HELGOLÄNDER MEERESUNTERSUCHUNGEN
Helgoländer Meeresunters. 40, 219–224 (1986)

Apomeiosis in *Acinetospora* (Phaeophyceae, Ectocarpales)

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ABSTRACT: *Acinetospora crinita* from the Mediterranean Sea has been studied in laboratory cultures. The plants formed monospores and unilocular sporangia. Both monospores and zoids from unilocular sporangia developed to new plants with the same habitus and chromosome number (average ca 47). This indicates that meiosis in unilocular sporangia fails, and that sexuality has been lost in the cultures studied. It is concluded that loss of sexuality is the cause of the great variability and establishment of distinct geographically isolated populations in the genus *Acinetospora*.

INTRODUCTION

The genus *Acinetospora* was introduced by Bornet (1891) for filamentous brown algae resembling *Ectocarpus*, referring to the presence of plurilocular reproductive structures with non-motile "acinetospores". Additional generic characters are multiple intercalary meristematic zones and short side branches named "crampons" in the French literature (Cardinal, 1964). In a study based on laboratory cultures Kornmann (1953) combined the two previously recognized taxa under the name *A. crinita* (Carmichael) Kornmann. The taxonomic status of this complex is at present unsatisfactory, and many questions are unresolved.

Reproductive structures in *Acinetospora* (normal plurilocular sporangia, plurilocular organs with "acinetospores", unilocular sporangia and monosporangia) may be present singly or in various combinations, or natural populations are entirely vegetative (Amsler, 1984). Morphological transitions between *Acinetospora* and *Giffordia* or *Feldmannia* in response to external conditions are discussed by Knoepffler-Péguy (1972, 1974).

Culture studies with *A. crinita* (Carmichael) Kornmann collected in List/Sylt (German Bight) and Southern Australia gave similar results: in both cases plurispores reestablished the *Acinetospora*-phase (Clayton 1974; Kornmann 1953). In addition Kornmann followed the development of zoids from unilocular sporangia in the material from List/Sylt. He obtained dwarf plants corresponding to two species of *Feldmannia* which he considered to represent haploid gametophytes. Both Kornmann's and Clayton's isolates lacked monosporangia, whereas plants from Helgoland cultured by Schmidt (1940) formed monosporangia as well as unilocular and plurilocular organs.

This short list indicates that the *Acinetospora* complex is quite heterogeneous and probably contains genetically different entities. Culture experiments on a new isolate from Naples, Italy now offer a possible explanation for this heterogeneity: the loss of

sexuality. This process allows the development and establishment of genetically isolated populations, thus creating the basis for great morphological and physiological variability.

MATERIALS AND METHODS

Fertile fragments of *Dictyopteris membranacea* were collected on 15 October, 1983 in Naples, Italy. Four weeks later, mats of *Acinetospora* with monospores and unilocular sporangia appeared in these raw cultures. One unilocular sporangium was isolated. Two germlings from this progeny were used to establish the clonal cultures on which all observations reported here are based.

Culture medium was natural North Sea water (German Bight, salinity 28 ‰) enriched after Provasoli (PES, Starr, 1978). Cultures were maintained in polystyrene petri dishes at various light and temperature regimes. White fluorescence light with photon fluence rates ranging from 3 to 24 $\mu E\ m^{-2}\ s^{-1}$ for daily periods of 14, 12 or 10 h were combined with temperatures of 20, 17, 12 and 8 °C.

Cytological observations and chromosome counts were made on specimens stained with acetocarmine and embedded in Euparal.

RESULTS

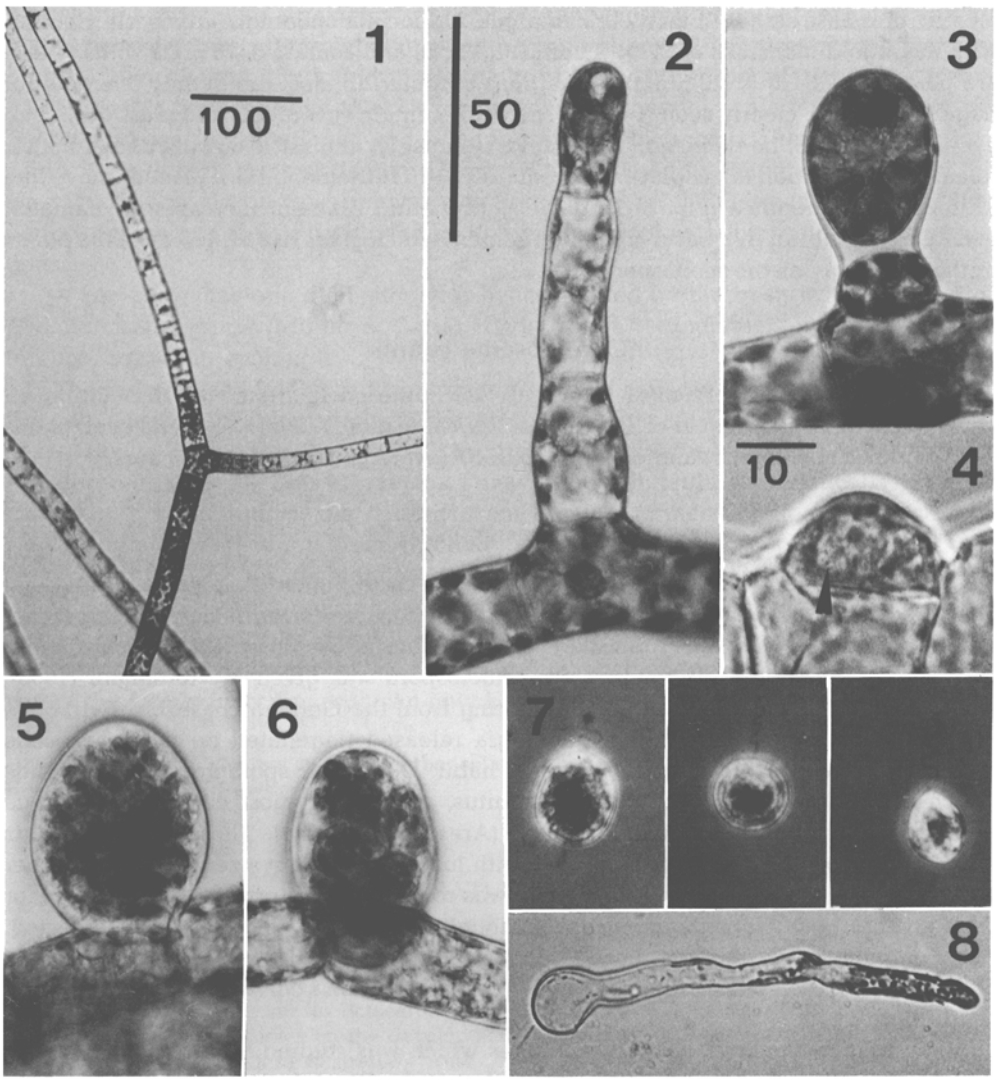
All combinations of culture conditions specified above including experiments with increased salinity (31 and 34 ‰) showed essentially similar results: typical morphological appearance of *Acinetospora* and formation of monospores and unilocular sporangia.

Morphology

Acinetospora in my cultures consists of uniseriate filaments with unlimited growth, localized in irregularly distributed meristematic zones (Fig. 1). Cell width is 25–30 µm, cell length varies from 12 µm in meristematic zones to 100 µm in fully differentiated cells. Filament cells contain up to 100 discoid to irregularly lobed plastids with 1 or 2 pyrenoids. Lateral branches of two types are inserted at right angles: new assimilatory filaments with unlimited growth, and few-celled rhizoid-like structures (crampons, Fig. 2). Lateral branching is often combined with a characteristic bend in the main filament. Pseudo-hairs with a basal meristem are formed in older cultures as lateral appendages inserted at right angles on the filaments (Fig. 1).

Monospores

Lateral outgrowths of filament cells often develop into sessile or stalked, slightly oblong reproductive bodies measuring on average 35 × 45 µm. A single nucleus is located in the centre of the cell which contains conspicuous strongly refractive material. These immobile monospores (Fig. 3) are discharged through an apical aperture. They germinate directly in uni- or bipolar manner to an inconspicuous creeping base, from which rise the typical *Acinetospora* filaments.



Figs 1–8. *Acinetospora crinita*. Fig. 1 Filament with intercalary growth zone and pseudo-hair with meristematic base. Fig. 2 Short side branch (crampon) on filament cell. Fig. 3 Mature monosporangium in the process of spore release. Fig. 4 Unilocular sporangium initial. Prophase with chromosome threads arranged asymmetrically (arrow). Acetocarmine staining. Fig. 5, 6 Unilocular sporangia, with individual zoids discernible (6). Fig. 7 Zoids from unilocular sporangia with front flagella. Fig. 8 Germling derived from zoid of unilocular sporangium, three days old. Scale bars in µm. Scale bar of Figure 2 valid for all figures except 1 and 4

Unilocular sporangia

Unilocular sporangia are formed concomitantly with monospores as sessile lateral appendages on filament cells. Occasionally, initials of unilocular sporangia showed asymmetrical arrangements of chromosome threads (Fig. 4), which are characteristic for

meiotic prophase stages in many brown algae. Unilocular sporangia are nearly globular with average dimensions of 37 × 43 µm (Figs 5, 6) and contain 8, 16 or 32 zoids. These are pear-shaped, 10 × 20 µm, or sometimes globular. In most cases, only one anterior flagellum can be clearly seen (Fig. 7). The zoids contain several discoid plastids, but an eye-spot could not be detected. They move sluggishly, and settle down within 1 h after release. Germination takes places immediately after settlement. Most plastids move into a tubular protuberance (Fig. 8), and the germinating filament increases in diameter, eventually resulting in a basal creeping filament which gives rise to *Acinetospora* plants in the same way as the monospores.

Chromosome counts

Prophase stages were most frequently encountered in filament cells cutting off lateral structures by unequal cell divisions. The same ploidy level was found in all plants with chromosome counts ranging from 36 to 57 (average 47) on 16 prophases.

DISCUSSION

The morphology of the plants studied here corresponds closely to the material described by Sauvageau (1931) under the name *Ectocarpus crinitus* Carmichael, except that Sauvageau's specimens from the French Mediterranean coast lacked monosporangia. The most detailed information on *Acinetospora* was given by Kornmann (1953). Culture experiments with material originating from the German coast (List/Sylt) gave the following results: plurilocular zoidangia released flagellated or motionless cells which developed to plants with the same habit. Unilocular sporangia released zoids which grew up to plants of different habitus, resembling most closely *Feldmannia padinae* (Buffham) Hamel and *F. lebelii* (Areschoug) Hamel. These small plantlets showed plurilocular reproductive organs with loculi of different size. This fact together with their origin from unilocular sporangia was considered by Kornmann as evidence for their potential gametophytic character, although no sexual reactions could be detected. The *Feldmannia*-stages reproduced themselves through plurispores. Re-establishment of the *Acinetospora*-phase occurred only once in Kornmann's cultures under unspecified conditions.

The Mediterranean isolate from Naples which was studied here clearly differs in respect of its life history from Kornmann's material, although the *Acinetospora* stages appear similar. The regular occurrence of unilocular sporangia suggested the possibility of obtaining gametophytes from meiospores, an approach which has been successful in many cases (Müller, 1981, 1984; Henry & Müller, 1983; Peters, 1984). Contrary to this expectation, unispores reestablished the *Acinetospora*-habitus in continuous succession. This observation suggests failure of meiosis in unilocular sporangia of *Acinetospora*, which is confirmed by identical chromosome numbers in successive generations. Failure to reduce chromosome numbers in spite of the typical spireme stages (bouquet configuration) of chromosomes in unilocular sporangium initials has also been reported in *Ectocarpus siliculosus* (Müller, 1967) and *Haplospora globosa* (Kuhlenkamp & Müller, 1985).

Acinetospora can be considered as the sporophyte phase of a formely complete

sexual life history with a gametophyte phase. Apomeiosis eliminated sexuality and led to a variety of genetically isolated non-sexual populations. This process can explain the high degree of variability found in geographically separated populations. The former gametophytes may continue to exist independently as microscopic forms like the two *Feldmannia* species mentioned above, and propagate by apomixis through their plurizoids. Evolutionary steps of this type have been discussed by Feldmann (1952). In this connection it would be most important to know, whether the German material indeed underwent meiosis as was concluded by Kornmann (1953) without cytological confirmation.

A similar apomeiotic life history has been reported for the fresh-water brown alga *Bodanella lauterborni* (Müller & Geller, 1978) where reproduction occurs exclusively through unilocular sporangia.

The isolates used for the culture studies described here did not show the polymorphism and morphological transitions to characters of the genera *Giffordia* and *Feldmannia* as reported by Knoepffler-Péguy (1972) in cultures of *Acinetospora* from Banyuls (French Mediterranean coast). This discrepancy may be attributable to genetically different materials in both studies: the cultures from Banyuls formed plurilocular, those from Naples unilocular sporangia in addition to monosporangia.

In any case, the results of the culture experiments reported here clearly show that *Acinetospora crinita* (Carmichael) Kornmann from Helgoland is genetically different from *A. crinita* (Carmichael) Sauvageau from the Mediterranean Sea. They also suggest that the *Acinetospora* complex as well as the taxonomical status of many lower taxa within the family Ectocarpaceae can only be resolved by rigorous culture studies.

Acknowledgement. The raw cultures for the isolates used in this study were kindly provided by Dr. E. Henry, St. John's, Newfoundland.

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