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SEM COMPARISON OF RADULAE IN SIX TAIWANESE ARCHAEOGASTROPODS[1]

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Wen-Lung Wu (1991) SEM comparison of radulae in six Taiwanese archaeogastropods. *Bull. Inst. Zool., Academia Sinica* **30**(4): 299-310. This paper reports on the morphology and function of radulae in six intertidal archaeogastropods from Taiwan. The six Taiwanese archaeogastropods are *Haliotis diversicolor*, *H. varia*, *Collisella striata*, *Trochus lineatus*, *Lunella coronata* and *Septaria porcellana*. The radula of *C. striata* belongs to the docoglossan type and the others belong to the rhipidoglossan radula. These two types of radulae exhibit typical herbivorous function. The number, size and radular formula of the six archaeogastropods are described in detail. The radula of *Pleurotomaria rumphii* is also compared with the six species.

Key words: Mollusca, Radulae, SEM, Taiwan.

A basic element in gastropod design is the radula, an organ with one principal function, to feed the food. An account of the history of radular study was reviewed by Bowell (1928), and an interpretation of the median teeth of radular characteristics in the classification of gastropods was discussed by Howe (1930). In spite of arguments questioning the validity of radular characteristics in the diagnosis of species by various malacologists, radulae have been utilized in the systematics of mollusks in monographs such as reported by Thiele (1931), Cox (1960) and Hyman (1967). Fretter and Graham (1962) suggested that radular characteristics remain fairly constant within a single species although the shape of the teeth differs from species to species. Wu (1965) also suggested that radular studies are important in the classification of the Muricacea if the orientation of the radula is standardized.

In Taiwan, Wu (1965) reported on the radulae of various muricid gastropods and discussed the relationships among the Muricacea from the point of view of the rachidian structures. The radula of *Pleurotomaria rumphii* was also discussed by Tan (1974) and Wang-Chu *et al.* (1976) but not in detail. Other than the above mentioned papers, there are no other articles concerning the functional morphology of radular except for Wu (1987) and Wu and Lin (1987).

The purpose of the present work is to clarify the functional morphology and ultrastructures of radulae among six archaeogastropods from Taiwan through the use of a SEM. The six species studied are *Haliotis diversicolor*, *H. varia*,

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Collisella striata, Throchus lineatus, Lunella coronata and *Septaria porcellana*

MATERIALS AND METHODS

The mollusks studied for this paper were collected during low tide periods from along the shorelines and estuarine areas of Pa-li Stream, Ping-Tong County in southern Taiwan.

The radulae were prepared by utilizing a modified SEM techniques (Wu, 1985). Briefly, the procedure was as follows: 1) the radular ribbon was removed from the buccal cavity of the mollusks and soaked in a 10-20% solution of sodium hydroxide for 10-20 minutes or more, 2) the ribbons were rinsed in distilled water and cleaned thoroughly in an ultrasonic cleaner for 10-20 seconds, 3) the radular ribbons were fixed in 1% osmium tetroxide-glutaraldehyde fixer at 4°C for 1-2 hours and then washed with phosphate buffer, 4) the fixed radulae were then dehydrated in a series of increasing alcohol grades, 5) the dehydrated ribbon was then put in a critical-point drying unit by using absolute alcohol as the transfer fluid and liquid carbon dioxide as the drying medium. The tissues were then coated with a thin layer of gold for 3-5 minutes and observed with SEM (Hitachi S-450 and S-2500).

RESULTS

Haliotis diversicolor

The rachidian (or central tooth, R, 75 μm×250 μm) is flat with no cuspid on the top but with biforked shapes on both sides (R in Plate I-b). The first central lateral tooth (cL1 in Plate I-b) is similar to the rachidian; the second central lateral tooth (cL2 in Plate I-c) is smaller than cL1 but sharper. There are three strong marginal lateral teeth (mL1, mL2 and mL3, in Plate I-c). There are two kinds of marginal teeth: 1. 20-25 feathered teeth with 7-8 slits on the tips of the marginal teeth (M1 in Plate I-e), and 2. 35-40 marginal teeth slender in shape but without slits (M2 in Plate I-f). The radular formula for *H. diversicolor* is 55-65, 5, R, 5, 55-65.

Haliotis varia

The rachidian (75 μm × 145 μm) is shaped like a flat hexagon (R in Plate II-b). The first central lateral tooth (cL1, 85 μm) is rectangular and slightly concave on both sides (Plate II-b); the second central lateral tooth (cL2 in Plate II-b) is smaller than cL1. Three sharp marginal lateral teeth with large lamella in the basal region (mL1, mL2 and mL3 in Plate II-c) are arranged between the central lateral and marginal teeth. There are two types of marginal teeth: 1. 30-40 feathered teeth with 20-30 slits on the top edge (M1 in Plate II-d, e), and 2. 45-50 teeth with small slits on the top edge of the marginal teeth (M2 in Plate II-f). The radular formula for *H. varia* is 75-90, 5, R, 5, 75-90.

Collisella striata

The retrogressive rachidian (45 μm ×120 μm) is shaped like a small leaflet with a lunar fold in the central region (R in Plate III-b). Two large lateral teeth (85 μm×190 μm) are perpendicular to each other (L1 and L2 in Plate III-d). The thickest fold is found at the edge of L1. The third smallest lateral tooth (L3, 75 μm) is attached to the edge of the second lateral tooth (L2). Two very small retrogressive hooked marginal teeth are arranged on both sides of the radular ribbon (M in Plate III-d). The radular formula for *C. striata* is 2, 3, R, 3, 2.

Trochus lineatus

The rachidian (90 μm × 130 μm) is shaped like a flat rectangle (R in Plate IV-b). Three small triangular central lateral teeth are arranged on both sides of the rachidian (cL in Plate IV-b). There are three marginal lateral teeth: two large dagger shaped marginal lateral teeth (mL1 and mL2, 330 μm in Plate IV-c); and one small sharp triangular marginal lateral tooth (mL3 in Plate IV-c). These are close to the central lateral teeth (Plate IV-c). There are 30-31 long rectangular feathered marginal teeth with 6-10 small hooks on both sides of the teeth (M in Plate IV-d). The radular formula for *T. lineatus* is 30-31, 6, R, 6, 30-31.

Lunella coronata

The rachidian (70 μm×90 μm) is rectangular shaped and slightly concave in the center (R in Plate V-b). Five small elliptical lateral teeth are located on both sides of the rachidian (L, 50 μm×110 μm, in Plate V-b and c). There are two kinds of marginal teeth: 10-12 daggered with one hook at the base of the marginal teeth (M1 in Plate V-e and f); and 60-73 smooth and slender marginal teeth (M2 in Plate V-a). The radular formula for *L. coronata* is 70-85, 5, R, 5, 70-85.

Septaria porcellana

The rachidian (75 μm×95 μm) is rectangular shaped and slightly concave in the central area (R in Plate VI-b). One long central lateral tooth (cL, 270 μm in width, Plate VI-a) is jointed with two small retrogressive central lateral teeth (rcL in Plate VI-a); and one strong lunate marginal lateral tooth (mL in Plate VI-a and c) is just attached to the retrogressive central lateral teeth (Plate VI-c). There are 65-80 feathered marginal teeth with 10-12 hooks on the top side of the margins (M in Plate VI-e and f). The radular formula for *S. porcellana* is 60-80, 4, R, 4, 65-80.

DISCUSSION

The radula has been found in all classes of Mollusca except in Bivalvia. The main function of the radula in mollusks is to cut the food into sufficiently small pieces or chunks so that the food can swallow more easily (Solen, 1974). All generalized archaeogastropods depend on the protrution a tongue-like organ coated with many thousands of teeth on the surface which rasp or tear loose pieces of food. Many drawings have been made of gastropod radula cusps over the years, but their complex form and usually small size have made understanding their structure and function extremely difficult (Purchon, 1977). The availability in the late 1960s of a new research tool, the scanning electron microscope, has facilitated considerable advances and greatly simplified illustration problems (Wu and Lin, 1987).

Very few papers on the radula have been published in Taiwan. However, Tan (1974) and Wang-Chu *et al.* (1976) described the radula of *Pleurotomaria rumphii* and Wu (1965) suggested that radular studies are important to the classification of the Muricacea if the orientation of the radula is standardized. Recently, Wu (1987) and Wu and Lin (1987) stated that the radula studies are more important to understanding the functional morphology rather than in classification.

Six kinds of Taiwanese archaeogastropods live along the rocky shorelines and estuarine areas, either on the surface of the upward facing rock or sometimes on the under surface of boulders. They feed on the filamentous algae and other fine algae growing on the surface of the rock. These animals browse on algae by

protruding their radulae through the mouth and by withdrawing it again with a licking action. This motion makes it necessary for the animal to have a flat central tooth (R in Plates I to VI) for cutting algae into small pieces and the long, spoon-like marginal teeth (M in Plates I to VI) for swinging small pieces of algae into their mouths (Wu and Lin, 1987).

The most primitive mollusks such as *Haliotis* (Dai and Wu, 1989) can be recognized by having two ctenidia in the anterior mantle cavity. In all such cases, there is an extremely large number of slender teeth in each transverse tooth row on the radula (Plates I and II). This is also true for several genera in which there is only one ctenidium which therefore makes them less primitive, e.g. *Trochus*, *Lunella* and *Septaria*. This kind of radula is described as "rhipidoglossan" (Plates I, II, and IV to VI).

Six archaeogastropods in this paper have a rhipidoglossate radula except for *C. striata*, which is known by it having huge numbers of small marginal teeth (M in Plates I to VI). These are used to catch and pull food particles into the mouth after they have been torn or ripped loose by the much larger lateral teeth (mL, cL and L in Plates I to VI). In the middle of the radula a single central tooth (Rachidian, R in Plates I to VI) is flanked on each side by 5-6 mirror-image teeth in front of the insertion of the marginal teeth (M in Plates I to VI). In general, the six radulae are symmetrical, having marginal-lateral-central-lateral-marginal teeth from left to right in each transverse row of the radular ribbon. Comparisons of radulae in the Taiwanese archaeogastropods are summarized in Table 1. The radular formula for *Pleurotomaria rumphii* is similar to that of the rhipidoglossate radula with the exception of the former having more lateral and marginal teeth. Tan (1974) dissected the digestive system of *P. rumphii* showing that the animal feeds on sponges and bits of food growing on rocks or other surfaces by scraping. The same feeding behavior and radular formula are also found in the six studied Taiwanese archaeogastropods (Table 1; Plates I, II and IV to VI).

The central tooth of each of the six Taiwanese archaeogastropods has an unserrated upper edge, and when the radula is curved as in a feeding stroke, it seems to act as a support for the teeth on either side. When protruded, the radula passes over a "bending plane", at which point the radula membrane becomes flat with the marginal teeth swinging outwards. The radula curls backwards under the proboscis with the

Table 1
Comparison of radulae in the Taiwanese archaeogastropods

Species	Radula			Author
	Rachidian	Lateral	Marginal	
Pleurotomaria rumphii	1	21+16	72+13	Wang-Chu (1976)
Pleurotomaria rumphii	1	27+14	∞	Tan (1974)
Haliotis diversicolor	1	2+3	20-25+35-40	the author
Haliotis varia	1	2+3	30-40+45-50	the author
Trochus lineatus	1	3+3	30-31	the author
Lunella coronata	1	5	10-12+60-73	the author
Septaria porcellana	1	1+2+1	65-80	the author
Collisella striata	1	3	2	the author

toothed surface pressed against the algal food source (Purchon, 1977). The long, spoon-like marginal teeth with cusps of slits on their upper edge (Plates I to VI) greatly reduced in size, brush scattered fragments of potential food material towards the median line as they swing inward prior to returning over the bending plane into the mouth (Wu and Lin, 1987). The shape and inter-relationships of these teeth are very complicated, except for the limpet, *C. striata*, which has a greatly modified type of teeth with the thickest part running along the margins of the teeth (Plate III). Thus, the rhipidoglossate radula is considered as one of the most important characteristics in Archaeogastropoda.

Limpets in the Patellacea adapt to life along exposed rocky shores. By rasping on the surface of the rocks themselves, they are able to feed on fine algal growths (Wu, 1978a, 1978b). The radula is robustly built for this heavy work, with only ten to thirteen teeth in each transverse row. Each tooth is large and heavily built, such as in *Patella* (Graham, 1931, 1964), in *Cellana*, *Acamaea* and *Patina* (Graham and Fretter, 1947) and in *Collisella striata* (Plate III). This type of radula is known as "docoglossan". Both rhipidoglossate (Wu and Lin, 1987) and docoglossate radulae enable the mollusks to adapt to their herbivorous feeding behavior on rocky surfaces.

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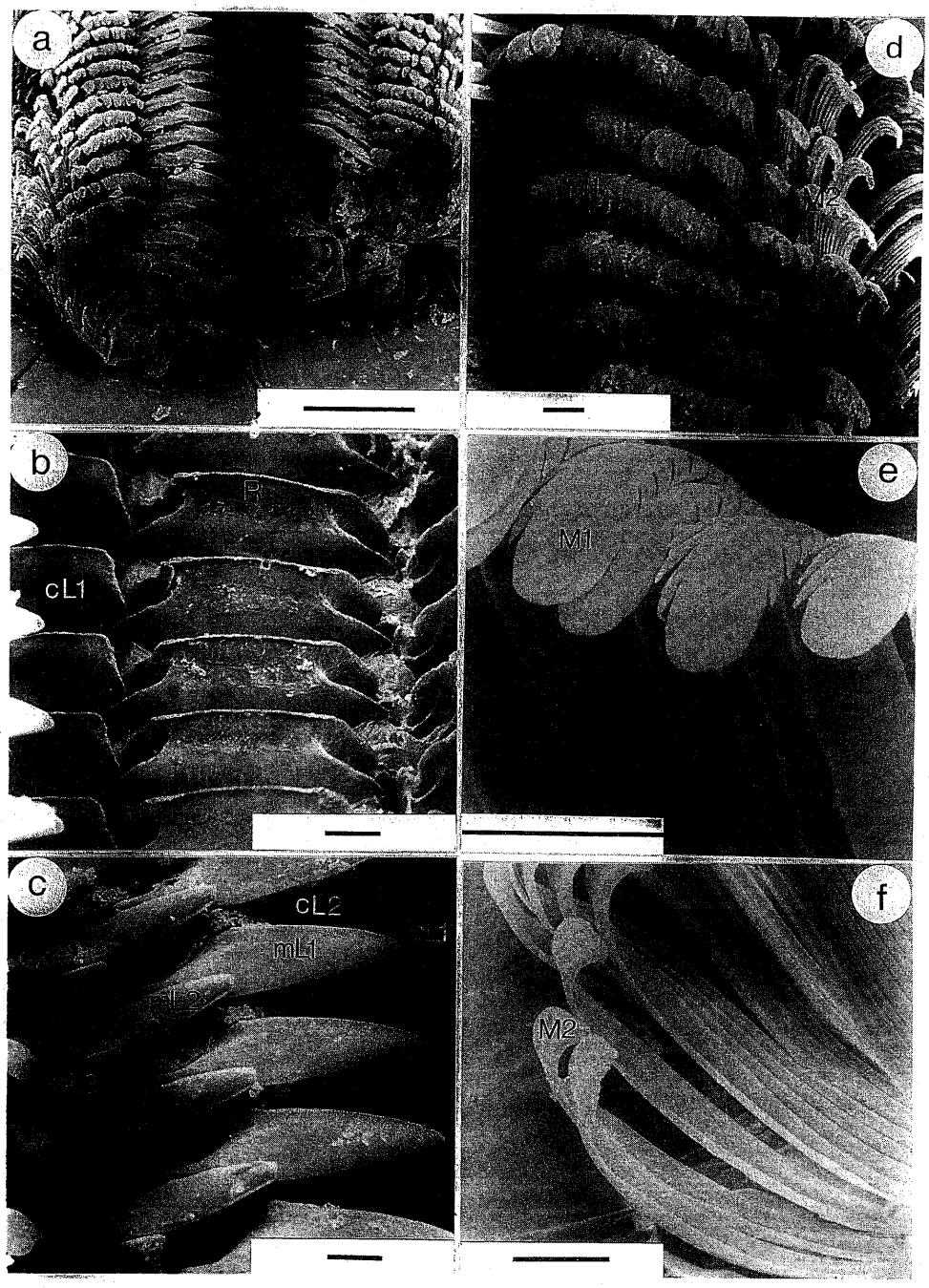

Plate I. SEM micrographs of the radula of *Haliotis diversicolor*

a. The radular ribbon, scale is 500 μm.
b. Detail of (a) shows the rachidian (R) and the first central lateral tooth (cL1), scale is 50 μm.
c. Detail of (a) shows the two central lateral teeth (cL1 and cL2) and three marginal lateral teeth (mL1, mL2 and mL3), scale is 50 μm.
d. Detail of (a) shows the marginal teeth (M1 and M2), scale is 50 μm.
e. Detail of (d) shows the marginal teeth M1, scale is 50 μm.
f. Detail of (d) shows the marginal teeth M2, scale is 50 μm.

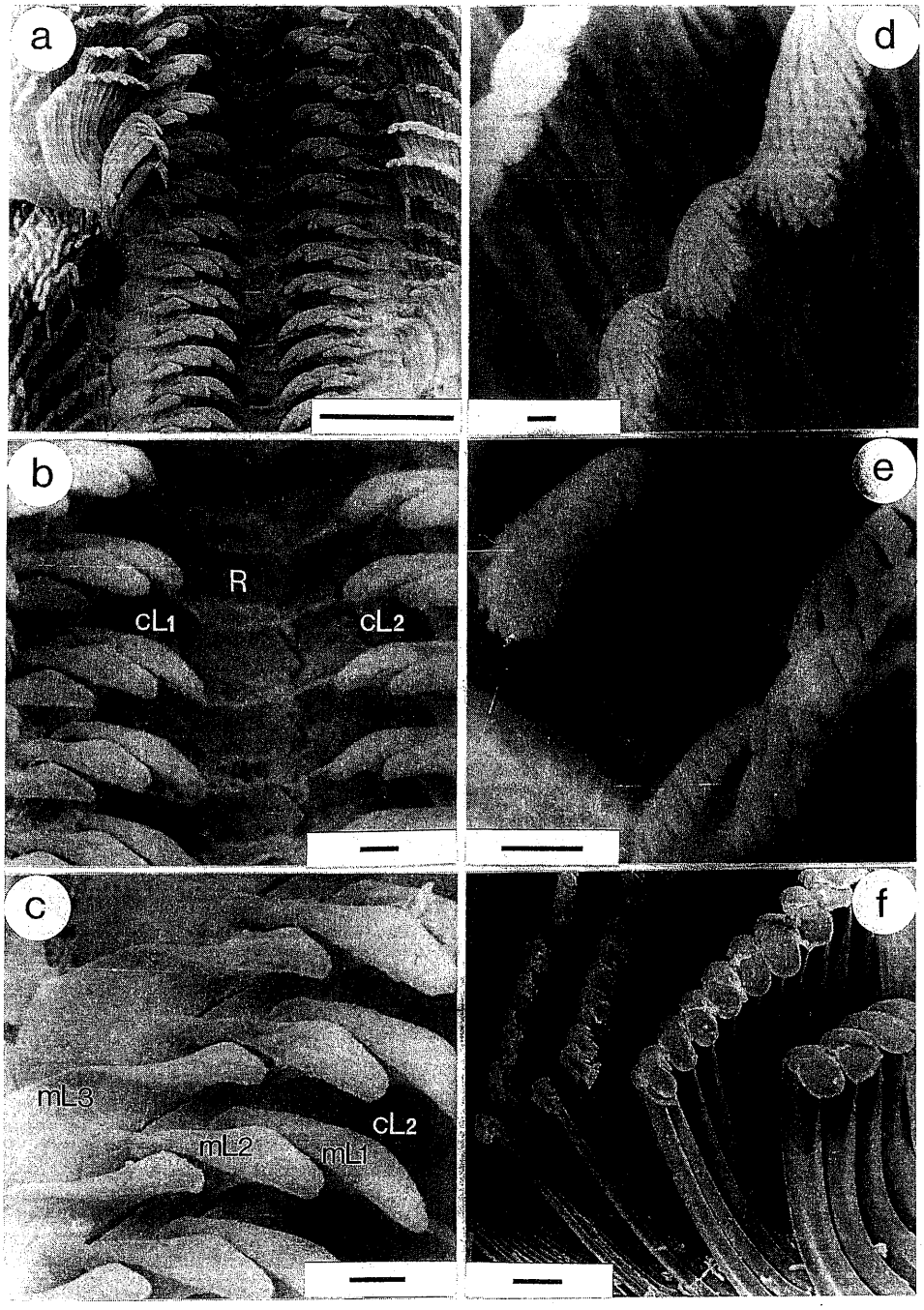

Plate II. SEM micrographs of the radula of *Haliotis varia*

a. The radular ribbon, scale is 500 μm.
b. Detail of (a) shows the rachidian (R) and the two central lateral teeth (cL1 and cL2), scale is 50 μm.
c. Detail of (a) shows the three marginal lateral teeth (mL1, mL2 and mL3), scale is 50 μm.
d. The enlarged marginal teeth M1, scale is 5 μm.
e. The enlarged marginal teeth M1, scale is 5 μm.
f. The enlarged marginal teeth M2, scale is 50 μm.

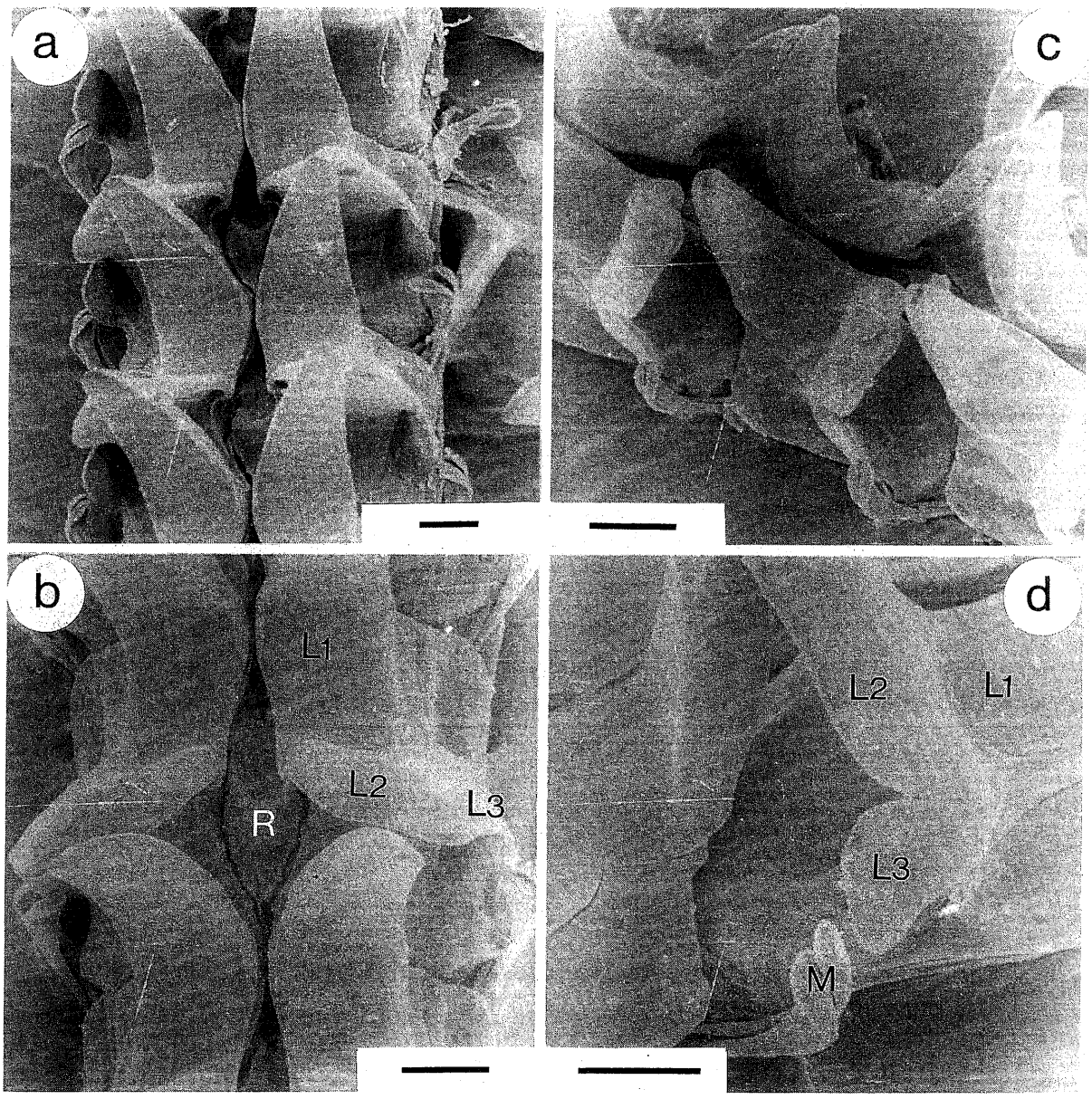

Plate III. SEM micrographs of the radula of *Collisella striata*

a. The radular ribbon, scale is 50 μm.
b. Detail of (a) shows the rachidian (R) and the three lateral teeth (L1, L2 and L3), scale is 50 μm.
c. Lateral view of (b), scale is 50 μm.
d. Lateral view of (b) shows the three lateral teeth (L1, L2 and L3) and two marginal teeth (M), scale is 50 μm.

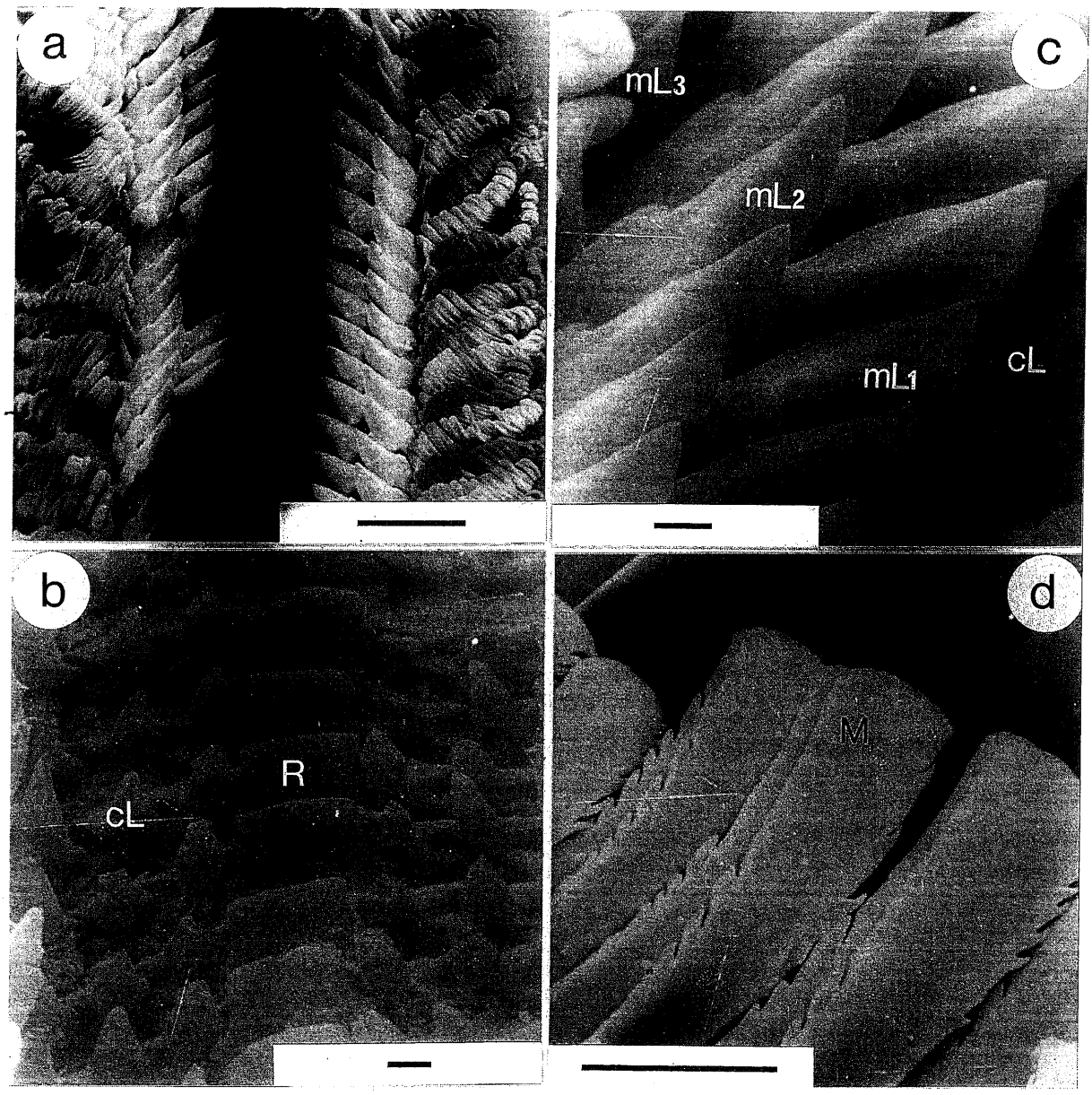

Plate IV. SEM micrographs of the radula of *Trochus lineatus*

a. The radular ribbon, scale is 500 μm.

b. Detail of (a) shows the rachidian (R) and the central lateral teeth (cL), scale is 50 μm.

c. Detail of (a) shows the three marginal lateral teeth (mL1, mL2 and mL3) and the central lateral teeth (cL), scale is 50 μm.

d. Detail of (a) shows the marginal teeth (M), scale is 50 μm.

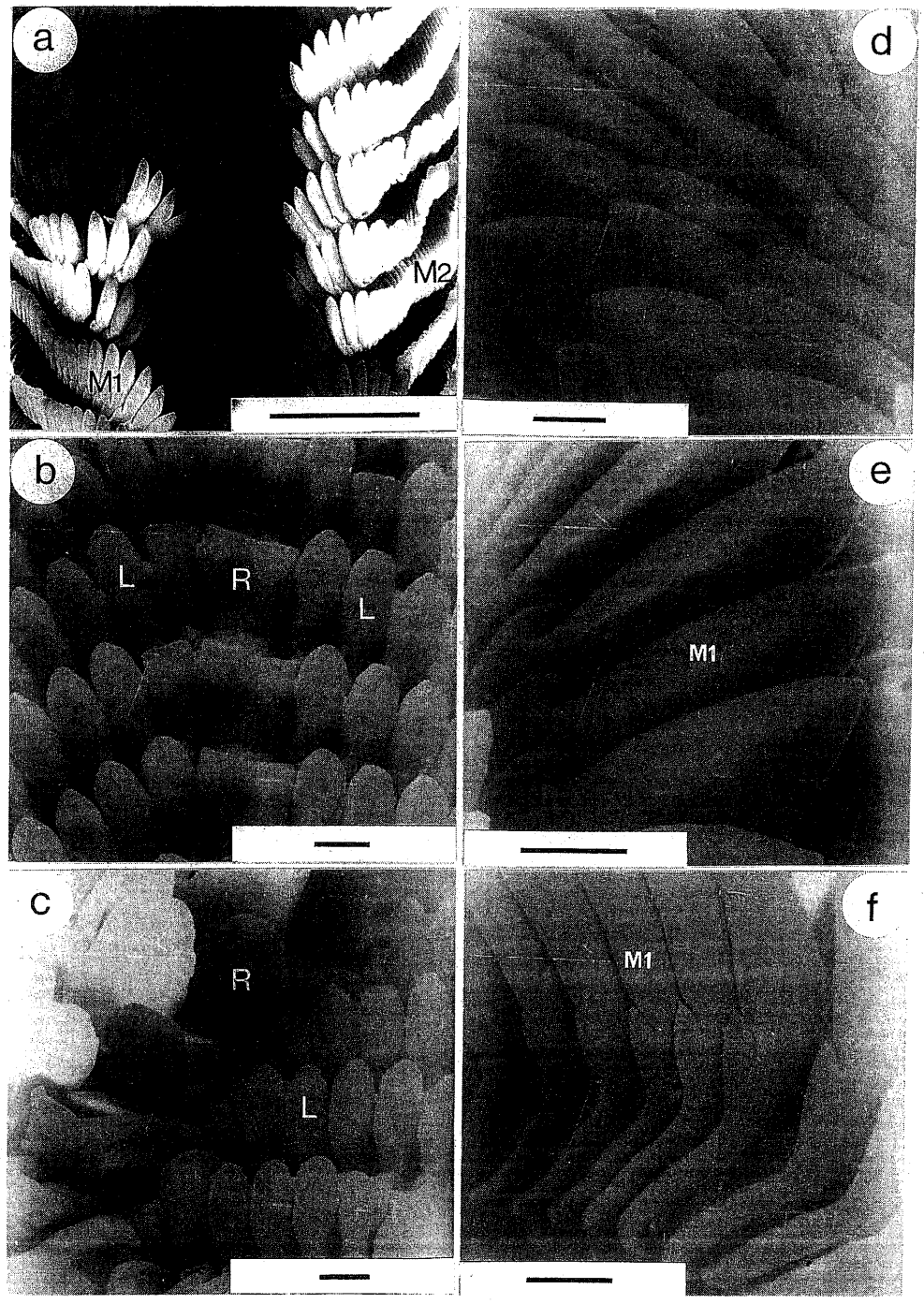

Plate V. SEM micrographs of the radula of *Lunella coronata*

a. The radular ribbon and the marginal teeth (M1 and M2), scale is 500 μm.
b. The rachidian (R) and the lateral teeth (L), scale is 50 μm.
c. The lateral view of (b), scale is 50 μm.
d. The marginal teeth M1, scale is 50 μm.
e. The marginal teeth M1 shows a hook on the basal region, scale is 50 μm.
f. The marginal teeth M1 shows a hook on the basal region, scale is 50 μm.

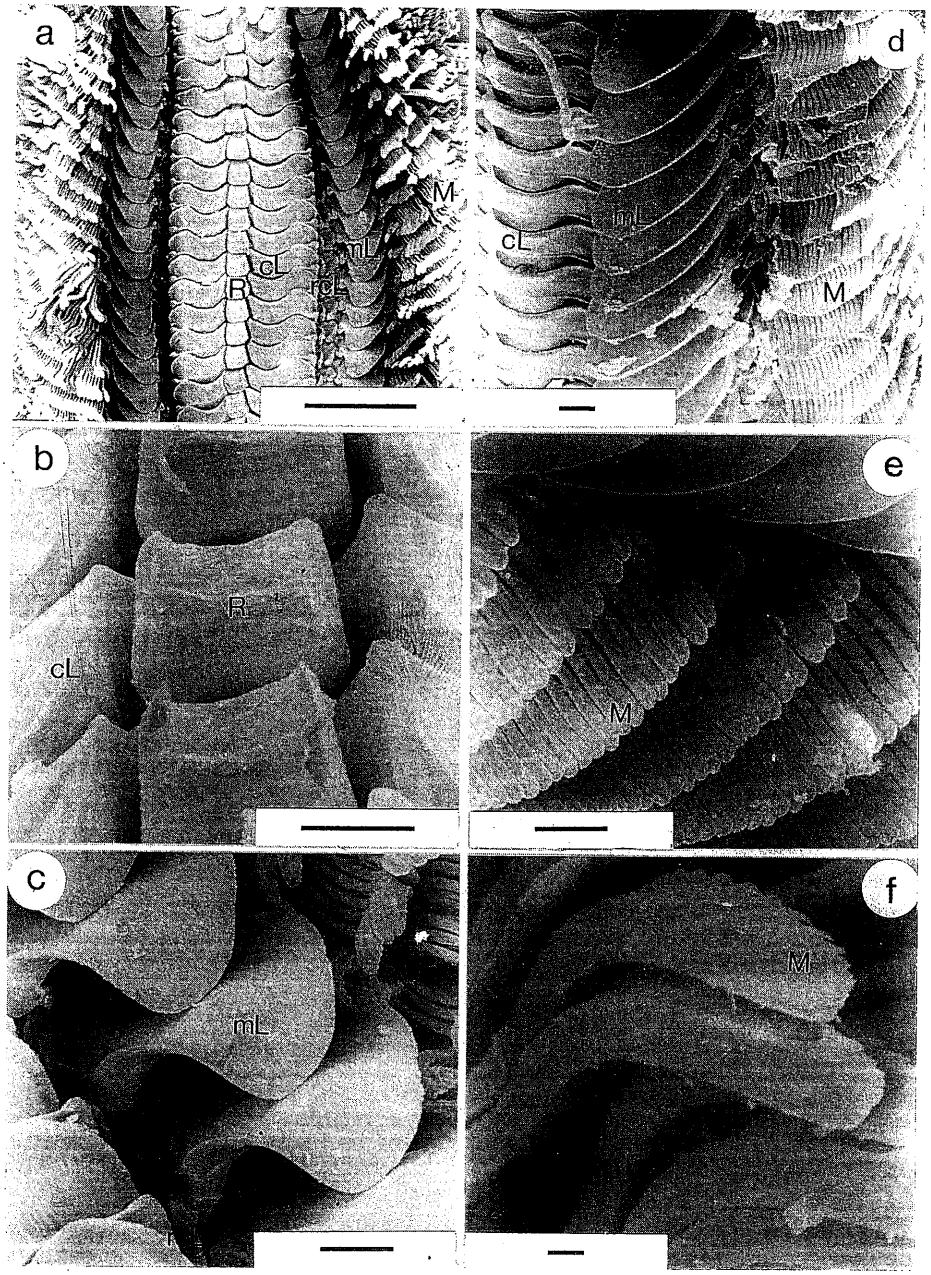

Plate VI. SEM micrographs of the radula of *Septaria porcellana*

a. The radular ribbon shows the richidian (R), central lateral teeth (cL), retrogressive central teeth (rcL), marginal lateral teeth (mL) and marginal teeth (M), scale is 500 μm.

b. Detail of (a) shows the rachidian (R), scale is 50 μm.

c. Detail of (a) shows the lunate marginal lateral teeth (mL) and retrogressive central lateral teeth (rcL), scale is 50 μm.

d. Detail of (a) shows the lateral teeth (cL and mL) and the marginal teeth (M), scale is 50 μm.

e. Detail of (a) shows the marginal teeth (M), scale is 50 μm.

f. The enlarged marginal teeth (M), scale is 5 μm.

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臺灣產原始腹足動物齒舌的電鏡比較研究

巫　文　隆

本文係討論臺灣產六種原始腹足綱軟體動物的齒舌比較研究。由於普通光鏡無法作微小邊緣齒之描述，因此利用掃描電鏡來觀察是相當理想的工具。九孔、扁鮑、鐘螺、蠑螺及壁蜑螺的齒舌是相當類似的：具有一個扁而鈍的中間齒，五或六個尖銳或扁平的側齒以及爲數甚多的小而細且排列緊密的邊緣齒。這些特徵都是草食性貝類齒舌的共同點。另一種笠螺雖然迥異於上述五種，但是因爲具有寬闊而且邊緣加厚的側齒，適合於啃食附著在岩壁上之海藻，因此也是另外一種草食貝類齒舌的特徵。本文另外再比較本省著名的另一種原始腹足類—龍宮翁戎螺，發現其齒舌亦相似於前五種，但邊緣齒及側齒數目均較多而推測龍宮翁戎螺應比前五種更爲原始。