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The life history of *Acrochaete wittrockii* (Ulvellaceae, Chlorophyta)

P. Kornmann

Biologische Anstalt Helgoland (Meeresstation); D-27483 Helgoland, Federal Republic of Germany

ABSTRACT: *Acrochaete wittrockii* (Wille) Nielsen is a heteromorphic diplohaplont. The haplophase consists of isomorphic, dioecious filamentous epiphytes on brown algae. Several generations follow each other by triflagellate zoospores from spring to early summer. By late summer and throughout autumn, quadriflagellate zoopores are produced by the epiphytic thalli; they give rise to male and female gametophytes of a globular, pseudoparenchymatic appearance in culture. The gametophytes produce anisogamic biflagellate gametes which, after gametic union, develop into diploid unicellular sporophytes. After 6–7 days, the sporophyte produces triflagellate zoospores, repeating the life history when germinating on brown algal hosts. Alternatively, triflagellate zoospores which settle on the bottom of petri dishes, develop into unicellular, autonomous sporangial plants. Their triflagellate spores repeat the epiphytic stage on brown algal hosts, or the sporangial plant cycle on non-living substrate, respectively.

INTRODUCTION

The few facts that are known about the biology of the small chlorophytan epiphytic species *Acrochaete wittrockii* have been compiled by Burrows (1991). Triflagellate zoospores with two eyespots were first observed by Kylin (1938), and subsequently noted by several authors, while additional epiphytic thalli with quadriflagellate zoopores "and a possible sexual process involving biflagellate zoopores" (Burrows 1991, p. 115) were reported Kornmann (1959, mimeogr.). Nielsen (1983) mentioned the occurrence of all three types of zoospores in the same culture. The present paper summarizes investigations of *A. wittrockii* life history performed in 1957 and 1958 in List/Sylt, North Sea, which were intended to be continued after my return to Helgoland in 1959, but were left unpublished up to now.

MATERIAL AND METHODS

This study was facilitated by a most favourable circumstance: a mussel bank with the brown alga *Elachista fucicola* (Vell.) Aresch., and its year-round fertile epiphyte *Acrochaete wittrockii* was only 100 m apart from my laboratory near Ellenbogen, Sylt. The main results on the above life history had been revealed by preliminary culture experiments and observations by autumn 1957; they were substantiated by further investigations on natural material from June to December 1958.

Samples of freshly cut filamentous thalli of *E. fucicola* were transferred into petri dishes filled with sterile seawater or Erdschreiber seawater medium. Sometimes a sufficient number of zoospores for cultures was obtained on the next day, or within a short time. Cultures of *E. fucicola* or *Pilayella* spp. were permanently maintained for infection experiments. Cultures were kept at room conditions, since controlled culture cabinets were not available on Sylt in those days.

RESULTS AND DISCUSSION

Observations on field material

Epiphytic thalli of *Acrochaete wittrockii* collected on August 26, 1958, and photographed recently from a permanent slide (Fig. 1), were surprisingly free of other epiphytic species. This was possibly due to the strong tidal current passing across the mussel bank. As to the growth rate balance between *A. wittrockii* and its host, *Elachista fucicola*, one might expect that the epiphyte grows as fast as the host, which secures immediate colonization of the newly-formed host surface.

In 1958, 17 samples of field-collected material of *A. wittrockii* were examined. Thalli collected from June to July produced triflagellate zoopores. Epiphytic *A. wittrockii* cells with hairs were observed twice in nature (Fig. 1) and frequently in older cultures. A few quadriflagellate zoospores, among many triflagellate ones, were observed for the first

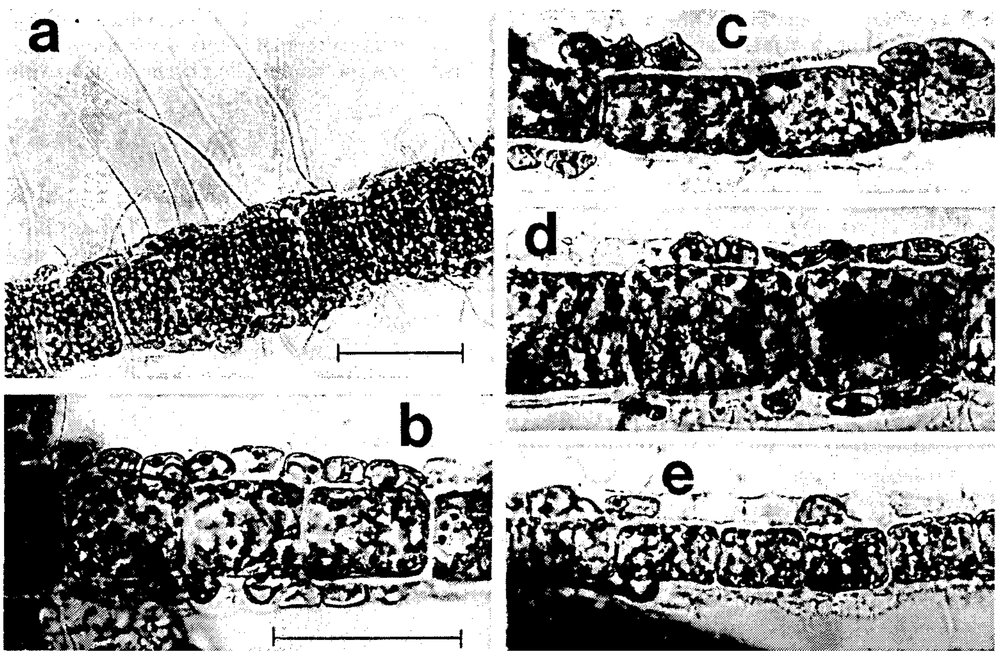

Fig. 1. *Acrochaete wittrockii* on *Elachista fucicola*. Vegetative epiphytes and fertile stages. Material collected at Ellenbogen, List, Sylt, North Sea, on 10 September 1957 (upper left; with hairs), and 26 August 1958 (other four pictures). Photographed in 1993, from permanent slides. a: filament with setae; b: vegetative filament; c and d: the release of spores is imminent; e: most of the sporangia are empty. Scales equal 50 µm

time in a sample collected on 1 August, 1958. Quadriflagellate zoospores had considerably increased in number in thalli tested on 26 August; they dominated the above triflagellate zoospores from September until mid November, in all collections. They decreased in number in a collection of 27 November, in relation to triflagellate zoospores, and became rare in a sample of 17 December.

Observations in cultured material

Development of triflagellate zoospores

In culture, triflagellate zoospores developed differently with regard to the substrate. On host filaments of *Elachista fucicola* or *Pilayella* spp. filamentous thalli, as in field material, were the result. On the bottom of petri dishes, however, they grew into unicellular sporangial plants (Fig. 2), which became fertile within a few days and again released triflagellate zoospores. The latter developmental pathway was formerly described and illustrated by Kylin (1938; see his Fig. 4, B–H).

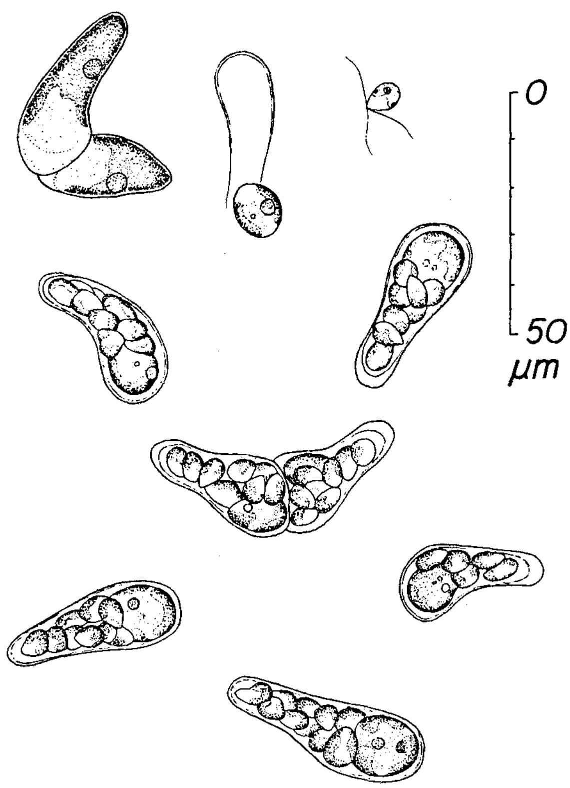

Fig. 2. *Acrochaete wittrockii*. Unicellular sporangial plants on bottom of Petri dish, originating from and recycling by triflagellate zoospores. These are not obligatory parts of the life history

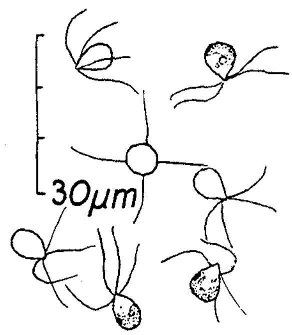

Fig. 3. *Acrochaete wittrockii.* Quadriflagellate zoospores from epiphytic thalli collected on 26 August 1973 at Helgoland

Development of quadriflagellate zoospores and formation of gametophytes with biflagellate gametes

Quadriflagellate zoospores (Fig. 3) germinating on the bottom of petri dishes developed into filamentous germlings, which soon formed globular plantlets. By the age of one month, the plantlets had turned into fertile cell masses. Plantlets with pale, bottle-like gametangia were full of many small swarmers; others with darker-coloured gametangia contained fewer and larger swarmers (Fig. 4). It was easy to induce the release of swarmers by increasing the light intensity. Upon release, the small swarmers often surrounded the releasing thalli like dense clouds.

The swarmers were biflagellate. After many unsuccessful trials, gametic union of

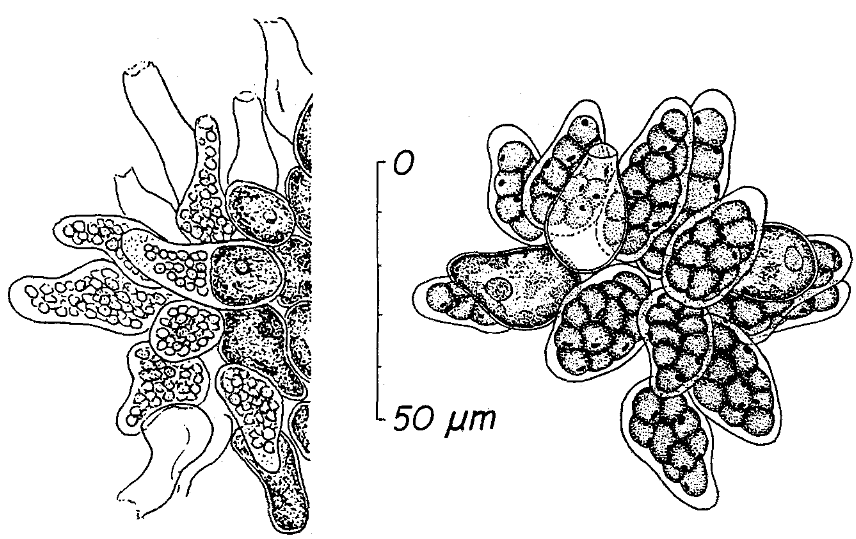

Fig. 4. *Acrochaete wittrockii.* Male (left) and female (right) gametophytes. The somewhat senescent male gametophyte originated from a culture started from field material collected on 26 July, 1973 at Helgoland

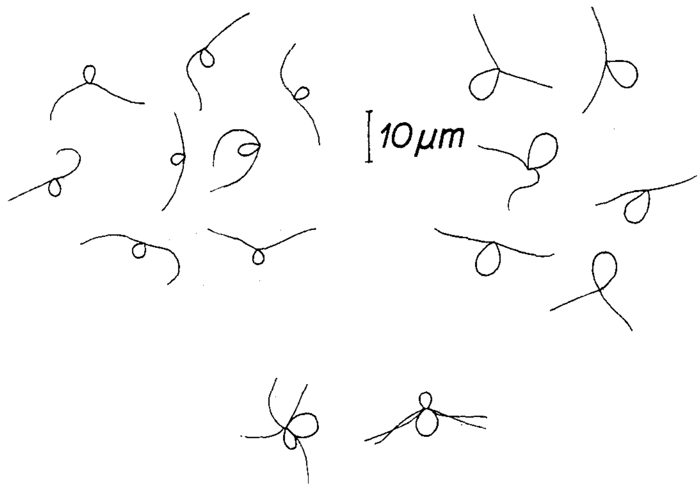

Fig. 5. *Acrochaete wittrockii.* Gametes and copulants

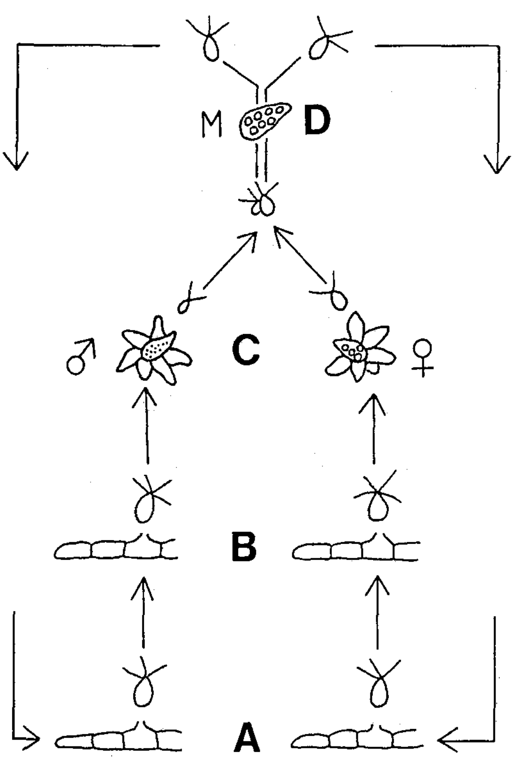

Fig. 6. *Acrochaete wittrockii.* Developmental scheme: A, B: epiphytic stages propagate in summer by zoospores and precede gametophytic phases (C), which are formed in late summer and autumn. D: sporophyte. M = presumed meiosis. See text for further explanation

anisogamic gametes was observed for the first time on 3 April 1958, in a culture started in autumn 1957 (Fig. 5). In the gametic pairs, the male gametes were 3.5–4.5 μm, the female 5–7.5 μm long. They were thus somewhat larger than the biflagellate swarmers observed by Nielsen (1983) in her cultures. Besides gametes, larger swarmers of unknown origin with 2, 3 or 4 flagellae were observed in older cultures of the convoluted cell masses. Numerous culture experiments starting from quadriflagellate zoospores were conducted in 1958; they often resulted in the formation of gametophytes, and permitted observation of gametic union. Zygotes were isolated and grew into unicellular sporophytes. Their triflagellate zoospores recycled the life history via isomorphic epiphytic thalli.

CONCLUSION

The haplontic phase of *Acrochaete wittrockii* consists of isomorphic, dioecious, asexually propagating epiphytic phases (Fig. 6A, B) preceding the gametophytes (Fig. 6C) which are only known from cultures. Up to midsummer, several generations of epiphytic thalli (Fig. 6A) follow each other by triflagellate zoospores. Spores not settled on living host plants develop into unicellular sporangia with triflagellated spores (Fig. 2). This additional way of reproduction is only known from cultures and omitted in the scheme illustrated in Figure 6. By the end of July, and in autumn, quadriflagellated zoospores are produced by the epiphytic thalli (Fig. 6B); these give rise to male and female gametophytes (Fig. 6C). The anisogamous biflagellate gametes develop into unicellular sporophytes (Fig. 6D). Their triflagellated zoospores lead back to the epiphytic stage (Fig. 6A).

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