The remarkable story of the "Viecherl" *Balanion planctonicum* (Ciliophora, Prostomatida)*

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Abstract: This article reviews how, within less than 20 years, an unknown freshwater ciliate became a widely known and intensely investigated species, once it had been properly described and named.

Key words: Brush, ecological niche, Lake Constance, model ciliate, *Pseudobalanion*, ultrastructure.

Introduction

The word "Viecherl" stands, in the dialect of Austria, for a friendly little, wee beast. The small ciliate, the story of which I am going to tell, initially had no other name. In August 1986, I carried it from Konstanz to Salzburg in mercury-chloride fixed water samples. At this time I had just started to study planktonic ciliates within the newly founded Special Collaborative Program "Cycling of Matter in Lake Constance" (Deutsche Forschungsgemeinschaft, SFB 248). I was looking forward very much to this job, considering that for Lake Constance, with its long tradition of limnological research (LAUTERBORN 1925) virtually no information existed on the heterotrophic protists. There was just one major problem: my knowledge of plankton ciliates also was virtually non-existent. In this situation, I consulted my former teacher, the protozoologist Karl Gottlieb GRELL, and this is what he told me: "The best thing you can do is go to Salzburg and see Wilhelm FOISSNER".

When I introduced myself, FOISSNER immediately invited me to come to his lab. On this first visit (Fig. 1) I was impressed threefold: by Wilhelm FOISSNERS immense and endless working capacity, by his generosity to share both his knowledge and his laboratory facilities with me, but most of all by his unlimited enthusiasm for the diversity and beauty of the ciliated protists. When I left two weeks later, I had gained a lot. I had acquired some basic knowledge of the most common plankton ciliates, I had learned the technique of protargol staining, and I knew that the "Viecherl" in my samples from Lake Constance indeed belonged to a new, hitherto undescribed species. Live observation, however, was still lacking, and since I had not attempted to isolate and cultivate the "Viecherl", I could not bring live specimens to Salzburg. So FOISSNER came to Konstanz in April 1988, at the season of the phytoplankton spring bloom, when the small ciliate was likely to be abundant in the epilimnion of the lake. At this occasion, I admired FOISSNERS ability to pick a single small, rapidly moving ciliate from a field sample, observe it under high magnification and make an exact, informative drawing (Fig. 2). After this task was completed, the "Viecherl" got its professional species description and scientific name: *Pseudobalanion planctonicum* FOISSNER, OLEKSIV & MÜLLER, 1990.

Taxonomy

The genus *Pseudobalanion* was established since the new ciliate largely resembled the genus *Balanion* as defined by SMALL & LYNN (1985), except for one important detail: FOISSNER et al. (1990) did not find a "brush" (adoral organelles) located inside the circle of oral dikinetids, which is a characteristic feature of *Balanion* according to SMALL & LYNN (1985). Only when laboratory cultures of the Lake Constance population were available, BARDELE (1992, 1999) could show, by scanning (Fig. 3) and transmission electron microscopy, the existence of a very small brush consisting of just two dikinetids, with one kinetosome ciliated and the other one barren (Fig. 4). Based on this evidence, the species was transferred to the genus *Balanion* by FOISSNER et al. (1994). The proper name of the "Viecherl" therefore is now: *Balanion planctonicum* (FOISSNER, OLEKSIV & MÜLLER, 1990) FOISSNER, BERGER & KOHMANN, 1994.

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* Dedicated to Professor Dr. Wilhelm FOISSNER on the occasion of his 60th birthday.

Fig 1: Professor Foissner at his microscope, in August 1986. Foto: H. Müller.

It is the only freshwater species described in this genus. The type species *B. comatum* Wulff, 1919 is marine; according to the redescription by Jakobsen & Montagnes (1999) it also possesses a very small brush, which is only recognizable by electron microscopy. A second marine species, *B. masanensis*, with a more prominent brush, was recently described by Kim et al. (2007).

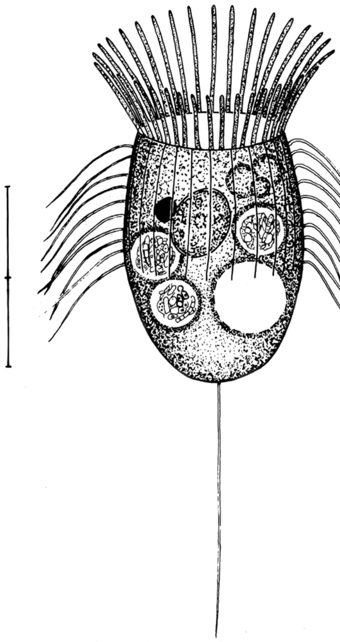

Fig 2: Morphology of *Balanion planctonicum,* from life. Scale bar: 20 µm. From Foissner et al. (1990).

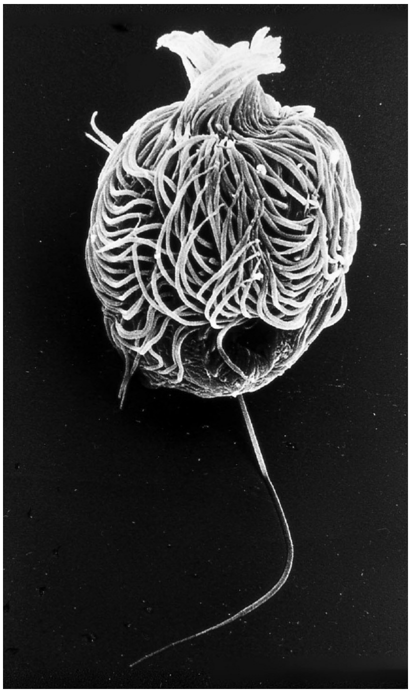

Fig 3: Scanning micrograph of *Balanion planctonicum*; from Bardele (1999).

Field studies

Within the following years, ecological research revealed that the "Viecherl" was anything but a rare ciliate. In Lake Constance, *Balanion planctonicum* was the most abundant ciliate species in the pelagic zone during a 3-years field study (Müller 1989, 1991, Müller et al. 1991). Annual averages accounted for 30 %, 35 % and 43 % of total ciliate numbers in the uppermost 20 m of the water column in 1987, 1988 and 1989, respectively. Its population dynamics showed a recurrent seasonal pattern, with highest cell densities (up to 60 cells ml^{-1}) in early spring (Fig. 5). Worldwide, *B. planctonicum* was found in several freshwater lakes in the temperate zone of both hemispheres (cf. Foissner et al. 1994, 1999). Reports exist from the Austrian lakes Mondsee (Salbrechter & Arndt 1994), Piburger See (Sommaruga & Psenner 1993, 1995), Neusiedler See (Schönberger 1994), Traunsee, Attersee and Hallstätter See (Sonntag et al. 2002, 2006), from the German lakes Schöhsee (Jürgens et al. 1994), Belauer See (Zimmermann 1994, 1996) and Heiligensee (Skibbe 1998), from Lake Pavin, France (Carrias et al. 2001), from Lago Maggiore and Lago di Garda, Italy, (Callieri & Heinimaa 1997), from Saginaw Bay, Lake Huron, USA (Lavrentyev et al. 1995), Lago Morenito, Patagonia Argentina, (Modenutti & Perez 2001), Lago Riñihue and Lago Pirehueico, South Chile, (Wölfl 1996), Lago Parque Ródó, Uruguay (Sommaruga 1993), and Lake Taupo, New Zealand (James et al. 1995).

Most of these studies report high abundances of *B. planctonicum* during phytoplankton blooms, apparently a characteristic response of this ciliate. Such periods can be used to determine ecological parameters in natural populations. Macek et al. (1996) studied growth of plankton ciliates in oligo-mesotrophic Piburger See (Tyrol, Austria) in prescreened natural water samples (i.e. with crustacean predators removed), which were incubated in transparent glass bottles for 2–3 d under in situ conditions. For *B. planctonicum*, these experiments yielded a mean growth rate of 0.65 ± 0.32 d^{-1} at ambient temperatures from 9.5–16.5 °C. In a parallel study, Simek et al. (1996) determined uptake rates of fluorescently labelled prey (bacteria, picocyanobacteria and nanoflagellates) by the same ciliate community. The results of these authors clearly identified *B. planctonicum* as a raptorial feeder mainly feeding on algae >2 µm, while uptake of picoplankton was negligible. In Lake Pavin, France, Carrias et al. (2001) studied growth of planktonic protists during an early phytoplankton spring bloom, using a similar approach as Macek et al. (1996). For *B. planctonicum*, they report a mean in situ growth rate of 0.49 ± 0.16 d^{-1} at ambient temperatures from 3.8–8.8 °C. In mesotrophic Schöhsee (northern

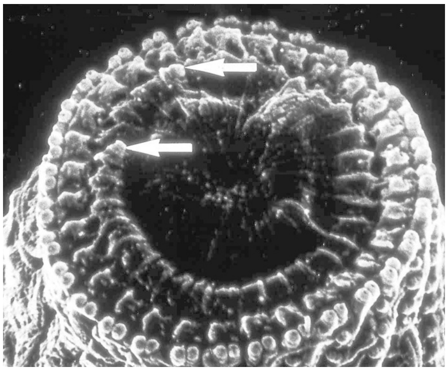

Fig 4: Scanning micrograph of an artificially deciliated cell of *Balanion planctonicum*. Arrows point to the stubs of the two adoral cilia of the "brush"; from BARDELE (1999).

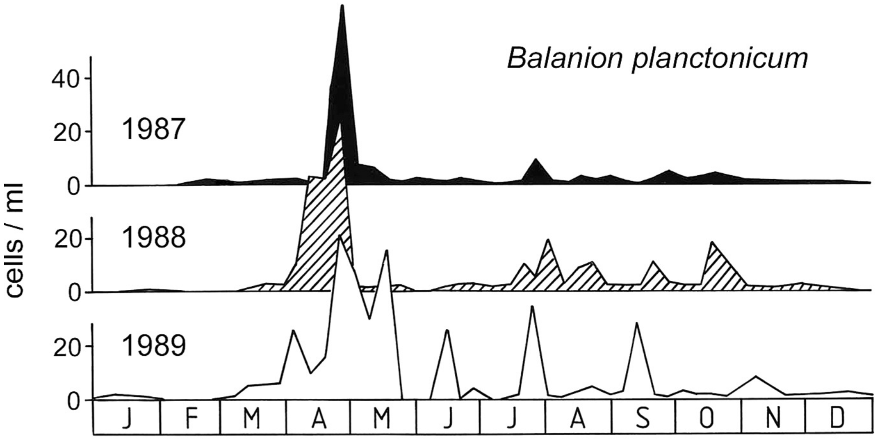

Fig 5: Seasonal pattern of abundance of *Balanion planctonicum* in Lake Constance over three annual cycles, given as mean cell concentrations in the uppermost 8 m of the water column. Modified from MÜLLER et al. (1991).

Germany) JÜRGENS et al. (1994) studied the impact of crustacean predators on components of the microbial food web (bacteria, flagellates and ciliates) in enclosure experiments. These mesocosms were manipulated so that either *Daphnia* or copepods were dominating, or that metazooplankton was virtually absent. Results revealed distinct differences in top-down control of copepods and daphnids on a population of *B. planctonicum*, which was only moderately affected by copepod predation, but drastically reduced in the presence of *Daphnia*.

Laboratory studies

Balanion planctonicum was first isolated from surface waters of Lake Constance and cultured on a diet of small cryptomonads in April 1989 (MÜLLER 1991). Later on, two more strains were established: from Lake Constance in 1993, and from Mondsee, Austria, in 1999 (MÜLLER & SCHLEGEL 1999; WEISSE et al. 2001). Maintenance of cultures (Fig. 6) over many years proved to be relatively easy, though labour-intensive, since these voraciously feeding and rapidly multiplying ciliates had to be transferred weekly to fresh medium and food.

These strains served to determine ecophysiological parameters under controlled conditions. MÜLLER (1991) studied the temperature response of *B. planctonicum* by measuring intrinsic growth rates at non-limiting food concentrations (>35 × 10^3 cells ml^{-1}) of a small cryptomonad, namely SAG strain # 26.80, provided by the Culture Collection of Algae in Göttingen, Germany, at temperatures from 5.5–21.5 °C. For the interval 5.5–18 °C there was a linear relationship between intrinsic growth rate and temperature, with highest and lowest rates equivalent to generation times of 11 h and 36 h, respectively. Surprisingly, temperatures >21 °C were lethal. MÜLLER & SCHLEGEL (1999) investigated the numerical response (growth rate versus food concentration) and functional response (ingestion rate versus food concentration) of *B. planctonicum* over the range from 10^2 to 10^5 cryptomonad cells ml^{-1} at a constant temperature of 15 °C. As evident from Figure 7, the ciliates were able to grow at very low food concentrations and they did not stop feeding when virtually all food was depleted, (that is the threshold for zero growth was very low and there was no significant threshold for zero ingestion). WEISSE et al. (2001) found in principle the same responses in the *B. planctonicum* strain from Mondsee, including the unusual sensitivity to moderately high temperatures (lethal >22 °C). These authors conducted similar growth experiments with *Urotricha furcata*, a prostome ciliate frequently observed during

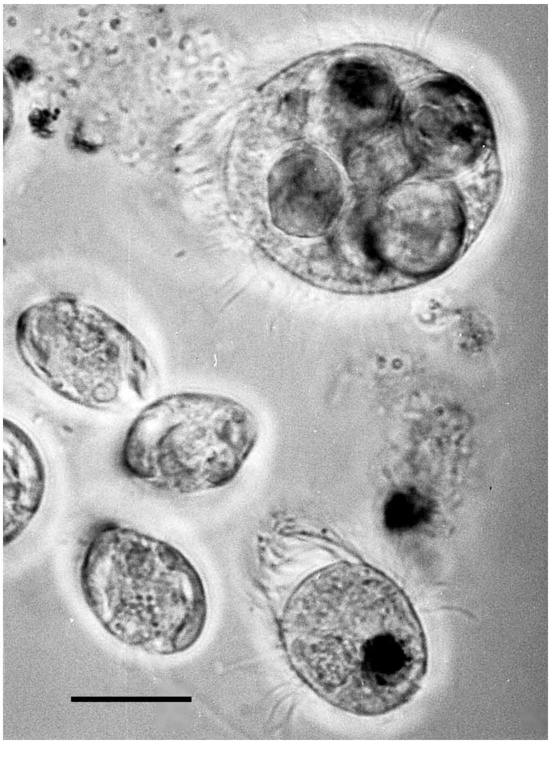

Fig. 6: Size variability of *Balanion planctonicum:* an extremely large ciliate with a small one, and food algae (cryptomonads) for comparison. The large ciliate contains ingested algal cells. Cultured material fixed with $HgCl_2$. Bar = 10 µm. Modified from MÜLLER (1991).

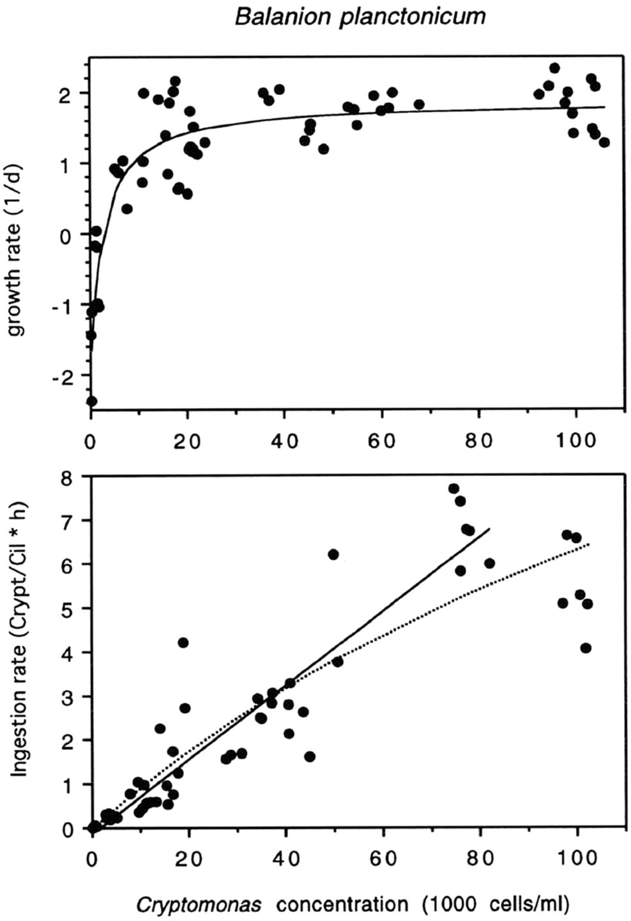

Fig. 7: Numerical response (top) and functional response (bottom) of *Balanion planctonicum* to cryptomonad food at 15 °C. From MÜLLER & SCHLEGEL (1999).

phytoplankton spring blooms together with *Balanion planctonicum* (MÜLLER et al. 1991; SOMMARUGA & PSENNER 1993) with the aim to characterize the ecological niches of these sympatric species, which obviously are competitors for the same prey. According to these data, *B. planctonicum* is the superior competitor at low to moderate water temperatures, due to its higher growth rates under these conditions. *Urotricha furcata*, in contrast, which tolerates a range from 8–27 °C, will benefit from water temperatures which are lethal for *Balanion planctonicum*.

WEISSE & FRAHM (2002) investigated predator-prey relationships of *B. planctonicum* and *Urotricha furcata* with the rotifers *Keratella cochlearis* and *K. quadrata*. These experiments revealed species-specific mutual interactions between the ciliates and their rotifer predators, with *Balanion planctonicum* being highly susceptible to grazing by *K. quadrata*, but unaffected by *K. cochlearis*, whereas *Urotricha furcata* was moderately affected by both rotifer species.

MÜLLER & SCHLEGEL (1999) studied selective feeding of *Balanion planctonicum* in comparison to the oligotrich *Rimostrombidium lacustris*, using cryptomonads and the small centric diatom *Stephanodiscus hantzschii* as prey. The food value of the latter apparently was low, since neither of the ciliates could be cultivated on a sole diet of *S. hantzschii*. When offered a mixed diet, food selectivity depended on feeding mode. The filter feeding *Rimostrombidium lacustris* ingested both prey items, though with a clear preference of the cryptomonads. *Balanion planctonicum*, due to its raptorial feeding mode, was able to select almost exclusively for the cryptomonads.

Use as a model organism

The availability of easily to maintain laboratory cultures rendered *Balanion planctonicum* useful to serve as a model ciliate. ROSENSTOCK & SIMON (2001) studied the microbial cycling of dissolved free amino acids and protein in mesotrophic Lake Constance by examining their release by phytoplankton and various heterotrophic organisms. On the basis of experiments with *B. planctonicum*, which served as a representative of algivorous ciliates, they estimated that ciliates contributed 18 % on average, but up to 50 % of the amino acid release in the microplankton fraction (1–140 µm) which included phytoplankton, protozoans and rotifers.

KENTER et al. (1996) investigated feeding of *B. planctonicum* on cryptomonads by flow cytometry. Starved ciliate cultures and algal cultures were separately stained in vivo with the fluorochrome 4,6-diamino-2-phenylindole (DAPI, final concentration 1 µg ml^{-1}) and then combined. This sample was analyzed by flow cytometry at 2–3 min intervals over 1h. The intensity of blue and red signals caused by DAPI-stained nuclei and photosynthetic pigments was used to identify different particles: cryptomonads (strong red, weak blue), *Balanion* starved (strong blue), *Balanion* with ingested cryptomonads (strong red, strong blue) and *Balanion* which had recently digested/egested their algal food (strong blue and faint red signals). Ingestion rates deducted from these data were 1.6–1.7 algal cells ciliate^{-1} h^{-1}. On average 20–30 min elapsed between ingestion and egestion. LINDSTRÖM et al. (2002) developed a fast and simple protocol for accurate quantification of small freshwater ciliates by flow cytometry, using several nucleic acid stains. Cultures of *B. planctonicum* and *Urotricha farcta* were used as model organisms. Flow cytometry in combination with the nucleid acid stain TO-PRO-1 allowed unequivocal discrimination in cases of overlapping size distribution between the target population and other particles.

BOËCHAT & ADRIAN (2006) evaluated population growth of the rotifer *Keratella quadrata* fed with four protists growing on either an algal or a bacterial diet. Feeding on the algivorous ciliates *Balanion planctonicum* and *Urotricha farcta* resulted in enhanced population growth rates and high egg production by *Keratella quadrata*, whereas feeding on the bacterivores *Cyclidium* sp. and *Chilomonas paramaecium* supported only moderate egg production, but no population growth. BOËCHAT & ADRIAN (2005) and BOËCHAT et al. (2007) analyzed the biochemical composition of *Balanion planctonicum* and *Urotricha farcta* in comparison to their algal food *Cryptomonas phaseolus*. The higher concentrations of some fatty acids, amino acids and sterols found in the ciliates suggest that these are capable to efficiently accumulate and transform these organic compounds. According to the authors, the high cellular concentrations in *Balanion planctonicum* and *Urotricha farcta* of fatty acids and amino acids make them a "prey of upgraded quality" for metazooplankton predators.

While this latter statement may be sad news for the fans of the „Viecherl“, I am confident that it will continue to thrive in freshwater lakes and surprise with further interesting studies in the literature.

Conclusions

This is the story how, within less than 20 years, an unknown and undescribed „Viecherl“ became the widely known and intensely investigated species *Balanion planctonicum*. Obviously, a large number of scientists have contributed to this development, but the first credit goes to Wilhelm FOISSNER. Who would have wanted to study the population dynamics of an undefined freshwater ciliate in the size class 10 to 20 µm? Who would have been interested to isolate and cultivate it, to study its ultrastructure, to define its ecological niche and to use it as a model organism? Obviously, it all started with the professional species description and differential diagnosis published by FOISSNER et al. (1990). The take-home message of the present article, therefore, is identical with the advice I received many years ago: „The best thing you can do is go to Salzburg and see Wilhelm FOISSNER.„

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