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FROM THE ARCHIVES

Robert Lauterborn (1869—1952) and his *Paulinella chromatophora*

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In 1895, in his second, short contribution about protozoa (*Protozoenstudien II.*), Robert Lauterborn, then at the Zoology Department of the University of Heidelberg, described a novel organism (nov. gen. et nov. spec.) which he named *Paulinella chromatophora*. He must have been very exited about his discovery which he made on Christmas Eve 1894, since he clearly recognized the importance of his observations for symbiosis research and biology, in general. And although his *Paulinella* featured only occasionally in scientific publications during the next 100 years, it now appears to be taking center stage in discussions about the endosymbiotic origin of plastids (some recent reviews in this field that mention *Paulinella* include Bhattacharya et al. 2003; Delwiche 1999; Keeling 2004; McFadden 2001). Who was the discoverer, what characterized his time, socio-economically and scientifically, and finally what did Lauterborn discover about *Paulinella chromatophora* that made him write (in the first sentence of his publication, p. 36; translated from German) "Among the many protozoa that populate the extensive diatom mats of the *Altrhein* near *Neuhofen* (*about 6 km south of Ludwigshafen on Rhine, Germany*) during the cold season, I found, on December 24 last year, a new rhizopod, that in more than one respect can demand to be ranked among the most interesting representatives of its division in freshwater." ?

In the second half of the 19th century the socio-economic situation in Germany (i.e. urbanization, industrialization and the rise of an urban proletariat) led to pronounced and lasting environmental changes (e.g. degradation of soil and natural waters, epidemic human diseases, plant diseases, decline of forests). The Janus face of prosperity were difficulties of supply, lack of hygiene in settlements, and various kinds of diseases. Gradually, questions were raised which today are known as problems of waste disposal. Careful observers such as Ferdinand Cohn (1828—1898) had early recognized the problems and with the methods then available initiated simple environmental monitoring systems (Cohn 1853; Kolkwitz and Marsson 1908; Mez 1898). Jörg Lange, Günther Leps (1934—2000; bibliography in Jahn 2001), Thomas Potthast and Astrid E. Schwarz have described the circumstances of the "Wilhelminian" epoch and the early period of the "republic of Weimar" and their influence on the development of science in Germany (Lange 1990, 1994; Leps 1998; Potthast 2001; Schwarz 2001).

The economic boom came after the German French war and finally led to overheating during the *Gründerzeit* ("founder period"; 1871—1873) and in consequence to many bankruptcies. During such phases of prosperity interest is initially focused on the requirements for economic growth: production and delivery of food and raw materials. Concomitantly, the older "humus

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theory" of Albrecht Thaer (1752—1828; Fördergesellschaft Albrecht Daniel Thaer e.V. Möglin 2004) was superseded by the modern concept of the mineral nutrition of plants by Justus von Liebig (1803—1873). The victory of this concept and the first successes of the production-oriented view diverted attention from the problem of waste disposal that usually seems to be of less importance to the public. However, the above-mentioned problems leading to increasing waste landfills and the omnipresent wastewater, made it the more important to try to better understand the decomposition process (today known as recycling). Wastewater treatment using artificial wetlands and trickling filters was introduced during this time (see Kolkwitz 1922).

The scientific study of aquatic ecosystems had just been initiated. François Alphonse Forel (1841—1912) in Geneva had introduced the term limnology (the science of inland waters; Forel 1882); many new ideas came from the aspiring ecological research in the U.S.A. and with the book of Stephen Alfred Forbes (1844—1930) entitled "The Lake as a Microcosm" (Forbes 1887), the programmatic catchword of the further development was born (Schwarz 2001).

After the First World War, August Thienemann (1882—1960) became the champion first of German and soon also of international limnology (Thienemann 1956, 1959). He came from fisheries science and had studied the chironomid midges (a group of Diptera comprising about 10,000 species), an important component of the aquatic food web. The chironomid larvae develop in the profundal zone at the bottom of water bodies. There, they form characteristic communities depending on oxygen and nutrient levels. Based on the presence or absence of certain benthic chironomid larvae, Thienemann introduced his first system of lake classification, which he soon extended in collaboration with his swedish colleage Einar Naumann (1891—1934) by adding the appropriate types of phytoplankton. This resulted in the typification of complex biotopes by their biocoenoses: the primary producers, the consumers, the secondary consumers and the decomposers. The inland lakes became a test-case for ecological thinking. The further elaboration of lake classification through studies of nutrient cycles appeared predetermined.

August Thienemann originated from Thuringia and had studied in Greifswald, Innsbruck, and also in Heidelberg. To Heidelberg he was drawn by the legendary reputation of the zoologist and protistologist Otto Bütschli (1848—1920). However, Bütschli fell ill during the time when Thienemann was there and could not give lectures. This brought Thienemann closer to the junior lecturer (*Privatdozent*) Robert Lauterborn (1869—1952). The meeting between the 21-year old zoology student from Thuringia and the 34-year old lecturer from the Palatinate was fateful. August Thienemann in his research has always dealt with both the fruitful suggestions as well as the pitfalls that "holism" held for biology. He placed his life under the motto *Schau auf zu den Sternen, hab acht auf die Gassen* ("look up to the stars, pay attention to the alleys"). This phrase was introduced by the lower-saxon poet and writer Wilhelm Raabe (1831—1910), whom Thienemann valued highly (see Thienemann 1949). Raabe had dealt with environmental issues in his lesser known novel *Pfisters Mühle* (Raabe 1970 [originally 1884]), not casually or in a general way but specifically using records from a publicly discussed lawsuit that dealt with water pollution about which the pharmaceutical chemist Heinrich Beckurts (1855—1929) from Brunswick had informed him (see also Beckurts 1882; Denkler 1980; Popp 1959; Thienemann 1925a,b; Vaupel 1985). The endurance of the constant tension between the duty to study the details and the danger of losing context with the large picture, was what Thienemann saw realized in an exemplary way in Lauterborn's life and research. Lauterborn became Thienemann's hero, whom he felt obliged during his whole life. But then who was Robert Lauterborn?

Robert Lauterborn's rather unspectacular life has been described in several obituaries and biographies, most recently by Lange (2001; using preparatory work done by Jürgen Schwoerbel [1930—2002]). Born in Ludwigshafen (October 23, 1869) as the son of a local publisher, Robert went to school in Ludwigshafen and Mannheim where he received his school-leaving degree (*Abitur*) from the *Realgymnasium* in 1889. He studied zoology and botany in Heidelberg (1889—1898) where he graduated as "Dr. phil. nat." in 1897 and received his *Habilitation* (entrance examination for university lecturers) 2 years later. Originating from a non-wealthy middle-class background, he was familiar with austere living conditions and had to seek additional income during his years as a student and non-tenured lecturer (*Privatdozent*). Income was generated by consulting. The young man changed need to virtue and obtained valuable knowledge and know-how in the transitional field between theoretical and applied hydrobiology/limnology. His knowledge about organismal biology (animals, plants and microorganisms) was phenomenal. One could envisage that he, who was a professor of forest zoology between 1918 and 1935, first in Karlsruhe, then in Freiburg (Fig. 1), could as well have succeeded as a professor of limnology or botany. This extremely unpretentious and modest man, unfortunately was not spared blows of destiny. His mother died when he was 2 years old, his aunt Pauline became his stepmother when his father married his mother's sister. Robert remained single and lived together with his two sisters, Ella and Paula. Paula died in 1939, and Ella was killed during an air-raid on Freiburg in 1945 during which his house and library were also destroyed. A little earlier he lost his collection at the forestry institute through world-war II bombings; his father's (later his brother's) lithographic facility in Ludwigshafen which housed the back files of Robert Lauterborn's publications was similarly lost in 1943. Nevertheless, Lauterborn did not resign and resumed his scientific work (Fig. 2) during the seven remaining post-war years of his life (he died on September 11, 1952 in Freiburg).

Of the many research areas in which Lauterborn excelled, we will deal here mainly with protistology and its relation to limnology and the biology of wastewater. Lauterborn's Ph.D. thesis described the peculiar mitotic features of dinoflagellates, using *Ceratium hirundinella* as an example. Of even greater significance is his work entitled *Untersuchungen über den Bau, Kernteilung und Bewegung der Diatomeen* ("Studies on the morphology, nuclear division and motility of diatoms"; Lauterborn 1893, 1896). The observations were described and illustrated with extraordinary detail and clarity, especially those relating to the mitotic spindles and centrosomes. And although the latter observations were sometimes questioned (by eminent scientists such as F.E. Fritsch and

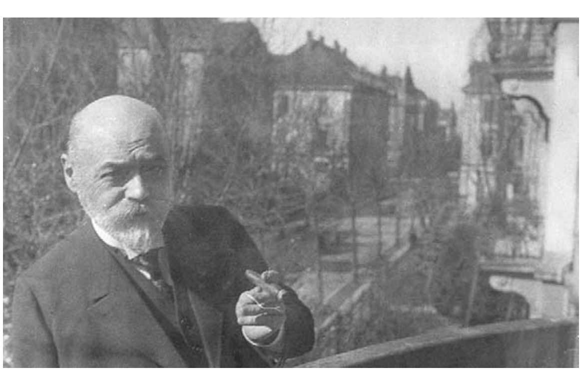

Figure 1. Robert Lauterborn in Freiburg (1928).

Figure 2. Robert Lauterborn (together with H. Utermöhl, right) at the 10th International Limnological Congress in Switzerland, 1948.

E.B. Wilson), they have been verified in every detail almost 100 years later by Jeremy Pickett-Heaps and collaborators (Pickett-Heaps 1983; Pickett-Heaps et al. 1984). Robert Lauterborn's contributions to phycology were honored by a special exhibition during the 1st European Phycological Congress held in Cologne in 1996.

Lauterborn set the standards of his time with his studies about saprobial life and with his contribution to the development of the "saprobial system" championed by Richard Kolkwitz (1873—1956) und Maximilian Marsson (1845—1909). When preparing this article, we noticed an interesting terminological detail: In the German language, a differentiation is made between the different processes occurring during the decay of dead organisms, i.e. whether they take place in the presence or absence of oxygen and are caused by bacteria or fungi, respectively (*Fäulnis*, *Verrottung*, *Verwesung*; similar expressions exist in the French language). In colloquial English, however, this distinction is not made (only the old terms rot or rottenness exist) and one has to rely on foreign words such as decomposition, putrefaction or saprobic. Perhaps, it is not by accident that the "saprobial system" originated in Germany and continental Europe. Sometimes, it appears, that in the prevailing unilingual scientific language the fine level of expression inherent in colloquial languages has been lost. Now familiar processes such as aerobiosis, anaerobiosis, respiration, and fermentation were hotly debated during Lauterborn's student days or were just being solved. Biochemistry had just started as a scientific discipline and many phenomena needed attention. Only in 1866 had Heinrich Anton de Bary

(1831—1888) introduced the terms mycotrophic and saprotrophic, and Louis Pasteur (1822—1895) described fermentation as a *conséquence de la vie sans air* ("a consequence of life without oxygen").

In connection with these debates, which also touched on human pathology, epidemiology, fisheries, water supply, urban hygiene, etc., Robert Lauterborn intensively studied saprobes, organism living immediately above or in rotten sludge (*Faulschlamm*; Lauterborn 1901). According to studies of Swedish limnologists and soil scientists who had intensively analyzed the formation of lake sediments, there exist different zones in the sediment, for which the Swedish language has its own terms (Gyttja, Äfja, etc.; summarized by Naumann 1931), which were in part incorporated into the earlier period of limnology. The chemical composition of these zones is as typical as is the biological phenomena taking place in the different zones as can be demonstrated today using microprobes. During Lauterborn's times, however, intuition and careful observation were necessary, to characterize such habitats. Lauterborn also knew much about ethnobiology and profited from the experience of inland fishermen and water authorities. His pioneering studies about the saprobial organisms (Lauterborn 1901) made him well-known, and he was officially asked to participate in the large-scale analysis of pollution of the river Rhine (Lauterborn 1905, 1907, 1908a—c, 1909a,b, 1910, 1911). With this long-term monitoring program, the imperial public health office in Berlin reacted to complaints about the increasing pollution of the river Rhine. This pollution was not only caused by the ever increasing discharge of industrial and domestic effluents into the river, but in part was also related to non-consideration of the risks and side-effects of the large-scale physical regulation of the river performed by Johann Gottfried Tulla (1770—1828), an engineer from Baden, which began in 1817 in the upper Rhine valley. During his studies on the Rhine, Lauterborn collaborated with his colleagues Kolkwitz, Marsson and Schaudinn, who came over from Berlin. Over a dozen years later, Lauterborn summarized his knowledge about the inhabitants of the saprobes again (Lauterborn 1915).

Trained in the study of protists and familiar with the practice of limnology and the study of wastewater, Lauterborn made remarkable discoveries (Fig. 3). One of those was the description of the only presently known amoeba with blue-green intracellular symbionts, the filose, testate amoeba

Figure 3. "The public and the naturalist" (R. Lauterborn, 1934).

Paulinella chromatophora, the generic name given by him to honor his stepmother (and aunt), although he made no mention of this in the published paper. The work about *Paulinella* (Lauterborn 1895) was published before Lauterborn received his doctorate. The nestor of British phycology, Felix Eugen Fritsch (1879—1954), who intimately knew the phycological literature of continental Europe wrote about the discovery of *Paulinella*: "The classical instance of the occurrence of a blue-green endophyte within a colorless organism is furnished by the Rhizopod *Paulinella*. . .. which, since its first discovery, has been found in many parts of the world. The blue-green symbiont . . . here takes the form of two large sausage-shaped structures (*Synechococcus*?), which remain alive for some hours when squeezed out of the host. During the division of *Paulinella*, one of the two Cyanellae passes through the narrow aperture of the test into the new daughter-individual and, like that left in the parent, soon divides into two. Little success has hitherto attended the efforts to cultivate these endophytes outside their host, which is probably due to their profound adaptation to the environment so that suitable conditions of existence are not readily reproduced. That the Cyanellae play an important part in the nutrition of the hosts is shown by the capacity of the latter to lead an autotrophic existence and by the absence of holozoic nutrition in *Paulinella*" (Fritsch 1945, p. 876). John W.G. Lund, who studied under Fritsch, added: "The cyanelles differ from the symbiotic Cyanophytes . . . in that they cannot be grown outside the host organism. They can be considered to be symbionts which in the course of time have become an integral part of the host cell, that is organelles just as chloroplasts are organelles. Paulinella can then be looked upon as a photosynthetic animal" (Canter-Lund and Lund 1995, pp 252—253). But what did Lauterborn himself find out?

As already indicated, Lauterborn found the material on which his description was based in 1894 in an old riverbed of the river Rhine near *Neuhof*en in what was then the Bavarian Rhine-Palatinate. The town *Neuhofen* is located in the floodplain of the upper Rhine valley southeast of Ludwigshafen between *Limburgerhof* and *Altrip* on the left bank of today's river. Later Lauterborn found *Paulinella* also in the Black Forest. His observations were soon confirmed by Eugène Penard (1855—1954) from Geneva, who observed the morphology and arrangement of the silica scales of the test in apical view (Penard 1905). Surprisingly, Penard described and illustrated only a single endosymbiont per amoeba, and presumably regarded the second one described by Lauterborn as only a pre-division situation. Finally, Hoogenraad who studied cell division and formation of the new test in *Paulinella* in detail (Hoogenraad 1927) clarified this aspect and wrote (translated from Dutch) "Thus we can state with certainty that *Paulinella* reproduces by bipartition as do *Euglypha* species and their relatives. During this process one of the daughter individuals receives a new test built up from reserve scales secreted into the protoplasm by the mother individual before division. One of the chromatophores moves into the daughter individual, while the other stays inside the test of the mother individual. The normal situation of two chromatophores per cell is brought about by transverse division of each of the two chromatophores" (Hoogenraad and De Groot 1927, p. 12). Cell division of *Paulinella chromatophora* is thus similar to that of *Euglypha alveolata*, as illustrated by Grell (1956, p. 81; 1973, p. 124) based on observations by Schewiakoff.

Paulinella also attracted the interest of prominent phycologists among them Lothar Geitler (1927, 1959) and Adolf Pascher (1929a, b) who, during these studies, introduced the terms cyanelle (Pascher 1929b) and syncyanosis (Pascher 1914; see Geitler 1959). Lackey (1936) and Lederberg (1952) discussed whether the endosymbionts of *Paulinella* should be regarded as "cell organelles". Finally, morphological studies on *Paulinella chromatophora* were concluded by Kies (1974, 1992) who was the first to investigate the organism by transmission electron microscopy. He found the "cyanelles" "lying within vesicles in the cytoplasma of the host". Following Geitler (1924), Kies (1974) arranged "blue-green endosymbionts" (i.e. cyanelles in Pascher's sense; Pascher 1929a) in a series of decreasing morphological and functional complexity starting with the "cyanelles" of *Geosiphon* (which can be cultivated outside their host and represent the cyanobacterium *Nostoc punctiforme*; Mollenhauer et al. 1996), then the cyanelles of *Paulinella chromatophora* (Pascher had in one case observed division of an isolated cyanelle outside its "host" [he squeezed out the cyanelles from the amoebae by pressure, a procedure that frequently resulted in breakage of the cyanelle caused by the sharp edges of the silica scales]; Pascher 1929b, pp 192—193), and finally the cyanelles of *Cyanophora*, *Glaucocystis* and the like, organisms which Kies and Kremer (1990) placed into the division Glaucocystophyta and which are now known to be part of the kingdom Plantae (here termed subkingdom Glaucoplantae). And while the cyanelles of the Glaucoplantae are genuine plastids (albeit uniquely retaining the peptidoglycan cell wall of their cyanobacterial ancestors), which together with the plastids (i.e. the rhodoplasts) of the Rhodoplantae (i.e. the red algae) and the plastids (i.e. the chloroplasts) of the Viridiplantae (i.e. the green algae and embryophytes) are of monophyletic origin within the cyanobacteria (Helmchen et al. 1995; Martin et al. 1998; Turner et al. 1999), the status of the cyanelles of *Paulinella chromatophora* still remains to be determined using a molecular approach. What is very likely, though, is that the cyanelles of *P. chromatophora* originated by a separate endocytobiotic event than the cyanelles of the Glaucoplantae, irrespective of whether they are genetically reduced (such as plastids) or not (in which case they may represent an intracellular cyanobacterial symbiont such as *Nostoc punctiforme* in *Geosiphon*). This conclusion is based on the fact that the host, the testate amoeba, has been firmly placed within the Euglyphidae (Bhattacharya et al. 1995), which together with other filose amoebae, zooflagellates, foraminifera, polycystines and acantharia form a new superassemblage of eukaryotes, the Rhizaria (Cavalier-Smith 2002), and thus that *Paulinella* is not monophyletic with the Glaucoplantae. The alternative hypothesis, although unlikely, namely that the cyanelles of the Glaucoplantae and those of *Paulinella* are indeed monophyletic and that *Paulinella* received its cyanelles through a secondary endocytobiosis involving a glaucoplant symbiont should not a priori be dismissed.

Geitler (1927), Pascher (1929b) and Kies (1974) have all concluded that the cyanelles of

P. chromatophora are closely related to free-living cyanobacteria and Pascher (1929b) even suggested that the cyanelle of *Paulinella* may represent a species of the extant genus *Synechococcus* (Lukavský and Cepák 1992 studied the nucleoids of *P. chromatophora* by DAPI fluorescence and concluded that they most closely resembled those of *Synechococcus elongatus f. thermalis*). And what did Robert Lauterborn conclude?

In his description, Lauterborn (1895) cautiously referred to the blue-green endosymbionts of *P. chromatophora* as "chromatophore-like structures" (*chromatophorenartige Gebilde*). He observed an outer pigmented part and a central non-pigmented part in the cyanelle, the latter containing fine granules often arranged like a string of pearls in the center of the cyanelle (Fig. 4). About the possible nature of the cyanelles Lauterborn wrote "A priori the following possibilities can be taken into consideration about the nature of the said inclusions. Either the blue-green structures represent algae from the division Cyanophyceae which are taken up as food or they are independent organisms — in this case again Cyanophyceae — that live with the rhizopod in an intimate symbiosis, or finally they are integral components, real organs of the rhizopod cell body. The first assumption is untenable, because their universal presence in over 200 individuals studied, the absence of such structures in the natural environment, and the ability of the structures to divide within the plasma rule out the possibility that said structures are only accidental components of the cell body of the rhizopod. More difficult, and perhaps currently impossible, is the decision between the last two possibilities. In favor of a symbiosis one may refer to many known examples in which algae from the group of the Cyanophyceae enter intimate associations with other organisms — for example one may think of the lichens which are nothing else than fungi (mostly ascomycetes) living intimately together with certain blue-green (more rarely green) algae. Also the above-mentioned fine structure of the "chromatophores" can be regarded as support for their independent status, the central non-pigmented part representing the nucleus (or "central body") of typical Cyanophyceae (e.g. *Oscillatoria*, *Merismopedia*, etc.). In support of the chromatophore nature of the blue-green inclusions, one may refer only to the fact that, as far as I am aware, no free-living Cyanophyceae exists or at least occurs in the natural environment of *Paulinella* that resembles the "chromatophores" of *Paulinella* in shape and structure." Lauterborn then goes on (p. 541) with an interesting comparison "Perhaps the difference between a symbiotic alga and a chromatophore may not be so significant after all because it may not be impossible that the chromatophores in general exist in a symbiotic relationship with the cells containing them." Here, he seems to touch on the possible endosymbiotic origin of the chromatophores (i.e. plastids) without explicitly advancing this hypothesis (as did Mereschkovsky 10 years later). Finally, Lauterborn concludes "A decision about this question (*the nature of the chromatophores of Paulinella*) must be left to the future, however, there can presently be no doubt that the blue-green inclusions in the plasma of *Paulinella* function as real chromatophores, i.e. the products of their assimilation nourish the rhizopod body. I reach this conclusion because in none of the 200 studied individuals of the rhizopod, I observed any uptake of food particles, although I focused my attention specifically on this aspect." Lauterborn's remarkably insightful conclusions still hold today!

It is noticeable that the older literature is largely silent about the type of habitat in which *Paulinella chromatophora* thrives. Penard took over Lauterborn's description "in diatom mats" and provided no further information. Similarly, Kies (1974), Grospietsch (1958), Schönborn (1966), Thomasson (1952), Skuja (1964), and Canter-Lund and Lund (1995) all made only very general statements about the occurrence of *Paulinella*. However, our own experience suggests that the habitat of *Paulinella chromatophora* can be described more precisely. Lauterborn's location already gives some hints. The old riverbeds in the fertile plain of the Rhine often lead water with low oxygen content, which ascends from the soaked and oxygen-depleted subsoil. In addition, oxygen is largely consumed by saprobial organisms, leading to anoxic or microaerophilic conditions including trace amounts of hydrogen sulfide near the sediment surface. *Paulinella chromatophora* occurs as part of a very characteristic community of organisms that include (as already noticed by Lauterborn) *Gymnodinium aeruginosum*, *Glaucocystis nostochinearum*, *Chroomonas nordtstedtii* and several cyanobacteria (Lauterborn mentions "*Merismopedia elegans*", "*Microcystis* spp.", "*Spirulina* spp." and others). These organisms are adjusted to this peculiar environment and may be adversely affected when transferred to oxygen-rich conditions. In addition, their habitat is rich in organic compounds, the salinity is higher (up to brackish conditions; see also Pankow 1982 who

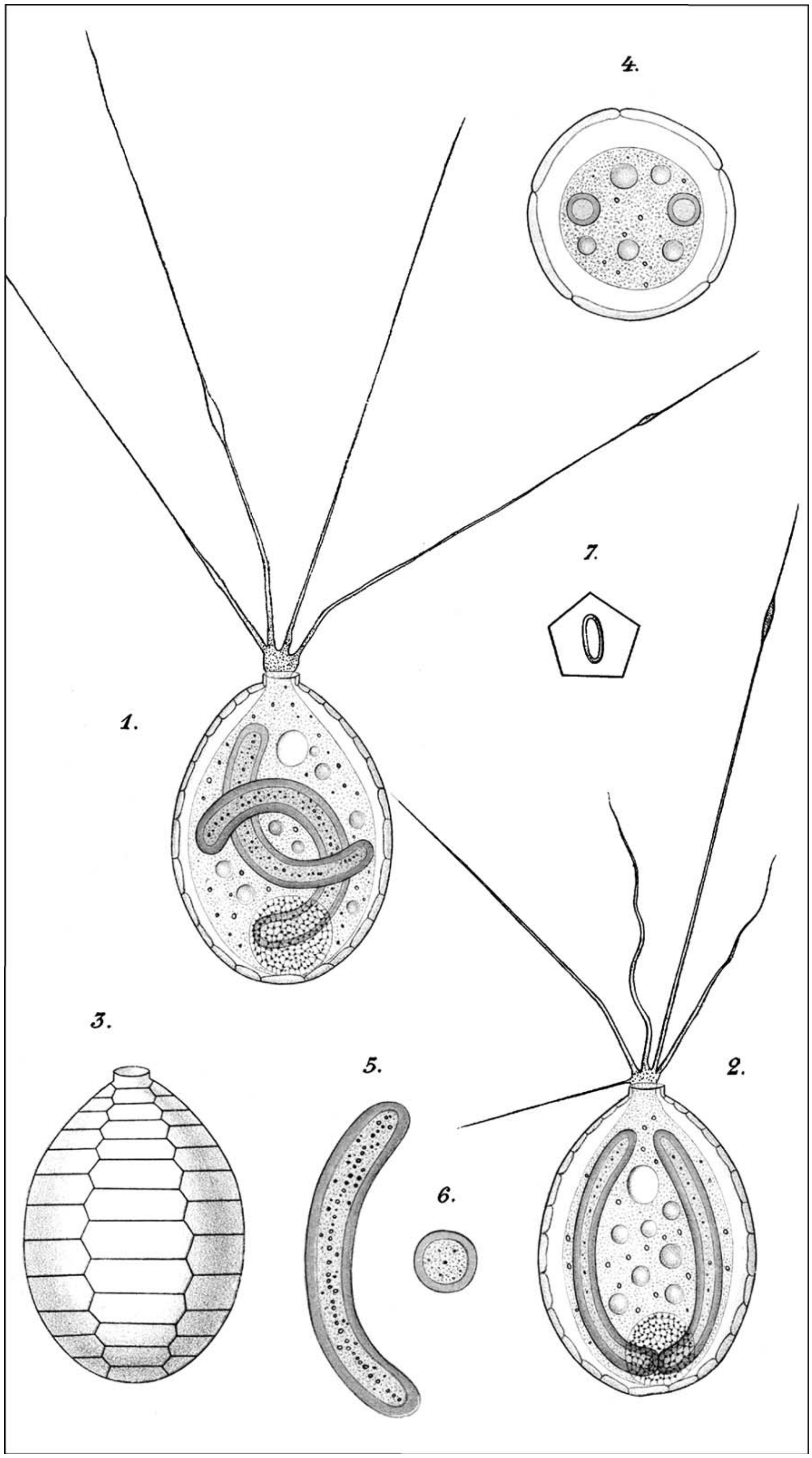

Figure 4. Plate 30 with 7 figures of various aspects of *Paulinella chromatophora* taken from Robert Lauterborn's original description published in *Zeitschrift für wissenschaftliche Zoologie* (Vol. 59, 537—544, 1985). Figs. 1, 2 and 4 illustrate cells of *Paulinella chromatophora* in longitudinal (1,2) or cross section (4), a surface view of the test (3), "chromatophores" in side view (5) and optical cross section (6), and the apical, five-sided plate with the oval opening ("mouth") (7).

found *P. chromatophora* in the shallow bays of the Darss and Zingst in the Southern Baltic Sea; other species of *Paulinella*, e.g. *P. ovalis*, have been found in the marine environment feeding on cyanobacteria: Hannah et al. 1996; Johnson et al. 1988; Vørs 1993) and often the pH is low. It is apparently difficult to reproduce these conditions in the laboratory and this may be one of the reasons for the failure to grow some of the organisms of this community ex situ.

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