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

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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: Corniostriidae Ponder, 1990, Xylodisculidae Warén, 1992 and Hyalogyriniidae 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; Corniostriidae: Ponder, 1990b; Bieler, Ball, & Mikkelsen, 1998; Hyalogyriniidae: 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 Hyalogyriniidae 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 Orbitellidae, a heterobranch family now considered only distantly related to the Ectobranchia (Hawe et al., 2014). Later, Warén (1992) removed Xylodiscula from the (gill-less) Orbitellidae, 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. Hoisæter & 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 biliputia Laseron, 1954 and Vitrinorbis calistus Pilbry & 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://sealugsofhawaii.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, Hoisæter & Johannessen (2001: 332) argued in support of this family as an example of the ‘stepping-stone’ hypothesis (e.g. Disel 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 orbitellid 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; Hoisæter & 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Protoconch</th>
<th>Teleoconch</th>
<th>Shell shape</th>
<th>Operculum</th>
<th>Radula</th>
<th>Soft parts</th>
<th>Eyes</th>
<th>References/first description</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Size (µm)</td>
<td>Hetero-strophy</td>
<td>Size (mm)</td>
<td>Height-width ratio</td>
<td>No. of whorls</td>
<td>Formula</td>
<td>Anatomy</td>
<td>no</td>
</tr>
<tr>
<td><em>X. analoga</em></td>
<td>?</td>
<td>?</td>
<td>3.00</td>
<td>0.500</td>
<td>Multispiral</td>
<td>1-1-0-1-1</td>
<td>Anatomy and histology</td>
<td>Warén &amp; Bouchet (2001), herein</td>
</tr>
<tr>
<td><em>X. boucheti</em></td>
<td>255 µm</td>
<td>Yes</td>
<td>1.72</td>
<td>0.436</td>
<td>?</td>
<td>2-1-0-1-2</td>
<td>Short description</td>
<td>yes</td>
</tr>
<tr>
<td><em>X. lens</em></td>
<td>215 µm</td>
<td>Yes</td>
<td>1.74</td>
<td>0.353</td>
<td>?</td>
<td>?</td>
<td>Short description</td>
<td>yes</td>
</tr>
<tr>
<td><em>X. major</em></td>
<td>275 µm</td>
<td>Yes</td>
<td>3.88</td>
<td>0.384</td>
<td>Multispiral</td>
<td>2-1-0-1-2</td>
<td>–</td>
<td>?</td>
</tr>
<tr>
<td><em>X. osteophila</em></td>
<td>270 µm</td>
<td>No</td>
<td>1.60</td>
<td>0.668</td>
<td>Multispiral</td>
<td>2-1-0-1-2</td>
<td>–</td>
<td>?</td>
</tr>
<tr>
<td><em>X. planata</em></td>
<td>?</td>
<td>No</td>
<td>1.70</td>
<td>0.441</td>
<td>6</td>
<td>2-1-0-1-2</td>
<td>+</td>
<td>yes</td>
</tr>
<tr>
<td><em>X. vitrea</em></td>
<td>270 µm</td>
<td>No</td>
<td>1.75</td>
<td>0.400</td>
<td>?</td>
<td>2-1-0-1-2</td>
<td>Short description</td>
<td>?</td>
</tr>
</tbody>
</table>

Table 2. Ecology of *Xylodiscula* species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Locality</th>
<th>Depth</th>
<th>Habitat</th>
<th>References/first description</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>X. analoga</em></td>
<td>Mid-Atlantic Ridge, Menez Gwen and Lucky Strike</td>
<td>850–1728 m</td>
<td>Hydrothermal vent</td>
<td>Warén &amp; Bouchet (2001), herein</td>
</tr>
<tr>
<td><em>X. boucheti</em></td>
<td>Corsica and Tuscan Sea, Mediterranean Sea</td>
<td>90–400 m</td>
<td><em>Posidonia</em> detritus and an amphora</td>
<td>Warén (1992)</td>
</tr>
<tr>
<td><em>X. lens</em></td>
<td>Corsica and Tuscan Sea, Mediterranean Sea</td>
<td>90–400 m</td>
<td><em>Posidonia</em> detritus and sunken driftwood</td>
<td>Warén (1992)</td>
</tr>
<tr>
<td><em>X. major</em></td>
<td>North Fiji Basin, Pacific Ocean</td>
<td>2000 m</td>
<td>hydrothermal vent “La Dame Blanche”</td>
<td>Warén &amp; Bouchet (1993)</td>
</tr>
<tr>
<td><em>X. osteophila</em></td>
<td>Off Mernoo Bank, Chatham Rise, New Zealand</td>
<td>ca. 900 m</td>
<td>Decaying whale bone</td>
<td>Marshall (1994)</td>
</tr>
<tr>
<td><em>X. planata</em></td>
<td>Western Norway</td>
<td>34–56 m</td>
<td>Associated with surplus fish feed</td>
<td>Høisæter &amp; Johannessen (2001)</td>
</tr>
</tbody>
</table>
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* Wareń & Bouchét (2001: 208, figs 44b-d, 47c, 49h) were kindly provided by Dr Anders Wareń 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 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; CPL, 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 prelab views and to change surface visualization (e.g. lighting, render mode, crop, etc.).
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 cerebropleural nerve ring is epiathroid. The cerebropleural ganglia (Fig. 1E–G: CP) 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 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.
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 statocystonia (Fig. 5B).

**DISCUSSION**

**General remarks**

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

10. Anatomy of Tjaernoidae, and Graphidae is nearly unknown (Warén 1991, 2013), and the shell-less Rhodopidae (see...
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 xylodisciulids 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. Jörg er 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* Ware`n & 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* Ware`n & 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. librae Marshall, 1988 (cf. Marshall, 1998, Höisæter & Johannessen, 2001). This is contrary to the situation found in the type species, X. vitrea Marshall, 1998, where a clearly hyperstrophic protoconch suggests planktotrophic development. The latter conforms to the heterobranch affinities of Xylodiscus.

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; Falniowski, 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 Xylodiscus and the presence of two pedal glands are all typical characteristics of Ectobranchia. It is doubtful, however, whether the propodial ‘auricles’ or ‘lappets’ found in Architetctonicoidea (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 Orbitellidae and Architetctonicoidea including Omalogyridae.

The array of pedal calcium cells in Xylodiscus 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 Xylodiscus (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. Orbitellidae, 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 oesophagus to the posterior end of the pallial cavity. However, there is no opposing tract at the ventral side.

The ectobranch condition of Xylodiscus (gill extendable, bipedate, 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. Orbitellidae, Omalogyridae, Risselididae, 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 Lirijax vitreus, where a distinct portion of the posterior mantle epithelium consists of bacterioocytes (Hawe & Haszprunar, 2013), X. analoga does not exhibit any trace of bacterial endosymbiosis.

Excretory system

The pallialy 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 Xylodiscus. As this character is also present in rhipidoglossate and caenogastropod taxa (e.g. Andrews, 1981), this is probably a pleisiomorphic 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 Xylodiscusidae 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). Xylodiscus analoga is exceptional among known Xylodiscusidae with a radula formula 1-0-1-1, but only few species have been investigated thus far (Table 1).

The ectobranch Hyalogyrinidae exhibit a likely pleisiomorphic 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 Xylodiscus the musculature of the buccal apparatus is only weakly developed as described for, e.g. Valvata rictula (Rath, 1986)—contrary to the situation found in Boryxinia naticea, 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 Xylodiscus lacks any glandular modification. Indeed, the condition of the oesophagus differs significantly between the clades of basal Heterobranchia: Ectobranchia and Orbitellidae possess a ciliated oesophagus with abundant mucous cells, Architetctonicoidea 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 homoplasny of the crystalline style in caenogastropods and heterobranchs, we consider these conditions to be pleisiomorphic 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 Architectonicoidea, 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 rhigidoglossate taxa.

Genital system
With a few exceptions among the panpulmonate acoelidlian slugs, all Heterobranchia are hermaphroditic. However, eutheuryneans usually possess truly hermaphroditic gonadal follicles that produce both egg and sperm, whereas most basal heterobranchs (including Xylodiscus) possess regionated gonads with outer follicles specialized for spermogonesis and inner follicles specialized for oogenesis.

Hyalogyridae, Cornirostridae and Valvatidae possess a diaulic genital system with a separate vas deferens. In contrast, Xylodiscus has a monaulic genital system resembling that of the Orbitestellidae. However, as in Architectonicoidea and Mathildidae (both with diaulic genital systems) there is a separate receptacular apparatus with a duct opening to the rear mantle roof. The lack of copulatory organs in all Xylodiscus examined suggests sperm transfer via spermatozoids 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 cerebral-innervated one in ectobranchs excluding Xylodiscus. 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 Xylodiscus 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), this hypothesis should occur within the female genital tract.

Only Kohnert & Storch (1984) (Valvatidae) and Healy (1990, 1991, 1993, 1995) (Valvatidae, Hyalogyridae, Cornirostridae, Orbitestellidae, Architectonicoidea, Murchisonellidae and Rissoellidae) have described spermatozoa and the fine structure of mature sperm of ectobranchs. All other basal heterobranchs. Of note is a description by Healy (1993) of the sperm of “Halyomyrna sp. from the hydrothermal vents off Fiji”, which could represent Xylodiscus major Warén & Bouchet, 1993 from the same locality. If this is correct, then sperm ultrastructure of Xylodiscus 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, streptomereous 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 eutheuryneous 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 Xylodiscus.

Xylodiscus analoga is unique among known xylodisculid species in lacking eyes. The simple ophthalm 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 ophthalm of Mathildidae (Haszprunar, 1985b, d); an ophthalm is lacking in Omalogyridae and Rhodopidae.

A statocyst with several statoconia, as found in Xylodiscus, 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 Xylodiscus 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 Xylodiscus 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 pleiomorphic 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 pleiomorphic for conchiferan Mollusca and thus of Heterobranchia.

Within the Ectobranchia, Xylodiscus 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 radiula 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.
5. A dorsal ciliated ridge behind the ophthalm (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.

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