

Morphogenesis of the marine spirotrichous ciliate, *Trachelostyla pediculiformis* (Cohn, 1866) Borrór, 1972 (Ciliophora, Stichotrichia), with consideration of its phylogenetic position

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Abstract

The cortical development during binary fission of the relatively poorly known stichotrich ciliate, *Trachelostyla pediculiformis* (Cohn, 1866) Borrór, 1972, found in coastal waters near Qingdao, China, was investigated using the protargol impregnation method. The morphogenetic process reveals some pretty unusual characteristics, which do not follow the *Oxytricha*-pattern: (1) the parental oral apparatus is entirely renewed from an oral primordium formed de novo in the proter; (2) in the proter, the parental undulating membranes are not involved in the formation of the newly formed oral primordium; both undulating membrane-anlagen (UM-anlage) and frontoventral-transverse cirral anlagen (FVT-anlagen) develop from the oral primordium in the proter; (3) the dorsal kineties (DK) are generated in a unique way, that is, in both dividers, two separate groups of DK-anlagen develop in the right- and left-most DK, generate all the DK and evolve to replace the old structures; (4) three caudal cirri are formed at the posterior ends of three right-most dorsal kinety anlagen; (5) eight frontal, five ventral and five transverse cirri are derived from six streaks, namely, the UM-anlage and 5 FVT-anlagen; the cirri are segregated from these anlagen in the pattern 1:3:3:3:4:4 (from left to right) in the *Oxytricha* mode. Based on both SSrRNA gene sequencing and morphogenetic data, the systematic positions of the genus *Trachelostyla* Borrór, 1972 as well as the family Trachelostylidae Small and Lynn, 1985 are briefly analyzed. The results indicate that this genus/family could be a highly isolated lineage and might be ancestral to other well-known oxytrichids.

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Introduction

The marine stichotrich, *Trachelostyla pediculiformis*, was recently redescribed and neotypified by Gong et al. (2006). Its ciliature shows generally similar features to

that of oxytrichids, e.g. 18 frontoventral-transverse (FVT) cirri, constantly 11 cirri in the frontal area and two ventral ones together with five enlarged transverse cirri, three inconspicuous caudal cirri and six dorsal kineties (DK) with prominent cilia. To the authors' knowledge, the morphogenesis of no species of this genus (or even of any member of the whole family) has been fully investigated (Berger 1999; Foissner 1996), hence, morphogenetic characteristics important for

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assessing its phylogenetic position are still unknown (Gong et al. 2006; Kool 1970).

Recently, we were fortunate to find a population of *T. pediculiformis* in a sandy beach near Qingdao, north China, and successfully kept a pure culture in the laboratory, which allowed a detailed observation of its morphogenesis. In this paper, the details of its morphogenesis and a comparison with some closely related taxa are presented. In addition, we present data about the systematic position of these poorly known ciliates.

Materials and methods

Morphogenetic studies

The population of *T. pediculiformis* used for morphogenetic studies was collected from the top 10 cm of sandy littoral sediments of Jiaozhou Bay near Qingdao (36°08'N; 120°43'E), China. Specimens were maintained for several weeks in the laboratory at room temperature. Squeezed wheat grains were added to the medium as a food source to enrich bacteria. Cells in division were selected and then impregnated using the protargol method (Wilbert 1975). Drawings were made with the help of a camera lucida at 1250× magnification. For clarity, parental cirri are shown in diagrams of morphogenetic stages only by outline, whereas new ones are shaded black.

Terminology and systematics are mainly according to Gong et al. (2006), Berger (1999) and Lynn and Small (2002).

Phylogenetic analyses

The SSrRNA gene sequences of species used in tree construction in the present work are available in GenBank/EMBL. The alignment was edited by a computer-assisted procedure, Clustal W (Version 1.80) (Thompson et al. 1994), and refined by considering the conservation of both primary and secondary structures (Elwood et al. 1985). The computer program, MrBayes v3.0b4 (Huelsenbeck and Ronquist 2001) was used for Bayesian tree construction with 100,000 cycles for the Markov chain Monte Carlo algorithm under the GTR model of substitution (Lanave et al. 1984; Rodriguez et al. 1990; Tavare 1986) and considering a gamma-shaped distribution of the rates of substitution among sites. The PHYLIP package, version 3.57c (Felsenstein 1995) was used to calculate the sequence similarity and evolutionary distances between pairs of nucleotide sequences using the Kimura (1980) two-parameter model. Distance-matrix trees were then constructed using the Fitch and Margoliash (1967) least-squares

(LS) method and the neighbor-joining (NJ) method (Saitou and Nei 1987).

Results

Divisional morphogenesis of *T. pediculiformis* (Figs 1–5)

Oral primordia and cirral streaks

Morphogenesis commences apokinetally with the appearance of two fields of sparsely distributed basal bodies (oral primordia) about 1/3 and 2/3 along the anterior/posterior axis (Figs 1C and 4A). Evidently, no old structures (cirri, UM) are involved in the formation of these two anlagen and thus all the old cirri and fibres nearby remain intact.

These two oral fields (primordia) develop with further proliferation of basal bodies. Development in both dividers is very similar and takes place at about the same pace. Cirral streaks develop slightly later at the right of the primordia (Figs 1D and 4B).

In the following stage, the new membranelles begin to organize at the anterior ends of primordia in both proter and opisthe. Two groups of undulating membranelle-anlagen (UM-anlagen, Figs 1F and 4E) and frontoventral-transverse cirral anlagen (FVT-anlagen) consisting of five streaks develop to the right of the oral primordia (Figs 1F and 4E).

A middle divider is shown in Figs 1H and 4F. The old structures, e.g., UM and proximal end of adoral zone begin to be resorbed. The new membranelles and UM-anlage differentiate posteriad in each divider. A single cirrus develops from the anterior end of the UM-anlage, later becoming the leftmost frontal cirrus. Commencing at the anterior ends of FVT streaks and proceeding posteriad, cirri form at the ends of the FVT-anlagen in both dividing parts (Fig. 1H). Commonly, more than 18 cirral segments were identified in this stage, but the “surplus” ones were later resorbed (Figs 1H and 4F).

Subsequently, the anterior end of the newly built adoral zone of membranelles bends to the right and the differentiation of membranelles is almost completed forming the new oral structures for both the opisthe and proter. The segregation of cirri from FVT-anlagen is complete (Figs 1J and 4H).

Thus, the UM-anlage and the FVT-anlagen I–V generate 1:3:3:3:4:4 cirri, respectively, in both in the proter and the opisthe, as most oxytrichids. That is, in each daughter cell: 3 anterior-most frontal cirri originate (one each) from the UM-anlage and cirral anlagen I and II; 4 frontoventral cirri develop from anlagen II (1), III (1), V (2); one buccal cirrus comes from anlage I; 3 “ventral cirri” are differentiated from anlagen III (1) and IV (2); while 2 pre-transverse ventral

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