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Eccentricity of the Apical System and Peristome of Sand Dollars (Echinodermata: Echinoidea: Clypeasteroidea: Scutellina)

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Eccentricity, location of structures away from a central position, is associated with directional movement. Although sand dollars have directional movement, only eccentricity of the anus is apparent. Eccentricity of the apical system and peristome is less apparent. We have found the apical system and the peristome are statistically significantly slightly anterior in *Mellita tenuis*, *Mellita quinquesperforata*, *Mellita isometra*, and *Encope aberrans*. The apical system of *Leodia sexiesperforata* is central and that of *Echinarachnius parma* is anterior, whereas the peristome of both is statistically significantly slightly posterior. The usual selective pressure for pronounced anterior location of the mouth in animals with directional movement may be countered by the mode of feeding in sand dollars that utilizes the oral surface. The basis for the eccentricity of the apical system is not known.

Knowledge of body form gives insight into the biology and ecology of species. Symmetry is a major aspect of body form, and Beklemishev (1969) noted the wide variety that exists. He concluded that the origin of bilateral symmetry in echinoids was clearly associated with a fossorial mode of life and suggested resistance of the particulate substrate to movement was sufficient to make it advantageous. Bilateral symmetry is usually associated with differentiation of the anterior and posterior ends of the body, with the peristome (mouth) located anteriorly and the anus posteriorly (Wainwright et al., 1976). In clypeasteroids, the periproct (anus) has moved out of the apical system toward the posterior edge of the test (Durham, 1966). This movement has been thought to be adaptive because it separates the feces from the aboral respiratory structures (Bather, 1900).

Smith (1984) stated "During the evolution of irregular echinoids there is a pronounced tendency for the peristome to shift anteriorly." However, this expected, pronounced anterior location of the peristome is not present in clypeasteroids. Indeed, Mortensen (1948) stated that the apical system and peristome of Clypeasteroidea usually is central. Dafni (1988) did not even mention the peristome in his discussion of the relation between bilateral symmetry and the anus. Slight eccentricity of the peristome, both anterior and posterior, has been reported for many species without documentation (Clark and Twitchell, 1915; Nisiyama, 1966). An exception is the famous pronounced posterior eccentricity of the apical system and mouth of some *Dendraster* species (Clark and Twitchell, 1915; Woodring et al., 1940; Dur-

ham, 1949; Raup, 1956; Alexander, 1972; Stanton et al., 1979; Beadle, 1995; Mooi, 1997) associated with its unique feeding behavior. Actual measurements of the location of the apical system and peristome are few (Woodring et al., 1940; Durham, 1949; Kier, 1972; Mooi and Harold, 1994; Beadle, 1995; Mooi, 1997; Ali, 1998).

Raup (1956) wondered whether the variation he found in the posteriorly eccentric apical system of *Dendraster excentricus* would be paralleled by that of the peristome. Beadle (1995) reported a strong correlation between the two did exist. Here we report the location of the peristome and apical system in six species of scutellid sand dollars and test the hypothesis that the two are eccentric.

MATERIALS AND METHODS

Six species of scutellid sand dollars were studied: *Encope aberrans* Martens, *Leodia sexiesperforata* (Leske), *Echinarachnius parma* (Lamarck), *Mellita quinquesperforata* (Leske), *Mellita isometra* Harold and Telford, and *Mellita tenuis* Clark. Two populations of *M. tenuis* were studied, one for two successive years.

Dimensions used for eccentricity calculations (see Beadle, 1995) were measured to the nearest 0.1 mm with vernier calipers. Eccentricity of the apical system was calculated by the ratio used by Raup (1956), Stanton et al. (1979), and Beadle (1995): $2x/y$, where x is the distance from the center of the apical system to the posterior test margin and y is the test length. For consistency, eccentricity of the peristome was calculated by the same ratio, where x is the distance from the posterior edge of the

peristome to the posterior test. Ratios >1 indicate anterior eccentricity; ratios <1 indicate posterior eccentricity. The means of the eccentricity ratios for the apical system and peristome were used to calculate whether the positions of the apical system and peristome were the same (apical system ratio/peristome ratio).

A one-sample t-test was used to test eccentricity values for departures from 1. One-way ANOVA and the Tukey-Kramer multiple comparison test were used to test for differences in eccentricity values among the populations. Normality of the data was tested by the Anderson-Darling test and equality of variances by Bartlett's test. Alpha = 0.05 was considered significant for all tests.

RESULTS

Although the eccentricity values were small, all except one were significantly different from one, which indicates they are eccentric (Table 1). The apical system was anterior in all species except *L. sexiesperforata*, in which it was central (no eccentricity). The peristome was anterior in all species of *Mellita* and in *E. aberrans*, whereas it was posterior in *L. sexiesperforata* and *E. parma*.

The anterior eccentricity of the peristome was significantly more in the mellitids than in *E. aberrans* (Table 2). Among the mellitids, the eccentricity ratios of *M. isometra* and *M. quinquesperforata* did not differ significantly, but both were greater than those of *M. tenuis*. The ratios for the three samples of *M. tenuis* collected at different times and sites did not differ. The ratios of *L. sexiesperforata* and *E. parma* did not differ.

The eccentricity ratios of the apical system of the species showed much more overlap (Table 2). The ratio of *L. sexiesperforata* differed from all others. The ratios of *E. parma* and one population of *M. tenuis* differed from those of *M. isometra* and a second population of *M. tenuis*. Other combinations showed considerable overlap.

The ratios of the apical system to the peristome differed (Table 1). Both were anterior and nearly identical in *M. tenuis*. Both were anterior, with the peristome being more anterior in *M. isometra* and *M. quinquesperforata*. Both were anterior, with the apical system being more anterior in *E. aberrans*. *Leodia sexiesperforata* was the only species with the apical system central, whereas the peristome was posterior, and *E. parma* was the only one with the apical system anterior and the peristome posterior.

TABLE 1. Eccentricity ratios for the apical system (AS) and peristome (P) of sand dollars. Ratios >1 indicate anterior eccentricity. Ratios <1 indicate posterior eccentricity.

Species	Provenance	n	Length ^a	Eccentricity ratio		AS/P
				Apical system	Peristome	
<i>Mellita tenuis</i>	Mullet Key, FL 1995	92	34 ± 1	1.215* ± 0.004	1.198* ± 0.006	1.014
<i>Mellita tenuis</i>	Mullet Key, FL 1996	21	57 ± 2	1.179* ± 0.005	1.178* ± 0.015	1.001
<i>Mellita tenuis</i>	Naples, FL 1996	70	54 ± 3	1.143* ± 0.005	1.149* ± 0.006	0.994
<i>Mellita quinquesperforata</i>	Playa Guria, Venezuela 1997	13	88 ± 3	1.180* ± 0.011	1.280* ± 0.022	0.920
<i>Mellita isometra</i>	Pritchard's Is., SC 1996	76	62 ± 1	1.182* ± 0.003	1.225* ± 0.005	0.964
<i>Leodia sexiesperforata</i>	Curacao, Netherlands Antilles 1998	24	75 ± 2	1.011 ± 0.007	0.931* ± 0.009	1.086
<i>Encope aberrans</i>	Mullet Key, FL 1998	49	100 ± 1	1.173* ± 0.004	1.024* ± 0.044	1.146
<i>Echinarachnius parma</i>	Isle of Shoals, ME 1996	120	90 ± 48	1.114* ± 0.007	0.901* ± 0.005	1.236

* Ratios significant at the 0.01 level.
^a Body length in mm; mean ± SE.

TABLE 2. Statistical differences in the eccentricity ratios of the apical system and peristome of sand dollars. The species are ranked from the lowest to the highest ratio. Ratios >1 indicate anterior eccentricity, $= 1$ no eccentricity, and < 1 posterior eccentricity. Species with the same letter do not differ significantly ($P > 0.05$).

Apical system	Ratio	Peristome	Ratio
<i>Leodia sexiesperforata</i> A	1	<i>Echinarachnius parma</i> A	<1
<i>Echinarachnius parma</i> BC	>1	<i>Leodia sexiesperforata</i> A	<1
<i>Mellita tenuis</i> Naples C	>1	<i>Encope aberrans</i> B	>1
<i>Encope aberrans</i> CD	>1	<i>Mellita tenuis</i> Naples C	>1
<i>Mellita tenuis</i> Mullet Key 1996 CD	>1	<i>Mellita tenuis</i> Mullet Key 1996 C	>1
<i>Mellita quinquesperforata</i> CD	>1	<i>Mellita tenuis</i> Mullet Key 1995 C	>1
<i>Mellita isometra</i> D	>1	<i>Mellita isometra</i> D	>1
<i>Mellita tenuis</i> Mullet Key 1995 D	>1	<i>Mellita quinquesperforata</i> D	>1

DISCUSSION

The apical system of five of the six species of sand dollars studied here was slightly anteriorly eccentric as was the peristome in four species. The apical system of *L. sexiesperforata* was central, and the peristome of *L. sexiesperforata* and *E. parma* was posteriorly eccentric. That the eccentricity ratios of the peristome of three samples of *M. tenuis* did not differ significantly gives confidence in the validity of the ratios. The variation in the eccentricity ratios of the apical system in the three samples of *M. tenuis* suggests the control of the location of the apical system is less fixed. The location of the apical system in *D. excentricus* (which is posterior) varies with habitat (Raup, 1956; Stanton et al., 1979).

Beadle (1995) reported a range for the eccentricity ratio of the peristome of *E. parma* of 0.95–1.05. The range for the eccentricity ratio of the apical system was estimated from his graph to be ca. 0.98–1.10. Beadle selected values nonrandomly to maximize variation, and those given are the basis for his conclusion that neither the apical system nor the peristome of *E. parma* shows any pronounced tendency toward posterior displacement. Our statistical analysis showed that the peristome of the population of *E. parma* sampled is displaced posteriorly and that the apical system is decidedly anterior. Hashimoto and Ujić (1965) reported both the peristome and apical system of *Echinarachnius microthyroides* are very slightly anteriorly eccentric.

Mooi and Harold (1994) reported the distance from the front ambitus to the madreporite of the neotype of *M. quinquesperforata* is 43.9%. This is equivalent to an eccentricity ratio of 1.14, similar to the mean found for the population from Venezuela. However, the distance from the front ambitus to the anterior

edge of the peristome of the neotype of *M. quinquesperforata* is 41% not 29.9% as in Mooi and Harold (1994) (Mooi, pers. comm.). This is equivalent to an eccentricity of 1.43, much greater than the mean of 1.280 found here. Clark and Twitchell (1915) reported slightly posteriorly eccentric peristomes have been reported for the extinct species *Scutella mississippiensis* and *Periarachus altus*. They reported slightly anteriorly eccentric peristomes for all other species except the dendrasterids.

Beadle (1995) reported a strong correlation between the location of the peristome and apical system in a sample of specimens pooled from three species of *Dendraster* but did not report whether the locations were correlated for individual species. In contrast, he found no correlation between the location of the two in *Echinarachnius parma*. We found the eccentricity ratio of the apical system and peristome are similar only for *M. tenuis*. The two structures are obviously uncoupled in development and function in general as Beadle (1995) concluded for dendrasterids.

Cassiduloids are in the same clade as clypeasteroids (Suter 1994a, 1994b; Smith et al. 1995), and it is instructive to consider them in this analysis. Kier (1972) made generalizations regarding the position of the peristome of cassiduloids although he did not quantify its position. For example, the peristome was usually only slightly anterior in Jurassic cassiduloids and was actually central or posterior in the genus *Clypeus*. In *Gentilia syriensis* of the Cretaceous, Kier reported a peristome located "very eccentric anteriorly." In this genus, the anterior ambulacrum III is very short or absent. Mooi (1990) reported without comment interesting correlations between test shape and position of the peristome in his key to the living cassiduloids. For example, despite showing di-

rectional movement, the test margin of species in the genus *Conolampas* is circular and the peristome is central or slightly posterior. In contrast, the test margin of species in the genus *Echinolampas* is oval and the peristome is slightly anterior. Once again, we see no pronounced change in body form or anterior position of the mouth in this group with directional movement.

The final question is why the peristome is not located anteriorly in a more pronounced way as predicted for species that show directional movement. Sand dollars do not move rapidly (Parker, 1927; Weihe and Gray, 1968; Bell and Frey, 1969), and one hypothesis is that the speed of movement is not sufficient to result in selection for an anterior location of the peristome.

A second hypothesis concerns the mode of feeding. Phelan (1977) suggested the greatly expanded ambulacral columns and adjacent regions of the interambulacra that support accessory tube feet are homologous to the more recognizable but less expansive phylloides of the cassiduloids. These tube feet accomplish food gathering and are associated with the food grooves on the oral surface of sand dollars (Ellers and Telford, 1984; Telford et al., 1985; Telford and Mooi, 1996). Cowen (1981) made an imaginative analogy between the pattern of arm branching in camerate crinoids and the pattern of harvesting roads on banana plantations. He showed the similarity of the food grooves on the sand dollar and the crown of a camerate crinoid to the ideal road layout of a banana plantation. Thus, the posterior location of the peristome in *D. excentricus* would be associated with its unique feeding behavior (Timko, 1976; O'Neill, 1978). The posterior position would be an adaptive relocation because the food-groove system is much more extensively developed posteriorly than anteriorly (Durham 1955). Possibly an anterior location of the peristome in sand dollars that have the usual prone position would decrease efficient feeding and thus be selected against.

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