Anatomy and systematics of bathyphytophilid limpets (Mollusca, Archaeogastropoda) from the northeastern Pacific

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Bathyphytophilus diegensis sp. n. is described on basis of shell and radula characters. The radula of another species of *Bathyphytophilus* is illustrated, but the species is not described since the shell is unknown. Both species feed on detached blades of the surfgrass *Phyllospadix* carried by turbidity currents into continental slope depths in the San Diego Trough. The anatomy of *B. diegensis* was investigated by means of semithin serial sectioning and graphic reconstruction. The shell is limpet-like; the protoconch resembles that of pseudococculinids and other lepetelloids. The radula is a distinctive, highly modified rhipidoglossate type with close similarities to the lepetellid radula. The anatomy falls well into the lepetelloid bauplan and is in general similar to that of Pseudococculini-dae and Pyropeltidae. Apomorphic features are the presence of gill-leaflets at both sides of the pallial roof (shared with certain pseudococculinids), the lack of jaws, and in particular many enigmatic pouches (bacterial chambers?) which open into the posterior oesophagus. Autapomor-phic characters of shell, radula and anatomy confirm the placement of *Bathyphytophilus* (with *Aenigmabonus*) in a distinct family, Bathyphytophilidae Moskalev, 1978. As revealed by a cladistic study, the Bathyphytophilidae should be classified within the Lepetelloidea close to the Lepetelli-dae, Pyropeltidae, and Pseudococculinidae. © 1996 The Norwegian Academy of Science and Letters.

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Introduction

Wolff (1976, 1979) studied the usage of plant remains as the food source for diverse groups of macrofaunal in-vertebrates in the Puerto Rico and Cayman Trenches. He figured (Wolff, 1976: 167, fig. 2K) some minute (2–3 mm) limpets obviously feeding on detached blades of the turtle grass, *Thalassia testudinum* (Hydrocharitaceae). This limpet species was subsequently described by Moskalev (1978) as *Bathyphytophilus caribaeus* in the new family Bathyphytophilidae. At the same time, Moskalev also added a second genus and species, *Aenigmabonus kuri-lokamtschaticus*, from the abyssal Kurile–Kamchatka Trench. Moskalev (1978) described shell, external mor-phology, and radula of these species and observed brood-ing in *B. caribaeus*.

In this paper, we first illustrate the bathyphytophilid radula with SEM and provide details on the internal anatomy of the genus. We describe a second species of *Bathyphytophilus*, *B. diegensis* sp. n., from continental slope depths in the San Diego Trough, eastern Pacific Ocean, and illustrate the radula of a third species, also from the San Diego Trough. The latter species is not named because the shell is unknown. We provide the first description of the anatomy of a bathyphytophilid limpet.

The anatomy of all other known families of the Cocculini-formia (Addisoniidae, Cocculinidae, Cocculinellidae, Osteopeltidae, Pseudococculinidae, Choristellidae; cf. McLean & Haszprunar, 1987; Haszprunar 1987*a,c*, 1988*a,b*, 1992) has been outlined in detail or given at least briefly (Bathysciadiidae, Lepetellidae; cf. Haszprunar 1988*c*, 1996). This paper provides the missing information on the solely known* remaining family for which anatom-ical information was previously lacking.

In order to clarify the systematic position of the Bathy-phytophilidae within the Lepetelloidea, and the inter-relationships of the remaining lepetelloidean families, a cladistic analyis was utilized.

Material and methods

External morphology and anatomy

Sources and localities for the two species of *Bathyphytophilus* are detailed in the systematic section that follows. All specimens are

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* According to Warén (1991: 82) a new family might be necessary for *Pilus conica* (Verrill, 1884), for which the anatomy and radula are unknown.

deposited in the Los Angeles County Museum of Natural History (LACM).

In addition to standard photography, shells were examined with SEM. Radulae were examined using SEM, following extraction by dissolution of tissues with 10% NaOH at room temperature for 48 hr, washing in distilled water, drying from a drop of distilled water, and coating with gold palladium.

A single paratype specimen of *Bathyphytophilus diegensis* was prepared for semithin serial sectioning. The specimen was originally preserved in 70% ethanol, which resulted in a good fixation, although histological details cannot be given satisfactorily for all tissues (see results). After dehydration, the specimen was embedded in plastic (araldite) and serially sectioned (2 μm) with "Ralph-knives" according to the method of Smith & Tyler (1984). Monochromatic staining was done by Methylene Blue (Richardson *et al.*, 1960).

The plastic block was trimmed symmetrically, so that the edges of the sections could be used as reference lines. Before embedding, the specimen was photographed from dorsal and lateral perspectives, so that the projected contours could be used as reference lines in addition to the symmetry plane of paired structures such as pedal cords or shell muscle. For graphic reconstruction, each section was represented by a transverse line, and the structures and organs were projected onto a horizontal plane. After some jagged lines had been smoothed, the graphic reconstructions were used as illustrations with some shading and semischematic patterning added.

Cladistic analysis

Large agreement exists that the monophyly of the lepetelloidean families is generally well founded on autapomorphic conditions of radula and anatomy (Marshall 1983, 1986; McLean 1985, 1988; McLean & Haszprunar 1987; Haszprunar 1987a, c, 1988a, b, c, d, 1992, 1996; Dantart & Luque 1994). The only exception concerns the Pseudococculinidae, the status of which as a holophyletic versus a paraphyletic taxon is still open (Haszprunar 1988). Accordingly, we coded the two nominal subfamilies, Pseudococculininae and Caymanabysiinae, as separate taxa.

The cladistic analysis was done using PAUP 3.1.1. (Swofford 1993). Coding of characters (Tables II, III) followed the NEXUS-format of PAUP. Each character state was represented by a numeric value; unknown or questionable states were coded by '?'. Multistate characters were generally considered as unordered, all characters being equally weighted. Generally the 'heuristic' and 'branch and bound' options of PAUP 3.1.1. were applied to create the trees, and the ACCTRAN option was applied to optimize the character states. The trees were rooted by using the outgroup method.

During the analysis, it became increasingly clear that the topology of the trees heavily depends on the selected outgroup(s). Because a thorough discussion on the relationships of cocculiniform groups among the Gastropoda is beyond the scope of this contribution, we decided to use an artificial outgroup. By coding the respective characters with '?', we left open the controversial question of whether the lepetelloidean ancestor was a primary limpet (Haszprunar 1988d) or a coiled organism (Ponder & Lindberg 1995).

Systematics

Superfamily LEPETELLOIDEA Dall, 1892
Family BATHYPHYTOPHILIDAE Moskalev, 1978

The family includes two monotypic genera: *Bathyphytophilus*, type species *B. caribaeus* from 5800–6500 m in the western Atlantic Cayman Trench, in which the protoconch was said to have "large pitted sculpture" and the radula five pairs of marginal teeth, and *Aenigmabonus*, type species, *A. kurilokamtschaticus* from 6160–6120 m in the northwest Pacific Kurile–Kamchatka Trench, in which the protoconch was said to have a "micropitted sculpture" and the radula 20 pairs of marginal teeth per row.

The new family was mainly justified on the food source of detached seagrasses transported to the deep sea and the corresponding radular distinctions. A study of the internal anatomy reported in this paper supports the family level distinction (see discussion part).

Genus *Bathyphytophilus* Moskalev, 1978

Description. Shell small, thin and fragile, elevated, apex at one-quarter length of shell from posterior margin, below highest elevation of shell; anterior slope broadly convex, posterior slope slightly concave; sculpture of fine concentric growth lines and faintly indicated radial striae. Protoconch with lateral indentation and flared lip, partially immersed in posterior slope; sculpture of numerous longitudinal rows of pits.

Radula with rachidian, four lateral elements (small pair of inner laterals, large second lateral here termed the pluricuspid, inner and outer basal elements) and three to five pairs of reduced marginals. Tooth rows markedly asymmetric, resulting from alternating positions on left and right sides of massive pluricuspid teeth. Rachidian broad, membranaceous, shaft broad, tip overhanging, overhang with single centrally placed, weakly projecting denticle, edge of overhang slanted down to right, corresponding to asymmetry derived from alignment of pluricuspid teeth; rachidian also with narrow lateral flanges, usually obstructed by pluricuspid teeth. Inner lateral teeth reduced, mostly hidden behind pluricuspid teeth, tips with single cusps. Pluricuspid with broad base; shaft massive, concave on inner side, outer edge continuous with overhang, evenly convex; entire tip projecting inwardly, tip with four cusps, an acutely tapered main cusp, strong lesser cusps on either side and a small nub-like outer cusp. Edge of ribbon bordered by flat-surfaced outer basal element, forming nearly straight outer edge. Inner basal plate exposed only near outer base of pluricuspid tooth. Marginal teeth three to five pairs, vestigial, appearing to arise between inner and outer basal plates below base of pluricuspid; shafts of marginals relatively short, strap-like, curved; tips finely digitate.

Snout broad, eyes and oral lappets lacking, single posterior pair of epipodial tentacles; smooth cephalic tentacles moderately long in preserved condition, right cephalic tentacle with ciliary band extending along neck to genital opening; shell muscle horseshoe-shaped, markedly asymmetrical. A single, reduced gill-leaflet at the left mantle roof, many well-developed gill-leaflets at right mantle roof and in right subpallial groove; gill-leaflets with sensory pockets but lacking skeletal rods. No hypobranchial gland; heart large and monotocardian. Left kidney small and pallial, large right kidney ramifies between viscera at left side. Testis and ovary separated, with a common hermaphroditic gonoduct; a urinogenital opening with the right kidney; broader. No jaws, no salivary glands (?) and two pairs of radular cartilages. Anterior oesophagus with dorsal food channel and lateral pouches, posterior oesophagus uniquely embedded in a mass of enigmatic pouches (bacterial chambers?). Stomach large, two digestive glands with food particles inside. Very long intestine shows several loops, rectum runs through ventricle. Nervous system streptoneurous and hypoathroid; osphradial epithelium well developed, statocysts contain several small statoconia.

Remarks. The radular description given above is based on the SEM micrographs of the two species treated here. Moskalev's (1978) radular description and drawing for

Bathyphytophilus caribaeus were based on polarizing and phase contrast microscopy of the type species. His drawing shows a larger inner basal plate that underlies the entire base of the pluricuspid tooth. The extent of that tooth is not directly confirmed by our SEM micrographs, but it may be that Moskalev's rendition is correct, the process of drying the radula for SEM study resulting in shrinkage in our preparations.

Sizes of the limpets are similarly small in the three known species of *Bathyphytophilus*, although the width of the blades for each seagrass differs. The type species occurs on detached blades and rhizomes of the broad-
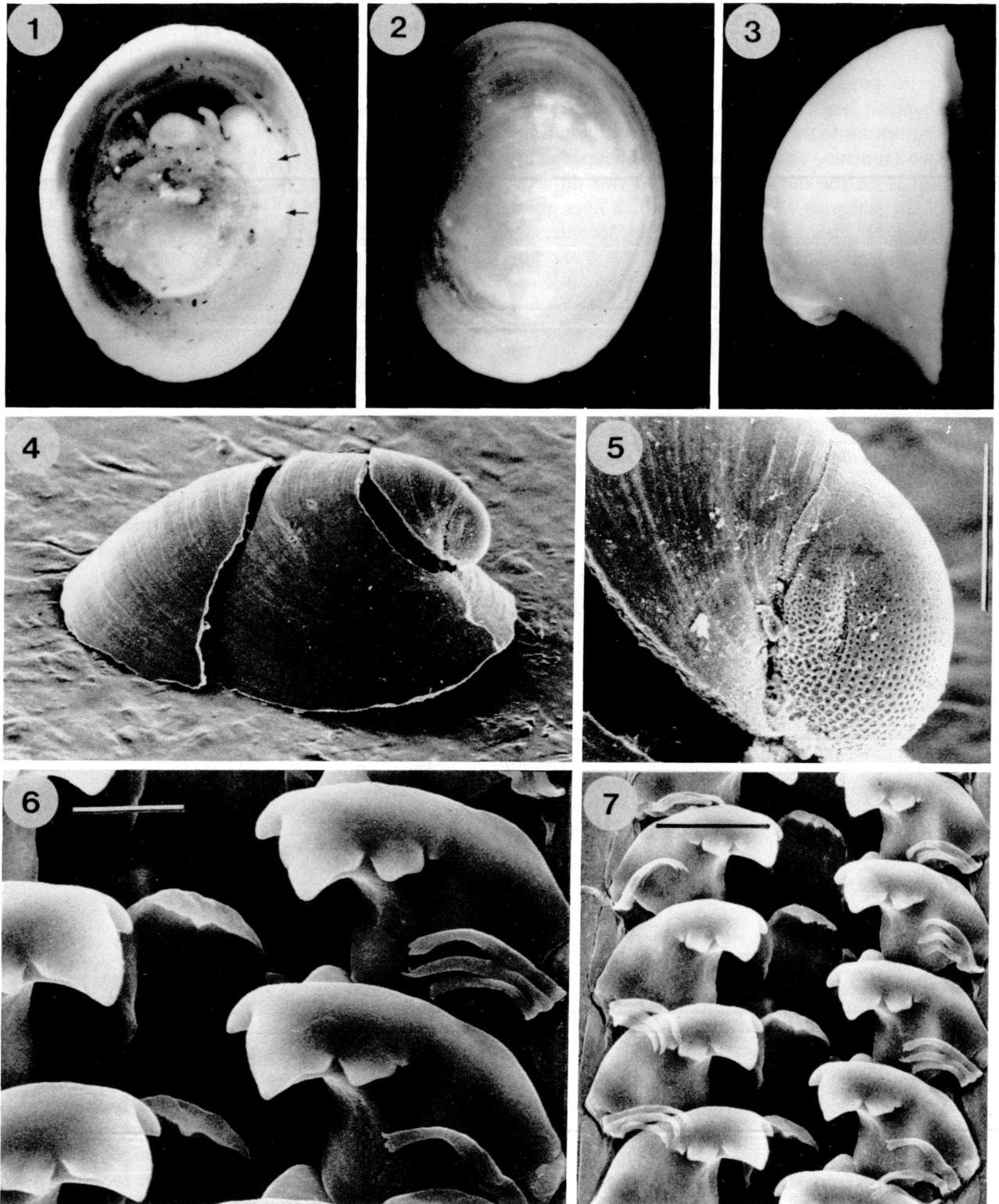
Figs 1–7. Bathyphytophilus diegensis sp. n. from San Diego Trough. 1.224 m.—*1–3*. Holotype, anterior at top, shell length 1.9 mm.—*1*. Ventral view of intact specimen, showing snout, projecting cephalic tentacles, foot sucker, and brooded eggs (arrows) in left subpallial cavity.—*2*. Dorsal view of shell.—*3*. Right lateral view of shell.—*4–5*. Paratype, SEM views of left side of shell showing protoconch; shell broken during mounting. Length 1.1 mm.—*4*. Left side showing protoconch.—*5*. Protoconch, scale bar = 100 μm.—*6–7*. SEM views of radula of paratype.—*6*. Scale bar = 10 μm.—*7*. Scale bar = 20 μm.

Table 1. *Dimensions (in mm) of type material of* Bathyphytophilus diegensis

No.	Length	Width	Height	Remarks
1	1.9	1.5	1.0	Holotype
2	1.9	1.4	—	Sectioned, shell intact
3	1.7	1.2	—	Shell only
4	1.1	—	—	SEM, shell and protoconch
5	0.8	0.6	—	Shell broken
6	0.7	0.4	—	
7	0.6	0.5	—	

bladed turtle grass *Thalassia*, which lives in shallow water. *Thalassia* blades are commonly transported by turbidity currents into the hadal depth of the Cayman and Puerto Rico Trenches. The two eastern Pacific species are here reported on the detached blades of two different species of the surfgrass *Phyllospadix*, which lives abundantly along rocky shores in California. Type localities for each are close to the base of Coronodo Canyon at continental shelf depth on the eastern flank of the San Diego Trough. Turbidity currents frequently occur in the submarine canyons along the Californian coast. Thus there is likely to be a steady supply of food for the bathyphytophilid limpets.

Bathyphytophilus diegensis sp. n. (Figs 1–7)

Holotype. LACM 2398.

Type locality. San Diego Trough at base of Coronodo Canyon, off Tijuana, Baja California, Mexico (32°18.2'N, 117°29.8'W), 1224 m.

Paratypes. Six specimens collected along with partially decomposed surfgrass *Phyllospadix scouleri* Hooker (Zosteriaceae) from type locality, collected by Peter A. Jumars, Scripps Institution of Oceanography, 6 December 1971. Six specimens, including one section series, LACM 2399. No other specimens are known.

Description. Shell (Figs 1–5) small, thin, fragile, elevated, apex at one-quarter length of shell from posterior margin, below highest elevation of shell; outline of margin asymmetric, right side more convex than left; anterior slope broadly convex, posterior slope slightly concave; sculpture of fine concentric growth lines and faintly indicated radial striae. Protoconch length 200 μm, with lateral indentation on each side and flared lip, sculpture of numerous pit rows, pits more weakly developed near protoconch rim.

Dimensions. See Table I for measurements. Radula (Figs 6, 7) as described for the genus. Lateral flanks of rachidian and tips of inner laterals concealed behind pluricuspid; three pairs of marginal teeth.

Remarks. *Bathyphytophilus diegensis* differs from *B. caribaeus* in having less pronounced concentric sculpture (compare Moskalev 1978: fig. 7), and three pairs of marginal teeth rather than five pairs. Its marginal tooth count also differs from *Bathyphytophilus* sp. treated here, which also has five pairs. Asymmetry of the shell outline, which is apparent in Figs 1 and 2, was not mentioned for the type species, which was shown only in oblique view, but such asymmetry may prove to be a specific character.

As described for the type species by Moskalev (1978),

the shell of *B. diegensis* is extremely thin and fragile, as is evident from the breakage illustrated in Fig. 4.

Leaves of the preserved plant material are 2 mm wide and are nearly flat in cross-section. It is identified as *Phyllospadix scouleri* Hooker (see Abbott 1975). The leaves of the plant are thus much wider than the width of any of the limpet specimens.

Bathyphytophilus sp. (Figs 8–11)

Material examined. LACM 147454. One specimen, body only, radula removed for SEM preparation, preserved with original material of partially decomposed surfgrass *Phyllospadix torreyi* Watson (Zosteriaceae). San Diego Trough, off Tijuana, Baja California (32°23.5' to 18.8'N, 117°31.75' to 31.01'W), R/V *Melville*, 16 December 1969, 25 foot otter trawl, 1207–1234 m.

Description of radula (Figs 10, 11) supplemental to the detailed generic description: marginal teeth pairs five; inner lateral of left side of ribbon well-formed with large tip, not hidden behind pluricuspid; lateral flanges of rachidian well marked.

Remarks. The radula differs from that of *B. diegensis* in having five rather than three pairs of marginal teeth. Other radular differences may be due to size differences and relative shrinkage of the radula during drying, exposing the flanges of the rachidian and tips of the inner laterals to various degrees. The marginal tooth count is considered to be a generic character, although it is possible that the number of marginal teeth may vary intraspecifically and that the specimen is actually conspecific with *B. diegenensis*. Until further material is available, it seems prudent not to name a new species in the absence of the shell.

Leaves of the preserved plant material are 1 mm wide and are elliptical in cross-section. The host plant is identified as *Phyllospadix torreyi* Watson (see Abbott 1975). In this case, the width of the body matches the width of the leaves of the host plant. This limpet occurred on the other of the two species of *Phyllospadix*, and it may be that the two limpet species are host specific.

Anatomy and histology of *Bathyphytophilus diegensis* sp. n.

External structures

For external morphology see the diagnosis part.

The foot sole shows two zones (Figs 8, 22). Centrally the epithelial cells are flat and lack cilia, the visible 'cuticula' of the cells is probably a microvillar border. This area is surrounded by a broad zone of elongated and densely ciliated cells. Laterally, the foot extends considerably; here the dorsal epithelium is composed of large, flat and glandular cells. A large, anterior pedal gland opens at the anterior edge of the foot sole; a distinct propodium is not present, however. Otherwise, many subepidermal glands are present, particularly laterally. A single pair of epipodial tentacles is present at the posterior end.

The mantle margin is quite simply structured. Special

sensory elements are represented by very small and short papillae; otherwise the mantle margin is smooth. The mantle sinus (i.e. a vessel lacking an endothelium) of the mantle is very wide (Fig. 16: *ms*). Gill-leaflets are present (see below).

Muscle system

The shell muscle is well developed and asymmetrically horseshoe-shaped (Fig. 13: *sm*). It is interpreted as paired because of the type of innervation (Haszprunar 1985).
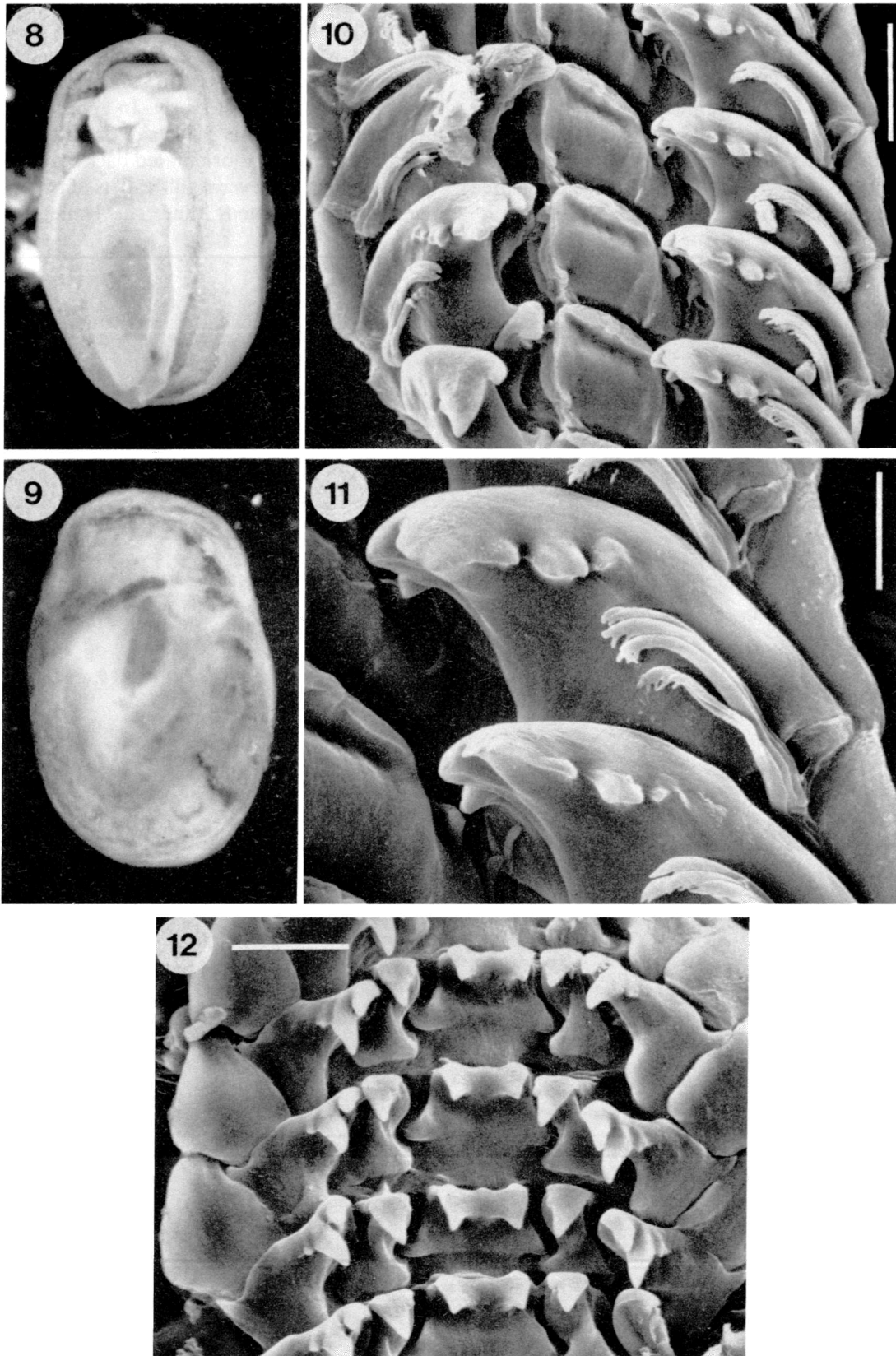
Figs 8–12. Bathyphytophilidae and Lepetellidae.—*8–11. Bathyphytophilus* sp. from San Diego Trough, 1.207–1.234 m.—*8–9.* Intact body prior to removal of radula, length 1.5 mm.—*8.* Oblique ventral view; note the head without oral lappets and the two zones of the pedal sole.—*9.* Dorsal view.—*10–11.* SEM views of radula.—*10.* Scale bar = 20 μm.—*11.* Scale bar = 10 μm.—*12.* SEM view of radula of *Lepetella* sp. (730–750 m off Punta Topocalma, Chile, LACM 66–152), for comparison with bathyphytophilid radula. Scale bar = 20 μm.

The shell muscle is a solid organ penetrated by nerves (to the mantle margin or to the epipodial tentacles) only. As usual, in limpets, the dorsoventral muscle fibres are intercrossed ventrally. The foot musculature is weakly developed (Fig. 18). In accordance with the somewhat asymmetrical shell (see *Diagnosis*), the paired head retractors of *B. diegensis* show an asymmetrical arrangement. The right retractor forms a hook at the anterior edge of the right shell muscle similar to conditions in many other lepetelloid (*Pyropelta, Cocculinella, Osteopelta*; see McLean & Haszprunar 1987; Haszprunar 1988*a*) or fissurelloid limpets. In contrast, the left head retractor has its insertion area much more centrally situated, while there is no connection with the insertion area of the left shell muscle (Figs. 13, 17: *hr*).

Mantle roof (Fig. 13)

The mantle cavity is very shallow in *B. diegensis*; to the left and right the 'cavity' is deeper than in the central region, which is occupied by the heart. Indeed, the central posterior border of the mantle roof is more anteriorly situated than the anterior end of the shell muscles. The anterior mantle roof contains numerous blood sinuses. The right mantle roof is mainly occupied by the left kidney and also the anus, while the urinogenital opening is positioned more posteriorly. In general, the arrangement of mantle organs reflects a 'detorted' condition in that the anal region is orientated backwards to the right.

B. diegensis has several gill-leaflets of two kinds. In the investigated specimen, nine gill leaflets occupy the
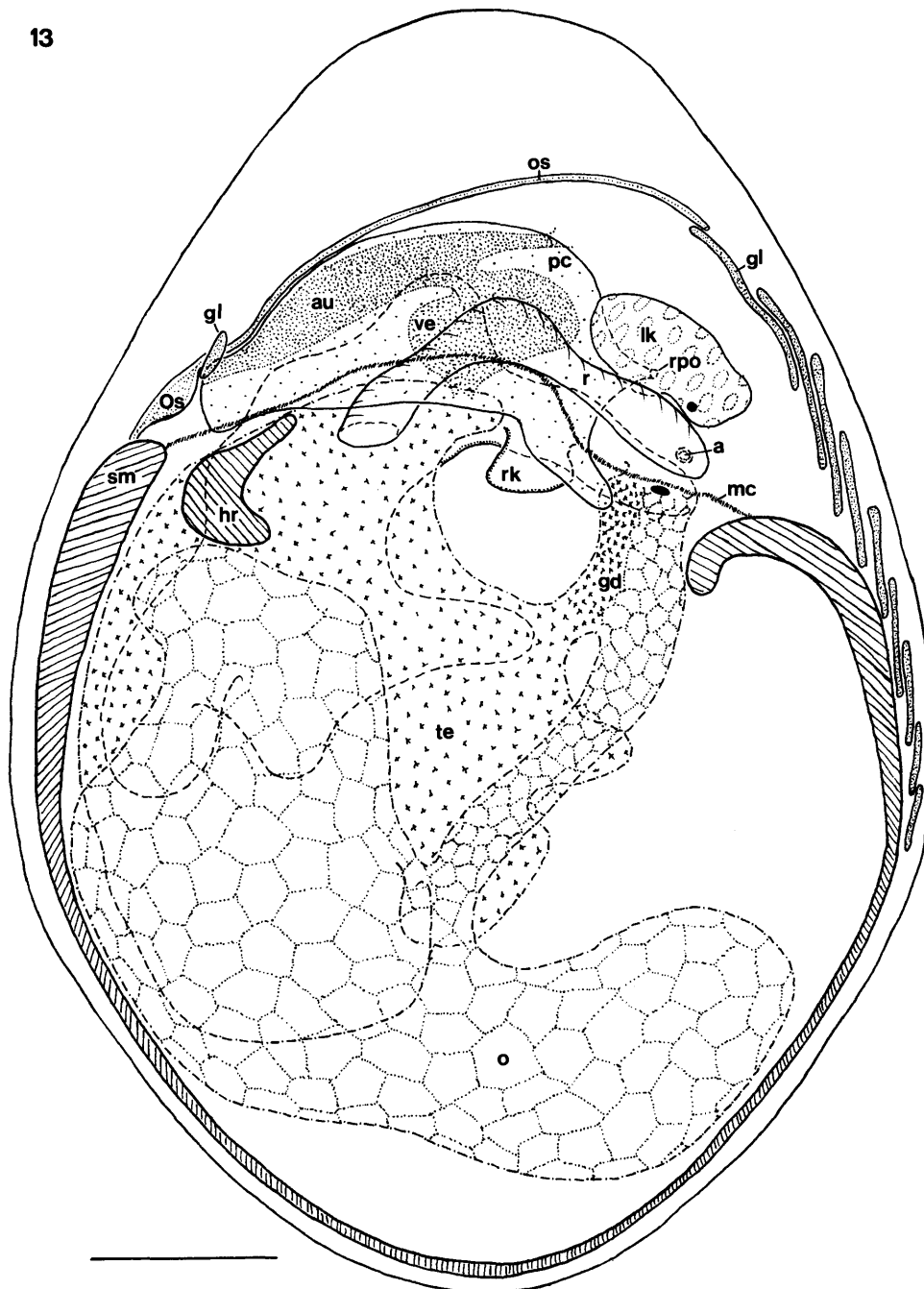

Fig. 13. Bathyphytophilus diegensis paratype. Mantle organs and coelomic system (dorsal view). *a* anus; *au* auricle; *gl* gill-leaflet; *gd* gonoduct; *hr* attachment zone of head retractor; *lk* left kidney; *mc* posterior end of mantle roof; *o* ovary; *Os* osphradial ganglion; *os* osphradial nerve; *pc* pericard; *r* rectum; *rk* right kidney; *rpo* renopericardial opening; *sm* attachment zone of shell muscle; *te* testis; *ve* ventricle. Scale bar: 200 μm.

anterior right mantle roof and continue backwards into the right subpallial cavity. Posteriorly the leaflets become less and less distinct, and there is a continuum from typical gill-leaflets through simple folds to a non-differentiated epithelium covering the mantle sinus. A well-differentiated gill-leaflet is provided with a distinct efferent axis with dense and large cilia that are laterally situated (Figs 20, 21). The efferent axis also has a sensory pocket (bursicle), the short tube of which opens posteriorly and is heavily ciliated (Fig. 20: arrow). Three simple epithelial folds (respiratory), which lack sensory pockets, are situated at the outer left mantle roof adjacent to the mantle border (Fig. 17: *ml*). There is an additional, single gill-leaflet at the point of entrance of the mantle sinus into the auricle, immediately adjacent to the osphradial ganglion. This one has a well developed axis with dense ciliation and a sensory pocket, though it lacks a respiratory zone (Fig. 19).

An hypobranchial gland is lacking, but two glandular fields with very similar histology are found in front of the anterior ends of the shell muscles (see genital system).

Heart and excretory system

The large pericardium occupies the central and left mantle roof and includes a single, anteriorly left situated auricle and a ventricle, which is penetrated by the rectum (Figs 13, 16: *ve*). There is no pericardial gland, and the aorta is very short. The oxygenated blood from the gill-leaflets is collected by a mantle sinus, which fuses with numerous small sinuses of the anterior mantle roof before entering the auricle at the extreme right. In addition, a second pass of blood coming from the left mantle sinus enters the auricle at the very left side.

Two kidneys are present (Fig. 13). The left one is rather small, occupies the right anterior pallial roof in front of the rectum, and is connected to the pericardium via a ventrally situated, short reno-pericardial duct. The opening of the left kidney is provided with a distinct sphincter. The right kidney differs entirely in histology from the left, and forms a system of large coelomic cavities occupying free space between the elements of the alimentary tract and gonad at the left side (Figs 17, 18: *rk*). It is not connected to the pericardium and has a common opening with the gonoduct.

Genital system (Fig. 13)

B. diegensis is a simultaneous hermaphrodite, the gonad of which is divided into testis and ovary. The testis is situated anteriorly left, while the ovary is placed dorsally and occupies the whole left posterior part of the body. All stages of ovo- and spermiogenesis are exhibited. Ripe eggs are large (up to 140 μm diameter), filled with many yolk vesicles and have a large nucleus. They are covered by a distinct, dark egg-layer (Fig. 23). Ripe sperm cells have filamentous heads. The proximal oviduct and proximal vas deferens are simple, ciliated tubes, which fuse after a short distance, with the hermaphroditic part of the gonoduct lacking accessory glands. A common urinogenital opening with the right kidney is situated at the right posterior end of the mantle roof. Ventrally, a small glandular field is present, and for a short distance, a ciliated groove can be detected. This is continued forwards as a band of ciliated and mucous cells. The ciliated
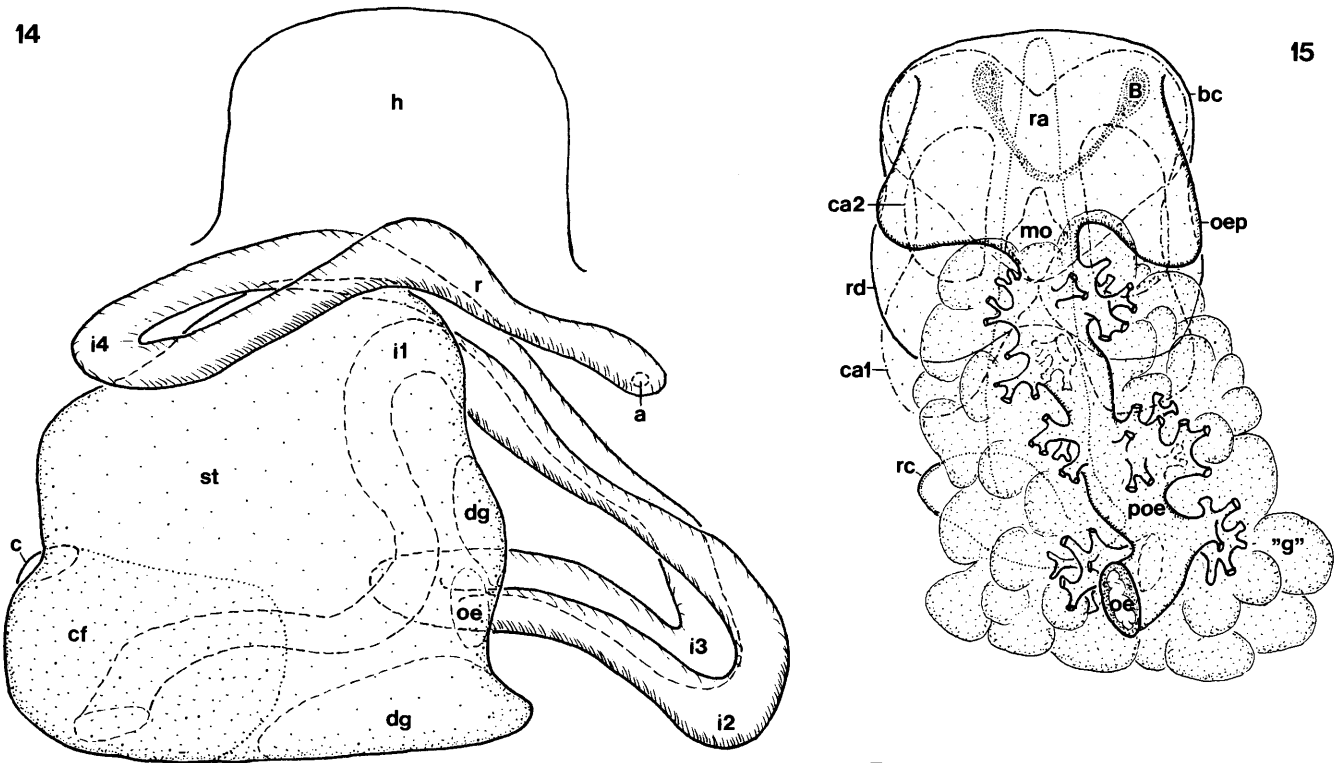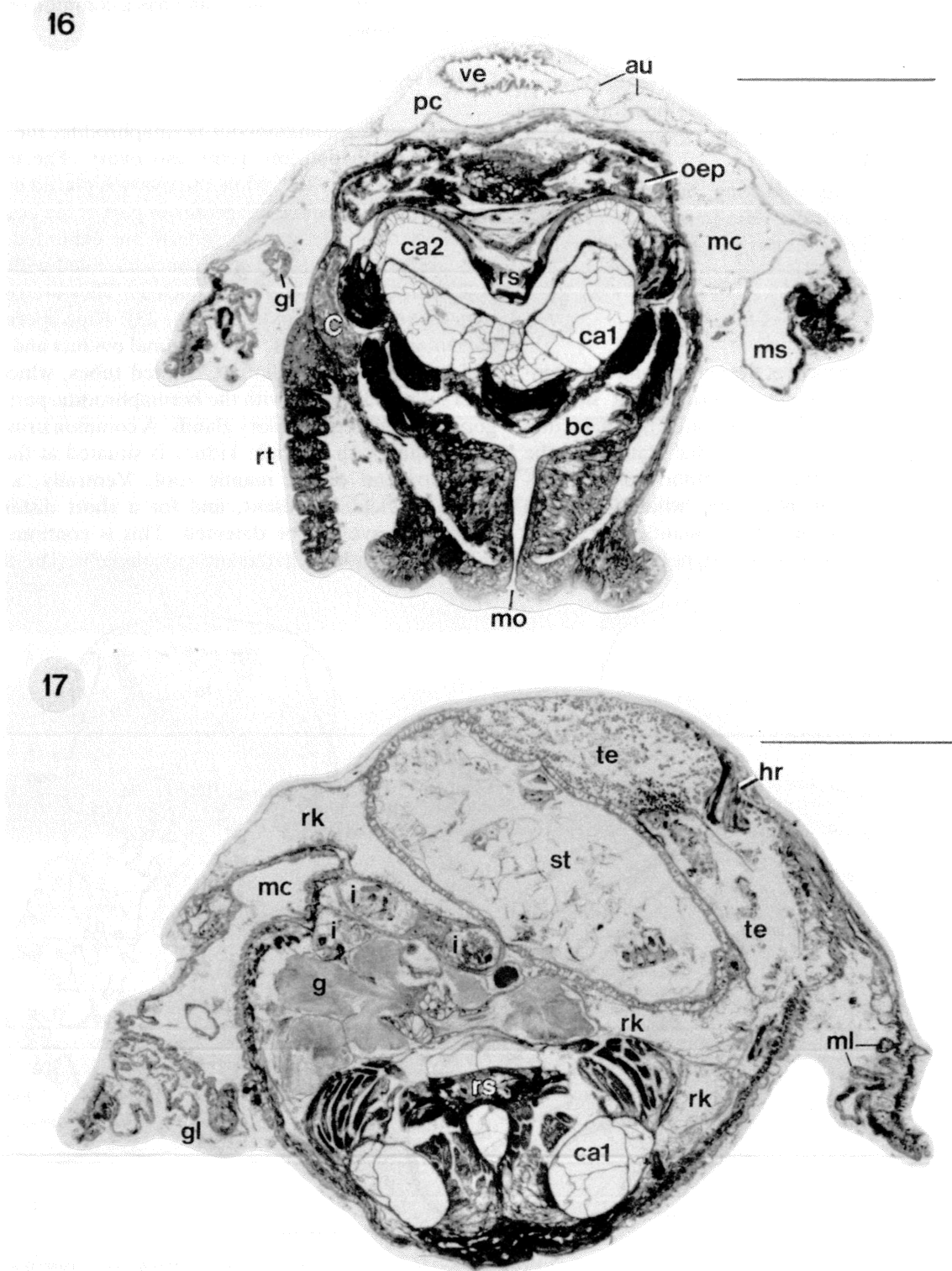

Figs 14–15. Bathyphytophilus diegensis paratype. Alimentary tract (dorsal view).—*14.* Head and posterior alimentary tract.—*15.* Buccal apparatus and anterior alimentary tract (stomach and intestine removed; the grape-like pouches are thought glassy). *a* anus; *B* buccal ganglion; *bc* buccal cavity; *c* caecum of stomach; *ca1,2* anterior and posterior cartilage; *cf* ciliary field of stomach; *dg* opening of digestive gland; *g* grape-like pouches (bacterial chambers); *h* head; *i1–4* course of intestine; *mo* mouth opening; *oe* opening of oesophagus into stomach; *oep* oesophageal pouches; *poe* posterior oesophagus; *r* rectum; *ra* radula; *rc* radular caecum ; *rd* radular diverticulum; *st* stomach. Scale bar: 200 μm.

band reaches the outer wall of the right cephalic tentacle which is not otherwise specialized (Fig. 16: *rt*). There is no trace of a receptaculum. An additional glandular field, which is histologically very similar to that near the genital opening, is situated immediately in front of the anterior end of the left shell muscle.

Like many other lepetelloid limpets, *B. diegensis* broods its eggs in the pallial cavity (Fig. 1: arrow).

Alimentary tract (Figs 14, 15)

The mouth opening is ventrally situated, and its lining appears to be cuticularized (Fig. 16: *mo*). Jaws are lacking, and the short and narrow sublingual pouch is devoid of a subradular organ. Salivary glands could not be detected; however, the respective region was tangentially sectioned, so the salivary glands might not have been

Figs 16–18. Bathyphytophilus diegensis paratype no. 2, semithin cross-sections (frontal view, compare with Figs 13–15).—*Fig. 16.* Line of mouth opening.—*Fig. 17.* Line of attachment zone of left head retractor.

distinct in this sectioning plane. Curving dorsally in the buccal cavity, there are two folds, which are densely ciliated at their inner surface. These form the food channel, which continues into the oesophagus.

The radula is described above. The radula sheath is short and straight, and the central tooth field is formed as a single, homogeneous, large tooth in the bulbous radular caecum, which bends downwards and slightly to the left. The radular diverticulum is very broad and flattened. There are two pairs of radular cartilages (Figs 16, 17: *ca1*, *ca2*). The anterior ones are large and consist of very large cells (diameter up to 80 μm). They are fused centrally for a considerable distance, and are connected ventrally by the horizontal muscle. Each anterior cartilage is connected via prominent muscles with the respective posterior one, and the latter are placed dorsally and are built up by much smaller elements. Otherwise the buccal muscles were not studied in detail.

The anterior oesophagus is broad and provided with a dorsal food channel as well as with a laterally situated glandular zone separated by longitudinal ciliary tracts. A short distance posteriorly, these zones form shallow oesophageal pouches (Fig. 16: *oep*).

The posterior oesophageal region of *B. diegensis* is peculiar. The oesophagus itself forms a tube, which runs ventrally to the stomach, straight backwards and slightly to the right of the midline. The oesophageal tube consists of cuboidal cells, and contains also various longitudinal, densely ciliated folds. A continuation of the dorsal food channel, the position of which would reflect torsion, could not be detected. Various embranchments of the oesophageal tube lead to prominent pouches, which are filled with densely packed cilia-like structures, resembling a vesicula seminalis (Figs 17, 18, 24: *g*). The whole region gives the impression of a bunch of grapes, but with a more or less equal diameter from the beginnning to the end. The epithelium of the embranchments resembles that of the oesophageal tube, but is generally ciliated, and the rows of basal bodies are well visible in the semithin sections. In contrast, the epithelium of the grape-like pouches is non-glandular, very flat, and basal bodies are not visible. Some larger cells are occasionally interspersed in the epithelium of the pouches. The whole structure is situated below the stomach anteriorly right and occupies a considerable volume (Figs 17, 18: *g*).

The oesophagus enters the very large stomach at the right ventral side between the very broad openings of the two large digestive glands (Fig. 18: *dg*). Like the stomach (*st*), these contain partly digested food particles of seagrass. The right digestive gland is situated anteriodorsally, whereas the left one occupies the posterioventral region. The stomach itself occupies the central dorsal region. It is provided with a cuticularized gastric shield forming a tooth, which is situated at the ventral left
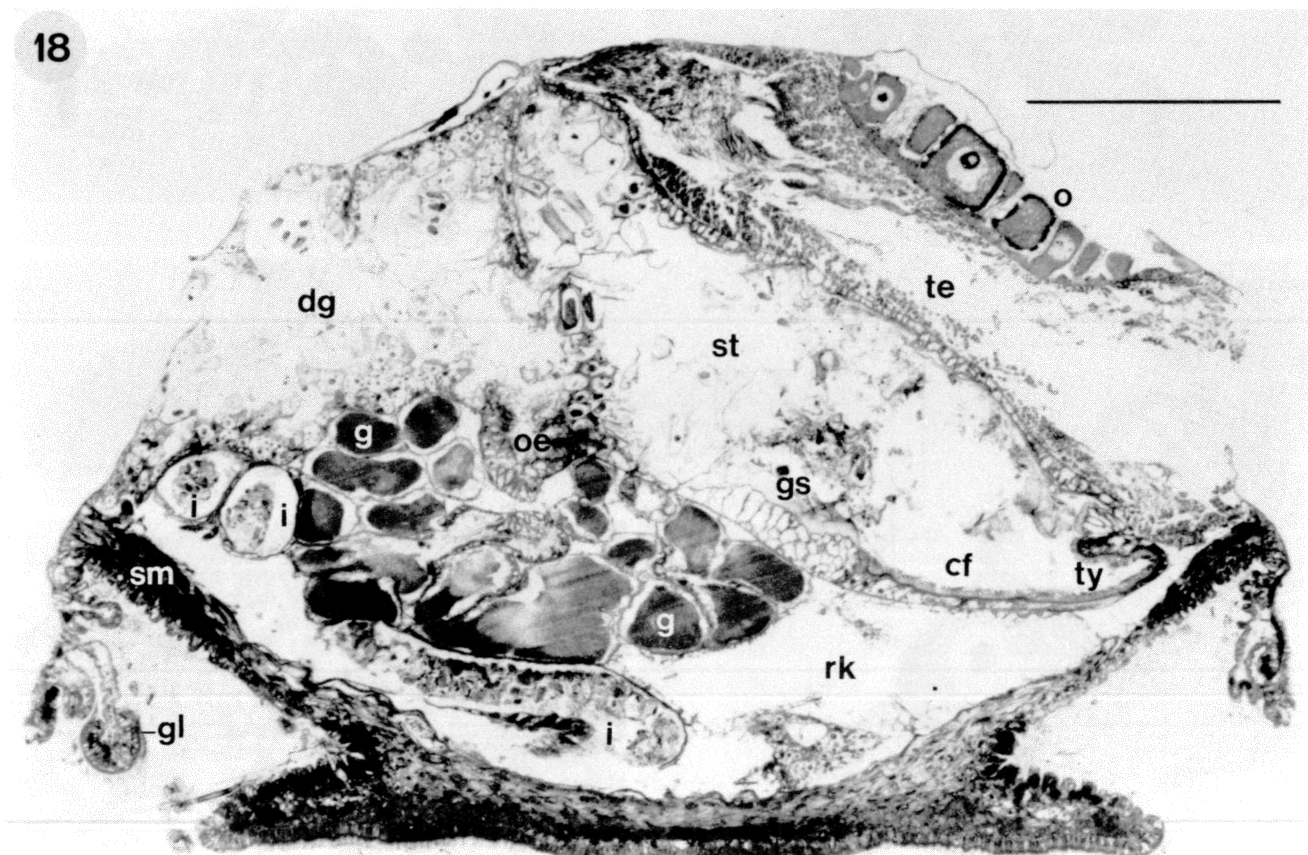

Fig. 18. Line of entrance of oesophagus into stomach; the specimen is slightly damaged at the left dorsal side (testis, ovary). *au* auricle; *bc* buccal cavity; *C* cerebral ganglion; *ca1,2* anterior (ventral) and posterior (dorsal) cartilage; *cf* ciliary field of stomach; *dg* digestive gland; *g* grape-like pouches (probably bacterial chambers of posterior oesophagus); *gl* gill-leaflets; *gs* gastric shield; *hr* left head retractor; *i* intestine; *mc* mantle cavity; *ml* mantle leaflets; *mo* mouth opening; *ms* mantle sinus; *o* ovary; *oe* opening of oesophagus into stomach; *oep* oesophageal pouch; *pc* pericard; *rk* right kidney; *rs* radular sheath; *rt* right cephalic tentacle; *sm* shell muscle; *st* stomach; *te* testis; *ty* typhlosolus of stomach; *ve* ventricle. All scale bars: 200 μm.

side, as well as a distinct ciliary field with typhlosolus (Fig. 18: *st*) and a short caecum.

The intestine emerges from the posterior left portion of the stomach. Being completely ciliated at the beginning, the ciliation becomes restricted to a typhlosole region after a short distance. The long intestine makes several loops (Figs 14, 17, 18: *i*). Finally, it curves dorsally, and the rectum runs through the ventricle and then to the right, terminating in an anus at the right posterior end of the mantle roof.

Nervous system

The nervous system of *B. diegensis* is weakly concentrated. The cerebropedal nerve ring surrounds the buccal apparatus and shows a hypoathroid condition having adjacent pleural and pedal ganglia. The cerebral ganglia are laterally situated at the basis of the cephalic tentacles (Fig. 16: *C*) and are interconnected by a long and thick cerebral commissure. The cerebral ganglia innervate the snout, and each cephalic tentacle is supplied with a simple, thick nerve. An optic nerve could not be detected. At each posterior ventral end, a so-called labial lobe is formed, from which the buccal connective emerges. The buccal commissure lies, as usual, at the emergence point of the oesophagus; the buccal ganglia are situated more anteriorly (Fig. 15: *B*). Posteriorly, two connectives emerge from each cerebral ganglion and run side by side backwards to the pleuropedal complex.

The pedal ganglia are large and are interconnected by a
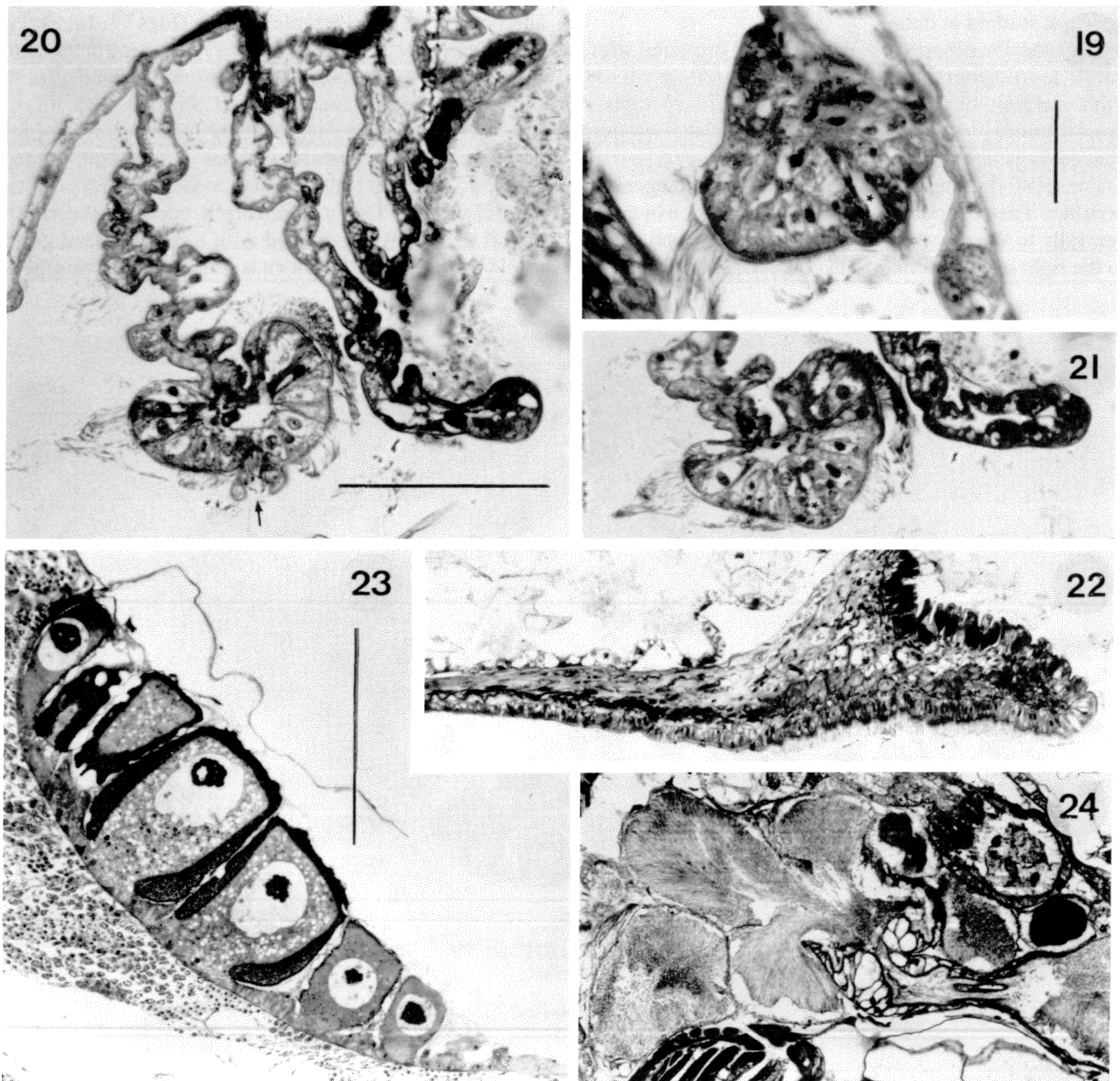
Figs 19–24. Bathyphytophilus diegensis paratype. Histological details.—*19.* Left gill-leaflet with prominent bursicle (channel marked by asterisk). Note the lack of a respiratory zone. Scale bar = 20 μm.—*20.* Right gill leaflets, the posterior (left) one with ciliated axis and entrance of bursicle (arrow); the anterior (right) one with respiratory zone alone. Scale bar: 50 μm.—*21.* Same leaflet as is Fig. 20 (also same scale bar), slightly posterior showing channel of bursicle (asterisk).—*22.* Foot sole showing outer, higher, ciliated cells (to the right) and central, lower, non-ciliated cells (to the left). Scale bar as in Fig. 23.—*23.* Ovary showing yolky eggs with large nucleus (bright) and nucleolus (dark). Scale bar: 100 μm.—*24.* Detail of Fig. 17. Posterior oesophagus (with few bright epithelial cells) with adjacent grape-like pouches (with filamentous bacteria?). Scale bar as in Fig. 23.

thick commissure and a very thin, posteriorly situated parapedal commissure. Two main nerves emerge from each pedal ganglion. The anterior nerve supplies the anterior foot sole and the pedal gland, the posterior one is not cord-like and innervates the rest of the foot sole and the epipodial tentacles. A relatively thin shell muscle nerve emerges laterally. The pleural ganglia are situated adjacent laterally to the pedal ones. Their main nerves are the mantle nerves, which penetrate the shell muscle and supply the mantle border, where they form a dense neural net that encircles the animal.

The visceral loop is weakly developed. Because of the strongly anterior position of the shallow mantle 'cavity', it is situated more anteriorly than the pleuropedal complex. From the suboesophageal ganglion, a thin nerve innervates the region of the anus and urinogenital opening. The elongated and depressed visceral/genital ganglion is situated along the posterior end of the mantle roof. From the supraoesophageal ganglion, a nerve runs dorsally to the left. Anteriorly to the left shell muscle, the nerve swells abruptly and forms a thick osphradial ganglion. From there, a short nerve supplies the osphradial epithelium, which is placed to the left of the ganglion. A second, thick nerve runs forward and then to the very right, innervating the mantle roof and the gill-leaflets (Fig. 13: *os*).

Sense organs

The cephalic tentacles are provided with small, but distinct ciliary tufts, which probably represent the sensory elements. These occur predominately at the inner, lower side of the tentacles. Distinct papillae, such as those of the mantle margin, are lacking, however. The tips of the epipodial tentacles bear a distinct sensory epithelium, which consists of highly cylindrical cells.

Eyes and subradular organ are lacking. The osphradium is represented by a distinct sensory epithelium. It is situated to the left of the osphradial ganglion being bordered by the single, inner gill-leaflet and the several outer left mantle folds. The bursicles of the gill-leaflets have been described above (Figs 19, 20, 21: asterisks).

The small statocysts are placed adjacent to each other at the pedal commissure. They contain few, tiny statoconia.

Cladistic analysis

Character analysis

The significance and evolution of organ systems of the Cocculiniformia as a whole have been reviewed and discussed in detail (Haszprunar 1988c,d, 1996). Here, specific attention is paid to the unique characters of *Bathyphytophilus*; remarks on the actual coding of characters are also given.

Shell characters of *Bathyphytophilus* are similar to most other lepetelloid families, so we restrict the coding for helicoid versus limpet-like shell (Tables II, III: no. 1) and presence versus absence of an operculum (no. 2). The surface sculpture of bathyphytophilids remains intact,

whereas all pyropeltids, certain cocculinids and many pseudococculinids are known only from specimens having a deeply eroded apex (see Marshall 1986; McLean 1987, 1988, 1991; McLean & Haszprunar 1987). We did not code the latter character because it may be an environmental artifact.

Protoconchs with lateral pouches (no. 3) are diagnostic for lepetelloid limpet families such as Lepetellidae, Pseudococculinidae, Cocculinellidae, and Addisoniidae (no data on Pyropeltidae and Osteopeltidae), but are not present in Choristellidae. Pit row protoconch sculpture occurs in several pseudococculinids, whereas such sculpture has not been observed in Lepetellidae and Cocculinellidae (see Marshall 1983, 1986; McLean 1991; Warén 1991: fig. 6B and pers. comm.; Dantart & Luque 1994). This character may be well suited for generic or species identification, but again does not seem to be significant for higher systematics.

The presence of mantle papillae is shared with the Pseudococculinidae (cf. Haszprunar 1988b: fig. 7F; Dantart & Luque 1994: fig. 67), certain lepetellids (Dantart & Luque 1994: fig. 49; G. H. pers. obs.), and *Addisonia excentrica* (Dantart & Luque 1994: fig. 88). However, fine-structural investigations are necessary to confirm the direct homology of these structures; therefore we did not code this character.

If it proves to be characteristic for the group, the asymmetry of outline (in which the right side is more projecting) and shell muscles (no. 4) may be an autapomorphic character of the Bathyphytophilidae, which is, however, paralleled by certain cocculinids (Marshall 1986) and even more pronounced in the addisoniids (McLean 1985). In contrast, the remarkable asymmetry of the head retractors appears to be an uninformative autapomorphy of the Bathyphytophilidae.

Paired shell muscles, which form a solid horseshoe-shaped organ, are typical for all lepetelloids, except certain (not yet described) lepetellid limpets (cf. Haszprunar 1996) which resemble patellogastropods and cocculinids in this character. Also the presence of a pedal gland and a foot sole being composed of two zones are typical for the superfamily. None of these characters is informative for internal relationships of the Lepetelloidea.

The presence of gill-leaflets in the mantle roof of *Bathyphytophilus diegensis* challenges the lack of respiratory organs in *B. caribaeus* and *Aenigmabonus kurilokamtschaticus* reported by Moskalev (1978). However, Moskalev (1978) did not investigate his specimens by means of serial sectioning or by scanning of the soft body, and there is a strong possibility that he overlooked small (or vestigial) gill-leaflets in his material. In any case, the arrangement and structure (no. 5, no. 7) of the gill-leaflets of *B. diegensis* strongly resembles conditions found in the Pseudococculinidae, in particular the Caymanabyssiinae (cf. Haszprunar 1988b) as well as in certain Lepetellidae (G.H. pers. obs.).

The additional single gill-leaflet at the entrance of the left mantle roof (no. 6) requires some attention. Lacking a respiratory zone, it is probably not used for gas exchange but for ventilation. Moskalev (1978) reported brooding in the left mantle cavity of *B. caribaeus*, and

brooding could be confirmed also for *B. diegensis* occurring at the left side of the mantle roof and subpallial cavity (Fig. 1: arrows). Therefore, one might speculate that this extra gill-leaflet is necessary to supply the brooded eggs with fresh, oxygen-rich water. This view is supported by the somewhat similar conditions found in certain lepetellid species (Haszprunar, unpubl.), which also are brooders (Warén, 1972; G.H. pers. obs.). However, similar leaflets are also found (at the right mantle roof) in *Cocculinella minutissima* (cf. Haszprunar 1988a), in which brooding has not been confirmed.

Among the Lepetelloidea, only Addisoniidae and Choristellidae have a gill skeleton (no. 7). These two families are additionally characterized by a hypobranchial gland extending at the gill-leaflets (no. 8).

The presence of two kidneys and of a monotocardian heart is typical for the Lepetelloidea. Penetration of the heart by the rectum certainly is a plesiomorphic trait in gastropods (Haszprunar 1988d), among the Lepetelloidea the rectum passes the heart only in addisoniids and choristellids (no. 9).

Because of the lack of a distinct receptaculum (no. 10) and judging from the reports of brooding in *B. caribaeus* and *B. diegensis* (Moskalev 1978; herein), fertilization probably occurs in the mantle 'cavity'. The role of the genital gland remains unresolved. Its secretions might be necessary for clumping sperm cells or eggs or both. Similar glands are present in the Lepetellidae, Pyropeltidae, Cocculinellidae, and Choristellidae, but their homology is highly doubtful, so we did not code this character.

The presence of a hermaphroditic gonoduct versus distinct vas deferens and oviduct separates the hermaphroditic Osteopeltidae, Cocculinellidae, Addisoniidae, and the gonochoristic Choristellidae from the remaining families (no. 11).

The bathyphytophilid condition of a common urinogenital opening (no. 12) is likewise found in Lepetellidae, Pseudococculinidae and Pyropeltidae (cf. McLean & Haszprunar 1987 for review). Based on the presence of the ciliary band, sperm transfer probably takes place by using the right cephalic tentacle as a copulatory organ.

Among the Lepetelloidea, distinct oral lappets (no. 13) are restricted to certain Lepetellidae and the Pseudococculinidae.

Bathyphytophilids share a complete lack of jaws (no. 14) with the Lepetellidae, Cocculinellidae and Addisoniidae. However, multiple convergence of this loss cannot be excluded.

The bathyphytophilid radula shows close similarities with that of Lepetellidae (Fig. 12) as illustrated by Warén (1972, fig. 21), Moskalev (1978, fig. 1), Hickman (1983, fig. 39), and Dartart & Luque (1994, figs 25–27, 31–33, 37–39). The lepetellid radula has the same elements as the bathyphytophilid radula, including the broad rachidian (no. 15), narrow inner lateral, large pluricuspid second lateral of similar morphology, and non-cuspidate basal plate. Compared to that of *Bathyphytophilus*, the elements missing in the lepetellid radula are the marginals and the small plate that defines the outer edge of the bathyphytophilid radula. The shared elements differ in the details of morphology: the lepetellid rachidian has a different cusp pattern, the first lateral is larger, the pluri-

cuspid is smaller and has one less cusp, and the basal plate is broader. In addition, the lepetellid radula is symmetrically structured, whereas the bathyphytophilid radula shows strong asymmetry. So many characters are shared, however, that common ancestry is likely. Coding of all these radular characters certainly would result in a sister-group relationship of Lepetellidae and Bathyphytophilidae. We decided to prove these relationships by other characters as well; therefore we only coded general radular characteristics.

The few marginal teeth of *Bathyphytophilus* (no. 16) are so weakly developed that they are probably without function. Moskalev's (1978: fig. 4)) drawing of the marginal teeth of *Aenigmabonus* shows them to have the same relative length compared to the pluricuspid, but it seems best to refrain from comment further on them until they can be examined by SEM. It is evident that the loss of marginal teeth is a trend in the Bathyphytophilidae, one that has been completed in the Lepetellidae (and in parallel in the Cocculinellidae, Addisoniidae and Choristellidae; see Table IV).

The presence of two pairs of radular cartilages (no. 17), a radular diverticulum and the conditions of the anterior oesophagus all reflect primitive conditions of the Lepetelloidea (cf. Haszprunar 1988c). Specific positional conditions of the two cartilages are found in the Cocculinellidae and Choristellidae (no. 18).

The presence of oesophageal pouches (no. 19) is a plesiomorphic gastropod (conchiferan) feature (Haszprunar 1988d), whereas true glands with narrow openings or ducts are present in Osteopeltidae, Cocculinellidae, and Addisoniidae.

The conditions of the posterior oesophageal region of *Bathyphytophilus* are unique (therefore uninformative in the present analysis) and difficult to interpret. The grape-like pouches cannot be directly homologized with organs of any other cocculiniform family. Oesophageal appendages in a similar position are present in the Choristellidae (Haszprunar 1992). However, in choristellids, these structures are glandular and lack the 'cilia' within, contradicting any direct homology.

Although the first impression of the content of the 'grapes' is 'densely packed cilia', this conclusion is unlikely, because basal bodies are not visible in the cells of the respective epithelium. In addition, we cannot imagine any function of such a mass of cilia. Sperm storage can be excluded, because this is a structure of the alimentary canal. Therefore, we speculate that the 'cilia' are endosymbiotic spirochaete-like (? because of the shape) bacteria for digestion of plant material analogous to conditions in teredinid bivalves, termites or ruminant mammals.

The bathyphytophilid type of the stomach (no. 20) and the course of the posterior alimentary tract (no. 21) is nearly identical to that of the Pseudococculinidae, probably reflecting primitive conditions among the Lepetelloidea. Compared with Pseudococculinidae, the stomach is larger and the presence of partially digested food in the digestive gland is shared with the Lepetellidae (G.H. pers. obs.).

Nervous system and sense organs of *Bathyphytophilus* do not show distinct specializations compared with other

Table II. *Character-matrix of cladistic study of the Lepetelloidea. Data based on Marshall (1983, 1986), McLean (1985, 1988), McLean & Haszprunar (1987), Haszprunar (1987, 1988a, b, c, d, 1992, 1996), and Dantart & Luque (1994)*

No. character	12345	67890	12	3	45	67890	12345
ANCESTOR	??0?0	00000	?0	?	01	00000	00011
Lepetellidae	00100	00100	00	{0,1}	10	22?01	00011
Pseudococculininae	00101	00100	00	0	01	01000	00111
Caymanabyssiinae	00101	10100	00	0	01	01000	00111
Bathyphytophilidae	00111	10100	00	1	10	11000	00011
Pyropeltidae	00?01	00100	00	1	00	01000	00011
Osteopeltidae	00?01	00100	11	1	01	02?10	00001
Cocculinellidae	00100	00100	11	1	11	21110	10000
Addisoniidae	00111	01211	11	1	11	21011	11000
Choristellidae	1101?	01211	11	0	01	21100	01002

The column group header above columns "12 3 45 67890" is labelled **1**, and the column group header above "12345" is labelled **2**.

Table III. *Coding of characters of cladistic study of the Lepetelloidea*

1. Shell: 0 = limpet; 1 = coiled.
2. Operculum (adult): 0 = absent; 1 = present.
3. Protoconch: 0 = otherwise; 1 = with lateral pouches.
4. Shell muscles: 0 = symmetrical; 1 = markedly asymmetrical.
5. Gill: 0 = only in mantle cavity; 1 = extending into subpallial cavity.
6. Vestigial knob(s) at left side: 0 = absent, 1 = present.
7. Ctenidial skeleton: 0 = absent, 1 = present.
8. Hypobranchial gland: 0 = present; 1 = absent; 2 = at gill-leaflets.
9. Rectum: 0 = penetrates the heart; 1 = passes the heart.
10. Receptaculum: 0 = absent; 1 = present.
11. Gonoduct: 0 = hermaphroditic; 1 = gonochoristic.
12. Common urinogenital opening: 0 = present; 1 = separate openings.
13. Oral lappets: 0 = present; 1 = absent.
14. Jaw: 0 = two, lateral; 1 = absent.
15. Rhachis tooth: 0 = prominent; 1 = vestigial or absent.
16. Marginal teeth: 0 = many, 1 = few, 2 = none.
17. Radular cartilages: 0 = three or more; 1 = two; 2 = one.
18. Second cartilage (if present): 0 = otherwise; 1 = above the first one.
19. Oesophageal glands: 0 = pouches; 1 = glands with duct.
20. Gastric shield: 0 = present; 1 = absent.
21. Intestine: 0 = regular; 1 = extremely widened.
22. Feeding on chondrichthyean eggs: 0 = absent; 1 = present.
23. Tentacles: 0 = smooth; 1 = papillate.
24. Bursicles: 0 = absent; 1 = present.
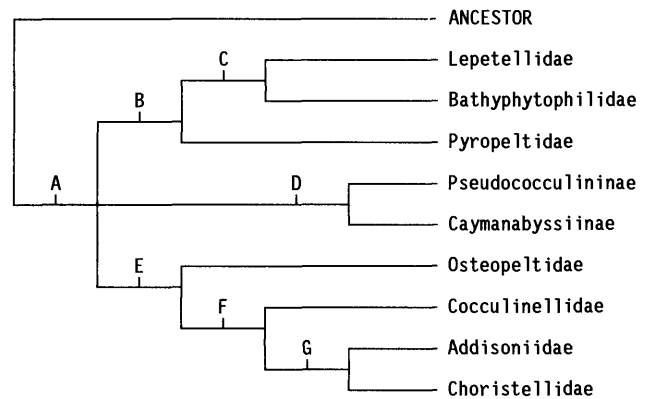25. Epipodial tentacles: 0 = none; 1 = single pair, 2 = several.

Fig. 25. Phylogenetic analysis of the Lepetelloidea. Strict consensus of three trees (= original tree no. 2). Indices of original trees: 43 steps; CI = 0.674; RI = 0.659; RC = 0.444.

Table IV. *Character state changes at nodes and taxa of Fig. 25 (H = homoplasy occurs, R = reversal occurs)*

A: no. 3:0 → 1(R); no. 5:0 → 1(R); no. 8:0 → 1; no. 17:0 → 1;
B: no. 15:1 → 0;
C: no. 14:0 → 1(H); no. 16:0 → 1;
D (Pseudococculinidae): no. 13:1 → 0(H); no. 23:0 → 1;
E: no. 11:0 → 1; no. 12:0 → 1; no. 19:0 → 1(R); no. 24:1 → 0;
F: no. 16:0 → 2(H); no. 25:1 → 0;
G: no. 4:0 → 1(H); no. 7:0 → 1; no. 8:1 → 2; no. 9:0 → 1; no. 10:0 → 1; no. 22:0 → 1;
Lepetellidae: no. 5:1 → 0(R,H); no. 16:1 → 2(H); no. 17:1 → 2(H); no. 20:0 → 1(H);
Pseudococculininae: no autapomorphies based on the matrix;
Caymanabyssiinae: no. 6:0 → 1(H);
Bathyphytophilidae: no. 4:0 → 1(H); no. 6:0 → 1(H);
Pyropeltidae: no autapomorphies based on the matrix;
Osteopeltidae: no. 17:1 → 2(H);
Cocculinellidae: no. 5:1 → 0(R,H); no. 14:0 → 1(H); no. 18:0 → 1(H); no. 21:0 → 1(H);
Addisoniidae: no. 14:0 → 1(H); no. 20:0 → 1(H); no. 21:0 → 1(H);
Choristellidae: no. 1:0 → 1; no. 2:0 → 1; no. 3:1 → 0(R); no. 13:1 → 0; no. 18:0 → 1(H); no. 19:1 → 0(R); no. 25:0 → 2;

lepetelloid families; therefore we did not code this character.

In contrast to pseudococculinids, papillae are lacking at the cephalic tentacles of *Bathyphytophilus* (no. 23). The loss of eyes certainly is a derived feature. However, because of the high probability of convergence, we did not code this character.

Sensory pockets (bursicles; no. 24) of the gill-leaflets are typical for Bathyphytophilidae, Lepetellidae, Pseudococculinidae, and Pyropeltidae. Outside the Cocculiniformia, very similar (homologous?) structures are found in the ctenidial leaflets of the hot-vent archaeogastropod *Melanodrymia aurantiaca* Hickman (see Haszprunar 1989), in the Vetigastropoda in general (Szal 1971, Haszprunar 1987*b*, 1988*d*) and (contrary to Haszprunar 1988) have been recently found also in seguenziids (Haszprunar 1993). Based on this resemblance, one might speculate that the gill-leaflets of the Lepetelloidea likewise are modified ctenidia. To the contrary, however, the smooth gradations from true gill-leaflets through high- to low folds of the mantle in *Bathyphytophilus diegensis* again suggest that the lepetelloid gill-leaflets are derivatives of this sinus and are not homologous with a ctenidium (Haszprunar 1988*c*, *d*).

The osphradial ganglion also supplies the gill of the right side. This condition is likewise present in all investigated limpet members of the Lepetelloidea (Haszprunar 1987*a*, 1988*a*, *b*, *d*, unpublished) as well as in the Cocculinidae (Haszprunar 1987*c*) and Bathysciadiidae (Haszprunar 1988*c*, unpublished). Since this arrangement differs from that of limpets of other archaeogastropod groups (Patellogastropoda, Neritimorpha, Vetigastropoda) and can hardly be interpreted as a plesiomorphic feature, it might represent a synapomorphy of the Cocculiniformia as a whole. Because this question is out of the scope of the present contribution, we did not code this character.

The presence of a single pair of epipodial tentacles in *Bathyphytophilus* (no. 25) probably is a primitive character among gastropods (Haszprunar 1988*d*, 1993), and loss or multiplication may have phylogenetic significance at the family level.

Systematic position of *Bathyphytophilus*

The classification of *Bathyphytophilus* among the Archaeogastropoda–Lepetelloidea (Lepetellacea) is beyond doubt. The archaeogastropod nature (cf. Haszprunar (1993) for recent review and the use of Archaeogastropoda as a paraphyletic taxon) of the family is reflected by the streptoneurous and hypoathroid nervous system, the presence of two kidneys, and by various characteristics of the alimentary tract. Lepetelloid characters of the Bathyphytophilidae are: (1) the limpet shell lacking an early coiled phase of the teleoconch; (2) the solid horseshoe-shaped shell muscle; (3) the arrangement of organs in the mantle roof; (4) in particular the position and structure of the gill-leaflets including bursicles; (5) the divided hermaphroditic gonad and the urinogenital opening; and (6) the specialization with respect to nourishment.

In accordance with earlier studies (Haszprunar 1992),

the resulting trees of the cladistic analysis (Fig. 25) show holophyly and sequential arrangement of {Osteopeltidae [Cocculinellidae (Addisoniidae & Choristellidae)]}. The phylogenetic relationships of the remaining families are less clear. Whereas a holophyletic sequence [Pyropeltidae (Bathyphytophilidae & Lepetellidae)] is strongly favoured, the position of the Pseudococculinidae is still open to question; the holophyly of the latter family is still weakly founded.

According to the analyses given above, the diagnostic characters of the Bathyphytophilidae are the asymmetry of head retractors, the distinct radula morphology, and the unique grape-like pouches of the posterior oesophagus. Additional autapomorphies are the lack of oral lappets and jaws, the lack of eyes and the specific gill conditions, although each of the latter characters is paralleled in at least one of the remaining lepetelloid families (Table IV).

However, one should still bear in mind that the indices of the trees are quite poor. The conditions of the soft body in the remaining bathyphytophilid species, which would potentially clarify the problem, are completely unknown. Also, the variability of anatomical characters within the Lepetellidae, where shell and radular characters are remarkably constant (Dantart & Luque 1994; A. Warén pers. comm.), still needs to be studied in detail. In general, the need of a fine structural character, in particular on sperm and sensory organs, has once more become obvious.

Thus, at the present stage of knowledge, it is not possible to present a final conclusion as to the origin of the Bathyphytophilidae, although a sister-group relationship with the Lepetellidae appears very likely. Pseudococculinidae, Pyropeltidae, Lepetellidae and Bathyphytophilidae may together represent a distinct grade or a clade. At present, it appears prudent to retain the Bathyphytophilidae Moskalev, 1978, which is, with certainty, a monophyletic taxon, as a distinct family close to the Lepetellidae and Pyropeltidae.

Acknowledgements

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