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The evolution of the radula in molluscs: what was first, flexoglossy or stereoglossy?

E.V. Vortsepneva[1*], A.L. Mikhlina[2], Yu.I Kantor[3]

[1] Invertebrate Zoology Department, Lomonosov Moscow State University, Leninskie Gory 1-12, Moscow 119234 Russia.
[2] White Sea Biological Station, Lomonosov Moscow State University, Leninskie Gory 1-12, Moscow 119234 Russia.
[3] Laboratory of Marine Invertebrate Morphology and Ecology, A.N. Severtsov Institute of Ecology and Evolution RAS, Leninsky Prospekt 33, Moscow 119071 Russia.
Elena Vortsepneva: vortcepneva@gmail.com ORCID https://orcid.org/0000-0002-8163-2733
Anna Mikhlina: mikhleanna@gmail.com ORCID https://orcid.org/0000-0002-9231-0545
Yuri Kantor: kantor.yuri1956@gmail.com ORCID https://orcid.org/0000-0002-3209-4940
** Corresponding author*

ABSTRACT: Two fundamental types of radulae in Mollusca have been recognized: stereoglossate and flexoglossate. The former is characterized by a fixed connection between the teeth and the radular membrane, a membrane that is not folded longitudinally, and parallel feeding tracks where the teeth act as a rasp. This type of radula has been considered present in Monoplacophora, Polyplacophora, Scaphopoda, and one gastropod subclass, the Patellogastropoda, and is therefore thought to represent the ancestral state of radulae in Gastropoda. In contrast, the flexoglossate radula is characterized by a mobile connection between the teeth and the radular membrane, longitudinal folding of the membrane within the radular sac, and the mobility of rotating marginal teeth, which follow different trajectories during feeding. The flexoglossate radula is typical of all Gastropoda except Patellogastropoda.
A detailed examination of the radular apparatus of ten gastropod species from different subclasses, including Patellogastropoda, as well as three Polyplacophora species, has allowed us to reevaluate the stereoglossate condition in gastropods and polyplacophorans. We demonstrate that the radular membrane is folded longitudinally in the radular sac in all the species studied. Among Patellogastropoda, this was most obvious in *Scutellastra longicosta*, which has a broader and more complete radular transverse row (13 teeth), though traces of folding were observed even in *Testudinalia testudinalis*, which has only 4 teeth in a transverse row. Similarly, the radular membrane was folded longitudinally in the radular sac of chitons, which were previously thought to have a stereoglossate radular type. Our data allowed us to re-evaluate the established views on the evolution of radula. Most likely, the plesiomorphic state of molluscan radula is a flexible flexoglossate condition. We conclude that the stereoglossate condition in Patellogastropoda is not a distinct radular type but rather a secondary modification of an originally flexoglossate radula. This modification is related to the reduction of teeth in the transverse row, retaining only the central portion of the radula, consisting of two pairs of lateral teeth.
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KEY WORDS: Gastropoda, Polyplacophora, docoglossate, taeniolgossate, rhipidoglossate, radula.

Devoted to memory of Claus Nielsen.

Эволюция радулы моллюсков: что появилось раньше, флексиглоссность или стереоглоссность?

Е.В. Ворцепнева[1*], А.Л. Михлина[2], Ю.И. Кантор[3]

[1] Кафедра зоологии беспозвоночных, Московский государственный университет им. М.В. Ломоносова, Ленинские горы 1-12, Москва 119234 Россия.
[2] Беломорская биологическая станция МГУ, Московский государственный университет им. М.В. Ломоносова, Ленинские горы 1-12, Москва 119234 Россия.
[3] Лаборатория морфологии и экологии морских беспозвоночных, Институт проблем экологии и эволюции им. А.Н. Северцова РАН, Ленинский проспект 33, Москва 119071 Россия.
Ответственный за переписку: vortcepneva@gmail.com

РЕЗЮМЕ: У моллюсков выделяют два основных типа радулы: стереоглоссный и флексиглоссный. Первый тип характеризуется жестким соединением зубов с радулярной мембраной, не складывающейся вдоль, и параллельными траекториями движения зубов при питании, действующими как терка. Считается, что этот тип радулы присутствует у Monoplacophora, Polyplacophora, Scaphopoda и одного подкласса брюхоногих моллюсков, Patellogastropoda. Соответственно, он считался исходным состоянием радулы у Gastropoda.
Флексиглоссная радула, в отличие от стереоглоссной, характеризуется подвижным соединением между зубами и радулярной мембраной, продольным складыванием мембраны внутри радулярного мешка и подвижностью вращающихся краевых зубов, которые следуют разным траекториям во время питания. Этот тип радулы характерен для всех брюхоногих моллюсков, за исключением Patellogastropoda.
Подробное исследование радулярного аппарата десяти видов Gastropoda из различных подклассов, включая Patellogastropoda, а также трех видов хитонов (Polyplacophora) позволило пересмотреть концепцию о стереоглоссном состоянии радулы у брюхоногих моллюсков и хитонов. Мы показали, что радулярная мембрана складывается продольно в радулярном мешке у всех изученных видов. Среди Patellogastropoda это наиболее заметно у вида *Scutellastra longicosta*, имеющего более широкую радулу с 13 зубами в поперечном ряду. Следы складывания наблюдались даже у вида *Testudinalia testudinalis*, обладающего радулой с 4 зубами в поперечном ряду. Аналогично, радулярная мембрана складывалась продольно в радулярном мешке у хитонов, которые ранее считались обладающими стереоглоссным типом радулы.
Наши данные позволяют переоценить устоявшиеся взгляды на эволюцию радулы у моллюсков. Вероятнее всего, флексиглоссное состояние радулы является плезиоморфным для моллюсков. Мы пришли к выводу, что стереоглоссное состояние у Patellogastropoda является не самостоятельным типом радулы, а скорее вторичной модификацией изначально флексиглоссной радулы. Эта модификация связана с уменьшением числа зубов в поперечном ряду, при котором сохраняется только центральная часть радулы, состоящая из двух пар латеральных зубов.
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КЛЮЧЕВЫЕ СЛОВА: Gastropoda, Polyplacophora, докоглоссная, рипидоглоссная, тениоглоссная, радула.

Introduction

Radular apparatus is the primary organ for obtaining food in all molluscs, except bivalves and aberrant forms of gastropods with highly specialized feeding types. The latter include, *e.g.* parasitic gastropods, radula-less gastropods with suctorial feeding mode (Ponder *et al*., 2020). The radula itself is a chitin ribbon of teeth, which is continuously renewing during the mollllusc lifetime (see, for example, Runham, 1962; Isarankura, Runham, 1968; Kerth, 1983; Mischor, Märkel, 1984; Mackenstedt, Märkel, 1987; Starobogatov, 1990a, b). This specific feature of radula, its ability for constant renewal, allowed the ancestral molluscan forms to exploit a rich but challenging food source, the biofilms and fouling found on the hard substrata (Ivanov, 1990).

The rasping feeding mode, specific to feeding on hard substrata fouling, can either imply the presence of hard teeth undergoing rapid wear during feeding (Shaw *et al*., 2010), of clever geometries of teeth that prosper the formation of a stiff tooth array transmitting high stresses (Krings, Gorb, 2024), or potentially by a high tooth turnover rate (Isarankura, Runham, 1968; Underwood, 1984). Consequently, this feeding strategy is available only for animals with continuously renewing buccal armature, such as the radula.

For the major classes of Mollusca, Monoplacophora, Polyplacophora, Cephalopoda, and Scaphopoda, a relatively narrow range of feeding strategies is typical, leading to a conserved morphology of the food-obtaining apparatus (Ivanov, 1990). In contrast, gastropods demonstrate the most diverse feeding strategies, a result of morphological plasticity of their food-obtaining apparatus, particularly the radula (Ponder *et al*., 2020). Over 35 terms have been used to describe different radula types within Gastropoda (see, for example, Gray, 1853; Troschel, 1856–1863; Mörch, 1865; MacDonald, 1869; Sars, 1878; Minichev, Starobogatov, 1979; Salvini-Plawen, 1988; Starobogatov, 1990a, b; Ponder, Lindberg, 1997). This extensive terminology stems from differences in the criteria used by authors to describe and classify radula types. Key characters of radula include the number of teeth per transverse row and the number of rows. Additional features include the mobility of tooth-membrane connection, the shape of radular ribbon within the radular sac, etc. (Starobogatov, 1990a, b; Ponder, Lindberg, 1997).

Salvini-Plawen (1988) proposed two basic radular types: *stereoglossate* and *flexoglossate*. The primary difference between these types lies in the movement of the radula during feeding. In the stereoglossate type, “the radular tongue acting as a simple rasp parallel to the longitudinal axis without lateral rotary movements of the teeth or an effective bending plane of the radula” (Salvini-Plawen, 1988: 359). Contrarily, flexoglossate radula, as defined by Salvini-Plawen (1988), is a “flexible tongue that causes each radular tooth to scrape the substratum when it moves over the bending plane” (Salvini-Plawen, 1988: 359).

Beside this definition, the terms “stereoglossate” and “flexoglossate radular condition” were frequently used by other authors to describe radular morphology and function (Salvini-Plawen, Haszprunar, 1987; Haszprunar, 1988, 1993; Schaefer, Haszprunar, 1996; Ponder, Lindberg, 1997; Guralnick, Smith, 1999).

Based on the literature data, the stereoglossate and flexoglossate radular conditions can be defined as follows:

(1) Stereoglossate radula (also referred to as docoglossan — Starobogatov, 1990; Ponder, Lindberg, 1997) is a rigid radula with fixed connection between teeth and radular membrane. The radular membrane is rather firm and does not fold longitudinally, neither at the working plane nor within the radular sac. The feeding tracks produced by this radula on the substratum are parallel, and the radula functions as a rasp (Ankel, 1938; Haszprunar, 1988; Salvini-Plawen, 1988; Ponder, Lindberg, 1997; Guralnick, Smith, 1999). Stereoglossate radula is typically found in Monoplacophora, Polyplacophora, Scaphopoda, and one gastropod subclass, the Patellogastropoda (Golikov, Starobogatov, 1975; Wingstrand, 1985; Haszprunar, 1988; Salvini-Plawen, 1988).

(2) Flexoglossate radula is a radula with mobile connection between teeth and radular membrane. The radular membrane is flexible, folding longitudinally within the radular sac and unfolding at the working plane. In flexoglossate radulae, the marginal teeth are mobile and can rotate, helping to gather the particles from a larger area compared to stereoglossate radula. The flexoglossate radular condition is characteristic of all Gastropoda, except Patellogastropoda. That includes Vetigastropoda, Neritimorpha,

Caenogastropoda, and Heterobranchia (Ponder, Lindberg, 1997; Ponder *et al*., 2020; Vortsepneva *et al*., 2023b).

The appearance of flexoglossate radula was a key event in the evolutionary history of gastropod molluscs. The development of longitudinal bending of the membrane facilitated the differentiation of radular teeth into morphologically distinct groups, allowing them to acquire new functions (Minichev, Starobogatov, 1979; Ponder, Lindberg, 1997), enabled the radula to function as diverse tools, such as brooms, scissors, etc. (Ankel, 1936; Hickman, Morris, 1985). This novel feeding mechanism provided early non-Patellogastropoda with a more efficient feeding strategy, which eventually resulted in a decline in patellogastropod diversity in habitats where the two listed clades coexisted (Ponder, Lindberg, 1997).

For a long time, the prevailing phylogenetic hypothesis on molluscan relationships was the morphology-based "Testaria" concept. According to this concept, gastropods, monoplacophorans, and polyplacophorans formed a monophyletic clade called Testaria. Polyplacophora were considered the sister clade to Conchifera, which comprises all shell-bearing molluscs, including Monoplacophora and Gastropoda. Furthermore, Monoplacophora were reconstructed as the sister group to other Conchifera (Salvini-Plawen, 1985; Salvini-Plawen, Steiner, 1996; Haszprunar, 2000). One of the synapomorphies of Testaria was the stereoglossate radular condition, found in Polyplacophora, Monoplacophora, Scaphopoda, Cephalopoda, and Patellogastropoda (previously considered the most basal gastropod clade) (Salvini-Plawen, 1988; Salvini-Plawen, Steiner, 2014). Therefore, the flexoglossate condition, characteristic of all Gastropoda except patellogastropods, was considered apomorphic, while the stereoglossate condition was deemed plesiomorphic for molluscs.

On the other hand, alternative hypotheses suggested the plesiomorphy of rhipidoglossan (wide flexoglossate) radula in gastropods (*e.g.* Fretter, Graham, 1962; Graham, 1973, 1979). However, they were doubted, as they implied an independent appearance of the stereoglossate radula in Patellogastropoda and other molluscan groups (Ponder, Lindberg, 1997).

However, the deep phylogenetic relationships within Mollusca were reconsidered, and currently the widely supported phylogenetic hypotheses favor the concept of Aculifera (Polyplacophora+Aplacophora) over Testaria (Polyplacophora+Conchifera) (Scheltema, 1993, 1996; Ivanov, 1996; Scheltema, Schander, 2000; Kocot *et al*., 2011, 2020; Smith *et al*., 2011). This suggests that the stereoglossate radula condition may have evolved independently in different molluscan lineages, doubting its previously assumed plesiomorphic status.

In preliminary studies, we obtained data on the histology of polyplacophoran radula, which has raised questions about its stereoglossate condition. This further challenges the previously proposed concept of stereoglossy as the plesiomorphic status for all molluscs. Therefore, the main purpose of this work is to verify the radular condition in Polyplacophora and Patellogastropoda and examine the validity of the "stereoglossate-as-plesiomorphic" concept. In our study, we examined the radular morphology of three polyplacophoran species and one patellogastropod species with a wide radula (*Scutellastra longicosta* (Lamarck, 1819)). We have also incorporated previously published data on radular morphology from other species representing all subclasses of Gastropoda.

Material and methods

MATERIAL. To trace the patterns of radula folding within the radular sac, we analyzed data from ten gastropod species (representing each subclass) and three polyplacophoran species (see Table 1). For the majority of these species, detailed descriptions of the radular morphology and formation process have been published previously. Here, we used the microphotographs of transverse semithin sections of radular sacs to illustrate the shape and location of the radular membrane.

Original data on radula morphology for *Scutellastra longicosta* (Patellogastropoda) are presented here for the first time. Five specimens of *S. longicosta* were collected from the subtidal rocky bottom at a depth of 25–30 m at the station NKR5 (22°19.8′S, 166°13.2′E) of KANAMECO 2024 expedition of Muséum national d'Histoire naturelle, Paris, France off Noumea, New Caledonia in March 2024.

Five specimens of *Buccinum undatum* were collected from the lower intertidal and upper subtidal zones near the N.A. Pertsov White Sea Biological Station (WSBS) of Lomonosov Moscow State University (MSU) in Kandalaksha Gulf, White Sea, Russia (66°33′N, 33°06′E) during the summer seasons of 2020–2022.

Table 1. List of species used in the present study.

Taxon	Species	References
Gastropoda		
Patellogastropoda	*Scutellastra longicosta*	Present study
	Testudinalia testudinalis (O.F. Müller, 1776)	Vortsepneva *et al*., 2019
Vetigastropoda	*Puncturella noachina* (Linnaeus, 1771)	Vortsepneva *et al*., 2021
Neritimorpha	*Nerita litterata* Gmelin, 1791	Vortsepneva *et al*., 2022
Caenogastropoda	*Lacuna pallidula* (da Costa, 1778)	Vortsepneva *et al*., 2023a
	Buccinum undatum Linnaeus, 1758	Present study
	Clavus maestratii Kilburn, Fedosov et Kantor, 2014	Vortsepneva *et al*., 2020
Heterobranchia	*Cadlina laevis* (Linnaeus, 1767)	Mikhlina *et al*., 2022
	Clione limacina (Phipps, 1774)	Vortsepneva, 2020
	Limapontia senestra (Quatrefages, 1844)	Mikhlina *et al*., 2024
Polyplacophora	*Leptochiton assimilis* (Thiele, 1909)	Present study
	Placiphorella stimpsoni (A. Gould, 1859)	Present study
	Tripoplax albrechtii (Schrenck, 1863)	Present study

Representatives of three polyplacophoran species: *Leptochiton assimilis* (3 specimens), *Placiphorella stimpsoni* (3 specimens), and *Tripoplax albrechtii* (3 specimens) were collected in Vostok Bay, Sea of Japan, near the Marine Biological Station Vostok, Institute of Marine Biology, Vladivostok, Russia (42°52′N, 132°43′E) in the tidal zone from under stones.

METHODS. Prior to fixation, radular sacs were dissected from all collected specimens. The radular sacs were then fixed with 2.5% glutaraldehyde diluted in 0.2 mol/L phosphate buffer (pH 7.2–7.4) with NaCl in a concentration of 16.07 g/L. After rinsing in the same buffer, the radular sacs were dehydrated through a graded ethanol series and transferred to acetone. The specimens were embedded in Spurr epoxy resin for semithin sectioning, performed using a diamond knife (Diatome Histo Jumbo, Diatome, Switzerland) on a Leica EM UC6 and UC7 ultramicrotomes (Leica Microsystems, Wetzlar, Germany). The semithin sections were stained with 1% toluidine blue and 1% methylene blue diluted in 1% sodium tetraborate and examined using an Olympus BS 61 VS slide scanner (Nikon, Japan).

To study the general morphology of the radulae in the aforementioned species, the radulae were dissected and incubated in a Proteinase K lysis buffer solution following the protocol of Ivanova *et al*. (2006) at 60 °C for 5–6 h to dissolve connective and muscular tissues. After rinsing in distilled water, the radulae were air-dried, coated with gold, and examined using a Jeol JCM-7000 (Neoscope) (Jeol, Japan) scanning electron microscope (SEM).

Results and Discussion

Radula folding in Gastropoda

A direct observation of the radular movements *in situ* in most cases is impossible. Therefore, to reconstruct the trajectories of the tooth movement during feeding, many studies utilized micrographs of radula arrangement combined with either slow-motion photography of radular movements *in vitro* or micrographs of feeding tracks (see, for example, Eigenbrodt, 1941; Carriker, 1969; Carriker *et al*., 1974; Wägele, 1983; Runham *et al*., 1997). In our turn, we suppose that studying the folding of the radular membrane within the radular sac and on the working plane is also helpful for reconstruction of the radular movements.

DOCOGLOSSATE RADULA OF PATELLOGASTROPODA. The docoglossate radula of Patellogastropoda is considered a stereoglossate and is characterized by the impregnation of the lateral teeth with iron oxide, specifically goethite, and silicon (Runham *et al*., 1969; Rinkevich, 1993; Liddiard *et al*., 2004; Hua, Li, 2007). Goethite is the second hardest iron oxide isomorph after magnetite. The latter is present in radular teeth of chitons (Macey, Brooker, 1996; Wealthall *et al*., 2005). Both patellogastropods and chitons rasp biofilm from hard substrata, which necessitates the presence of durable teeth.

This feeding mode leads to a high rate of tooth wear. The patellogastropod radula can exceed nearly twice the length of the shell. Potentially, the long maturation phase is necessary to incorporate the high proportions of minerals in the teeth.

Apart from mineralization with iron oxides, the main trend in modifications of the patellogastropod radula is the reduction of teeth within the transverse row, specifically, the partial or total loss of the rachidian and marginal teeth (Sasaki, 1998). The complete set of teeth in the transverse row in the patellogastropod radula consists of 13 teeth: one rachidian tooth flanked by three lateral and three marginal teeth on each side (radular formula: 3.3.1.3.3). A similar radular formula is observed in *Scutellastra longicosta* (Patellogastropoda, Patellidae) (Fig. 1A–D). Its radula consists of a narrow rachidian tooth, flanked by two small, unicuspid lateral teeth, a large, four-cuspid lateral tooth, and three elongated marginal teeth on each side. The radular sac in this species looks flattened, suggesting that the radula is not folded within the sac. However, transverse semithin sections reveal that the radular membrane does not fold in the central field where the highly mineralized rachidian and lateral teeth are located. Instead, two longitudinal folds are present in the zone of marginal teeth attachment to the radular membrane, situated in the lateral parts of the radular sac (Fig. 1D). Consequently, as the radula become mature and enters the working zone, the membrane unfolds. According to the position of the teeth, the marginal teeth do not move in straight lines but rather move from sides towards the center of the membrane.

The second species examined to illustrate the docoglossate radula is *Testudinalia testudinalis* (Patellogastropoda, Lottiidae). In adult specimens of *T. testudinalis*, two pairs of highly mineralized lateral teeth are present. The inner and outer lateral teeth within one row are shifted longitudinally, with the outer laterals situated behind the inner ones. The radular formula is 2.0.2. Transverse semithin sections through the radular sac (mineralization zone) reveal that the radular membrane does not fold in the central field, where the mineralized teeth are located. However, there are longitudinal folds outside of the outer lateral teeth, on both sides of the central field (Fig. 1F). That is, similar to *S. longicosta*, the radula is folded within the radular sac.

Therefore, the radula of Patellogastropoda is folded longitudinally within the radular sac. This fact is particularly evident in species with wide radulae having a complete set of teeth, such as *S. longicosta*. That suggests that the stereoglossy in patellogastropod radulae is a secondary condition that arose from a shift from detritophagy to rasping on hard substrata. This change of feeding strategy has driven the evolution of a long, highly mineralized radula optimized for feeding on biofilms on hard substrata. Subsequently, mineralization, a key event in the patellogastropod evolution (Runham *et al*., 1969; van der Wal, 1989), has led to a decrease in the number of teeth within the transverse row and the loss of the flexoglossate condition due to the hardening of the radular teeth and membrane.

FLEXOGLOSSATE RADULA OF OTHER GROUPS OF GASTROPODA. The flexoglossate radula, found in other gastropods, demonstrates an exceptionally wide range of morphology and is represented by over 20 types. The rhipidoglossan radulae of Vetigastropoda, Neritimorpha, and lower Heterobranchia, along with the taenioglossan radulae of Caenogastropoda and Heterobranchia, form the basis of the current diversity of radular morphology.

RHIPIDOGLOSSAN RADULAE OF VETIGASTROPODA AND NERITIMORPHA. The rhipidoglossan radula of Vetigastropoda is characterized by a central field with a central (rachidian) tooth, typically flanked by five lateral teeth (one of which may be stronger than the others) and numerous (more than 10–12) elongated marginal teeth on each side within a transverse row (Hickman, 1980, 1984). Many authors have considered this radular type to be plesiomorphic for all gastropods except Patellogastropoda (Haszprunar, 1988; Ponder, Lindberg, 1997; Ponder *et al*., 2020). The rhipidoglossan radulae, with its numerous flexible marginal teeth, along with paired jaws bearing rodlets on the masticatory border, are well-suitable for detritophagy. Vetigastropoda have a rather wide range of feeding preferences, from detritus to seston and fouling organisms, such as sponges and cnidarians (Fretter, 1955, 1975; Nisbet, 1973; Hickman, 1984; Salvini-Plawen, Haszprunar, 1987).

The rhipidoglossan radula is also characteristic of Neritimorpha (Ponder, Lindberg, 1997; Ponder *et al*., 2020). Transverse semithin sections

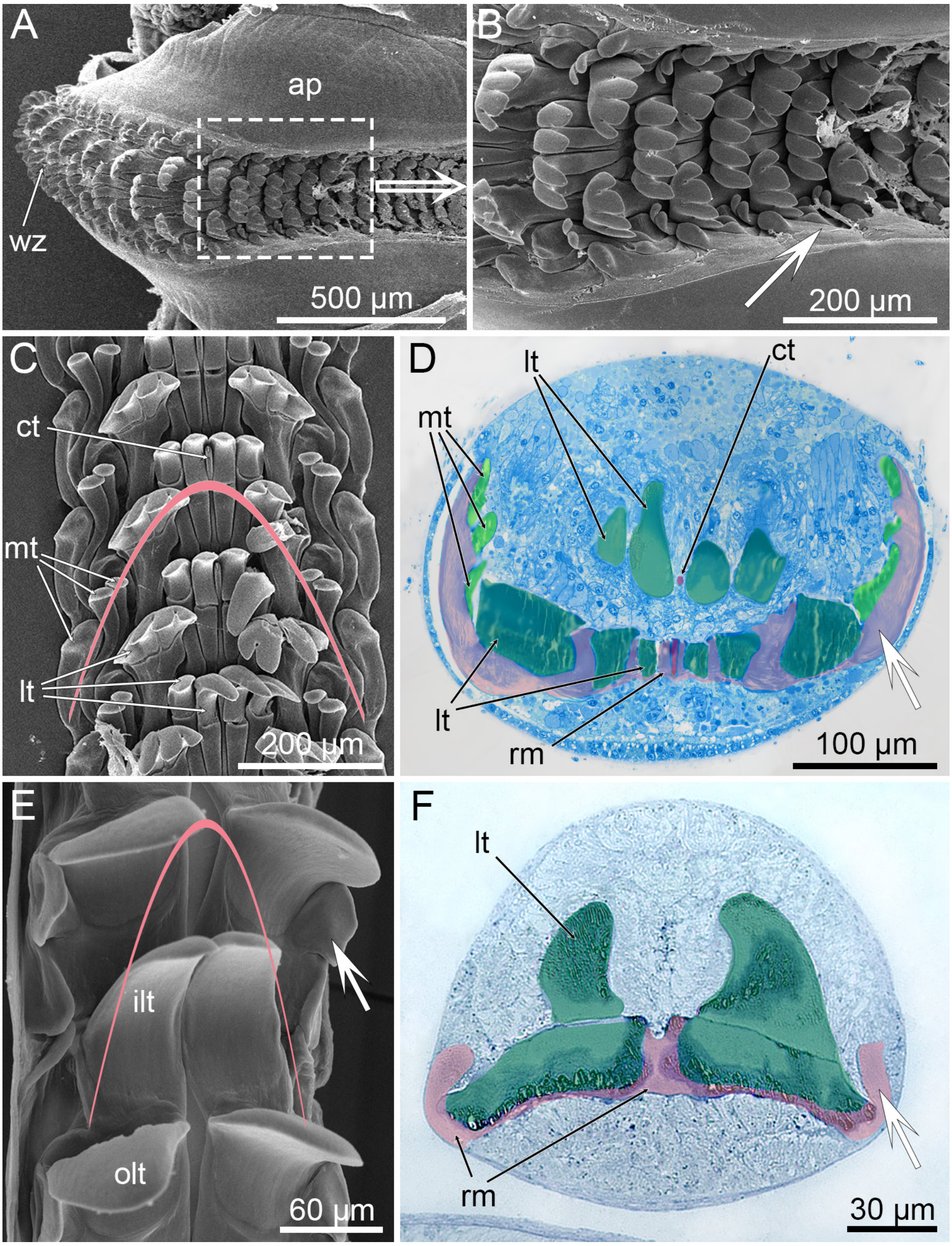

Fig. 1. Morphology of docoglossate radula of Patellogastropoda (Gastropoda). A–C — top view on the radula of *Scutellastra longicosta*, SEM micrograph; pink curved line marks teeth location within the transverse row on the flattened radula; D — transverse semithin section through the middle part of the radular sac of *S. longicosta*; E — general morphology of the radula of *Testudinalia testudinalis*, SEM micrograph; F — transverse semithin section through the zone of matured teeth in the radular sac of *T. testudinalis*. Radular parts on plates D and F are indicated by semitransparent colors: radular membrane — pink, central tooth — dark pink, lateral teeth — dark green, marginal teeth — pale green. White arrows on plates B, D, E, and F mark folds of the radular membrane and borders of the central field of radula.

Abbreviations: ap — alary process; ct — central tooth; ilt — inner lateral tooth; lt — lateral tooth; mt — marginal tooth; olt — outer lateral tooth; rm — radular membrane; wz — working zone of the radula.

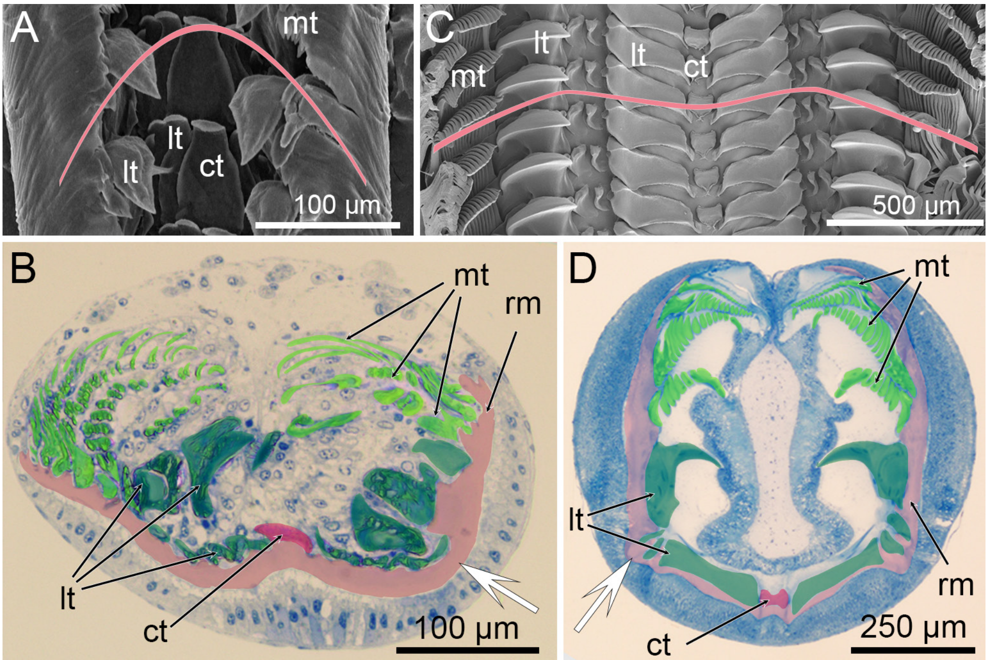

Fig. 2. Morphology of rhipidoglossan radula. A — general morphology of the radula of *Puncturella noachina* (Vetigastropoda, Gastropoda), SEM micrograph; B — transverse semithin section through the radular sac of *P. noachina*; C — general morphology of the radula of *Nerita litterata* (Neritimorpha, Gastropoda); D — transverse semithin section through the radular sac of *N. litterata.* In both species, longitudinal folds of radula (marked by white arrows) on the border between lateral teeth. Pink curved lines on the plates A and C mark teeth location within the transverse row on the flattened radula. Radular parts on plates B and D are indicated by semitransparent colors: radular membrane — pink, central tooth — dark pink, lateral teeth — dark green, marginal teeth — pale green. White arrows on plates B and D mark folds of the radular membrane and borders of the central field of radula.
Abbreviations: ct — central tooth; lt — lateral tooth; mt — marginal tooth; rm — radular membrane.

through the radular sacs both of vetigastropods and neritimorphs (Fig. 2) clearly show that the radular membrane folds twice longitudinally in the central field, and the elongated marginal teeth lie dorsally inside the sac, covering the central field of the radula. Notably, cross-sectional views of the radulae of patellogastropods having wide radulae are similar to those of neritimorph radulae with large teeth in the central field. These radulae have highly mineralized teeth in the central field, making it difficult to bend the radular membrane in this area. The longitudinal folds in these radulae lie between the lateral and marginal teeth, suggesting that this way of radula folding is the most optimal given the mentioned conditions.

According to the currently accepted phylogenetic hypotheses, vetigastropods and neritimorphs are not closely related groups (Cunha, Giribet, 2019; Uribe *et al*., 2019, 2022; Zhong *et al*., 2022). Their radulae, though similar in type, have a number of significant morphological differences in the configuration and organization of the radula formation zone (Vortsepneva *et al*., 2022). These characters suggest a convergent origin of rhipidoglossan radulae with elongated marginal teeth in these two subclasses. Moreover, the multilayered epithelium in the zone of formation of marginal teeth likely evolved as an adaptation for the synthesis of numerous elongated teeth and compacting them within the radular sac.

TAENIOGLOSSAN RADULAE OF CAENOGASTROPODA AND HETEROBRANCHIA. Most of Caenogastropoda possess taenioglossan radula, consisting of seven teeth per transverse row (Fig. 3), a plesiomorphic condition for this group (Ponder, Lindberg, 1997; Strong, 2003; Ponder *et al*., 2008, 2020). This basic radular type

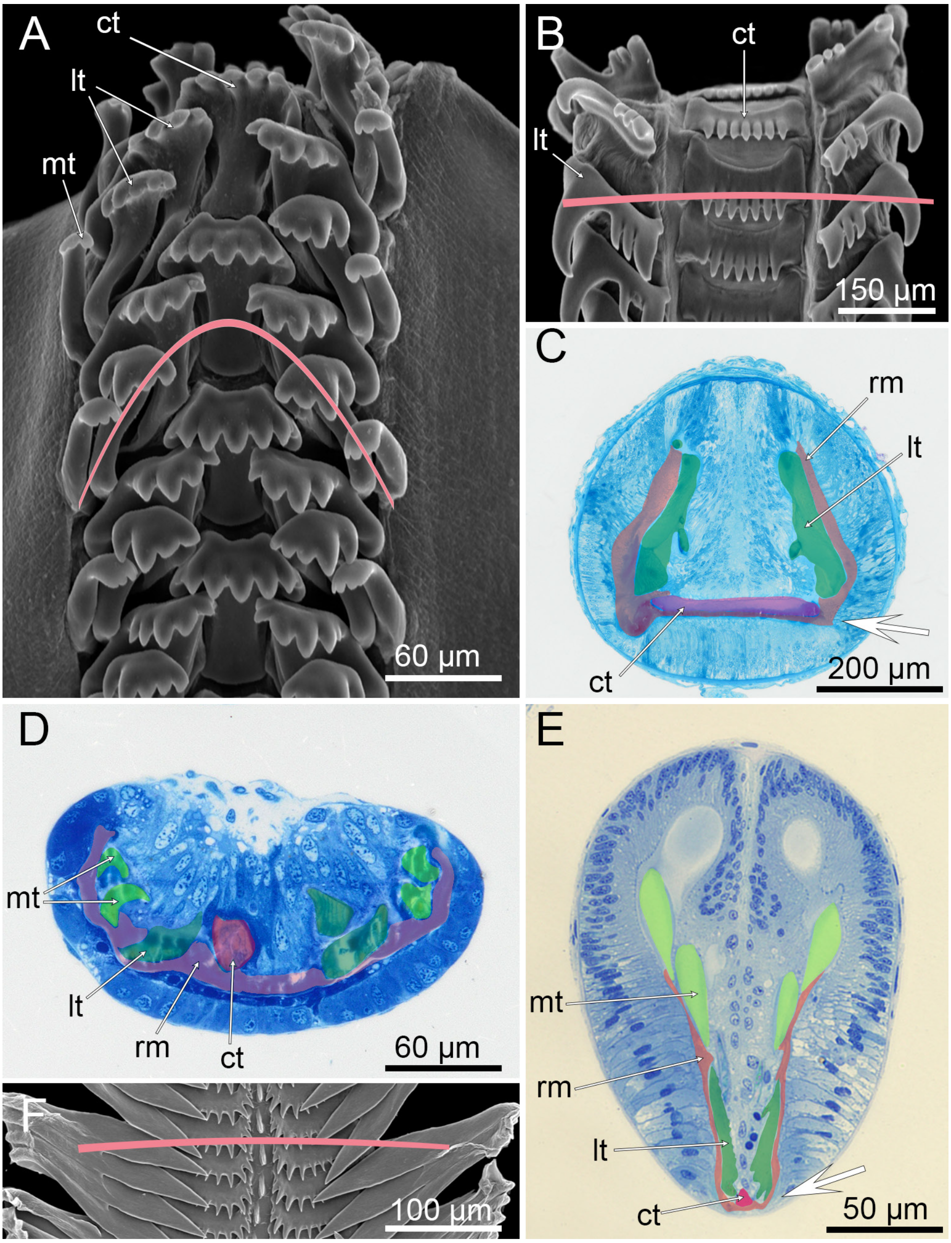

Fig. 3. Radular morphology of Caenogastropoda. A, D — taenioglossan radula of *Lacuna pallidula* (Littorinimorpha); general morphology of the radula of *L. pallidula*, SEM micrograph (A) and transverse semithin section through the radular sac (D); B, C — stenoglossate radula of *Buccinum undatum* (Neogastropoda); general morphology of the radula, SEM micrograph (B) and transverse semithin section through the radular sac (C); E, F — toxoglossan radula of *Clavus maestratii* (Neogastropoda); general morphology of the radula, SEM micrograph (F) and transverse semithin section through the radular sac (E). Pink curved lines on the plates A, B and F mark teeth location within the transverse row on the flattened radula. Radular parts on plates C, D, and E are indicated by semitransparent colors: radular membrane — pink, central tooth — dark pink, lateral teeth — dark green, marginal teeth — pale green. White arrows on plates C and E mark folds of the radular membrane and borders of the central field of radula.
Abbreviations: ct — central tooth; lt — lateral tooth; mt — marginal tooth; rm — radular membrane.

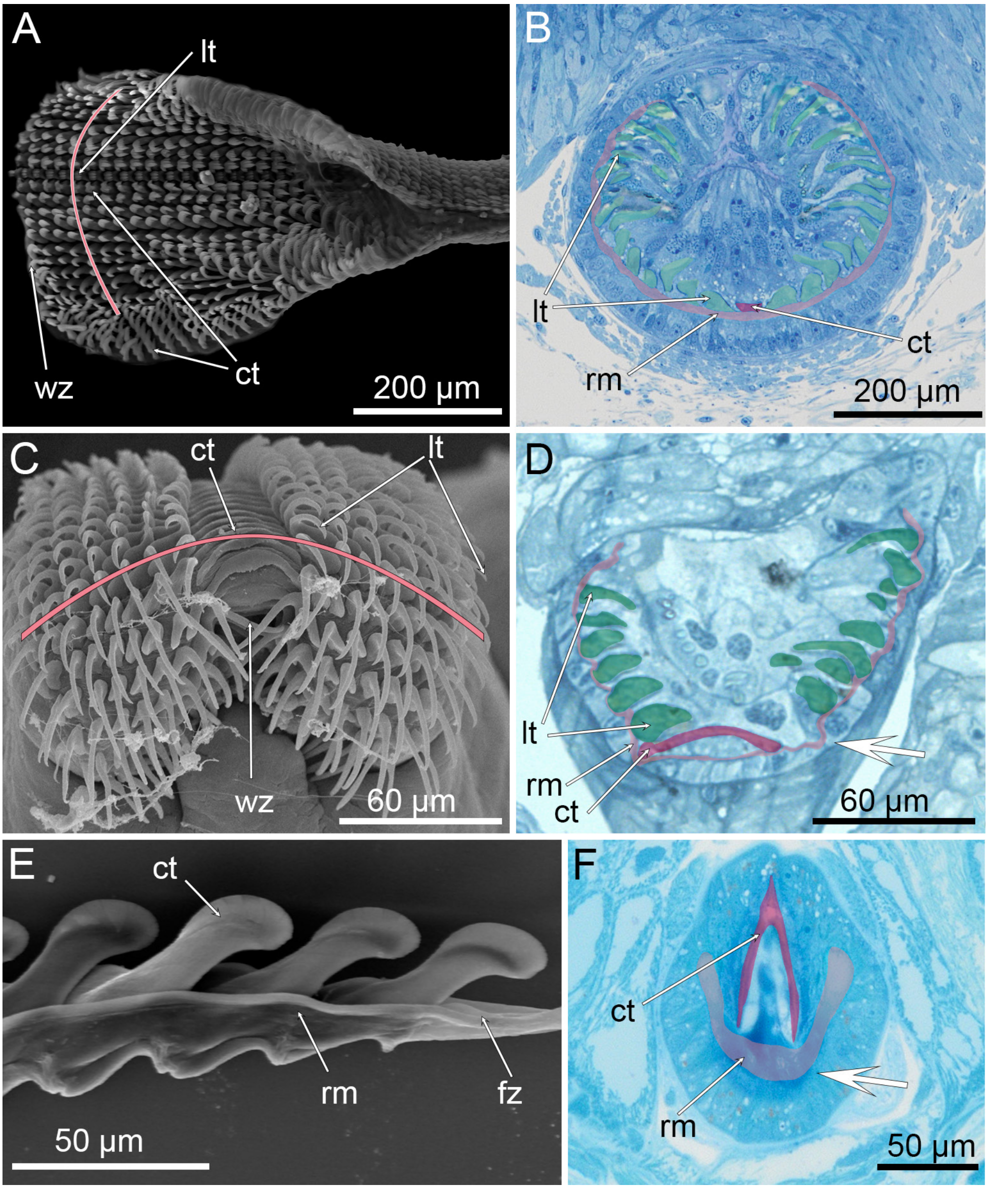

Fig. 4. Radular morphology of Heterobranchia (Gastropoda). A — general morphology of the radula of *Cadlina laevis* (Nudibranchia, Doridina), SEM micrograph; B — transverse semithin section through the radular sac of *C. laevis*, SEM micrograph; C — general morphology of the radula of *Clione limacina* (Pteropoda, Gymnosomata), SEM micrograph; D — transverse semithin section through the radular sac of *C. limacina*; E — general morphology of the radula of *Limapontia senestra* (Sacoglossa), lateral view, SEM micrograph; F — transverse semithin section through the radular sac of *L. senestra*. Pink curved lines on the plates A and C mark teeth location within the transverse row on the flattened radula. Radular parts on plates B, D, and F are indicated by semitransparent colors: radular membrane — pink, central tooth — dark pink, lateral teeth — dark green. White arrows on plates D and F mark folds of the radular membrane and borders of the central field of radula.

Abbreviations: ct — central tooth; fz — formation zone of the radula; lt — lateral tooth; rm — radular membrane; wz — working zone of the radula.

serves as a foundation for other caenogastropod radulae, including highly specialized forms adapted for predation, such as the toxoglossan radula of Neogastropoda (Fig. 3E–F) (Ponder, Lindberg, 1997; Strong, 2003; Ponder *et al*., 2008, 2020). Taenioglossan radulae are also found in Vetigastropoda (*e.g.*, Seguenziidae, Lepetellidae, *Conjectura*) and are in fact secondarily simplified rhipidoglossan radula that evolved in aberrant taxa with specialized feeding modes (Hickman, 1983; Salvini-Plawen, Haszprunar, 1987; Haszprunar, 1988; Haszprunar *et al*., 2016). In contrast, the taenioglossan radula type is most likely plesiomorphic for Heterobranchia, as it is occasionally found in various clades of this subclass, including basal lineages (Bieler, 1988; Climo, 1975; Ponder, Yoo, 1977; Warén, Bouchet, 1993). The close phylogenetic relationships of Caenogastropoda and Heterobranchia are well-established (Cunha, Giribet, 2019; Uribe *et al*., 2022).

In both caenogastropods (Fig. 3) and heterobranchs (Fig. 4), all radulae are flexoglossate, since the radular membrane with teeth folds within the radular sac and unfolds on the working plane, regardless of the radular type.

The teeth feeding tracks in flexiglossate radulae are diverse, with different groups of teeth having distinct trajectories during the feeding process. This distinguishes flexoglossate radulae from the stereoglossate (Ankel, 1936, 1938; Eigenbrodt, 1941; Morris, Hickman, 1981; Janssen, Triebskorn, 1987; Hawkins *et al*., 1989; Franz, 1990; Mackenstedt, Märkel, 2001; Krings *et al*., 2019; Scheel *et al*., 2020).

Radula folding in Polyplacophora

According to previously published works, polyplacophoran (chiton) radula belongs to the docoglossate type (stereoglossate condition), similar to the radulae of Patellogastropoda, Monoplacophora, and Scaphopoda (Wingstrand, 1985; Haszprunar, 1988; Salvini-Plawen, 1988). Chitons typically have the rasping feeding mode, and their radular morphology is conserved. The chiton radula is typically composed of 17 teeth in the transverse row, rarely 15 or 13. The typical radular formula for chitons is 3.5.1.5.3 (Eernisse, Reynolds 1994). The transverse row comprises the central tooth, a pair of centro-lateral teeth, a pair of magnetite-impregnated major laterals, two pairs of small laterals, a pair of elongated lateral teeth called major uncinus, and three pairs of marginal plates (Saito, 2004) (Fig. 5A–C, F).

Despite the generally assumed stereoglossate condition of the chiton radula, studies on radular feeding tracks suggest otherwise (Shaw *et al*., 2010; Pohl *et al*., 2020; Scheel *et al*., 2020; Krings *et al*., 2022). These studies demonstrated that the lateral teeth in polyplacophoran radulae are mobile and rotate during feeding, indicating that the radula does not function as a rasp like stereoglossate radulae (Scheel *et al*., 2020). Our findings, based on three studied polyplacophoran species, have shown that the radula is folded within the radular sac. The radular membrane folds longitudinally between the centro-lateral teeth and major laterals, as well as between the major uncinus and marginal plates (Fig. 5D, E, G). Therefore, based on both morphology and function, the radula of Polyplacophora should be classified as flexoglossate.

Plesiomorphic condition of the molluscan radula

Considering the data on radular conditions within the radular sac and on the working plane for different gastropods and chitons, we propose that the plesiomorphic state of molluscan radula is a flexible flexoglossate condition, when the radula is longitudinally folded within the radular sac and unfolds on the working plane.

In Patellogastropoda, the radula is secondarily modified due to a shift from grazing on soft fouling organisms to rasping biofilms on hard substrata. In that case, the originally wide and flexible flexoglossate radula transformed into a narrower, more rigid stereoglossate. Most likely, the outermost fields with mobile marginal teeth were reduced in patellogastropod radulae, retaining only the central field with highly mineralized teeth firmly attached to the radular membrane. This suggests that the flexoglossate radular condition was plesiomorphic for gastropods, and the stereoglossate radula of Patellogastropoda represents a special case of flexoglossate radula with reduced outermost fields (Figs 6, 7).

The studies of the polyplacophoran radular morphology and function, particularly regarding the folding of the radula within the radular sac (Fig. 7) and feeding tracks of the radular teeth (Shaw *et al*., 2010; Pohl *et al*., 2020; Scheel *et al*., 2020; Krings *et al*., 2022), demonstrate that the radulae of Polyplacophora should be classified

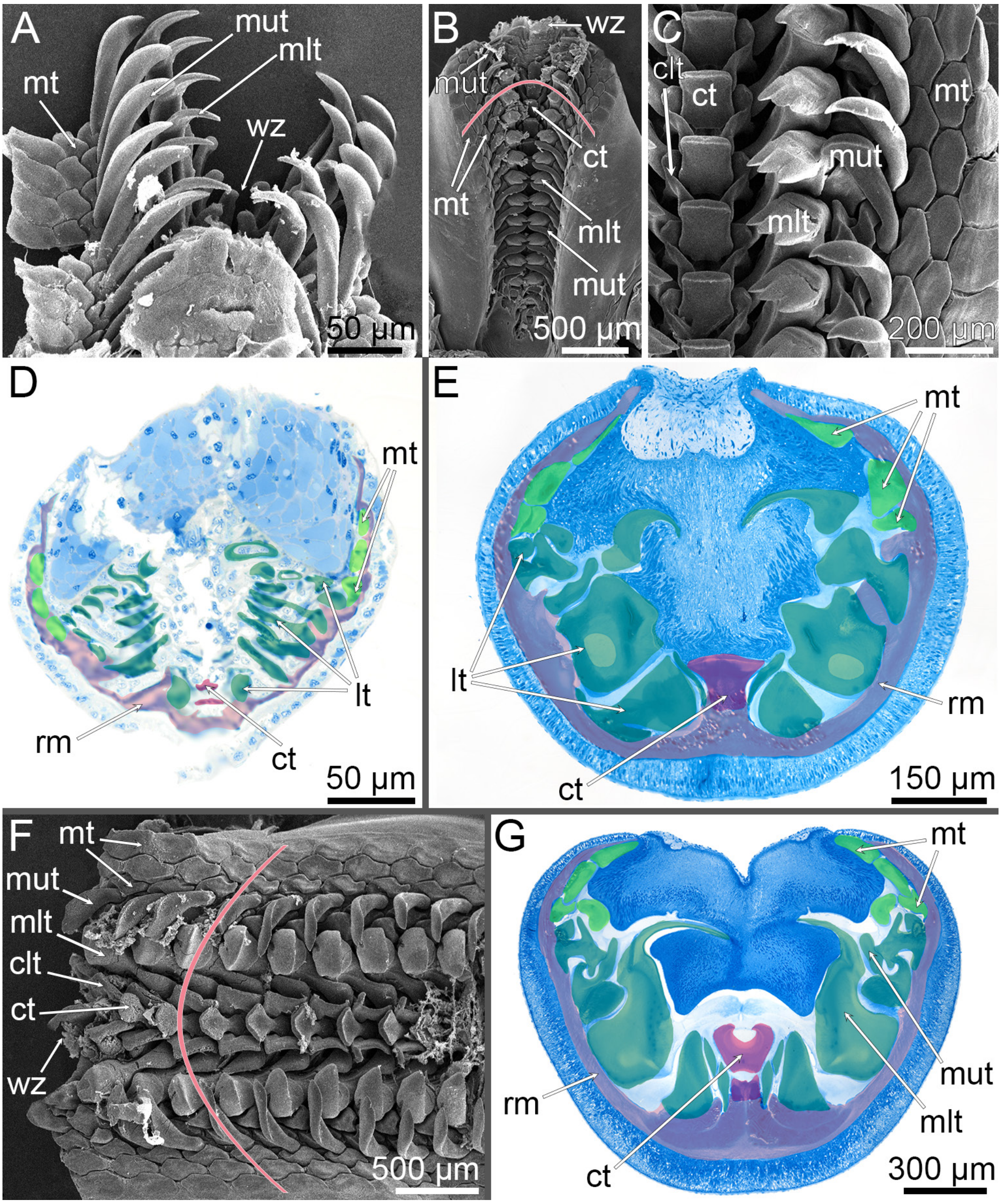

Fig. 5. Radular morphology of Polyplacophora. A, D — radular morphology of *Leptochiton assimilis* (Lepidopleurida); general morphology on the working plane, SEM micrograph (A) and transverse semithin section through the radular sac (D); B, C, E — radular morphology of *Placiphorella stimpsoni* (Chitonida); general morphology on the working plane (B) and magnified area of the half-row (C); transverse semithin section through the radular sac (E); F, G — radular morphology of *Lepidozona albrechti* (Chitonida); general morphology on the working plane (F) and transverse semithin section through the radular sac (G). Pink curved lines on the plates B and F mark teeth location within the transverse row on the flattened radula. Radular parts on plates D, E, and G are indicated by semitransparent colors: radular membrane — pink, central tooth — dark pink, lateral teeth — dark green, marginal teeth — pale green.

Abbreviations: clt — centro-lateral teeth; ct — central tooth; ilt — inner lateral tooth; lt — lateral tooth; mlt — major laterals; mt — marginal tooth; mut — major uncinus; rm — radular membrane; wz — working zone radula.

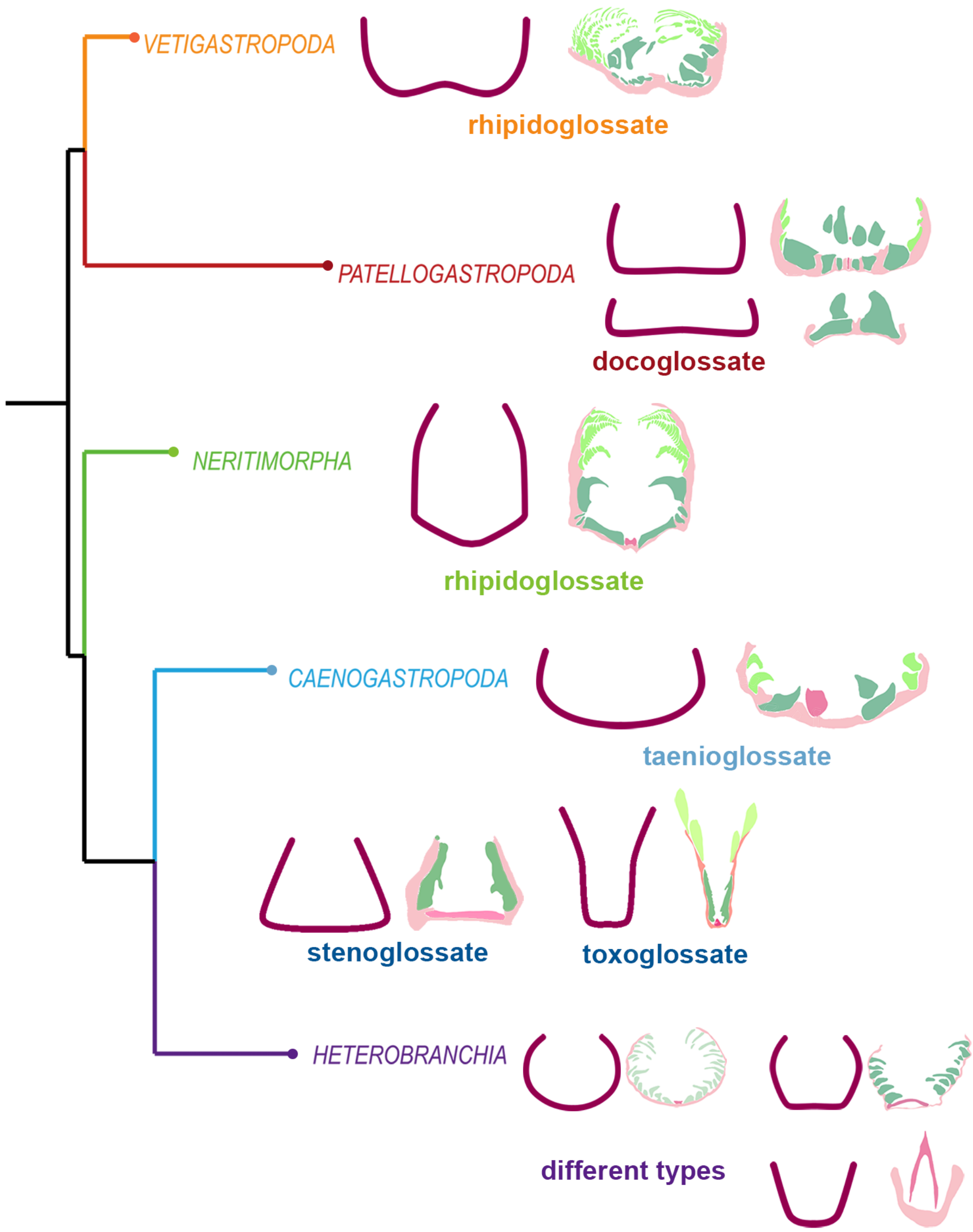

Fig. 6. Distribution of the radular types among Gastropoda with the indication of the flexoglossate condition (dark pink curved lines near the schematic overviews of transverse sections through the radular sac). Radular parts on the diagrams of transverse sections through radula are indicated by semitransparent colors: radular membrane — pink, central tooth — dark pink, lateral teeth — dark green, marginal teeth — pale green. Phylogeny based on Cunha & Giribet (2019).

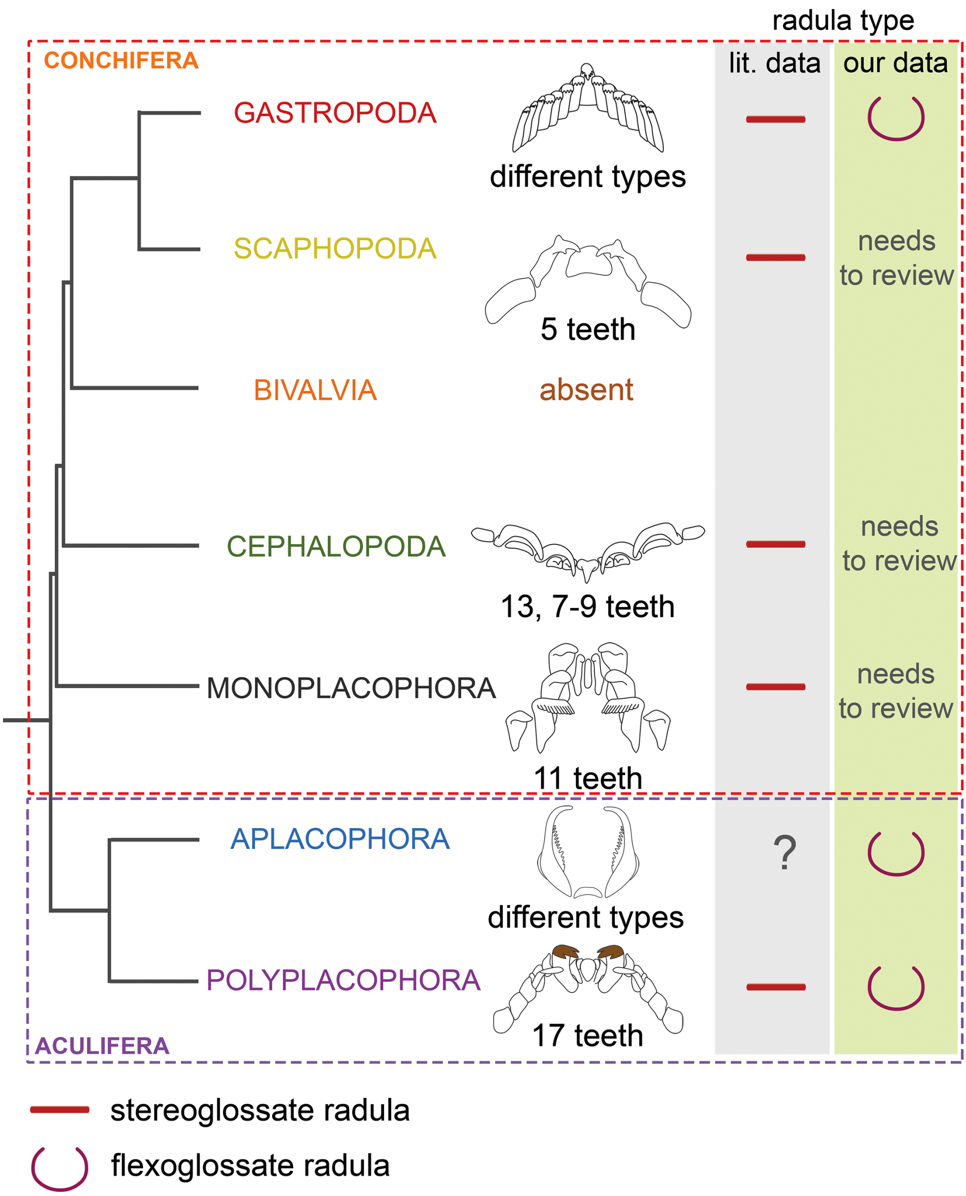

Fig. 7. Distribution of the radular types among Mollusca. Grey column — radular types according to literature data; light green column — present study. Phylogeny based on Kocot *et al.* (2020).

as flexoglossate rather than stereoglossate, as previously incorrectly assumed in earlier works.

Analysis of radular movements and radula folding within the radular sac allows to reconsider the evolution of the molluscan radula (Fig. 7). The flexoglossate radula is a plesiomorphic condition for at least two classes of molluscs, Gastropoda and Polyplacophora. This raises questions about established views on the evolution of radula, highlighting the need for more detailed studies on the morphology and function of stereoglossate radulae of other molluscan classes, *e.g.*, Monoplacophora and Scaphopoda. It is possible that their radulae may also have features of both stereoglossy and flexoglossy, similar to those observed in Patellogastropoda. Given that the stereoglossate radulae in patellogastropods are just the special case of flexoglossate radulae, defining these two types as fundamentally distinct may be an oversimplification and possibly unnecessary. Instead, focusing on the radular biomechanics and classifying the radulae based on their multi- and monofunctionality, as proposed by Krings and Gorb (2024), could provide a more precise understanding of the evolution of radula.

Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

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