

Rotifera X

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K. Martens

Rotifera X

Rotifer Research: Trends, New Tools and Recent Advances

Proceedings of the Xth International Rotifer Symposium,
held in Illmitz, Austria, 7–13 June 2003

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Preface

The Xth International Rotifer Symposium was held in Illmitz, Austria, 7–13 June 2003, at the Information Centre of the National Park Neusiedler See – Seewinkel. The Symposium was returning to Austria 27 years after the first rotifer meeting was organized there by Prof. Agnes Ruttner-Kolisko at the Biological Station Lunz in 1976. The Xth meeting was attended by 113 participants from 28 countries. It was organized by Alois Herzig with the assistance of Christian Jersabek, Institute of Zoology, University of Salzburg and Alois Lang, Information Centre of the Nationalpark Neusiedler See – Seewinkel. It was hosted by the Biological Station Neusiedler See (Provincial Administration of Burgenland) and the National Park Society. The symposium venue provided an excellent opportunity for the community of rotifer researchers to follow the scientific programme combined with enjoyable breaks and nice sundowners.

After the opening ceremony and a short appraisal by Alois Herzig of the contents and topics of the last nine meetings, Norbert Walz paid a tribute to the life-time works of Walter Koste. Subsequently, the scientific programme followed the traditions of the previous symposia with 6 invited main lectures, 56 oral contributions and 45 poster presentations. The papers were grouped into thematic sessions: Phylogeny, evolution and genetics; Molecular ecology; Biogeography and development; Diapause, anhydrobiosis and resting eggs; Morphology, ultrastructure and behaviour; Feeding; Population ecology; Culture of rotifers; Physiology and ecotoxicology. In addition, two late afternoon sessions were devoted to the careers in rotiferology of John Gilbert and Henri Dumont.

Special thanks to John J. Gilbert, Ramesh D. Gulati, Charles E. King, Linda May, Claudia Ricci, Terry W. Snell and Robert L. Wallace for their involvement with the arrangements for the scientific programme.

Social activities began with a Welcome Party that was held on Saturday evening at the Information Centre of the National Park. The

occasion was made all the more enjoyable by the wonderful atmosphere created by a brass band playing music typical of Czech Republic, Slovakia and eastern Austria. A full-day excursion was organized on the Wednesday. The participants enjoyed a cruise around Neusiedler See, a visit and an introduction to the activities of the Wine Academy at Rust (which runs courses in the Science of Wine Making) combined with a short wine tasting, a guided tour through the old town of Rust (buildings dating back to the 16th century), and a visit to the Baroque Esterházy Palace at Eisenstadt. As an preamble to Joseph Haydn's music, a chamber concert was given in the famous Haydn Hall of the Esterházy Palace. Participants were invited to a lunch by the Head of the Government of the Province of Burgenland, which took place in representative rooms of the Palace. The excursion in the afternoon to Hungary included a visit to typical farm houses in a small village situated south of Neusiedler See (Fertőszéplak) and the baroque Esterházy Castle of Fertőd, the place where Haydn spent nearly two decades of his creative life. The Conference Dinner was hosted by the Government of the Province of Burgenland on Friday at Johanneszeche, a typical restaurant with Hungarian ambience and Croatian (Tamburizza) and gypsy music in the backdrop. Accompanying guests made several day trips to places of natural, cultural and historical interests in the Neusiedler See area and the adjacent Hungarian neighbourhood townships.

Kluwer Academic Publishers, now Springer Aquatic Sciences, and Prof. Dr. Koen Martens, *Editor-in-chief Hydrobiologia*, have accepted to publish the symposium proceedings as a special volume in the series *Developments in Hydrobiology*. The manuscripts accepted for publication have undergone a careful review and revision process and appropriate editorial amendments needed for clarity and conciseness. The final product is the result of the efforts of the authors, reviewers, editors and the Editor-in-chief.

The *Proceedings* are composed of nine parts (See Contents). The introductory paper by Funch et al. (Part I) offers a detailed discussion of the phylogenetic position of rotifers *vis-a-vis* gnathiferan groups. Originally, Gnathifera only comprised the hermaphroditic Gnathostomulida and the Syndermata. On the basis of the ultrastructure of the trophi, the rotifers belong to the Gnathifera; moreover, molecular evidence strongly suggests that they are closely related to the parasitic acanthocephalans and the two together form the clade Syndermata. In his paper Mark Welch provides evidence for a monophyletic Eurotatoria based on maximum likelihood and Bayesian analysis of the protein-coding gene *hsp82* and for the placement of Acanthocephala within the Phylum Rotifera as a sister clade to either Eurotatoria or Seisonidea.

Substantial differences in both life-table characteristics and reproductive patterns distinguish bdelloid rotifers from monogonont rotifers. King et al. explore some of the adaptive consequences of these life-history differences using a computer model to simulate the evolutionary acquisition of new beneficial mutations. Birky et al., isolated more than 100 females of the obligately asexual bdelloid rotifers from nature and sequenced their mitochondrial *cox1* genes and conclude that in the absence of sexual reproduction the bdelloids have undergone substantial cladogenesis; bdelloid clades are adapted to different niches and have undergone substantial speciation. The authors failed to detect a decrease in the effectiveness of natural selection on bdelloid genes.

The development of cost-effective molecular tools that allow the amplification of minute amounts of DNA, effectively opened the field of molecular ecology of rotifers. In Part II (*Genetics and Molecular Ecology*), Gómez critically reviews: (1) methodological advances that have facilitated the application of molecular techniques to rotifers, (2) recent advances in the field of rotifer molecular ecology, and (3) future developments and areas which are likely to benefit further from the molecular ecological approach. It is now feasible to obtain representative DNA sequences from identified rotifer species for use in genomic-based surveys for determining rotifers in new sample collections, circumventing the difficulties that go with traditional surveys. D.B. Mark Welch and

J.L. Mark Welch discuss in their paper the application of two genomic-based tools used in surveys of microbial communities to rotifer taxonomy: serial analysis of gene tags (SAGT) and microarray hybridization. They also report the construction and hybridization of a small microarray of rotifer sequences, thereby demonstrating that these techniques are most powerful if combined with traditional rotifer systematics.

Bdelloids show a rather uniform morphology of jaws (trophi), most recognizably feature is the presence of a series of teeth forming unci plates, each with one to ten major median teeth. Using SEM photomicrographs of trophi and literature data, Melone and Fontaneto deduce that few major teeth are common in species living in water bodies, where these species possibly eat unicellular algae, while more major teeth are more common in species inhabiting mosses and lichens, where they possibly consume bacteria.

Modern techniques can contribute significantly to our understanding of the rotifers anatomy, especially relating to the musculature and the nervous system. Very recently, immunostaining has been applied in combination with confocal laser scanning microscopy (CLSM). Santo et al., applied CLSM to describe the muscle arrangement of *Brachionus urceolaris*, *Floscularia ringens*, *Hexarthra mira* and *Notommata glyphura*. Sørensen describes the musculature of *Testudinella patina*. Kotikova et al. presents data on the immuno-reactivity patterns in the nervous system of *Platyas patulus*, *Euchlanis dilatata* and *Asplanchna herricki* using CLSM. That species considered to be cosmopolitan can be complexes of sibling species has been recently clearly demonstrated for the rotifer *Brachionus plicatilis*: within the Iberian Peninsula three species have been described and another three have been identified (see Gómez, Part II). Gilbert and Walsh who observed mating behaviour and genetic differentiation among four geographically isolated strains of *Brachionus calyciflorus* conclude that it is a species complex in which some geographically and genetically distinct strains are reproductively isolated from one another.

Bdelloid rotifers can withstand desiccation by entering a state of suspended animation: anhydrobiosis. Ricci and Covino describe and discuss costs and benefits of anhydrobiosis of a new

species, *Adineta ricciae*, a new species described by Segers and Shiel (see part III). A comparison of this with *Macrotrachela quadricornifera* reveals both species suspend their life activities during desiccation as well do not “age” during anhydrobiosis. This meets the prediction of the “Sleeping Beauty” model. Anhydrobiosis is thought to require accumulation of the non-reducing disaccharides trehalose (in animals and fungi) or sucrose (in plant seeds and resurrection plants), which may protect proteins and membranes by acting as water replacement molecules and vitrifying agents. However, in clone cultures of the bdelloids *Philodina roseola* and *Adineta vaga* Tunnacliffe et al. were unable to detect trehalose or other disaccharides. Instead, on dehydration, *P. roseola* upregulates a hydrophilic protein related to the *late embryogenesis abundant* (LEA) proteins associated with desiccation tolerance in plants. It could well be that hydrophilic biosynthesis represents a common element of anhydrobiosis.

A number of studies examine spatial and temporal variability in rotifer abundance and community structure in relation to variations in abiotic and biotic factors along gradients in natural water bodies, and in laboratory. M. Gophen presents the results of a long-term study on seasonal rotifer dynamics in Lake Kinneret (Israel) and T.E. Andrew and J.A.M. Andrew in Lough Neagh (Northern Ireland). N. Lair focussed on rotifers in river plankton, especially the response of various rotifer taxa to hydraulic conditions, and the role of rotifers in the river food web.

As a special topic, Z. Brandl reviews the trophic relationship between freshwater copepods and rotifers. Most copepod species, at least in their later developmental stages, predate efficiently, preferably on rotifers. Generally, soft-bodied species of rotifers are more vulnerable to predation than those that possess spines or lorica. But also behavioural characteristics, e.g., movements and escape reactions, and temporal and spatial distribution of rotifers are important in these trophic interactions. The reported predation rates by freshwater copepods can effectively exercise a top-down control of rotifer populations.

During the preparation of the present proceedings, we heard about the sudden death of Andrzej Karabin, who had designed logos for

previous Rotifer Symposia as well as contributed a paper to this volume. On behalf of the rotifer family, we extend our profound sympathy to Andrzej’s wife, Jolanta Ejsmont-Karabin.

The editors wish to thank the “local organizers” for their invaluable help during the symposium. They also wish to acknowledge the Government of the Province of Burgenland for financial support.

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Walter Koste - a K-strategist? A laudatio

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Key words: Rotifers, taxonomy, publications, long life

Abstract

Walter Koste is one of the architects of modern rotiferology. Here I take a look at his scientific career using ecological concepts. Although he has more than 150 publications to his credit, he did not start publishing his works on rotifers before the age of 49, and then most of his publications appeared after his retirement. Long life and late reproduction are characteristics for K-strategists. Thus, it appears that Koste has followed K-strategy for his contributions to rotiferology.

Introduction

On July 19th, 2003 Walter Koste celebrated his 91th birthday (Fig. 1). At the Xth Rotifer Symposium in Illmitz in 2003 this laudatio was presented in his honour. For additional information on this remarkable scientist the reader is requested to consult Ruth Laxhuber's review of his curriculum vitae (Laxhuber, 1993) and Jürgen Schwoerbel's tribute presented on the occasion of his 75th birthday (Schwoerbel, 1987).

Although in retrospect Koste's contributions have been outstanding, the way to his success was hard and difficult. While he was interested in biology, especially in aspects of biodiversity since his school days, circumstances prevented him from attending university. This did not deter Koste's innate interest to become skilled at about rotifers. After World War II he became a teacher and a headmaster of a one-class country school in a village in North-Western Germany. After additional training in education at the college level he received a certificate to teach at the secondary school level for biology and geography. Later he moved to Quakenbrück, a small town in Lower Saxony, where until his retirement he was headmaster of the Artland Secondary School. He still resides in this small town.

Even though he did not start to publish his works until he became 49 years Koste has more than 150 publications to his credit, that is the envy of many a university professor. Moreover, a good deal of this work was accomplished during his leisure time, i.e., after his school duties. On his retirement from teaching he continued to publish thereby establishing himself as one of the grand dons of rotiferology. Long life and long and late reproduction of qualitatively good offspring are the life history characteristics termed K-strategy (MacArthur & Wilson, 1967). K-strategists are more competitive and use their energy more efficiently. In contrast, r-strategists have rather high reproduction rates early in their life, compensating higher mortality of offspring. Based on these criteria I pose the question: is Walter Koste a r- or K-strategist?

Results

Koste's publication career began in 1961 and continued in a modest way with a total of four papers by the mid 1960s. At that point his efforts picked up momentum, so much so that by the end of 1970 he had already quadrupled the pace of his output of his early years. Koste continued to be



Figure 1. Walter Koste at the occasion of his 91st birthday at July 19th, 2003.

highly productive until his retirement in 1974. Nevertheless, retirement and aging did not slow down Koste's productivity for nearly 75% of his works, including his revision of Voigt's taxonomy of the rotifers (see below), were published after he had stopped formal teaching. However, teaching never left Koste's blood, as was witnessed by many at the rotifer symposia he attended. It was here that a second type of contribution to the rotifer world could be noted: the way Koste helped his colleagues sort out the details of rotifer taxonomy.

Koste's early studies were on the rotifer fauna of the countryside of north-western Germany, near his residence. Here he found many species for the first time. His very successful series, called "Das Rädertier-Portrait" (the rotifer

portrait), published in the monthly journal *Mikrokosmos*, is exemplary of the way Koste wedded his teaching interests with his scientific explorations of rotifers. In this series he examines different rotifers both on a scientific level as well as making them understandable for the general public. Through these early years he worked on a revision of the identification guide of M. Voigt "Rotatoria – the Rotifers of Middle Europe" which he published in two volumes in 1978 (Koste 1978). This enormous effort brought him a break-through in public perception. This book demonstrated for the first time to a wide public arena Koste's capacities to combine exact scientific observations of high accuracy with excellent artistic illustrations. Through this works we get a glimpse of how deeply impressed Koste was by the famous book of Ernst Haeckel (1899): "Art Forms in Nature", which he received as a present from a former teacher when he was about 16 years old.

Recognition of the importance of "Rotatoria" by the scientific community was a critical point in Koste's scientific career as it legitimised him in the field as a major force, but it also allowed him to expand his studies from Middle Europe to the whole world. Beginning about 1980 many scientists began to send him rotifer samples for identification from different countries and this contributed to his success as expert in the rotifer fauna from many geographical regions, including Australia and South America, especially the Amazon region, followed later by Africa, Canada, India, Sri Lanka, Malaysia, Indonesia, China, and others. Along with

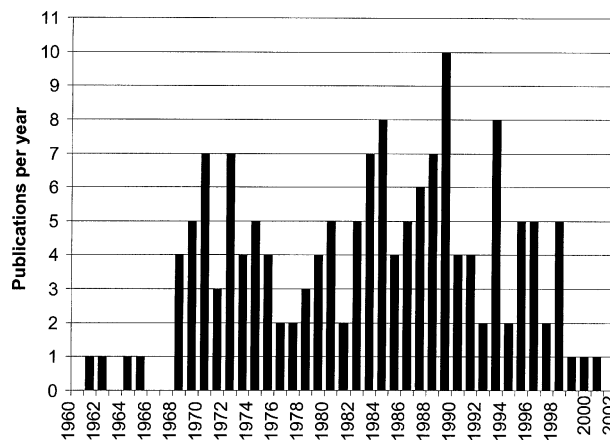


Figure 2. Number of scientific publications per year by Walter Koste.

this work he described many new species and sub-species (Schwoerbel, 1987). Altogether his publication record stands at 153 papers (Fig. 2).

One wonders if any other person will equal Koste's achievements, considering that he was equipped with only a good microscope and simple sampling equipment. Koste literally carried out all this work single handed and financed the costs from his pension as a retired teacher. I doubt very much if future generations will be able to exhibit such a patience and observe rotifers so precisely using a limiting equipment as Koste did. This is in sharp contrast with the present generation of taxonomists who are now using highly sophisticated techniques as scanning electron microscopy and molecular techniques to carry out their taxonomic studies. This, of course, is not an attempt to criticise those who aim at advancing the discipline. Clearly researchers must include other methods to reach other levels of understanding. So Koste – like a dinosaur – simultaneously marks the culmination of an ongoing development since the discovery of the animalcules by Antonio van Leeuwenhoek (1674). A few years after the publication of “Rotatoria” Koste began to win the honours appropriate to his accomplishments. In 1980 the University of Kiel promoted him to “Doctor honoris causa”, a title very rarely conferred on scientists in Europe. The *raison d'être* given by the university for this honour makes it especially interesting: “For his achievements in the assessment of freshwater and marine life. For his exemplary and outstanding achievements in the taxonomy, biogeography, biology and ecology of rotifers,” and: “For his efforts in imparting his knowledge and his enthusiasm for science to following generations”. The latter has been Koste's hobby horse. For many years he gave courses at the University of Osnabrück (Germany) and other locations (e.g., Plön, Germany; Illmitz, Austria) in rotifer taxonomy, limnology, hydrobiology, and plankton biology as well as helping countless students in rotifer taxonomy from all over the world to identify their samples. In 1981 the Federal Order of Merit of the Federal Republic of Germany was conferred upon him. And in 1985 he was elected to a Corresponding Member of the Senckenberg Museum in Frankfurt and as an Honorary Member of the Quekett Microscope Club of the British Natural History Museum in Lon-

don, and in 1986 he was established as an Associate Member of the Royal Society of South Australia of the South Australia Museum in Adelaide.

As Walter Koste had no external funding for his travels he was invited to many countries (Australia, Austria, Belgium, Brazil, China, England, France, Italy, Kenya, Romania, Scotland, Spain, Ukraine) to attend symposia or to introduce local scientists to the regional rotifer fauna at the expense of this hosting country.

Discussion

Koste's publication list of 153 papers is phenomenal! Between 1968 and 1998 he published at least 2 publications per year but often more so that he had on average 4.8 publications per year. It is however, most astonishing that he (1) did not start publishing his work until the age of 49, (2) published >75% of his work after his retirement in 1974 and (3) that he reached 77 years of age when he reached his output maximum 10 publications per annum. When Schwoerbel (1987) congratulated him to his 75th birthday he referred to Koste's publication list comprising over 100 publications, but he also reported that Koste was looking forward to go on with his scientific pursuits . . . Jürgen Schwoerbel was quite right in his prediction because Koste added nearly 50% more to his already long list of publications.

Has Koste been following a K-strategy? The answer: it appears he is because long life with delayed but repeated reproduction is characteristic for this life history (Table 1). However, Koste had also numerous offspring (papers), a characteristic that is typical for r-strategists. R-strategists produce many offspring but they usually do not invest much energy in each. Clearly, this is not the case with Koste's publications. His papers have appeared in respected international journals such as *Amazoniana*, *Annales de Limnologie*, *Archiv für Hydrobiologie*, *Australian Journal of Marine and Freshwater Research*, *Hydrobiologia*, *International Review of Hydrobiology*, *Limnologica*, and *Transactions of the Royal Society of South Australia*. In fact, Koste has succeeded in combining the characteristics of both r- and K-strategist into a super-K-strategist.

Table 1. Characteristics of r- and K-strategy according to Pianka (1978) with data from Walter Koste

Characteristics	r-strategy	K-strategy
Length of life	Short	Long <i>Koste: 91 years</i>
Reproduction	Early	Delayed <i>Koste: started at age 49</i>
Type of reproduction	Often: single reproduction	Repeated reproduction <i>Koste: every year</i>
Number of offspring	Many	Fewer offspring <i>Koste: 153 papers</i>
Quality of offspring	Low	High <i>Koste: offspring in excellent journals</i>
Intraspecific competition	Low	High <i>Koste: honours and decorations</i>
Use of resources	Maximum energy intake	Efficient energy intake <i>Koste: in retirement since 1974</i>
Body size	Small	Larger <i>Koste: >190 cm</i>
Environment	Variable	Constant <i>Koste: since 1962 in Quakenbrück</i>
Occurrence	Local	Ubiquitous <i>Koste: offspring in many libraries</i>

Not many are able to comprehend why Koste has been investing so much energy in scientific work at an age by which other senior people would have doing so already for long time. I think he simply could not have done otherwise. This way of life has been his hobby and his passion. I suppose his daily work observing rotifers is rather a contemplation for him from where he gets power for his life and for his contact with other people. This is the way how he could sustain such a steady output even long after his retirement. With this as basis Koste likes always to meet with friends and to share his humour. With this way of life Koste is a ‘living fossil’; in the contemporary scientific environment where, unfortunately, r-strategy is the predominant paradigm and where people are urged to present them as young as possible and to burn up early like meteors. We, his friends and his students, living today with a longer life expectancy

than ever before, have with Koste hopefully not a run-out model, which shows us how to combine scientific work and true life. He oversees his situation perfectly. Not for nothing is he often coquetting with his role as Methuselah. On the other side, nothing is farther away from him than to demonstrate his as a role as a super-K-strategist or as a king of rotiferologists. In fact, for all who like him, and these are many, he remains our “Uncle Walter”.

A robust health has been a physical prerequisite for his success. This we, the members of the international family of rotiferologists, wish him many more years of healthy life – and, of course, we wish him to study and discover many new species of rotifers under his microscope.

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References

- Haeckel, E., 1899–1904. *Kunstformen der Nature*: Leipzig und Wien, Verlag des Bibliographischen Instituts.
 Laxhuber, R., 1993. *Das Rädertierportrait: Walter Koste*. *Hydrobiologia* 255/256: xxiii–xxvi.
 MacArthur, R. H. & E. O. Wilson, 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton NJ, 216 pp.
 Pianka, E. R., 1978. *Evolutionary Ecology* (2nd edn). Harper & Row, Publishers, New York, 397 pp.
 Schwoerbel, J., 1987. Dr. h. c. Walter Koste zum 75. Geburtstag. *Archiv für Hydrobiologie* 110: 631–638.

Bibliography of Walter Koste

- Koste, W., 1961. *Paradicranophorus wockei* nov. spec., ein Rädertier aus dem Psammon eines norddeutschen Niederungsbaches. *Zoologischer Anzeiger* 167: 138–141.
 Koste, W., 1962. Über die Rädertierfauna des Darnsees in Epe bei Bramsche, Kreis Bersenbrück. *Veröffentlichungen Naturwissenschaftlicher Verein Osnabrück* 30: 73–137.
 Koste, W. & K. Wulfert, 1964. Rotatorien aus der Wüste Gobi. *Limnologia* 2: 483–490.

- Koste, W., 1965. Rotatorien des Naturdenkmals "Engelbergs Moor" in Druchhorn, Kreis Bersenbrück. Veröffentlichungen Naturwissenschaftlicher Verein Osnabrück 31: 49–82.
- Koste, W., 1968. Über moosbewohnende Rädertiere von Strohdächern alter Gebäude. Mitteilungen Kreisheimatbund Bersenbrück Nr. 15: 123–128.
- Koste, W., 1968. Über *Proales sigmoida* (Skorikow) 1896 (eine für Mitteleuropa neue Rotatorienart) und *Proales daphnicola* (Thomson) 1892. Archiv für Hydrobiologie 65: 240–245.
- Koste, W., 1968. Über die Rotatorienfauna des Naturschutzgebietes "Achmer Grasmoor", Kreis Bersenbrück. Veröffentlichungen Naturwissenschaftlicher Verein Osnabrück 32: 107–160.
- Koste, W., 1968. Das moosbewohnende Rädertier *Tetrasiphon*. Mikrokosmos 57: 334–337.
- Koste, W., 1969. Das parasitische Rädertier *Albertia naidis*. Mikrokosmos 58: 212–216.
- Koste, W., 1969. Das sessile Rädertier *Ptygura velata*. Mikrokosmos 58: 1–6.
- Koste, W., 1969. *Notommata copeus* und einige verwandte Arten. Mikrokosmos 58: 137–143.
- Koste, W., 1969. *Filinia*, eine pelagisch lebende Rädertiergattung. Mikrokosmos 58: 298–301.
- Koste, W., 1969. *Stephanoceros fimbriatus*. Mikrokosmos 58: 370–373.
- Koste, W., 1970. Über eine parasitische Rotatorienart. *Albertia reichelti* nov. spec. Zoologischer Anzeiger 184: 428–434.
- Koste, W., 1970. Das Putzer-Rädertier *Proales daphnicola*. Mikrokosmos 59: 49–51.
- Koste, W., 1970. *Collotheca trilobata*, ein seltenes sessiles Rädertier. Mikrokosmos 59: 195–200.
- Koste, W., 1970. Die Rädertiergattung *Lindia*. Mikrokosmos 59: 134–138.
- Koste, W., 1970. *Macrotrachela quadricornifera*, ein moosbewohnendes bdelloides Rädertier. Mikrokosmos 59: 328–332.
- Koste, W., 1970. Zur Rotatorienfauna Nordwestdeutschlands. Veröffentlichungen Naturwissenschaftlicher Verein Osnabrück 33: 139–163.
- Koste, W., 1970. Über die sessilen Rotatorien einer Moorblänke in Nordwestdeutschland. Archiv für Hydrobiologie 68: 96–125.
- Koste, W., 1971. Die Rädertiergattung *Collotheca*. Mitteleuropäische Arten mit besonders auffallenden Koronafortsätzen. Mikrokosmos 60: 161–167.
- Koste, W., 1971. Kurt Wulfert, ein Nachruf. Archiv für Hydrobiologie 68: 457–461.
- Koste, W., 1971. Kutikowa, L. A. Die Rädertiere der Fauna USSR (Unterkl. Eurotatoria, Ploimida, Monimotrochida, Paedotrochida). Best. Bücher zur Fauna USSR, Bd. 104: 1–744, Book Review. Archiv für Hydrobiologie 69: 142.
- Koste, W., 1972. Ein seltener Außenparasit an Süßwasser-Oligochaeten: *Cephalodella parasitica*. Mikrokosmos 61: 10–12.
- Koste, W., 1972. *Collotheca campanulata longicaudata*. Mikrokosmos 61: 97–99.
- Koste, W., 1972. *Rhinoglena frontalis*, ein vivipares Rädertier. Mikrokosmos 61: 358–360.
- Koste, W., 1972. Über zwei seltene parasitische Rotatorienarten, *Drilophaga bucephalus* Vejdovsky und *Proales gigantha* (Glascott). Osnabrücker Naturwissenschaftliche Mitteilungen 1: 149–218.
- Koste, W., 1972. Über ein sessiles Rädertier aus Amazonien. *Floscularia noodti* n. sp. Archiv für Hydrobiologie 70: 534–540.
- Koste, W., 1972. Rotatorien aus Gewässern Amazoniens. Amazoniana 3: 258–505.
- Koste, W., 1972. Ein Rädertier des Hochmoores: *Monommata arndti*. Mikrokosmos 61: 269–273.
- Koste, W., 1973. Über ein sessiles Rädertier aus Amazonien, *Ptygura elsteri* n. sp., mit Bemerkungen zur Taxonomie des Artkomplexes *Ptygura melicerta* (Ehrenberg) 1932. Internationale Revue der gesamten Hydrobiologie 57: 875–882.
- Koste, W., 1973. *Cupelopagis vorax*, ein merkwürdiges festsitzendes Rädertier. Mikrokosmos 62: 101–106.
- Koste, W., 1973. *Horaella thomassoni* n. sp., ein neues Rädertier aus Gewässern der Guiana-Brasilianischen Region der Neotropis. Archiv für Hydrobiologie 72: 375–383.
- Koste, W., R. Chengalath & C. H. Fernando, 1973. Rotifera from Sri Lanka (Ceylon). 2. Further studies on the Eurotatoria including new records. Bulletin of the Fisheries Research Station, Sri Lanka (Ceylon) 24: 29–62 pp.
- Koste, W., 1974. Die Gattung *Notholca*. Mikrokosmos 63: 48–52.
- Koste, W., 1974. Zur Kenntnis der Rotatorienfauna der "schwimmenden Wiese" einer Uferlagune in der Varzea Amazoniens, Brasilien. Amazoniana 5: 25–60.
- Koste, W., 1974. *Ptygura pectinifera*, die "Kammträgerin", eine Einwanderin in Warmwasseraquarien. Mikrokosmos 63: 182–187.
- Koste, W., 1974. Rotatorien aus einem Ufersee des unteren Rio Tapajos, dem Lago Paroni. Gewässer und Abwässer 53/54: 43–68.
- Koste, W., R. Chengalath & C. H. Fernando, 1974. Rotifera from Sri Lanka (Ceylon) 3. New species and records with a list of Rotifera recorded and their distribution in different habitats from Sri Lanka. Bulletin of the Fisheries Research Station, Sri Lanka (Ceylon) 25(1–2): 83–96.
- Koste, W., 1975. Macrochaeten, die "Igel" unter den Rädertieren. Mikrokosmos 64: 143–147.
- Koste, W., 1975. Über den Rotatorienbestand einer Mikrobiozönose in einem tropischen aquatischen Saumbiotop, der *Eichhornica-crassipes*-Zone im Litoral des Bung-Borapet, einem Stausee in Zentralthail and Gewässer Abwässer, 57/58: 43–58.
- Koste, W., 1975. *Seison annulatus*, ein Ektoparasit des marinen Krebses *Nebalia*. Mikrokosmos 64: 341–347.
- Koste, W., 1975. Ruttner-Kolisko, A., Plankton Rotifers, Biology and Taxonomy, In: Die Binnengewässer Bd. 16/1, Supplement. Stuttgart 1975, 146 pp., Book Review. Archiv für Hydrobiologie 76: 133–134.
- Koste, W., 1976. *Trochosphaera aequatorialis*, das "Kugelrädertier". Mikrokosmos 65: 266–268.
- Koste, W., 1976. Über die Rädertierbestände (Rotatoria) der oberen and mittleren Hase in den Jahren 1966–1969. Osnabrücker Naturwissenschaftliche Mitteilungen 4: 191–263.
- Koste, W., 1977. *Ptygura pedunculata*. Mikrokosmos 66: 37–40.
- Koste, W., 1977. Über drei neue Formen des Genus *Hexarthra* Schmarda 1854: *H. jenkinsae* f. *nakuru* n. f., *H. brandorffi* n.

- sp. and *H. polyodonta soaplakeiensis* n. sp. Gewässer und Abwässer 62/63: 7–16.
- Koste, W., 1978. Über *Testudinella ohlei* Koste 1972, ein Rädertier der U. Ordnung Flosculariacea aus der Guiana-Brasilianischen Region der Neotropis. Archiv für Hydrobiologie 82: 359–363.
- Koste, W., 1978. *Synchaeta grandis*, ein in Mitteleuropa vom Aussterben bedrohtes Planktonrädertier. Mikrokosmos 67: 331–336.
- Koste, W., 1978. Die Rädertiere Mitteleuropas (Ü. Ordnung Monogononta), Begr. von M. Voigt, Textband: 1–8 + 1–673 pp., Tafelband: T. 1–234. Gebr. Borntraeger Verlagsbuchhandlung, Berlin-Stuttgart.
- Koste, W., 1979. *Hexarthra mira*, ein sechsarmiges Planktonrädertier. Mikrokosmos 68: 134–139.
- Koste, W., 1979. New Rotifera from the River Murray, South-eastern Australia, with a review of the Australian species of *Brachionus* and *Keratella*. Australian Journal of Marine and Freshwater Research 30: 237–253.
- Koste, W., 1979. *Lindia deridderi* n. sp., ein Rädertier der Familie Lindiidae (Überordnung Monogononta) aus SE-Australien. Archiv für Hydrobiologie 87: 504–511.
- Koste, W. & R. J. Shiel, 1979. Rotifera recorded from Australia. Transactions of the Royal Society of South Australia 103: 57–68.
- Koste, W., 1980. *Brachionus plicatilis*, ein Salzwasserrädertier. Mikrokosmos 69: 148–155.
- Koste, W., 1980. Zwei Plankton-Rädertertaxa *Filinia australiensis* n. sp. und *Filinia hofmanni* n. sp., mit Bemerkungen zur Taxonomie der *longiseta-terminalis* Gruppe. Genus *Filinia* Bory de St. Vincent 1824, Familie Filiniidae Bartos 1959 (Überordnung Monogononta). Archiv für Hydrobiologie 90: 230–256.
- Koste, W. & R. J. Shiel, 1980. On *Brachionus dichotomus* Shephard 1911 (Rotatoria), Brachionidae from the Australian region. With a description of a new subspecies *Brachionus dichotomus reductus*. Transactions of the Royal Society of Victoria 91: 127–134.
- Koste, W. & R. J. Shiel, 1980. Preliminary remarks on the characteristics of the rotifer fauna of Australia (Notogaea). Hydrobiologia 73: 221–222.
- Koste, W. & R. J. Shiel, 1980. Rotifera from Australia. Transactions of the Royal Society of South Australia 104: 133–144.
- Koste, W., 1981. Zur Morphologie, Systematik and Ökologie von neuen monogononten Rädertieren (Rotatoria) aus dem Überschwemmungsgebiet des Magela Creek in der Alligator-River-Region Australiens, N. T., Teil 1. Osnabrücker Naturwissenschaftliche Mitteilungen 8: 97–126.
- Koste, W., 1981. Einige auffällende *Synchaeta*-Arten aus Küstengewässern. Mikrokosmos 71: 169–176.
- Koste, W., 1982. *Ploesoma truncatum*, ein räuberisches Plankton-Rädertier. Mikrokosmos 71: 167–173.
- Koste, W., 1982. Über *Dicranophorus robustus* Harring 1928, ein seltenes carnivores Rädertier aus der Familie Dicranophoridae (Überordnung Monogononta, Klasse Rotatoria). Osnabrücker Naturwissenschaftliche Mitteilungen 9: 65–84.
- Koste, W., G.-O. Brandorff & N. N. Smirnov, 1982. The composition and structure of rotiferan and crustacean communities of the lower Rio Nhamunda, Amazonas, Brazil. Studies on Neotropical Fauna and Environment, Amazonas, Brazil Environment 17: 69–121.
- Koste, W. & S. Jose de Paggi, 1982. Rotifera of the Superorder Monogononta recorded from Neotropis. Gewässer und Abwässer 68/69: 71–102.
- Koste, W. & E. Wobbe, 1982. Kleiner Führer für den Moorlehrpfad durch das Hahlener Moor, Gemeinde Menslage, Ortsteil Hahnenmoor, Landkreis Osnabrück, 1. Aufl., 1–42, Berge Krs. Osnabrück.
- Koste, W., 1983. *Lecane*, eine formen- und artenreiche Rädertiergattung. Mikrokosmos 72: 174–180.
- Koste, W. & R. Chengalath, 1983. Rotifera from northeastern Quebec, Newfoundland and Labrador, Canada. Hydrobiologia 104: 49–56.
- Koste, W. & J. Poltz, 1983. Über einen Fund des seltenen schlammbewohnenden *Paradicranophorus hudsoni* (Glascott, 1893), einem schlammbewohnenden Rädertier im Dümmer, NW-Deutschland. Osnabrücker Naturwissenschaftliche Mitteilungen 10: 27–41.
- Koste, W. & B. Robertson, 1983. Taxonomic studies of the Rotifera (Phylum Aschelminthes) from a Central Amazonian varzea lake, Lago Camalleao, Ilha de Marchantaria, Rio Solimões, Amazonas, Brazil. Amazoniana 8: 225–254.
- Koste, W. & R. J. Shiel, 1983. Rotifer communities of billabongs in northern and south-eastern Australia. Hydrobiologia 104: 41–47.
- Koste, W. & R. J. Shiel, 1983. Morphology, systematics and ecology of new monogonont Rotifera (Rotatoria) from Alligator river region, Northern Territory. Transactions of the Royal Society of South Australia 107: 109–121.
- Koste, W., R. J. Shiel & M. A. Brock, 1983. Rotifera from Western Australian wetlands with descriptions of two new species. Hydrobiologia 104: 9–17.
- Koste, W., 1984. *Trichotria tetractis* (Ehrenberg) und verwandte Arten. Mikrokosmos 73: 113–118.
- Koste, W. & J. Poltz, 1984. Über die Rädertiere (Rotatoria, Phylum Aschelminthes) des Dümmers, NW-Deutschland. Osnabrücker Naturwissenschaftliche Mitteilungen 11: 91–125.
- Koste, W., B. Robertson & E. R. Hardy, 1984. Further taxonomical studies of the Rotifera from Lago Camaleao, a Central Amazonian varzea lake (Ilha de Marchantaria, Rio Solimões, Amazonas Brazil). Amazoniana 8: 555–576.
- Koste, W. & E. R. Hardy, 1984. Taxonomic studies and new distribution records of Rotifera (Phylum Aschelminthes) from Rio Jatapu and Uatuma, Amazonas, Brazil. Amazoniana 9: 17–29.
- Hardy, E. R., B. Robertson & W. Koste, 1984. About the relationship between the zooplankton and fluctuating water levels of Lago Camaleão, a Central Amazonian varzea lake. Amazoniana 9: 43–52.
- Jose de Paggi, S. & W. Koste, 1984. Checklist of the Rotifers recorded from Antarctic and Subantarctic areas. Senckenbergiana biologica 65: 169–178.
- Lair, N. & W. Koste, 1984. The rotifer fauna and population dynamics of Lake Studer 2 (Kerguelen Archipelago) with description of *Filinia terminalis kergueliensis* n. sp. and a new record of *Keratella sancta* Russel 1944. Hydrobiologia 108: 57–64.

- Tait, R. D., R. J. Shiel & W. Koste, 1984. Structure and dynamics of zooplankton communities, Alligator Region N.T., Australia. *Archiv für Hydrobiologie* 113: 1–13.
- Koste, W., 1985. Zur Morphologie, Anatomie, Ökologie und Taxonomie von *Paradicranophorus wockei* Koste 1961 (Aschelminthes, Rotatoria, Dicranophoridae). *Senckenbergiana biologica* 66: 153–166.
- Koste, W., 1985. Das Rädertier-Porträt. *Cephalodella gigantea*, ein seltenes Rädertier der Faulschlammzone. *Mikrokosmos* 74: 168–173.
- Koste, W. & R. J. Shiel, 1985. New species and new records of Rotifera (Aschelminthes) from Australian Waters. *Transactions of the Royal Society of South Australia* 109: 1–15.
- Shiel, R. J. & W. Koste, 1985. Records of rotifers epizoic on cladocerans from South Australia. *Transactions of the Royal Society of South Australia* 109: 179–180.
- Koste, W., 1986. Über die Rotatorienfauna in Gewässer südöstlich von Concepcion, Paraguay, Südamerika. *Osnabrücker Naturwissenschaftliche Mitteilungen* 12: 129–155.
- Koste, W., 1986. *Collotheca edentata*, ein sessiles Rädertier “ohne” Zähne? *Mikrokosmos* 75: 302–305.
- Koste, W., & R. J. Shiel, 1986. Rotifera from Australian inland waters, 1. Bdelloidea (Rotifera: Digononta). *Australian Journal of Marine and Freshwater Research* 37: 765–792.
- Koste, W. & R. J. Shiel, 1986. New Rotifera (Aschelminthes) from Tasmania. *Transactions of the Royal Society of South Australia* 109: 93–106.
- Shiel, R. J., & W. Koste, 1986. Australian Rotifera: Ecology and Biogeography. In: De Deckker, P., & W. D. Williams (eds), *Limnology in Australia* CSIRO. Australia, Melbourne, *Monographiae Biologicae* 61: 141–150.
- Koste, W., 1987. *Asplanchnopus multiceps*, ein Rädertier, das Krebse frißt. *Mikrokosmos* 76: 170–175.
- Koste, W. & J. Poltz, 1987. Über Rädertiere (Rotatoria, Phylum Aschelminthes) des Alflsees, NW-Deutschland. *Osnabrücker Naturwissenschaftliche Mitteilungen* 13: 185–220.
- Koste, W. & R. J. Shiel, 1987. Tasmanian Rotifera: Affinities with the Australian mainland fauna. *Hydrobiologia* 147: 31–43.
- Koste, W. & R. J. Shiel, 1987. Rotifera from Australian inland waters, 2. Epiphaniidae and Brachionidae, (Rotifera: Monogononta). *Invertebrate Taxonomy* 1: 949–1021.
- Koste, W. & W. Tobias, 1987. Zur Rotatorienfauna des Sankarani-Stausees im Einzugsgebiet des Niger, Republik Mali, Westafrika. *Archiv für Hydrobiologie* 108: 499–515.
- Chengalath, R. & W. Koste, 1987. Rotifera from Northwestern Canada. *Hydrobiologia* 147: 49–56.
- Koste, W., 1988. Das Rädertierporträt. Die Gattung *Squatinella*. *Mikrokosmos* 77: 140–145.
- Koste, W., 1988. Rotatorien aus Gewässern am Mittleren Sungai Makaham, einem Überschwemmungsgebiet in E-Kalimantan, Indonesian Borneo. *Osnabrücker Naturwissenschaftliche Mitteilungen* 14: 91–136.
- Koste, W., 1988. Über die Rotatorien einiger Stillgewässer in der Umgebung der Biologischen Station Panguana im tropischen Regenwald in Peru. *Amazoniana* 10: 303–325.
- Koste, W. & S. Jose Paggi, 1988. Rotifers from Saladillo River Basin (Santa Fe Province, Argentina). *Hydrobiologia* 157: 13–20.
- Koste, W., R. J. Shiel & L. W. Tan, 1988. New rotifers (Rotifera) from Tasmania. *Transactions of the Royal Society of South Australia* 112: 119–131.
- Koste, W. & E. Vasquez, 1988. Form variations of the rotifer *Brachionus variabilis* (Hempel, 1896) from the Orinoco River, Venezuela. *Annales de Limnologie* 24: 127–129.
- Chengalath, R. & W. Koste, 1988. Composition of littoral rotifer communities of Cape Breton Island, Nova Scotia, Canada. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 23: 2019–2027.
- Koste, W., 1989. Über Rädertiere (Rotatoria) aus dem Lago do Macaco, einem Ufersee des mittleren Rio Trombetas, Amazonien. *Osnabrücker Naturwissenschaftliche Mitteilungen* 15: 199–214.
- Koste, W., 1989. *Octotrocha speciosa*, eine sessile Art mit einem merkwürdigen Räderorgan. *Mikrokosmos* 78: 115–121.
- Koste, W. & K. Böttger, 1989. Rotatorien aus Gewässern Ecuadors. *Amazoniana* 10: 407–438.
- Koste, W. & R. J. Shiel, 1989. Rotifera from Australian inland waters. 3. Euchlanidae, Mytilinidae, Trichotriidae. *Transactions of the Royal Society of South Australia* 113: 85–114.
- Koste, W., & R. J. Shiel, 1989. Rotifera from Australian inland waters. 4. Colurellidae. *Transactions of the Royal Society of South Australia* 113: 119–143.
- Koste, W. & R. J. Shiel, 1990. Rotifers from Australian inland waters. Lecanidae. *Transactions of the Royal Society of South Australia* 114: 1–36.
- Koste, W. & R. J. Shiel, 1989. Classical taxonomy and modern methodology. *Hydrobiologia* 186/187: 279–284.
- Koste, W. & W. Tobias, 1989. Die Rädertierfauna der Sélingue-Talsperre in Mali, Westafrika (Aschelminthes: Rotatoria). *Senckenbergiana biologica* 69: 441–466.
- Chengalath, R. & W. Koste, 1989. Composition and distributional patterns in arctic rotifers. *Hydrobiologia* 186/187: 191–200.
- Herzig, A. & W. Koste, 1989. The development of *Hexarthra* spp. in a shallow alkaline lake. *Hydrobiologia* 186/187: 129–136.
- Shiel, R. J., W. Koste & L. W. Tan, 1989. Tasmania revisited: Rotifer communities and habitat heterogeneity. *Hydrobiologia* 186/187: 239–245.
- Koste, W. & B. Robertson, 1990. Taxonomic studies of the Rotifera from shallow waters on the Island of Maraca, Roraima, Brazil. *Amazoniana* 11: 185–200.
- Koste, W. & R. J. Shiel, 1990. Rotifers from Australian inland waters. 6. Proalidae, Lindiidae. *Transactions of the Royal Society of South Australia* 114: 129–143.
- Koste, W. & W. Tobias, 1990. Zur Kenntnis der Rädertierfauna des Kinda Stausees in Zentral-Burma (Aschelminthes: Rotatoria). *Osnabrücker Naturwissenschaftliche Mitteilungen* 16: 83–110.
- Koste, W., 1991. *Anuraeopsis miraclei*, a new planktonic rotifer species in karstic lakes of Spain. *Hydrobiologia* 209: 169–173.
- Koste, W., W. Janetzky & E. Vareschi, 1991. Über die Rotatorienfauna in Bromelien-Phytotelmata in Jamaika (Aschelminthes: Rotatoria). *Osnabrücker Naturwissenschaftliche Mitteilungen* 17: 143–170.
- Koste, W. & R. J. Shiel, 1991. Rotifers from Australian inland waters. 7. Notommatidae (Rotifera), Monogononta. *Transactions of the Royal Society of South Australia* 115: 11–159.

- Koste, W., E. Vasquez & M. L. Medina, 1991. Variaciones morfológicas del rotífero *Keratella americana* (Carlin, 1943) de una laguna de inundación del Río Orinoco, Venezuela. *Revue d'Hydrobiologie Tropicale* 24: 83–90.
- Koste, W. & K. Böttger, 1992. Rotatorien aus den Gewässern Ecuadors. 2. Amazoniana 12: 263–303.
- Shiel, R. J. & W. Koste, 1992. Rotifera from Australian inland waters. 8. Trichocercidae (Monogononta). *Transactions of the Royal Society of South Australia* 116: 1–27.
- Koste, W., et al. (eds.), 1993. Rotifera: Guides to the identification of the microinvertebrates of the continental waters of the world. The Hague, Vol. 4: 1–7, 1–137.
- Koste, W. & E. D. Holloway, 1993. A short history of western European rotifer research. *Hydrobiologia* 255/256: 557–572.
- Brain, C. K. & W. Koste, 1993. Rotifers of the genus *Proales* from saline springs in the Namib desert, with the description of a new species. *Hydrobiologia* 255/256: 449–454.
- Hirschfelder, A., W. Koste & H. Zucchi, 1993. Bdelloid rotifers in aerophytic mosses: influence of habitat structure and habitat age on species composition. *Hydrobiologia* 255/256: 343–344.
- Jersabek, C. D. & W. Koste, 1993. Additional notes on taxonomy and ecology of *Anuraeopsis miraclei* Koste, 1991 (Rotatoria: Monogononta) from an Austrian alpine lake. *Hydrobiologia* 264: 55–60.
- Kizito, Y. S., A. Nauwerck, J. Chapman & W. Koste, 1993. A limnological survey of some Western Uganda crater lakes. *Limnologia* 23: 335–347.
- Peters, U., W. Koste & W. Westheide, 1993. A quantitative method to extract moss dwelling rotifers. *Hydrobiologia* 255/256: 339–341.
- Shiel, R. J. & W. Koste, 1993. Rotifera from Australian inland waters. 9. Gastropodidae, Synchaetidae, Asplanchnidae (Rotifera: Monogononta). *Transactions of the Royal Society of South Australia* 117: 111–139.
- Koste, W., W. Janetzky & E. Vareschi, 1994. Zur Kenntnis der limnischen Rotatorienfauna Jamaikas (Rotatoria: Aschelminthes). Teil I. Osnabrücker Naturwissenschaftliche Mitteilungen 19: 103–149.
- Janetzky, W., W. Koste & E. Vareschi, 1994. Rotifers of Jamaica: ecology, diversity and biogeography. *Jamaica Naturalist* 4: 16–20.
- Koste, W., W. Janetzky & E. Vareschi, 1995. Zur Kenntnis der limnischen Rotatorienfauna Jamaikas (Rotifera). Teil II. Osnabrücker Naturwissenschaftliche Mitteilungen 20/21: 399–433.
- Koste, W. & Y. Zhuge, 1995. On *Paradicranophorus aculeatus* (Neistwestnova-Shadina 7, 1935), with remarks on all other species of the genus (Rotifera: Dicanophoridae). *Internationale Revue der gesamten Hydrobiologie* 80: 121–132.
- Janetzky, W., W. Koste & E. Vareschi, 1995. Rotatorien in limnischen Mikrohabitaten: Phytotelmata und Gastrotelmata. *Deutsche Gesellschaft für Limnologie, Jahrestagung 1994 Hamburg. Erweiterte Zusammenfassungen.* 933–937.
- Janetzky, W., W. Koste & E. Vareschi, 1995. Rotifers (Rotifera) of Jamaican inland waters. A synopsis. *Ecotropica* 1: 31–40.
- Jose de Paggi, S. & W. Koste, 1995. Additions to the checklist of rotifers of the superorder Monogononta recorded from Neotropis. *Internationale Revue der gesamten Hydrobiologie* 80: 133–140.
- Koste, W., 1996. On soil Rotatoria from a Lithotelma near Halali Lodge in Etosha National Park in N-Namibia, South Africa. *Internationale Revue der gesamten Hydrobiologie* 81: 353–365.
- Koste, W., 1996. Über die moosbewohnende Rotatorienfauna Madagaskars. *Osnabrücker Naturwissenschaftliche Mitteilungen* 22: 235–253.
- Koste, W. & Y. Zhuge, 1996. A preliminary report on the occurrence of Rotifera in Hainan. *Quekett Journal of Microscopy* 37: 666–883.
- Segers, H., W. Koste & S. M. Yussuf, 1996. Contributions to the knowledge of the monogononta Rotifera of Zanzibar, with a note of *Filinia novaezealandiae* Shiel & Sanomuang, 1993. *Internationale Revue der gesamten Hydrobiologie* 81: 597–603.
- Zhuce, Y. & W. Koste, 1996. Two new species of Rotifera from China. *Internationale Revue der gesamten Hydrobiologie* 81: 605–609.
- Janetzky, W. J. & W. Koste, 1997. Rotifera in broemeliad phytotelma. <http://www.ifas.ufl.edu/~frank/robrom.htm>.
- Zhuce, Y. & W. Koste, 1997. Rotiferology in China. *Rotifer News* 1997: 9–10.
- Koste, W. & W. Tobias, 1998. Rädertiere des Manantali-Stausees in der Republik Mali, Westafrika (Aschelminthes: Rotatoria). *Senckenbergiana biologica* 77: 257–267.
- Koste, W. & Y. Zhuce, 1998. Zur Kenntnis der Rotatorienfauna (Rotifera) der Insel Hainan, China. Teil II. *Osnabrücker Naturwissenschaftliche Mitteilungen* 24: 183–222.
- Holst, H., H. Zimmermann, H. Kausch & W. Koste, 1998. Temporal and spatial dynamics of planktonic rotifers in the Elbe Estuary during spring. *Estuarine Coastal and Shelf Science* 47: 261–273.
- Leutbecher, C. & W. Koste, 1998. Die Rotatorienfauna des Dümmer unter besonderer Berücksichtigung der sessilen Arten. Teil 1. *Osnabrücker Naturwissenschaftliche Mitteilungen* 24: 223–255.
- Zhuce, Y., H. Xiangfei & W. Koste, 1998. Rotifera recorded from China, 1893–1997, with remarks on their composition and distribution. *International Review of Hydrobiology* 83: 217–232.
- Koste, W., 1999. Über Rädertiere (Rotifera) aus Gewässern des südlichen Pantanal (Brasilien). *Osnabrücker Naturwissenschaftliche Mitteilungen* 25: 179–209.
- Koste, W., 2000. Study of the Rotatoria-Fauna of the littoral of the Rio Branco, South of Boa Vista, Northern Brazil. *International Review of Hydrobiology* 85: 433–469.
- Koste, W. & H. Terlutter, 2001. Die Rotatorienfauna einiger Gewässer des Naturschutzgebietes "Heiliges Meer" im Kreis Steinfurt. *Osnabrücker Naturwissenschaftliche Mitteilungen* 27: 113–177.

Part I
Phylogeny and Evolution

On the phylogenetic position of Rotifera – have we come any further?

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Abstract

Rotifers are bilateral symmetric animals belonging to Protostomia. The ultrastructure of the rotiferan trophi suggests that they belong to the Gnathifera, and ultrastructural similarities between the integuments and spermatozoa as well as molecular evidence strongly suggest that rotifers and the parasitic acanthocephalans are closely related and form the clade Syndermata. Here we discuss the phylogenetic position of rotifers with regard to the gnathiferan groups. Originally, Gnathifera only included the hermaphroditic Gnathostomulida and the Syndermata. The synapomorphy supporting Gnathifera is the presence of pharyngeal hard parts such as jaws and trophi with similar ultrastructure. The newly discovered Micrognathozoa possesses such jaws and is a strong candidate for inclusion in Gnathifera because their cellular integument also has an apical intracytoplasmic lamina as in Syndermata. But Gnathifera might include other taxa. Potential candidates include the commensalistic Myzostomida and Cyclophora. Traditionally, Myzostomida has been included in the annelids but recent studies regard them either as sister group to the Acanthocephala or Cyclophora. Whether Cyclophora belongs to Gnathifera is still uncertain. Some analyses based on molecular data or total evidence point towards a close relationship between Cyclophora and Syndermata. Other cladistic studies using molecular data, morphological characters or total evidence suggest a sister group relationship between Cyclophora and Entoprocta. More molecular and morphological data and an improved sampling of taxa are obviously needed to elucidate the phylogenetic position of the rotifers and identify which phyla belong to Gnathifera.

Introduction

Our knowledge about the phylogenetic affinities of the Rotifera has increased a lot within the latest decade. Throughout time they have been considered relatives to the Infusoria, Crustacea, Tardigrada, Nematoda, Annelida, Mollusca, Gastrotricha and Platyhelminthes (Remane, 1929–1933; Hyman, 1951; Clément, 1985) and more recently as a member of the obviously polyphyletic group named ‘Aschelminthes’ (Ruppert & Barnes, 1994; Wallace et al., 1996). A close relationship between the

Rotifera and Acanthocephala has been broadly accepted since Storch & Welsch (1969, 1970) demonstrated the ultrastructural similarities in the integuments of the two groups, and today most taxonomists unite them in the taxon Syndermata Ahlrichs, 1995.

A possible homology between the jaws of rotifers and gnathostomulids was first suggested by Ax (1956) and Reisinger (1961). An increasing amount of data now supports a close relationship between Rotifera, Gnathostomulida, Micrognathozoa and Acanthocephala united in a group

named Gnathifera (Ahlrichs, 1995a, b, 1997; Rieger & Tyler, 1995; Haszprunar, 1996a; Melone et al., 1998; Kristensen & Funch, 2000; Sørensen, 2000, 2003; Jondelius et al., 2002; Sørensen & Sterrer, 2002; Zrzavý, 2003). Several synapomorphies have been proposed for Gnathifera, and even though some of these may be questionable (see Jenner, 2004), the presence of jaws with a unique ultrastructure appears to be a strong support argument for gnathiferan monophyly.

Some problems, however, still remain and new questions appear. The phylogenetic position of Gnathifera in the Metazoa is still uncertain and recently, new studies have questioned the monophyly of Gnathifera (Giribet et al., 2004). Cladistic analyses based partly or solely on molecular data imply that Gnathifera might be polyphyletic (Littlewood et al., 1998; Zrzavý et al., 1998; Peterson & Eernisse, 2001) or paraphyletic, for example, in respect to Cycliophora, Gastrotricha or Myzostomida (Cavalier-Smith, 1998; Giribet et al., 2000; Zrzavý et al., 2001; Giribet, 2002). Many studies based on morphological as well as molecular data have proposed that the Acanthocephala should be considered highly advanced rotifers (Lorenzen, 1985; Garey et al., 1996; Ahlrichs, 1997; Garey et al., 1998; Mark Welch, 2000; Herlyn et al., 2003) and most recently it was suggested that the newly described taxon Micrognathozoa (Kristensen & Funch, 2000) is sister group to the monogonont rotifers (De Smet, 2002).

Here we will discuss some of the conflicting proposals about rotifer relationships. We focus primarily on two newly described taxa, Cycliophora and Micrognathozoa, but also make some comments to the position of the Acanthocephala, Myzostomida, and Gnathifera within the Metazoa.

Discussion

Cycliophora – newly discovered taxon with rotifer affinities?

Among metazoans the Cycliophora is the most recently described major taxon. So far, only one marine species *Symbion pandora* Funch & Kristensen 1995 is known. This microscopic animal lives as a commensal on the mouth parts of the Norway lobster *Nephrops norvegicus* (Linné).

Throughout the metagenetic life cycle of *S. pandora* six different stages emerge of which the sessile feeding individual is the largest (approx. 350 μm) and most prominent one. It is the only stage with an alimentary tract and is permanently attached to the host with an adhesive disc (Fig. 1, ad). The body of the feeding individual has a bell-shaped buccal funnel (Fig. 1, bf) and an ovoid trunk. The buccal funnel carries a mouth ring (Fig. 1, mr₁) consisting of multiciliated cells with compound cilia. The feeding apparatus works as a downstream collecting system (Riisgård et al., 2000) that filters food particles generated from the feeding activities of the host. The mouth leads into a U-shaped gut that terminates in an anus that is situated close to the buccal funnel (Fig. 1, an). The entire alimentary apparatus is periodically replaced by internal budding (Fig. 1, ib). A fluid-filled body cavity is absent (Funch & Kristensen, 1997).

Three different stages develop in the brood chamber of the feeding individual (Fig. 1, bc). The asexual developed Pandora larva (Fig. 1, pl) is approximately 120 μm long and equipped with an antero-ventral ciliated disc, various frontal glands, long and stiff, sensory cilia, and an internal bud from which a new feeding individual will arise. The asexually developed male larva (Prometheus larva) is approximately 100 μm long and has an antero-ventral ciliated disc, various glands and several pairs of long, stiff cilia anteriorly. Several dwarf males arise from internal buds within this larva (Obst & Funch, 2003). The dwarf male, approximately 33 μm in length, has a complex morphology with two ciliated fields covering the anterior and ventral body. It has various sensory structures, gland complexes, a relatively large brain connected to a pair of ventral longitudinal nerves, and numerous muscle cells. The reproductive system of the male is located in the posterior part of the body and consists of an unpaired testis, several adjacent gland cells, and a ventral penis connected to some of the muscle cells. The female, which is also developed in the brood chamber of the feeding individual (Fig. 1, bc), grows to a size of about 150–190 μm , and is morphological like the Pandora larva. However, the female contains a single egg instead of a bud. After fertilization the embryo grows inside the female, nourished by the degenerating maternal tissue and develops into a chordoid larva with a size of about 200 μm and a

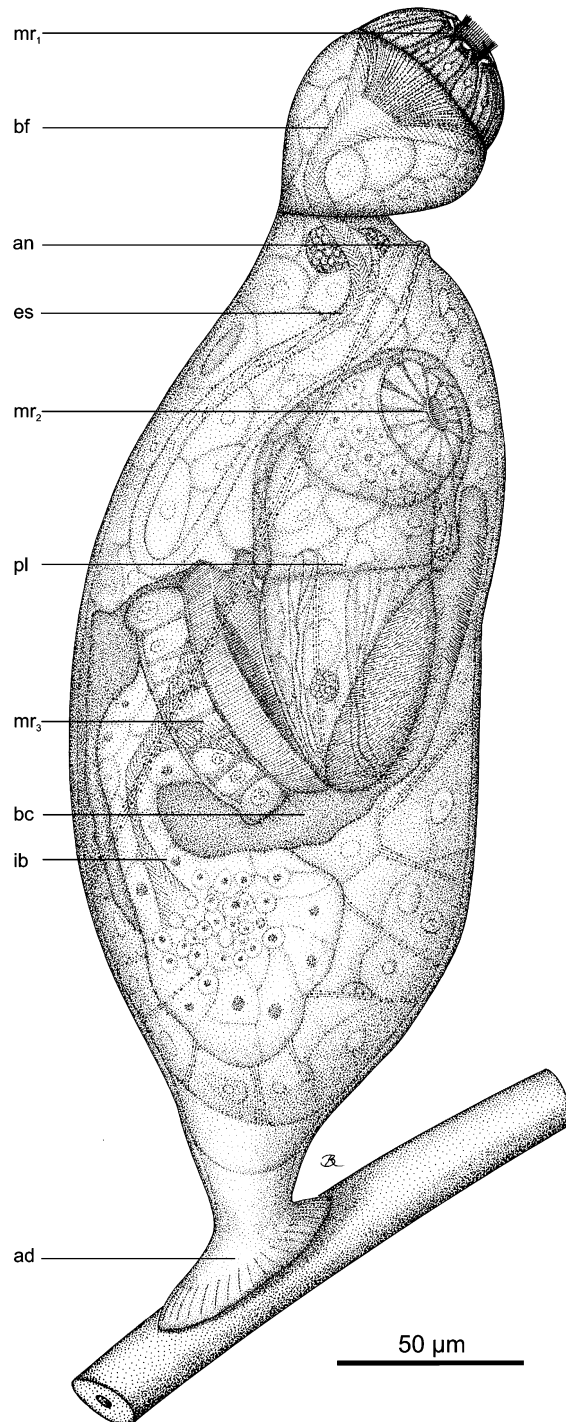


Figure 1. A young feeding stage of *Symbion pandora* (Cycliophora) on a seta from the host *Nephrops norvegicus*, lateral view. ad – adhesive disc; an – anus; bc – brood chamber; bf – buccal funnel; es – esophagus; ib – inner bud; mr₁ – functional mouth ring on feeding stage; mr₂ – mouth ring inside developing Pandora larva; mr₃ – developing mouth ring on inner bud; pl – Pandora larva. From Funch & Kristensen (1997).

complex morphology (Funch, 1996). The external ciliation of the chordoid larva consists of two anterior bands, two large ventral fields, and different sensory structures. The ciliated areas of the chordoid larva have been proposed to be homologous to those of a trochophore (Funch, 1996). Internally, the chordoid larva possesses a brain connected to a pair of ventral longitudinal nerves, a pair of protonephridia, a longitudinal rod of stacked muscle cells (chordoid organ), several gland and muscle complexes and one or two clusters of budding cells. Only a single host is known in the life cycle, and the chordoid larva is regarded as the dispersal stage between hosts.

Evaluation of the phylogenetic affinity between Cycliophora and Syndermata

In the original description of *Symbion pandora*, Funch & Kristensen (1995) proposed a close relationship between Cycliophora and Entoprocta and/or Bryozoa. Since then phylogenetic analyses have resulted in two competing hypotheses. Some analyses based on morphological data or total evidence support a Cycliophora–Entoprocta relationship (Zrzavý et al., 1998; Sørensen et al., 2000; Zrzavý, 2003), while others support a Cycliophora–Syndermata relationship (Peterson & Eernisse, 2001; Zrzavý et al., 2001). Analyses using molecular data or total evidence often favour a Cycliophora–Syndermata relationship (Winnepenninckx et al., 1998; Giribet et al., 2000; Peterson & Eernisse, 2001; Zrzavý et al., 2001). Based on both morphological and molecular data Zrzavý et al. (2001) proposed a monophyletic group including Cycliophora, Myzostomida, and Syndermata. This putative group was supported by three synapomorphies: (1) sperm with anteriorly inserted flagellum, (2) sperm without an accessory centriole, and possibly (3) the general tendency to live in association with crustaceans. However, it is not known if the flagellum in the cycliophoran sperm inserts anteriorly (Funch & Kristensen, 1997). An accessory centriole is apparently lacking in the sperm of *S. pandora*, but is also absent in several other taxa, i.e. some Gastrotricha and Platyhelminthes (Ferraguti & Balsamo, 1994; Ahlrichs, 1995b). Furthermore, the lack of an accessory centriole could be correlated with the evolution of the filiform sperm which probably

occurred more than once (Jenner, 2004). The association with crustaceans as a ‘possible support’ for Cycliophora, Myzostomida, and Syndermata being monophyletic (Zrzavý et al., 2001) is of dubious character. Most rotifers, acanthocephalans, and all myzostomids are not associated with crustaceans, and this synapomorphy would require numerous independent losses of symbiosis with crustaceans. One also may speculate whether the cycliophoran affiliation to the lobster’s mouth parts, the seisonid association with *Nebalia*, and the acanthocephalan endoparasitism in various crustaceans are so similar that they are products of one unique evolutionary event.

In a phylogenetic analysis using morphological data Peterson & Eernisse (2001) placed Cycliophora in a trichotomy with Rotifera and Gnathostomulida + Platyhelminthes, but Acanthocephala and *Seison* were not included. No unambiguous support for a Cycliophora–Rotifera relationship was found and the entire clade had a low Bremer and bootstrap support. Hence, none of the morphological analyses are able to produce consistent support for the suggested affinities between Cycliophora and Syndermata, even though they do share some superficial similarities.

Both the cycliophoran mouth ring and the rotiferan corona have bands of compound cilia that function as a downstream-collecting system, but this seems to be a general feature of ciliary suspension feeding protostomes (Riisgård et al., 2000; Nielsen, 2001). Also, the ability to retract the feeding structures differs, while the corona of rotifers can be retracted into the trunk, the mouth ring of cycliophorans cannot (Funch & Kristensen, 1997). The cycliophoran chordoid larva possesses one pair of multiciliated lateral pits and one paired dorsal ciliated organ, somewhat resembling the lateral and dorsal antennae in rotifers (Funch, 1996). In addition the sensory structures of rotifer and cycliophoran dwarf males have a somewhat similar morphology but their homology has yet to be assessed (see Obst & Funch, 2003).

Based on an ultrastructural study of the cycliophoran male and comparison with literature descriptions of rotiferan males, Obst & Funch (2003) argued that the presence of dwarf males in Rotifera and Cycliophora is a result of a convergent evolution. This is in agreement with the

generally accepted idea that dwarf males have evolved within Syndermata (Wallace & Colburn, 1989; Ahlrichs, 1997; Melone et al., 1998; Sørensen, 2002), since *Seison* (Ricci et al., 1993) and some monogonont rotifers (Wesenberg-Lund, 1923; Hermes, 1932) possess fully developed males. The ontogeny differs as well, while the males of monogonont rotifers develop from haploid eggs produced by mictic females (Wallace, 1999); cyclophoran males develop from budding cells inside a male larva. Also, the copulatory organ in monogonont males consists of several cell types (Aloia & Moretti, 1973; Gilbert, 1983), and sometimes bears a ciliated crown around the genital pore (Clément et al., 1983). The cuticular penis of *S. pandora* is more simple and without cilia (Obst & Funch, 2003). The external ciliation of the dwarf male of *S. pandora* is more extensive than in rotiferan males and consists of two separated ciliated fields (Obst & Funch, 2003). The corona of monogonont dwarf males usually consists of a single anterior terminal disk of cilia or a girdle surrounding bundles of cilia (Hyman, 1951).

In contrast to syndermates *S. pandora* has a true cuticle that is formed from the cellular epidermis. The regenerative powers between rotifers and cyclophorans differ as well; while rotifers are poor in regeneration and apparently lack cell divisions in the adults (Hyman, 1951), *S. pandora* is able to replace the alimentary apparatus periodically or develop individual stages from internal buds. Also cuticular jaws are absent in *S. pandora*.

In summary, the morphological data supporting cyclophoran–syndermate affinity are weak and since all molecular analyses including cyclophorans mentioned above, used the same partial 18S rDNA sequence, the resulting relationships have to be treated with caution. For example Zrzavý et al. (2001) found support for the Syndermata relationship and Zrzavý (2003) for the Entoprocta relationship. Both studies used total evidence with 18S rDNA data. In a recent cladistic study Giribet et al. (2004) used four molecular loci (18S rDNA, a fragment of 28S rDNA, the nuclear protein-coding gene histone H3 and the mitochondrial gene cytochrome *c* oxidase subunit I) and a dense sampling of gnathiferan taxa, but the phylogenetic position of Cyclophora was still unstable. All four loci tended to place Cyclophora with Syndermata. Ribosomal and nuclear loci

tended to place Cyclophora with Entoprocta. Alternatively, nuclear loci tended to place Cyclophora with Micrognathozoa and Syndermata. The support for closely related syndermates and cyclophorans is too weak (Fig. 6), and a relationship between Cyclophora and Entoprocta cannot be ruled out. Better comparative morphological studies of the possible homologies mentioned here are clearly needed to clarify a possible relationship between Cyclophora and Syndermata.

Micrognathozoa – sister group to Syndermata or aberrant rotifer?

Recently, a new microscopic taxon named Micrognathozoa was described from a cold spring on Disko Island, Greenland (Kristensen and Funch, 2000). At present it comprises a single species named *Limmognathia maerski* Kristensen and Funch and its possession of an intracytoplasmic lamina and complicated pharyngeal hard parts (Fig. 2, ja) suggest a close relationship with Rotifera.

With more than 15 paired or unpaired sclerites the micrognathozoan jaws are more complex than the pharyngeal hard parts found in any other microinvertebrate (Fig. 3). However, Kristensen & Funch (2000) demonstrated that the ultrastructure of the sclerites was very similar to that of the rotifer trophi. Based on a detailed comparison with the rotifer trophy, Kristensen & Funch (2000) proposed that the micrognathozoan main jaws and symphysis were homologous with the rotifer incus and that the micrognathozoan pseudophalugia and associated sclerites corresponded to the rotifer mallei, and these proposals were later supported by Sørensen (2003). Furthermore, Sørensen (2003) noted that the pharyngeal lamellae could be homologous with parts of the rotifer epipharynx, but it would be premature to draw this conclusion since the ground pattern of the rotifer epipharynx is not yet fully understood.

De Smet (2002) recently made a new attempt to understand the highly complicated jaws of Micrognathozoa. In a comprehensive description of the hard parts he pointed out several previously undescribed structures, such as the prominent brush on the main jaws and the circular platelet between the basal plates (Fig. 3, (cp), mj, vmj). Furthermore, he reinterpreted the already known

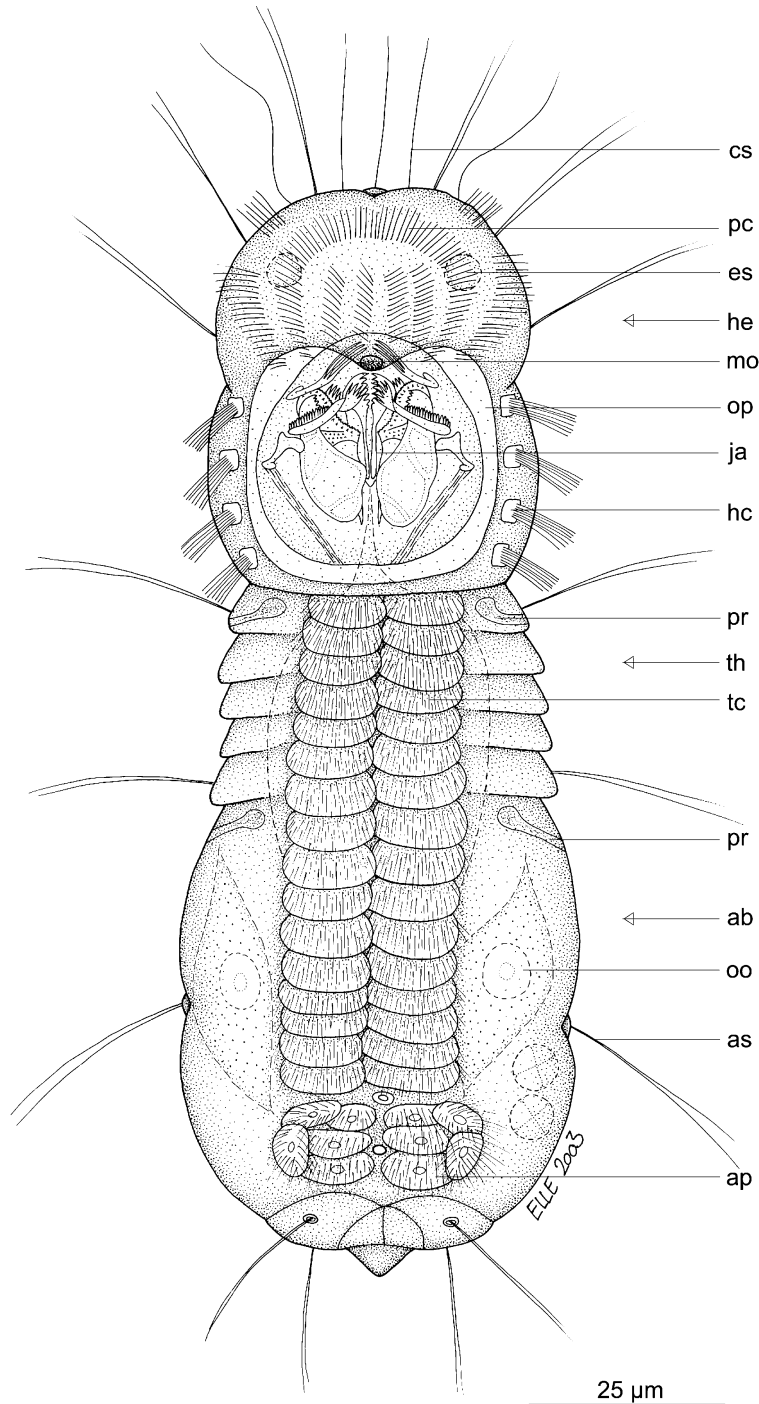
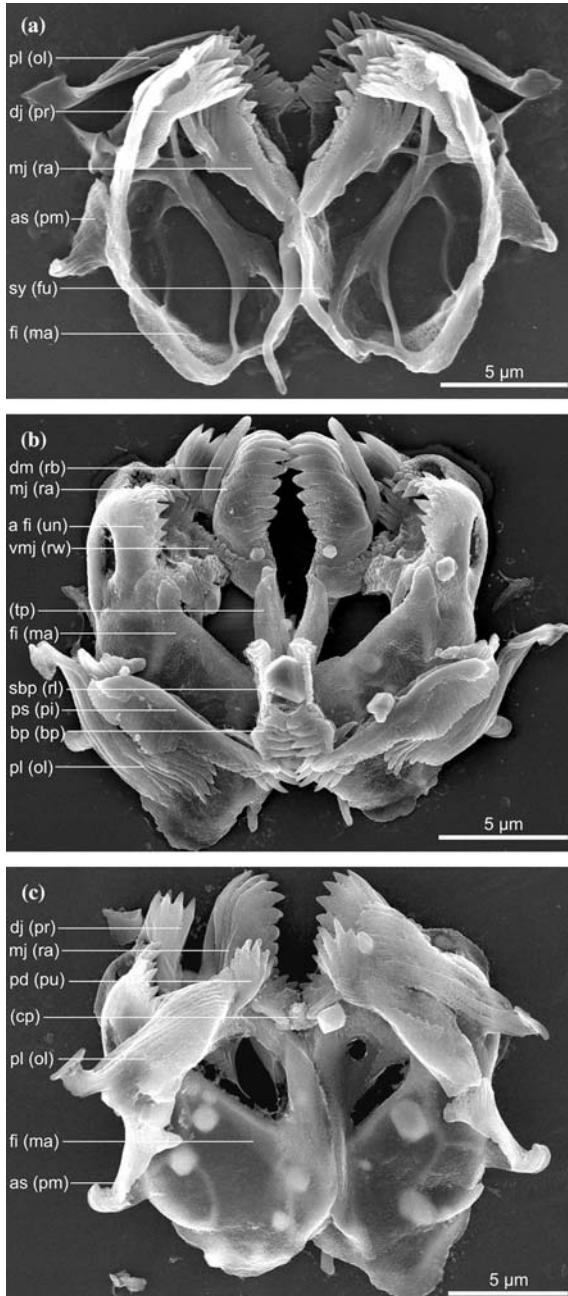


Figure 2. Drawing of *Limnognathia maerski* (Micrognathozoa), ventral view. ab – abdominal sensory bristle; ap – adhesive pad; cs – cephalic sensory bristles; es – eyespot; hc – head ciliophore; he – head; ja – jaws; mo – mouth; oo – oocyte; op – oral plate; pc – preoral ciliary bands; pr – protonephridium; tc – trunk ciliophores; th – thorax. Courtesy of R. M. Kristensen, Zoological Museum, University of Copenhagen.



structures and made a detailed comparison with the rotiferan trophi. Based on these observations De Smet (2002) supports the previously proposed homology between the main jaws, plus symphysis (Fig. 3, mj, sy, vmj) and the rotifer incus, but rejects a possible homology between the pseudophalugia (Fig. 3, ps) including the associated

Figure 3. *Limnognathia maerski* (Micrognathozoa), SEM photographs of jaws. (a) Dorsal view. (b) Ventral view, note that basal plates, pharyngeal lamellae and pseudophalugia are tilted backwards. (c) Ventral view. Abbreviations are given *sensu* Kristensen & Funch (2000) and Sørensen (2003). Abbreviations in parenthesis are *sensu* De Smet (2002). a fi (un) – anterior part of fibularium (uncus); as (pm) – associate sclerite (pseudomanubrium); bp (bp) – basal plate (basal platelets); (cp) – (circular platelet); dj (pr) – dorsal jaw (pleural rod); dm (rb) – dentes medialis (rami brush); fi (ma) – fibularium (manubrium); mj (ra) – main jaw (ramus); ps (pi) – pseudophalangium (pseudintramalleus); pd (pu) – pseudodigits (pseuduncus); pl (ol) – pharyngeal lamella (oral lamella); sbp (rl) – shaft of basal plate (reinforced ligament); sy (fu) – symphysis (fulcrum); (tp) – triangular plate; vmj (rw) – ventral part of main jaw (reinforced web).

sclerites and the rotifer mallei, and homologizes instead the mallei and the micrognathozoan fibularia (Fig. 3, fi). Moreover, he compares several of the remaining micrognathozoan sclerites with the rotifer trophi and homologizes them with different epipharyngeal sclerites, and concludes that these similarities support ‘a sister-group relationship between Micrognathozoa and Rotifera Monogononta’ (De Smet, 2002).

Evaluation of the proposed relationship between Micrognathozoa and Monogononta

De Smet’s (2002) interpretation of the micrognathozoan jaws and suggested homologies with the rotiferan trophi are interesting in a phylogenetic as well as a comparative context and deserve some comment. The suggested homology between the fibularia (Fig. 3, fi) and the mallei are possible, but on the other hand it is difficult to find consistent morphological support for this assumption. De Smet (2002) interprets the anterior part of the fibularium as an uncus that is fused caudally with the manubrium, and notes that such an arrangement is not uncommon in rotifers. Fused unci and manubria are truly present in different taxa, for example, in all bdelloids and several monogonont taxa, such as *Birgea*, *Tylotricha*, and Testudinellidae, but this character is nevertheless problematic. First, nothing indicates that fusion of the unci and manubria in *Birgea* and *Tylotricha* is homologous with the arrangement found in Flosculariaceae and Bdelloidea. Second, the general appearance of the micrognathozoan fibularium differs significantly from the mallei in Bdelloidea

as well as in Flosculariacea and Ploima. In Micrognathozoa the fibularium has four chambers (exclusive the anterior-most one), whereas the rotifer manubrium has three or fewer. The fibularium is moreover connected with the main jaws via a unique structure named the reinforced web (Fig. 3, vmj (rw) (De Smet, 2002). Such an interconnection is not known in rotifers. Hence, from our point of view, nothing indicates that a homology between the malleus and fibularium is more likely than a homology between the malleus and the pseudophalangium with its associated sclerite. Nothing really favours the latter possibility, so at present this problem must be considered unresolved.

De Smet (2002) also homologizes the micrognathozoan dorsal jaws and pseudophalangia + associated sclerites (Fig. 3, dj, ps) with the rotiferan pleural rods and pseudomallei, respectively, but this assumption is questionable. First, the morphology of the epipharyngeal elements is very diverse, and our understanding of their basic patterns is still very limited. Thus, comparisons based on morphological similarities should be done with great care. The question can, however, be analyzed from a cladistic point of view. If *Limnognathia* is considered sister group to Rotifera, or even sister group to the Monogononta, and possesses pleural rods and pseudomallei that are homologous with those found in different ploimid taxa, it implies that these sclerites were present in the rotifer or monogonont ground plan. Pleural rods and pseudomallei are only present in some rotifers, and the structures do not necessarily co-occur in the same species. *Lindia* has pseudomallei, but lack pleural rods, while *Birgea* has pseudounci but lacks other pseudomallei sclerites. If all these elements should be present in the rotiferan ground plan it would require numerous secondary reductions, and if the presence of fused unci and manubria is added to this ground plan the number of necessary character transformations increases even more. Hence, we do not agree with the statement by De Smet (2002): ‘that the jaws of *Limnognathia* can be homologized easily with the trophi of the monogonont Rotifera’. These uncertainties clearly demonstrate that it is premature to include Micrognathozoa as a subtaxon in Rotifera. It is furthermore noteworthy that Micrognathozoa deviate from monogonont rotifers at several points.

The integument is, as noted above, syncytial in both Acanthocephala and Rotifera, whereas the micrognathozoan epidermis is cellular. The structure of the integuments of Micrognathozoa and Syndermata could be explained by the following evolution: the ancestor of Micrognathozoa + Syndermata acquired a dense apical intracytoplasmic lamina that perhaps served as a cytoskeleton, and after the deviation of Micrognathozoa, the epidermis in the syndermate ancestor became a syncytium. Bender & Kleinow (1988) have shown that the intracytoplasmic lamina consists of keratin-like proteins in *Brachionus*. The integument of Acanthocephala also contains keratin (Dunagan & Miller, 1991), while the biochemical composition of the lamina in Micrognathozoa is unknown.

The ventral epidermis in *Limnognathia* is ciliated but posterior to the mouth the epidermis secretes a conspicuous cuticular oral plate (Fig. 2, op). This is in contrast to all known rotifers, where the ciliation of the epidermis is confined to the anterior corona and where no external cuticular oral plate is known. It is, however, interesting that Micrognathozoa has a ventral ciliation like in Gastrotricha. According to Rieger (1976) Gnathostomulida and Gastrotricha represent the most primitive bilaterians with respect to the construction of their integument, and Beauchamp (1909, 1965) actually suggested that both rotifers and gastrotrichs evolved from a ciliated crawling ancestor.

The gut epithelium of the micrognathozoans lacks cilia and has a brush border of microvilli as in Seisonidea (Ricci et al., 1993; Ahlrichs, 1995b) and Gnathostomulida (Lammert, 1991). The gut epithelium in monogonont rotifers is both ciliated and with microvilli, while a syncytial stomach epithelium seems to be autapomorphic for bdelloids (Clément & Wurdak, 1991; Melone et al., 1998). Of importance is also the fact that the micrognathozoan body plan is compact and has no fluid-filled extracellular compartment such as the often spacious pseudocoel in Syndermata (Wallace et al., 1996).

The Micrognathozoa possesses protonephridia (Fig. 2, pr) with two pairs of terminal cells. Interestingly, all the cells of these organs are monociliated as in Gnathostomulida and some Gastrotricha but contrary to all protonephridial