

RICHARD U. GOODING AND JØRGEN LÜTZEN

STUDIES ON PARASITIC  
GASTROPODS FROM ECHINODERMS

III.

A DESCRIPTION OF *ROBILLARDIA CERNICA* SMITH 1889,  
PARASITIC IN THE SEA URCHIN  
*ECHINOMETRA* MEUSCHEN, WITH NOTES ON ITS BIOLOGY

Det Kongelige Danske Videnskabernes Selskab  
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### Synopsis

The prosobranch gastropod *Robillardia cernica* is reported from the regular echinoids *Echinometra mathaei* in the Red Sea and at Amboina, and *E. insularis* at Easter Island (SE Pacific Ocean). The original specimen was recorded "on an *Echinus*" at Mauritius (W Indian Ocean) but all our specimens occurred in the host's rectum.

At Easter Island specimens were examined alive. Fifty-nine of 213 urchins were infected in January 1971.

The soft parts are described for the first time. The foot has a well-developed creeping sole. A large fold mainly of pedal origin is reflected over part of the fragile shell, its anterior left portion drawn out into a siphon, probably for inspiration. In the female the anterior right part of the fold forms a brood-pouch for protection of the stalked egg capsules, which are cemented at the base of the snout. Special emphasis is placed on the anatomy of the alimentary tract and reproductive organs. The species is presumably a consecutive hermaphrodite.

In the host the female's mobility is limited by attachment to the test at the point where her snout pierces the rectal wall and she normally lies with her siphon extending to the host's anus. The much smaller male is fully mobile but usually occurs in the female's brood-pouch. Both sexes feed probably on the sea urchin's internal organs—particularly the gonad—by invaginating a long proboscis through the rectal wall.

The position of *Robillardia* in the complex of parasitic prosobranchs is not clear.

## Introduction

Smith (1889) briefly described the shell of a gastropod, which he named *Robillardia cernica*. His account begins, "About a year ago the British Museum purchased of Mr. Robillard, of the Mauritius, . . . a single example of a shell, which, according to his statement, appears to have been 'found living on an *Echinus*.'" Only a small dried portion of the animal remained, attached to the shell, but "some minute, glassy, grain-like objects adhering to it proved . . . to be minute shells and doubtless the young of the species". The original dried shell is still in the British Museum (Natural History), London.

No new specimens of *R. cernica* have been reported since and no further species have been added to the genus.

In 1970, Dr. John M. Lawrence (Dept. of Zoology, University of South Florida) referred to one of us (J. L.) material of the sea-urchin *Echinometra mathaei* (de Blainville) s.s. from Elat (Gulf of Aqaba, Red Sea) carrying an endoparasitic gastropod. Independently, in 1971 at Easter Island (= Rapa Nui, Isla de Pascua, SE Pacific Ocean), the other of us (R. U. G.), noting that the rectum of *Echinometra insularis* H. L. Clark frequently contained parasitic gastropods, made observations on live material and preserved several specimens.

The identification of this new material obviously rests on a similarity of shell characters, but it is consistent with most of the available data.

The range of material from Easter Island has allowed us to study the anatomy of the species in some detail and to consider certain aspects of its biology.

## Acknowledgements

The study was supported by a grant from the Danish State Research Foundation to J. L. Collecting on Easter Island was made possible in part through a Singapore-Barbados passage furnished R.U.G. by the University of Singapore. His laboratory work was carried out during tenure of a Visiting Postdoctoral Research Associateship at Smithsonian Institution, Washington, D.C., where facilities, information and advice were kindly provided by David L. Pawson, Roger F. Cressey, and other members of the Department of Invertebrate Zoology.

We should also like to thank Dr. Lawrence for making available to us the material from the Red Sea; Dr. Pawson for identifying the host of our specimens from Easter Island; and several people, named in the text, for allowing us to quote their unpublished data.

## Material and Methods

### Mauritius

Smith's original shell, holotype of *R. cernica* (BMNH, registration number: 1888.1.9.88.).

### Gulf of Aqaba

One ovigerous female and one male, from inside *Echinometra mathaei*, reef S of the Heinz Steinitz Marine Biology Laboratory, Elat, Israel. Dried. Plus Kodachrome of live host and parasite. Collected by Dr. J. M. Lawrence, who has informed us that this host-specimen was of the typical *mathaei* form.

### Amboina (Banda Sea)

One small cleaned shell from *Echinometra mathaei*, collected "at the coast", Feb. 1922. Zool. Mus., Copenhagen.

### Easter Island

All collections were made from *Echinometra insularis* on January 15th–21st, 1971. With the exception of No. 12, all samples derive from near Hanga-Piko Bay.

1. 3 single ♀♀, 3 ovig. ♀♀ + ♂♂ from 18 hosts; high-tide level.
2. 2 young ♀♀, 2 ovig. ♀♀ + ♂♂ from 15 hosts; high-tide level.
3. 2 young ♀♀ from 10 hosts; high-tide level.
4. 4 single ♀♀, 3 ovig. ♀♀ + ♂♂, and 5 parasitized hosts cut in half from 28 hosts; mid-tide level.
5. 3 young ♀♀, 2 ovig. ♀♀ + ♂♂ from 12 hosts; mid-tide level.
6. 2 single ♀♀, 1 large (ovig.?) ♀ + ♂; ca. 1.5 m. subtidal.
7. 3 young ♀♀, 1 ovig. ♀ + ♂ from 24 hosts; splash-zone.
8. 4 young ♀♀, 1 ovig. ♀ + ♂ from 13 hosts; mid-tide level.
9. 8 young ♀♀ (2 in 1 host), 3 ovig. ♀♀ + ♂♂, 1 ovig. ♀ without ♂ from 52 hosts; ca. 1 m subtidal.
10. 4 young ♀♀ (2 in 1 host), 1 ovig. ♀ + ♂ from 20 hosts; splash-zone.
11. 1 large ♀, 2 ovig. ♀♀ + ♂♂ from 6 hosts; mid-tide level.
12. 1 ovig. ♀ + ♂ from 10 hosts, crevices on inner side of rocks forming SW side of entrance to small bay off Vaihu (27°09.8' S, 109°22.3' W), S coast; mid-tide level.

Sixteen of the parasites were fixed in Bouin's fluid (seawater formula), 9 rotted to shells in freshwater, and the remainder, including the 5 specimens *in situ*, preserved in ca. 10 % neutralised seawater formalin. Twenty were serially sectioned (tissuemat embedding at 6, 8, or 10  $\mu$ ; celloidin at 30  $\mu$ ) and stained with H + E, Azan, or tetrachrome.

The bulk of the material is being kept in the Zoological Museum, Copenhagen. Specimens and complete serial sections of a female and male have been deposited in the Division of Mollusks, National Museum of Natural History, Washington, D.C.; specimens in the Australian Museum, Sydney; and in the Museo Nacional de Historia Natural, Santiago, Chile.

### External Appearance

The shell (Pl. I) bears a distinct mucro consisting of  $2\frac{1}{2}$  nuclear whorls. It is apically smoothly rounded, ca. 0.3 mm in height and 0.25 mm in largest diameter. The mucro as well as part of the first adult whorl is whitish and nontransparent, in sharp contrast to the rest of the shell which has a glassy texture. The adult whorls increase rapidly in width and, since the individual whorls are fairly low, this results in the shell being much broader than high. Maximum number of adult whorls is  $3\frac{1}{2}$ , corresponding to a width of 10 mm. The suture is double. The shell is polished and glossy, with a smooth surface and very many closely placed growth lines. It is rather fragile.

There is no operculum.

Soft parts of the female (Pls. II & III). The foot has the shape of a sole. It is comparatively large, longer than broad, fleshy, and pointed posteriorly. Anteriorly it tapers into an obviously very mobile portion, at the tip of which is located the opening of the anterior pedal gland; the opening is usually surrounded by an upper and a lower lip. A little in front of the mid of the under side is the opening of the posterior pedal gland. This opening often appears as a distinct short, longitudinal slit.

The head is displaced a little to the left with respect to the foot; the snout is broad and very conspicuous. Where the head emerges from the mantle aperture, it bears two tentacles; at the base of each a small pigmented ocellus may be distinguished. The tentacles are fairly long, pointed, and somewhat flattened.

A very conspicuous fold of skin arises from each side of the head and foot. That of the left side starts just beneath the left tentacle and continues backwards to the mid-dorsal part of the foot where it meets the fold of the opposite side with which it is sometimes confluent. The anterior part of the fold of the left side is rolled back on itself to form an open tube (the siphon) with a narrow terminal aperture and a broad opening at its base. This is presumably a permanent structure since it occurred in all specimens seen. The left tentacle was very often observed to be introduced into the basal part of the siphon. The remainder of the left fold together with the hindmost part of the right fold is reflected to cover part or almost all of the shell. While in preserved specimens these parts of the folds were contracted in varying degrees to expose a considerable part of the shell, in live specimens they were observed to cover the shell entirely save for the mucro and one or two spire whorls. Consequently we consider that they serve to protect the fragile shell from the abrasive action of the host's faeces.

The anterior part of the right fold, which starts slightly behind the right tentacle, is expanded into a thin-walled vesicular structure with a broad opening that is usually directed towards the body. It reaches its maximum size in ovigerous females, where it extends to cover the mass of egg capsules entirely, thus serving as a brood-pouch. Its opening was often observed to oppose the basal opening of the siphon.

Soft parts of the male (Pls. I & III). These are very similar to those of the female. However, the siphon is comparatively much shorter and that part of the cephalo-pedal fold which in the female forms the brood-pouch is rudimentary in the male. In its place

a large penis emerges from the right side of the head behind the right tentacle. In preserved specimens the penis is usually longer than the siphon and tapers from a broad base to a pointed tip.

The colour of the animal in life, including that part of the body which could be seen through the transparent shell, is generally pinkish. The kidney region, however, is characteristically purple and those parts of the whorls containing the digestive gland and reproductive glands appear yellowish-brown. The colour of the siphon, particularly towards its end, is yellow. The egg capsules were usually pink, becoming pinkish-brown as they matured.

### **Occurrence and Orientation in Host at Easter Island**

All specimens were found in the rectum. This lies under the interambulacrum containing the madreporite (3 in Lovén's scheme, = CD of Carpenter). Normally, only one female infests a particular host: if young, she is alone but, when she bears eggs, a male is present.

All but 3 of the females were oriented in the same way (the terms "dorsal", "left", etc. are used in relation to the host in its normal position). The body lies in the lumen of the rectum, with the siphon extending to or just through the host's anus. The snout penetrates the rectal wall on the left side and is attached, together with the portion of wall at this point, by a cap of dark secretion to the test in the interambulacrum 2 (= BC; the left of the madreporic interambulacrum). The foot is applied to the rectal wall dorsally; the shell and visceral mass extend ventrally, and the external side of the brood-pouch facing the intestinal end of the rectum. When protruded, the proboscis snakes as a thin white tube among the organs of the host's body-cavity; it is sufficiently extensible to reach any part of the latter.

That the female can detach (or is detached) occasionally from its position and later reattach is suggested by the presence of 2-3 dark spots within ca 10 mm of each other on the inner side of test of some hosts. These are probably not related to growth, since they are randomly oriented.

Of the 3 females occupying an unusual position (all young specimens, without males or egg capsules) one was attached in the normal way to the left of the rectum but reversed in orientation, so that the siphon pointed up the rectum. This indicates that the females may retain a certain mobility within the rectum but that movement is limited by the attachment of the snout. The 2 other females, attached and oriented as described above, were each paired with a similar young female. In one case, the additional female was attached in the normal way to the test but on the right side of the rectum and closer to its intestinal end; the siphon extended toward the anus as usual. The situation of the second additional female was not noted.

Males were never found except accompanying large females. When the host's rectum is first opened, the male is usually discovered in the female's brood-pouch. But males are quite active, gliding on the relatively large foot, and sometimes occurred on



other parts of the female or on the inner side of the host's rectal wall. At least one of these last had the proboscis extending through the wall a short way into the body-cavity. But the snout is never anchored to the test as in the female.

When removed to a dish of seawater, young females crawl actively (though not as fast as males). Large ovigerous females could adhere by and balance on the foot but did not move very far in these circumstances.

Smith (l.c.) reported his specimen of *R. cernica* to live on an echinoid. It is possible that the original collector might have assumed that the gastropod was external if its host had been damaged and the parasite found nearby. Such cases are known; and on Easter Island specimens were occasionally observed to wash out of *E. insularis* which had been cut in half and left in a quiet pool for a short time before examination.

## Internal Anatomy

### Structure of the Foot and the Cephalo-pedal Derivatives

The thickness of the foot is made up of a loose connective tissue supplied with very few criss-crossing muscle fibers that seldom accumulate into bundles. Ciliation is limited to the sole and the margins.

Except in the interior of the siphon, cilia are absent on the components of the cephalo-pedal folds, the external surfaces of which tend to be thinly cuticularized.

The epithelium lining the inner wall of the siphon is made up of small, cuboidal, ciliated cells interspersed with numerous mucocytes which increase in number towards its base. These are absent in the epithelium of the outer wall, the cells of which are non-ciliated and appear cuticularized. Underlying both epithelia occur a few muscle fibers running transverse to the long axis of the siphon and in addition, along the interior wall, distinct bundles and longitudinal fibers; the latter are especially powerful in the female. Separating inner and outer wall is a loose connective tissue with a very few randomly oriented muscle fibers.

The folds which surround the shell and, in the female, the one which forms the brood-pouch are extremely delicate and built on the same plan. The epithelial covering consists of short cylindrical or cuboidal cells which are cuticularized to a varying extent; it rests on an indistinct layer of irregularly oriented muscle fibers. The thickness of the fold is occupied by a loose connective tissue and a few muscle fibers; the latter extend from side to side. Beneath the interior wall of the brood-pouch and obviously more or less radiating from its base occurs a layer of muscle bundles; the action of these is likely to reduce the pouch in size by infolding its margins. On whole mounts of the brood pouch a system of radiating, branching canals is visible in its walls; these by filling the spaces in the connective tissue may again extend the fold and thereby antagonize the muscles.

We have been unable to find data on the fluid content of the rectum in sea urchins. Although some sea water may enter the anus at defecation, the interior of the rectum is

presumably poor in oxygen; the siphon in *Robillardia* has probably developed to cope with this situation. The structure of the siphon shows that it is capable of elongating and shortening by contraction of the subepithelial circular muscle fibres and the longitudinal muscle bundles respectively. Although contracted in preserved specimens, in live females it was often observed to reach and penetrate the host's anal opening. Arising from the left pedal fold, its broad base could be applied to the mantle aperture of that side (Pl. II, fig. 8; Pl. III, fig. 10). In this position ciliary activity on the gill would draw in a water current through the siphon, the ciliation of the interior wall of the siphon presumably being too weak to maintain a current although aiding, perhaps, in reducing the frictional resistance.

The broad opening of the brood pouch faces the right part of the mantle aperture and sea water is likely to enter it either directly from the siphon or by way of the mantle cavity. The males probably meet their oxygen requirements by exploiting the female's exhalent water current with their short siphon. This agrees well with the location of the males as related elsewhere (p. 6).

#### **The Anterior and Posterior Pedal Glands**

These are more or less tubular bodies comparable in structure to those of other gastropods. They are accommodated centrally in the thickness of the foot, with their blind ends directed towards and touching the wall of the central body sinus. Both glands are comparatively more conspicuous in the male than in the female.

#### **Mantle Cavity and Pallial Complex**

The mantle opening is very wide. Although fairly deep, the mantle cavity is not very spacious when the proboscis is redrawn into the body. A large, monopectinate gill with up to ca 42 leaflets in a large female and more than 20 in a medium-sized male occupies the left side of the mantle wall. A hypobranchial gland occurs along part of the right side of the gill. The anus opens far back in the mantle cavity, close to the genital aperture and to the right of the hypobranchial gland. An aperture for the kidney is found in the roof of the mantle cavity to the left of the anus.

In young females the right wall of the mantle cavity posterior to the anus is raised into numerous folds and diverticles, each supported by a core of connective tissue rich in vascular spaces. The epithelial lining consists of very high, cylindrical cells the nuclei of which are either (and most frequently) basal or apically placed. The plasma appears finely granulated and the epithelium may well be secretory. A similar structure is absent in the males and there is indication that it atrophies when the females attain maturity.

#### **The Alimentary Canal. General Structure** (Pl. IV)

The alimentary tract is very elaborate. It is essentially similar in the two sexes and consists of an acrembolic proboscis capable of considerable extension; a pharyngeal bulb; an oesophagus of great length, divisible into two parts; a small stomach in

continuity with the digestive gland; and an intestine. In addition, a conspicuous convoluted gland discharges into the dorsal aspect of the proboscis sheath. There is no radula.

The first part of the proboscis sheath is supplied with very many stout muscles, which radiate into the interior of the snout and of which a few even extend far back in the body to become continuous with the columellar muscle. The remainder of the proboscis sheath, the pharynx and the entire oesophagus lies completely free within a very spacious sinus situated immediately under the skin of the dorsal side of the body. The sinus is everywhere lined by connective tissue; its posterior portion is subdivided by a few connective tissue strands and septa, which serve to support most of the ganglia of the central nervous system and their associated nerves, at the same time leaving an open tube for the movement of the oesophagus. Especially in the male, the blind portion of the pedal glands participate in the formation of the sinus' ventral wall. Although most of the gland of the proboscis lies free within the sinus, its hind portion appears to be fixed in the connective tissue. Two distinct retractor muscles originate in the columellar muscle and run through the sinus to penetrate the wall of the proboscis sheath far anteriorly.

The terminal part of the snout is closely opposed the host's rectal wall which also plugs the opening of the proboscis sheath although leaving an aperture for the penetration of the proboscis into the coelomic cavity of the host (Pl. III, fig. 10). When the proboscis is extruded the epithelium of the sheath is everted and faces the exterior. In this position the proboscis gland opens to the exterior on the base of the proboscis at a point which lies immediately on the coelomic side of the host's rectal wall.

When the proboscis is inverted the alimentary tract is greatly reduced in length (as evidenced by the increase in thickness of the muscular investments), but in order to be accommodated within the sinus it is in addition considerably convoluted.

### **Histology of the Alimentary Canal**

The first part of the proboscis sheath is short and has an epithelial covering of close-set, very tall, cylindrical cells; a thick sheath of longitudinal muscle fibers underlies the epithelium. The next part of the sheath is in contrast very long; the epithelium of this region consists of cylindrical, finely ciliated cells with basal nuclei. Underlying the epithelium occurs a layer of circular muscle fibers surrounded by a layer of longitudinal fibers which diminish in thickness posteriorly. An arrangement of the epithelial cells into very many minute transverse folds was noted when the everted proboscis was examined at high magnification (scanning electron microscope).

The pharynx forms a powerful muscular bulb. Its lumen, which is triangular in cross section, is clothed by a very flat epithelium with very few cells. The muscular wall consists of a thick inner layer of radial fibers, in the periphery of which occur also a number of circular fibers. Encircling these is a thin layer of longitudinal fibers. Two buccal ganglia are embedded in a collar of connective tissue surrounding the posterior base of the bulb.

The oesophagus is very long. The epithelium lining it consists of cells of varying length raised to form numerous villi and containing secretory granules which are constantly nipped off the apical part. Underlying the epithelium occurs a very thick layer of longitudinal muscle fibers ensheathed by a few circular fibers. Posteriorly the muscular investments diminish considerably in thickness.

The oesophagus leads into a small stomach region the wall of which shows many folds. The epithelium is columnar and ciliated here and there, and the cells contain a variety of secretory vacuoles and inclusions. The stomach has one major and a few minor openings into the digestive gland. This is very large and occupies all available space in the visceral hump left by the gonads. From the stomach a fairly short intestine loops through the kidney. The wall of the intestine is thrown into many longitudinal folds, its lining epithelium consists of tall ciliated cells.

The proboscis gland occupies a dorsal position with respect to the retracted proboscis. It opens by way of a narrow duct into the proboscis sheath at the point separating its first and second part. The epithelial lining of the gland may be irregularly folded and consists of a variety of non-ciliated cells, mostly with basal nuclei, containing vacuoles and granules which show a wide range of staining properties. A smaller anterior part of the gland has a very minute lumen and only one kind of secretory cells; these are very large, globular, and filled with numerous small granules that stain with Alcian blue. In contrast to the much larger posterior portion of the gland, this part is encapsulated by a thin covering of muscle fibers and connective tissue.

Whenever material obviously of hostal origin is observed in the alimentary canal, it occurs exclusively in the proboscis sheath, pharynx or oesophagus. The contents of the gland seems to be entirely secretory. The actual function of the proboscis gland is nevertheless obscure. The fact that it is unpaired and discharges into the proboscis sheath makes it difficult to suggest a homologous structure in other prosobranchs.

The contraction and extension of the proboscis obviously results from terminal involution. Contraction of the extended proboscis is apparently brought about by muscular activity; the involved muscles are 1) those associated with the anterior section of the proboscis sheath which draw the proboscis base back into the snout; 2) the retractor muscles which act on the anterior part of the next section of the proboscis; 3) the longitudinal muscles of the proboscis sheath which, since they increase in thickness anteriorly, are likely to contract especially the mid portion of the proboscis; 4) the powerful longitudinal fibers of the oesophagus which pull back the pharynx bulb and involute the remainder of the proboscis aided, perhaps, by the circular muscles associated with the sheath which on contracting will exert a pressure on the fluid in the proboscideal space thus tending to reduce this in size.

To explain how the proboscis is extruded is more difficult, since no muscles are obviously involved. It is conceivable, however, that it may result from an internal hydrostatic pressure formed by the very involution of the proboscis.

### **The Nervous System and Sense Organs**

The central nervous system forms a concentrated ring of ganglia around the middle part of the oesophagus; five ganglia could be distinguished: two pedal ganglia, the sub-oesophageal ganglion, and two cerebro-pleural ganglia. In addition to these two buccal ganglia, a visceral ganglion and a supra-oesophageal ganglion are present. Neither accessory buccal ganglia or an osphradial ganglion were found.

From the pedal ganglia strong nerves issue to the foot, the penis, and all parts of the pedal fold; the nerves supplying the latter seem predominantly to arise in the left pedal ganglion.

The sense organs comprise the osphradium, a folded epithelial strip near the left entrance to the mantle cavity; two statocysts; and two ocelli. The latter are embedded in connective tissue very close to the anterior wall of the great sinus around the alimentary tract and in the region close to the tentacle base. The epithelium lining the oval optical vesicle is divided into a translucent cornea and a pigmented retinal cup. The spherical lens is 35–40  $\mu$  in diameter in an average male, 60–70  $\mu$  in an average female.

### **Musculature, Kidney, and Circulatory Apparatus**

The columellar muscle is inconspicuous and restricted to the body whorl, a few of its fibers spreading diffusely into the thickness of the foot.

The kidney is a capacious sac lying dorsally in the body whorl posterior to the mantle cavity and in between the digestive gland, the pericard, and, in the female, part of the genital duct. It is penetrated by the rectum and has a simple aperture into the mantle cavity. The pericard lies to the left of the kidney. The heart has a well-developed auricle and ventricle.

### **The Reproductive Apparatus of the Male**

Seventeen specimens identified as males by the presence of a well-developed penis and accompanying females, showed a shell diameter from 1.7 to 3.9 mm. Four of these were sectioned (shell diameter: 2.4, 2.5, 3.2, and 3.9 mm).

The testis occupies a central position in the columellar side of the spire whorls, its volume being moderate compared with that of the digestive gland which almost envelops it everywhere. It is divided into several lobules, all of which ultimately discharge into a short vas deferens lined with cuboidal non-ciliated cells. Upon coiling a few times the vas deferens expands into an ovoid vesicula seminalis containing un-oriented sperm cells. The walls of the vesicula are composed of cuboidal cells bearing long cilia. A short and very narrow duct connects the vesicula with the prostatic gland, which opens broadly into the rear end of the mantle cavity. From the prostatic aper-

ture, an open seminal groove can be traced along the right side of the body to the penis base.

The shape of the penis has been noted earlier. A deep ciliated groove in continuity with the open seminal groove runs from its base to the very tip. Underlying the epithelium is an ill-defined layer of longitudinal muscle fibers, while the central core is occupied by connective tissue, unoriented muscle fibers, and spaces continuous with the body sinus. Although this arrangement suggests that the penis is capable of spiraling and coiling, as was actually observed, it probably never fully redraws into the mantle cavity, since it was invariably found in an exposed position.

### **The Reproductive Apparatus of the Female**

The diameter of the shell in the females ranged between 3.8 and 10.0 mm, the largest usually being ovigerous. The reproductive organs in 2 mature females (6.5 and 7.3 mm) showed the following structure:

The ovary is voluminous and occupies almost all of the visceral hump, the digestive gland being restricted to a narrow layer along the surface of the whorls. The genital duct is placed far to the right in the body whorl, its main part being included in the thickened right wall of the mantle cavity. It comprises an oviduct, an albumen gland, a bursa copulatrix, a receptacle for the sperm, and a capsule gland.

The ciliated oviduct is extremely short, probably because the albumen gland—into which it exits—is intimately associated with the anterior part of the ovary, being partially embedded in its right side. The albumen gland has the shape of an elongate sac that lies immediately beyond the surface of the right side of the body whorl. Its walls are moderately folded and composed of elongate, profusely ciliated cells of two types; one has very basal nuclei, while in the other the nuclei are more apically placed. Both cells secrete a secretion that stains intensively with Alcian blue.

The short section of the genital duct which unites the anterior part of the albumen gland and the capsule gland is thin-walled and strongly folded. The cells of the wall are small and ciliated, and obviously not secretory. The duct actually opens into the rear end of the mantle cavity and, although sperm cells were not observed in it, its location suggests that it may represent a bursa copulatrix. From the left side of the bursa arises a moderately large seminal receptacle, which lies included in the kidney wall and contains sperm cells.

The capsule gland has a slit-like lumen and occupies the thickened upper right wall of the mantle cavity, into which it opens throughout its entire length except for the most anterior blind portion. Along its interior left surface runs a deep, ciliated gutter which is opposed to a longitudinal region of similar gutters in the right wall. These can be traced back almost to the region where the gland and the bursa unite. If the two walls of the capsule gland are pressed together, these gutters are likely to form a ciliated tube along which sperm could be transported.

## On the Reproduction and Life History

### Copulation

With a single exception each of the 20 ovigerous females was accompanied by a single male specimen. Similarly, all except one of the females accompanied by a male were ovigerous.

Sperm stored in the male's vesicula seminalis is discharged into the prostate where it mingles with prostatic secretion to form the seminal fluid. The length of the penis of preserved specimens never exceeded 2 mm, whereas the distance from the mantle edge to the opening of the bursa copulatrix in larger females approached 4 mm. Unless the penis is capable of considerable extension, which it probably is, sperm could not be deposited directly in the bursa. However, the presence of ciliated gutters in the wall of the female pallial duct has been mentioned earlier. If these are active in sperm transportation, the degree to which the penis has to be extended is considerably reduced.

### Oviposition

Each egg capsule usually contains 300–500 eggs. It is elongate, ovoid and furnished with a long stalk. Until the larvae hatch, the capsules are attached by this stalk to the base of the snout, glued onto its surface by a secretion. By continuous addition of new capsules the mass gradually grows to a branched tree-like structure. Thus it carries a number of capsules (up to 26 at a time) containing embryos in various stages of development, as well as empty decayed ones from which the larvae have escaped. Since the point of attachment on the snout is always on the right side, immediately opposite the opening of the anterior pedal gland, the secretion may well be produced by this gland (Pl. III, fig. 11).

The eggs of the single unaccompanied female had not developed and were probably not fertilized.

In live females the brood-pouch was observed to envelop the mass of egg capsules completely, thereby protecting them from the abrasive action of the host's faeces. Its opening is more or less opposite the proximal opening of the siphon; thus part of the inhalant water might enter the brood-pouch and aerate the capsules.

### Considerations on Life History

When live ovigerous females were removed to a dish of seawater, some of the capsules usually hatched. Under natural conditions, the larvae probably escape into the rectum and pass out with the faeces. The fact that the females retain the egg capsules until hatching of the larvae may be correlated with the habitat preferred by the host (p. 18). If the capsules were expelled into the turbulent seawater of the tidal zone immediately upon their formation, their chance of survival would in all probability be very small. It is true that *Stilifer linckiae*, a gastropod parasite of the littoral starfish, *Linckia multifora*, liberates the egg capsules into the sea as soon as they are manufactured (Lützen, 1972a), but parasitized host specimens live mainly subtidally.

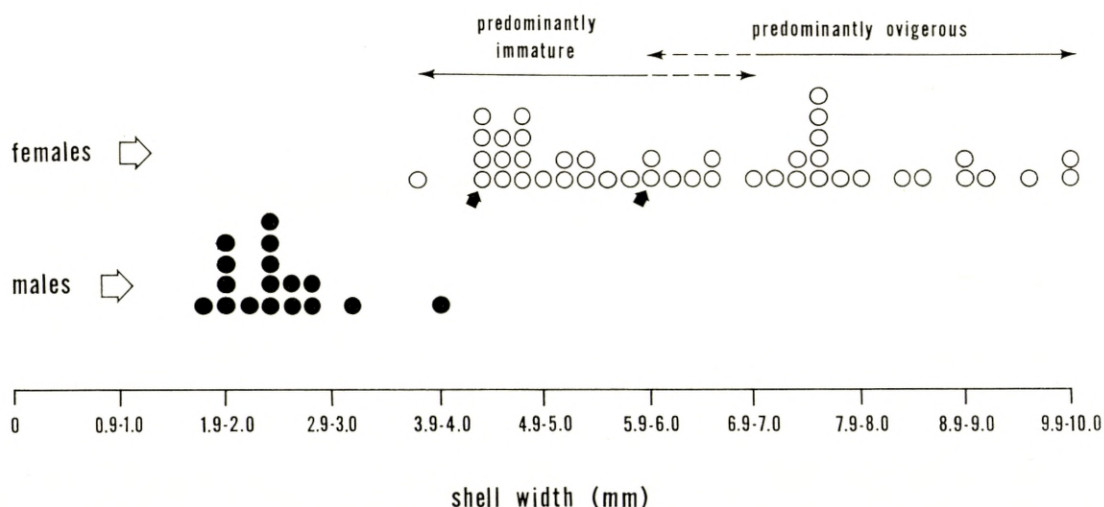


Fig. 1. *Robillardia cernica* Smith. Size-frequency analysis of 61 specimens collected near Hanga-Piko Bay, Easter Island, January 15th–21st, 1971. Arrows indicate specimens with vestige of penis.

Using the greatest width of the shell (measured to the nearest 0.1 mm) as reference, a size frequency diagram was constructed (Fig. 1). It comprises only 61 individuals, as a number of specimens had been used for other purposes before they were measured. The sex is indicated when it was immediately apparent (males and ovigerous females) or examined by sectioning.

The fact that the smallest shell-width recorded was 1.7 mm might suggest either that the very young gastropods do not occur in the rectum (at least not at the particular time of the year when the collections were made) or, that if they do so, their growth is extraordinary fast. However, we suspect that some may actually have occurred but on account of their minute size, were not discovered, because collecting was performed by eye rather than with a lens.

The males (range of shell width: 1.7–3.9 mm) make up a very well-defined size-group, separated by a distinct gap in which almost no overlapping occurs from the next group. The latter comprises young females and mature, ovigerous females.

It proved impossible to discriminate sharply between young and ovigerous females as the egg capsules had often been removed or detached. We are confident, however, that the great majority of the females with a shell width less than 7.0 mm are non-ovigerous and that those above that size were nearly always ovigerous; the smallest ovigerous female observed had a shell width of 6.0 mm.

No female less than 3.8 mm was found. It cannot be argued that smaller ones were overlooked. It is also inconceivable that the females as young should live outside the rectum: measurements performed on a number of cleaned tests of *E. mathaei* and *lucunter* (material of *E. insularis* not being available) showed the anal opening in medium-sized specimens to measure 1–1.5 mm across; even if the flexibility of the pe-



riproct would allow some expansion of the anal opening, we doubt that parasites with a shell width larger than 1.5–2 mm could penetrate through the anus. And penetration through the mouth seems out of question, the activity of the teeth presumably forming an effective barrier.

All of the young females were carefully examined externally and 14 (shell diameter 3.8 to 6.0 mm) were sectioned. They differed from ovigerous females merely in that the ovary is less voluminous, the albumen gland generally smaller, and the receptaculum empty. But in two of them (4.4 and 6.0 mm, marked by arrows in fig. 1) occurred a penis, smaller than in most males, behind the right tentacle.

The presence in these two females of a penis is suggestive of a prior male phase or at least of male potentialities. Although such females were remarkably few, we incline to consider *Robillardia* to be a consecutive hermaphrodite. Assuming that the species as young functions as a male and after that transforms into a female explains the total absence in our material of females less than 3.8 mm as being apparent only. Implicitly a sex change seems obligatory, all females having originally passed through a male phase.

The reproductive organs in none of the young females examined revealed any trace of a former male phase. Neither had any of the four males sectioned entered a transitional phase. The cause for this is presumably that the change from male to female in *Robillardia* proceeds very rapidly. In the protandric hermaphroditic gastropod, *Stilifer*, parasitic in tropical starfishes, Lützen (1972a) presumed that the proximity of the female prevents sex change in the male. It is possible that the data on *Robillardia* could be interpreted along the same lines.

### The Veliger

The larvae hatch as veligers equipped with a transparent shell consisting of  $1\frac{1}{4}$  whorls (Pl. I, fig. 6) and a horny operculum. The veligers possess pigmented ocelli, two statocysts, and a bilobed, ciliated velum.

The fact that the protoconch has only  $1\frac{1}{4}$  whorls as compared with  $2\frac{1}{2}$  nuclear whorls in the shell of the adult, and the presence of an elaborate velum, indicate that the larvae lead a planktonic life for some time before they seek out a host.

### Incidence at Easter Island

At the collecting site near Hanga-Piko, 213 specimens of *E. insularis* were examined, of which 59, or 27.7%, were parasitised. Since other species of *Echinometra* are known to move little once they are established (Mc Pherson, 1969; Khamala, 1971) and observations at Easter Island suggest a similar type of behaviour in *E. insularis*, it seems valid to divide the figures according to the tide-levels from which the urchins were collected (Table 1). Then it becomes apparent that the highest rate of infestation

Table 1. Tide-level distribution of *Echinometra insularis* and its parasitic snail, *Robillardia cernica*, examined near Hanga-Piko Bay, Easter Island.

Habitats	Number of urchins			Percentage of urchins		Percentage of parasitized urchins doubly infected
	examined	parasitized	parasitized by 2 snails	parasitized	parasitized by 2 snails	
	1	2	3	4	5	6
subtidal . . . . .	62	14	5	22.6	8.1	35.7
water level . . . . .	59	25	10	42.4	16.9	40.0
high-water . . . . .	48	12	5	25.0	10.4	41.7
splash-zone . . . . .	44	8	3	18.2	6.8	37.5
Total . . . . .	213	59	23			

occurred at water level (column 4). This also holds when the number of urchins with a double infestation is related to the total number of urchins examined at each tide-level (column 5). But more uniform rates obtain if the numbers of parasitised urchins (i. e., those with both one or 2 snails) are used as the denominator (column 6).

The smallest urchin parasitised measured 38×32 mm (horizontal axes); the smallest with a double infestation (ovigerous female plus male), 44×40 mm. The peak of infestation seemed to centre in urchins about 60×52 mm. Singly infested urchins occurred throughout the sampled population and there was no tendency for double infestations to predominate among larger urchins.

### Feeding and Effect on Host

The fact that proboscides of both females and males were observed extending among the internal organs of freshly opened urchins indicates that *Robillardia* feeds either on the coelomic fluid or the tissues of its host. We incline to the latter theory—and specifically suggest that the gonad is the main source of nutriment—for several reasons:

1) Since the perforation made by *Robillardia* in the rectal wall leads directly into the main coelomic cavity, utilization of the coelomic fluid alone would not require an extensible and elaborate proboscis.

2) Ingested food found in a few of the sectioned specimens (in the proboscis and pharynx) when at all identifiable, proved to consist of yolk granules.

3) The female is attached in the region of one of the sections of gonad, which could then be exploited while her proboscis is short and would be available constantly to the smaller male.

4) This section of gonad in infected hosts is usually smaller than the others. In some cases the degeneration is distinctly greater oral to the attachment of the female parasite, a gross effect similar to that reported by Pearse & Timm (1968) for the nematode *Echinocephalus pseudouncinatus* Millemann in the gonads of the echinoid *Centrostephanus coronatus* Verrill and attributed by them to blocking of a gametogenic regulating hormone.

5) Gonad is nutritionally a very rich food. Egg-production at the level on which *Robillardia* appears to operate would seem to require such a source of nutriment and gonad to be a particularly suitable one for this biochemical conversion.

It is possible, however, that other tissues may supplement or even seasonally supplant gonad in the parasite's diet. At the time when the work on Easter Island was being carried on, it seemed obvious that *Robillardia* had a definite effect on the whole gonad of its host (apart from the local deterioration of the section in interambulacrum 2), small females causing little or no diminution nor change in colour and large ones usually living in urchins with small, very darkly coloured gonads. Following Pearse's observations (1968, 1969) that individuals in many populations of *E. mathaei* are asynchronous in their breeding and that the condition which had appeared extreme in parasitized *E. insularis* could be normal, we reexamined our data more closely. But the correlation still appears significant.

Large females stretch the wall of the rectum considerably and presumably cause some mechanical impediment to the passage of the host's faecal pellets. They may thus interfere with its nutrition. But it is unlikely that these effects are severe.

In some cases there was a slight local thickening of the echinoid's test on the inner side immediately under the attachment of the female's snout. It is interesting that continuous extrusion of the female parasite's proboscis through the rectal wall and intermittent penetration of it by the male's proboscis seems to do little or no damage and to provoke no tissue reaction on the part of the host.

## Hosts: Distribution and Habitat

Smith (l.c.) simply stated that his specimen of *R. cernica* parasitized "an *Echinus*". Although the Linnean concept of *Echinus* as a genus comprising all echinoids had been considerably refined by the time Smith wrote, the name persisted as a convenient vernacular for an unidentified echinoid, particularly those belonging to the order Echinoida (= Camarodonta), and its plural, Echini, for the class as a whole for many years. It is possible, then, that Smith was using it in this way. No species of *Echinus*, as the genus is defined today, occurs at Mauritius (Mortensen, 1943), but a species of *Echinometra*, *E. mathaei*, is quite common around the island (actually it is properly the *oblonga* form which occurs there (Mortensen, 1943)).

The taxonomy of the Pacific species of *Echinometra* appears confused:

*E. mathaei* is widely distributed in the tropical and subtropical Indo-W Pacific area, being mainly littoral (but at least to 34 m). It occupies a variety of habitats (particularly rocky); sometimes in the open, sometimes partly hidden under rocks and ledges and sometimes deep in holes or crevices (Mortensen, 1943; Kelso, 1970, unpublished; Clark & Rowe, 1971). There is little movement of individuals from an established position (Khamala, 1971).

Whether this species extends into the Eastern Pacific depends on the status accorded to *E. oblonga* (de Blainville), since it is the latter which occurs there (at Clarion, Socorro and the northern Galapagos Island). While Mortensen considers the two as varieties (with a similar Indo-W Pacific distribution), Clark (1948) concludes that *oblonga* is gradually differentiating into a distinct species and, in the Eastern Pacific, has attained such distinction. Kelso (1971) also decided that the species were separate in Hawaii.

A similar problem exists in deciding the distribution of *E. insularis*, because of uncertainty about its relation to *vanbrunti* A. Agassiz. Mortensen treats these as separate species, with *insularis* ranging from Easter Is to Socorro, the Galapagos and possibly Cocos Is; *vanbrunti* from central California to Peru, including the Pearl Island, with Cocos and the Galapagos as possibilities. Clark thought the fact that none of his specimens from Clarion, Socorro or the Galapagos Islands were *insularis* "justifies the suspicion that that supposed species is not really valid" (it should be remembered that he was its author). However, in a paper soon to go to press, Mr. F. J. Fell (University of Maine), who has reexamined the extant type material of *insularis*, shows that this species is restricted to Easter Is.

Dr. Pawson informs us that, in his opinion, the relation of *insularis* to *mathaei* is uncertain at present, but there are some grounds for considering the former to be a junior synonym of *mathaei*.

These changes make for a much simpler distribution-pattern of the species. The closer identity of *insularis* with *mathaei* also helps to explain the host-preference of *R. cernica*.

At Easter Is *E. insularis* is very abundant, occupying individual holes in the surf-swept lava rocks on all coasts. Specimens are densest at mid-tide level on the lee side of the island, where large stretches may resemble honey-combs.

Another echinometrid, probably *Echinostrephus molaris* (de Blainville), is also common in the same habitat but usually subtidal and in places with slightly more protection, such as the sides of the deeper rock-pools. Since they live in close-fitting tubular holes 15–20 cm deep and have long sharp spines on the outer side, they are relatively inaccessible, and none were sampled.

Near parasitized *Echinometra* at Easter Is, a few specimens of the following urchins also were examined, with a negative result: *Diadema savignyi* Michelin, occasionally occurring in the open pools, and *Tripneustes gratilla* (L.) from rocky algal flats further offshore.

Because of *R. cernica*'s association with Pacific species of *Echinometra*, we may

note that there are 2 warm-water Atlantic species of this echinoid genus, *lucunter* (L.) and *viridis* A. Agassiz, which occupy habitats similar to those in the Pacific.

On the other hand, in several recent studies, the internal organs of various species of *Echinometra*—particularly from the Pacific—have been examined, for other purposes but under conditions which suggest to us that *Robillardia* would have been seen if it had occurred. The data are:

*E. mathei* s.l.

RED SEA: Gulf of Suez and NW Red Sea; ca 850, 40–69 (53) mm, May 65–Apr. 67 (Pearse, 1969).

Gulf of Suez; 20, 60–90 mm, Jun. 70 (comm. by J. M. Lawrence).

S Sinai; 30, 30–50 mm, Mar. 70 (comm. by J. M. Lawrence).

Elat; 120, 16–52 mm, Nov. 69–Mar. 70 (comm. by J. M. Lawrence).

Ras Burka, Gulf of Aqaba; 10, 37–52 mm, Feb. 70 (comm. by J. M. Lawrence).

KENYA: Diana Beach; 157, 14–61 mm, Apr.–Sep. 70 (Khamala, 1971).

MALDIVES ISLANDS: Male Atoll; 10, Nov. 64 (Pearse, 1968).

AUSTRALIA: Rottneest Is, W. A.; 290, 40–67 (52) mm, Apr. 65–Jun. 67 (Pearse & Phillips, 1968).

Heron Is, Gt Barrier Reef; 20, Apr. 65 (Pearse, 1968).

BORNEO: Darvel Bay, Sabah; 21, 31–51 mm, Feb. 65 (Pearse, 1968).

JAPAN: Seto Mar. Lab.; > 500, 5–47 mm, Feb.–Sep. 67 (Tahara & Okada, 1968).

NEW BRITAIN: Rabaul; 35, 20–38 mm, Feb. 65 (Pearse, 1968).

SOLOMON ISLANDS: Kieta, Bourgainville Is; 24, 32–45 mm, Mar. 65 (Pearse, 1968).

Honiara, Guadalcanal Is; 21, 23–38 mm, Mar. 65 (Pearse, 1968).

NEW HEBRIDES: Vila, Efate Is; 16, 23–43 mm, Mar. 65 (Pearse, 1968).

NEW CALEDONIA: Nouméa; 25, 23–28 mm, Mar.–Apr. 65 (Pearse, 1968).

near Yaté; 8, 45–64 mm, Apr. 65 (Pearse, 1968).

FIJI: Viti Levu; 43, May 65 (Pearse, 1968).

SAMOA: Pago Pago, Tuitilla Is; 20, Jul. 64 (Pearse, 1968).

MARSHALL ISLANDS: Eniwetok Atoll; 28, Jul. 63 (Berger, 1964). 27, 21–69 gm wet wt, Aug. 68 (comm. by J. M. Lawrence).

HAWAII: Kapapa Is and Black Point, Oahu; 440, 14–60 mm, Jan. 67–Jan. 69 (comm. by D. P. Kelso).

*E. vanbrunti*

PANAMA: City; 34, Jan.–Feb. 63 (Berger, 1965).

Pta Paitilla; 550, 16–50 gm wet wt, Jan. 68–Jul. 72 (comm. by P. W. Glynn).

MEXICO: Acapulco; 25, 42–70 mm (comm. by J. S. Pearse).

Capo San Lucas, Baja California; 35, 59–78 mm, Nov. 63 (comm. by J. S. Pearse).

Bahia Tortola, Baja California; 5, 130–165 mm, Nov. 63 (comm. by J. S. Pearse).

GALAPAGOS ISLANDS: Academy Bay, Santa Cruz Is; 24, 33–57 mm, Sep. 63 (comm. by J. S. Pearse).

*E. lucunter*

FLORIDA KEYS: 200–300, 25–65 mm, Jan. 65–Aug. 66 (McPherson, 1969).

BARBADOS: 200, 8–70 mm, Oct. 65–Sep. 66 (comm. by Doran).

PANAMA: Galeta Pt., C. Z.; 520, 10–40 gm wet wt, May 68–Jul. 72 (comm. by C. Glynn).

*E. viridis*

FLORIDA KEYS: 200–300, 25–65 mm, Jan. 65–Aug. 66 (McPherson, 1969).

### Comparison with other Parasitic Gastropods

Several genera of gastropods have been recorded living on the skin between the spines, or within cysts in the spines, of regular sea urchins (Franc, 1968), but *Robillardia* is the only one now known to occupy the interior.

Those features which particularly characterize *Robillardia* as compared with other parasitic gastropods from echinoderms of the same level of organization can be summarized as follows:

1) The foot has retained a primitive structure forming a well-developed creeping sole. This is actually a unique feature, since in parasitic forms the foot tends to become vestigial or has been modified into a fleshy non-locomotory appendix to the body.

2) A pseudopallium, a structure characterizing the Stiliferidae (*Stilifer*, *Megadenus*, *Paramegadenus*, and *Asterophila*), is absent.

3) Most of the body is wrapped in skin folds which arise from the foot and, to a less extent, the head region. They could be compared with the fold (mainly of pedal origin) which, in the Pelseneeridae (*Pelseneeria* and *Parastilifer*), envelops the shell (Rosén, 1910). However, those of *Robillardia* are much more extensive and elaborate and serve several purposes (protection of shell and egg cases, inspiration of respiratory water).

4) A muscular pharynx may occur in some Stiliferidae and Pelseneeridae, but an acrembolic proboscis as well as the accompanying proboscis gland are absent in these.

5) The sexual apparatus shows great resemblance to that of the Stiliferidae and there are indications that *Robillardia* resembles *Stilifer* in being a consecutive hermaphrodite. It seems advisable, however, not to lay too much emphasis upon the latter point, since several other parasitic gastropods with diminutive males, when more adequately studied, may well turn out to be consecutive hermaphrodites. But in the Pelseneeridae and *Goodingia* (Lützen, 1972b), which are simultaneous hermaphrodites, the reproductive organs differ distinctly from those of *Robillardia*.

We would like to suggest, however, that the ancestor of the family Paedophoropodidae, might well be a type closely similar to *Robillardia*. This family comprises two species: *Paedophoropus dicoelobius* Ivanov 1937, found in the Polian vesicles or in the respiratory organ of the holothurian *Eupyrgus pacificus* Östergren; and *Molpadicola orientalis* Gruzov 1957, parasitic in the body cavity of the holothurian *Molpadia* sp. The sexes are separate, the male being substantially smaller than the female and provided with a very large penis. Both sexes possess a long proboscis which is applied to the alimentary canal of the host. The foot is sole-shaped in *Molpadicola*, and reduced to a small lump in *Paedophoropus*. In both it is produced into right and left lateral lobes, which in the female *Paedophoropus* join along the mid line, forming a large sac, opening

ventrally, within which the embryos are incubated. The structure of the reproductive apparatus in both sexes is very similar to that of *Robillardia*. Further comparisons are difficult, since the two species are considerably reduced in several respects; thus, a shell, gills, and ocelli are lacking, the visceral mass is not spiral, and the mantle cavity is reduced to a diverticulum with an orifice for the kidney.

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PLATES

PLATE I

*Robillardia cernica* Smith

Figs. 1-4. Male seen from in front, in oblique left view, in dorsal aspect, and from the left. Scale 1 mm.

Fig. 5. Female. Scale 2 mm.

Fig. 6. Shell of veliger in apertural view. Scale 100  $\mu$ .

Fig. 7. Mucro of male. Scale 200  $\mu$ .

Symbols

- 1, brood pouch
- 2, foot
- 3, opening of anterior pedal gland
- 4, opening of posterior pedal gland
- 5, penis
- 6, siphon
- 7, skin fold of left side
- 8, skin fold of right side
- 9, snout
- 10, tentacle

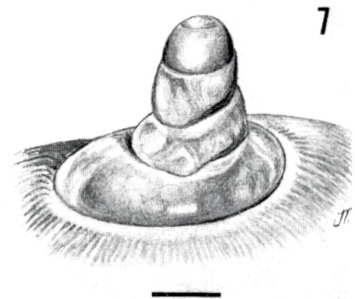
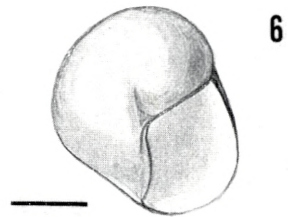
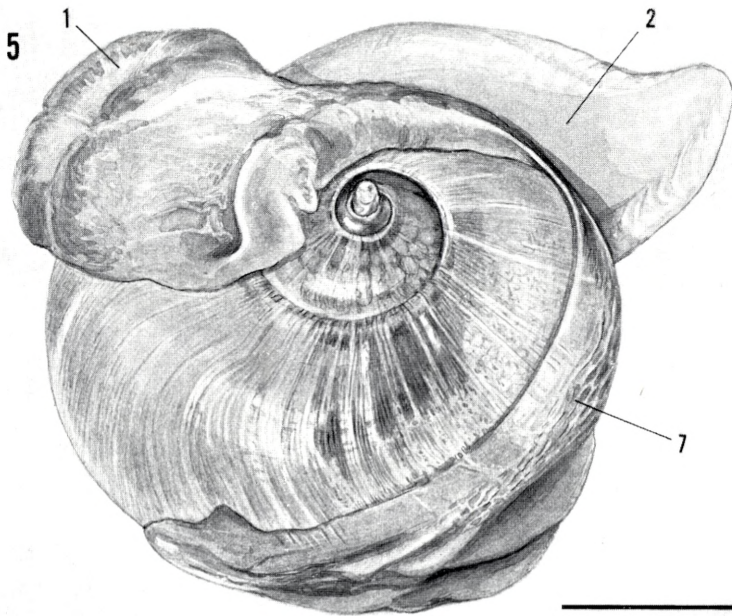
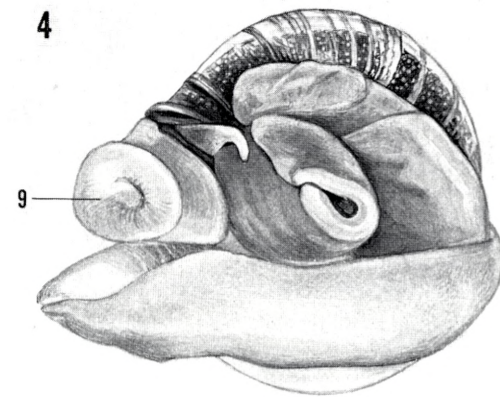
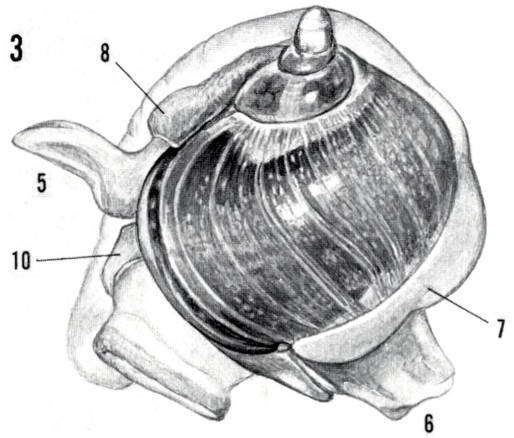
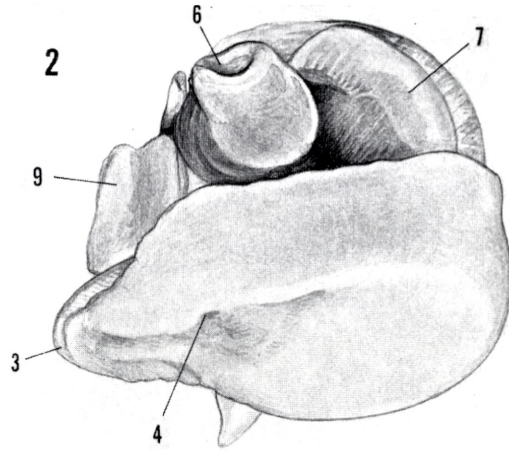
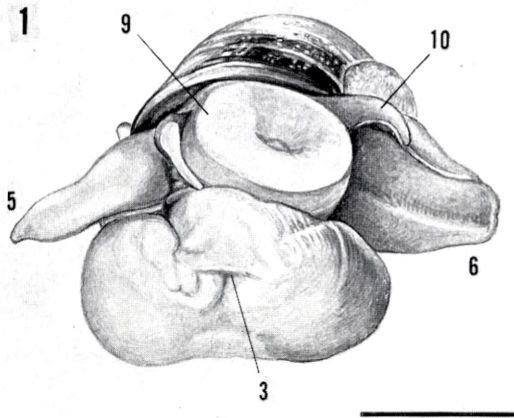


PLATE II

*Robillardia cernica* Smith

Fig. 8. Female, shell removed by decalcification. Scale 2 mm.

Fig. 9. Ovigerous female, shell removed by decalcification. Scale as above.

Symbols

- 1, albumen gland
- 2, brood pouch
- 3, capsule gland
- 4, digestive gland
- 5, egg capsules
- 6, foot
- 7, gill
- 8, kidney
- 9, pericardium
- 10, siphon
- 11, skin fold of left side
- 12, skin fold of right side
- 13, snout

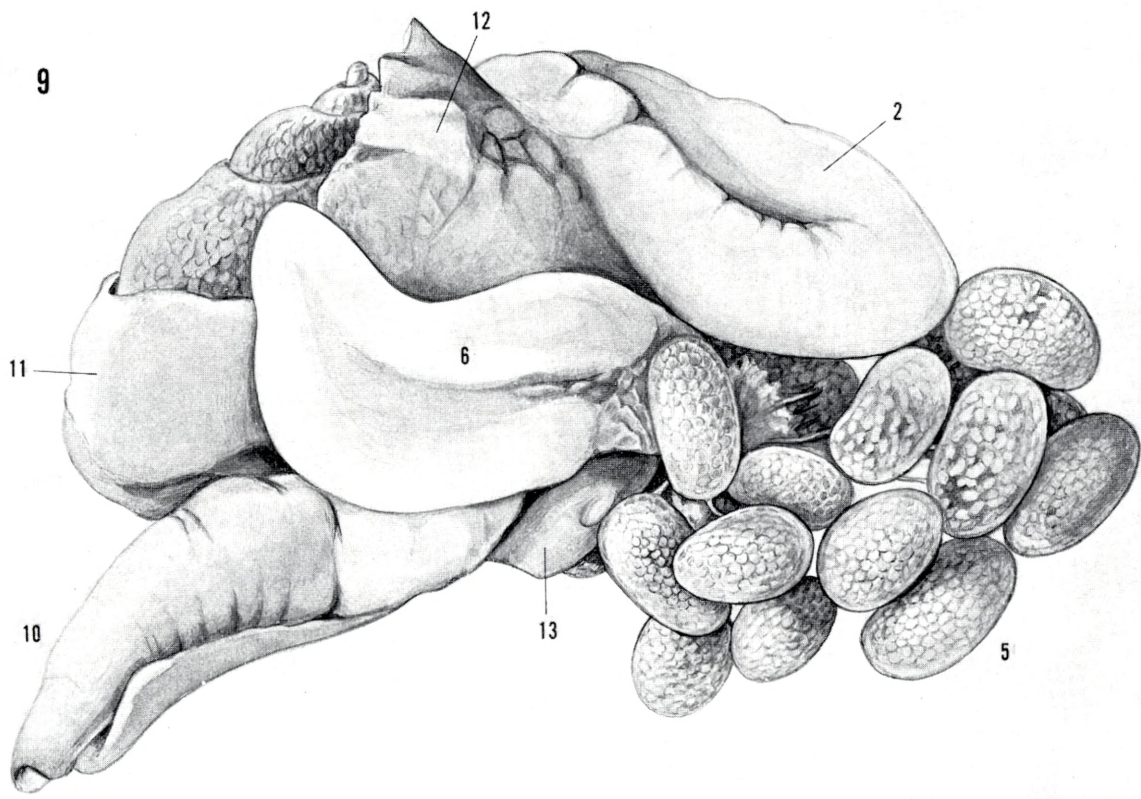
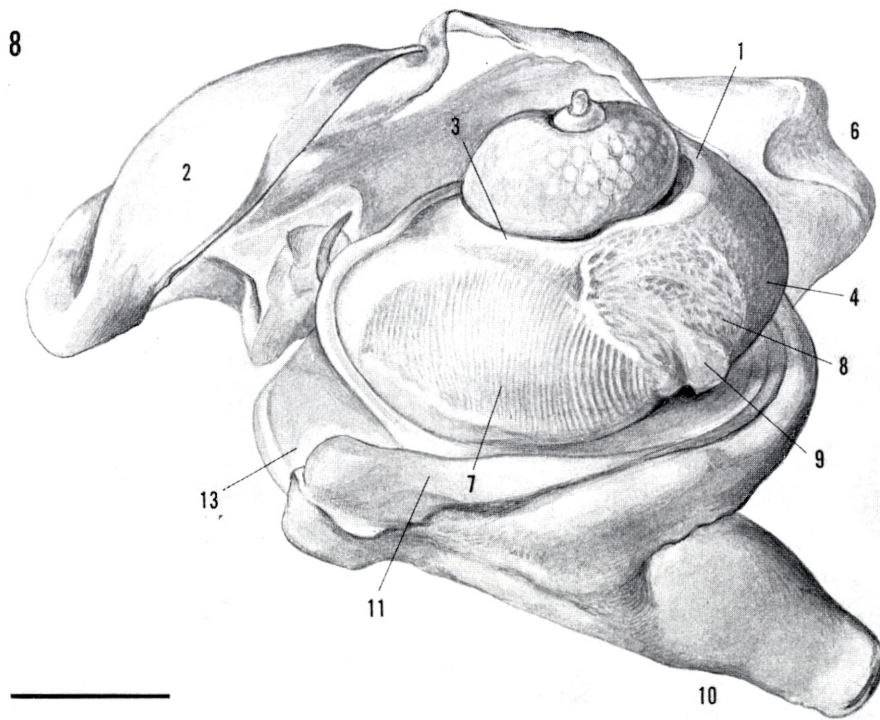


PLATE III

*Robillardia cernica* Smith

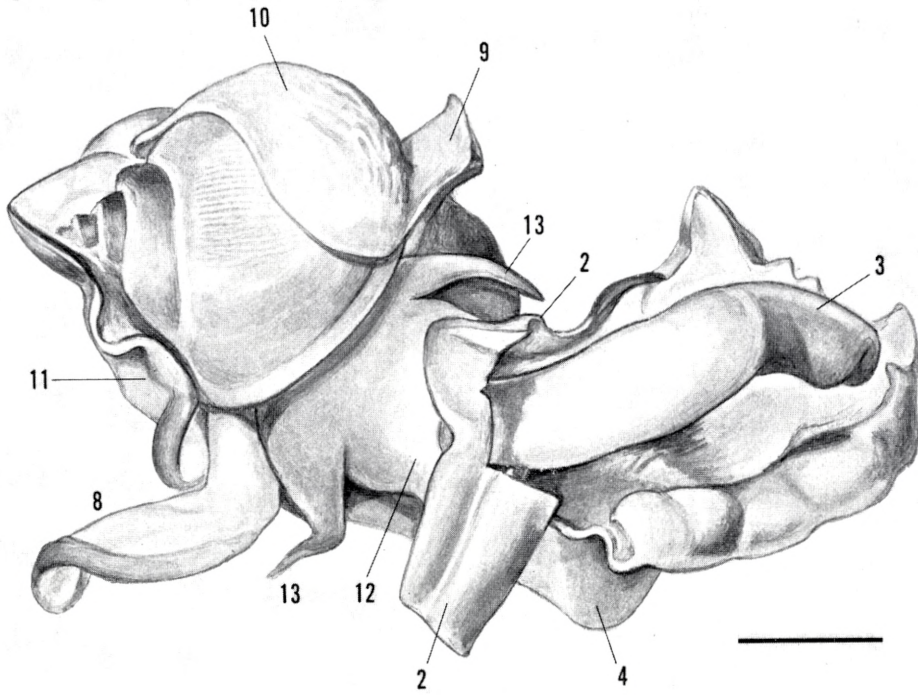
Fig. 10. Male in dorsal aspect, shell removed by decalcification. Scale 1 mm.

Fig. 11. Female seen from the under side, shell removed by decalcification. Scale 2 mm.

Symbols

- 1, anterior portion of proboscis sheath, everted
- 2, collar of host's rectal wall, enveloping  
base of proboscis
- 3, extended proboscis
- 4, foot
- 5, mucus, secreted on the snout by the anterior  
pedal gland for attachment of egg capsules
- 6, opening of anterior pedal gland
- 7, opening of posterior pedal gland
- 8, penis
- 9, siphon
- 10, skin fold of left side
- 11, skin fold of right side (brood pouch in female)
- 12, snout
- 13, tentacle

10



11

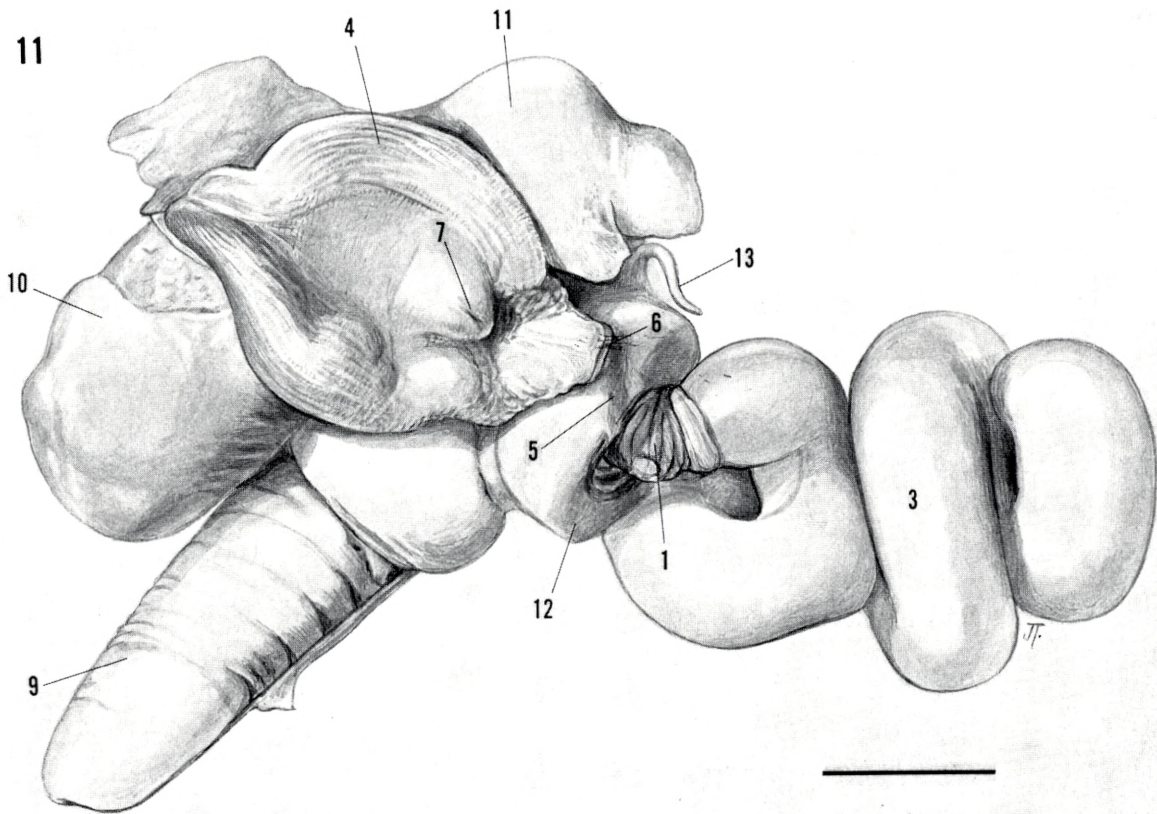


PLATE IV

*Robillardia cernica* Smith

Longitudinal sections through ovigerous female. Celloidin, 30  $\mu$ , tetrachrome. Scale 1 mm.

Symbols

- 1, albumen gland
- 2, anterior pedal gland
- 3, anterior tip of foot with opening of  
anterior pedal gland
- 4, capsule gland
- 5, digestive gland
- 6, foot
- 7, gill
- 8, glandular folds present in female
- 9, kidney
- 10, mantle skirt
- 11, oesophagus
- 12, opening of proboscis sheath
- 13, ovary
- 14, pharynx
- 15, posterior pedal gland
- 16, proboscis gland
- 17, proboscis gland (anterior narrow part)
- 18, proboscis sheath (retracted)
- 19, skin fold of right side
- 20, snout



