



Review Paper

The undiscovered country: ten grand challenges in rotifer biology

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Abstract Authors have attributed the statement “All science is either physics or stamp collecting” to the Physicist, Ernest Rutherford. Putting this sarcastic quip aside, we know that scientific disciplines come of age when they can generate testable, repeatable, and falsifiable hypotheses; yet disciplines begin, and continue, by simply collecting observational information. It is clear, even with a casual assessment of all 16 International Rotifer Symposia, as well as the extensive literature published since our first congress, that rotifer research has moved beyond describing species, making lists of their occurrences, and describing changes in their population dynamics. In spite of the excellent progress that has been made in rotiferology we believe more remains to be done. In

this review we nominate 10 fields in rotifer research that we believe will advance understanding of rotiferan biology; these include the following topics: (1) neurobiological connectomes, (2) genomic architecture and control systems, (3) physiology, (4) life history, including sexuality, development, and aging, (5) ecological responses to stresses, (6) biogeography and distribution of cryptic species, (7) analysis of rotiferan morphospace, (8) rotifer evolution within Gnathifera including Acanthocephala, (9) educational opportunities for beginning students, and (10) fostering international collaboration.

Keywords Biogeography · Ecology · Evolution · Genetics · Morphology · Physiology

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Rotifers in Diverse Ecosystems

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Introduction

All science is either physics or stamp collecting—physicist, E. Rutherford (Johnson, 2007; Gonzalez-Gualda et al., 2021).

Before scientific disciplines come of age, they collect information (observational data); thus, to *Rutherford's* perspective they would appear to be little more than stamp collecting. But gathering additional information is absolutely necessary, and once a certain amount is accumulated, it is possible for scientists to begin generating rigorous testable, repeatable, and falsifiable hypotheses. That is how all disciplines

start, including physics, and, of course, they all continue gathering data in that manner. We offer four well-known examples to illustrate this point. (1) It can be said that evolutionary biology began its real maturation when Darwin and Wallace, and before them von Humboldt, collected enormous amounts of data on the forms and biogeography of life (Schrodt et al., 2019). (2) Understanding cosmology and the expanding universe was not possible until the meaning of the redshift in light from stars and galaxies, gravitational waves, and the background radiation at ~ 2.73 K was understood (Fraknoi et al., 2018). (3) Mapping the ocean floor initiated a profound shift in our perception of the structure of the earth's crust and mountain building, which led to the theory of plate tectonics (Hazen, 2010). (4) A compelling construct that explained the Cretaceous-Paleogene mass extinction of Mesozoic life could only become established after the Chicxulub structure was identified and elucidated (Goderis et al., 2021). Each of these examples was essential and afforded a tipping point—a paradigm shift—within their discipline from which significant advances were made (Kuhn, 1970).

Here we are concerned with rotifers (*L. rota*, wheel, *L. ferra*, to bear) —the ‘wheeled animalcules’—and how their studies may provide insights into the ecology and evolution of life (Wallace et al., 2006). There are several reasons to study rotifers. While the following are important examples, we recognize that they are not an exhaustive accounting. (1) As grazers, rotifers play significant roles in energy flow and biomass, especially in freshwater food webs. (2) Rotifers display a wide variety of reproductive strategies across their ecological and phylogenetic spectra. The marine epizoic seisonids are obligately sexual; most marine and freshwater monogononts are cyclical parthenogens (but some populations/species have apparently become totally asexual through the loss of sex); and bdelloids are entirely asexual. The evolution of these different reproductive strategies remains poorly known, but bdelloid asexuality appears to be linked to horizontal gene transfer. (3) Dormancy and resistance to prolonged desiccation is seen in both bdelloids and monogononts; study of that phenomenon has ecological, as well as important, potentially practical importance (i.e., developing preservation techniques for cells or organs). (4) Some rotifers (e.g., *Asplanchna*, *Brachionus*) undergo transgenerational changes in body shape induced

by environmental factors in the F1 generation. (5) Recently a few species have been demonstrated to release interesting biomolecules that may have important health implications. (6) Rotifers are small and easily and inexpensively cultured; this makes them ideal models for a variety of studies, including aging, ecotoxicology, phylogeny, and population dynamics. Moreover, they are natural food for larvae of invertebrates and vertebrates, making them important in commercial aquaculture.

Within this panoply of topics, rotifer research has progressed to the point that it is no longer exclusively rotifer-centric; to a greater extent investigators are crossing disciplinary boundaries to include comparisons to other aquatic taxa, as well as using techniques and topics gleaned from other fields. Indeed, maturation of rotiferology is easily seen by inspection of publications from all 16 meetings of the IRS, as well as numerous other venues. Rotifer biology has come a long way from describing new species, documenting their anatomy, making lists of their occurrences, and describing the changes in their population dynamics. Undeniably, so much has been published over the past few decades that it is impossible to appraise the entire scope of rotifer research; and clearly many unresolved, controversial issues remain to be explored. It is obvious that more remains to be done. Here we review 10 grand challenges that we believe warrant greater attention from rotiferologists. Nevertheless, we recognize that this brief compendium is by no means exhaustive, either in scope of what we cover or in what we excluded due to lack of space. All the topics we advance are amenable to being developed into testable hypotheses with appropriate technologies.

Neurobiological connectomes

An understanding of the design of an invertebrate nervous system may shed light on the construction of nervous systems in general—D. Kennedy (1971).

With advances in imaging and genetics, it is now possible to map the connectomes of invertebrates: i.e., determine the structural connectivity of an entire nervous system, thereby creating a map of all the neurons. The next step would be to associate neurological pathways to specific behaviors. This has been advanced for many species including

Caenorhabditis elegans (Maupas, 1900) (Sohn et al., 2011; Bentley et al., 2016). Yet there are advantages to using rotifers in the study of connectomes. They often occur in large numbers in natural habitats; many species are easily cultured (Wallace et al., 2006); they are considered eutelic (Hyman 1951) [but compare (Ricci & Covino, 2005)]; neural topology is relatively conservative (Kotikova et al., 2005; Hochberg, 2007; Leasi et al., 2009; Hochberg & Hochberg, 2015; Gasiorowski et al., 2019) and the cerebral ganglion is simple and innervation is uncomplicated (Clement et al., 1983; Hochberg, 2009). Moreover, rotifers exhibit a wide behavioral repertoire that may be examined for phenotypic correlations with neurology; these include egg laying and guarding, mating, substrate selection, food preferences, and swimming (Wallace, 1980; Clement et al., 1983; Clément, 1987; Mimouni et al., 1993; Joanidopoulos & Marwan, 1998; Snell et al., 2007; Gilbert, 2019).

Challenges

Early studies provided interesting insights into the rotifer nervous system. Hyman (p. cit.: pp 99) reported the work of Martini (1912) who recorded the number of nerve cells in *Epiphanes senta* (Müller, 1773): i.e., brain ($n=183$) and peripheral nervous system (PNS) ($n=63$), for a total of 246 cells in the nervous system (NS). Therefore, with ~950 total cells we estimate that in *E. senta* the connectome comprises ~26% of all cells, with the brain consisting of ~19% and the PNS ~7%. Moving on from these early descriptive studies, rotiferologists have taken advantage of new developments in immunocytochemistry and imaging (CLSM) to substantially improve our understanding of the rotiferan NS. Yet data still are limited to relatively few species and do not reveal substantial insights into connectome diversity across the phylum. Thus, several questions about rotiferan neurobiology remain unanswered; these include the following. (1) What is the significance (i.e., functional, systematic) of the different neural patterns observed in cerebral ganglia (Kotikova et al., 2005)? (2) Are there functional centers in the rotifer brain? (3) How many types of neural circuits (motifs) are present in the connectome? (4) Can the connectome circuitry be linked to specific behaviors? (5) Do female (amictic, mictic) and male connectomes differ (Gasiorowski et al., 2019)? (6) Do connectomes

change during metamorphosis of indirectly developing species (Hochberg & Hochberg, 2015; Preza et al., 2020)? (7) Is there a correlation between connectome and life history strategy (benthic, planktonic, sessile, parasitic)? (8) How does the rotiferan connectome compare to that of other gnathiferans: micrognathozoans (Bekkouche & Worsaae, 2016), gnathotomulids (Gasiorowski et al., 2017), and chaetognaths (Fröblius & Funch, 2017)?

Opportunities

As noted above, research has supplied information on some aspects of the NS of several rotifer species, but use of these techniques needs to be expanded and new techniques need to be incorporated. These include the following: (1) application of chemical agonists and antagonists (Mekdara et al., 2022) combined with histochemical techniques to locate neurological components of behavior (Pérez-Legaspi et al., 2014); (2) use of precision laser ablations of NS components (Chung & Mazur, 2009); (3) employing patch clamps to monitor NS activity in cells of at least ~10 μm (Anecchino & Schultz, 2018); (4) use of more neurotransmitter antibodies to map phenotype expression; (5) employ correlative light and electron microscopy (CLEM) to collate serial images of the nervous system and map its neurocircuitry (Kolotuev et al., 2012); and (6) computer-assisted imaging (Gasiorowski et al., 2019; Preza et al., 2020) and modeling of connections.

We know a good deal about rotifer behavior including studies of mate-recognition (Snell & Rico-Martinez, 1996; Snell & Stelzer, 2005; Gribble & Mark Welch 2012), including mate guarding behavior in *Epiphanes senta* (Müller, 1773) (Schröder, 2003; Schröder & Walsh, 2010), surveillance behavior and predatory attack in *Cupelopagis vorax* (Leidy, 1857) (Bevington et al., 1995; Espinosa-Rodríguez et al., 2021), feeding preferences in several species (Gilbert & Starkweather, 1977, 1978; Clément et al., 1980), avoidance of predators (Gilbert, 1985, 1987; Kirk & Gilbert 1988), oviposition (Walsh, 1989), phototactic responses (Colangeli et al., 2019), mechanoreception (Joanidopoulos & Marwan, 1998), and attachment behaviors, either by adults (Gilbert 2019) or larvae of sessile rotifers (Wallace, 1978; Wallace & Edmondson, 1986). With this information, we posit that it is possible to develop connectome maps and

then compare them across a diverse array of taxa (Leasi et al., 2009; Gasiorowski et al., 2019; Preza et al., 2020). Thus, with sufficient information on the connectomes of selected species, rotiferologists should be able to develop a schematic model of the rotiferan neuronal workspace; then building on those models, develop algorithms that infer specific behaviors, which could be tested (Clément & Wurdak, 1991; Luo, 2021). In this way we can advance our understanding of simple nervous systems in general, and potentially how they relate to phylogeny, traits, and life history strategies. We suspect that unforeseen neurological properties will emerge from such studies.

Genomic architectures and control systems

The maintenance of favorable combinations of traits is essential for the evolution of sex determination, mating systems, local adaptation, and speciation—(Gutierrez-Valencia et al., 2021).

The study of rotifer genomes is still in its infancy, but our appreciation for rotifer genetics goes back to the first IRS. At that meeting our understanding of rotifers was simple and assumed to be stably linked to the reproductive strategies of the three major taxa (noted above). Since then, our knowledge of the ties between sexuality and genetics has advanced rapidly and changed some of our earlier views (Mauer et al., 2021). For example, recent genetic research on bdelloids has provided insights into polyploidy and yet also questioned the modes of genetic exchange in these obligate parthenogens (Flot et al., 2013; Serra et al., 2018; Lainea et al., 2020; Vakhrusheva et al., 2020); we now have evidence for recombination between homologous chromosomes (Simion et al., 2021). Moreover, the importance of horizontal gene flow in bdelloids is now well recognized (Gladyshev et al., 2008; Boschetti et al., 2012; Eyres et al., 2015; Debortoli et al., 2016; Nowell et al., 2018). Monogononts are largely cyclically parthenogenetic, yet how genetics (as well as epigenetics) play a role the switch from asexuality to sexuality remains a significant question. Still, inroads into how genetics may affect reproductive isolation are being made (Jezkova et al., 2022b). For many species of monogononts evidence of sex still has not been documented (Serra et al.,

2018). While information deposited in online repositories such as GenBank is improving, it is still incomplete. For example, to our knowledge, sequences for Ploima currently account for only ~60% of families and ~40% of genera, and these cover a limited number of genetic markers (<5). Also, what we know about rotifer phylogenetics mainly comes from a small suite of genes (18S rRNA, 28S rRNA, COI, ITS).

Challenges

Current status of our understanding of rotifer genetics and genomics leaves several areas with unanswered questions. (1) Comprising two genera with only four described species, seisonids offer the challenge of collecting sufficient study material (Mauer et al., 2021). For example, have particular gene families changed with the adherence to a strictly sexual lifestyle relative to other bdelloids and monogononts? (2) Research indicates presence of viral and fungal genetic elements in bdelloids: alienomics (Simion et al., 2021; Vakhrusheva et al., 2020). How did these elements become established? Are they present in seisonids and monogononts and, if so, how do they differ and what function do these elements play? (3) Does the genomic architecture of rotifers contain supergenes and, if so, how do they compare to those present in other organisms and can knowledge of their genomic architecture shed light on the evolution of Rotifera (*sensu lato*) (Gutierrez-Valencia et al., 2021)? (4) Allele sharing has been reported in the bdelloid *Macrotrachela quadricornifera* Milne, 1886 thereby suggesting “a cross and sexual reproduction” (Signorovitch et al., 2015). We need to determine how widespread this phenomenon is in this putatively asexual taxon. (5) Are there similarities in the genetic controls of sex regulation, anhydrobiosis, diapause, and aging in bdelloids and cyclical parthenogenetic monogononts (Gribble & Mark Welch, 2017). (6) How are lesions in DNA repaired so that bdelloid chromosomes are faithful restored (Terwagne et al., 2022)? (7) Is the genetic basis for induction of predator-induced defense structures the same across taxonomic lines within rotifers and outside of the phylum: e.g., ciliated protozoa (Fyda et al., 2005)? (8) Given that acanthocephalans are considered to be closely related to or actually specialized rotifers, collectively termed the Syndermata (García-Varela & Nadler 2006; Sielaff et al., 2015; Gazi et al., 2016), how do

their genetic signatures different from rotifers (*sensu stricto*)?

Opportunities

Clearly, if we are to understand rotifer genetics and genomics, researchers will need to survey the complete genomes of a wide array of taxa across all of Syndermata (= Rotifera, *sensu lato*). Recent advancements in established technologies have reduced the number of animals needed to get adequate results (Kang et al., 2020). Thus, successful application of technologies such as single-cell genetic sequencing and RNA*Later*® will be an enormous advancement (Gawad et al., 2016; Hernández-Rosas et al., 2017). Many next-generation sequencing approaches for whole-genome or whole-transcriptome sequencing are designed for higher quantities of starting material that may require pooling animals. Nonetheless, advanced approaches for long-read sequencing to facilitate genome assembly and mapping of non-model organisms, coupled with increasing efforts to reduce input requirements (e.g., single-cell sequencing), provide avenues to address some such challenges (Saviano et al., 2020). Furthermore, ability to generate clonal populations (bdelloids, amictic monogononts) presents a unique opportunity to use clonal lineages as replicates. Clonality coupled with the short generation times of many species provides a promising foundation for experimental evolution studies to investigate adaptation to different environments or conditions. Tools such as interference RNA and newer approaches like CRISPR-Cas enable functional investigation of the roles of genes (Li et al., 2019). Future work combining high-throughput molecular approaches (proteomics, metabolomics, next- and third-generation sequencing) can facilitate systems biology perspectives.

Physiology

For such a large number of problems there will be some animal of choice or a few such animals on which it can be most conveniently studied—
A. Krogh (1929).

As a group, Rotifera (*sensu lato*) may come closest of any animal taxon to match the qualities expressed

by Krogh, both in terms interesting physiological characteristics and advantages of use in studies (Wallace et al., 2015). These characteristics and advantages include the following. (1) Rotifers exhibit a wide tolerance for variation in pH, oxygen, and ionic concentrations, and to both organic and inorganic pollutants; (2) they procure nutrition as herbivores, predators, scavengers and parasites (e.g., of algae and oligochaetes); (3) as rotifers (*sensu lato*), acanthocephalans are parasites of arthropods and vertebrates. Finally, (4) culture techniques that are both easy and inexpensive have been established for a range of species that exhibit varied life history features.

Challenges

There is an embarrassment of topics of rotifer physiology that have not been fully explored. We nominate the following short list of outstanding questions for additional research. (1) How is homeostasis maintained in extremophiles, especially under stressful conditions such as low pH (Weithoff et al., 2019), high saline conditions (Fontaneto et al., 2006), and waters with high levels of heavy metals (Garza-León et al., 2021), organic pollutants (Vanjare et al., 2010), and materials from anthropogenic sources (Shin and Jeong 2022; Shin et al., 2022)? (2) By what specific processes are xerosomes (Nowell et al., 2018) and diapausing monogonont embryos (Jones et al., 2012) able to withstand desiccation and extreme ionizing radiation (Simion et al., 2021); are they the same? (3) What controls development and hatching of amictic and resting embryos (Denekamp et al., 2010, 2011, Schröder et al., 2007; Rozema et al., 2019; Yin et al., 2021)? (4) How does digestion physiology vary among taxa (Lindemann & Kleinow 2000; Lindemann et al., 2001). (5) Can we develop a lipidomic and metabolomic profile for rotifers and investigate it with regard to their normal and stressful conditions, as well as under culture conditions of caloric restriction (Snell et al., 2015; Lee et al., 2019)? (6) How do higher temperatures and elevated nutrient levels affect the level of polyunsaturated fatty acids (PUFAs) and how will changes influence rotifer physiology (Kim et al., 2014) and nutritional value (Coutinho et al., 2020; Schalicke et al., 2020), and thus, ultimately altering trophic dynamics (Strandberg et al., 2022)? (7) Is there a pattern to the rotifer microbiome based on their trophic state (diet) (Turgay et al., 2020) and,

if so, what role does it play in such features as digestion and stress tolerance (Eckert et al., 2021, 2022)? (8) How do rotifers produce and release bioactive metabolites (Stirewalt & Lewis, 1981; Gao, et al., 2019; Datki et al., 2021; Datki & Sinka 2022) and unpalatability chemicals (Felix et al., 1995; Walsh et al., 2006; Wallace et al., 2023)? (9) How does coloniality affect growth, respiration, and behavior (Wallace, 1987; Garcia, 2004)? (10) What are the dynamics of infection by viruses, fungi, and sporozoans (Wallace et al., 2015)? (11) How do parasitic rotifers evade immune responses from their host (Rees, 1960)?

Opportunities

Several research teams are making good progress in investigating the questions noted above, but applying emerging techniques will no doubt yield additional insights. For example, polymeric nanoparticles can be used as chemical delivery systems to bring bioactive materials into rotifers, thereby bypassing the crude methods of culturing or bathing animals in solutions of the target chemical (Begines et al., 2020). Despite challenges of the glycocalyx on the cell surface (D. Light, pers. commun.), it may be possible to perform patch clamps (see above) on rotifer organs to study ion channel physiology in tissues. The study of cellular senescence (e.g., cessation of cell division) may be possible using immunohistochemistry (Gonzalez-Gualda et al., 2021).

Life history, including sexuality, development, and aging

Ex ovo omnia (Everything from an egg)—W. Harvey (Slack, 1999).

Indeed, it all starts with the egg—actually an embryo—and then what happens? In most rotifers there is minimal further development after hatching except for increase in body size (Fontaneto & Melone, 2005); it is only in the sessile taxa where juveniles (larvae) do not resemble the adult (Hochberg et al., 2019). Once the adult state is achieved, reproduction begins, but across the phylum reproduction is complicated (Wallace et al., 2015); and it may or may not include sexuality as commonly considered (Serra &

Snell, 2009). Aging proceeds at different rates among taxa and can be modified by diet or culture conditions (Snell et al., 2012; Snell, 2014). Each of these aspects of rotifer biology need to be considered through the lens of the life history of the species. Unfortunately, their study has not kept pace with advancements in other fields. The nature of their unique reproductive modes challenges application of traditional concepts such as biological species.

Challenges

Once again there is much to be learned, but the following questions are worthy of our consideration. (1) How is the mictic switch initiated in monogononts so that male embryos are produced rather than female embryos (Serra & Carmona, 1993; Gilbert, 2003; Schröder & Gilbert, 2004; Schröder et al., 2007; Serra et al., 2011, 2004; Smith & Snell, 2012; Snell, 2011, 2017; Snell et al., 2011)? (2) How is the switch from producing amictic, subitaneous embryos to producing amictic, diapausing embryos (polyphenism) in *Synchaeta pectinata* Ehrenberg, 1832 regulated internally (Gilbert & Schreiber, 1998)? (3) How does the loss of sex arise and once lost, is the loss permanent (Serra & Snell, 2009; Pajdak-Stós et al., 2014)? (4) How does embryonic development proceed across the phylum (Gilbert, 1989; Castellanos Paez et al., 1998; Boschetti et al., 2005) and how are non-genetic polymorphisms (e.g., polyphenisms, such as spines and body wall outgrowths) initiated (Riggs & Gilbert, 1972; Gilbert, 2016)? (5) How does coloniality affect growth and development: e.g., in *Sinantherina socialis* (Linnaeus, 1758) (Garcia, 2004)? (6) In some species trophi size and shape change after hatching, but not in others: how is that controlled (Fontaneto & Melone, 2005)? (7) Several questions on lifespan should be examined: do geographical strains vary in lifespan; how important are allelopathic effects from hydrophytes (Viveros-Legorreta et al., 2022); what drugs are capable of extending lifespan; what is the relationship between the rotifer microbiome and lifespan (Turgay et al., 2020; Eckert et al., 2021); what is the optimal schedule of fasting to produce lifespan extension (Gribble & Mark Welch 2017; Snell et al., 2015; Viveros-Legorreta et al., 2020)? (8) Additional research also is needed to confirm some unusual behaviors that have recently been described in *Brachionus calyciflorus* Pallas, 1766: linear swimming

aggregation (Cheng et al., 2021) and floating response to avoid predation by *Asplanchna* (Zhang et al., 2021a).

Opportunities

The study of development requires study of a diverse array of taxa. However, because their amictic embryos are in near developmental lock step, both *Laciniaria flosculosa* (Müller, 1773) and *S. socialis* are good candidates for developmental studies (Champ & Pourriot, 1977; Wallace, 1980).

When compared to the abundance of studies in other microscopic taxa with similar life histories (e.g., *Artemia*, *Daphnia*), it is evident that rotiferologists have much work to do. Even beyond microcrustaceans, there is a world of life history and aging research in many other taxa (including vertebrates) that can have applications to rotifers, including studies of senescence (Gonzalez-Gualda et al., 2021). Answers to the questions posed above may have applications both in using rotifers as ecological sentinels, and for addressing, themes with applications across organisms such as the relation between diet, longevity, and reproduction.

Ecological responses to stresses

All nature is linked together by invisible bonds—G.P. Marsh (1864)

Studying how rotifer populations respond through time to changes in prevailing conditions provides insight into ecological processes governing community development (Kuczyńska-Kippen & Basińska, 2014; May & Wallace, 2019). Such research gives context to understanding how communities respond to periodic natural changes. But while these investigations have remained a substantial focus in rotifer research, ecological research has expanded to include studies where natural communities have been impacted by anthropogenic stressors, chiefly climate change (Obertegger & Flaim, 2021). In lakes the array of topics includes trophic mismatch (Winder & Schindler, 2004), and natural (Weithof, 2005) and artificial (Gonzalez & Frost, 1994) stresses from acid or changes in salinity (Halse et al., 1998; Tiffany et al., 2002). In experimental work topics have

included studies of temperature tolerance (Saucedo-Ríos et al., 2017) and effects of heavy metals (Garza-León et al., 2021), organics (Arnold et al., 2010; Han et al., 2016; Rivera-Davila et al., 2022), and nanoparticle microplastics (Shin & Jeong, 2022; Sui et al., 2022), as well as combinatorial effects (Kim et al., 2022; Ríos-Arana et al., 2005). Exploration of these topics also should include the study of psammic (interstitial) habitats in lakes (Ejsmont-Karabin & Karpowicz, 2021), humic waters (bogs) (Bielańska-Grajner et al., 2017; Ejsmont-Karabin et al., 2020), and marine systems (Fontaneto et al., 2006), as well as terrestrial (Devetter et al., 2017) and bog soils (Błędzki & Ellison, 2002). Thus, understanding rotifer responses to stress have advanced along two avenues of investigations: long-term field studies and experiments assessing effects of toxic agents (Kang et al., 2020). Also, the recent call for the use of multi-omics in assessing aquatic ecotoxicology should prove useful (Nam et al., 2022). In general, ecotoxicological studies have done much to advance our understanding of the physiological responses of rotifers to toxic agents (Park et al., 2020, 2022; Shin & Jeong, 2022). One important knowledge gap that has not been fully explored is that responses to toxins may vary among species (Rico-Martínez et al., 2016; Pérez-Legaspi & Rico-Martínez, 2001). Yet, with this information we may be better able to identify field sites at risk from specific toxins or their combinations (Escher et al., 2020).

Challenges

While costly and difficult to maintain, more long-term field studies on rotifer population dynamics and community structure are needed (May & Wallace, 2019; Powers et al., 2022). Questions that require our immediate attention include the following. (1) How do seasonal changes in various waterbodies influence food web networks (e.g., intraguild predation and the microbial loop)? Variations in waterbodies could include size differences, permanent v. temporary basins, and habitats that range from ultra-oligotrophic to hypereutrophic conditions (Obertegger et al., 2011). (2) How often do compensatory dynamics in rotifers occur and, in those events, how many species can be deemed to be fungible (i.e., performing similar ecological functions) (Fischer et al., 2001)? Is fungibility located within the same taxonomic units

(e.g., families and genera) (Vinebrooke et al., 2003)? Does fungibility correlate with phenotypic traits such as trophic structure or life history strategies such as reproductive strategy (cyclical parthenogenesis; permanent asexuality; etc.) (Obertegger et al., 2011)? (3) When a perturbation to a habitat is followed by a return to starting conditions, do rotifer populations follow hysteretic or non-hysteretic patterns in community composition (Frost et al., 2006)? Attention should be given to changes exhibiting non-canonical trophic cascading (Reissig et al., 2004).

Opportunities

The use of aquaculture offers promising alternatives avoid the difficulties and costs associated with long-term ecological studies of natural habitats. This rich discipline has already provided an immense contribution to our understanding of rotifer biology including food requirements, population growth, and dormancy of resting eggs under a wide variety of conditions (Lubzens et al., 1989, 1993; García-Roger et al., 2019; Rozema et al., 2019). Thus, utilizing the well-established methodologies of aquaculture a variety of ecological questions can be addressed. While small systems have been used (e.g., 2 L systems; Lemmen et al., (2021)), we suggest using a multifactorial design with larger volumes (≥ 1000 L), which would presumably mimic natural systems more reliably (Zhang et al., 2021b). An area for improvement is to increase the diversity of rotifer taxa used in aquaculture to expand findings and benefits beyond the current handful of species (mostly *Brachionus*).

Network graph analysis may be a valuable way to analyze changes in community structure, specifically details of interspecific relationships across a wide array of habitats (Gozdziejewska & Kruk, 2022). These concepts may be investigated using 3-D food web imaging (Yoon et al., 2005), application of the Minimum Microbial Food Web model (Prowe et al., 2022), and using computer program that calculates indices of diet variation based on network theory (Araújo et al., 2008). Studying effects of stress on community dynamics by manipulating edaphic conditions in micro- and mesocosms will likely prove useful (Sanderson et al., 2009). Such studies have been done in which vessels are seeded with a community comprising various species (Dickerson & Robinson, 1985; Robinson & Dickerson, 1987). This concept

could be extended into benthic experiments using a series of small vessels with sterile glass beads of different sizes set in an R x C factorial design in which physical and chemical conditions are varied. Unfortunately, these kinds of experiments use destructive sampling and are labor intensive. However, they could be made less labor intensive using automated systems that process images and use visual recognition programs to identify the species (Orenstein et al., 2022). Thus, in the type of systems we describe above, it might be possible to use a pump that gently removes fluid from the microcosm, passes it through and automated visualization system, and then returns it to the vessel. This would eliminate destructive sampling and decrease time to assess community constituents.

Biogeography and distribution of cryptic species

“Alles is overal: maar het milieu selecteert”
(*Everything is everywhere: but the environment selects*) —Baas Becking (de Wit and Bouvier, 2006)

Rotifers have fascinated microscopists since they were first described in the late 17th Century (Wallace et al., 2006). Much research since then has been devoted to species descriptions and recording their presence in specific habitats. This was necessary and valuable; it still is. The results of early research led Rousselet (1909) to the conclusion that rotifers have no biogeography, but are distributed everywhere (i.e., cosmopolitanism). However, if they do have a biogeography then we ought to see, within their genetic systems, evidence of isolation by distance (IBD) and, if not, evidence supporting the Baas Becking hypothesis (BBH, noted above) should be evident (Liang et al., 2021). These hypotheses present a binary situation, but emerging science offers a different model (Artois et al., 2011). Over time, any species will disperse everywhere and depending on the local conditions upon arrival it may survive to colonize a habitat (Rivas et al., 2018). Then with each passing generation the population will evolve becoming more closely adapted to the habitat (i.e., vicariance) (De Meester et al., 2016; Brown et al., 2022). If morphological changes do not keep pace with genetic changes that lead to incipient reproductive isolation,

the result will be cryptic species (Jezkova et al., 2022a). Yet as habitats change due to forces small and large (e.g., climate change), evolutionary pressures may not be constant, and the endpoint of habitat colonization may more closely resemble an evolutionary waltz than a static situation.

Challenges

There are several issues to be resolved regarding rotifer distribution. (1) Rotifers may disperse by anemochory, hydrochory, and zoochory, but on a global scale we do not know the relative importance of each (Brown et al., 2022). Moreover, the relative importance of each of these dispersal agents vary globally: anemochory may dominate in aridlands, hydrochory in flowing water and where flooding is prevalent, and zoochory in habitats frequented by migrating waterfowl. (2) Also, we do not understand how quickly vicariance will allow a colonist to become permanently established and whether or not models focusing solely on one method of dispersal are sufficient to explain cryptic speciation (Mills et al., 2017). (3) Most biogeographical research focuses on easily accessed habitats: i.e., lakes, ponds, and rivers. Thus, study of poorly known habitats not usually included in surveys may provide additional insights; these would include cryoconite holes (Grøngaard et al., 1999), ice fields (Shain et al., 2016), and shallow pools that can form in alpine fellfields, desert playas (Rivas Jr. et al., 2019), rock pools (Schröder et al., 2007), aerobic sewage systems (Nogrady, 1982), subterranean waters (Pejler, 1995), and artificial container habitats such as birdbaths (Örstan 2022). (4) We also need to know more about differences in life history characteristics within cryptic species complexes (Zhang et al., 2019).

Opportunities

Sampling techniques adopted from the study of wind-driven dust have been used to successfully study rotifers and other biota travelling via anemochory (Fontaneto, 2019; Rivas Jr. et al., 2019). Hydrochory is well-documented from a variety of biogeographic realms (Segers et al., 2004; Bertani et al., 2010; Martins et al., 2020), but most studies sample from a few permanent stations. We suggest that Lagrangian sampling (Scherwass et al., 2010) be used and that besides examining community composition, data on

both morphometrics and genetic composition be collected. Zoochory has been implicated in rotifer dispersal by elephants (Vanschoenwinkel et al., 2011), wild boar (Vanschoenwinkel et al., 2008), birds (de Morais Jr. et al., 2019), and fishes (Battauz et al., 2015), but in our estimation, it is an understudied dispersal mechanism. Assessing the relative contribution of these dispersal mechanisms in varied of habitats worldwide cannot easily be addressed by individual researchers, or even those comprising a specific laboratory. Thus, more collaborative work by researchers from across the globe is needed: e.g., (Cakil et al., 2021). We believe that purpose-driven, coalitions among many laboratories could develop specific projects (see also Challenges #9 and 10).

Analysis of rotiferan morphospace

The variation and diversity of shapes in nature is a central focus of both evolutionary and developmental biologists—Moulton and Goriely (2020)

Rotifers exhibit an extraordinary array of shapes and appended features (Wallace et al., 2015). However, our understanding of this diversity is incomplete; we need to take steps to “explore the intersection of geometric morphometrics and functional morphology” (Cooke & Terhune, 2015). One way to do that is to evaluate rotiferan structures using anthropogenic analogs. Here we suggest three topics whose study could improve our understanding of rotifer diversity by examining their mechanics. These topics are (1) jointed appendages as lever-arm systems, (2) trophi as class-3 levers, and (3) body shape of loricate species. Analyzing the first two of these involves the mechanics of complex lever-arm systems, while that of the third necessitates understanding of the architectural basis of durable buildings. These are only three traits that have a functional significance to rotifers; other should be explored. Analytical approaches like machine learning may improve understanding of rotiferan morphospace (Orenstein et al., 2022).

Challenge: jointed lever-arm appendages.

Several types of articulating elements are seen in rotifers. These include (1) the spines in *Brachionus*

that act as foils fending off predators (Gilbert, 1967), (2) the arms and paddles that in *Hexarthra* and *Polyarthra* permit rapid jumps to escape predators (Allen, 1968; Gilbert 1985; Hochberg & Ablak Gurbuz, 2008), and (3) a long foot with toes in *Scaridium* (Segers, 1995). Mechanically these systems are probably all class-3 lever arms; effort moving the lever-arm is applied between the fulcrum and the load. The first two examples (spines and arms/paddles) are 1-bar lever-arm systems; the third is a 3-bar system. While we understand something of the dynamics of the first two, little is known of the mechanics of rotifers possessing a long foot with toes (i.e., species in *Beauchampiella*, *Cephalodella*, *Monommata*, *Scaridium*, and *Trichocerca*). While these 3-bar lever arms are at least 4–5 orders of magnitude smaller than those of human invention, they may be studied using appropriate mechanical equations.

Opportunities

Comprehending the musculature of rotifers will aid in our understanding of rotiferan behaviors (Hochberg & Litvaitis, 2000; Hochberg et al., 2010) and their evolutionary ground pattern (Sørensen, 2005; Riemann et al., 2008; Leasi & Ricci, 2010), as well as the evolution within taxonomic groups including, for example, Proalidae (Wilts et al., 2009; Wilts & Ahlrichs, 2010) and Scaridiidae (Segers, 1996).

Challenge: mechanics of trophi.

Interest in the structure and function of rotifer trophi has led to insights into a variety of topics including community structure (Obertegger et al., 2011), feeding dynamics (Salt et al., 1978), identification of species (Obertegger et al., 2006), ontogeny (De Smet & Segers, 2017), and phylogeny (Wilts et al., 2010). However, a relatively unexplored topic is mechanics of trophi movement. Rotifer trophi resemble forceps (Wallace et al., 2006). In their simplest form, such as the incudate trophi of *Asplanchna*, the mechanical system is that of a class-3 lever: the effort is applied between the load and the fulcrum. However, trophi can be much more complex, such as cardate trophi of Lindiidae (Nogrady & Segers, 2002) and forcipate trophi in the Dicranophoridae (e.g., *Encentrum*, *Dicranophorus*, *Paradicranophorus*, and *Wierzejskiella*) (De Smet & Pourriot, 1997). Also, while

the trophi of most species are symmetrical, some species exhibit asymmetry in one or more elements; this can range from moderately asymmetrical in *Cephalodella changdensis* Wei, Jersabek & Yang, 2020 to pronounced asymmetry, as in *Trichocerca kostei* Segers, 1993. With nine major parts, the mechanics of rotifer trophi will be more difficult to understand than the jaws of vertebrates. In the latter, functional divergence appears to follow a constrained, level model (Singleton, 2004). Nevertheless, Finite Element Analysis, a tool used in musculoskeletal biomechanics of vertebrates, may be helpful in exploring functionality in rotifer trophi (Nanova et al., 2017).

Opportunities

It may be possible to atomize the elements of even complex trophi and then analyze their movements separately, ultimately reconstructing mechanics of the entire structure. Such studies would rely on the rich literature of the jaws of modern and extinct invertebrates and vertebrates and, of course, forceps, scissors, and certain types of catapults (Wroe et al., 2008). Because the size differences between trophi and both artificial and natural systems is > 5 orders of magnitude, and viscosity of their media is drastically different, we need to know whether the mechanics of rotifer jaws function in the same way as these analogs. While analysis of the musculature of rotifer trophi will be difficult, it may be possible to better understand their dietary preferences as Ferrara et al., (2011) have done for certain sharks. Using advanced technologies, it seems likely that measurements can be obtained of their ability to resist wear by determining values of Hardness, i.e., resistance to surface deformation (H), or Scratch Hardness (H_s) and/or Young's Modulus, i.e., structural elasticity (E) (Vogel 1988). These metrics, as well as analysis of bite force performance, across trophi type may provide insight into rotifer food preferences.

Challenge: Rotiferan lorica form.

Defensive mechanisms in rotifers against predators are well-known; these include behavioral (jumps in *Hexarthra* and *Polyarthra*), morphological (permanent and inducible spines in *Brachionus* and *Keratella*) and increased lorica thickness in *Brachionus* (Yin et al., 2017), and chemical (*Sinantherina*)

strategies. However, many loricate species have unique morphologies that resemble buildings. For example, most *Keratella* have architectural features called facet patterns that resemble, and appears to function as, geodesic domes. Species of *Lecane*, *Lepadella*, *Notholca*, and *Ploesoma* have architectures composed of elongate ridges and elevated domes are seen in *Dipleuchlanis*, *Euchlanis*, and *Tripleuchlanis*. While Kuszty et al., (2023) explored the architecture of the facet patterns in *Keratella*, clearly much more remains to be investigated about the adaptive forms in rotifers.

Opportunities

An analysis of these architectural features could employ physical models, software applications such as SkyCiv© (skyciv.com) (Carigliano and Comino, 2020) and/or rigorous mathematical analyses (Barbieri et al., 2016; Lanzoni & Tarantino, 2020). Investigations of these features may lead to novel biometric advances.

Rotifer evolution within Gnathifera including Acanthocephala

Nothing in biology makes sense except in the light of evolution—T. Dobzhansky (1973)

Understanding rotifer evolution has improved over early attempts, but in spite of recent significant efforts, we still have not worked out the details of their phylogeny and there has yet to be a clear consensus of the evolution of the major clades (Bininda-Emonds, 2021; Mauer et al., 2021), nor why the distribution of morphospecies within rotiferan genera shows a strong hollow curve (Beres et al., 2005).

Challenges

The questions that we need to explore appear legion and range widely in scope. Following is a list of some outstanding issues. (1) We do not understand the relationship of rotifers to the rest of the jawed micro-metazoans (the Gnathifera), nor do we understand

the evolution leading to the parasitic specialization of Acanthocephala within Rotifera (*sensu lato*) (Clément, 1980; Garey et al., 1998; Melone et al., 1998; Near et al., 1998; Bininda-Emonds, 2021). (2) We do not understand how rotiferan life styles are controlled and whether specific traits evolve in a coordinate fashion. (3) What are the evolutionary drivers and underlying genetic mechanisms that led to bdelloid rotifers losing capacity for archetypal sexual reproduction? (4) What were the evolutionary drivers that led to males with reduced size, including non-feeding dwarf males, in monogononts? (5) What selection pressures led to the sessile life style? (6) How did coloniality evolve once and then diversify or did it evolve multiple times across the phylum? (7) Is amphoterism (a female monogonont produces both diploid eggs by mitosis and haploid eggs by meiosis) ancestral or derived within the Rotifera?

With better appreciation of the topics posited above we can approach more specific questions about the phylum: these include the following. (1) Why have we not been able to resolve the phylogeny of many families (Sørensen, 2002; Sørensen & Giribet, 2006)? (2) How did the Ploima and Gnesiotrocha diversify? (3) Can we resolve the relationship between the Conochilidae and *Ptygura* and Collotheidae v. Flosculariidae (Meksuwan et al., 2015)? (4) What features of rotifer genomes promote adaptation and speciation and what does it reveal about the architecture of animal genomes in general? Regardless of how these questions are approached we need to be cognizant that selection happens to the entire animal as it lives in its multidimensional world (White et al., 2022) and that no phenotype can be optimized for all tasks: i.e., Pareto optimality (Szekely et al., 2015; Tendler et al., 2015).

Opportunities

The use of total evidence —morphological and molecular—has been and undoubtedly will continue to be the best research strategy (Funch et al., 2005; Sørensen & Giribet, 2006; Wilke et al., 2020). However, for that to be productive we need information on more genera in more families within all Rotifera (*sensu lato*).

Educational opportunities for beginning students

“Le hazard ne favorise que les esprits préparés” (Chance only favors prepared minds)
—L. Pasteur (1854).

Pasteur had great insight when he noted that keen observations are made by people who, being thoroughly prepared by their education and experiences, are better equipped to see what remains hidden to others. As scientists we ask: who prepares those minds and how is that preparation best accomplished?

Challenges

It is obvious to even the most casual observer that a simple search on the Internet using the search term “rotifer” yields a number of ‘hits’ that is truly astounding. These hits include posts from Wikipedia, encyclopedias, dictionaries, and other educational venues, personal websites, advertisements for sundry products (including books, resting eggs, rotifer food, and toys), images (both line art and photomicrographs), and videos. Some of the art has been copied from proprietary publications with minor modifications. While some of the images range from poor to adequate in quality, others are excellent. Unfortunately, many of the taxa depicted are not identified. There are also a several Internet sites that provide informative text, although a few that we have reviewed use outdated terminology or incorrect taxonomy. We believe that this sort of ‘citizen science education’ is, on the whole, a positive phenomenon. This is especially important because it is the easiest and least expensive way for many beginning students to gain knowledge. However, there are troubling issues with the Internet as an educational medium. (1) It is a forum with no significant corrective filter to challenge errors, nor is that process easy. (2) Some sites are not kept up to date and there is a no consistent educational platform covering general rotifer biology. (3) In many cases specialized knowledge is required to initiate even a basic search; existence of these microscopic metazoans is far less well-known than that of more visible charismatic megafauna. Yet, in this chaos there is opportunity for us to advance the study of rotifers.

Opportunities

Many years ago, Henri Dumont and his colleagues ran extensive workshops on the taxonomy of freshwater zooplankton (including rotifers), but to our knowledge these intensive introductory practicums have not been offered for nearly 30 years. However, some laboratories have endeavored to fill this void. For example, (1) short courses that focus on a variety of topics in aquatic ecology including rotifers have been held at the Universidad Nacional Autónoma de México in Mexico City, (2) intensive studies have been run on specialized topics such as a workshop on the *Brachionus plicatilis* Müller, 1786 species complex (Wallace et al., 2014), and (3) workshops also have been held at each of the IRS meetings (Wallace et al., 2013). However, these educational venues often do not meet the criteria of being easy to attend and low cost. However, operating introductory practicums are difficult. They would have to be held in a convenient place and external funding would be needed for them to be successful. But another educational opportunity already exists. Since late in 2021, an electronic venue—the *Virtual Rotifer Collaboration*© (VRC)—has been offered to students of rotifers worldwide online. While the attendance has been modest (15–30), VRC meeting show promise as a potential alternative educational platform. As of this writing > 12 VRC meetings have been held covering a variety of advanced topics including: predatory-prey relationships, community development, and biochemistry (see announcements in *Rotifer News*: URL noted below). Finally, we advocate that researchers record their careers and that of their colleagues in a convenient place to provide records for historians to chronicle our history (Wallace et al., 2006).

Fostering international collaboration

[People] work together, I told him from the heart, Whether they work together or apart—R. Frost (1915)

Just as the Internet can be employed to educate the next-generation of rotiferologists, it also should be used with more effect to advance rotifer research on a global scale by making fruitful connections among

independent researchers and groups. As noted above, we envision improved data sharing, better analysis of complex datasets, and ultimately more collaborative publication. Of course, alliances have been made throughout the history of scientific research and certainly partnerships have been becoming more common among rotiferologists. Now the Internet permits rapid and direct contact, but the question is: how can we make data sharing advantageous to all researchers?

Challenges

We acknowledge three serious impediments to data sharing. (1) Since the start of the scientific revolution, reputation and career advancement has been linked to publication. Thus, sharing data exposes researchers to potentially losing priority in publication; this could make researchers reluctant to share their data without tangible recompense. (2) Some funding agencies require that when the research they fund is published, it is to be made available electronically as an open access version. Yet, this requirement is not uniform, nor is it always required that the dataset used be provided. Also, because the process of bringing a manuscript to publication is costly, many journals require a fee for open access, including access to supplemental datasets. This cost is beyond the capacity for many researchers. (3) The format in which the data are stored must meet the basic requirements of being easy to locate on the Internet and accessible by older generation computers.

Opportunities

What can be done? First, we should not underestimate the power of collaboration, especially when it includes interdisciplinary research. To expedite those elements of our scholarship we need to work towards establishing a research ‘commons.’ That is, a venue where data may be easily and openly shared. It may be possible to model this by emulating three models that already function in that regard. (1) *Rotifer News* began in the mid-1970s in print form as a newsletter. After many years it ceased printing, but it was restarted on-line form (<https://sitios.iztacala.unam.mx/rotifernews/>). (NB: *Rotifer News* also provides a list of recent publications on rotifers, short biographies, and brief synopses of research.) (2) A similar

model is *The Rotifer World Catalog* (<http://rotifera.hausdernaatur.at>) (Jersabek and Leitner, 2013). (3) One organization that provides a more extensive model is the *Global Lake Ecological Observatory Network* (GLEON), a grass roots organization that encourages data sharing about inland waters (<https://gleon.org>). We do not suggest that these are the only methods of database archiving and sharing data (e.g., GenBank, FlyBase, WormBase). However, they do provide tangible models from which others may develop. Also new strategies for data mining should be created. A recent development that will aid in the searching genetic databases for rotifers is *RotiferMiner*, which was developed at the University of Texas El Paso and presented at the International Rotifer Symposium XVI.

Conclusions

*We have joined the caravan, you might say,
at a certain point; we will travel as far as we
can, but we cannot in a lifetime see all that we
would like to see or learn all that we hunger to
know—(L. Eiseley 1957)*

Rotiferology began with the observations of van Leeuwenhoek and Harris late in the seventeenth century (Harris, 1695; Dobell, 1958; Ratcliff, 2000) and since then, study of rotifers has been instructive for the biological sciences in many ways, as we have reviewed here. Indeed, what we have collectively witnessed since the first congress in 1976 has been exciting and we predict even greater insights being produced in the coming years. However, it is clear that rotiferology has not yet reached the zenith. To do so the discipline must move beyond a focus on species in the *B. calyciflorus* and *B. plicatilis* species complexes—the so-called white mice of rotiferologists. While their study has been instrumental in advancing our understanding of the phylum and, no doubt, will continue to do so, the diversity of rotifer biology should summon a wider research agenda. Thus, work on other species should be privileged. Indeed, the past few IRS illustrate that expansion. Thus, we suggest that the taxonomic scope of the species studied be expanded, more novel environments be explored, and that scientific questions be undertaken with a wider interdisciplinary curiosity.

We regret that however inclusive we attempted to be in this review, due to space limitation, we could not provide exhaustive coverage of several topics, thus, some topics are underserved in our review. However, recognizing that rotiferology continuously build upon itself, and each new discovery may herald new hypotheses to test, we conclude that the future of rotifer research is bright: many opportunities remain to be explored.

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