Interactive 3D Anatomy and Affinities of Bathysciadiidae (Gastropoda, Cocculinoidea): Deep-Sea Limpets Feeding on Decaying Cephalopod Beaks

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ABSTRACT The anatomy of five bathysciadiid limpets, the type species *Bathysciadium costulatum* (Locard, 1898), *Bathysciadium* sp. B (off New Zealand), *Bathypelta pacifica* (Dall, 1908), *Bathypelta* sp. A (off New Zealand), and *Bathyaltum wareni* n.g., n.sp. (deep East Atlantic Ocean Basins), which all feed on decaying cephalopod beaks, has been investigated by means of semithin serial sectioning and interactive, computer-aided 3D reconstructions. *Bathyaltum wareni* is described as a species new to science based on additional SEM photos of shell and radula. Differences between species are found in conditions of shell, protoconch, mantle papilla, copulatory organ, receptaculum openings, oral lappets, and rectal histology. The Bathysciadiidae share several synapomorphies with the Cocculinidae (s. str.), namely the pseudoplicatid gill, a single, left kidney, the hermaphroditic gonad with the single, glandular gonoduct, and the statocysts with single statoliths. Therefore, these families are united in a clade Cocculinoidea, which is considered to be highly modified offshoot of early gastropods independent of the likewise "cocculiniform" Lepetelloidea, which should be classified among the Vetigastropoda. J. Morphol. 272:259–279, 2011.   © 2010 Wiley-Liss, Inc.

KEY WORDS: Gastropoda—Cocculinida—Bathysciadiidae; anatomy; systematics; feeding biology; 3D reconstruction

INTRODUCTION

At the very end of the 19th century, Dautzenberg and Fischer (1899) described an unusual limpet species from deep waters of the Azores, *Bathysciadium conicum* (junior synonym of *Lepeta costulatum*/(Locard, 1898); cf. Warén, 1996), and based a new family on it, Bathysciadiidae. The family was characterized by a fragile shell with circular aperture and distinct, centrifugally arranged, periostracal fringes, a unique radula, and a prominent copulatory organ. Pelseneer (1899) added a brief anatomical description and concluded that the family should be placed among the Docoglossa (now Patellogastropoda). A few years later, a second species, *Bathysciadium pacificum,* was described by Dall (1908), and Thiele (1908) published a brief but (as will be shown) concise anatomical description of this species, stating several severe differences to the description by Pelseneer (1899). Already these early authors noted the enigmatic habitat of these limpets, most of which live and feed on decayed cephalopod (squid) beaks.

Based on the different anatomical descriptions by Pelseneer (1899) and Thiele (1908), Moskalev (1971, 1973) placed *Bathysciadium pacificum* in a new genus, *Bathypelta*. Another new species and genus, *Bonus petrochenkoi* was described from abyssal depths, again feeding on cephalopod beaks. In addition, Moskalev (1973) erected Bathysciadioidea for *Bathysciadium* plus *Bonus* and Bathypeltoidea for *Bathypelta* and placed both superfamilies among the Docoglossa (Patellogastropoda). However, these higher categories were ignored or rejected by all later authors (e.g., Hickman, 1983; Haszprunar, 1988a, 1998; Warén, 1993, 1996).

In her review on deep-water limpets, Hickman (1983) mentioned once more the unusual habitat and radula of the Bathysciadiidae. She presented SEM photos of the radula of *B. pacificum*, but her photos were misleading, because the radula was mounted upside down. More informative SEM photos of the unique bathysciadiid radula were provided by Warén (1993, 1996), confirming largely the drawings already made by Pelseneer (1899) and Thiele (1908, 1909). The first SEM pictures of a bathysciadiid protoconch were presented by Warén (1993, 1996), this structure usually is lost in adult animals.

Warén (1993) also described a new species and genus, *Xenodonta bogasoni*. In contrast to other bathysciadiids, the apex of *Xenodonta* is bended backward and deflected to the right, and the periostracum does not show fringes. Warén (1993) tentatively added another genus and species, *Pilus conica* (Verrill, 1884) (cf. Warén, 1991), to the Bathysciadiidae. Later, Warén (1996) described another new species, *Bathysciadium xylophaga* (Warén and Corolla, 1996), which feeds on sunken wood, from the Mediterranean Sea, figured various features of four more (still undescribed) species, and stated the probable existence of several hundreds of different species of the family worldwide.

Based on preliminary anatomical investigations Haszprunar (1988a,b, 1992b, 1998) classified the Bathysciadiidae with the Cocculinidae in a superfamily Cocculinoidea and noted several distinct anatomical similarities between the two families. This study outlines the anatomical and histological features of these enigmatic limpets and reveals a very unusual morphology in particular of the alimentary tract. In addition, a new species and genus is described and certain anatomical criteria for the generic classification of the family are presented. Finally, we discuss the new data with respect to the phylogenetic framework on "cocculiniform" gastropods, which has been developed and variously modified through the last two decades (Haszprunar, 1988a,b, 1992, 1993, 1998; Ponder and Lindberg, 1997; Strong et al., 2003; see recent reviews by Aktipis et al., 2008; Lindberg, 2008; Geiger et al., 2008).

(Principal Investigator: Dr. Claude Monniot). The specimens have been found "free in sediment, but have probably fallen off something, perhaps squid jaws" (Warén, pers. Comm. 1987-06-29). Details of the collecting and the ecology and fauna of the various stations have been described by Monniot and Segonzac (1985).

Holotype. MNHN Paris 0602: one empty, dry shell. Type locality: ABYPLAINE sta. 6, CP08: from 33° 00,8′ N, 21° 59,5′ W to 33° 02,1′ N, 21° 59,3′ W, 5230 m, May 24, 1981.

Paratypes. NMHN Paris 0602: one shell. ABYPLAINE sta. 4, CP03: from 36° 48,7′ N, 19° 09,2′ W to 36° 49,4′ N, 19° 09,8′ W, 5500 m, May 20, 1981. NMHN Paris 0602: two shells. ABYPLAINE sta. 8, CP11: from 34° 06,1′ N, 17° 06,3′ W to 34° 07,9′ N, 17° 07,7′ W, 4270 m, May 30, 1981. NMHN Paris 0602: one shell. ABYPLAINE sta. 12, DS 13: from 44° 41,2′ N, 17° 49,0′ W to 44°41,8′ N, 18° 01,8′ W, 4990 m, July 20 1983.

Paratypes. NMHN Paris 0602: SEM photos (see Table 1). ABYPLAINE sta. CP11 (an adult specimen). NMHN Paris 0602: SEM photos "DS12" (a juvenile). MNHN Paris 0602: "DS13" (same specimen as "DS12").

Paratypes. MNHN Paris 0602 from the type locality (CP08). In 1991, two section series of 2-μm thick, plastic (Spurr's resin) sections were made at the Institute of Zoology of the University of Innsbruck, Austria, and stained with methylene blue: A1–A11 (block 61A) and B1–B8 (block 62A). These specimens were very well preserved.

DESCRIPTION OF *Bathyaltum wareni* Haszprunar n.g., n.sp.
Type material

All type material of *Bathyaltum wareni* comes from the R/V "Jean-Charcot," cruise ABYPLAINE

Etymology

Bathyaltum refers to the deep water habitat and the high back of the shell. The species is dedicated to Dr. Anders Warén (Naturhistoriska Riksmuseet Stockholm, Sweden), who not only has signifi-

TABLE 1. SEM photos (made by Dr. Anders Warén) of Bathyaltum wareni available

BATHYALTUM WARENI	Subject	Original number	Figure herein	Original magnification	Scale (55 mm = edge length of photo), E = scale bar on photo
Abyplane DS12	Shell lateral	#5444	1A	×40	55 mm = 1,35 mm
	Shell dorsal	#307	1C	×42	55 mm = 1,39 mm
	Radula total	#3957	2A	×528	55 mm = 104,1 μm
	Radula central	#287	–	×1630	55 mm = 33,75 μm
	Radula central	#288	–	×1630	55 mm = 33,75 μm
	Radula lateral	#289	–	×1630	55 mm = 33,75 μm
	Radula marginal	#290	–	×1630	55 mm = 33,75 μm
Abyplaine DS13	Shell posterior	#3053	1B	×42	55 mm = 1,31 mm
(= DS12)	Detail of apex	#1864	–	×264	55 mm = 208 μm
Abyplaine CP11	Shell lateral	#5151	1D	×18	55 mm = 3,05 mm
	Shell dorsal	#5154	1E	×26	55 mm = 2,12 mm
	Radula total	#0040	2C	×480	E = 10 μm
	Radula central	#0041	–	×1200	E = 10 μm
	Radula central	#0021	–	×1500	E = 10 μm
	Radula marginal	#0042	–	×1300	E = 10 μm
	Radula lateral	#0043	2B	×1500	E = 10 μm
	Radula left	#0044	–	×1300	E = 10 μm
	Radula broken	#0045	–	×1000	E = 10 μm

cantly contributed to our knowledge of bathysciadiid taxonomy but also generously provided his SEM photos of shell and radula for this study.

Description

Shell. Shell (Fig. 1A–E) of medium size for Bathysciadiidae (max. 2.75 mm), thin-shelled, colourless, ovate to slightly asymmetrical, anterior part convex, posterior part concave, radially ribbed. Periostracum eroded, no fringes. Apex posteriorly placed at median line or slightly shifted to the right. Adult shells lack a protoconch but show an apical septum similar to that found in postmetamorphic Patellogastropoda (Fig. 1B). Relative shell height and overall shape in lateral view varies significantly (ratio shell length to shell heights varies from 1.0 to 1.5; cf. Fig. 1A,D).

Radula. Radula (Fig. 2) typically bathysciadiid: The central field is reduced but maintains a shield-like area in the central part of each transverse row, the most central part and the most lateral parts slightly protruding (like longitudinal folds) from the radular membrane. The cutting edge of the first true lateral tooth is S-shaped in dorsal view, and the whole tooth is quite a flattened structure. The second tooth is the largest and quite robust with the most prominent cutting edge at the inner posterior area. The third element consists of three indistinct lamella-like structures and may represent a fusion of several teeth.

Diagnostic soft parts. Diagnostic soft parts (for details see below): Oral lappets small, suckers very small; few, very small, probably unicellular mantle papillae; copulatory organ with external seminal groove; spiral sperm; duct of receptaculum opens into distal gonoduct.

Remarks

Comparisons with related species are summarized in Table 2. *Bathyaltum wareni* differs significantly from all other bathyscidadiids: Unfortunately protoconch features are unknown, but the smooth shell with posterior apex is untypical and plesiomorphic by outgroup comparison with
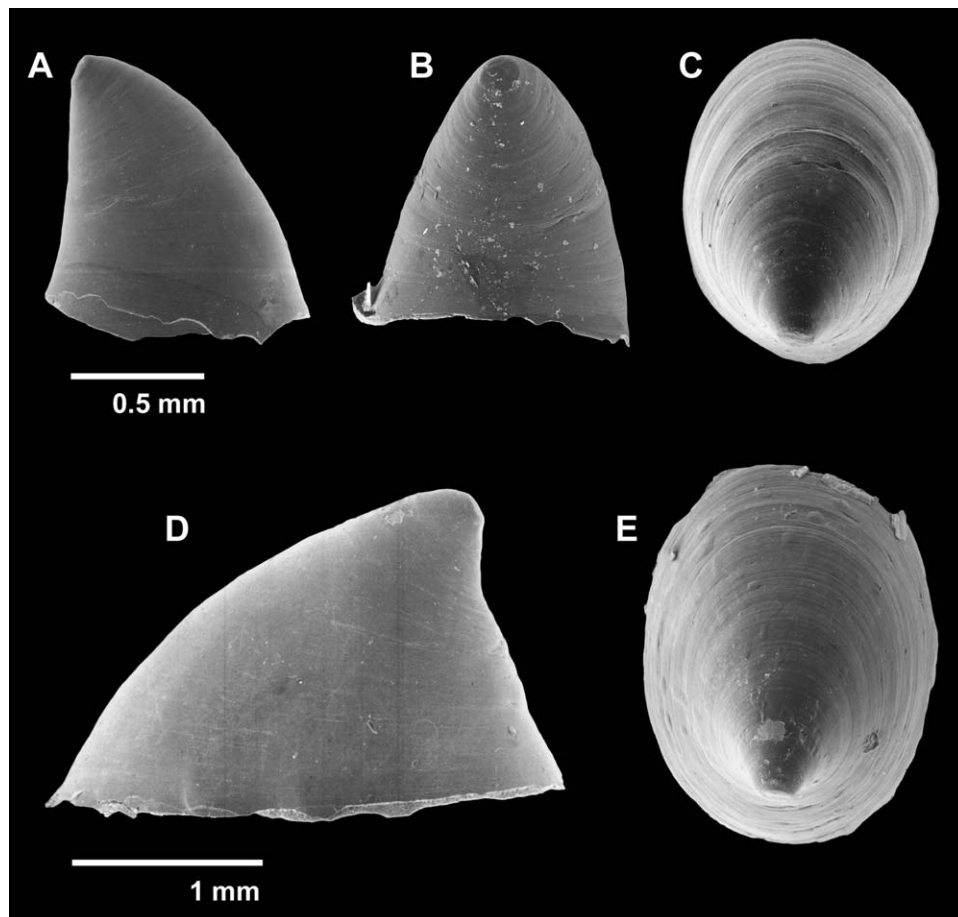

Fig. 1. Shell features of *Bathyaltum wareni* n. sp. **A–C:** Holotype (Abyplaine DS12). (A) From right side, (B) in posterior view, (C) and in dorsal view. **D,E:** Paratype (Abyplaine CP11), note the size difference to holotype. (D) From left side and (E) dorsal view.
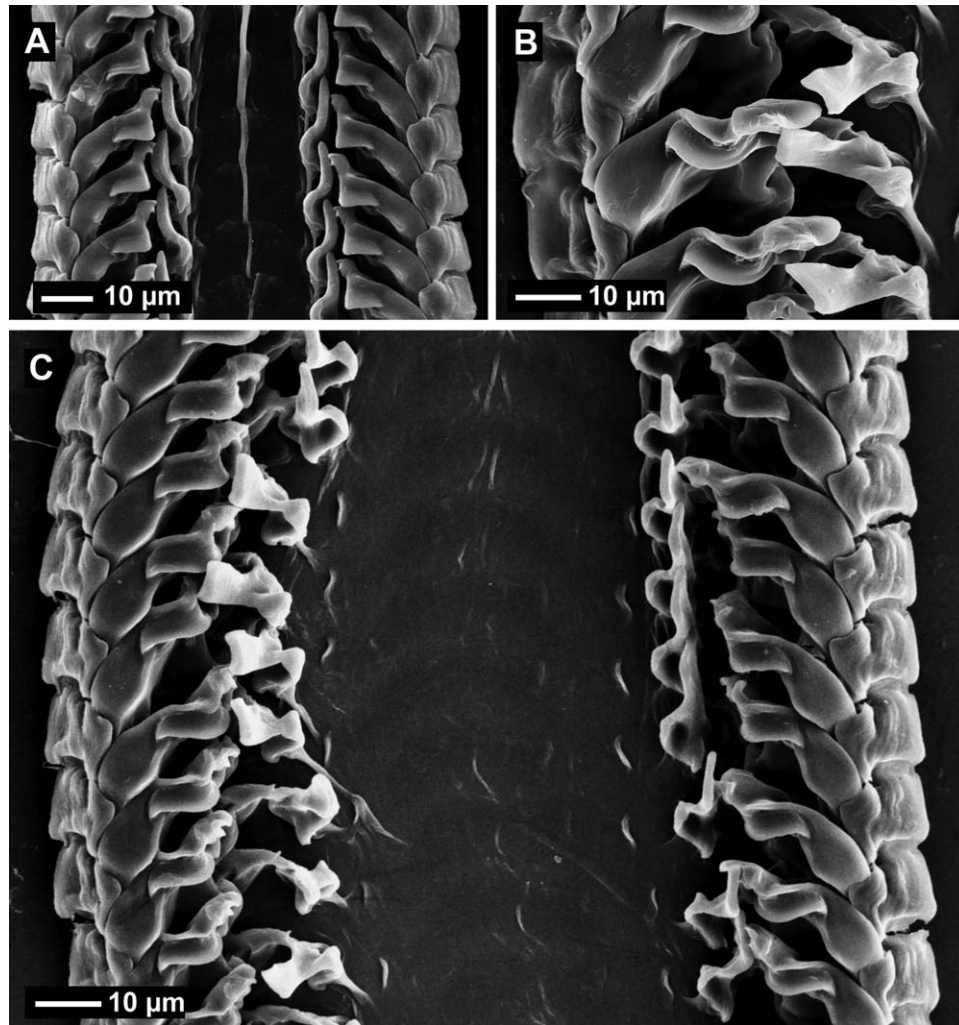
Fig. 2. Radular features of *Bathyaltum wareni* n.sp.. **A:** Holotype (Abyplaine DS12). **B:** Detail from paratype (Abyplaine CP11). **C:** Overview from the same paratype (Abyplaine CP11), note the size difference to holotype.

TABLE 2. Comparison of Bathysciadiid limpets

	Bathysciadium costulatum (Locard, 1898)	*Bathysciadium* sp. B (NMNZ: S153/1048)	*Bathypelta pacifica* (Dall, 1908)	*Bathypelta* sp. A (NMNZ: S151/1138)	*Bathyaltum wareni* n.sp.
Size	Max. 1.2 mm	Max. 1.5 mm	Max. 12 mm	Max. 1.7 mm	Max. 2.75 mm
Shell	Circular, low	Circular, low	Circular, low	Circular, low	Oval, medium to high
Apex	Central	Central	Central	Central	Posterior
Periostracum	Fringes	Fringes	Fringes	Fringes	Smooth
Radula	Diagnostic	Diagnotic	Diagnostic	Diagnostic	Diagnostic
Suckers	Small	Large	Large	Large	Very small
Oral lappets	Large	Large	Large	Large	Small
Mantle margin	Complex papillae	Complex papillae	Complex papillae	Complex papillae	Unicellular papillae
Gill	Small	Medium	Very large	Medium	Medium
Anal gland	Absent	Absent	Present	Present	Absent
Copulatory verge	Ciliated seminal groove	Ciliated seminal groove	Distal, glandular seminal duct	Distal, glandular seminal duct	Ciliated seminal groove
Sperm	Elongate	Elongate	Elongate	Elongate	Elongate, spiral
Receptaculum	Separate opening to the right	Separate opening to the left	Separate opening to the right	Separate opening at central position	Opens into distal gonoduct

Cocculinidae (apomorphic in *Bathysciadium*, *Bathypelta*, and *Xenodonta*), whereas the radula fully confirms the bathysciadiid nature. Additional differences to other bathysciadiids are the very small oral suckers and small oral lappets as well as the unicellular mantle papillae.

MATERIAL AND METHODS
Additional Material

Bathysciadium costulatum (Locard, 1898) = *Bathysciadium conicum* Dautzenberg and Fischer, 1899. Pelseneer's (1899) sample (Collections du Prince Albert Ier de Monaco; Stn. 244; 1266m; 38° 33′ 57″ N, 28° 19′ 15″ W—Azores on beak of the squid *Architeuthis* sp.; returned to the Musée Oceanographique, Monaco) includes numerous (more than 100) specimens, the shells of which are largely dissolved. Warén (1996) has provided SEM photos of shell, radula, and soft body of specimens of the same sample. In 1986, two specimens were embedded in plastic (araldite) and single, 1-μm thick sections were made with glass knives at the Zoological Institute of the University of Vienna, Austria. Staining was effected by Regaud's fluid (iron hematoxylin). The section series are now deposited in the Zoologische Staatssammlung München (ZSM: Mol 20100280).

Bathysciadium sp. B [National Museum of New Zealand (NMNZ): S153/1048]: Two section series were made at the Zoological Institute of the University of Vienna, Austria, one (1984) of 5-μm thick, paraffin sections and stained by Haidenhain's Azan method (very poor), and the other (1986) of 2-μm thick, serial, plastic (araldite) sections stained by Regaud's fluid. The section series are now deposited in the Zoologische Staatssammlung München (ZSM: Mol 20100281).

Bathypelta pacifica (Dall, 1908): We re-examined the section series which was the base of Thiele's (1908) anatomical description. The whole series (nine slides, 10-μm sections made by the paraffin/celloidin technique, stained by hemalaun-eosin) is deposited in the Museum für Naturkunde in Berlin (inventory number ZMB 114157).

Bathypelta sp. A (NMNZ: S151/1138): In 1985, two section series were made at the Zoological Institute of the University of Vienna, Austria, one of 5-μm thick paraffin sections and stained by Haidenhain's Azan method (very poor), and the other of 1-μm thick, single plastic (araldite) sections stained by Regaud's fluid (good). The section series are now deposited in the Zoologische Staatssammlung München (ZSM: Mol 20100282).

Methods

Generally the specimens were originally (i.e., decades or years ago) preserved in 70% ethanol or spirit resulting in a good to very good fixation, although histological details cannot be given satisfactorily for all tissues (see results). After dehydration most specimens were embedded in araldite or Spurr's (1969) resin and serially sectioned. Either 1-μm thick single sections were made or serial 2-μm thick sections were made by so-called Ralph knives after the method of Smith and Tyler (1984). Also, 5-μm thick, serial paraffin sections were made with steel knives, but the results were very poor in the latter case. Monochromatic staining of the plastic sections was done by Regaud's fluid or by methylene blue (Richardson et al., 1960), the latter with initial better results. Embedding in cedarwood oil resulted in bleaching over 18 years, whereas those sections, which were embedded in the original plastic, retained the staining. Highly resolved digital images (light microscopy) were created directly from selected sections to visualize histological details.

One section series of *Bathysciadium costulatum* and *Bathyaltum wareni* each were further treated for computer-aided 3D reconstructions. The semithin section series were digitally photographed on a standard optical microscope under bright-field illumination. Bleached sections have been photographed with phase contrast microscopy to enhance contrast. Most slice profiles easily fitted into a field-of-view of 1,178 × 884 μm of the 10×-objective (2,592 × 1,944 pixels), but the largest profiles in the middle of the section series had to be imaged by two or three overlapping pictures, which were combined subsequently. In the case of rippled slices, the extended focal imaging function of the Olympus dotSlide system was used to reveal acute images. To create a scale reference an object micrometer (1 mm in 100 parts) was photographed with the same imaging parameters. To prepare image stacks for 3D reconstruction, the original images were preprocessed with Adobe Photoshop: converted to eight bit greyscale, autoscaled, unsharp masked, and resampled from 2.2 to 1 pixels/μm, a resolution sufficient for the reconstruction of most histological details. The stacks were then imported into the visual display and rendering software Amira version 4.1.1 (TGF Template Graphics Software, USA) on a powerful imaging PC (Dell Dimension 8300, 2.7 GHz Pentium IV, 2 GB RAM, NVIDIA GeForceFX 5200), voxel size specified to 1 μm × 2 μm and aligned semiautomatically. The profiles of the whole soft body and of all organ systems separately were traced manually on every digital slice and stored in a 3D "label field." Single distorted slices were skipped and interpolated. For every set of contour lines, a slightly smoothed surface model was computed (triangulation, surface rendering), resulting in a set of "digital organs." These data can be visualized in color, free perspective, organ combination, and transparency and stored in digital surface models (3D) or snapshots (2D). In addition, the software provides the possibility for morphometric evaluations (measuring of distances, volumes, etc.).

The interactive 3D presentation within the PDF format follows the protocol of Ruthensteiner and Heß (2008).

RESULTS
General Remarks

The anatomy of the species investigated is quite similar. Accordingly, we provide a common description. Differences between species will be mentioned where they occur.

Shell

The typical central apex of bathysciadiids, the circular aperture and the centrifugally arranged, periostracal fringes are present in species of *Bathysciadium*, *Bathypelta*, and *Bonus*, whereas shell features are cocculinid-like in *Xenodonta bogasoni* and *Bathyaltum wareni* (for details see the species description above and Fig. 1).

External Morphology

Usually the bathysciadiid shell height is lower than the diameter of the shell aperture. The exception is *Bathyaltum wareni*, where shell height may exceed the diameter of the aperture.

The large head of bathysciadiids typically bears very short and smooth tentacles. In addition, a prominent copulatory organ is visible behind the right cephalic tentacle. *Bathypelta pacificum* alone shows an epipodial ridge, which surrounds the posterior half of the body, and a pair of prominent epipodial lappets near the posterior end of the animal, whereas epipodial ridges or tentacles are lacking in all other species.

The large mouth opening is flanked by oral lappets in all species investigated (Figs. 3 and 4B); the size and histology of the lappets vary between the species, however. In *Bathyaltum wareni*, the oral lappets are quite small (Fig. 4B). A strongly cuticularized area is situated anteriorly to the mouth opening and continues by narrow, highly cuticularized bands to the left and right of the mouth opening. Many thick muscles insert at the basement membrane of the cuticularized epithelium. All remaining species have prominent oral lappets, and the cuticularized area is present left and right but not anterior of the mouth opening (Fig. 3). In *B. costulatum*, the cuticularized areas are smaller than in the other species; however, prominent retractor muscles inserting at the basement membrane of the cuticularized zones are present in all species. In all species, the inner and outer borders of the cuticularized area are formed by longitudinal folds and clefts, and the lateral area of the oral lappets is ciliated, and many large subepithelial mucous cells are present in this part (Fig. 5C).

The circular, sucker-like foot shows two zones: The central area is bulged (possibly by contraction during fixation and by the voluminous stomach, see below) and is covered by a nonciliated epithelium, whereas the peripheral zone is ciliated (Fig. 3). The anterior edge is composed of many subepidermally placed, darkly staining mucous cells, the remaining sole has epithelial mucous cells interspersed. A true pedal gland with a distinct opening is lacking in all species investigated.

The conditions of the mantle margin differ between species: *Bathyaltum wareni* shows only few, very small, probably unicellular papillae. In *Bathypelta* sp. A, there are prominent mantle tentacles being composed of several highly cylindrical cells. The mantle tentacles of *Bathysciadium costulatum* (Fig. 3), *Bathysciadium* sp. B and *Bathypelta pacifica* (see also Warén 1996: Figs. 4 and 12B) are even more complicated in having distinct retractor muscles and nerves. In addition, a central bud is flanked by two lateral flaps. In general, the mantle is heavily retracted in all specimens investigated and contains a network of blood lacunae, which are continued by passages between the shell muscles with the haemocoel in the visceral part of the body.

Muscle System

Compared with patellid or cocculinid limpets, the shell muscle system appears weak. It is paired based on innervation, and its insertion zone is horse shoe-shaped (Fig. 4C) with the right anterior end placed somewhat more backward than the left one. The shell muscle system consists of distinct bundles similar to Patellogastropoda and Cocculinidae, and the innermost fibres
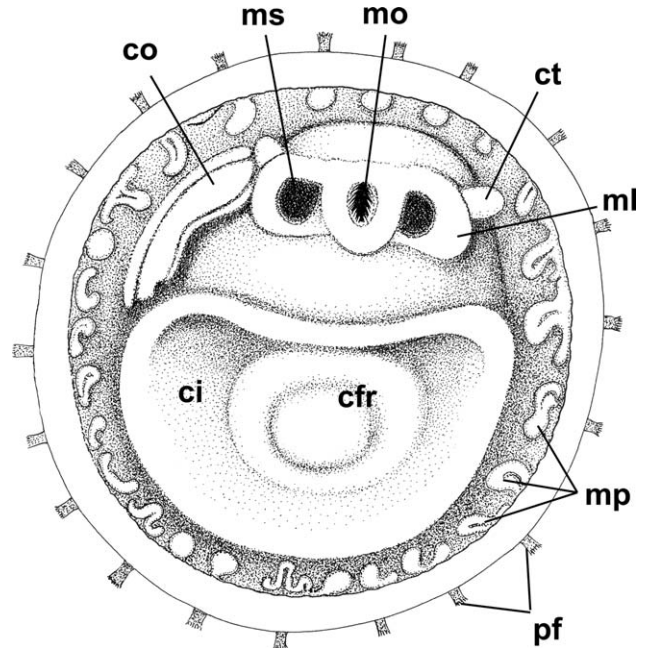

Fig. 3. Drawing of ventral view of *Bathysciadium costulatum*. Combined by Ruth Kühbandner after Pelseneer (1899: fig. 1) and SEM photos in Warén (1996: fig. 3). Shell diameter about 1 mm. cfr, central (nonciliary, bulged) portion of foot; ci, outer (ciliated) portion of foot; co, copulatory organ; ct, cephalic tentacle; ml, mouth (oral) lappet; mo, mouth opening; mp, mantle papilla; ms, mouth (oral) sucker; pf, periostracal fringes.

intercross midventrally. The head retractors have their insertion areas inward the anterior end of the left and right shell muscle and form the longitudinal muscles of the lateral wall of the head. Contrary to the buccal musculature (see below), shell and head retractors consist of smooth muscle fibres. The insertion areas generally are composed of so-called tendon cells with prominent distal-basal actin filaments.

Mantle Cavity

The bathysciadiid mantle cavity is very shallow and may be better termed a "nuchal cavity" (Fig. 4F). In *Bathypelta* sp. A, the posterior line is situated even more anteriorly in the central area than lateral, so that there is no real "cavity." The depth of the mantle cavity also depends on the actual volume of the gonad (particularly the ovary), which may bulge forward into the central area. The whole mantle roof is provided with a dense net of subepidermal blood lacunae representing the main respiratory surface aside of the mantle. The single, left kidney occupies the central anterior roof, and the pericardium is situated in the left posterior roof (Fig. 4C,F). To the right, the mantle cavity is deeper than in the central region, here the nephridioporus, the distal part of the rec-
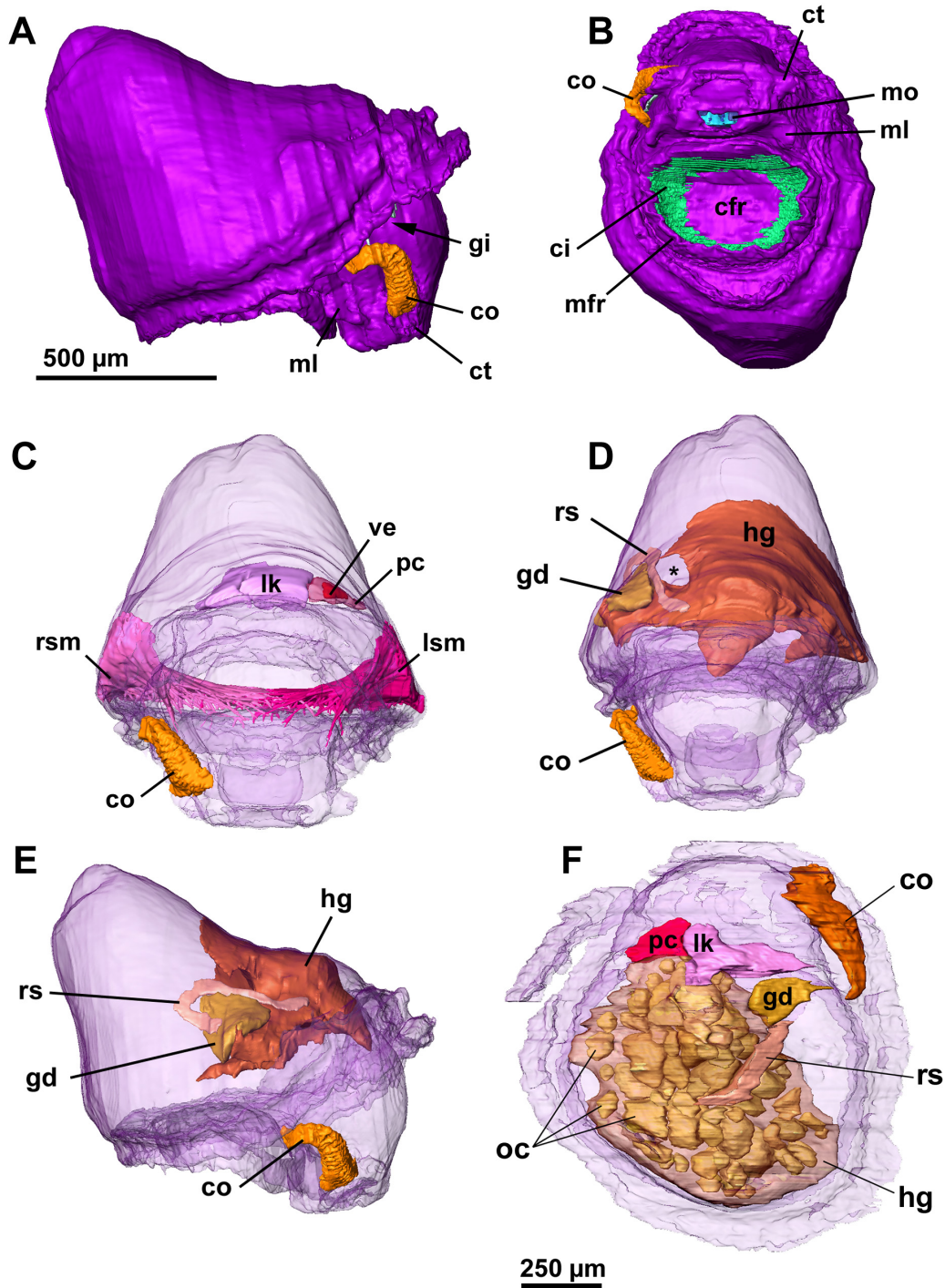
Fig. 4. 3D reconstructions. **A–E:** *Bathyaltum wareni* n.sp. A: External morphology from the right side. B: External morphology from the ventral side. C: Copulatory organ, shell muscle, nephridium, and heart in frontal view. D: Genital system in frontal view. E: Genital system in lateral view. **F:** *Bathysciadium costulatum*. Coelomic organs in dorsal view. cfr, central (nonciliary, bulged) portion of foot; ci, outer (ciliated) portion of foot; co, copulatory organ; ct, cephalic tentacle; gd, gonoduct; gi, gill; hg, hermaphroditic gland; lk, left kidney; lsm, left shell muscle; mfr, marginal (ciliary) foot region; ml, mouth (oral) lappet; mo, mouth opening; oc, oocytes; pc, pericardium; rs, receptaculum seminis; rsm, right shell muscle; ve, ventricle of heart. The **interactive 3D model** of *Bathyaltum wareni* n.sp. can be accessed by clicking into Figure 4 (Adobe Reader Version 7 or higher required). Rotate model by dragging with left mouse button pressed, shift model: same action + ctrl, zoom: use mouse wheel (or change default action for left mouse button). Select or deselect (or change transparency of) components in the model tree, switch between prefab views or change surface visualization (e.g., lightning, render mode, crop, etc.).
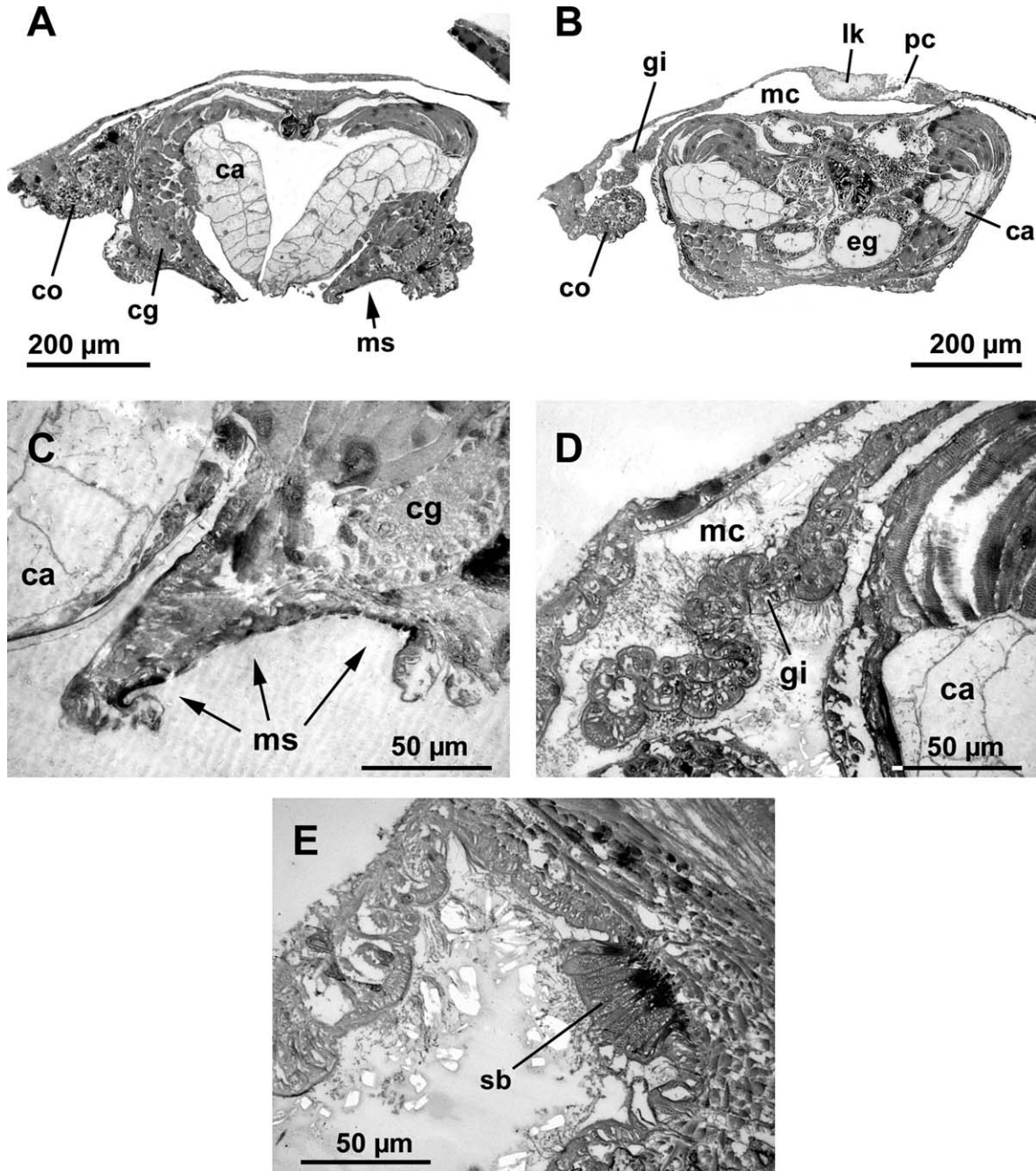
Fig. 5.   Histological details of *Bathysciadium costulatum*. **A:** Plane of mouth opening. **B:** Plane of gill. **C:** Oral Sucker in cross-section. **D:** Gill in cross-section (detail of B). **E:** Seminal band in right pallial cavity. ca, radular cartilage; cg, cerebral ganglion; co, copulatory organ; eg, esophageal gland; gi, gill; lk, left kidney; mc, mantle cavity; mo, mouth opening; ms, mouth (oral) sucker; pc, pericardium; sb, seminal band.

tum with the anus, and the genital opening(s) are placed.

Although the gill is only a quite simple, ciliated fold in *Bathysciadium costulatum* (Fig. 5B,D), all other species investigated show a prominent "pseudoplicate" gill, which is very similar to those of cocculinids (Haszprunar, 1987b; Thiele, 1904). *Bathypelta pacifica* in particular has a very large gill. The gill is always highly vascularized, the homogeneous epithelium consists of squamous cells, and ciliary cells are interspersed and denser in the small species. In one specimen of *Bathyaltum wareni* of nearly the same size as the reconstructed one but with immature gonad, the gill was entirely lacking. A hypobranchial gland is generally absent.
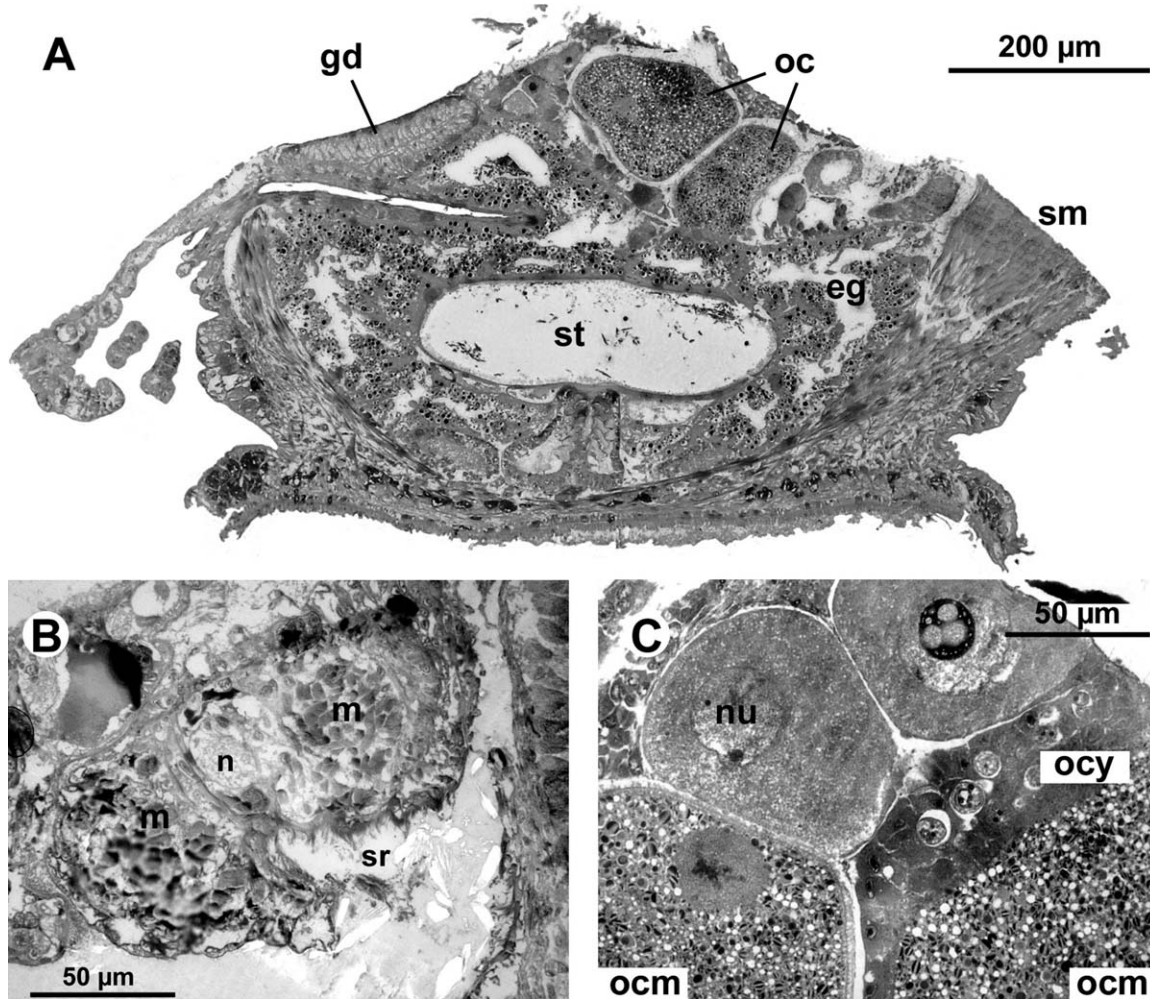
Fig. 6. Histological details of *Bathysciadium costulatum*. **A:** Cross-section at plane of posterior end of mantle cavity. **B:** Cross-section of copulatory organ. **C:** Details of eggs. eg, esophageal gland; gd, gonoduct; m, retractor muscle of copulatory organ; n, nerve of copulatory organ; nu, nucleolus of oocyte; oc, oocytes; ocm, mature oocyte; ocy, immature (young) oocyte; sm, shell muscle; sr, seminal rim of copulatory organ; st, stomach.

Heart and Excretory System

The large pericardium occupies the left posterior mantle roof and extends considerably backward. It includes a single auricle and a ventricle. In *Bathysciadium* (Fig. 4F) and *Bathypelta* species, the auricle is situated anteriorly left, whereas in *Bathyaltum wareni* it is situated anteriorly right.

The single, left kidney is large and is situated in the anterior central roof of the mantle cavity to the left of the gill basis. It extends slightly backward into the visceral part of the animal (Figs. 4C,F, and 5B). A short, ciliated (renopericardio-) duct connects the kidney with the pericardium at the ventral side. A distinct nephridial gland (sensu Andrews, 1985, 1988) could not be detected, and the nephridial epithelium does not show papillae as in vetigastropods. The nephridiopore lies at the right side close to the anus and is provided with a sphincter muscle.

Genital System

All bathysciadiid limpets are simultaneous hermaphrodites with a single gonad, which is dorsally situated and extends more backward to the left. The hermaphroditic gonad, the ovary portion in particular, occupies a considerable volume of the animal's posterior body (Figs. 4F and 6A). The ovary part occupies the central area, whereas the testis part is always placed peripherally. All stages of oogenesis are present. The ripe eggs are very large (up to 250 μm in diameter), very yolky and show a large nucleus, but lack the typical vitelline layer of vetigastropods (Figs. 6C and 7C). All stages of spermiogenesis also occur: In *Bathyaltum wareni* alone the ripe sperm are elongated and spiral (Fig. 7A) similar to those of euthyneurans (e.g., Thompson, 1973; Healy, 1996).

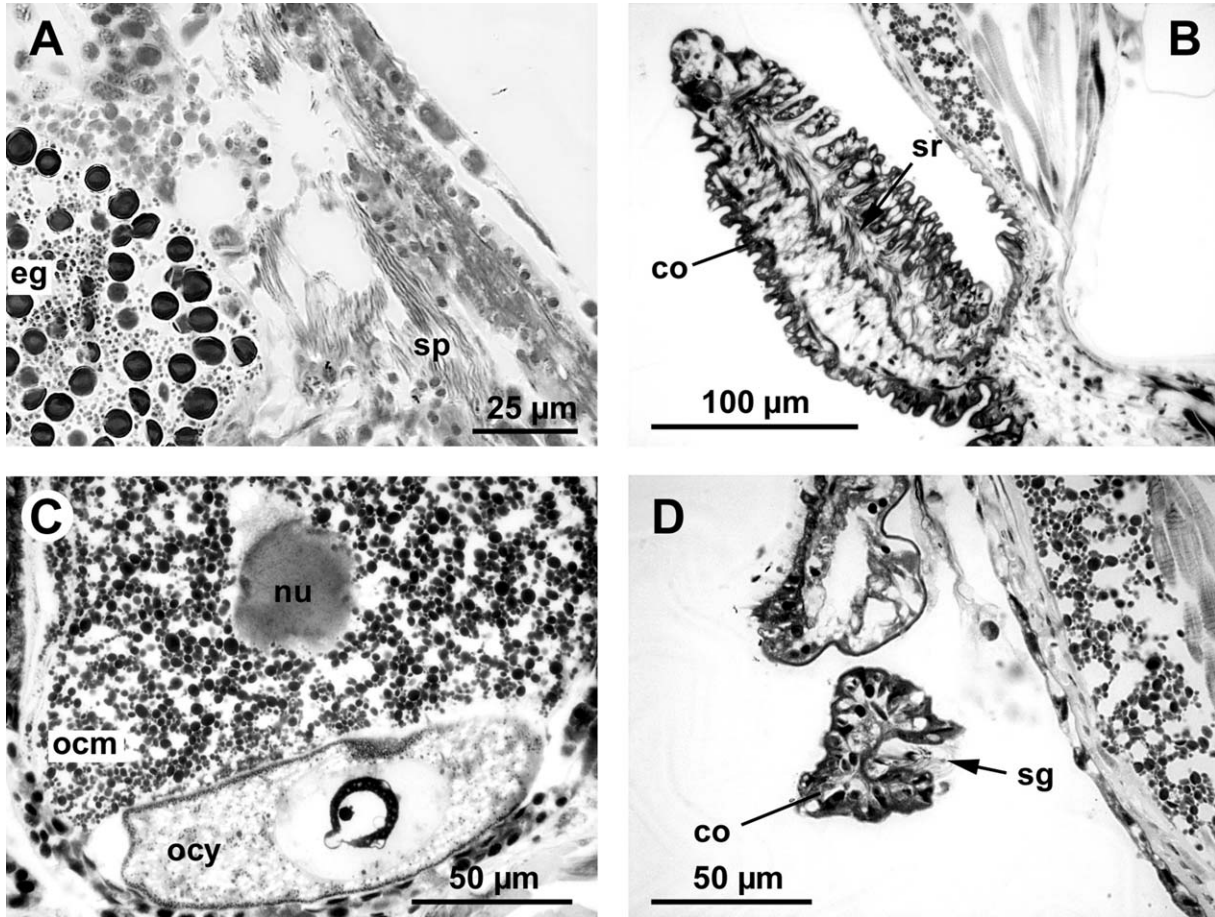At the right side a short, wide, glandular gonoduct runs forward and opens into the right poste-

Fig. 7.   Histological details of genital system of *Bathyaltum wareni* n.sp. **A:** Peripheral portion of hermaphroditic gland showing spiral sperm. **B:** Longitudinal section of copulatory organ. **C:** Oocytes. **D:** Cross-section of copulatory organ. co, copulatory organ; eg, esophageal gland; nu, nucleolus of oocyte; ocm, mature oocyte; ocy, immature oocyte; sp, sperm cells; sg, seminal groove.

rior end of the mantle cavity (Fig. 6A). In *Bathypelta pacifica*, the proximal duct shows granular cells, the distal part mucous cells with homogeneous content. In the specimen investigated (that of Thiele, 1908), two ripe eggs were found adjacent to the basis of the gill.

All species studied have a distinct receptaculum seminis. In *Bathyaltum wareni*, it is situated dorsally of the gonad and opens into the most distal part of the gonoduct (Fig. 4F), whereas in all other species, the receptaculum is a completely separated organ with its own opening. In *Bathysciadium costulatum* (Fig. 4F) and *Bathypelta* sp. A, the receptaculum opens into the right posterior mantle cavity. In *Bathysciadium costulatum*, an elongated tube runs backward and to the left side crossing the centre of the body (Pelseneer, 1899; Fig. 3: "testicule"), whereas in *Bathypelta* sp. A, the tube ends in the centre of the body. In *Bathysciadium* sp. B, however, the receptaculum is situated as a wide tube along the left shell muscle and opens into the left posterior mantle cavity. In *Bathypelta pacifica*, the receptacular conditions were correctly described by Thiele (1908: 85, Fig.

15): "Posterior of the openings of rectum and releasing duct (i.e., gonoduct) the mantle cavity narrows to a duct (Fig. 15, rec), which runs below and more backward to the right of the releasing duct of the gonad, then curved (slightly: pers. obs.) to the left behind the end of the gonoduct, and finally ends with a wide, sac-like cavity below the dorsal wall slightly right of the centre of the body. This sac contains ripe sperm, it is therefore a 'receptaculum'" (translated from the original German). These conditions resemble those of *Bathysciadium costulatum*.

All bathysciadiids have a prominent copulatory organ, which is bended backward and is situated immediately below the gill (Figs. 3, 4, and 5A,B). The copulatory organ is always supplied by a separate nerve emerging from the right cerebral ganglion. In *Bathysciadium costulatum* (Fig. 6B), *Bathysciadium* sp. B, and *Bathypelta* sp. A, the copulatory organ is equipped with a thick retractor muscle, which inserts at the central part of the neck. From the emergence point to the tip, there is a deep ciliated groove at the ventral, inner side (Fig. 6B). In *Bathysciadium costulatum* and

Bathysciadium sp. B this groove continues up to the tip, whereas the distal half of the copulatory organ in *Bathypelta* sp. A is tubular. In *Bathyaltum wareni*, the elongated copulatory organ does not show specific retractors but has again a deep ciliated groove at the inner side up to the tip (Fig. 7B,D).

The complicated copulatory organ of *Bathypelta pacificum* was again correctly described and figured by Thiele (1908: p. 85, Figs. 12 and 13) and Warén (1996: Figs. 7A–C) provided SEM-images. A ciliated seminal groove runs from the end of the gonoduct forward along the right neck and reaches the basis of the copulatory organ, where a slit-like opening at the ventral side is present. The whole copulatory organ is a hollow tube with an additional, small process at the outer basis. A high, glandular epithelium covers the tube anteriorly and posteriorly of the opening. This part opens backward via a narrow opening in a dorsally situated, wide portion, which is covered by a quite flat epithelium with vacuole-like nuclei. From here a long, narrow process continues dorsally, then runs obliquely backward and is provided until its tip with a narrow tube.

Alimentary Tract

Contrary to earlier statements (Haszprunar, 1988a; but see Haszprunar, 1998) jaws are absent or at best vestigial. A subradular organ is also lacking in all species investigated. Small, pouch-like salivary glands are present at the front end of the pharynx (Fig. 8C). The sublingual cavity is shallow, and its posterior part is glandular. The anterior and lateral walls of the buccal cavity are cuticularized, a densely ciliated band, which is situated centrally, continues into the esophagus. As a whole the buccal apparatus is a very prominent organ occupying a considerable volume of the anterior animal (Fig. 9A,B).

The bathysciadiid radula is generally composed by a weak or absent central tooth, and there are few prominent lateral teeth and only one or two small plate-like marginals. The radula of *Bathyaltum wareni* is depicted in the species description (see above and Fig. 2).

There is always a single pair of prominent radular cartilages, which consist of large, optical empty cells being typically arranged in two layers (Fig. 5A,B). The most anterior portion of the cartilages is covered by many small cells. Anteriorly, the cartilages are interconnected by a horizontal muscle located ventrally (Fig. 9C), further anatomical details of the prominent buccal musculature have not been determined. All buccal muscles are cross-striated (Fig. 8E) and show centrally placed cytoplasm surrounded by myofibrils resulting in a hollow appearance of the muscle fibers in cross-

sections (Fig. 8F). A small but distinct radular caecum is present, and the radular membrane is prominent (Fig. 8C). The radula sheath runs obliquely backward and ends at about the midline of the animals in a bifid formation zone of the teeth (Figs. 8D, 9D, and 12D).

The esophagus becomes restricted to a narrow, densely ciliated tube immediately behind its emergence from the buccal cavity (Fig. 10B,D,F). The tube runs dorsally backward to the right, then back to a more central position and makes a narrow loop downward. Running backward, it forms a pocket, which opens laterally into two very voluminous esophageal glands. Each of these glands splits into several branches occupying all free space between the remaining viscera (Fig. 10A). The epithelium of the esophageal glands is characterized by brownish to black "pellets" of two different size classes, the larger of about 5 μm and the smaller of about 1 μm (Figs. 7A and 11B, D). These pellets are relatively hard structures, because they easily break out during sectioning. The posterior esophagus makes another wide loop, then runs backward between the main parts of the stomach and enters ventrally into the anterior part of the stomach slightly to the right. The exact course of the esophagus also depends on the volume of the gonad, but in principle it is constant in all species investigated (Fig. 10B,F). In one section series of *Bathyaltum wareni*, the posterior esophagus is partly widened by an unknown ingested subject reflecting a high amount of elasticity.

In all species investigated, the stomach forms a large sac, which it is filled with characteristic, needle-like pieces of food, occasionally some larger food particles are also visible (Fig. 11A,C). The stomach lacks a gastric shield as well as a caecum and distinct ciliary fields, and the epithelium is homogeneously glandular throughout (Fig. 11C). There is no midgut gland, but the large branches of the esophageal glands surround the stomach in a similar way as the midgut glands in other gastropods (Fig. 11).

From the stomach the intestine emerges forward. Partly, it is a very narrow, ciliated tube, often collapsed and sometimes very difficult to detect. A typhlosole is absent. In general, the ciliated intestine (and sometime the rectum too) also contain the pellets of the esophageal glands, but now the large ones alone being placed only in the lumen of the duct (Fig. 11B–D). In *Bathysciadium costulatum*, the intestine runs forward up to the line of the posterior end of the radular cartilages, then curves to the left and dorsal, and makes a narrow loop backward. There, in the region of the openings of the esophageal glands (and thus very confusing at first glance), the intestine widens significantly. This widened, S-shaped tube runs forward and upward and is continued by the rectum (Fig. 10E,F). The latter crosses again to the right side by passing the peri-
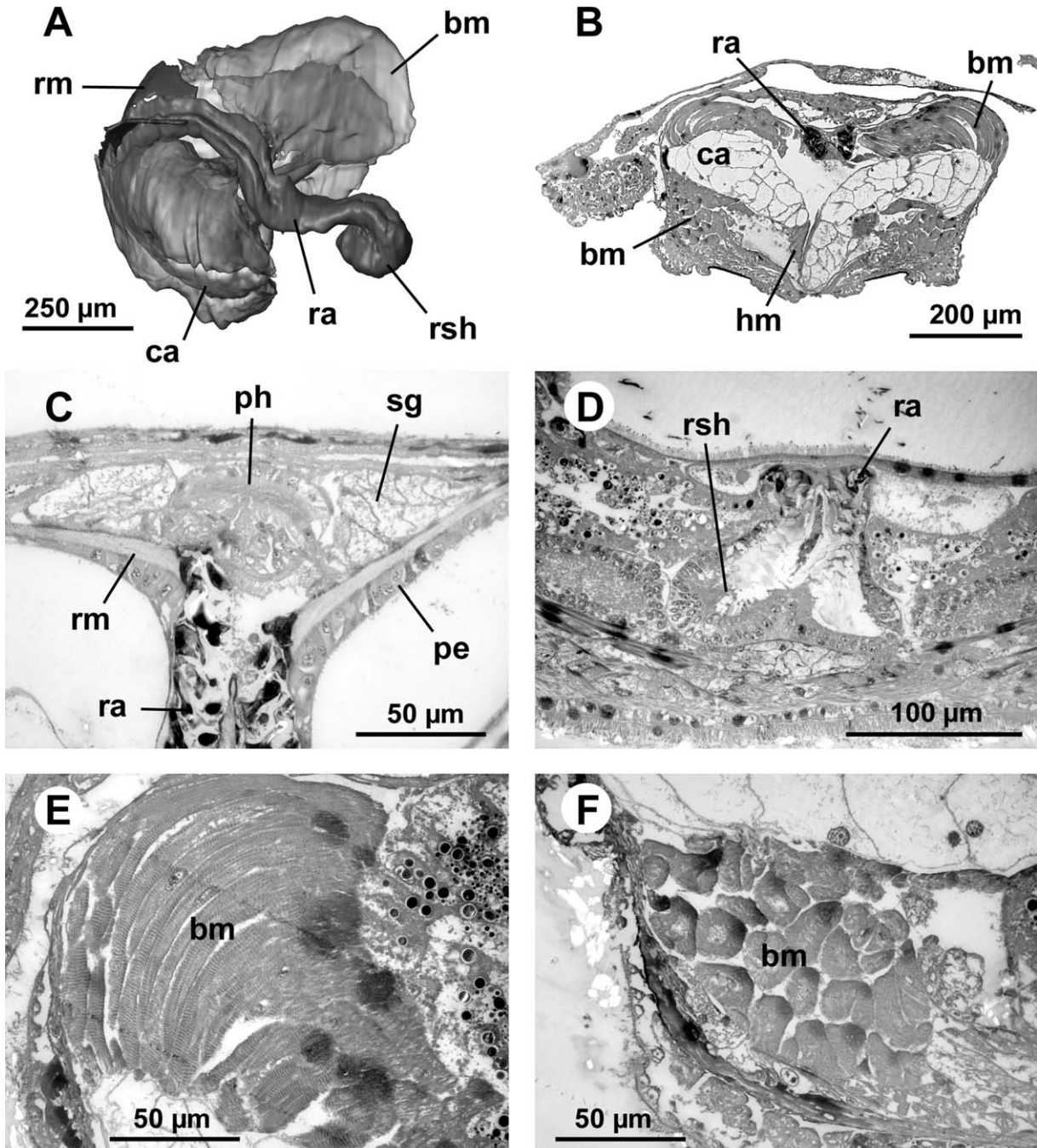
Fig. 8. Anterior alimentary tract of *Bathysciadium costulatum*. **A:** 3D reconstruction of buccal apparatus. **B:** Cross-section at plane of posterior pharynx. **C:** Salivary glands. **D:** Posterior end of radula. **E:** Longitudinal section of buccal muscles showing cross striation. **F:** Cross-section of buccal muscles. bm, buccal muscles; hm, horizontal buccal muscle; pe, peripheral portion of radular cartilage; ph, pharynx; ra, radula; rm, radular membrane; rsh, posterior end of radula sheath; sg, salivary gland.

cardium and opens via an anal opening into the right mantle cavity. Similar conditions exist in *Bathysciadium* sp. B and in *Bathyaltum wareni*, where the widening of the intestine is even more prominent than in *Batyhsciadium costulatum*.

In *Bathypelta pacifica*, Thiele (1908: Fig. 15) correctly described and figured, that the rectum is enormously developed and glandular. Indeed, the first impression is that this structure is an additional genital gland rather than the rectum. However, we could clearly confirm its continuity with the narrow intestine, the distal part of which makes several narrow loops in the left head's region. The glandular part opens via a very small anal opening into the mantle cavity. Similar conditions exist in *Bathypelta* sp. A, where the rectum
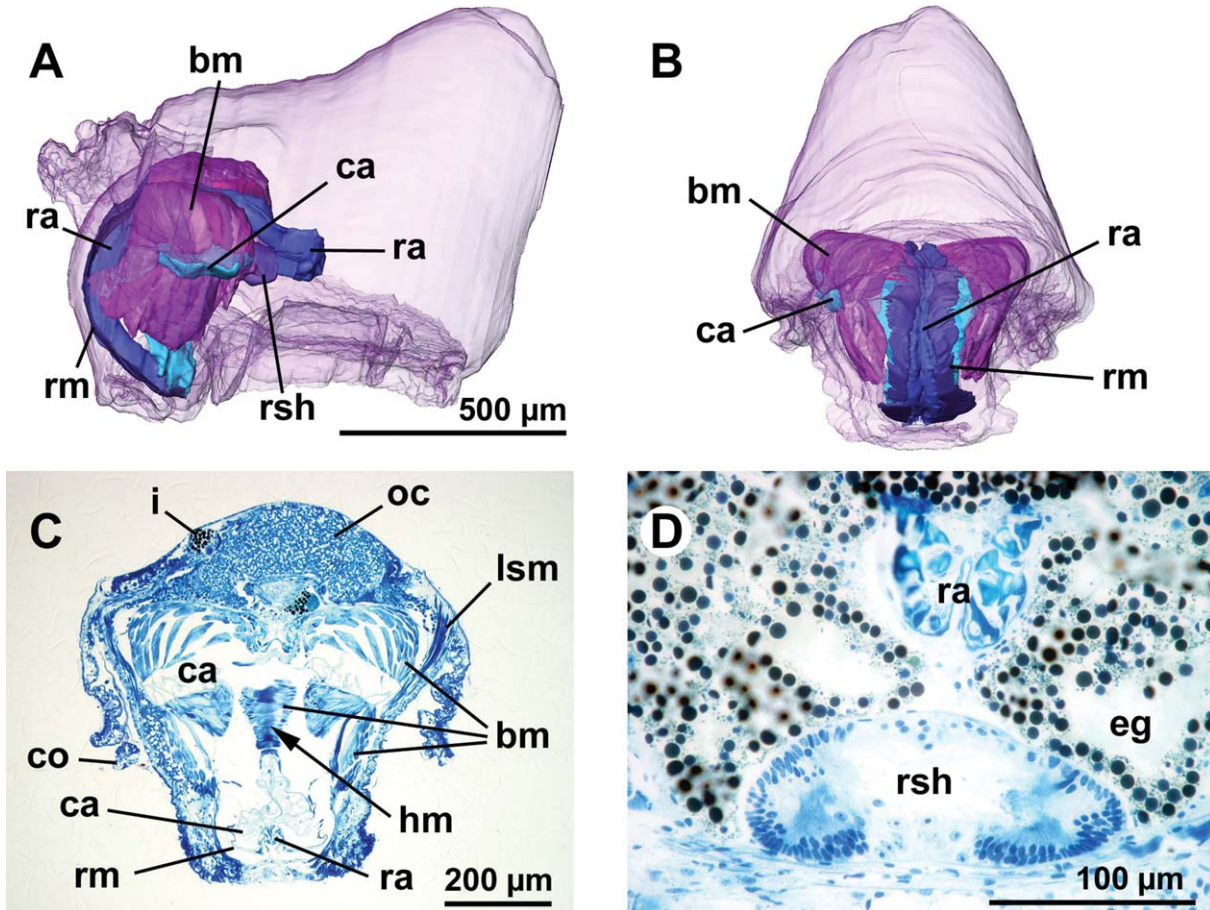
Fig. 9. Anterior alimentary tract of *Bathyaltum wareni* n.sp. **A,B:** 3D reconstructions. A: View from the left side. B: Frontal view. **C,D:** histological details. C: Cross-section of buccal apparatus. D: Cross-section of posterior end of radular sheath. bm, buccal muscles; ca, radular cartilage; co, copulatory organ; eg, esophageal gland; hm, horizontal buccal muscle; i, intestine; lsm, left shell muscle; oc, oocyte; ra, radula; rm, radular membrane; rsh, posterior end of radula sheath.

is likewise highly glandular though comparatively smaller than in *Bathypelta pacifica*. Again the distal part of the intestine makes several narrow loops in the left region of the head.

Nervous System

The bathysciadiid central nervous system is weakly concentrated and is uniformly developed throughout the family. The wide cerebropedal nerve ring surrounds the buccal apparatus and shows a hypoathroid situation in having adjacent pleural and pedal ganglia (Fig. 12A,B). The cerebral ganglia are laterally situated at the basis of the cephalic tentacles and are interconnected by a long and thick cerebral commissure. Cerebral nerves supply the mouth opening region, and each cephalic tentacle is supplied with a simple, thick nerve. An optic nerve could not be detected. At each posterior ventral end a labial lobe is formed, from which the buccal connective emerges. However, a labial commissure is lacking. The small buccal ganglia are situated as usual at the emer-

gence point of the esophagus (Fig. 12C). Two connectives emerge from each cerebral ganglion running side by side backward to reach the pedal and the pleural ganglia, respectively.

The large pedal ganglia are interconnected by a thick commissure and by a very thin parapedal commissure behind it. Each pedal ganglion has two main nerves: The anterior nerve ramifies into the anterior foot, and the posterior one supplies the rest of the foot sole and the epipodial region. Although this nerve is cord-like in both *Bathypelta* species, nerve cell somata are lacking in the remaining species. A relative small shell muscle nerve emerges laterally at each side. The pleural ganglia are situated adjacent to the pedal one. Their main nerves are the mantle nerves, which penetrate the shell muscle and ramify into the mantle border, where they form a dense net that encircles the whole animal.

The wide visceral loop could not be reconstructed in detail, but its main characteristics can be provided: It is streptoneurous and cord-like throughout, true ganglia cannot be distinguished.
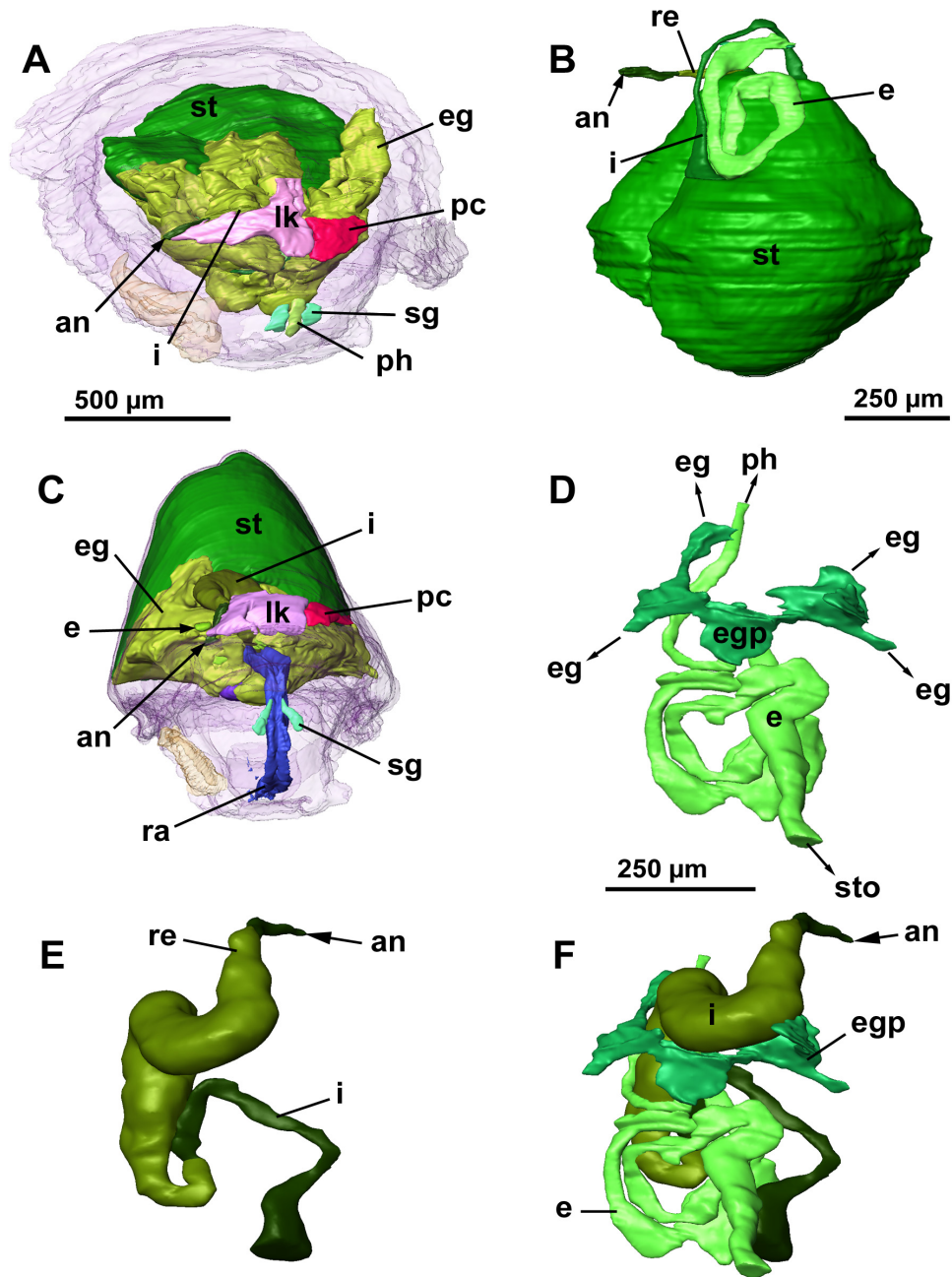
Fig. 10. 3D reconstructions of alimentary tract. **A,B:** *Bathysciadium costulatum*. A: Position and volume occupation in the whole animal in dorsofrontal view. B: Posterior alimentary tract alone from ventral view. **C–F:** *Bathyaltum wareni* n.sp. C: Position and volume occupation in the whole animal in frontal view. D: Esophagus and main branches into esophageal gland in dorsal view. **E:** Intestine and rectum in dorsal view. F: Combination of D and E. an, anal opening; e, esophagus; eg, esophageal gland; egp, esophageal gland pouch; i, intestine; lk, left kidney; pc, pericardium; ph, pharynx; ra, radula; re, rectum; sg, salivary gland; st, stomach. Scales: 500 μm for A and C; 250 μm for B; 250 μm for D–F. The **interactive 3D model** of *Bathysciadium costulatum* can be accessed by clicking into Figure 10 (Adobe Reader Version 7 or higher required). Rotate model by dragging with left mouse button pressed, shift model: same action + ctrl, zoom: use mouse wheel (or change default action for left mouse button). Select or deselect (or change transparency of) components in the model tree, switch between prefab views or change surface visualization (e.g., lightning, render mode, crop, etc.).

Because of the shallow mantle cavity, the visceral loop is situated more anteriorly than the pedal ganglia. The visceral part crosses immediately behind the posterior end of the mantle cavity.

From the most dorsal, left point of the visceral loop the osphradial connective enters the left mantle roof and forms a small swelling, which supplies in particular the gill.
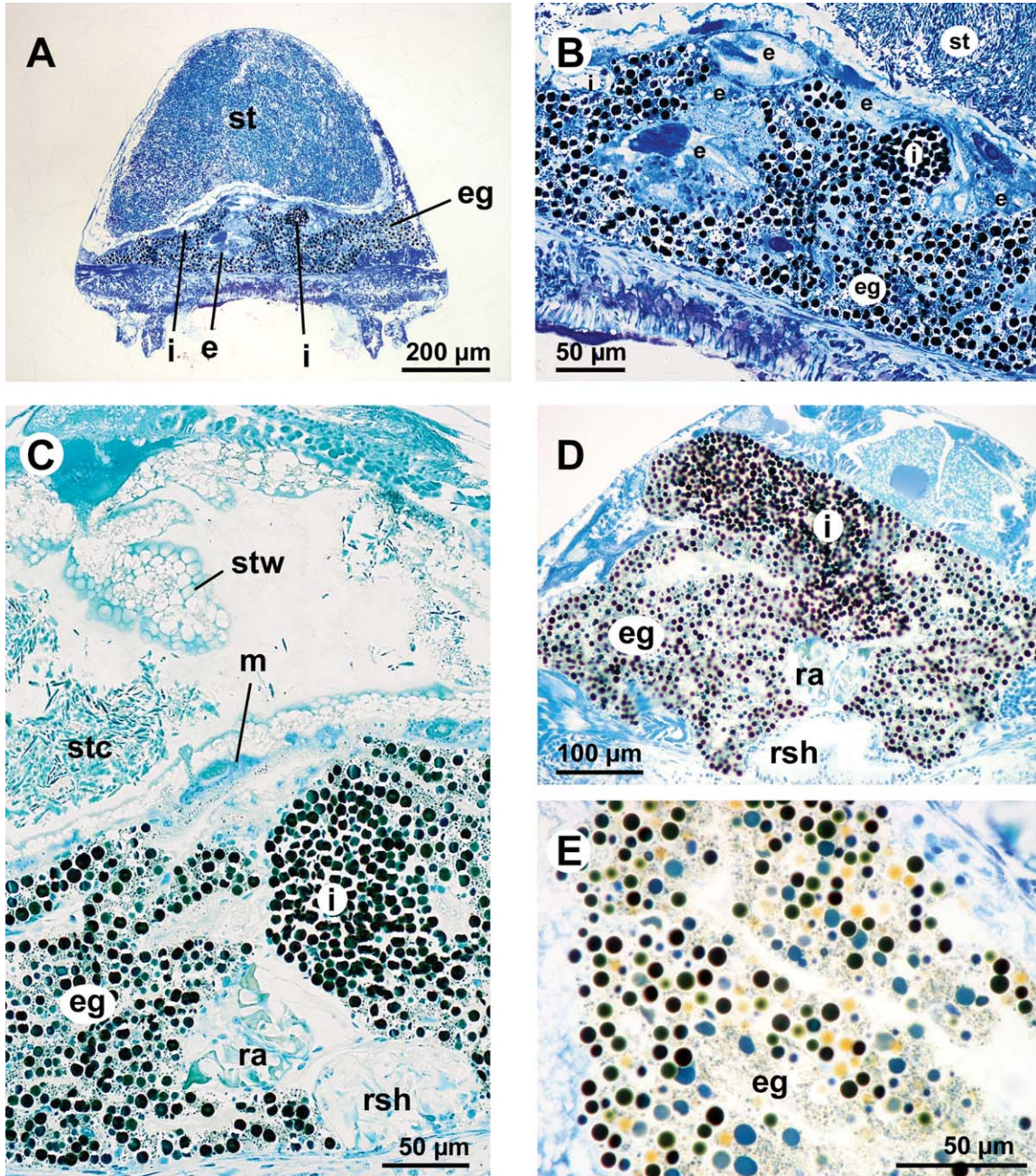
Fig. 11. Histological details of posterior alimentary tract of *Bathyaltum wareni* n.sp. **A:** Cross-section of stomach. **B:** Detail of A showing esophageal and intestinal loops. **C:** Cross-section at plane of anterior stomach. **D:** Cross-section at plane of end of radular sheath. **E:** Detail of esophageal gland. e, esophagus; eg, esophageal gland; i, intestine; m, mucous cell of stomach epithelium; ra, radula; rsh, posterior end of radular sheath; st, stomach; stc, stomach content; stw, glandular wall of stomach.

Sense Organs

The small cephalic tentacles are smooth. Distinct sensory elements could not be detected. Eyes and a subradular organ are lacking in all species. A distinct osphradial epithelium is also lacking. The small statocysts are placed adjacent to each other at the pedal commissure. Each statocyst contains a single, concentrically structured statolith (Fig. 12D).

For conditions of the mantle papillae see above. It is unclear whether the ciliary tufts in the subpallial cavity represent sensory structures or are used for cleaning.

Parasites

One specimen of *Bathysciadium costulatum* contained a large parasitic (commensal?) crustacean
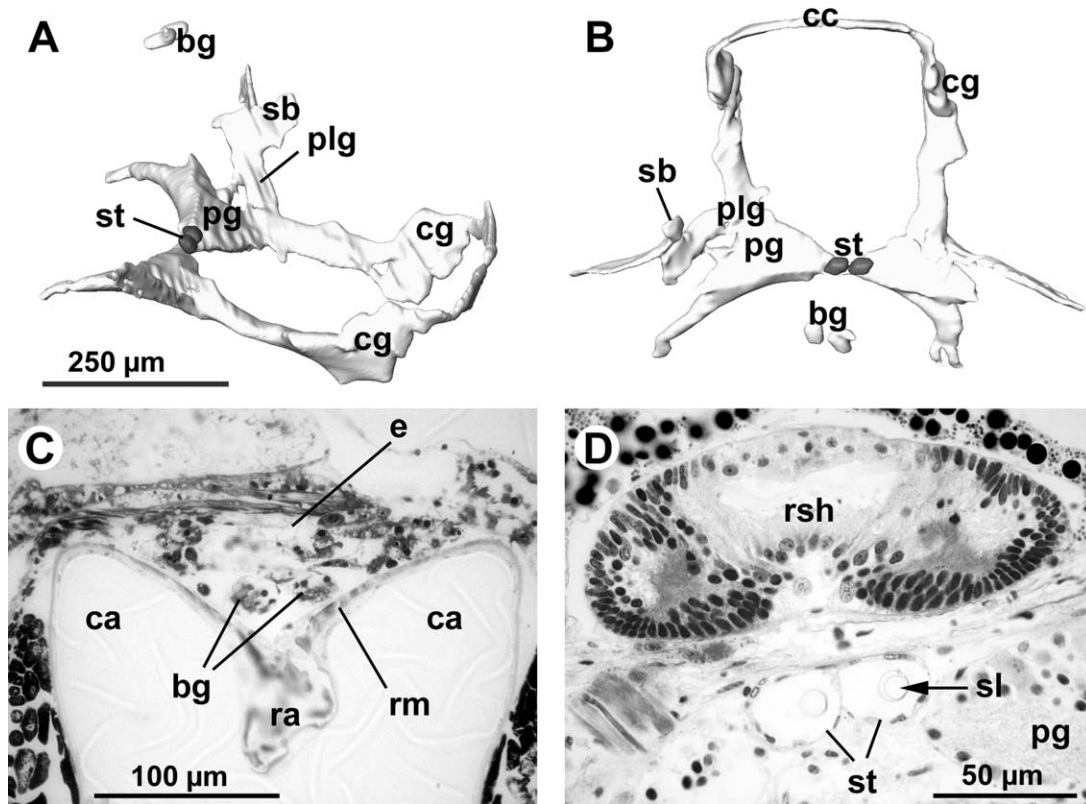
Fig. 12. Nervous system of *Bathyaltum wareni* n.sp. **A,B:** 3D reconstruction of anterior nerve ring. A: Laterodorsal view from the right side. B: Dorsal view. **C:** Buccal ganglia. **D:** Statocysts. bg, buccal ganglia; ca, empty space of radular cartilage; cc, cerebral commissure; cg, cerebral ganglia; e, esophagus; pg, pedal ganglia; plg, pleural ganglia; ra, radula; rm, radular membrane; rsh, posterior end of radular sheath; sb, subesophageal ganglion; sl, statolith; st, statocysts.

[probably a copepod, the sections look similar to those of the chitonophilids recently described by Tunnicliffe et al. (2008) for *Lepetodrilus* and by Huys et al. (2002) in *Lepetellids*] in its mantle cavity, which fills the volume nearly completely.

DISCUSSION
Character Analysis

The significance and evolution of the various organ systems of the cocculiniform Gastropoda have been discussed in detail by Haszprunar (1988a,b; 1992, 1993, 1998) and later on by Ponder and Lindberg (1997), Sasaki (1998), and Strong et al. (2003). Here, specific attention is paid to the peculiar characters of the Bathysciadiidae with respect to function(s) and their systematic significance.

Detailed descriptions of the bathysciadiid shell have been provided by Dautzenberg and Fischer (1899), Dall (1908), Thiele (1908, 1909), Moskalev (1973), and Warén (1991, 1993, 1996). Warén (1993, 1996) also figured with SEM the symmetrical protoconch with a bowl-shaped initial part and reticulate (*Bathysciadium* and *Bathypelta* spp.) or pitted (*Xenodonta*) pattern of the surface. The doubtfully included *Pilus conica* shows a wide helicoid shell (cf. Warén, 1991, 1993).

The teleoconchs of *Xenodonta bogasoni* and *Bathyaltum wareni* with their posterior apex resemble those of cocculinids and pseudococculinids in having weak sculpture and more or less oval aperture. In contrast, the adult shell of *Bathysciadium*, *Bathypelta*, and *Bonus* species is aberrant and diagnostic in showing a circular aperture and typical rows of periostracal fringes. Obviously the presence of prominent mantle tentacles is directly correlated with the conditions of the periostracal fringes, the functional significance of the latter remains obscure. Both characters form a complex, synapomorphic feature suggesting a monophyletic subclade of these three genera within the Bathysciadiidae. It is uncertain at present, whether or not protoconch features will support this clade.

As in Patellogastropoda, Cocculinidae, and most Lepetelloidea and contrary to all other limpet taxa, there is no helicoid larval or juvenile stage of the shell. Haszprunar (1988a,b) provided evidence that such shell conditions are probably plesiomor-

phic for Gastropoda (primary limpets). In contrast, Lindberg (1981b, 1988; Ponder and Lindberg, 1997) suggested that the left-side angle between the protoconch and the teleoconch, which is present in many species, indicates a coiled, hyperstrophic ancestor of these groups. However, the conditions of *Xenodonta bogasoni* with a right-side angle (Warén, 1996) cast doubts on the latter hypothesis. In addition, the angle between protoconch and teleoconch varies substantially (i.e., left or right in the same sample of a single species) in certain pseudococculind species (Haszprunar, unpublished data) and thus is probably of minor significance concerning ancestral conditions. Again the protoconch itself is bilaterally symmetrical in bathysciadiids (Warén, 1993, 1996; Haszprunar, 1998) as in other cocculiniform gastropods. The strongly asymmetric teleoconch of the doubtfully placed *Pilus conica* (cf. Warén, 1991, 1993) probably is an autapomorphic feature in parallel with adult *Addisonia* (cf. Haszprunar, 1987a; Warén, 1996).

External morphology of the species studied agrees in principle with previous descriptions (Pelseneer, 1899; Thiele, 1908, 1909; Warén, 1993, 1996) (Fig. 3). According to Warén (1996: Figs. 4, 12B, and 13B), *Bathysciadium* species (*B. costulatum*, *B.* cf. *xylophagum* and a further undescribed species) are characterized by numerous ciliary tufts at the subpallial epithelium, which may function for cleaning from mud particles.

The type of a paired, horse shoe-shaped shell muscle with separate bundles and the shallow mantle cavity is shared with the Patellogastropoda, Cocculinidae, and Lepetellidae and also with certain Neritimorpha (= Neritopsina). We regard these characters as plesiomorphic (see Haszprunar, 1988a,b, 1992b, 1998), although homoplasy cannot be excluded (Ponder and Lindberg, 1997).

Figure 12 of *B. pacificum* of Thiele (1908) shows only the most distal third of the very large gill of this species; however, Warén (1996: Fig. 7A) depicted a SEM-photo of another specimen, which gives the impression of a true bipectinate ctenidium, which does not agree with the sections. The pseudoplicatid gill-type is generally shared with the Cocculinidae. Among the Patellogastropoda, *Rhodopetala rosea* (Acmaeidae) alone shows a similar type (Lindberg, 1981a). In all cases, this gill-type probably is a modified ctenidium (Haszprunar, 1988a,b; Ponder and Lindberg, 1997; Sasaki, 1998). The ciliation of the gill clearly is responsible for the ventilation of the shallow mantle cavity. Judged from its high degree of vascularization and the thin, squamous epithelium the gill is also a respiratory organ as in bullomorph opisthobranchs. However, the respiratory surfaces of the pallial roof and of the mantle (extended to the shell margin in living animals) by far exceed that of the gill. The immature, gill-less specimen of

Bathyaltum wareni suggests that the gill occurs very late in ontogeny, probably not before sexual maturity. Accordingly, it is not necessary for respiration in juvenile animals. In contrast to the Cocculinidae but similar to Patellogastropoda there is no hypobranchial gland.

As typical for cocculinoid and all higher gastropods, the heart is monotocardian. The significance of the exact position of the auricle (anteriorly right in *Bathyaltum wareni*, anteriorly left in all other species) is uncertain at present.

The presence of a single, left kidney, a single hermaphroditic gonad, and a single, glandular gonoduct are probably synapomorphies shared with the Cocculinidae. We agree with Ponder and Lindberg (1997) that the loss of the right kidney occurred independently several times in gastropod evolution, namely also in Neritimorpha, Neomphalida, and Apogastropoda (Caenogastropoda and Heterobranchia). The lack of a distinct nephridial gland is shared with Cocculinidae and Neritimorpha, whereas a (homologous?) nephridial gland is present in the left kidney of Patellogastropoda, Vetigastropoda, Neomphalida, and Apogastropoda (Andrews, 1985, 1988; Ponder and Lindberg, 1997).

As in cocculinids, the conditions of the copulatory organ and receptaculum serve for species and generic diagnosis in the Bathysciadiidae (see below) and reflect entaquatic (i.e., in the mantle cavity) or truly internal (i.e., in the gonoduct) fertilization. The presence of all stages of spermiogenesis and oogenesis suggests continuous reproduction, which is common among deep-water animals. A vitelline layer of the eggs is diagnostic for Vetigastropoda (including Lepetelloidea), thus its absence excludes the Bathysciadiidae from this major clade. At first glance, the presence of eggs at the basis of the gill in *Bathypelta pacifica* suggests brooding, however, this might be the artificial result of mechanical treatment during collection or preservation.

Bathysciadiidae, Cocculinidae, and Neritimorpha share vestigial to absent jaws, a feature, which is clearly independent of their (extremely variable) feeding biology. Ponder and Lindberg (1997) and Sasaki (1998) considered this character as a synapomorphy of Cocculinoidea and Neritimorpha. However, the presence of a prominent jaw of the patellogastropod type in *Teuthriostria cancellata* (Moskalev, 1976), a cocculinoid limpet with cocculinid-like radula also feeding of cephalopod beaks (Moskalev, 1976), suggests independent reduction even within the Cocculinoidea (Strong et al., 2003).

The bathysciadiid radula is diagnostic for the family, the details even enable diagnosis of species and genera (see Thiele, 1908, 1909; Moskalev, 1973; Warén, 1993, 1996). Warén (1993) presented informative SEM-photos of the radula of *Bathy-*

sciadium cf. *pacifica* and *Xenodonta bogasoni*; Warén (1996: Figs. 5A–B, 6A–C, 8A–D, and 11A–C) showed SEM photos of the radula of *Bathypelta pacifica*, *Bathysciadium costulatum*, *Bonus petrochenkoi*, *Bathysciadium* cf. *xylophagum*, and *Bathysciadium xylophagum*. As in cocculinids, the central tooth is weakly developed or vestigial or lost.

Conditions of the radular cartilages (a single pair) are shared with cocculinids again, but are also found in Neomphalida (Haszprunar, 1987b, 1988a, 1998; Heß et al., 2008). In contrast, the remaining gut is strongly specialized and modified. The peculiar cuticularized area of the oral lappet probably functions as suckers (Warén, 1996). Pelseneer (1899: Fig. 3) depicted a "foie" (liver = midgut gland) in *Bathysciadium costulatum* and Thiele (1908: p. 84) noted in *Bathypelta pacifica* that "the liver (= midgut gland) surrounds the stomach and contains very similar granules like the esophageal gland," but he failed to detect the midgut opening. In fact, however, there is no midgut gland at all. Indeed, the bathysciadiids are the only nonparasitic gastropods (molluscs) entirely lacking a midgut gland, which appear to be functionally substituted by the very large esophageal glands. However, the role of the pellets within the epithelial cells remains obscure. It is likely that bacterial symbionts are necessary to digest the unusual food, that is, fine raspings of chitinous cephalopod beaks. Presence of symbiotic bacteria in the esophageal glands and their direct consumption by the host would explain the unique absence of the midgut gland, but if so, why the fine pieces of food are stored in the (subsequently placed) large stomach? Anyway, the presence of bacteria in the esophageal glands and/or in the stomach and intestine awaits confirmation by future fine-structural or molecular investigations. Needless to say that the anatomical conditions of the doubtless bathysciadiid *Xenodonta*, which probably feeds on shell periostracum (again a chitinous substrate) and of the addisoniid *Helicopelta* (cf. Marshall 1996), would be of greatest interest.

The presence of a glandular rectum in *Bathypelta* species defines the genus independently from the conditions of the copulatory organ (see above). This character is certainly not homologous with the anal gland of neogastropods, where symbiotic bacteria enable or assist in extraction of cations and macromolecules (Andrews, 1992). An anal gland has also been described by Andrews (1992) in the trochid *Gibbula,* where it might function in enveloping the fecal strings. However, this is quite unlikely for *Bathypelta*, which share the same nourishment as *Bathysciadium* species. Again fine-structural or physiological data are needed to proceed in this enigma.

The hypoathroid nervous system reflects the "archaeogastropod" nature of the family (see Haszprunar, 1993). The cord-like visceral loop is plesio-morphically shared with Patellogastropoda and many vetigastropods, whereas the formation of true pedal ganglia is a matter of multiple convergency (Haszprunar, 1988b, Ponder and Lindberg, 1997) in the Gastropoda.

Loss of sense organs is a very common phenomenon among cocculiniform gastropods (Haszprunar, 1988a,b, 1998). Among the main rhipidoglossate taxa, the conditions of the statocyst with their single statolith are again shared with the Cocculinidae and Neomphalida but differ from Neritimorpha and Vetigastropoda, where several statoconia are the rule.

Generic Definitions of Bathysciadiids

In the complete absence of molecular characteristics and based only on a couple (of may be hundreds; Warén, unpublished data) of species, a thoroughly based phylogenetic system of the Bathysciadiidae cannot be inferred. Warén (1996) concluded that it is best to retain all species in the genus *Bathysciadium* until a sound phylogeny is available. However, we think it more useful to attempt to apply various generic names, if they can be thoroughly defined by apomorphic characters. As a basis, Table 2 presents all differences in the species studied so far by means of serial sections.

Accordingly, we redefine *Bathypelta* (Moskalev, 1971) (type species: *Bathysciadium pacificum*) (Dall, 1908) by the synapomorphic copulatory verge with distal, glandular seminal duct, and a prominent anal gland. In addition, we place the new species in a separate genus (*Bathyaltum*) due to severe differences in shell shape and anatomy (see above).

There are many already collected but still undescribed bathysciadiid species from the Atlantic and from the New Zealand region (Warén and Marshall in letter). The current contribution may not only improve our knowledge of these enigmatic limpets but also should encourage colleagues to increase attention to these taxa.

Systematic Position of Bathysciadiidae

The original placement of the Bathysciadiidae among the Patellogastropoda was based on the short anatomical report of Pelseneer (1899) and during the last decades only reconsidered by Moskalev (1973). The present investigation clearly showed that Pelseneer's (1899) study included several severe errors, whereas the observations of Thiele (1908) could be largely confirmed. Accordingly, the splitting into separate families and superfamilies as proposed by Moskalev (1973) as well as the inclusion among the Patellogastropoda can no longer be supported. To some extend, mistakes of Pelseneer's (1889) can be explained by the

smallness of his specimens; we also failed to investigate the detailed anatomy of any small bathysciadiid by classic paraffine sectioning.

The assumption of a close relationship between the Bathysciadiidae and the Cocculinidae, which were united in Cocculinoidea by Haszprunar (1987b, 1988a,b, 1998) is supported by the following characters: Retained plesiomorphies are the symmetrical limpet shape (i.e., no helicoid juvenile stage, see above for discussion), the shell muscle being composed of distinct bundles, the shallow mantle cavity, and the single, dorsal jaw (reduced in cocculinids, lacking or vestigial in bathysciadiids, but prominent in *Teuthirostria*). All these characters are likewise present in the Patellogastropoda, which are now generally considered to be the earliest gastropod offshoot (Haszprunar, 1988b; Ponder and Lindberg, 1997; Sasaki, 1998; Aktipis et al., 2008; Lindberg, 2008). Synapomorphies of Cocculinoidea are the pseudoplicatid gill, the single (left), kidney, the single, hermaphroditic gonad with glandular gonoduct, and the statocysts with single, concentrically structured statoliths. Although confirmation by molecular characters will be welcome, there is already considerable evidence by morphology that the taxon Cocculinoidea forms a clade.

Cocculinoidea and Lepetelloidea, formerly united as "Cocculiniformia" by the senior author (Haszprunar, 1988a,b, 1998), differ from each other in many fundamental characters, contradicting their monophyletic origin. Indeed, the Lepetelloidea alone share several features with the Vetigastropoda (papillate tentacles or mantle margin, paired jaw with teeth-like elements, bursicles, intestine with typhlosole, vitelline layer of eggs) (cf. Ponder and Lindberg, 1997). In addition, molecular data also support inclusion of Lepetelloidea in the Vetigastropoda to the exclusion of Cocculinidae (Kano, 2008); however, sequence data on Bathysciadiidae are still missing. The hypothesis of monophyletic "Cocculiniformia" cannot longer be adhered and should be abandoned.

Accordingly, all similarities between Cocculinoidea and Lepetelloidea are either plesiomorphic or but homoplastic characters. The latter is probably true for the functional overlapping of the marginal radular teeth (Hickman, 1984) and a distinct pattern of esophageal folds (Salvini-Plawen and Haszprunar, 1987) shared by Cocculinidae and Pseudococculinidae due to common nourishment mostly on decaying wood. Members of both clades have their gill (leaflets) situated at the right side, whereas it is supplied by the left osphradial ganglion. As outlined by Ponder and Lindberg (1997) this might be a parallel case of heterochrony or paedomorphism respectively.

The inclusion of Lepetelloidea in the Vetigastropoda leaves only the Cocculinoidea to be placed and various trees have been proposed in the last two decades as recently reviewed by Aktipis et al. (2008) and Lindberg (2008). The morphological analyses by Salvini-Plawen and Steiner (1996) and Ponder and Lindberg (1997) favored that Cocculinoidea are the sister-group to the Neritimorpha (= Neritopsina): Shared characters include symplesiomorphic conditions of the shell muscles, rhipidoglossate radula and lack of gill-skeletons, and apomorphic conditions like the single, left kidney, the glandular gonoduct, and the reduction of jaws and salivary glands. However, the first apomorphy is paralleled by the Neomphalida and the Apogastropoda (all higher gastropods), the latter is contradicted by the conditions in the cocculinid-like *Teuthirostria cancellata* with prominent jaws and salivary glands (Strong et al., 2003).

In contrast, molecular analyses of Cocculinidae (up to now five genes of *Cocculina messingi*, two genes of *Coccopigya punctoradiata,* and three genes of *Cocculina* sp.) lack resolution among the major rhipidoglossate groups (Geiger and Thacker, 2005; Kano, 2008; Williams et al., 2008) or suggest (with weak support) a closer relationship of Cocculinoidea and Neomphalida (McArthur and Harasewych, 2003; Aktipis et al., 2008). The latter two groups share in particular the presence of a single, left kidney and true statoliths (as in Neritimorpha and Apogastropoda). Because of the modification of the ctenidium in Cocculinoidea, the absence of bursicles (contrary to Neomphalida and Vetigastropoda) (cf. Heß et al., 2008) is not significant, but the jaw conditions (paired, teeth-like in Neomphalida and Vetigastropoda) contradict a close affinity. To proceed here in particular molecular data on bathysciadiids are a must. At the present stage of knowledge, we prefer to keep the Cocculinoidea (Cocculinida) as an independent clade of rhipidoglossate Gastropoda.

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