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Morphology and formation of jaw structures in some gastropod species

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ABSTRACT. The gastropod feeding apparatus originally comprises the radula and jaws. While the radula has been extensively studied, data on jaws remain limited. Nevertheless, investigating jaw morphology is essential for understanding feeding mechanisms and morphofunctional adaptations. This study addresses this gap by presenting novel data on jaw morphology across a range of gastropod species from various clades, including Vetigastropoda, Littorinimorpha, and Neogastropoda. Based on our data and previously published research, we propose the existence of two distinct types of jaws: simple and complex. Simple jaws (found in the majority of Patellogastropoda and some Neogastropoda) consist of solid plates, whereas complex jaws (found in Vetigastropoda, Caenogastropoda, and Heterobranchia) are composed of both a solid homogeneous layer and a layer of solitary structures, such as rods or hooks, referred to as rodlets (as in some heterobranchs). Electron microscopy data enabled us to homologise the complex jaws of Vetigastropoda and Caenogastropoda. The jaws of representatives from both subclasses exhibit a similar synthesis mechanism, in which a single gnathoblast synthesises an individual rodlet. The jaws of Neogastropoda and Tonnoidea display considerable diversity, both in their localization within the buccal complex and in their morphology, ranging from paired smooth or complex structures to highly modified structures acting as a stylet. Furthermore, the varied localization of jaws in neogastropods suggests a high potential of the buccal epithelium for the formation of diverse jaw structures.

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Особенности морфологии и формирования челюстных структур у некоторых видов брюхоногих моллюсков

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РЕЗЮМЕ. Пищедобывательный аппарат брюхоногих моллюсков исходно включает радулу и челюсти. Несмотря на то, что радула была хорошо изучена, данные по челюстям весьма ограничены. В то же время изучение морфологии челюстей имеет ключевое значение для понимания механизмов питания и морфофункциональных адаптаций. Данное исследование призвано устранить этот пробел, и представляет новые данные о морфологии челюстей ряда видов брюхоногих моллюсков из разных клад, включая Vetigastropoda, Littorinimorpha и Neogastropoda. Основываясь на наших данных и ранее опубликованных исследованиях, мы предполагаем существование двух типов челюстей: простых и составных. Простые челюсти (описанные для большинства Patellogastropoda и некоторых Neogastropoda) представляют собой монолитные пластинки, в то время как составные (обнаруженные у Vetigastropoda, Caenogastropoda и Heterobranchia) имеют как монолитную часть, так и часть с дискретными элементами (палочками, крючьями), называемыми родлетами, по аналогии с челюстями у некоторых Heterobranchia. Данные электронной микроскопии позволили провести гомологию между составными челюстями Veti-

gastropoda и Caenogastropoda. Для челюстей представителей обоих подклассов характерен схожий механизм синтеза, при котором один гнатобласт синтезирует один родлет. Челюсти Neogastropoda и Tonnoidea демонстрируют большое разнообразие как по своей локализации в буккальном комплексе, так и по морфологии, варьируя от парных гладких или составных, до видоизмененных челюстей, функционирующих как стилет. Кроме того, разнообразие локализации челюстей неогастропод говорит о высокой способности буккального эпителия к формированию различных челюстных структур.

Introduction

The gastropod feeding apparatus typically comprises two hard structures: the radular apparatus and the jaws. While data on the function, general morphology, ultrastructure, and mineralisation of the radula are abundant, data on jaws is limited to a few groups where jaw morphology serves as a key character in taxonomic descriptions or where jaws play a critical role in the feeding process [Fretter, Graham, 1962; Haszprunar, 1985; Ponder, Lindberg, 1997]. However, to understand the functional mechanisms of jaws and to reveal the principal morphofunctional adaptations of the gastropod feeding apparatus, it is crucial to study the morphological diversity of jaws and their synthesis mechanisms.

To address this knowledge gap and summarise existing data on the morphological diversity of jaws, we present here new data on jaw morphology in some gastropod species from different clades, including one species of Vetigastropoda, four species of Littorinimorpha, and four species of Neogastropoda (both Caenogastropoda).

Margarites helicinus (Phipps, 1774) (Trochoidea, Margaritidae) is a common vetigastropod species in the White Sea, typically found near the border of intertidal and upper subtidal zones, as well as within the upper subtidal zone. This small gastropod, with a shell height not exceeding 6 mm, possesses a depressed conical, iridescent and nacreous shell (Fig. 1A, B). *M. helicinus* is a grazer, feeding on the organic film present on substrata [Fretter, 1955; Golikov, 1987]. The radula of *M. helicinus* is rhipidoglossan, consistent with the majority of Vetigastropoda [Vortsepneva *et al*., 2021a; 2021b].

To study jaw morphology in Caenogastropoda, we examined representatives from the orders Littorinimorpha and Neogastropoda.

Three of the selected littorinimorph species inhabit the intertidal and subtidal zones of the White Sea. *Skeneopsis planorbis* (O. Fabricius, 1780) (Skeneopsidae) is a small gastropod with nearly planorboid shell, reaching up to 2 mm in diameter (Fig. 1C). Specimens are commonly found in the intertidal and upper subtidal zones among the rhizoids of kelps and other algae, and they may also inhabit tidal pools. *S. planorbis* is a grazer, feeding on diatoms and single-celled algae from hard substrata [Fretter, 1948]. *Peringia ulvae* (Pennant, 1777) (Hydrobiidae) is a gastropod species characterised by an elongated conical shell, rarely exceeding 3 mm in height (Fig. 1D). This species inhabits tidal pools in the middle littoral zone and feeds on algae and bacterial films [Newell, 1962; Golikov, 1987; Araújo *et al*., 2015]. *Velutina velutina* (O. F. Müller, 1776) (Velutinidae) is a relatively large gastropod with an ear-shaped shell, typically measuring 13–14 mm in diameter, with the last whorl comprising the majority of the shell. Specimens are usually found epibenthically on the surface of muddy rocky sediments [Golikov, 1987; Gulbin, Golikov, 1999]. *V. velutina* specialises in feeding on tunicates [Sargent *et al*., 2019], using its jaws to grate the hard covers of its prey. All three of these Littorinimorpha representatives possess taenioglossan radulae, with seven teeth per transverse row [Fretter, 1948; Golikov, 1987; Gulbin, Golikov, 1999].

We also studied jaw morphology in four species of gastropods with a proboscis: one species of Tonnoidea (Littorinimorpha) and three species of Neogastropoda. A key morphological feature of the foregut in Tonnoidea and Neogastropoda is the presence of a well-developed proboscis, a retractable and highly mobile organ that originates as an elongation of the snout [Fretter, Graham, 1962; Kantor, 1991]. The proboscis typically contains the buccal mass and the anterior oesophagus.

To examine jaw morphology of Tonnoidea, we studied *Phalium glaucum* (Linnaeus, 1758) (Tonnoidea, Cassidae). Like other members of the family, *Ph. glaucum* is a specialised predator that feeds on various species of sea urchins [Hughes, Hughes, 1981]. Using its long, muscular and mobile proboscis, it can remove the spines and drill through the urchin's test to access the soft tissues of the urchin [Hughes, Hughes, 1981].

The typical feeding apparatus of Neogastropoda is characterised by a radula that can be morphologically modified due to a shift towards carnivory [Ponder, 1973]. In most neogastropod species, the reduction of jaws has been reported [Ponder, Lindberg, 1997]. However, a few families within Neogastropoda have unusual jaws shaped like a semi-closed funnel, as observed in Volutomitridae [Kantor, Harasewych, 1992] and Cancellariidae [Harasewych, Petit, 1986]. In this study, we provide new data on jaw-like structures in four species of the Neogastropoda: *Rapana rapiformis* (Born, 1778) (Muricidae), *Trigonostoma lamberti* (Souverbie, 1870), *Sydaphera lactea* (Y.-C. Lee et T. C. Lan, 2002), and *Admete viridula* (O. Fabricius, 1780) (all Cancellariidae). *Rapana rapiformis* is a subtidal predator that drills into the shells of bivalves, a feeding strategy typical of

Table 1. Material of different species of gastropods used for jaw morphology. The asterisk indicates the same sample used for both 3D and micro-CT.

		Light microscopy	TEM	cLSM	Micro-CT	3D	SEM	TOTAL no. of spms
Vetigastropoda								
Trochida								
Trochoidea	*Margarites helicinus*	3	2				3	**8**
Caenogastropoda								
Littorinimorpha								
Littorinoidea	*Skeneopsis planorbis*	3	2			1	2	**8**
Truncatelloidea	*Peringia ulvae*	2		2				**4**
Velutinoidea	*Velutina velutina*	2	2				2	**6**
Tonnoidea	*Phalium glaucum*				1	1*		**1**
Neogastropoda								
Muricidae	*Rapana rapiformis*				1			**1**
Cancellariidae	*Trigonostoma lamberti*						1	**1**
	Sydaphera lactea						1	**1**
	Admete viridula	2	1	2				**5**

other members of the Muricidae family. *Sydaphera gigantea* and *Admete viridula* belong to the poorly studied family Cancellariidae, a highly specialised group of neogastropods inhabiting soft-bottom environments from subtidal to bathyal depths across the world's oceans. The studied cancellariids are suctorial feeders, preying on a wide range of organisms, from fish [O'Sullivan et al., 1987] to other molluscs [M.-V. Modica, personal observation]. The feeding apparatus of cancellariids includes a nematoglossan radula with elongated central teeth alone and a highly modified jaw. *Admete viridula* is a common benthic species found on soft sediments in the subtidal zone of the White Sea (Fig. 1E, F). This species lacks a radula, and its buccal cavity is equipped with a modified jaw. Despite its distinctive feeding apparatus, the diet of *A. viridula* remains unknown [Harasewych, Petit, 1986].

Material and methods

Nine species in total were studied by different morphological methods (Table 1).

Specimens of *Margarites helicinus, Skeneopsis planorbis*, and *Peringia ulvae* were collected near the Biological Station of the Moscow State University in Kandalaksha Bay, White Sea, Russia (WSBS; 66°34`N, 33°08`E) during the summer seasons from 2018 to 2022. Specimens of *Velutina velutina* were collected using SCUBA diving equipment in the vicinity of Cape Kindo near the WSBS at depths of 18–25 m. *Admete viridula* specimens were collected by trawling soft sediments at depths of 50–70 m near the WSBS. Specimens of *Rapana rapiformis* and *Phalium glaucum* were collected via SCUBA diving in Nha Trang Bay, Vietnam, near Mot Island (12º10.443'N, 109º16.298'E, 15–18 m) and Mun Island (12º10.084'N, 109 º17.771'E, 10 m), respectively. The specimens of *Trigonostoma lamberti* (Souverbie, 1870) and *Sydaphera lactea* (Deshayes, 1830) were collected in Koumac, New Caledonia (20°38'24''S, 164°12'43.2'', 15 m; expedition KOUMAC 2.1, Stn KR616 of Muséum National d'Histoire Naturelle, Paris, France) and Tasmania, correspondingly.

The morphology of the buccal complex was studied using different morphological methods including light, scanning electron microscopy (SEM) and transmission electron microscopy (TEM), confocal laser scanning microscopy (cLSM), and micro-computed tomography (micro-CT). The jaw morphology was examined in five specimens of *M. helicinus*, 12 specimens of *S. planorbis*, six specimens of *P. ulvae*, five specimens of *V. velutina*, and five specimens of *A. viridula*. The proboscis morphology of *Phalium glaucum* and *Rapana rapiformis*, was studied using micro-CT, with one specimen analysed per species. The list of used methods with the respective number of specimens is presented in Table 1.

Prior to morphological studies, specimens were relaxed in a solution of magnesium chloride ($MgCl_2$) isotonic with seawater, diluted 1:1 with seawater, for a minimum of 90 min at 4°C.

For TEM studies, two specimens of each species (*M. helicinus*, *S. planorbis*, *V. velutina*, and *A. viridula*) were examined. For histological and TEM studies, relaxed specimens were fixed in 2.5%

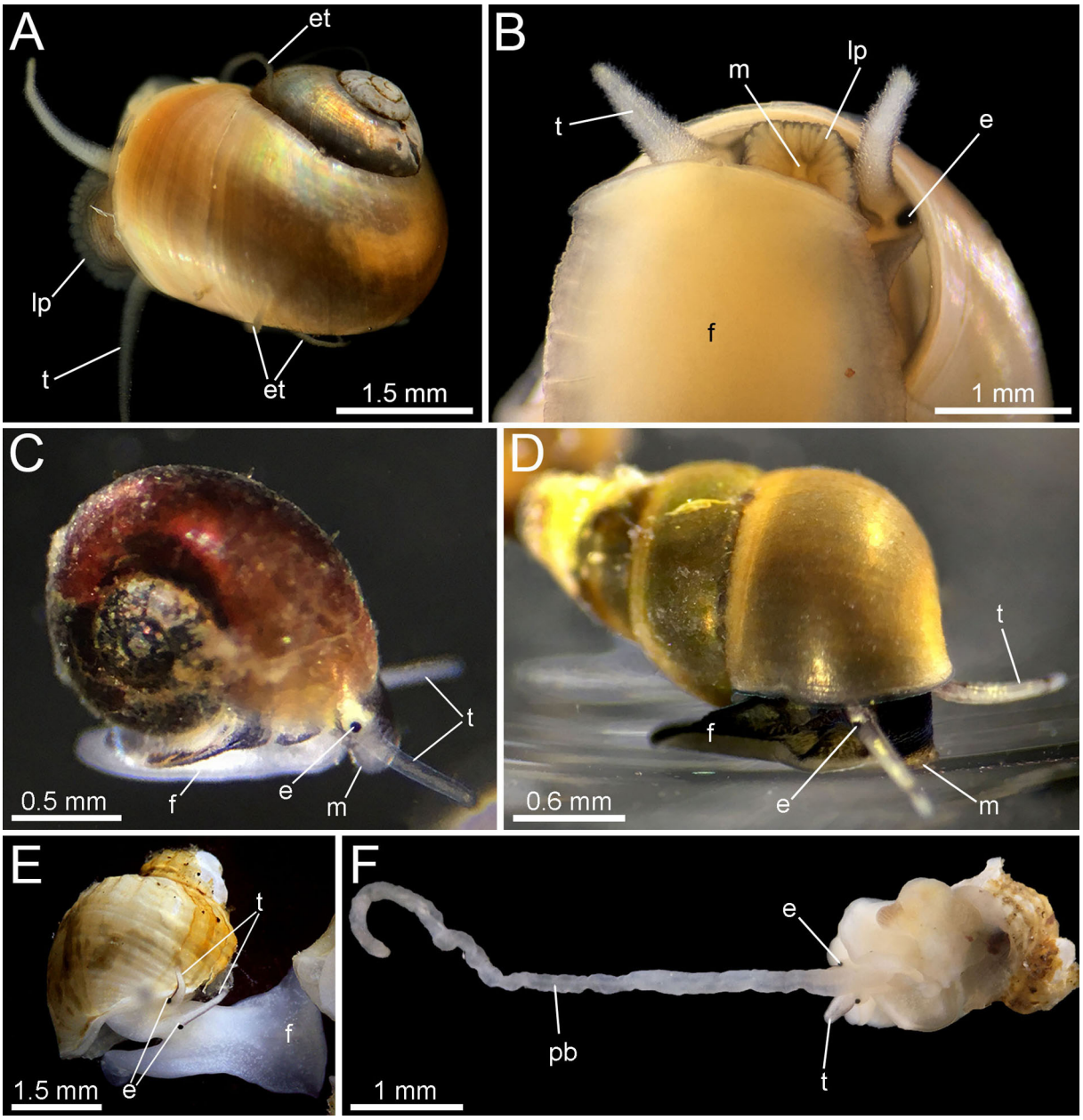

FIG. 1. Photos of alive molluscs *Margarites helicinus* (**A, B**), *Skeneopsis planorbis* (**C**), *Peringia ulvae* (**D**), *Admete viridula* (**E, F**). Abbreviations: e – eye; et – epipodial tentacle; f – foot; lp – lips; m – mouth; pb – proboscis; t – cephalic tentacle.

glutaraldehyde in 0.1 M phosphate-buffered saline (PBS; pH 7.2–7.4) at 4°C for 3 h, with the solution replaced after the first hour. Specimens were then rinsed with 0.1 M PBS, dehydrated through a graded ethanol series (20–25 min per step), transferred to acetone, and embedded in Spurr resin (EMS, Pennsylvania) using a graded acetone/resin series (1:3, 1:1, 3:1). Series of semi-thin (1 µm) and ultrathin (70–80 nm) sections were prepared using a diamond knife (Diatome, Jumbo) and Leica EM UC6 and UC7 ultramicrotomes (Leica Biosystems, Germany). Semi-thin sections were stained with 1% toluidine blue and 1% methylene blue diluted in 1% sodium tetraborate for 10–15 sec at 60°C. Histological sections were photographed using an Olympus BX 61 VS slide scanner (Olympus Inc., Japan). Three-dimensional (3D) reconstructions were prepared for *S. planorbis* from a transverse series of semi-thin sections, as described by Ruthensteiner and Heß (2008). Image stacks were aligned using AMIRA 5.2.2 (Amira Visaging GmbH, Germany). A computer-based 3D-reconstruction was conducted using the software Imaris 7.2.1 (Bitplane AG, Zurich, Switzerland). Ultrathin sections were stained with 1% uranyl acetate for 40 min at 37°C, followed by 0.4% lead citrate for 10 min at room temperature in the dark. Ultrathin sections were examined using a JEOL JEM 1011 transmission electron microscope (JEOL Ltd., Japan).

Additionally, the jaws of *P. ulvae* and *A. viridula*

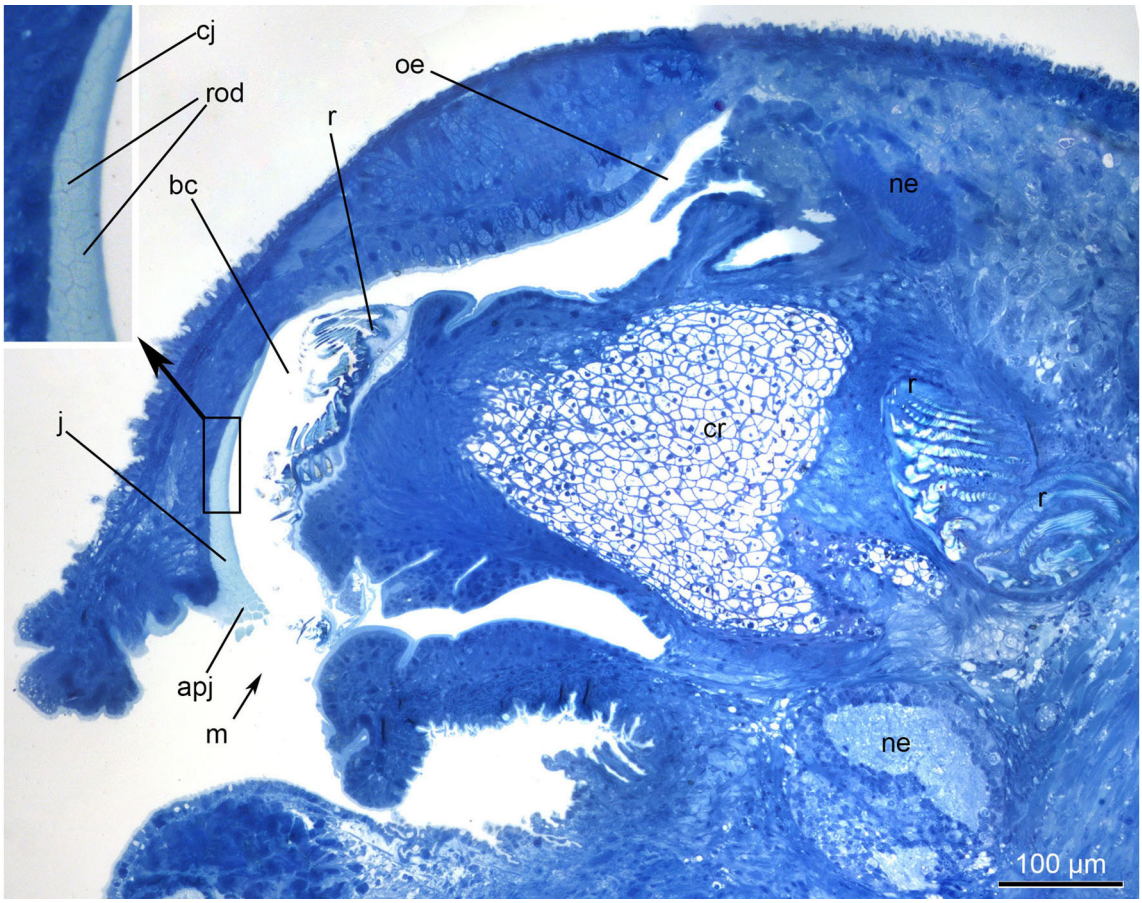

FIG. 2. Longitudinal histological section through the buccal cavity of *Margarites helicinus*. The jaw in higher magnification is in the rectangular insert. Abbreviations: apj – apical part of the jaw; bc – buccal cavity; cj – cover layer of the jaw; cr – odontophoral cartilages; j – jaw; m – mouth; ne – nervous; r – radula; rod – rodlets.

were studied using cLSM. After relaxation, the specimens were dissected and fixed in 4% paraformaldehyde in 0.1 M PBS for 4–12 h at 4°C with shaking. They were then washed three times over 3 h in PBS with shaking, stained with Calcofluor white (CfW; Fluorescent Brightener 28, Sigma F3543) to visualise amorphous chitin and identify newly formed jaws. Then, the samples were stained with Phalloidin 488 in 0.1 M PBS for 1 h at 4°C with shaking, washed three times (20 min each) with 0.1 M PBS, and mounted in glycerol under a coverslip. They were examined using a Nikon A1 confocal laser scanning microscope (Nikon Corporation, Japan) with 405 nm excitation (for CfW) and 488 nm excitation (for phalloidin). Prior to detection of the results of immunostaining, the microphotographs of the jaws in the bright field were taken using the same microscope.

The general morphology of the jaws of *M. helicinus, S. planorbis, P. ulvae*, *V. velutina, T. lamberti*, and *S. lactea* was examined using SEM. The jaws were soaked in Proteinase K lysis buffer solution at 60°C for 4–12 h to dissolve connective and muscular tissues. After washing in distilled water, the jaws were air-dried and sputter-coated with gold. Samples were examined using a JEOL JSM 7000 scanning electron microscope (JEOL Ltd., Japan).

To study the location and morphology of the jaws in *Ph. glaucum* and *R. rapiformis* the specimens were fixed and dehydrated in graded ethanol and acetone series, similar to the way described for light microscopy and TEM. Then the specimens were dried via a critical point with CO2 and were qualitatively studied with X-ray microtomography using the microtomography SkyScan 1272 (Bruker MicroCT, Belgium). For reconstruction of the shadow image array an NRecon software package (BrukerMicroCT, Belgium) was used. Microtomographic sections were analysed using CTVox software packages. Three-dimensional (3D) reconstruction was prepared for *Ph. glaucum* from a series of microtomographic sections using the software Imaris 7.2.1 (Bitplane AG, Zurich, Switzerland).

Results

Jaw morphology of *Margarites helicinus*

The mouth opening of *M. helicinus* is surrounded by horseshoe-shaped lips bearing numerous folds

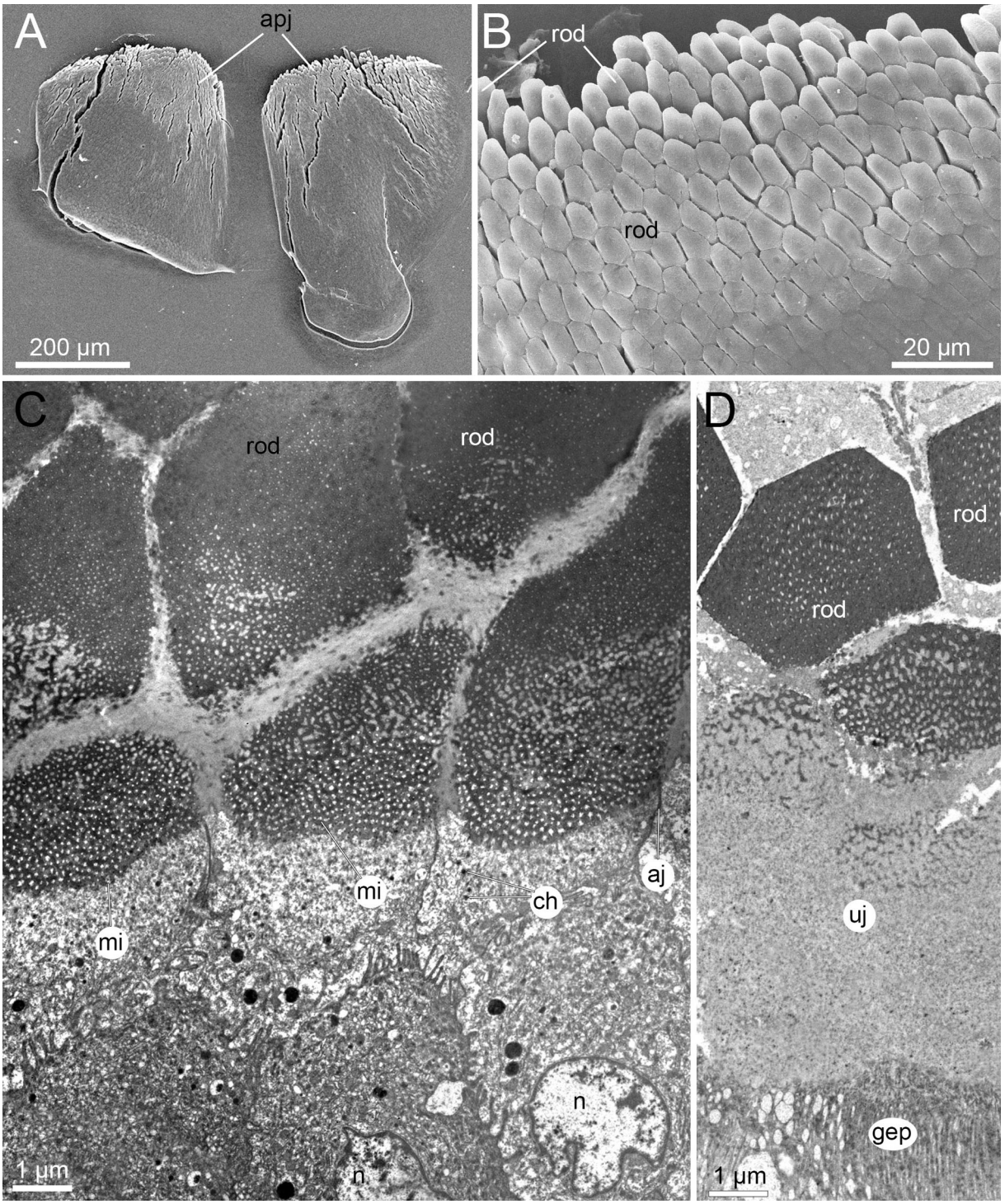

FIG. 3. Jaw morphology of *Margarites helicinus*. **A.** General morphology of jaws, SEM photo. **B.** Apical part of the jaw with rodlets in higher magnification, SEM photo. **C.** Longitudinal ultrathin section through the gnatoblasts and rodlets, TEM photo. **D.** Longitudinal ultrathin section through the apical part of the jaw. Abbreviations: aj – adherens junctions; apj – apical part of the jaw; ch – chitosome; gep – gnathoepithelium; mi – microvilli; n – nucleus; rod – rodlets; uj – layer of jaw under rodlets

(Fig. 1B). The mouth continues into the buccal cavity, where the paired jaws and the radular apparatus are located (Fig. 2). The morphology and formation process of the radula have been described in detail in our previous work [Vortsepneva *et al*., 2021b]. The paired jaw plates are triangular and positioned opposite the working zone of the radula. Several rows of rodlets are present at the external edge of the jaw plate (Fig. 3A, B), resembling the jaw structure of *Puncturella noachina* (Linnaeus, 1771) (Fissurellidae) [Vortsepneva *et al*., 2014]. The external homogeneous layer covers the internal layer, which contains the rodlets (Fig. 2). Each rodlet corresponds to a single cell, called gnathoblast, measuring up to 3.8–4 × 7.5–8.2 µm. The apical surface of the gnathoblast bears numerous microvilli, which reach into

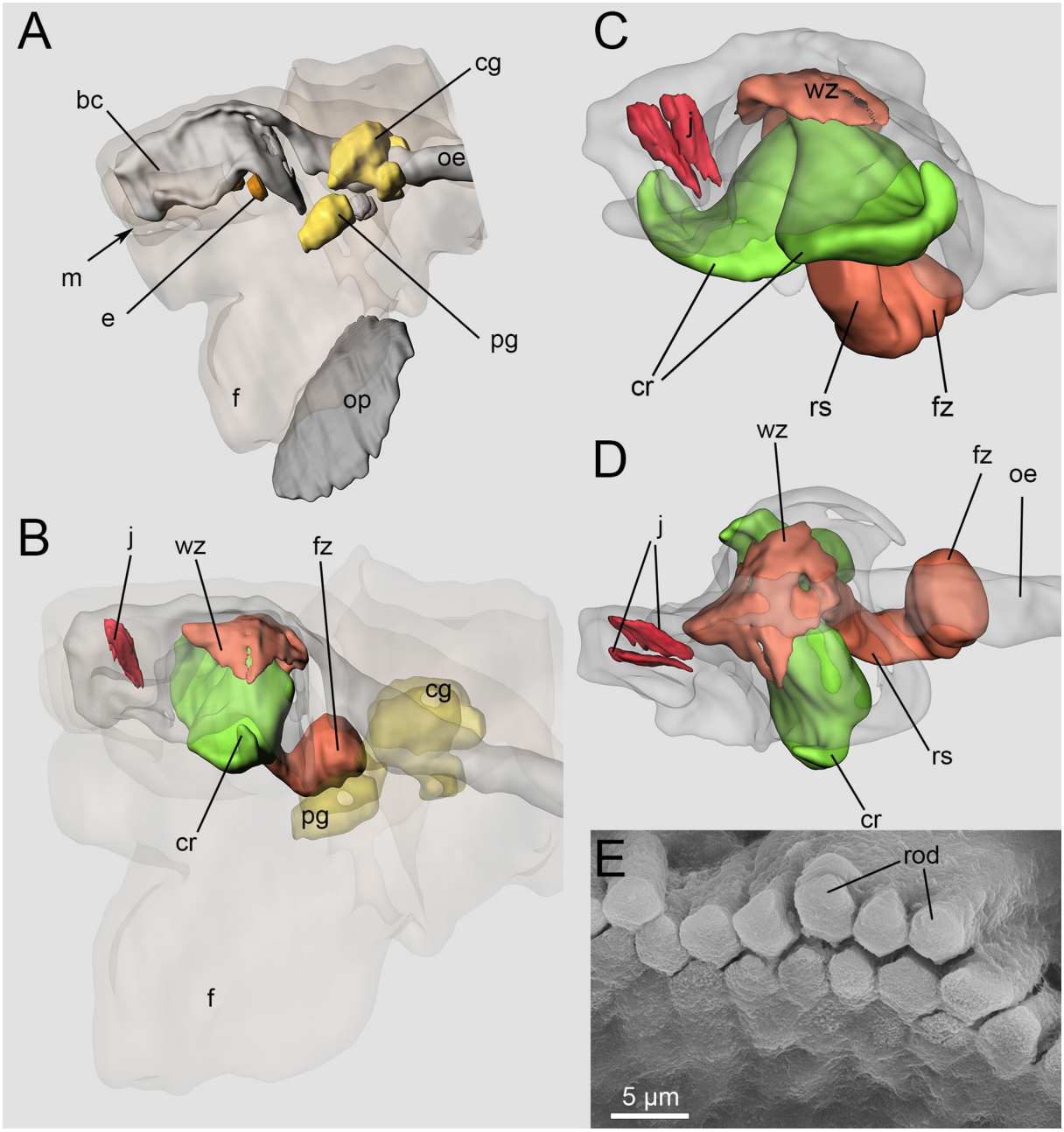

FIG. 4. Morphology of the buccal cavity of *Skeneopsis planorbis*. **A**–**D.** Three dimensional reconstruction of the head. **A.** Body coverings are semi-transparent; the outline of the buccal cavity and esophagus is opaque gray. Side view. **B.** Body coverings and wall of the buccal cavity are semi-transparent. Side view. **C**–**D.** Buccal apparatus in higher magnification. Side view (**C**) and view from above (**D**). **E.** Apical part of the jaws with rodlets, SEM photo. Abbreviations: bc – buccal cavity; cg – cerebral ganglion; cr – odontophoral cartilages; fz – formation zone of radula; j – jaw; m – mouth; oe – oesophagus; op – operculum; pg – pedal ganglion; rod – rodlets; rs – radular sac; wz – working zone of radula.

the synthesised rodlet by 1.5–1.7 µm (Fig. 3C, D). Gnathoblasts are secretory cells, as evidenced by the presence of well-developed granular endoplasmic reticulum (gER). The apical regions of gnathoblasts are connected by adherens junctions (Fig. 3D). Within the apical part of the gnathoblast, chitosome – vesicles (d: 0.05–0.1 µm) with globular chitin – are found. The nucleus of the gnathoblast is located in the central region of the cell (Fig. 3C).

Jaw morphology of *Skeneopsis planorbis*

The round mouth opening of *S. planorbis* lies ventrally and is surrounded by lips (Figs 1C; 4A). The buccal cavity of *S. planorbis* is relatively small. The buccal armature consists of a radula and paired jaws (Fig. 4B). The jaws are situated laterally within the buccal cavity, opposite the working zone of the radula (Fig. 4B–D). Ventrally, the jaws are connected

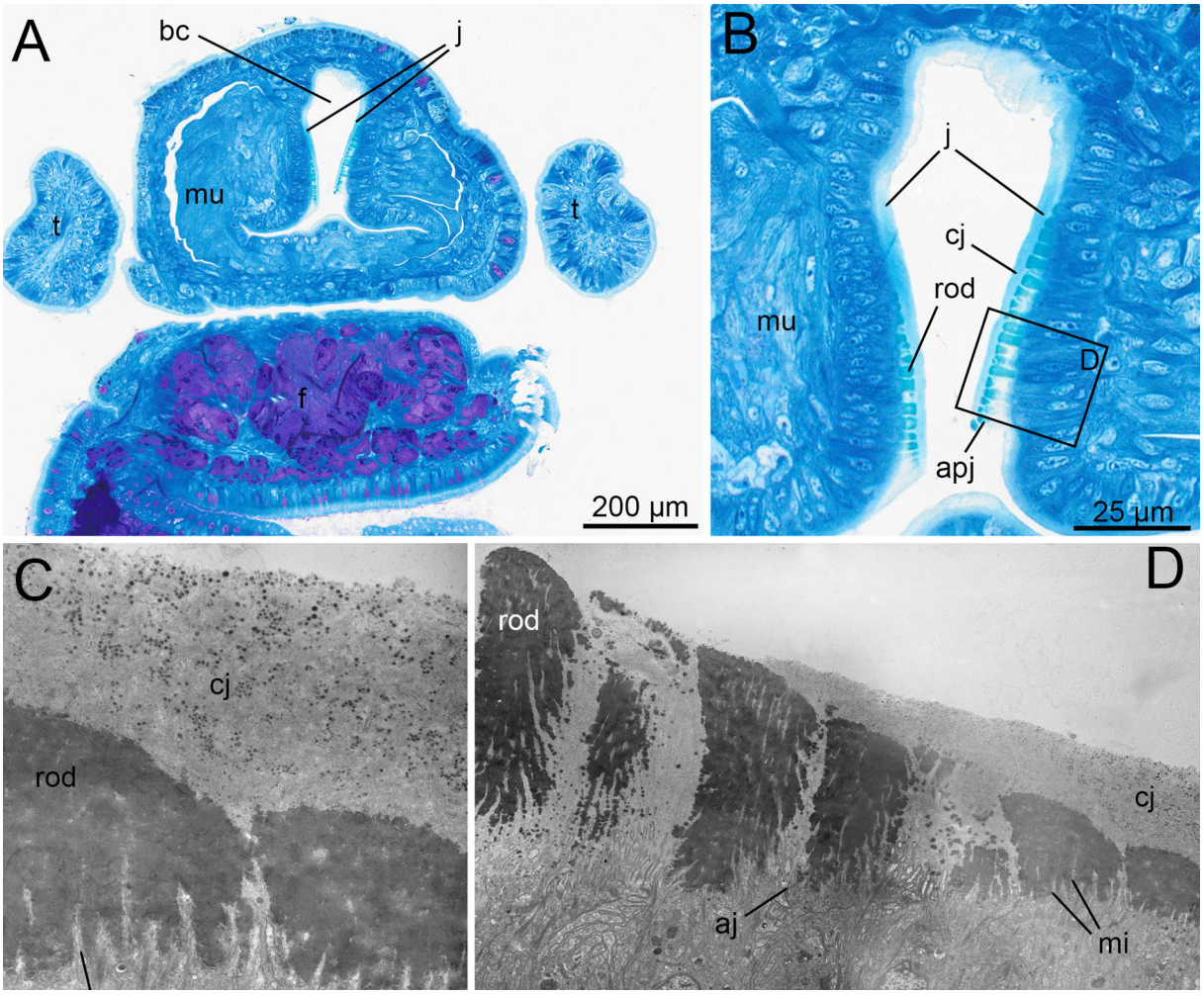

FIG. 5. Jaw morphology of *Skeneopsis planorbis*. **A.** Transverse histological section through the jaws located on the lateral sides of the buccal cavity. **B.** Transverse section through the jaws with rodlets in higher magnification. **C.** Transverse ultrathin section through the gnathoblasts and rodlets, TEM photo. **D.** Transverse ultrathin section through the apical part of the jaw, TEM photo. Abbreviations: aj – adherens junctions; apj – apical part of the jaw; bc – buccal cavity; bl – basal lamella; ch – chitosome; cj – cover layer of the jaw; j – jaw; mi – microvilli; mu – muscles; n – nucleus; rod – rodlets; tf – tonofilaments.

by a thick cuticle (Fig. 5A, B). Each jaw comprises two layers: a lower layer formed by rodlets and an upper homogeneous layer (Fig. 5B–D). The jaw plate is underlain by secretory epithelium composed of gnathoblasts (Fig. 5B–D). Similar to *M. helicinus*, each gnathoblast corresponds to a single rodlet, and the microvilli of the gnathoblast reach into the rodlet by 0.5–1 µm (Fig. 5C, D). The gnathoblasts of *S. planorbis* are narrow cells (2 µm wide, 7–8 µm high) with large oval centrally located nuclei (Fig. 5D). Chitosomes (diameter: 0.05–0.1 µm) are present in the apical region of the gnathoblasts (Fig. 5C). The gnathoblasts are connected by adherens junctions, and the basal portion of each cell secretes a basal lamina. Beneath this lamina lies a layer of musculature (Fig. 5D). Each gnathoblast contains bundles of tonofilaments oriented apicobasally, which connect to the underlying muscle layer (Fig. 5C, D).

Buccal armature morphology of *Peringia ulvae*

We have documented the radula and paired jaws of *P. ulvae* (Fig. 6A). The radula is short (up to 0.5 mm) and terminates with an expanded zone of formation (Fig. 6A). The small, paired rectangular jaws (150 × 200 µm) bear several rows of rodlets along their external edges (Fig. 6C, D). The rodlets are clearly visible while stained with CfW, which marks unpolymerised chitin (Fig. 6B).

Jaw morphology of *Velutina velutina*

The jaws of *V. velutina* are paired strong plates, up to 800 µm in length and 450 µm in width (Fig. 6E, F), covered by rodlets or rather denticles, arranged in regular longitudinal rows (Fig. 6G). The jaw plates are located laterally and are connected to

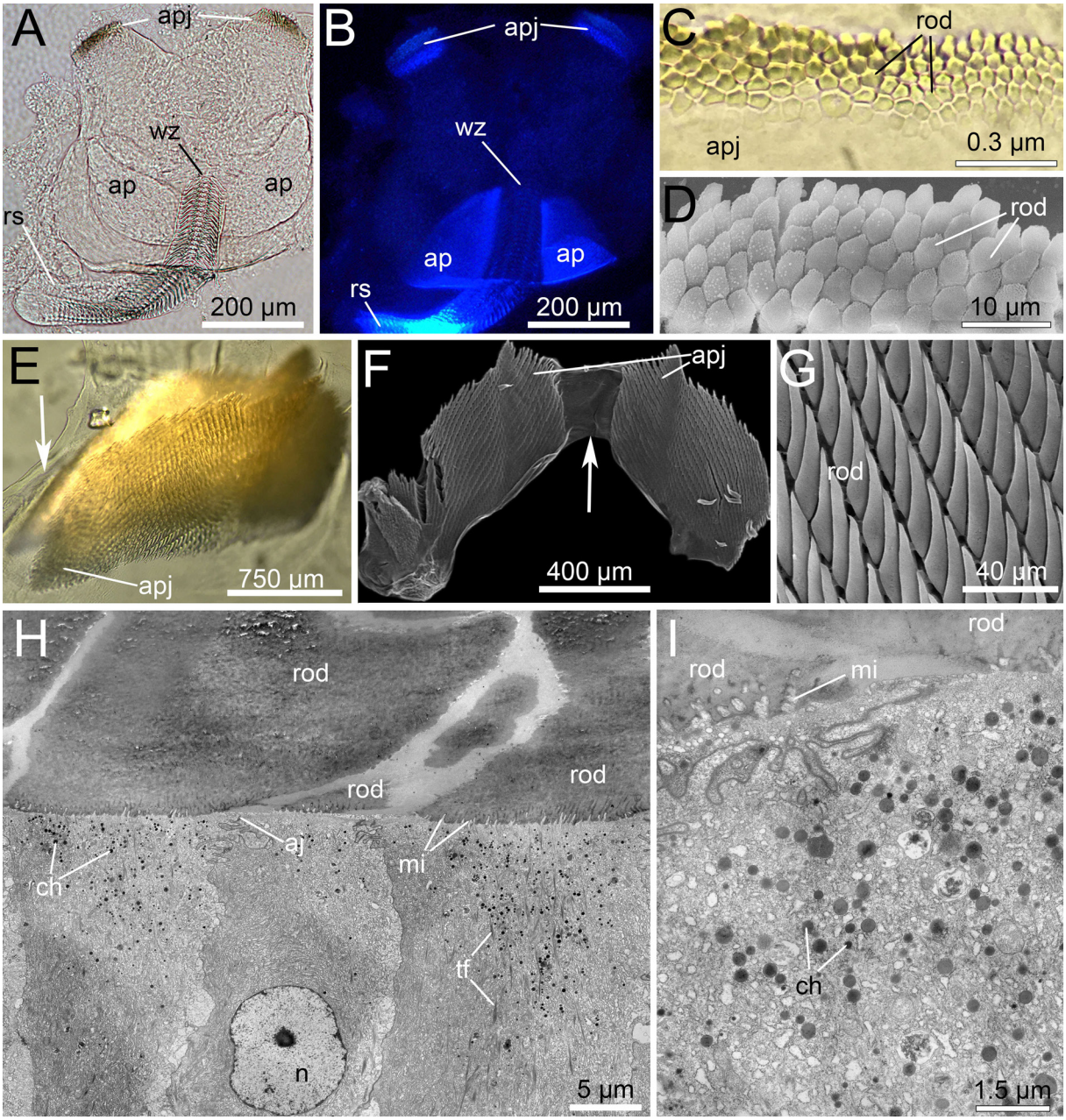

FIG. 6. Jaw morphology of *Peringia ulvae* (**A–D**) and *Velutina velutina* (**E–I**). **A.** Light microscopy of buccal apparatus consisting of radula and jaws of *P. ulvae*. **B.** Feeding apparatus of *P. ulvae* stained with CfW (laser 405 nm) on amorphous chitin. Radula and jaws are stained blue. **C.** Light microscopy of apical part of the jaw of *P. ulvae*. **D.** Apical part of the jaw with rodlets, SEM photo. **E.** Jaws of *V. velutina* by light microscopy. **F.** View from above of the jaws connecting on the dorsal side (arrow) by cuticle, SEM photo. **G.** Part of the jaw with rodlets on higher magnification, SEM photo. **H.** Ultrastructure of gnathoblasts and rodlets, TEM photo. **I.** Apical part of gnathoblast, TEM photo. Abbreviations: aj – adherens junctions; ap – alary processes of the subradular membrane; apj – apical part of the jaw; ch – chaetosoma; mi – microvilli; n – nucleus; rod – rodlets; tf – tonofilaments.

each other ventrally by thin cuticle (Fig. 6F). The covering homogenous layer, which was found in *S. planorbis*, is absent (Fig. 6 E, F). Under the jaw plate the gnathoblasts are found. They are connected in the apical parts by adherens junctions (Fig. 6H). Each gnathoblast (15–17 µm in height, 12–15 µm in width) corresponds to a rodlet (Fig. 6H). The apical surface of a gnathoblast bears microvilli, which reach into a rodlet by 1–1.5 µm; also there are numerous chitosomes (d: 0.05–0.1 µm) in the apical part of the cell (Fig. 6H, I). The gnathoblast nuscleus is round (d: 10–12 µm) and locates basally. The gnathoblast contains bundles of tonofilaments directed apico-basally (Fig. 6H).

Jaw morphology of *Rapana rapiformis*

The pharynx of *R. rapiformis* (Muricidae) is a muscular dilation of the foregut, which contains

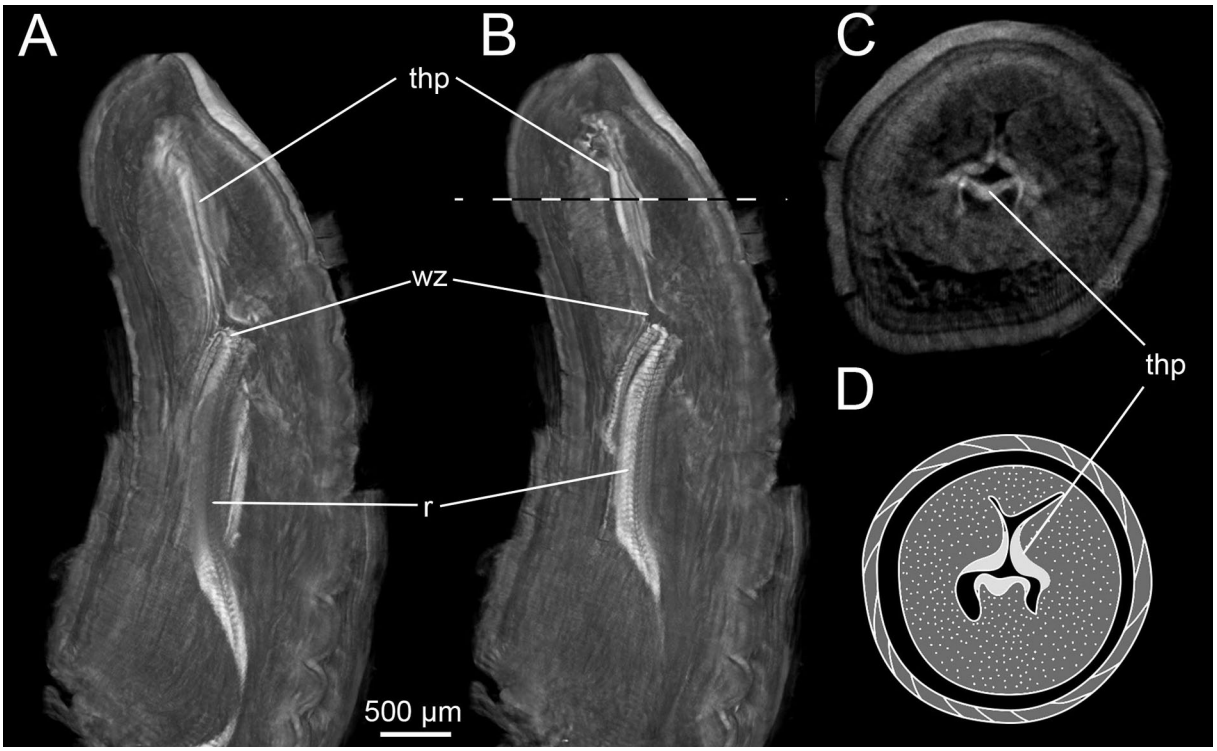

FIG. 7. Morphology of proboscis of *Rapana rapiformis* based on micro-CT data. **A**–**B.** Longitudinal section through the anterior proboscis. **C.** Transverse section through the oral tube (identified by black-white line on figure B) with three thickenings (two lateral and one ventral) of the tube cuticle. **D.** Schematic overview of transverse section through the oral tube. Abbreviations: r – radula; thp – thickness of the oral tube cuticle; wz – working zone of radula.

voluminous and complex musculature and an odontophore. These structures comprise the buccal mass, occupying a significant part of proboscis (Fig. 7A, B). According to micro-CT data, the pharynx has a three-lobed lumen with a thickened lining on the lateral and ventral walls (Fig. 7C, D). These cuticular thickenings are up to 750 µm long and 80 µm thick. Currently, it's uncertain whether these thickenings represent distinct jaws. This thickness may represent an early stage of jaw evolution.

Jaw morphology of *Phalium glaucum*

The jaws of *Phalium* (Cassidae) consist of paired, vertical trapeziform smooth lateral plates, located within the buccal cavity on either side of the radula's working zone. According to micro-CT data, the jaws have sizes up to 3 mm in length and 2 mm in width, their thickness is up to 200 µm. The plates almost reach the height of the buccal cavity (Fig. 8).

Jaw morphology of representatives of Cancellariidae

Three representatives of Cancellariidae, *Trigonostoma lamberti* (Fig. 9A), *Sydaphera lactea* (Fig. 9B), and *Admete viridula* (Fig. 9 C–H), also possess jaws. In these species, the jaw is represented by a single plate longitudinally split by a dorsal slit. The anterior part of the jaw is modified into a tube (Fig. 9E). In *Trigonostoma lamberti*, which has a well-developed radula, this tube is formed by the left and right margins of the jaw plate, which overlap ventrally without fusing. The jaw tube continues from the oral tube to the buccal mass. The posterior part of the jaw is broad and consists of two halves that cover the buccal mass laterally (Fig. 9A). The jaw of *Sydaphera lactea*, species with radula, has a jaw fused in the apical part to the tube (Fig. 9B).

Admete viridula is a radula-less species. The jaw in *Admete* has a puncturing function [Harasewych, Petit, 1986]. In this species, the left and right parts of the anterior part of the jaw plate fuse to form a tube, which can extend out of the proboscis through the mouth opening. The broad posterior part of the jaw plate is bilobed and surrounds the buccal cavity laterally (Fig. 9 C–F). The jaw is a chitinous thickening that lines the buccal cavity. According to cLSM data, the posterior part of the jaw plate stains intensively with Calcofluor white, indicating the presence of unpolymerised chitin, whereas the anterior part (the tube) does not (Fig. 9 D–F). This suggests that the tube may contain polymerised chitin. Ultrathin sections reveal that the jaw plate is electron-dense and solid (Fig. 9 G–H). Beneath the jaw lies a layer of gnathoepithelium, composed of flattened gnathoblasts (1.5–2 µm in heigth, 3–4 µm in width) with electron-translucent cytoplasm (Fig. 9G). The microvilli of the gnathoblasts reach into the jaw plate by 1.5–2 µm (Fig. 9H).

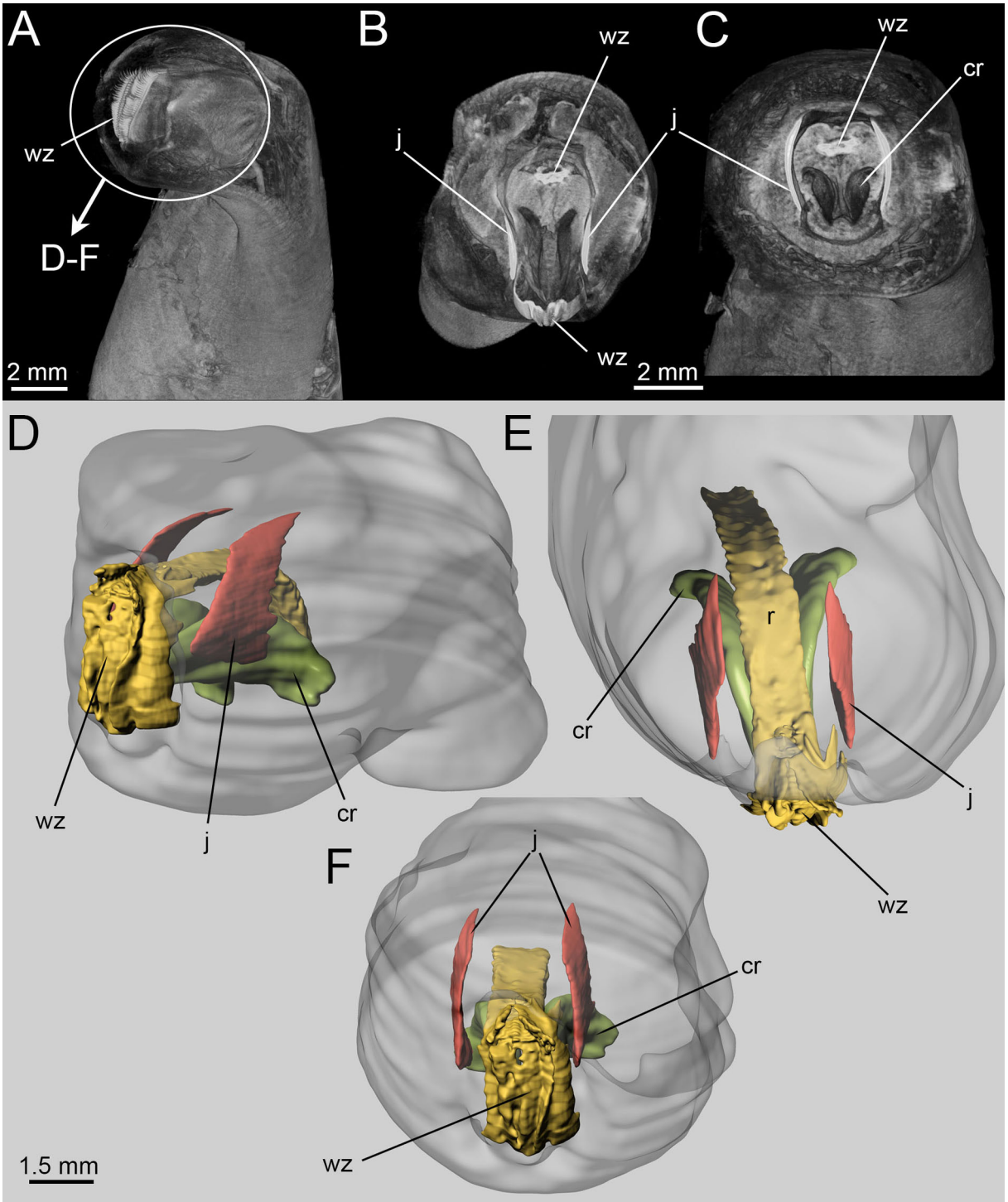

FIG. 8. Morphology of proboscis of *Phalium glaucum* based on micro-CT data. **A.** General view on the tip of proboscis, micro-CT. **B–C.** Sections through the buccal apparatus on different levels, micro-CT. **D–F.** Three-dimensional reconstruction of buccal complex labelled by circus on the figure A. Body cover is semi-transparent. Lateral view (**D**), view from above (**E**) and frontal view on the buccal complex (**F**). Abbreviations: cr – odontophoral cartilages; j – jaw; r – radula; wz – working zone of radula.

Discussion

According to the published data, the jaws in all vetigastropods – except for the majority of the representatives of deep-sea family Cocculinidae [Haszprunar 1987; Dantart, Luoue, 1994], which have unpaired jaws – usually consist of paired lateral plates positioned opposite the working zone of the radula. Sometimes these plates are connected with a thin cuticle and look like a single one (e.g., in pleurotomariid *Perotrochus*) [Harasewych, Askew, 1993]; the similar situation is described for some Neritimor-

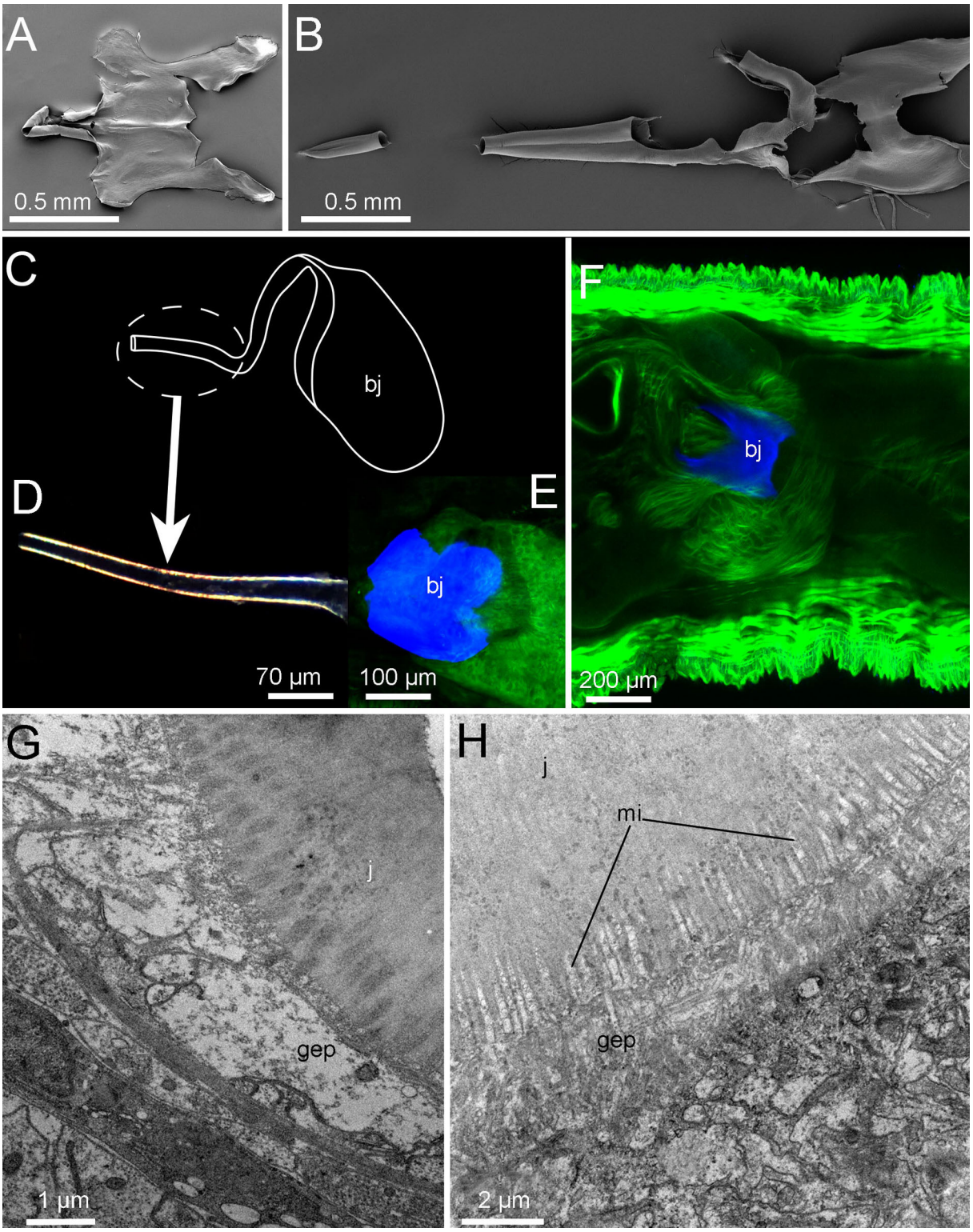

FIG. 9. Jaw morphology of Cancellariidae. **A.** General morphology of jaw of *Trigonostoma lamberti*, SEM photo. **B.** General morphology of jaw of *Sydaphera lactea*, SEM photo. **C-H.** Jaw morphology of *Admete viridula*. **C.** Schematic overview of the jaw. **D.** Light microscopy photo of the apical part of the jaw. **E.** Basal part of the jaw, cLSM photo. **F.** Part of the proboscis with basal part of the jaw, cLSM photo. Blue – jaw stained with CfW (laser 405 nm) on amorphous chitin, green – muscles. **G.** Ultrastructure of the apical part of the jaw, TEM photo. **H.** Ultrastructure of the basal part of the jaw, TEM photo. Abbreviations: bj – basal part of the jaw; gep – gnathoepithelium; j – jaw; mi – microvilli.

pha [Sasaki, 1998]. The masticatory edge of the jaw plate usually bears rodlets (Haliotidae [Crofts, 1937], Fissurellidae [Sasaki, 1998], Lepetodrilidae, Seguenzioidea [Kunze, et al., 2016]), though it is smooth in some families (Pleurotomariidae [Harasewych, 2002], Trochidae [Marshall, 1988; Simone, Cunha, 2006]). However, the jaws of *Margarites helicinus* (Trochidae), described in this study, have rodlets in contrast to other representatives of this family. A similar morphology has been reported for the jaws of *Puncturella noachina* (Fissurellidae) [Vortsepneva et al., 2014]. Both species possess paired dorsolateral jaws with rodlets on the working edge, a feature characteristic of species specialised in detritivory. This type of jaw, combined with a rhipidoglossan radula, is highly effective for collecting soft detritus particles: the jaws are pressed against the tip of the odontophore while a specimen swallows the collected detritus, preventing the food particles from falling out. This function was previously described for Vetigastropoda and Caenogastropoda [Starmühlner, 1952; Hawkins *et al*., 1989]. The jaw is formed by a cuticular plate, which is synthesised by microvilli of the underlying gnathoepithelium. In both listed species, the anterior edge of the jaw consists of two layers: an external chitinous matrix and an internal layer of short rodlets arranged in multiple rows. A key feature of this jaw type is its synthesis mechanism: each rodlet is secreted by a single cell.

Data on the jaws of Littorinimorpha in literature is limited, since jaws are completely reduced in the majority of species within this group [Ponder, Lindberg, 1997]. When present, the jaws in Littorinimorpha typically appear as paired lateral plates with rodlets on the working edge [Ponder, Lindberg, 1997]. In *Skeneopsis planorbis*, *Peringia ulvae*, and *Velutina velutina*, paired lateral chitinous jaw plates are positioned opposite the working edge of the radula. In the case of small-sized gastropods (*S. planorbis* and *P. ulvae*), the jaws are small, with working edges similar in width to the radula, and the rodlets are tiny and scale-like. In contrast, *V. velutina* possesses large jaw plates, with the width of the working edge exceeding that of the radula by four times. Sharp denticles cover nearly the entire surface of the jaw plate, and their size is comparable to that of the radular teeth. Based on these observations, we hypothesise that the jaws play a significant role in the feeding process of these species, helping to grate the hard covers of its prey [Sargent *et al*., 2019].

The internal structure of the jaws in Littorinimorpha is similar to that described in Vetigastropoda. Based on histological data, it was shown that the jaw plates of *S. planorbis* and *V. velutina* consist of two distinct layers: an external homogeneous layer and an internal layer of rodlets. Each rodlet is synthesised by a single cell, a process similar to that described for the jaws of *Marisa cornuarietis* (Linnaeus, 1758) (Architaenioglossa, Caenogastropoda) [Lufty, Demian, 1967] and the jaws of Vetigastropoda [Vortsepneva *et al*., 2014; present study]. Consequently, the jaws of Vetigastropoda, Architaenioglossa, and studied Littorinimorpha exhibit similar morphology and renewal mechanisms. We propose the term ‘complex jaw’ to describe this type of jaw structure, characterised by an upper (external) homogeneous layer and a lower (internal) layer of rodlets, in contrast to the ‘simple jaw’, previously described in Patellogastropoda [Vortsepneva *et al*., 2013]. These terms partially overlap with those proposed earlier by Ponder and Lindberg [1997]. However, in their work, ‘complex jaws’ were defined as structures composed exclusively of solitary elements, with no mention of the external homogeneous layer that integrates these elements into a unified structure.

The renewal mechanism of this complex jaw partially resembles that of the radula. In the case of the radula, the teeth of each transverse row are synthesised almost simultaneously. During this process, the cells which secrete the radular tooth (odontoblasts) develop numerous microvilli that extend into the forming tooth [Mischor, Markel, 1984; Mackenstedt, Markel, 1987; Vortsepneva et al., 2023; Wiesel, Peters, 1978]. The tooth is thus formed through microvillar secretion, a process similar to the formation of rodlets. A single group of odontoblasts secretes one tooth and is capable of sequentially secreting multiple teeth. Specifically, once a tooth is fully formed, it detaches from the odontoblasts. The microvilli of the odontoblasts then dissolve, allowing the tooth to move away from the odontoblasts. Over time, the odontoblasts develop new microvilli and initiate the synthesis of a new tooth. This intermittent activity of the odontoblasts enables the formation of a serial radula, consisting of repeated rows of transverse teeth. We hypothesise a similar mechanism for rodlet synthesis, as a single gnathoblast secretes a single rodlet. Following secretion, the rodlet detaches from the gnathoblast, the microvilli dissolve, and new microvilli subsequently form, initiating a new cycle of rodlet secretion. A similar synthesis mechanism for serial structures has been previously proposed for the jaws of *Puncturella noachina* (Vetigastropoda) [Vortsepneva *et al*., 2014]. We suggest that gnathoblasts, like odontoblasts, are capable of repeatedly transitioning between synthesis and resting phases. This process also bears resemblance to the moulting mechanisms observed in ecdysozoans [Aguinaldo et al., 1997] and leeches [Berchtold et al., 1985; Vortsepneva, Lavrov, 2021], where the underlying epithelium intermittently synthesises new cuticular layers.

In contrast to the aforementioned gastropod species, *Phalium* (Cassidae) possesses paired simple and solid jaw plates devoid of rodlets. These plates are located on each side of the radula’s working zone.

However, in some other representatives of the same superfamily (e.g., *Cymatium*) the jaws bear rodlets [Houbrick, Fretter, 1969; Barkalova *et al.*, 2016].

In Neogastropoda, the jaws are often absent [Ponder, Lindberg, 1997]. Nevertheless, various forms of jaws and buccal cuticle thickenings have been documented in certain species [Carriker, 1943; Wu, 1965; Harasewych, Petit, 1986]. The most typical jaw-like structure in this group is a thickening of the buccal cuticular lining, as observed in Muricidae. In this case, the ventral ridges of the oral tube extend into the lateral ridges and fuse with a dorsal sclerite. This dorsal sclerite is likely a rudimentary jaw plate, which is thought to aid in cleaning the radula of food particles and preventing damage to the oral tube wall during radula movements [Carriker, 1943]. In some muricid species, both ventral and dorsal jaw structures have been reported [Wu, 1965]. A highly specialised type of jaw is found in Cancellariidae [Harasewych, Petit, 1986; present study]. In cancellariids, we propose that initially paired jaw plates have fused dorsally. The broad posterior part of the jaw surrounds the odontophore laterally, while the anterior part is modified into a tube. In species with a radula, the tube is not fully closed, whereas in radula-less cancellariids, it forms a hollow stylet. The jaw is synthesised via microvillar secretion. The internal structure of neogastropod jaws is homogeneous, lacking rodlets or other solitary structures. These jaws are continuously secreted in specialised growth zones, similar to the process described for patellogastropod and cladobranch jaws [Vortsepneva *et al*., 2013; Mikhlina, Vortsepneva, 2023; Mikhlina *et al*., 2018].

The diversity of jaw morphotypes and their varying locations within the oral tube (lateral, dorsal, and ventral) in neogastropods highlights the buccal epithelium's remarkable capacity to form jaw structures along the entire perimeter of the buccal cavity.

Conclusion

Our morphological data, along with data from the literature, indicate that gastropod jaws can be classified into two categories based on their internal structure and synthesis mechanism: complex and simple. The first type, found in Vetigastropoda and the majority of Caenogastropoda, exhibits a similar two-layered structure and an intermittent type of synthesis mechanism, which resembles the process of radula synthesis. This type of synthesis is likely a unique characteristic of molluscan jaws and the radula. However, a similar mechanism can also be observed during the moulting process of ecdysozoans and leeches. Additionally, in representatives of the aforementioned two subclasses, each jaw rodlet is synthesised by a single gnathoblast.

The second type of jaws is found in Neogastropoda, one species of Cassidae (Littorinimorpha), Patellogastropoda, and Cladobranchia. The jaws in these groups are solid and secreted continuously via the activity of microvilli of gnathoepithelium. The location of the jaws may vary among different Neogastropoda, suggesting a high degree of plasticity in the buccal epithelium to synthesise jaws or jaw-like structures. This variability complicates the identification of homology in jaw structures based solely on positional criteria.

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