

Interactive 3D-anatomical reconstruction and affinities of the hot-vent gastropod *Xylodiscula analoga* Warén & Bouchet, 2001 (Ectobranchia)

Andreas Hawe¹, Claudia Paroll¹ and Gerhard Haszprunar^{1,2}

¹Department Biology II and GeoBio-Center, LMU München, Biozentrum, Großhaderner Str. 2, Planegg D-82152, Germany; and

²SNSB- Zoologische Staatssammlung München, Münchhausenstraße 21, München 81247, Germany

Correspondence: A. Hawe; e-mail: a.hawe@gmx.de

ABSTRACT

The heterobranch family Xylodisculidae Warén, 1992 includes about a dozen described species, the taxonomy of which is mostly based on hard parts (shell, operculum, radula) with occasional reports on the external morphology. By applying semithin sectioning, digital photography and 3D-reconstruction, we describe for the first time the anatomy and histology of a xylodisculid, *Xylodiscula analoga* Warén & Bouchet, 2001. Described from hot-vent habitats, this species is exceptional among Xylodisculidae for its extraordinary size and atypical taenioglossate-like radula. Anatomy and histology confirm a placement of monophyletic Xylodisculidae among the Heterobranchia: Ectobranchia. Members of the family combine a unique radula type with a plesiomorphic alimentary and genital system; the latter is monaulic, lacks a copulatory organ and possesses a separated receptacle apparatus. Due to lack of data on soft bodies of other xylodisculid species and because molecular data are entirely missing for the family, a robust hypothesis on the systematics of Xylodisculidae cannot yet be provided.

INTRODUCTION

The superfamily Valvatoidea (= Heterobranchia: Ectobranchia) currently comprises four families. The freshwater Valvatidae Gray, 1840 have been known for more than 170 years and have long been considered as ‘primitive mesogastropods’. Shortly after their new placement as basal Heterobranchia (Haszprunar, 1985a, 1988; Rath, 1988), their marine relatives were recognized: Cornirostridae Ponder, 1990, Xylodisculidae Warén, 1992 and Hyalogyrinidae Warén & Bouchet, 1993. Whereas the anatomy of one or a few representatives of most families has been investigated (Valvatidae: Bernard, 1890; Cleland, 1954; Rath, 1986, 1988; Hawe *et al.*, 2013; Cornirostridae: Ponder, 1990b; Bieler, Ball, & Mikkelsen, 1998; Hyalogyrinidae: Haszprunar *et al.*, 2011), Xylodisculidae have remained anatomically unstudied. In addition, the relationships between ectobranch families are still obscure, although the rhipidoglossate-like radula of the Hyalogyrinidae suggests a basal position of this family and of Ectobranchia as a whole among the Heterobranchia (Haszprunar *et al.*, 2011; Hawe, Heß, & Haszprunar, 2013; Hawe, Gensler, & Haszprunar, 2014; Brenzinger, Haszprunar, & Schrödl, 2013a, Brenzinger, Wilson, & Schrödl, 2013b).

Xylodiscula Marshall, 1988 was originally assigned to Orbitestellidae, a heterobranch family now considered only distantly related to the Ectobranchia (Hawe *et al.*, 2014). Later, Warén (1992) removed *Xylodiscula* from the (gill-less) Orbitestellidae, elevated it to family rank and placed the family within the Ectobranchia, a view confirmed by the presence of an ectobranch gill in *X. planata* (cf. Høisæter & Johannessen, 2001).

This view was followed by Warén & Bouchet (2001). Currently, Xylodisculidae comprises about 10 extant and one fossil species (Tables 1 and 2). Two more species, *Helisalia liliputia* Laseron, 1954 and *Vitrinorbis callistus* Pilsbry & Olssen, 1952 have been tentatively assigned by Marshall (1988: 988), and several more are still undescribed (see e.g. Sasaki *et al.*, 2010: 243 or <http://seaslugsofhawaii.com/species/Xylodiscula-sp1-a.html>).

As far as is currently known, all xylodisculids live in chemosynthetic habitats (Table 2), including a still undescribed species from cold seeps (Sasaki *et al.*, 2010: 245). Indeed, Høisæter & Johannessen (2001: 332) argued in support of this family as an example of the ‘stepping-stone’ hypothesis (e.g. Distel *et al.*, 2000) for the colonization of chemosynthetic habitats from shallow water via whale bones or sunken driftwood. Recently, the first case of bacterial endosymbiosis was reported in a hot-vent heterobranch, the orbitestellid *Lurifax vitreus* Warén & Bouchet, 2001 (Hawe *et al.*, 2014), and similar conditions may occur among the Ectobranchia, particularly within the Xylodisculidae.

Heretofore, species descriptions of xylodisculids have been based exclusively on hard parts (shell, operculum and radula), with external soft-body morphology reported only occasionally (Table 1). The family has been diagnosed by the radula formula 2-1-0-1-2 (Warén, 1992; Høisæter & Johannessen, 2001), but *Xylodiscula analoga* Warén & Bouchet, 2001 exceptionally possesses a radula with the formula 1-1-0-1-1.

This study presents anatomical and histological data for a xylodisculid species for the first time. The results are discussed

Table 1. List of *Xylodiscula* species and available data.

Species	Protoconch		Teleoconch	Shell shape	Operculum	Radula	Soft parts	Eyes	References/first description
	Size (µm)	Hetero-strophy	Size (mm)	Height-width ratio	No. of whorls	Formula	Anatomy		
<i>X. analoga</i>	?	?	3.00	0.500	Multispiral	1-1-0-1-1	Anatomy and histology	no	Warén & Bouchet (2001), herein
<i>X. boucheti</i>	255 µm	Yes	1.72	0.436	?	2-1-0-1-2	Short description	yes	Warén (1992)
<i>X. eximia</i>	233 µm	No	1.95	0.487	?	2-1-0-1-2	Short description	?	Marshall (1988)
<i>X. lens</i>	215 µm	Yes	1.74	0.353	?	?	Short description	yes	Warén (1992)
<i>X. librata</i>	267 µm	No	1.20	0.416	?	?	–	?	Marshall (1988)
<i>X. major</i>	275 µm	Yes	3.88	0.384	Multispiral	2-1-0-1-2	–	?	Warén & Bouchet (1993)
† <i>X. okutanii</i>	211 µm	Yes	1.03	–	?	?	–	?	Kiel & Goedert (2007)
<i>X. osteophila</i>	270 µm	No	1.60	0.668	Multispiral	2-1-0-1-2	–	?	Marshall (1994)
<i>X. planata</i>	?	No	1.70	0.441	6	2-1-0-1-2	+	yes	Høisæter & Johannessen (2001)
<i>X. vitrea</i>	270 µm	No	1.75	0.400	?	2-1-0-1-2	Short description	?	Marshall (1988)
? <i>X. wareni</i>	250 µm	No	1.10	0.600	?	?	?	?	Bogi & Bartolini (2008)

Table 2. Ecology of *Xylodiscula* species.

Species	Locality	Depth	Habitat	References/first description
<i>X. analoga</i>	Mid-Atlantic Ridge, Menez Gwen and Lucky Strike	850–1728 m	Hydrothermal vent	Warén & Bouchet (2001), herein
<i>X. boucheti</i>	Corsica and Tuscan Sea, Mediterranean Sea	90–400 m	<i>Posidonia</i> detritus and an amphora	Warén (1992)
<i>X. eximia</i>	Off White Island, New Zealand	1075–1100 m	On sunken driftwood	Marshall (1988)
<i>X. lens</i>	Corsica and Tuscan Sea, Mediterranean Sea	90–400 m	<i>Posidonia</i> detritus and sunken driftwood	Warén (1992)
<i>X. librata</i>	Off White Island, New Zealand	1075–1100 m	On sunken driftwood	Marshall (1988)
<i>X. major</i>	North Fiji Basin, Pacific Ocean	2000 m	hydrothermal vent “La Dame Blanche”	Warén & Bouchet (1993)
† <i>X. okutanii</i>	Merrick’s Bay, Clallam County, Washington State, USA	?	Upper Oligocene to lower Miocene, Pysht Formation	Kiel & Goedert (2007)
<i>X. osteophila</i>	Off Mermoo Bank, Chatham Rise, New Zealand	ca. 900 m	Decaying whale bone	Marshall (1994)
<i>X. planata</i>	Western Norway	34–56 m	Associated with surplus fish feed	Høisæter & Johannessen (2001)
<i>X. vitrea</i>	Off White Island, New Zealand	439–714 m	On sunken driftwood	Marshall (1988)
? <i>X. wareni</i>	Off Sicily, Mediterranean Sea	35–52 m	?	Bogi & Bartolini (2008)

in the context of ecomorphological characteristics of the hot-vent habitat and should improve our understanding of relationships within the Xylodisculidae and between the ectobranch families.

MATERIAL AND METHODS

Two paratypes (SMNH 43247) of *Xylodiscula analoga* Warén & Bouchet (2001: 208, figs 44b-d, 47c, 49h) were kindly provided by Dr Anders Warén of the Swedish Museum of Natural History (SMNH). Specimens were collected from the Lucky Strike vent field (37°17'N, 032°17'W) of the Mid-Atlantic ridge at a depth of 1620–1720 m in July 1998. The semithin sections described here are deposited in SMNH.

Treatment of specimens and sections, histological photography, 3D-reconstruction using the software Amira®, and embedding of the voxel graphic files into the pdf-format followed the protocols as described in detail in the foregoing papers on ectobranch and orbitestellid anatomy (Haszprunar *et al.*, 2011; Hawe *et al.*, 2013, 2014; Hawe & Haszprunar, 2013).

RESULTS

Headfoot morphology

The head of *Xylodiscula analoga* bears a pair of lateral cephalic tentacles behind the bilobed snout (Fig. 1A). A single pallial tentacle arises within the right mantle cavity roof and tapers to the tip (Fig. 1A). Its epithelium consists of highly cylindrical, ciliated cells. Only the left shell muscle is present.

The foot is retracted due to fixation. The anterior foot is bilobed; the foot sole is densely ciliated and lacks epipodial tentacles. The pedal epithelium contains scattered tall, cylindrical epithelial and subepithelial glandular cells. Two pedal glands (Fig. 1A) differing in their fine structure are present. The anterior gland consists of thick, darkly stained cells. The mucus is collected in a broad, ciliated channel, which opens anteriorly between the two pedal lobes. The posterior pedal gland, with large and brightly stained cells, opens to the foot sole via a small, mid-ventral duct between the two pedal glands. Within the foot, whitish calcium cells can be found dispersed among muscle fibres, blood spaces and connective tissue behind the posterior pedal gland.

Mantle cavity and its organs

The anterior roof of the deep mantle cavity is covered by a thin, non-ciliated epithelium. To the far left is a prominent mantle gland bordered on the right by the osphradium. To the right of the osphradium and continuing posteriorly within the mantle roof is a densely ciliated tract.

The triangular gill occupies the right anterior part of the mantle cavity (Figs 1B, 2D) and is comprised of six alternating lamellae without skeletal rods or bursicles. The epithelium of the gill is very thin, densely ciliated and underlain by large haemolymph lacunae. The mantle epithelium lining the efferent gill sinus is similarly very thin. From the left posterior end of the gill, the efferent gill sinus (Fig. 2D: egs) leads to the kidney, where it forms the afferent kidney sinus.

The single (left) kidney lies medio-dorsally in the mantle cavity roof behind the gill (Figs 1B, 2E) and comprises two lobes posteriorly enclosing the pericardium. The wall of the kidney is extensively penetrated by haemolymph lacunae. A nephridial gland is situated at the posterior end of the kidney (Figs 1B, 2E: ng), and anterior to the heart. The monotocardian heart, with anterior auricle and posterior ventricle, is also

pallially situated and extends to the anterior tip of the receptaculum seminis and is surrounded by a pericardium (Figs 1B, 2F: pc). The pericardium is bordered posteriorly by the intestine (Fig. 2E, F). A reno-pericardial duct is lacking. A simple nephropore is present adjacent to the posterior end of the gill and anterior to the rectum, which ends between kidney and gill.

Both gonoduct and rectum open at the line of the posterior end of the gill on the mantle floor, the gonoduct slightly further anteriorly. The opening of the receptaculum duct is situated more posteriorly, approximately at the line of the intestine.

Digestive system

The small mouth opening lies at the tip of the bilobed snout and is surrounded by a tall, columnar epithelium, whereas the epithelium of the dorsal side of the snout contains scattered vacuolated cells. The oral tube is star shaped in cross section and bears a ciliated dorsal channel that continues into the buccal cavity. A pair of cuticularized jaw plates flanks the mouth latero-ventrally and consists of many rectangular teeth (Fig. 2A). The oral tube continues to the buccal cavity containing a small radula. The underlying odontophore is purely muscular; cartilages are lacking. The paired salivary glands consist of two parts: the distal, fused (?) portion lies directly below the buccal cavity and comprises bright unstained, parenchyma-like gland cells (Figs 1C, 2B). This portion extends backwards flanking the oesophagus and continues into the dorsal portion. These proximal parts are twisted, extend forward again and show a distinct lumen, which is enclosed by darkly staining cells. Salivary ducts to the buccal cavity could not be found.

A densely ciliated oesophagus (Fig. 2B) continues posteriorly from the buccal cavity as a narrow tube and opens roughly mid-ventrally to a large, densely ciliated stomach (Fig. 2C). The stomach contains a prominent (~130 µm long and ~43 µm wide) crystalline style (Figs 1D, 2C) that is dorsolaterally enclosed by a gastric shield (Fig. 1D). The duct for the anterior digestive gland opens ventrally immediately adjacent to the oesophageal opening, whereas the duct for the posterior digestive gland lies near the posterior end of the anterior digestive gland. The posterior digestive gland starts on the left side of the stomach and fills the entire left half of the visceral whorls. Both digestive glands have highly glandular epithelia and large lumen. The anterior end of the stomach narrows into a short, ciliated intestine, that proceeds to the right, completing a tight loop, before continuing forward as a densely ciliated rectum. The rectum lies along the right side of the mantle cavity, and terminates between the kidney and gonoduct.

Genital system

The hermaphroditic genital system is simple and monaulic (Figs 3, 4). The large hermaphroditic gonad fills the entire right half of the visceral whorls, its anterior part dorsally enclosing the stomach on the right and ending at the line of the intestine. The follicular gonad is subdivided into an outer portion comprising the testis and an inner portion comprising the ovary (Fig. 3B), both filled with gametes.

The eggs increase in size and yolk content from the distal to the proximal portion of the ovary, eventually reaching about 55 µm in diameter. Due to poor fixation, details of sperm morphology could not be assessed.

Near the line of the posterior end of the stomach, the hermaphroditic gland opens ventrally to a vesicula seminalis densely filled with sperm and enclosed by a thin epithelium. The anterior vesicula seminalis narrows to a short, narrow, coiled hermaphroditic

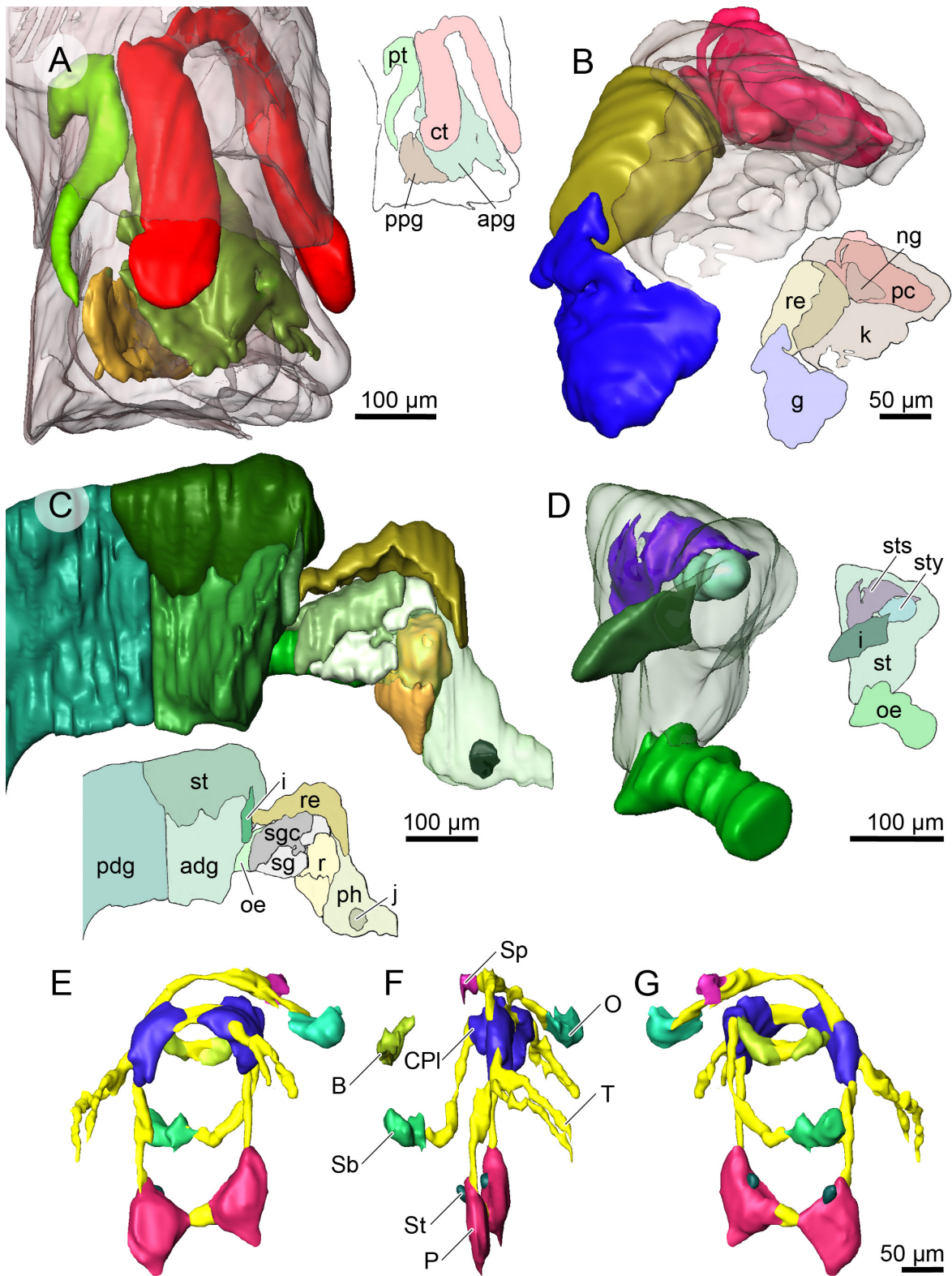


Figure 1. 3D reconstructions (interactive) and schematic overviews of the digestive, nervous and excretory systems of *Xylodiscula analoga*. **A.** Headfoot morphology (frontal view). **B.** Gill and excretory system (frontal view). **C.** Digestive system (right lateral view). **D.** Stomach (frontal view). **E–G.** Nervous system (anterior, right lateral and posterior views). Abbreviations: Adg, anterior digestive gland; apg, anterior pedal gland; B, buccal ganglia; CPI, cerebro-pleural ganglia; ct, cephalic tentacles; g, gill; i, intestine; j, jaws; k, kidney; ng, nephridial gland; O, osphradial ganglion; oe, oesophagus; P, pedal ganglia; pc, pericardium; ph, pharynx; ppg, posterior pedal gland; pt, pallial tentacle; r, radula; re, rectum; sg, salivary glands (whitish portion); sgc, salivary glands (dark-staining portion); Sb, suboesophageal ganglion; Sp, supraoesophageal ganglion; St, statocysts; st, stomach; sts, stomach shield; sty, crystalline style; T, bifid tentacular nerves. The interactive 3D model can be accessed by clicking on the figure (Adobe Reader v. 7 or higher required). To rotate model, drag with left mouse button pressed. To shift model use same action plus ctrl; to zoom use mouse wheel (or change default action for left mouse button). It is also possible to select or change transparency of components in the model, to switch between prefab views and to change surface visualization (e.g. lighting, render mode, crop, etc.).

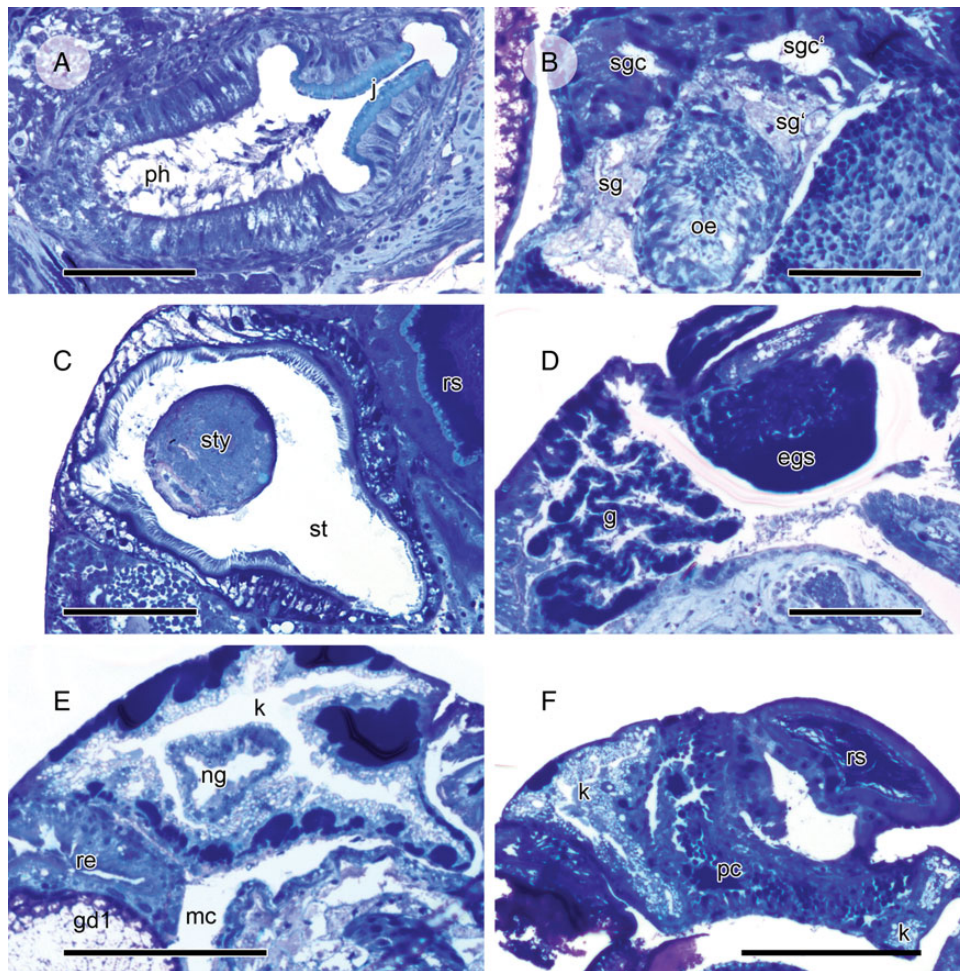


Figure 2. Histology of the gill and digestive and excretory systems of *Xylodiscula analoga*. **A.** Ciliated oral tube with jaws. **B.** Oesophagus with presumed salivary glands. **C.** Stomach with crystalline style. **D.** Gill and efferent gill sinus. **E.** Kidney and nephridial gland. **F.** Kidney and pericardium. Abbreviations: Egs, efferent gill sinus; g, gill; j, jaws; gd1, part of gonoduct; k, kidney; mc, mantle cavity; ng, nephridial gland; oe, oesophagus; pc, pericardium; ph, pharynx; re, rectum; rs, receptaculum seminis; sg, salivary glands (whitish portion); sgc, salivary glands (dark stained portion); st, stomach; sty, crystalline style. Scale bars: **A–C** = 50 μm ; **D–F** = 100 μm .

duct, which connects dorsally to the proximal glandular gonoduct (Fig. 3C, D: gd1 + gd2). The proximal gonoduct consists of two types of tall, columnar glandular cells that stain differently with Richardson's reagent. The proximal gonoduct leads backwards and ventrally, connecting with the distal gonoduct, again with two histologically distinct tall, columnar glandular cells: a dark-staining dorsal and a bright-staining ventral portion. The lumen of the distal gonoduct is compressed, forming a narrow slit. The thick distal gonoduct leads forward below the rectum, occupying most of the right mantle roof, opening to the mantle cavity near the anus. No seminal groove or copulatory organ is present.

A prominent receptacle apparatus is present. The large receptaculum seminis is situated in the pallial roof beneath the anterior stomach to the left of the heart (Fig. 3A). The epithelium is densely ciliated and the lumen completely filled with sperm (Fig. 3A). The anterior end of the receptaculum is cone-shaped and continues into the receptacular duct. The narrow duct is lined by small, cylindrical, densely ciliated cells and proximally bears a thin layer of circular muscles. The duct continues ventrally, expanding slightly at the level of the gonoduct, before turning anteriorly to open to the mantle cavity at the line of the intestine.

Nervous system

The cerebropedal nerve ring is epiathroid. The cerebropleural ganglia (Fig. 1E–G: CPI) lie below the base of the cephalic tentacles and are connected by a short commissure. On each side, a bifid tentacular nerve innervates the cephalic tentacle (Fig. 1E–G: T). The cerebropleural ganglia are connected to the pedal ganglia by cerebropedal and pleuropedal connectives, respectively. The pedal ganglia are ventrally located (Fig. 1E–G: P) and joined by a short commissure. Several pedal nerves supply the foot.

The visceral loop leads dorsally and across the oesophagus from the right cerebropleural ganglion to the supraoesophageal ganglion (Fig. 1E–G: Sp) located above the buccal cavity on the left. The supraoesophageal ganglion produces a nerve that supplies the osphradial ganglion in the left mantle roof (Figs 1E–G, 5A: O). From the left cerebropleural ganglion, the visceral loop leads ventrally and crosses below the oesophagus to the right, to the suboesophageal ganglion (Fig. 1E–G: Sb) deeply embedded in the columellar muscle and which innervates the pallial tentacle. The posterior portion of the visceral loop could not be followed. However, the flat visceral ganglion is situated below the posterior end of the mantle cavity, immediately dorsal to the oesophagus before it enters the stomach.

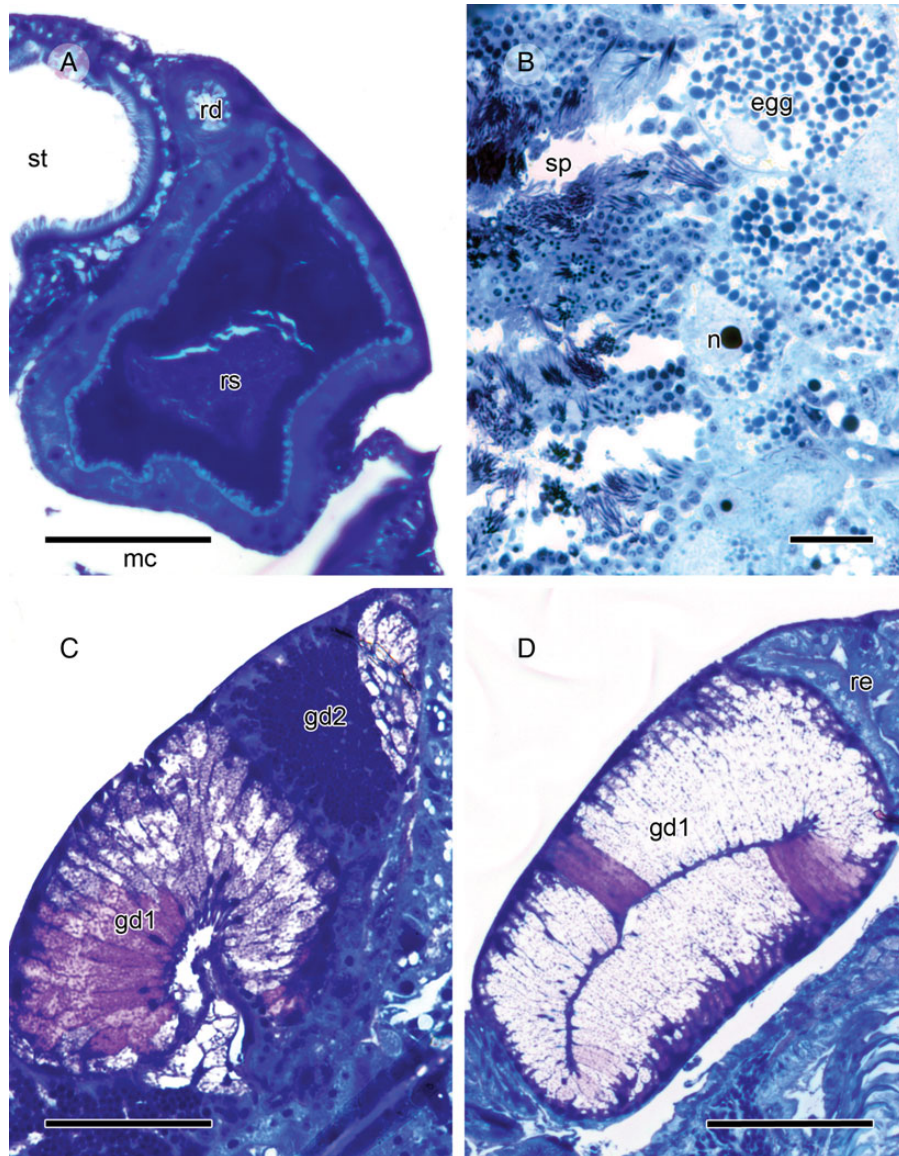


Figure 3. Histology of the genital system of *Xylodiscula analoga*. **A.** Receptaculum seminis. **B.** Hermaphroditic gland showing both ovary and testis portions. **C, D.** distal to proximal pictures of the glandular gonoduct. Abbreviations: Egg, egg; gd1, gd2, gonoductal glands; n, nucleus; re, rectum; rd, receptaculum duct; rs, receptaculum seminis; sp, sperm; st, stomach. Scale bars: **A, C, D** = 50 μm ; **B** = 20 μm .

The paired buccal ganglia (Fig. 1E–G: B) lie far behind the cerebropedal ring, at the junction between the buccal apparatus and oesophagus.

Sense organs

The paired cephalic tentacles lack papillae, bear scattered ciliated cells and are penetrated by a muscular hydrostat system with only narrow blood spaces. Eyes and epipodial tentacles are lacking. The osphradium forms a small, ciliated ridge underlain by the osphradial ganglion (Figs 1E–G, 5A: O). At the posterior end of each pedal ganglion is a round statocyst with several statoconia (Fig. 5B).

DISCUSSION

General remarks

For anatomical comparisons, we focus on other basal Heterobranchia. Anatomical data on these families are taken from:

- (1) Ectobranchia—Hyalogyrinidae: Haszprunar *et al.* (2011), Warén *et al.* (1993).
- (2) Ectobranchia—Cornirostridae: Ponder (1990b, 1991), Bieler *et al.* (1998).
- (3) Ectobranchia—Valvatidae: Bernard (1890), Cleland (1954), Rath (1986, 1988), Hawe *et al.* (2013).
- (4) Orbitestellidae: Ponder (1990a, 1991), Simone & Zelaya (2004), Hawe *et al.* (2014), Hawe & Haszprunar (2013).
- (5) Architectonicoidea—Architectonicidae: Robertson (1974), Haszprunar (1985c).
- (6) Architectonicoidea—Mathildidae: Haszprunar (1985d).
- (7) Architectonicoidea?—Omalogyridae: Fretter (1948), Bäumlér, Haszprunar, & Ruthensteiner (2008), Bieler & Mikkelsen (1998).
- (8) Rissoellidae: Fretter (1948), Simone (1995), Wise (1998), pers.obs.
- (9) Murchisonellidae: Warén (2013), Brenzinger *et al.*, (2013b and pers. comm.)
- (10) Anatomy of Tjaernoidae, and Graphidae is nearly unknown (Warén 1991, 2013), and the shell-less Rhodopidae (see

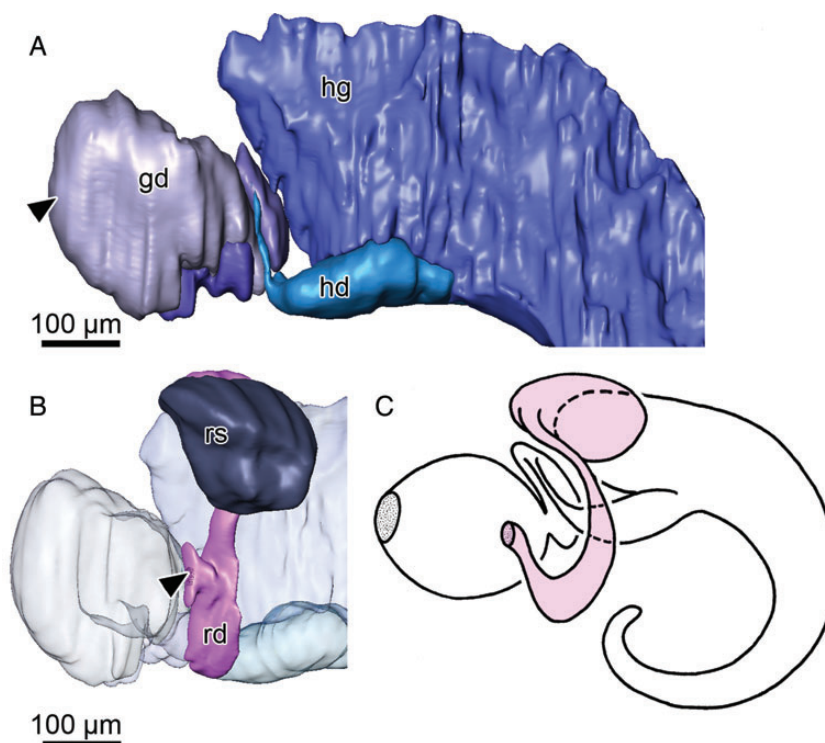


Figure 4. 3D reconstruction and schematic views of the genital system of *Xylodiscula analoga*. **A.** Genital system without receptaculum seminis. **B.** Receptacle apparatus with transparent gonoduct in the background. **C.** Schematic overview of receptacle apparatus. Abbreviations: Gd, gonoduct; hd, hermaphroditic duct; hg, hermaphroditic gland; rd, receptaculum duct; rs, receptaculum seminis. Arrowheads: openings of gonoduct (**A**), receptaculum duct (**B**).

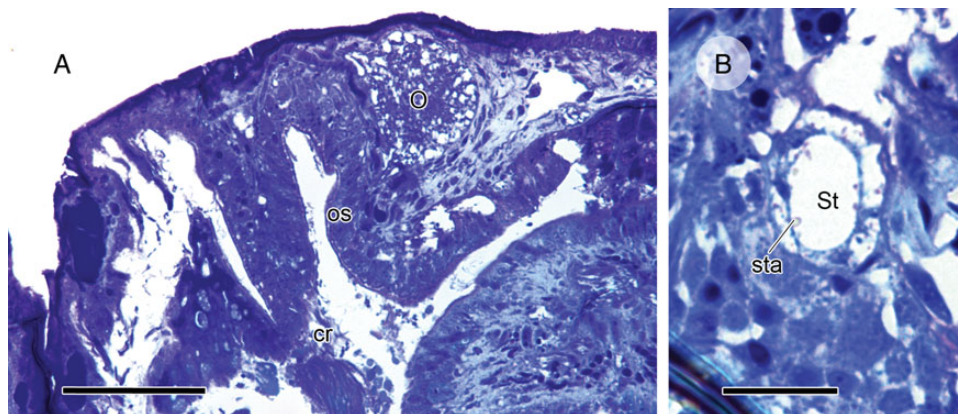


Figure 5. Histology of the sense organs of *Xylodiscula analoga*. **A.** Osphradium and osphradial ganglion. **B.** Statocyst with several statoconia. Abbreviations: Cr, ciliated ridge; O, osphradial ganglion; os, osphradium; St, statocyst; sta, statocone. Scale bars: **A** = 50 µm; **B** = 20 µm.

recent reviews by Brenzinger *et al.*, 2011, 2013a) are too highly derived for meaningful comparison.

Shell

The shells of *Xylodiscula analoga* and *X. major* are up to 3 mm in diameter and are exceptionally large for the genus (Table 1). Both species are hot-vent inhabitants suggesting a correlation between size and habitat. However, all xylodisculids are associated with chemosynthetic habitats. The thick periostracum prevents the acidic sea water of the hot-vent environment from dissolving the shell.

The smooth, subplanispiral shell of *Xylodiscula* species may be easily confused with other, distantly related heterobranchs, e.g. certain Omalogyridae (Architectonicoidea) or the pyramidellid genus *Cyclostremella* Bush, 1897 (Marshall, 1988: 988) (now Euthyneura: Panpulmonata; cf. Jörger *et al.*, 2010; Dinapoli & Klussmann-Kolb, 2010; Dinapoli, Zinssmeister, & Klussmann-Kolb, 2011). Even stronger similarities in shell shape exist between *Xylodiscula* and the cornirostrid genus *Noerrevangia* Warén & Schander, 1993 (see Høisæter & Johannessen, 2001: 330) and certain Hyalogyrinidae. Thus, the fossil *X. okutanii* Kiel & Goedert, 2007 was first classified among Hyalogyrinidae (Kiel & Goedert, 2006).

The shells of *X. analoga*, *X. okutanii* and *Hyalogyrina umbellifera* Warén & Bouchet, 2001 also share ‘intersected crossed platy

structure'. However, this type of shell structure may not indicate close phylogenetic affinity but more likely is correlated with the small size and thinness of the shells (Kiel, 2004: 181; Kiel & Goedert, 2007: 45).

Unfortunately, the protoconch of *X. analoga* is unknown due to corrosion (Warén & Bouchet, 2001). However, because of the large yolk content of the eggs (see below), we assume a protoconch type correlated with a lecithotrophic mode of development, as in *X. librata* Marshall, 1988 (cf. Marshall, 1988, Høisæter & Johannessen, 2001). This is contrary to the situation found in the type species, *X. vitrea* Marshall, 1988, where a clearly hyperstrophic protoconch suggests planktotrophic development. The latter confirms the heterobranch affinities of *Xylodiscula*.

Among the Ectobranchia, structure and form of the teleoconch provide few significant features for phylogenetic analyses. For example, teleoconch features of the freshwater Valvatidae (e.g. the widespread *Valvata piscinalis*) are highly variable due to ecophenotypic or ontogenetic variation (e.g. Favre, 1927, 1935; Haas, 1938; Falmiowski, 1989a, b; Hauswald, Albrecht, & Wilke, 2008); hydrobiid species with superficially similar shells often have been misidentified as valvatids (Haszprunar, 2014).

Soft-body morphology

The bilobed snout and foot of *Xylodiscula* and the presence of two pedal glands are all typical characters of Ectobranchia. It is doubtful, however, whether the propodial 'auricles' or 'lappets' found in Architectonicoidea (Haszprunar, 1985c, d) are homologous with those of the Ectobranchia. The same is true of the possible homology of the posterior pedal gland of most ectobranchs, which is shared with Orbitestellidae and Architectonicoidea including Omalogyridae.

The array of pedal calcium cells in *Xylodiscula* is the typical condition in gastropods, but contrasts to the compact mass of calcium cells found as an autapomorphy of the Hyalogyrinidae.

In contrast to all other known specimens of *Xylodiscula* (see Table 1), *X. analoga* lacks a second pallial tentacle to the right. Pallial tentacles are typical for all Ectobranchia and occur also in other, only distantly related, basal heterobranchs (e.g. Orbitestellidae, Murchisonellidae and Graphidae).

Mantle cavity

All Ectobranchia studied thus far lack opposing ciliary tracts in the mantle cavity, but generate ventilation currents with the dense ciliation of the gill and of the pallial tentacles. In *X. analoga* we found a ciliated tract within the left mantle roof leading from the osphradium to the posterior end of the pallial cavity. However, there is no opposing tract at the ventral side.

The ectobranch condition of *Xylodiscula* (gill extendable, bipeccinate, alternating lamellae, lack of skeletal rods and bursicles) is diagnostic for all Ectobranchia and is independent of size (shell diameters of Valvatidae range from 1 to 10 mm, i.e. 1:1,000 in volume). Accordingly, the absence of gills in other basal heterobranchs (e.g. Orbitestellidae, Omalogyridae, Rissoellidae, Murchisonellidae and Graphidae) cannot be explained by small size alone [e.g. Scissurellidae (Vetigastropoda); see, e.g. Zelaya & Geiger, 2007]. The thin epithelium and prominent sinuses of the gill suggest significant respiratory function. Also the lack of a pigmented mantle organ is typical for Ectobranchia and is in contrast to most other basal heterobranchs (e.g. Robertson, 1985; Haszprunar, 1985a, 1988; Ponder, 1991; Ponder & Lindberg, 1997).

In contrast to the hot-vent inhabitant *Lurifax vitreus*, where a distinct portion of the posterior mantle epithelium consists of bacteriocytes (Hawe & Haszprunar, 2013), *X. analoga* does not exhibit any trace of bacterial endosymbiosis.

Excretory system

The pallially situated renopericardial complex is typical of all basal heterobranch groups listed above. The thin pallial epithelium of the kidney and efferent sinus and the large sinuses in the nephridial wall suggest a substantial respiratory function in addition to that of the gill. Among the Ectobranchia, nephridial glands have been described only in Hyalogyrinidae and in *Xylodiscula*. As this character is also present in rhipidoglossate and caenogastropod taxa (e.g. Andrews, 1981), this is probably a plesiomorphic condition among Heterobranchia and thus cannot be used to infer close relationships between the two families.

Digestive system

The simple digestive system agrees with those of all other investigated ectobranchs. The folded oral tube suggests expansion during the feeding process. A weak jaw is typical for Ectobranchia, but the characteristics of the oral tube with a dorsal, ciliated tract and a ventral jaw are uncommon.

Typically, the radula formula for Xylodisculidae is 2-1-0-1-2 (Table 1), and the marginal teeth are generally broad and serrate. This "unusual radula type (Marshall, 1988) may give a hint of unusual or specialized feeding biology" (Sasaki et al., 2010: 201). *Xylodiscula analoga* is exceptional among known Xylodisculidae with a radula formula 1-1-0-1-1, but only few species have been investigated thus far (Table 1).

The ectobranch Hyalogyrinidae exhibit a likely plesiomorphic rhipidoglossate radula type such that the various taenioglossate types among the remaining ectobranch families and other heterobranchs appear as derived. However, it is very likely that reduction in the number of marginal teeth occurred several times independently. Among the Ectobranchia, reduction of radular teeth reaches its maximum extent in *X. analoga*. The Murchisonellidae have reduced the radula even further and have retained only two teeth per row, while the radula of Omalogyridae comprises only a single (rachidian) tooth per row.

All basal Heterobranchia have functionally replaced the original odontophoral cartilages by a purely muscular cushion, and only certain pulmonate species have regained cartilages. In *Xylodiscula* the musculature of the buccal apparatus is only weakly developed as described for, e.g. *Valvata relicta* (Rath, 1986)—contrary to the situation found in *Borysthenia naticina*, the Hyalogyrinidae and Cornirostridae.

The salivary glands of *X. analoga* have a unique shape and histology (Fig. 2B). The distal portions of the paired salivary glands appear fused in histological section and the opening to the buccal cavity could not be found.

In contrast to Hyalogyrinidae, Cornirostridae and Valvatidae, the ciliated oesophagus of *Xylodiscula* lacks any glandular modification. Indeed, the condition of the oesophagus differs significantly between the clades of basal Heterobranchia: Ectobranchia and Orbitestellidae possess a ciliated oesophagus with abundant mucous cells, Architectonicoidea possess a cuticularized oesophagus (like Euthyneura) and Murchisonellidae possess a highly glandular oesophagus (B. Brenzinger, pers. comm.).

The presence of a complex stomach with gastric shield and tooth, ciliated areas and a crystalline style is shared with the other ectobranch families. Yet an apparent style sac was not found. Similar conditions are found in the Monoplacophora, Bivalvia (e.g. Salvini-Plawen, 1981) and also in 'archaeogastropods' and caenogastropods (Strong, 2003). Contrary to Ponder & Lindberg (1997: 150), who argued for homoplasy of the crystalline style in caenogastropods and heterobranchs, we consider these conditions to be plesiomorphic for conchiferan Mollusca and thus also for Heterobranchia (Haszprunar, 1988).

The presence of a posterior and an anterior digestive gland with distinct openings into the stomach is identical to the conditions of other ectobranch families and most other basal heterobranch groups except Architectonicidae, where the openings are fused (Haszprunar, 1985c). Similarly, a short intestine is common to all basal Heterobranchia, but differs significantly from the long, coiled intestine of the likewise detritivorous docoglossate or rhipidoglossate taxa.

Genital system

With a few exceptions among the panpulmonate acochliidian slugs, all Heterobranchia are hermaphrodites. However, euthyneurans usually possess truly hermaphroditic gonadal follicles that produce both egg and sperm, whereas most basal heterobranchs (including *Xylodiscula*) possess regionated gonads with outer follicles specialized for spermiogenesis and inner follicles specialized for oogenesis.

Hyalogyrinidae, Cornirostridae and Valvatidae possess a diallic genital system with a separate vas deferens. In contrast, *Xylodiscula* has a monaulic genital system resembling that of the Orbitestellidae. However, as in Architectonicidae and Mathildidae (both with diallic genital systems) there is a separate receptaculum apparatus with a duct opening to the rear mantle roof. The lack of copulatory organs in all Xylodisculidae examined suggests sperm transfer via spermatophores as in the likewise aphyllate Architectonicoidea. There is a great variety of copulatory organs among the remaining ectobranch families, including a pedally-innervated organ in the Orbitestellidae and a cerebrally-innervated one in ectobranchs excluding *Xylodiscula*. Consequently, it is likely that copulatory organs were primitively absent and have arisen repeatedly in the course of heterobranch evolution. It remains somewhat unclear, however, where fertilization in *Xylodiscula* occurs: assuming that the spawn are similar to most heterobranchs, including the aphyllate Architectonicoidea (i.e. eggs connected by chalazae embedded in a gelatinous mass; Robertson, 1974, Haszprunar, 1985a), then fertilization should occur within the female genital tract.

Only Kohnert & Storch (1984) (Valvatidae) and Healy (1990, 1991, 1993, 1995) (Valvatidae, Hyalogyrinidae, Cornirostridae, Orbitestellidae, Architectonicoidea, Murchisonellidae and Rissoellidae) have described spermatogenesis and the fine structure of mature sperm of ectobranchs and other basal heterobranchs. Of note is a description by Healy (1993) of the sperm of "*Hyalogyrina* sp. from the hydrothermal vents off Fiji", which could represent *Xylodiscula major* Warén & Bouchet, 1993 from the same locality. If this is correct, then sperm ultrastructure of *Xylodiscula* compares well with that known of other ectobranchs. We recommend studying sperm structure among basal Heterobranchia as a significant character set for systematics, as it can be reasonably applied also to highly derived taxa such as the shell-less Rhodopemorpha.

Nervous system and sense organs

An epiathroid, streptoneurous nervous system is typical for all ectobranch gastropods. Indeed the nervous system is quite uniform throughout the Ectobranchia and most other basal Heterobranchia (with the euthyneurous Rhodopidae as a notable exception) and only minor differences occur. Variability mainly concerns the position of the cerebropedal nerve ring in relation to the buccal apparatus. However, this may be due to different contraction states in the preserved material studied. The bifid tentacular nerve also is typical for basal heterobranch taxa.

Nerves from the retractor musculature of the proboscis (Architectonicoidea) or buccal apparatus (Valvatidae), and leading towards the stomach alongside the oesophagus, have been described in Valvatidae (e.g. Rath, 1986, 1988; Hawe

et al., 2013) and in Architectonicoidea (Haszprunar, 1985c) but could not be detected in *Xylodiscula*.

Xylodiscula analoga is unique among known xylodisculid species in lacking eyes. The simple osphradium of *X. analoga* resembles that of all other investigated ectobranch gastropods. Exceptions to this morphology among basal Heterobranchia include the radiating, finger-like ridge found in the Architectonicoidea (Haszprunar, 1985b) and the bipectinate osphradium of Mathildidae (Haszprunar, 1985b, d); an osphradium is lacking in Omalogyridae and Rhodopidae.

A statocyst with several statoconia, as found in *Xylodiscula*, is highly unusual, as all other investigated ectobranch species possess statocysts with a single statolith. Statoconia are likewise present in the Architectonicoidea and Mathildidae, whereas Omalogyridae possess statoliths. Since statocyst condition also varies among the Orbitestellidae, this character is likely of low phylogenetic significance.

Systematic considerations

There are several differences between *X. analoga* and other xylodisculids studied thus far, including lack of the second pallial tentacle, lack of the second outer marginal tooth and lack of eyes. However, these differences all represent autapomorphies, which are not informative in assessing affinity. Studies on the anatomy of Xylodisculidae are still in their infancy (see Table 1), and many more species remain to be described. Many more phenotypic (morphological), ecological and genotypic (molecular) characteristics of xylodisculids require analysis before a robust hypothesis on the internal classification of the family can be produced.

The placement of *Xylodiscula* among the Heterobranchia appears well-founded based on several characteristics: shell with a hyperstrophic protoconch, bilobed snout and anterior foot, two pedal glands, pallial kidney, muscular buccal apparatus lacking radular cartilages, large salivary glands with duct, bifid tentacular nerve and spiral sperm lacking dimorphism.

In addition, the placement of *Xylodiscula* among the Ectobranchia, rather than in the Orbitestellidae where it was originally classified (Marshall, 1988), appears well established based on several presumably apomorphic features, including: the presence of a weak (vs. very strong) jaw, lack of a (vs. a pedally innervated) penis, and the presence of a typical ectobranch (vs. lack of a) gill. However, both families share a likely plesiomorphic monaulic genital system. Ectobranchia and Orbitestellidae both have retained a very similar sperm morphology (Healy, 1993) and a digestive system with a ciliated oesophagus and a stomach with gastric shield, crystalline style, and ciliated areas. All these characters are probably plesiomorphic for conchiferan Mollusca and thus of Heterobranchia.

Within the Ectobranchia, *Xylodiscula* can be characterized by several characters (features in bold are currently known only from *X. analoga*; see Table 1):

- (1) A diagnostic and apomorphic, taenioglossate-like radula with the formula 2-1-0-1-2 or 1-1-0-1-1 (*X. analoga*) showing broad marginal teeth with numerous cusps.
- (2) Two pairs (one in *X. analoga*) of pallial tentacles.
- (3) A simple, monaulic genital system with a separate receptaculum apparatus.
- (4) Absence of a copulatory apparatus.
- (5) A dorsal ciliated ridge behind the osphradium (on the left).
- (6) Statocysts with several statoconia.

With the present study, anatomical data are now available for all families currently placed in the Ectobranchia and the (now excluded) Orbitestellidae. A thorough cladistic analysis of these data is beyond the scope of this paper and will be provided elsewhere. However, there is little doubt that only an integrative

approach of morphological and molecular analyses can provide a robust hypothesis on ectobranch and early heterobranch evolution.

ACKNOWLEDGEMENTS

We are deeply indebted to Anders Warén (Swedish Museum of Natural History, Stockholm) for sending us the specimens of *Xylodiscula analoga* and for his helpful comments on the manuscript. We also wish to thank Martin Heß (LMU München) for compiling the interactive pdf figure and Bastian Brenzinger (LMU München and Zoologische Staatssammlung München) for his comments on murchisonellid anatomy. The Bayerische Eliteförderung provided a PhD-fellowship for A. Howe. We want to thank another anonymous reviewer for most helpful comments on the manuscript.

REFERENCES

- ANDREWS, E.B. 1981. Osmoregulation and excretion in prosobranch gastropods part 2: structure in relation to function. *Journal of Molluscan Studies*, **47**: 248–289.
- BÄUMLER, N., HASZPRUNAR, G. & RUTHENSTEINER, B. 2008. 3D interactive microanatomy of *Omalogyra atomus* (Philippi, 1841) (Gastropoda, Heterobranchia, Omalogyridae). *Zoosymposia*, **1**: 101–118.
- BERNARD, F. 1890. Recherches sur *Valvata piscinalis*. *Bulletin Scientifique de la France et de la Belgique*, **22**: 253–361.
- BIELER, R., BALL, A.D. & MIKKELSEN, P.M. 1998. Marine Valvatoidea—comments on anatomy and systematics with description of a new species from Florida (Heterobranchia: Cornirostridae). *Malacologia*, **40**: 305–320.
- BIELER, R. & MIKKELSEN, P.M. 1998. *Ammoniceria* in Florida: notes on the smallest living gastropod in the United States and comments on other species of Omalogyridae (Heterobranchia). *Nautilus*, **111**: 1–12.
- BOGI, C. & BARTOLINI, S. 2008. *Xylodiscula waveni* n. sp., una nuova specie per le coste orientali della Sicilia. *Iberus*, **26**: 43–46.
- BRENZINGER, B., HASZPRUNAR, G. & SCHRÖDL, M. 2013a. At the limits of a successful body plan—3D microanatomy, histology and evolution of *Helminthope* (Mollusca: Heterobranchia: Rhodopemphra), the most worm-like gastropod. *Frontiers in Zoology*, **10**: 1–26.
- BRENZINGER, B., NEUSSER, T.P., JÖRGER, K.M. & SCHRÖDL, M. 2011. Integrating 3D microanatomy and molecules: natural history of the pacific freshwater slug *Strubellia* Odher, 1937 (Heterobranchia: Acochlidia), with description of a new species. *Journal of Molluscan Studies*, **77**: 351–374.
- BRENZINGER, B., WILSON, N.G. & SCHRÖDL, M. 2013b. A glimpse into early heterobranch evolution—microanatomy of Murchisonellidae. In: *Abstracts of the 18th WCM, Ponta Delgada, Azores* (A.M. de Frias Martins, A.C. Costa, R.T. da Cunha, S. Avila, S.C. Monteiro & P. Raposeiro, eds). *Açoreana Suplemento*, **8**: 180–181.
- BUSH, K.J. 1897. Revision of the marine gastropods referred to *Cyclostrema*, *Adeorbis*, *Vitrinella* and related genera; with descriptions of some new genera and species belonging to the Atlantic fauna of America. *Transactions of the Connecticut Academy of Science*, **10**: 97–144.
- CLELAND, D.M. 1954. A study of the habits of *Valvata piscinalis* (Müller) and the structure and function of the alimentary canal and reproductive system. *Journal of Molluscan Studies*, **30**: 167–203.
- DINAPOLI, A. & KLUSMANN-KOLB, A. 2010. The long way to diversity—phylogeny and evolution of the Heterobranchia (Mollusca: Gastropoda). *Molecular Phylogenetics and Evolution*, **55**: 60–76.
- DINAPOLI, A., ZINSSMEISTER, C. & KLUSMANN-KOLB, A. 2011. New insights into the phylogeny of the Pyramidellidae (Gastropoda). *Journal of Molluscan Studies*, **77**: 1–7.
- DISTEL, A.L., BACO, A.R., CHUANG, E., MORRILL, W., CAVANAUGH, C. & SMITH, C.R. 2000. Do mussels take wooden steps to deep-sea vents? *Nature*, **403**: 725–726.
- FALNIOWSKI, A. 1989a. Przodoskrzelne (Prosobranchia, Gastropoda, Mollusca) Polski I: Neritidae, Viviparidae, Valvatidae, Bithyniidae, Rissoidae, Aciculidae. *Zeszyty naukowe Uniwersytetu Jagiellońskiego CMX. Prace Zoologiczne*, **35**: 1–148.
- FALNIOWSKI, A. 1989b. A critical review of some characters widely used in the systematics of higher taxa of freshwater prosobranchs (Gastropoda: Prosobranchia), and a proposal of some new, ultrastructural ones. *Folia Malacologica*, **3**: 73–93.
- FAVRE, J. 1927. Les mollusques post-glaciaires et actuels du bassin de Genève. *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève*, **40**: 171–434.
- FAVRE, J. 1935. Études sur la partie occidentale du Lac de Genève II. Histoire malacologiques du Lac de Genève. *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève*, **41**: 295–414.
- FRETTER, V. 1948. The structure and life history of some minute prosobranchs of rock pools: *Skeneopsis planorbis* (Fabricius), *Omalogyra atomus* (Philippi), *Rissoella diaphana* (Alder) and *Rissoella opalina* (Jeffreys). *Journal of the Marine Biological Association of the United Kingdom*, **27**: 597–632.
- GRAY, J.E. 1840. *Synopsis of the contents of the British Museum, Edn 42*. British Museum, London.
- HAAS, F. 1938. Über potenzielle Skulpturbildung bei *Valvata* (*Cincinna*) *piscinalis antiqua* (Sow.). *Archiv für Molluskenkunde*, **70**: 41–45.
- HASZPRUNAR, G. 1985a. The Heterobranchia—a new concept of the phylogeny of the higher Gastropoda. *Journal of Zoological Systematics and Evolutionary Research*, **23**: 15–37.
- HASZPRUNAR, G. 1985b. The fine morphology of the osphradial sense organs of the Mollusca. II. Allogastropoda (Architectonicidae, Pyramidellidae). *Philosophical Transaction of the Royal Society of London Series B*, **307**: 497–505, 1 pl.
- HASZPRUNAR, G. 1985c. Zur Anatomie und systematischen Stellung der Architectonicidae (Mollusca, Allogastropoda). *Zoologica Scripta*, **14**: 25–43.
- HASZPRUNAR, G. 1985d. On the anatomy and systematic position of the Mathildidae (Mollusca, Allogastropoda). *Zoologica Scripta*, **14**: 201–213.
- HASZPRUNAR, G. 1988. On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. *Journal of Molluscan Studies*, **54**: 367–441.
- HASZPRUNAR, G. 2014. A nomenclator on extant and fossil taxa of the Valvatidae (Gastropoda: Ectobranchia). *ZooKeys*, **377**: 1–172.
- HASZPRUNAR, G., SPEIMANN, E., HAWE, A. & HEB, M. 2011. Interactive 3D anatomy and affinities of the Hyalogyrinidae, basal Heterobranchia (Gastropoda) with a rhipidoglossate radula. *Organisms, Diversity & Evolution*, **11**: 201–236.
- HAUSWALD, A.-K., ALBRECHT, C. & WILKE, T. 2008. Testing two contrasting evolutionary patterns in ancient lakes: species flock versus species scatter in valvatid gastropods of Lake Ohrid. *Hydrobiologia*, **615**: 169–179.
- HAWE, A., GENSLER, H. & HASZPRUNAR, G. 2014. True bacteriocytes in the mantle cavity of *Lurifax vitreus* Warén & Bouchet, 2001 (Orbitestellidae), the first case among heterobranch Gastropoda. *Journal of Molluscan Studies*, **80**: 337–340.
- HAWE, A. & HASZPRUNAR, G. 2013. 3D-microanatomy and histology of the hydrothermal vent gastropod *Lurifax vitreus* Warén & Bouchet, 2001 (Heterobranchia: Orbitestellidae) and comparisons with Ectobranchia. *Organisms, Diversity and Evolution*, **14**: 43–55.
- HAWE, A., HEB, M. & HASZPRUNAR, G. 2013. 3D-reconstruction of the anatomy of the ovoviviparous (?) freshwater gastropod *Borysthenia naticina* (Menke, 1845) (Ectobranchia: Valvatidae). *Journal of Molluscan Studies*, **79**: 191–204.
- HEALY, J.M. 1990. Spermatozoa and spermiogenesis of *Cornirostra*, *Valvata* and *Orbitestella* (Gastropoda: Heterobranchia) with a discussion of valvatoidean sperm morphology. *Journal of Molluscan Studies*, **56**: 557–566.
- HEALY, J.M. 1991. Sperm morphology in the marine gastropod *Architectonica perspectiva* (Mollusca): unique features and systematic relevance. *Marine Biology*, **109**: 59–65.
- HEALY, J.M. 1993. Comparative sperm ultrastructure and spermiogenesis in basal heterobranch gastropods (Valvatoidea,

- Architectonicoidea, Rissoelloidea, Omalogyroidea, Pyramidelloidea) (Mollusca). *Zoologica Scripta*, **22**: 263–276.
- HEALY, J.M. 1995. Sperm and spermiogenetic ultrastructure in the Mathildidae with a review of sperm morphology and its systematic importance in the Architectonicoidea (Gastropoda). *Journal of Molluscan Studies*, **61**: 361–373.
- HOISAETER, T. & JOHANNESSEN, P.J. 2001. *Xylodiscula planata* sp. nov., a “lower” heterobranch gastropod from Norwegian waters. *Sarsia*, **86**: 325–332.
- JÖRGER, K., STÖGER, I., KANO, Y., FUKUDA, H., KNEBELSBERGER, T. & SCHRÖDL, M. 2010. On the origin of Acochlidia and other enigmatic euthyneuran gastropods, with implications for the systematics of Heterobranchia. *BMC Evolutionary Biology*, **10**: 1–20.
- KIEL, S. 2004. Shell structures of selected gastropods from hydrothermal vents and seeps. *Malacologia*, **46**: 169–183.
- KIEL, S. & GOEDERT, J.L. 2006. Deep-sea food bonanzas: early Cenozoic whale-fall communities resemble wood-fall rather than seep communities. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **273**: 2625–2631.
- KIEL, S. & GOEDERT, J.L. 2007. New mollusks associated with biogenic substrates in Cenozoic deep-water sediments of Washington State. *Acta Palaeontologica Polonica*, **52**: 41–52.
- KOHNERT, R. & STORCH, V. 1984. Vergleichend-ultrastrukturelle Untersuchungen zur Morphologie eupyrener Spermien der Monotocardia (Prosobranchia). *Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere*, **111**: 51–93.
- LASERON, C.F. 1954. Revision of the Liotiidae of New South Wales. *Australian Zoologist*, **12**: 1–25.
- MARSHALL, B.A. 1988. Skeneidae, Vitrinellidae and Orbitestellidae (Mollusca, Gastropoda) associated with biogenic substrata from bathyal depths off New Zealand and New South Wales. *Journal of Natural History*, **22**: 969–1004.
- MARSHALL, B.A. 1994. Deep-sea gastropods from the New Zealand region associated with recent whale bones and an Eocene turtle. *Nautilus*, **108**: 1–8.
- PILSBRY, H.A. & OLSSON, A.A. 1952. Vitrinellidae of the Panamic Province: II. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **104**: 35–88.
- PONDER, W.F. 1990a. The anatomy and relationships of the Orbitestellidae (Gastropoda: Heterobranchia). *Journal of Molluscan Studies*, **56**: 515–532.
- PONDER, W.F. 1990b. The anatomy and relationships of a marine valvatoidean (Gastropoda: Heterobranchia). *Journal of Molluscan Studies*, **56**: 533–555.
- PONDER, W.F. 1991. Marine valvatoidean gastropods—implications for early heterobranch phylogeny. *Journal of Molluscan Studies*, **57**: 21–32.
- PONDER, W.F. & LINDBERG, D.R. 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean Society*, **119**: 83–265.
- RATH, E. 1986. *Beiträge zur Anatomie und Ontogenie der Valvatidae (Mollusca: Gastropoda)*. PhD thesis, Faculty of Biology, University of Vienna, Vienna.
- RATH, E. 1988. Organization and systematic position of the Valvatidae. *Malacological Review, Supplement*, **4**: 194–204.
- ROBERTSON, R. 1974. The biology of the Architectonicidae, gastropods combining prosobranch and opisthobranch traits. *Malacologia*, **14**: 215–220.
- ROBERTSON, R. 1985. Four characters and the higher category systematics of gastropods. *American Malacological Bulletin*, **1**: 1–12.
- SALVINI-PLAWEN, L.V. 1981. The molluscan digestive system in evolution. *Malacologia*, **21**: 371–401.
- SASAKI, T., WARÉN, A., KANO, Y., OKUTANI, T. & FUJIKURA, K. 2010. Gastropods from recent hot vents and cold seeps: systematics, diversity and life strategies. In: *The vent and seep biota* (S. Kiel, ed.). *Topics in Geobiology*, **33**: 169–254.
- SIMONE, L.R.L. 1995. *Rissoella ornata*, a new species of Rissoellidae (Mollusca: Gastropoda: Rissoelloidea) from the southeastern coast of Brazil. *Proceedings of the Biological Society of Washington*, **108**: 560–567.
- SIMONE, L.R.L. & ZELAYA, D.G. 2004. A new *Orbitestella* (Gastropoda: Heterobranchia: Orbitestellidae) from Tierra del Fuego, Argentina. *Nautilus*, **118**: 160–166.
- STRONG, E.E. 2003. Refining molluscan characters: morphology, character coding and a phylogeny of the Caenogastropoda. *Zoological Journal of the Linnean Society*, **137**: 447–554.
- WARÉN, A. 1991. New and little known Mollusca from Iceland and Scandinavia. *Sarsia*, **76**: 53–124.
- WARÉN, A. 1992. New and little known “skeneiomorph” gastropods from the Mediterranean Sea and the adjacent Atlantic Ocean. *Bollettino di Malacologico*, **27**: 149–248.
- WARÉN, A. 2013. Murchisonellidae: who they are, where are they and what are they doing? (Gastropoda, lowermost Heterobranchia). *Vita Malacologica*, **11**: 1–14.
- WARÉN, A. & BOUCHET, P. 1993. New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. *Zoologica Scripta*, **22**: 1–90.
- WARÉN, A. & BOUCHET, P. 2001. Gastropoda and Monoplacophora from hydrothermal vents and seeps; new taxa and records. *Zoologica Scripta*, **44**: 116–231.
- WARÉN, A., GOFAS, S. & SCHANDER, C. 1993. Systematic position of three European heterobranch gastropods. *Veliger*, **36**: 1–15.
- WISE, J.B. 1998. Morphology and systematic position of *Rissoella caribaea* Rehder, 1943 (Gastropoda: Heterobranchia: Rissoellidae). *Nautilus*, **111**: 13–21.
- ZELAYA, D.G. & GEIGER, D.L. 2007. Species of Scissurellidae and Anatomidae from sub-Antarctic and Antarctic waters (Gastropoda: Vetigastropoda). *Malacologia*, **49**: 393–443.