Short Contribution

Sexually dimorphic radular morphology in *Euplica varians* and *E. versicolor* (Neogastropoda: Columbellidae)

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Abstract

Radular morphology in two species of *Euplica* (Gastropoda: Neogastropoda: Columbellidae) was investigated for the occurrence of sexual dimorphism. Sexual dimorphism was found to occur in these columbellid species, as it does in some species of muricids, with adult males having tooth modifications including differences in cusp shape, larger tooth size in one species and more tooth rows in both. The functional significance of the dimorphism is unknown.

Additional keywords: Gastropoda, Mollusca, ontogeny, sexual dimorphism.

Introduction

The morphology of the radula, the chitinous strip of teeth found in molluscs, has traditionally been one of the most commonly used sources of data for studies on molluscan systematics. The shape and form of molluscan radular teeth are typically unique to a species or genus, and some features of the radula, such as tooth numbers, have been used to investigate higher level molluscan taxonomic relationships. Thus intraspecific variations in radular characteristics are important and must be documented if molluscan relationships are to be reconstructed rigorously.

Sexual dimorphism in radular morphology is known in one member of a basal gastropod group, the trochoidean species *Tricolia variabilis* (Robertson 1971). It is more common in caenogastropods and has been documented in muricid gastropods by Arakawa (1957) and Maes (1966), who studied species of *Drupella* and *Nassa* respectively. In both cases, variation was present primarily in the size and shape of the rachidian teeth, and *Drupella* also showed variation in aspects of lateral tooth size. Fujioka (1982) later investigated four species of *Drupella* in greater detail and found that the sexual dimorphism in radular tooth shape was not present in the juveniles, which had tooth shapes similar to adult females; change in tooth shape only occurred in the adult males. Fujioka (1984) studied the radulae of *Cronia margariticola* and *Morula musiva*, also muricids, and found sexual dimorphism to occur in the larger size and simpler shape of the rachidian teeth in adult males, similar to the situation in *Drupella*. Fujioka (1984) suggested that this may be linked to a difference in diet between the adult males and females. One buccinid species, *Pisania luctuosa*, was shown by Cernohorsky (1971) to exhibit sexual dimorphism in radular tooth row numbers, wherein males have fewer tooth rows and a wider radula.

The purpose of this paper is to describe dimorphic radulae present in *Euplica varians* and related species of columbellid gastropods. Columbellids are a diverse family of buccinoid neogastropods. Although they are mostly opportunistic carnivores, some members of the family, including species in the genus *Euplica*, are facultative herbivores. Radular morphology is one of the preferred character sets for investigating columbellid

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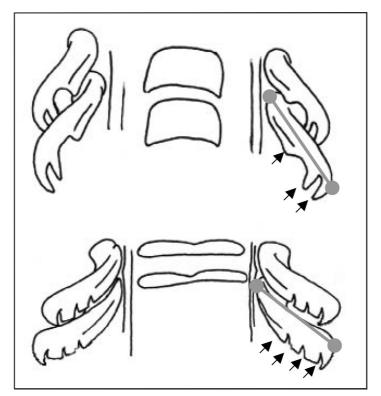


Fig. 1. Drawings of two rows each from a *Mitrella* radula (top) and that of *Euplica* (bottom). The double-ended lines on each indicate the main axis of the primary lateral tooth cusp, along which tooth length was measured. The arrows indicate the secondary (posterior) lateral cusps in each.

systematics at the generic level (Radwin 1977; Bhatti 1992) because it varies little within columbellid species or between closely related species, whereas shell morphology is often highly variable.

The columbellid radula is stenoglossate, but with an acuspate centre plate rather than a typical rachidian (Guralnick and deMaintenon 1997), and tall, sigmoid lateral teeth that rotate obliquely on narrow bases. Each lateral tooth has one primary cusp, with three to four secondary cusps along the posterior edge (Fig. 1 shows a typical columbellid radula compared with the radula of *Euplica*). Tooth wear patterns suggest that the lateral teeth contact the substrate obliquely along the posterior edge, most strongly at the end. Because radular morphology is conserved within columbellid species groups, intraspecific dimorphism in radular morphology may be both interesting from a functional perspective, and it may in itself be systematically informative.

Euplica, the focus of this study, is a group of about nine Indo-Pacific columbellid species, 5–25 mm in shell length, found commonly in shallow rocky or seagrass habitats. Radular morphology is similar in all members of the genus. The end-most (distal) secondary cusp is flat or pointed, the two medial secondary cusps are flat-edged and the proximal secondary cusp is blade-like, giving the posterior edge of the tooth a scraper-like form (Fig. 1, bottom). This state is characteristic of many columbellid species with a

partially herbivorous diet, whereas carnivores (Fig. 1, top) will typically have pointed secondary cusps with large spaces between them (deMaintenon 1999).

Materials and methods

Specimens of *Euplica varians*, a small widespread species, were collected from sites in the Hawaiian Islands and preserved in 70–90% ethanol. Specimens of *Euplica versicolor* (Sowerby, 1832), a larger species of *Euplica* native to the south-west Pacific, were available from collections made in New Caledonia. Sex, shell length and stage (juvenile or adult) were recorded for each specimen. Columbellids have determinate growth; the shell in a growing individual has a thin, fragile aperture edge, which becomes thickened and denticulate when the growth period is terminated. Thin-lipped individuals were recorded as juveniles, individuals with a thickened denticulate labial edge were recorded as adults. Because of this, recognition of adults in this study is likely to be conservative. Sex was determined by the presence of secondary sexual characteristics, including a penis in males or reproductive glands in females (the male pallial gonoduct is non-glandular).

Each specimen was dissected and the radula removed. Tooth rows were counted and the total number recorded, and radular tooth measurements made using an Olympus compound microscope with an ocular micrometer (Olympus, Melville, NY, USA). Two sample *t*-tests were used to investigate differences in mean radular measurements between adult males and females, and simple linear correlations were used to investigate ontogenetic changes in radular measurements as indicated by increasing shell size. For illustration, radulae from several individuals were mounted on stubs with double-stick conductive tape, and the radulae were sputter coated and viewed using an ISI electron microscope (Topcon America Corporation, Paramus, NJ, USA).

Results and discussion

Hawaiian *Euplica varians* has a maximum shell length of ~10 mm, and individuals cease growth and develop a thickened lip at 8.5–9.0 mm shell length or larger. Secondary sexual characteristics (and perhaps sexual maturity) appear before growth is completed, at ~7 mm shell length.

Radular morphology in *E. varians* is sexually dimorphic, but shape only differs in adults. Adult male and female *E. varians* differ in the shape of the outermost secondary lateral tooth cusp. Adult males have a pointed outermost cusp that extends past the posterior edge of the rest of the tooth (Fig. 2a), whereas subadult males and females have flat-tipped outer cusps with only a very slight point, giving the distal cusp a notched appearance (Fig. 2b). Two transitional specimens (both adults) were found with a longer distal cusp and a very small point at its base (the male in Fig. 2a is one of these), suggesting that the shift in radular form occurs after growth ceases. The specimens observed all had similar teeth from one end of the radula to the other (not counting wear), so no transitions were observed within individual radulae.

The width of the centre plates, lengths of the lateral teeth, and the number of tooth rows were recorded in each specimen of E. varians and compared relative to shell length to investigate ontogenetic trends (Fig. 3). The lateral tooth length and number of tooth rows both increase linearly with increasing shell length (Pearson's correlation coefficient and P-value given in Fig. 3), and those trends do not show any definitive quantitative change associated with cessation in growth or with sexual maturity. Radulae of adult males and females differ in one aspect of size; adult males have more tooth rows than adult females (t-test, P = 0.008, see Table 1 for means), though adult shell size and tooth length do not differ significantly.

Several adult specimens of *Euplica versicolor* were available from New Caledonia, and radular morphology was examined in eight of these. Because all available specimens were adults, no ontogenetic changes could be observed. The radula in this species differs from that of *E. varians* primarily in size; the basic tooth morphology is the same. The divergent

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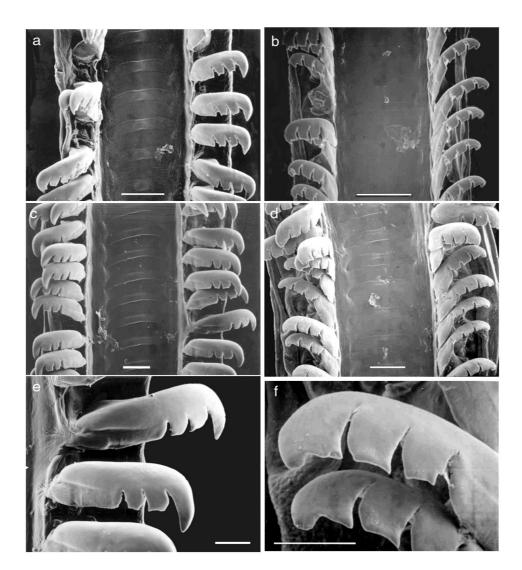
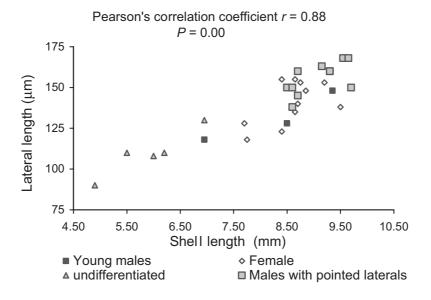


Fig. 2. (a) Euplica varians radula, adult male, 9.30 mm shell length, scale bar = $100\mu m$. (b) Euplica varians radula, adult female, 8.40 mm shell length, scale bar = $100\mu m$. (c) Euplica versicolor radula, adult male, 16.75 mm shell length, scale bar = $100\mu m$. (d) Euplica versicolor radula, adult female, 17.90 mm shell length, scale bar = $100\mu m$. (e) Lateral teeth, close-up of (c), scale bar = $50\mu m$. (f) Lateral teeth, close-up of (d), scale bar = $50\mu m$.

morphology found in *Euplica varians* was present in this species, with all four males having a pointed distal lateral cusp (Fig. 2c,e) and the females having a flatter distal secondary cusp (Fig. 2d,f). Lateral tooth length and number of tooth rows are also higher in males than in females (t-test, P = 0.007 and P = 0.002, respectively, see Table 2 for means) even though shell lengths are similar, but the available sample size was rather small.

The sexual dimorphism in the columbellid radulae appears to take the same form as seen previously in muricids: a variation in tooth cusp shape and size that only appears in adults. The buccinid *Pisania* may be similar, but female *Pisania* have more tooth rows than males



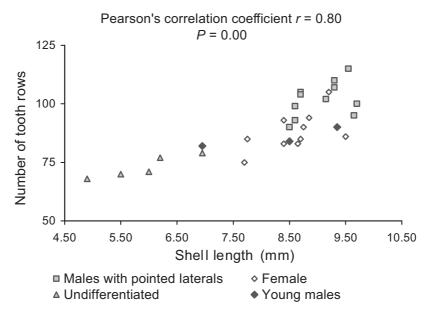


Fig. 3. (a) Scatter plot of shell length v. lateral tooth length for specimens of *Euplica varians* showing Pearson's correlation coefficient and probability. (b) Scatter plot of shell length v. number of tooth rows for specimens of *Euplica varians* showing Pearson's correlation coefficient and probability.

(Cernohorsky 1971), whereas female *Euplica* have less. The function of the dimorphism is unknown in both cases. Robertson (1971) suggested that it may be linked to dietary differences, but that possibility has not been investigated in these taxa. The presence of a similar characteristic evolving sporadically in members of four different families suggests that radular dimorphism might have some particular function.

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Table 1. Means and standard errors for tooth measurements from male and female *Euplica varians* radulae

Asterisks indicate measurements that differed significantly between sexes

	n	Shell length (mm)	Lateral tooth length (µm)	Number of tooth rows*
Males Females	11 8	9.07 ± 0.14 8.84 ± 0.12	155.64 ± 2.92 147.13 ± 2.91	$101.8 \pm 2.3 \\ 90.9 \pm 2.8$

Table 2. Means and standard errors for tooth measurements from male and female *Euplica* versicolor radulae

Asterisks indicate measurements that differed significantly between sexes

	n	Shell length (mm)	Lateral tooth length (µm)*	Number of tooth rows*
Males Females	4 4	16.65 ± 0.84 16.14 ± 0.50	261.25 ± 7.18 225.13 ± 5.40	140.0 ± 4.4 112.3 ± 2.8

Sexual dimorphism in columbellids was investigated in two congeneric species, *Euplica varians* and *E. versicolor* in the present study. These species' radulae have rarely been illustrated. Sleurs (1985) figured the radula of *E. varians* and deMaintenon (1999) figured the radula of *Euplica bidentata*, a species very similar to *E. versicolor*; the latter was taken from an adult male and its tooth morphology is consistent with that. Sleurs (1985) appeared to have a female or young male. Radulae of other *Euplica* species and of members of the genus *Metanachis* are morphologically similar to the point of being indistinguishable, so the dimorphism may be present in these other species as well. In *E. varians*, the dimorphism has an ontogenetic basis and does not appear until the animal ceases growth.

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