Zoosymposia 1: 101–118 (2008)
www.mapress.com/zoosymposia/

ISSN 1178-9905 (print edition)
ZOOSYMPOSIA
ISSN 1178-9913 (online edition)

3D interactive microanatomy of *Omalogyra atomus* (Philippi, 1841) (Gastropoda, Heterobranchia, Omalogyridae)

NATALIE BAEUMLER[1], GERHARD HASZPRUNAR[1] & BERNHARD RUTHENSTEINER[1,2]
[1] *Zoologische Staatssammlung München, Münchhausenstrasse 21, D-81247 Munich, Germany*
Email: natalie.baeumler@t-online.de, haszi@zsm.mwn.de, BRuthensteiner@zsm.mwn.de
[2] *Corresponding author*

Abstract

Omalogyridae are minute gastropods with a shell diameter usually less than one millimeter and have a worldwide distribution. A reinvestigation of the type species, *Omalogyra atomus* (Philippi, 1841), should help to unravel the systematic affinities of this family. Furthermore, direct comparisons of previous and the present results enable the evaluation of the advantages of the innovative methods applied—"semithin" serial sectioning and computer-aided 3D reconstruction. Our data provide substantial new information and show that the resolution of methods used for previous studies was insufficient. The methods applied herein provide more detailed and accurate results and in combination with interactive 3D illustrations in the electronic publication version offer many novel options for exploration of the results by the reader.

The highly glandular nature of the foot and the mantle cavity, the complete lack of a gill being functionally replaced by prominent, dorsal and ventral ciliary tracts on the right side of the mantle cavity, the relative simplicity of the gut and the high complexity of the hermaphroditic reproductive system adapted for internal fertilization but lacking a copulatory verge are the most outstanding features of the snail's anatomy.

Most characteristics reflect affinities with basal heterobranchs, such as Rissoellidae and Pyramidellidae, of *O. atomus* and thus of Omalogyridae, while a closer relationship with Architectonicoidea appears less likely. Only a few features, *e.g.*, the lack of any respiratory structure, can be ascribed functionally to the extreme smallness of the animals. Some characters, such as the modification of the cephalic tentacles into small lobes, remain to be understood.

Key words: *Omalogyra*, 3D interactive microanatomy, phylogeny

Introduction

Omalogyridae G.O. Sars, 1878 represent a poorly known family of extremely minute, marine snails, their most characteristic feature being the more or less planispiral shell with a diameter usually less than one millimeter. Traditionally the family was placed within the "rissoacean prosobranchs" (*e.g.*, Thiele 1931; Ankel 1936; Fretter & Graham 1978), but already Fretter (1948) noted the "opisthobranch" (*i.e.*, heterobranch) affinities. Currently the omalogyrids are considered basal members of the heterobranch gastropods (*e.g.*, Haszprunar 1985a, 1988; Ponder 1991; Bieler 1992; Ponder & Lindberg 1997; Kurabayashi & Ueshima 2000). However, their exact systematic affinities, in particular the supposed closer relationship to the Architectonicoidea (Haszprunar 1985a, b, 1988; Bieler 1988; Healy 1988), are still unclear. At present three genera, *Omalogyra* Jeffreys, 1859, *Ammonicera* Vayssière, 1893 and *Retrotortina* Chaster, 1896, comprise the family (Bieler & Mikkelsen 1998). In recent

Accepted by D.L. Geiger: 1 May 2008; published 25 Jul. 2008

times, several new omalogyrid species were described from all over the world (Sleurs 1984, 1985a,b; Palazzi 1988, 1992; Castellanos 1989; Rolán 1991, 1992; Simone 1997, 1998; Bieler & Mikkelsen 1998; Chernyshev 2003) demonstrating the increasing interest in these tiny gastropods.

The best known and the type species of Omalogyridae, *Omalogyra atomus* (Philippi, 1841), is said to have a wide distributional range. It is the only species so far reported from both sides of the Atlantic Ocean, with findings on the western coast from Maine to Rhode Island and on the eastern coast from Norway, Iceland, Greenland, Great Britain, Madeira, the Azores and the Cape Verde Archipelago, the whole Mediterranean and also the Pacific Ocean (*e.g.*, Ankel 1936; Fretter & Graham 1978; Bieler & Mikkelsen 1998; Hasegawa 2000). However, the assumed conspecifity with the Antarctic *Omalogyra atomus burdwoodianus* Strebel, 1908 (see Egorova 1991), for instance, requires confirmation by detailed anatomical or molecular studies. The animals often are abundant in intertidal rock pools and shallow water, near-shore habitats to a depth of 20 m, where they feed on algae such as *Ulva* sp. and *Enteromorpha* sp. (Fretter 1948; Fretter & Graham 1978). Originally described as *Truncatella atomus* by Philippi (1841) from Sorrent (Italy) our knowledge of this species has increased due to an account of the gross morphology and the radula by Sars (1878), information on the central nervous system by Huber (1993), a transmission electron microscopic (TEM) analysis of the spermatozoa by Healy (1993) and a scanning electron microscopic analysis (SEM) of the radula by Gofas and Warén (1998). Even molecular data such as the partial mitochondrial genome (Kurabayashi & Ueshima 2000) are available. But no investigation has promoted our knowledge of this species like the detailed anatomical study of Fretter (1948), up to now the sole study on soft part anatomy of the whole family. Although information on the methods applied in Fretter's study (1948) is missing, it seems likely because of the small size of the animals that this examination was carried out by paraffin sectioning, the method available at that time. The current study thus provides the opportunity for a direct methodological evaluation. We applied "semithin" sectioning and computer based 3D reconstruction (see Ruthensteiner 2008), enabling a more detailed examination and offering many visualization options.

The taxonomy of the genus *Omalogyra* as well as the synonymy of *O. atomus* has been treated in detail elsewhere (Bieler & Mikkelsen 1998).

Material and methods

Specimens of *Omalogyra atomus* were collected in northern Sardinia (Italy), in the west of the Isola Gabbiani peninsula (shallow water habitats) in early April 2007, the Station Biologique de Roscoff (France) (intertidal rock pools off the station (Fig. 1A,B) and from a bay somewhat south of the station) in June 2007 and the Observatoire Océanologique de Villefranche sur Mer (France) (tidal pool off the station) in June 1983.

After anaesthetization with magnesium chloride, specimens were fixed like for TEM [specimens from Sardinia and Roscoff, see protocols for TEM fixation for marine invertebrates, decalcification with ascorbic acid and embedding in Spurr's resin in Ruthensteiner (2008)], in ethanol [specimens from Sardinia (80%) and Roscoff (100%)] and Bouin's fixative fluid (specimen from Villefranche). The latter specimen was embedded in an epon-araldite mixture (Mollenhauer 1964).

Six specimens were serially sectioned with a thickness of either 1.5 µm (four specimens, from Sardinia and Villefranche) or 0.75 µm (two specimens, from Sardinia), stained with methylene blue-azur II (see Ruthensteiner 2008) and used for examination. For reconstruction, section series of two specimens—an adult one (1.5 µm thickness, Villefranche) and a juvenile one (0.75 µm thickness, Sardinia)—were selected. After taking digital images of every section, specimens were further 3D-processed with the software package *AMIRA* (versions 3.1.1 and 4.1.1, TGS Europe, S.A., Merignac Cedex, France, Mercury Computer Systems Inc., Chelmsford, MA USA) as described by Ruthensteiner (2008). Preparation of 3D models for embedding in the electronic (pdf) version was done as given by Ruthensteiner & Heß (in press).

For SEM of the shell, specimens (seven from Roscoff) stored in 100% ethanol were air-dried. For soft part SEM preparation, whole specimens (six from Roscoff) fixed in 1.5% glutaraldehyde were decalcified in 1% ascorbic acid, dehydrated in an acetone series and subjected to critical point drying. For radula SEM preparation, specimens (in total 15 from Roscoff and Sardinia) were immersed for about five to ten minutes in Bouin's fixative fluid for shell removal and macerated for about one to two minutes in a 1:1 mixture of the cleansing agent DanKlorix (Colgate-Palmolive GmbH, Hamburg) and distilled water while maceration progress was watched under the microscope. When tissue started to clarify, the remaining specimens—held together by the periostracum—were transferred to a drop of distilled water on a cover-slip (Geiger *et al.* 2007) and the radula removed from the residual tissue by means of needles. Then the radula was rinsed in distilled water and air-dried. Shells, soft part specimens and cover-slips with radulae, were mounted on SEM stubs and sputter coated with gold. Investigations were performed with a LEO 1430 VP scanning electron microscope.

Results

Shell and operculum. With a diameter of up to 0.4 mm, the examined specimens of *Omalogyra atomus* were very small. The shell surface is smooth and reddish brown, also fairly transparent so that some internal organs can be seen shining through. It is planispirally coiled (Fig. 2A,B) with up to three rounded whorls. The diameter of the coils is increasing constantly from the protoconch towards the aperture. A distinct suture marks the border between protoconch and adult shell. The protoconch is smooth, whereas the teleoconch is smooth except for thin, delicate, irregular striae representing growth lines. The shell aperture is nearly circular except for the side in contact with the previous whorl, which is flattened.

The operculum (Fig. 2C,D) is flat, circular, perfectly fitting the shell's opening and paucispiral with the nucleus located at its posterior half. Where the operculum is attached to the foot, its external side is smooth, whereas the rest shows thin, curved lines radiating to its edge.

Figure 1. A, B. Typical habitats of *Omalogyra atomus*—near the Station Biologique de Roscoff, France. **A.** Intertidal area. **B.** Detail of rock pool with typical algal contents. **C.** Living specimen of *Omalogyra atomus*.

External morphology and live observations. In living specimens, when creeping rapidly over the substratum, the shell is held uprightly above the uniformly yellowish-whitish head and foot (Fig. 1C). The broad, flexible head bears no tentacles. They are functionally replaced by a pair of characteristic, flat, semicircular head lobes (Figs 1C, 2C, 4A, 5A: hl), which are very agile in life. When creeping they are swayed in all directions, probably sensing the environment. The lobes bear solitary tufts of stiff cilia along their edges. At the base of the head lobes a pair of big, black eyes (Fig. 1C) can be

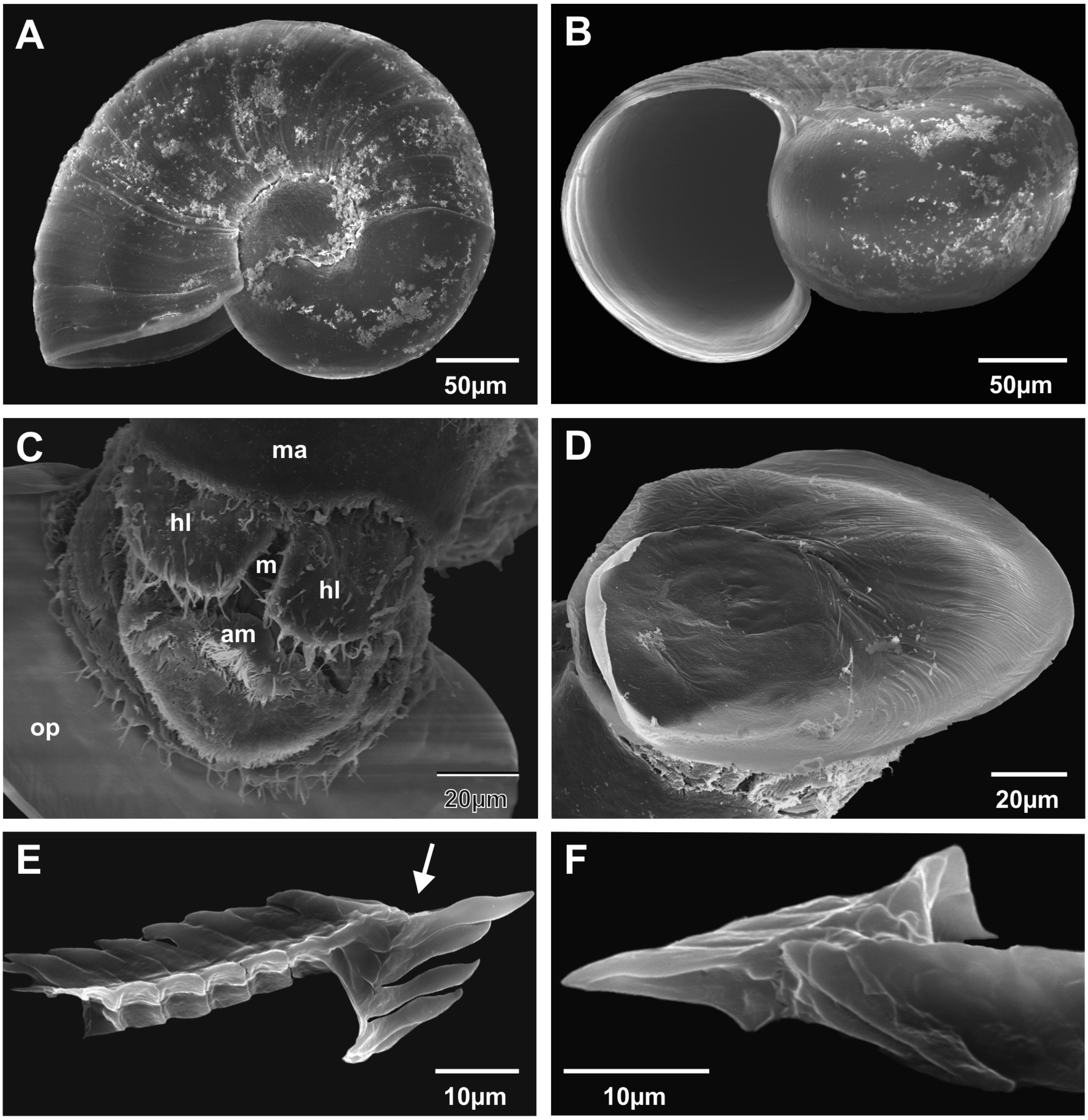


Figure 2. *Omalogyra atomus*. SEM. **A.** Shell with protoconch, left side view (specimen from Roscoff). **B.** Shell, apertural view. **C.** Head-foot region from anterior (shell removed) (specimen from Roscoff). **D.** Operculum attached to soft parts, external view obliquely from the left (specimen from Roscoff). **E.** Radula, laterally right view (specimen from Sardinia). **F.** Bent portion (arrow) enlarged and viewed from a different angle in. am, median ciliated depression; hl, head lobe; m, mouth; ma, mantle; op, operculum.

observed. When disturbed, the animals retract far back into their shell. By this the posterior half of the foot is tucked in at 180 degrees, thus bringing the operculum tightly attached to the upper posterior foot in the right position to block the aperture.

The foot is relatively short and rarely protrudes underneath the head lobes anteriorly and beyond the posterior end of the shell. It has an even width along its entire length and anteriorly as well as posteriorly it is rounded. The creeping sole and the upper side of the anterior foot are covered with a dense layer of cilia and single tufts of cilia are found along the rim of the posterior foot.

The mantle cavity (Fig. 3: mc) is very deep and distinctly elongate. It extends from the base of the head lobes to the most dorsal expansion of the last whorl. In the area of the nervous system it shows a constriction from the right side. Posterior to this it widens ventrally forming a wedge jammed between the buccal apparatus on the left and the capsule gland of the genital system on the right. Dorsally the mantle cavity is compressed by two mantle glands and the renopericardial system. In the middle of the mantle cavity the anus is located. From the latter, two ciliary strips run anteriorly. The dorsal strip continues to the opening of the mantle cavity, while the ventral one ends in the area of the central nervous system. The dorsal strip and posterior portion of the ventral one lie on the right side of

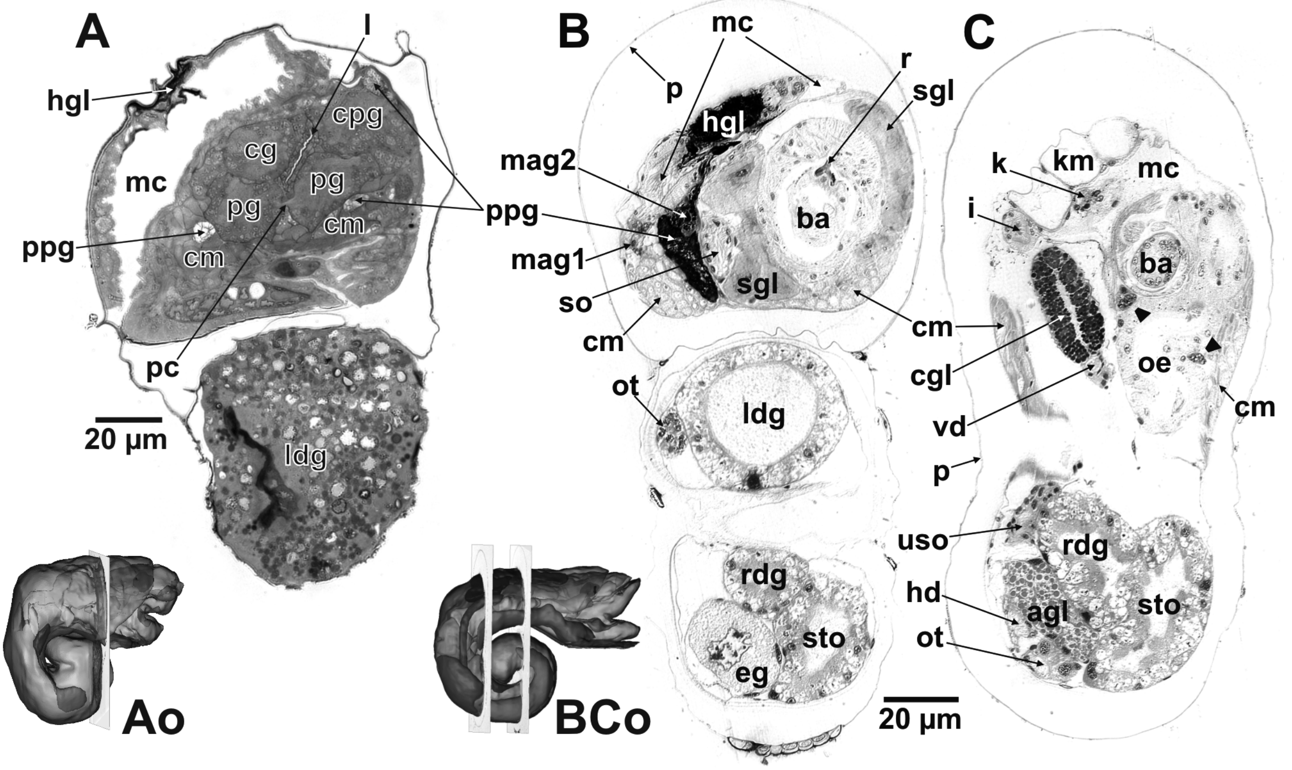


Figure 3. *Omalogyra atomus*. Histological sections. **A.** Juvenile specimen (same as Figure 5). **B–C.** Adult specimen (same as Figure 4). Ao, BCo. Section planes in respective specimens. Arrow heads in C. point towards the paired elliptic-shaped structure. agl, albumen gland; ba, buccal apparatus; cg, cerebral ganglion (right side); cgl, capsule gland; cm, columellar muscle; cpg, cerebropleural ganglion (left side); eg, egg in ovotestis; hd, hermaphrodite duct; hgl, hypobranchial gland; i, intestine; k, kidney; km, mantle gland; l, lumen of oral duct; ldg, left digestive gland; mag 1,2, mantle glands 1,2; mc, mantle cavity; oe, oesophagus; ot, ovotestis (in B. testis portion, in C. ovary portion with small eggs); p, periostracum; pc, pedal commissure; pg, pedal ganglion; ppg, posterior pedal gland; r, radula; rdg, right digestive gland; sgl, salivary gland; so, spermoviduct; sto, stomach; uso, upper spermoviduct; vd, vas deferens.

the mantle cavity. Anteriorly the ventral strip runs approximately in the middle of the mantle cavity. As already noted by Fretter (1948), these ciliary bands probably are responsible for the evacuation of the faeces. They also ventilate the mantle cavity, necessary for respiration, since no trace of a gill could be found. Posterior to the anus no continuous ciliary strips are found, but separate tufts of cilia are located mainly along the ventral wedge.

Glands. A striking feature of the snail's organization is its large amount of glandular tissue. The foot is equipped with two pedal glands, an anterior and a posterior one (Figs 3A,B, 4C: apg, ppg). The former is small and situated in the anterior part of the foot directly underneath the constriction between the head lobes. It opens on the dorsal side of the foot via a heavily ciliated pore right in front of the mouth. The posterior pedal gland is very large and consists of paired thin ducts with large bulb-like glandular masses. The left glandular mass is situated between body wall and cerebral ganglion, whereas the right, more posteriorly located part extends between the reproductive system and the right portion of the columellar muscle. Anteriorly, the paired duct opens into a common chamber provided with a broad ventral ciliary band, which opens via a small pore posteriorly on the pedal sole.

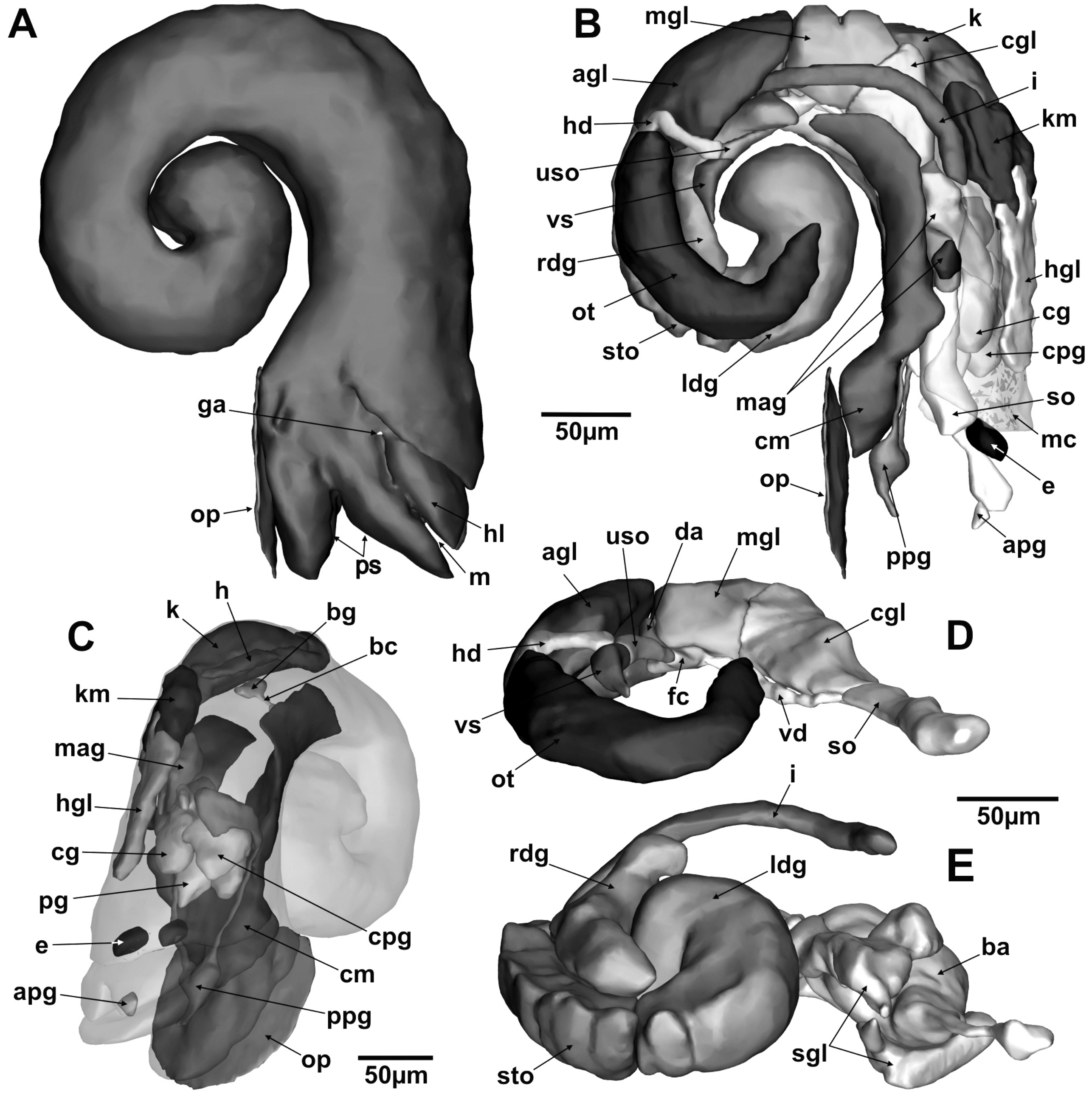
Further glands are arranged around the mantle cavity (Figs 3, 4C: hgl, km). The most anterior one of these is the hypobranchial gland situated anteriorly in the roof of the mantle cavity. Its tissue is stained pink and its cells seem to open individually into the mantle cavity. Another gland lies postero-dorsally to the hypobranchial gland adjacent to the latter and the mantle cavity. It consists of few, very large, unstained cells that are visible shining through the shell in living specimens.

There are two more glands associated with the mantle cavity positioned on the right side of the animal (Figs 3B, 4C: mag1,2). They open ventrally into the latter. The smaller one (mag 2) opens into the right, outermost corner of the mantle cavity. The pore of the larger one (mag 1) lies approximately

→

Figure 4 (next page). *Omalogyra atomus*. Adult organization from 3D reconstruction/visualization. **A.** External surface from the right. **B.** Overview of internal organs from the right. **C.** Obliquely from anterior-left with transparent external surface with reproductive and digestive system ommitted. **D.** Reproductive system from obliquely ventral. **E.** Digestive system from obliquely ventral. agl, albumen gland; apg, anterior pedal gland; ba, buccal apparatus; bc, buccal commissure; bg, buccal ganglion; cg, cerebral ganglion (right side); cgl, capsule gland; cm, columellar muscle; cpg, cerebropleural ganglion (left side); da, duct of albumen gland; e, eye; fc, fertilization chamber; ga, genital aperture; h, heart; hd, hermaphrodite duct; hgl, hypobranchial gland; hl, head lobe; i, intestine; k, kidney; km, mantle gland; ldg, left digestive gland; m, mouth; mag, mantle gland; mc, mantle cavity; mgl, mucous gland; op, operculum; ot, ovotestis; pg, pedal ganglion; ppg, posterior pedal gland; ps, pedal sole; rdg, right digestive gland; sgl, salivary gland; so, spermoviduct; sto, stomach; uso, upper spermoviduct; vd, vas deferens; vs, vesicula seminalis.

If viewed with *Adobe Reader* (from version 7.0.7 or better 8.1.1 and higher) click the image plate to activate the 3D mode. A variety of tools allows interactive manipulations ranging from free rotating or moving the model to changing the appearance by viewing only selected portions (use *Model Tree*—check or uncheck objects) or changing surface visualization (*Render Mode*, *Lightning*). In addition to the *default view* some *views* (named self-explanatory) are prefabricated and available by clicking on them in the middle of the *Model Tree* interface part. Some of the *views* correspond to images of the figure plate. 3D mode is disabled (figure reappearing) when *Disable 3D* is selected from the context menu (right-click on 3D model) or when page containing the figure is left.



in the middle of the mantle cavity next to the ventral ciliary band that leads from the anus anteriorly. This gland is stained dark purple and sits atop the right glandular mass of the posterior pedal gland.

Musculature. The columellar muscle system (Figs 3, 4B,C: cm) is very prominent. It consists of a pair of smooth muscles that dorsally end on the columellar side of the body wall. Ventrally the two portions are merging and extend to the epithelial attachment of the operculum on the posterodorsal side of the foot. Along the whole length of the columellar muscle more or less big muscle strands are branching off and extend towards different body portions such as the foot.

Digestive system. The simply organized digestive system (Fig. 4B,E) occupies the left body side. The mouth opening lies underneath the constriction between the head lobes and directly posterior to a ciliated depression representing the opening of the anterior pedal gland (Fig. 2C: am). Posterior to the mouth opening there is a small cavity that bears two thickenings in its lateral walls possibly functioning as jaws. Other structures resembling jaws could not be discerned. From this cavity, starting in the area of the eyes, an unciliated, thin oral duct runs straight posteriorly. In the area of the nervous system the duct widens again forming a laterally compressed slit-like lumen (Fig. 3A: l) before merging with the prominent, highly muscular buccal apparatus (Fig. 3B,C: ba).

Embedded in the middle of the buccal mass lies the hook-shaped radula (Fig. 2E,F), its anterior part bent ventrally, thus, standing at an angle of approximately 45° to the much longer dorsoposterior part. The anterior tip of the radula points towards the opening of the oral duct into the buccal apparatus. The radula itself is 60 to 70 µm long. Its dorsal part comprises six or seven rows of teeth, whereas the ventral part has five or four rows resulting in a total number of eleven rows for the whole radula. Each row shows a single (but see discussion for presence of lateral plates), unicuspid, triangular tooth. Each tooth is hollowed out on the posterior side and curved on the other side so that they fit into each other. The hollow side basally bears two bulges to form an interlock with the preceding tooth.

Two glandular masses lie on both sides adjacent to the buccal apparatus (Figs 3B, 4E: sgl). These represent the salivary glands, the opening of which into the digestive tract could not be traced. The oesophagus (Fig. 3C: oe) emerges from the dorsal, rear third of the posteriorly tapering buccal apparatus. The diameter of the oesophagus remains constant over its length apart from the slightly thinner anterior origin. The posterior part meanders in five to six, short loops before entering the stomach at its left, anterodorsal side. Next to one of the anterior oesophagal loops, a pair of distinct, elliptically-shaped, purple-stained structures (Fig. 3C: arrow heads) were found. Function and homology relations of these structures are unclear, but they seem to be associated with the digestive system. Internally the oesophagus contains a distinct ventral ciliary band that starts at about one quarter and ends at about three quarters of the length.

The stomach (Figs 3B,C, 4E: sto) is positioned posteriorly in the outer whorl of the visceral mass. It shows constrictions at regular intervals, but interiorly there are no differentiations discernable. From anterior left it receives the oesophagus via a broad, unciliated opening. One digestive gland (left according to Fretter 1948) opens posteriorly, whereas the other (right) opens right anteriorly into the stomach (Figs 3, 4E: ldg, rdg). Stomach and digestive glands have an overall curved shape in accordance with the whorls of the visceral mass. The innermost whorl is almost completely filled by the voluminous left digestive gland. The right gland is slightly smaller and lies adjacent to the right side of the stomach.

The intestine (Figs 3C, 4B,E: i) emerges anteriorly on the right side from the stomach, slightly posterior to where the oesophagus enters the stomach. Its internal surface is ciliated. It runs anteriorly along the right body side, passes the heart, and finally opens on the right side into the mantle cavity at about the middle of its length.

Renopericardial system. The kidney (Figs 3C, 4B,C: k) lies underneath the dorsal mantle in the middle of the animal. It opens via a small pore into the central mantle cavity. From this pore a narrow and non-ciliated duct proceeds posteriorly and enlarges forming the voluminous kidney sac. The kidney is a simple vesicle bordered by bubble-like tissue. The monotocardian heart (Fig. 4C: h) is composed of very delicate membranes and is located posteroventrally on the right side adjacent to the kidney. Posteriorly, the heart reaches as far back as the end of the mantle cavity.

Reproductive system. All adult specimens examined (collected in early April and June in the Mediterranean Sea) showed the same organization of the reproductive system. The terminology used by Fretter (1948) for the reproductive system of *Omalogyra atomus* is given in quotation marks below where required in order to enable and facilitate comparison. These terms in some cases imply a questionable function or homology, which contradict our observations.

The complex, hermaphroditic reproductive system occupies the right side of the visceral mass (Fig. 4B,D). The ovotestis (Figs 3B,C, 4B,D, 6A: ot) lies on the right side adjacent to the stomach and the left digestive gland and has an overall crescent shape. It extends from the middle of the stomach to the middle of the left digestive gland. The posterior part contains the testis (Figs 3B, 6A: te), recognizable by the grouped sperm heads in sections. The ovary part (Figs 3C, 6A: ov) is represented by the larger anterior portion, where eggs, lined up in increasing stages of size and maturity, are discernable. In all specimens investigated one egg distinctly was the ripest and largest (Fig. 3B: eg). The largest one found had a diameter of 90 µm. Such an egg sits anteriorly next to the opening of the small, ciliated hermaphrodite duct, the "ovarian duct" of Fretter (1948) (Figs 3C, 4B,D, 6A: hd). Sperm cells can also be found in the cone-shaped vesicula seminalis (Figs 4B,D, 6A: vs) on the right of the right digestive gland. It is unclear whether the contents of this vesicula seminalis represent autosperm produced by the testis or allosperm received during copulation. The vesicle continues as a small duct ("testicular duct") that fuses after a short distance with the upper spermoviduct (Figs 3C, 4B,D, 6A: uso). The latter proceeds anteriorly and slightly widens forming a small, ciliated fertilization chamber (Figs 4D, 6A: fc). It is flanked by the oesophagus on the left and by the right digestive gland on the right. The chamber anteriorly is continued by the narrow, straight, ciliated vas deferens (Fig. 3C: vd) that lacks prostate or glandular tissue. It passes into the broader spermoviduct ("hermaphrodite duct") next to the anterior connection of the glandular complex (Figs 3B, 4B,D, 6A: so).

The glandular complex (Figs 4B,D: 6A) comprises three different, consecutive glands associated with each other. The most anterior, second-largest capsule gland (Fig. 3C: cgl) is located on the front face of the last whorl between the buccal apparatus on the left and the end of the intestine on the right. Its tissue stains reddish-purple and contains circular to elliptic granules that are all about the same size and arranged in groups around the unciliated, slit-like lumen of the gland. Posteriorly, it is merged with the second and smallest gland, the mucous gland, lying dorsally between the oesophagus and the intestine. The internal surface of this lobate gland is densely ciliated. Its tissue is dark-purple staining and this way distinguishable from the previous gland. Via a broad, dark-blue staining duct the mucous gland is linked to the third one, the albumen gland (Fig. 3C: agl). The latter has a turquoise tissue with circular granules of different sizes that surrounds a large lumen. The internal surface is unciliated. The gland is composed of two lobes: a large, dorsal one and a small ventral one, which is connected to the mucous gland.

The entire glandular complex has two connections to the remaining portions of the reproductive system, which are located ventrally: (1) posteriorly, via a small, short connection between the large lobe of the albumen gland and the fertilization chamber (Figs 4D, 6A: da) and (2) anteriorly, via the opening of the capsule gland into the vas deferens forming the connection to the fertilization chamber. The spermoviduct (Figs 3B, 4B,D, 6A: so) emerges anteriorly from the capsule gland together with the vas deferens and runs forwards as a straight, wide, round tube. The wall of its anterior half is highly muscular consisting of mainly longitudinal but also circular muscles. The spermoviduct opens to the outside via a prominent genital pore (Fig. 4A: ga) situated just beneath the mantle border at the base of the right head lobe. A copulatory verge is absent.

In the juvenile individual studied, the reproductive system (Figs 5B, 6C) was at the beginning of development. Solely the anlagen of components of the organ system were found. The anlage that may give rise to the spermoviduct is located anteriorly. Posterior to this the middle portion anlage is found, which seems to be the predecessor of structures like the female gland or the fertilization chamber. The posterior anlage, which is already connected to the middle portion, appears to give rise to the ovotestis.

Nervous system and sensory organs. The nervous system is fairly concentrated and as a whole somewhat shifted to the left side of the animal. This left-side shift was found in all adult specimens investigated and may be due to the presence of the ripe, voluminous reproductive system on the right side.

A pair of elongate pedal ganglia (Figs 3A, 4C, 5B, 6D: pg) is positioned anteriorly. From the anterior end of each pedal ganglion, three nerves emerge, one emanates dorsally, the other two ventrally, but all three run forward. Posterodorsally almost perfectly spherical statocysts rest atop the pedal ganglia (Figs 5B, 6D: st). The pedal commissure (Fig. 3A: pc) arises centrally. The ganglia are double-linked with the dorsally situated cerebropleural complex (Figs 5B, 6D): first by the cerebropedal connective arising slightly more anteriorly and secondly by the pleuropedal connective emerging dorsally from the rear pedal ganglia just anterior to the statocysts.

The cerebropleural complex (Figs 5B, 6D) is quite prominent and sits atop the buccal apparatus. A thick cerebral commissure connects the cerebral ganglia anteriorly to each other. The frontal part of each ganglion receives two incoming nerves, dorsally the thin optic nerve and more ventrally a stron-

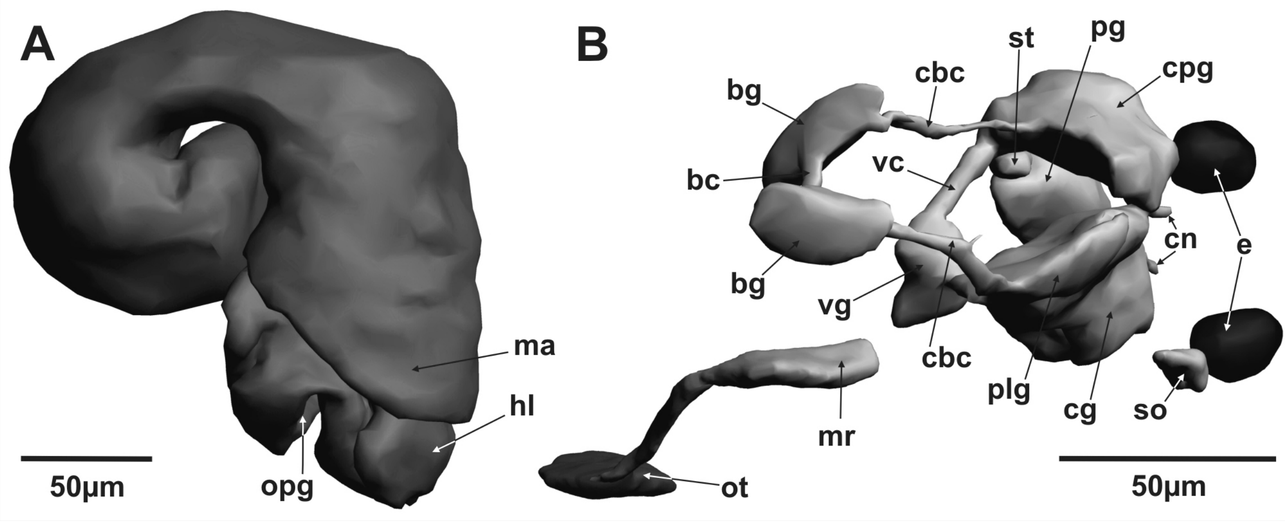


Figure 5. *Omalogyra atomus*. Juvenile specimen from 3D reconstruction/visualization. **A.** External surface from the right. **B.** Nervous system and anlagen of reproductive system from dorsal. bc, buccal commissure; bg, buccal ganglion; cbc, cerebrobuccal connective; cg, cerebral ganglion (right side); cn, cerebral nerve; cpg, cerebropleural ganglion (left side); e, eye; hl, head lobe; ma, mantle; mr, middle portion of reproductive system; opg, opening of posterior pedal gland; ot, ovotestis; pg, pedal ganglion; plg, pleural ganglion (right side); so, spermoviduct; st, statocyst; vc, visceral connective; vg, visceral ganglion.

See Figure 4 for the interactive 3D mode if viewed with *Adobe Reader*.

ger nerve from the head region. The pleural ganglia are entirely fused with the cerebral ganglia. Only the right pleural ganglion (Figs 5B, 6D: plg) is slightly silhouetted against the right cerebral ganglion (Figs 5B, 6D: cg) in the form of a projecting bulge at the posterior end of the latter. From this bulge the right branch of the visceral connective originates ventrally, whereas the left branch emanates directly from the rear of the left, compact cerebropleural ganglion (Figs 5B, 6D: cpg).

The visceral loop (Figs 5B, 6D: vc) is short and euthyneurous due to the shortening of the visceral connectives. There are no distinct supra- and suboesophageal ganglia. The unpaired visceral ganglion is located slightly posteriorly of the cerebropleural complex. An osphradial ganglion and an osphradium could not be found.

The paired buccal ganglia (Figs 5B, 6D: bg) are far posteriorly positioned, where the oesophagus arises from the buccal apparatus. The ganglia lie on the left side of the animal, obliquely orientated with the left ganglion lying further ventrally than the right one. The ganglia are connected to the cerebral ganglia via long, delicate buccal connectives. Just anterior to the buccal ganglia, each buccal connective dorsally gives off a very thin nerve supplying the buccal apparatus.

The eyes have a perfectly spherical, blue-staining lens. Except for anteriorly, this lens is embedded in a dark-tinted pigment epithelium. The statocysts contain a single statolith with a diameter of about one quarter of the spherical statocyst lumen.

Discussion

Methodology. This study represents a case where modern methods (sectioning technique plus 3D computer reconstruction, see Ruthensteiner 2008) for investigation of soft part morphology provide substantial novel information. This becomes particularly evident in the case of the reproductive and nervous system (see below). Older data on the reproductive system of *Omalogyra atomus* provided by Fretter (1948) appear dubious if compared to our findings and information on the nervous system is provided for the first time. Particularly for small specimens, such as the micromolluscs treated herein, the resolution of paraffin sectioning or whole mount investigation is insufficient to address detailed anatomical questions. In addition, the results provided herein are by far superior concerning interactive visualization, supplying the reader with 3D—and thus extremely detailed—information on various organ systems. Because of this morphological information, the fine-structural data on sperm (Healy 1988, 1993) and the molecular data sets (*e.g.*, partial mitochondrial genome by Kurabayashi & Ueshima 2000; also GenBank AY081998: 28S rDNA by Lydeard *et al.* unpubl. data), *O. atomus* now is one of the best-known microgastropods.

Morphological structures as functional and evolutionary units. The planispiral teleoconch of *Omalogyra atomus* is also found in several other, unrelated gastropod clades. Among basal Heterobranchia, it is also found in *e.g.*, the ectobranch *Valvata cristata* O.F. Müller, 1774, and the pyramidellid genus *Cyclostremella* (*cf.* Robertson 1973). The lack of a distinctly hyperstrophic protoconch, otherwise typical for basal heterobranchs (Haszprunar 1985a, 1988; Robertson 1985), is probably due to the non-planktonic mode (Fretter 1948) of development. It is noteworthy, that the closely related *Retrotortina* shows a slightly hyperstrophic teleoconch, which might be interpreted as a paedomorphic larval shell.

The reduction and modification of the cephalic tentacles to small lobes is difficult to interpret functionally, since many other basal heterobranchs of similar size do have regular cephalic tentacles. Among Omalogyridae, this feature is shared with *Retrotortina fuscata* Chaster, 1896 (cf. Gofas & Warén 1998; N. Baeumler, G. Haszprunar pers. obs. 6/2007), but not with *Ammonicera* species, which all have regular tentacles. Accordingly, this feature is in any case a parallelism to cephalic lappets found in certain pyramidelloids or bullomorph opisthobranchs.

The highly glandular body represents both, a functional and a phylogenetic feature. A tiny gastropod in a tide pool is always in danger of being washed away by heavy waves and cannot overcome such forces by powerful musculature akin to those of limpets. Adhesion by mucus from the anterior and especially from the posterior pedal gland gives *Omalogyra atomus* an anchorage. Probably, it also profits from physical laminar effects due to its smallness. In addition, hiding behavior in small crevices may also enable permanent occupation of such difficult habitats. On the other hand the presence of additional, posteriorly placed pedal glands and additional mantle glands is typical for primitive heterobranchs and also found in rissoellids (Fretter 1948), architectonicids (Haszprunar 1985b; Bieler 1988), mathildids (Haszprunar 1985c), and pyramidellids (Fretter & Graham 1949). The same holds true for other mantle cavity related organs (pallial kidney, ciliary strips). Since the ciliary strips replace the ctenidial function of pallial water movement (ventilation), the lack of a (purely respiratory) gill is easily explained by the small size of the animals. In contrast to the assumption of Haszprunar (1988), but in accordance with Fretter (1948), the ciliary strips are located on the right side of the mantle cavity, thus showing an arrangement typical for all lower heterobranchs so far studied (if they are dextral) except for Architectonicidae and Mathildidae, where the strips are placed on the left side (Haszprunar 1985b,c, 1988).

There are major discrepancies between previous studies and the current investigation concerning the reproductive system. Although *in situ* organization (Fretter, 1948: pl. IV, fig. 2, same as Fretter & Graham 1962: fig. 184) and schematic drawing (Fretter & Graham 1962: fig. 187C same as Fretter & Graham 1994: fig. 179C) do not totally correspond (connectivity of vesicula seminalis), we tried to infer the organization of the reproductive system as given by Fretter (& Graham) graphically (Fig. 6B). Differences to present investigation (compare Fig. 6A and 6B) concern for instance the ovotestis (typical in the present study but separate testis and ovary with separate ducts in Fretter's

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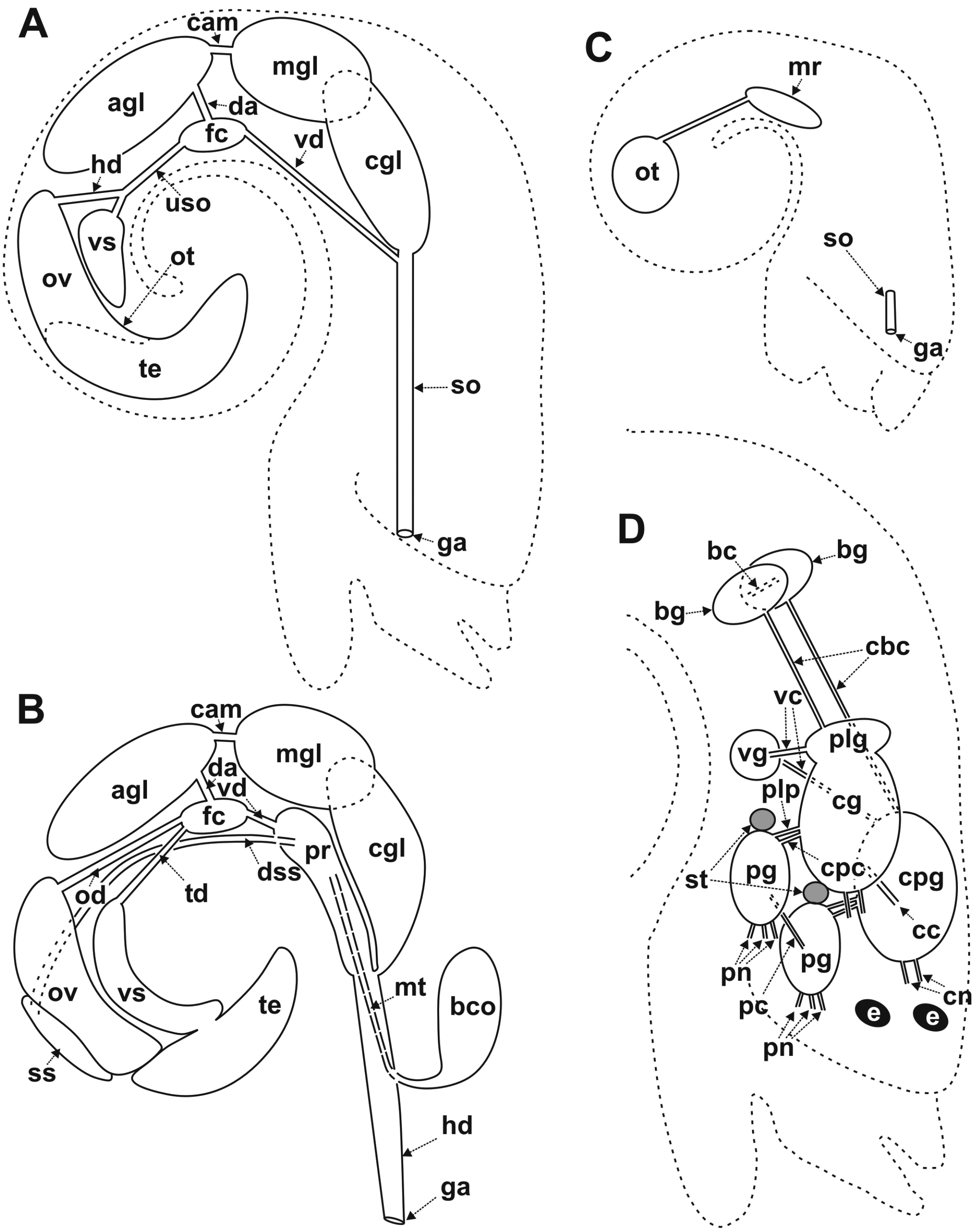
Figure 6 (next page). *Omalogyra atomus*. Schematic drawings, all right side views. **A.** Reproductive system. **B.** Reproductive system as reported by Fretter. Combined from text and figures of Fretter (1948) and Fretter and Graham (1962, 1994). **C.** Anlagen of the reproductive system of a juvenile—corresponding to the juvenile specimen of Figure 5. **D.** Nervous system. agl, albumen gland; bc, buccal commissure; bco, bursa copulatrix; bg, buccal ganglion; cam, connection between albumen and mucous gland; cbc, cerebrobuccal connective; cc, cerebral commissure; cg, cerebral ganglion (right side); cgl, capsule gland; cn, cerebral nerves; cpc, cerebropedal connective; cpg, cerebropleural ganglion (left side); da, duct of albumen gland; dss, duct of sperm sac; e, eye; fc, fertilization chamber; ga, genital aperture; hd, hermaphrodite duct; mgl, mucous gland; mr, middle portion of reproductive system; mt, muscular tube; od, ovarian duct; ot, ovotestis; ov, ovary (in A. portion of ovotestis); pc, pedal commissure; pg, pedal ganglion; plg, pleural ganglion (right side); plp, pleuropedal connective; pn, pedal nerves; pr, prostate; so, spermoviduct; ss, sperm sac; st, statocyst; td, testicular duct; te, testis (in A. portion of ovotestis); uso, upper spermoviduct; vc, visceral connective; vd, vas deferens; vg, visceral ganglion; vs, vesicula seminalis.

study), vesicula seminalis (sac-like in the present study but widened "testicular duct" in Fretter's studies), bursa copulatrix (absent in the present study but found in all specimens by Fretter) and the muscular tube (absent in the present study but extending from the bursa copulatrix to the hermaphroditic duct in Fretter's studies).

In addition, Fretter (1948) reported significant differences in the reproductive system organization among her specimens examined. She attributed these to seasonal differences. According to this, "spring animals" are male with female organs not fully developed and not functional. "Summer animals" do not show full anatomical male characteristics and pass directly into feminized individuals.



However, we cannot confirm these findings in our study. The specimens we examined anatomically cover both seasons, spring (Sardinia) and early summer (Villefranche) and all fully-grown specimens exhibit a more or less constant organization with regard to the reproductive system (and also to other organ systems—see below).

The discrepancies between our results and those of Fretter may be due to different reasons: (a) Because of relatively lower seasonal variations in the Mediterranean than in the Atlantic Ocean, Mediterranean populations of *Omalogyra atomus* do not follow the same pattern of anatomical changes as Atlantic Ocean populations. (b) Investigated populations may not be conspecific. This seems possible since the specimens studied by Fretter (1948) are—according to the scale bar—about 1.3 mm in diameter and, therefore, much larger than the specimens we found (diameter of the large ones approximately 0.4 mm). Unfortunately, there is no information provided in the Fretter (1948) study on the collection locality or on radula and shell morphology for species identification. On the other hand, there are soft-part morphological details that correspond to those found in the material we investigated. It may be noted that the specimens we used for anatomical examination are from localities (western Mediterranean) closer to the type locality (Sorrent, Italy) than the specimens of Fretter (probably British islands). (c) Differences are based on methodological limitations in Fretter's study (see above).

Fretter (1948) regarded the mode of copulation of *Omalogyra atomus* to be unique among molluscs. This assumption is mainly based on the presence of the muscular tube and the absence of a true penis, which Thiele (1931) and Ankel (1936) erroneously thought to be present. However, aphallic hermaphrodites with internal fertilization are also known, for instance, in Architectonicidae (Haszprunar 1985b,c; Bieler 1988), Pyramidellidae (Fretter & Graham 1949; Fretter 1953; Robertson 1978), or Orbitestellidae (Ponder 1990). It is likely that sperm transfer is performed via spermatophores like in the latter taxa (Robertson 1989), although this needs confirmation.

Sars (1878: pl. 8, fig. 1a-c) first described the radula of *Omalogyra atomus* and produced a remarkably accurate drawing, later adopted by Ankel (1936), showing each radular row to consist of three components: a triangular, unicuspid, central tooth flanked on both sides by a small, rectangular plate. Sars found this radula to be so special that he created the discrete taxon Prionoglossa for the omalogyrid family alone. Indeed, his drawing of the central tooth is in good accordance with modern SEM images of the radula (Gofas & Warén 1998; present study) of *O. atomus*. However, we could not find the thin, flat lateral plates mentioned by Sars (1878), Egorova (1991) and Gofas & Warén (1998). The latter confirmed the presence of these lateral plates by light, but not by scanning electron microscopy. Since we used only SEM, it is most likely that the radulae examined were also flanked by lateral plates. In terms of the number of radular rows, 11 were counted in this study, Sars (1878) showed 12 in his lateral drawing of the radula. Egorova (1991) reported 18–19 rows of teeth for the radular ribbon of another species, *O. antarctica* Egorova, 1991. *Retrotortina fuscata* has a very similar radula to that of *O. atomus*, consisting of the triangular central tooth, whereas the lateral plates are completely missing (Gofas & Warén 1998). In contrast, the radula of *Ammonicera* species (*e.g.*, Sleurs 1985a,b) shows on each radular row two bent, dagger-like teeth, which articulate on the outside with a very small marginal plate, resulting in a formula of 1-1-0-1-1. If *Ammonicera* is correctly placed within Omalogyridae (might be questioned—see below), the condition found in *O. atomus* [formula: 0-(1)-1-(1)-0] is a feature being evolved within the family with a remarkable (analogous) similarity to those of Sacoglossa.

The relative simplicity of the digestive system has already been noticed by Fretter (1948) and is generally found in basal heterobranchs (Haszprunar 1988). As for the reproductive system, Fretter reported a kind of seasonal variation: (a) The salivary glands are smaller (winter) or relatively larger (summer). (b) The oesophagus is narrower (winter) or broader (summer). (c) The oesophagus is ciliated at its extreme anterior end, along the entire length of its dorsal wall and for a narrow longitudinal strip along the mid-ventral wall (winter) or there are no cilia (summer). (d) The oesophagus and the stomach are lined by the digestive epithelium (winter) or only the stomach is lined by digestive cells (summer). Again, we could not confirm these findings based on the material we investigated. According to Fretter (1948) the extension of the digestive tissue into the stomach is correlated with the type of food (plant sap) of *Omalogyra atomus*. Since plant sap does not need mechanical treatment or sorting, the stomach can support the digestive task of the digestive glands.

Fretter (1948) did not provide information on the nervous system at all. Fretter & Graham (1962, 1994) added some data, but not mentioning relatively large components such as the visceral ganglion. Up to now, the only neural details on *Omalogyra atomus* were provided by Huber (1993) in his comparative study on the cerebral nervous system of marine heterobranchs. Huber investigated two omalogyrid species, *O. atomus* and *Ammonicera rota* (Forbes & Hanley, 1850), and provided a figure of the nervous system of the latter. Since he stated that both species show the same characters in their nervous system, this figure holds true for *O. atomus* as well. However, there are some major differences to the results of the present study. There is no discrete supraoesophageal ganglion, which was clearly illustrated by Huber, and which is usually present in almost all the lower heterobranchs so far reported (Huber 1993). Huber furthermore found four nerves emerging from the cerebral ganglia: a labial, a static, a tentacle and an optic nerve. In the current study only two, the optic and the (possibly) tentacle nerves, could be confirmed. We might have overlooked those, because we could not discern the static nerve and such a nerve must be present for supplying the statocysts. Huber stated that the optic nerve is very short because the eye is attached to the cerebral ganglion. The present observations contradict this. The eyes are located fairly distantly to the cerebropleural complex and the optic nerve is thus long. This reduction in the number of cerebral nerves compared to other heterobranchs according to Huber is due to the small size of the animal.

As outlined by Haszprunar (1988) an euthyneuran visceral loop in gastropods is a matter of multiple evolutionary parallelism due to (a) shortening of the visceral loop (*e.g.*, in Cingulopsidae or Pyramidellidae; cf. Fretter & Graham 1949; Huber 1993), (b) detorsion (most opisthobranchs), or (c) both (most pulmonates). In the case of *Omalogyra atomus,* this seems to be due to (a) since there is no trace of detorsion in its general organization. At present we can not account for the whereabouts of the supra- and suboesophageal ganglia. Were they simply reduced or fused with the visceral ganglion or the cerebropleural ganglia? Unfortunately there is no distinct osphradial ganglion, because the site where the respective nerve branches off from the visceral loop would clearly indicate the position of the supraoesophageal ganglion.

Taxonomy and phylogenetic position. Taxonomic problems regarding both the genus *Omalogyra* and the species *O. atomus* including synonymy have been treated in detail by Bieler and Mikkelsen (1998). We concur that the species *O. atomus* should be based on Philippi's (1841) shell description of *Truncatella atomus*.

The identification of the studied specimens is based on the scanned shell and radula, which appear identical to those of Sars (1878) from the north coast of Norway, Egorova (1991) from the White Sea (Russia) and Gofas & Warén (1998) from Iceland (but see discussion on the presence of radular lateral plates above). We must leave the question open if differences in the genital apparatus compared to Fretter's (1948) description of British specimens are due to different species identity (see above).

There are several lines of evidence for a position of *Omalogyra atomus* and thus Omalogyridae among the basal Heterobranchia (*i.e.*, within the allogastropod or heterostrophan grade; *cf.* Haszprunar 1988): two pedal glands, replacement of the ctenidium by opposite ciliary strips, a pallially situated kidney, lack of true radular cartilages, simplification of the gut, epiathroid nervous system, and in particular sperm fine-structure (Healy 1993). In addition, all molecular data available (*e.g.*, Kurabayashi & Ueshima 2000) call for a heterobranch placement of *O. atomus*, although a hyperstrophic larval shell is missing due to the putative non-planktonic mode of development. At first glance the kind of gonad (ovotestis with locally separated spermio- and oogenesis, versus "normal" hermaphroditic ovotestis lobes like in valvatoids, pyramidelloids, opisthobranchs and pulmonates) suggests close affinities with Architectonicidae and Mathildidae (Architectonicoidea). However, whereas in Architectonicoidea testis and ovary are separated lobes, there are only regions in a single lobe in *Omalogyra*. In any case, the erroneously stated (Haszprunar 1988) left-side position of the ciliary strips is herewith corrected and can no longer be used to support affinities with architectonicoids.

The (small *versus* large) size of the hypothetical stem species of the Heterobranchia is still a matter of debate: on the one hand direct outgroup comparison with the Caenogastropoda and the basic planktotrophic mode of development (*cf.* Chaffee & Lindberg 1986) suggest a large ancestor. In contrast, most basal groups and in particular the rhipidoglossate ones (Ectobranchia: Hyalogyrinidae) are small organisms of 1–3 mm. Accordingly, it remains open, whether the smallness of Omalogyridae is a plesiomorphic feature or is caused by progenesis of a larger ancestor.

Summing up, the present study supports affinities of *Omalogyra atomus* to other lower heterobranchs, such as Rissoellidae and Pyramidellidae, by dismissing previously reported contradicting peculiar characters, such as the left sided ciliary tracts and unusual structures in the reproductive system. At present, the striking morphological differences between *Omalogyra* and *Ammonicera* (*e.g.*, radula and head appendages) make the interpretation of the organization of the Omalogyridae difficult. Therefore, anatomical investigation of the latter genus suggests itself as the next step to further unravel the systematic affinities of Omalogyridae among the basal heterobranchs.We are still at the very beginning of investigating the anatomy of heterobranch microgastropods. The methodology applied herein should not only provide, but also visualize, the details much better than in previous studies and should encourage students to focus on this highly interesting field of gastropod evolution.

Acknowledgements

We thank Eva Lodde (ZSM) for embedding and sectioning of specimens and general technical support. Rebecka Zernecke helped with 3D reconstruction procedures. We are indebted to Martin Heß (LMU Munich) for the image of the living *Omalogyra atomus*. The GeoBio-Center of the LMU Munich provided a license of AMIRA. Many thanks to Paula Mikkelsen, Kazunori Hasegawa and Daniel Geiger for providing most helpful comments, that served as base for substantial improvements.

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