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11. SIPUNCULA

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I. INTRODUCTION

Sipunculans are generally dioecious, although externally they show no signs of sexual dimorphism (see Section II below). The ovary or testis occurs at the base of the ventral retractor muscles as a narrow band of tissue from which oocytes or spermatocytes are released into the coelomic cavity at an early stage of development. Gametes complete their differentiation within the coelom where, in many sipunculans, developmental stages of oocytes or spermatocytes are present throughout much of the year (see Rice, Volume I of this series, for details).

The only exception to dioecism in the Sipuncula is found in *Golfingia minuta* from European and Scandinavian coastal waters (Section III). This species was first reported as hermaphroditic in 1910 by Paul, whose findings have been confirmed more recently by Åkesson (1958) and Gibbs (1975).

An unusual sex ratio in which females are dominant has been noted for several species of sipunculans (Claparède, 1863; Keferstein, 1863; Cole, 1952; Awati and Pradhan, 1936; Pilger, 1978, 1987). The significance of this biased sex ratio is uncertain, although in one species, *Themiste lageniformis*, it has been related to parthenogenetic development (Pilger, 1978, 1987; see also Rice and Pilger, Volume VI of this series, for review).

II. SEXUAL DIMORPHISM

The sexes of sipunculans are not distinguishable by external morphological features. However, in species in which the body wall is thin or transparent, sexes may be discerned by a distinctive pigmentation of gametes visible through the body wall.

For example, in *Phascolosoma perlucens* the females appear reddish due to the pigmentation of the coelomic oocytes, and the males, at seasons when the coelom has a high concentration of sperm, appear yellowish. The sex of an animal also may be readily revealed by microscopic examination of a sample of coelomic fluid in which developing sex cells are present.

Internally, the sexes can often be distinguished by a comparison of the general morphological features of the gonad. At its distal border the gonad is divided into numerous digitations. In males the digitations are finer and more numerous than in females.

III. HERMAPHRODITISM

The only known example of hermaphroditism occurring as a normal means of reproduction in sipunculans is found in the species *Golfingia minuta*. The first to describe hermaphroditism in this species was Paul (1910), who documented the presence of both sperm and oocytes in the body cavity of living material from Helgoland in the North Sea and preserved specimens from the coasts of Normandy and west Sweden. Later, his observations were confirmed by Åkesson (1958) on populations from Gullmar Fjord, west Sweden, and by Gibbs (1975) on material from the coast of Wemburg, southwest England. On the other hand, populations of *G. minuta* from the northwestern and northern Atlantic have been reported as dioecious (Gerould, 1913; Wesenberg-Lund, 1930, 1937; Cutler, 1973). Gerould (1913) proposed that, pending confirmation by further investigation, the dioecious form should be regarded as a separate species, *Golfingia diaphanes*. Åkesson (1958) and Gibbs (1975) have concurred with Gerould's (1913) proposal for the recognition of two morphologically similar species, one a monoecious form occurring near-shore in European and Scandinavian waters, and the other a dioecious form from deep waters of the western and northern Atlantic.

Histological studies of the hermaphroditic species *Golfingia minuta* have demonstrated that both male and female germ cells originate from the same gonad (Paul, 1910; Åkesson, 1958). Paul (1910) reported that clusters of readily identifiable oocytes occurred between groups of smaller cells with dense chromatin, which he presumed to be male sex cells. These smaller cells, which resembled coelomic spermatocytes, were observed at the distal border of the gonad in the position for release into the coelom. Åkesson (1958) observed further that the gonad was divided into specialized regions, the more median parts producing oocytes and the lateral parts producing both oocytes and spermatocytes separated by layers of connective tissue.

Paul (1910) as well as Åkesson (1958) supposed that animals might alternate the production of ova and sperm. Paul (1910) based his supposition on one individual in which large oocytes were present in the coelom, but only male cells in the gonad. Åkesson (1958) found oocytes and spermatocytes occurring together in the coelom of some animals and only oocytes in others. In those animals having gametes of both sexes, the oocytes were immature. During the course of the breeding season,

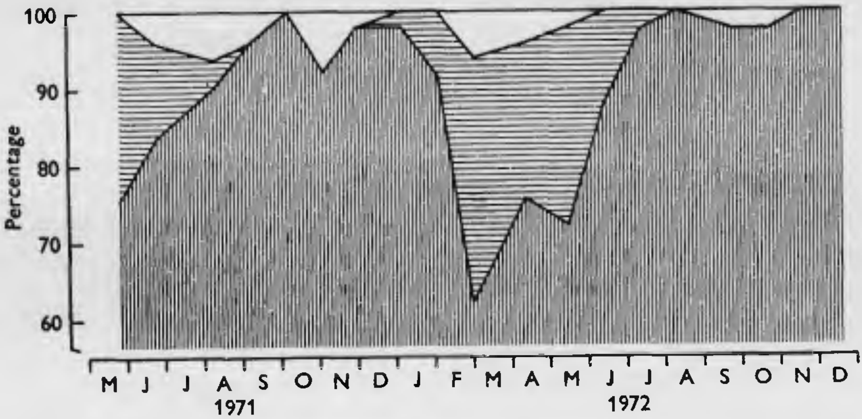

Fig. 1. Seasonal changes in percentages of males, females, and hermaphrodites in a population of *Golfingia minuta* from West Reef, Wembury, England. Vertical hatching indicates hermaphrodites, horizontal hatching apparent females, and clear space apparent males. (Reproduced from Gibbs, 1975 with permission of Cambridge University Press, New York.)

the percentage of animals with only oocytes increased, whereas the percentage with both oocytes and spermatocytes decreased. Thus, Åkesson (1958) presumed that spermatocytes required a shorter time than oocytes to mature and that an animal functioned first as a male and later as a female. In observations of animals after the spawning of eggs, the coelomic fluid revealed the presence of developing stages of oocytes but an absence of coelomic sperm. Moreover, attempts to demonstrate self-fertilization were unsuccessful; no development was observed in eggs spawned by isolated individuals. Åkesson (1958) concluded from these studies that mature or fully developed coelomic oocytes and sperm did not occur simultaneously and that the hermaphroditism in the population of *Golfingia minuta* from the west coast of Sweden could be classified as 'protandric'.

In contrast to Åkesson's (1958) findings on Scandinavian populations, Gibbs (1975) found that sperm and eggs developed simultaneously within the coelom in *Golfingia minuta* from the southwest coast of England. A seasonal study, covering a period of 20 months, revealed that the population was almost exclusively hermaphroditic during the spawning season (November—January), decreasing to about 70 per cent hermaphrodites in the post-spawning period (Fig. 1). As the hermaphrodites decreased, the percentage of females increased. Oocytes were present in most individuals throughout the year, whereas the percentage of animals with sperm decreased for a period of three to four months after spawning. Gibbs (1975) further demonstrated that during the breeding season not only were sperm and eggs present simultaneously in the coelomic cavity, but also they were spawned simultaneously. Although he did not observe the act of spawning, he found that spawnings from isolated individuals resulted in normally developing embryos and larvae. Thus, unlike Åkesson's (1958) findings for the population from Gullmar Fjord, Gibbs' (1975) data provided evidence for self-fertilization in the Wembury population. Gibbs (1975) found further that spawning of one member of a group of specimens did not induce spawning of the others. Thus he suggested that self-fertilization might be a common occurrence under natural conditions.

In addition to the well-documented example of hermaphroditism in *Golfingia minuta*, occasional reports have appeared in the literature of apparently anomalous hermaphroditic individuals among sipunculan populations that are otherwise dioecious. Two hermaphroditic specimens of *Physcosoma lanzarotae* (= *Phascolosoma granulatum*) were found among several hundred specimens that were examined by Harms (1921). Fisher (1952) remarked on two hermaphroditic specimens of *Themiste dyscritum*, one of which contained sperm in one nephridium and eggs in the other. Rice (unpublished data) found a single specimen of *Themiste lageniformis* from the central east coast of Florida with both eggs and sperm in the coelom. Further examination of hundreds of individuals from this same population revealed no other hermaphrodites.

IV. CONCLUSION

Nothing is known on sexual differentiation in the phylum.

As a general rule sexes are separate in the Sipuncula. The one known example of hermaphroditism occurs in populations of *Golfingia minuta* from the nearshore waters around Europe and Scandinavia, but not in morphologically identical populations from deeper waters of the northern and western Atlantic. Even within the hermaphroditic populations, there are differences in the manner in which hermaphroditism is expressed. Scandinavian populations are thought to be protandrous hermaphrodites, whereas European populations display simultaneous hermaphroditism and the capacity for self-fertilization. These differences present challenging problems concerning the use of hermaphroditism in taxonomic classification and its significance in systematic relationships. Fundamental questions for future research on hermaphroditism, as it occurs in this species, relate to an understanding of the adaptive value of the phenomenon, its evolution, and its relevance to geographical distribution.

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