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Reproduction in British zoanthids, and an unusual process in *Parazoanthus anguicomus*

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Specimens of three zoanthid species, *Epizoanthus couchii*, *Parazoanthus anguicomus* and *P. axinellae* were sectioned. All were gonochoric, with gametes developing during summer. Oocytes in *P. anguicomus* originate in a single-layered ribbon down the perfect septa, but the ribbon becomes moniliform as, at regular intervals, it folds laterally into lens-shaped nodes, packed with oocytes, doubling polyp fecundity.

Zoanthids are mainly tropical anthozoans but a few species (all suborder Macrocnemina) occur in cooler latitudes, five being present around the British Isles: *Epizoanthus couchii*, *E. papillosus (=incrustatus)*, *Isozoanthus sulcatus*, *Parazoanthus anguicomus* and *P. axinellae* (Manuel, 1988). Manuel reported 'no recent records' of *E. papillosus*, but it has since been found in both the North Sea (54–61°N, west of 2.5°E) and St George's Channel (~51.7°N 6.5°W: S. Jennings and J.R. Ellis, personal communications). Additionally, a sixth species, *E. arenaceus*, in the Adriatic found on the shell of live or pagurid-occupied *Aporrhais pespelicani*, is said to extend through the Mediterranean to Roscoff, Guernsey and Boulogne (Pax & Müller, 1962).

Colonies were examined for gametogenic activity. Anthozoans lack gonads but gametes develop in the septa; primordial germ cells arise in the endoderm along a region centrifugal to the filament (Ryland, 1997, for review of zoanthid reproduction). Oogonia proliferate. Developing oocytes bulge or migrate into the mesogloea but—in some species—remain in intimate contact with the endoderm cells through vitellogenic 'trophonemata', marked by the peripheral position of the germinal vesicle, fully described in actinians (Larkman & Carter, 1982; Larkman, 1983). Spermatogonia proliferate into subspherical cysts, which enlarge as spermatogenesis progresses, generally approximating to the size of the oocytes. These cysts appear also to have a trophonema, or homologous structure, which later functions as a gonopore or exit for mature sperm (Carlgren, 1923; Muirhead et al., 1986).

I have examined material belonging to *Epizoanthus couchii*, *Parazoanthus anguicomus* and *P. axinellae* by standard histological methods and light microscopy. Following desilicification in 20% HF for 24 h (to remove sand particles embedded in the mesogloea: see Ryland & Babcock, 1991), wax embedded polyps were sectioned at 7 μm and stained with Mallory's triple. All three species have gonochoric colonies (Ryland, 1997, for discussion) and follow a broadly similar breeding cycle; though, as often happens with zoanthids (Ryland, 1997), a number of colonies—even in summer—were non-reproductive. Using video image analysis, oocyte diameters were measured in those sections which both passed through the germinal vesicle (which lies in the median plane) and included the nucleolus, which provides a marker. Previtellogenic oocytes and small testis cysts were seen during May and June. In *P. axinellae* the youngest previtellogenic oocytes formed a double row separated by mesogloea. They therefore arise from both the endo- and exocoelic endoderm, not just the former as in *Isozoanthus giganteus* (Carlgren, 1923).

Oocytes had reached ~100 μm diameter by August–October, the sperm cysts a little more (Figure 1). Oocytes and cysts will have shrunk by 10–25% during processing (Ryland & Babcock, 1991; Ryland, 1997). Even so, if these oocytes were nearly mature they are smaller than recorded in other zoanthids (170–450 μm diameter: Ryland, 1997). Testis cysts in June contained spermatogonia, later samples spermatocytes; none contained mature spermatozoa. In *E. couchii* collected in Lough Hyne, the germinal vesicles were central (Figure 2B–F) and no trophonemata were observed. The three species appear to have annual reproductive cycles, with spawning not before late autumn, or even winter, when no collections could be made. All appear oviparous but it is now assumed that macrocnemic zoanthid embryos do not develop into distinctive Semper's larvae (Pax, 1937; Ryland et al., 2000). While the breeding cycles were thus not fully resolved, a curious phenomenon was observed in female *P. anguicomus* from St Kilda.

Oogonia develop in the distal part of the filament-bearing portion of the perfect septa. Later, the oocytes form a single-layered germinal ribbon down the mesogloea of the central third (as seen in cross section: Figure 2) of the septa. The septa appear slightly to extend centripetally to accommodate the line

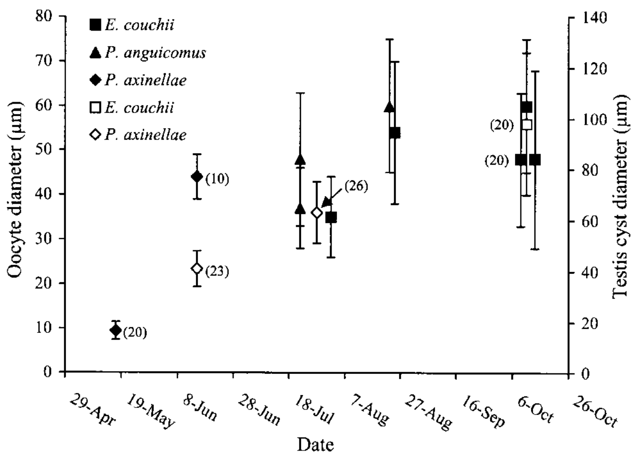

Figure 1. State of gametogenesis in three zoanthid species (*Epizoanthus couchii, Parazoanthus anguicomus, P. axinellae*) in samples collected between 1990 and 1995. Black symbols (left ordinate), oocyte diameters; open symbols (right ordinate), sperm cyst diameters. N=100 except where indicated in parentheses; values are means, error bars ±1SD. The October dates for some *E. couchii* samples may be misleading, since they had been kept in aquaria since September.

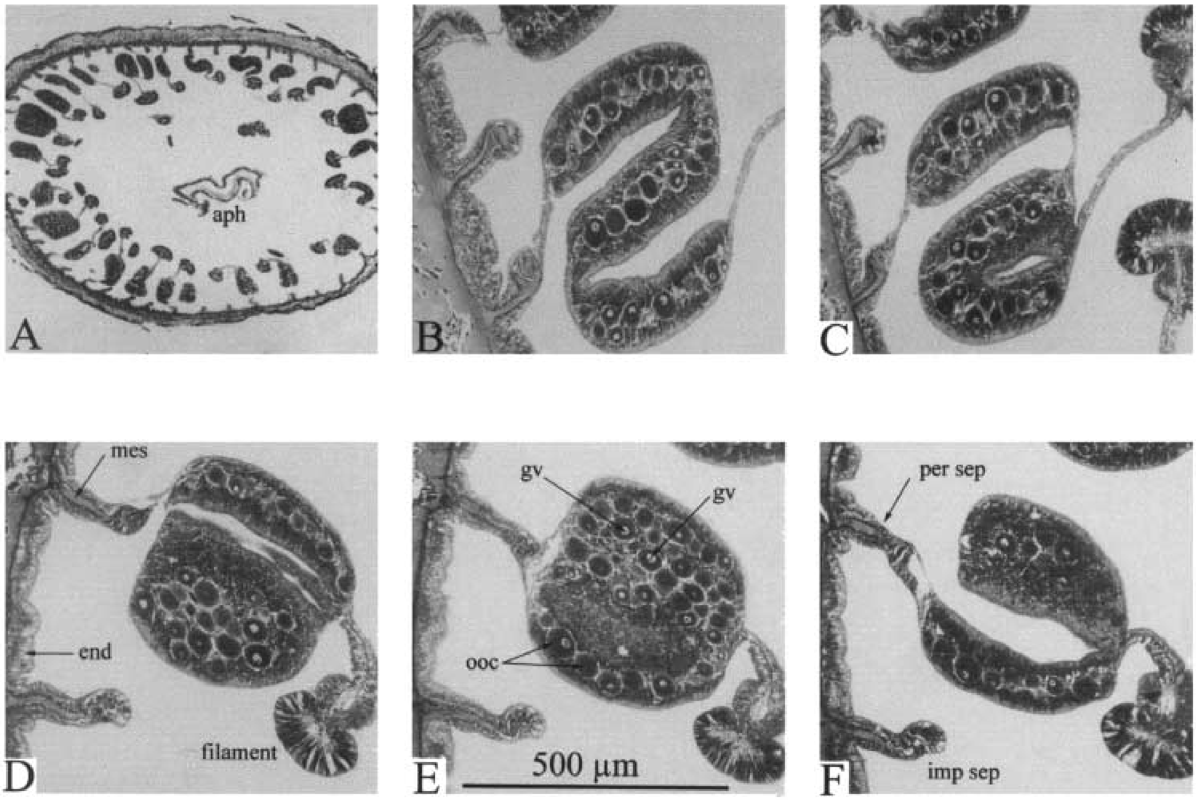

Figure 2. Oogenesis in *Parazoanthus anguicomus* showing formation of nodes in the gravid perfect septa. (A) TS whole zooid at the level of the basal extremity of the actinopharynx (centre). Note the extent to which the sectioned septa differ in appearance; column 6×4.5 mm diameter. (B) Germinal ribbon of septum folded but with oocytes in single series. (C) Same septum as in B, with two surfaces fusing. (D–F) Sections of the same septum 343, 406, and 434 μm from actinopharynx, with partial fusion in D and F, total fusion in E. end, endoderm; gv, germinal vesicle; imp sep, imperfect septum; ooc, oocyte; mes, mesogloea; per sep, perfect septum.

of enlarging oocytes. Then, the germinal ribbon develops a sequence of swollen nodes, where the septum folds locally in an S (in cross section: Figure 2B,C) and the layers fuse. Each node, with its triple layer of oocytes (Figure 2D,E), measures ~460 μm in the radial axis, ~435 μm across, but only ~150 μm vertically. Internodes, with a single layer of oocytes extending radially for ~470 μm, also extend vertically for ~150 μm. The whole ribbon resembles a string of beads, with 5–6 nodes per mm down its length. At any given point, a transverse section through the polyp displays a mixture of nodes, internodes and intermediate stages (Figure 2A). While the function of this remarkable process remains conjectural, an undoubted consequence is that the number of oocytes per septum can be doubled with no concomitant increase in radial length. The lens shape of the nodes ensures that inner oocytes remain close enough to the endoerm for oxygen to diffuse. Although the oocytes of all anthozoans develop in essentially the same way, I am not aware of any previous description of this phenomenon. Unfortunately, neither male *P. anguicomus* nor female *P. axinellae* were obtained at a comparable stage of development, but the same process evidently occurs in the latter (see figure 7 in Pax, 1937); in an immature male *P. axinellae* from Skomer, 29 July 1995, the septa were folded tightly but the parallel portions of the S, though contiguous, had not fused. Folding and fusion did not occur in *E. couchii*.

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