HOMOSYNDROME IN PLANKTONIC GRAPTOLITES: IMPLICATIONS FOR REPRODUCTIVE BIOLOGY, POPULATION ECOLOGY, AND MACROEVOLUTION

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Fusion (soft tissue merger and coordinated growth) of conspecific colonies originating from different larvae (i.e., homosyndrome) occurs rarely among a wide variety of benthic colonial organisms, including cnidarians, bryozoans and tunicates. Whether or not individuals fuse upon contact is determined by similarity in their histocompatibility complex. Among higher invertebrates fusion is genetically controlled and largely restricted to close kin (parent-offspring and sib-sib pairs).

Two large collections of three-dimensionally preserved graptolites, etched out of Upper Ordovician limestones, contain three homosyndrome colonies. In each a sicula (**B**) fused with the distal portion of a somewhat more mature but still small rhabdosome (**A**). In the two *Geniculograptus pygmaeus* homosyndromes, **B** passes through the lateral wall of **A**, and is enveloped by its periderm, including a secondary cortical layer that is continuous across the suture between **A** and **B**. The intertheal septa of one **A** colony (which ordinarily attach to the nema) are instead inserted on **B**. The **B** colony of the *Orthograptus quadrimucronatus* homosyndrome is a mature sicula and immature first theca that incorporated the nema of **A** in its structure as it developed.

Unlike previously reported homosyndromes, these graptolites were planktonic. This, the consistent age difference between **A** and **B** colonies, and fusion compatibility studies of other invertebrates together indicate that the **B** colonies were offspring of the **A** colony. The most likely scenario for their formation is that a mature larva, brooded within the central lumen of the parent colony, moved out along the colony's nema. There, rather than swimming off into the surrounding water as usual, the larva underwent metamorphosis within or near the open growing end of the parent colony. Subsequent growth of parent and offspring lead to fusion (see figure).

In one of the *G. pygmaeus* homosyndromes the nema of **A** terminates against **B** at the level of the fourth thecal pair. The nema in this species ordinarily projects about 0.9 mm beyond the growing edge of the colony. If **B** in this homosyndrome represents a daughter larva that metamorphosed at the growing tip of the nema, then the parent colony must have begun sexual reproduction when it comprised no more than five zooids. Large colonies of *G. pygmaeus* commonly contain 30 to 50 zooids. Thus, sexual reproduction in this species may have commenced at a quite early age. Early onset of sexual reproduction, and the resultant high population growth rates, is consistent with sedimentological evidence that suggests both species typically occurred as ephemeral, monospecific swarms within relatively shallow water.

Among modern colonial organisms these graptolites appear most similar ecologically to thaliacean tunicates. Both are planktonic, colonial organisms that exhibit low levels of zooid specialization. Both display a combination of depth and water mass specificity in their habitat preferences and frequently occur in swarms. Thus, it is likely that graptolites, like thaliaceans, were primarily opportunist suspension feeders, with high inherent population growth rates as an adaptation to tracking plankton blooms. The multiple macroevolutionary trends toward reduction in colony size and complexity, which pervade graptoloid macroevolution, accordingly become interpretable as a common response to selection for accelerated sexual reproduction and enhanced rate of population increase.