

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: *cal*, *ca2*). The anterior ones are large and consist of very large cells (diameter up to $80\ \mu\text{m}$). 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 beginning 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 sea-grass. The right digestive gland is situated antero-dorsally, whereas the left one occupies the postero-ventral 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

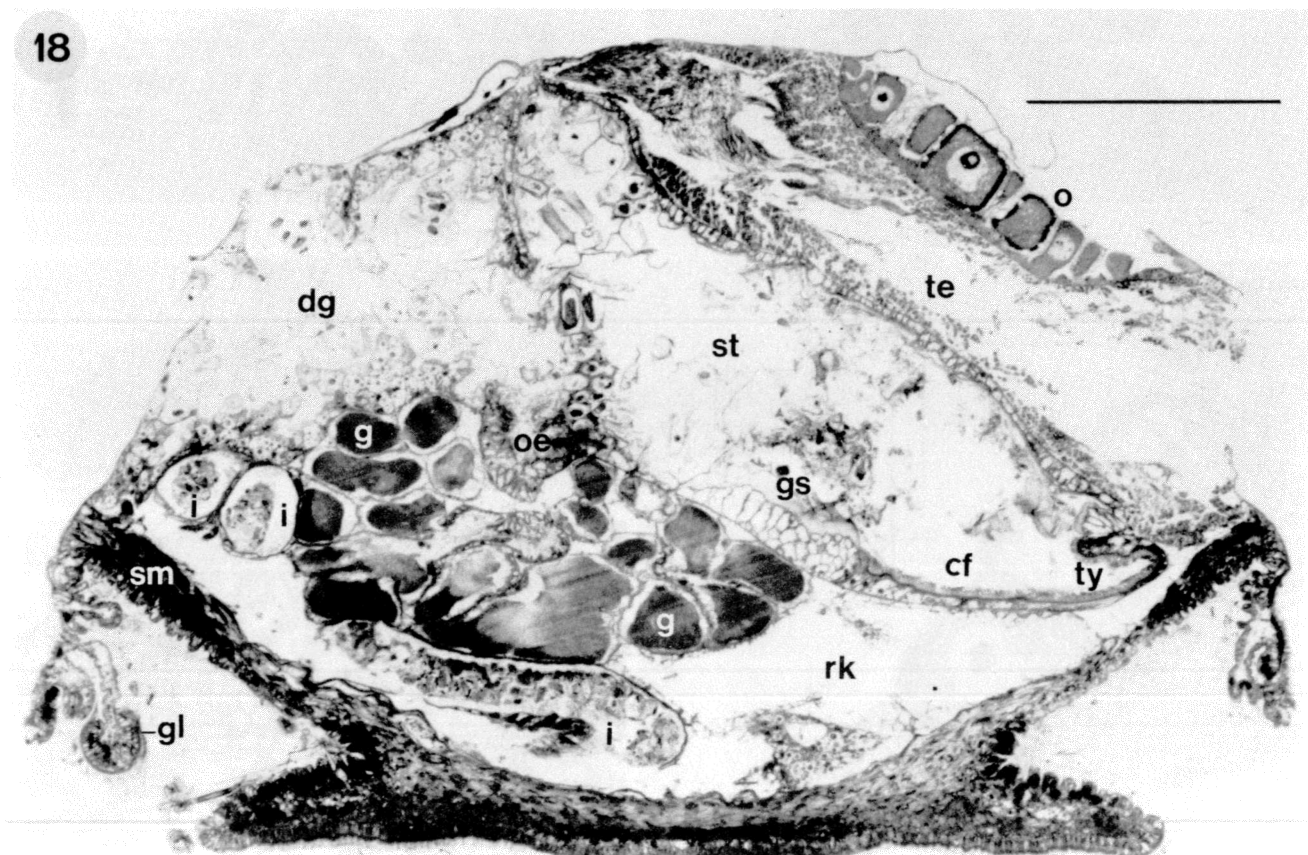


Fig. 18. Line of entrance of oesophagus into stomach; the specimen is slightly damaged at the left dorsal side (testis, ovary). *au* auricle; *bc* buccal cavity; *C* cerebral ganglion; *cal*, 2 anterior (ventral) and posterior (dorsal) cartilage; *cf* ciliary field of stomach; *dg* digestive gland; *g* 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: $200\ \mu\text{m}$.

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

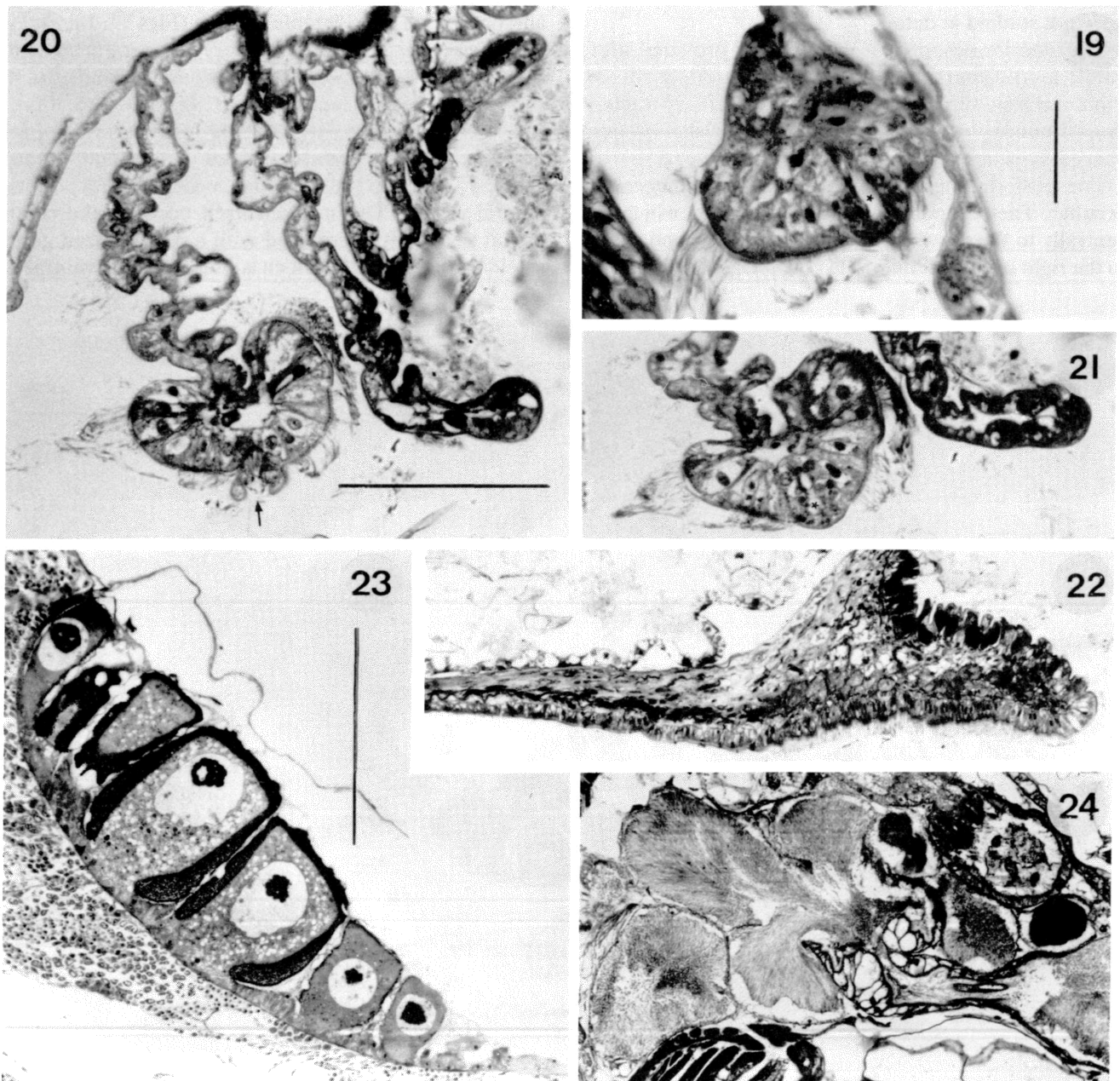
The intestine emerges from the posterior left portion of the stomach. Being completely ciliated at the beginning, the ciliation becomes restricted to a typhlosole region after a short distance. The long intestine makes several loops (Figs 14, 17, 18: *i*). Finally, it curves dorsally, and the rectum 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 in 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 statocystonia.

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. caribaesus* 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	1					2	
	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

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 chondrichthyan 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.

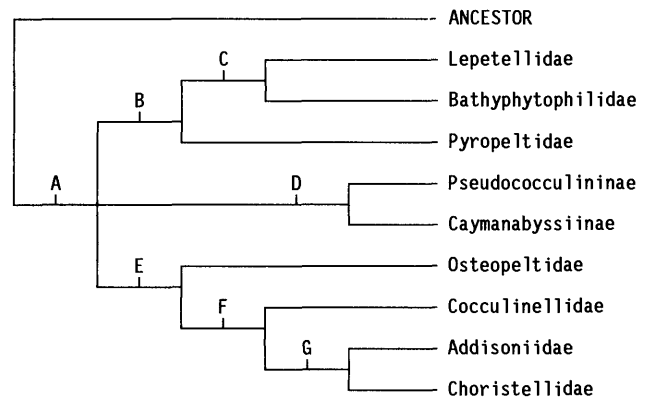


Fig. 25. Phylogenetic analysis of the *Lepetelloidea*. Strict consensus of three trees (= original tree no. 2). Indices of original trees: 43 steps; CI = 0.674; RI = 0.659; RC = 0.444.

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 1987b, 1988d) 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 1988c, 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 1987a, 1988a, b, d, unpublished) as well as in the Cocculinidae (Haszprunar 1987c) and Bathysciadiidae (Haszprunar 1988c, 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 1988d, 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.

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