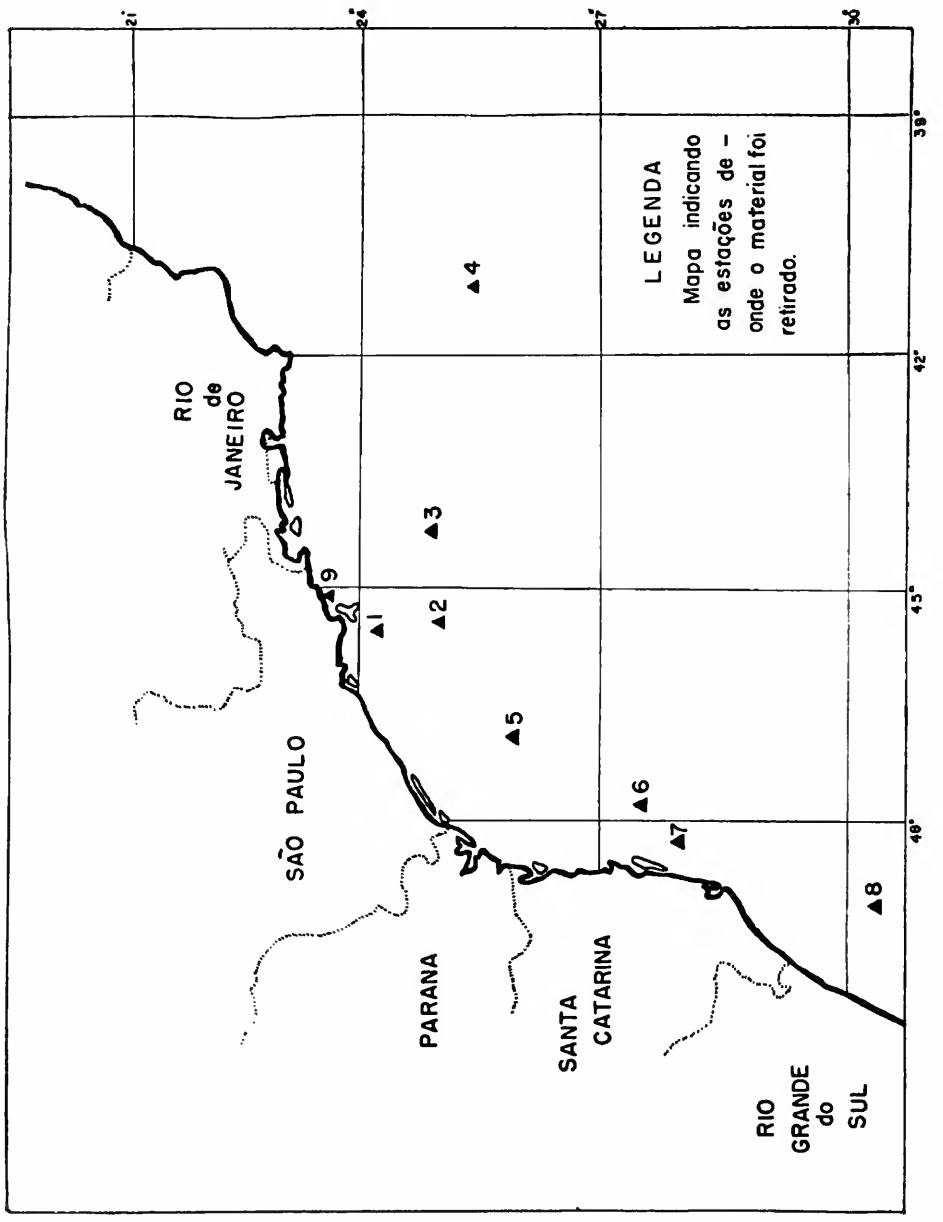
LOCALIZAÇÃO DAS ESTAÇÕES

Várias amostras de fundo foram coletadas em diferentes viagens, pelo I. O., tais como as da Expedição ao chamado "Mar Novo", com o iate "Igaratí" (1954) e da viagem realizada pelo "Presidente Vargas" (1955).

Três amostras de fundo foram coletadas pelo "Igaratí" e cinco pelo "Presidente Vargas"; além dessas estações foi recebida também uma amostra de Ubatuba, de pequena profundidade. O quadro seguinte mostra a localização, a profundidade e a natureza das amostras.

Estação	Estação hidrográfica correspondente	Local	Situação	Profundidade	Natureza da amostra
1	—	Ilha dos Alcatrazes	Lat. 24° 03' S. Long. 45° 40' O.	32 m	Lôdo
2	Est. 5 Alcatrazes	—	Lat. 25° 26' S. Long. 45° 25' O.	106 m	—
3	Est. 7 Alcatrazes	—	Lat. 25° 02' S. Long. 44° 42' O.	136 m	Lôdo com conchas
4	Est. 4 Pres. Vargas	—	Lat. 25° 45'5 S. Long. 40° 36'9 O.	125 m	"
5	Est. 5 Pres. Vargas	—	Lat. 26° 19'7 S. Long. 46° 58'5 O.	150 m	"
6	Est. 7 Pres. Vargas	—	Lat. 27° 36'5 S. Long. 47° 56' O.	95 m	Lôdo
7	Est. 8 Pres. Vargas	—	Lat. 28° 0'75 S. Long. 48° 12' O.	63 m	Areia
8	Est. 13 Pres. Vargas	—	Lat. 30° 22' S. Long. 49° 19' O.	120 m	Lôdo com conchas
9	—	Ubatuba	Lat. 23° 27' S. Long. 45° 6' O.	10 m	Lôdo

MAPA


21°
24°
27°
30°
39°
42°
45°
48°
LEGENDA
Mapa indicando as estações de - onde o material foi retirado.
RIO de JANEIRO
SÃO PAULO
PARANA
SANTA CATARINA
RIO GRANDE do SUL
1
2
3
4
5
6
7
8
9

AS LAGENIDAE E NODOSARIIDAE DO BRASIL

A lista seguinte contém as espécies das Famílias Lagenidae e Nodosariidae até agora assinaladas nas costas brasileiras. Da região norte nada sabemos além da relação apresentada por SCHOTT, resultado das sondagens feitas pela "Expedição Atlântica Alemã". As estações foram feitas em grandes profundidades sendo que poucas na plataforma continental.

Na região do nordeste, além do trabalho de SCHOTT e do "Challenger", temos ainda a coleta do "Plumper" com material do banco de Abrolhos entre Bahia e Cabo Frio. Desta região há ainda o trabalho de TINOCO, que apresenta apenas uma espécie.

Na região sudeste, os trabalhos de CUSHMANN & PARKER, PAIVA CARVALHO & CHERMONT e o de BOLTOVSKOY, referem-se a material do Rio de Janeiro, São Paulo e sul do Brasil, respectivamente.

As ocorrências das espécies coloco à maneira dum catálogo sem comentar ou modificar as classificações encontradas na literatura. A região norte abrange as espécies desde Cabo Orange até Cabo de São Roque. No litoral nordeste, as da região de Cabo de São Roque até Cabo Frio e o litoral sudeste de Cabo Frio até o Sul do Brasil.

Região Norte

Robulus lucidus Cushman
Robulus papillosa (Fichtel & Moll)
Robulus occidentalis Cushman, var. *torridus* Cushman
Lenticulina gibba (d'Orbigny)
Nodosaria scalaris (Batsch)
Lingulina seminuda Hantken
Lagena flintiana Cushman
Lagena globosa Montagu
Lagena gracillima (Seguenza)
Lagena hispida Reuss
Lagena marginata Walker & Boys
Lagena orbignyana, var. *elliptica* Cushman
Lagena staphyllearia (Schwager)

Região Nordeste

Cristellaria calcar Linné
Cristellaria cassis Fichtel & Moll
Cristellaria cultrata Montfort
Cristellaria rotulata Lamarck
Cristellaria crepidula Fichtel & Moll
Cristellaria variabilis Reuss
Nodosaria pyrula d'Orbigny
Nodosaria (*D.*) *mucronata* Neugeboren
Nodosaria obliqua Linné
Nodosaria hispida d'Orbigny
Nodosaria hispida var. *sublineata* Brady
Vaginulina spinigera Brady
Vaginulina linearis Montagu
Rhabdogonium tricarinatum d'Orbigny
Lagena sulcata Walker & Jacob
Lagena striata d'Orbigny
Lagena lineata Williamson
Lagena laevigata Reuss
Lagena marginata Walker & Jacob
Lagena orbignyana (Seguenza)
Lagena lagenoides Williamson

Região Sudeste

Robulus calcar (Linné)
Robulus rotulatus (Lamarck), forma typica
Robulus rotulatus, forma *cultrata* Montfort
Robulus orbicularis (d'Orbigny)
Robulus convergens (Bornemann)
Robulus limbosus (Reuss) s. l.
Robulus cf. nikobarensis (Schwager)
(?) *Robulus clericii* (Fornasini)
Darbyella (?) *argentinensis* Boltovskoy
Lenticulina peregrina (Schwager)
Astacolus crepidulus (Fichtel & Moll)
Astacolus planulatus Galloway & Wissler
Planularia cassis (Fichtel & Moll)

Marginulina glabra d'Orbigny
Marginulina bacheii Bailey
Marginulina schlönbachi (Reuss)
Marginulina marginuloides (Goës)
Dentalina communis (d'Orbigny)
Dentalina consobrina emaciata Reuss
Nodosaria scalaris (Batsch), forma typica
Nodosaria scalaris, forma *separans* Brady
Nodosaria pyrula d'Orbigny
Nodosaria candei d'Orbigny
Nodosaria catesbyi d'Orbigny
Nodosaria sublineata Brady
Nodosaria vertebralis albatrossi Cushman
Saracenaria italica Defrance
Lingulina seminuda Hantken
Lagena sulcata (Walker & Jacob), forma typica
Lagena sulcata, forma *lyellii* (Seguenza)
Lagena laevis (Montagu), forma typica
Lagenda laevis, forma *perlucida*
Lagena caudata (d'Orbigny)
Lagena striata (d'Orbigny), forma typica
Lagena striata var. *pustulata* Boltovskoy
Lagena interrupta Williamson
Lagena distoma Parker & Jones
Oolina melo d'Orbigny
Oolina hexagona (Williamson)
Oolina acuticosta (Reuss)
Oolina caudigera (Wiesner)
Fissurina marginata (Walker & Boys)
Fissurina lineata (Williamson)
Fissurina laevigata Reuss
Fissurina lagenoides (Williamson)
Fissurina orbignyana Seguenza
Fissurina semimarginata (Reuss)
Fissurina quadricostulata (Reuss)
Fissurina falcata (Chaster)
Fissurina heinzi (Matthes)

Parafissurina lateralis (Cushman)
Parafissurina cf. quadrata Parr
Lagena orbignyana (Seguenza)
Nodosaria calomorpha Reuss

Das quase noventa espécies encontradas nas costas do Brasil cêrca de sessenta das Famílias aqui tratadas haviam sido registradas da região de Cabo Frio para o Sul. Vê-se daí que os trabalhos de SCHOTT, BRADY, PARKER & JONES e o de BOLTOVSKOY fornecem a base do nosso conhecimento da distribuição geográfica das Legenidae e Nodosariidae nas águas brasileiras.

EVOLUÇÃO DE CERTOS FORAMINÍFEROS

O estudo dos fósseis deveria levar à taxonomia *filogenética* ideal. Nas Famílias tratadas por mim, de exoesquelto completamente calcáreo, a sistematização baseada no material fóssil é variável. Para os foraminíferos em geral, tantas vêzes de esqueleto arenoso, pseudoquitínico ou até gelatinoso, as possibilidades da fossilização são restritas ou inexistentes. Não discuto, por isso, as raízes das Famílias, esboçadas diferentemente pelos vários autores.

Prefiro, baseado na ornamentação, demonstrar nos gêneros *Robulus e Fissurina,* a seqüência do tempo, e com isso, a presumível origem de certas formas recentes. Na discussão e descrição seguintes adoto o sistema de PARR (1947). Separou duas Famílias, Lagenidae monotálamas, isto é, de uma câmara e Nodosariidae politálamas, quer dizer, de muitas câmaras. A maioria dos autores considera a monotalamia dos Lagenidae como caráter secundário. No sistema de CUSHMAN (1927), as Nodosariidae formam uma subfamília das Lagenidae, no de RHUMBLER (1909), dá-se o contrário.

Robulus das Nodosariidae aparece no Liássico (*R. iota*) com quilha larga. Em *R. lucidus* (outrora *articulata*), do Cretácio, a quilha é estreita, mas no Terciário aparece larga generalizadamente como base de vários apêndices. As linhas principais da evolução de *Robulus* no Terciário caracterizam-se pela evolução de espinhos, pelo serrilhamento da quilha e uma, a mais ricamente ramificada, pelas elevações na sutura. A figura A ilustra estas linhas.

FIGURA A

1. *Robulus lucidus* (CUSHMAN)
2. *Robulus denticuliferus* (CUSHMAN)
3. *Robulus submamiligerus* (CUSHMAN)
4. *Robulus calcar* (LINNE')
5. *Robulus yanquensis* BERMUDEZ
6. *Robulus echinatus* (D'ORBIGNY)
7. *Robulus formosus* (CUSHMAN)
8. *Robulus mamiligerus* (KARRER)
9. *Robulus bowdenensis* (CUSHMAN)
10. *Robulus antilleus* (CUSHMAN)

FIGURA A

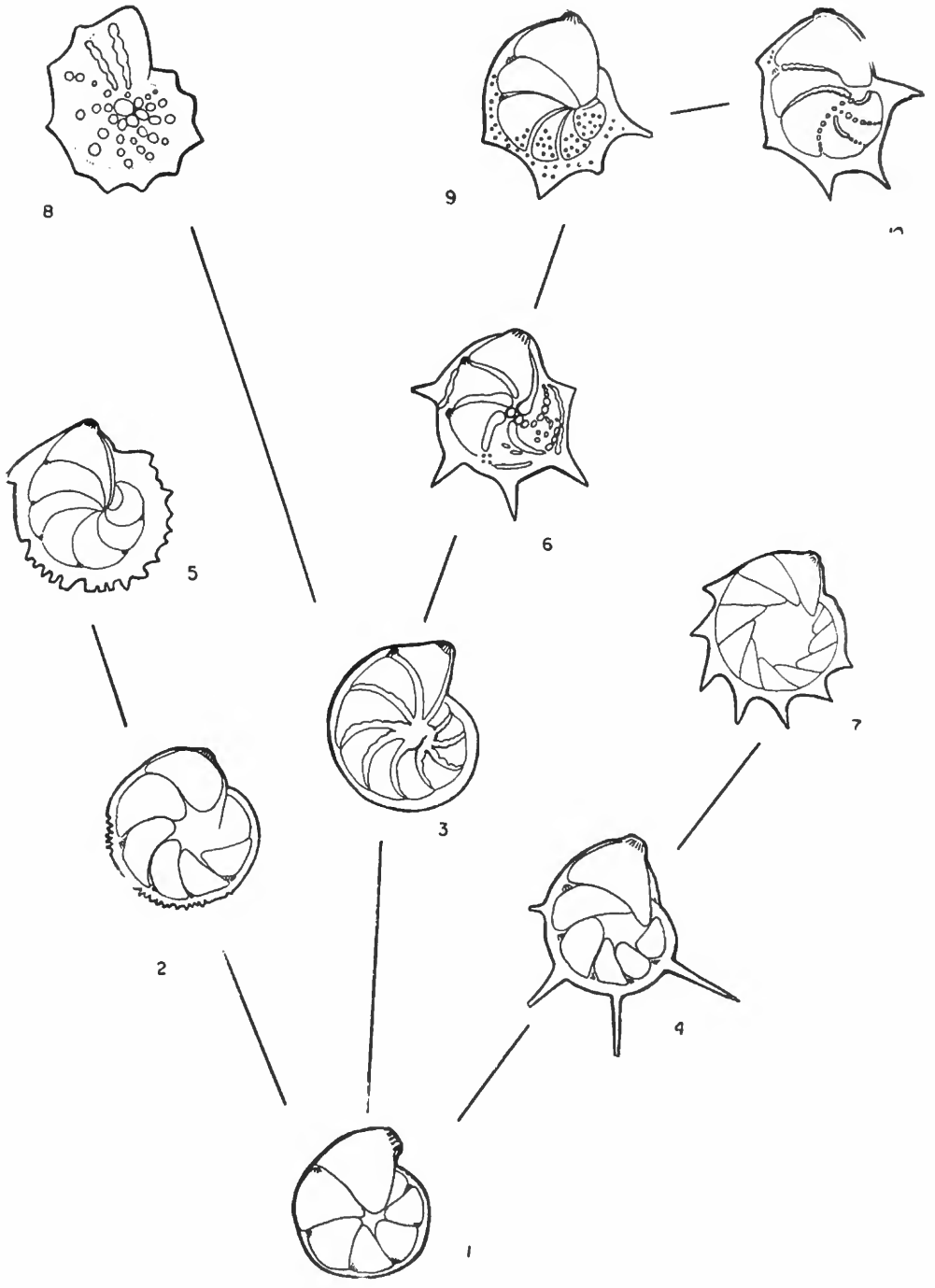


FIGURA B

1. *Fissurina laevigata* (REUSS)
2. *Fissurina marginata* (REUSS)
3. *Fissurina quadricostulata* (REUSS)
4. *Fissurina acuta* (REUSS)
5. *Fissurina annectens* (BURROWS & HOLLAND)
6. *Fissurina lucida* (WILLIAMSON)
7.-9. *Fissurina staphyllearia* SCHWAGER
10. *Fissurina lucida* (WILLIAMSON)

FIGURA B

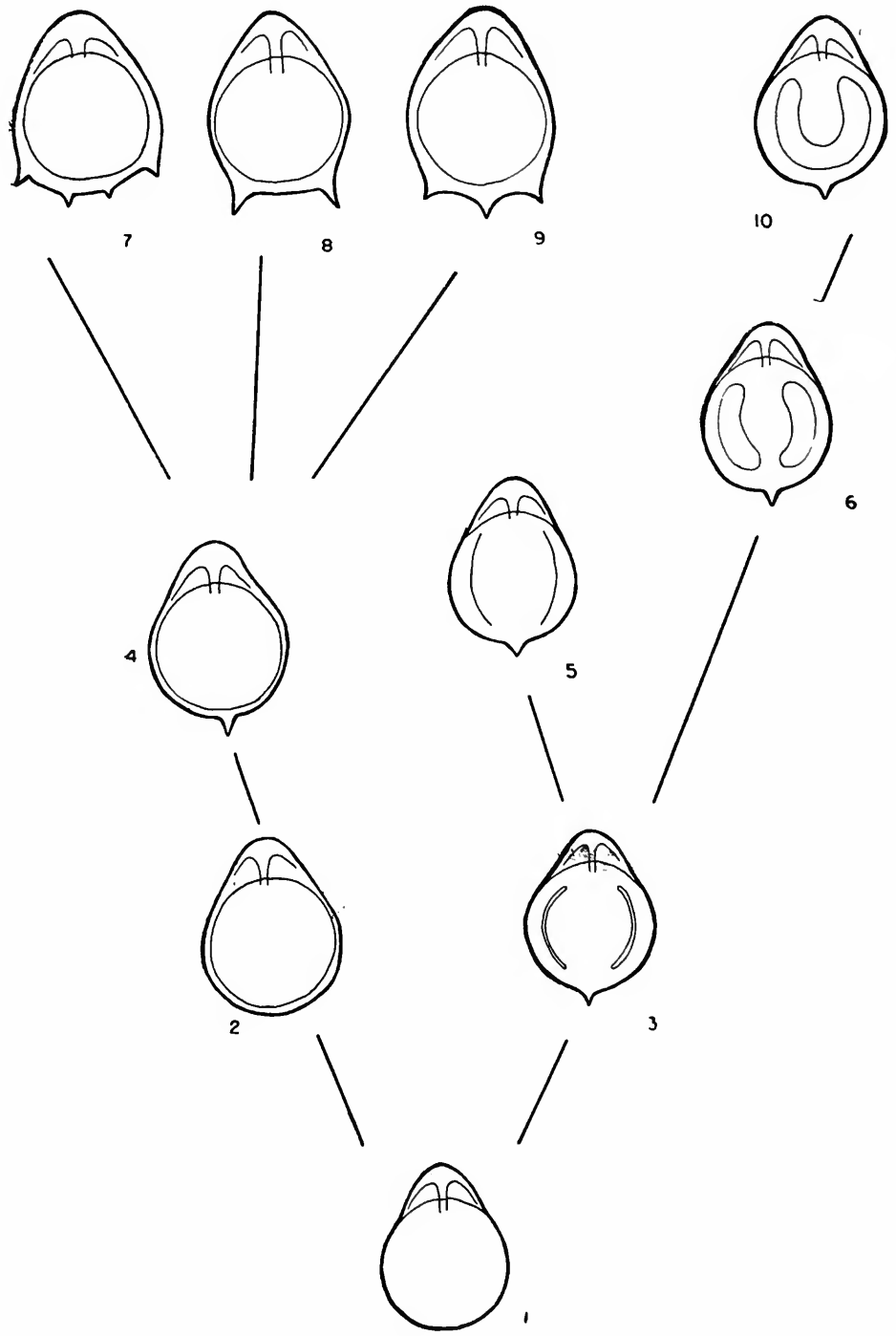
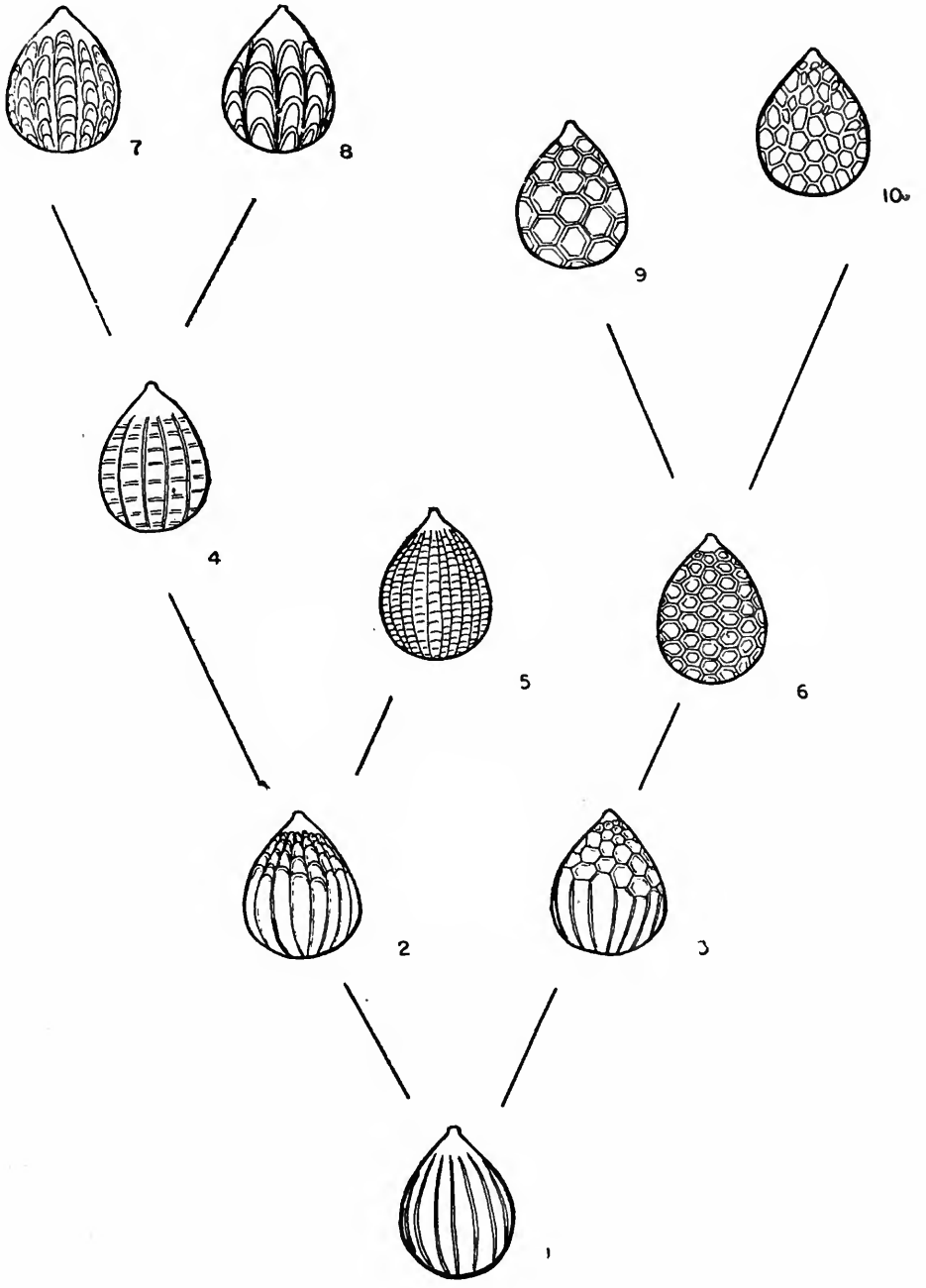


FIGURA C

1. *Oolina costata* (WILLIAMSON)
2. *Oolina melo* d'ORBIGNY
3. *Oolina scalariforme sulcata* (WIESNER)
4. *Oolina melo* d'ORBIGNY
5. *Oolina catenulata* (WILLIAMSON)
6. *Oolina hexagona* (WILLIAMSON)
7.-8. *Oolina squamosa* (MONTAGU)
9. *Oolina scalariformis* (WIESNER)
10. *Oolina montagui* (SILVESTRI)

FIGURA C



A da direita, de espinhos, existe desde o Mioceno (*R. calcar*) até hoje, sendo até a espécie idêntica.

A da esquerda, com dentes na quilha, é representada por duas espécies, também do Mioceno, sendo a de dentes menos fortes ainda encontrada atualmente.

A terceira linha, de elevações na sutura, contém muitas espécies do Terciário e algumas da fauna recente. Num ramo, de quilha estreita provida de numerosos dentes pequenos, caracteriza-se por *R. mamiligerus* (Fig. A-8), sem que seja possível derivar espécies recentes dêste. Outro ramo, de quilha larga e provida de poucos espinhos, sobrevive com *R. antilleus* (fig. A-10), dificilmente separável de *R. bowdenensis* (Fig. A-9), do Terciário. A variabilidade de *R. antilleus* será demonstrada na parte de sistemática especial.

Fissurina (Fig. B), das Lagenidae, começa no Eoceno com *F. laevigata* (Fig. B-1) sem quilha e sem espinho basal. O aparecimento destas complicações pode ser representado em duas linhas divergentes, ambas ainda na fauna recente.

A linha da direita mostra além do espinho basal ainda quatro costelas (*F. quadricostulata*), que num ramo diminuem (*F. annectens*) e no outro se desenvolvem de tal modo que confluem na base (*F. lucida*).

Na linha da esquerda coloco, no início, *F. marginata*. Do Mioceno, conhece-se *F. acuta,* na linha em questão. No Plioceno e na fauna atual, a quilha é provida de dois a quatro espinhos basais (*F. staphyllearia*).

Sem poder acompanhar os dados paleontológicos, apresento ainda algumas espécies de *Oolina* (Fig. C), das Lagenidae, para demonstrar a diversificação da escultura em várias direções. De uma espécie com costelas simples passo às que apresentam gradativamente a substituição das costelas por hexágonos que podem transformar-se em malhas nas terminações da linha. As espécies com hexágonos e malhas conhecem-se da fauna recente.

Outra linha derivável do tipo de costelas simples mostra o aparecimento de traves transversais que tornam a escultura constituída por retângulos ou até escamas. Tanto as espécies quadriculadas quanto as de escamas fazem parte da fauna atual.

RELATÓRIO DAS ESPÉCIES ENCONTRADAS

O meu material pertence aos seguintes gêneros:

Família Lagenidae

Gêneros

Lagena WALKER & JACOB, 1798
Oolina d'ORBIGNY, 1839
Fissurina REUSS, 1850
Parafissurina PARR, 1945

Família Nodosariidae

Gêneros

Nodosaria LAMARCK, 1812
Dentalina d'ORBIGNY, 1826
Frondicularia DEFRANCE, 1826
Saracenaria DEFRANCE, 1824
Robulus MONTFORT, 1808
Marginulina d'ORBIGNY, 1826
Astacolus MONTFORT, 1808

Família Lagenidae

Gênero

Lagena WALKER & JACOB, 1798

LAGENA CAUDATA (d'ORBIGNY, 1839) (Fig. 6)

Oolina caudata d'ORBIGNY, 1839

Lagena caudata HERON-ALLEN & EARLAND, 1932; BOLTOVSKOY, 1954.

Carapaça sub-globular, oblonga, com pequena saliência na região basal. Na porção anterior, pescoço curto com abertura. Tôda a carapaça é coberta por estritas longitudinais.

A figura de HERON-ALLEN & EARLAND difere do meu exemplar pela região anterior bem mais alongada.

Tôdas as espécies foram medidas em milímetros.

Comprimento: 0,23; largura 0,11.

Ocorrência — Estação 1.

Distribuição — Atlântico Sul (Falkland Islands, Patagônia, Argentina, Sul do Brasil, Rio de Janeiro).

LAGENA DISTOMA PARKER & JONES, 1857 (Fig. 5)

Lagena laevis var. striata PARKER & JONES, 1857.

Lagena distoma BRADY, 1884; SIDEBOTTOM 1913; CUSHMAN 1913, 1923; HERON-ALLEN & EARLAND 1932; EARLAND 1934.

Carapaça cilíndrica alongada, estreitada na base, onde pode formar curto tubo ponteagudo. Na região anterior há ligeiro estreitamento. Com aumento médio, verificam-se costelas longitudinais que percorrem tôda a testa.

Comprimento: 0,53; largura 0,08.

Ocorrência — Estação 1; sòmente poucos exemplares em bom estado.

Distribuição — Atlântico Sul (Sul do Brasil, ao largo de Pernambuco, Ascencion Island); Atlântico Norte (Índias Ocidentais, Ilhas Britânicas); Oceano Índico (Kerguelen Islands); Pacífico Sul (Raine Island); Pacífico Norte(Sul do Japão).

LAGENA GRACILIS WILLIAMSON, 1848 (Figs. 7, 8).

Lagena gracilis WILLIAMSON, 1848; BRADY 1884; CUHSMAN 1913, 1923, 1933; HERON-ALLEN & EARLAND 1932; EARLAND 1934, 1936.

Carapaça ovóide ou fusiforme, às vêzes estreita e alongada; pescoço cilíndrico com abertura. A largura máxima localiza-se no último terço da testa; extremidade basal pode apresentar espinho terminal. Em algumas espécies existe escultura no pescoço em forma de espiral.

Embora diferindo muito da forma apresentada por WILLIAMSON, inclusive pela ausência de rebordo ao redor da abertura, sua semelhança é muito grande aos desenhos apresentados por BRADY (1844 pl. 58 f. 9, 10, 23) e CUSHMAN (1933 pl. 8 f. 5).

Comprimento: 0,25; largura 0,08.

Ocorrência — Estação 6.

Distribuição — Atlântico Sul (Falkland Islands, Argentina); Atlântico Norte (Nova Inglaterra, Ilhas Britânicas, Mediterrâneo); Pacífico (Guam, Midway Islands).

LAGENA GRACILLIMA (SEGUENZA, 1862) (Figs. 11, 12)

Lagena gracillima BRADY, 1884; SIDEBOTTOM 1913; CUSHMAN 1913, 1923; HERON-ALLEN & EARLAND 1932; EARLAND 1934, 1936; BOLTOVSKOY 1954.

Testa finamente perfurada, pouco espêssa, alongada, mais larga no meio e estreitada nas extremidades. Nestas existem projeções cilíndricas finas cujos tamanhos variam, pois quebram-se com facilidade.

As figuras de BRADY (pl. 56 f. 20, 24) assemelham-se muito às formas encontradas por mim. Espécie rara nas amostras presentes. BOLTOVSKY (1954, p. 153), observou um exemplar no Gôlfo San Jorge.

Comprimento: 0,22 (Fig. 11) a 0,33 (Fig. 12); largura 0,06 Fig. 11) a 0,08 (Fig. 12).

Ocorrência — Estação 2.

Distribuição — Antártica; Atlântico Sul (Falkland Islands, Argentina); Atlântico Norte (Índias Ocidentais; Leste dos Estados Unidos, Ilhas Britânicas, Mediterrâneo, Guiné Portuguêsa); Oceano Índico (Kerimba Islands); Pacífico (Califórnia, Japão, Austrália, Nova Zelândia).

LAGENA HISPIDULA CUSHMAN, 1913 (Fig. 18)

Lagena laevis BRADY (em parte), 1884.

Lagena hispidula CUSHMAN, 1913; HERON-ALLEN & EARLAND 1932; EARLAND 1934, 1936.

Lagena submagnifica CUSHMAN & Mc. CULLOCH, 1950.

Carapaça elipsóide, arredondada na base, levemente alongada para o ápice onde ocorre pescoço comprido, tubiforme com abertura simples. Grupos de pequenos espinhos fundem-se na superfície e constituem fina parede externa que se rompe fàcilmente. O nome *L. submagnifica* refere-se a exemplares recentes e pleistocênios de *L. hipidula,* com parede externa incompleta.

Nos desenhos de EARLAND vê-se ausência parcial ou total desta parede.

Comprimento: 0,62; largura 0,25.

Ocorrência — Estações, 6, 7.

Distribuição — Pacífico (Japão, Hawaiian Islands).

LAGENA LAEVIS (MONTAGU, 1803 (Fig. 14)

Oolina striaticollis d'ORBIGNY, 1839.

Lagena laevis WILLIAMSON, 1848; BRADY 1884; SILVESTRI 1902; SIDEBOTTOM 1913; HERON ALLEN & EARLAND 1913, 1932; CUSHMAN 1923, 1933; EARLAND 1934, 1936; BOLTOVSKOY 1954.

Carapaça lisa, bem translúcida, em forma de garrafa com pescoço tubular que se abre distalmente. Nas amostras presentes, encontrei poucos exemplares.

São muito semelhantes à figura 12 (pl. 56) de BRADY.

Comprimento: 0,31; largura 0,11.

Ocorrência — Estação 1.

Distribuição — Universal.

LAGENA LYELLI (SEGUENZA, 1862) (Fig. 15)

Lagena lyelli SILVESTRI, 1902; HERON-ALLEN & EARLAND 1913, 1932; CUSHMAN 1923; CUSHMAN & PARKER 1931; BOLTOVSKOY 1954.

Carapaça consistente, firmemente calcificada, esférica com série de costelas. Estas estendem-se da base do prolongamento anterior até o espinho posterior, mais curto que o primeiro. Abertura rodeada por rebordo recortado, na extremidade do tubo anterior. Em alguns exemplares, ocorre refôrço nas costelas, estas param bruscamente no pescoço, como se fôssem continuar na outra câmara.

SILVESTRI (1902, p. 164) considera a espécie como sendo o "proloculus" de uma espécie de Nodosaria.

Comprimento: 0,27; largura 0,15.

Ocorrência — Estação 1.

Distribuição — Atlântico Sul (Falkland Islands, Argentina, Sul do Brasil, Rio de Janeiro); Atlântico Norte (Ilhas Britânicas, Mediterrâneo); Oceano Índico (Kerimba Islands).

LAGENA SEMISTRIATA WILLIAMSON, 1848 (Figs. 2-4)

Lagena striata var. semistriata WILLIAMSON, 1848.

Lagena semistriata BRADY, 1884; SIDEBOTTOM 1906; CUSHMAN 1933; EARLAND 1934.

Lagena Howei BERGQUIST, 1942.

Carapaça piriforme, com pescoço curto cilíndrico e rebordo estreito ao redor da abertura. A região basal termina abruptamente e apresenta uma série de curtas costelas longitudinais. A escultura do pescoço pode ser mais ou menos retílinea ou espiralada.

BRADY desenhou vários espécimens e o da f. 17 pl. 57 é idêntico ao meu da figura 2. A *L. Howei* BERGQUIST (1942) é uma variedade de *L. semistriata*.

Comprimento: 0,387 (Fig. 2) a 0,25 (Fig. 3); largura 0,16 (Fig. 2) a 0,11 (Fig. 3).

Ocorrência — Estação 1.

Distribuição — Atlântico Norte (Ilhas Britânicas, Mediterrâneo); Pacífico (Caroline Islands).

LAGENA SULCATA (WALKER & JACOB, 1798) (Fig. 13)

Lagena striata WILLIAMSON, 1848.

Lagena caepulla SCHWAGER, 1866.

Lagena sulcata BRADY, 1884; CHAPMAN 1902; CUSHMAN 1913, 1923; HERON-ALLEN & EARLAND 1932; EARLAND 1934, 1936; BOLTOVSKOY 1954.

Carapaça globular, com pescoço bem alongado em cuja extremidade se situa a abertura. Costelas longitudinais cobrem tôda a carapaça.

Dos desenhos de BRADY a figura 26 (pl. 57) assemelha-se à minha.

Comprimento: 0,42; largura 0,18.

Ocorrência — Estação 4.

Distribuição — Universal.

LAGENA SULCATA VAR. INTERRUPTA WILLIAMSON, 1848 (Fig. 16).

Lagena striata var. interrupta WILLIAMSON, 1848

Lagena sulcata var. interrupta BRADY, 1884; CUSHMAN 1905.

Carapaça globular ou piriforme com prolongamento anterior, ornamentado por elevações anelares. Na extremidade dêste se encontra a abertura simples. Superfície da testa com costelas longitudinais algumas das quais prolongam-se no pescoço. Na região basal as costelas terminam abruptamente formando uma corôa. Algumas costelas terminam anteriormente, no meio, ou no terço inferior.

Comprimento: 0,36; largura 0,17.

Ocorrência — Estação 6.

Distribuição — Atlântico Norte (Ilhas Britânicas); Pacífico (Rotonga).

LAGENA STRIATA (d'ORBIGNY, 1839) (Figs. 9, 10)

Oolina striata d'ORBIGNY, 1839.

Lagena substriata WILLIAMSON, 1848.

Lagena tenuistriata STACHE, 1865.

Lagena striata BRADY, 1884; BRADY, PARKER & JONES 1888; CUSHMAN 1913, 1923, 1933; HERON-ALLEN & EARLAND 1932; EARLAND 1934, 1936.

Forma da carapaça variável, circular a oval, com longo pescoço cilíndrico. Superfície com numerosas estrias longitudinais que podem continuar no pescoço, onde aparecem espiraladas.

A figura de BRADY (pl. 57 f. 22) corresponde perfeitamente aos espécimens presentes.

Comprimento: 0,28; largura 0,16.

Ocorrência — Estações 1, 7.

Distribuição — Atlântico Sul (Falkland Islands, Argentina, Sul do Brasil, Banco dos Abrolhos); Atlântico Norte (Índias Ocidentais, Ilhas Britânicas, Mediterrâneo); Pacífico (Hawaiian Islands, Guam, Japão, Austrália).

LAGENA STRIATA VAR. STRUMOSA REUSS, 1858 (Fig. 17)

Lagena striata var. strumosa CUSHMAN, 1913, 1918, 1921, 1933; EARLAND 1934.

Carapaça globular com estrias longitudinais como na forma típica de d'ORBIGNY. As estrias continuam no prolongamento anterior, tubular, em cuja extremidade se situa a abertura, que apresenta uma projeção labiada.

Os exemplares de CUSHMAN são piriformes e, assim sendo, lembram *L. caudata*. Os de BRADY (1884, pl. 57 f. 28) têm forma geral semelhante à dos meus, diferindo, porém, pela ausência da ornamentação no pescoço.

Comprimento: 0,22; largura 0,11.

Ocorrência — Estação 1.

Distribuição — Indo-Pacífico (Filipinas); Pacífico (Japão, Fiji Islands, Midway Islands, Guam).

LAGENA YCATUPE SP. N. (Fig. 1)

Carapaça ovóide, alargada na região central, continuando-se para as extremidades em duas grandes projeções apiculadas. Parede da testa pouco espêssa, finamente perfurada. Extremidade anterior mais

desenvolvida apresentando abertura circundada por rebordo. Região basal ornamentada por estrias longitudinais finas.

Os desenhos de BRADY (1884, pl. 56 f. 22), muito semelhantes aos meus, não apresentam estrias, nem rebordo na abertura, o que poderia ocorrer devido à fragilidade da espécie.

Parece-me indicado separar *L. ycatupe* especìficamente. Distingue-se de *gracillima* e das variedades desta pela forma ovóide da carapaça, estrias na região inferior, rebordo na abertura e prolongamento inferior menor que o superior.

Holótipo da espécie encontra-se na coleção de foraminíferos da Divisão de Oceanografia Biológica do Instituto Oceanográfico, sob n.º 19/1.

Comprimento: 1,12; largura 0,21

Ocorrência — Estações, 4, 7

Gênero *FISSURINA* REUSS, 1850

FISSURINA ACUTA REUSS, 1858 (Fig. 52)

Lagena acuta BRADY, 1884; CUSHMAN 1913, 1923; EARLAND 1934.

Carapaça globosa, biconvexa, elíptica em secção transversal; quilha fraca na periferia e espinho na base, êste é caráter específico. Abertura em forma de fenda e tubo entosoleniano curto, perpendicular. Os poucos exemplares encontrados estavam òtimamente conservados.

Comprimento: 0,28; largura 0,20.

Ocorrência — Estação 1.

Distribuição — Atlântico Sul (Falkland Islands); Atlântico Norte (Ilhas Britânicas); Pacífico (Hawaiian Islands).

FISSURINA AEQUILLABIALIS (BUCHNER, 1940) (Figs. 48, 49)

Lagena aequillabialis BUCHNER, 1940.

Carapaça biconvexa, circundada por quilha, estreita na região da abertura, alargada para trás. Abertura em forma de fenda; tubo entosoleniano contíguo com a parede ventral. Com exceção da quilha menor do material de BUCHNER, o meu concorda com o dêle (1940, pl. 21, f. 443).

Comprimento: 0,27; largura 0,23.

Ocorrência — Estação 1.

Distribuição — Atlântico Norte (Mediterrâneo).

FISSURINA ANNECTENS (BURROWS & HOLLAND, 1895) (Fig. 45)

Lagena annectens HERON-ALLEN & EARLAND, 1932; EARLAND, 1936.

Carapaça sub-globular, piriforme ou alongada. Região basal arredondada. Comumente aparecem duas áreas branco-esfumaçads, foscas, que não se unem na região basal. O exemplar desenhado, cuja configuração quase globular diverge da típica, mostra pertencer a diferenciação estrutural ao lado interno da testa. Em certos espécimes, a esculturação permite reconhecer um canal interno.

SILVESTRI (1912) considera *F. annectens* como sinônimo de *F. quadricostulata* (REUSS, 1870) que possui quatro costelas verdadeiras. De fato, as duas espécies são muito semelhantes. Os próprios autores de *annectens* separam a *quadricostulata* de BRADY (1884, pl. 59, f. 15) de *quadricostulata* (REUSS) e reunem-na com *annectens*. Nisto, não são acompanhados por HERON-ALLEN & EARLAND (1932), cujo conceito de *annectens* foi adotado por mim.

Comprimento: 0,20; largura 0,13.

Ocorrência — Estações 1, 9.

Distribuição — Atlântico Sul (Falkland Islands); Atlântico Norte (Ilhas Britânicas).

FISSURINA COACATU SP. N. (Figs. 43, 44)

Carapaça elipsóide, comprimida lateralmente e com pescoço curto. Abertura circundada por rebordo. Tudo entosoleniano curto, terminando no início da cavidade. Quilha transparente ao redor da testa tornando-se mais larga próximo ao pescoço e apresentando reentrância na região basal.

Quilha na região basal e rebordo na abertura distinguem a nova espécie de *F. quadrada* (WILLIAMSON, 1848). Em *F. rizzae* SEGUENZA, 1862, o tubo entosoleniano ultrapassa o centro da concavidade sendo a quilha opaca, destituída de reentrância. Duas quilhas ocorrem em *F. bicarinata* TERQUEM, 1882.

Holóitipo da espécie encontra-se na coleção de foraminíferos da Divisão de Oceanografia Biológica do Instituto Oceanográfico, sob n.º 23/5.

Comprimento: 0,24; largura 0,16.

Ocorrência — Estação 1.

FISSURINA EVELINAE SP. N. (Figs. 34-36)

Carapaça biconvexa de limite circular. Duas quilhas pouco desenvolvidas circundam a testa formando um anel contínuo. Região central ligeiramente elevada. Na região basal existem três espinhos que são prolongamentos da região mediano-basal do anel. Abertura, uma fenda alongada que se encontra numa elevação da testa e continua para o interior da mesma com um tubo entosoleniano comprido.

O aspecto geral lembra muitas espécies de *Fissurina*. *F. fasciata var. spinosa* não apresenta o anel concêntrico mediano nem costelas que aparecem nos lados da carapaça. *F. bicaudata var. tricaudata,* apresenta duas quilhas marginais, não porém, cinturão mediano. *F. neptuni* assemelha-se a *evelinae,* mas as suas duas quilhas laterais fundem-se na região basal, onde encontramos três espinhos. Além disso, ocorre região fosca em forma de ferradura em *F. neptuni* e o tubo entosoleniano é curto. Quilha mediana forte e ausência de espinhos basais separam *F. orbignyana* var. *walleriana* e var. *alata* (EARLAND, 1936, pl. 1).

Holótipo da espécie dedicada à Sra. D. EVELINE DU BOIS-REYMOND MARCUS, encontra-se na coleção de foraminíferos da Divisão de Oceanografia Biológica do Instituto Oceanográfico sob o nº 23/1.

Comprimento: 0,23; largura 0,16.

Ocorrência — Estação 1.

FISSURINA JURUTA SP. N. (Figs. 40-42)

Carapaça ovóide ou piriforme, pouco comprimida lateralmente. Uma quilha longitudinal começa na região da abertura acentuando-se na basal. A superfície da testa é perfurada por póros grandes. Uma projeção plicada da região apical termina com fenda estreita. O tubo entosoleniano corre perpendicularmente até a região do pescoço, de onde se encurva para o lado ventral (fig. 42)

A forma mais semelhante à nova espécie é *F. marginata* var. *semimarginata* (REUSS, 1870). Esta tem carapaça globosa, margem carinada na região do ângulo entre o pescoço e corpo. Diferem também o tubo entosoleniano e a ornamentação na região da abertura.

Holótipo da espécie encontra-se na coleção de foraminíferos da Divisão de Oceanografia Biológica do Instituto Oceanográfico, sob o n.º 23/3.

Comprimento: 0,22; largura 0,13.

Ocorrência — Estações 1, 4.

FISSURINA LAGENOIDES (WILLIAMSON, 1848) (Fig. 38)

Lagena lagenoides BRADY, 1884; SIDEBOTTOM, 1912, 1913; CUSHMAN, 1913, 1923, 1933; HERON-ALLEN & EARLAND, 1932; EARLAND, 1934, 1936; BOLTOVSKOY, 1954.

Carapaça ovóide; pescoço curto termina na abertura e continua como tubo entosoleniano. Testa circundada por lâmina periférica com tubinhos paralelos entre si e radialmente dispostos. O rebordo da abertura, nítido no único exemplar presente, nem sempre se vê nos desenhos muito variáveis que existem na literatura; reconhece-se bem no material de HERON-ALLEN & EARLAND (1932, pl. 11, f. 5).

Comprimento: 0,26; largura 0,16.

Ocorrência — Estação 1.

Distribuição — Atlântico Sul (Falkland Islands, Argentina, Sul do Brasil, Banco dos Abrolhos); Atlântico Norte (Índias Ocidentais, Ilhas Britânicas, Mediterrâneo); Pacífico (Midway Islands, Guam, Japão, Fiji Islands, Austrália).

FISSURINA LUCIDA (WILLIAMSON, 1848) (Fig. 50)

Entosolenia marginata var. lucida WILLIAMSON, 1848.

Lagena lucida SIDEBOTTOM, 1906; CUSHMAN, 1923; EARLAND, 1934.

Carapaça piriforme, alongada, lateralmente comprimida. Apresenta tubo entosoleniano livre. Região superior, central e média-inferior transparentes, a lateral de um branco fosco.

O desenho de WILLIAMSON mostra tôda a margem inferior uniformemente branca. Espinho basal e quilha, presentes nos espécimes originais, faltam nos meus e nos de SIDEBOTTOM (1906, pl. 1, f. 10 a-b).

Comprimento: 0,20; largura 0,12.

Ocorrência — Estação 9.

Distribuição — Atlântico Sul (Falkland Islands); Atlântico Norte (Ilhas Britânicas, Mediterrâneo); Pacífico (Japão, Guam, Austrália).

FISSURINA QUADRICOSTULATA (REUSS, 1870) (Fig. 39)

Lagena quadricostulata BRADY, 1884; CUSHMAN, 1913, 1923; HERON-ALLEN & EARLAND, 1932.

Fissurina quadricostulata SILVESTRI, 1912; BOLTOVSKOY, 1954.

Carapaça piriforme, dorso ventralmente comprimida; região basal arredondada com saliência. Duas costelas de cada lado acompanham o bordo da testa terminando livremente, sem união basal.

F. quadricostulata e *F. annectens* (BURROWS & HOLLAND, 1895) são consideradas por alguns autores como sinônimas.

Comprimento: 0,17; largura 0,12.

Ocorrência — Estação 1.

Distribuição — Atlântico Sul (Falkland Islands, Argentina, Sul do Brasil); Atlântico Norte (Faroe Channel); Oceano Índico (Kerguelen Islands); Pacífico (Sydney).

FISSURINA STAPHYLLEARIA SCHWAGER, 1866 (Figs. 46, 47)

Lagena staphyllearia BRADY, 1884; SIDEBOTTOM, 1912; CUSHMAN 1913, 1923; HERON-ALLEN & EARLAND, 1932; EARLAND, 1934, 1936; BERMUDEZ, 1949.

Carapaça biconvexa, globular, elíptica em secção transversal. Margem ligeiramente proeminente ao redor da testa, com três espinhos na região inferior. Numa proeminência da região anterior, abertura em forma de fenda continuada para dentro com tubo entosoleniano que não ultrapassa o terço anterior. O exemplar desenhado por SCHWAGER não mostra quilha marginal; no meu material e no de SIDEBOTTOM, a quilha é incipiente. No último, aliás perfeitamente comparável com o meu, há dois espinhos (1912, pl. 17, f. 22, 23); encontrei um exemplar com quatro, procedente da Ilha dos Alcatrazes.

Comprimento: 0,21; largura 0,15.

Ocorrência — Estação 1.

Distribuição — Atlântico Sul (Falkland Islands); Atlântico Norte (Índias Ocidentais, Ilhas Britânicas, Mediterrâneo); Indo-Pacífico (Filipinas); Pacífico (Hawaiian Islands, Midway Islands).

FISSURINA VARIOPERFORATA (BUCHNER, 1940) (Fig. 51)

Lagena (Entosolenia) marginata var. semimarginata WIESNER, 1931.

Lagena varioperforata BUCHNER, 1940.

Carapaça globosa, perfurada por grossos poros, biconvexa, elíptica em secção transversal e acuminada para a frente. Quilha transparente pouco desenvolvida ao seu redor. Tubo entosoleniano atingindo o centro da carapaça. Abertura pequena em forma de fenda. O espécime presente concorda nos caracteres gerais com os desenhos dos autores citados, principalmente com a f. 357 de BUCHNER (1940), diferindo em alguns pormenores, que enquadram-se na amplitude da variação da espécie.

Comprimento: 0,18; largura 0,13.

Ocorrência — Estação 4.

Distribuição — Antártica (Gauss st. 56); Atlântico Norte (Mediterrâneo).

Gênero *PARAFISSURINA* PARR, 1947

PARAFISSURINA LATERALIS (CUSHMAN, 1913) (Fig. 37)

Lagena lateralis CUSHMAN, 1913.

Ellipsolagena lateralis WIESNER, 1931.

Parafissurina lateralis BOLTOVSKOY, 1957.

Carapaça globular, elíptica em secção longitudinal, quase esférica em secção transversal, com abertura sub-terminal semilunar situada na região anterior. Ela é recoberta por uma extensão da parede ventral com forma de arco. Tubo entosoleniano curva-se para o lado ventral e abre-se dilatado.

Comprimento: 0,18; largura 0,13.

Ocorrência — Estação 1.

Distribuição — Antártica (Gauss st. 56); Atlântico Sul (Argentina, Sul do Brasil); Pacífico (Guam, Japão).

Gênero *OOLINA* d'ORBIGNY, 1839

OOLINA AIACA SP. N. (Fig. 58)

Lagena melo BRADY, PARKER & JONES, 1888, pl. 44, f. 21.

Carapaça globosa ou ligeiramente piriforme, vítrea e espêssa, com abertura apical e tubo entosoleniano curto. Superfície com cêrca de 15 quilhas longitudinais que terminam anteriormente à base. Traves arqueadas entre as quilhas tornam a superfície reticulada. Base da

testa truncada, provida de expansão anelar ou poligonal, de tamanho medíocre. Esta expansão separa a espécie imediatamente de *O. melo* e *O. squamosa,* de resto semelhantes. Às vêzes, as quilhas longitudinais terminam no terço posterior da testa; seu número é de 12 a 15.

Holótipo (com 15 quilhas), encontra-se na coleção de foraminíferos da Divisão de Oceanografia Biológica do Instituto Oceanográfico, sob n.º 23/7.

Comprimento: 0,27; largura 0,24.

Ocorrência — Estação 1.

OOLINA HEXAGONA (WILLIAMSON, 1848) (Fig. 54)

Entosolenia squamosa var. hexagona WILLIAMSON, 1848.

Lagena hexagona BRADY, 1884; SIDEBOTTOM, 1913; CUSHMAN, 1913, 1923; WIESNER, 1931; HERON-ALLEN & EARLAND, 1932; EARLAND, 1934, 1936.

Oolina hexagona BOLTOVSKOY, 1954.

Carapaça piriforme, tendo na superfície hexágonos. Abertura circular com tubo interno sòmente visível em exemplares de carapaça tênue. O tamanho dos hexágonos varia; um dos meus exemplares tem-nos relativamente grandes e em pequeno número, os demais, menores como na Figura 54.

Comprimento: 0,15; largura 0,11.

Ocorrência — Estação 1.

Distribuição — Atlântico Sul (Falkland Islands, Argentina, Sul do Brasil); Atlântico Norte (Leste dos Estados Unidos, Ilhas Britânicas, Mediterrâneo); Pacífico (Midway Islands, Japão, Guam).

OOLINA MELO d'ORBIGNY, 1839 (Fig. 53)

Entosolenia squamosa var. scalariformis WILLIAMSON, 1848.

Lagena melo CUSHMAN, 1932; HERON-ALLEN & EARLAND, 1932; EARLAND, 1934.

Oolina melo BOLTOVSKOY, 1954.

Carapaça piriforme. Superfície com costelas longitudinais ligadas por transversais. Surgem, assim, malhas aproximadamente quadrangulares que são côncavas. Às vêzes, as malhas são justapostas, outras vêzes as entre duas costelas longitudinais se alternam. Os limites transversais das malhas são ou retos ou arqueados para frente. Abertura circular alongada no tubo interno.

Comprimento: 0,22; largura 0,17.

Ocorrência — Estações 1, 4.

Distribuição — Atlântico Sul (Falkland Islands, Argentina, Sul do Brasil, Banco dos Abrolhos); Atlântico Norte (Ilhas Britânicas, Flórida ao Labrador).

OOLINA SQUAMOSA (MONTAGU, 1803) (Fig. 35)

Entosolenia squamosa WILLIAMSON, 1848.

Entosolenia globosa var. squamosa PARKER & JONES, 1857.

Lagena squamosa SILVESTRI, 1902; CUSHMAN, 1913, 1923; HERON-ALLEN & EARLAND, 1932; EARLAND, 1934, 1936.

Oolina squamosa BOLTOVSKOY, 1954.

Carapaça piriforme, com abertura circular e tubo interno. Escultura da carapaça lembra escamas sobrepostas, mas varia consideràvelmente.

As figuras 24 (1888, pl. 44) de BRADY, PARKER & JONES e 26 de HERON-ALLEN & EARLAND (1932, pl. 10) concordam com a observação de BRADY de passar *O. squamosa* a *O. hexagona*.

Comprimento: 0,23; largura 0,18.

Ocorrência — Estações 1, 4.

Distribuição — Atlântico Sul (Falkland Islands, Argentina), Atlântico Norte (Ilhas Britânicas, Mediterrâneo); Pacífico (Japão, Guam, Midway Islands).

Família Nodosariidae.

Gênero *NODOSARIA* LAMARCK, 1812

NODOSARIA CATESBYI d'ORBIGNY, 1839 (Fig. 27)

Nodosaria catesbyi CUSHMAN, 1931; CUSHMAN & CAHILL, 1933; CARVALHO & CHERMONT, 1952.

Carapaça constituída por duas câmaras. A inicial com espinho basal e a seguinte piriforme ou sub-globular, apresenta abertura radiada num prolongamento apical. Costelas longitudinais da superfície passam sôbre a sutura e continuam até a abertura. No meu material de *catesbyi* encontrei 1 exemplar com 3 câmaras.

Comprimento: 0,41; largura 0,16.

Ocorrência — Estação 1.

Distribuição — Atlântico Sul (São Paulo, Rio de Janeiro); Atlântico Norte (Índias Ocidentais, Flórida).

NODOSARIA HISPIDA d'ORBIGNY, 1826 (Fig. 24)

Nodosaria hispida PARKER, JONES & BRADY, 1871; BRADY, PARKER & JONES, 1888; BERMUDEZ, 1949.

Marginulina aff. M. hirsuta PALMER & BERMUDEZ, 1936.

Nodosaria hirsuta CUSHMAN, 1913.

Carapaça formada de várias câmaras dispostas em série, sendo as iniciais globosas e as distais piriformes; suturas aprofundadas. Superfície áspera pela ocorrência de espinhos curtos. Tubo distal comprido, sendo a abertura rodeada por corôa terminal.

Comprimento: 1,2; largura 0,3.

Ocorrência — Estação 3.

Distribuição — Atlântico Sul (Pernambuco, Banco dos Abrolhos); Atlântico Norte (Índias Ocidentais, Mediterrâneo); Indo-Pacífico (Filipinas); Pacífico (Japão).

? NODOSARIA INTERCELLULARES BRADY, 1884 (Figs. 25, 26).

Os dois exemplares disponíveis, ambos com espinho basal e rebordo da abertura partido, poderiam ser fases jovens de *N. intercellularis,* até agora não descritas, mas também pertencer a *N. scalaris* (BATSCH, 1791). A ocorrência do meu material não facilita a decisão, pois as duas espécies mencionadas, são conhecidas da mesma região.

Comprimento: 0,5 (Fig. 25) a 0,8 (Fig. 26); largura 0,1 (nos dois exemplares).

Ocorrência — Estação 3.

NODOSARIA BOIGRA SP. N. (Fig. 19)

Fragment of N. scalaris BATSCH, sp. (?), BRADY, PARKER & JONES, 1888, pl. 44, f. 19.

Carapaça alongada, retilínea, sem espinho basal. Composta por cinco câmaras, a primeira das quais ligeiramente inflada, as outras, piriformes separadas por suturas distintas e a última por um pequeno tubo. Superfície com quilhas longitudinais que ou passam de uma câmara à outra, ou terminam em ponta, na mais distal. Última câmara com projeção anterior ornamentada por elevação espiralada.

A espécie mais semelhante, *N. intercellularis* BRADY, 1884 difere pela esculturação das câmaras distais e pelo espinho basal. Êste ocorre também em *N. scalaris* (BATSCH, 1791) cuja forma geral, número menor de quilhas e relêvo das mesmas a distinguem de *boigra.*

Identifico como pertencente à nova espécie, a câmara desenhada por BRADY, PARKER & JONES (1888, pl. 44, f. 19) e determinada, duvidosamente como fragmento de *N. scalaris*.

Holótipo se encontra na coleção de foraminíferos da Divisão de Oceanografia Biológica do Instituto Oceanográfico, sob o n.º 25/1.

Comprimento: 1,2; largura 0,2.

Ocorrência — Estação 3.

Distribuição — Atlântico Sul (Banco dos Abrolhos, 22º54'S, 40º37'O).

NODOSARIA PYRULA d'ORBIGNY, 1826 (Figs. 22, 28)

Nodosaria pyrula SCHWGER, 1866; BRADY, PARKER & JONES, 1888; HERON-ALLEN & EARLAND, 1913; CUSHMAN, 1913, 1923; BERMUDEZ, 1949.

Carapaça frágil constituída por câmaras ovóides, às vêzes, piriformes e de tamanho variável. Tubo distal alongado com abertura radiada, típica da espécie. Ocorrem câmaras assimètricamente infladas.

Encontrei sòmente fragmentos, especialmente o tubo distal fino, fàcilmente quebradiço, devido à fragilidade de *N. pyrula*.

Comprimento: 0,8 (Fig. 22); largura 0,1 (Fig. 22)

Ocorrência — Estações 2, 4.

Distribuição: Atlântico Sul (Sul do Brasil, Banco dos Abrolhos); Atlântico Norte (Índias Ocidentais, Georgia, Ilhas Britânicas, Mediterrâneo, Ilhas Canárias); Indo-Pacífico (Filipinas); Pacífico (Japão).

NODOSARIA SCALARIS (BATSCH, 1791) (Figs. 30-33)

Nodosaria longicauda d'ORBIGNY, 1826.

Nodosaria sulcata d'ORBIGNY, 1826.

Nodosaria subradicula SCHWAGER, 1866.

Nodosaria scalaris BRADY, 1884; CUSHMAN, 1913, 1923; HERON-ALLEN & EARLAND, 1913, 1932; BOLTOVSKOY, 1954.

Carapaça constituída por uma série de câmaras com costelas longitudinais, estendidas da base até a abertura circundada por corôa radiada. Suturas acentuadas entre as câmaras. Proloculus globoso com curto espinho basal.

Das figuras de CUSHMAN & Mc-CULLOCH duas, 30 e 32 (1950, pl. 41) evidentemente retratam outra espécie, não *N. scalaris*.

Comprimento: 0,3 (Figs. 30, 31), 0,4 (Fig. 32), 0,7 (Fig. 33); largura 0,14 (Figs. 30-32), 0,16 (Fig. 33).

Ocorrência — Estação 1.

Distribuição — Atlântico Sul (Falkland Islands, Argentina, Sul do Brasil, Banco dos Abrolhos, Cabo da Boa Esperança); Atlântico Norte (Índias Ocidentais, Bermuda, Ilhas Britânicas, Mediterrâneo, Ilhas Canárias); Indo-Pacífico (Filipinas); Pacífico (Japão, Guam, Hawaiian Islands, Austrália, Nova Zelândia).

NODOSARIA SUBLINEATA BRADY, 1884 (Fig.s 20, 21)

Nodosaria hispida var. sublineata BRADY, 1884.

Nodosaria sublineata CUSHMAN, 1913.

Carapaça alongada formada por várias câmaras cuja sucessão perfaz um conjunto ligeiramente curvo. Última câmara com a abertura num prolongamento alongado. Superfície coberta por costelas longitunais que percorrem as câmaras até a base ou até o meio. No último caso, numerosos acúleos situam-se na metade basal de cada câmara. Às vêzes ocorre espinho basal na primeira câmara, e as outras seguem sem intervalos (Fig. 21). Sòmente a última, ligada ao pescoço da penúltima, afastou-se mais. O exemplar da Fig. 20 representa a geração macro-esférica e concorda completamente com o material de BRADY.

Comprimento: 1,0 (Fig. 20) e 0,7 (Fig. 21).

Ocorrência — Estação 4.

Distribuição — Atlântico Sul (Sul do Brasil, Pernambuco); Atlântico Norte (Índias Ocidentais até Cape Hatteras, Bermuda); Indo-Pacífico (Filipinas).

NODOSARIA VERTEBRALIS VAR. *ALBATROSSI* CUSHMAN, 1923 (Fig. 23)

Nodosaria fascia PARKER, BRADY & JONES, 1865.

Nodosaria vertebralis BRADY, 1884; BAGG, 1912.

Nodosaria vertebralis var. albatrossi CUSHMAN, 1923.

Carapaça composta por muitas câmaras que se sucedem, formando conjunto reto ou ligeiramente encurvado; as linhas de sutura entre as câmaras são retas. Na superfície existem costelas longitudinais cuja reunião basal forma um espinho robusto. As costelas passam sôbre as constrições entre as câmaras; essa região é tênue e transparente.

Na sua maioria, os meus exemplares estão quebrados. O desenhado (Fig. 23) mostra o início de nova câmara e, com isso, a constrição entre as costelas.

Comprimento: 2.

Ocorrência — Estações 4, 5, 8.

Distribuição — Atlântico Sul (Sul do Brasil); Atlântico Norte (Índias Ocidentais, Sudeste dos Estados Unidos, Bermuda, Açores).

Gênero *DENTALINA* d'ORBIGNY, 1826

DENTALINA ADVENA (CUSHMAN, 1923) (Fig. 67)

Nodosaria (Dentalina) roemeri BRADY, 1884.

Nodosaria advena CUSHMAN, 1923; PINTO, 1950.

Carapaça sólida constituída por oito câmaras, a última das quais volumosa, oblíqua e circular em secção sendo inclinada contra as precedentes. Primeira câmara arredondada, pequena como as adjacentes. Suturas superficiais entre as iniciais e profundas entre as distais.

Meu exemplar é muito menor que o descrito por CUSHMAN (7 mm). Os achados anteriores provêm de profundidades entre 713 e 960 m.

Comprimento: 2,1; largura 0,4.

Ocorrência — Estação 4.

Distribuição — Atlântico Norte (Índias Ocidentais, Bermudas, Ilhas Canárias).

DENTALINA CALIFORNICA CUSHMAN & GRAY, 1946 (Fig.63)

Dentalina californica CUSHMAN & Mc. CULLOCH, 1950.

Carapaça translúcida, composta de três câmaras elipsóides. Proloculus com curto espinho basal. Abertura radiada. Rara em nosso material.

A espécie foi descrita do Pleistoceno da Califórnia (Timms Point). O espécime presente concorda com a descrição e a figura de material recente (CUSHMAN & Mc. CULLOCH, 1950, pl. 41, f. 8).

Comprimento: 0,3; largura 0,07.

Ocorrência — Estação 2.

Distribuição — Atlântico Norte (Est. 601, 611, 613 da col. ALLAN HANCOCK, provenientes da Europa); Pacífico (Gorgona Island, Galapagos, Bahia Honda).

DENTALINA COMMUNIS d'ORBIGNY, 1826 (Fig. 62)

Dentalina communis PARKER & JONES, 1857; CUSHMAN & Mc. CULLOCH, 1950; BOLTOVSKOY, 1954.

Nodosaria Neugeboreni SCHWAGER, 1866.

Nodosaria communis BRADY, 1884; BAGG, 1912; HERON-ALLEN & EARLAND, 1913; CUSHMAN, 1923; EARLAND, 1934, 1936.

Carapaça ligeiramente encurvada, formada por número variável de câmaras, dispostas oblìquamente uma sôbre a outra e separadas por sutura profunda. Abertura radiada na região periférica e terminal. Encontrei exemplares com 5 e 8 câmaras. Os de SCHWAGER e de BRADY tiveram número maior de câmaras, os de BAGG do Plioceno e Pleistoceno da Califórnia, número menor. A espécie de BOLTOVSKOY (1954, pl. 5, f. 12a-b) com apenas duas câmaras não pertence, evidentemente, a *communis*.

Comprimento: 0,51; largura 0,17.

Ocorrência — Estações 2,4.

Distribuição — Atlântico Sul (Falkland Islands, Argentina, Sul do Brasil); Atlântico Norte (Índias Ocidentais, Ilhas Britânicas); Pacífico (Japão, Guam, Hawaiian Islands, São Francisco).

DENTALINA CONSOBRINA VAR. *EMACIATA* REUSS, 1851 (Fig. 29)

Nodosaria consobrina var. emaciata BRADY, 1884; BAGG, 1912; CUSHMAN, 1923; PINTO, 1950.

Carapaça lisa, porcelânica, retilínea; conjunto formado por série de câmaras separadas por sutura superficial. Proloculus arredondado, as demais aumentam gradualmente de volume. Devido ao comprimento e à fragilidade da carapaça encontrei apenas exemplares quebrados. Todavia verifiquei a configuração radiada, genèricamente típica da abertura.

Comprimento: 4; largura 0,4.

Ocorrência — Estação 4.

Distribuição — Atlântico Sul (Sul do Brasil, Pernambuco, Cabo da Boa Esperança); Atlântico Norte (Açores); Pacífico (Japão, Guam, Hawaiian Islands).

DENTALINA MUCRONATA NEUGEBOREN, 1856 (Fig. 61)

Nodosaria (Dentalina) oblíqua d'ORBIGNY, 1826.

Dentalina communis, sub. var. oblíqua PARKER, JONES & BRADY, 1879.

Nodosaria mucronata BRADY, 1884; GOES, 1891; BRADY, PARKER & JONES, 1888; CUSHMAN, 1913, 1923; EARLAND, 1936.

Dentalina mucronata BERMUDEZ, 1949; CUSHMAN & Mc. CULLOCH, 1950.

Carapaça constituída por câmaras quase retilineamente dispostas, com exceção da distal, muito volumosa, disposta em ângulo acentuado. As suturas são oblíquas e incisadas; a abertura radiada situa-se numa curta projeção da última câmara.

BRADY (pl. 62, f. 27) apresenta exemplares muito semelhantes aos meus; encontrou a espécie sempre em águas profundas. BRADY, PARKER & JONES relatam-na da região do Banco dos Abrolhos.

Comprimento: 0,72; largura 0,18.

Ocorrência — Estações, 1, 4, 6, 7.

Distribuição — Atlântico Sul (Falkland Islands, Argentina, Banco dos Abrolhos); Atlântico Norte (das Índias Ocidentais até New York, Bermuda, Ilhas Britânicas).

DENTALINA MUTSUI HADA, 1931 (Fig. 64)

Dentalina mutsui PARR, 1945.

Carapaça ligeiramente encurvada, formada por cinco câmaras elipsóides. Estas providas de fortes costelas longitudinais, com exceção da câmara distal, lisa. Abertura terminal radiada. Suturas distintas, aprofundadas. Proloculus com espinho forte. O tamanho varia, sendo o do material original de 3, 65, o de PARR 2, e o meu de 1 mm.

Comprimento: 1; largura 0,2.

Ocorrência — Estação 6.

Distribuição — Pacífico (Victoria, Japão).

DENTALINA STRIOLATA (GOËS, 1891) (Fig. 60)

Nodosaria soluta BRADY, 1884.

Nodosaria striolata Goës, 1891.

Carapaça constituída por 10 câmaras formando uma série ligeiramente encurvada. Câmaras globulares, lembrando contas; a inicial

maior que as duas seguintes. Superfície ornamentada por estrias superficiais com exceção das últimas câmaras que são lisas.

Comprimento: 3; largura 0,6.

Ocorrência — Estação 8, um exemplar completo, 8 quebrados.

Distribuição — Atlântico Norte (Índias Ocidentais).

Gênero *SARACENARIA* DEFRANCE, 1824

SARACENARIA ANGULARIS NATLAND, 1938 (Fig. 59)

Saracenaria angularis CUSHMAN & Mc. CULLOCH, 1950.

Carapaça alongada, triangular em secção transversal. Margens com quilhas translúcidas; paredes transparentes, mais finas do que as de *S. italica* DEFRANCE. Abertura radiada situada na região apical da câmara. Suturas distintas um pouco aprofundadas e dispostas obliquamente. O meu único espécime é um pouco maior que o material da descrição original, e a câmara distal é menor. Concorda, porém, com os desenhos de CUSHMAN & Mc. CULLOCH nomeadamente com a figura 8 da estampa 42.

Comprimento: 1; largura 0,7.

Ocorrência — Estação 5.

Distribuição — Pacífico (Califórnia).

SARACENARIA ITALICA DEFRANCE, 1824 (Fig. 66)

Cristellaria (Saracenaria) italica d'ORBIGNY, 1826.

Cristellaria italica PARKER, JONES & BRADY, 1865; BRADY, 1884; GOËS, 1891; CUSHMAN, 1923.

Saracenaria italica BERMUDEZ, 1949; COLOM, 1952.

Carapaça tão longa quanto larga, formando em secção transversal um triângulo equilátero. Paredes grossas, margens com quilhas opacas que terminam abruptamente. Suturas profundas. Os poucos exemplares que encontrei, se bem que grandes, ficam aquém dos de BRADY que atingiram 5 mm.

Comprimento: 1,3; largura 0,5.

Ocorrência — Estações 4, 5, 8.

Distribuição — Atlântico Sul (Sul do Brasil); Atlântico Norte (Índias Ocidentais, Sudeste dos Estados Unidos, Bermuda, Ilhas Britânicas, Mediterrâneo); Pacífico (Japão, Fiji Islands).

SARACENARIA LATIFRONS (BRADY, 1884) (Fig. 79)

Cristellaria latifrons BRADY, 1884; CUSHMAN, 1923.

Saracenaria latifrons BERMUDEZ, 1949.

Saracenaria sp. CUSHMAN & Mc. CULLOCH, 1950 (pl. 42, f. 13)

Carapaça alongada, triangular em secção transversal, larga no meio, mais estreita nas extremidades. Câmaras iniciais pequenas em curva envolvente sendo as terminais maiores. Última câmara curvada quase perpendicularmente sôbre as anteriores, tendo na região apical abertura radiada. Face ventral côncava de contôrno oval; a dorsal possui margem aculeada e quilha. Num dos dois exemplares de BRADY ocorrem quilhas periféricas; no meu existe apenas quilha posterior incipiente como na figura 19 (pl. 68) de BRADY. A distinta fenda mediana da abertura radiada do meu exemplar, um pouco menor do que a de BRADY (1884, pl. 113, f. 116) corresponde à daquele espécime.

Comprimento: 0,6; largura 0,2.

Ocorrência — Estação 4.

Distribuição — Atlântico Norte (Índias Ocidentais, Flórida, Bermuda); Indo-Pacífico (Filipinas); Pacífico (Austrália, Nova Zelândia).

SARACENARIA TAYAÇU SP. N. (Figs. 56, 57)

Carapaça curta, triangular em secção transversal. Suturas distintas, aprofundadas, oblìquamente dispostas. Cinco câmaras sucessivas aumentam de volume; paredes translúcidas e lisas, sem quilha. Última câmara grande encobre as anteriores.

Abertura radiada com fenda mediana na face ventral. As duas faces laterais da carapaça ligeiramente comprimidas, formam uma concavidade; face ventral um pouco convexa.

S. subglobosa BANDY, 1951 difere de *tayaçú* pela face da abertura redonda, pelo número de câmaras e ausência de fenda mediana na abertura.

S. moresiana HOWE & WALLACE, 1932, do Eoceno superior, assemelha-se mais à espécie presente, dela diferindo, porém, pela periferia arredondada e ausência de fenda mediana na abertura.

O holótipo encontra-se na coleção de foraminíferos da Divisão de Oceanografia Biológica do Instituto Oceanográfico, sob n.º 27/1.

Comprimento: 0,7; largura 0,3.

Ocorrência — Estação 4.

Gênero *FRONDICULARIA* DEFRANCE, 1826

FRONDICULARIA ALATA d'ORBIGNY, 1826 (Figs. 65, 68)

Frondicularia alata PARKER, JONES & BRADY, 1871; BRADY, 1884; GOËS, 1891.

Carapaça plana, constituída por uma série de câmaras triangulares em cujo vértice se localiza a abertura radiada. Proloculus globular com espinho no meio do seu bordo basal. Externamente as câmaras podem apresentar expansões em forma de espinhos.

O maior dos meus espécimes (Fig. 68) começa como triângulo tornando-se foliáceo pela superposição das câmaras sucessivas. Ocorrem, no meu material, exemplares com 2 espinhos basais e, na literatura (BRADY, 1884, pl. 65, f. 20-22) outros cuja etapa de crescimento parou na fase triangular.

Comprimento: 3 (Fig. 65) e 8 (Fig. 68); largura 3 (nos dois).

Ocorrência — Estação 4.

Distribuição — Atlântico Norte (Índias Ocidentais, Bermuda, Mediterrâneo).

Gênero *ROBULUS* MONTFORT, 1808

ROBULUS ANTILLEUS (CUSHMAN, 1923) (Fig. 78)

Cristellaria antillea CUSHMAN, 1923.

Carapaça achatada com câmaras distintas, às vêzes infladas, formando espiral fechada, exceção feita às 2-3 últimas câmaras não enroladas. Suturas distintas, aquelas entre as câmaras iniciais com contas, às vêzes reunidas. Periferia com quilha que apresenta grandes espinhos. Abertura radiada formando grande crista no meio da última câmara. Quando ocorrem contas na superfície das câmaras quer iniciais ou distais, o aspecto da espécie aproxima-se ao de *R. papillosus* (FICHTEL & MOLL, 1803). Os oito espécimes de CUSHMAN provêm de profundidades entre 100 e 800 m; os trinta e dois presentes, de 32 a 125 m.

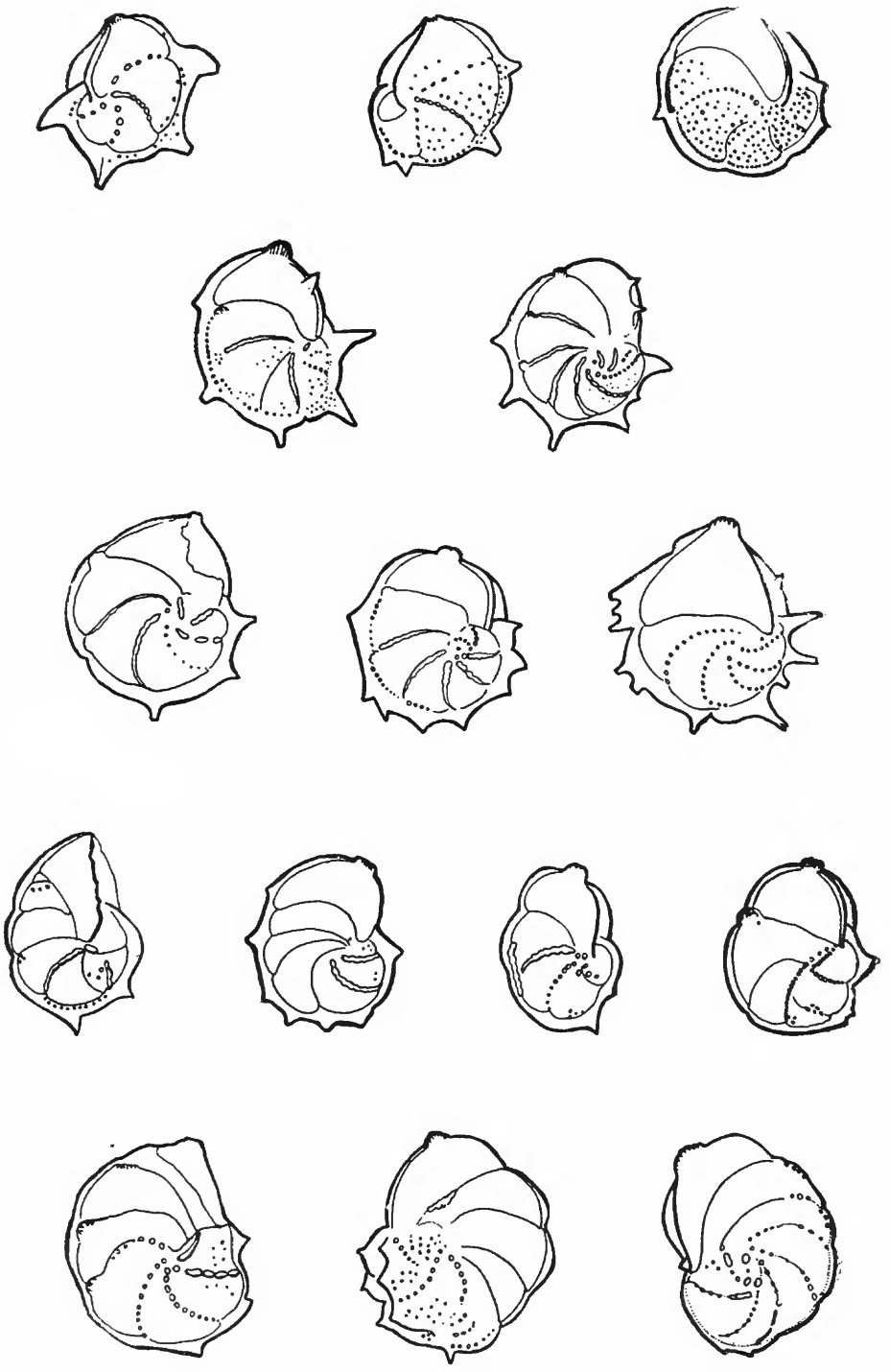
A presença de quilha com espinhos, contas e suturas elevadas, varia de exemplar a exemplar, dificultando a distinção da espécie. Os 15 espécimes da figura D mostram a grande variabilidade da espécie.

Comprimento: 4; largura 2.

Ocorrência — Estações 1, 4, 8.

Distribuição — Atlântico Norte (Índias Ocidentais, Sudeste dos Estados Unidos).

FIGURA D



Variação em *Robulus antilleus*

ROBULUS ARGENTINENSIS (BOLTOVSKOY, 1954) (Figs. 80, 81)

Darbyella argentinensis BOLTOVSKOY, 1954, 1959.

Carapaça constituída por sete câmaras formando espiral. A última salienta-se fortemente para o lado. Periferia aguda e angulada entre câmaras adjacentes. Abertura radiada com fenda alongada no centro. No material original, os ângulos do contôrno são restritos às últimas câmaras, existindo no atual, também nas primeiras.

O comprimento do exemplar argentino é ligeiramente inferior ao do meu.

BOLTOVSKOY considerou a espécie no gênero *Darbyella* HOWE & WALLACE, 1933 no que eu não posso acompanhá-lo, pois o animal não concorda com as características básicas do gênero.

Comprimento: 0,5; largura 0,3.

Ocorrência — Estação 4.

Distribuição — Atlântico Sul (Sul do Brasil, Argentina).

ROBULUS CALCAR (LINNE', 1767) (Figs. 69-71, 74)

Robulina aculeata d'ORBIGNY, 1826.

Cristellaria calcar PARKER, JONES & BRADY, 1871; BRADY, 1884; BRADY, PARKER & JONES, 1888; CUSHMAN, 1913, 1923.

Robulus calcar CUSHMAN, 1933, 1950; BERMUDSZ, 1949.

Carapaça lenticular, periferia com quilha estreita provida de espinhos de comprimento e posição variáveis. Ora situam-se no meio da câmara, ora ao nível entre duas delas. Paredes lisas, transparentes que permitem observar a disposição e as aberturas das câmaras. Na estação 4, encontrei fases jovens com 2 e 3 câmaras. O espinho basal do proloculus parece ser o início da quilha periférica.

Comprimento: 0,5 (figs. 71, 74); largura 0,4 (figs. 71, 74). Estas medidas não incluem os espinhos.

Ocorrência — Estações 4, 8.

Distribuição — Atlântico Sul (Sul do Brasil, Banco dos Abrolhos); Atlântico Norte (Índias Ocidentais, Flórida até Cape Hatteras, Açores, Mediterrâneo); Indo-Pacífico (Filipinas); Pacífico (Japão, Hawaiian Islands).

ROBULUS CULTRATUS MONTFORT, 1808 (Fig. 85)

Robulina cultrata d'ORBIGNY, 1826.

Cristellaria gyroscalpum STACHE, 1864.

Cristellaria cultrata BRADY, 1884; BRADY, PARKER & JONES, 1888; HERON-ALLEN & EARLAND, 1913, 1932.

Carapaça discoidal, biconvexa, com quilha translúcida, cuja largura varia consideràvelmente. Paredes lisas, suturas não atingindo o centro da testa.

Depreende-se, das profundidades indicadas, provir o material de BRADY, do Atlântico Sul, da latitude de Pernambuco, pois as duas estações do "CHALLENGER" daquela região têm idêntica indicação batimétrica.

Comprimento: 1,5; largura 1,3.

Ocorrência — Estação 5.

Distribuição — Atlântico Sul (Falkland Islands, Patagônia, Sul do Brasil, Banco dos Abrolhos, Ilhas Britânicas); Indo-Pacífico (Filipinas); Pacífico (Hawaiian Islands, Mar de Bering); Ártico.

ROBULUS GIBBUS d'ORBIGNY, 1839 (Fig. 72).

Cristellaria gibba BRADY, 1884; BAGG, 1912; CUSHMAN, 1913, 1923; HERON-ALLEN & EARLAND, 1932; EARLAND, 1934, 1936.

Robulus gibbus CUSHMAN, 1933; BERMUDEZ, 1949; COLOM, 1952; BOLTOVSKOY, 1954.

Carapaça formando espiral fechada oblonga e biconvexa com cito câmaras na última volta. Paredes lisas e transparentes, com suturas arqueadas. Periferia com quilha forte. Abertura radiada com ranhura central longitudinal.

Comprimento: 1,5; largura 1,1.

Ocorrência — Estação 2.

Distribuição — Atlântico Sul (Falkland Islands, Argentina); Atlântico Norte (Índias Ocidentais, Bermuda, Ilhas Britânicas, Mediterrâneo); Pacífico (Fiji Islands, Hawaiian Islands, Japão).

ROBULUS LUCIDUS (CUSHMAN, 1923) (Fig. 83)

Cristellaria articulata BRADY, 1884.

Cristellaria lucida CUSHMAN, 1923.

Robulus lucidus BERMUDEZ, 1949.

Robulus articulata PINTO, 1950.

Carapaça formando espiral fechada com sete câmaras na última volta. Quilha na periferia larga e transparente. Suturas distintas

saem como raios da região central que não é saliente, mas lobulada e transparente, mostrando as câmaras iniciais. Abertura radiada na última câmara apresentando fenda mediana alongada. Os exemplares de CUSHMAN, embora maiores (2,5 mm e mais) que os meus, têm quilha menos desenvolvida.

Comprimento: 1,7; largura 1,5.

Ocorrência — Estações 4, 5.

Distribuição — Atlântico Sul (Falkland Islands, Tristan da Cunha), Atlântico Norte (Índias Ocidentais até Cape Cod, Bermuda, Espanha, Canárias); Pacífico (Japão, Hawaiian Islands).

ROBULUS OCCIDENTALIS (CUSHMAN, 1923) (Figs. 73, 86)

Carapaça biconvexa, disciforme, espiralada com até oito câmaras externas, a última das quais ressaltada. Paredes lisas, transparentes; quilha larga periférica. Abertura radiada com fenda mediana.

No material original, o comprimento ultrapassa 5 mm.

Comprimento: 1,3; largura 1,2.

Ocorrência — Estação 7.

Distribuição — Atlântico Norte (Nova Inglaterra).

ROBULUS ORBICULARIS (d'ORBIGNY, 1826) (Fig. 82).

Cristellaria orbicularis BRADY, 1884; CUSHMAN, 1923; HERON-ALLEN & EARLAND, 1932.

Robulus orbicullaris BERMUDEZ, 1949; BOLTOVSKOY, 1954.

Carapaça formando uma curva evolvente. As suturas saem do centro e se dirigem para a periferia em trajeto parabólico e espiral. Quilha periférica termina antes da última câmara, faltando no material da costa argentina. Centro umbilicado da carapaça salienta-se em vista lateral.

Comprimento: 0,8; largura 0,7.

Ocorrência — Estação 8.

Distribuição — Atlântico Sul (Falkland Islands, Argentina, Sul do Brasil); Atlântico Norte (Índias Ocidentais); Pacífico (Tahiti, Fiji Islands, Sydney, Nova Zelândia).

ROBULUS SUBMAMILLIGERUS (CUSHMAN, 1917) (Fig. 75)

Cristellaria mamilligera BRADY, 1884; CUSHMAN, 1913.

Cristellaria submamilligera CUSHMAN, 1923.

Robulus submamilligerus BERMUDEZ, 1949.

Carapaça biconvexa, lisa com quilha na periferia. Partindo da região umbilical uma série de elevações situadas nas suturas, das quais as anteriores são especialmente salientes. Abertura radiada.

Os exemplares que encontrei estavam quebrados na última câmara e são parecidos com os de BRADY (1884, pl. 70, f. 17).

Comprimento: 1,3; largura 1,0.

Ocorrência — Estação 5.

Distribuição — Atlântico Sul (Argentina); Atlântico Norte (Índias Ocidentais); Indo-Pacífico (Filipinas); Pacífico (Japão, Fiji Islands, Great Barrier Island).

Gênero *MARGINULINA* d'ORBIGNY, 1826

MARGINULINA BACHEII BAILEY, 1851 (Fig. 84)

Marginulina bacheei CUSHMAN, 1923.

Marginulina bacheei CUSHMAN & Mc. CULLOCH, 1950.

Carapaça subcilíndrica, alongada, ligeiramente curvada. Da espiral fechada da parte inicial surge uma série de câmaras sobrepostas. Suturas distintas pouco aprofundadas. Paredes lisas, consistentes e opacas. Abertura radiada, localizada no ângulo dorsal da última câmara.

Comprimento: 2; largura 0,6.

Ocorrência — Estações 5, 8.

Distribuição — Atlântico Sul (Sul do Brasil); Atlântico Norte (Índias Ocidentais, Flórida até New York, Ilhas Britânicas); Pacífico (Gôlfo da Califórnia).

Gênero *ASTACOLUS* MONTFORT, 1808

ASTACOLUS CREPIDULUS (FICHTEL & MOLL, 1803) (Figs. 76, 77)

Hemirobulina compressa Stache, 1864.

Cristellaria crepidula PARKER & JONES, 1865; BRADY, 1884; RHUMBLER, 1909; CUSHMAN, 1918, 1923.

Astacolus crepidulus BOLTOVSKOY, 1954.

Carapaça lateralmente comprimida, alongada, câmaras lisas obliquamente sobrepostas. Suturas ligeiramente aprofundadas. Abertura radiada na última câmara.

Comprimento: 0,9; largura 0,3.

Ocorrência — Estação 1.

Distribuição — Atlântico Sul (Falkland Islands, Argentina, Sul do Brasil, Banco dos Abrolhos); Atlântico Norte (Índias Ocidentais, Ilhas Britânicas, Mediterrâneo); Pacífico (Hawaiian Islands, Midway Islands, Guam, Japão).

RESUMO

Das famílias Lagenidae e Nodosariidae foram descritas 59 espécies. Destas 6 são novas e uma foi separada de espécie duvidosamente determinada. Das 52 espécies conhecidas, 26 do Atlântico Meridional são pela primeira vez assinaladas no presente trabalho.

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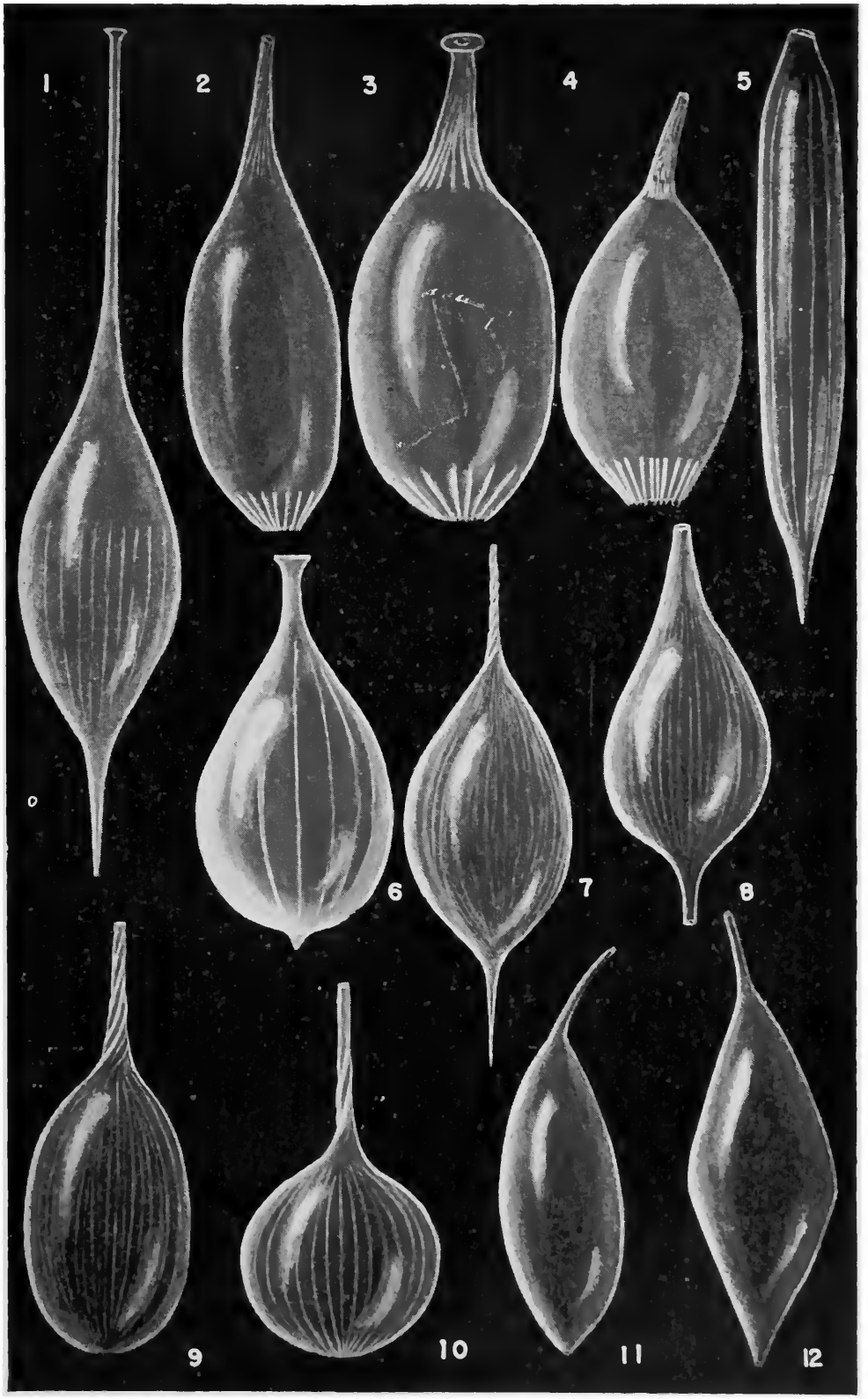
ESTAMPAS

ESTAMPA 1

Fig. 1 — *Lagena ycatupe* sp. n.
Fig. 2-4 — *Lagena semistriata* Williamson
Fig. 5 — *Lagena distoma* Parker & Jones
Fig. 6 — *Lagena caudata* (d'Orbiny)
Fig. 7, 8 — *Lagena gracilis* Williamson
Fig. 9, 10 — *Lagena striata* (d'Orbigny)
Fig. 11, 12 — *Lagena gracillima* (Seguenza)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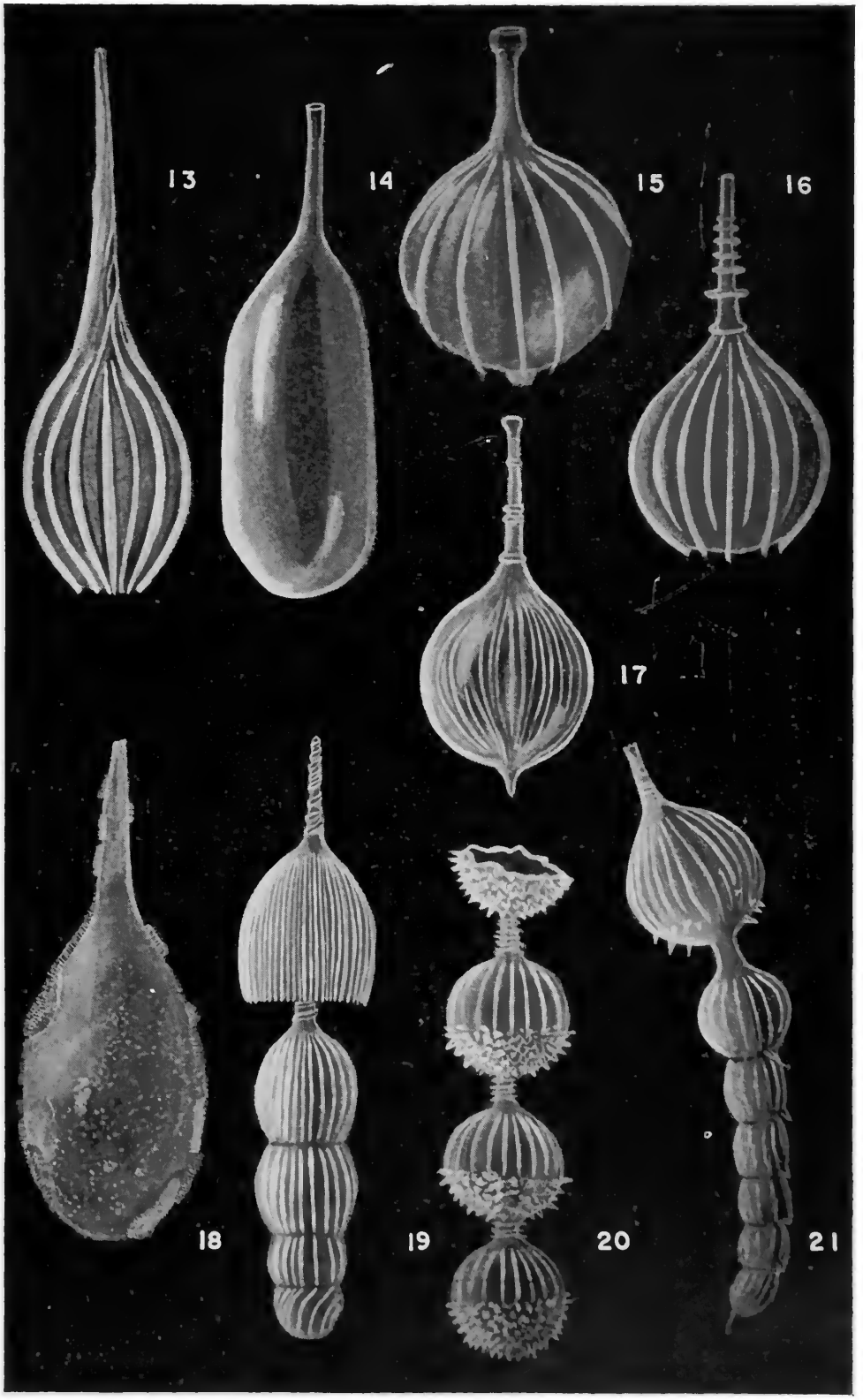
ESTAMPA 2

Fig. 13 — *Lagena sulcata* (Walker & Jacob)
Fig. 14 — *Lagena laevis* (Montagu)
Fig. 15 — *Lagena lyelli* (Seguenza)
Fig. 16 — *Lagena sulcata* var. *interrupta* Williamson
Fig. 17 — *Lagena striata* var. *strumosa* Reuss
Fig. 18 — *Lagena hispidula* Cushman
Fig. 19 — *Nodosaria boigra* sp. n.
Fig. 20, 21 — *Nodosaria sublineata* Brady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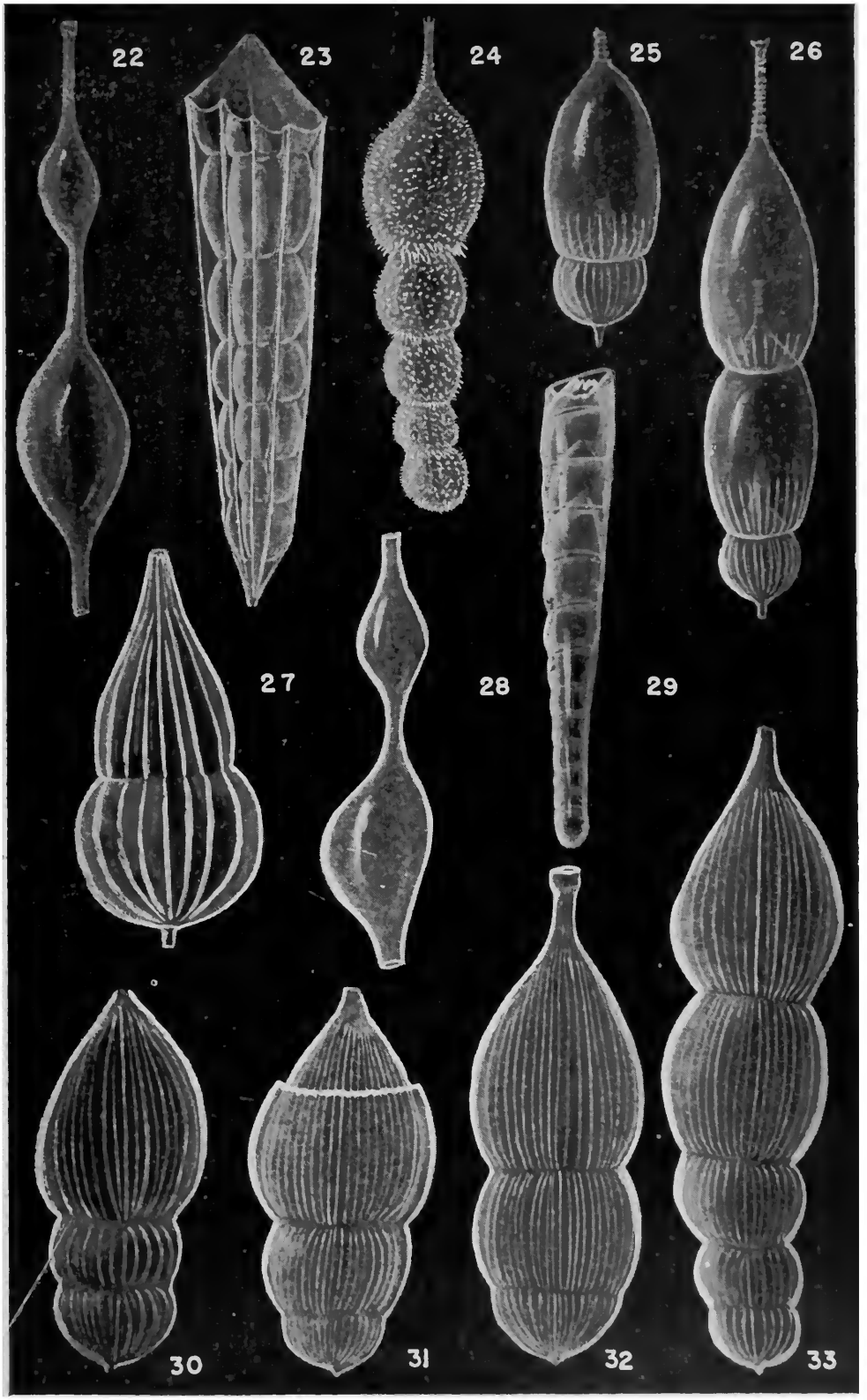
ESTAMPA 3

Fig. 22, 28 — *Nodosaria pyrula* d'Orbigny
Fig. 23 — *Nodosaria vertebralis* var. *albatrossi* Cushman
Fig. 24 — *Nodosaria hirsuta* d'Orbigny
Fig. 25, 26 — *? Nodosaria intercellularis* Brady
Fig. 27 — *Nodosaria catesbyi* d'Orbigny
Fig. 29 — *Nodosaria consobrina* var. *emaciata* Reuss
Fig. 30-33 — *Nodosaria scalaris* (Batsch)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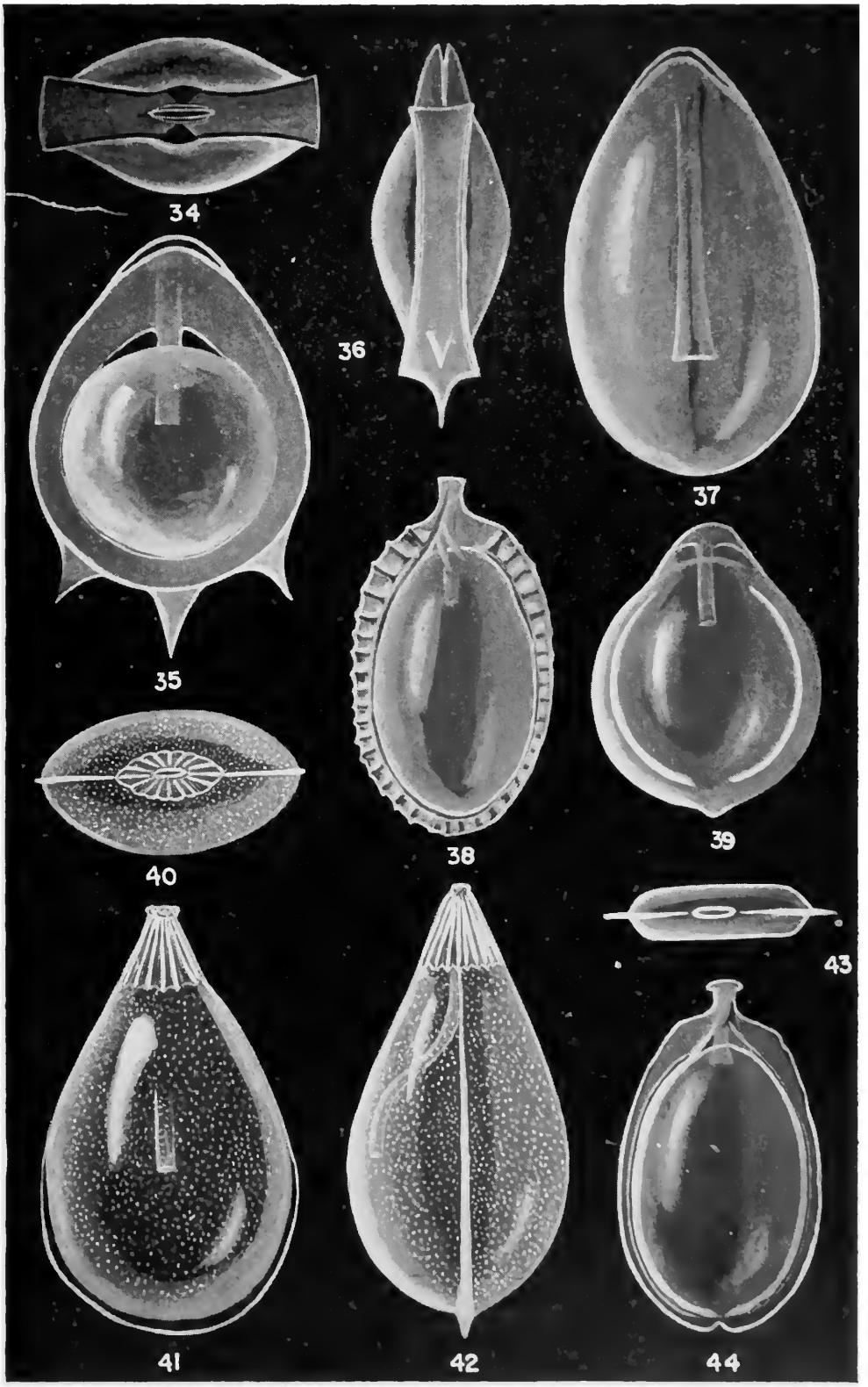
ESTAMPA 4

Fig. 34-36 — *Fissurina evelinae* sp. n.
Fig. 37 — *Parafissurina lateralis* (Cushman)
Fig. 38 — *Fissurina lagenoides* (Williamson)
Fig. 39 — *Fissurina quadricostulata* (Reuss)
Fig. 40-42 — *Fissurina juruta* sp. n.
Fig. 43, 44 — *Fissurina coacatu* sp. n.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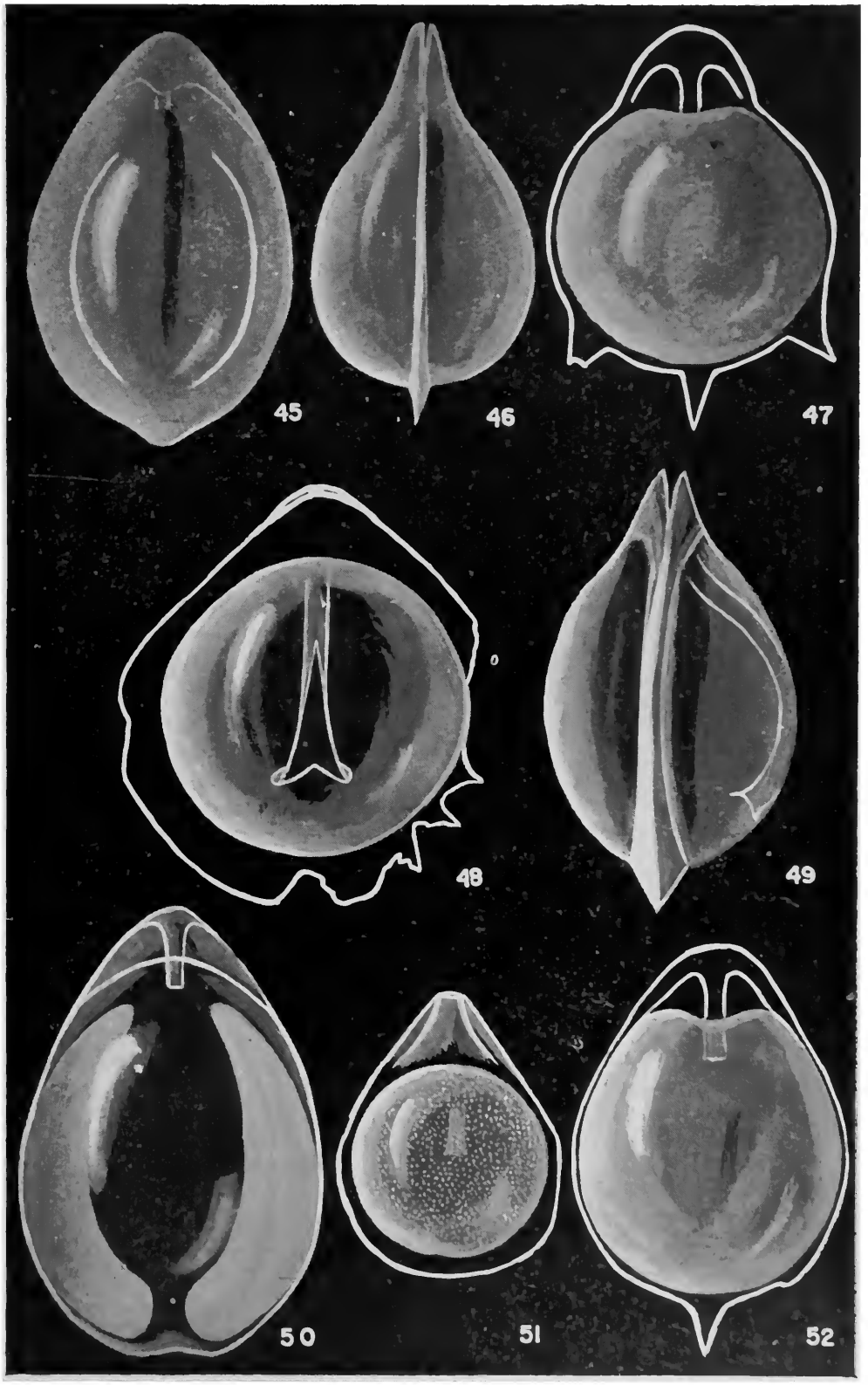
ESTAMPA 5

Fig. 45 — *Fissurina annectens* (Burrows & Holland)
Fig. 46, 47 — *Fissurina staphyllearia* Schwager
Fig. 48, 49 — *Fissurina aequilabialis* (Bachner)
Fig. 50 — *Fissurina lucida* (Williamson)
Fig. 51 — *Fissurina varioperforata* (Buchner)
Fig. 52 — *Fissurina acuta* Reuss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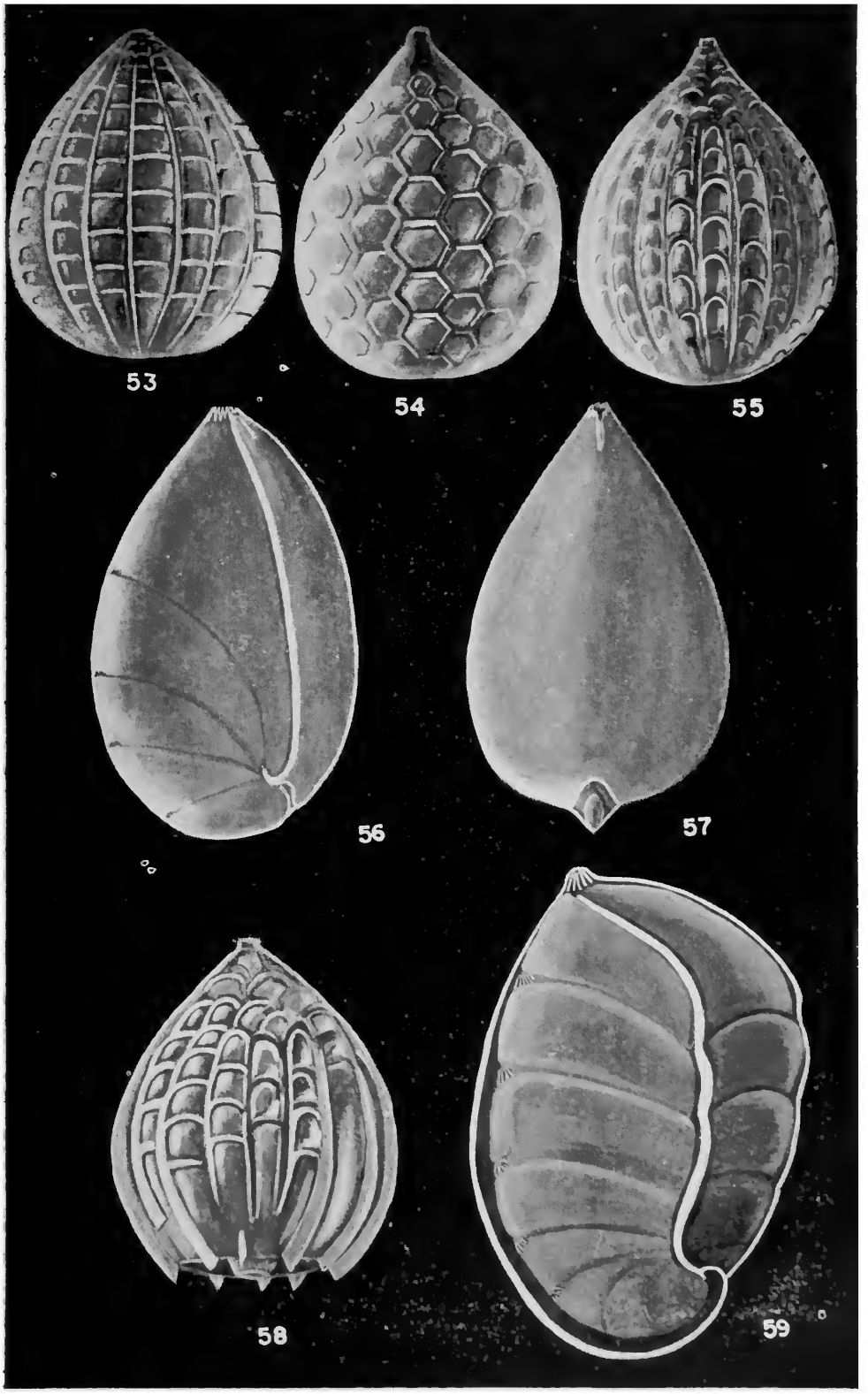
ESTAMPA 6

Fig. 53 — *Oolina melo* d'Orbigny
Fig. 54 — *Oolina hexagona* (Williamson)
Fig. 55 — *Oolina squamosa* (Montagu)
Fig. 56, 57 — *Saracenaria tayaçu* sp. n.
Fig. 58 — *Oolina aiaca* sp. n.
Fig. 59 — *Saracenaria angularis* Natland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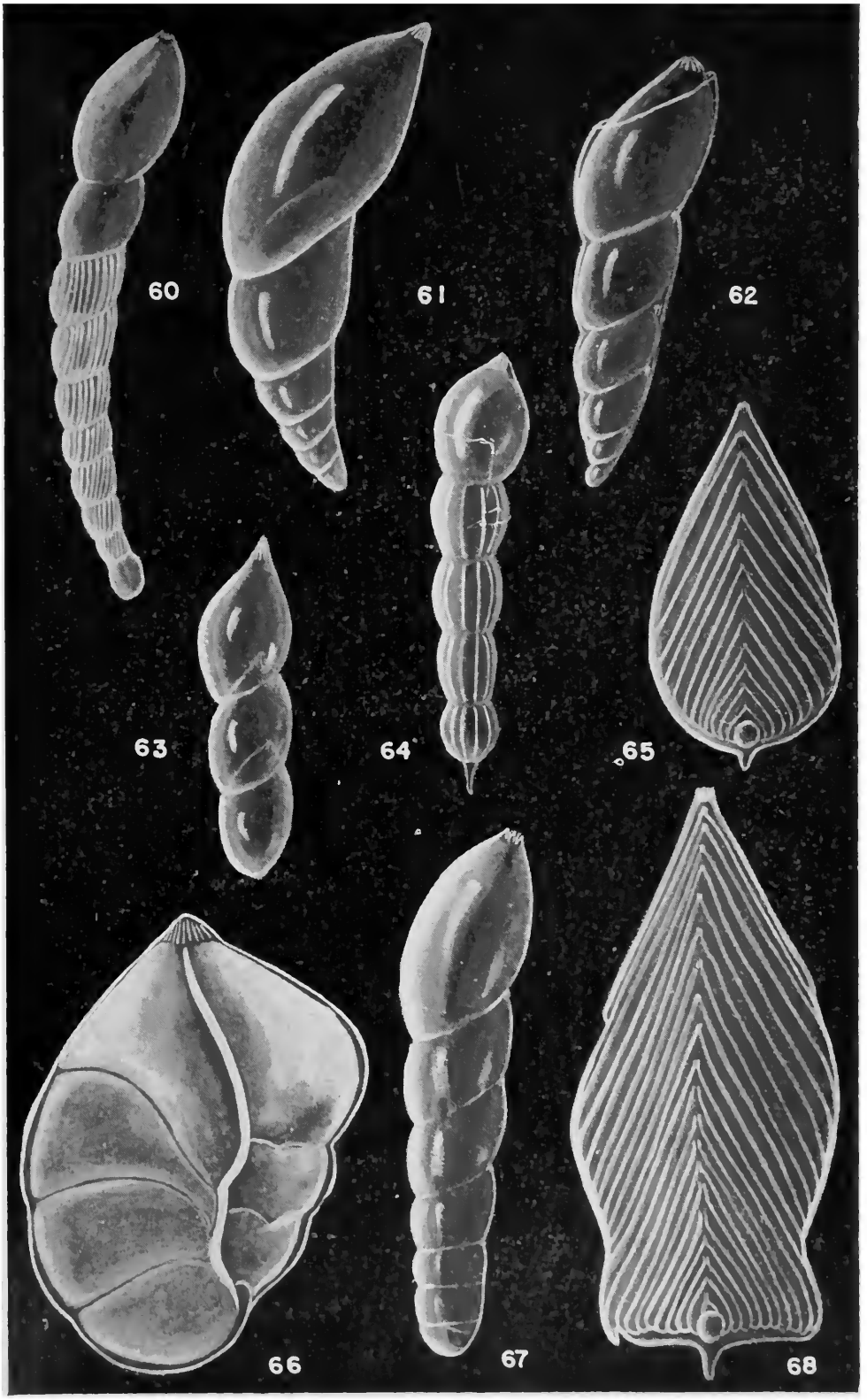
ESTAMPA 7

Fig. 60 — *Dentalina striolata* (Goës)
Fig. 61 — *Dentalina mucronata* Neugeboren
Fig. 62 — *Dentalina communis* d'Orbigny
Fig. 63 — *Dentalina californica* Cushman & McCulloch
Fig. 64 — *Dentalina mutsui* Hada
Fig. 65, 68 — *Frondicularia alata* d'Orbigny
Fig. 60 — *Saracenaria italica* Defrance
Fig. 67 — *Dentalina advena* (Cushman)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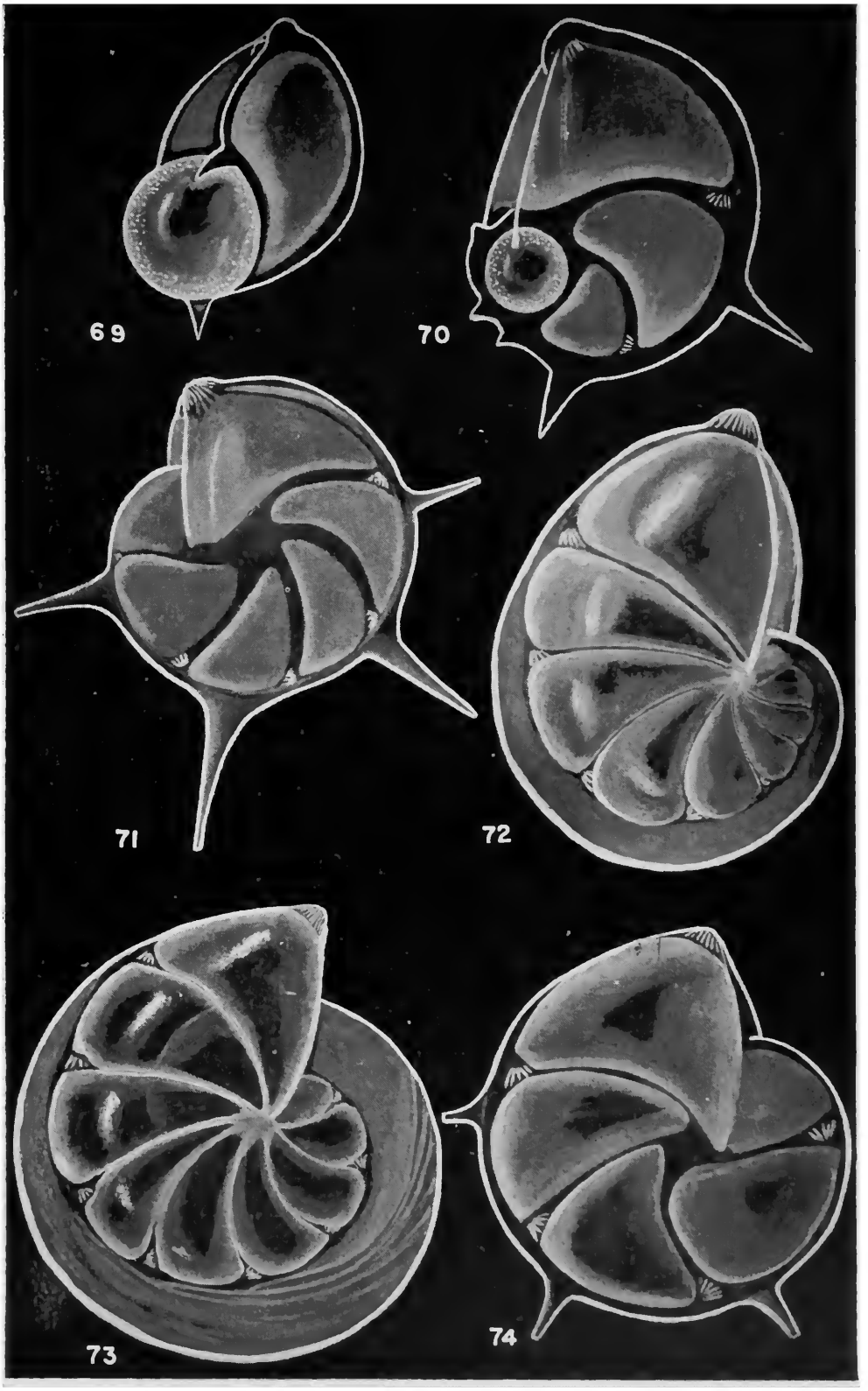
ESTAMPA 8

Fig. 69, 71, 74 — *Robulus calcar* (Linné)
Fig. 72 — *Robulus gibbus* d'Orbigny
Fig. 73 — *Robulus occidentalis* (Cushman)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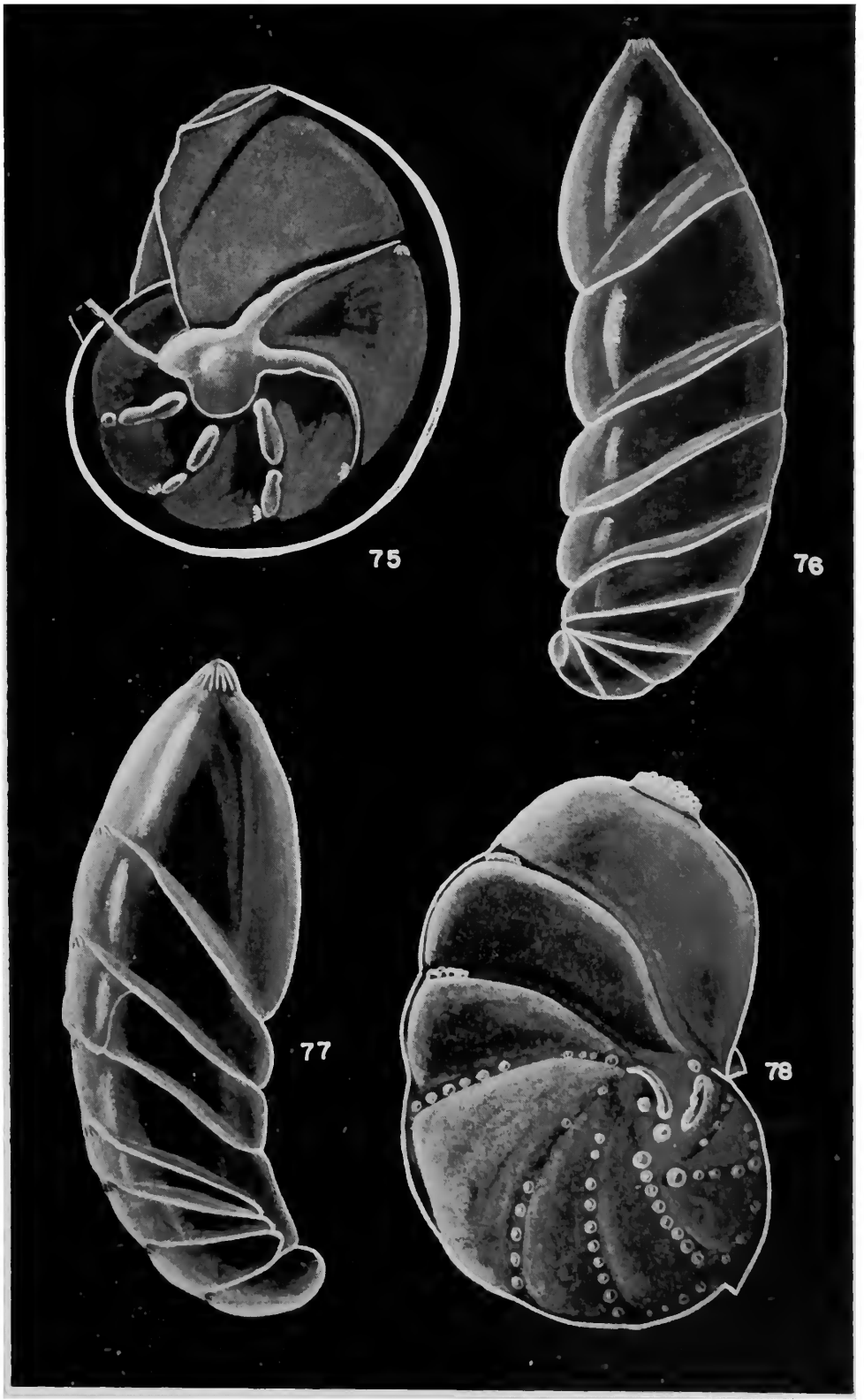
ESTAMPA 9

Fig. 75 — *Robulus submamilligerus* (Cushman)
Fig. 76, 77 — *Astacolus crepidulus* (Fichtel & Moll)
Fig. 78 — *Robulus antilleus* (Cushman)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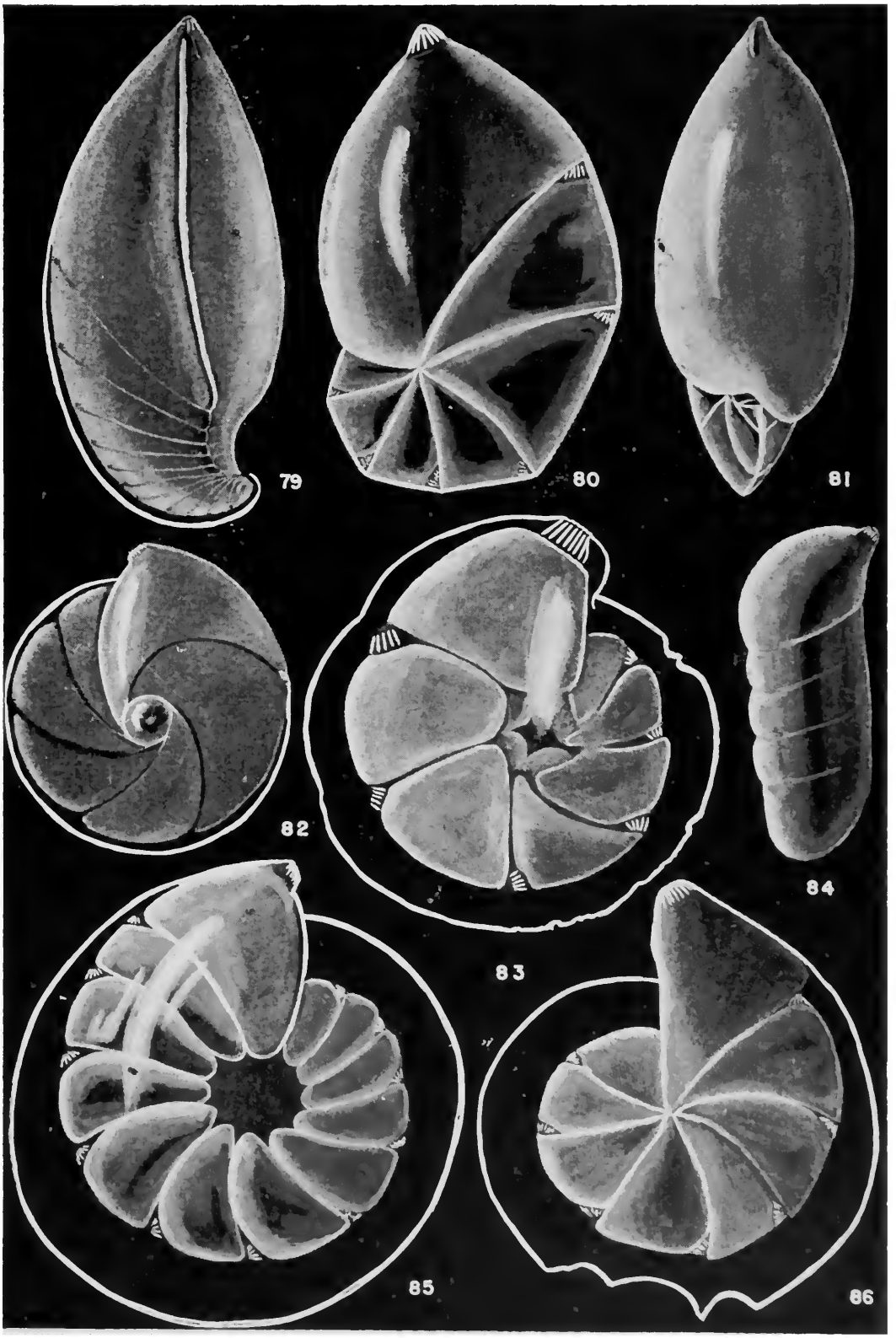
ESTAMPA 10

Fig. 79 — *Saracenaria latifrons* (Brady)
Fig. 80, 81 — *Robulus argentinensis* (Boltovskoy)
Fig. 82 — *Robulus orbicularis* (d'Orbigny)
Fig. 83 — *Robulus lucidus* (Cushman)
Fig. 84 — *Marginulina bacheei* Bailey
Fig. 85 — *Robulus cultratus* Montfort
Fig. 86 — *Robulus occidentalis* (Cushman)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BODY TEMPERATURES IN TWO BRAZILIAN PRIMATES [1]

by PETER MORRISON and J. SIMÕES JR.

Department of Physiology, University of Bahia, Salvador, Brasil, and the Department of General and Animal Physiology of the University of São Paulo. The Departments of Zoology and Physiology, University of Wisconsin, Madison, E.U.A.

A considerable literature of temperature data on monkeys exists, but this is largely confined to old world species and several of the larger new world forms (Wislocki, 1933). The current report describes two of the smaller South American species, the night monkey (*Aotus trivirgatus*) and the common marmoset (*Callithrix jacchus*). The latter is a representative species of this typically tropical group, the marmosets (*Callithricidae*) being a large family with many species. These are common in collections and as pets so it is surprising that more is not known of them. While the marmosets are typical diurnal monkeys, *Aotus* is unique as the only nocturnal, new-world, primate. Perhaps in keeping with its nocturnal habit, *Aotus* has a fine thick fur. The light fur and long limbs of the marmosets suggest a limited thermoregulatory ability in the cold, a condition, however, which will not be encountered in its normal environment. Current information on *C. jacchus* has been summarized by Simões (1958).

MATERIALS AND METHODS

The marmosets were captured locally and maintained as a group in a large cage in the Physiology Department. Four individuals, all males (*ca* 190g) were studied. Experimental observations were carried out on singly caged individuals at the Hospital das Clínicas where we

(1) This is paper 4 in a series describing results from the Wisconsin South American Physiological Expedition, 1959-60. Support was provided under N.S.F. grant (G-7073) and senior postdoctoral fellowship (PRM); and logistic assistance through O.N.R. contract (No. 2247(00)).

were indebted to Prof. Roberto Santos for the hospitable provision of facilities in his laboratories. The pair of night monkeys (♂, 660g; ♀ 590g) were made available to us for study from the Zoological State Garden through the kindness of the director, Dr. Valle. They were also caged singly during the series of observations, being maintained in a large general laboratory rather than in isolated quarters.

Body temperatures were measured with a YSI thermister thermometer using the ordinary (3 mm.) plastic coated probes. Metabolic measurements were made using a Manometric apparatus (Morrison, 1952). We are grateful to W. R. Holthaus and B. K. McNab for their assistance in some of these experiments.

RESULTS

Daily Cycles: Figure 1 presents the temperature measurements on *Aotus* as a function of the hour of day. Although only 21 values were obtained a rather well defined daily cycle is manifested. This might be expected in an animal with such a striking behavioral cycle since *Aotus*, like the flying squirrel, stayed curled up and quiet during the daylight hours despite light and disturbance about him. However, it was unfortunate that the subjects should have been subjetc to some

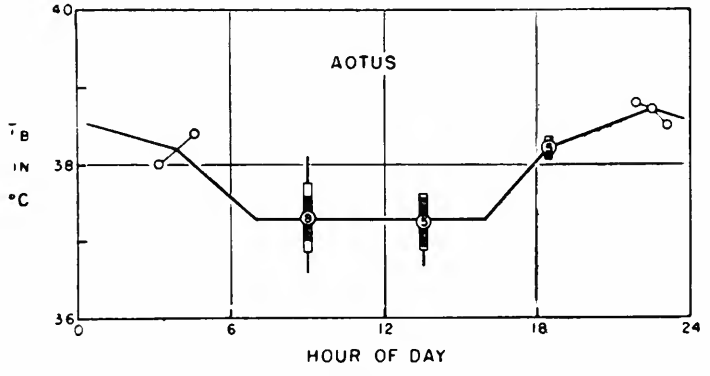

Fig. 1

disturbance during these normally resting hours. It is quite possible that considerable of the dispersion in the daytime points resulted from this abnormal disturbance. Under more favorable conditions a somewhat larger amplitude than the 1.4° observed here might be revealed. Although the data is limited, an equal division of 12 hours each was indicated for the active and resting phases.

Aotus is a very quiet, well-mannered animal which is easy to handle and usually does not try to bite or escape. On the other hand marmosets in general, and *C. jacchus* in particular, are usually excitable and aggressive. They were difficult to capture and struggled incessantly while being held. Part of this difference in behavior can be related to the fact that the nocturnal *Aotus* is in the depressed activity phase during the day when he is normally seen, whereas this is the active period for the marmoset. But while *Aotus* was much more responsive when handled at night, most of this difference relates to a basic contrast in the behavioral characteristics of the species.

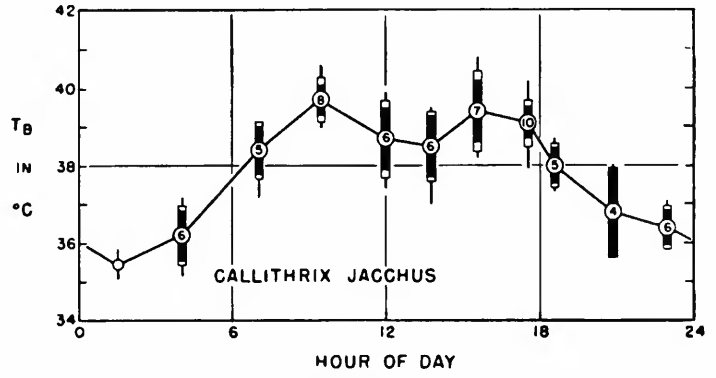

Fig. 2

Figure 2 shows the daily temperature cycle in *Callithrix*. Although there were considerably more measurements (66), the unstable nature of this species introduced considerable dispersion into the data. But the daily pattern is clearly revealed and shows a striking 4.3° amplitude between the minimum of 35.4° at 09^{30} hours and the maximum of 39.7° at 09^{30} hours. The mean temperature over the active period (0800 — 1800 hours, 37 values) was 39.1° and the mean value over the quiet period (21^{00} — 05^{00} hours, 14 values) was 36.2°. Again, the two phases were almost equal in duration. An unusual feature was the clear-cut depression in the middle of the active period. Although this phenomenon is sometimes observed in crepuscular animals which are active after night fall and again before dawn, we have not observed it before in a diurnal species.

Activity: The temperature response of *Aotus* in relation to activity is shown in Figure 3. These data are rather unsatisfactory because this species shows almost no range of activity. At night, they were

always awake, but were usually quiet and the small cages used here gave little scope for activity. In the daytime they are always sleeping, or at most wake and very quiet even when disturbed. The *1+* activity values for *Aotus* could be divided into sharply defined upper and lower groups representing day and night. An indication of disturbance to this animal is the fact that so few truly sleeping values were observed. Probably the daytime values should be assigned a value of *0+* even though the eyes were open.

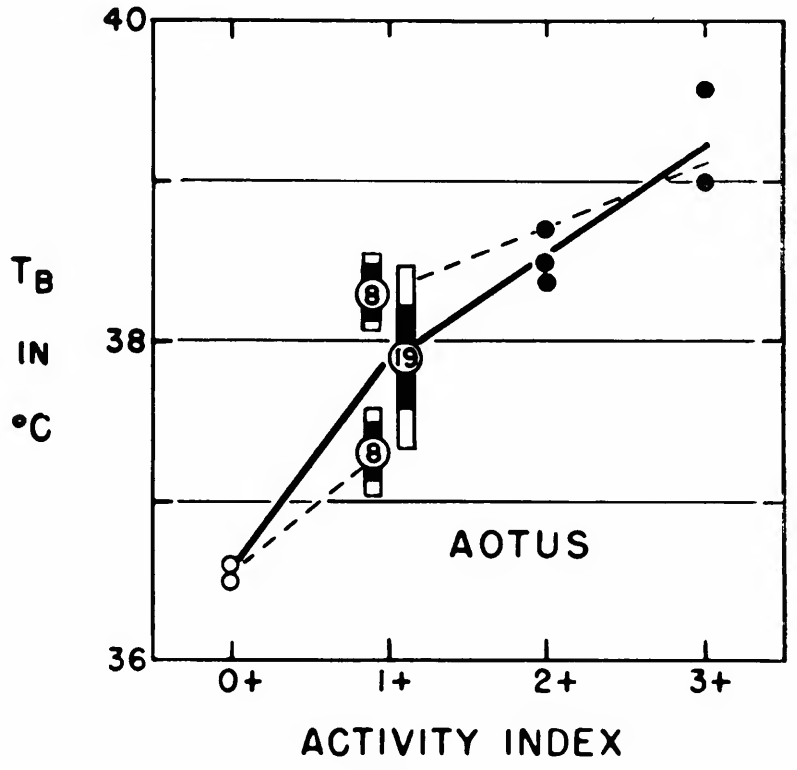

Fig. 3

The data on the marmoset was equally unsatisfactory in this regard to activity (Fig. 4). All sleeping values, were taken during the night. The *1+* activity values fell into three well defined groups of which the lower group included most of the transitional values in early morning of late afternoon between the active and resting periods. The upper group represented daytime values alone. If larger cages had been provided perhaps these waking values would have been more effectively divided.

Response to Ambient Temperatures: Body temperatures for both species following exposures at either high or low ambient temperatures are summarized in Figure 4. There were only three values

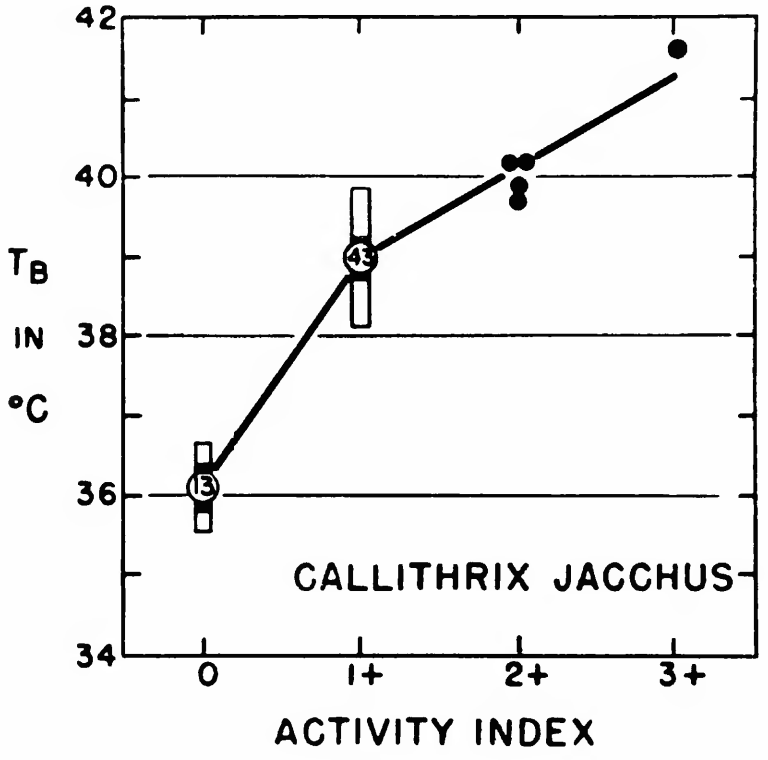

Fig. 4

on *Aotus,* but these showed a very steady, well-maintained body temperature at the level of 38° over an ambient range of 8 to 33°. This value is about midway between the night time and the daytime averages, although these experiments were carried out in the day. It may be presumed that handling and confining the animal to a small chamber elevated the temperature above the normal daytime value.

By contrast, the marmoset showed a definite depression of body temperature when exposed at either 16 or 8°. In the latter the average fall was 1.2° as referred to the average value in animals confined at near room temperature; or 1.7° as referred to the normal daytime average. The former value which is used to draw the average curves in Figure 5 is probably preferable as representing comparable

activity. At higher ambient temperatures (33 and 38°) the body temperature rose steeply, reaching a value of 41° at the latter temperature.

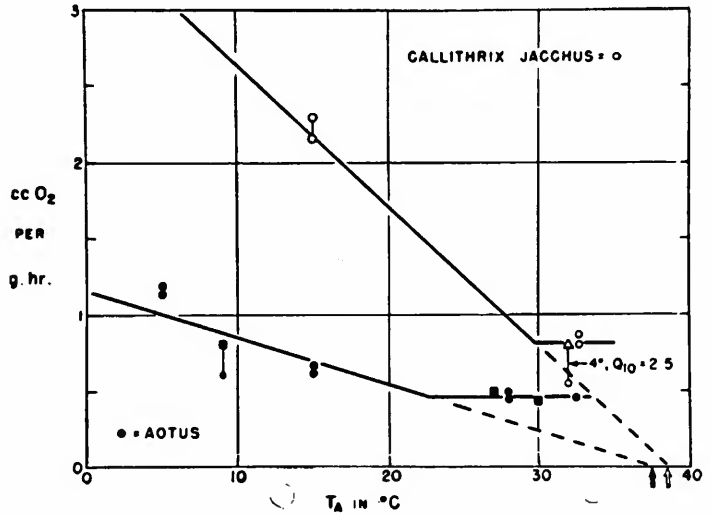

Fig. 5

Metabolism: The limited data on the metabolic response of both species is given in Figure 6. The basal metabolism in *Aotus* lay at a level of 0.45 cc $0_2 g^{-1} hr^{-1}$, equivalent to 2.57 cc $0_2 g^{-.73} hr^{-1}$. Scholander, *et al* (1950) report a slightly higher value of 0.51 cc

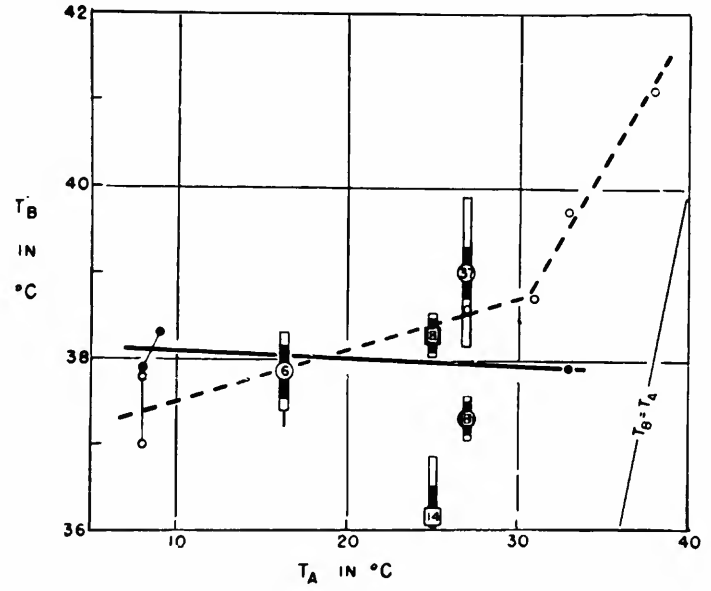

Fig. 6

g $^{-1}hr^{-1}$ for the Panamanian subspecies. This is below the standard value of 2.70 corresponding to the average for mammals (Brodie, 1945). The mean curve describing oxygen consumption below thermal neutrality has a value of 1.16 cc $g^{-1}hr^{-1}$ at 0°. The slope of this curve, 0.031 cc $0_2g^{-1}hr^{-1}C°$, or 0.149 cal $g^{-1}nr^{-1}°C^{-1}$ represents the thermal conductance of the animal and this value is distinctly lower than the average which we have observed in small temperature mammals, in particular, than that of the Franklin ground squirrel, an animal of comparable size (Morrison and Ryser, 1951). The critical temperature for this species lay at 23°.

The basal level for *Callithrix* appears to be at 0.80 cc $g^{-1}hr^{-1}$. One very low value at 0.65 cc $0_2g^{-1}hr^{-1}$ was recorded but in this case the body temperature of the animal was only 33.7°. Adjustment of this value to correspond to 38.0°, the mean body temperature in the day, raised it to the level of 0.80 of cc $0_2g^{-1}hr^{-1}$. Scholander *et al* (1950) reported a somewhat higher value of 1.04 cc $0_2g^{-1}hr^{-1}$ for a related species, *Oedipomidas spixi*. The conductance curve for this species was placed from the data from a single experiment at 15° and gives a value of 0.093 cc $0_2g^{-1}hr^{-1}°C^{-1}$ 0.45 cal $g^{-1}hr^{-1}°C^{-1}$. Although *Callithrix* proved to be a rather poor regulator as judged by the depression of its body temperature at ambient temperatures of only 8 to 17°, this conductance value is at the normal level for temperate forms, being close to that of the 13 lined ground squirrel, a rodent of comparable size.

DISCUSSION

The daily temperature cycle in the marmoset, *Callithrix jacchus,* has a striking amplitude of 4.3°. No member of the Callithricidae have been measured in this regard previously except for a single set of values (12 points) from a tuberculin test on *Oedipomidas spixi* by Fox (1923). His values show a rather close correspondence with those seen here for *C. jacchus*. There are data on several of the other family of new world monkeys. In *Cebus* and in *Ateles,* lesser amplitudes of 2.1 and 2.0 respectively, or less than half the above have been reported (Fox, 1923). Such smaller values appear characteristic of the old world monkeys which have been studied as well.

Further, the form of the daily cycle in *Callithrix* is quite different than that found in the monkeys for which an almost saw-tooth pattern has been reported. *Callithrix* maintained a high level of temperature for about 10 hours, and this active period was clearly divided into two peaks with maxima at 09^{30} and 16^{30} and an intervening minimum at 14^{00}, the time of maximum body temperature in other species. This secondary daytime minimum appears shallow compared to the nocturnal low, but it may be noted that its amplitude was almost as large (1.2 vs. 1.40) as the entire daily cycle in *Aotus*. Such bimodal activity or temperature cycles are sometimes seen in crepuscular animals such as bats which are active at dusk and then again at dawn (Pearson, 1947). The maxima seen here appear either too late (09^{30}) or too early (16^{30}) to qualify for crepuscularity. But in animals such as the marmosets which characteristically live in the dense rain forest, where light levels are greatly reduced, a mid-day cessation of activity has often been described for animals exposed to heat. This might represent a displacement of dawn and dusk.

Aotus trivirgatus shows a temperature cycle that contrasts to *Callithrix* in almost every aspect. The amplitude of 1.40 between minimum and maximum is very modest. The phasing of the cycle, of course, corresponds to the activity of the animal with the maximum at 11^{00}. Insufficient data were available to define the cycle more precisely, but it appeared to represent a rough "square" wave with a maintained lower temperature ($07^{00} \rightarrow 16^{00}$) of 37.3 and a fairly well maintained active temperature, at least much more so than in monkeys in the literature referred to above. *Aotus* may be compared to another primate of similar habit, but of a quite different group, the west African Potto. *Perodicticus potto* is a rather sluggish nocturnal lemur and its temperatures cycle is very similar to *Aotus* with an identical amplitude of 1.4^{o}. It is of interest that both these nocturnal members of an almost strictly diurnal order are of such a quiet habit and show such a reduced temperature cycle. One might speculate that the diurnal habit was so strongly impressed on this order that it was not possible to switch from day to night with a complete (intensity) reversal of the activity pattern. Body temperatures for marmosets and for *Aotus* are summarized in Table 1.

TABLE 1

Body temperatures in Marmosets and Night monkeys

Species	Tb	#	*S.D.*	*Hour*	Ta	*Sex*	*Reference*
Oedipomidas spixi	38.8	(8:?)	—	Day	(25)		Britton and Klein, 1939
" "	39.1	(9:1)	0.33	15^{00}			Fox, 1923
	37.0	(3:1)	—	Night			
Callithrix jacchus	39.1	(?:2)	—	Day	19	♂	Brown, 1909
" "	39.1	(37:4)	0.88	Day	27	♂	this study
	36.2	(14:4)	0.72	Night	25		this study
A. trivirgatus	38.0	(?:2)	0.80	15^{00}	19	♂,♀	Brown, 1909
A. t. griseimembra	38.5	(3:?)	—	Day	(25)		Britton and Klein, 1939
A. t. trivirgatus	37.3	(13:2)	0.40	Day	27	♂,♀	this study
	38.4	(10:2)	0.25	(Night)	25		this study

A contrast between the two species is also seen in the influence of cold on body temperature. The data indicate that *Aotus* is a quite adequate regulator, at least within the rather modest test limits of 8°, since there was no fall in body temperature. By contrast, *Callithrix* was quite thermolabile over the whole temperature range showing a slope of 0.10 (Δ_1 Tb/Δ Ta) between 8 and 31°; and a slope of above 31. *C. jacchus* is confined to eastern Brazil where a uniform temperature is the rule. *A. t. trivirgatus* is also found over about the same range, but other subspecies range into the lower Andes at altitudes up to 5.000' where cold of a degree appropriate to its dense fur is encountered. The metabolic measurements gave a conductance value for *Aotus* which was, in fact, lower than that seen in some "temperate" mammals of comparable size (Morrison and Ryser, 1951). The value for *Callithrix* was comparable to that seen in "temperate" rodents, and it would appear that either huddling or the development of an axial temperate gradient (Scholander, 1957) had compensated for the longer limbs and greater surface area.

SUMMARY

1. The daily body temperature cycle in the common marmoset, *Callithrix jacchus,* (4 ♂) had and amplitude of 4.3°C, about twice that observed in other primates and higher than that seen in any other mammal. The maximum was at 09^{30} hours (39.7 ± 0.98°) and the minimum was at 01^{30} (35.4 ± 0.4°).

2. The night monkey, *Aotus trivirgatus,* (1 ♂, 1 ♀) showed a reversed (nocturnal) temperature cycle with an amplitude of 1.4°, less than is seen in most monkeys. The maximum was at 23^{00} (38.5°) and a minimum of 37.3° was maintained between 07^{00} and 17^{00} hours. The ♂ averaged 0.6° higher than the ♀.

3. *Aotus* maintained its normal body temperature on cold exposure down to 8°, while in *Callithrix* the body temperature fell continuously from 38.8 at 31° ambient to 37.3 at 8° ambient.

4. Metabolic measurements in the cold gave values of thermal conductance of 0.149 for *Aotus* and 0.45 cal $g^{-1}hr^{1}°C^{-1}$ for *Callithrix;* (0.031 and 0.093 cc 0_2 $g^{-1}hr^{1}°C^{-1}$) and critical temperatures of 22.5 and 29.7 respectively. The basal metabolic rate was 0.80 in *Callithrix* and 0.45 cc 0_2 $g^{-1}hr^{-1}$ in *Aotus*.

SUMÁRIO

1. O ciclo de temperatura corpórea diário do saguí *Callithrix jacchus* (4 ♂) tem uma amplitude de 4,3°C, cêrca de 2 vêzes a observada em outros primatas e mais elevada em qualquer outro mamífero. O máximo foi às 9,30 horas (39,7 ± 0,98°) e o mínimo foi às 1,30 horas (35,4 ± 0,4°).

2. O macaco noturno *Aotus trivirgatus* (1 ♂, 1 ♀) exibiu um ciclo de temperatura reverso (noturno) com uma amplitude de 1,4°, menor do que a vista na maioria dos macacos. O máximo foi às 23 horas (38,5°) e um mínimo de 37,3° foi mantido entre 7 e 17 horas. O macho teve uma média 0,6° mais elevada do que a fêmea.

3. *Aotus* manteve sua temperatura do corpo normal na exposição ao frio até 8°, enquanto que em *Callithrix* a temperatura do

corpo caiu contìnuamente de 38,8 a 31° ambientais para 37,3 a 8° no ambiente.

4. Medidas metabólicas no frio deram valores de condutância térmica de 0,149 para *Aotus* e 0,45 $g^{-1}h^{1}{}^{o}C^{-1}$ para *Callithrix;* (0,031 e 0,093 cc 0_2 $g^{-1}h^{1}{}^{o}C^{-1}$) e temperaturas críticas de 22,5 e 29,7 respectivamente. A taxa metálica basal foi de 0,80 para *Callithrix* e 0,45 cc 0_2 $g^{-1}h^{-1}$ para *Aotus*.

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CONTRIBUIÇÃO PARA O ESTUDO DA NUTRIÇÃO DE DROSOPHILA WILLISTONI *STURT*

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I

INTRODUÇÃO

Muitas vêzes, nos estudos da nutrição de organismos é desejável, e mesmo necessária, a determinação de um meio de cultura quìmicamente definido de modo a permitir o desenvolvimento do organismo escolhido em boas condições. Sempre que possível o meio de nutrição deve ser asséptico, providência esta que elimina a análise e síntese que realizam microorganismos concorrentes, proporcionando assim apreciável redução dos fatôres variáveis, o que é de importância para melhor avaliação dos resultados.

Estudos dêste tipo em animais pluricelulares são relativamente raros na literatura, se considerarmos o grande número de trabalhos realizados com micro-organismos.

Nas pesquisas de fisiologia comparada, principalmente, é de interêsse conhecer a influência decisiva no crescimento, na reprodução, enfim na biologia de certos animais bastante utilizados em diversas pesquisas. Dêstes animais, sobressaem-se pela intensidade de investigação já realizada, as môscas do gênero *Drosophila*, o díptero de eleição para os estudos de genética, como bem é conhecido. Culturas dêste inseto fazem-se no mundo inteiro, e pareceu-me de importância verificar a influência que nelas possam exercer certos e determinados fatôres, principalmente os aminoácidos e vitaminas.

Assim, dispus-me a trabalhar êste tema que me pareceu relevante, como contribuição para o melhor conhecimento da biologia das *Drosophila*.

No presente trabalho tive em mira principalmente o seguinte:

a) determinar um meio de cultura quìmicamente definido no qual *D. willistoni* pudesse desenvolver-se normalmente, isto é, que permitisse pupação de tôdas ou quase tôdas larvas até atingirem inclusive o estado adulto;

b) experimentar em tal meio de cultura, linhagens de *D. willistoni* oriúndas de populações naturais e transformadas em homozigotas para determinado cromosoma, o que possibilitava verificar diferenças bioquímicas em linhagens genèticamente diversas.

Como se sabe, no estudo da genética de populações, a espécie *D. willistoni* é uma das Drosophilas mais empregadas no Brasil, e daí ser uma das espécies brasileiras mais bem conhecidas genèticamente (Pavan et al. 1951, Cordeiro 1952, 1954), Pavan et al. 1954.

Populações de *D. willistoni* costumam apresentar grandes quantidades de mutações recessivas, letais, semi-letais, de esterilidade, morfológicas, etc. Evidentemente, muitas outras mutações devem ter passado desapercebidas ao investigador se não utiliza métodos especiais para conhecê-las. Com êste propósito foi o método da análise espectrofotométrica dos pigmentos do olho de Drosophila empregado por Nolte e outros (1952, 54). Por sua vez, Hadorn (1953) preferiu a análise cromatográfica para estudo dos mutantes em linhagens homozigotas aparentemente normais. Recentemente Tondo e Cordeiro (1956), utilizando eletroforese, descreveram "mutantes eletroforéticos". Coube, porém, a Hinton (1951) determinar as mutações metabólicas que afetam necessidades nutricionais nestes Dipteros.

Com a finalidade de proporcionar aos geneticistas mais um método aplicável ao estudo das variações genéticas metabólicas em *D. willistoni* foi êste trabalho realizado por sugestão do Dr. Antônio R. Cordeiro, sob a orientação do Dr. Taylor Hinton no Departamento de Zoologia da Universidade da Califórnia e do Dr. Paulo Sawaya do Departamento de Fisiologia Geral e Animal da Universidade de São Paulo, durante o estágio na Universidade de Los Angeles, gra-

ças a uma bôlsa de estudos patrocinada pela Fundação Rockefeller. Aos Professôres citados que se tornaram credores de minha gratidão adiciono o nome de minha espôsa, Lic. Euterpe Cauduro Jaeger, auxiliar imprescindível na realização dêste trabalho.

II

MATERIAL E MÉTODOS

Estoques balanceados de linhagens de *D. willistoni* tornadas homozigotas para o II cromosoma pelo método empregado por Pavan et al. (1951) seguindo o clássico método CLB, e originárias de môscas coletadas de populações naturais em El Destino, República Argentina, foram gentilmente cedidas pelo Dr. Antônio R. Cordeiro para a realização dêste trabalho.

Coletaram-se os ovos por técnica especial, utilizando um prato raso de vidro provido de uma base de agar-agar a 4%, que era coberta por uma mistura de fermento com Terra de Fuller formando uma camada de um a dois milímetros de espessura sôbre a base de agar. Sôbre o prato assim preparado eram emborcados durante algumas horas garrafas de 1/4 de litro contendo as fêmeas adultas. A camada de fermento e Terra de Fuller assim utilizada era raspada com uma pequena espátula e colocada em cestinhos de tela medindo 1 x 1 x 0,5 cm com malha menor que o diâmetro transversal do ovo de *D. willistoni*. A lavagem dos ovos era feita segurando com uma pinça dois cestinhos de cada vez e aplicando fino jato de água distilada que retirava tôda a mistura de fermento e Terra de Fuller, bem como os detritos visíveis, liberando assim os ovos. A esterilização dos ovos era feita de acôrdo com a técnica de Hinton (1955). Os cestinhos contendo os ovos eram lavados várias vêzes em água distilada corrente, e após lavados também várias vêzes em álcool 70°. Depois, colocados durante 45 minutos em placas esterilizadas cobertas com tampa de vidro e novo álcool 70°. A seguir, os cestinhos eram transferidos individualmente para placas de Petri pequenas, devidamente esterilizadas, contendo uma base de agar a 2%. Estas eram guardadas na estufa a 25°C durante à noite, para a eclosão dos ovos. Êste tratamento mostrou-se eficaz e não injuriava os ovos. Na manhã seguinte, utili-

zando precauções bacteriológicas comuns, as larvas eclodidas eram transferidas para os tubos de ensaio contendo o meio sintético utilizando-se uma alça de platina achatada na ponta. Vinte larvas eram inoculadas por tubo e não mais do que por duas manipulações retiradas da mesma placa de Petri. Como as larvas aderiam fàcilmente à ponta da alça de platina, uma placa de Petri fornecia larvas para dois tubos. Os tubos eram mantidos na estufa a 25°C sendo as larvas e pupas contadas diàriamente até a eclosão dos adultos. Os tubos eram então testados, quanto à contaminação, adicionando-se caldo nutritivo e incubando-os por 48 horas na estufa a 37°C. Em seguida placas de Petri estéreis contendo agar nutritivo eram inoculadas com conteúdo dos tubos e incubadas. De todo tubo que apresentasse contaminação não se considerou nos resultados. As contaminações eram infreqüentes e nunca atingiram mais do que 5% dos tubos.

TABELA I

Meio de cultura químicamente definido para D. willistoni

	mg/ml		ug/ml
L-Arginina	0,559	Biotina	0,02
L-Cisteina	0,480	Pantotenato de Ca	16,0
L-ác. Glutâmico	4,418	Colina	75,0
Glicina	1,745	ác. Fólico	3,0
L-Histidina	0,484	Piridoxina	2,5
L-Isoleucina	1,260	Riboflavina	10,0
L-Leucina	2,345	Tiamina	2,0
L-Lisina	1,337	Niacinamida	12,0
DL-Metionina	0,339		
L-Fenilalanina	1,008		mg/ml
DL-Treonina	0,756		
L-Triptofano	1,745	KH_2PO_4	1,83
L-Valina	1,355		
		NaH_2PO_4	1,89
Frutose	7,5		
Colesterol	0,3	$NaHCO_3$	1,4
ác. Ribonucleico	4,0	Agar	20,0

O meio sintético era preparado segundo o método descrito por Hinton *et al.* (1951). Depois de planejada a experiência, colocavam-se 20 mg de agar em pó em cada tubo de ensaio utilizando-se um dosador automático. Adicionava-se em seguida o colesterol diluído em

éter ao agar em cada tubo. Os aminoácidos e açúcar (sacarose ou frutose) foram pesados em quantidades necessárias para 100 ml finais de meio e depois de misturados em moinho de bolas, dissolvidas em 50 ml de água distilada eram neutralizados com NaOH 0,1 N. A esta mistura adicionavam-se de soluções estoques, conforme o plano da experiência, ácido nucleico, fosfatos, cloretos, sulfatos (exceto $FeSO_4$ que era preparado na ocasião), carbonatos e as vitaminas (exceto ácido fólico que era diluído em álcool a 20%). A seguir juntavam-se $FeSO_4$ e ácido fólico. Como cada tubo continha 4 ml de meio de cultura e 6 tubos idênticos eram feitos em cada experiência, necessitávamos para uma experiência sòmente 24 ml de meio de cultura. Assim os 100 ml de meio eram divididos em 4 partes de 25 ml cada uma, possibilitando a realização de 4 experiências concomitantes. Depois de divididos os 100 ml em partes iguais eram então adicionadas as substâncias que representavam as variáveis experimentais. Os meios de cultura finais eram então novamente neutralizados e em seguida pipetados nos tubos de ensaio. Êstes depois de arrolhados com algodão não absorvente eram autoclavados durante 15 minutos a 15 libras de pressão e inclinados para solidificação.

A viabilidade foi medida considerando-se a porcentagem do número original de larvas e o número das que puparam, o tempo médio em dias da inoculação até a pupa e a porcentagem de pupas que produziram adultos. Outros fatôres como o tempo gasto na pupa não foram considerados pois independem do meio de cultura (Hinton et al., 1951).

III

PARTE EXPERIMENTAL

Com o propósito de estabelecer o meio de cultura quìmicamente definido, de modo a permitir um bom desenvolvimento normal de *D. willistoni,* inicialmente vários experimentos de contrôle foram realizados e alguns mantidos paralelamente aos meios experimentais durante todo o trabalho. Para provar a eficácia dos meios experimentais utilizaram-se môscas provenientes de fêmeas coletadas na natureza assim como as obtidas pelo intercruzamento de duas linhagens

diferentes dos estoques mencionados na página 3, indivíduos agora portadores de dois II cromosomas existentes em animais capturados no ambiente natural (Cordeiro et al., 1958).

Várias fórmulas básicas que deram bons resultados para *D. melanogaster* (Hinton etl al., 1951) foram provadas para *D. willistoni*, apresentando tôdas elas parco desenvolvimento e longo tempo para pupação em relação ao contrôle.

TABELA II

Experimentos contrôle — 25°C

Linhagem número	N.º orig. de larvas	Meio d/cultura	% pupas	Tempo médio em dias p/ pupação	% adultos
220/5	120	Farinha de milho	75,0	9,1	95,5
141	120	" " "	53,3	7,4	90,6
8	120	" " "	55,0	6,8	93,9
7	120	" " "	76,0	6,6	86,9
220	120	" " "	86,6	7,0	94,2
38	112	Fermento morto Meio para *D. melanogaster*	68,8	9,6	69,1
220/6	91	Hinton, 18 AA	43,9	17,8	75,0
220/6	116	Hinton, 13 AA	56,0	17,1	83,1
8/220	149	" " "	14,8	14,9	90,9
141/220	124	" " "	19,4	14,3	100,0 *)
141/7	148	" " "	16,9	13,0	100,0 *)
7/8	148	" " "	22,3	14,4	100,0 *)
Selvagem **	115	Sang, caseina	11,6	7,1	22,2
Selvagem	120	" "	10,0	11,3	25,0
Selvagem	131	Difco, K 115 225	33,0	17,8	77,4

*) Êstes dados não são significativos, indicam apenas que tôdas as pupas eclodiram.

**) Linhagens originadas de fêmeas coletadas na natureza e não analisadas genèticamente.

A tabela I sumaria os dados obtidos com êstes meios assim como os experimentos testemunhos com animais homo e heterozigotas. O meio de cultura com caseína Sang, (1956) para *D. melanogaster* foi também experimentado em *D. willistoni*, segundo a fórmula de Sang, assim como substituindo-se a caseína pela mistura de 13 ami-

noácidos que contém os 10 essenciais para Drosóphila e mais Cisteína, Glicina e ác. Glutâmico que possuem efeito desintoxicante.

Por cortesia do Dr. Taylor Hinton e dos Laboratórios Difco foi também possível provar o meio experimental K115 225 que possui a mesma composição do usado por Hinton (1951). Êstes meios não produziram bons resultados conforme sumaria a Tabela II.

Em face da ineficácia dos meios de cultura existentes no tocante a permitir o desenvolvimento de *D. willistoni* passamos a pesquisar novas fórmulas. Evidentemente, tôda modificação introduzida que desse bons resultados era logo incorporada no experimento seguinte. Durante o trabalho realizamos 222 experimentos com 76 meios diferentes quìmicamente definidos (exceção feita dos poucos com caseína e outros com resíduos de fermento). Tôdas experiências foram repetidas no mínimo uma vez. O número de larvas por experiência foi sempre ao redor de 120 (menor em casos de contaminação) o mesmo ocorrendo nas repetições.

a) *Necessidades de aminoácidos.*

Experimentamos o emprêgo de um número variável de aminoácidos de modo a iniciar com os 10 essenciais para Drosophila (Hinton et al., 1951) e depois aduzir outros em várias combinações dos não essenciais de tal modo a conseguir misturas de 10, 11, 13, 18 e 19 aminoácidos. Como outra variável experimental, a quantidade de certos aminoácidos foi alterada especialmente dos de efeito desintoxicante, como o ácido glutâmico, a cisteína e a glicina. Uma resposta a doses foi feita para fenilalanina e triptofano. A combinação de aminoácidos que melhores resultados ofereceu foi a de Hinton (1956) contendo 13 aminoácidos nas proporções apresentadas na tabela I.

b) *Necessidades de carbohidratos.*

Hasset (1948) revisou os trabalhos sôbre necessidades de carbohidratos em insetos e demonstrou os diferentes valores de uma série de açúcares na nutrição de Drosophila adultas. Demonstrou a seguinte ordem de utilização dos açúcares: frutose > maltose > sacarose > glicose > galactose > xilose > lactose. Sang (1956), por sua vez, provou que a frutose é mais conveniente para a Drosophila.

Frutose na proporção de 7,5 mg/ml do meio deu melhores resultados com *D. willistoni* do que com sacarose.

c) *Necessidades lipoídicas.*

Lecitina, ergosterol e colesterol foram experimentados individualmente em várias concentrações. Lecitina não é essencial para Drosophila (Hinton, 1952, Sang, 1956). Também aqui verifiquei que esta substância não melhora as qualidades do meio quando a êle adicionada. Ergosterol utilizado a 0,3 mg/ml não deu melhores resultados que o colesterol, pois na ausência dêste as larvas não crescem. A quantidade de colesterol que proporciona melhores resultados é de 0,3 mg/ml.

d) *Necessidades de ácido nucleico.*

Schultz et al. (1946) e Villee & Bissel (1948) demonstraram não residir o fator crescimento representado pelo ácido ribonucleico no desenvolvimento de Drosophila no próprio RNA total, mas sim nas bases purínicas e pirimidínicas que o compõem.

Drosophila tem uma capacidade limitada de sintetizar o ácido nucleico de que necessita, e pode fazê-lo se forem fornecidas as bases purínicas e pirimidínicas. Um mutante que perdeu esta capacidade, não se desenvolve sem adição de adenina (Hinton, 1952). A proporção de RNA e a de seus componentes foram experimentados na dieta. Melhor desenvolvimento obtivemos com 4 mg/ml de RNA. Tôdas as outras combinações de bases purínicas e pirimidínicas produziram menor efeito. Segundo Sang (1956) uma ótima quantidade de ácido ribonucleico na dieta é suficiente para um bom desenvolvimento.

e) *Necessidades de vitaminas.*

Tôdas vitaminas incluídas na tabela III mostraram ser essenciais ao desenvolvimento de *D. willistoni*. Inositol e ácido paraminobenzóico que Hinton (1951) comprovou não serem fator de crescimento para *D. melanogaster,* também não o são para *D. willistoni*. B_{12} que parece aumentar o número de pupas em *D. melanogaster* não tem efeito algum quando retirada da dieta de *D. willistoni*.

f) *Necessidades de sais minerais.*

Sang (1956) demonstrou que as necessidades de sais minerais não podem ser exatamente definidas em meios sintéticos devido à contaminação do agar e outros constituintes com vários metais. As experiências que efetuamos mostram que *D. willistoni* se desenvolve melhor na ausência de Mg, sendo o K, P e Na essenciais.

IV

DISCUSSÃO

Os resultados obtidos com o meio sintético para *D. willistoni* tanto para linhagens homo e heterozigotas como para selvagens estão sumariados na tabela III. A análise dêstes dados revela que o meio fornecido foi o melhor conseguido dentro das limitações impostas pelas condições assépticas exigidas por êste tipo de experiência. Evidentemente, não se pode comparar êste crescimento asséptico com o que a môsca encontra na natureza, mas por outro lado pode êle ser confrontado com os experimentos de contrôle (Tabela II) nos quais se deu aos ovos o mesmo tratamento asséptico, utilizando-se meio padrão de farinha de milho (Burdick, 1954) ou fermento inativo. Os resultados mostram que o melhor meio obtido permitiu a pupação de 70,9 a 99,8% das larvas inoculadas, no período de 9,3 a 13 dias, resultado aqui considerado bom se comparado com os 6,6 a 9,9 dias de pupação de 69,1 a 96,8% requeridos por larvas inoculadas em meio de farinha de milho. Para a maior parte das finalidades às quais servirá êste meio sintético esta diferença é de pouca monta.

"Mutações metabólicas"

O exame dos resultados obtidos criando homozigotos em meio de cultura quìmicamente definido para *D. willistoni* (tabela III) revela que estas linhagens do ponto de vista de sua viabilidade, morfologia, etc., classificadas como *normais* em meio de cultura comum, apresentam aqui viabilidades diferentes, isto é, mostram diferentes capacidades de aproveitar as substâncias presentes no meio para realizar totalmente suas sínteses orgânicas.

Estas linhagens são distribuídas numa seqüência contínua de valores de viabilidade, o que indica a grande diversidade de efeitos produzidos pela homozigose do II cromosoma.

TABELA III

Resultados obtidos com meio quìmicamente definido para D. willistoni contendo 13 aminoácidos indicados na Tabela I — 25°C

Linhagem número	N.° orig. de larvas	% de pupas	Tempo médio em dias p/ pupação	% de adultos
Selvagem *)	120	60,0	9,6	88,8
"	120	70,8	9,3	70,9
"	160	68,7	9,6	69,0
"	180	60,0	9,5	88,9
"	180	61,6	13,0	78,3
Homozigotos				
141	117	33,3	13,7	74,3
8	104	5,8	16,0	66,7
8	110	7,3	14,8	75,0
7	124	26,6	14,2	75,7
220	123	22,7	13,7	78,6
38	119	50,8	18,6	66,7
15	120	45,8	23,4	67,3
212	119	5,0	22,7	100,0**)

*) Êste dado indica apenas que tôdas as pupas desenvolveram adultos.

**) Linhagens originadas de fêmeas coletadas na natureza e não analisadas genèticamente.

As linhagens homozigotas D8 e D212, principalmente, poderiam ser consideradas portadoras de "mutações metabólicas" devido à sua decidida incapacidade de se desenvolverem no meio sintético. Disso decorre a existência de uma provável herança de diferenças bioquímicas oriundas de deficiências nutricionais em conseqüência da condição de homozigose.

Embora numerosos experimentos tenham sido realizados, os resultados conseguidos não foram de êxito durante o trabalho de modo a permitir identificar necessidades nutricionais específicas de tais linhagens. Nestes experimentos além de variar individualmente a concentração de diferentes substâncias incluídas na dieta da tabela I fo-

ram ainda adicionados em outras experiências as substâncias que aparecem abaixo com as quantidades usadas. Isto na tentativa de identificar alguma mutação metabólica.

	mg/ml
Resíduo de fermento C,	2,0
Resíduo de fermento C,	2,0
Piridoxamina	0,003
Piridoxal	0,003
Glutatião	0,4
Betaina	1,7
Ác. cisteico	0,5
Citrulina	18,0
Homocistina	0,4
Homoscrina	1,26
Sarcosina	1,7
Quinurenina	1,7

Até agora o que se conseguiu foi a acentuada incapacidade de estas Drosophilas se desenvolverem em meio de cultura quìmicamente definido.

V

CONCLUSÕES E SUMÁRIO

1. Teve-se em mira determinar um meio sintético asséptico que possibilite o desenvolvimento de largas de *D. willistoni*.
2. Descreveu-se uma técnica especial para coletar ovos de *D. willistoni*.
3. No meio sintético asséptico determinado experimentou-se a viabilidade de linhagens de *D. willistoni* homozigotas para o II cromosoma.
4. Linhagens que decididamente não se desenvolveram neste meio foram consideradas como portadoras de "mutações metabólicas".

VI

SUMMARY

1. A chemically defined medium for raising *D. willistoni* in asceptic conditions is formulated.

2. Special technique for collecting *D. willistoni* eggs is described.
3. On the basis of this medium II chromosome homozygous strains of *D. willistoni* were tested for viability.
4. Strains that consistently failed to grow in this medium were described as carriers of "metabolic mutants".

VI

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ALGUMAS ASCÍDIAS DO LITORAL SUL DO BRASIL

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I — INTRODUÇÃO

Durante meu estágio no Laboratório de Biologia Marinha de São Sebastião (L.B.M.), por sugestão do Prof. Dr. Paulo Sawaya, venho coletando, sistemàticamente, exemplares representativos da fauna local, tendo sido encarregado do estudo das ascídias (Sub-phylum *Tunicata,* Classe *Ascidiacea*).

No intuito de alargar o conhecimento sôbre a distribuição geográfica dêstes animais realizei, em outubro de 1961, uma excursão ao sul do país, tendo assim oportunidade de acrescentar à coleção do L.B.M. novos espécimes obtidos na Ilha de Florianópolis e nas proximidades da Ponta de Garopaba, um pouco mais ao sul.

Darei a seguir a descrição das espécies coletadas, uma das quais tenho por nova. Ao tratar de cada espécie darei os caracteres não mencionados ou que são diferentes dos descritos, para as mesmas, na bibliografia.

Na citação bibliográfica de cada espécie indico apenas a bibliografia principal. Vali-me principalmente da monografia de Van Name (1945) e do trabalho de Millar (1958) sôbre ascídias do Brasil.

Como se verá, a distribuição das espécies estende-se mais ao sul do que a assinalada na literatura.

Seja lembrado que os Ascidiacea do litoral sul do Brasil foram objeto de considerações também por Luederwaldt (1929), Moure, Björnberg e Loureiro (1954) e Börnberg (1956).

II — DESCRIÇÃO DAS ESPÉCIES

Família *Synoicidae* Hartmeyer, 1908.
Gênero *Polyclinum* Savigny, 1816.

Polyclinum constellatum Savigny, 1816.

Van Name, 1945, p. 68-70, f. 28, pr. 13, f. 1-2.
Millar, 1955, p. 176, f. 7, 1958, p. 498.

Distribuição geográfica.

Ampla através das regiões quentes. No Brasil esta espécie foi encontrada no Rio de Janeiro, Santos (registro não publicado) e em Cananéia.

Localidades.

S. Sebastião (Praia de Barequeçaba). Zona litoral média. Sôbre rochas de superfície relativamente lisa, em local de pouca profundidade, entre a faixa de cirripédios do gênero *Tetraclita* e a areia do fundo.

A presença de numerosos grãos de areia e grânulos fecais na superfície do manto, entre os orifícios dos zooides, empresta à colônia um aspecto pardo esverdeado, tornando-a fàcilmente confundível com uma saliência de rocha.

Discussão.

A estrutura dos zooides concorda com a espécie, porém o arranjo dos mesmos é menos nítido, como também observou Millar (1958, p. 498). Nas colônias observadas em setembro constatei a presença de embriões.

Família *Didemnidae* Verrill, 1871.
Gênero *Didemnum* Savigny, 1816.

Didemnum candidum Savigny, 1816.
Van Name, 1945, p. 83-86, f. 35, pr. 3, f. 4.

Distribuição geográfica.

Mares tropicais e mesmo subtropicais do Novo e do Velho Mundo. No Brasil foi assinalada na Bahia, Cananéia e Paranaguá.

Localidades.

São Sebastião, até 7 m de profundidade, sôbre a superfície de rochas ou envolvendo corais (*Telesto sp.*) e tubos de poliquetos (*Daschone sp.*), Florianópolis e Garopaba, zona litoral, sob pedras em reentrâncias mais protegidas do costão.

As colônias apresentam colorido variando de branco muito puro, homogêneo, a levemente leitoso, com manchas de fraca transparência.

Discussão.

O material analisado concorda com as descrições de Van Name e também com as observações de Moure, Björnberg e Loureiro (1954, p. 235, 236) para exemplares da Baía de Paranaguá.

Gênero *Polysyncraton* Nott, 1892.

Polysyncraton amethysteum Van Name, 1902.

Polyncraton amethysteum Van Name, 1902, p. 366, pr. 54, f. 62, 64-67; pr. 58, f. 102.

Didemnum (*Polysyncraton*) *amethysteum* Van Name, 1945, p. 95, 96, f. 41; pr. 18, f. 3.

Polysyncraton amethysteum Pérès, 1948.

Polysyncraton amethysteum Millar, 1953, p. 298-300, f. 11; 1958, p. 499, 500.

Didemnum (*Polysyncraton*) *amethysteum* Moure, Björnberg e Loureiro, 1954, p. 236 e 237.

Distribuição geográfica.

Bermudas, Caribe, Senegal, Costa do Ouro. No Brasil foi assinalada em São Sebastião, Rio de Janeiro e Cananéia.

Localidades.

São Sebastião e Garopaba. "Habitat" idêntico ao da espécie anterior.

Colônia incrustante, medindo 6 a 12 cm. Colorido vermelho arroxeado vivo, notadamente ao redor dos orifícios atriais; no restante apresenta-se mais pálido, devido à finíssima pontuação esbranquiçada resultante de pequenas espículas, quase esféricas, notadamente abundantes no folheto superficial da túnica comum.

Zoóides apresentando orifício branquial com seis lobos pouco pronunciados, lingueta atrial bem desenvolvida, quatro fileiras de estigmas e musculatura torácica forte.

No abdome, sôbre a porção inferior da alça intestinal ascendente, encontram-se os testículos formados por quatro lobos piriformes. Ducto espermático espiralado em quatro voltas frouxas. Ovário simples, com poucos óvulos, sendo os maduros de grande tamanho e superiormente situados.

Discussão.

Êstes exemplares não concordam inteiramente com os de Van Name, divergindo quanto ao tamanho das colônias, que, no presente caso, são um pouco maiores.

Família *Clavelinidae* Forbes e Hanley, 1848.
Gênero *Clavelina* Savigny, 1816.

Clavelina oblonga Herdman, 1880.
Herdman, 1882, p. 246, pr. 35, f. 6-10.
Van Name, 1945, p. 136-138, f. 63, 64, pr. 16, f. 6.

Distribuição geográfica.

Índias Ocidentais, África Ocidental. Nas costas do Brasil foi assinalada em Niterói, Ubatuba, São Sebastião.

Localidades.

Florianópolis (Baía Sul, Ilha das Vinhas), local protegido, de pouca profundidade e em substrato rochoso; São Sebastião (Praia do Araçá), zona litoral inferior sôbre rochas ou tubos de *Chaetopteras* sp.

Examinados com vida os zoóides apresentam aspecto característico: túnica perfeitamente transparente, corpo com pequenas má-

culas de pigmento branco na cesta branquial e região abdominal amarelada.

Discussão.

Esta espécie foi freqüentemente confundida com *Clavelina picta* (Verrill), 1900, também assinalada no Brasil. Os trabalhos de Berrill (1932, p. 84) permitem a distinção entre as duas espécies.

Família *Perophoridae* Giard, 1872.
Gênero *Perophora* Wiegmann, 1835.

Perophora bermudensis Berrill, 1932.
Berrill, 1932, p. 78-82, f. 3 a.
Van Name, 1945, p. 167, 168, f. 81 a, 82 e, 84.
Millar, 1958, p. 501, 502.

Distribuição geográfica.

Índias Ocidentais. No Brasil a espécie foi assinada em Cananéia.

Localidade.

Florianópolis. Zona litoral superior, em local de pouca profundidade, sôbre conchas de moluscos do gênero *Crepidula* e *Ostrea,* ou envolvendo a base de talos de algas de gênero *Codium*.

Discussão.

Colônias pequenas, apresentando de 10 a 20 zoóides bem isolados, com a 2 a 2,5 mm no maior diâmetro. Os exemplares examinados não se encontravam maduros.

Família *Ascidiidae* Herdman, 1880.
Gênero *Ascidia* Linnaeus, 1767.

Ascidia nigra (Savigny), 1816.
Van Name, 1945, p. 184-186, f. 98, pr. 15, f. 1 e 2.
Kott, 1952, p. 305, 306.

Distribuição geográfica.

Índias Ocidentais, Mar Vermelho, Gôlfo de Aden, Gôlfo de Guiné, Austrália. No Brasil a espécie foi assinalada no Rio de Janeiro, Ubatuba e São Sebastião.

Localidade.

São Sebastião. Rochas de ambos os lados do canal, até 10 m de profundidade.

Discussão.

E' seguramente a espécie mais comum dessa região, podendo ser encontrada, com facilidade, durante todo ano.

Ascidia sydneiensis Stimpson, 1855.

Figuras 1, 2, 3 e 4.

Van Name, 1945, p. 188-190, f. 101.
Kott, 1952, p. 310-312, f. 173.
Millar, 1955, p. 190, f. 18.

Distribuição geográfica.

Bastante ampla através das regiões tropicais. No Brasil foi encontrada em Ubatuba, São Sebastião e Santos.

Localidades.

São Sebastião (Praia do Araçá, Praia do Segrêdo), sob e sôbre rochas até 7 m; Florianópolis (Baía Sul, Ilha das Vinhas), rochas à pouca profundidade (0,5 a 1,5 m).

Corpo alongado, sifões de tamanho variável, comumente longos. O branquial, superiormente situado, o atrial emergindo aproximadamente da região mediana do corpo. Abertura branquial com 6 ou 8 lobos, atrial com 6. Tamanho máximo dos exemplares examinados: 40 a 50 mm.

Musculatura formando anéis nítidos ao redor das aberturas. Lado esquerdo do corpo quase completamente destituído de músculos. Lado direito com faixas musculares nas margens, formando um traçado paralelo que deixa a porção central nua.

Tentáculos em número de 80 a 90, dispostos em várias ordens.

Cesta branquial com cêrca de 35 vasos longitudinais de cada lado e vasos transversais dispostos em 4 ordens. Papilas finas e recurvadas.

Tubérculo dorsal de abertura irregular, por vêzes com desenho complicado.

Intestino formando uma grande bôlsa na região subterminal, freqüentemente muito dilatada, determinando visível saliência no lado esquerdo do animal.

Discussão.

A musculatura, o grande número de tentáculos e a forma do tubérculo dorsal caracterizam fàcilmente a espécie. Porém, o aspecto menos comum dos sifões e do intestino levaram-me a descrever mais pormenorizadamente o exemplar.

Família *Botryllidae* Verrill, 1871.

Gênero *Botryllus* Gaertner, in Pallas, 1774.

Botryllus tabori sp. n.

(Figuras 8, 9, 10 e 11)

Diagnose.

Orifício cloacal formando sifão bem nítido, comumente longo. Oito tentáculos. Nove fileiras de estigmata. Estômago com nove pregas glandulares e ceco pilórico muito longo, dobrado em ângulo reto. Um ou dois óvulos dorsalmente situados em relação aos testículos. Anus bilobado.

Localidade.

São Sebastião: Praia do Araçá, zona litoral, uma colônia sôbre talo de *Padina* sp. (20-X-1961), duas colônias envolvendo tubos de poliquetos do gênero *Dasichone* sp. (10-IX-1961); Praia do Segrêdo, três colônias sob rochas, nível mínimo absoluto de maré (9-IX-1961).

Aspecto da Colônia.

Colônias pouco espêssas, incrustantes, apresentando as menores sistemas regulares elipticos e alongados com 5, 17 e 28 zoóides nos

exemplares examinados; as maiores possuem grande número de zoóides agrupados em sistemas menos regulares, ramificados, semelhantes aos de *Botryllus planus* (Van Name).

Coloração.

Róseo violécea homogênea. Ampôlas marginais numerosas, pequenas e de coloração idêntica ao restante da colônia. Em material fixado em formol a coloração muda para amarelo pardacento ou amarelo esverdeado.

Zoóides.

Tamanho variando de 1 a 1,5 mm no máximo. Musculatura pouco nítida, quase invisível. Abertura branquial circular, atrial projetando-se em um sifão de tamanho variável, às vêzes muito longo, levemente recurvado.

Tentáculos.

Oito de igual tamanho em exemplares adultos.

Cesta branquial.

Apresentando 3 vasos longitudinais, 8 fileiras de fendas branquiais. Em cada fileira da região anterior da cesta branquial as fendas estão assim distribuídas:

E 4 v 2 v 2 v 4 L D.

Aparelho digestivo.

Esôfago curto. Estômago alongado, um pouco mais dilatado na região cardíaca, apresentando 9 pregas glandulares e 1 ceco pilórico longo, curvado em ângulo reto e tocando o intestino. O ângulo formado pelo ceco determina um plano perpendicular ao dos vasos longitudinais. Intestino formando uma alça que passa junto ao esôfago. Anus bilobado.

Aparelho genital.

Testículos subdivididos em aproximadamente 12 lobos nítidos, formando inclusive massas isoladas. Ovários um de cada lado, com 1 ou 2 óvulos e situados dorsalmente em relação aos testículos.

Discussão.

Quanto ao aspecto do sifão cloacal os exemplares assemelham-se a *Botryllus primigenus* Oka, mas diferem dêste pelo maior número de fileiras de fendas branquiais, pois a espécie descrita por Oka apresenta 4 fileiras de fendas e a que agora descrevemos possui 9.

O aspecto geral da colônia e o comprimento do ceco pilórico lembram *Botryllus planus* (Van Name), porém o número de fileiras de fendas branquiais é mais elevado em *Botryllus planus* (11 a 13), além desta espécie possuir um único óvulo de cada lado, ao passo que a presentemente descrita pode possuir 2.

Dedico esta nova espécie ao Prof. A. A. Tabor, meu primeiro professor de Zoologia.

Gênero *Botrylloides* Milne Edwards, 1841.

Botrylloides nigrum Herdman, 1886.

(Figuras 5, 6 e 7).

Herdman, 1886, p. 50, pr. 1, f. 8; pr. 3, f. 19-21.
Van Name, 1945, p. 227-229, f. 133 c, 137.
Kott, 1952, p. 257, f. 73, 74.

Distribuição geográfica.

Bermudas, Índias Ocidentais, África e Austrália. Espécie não assinalada até agora na América do Sul.

Localidades.

São Sebastião (Praia do Araçá), zona litoral. Neste local a espécie é muito comum. As colônias crescem em substratos variáveis, tais como outras ascídias (*Styela plicata* e *Clavelina oblonga*), talos de algas (*Padina* sp.), tubos de poliquetos (*Dasichone* sp.) e caules de Monocotiledôneas marinhas da ordem Helobiae. Florianópolis (Baía Sul, Ilha das Vinhas), zona litoral média, sôbre colônia de *Clavelina oblonga*.

Colônias de tamanho relativamente grande: 3,5 a 5 cm no diâmetro maior. Número de zoóides muito elevado, dispostos em siste-

mas irregulares e alongados. Em colônias pequenas alguns sistemas regulares podem ser observados apresentando, aproximadamente, 12 zoóides em tôrno de uma cavidade cloacal comum.

Coloração muito nítida e constante em tôdas as colônias examinadas. Os zoóides apresentam-se de côr marron arroxeado bem escuro com um anel amarelo gema alongado ao redor do orifício branquial. Em exemplares fixados em formol a coloração muda para marron escuro quase negro e os zoóides destacam-se fàcilmente da túnica comum.

Comprimento dos zoóides: 1,5 a 2 mm. Vista superior, com a lingueta dorsal expandida, de aproximadamente 2 mm.

Tentáculos em número de 8, sendo 4 mais desenvolvidos.

Cêsta branquial com 10 ou 11 fileiras de estigmas. Lâmina (goteira) dorsal plana.

Estômago grande, dilatado na região do esôfago e afunilado na região pilórica, apresentando 8 a 9 pregas glandulares e um ceco curto, capitado.

Aparelho genital formado por ovários grandes, um de cada lado, com um único óvulo e situados posteriormente em relação aos testículos. Êstes encontram-se aderidos aos ovários e possuem 6 a 7 lobos bem delimitados dando a impressão de massas isoladas.

Os exemplares coletados de julho a setembro possuiam embriões.

Família *Styelidae* Sluiter, 1895.
Gênero *Symplegma* Herdman, 1886.

Symplegma viride Herdman, 1886.
Herdman, 1886, p. 144, pr. 18, f. 7-14.
Berrill, 1932, p. 78, 86, 88, f. 5.
Van Name, 1945, p. 232-234, f. 139, 140, pr. 18, f. 2.
Kott, 1952, p. 252-253, f. 68 e 69.

Distribuição geográfica.

Índias Ocidentais, África, Mar Vermelho, Oceano Índico, Filipinas, Austrália. No Brasil a espécie foi assinalada no Rio de Janeiro, Ubatuba e Santos.

Localidades.

São Sebastião (Praia do Araçá, Praia Grande, Praia do Segrêdo). "Habitats" diversos.

Discussão.

A estrutura das gônadas, a presença de 4 vasos longitudinais e 11 a 12 fileiras de fendas branquiais caracterizam a espécie.

Analisando o material coletado, pudemos observar a presença de 3 agrupamentos distintos que diferem entre si não só pela aparência e colorido, como também pelas características morfológicas e ecológicas. Êstes agrupamentos parecem apresentar isolamento nítido, mas, para considerá-los como variedades, creio serem os dados ainda insuficientes, além dessa espécie ser, por excelência, muito variável.

Gênero *Polyandrocarpa* Michaelsen, 1904.

Polyandrocarpa maxima Sluiter, 1904.
Van Name, 1945, p. 244, 245, f. 146.

Distribuição geográfica.

Filipinas, Ilha de Salibabú e Flórida. No Brasil a espécie já havia sido assinalada em São Sebastião.

Localidade.

São Sebastião (Praia de Baraqueçaba), sôbre rochas, a 1,5 m de profundidade. Uma única colônia coletada em 8-IX-1960.

Discussão.

Para confirmar melhor a identificação comparamos o presente exemplar com os coletados por Luederwaldt, determinados por Van Name, e que se encontram atualmente nas coleções do Museu Paulista.

Polyandrocarpa zorritensis (Van Name), 1935.
Stolonica zorrientensis Van Name, 1931, p. 218, f. 6.
Polyandrocarpa zorritensis Van Name, 1945, p. 245-247, f. 147.
Polyandrocarpa zorritensis Millar, 1958, p. 505-507, f. 5.

Distribuição geográfica.

Perú, África do Sul (?), Austrália (?). No Brasil a espécie foi assinalada em Santos e Cananéia.

Localidade.

São Sebastião (Praia do Araçá). Zona litoral inferior. Sôbre tubos de poliquetos (*Dasichone* sp.).

Discussão.

Os exemplares examinados concordam com as descrições de Van Name, salvo pela presença de um pequeno ceco pilórico no estômago, fato aliás já observado por Millar (1958). Duas espécies muito semelhantes à *P. zorritensis* foram descritas: *P. durbanensis* Millar da África e *P. australiensis* Kott da Austrália. E' possível que as três espécies sejam sinônimas, porém não há ainda evidência suficiente para elucidar a questão.

Gênero *Polycarpa* Heller, 1877.

Polycarpa spongiabilis Traustedt, 1883.
Traustedt, 1883, p. 125-134, pr. 5, f. 9.
Van Name, 1945, p. 259-261, f. 157, pr. 19, f. 3.

Distribuição geográfica.

Flórida e Pôrto Rico. Traustedt (1883) dá como referência simplesmente Índias Ocidentais e Brasil.

Localidade.

Florianópolis (Baía Sul, Ilha das Vinhas), substrato rochoso, 0,5 a 1,5 m de profundidade.

Corpo globoso, com 4 a 5 cm de comprimento. Túnica marron côr de terra. Metade inferior incrustada por material estranho. Metade superior e sifões de aspecto fibroso, livre de incrustações, salvo pela presença de moluscos bivalvos, muitas vêzes profundamente mergulhados na túnica. Orifícios aproximadamente quadrangulares e não contraídos nos exemplares fixados em formol.

Discussão.

Esta espécie, quanto à morfologia interna, assemelha-se bastante à *P. obtecta* Traustedt, 1883, porém a aparência externa fornece as melhores indicações para sua separação.

Gênero *Styela* Fleming, 1822.

Styela plicata (Lesueur), 1823.
Van Name, 1945, p. 295-298, f. 192-194.
Moure, Björnberg e Loureiro, 1954, p. 238, 240.

Distribuição geográfica.

Ampla através de tôdas as regiões quentes do globo. No Brasil foi assinalada em Niterói, Santos, Paranaguá.

Localidades.

São Sebastião (Pràia do Araçá, Pitangueiras e Cabelo Gordo). Florianópolis (Baía Sul, Ilha das Vinhas).

Observações.

A espécie é muito abundante em São Sebastião, principalmente na Praia do Araçá, local de pouca profundidade, ficando a descoberto com as marés de lua cheia e lua nova. Apresenta-se em grupos ou isoladamente, sôbre substratos variáveis: superfície de rochas, fragmentos de conchas, talos de algas, tubos de poliquetos sedentários (*Dasichone* sp., *Chaetopterus* sp.) ou simplesmente o lôdo do fundo.

Em outras praias da mesma região (Pitangueiras, Cabelo Gordo) a espécie ocorre em nível mais inferior, podendo ser encontrada nas rêdes dos pescadores.

Família *Pyuridae* Hartmeyer, 1908.
Gênero *Herdmania* Lahille, 1887.

Herdmania momus (Savigny), 1816.
Van Name, 1945, p. 341-344, f. 225-226.
Kott, 1952, p. 279-283, f. 123-129.

Distribuição geográfica.

Ampla através dos mares quentes do globo. No Brasil foi assinalada no Rio de Janeiro e Ubatuba.

Localidade.

São Sebastião. Zona litoral inferior.

Discussão.

Esta espécie é fàcilmente reconhecida pela presença de espículas alongadas na superfície do revestimento muscular, e, até mesmo, nos órgãos internos do animal.

Nos arredores do Laboratório de Biologia Marinha (São Sebastião) a espécie ocorre na superfície ou reentrâncias de rochas, no mínimo de maré, só ficando a descoberto, via de regra, pelas grandes marés de setembro.

Encontra-se comumente em associação com outras ascídias simples (*Ascidia sydneiensis, Microcosmus exasperatus*) e coloniais (*Simplegma viride, Didemnum candidum*), como também com poliquetos da família Sabellidae e Terebelidae.

Gênero *Microcosmus* Heller, 1878.

Microcosmus exasperatus Heller, 1878.
Van Name, 1945, p. 346-349, f. 230, 231, pr. 16, f. 3.
Millar, 1955, p. 210, 211, f. 35.

Distribuição geográfica.

Ampla através das regiões quentes do globo. No Brasil a espécie foi assinalada em Santos e São Francisco do Sul.

Localidades.

São Sebastião (Praia do Araçá, Pitangueiras e Praia do Segrêdo) sôbre rochas, tubos de *Chaetopterus* sp. ou o lôdo do fundo, até 6 m de profundidade. Florianópolis (Baía Norte e Baía Sul, Ilha das Vinhas), rochas a 0,5 m de profundidade.

Discussão.

Parece haver relação entre o aspecto geral e o habitat. Exemplares coletados a pequena profundidade apresentam coloração violeta suja, com incrustação de material estranho; os recolhidos a mais de 3 m têm túnica avermelhada, mais lisa e quase sem incrustação.

III — CONSIDERAÇÕES ZOOGEOGRÁFICAS

Tendo em vista a distribuição geográfica indicada, reuni no quadro abaixo as espécies por mim encontradas, a saber:

Espécies	*São Sebastião*	*Florianópolis*	*Índias Ocidentais*	*África Tropical*	*outras ocorrências*
P. constellatum	*		*		outros mares tropicais
D. candidum	*	*	*	*	outros mares tropicais
P. amethysteum	*	*	*	*	——
C. oblonga	*	*	*	*	——
P. bermudensis		*	*	(?)	——
A. nigra	*		*	*	outros mares tropicais
A. sydneiensis	*	*	*	*	outros mares tropicais
B. tabori	*				——
B. nigrum	*	*	*	*	Austrália
S. viride	*		*	*	outros mares tropicais
P. maxima	*		*		Filipinas
P. zorritensis	*			(?)	Peru. Austrália (?)
P. spongiabilis		*	*		——
S. plicata	*	*	*	*	outros mares tropicais
H. momus	*		*		outros mares tropicais
M. exasperatus	*	*	*	*	outros mares tropicais

Analisando o quadro podemos observar que, com exceção de *P. zorritensis,* tôdas as espécies assinaladas tanto em São Sebastião como em Florianópolis pertencem à fauna da região das Índias Ocidentais, ou são comuns a essa fauna e à da região Tropical Africana Ocidental.

Como se sabe, a região faunística das Índias Ocidentais — ou Região Atlântica Tropical Americana — abrange as Ilhas das Bermudas, a costa da Flórida, o Gôlfo do México, as Ilhas do Caribe e estende-se para baixo, ao longo da costa atlântica da América do Sul, até onde predominam as condições tropicais. O limite sul desta região foi, de início, freqüentemente considerado como sendo Cabo Frio, Estado do Rio de Janeiro. Porém, essa zona não constitui, aparentemente, barreira zoogeográfica para os tunicados do bentos litoral, pois tôdas as ascídias encontradas em São Sebastião e Florianópolis são espécies tìpicamente tropicais. Van Name (1945), em sua importante monografia sôbre as ascídias das Américas, julgou ser possível estender o limite sul até Santos, Estado de São Paulo, e os dados de Björnberg (1956) e Millar (1958) permitem levá-lo até Cananéia, ainda no Estado de São Paulo. As minhas observações, feitas com base no material coletado, permitem prolongar o limite da referida região faunística, pelo menos para os Ascidiacea, até Florianópolis, pois tôdas as 9 espécies examinadas pertencem à fauna das regiões tropicais. Estas 9 espécies são aqui registradas pela primeira vez na região de Florianópolis, sendo que uma delas é também pela primeira vez indicada para a América do Sul.

Finalmente, cumpre ainda assinalar que, ao sul do Estado de São Paulo, registram-se apenas 3 espécies na Baía de Paranaguá (Moure, Björnberg e Loureiro, 1954) e 2 na Ilha de São Francisco do Sul (Van Name, 1945). Para a região de Florianópolis a Garopaba não existem, pois, referências bibliográficas.

IV — SUMMARY

1 — A group of sixteen species of ascidians is described from the shores of São Sebastião (Estado de São Paulo) and Florianópolis (Estado de Santa Catarina). One species is new to science and another (*Botrylloides nigrum*) is first recorded from South America.

2 — The new species (*Botryllus tabori*) has the chiefly following characteristics: atrial opening projeting in siphon often long (like *B. primigenus* Oka); 8 tentacles and 9 rows of stigmata in adult zooids; stomach with about 9 glandular folds almost indistinct and a long pyloric caecum resembling that of *B. planus* (Van Name), but curved in right angle; ovary with 1 or 2 eggs dorsal to the testis; anal border with two lips.

3 — This is the first collection of ascidians from Florianópolis (27° 40' lat. S. — 49° 35' long. W.). Its characteristics supports the indication that the tropical conditions are prevailing in that place.

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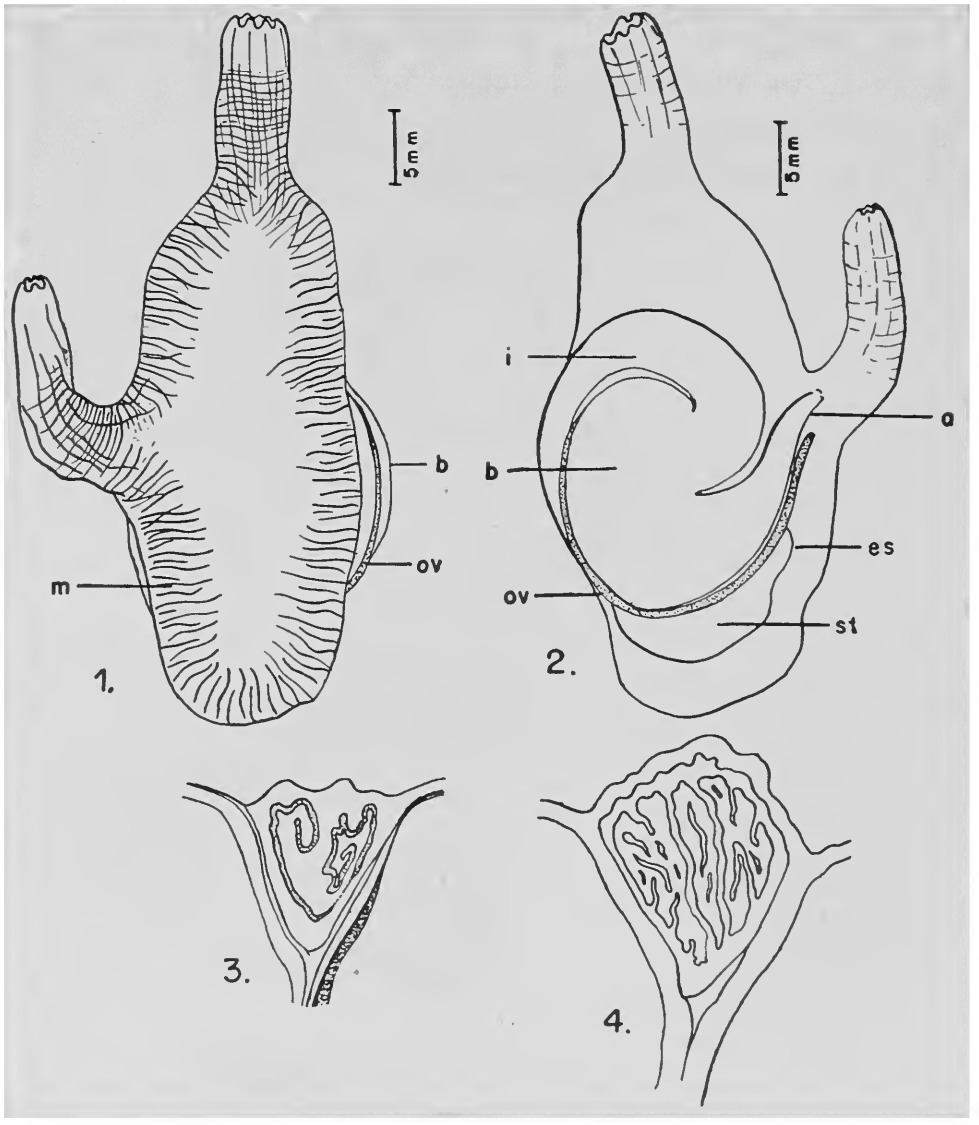
ABREVIATURAS UTILIZADAS NAS PRANCHAS

a — anus.
an — anel amarelado.
b — bôlsa intestinal.
c — ceco pilórico.
cb — cesta branquial.
es — esôfago.
ld — lingueta dorsal.
i — intestino.
m — musculatura.
ov — oviduto.
p — pregas glandulares.
sc — sifão cloacal.
st — estômago.
t — tentáculos.

PRANCHA I — *Ascidia sydneiensis* Stimpson

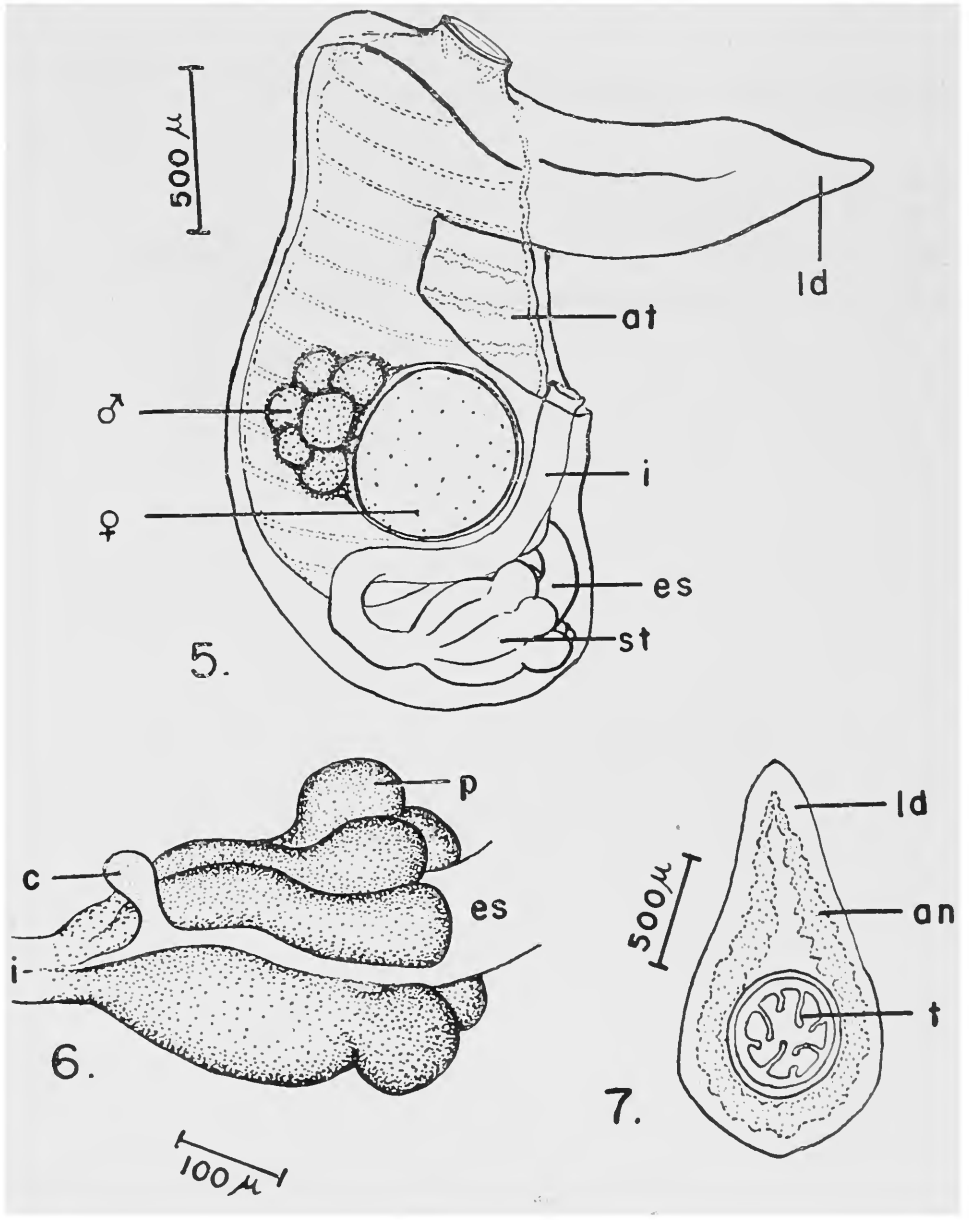
Fig. 1 — Lado direito do corpo.
Fig. 2 — Lado esquerdo do corpo.
Fig. 3 — Tubérculo dorsal de um exemplar jovem.
Fig. 4 — Tubérculo dorsal do exemplar representado nas figs. 1 e 2.

Sérgio A. Rodrigues — Ascídias do Litoral Sul do Brasil — Est. 1 — Fig. 1-4



PRANCHA II — *Botrylloides nigrum* Herdman

Fig. 5 — Vista lateral de um zoóide.
Fig. 6 — Estômago.
Fig. 7 — Vista superior de um zoóide.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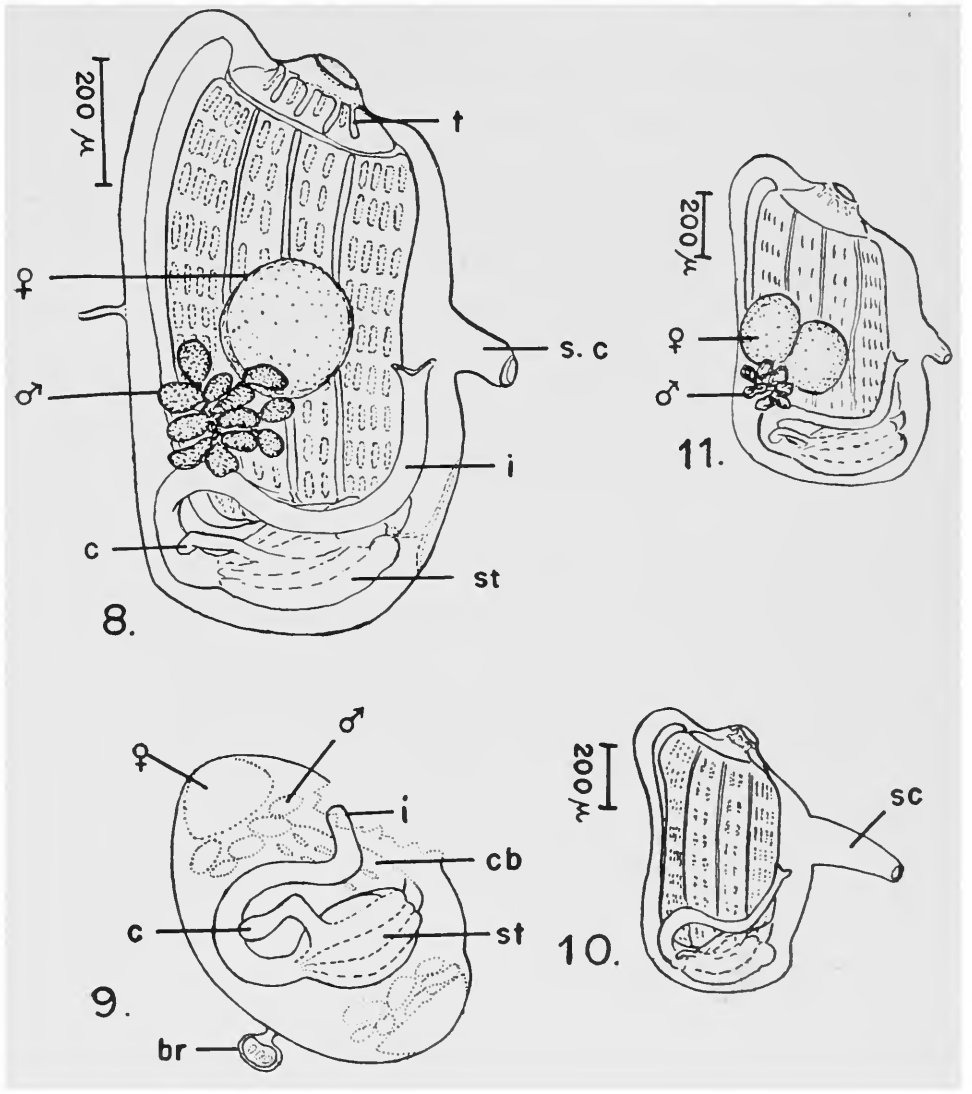
PRANCHA III — *Botryllus tabori* sp. n.

Fig. 8 — Vista lateral de um zoóide.
Fig. 9 — Vista inferior de um zoóide.
Fig. 10 — Exemplar com sifão cloacal bem pronunciado.
Fig. 11 — Exemplar apresentando dois óvulos.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ON UNCANCYLUS TICAGUS

by EVELINE and ERNST MARCUS

(with 4 plates)

Contents

Numerous ancylids in an aquarium of our Department, to which our attention was called by Docent Dr. Claudio G. Froehlich, belong to *Uncancylus* Pilsbry, 1914. As the anatomy with exception of two radulae is not known of any representative of this genus (Hubendick 1955, p. 319-320), we studied the species. It does not agree completely whith any of the previously described ones and is therefore considered as new and called *Uncancylus ticagus* sp. n. It can be shortly characterized as follows: Length of shell up to 6,5 mm; cephalic lobes distinct; tentacles long. Shell oval, translucent, nacreous; apex between second and last third and mid-line and right margin, minutely pitted, with flattened top. Posterior shell muscle to the left. Mantle with 3 fields of dark pigment cells. Pallial cavity and its aperture large. Infrapallial lobe with retractor and small dorsal and big ventral branchial appendage; anus between them. Concentration of ganglia varies individually. Bow of separate mandibular lamellae surrounding antero-dorsal plate. Radula with tricuspid laterals and asymmetrical principal cusps of central. Ejaculatory duct terminates with small penial papilla. Duct of bursa immediately inside female aperture. Together with the holotype, a 4,5 mm long snail in alcohol, further preparations are kept in the Department of Zoology, Faculty of Philosophy, Sciences and Letters of the University of São Paulo.

1. SYSTEMATIC DISCUSSION

The system of the Ancylidae is still largely based on characters of the shell, but these are variable (Hoff 1940, p. 224). *Hebetancylus moricandi* (d'Orb.) for example has a broad shell and *H. ploecarius* (Bgt.) a narrow one. The extremes are connected by intermediate forms, and broad-shelled and narrow-shelled snails occur at the same locality in Ceará (Haas 1939, p. 267) Therewith Walker's supposition that *moricandi* and *ploecarius* are individual variations is proven. A pitted apex appears in slightly eroded shells of species of *Uncancylus,* while perfect shells of the same species may have smooth apices (Pilsbry 1925, p. 58, note 10). As Connolly (1939) considered nature and area of the apical sculpture as of primary importance in specific determination of the Ferrissiinae, eroded specimens cannot be classified. In a collection of numerous animals from different places a purely conchological separation of the species (Biese 1949, p. 217-236) may be possible. But a systematization according to the localities whence the specimens proceed is impossible, because ancylids are known to be transported adherent to the elytra of water beetles (Hesse 1924, p. 56; Allan 1950, p. 411-412; Fischer 1950, p. 65; Buttner 1953), and possibly together with mud on the feet of aquatic birds. Baker (1945, p. 40) explained the spreading of some planorbids from the West Indies into South America by "avian dispersal". Also Boettger (1932, p. 273; 1951, p 78; 1954a, p 35) supposed transportation of *Potamopyrgus jenkinsi* (E. A. Smith) by birds.

The insufficiency of the shell for the taxonomy of the Ancylidae became evident when Haas (1955, p. 8) allocated material from Lake Titicaca to *Anisancylus* Pilsbry (1925, p. 8) due to the shells. The subsequent study of the radulae (Hubendick 1955a, f. 44, 52) however revealed their incompatibility with the radula of the genotype (Pilsbry 1925, f. 6).

Hebetancylus and *Uncancylus,* genera or subgenera of *Ancylastrum,* were characterized by their shells (Pilsbry 1914, p. 671, note 6). The apex of the first was described as obtuse, rounded, that of the latter as acute. Also further indications (Pilsbry 1925, p. 57, 58; Thiele 1931, p. 483), the rather large, thin and longish-oval shell

of *Hebetancylus* and the small one in *Uncancylus,* are gradual and are difficult to interpret (Hoff 1940, p. 224). According to Scott (1954) *Hebetancylus* is a synonym of *Gundlachia.*

Without Baker's drawings of the radulae of two species of *Uncancylus* (Pilsbry 1921, f. 5; 1925, f. 7; Walker 1925, figure on p. 3) we hardly would have recognized our species as belonging to this genus. For specific separation conchological characters cannot be avoided yet, because the radula is only known of *U. leucaspis* (Anccy, 1901) from Mato Grosso and the State of Rio de Janeiro, Niteroi and Pernambuco (Walker 1925, p. 2; van Benthem Jutting 1943, p. 484), and of *U. calverti* Pilsbry (1921, p. 7) from Costa Rica. The first with an apex depressed towards the tip and slightly S-shaped rows of the radular teeth is evidently nearest to *ticagus,* but differs by its symmetrical principal cusps of the central tooth. In *U. calverti* the left cusp is longer (Baker in Pilsbry 1925, p. 58) as in *ticagus,* but the asymmetry is slighter. Besides the transverse radular rows are nearly straight in *calverti,* and the hooked apex of the shell is acute. The last character separates also the other species of *Uncancylus* (Pilsbry 1921, p. 7-9) from *ticagus.*

The systematic arrangement (Thiele 1931) followed here is obsolete, but makes a survey possible for those who know ancylids from general texts. In the modern system (Wenz &Zilch 1959) the Protancylinae are a subfamily of the Planorbidae (though not in Hubendick 1955b); *Uncancylus, Anisancylus, Hebetancylus* and others belong to the Ferrissiidae; the Ancylidae are restricted to *Ancylus;* the older, dextrally whorled Acroloxidae comprise *Pseudancylastrum* and *Acroloxus.*

2. SHELL (Figs. 1-6)

The shell is fragile, oval, moderately elevated: its height is less than half the breadth. The anterior border is more obtuse, the posterior narrower. The right border is rather straight, the left convex. The apex lies on the limit of the second and last thirds, approximately in the middle between mid-line and right margin. The top of the apex is flattened. The right and posterior slopes are somewhat concave, the left and anterior ones rather convex, but often irregular,

probably due to repairs of lesions. The shell it translucent, but not glossy; the colour is nacreous, with a light brown periostracum.

With low power only the fine concentric growth-rings are seen, with higher power the apex appears pitted (Fig. 3), and in some of the 50 dry shells examined in detail radial lines were seen produced by slight ribs on the inner surface.

Measurements of some shells in mm:

Length	Breadth	Height	Proportion of length to breadth
6,5	5,0	2,0	1,3
6,0	4,2	1,8	1,43
5,8	4,0	1,8	1,43
5,5	4,0	1,5	1,38
5,0	3,5	1,3	1,43
4,1	2,8	—	1,46
3,5	2,5	1,3	1,4
3,0	2,0	1,0	1,5
0,85	0,55	—	1,54

The shell agrees with that of an unnamed ancylid from Lassance, north of Belo Horizonte, Minas Gerais (Walker 1925, p. 6, pl. 1, f. 10-11).

The three shell muscles are visible without removal of the shell (Fig. 19). The biggest is the left, and the smallest the posterior muscle. The left muscle lies a little farther in front than the right one, and the posterior lies to the left (Hubendick 1955, f. 40, 43), not in the middle as in *Ferrissia tarda* (Hoff 1940, f. 2).

Parts of the shell border damaged by manipulation were repaired in the course of two days (21° C.) provisionally.

3. EXTERNAL FEATURES

The creeping snails attain 7,5 mm in length, without the tentacles. When the animal moves, the gill often stands out over the shell, and the pointed tail projects with about 1 mm. Of the 4 mm long tentacles 3 mm appear in front of the shell. The body is rather transparent with yellowish flesh. The muscles of the buccal bulb and gizzard are reddish due to haemoglobin (Pelseneer 1935, p. 156; Carriker 1946, p 36).

Some gland cells of the mantle border contain crystals which are white in reflected light, while others in this region show dark blue contents in transmitted light. This colour disappears in fixed material. In three fields the epithelial cells of the mantle are crowded with purplish black pigment granules (Fig. 19, last phase) which leave the nuclei free, as in the species of *Ancylus* and *Acroloxus* studied by Hubendick (1960, pp. 499, 512-514). The left anterior of these fields emits an anterior and a posterior branch which vanish peripherally, while the corresponding right and the posterior field are concentrated. These pigments do not pass into the shell. The liver of young animals is brown; with age it becomes dark red, violet or purple. The pedal sole has blue or black glands whose colour disappears in fixed material, as that in the mantle skirt. In sections they stain blue with hematoxylin and appear as long tubes which extend far into the tissue of the foot. Into the fold between head and foot the cells of the suprapedal gland (Simroth 1909, pp. 142-143) or anterior pedal mucous gland (Graham 1957, p. 141) open near one another without a common duct. Big melanophores with light nuclei are scattered on the back of the head; sections reveal their submuscular position in the wall of the cephalic cavity.

The head is well separated from the foot and can be withdrawn into the deep fold (x) between mantle and foot beyond the anterior shell muscles. This is the supranuchal cavity of *Lymnaea* (Régondaud 1961, p. 180). The fibres of the cutaneous cephalic muscles concentrate behind forming a strong retractor (h) which originates in the middle of the dorsal mantle surface to the right of the pericardium. In comparison with some other ancylids (Hoff 1940, f 2; Hubendick 1947b, f. 4) the lobes of the head (Fig. 12) and the anterior depression between them are more distinct. The tentacles are very long, nearly as long as the foot; they are pointed and circular in transverse section. Behind the eyes the tentacles are continued backwards forming bulges (j) which bear sensory cells. They correspond to the auricles, foliate appendages or undulate folds of *Ancylus fluviatilis* *) (Moquin-Tan-

(*) Contrary to Boettger (1944) who applies the rules of nomenclature, we follow Hubendick (1947b, p. 142, note 1; 1960) who uses the traditional generic names of *Ancylus fluviatilis* and *Acroloxus lacustris*. Hubendick's argument of the *"Ancylus-sea"* is striking (see also Opinion 363, Comm. Zool. Nomencl. vol. 11, 1955, p. 183-202).

don 1852, p. 12; Lacaze-Duthiers 1899, p. 46), to the pouches of *Protancylus* (Simroth 1909, pp. 210, 215, pl. 8, f. 13, pl. 12, f. 1) and to the sensory lobes or furrows of other basommatophores (Lacaze-Duthiers 1872, p. 448-449, 473, 477). In *Ancylus fluviatilis* such a bulge is developed especially on the left, the genital side (Hubendick 1947b, p. 143). The head ends with broad latero-ventral lobes. The mouth (Fig. 12) lies on the ventral side of the head between small folds, the lips. On the inner border of the lips the lining cuticle of the buccal cavity is strengthened with a single row of about 40 separate broad obtuse mandibular lamellae (ic). These show almost black around the mouth in life, brown in mounts. The bow of lamellae leaves the middle of the hind border free. On the roof of the buccal cavity the cuticle is reinforced and forms a broad, colourless plate (ui) which does not protrude in living snails. A superior median jaw is also mentioned for *Ferrissia tarda* (Hoff 1940, p. 230).

4. PALLIAL CAVITY AND KIDNEY

The pallial cavity (c) and its opening (Fig. 7) are larger than in all other known members of the family. The limits are the anterior and posterior shell muscles (sm) of the left side. The cavity is slit-like and extends a little beyond the mid-line to the right (Fig. 10). The epithelium of roof and floor (diaphragm; Hubendick 1960, p. 501) bears scattered tufts of cilia. The roof has some inconspicuous folds under the pericardium, and in this region a small area of the epithelium (ru) consists of goblet cells of glandular character discharging into the mantle cavity. Remnants of a hypobranchial gland occur in all genera of the Ellobiidae (Morton 1955b, p. 153), while Hubendick (1947a, p. 107-108; 1947b, p. 144, 146) has described differentiations of the connective tissue in the roof of the mantle cavity in lower and higher aquatic pulmonates. Régondaud's recent research (1961) makes it doubtful, whether we may continue to call the respiratory cavity of the Lymnaeaceae a pallial cavity with vestiges of a hypobranchial gland.

Aerial respiration was not recorded for ancylids (Pilsbry & Bequaert 1927, p. 148). It occurs in *Uncancylus ticagus*. In boiled, but also in aquarium water, we saw snails hanging to the surface film take

an air bubble into their pallial cavity. We describe this process in chapter 10.

The kidney (Fig. 7, k, z) lies in the connective tissue of the roof of the pallial cavity. It is for the most of its extension bathed in the arterial blood of the mantle sinus (s) and corresponds fundamentally to the kidney of *Ancylus* and *Acroloxus* (Sharp 1884, p. 236f.). It consists of an excretory (z) and an ureteric (k) portion which Sharp termed saccular and tubular parts. The first appears as a sausage--shaped winding organ. Its high epithelium is generally stuffed with concretions. These are most frequently sulphur-yellow, sometimes white or pink, and rarely bluish green. The wall of the excretory portion is smooth in young snails, while its surface is enlarged by irregular folds in bigger animals. A short canal (eo) whose cilia can be seen beating under favourable conditions connects the excretory part with the left wall of the pericardium (er). The reno-pericardial duct lies on the ventral side of the kidney, approximately in the middle of the organ. From here the kidney curves backwards and to the left, then forwards and to the middle, again to the left, then to the middle, and finally turns backwards. Here the excretory epithelium disappears and is substituted by a flat, smooth epithelium with scattered cilia which line the entire tubular part, the ureter. This emptying duct accompanies the windings of the excretory portion on the left side. A little behind the latter the ureter is dilated into a urinary chamber where the concretions of excretory matter may be seen revolving or are expelled backwards through the renal pore (n). The current produced by the cilia of the pallial cavity carries the excreta outwards.

5. INFRAPALLIAL LOBE

The infrapallial (auriform or anal) lobe (pseudobranchia, gill) begins at the anterior end of the pallial aperture and extends along the whole length of the mantle cavity (c). The inferior border of the latter constitutes the base of the lobe. The rectum (r) runs inside the base along its entire postero-anterior direction, and is surrounded by and ample blood sinus (s); it opens near the anterior end of the lobe. The absence of an anterior lobe shows that the infrapallial lobe at least in *Uncancylus ticagus,* is not specially related with the double

lobe (anal lobe and gill) of the Planorbidae (Hubendick 1947b, p. 156-157). The gill itself is similar in our species with that of the planorbid *Plesiophysa ornata* (Hubendick 1950, f. 5). In young snails the base bears a single, ventrally directed appendage. In older snails the ventral appendage (p) is folded longitudinally, and still later a smaller dorsal, also folded appendage (no) of the base develops. The anus (ar) lies between ventral and dorsal appendage. Number and depth of the folds increase enormously with age. Both appendages have the same structure (Fig. 8), viz. a ciliated epithelium (zi) with scattered gland cells and muscular trabeculae (xa) between the blood lacunae (s). Thus the pseudobranchia of *Uncancylus* resembles the gill of *Acteon* (Perrier & Fischer, 1911, p. 32, fig. H) and other Cephalaspidea. The gill can be contracted by a strong muscle along its anterior border which accompanies the sinus described in the following. The muscle originates from the left anterior shell muscle, divides during its course outwards (rm) and inserts on several branchial folds. The edge of the mantle is underlain by a wide circular blood sinus (s) (Simroth 1912, p. 477, f. 157) which is in front and on the left side broader than behind and on the right side. The muscle fibres of the sinus are similar to the trabeculae of the pseudobranchia; they traverse the sinus obliquely and are in connection with the three shell muscles. These fibres constitute the so-called mantle retractor (Hoff 1940, p. 226, f. 2, mt). When the snail is manipulated with tweezers, the mantle narrows to half its breadth at the spot where the tweezers touch it. The muscle fibres bring about circulation within the mantle sinus, hence act like the trabeculae in the pseudobranchia. Pulsation of the mantle sinus was occasionally seen at the place where the sinus passes to the kidney.

6. HEART AND CIRCULATION

The pericardium (er) lies to the right of the kidney; the auricle to the left of the ventricle (w). The aorta divides soon into two branches, an anterior and a posterior one. They enter the cephalic and visceral cavities which are incompletely separated by the diaphragm, Hoff's "membrane of André" (1940, p. 236). In the head cavity the organs are loosely suspended. The muscles of buccal mass and gizzard are reddish, according to Leydig due to haemoglobin (Pelseneer 1935, p. 156).

Arterial blood supplies the organs of the head, the foot and the viscera. The venous blood passes from the cephalic cavity to the body sinus whose lacunae communicate with the marginal sinus of the mantle in the posterior region, where they are in contact. As the pedal border is richly provided with blood lacunae, a certain oxygenation may take place here. The blood goes from the foot of the peripheral mantle sinus and the perirectal sinus through multiple communications. This intestinal sinus is connected with the mantle sinus at the hind end of the pseudobranchia and in front of the anus on the level of the osphradium (o). Hence the base of the pseudobranchia is supplied with blood from the mantle sinus. The branchial lacunae communicate with the mantle sinus. The blood flows through the lacunae (s) of the pseudobranchia in logitudinal direction, not transversely as in André's figures (Simroth 1912, p. 477, f. 157). Contrary to *Ferrissia tarda* (Hoff 1940, p. 234) the richly folded and long organ of *Uncancylus ticagus* is evidently efficient for oxygenation. The arterial blood flows around the osphradium, the kidney, where it is cleaned, and to the auricle. The rhythm of the circulation is a complex phenomenon which is difficult to analyze. Though the heart of our young snails generally pulsates more slowly than that of older animals, in contrast with indications for *Lymnaea* (Hoffmann 1924-28, p. 977, 979; Boettger 1944, p. 334), and in most cases heartbeats are more numerous at higher temperatures, there are exceptions in our protocols. Possibly local

Length (in mm)	Heartbeats per minute	Temperature (in centigrades)
0,6	46	18
0,6	89	18
0,65	65-72	17
0,65	73	20,5
0,65	65	21,5
3	30	17
4	74	18
4	170	31
5	96	20,5
5,5	78	17
5,5	42	18
5,5	64	18

muscle contractions exert influence upon the flow of the blood in the chiefly lacunar circulatory system of our snail.

Moquin-Tandon (1852, p. 128) observed 50-60 heartbeats in young *Ancylus fluviatilis* and Saint-Simon (1852, p. 121) the same in adult *Acroloxus lacustris*. Both authors did not indicate the temperature.

7. NERVOUS SYSTEM AND SENSORY ORGANS

The central nervous system (Fig. 11) is as highly concentrated as in the other ancylids (Hubendick 1947b, p. 149). The ganglia are however in some specimens more and in others less distinctly circumscribed and set off from one another, and the lengths of the commissures vary individually. The cerebral ganglia (1) are biggest; their commissure is less than half the diameter of one of them. The next in size, the pedal ganglia (3) are ventrally apposed to the posterior third of the cerebral ganglia and bear the statocysts (oc) with many statoliths on their dorsal surface. The pleural (4) and parietal (5, 6) ganglia are frequently separate as in several planorbids (Hubendick 1955b, figs. on p. 230). These ganglia or this complex of ganglia is somewhat bigger on the left than on the right side. The separation of pleural and parietal ganglia explains the indication of 3 visceral besides the pleural ganglia (Aeberhardt 1905, quoted from Hubendick 1947b, p. 149).

The abdominal (Hoff 1940, p. 237: left posterior visceral) ganglion (7) is big and lies to the left of the mid-line. The length of the cerebro-buccal connectives varies; the buccal commissure is as long as or longer than the diameter of one buccal ganglion (2). In snails with separate pleural and parietal ganglia sometimes a further small visceral ganglion (8) was seen between right parietal and abdominal ganglion. As in these cases the left parietal (supra-intestinal) ganglion is contiguous with the abdominal ganglion, the whole visceral loop consists of ganglia.

A nerve from the left parietal ganglion innervates the osphradium which lies in front of the entrance of the mantle cavity under the left anterior shell muscle. It is a deep, narrow pit (Fig. 9) coated with a fine tunic of connective tissue and lined with an epithelium whose long cilia beat lively. The ciliated cells enter the osphradial concavity,

but do not continue around the whole lumen. The cells of the bottom (sc) bear short rods, not long cilia, and their nuclei are big and spherical, not narrow and longish as in the external cells. Lacaze-Duthiers (1872, p. 483) discovered the osphradium of limnic Basommatophora, though not in ancylids, and distinguished the external and internal cells of the pit in *Planorbis* (p. 486). Both types are distinctly separated, and at the limit between outer and inner cells clusters of subepithelial cells (wo) form a corona around the osphradium. These cells are glandular and discharge their secretion into the pit. In *Planorbis* Lacaze-Duthiers (p. 491) observed mucous secretion expelled when the aperture of the osphradium was stimulated, and Bernard (1890, p. 242) noted mucus cells. The bottom cells are evidently sensory. The big, cup-like osphradial ganglion (oa) around the fundus of the pit was in ancylids first described by Sharp (1884, p. 231).

The origin of the four anterior cerebral nerves is not as separate as in *Acroloxus lacustris* (André 1893, quoted from Simroth 1910, fig. 74 E). The inner nerve trunk divides into inner and outer cephalic nerves nearly as in *Ferrissia tarda* (Hoff 1940, f. 17), but the outer trunk is different. Optic and tentacular nerve are united for a long distance in *Uncancylus ticagus;* this corresponds to the "most lateral main nerve" of *Ancylus tapirulus* (Hubendick 1960, p. 504). Near the surface of the bulge (j) behind the base of the tentacle the tentacle nerve forms a club-shaped ganglion (9) connected with the sensory cells of the bulge. These cells stand in subepithelial groups, and sections of the bulges with the secondary ganglion and subepithelial clusters of sensory cells resemble those of the Hancock's organ of the Cephalaspidea. The "cup-shaped ganglion" of *Protancylus* (P. & F. Sarasin 1898, quoted from Simroth 1909, p. 210, pl. 12, f. 1) may be the complex of subepithelial sensory cells. The tentacle nerve runs forward into the tentacle (t) entally to the ganglion of the bulge.

8. ALIMENTARY CANAL (Fig. 14)

The jaws were described at the end of chapter 3. The radula (Fig. 13) consists of 125-145 slightly opisthocoelous rows with about 20.1.20 teeth. The rhachidian tooth (R) has two principal cusps, each flanked by an accessory cusp. The left principal cusp in distinctly longer than the right one. The lateral teeth are fundamentally

tricuspid. The first has besides the ental cone, mesocone and ectocone, one entoconal and two to four ectoconal accessory cusps. The following laterals are similar; sometimes two accessory entoconal cusps were observed. Farther outwards the size of the ectocone decreases, an interstitial cusp may appear also between mesocone and entocone, and the latter may split into two as do the principal cusps in *U. leucaspis* (Walker 1925, p. 4). From the 16th or 17th tooth outwards the teeth are very weak. The radula of a 0,66 mm long snail has already 85 rows, the oldest of which contains three, the newest six tiny teeth on each side of the rhachidian tooth. The latter has two principal cusps and a single accessory one beside the left and larger of these. The cushions of supporting tissue (radular cartilages) are separate.

The rather short salivary glands (sa) are tubular, not lobate, dorsal to the cerebral commissure and coalesced over the oesophagus (oe) behind, as Hubendick (1955a, p. 317) had supposed in his material. The narrow oesophagus has very long cilia (Hoff 1940, p. 231: "flagellated cells") and a few longitudinal folds. It opens suddenly into a wide crop (cr) where the folds become irregular, and the long cilia stop. Only a dorsal and a ventral median band of higher cells are ciliated. Near the passage to the gizzard (mu) there is a narrow belt of cilia which are much shorter. The gizzard has a high epithelium without cilia thrown into about a dozen folds. The cuticle is very thin, not "relatively thick" as in *Lymnaea stagnalis* (Carriker 1947, p. 33). The muscle mantle of the gizzard contains haemoglobin as in *Lymnaea* (ibid., p. 36). It is composed of four circular layers separated by three longitudinal ones, while *Ancylus fluviatilis* has five and four layers respectively (Heidermanns 1924, p. 350). The muscle coat is of equal thickness all round as in *Ancylus fluviatilis* and *Acroloxus lacustris* (ibid.), contrary to lymnaeids and planorbids with two muscular pads. According to Heidermanns (p. 365-366) only gizzards with muscle pads can grind. He supposes that the gizzard of ancylids only functions as press forcing the food into the digestive gland and the intestine (p. 352).

The contents of the gizzard of *Uncancylus ticagus* are mingled with numerous sand grains which are moved to and fro, but rarely evacuated. This indicates that they are biologically significant, possibly slitting the membranes of plant cells. The following region, the py-

lorus of Hoff (1940) and Carriker (1947), "Hintermagen" of Heidermanns (1924), may be called stomach (ac), because it communicates with the digestive gland (l). The latter has a single duct, already seen by Moquin-Tandon (1852, p. 52). The wall of the stomach has a thin muscle coat and a ciliated epithelium with several folds. These are difficult to analyze due to the small size of the animals. We found a curved major pyloric fold (Carriker 1946, p. 35) which probably acts as a valve protecting the opening of the hepatic duct against the entering of stones or other big particles. This fold occurs also in *Gadinia peruviana* (Schumann 1911, p. 32). The atrial and hepatic corrugations (Carriker 1947, f. 13, p. 28-29) which enter the small caecum (cu) represent a posterior sorting area. The caecum opens after the entrance of the hepatic duct, but lies in front of it due to the winding of the alimentary tract. The caecum has a high folded epithelium of glandular character beset with cilia; it is a sorting organ and contributes to the mucus of the faecal string as in *Lymnaea* (Morton 1953, p. 244). The epithelium of the stomach near the opening of the caecum is similar to the description of an elementary style-sac (Morton 1955a, p. 127). The height of the cells (18μ) is less than in *Otina* (30μ), and they have only one nucleolus.

In a rather transparent living snail that had fed on lettuce the gut contained fine homogenous green particles which made it possible to observe the movements of the food. The contents of the gizzard, food as well as sand, were pumped alternately into the crop and the stomach and sucked back into the gizzard many times. The green masses, not the sand, are also driven into the lobes of the digestive gland and regurgitated repeatedly. Also the caecum is filled with food masses. The described process does not support Heidermanns' above cited idea of the ancylidan gizzard as a simple force pump which presses the food through the flexure of the stomach. It is true that Heidermanns dealt with other species. His observations (1924, p. 353-354) refer only to intestinal peristalsis.

The peristaltic intestine (i) carries the digested masses to the rectum (r), gradually concentrating the faecal string. The intestine first runs in a loop around the gizzard, anteriorly from right to left, then backwards, and again to the right around the hind lobe of the

liver to the ventral side, turning along its own course to the left and forwards. The intestine has a glandular ciliated epithelium and an inconspicuous intestinal groove till it enters the blood sinus in the infrapallial lobe (p). The ring of high cells described in *Ancylus fluviatilis* (Sharp 1884, p. 221) is absent. In its terminal course forwards the ciliated epithelium of the alimentary tract is lower and no longer glandular, hence this outermost portion of the intestine can be called a rectum. According to the contraction of the infrapallial lobe the anal opening (ar) is directed to the dorsal or to the ventral side.

9. REPRODUCTIVE ORGANS (Fig. 15)

The acini of the orange hermaphrodite gland (ov) are surrounded by the liver and lie over the descending portion of the intestine. The female germ cells are the more ental (proximal), the male cells the more ectal (distal) elements. The hermaphrodite duct (so) has an inner and an outer portion separated by the irregularly coiled seminal vesicle (vs). The latter and the ental portion of the duct were filled with sperms in July 1961, while the ectal course was empty. This ends at the "crible ou carrefour génital" (Lacaze-Duthiers 1899, p. 36, 64 ff.), where the male and female ducts separate. Own sperm is absorbed by the epithelium of the vesicula seminalis as in *Acteon* (Fretter & Graham 1954, p. 574).

The male or efferent duct begins prostatic (q) as a convolute glandular tube whose epithelium contains big spherules of secretion. The cells of the prostatic section are very big, their nuclei are 20μ in diameter. The following muscular portion of the efferent duct (d) passes through the left anterior shell muscle and unites with the flagellum (u), a long tube with big gland cells in its ental widened part, decreasing towards the narrower, so-called flagellum duct. Ectally to the junction (un) of efferent and flagellum duct the male canal can be called ejaculatory duct (Hubendick 1955, p. 318). Its circular muscle layer is thicker than that around the precedent efferent duct. A retractor (re) originating in front of the head inserts on its base. The flagellum duct enters the male canal on the same level as in *Uncancylus ticagus* in *Ferrissia parallela,* according to Hoff (1940,

p. 241), and in Haas' so-called *Anisancylus*-species (Hubendick 1955a, f. 46, 47, 53), but farther ectally in other ancylids (Lacaze-Duthiers 1899, pl. 7, f. 30; Hoff 1940, pl. 2, f. 11; Hubendick 1947b, f. 23 on p. 153; 1960, p. 507, f. 11 on p. 509).

The outlet of the ejaculatory duct is permanent on a small papilla thickened by insunk glands. It hangs into the male atrium (e) that is entirely evaginated during copulation. In this state the atrium forms an up to 1,3 mm long tube of 0,1 mm diameter (Fig. 18). The retracted papilla measures about 0,12 mm in both directions and is surrounded by an annular fold. The male pore lies behind the basal bulge of the left tentacle.

In the literature the male copulatory organ is generally studied in fully retracted condition; then the atrium is composed of two compartments, an inner and an outer one. The former is called "deuxième prépuce" (Lacaze-Duthiers 1899, p. 87), penis sheath (Hoff 1940, p. 240; Hubendick 1947b, p. 150), or vergic sac (Baker 1945, p. 7; Hubendick 1955a, f. 46, 47, 53, vs), the latter "premier prépuce" (Lacaze-Duthiers 1899, p. 86) or praeputium (other authors). Penis sheath and praeputium are separated indistinctly by an oblique ring-shaped fold, the diaphragm (Baker, l. c.) or velum (Hoff 1940, p. 241; Hubendick 1947b, p. 154; 1955a, p. 317). In his figure 11 (pl. 2) Hoff called the velum 'sarcobellum", but Baker's description of the "sarcobelum" refers to a special organ of stimulation which occurs in *Planorbarius*.

The hermaphrodite duct conveys the eggs to the carrefour (ca) whose entrance is provided with a strong sphincter. This muscle blocks the way into the chamber for the own sperms. The carrefour is entally connected with the transparent yellow albumen gland (an), ectally with the capsule (nidamental or mucus) gland (cm). The cilia which also occur in the hermaphrodite duct, in the carrefour, and in its connection with the albumen gland are especially strong in the canal between the chamber and the capsule gland. Topographically Hoff's papilla of *Ferrissia tarda* (1940, p. 239) corresponds to the carrefour of our species; the carrefour belongs to the oviduct.

We suppose, as Simroth (1912, p. 498 did, that the carrefour of *Uncancylus ticagus* is a fertilization chamber, but as we have not yet seen sperm in the inner part of the female duct, we cannot affirm

it. According to the literature concerning neighbouring families mentioned by Alaphilippe & Régondaud (1959, p. 491) fertilization takes place still farther inwards, in the ectal part of the hermaphrodite duct.

The fertilized eggs supplied with the secretion of the albumen gland, which in the present species resembles the white of a hen's egg, enter the broad yellow capsule gland. This gland is connected with the female pore by the muscular nidamental duct which begins with an inward fold (va) of its wall. The nidamental duct (ni) which has no glands is in other Lymnaeacea subdivided into an inner portion (uterus) between capsule gland and entrance of the bursa canal, and an outer part (vagina) from this entrance to the female aperture. In the present species this subdivision is merely topographic. The outer opening (v) of the female organs lies beneath the osphradium or under the anterior end of the pseudobranchia. The duct of the bursa copulatrix (b) (spermatheca) opens immediately inside the female aperture.

A couple of snails (Figs. 17, 18) was preserved during its copulation. In the animal that has functioned as female the wall of the female opening is protruded and forms a cylindrical papilla (Lacaze-Duthiers 1899, pl. 3, f. 3, Va). In sections a plug of sperm and secretion sticks out of this papilla and fills the canal and the ampulla of the bursa copulatrix. The fold at the entrance of the capsule gland closed the latter, evidently to avoid the immediate ascent of the spermatozoa. Also in specimens preserved one and three hours after mating only the bursa contained sperm.

10. OBSERVATIONS ON LIVING SNAILS

The animals lived for months and in great numbers mating and laying eggs in two aerated aquaria, 80 cm in length, 40 cm in breadth, height of water 25 cm. The aquaria stood near a window, but were not exposed to direct sunlight; they contained a layer of coarse sand and small (2-6 cm) stones, algae and *Elodea,* some *Xiphophorus helleri,* green hydrae, many *Macrostomum* and *Chaetogaster*. Tufts of *Stentor* are attached to the shell of the ancylids with their gelatinous investment, and irregular patches of green algae fasten themselves in the growth-rings. *Macrostomum gigas* Okugawa, 1930, a

macrophagous rhabdocoel, preyed upon our young ancylids. In one of the aquaria *Chaetogaster parvus* Pointner, 1914, was found on the surface of the snails, while in the other *Chaetogaster limnaei* C. Baer, 1827, gathered in their pallial and supranuchal cavity, sometimes up to 25 worms. They fed upon the faecal pellets of the snails and also upon Ciliata. They do not seem to be harmful to their host, as a richly infected isolated snail produced three capsules with 12-14 eggs each in the course of three days.

During the months of observation, May to September 1961, the temperature in the aquarium varied from 17° to 22° C.

The food of the snails consists of micro-organisms growing on stones, plants, and the glass panes of the aquaria, and decaying leaves and other organic detritus. Sometimes green spherical algae and eggs of *Macrostomum* in the faecal pellets had passed the alimentary canal entire. The youngest 0,66 mm long animals found in the aquarium had already a sand grain in the stomach. When adult snails with sand grains in the gizzard are kept in a dish and fed with clean lettuce the grains are retained, not evacuated.

The faecal pellets are greenish cylinders of 1-1,7 mm length and about 0,16 mm diameter in big specimens. There are also a few dark brown masses composed of conglutinated excreta from the digestive gland (Fretter 1939, p. 636-637). At a water temperature of 20° C. snails living with abundant food defecated thrice per minute. Measurements of pellets and frequency of evacuations are a little superior to those indicated of *Ancylus fluviatilis* (Heidermanns 1924, p. 353).

In the aquaria the snails sat on the light and on the dark walls, on the bottom, on rooted and on detached *Elodea*. They can reach the latter falling down from the surface where they glide with perfection as do other ancylids (Hoffmann 1924-1928, p. 1079). Moquin-Tandon (1852, p. 136) and Sharp (1884, p. 217-218) never saw the snails creep on the surface film. In this position and also while moving on a solid substratum, e. g. a slide, our species uses its cilia which cover the whole sole. This is facilitated by secretion from the anterior pedal gland, a ribbon of rather fluid mucus. We did not see the snails descending from the surface hanging on this thread, as was observed in *Ancylus fluviatilis* (Pelseneer 1935, p.

362), but proved its existence by drawing the snails backwards through the water with it (Kaiser 1959, p. 379). The mucous trail can also be shown by letting the snail creep on a greased slide, then the water adheres to the track. As Kaiser (p. 375-376) observed in bigger basommatophores also *Uncancylus ticagus* adheres to the surface by means of suction performed by dorso-ventral and oblique muscle fibres of the foot. The oscillation of these muscles ("die muskuläre Unruhe") produces concavities on the surface film which change their place continuously, while the mutual position of the pigment cells in the sole remains constant. In the present species whose pallial cavity generally does not contain air, the suction alone must overcome gravity; if it is relaxed, the snail loses its contact with the surface film and sinks. As long as the animal adheres to the surface a second of these positively thigmotactic snails can fix itself with its sole to the shell of the first, and even a third to that of the second, and all three are maintained suspended by the muscular action of one. The force of the cilia is responsible for locomotion. On a solid substratum the snails run on their mucous trail by means of the cilia. Compared with *Protancylus* (Simroth 1908, p. 11, note), and *Ancylus* (Moquin-Tandon 1852, p. 135; Wesenberg-Lund 1937, p. 740) *Uncancylus ticagus* is a vagrant snail. It moves about frequently and creeps 3 mm per minute at 17° C., 25 mm at 26° C. Hunter (1953, p. 625) indicates 1-2 mm per minute for feeding *Ancylus fluviatilis*, hence much more than Moquin-Tandon and Wesenberg-Lund.

Snails fallen upside down on a solid substratum, e. g. glass, recover their normal position rapidly (Fig. 19). However when the same snail is laid on its back several times, reversion becomes slow. The snail tries to regain contact with the substratum moving the anterior border of its maximally extended foot to all sides. It does not succeed to reach the substratum in front or over the right side, but when it touches the substratum on the left side, where the shell is not as steep as on the right one, it turns over immediately. When the snail moves on loose sand, the mucus forms a thick carpet to which the superficial sand grains stick. If it has fallen upside down, the carpet helps it to recover. If a snail falls on to loose sand, where it has no tract, it cannot turn round till it has grasped so many sand grains

with its foot and agglomerated them to a ball that this is heavy enough to counterbalance the snail while turning over.

A slight, by no means pronounced preference for the dark side in the aquarium led us to test the reactions of *Uncancylus ticagus* to light. In a first series of experiments snails which had lived under the normal rhythm of day and night were brought into a dish with one half dark and the other exposed to diffuse daylight. In a second series snails kept in the dark for 24 hours were submitted to the same conditions as the first. The results of both experiments were the same: the snails behaved indifferently, without preference to dark or light. However to direct sunlight they react negatively, avoiding it. They respond to this stimulus in form of a phobotaxis. Ancylids fleeing from sunbeams were several times mentioned in the literature, e. g. by Moquin-Tandon (1852, p. 134) and Pelseneer (1935, p. 231).

A snail wanting to take air into its pallial cavity curves its foot so that a concave angle at the left side results. Here the concavity of adhesion is deepened so far that only a narrow rim of the sole remains in contact with the surface film. Also the left mantle border touches the film. Then the gill is apposed to the side of the foot, and the pallial cavity drawn widely open, so that air enters. The gill closes over the air bubble. Later on the shell muscles contract and press the air out of the cavity again.

As all basommatophorans (Boettger 1944, p. 396) also *Uncancylus ticagus* mates unilaterally, not reciprocally. Mutual copulation is excluded by the position of the genital apertures (Fig. 18). Lacaze-Duthiers' description and figure (1899, p. 93, pl. 3, f. 5) of a penis penetrating into the female orifice was repeated by Simroth (1912, p. 500, pl. 25, f. 12) and Hoffmann (1924-28, p. 1118). According to Moquin-Tandon (1852, p. 346) however *Ancylus fluviatilis* copulates in the same way as *Uncancylus ticagus,* not introducing the penis into the female aperture, but clasping the female papilla tightly ("presse fortement le mamelon vaginal"). We saw also chains of three copulating snails, the undermost functioning as female, that in the middle as male and female, and the uppermost as male. A mating couple is firmly united (Fig. 17) so that it can be turned upside-down for observation. In the transparent penis (e) the ejaculatory duct (d) and the entrance of the flagellum duct (un)

near the end of the former could be seen, as well as the whole extension of the flagellum (u) which remains enclosed in the evaginated male atrium of the active partner. Even when preserved, a couple stayed united, and separated only after decalcification. Evidently the snails are sticking together due to secretion of the flagellum. In the preserved animal the erected penis reached the right border of its foot; it measures 1,3 mm in length and 0,1 mm in diameter.

In the middle of July, at water temperatures of 18° C. in our dishes in the early morning and 25° at noon six snails produced 8 egg capsules in 24 hours. In the course of 48 h. we obtained 16, in 72 h. 26 capsules. These contain up to 14 eggs which can all hatch. After some days the number of capsules and that of eggs contained in them decreased. The size of the capsules corresponds to the number of eggs. With one and two eggs they measured 1 x 0,9 mm, with three eggs 1 x 1 mm, with five eggs 1,3 x 1,3 mm, and with six eggs 1,5 x 1,3 mm. The biggest capsules (Fig. 16) with 12-14 eggs were 2 mm in length and breadth. As the margin is about 0,1 mm broad, the diameter of the central space is about 1,8 mm. When recently laid capsules are detached, they become globular. The unsegmented egg is 80μ in diameter. The developing embryo grows considerably and measures 0,12-0,14 mm on the third day, on the fourth 0,25-0,3 mm, and on the seventh 0,5 mm. The embryo rotates in its membranes on the fourth day. The snails hatch in 8-10 days with the shell 0,65 mm long and 0,4 mm broad. The time of hatching is quite variable in the ancylids (Basch 1959, p. 274). Hatching snails have only 40μ long tentacles and still yolk in the digestive gland; they feed already and have a green alimentary canal. With a length of 0,8 mm the mandibular teeth are present. The tentacles grow slowly, 1 mm long snails have them 60μ long, in 2 mm long animals they are 0,4 mm. The pigment cells appear at a length of 2 mm, but their development is not always correlated wich size.

Ferrissia shimekii studied by Basch (1959) and *Uncancylus ticagus* become mature before their somatic growth ends. This seems to be the case in all basommatophores, but contrasts with most of the Stylommatophora (Hoffmann 1924-1928, p. 1116). The capsules of the mentioned *Ferrissia* always contain only a single egg

(Basch 1959, p. 269). *Uncancylus ticagus* is bigger than *F. shimekii,* and in our dishes produced egg capsules already at a length of 3 mm. Once such a small snail isolated after copulation laid a capsule containing 3 eggs about 12 hours later, and on the 7 following days 7 further capsules with 3 eggs each. During this time the animal did not increase its size.

11. GENERAL CONSIDERATIONS

The surface of the ancylids, as small snails, is relatively large. Hence cutaneous aquatic respiration facilitated by a patelliform, not coiled, body and locally reinforced by a gill is suficient for them. The shell surface exposed to the movement of the water is only one and a half or two times larger than that of adhesion, against 12-20 times in planorbids of stagnant water (Hoffmann 1924-1928, p. 1323). So equipped ancylids can enter brooks and torrents, where oxygen contents are highest. Food is scarce in this oligotrophic environment and gathers in sheltered niches at the bottom. As a bottom-dweller *Ancylus fluviatilis* may perhaps be called "earthworm of brooks" (Heidermanns 1924, p. 351), though it moves about much less than an earthworm. Moreover many members of the family Ancylidae (sensu latiore) live in quiet, eutrophic waters, e. g. *Acroloxus lacustris* (Wesenberg-Lund 1937, p.741; Boettger 1944, p. 439), *Ferrissia parallela* (Taylor 1960, p. 61), our *Uncancylus ticagus* and others. *Acroloxus lacustris*, it is true, from stagnant waters has a low shell, and so it opposes less resistance to mechanical aquatic action than the high-shelled rheophile *Ancylus aquaticus* (Berg 1952, f. 1 and p. 264).

During active life, e. g. on stones exposed to spray (Boettger 1944, p. 323), and during winter, with reduced activity (Pelseneer 1935, p. 314) ancylids can breathe air. This respiratory amplitude is common in the Basommatophora. *Chilina* takes air or water into its mantle cavity, and higher limnic forms can live without air with aquatic cutaneous (*Lymnaea, Galba*) or branchial respiration (planorbids). The systematic position of the ancylids cannot be derived from their on the whole aquatic respiration. Pondering their relation with the Patelliformia (Hubendick 1947a, p. 162-163), the

Amphibolidae, and Chilinidae (id., 1947b, p. 1956-1957), or with the Planorbidae, Hubendick favours the last position. He considers the patelliform shell and diminution of the mantle cavity as secondary specializations.

Within the family *Uncancylus ticagus* has several primitive characters: the well developed head lobes (Hubendick 1947b, p. 156), the relatively large mantle cavity, the sometimes separated pleural and parietal ganglia, and the occasional occurrence of a commissural ganglion between right parietal and abdominal ganglion. The penis of *Uncancylus ticagus* is intermediate between the more complex one of *Ancylus* and *Ferrissia* and the simpler one of Hubendick's species (1955a). These have all a flagellum. Hubendick (1947a, p. 131) stressed the lability of the distal reproductive organs and points to histological differences (1947b, p. 159-160) between a flagellum and the tubiform organ of *Amphibola*. It is however the only topographically comparable organ in these snails that may belong to the ancestry of ancylids. The ental part of the reproductive system in ancylids as well as planorbids is similar to that of the lymnaeids which hints to *Chilina*.

Besides the general organization of the generative organs the central nervous system and the alimentary canal offer criteria which unite the higher limnic Basommatophora or Lymnaeacea. Morton (1955b, p. 163) called them Branchiopulmonata, but as Physidae and Lymnaeidae have no gills, the choice of the name is strange. As far as Heidermanns' studies of some species (1924) inform, Physidae have the least, Planorbidae and Lymnaeidae the most developed gizzard; the Ancylidae stand between Physidae and Planorbidae. The weak gizzard of the physids coincides with the radula more elaborate than in the other lymnaeaceans. A posterior caecum (caecum pyloricum) is a feature of the earliest gastropod stock (Morton 1953, p. 244). It occurs in all families of the Lymnaeacea; in *Uncancylus ticagus* there is also a vestigial style-sac.

Beyond the known relationships between Cephalaspidea and Basommatophora in nervous system, radula, gizzard, and hermaphroditism there are no special affinities of ancylids to opisthobranchs. Burch,

Basch, and Bush (1960, p. 202, note) think that the chromosome numbers might suggest such.

Hubendick (1947a, b) and Morton (1955a, b) agree in a main bipartition of the Basommatophora, distinguishing the more primitive Archaeopulmonata (Morton 1955a, p. 148) and the higher limnic Basommatophora (Branchiopulmonata or Lymnaeacea). The families of the latter were already mentioned; the former comprise Ellobiidae, Chilinidae, Latiidae, Amphibolidae, Siphonariidae, and Gadiniidae.

An operculum in the adult or in the embryo, free swimming veligers (*Melampus, Amphibola, Siphonaria, Gadinia*), embryonic vestiges of a velum, the nervous system, sometimes with vestigial streptoneury, parallels in the reproductive organs, and a general compatibility of the stomach of *Amphibola* with the ellobiid type (Morton 1955b, p. 163) justify the name Archaepulmonata, and make it probable that the two parallel lines, viz. Ellobiidae and the other families, have their origin in common (Hubendick 1947a, p. 160).

Pelseneer (1894, p. 117: diagram) derived the Lymnaeacea from *Chilina,* and Plate (1895, p. 203), Thiele (1935, p. 1110), Boettger (1944, p. 269; 1954b, p. 269), and Hubendick (1947b, p. 156: Amphibolidae and Chilinidae) are of the same opinion. If the higher limnic Basommatophora were early land pulmonates reverted to freshwater (Morton 1955b, p. 162), their infrapallial lobe and osphradium would be convergences. Boettger (1944, p. 331; 1954b, p. 268) follows Herfs (1922, p. 20-30) and considers the mostly subepithelial position of the glands in the limnic basommatophores as testimony of ancestral terrestrial life, as a formerly necessary protection against dry air on the seashore. Certainly such glands arranged on different levels in the connective tissue can secrete more mucus than intra-epithelial goblet cells, and cutaneous secretion helps to shield the body of gastropods besides shell and operculum. But also limnic snails are exposed to drying. Many of their biotopes lose the water in summer or winter. A snail that passes from sea to freshwater must be equipped as well as or even better than one going to the land. It has to counterbalance not only dry periods but also a hypotonic medium and cannot withdraw into the shell like a terrestrial snail during heavy rains.

12. RESUMO

A espécie encontrada em aquários no Departamento de Zoologia da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo tem concha de até 6,5 mm de comprimento, com ápice achatado, finamente pontilhado. O comprimento da cúspide principal esquerda, no dente central da rádula, ultrapassa o da direita. A cavidade do manto é larga, e o animal serve-se dela para respiração de ar. Órgãos respiratórios aquáticos são a brânquia bilobada e o bordo do manto. A concentração dos gânglios varia individualmente. Grãos de areia evidentemente auxiliam na trituração do alimento, principalmente vegetal. A papila penial é pequena; o duto da bolsa copulatória que recebe os espermatozóides na cópula, abre-se perto do orifício feminino. Na locomoção na superfície dágua, músculos dorso-ventrais e oblíquos seguram, por sucção, o gastrópode, os cílios locomovem-no ao longo de uma fita de muco. Animais caídos de dorso voltam à posição normal virando sôbre o lado esquerdo da concha, menos íngreme que o direito. Os animais são indiferentes à luz difusa do dia e ao escuro, mas evitam, fobotàticamente, os raios solares. Os casulos de ovos contêm até 14 embriões; os animais podem tornar-se maduros antes de terminar o crescimento somático. Não há evidência de que os Lymnaeacea sejam caracóis outrora terrestres voltados para a água doce.

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14. EXPLANATION OF LETTERS

1 — cerebral ganglion
2 — buccal ganglion
3 — pedal ganglion
4 — pleural ganglion
5 — right parietal ganglion
6 — left parietal ganglion
7 — abdominal ganglion
8 — accessory visceral ganglion
9 — ganglion of the post-tentacular sensory organ
a — mantle skirt
ac — stomach
an — albumen gland
ar — anus
b — bursa copulatrix
c — pallial cavity
ca — carrefour
cm — capsule gland
cr — crop
cu — caecum
d — efferent duct
e — penis
eo — reno-pericardial duct
er — pericardial cavity
f — foot
g — glands of mantle skirt
h — retractor of head
i — intestine
ic — mandibular lamellae
im — pigment
j — post-tentacular sensory organ
k — ureteric part of kidney
l — digestive gland
m — male aperture
mo — mouth
mu — gizzard
n — renal pore
ni — nidamental duct
no — dorsal lobe of gill
o — osphradium
oa — osphradial ganglion
oc — statocyst
oe — oesophagus
ov — ovotestis
p — pseudobranchia
q — prostate
r — rectum
re — retractor of penis
rm — retractor of gill
ru — "hypobranchial" gland
s — blood sinus
sa — salivary gland
sc — sensory cells
sm — shell muscle
so — hermaphrodite duct
t — tentacle
u — flagellum

uc — buccal bulb
ui — mandibular plate
un — junction of flagellum and efferent duct
v — female aperture
va — valve closing capsule gland
vs — seminal vesicle (ampulla)
w — ventricle
wo — osphradial glands
x — supra-nuchal cavity
xa — trabeculae of gill
y — eye
z — excretory part of kidney
zi — ciliated cells of epithelium

PLATES

15. PLATES

PLATE 1

Fig. 1 — Broad shell, 6 x 4,5 mm.
Fig. 2 — Narrow shell, 4,2 x 2,8 mm.
Fig. 3 — Young shell, 0,85 x 0,55 mm.
Fig. 4 — Profile of 6,5 mm long shell.
Fig. 5 — Same of 5,0 mm long shell.
Fig. 6 — Same of 4,5 mm long shell.
Fig. 7 — Left side of living snail showing entrance (c-c) of pallial cavity.
Fig. 8 — Part of transverse section of pseudobranchia.
Fig. 9 — Section of osphradium.

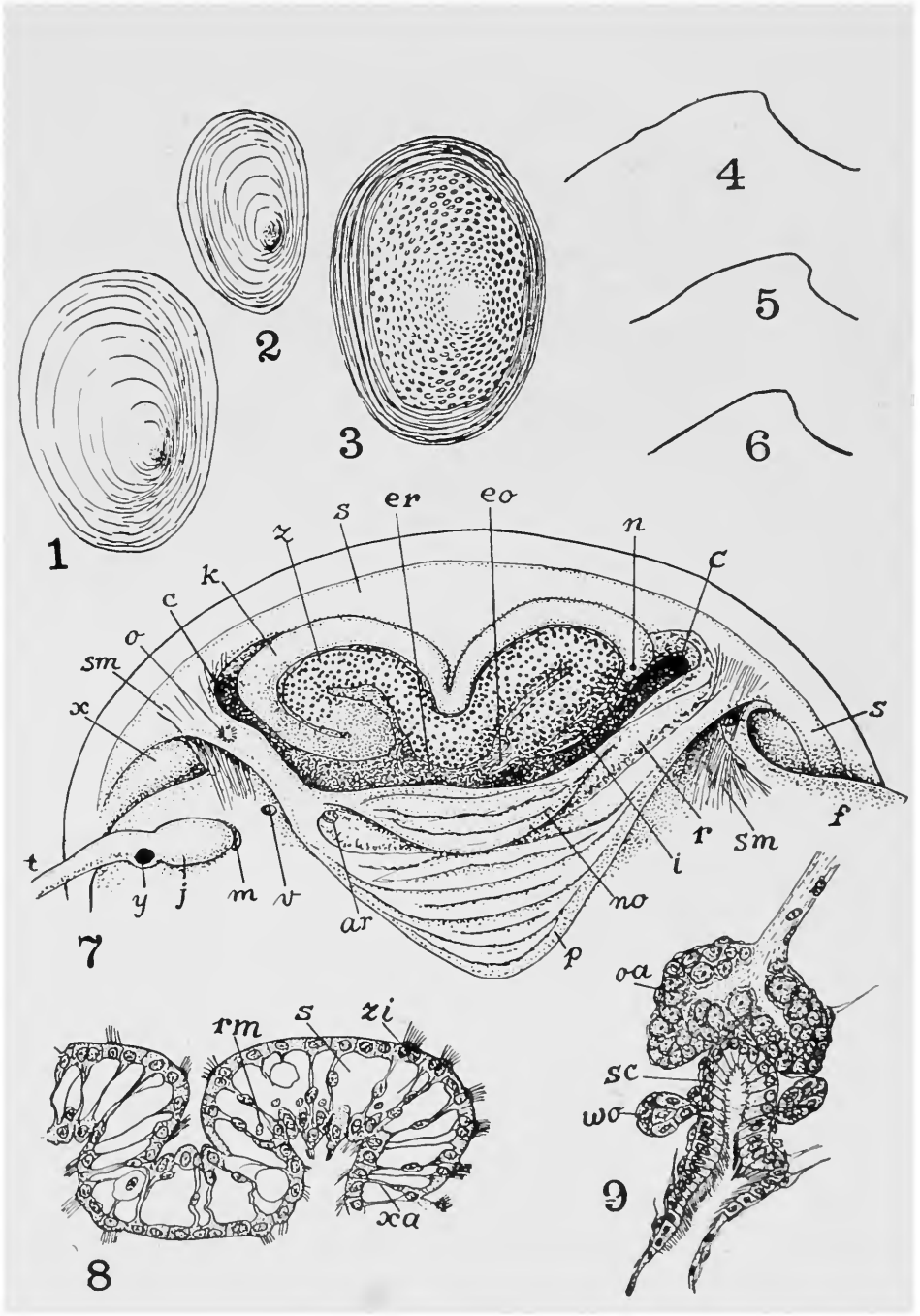
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PLATE 2

Fig. 10 — Combined transverse section of snail on level of pseudobranchia and pallial cavity.
Fig. 11 — Diagram of central nervous system.
Fig. 12 — Mouth.
Fig. 13 — Radular teeth of adult snail. R — rhachidian tooth.

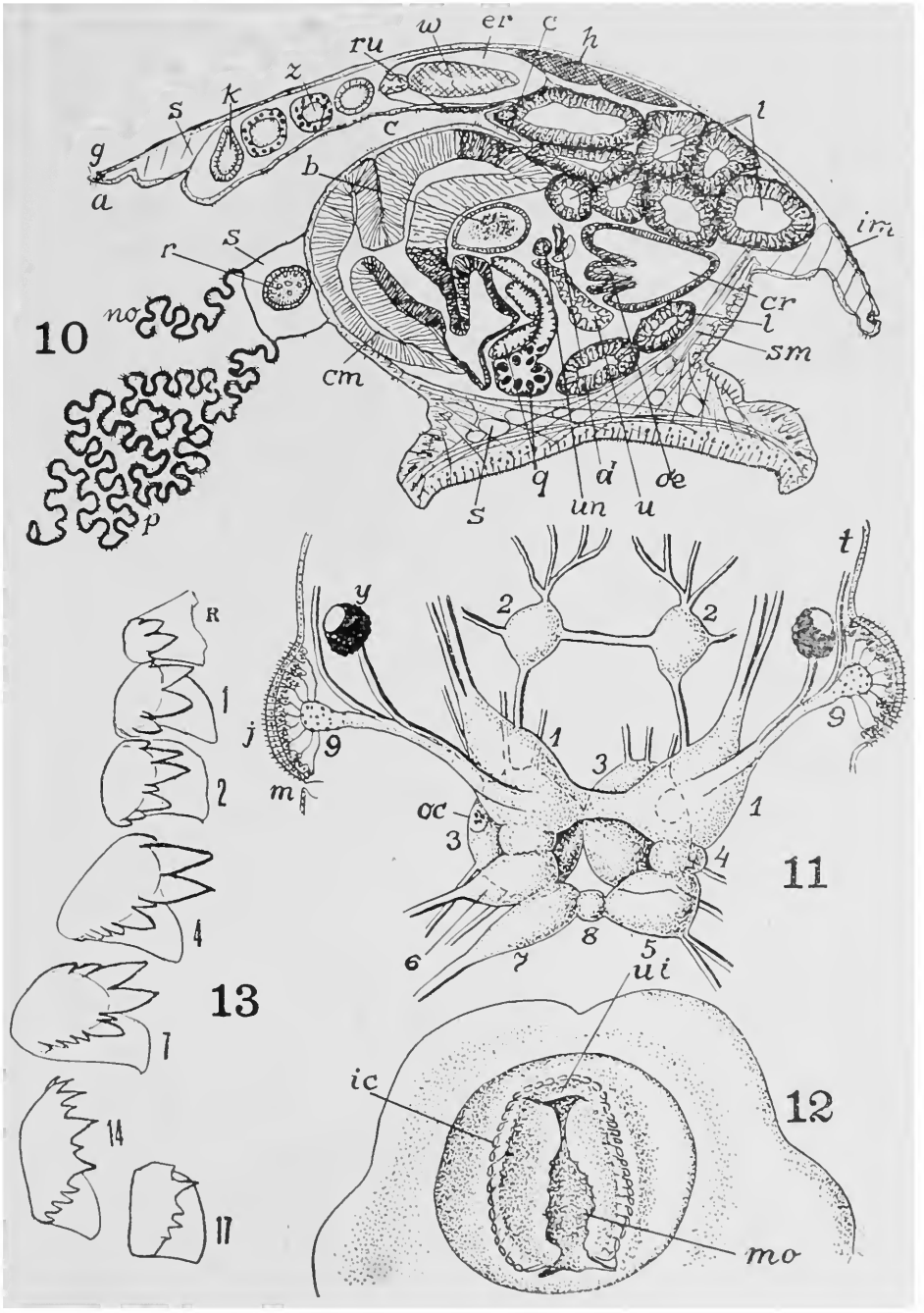
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PLATE 3

Fig. 14 — Alimentary canal.
Fig. 15 — Diagram of reproductive organs in ventral view.
Fig. 16 — Recently laid egg capsule.
Fig. 17 — Mating snails.
Fig. 18 — Details of same.

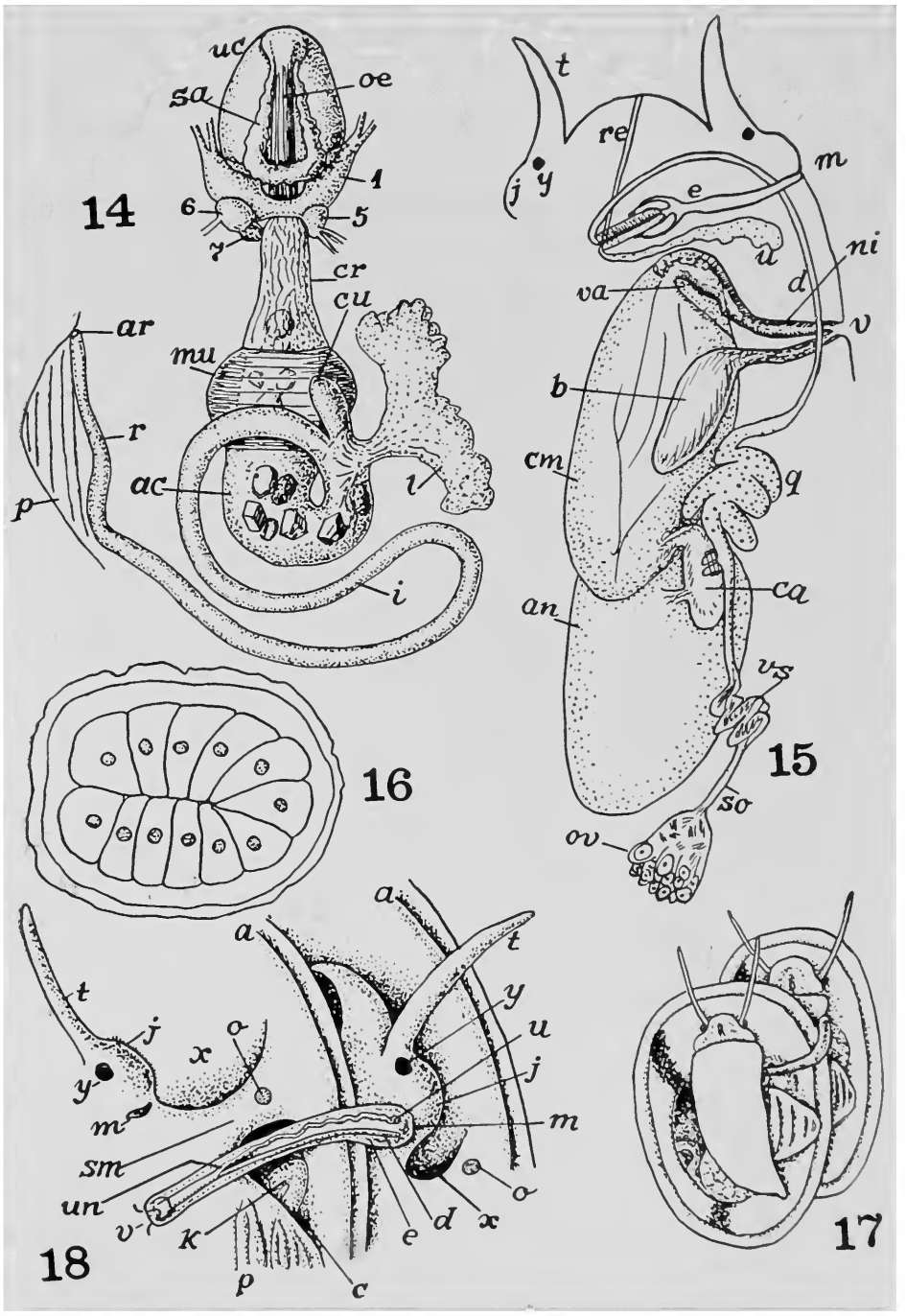
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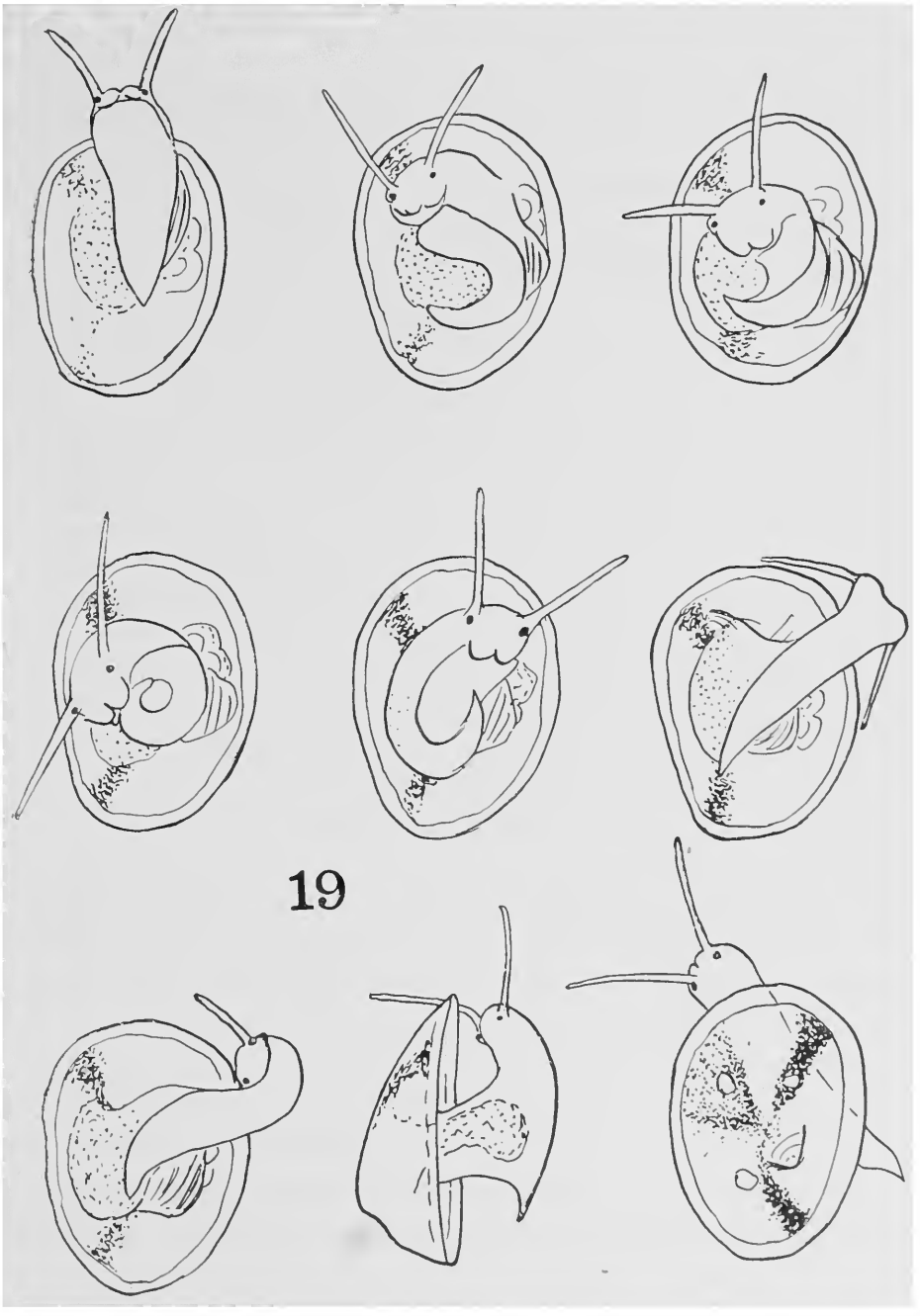
PLATE 4

Fig. 19 — Snail fallen upside-down recovering normal position; successive phases.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THE FEEDING MECHANISM OF BALANOGLOSSUS GIGAS *

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(9 Figs.)

INDEX

INTRODUCTION

Hitherto studies on the feeding mechanism and processes of alimentation in the Enteropneusta have been limited to those of Barrington (1941) and Knight-Jones (1953) on comparatively small species. The rediscovery in some quantity on certain shores in Brazil of *Balanoglossus gigas* Fr. Müller (Sawaya, 1951), the largest known species of Enteropneusta and probably one of the most robust, made a more detailed study possible.

Observations were made in the field and in the laboratory on the feeding mechanism and food transport through the gut.

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* Work carried out at the Marine Biological Laboratory of São Sebastião — Dept. of General & Animal Physiology — Univ. São Paulo, whilst visiting Brazil under the very kind auspices of the British Council and the National Research Council of Brazil.

Stock animals maintained in aquaria in the laboratory with and without their native substrate lived for many weeks. They varied in length from 75 cm. to almost 1.5 m., when fully relaxed with isotonic magnesium chloride solution.

The paths of the ciliary currents were plotted with the aid of Aquadag suspensions of graphite, talc, titanium oxide and copper phthalocyanide, having a particle size range of 1 to 50μ. Starch grains, miscellaneous diatoms, organic debris, carmine and various grades of sand and fine gravel up to 3 mm. in size were also used.

Dissections of the various regions of the animal lived for several days in clean running sea water and so enabled the observations to be repeated several times. Excised preparations were thoroughly irrigated in running sea water to remove excess mucus before being used.

HABITAT

Balanoglossus gigas occurs at several points along the Brazilian coast, but tends to favour comparatively sheltered shores with substrates of fine sand with underlying layers of fine to coarse gravel, a habitat common to many of the Enteropneusta (Burdon-Jones, 1950, 1956). A granulometric analysis of the various layers of sand and gravel from the surface down to a depth of 0.5 m. on a well populated shore, is given in Appendix p. 279.

The animals occupied tubular burrows which followed a sinuous course from the cast on the surface down to depths of almost 0.5 m. passing through several layers of sand and gravel. The burrows were circular or ovoid in cross section and from 1.5 to 2.0 cm. in diameter. They varied in length from 2 to 3 m. and were probably longer. A complete burrow was never exposed. They were lined with a thin layer of mucus, but could not be isolated from the surrounding substrate. Although numerous burrows were exposed an entrance hole was never found. Many surface holes that might have belonged to the burrow were seen within a radius of 2 to 3 m. from a cast, but when the burrow was exposed no contact could be established with any of them, and the search was usually abandoned when the animal was finally overtaken. These burrows tended to be

confined to the layers of sand lying between the strata of gravel, but made brief and shallow excursions into the gravel or passed directly through it into the sand below. There was no evidence that secondary burrows were formed, but their existence cannot be excluded, since it was never certain that the burrows examined were entire. The thin mucus lining of the burrows suggested that they were temporary structures. The failure to locate an entrance hole lends some support to this idea.

Specimens were collected immediately after the tide had receded and were located by the enormous casts they produced during the ebb. The frequency and volume of the casts produced indicated a considerable amount of activity either just prior to or during the ebb of the tide. To date it has not been possible to make observations on cast formation during the flood. It is reasonable to suppose that some specimens did not cast during the ebb, yet counts of up to 100 and more were not uncommon for a section of the shore extending 20 m. from mid-tide level down to low water springs and about 250 m. in length, on one well populated shore. Within this area the specimens were irregularly distributed, and were rarely less than 1 m. apart. There was no apparent tendency for them to aggregate at any one particular level of the shore, or to be localised in any way. Their offshore distribution is unknown.

During the ebb the water table was at, or very close to, the surface of the sand wherever the casts were seen. The population thinned out rapidly above the mid-tide level, and in the more heavily drained areas below this level.

The associated fauna consisted of a large population of the lamellibranch *Anomalocardia brasiliana* (Gmelin, 1792), some burrowing decapod crustacea, a variety of small errant polychaetes, and numbers of the very large polychaete *Eunice* sp. The latter was the next largest animal in the biocoenose and tended to occupy a higher level of distribution on the shore, but overlapping with that of the *Balanoglossus*. It also penetrated to greater depths in the substratum.

When handled *Balanoglossus* produced enormous quantities of thick mucus which adhered tenaciously to the hands and emitted a powerful smell of iodoform. This strong odour greatly facilitated the identification and tracking of the burrows in the field. It, and

the mucus, must serve as a effective deterent to any predator. When handled in a darkened room the animals luminesced strongly. The entire body produced a greenish light and this appeared to be associated in some way with the secretion of mucus, because the latter glowed for a very short period as it streamed off the body when the animal was swirled around in an aquarium.

CASTS AND CASTING

The casts resembled those of *Arenicola marina* (L.) in form, but were very much larger and consisting of continuous faecal cords of diameter 1.0 to 1.5 cm. and length ca. 0.5 to 1.0 m. Coiled upon themselves these cords formed a mass that measured 6 to 10 cm. in height and 10 to 15 cm. at the base, and weighed about 200-250 gm. when freshly cast. All the casts examined had evidently been made after the tide had receded.

The process of casting was similar to that described for *Saccoglossus*. The anus appeared very slowly at the exit of the burrow and equally slowly began to extrude the faecal cord. As the cord lengthened the posterior end of the animal was protruded further and further until it came to lie several cms. above the substratum, and except for the terminal centimeter or two it remained completely enveloped by the irregular coils of the cast. There was no circular movement of the extruded portion as noted for *Saccoglossus ruber* (Knight-Jones, 1953), so the cast did not assume the regular spiral form characteristic of many of the Harrimanidae. Instead it fell in loose irregular coils around the protruding tail region. The process of protrusion of the tail and the extrusion of the faecal cord took place simultaneously. The tail was not always withdrawn after the extrusion of the cord had ceased, but frequently remained visible within the coils of the cast until the next period of intestinal activity forced still more of the cord out through the anus. Shallow annulations on the cord resulted from the contractions of the anal orifice and the irregular rate of extrusion of the cord. The cords contained very little mucus, were loosely compacted, and readily dispersed by the incoming tide. There was no evidence, as in *Arenicola* which occupies a permanent burrow, of several casts being produced one

on top of another forming a shallow cone of sand upon which subsequent casts are extruded. Specimens kept in aquaria with a substrate of sand a few cms. deep made short burrows and extruded short very loose casts on the surface. The absence of an adequate depth of substratum prevented them from making deep burrows and producing large casts. In the field the terminal portion of the burrow immediately below the cast rose vertically through 20 to 30 cm. of sand to the surface, so that the posterior end of the animal would also be so orientated when casting. In the aquarium the terminal portion presented a very oblique angle to the surface so the cast tended to remain uncoiled.

Specimens kept for several days in aquaria devoid of a sandy substratum extruded two long thin yellow mucus cords which twisted upon each other as the animal moved around. These cords were rarely more than 0.5 to 1.0 mm. in diameter and were produced by the lateral furrows of the intestine (see p. 276). Similar but single cords have been observed in *Saccoglossus*. In *B. gigas* they are composed of the indigestible or partly digested fine particulate matter carried into the pharynx by the respiratory and ciliary feeding currents, embedded in mucus along with the secretions of the dorsal sacs.

The alimentary canal of newly caught specimens was often empty except for some fine sand in the hind gut and thin cords of mucus and sand within the anterior regions of the gut. Others were found in which the gut was gorged with sand throughout. In aquaria the burrowing activities of these animals were spasmodic so that the gut was sometimes distended with sand and at other times almost empty and flaccid.

Specimens placed on a substrate composed of alternate layers of sand and coarse gravel in an aquarium and irrigated by water flowing in at the bottom, rapidly burrowed down as far as one of the underlying layers of gravel. Graphite suspensions introduced into the substrata showed that in this position the respiratory stream entering the mouth was drawn primarily from the layer of gravel immediately adjacent to the proboscis. Subsequently the graphite appeared in the cords extruded from the intestine. Dissections showed that it had been extracted by the sieving action of the pharynx. Moreover this action of the pharynx could be demonstrated whenever an

animal had reversed its position and was drawing its respiratory water through the entrance to the burrow.

CILIARY FEEDING MECHANISM

1) *Proboscis* (figs. 1, 2 & 3)

The epidermis of the proboscis was uniformly ciliated and liberally supplied with mucus gland cells. The exudate from these seemed to be more copious when the animal was burrowing or feeding by engulfing the substrate. It formed an enveloping sheath around the proboscis and was propelled posteriorly at an even velocity towards the base of the proboscis. The base of the proboscis was surrounded by the crenated anterior margin of the collarette, a funnel-like extension of the collar to which it is attached by a short stalk middorsally.

The currents created by the cilia of the proboscis drive the mucus and any adhering sand and debris towards the margin of the collarette. At this point some selection takes place and whilst most of the mucus sheath appears to pass back over the collar, some of the finer material within the inner layers of the sheath are drawn into the vestibule of the collarette (see fig. 1). The cilia on the base of the proboscis all beat towards the stalk and the preoral ciliary organ which almost surrounds its point of insertion into the proboscis. The cilia on the base help to propel the sand and mucus aggregating within the vestibule radially towards the mouth.

During the process of ciliary feeding whether within a few cms. of the mouth of the burrow or deeper down in the vicinity of a layer of gravel, the proboscis moved gently to and fro around the walls of the burrow collecting any fragments of debris and sand as they were drawn into the burrow with the currents set up by the pharyngeal apparatus. At other times, when the animal was fully relaxed and quiescent, the proboscis became deeply fluted and almost immobile. Particulate matter entering the mouth on these occasions was sieved off by the branchial apparatus in the manner described on p. 259. When stimulated, or about to resume its activities the proboscis was inflated and resumed its normal elongated egg shape.

2) *Preoral Ciliary Organ* (Figs. 1 & 2)

This organ is present in many enteropneusts and in *B. gigas* it is a deep U-shaped depression in the base of the proboscis, the limbs of which almost meet in the mid-dorsal line above the stalk. This depression is surrounded by a raised epidermal ridge covered with strong densely packed cilia, which beat continuously inwards towards the depression. Within the depression the cilia beat ventrally from the ends of the limbs towards the bend of the U. The cilia on the ridges beat more rapidly than those on the surrounding epidermis.

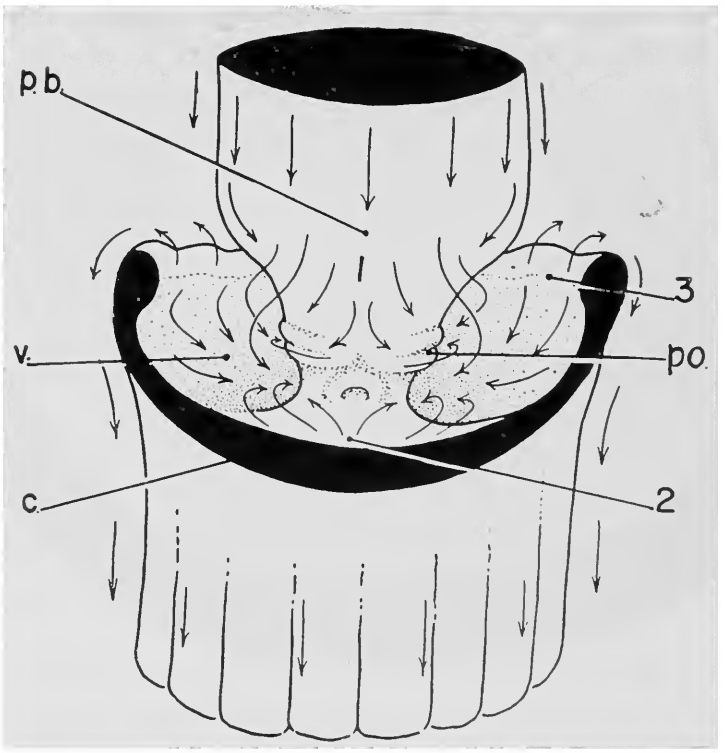

Fig. 1. Dorsal view of the proboscis and the collarette with a portion of the latter cut away to show the paths of the currents within the vestibule, indicated by arrows.

(1) mid-dorsal cleavage of currents over the base and stalk of the proboscis
(2) mid-dorsal cleavage of currents set up by the ciliated epithelial lining of the vestibule
(3) sub-marginal cleavage of currents around the rim of the collarette.

Lettering: — c. cut edge of collarette; p.b. proboscis; p.o. preoral ciliary organ; v. vestibule.

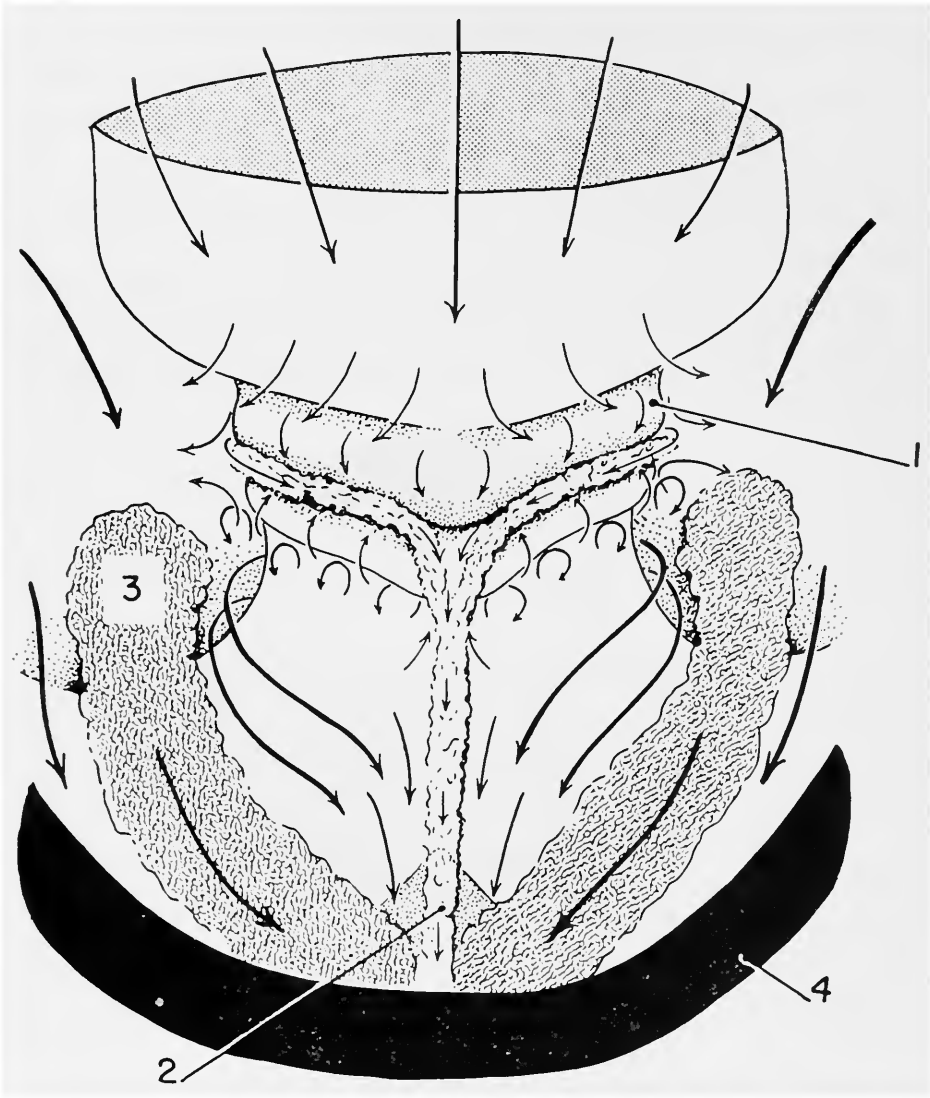

Fig. 2. A ventral view of the proboscis base and stalk. Currents caused by the cilia of these regions are indicated by arrows.

(1) anterior ridge of the preoral ciliary organ.

(2) fine particles and mucus formed into a cord in the depression of the preoral organ and passing ventrally under the proboscis towards the mouth

(3) food stream from the proboscis and margin of the collarette, shown entering from the dorso-lateral regions only. Food enters the vestibule from all parts of the margin.

(4) margin of collarette cut away to display the vestibule.

The cilia of the epidermis within a few mm. from the organ all beat towards it and help to create small eddies and vortices in its neighbourhood from which the cilia on the ridges draw off fine particles and thrust them into the depression. Here they are compacted into mucus cords which pass out of the organ ventrally and are swept into the mouth either by the respiratory current when the animal is filter feeding or with the main stream of sand etc. when the animal is engulfing and burrowing. By this simple process of drawing off minute quantities of the fine particles from the main respiratory and feeding streams the preoral organ seems to fulfil the function of a chemoreceptive organ. These observations tend to confirm those of Knight-Jones (1953) and the author's on *Saccoglossus* and *Protoglossus* (Burdon-Jones, 1956). Coarse particles entering the mouth were never caught up by the preoral organ during the process of ciliary feeding, but must inevitably brush past it when the animal is burrowing. Direct observations of the action of the organ on these occasions were difficult because of the masking effect of the sand being engulfed, but clearly only a very small percentage of the material being swallowed can come in contact with the organ. The comparatively feeble orally directed currents contributed very little to the powerful streams set up by the cilia of the vestibule of the collarette, the buccal cavity and the pharyngeal apparatus. The mucus cords produced by it were no more than by-products of its more likely function of testing the streams of sand, food and water entering the mouth.

3) *Collarette* (figs. 1, 3, 4 & 5)

The funnel-like vestibule of the collarette can embrace the greater part of the proboscis when the latter is fully retracted. It is a highly sensitive, versatile organ, which plays a very prominent role in the feeding and burrowing activities of the animal. The interior face of the vestibule is lined with densely packed cilia which are primarily responsible for propelling some of the material collected by the proboscis and anterior margin of the collarette into the mouth. The cilia lining the dorsal half of the vestibule beat latero-ventrally from the mid-dorsal line and so divide into two streams any material entering this region from the base and more anterior regions of the proboscis. The cilia on the lateral and ventral walls of the vestibule

beat towards the mouth. The cilia on the outer face of the collarette all beat posteriorly and their action helps to clear the excess mucus, sand and food material as it collects in and wells out of the vestibule.

When ciliary feeding is in progress the collar is dilated so that it almost fills the burrow. The margin of the collarette is slightly everted so that the ciliary surfaces of the vestibule are presented to the incoming stream of water and thus assist in propelling it into the pharynx. The mouth is held wide open and the proboscis contributes in the manner described above (see p. 260).

The smooth and sometimes crenate anterior margin of the collarette is capable of considerable flexure and is used to exclude and in some degree select material approaching the vestibule.

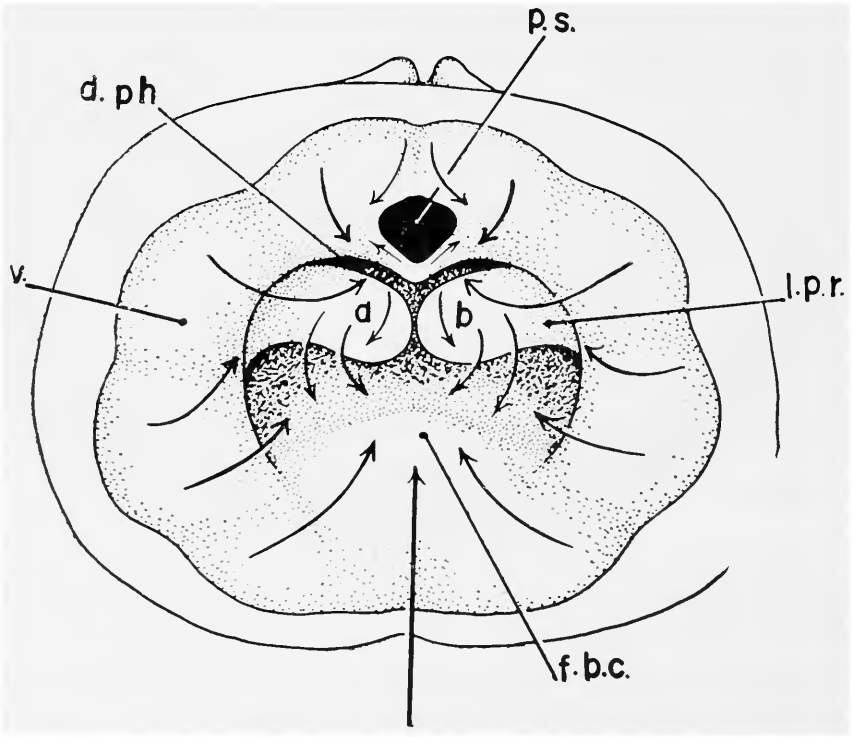

Fig. 3. Anterior of the vestibule, mouth and buccal cavity, with the proboscis cut away to show the ciliary currents, indicated by arrows, converging on the mouth and the rejection currents on the anterior ends of the parabranchial ridges.

Lettering: — d.ph. dorsal pharynx; f.b.c. floor of buccal cavity; l.p.r. swollen anterior end of the left parabranchial ridge; p.s. cut end of proboscis stalk; v. vestibule.

APPENDIX 1

The table given below is a granulometric analysis of 50 gm. samples of different substrates commonly traversed by the burrows of *Balanoglossus gigas,* and of the gut contents and casts. The samples ranged from the surface down to a depth of almost 0.5 m. Column 1 is a surface scraping and 2 was taken from within the next 10 cm depth. Columns 3 to 7 were taken from each succeeding distinct layer of sand and gravel. Columns 8 & 9 are of gut contents and cast respectively.

	Quantity of each size range expressed as a percentage.					
Sample no.	> 1.98 mm	1.98 — 1.65mm	1.65 — 1.17mm	1.17 — 0.88mm	0.88 — 0.42mm	0.42 — 0.3 mm
1	0.28	0.06	0.06	0.04	0.10	0.06
2	3.44	1.04	2.32	2.06	2.10	1.60
3	18.72	6.48	12.08	11.70	13.10	4.12
4	10.90	2.10	3.30	4.36	5.78	1.60
5	16.72	5.00	12.72	15.02	20.98	6.00
6	17.28	3.24	5.32	4.26	3.80	0.88
7	11.08	1.34	2.54	2.36	2.64	0.90
8	3.74	1.14	2.68	2.62	3.40	1.28
9	1.32	0.72	1.68	1.80	3.36	1.34

0.3 — 0.2mm	0.2 — 0.15mm	0.15 — 0.1 mm	0.1 — 0.07mm	0.07 — 0.05mm	0.05 — 0.04mm	< 0.04 mm
0.14	0.36	4.66	79.80	12.42	0.62	1.34
0.54	0.60	2.94	64.92	14.76	1.20	1.48
3.36	1.56	2.40	21.22	3.96	0.20	1.10
1.68	1.74	7.72	53.26	6.60	0.30	2.64
3.32	1.30	2.44	13.82	1.30	0.08	1.24
0.86	1.02	4.94	46.12	6.66	0.82	4.80
0.98	1.26	6.58	57.68	8.66	0.70	3.36
1.38	1.40	6.92	62.04	9.04	0.80	3.56
1.60	1.80	7.02	68.58	8.00	0.62	2.00

This it appears to do primarily according to the size of the object. It is much more selective when the animal is ciliary feeding than when it is engulfing. On the latter occasions the observer gets the impression that the animal is prepared to swallow anything that it can possibly squeeze into the mouth. The boundary between the inner and outer ciliated faces of the collarette was set just within the anterior margin, so that unless this margin was slightly everted the greater part of the material thrown back in the mucus sheath from the proboscis passed on over the collar. Retraction of the proboscis also produced the same result, and tended to stem the flow of material into the vestibule. Thus the intake of food is automatically minimised whenever the proboscis is adversely stimulated. By flexure, eversion and inversion and presentation of the inner or outer ciliated surfaces to the oncoming stream of sand from the proboscis the collarette exercised some degree of selection of the material to be ingested. Any larger particles of sand or debris which evaded this process of selection and entered the vestibule but could not be swallowed, were dealt with in a different way. Ciliary feeding ceased, the mouth closed, the proboscis and the walls of the collarette contracted and the unwanted object and everything else within the vestibule was squeezed out. Local inversion of the margin of the collarette facilitated the expulsion of the vestibular contents and was deepest in and around the objects to be evicted.

Pieces of shell and gravel up to 4 mm. in size have been found within the intestine of large specimens, but only in very small quantities and were probably swallowed when the animal was burrowing rapidly.

4) *Mouth and Buccal Cavity* (figs. 3, 4 & 5)

The mouth lies in the ventral half of the vestibule, immediately below the insertion of the proboscis stalk. The latter is keeled ventrally and triangular in cross section. The cilia on the sides of the keel beat towards the preoral organ and in consequence against the main currents entering the mouth. The food stream from the dorsal surface of the proboscis passes down on either side of the stalk into the mouth. The latter can be closed by muscular contraction and

elevation of the floor of the buccal cavity, thus sealing off the entrance to the ventral pharynx. Closure of the entrance to the dorsal pharynx is effected by the elevation and convergence of the anterior ends (a & b, fig. 3) of the parabranchial ridges.

The buccal cavity is short, about 4 to 5mm. long, circular in cross section and lined throughout with a strongly ciliated epithelium. The greater part of the dorsal half of the cavity is occupied by the protruding ends of the parabranchial ridges. Ventrally the cavity leads straight into the non-branchial region of the pharynx. The roof of the cavity is ridged median dorsally and the cilia on this ridge and on the roof beat latero-ventrally and obliquely down the right and left walls towards the pharynx. Everything solid that enters the mouth is thus driven ventrally onto the floor of the cavity where the cilia beat posteriorly towards the ventral pharynx. The oblique ventrally directed beat of the cilia on the walls of the buccal cavity helps to maintain the cleavage of the food stream produced by the proboscis stalk and the cilia on the dorso-lateral walls of the vestibule. Entry of these cords into the dorsal pharynx was prevented by the swollen anterior ends of the parabranchial ridges (see fig. 3), which moved upwards and inwards whenever any large quantities of sand entered the buccal cavity. As they moved upwards they converged mid-dorsally on the ridge running along the roof of the cavity. In this way the entrance to the dorsal pharynx was sealed off except for a narrow transverse slit which excluded all but the finest particles of sand, but permitted the passage of the respiratory current. The cilia on the anterior ends of the parabranchial ridges (see figs. 4 & 5) all beat antero-ventrally, so that any sand grains which, because of their size or angle of presentation at the entrance to the dorsal pharynx became lodged there were rejected and propelled downwards to join the main stream entering the ventral pharynx. The cilia on the walls of the buccal cavity all beat in a direction which assisted this process of rejection and cleansing at the entrance to the dorsal pharynx.

Under normal feeding conditions coarse material never enters the dorsal pharynx, but fine sand, silt and small organisms in suspension are not excluded and pass directly into the pharynx with the respiratory current. If when the animal is filter feeding, as described

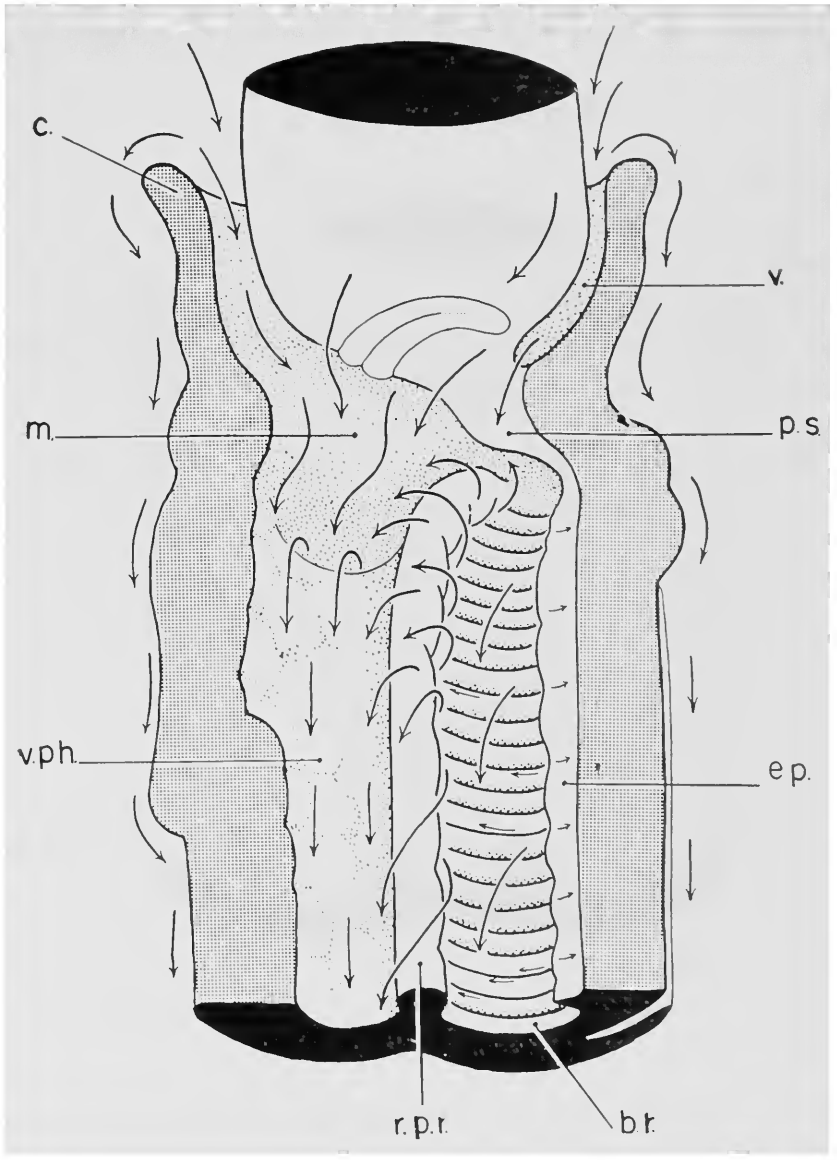

Fig. 4. An almost median vertical section through the anterior end of the pharynx and collar to show the arrangement of the organs within the vestibule and buccal cavity when feeding, and the rejection and cleansing currents set up by the parabranchial ridges.

Lettering: b.r. branchial ridges in dorsal pharynx; c. collarette; ep. epibranchial ridge; m. mouth; p.s. proboscis stalk; r.p.r. right parabranchial ridge; v. vestibule; v.ph. ventral pharynx.

on p. 270, any stray sand grains settle on the ventral side of the vestibule they are borne directly into the ventral pharynx, but any that settle in the dorsal region of the vestibule are carried down one

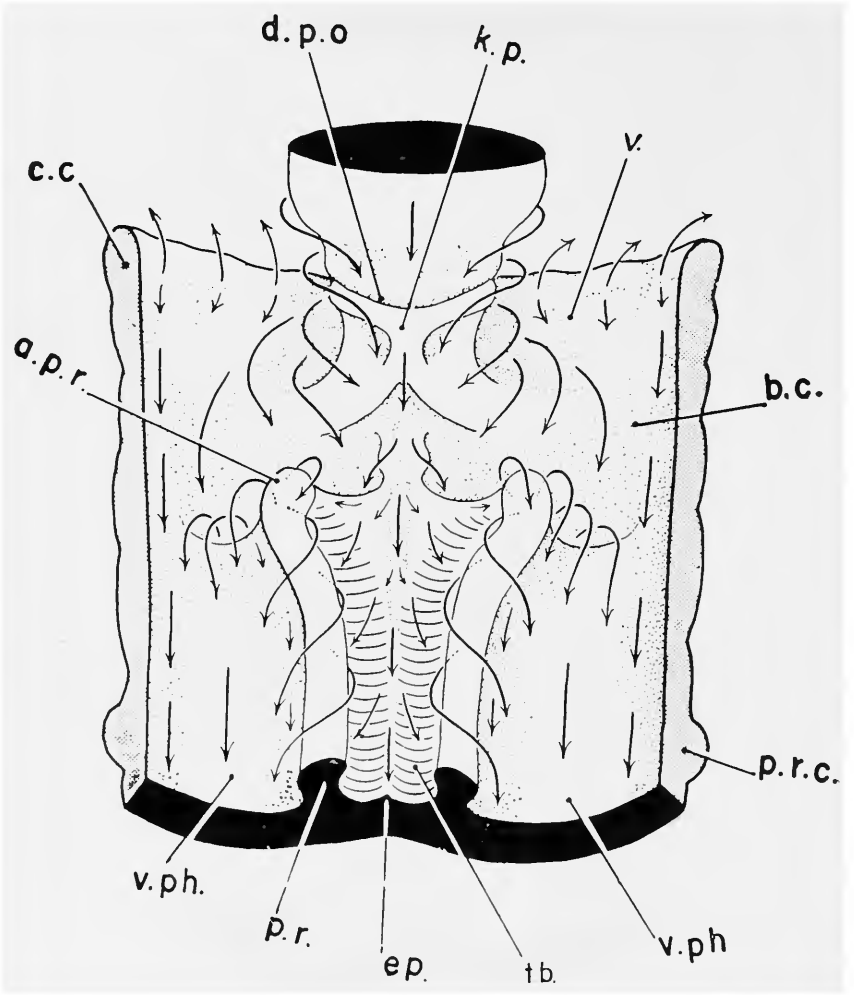

Fig. 5. A dissection from the mid-ventral line showing the ciliary currents, indicated by arrows, within the vestibule, buccal cavity and the anterior region of the pharynx.

Lettering: — a.p.r. swollen anterior end and parabranchial ridge showing rejection currents; b.c. buccal cavity; c.c. cut edge of collarette collar and collar; d.p.o. depression of preoral organ; ep. epibranchial ridge; k.p. keel of proboscis stalk; p. r. right parabranchial ridge; p.r.c. posterior rim of collar; t.b. tongue-bars separating branchial-clefts in dorsal pharynx; v. vestibule.

or the other side of the stalk and along the dorso-lateral walls of the buccal cavity towards the parabranchial ridges which deflect them into the ventral pharynx.

5) *Pharynx* (figs. 4, 5, 6 & 7)

In *B. gigas* the pharynx is separated into dorsal and ventral regions by two prominent parabranchial ridges which protrude from its lateral walls. The dorsal portion contains the branchial apparatus, which comprises about 300 to 350 pairs of branchial clefts extending vertically downwards from the base of a prominent median dorsal epibranchial ridge and terminating just short of the parabranchial

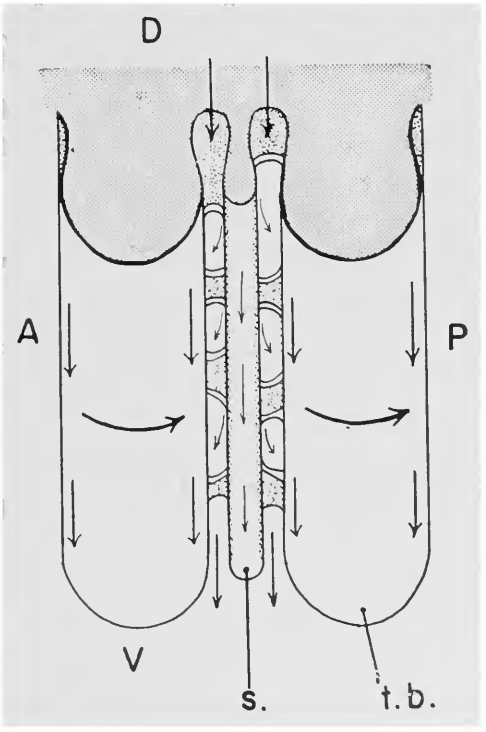

Fig. 6. A small portion of the dorsal pharynx, showing diagrammatically the septum with synapticulae on either side lying deep within the cleft bounded by the prominent tongue-bars, and the ciliary currents as indicated by the arrows.
Lettering: A, anterior; D, dorsal; P, posterior; t.b, tongue-bar; s, septum; V, ventral.

ridges. These ridges are highly glandular and densely ciliated structures. Their elevation and protrusion is under muscular control and determined by the amount of food material in the ventral pharynx over which they form a roof. They extend to the posterior limit of the branchial clefts after which they curve sharply upwards and converge on the mid-dorsal line where they terminate abruptly. When closely adpressed they serve to seal off the posterior end of the pharyngeal apparatus and so help to prevent any fouling of this region by regurgitated food. (see p. 271).

The branchial apparatus is made up of a series of clefts separated from one another by the strongly ciliated and glandular ridges of the tongue-bars and the thinner more deeply set septa. The tongue-bars are considerably thicker and more prominent than the septa and envelop them so completely that they cannot be seen from within the lumen of the pharynx. The synapticulae and apertures leading into the branchial chambers, and thence through the branchial apertures to the exterior, lie on either side of the septa deep within the clefts bounded by the tongue-bars. The frontal cilia on the pharyngeal surfaces of the tongue bars beat posteriorly. The cilia on the parabranchial ridges beat obliquely postero-ventrally from the dorsal into the ventral pharynx. Excision of these ridges showed that their cilia were responsible for the oblique element in the movement of the mucus film over the branchial clefts, because in their absence this film moved directly posteriorly. The cilia lining the lateral walls of the clefts beat ventrally towards the parabranchial ridges. (see fig. 6).

Thin graphite suspensions released at the margin of the collarette were swiftly drawn into the dorsal pharynx and onto the branchial ridges. They were then transported postero-ventrally and accumulated in shallow grooves at the base of the parabranchial ridges. The finer particles in the suspension were drawn into the clefts, sieved off by the mesh of synapticulae and transported slowly ventralwards and ultimately disgorged into the grooves alongside the ridges. Within these grooves the graphite and mucus from the clefts and ridges was gently rolled into a loose cord and transported slowly posteriorly until ultimately caught up by the powerful beat of the cilia on the parabranchial ridges and whisked over into the ventral pharynx. This sieving mechanism was very efficient and prevented particles 1 to 2μ

from passing out through the branchial pores. In this way the branchial apparatus was able to cleance itself within seconds of any fine suspended matter entering the dorsal pharynx and to make a small contribution to the main mass of food passing ventrally. Even coarse sand injected into the dorsal pharynx was dealt with speedily and rarely traversed more than 2 cm. of the pharynx before being swept over the ridges into the ventral regions.

TRANSPORTATION THROUGH THE GUT

1) *Oesophagus* (figs. 7 & 8)

This region is often three to four times as long as the branchial, presenting a wide lumen and a low obliquely grooved epithelium on its lateral walls. It is bounded dorsally by the genital pleurae throughout its length and the coloration of the genital sacs may be seen through its thin dorsal walls. There is no apparent differentiation into regions except for a shallow tranverse grooving on the lateral and ventral walls. The roof is comparatively smooth or only slightly grooved transversely. There are no oesophageal pores.

At the junction of the oesophagus and the pharynx there are two shallow dorso-lateral pockets, the cavities of which are posteriorly directed. Their function is not certain, but they may serve as safety valves to prevent regurgitation of food into the dorsal pharynx in the event of back pressure being exerted upon the food cord in the oesophagus, when the animal retracts quickly or even during the normal rhythmic contractions of the body as the animal burrows. The inflation of these pockets by such a back pressure would also tend to force the parabranchial ridges closer together and so help to seal off the dorsal pharynx as mentioned above.

The epithelium on the walls of the oesophagus is transversely grooved and the fine cilia within these grooves beat dorsally whilst the more powerful ones on the intervening ridges beat posteriorly. Median dorsal and ventral grooves are also present and in them the cilia also beat posteriorly. The transport of the food cord through this region is assisted by peristaltic movements of the walls. Posteriorly, in the transitional region, the grooving of the walls becomes progressive-

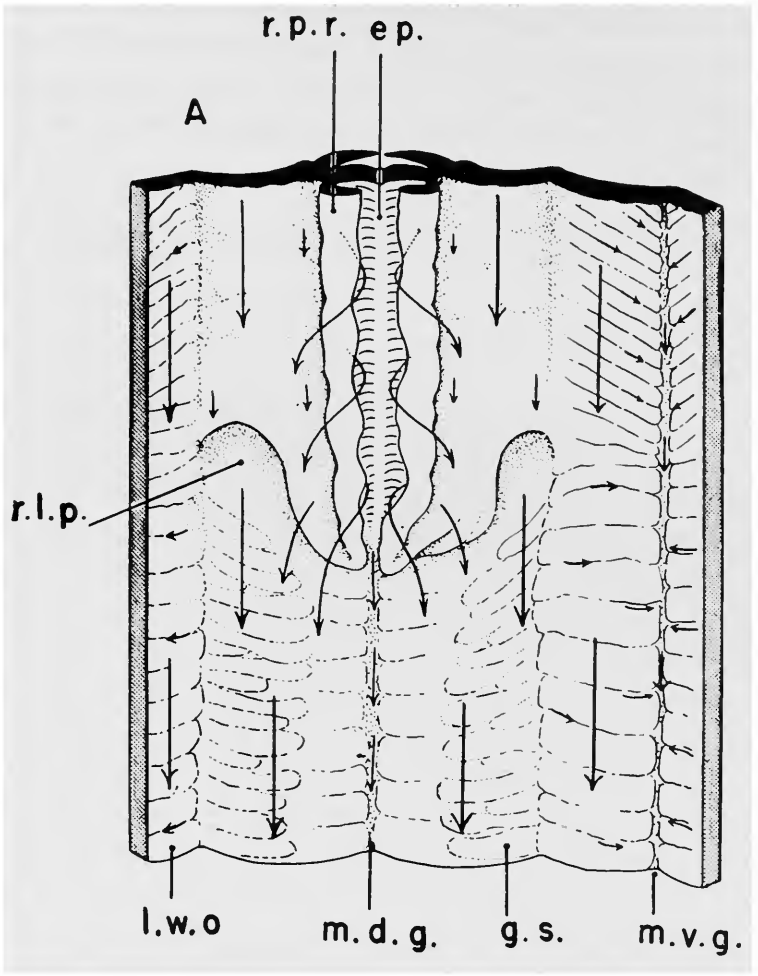

Fig. 7. A view of the posterior branchial region dissected from the ventral side, showing the termination of the parabranchial ridges mid-dorsally and the lateral pockets. The ciliary currents are indicated by arrows.

Lettering: A, anterior; ep, epibranchial ridge; g.s. genital sacs showing through the thin roof of the oesophagus; l.w.o, lateral wall of oesophagus; m.d.g, median dorsal groove; m.v.g, median ventral groove; r.l.p, right lateral pocket; r.p.r, right parabranchial ridge.

ly more oblique and subtends an angle of 45° or more to the mid-ventral line.

2) *Transitional Region* (fig. 8)

Within this region the posterior end of the oesophagus overlaps with the non-sacculated anterior end of the intestine. At this level there are two more shallow depressions in the dorso-lateral walls of the gut, at the point where the genital pleurae terminate externally. The cilia within the grooves bordering on these depressions all beat towards them, whilst those on the neighbouring ridges are very much stronger and beat obliquely towards the mid-dorsal line (see fig. 8). Thus in the transitional region the gut contents are subjected to the action of two major currents converging mid-dorsally, and a number of minor ones converging on the depressions. Such an arrangement will tend to loosen and disperse the food before it passes into the intestine.

3) *Intestine* (figs. 8, 9)

The walls of the intestine are grooved throughout. Anteriorly the grooves on the lateral walls are inclined towards the mid-dorsal line and merge with those of the oesophagus. Dorsally the transition from the deep transverse ridging of the intestine to the smooth epithelium of the oesophagus is more abrupt (see fig. 8).

Posterior to the short transitional region, the roof of the intestine becomes deeply sacculated for about 25% of the overall length of the gut. This is the 'hepatic' region and is divisible by colour into three distinct regions and for convenience these have been designated 1, 2 and 3.

In region 1 the first few sacs are elongated and ovoid in shape and irregularly arranged dorsally. The succeeding 20 or more pairs are flattened antero-posteriorly and auriculate, serially arranged on either side of the mid-dorsal line and a deep brown in colour. In region 2 the sacs are similar in form and arrangement and have a pale olive green to fawn colour. The first 10 pairs of sacs often have a lighter colour than the succeeding 50 or more pairs. Posteriorly

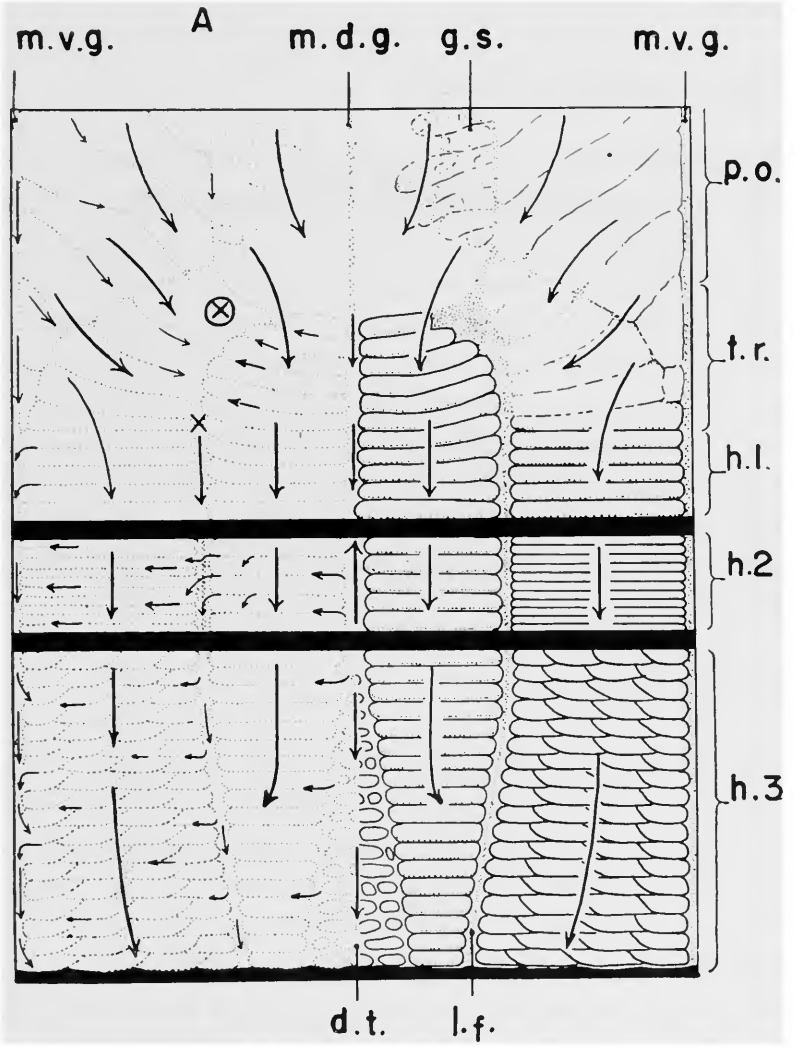

Fig. 8. A semidiagrammatic view of the posterior oesophagus, transitional region and the sacculated anterior end of the intestine as seen in ventral dissection. Stippling has been used to outline the structures on the left of the diagram so that the arrows indicating the directions of the ciliary currents can be inserted. Lettering: A, anterior; d.t, dorsal tract of glandular lobules; g.s, genital sacs showing through the dorsal wall of the oesophagus; h.1, h.2, h.3, first, second and third sacculated regions of the intestine; l.f, lateral furrow; m.d.g, median dorsal groove; m.v.g, median ventral groove; p.o, posterior limit of oesophagus; t.r, transitional region; X, right dorso-lateral depression.

these sacs lose their serial arrangement and laminar form and become bunched ovoid sacs. This form and arrangement persists for the first few centimeters of region 3, but their colour becomes dominantly pink shaded with brown. Posteriorly these ovoid sacs become progressively more widely spaced and once again arranged in a single series on either side of the mid-dorsal line. Their size and shape diminishes from elongated ovoid sacs anteriorly to small globular elevations posteriorly. The total number of sacs in each region is roughly in the proportion of 1 : 2 : 10. Thus in region 3 the number of pairs of sacs may exceed 200.

The pigmentation of these regions is distinguishable internally, the epithelial linings of the cavities of the sacs of 1 and 3 being brown and pink respectively, whilst those of region 2 are a pale yellow or fawn. There is also a ring of deep green pigmentation about 2 mm. wide around the lumen at the junction of regions 1 and 2.

The cavities of the sacs of regions 1 and 2 open into the intestine through slit-like orifices which lie in between the transverse ridges on the roof. These prominent ciliated ridges are opposable and control the opening and closing of the orifices. In region 3 they are replaced by small circular pores at the base of conical depressions. The cilia on the lips of the sacs of region 1 beat towards the mid-dorsal line, whilst those in the transverse grooves on the ventral walls beat ventrally. This mid-lateral divergence of the currents traversing the grooves may further assist in the dispersal of intestinal secretions at this level and in the mixing of the contents of the lumen. At the junction of regions 1 and 2 this divergence ceases and the currents in the transverse grooves all travel ventrally, whilst the median dorsal convergence of the currents which persists throughout region 1 is replaced by a divergence.

In region 1 the median dorsal groove is a shallow depression in which the cilia create a posteriorly directed current. In region 2 the groove is much deeper and tends to form a channel partially cut off from the lumen of the intestine by the overlapping dorsal extremities of the lips of the sacs. Within this channel the ciliary currents are anteriorly directed. Any fine particulate matter introduced at its posterior end is rapidly transported forwards and wells out at the junction of regions 1 and 2. There is also some degree of lateral

dispersion over the lips of the sacs. (see fig. 8). In the absence of a more detailed knowledge of the secretions of the dorsal sacs and other glandular regions in this part of the intestine the nature of the fluids which pass through this channel must *pro tem* remain obscure. In region 3 the channel opens out gradually and the ridging on the roof breaks down and becomes irregularly lobular.

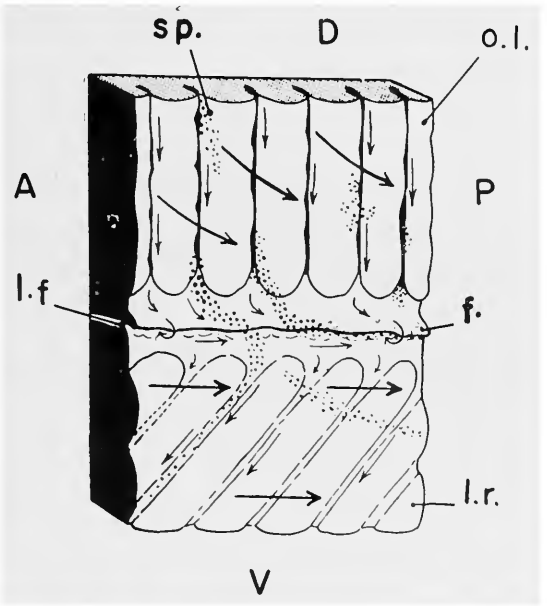

Fig. 9. A portion of the right lateral wall of the intestine (region 2), showing the lateral furrow, and the currents (as indicated by arrows) which disperse the yellow spherules exuding from the dorsal sacs. (Diagrammatic)

Lettering: A, anterior; D, dorsal; f, flange overlapping lateral furrow; l.f, lateral furrow; l.r, oblique ridges on lateral walls of intestine; o.l, opposable lips of dorsal sacs; P, posterior; sp, yellow spherules; V, ventral.

The sacs of regions 1 and 2 move constantly in a rhythmic fashion to and fro as waves of contraction and dilation pass over them in an anteroposterior direction, whilst internally the transverse ridges on the roof roll laterally over one another exposing alternately the linings of the anterior and posterior walls of the sacs. In region 2 this activity of the ridges appears to assist in the extrusion of fine streams

of yellowish cream spherules which seep slowly out of the sacs onto the walls of the intestine, and ventrally towards the lateral furrow (see fig. 9).

These furrows are a prominent feature of the intestine at this level, and consist of two dorso-laterally placed depressions which extend longitudinally from the orifices of the first pair of dorsal sacs (see X fig. 8) throughout the intestine to within a few centimeters of the anus. The ridging on the roof of the intestine ceases abruptly just above the furrows, which are acute depressions in the intestinal walls with an overlapping flange dorsally. Both the furrow and the flange are strongly ciliated and the cilia on the outer face of the flange beat ventrally towards the margin, whilst those on the inner face beat obliquely inwards and posteriorly. The cilia deep within the furrow beat posteriorly.

Posterior to region 3 the ventral groove and the lateral furrows retain their identity to within a short distance of the anus, but the overlapping flange loses its prominence towards the latter end of region 3. The glandular lobules on the roof and immediately lateral to the furrows become more widely spaced until finally those within the furrows disappear whilst those outside them become elongated in an antero-posterior direction before disappearing. (see fig. 8). The grooves on the ventral walls of the intestine become more and more widely spaced posteriorly, so that near the anus they are several millimeters apart, whilst in region 1 they are less than 0.5 mm apart. Latero-dorsally the ridges and the grooves are shallow and set obliquely against the direction of flow of the faecal cord, but the cilia within the grooves on the walls all beat ventrally and those on the shallow ridges beat very strongly analwards. The passage of the faecal cord along this part of the intestine is primarily effected by ciliary activity assisted in some degree by a weak peristalsis of the walls. The anus is terminal and closed by a sphincter.

CONCLUSIONS

Balanoglossus gigas obtains its food in three ways:

a) by engulfing large quantities of the substratum collected and selected by the proboscis and the collarette, and digesting the debris

and organisms taken in with it as well as the bacterial film on the sand grains,

b) by ciliary feeding with the proboscis and collarette on the detritus and suspended matter washed into the burrow by the tide, or draining into it from a gravel substrate, or drawn into it by the respiratory current, and

c) by sieving the respiratory current, which although it is automatic and always accompanies a) and b) can also provide a steady trickle of nutrient material into the ventral oesophagus when both are inoperative.

The interstitial fauna engulfed or seived out of the sand and gravel layers may also be a potential source of food, although little is known of its composition in these substrates.

The granulometric analysis given in Appendix 1 indicates a certain degree of selectivity in favour of sand within the range 0,05 to 0.1 mm. Over 80% of the gut contents and the casts was within this range. Since fine sand of this size was also dominant in the surface layers (columns 1 and 2) it seems probable that these animals had been feeding at or near the surface. Alternatively selective feeding may have taken place at or within one of the gravel layers, because these also contain 40 to 60% of sand within this range (columns 4 and 6).

Whereas the greater proportion of the contents of the gut are derived from method a) the most nourishing component will probably be collected by method b) supplemented by c).

SUMMARY

Balanoglossus gigas lives in substrates composed of layers of sand and gravel. The collection of food material in this very large enteropneust is effected by a combination of engulfing and ciliary feeding. On the shores examined, it tended to feed selectively on fine particulate matter, the collection of which involved the cilia of the proboscis, collarette, vestibule, buccal cavity and the pharynx. Fouling of the branchial apparatus was prevented by a ciliary cleansing mechanism which automatically supplemented the general supply of food in the ventral pharynx.

The ciliary tracts and currents throughout the intestine and their role in the propulsion of the food cord, the mixing of the gut contents and dispersal of intestinal secretions are described.

RESUMO

Balanoglossus gigas vive em substrato de camadas de areia fina e grossa (cascalho). A coleta de material alimentar por êste enorme enteropneusto efetua-se por meio de uma combinação de tomada de alimento por engolimento e de movimento ciliar. Nas praias examinadas, êste animal procura alimentar-se seletivamente com material finamente reduzido, participando na coleta do mesmo os cilios da proboscis, do colar, do vestíbulo, da cavidade bucal e do faríngе. Obstrução do aparelho branquial é prevenida por um mecanismo de limpeza por meio dos cilios que, automàticamente, suprem a tomada de alimento pelo faríngе ventral.

Descrevem-se os tratos ciliares e as correntes através do intestino e sua função na propulsão do cilindro de alimento, a mistura do conteúdo intestinal e a dispersão das secreções intestinais.

ACKNOWLEDGEMENTS

I am very grateful to the University of São Paulo for its financial support and for all the facilities placed at my disposal during my visit. I am also very grateful for the invaluable assistance given by Professor Paulo Sawaya — Director of the Marine Biological Laboratory of São Sebastião and Head of the Departament of General and Animal Physiology of the University of São Paulo — and his staff and in particular Mr. J. A. Petersen, and to whom I am further indebted for the data give in Appendix 1.

The Aquadag suspensions were very kindly prepared by Acheson Colloids Ltd.

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ON SOME LUNULITIFORM BRYOZOA

by EVELINE and ERNST MARCUS

(with 5 plates)

Contents

MATERIAL AND LOCALITIES

The present study comprises: a) *Cupuladria canariensis* (Busk, 1859), b) *Discoporella umbellata* (Defrance, 1823), c) its var. *conica* (Canu & Bassler, 1930), and d) *Mamillopora cupula* Smitt, 1873. Forms a, c, and d are new for the Brazilian coast. We obtained material from seven different localities which follow in the sequence from South to North:

1) Off the coasts of Paraná and São Paulo, Lat. 26° 19' — 25° 45' S, Long. 46° 36' — 46° 58' W, 125 — 150 m; 26. IX. 1955 (a, c).

2) Alcatrazes Island, Lat. 24° 03' S, Long. 45° 40' W, 32 m (principally b, a few c).

3) E of Santos, Lat. 24° 02' S, Long. 46° 07' W, 23 m (b).

3a) Ibid., Lat. 23° 57' S, Long. 46° 09' W, 16 m; 1. VII. 1960 (b).

4) Bay of Flamengo, 14 km W of Ubatuba, Lat. 23° 57' S, Long. 45° 06' W, about 4 m (b).

5) Canal between Anchieta Island (former Porcos Island) and the continent, 14 km W of Ubatuba (see 4), 30 m; 6. V. 1958 (b, c).

6) Near Cabo Frio, Lat. 22° 57' S, Long. 42° 01' W, about 3 m; VII. 1957 (a, c).

7) Off mouths of River Amazon, Lat. 02° 23' N, Long. 48° 26' W, 70 m (a-d).

7a) Ibid., Lat. 02° 58' N, Long. 49° 19' W, 71,5 m (a-d).

The bottom of localities 7 and 7a is silt, that of the others silty sand. The sand grains of our most important locality, no. 4, whence living colonies were examined, generally measure 50-200μ and more, up to 300μ. The sand is especially coarse (grains 0,5-3 mm) at locality 5, whose sand is rich in fragments of shells. The sample of locality 6 consists of fragments of shells, broken and complete Bryozoa.

ACKNOWLEDGMENTS

Dr. Edmundo F. Nonato, Head of the Northern Research Base of the Oceanographic Institute São Paulo, during his ecological survey of the Bay of Flamengo (locality 4) found colonies of *Discoporella umbellata,* collected further specimens together with us, and set up aquaria for observing them alive. Lic. Luiz Roberto Tommasi kindly gave us his samples collected at localities 3, 3a, and 6. From the Oceanographic Institute (Director: Dr. Ingvar Emílsson) we received the material from localities 1, 2, 5, 7, and 7a by courtesy of Drs. Liliana Forneris and Walter Narchi. To our helpful colleagues we express our cordial thanks, and remember our dear friend, the late João de Paiva Carvalho, gratefully, who collected the material of locality 5 together with Dr. Edmundo F. Nonato.

ENVIRONMENT OF LUNULITIFORM BRYOZOA

Mud, silt, and sand are unfavourable for most of the Bryozoa whose larvae generally settle on rocks, stones, shells, algae and other substrata. However species whose larvae undergo metamorphosis after fixation on a sand grain or foraminifer, and whose colonies grow out free beyond this small point of attachment, can thrive on sand or mud. Some of them are anchored to the soft bottom by chitinous or membranous rootlets which may terminate with delicate ramifications (Harmer 1957, p. 649); others, e. g. those of the present study, lie loosely on the bottom. Here competition with arborescent species is insignificant, and that with encrusting ones nearly absent. So the number of free colonies is often abundant in this biotope. At locality 4 a grab whose surface is about 10 × 10 cm hauled 1 litre of sand per sample. As 100 living colonies were obtained with 4 seizings, the density of the population can be computed to 2-3 thousand zoaria per sq. metre. In the eastern Atlantic, near the Cape Verde Islands, and on the coast of Liberia Studer (1887, p. 13, 27) dredged so many lunulitiform Bryozoa that the dead colonies constituted a noticeable component of the bottom.

In the upper littoral where wave action is strongly felt (Stach 1936, p. 63) species with free colonies do not occur. On the other hand, they exceed an upper limit of about 25 m (l. c.) in sheltered localities. This is shown by our localities 4 and 6, and indicated in the literature, e. g. Robertson (1908, p. 315) 7 m near San Pedro, S of Los Angeles, and Osburn (1947, p. 18) 3,7 m in the Gulf of Maracaibo. Samples with all or almost all colonies dead, as those of our localities 7 and 7a, were probably accumulated by currents and do not represent the normal biotope of these species. This possibility should be taken into consideration when isolated findings of numerous lunulitiform Bryozoa are evaluated paleoecologically.

Exceptionally lunulitiform Bryozoa (species a) were caught at the surface of the ocean (Silén 1942a, p. 13; 1947, p. 10). Probably they were lifted by upwelling water. According to Stach (1936, p. 63) the benthic lunulitiform Bryozoa are restricted to places on the bottom where current action is strong. *Species a* found in the pelagial has neither voluminous nor heavily calcified zoaria, so that

they may be able to float for a certain time, but we do not believe that they swim actively.

The shape of lunulitiform Bryozoa, resembling a disc with a more or less elevated centre, a bowl, umbrella, or cup, is not natatory. This form is suitable for an aquatic animal that lies on soft bottom. When the colony is cupuliform, sediments drifting down upon the sea floor will not bury the individuals. Moreover vibracula, these cleaners developed especially in anascan Cheilostomata with their membranous frontal wall, occur in the lunulitiform colonies of widely different species. Full conical colonies as those of form c are heavier than the inverted saucer-shaped ones. They remain smaller, so evidently avoiding to be buried in the sand by their weight.

SYSTEMATIC REMARKS

By natural selection the free round colonies of systematically distant species have become similar, and, as in our material, were found together at the same locality (Canu & Bassler 1918, p. 119; 1923, p. 81). "Lunulitiform" and "selenariiform" are descriptive terms used for such colonies, indifferently to which family the species belongs. Convergent shape and high geological age makes the taxonomy of the Bryozoa with lunulitiform colonies rather complex. It is not our intention to exhaust this subject. However for an evaluation of the morphology, in part specific and in part phenotypic, we cannot avoid a summary systematic discussion. Moreover a survey of the geographical distribution of the species studied here requires critical comparison of the previous descriptions and figures.

Three cup- or saucer-shaped Bryozoa of the present material belonging to different taxa of the Cheilostomata occur on the Brazilian coast, in the West Indian region (Osburn 1947, p. 46) and on the American Pacific coast (Hastings 1930, p. 714, 718, 733). These are:

1) *Cupuladria canariensis* (Busk 1859a, p. 66) of the Suborder Anasca (Levinsen 1909, p. 12, 88, 91), Division Malacostega (Levinsen 1902, p. 2), Family Cupuladriidae (Lagaaij 1952, p. 31);

2) *Discoporella umbellata* (Defrance 1823, p. 361) of the Anasca, Division Coilostega (Levinsen 1902, p. 2), Family Calpensiidae (Canu & Bassler 1923, p. 67); and

3) *Mamillopora cupula* Smitt (1873, p. 33) of the Suborder Ascophora (Levinsen 1909, p. 12, 88, 213), Division Ascophora Vera (Harmer 1957, p. 645), Family Mamilloporidae (Canu & Bassler 1927, p. 9, 22).

These species evidence the marine Central America connexion of older Tertiary times (Ekman 1935, p. 57).

CUPULADRIA CANARIENSIS

The name of the genus is justified in the introduction to the following *Discoporella umbellata;* our concept of the species *C. canariensis* is evidenced by the succeeding list of the geographic distribution:

Brazil, off the coasts of Paraná and São Paulo, 125-150 m; near Cabo Frio, about 3 m; off mouths of River Amazon, 70-71,5 m (present material). Caribbean Sea, from N coast of Venezuela (Osburn 1947, p. 10) to Yucatan (Silén 1942a, p. 14); Gulf of Mexico (Canu & Bassler 1928b, p. 16). Lesser Antilles, also from the stomach of a sea-urchin (Silén 1942a); Pôrto Rico (Osburn 1940, p. 354); Florida, incl. Tortugas Keys and Key West (Smitt 1873, p. 10; Osburn 1914, p. 194; Canu & Bassler 1928b; Silén 1942a). Azores, also on the surface of the ocean (Silén 1942a); Madeira (Busk 1859a, p. 66; Norman 1909, p. 289); Canaries (Busk 1859a; Calvet 1907, p. 393). Coast of Liberia (Waters 1888, p. 37); Mauretania, Cape Blanco (Calvet 1907; Canu & Bassler 1928a, p. 16); coast of Morocco (Smitt 1873; Canu & Bassler 1925, p. 13) and Algeria (Waters 1921, p. 412; Dartevelle 1935, p. 560; Gautier 1955, p. 231). American Pacific coast from Cedros Island, Lat. 28° 12' N, Long. 115° 15' W (Osburn 1950, p. 34) and Gulf of California (Canu & Bassler 1929, p. 73; Soule 1959, p. 8-9) along the coasts of Mexico, Costa Rica and Panama to Colombia (Hastings 1930, p. 714), Galapagos and Ecuador (Osburn 1950).

C. canariensis was found in shallow water, about 3 m (present material from Cabo Frio, and Osburn 1947, p. 10) to 259 m (Calvet 1907). According to Osburn's rich material (1950, p. 34) the species is most frequent between 18 and 36 m. Geologically it appears first

in the Lower Miocene (Canu & Bassler 1923, p. 29; Lagaaij 1952, p. 34).

The preceding list is based on the exclusion of *Cupuladria guineensis* (Busk 1854, p. 98) and *C. monotrema* (Busk 1884, p. 207). For the inclusion of the material from the coast of Liberia Waters' figure 12 (1921, pl. 30) with numerous basal pores was decisive.

C. canariensis to which our material belongs is characterized by parallel series of chambers which permeate the basal wall of the zoarium. They were first drawn by Busk (1859b, pl. 13, f 2 e) and analyzed by Waters (1921, p. 400). In *C. guineensis* these chambers do not occur; the basal wall contains fine striations, perpendicular to the surface of the colony (Hastings 1930, pl. 8, f. 39). In many cases the zoaria of *guineensis* are thinner than those of *canariensis* (Silén 1942a, p. 9).

Hastings (l. c.) confirms Harmer's statement (1926, p. 267) that *canariensis* has longer and narrower zooecia than the Indowestpacific *guineensis,* narrower cryptocyst, and larger pores on the basal surface. We do not contest these differences when numerous colonies proceeding from the Atlantic and Indic Ocean are compared. However within a given material, as the present one, the measurements of the zooecia vary, and the same holds for the breadth of the cryptocyst. Large and small pores as well as smooth basal surfaces occur in our colonies. The diameter of these pores depends on the stage of growth of the basal chambers (Silén 1942a, p. 9).

According to Hastings (1930, p. 715) also the largest colonies of *C. monotrema,* which are as large as the largest of *canariensis* in the British Museum, have only one layer of kenozooecia on their basal surface. By reason of this character we have classified our material collected N and S of the locality of *monotrema,* off Bahia, as *canariensis*. As young colonies of *canariensis* have one layer too, it was necessary to determine our material from Cabo Frio, rich in young colonies, with help of the relatively few large ones. The "monotrematous" condition of the basal surface of *monotrema* has been emended by Hastings' re-examination of the "Challenger" material. "There are fewer pores on the basal surface of *C. monotrema,* and, though those at the edge are larger than those in *canariensis,* they are soon nearly filled up" (p. 715). We therefore think that the

above-mentioned material from Liberia can be placed with *canariensis*. Our material contains small colonies with single pores only, but the larger ones have one pore in some areae and several in others. We cannot judge the operculum of *monotrema*, because our material is *canariensis*. In the latter the operculum can assume the appearance of a basal thickening set off from the frontal membrane, when it becomes somewhat curved by drying. The distal and lateral rims of the opercula in our material are thick; proximally only two lateral sclerites on which the occlusors insert are thickened, the middle passes without limits into the frontal membrane.

The large heterozooecia of *monotrema,* described by Busk as avicularia, and also seen by Kirkpatrick (Waters 1888, p. 37), do not constitute a specific character. They are actually vibracula (Hastings 1930, p. 715) and will be mentioned in the following.

The ancestrula of *C. canariensis* is single (Fig. 1, a), not double (Waters 1926, p. 426). The primary can be recognized by its regular oval form, while the opposite zooecium, which Waters considered as also ancestrular, has somewhat irregular outlines. In Waters' diagram (p. 425), it is true, the contours of this zooecium are as regular as all others, but in his drawing (pl. 18, f. 10) the single primary is the one directed downwards, and the opposite zooecium is not completely ovoid. Young colonies with the zooids d still developing evidence the sequence of the central individuals clearly. Zooecium c, Waters' presumed second primary, occupies the space left between the earlier formed zooids b, and its shape is influenced by their walls. Hence it is often narrower than the primary and the first buds, and its contours are irregular.

The actual centre of young colonies is generally triaxial. The distal-proximal extension of the ancestrula (a) is the first axis; the two first buds (b) form the two other axes and diverge from the primary at angles of 120°. By the development of the third bud (c) between the two first, and of two further individuals (d) between the first buds and the ancestrula, a six-rayed star is brought about as in Waters' figure 11 (1921, pl. 30). Occasionally the first buds stand at right angles to the primary. After development of zooid c, the intervals between c and the two zooecia b allow for budding two further individuals d, and so the centre of the colony appears as an

8-rayed star. The primary and the two first developed zooecia (b) are generally smaller than the later ones, whose growth is sustained by food supplied by more numerous polypides.

Sometimes the larva settles on very small substrata, in other cases on bigger ones, measuring, e. g., 1 × 2 mm. A zoarium on a large sand grain was drawn by Waters (1921, pl. 30, f. 12). Under these conditions the colony grows encrusting for a long time before it incorporates the substratum, or even attains its specific size before it reaches the borders of the stone which remain free. Colonies on big substrata which had grown distorted were found by Osburn (1950, p. 34). He was right to consider *Cupuladria elongata* Sakakura (1935, p. 6) as a distorted *C. guineensis* (Bsk.).

Our material contains many young colonies consisting of the central star only and evidently without any substratum. Some were slowly and partially decalcified in order to preserve a possible minute grain or the vestiges of its incorporation by the basal walls of the first zooecia. It is difficult to explain the inexistency of a substratum satisfactorily. Perhaps the least improbable hypothesis is the settlement of the larva on a substratum to which it did not adhere firmly with its basal wall and fell off immediately after metamorphosis. Another possibility is, if the first hold was a calcareous fragment, its absorption for building the walls of the first zooecia.

Of course the first polypides of the colony normally degenerate first. In our material dead central zooecia are not closed by a more or less porous cryptocyst, as happens in *Cupuladria capriensis* (Waters 1926, p. 432) or in the colony from Anguilla, Lesser Antilles, which Silén (1942a, p. 14) considers as possibly belonging to *canariensis*. As far as our zoaria were caught alive, their central individuals were complete or regenerated (Fig. 2). Regeneration had brought forth an autozooid or a vibraculum (av-dv) bigger than that (v) at the distal end of the autozooecia and with a broader, not longer, seta (si) than the ordinary ones (s). Replacement of an autozooecium by an avicularian heterozooecium was discovered by Levinsen (1907, p. 154) and later described by Buchner (1918, p. 458), Canu & Bassler (1920, p. 67), Silén (1938, p. 329), and Marcus (1938, p. 74). In the present cases of substitution of an autozooid by a vibraculum the original proximal-distal direction is sometimes inverted (Fig. 2, cv), and

the old walls are included in the rebuilding. In one of our colonies the six autozooids of the central star and further nine were replaced by large vibracula. This type of total regeneration was first observed by Hastings (1930, p. 714); it is common in *C. canariensis*. In the 8-rayed central star of Smitt's figure 70 (1873, pl. 2) the primary directed to the right and downwards and the adjacent first buds directed to the right and left are evidently regenerated large vibracula with the characteristic oblique chambers. Also in the central region of Hastings' colony from the coast of Colombia (1930, pl. 8, f. 40) and in the ancestrula of a zoarium from the Pliocene (Lagaaij 1953, pl. 1, f. 1 a) substitution of an autozooid by a vibraculum is figured. Several large vibracula are also found in the new central area of colonies originated by regulative budding of a fragment. This zoarial regeneration is described in the following. When the vibracular bristle is lost, as frequently in our material, the rostrum or beak-like opesia (subopercular field) resembles an avicularian opesia. This was certainly the case in Busk's material of *monotrema*.

Autozooecia as well as vibracula produce the above-mentioned basal chambers. They are morphologically kenozoecia (Waters 1921, p. 400; Hastings 1930, p. 715) connected with one another by pores (Waters, pl. 29, f. 2). The one to four series of thick-walled chambers corresponding to one surface zooecium form a common prismatic block whose limits are indicated by stronger brown lines of the basal membrane or epitheca. These limits do not coincide with those of the frontal zooids but with the mid-lines of the latter. Young colonies have thin-walled kenozooecia with spacious central cavities. Their weight is certainly lower than that of older zoaria. In no case, however, is their specific weight so reduced that the 9 colonies fished in the plancton (Silén 1942a, p. 13, no. 7; 1947, p. 10) could float without a sustaining current.

Our material contains fragments along whose breaking-lines numerous zooids produce regenerative buds. Such will be described in *Discoporella umbellata*. Our biggest colony of *C. canariensis* (Fig. 3) has originated from a fragment. This is recognized by the directions of the rows of prisms on the underside. In the centre of this zoarium there is an area with parallel rows of prisms belonging to the fragment. This area is surrounded by radiating rows of the

growth after breaking. By comparison of lunulitiform, fossil and recent (*C. canariensis*) species from different localities Dartevelle (1933, p. 69-71; 1935, p. 560) came to the conclusion that agitated water is responsible for the breaking of the colonies (see also Brown 1952, p. 140). Our following observations concerning *Discoporella umbellata* confirm Dartevelle's statement that the regenerative reconstitution of the zoarial form proceeds rapidly. When the zooids near the break produce buds, budding is stopped temporarily on the opposite side. So the colony grows as a coordinated whole, though there is no colonial centre. Silén (1942a, pl. 3, f. 10-12) gave instructive photographs of a regenerated zoarial fragment of *Cupuladria guineensis* (Busk).

DISCOPORELLA UMBELLATA

Smitt (1873, p. 14), Levinsen (1909, p. 155) and Harmer (1926, p. 262-63, 266) recognized that membraniporine as well as microporine species had been united in *Cupularia*. Waters (1921, p. 415) also declared that "a new genus must probably be created for *Cupularia lowei* Busk (1854, p. 99) and *C. umbellata* (Defrance 1823, p. 361, pl. 47, f. 1-1 b)", but did not mention their microporine character.

Canu & Bassler (1919, quoted from 1920, p. 103) introduced the genus *Cupuladria* for a membraniporine species whose original name (Busk 1859a, p. 66; 1859b, p. 87) is *Cupularia canariensis,* not *Membranipora canariensis,* as Canu & Bassler wrote. *Membranipora canariensis,* erroneously given as original name by Jelly (1889, p. 79), is the name used by Smitt (1873, p. 10) in connexion with his above-mentioned distinction between membraniporine and microporine species of *Cupularia*.

The name *Cupularia* was applied by Canu & Bassler (1923, p. 75) to *Lunulites umbellata* Defrance 1823 (see above), a microporine form. Hastings (1930, p. 717-18) did not accept this arbitrary nomenclature. She explained that the first generic name for a microporine "*Cupularia*" is *Discoporella* d'Orbigny (1852, p. 472) and abandoned *Cupularia* whose fossil type-species cannot be defined as membraniporine or microporine. As Bassler (1935, p. 86, 99) formally adopted Hastings' view, the nomenclature of the three genera is now established.

However the confusion as to their contents continues. Canu & Bassler (1923) allocated their genus *Cupularia* to a new family Calpensiidae (p. 67) characterized by the diagnosis "No ovicell. The cryptocyst is perforated by one or two opesiules". Not even the type-species, *C. umbellata* corresponds to this diagnosis, as it has a row of opesiular pores on each side of the cryptocyst. In the description of *C. robertsoniae* (ibid., p. 82) the cryptocyst is described as perforated laterally by seven large opesiules, hence in contrast with the diagnoses of genus and family. Also in the treatise on invertebrate paleontology (1953) Bassler gave a generic diagnosis of *Discoporella,* "zooecia porous with 2 rounded opesiules", discordant with the type-species.

As *Discoporella* d'Orbigny has received a complete and modern definition (Hastings 1930, p. 718), the mentioned incongruities do not affect the state of *D. umbellata* (Defrance 1823). Worse is Canu & Bassler's incorporation of membraniporine species in their microporine genus *Cupularia*. *Lunulites haidingeri* Reuss 1847 (see Lagaaij 1953, p. 35), *Discoflustrella doma* d'Orbigny 1853, frequently called *Cupularia johnsoni* Busk (1859a, p. 67) by neozoologists (Waters 1921, p. 413; Silén 1942a, p. 17), and other malacostegous species come in Canu & Bassler's system under the Coilostega Levinsen 1902, or Coelostega as Harmer (1926, p. 188), Silén (1942b, p. 53 etc.), Brown (1952, p. 122), and Lagaaij (1952, p. 37) prefer to write. Canu & Bassler knew (1929, p. 144) that a microporine cryptocyst with a broken centre is similar to a membraniporine opesia into which calcareous denticles project from the edge of the cryptocyst, and that only microscopic examination reveals the difference of these two types. Nevertheless Bassler (1935) codified the zoological error of 1923 in his widely distributed catalogue (p. 86, 99) alotting all species of *Cupularia* published by Busk, Canu & Bassler, and others to *Discoporella*.

Therefore Silén (1942a, p. 15) following Canu & Bassler (1928; 1929) applied *Cupularia* to *umbellata, lowei,* and *johnstoni,* two coilostegous and one malacostegous form, and Osburn (1940, p. 374), after Bassler's catalogue (1935) called *doma* a *Discoporella,* though he correctly mentions that the spinous processes of its cryptocyst never coalesce. Maturo (1957, p. 41) followed Osburn.

Discoporella umbellata occurs in warm and warm-temperate waters of the Atlantic Ocean, enters the western Mediterranean Sea and reaches the eastern Pacific. Canu & Bassler's opinion (1928b, p. 64) that the species on the American side of the Atlantic is now much less common than in the E Atlantic and in course of extinction is not supported by the following list.

Argentina, Puerto Militar of Bahia Blanca (Canu 1908, p. 275) Post-Pampean, i. e., Recent (p. 327); off La Plata (Silén 1942a, p. 16). Brazil, off coasts of Paraná and São Paulo; São Paulo, between Santos and Ubatuba (present material); off Rio de Janeiro and at Cabo Frio (Silén 1942a); off mouths of Amazon (present material). Caribbean Sea, from the northern coast of Venezuela to Yucatan (Silén 1942a; Osburn 1947, p. 18). Gulf of Mexico (Canu & Bassler 1928b; Silén 1942a). Florida, incl. Tortugas Keys and Key West (Smitt 1873, p. 15; Osburn 1914, p. 194; Silén 1942a). North Carolina, off Cape Fear River and Beaufort (Smitt 1873; Osburn 1914), both localities S of Cape Hatteras. Middle Atlantic (Silén 1942a); Madeira (Busk 1854, p. 99; Norman 1909, p. 290; Soule & Duff 1957, p. 100 mistook this for "Spain"); Canaries (Calvet 1907, p. 393); coast of Algeria (Waters 1905, p. 11; 1921, p. 413; Canu & Bassler 1923, p. 76: explanation of text-fig. 13 A). ?South Africa, Cape St. Blaize, Lat. 34° 11' S, Long. 07° 10' E (O'Donoghue 1924, p. 39). American Pacific coast, from Point Conception (Lat. 34° 25' N, Long. 120° 30' W), the northern Channel Islands (Osburn 1950, p. 114) and San Pedro (Robertson 1908, p. 314), the Gulf of California (Soule 1959, p. 34), along the Central American coast (Hastings 1930, p. 718) to the Galapagos Islands (ead.; Canu & Bassler 1930, p. 11; Silén 1942a) and the continental coast of Colombia (Hastings 1930) and Ecuador, Point of Santa Elena, Lat. 02° 15' S, Long. 80° 55' W (Osburn 1950) and Gulf of Guayaquil (Silén 1942a). Pacific Ocean, between California and Hawaii, Lat. 29° 50' N, Long. 141° 40' W (Canu & Bassler 1929, p. 144).

Discoporella umbellata was found in depths from 4 m (Osburn 1947; present material) and 7 m (Robertson 1908) to 4.979 m (Canu & Bassler 1929). In the regions explored by the Allan Hancock Foundation (Osburn 1947; 1950) it is most abundant between 36 and 73 m. For the first time the species appeared in the Upper Aqui-

tanian of France (Canu 1916, p. 322), that is Lower Miocene (l. c., p. 321).

In the preceding list *Cupularia lowei* Busk (1854, p. 99) is considered as identical with *D. umbellata*. The doubts as to this identity (Hastings 1930, p. 719) disappear in the following study. As Hastings (l. c.) re-examined O'Donoghue's material (1924, p. 39) we also include its locality with a question mark, though O'Donoghue's reference to a malacostegous species, *Cupuladria owenii* (Gray 1828, see Busk 1854, p. 99), indicates that his classification was influenced by a geographic conception. Waters (1905, p. 11), Hastings (1930, p. 719), and Osburn (1950, p. 113) have shown that *Discoporella berardana* d'Orbigny (1853, p. 474), *Cupularia canariensis* Robertson (1908, p. 314; non Busk), and *Cupularia robertsoniae* Canu & Bassler (1923, p. 82) are synonyms of *Discoporella umbellata*. Hincks' *Cupularia umbellata* from the Mergui Archipelago on the coast of Tenasserim (1887, p. 125), already questioned by Waters (1921, p. 414), belongs to *Cupuladria guineensis* (Busk 1854, p. 98), as verified by Hastings (l. c.). In the dredgings of the Travailleur and Talisman (Calvet 1907, p. 393) only the colony from the Canary Islands comes under *D. umbellata,* while the material from 1900 m near the Cape Verde Islands, compared with Busk's *Cupularia denticulata* (1859b, p. 85), seems to be a *Cupuladria* (see Lagaaij 1952, p. 35).

THE COLONY

The colour of living colonies is yellowish red, darker on the upper than on the basal surface. The skeleton begins transparent, so that the black digestive tracts shine through the basal walls, and becomes opaque white with increasing thickness. The polypides and the soft parts of the vibracula are red, storing alimentary amoebocytes dark red. In the vibracular chambers and the opesiular passages the dark red cords of these cells are especially distinct.

The diameter of the colonies is commonly up to 6 mm, and the centre of such zoaria rises 1-1,5 mm above the border. One fragment from locality 2, whose centre and border are wanting, is 7 mm long; the diameter of the complete colony must at least have been 15 mm.

Some thin-walled colonies from locality 5 are rather high, they measure 3 mm in height, 9 mm in diameter.

The origin of a zoarium from a larva, or by the process described as zoarial budding in the following, can be recognized in all colonies, not only by details of the centre, but also by the zoarial shape. Due to the included substratum ancestrular colonies are higher than those that began as buds. To the latter the description "inverted saucer--shaped" is appropriate. Ancestrular colonies begin encrusting, later they incorporate the substratum if possible, and often become distorted. A colony of typical *umbellata* had grown longish, because it had incorporated a 3 mm long stone. Most of our irregular colonies belong to the variety *conica* (Canu & Bassler 1930, p. 12).

Many colonies are quite round. Those whose zoarial buds were detached recently have ragged outlines as that of figure 8 of Norman's *Cupularia lowei* (1909, pl. 37). Zoarial buds and also fragments of colonies broken by mechanical factors generally regulate their orbicular form rapidly (Fig. 22). Under certain conditions the regulation of buds or fragments becomes irregular. This happens when the zoarial bud is already very large at the time of its separation, or when a fragment is nearly as big as the common size of a colony, or perhaps when zoarial budding is delayed by cold or scarce food. Possibly O'Donoghue's zoaria (1924, p. 39; Hastings 1930, p. 719) are irregularly regenerated fragments. Presumably also Busk's colony of *lowei* (1854, pl. 116, f. 1) is a fragment. We have fragments of *D. umbellata* with 5 mm long complete outer border and 6 mm long broken sides which are far from reaching the colonial centre. They must come from colonies about 25 mm in diameter.

THE AUTOZOOECIA

The autozooecia are 0,4-0,5 mm, rarely 0,6 mm long, and 0,3-0,4 mm broad. Their limits are brown chitinous lines. The opercula are broader than high and have thickened rims, also proximally. Their proportions vary; in one and the same colony the height of one operculum was 43,5% of the breadth, that of another 83%. The frontal membrane is thickened around the operculum; this smooth rim ends proximally with two "curves" level with the base of the operculum (Waters 1921, p. 413, pl. 30, f. 1; Hastings 1930, p. 719).

Fig. 4 shows the formation of the frontal cryptocyst by coalescing processes. Sometimes irregular perforations remain in the middle beside the specific 5-10 peripheral opesiules. The latter are all penetrated by parietal muscles which depress the frontal membrane. There are 13-16 tentacles.

The zooids are separated by thick calcareous walls (Fig. 5, ca) and connected with one another by epidermal tubes (Figs. 7, 21, u, w) containing mesenchymal cords. Generally there are two, but also one or three oblique lateral tubes in each quadrant of a zooecium, and one (Fig. 5, me) to each of the vibracula. Exceptionally two tubes are connected with one another. Each tube begins with a chamber (Fig. 6, k) which develops as an outward fold of the body-wall. The fold forms two narrow diaphragms, one at its zooecial origin, and another where it communicates with the tube. The cellular layer of the chamber, the epidermis accompanied by the peritoneum is scarcely distinguishable from the loose mesenchymal cords. The exoskeleton of the chamber is chitinous, not calcified.

Under normal budding conditions the chambers belong to the proximal zooecium, whose tubes form the distal individuals. Here the tubes pass into the body-wall without folds. Where chambers occur in the proximal tubes of a distal zooecium, these have contributed to the regeneration of a proximal zooecium. The frequent destruction of the frontal membrane and cryptocyst with the consequent entrance of water and sand into the body-cavity of a zooecium evidently exercises a stimulus upon the adjacent zooids. Of these also the distal ones react (Fig. 7). These, originally receivers of proximal tubes become producers and develop a chamber at their former entrances, now outlets, of the proximal tubes. The sand grains which fill the broken zooecium are not removed by the budding tissue which produces a new cuticular basal wall over them.

The basal zooecial endocyst (Fig. 5, ez) that is inwards peritoneum and outwards epidermis lies over and produces a thick calcareous base. The external surface of the base is also covered by two layers of cells and an external cuticle. The zooecial and zoarial strata and the basal cuticle are connected by rows of tubules (l). Seen from the basal surface these have the aspect of pores, especially where they end in pits. These pits were described as pores (Waters 1921, p. 400,

pl. 30, f. 4), and are retouched in a photograph of Canu & Bassler (1918, pl. 53, f. 4). The series of tubules generally go out from the the mid-line of the zooecia or from a more lateral plane. Waters (1921, p. 412) called the tubules muscles, but they are neither topographically nor histologically myofibrils. They are principally cuticular, and their cellular layers are not visible in the part of the tubules that runs within the calcareous mass. The shallow furrows on the underside (Smitt 1873, pl. 3, f. 76, 80) branching dichotomously from the zoarial centre outwards correspond to the rows of tubules. The calcareous base of the colony secreted by the tubules as well as by the individual basal walls does not show zooecial limits. Only in the centre of young colonies such are recognizable (Fig. 19). In older zoaria calcareous tubercles develop. They are well figured on Canu & Bassler's photograph 16 (1923, pl. 2), rather uniformly distributed, or in about two rows on the bulge between the above-mentioned furrows. By further calcification these tubercles coalesce into a general granular crust. This can later be covered by a new calcareous layer which develops from the margins towards the centre of the basal surface; such a covering can be formed repeatedly. Canu & Bassler (1929, pl. 15, f. 9) figured an under surface whose superposed layers grow from the centre towards the margin.

The polypides are evidently short-lived. The number of such in degeneration and regeneration frequently exceeds that of the functioning ones by far. In a small colony originated by budding which consisted of 5 rows with a total of 27 autozooids only 5 polypides functioned. These were situated in the two outer circles, the outermost individuals were in development, and those of the three inner circles were all in de- and regeneration. The rests of the brown bodies are not accumulated in the zooecial cavity but eliminated by the regenerated polypide, whose digestive tract grows rapidly around them. An optical section of budding or regenerating, hence short polypides, or possibly also completely retracted ones, brings about the aspect of Waters' figure 2 (1921, pl. 30). Such phases did evidently not occur in Hastings' material (1930, p. 719). The present explanation of Waters' figure 2 deprives *Cupularia lowei* Busk (1854, p. 99) of the last distinguishing character from *Discoporella umbellata*.

In none of our well preserved colonies belonging to the budding population did we find any traces of germ cells.

THE VIBRACULA

The vibraculum lies distal to the autozooecium. Its frontal side is generally 0,15 mm, exceptionally 0,2 mm long. The seta is almost colourless, grey to light yellow, smooth, and slightly curved at the tip. Setae of central vibracula are 0,4-0,5 mm long, those of marginal ones 1-1,5 mm. Budding and regenerating vibracula evidence that the area of the frontal membrane (opesia, subopercular field, aperture) is the distal, short part of the chamber, and the proximal long one is the area of the orifice (oral shelf, opercular field). Over the latter rests the developing bristle enclosed in a bag of formative cells, so that it appears broad and beak-like (Fig. 7, sr). The narrowed opercular part of the chamber is asymmetrical, directed to the right or to the left side of the autozooecium. A rule for the distribution to right or left was not recognized in large colonies, but in 65 primaries the distal vibraculum pointed 64 times to the left, only once to the right. The vibracula of the two first buds are symmetrical to one another, both pointing inwards.

A narrow cryptocyst is developed in the opercular and the subopercular area. The cuticle of the gymnocyst is thickened and contiguous with that of the adjacent opercular region of the autozooecium. On the opposite side the thickening is stronger. Also the cystidial projection or hinge-tooth (Fig. 8, h) on this side is bigger than the other. The bigger tooth is more distal than the smaller one. This oblique position of the hinge-teeth contributes to amplify the mobility of the seta.

A concave thickening (Fig. 9, 10, x) of the frontal membrane which corresponds to the frontal plate of certain avicularia (Marcus 1939, figs. 47-48, 50, s) is connected with the base of the bristle (s). At this plate numerous smooth abductor fibres (au) insert, each with its own tendon as in the cited avicularia. The nuclei of the epidermal cells that become tendinous fibres lie all at the same level, in the middle of the tendons. The antagonistic cross-striated adductor fibres (ac) have a long common tendon which inserts on the basal arch of

the bristle. Two further bundles of smooth muscle fibres, also with collective tendons, insert at the right and left basal knobs of the seta and act as gyrators (j). The knobs are fastened to the hinge-teeth with tendinous fibres.

The vibracular polypide, though rudimentary, allows to discern tentacle sheath (p) sensory organ (q) with tuft of cilia (ci), ganglion (g), and a tiny gland (r) attached to the tentacle sheath. The two small glands of Waters' figure 15 (1921, pl. 29) are not developed in our material. The nerve going out from the ganglion enters the proximal autozooecium.

The biological significance of the vibracula can be deduced from their substitution in the centre and in other regions of the colony, where the surrounding autozooecia are closed by secondary calcification. Maybe their most important function is the protection of frontal membranes and polypides when the colonies fall upside down. When they are thrown into the aquarium, this position occurs frequently, and the stiff bristles prevent the active surface of many autozoids from touching the sand. On the other hand the setae do not hold the zoaria completely clean from other organisms. The heterotrichous ciliate *Folliculina* is frequent on the basal surface; Foraminifera settle on living colonies; sometimes stolons of thecate hydrozoans grow from the underside on to the upper surface, and one or other incipient encrusting colony of Bryozoa was also seen, oddly enough not *Beania cupulariensis* Osburn (1914, p. 190) which occurs in the littoral of Brazil (Marcus 1944, p. 1). Some boring Ctenostomata had attacked the basal surface of living *Discoporella umbellata* var. *conica*.

LIVING COLONIES

In living colonies the vibracular setae are abduced. This is their resting position. The abduced bristles of the marginal zone project far beyond the border increasing the diameter of the colony, e. g., from 5 to 7,5 mm, and prevent it from sinking into the soft bottom. A mechanical stimulus applied to the frontal membrane of an auto- or heterozooecium is answered by rapid adduction of the neighbouring bristles. According to the intensity of the stimulation a larger or smaller area of vibracula responds. This proves the existence of colonial ner-

vous connexions in addition to that observed between vibraculum and proximal autozooecium.

Adduction is followed by slow abduction after about 4 seconds at 28° C. The bristles react to a single stimulus by several adductions and abductions. The rapid adductions and relatively slow abductions correspond to the striated and smooth fibres of the effecting muscles. The bristle moves downwards in a plane vertical to the surface of the colony; upwards the seta sweeps in a curve. The inclination of the vibracula to the right and the left brings forth a crossing of the opening bristles. They act like tweezers grasping particles and removing them from the surface. However they always act over the same spot and do not attain the areae between their radii of action. The threshold of the stimulus is rather high, at least when the polypides are retracted. Under these conditions a small nematode or mite moving about on the frontal membrane of a vigorous colony did not provoke any reaction of the setae.

The reaction of a colony lying upside down was surprising. A mechanical stimulus applied to the basal surface was evidently strong enough to press the vibracula against the sand. Thereupon the entire colony wavered, set in motion by repeated adductions and abductions of the setae. Locomotion was not brought forth by this general wavering, but may perhaps happen if a localized basal stimulus is responded only by the bristles of the corresponding sector of the upper surface. Such a displacement cannot be called a progressive movement. The vibracula of *Discoporella umbellata* are not locomotive. This function was considered as possible for the vibracula of lunulitiform cheilostomes and even indicated in the older literature (Busk 1854, p. 97, 106; Hincks 1878, p. 9; Tenison-Woods 1880, p. 3), but never confirmed (Harmer 1926, p. 263; 1931, p. 151 ff.; 1957, p. 649).

Upset colonies cannot return to their normal position by themselves. When they lie like saucers on the bottom, they are more exposed to movements of the water than in normal position. This exposure together with the wavering may favour their turning upwards.

ZOARIAL GROWTH

The centre of the colony agrees with that of *Cupuladria canaricnsis*. The ancestrula is single, and together with it the first zooids form a 6-rayed star (Fig. 11). Sometimes the ancestrula has its first two buds developed laterally, not latero-proximally as is more frequent. In these cases the ancestrula ,the first lateral buds, and the zooid opposite to the ancestrula constitute a cross, and the following 4 zooids transform it into a 8-rayed star (Fig. 12). This type of centre is known of several lunulitiform zoaria (Stach 1938, p. 412). Ancestrular colonies of *Discoporella umbellata* are photographed, e. g., by Canu & Bassler (1928b, pl. 7, f. 1) and by Lagaaij (1953, pl. 1, f. 3a); the former has a 6-rayed, the latter an 8-rayed centre. In one of our zoaria two larvae had settled one beside the other on a stone. One perfectly round colony developed with only slight irregularities in the zone of coalescence.

As in other lunulitiform colonies the frontal wall of old autozooecia in the centre of the zoarium is closed by secondary calcification (Fig. 11). Some opesiulae may continue pervious, but the polypides can no longer function. The endocyst and the funicular cords persist and conduct material for the vibracula which continue active after the central and later on also more peripheral autozooecia are calcified. The outermost zooecia of a colony are vibracula. Between and beyond these heterozooecia the autozooecia produce a thin, not yet individualized budding zone which comprises the frontal as well as the basal side. On the latter the above-mentioned secondary calcification begins early. This is especially distinct in sectors of the zoarial periphery where a further outward growth is hindered by juxtaposed zoarial buds. The young budding zone needs careful examination of colonies preserved in neutral liquids; it collapses in dry zoaria, and if the liquid of preservation is even only a little acid, its thin lime is dissolved. In the following phase calcification and individualization of auto- and heterozooids proceed rapidly. The longest lasting process is the formation of the polypide and the seta.

We have only fragments of colonies of *D. umbellata* without budding zone or without zoarial buds on their margin. These are the above-mentioned parts of colonies with a diameter of about 25 mm.

Their border has ceased to grow and has assumed the characters described later on of *D. umbellata* var. *conica* that frequently has definitive borders in our material.

ZOARIAL BUDDING

The most interesting feature observed in our *D. umbellata* is the vegetative reproduction by colonial buds. Many colonies from the localities 3, 3a and 4 were budding; few were seen from locality 2 (32 m), and some from 5 (30 m) had probably shed their buds. The deep-water samples from 70-150 m did not contain any zoarial buds. We have numerous ancestrular colonies from depths of 30 to 150 m, none at all in 3 and 4 m. Perhaps the settlement of the larva is difficult in irregularly agitated shallow waters. However by budding the species succeeds to populate this biotope. As we have material collected in summer (December, January), autumn (March and April), and winter (June to August), with colonial buds, this propagation seems to be independent of the season. Buds are sometimes already produced by zoaria of 4 mm diameter. As far as can be judged from the small number of colonies that are just beginning to bud, the first two buds arise on opposite sides. The largest colony with buds measured 9 × 7 mm. Up to 15 buds were counted on the periphery of one colony (Figs. 13, 14), but as their connection with the mother-zoarium is fragile, they fall of easily during manipulation, and so still more may occur. In some old colonies encrusted with covering black sediments and with opaque white basal surface the only active zooids were the marginal vibracula. Their buds however continue with transparent calcareous walls and red functioning zooidal organs.

The first step to colonial budding consists in a slight advancement of an autozoid and its vibraculum. Simultaneously the buds beside this zooecium do not develop. On the frontal surface the primordial zooid of the zoarial bud exhibits the same aspect as the adjacent proximal invididuals, but on the basal side it is set off from these by a deep furrow. Sections (Fig. 15) show that the basal membrane of this zooecium is considerably thickened (uc). This cuticular area is less strongly calcified than the further basal surface of the zoarial bud, and constitutes a preformed zone through which the bud

readily breaks off. As first individual of a new group this zooid (f) may be called a pseudoancestrula (Canu & Bassler 1923, p. 20; Marcus 1938, p. 70). Its shape differs as little as that of the ancestrula from common autozooids. Canu & Bassler's "membraniporoid ancestrula" (1923, pl. 2, f. 19) is a common autozooecium with broken cryptocyst. The pseudoancestrula is nourished by the two neighbouring proximal autozooecia whose distal connective tubes communicate with it. Exceptionally also material from the undifferentiated budding zone contributes to the formation of the pseudoancestrula. The complete pseudoancestrula emits two distal tubes on either side, thus giving origin to two latero-distal individuals. If such a zoarial bud composed of three autozooids and one heterozooid breaks off, it can already live independently, but generally 10-30 autozoids with their vibracula develop, before the young zoarium detaches. Of course, budded colonies have no central sandgrain or other substratum.

When numerous buds are produced at the same time, the daughter-colonies grow narrow (Fig. 17) and are brimmed with an inhibited and undifferentiated budding zone along their sides. With a smaller number of buds these assume a broad, flabellate shape (Fig. 16) whose budding zone is individualized all round. The detachment of the bud generally takes place by the pseudoancestrula breaking in two (Fig. 17, f). Rarely its proximal end loses the contact with the mother-zoarium. Subsequently the pseudoancestrula, or, in most cases, its distal half, produces a proximal zooecium or a new half (Figs. 16, 18). This regenerated half is a distal one with operculum and a vibraculum. Also the complete zooecium and vibraculum developed in exceptional cases lie opposite to the pseudoancestrula. Therewith the polarity is seen to be inverted in the regeneration or the regulative budding which proceeds from the pseudoancestrula. The direction of the new vibraculum to the right or to the left is not correlated with that of the pseudoancestrular vibraculum. This heterozooid continues active while the original operculum of the pseudoancestrula is closed by calcification. The first polypide of the pseudoancestrula degenerates and a new one appears which is orientated towards the new orifice. The inversion of the polarity of the pseudoancestrula is accompanied by generalized budding of zooids in the sector hitherto facing the mother-colony. So the fan-shaped daughter-colony closes to a circle.

When a large zoarial bud is freed, e. g., one with 40 autozooids, the zooecia on the two sides budding towards one another do not coalesce (Fig. 21, cu). Sometimes this gap remains visible only on the basal surface.

ZOARIAL FRAGMENTS

Of the fragments we treat first those containing parts of the original budding zone. The broken or complete zooecia along the breaking-line produce new opercula and vibracula opposite to the old ones. As in total regeneration (Fig. 7) and regulation of liberated buds (Fig. 18, 19) the reparation of fragments begins with the development of connective tubes. The polarity of the tubes and buds may be inverted, but otherwise the mentioned processes agree with the outward budding in the normal zone of growth of the colony. The production of proximal buds in the fragment stops for a while the development of distal ones in the original budding zone. Thus the fragment approaches circular form and attains it rapidly. By the great number of new zooids in the fragment a somewhat irregular growth of the different sectors takes place, contrary to the colonial bud whose regulation goes out from a single autozooid. We interpret Norman's irregular colonies (1909, pl. 37, f. 7, 9) of *Cupularia lowei* as regulating fragments, and his figure 8 as a zoarium that has recently shed its buds. What Canu & Bassler (1923, p. 81) called an "ancestrula replaced by a special region in which the zooecia are arranged in contrary order" evidently refers to regulating fragments (pl. 2, f. 17-18), whose explanations "ancestrular region" are not correct.

Frequently fragments broken in several directions have defective borders all round and have no original budding zone left (Fig. 22). Their regulation to circular form begins with buds directed proximally and proximo-laterally, while growth in the normal, distal, direction pauses. In our opinion this phenomenon explains the first processes in fragments broken off and in zoarial buds separated from the mother-colony. In all these cases, even when a colonial bud becomes free with an unbroken pseudoancestrula, the proximal continuity is interrupted. Evidently this interruption of the proximal continuity produces an inverted proximal budding and a standstill of the distal

budding. It is not known whether this effect is brought about by nervous conduction between the zooecia or by an inverted transport of food in the mesenchymal cords or by both.

DISCOPORELLA UMBELLATA var. CONICA

The colonies of this form are smaller than typical *umbellata,* solid, and their zooecia smaller. The preserved or dry zoaria caught alive are ivory, the bristles of the vibracula golden-yellow. Three millimetres in diameter and 1,6-2 mm in height are common measurements. There are also bigger colonies, 4,7 × 2,8 mm, but these are worn and cannot be determined with certainty. The same holds for flat (5 × 1,5 mm) and hollow (5 × 3 mm) zoaria which might be typical *umbellata,* though the zooecia are smaller.

The autozooecia are 0,2-0,3 mm long, rarely up to 0,4 mm. Their breadth is 0,15-0,25 mm. The periancestrular vibracula have 0,5 mm long bristles, the marginal ones up to 1,1 mm long setae.

Old zoaria are approximately hemispherical or a little broader; some are irregularly longish, due to the shape of the enclosed substratum. Many colonies are middle-sized or young. They begin encrusting on generally small, but sometimes also up to 5 mm big substrata. Old worn colonies expose their substratum under the apex. The colonies are neither lobed nor do they produce zoarial buds. Typical basal surfaces are plane and smooth with or without slight traces of radiate striation (Fig. 23, 24). As solid and hollow zoaria occur in *Cupuladria johnsoni* (Busk 1859a, p. 67) (see Silén 1942a, p. 7), the hollow colonies with small zooecia whose basal surface is radiate, or rough without radial structure, are difficult to be referred to typical *umbellata* or to var. *conica*. Probably they belong to the latter, because the zooecia are small. These hollow colonies have the same structure of the edge as typical *umbellata*. A single row of vibracula, whose chambers appear as long cylinders on the basal surface, projects over the periphery. All young colonies have this aspect and can be recognized as var. *conica* only when their basal side is filled.

Colonies of *D. umbellata* var. *conica* attain their definitive size much earlier than those of typical *umbellata*. The configuration of

the zoarial border which ceases to grow is the same in the typical form and the variety. This definitive border (Fig. 25) is smooth, because kenozooecia (z) are formed between the marginal vibracula. Also the autozooids proximal to these vibracula are closed by a granular cryptocyst which sometimes leaves several opesiules open. There are stages of transition between these closed autozooecia and the functioning autozooids farther inwards, viz. small zooecia with low operculum, evidently restricted by the growing cryptocyst. Smooth and shining chitinous bulges (ei) overlie the closed autozooecia of the marginal zone as distal caps; they correspond to the chitinous thickenings which surround the opercular region of typical autozooecia in *umbellata* and var. *conica*. The margin of *umbellata* and its var. *conica* is similar to the basal surface ("face supérieure" in Duvergier's terminology, 1924, p. 19) of *Discoporella peyroti* (Duvergier 1921, p. 2; description: 1924, l. c.), where vibracula between porous cryptocysts are developed. As the definitive edge also the older regions of the colonies agree in *umbellata* and in var. *conica*. The ancestrula and the periancestrular autozooids are closed by secondary calcification, but the vibracula of the centre have their setae and are evidently still functioning.

MAMILLOPORA CUPULA

Geographic distribution: Northern coast of Brazil, off mouths of River Amazon (localities 7 and 7a of the present material). Caribbean Sea, Margarita, Tortuga, Aruba Islands, Gulf of Maracaibo, and Cape de la Vela, eastern Colombia (Osburn 1947, p. 46). Gulf of Mexico, W off Florida, Straits of Florida (Canu & Bassler 1928b, p. 155), Florida (Smitt 1873, p. 33). American Pacific coasts: Gulf of California, Angel de la Guarda Island (about Lat. 29° N); W coast of Lower California, Mexico, Costa Rica, and Panama (Osburn 1952, p. 518); Gorgona Island, Colombia (Hastings 1930, p. 733); Galapagos Islands (Canu & Bassler 1930, p. 45; Osburn 1952), to Lat. 1° 17' S, Long. 90° 30' W.

In depths from 18 to 130 m; first fossil findings in the Lower Miocene. As Osburn (l. c.) informed that the species is abundant in the Gulf of California and about the Galapagos, Canu & Bassler's

opinion (1930, p. 46) that it has degenerated in the Pacific since the formation of the Isthmus of Panama cannot be maintained.

Our material, 6 dead colonies, up to 1 mm in height, and 2 mm in diameter, does not allow for additions to the good descriptions of Smitt (1873, p. 33) and Hastings (1930, p. 733). But the literature concerning *M. cupula* requires some comments. The occurrence of avicularia on the basal surface seems to have caused Osburn's idea (1947, p. 66) that "the colony may have some small capacity for movement by means of the avicularia or vibracularia". There are no vibracula, and that the short, semicircular avicularian mandibles of the basal side should produce a locomotory effect by opening and closing is not easy to conceive. Still less probable is that living colonies float with the top of the cone touching the surface and "at their pleasure rise or descend" (Canu & Bassler 1928b, p. 153, 155). The experience with a dry colony plunged into water is not convincing. "The larva is not fixed then, but it is transformed into a swimming larva (misprint for colony)". Canu & Bassler continue calling this transformation "a very curious phenomenon", but we must state that it is a mere supposition and moreover a quite improbable one.

Canu & Bassler (1928b, p. 155) did not find substrata in their sections, and such are absent also in the typical material (Silén 1947, p 6). Evidently the ancestrula is only loosely fixed to the substratum (ibid., p. 29) and detaches from it when the colony grows. The zoaria of *Mamillopora cupula* lie on the bottom as do those of *Cupuladria canariensis and Discoporella umbellata*.

The Suborder Hexapogona Canu & Bassler (1927, p. 9, 22) criticized by Harmer (1931, p. 159-162) is now abandoned (Harmer 1957, p. 854, 887), also in North American papers (Osburn 1952, p. 517; Bassler 1953, p. 327). The Mamilloporidae are a Family of the Ascophora Vera (Harmer 1957, p. 645).

RESUMO

Há Briozoos de várias famílias dos Cheilostomata cujas larvas se fixam em grãos de areia, Foraminíferos ou outros substratos pequenos. As colônias assim originadas crescem em forma de disco, cone ou cúpula ao redor do ponto de fixação, e deitam-se sôbre fundo

arenoso ou lodoso. Quatro espécies com tais colônias, chamadas de lunulitiformes, foram obtidas do litoral brasileiro entre 26° 19' S e 2° 58' N, em profundidades de 3-150 m. Estudamos, principalmente, *Discoporella umbellata* (Defr.) da Enseada do Flamengo, 14 km. oeste de Ubatuba. A cêrca de 4 m. de profundidade, em certa região de areia fina e lodosa desta baía, ocorrem 2-3.000 colônias de *D. umbellata* por m^2. Durante o ano inteiro reproduzem-se vegetativamente, por brotamento colonial. Colônias originadas da larva metamorfoseada encontramos sòmente em material de maiores profundidades.

A agitação irregular do mar raso parece ser desfavorável à fixação das larvas de *D. umbellata*. No brotamento, até 15 botões ligados cada um à colônia-mãe por um único zoécio projetam-se no bordo da colônia (Fig. 13). Separam-se com tamanho muito diferente, sendo 10-30 autozoécios e outras tantas vibráculas o número comum de botões individualizados. Os autozoécios são ligados entre si por tubos com câmaras especiais na sua base (Fig. 6). Cada autozoécio forma 2 tubos látero-distais direitos e 2 esquerdos para os zoécios correspondentes, e um distal para a vibrácula.

As vibráculas têm músculos abdutores e giradores lisos, adutores transversalmente estriados, órgão sensorial com cílios e gânglio cujo nervo passa ao autozoécio proximal. As cerdas das vibráculas encontram-se, normalmente, abduzidas. Nesta posição as cerdas marginais, projetadas sôbre o bordo (Figs. 13, 14) sustentam a colônia. Estímulos mecânicos provocam adução rápida da cerda cuja volta à posição abduzida se processa lentamente. Na colônia caída, com a superfície frontal para baixo, as cerdas abduzidas das vibráculas encontram-se interpostas entre a areia e a membrana frontal dos indivíduos.

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EXPLANATION OF LETTERS

a — ancestrula.
ac — adductor.
ar — rectum.
au — abductor.
av — vibraculum substituting ancestrula.
b — first buds of ancestrula.
bv — vibraculum substituing one of first buds.
c — second bud of ancestrula.
ca — calcareous wall.
ci — cilia of vibracular polypide.
cu — kenozooecial structure.
cv — vibraculum substituting second bud.
d — third buds of ancestrula.
dv — vibraculum substituting one of third buds.
e — stomach.
ei — chitinous thickening of closed zooecia.
en — tentacles.
ez — endocyst.
f — pseudoancestrula.
g — ganglion.
h — hinge-tooth.
i — cryptocyst.
is — hypostegia.

j — gyrators.
k — chamber of connecting tube.

l — cuticular tubes.
m — frontal membrane.
me — connecting tube.
n — basal membrane.
nc — amebocytes.

o — operculum.
oe — opesiule.

q — tentacle sheath of vibraculum.
r — vibracular gland.

re — retractor of polypide.
s — vibracular seta.

si — seta of substitutive vibraculum.
sr — vibracular seta in regeneration.
t — budding polypide.
u — distal connecting tube.
uc — basal cuticle of pseudoancestrula.
v — vibraculum.
ve — vestibulum.
w — proximal connecting tube.
x — frontal plate.
y — destroyed autozooecium.
z — kenozooecium.

PLATES

PLATE 1

Fig. 1 — Young colony of *Cupuladria canariensis*.

Fig. 2 — Centre of older colony of *Cupuladria canariensis* with substitution of autozooecia by vibracula.

Fig. 3 — Basal surface of big colony of *Cupuladria canariensis* regenerated from a fragment.

Fig. 4 — Formation of cryptocyst in *Discoporella umbellata*, calcined.

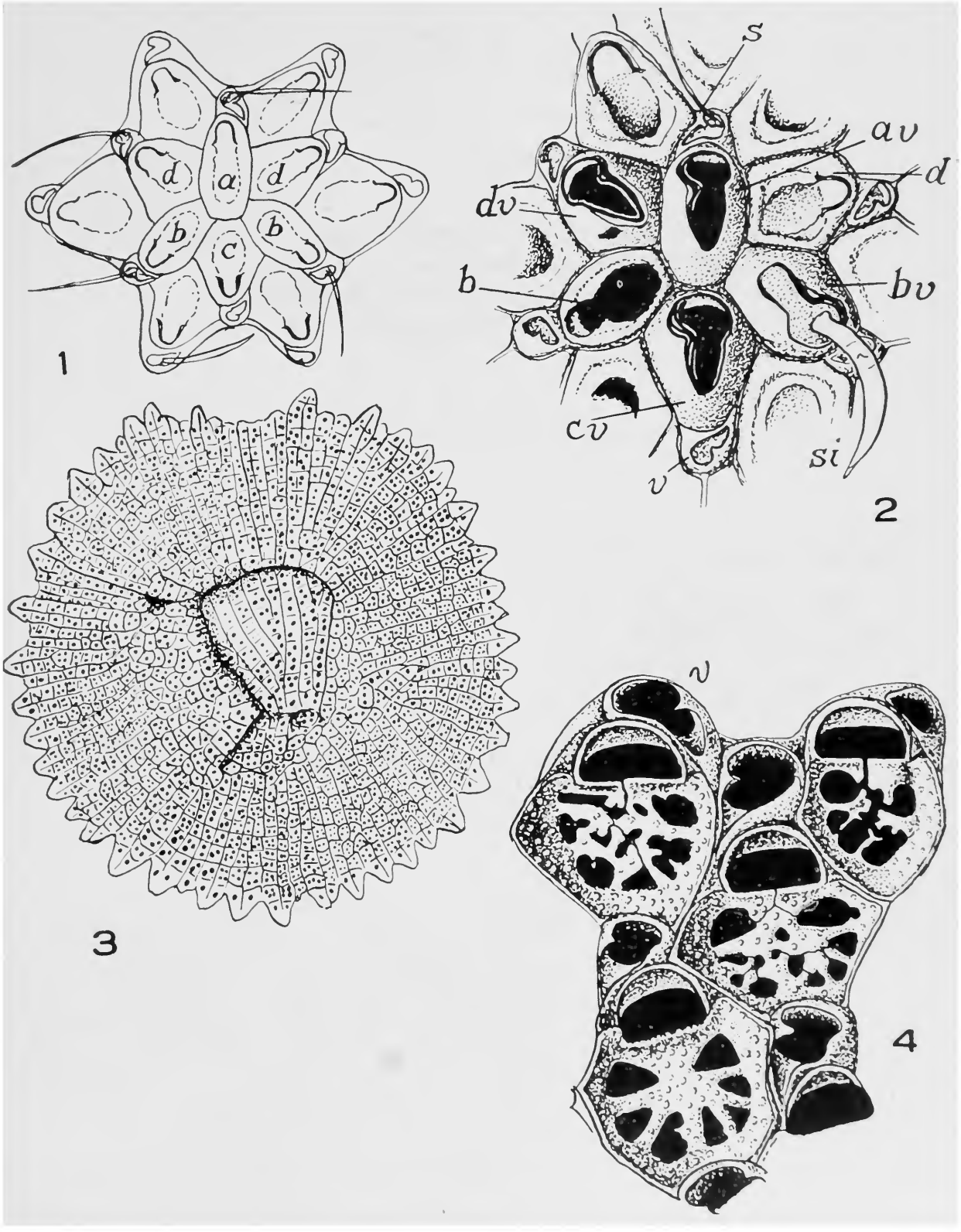
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PLATE 2

Fig. 5 — *Discoporella umbellata,* combined sagittal section of autozooecium and two vibracula.

Fig. 6 — Connective tube with chamber of *D. umbellata*.

Fig. 7 — Total regeneration in *D. umbellata*.

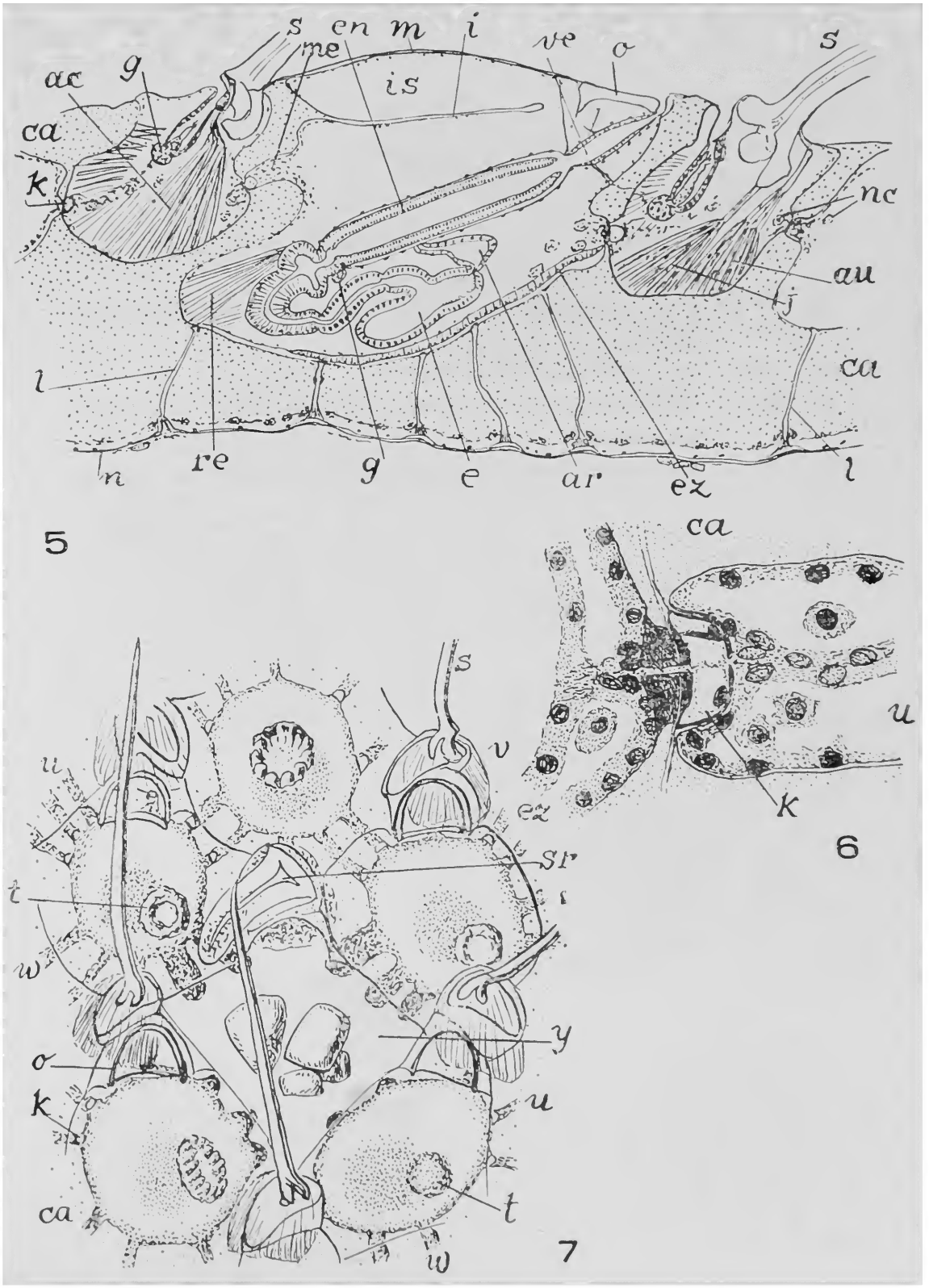
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PLATE 3

Fig. 8 — Vibraculum of *Discoporella umbellata,* decalcified and clarified; abductor omitted.

Fig. 9 — Combined sagittal section of open vibraculum of *D. umbellata*.

Fig. 10 — Same of closed vibraculum.

Fig. 11 — Six-rayed centre of colony of *D. umbellata* with closed autozooecia.

Fig. 12 — Eight-rayed centre of colony of *D. umbellata* var. *conica*.

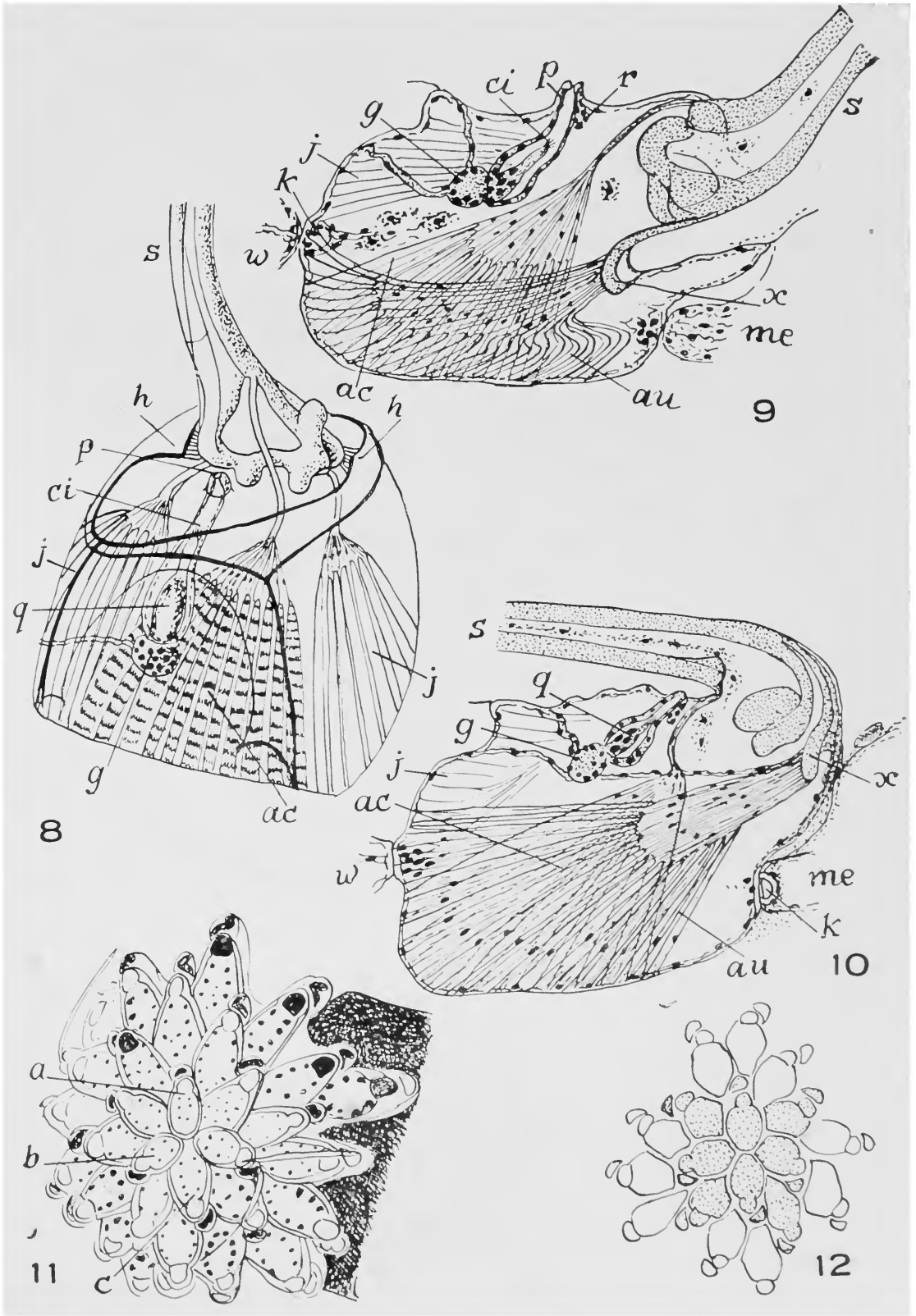
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PLATE 4

Fig. 13 — Budding colony of *Discoporella umbellata,* frontal view; buds stippled.

Fig. 14 — Basal view of same; buds not stippled.

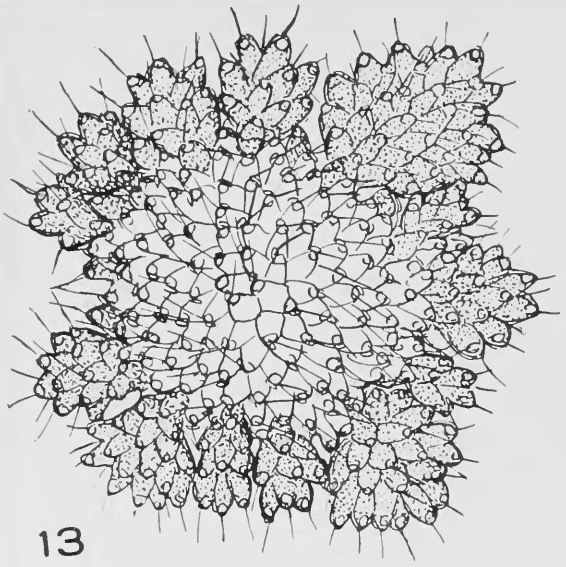
Fig. 15 — Combined sagittal section of incipient zoarial bud of *D. umbellata*.

Fig. 16 — Flabellate colony of *D. umbellata* arisen from bud.

Fig. 17 — Narrow colony of *D. umbellata* shed recently; pseudo-ancestrula (f) not regulated yet.

Fig. 18 — Budded colony of *D. umbellata,* regulated.

Fig. 19 — Basal surface of young budded colony of *D. umbellata.*



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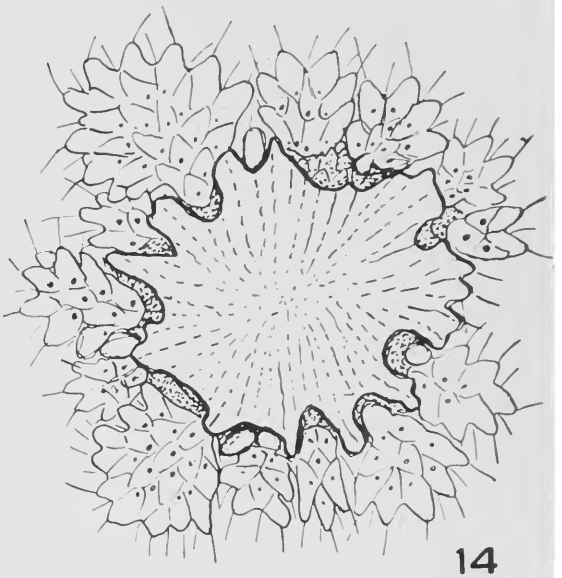

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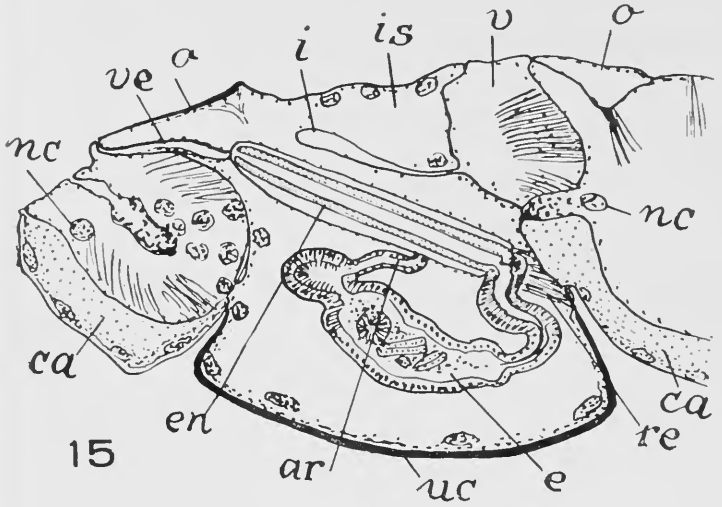

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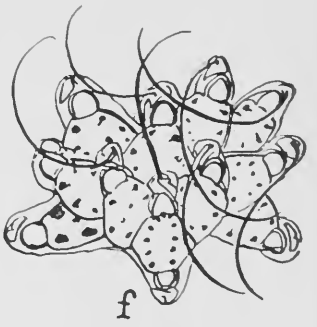

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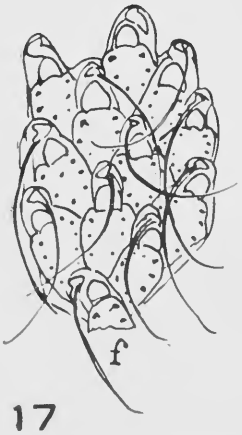

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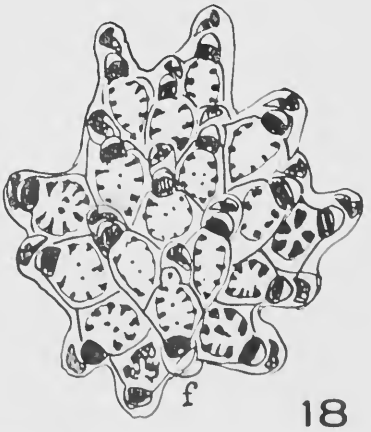

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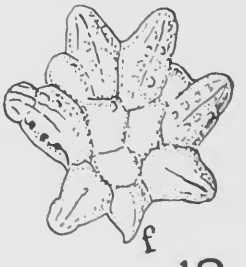

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PLATE 5

Fig. 20 — Budded colony of *Discoporella umbellata* not completely regulated and producing buds. Stippled part magnified in Fig. 21.

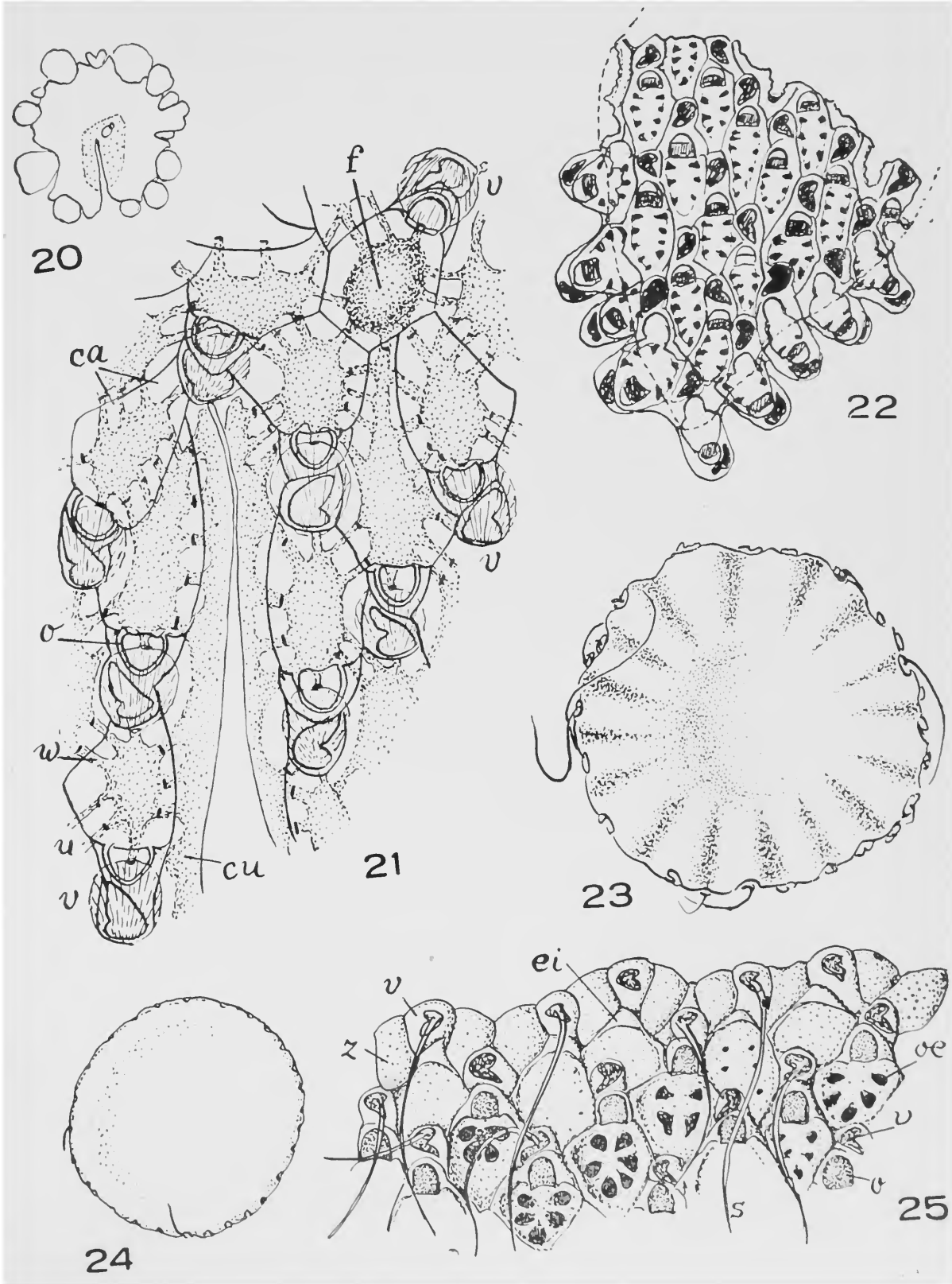
Fig. 21 — Gap of Fig. 20, bordered by kenozooecial structure (cu).

Fig. 22 — Fragment of *D. umbellata* with proximal and latero-proximal regulative zooidal buds; the dashed line indicates the break.

Fig. 23 — Concave basal surface of *D. umbellata* var. *conica*.

Fig. 24 — Plane basal surface of *D. umbellata* var. *conica*.

Fig. 25 — Definitive border of old colony of *D. umbellata* var. *conica*.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A PERIPATUS FROM BARBADOS

By CLAUDIO G. FROEHLICH

No species of *Peripatus* was known from Barbados, British West Indies. As a matter of fact, onychophores were supposed to be absent from this island on account of its greater isolation from the other Lesser Antilles, and the nature of its fauna (Clark, 1915; cf. also Cuénot, 1949, p. 34). Recently, however, the Rev. E. J. Pearce succeeded in discovering some examples of *Peripatus* in Barbados, one of which he sent to Prof. Dr. Ernst Marcus, head of our Department, and two others he deposited in the Science Museum of the Jamaica Institute. Prof. Marcus handed over his specimen to me for determination, and the two specimens of the Jamaica Institute were also kindly forwarded to me. The specimens proved to be a form closely related to *Peripatus dominicae* Pollard, 1894, of which I consider it to be a new subspecies.

PERIPATUS (s. str.) DOMINICAE BARBADENSIS, n. subsp.

All three specimens are females with 31 pairs of legs. Their sizes are 32 mm. long by 4.5 mm. broad, 25 mm. by 4 mm., and 17 mm. by 2 mm., resp. The latter is very young. The body is broader than high, the dorsal side is convex, the ventral flat to slightly concave. In the middle-sized specimen, which appears to be somewhat shrunken, the dorsal surface is depressed along a line on each side, resulting in a three-lobed appearance. The colour of the preserved specimens is a uniform reddish-brown above, due in a large measure to the colour of the subepidermal muscles. The middle-sized specimen is much the darker one. The scales of the papillae are brown, the rest of the scales are lighter in colour (fig. 1). The middorsal light line is more distinct on alternate plicae. On a narrow band on each side of the light line the skin scales are all dark and, as a rule, no principal papillae occur (figs. 1-5). The light organs (hyaline organs, "organes

claires") are hardly visible. As usual, the ventral side is lighter than the dorsal.

There are 12 plicae per segment on the back, but at the level of each pair of legs two of them are incomplete, ending about halfway to the margins (figs. 3-5). Seven of the plicae generally pass to the ventral side, where they are continuous. Between these, irregular plicae occur. The ventral organs are distinct, the preventral ones also frequently so.

The youngest specimen has large principal papillae separated by one to six or occasionally even more accessory papillae; the most common number is three, of which the middle one is larger. All papillae are on the crest of the plicae and the principal ones are manifestly prominent (fig. 5). The middle-sized specimen presents small to medium-sized accessory papillae on the slopes of the plicae, besides those on the crest (fig. 4). In the largest specimen the distribution of the papillae is similar, but the plicae are broader and the furrows less deep (fig. 3). The basal diameter of the larger accessory papillae is about the same as that of the smaller principal ones, but on the whole the principal papillae appear clearly dominant. The principal papillae have a conical base and an upper part which is rather short and conical in the mesial papillae (fig. 6) but gets longer and cylindrical toward the margins (figs. 7-9). The terminal spine is commonly almost as long as the upper cylinder. The principal papillae of contiguous or of alternate plicae may be disposed in short longitudinal rows.

The antennae, which are about as dark as the dorsal side, have ca. 42 large rings. The eyes are small, measuring 130 × 90μ in the largest specimen. The frontal organs are present, their length corresponding to three or four principal papillae of the ocular ring.

Both blades of the jaw (fig. 10) have but one accessory tooth. The saw of the inner blade has 9 denticles in the largest specimen, 8 in the smallest. The denticles diminish slightly in size backwards. The buccal crest ("tongue") has 9 denticles and, at its posterior end, 3 or 4 minute lateral spines.

The creeping pad of the feet comprises four arcs. The papillae of the row next to the fourth arc are mostly spiny as the pad, and some

occasionally coalesce, forming rudiments of a fifth arc. The nephridial tubercle of the fourth and fifth pairs of legs is independent of the third arc in all specimens. The third arc is a little emarginate and the fourth pushed aside by the tubercle.

The largest specimen has been dissected. The salivary glands extend to the fourth preanal legs, its reservoir to the second leg-bearing segment. The funicle of the ovaries is long and simple. The ovaries are short and are located at the level of the twelfth preanal legs. The ovoid seminal receptacles are 250 × 300μ. Two advanced embryos, one in the terminal part of each uterus, are close to 20 mm. long by 1.5 mm. broad. Both have 31 pairs of legs and seem to be females.

Collection Data. St. John, Barbados, B. W. I., The Rev. E. J. Pearce coll.: Holotype ♀, 32 mm. long, on leaf mould, Codrington College, 5. viii. 1960 (Dept. of Zoology, Fac. of Philosophy, Univ. of São Paulo). Paratype ♀ ♀, 25 mm. and 17 mm. long resp., Codrington College Grounds, Sept. 1960 (Science Mus., Jamaica Inst.). According to the collector (letter of Nov. 9th, 1960): "I was surprised to find *Peripatus* here, as I would have thought that our frequent very dry periods would not provide sufficiently humid conditions for its survival here. I have so far found it in two different localities on Barbados, some miles apart. It seems to be decidedly rare here."

DISCUSSION

Peripatus dominicae barbadensis is closely related to the type subspecies and to *P. d. antiguensis* Bouv. The distribution of the skin papillae is much the same as in *dominicae* s. str., our largest specimen being in this respect very similar to the one picture by Bouvier, 1905, pl. VII, fig. 59. As regards the smallest specimen, the scarcity or absence of accessory papillae on the slopes of the ridges is usual in young specimens of *Peripatus* s. lato. The number of pairs of legs in five females (two of them advanced embryos) is 31, indicating a slightly higher average than in *dominicae* s. str., which has 29 or 30 pairs as the most common numbers. Females of *antiguensis* have from 29 to 31 pairs. The nephridial tubercle of the fourth and fifth legs is independent of the third arc as in *antiguensis*. In *dominicae* s. str. it is connected to the third arc by a narrow bridge.

As regards the internal anatomy, the salivary glands of three forms under discussion are similar. The ovaries and seminal receptacles of *barbadensis,* being about the level of the 12th and 13th preanal legs, are much in advance than in either *dominicae* s. str. or *antiguensis* and resemble those of one female of *P. d. juanensis* Bouv., in which the ovaries were at the level of the 14th preanal legs. In the other female of the same form examined by Bouvier, however, the ovaries were at the level of the 7th preanal legs (Bouvier, l. c., p. 268). If Bouvier had really homogenous material, then this character cannot be much reliable for taxonomic purposes.

Some forms from Haiti described by Brues, 1935, as varieties of *dominicae,* viz. *basilensis, darlingtoni* and *lachauxensis,* differ rather widely from *dominicae* s. str. and its closer "varieties" in the distribution of skin papillae, number of legs, or number of denticles of the saw of the inner jaw blades. Their taxonomic position merits a revision, which at the moment I am unable to carry on.

FURTHER REMARKS

The occurrence of *Peripatus* in Barbados raises some zoogeographic and other problems. Barbados is a very young island, its last emergence dating from late Pleistocene to Recent (see Schuchert, 1935; Beard, 1949; Woodring, 1954). Both its terrestrial fauna and flora have the character of accidental arrivals. Any land connection with neighbouring islands is out of question, so the *Peripatus* of Barbados could only have arrived as waifs or through human agency. Waif transport has been considered absolutely impossible for onychophores but, as has happened in some other cases of animal dispersion, that notion may prove to be wrong (see Darlington, 1938). In either case, the establishment of *Peripatus* in Barbados must be a relatively recent event. One may ask if their isolation has been sufficiently long to allow a significant degree of variation from the parent stock, so as to deserve a special name. As, however, of all known forms none fits entirely, the most similar being discussed above, I thought it more prudent to distinguish it from its near relatives. As a matter of fact, the onychophore fauna of the West Indies (and, for that matter, that of Latin America generally) is only partly

known. Some forms, like *P. danicus* Bouv. from St. Thomas, *P. bavayi* Bouv. from Guadeloupe, and the form from Carriacou (Brues, 1914), are insufficiently known; others probably have not yet been found. No species of *Peripatus* is known, for example, from St. Lucia or Martinique, there being no apparent reason for their absence in these islands.

From the Science Museum of the Jamaica Institute I received also a specimen collected in British Guiana by the Rev. Pearce. The specimen is a female, ca. 38 mm. long, with 30 pairs of legs, dark purplish-brown on the back, lighter below. Although badly macerated, it can be identified with *Peripatus* (*Epiperipatus*) *imthurmi* Sclater. Collection data: Wakapor, Pomeroon, British Guiana, 8. viii. 1959. The Rev. E. J. Pearce coll.

RESUMO

Peripatus (s. str.) *dominicae barbadensis,* n. subsp., proveniente da ilha de Barbados nas Pequenas Antilhas, é descrito. A nova subespécie assemelha-se a *P. d. dominicae* e a *P. d. antiguensis*. Aproxima-se da primeira pela distribuição das papilas da pele, da segunda pela disposição do tubérculo excretor do 4.º e 5.º pares de patas, que é independente do 3.º arco do pé. Todos exemplares da nova subespécie têm 31 pares de patas, o que indicaria ter em média um a dois pares a mais que as duas outras subespécies.

A ocorrência de *Peripatus* em Barbados é de interêsse zoogeográfico. Barbados emergiu muito recentemente e até seu ponto culminante, 330 m acima do nível do mar, é recoberto por corais do Pleistoceno. Desde sua emergência está seguramente isolada. Por outro lado, os onicóforos são animais muito sensíveis a condições adversas, o que levou vários autores a considerar impossível para êsses animais dispersão acidental que implicasse travessia de mar. Darlington, 1938, contudo, acredita que as Antilhas, exceto Trinidad, foram colonizadas inteiramente por sêres que, de qualquer forma, atravessaram o mar. A ocorrência de *Peripatus* em Barbados, se não se deve à interferência humana, só pode ser explicada por travessia acidental do mar. A pátria de origem de *P. d. barbadensis* ainda não pode ser determinada.

Um exemplar proveniente da Guiana Britânica, apesar de mal conservado, pode ser classificado como *Peripatus* (*Epiperipatus*) *imthurmi* Sclater. Tanto os exemplares de Barbados, como o último, foram colecionados pelo Rev. E. J. Pearce.

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EXPLANATION OF THE FIGURES

Fig. 1 — Holotype. Photograph of skin at the level of the 16th pair of legs: skin scales, papillae, median light line, and some spiracles.

Fig. 2 — Ink outline of the same. The spiracles are drawn with double thin lines.

Fig. 3 — Holotype. Skin of the same region as above: distribution of principal and accessory papillae, two incomplete plicae, and median light line.

Fig. 4 — Larger Paratype. Skin at the level of the 15th pair of legs: same structures as in fig. 3.

Fig. 5 — Smaller Paratype. Skin at the level of the 14th pair of legs: same structures as in fig. 3.

Fig. 6 — Larger Paratype. A principal and an accessory papilla close to the median line.

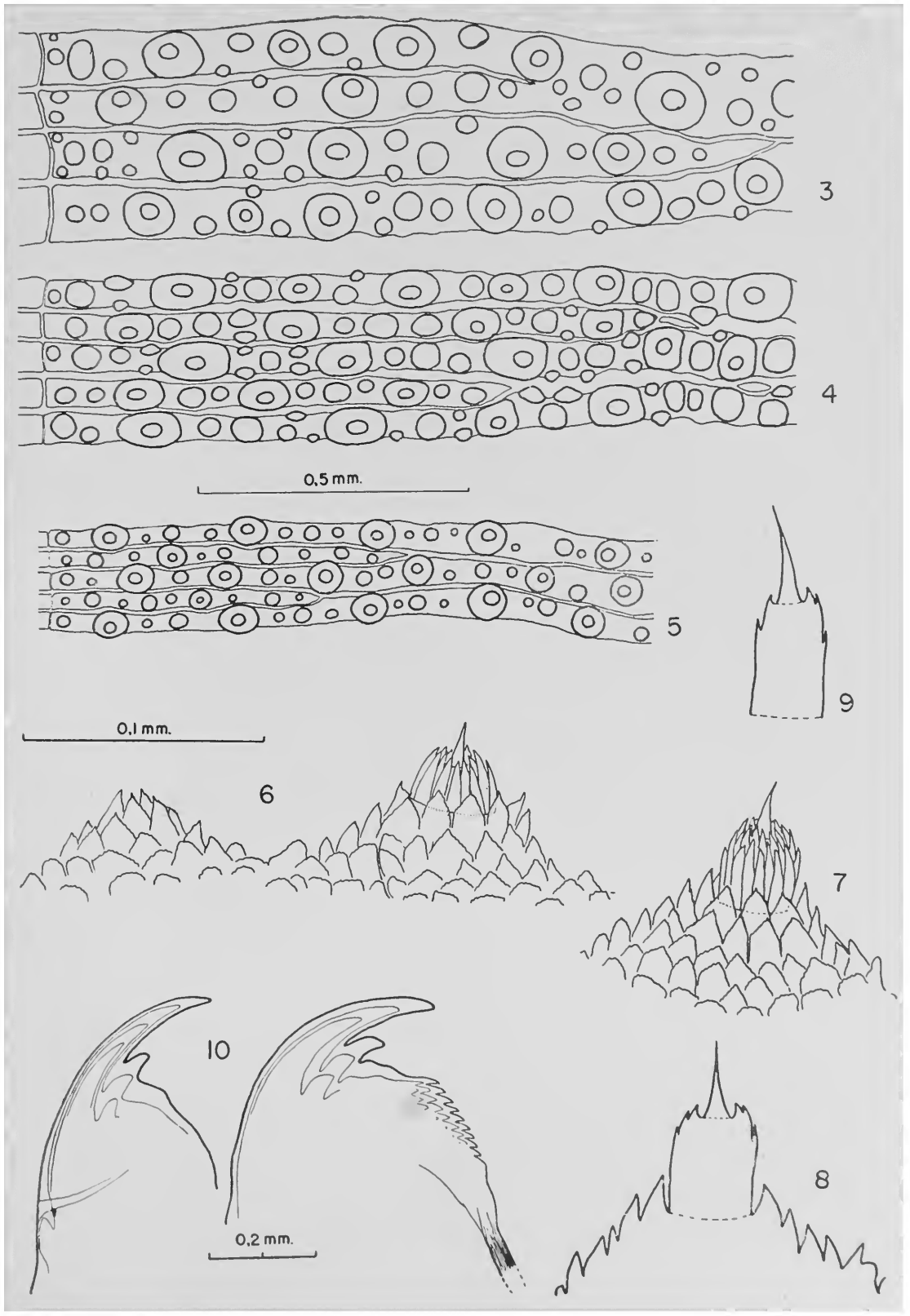
Fig. 7 — Ibid. A principal papilla of the lateral portions of the body.

Fig. 8 — Holotype. Outline of a principal papilla close to the legs.

Fig. 9 — Ibid. Upper cylinder of another principal papilla of the same area.

Fig. 10 — Outer and inner blades of the jaw.

Figs. 3-10 are camera lucida drawings. Figs. 3-5 drawn to scale above fig. 5; figs. 6-9 to scale above fig. 6. The skins and papillae figured are all from the dorsal surface.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STUDIES ON COLUMBELLIDAE

by EVELINE and ERNST MARCUS

(with 8 plates)

Contents

INTRODUCTION

The exterior aspect of the soft parts of a *Columbella, C. rustica* (L.), was drawn and rapidly described more than 100 years ago (Joannis, 1834), but the classical French papers of the last decennia of the past century which constitute the basis of modern malacology do not include the Columbellidae. Thiele (1924, p. 208) still called

the anatomy of the columbellids unknown, and 30 years later Risbec (1954) began his study of the inner organs of 6 columbellids from the coast of New Caledonia with the words: "l'anatomie des Columbellidae est complètement inconnue". Risbec's conditions for work (1937, p. 189-192) allowed only for an anatomical foretaste without microtomy. Hence we took the opportunity to continue his studies, but with 8 other species, mainly from the coast of São Paulo.

We are grateful to the Director of the Oceanographic Institute, Dr. Ingvar Emilsson, for his permission to stay repeatedly at the Base of Research, 14 km W of Ubatuba, whose Head, our friend Dr. Edmundo Nonato, made our work most agreeable.

Drs. Roger Jean Lavallard and Edmund Hobart Smith found a locality where *Columbella mercatoria* was obtained, and collected many specimens for us. We are most thankful to them, because some particularities of *C. mercatoria* and also of *C. rustica* which we owe to the Zoological Station of Naples extended our knowledge of the anatomy and biology of the columbellids.

We thank Dr. Woutera S. S. van der Feen van Benthem Jutting--Amsterdam for her elucidative information by letter, and Dr. Germaine L. Warmke-Puerto Rico for her and Dr. Abbott's book on Caribbean Seashells (1961). This most recent synopsis of a neighbouring fauna serves to classify also Brazilian shells.

SYSTEMATIC NOTES

As 100 years ago, Reeve's Shakespearean motto (1859) holds to-day for the Columbellidae: "mis-shapen chaos of well seeming forms". Certainly Pace's list (1902b) is the first step to bring order into this chaos. Comparative revision, however, must be done with a great collection as basis and the possibility to loan further material. Since Thiele's survey (1931, p. 302-305) the number of taxa has increased considerably, as the "Zoological Record" shows as well as any regional list, e. g., Macpherson and Chapple's of the columbellids of Victoria (1951, p. 131). Therefore we leave aside the discussion of genera, subgenera and sections, adopt the nomenclature of Abbott (1955), and try to evidence that we combined uniform and recognizable material with every name. Hence we describe shells, colours of soft

parts, and radulae merely as far as seen in our material. The first 6 of our species were collected on algae, chiefly *Sargassum cymosum stenophyllum* immediately beneath the low water-line, 14 km W of Ubatuba (23°27'S, 45°6'W). *Anachis sparsa* and *veleda* also occur on and under stones in the vicinity of the algae. A female of *veleda* laid an egg capsule in a dish (1-I-1961) and so made possible to identify capsules found on *Sargassum*. Other capsules which we combine (see chapter "Eggs and larvae") with *A. brasiliana* and *A. sparsa* occurred in winter (July 1960) and summer (December 1960-January 1961) on *Sargassum*. The egg capsules were fixed to the young broad "leaves" of the short lateral branches near the holdfast which are smooth, not overgrown by polychaetes, bryozoans, and compound ascidians.

Columbella mercatoria was found among algae, chiefly *Acanthophora spicifera,* grown on stones and boulders at the mean low water-line on the continental coast of the Canal of São Sebastião. The point, called Ponta da Prainha, is 23°45' S, 45°25' W.

On the inside of the shells of living columbellids the colour pattern of the outside appears by translucence. We collected principally live snails whose shells are still translucent after preserving or drying. Some shells inhabited by hermit crabs were also taken. Their inner layer is opaque. We did not gather dry shells from the beach, because they are generally much lighter, and the grinding action of waves and sand can modify the sculpture to such a degree that classification becomes insecure, e. g. in *Anachis cancellata* (Gaskoin, 1851) (see Kobelt, 1897, p. 226).

1. *Anachis brasiliana* (v. Martens, 1897) (Fig. 1)

Length up to 11 mm, breadth about 4 mm, smallest shells seen 5 mm. About 9 whorls, 4 of which, smooth and convex, are nuclear. Outline of shell straight, even, only axial ribs of body whorl project slightly on the sides. Body whorl with about 12 ribs ending in front of suture. Ribs narrower than interspaces. Other whorls smooth. Spiral lines absent, except on base of body whorl. Young shells with incipient ribs behind outer lip. Aperture narrow, elliptical, with thickened varix on outer lip. Flattening behind varix may suppress

up to 7 ribs. Inside of outer lip with 7-9 denticles, sometimes the 2nd from behind biggest. Inner lip frequently with white callus which bears a longitudinal crest.

Dry shells may have opaque, sometimes iridescent inside. Protoconch, including apex, light. Suture with white band in front; rest of shell generally whitish with many rusty brown meshes of different, sometimes considerable, width and light spots between. Some shells are quite dark. The ribs are often light.

Siphon white, mottled, or with 3 black rings. Tentacles white with black base and a black ring farther in front. Proboscis white. Foot with brownish and greyish spots, in front with black and yellow pattern. Mantle under shell black up to apex. Operculum oval, colourless or light yellow.

Discussion of *Anachis brasiliana*

Our material agrees with v. Martens' description (1897, p. 171-172) and figure (pl. 16, f. 10). His and our shells differ by smooth interspaces between the ribs from *A. avara* (Say, 1826). Also in *A. avara semiplicata* (Stearns, 1873), a hypotype of which was figured by Puffer and Emerson (1953, pl. 56, f. 7), spiral lines occur in these interstices.

Similar to *A. brasiliana* is *Columbella sertulariarum* d'Orbigny (1841, p. 431; 1846, pl. 61, f. 13-17), whose distribution Carcelles (1944, p. 253) gives from Key West and the Antilles to Brazil, Uruguay, and Argentina, Gulf of San Matias. The shell of this species is a little bigger than that of *brasiliana*, and the colour of the body differs slightly.

Distribution: Brazil: Bahia (v. Martens), São Paulo, Ubatuba (present material), Sta. Catharina (v. Martens); Uruguay (id.).

2. *Anachis sparsa* (Reeve, 1859) (Fig. 2)

Length 8-9 mm, breadth 4 mm; smallest shells of 2 mm have already some brown marks. Protoconch smooth, light, comprising 3 whorls with impressed, sometimes dark suture. Total number of whorls about 8. Axial ribs broader than interspaces, end in front of suture. Faint spiral lines between the ribs; base with stronger

spiral lines. Number of ribs on body whorl about 16. Aperture small, narrowed behind; outer lip frequently with varix and regularly with dorsal flattening which may suppress up to 7 ribs. Inside of outer lip with 6-7 denticles. Inner lip with or without callus, whose presence or absence is independent of age. On callus, when present, a row of about 6 denticles corresponding to basal spirals.

Periostracum thick, longitudinally fibrous. Some shells vitreous with colour pattern translucent on inside, others opaque and with iridescent inside. Ground colour whitish; a white stripe in front of suture. On the ribs chestnut brown or darker marks alternating with white ones, corresponding to the dark blotch of one rib a white mark on the two neighbouring ribs. On the basal spiral lines the brown blotches form rows or meshes.

Siphon white with grey spots or with 3-4 grey rings, tentacles white with black band, proboscis white, foot spotted, in front of operculum and at anterior border with black marks; sole with small spots and white anterior border. Mantle under shell black. Operculum yellow, rather narrow, pointed on one, broad on the other end.

Discussion of *Anachis sparsa*

As this species is common near Ubatuba, it should be expected in Lange's catalogue (1949). Possibly it is hidden there under the name *pulchella* Kiener, Sowerby, 1844, which Lange indicated (p. 96) from Guarujá near Santos. According to Johnson (1934, p. 120) this species appears with the name *catenata* in the literature. By comparison of our material with figures of *catenata* (Reeve 1859, pl. 21, f. 119a, b; Warmke & Abbott 1961, pl. 20 r), *pulchella* (Warmke & Abbott, pl. 20 g), and *sparsa* (Reeve, pl. 31, f. 200) the differences between them become evident, and the classification of our material as *sparsa* is beyond doubt.

Distribution: West Indies: Brazil, coast of São Paulo, Ubatuba (present material).

3. *Anachis obesa* (C. B. Adams, 1845)

Up to 5 mm long, 2,2 mm broad. Whorls about 7, 3 1/2 of which nuclear and smooth. The others with sharp axial ribs, about

18 on body whorl, narrower than interspaces. These with spiral lines not crossing the ribs. First definitive whorl with 4 lines, next whorls with 5-6, body whorl with about 16 besides 10 basal ones. Suture concealed by posterior knobs of ribs. Outer lip with thick varix; flattened area behind varix may suppress 4-6 ribs. Inside of outer lip with 3-6 white denticles projecting from a brown longitudinal ribbon not always present. Inner lip with narrow, sharply edged callus, sometimes with longitudinal fold. Aperture oval, simple or constricted by projecting outer lip and parietal shield.

Shell light or darker brown with quite light apex. Suture accompanied in front by white line. Colour pattern variable. Sometimes two more or less distinct darker brown spiral bands on body whorl, the posterior of which continues on to spire. In some shells the bands substituted by crescent-shaped spots prolonged into undulate lines.

Siphon and all soft parts white; mantle under shell pigmented; operculum pumpkinseed-shaped, light yellow.

Discussion of *Anachis obesa*

Lange de Morretes (1949, p. 96) records *A. ostreicola* as separate species. Melvill (1881, p. 160) described it sketchy, Sowerby (1882, p. 119, pl. 5, f. 10) completely. The typical locality is northwest Florida. It belongs to *obesa* (Dall 1889, p. 188; Kobelt 1897, p. 140) as a dark colour-form. Light and dark shells of our material are linked by such of intermediate shades. Therefore we think that the darkest shells do not deserve a special name, as little as other varieties without restricted geographic range (Pace 1902b, p. 39).

Nassa isabellei d'Orbigny (1841, p. 433; 1846, pl. 61, f. 18-21) from Santos to Argentina, Gulf of San Matias (Carcelles 1944, p. 253) is probably identical with *obesa*. Both have white bodies. The size of the shell in the type of *isabellei* agrees with *obesa;* southern *isabellei* are bigger. The question can be decided only with material from Argentina.

Distribution: Virginia to Florida; the Gulf States and the West Indies (Abbott 1955, p. 221); Brazil, Ubatuba and Itanhaen (present material), Island of São Sebastião (as *ostreicola;* Lange), coast of Paraná and Sta. Catharina (Lange).

4. *Anachis veleda* (Duclos, 1846) (Fig. 3)

Length up to 18 mm, breadth up to 8 mm; no shells smaller than 7 mm were seen. Adult shells thick-walled, young ones thin. Whorls 10-11, 2 1/2 of them nuclear, smooth. All whorls little convex, but suture somewhat impressed. About 17 axial ribs on body whorl, narrower on other whorls; all ending in front of suture and narrower than interspaces. These smooth; spiral lines only in anterior half of body whorl. In young shells the ribs of each whorl with 4 spiral rows os beads. Similar knobs at base of shell on crossings of spiral lines with axial ribs. Aperture elliptical or narrowed posteriorly. In old shells allusive varix on outer lip marked by posterior flattening, and slight white callus on inner lip. Inside of outer lip with about 6 denticles; pillar without denticles.

Shell whitish with light or greenish protoconch; distinct white band in front of suture and a second farther in front. Interspaces between ribs darker. Between white bands on ribs of body whorl an anterior and a posterior row of blackish brown dashes; on other whorls only posterior row visible. Anterior spirals with brown spots.

Siphon white with 2-3 black bands, tentacles white with 2 black rings, upper side of foot spotted with brown, around the margin black; sole lighter. In some cases the hind end of the sole was white, evidently due to recent regeneration. Mantle under shell pigmented. Operculum brown, longish, more pointed than that of *sparsa*.

Discussion of *Anachis veleda*

Though Duclos' species was only figured, not described, we use its name which v. Martens (1897, p. 171) applied to Brazilian shells. His drawings (pl. 16, f. 8, 9) and the copy of Duclos' figure (Kobelt 1897, pl. 43, f. 18) agree well with our material.

Possibly Lange de Morretes' (1949, p. 96) *A. lyrata* Sowerby, from the coast of Ceará to Paraná, refers to the same species. *A. lyrata* is Pacific (Kobelt 1897, p. 58-59). The corresponding western Atlantic (Keen 1958, p. 382) *A. terpsichore* Sowerby, 1822 which Lange (l. c.) records from Bahia, may be our species too. Duclos'

and v. Martens' figures of *veleda* however agree better which our material than Kobelt's of *terpsichore* (1897, pl. 8, f. 5-7).

Kobelt (p. 40-41, 321) follows Tryon and considers *veleda* as a variety of *A. varia* (Sowerby, 1832) from the Pacific coast of Mexico, Sonora, to Panama, and A. Myra Keen (1958, p. 386) gives it as a mere synonym of *varia*. Though that species is a little bigger than *veleda,* it has less ribs on the body whorl, and its colour pattern (Kobelt, pl. 5, f. 8-14) differs from that of Duclos', v. Martens' and our *veleda*.

Our material is the shell that is called "felicidade" (happiness) on the beach of São Paulo, where it is collected for ornamental purposes.

Distribution: Brazil: ? Bahia (Lange, *terpsichore*), Ubatuba (present material), Desterro (to-day Florianopolis), Sta. Catharina (v. Martens); probably also Lange's localities on the coasts of Ceará, Bahia, São Paulo, and Paraná that refer to *lyrata*.

5. *Nitidella dichroa* (Sowerby, 1844) (Fig. 4)

Length 7, rarely 8 mm, breadth up to 3 mm; the smallest shells were 1 mm long. Whorls 6-8, the 3 of the protoconch flat. Shell smooth and of nearly straight sides, when dry, mat on outer, glossy on inner side. Suture shallow, spiral lines only on anterior third of body whorl. Aperture narrow, about 2/3 of the length of body whorl. Outer lip with 3-8 denticles in shells thickened by age, columellar lip not denticulated, sometimes with glossy brown callus contrasting with white pillar farther inwards.

Whorls of protoconch without spots, quite dark, the forward whorls with superficial black or dark chestnut brown pigment and highly variable white pattern. An opaque white line in front of suture generally appears as row of dots interrupted by black or is nearly completely concealed. More or less densely disposed round spots, especially on spiral lines around anterior canal and first definitive whorl; other parts with spots and several axial blotches of irregular outlines.

Siphon and tentacles black with 2-3 white rings or white with black spots. Proboscis black with white tip and ventral line. Foot

black with narrow white line at anterior border. Mantle under shell light. Operculum short oval, quite light yellow.

Discussion of *Nitidella dichroa*

In the beginning we took our snails for small specimens of the typically 10-14 mm long *Nitidella ocellata* (Gmelin, 1791). Lange's catalogue does not contain *ocellata* nor its synonym *cribraria* (Lamarck, 1822). Therefore we compared *parvula* (Dunker, 1847) and *moleculina* (Ducios, 1846), both indicated by Lange from the northeastern coast of São Paulo, with our material. Kobelt (1897, p. 86-87) identified *parvula* with *ocellata;* Johnson (1934, p. 120) maintained it separate, and *parvula* is really considerably smaller. Its colour pattern consists of blotches (Philippi 1851, pl. 2, f. 7). Also *moleculina* indicated from deeper water of Northern Argentina by Dall (1889, p. 186) is, according to Kobelt's copy (1897, pl. 40, f. 7) of Duclos' figure, smaller than *ocellata* and its pattern is rather dots than blotches. We leave the definition of *parvula* and *moleculina* to the conchologists with ample collections and bibliography.

Our material must be classified as *N. dichroa,* according to text and figure of Warmke & Abbott (1961, p. 112, pl. 20 k). Colour pattern and size distinguish it from *ocellata*. Nearly all our shells collected alive have an entire spire with protoconch, while the apex of adult shells of *ocellata* is generally decollated (Kobelt 1897, p. 86; Lamy 1941, p. 306, note 2; Abbott 1955, pl. 25 hh; Coomans 1958, pl. 14; A. Myra Keen 1958, f. 484). Besides the occurrence of *dichroa* near Ubatuba we know it also from the Bay of Santos.

Distribution: West Indies; Brazil, coast of São Paulo, Ubatuba (present material).

6. *Mitrella lunata* (Say, 1826)

Length 3-4 mm, breadth 1,7-1,8 mm; the youngest shell 1 mm. Whorls 5-7, the 3 of the protoconch convex and with deep suture, the others flatter with not impressed suture. Shell smooth, of variable thickness, in adults rather thick, mat on outer, glossy on inner side. Spiral lines only around siphonal canal. Aperture constricted

by projecting outer lip. Inside of outer lip with 2-9, frequently 7, denticles of somewhat different size, often the 2nd from behind biggest. Sometimes a varix-like thickening on outer lip and flattening behind it. Inner lip with narrow callus bearing longitudinal fold, without denticles.

Dark brown line along callus continued around whole aperture. First nuclear whorl generally brown, rarely light, following whorls lighter than definitive ones. These are light olive with white band in front of suture, sometimes concealed, sometimes dissolved into a row of dots. On the band brown crescents from which 1-3 wavy lines run forwards which may anastomose. Occasionally very dark shells occur.

Siphon white with some black spots, tentacles white with black ring, proboscis white. Back of foot white with thin black meshes, sole white. Mantle under shell dark grey. Operculum broad oval, colourless.

Present shells frequently attacked by boring ctenostomatous Bryozoa.

Discussion of *Mitrella lunata*

Our shells do not show the fine axial stripes described by Kobelt (1897, p. 145), hence agree with Abbott's (1955) and Warmke & Abbott's (1961) indication "smooth".

Distribution: Massachusetts to Florida, Texas and the West Indies (Abbott 1955, p. 223); Brazil: São Paulo, Ubatuba (present material), Island of São Sebastião (Lange de Morretes 1949, p. 97); coast of Paraná (Gofferjé 1950, p. 243), not common.

7. *Columbella mercatoria* (Linné, 1857) (Fig. 5)

Length of 50 present shells up to 20 mm, breadth 11 mm. Up to 8 convex whorls, 3 of which belong to the whitish or yellowish protoconch, whose uppermost one, the shell of the veliger, is very large. Body whorl more than half the height; spire low, acuminate. Sutures distinct. Growth lines appear in the periostracum; no axial ribs. Distinct revolving ridges on the whole surface, sometimes those on

base of body whorl a little higher. Aperture narrow, 13 mm high, as long as body whorl. Outer lip thickened, its inner margin with central convexity and crenulation extended from basal end to a point below anal angle, comprising up to 14 white crenations with more or less distinct mauve-brown marks between them. Inner lip with 4-7 small beads. Columella curved, with thickening divided by a furrow.

Periostracum thick whitish, very fibrous, firmly adherent. Ground colour whitish, maculated, banded or reticulated with black or brown, sometimes colour nearly uniformly brown. Inner side of shell white or purple. Siphon black on outside, white on inside; tentacles black with white tips; proboscis orange, containing haemoglobin. Foot with black dorsum, white anterior stripe, and reddish-brown sole; moulding gland white. Mantle under shell white or pigmented. Pericardium white due to filling with sperm; kidney purplish; stomach green; digestive gland olive; intestine greyish green. Ovocytes in ovary olive; capsule gland white.

Operculum small, thin, nearly triangular, light yellow, with terminal nucleus and conchinous ridge in middle of thin area, where muscle inserts. Absence of pigment at hind tip of foot and comparison with present complete operculum of *rustica* suggest that all present opercula of *mercatoria* were in regeneration.

Discussion of *Columbella mercatoria*

The mauve-brown marks between the crenulations (Abbott 1955, p. 220: *rusticoides*), the very fibrous periostracum (Perry & Schwengel 1955, p. 160: "hispid epidermis" of *rusticoides*), and the geographic indications for Brazil (Lange de Morretes 1949, p. 95-96) made us doubt how to call our material, till we saw Warmke & Abbott's figure (1961, pl. 20 a). *C. rusticoides* is up to 28 mm long, smooth on the centre of the body whorl, and slender, not squat as our snails. This becomes evident by the proportion of length and breadth (1) of the shells: *rusticoides* (Heilprin 1887, pl. 8, f. 9) 2,0; *rusticoides* (Perry & Schwengel, f. 223) 2,05; *mercatoria* (Abbott 1955, pl. 25 bb) 1,68; *mercatoria* (Warmke & Abbott 1961, pl. 20 a) 1,67; present material (10 shells measured) 1,67; *mercatoria* (Coomans 1958, pl. 14) 1,51 (spire worn).

The name of the genus refers to the comparison of the Dove-shell *C. mercatoria* to a breeding dove, whose apex is the head, and the outer lip the lowered left wing. The translation "pretty column" (Perry & Schwengel, note 295) is untenable, as are others (294, 296). *Nitidula* is the diminutive form of *nitida,* while *nitedula,* the dormouse (*Muscardinus avellanarius*) alludes to the verb "nitor" (I climb). In contrast to the commercial *mercatoria* sold for ornamental purposes, *rustica* is simpler, more rustic, and *rusticoides* is similar to *rustica.*

8. *Columbella rustica* (Linné, 1758) (Fig. 6)

The available nine shells are up to 24 mm long, 12 broad. A total of 8 whorls, 3 of which belong to the brownish or whitish protoconch. Body whorl considerably more than half the height, e. g. 12,5 mm in a 16,5 mm long shell. Whorls less convex than in *mercatoria,* but sutures also distinct. Spire short, pointed. Growth lines as in *mercatoria;* no ribs. Spiral lines slight, stronger at base. Aperture as long as body whorl, narrow. Outer lip sometimes thick, with central convexity and up to 14 crenations of inner margin, sometimes thin, smooth, without crenulation. When the outer lip is thick, it has a varix and a flattening behind it. Up to 4 beads on the inner lip and a thickening of the columella divided by a furrow occur in shells whose outer lip is thickened, not in the others.

Periostracum thick. Ground colour whitish, also on inside. Black or dark brown colour marks leave more or less transverse white spots free on surface. Foot with sometimes light sometimes dark sole, the sides are spotted and dark below; the anterior border is light. Also the colour of the siphon varies: it may be hardly pigmented, maculated, or nearly black. Proboscis white. Tentacles spotted to nearly black with white tips. Mantle white or black with white border. Operculum almost black; 7 mm long, 3,5 mm broad; nucleus apical, at the pointed end. Of the 9 present snails all but one had regenerating hind ends with incomplete opercula.

Discussion of *Columbella rustica*

The great variability of the shell with regard to shape and colour is shown by Kobelt's 14 figures (1897, p. 6, pl. 1). The preceding

description refers only to material preserved in Bouin's liquid at the Zoological Station of Naples.

The range of *rustica* comprises the Mediterranean Sea, the warm temperate Eastern and the Middle Atlantic Ocean, where it extends southwards to the Gulf of Guinea.

GENERAL REMARKS ON THE SHELLS

The beads or denticles on the inside of the outer lip are taxonomically of little use, because their occurrence is quite irregular. When the outer lip is growing fast and therefore thin, the beads are absent; if growth is slow and the lip thickens, they are developed. The same holds for the callus of the inner lip. The character used in Keen's key (1958, p. 378) for the genera "outer lip smooth in the adults" opposed to "outer lip with teeth in the adult" cannot be applied to the species we have seen.

Already Pace (1902b, p. 39) mentioned that simple, thickened, or denticulate lips are individual, not specific characters. He also denied the systematic significance of shell-size and shape, long and narrow, or short and stumpy, almost globose. According to Pace even the sculpture is subjected to a wide variability. One and the same species may have a longitudinally ribbed, transversely striped, or smooth shell. If this was true, *A. brasiliana* would be a synonym of *A. avara*. However, we do not feel authorized to apply Pace's criteria. They contrast whith the conchological tradition exemplified in A. Myra Keen's key to the genera of Columbellidae (1958, p. 378). We agree with Pace (p. 40) in the diagnostic value of the colour plan from which patterns, often very diverse in a great number of conspecific specimens, can be derived.

The apical angles in our species are: *brasiliana* 40°, *sparsa* 40-50°, *obesa* 55°, *veleda* 50°, *dichroa* 40°, *lunata* 50°, *mercatoria,* 60-70°, and *rustica* 66°. Thence a narrow mantle cavity can be inferred for the first six species.

HEAD AND FOOT

The head is small, without snout, only developed as a salient common socket of the short, pointed, and divergent tentacles. Late-

rally and basally the tentacles contain the eyes, whose structure corresponds to the *Murex*-type (Hesse 1934, fig. 58, C). The inconspicuous opening of the proboscis sheath lies beneath the base of the tentacles.

The siphon (Figs. 9, 22, so) is about half the length of the foot and open on its ventral side without curling one border over the other. The ciliated edges to the sides of the ventral slit are straight. Blue-staining subepithelial glands open principally on the inner surface whose epithelium is flat. The siphonal musculature is chiefly longitudinal with sparse radial fibres. The muscle layer is thicker on the ventral than on the dorsal side. As the fibres of the retractor insert on the left dorsal side, the musculature of the corresponding right side is especially weak. The inner and outer muscle layers are separated by a thin stratum of connective tissue containing the siphonal nerves, up to 20 near the tip. Blood lacunae occur between the outer muscles and the epidermis whose cells are higher than those of the inner epithelium.

The left border of the siphon is continued into a massive retractor lodging the siphonal ganglion. This retractor (Fig. 8, ms) accompanies the broad columellar muscle (Fig. 33, c) to the columella. The right border of the siphon is extended inwards into a high, ciliated fold whose loose conective tissue contains blood spaces and subepithelial glands. This fold broadens behind and ends with a small flap in front of the gill.

On the right side of the head the pallial suture forms an acute angle jutting as a minute flap. The columellar muscle originates near the apical suture of the penultimate whorl.

The foot is narrow, truncate in front, without mentum, and pointed behind. An operculum is present in all our species, while it is absent in two small species of Risbec's columbellids (1954, p. 132). The operculum (Fig. 7, oc) lies obliquely on a pad (za) set off from the back of the foot and stands out over its sides. The thickly ciliated sole (Fig. 8, sc) is separated from the sides by a longitudinal furrow (mr) which runs from the fore end of the foot to the hind point.

The sole glands (Fig. 8, iv) (Graham 1957, p. 141) lie in the connective tissue under the epithelium of the entire sole and attain

the furrow. The anterior pedal mucus glands (l. c.) discharge into the deep ciliated groove (Fig. 7, an) that runs across the anterior end of the foot, and into an about 0,1 mm long canal coursing from the middle of the groove backwards. In *dichroa* the glands of the groove are, in part, red-staining. A small median invagination or folded pouch (vn) of the ciliated epithelium in front of the middle of the sole is the ventral pedal gland (l. c., p. 142). It contains few gland cells and is only quantitatively less developed in males. The same was found in *Lintricula auricularia* (Marcus 1959, p. 115). In *sparsa* the sexual difference of the ventral pedal gland is slight, in *dichroa* this gland is much more conspicuous in females where it is macroscopically recognizable as a white pit in the black sole. Also the ventral pedal gland of *brasiliana* and *veleda* (Fig. 7, vn) can be seen in the living female. It is, however not very distinct, so that the root of the penis showing when the mantle border is lifted in a snail taken out of its shell is the best character to distinguish the sexes.

At the hind tip of the foot, under the operculum, or under its anterior border (*obesa*) opens the posterior pedal gland (Fig. 8, uo) of Graham's terminology (1957, p. 142). Its round, ciliated and straight canal (ow) attains the region of the nervous system (ea, eu) and contains stretches with mucus glands. The inner end of the canal receives the ducts of numerous mucus glands that lie around the nerve ring, the statocysts, and part of the salivary glands. In *veleda* and *lunata* examined in this respect the pedal mucus glands on the right side of the brain are several times as voluminous as the rudimentary ones on the left side. As in *Cerithiopsis tubercularis* the posterior pedal gland of the columbellids produces the "viscid climbing rope which allows the snail to lower itself from its inverted swimming position on the surface film, or to climb along it with its narrow sole, or it may be used to secure the animal" (Fretter 1951, p. 569). *Rissoa membranacea* (Johansson 1939, p. 298), *Skeneopsis planorbis* (Fretter 1948, p. 599), *Omalogyrus atomus* (ibid., p. 608), *Rissoella diaphana, R. opalina* (ibid., p. 618, 624), and *Cingulopsis fulgida* (Fretter & Patil 1958, p. 115-116) are examples of similar posterior pedal glands in small, "spinning" prosobranchs, but

those of the mentioned Rissoacea and Cerithiacea have branched canals and open farther in front; the secretion is conveyed to the posterior tip of the foot in a groove of the sole.

LOCOMOTION

A few preliminary observations were made on locomotion of species 1-6. As other small snails (Ankel 1936, p. 82) the columbellids have the ability to glide on the surface film. We saw it principally in *dichroa* and *lunata*. Also the other species, e. g., *brasiliana* and *sparsa* "spin" a thread of mucus which is attached to the seaweed or the surface film, and the snail then "dangles and swings on its elastic support" (Myra Keen 1958, p. 378). Rhythmical locomotion, an even gliding on a substratum by undulations of the sole, occurs in all species, but also arhythmical locomotion, gliding alternating with jerks (Weber 1924, p. 112). The foot maintains its contact with the substratum and advances in front of the shell. Then the latter is drawn forwards by contraction of the columellar muscle. This type of locomotion is more frequent in *veleda* and *brasiliana* than in *dichroa* and *lunata*. Species with bigger, heavier shells and relatively shorter foot move arhythmically oftener than those with smaller shells and relatively longer foot (ibid., p. 120). As the foot is narrow in these species, one can compare the proportion of length of shell and foot in our extreme species. In the following proportions 1 is the length of the foot. We obtained for *veleda* 1,64-2,0: 1, and for *lunata* 0,8-1,17: 1.

Weber (1924, p. 113) derived the arhythmical locomotion from digging. In his example, *Conus,* this is conceivable, but not so easily in Buccinacea. Though some columbellids plow about in tide pools (Myra Keen, l. c.), they are not so pronounced diggers as, e. g., the Nassariidae.

Mitrella lunata frequently assumes a peculiar attitude. Fixed only with the hind end of its foot to the bottom of a watch-glass, as if standing on its tail, it rises and stretches its siphon upwards moving it in all directions.

The highly extensible foot of the columbellids makes it easy for them to recover when they have fallen upside down. As Weber

(1926, p. 400) observed at Naples, they grasp with the anterior pedal border. This projects from the aperture and searches in all directions, to the right or left side or even over the middle in front of the shell. Where the pedal border finds a hold, it seizes it and turns over.

PALLIAL ORGANS (Figs. 8, 9, 33)

The inferior mantle border is thinly ciliate, the upper one is strongly innervated and lodges numerous glands. Where the hind border of the mantle is united with that of the roof of the pallial cavity on the right side, in all species the suture is developed as a prominent fleshy ridge, as already figured by Joannis (1834). The roof of the mantle cavity is richly supplied with blood lacunae, hence probably respiratory. In the innermost part of the floor begins a patch of cilia (Fig. 33, x). The pallial communication (Figs. 25-29, ra) of the renal sperm duct, described in the following, opens in this region on the left side. Farther in front the ciliated area divides into two stripes of small cilia. The left one is short and ends at the posterior level of the ctenidium (b). The right stripe continues beyond the mantle cavity for a short extension under the root of the penis. This right stripe evidently affords an efficient exhalant current.

Generally the epithelium is flat in the mantle cavity (Fig. 9), but a conspicuous hypobranchial gland (y) is developed on the right side of the roof behind the area underlain by blood spaces (si). An interruption of the hypobranchial gland by a penial pouch (Fig. 33, eo) in the male will be described in connexion with the reproductive organs. It is absent in *mercatoria* and *rustica*. On the left side the narrow ctenidium (b) extends far backwards. On the afferent side its leaflets bear a pad of glandular epithelium.

The osphradium, though shorter than the gill, is large (Fig. 9, os). In our smallest species, *lunata,* it is unipinnate. Also Risbec (1954, p. 132-133) found the left leaflets of the osphradium very reduced in size in *C. ligula* and absent in *C. troglodytes*. Even in our bigger species the right osphradial leaflets are more numerous and broader than the left ones. The following table refers to average snails of our eight species.

Species:	Osphradium				Gill		
	n.° of left leaflets	breadth of same	breadth of ganglion	breadth of right leaflets	n.° of same	n.° of leaflets	breadth of same
lunata	0	—	0,1	0,3	33	50	0,3 mm
obesa	17	0,1	0,25	0,35	40	72	0,5 mm
dichroa	19	0,1	0,2	0,35	45	68	0,6 mm
sparsa	24	0,2	0,2	0,4	53	90	0,7 mm
brasiliana	34	0,25	0,25	0,7	65	125	1,2 mm
veleda	50	0,3	0,2	0,8	95	200	1,3 mm
mercatoria	31	0,6	0,4	0,8	50	160	2,2 mm
rustica	39	0,7	0,3	0,8	58	120	4 mm

By counting and measuring sections we found that the mass of the central ganglia exceeds that of the osphradial ganglion by 10%.

NERVOUS SYSTEM (Fig. 11)

The ganglia of the nerve ring lie near together, but are all set off from one another. As in the species examined by Risbec (1954, p. 131) the longish pedal ganglia (ea) are biggest. The right, more dorsal ganglion, which emits the penial nerve (xn), lies farther in front than the left, farther ventral one. A number of pedal nerves leave the anterior margins of the ganglia. These are, as in Risbec's figure B, 5 (p. 133), subdivided into several cones. One pair of nerves (na) supplies the anterior border of the foot, the others, about 3 pairs (nv), run parallel to the duct of the posterior pedal gland (ow) and branch in the region of the operculum. In *dichroa* the pedal ganglia are strongly pigmented with black. In *mercatoria* and *rustica* the roots of the nerves (na) which supply the anterior border of the foot are separated as conical propodial ganglia by a furrow from the rest of the pedal ganglia.

The cerebral ganglia (er) are almost globular, and the right one is bigger than the left as in Risbec's species. In *brasiliana, sparsa, obesa, veleda, dichroa,* and *lunata* the cerebral ganglia lie to the sides of the oesophagus (e), over which their posterior halves are broadly connected without interruption of the layer of nerve cells. In *mercatoria* and *rustica* these ganglia are connected by a true supra-oesophageal commissure which is twice as long as broad, hence shorter and broader than that of *C. versicolor* (Risbec, 1954, f. A, 7), but essentially comparable. The cerebro-pedal and cerebro-buccal connectives are short, internal connexions in our material. The buccal ganglia (cc) are contiguous without external comissure. They lie between the anterior part of the cerebral ganglia. Much farther ventral are the statocysts (sz) with a single spherical statolith. Their position varies. They lie to the right, sometimes close to the pedal ganglia, sometimes embedded in the racemose salivary glands.

In *veleda, mercatoria* and *rustica,* not in our smaller species, each cerebral ganglion has on its anterior and outer side a cap (cz) which consists of small, dark staining nerve cells around a core of

fibres. Such areae are known from several prosobranchs, also from *Buccinum* (Hanström 1928, p. 170). In his discussion of the homology of these caps with the procerebrum of pulmonates Hanström (p. 172) ponders their possible relation with the tentacle nerves. In our columbellids these nerves (nn) enter the cerebral ganglia farther dorsally than the caps lie, hence are evidently independent from the caps. The cerebral proboscis nerves unite with those going out from the buccal ganglia and run back to the root of the proboscis.

The pleural ganglia (eu) are of approximately equal size, nearly globular, and delimited against the cerebral ganglia by constrictions. They also touch the pedal ganglia. Yellow pigment occurs in nerve cells of the pleural ganglia as in *Olivella verreauxii* (Marcus 1959, p. 116). Of the nerves that leave the left pleural ganglion the thickest is the pallial-siphonal nerve (sn). It forms a swelling (sw) covered with nerve cells, hence a peripheral ganglion, at the base of the siphon, and from this secondary centre several branching nerves pass into the siphon. There is a left zygosis (zi) between the pallio-siphonal and the osphradial-branchial nerve (on). From the region where right pleural and subintestinal ganglion are in broad contact, a strong pallio-parietal nerve (wi) arises. It may correspond to the sole nerve which originates from the right pleural ganglion of *Buccinum* (Bouvier 1887, p. 268), but this comes from the limit between right pleural ganglion and pleuro-pedal connective (Dakin 1912, fig. 6 on p. 69, r.pl.n.).

Of the short connexions between the pleural ganglia and those at the root of the visceral loop the zygosis between the subintestinal (iu) and the right pleural ganglion is shortest; both these ganglia are fused as in *Buccinum* (Bouvier 1887, p. 259). Also Risbec (1954, p. 131) stressed this maximum zygoneury on the right side.

Contrary to the position of the supra-intestinal ganglion in Risbec's species (ibid., and f. A, 7, sp) this ganglion (ai) is in ours apposed to the right pleural ganglion. When concentration of the central nervous system is judged, the distance of the supra-intestinal ganglion from the right pleural ganglion must not be overrated; to Thiele's examples (1935, p. 1097) in this connexion two volutids can be added, *Adelomelon ancilla* (Woodward 1900, p. 11) and *Voluta*

musica (Pace 1902a, p. 24). In the former the supra-intestinal ganglion is close to the right pleural ganglion, in the latter it is far away from it and near the osphradium. The visceral cords (vc) pass through the diaphragm between anterior and posterior body cavity, together with the oesophagus and the diverticulum of the gland of Leiblein. Close behind the passage, at the level of the hind end of the gill and in front of the heart, lie the two visceral ganglia (va) apposed to one another. They belong to the supra-oesophageal, left branch of the visceral loop; the subintestinal one contains an accumulation of nerve cells (su) farther in front. The posterior curve of the loop emits a nerve which goes to the genital aperture.

ALIMENTARY TRACT (Figs. 10, 12-21)

The sheath of the proboscis is connected with the dorsal body wall for a certain distance. As in the other Stenoglossa only the part that connects the free hind ends of sheath and proboscis is eversible. When the proboscis (ro) is extended, the sheath encloses its base. The epithelium lining the sheath is flat on the dorsal side and appears higher on the ventral side, perhaps due to contraction. Here, on the floor of the sheath, the transverse layer of muscle fibres is thick. Risbec (1955, p. 71) described this "grande lame musculaire" in his Pacific species.

The pleurembolic proboscis is a little shorter than the shell. Generally it is silky white, orange in *mercatoria,* and pigmented black with a white tip and ventral line in *dichroa*. As a very unusual feature a pigmented introvert of *Voluta musica* was noted by Pace (1902a, p. 22). The high mobility of the very muscular proboscis is evidenced while feeding and by the fact that it can reach every point of the shell and remove sediments which are often swallowed. The two herbivorous species, *mercatoria* (Fig. 10) and *rustica,* have a cuticular ring around the anterior opening of the proboscis. This cuticle is dark in *mercatoria,* colourless in *rustica*. Evidently by use among the hard algae (*mercatoria*: *Acanthophora spicifera; rustica*: possibly also Rhodomelaceae) the ring is irregularly worn, so that nodules separated by gaps are brought about.

The buccal cavity is short, as the radular sac (cs) separates from its hind end close behind the tip of the proboscis, i. e. the

mouth. Only in *veleda* the radula ends approximately in the middle of the proboscis, in the other species it is as long as the proboscis (*mercatoria, rustica*) or projects from its base (remaining species). Radular sac and oesophagus (c) lie in the proboscis as two tubes, each surrounded by its own muscle layer. The tubes are connected with one another by radial and oblique fibres and with the wall of the proboscis by three pairs of longitudinal muscles which insert close to the tip of the proboscis. At the confluence of the radular sac with the buccal cavity the sac forms a ventral pouch (us) into which the foremost oldest and worn teeth of the radula are folded back. The salivary ducts (Fig. 12, w) of *mercatoria* and *rustica* open into this pouch. In these species radular sac and oesophagus are united only quite in front, at the tip of the proboscis, so that these snails which feed on algae have a more freely movable rasping organ than the others.

The odontophoral cartilages (Fig. 12, rc) are paired behind and, as in *Buccinum* (Amaudrut, 1898, p. 71), coalesced in front for about 1 mm of their length in *sparsa,* for 1,75 mm in *mercatoria*. The paired parts are connected by a transverse muscle, conspicuous in *mercatoria* and *rustica,* thin in the other species. Each cartilage is formed by a single layer of vesicular cells; *mercatoria* and *rustica* have several layers.

The radulae of the examined species are rather uniform. All have a rhachidian plate-like tooth whose posterior border is thickened and smooth. The lateral tooth is movable; it has a pronged cusp and is fixed to the radular membrane only with its base. Right and left cusp may touch over the central tooth or be turned outward. The posterior side of each lateral tooth bears two secondary cusps or "lamellae" (Thiele, 1924, 1931). Shape and size of these cusps as well as their distances from one another are different in the different species (Figs. 13-20). In young *lunata* with 11-18 micra long lateral teeth the undermost secondary cusp is broad and blunt, really lamella-shaped. As the radulae are not known for all type-species of the genera and subgenera, A. Myra Keen (1958, p. 378-9) arranged the columbellids conchologically. Thiele (l. c.) tried to combine characters of the radulae with those of the shells. This is difficult, e. g. in *Nitidella*. The spaces between the cusps are not as narrow in *dichroa* as in the

type-species *nitida* (Fischer, 1887, f. 393; Simroth, 1901, f. 122). Also the reproductive organs of *dichroa* differ widely from those of Thiele's genus *Columbella* with narrow-spaced lamellae. On the other hand *obesa* and *lunata* with wide-spaced lamellae have reproductive organs similar to *mercatoria* and *rustica* with narrow-spaced lamellae.

The measurements, in micra, are as follows:

Species	Central tooth		Breadth of	number of
	breadth	height	lateral tooth	rows
1) *brasiliana*	38	24	52	215
2) *sparsa*	40	20	70	100
3) *obesa*	25	12	28	80
4) *veleda*	50	31	67	330
5) *dichroa*	36	20	50	125
6) *lunata*	20	15	26	120
7) *mercatoria*	115	31	210	115
8) *rustica*	140	25	180	100

In the carnivorous species 1-6 a certain proportion between the size of the snails and the number of radular rows can be recognized, but the small *lunata* is an exception. The herbivores whose higher mobility of the radula and its stronger cartilaginous support were already mentioned have also a radula twice as broad as that of the carnivores, and its plates are thicker.

The clustery salivary glands lie around the central nervous system and the pharynx of Leiblein. In all our species the ducts do not pass through the nerve ring. At first they are ciliate, but lose their cilia in their intra-proboscidial course, except for *mercatoria* and *rustica* where they continue ciliated. The long tufts of cilia are developed on either side of the duct on a row of single cells which project on the basal side of the epithelium. In *brasiliana, sparsa, obesa, veleda, dichroa,* and *lunata* the ducts run in the lateral folds of the anterior oesophagus which accompany the dorsal food channel. Far in front they pass on both sides through the oesophageal muscles, curve ventrally, enter into the muscle wrapping of the radular sac, and open on both sides into the foremost part of this sac. In *mercatoria* and *rustica* the epithelium of the intra-proboscidial oesophagus (Fig. 12, e)

is thrown into many longitudinal folds behind, and in front is differentiated into lateral folds and dorsal food channel. Behind the salivary ducts run on either side of the ventral midline, in front, in the lateral folds. Right and left duct (w) leave the folds on different levels, and each duct forms a long, unciliate vesicle (a), evidently a salivary ampulla or reservoir beside the oesophagus. As mentioned before, the outlets of the reservoirs open separately through the antero-ventral wall of the radular pouch (us).

The muscles of the anterior oesophagus are connected with those of the wall of the proboscis in the foremost region. Between these muscle layers lie glands, which discharge to the outside around the mouth, i. e. the tip of the proboscis. In *mercatoria* and *rustica* there are also glands opening into the radular sac and subepithelial oesophageal glands. The part of the oesophagus, that is X-shaped in transverse sections (Fig. 12, e) due to the lateral folds, has a thin, sometimes rough, cuticle, but no cilia. This refers to the entire intra-proboscidial oesophagus of the carnivores and the anterior part in the herbivores. Cuticle without cilia also lines the posterior intra-proboscidial, folded part of the oesophagus of the herbivores.

Behind the proboscis the epithelium of the oesophagus of the carnivores is thrown into many longitudinal folds, so that the dorsal food channel is no longer recognizable. Hence this part of the anterior oesophagus which curves forwards and then runs transversely has the same aspect in carnivores and herbivores, and is in both cuticularized and ciliate. The oesophagus enters the pyriform pharynx of Leiblein whose greatest extension is dextro-sinistral. Its lumen is not folded, but the entrance of the oesophagus is a regularly folded funnel. The outside of this infundibuliform projection into the pharynx is surrounded by blue-staining glands and ciliated cells, as the mucous pad in Graham's Stenoglossa (1941, p. 6, 12) and in *Oliva* (Marcus 1959, p. 125-126). The high epithelium of the pharynx of Leiblein which consists in unciliated gland and slender ciliated cells corresponds to the mentioned snails too. The pharynx of Leiblein of our columbellids is similar in shape to that of the muricids, but does not show the effect of torsion characteristic for this family (Graham 1941, p. 17).

The mid-oesophagus from the pharynx of Leiblein, through the nerve ring, to the entrance of the duct of the gland of Leiblein pre-

sents a rather regular array of longitudinal folds; the epithelium is ciliated, without cuticle and glands. In this region we tried to identify the strip of unciliated cells that marks the effect of torsion in *Buccinum* (Graham 1941, f. 5, VC), but did not succeed.

The broad communication between oesophagus and gland of Leiblein is not glandular. As in Risbec's species (1954, p. 130) this communication is differently developed in ours, leaving in 7 of them the anterior end of the gland, in *veleda* the middle. It is wide in *sparsa,* narrow in *lunata,* long in *veleda,* short in *brasiliana* and *dichroa,* and quite short in *obesa, mercatoria,* and *rustica*. Even in proportion to the greater size of *veleda, mercatoria,* and *rustica* their gland of Leiblein is voluminous, in the other species it is small. It is transverse to the main direction of the gut, and its rather flat epithelium whose cells contain some brown pigment is thrown into folds. As in *Buccinum* (Graham, 1941, p. 17) it is in the columbellids less a secreting gland than in the Muricacea and some Volutacea (Woodward, 1900, p. 119, 120; Pace, 1902a, p. 23, 28). The gland is elongated into a tubular canal lined with a simple, flat epithelium as in *Buccinum* and others (Simroth, 1901, p. 516, pl. 38, f. 5). This canal goes out from the hind end, in one exceptional case of *rustica* from the middle. It accompanies (Fig. 43, ei) the afferent renal vessel that originates from the cephalic blood sinus and supplies the villosities of the kidney (k). Also in *Leucozonia nassa* studied by us and in *Vasum turbinellum* the gland of Leiblein ends within the kidney (Risbec, 1955, p. 50). Bouvier (1887, p. 278) mentioned the similarity of the long tubular glands of Leiblein ending with a small ampulla in Buccinidae and Fasciolariidae (e. g. Fischer & Bouvier, 1892, p. 152, note 1, pl. 2, f. 10, Le).

The epithelium of the posterior oesophagus (Fig. 21, e) is thrown into numerous longitudinal folds. It is rather high and contains some glands. Brown pigment lies in the apical half of its cells. The folds are irregular, of variable height and length. After its passage from the anterior to the posterior visceral cavity the oesophagus courses first in transverse and then again in longitudinal direction. As the posterior oesophagus dilates gradually into the stomach, its limit against the latter cannot be indicated exactly. However we think that the "entonnoir transparent", the gastric shield (is), does not as

Risbec indicated (1954, p. 130) lie in the cardia. In dissections the limit between the oesophagus and the stomach appears to be between the brown oesophageal and the white gastric limb of the U-shaped organ.

Thus the stomach would be rather similar to that of *Trivia monacha* (Graham, 1949, p. 748, f. 20), except for the more numerous and more densely disposed folds of the oesophagus and the sorting area (sa) in the columbellids. The right liver duct (l) opens short behind the entrance of the oesophagus. The gastric shield (is) is free, only fastened to the wall with one short side, as observed by Risbec (1954, p. 130) and well developed in *mercatoria* and *rustica*. In the other species it covers a small area, but the thin cuticle around it extends farther. In a concavity between gastric shield and major typhlosole (rm) particles of food accumulate, rotate, and become agglutinated to a string (oo). The left liver duct (l) opens between the typhlosoles at the beginning of the intestinal groove (ir). The left, minor, typholosole (mi) reaches almost to the oesophageal opening as in *Trivia*. The intestine (i) is rather short; an anal gland does not occur.

Oesophagus, stomach, and intestine of *rustica* contain pieces of algae whose sections are similar to those of Rhodomelaceae. The quantity of algal fragments is so great in several specimens that we feel justificied to consider brown algae as the principal food of *rustica*. Also the recognizable contents of the gut of *mercatoria* are algae. In the alimentary tract of the 6 other species we found polychaetes and their setae, crustacean muscles and tubes which we consider to be abdomina of composite ascidians. We suppose that these were torn off from their pharynges. Enormous balls of sperm several times found can have been engulfed together with the abdomina. Also *Trivia* feeds on colonial ascidians (Fretter 1951a). In the laboratory specimens of our 6 carnivorous columbellids accepted pieces of lamellibranchs, crustaceans, and fish. We did not keep *mercatoria* alive yet.

RENAL ORGAN (Fig. 22)

The kidney (k) is a longish undivided sac situated on the outside of the penultimate whorl, on the left side. It lies on the apical

border of this whorl. The posterior oesophagus (ma) is apposed to its anterior border but extends a little farther backwards than the kidney. The renal sac lies principally behind the heart, but the urinary chamber (Figs. 42, 43, ui), the foremost part of the nephridium, in front of it. This lobe is situated in the roof of the mantle cavity and opens into the cavity with a slit-like aperture (Figs. 9, 43, ni). The anterior part of the kidney is separated from the rest by the heart. The reno-pericardial communication (Fig. 43, re) is located where the reno-pallial opening is nearest to the heart. In most cases this communication is a minute tube, but in *mercatoria* and *rustica* it is a well developed, about 0,3 mm long canal in both sexes. In the females of *lunata* and *obesa* is is a wide, long, and strongly ciliated canal. In the description of the female reproductive organs we will return to this peculiarity as well as to the character of the epithelium that surrounds the pallial renal aperture in the females of the mentioned species.

On the whole the wall on the outer side of the kidney is smooth and thin, the inner wall of species 1-6 bears folds (Figs. 22, 43, f) which are a little branched in the bigger species. The folds are high in dorso-ventral, flat in antero-posterior direction. In *mercatoria* and *rustica* the folds are richly sub-divided and cover also part of the outer wall. The afferent renal vessel enters the bottom of the kidney from the anterior side and ascends towards the upper hind end. Along its dorsal course this vessel bears one row of villosities (vi) on either side and emits branches into the folds of species 1-6. In the big species, *mercatoria* and *rustica,* the villosities are more numerous, and occur also on the outer wall beside the vessel; their cells contain the known red-staining granules (Cuénot, 1914, p. 281). The blood from the folds flows into the afferent branchial vessel, that from the villosities through the small nephridial gland (Fig. 33, oa) into the auricle (au). The spongy tissue of the gland protrudes into the auricle (Fig. 43, oa). Some tubules formed by ciliated renal epithelium penetrate into the spongy tissue.

Nearly on its whole length the afferent renal vessel contains the tubular elongation of the hind end of the gland of Leiblein (Fig. 43, ei) which ends without dilatation.

MALE REPRODUCTIVE ORGANS (Figs. 23-33)

The testis lies in the apex as uppermost organ or beside the digestive gland, but unlike in *Ocenebra erinacea* (Fretter, 1941, p. 174) on the outer side. The long efferent duct runs coiled on the columellar side. It is unciliate, hence a gonadial or testicular sperm duct. It is distended (sv) by eupyrene sperms with thin heads. In *mercatoria* (Fig. 23) and *rustica* (Fig. 24) the latter lie around the dyspyrene (Ankel, 1926, p. 154, note 7) sperms whose pink cylinders were only found within the coiled region of the sperm duct in the two mentioned species. In *brasiliana* (Fig. 25), *sparsa* (Fig. 26), *dichroa* (Fig. 27), and *veleda* (Fig. 28) the duct opens into a seminal vesicle (rv), absent in the 4 other studied species. In *sparsa* and *dichroa* the duct passes along this vesicle and opens into its anterior end; in *brasiliana* it enters the vesicle near its middle, and in *veleda* near its posterior end. The epithelium of the vesicle is quite flat, unciliated, not prostatic. The seminal vesicle lies beneath the fundus of the pallial cavity, between renal aperture and anus. In *brasiliana* and *veleda* the vesicle receives the unciliated gonadial, in *sparsa* and *dichroa* the ciliated renal sperm duct. The 4 species with seminal vesicle, as well as *mercatoria* and *rustica* without it, have atypical sperms. In the first these were found only in the vesicle where eupyrene ones are rare, except for *veleda*. In the long seminal vesicle of this species masses of typical sperms lie near the entrance of the sperm duct, while the atypical ones occupy the fundus.

In the reproductive organs of females dyspyrene sperms were noted only in one doubtful case (*brasiliana*); as the available females of *rustica* had not copulated, this species must be left aside for this statement.

Odette Tuzet (1930, p. 160-61, pl. 9, f. 284-85) and others (see her bibliography) described the atypical sperms of *Columbella rustica.* Three possible functions of these sperms have been considered. The first, transference of eupyrene sperms by dyspyrene ones (Ankel, 1930, p. 540; Graham, 1954), cannot be supposed in the columbellids, all with penis. The second, determination of nurse-eggs by atypical fertilization, is probable in *Fasciolaria tulipa* (Hyman, 1925) *Buccinum undatum* (Portmann, 1926, 1927), and *Thais lapillus* (id., 1930),

evidently not in *Pisania maculosa* and *Fasciolaria lignaria* (Staiger, 1950, p. 499). The species with atypical sperms whose spawn we have kept alive, *brasiliana* and *sparsa,* have no nurse-eggs. The third function of the dyspyrene sperms, to provide nourishment for the eupyrene ones has been suggested by Hanson, Randall and Bayley (1952, p. 77). They generalize the lack of accessory glands in *Viviparus* for the reproductive system of all male prosobranchs in order to support their hypothesis. Our species *brasiliana* and *veleda* without prostate and with dyspyrene sperms as well as *lunata* and *obesa* with prostate and without dyspyrene sperms seem to favor the idea of Hanson and his collaborators, but *mercatoria* and *rustica* with prostate and with dyspyrene sperms do not.

A spermiducal-pallial communication (ra) belonging to the renal section of the sperm duct occurs in all our species. It is a long, narrow canal in *brasiliana* (Fig. 25), and *sparsa* (Fig. 26); a shorter canal in *lunata* (Fig. 29), *obesa* (Fig. 30), and *rustica* (Fig. 24); a quite short funnel in *dichroa* (Fig. 27), and short and thin in *veleda* (Fig. 28). In *mercatoria* (Fig. 23) it is bigger than in all other species and has a wide opening. In *dichroa* this connexion lies entally (proximally) to the seminal vesicle, in *veleda* at its beginning, and in *brasiliana* and *sparsa* ectally (distally) to it. A slight gonopericardial strand of connective tissue was noted in *dichroa;* it goes out from the sperm duct opposite to the spermiducal-pallial communication. In *mercatoria* the flat-celled pericardium emits a diverticulum whose lining epithelium is higher. This diverticulum nearly attains the sperm duct at the limit of gonadial and renal section.

The pallial sperm duct (d) is characterized by a thick muscle layer. In transverse section it is circular, and its narrow lumen is lined with a ciliated epithelium. The duct passes along the mantle cavity underneath the floor to the penis with the same diameter throughout and without prostatic glands in four of our eight species (*brasiliana, sparsa, dichroa, veleda*). In the others there are prostatic glands (rs), a pair of free ones in *lunata* (Fig. 31), and a single intercalary gland in *obesa* (Fig. 32), *mercatoria* (Fig. 23), and *rustica* (Fig. 24).

In *lunata* the pallial sperm duct becomes thicker at a point where it receives the red-staining coarse granules secreted by the two tubular glands. One of these opens directly into the sperm duct, while the other is connected with it by a long ciliate and muscular canal. The glands are unbranched coiled around one another, and lie beside the other organs of the visceral mass (Fig. 33). Their lining consists of high merocrine cells with basal nuclei and fine ciliated supporting cells with small apical nuclei between them as in *Littorina* (Linke, 1933, p. 16). Ectally to the entrance of the prostatic glands the epithelium of the sperm duct becomes high and stores granules; the supporting cells between the storing cells are ciliated.

In *obesa, mercatoria,* and *rustica* the efferent duct widens suddently and bends backwards. In *mercatoria* and *rustica* it forms a single, in *obesa* a double loop, runs forward again and continues with the same width to the root of the penis. In *obesa* the epithelium of the widened section is exactly like that of the glands of *lunata;* in *mercatoria* and *rustica* the nuclei of the supporting cells are basal or central, not apical.

The small single gland that opens on the outside of the penis of *Columbella flava* (Risbec, 1954, p. 132, f. 6, gl) may be prostatic too, but cannot be compared morphologically with the prostates of the 4 precedingly mentioned species. In *mercatoria* and *rustica* a great number of blue-staining subepithelial glands open on the tip of the penis around the male opening.

The prostatic gland cells continue along the ejaculatory duct of *obesa, mercatoria* and *rustica*. In the middle part of this duct there are red-staining glands in *sparsa, lunata* and *dichroa*. Besides blue--staining glands occur in the terminal part of the ejaculatory duct of *sparsa*. Some of the high epithelial cells of this duct contain blue--staining granules in *rustica*. In *veleda* the epithelium of the penial sperm duct includes pink-staining glands; in *brasiliana* only the basal part of the duct is glandular. Probably occurrence and colourability of the glands in the ejaculatory duct (Fig. 33, eo) vary according to the reproductive phase. The muscular duct of *veleda* is sometimes sinuous, that of *brasiliana* is commonly winding. In the other species it runs more or less straight to the tip where it opens in all our species.

All have a male copulatory organ which is flattened in resting state. Except in *mercatoria* and *rustica* the outer half of the penis lies in a pouch (Figs. 9, 33, eo) which opens about in the middle of the hypobranchial gland (y). The glandular cells are interrupted at the entrance of the pouch, but backwards they fuse over it. In *lunata* the entrance lies at the limit between ctenidium and hypobranchial gland. The pouch extends backwards maximally to over the kidney, hence far beyond the fundus of the mantle cavity. The pouch is lined with a flat epithelium. This pouch, as far as we know, unique in prosobranchs, seems to be biologically significant for snails whose penis is big also in resting state (Fig. 9, q). If it was tucked into the rather narrow mantle cavity, it might interfere with the respiratory current. The penis lies in the pouch with its tip directed backwards. The two species with a wider pallial cavity, *mercatoria* and *rustica,* have no penial pouch; their penis lies bent into the mantle cavity. The projecting male organ of Joannis' figure and text (1834) is evidently in beginning erection. The mantle cavity of the female is free from the swollen penis during copulation in *Skeneopsis planorbis* (Fretter, 1948, p. 606; 1953, p. 220) whose male organ is inserted between mantle and shell of the female.

In proportion to the length of the shell the preserved resting penes are relatively shortest in our biggest species, *mercatoria* 0,67:1, and *veleda* 0,66:1. In *lunata,* our smallest species, the proportion is 0,71:1; the penial pouch of this species is short. The other proportions are: *brasiliana* 0,73:1; *sparsa* 0,77:1; *dichroa* 0,86:1; and *obesa* 1:1. In *rustica* the males were evidently not in their reproductive period, as their penes were only 0,38:1. The material was preserved at Naples in September; also the females did not contain sperm in oviduct and annexes. The penis of *rustica* and *mercatoria* is broad and flat, that of *sparsa* broad (Fig. 9, q), that of *dichroa* has a specially thin middle and terminal part which lie in the pouch. Also in *brasiliana* these parts are thin, the base is thicker. The penis of all species is white, except that of *sparsa* whose base is pigmented. In *rustica* the pigmentation and the length of the penis exhibit variation; the organ is sometimes white, sometimes black. One full-grown male whose pallial and penial sperm duct shone black through the skin had a 1 mm long, 0,12 mm thick penis, hence a proportion of 0,04:1.

FEMALE REPRODUCTIVE ORGANS (Figs. 34-43)

The ovary extends with its lobules between those of the subjacent digestive gland in the uppermost whorls. Thence the straight unciliate oviduct runs forward on the columellar side. In the smaller species (n.^{o}s 1-6) the epithelium of the incipient oviduct is quite low (ovarian oviduct), whence it becomes a little higher (renal oviduct); in *mercatoria* and *rustica* the outer part of the oviduct can with certainty be defined as renal oviduct by high cells of the epithelium and longitudinal folds. Though the efferent female organs are different in all our eight examined species, two main groups are clearly distinguished, one without gonopericardial duct, with albumen gland, and with oviducal sperm-storing organs, and the other with such a duct, without albumen gland, and the pericardium storing sperm. The first group comprises *brasiliana* (Fig. 34), *sparsa* (Fig. 35), *dichroa* (Fig. 36), and *veleda* (Fig. 37); the second *lunata* (Fig. 38), *obesa* (Fig. 40), *mercatoria* (Fig. 42), and *rustica* (Fig. 43).

In the first group the lumen of the albumen gland (az) is surrounded by the typcial tubes of reddish-staining gland cells. Also the following part, the capsule gland (cn), corresponds to the general scheme of the Stenoglossa (Fretter 1941). The lateral walls consist of long glandular tubes which stain differently in the different zones of the organ. The central lumen is high in dorso-ventral, narrow in dextro-sinistral extension. The cilia of this lumen are absent on the ventral side which corresponds to the sperm channel (l. c., f. 5, VC). In *veleda* the ventral gutter is set off from the central lumen by two symmetrical folds similar to those in *Nassarius reticulatus* (l. c., f. 5c); in *brasiliana* one fold on the columellar side is developed; in *sparsa* and *dichroa* there are no limiting folds.

The capsule gland opens into a ciliate vestibule (v). Except for *sparsa* the vestibule is strongly muscular. The vestibular lumen is distended into irregular pouches in *brasiliana, sparsa,* and *veleda;* in *dichroa* it is smooth. The outer opening (u) of the vestibule lies close to the anus (ar); it is especially broad in *veleda* (Fig. 37). In *sparsa* (Fig. 35) the narrow outlet (xi) of the vestibule (v) runs on

the columellar side of the anus (ar). It is lined with a flat, not folded epithelium. The connective tissue around this duct up to the outermost region of the vestibule is interwoven with muscle fibres. Evidently this duct functions as nidamental duct, not for the entrance of the copulatory organ. The wide and folded vagina of *sparsa* is a second communication (u) of the mantle cavity with the outer region of the vestibule. It is sparsely ciliated and is functionally continued into the likewise folded canal of the bursa (ur) to be described in the following.

Vestibular appendages which receive sperms during copulation and store them occur in all species of the first group. Morphologically these organs are distal copulatory bursae (ur); proximal sperm reservatories between capsule and albumen gland which are frequent in Stenoglossa do not occur. The bursa is globular or nearly so, except for *veleda* where it is sausage-shaped (Fig. 37, ur).

In *brasiliana* and *dichroa* the ciliate appendage has a central cavity and peripheral tubules. In *brasiliana* (Fig. 34) these are numerous and surround the cavity; in *dichroa* (Fig. 36) they amount to 6-8 and lie around the fundus. The cavity of *brasiliana* contains eupyrene sperms and possibly dyspyrene ones, though the long cilia of the epithelium make it difficult to distinguish them from the contents of the lumen. The peripheral tubules contain eupyrene sperms only. Possibly the atypical sperms as well as the excess of the typical ones are digested in a phase following that of our sections. In *dichroa* ingestion of sperm by the lining epithelium of the bursal cavity is distinct in some areae, though the mass of coiled sperms obscures great stretches of this epithelium. The tubules (zs) store sperms whose heads are orientated towards the walls. Thus *dichroa* has the bursa functionally divided into a sperm-receiving and a sperm-keeping part. As mentioned above, vestibular pouches are absent in *dichroa*.

In *sparsa* (Fig. 35) and *veleda* (Fig. 37) the bursa (ur) has no separate central cavity and peripheral tubules. The folded unciliate bursal canal of *sparsa* leads into a thick-walled, broadly ovoid vesicle. The epithelium of this vesicle ingests sperm, and the same holds for *veleda*.

The vestibular pouches (zs) store sperms in the species of the group which have these organs, viz. *brasiliana, sparsa,* and *veleda*. In *brasiliana* we verified that the sperms in these pouches are exclusively of the eupyrene type.

The ciliate gonopericardial duct (no) of the second group (Figs. 38-40, 42-43) connects the pericardium (ca) with the oviduct (io) where it enters the capsule gland (in) (*lunata, mercatoria*) or with the inner part of the capsule gland (*obesa, rustica*). The duct is muscular in its whole length in *lunata;* in *obesa* it widens when it enters the pericardium, and this entrance is marked by a constriction produced by a thin sphincter. The duct of *mercatoria* and *rustica* begins thin and coiled on the oviducal side, then becomes folded and strongly muscular, and merges into a diverticulum of the pericardium without limit, except for a slight sphincter in *rustica*.

In 3 species of the second group the pericardial cavity contains sperm mixed with prostatic secretion. Our females of *rustica* were mature, but had not copulated. They have, however, the same high and ciliate pericardial epithelium (ca) as the other species, while that of the males is quite flat and unciliated. Red-staining granules were seen in the pericardial epithelium, but no ingestion of sperm. In the females of *mercatoria* and *rustica* (Figs. 42-43) the modified pericardial epithelium coats also auricle and ventricle. In *mercatoria* pericardium and gonopericardial duct appear to have different function. The pericardium contains disorderly sperms (se) and secretion, as in a bursa copulatrix; the duct (no) only oriented sperms, in part attached to the wall, as in a receptaculum seminis. In some sections this seminal receptacle seems to function as ingesting gland (Fretter, 1941, p. 182, 189, 192).

In 3 species of the second group (*obesa, mercatoria, rustica*) a gonopericardial-pallial communication (g), morphologically a right ureter, occurs regularly; in *lunata* exceptionally (Fig. 39). In *obesa* (Fig. 40) a long and thin tube (g) begins with a sphincter opposite to the pericardial opening of the gonopericardial duct (no). It runs forwards to open into the mantle cavity at the limit between pericardium (ca) and kidney (k). The place of the opening is the same in *mercatoria* and *rustica*. It begins in the widened part of the gonopericardial duct, in *rustica* with a feeble sphincter. In *rustica* (Fig.

43) the gonopericardial-pallial communication (g) is short and wide, in *mercatoria* (Fig. 42) longer and thinner.

In *lunata* (Fig. 38) whose gonopericardial duct (no) is very thin and long one of 10 sectioned females had a pericardial-pallial communication (Fig. 39). This is a narrow, about 50 micra long canal which begins close to the pericardial opening of the gonopericardial duct. It is lined with high cells without the cilia and granules of the pericardial epithelium (ca) and opens into the mantle cavity (p) as in the other species, between pericardium and kidney.

In *lunata* and *obesa* the renopericardial duct and the renal aperture are different in females and males. The duct of the female is a wide, densely ciliated canal (Figs. 38, 40, 41, re), that of the male inconspicuous. The epithelium of the mantle cavity around the renal aperture (ni) is composed of high and narrow gland cells containing blue-staining droplets. Possibly the secretion of these glands has one of the functions attributed to those of the female aperture of the right ureter in Trochacea (Fretter 1946, p. 334), viz. making the discharge of the egg capsules from the mantle cavity easier, or adding some substance to them. In the males the pallial epithelium is a little richer in cells around the renal aperture than farther outwards, but does not include gland cells. In *mercatoria* and *rustica* the sexes do not differ with regard to the renopericardial duct and the epithelium around the renal aperture.

As mentioned above, the pallial oviduct of the second group is represented only by the capsule gland (cn). The unciliated ventral channel of this organ is not limited against the central lumen by folds in all 4 species. In *lunata* and *obesa* some sperms were seen high up in this channel near the gonopericardial duct. The capsule gland discharges into a muscular vestibule (Figs. 38, 40, v). This opens (u) into the mantle cavity between hypobranchial gland and rectum (ar). In *mercatoria* and *rustica* the vestibule (Figs. 42, 43, v) is short and folded, not specially muscular.

EGGS AND LARVAE (Figs. 44-52)

On the *Sargassum* where the adult snails live we found egg capsules of two species. They are similar to those of *Anachis iontha*

(Ravenel, 1861) (Perry and Schwengel 1955, pl. 50, f. 344). One kind was determined as laid by *brasiliana* (Fig. 45) by the capsules fastened to the panes of an aquarium in which only *brasiliana* was present. We attribute the second type (Fig. 44) to *sparsa* due to the comparison of the shell of the hatching veligers (Figs. 51, 52) with the protoconch of the adult snails. Already Pace (1902b, p. 40) emphasized the diagnostic value of the protoconch for distinguishing the adult shells specifically. In both species the adhesion disc of the egg capsule is polygonal. In *sparsa* it is 1,1-1,2 mm long, 0,6 mm broad; in *brasiliana* 0,8 mm in diameter. From this disc rise the walls of the capsule. This is flask-shaped and about 0,5 mm high in *brasiliana,* like an obtuse cone and 0,7 mm high in *sparsa*. In the latter about 20 fine irregularly spaced ridges support the wall which ends with a projecting edge around the flat, 0,6 mm long, 0,4 mm broad top closed by a membrane. In *brasiliana* a collar expands from the circular top whose lid bears a cruciform fold. The collar is 0,6 mm in diameter and stiffened by about 10 ribs, in part continued down the side walls. The species studied by Perry and Schwengel (l. c.) and *Columbella blanda* (Thorson 1940, p. 206) have a similar collar around the top of the capsule, but without ribs. The capsules of *brasiliana* and *sparsa* are so transparent that the eggs are visible through the walls.

The developmental stage of the embryos makes it possible to estimate the number of egg capsules laid at one time with 10-20. We found, it is true, 37 (*sparsa*), 49 (*brasiliana*) and even 64 (*brasiliana*) capsules in one patch, but they contained embryos of different ages (Fig. 46), hence had been laid at different times or by several females. The number of eggs in each capsule is about 10 in *brasiliana* and about 20 in *sparsa*.

The single spawn of *veleda* mentioned in the introductory chapter produced in a dish (Fig. 49) made it possible to identify 18 empty capsules of this species (Fig. 48) found on one leaf of *Sargassum*. The capsules are shaped like upside down mugs with concentric ridges; the one laid in the dish contained 30 eggs, 0,2 mm in diameter.

As is also shown in the figure of the egg capsules of *Anachis iontha* (l. c.), the newly laid eggs, 0,14 mm (*brasiliana*) and 0,18 mm (*sparsa*) in diameter, do not fill the inner space of the capsule.

During its development the embryo distends and forms inner cavities, and so its size increases. As in *Anachis avara semiplicata* (Perry and Schwengel 1955, p. 159) also in *brasiliana* and *sparsa* the number of laid eggs and hatching veligers remains the same. In several other columbellids of the intertidal zone in warm waters the embryos in the capsule feed on nurse-eggs (Petit et Risbec 1929, p. 568; Thorson 1940, p. 206-207).

At about 23-25°C. the veligers of *sparsa* and *brasiliana* hatch within 10-12 days. They have two velar lobes (Fig. 50), the right of which is bigger. The same holds for the veliger of the *Mitrella-spec.* drawn by Habe (1944, p. 189, f. 5), but this veliger has two tentacles, while ours hatch with one. Two eyes with lenses, and a big pedal gland are already developed. The shell has one and a half whorl, while the protoconch of the adult shell has 3-4 whorls. Therefore it is probable that these veligers live pelagically for a certain time, developing not only one to two and a half whorls more, but possibly also two more velar lobes. In the pelagic veliger of *Columbella costulata* (*haliaëti*) whose shell consists of 3 whorls, there are 4 velar lobes (Pelseneer 1906, p. 140).

Some preliminary observations refer to egg capsules of *obesa* and *lunata,* found in sectioned capsule glands. In the latter the capsule is 0,16 mm long, 0,1 mm broad, and 0,08 mm high. In *obesa* the corresponding measurements are 0,2 mm, 0,13 mm, and 0,1 mm. The capsule of *obesa* has somewhat irregular slightly shrunken walls. The measurements of full grown ovocytes in the ovary and those of the contents of the capsule suggest that only one egg is enclosed in the capsules of *obesa* and *lunata*.

PARASITES

Algae, small oysters, serpulids, and Bryozoa, principally incrusting Malacostega, as Membraniporidae and allied families, grow on the shells of all our species. Boring Ctenostomata of the family Immergentiidae Silén (1946, p. 6) bore in the shells. In July 1960, 24 of 82 counted living *brasiliana* had their shells inhabited by these Bryozoa. We found them in all our Brazilian columbellids except *obesa;* this may be due to the relative rarity of this species.

One *C. rustica* from Naples had polychaetes, probably of the genus *Polydora,* in its shell whose calcification was thickened around the worms.

A polyclad flatworm, *Hoploplana usaguia* Edmund H. Smith (1960) occurs in the mantle cavity of many of our columbellids, in the buccinids *Cantharus auritula* Link and *Pisania janeirensis* Philippi, and the fasciolariid *Leucozonia nassa* (Gmelin). All worms found in the columbellids were much smaller than those from the larger snails, viz. up to 1,5 mm in length, and immature, or in the first, the male, sexual phase. We have found the following, female, phase only in bigger worms from *Cantharus, Pisania,* and *Leucozonia*. As was seen in sections, the polyclads lay with their dorsal side against the ctenidium, and the pharynx towards the mantle cavity, whose current produced by the branchial cilia brings micro-organisms into the pallial cavity. Here they are stuck together with mucus, so that the polyclad profits of protection, current water, and food.

During the periods while we studied the life of our columbellids, in July 1960 and December 1960-January 1961 the digestive gland of *brasiliana* was infested with sporocysts and cercariae whose tails are much longer than those of *Cercaria columbellae* Pagenstecher (1863, p. 306) discovered in *Columbella rustica* at Spezia (Italy). Pagenstecher defined the larval sacs as rediae. Arvy (1952) who thinks that the larval sacs and short-tailed cercariae he found in *C. rustica* at Villefranche (France) belong to *Cercaria columbellae,* calls the sacs sporocysts in his and Pagenstecher's material. In ours the nature of the larval sacs as sporocysts was verified in sections. Stomach and digestive gland of our *mercatoria* contained larvae of another trematode in November 1960. The cercariae were long, slender, and had big eyes, while those from *brasiliana* were eyeless. The definitive hosts of the flukes whose larvae live in columbellids must be fishes, which are known to feed on these snails (Nobre 1938-40, p. 199).

A living tetraphyllid plerocercoid was once found free, not encysted, in the stomach of an *Anachis veleda,* in December 1960. Probably it has reached the snail with its first host, a copepod (see Reichenbach-Klinke, 1956).

Females of parasitic copepods belonging to the Lernaeopodoida occur in *brasiliana* and *sparsa*. In winter and summer 1960, 5-10% of the examined snails bore these parasites, and up to 4 of them were found in one snail. The crustacean lives embedded in the tissue behind the mantle cavity of the host, and the two cylindrical sacs with the multiseriate eggs hang into the pallial cavity.

Small white axially and spirally sculptured pyramidellids, similar to certain *Odostomia* (Abbott 1955, text-fig. 62, a, j), were found crawling on shells of living *Mitrella lunata,* and once a snail sitting on a *lunata* with its proboscis widely everted sucked at the foot of the columbellid. According to Robertson (1957) his finding of *Odostomia* (*Chrysallida*) *seminuda* (C. B. Adams) on *Crepidula fornicata* (Linné) at Woods Hole was the first observation of a gastropod host of pyramidellids; Ankel (1959, p. 13-17) mentioned further cases.

CONCLUSIONS

The shell of many columbellids is bucciniform. Nevertheless Bouvier (1887) did not consider them in his "Tableau résumant" of classification, probably because the nervous system was not known at that time. In the text (p. 472) the columbellids are placed in Troschel's Rhachiglossa, according to the radula. This position is maintained by Fischer (1887, p. 597) and is consonant with that of to-day. Thiele who studied the radula of many species (1924) allocated the Columbellidae to his superfamily ("stirps") Buccinacea (1925). Evidently Bouvier (1887, p. 247) and Thiele (1935, p. 1039) were quite right to consider the radula as an excellent character for the definition of natural groups in the prosobranchs, not as overrated (Pace, 1902a, p. 24-25). As Bouvier stressed (l. c., and p. 463), aberrant radulae should not be used to assemble snails with no other similarities. The radulae of the Columbellidae, however, are not aberrant. They are sufficiently peculiar to characterize them as a family of the Buccinacea. This refers less to the median tooth than to the lateral plates. Rhachidian teeth without cusp occur also in the Buccinidae, e. g. in *Liomesus* and *Beringius,* and exceptionally in *Cantharus* (Cooke, 1895, f. 123).

The lateral teeth of the columbellids are versatile plates which may be turned inwards and outwards. They correspond functionnally, not morphologically, to those of *Olivella,* whose accessory plates or rectangular bases (Marcus, 1959, p. 121) articulate with the lateral teeth. In the first figure of the radula of *Pseudanachis duclosiana* Thiele (1924, pl. 9, f. 7 b) gave a columbellidan base of the lateral tooth, but did not in the second one (1931, f. 337), so that the systematic position of this genus becomes somewhat doubtful. Rhachidian plates with multidentate cusp as in *Pseudanachis* occur also in the Buccinidae *Macron* and *Clea* (ibid., f. 352, 354) and in several nassariids (e. g., f. 373).

Excepting the genera *Pseudanachis* and *Pseudamycla* whose radulae are not columbellidan, this organ does not diverge widely within the Columbellidae. Already Pace (1902b, p. 40) considered it as rather uniform and only useful for separating species. As other inner organs were not known at that time, Pace called the family, exceedingly homogeneous, and so did Risbec (1954, p. 132) adding "as far as can be judged from the few dissected species". By the present dissections and microtomic studies the homogeneneity becomes considerably restricted.

For the most part the inner organs of the Columbellidae are buccinacean. This is shown by the salivary glands, the gland of Leiblein and its posterior elongation. Though a prominent pharynx of Leiblein is not developed in *Buccinum* (Graham, 1941, p. 12), it is not a divergent feature, because it occurs in the buccinid genus *Pisania,* as Mr. Edmund H. Smith recently verified in our Department. The muricacean effect of torsion (ibid., f. 2) does not occur in the pyriform pharynx of Leiblein of *Pisania* nor in our columbellids. It seems that this character distinguishes Muricacea and Buccinacea better than the shape of this pharynx.

The stomach of *Buccinum* (Dakin, 1912, f. 12, 13) and that of the Nassariidae *Nassarius* (Graham, 1949, f. 22) and *Cyclope* (Morton, 1960, f. 5) has a caecum, and is thus different from that of our columbellids. The loss of the caecum is a specialization (Graham, 1949, p. 749). The gastric shield present in the mentioned nassariids and our columbellids is a primitive character in Steno-

glossa. On the whole the Buccinacea are not as highly specialized in their diet as the shell-boring and suctorial feeding Muricacea (Morton, 1960, p. 104). This is confirmed by our columbellids which comprise the carnivorous species 1-6 and the herbivorous *mercatoria* and *rustica*.

Oral cuticle, mobility, breadth and thick support of the radula, stronger teeth, salivary reservoirs, proboscideal glands opening into anterior oesophagus and radular pouch, as well as strenghtened and more extended gastric shield characterize our algae-feeding snails.

The central nervous system agrees essentially with the highly concentrated one of *Buccinum*. The coalesced buccal ganglia without commissure and the broadly connected cerebral ganglia in species 1-6 attain an even higher degree of concentration than *Buccinum*. The nervous system of the herbivorous species with cerebral commissure is a little less concentrated. The farther distant position of the supraintestinal ganglion in *C. versicolor* studied by Risbec (1954) was mentioned above.

Though only known since Tertiary times, hence relatively new, the columbellids have conquered an enormous extension of the littoral and even penetrated into deep water (Watson, 1886, p. 236-38, 240). To their vast distribution from the Arctis to the Subantarctis corresponds the great number of species. This success is due to the organization of these mobile snails which quickly respond to any stimulus. The narrow peduncle of the foot and the concentrated, extremely zygoneurous central nervous system may be correlated with the efficiency of movements and reactions. Specialized are also the lateral teeth of the radula which probably function as tweezers.

The reproductive system combines extreme features, primitive ones as a gonopericardial-pallial communication, homologous to a right ureter, and secondary novelties as a pouch lodging the resting penis. Contrary to the radula whose wider and narrower interspaces between the lamellae of the lateral teeth do not divide the family into two distinctly separated groups the reproductive system allows for such a classification. The valid names of these groups cannot be established, as long as the generative organs are unknown for the type-species of the genera and subgenera belonging to them.

The first group comprises *brasiliana, sparsa, dichroa,* and *veleda*. In this group the males have a seminal vesicle (rv), but no prostate; the females have an albumen gland (az) and sperm-receiving organs (ur) which belong to the efferent reproductive organs. The second group includes *lunata, obesa, mercatoria,* and *rustica*. The males have no seminal vesicle, but a prostate (q); the females have no albumen gland, and the pericardium (ca) contains sperm.

Within the first group it is possible that the names *Nitidella* for *dichroa* and *Anachis* for the 3 other species can be maintained, because *dichroa* has a smooth vestibule (v), and pouches are formed by the canal of the bursa, while in the others the pouches are vestibular.

For a subdivision of the second group the gonopericardial-pallial connection cannot be used, because it is not always absent in *lunata*. It seems better to separate *mercatoria* and *rustica* as taxon without penial pouch, possibly maintaining for them the name *Columbella* as Abbott (1955) and Warmke & Abbott (1961) do. The two other species, with penial pouch, are different in their prostates, paired and free in *lunata,* simple and intercalary in *obesa*. If *Mitrella scripta* (L.) turns out to have two free prostates, *lunata* can preserve its generic name.

Though the anatomical study will perhaps lead to some alterations in generic and subgeneric names, the coincidence of anatomical and conchological cuts in the majority of cases obliges to recognize the taxonomic competence of the past century's conchologists.

RESUMO

Estudámos 1) *Anachis brasiliana,* 2) *A. sparsa,* 3) *A. obesa,* 4) *A. veleda* (têrmo popular: "felicidade"; nome não certo: *lyrata*), 5) *Nitidella dichroa,* 6) *Mitrella lunata,* 7) *Columbella mercatoria* e 8) *C. rustica*. Espécies 1-6 ocorrem durante o ano inteiro em *Sargassum cymosum stenophyllum* na Base de Pesquisas de Ubatuba (Enseada do Flamengo) do Instituto Oceanográfico da Universidade de São Paulo. *Columbella mercatoria* obtivemos na Ponta da Prainha, na costa do Canal de São Sebastião, perto do Bairro de São Francisco; *C. rustica,* de Nápoles.

Verrugas e calo no lábio interno da concha e dentículos no externo não são taxonômicamente importantes, pois com crescimento lento desenvolvem-se; com rápido, não. Também a configuração da concha e, segundo Pace (1902b), a escultura variam grandemente. Pelo ângulo apical da concha define-se como estreita a cavidade palial das espécies 1-6.

Os olhos, do tipo de *Murex,* situam-se nos tentáculos, látero-basalmente. A glândula pedal ventral difere pouco nos dois sexos de *sparsa;* em *dichroa, brasiliana,* e *veleda* é maior na fêmea. Em oposição às duas pequenas espécies de Risbec (1954), as nossas têm tôdas opérculo. Ocorre também em tôdas a glândula pedal posterior. Esta produz o cordão de muco com que os animais se seguram trepando nas algas ou descendo do filme da superfície da água. Às mais das vêzes, as espécies pequenas rastejam continuada e ritmicamente; as maiores, também arritmicamente, aos passos.

Numerosas lacunas sangüíneas no teto da cavidade do manto sugerem função respiratória auxiliar desta região. Cilios no assoalho da dita cavidade intensificam a correnteza exalante.

A concentração do anel nervoso abrange também comissura e conectivos bucais; os gânglios subintestinal e pleural direito coalescem-se. Sòmente nas espécies algófagas, *mercatoria* e *rustica* que comem Rhodomelaceae, existe comissura cerebral supra-esofágica; nas outras, carnívoras, os gânglios cerebrais tocam-se. Ainda as espécies herbívoras distinguem-se das carnívoras pela cutícula ao redor da bôca, rádula mais larga, mais móvel, de dentes mais grossos e suporte mais firme, pelos reservatórios das glândulas salivares, número maior de glândulas esofágicas, e escudo gástrico mais desenvolvido. As espécies carnívoras comem políquetos, crustáceos e arrancam a parte abdominal de ascídias compostas.

Tubo posterior alongado da glândula de Leiblein entra no rim que corresponde ao dos Pycnonephridia (Perrier).

Os órgãos reprodutivos permitem reconhecer dois grupos de espécies, o primeiro compreende *brasiliana, sparsa, veleda,* e *dichroa;* o segundo *obesa, lunata, mercatoria,* e *rustica*. O primeiro tem vesícula seminal não ciliada nem glandular no duto eferente interno, glândula de albumina, receptáculo seminal ou bôlsa copulatória no oviduto, sendo ausentes próstata e, na fêmea, duto gonopericardial.

O segundo tem próstata no duto eferente palial, duto gonopericardial feminino, e pericárdio armazenador de espérmios, não ocorrendo vesícula seminal interna, glândula de albumina, e órgãos espérmi-receptores no oviduto.

Comunicação do duto eferente renal com a cavidade palial ocorre em tôdas as espécies; espérmios dispirenos faltam sòmente em *obesa* e *lunata*. Em *sparsa,* o orifício nidamental do vestíbulo e o vaginal da bôlsa copulatória são separados; *dichroa* possui divertículos no canal da bôlsa copulatória, não no vestíbulo como as outras espécies do primeiro grupo.

No segundo grupo há um par de próstatas livres em *lunata;* uma intercalar comprida, nas outras espécies. Excepcionalmente em *lunata* (em 1 fêmea de 10 microtomizadas), regularmente nas outras, existe ligação gonopericardial-palial, morfològicamente, ureter direito. Duto renopericardial largo e abertura renal glandular ocorrem nas fêmeas de *lunata* e *obesa*.

Afora em *mercatoria* e *rustica,* a metade externa do pênis em repouso situa-se numa bôlsa da cavidade palial. A bôlsa estende-se da glândula hipobranquial até a região renal; evidentemente a bôlsa alivia a correnteza respiratória e a eliminação dos produtos da digestão e excreção, pois o grosso órgão copulador masculino desocupa a cavidade do manto, não larga nas espécies 1-6.

As cápsulas ovulares de *brasiliana, sparsa,* e *veleda,* contêm sòmente ovos regulares, não alimentares. A concha dos velígeres tem uma volta e meia; a protoconcha adulta, 3-4 voltas. Daí depreende-se vida pelágica durante certo tempo dos velígeres. As cápsulas de *obesa* e *lunata* incluem apenas um ovo.

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EXPLANATION OF LETTERS

a — salivary ampulla.
ai — supra-intestinal ganglion.
an — groove of anterior foot glands.
ao — aorta.
ar — anus.
au — auricle.
az — albumen gland.
b — ctenidium.
c — columellar muscle.
ca — pericardium.
cc — buccal ganglia.
cn — capsule gland.
cs — radular pouch.
cz — caps of small cells on cerebral ganglia.
d — efferent male duct.
e — oesophagus.

ea — pedal ganglia.
ei — gland of Leiblein.
eo — penial pouch.
er — cerebral ganglia.
eu — pleural ganglia.
f — renal folds.
g — gonopericardial-pallial connection.
i — intestine.
io — oviduct.
is — gastric shield.
ir — intestinal groove.
iu — subintestinal ganglion.
iv — glands of sole.
j — ejaculatory duct.
k — kidney.
l — duct of digestive gland.
ma — posterior oesophagus.
me — mantle.
mi — minor typhlosole.
mr — furrow of foot.
ms — siphonal retractor.
mv — mantle border.
n — nerve.
na — nerves to anterior border of foot.
ni — renal aperture.
nn — tentacle nerve.
no — gonopericardial duct.
nv — posterior pedal nerves.
o — ovary.
oa — nephridial and blood gland.
oc — operculum.
on — osphradial-branchial nerve.
oo — food string.
os — osphradium.
ow — duct of posterior foot gland.
p — pallial cavity.
q — penis.
r — radular teeth.
ra — pallial connection of sperm duct.
rc — radular cartilage.
re — renopericardial duct.
rm — major typhlosole.
ro — proboscis.
rs — prostatic gland.
rv — seminal vesicle.
rz — proboscis pouch.
s — salivary gland.
sa — sorting area.
sc — sole of foot.
se — sperm.
si — blood space.
sn — siphonal nerve.
so — siphon.
su — swelling of visceral loop.
sv — coiled part of sperm duct.
sw — siphonal ganglion.
sz — statocyst.
t — tentacle.
u — female aperture.
ui — urinary chamber.
uo — posterior pedal gland.
ur — bursa copulatrix.
us — anterior diverticulum of radular sac.
v — vestibule.
va — visceral ganglia.
vc — visceral loop.
ve — ventricle.
vi — renal villosities.
vn — ventral pedal (moulding) gland.
w — salivary duct.
wi — right pallio-parietal nerve.
x — cilia.
xi — vestibular opening of *sparsa*.
xn — penial nerve.
y — hypobranchial gland.
z — blood vessel.
za — opercular pad.
zi — left zygosis.
zs — vestibular or bursal pouches.

PLATES

PLATE 1

Fig. 1 — *Anachis brasiliana*.
Fig. 2 — *Anachis sparsa*.
Fig. 3 — *Anachis veleda*.
Fig. 4 — *Nitidella dichroa*.
Fig. 5 — *Columbella mercatoria*.
Fig. 6 — *Columbella rustica*.
Fig. 7 — Sole of female *veleda*.

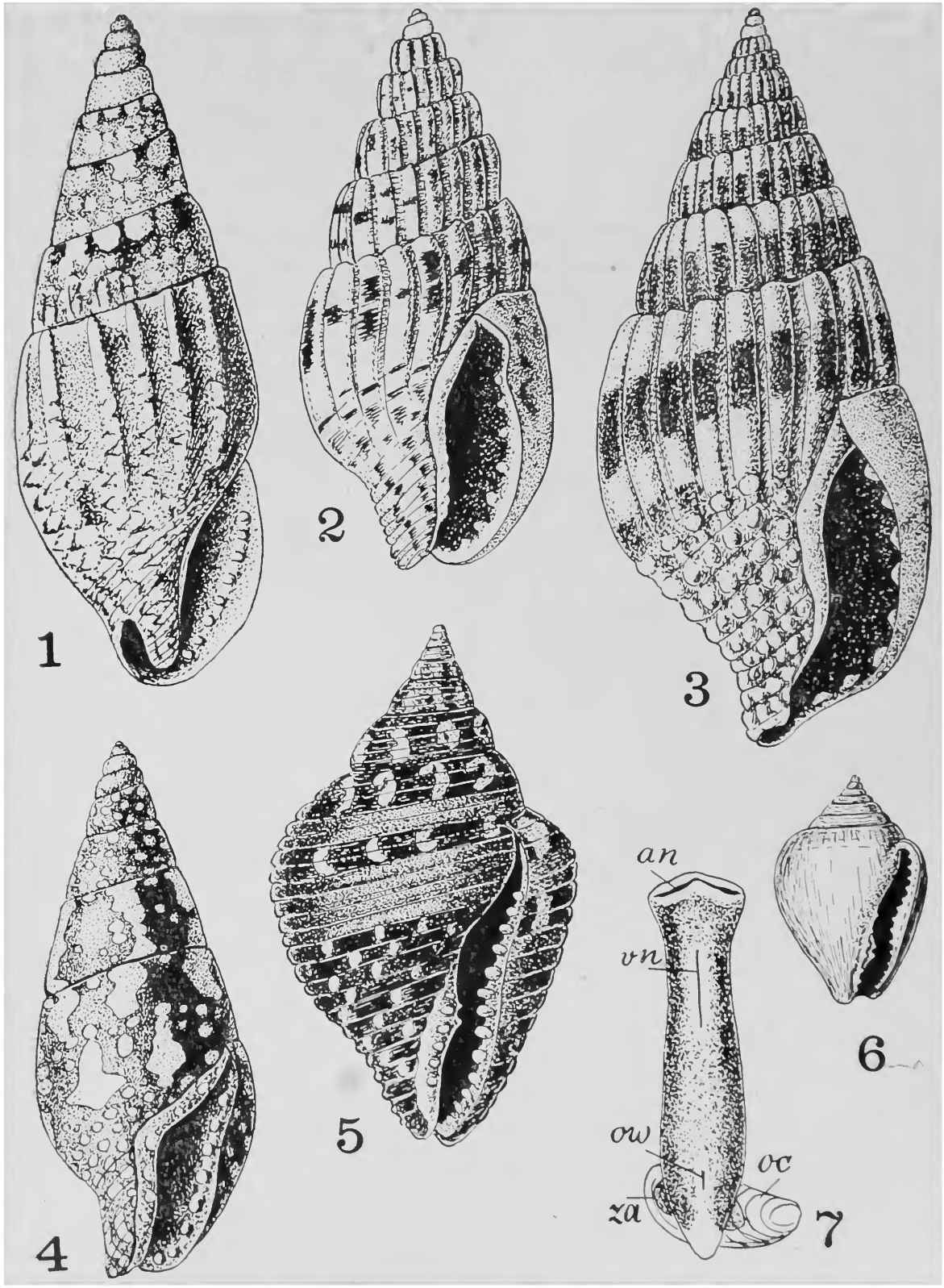
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PLATE 2

Fig. 8 — Combined transverse section of male *lunata*.
Fig. 9 — Male *sparsa* removed from shell, pallial cavity opened.
Fig. 10 — Tip of proboscis with protruded radula of *mercatoria*.
Fig. 11 — Central nervous system of male *veleda*.

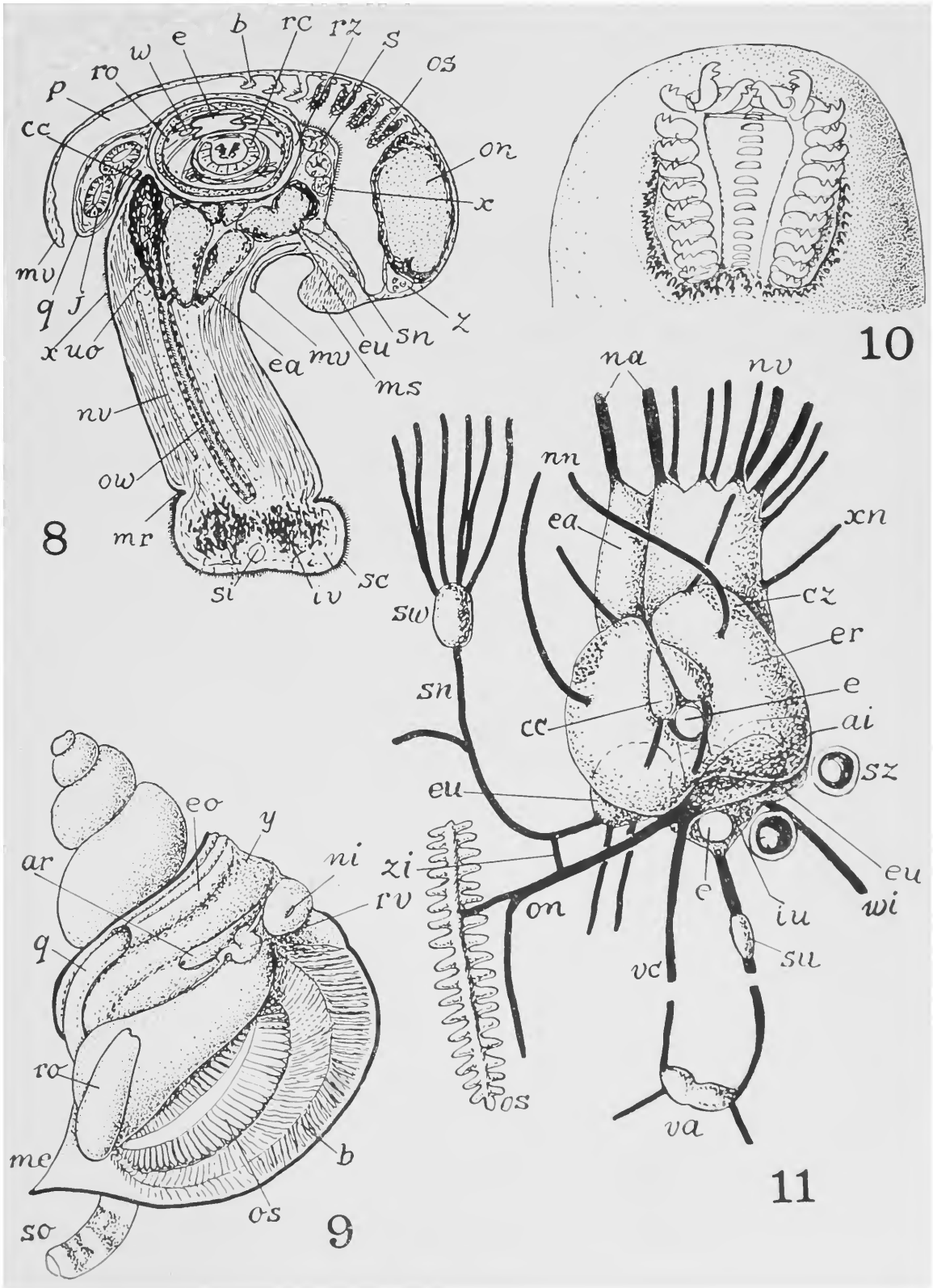
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PLATE 3

Fig. 12 — Transverse section of proboscis of *rustica,* near tip.
Fig. 13 — Lateral radular tooth of *brasiliana*.
Fig. 14 — Same of *sparsa*.
Fig. 15 — Same of *obesa*.
Fig. 16 — Same of *veleda*.
Fig. 17 — Same of *dichroa*.
Fig. 18 — Same of *lunata*.
Fig. 19 — Three lateral radular teeth of *mercatoria*.
Fig. 20 — Same of *rustica*.
Fig. 21 — Stomach of *veleda* opened on dorsal side.

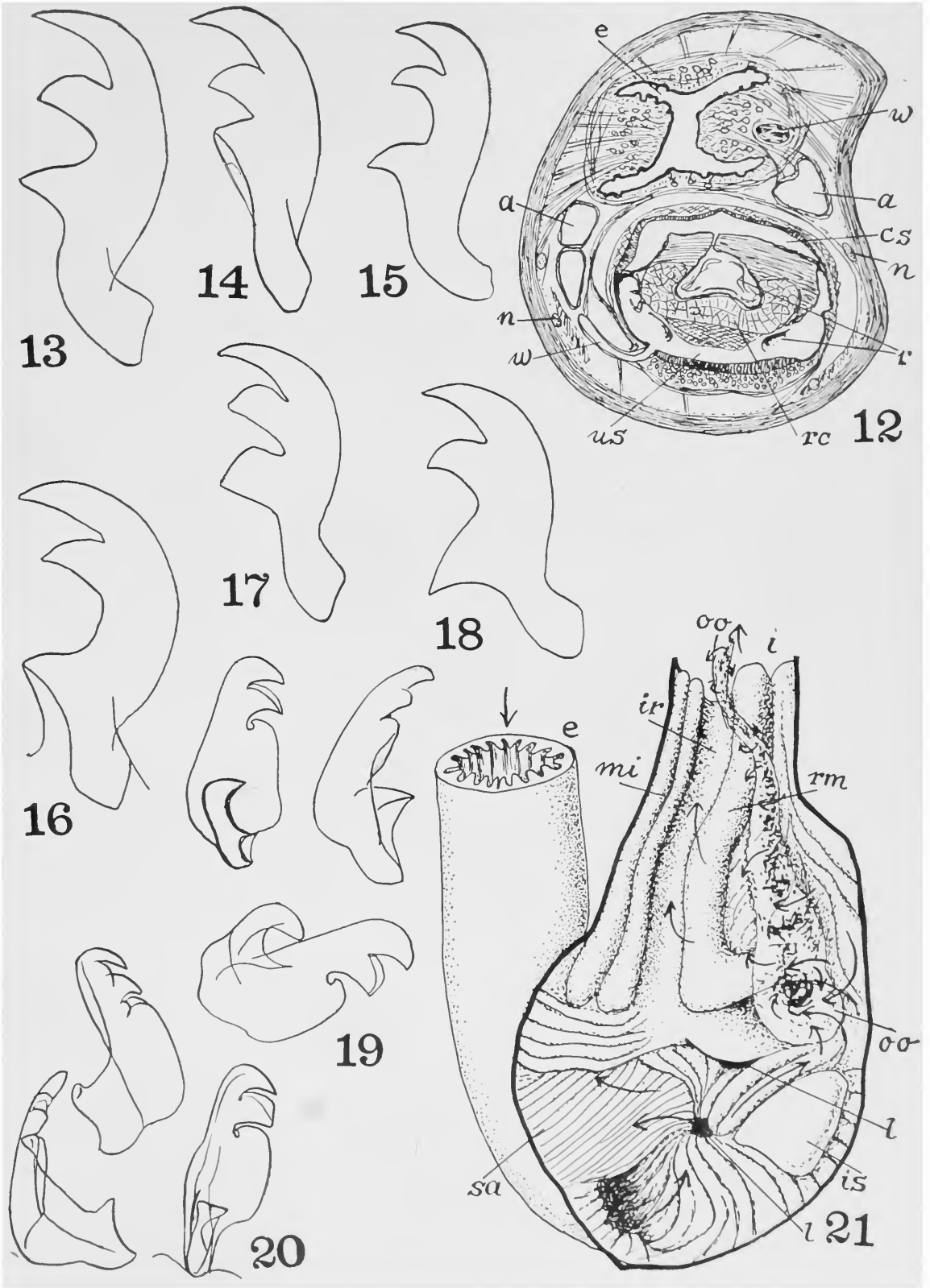
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PLATE 4

Fig. 22 — *dichroa* removed from shell.
Fig. 23 — Diagram of male organs of *mercatoria*.
Fig. 24 — Same of *rustica*.
Fig. 25 — Reconstruction of middle sperm duct of *brasiliana*.
Fig. 26 — Same of *sparsa*.
Fig. 27 — Same of *dichroa*.
Fig. 28 — Same of *veleda*.
Fig. 29 — Same of *lunata*.
Fig. 30 — Same of *obesa*.
Fig. 31 — Diagram of male organs of *lunata*.

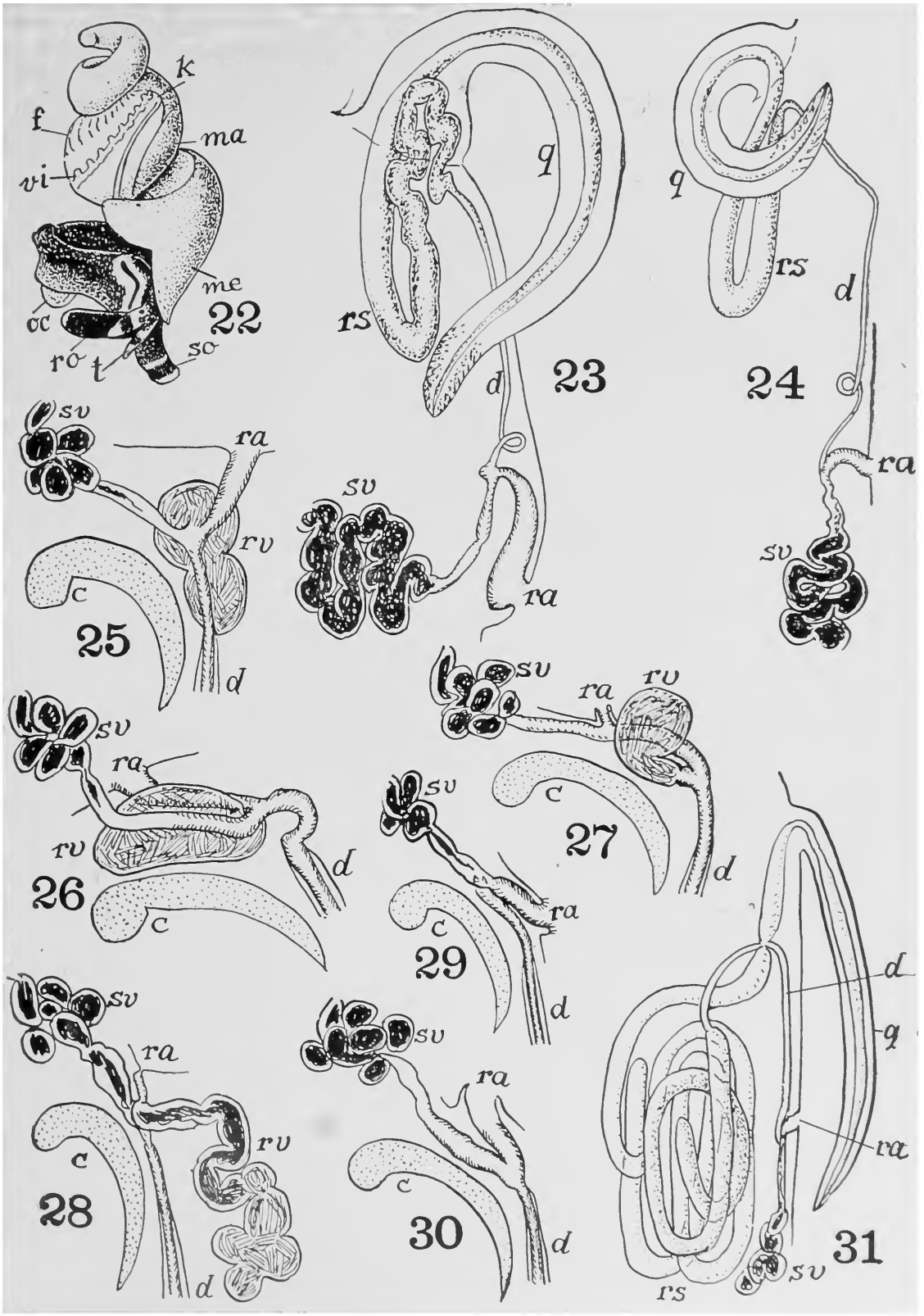
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PLATE 5

Fig. 32 — Diagram of male organs of *obesa*.
Fig. 33 — Transverse section of male *lunata*.
Fig. 34 — Diagram of female organs of *brasiliana*.
Fig. 35 — Same of *sparsa*.

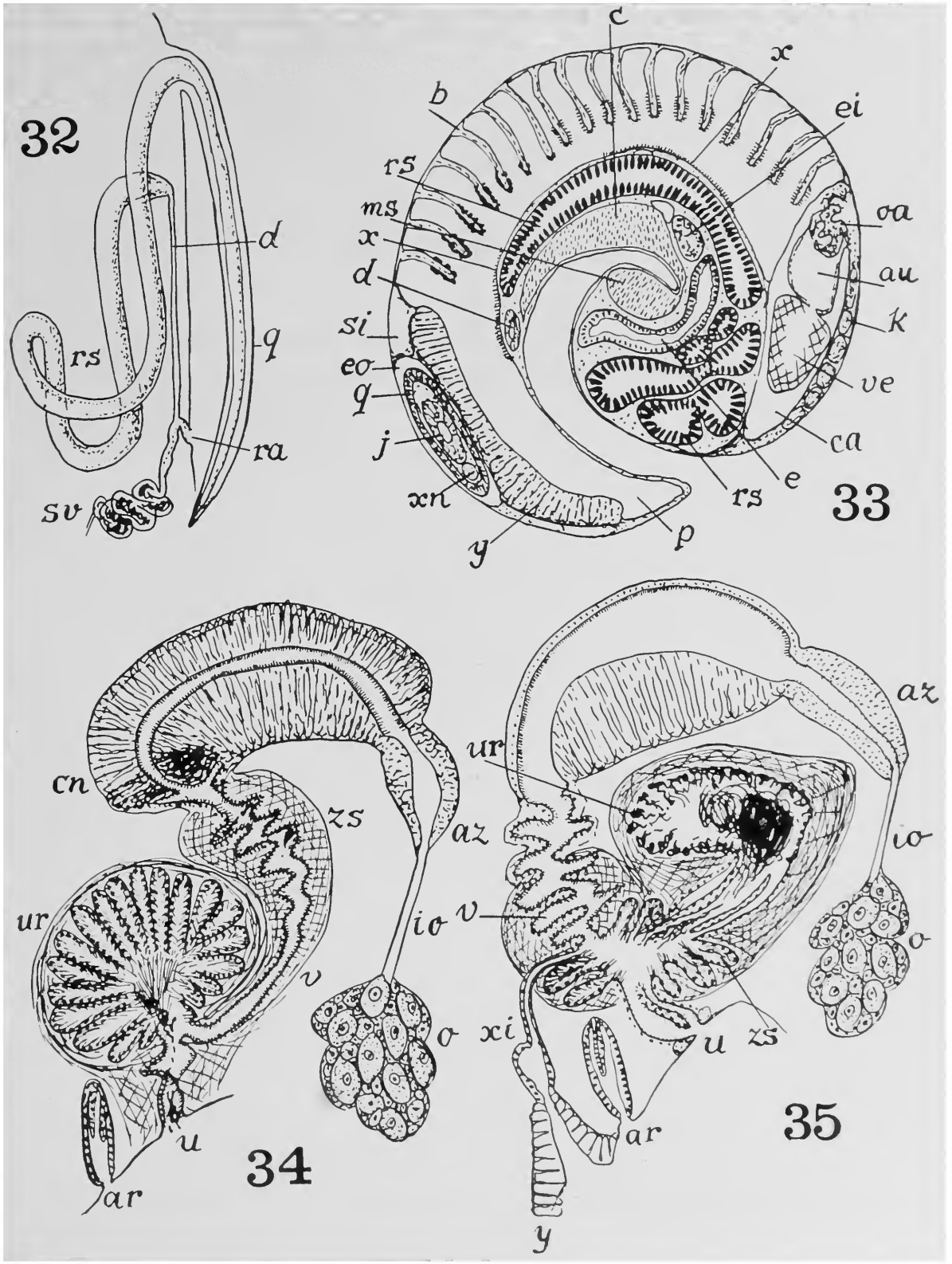
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PLATE 6

Fig. 36 — Diagram of female organs of *dichroa*.
Fig. 37 — Same of *veleda*.
Fig. 38 — Same of *lunata*.
Fig. 39 — Exceptional gonopericardial-pallial connection in *lunata*.
Fig. 40 — Diagram of female organs of *obesa*.

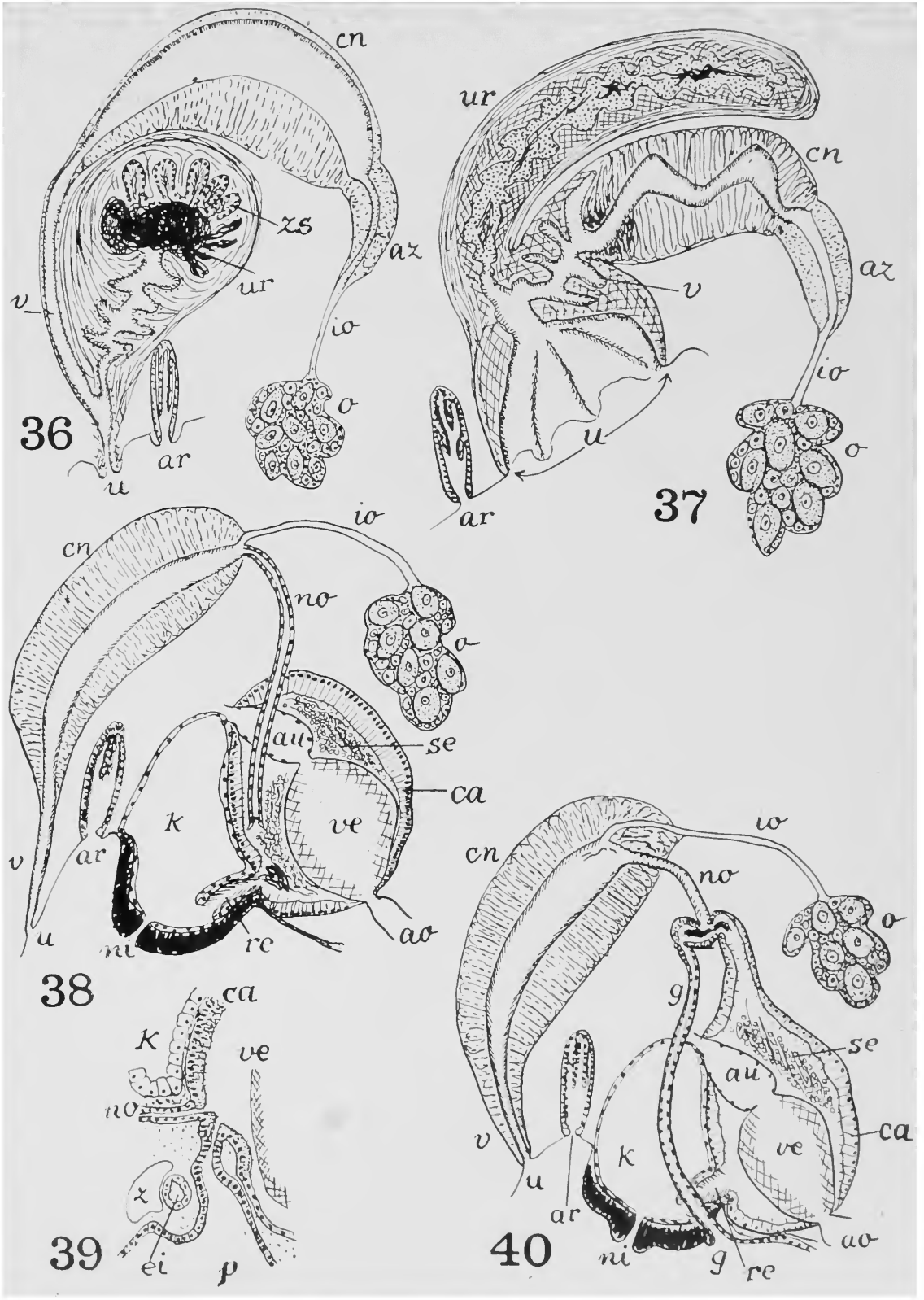
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PLATE 7

Fig. 41 — Combined section of pericardium and neighbourhood in female *obesa*.

Fig. 42 — Diagram of female organs of *mercatoria*.

Fig. 43 — Same of *rustica*.

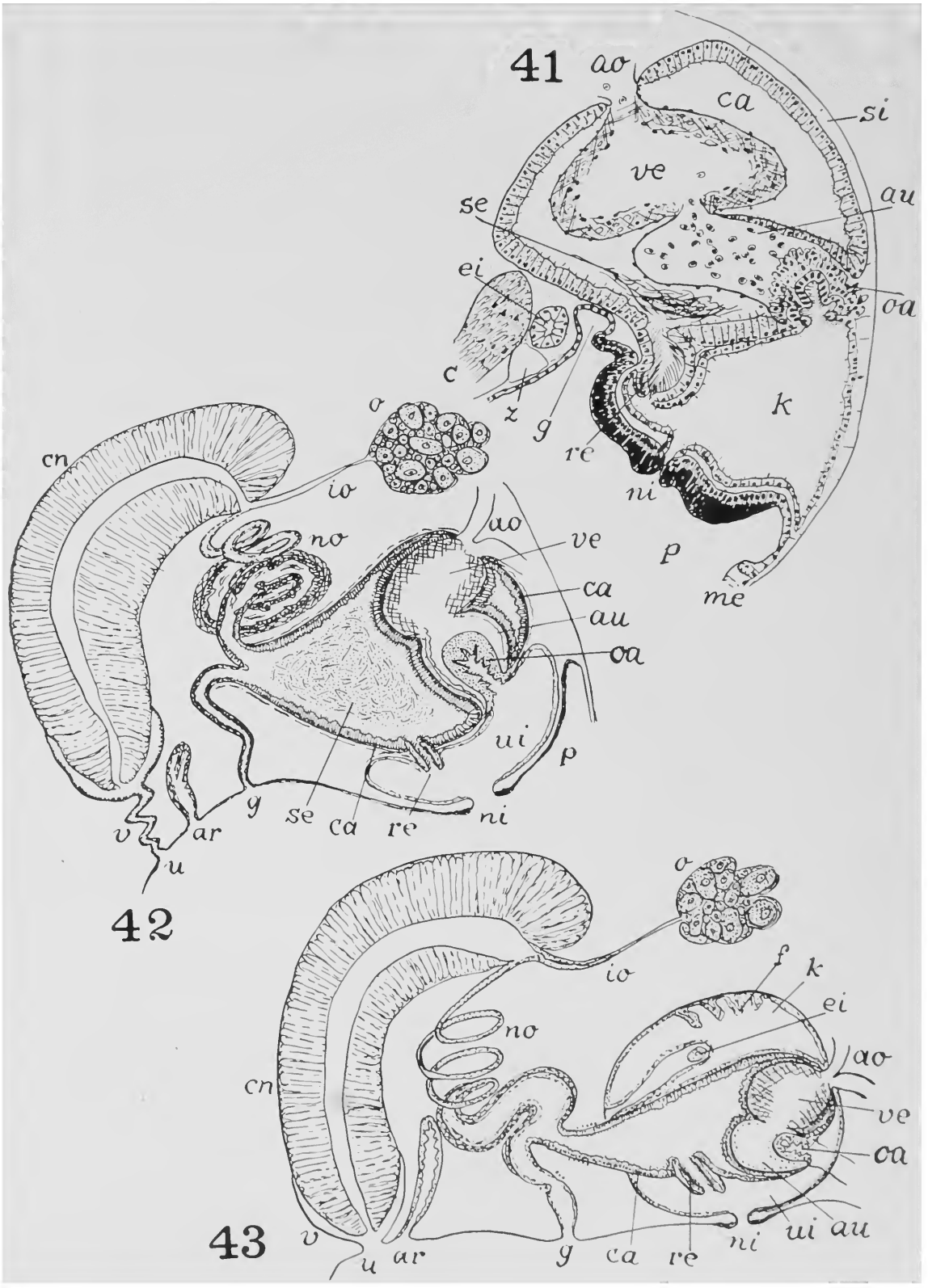
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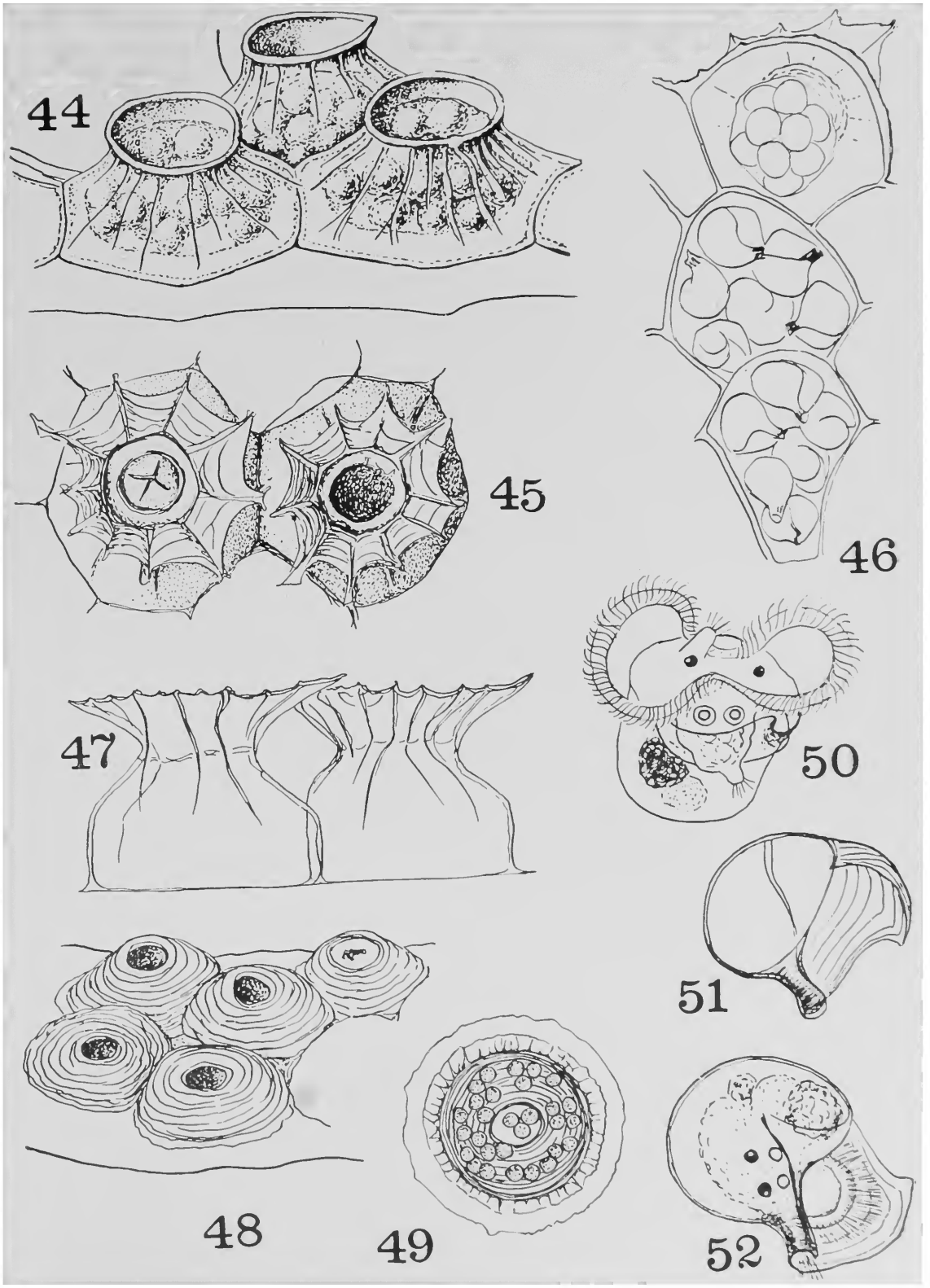
PLATE 8

Fig. 44 — Three egg capsules of *sparsa*.
Fig. 45 — Two egg capsules of *brasiliana,* seen from above.
Fig. 46 — Basal view of egg capsules of *brasiliana* with newly laid eggs and veliger shells.
Fig. 47 — Two egg capsules of *brasiliana,* side view.
Fig. 48 — Five eff capsules from a spawn of *veleda*.
Fig. 49 — Egg capsule of *veleda,* basal view.
Fig. 50 — Veliger of *brasiliana*.
Fig. 51 — Shell of same.
Fig. 52 — Shell of veliger of *sparsa*.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