Sexual behaviour of the terrestrial fern *Platyzoma microphyllum* R.Br.: a morphogenetic look at the origins of heterospory

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Platyzoma produces 32 small spores and 16 larger spores in small and larger sporangia respectively. By contrast to the obligate, unisexual endosporic condition found in heterosporous lycopsids and water ferns, the photosynthetic gametophytes of *Platyzoma* are exosporic and partially bisexual. The small spores produce filamentous male gametophytes and the larger spores form spathulate individuals which are initially female but subsequently produce antheridia (Tryon 1964).

This pattern of sexuality, determined during sporogenesis, may be modified by subculturing the gametophytes. Fragments from both kinds of spores produce the following types of regenerant: (1) much branched filaments bearing antheridia alone; (2) spathulate proliferations bearing archegonia which subsequently develop antheridia either on the lobe margins or on separate filamentous branches; and (3) a mixture of filamentous antheridial and spathulate archegonial branches.

The frequencies of these secondary male and female outgrowths (now taken through 3 sets of subcultures) vary according to the nature of the fragment rather than the kind of spore from which the material is derived. Gametophyte dimorphism and unisexuality, determined during sporogenesis, has been overridden: the expression of the sex-determining process has been transferred from the sporophyte to the gametophyte stage in the life cycle. In all other extant heterosporous ferns, the unisexual condition is, as far as we are aware, fixed irrevocably during or before sporogenesis. Modifications to sexuality are only possible at the sporophyte level.

The sexual behaviour of both intact and subcultured gametophytes of *Platyzoma* closely resembles that in *Equisetum* (Duckett 1977) although the latter is unequivocally homosporous and sex is determined by environmental conditions *after* spore germination. The failure, in both cases, of male gametophytes to produce archegonia (except on adventitious outgrowths) appears to be related to the presence of a meristem totally committed to antheridium formation and very little sexually undifferentiated tissue. This situation suggests that a crucial step in the development of heterospory may have been an intimate association between gametophyte morphogenesis and sex organ formation. In this morphogenetic context, the notion that gametophyte dioecism, and the dimorphism resulting from it, preceded heterospory in evolution (Sussex 1966) appears particularly credible. When viewed in this way, the development of heterospory is readily reconciled with the concept of gradual evolution and there is no requirement for the presupposition that bisexuality is primitive (Duckett and Pang 1984).

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