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RELATIONS BETWEEN SHELL SIZE AND RADULA SIZE IN MARINE PROSOBRANCHS (MOLLUSCA: GASTROPODA)

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ABSTRACT

The Gastropoda presents the highest adaptative radiation among the mollusks. This characteristic allowed the appearance of many forms of feeding, and with it, many strategies of capture and food processing. In this work, specimens belong to 14 marine prosobranch gastropod species were collected in the coast of Ceará State Northeast Brazil with the purpose to investigate the relation between shell size and radula size in gastropods with different diets and radula type. It was found significative correlations in *Cerithium atratum, Collisella subrugosa, Fissurella rosea, Neritina virginea, Olivella minuta, Pisania pusio, Tegula viridula,* and *Thais haemastoma*. Non-significative results were found in *Littorina flava, Littorina ziczac, Nassarius vibex, Natica marochiensis, Pleuroploca aurantiaca,* and *Pugilina morio*. The species with *rhipidoglossate* radula and the driller carnivores with *rachiglossate* radula are the ones that presented significative correlation among shell size and radula size. Other parameters that could influence the radular morphology (besides the radula type or diet) are environment pressure, prey searching and capture strategies and species ontogeny.

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RESUMO

A classe Gastropoda é o grupo que possui a maior radiação adaptativa entre os moluscos. Essa característica permitiu o surgimento de várias formas de alimentação e, com elas, diversas estratégias de captura e processamento do alimento. Neste trabalho, 14 espécies de gastrópodes prosobrânquios marinhos foram coletados no litoral do Estado do Ceará nordeste do Brasil, com o objetivo de analisar a relação entre o tamanho da concha e o tamanho da rádula em animais com diferentes dietas e tipos radulares. O teste revelou correlações significativas em *Cerithium atratum, Collisella subrugosa, Fissurella rosea, Neritina virginea, Olivella minuta, Pisania pusio, Tegula viridula* e *Thais haemastoma*. Resultados não significativos forma encontrados em *Littorina flava, Littorina ziczac, Nassarius vibex, Natica marochiensis, Pleuroploca aurantiaca* e *Pugilina morio*. As espécies com rádula *rhipidoglossa* e os carnívoros perfuradores com rádula *rachiglossa* apresentaram correlação significativa na relação estudada. Outros parâmetros que podem influenciar na morfologia radular (além do tipo de rádula e dieta,) são a pressão do meio, as estratégias de procura e captura da presa e a ontogenia das espécies.

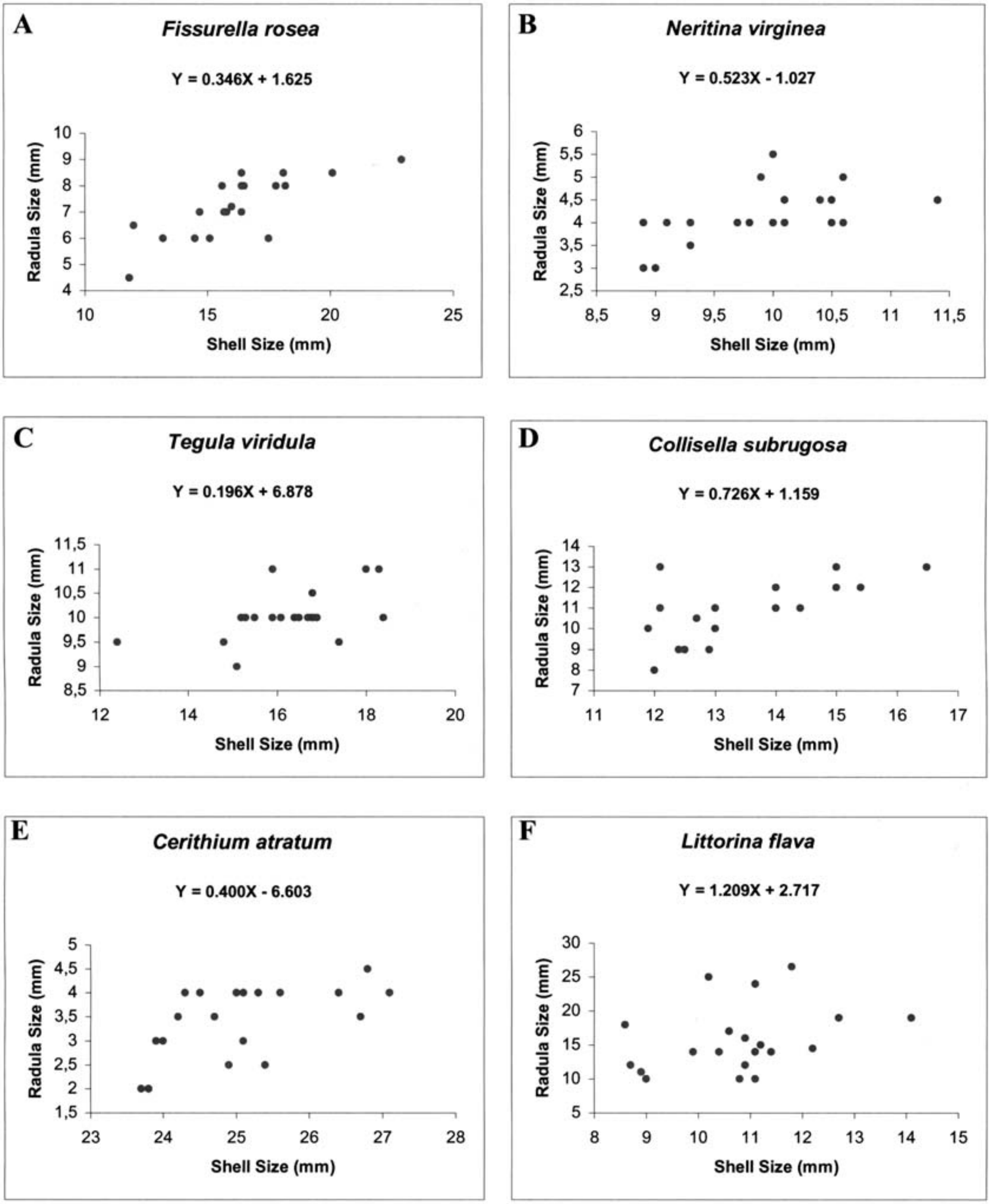

Figure 1.
Relation between shell and radula size in marine gastropod prosobranch mollusks. Radula Rhipidoglossa: A. Fissurella rosea*. B*. Neritina virginea*.* C. Tegula viridula*. Radula Docoglossa:* D. Collisella subrugosa*. Radula Taenioglossa:* E. Cerithium atratum. F. Littorina flava.

INTRODUCTION

The structure of the mollusk radula has been the subject of many studies, specially among the gastropods and chitons (Fretter & Graham, 1994). These studies have show interactions among physical structures of buccal muscles and cartilages of the odontophore , in the characterization of form and function of each radula type (Black *et al.*, 1988).

The radula has been used as an important instrument in the systematic studies of gastropods (Reid & Mak, 1999). It has been used in the resolution of problems with critical species, which are practically impossible to set apart based only in the morphological analysis of the shell or soft parts (Simison & Lindberg, 1999).

One question that arose from these studies (Kool, 1987 and 1993) is in which extention the environment could influence the radula morphology. Kool (1987 and 1993) made correlation analyzes among species from the Thaididae family, and found no significant relationship among radula morphology and diet. Other researches, as Bandel (1984) and Wu (1985), got similar results, and considered the radula a structure morphologically conservative, for not be greatly influenced by factors such as feeding resources.

Other studies about intraspecific variation in the radula teeth have investigated sexual dimorphism in Muricidae (Fujioka, 1985), ontogenic variation in the genus *Conus* (Nybakken, 1990; Nishi & Kohn, 1999), phenotypic plasticity of the morphology of the radula teeth on *Lacuna* in relation to the feeding habits (Padilla, 1998) or in *Littoraria* in relation to the type of substratum (Reid, 1999; Reid & Mak, 1999) and similarity in the radula morphology among species phylogenetically distant but that have the same diet (Solem, 1973; Harasewych, 1984).

The Gastropoda is represented by species with tremendous adaptative success. Regarding the strategies of food search and food capture (Taylor *et al.*, 1980; Hughes, 1986), we can find forms with many feeding habits, such as herbivores, detritus eaters, suspension eaters, carnivores and parasites. Given the importance of the radula, not only in feeding, but also in taxonomic and phylogenetic studies, the objective of this work is to verify the existence of correlation between radular size and shell size in marine prosobranch gastropod mollusks that have different types of radula and feeding habits.

STUDY AREAS

The animals used in this study were collected in seven locations in the coast of Ceará State, Northeast Brazil: Flexeiras Beach, located in Trairí County (3º 22' S, 39º 25' W); Pacheco Beach (3º 41' S, 38º 37' W) and Tabuba Beach (3º 41' S, 38º 39' W), in the Caucaia County; Ceará River's estuary (3º 41' S, 38º 35' W), Meireles Beach (3º 43' S, 38º 28' W) and Cocó River's estuary (3º 45' S, 38º 26' W) in Fortaleza County and Redonda Beach, in Icapuí County (4º 40' S, 37º 20' W).

The collecting areas, Flexeiras, Pacheco, Meirelles e Redonda, have a rocky substratum, while the animals from Tabuba were collected from a hyper-saline lagoon near the beach that has a sandy-muddy substratum. The collecting place in Ceará and Cocó River are located in urbanized areas.

MATERIAL AND METHODS

Twenty individuals of each one of the 14 studied species of marine prosobranch gastropods were collected during the low tide, in the intertidal zone, from 1997 to 2000 in one or more of the seven different collecting sites (table 1).

The individuals were anesthetized in saturate solution of magnesium chloride and sea water for two hours or frozen (at 0ºC) for 24 hours. Then, they were fixed in 70% alcohol and had their shells measured with a vernier caliper to 0.1mm precision. The shell measures in *Collisella subrugosa* and *Fissurela rosea* were done by measuring the distance from the anterior end to the posterior end, while in *Natica marochiensis*, *Neritina virginea* and *Tegula viridula* it was measured the distance from the apex to the farthest point of the outer lip. In the remaining species it was measured the distance from the apex to the tip of siphonal canal.

Littorina flava, L. ziczac, Natica marochiensis and *Olivella minuta* individuals were removed from their shells and submitted to a saturated potassium hydroxide (KOH), solution, then,they were boiled at

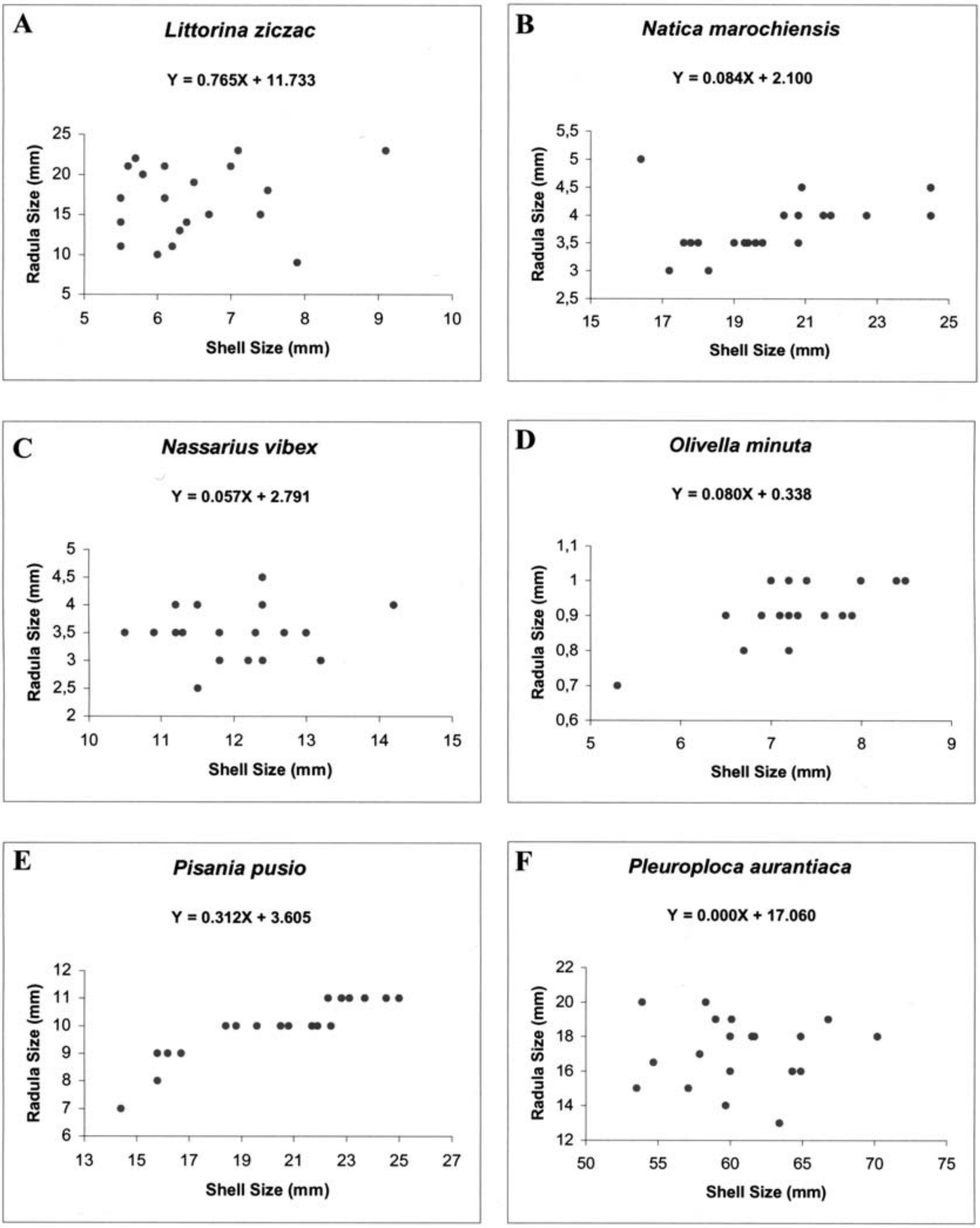

Figure 2.
Relation between shell and radula size in marine gastropod prosobranch mollusks. Radula Taenioglossa: A. Littorina ziczac. B. Natica marochiensis*. Radula Rachiglossa:* C. Nassarius vibex. D. Olivella minuta. E. Pisania pusio. F. Pleuroploca aurantiaca.

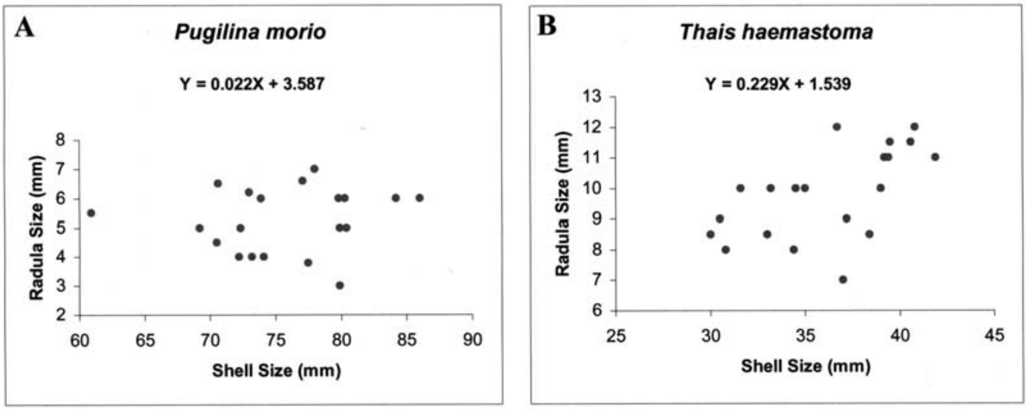

Figure 3.
Relation between shell and radula size in marine gastropod prosobranch mollusks. Radula Rachiglossa: A. Pugilina morio. B. Thais haemastoma.

100ºC until the soft parts disappeared and just the radula remained. Individuals from the other species had their radulae removed through dissection. The measure of radulae was done with a milimetric slide under a stereoscopic microscope. After this procedure, the radulae were fixed in 70% alcohol.

The radulae were submitted to dehydration in increasing alcoholic series (70% - 80% - 90% and absolute). After, they were stained with hot Congo Red, clarified with Creosote of Faia, mounted in Canada Balsam, and photographed on an optic microscope.

RESULTS

Rhipidoglossate and Docoglossate Radulae

The species with microherbivore diet and *Rhipidoglossate* radula (*Fissurella rosea, Neritina virginea* and *Tegula viridula*) or *Docoglossate* radula (*Collisella subrugosa*) presented shell size positively related to radula size (Tab. 2, Fig.1).

These species presented a relatively long radula, specially *Collisella subrugosa*, the form with *Docoglossate radula*, where the radula size corresponded in average to 81,65% of the shell size (Tab.3).

Taenioglossate Radula

Among the species with *Taenioglossate* radula, shell size was positively related to radula size just in *Cerithium atratum*, that feeds on detritus, and presents a relatively small radula (Tab. 3).

There was no relation between radula and shell size in *Littorina flava* and *L. ziczac*, that have herbivore diet and also in *Natica marochiensis* (Tab.2, Fig.2B), that has a carnivore diet. *Littorina flava* had the longest radula in relation to shell size (Tab.3). The *Natica´s* radula, just as in *C. atratum*, didn´t show a high radula size percentual related to the shell´s size, reaching a 18,84% average (Tab. 3).

Rachiglossate Radula

The negrophagous *Nassarius vibex* and the mollusks predators *Pleuroploca aurantiaca* and *Pugilina morio* did not present a relation between shell and radula size. The latter species presented the smallest radula with relation to shell size (Tab. 3).

Olivella minuta feeds on bivalves in a process where it swallows its prey. This species is characterized for presenting an exception in the *rachiglossate* radula structure for presenting marginal teeth, along with the usual rachidian and lateral teeth.

Table 1. *Studied species*

SPECIES	FAMILY	SITES
Collisella subrugosa (Orbigny, 1846)	Acmaeidae (Carpenter, 1857)	Pacheco Beach, Caucaia-CE
Cerithium atratum (Born, 1778)	Cerithiidae (Fleming, 1822)	Ceará River, Fortaleza-CE
Fissurella rosea (Gmelin, 1791)	Fissurellidae (Fleming, 1822)	Pacheco Beach, Caucaia-CE
Littorina flava (King & Broderip, 1832)	Littorinidae (Gray, 1840)	Meireles Beach, Fortaleza-CE
Littorina ziczac (Gmelin, 1791)	Littorinidae (Gray, 1840)	Meireles Beach, Fortaleza-CE
Nassarius vibex (Say, 1822)	Nassariidae (Iredale, 1916)	Cocó River, Fortaleza-CE
Natica marochiensis (Gmelin, 1791)	Naticidae (Forbes, 1838)	Redonda Beach, Icapuí-CE
Neritina virginea (Linnaeus, 1758)	Neritidae (Rafinesque, 1815)	Tabuba Beach, Caucaia-CE
Olivella minuta (Link, 1807)	Olividae (Latreille, 1825)	Flexeiras Beach, Trairí-CE
Pisania pusio (Linnaeus, 1758)	Buccinidae (Rafinesque, 1815)	Pacheco Beach, Caucaia-CE
Pleuroploca aurantiaca (Lamarck, 1816)	Fasciolariidae (Gray, 1853)	Pacheco Beach, Caucaia-CE
Pugilina morio (Linnaeus, 1758)	Melongenidae (Gill, 1867)	Ceará River, Fortaleza-CE
Tegula viridula (Gmelin, 1791)	Trochidae (Rafinesque, 1815)	Meireles Beach, Fortaleza-CE
Thais haemastoma (Linnaeus, 1767)	Thaididae (Jousseaume, 1888)	Meireles Beach, Fortaleza-CE

It presented a positive relation between radula and shell size (Tab. 2, Fig. 2D). The radula size corresponds in average 12,6% of the shell size (Tab. 3).

The remaing species with *Rachiglossate* radula; the predators *Olivella minuta, Pisania pusio* and *Thais haemastoma*, also presented a positive relation between shell size and radula size (Tab. 2, Fig.2D, 2E, 3B).

Table 2.
Relation between shell size and radula size in 14 species of marine prosobranchs mollusks

RADULA	SPECIE	DIET	p
Rhipidoglossate	*Fissurella rosea*	Herbivore	< 0,0001
	Neritina virginea	Herbivore	0,0078
	Tegula viridula	Herbivore	0,0174
Docoglossate	*Collisella subrugosa*	Herbivore	0,0018
Taenioglossate	*Cerithium atratum*	Detritivore	0,0100
	Littorina flava	Herbivore	0,1469
	Littorina ziczac	Herbivore	0,5003
	Natica marochiensis	Carnivore	0,1024
Rachiglossate	*Nassarius vibex*	Necrophage	0,6553
	Olivella minuta	Carnivore	0,0005
	Pisania pusio	Carnivore	< 0,0001
	Pleuroploca aurantiaca	Carnivore	0,9981
	Pugilina morio	Carnivore	0,6241
	Thais haemastoma	Carnivore	0,0066

DISCUSSION

A clear pattern between type of diet and the existence of a positive relation between radula size and shell size was not found in the present study. However, such positive relation was found in the microherbivore animals that have *Rhipidoglossate* (Figs. 4A and 4B) and *Docoglossate* radula types. According to Fretter and Graham (1994) the enlargement of the radula in gastropods with *Rhipidoglossate* radula type made possible the use of a larger area of substratum during the food scraping.

The *Littorina* species didn´t present positive relation between radula size and shell size, although they have an herbivore diet very similar to those species with *Rhipidoglossate* radula type. This may be related to the fact that their *Taenioglossate* radula type doesn´t have a very efficient system that allows a high contact with the surface of the substratum (Graham, 1985).

In the *Taenioglossate* group, *Cerithium atratum* was the only species that had a positive relation between radula size and shell size. *C. atratum* individuals, which feed on detritus, have very long marginal teeth (Fig. 4D), well adapted for capture of particles from the substratum (Morton, 1968). *C. atratum* has one of the smallest studied radulae related

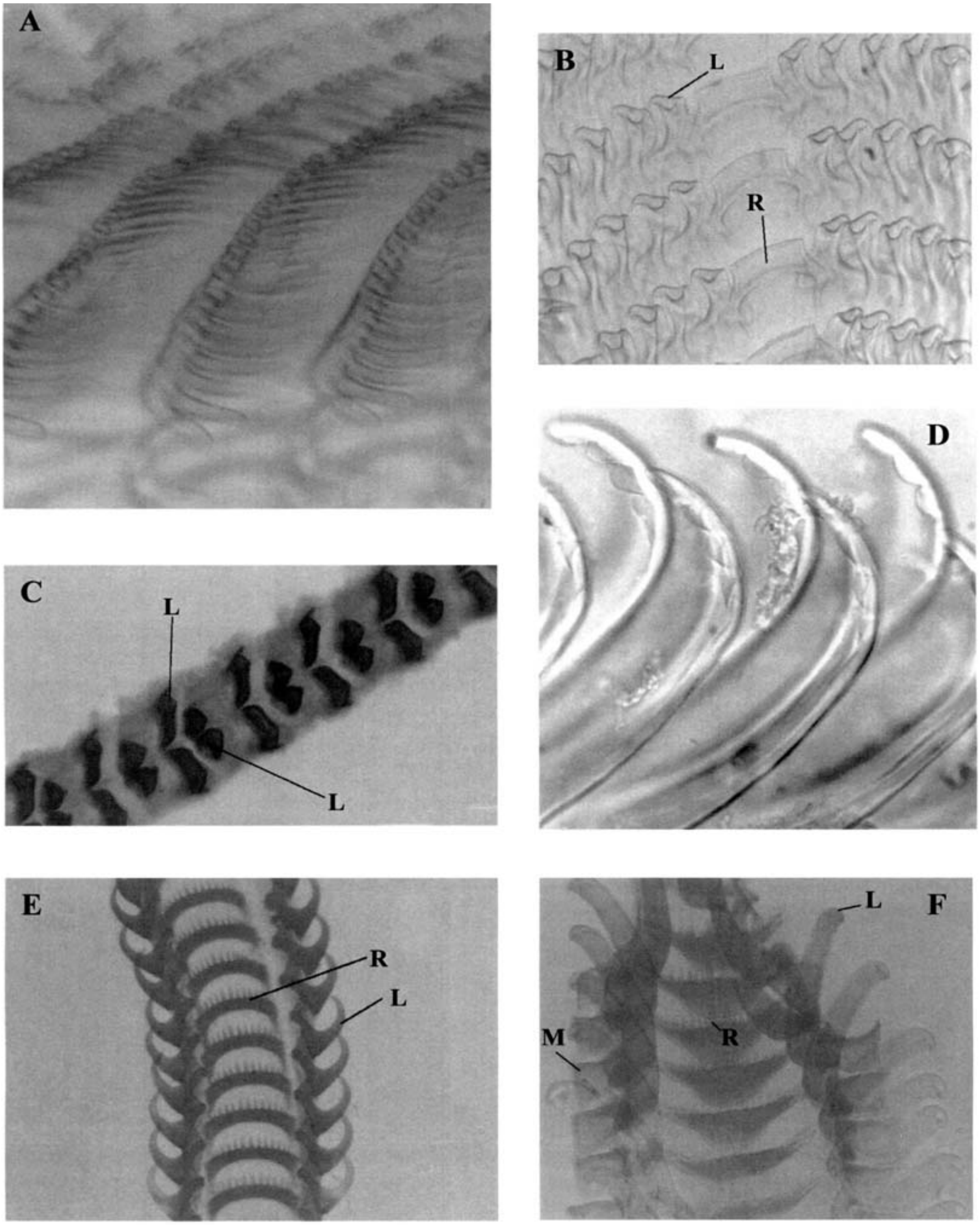

Figure 4.
A. Tegula viridula *radula showing the marginal teeth (252X).* B. Tegula viridula *radula showing the rachidian (R) and lateral (L) teeth (252X).* C. Collisella subrugosa *radula showing the lateral teeth (L) (63X).* D. Cerithium atratum *radula showing the marginal teeth (252X). Nassarius* 'vibex *radula showing the rachidian (R) and lateral (L) teeth (63X).*
F. Olivella minuta *radula showing the rachidian (R), lateral (L) and marginal (M) teeth (630X).*

Table 3. *Radulae size percentual related to the shell size in 14 species of marine prosobranchs mollusks.*

SPECIES	MSS (mm)	MRS (mm)	MRS / MSS
Collisella subrugosa	13,44	10,92	0,810
Cerithium atratum	25,06	3,42	0,136
Fissurella rosea	16,23	7,23	0,445
Littorina flava	10,78	15,75	1,461
Littorina ziczac	6,49	16,7	2,573
Nassarius vibex	11,98	3,47	0,289
Natica marochiensis	20,01	3,77	0,188
Neritina virginea	9,89	4,15	0,419
Olivella minuta	7,29	0,92	0.126
Pisania pusio	20,33	9,95	0,489
Pleuroploca aurantiaca	60,84	17,07	0,280
Pugilina morio	75,65	5,25	0,069
Tegula viridula	16,21	10,05	0,620
Thais haemastoma	36,13	9,82	0,271

MSS: Mean Shell Size
MRS: Mean Radula Size

to shell size, so the length of marginal teeth seems to be efficient enough for the food capture.

According to this study, the carnivorous animals have smaller radulae than herbivorous ones. *N. marochiensis* had a smaller radula than *T. haemastoma*, but the first one didn´t show a significant relation between radula size and shell size while that the second one did.

The relation between radula size and shell size was not significant for animals that don´t use radula to capture their food, as *Nassarius vibex* (Fig. 4E), *Pleuroploca aurantiaca* and *Pugilina morio*, but there was an exception *Olivella minuta*, which has a modified radular morphology, i.e., the presence of marginal teeth (Fig. 4F). According to Bandel (1984), the origin of the Olividae family doesn´t come directly from Muricacea or Buccinacea, but from a common link between these two, followed by the parallel development of *Oliva* e *Olivella*. The flexibility of these radular teeth allows the passage of the prey to the mouth and the rest of the swallowing process. Bandel (1984) e Nybakken (1990) observed in animals with *Rachiglossate* radula (*Fasciolaria, Thais*) and *Toxoglossate* radula a morphologic ontogenic radular change, related not only to the size of the animal, but also with the changes in the diet during the animal development. Young animals usually live in different places in relation to the adults, therefore, they have different diets (Paine, 1963). *Thais* doesn´t have all cusps developed in the lateral teeth when it is young and *Fasciolaria*, which usually lives upon coral and rocks with calcareous algae (Schmitt, 1994; Matthews-Cascon *et al.*, 1989), has the number of rachidian cusps varying according to the size of the animal.

According to Guralnick & De Maintenon (1997) not only the radula type or diet will have influence in the morphological characteristics of each individual from each species. There are others influences such as the prey capture strategies and the food processing mechanism (how the whole radula teeth are used and the time taken to they being reconstructed), the environment pressures (phenotypic plasticity and food competition) and the species ontogeny.

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