

**TRACE FOSSILS AND GRAZING TRACES
PRODUCED BY LITTORINA AND LEPIDOCHITONA,
DUTCH WADDEN SEA¹**

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ABSTRACT

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Fossil grazing traces of molluscs are regularly encountered but have not yet been studied in detail. This paper presents data on the grazing traces produced by a periwinkle (*Littorina littorea*) and by a chiton (*Lepidochitona cinereus*) both under laboratory conditions and in the Dutch Wadden Sea. It is found that the traces are different for both species, but that the traces made by one particular species are not necessarily uniform.

INTRODUCTION

ANKEL (1937-a, b) and RICHTER (1962) classified the molluscs according to food uptake. They distinguish the following groups:

- (1) Grazers, scraping algal films from a substratum.
- (2) Biters, carnivores and carrion-feeders tearing up their food.
- (3) Swallowers, swallowing undivided animals.
- (4) Ciliary-feeders, feeding on small particles filtered out of the water by cilia.
- (5) Mucoïd-net feeders, plankton is caught in mucoïd fibres.
- (6) Ectoparasites.
- (7) Endoparasites.

The characteristic feeding organ of molluscs is the radula, absent only in ciliary-feeders and parasites. The radula apparatus consists of the radula (a toothed belt) that passes over a supporting rod (the odontophore) and the radula sac

around the radula. When the radula is used for scraping, the odontophore, a firm choroid tissue, is thrust out of the mouth by contraction of the protractor muscles. In this position the radula can be moved to and fro across the odontophore by contraction of respectively the radula protractor and retractor. Drawing in of the radula is accomplished by contraction of the odontophore retractor. If the radula is protruded the recurved teeth engage particles from the substratum pulling them away from the surface as the odontophore

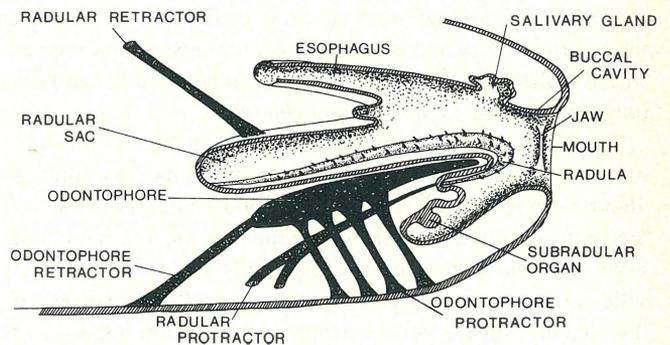


Fig. 1
Diagram of mollusc buccal cavity and radular apparatus (drawn after Meglitsch, 1972).

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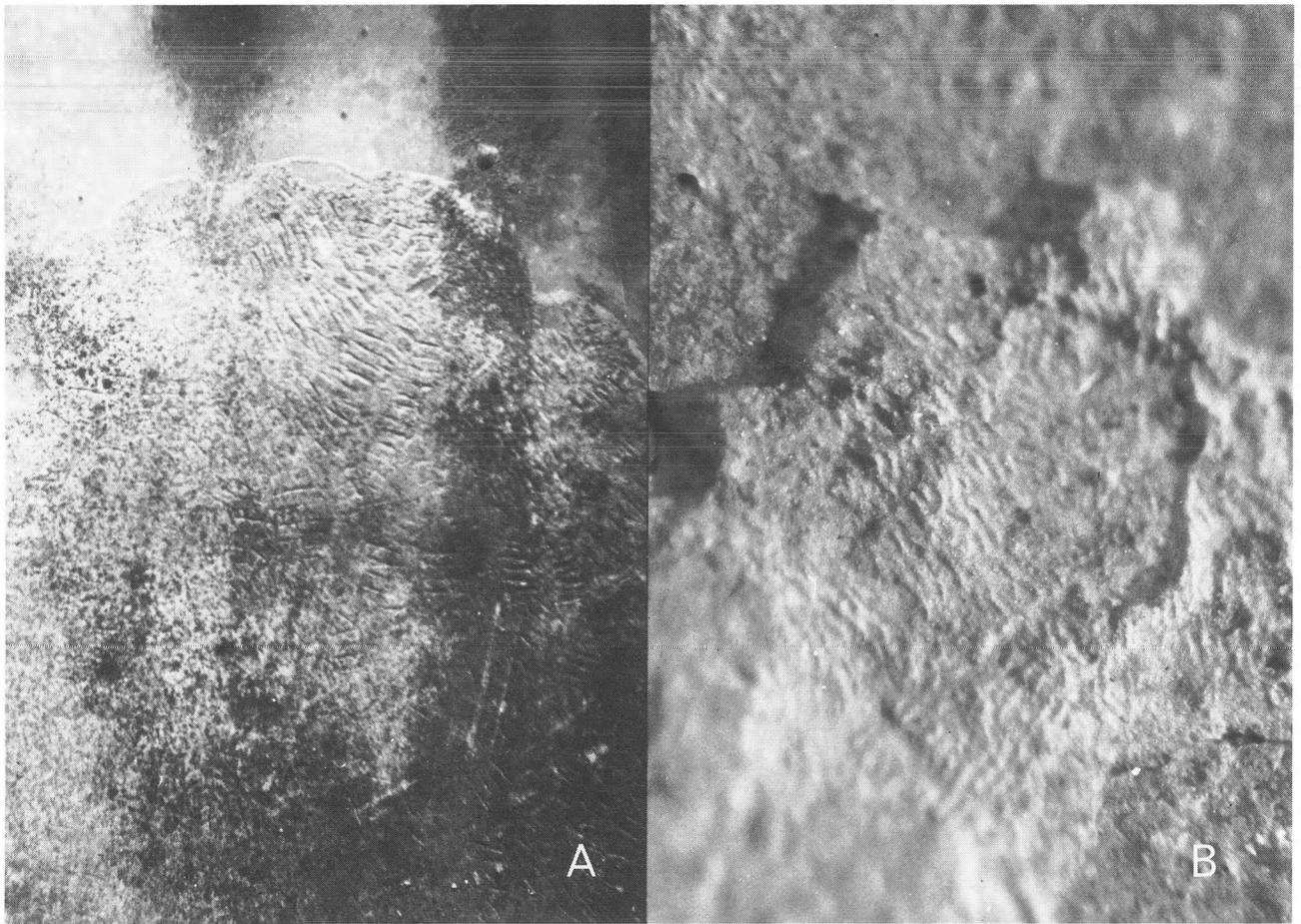


Fig. 2
 A: Chiton grazing traces on the adductor scar of *Pecten* (6.3×). Recent; Algarve, Portugal.
 B: Chiton grazing traces on the inside of *Pygocardia* (25×). Pliocene; Tielrode, Belgium.

is retraced. Figure 1 presents a general diagram of this structure.

It is evident that when algal-coated surfaces are browsed by the radula, grazing traces will be produced. If the radula scratches the substratum also, its traces may be preserved as fossils. They were recorded by BOEKSCHOTEN (1967) and VOIGT (1977). An example is shown in figure 2. To understand fossil grazing traces it is necessary to study the browsing traces and their formation of recent molluscs. The present study deals with this theme in the gastropod *Littorina littorea* L., and the polyplacophoran *Lepidochitona cinereus* L.

The habitat of the periwinkle *Littorina* is the eu- and sublittoral zone, on sea weeds, rocks or mudflats. Its radula is about 6 cm long and carries about 600 transverse rows of teeth; the part in use comprises about 24 rows. The habitat of *Lepidochitona* is the littoral, especially the tidal zone, on solid substrata such as rocks and empty shells of bivalves. In the area investigated solid calcareous substratum is limited to shells, especially *Mya arenaria* L. Endo- and epilithic algae and lichens living on the shells form the food supply.

The first records of the browsing traces of *Littorina* were

given by ANKEL (1936, 1937-a, b). He studied the grazing mechanism of the radula and the grazing behaviour of some living molluscs, in particular *Littorina littorea*. On a thin film of algae covering the wall of an aquarium these snails grazed meandering paths while crawling slowly sideways. The grazing produced a series of isolated, adjacent spots with characteristic longitudinal striation. The mouth of the snail is in pendulous motion, simultaneously with the crawling progress. On grazing the radula touches the substratum, browsing the algal layer and producing regular marks arranged side by side. The browsing-traces showed a number of striae, more or less situated in a transverse direction, corresponding to the number of teeth of one row of the radula. Ankel did not study traces formed under natural conditions. EIGENBRODT (1941), NEUMANN (1961) and RICHTER (1962) also studied grazing traces under artificial conditions, namely on glass plates covered with a thin fat layer. Richter compared the classes of molluscs with regard to their radula structure, and presented a general scheme for this organ in these groups.

Grazers have radula teeth with spade-like, lobed dissecting

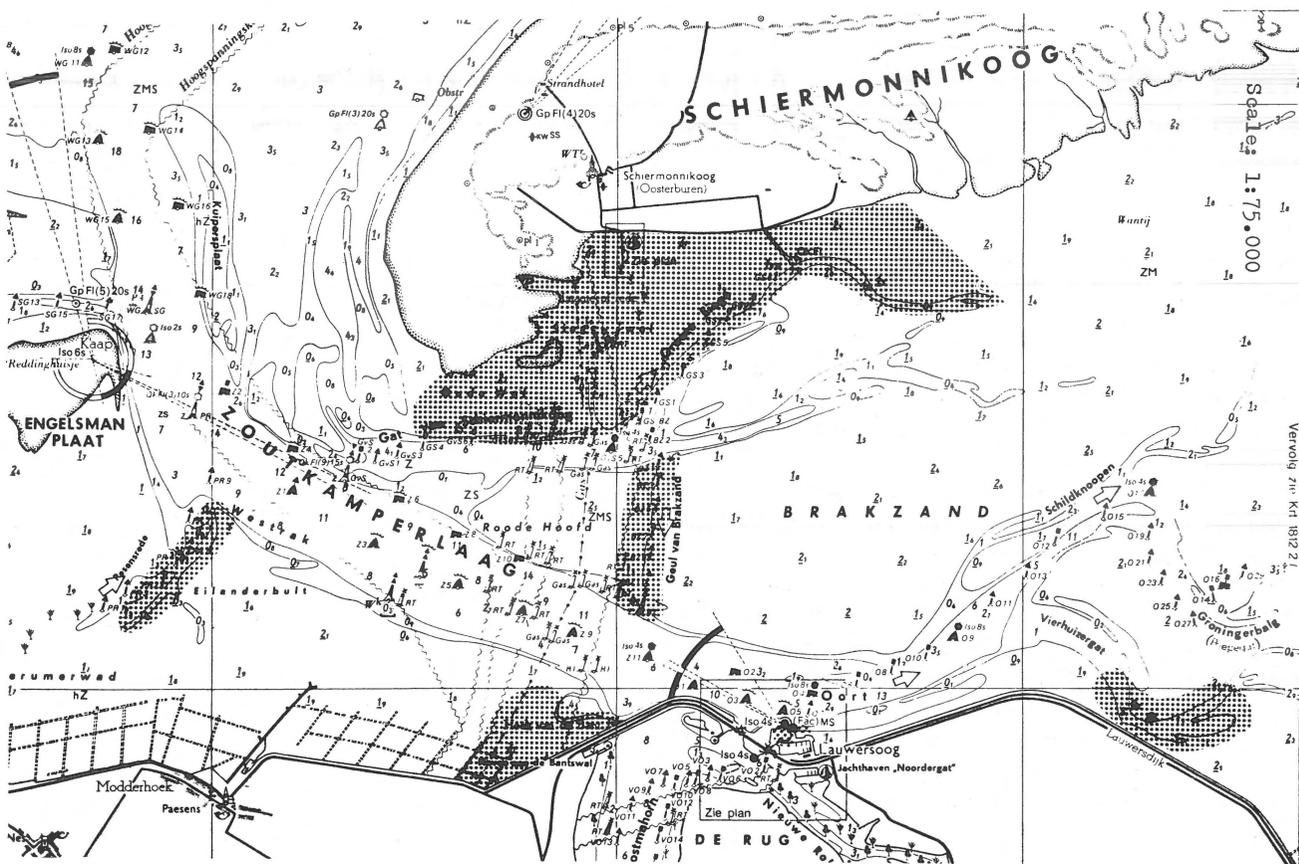


Fig. 3
Map of area investigated; dotted regions were studied in detail.

edges. The tooth shaft is often strong and seldom smooth, often with reinforcement buttresses. This type of radula is a general tool for gathering loose food particles, grazing off hard algal crusts, or eating holes in soft tissues of Phaeophyceae. It may also loosen balanids from their substratum. Richter postulates therefore that the radula of *Littorina* is a general tool for gathering several types of food.

BOEKSCHOTEN (1966, 1967) first recorded browsing-traces of chitons (*Lepidochitona*) and fossil examples (Fig. 2). VOIGT (1977) compared recent grazing traces with fossil specimens. Shells of bivalves and gastropods dating from Jurassic, Cretaceous and Tertiary strata showed grazing traces. Some traces were recognized as probably due to chitons, as indicated by the aquarium experiments by Richter.

MATERIAL AND METHODS

The Wadden Sea between the provinces of Friesland and Groningen on one side and the Frisian island Schiermonnikoog on the other side was investigated (Fig. 3).

In order to acquire empty shells of bivalves with grazing traces trips were made by boat or by walking offshore during

low tide. The shells were collected not only from parts of the shallows falling dry, but also out of small canals and gullies up to 0.5 m depth. The major part of the shells came from larger aggregations, washed out by tidal currents. Most specimens in the samples were *Mya arenaria*, but also some specimens of *Mytilus edulis*, *Cerastoderma edule*, *Macoma baltica* and *Scrobicularia plana* were studied. After drying at room temperature, the shells were inspected under a binocular. Specimens found together with living periwinkles or chitons were marked to indicate which grazing traces were formed by a given mollusc.

The living material was collected from several localities. In the first place littorinas and chitons from the shells mentioned above were considered. Other specimens were acquired from the building stones of the sea-wall. The molluscs used for the grazing experiments were transported in salt-water tanks and stored in aerated water in a climate chamber at 18°C. Specimens for anatomical investigation were killed and fixed in a 4% formalin solution.

The laboratory experiments were two-fold. The first part was intended to indicate how grazing traces are formed by the radula. For this purpose the living molluscs were put on a moistened glass-plate. After settling of the animal the plate

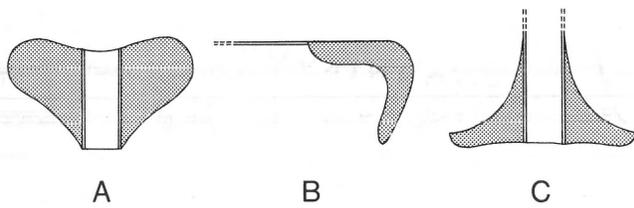


Fig. 4
Kink of radula of *Littorina littorea*, with the membrane (dotted).
A: rostral; B: lateral; C: dorsal (25 \times).

was turned over and the grazing movements were investigated under a binocular. It appeared to be necessary to starve chitons for several days, otherwise grazing movements would not occur.

The second part of the experiments concerned the conditions under which eating behaviour takes place. To investigate whether the traces were formed during day- or night-time, littorinas or chitons were put in tanks containing algal-coated bivalves without any grazing traces. After a period of 12 hours of total darkness, the shells were taken out of the water and dried for further investigation. The same procedure was applied for a period of 12 hours of exposure to light. Also periods of 36 hours for both conditions were tested. To check whether the presence of an algal-coated shell surface is necessary for the formation of grazing traces, the algal sheets were wiped off completely in order to remove all epilithic algae. With these shells tests were performed under the same conditions as described above. No experiments were done with shells cleared of all endo- as well as epilithic algae.

To investigate the structure of the radula apparatus firstly animals fixed in a 4% formalin solution were used. Living animals were placed in an anaesthetic solution of MS 222 (Sandoz), in order to stretch the soft parts and facilitating the anatomical investigation. Although this solution was applied in high concentration, the anaesthetic had little or no influence. The most successful method was killing the animal in a boiling 10% KOH solution for 5 minutes. For *Littorina* the shell had to be cut away, because the animal retreated completely; the shell of *Lepidochitona* fell off during boiling, so the dissection of the material could start immediately. In both species further investigation took place under a binocular microscope when the radulas had been removed. A darkfield illumination was used when photographing with an Olympus PM-6.

RESULTS

Field observations

The range of the periwinkles habitat is large. Important aggregations were found on the rocks of sea-wall in the tidal zone. No migration of the snails was established during tides coming in or going out. Once out of the water, the peri-

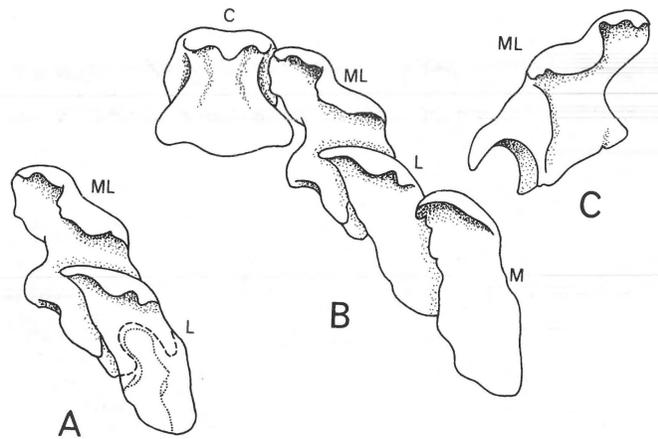


Fig. 5
Teeth of the radula of *Littorina littorea* (400 \times).
A: Major-lateral and lateral tooth of the right side.
B: One right half row of radula teeth.
C: Left major lateral tooth; the bowl of the joint is indicated by the dotted and striped lines in A.
C= rhachis; ML= major lateral; L= lateral; M= marginal tooth.

winkles fixed on the rocks and no activity was undertaken during low tide. When they were covered by the water again, crawling behaviour was displayed.

Another place where large numbers of this species were found is on mussel banks. Here the same pattern of activity was noticed. A third habitat was found on and between seaweeds, growing at the foot of the sea-wall. These seaweeds were always partly or completely submerged. Finally isolated periwinkles were found on those parts of the shallows that remain covered by a thin layer of water during low tides. Here the molluscs were crawling across the surface of the sediment.

The habitat of *Lepidochitona* is less extensive than that of *Littorina*. Most specimens were found on the downward-facing inner side of empty shells of *Mya arenaria*, never on the upper side. Such shells were often found near the aggregations of *Mytilus* as well as in or on the edge of the canals and gullies. Chitons were never seen in environments that are left dry for long periods. The sea-wall was found also to be a part of its habitat. Here *Lepidochitona*s were always situated on the under side of rocks. The spaces between the rocks remained water-logged during low tides.

Structure of the radula of *Littorina littorea*

The length (about 6 cm) of the toothed belt is very striking considering the length of the body of the animal. Across its whole length the belt is set with about 600 transverse rows, and passes over the odontophore. The radula changes its direction of movement at a place called the 'kink'. A basal membrane is present in this part of the radula. On the rostral side of the kink, the membrane is convex; otherwise it is concave. Figure 4 is a diagram of the distal end of the belt

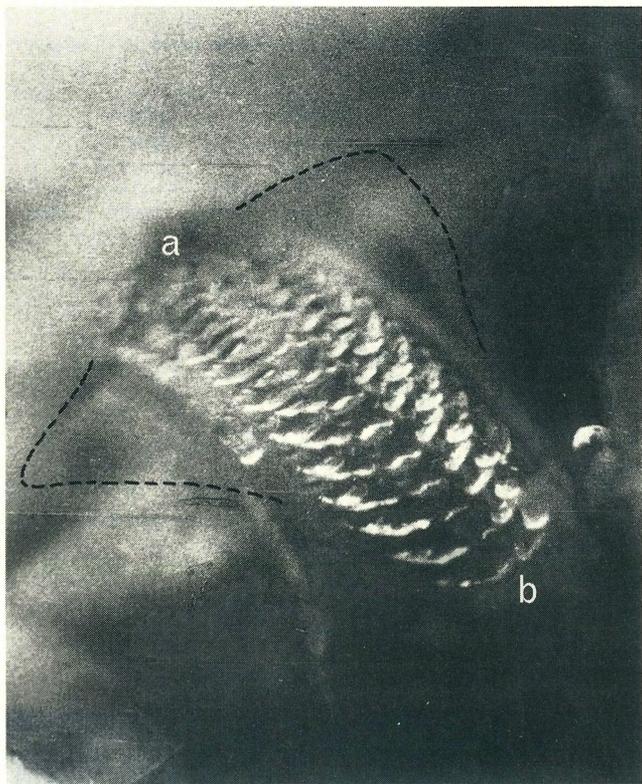


Fig. 6
Radula of *Littorina* showing the part used for scraping with several rows of teeth (16 \times). a= kink; b= distal end. The dotted lines are the outline of the basal membrane.

where the radula carries this membrane; its maximal width is situated at the side used for grazing. When active it glides together with the toothed belt across the odontophore. The shape of the membrane prevents the radula from slipping away during scratching, and also restricts movement in a rostral-caudal direction. Each transverse row of teeth on the radula consists of 7 elements. In the middle the rhachis is present, on the left and right side the paired major-laterals are found. Next to these the lateral teeth are situated, followed by the marginal teeth. Figure 5 shows the teeth of one half row in natural situation.

The rhachis has the shape of a trapezium and is bent at the top, forming a hook. This hook is perpendicular to the plane of the trapezium, supported by a consolidating column in the median plane. According to ANKEL (1937-b) more hooks should be present on the central tooth. These hooks were not observed during this investigation.

The major-lateral teeth are more adapted to scraping. On the top side two more or less lobed hooks are situated; this extends its active surface. On the bottom of the lateral side a bowl of the joint-like connection with the lateral teeth is seen, making rostral-lateral movement feasible for the latter. The most conspicuous feature of the lateral and marginal teeth is their spoon-shaped upper edge, somewhat lobed in the for-



Fig. 7
Distal part of radula of *Littorina* (100 \times). c= rhachis; ml= major-lateral; l= lateral; m= marginal.

mer. The freedom of movement for the outer teeth is well developed, particularly in the rostral-lateral direction. They may be rotated around their basis to a certain extent relative to the basal membrane. Figures 6 and 7 show details of the radula of the periwinkle.

Structure of the radula of Lepidochitona cinereus

The radula of *Lepidochitona* is quite different from that of *Littorina*. The total length of grazing apparatus measures up to 0.7 cm and does not possess a coiled basal end; it terminates straight in the form of a club. The belt is firm and does not allow much freedom of movement in a lateral direction. The radula carries about 40 transverse rows of teeth, diminishing in size in a caudal direction. In its basal part the rows are hardly visible and near the radula sac they are absent. The part in use comprises about 10 rows of teeth. Each row is composed of one central tooth (rhachis), two lateralia and six marginalia (Figs. 8 and 9). The lateral tooth is large and is spread out at the top side, supplied with a dark-brown crown with three sharp points. The central, major-lateral and major-marginal teeth have a spoonlike top side, while the

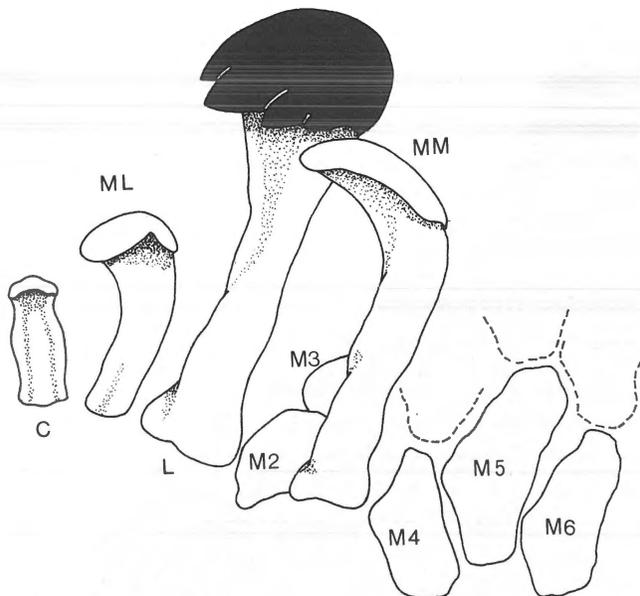


Fig. 8
One right half row of radula teeth of *Lepidochitona* (400×).
C= rhachis; ML= major-lateral; l= lateral tooth with magnetite cap; MM= major-marginal; MM₂-MM₆= marginal teeth.

Table I
Grazing traces of *Littorina* and *Lepidochitona* on shells of *Mya arenaria*.

		epilithic algae present		epilithic algae removed	
		light	dark	light	dark
<i>Littorina littorea</i>	12 hours	+	+	-	-
	36 hours	+	+	-	-
<i>Lepidochitona cinereus</i>	12 hours	-	+	-	+
	36 hours	±	+	±	+

+ present; - absent; ± some present.

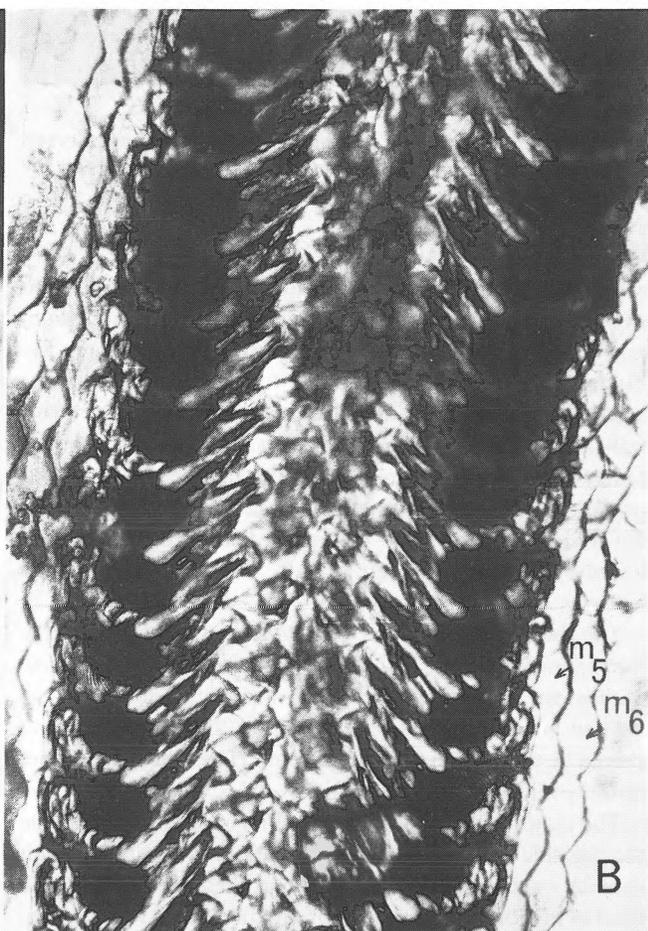
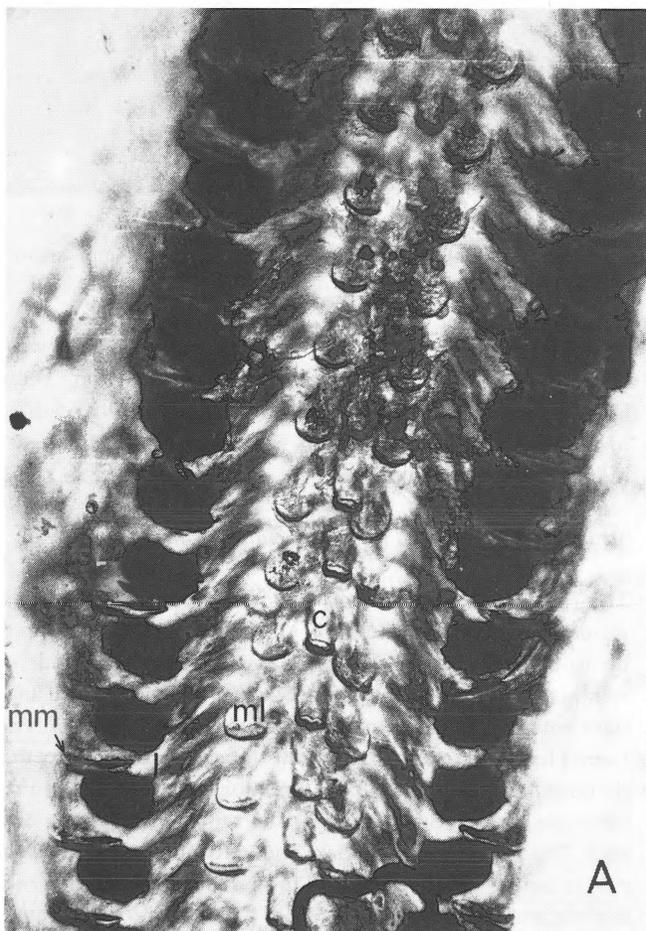


Fig. 9
Part of radula of *Lepidochitona* (400×).
A: focused on the upper surface;

B: focused on the basal surface.
Explanation of abbreviations same as in figure 7.

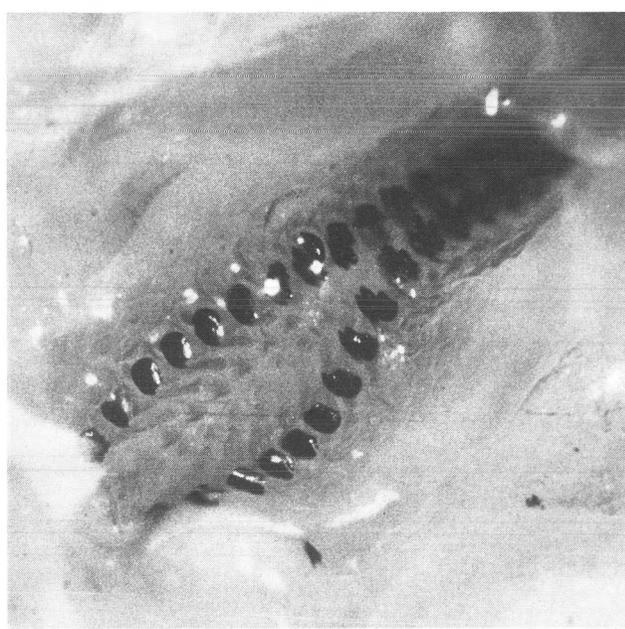


Fig. 10
Radula of *Lepidochitona* in situ, showing the rostral part and the kink (40×).

remaining marginals are irregularly plate-shaped. At the kink the radula belt changes in direction during grazing. Figure 10 shows this kink and the rows of teeth in use.

Laboratory experiments

The formation of grazing-traces under varying conditions with respect to day and night time, is rendered in table 1.

Movements during grazing by Littorina and Lepidochitona

A model of the radula apparatus was given by ANKEL (1937-b). The basal membrane is represented by a flat flexible belt; the radula teeth by driven-in hooked nails, from the inner to the outer side; the odontophore by a revolving cylinder. This model can be moved to and fro in a shaft (Fig. 11). When turning the cylinder around its axis with rhythmic intervals, the belt follows this movement by lowering and elevating. When the apparatus is moved along the axis a-b to the left against the substratum during elevation, browsing takes place.

During grazing the head of the *Littorina* describes a segment of a circle relatively to the foot of the animal. The lowering movements of the radula always take place rostral, perpendicular to the tangent of the circle. Simultaneously with lowering, the head moves along a new segment of the circle and the radula is lowered again with a new spot situated beside the first bite. In this way 8-12 bites are made in a segment of a circle. The bites always succeed each other in one direction, to the left or to the right (see Fig. 12a). Besides

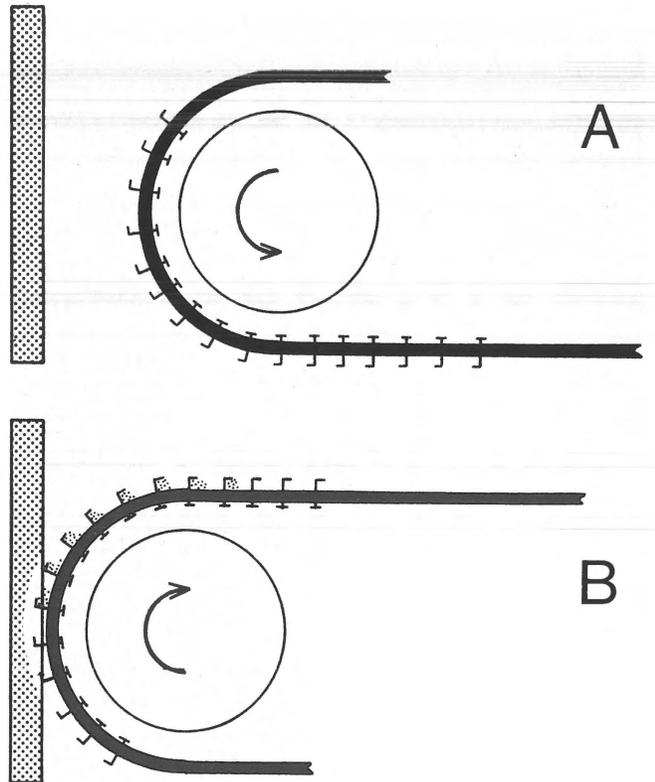


Fig. 11
Model of radula.
A: lowered; B: elevated (modified after Ankel, 1937).

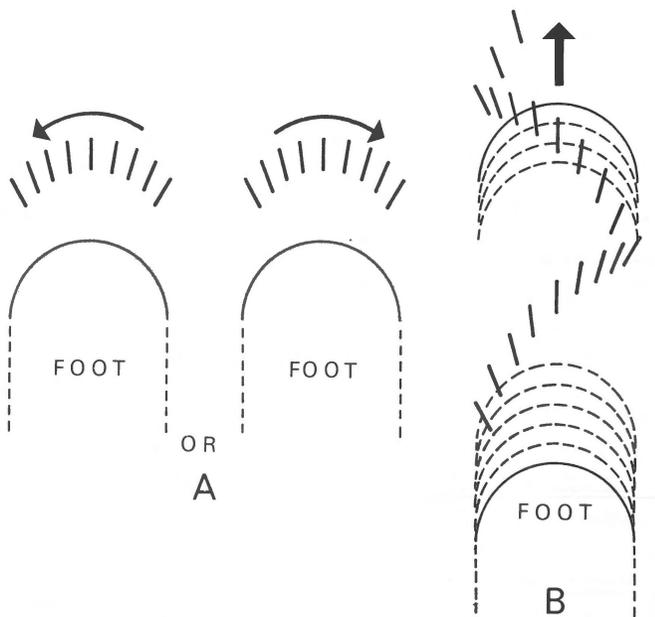


Fig. 12
Grazing of *Littorina* (25×). Each thick line is one bite.
A: Bites during one movement of the head in left or right sequence.
B: Bites as a result of the complex of movements of the head and the crawling animal.

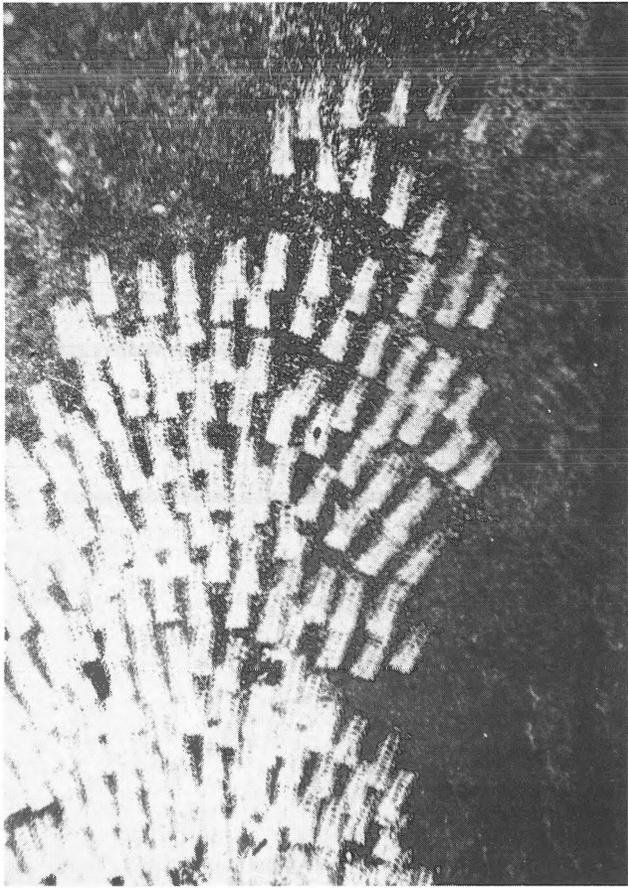


Fig. 13
Algal coated inside of *Mya arenaria* with traces of intensive grazing of *Littorina* (6 \times).

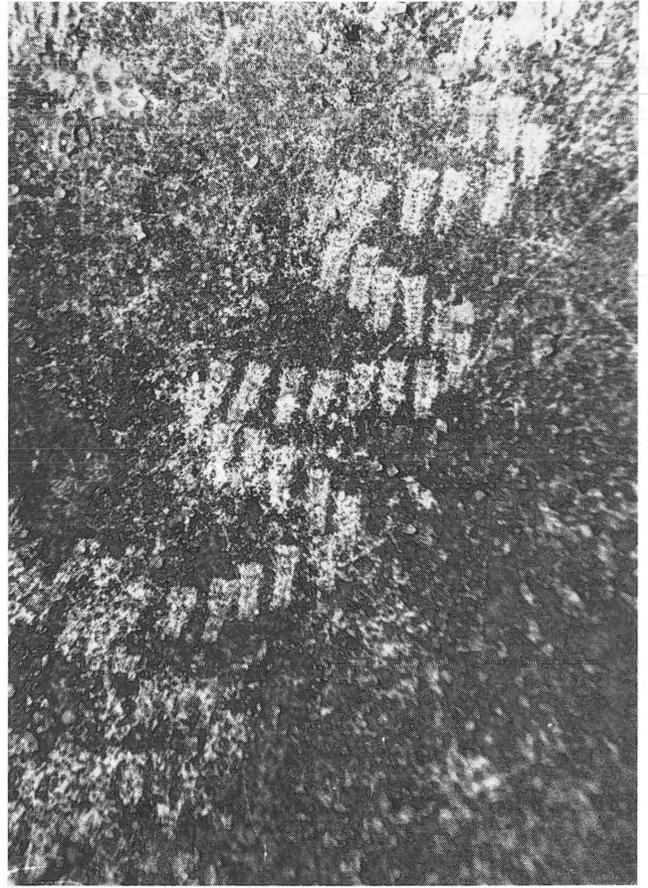


Fig. 14
Zigzag grazing pattern of *Littorina* in algal coated shell of *Mya arenaria* (6 \times).

this motion the animal moves as a whole in a rostral direction, and the result is a zigzag line on which bites are seen (Fig. 12b). The pendulous motions come closer together when the speed of the rostral movement decreases and/or the lateral one increases.

The grazing of *Lepidochitona* has a different speed of biting. One elevation takes about 1-2 seconds, while for *Littorina* this is up to 0.5 sec. Also the displacement from one biting spot to another takes several seconds as opposed to *Littorina* with up to 1 sec. Another difference of grazing with regard to the periwinkle consists in lack of rostral movement, so the bites are not made on a zigzag line but only on a segment of a circle. After the end of lateral movement the animal moves up for several mm and grazing is resumed. The number of bites during one lateral motion varies from 1-8. In contrast with *Littorina*, which produces bites at one place at a time, *Lepidochitona* performs elevation of the radula at the same biting spot several times.

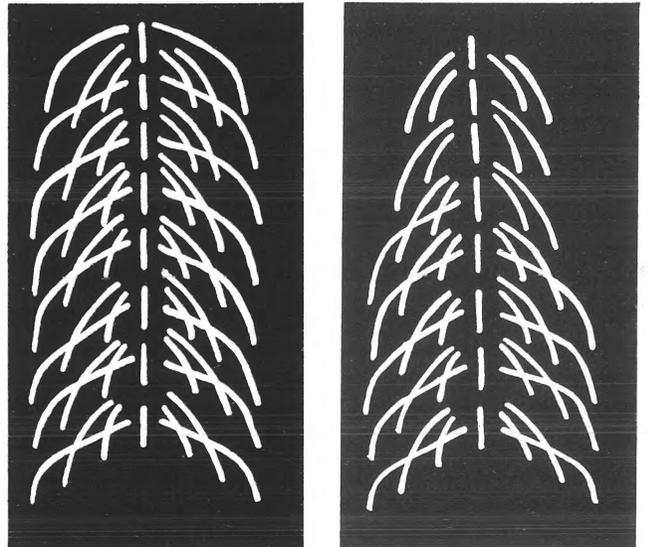


Fig. 15
One single bite of the grazing-trace of *Littorina* (60 \times).
A: intensive grazing; B: zigzag grazing.



Fig. 16
Detail of grazing trace of *Littorina* in which part the substratum is eroded (40×).

GRAZING TRACES OF *LITTORINA LITTOREA*

The browsing traces of *Littorina* found on *Mya arenaria* were situated in most cases at the inner side of the shell. No preference for certain places was observed. Sometimes traces were situated on the upper side of the shell, when an algal film grew there. If an algal cover was absent traces were never discovered.

Two different grazing patterns were observed. In the first pattern (Fig. 13) the surface of the substratum is covered with densely packed bites, arranged on curved lines, lying behind each other. This pattern gives the impression of intensive grazing behaviour. The second pattern is a zigzag grazing trace (Fig. 14), consisting of 5-8 bites that are part of one track (zig or zag). The distance between two bites is equal in both patterns, and is $\frac{2}{3}$ of the width of one single bite. Precise study of the separate bites belonging to the two patterns revealed some difference between these bites. Before going into this subject the structure of the single bite has to

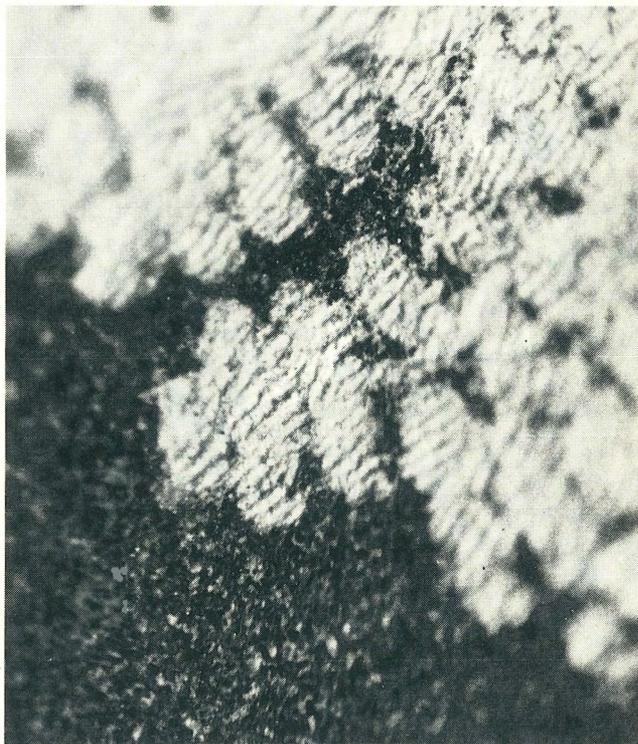


Fig. 17
Several series of parallel furrows in grazing traces of *Lepidochitona* (25×).

be discussed.

The pattern of one bite is bilateral, width and length of about 0.5 mm, (varying up to 0.1-0.2 mm) and a width of 0.2 mm. In the middle a striped line is to be seen. The number of these stripes is directly proportional to the length of the bite. Curved lines accompany the middle stripes, and between these two at both sides in most cases a thick vague line running parallel to the middle is situated. Sometimes in this vague line two more somewhat curved lines can be discovered. An idealized bite pattern is presented in figure 15a. The direction in which the curved lines point is the direction in which the bites are made, so the front and the back of the bites can be identified. It is evident that the front of the bite of the zigzag pattern lacks the outer curved lines. This implies that the outer teeth of the radula, the marginal teeth, did not touch the substratum. An idealized bite pattern of this type is presented in figure 15b. The difference of the two bites cannot be due to the substratum, as both patterns do appear on the same shell.

When the algal sheet is wiped off the traces, imprints of the bites are rarely left in the substratum. In one specimen of *Mya arenaria*, after removal of the algal layer, the grazing trace remained visible (Fig. 16). In this case the nacreous layer of the ostracum was very soft. Grazing traces of *Littorina* in the fossil state should be rare; they have not as yet been observed by the present authors.

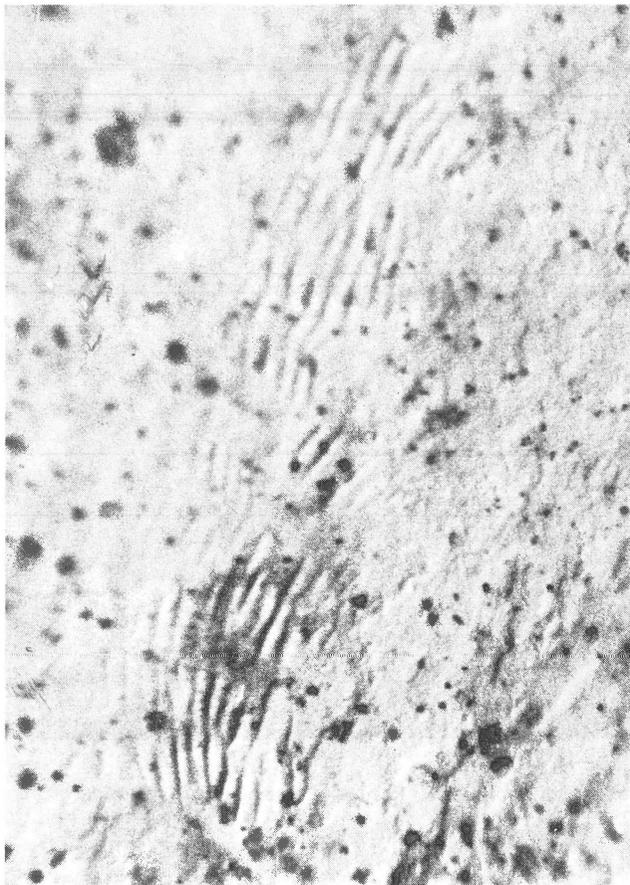


Fig. 18
Grazing traces of *Lepidochitona* at the inside of a *Mya* shell, shorn of epilithic algae in advance (25 \times).

GRAZING TRACES OF *LEPIDOCHITONA CINEREUS*

It was seen that the inside of empty *Mya* shells was preferred for grazing. The apical inside of the shell especially was densely covered by traces. In traces on the outside of *Mytilus* shells, the periostracum was very thin or completely absent, so in fact the ostracum had been scratched off. In comparison with the traces on the inner side, traces were minute and not so densely spaced.

The grazing traces show sharp sub-parallel or slightly ar-

ched non-parallel furrows arranged perpendicularly to the axis of the browsing animal, in contrast to *Littorina* where scratches are parallel to the body axis. The scratches are arranged in series of 2-30, and the interspatial of two scratches varies in case of dense packing from 1/3 of the width of one scratch to 2 \times this width in case of slight grazing. The length of one scratch is about 0.5 mm. The erosive character of this grazing is striking (Fig. 17). At first sight also a wavy pattern seems present, but the direction of the scratches in this pattern cannot be compared with the zigzag grazing pattern of *Littorina*. The polyplacophoran is also able to form grazing-traces on surfaces wiped clean of epilithic algae (Fig. 18). In all cases after removal of the algal sheet the scratches remained distinctly visible.

Investigations of traces found on other shells revealed that the traces found on *Mytilus edulis* were always situated on the outside of the shell and never on the inside. Apparently, the large shells of *Mya* give opportunity for grazing when empty; but *Mytilus* shells are scratched off only by chitons living between the densely packed living bivalves in mussel banks. Subfossil *Lepidochitona* traces are often seen.

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