

SECONDARY SEX CHARACTERS IN *COELOPLEURUS FLORIDANUS*
A. AGASSIZ, 1872 (ECHINODERMATA: ECHINOIDEA)

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ABSTRACT—Male specimens of *Coelopleurus floridanus* have tubular genital papillae which are conspicuous during spawning. Papillae are also visible in live, alcohol-preserved, and dried specimens. Females have small, inconspicuous, conical papillae. No other external differences between males and females of this species were found, and no secondary sex characters of this nature were found in any other genera in the Order Arbacioida. This is apparently the first record of dimorphic genital papillae in a deep-sea regular echinoid. A survey for dimorphic papillae in some other deep-sea regular echinoids was negative.

Secondary sex characters have been recorded for many species of echinoids. Usually these take the form of differences in sizes of genital pores (Mortensen, 1928), but in several species where the females brood young, the differences are rather more obvious, often involving development of deep brood pouches in the test of the female. Kier (1969) discussed sexual dimorphism in fossil echinoids.

Dimorphic genital papillae, also secondary sex characters, have been described for several species of shallow-water echinoids (Chia, 1977). Mortensen (1935) noted that the western Atlantic arbacioid *Coelopleurus floridanus* A. Agassiz has the genital pores "covered by distinct genital papillae . . ." (p. 615), but he did not comment on differences between males and females. While studies were being conducted on spawning and larval development of *C. floridanus*, one of us (J.E.M.) observed that the spawning males possess conspicuous tubular papillae, while spawning females have at best short conical papillae. This paper includes a brief description of the papillae in live and preserved material, notes the time of first appearance of the papillae in young urchins, and presents results of a brief survey for secondary sex characters in other arbacioids and in a small number of regular deep-sea echinoids.

MATERIALS AND METHODS

C. floridanus occurs off the southeastern United States and in the Caribbean at depths of 90-2,385 m. Specimens were collected in July 1978 during a dive aboard the research submersible JOHNSON-SEA-LINK, off Cape Canaveral, Florida, at a depth of 91 m. A benthic scoop or net held by the submersible's manipulator was used to collect the urchins, which were then transferred to a basket. Thirty-six specimens were returned live to the laboratory. Spawning was induced by injection through the peristomial membrane of 0.3 ml of 0.5 molar potassium chloride. Specimens were photographed with a Zeiss Tessovar photomacrographic apparatus or with a Nikon camera with bellows attachment.

Alcohol preserved and dried specimens of this and other species of echinoids were studied at the National Museum of Natural History, Smithsonian Institution.

RESULTS

Genital papillae in live specimens.—The genital papillae of male and female *C. floridanus* differ as follows:

MALE papillae are essentially tubular (Figs. 1 and 2A), nonretractile, protruding a distance of slightly more than 1 mm. The proximal two-thirds of each papilla is dark brown; the distal one-third is transparent, with flecks of dark brown pigment.

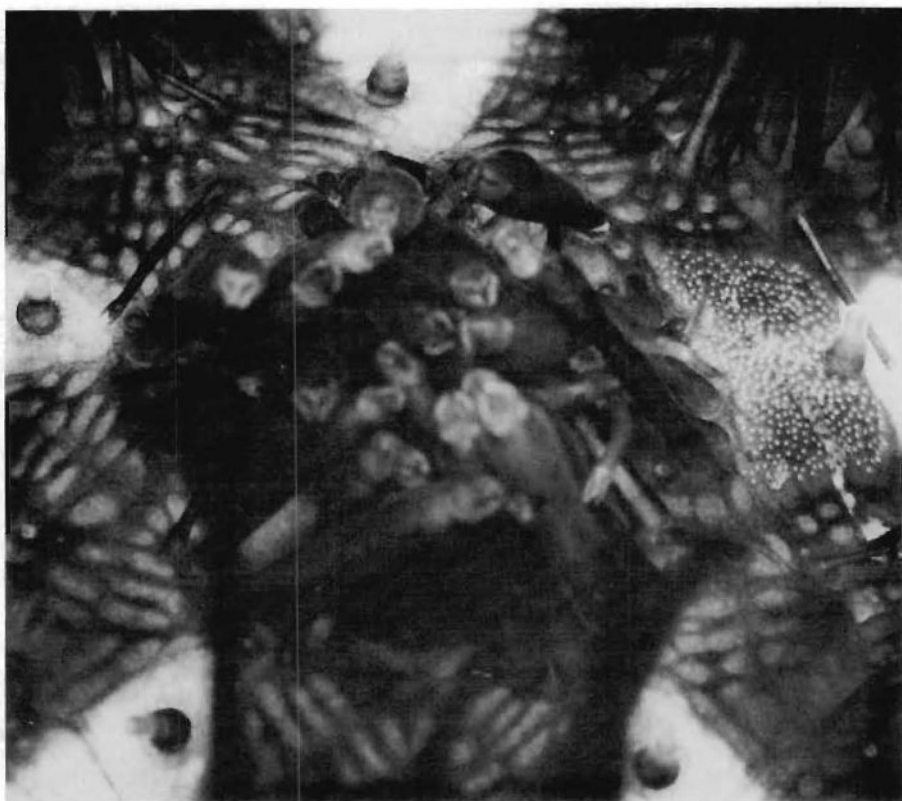


Figure 1. Adapical area of male specimen of *C. floridanus*, showing five conspicuous genital papillae in interradii.

FEMALE papillae are conical (Fig. 2B), either slightly sunken into the genital pores or slightly protruding. The area surrounding the papilla is yellow, the basal portion of the papilla is yellowish green, and the tip is transparent.

When spawning, males eject a stream of sperm cells from each papilla. The stream is carried upwards, away from test and spines and the sperm cells soon disperse into the surrounding seawater. Females eject eggs which are slightly negatively buoyant; these fall onto the test and spines in large numbers. Movements of spines, tube feet and pedicellariae help to move the eggs away from the urchin.

We attempted to test the efficacy of the genital papillae by removing them from two male specimens. On both specimens, three papillae were removed to the level of the test, and in the remaining two only the distal half was removed. One specimen was injected with potassium chloride immediately; the other was held for 24 h before injection.

A specimen with intact genital papillae can eject sperm in a fine stream a distance of 7–10 mm upwards into the water column. This ejection in turn creates a local current which pushes the sperm even further as it begins to disperse into a cloud. This process keeps the area around the gonopore free from flooding by

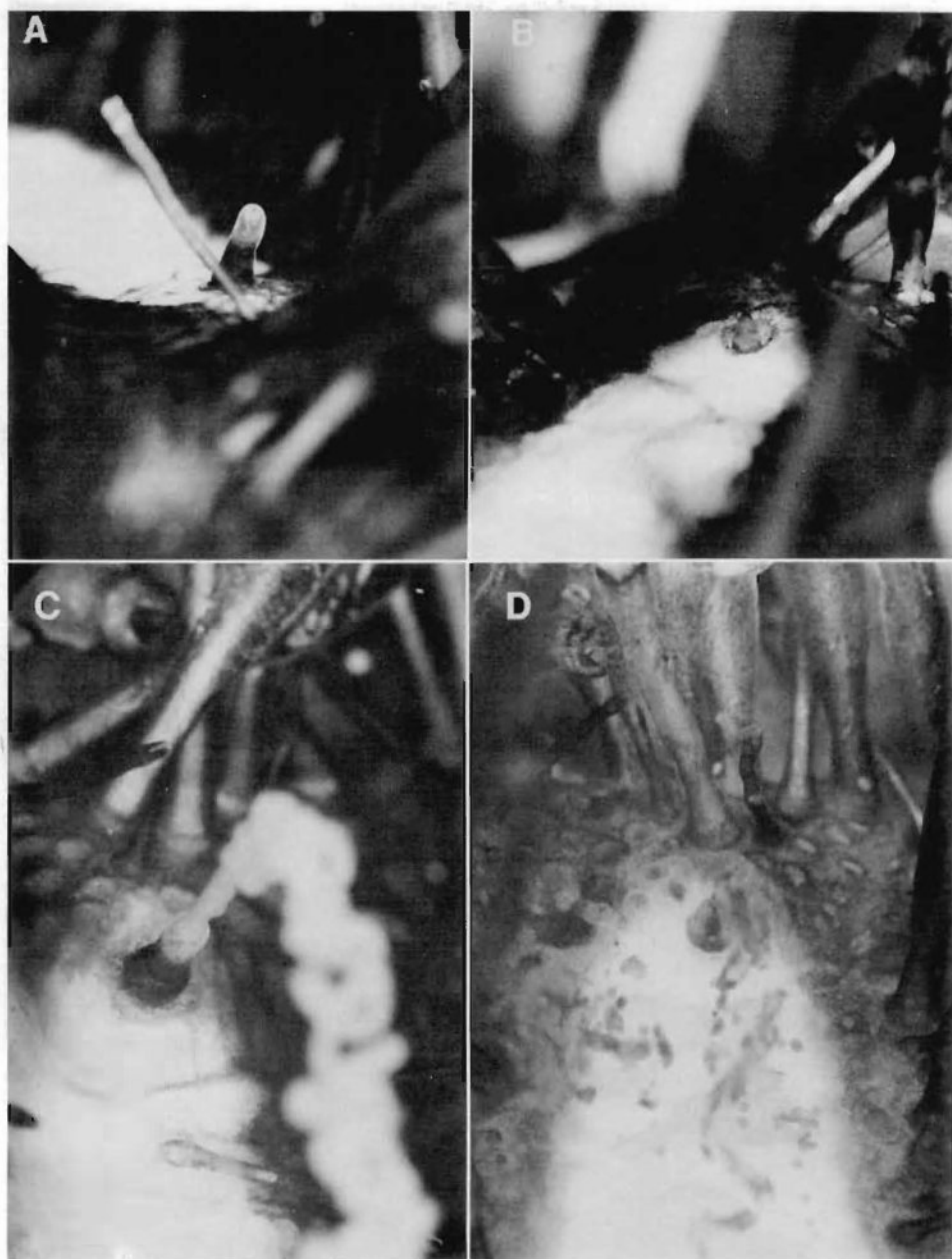


Figure 2. *C. floridanus*, genital papillae and spawning activity. A. male genital papilla, viewed from the side; B. female genital papilla, slightly sunken into genital pore; C. male in act of spawning. Note stream of sperm cells being ejected upwards, away from test and spines; D. female in act of spawning. Note loose stream of eggs, which fall onto test almost immediately.

sperm cells. A papilla from which the distal half has been removed is also capable of ejecting a stream of sperm cells, but only a few millimeters from the test. Within a few seconds after ejection, the sperm stream dissociates into a cloud which covers the area around the gonopore. When a papilla is completely re-

Table 1. Incidence of Papillae in Arbacioida

Genus and species	Dimorphic papillae present	Source
<i>Arbacia punctulata</i>	no	Harvey (1956); present study
<i>Arbacia lixula</i>	no	Swann (1954)
<i>Podocidaris sculpta</i>	no	present study
* <i>Tetrapygas niger</i>	no	present study
<i>Habrocidaris</i> spp.	no?	Agassiz & Clark (1908), Mortensen (1935)
<i>Pygmaeocidaris prionigera</i>	no?	"... no genital pores" Mortensen (1935)
<i>Dialithocidaris gemmifera</i>	no?	"... genital openings not found" Agassiz & Clark (1908)
<i>Arbaciella elegans</i>	no?	Mortensen (1935)
<i>Coelopleurus floridanus</i>	yes	present study

* In *Tetrapygas niger* male and female specimens have large gonopores with very short conical genital papillae. No sex differences were observed.

moved, no stream is produced, and the sperms are released as a cloud, which immediately floods the gonopore area and the test. No differences in spawning method were noted between the specimen injected immediately and the specimen held for 24 h.

Genital papillae in preserved specimens.—In cleaned, dried tests, the genital pores of males and females are indistinguishable. The dimorphism of the papillae is clearly evident in alcohol-preserved and in complete dried specimens. On the basis of presence or absence of tubular genital papillae, specimens were separated into "males" and "females." Confirmation of the sex of alcohol-preserved specimens was obtained by examination of teased samples of gonad. In all cases examined, only males were found to have tubular genital papillae.

First appearance of genital papillae.—Study of juvenile specimens collected on March 9, 1978 from 117 meters off St. Lucie Inlet, Fort Pierce, Florida, and maintained live in the laboratory revealed that genital pores first appear at a horizontal test diameter of approximately 12 mm. When a test diameter of 13–14 mm is attained, genital papillae of males are present and conspicuous.

Survey of other arbacioids.—A survey of the literature and an examination of specimens of representative genera within the Order Arbacioida was undertaken to determine the incidence of papillae in the group. Table 1 summarizes our findings.

Survey of some non-arbacioid deep-sea regular echinoids.—In the following species, no dimorphic genital papillae were found: *Plesiadiadema antillarum* (A. Agassiz), *Salenocidaris varispina* A. Agassiz, *Echinus affinis* Mortensen, *E. gracilis* A. Agassiz, *E. alexandri* Danielssen and Koren, *Allocentrotus fragilis* (Jackson).

At least, dimorphic papillae were not visible in alcohol-preserved specimens. It is possible that a study of live material might produce a different result.

DISCUSSION

The genital papillae in *C. floridanus* conform to the "Tripneustes" type described by Tahara et al. (1958). In their study of development of genital papillae in *Echinometra mathaei*, Tahara and Okada (1968) found that genital pore for-

mation took place in the size range 8×10 mm to 12×14 mm (short diameter \times long diameter); papilla formation occurred in the range 13×15 mm to 19×22 mm. In *C. floridanus* the male genital papillae appear soon after initial appearance of the genital pore, test diameter increasing by only 1 mm in the intervening time.

The striking difference of genital papillae in male and female *C. floridanus* raises the question of the functional significance of elongate papillae. As the sperm cells are released in a stream which easily adheres to solid substrates, it would be of value to the male to eject the sperms so that they do not fall onto the test and spines. This also affords the maximum opportunity for dispersal. In the female, the eggs are not sticky, and when they do land on test and spines, gentle movements of the appendages sweep the eggs away from the echinoid. Chia (1977) suggested that elongate papillae in irregular echinoids are required to ensure that gametes are liberated into the water above the substrate in which these echinoids are buried. He could offer no explanation for their occurrence in regular echinoids, except to note that they are known from few regular echinoids, perhaps because these echinoids generally live in areas of reasonably swift currents, and that gametes can be dispersed without difficulty. Nonetheless, a total of 17 shallow water regular echinoids is now known to possess dimorphic papillae, and undoubtedly other species have them. While the covering reaction in some species might require them to have elongate papillae to ensure that gametes are released clear of the fragments of shells and debris held on the urchins' upper surface (Chia, 1977), at least seven of the species he lists do not exhibit the covering reaction, but still have elongate papillae.

In an effort to determine whether regular echinoids living in relatively quiet habitats might require dimorphic papillae, we surveyed six typically deep-sea species, and found that none possess them. This survey included three species of *Echinus*, and we were surprised to obtain a negative result for this genus, as Swann (1954) had found dimorphic papillae in the shallow water *Echinus esculentus* Linnaeus. Mortensen (1935) noted that in the usually deep-sea echinothurioid urchins genital papillae occur often, but unfortunately in his species descriptions he does not call attention to any sexual dimorphism in this character. The preserved echinothurioids in the National Museum of Natural History, Smithsonian Institution, were not preserved well enough to allow comparison of relative sizes of the fragile genital papillae in this group.

We can offer no explanation for the occurrence of dimorphic genital papillae in only *C. floridanus* among the deep-sea forms studied, nor can we account for the fact that *Coelopleurus* is apparently the only arbacioid genus known to possess them.

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