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Comparative Morphology of the Radulae in *Pomatias elegans* and in *Littorina littorea* (Gastropoda: Taenioglossa)

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Abstract

The micromorphology of the radulae of *Littorina littorea* and of *Pomatias elegans* is compared, evaluating scanning electron microscopal findings and radula prints in agar-covered slides. Stress is laid on the morphological adaption of the redulae to the special food and feeding behaviour of each species. The general anatomy and function of the taeniogloss radula is reviewed.

Introduction

The radula organ of the Gastropoda is a complex rasping apparatus, the function of which is not yet fully understood. The interest of many authors only concentrates on the radulae as easily accessible hardstructures and organs of merely systematic value. Only early papers by Ankel (1936, 1938) deal with morphology and function of the radulae. These studies are continued by Märkel (1957, 1965, 1966, 1969). Recent papers focus on radula regeneration and teeth transport, e.g. Kerth (1976), Mischor and Märkel (1984), Mackenstedt (1985). While the classical electron microscopy allowed better resolution of the different epithelia envolved in teeth formation and teeth transport, the use of radioactive tracers and autoradiographic techniques as well as electron energy dispersive microanalysis opened new ways of understanding of the different components of the radulae. New structures, like a retaining cuticula which locks the mouth of the radula pouch, were described and their formation was studied (Mackenstedt 1985).

Many systematic categories of the Gastropoda are characterized by certain types of radulae, e.g. Taenio-, Rhipido-, Pteno-, Rhachi-, Toxoglossa, etc. However, only few recent papers lay stress on comparative morphology in this field. The various ways of adaptation and specialisation of the radula apparatus to a certain food or to specific ways of nutrition have been widely neglected. To meet this lack of morphological studies the radulae of two related prosobranch Gastropoda adapted to different nutrition and living in different biotops are compared. *Littorina littorea* (Littorinidae) is a marine prosobranch grazing in the upper eulitoral zone on layers of micro algae covering rocks. *Pomatias elegans* (Pomatiasidae) is the most common of the native terrestrial prosobranchs. It feeds on leaf litter, which at our collecting site predominantly derives from Fagus silvatica, Castanea sativa, and of Quercus robur.

Material and Techniques

Littorina littorea were collected at low tide from different sites of the German wadden sea. *Pomatias elegans* were collected from a narrow forest area at Heidelberg-Handschuhsheim, where a small endemic population exists. The radulae were dissected and macerated in 10% KOH, thoroughly rinsed in distilled water and dried in a Balzer critical point drier using liquid carbon dioxide. Then the specimens were mounted on stubs, sputtered with gold and examined in a Cambridge stereoscan (SEM).

For the visualisation of radula prints glass slides were coated with a suspension of agar and starch following a prescription of Ankel (1936): 2 g agar + 2 g starch + 96 ml water. Slides were dipped into the heated mixture and allowed to cool. The coated slides were offered to the snails which fed on the agar layer. The imprints of the radulae can be better discerned when the slide is treated with Lugol's solution so that the layer becomes bluish.

Results

1. General situs of the radula

Any radula is nearly entirely enveloped by its pouch, which is located ventrally of the esophagus. It is born by a tongue like structure called odontophor. The odontophor partly consists of a kind of cartilaginous connective tissue which acts as support for the muscle tissue. The fore end terminates in a sharp edge over which the radula is pulled back and forth when in action. Odontophor and radula pouch are equipped with a well developed muscular apparatus rendering the whole organ highly motile.

The radula teeth are arranged in regular transversal and longitudinal rows. In the Taenioglossa, any transversal row consists of one rhachis tooth, accompanied by a right and left lateral tooth, eventually followed by two marginal teeth on each side which may be expressed by the formula "1 + 2 + 4". According to Ankel (1936) the middle and lateral teeth are rigidly attached to the supporting membrane of the radula, so that only the four marginal teeth can be shifted.

2. Function of the taeniogloss radula

The function of a taeniogloss radula may be described as follows: By muscle action the radula is passed forward over the terminal edge. Running forward, the supporting membrane changes its profile in cross section from concave to convex. The teeth of the radula, which in the beginning point towards the axis of the trough formed by the concavely indented basemembrane, open and spread out like a zip-fastener. The marginal teeth tilt apart and reach their working position. If a transversal row is pulled back over the edge, the marginal teeth move back following the supporting membrane shifting this time from convex to concave, until the initial position is regained (tips pointing into the radula trough). When the teeth move back, they scrape over the grazed surface. Their tips follow a crescent shaped curve running from distal to proximal and leave a characteristic print on the grazed surface. The serrated points and the spoon like protrusions of the teeth slide the scraped-off particles into the oral cavity. Highly motile folds at the entrance of the esophagus or a kind of peristaltic movement in the upper region of the buccal cavity then apparently exercise a sucking influence on the ingested particles thus transporting them further into the ciliated esophagus (Kerth 1976).

When the radula is pulled backward, the odontophor is simultanously moved forward. This guarantees, that one transversal row of teeth after another touches fresh surface. Thus the surface is grazed line by line, until all the rows of teeth belonging to the so-called working area have scraped over the surface. Worn or broken teeth are abandoned in groups at the fore end of the working area of the radula. Lost teeth are replaced by the odontoblast region at the distal end of the radula pouch. For the continuous transport of replaced teeth to the working area of the radula see MACKENSTEDT (1985). By this mechanism teeth ready-to-use are continuously delivered to the working area of the radula.

3. Special features of the radulae of *Littorina littorea* and of *Pomatias elegans*

The radula of a *L. littorea* from the German North Sea may reach a maximal length of 50 mm, if stretched out. This is twice the height of the shell. The bulk of the radula pouch is coiled up on the right side of the body dorsally of the esophagus (Fig. 1).

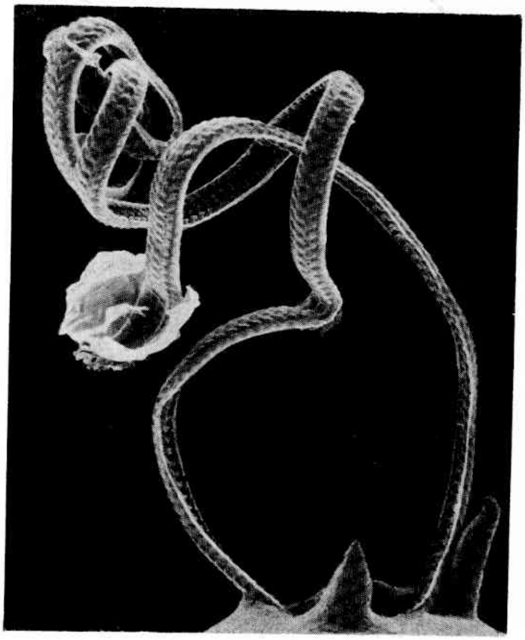

Fig. 1. *Littorina littorea*. Total view of a macerated radula

Feeding prints show the characteristic teeth arrangement of a taeniogloss radula: one transversal row comprises one rhachis, two lateral and four marginal teeth (Fig. 2). The rhachis tooth is attached to the radula membrane by a broad base. It possesses one strong medial tooth accompanied by two small pointed lateral projections (Fig. 3). The lateral teeth also insert with a broad base, but show two lobular projections at their distal ends, which are proximally followed by smaller comb-like structures (Fig. 4). The marginal teeth differ from the others in having a peduncle of conspicuous length which changes to a broad terminal part curved to the median plane which due to a finger like serration looks like a hand (Fig. 5). In resting position all the teeth are folded into one another (Fig. 6).

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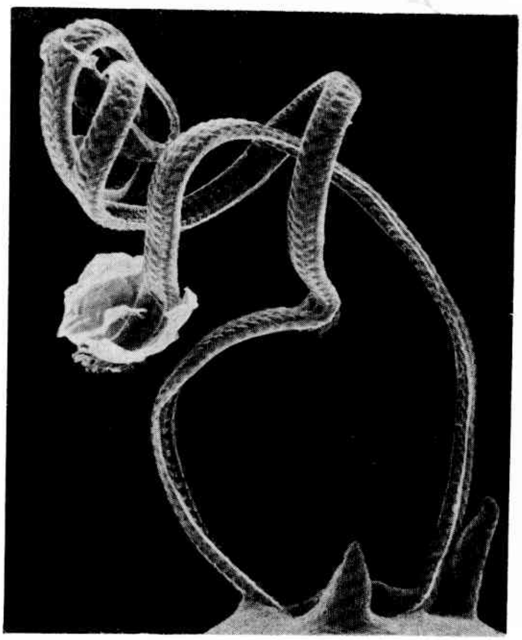

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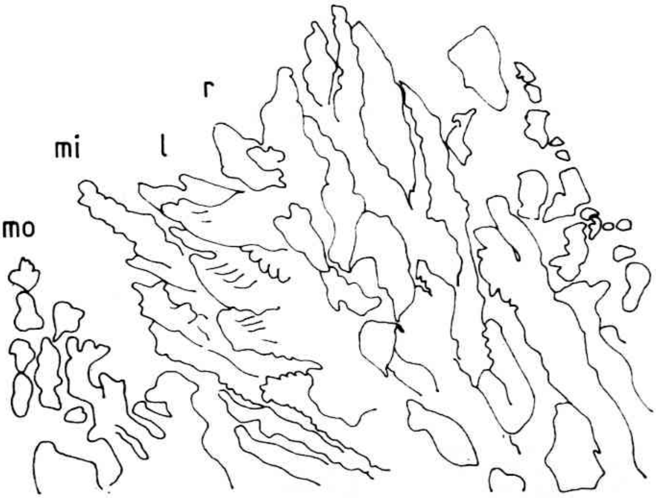


Fig. 2. *L. littorea*. Feeding print. Abbreviations of teeth: mo = outer marginal, mi = inner marginal, l = lateral, r = rachis tooth

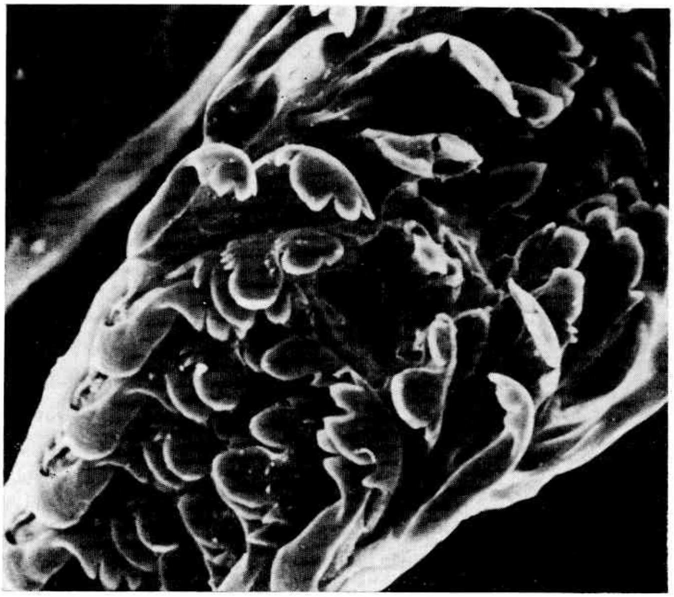


Fig. 3. *L. littorea*. View on the slightly opened radula

The radula of *P. elegans* is only 15 mm to 20 mm long. Its rear end is not coiled up into a spiral, only is anterior part is slightly bent (Fig. 7). The radula prints show the imprints of seven teeth as in *L. littorea*. However, the track of the rhachis tooth is very inconspicous, if visible at all. The picture is dominated by the tracks of the outer marginal teeth (Fig. 8). The reason for this becomes obvious in an SEM specimen: the medial

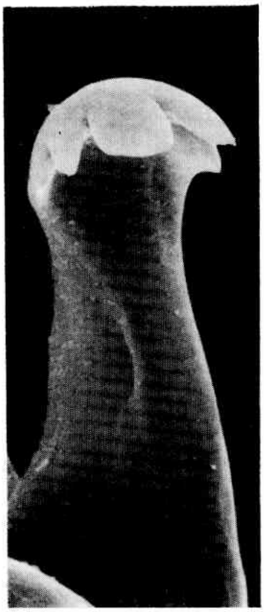
Fig. 4. *L. littorea.* Laterial teeth of the radula

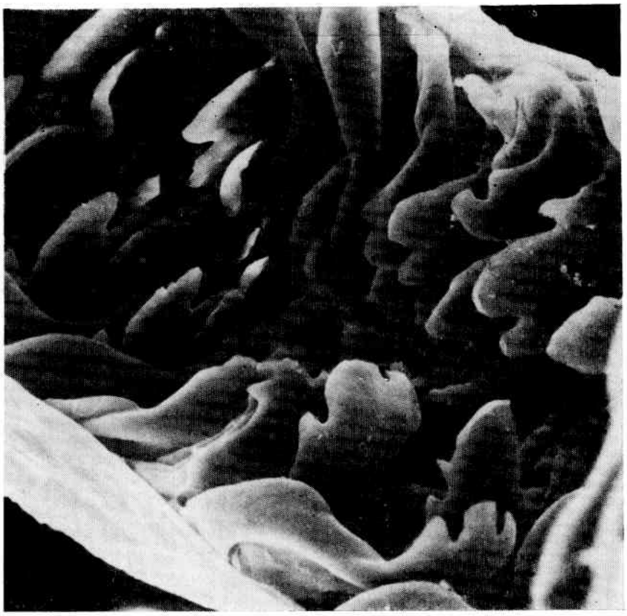
tooth of *P. elegans* is greatly reduced in size and does not show any conspicuous tip. The broad-based peduncle is extremely short and ends in a trilobular terminal part. The lateral teeth as well as the inner marginal teeth are very similar to the marginal teeth of *L. littorea* (Fig. 9). However, the outer marginal teeth of *P. elegans* are of special shape: they have a broad flat wing which is mounted only with a narrow central peduncle onto the supporting membrane (Fig. 10). From the point of insertion a low ridge runs to the terminal end of each tooth, the end of this ridge splitting up into three small lobes. To the lateral side of the ridge a wing-like structure protrudes which is not attached to the radula membrane (Fig. 11). The terminal edge of this lateral wing is different from the terminal zone of the ridged part in showing a series of regular tips which are often destroyed or totally worn in the working area of the radula (Fig. 12).

Discussion

The different micromorphology of radulae is often used to define systematic taxa within the Gastropoda. Additionally, comparative radula analysis within one systematic category may yield insight into feeding behaviour or nutrition. In the present paper this was tried for two prominent representatives of the taeniogloss Prosobranchia.

L. littorea grazes layers of micro algae from litoral rocks and possesses a radula that is well adapted to its way of nutrition. Long peduncles of the teeth allow the scraping off of extensive surface areas with one stroke. The working edge of each tooth is enlarged by a serrated terminal part. Both the long peduncles and the long, multipronged points guarantee, that all teeth simultanously touch the surface and take an active





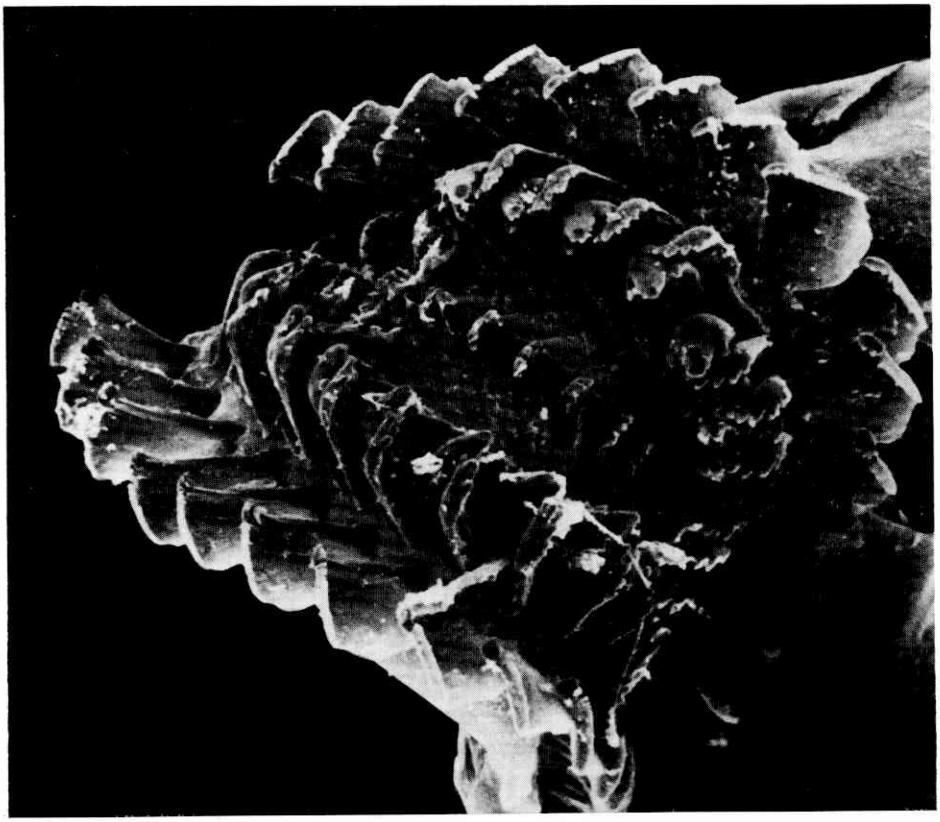


Fig. 5. *L. littorea.* Single lateral tooth of the radula

Fig. 6. *L. littorea.* View on the closed radula

Fig. 7. *Pomatias elegans.* View on the widely opened working area of a macerated radula

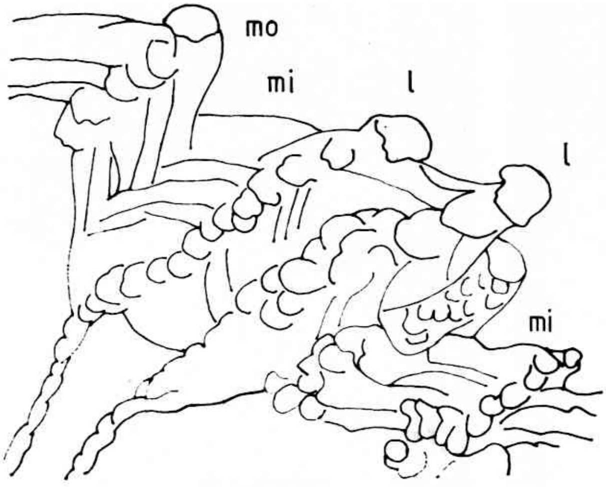


Fig. 8. *P. elegans*. Feeding print. Abbrevations of teeth as in Fig. 2. Note that the rachis tooth does not contribute to the imprints

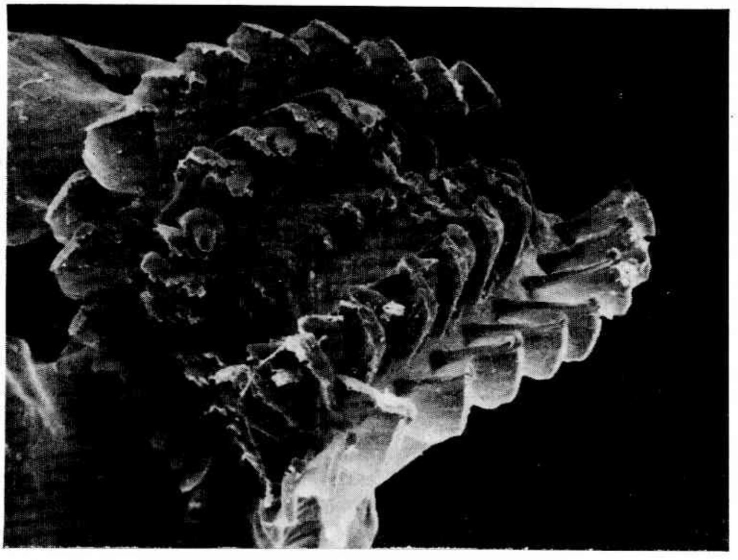
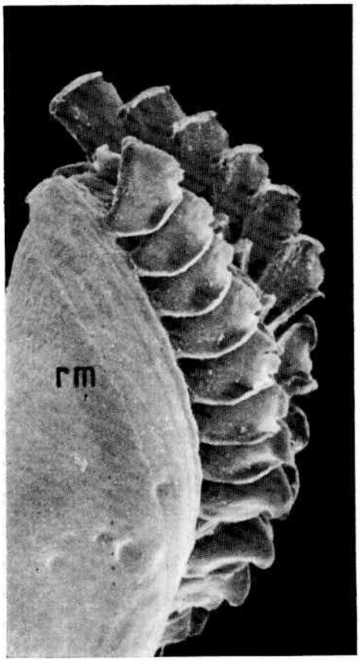
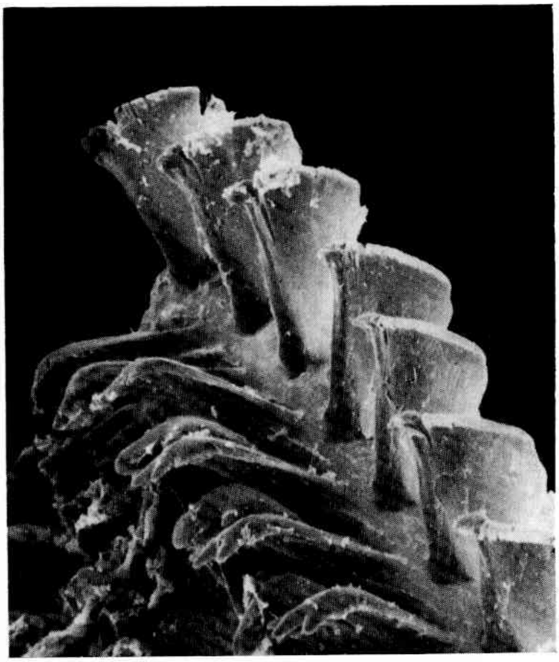


Fig. 9. *P. elegans*. View of the slightly opened radula

hand in collecting and ingesting food particles. The long prongs as well as the remarkable length of the radula are understandable considering the extremely hard ground the animal grazes on leading to speedy wear and tear of the teeth. As newly secreted teeth require a certain period of time for mineralization and hardening (MACKENSTEDT 1985, KERTH 1983b), the radula had to be prolonged in order to process more teeth in a given period of time, so that there is always a sufficient number of teeth available for continuous replacement.





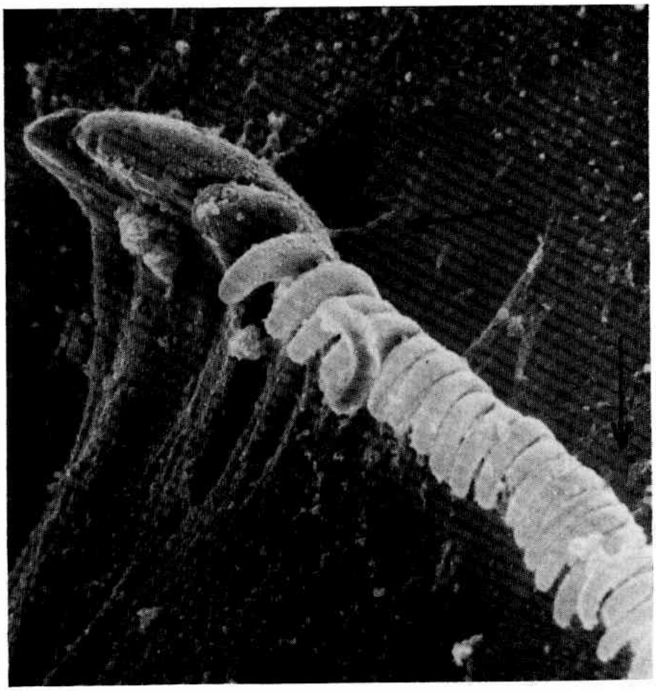


Fig. 10. *P. elegans*. Lateral view on the radula. rm = supporting membrane of the radula
Fig. 11. *P. elegans*. Outer marginal teeth of the radula
Fig. 12. *P. elegans*. Higher magnification of a lateral tooth showing the tooth proper and its lateral wing (arrows) ending in a row of densly arranged fingerlike prongs

P. elegans does not graze like *L. littorina*, but bites off pieces off leaf litter. For this method of ingestion strong teeth are required. Thus the outer marginal teeth have become specially transformed for biting and cutting. Only the medial ridge of such a tooth ending with three terminal lobelets corresponds to the shape of an original one as it is still found as the inner marginal tooth. The lateral parts of the outer marginal teeth have been enlarged to wings. By means of these robust teeth the animal can easily shred considerable amounts of leaves. These teeth are used for a long time, even if their terminal parts are worn and the row of tips is destroyed. Hence the radula may be considerably shorter than in *L. littorea*, as only very few teeth have to be replaced per time unit. According to PURCHON (1977) teeth similar to the marginal ones in *Pomatias elegans* are found in *Neopilina galathea* ("lateral tooth no. 5") so that the radula of *Neopilina* should not be regarded as primitive.

Long radulae with considerably differentiated teeth are typical for grazing Gastropoda. e.g. 5 to 8 cm in *Patella vulgata* (RUNHAM 1961). Whether short radulae with less modified teeth are generally characteristic of prosobranch Gastropoda feeding on leaves still has to be confirmed. The marine *L. obtusata* is closely related to *L. littorea*, but feeds on the phylloids of the brown algae Fucus spp. in a manner comparable to *P. elegans* feeding on leaves. Studies completing the presented findings are under way.

Acknowledgements

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Zusammenfassung

An Hand rasterelektronenmikroskopischer Befunde sowie von Bißspuren auf agarbeschichteten Objektträgern werden Feinbau und Funktion der Radulae von *Littorina littorea* und von *Pomatias elegans* verglichen. Dabei liegt das Schwergewicht auf der morphologischen Anpassung der Radulae an die unterschiedliche Nahrung und an das Freßverhalten der beiden Arten. Neuere Befunde zur allgemeinen Mikromorphologie und Funktion der taenioglossen Radula werden mit aufgegriffen und diskutiert.

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