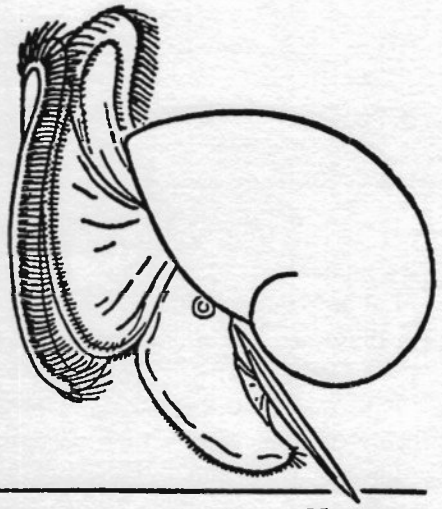
THE VELIGER



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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, *Genus, (Subgenus)*
New Taxa

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Structures of Recent Cephalopod Radulae

BY

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(4 Plates)

ATTEMPTS TO DETERMINE the possible affinities of the isolated Carboniferous nautiloid radula recently described as *Paleocadmus herdinae* Solem & Richardson, 1975 have led first to an examination of a few recent cephalopod radulae, and then, on the basis of these results, to a systematic review of radular patterns in the Cephalopoda. Scanning electron microscope (hereafter SEM) photographs from the extended survey, including observations on the pattern of variation found in sympatric congeneric species, will be published subsequently. Here we present examples from most major systematic groups, selected to show typical overall structural patterns and to indicate deduced functional differences.

SEM photographs of cephalopod radulae have been published previously by ALDRICH, BARBER & EMERSON (1971), who surveyed 22 species, covering the sepiolid *Rossia,* loliginid squids *Loligo* and *Lolliguncula,* ommastrephid squids *Illex, Todaropsis,* and *Ommastrephes,* and the octopods *Octopus, Pteroctopus,* and *Eledone.* Subsequently SOLEM & RICHARDSON (1975) illustrated the radula of *Nautilus* and discussed its function.

The species reviewed here, their systematic position and the specimens are:

CEPHALOPODA Cuvier, 1798

Coleoidea Bather, 1888

TEUTHOIDEA Naef, 1916

Myopsida Orbigny, 1845

LOLIGINIDAE Steenstrup, 1861

Loligo plei Blainville, 1823
USNM 577080, "*Geronimo*" Cruise 6, station 7-2, 26 October 1966, 18°25'N, 67°12'W, Caribbean Sea. ML (Mantle Length) =137 mm

Oegopsida Orbigny, 1839

HISTIOTEUTHIDAE Verrill, 1881

Histioteuthis dofleini (Pfeffer, 1912)
USNM 729468, *Oregon* station 6703, 21 May 1967, 16°53'N, 61°53'W, Caribbean Sea. ML=57 mm

VAMPYROMORPHA Pickford, 1939

VAMPYROTEUTHIDAE Thiele, 1915

Vampyroteuthis infernalis Chun, 1903
USNM 729469, *Walther Herwig* station 482-III, 13 April 1971, 04°38'N, 19°41' W, North Atlantic Ocean, off western Africa. ML=47mm

OCTOPODA Leach, 1817

Incirrata Grimpe, 1916

OCTOPODIDAE Orbigny, 1845

Octopus briareus Robson, 1929
USNM 574777, J. Russell, 10 July 1937, 24°38'N, 82°55'W, Gulf of Mexico, Dry Tortugas. ML=39 mm

When combined with the previously published SEM illustrations of cephalopod radulae, the information presented here permits a definition of the basic strategies of radular function and an indication of patterns within the major groups of extant cephalopods.

ACKNOWLEDGMENTS

We are indebted to Anne Cohen, Michael J. Sweeney, and Barbara Walden for assistance in the extraction of buccal masses and preparing them for SEM study. The photographs illustrating this paper were made by Alan Solem on a Cambridge S4-10 scanning electron microscope provided to Field Museum of Natural History through National Science Foundation grant BMS 72-02149 A01. The enlargements were made by Fred Huysmans and mounted by Dorothy Karall. For help with manuscript preparation, we are indebted to Jayne Freshour, Barbara Walden, and Michael J. Sweeney. We thank C. C. Lu, M. J. Sweeney and R. E. Young for reading the manuscript.

METHODS

Buccal masses were prepared for SEM viewing using the technique outlined by SOLEM (1972). The masses were soaked in a concentrated KOH solution until the beaks could be pulled out and the muscles surrounding the radula itself were weakened enough so that the radula could be removed easily. Frequently the radula was left in KOH for an additional period, until connective tissue and muscle fibers were virtually detached. The radular membrane then was soaked briefly in alcohol and plunged into a sonic cleaner for 10 to 20 seconds in order to remove extraneous particles. Rubber cement was used to mount each radula onto an SEM stub. After drying onto the mounts, 6 stubs at a time were given first a coating of carbon and then gold in a vacuum evaporator with continuous rotation and varying tilt of the stubs during the coating processes. This insured covering of nearly all surfaces and greatly reduced the problems of charging during SEM viewing. Photographs were made on Polaroid Type 55 P/N film. The accelerating voltage ranged from 3-20 kv, depending upon the condition of individual specimens.

DESCRIPTION AND FUNCTION OF STRUCTURES

Traditionally the radular teeth of cephalopods have been termed rachidian, first lateral, second lateral and third lateral teeth and marginal plate (or tooth) (see ROB-

Explanation of Figures *1* to *6*

Loligo plei Blainville, 1823

USNM 577080; 18°25'N; 67°12'W; ML=137 mm

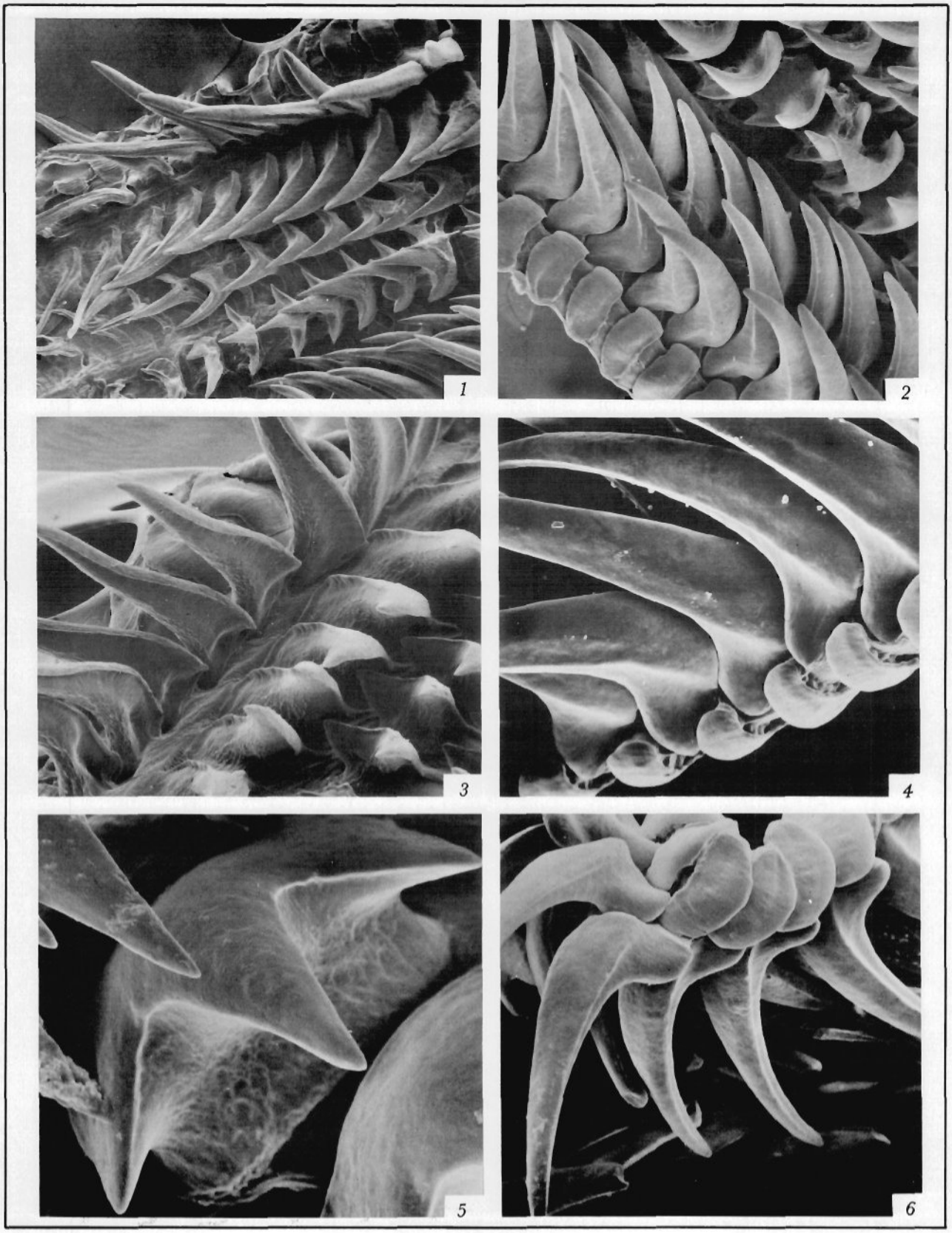
Figure *1*: Part row at posterior end showing newly formed, only partly hardened teeth × 72
Figure *2*: Part row of mature teeth × 94
Figure *3*: Inner side of outer marginal teeth and inner marginal teeth × 142
Figure *4*: Detail of outer marginal teeth and marginal plates × 194
Figure *5*: Rachidian tooth showing margin of posterior basal plate and cusps × 480
Figure 6: Outer marginal teeth at artificially curved point of basal membrane to show functional relationship between marginal plates and outer marginal teeth × 136

Explanation of Figures *7* to *12*

Histioteuthis dofleini (Pfeffer, 1912)

USNM 729468; 16°53'N; 61°53'W; ML=57 mm

Figure *7*: Part row in near-vertical view × 123
Figure *8*: Anterior view of part row × 200
Figure *9*: Rachidian and lateral teeth × 188
Figure *10*: Nearly vertical view of outer marginal teeth and remnants of marginal plate × 158
Figure *11*: Outer marginal teeth bent outwards, inner marginal teeth, and marginal tooth ligament (arrows) × 176
Figure *12*: Detail of marginal plate remnant × 875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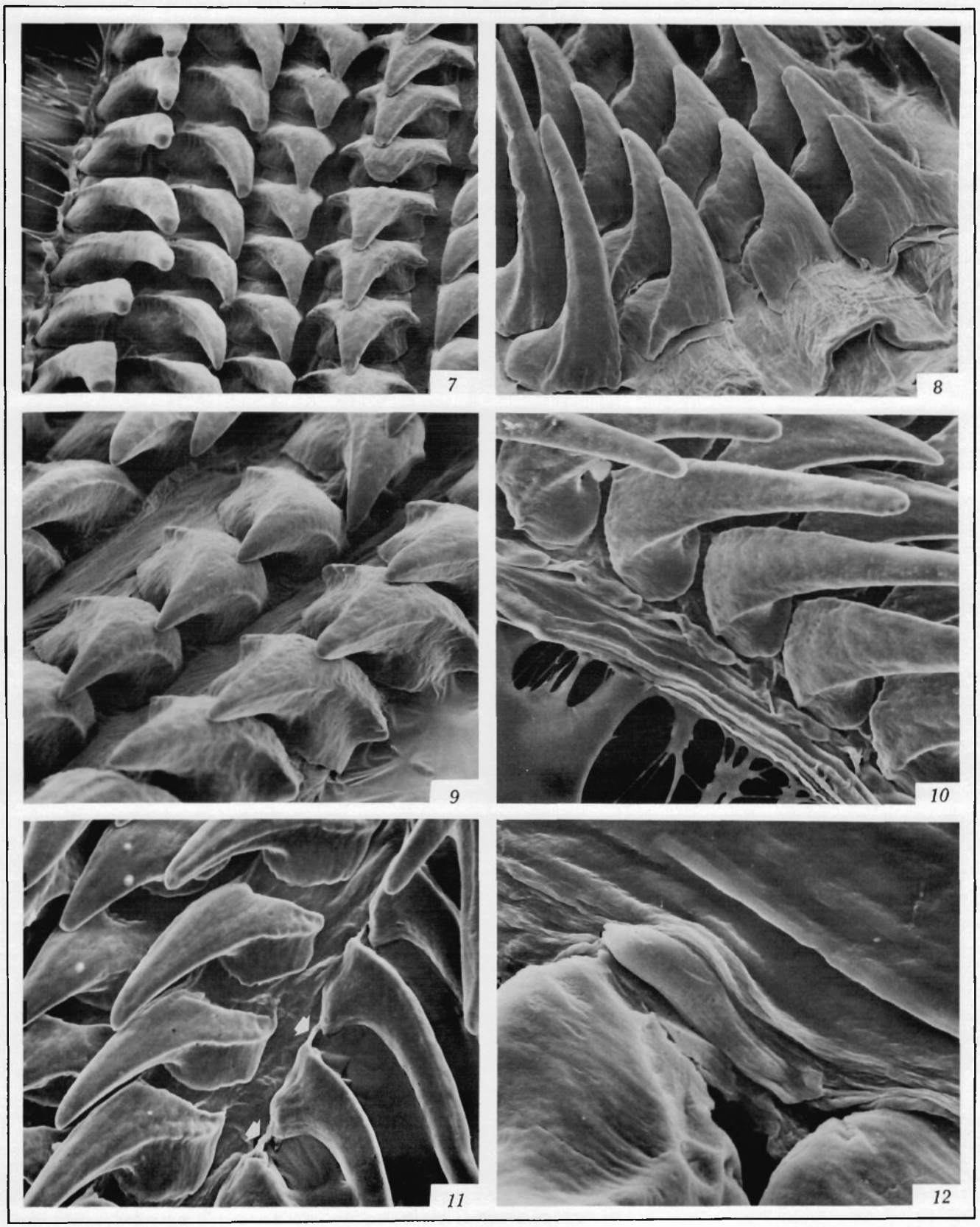
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SON, 1932; Voss, 1956). We alter the terminology somewhat by calling the second and the third lateral teeth, respectively, the inner and the outer marginal teeth. This terminology parallels that applied in other molluscan groups and is equivalent to that of taenioglossate gastropods which also have seven rows of radular teeth (FRETTER & GRAHAM, 1962: 169, 171; fig. 105D). More importantly, the designation of inner and outer marginal teeth takes into account the close functional relationship of these two teeth in the process of compaction or folding (Figures *1, 8, 16, 23*). In the majority of taxa examined (unpublished survey) the inner and outer marginal teeth are structurally much more similar to each other than they are to the lateral tooth (Figures *1, 8, 18, 20*).

We define "cusp" more narrowly than previous authors. We consider it to be an elevated, pointed projection from the base of a tooth or laterally from a main cutting projection. We distinguish a cusp from a lower, laterally extending support ridge, which may appear cusp-like from some angles of viewing. This difference is demonstrated by *Loligo plei*. For example, in Figure *3* the lateral teeth, lower right, show an elevated "wing-like" lateral cusp, that when viewed from directly above (Figure *1*) appears as a pointed projection. In contrast, the inner marginal tooth in Figure *3* (second tooth row from right) has a raised laterally extending edge that effectively is a low, unpointed version of the cusp on the lateral tooth. When it is viewed from directly above (Figure *1*), this is clearly a support ridge rather than a cusp. As can be seen in the upper right of Figures *1* and *3*, the outer marginal teeth can fold down on top of the inner marginals, with the support ridge of the inner marginals fitting into the groove on the median side of the outer marginal teeth (see left of center in Figure *3*). Both support ridge and cusp share a common derivation, but their functions have diverged – cusps operate in holding, tearing, or conveying particles of food, while the support ridges function during the process of compaction, *i.e.*, when the teeth are folded down.

Marginal Plate:

Marginal plates long have been recognized as discrete structures, but this is the first attempt to define functional differences. In *Nautilus* (SOLEM & RICHARDSON, 1975: figs. 14, 15, 17, 18) the outer marginal plate functions as a mechanism for tooth erection through interaction between the free inner edge of the plate and the laterally curved posterior tip found on the basal plate of the outer marginal tooth. The series of teeth shown from upper right to the middle of fig. 15 (*loc. cit.*) suggests the sequence of moves in tooth elevation in *Nautilus* through shifting alignment between the marginal plate and the base of the outer marginal tooth.

The inner marginal plate that occurs in nautiloids does not exist in recent coleoids.

A function equivalent to that in *Nautilus* apparently is served by the (outer) marginal plates in myosid squids such as *Loligo* (Figures *2, 4, 6*), with interactions between the basal flare of the outer marginal tooth and the free edge of the plate. The marginal plate is reduced to a remnant (*Histioteuthis dofleini*, Figures *10, 12, 13*) or is lost (unpublished data) in most oegopsid squid (except, *e.g.*, *Cranchia*) and sepiolids (unpublished; also ALDRICH, BARBER & EMERSON, 1971). In *Vampyroteuthis infernalis* (Figures *15, 16, 18*) and incirrate octopods (*Octopus briareus*, Figures *19, 20, 23*), the marginal plate seems to act as a "stress support" buttress, rather than as an erection device. The plate itself is without a free edge, has a truncated inner margin and articulates with an indentation (Figure *23* for *Octopus*) or a truncation (Figure *18* for *Vampyroteuthis*) on the outer marginal tooth.

The change between an erectional and supporting function for the outer marginal plate is of uncertain phylogenetic significance. SOLEM & RICHARDSON (1975: 239) hypothesized that in the Carboniferous genus *Paleocadmus* the outer marginal plate had a support function, but that in the recent *Nautilus* it serves a "triggering function." The function of the plate in such octopods as *Eledone* and *Octopus salutii* (ALDRICH, BARBER & EMERSON, 1971: figs. 18, 19) is uncertain, but the appearance suggests reduction toward a remnant state, while in taxa such as *Bathypolypus* (unpublished) the plate may serve partly as a triggering mechanism, rather than a support system. Quite probably the change has occurred repeatedly within major lineages as selection for more efficient feeding on differing prey organisms has proceeded.

In taxa with greatly reduced marginal plates, a new structure frequently is present. A strand of ligamentous tissue extends from the anterior tip on the base of the outer marginal tooth to either the posterior edge of the base of the next outer marginal tooth anteriorly (*Enoploteuthis*, unpublished), or to the basal membrane itself (*Histioteuthis*, see arrows in Figures *11, 14*). Equivalent structures are known for the carnivorous land snail *Oophana* (SOLEM & RICHARDSON, 1975: fig. 24) and are a normal part of the radular complex in the fresh water pulmonate family Physidae (BAKER, 1928: 414). We are not aware that this has been reported in other mollusks. Similar structures in other taxa with long slicing teeth can be predicted, but because of the unusual viewing angle required to detect this structure, it easily can be over-

looked. We call this structure in cephalopods the *marginal tooth ligament.*

The inner marginal support plate in *Nautilus* (SOLEM & RICHARDSON, 1975: figs. 17, 18, 21) is a uniquely nautiloid feature, and it functions both as a trigger for the erection of the inner marginal tooth and as a folding support for the outer marginal tooth. It also is found in *Paleocadmus* (*loc. cit.*: 239; fig. 25), but has not been observed in other cephalopods.

Outer Marginal Tooth:

Structure of the outer marginal tooth differs drastically with the apparent function of the marginal plate. The outer marginal tooth in all taxa is unicuspid, but its shape and basic angle or alignment varies greatly. In taxa with a strong lateral basal flare on the outer marginal tooth which correlates with the triggering or erectional function of the marginal plate, distinct grooves occur on the medial side of the tooth (*Nautilus*, SOLEM & RICHARDSON, 1975: fig. 20), or the medial side is indented (*Loligo*, Figure *3*). In taxa in which the basal plate of the tooth is greatly reduced or lost, such as *Histioteuthis* (Figure *11*), the medial edge of the outer marginal tooth lacks these grooves. The functional difference basically involves the way in which teeth are folded when they are not being used for feeding. The type of folding pattern represented by *Loligo* involves interlocking of the outer marginal tooth onto the inner marginal tooth during folding, whereas in *Histioteuthis* the pattern of folding does not involve such an interlocking with the adjacent inner marginals.

The degree of curvature of the outer marginal teeth varies greatly from species to species, both in those in which the marginal plate functions as a trigger and those that possess greatly reduced marginal plates. For taxa in which the marginal plate functions as a support, the tendency is for the outer marginal tooth to be a simple, only slightly curved shaft, that tapers slightly from tip to base (Figures *15, 18, 20, 23*) and that folds down (medially) against the inner marginal tooth. The inner marginal tooth can be very strongly extended laterally via a deep groove into which the outer marginal tooth fits (*Octopus*, Figure *23*), or the outer marginal tooth can fold against the grooved side of the inner marginal (*Vampyroteuthis*, Figure *18*).

None of the outer marginal teeth of cephalopods examined so far demonstrate a "slicing" form equivalent to that seen in carnivorous land snails such as *Euglandina, Systrophia,* and *Haplotrema* (see SOLEM, 1974). Instead they are of the "stabbing" or "tearing" form.

Inner Marginal Tooth:

The inner marginal teeth in nautiloids are very similar in form and function to the outer marginal teeth (see SOLEM & RICHARDSON, 1975: figs. 1, 15, 17, 25) and quite different from the lateral and central teeth. In the coleoid species discussed and illustrated here, the cusped portion of the inner marginal tooth is of the same size as the lateral tooth and much shorter than the outer marginal. Very great differences occur in the degree of lateral extension of the inner marginal tooth. In *Octopus briareus* (Figure *23*) and *Vampyroteuthis infernalis* (Figure *16*) a very strong lateral extension exists on the inner marginal tooth onto which the outer marginal tooth lies in the folded position. In *Loligo plei* (Figures *1, 3*) the lateral extension of the inner marginal tooth is shorter than in the two previous taxa, but the function appears to be the same (although the outer marginal tooth may not lie as flat). *Histioteuthis dofleini* (Figures *8, 9, 11*) has a very short, ridged extension on the inner marginal tooth, a structure that is typical of taxa with reduced marginal plates.

Lateral Tooth:

The lateral teeth are equal in height to the inner marginal teeth (*e.g.*, Figures *1, 7*), except in *Octopus* (Figure *19*). They may be unicuspid (*Vampyroteuthis*, Figure *17*), or have a very slightly elevated lateral "cusp" that is more of a shoulder than a projection (*Histioteuthis*, Figure *9*), or have a markedly elevated lateral cusp that is distinctly lower in elevation than the main cusp (*Loligo*, Figures *1*,

Explanation of Figures *13* to *18*

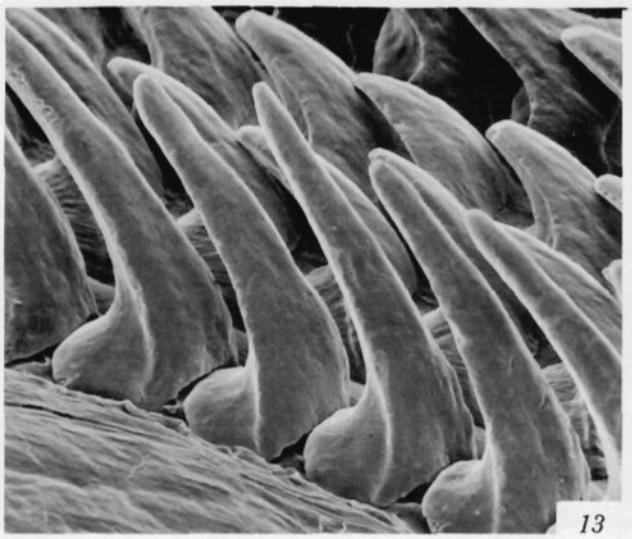
Histioteuthis dofleini (continued)

Figure *13*: Outer marginal teeth and marginal plate remnants × 200
Figure *14*: Detail of marginal tooth ligament (arrow) × 550

Vampyroteuthis infernalis Chun, 1903

USNM 729469; 04°38′N; 19°41′W; ML=47 mm

Figure *15*: Detail of marginal plates and outer marginal teeth × 96
Figure *16*: Part row of teeth × 48
Figure *17*: Rachidian and lateral teeth × 169
Figure *18*: Marginal teeth and marginal plates × 95



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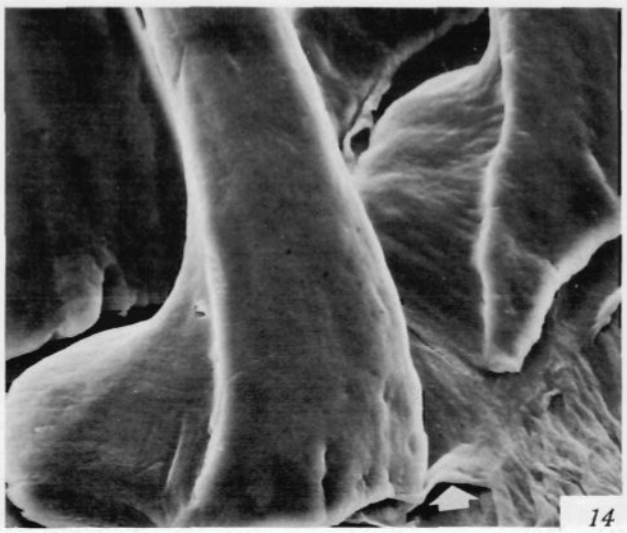

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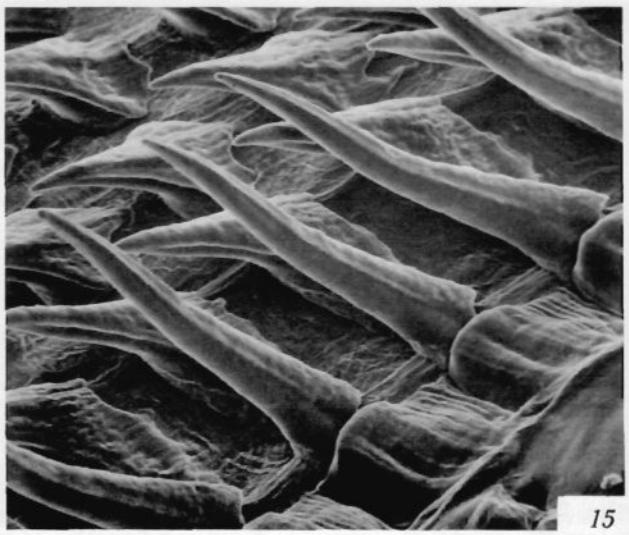

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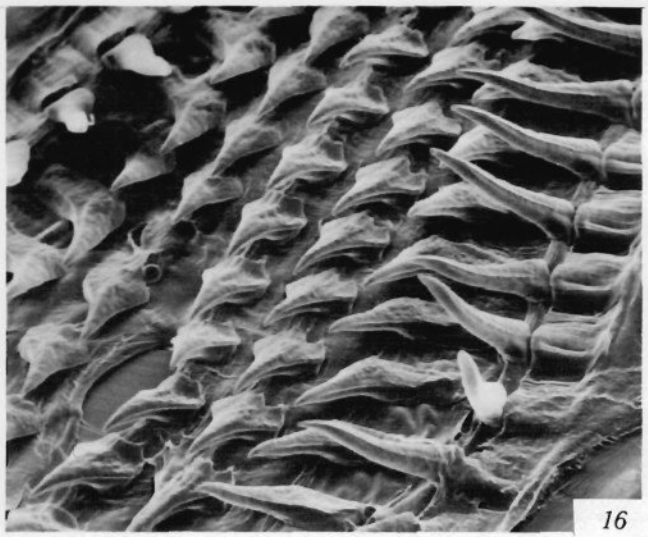

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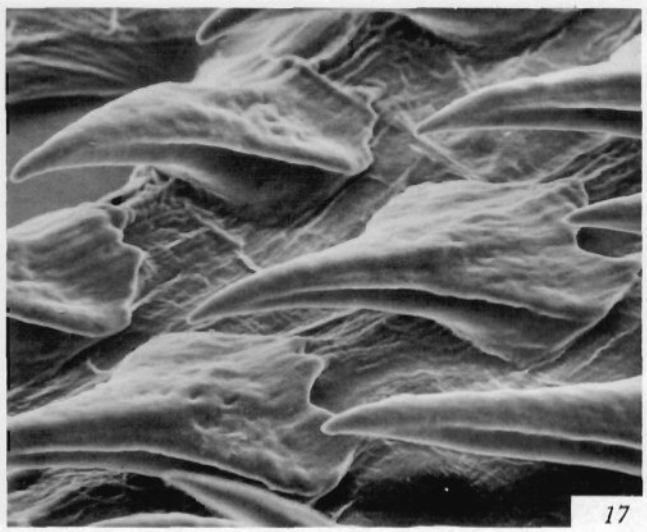

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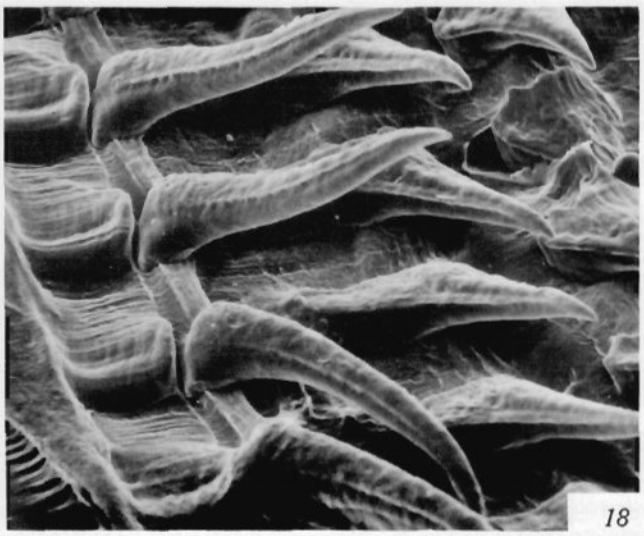

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3). In octopods (Figures *19, 20, 22*), the lateral tooth is rudimentary, consisting of a small lateral cusp and a medial extension (see also ALDRICH, BARBER & EMERSON, 1971: figs. 18, 19). The lateral tooth appears so underdeveloped compared with the cusps on the neighboring teeth, that it is difficult to imagine how it could take part in the feeding process.

Rachidian Tooth:

Rachidian teeth are equally variable, ranging from the almost equally tricuspid structure with narrow base found in *Loligo* (Figure *5*), to the very large multicuspid structure seen in *Octopus* (Figures *21, 22;* also ALDRICH, BARBER & EMERSON, 1971: figs. 18, 19). All of the squid species examined by ALDRICH, BARBER & EMERSON (1971: figs. 2-8, 12-17) had tricuspid rachidian teeth, although these authors document considerable intraspecific variation in tooth width and relative size of the cusps. They found species of the sepiolid *Rossia* to have unicuspid rachidian teeth (*loc. cit.:* figs. 9-11). Every degree of variation seems to exist between the tricuspid and unicuspid structures. In *Histioteuthis dofleini* (Figures *7,8,9*) there are "pointed shoulders" to the rachidian tooth that equal the weak extensions of the lateral teeth (Figure *9*). The low degree of elevation is such that they must play a secondary role in actual feeding. *Vampyroteuthis* (Figures *16, 17*) has a sharply pointed unicuspid rachidian tooth, that tapers gradually at first, then flares to a broad base. The strong grooves on the lateral surface of both rachidian and lateral teeth in *Vampyroteuthis* are clearly visible in Figure *17*.

In contrast, the large, highly variable rachidian teeth in *Octopus* have a very different orientation and cusp structure. The well-known pattern of variation in number and position of subsidiary cusps on successive rachidian teeth is shown clearly in *Octopus briareus* (Figures *20, 22*). The pattern occurs over 4 teeth, with an initial two side-cusps (fourth tooth from bottom in far left of Figure *20*), one high and one very low cusp. This is followed by loss of the upper, then size increase and upwards migration of the lower cusp on the next two teeth, then size reduction of the upper and reappearance of a lower cusp in the 4th tooth, thus duplicating the first state. ROBSON (1929: 12, 28) discusses this phenomenon in detail. ALDRICH, BARBER & EMERSON (1971: figs. 18, 19) report a similar two-tooth change in *Octopus salutii*. The angle of the rachidian teeth, concave anterior margins, and very crowded positions contrast greatly with the shape and spacing in the other cephalopods.

One additional structural pattern requires comment. When the radula of virtually all coleoid cephalopods, whether octopods or teuthoids is viewed from the anterior end, the teeth have a characteristic indention on the anterior base (compare *Histioteuthis,* Figure *8,* and *Octopus,* Figure *20;* also ALDRICH, BARBER & EMERSON, 1971: figs. 2-6, 9-10, 12-16 for various sepiolids and teuthoids). The only exception noted to date in our survey is *Vampyroteuthis* (Figures *15-18*) in which the rachidian and lateral teeth have a prolongation of the anterior basal support. This is the same type of extension seen in the radulae of carnivorous land snails such as *Ptychorhytida* (SOLEM, 1974: fig. 14), marginal teeth of *Haplotrema* (SOLEM, *loc. cit.:* fig. 6), and *Torresiropa* (SOLEM, *loc. cit.:* figs. 23, 24). It is analagous to the stress support flare seen in many land snails (SOLEM, 1972: figs. 22, 23), although the latter is not attached to the radular membrane, while in *Ptychorhytida* and *Vampyroteuthis* the anterior flare is anchored to the basal membrane. This prolongation functions as support against stress from bending during feeding. It effectively locks the tooth into a fixed angle, whereas the anterior margin of the rachidian and lateral teeth in other cephalopods permits more flexibility in tooth orientation.

The presence of grooves on the teeth is most marked in the nautiloid cephalopods (see discussion in SOLEM & RICHARDSON, 1975), but they are also quite prominent in the coleoid taxa that have prominent marginal plates, whether of the trigger-erection (*Loligo,* Figure *3*) or support function (*Vampyroteuthis,* Figure *17* and *Octopus,* Figure *23*). These grooves are greatly reduced or absent in taxa with reduced or missing marginal plates (*Histioteuthis,* Figure *11*). The grooves function during the compaction or infolding of the teeth toward the midline of the radula. Their presence is to be expected in taxa with a marked radial (to and from midline of radula) shift in tooth erection and folding. Their reduction or loss in taxa where tooth movement is more "up and down" (*i.e.,* non-folding) rather than "out and up, then in and down" is reasonable.

SUMMARY OF STRUCTURAL PATTERNS

On the basis of the observations outlined above. the pattern of teeth in radulae of recent cephalopods is relatively simple. The largest number of structural elemcnts occur in *Nautilus* which has the following teeth in order from radular midline to outer margin: one rachidian, two laterals, one inner marginal, one outer marginal, and one each of inner and outer marginal support plates. A total of 9 teeth and 4 support plates occur in a transverse row of teeth. Both marginal teeth are much larger and very different in shape from the lateral teeth.

The generalized pattern in extant coleoids appears to be a rachidian, one lateral, one inner marginal, and one

outer marginal tooth, plus the marginal plate. The inner marginal tooth tends to be different in size from the outer marginal tooth, but similar instead to the lateral tooth.

Reduction and loss of the marginal plate is frequent in teuthoids. Unicuspid, bicuspid, and tricuspid rachidian teeth and unicuspid or bicuspid lateral teeth are seen in many groups. The shape of the inner marginal tooth is correlated with the function of compaction and support against stress of the outer marginal tooth.

Octopods differ in having the lateral tooth on each side reduced to a small remnant, the rachidian tooth enlarged —often with variable cusps, and, usually, a massive outer marginal plate.

Once the clear distinction is made between cusp-bearing teeth and the marginal plates, which function for erection, support against stress, or compaction (folding), or both, then much of the discussion concerning numbers of teeth in a transverse row in the Cephalopoda becomes irrelevant. The nautiloids do differ in having 9 teeth and 4 plates in each row, that is, an additional pair of lateral teeth and an additional pair of support plates over those found in typical coleoids. The coleoids characteristically have 7 teeth and 2 plates in each row, with the support plates reduced or lost in sepiolids and many oegopsid squids. Some gonatids have only 5 teeth per row. The inner marginal tooth of teuthoids is more modified than the outer marginal. Octopods generally are characterized by having a modified and enlarged rachidian, greatly reduced laterals, and very large marginal plates. Some cephalopods lack radulae altogether.

Thus the coleoids have rather limited variations on a basic plan, rather than showing the more radical differences implied by counting the outer plates as teeth or by overlooking the minute lateral tooth of most octopods. Some cephalopods, such as *Spirula* and cirrate octopods *e. g.*, *Opisthoteuthis* (Solem & Roper, unpublished), totally lack a radula (see also Robson, 1932: 9).

A thorough discussion of the phylogenetic implications of the radula will appear in our later work. Although the topic has been discussed in the literature (Robson, 1932: 7-12), no conclusions have been reached, nor is there agreement on which type of radula represents the primitive form. We do know, however, that the radula of nautiloid cephalopods is a very conservative structure that has persisted nearly unchanged in basic structure for about 300 million years (Solem & Richardson, 1975). The radula in the orders of living coleoids also is similar in basic structure. The details of structure do vary at different taxonomic levels, even to the extent that some congeneric sympatric species have dissimilar radulae. The variations on the conservative structural plan of the radula appear to be an overlay imposed by the evolution of a variety of feeding characteristics throughout the cephalopods.

SUMMARY

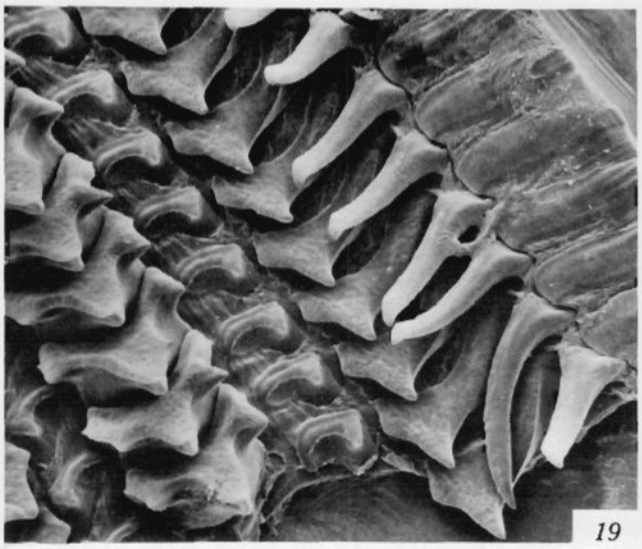
A review of published scanning electron micrographs of cephalopod radulae, together with illustrations of the radula of *Loligo plei, Histioteuthis dofleini, Vampyroteuthis infernalis,* and *Octopus briareus* permit identification of different functions for marginal plates, clear distinction between teeth and plates, and clarification of the basic number and patterns of teeth and plates in major taxonomic categories. Marginal plates may function either to erect outer marginal teeth or to support them against stress. Nautiloid cephalopods differ from coleoids in having two extra lateral teeth and two inner marginal support plates. Coleoids vary in cusp patterns on the rachidian and lateral teeth, with the teuthoids varying from possession of strong marginal plates to their complete loss. Octopods are characterized by a greatly reduced lateral tooth, a very enlarged and usually multicuspid rachidian tooth, and massive marginal plates. *Vampyroteuthis* is unique among examined species in having an anterior prolongation of the rachidian that provides support against stress during feeding. The conspicuous grooves present on the teeth of many cephalopods function during compaction or infold-

Explanation of Figures *19* to *23*

Octopus briareus Robson, 1929

USNM 574777; 24°38′N; 82°55′W; ML = 39 mm

Figure *19*: Part row of teeth	× 90
Figure *20*: Anterior view of teeth	× 96
Figure *21*: Rachidian teeth in lateral view	× 189
Figure *22*: Cusp variation on rachidian teeth	× 189
Figure *23*: Details of folding pattern of marginal teeth	× 194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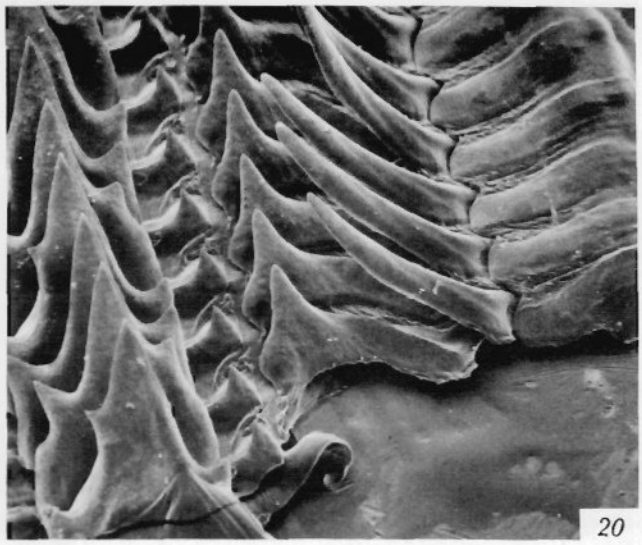
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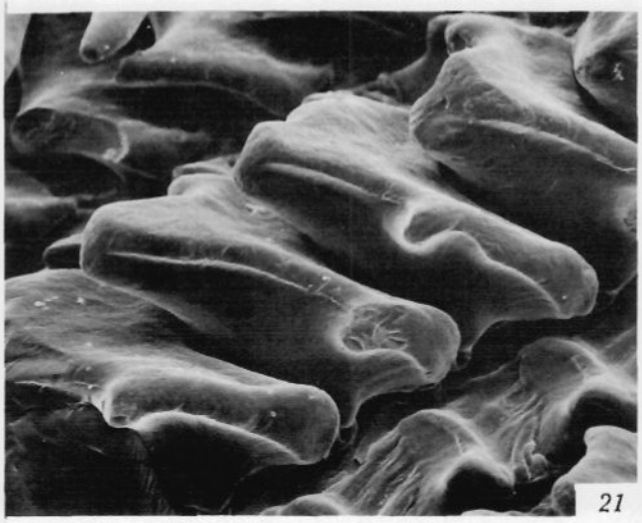
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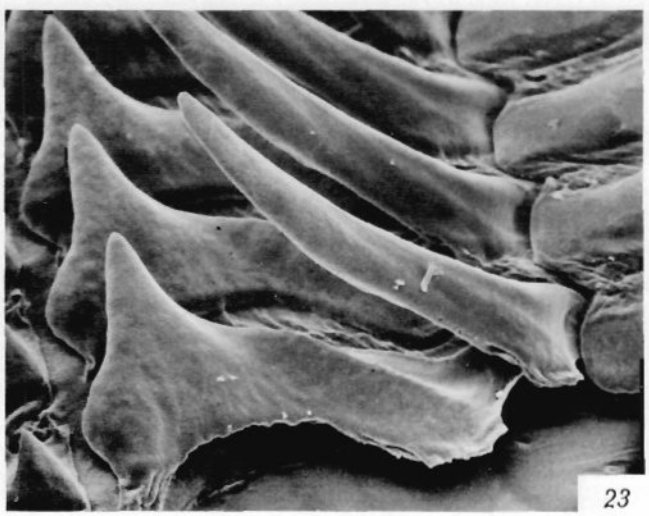
23

ing of the teeth towards the midline of the radula. These grooves cause the outer teeth to "lock" down either on the support plates (*Nautilus*) or against the inner marginals and laterals (coleoids). When the outer marginal plates are greatly reduced or lost, the grooving on the teeth often is reduced or lost and a different pattern of tooth folding or erection, or both, is evolved. In some teuthoid taxa that lack marginal plates an entirely new structure is present, a marginal tooth ligament that extends from the anterior basal plate of the outer marginal tooth to either the basal membrane or the posterior part of the basal plate of the next anterior outer marginal tooth. This structure was not reported previously.

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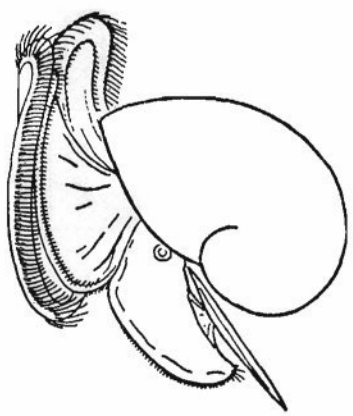

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