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NEW ARCHAEOGASTROPOD LIMPETS FROM HYDROTHERMAL VENTS; SUPERFAMILY LEPETODRILACEA
II. ANATOMY

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CONTENTS

The anatomy of nine species (two genera) of lepetodrilacean limpets is described and the mode of life deduced therefrom.

The unique action of the odontophore sets them apart from all prosobranchs yet known: its initial ventral movement is all but suppressed and the dorsal movement, before withdrawal, exaggerated. This action is facilitated by the freedom of the odontophore from the restraining action of the snout which is controlled by special cephalic levator and retractor muscles. Evidence indicates that the jaws are used as scrubbers, loosening particles from the substratum over the animal's head which are then collected by the specialized rhipidoglossate radula. This is the only method of feeding in the more primitive of the two genera, *Gorgoleptis*, in which the possession of a metapodium with an operculum indicates that the transformation to the limpet form is incomplete. All members of the superfamily have a single left gill typically bilamellate and with a pectiniform skeleton. The dorsal (left) lamellae are reduced in number and size, particularly in *Lepetodrilus* (lost in *Lepetodrilus ovalis*), and the ventral (right) ones exaggerated and their numbers increased with the enlargement of the mantle cavity. Although the ciliary bands on the lamellae of *Lepetodrilus* are as in other prosobranchs, at the tips of the lamellae the frontals and abfrontals expand to form pads and the laterals encircle the tips between them. This unusual modification relates to suspension feeding: the two methods of feeding may proceed concurrently.

The nervous system has a high degree of fusion of the postcephalic ganglia. The pedal ganglia are large, their short commissure continuous with a pleural commissure, and the supra- and suboesophageal ganglia are contiguous with the right and left pleurals respectively. Nerves to the mantle and foot are compound.

The epipodium is well developed, confined to the region of the foot in *Gorgoleptis* and with elongated tentacles, but spreading on to the head and forming a fold surrounding the base of each cephalic tentacle in *Lepetodrilus*, which has shorter tentacles round the foot; cilia on the right cephalic fold pass particulate matter from the mantle cavity to the mouth. The penis of *Lepetodrilus* is also of epipodial origin as opposed to its development from the left side of the snout in *Gorgoleptis*. In both genera a right pallial tentacle is associated with the exhalant passage from the mantle cavity, though this is greatly reduced in *Lepetodrilus*.

The shell of *Gorgoleptis* species indicates that these limpets have followed a different evolutionary course from that of *Lepetodrilus* in that the columellar lip remains as an integral part of the peristome. In species of both genera the mantle edge has two folds, the inner probably represents the fusion of the inner and middle folds of zeugobranch limpets: the remoteness of the periostracal and shell secreting areas results in an inturned band of periostracum particularly broad in *Lepetodrilus* species. In each, the shell muscle is approximately bilaterally symmetrical, but details of its constituent parts, pedal and pallial, differ. In addition to the bilamellate gill and epipodium, the alimentary, circulatory, nervous and excretory systems indicate that relationships are at the archaeogastropod level. Although similar to the trochaceans, these limpets differ from them in a number of respects.

The reproductive system approaches that of monotocardians in the length of the gonadial duct, which in the male is a vesicula seminalis; in the separation of that part of the right kidney through which gametes pass to the urinogenital opening; in the presence of a prostate and penis in the male, and in the female *Lepetodrilus* of a receptaculum seminis. The female has no hypertrophied pallial oviduct, and eggs with no secondary investments are apparently fertilized in the mantle cavity, and then shed.

Although the anatomy of *Neomphalus* indicates that it had a different origin and evolution from the more conservative lepetodrilaceans, all these prosobranchs share a common characteristic in the attainment of the limpet form by having a narrow section between the enlarged head and the visceral mass marked by the end of the oesophageal pouches and tight chiastoneury.

INTRODUCTION

Limpets are one of the most abundant invertebrate groups in the rich biomass of the east Pacific vent communities, occurring on bushes of *Riftia* tubes, on basaltic substrata and in sulphide particle deposits at the foot of chimneys (Desbruyères & Laubier 1983). A rich source of food is available both in suspension (Corliss *et al.* 1979; Karl *et al.* 1980) and as mats of microorganisms on substrata in the vicinity (Jannasch & Wirsen 1981). In 1983, undescribed limpets were assigned to three groups, referred to as A, B and C (Hickman 1983) on the basis of radular structure. A study of their external features indicated that the functional anatomist would find the second group, previously called the dimorphs (McLean 1985), the most rewarding. These preserved animals were not all deeply contracted into their shells. Some showed the odontophore at various stages of protrusion, even with food on the modified rhipidoglossate radula, and through the semitransparent mantle the specialized gill could be seen. Moreover, it was hoped that anatomical studies might indicate the necessity for the exceptionally conspicuous penis.

The source of the animals has been given in McLean (1988) (hereafter referred to as part I). Specimens were fixed at normal atmospheric pressure in formalin (10% by volume) in seawater, neutralized with sodium borate, except for *Lepetodrilus fucensis* in which the pH was controlled by phosphate buffer. After fixation for at least 24 h they were thoroughly rinsed in freshwater to remove the salts, and then transferred to ethanol (70% by volume). Their anatomy was studied by dissection with the help of a stereomicroscope and wholemounts stained in haemalum. More detailed information was obtained from serial sections 12–15 μm thick, stained in either haematoxylin and eosin or azan; the fixation allowed only limited histological detail to be investigated. Whole animals and parts dissected from them were examined in a Cambridge SM4 scanning electron microscope. For some species the number of specimens available was extremely restricted, in which case this is mentioned under the species description.

The anatomy of *Lepetodrilus pustulosus* is described and only important differences between this and the other five species of the genus are given. For the second genus, *Gorgoleptis*, the number of specimens of *emarginatus* allowed anatomical investigation to be moderately complete, but comparison with the other two species, *spiralis* and *patula*, was limited.

ANATOMICAL DESCRIPTIONS

Lepetodrilus pustulosus

External features

The snout is extensile, broad and truncated with the oral surface directed ventrally. The mouth is a longitudinal slit bifurcating dorsally with the lips surrounded dorsally and laterally by a rim (figure 4*a*) that is rich in sensory cilia. The tentacles arise laterally at the base of the snout and may extend well beyond the shell margin or contract to less than half this length. Their longitudinal muscles, better developed than the outer circular ones, are grouped in a dozen or so bundles surrounding a blood space and a stout central nerve, each bundle isolated by a sheath of connective tissue. The surface of the tentacle has numerous groups of sensory cilia (figure 26, plate 1), arising from pits into which they may be withdrawn, and to which pass branches from the main nerve; at the base of the pits are openings of glands. There are no eyes.

The base of each tentacle is encircled, except medially, by a glandular fold, and a band of ciliated cells encircles the right fold. At its median limit the ventral part of the fold around the right tentacle of females recurves and abuts against a lobe of the epipodial fold passing forwards from the foot (figure 4*b*): in males the fold does not recurve and the anterior end of the epipodium takes a more ventral course to end beneath the snout; it expands near the base of the tentacle to form the penis (figures 4*a* and 5). The contractility of the head is indicated by the deep transverse furrows on its walls; it would appear to be capable of extending well beyond the shell margin.

The sole of the foot is ovate. Anteriorly, a double edge indicates the opening of the anterior pedal gland passing back on each side for approximately half its length. The epipodium forms a fold set towards the dorsal limit of the foot laterally and posteriorly and bearing three pairs of outgrowths, the first and last tentacular and extensile, the second apparently truncated; its extension on to the left side of the head in both sexes is insignificant compared with that on the right. The fold is broadest anteriorly at the opening to the mantle cavity where its anterior edge is recurved ventrally, whereas laterally is the most anterior tentacle which has a sense organ at its base (figure 3*b*). This organ is a raised area where nerve fibres pass between tall epithelial cells, and it resembles the epipodial sense organs of *Fissurella costaria* (Haller 1894). All the epipodial outgrowths are covered by stereocilia, most numerous at the tips. In a few specimens the tentacular ones extended slightly beyond the shell margin, but in most they were fully contracted.

The shell muscles, homologous with the columellar and pallial retractor muscles of coiled gastropods, have right and left longitudinal limbs, each broadest anteriorly, the left somewhat larger than the right (figures 1*a* and 2). Their origins lie well in from the growing edge of the shell, which gives the muscle an increased mechanical advantage. They are joined posteriorly by a narrow band of muscle continuous with the lateral part of each. The band is made up of fibres of the right and left pallial retractors (figures 1*b* and 2) which attach posteriorly on the shell, others from the posterior pallial edge passing forwards to attach and a few from the foot.

The free edge of the mantle skirt, which encircles the animal, has two folds: the inner, the broader, has a band of epithelial glands covering its ventral wall, small tentacles at the free edge, and dorsally, near its base, a shallow groove where the periostracum is secreted; the outer, deep and narrow, lies under the newly formed periostracum (figure 23, plate 1), between this and the overlying shell, though free from both (figure 3*b*). Distally the outer fold is double – though this is not apparent in very small individuals – and whereas the narrow inner part may manipulate the periostracum as it is secreted, the outer, more muscular, secretes the growing edge of the calcareous part of the shell; it has some ciliation on its ventral wall. In most limpets the pallial folds were contracted away from the growing edge and in some the periostracum was torn from its origin. The pallial muscles arise at the level of the outer and anterior edges of the shell muscle (figure 19*d*). The bulk of the fibres pass to the inner pallial fold and are associated with a complex array of nerves, many relating to the circlet of tentacles at its edge. The tentacles, which have been seen only in a contracted or semicontracted state, have their tips covered by cells bearing microvilli. Median to them in the region of the exhalant passage from the mantle cavity arises an isolated tentacle, short and contracted (figure 4*b* and figure 36, plate 3).

The mantle cavity is shallow, but extends nearly four fifths of the body length, occupying the

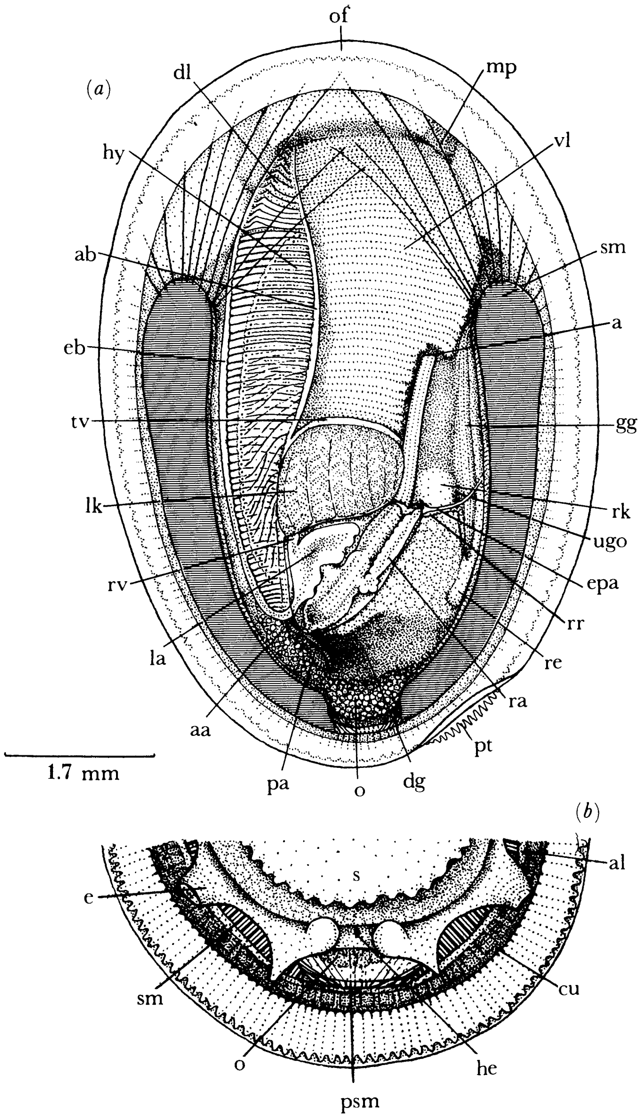

FIGURE 1. *Lepetodrilus pustulosus* female. (*a*) Dorsal view. (*b*) Ventral view, posterior end.

breadth of the shell anteriorly and restricted by the shell muscle more posteriorly (figures 1*a* and 2). Posteriorly, it approaches the summit of the visceral mass, underlying the left kidney and part of the right one, the left auricle, the anterior part of the ventricle and the rectum. It extends more posteriorly on the left where the posterior gill filaments underlie the heart. The posterior part of the ventricle with part of the digestive gland lie at the summit of the visceral mass; in young individuals the gland extends into the shell apex and later withdraws. The rectum passes through the ventricle and leads forwards within the mantle skirt to open to the right side of the mantle cavity about halfway along its length.

The bulk of the mantle cavity is filled by a large left gill, mostly monopectinate (figure 1*a*); its narrow axis is fused to the mantle skirt except for the tapering anterior fifth where the gill is free and bipectinate. Its axis lies horizontally and the dorsal lamellae are small and relatively inconspicuous (figure 30, plate 2). The free tip of the axis bears very long cilia and even longer sensory processes projecting forwards from the mantle cavity. Behind the tip the ventral lamellae extend across the breadth of the cavity anteriorly, their length exceeding ten times their depth, but they shorten posterior to the anus; they separate a ventral inhalant chamber from a dorsal exhalant one into which the faeces are discharged. The afferent and efferent branchial veins of the monopectinate part of the gill are widely separate, but this does not correspond with the breadth of the gill axis because between them lies the hypobranchial gland composed of tall, epithelial secreting cells and interspersed ciliated cells; in large individuals the epithelium is slightly folded. Vessels of small dimensions pass through the gland from the afferent branchial vein, each entering a gill lamella not far from the gill axis (figures 1*a* and 2).

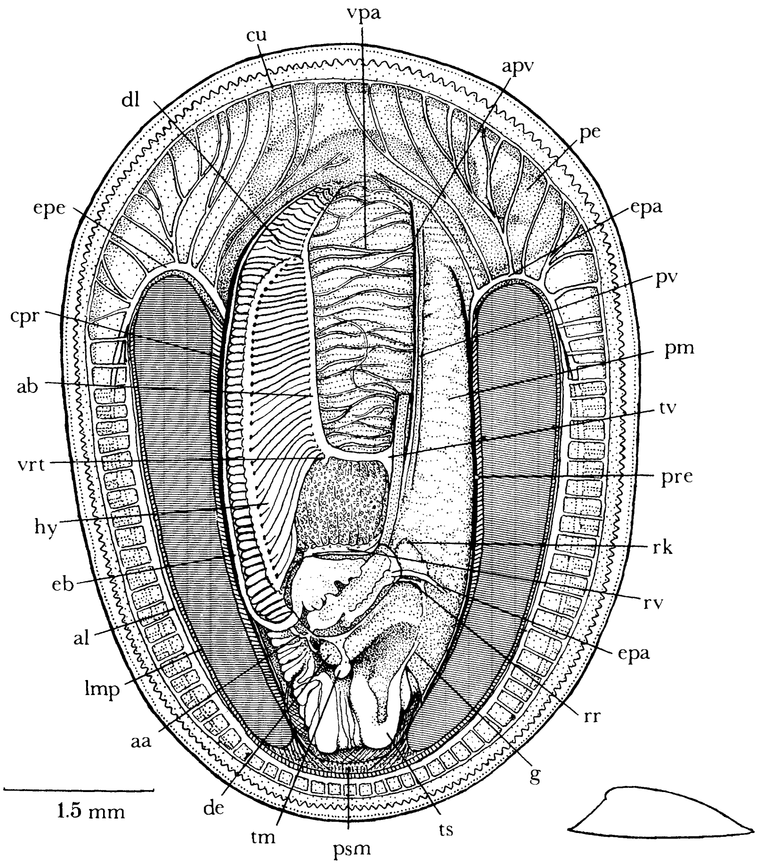

FIGURE 2. *Lepetodrilus pustulosus* male, dorsal view; the pallial vascular system was well displayed in this individual. Bottom right, outline of right side of shell.

The ctenidial skeleton is pectiniform: the skeletal rod supporting the frontal surface of each lamella fuses with, and so strengthens, the axial rod; the skeleton of the reduced dorsal lamellae forms a minute accessory comb. The basal third of each lamella is thickened by the rod and by tall columnar cells bearing very long lateral cilia which border the efferent branchial vein. This vessel is strengthened by septa passing dorsally from the rod. Elsewhere, except along the course of the afferent branchial, the lateral walls are thin and puckered. The free tip of each lamella related to the exhalant passage from the mantle cavity has a unique elaboration. The bands of cilia, frontals, abfrontals and laterals run as in other prosobranchs, but at the tip frontals and abfrontals expand to from large ciliated pads, and the laterals encircle the tip between the two (figures 27, 29 and 32, plate 2). The epithelial cells of the lamellar tip are tall, glandular, with muscle fibres penetrating between the cells of the pads; their cilia, to which particles less than 4 μm diameter have adhered, are fine and may attain three times the height of the cells (figure 7*b*) (in preparations for scanning electron microscopy (SEM) these cilia were damaged). The tips dip ventrally to a ciliated tract conspicuous along the dorsal body wall anteriorly and on the right side of the head; in a number of limpets particles embedded in secretion, presumably hypobranchial, were most frequently associated with the band of cilia between the pads. The majority of these particles were identical with prokaryotic cells of the microbial mat covering the surfaces exposed to vent plumes, and others were apparently stalks of *Hyphomonas*-like organisms (Jannasch 1984; Jannasch & Wirsen 1979).

The osphradium is a raised strap-shaped band curving around the anteromedian border of the left limb of the shell muscle and extending back a short distance beneath the gill axis. Its ganglion is large and in some areas separated by blood spaces from the nerves running to its sensory epithelium.

Internal anatomy

The pedal glands and retractor muscles. In many specimens the sole of the foot appears as a sucker with a broad peripheral rim surrounding a cavity (figure 5). The rim is the ventral wall of a thick flange with its own muscles and not served by the shell muscle. It is distended by blood and the surface applied to the substratum is ciliated. The periphery is remarkably glandular: the anterior pedal gland opens around the anterior half and more posteriorly ducts open from scattered subepithelial glands. The staining properties of the cells of the anterior gland indicate that their secretion is different from that produced elsewhere by the foot: it is in the form of minute protein spherules whereas glands opening to the periphery more posteriorly respond, though weakly, to stains for mucus. Fibres of the shell muscle pass to the insunken area of the sole: the lateral ones run dorsoventrally to an ipsilateral origin, the median obliquely transverse, decussating in the mid-line to a contralateral origin; median dorsoventral fibres intermingle with the latter. A transverse sheet of muscle passes from side to side across the insunken sole, thickest in the mid-line where it is concentrated beneath the epithelium; laterally the fibres scatter and lie more deeply. Large numbers of gland cells, with a somewhat amorphous secretion, lie in the connective tissue, mainly deeper than the transverse muscles, and open on the insunken sole, which is not ciliated.

The foot is muscular enough to indicate locomotor activity as well as adhesion. When used as a sucker the intrinsic sheet of transverse muscle is seen to be relaxed and the dorsoventral components of the shell and pedal muscles contracted, raising the sole, except at the periphery where they are absent. Fluid pressure beneath the raised area will fall, but the viscosity of the fluid is presumably increased by copious secretion from the sole glands, whereas the peripheral flange will be pressed against the substratum by the higher pressure of the external medium, and so form a seal improved by secretion from its glands.

Median to each lateral limb of the shell muscle is a longitudinal muscle band which is insignificant posterior to the heart. Its narrow posterior end runs adjacent to the shell muscle, along the length of which its fibres originate, increasing in numbers anteriorly. It diverges from the shell muscle and forms a band beneath the dorsal body wall before entering the head where it gives rise to the cephalic levators and retractors of the tentacles and snout.

The alimentary canal. The lateral lips are broad and furrowed transversely when the mouth is closed. Their surface is covered by groups of sensory cilia arising in pits. Some limpets showed the mouth partly opened and with relaxation of the oral sphincter the tip of the odontophore was protruded and a rim of buccal wall everted laterally and dorsally, exposing a pair of dorsolateral jaws (figures 22 and 24, plate 1). Each jaw lies on a crescent-shaped buccal fold alongside the odontophore. On its median face lie numerous rows of chitinous rods, slightly flattened and with pointed tips which diverge from one another on protrusion, when they present the appearance of a brush, and some rods can be seen to be worn and chisel-shaped. During the initial stages of protrusion of the odontophore the eversion of the buccal wall is accompanied by an out-turning of the jaw fold so that the rods project upwards. On full protrusion of the odontophore the jaw is swung back and down so that the rods face inwards and are hidden. The withdrawal and protrusion of the rods must, in part, be related to striped muscles passing to the epithelial cells secreting them. The fact that they are worn indicates that they have an abrasive action.

As the odontophore is protruding the snout is shortened, the tentacles retracted and the head raised by the action of the median longitudinal element of the shell muscle (figure 4*b*). A depression at the inner margin of the lips formed by the attachment of the protractor muscles of the odontophore, marks the outer limit of the everted buccal wall. The dorsal and lateral protractors originate on the snout and pass back as a number of converging strands to insertions on the posterior edge of the right and left posterior odontophoral cartilages, whereas the ventral protractors originating on the ventral lip insert ventrally (figure 3*a*). Their action is synchronized with that of a pair of levator muscles arising on the body wall posterior to the cerebral ganglia and inserted laterally on the anterior third of each anterior cartilage. These cartilages are enveloped posteriorly by the posterior ones which broaden the odontophore.

In other specimens the mouth was more widely open and the odontophore protruded further, often tilted towards the right (figure 5). Its tip then appears as an inverted cone, the apex overhanging the ventral lip and the opening radula spread across the broad base. The conical projection is covered by the subradular membrane, the sublingual pouch becoming everted under its apex. Here the tips of the anterior cartilages lie covered by layers of tough connective tissue from which a few muscles pass to the anterior limit of the radular membrane and the subradular membrane adjacent to that point. These are presumably tensors regulating the relation of one structure to another. Examination of the resting odontophore shows the tips of the cartilages against the membrane immediately beneath the radula, and anterior to them a loosely puckered subradular membrane. This slack area has subepithelial glands beneath which are circular and longitudinal muscle fibres. When the odontophore is protruding and the tips of the cartilages are bent ventrally, the membrane becomes taut, stretching the epithelium and simultaneously flattening the dorsal groove of the radular membrane, so erecting the teeth. The bending of the anterior cartilages, which at this stage of protrusion directs their tips ventrally (figure 3*a*), is effected by broad, ventral, cartilage flexor muscles; posteriorly the cartilages are linked ventrally by chondroid tissue external to which are ventral approximator muscles. The stretching of the subradular membrane depends not only on the ventral swing of the cartilage tips, but also on a surge of blood from the buccal sinus and the action of muscles associated with the subradular membrane. These include the lateral protractors of the membrane originating on the posteroventral surface of each cartilage and running forwards as straps dorsal to the ventral protractors of the odontophore. They insert transversely to the under surface of the membrane, except the most median part where lies a pair of median protractors.

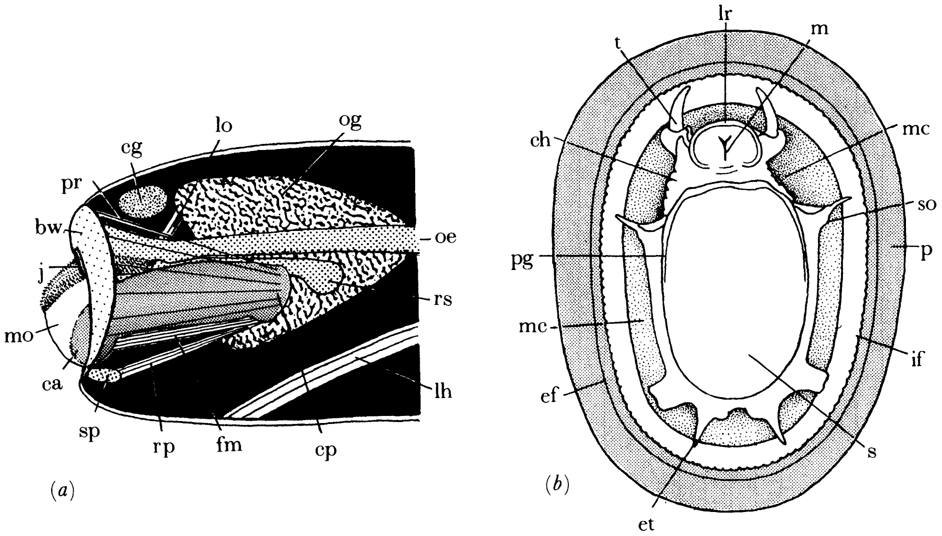

FIGURE 3. *Lepetodrilus pustulosus*. (*a*) Diagram of protruding odontophore and some muscles related to it. (*b*) Female, ventral view to show epipodium and most recently secreted periostracum enclosing contracted outer pallial fold.

It is not uncommon to find limpets with the odontophore partly protruded, but only two showed full protrusion (figures 20 and 21, plate 1). The whole buccal area was everted, giving the appearance of a short proboscis. The radula was resting on the anterior cartilages which apparently had been uplifted by a final forward surge of blood. It grasped a bolus of food which overlay the rachidian teeth with marginals applied to it laterally. All limpets had inevitably been subjected to harsh treatment when removed from their habitat and subsequently, so it was not surprising to find some damage to the exposed tip of the radula; otherwise no injury to the head was apparent.

At certain points tendons limit the forward motion of the odontophore. A buccal tendon on each side runs from the body wall lateral to the levator muscle and joins the outer surface of the cartilage near the anterior limit of its flexor muscle. The two are joined by a transverse tendon lying between the radular diverticulum and oesophagus. This median tendon also extends back for a short distance along the line of closure of the radular sac where it serves for the attachment of muscles related to the sac and the oesophagus.

As soon as the forces maintaining the feeding position cease to act the odontophore assumes the resting position and simultaneously, the cephalic section of the shell muscle relaxes allowing the snout and tentacles to lengthen and the head to lower. Other important muscles brought into action are the retractors of the subradular membrane, which pass back to a posterodorsal origin on the ipsilateral cartilage, and the retractors of the radular sac inserted on its lateral and ventral walls and passing to the posterior wall of the adjacent posterior cartilage.

Along the roof of the buccal cavity are two muscular ciliated folds, deep anteriorly where their free edges rest against the retracted radular teeth. The folds delimit the food channel and lateral to each is an outpushing of the wall into which the short duct of a sac-like salivary gland opens. The epithelium of the pouch and the gland has mucous cells alternating with ciliated cells. The dorsal folds diverge and shallow posteriorly as they continue into the oesophagus. The oesophageal opening and that of the underlying radular diverticulum are wide and shallow, especially the former. Behind this area each dorsal fold overlies a ventral fold of similar

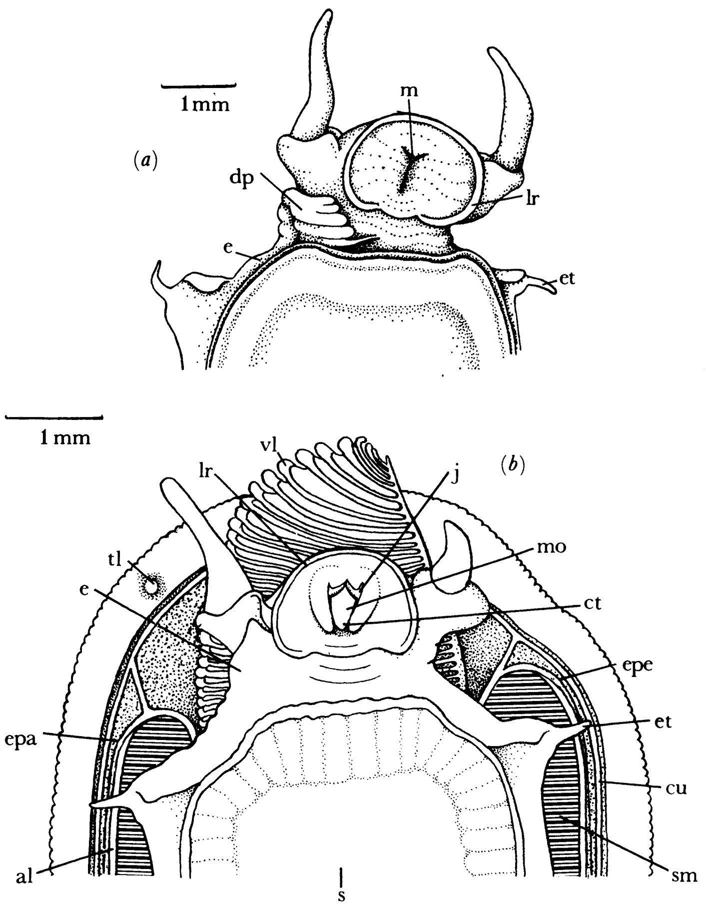

FIGURE 4. *Lepetodrilus pustulosus.* (*a*) Young male to show development of penis from epipodium. (*b*) Female, odontophore beginning to protrude.

size and between them, on each side, is the opening of a large oesophageal gland (figure 6*a*, *b*). The right and left glands extend anteriorly beyond their openings, especially dorsally, where they approach the cerebral ganglia; posteriorly the glands extend to the site of torsion whilst ventrally they spread around the odontophore; behind the posterior end of the cartilages right and left glands meet mid-ventrally. Except near the anterior limits of the glands and where they extend ventrally round the cartilages the epithelium is folded; everywhere it comprises ciliated cells and a single type of gland cell. Anteriorly the lumen of each gland is large because the folds are neither deep nor close-set and between them the wall is sparingly papillate; posteriorly, the folds are deeper and more numerous and some contain thick muscle strands. At the level of the posterior end of the retracted cartilages a complex network of dorsoventral muscle fibres passes through the oesophageal gland on each side, anchoring it to the body wall, and, anterior to this, a short muscle from the posterior end of each posterior cartilage inserts on the adjacent median wall. Still further back, towards the level of the pleuropedal ganglia, the dorsal longitudinal folds converge and, affected by torsion, rotate to the left; the ventral folds are lost and the pouches reduced in size. The right pouch ends and, immediately behind the radular sac, the left swings ventrally to the right and expands to form a blind sac. Meanwhile, the right originally dorsal fold flattens and the left curves ventrally and to the right; on the way it separates the pouch from the posterior oesophagus and forms the ventral limit of the oesophageal opening, the dorsal limit being the flattened right fold.

The posterior oesophagus crosses to the right side of the haemocoel and passes back ventrally between lobes of the digestive gland to open to the right wall of the stomach. The epithelium is ciliated and has goblet cells.

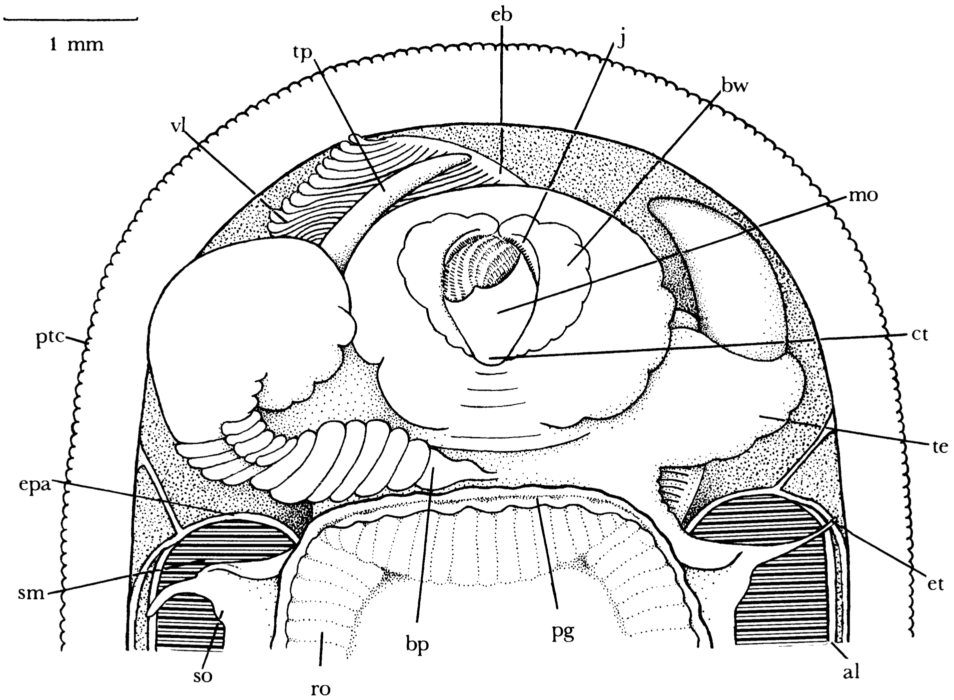

FIGURE 5. *Lepetodrilus pustulosus* mature male with odontophore partly protruded.

The stomach is a relatively small sac embedded in the digestive gland, the intestine leaves it anteriorly (figure 6*a*). At the apex of the stomach the vestige of a spiral caecum has been found, but only in two individuals from the Galapagos Rift (dive 880). The stomach is connected to the digestive gland by three broad openings adjacent to the oesophageal opening where the epithelium is ciliated. Elsewhere most of the gastric epithelium is cuticularized and this area must represent the gastric shield of other prosobranchs. Towards the entrance to the intestine is a shallow ciliated groove bordered by slight typhlosoles, an area corresponding to the style sac, and between this and the cuticle is a ciliated sorting area, often ill defined owing to poor fixation and the distension of the stomach with food. The intestine, surrounded by lobes of the digestive gland, passes from the stomach to describe an anterior loop. It turns back on itself just posterior to the site of torsion and dorsal to the origin of the posterior oesophagus. The posteriorly directed limb extends towards the posterior end of the pericardium and then curves abruptly forwards to pass through the ventricle. The rectum emerges from the right anterior wall of the pericardial cavity and leads forwards within the mantle skirt to open on a short papilla. The intestine is ciliated throughout and produces a mucous secretion which consolidates the faecal matter.

The tubules of the digestive gland are lined by club-shaped cells, with many vacuoles containing homogeneous spherules which are lightly staining and smallest distally. These

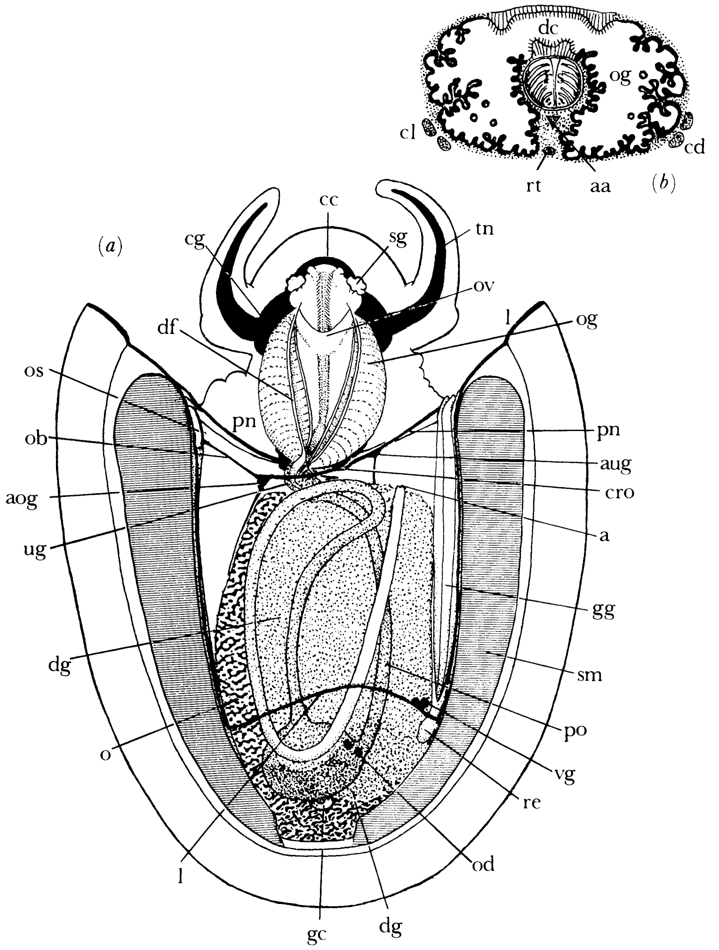

FIGURE 6. *Lepetodrilus pustulosus*. (*a*) Female, dorsal view, stained in haemalum and cleared in cedar-wood oil; mantle skirt removed to show by transparency the alimentary canal, nervous and reproductive systems, omitting renal section; in front of the nerve ring the osesophagus and buccal cavity are drawn as transparent objects revealing their structure and the underlying median radular sac, which lies over and between the radular cartilages. (*b*) Transverse section of oesophagus immediately posterior to radular cartilages; secreting epithelium of the oesophageal glands black.

correspond to the digestive cells of other prosobranchs. Other cells grouped mainly in the crypts of the tubules and forming outpouchings into the haemocoel have broad bases and taper distally. Each contains one or two light brown spherules or larger concretions with an irregular outline. They would appear to be excretory cells: their contents are not infrequent in the faeces. In limpets from the Galapagos Rift obtained from mussel washings the stomach contained indigestible particles including radiolarian and foraminiferan shells, scraps of crustacean skeleton and grit, none of which were found on the gills. All were embedded in mucus. Much of the food had been digested and was unidentifiable except for what appeared to be, from size and shape, cyanobacteria-like trichomes (Jannasch & Wirsen 1979) which may be more resistant to enzymes. Their presence would indicate that the limpet abrades the surface of the microbial mat which covers the mussel shell (Jannasch 1985). Particles loosened, but not collected by the radula, together with bacteria already in suspension, may enter the pallial water stream and be collected by the gill lamellae. The inorganic particles may be too firmly embedded in the mat to be free, or, if freed they sink. The stomach of limpets from *Riftia* washings (21° N) had similar inorganic contents and numerous cut-off pieces of *Riftia* tube of approximately the same size with the bacteria associated with its surface partly digested. In some individuals a continuous faecal rod, indicating the rotary action of cilia and well supplied with mucus, filled the intestine, and lengths of it were discharged into the mantle cavity. Some faeces contained cleaned scraps of *Riftia* tube.

The kidneys. The left kidney, situated wholly within the mantle skirt, is of compact construction (figures 1*a* and 2). It is bordered anteriorly by the transverse pallial vein, posteriorly by the pericardium, on the left by the hypobranchial gland traversed by afferent vessels to the gill lamellae, and on the right by the rectum and that part of the transverse pallial vein running alongside it. The renal epithelium is folded except over the wall of the transverse pallial vein in the vicinity of the rectum, along the ventral wall near the renal opening and the more posterior opening of the renopericardial canal. The epithelial cells covering the folds are cuboidal with long basal processes passing through the blood sinus that underlies them and may penetrate between them: these maintain a resistance to the blood flow through the sac. Long microvilli extend from the free surfaces of the cells and in some places there are clusters of cilia. A thin layer of muscles covering the outer surface of the kidney is attached to the lamina at the base of the folds. There is an anterior and a posterior blood vessel, both short. The anterior is a venous connection with the transverse pallial vein near its junction with the afferent branchial vein, and the posterior connects with the anterolateral wall of the left auricle. Over the dorsal surface of the kidney can be seen fine longitudinal blood spaces associated with the bases of the epithelial folds and these join a transverse vessel along the posterior renal wall which passes to the posterior renal vessel. In the deeper part of the kidney where it abuts the wall of the pericardium the tubular arrangement of its tissues indicates the presence of a nephridial gland, but the fixation does not allow detailed observations.

The right kidney is divided into a small genital part, essentially a conduit, and a lobed sac. One lobe, which opens to the mantle cavity, lies dorsally in the mantle skirt, the others act as a visceral coelom with smooth walls providing a large area in contact with the haemocoel. The urinogenital opening is a longitudinal slit in the right wall at the base of the genital groove (figure 1*a*). The genital part, which shows sexual differences, is lined by ciliated cells and, from the material examined, appears to have lost its excretory function and to have been taken over as the renal section of the genital duct. It passes back from the posterior lip of the urinogenital opening, at first contiguous with the dorsal lobe of the excretory part, and receives dorsally the renopericardial canal from an overlying extension of the pericardial cavity penetrated by the right anterior pallial vein. In males the genital conduit is narrow and closed from the kidney except in the immediate vicinity of the urinogenital opening. It receives the gonadial duct near the opening of the renopericardial canal which is narrower than in females (figure 2). In two females examined the genital part of the kidney had a slit-like opening to the excretory part near the urinogenital opening; in others that were larger it was completely separate. It continues posteriorly to near the level of the receptaculum seminis as a moderately broad duct and receives a narrow gonadial duct. In both sexes the renopericardial canal has cilia that spread on to the pericardial wall around its opening.

The excretory part of the kidney (figures 1*a* and 2) passes back between the rectum and the genital tract and borders the ventral and ventrolateral walls of the pericardium to its posterior limit. Posterior to the mantle cavity lobes of the digestive gland invaginate its posterior wall and its lumen becomes subdivided to form tubules penetrating between the lobes and running back alongside the pericardium: these are the sites of excretory activity. The kidney also extends anteroventrally around the right posterior wall of the mantle cavity and passes forward to ramify through enlarged haemocoelic spaces between lobes of the digestive gland in the anterior part of the visceral haemocoel. The renal epithelium appears to be made up of one type of cell, cuboidal–columnar with a large spherical nucleus, vacuolated cytoplasm and microvilli. The contents of the vacuoles vary, some are unpigmented whereas others are yellowish brown. The vacuoles with their contents are nipped off from the cell apex and accumulate in the lumen of the kidney; sometimes all cell contents are evacuated.

The circulatory system. The pericardial cavity is approximately triangular in dorsal view: the posterior part underlies the shell apex and the anterior abuts the posterior wall of the left kidney and spreads around the rectum on the right. Its left wall is alongside the back end of the right margin of the ctenidial axis and the posterior gill filaments spread beneath it. The ventricle (figure 2) extends obliquely from the posterior angle of the cavity, close to which the rectum enters it, to the proximity of the posteroventral limit of the left kidney. It is bordered on each side by an auricle. The larger left auricle receives the efferent branchial vein posteriorly and anteriorly a short, broad vessel from the left kidney. Posterior to the entry of the efferent branchial vessel fibres originating on the shell alongside the adjacent shell muscle insert on the pericardial wall stabilizing the position of the heart. The right auricle receives only one vessel, the right efferent pallial vein which enters its anterior limit; this vessel is joined near its base by a very narrow connection with the transverse pallial vein. The auriculoventricular opening is on the posteromedian wall of the ventricle opposite the corresponding opening of the left auricle; each is regulated by a valve. Along the paraventricular wall of each auricle are filtration chambers, the primary sites of filtration of the blood (Andrews 1976), which are smaller and more numerous in the right auricle. Muscle strands separate the lumen of the filtration areas from the main part of the auricle.

The pericardial cavity communicates with the left and right kidneys by renopericardial canals lined by an epithelium with long cilia and with glands covering the lips of the funnel at each renal end, which can be closed by a sphincter. Both canals connect with the anterior part of the pericardial cavity; that from the left kidney ventral to the opening of the renal vessel passing to the left auricle, that from the right kidney adjacent to the entrance of the efferent pallial vein.

The ventricle narrows posteriorly to a short bulbus which passes out of the pericardial cavity and divides into anterior and posterior aortae. The posterior aorta leads back beneath the mantle and then ventralwards where it branches to the tissues of the gonad, digestive gland and stomach and then curves anteriorly to supply the right kidney. The anterior aorta curves beneath the pericardium to the floor of the mantle cavity and passes forward under the body wall on the extreme left. Along its course it gives vessels to the viscera. At the site of torsion the aorta curves over the supraoesophageal connective to the ventral side of the gut, passes through the nerve ring and gives rise to the right and left pedal arteries. It continues forward beneath the radular sac in the floor of the cephalic haemocoel between the ventral extension of the oesophageal glands and divides into radular and buccal arteries. The former surrounds the radular sac; the latter passes forward between the protractor muscles of the radular membrane and soon opens into a space within the odontophore, the buccal sinus. The sinus lies between the left and right cartilages, dorsal to their approximator muscles and plays an important role in the protrusion of the buccal mass.

The venous spaces in the head connect posteriorly with paired ventrolateral and dorsolateral sinuses, and, posterior to the pedal commissure, these unite with the pedal sinus to form the cephalopedal sinus or vein. Posteriorly this joins the visceral sinus which passes back between the viscera and foot and supplies blood to the right kidney and the shell muscle which is permeated by fine transverse blood spaces. From the muscle the blood collects in a **U**-shaped vein along its outer edge, the afferent pallial vein (figure 2). There is an alternative route for blood from the visceral sinus: anteriorly on the right a sinus separates from it and leads back towards the posterior end of the mantle cavity. Here, as in trochids, it is joined by the efferent vessel from the right kidney (Fretter & Graham 1962) and blood from both sources flows into a large vein which passes dorsally near the posterior limit of the mantle cavity to enter the mantle skirt; this is the origin of the transverse pallial vein. At its origin tough connective tissue strengthens its walls and projects into the lumen to form a prominent valve which will regulate the flow of blood taking this course. The valve and walls of the vein are innervated by the adjacent visceral ganglion. The vein runs beneath the rectum from right to left, and then forwards along its left wall; it appears as a prominent vessel in the mantle skirt passing to the left parallel with the anterior wall of the left kidney. It then curves forwards to become the afferent branchial vein, but before doing so connects with the kidney. Near the rectum it gives rise to the perirectal sinus, the posterior part of which has the lumen traversed by strands of connective tissue. This sinus continues anteriorly as the anterior pallial vein which vascularizes the mid-dorsal part of the mantle skirt from which blood drains to the afferent branchial or right pallial veins.

The main supply of blood to the mantle originates not from the transverse pallial vein but the **U**-shaped afferent pallial associated with the shell muscle (figure 2). This vein has numerous fine connections with a circumpallial vein at the mantle edge from which efferent vessels supply a left and right efferent pallial vein; the former joins the efferent branchial, the latter takes a course similar to this branchial vein but enters the right auricle. The efferent pallial vessels, especially anterior to the shell muscle, give rise to capillary beds which suggest the importance of pallial respiration.

The reproductive system. Males are distinguished by a large penis arising beneath the right cephalic tentacle and innervated from the labial lobe of the right cerebral ganglion, though in small animals it forms only a broadening of the most anterior part of the epipodial fold (figure 4*a*) which extends on to the right side of the head. In all adult specimens it was contracted into a spiral (figure 5) with a narrow terminal part directed forwards under the anterior tip of the gill. There is a deep, dorsal, densely ciliated seminal groove. The expanded base is also ciliated on the anterior surface and forms the anterior end of the food groove.

In both sexes the gonad is placed ventral to the stomach and intestine, spreading beyond them on the left and posteriorly. Anteriorly it comprises a number of broad tubules which open in the vicinity of the stomach to the posterior part from which the gonadial duct arises. The duct passes to the right posterior corner of the mantle cavity: it is straight in females, but in the male describes a few loops which act as a vesicula seminalis. It opens to the renal section of the gonadial duct already described. The urinogenital opening is at the posterior end of a groove which runs forwards median to the right shell muscle. Details of the groove differ in the two sexes. In males it lies on the mantle skirt and overlies the seminal groove on the penis anteriorly where it faces ventrally. Alongside the rectum the groove is broader and deeper, but its opening is narrower and faces to the right. The pallial epithelium alongside it, especially laterally, becomes glandular and folded to form a prostate which extends from immediately anterior to the shell muscle to a diverticulum posterior to the urinogenital opening (figure 2). The glands are epithelial and eosinophile. The sperm have elongated heads and are deposited in the female in discrete masses embedded in, and surrounded by, prostatic secretion.

The genital groove in the female lies more laterally, at the junction of mantle skirt and body wall, and extends to the anterior end of the adjacent limb of the shell muscle (figure 1*a*). Anteriorly the groove is separated from the tips of the gill filaments by a deep longitudinal fold directed dorsally from the body wall. The fold diminishes in height posteriorly and is replaced by an even deeper longitudinal fold in the mantle skirt, in which runs the rectum surrounded by the perirectal sinus. The epithelium of the groove is columnar, ciliated and sparingly glandular. The development of the subepithelial musculature and the longitudinal folding of the walls indicate that the groove can be considerably distended. Its main breadth alongside the shell muscle leads to a receptaculum, the median part to the urinogenital opening. The receptaculum separates posterior to the opening in most individuals examined, immediately anterior in others. Sperm within the receptaculum are typically orientated with their heads penetrating the epithelium, but there were also a few unorientated sperm in two sexually mature individuals 3 mm in shell length, and other sperm were in the mantle cavity, into which a few eggs had been liberated. Three larger limpets with the receptaculum well filled had eggs in the pallial groove and suprabranchial chamber of the mantle cavity, and sperm, both in prostatic secretion and free, occurred with them. In each individual the freed eggs were few (four to six), heavily yolked and without secondary membranes. All were slightly distorted and their size difficult to assess; large eggs in the ovary had a diameter of 120 µm. This is the only species in which eggs were found in the mantle cavity.

The nervous system. The nervous system is primitive in its general plan and in the fact that nerve cells are not wholly concentrated in ganglia, but spread along the nerves. The cerebral ganglia are ovoid, situated near the base of the cephalic tentacles and linked by a broad commissure which passes around the anterior wall of the buccal cavity ventral to the salivary glands (figure 6*a*). Stout nerves from the commissure innervate the muscles of the anterior buccal wall. Each cerebral ganglion gives nerves to the lips and jaw muscles and a stout nerve to the tentacle which is rich in nerve cells for a short distance from its origin. Posterior to this a large labial lobe extends ventrally and innervates the lips. Short buccal connectives arise from the labial lobes, and from the right lobe a stout penial nerve. Posteriorly each cerebral ganglion gives rise to a pleural and a more ventral pedal connective: both pass back in a small subsection of the cephalic haemocoel, at first lateral and then ventrolateral. Ultimately the two connectives approximate and enter the anterior limit of the pleural and pedal ganglia which, as they enlarge, spread ventrally under the radular sac and fuse, the compound ganglion of one side adjoining that of the other. Each pleural has a ganglion contiguous with it dorsally: the right, the larger, is the supraoesophageal and the left the suboesophageal. Between the suboesophageal and the left pleural ganglia a very stout nerve from the left pallial edge, where it joins a circumpallial nerve, enters and sends fibres to the pedal, pleural and suboesophageal centres. Along its course this nerve passes through the anterior end of the shell muscle and better-fixed material might verify the indication that the muscle is innervated by it. Near it a smaller nerve, with fibres related to pleural and pedal ganglia, passes from the left pleural to innervate the muscle, and there is a similar innervation of the right limb of the muscle from the right pleural, but the innervation of the right mantle edge is dissimilar. Streptoneury is tight. The suboesophageal connective passes abruptly to the right immediately behind the statocysts and, on the same level, the supraoesophageal connective passes over it as it is directed to the left over the radular sac and oesophagus which lie side by side. The statocysts, each with numerous statoconia, are embedded in the nerve centre formed by the pleuropedal ganglia: immediately posterior to them a ventral pedal tract and a slightly more dorsal pleural tract connecting the posterior parts of the ganglia form a continuous sheet of fibres; in addition there are also ipsilateral pleuropedal fibres. From the posterior end of each pleural area two nerves with pleural and pedal connections pass to the adjacent shell muscle.

The right mantle edge is innervated by a nerve from the visceral loop. From its course beneath the oesophagus and radular sac the suboesophageal connective passes dorsolaterally to a site beneath the median part of the longitudinal cephalic muscles under the dorsal body wall. A few scattered nerve cells are at its periphery and these increase to form an accessory suboesophageal ganglion from which the right part of the visceral loop passes posteriorly and which receives laterally a stout nerve from the pallial edge originating from the circumpallial nerve. There is also an accessory supraoesophageal ganglion at about the same level, though median to the left longitudinal muscle band, and from it the left part of the visceral loop passes posteriorly and the osphradiobranchial nerve is directed laterally, between the muscle and the body wall. This nerve leads to a prominent ganglionic mass running through the osphradial blood sinus from which arises the ctenidial nerve. The right half of the visceral loop leads straight back from the accessory suboesophageal ganglion beneath the right cephalic retractor, and, as it approaches the posterior end of the mantle cavity, it penetrates the muscle, here comparatively thin, and comes to lie beneath the body wall on the extreme right: in the female this is adjacent to the genital groove. At this level it joins the visceral ganglion. On leaving the accessory supraoesophageal ganglion the left half of the visceral loop passes straight back ventral to the anterior aorta, then crosses the viscera to the right to approach the visceral ganglion. This ganglion is transversely elongated and lobed. Nerves from it have been traced to the pericardium, the left kidney in the vicinity of the rectum, the right kidney, the urinogenital opening and the posterior part of the genital groove.

Each pedal ganglion gives rise to three anterior nerves, an anterolateral epipodial nerve, and posteriorly, a stout pedal cord. At least some of these nerves are compound, having fibres running to the pleural centres. The epipodial nerve swells considerably within each epipodial outgrowth, into which it is accompanied by a branch of the pedal sinus. The cords extend the length of the foot, gradually diverging and becoming more slender. They are linked by three or more commissures, the posterior being the most slender. Numerous nerves pass laterally from the cords innervating the pedal musculature.

Specimens from the Galapagos Rift and 21° N were similar anatomically.

Lepetodrilus elevatus

The body is relatively narrower than in *Lepetodrilus pustulosus* and in dorsal view has a slight clockwise twist reflected in an asymmetry of the two limbs of the shell muscle. Certain features of the head are diagnostic. The fold embracing the base of the left cephalic tentacle (figure 7*a*) extends medially around the lateroventral wall of the snout; immediately posterior to it a sensory process projects forwards from above the propodium which hides a ridge connecting the base of the process with the epipodium. The fold at the base of the right tentacle is deeper than that on the left and ends ventrally near the base of the snout; it is underlaid by a triangular epipodial fold which in males enlarges to form the penis. The penis has no filamentous tip; its furrowed wall indicates the possibility of considerable elongation.

Anterior to the shell muscle the ctenidial axis is free and the gill bipectinate, with thirty or

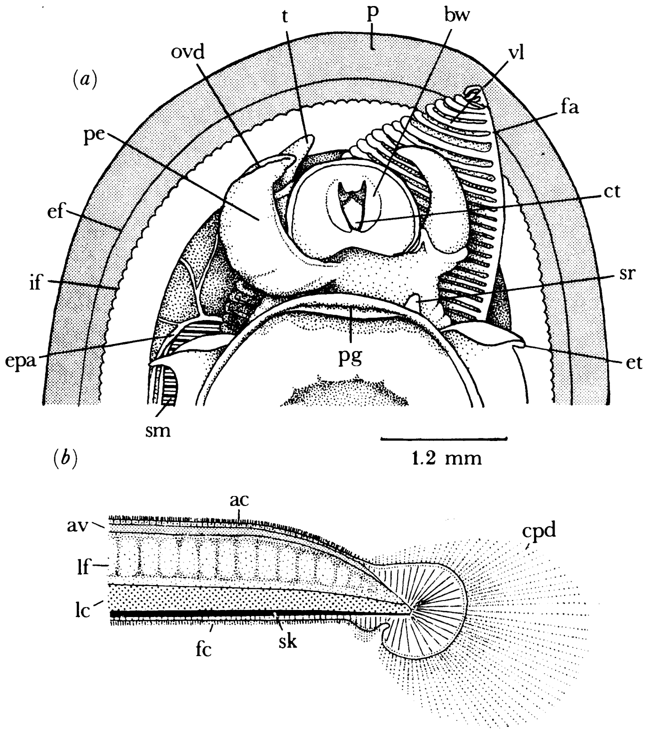

FIGURE 7. *Lepetodrilus elevatus*. (*a*) Male, ventral view, odontophore partly protruded. (*b*) Part of the lateral surface of a gill lamella to which has been added a section of its tip to show the relative lengths of the cilia not always evident in SEM.

more short dorsal filaments; this represents about half the length of the gill. The gill axis is broad, especially posteriorly. The pallial seminal groove is shallow posteriorly where it faces ventrally, and deepens considerably as it approaches the anus where its mouth becomes lateral and its epithelium of ciliated and gland cells increases in height threefold. The prostate gland spreads across the mantle skirt anterior to the anus, and posterior to this forms a blind pouch. The genital groove of the female is similar to that of *Lepetodrilus pustulosus*, but there is no upfolding of the dorsal body wall isolating it from the tips of the gill lamellae anteriorly. Packets of sperm in prostatic fluid were in the groove and orientated sperm in the receptaculum.

Distinguishing features of the vascular system include the infiltration of blood from the visceral haemocoel into the posterior wall of the pericardium, the numerous filtration chambers in the auricular walls, the short transverse pallial vein (figure 8) communicating with the left kidney on entering the mantle skirt, and the median position of the afferent branchial vein. The hypobranchial gland not only borders vessels leading to the gill lamellae but is also well developed to the right of the afferent branchial vein.

The right kidney is characterized by numerous small tubules to the right of and ventral to the pericardium, and anteriorly, ventral to the mantle cavity, fewer larger tubules with groups of ciliated cells scattered among the excretory cells.

Lepetodrilus ovalis

This is one of the smaller limpets. It can be identified by the fold of tissue encircling the base of the left cephalic tentacle extending posteriorly around the lateroventral wall of the snout,

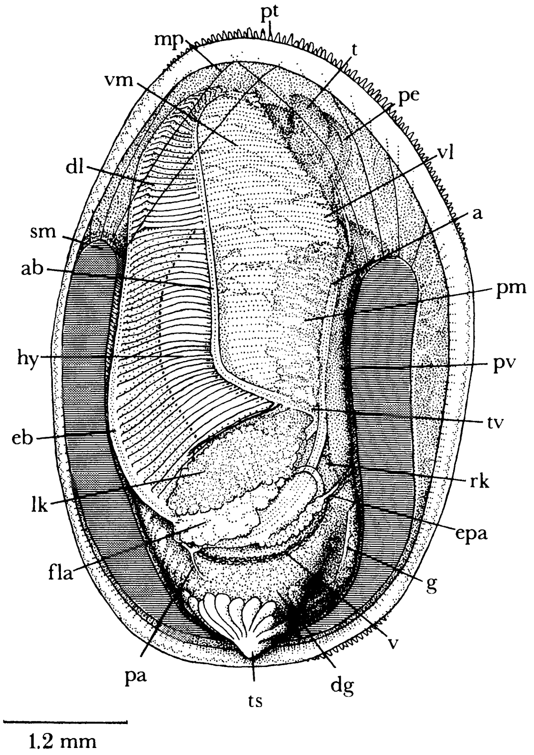

FIGURE 8. *Lepetodrilus elevatus* male, dorsal view.

where it connects by a low ridge to the anterior limit of the left epipodial fold (figure 9). The fold encircling the base of the right tentacle ends anteromedially in a prominent forwardly directed process. Ventral to it is an epipodial fold at the base of which a ciliated sensory process projects forwards from above the propodium. In females the fold is small and triangular, in males it enlarges to form the penis which retains a similar triangular outline when retracted, but when extended the tip is filamentous. The penis is short compared with that of *Lepetodrilus pustulosus*.

In the specimens examined the mantle cavity between the anterior third of the two limbs of the shell muscle was narrower than in the two species already described and relatively higher.

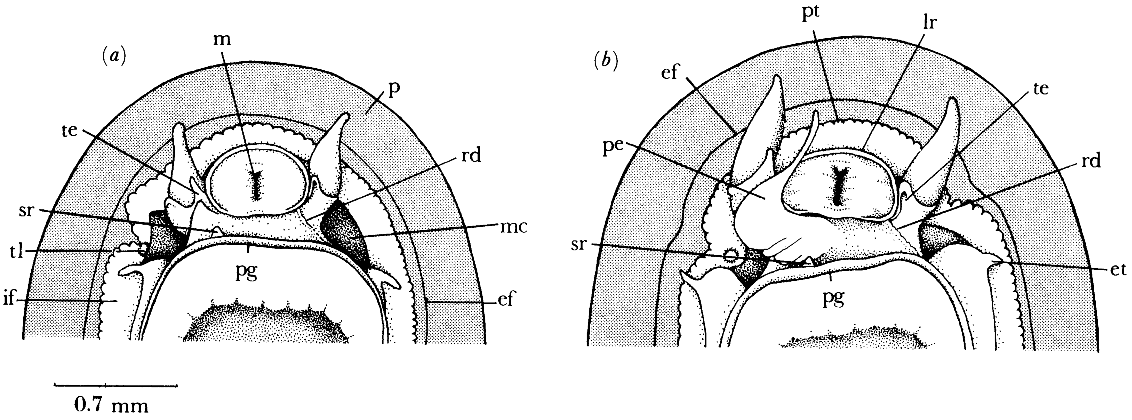

FIGURE 9. *Lepetodrilus ovalis*. (*a*) Female. (*b*) Male.

The gill axis is tied to the mantle skirt throughout its length so the gill does not project further than the mantle edge; it is monopectinate throughout with only ventral lamellae and these, especially anteriorly, are not as broad (figure 10) as in *Lepetodrilus pustulosus*. In females the genital groove, which opens ventrally, is bounded by a deep median pallial fold through which runs the right pallial vein. No fold separates the channel anteriorly from the tips of the gill lamellae. The main part of the groove closes some distance anterior to the urinogenital opening and forms a long receptacular duct which lies alongside the shell muscle; the median part leads back to the urinogenital opening. From the point of closure of the receptaculum the sperm, initially in discrete bundles, are found throughout its length. Measurements of the penial filament and the receptacular duct suggest that seminal fluid is deposited directly into it. Only in the terminal receptacular pouch, which is at a level posterior to the heart, are the sperm freed from prostatic fluid and orientated. The renal oviduct is median to the receptacular duct and has no communication with the kidney; its connection with the pericardium is by a broad and well-ciliated canal. In males the pallial prostate is particularly conspicuous anterior to the anus, spreading on either side of the seminal groove; its histology is uniform throughout, tall gland cells with large spherules which stain with azocarmine, though less intensely than the cytoplasm. The groove is open ventrally and lined by gland cells alternating with cells with long cilia: although the glands respond to mucous stains near the penis, posteriorly they stain red with azocarmine, but lack the large spherules characteristic of the anterior prostate cells.

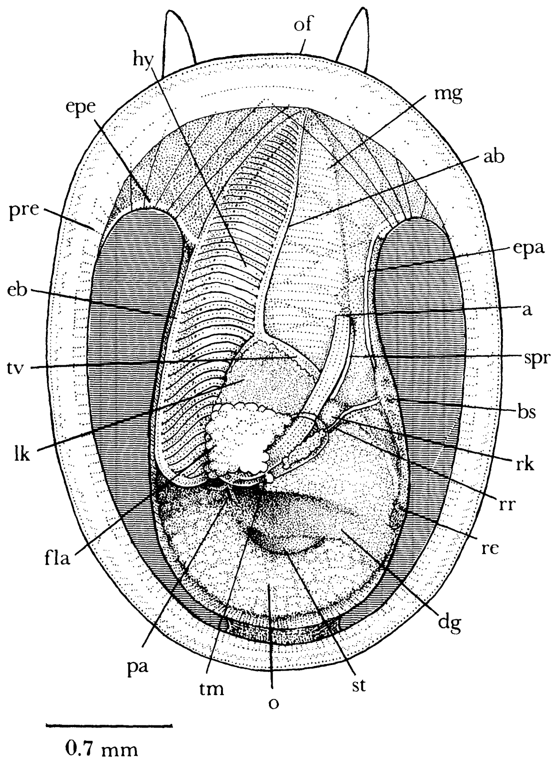

Figure 10. *Lepetodrilus ovalis* female, dorsal view.

The heart is conspicuous on account of numerous filtration chambers on the wall of each auricle especially the left where they are larger. The dorsal part of the right kidney adjacent to the pericardium subdivides to form numerous fine tubules, but where the kidney spreads among lobes of the digestive gland the tubules are fewer and larger and their epithelium has scattered groups of cells with exceptionally long cilia.

In some limpets the gut contained numerous pieces of *Riftia* tube, whereas in others it was filled with small particles, including bacteria similar to those collected on the gill filaments.

Lepetodrilus cristatus

Four specimens were examined: one mature male and female removed from their shells (figures 11*a*, *c* and 12*a*, *b*) and later sectioned, and a smaller female (figure 11*b*) and male (figures 37 and 38, plate 3). No specimen was fully contracted: on the contrary, each suggested considerable activity. In this species the head is elongated and the foot relatively short with a prominent epipodium. In the mature female the epipodial vessels were distended, their cephalic extensions passing forwards to the base of each cephalic tentacle. A small sensory process is associated with the extension on the left and in the male SEM revealed a vestigial process on the right (figure 38). The bipectinate part occupies about a quarter of the total ctenidial length and the ventral lamellae are shorter than in other species, especially anteriorly.

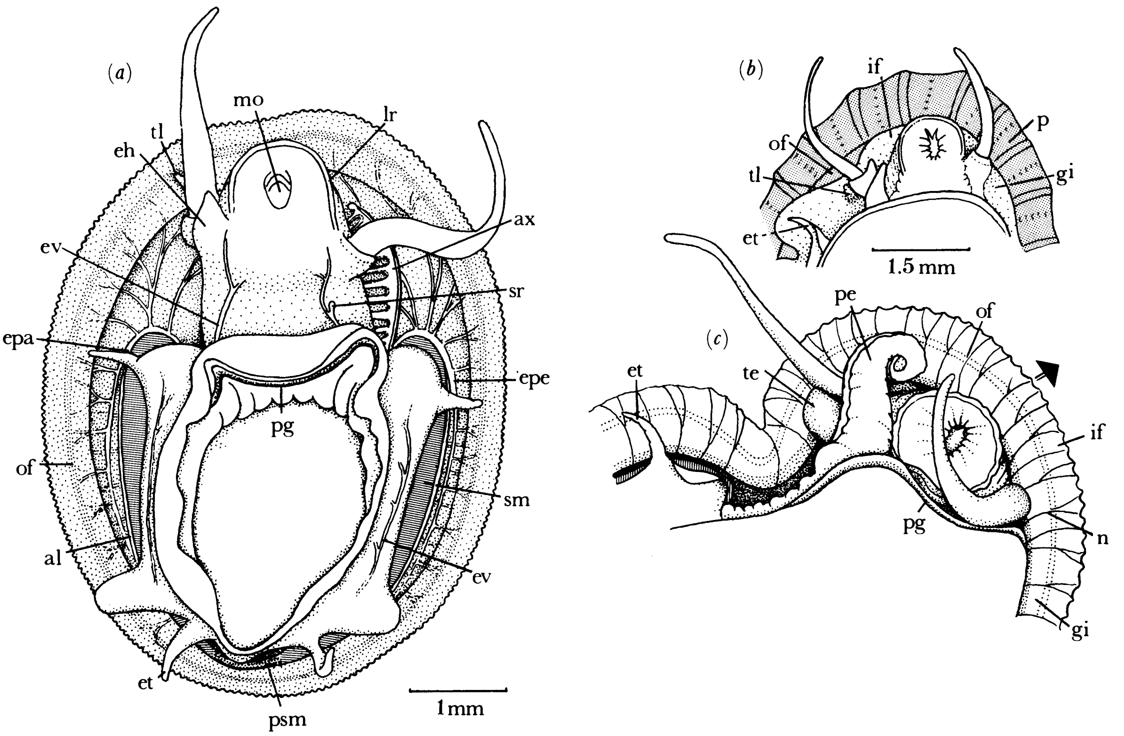

FIGURE 11. *Lepetodrilus cristatus* ventral view. (*a*) Female. (*b*) Female to show breadth of inturned periostracum. (*c*) Male, arrow indicates anterior.

Certain characters of the reproductive system set *Lepetodrilus cristatus* apart. The penis is elongated, tapering to a long flagellar tip, and its base is not extended below the snout. There is an unusually large prostate between the shell muscle and the glandular epithelium associated with the pallial vas deferens. Its walls are deeply folded and its glands, all epithelial, are filled with large spherules staining with azocarmine. The vas deferens is a deep groove lined by ciliated cells and tall epithelial glands with contents staining blue with azan; its walls are

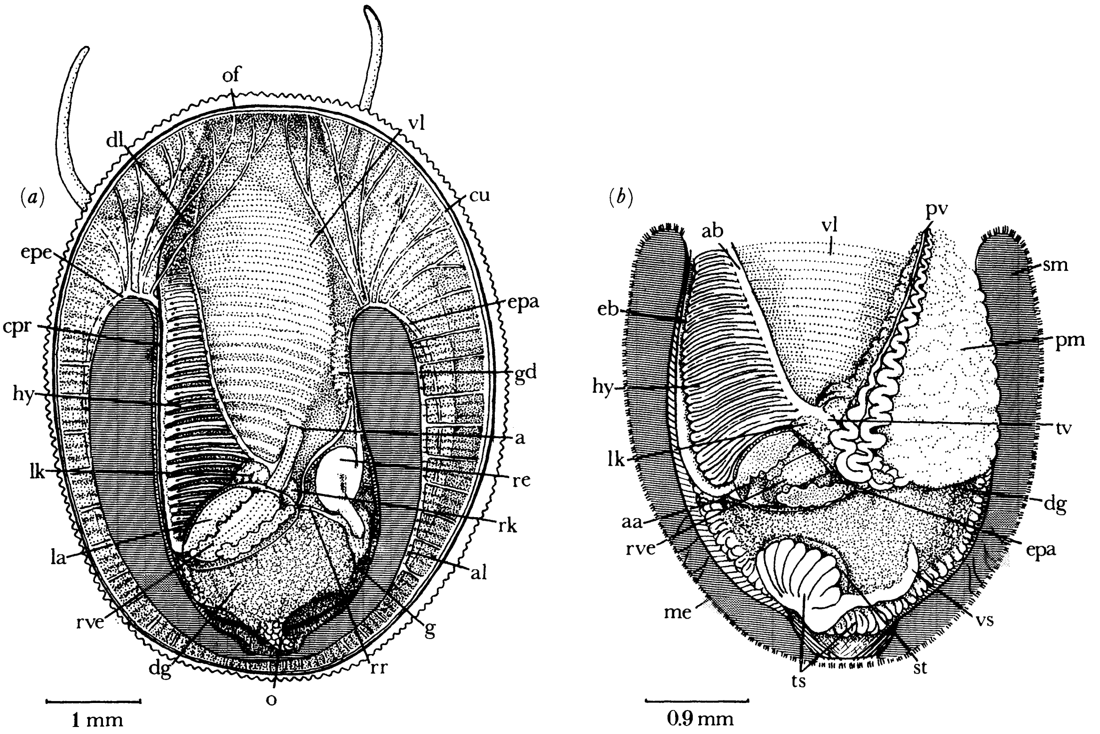

FIGURE 12. *Lepetodrilus cristatus* dorsal view. (*a*) Female. (*b*) Male.

folded, particularly posteriorly; it hides the rectum and dorsal lobe of the right kidney from surface view. A similar epithelium lines an area to the left of the rectum anteriorly and median to this is a narrow longitudinal strip of gland cells similar to those of the prostatic gland. The renal vas deferens is a moderately narrow duct connecting proximally by a wide aperture with the ciliated renopericardial canal; owing to the state of the material details of the area leading to the urinogenital opening cannot be given.

In the female the receptaculum is large, filled with sperm and with a relatively narrow duct which is ciliated and with epithelial glands; anteriorly this groove leading to the duct is overlain by a patch of pallial glands. The renal oviduct is broad, its epithelium ciliated and sparingly glandular. It receives the wide opening of the renopericardial duct, the epithelium of which has exceptionally long cilia. As it approaches the mantle cavity it narrows and forms a papilla which is urinogenital; on its median side the papilla connects with the dorsal lobe of the kidney and on its lateral with the mantle cavity. There must be considerable distension of this terminal part of the renal oviduct to allow the passage of eggs which are 140–150 μm in diameter.

The arrangement of the vessels of the pallial circulation is bilaterally symmetrical, consequently the right auricle is well developed.

Lepetodrilus guaymasensis

Examination of this species was done on one intact, but fully retracted female, which was dissected, and the external features compared with the holotype, and one male which was shattered posteriorly and allowed only examination of the head, anterior gill filaments and overlying mantle skirt. A number of features distinguish the species. A ventral view of the head (figure 13) shows that the fold surrounding the base of each cephalic tentacle is broad and its median limit free from the snout. It may be moved well away from the tentacle and contracted to half its length when the limpet is withdrawn into its shell. The epipodial lobe at the base of the right tentacle is well developed, approximately triangular in females and enlarged in males to form a penis without elongated tip and a broad base extending medially to the mid-region of the snout. Males can also be distinguished by two sensory processes of unequal size between the base of the left cephalic tentacle and the anterior end of the epipodial fold. Dorsally (figure 14) it can be seen that the mantle cavity is broad and elongated, reflecting the length

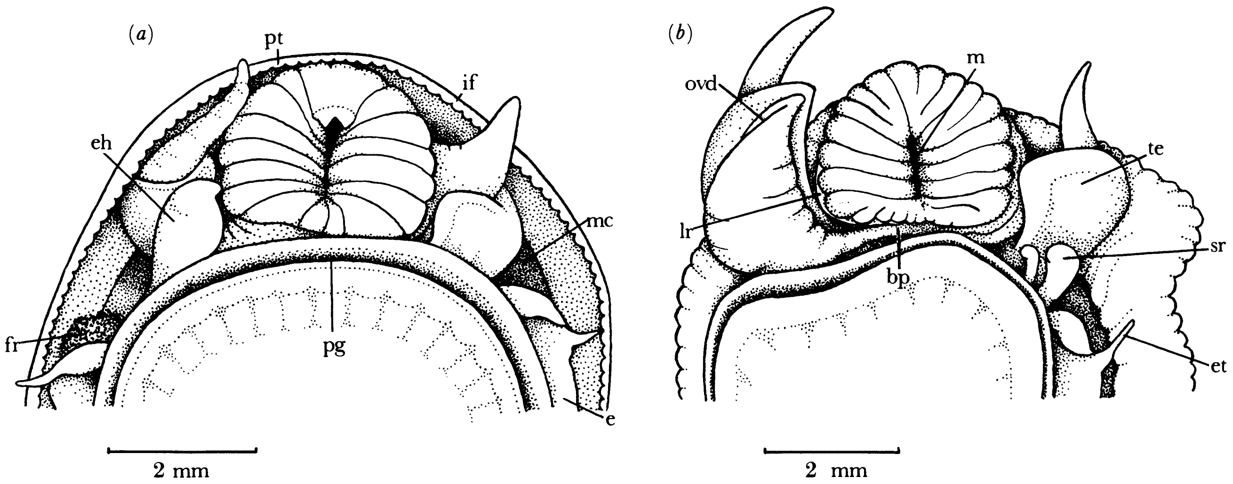

FIGURE 13. *Lepetodrilus guaymasensis* ventral view. (*a*) Female. (*b*) Male.

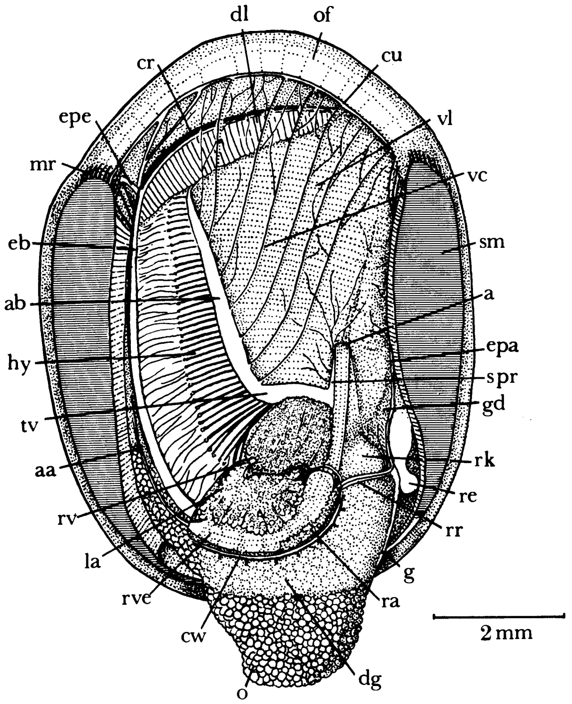

FIGURE 14. *Lepetodrilus guaymasensis*. Female that was fully contracted into shell, dorsal view; dorsal wall of pericardium removed together with a portion of the left kidney spreading over it.

and distance separating the two limbs of the shell muscle which in turn are related to the length and breadth of the foot. The gill is large, its axis relatively broad, and the bipectinate free tip occupies nearly half its length, even in the contracted state, when it stretches across the mantle cavity, exposing the thick ctenidial retractor muscle. A considerable quantity of particulate material was accumulated on the frontal surfaces of the ventral filaments, which span the breadth of the mantle cavity, and also on their free tips (figure 29).

The pericardial wall carrying vessels connected with the visceral haemocoel, is thick and opaque so that the heart can be seen only after its removal. The left auricle is exceptionally large and very numerous filter chambers cover its dorsal surface; they are isolated into groups by muscles radiating from the central part of the auricle. A nephridial gland in the left kidney indents the anterior pericardial wall; when part of the gland is removed the short vessel connecting auricle and kidney is revealed. Much of the blood from the circumpallial vein flows through the roof of the mantle cavity to the afferent pallial vein, resulting in a reduction in importance of the right efferent pallial vessel and the right auricle. The filtration chambers of this auricle are numerous, though smaller than those of the left.

The general outlay of the female reproductive system is similar to that of *Lepetodrilus pustulosus*; owing to inadequate material details of the urinogenital duct are unknown. A major difference is the presence of a pallial gland of unknown significance extending forwards from the urinogenital opening parallel with the duct of the receptaculum. The uninjured part of the mantle skirt of the male had a well developed prostate gland.

Lepetodrilus fucensis

This species has a number of characters that set it apart from those already described. One relates to the increased length and breadth of the mantle cavity. The shell is steep-sided, the right and left limbs of the shell muscle, which extend to the level of the base of the head, are set apart and inserted on a steeper slope than in other species, especially the left; the narrow posterior band uniting them undercuts the visceral coil (figure 15*a*). The mantle cavity lies between the two shell muscles as far as the base of the coil where the pericardial cavity overlies the stomach; its depth is over seven tenths of the body length. The gill extends over the head which is broadened by anterior prolongations of the epipodial folds. The right fold, especially deep, projects forwards to form a triangular process beneath the cephalic tentacle and enlarges in the male to form a scroll-shaped penis with a dorsal seminal groove (figure 15*b*, *c*). The ciliated food tract leading to the base of the right cephalic tentacle and abutting the median wall of these epipodial processes is pronounced. On the left the epipodium reaches to the fold of tissue around the base of the tentacle which, unlike that associated with the right tentacle, spreads around the ventrolateral wall of the snout. Posterior to this there is a sensory process. The lateral pallial cavities, subdivided by the epipodial fold, are deep. The first pair of epipodial tentacles is placed at the broadest part of the fold, the second and third lie close together posteriorly with the last two separated by a median lobe. The outer fold of the mantle edge is not subdivided as in other species; the inner has a broad ventral glandular area. Some irregularities in the shell outline of larger limpets may be due to the fact that clusters adjacent to thermal vents are reported to live predominantly in stacks of up to six individuals each fitting closely to the shell beneath (De Burgh & Singla 1984). This is a suitable arrangement for a suspension feeder.

The gill is bipectinate for half its length and the anterior third is free. The left lamellae are

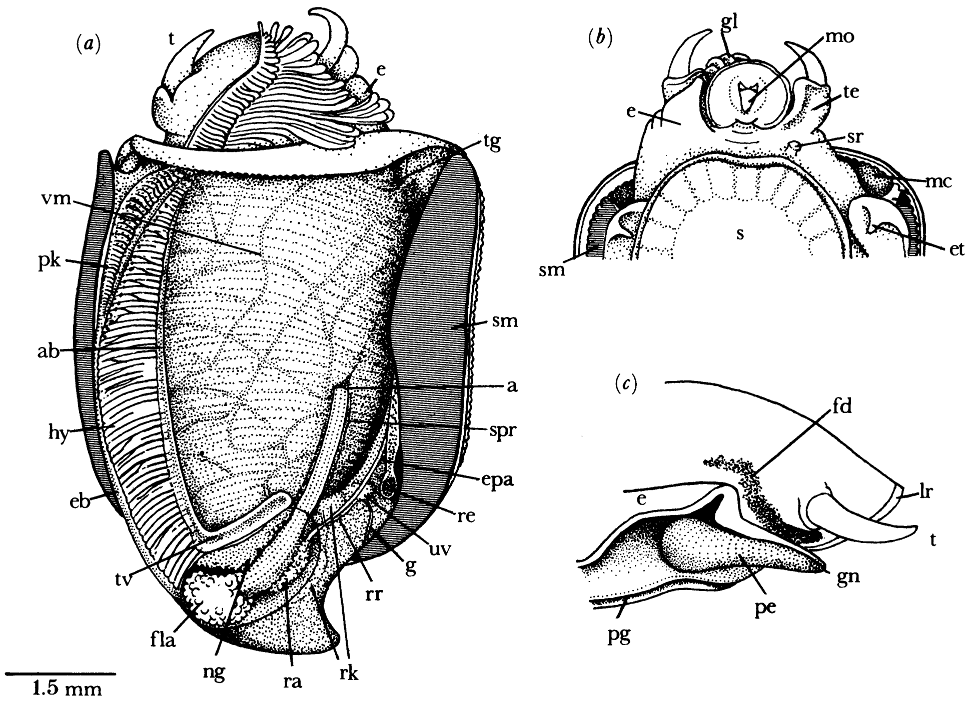

FIGURE 15. *Lepetodrilus fucensis*. (*a*) Female, dorsal view, mantle skirt turned back to expose head. (*b*) Female, ventral view. (*c*) Male, right side of head.

short and posterior to the free tip are enclosed in a pocket formed by the fusion of an afferent membrane with the mantle skirt; the right ones are not only exceptionally long, but deeper than those of other species. The afferent area of each lamella is covered by pseudostratified epithelium with which a thick layer of filamentous bacteria is associated, limited to this area (figure 31, plate 2). De Burgh & Singla (1984) have shown that the bacteria are frequently endocytosed by the epithelial cells and broken down in lysosome-like organelles. The folded lateral wall of the lamella is white and iridescent and at the ventral limits of the folds groups of stout cilia interlock with similar groups on the adjacent lamella making them difficult to separate. These ciliary junctions are unknown in other rift limpets (figures 33, 34 and 35, plate 2). The structure of the lamellar tip and the accumulation of particles, especially anteriorly, suggest that the limpet is a suspension feeder. But the fact that the buccal mass has been seen to be everted with the radula open as in *Lepetodrilus pustulosus*, and the wear of the jaws, indicate that, as in that species, it has an alternative method of obtaining food.

The left kidney is elongated and narrow, extending along the posterior wall of the transverse pallial vein and spreading back over the pericardium. It opens to the mantle cavity to the left of the perirectal sinus and communicates with the pericardium by a broad, short duct with exceptionally long cilia. The lumen is larger than in *Lepetodrilus pustulosus* and subdivided by a few septa, but the epithelium is similar. A nephridial gland is developed not only in relation to the pericardium, but to a lesser extent over the transverse pallial vein.

There are two important features in which the right kidney differs from that of other species. Whereas in females the urinogenital duct connects with the renal section of the oviduct, in males it extends towards the excretory lobe of the kidney adjacent to the urinogenital opening; it then unites with the male duct to form a very short connection to the kidney which is linked by a ciliated groove to the urinogenital opening. It would appear that the renal section of the vas deferens is greatly reduced and the gonadial duct lengthened. Females have a complex renal section of the oviduct with functions not apparently confined to conduction. Distally it terminates in a vesicle with a glandular and ciliated epithelium underlain by muscles which would allow compaction and expulsion of its contents; the excretory part of the kidney opens to it. The size of the vesicle suggests that it could accommodate four to six eggs of the diameter of those at the base of the gonadial duct, 100–140 μm. Between the vesicle and the opening of the renopericardial duct the wall of the renal section of the oviduct has three longitudinal folds, the central the largest. Anteriorly they are ventral, but as they pass posteriorly they curve to the left where the uppermost one overlies the opening of the renopericardial canal and the other two enclose a ciliated pathway from the ovarian duct. Here sperm occur in the lumen and in the epithelial cells of the folds, where there are indications that they are ingested.

The postcephalic nerve mass has the same general plan as in other species, but the visceral connectives arise from the supra- and suboesophageal ganglia anterior to the fusion of the right and left pleuropedal ganglia. The course of some fibres within the ganglia is more easily traced, particularly those related to the compound nerves of the left mantle edge, the shell muscle and some pedal muscles with large tracts passing to the pleural ganglia. Fibres of the pallial nerve pass to the pleural and pedal ganglia and a large component to the suboesophageal ganglion whence they enter the visceral loop leading to the accessory suboesophageal ganglion.

The anterior end of the gonad is closely associated with the ventral wall of the aorta with which it has vascular connections. Its anterior limit is immediately left of the mid-line, near the site of torsion, where it projects into a haemocoelic space with restricted communication with other parts of the blood system.

Gorgoleptis emarginatus

External features

The general form of the body is unusual. Although limpet-like with folds of the mantle edge bordering the periphery of the shell there is a metapodium with an operculum, though this is too small to close the shell. The visceral mass, elongate and with a small dextral coil at its posterior limit, is directed posteriorly over the metapodium (figure 17) and covered ventrally by a sheet of tissue arising anteriorly at its junction with the foot and spreading posteriorly and laterally to the mantle edge. Typically in prosobranchs other than limpets the visceral mass is directed posterodorsally and the mantle skirt encircles its base, being narrow posteriorly at its junction with the foot. It is the enlargement of this posterior part of the mantle skirt that forms the protective ventral covering of the visceral mass and brings the two folds of the mantle edge to its periphery, except in the mid-line. Here the outer fold continues from side to side, but the inner fold with the periostracal groove turns forwards to form a narrow sinus stretching as far as the junction of the visceral mass with the head–foot. As a result, a narrow longitudinal strip of periostracum extends posteriorly and underlies the mantle skirt and the visceral mass.

The ovate outline of the shell is broken posteriorly by a narrow embayment in the mid-line. The inner margin of this interruption marks the columellar edge of the aperture. From this level the lips of the aperture have expanded abruptly at each end of the columellar edge, and especially anteriorly, to give rise to the limpet shape, whereas at the columellar edge, except for some thickening and broadening, there has been less growth. Here a grooved area, the umbilical groove, is overlaid by periostracum continuous posteriorly with that covering the dextral coil and anteriorly with the longitudinal strip underlying the visceral mass (figure 19*a*), its breadth related to that of the columellar edge. The outer pallial fold, not so deep as in *Lepetodrilus*, secretes the calcareous part of the shell, the edge of which is overlaid by a narrow band of periostracum secreted at the base of the inner fold. The latter has a ventral glandular band conspicuous at the mantle edge until reaching the posterior embayment of the shell where it narrows abruptly as the fold inturns.

The snout, which may project beyond the mantle anteriorly is broad and truncated with the oral surface directed ventrally (figure 16*a*). A pair of lateral tentacles arises near its base, elongated and gradually tapering to a pointed tip. They bear no eyes. In gross anatomy they are similar to five other pairs of tentacles projecting laterally from the body, the third pair thick, truncated and not extending beyond the mantle edge in any specimen examined, the others long and tapering; all are epipodial except the anterior one on the right which is pallial and overlies the exhalant passage from the mantle cavity marked by a marginal shell notch. Each tentacle has a stout nerve running to sensory epithelium at its tip and there are peripheral bundles of longitudinal muscle separated by transverse muscle passing from wall to wall. Near the base of the first two epipodial tentacles on the left and the first on the right there is a sense organ appearing as a hemispherical boss. Each epipodial fold is broad anteriorly, its anterior edge slightly flexed ventrally; it narrows posteriorly and ends at the base of the last pair of tentacles.

In males (figure 16) a stout process arises from the left wall of the snout and passes beneath the left cephalic tentacle, either to a position of rest on the floor of the mantle cavity left of the gill, or to extend laterally beyond the shell edge, though full extension may not have been observed. It is innervated by a stout nerve from the labial lobe of the left cerebral ganglion and a blind tube runs inward from an opening at its tip. The outer wall of the process has inner circular and outer longitudinal muscles which are separated from the muscles of the tube by a large blood sinus which must be related to its extension. The wall of the tube has a thick layer

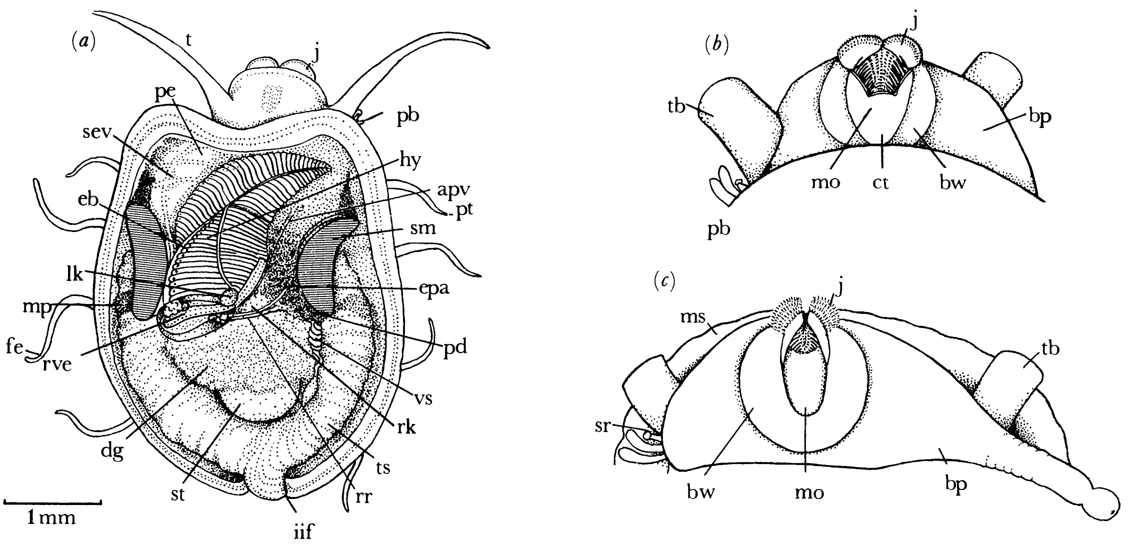

FIGURE 16. *Gorgoleptis emarginatus*. (*a*) Dorsal view. (*b*) Ventral view of head of (*a*), odontophore protruding, cephalic tentacles cut short, penis retracted. (*c*) Ventral view of head showing earlier stage in odontophore protrusion and penis partly protracted.

of circular muscles from which radial muscles pass through the blood space to the outer wall. Although placed in an unusual position this process is assumed to be copulatory in function, pipetting seminal fluid from the mantle cavity and transferring it to the female.

The mantle cavity is broad anteriorly, but restricted posteriorly by the right and left shell muscles which extend back to the base of the visceral mass; it underlies the anterior part of the pericardium on the left and the anterodorsal part of the right kidney on the right. The single gill is bipectinate for at least two thirds of its length. It tapers to a pointed tip and on retraction is directed to the right. The axis of the free part of the gill is vertical and right and left lamellae are of equal size. Posteriorly the axis, remaining narrow, rotates through 90° so that the left side becomes dorsal and is attached to the mantle skirt. The lamellae on the right become longer than those on the left and at the posterior end the left ones are lost and the right ones traverse most of the breadth of the mantle cavity. Some of the most posterior left lamellae lie in a pocket formed by a short afferent membrane extending from gill axis to mantle skirt. In the holotype the free end of the gill is retracted and the dorsal filaments turned back over the ventral ones revealing the gill axis. The osphradium can be seen where the axis approaches the left shell muscle; it is conspicuous because of its large ganglion lying alongside the muscle parallel with the axis. As in *Lepetodrilus*, the afferent branchial vein diverges from the ctenidial axis posteriorly where they are separated by hypobranchial gland and fine vessels from the afferent branchial cross the gland and enter the gill lamellae near the efferent branchial. Similarities in the gill of the two genera also extend to the skeleton and the elaboration of the tips of the lamellae. In each lamella the bands of frontal and abfrontal cilia end in the ciliated pad, most prominent on the ventral filaments, and lateral cilia extend to the tip between the pads. The dorsal, posterior and posteroventral walls of the mantle cavity have a tall glandular epithelium – an extension of the hypobranchial gland – and ventrally, in the exhalant area, the epithelium is ciliated. The exhalant area contains faecal rods, loosely compacted, and particulate matter from the mantle cavity which is not used as food, but is apparently directed away from the body by the pallial tentacle and two tentacular processes at the base of the right cephalic tentacle; median to those processes is a shorter one capped with sensory cells.

Internal anatomy

The pedal glands and components of the shell muscle. The sole of the foot is broad anteriorly where the groove between a double edge marks the opening of the anterior pedal gland; posteriorly it tapers to a blunt point. In some specimens the sole was almost flat except for one or two transverse furrows suggestive of locomotor waves, whereas in others the posterior tip was contracted and the centre deeply insunken so that the whole appeared as a sucker. The surface of the peripheral rim of the sole is ciliated and as in other limpets (Fretter 1984) the rim contains no fibres of the shell muscle, but has its own intrinsic musculature and ample blood lacunae; elsewhere the arrangement of the pedal musculature and glands is similar to that described for *Lepetodrilus*. However, in *Gorgoleptis* the foot is shorter as indicated by the length of the pedal shell muscles which are limited to the anterior part of the body. At their posterior ends, at the level of the origin of the metapodium, some median fibres from each shell muscle pass ventromedially to form a transverse muscle which subdivides into a band at the base of the visceral mass and a more ventral one at the base of the metapodium. The anterior end of the metapodium projects forwards in the narrow space between them and some muscles of the ventral band insert on the operculigerous disc. Posterior to this all pedal muscles are intrinsic,

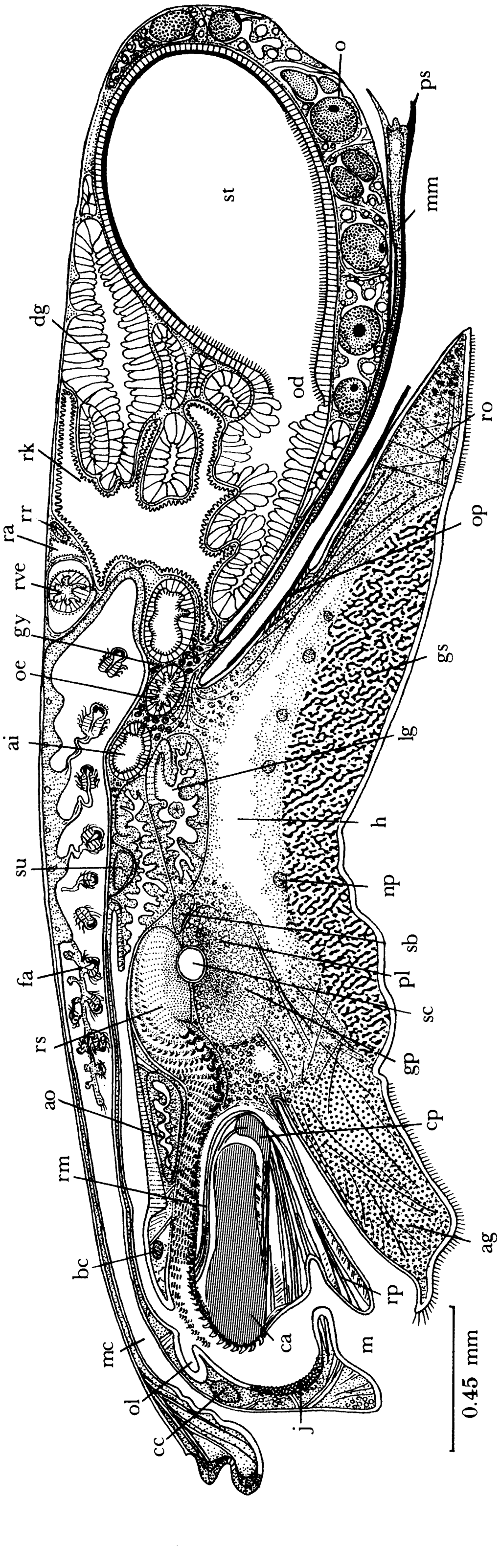

FIGURE 17. *Gorgoleptis emarginatus*. Female with odontophore retracted, oblique longitudinal section.

the dorsoventral and oblique arising from the metapodial surface. The median longitudinal component of the shell muscle passing to the head is important, but in contrast to *Lepetodrilus* most fibres arise from the posterior part of each muscle, passing forwards lateral to the oesophageal pouches and cerebral ganglia to insert dorsally, laterally and ventrally on the head. The dorsal ones, which raise the head and shorten the snout when the odontophore is protruding, form the stoutest band.

The shell shows pallial muscle scars continuous with those of the two pedal shell muscles (figure 19*a*), an anterior scar projecting forwards from each and a posterior scar passing laterally from near the posterior margin, then narrowing and encircling the shell posteriorly though particularly narrow in the region of the inturned periostracum.

The alimentary canal. In some limpets the mouth was slightly open and the buccal wall partly everted revealing a U-shaped buccal fold open ventrally and narrow mid-dorsally. On each side the median wall of the fold bears a chitinous plate beset with rows of rods, hexagonal in transverse section, and hidden except for their tips. These compose the jaws. As the mouth opens further and the radula emerges (figure 16*b*, *c*) the fold, which is free from the buccal wall ventrally, is inflated with blood, everted to expose the jaws and directed dorsally to appear as two, large, ovate protuberances with the jaw teeth directed away from the buccal area. Each protuberance forms a scrubber, the complex array of muscles passing to the epithelium which secretes the rods and their worn tips indicating that it abrades some surface. This must be over the animal's head and may be the roof of a crevice into which it has crept. The particles loosened by the jaws will be gathered by the rhipidoglossate radula which emerges when the jaws are brought into action and is directed dorsally. No detailed study has been made of the odontophore, but it certainly functions in a similar way to that of *Lepetodrilus*.

The alimentary tract has the same general plan in the two genera. In *Gorgoleptis* the simple tubular salivary glands opening to the buccal cavity lateral to each dorsal fold are relatively broader and longer. The ventral wall of the oesophagus back to the site of torsion is reduced to a median ridge varying in breadth and in its glandular equipment. On each side it borders the opening of an oesophageal gland. The glands follow a course similar to that described for *Lepetodrilus pustulosus*, but throughout their length the lumen is reduced by glandular folds, and there are no dorsoventral muscles anchoring them to the body wall. In the area of torsion the glands are reduced, the right becomes dorsal and ends, the left, at first ventral, curves to the right, closes off from the oesophagus, and forms a blind sac similar histologically to its anterior portion and continues to near the base of the visceral hump where it lies under the anterior loop of the intestine. The stomach is larger than in *Lepetodrilus*; the oesophagus enters posteroventrally, the broad ducts of the digestive gland open nearby, and the intestine leaves anteriorly. There is a thick gastric shield raised into a tooth-like eminence on the dorsal wall and the opposite wall is ciliated. In all specimens examined the stomach was full of particulate matter and it may be that this distension obliterated the typical folds of a sorting area. No spiral caecum was seen. From the style sac a deep typhlosole continues into the intestine and runs throughout its length. The contents of the gut indicate that the food of these limpets is similar to that taken by *Lepetodrilus pustulosus*.

The kidneys. In contrast to *Lepetodrilus* the left kidney forms only a small vesicle, though situated in a similar position against the left wall of the rectum immediately posterior to the short transverse pallial vein. It spreads back for a short distance over the pericardial wall where there is a thickening of the renal tissue in the position of a nephridial gland, but the fixation is too poor to prove this and to describe the renal tissue elsewhere. The renal opening is anterior and, posterior to it in the left wall, is the opening of the renopericardial canal which it receives transversely from the ventral part of the pericardial cavity. The cilia of the epithelium of the canal and of the large glandular funnel at the renal opening are extraordinarily long. The walls of the kidney are glandular and a vessel connecting it with the transverse pallial vein has been traced, with only a suggestion that there might be a vascular connection with the left auricle. In contrast to the right kidney, in which the lumen has numerous vesicles budded from the epithelium, the lumen of the left appears empty, compatible with the idea that it fulfils a different function.

Gametes escape from part of the same opening as waste from the right kidney and this is situated at the inner end of the genital groove, median to the right shell muscle; the genital and renal parts of the kidney, although sharing this common opening, diverge almost at once. The former passes back as a moderately broad, strongly ciliated duct without excretory function apart from conducting fluid received from an unusually broad renopericardial canal which, in both sexes, is glandular, ciliated and long. From its opening into the renal genital duct, which is regulated by a sphincter, the canal passes medially and follows closely the right pallial vein to open to the pericardial cavity. Its size and glandular nature suggest that it is concerned with the modification and possibly with increasing production of the primary urine. The renal section of the genital duct, surrounded by a layer of circular muscles, continues posteriorly for a short distance before a sphincter separates it from the gonadial duct. In the two females examined it was glandular in the vicinity of, and behind, the renopericardial opening, near which mucous cells and cells with large protein spherules occurred among the ciliated epithelial cells and numerous mucous cells posterior to this. In males no glands were evident in the renal section of the vas deferens.

The excretory part of the right kidney (figure 17) is extensive. From the external opening it spreads around the right and ventral walls of the rectum, immediately anterior to the pericardium, to pass beneath the pericardium and spread dorsally under the shell and ventrally among tubules of the digestive gland, penetrating between them as fine tubules. Its epithelium appears to consist of a single type of excretory cell, which buds off the spherical tip filled with contents, and occasional ciliated cells.

The circulatory system. The organization of the vascular system is similar to that of *Lepetodrilus*, though it was not possible to trace all details of the pallial circulation. Filtration chambers in the auricular walls are numerous and sections show that at systole blood is isolated there by contraction of muscles across their openings when filtration of the blood will occur under pressure; they are fully open at diastole. The resultant filtrate in the pericardial cavity is added to by the tall cells of the epicardium, the tips of which are nipped off and then appear to disperse.

The reproductive system. In both sexes the gonad is large, U-shaped and extends into some unusual sites. It covers the ventral surface of the visceral mass posterior to the mantle cavity spreading beyond the rest of the viscera laterally and posteriorly, whereas anteriorly it penetrates beyond the visceral mass into a large haemocoelic space between each shell muscle and the mantle edge, filling it and so broadening this part of the body, and to a certain extent constricting the mantle cavity (figure 16*a*). In one moderately small female tubules of the digestive gland accompanied the developing gonad through the right haemocoelic space. Strands from the gonad containing gametes in the earliest stages of development penetrate deeply among the anterior viscera, extending dorsally and attaching to the wall of the posterior oesophagus and the adjacent anterior loop of the intestine. The gonadial duct arises from the posterior part of the gonad towards the right and passes anterodorsally to the renal genital duct. In the male it acts as a vesicula seminalis, superficial posteriorly, but under part of the prostate anteriorly. The prostate consists of a posterior diverticulum in the visceral mass with folded walls lined by tall gland cells, with contents staining bright red with azan, alternating with ciliated cells. Anteriorly the seminal groove associated with the prostate forms a gutter along the mantle skirt open ventrally and receiving posteriorly on the left the urinogenital opening. Its forward course is between the anterior pallial and right pallial veins. Its epithelium becomes lower, especially in the depth of the groove where mucous glands become numerous. There is a gradual reduction in its glandular equipment and dorsal to the tip of the retracted ctenidium it forms only a ciliated tract.

By comparison the pallial genital groove in females is inconspicuous. It is moderately deep covering the area between the rectum and the median wall of the right shell muscle. The muscles underlying the epithelium are contracted throwing the walls into longitudinal folds. The epithelium is ciliated and contains gland cells. There appears to be no receptaculum seminis and no sperm have been found in the female.

The nervous system. As in *Lepetodrilus* the nervous system is hypoathroid–dystenoid. The ovoid cerebral ganglia are linked by a stout commissure passing around the anterior buccal wall and from the ventral, labial lobe of each arises a buccal connective. The cerebropleural and cerebropedal connectives are long with nerve cells scattered along their length, distally they pass into the anterior ends of the ganglia; the two pleural ganglia, one on either side of the radular sac, are separated from the larger pedals by a transverse muscle arising from the shell muscle and stabilizing the position of the radular sac. Anterior to the statocysts the pedals fuse mid-ventrally and are linked by a stout commissure; posteriorly they fuse with the pleurals which have a commissure almost continuous with that of the pedals. As in *Lepetodrilus pustulosus* the supra- and suboesophageal ganglia appear as lobes of the right and left pleurals respectively; streptoneury of the visceral loop is tight and there are accessory supra- and suboesophageal ganglia at the sites at which the visceral loop passes posteriorly, and a nerve from the former passes laterally to the large osphradiobranchial ganglion and to the circumpallial nerve from the latter; the left and right pallial nerves have a dissimilar origin, both are large and compound. The size of the pedal ganglia is related to the well developed epipodium; they give rise to scalariform pedal cords. The visceral ganglia are at the posterior end of the mantle cavity between the body wall and oesophagus.

Gorgoleptis spiralis

Only two whole specimens were examined, both female. The ventral view of the holotype removed from the shell is illustrated; the second specimen was smaller and less well preserved; its anatomy was viewed by SEM.

The limpet form has been attained by the same modifications as in *Gorgoleptis emarginatus* and as much as could be seen of the internal anatomy is in close agreement. In contrast to *Gorgoleptis emarginatus*, however, the columella and its lip are elongated (figure 19*b*) and the visceral coil is larger (figure 18*a*). As a consequence, viscera overlying the operculum anterior to the umbilical lip are covered by a wide sheet of periostracum at the lateral margins of which the inner mantle fold and periostracal secreting groove can be traced to the base of the visceral mass

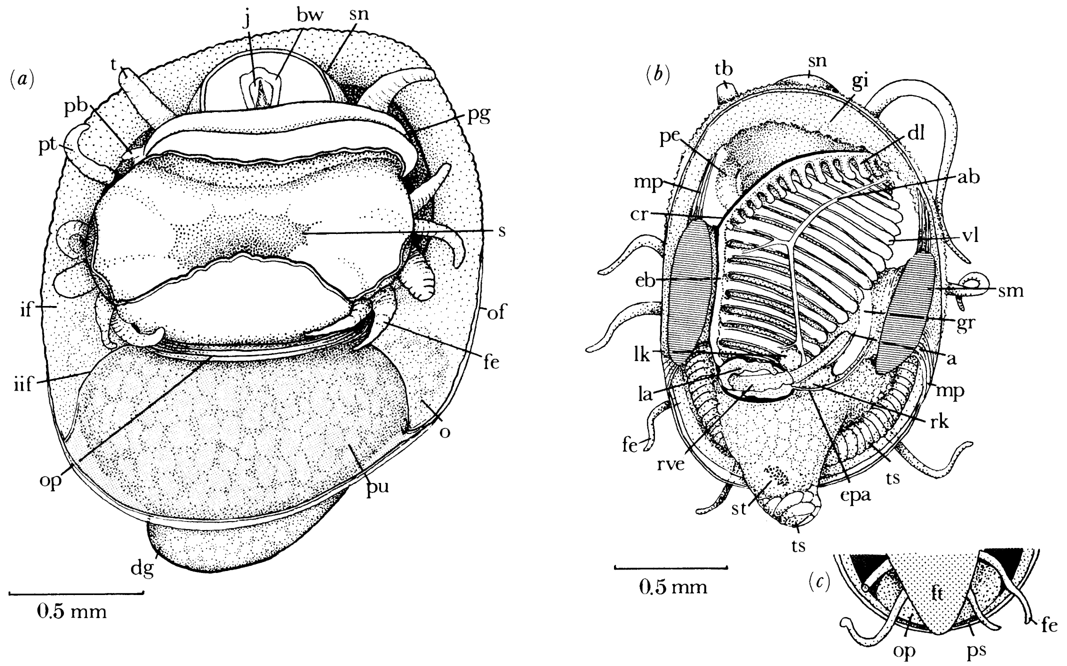

FIGURE 18. (*a*) *Gorgoleptis spiralis* female ventral view, holotype. (*b*, *c*) *Gorgoleptis patulus* male, holotype; (*b*) dorsal view; (*c*) ventral view posterior end.

not having shared the back growth of the rest of the mantle skirt to the posterior margin of the aperture (figure 42, plate 3). The ventral band of epithelial glands associated with the peripheral course of the inner mantle edge is broader than in *Lepetodrilus emarginatus* and increases in breadth towards the posterior ends of the two shell muscles, extending across the area where the gonad penetrates the haemocoelic space between the muscle and the mantle edge (figure 18*a*). The depth of the mantle is about half the body length, its limit being near the posterior ends of the shell muscle, and here the rectum crosses the body, passing through the ventricle on the left and curving forwards towards the anus on the right. This region of the body is stabilized on either side by a thick band of pallial muscles originating on the shell adjacent to the pedal shell muscle (figure 19*b*). The gill, similar to that of *Gorgoleptis emarginatus*, was contracted in both specimens and positioned across the mantle cavity anterior to the heart. The siting and number of epipodial appendages are similar in both species: the apparent shortness of these may be due to full contraction. The cephalic tentacles are characterized by clusters of sensory cells arranged in a few longitudinal rows and alternating with rows of kinetocilia (figure 25, plate 1). Although the gonads indicated that both species were mature there was no trace of a receptaculum.

Gorgoleptis patulus

One animal (the holotype), a male perhaps not fully grown, was examined externally. This showed that the limpet form (figure 18*b*) had been attained by the same method as in the other two species. However, the inturned band of periostracum dorsal to the operculum is relatively shorter, and the mantle cavity is elongated to over two thirds of the body length, half the length being anterior to the pedal shell muscles which remain short. In the region of the short, but

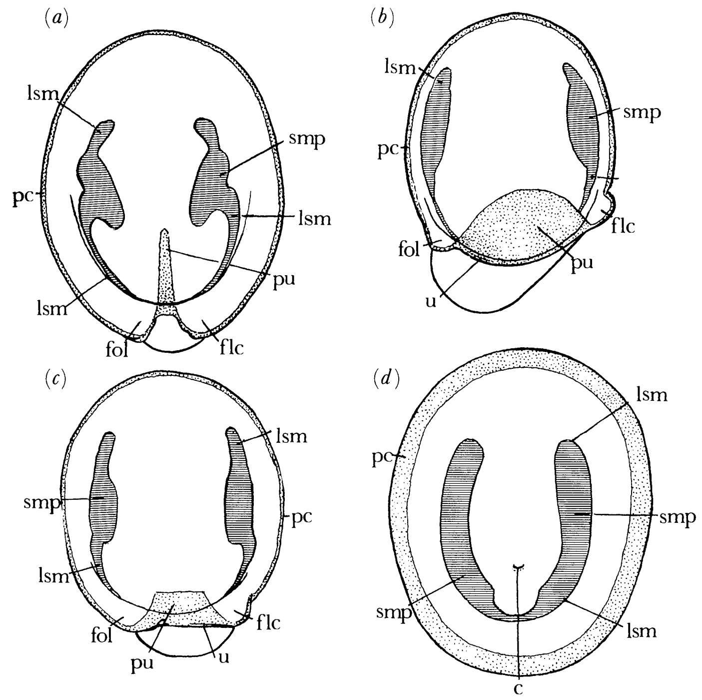

FIGURE 19. Diagrams of ventral views of shells to show muscle attachments and inturned areas of periostracum. (*a*) *Gorgoleptis emarginatus.* (*b*) *G. spiralis.* (*c*) *G. patulus.* (*d*) *Lepetodrilus pustulosus.*

prominent, columellar lip (figure 19*c*) growth of the shell and body is inhibited. At the posterior end of each pedal shell muscle a strong band of pallial muscles stabilizes the area where the gonad extends into the pallial edge, though in this specimen this extension of the gonad had not resulted in broadening the body as in *Gorgoleptis emarginatus*. With the lengthening of the body the gill is enlarged: the dorsal filaments are fewer and shorter, the ventral ones elongated (figure 18*b*); the former are turned back over the latter in the holotype

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DESCRIPTION OF PLATE 1

FIGURE 20. *Lepetodrilus pustulosus*: female, anterior end. The buccal walls are everted and the odontophore fully protruded. (Magn. × 51 approximately.)

FIGURE 21. *Lepetodrilus pustulosus*: female, anterior end. A broken piece of radula projects upwards. (Magn. × 50 approximately.)

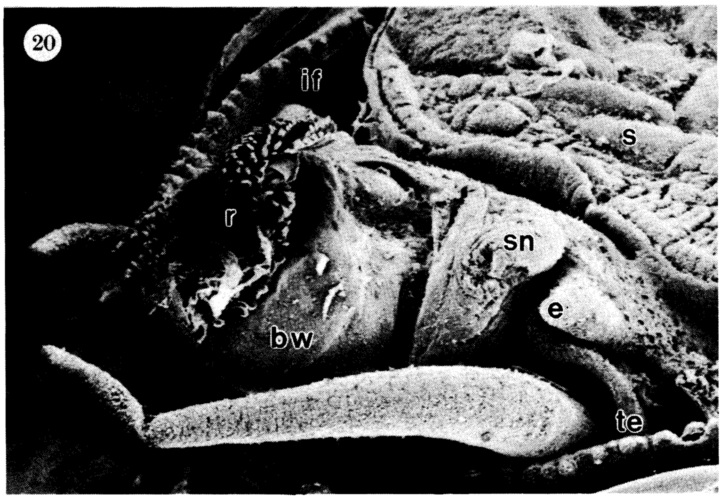
FIGURE 22. *Lepetodrilus pustulosis*: front view of snout with buccal wall, odontophore and jaws partly protruded. (Magn. × 52 approximately.)

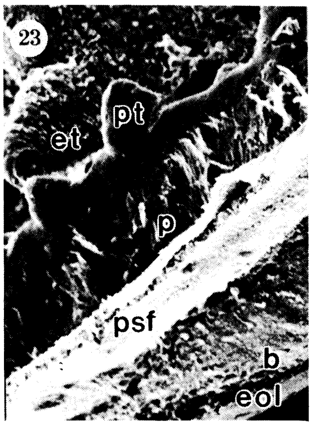
FIGURE 23. *Lepetodrilus pustulosus*: right mantle edge adjacent to first epipodial tentacle, lateroventral view. Periostracum secreted near base of inner fold from which the outer fold has contracted. (Magn. × 260 approximately.)

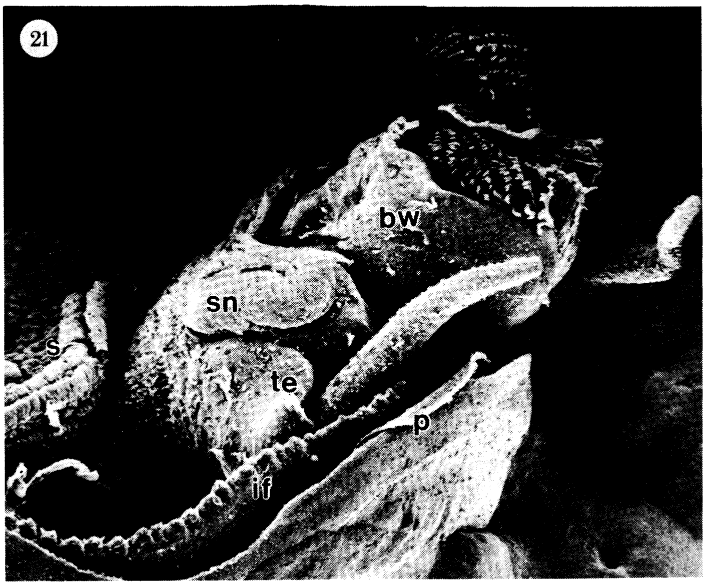
FIGURE 24. *Lepetodrilus pustulosus*: chitinous rods of jaw. (Magn. × 800.)

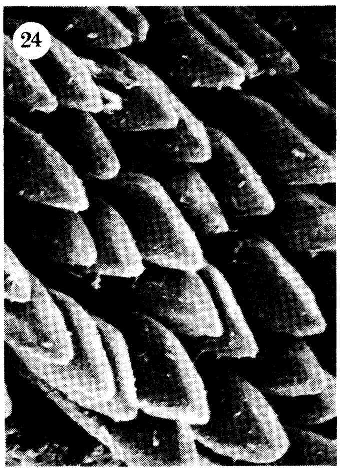
FIGURE 25. *Gorgoleptis spiralis*: frontal view of right half of snout and cephalic tentacle (broken at tip), both with groups of sensory cilia, also rows of vibratile cilia on tentacle. (Magn. × 140 approximately.)

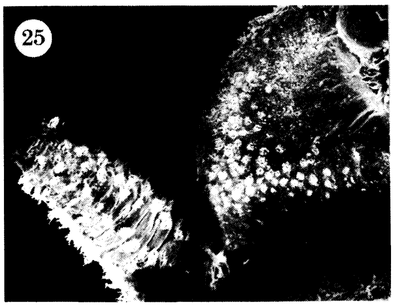
FIGURE 26. *Lepetodrilus pustulosus*: contracted cephalic tentacle with groups of sensory cilia. (Magn. × 420 approximately.)

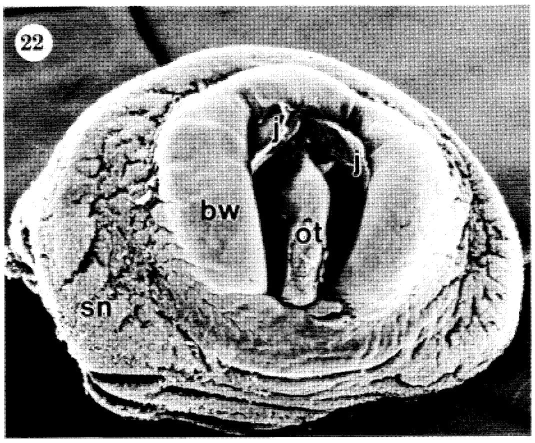


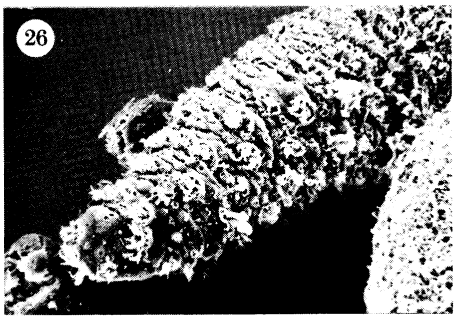




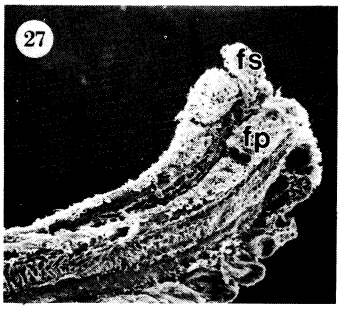


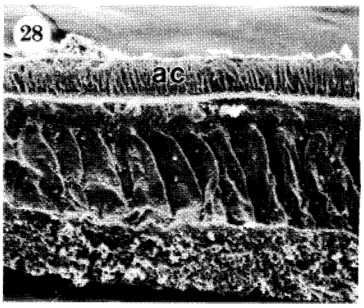


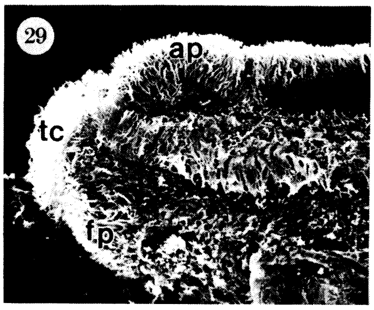


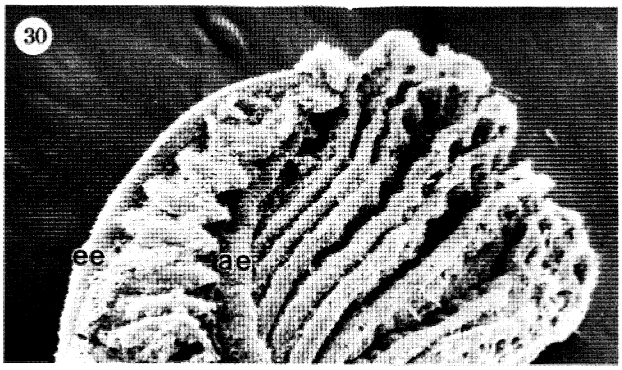


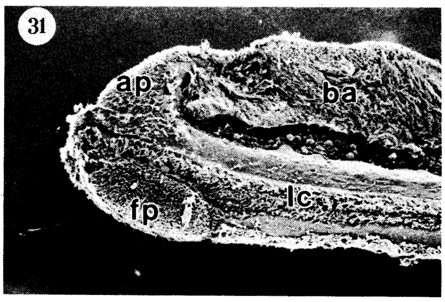
FIGURES 20–26. For description see opposite.

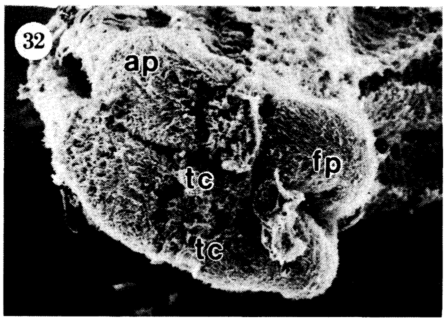


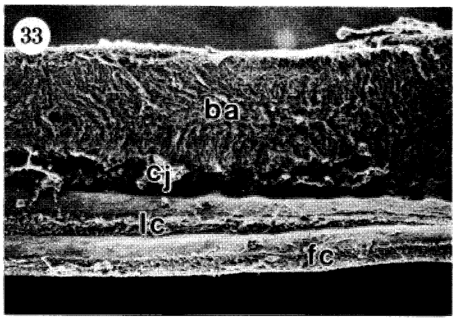


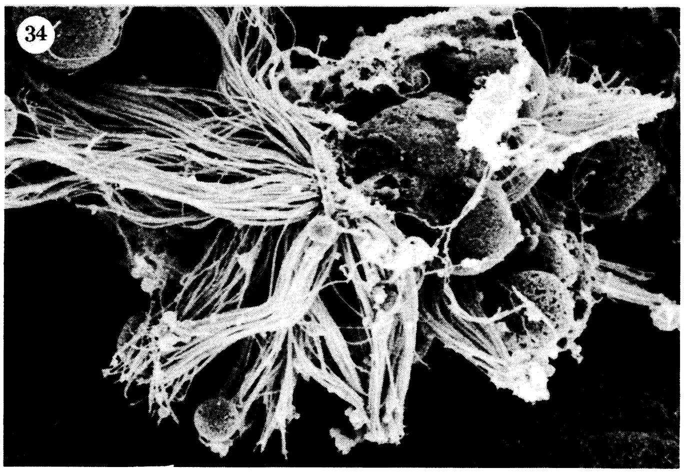


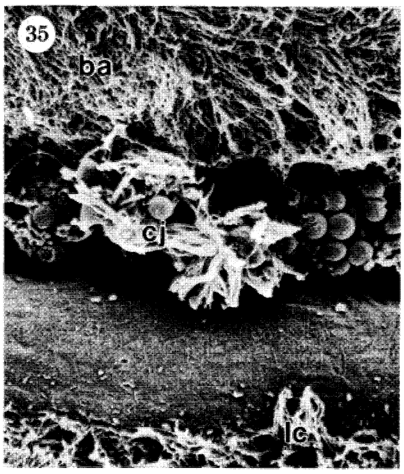












FIGURES 27–35. For description see opposite.

DESCRIPTION OF PLATE 2

Fine cilia, expecially those of the lamellar tip, were damaged during preparation for SEM, and this had the advantage of revealing their origin.

FIGURE 27. *Lepetodrilus pustulosus*: free ends of two consecutive gill lamellae, frontal surface uppermost. (Magn. × 115 approximately.)

FIGURE 28. *Lepetodrilus pustulosus*: part of gill lamella, lateral view. The lateral and frontal cilia are obscured by adherent food particles. (Magn. × 115 approximately.)

FIGURE 29. *Lepetodrilus guaymasensis*: free tip of gill lamella. (Magn. × 210 approximately.)

FIGURE 30. *Lepetodrilus pustulosus*: bipectinate tip of gill. (Magn. × 115 approximately.)

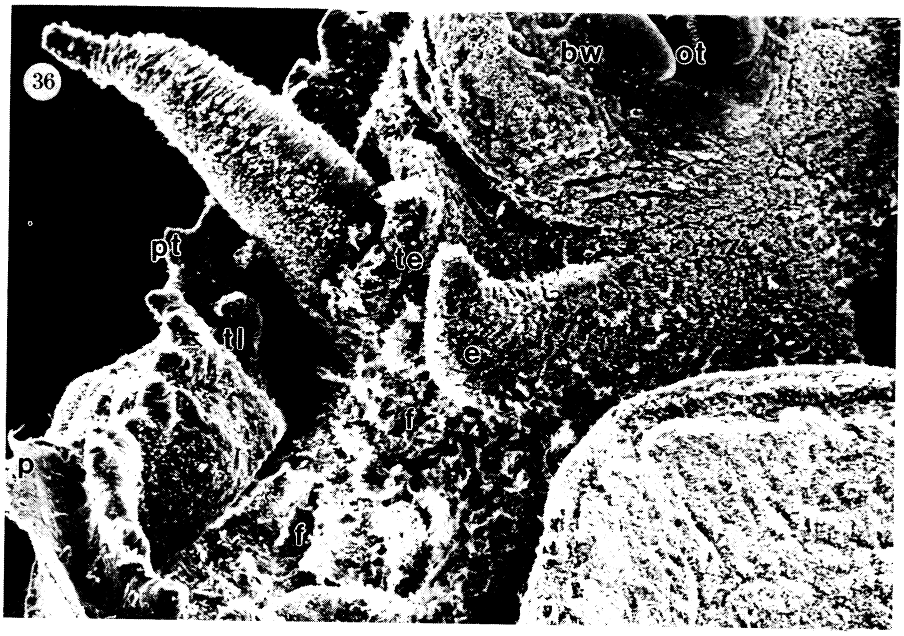
FIGURE 31. *Lepetodrilus fucensis*: free tip of gill lamella, frontal tip below. (Magn. × 105 approximately.)

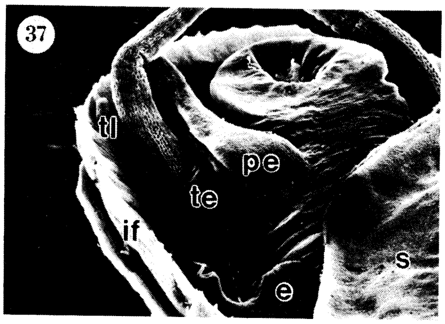
FIGURE 32. *Lepetodrilus fucensis*: tips of two consecutive gill lamellae. (Magn. × 160 approximately.)

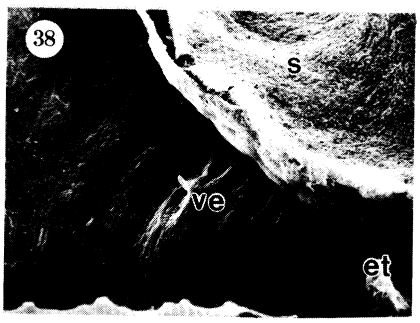
FIGURE 33. *Lepetodrilus fucensis*: part of gill lamella, lateral view, frontal edge below. (Magn. × 80 approximately.)

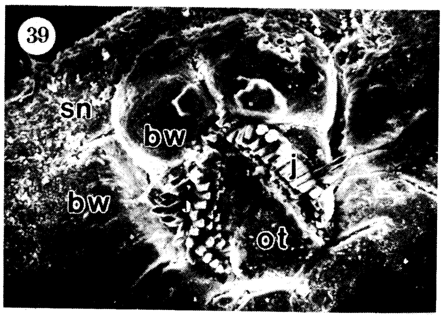
FIGURE 34. *Lepetodrilus fucensis*: enlargement of ciliary junction. (Magn. × 1690 approximately.)

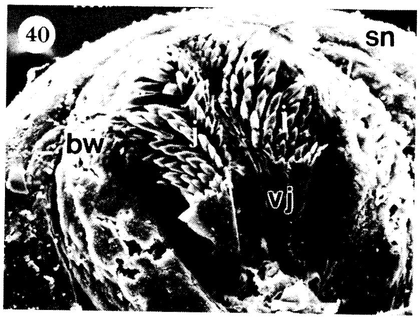
FIGURE 35. *Lepetodrilus fucensis*: ciliary junction; nature of spherules unknown. (Magn. × 380 approximately.)

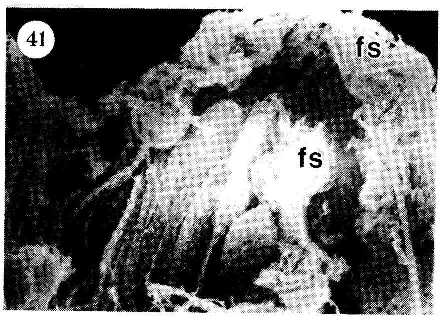


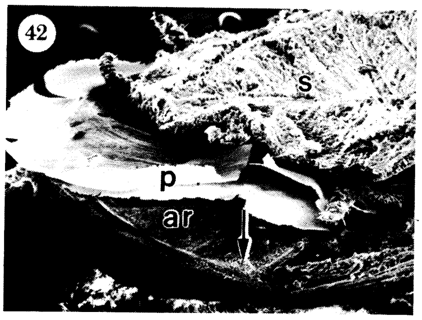












FIGURES 36–42. For description see opposite.

revealing the gill axis. The epipodium is relatively broad and more or less restricted to the length of the origin of the shell muscle. The arrangement of its tentacles, the single pallial tentacle on the right and the three processes related to the base of the right cephalic tentacle are similar to those of the other species.

One unusual character of the limpets belonging to this genus is the origin of the penis from the left side of the snout. In this specimen the penis is directed posterodorsally, resting over the base of the neck. Before copulation it must suck up sperm liberated from the urinogenital opening. A groove along the mantle skirt leads anteriorly from this opening (figure 18*b*) and curves to the left over the gill, suggesting that this is the course of the extended tip of the penis during this process. In contrast to *Gorgoleptis emarginatus* there is no prominent prostate. It is unfortunate that no female was available for investigation. The single male was in poor condition and rendered the course of the blood to the gill filaments and details of the urinogenital system uncertain.

DISCUSSION

Prosobranch limpets are derived from ancestors with spiral shells, a transformation well known in each Recent superfamily of archaeogastropods. It also occurs in some Neritacea, in Calyptraeacea and Hipponicacea among Mesogastropoda and in two genera of Neogastropoda, *Concholepas* and *Quoyula* (Robertson 1970). This body form is related to a sedentary and semisedentary existence in places where appropriate food is abundant. The food is varied. The archaeogastropods and neritaceans eat detritus gathered by the radula, *Concholepas* eats barnacles and the calyptraeaceans are suspension feeders. *Hipponix* (Yonge 1953) and *Capulus* not only collect particles from the water stream ventilating the mantle cavity, but with a pseudoproboscis take other food within their reach (Sharman 1956).

The clinging habit of limpets is associated with attainment of external bilateral symmetry, loss of the operculum, the migration of retractor muscles from the columella and the attachment of pallial muscles to the shell. For most the shell forms a complete cover when the body is clamped to the ground, and allows the mollusc to ride over temporarily adverse conditions.

DESCRIPTION OF PLATE 3

FIGURE 36. *Lepetodrilus pustulosus*: female, right side of head and front end of foot seen obliquely. (Magn. × 160 approximately.)

FIGURE 37. *Lepetodrilus cristatus*: male, anterior end of body seen ventrally from right. The flagellum of the penis broken off. (Magn. × 38 approximately.)

FIGURE 38. *Lepetodrilus cristatus*: vestigial sensory process on right. (Magn. × 107.5 approximately.)

FIGURE 39. *Gorgoleptis spiralis*: frontal view of snout with jaws and odontophore partly protruded. (Magn. × 225 approximately.)

FIGURE 40. *Gorgoleptis emarginatus*: frontal view of snout with jaws partly protruded (Magn. × 260 approximately.)

FIGURE 41. *Lepetodrilus pustulosus*: particles trapped on lateral cilia encircling tip of lamella. (Magn. × 2000 approximately.)

FIGURE 42. *Gorgoleptis spiralis*: posterior end of body, oblique lateroventral view. The inner mantle fold with the periostracal groove is reflected under the posterior end of the foot at point marked by arrow; the outer mantle fold which secretes the shell is not involved in this. The area between these two folds is expanded and covered by a double sheet of periostracum. (Magn. × 66 approximately.)

Shell, radula and anatomy are indicators of gastropod relationships: the palaeontologist relies on the first, and comments on anatomy must be deductive. Discovery of limpets from hydrothermal vents aroused considerable attention because they appeared to be archaic and would allow the palaeontologist to check deductions on living forms. The first hydrothermal-vent limpet to be described was *Neomphalus*: it showed no relationship with other genera and displayed a mosaic of archaeogastropod and mesogastropod characters, the latter outweighing the former. This reinforces the view that there are no rigid boundaries between these two groups, erected for convenience by the taxonomist. The organization of the nine other species now under discussion also excludes close relationship with genera previously known. The species show a number of dissimilarities in external features which allow grouping into two genera, a more advanced form, *Lepetodrilus*, and a less advanced one, *Gorgoleptis*, which still retains a reduced metapodium and operculum, though the outstanding feature in their organization is their many anatomical similarities, and it is clear that their transformation to the limpet form has followed different routes.

In species of both genera, generalized archaeogastropod characters are numerous. There are two auricles and the rectum passes through the ventricle; there are two kidneys each linked to the pericardium by a canal, and the gonad discharges into the right one; the gill is basically bipectinate. The radula is rhipidoglossate and enters the buccal cavity by a radular diverticulum; the salivary glands are simple pouches opening to the buccal roof; lateral glandular pouches along the oesophagus anteriorly overlap the posterior part of the buccal mass; their walls are folded and papillate. The intestine has a loop extending forwards from the stomach to near the origin of the posterior oesophagus. The nervous system is primitive in that the cerebral ganglia are far apart at the base of the tentacles and are linked by a stout commissure passing around the anterior wall of the buccal cavity; the cerebropleural and cerebropedal connectives are long, and the pedal and pleural ganglia partly fused; the pedals extend along the foot as elongated cords connected by commissures; nerve cells are not totally concentrated in ganglia; the statocysts have numerous statoconia. Unlike most archaeogastropods however, the labial ganglia are represented by lobes of the cerebrals. Other primitive features relate to the importance of the epipodium and its tentacles and sense organs, also to the discharge of eggs which at least in most species must be devoid of secondary membranes.

The most obvious anatomical links are with the trochaceans. These also have a single ctenidium, the left, which may be only in part aspidobranch, and a single osphradium; the left kidney lies within the mantle skirt and the right, larger and spreading among the viscera, receives the gonadial duct. In trochaceans, as in *Lepetodrilus* species, the epipodial fold all but encircles the foot and there is a neck lobe behind each cephalic tentacle, the base of which is surrounded by a cephalic lappet, perhaps homologous with the fold encircling the tentacle of *Lepetodrilus* species. The vascular system has a similar plan. It indicates descent from gastropods with two potentially equally well-developed ctenidial areas. In the venous system blood from the viscera traverses the right kidney and drains into its efferent vein. This vessel is joined by a branch from the anterior part of the ventral visceral sinus (Fretter & Graham 1962), and the combined flow supplies the transverse pallial vein, through which blood passes to the ctenidium, and the anterior pallial vein which supplies the roof of the mantle cavity. The vascular connections of the left kidney are also with the transverse pallial vein and with the efferent branchial vein near its entry to the left auricle, but directly with the auricle in

Lepetodrilus in which the posterior extension of the gill isolates the kidney from this vessel. There are two important ways in which *Gorgoleptis* does not exhibit these trochacean links: firstly, the epipodium is restricted to the sides of the foot, though the processes at the base of the right cephalic tentacle may have had such an origin. Secondly, the left kidney is small and no vascular connection with the left auricle has been traced, though this may be the result of poor fixation.

The concentration of the postcephalic ganglia is found in zeugobranchs and trochaceans (Haller 1886). They also exhibit a pleural commissural tract. The fact that nerves related to these ganglia are compound fits with the idea that pleurals and pedals at this level act as a single unit. There is no macroscopically visible pleural commissure in higher prosobranchs, apart from the neritaceans (Bourne 1908), but commissural tracts must persist, and, as the pleurals migrate towards the cerebrals, become incorporated in pleuropedal connectives and pedal commissure. In the unpredictable environment related to hydrothermal vents survival may depend on the rapid correlation of sensory- and motor-nerve centres enabling the limpet to retreat suddenly into the shell and remain motionless. To this end the compound nerves related to the pallial edge and the foot of lepetodrilaceans must be of the greatest importance. On the basis of size and complexity of connections the suboesophageal nerve centre could thus be regarded as of greater importance than the cerebral, whose activity may be limited to the control of the head.

The shell of *Lepetodrilus* species represents the last whorl of a helicocone with a minute apical protoconch. Beneath the apex a shelf projects forwards from the posterior face of the protoconch to form its columellar lip. During later growth it remains small and insignificant. From this stage growth has been radial: it is maximal anteriorly and minimal posteriorly, and in extreme cases this differential growth results in positioning the protoconch behind the posterior margin of the aperture (*Lepetodrilus guaymasensis*) and well below the highest elevation. Except for differences in rate of growth these are also characters of some fissurellids, the patellacean *Propilidium* and the neritacean *Phenacolepas*. In these limpets, and in prosobranchs in general, the periostracum is formed close to the site of secretion of the calcareous matter of the shell. It originates from the base of the median side of the outermost of three pallial folds. In lepetodrilaceans there are only two closely associated folds at the mantle edge; the periostracum arises towards the base of the outer surface of the inner, and encloses the outer. The inner fold, glandular and with sensory tentacles, probably represents a fusion of the middle and inner folds of zeugobranch limpets; any structure lateral to this must relate to the outer fold. The shell is secreted from an area near the edge of the outer fold which in *Lepetodrilus* is remote from the periostracal secreting groove. The remoteness results in a broad inturned band of periostracum free from the shell. The extreme flexibility of the recently formed secretion is evident when the limpet is fully contracted. In most species the edge of the outer fold is double and although the outermost part secretes the shell the inner may perhaps manipulate or control movement and positioning of the periostracum. A similar inturned rim in *Gorgoleptis* is narrow and somewhat thinner. Thus the periostracum not only protects the surface of the shell but also its growing edge against detrimental effects of a possibly adverse environment.

The shell of *Gorgoleptis* species indicates that these limpets have followed a different evolutionary course from *Lepetodrilus*. The columellar edge of the initially dextral shell of little more than one whorl remains an integral part of the peristome of the adult shell situated at the base of a posterior embayment. It is identified by the umbilical groove, in addition to its position, and here growth is limited except for some thickening and elongation. Its limits are marked by posteriorly directed flanges, dissimilar in detail, resulting from differences in their origin, the right being an outgrowth of the outer lip adjacent to the columellar edge and the left originating from the left limit of the columellar lip, as indicated by a groove in *Gorgoleptis patulus*.

The shell muscles of the two genera as indicated by scars are dissimilar from one another and from those of other limpets. They mark the attachment of pedal and pallial retractor muscles. Each pedal muscle of *Gorgoleptis* is short, not extending beyond the posterior end of the mantle cavity and continuous anteriorly and posteriorly with a thick band of pallial muscles, the posterior band narrowing and most reduced in the region of the inturned periostracum. The two limbs of the pedal muscle are considerably elongated in *Lepetodrilus* in accordance with its more advanced limpet form, but although the majority of its fibres are pallial the narrow band joining them has few passing to the foot. Pallial muscles also insert laterally and anteriorly alongside each pedal limb (figure 19).

The adoption of the limpet form affects the disposition of the gonad and digestive gland in relation to the depth and position of the mantle cavity, itself related to the size of the gill. In docoglossans viscera are accommodated solely posterior to the shallow cavity over the head, which either contains no ctenidium (Patellidae, Lepetidae) or only one lying across the cavity (Acmaeidae). In the neritacean limpets (Fretter 1984) and *Lepetodrilus*, each with a single large ctenidium, the mantle cavity attains a depth comparable to that of a coiled gastropod: not only is the length of the cavity aligned with the maximal anterior growth of the snail but the cavity also spreads back above some viscera. Its maximal depth is attained in *Lepetodrilus* because viscera are accommodated ventrally as far forwards as the head–foot; in those species in which there is an enlarged apex overhanging the posterior margin of the shell it occupies four fifths of the body length. *Gorgoleptis* is unique with respect to the position of the gonad, which spreads forwards into an enlarged haemocoelic space lateral to each shell muscle broadening the body and enhancing adhesion.

The method by which these limpets feed can be deduced only from the structure of the food-collecting apparatus, the varied positions of its parts in preserved specimens, food particles associated with them and the contents of the gut. The last two show that they must utilize the bacterial mat by brushing a nearby surface and ingesting the particles so loosened, or rely on the gill lamellae to collect bacteria in suspension. The former is the more primitive method of food collecting, characteristic of snails with a rhipidoglossate radula, and seems to be the only method employed by *Gorgoleptis emarginatus*, and probably the other two species of this genus. However, the action of both jaws and radula is unusual.

In *Monodonta lineata* it has been shown (Nisbet 1953; Fretter & Graham 1962) that the jaws – cuticular thickenings on a buccal fold – are concerned with an early stage in the feeding cycle: they press against the radula as the odontophore moves forward and prevent the teeth opening until a level more anterior than their tips has been reached. By contrast, the jaws of *Gorgoleptis emarginatus* must be protruded beyond the margin of the shell before the emergence of the odontophore to loosen particles from the substratum over the limpet's head. Each jaw fold is inflated by blood to bring it into position and maintain its turgidity, whereas the action of muscles to the individual rods will cause them to carry out a scrubbing action. The particles will then be collected by the radula which has been directed dorsally by the protruding odontophore. In all lepetodrilaceans the initial ventral movement of the odontophore tip typical of prosobranchs has been suppressed, and the second phase, when it is moved dorsally (figure 20, plate 1; figures 39 and 40, plate 3) and then withdrawn, is exaggerated. The dorsal movement has become more extensive because the odontophore is free from the restraining effect of the snout which is under the influence of the cephalic levator and retractor muscles. These muscles are in a position corresponding to the proboscis muscles of monotocardians.

The evidence collected infers that *Lepetodrilus* is a suspension feeder and also gathers particles loosened from a substratum: the two methods of feeding may proceed concurrently. Evidence for it being a suspension feeder soon became apparent, but wear on the jaws, sometimes excessive, indicates that they have played a more forceful role than ingestion of a food string from the mantle cavity. Like the jaws of *Gorgoleptis* they are scrubbers, their pointed rods diverging on protrusion, but, by contrast, these do not arise from dilated pads well removed from the protruded radula and retracted at the same time as the radula with the collected food. They must abrade the surface over the limpet's head shortly before the odontophore is fully protruded with the radula directed towards the site of their activity, then, as full protrusion of the radula occurs, swing back and down so that the rods face inwards and are hidden by the fold which bears them. Towards the completion of the radular withdrawal the tips of the jaws may protrude to aid in the final manipulation of the food mass. The radula is more highly specialized than in *Gorgoleptis*, in particular the lateral teeth: the first is comparatively large with a broad shaft and finely divided cusp (part I; Hickman 1983), the other four interlock by a lateral expansion on each shaft. Unlike other rhipidoglossate prosobranchs the central part of the tooth rows of the retracted radula dip posteriorly as in some flesh-tearing monotocardians (*Tiariturris libya* (Shimek & Kohn 1981)). When the radula comes into action the first laterals, separated by a small rachidian, will be the first teeth to protrude and act. The gut of limpets taken from *Riftia* washings contained pieces of *Riftia* tube of approximately equal size, perhaps initially ripped off by the jaws and then fragmented by the first lateral teeth; ingestion would be facilitated by the combined action of the four interlocking laterals on each side, while the marginals sweep up the loose particles so abundant on this substratum. This ingestion of *Riftia* fragments may relate to observations made by C. Van Dover and C. Berg. They collected *Riftia* tubes to which limpets were known to attach at 21° N, and some tubes had pockmarks thought to be caused by the rasping of the limpets (personal communication). Presumably, the tube is taken for its thick microbial covering: the latter appear to be digested whereas fragments of the tube remain (figures 20 and 21).

When *Lepetodrilus pustulosus* grazes the whole buccal area is protruded to reach an area beyond the shell margin: there is no evidence that the head emerges, or has need to emerge from under the shell, when the limpet ingests food collected by the gill.

All filter-feeding prosobranchs previously described have a single left filamentous gill with all filaments crossing the mantle cavity to the right side. The mantle cavity is elongated in accordance with the need for a longer gill, so increasing the force of the inhalant current and the filtration area. Particles are trapped on a mucous sheet (Werner 1959) and the tips of the filaments to which this is transported are related to a longitudinal pathway or groove on the dorsal body wall which leads to the mouth, though this pathway may only be well defined anteriorly (Calyptraeacea). Monotocardians with a single monopectinate gill have clearly made such adjustments with minimal modifications, but when this method of feeding is adopted by forms with aspidobranch gills, which are typically paired, greater change is required. This involves the loss of the right gill and the loss, reduction or realignment of the dorsal (left) lamellae of the left gill and elongation and change to a filamentous form of the ventral (right) ones. The only known trochacean filter-feeder, *Umbonium* (Fretter 1975), has developed a monopectinate gill by losing one row of lamellae; whereas in *Neomphalus* (Fretter *et al.* 1981), the only filter-feeding rift limpet already described, the positioning of the gill axis of the conspicuously enlarged left gill has been modified so that both sets of filaments are directed to the food groove. The modification of the gill of *Lepetodrilus* is similar to that of *Umbonium*, but the gill is lamellar, the anterior end typically free and biramous, and particles are trapped on cilia as in lamellibranchs (Owen 1974) and not on mucous sheets (figure 28, plate 2). Although the dorsal (left) lamellae at the free tip are insignificant compared with the ventral (right) lamellae, their ciliation will increase the force of the inhalant current to the mantle cavity, the folded anterior edges of the lateral epipodial folds obstructing its passage to the lateral pallial cavity: limpets with the deepest mantle cavity have the biramous area best developed. The increased respiratory surface provided by folded lateral surfaces of lamellae may be important in an environment of fluctuating conditions.

The effective beat of cilia on the gill lamellae is likely to be similar to that of other prosobranchs: the laterals beating abfrontally and frontals and abfrontals towards the tip, where, in prosobranch suspension feeders previously described there is a forwardly directed current (Yonge 1938). In the absence of living material the way in which particles are driven forwards in *Lepetodrilus* can only be surmised. Of the areas on the lamellar tip that might be responsible for this, the ciliated pads and intervening band of cilia, the last is frequently clogged with particles whereas the pads are clean (figures 31 and 32, plate 2; figure 41, plate 3). This suggests that the ciliary beat on the pads retains the alignment of that of the ciliary rows with which they are in contact, giving increased strength to the current directed on to the area between them where the cilia are responsible for the forward drive. The ciliated tract underlying the lamellar tips may add strength to the forward current, but the cilia appear too insignificant to be a major force; however, they become longer and more numerous as the tract continues around the fold at the base of the right tentacle. Numerous particles, some identical with prokaryotic cells, have been found between this fold and the underlying epipodial lobe (figure 36), that is towards the base of the penis in the male; all these are ciliated areas. In several limpets, especially *Lepetodrilus pustulosus*, the partly protruded odontophore was directed towards the right and in two the radula, although not fully open, was gripping a food mass.

A sedentary or semi-sedentary mode of life is associated with prosobranchs that are virtually exclusively filter feeders. It would seem that neither habit applies to *Lepetodrilus*. Video tapes have shown that *Lepetodrilus pustulosus* is fast moving over the tubes of *Riftia* (Galapagos Rift, *Alvin* dive, January 1979) and Verena Tunnicliffe (personal communication) has observed large numbers of *Lepetodrilus fucensis* quite mobile over the pitted surfaces of sulphide deposits (Endeavor Segment, Juan de Fuca Ridge) where bacteria and detrital material will accumulate.

Elongation of the post-tentacular region of the head, related to the method of feeding and maximal anterior growth, has affected features of the nervous and alimentary systems. The cerebropleural and cerebropedal connectives are long, extending the length of the paired oesophageal glands, and the visceral connectives cross near the origin of the posterior oesophagus; streptoneury is tight. These features of the nervous system are shared with *Neomphalus*. They contrast with *Pleurotomaria* (Woodward 1901) in which the mantle cavity is also deep, but the depth is not related to differential growth, and the visceral loop is long, so that a considerable length of the oesophageal glands is involved in torsion, and with the docoglossans (*Patella*, *Acmaea*) in which the general reduction in importance of the mantle cavity has resulted in the shortening of that part of the body and the visceral loop is almost vertical and anterior to the oesophageal glands (Fretter & Graham 1962). In archaeogastropods in general the lateral glandular pouches extend along the length of the mid-oesophagus and the lateral walls of the short anterior oesophagus form separate pouches which may accommodate food during feeding. In lepetodrilaceans there are buccal pouches, but none related to the anterior part of the oesophagus, which is indistinguishable as a separate entity because the paired oesophageal glands extend from the buccal region to the posterior oesophagus, as they do in *Mikadotrochus* (Fretter 1964). The dorsal expansion of the gland over the odontophore and ventral expansion posterior to the cartilages is atypical. In *Lepetodrilus* this unusual size may not only compensate for the slight degree of folding of the walls, but may relate to hydrostatic functions as suggested for the oesophageal sacs of monoplacophorans (Wingstrand 1985) for which it is said that anterior ones may influence the positioning of the radula. In the living lepetodrilid hydrostatic pressure set up by the anterior part of the gland, where the lumen is large, and which is separated from the posterior by a sheet of dorsoventral muscles attached to the body wall, may be important in the protrusion of the buccal mass.

The stomach displays typical features of prosobranch gastric anatomy. The oesophagus opens on the right posteriorly and the intestine emerges from the anterior end of the style sac. There is an extensive cuticularized area, the gastric shield, and between it and the intestinal groove is a sorting area. The broad openings to ducts of the digestive gland are near the oesophageal opening, surrounded by ciliated epithelium. The reduction or loss of the caecum may be related to the reduction or loss of coiling of the visceral mass and the adoption of a limpet form (Graham 1939). In all lepetodrilaceans the intestine is relatively short, contrasting with the long intestine of archaeogastropod limpets, with the exception of the fissurellaceans.

The well-developed pallial circulation of *Lepetodrilus* indicates that the respiratory surface provided by the enlarged gill may not always fulfil all respiratory requirements. Alternatively, because ctenidial and pallial circulations are to some extent independent, there may be occasions when only one can serve a major role. When the limpet is attached firmly to the substratum the vascular flow through the fine haemocoelic spaces in the contracted shell muscle must be reduced, even stopped; consequently, at such a time, the blood will take the alternative route and ctenidial circulation be of major importance. In the limpets examined, the shell muscle and pallial edge contracted simultaneously.

A striking feature of the vascular system is the number of filter chambers in the auricular walls, varying in number and size from auricle to auricle. They appear to be more restricted in occurrence in *Lepetodrilus pustulosus* than in some other species of that genus in which almost the entire auricular surface is involved. Their size and arrangement in the exceedingly large left auricle of *Lepetodrilus guaymasensis* approaches that of the freshwater prosobranch *Viviparus* (Andrews 1979). Muscles radiate from the central part of the auricle, which refills the ventricle at systole and isolates groups of filter chambers where blood is retained and subjected to pressure. Molecules up to a given size pass through the epicardium to the pericardial cavity: this constitutes the primary urine. Little quantitative work has been done on the porosity of the epicardium of the prosobranch ventricle. Økland (1982) has shown that it is porous in *Patella vulgata* and probably contributes to urine formation by ultrafiltration. The vascularization of the pericardial wall by haemocoelic spaces associated with the visceral haemocoel is particularly obvious in *Lepetodrilus elevatus*, *Lepetodrilus fucensis* and *Lepetodrilus guaymasensis*; this also occurs in *Haliotis* (Crofts 1929). The elaboration of the pericardium coupled with the activity of the auricular walls suggests a high cardiac filtration rate.

Because the functioning of the heart is dependent on the maintenance of a constant volume of the pericardial cavity, the mechanism for dealing with this high production of primary urine must be important. Fluid escapes from the cavity by renopericardial canals, and in both sexes of all known members of the Lepetodrilacea there is a canal to each kidney. The right canal is typically the longer and closely applied to the final course of the right pallial vein; its opening to the pericardial cavity is near the opening of the vein to the right auricle. Both canals are ciliated, the ciliation of the right spreading on to the pericardial wall in *Lepetodrilus*, and beneath the epithelium is a thin layer of muscles. Owing to poor fixation, little histological detail of the epithelium can be given. However, the glandular nature of the epithelium of the broad right canal in *Gorgoleptis marginatus* is very evident and this, with the close association with the right pallial vein, suggests that it is responsible for some modification of the primary urine passing through it. Of the species studied in detail, this one also stands apart in having a large funnel, glandular and ciliated, at the entrance of the canal to the left kidney.

The siting and histological detail of the left kidney conform with those of the papillary sac of trochaceans, but the wall is not folded to form papillae. The kidney is isolated from the rest of the viscera and has short, broad, vascular connections with the transverse pallial vein and directly with the auricle, not the base of the efferent branchial vein as in *Haliotis* (Crofts 1929), *Mikadotrochus* (Fretter 1964) and trochids (Fretter & Graham 1962). Its renopericardial duct, relatively short and broad, opens widely to that part of the pericardium directly under the influence of pressure changes brought about by the action of the large left auricle, and is likely to be of greater importance in regulating the pressure of the pericardial fluid than the longer right duct. It may be deduced that the function of the kidney is the same as that of the papillary sac of other diotocardians (Harrison 1962; Delhaye 1976; Andrews 1985) and that its primary concern is the resorption of solutes from the fluid it receives. Because the blood vessels associated with the kidney appear to have no valvular control, and one is directly under the influence of the heart beat and arises on the direct course of oxygenated blood entering the auricle, it is assumed that the vascular supply to the kidney is arterial, meeting a high metabolic demand, and is influenced by systole and diastole, the connection with the transverse pallial vein being of minor importance. A special part of the kidney is associated with the pericardial wall, in a position that would receive a direct supply of arterial blood at systole. This is the nephridial gland which is present in both genera. It is particularly pronounced in *Lepetodrilus fucensis* and *Lepetodrilus guaymasensis* appearing as papillae bathed in blood and covered by cuboidal cells. Delhaye (1976) observed the similarity of the gland in trochids and *Littorina* and for some time the function of regulating the ionic concentration of the blood has been assigned to it (Fretter & Graham 1962); this function agrees with its ultrastructure in *Littorina littorea* (Andrews 1981). Far from having a well-developed nephridial gland, *Lepetodrilus fucensis* has a reduced left kidney. It will be recalled that this is the only known limpet that harbours bacteria on the gill lamellae, the innermost of which are endocytosed (De Burgh & Singla 1984). It may be that these two features are interrelated. It is assumed that the strong ciliary junctions that unite the gill lamellae in this species are related to the presence of bacteria, because neither occurs in other species. These junctions will maintain the distance between the lamellae where the water current passes to the suprabranchial chamber, and they may also provide a measure of the growth of bacteria and stimulate their ingestion when growth might block the water passage.

The right kidney, in contrast to the left, is a ramifying system of spaces forming an extensive area closely associated with the visceral haemocoel, in particular the digestive gland on the right side of the body, accompanying it to the site of torsion anteriorly and to the anterior limit of the stomach posteriorly. Its lumen, unlike that of the left, contains spherules freed from the epithelium. Such characteristics conform with those of the right kidney of archaeogastropods, which is known to be responsible for nitrogenous excretion (Harrison 1962; Delhaye 1976; Andrews 1985).

The opening of the right kidney is urinogenital: in genera of archaeogastropods previously studied a short gonadial duct discharges to the renopericardial canal (Trochacea, *Diodora*) or the kidney (*Patella*), both near the external opening. In lepetodrilaceans, however, the gonadial duct approaches that of monotocardians in length and function. In the male it acts as a vesicula seminalis and in the female regulates the rate of liberation of the eggs. Except for the male of *Lepetodrilus fucensis* it discharges to a section of the right kidney contiguous and lateral to the excretory part, which receives the renopericardial canal anterior to the gonadial duct, and, with the exception of *Lepetodrilus pustulosus*, no communication with the excretory part has been traced. This section corresponds with the renal genital duct of monotocardians which, however, has lost the pericardial connection in males. In no known prosobranch does a separate renal genital duct coexist with a functional right kidney. In monotocardians this duct is solely conducting as it appears to be in most species of *Lepetodrilus*, but in *Lepetodrilus fucensis* its structure and the presence of sperm indicate that eggs may be fertilized there and receive secondary membranes. Further study may show that this additional function applies to *Gorgoleptis emarginatus*.

The pallial section of the genital duct of monotocardians provides prostatic fluid in the male, and in the female sperm pouches, albumen and protective covering for the eggs. In this respect the male lepetodrilacean is monotocardian, but not the female, except that in *Lepetodrilus* species there is a large receptaculum. The fact that a penis is present in all species of this new superfamily, and has evolved more than once, indicates that sperm are not broadcast. It ensures that the eggs are fertilized in a limited and more controlled environment than that of the external medium. *Lepetodrilus* species are characterized by an epipodial penis on the right side of the head with an open seminal groove: by contrast, the presumed penis of *Gorgoleptis emarginatus* and *Gorgoleptis patulus* is unlike that of any known prosobranch in origin and structure, because it arises from the left side of the snout, has no direct connection with the urinogenital opening and must function as a pipette. Observations on *Lepetodrilus pustulosus* indicate that copulation is not associated with internal fertilization. In three females a maximum of six eggs with no secondary membranes was in the mantle cavity surrounded by sperm freed from prostatic secretion; sperm were in the receptaculum, none had entered the renal section of the oviduct. In *Lepetodrilus fucensis*, the number of sperm in the renal section of the oviduct was negligible compared with those in the receptaculum. No eggs were present with the sperm, which were presumably a residue of a previous spawning when the liberation of eggs from the gonadial duct stimulated their entry into the oviduct. Because no embryos have been found in the mantle cavity of any species it is assumed that the fertilized eggs are soon liberated, naked except for a fertilization membrane, perhaps unusually resistant. The fact that animals of one species, *Lepetodrilus pustulosus*, found in widely separated vents are anatomically indistinguishable, is indicative of larval dispersal involving an extensive planktonic stage. Batten (1984) suggested this for *Neomphalus* as a result of a study of the protoconch.

There is evidence that female limpets attain sexual maturity at an early stage: some a third of their maximal size had ripe eggs and sperm in the mantle cavity (*Lepetodrilus pustulosus*, Galapagos Rift). However, in the males available for study the penis at a corresponding size was not always fully developed. The condition of the gonad and secondary sexual structures in both sexes indicate that spawning is a more or less continuous process, though the number of eggs liberated at any one time is perhaps limited. This may result in a short life-span.

In attempting to describe the descent of rift limpets it may be deduced that the immediate ancestor from which members of the Lepetodrilacea were derived had a low dextrally coiled shell with the columellar lip short and limited by columellar and labial expansions. These are characters of the shell of members of the more primitive family, the Gorgoleptidae, and there is evidence that members of the Lepetodrilidae exhibit them at a very early stage. Among sulphide particles on the foot of adult *Lepetodrilus fucensis* were two young limpets, 0.5 and 0.6 mm shell length, with the columellar lip similar to that of *Gorgoleptis*, but otherwise their appearance was lepetodrilid. The shell muscle of the ancestor would have been paired and related to the columella, with which it later lost contact, and with the pallial muscles originating closer to the apertural edge. The mantle edge had two folds, the inner with small tentacles at its edge, a single and more median larger tentacle near the exhalant area and the periostracal groove towards the base of its outer surface. The outer fold secreted the shell. There was a single left gill, wholly or partly bipectinate, without bursicles (Szal 1971). The foot had a well-developed metapodium with an operculum and an epipodium with sense organs. There was a well-developed snout, a rhipidoglossate radula and the odontophore turned dorsally to the feeding position. They were microphagous grazers. The paired cephalic tentacles were long, rich in sensory cilia which also occurred over the snout and epipodium. There were no eyes. Isolated sensory processes were related to the inhalant and exhalant parts of the mantle cavity. Sexes were separate. Because the penis has evolved more than once within the superfamily it was probably not present in the ancestor, though this does not exclude the possibility of fertilization within the mantle cavity of the female. The internal anatomy exhibited a number of characters that together indicate a primitive level of organization. These include large oesophageal pouches; an anterior loop of the intestine extending towards the level of the origin of the posterior oesophagus; the rectum passing through the ventricle, two auricles; two kidneys of dissimilar function, the right associated with the gonad; a hypoathroid–dystenoid nervous system with long cerebropleural and cerebropedal connectives and scalariform pedal cords.

Changes from this ancestral prosobranch are fewer in the Gorgoleptidae than in the Lepetodrilidae: the columellar lip is an integral part of the aperture, the pedal shell muscles are short, and the periostracal secreting groove related to the columellar edge inturns beneath the visceral mass and secretes a protective sheet of periostracum posterior to the insertion of those muscles. Of the three species that have been described, *G. spiralis* is the most primitive. It has the largest visceral mass, the longest columella and consequently the broadest sheet of protective periostracum: the most advanced is *G. emarginatus* with the shortest columella and narrowest periostracal inturning. Transformation from helicoid to patelliform shape as indicated by the breadth of the columella and consequent periostracal inturning starts progressively earlier in the three species.

The anatomy of only one rift limpet, *Neomphalus fretterae*, has been described previously and, as yet, no other species of this genus is known. Its assemblage of characters implies that it has a different origin and followed a different evolutionary pathway from the limpets described here; its morphological innovations related to the attainment of the limpet facies and to filter-feeding are, in many respects, unique, justifying its exclusion from any other group of living gastropods (McLean 1981; Fretter *et al.* 1981) and perhaps preventing further radiation into species. By contrast, nine species of lepetodrilaceans are now known, and if the relatively minor characters that are directly related to their environment be omitted, morphological innovations are few. Four species of *Lepetodrilus* (*Lepetodrilus pustulosus*, *Lepetodrilus elevatus*, *Lepetodrilus cristatus* and *Lepetodrilus ovalis*) have been collected from the 13° N and 21° N vents, and the first three also from the Galapagos vent. Because they have approximately identical radulae (Hickman 1983) and jaws used in an approximately identical manner, and because all four are also suspension feeders, they cannot be avoiding competition by trophic specialization. Unless there is sufficient food available to eliminate competition this must be minimized by spatial separation, each species in its own microhabitat. Although their anatomy is almost identical, specific isolation is ensured by differences in penis and female tract.

Neomphalus is also found at the same geographical sites and must therefore be involved in competition with the lepetodrilacean limpets. It also feeds in the same two ways, but because of the presence of a pronounced food-collecting groove and great hypertrophy of its gill, and because of our lack of observations on the use of the odontophore, owing to the failure to find specimens indicating its action and that of the jaws related to grazing, it is almost certain that the proportion of its total intake of food is greater from suspension feeding than by grazing. Nevertheless, the radula shows signs of wear. It would appear that most lepetodrilacean limpets explore more confined spaces than *Neomphalus* where the effective dorsal action of the odontophore (as opposed to the normal ventral one of *Neomphalus*) makes grazing possible, but suspension feeding less rewarding. This suggests that competition between these two totally unrelated limpet forms is partly based on habitat specialization and partly on trophic specialization.

The facts that two species of *Lepetodrilus* (*fucensis* and *guaymasensis*) both occur on sulphide rocks, do not occur with the others, are found in vents remote from them and each is apparently the only lepetodrilacean species there, indicate that they are detached occurrences. Fortuitous colonization of these sites may have been by more than one species, but only one survived in a habitat less endowed with a richness of ecological niches. Speciation may not have occurred because colonization is relatively recent, or at those sites there is little possibility of deme isolation.

The reader may find it helpful to have a concise summary of lepetodrilacean characters, and characters of the two genera indicating their relationship. Except for those marked with an asterisk, the features are those regarded as typical of archaeogastropods.

The shell of the lepetodrilacean represents the expanded last whorl of a low, dextrally coiled helicocone with the apex posterior to the highest elevation. The protoconch is small, its surface finely pitted. The teleoconch has radial ribs or lines, sometimes imbricate, sometimes beaded, and growth lines that may be more obvious than the ribs. There is *no nacreous layer. The periostracum is thick and *extensively inturned around the shell edge. The shell muscle scars, marking attachment of pedal and pallial muscles, are paired and may be united posteriorly. An epipodium with sense organs is well developed. There are *no eyes. The sexes are separate. The mantle cavity is deep and houses a *single left gill, typically bipectinate; a right pallial tentacle is associated with the exhalant passage and there are isolated sensory processes behind and ventral to the cephalic tentacles. There are two auricles with numerous filter chambers and the rectum passes through the ventricle; there are two kidneys, each with a renopericardial duct, the gonad discharging into a *special chamber of the right one by way of a *long gonadial duct which acts as a *vesicula seminalis. A *prostate is present. The radula is rhipidoglossate. The effective movement of the odontophore is *dorsal, that is the initial withdrawal phase of other prosobranchs; it collects particles loosened by the jaws from over the animal's head. The salivary glands are simple pouches, the lateral oesophageal pouches with *large cavities extend from the posterior end of the buccal region to the site of torsion, to which the anterior loop of the intestine also reaches. The stomach displays typical prosobranch features. Cerebral and labial ganglia are fused, the cerebropleural and cerebropedal connectives long; there is fusion of the postcephalic ganglia. The pedal cords are scalariform.

The initial whorl of the shell of *Gorgoleptis* (the more primitive genus) is pronounced. The columella forms an integral part of the peristome at the base of a *posterior embayment, with the umbilical groove alongside. Its extent is marked by posteriorly directed flanges, the right an outgrowth of the outer lip, the left originating from the left limit of the columella. The inturned rim of periostracum is narrow except in the region of the columellar edge where the groove secreting it *inturns beneath the visceral mass and secretes a protective sheet of periostracum beneath the viscera posterior to the mantle cavity. The two limbs of the shell muscle are short, not extending beyond the posterior limit of the mantle cavity. The epipodium is confined to the lateral regions of the foot and has elongated tentacles evenly spaced. There is a metapodium with a small operculum. The gonad is U-shaped, the two limbs spreading forwards between each shell muscle and the mantle edge, so broadening the body; the *penis is developed from the left side of the snout. Microphagous grazing is the only method of food collecting. In all these features *Gorgoleptis* differs from *Lepetodrilus*.

The initial coil of the shell of *Lepetodrilus* is very small and less than one whorl. Teleoconch growth is radial, maximal anteriorly, minimal posteriorly, and in some species results in the apex overhanging the posterior margin of the shell. The columellar lip, confined to the apical region, does not form part of the shell margin. Growth lines are marked and may be more prominent at intervals. The inflected edge of the periostracum is pronounced and of uniform breadth. The shell muscle is horseshoe-shaped, surrounding the viscera, the two lateral limbs connected posteriorly by a narrow band. The epipodium surrounds the foot laterally and posteriorly, bearing three pairs of short outgrowths, of which two are posterior; it extends on to the head, forming a *fold surrounding the base of each cephalic tentacle and the *penis at the base of the right one. The gonad is ventral to the stomach and intestine, speading beyond these on the left and posteriorly. In females there is a *receptaculum seminis. Ova are fertilized in the mantle cavity. The animals are suspension feeders as well as microphagous grazers, and both methods of feeding may proceed concurrently; *ciliary pads at the apex of the gill filaments are related to the former method.

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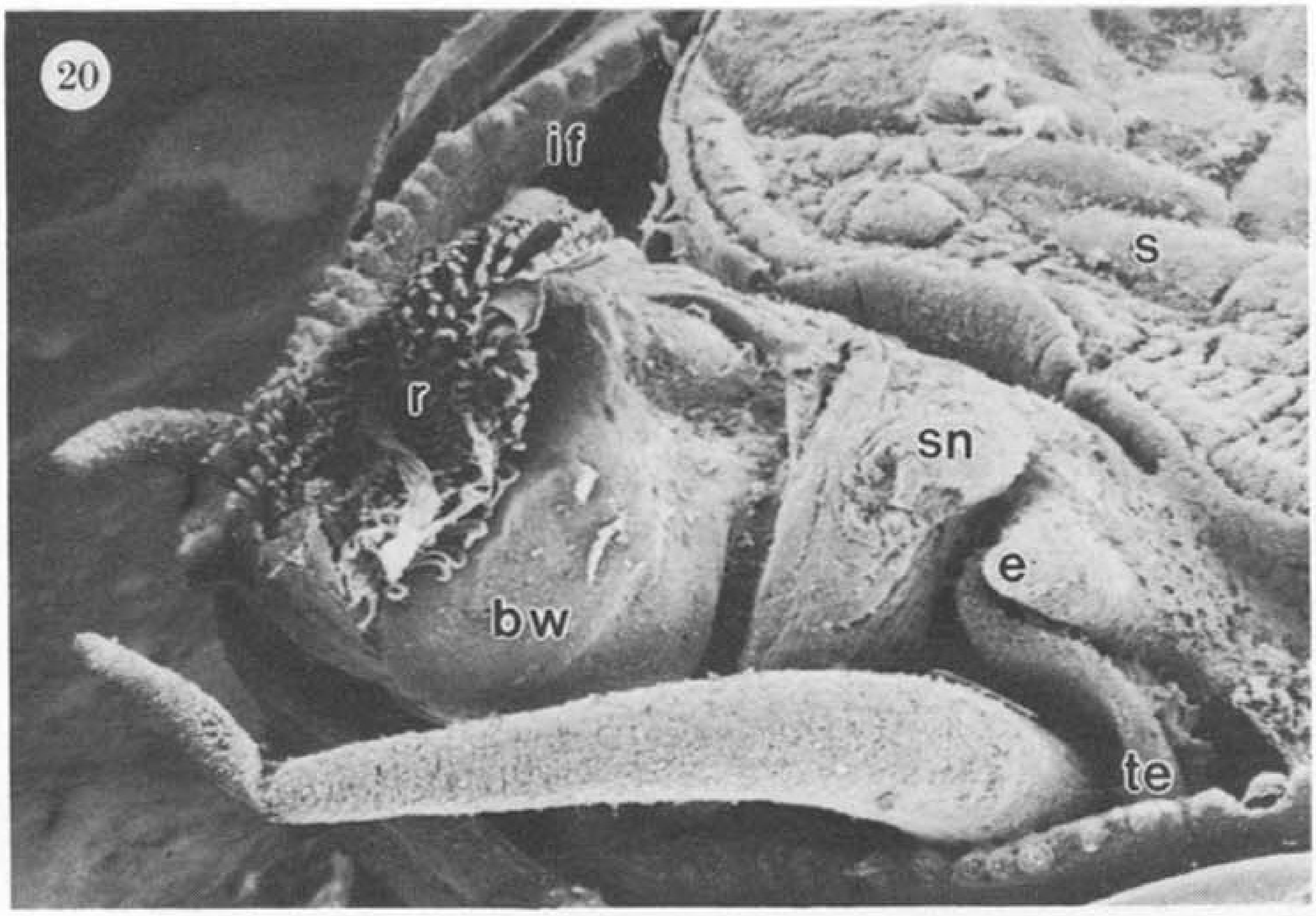
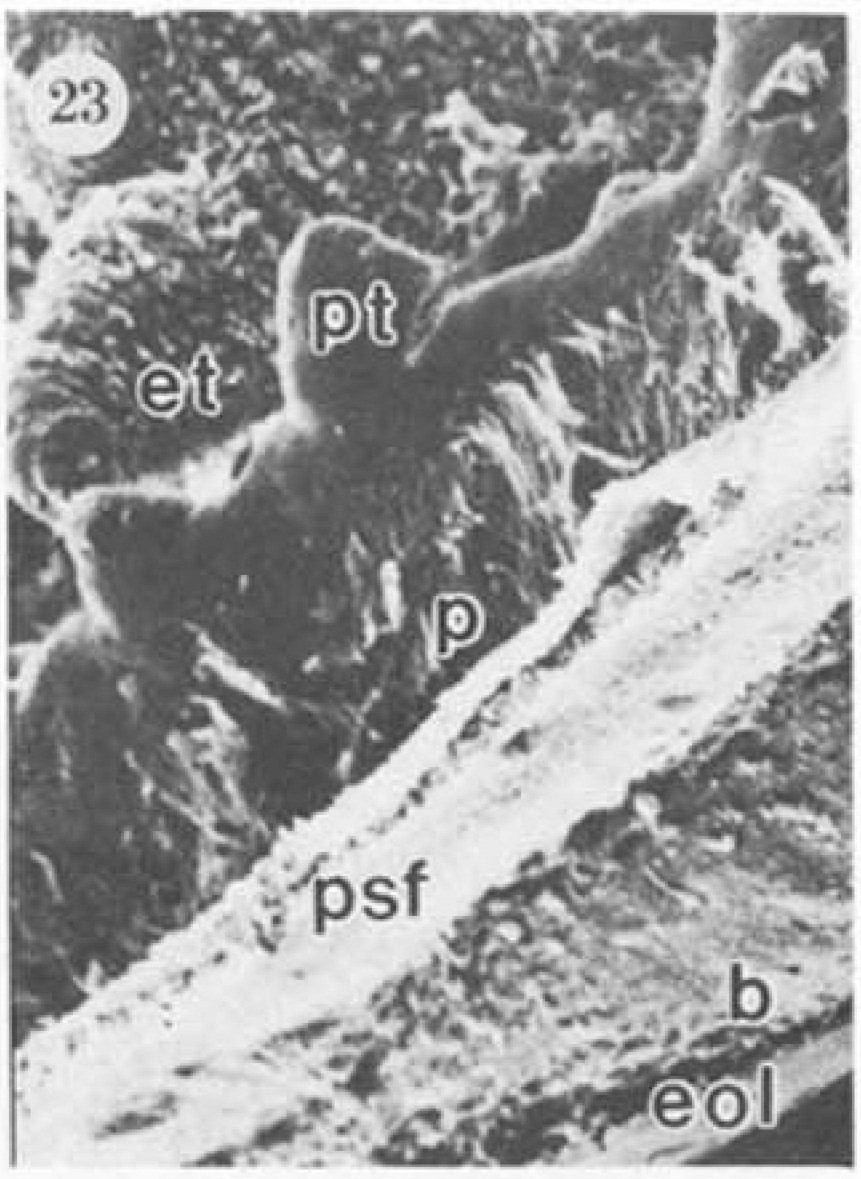
ABBREVIATIONS USED ON THE FIGURES

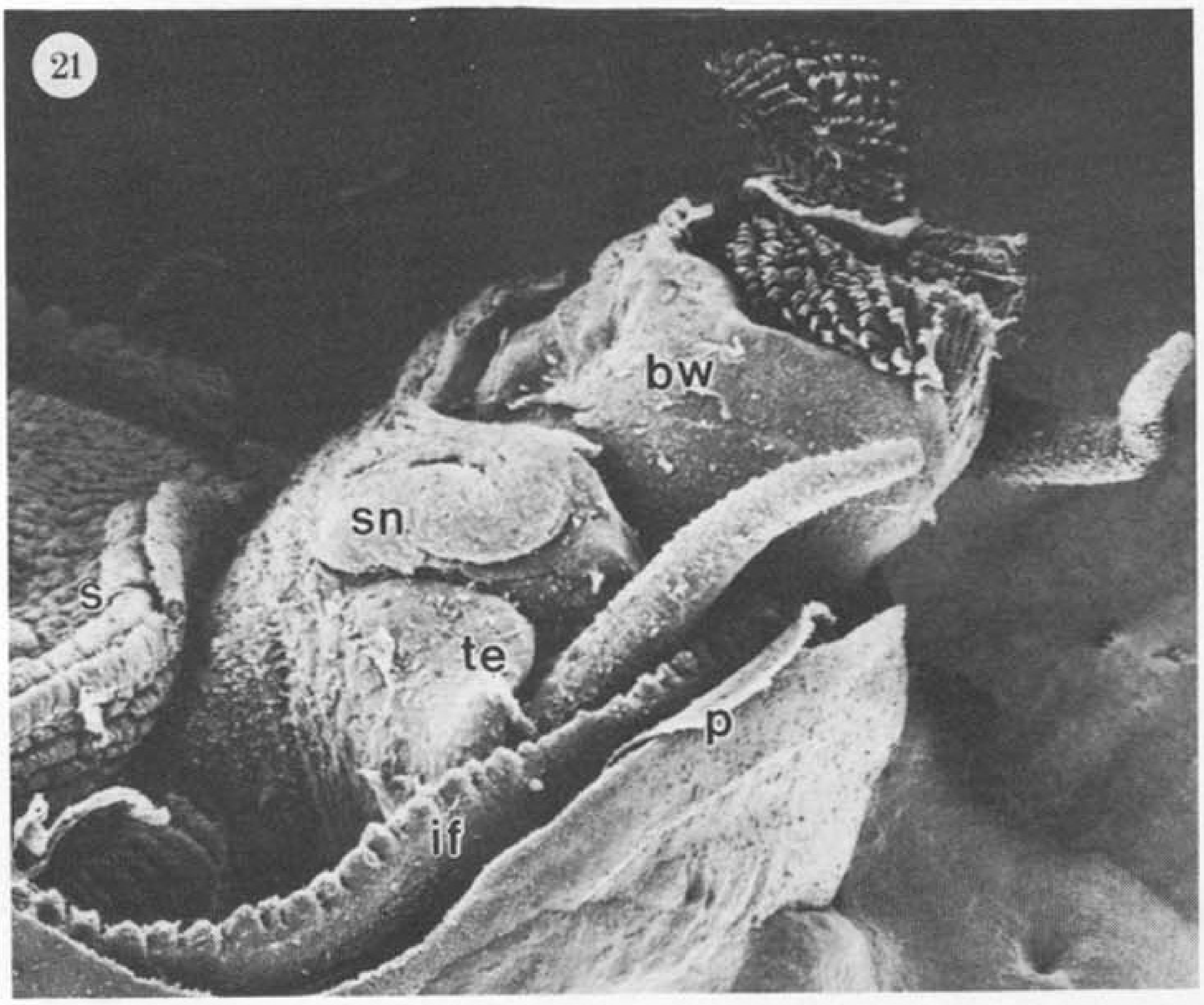
a	anus
aa	anterior aorta
ab	afferent branchial vein
ac	abfrontal cilia
ag	anterior pedal gland
ai	anterior loop of intestine
al	afferent pallial vein
ao	anterior part of oesophageal gland
aog	accessory supraoesophageal ganglion
apv	anterior pallial vein
ar	area separating mantle folds
aug	accessory suboesophageal ganglion
av	afferent vessel
ax	gill axis
b	base of outer pallial fold
ba	bacteria spreading ventralwards over lamellae
bc	buccal commissure
bp	base of penis
bs	bundle of sperm in receptaculum seminis
bw	everted buccal wall
c	columella of early growth stage
ca	anterior odontophoral cartilage
cc	cerebral commissure
cd	cerebropedal connective
cg	cerebral ganglion
cj	ciliary junction
cl	cerebropleural connective
cp	posterior odontophoral cartilage
cpd	cilia of pad
cpr	ctenidial and pallial retractor muscle
cr	ctenidial retractor muscle
cro	crossing of supra- and suboesophageal visceral connectives
ct	position of tips of anterior cartilages
cu	circumpallial vein
cw	cut wall of pericardium and its vascular connections with the visceral haemocoele
dc	dorsal food channel of oesophagus
de	digesive gland under apex of visceral mass which it initially filled
df	dorsal fold
dg	digestive gland
dl	dorsal gill lamella
dp	developing penis
e	epipodium
eb	efferent branchial vein
ee	efferent edge of gill axis
ef	outer pallial fold enclosed by inturned periostracum, retracted from shell edge
eh	extension of epipodium on to head
eol	edge of contracted shell muscle
epa	right efferent pallial vein passing to right auricle (renopericardial duct seen beneath in figure 8)
epe	left efferent pallial vein passing to efferent branchial vein
et	epipodial tentacle
ev	epipodial vessel
f	food leaving mantle cavity
fa	free ctenidial axis
fc	frontal cilia
fd	food mass
fe	4th epipodial tentacle
fla	filter chamber in wall of left auricle
flc	flange at left limit of columellar lip (= original abapical)
fm	cartilage flexor muscle
fol	outgrowth of outer lip adjacent to columella
fp	frontal pad of cilia
fr	faecal rod
fs	food particles embedded in secretion
ft	foot
g	gonadial duct
gc	gastric caecum
gd	pallial gland
gg	genital groove

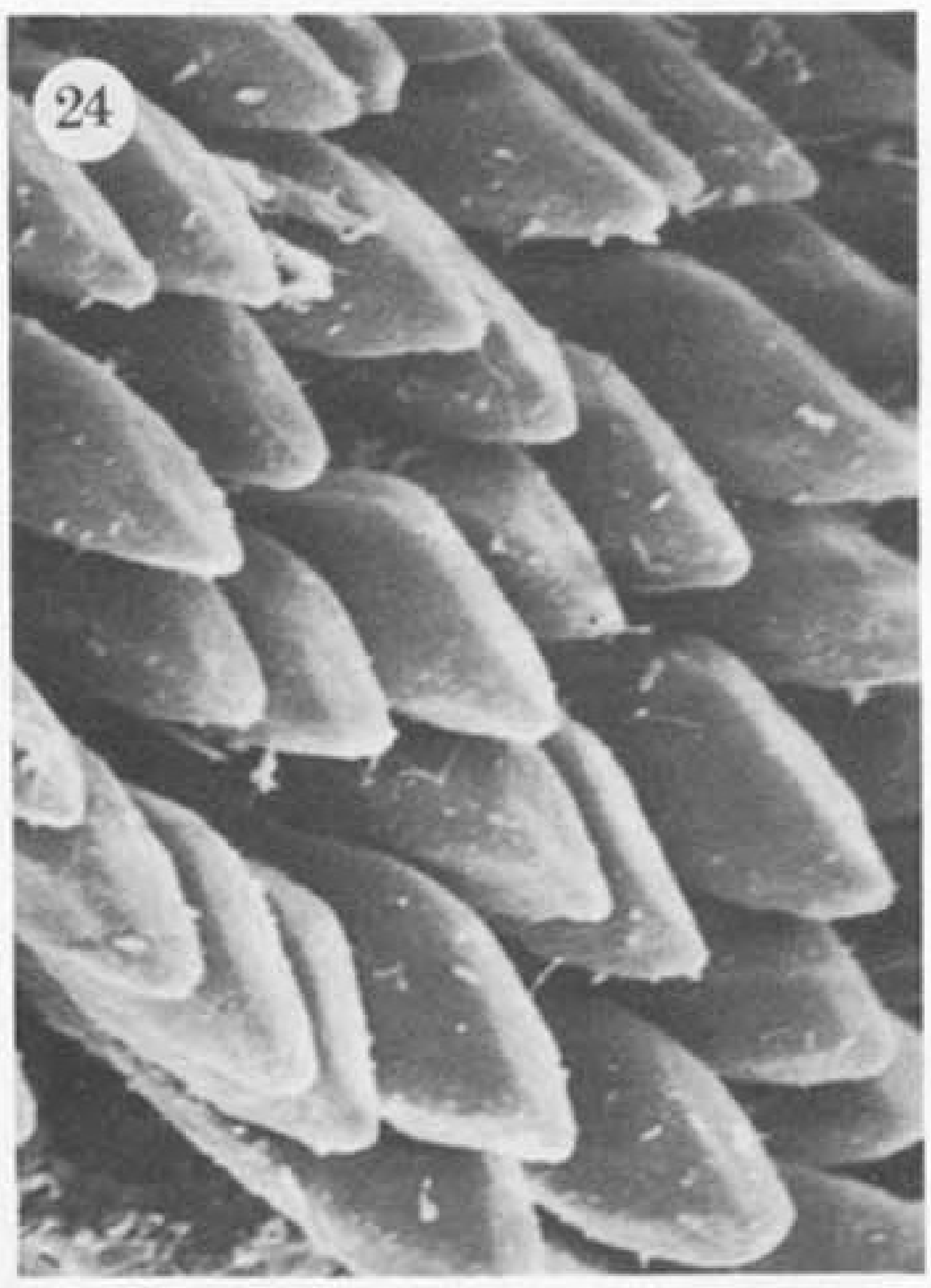
gi	ventral glandular area of inner pallial fold (seen by transparency in figure 18)
gl	gill lamella
gn	glandular tip of penis
gp	pedal ganglion
gr	groove along mantle skirt, suggesting path followed by extended penis
gs	sole gland
gy	young oocytes
h	visceral haemocoele
he	vascular connection between epipodium and foot
hy	hypobranchial gland bordering afferent vessel to gill lamella; dot marks entry of vessel to lamella
if	inner pallial fold
iif	inturning of inner pallial fold and groove secreting periostracum
j	jaw
l	cut edge of mantle skirt
la	left auricle
lc	lateral cilia
lf	transverse lamellar fold
lg	left oesophageal gland
lh	cephalic levator muscle
lk	left kidney
lmp	line of attachment of lateral pallial muscles
lo	odontophoral levator muscle
lr	labial rim
lsm	origin of pallial component of shell muscle
m	mouth
me	pallial muscles inserted along edge of shell muscle (some insert between fibres of this muscle)
mc	mantle cavity
mg	filament of monopectinate gill
mm	mantle covering ventral part of visceral mass
mo	subradular membrane covering protruding tip of odontophore
mp	pallial retractor muscle
mr	retracted pallial muscle
ms	mantle skirt
n	pallial nerve related to tentacles of inner pallial fold
ng	nephridial gland
np	pedal nerve
o	ovary
ob	osphradiobranchial nerve
od	opening of digestive gland duct
oe	oesophagus
of	outer pallial fold (retracted and seen by transparency in figure 11)
og	lateral oesophageal gland opening medianly to oesophagus
ol	opening of salivary gland
op	operculum
os	osphradium
ot	odontophoral tip
ov	oeophageal valve anterior to which the radular sac enters the buccal cavity
ovd	open penial duct
p	periostracum
pa	posterior aorta
pb	process arising near base of cephalic tentacle
pc	periostracal rim continuous with periostracum covering dorsal surface of shell
pd	posterior diverticulum of prostate gland
pe	penis
pg	opening of anterior pedal gland
pk	pocket enclosing posterior gill lamellae
pl	pleural ganglion
pm	prostate gland in mantle skirt
pn	pallial nerve
po	posterior oesophagus
pr	odontophoral protractor muscle
pre	pallial retractor muscle
ps	periostracum continuous with periostracum of shell
psf	periostracum covering free edge of outer pallial fold, severed from shell
psm	posterior part of shell muscle
ptc	contracted tentacle of inner pallial fold
pt	tentacle at free edge of inner pallial fold
pu	tongue of periostracum free from shell and underlying viscera, secreted by inner mantle fold not incorporated in back growth of mantle
pv	pallial vas deferens
r	radula
ra	right auricle
rd	ridge connecting epipodium with fold encircling base of tentacle
re	receptaculum seminis
rk	right kidney
rm	retractor muscles of subradular membrane
ro	peripheral rim of sole of foot
rp	retractor muscles of sublingual pouch
rr	right renopericardial duct
rs	radular sac
rt	radular protractor muscle
rv	renal vessel linking blood capillaries of left kidney with left auricle
rve	rectum passing through ventricle
s	sole of foot
sb	suboesophageal part of visceral loop
sc	statocyst
sev	pallial collecting sinus passing to efferent branchial vein
sg	salivary gland
sk	skeleton
sm	shell muscle
smp	origin of pedal component of shell muscle
sn	snout
so	epipodial sense organ
sog	supraoesophageal ganglion
sp	sublingual pouch
spr	perirectal sinus
sr	sensory process
st	stomach
su	supraoesophageal part of visceral loop
t	cephalic tentacle
tb	base of broken cephalic tentacle
tc	terminal cilia transporting food
te	fold encircling base of cephalic tentacle
tg	tip of right gill lamella
tl	inner pallial tentacle

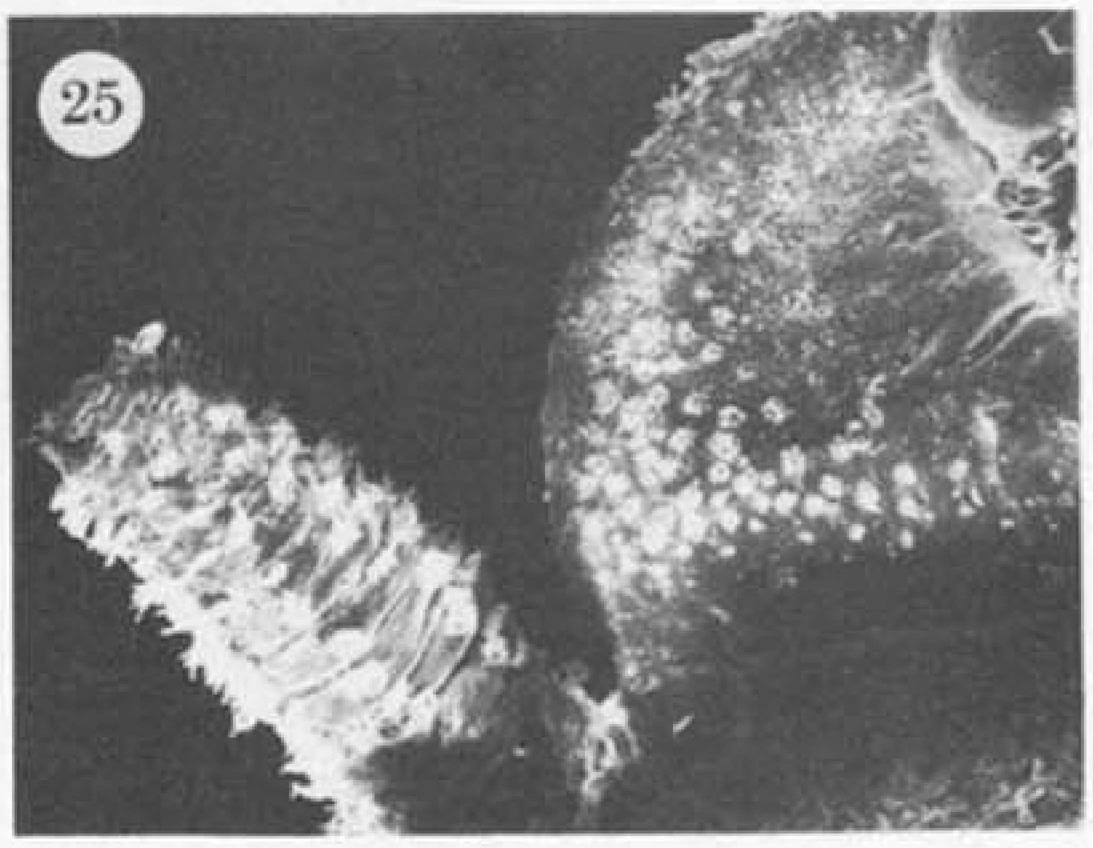
tm	tip of visceral mass
tn	tentacular nerve
tp	tip of penis
ts	testis
tv	transverse pallial vein
u	umbilical groove
ug	unpaired oesophageal gland
ugo	position of urinogenital opening
uv	urinogenital vesicle
v	vascular tissue in posterior wall of pericardial cavity
vc	vessels linking circumpallial and afferent branchial veins
vd	vas deferens
ve	vestigial sensory process anterior to first epipodial tentacle
vg	visceral ganglion
vj	jaw plate
vl	ventral gill lamella
vm	vascularization of mantle skirt
vo	oesophageal valve
vpa	vessels linking anterior pallial vein with afferent branchial vein
vrt	vessels linking transverse pallial vein with left kidney
vs	vesicula seminalis

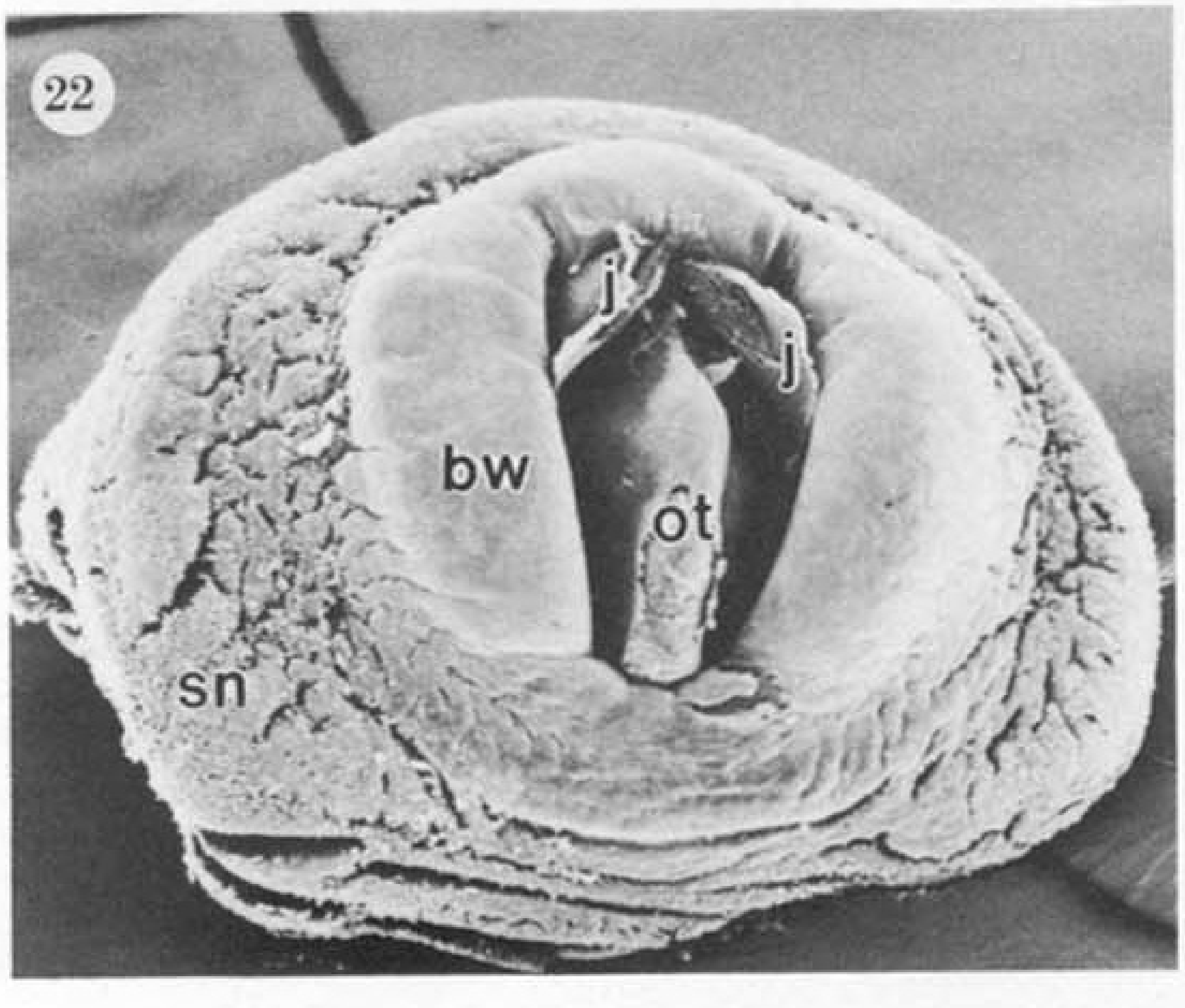


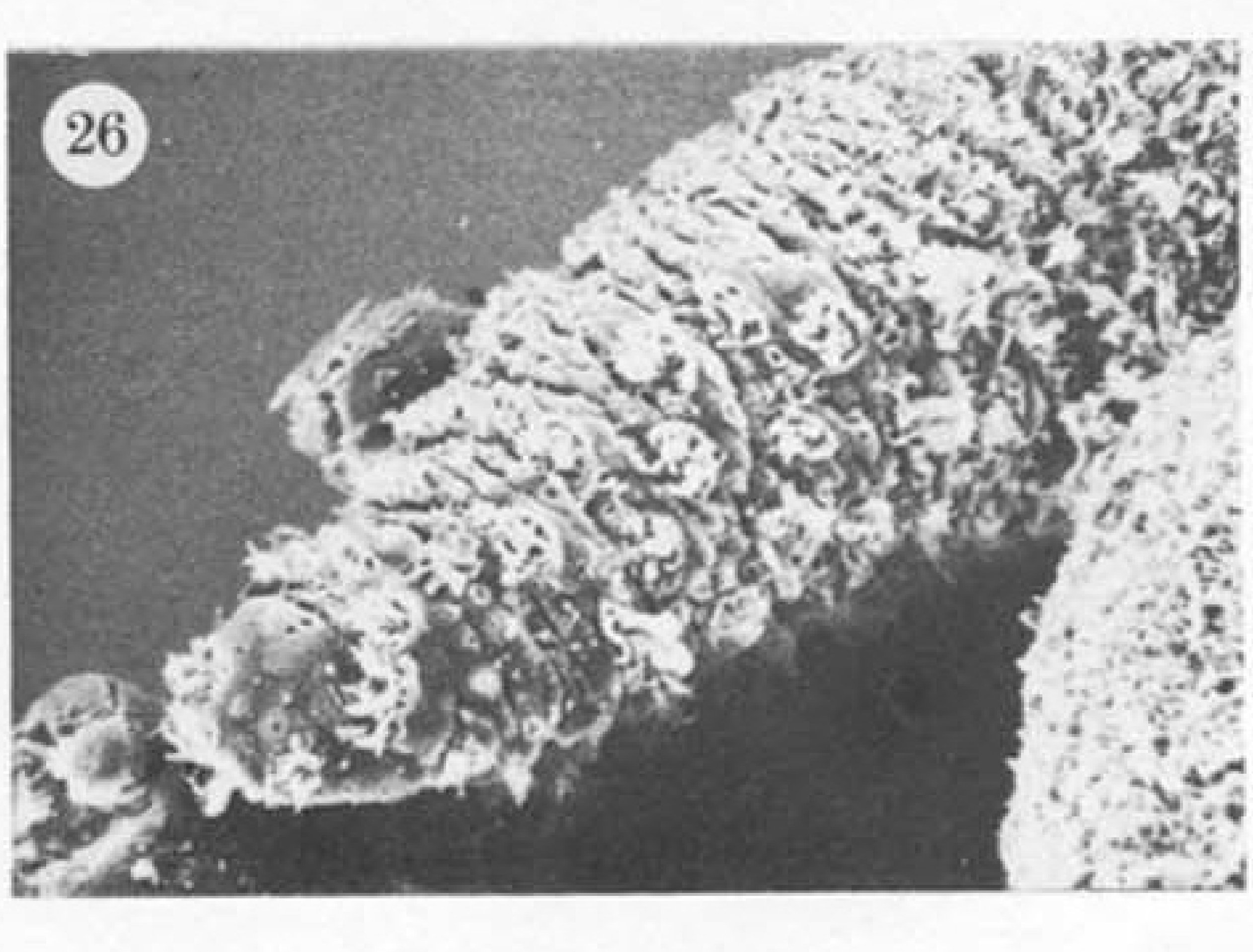




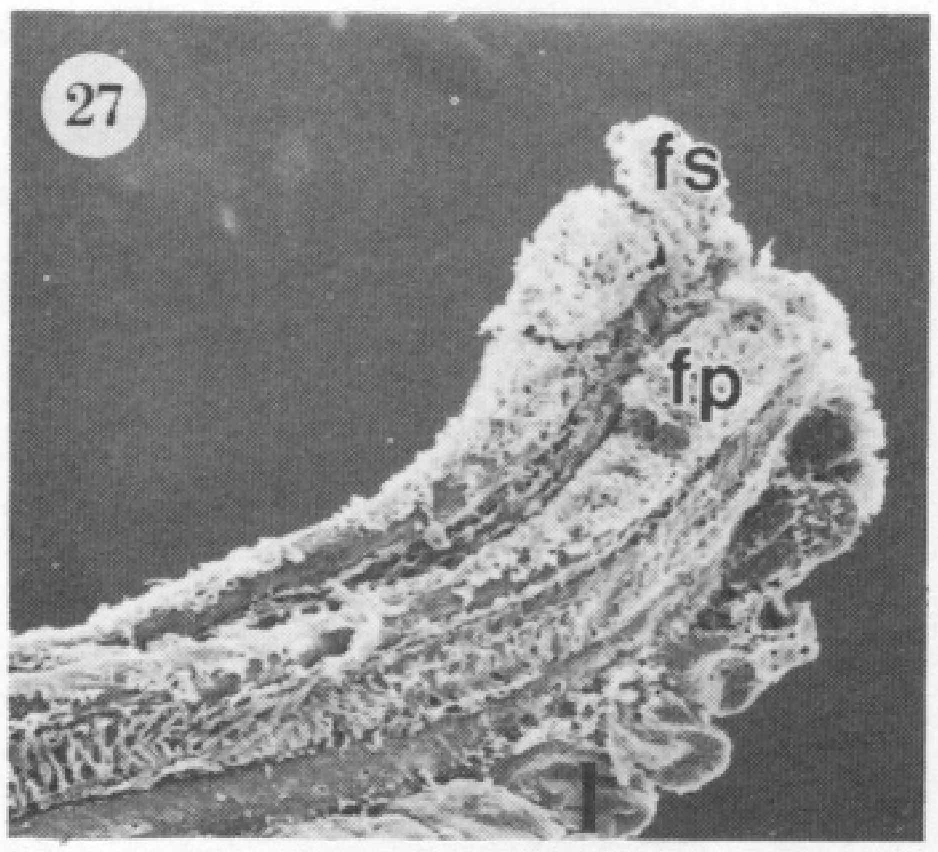


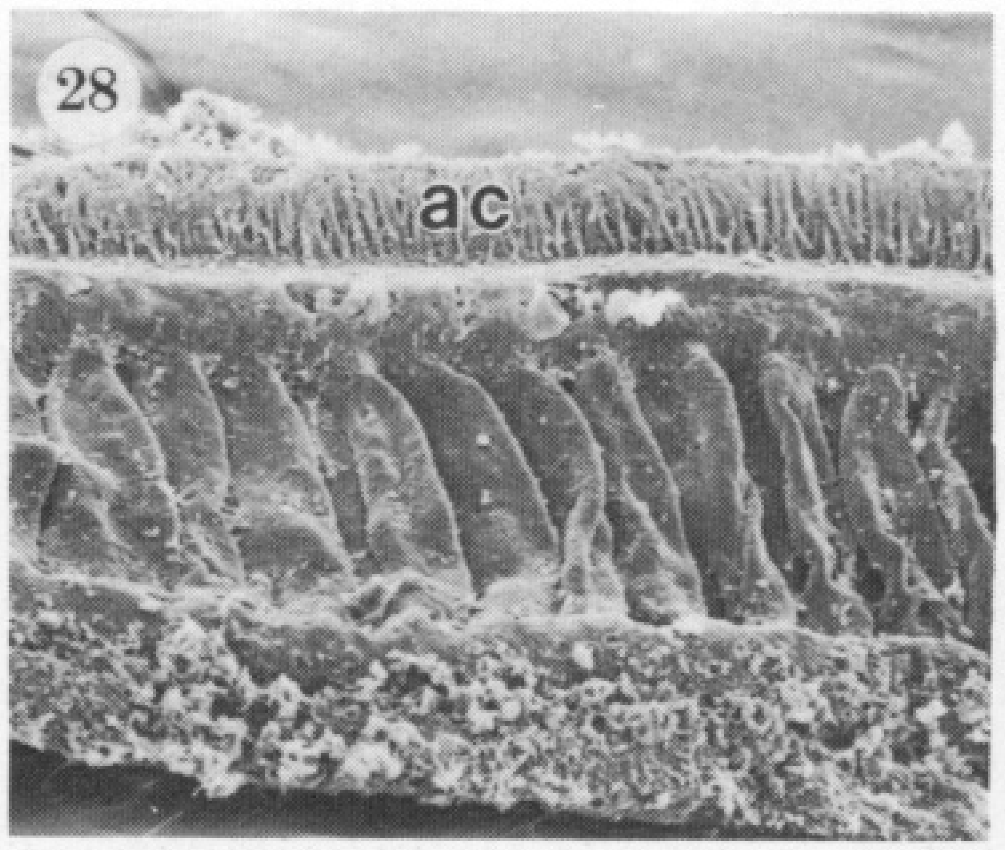


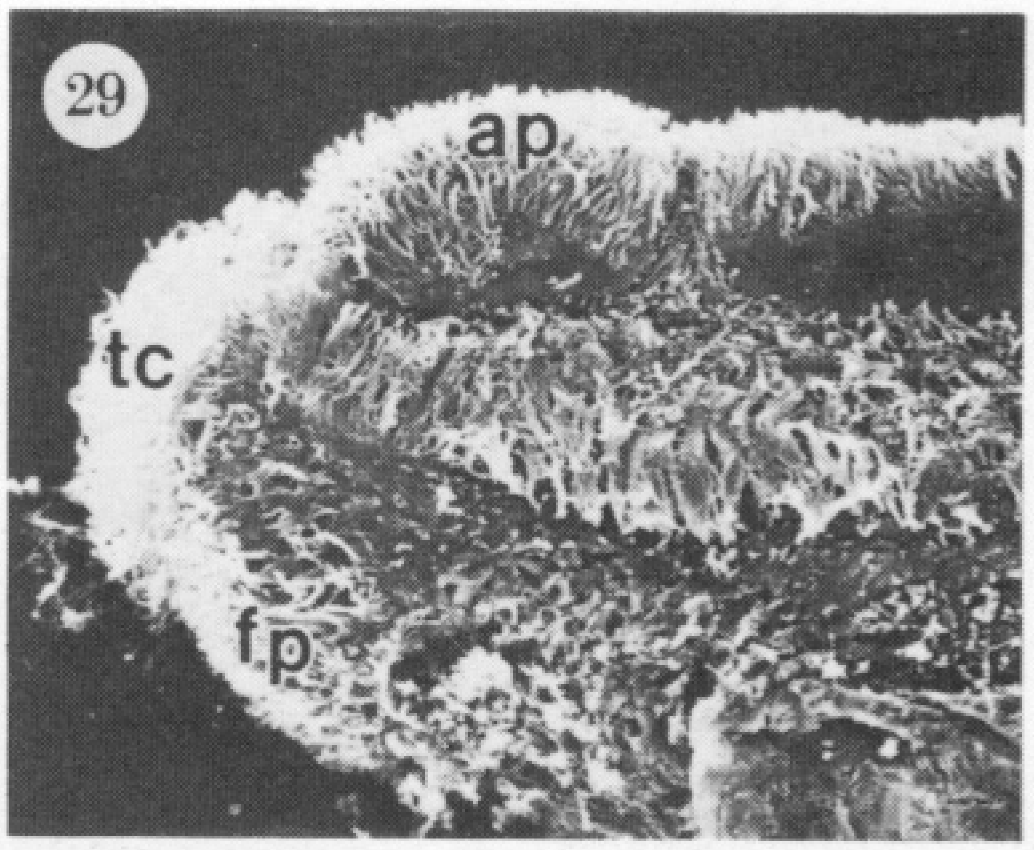


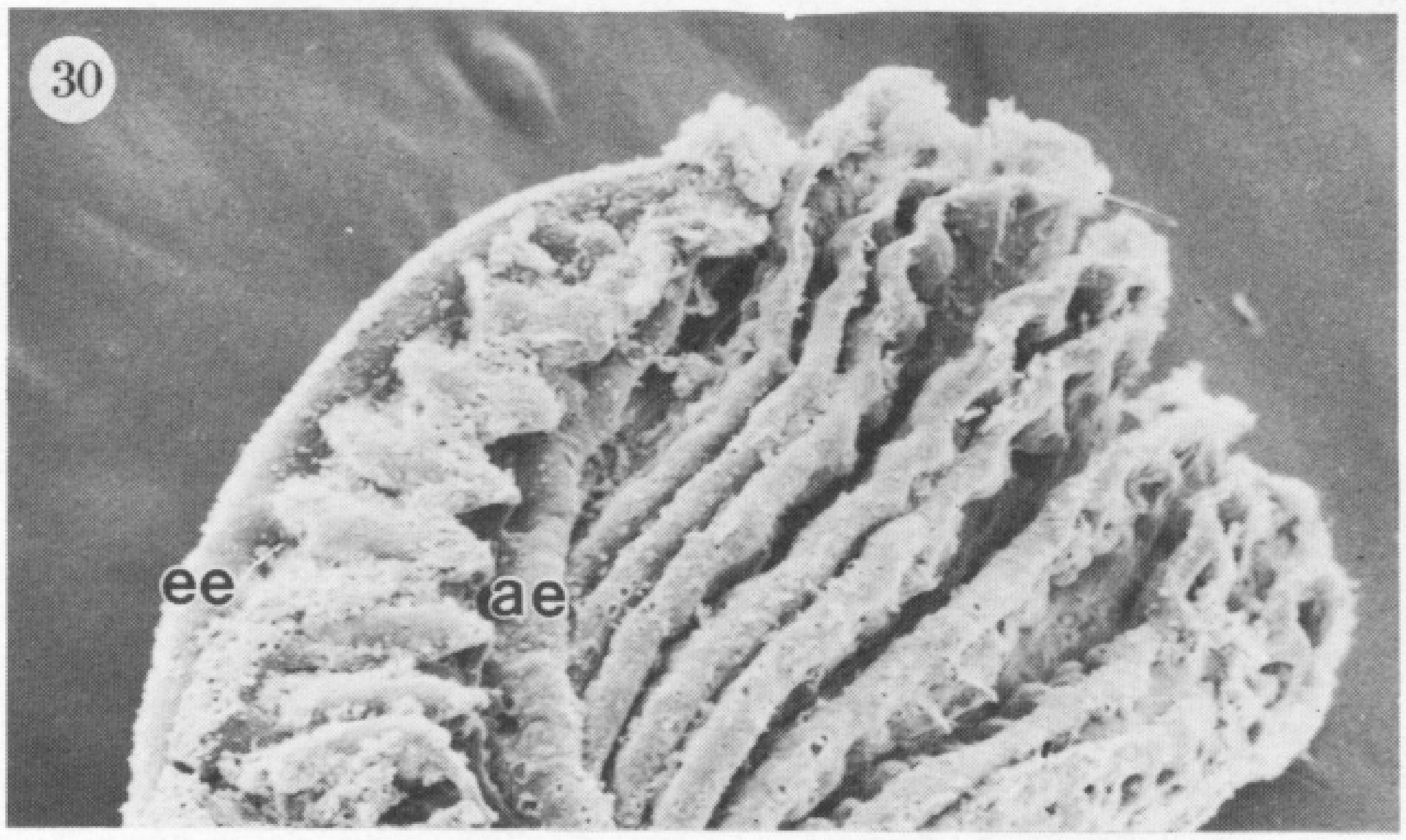


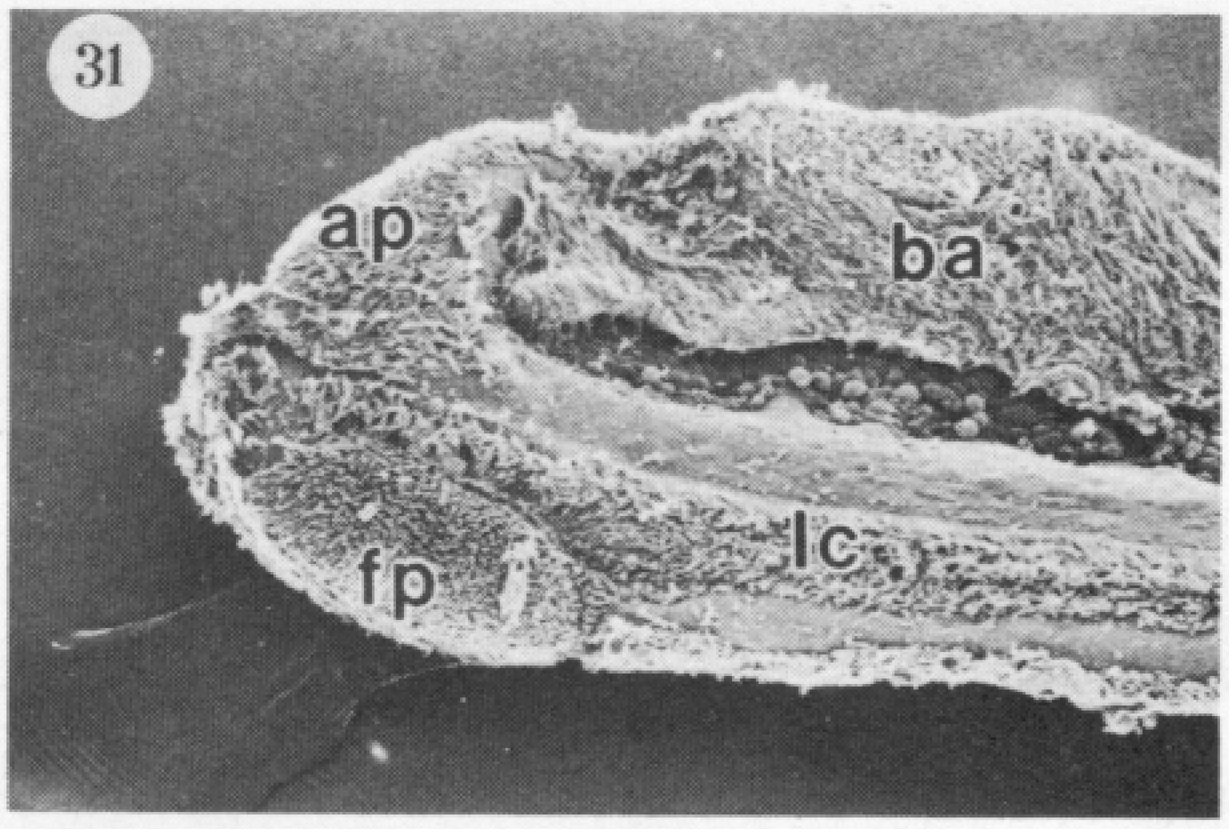
FIGURES 20–26. For description see opposite.

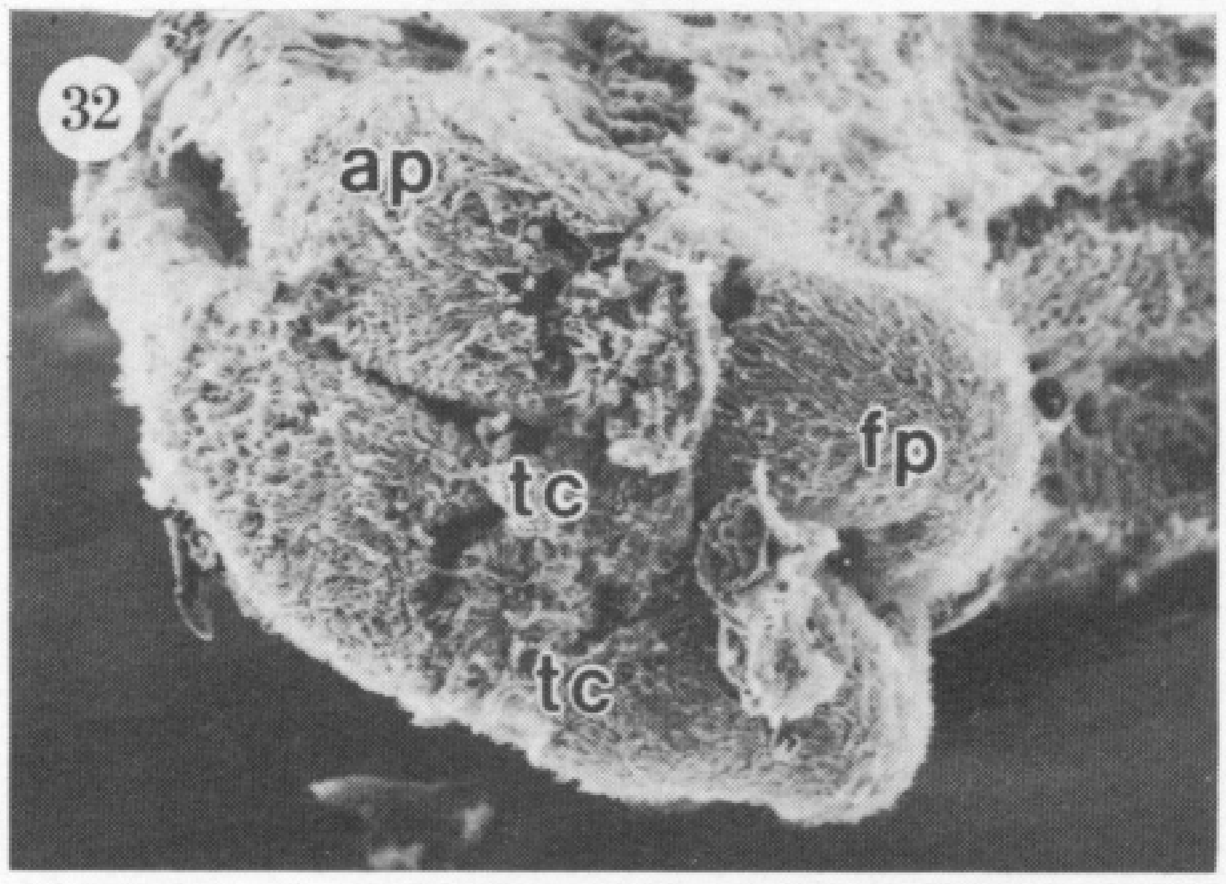


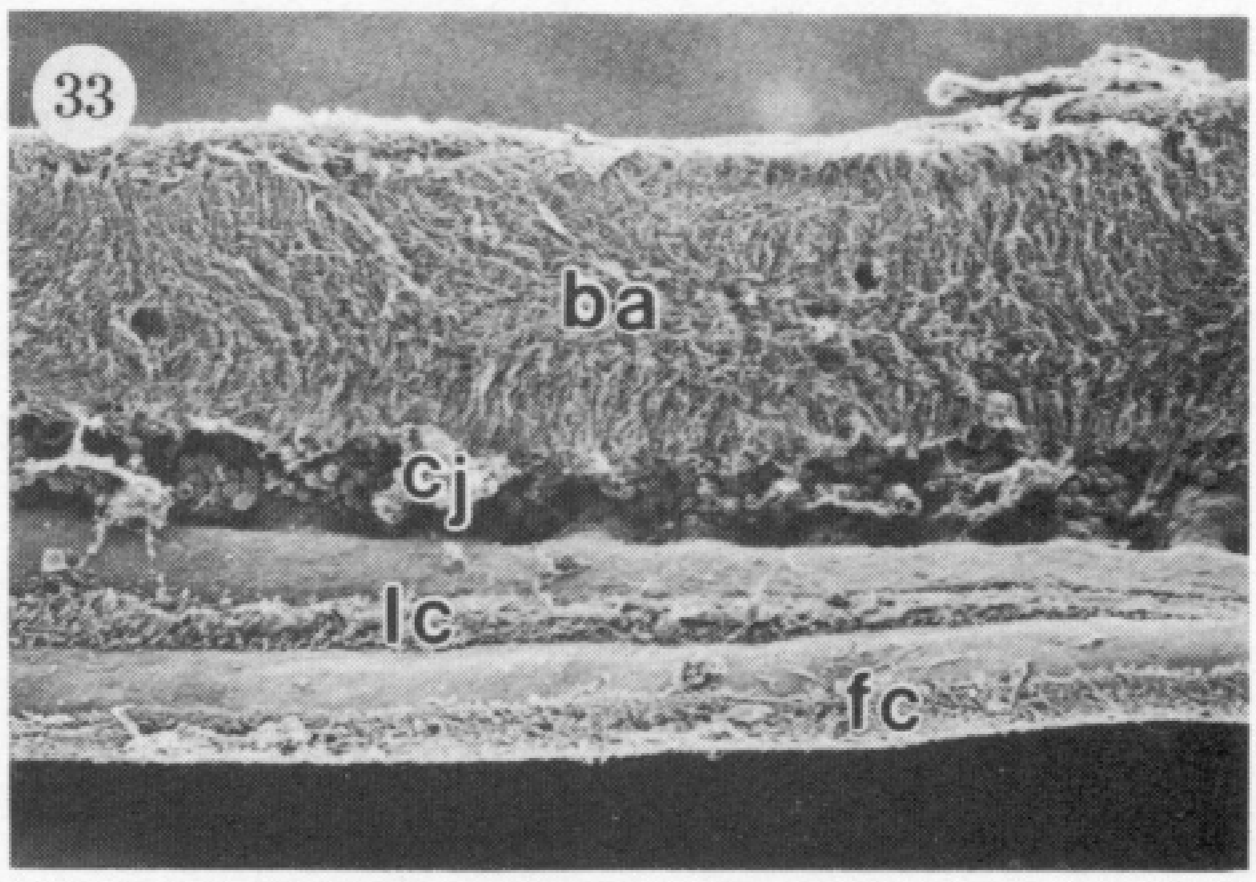


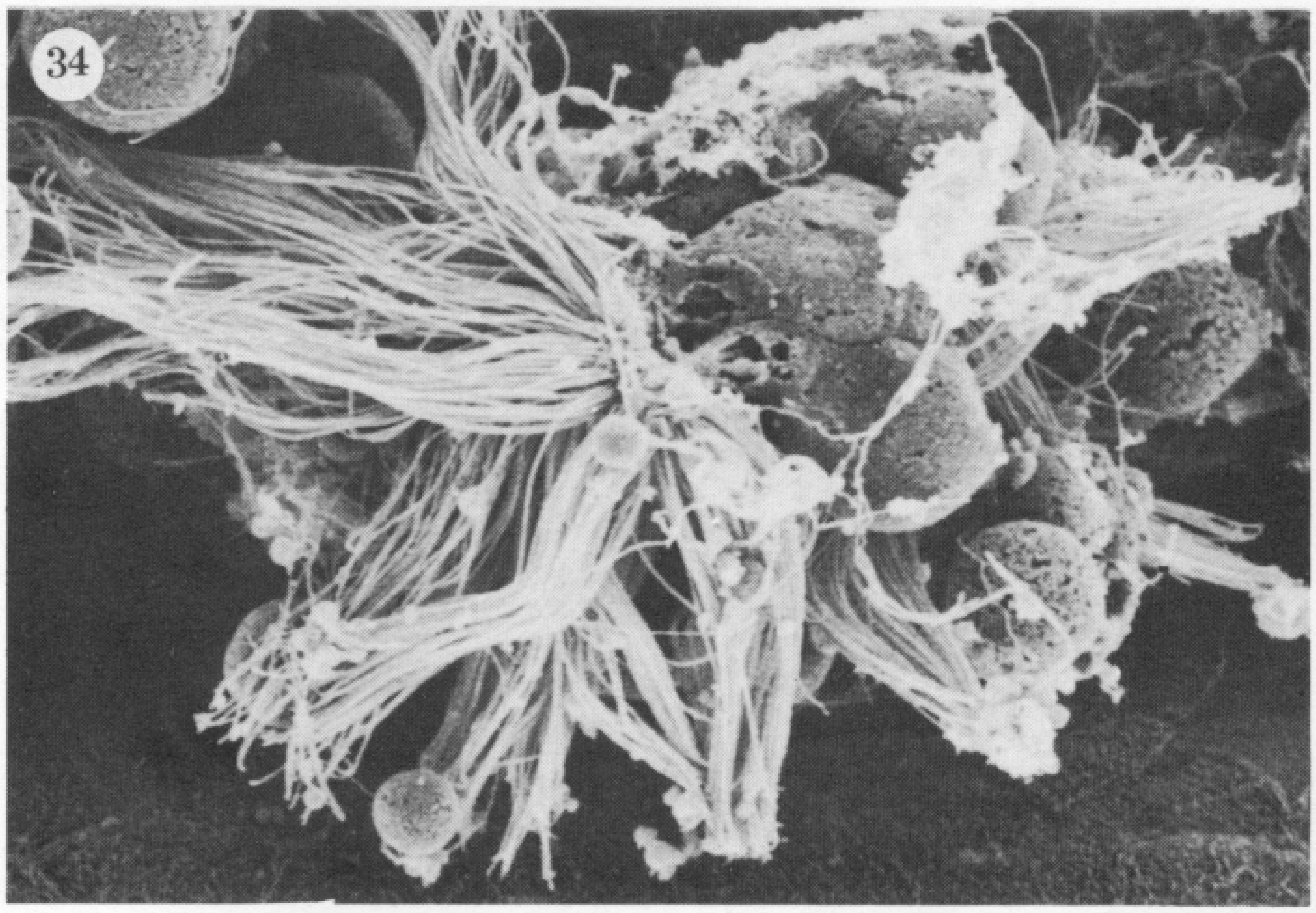


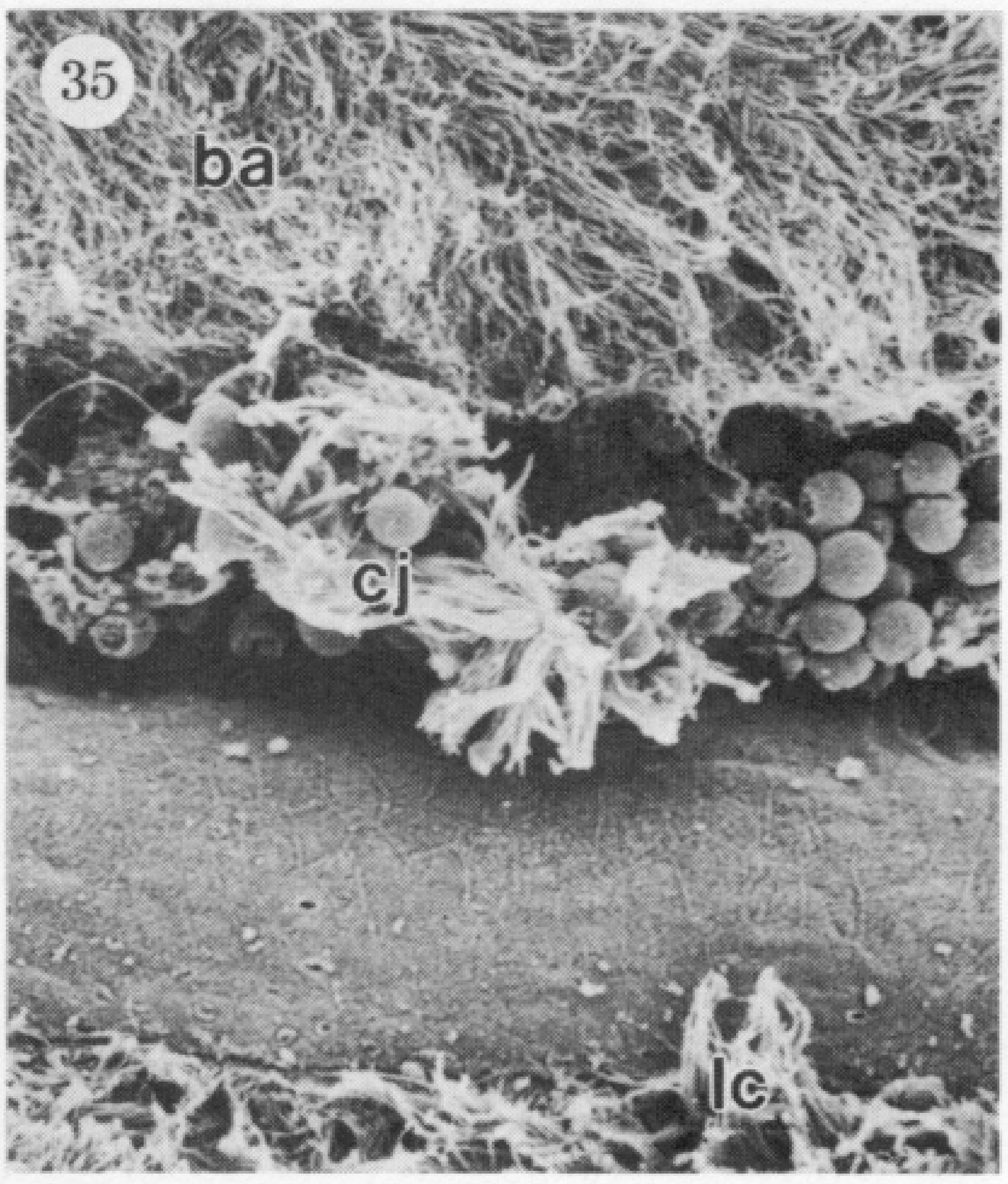




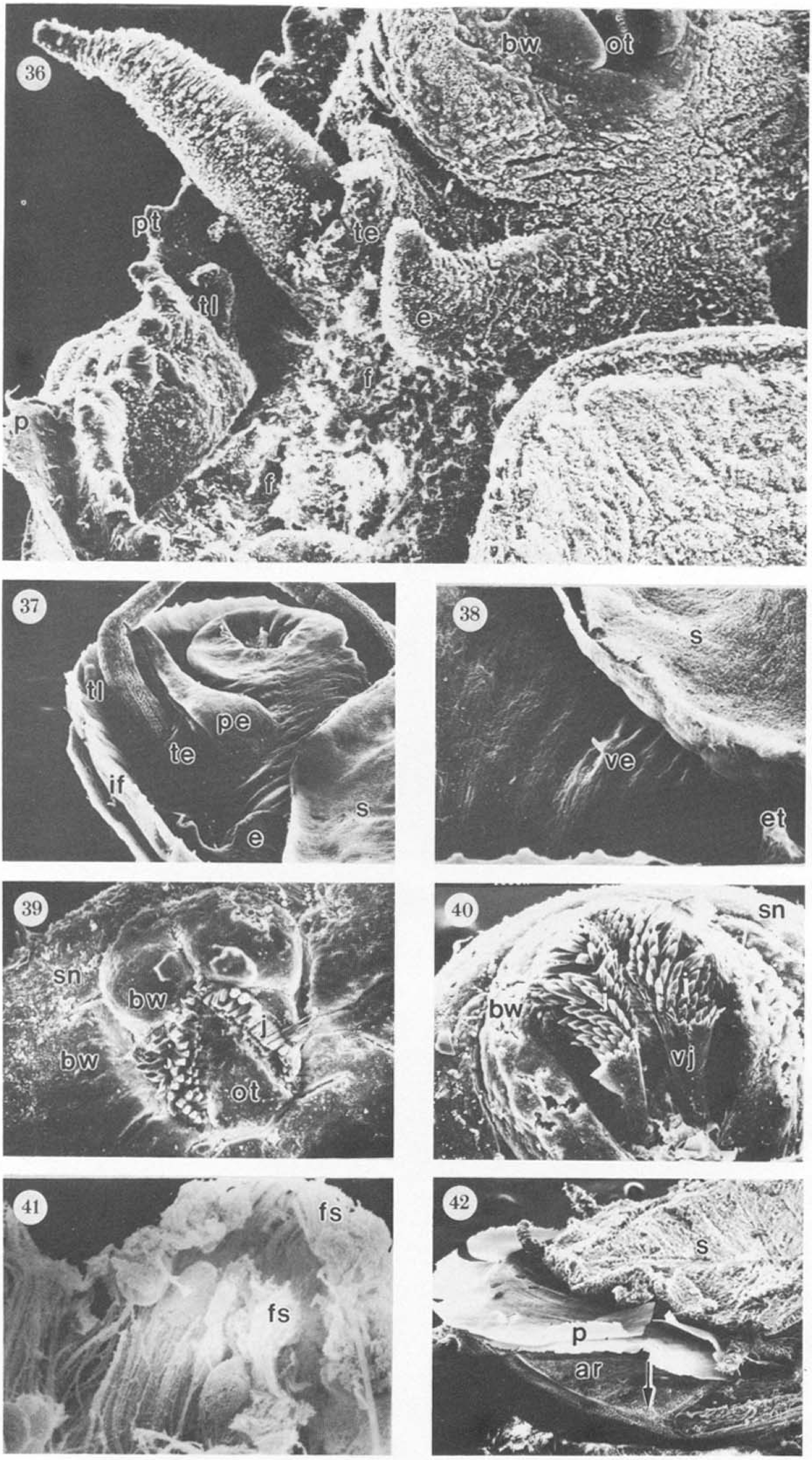








FIGURES 27–35. For description see opposite.



FIGURES 36–42. For description see opposite.