Taxonomical characterization of bdelloid rotifers in the family Philodinidae

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Summary

Taxonomically significant morphological, behavioral and ecological traits of bdelloid rotifers in the family Philodinidae are discussed. It is recommended that new morphospecies descriptions include information on all of these traits.

Introduction

I discussed the taxonomically significant morphological traits of bdelloid rotifers in the genus Adineta (family Adinetidae) in a previous paper [1]. Therein I recommended that a list of traits useful to separate the morphological variants (morphovariants) in every bdelloid genus should be prepared. I have since decided to make such lists more inclusive by adding behavioral and ecological traits. I have also decided that a separate list for each genus would be somewhat superfluous and that a list of taxonomically significant traits for each family would suffice. I am now following my own advice, and as a prelude to the descriptions of several new species that I am preparing, presenting an annotated list of what I consider to be the taxonomically significant traits for the family Philodinidae.

The family Philodinidae includes the following genera: Anomopus, Ceratotrocha, Didymodactylos, Dissotrocha, Embata, Macrotrachela, Mniobia, Philodina, Pleuretra, Pseudoembata, Rotaria and Zelinkiella.

This paper is not intended to be a primer on methodology, but I have included several brief recommendations concerning the best practices for the examination of certain traits.

Morphospecies of bdelloid rotifers

Although bdelloid rotifers appear to be exclusively parthenogenetic, their phenotypes do form clusters comparable to the species of sexually reproducing animals. Despite the increasing use of gene sequences in their taxonomy, the most practical criteria to

distinguish bdelloid species from each other are morphological.

the conceptualize morphological characterization of bdelloids we can visualize the distribution of the observed phenotypic traits in a multidimensional morphospace where each point represents one individual bdelloid. Some regions of the morphospace would probably be sparsely populated or even totally devoid of points, while other regions would have clusters of them (Fig. 1). Presumably, the clusters of morphologies would be at or near adaptive peaks [2, 3]. I will refer to each cluster of observed morphologies as a morphovariant and each morphovariant that has been recognized taxonomically and given a binominal as a morphospecies (hereafter species). The clusters may be diffuse or dense depending on how much variability in trait values have been created by genetic and environmental influences

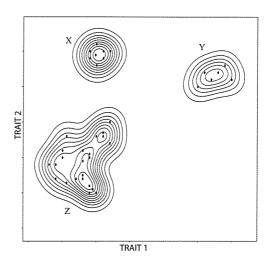


Fig. 1. A hypothetical morphospace of two phenotypic traits. Each point represents a bdelloid specimen and each cluster of points delimited by contours (surrounding an adaptive peak) a morphovariant. Morphovariants X and Y, with no shared contours, may be easily distinguished from each other morphologically. The cluster Z consists of three or more cryptic morphovariants with shared contours that may be resolved by comparisons of detailed morphology or DNA sequences.

(Fig. 1). The difficulty is in determining how much morphological variation to allow before designating a given morphovariant cluster to be a unique morphospecies. Conceptually, this scheme is not too different from the morphospecies definition proposed for ciliated protozoa [4, 5]. One caveat associated with the latter definition is also valid here [5]: genetic may be observed differences physiologically diverged bdelloid populations that may appear morphologically identical. For example, physiological divergence may cause morphologically similar populations to differ in mostly qualitative traits such as food preferences, habitat specificity or drying survival.

In the following, I have divided the taxonomically significant traits into loosely delimited groups. Although there is unavoidable overlap between the groups, this format will simplify discussion of the traits and their application when a specimen is being studied.

Morphological traits

Murray's [6] 115 year-old introduction to the morphology of bdelloid rotifers remains surprisingly accurate and useful, save for a few outdated terms, and is recommended reading for those just starting to study these animals. The body of a bdelloid has been divided traditionally into five parts: head, neck, trunk, rump and foot (Fig. 2A). Although there is no segmentation, the internal integument, especially around the foot, has well-defined divisions that appear transverse "pseudosegments". Thanks these to pseudosegments, the body is telescopic; the head, neck, rump and foot can be withdrawn fully into the trunk (Fig. 3). Body parts, often the head and neck, or various internal organs may be colored in shades of yellow, orange and red (Fig. 2B). The colored contents of the stomach are almost certainly due to ingested food and may reveal the feeding preferences of a specimen (see below).

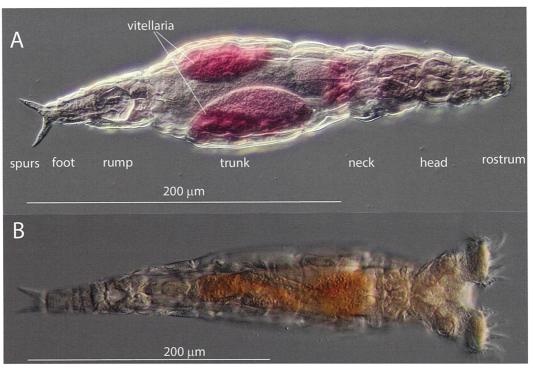


Fig. 2. General body plans of bdelloid rotifers. A. Preserved specimen of an undescribed *Macrotrachela* with corona withdrawn (stained with neutral red; stack of five images). B. Live swimming *Philodina* with an orange stomach and a lightly colored anterior body.

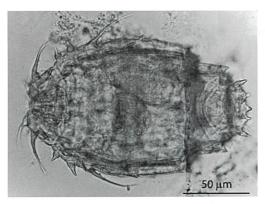


Fig. 3. *Macrotrachela multispinosa* (Thompson). Contracted specimen with multiple spines on its trunk (composite of 2 images).

Body surface: Many philodinid species, especially those in *Macrotrachela*, have various types of appendages, protuberances and spines on their integuments (Fig. 3), while the species in *Pleuretra* are characterized by the prominent thickness and folding of their integument [7]. Although the biological functions of these formations are unknown, they are useful taxonomically to delineate morphovariants. Attention should be paid to the dorsal surfaces of the rump and foot, which may carry various types of protuberances or spines.

All bdelloids have a dorsal antenna. Its length is useful to separate some species from each other, for example, in *Rotaria*. There is often a transverse ridge on each side of the antenna (Fig. 4B). This ridge may be difficult to notice in active animals unless one is looking for it. Occasionally, it forms a prominent structure. For example, in *Rotaria sordida* (Western) the ridge is raised and forms a small point at its lateralmost edge; in *Macrotrachela sonorensis* Örstan there is a lateral blunt spine on each side of the antenna.

All bdelloids probably have pores on their external surfaces first seen in electron micrographs [8]. In some morphovariants these pores may be too small to resolve under a light microscope, but in others they can be seen at high magnifications especially with a microscope equipped with differential interference contrast (DIC). In some species the pores form distinct papillae covering the entire body or parts of it. A mucus coat may also be present around the trunk and sometimes the rump. The presence of such a coat is often made obvious by the clumps of bacteria and microscopic debris adhering to it.

Corona and rostrum: Most philodinids carry on their heads the typical bdelloid corona consisting of two ciliated disks on pedicels (Fig. 2B, 5). Species in *Ceratotrocha* have

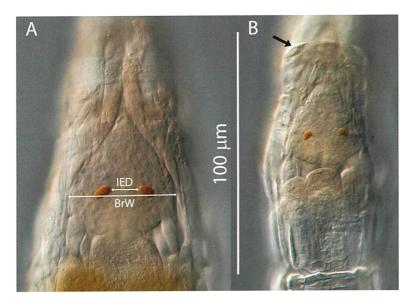


FIG. 4. Brains and eye spots of two undescribed *Philodina* morphovariants. The specimen A is larger but has a smaller IED/BrW value (closer eye spots) than specimen B. Also visible are several glands posterior to brains of both specimens (retrocerebral organ?) and the ridges lateral to the antenna of specimen B (arrow).

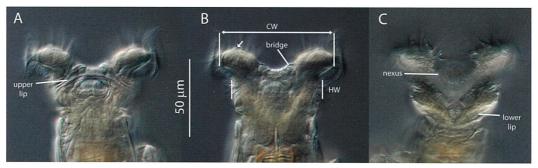


Fig. 5. Views of the corona of a *Philodina* morphovariant (also in Fig. 4B) as the focus was moved from the dorsal (A) through the median (B) to the ventral (C) surfaces.

modified coronas with horn-like structures extending from the sides of the head.

The corona and the mouth open during swimming or stationary feeding. The mouth is a funnel-like ciliated structure posterior to the corona on the ventral side of the head (Fig. 5C). When the corona is withdrawn into the head, the mouth is closed and the integument folds over itself to create a puckered structure encircling the closed mouth (Fig. 6). The opening of the corona moves the folds of the integument out of the way to form the dorsal upper lip between the pedicels of the coronal disks and the partially withdrawn rostrum and the ventral lower lip surrounding the mouth opening (Fig. 5).

The characteristics of the open corona and the associated structures, especially the upper lip, are taxonomically highly significant as they often help distinguish morphovariants from each other. Any unusual morphology of the corona should be described. The general shape of the head during feeding, as seen from above, should be stated. In some species the width of

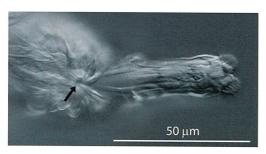


Fig. 6. Rostrum and the closed mouth (arrow) of Rotaria sordida.

the head narrows from the base of the corona to the neck, while in others it is more rectangular in shape. The upper lip usually has a complex layered morphology that should be described carefully. Additionally, there is often a bridge across the sulcus between the pedicels (Fig. 5B). This bridge usually has a membraneous appearance that should be distinguished from the layers of the upper lip. Posterior to the bridge but anterior to the mouth on the ventral side is the nexus between the pedicels that is sometimes visible in carefully focused photographs (Fig. 5C). When the corona is open, the rostrum retracts, but it may be long enough to cover the upper lip partially. In fact, some Rotaria species have unusually long rostrums that extend over the corona.

Less attention has been paid in the literature to morphology of the lower lip, which is somewhat less well defined and apparently less variable in its shape compared to the upper lip (Fig. 5C). Nevertheless, it is a potentially useful taxonomic trait and whenever the opportunity arises, its morphology should be included in species descriptions.

Near the center of each disk of the corona there is usually a small protuberance that carries a few setae that seem to remain stationary during feeding unlike the continuously beating cilia encircling the disks (Fig. 5B, arrow). I suspect these protuberances are present in most, if not all, species that have the usual corona morphology. Nevertheless, their presence (or absence) should be noted.

During creeping, the proboscis-like rostrum becomes the front end. There is a hood-like formation partially over the ciliated tip of the rostrum. I agree with Murray [9] that this is a single lamella that can appear to have two or more lobes (Fig. 6). Therefore, I will refer to it (unlike Murray) in the singular. The shape and the width of the lamella should be included in species descriptions. It is best examined and photographed when a rotifer is crawling upside down on the underside of a cover glass.

Eye spots: When eye spots are present they are either on the brain or in the rostrum. Their colors and shapes seem to be variable. Here I am proposing the use of the inter-eye distance (IED) as a potential trait to distinguish between morphovariants (Fig. 4). To my knowledge, IED has not been mentioned in any previous species descriptions, although Bartoš [10] used it qualitatively for three *Philodina* species in his key for the genus. Evaluation of the taxonomic usefulness of IED will require comparisons of many morphovariants. IED should be measured on photographs of uncompressed specimens and may best be expressed relative to some other measurement, such as the brain width (BrW in Fig. 4A).

Glands: There are a number of bag-like syncytial organs often referred to as glands in the heads, necks and feet of bdelloid rotifers (Figs. 4, 8). They have never been studied in detail and their functions have been inferred from their locations: those anterior to the stomach may secrete digestive fluids, while the ones in the foot probably secrete the substances for the attachment of the toes and spurs. The largest and the most prominent of these glands, which I refer to as the dorsotransverse gland, is located dorsal to the anterior stomach (Fig. 8). An elusive group of three glands, the retrocerebral organ, surrounds the posterior brain (Fig. 4). Available data suggest that there are phylogenetic differences in the presence, dimensions and arrangements of these glands. For example, the retrocerebral organ is missing in Adineta [11] and the foot glands of the marine bdelloid Zelinkiella synaptae (Zelinka) differ in their arrangement from those of the other philodinid species [7]. Students of bdelloids are encouraged to study these glands. They are easiest to examine in preserved specimens [12].

Trophi: In a live rotifer the trophi (jaws) are positioned at a steep angle to the longitudinal axis of the body. What would be the dorsal side of the trophi (when flattened) faces the mouth and the ventral side the stomach. The dorsal

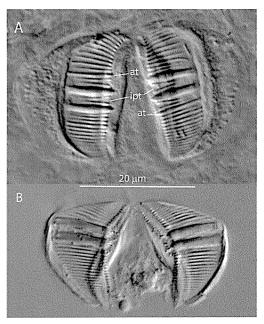


Fig. 7. A. Trophi of a *Philodina* morphovariant (also in Figs. 4B and 5). There are two major and one ancillary teeth (at) on each side (dental formula, 1+2/2+1) and two interproximal teeth (ipt) between the major teeth (stack of eight images). B. Trophi of *Rotaria sordida*. There are two major teeth on each side (dental formula, 2/2). The major teeth are very close to each other and no interproximal teeth can be seen between them (stack of nine images).

surface of each half of the trophi carries transverse teeth. There are major and minor teeth, distinguished by their widths, and sometimes ancillary teeth of an intermediate width (Fig. 7). The latter are always fewer in number and may be present on one half, but not the other. The teeth numbers are taxonomically significant and have traditionally been expressed formulaically as, for example, 2/2, when there are two major teeth on each side. Ancillary teeth are added as, for example, 1+2/2+1, when there is one asymmetrically placed on each side (Fig. 7A).

The number of minor teeth may also differ between species [13]. Although they are easiest to count in electron micrographs, they may also be counted in well-resolved high magnification photomicrographs preferably obtained using DIC. But because of the slight curvature of the trophi, the shortest teeth at the ends are usually difficult to make out (Fig. 7).

The presence of what appear to be curved minor teeth between the major teeth was first noted in electron micrographs [14]. I propose to call these "interproximal teeth". The potential taxonomic use of interproximal teeth has so far not been considered, but preliminary comparisons suggest that they may have some taxonomic value (Fig. 7). Because of their fineness and placement between major teeth, interproximal teeth are easy to overlook and best seen, once again, using DIC.

The dimensions of the trophi, especially its length, also differ between morphovariants [13]. The trophi should be measured on photographs taken either after a specimen and its trophi have been flattened under the cover glass or the trophi extracted. The trophi in a rotifer's body may have a yellow-orange color and wide granular outside borders (Fig. 7A). These characteristics disappear during the extraction process.

Stomach and intestine: In Philodinidae, Philodinavidae and Adinetidae a lumen is present in the stomach, but is absent in Habrotrochidae. When it is present, the lumen is usually obvious, but sometimes it may be hard to detect it. Feeding a specimen finely powdered charcoal or carmine or compressing it under the cover glass may make its lumen visible if it indeed has one (Fig. 8). Interestingly, the form of the excrement provides indirect evidence for stomach morphology: the excrement of species with a lumen consists of loosely and irregularly aggregated particles, but that of species without a lumen retains outside the body (long enough to observe and photograph)

the shape of the roughly spherical aggregates of food particles (pellets) present in their stomachs.

The lumen continues into the intestine, which is followed by a contractile cloaca in the rump that opens out through the anus near the posterior border of the second pseudosegment of the rump. It should be noted whether or not the insides of the lumen and intestine are ciliated. These organs are best examined in slightly compressed specimens (Fig. 8).

Reproductive organs and eggs: All (female) bdelloids have a pair of ovaries and a pair of associated vitellaria (yolk glands). The ovaries are usually inconspicuous clusters of small cells and, therefore, hard to notice (Fig. 8), while the vitellaria are large syncytial organs (and one vitellarium is usually larger than the other) with prominent nuclei that are hard to miss (Fig. 2A). The number of nuclei in each vitellarium is usually eight, although some variance has been noted in the literature. The taxonomic significance of the variable numbers of nuclei is not known, but it is good practice to report the number of nuclei in at least one vitellarium even if it is eight. These nuclei are easiest to count in the larger vitellarium when the specimen is slightly compressed and immobilized under the cover glass.

The number of nuclei in an ovary may also vary between morphovariants. However, counting of ovarian nuclei is tedious because their view is often blocked by the associated vitellarium. Also, to obtain their maximum numbers they must be counted in young specimens that have not yet reproduced.

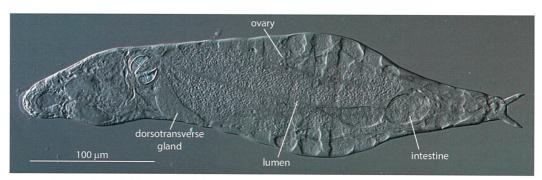


Fig. 8. Compression of this *Macrotrachela* specimen (also in Fig. 2A) revealed a very narrow lumen through its stomach that widened before entering the intestine. The insides of the lumen and intestine were ciliated. Also visible are the dorsotransverse gland and a cluster of ovarian nuclei.

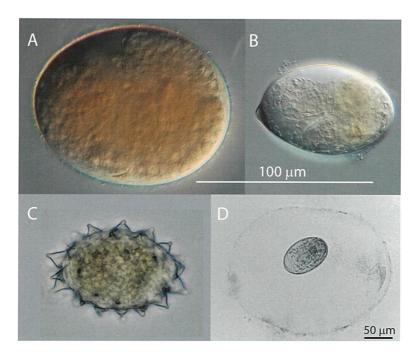


FIG. 9. A. Egg of the large predatory *Philodina* in FIG. 10. B. Egg of another *Philodina* morphovariant (also in Figs. 4B, 5, 7A). C. Egg of a *Macrotrachela* morphovariant (stack of three images). D. Egg of *Philodina duplicalcar* inside its capsule. A-C to the same scale.

Bdelloids may be oviparous or viviparous (strictly speaking, ovoviviparous). The eggs of oviparous species are more or less elongated ellipsoids. Their poles usually have either a uniform curvature (Fig. 9A) or a nipple-like protuberance (Fig. 9B). A few philodinids have eggs covered with spines of various shapes or other protuberances (Fig. 9C). *Philodina duplicalcar* (De Koning) deposits its eggs inside a mucus capsule (Fig. 9D). Besides their morphology, the dimensions of eggs should also be given.

Foot: The number of the pseudosegments of the foot has some taxonomic significance. However, it is not always clear whether the toes are on a pseudosegment separate from the one carrying the spurs and how different authors have counted the pseudosegments. As I have suggested [1], the easiest way to end this ambiguity is to give the number of only the prespur pseudosegments of the foot. Most species seem to have two or three of them, but occasionally higher numbers are encountered.

All philodinids have a pair of appendages called spurs near the end of the foot and either two to four toes or an adhesive plate at the end of the foot. These parts are taxonomically highly significant: the number of toes help determine

the genus of a specimen, while the spur shape and length help separate species from each other. The descriptions of the shapes of the spurs should be complemented with photographs (or drawings).

Dimensions: The total length during crawling (TL) and the length of the foot (FL) should be measured (excluding spurs). If the foot is relatively short, the combined length of the rump plus the foot (RF) may be used. When a philodinid is crawling, the end of its foot, carrying the toes or an adhesive plate, does not normally extend away from the rest of the foot (Fig. 2A). Therefore, measurements of TL and FL end at the posterior end of the spur pseudosegment. The ratio FL/TL (or RF/TL) may help distinguish some morphovariants from each other. Other dimensions considered significant, for example, the length of the rostrum may also be measured.

The widths of the open corona (CW) and the head (HW) should be given (Fig. 6B). The ratio CW/HW is a useful trait. The width of the gap (sulcus) between the pedicels may be given qualitatively as it is somewhat difficult to select points between which this gap may be measured reproducibly. Both the absolute length of the antenna and its length relative to the lateral

thickness of the head at the base of the antenna may be given.

Both the absolute length of a spur and its length relative to the width of the foot at the base of the spurs as well as the length of the interspace between the bases of the spurs should be given. Toe dimensions should be mentioned at least in qualitative terms (they are difficult to measure accurately).

I recommend that all body parts be measured on photographs, for even the tardiest bdelloid can be too unruly for the taking of accurate measurements directly under the microscope. Further details of measurement methodology are in [1].

Behavioral, ecological and other traits

Locomotion: Some bdelloid species are slow crawlers, for example, *Rotaria tardigrada* (Ehrenberg) true to its name, while others are fast crawlers that are difficult to follow under

the microscope, especially at high magnifications. Crawling speed is a good, but difficult to measure trait, so a qualitative indication of it as slow, moderate or fast, would suffice.

The tendency of bdelloids to swim is also variable. Some species almost always swim when they are feeding, some are almost exclusively stationary feeders and swim rarely, while others alternate between swimming and stationary feeding. The preference of a morphovariant for swimming or stationary feeding should be noted.

Only one philodinid, *Rotaria mento* (Anderson), has been noted to build a tubular case out of which it feeds [15]. If a new casebuilding morphovariant is encountered, information should be given about the structure of the case and how it is built.

Food: Most philodinids feed on suspended bacteria and organic particles that are small enough to pass through their mouths into their

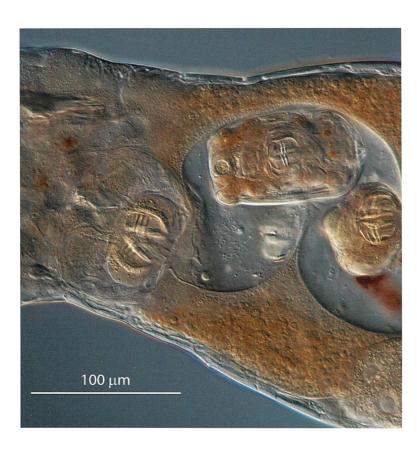


Fig. 10. Stomach lumen of an undescribed *Philodina* morphovariant (slightly compressed) that preys on smaller dead and live bdelloids. Two ingested and still alive bdelloids are visible in the wide lumen: a *Philodina* (elongated) and an *Abrochtha*.

stomachs. They do not seem to discriminate between digestible and indigestible matter [16]. For example, water insoluble particles of carmine, a salt of carminic acid that presumably has no nutritive value, are readily ingested and subsequently expelled through the anus. I have seen seemingly intact diatoms in the stomach lumens, intestines as well as in excrements of bdelloids; their silica walls are apparently too tough to be breached by the digestive fluids.

Some species are more specialized in their food requirements. Abrochtha intermedia (Beauchamp) feeds on unicellular and filamentous algae [16]. The bdelloid species that live in rock pools and birdbaths often have reddish orange stomachs, because they feed on the red cysts of the coinhabitant unicellular alga Hematococcus pluvialis (Fig. 2B). Although rare, carnivory is also practiced; I am preparing the description of a large philodinid that feeds on other bdelloids (Fig. 10).

Habitat: The specific habitat of a morphovariant should be mentioned in its description. If similar morphovariants have been found in different habitats, their morphologies should be compared carefully to determine whether they are identical.

The species in *Embata*, *Pseudoembata* and some in *Rotaria* have been reported to live epizoically on various freshwater arthropods, although sometimes they may also be found free. The marine bdelloid *Zelinkiella synaptae* lives on sea cucumbers. Whenever a new morphovariant in one of these genera is being described, an attempt should be made to determine its host.

Drying survival: Although many species of bdelloids survive drying [17], it is not known if all can. Habitats of bdelloids differ in the frequency and duration of the dry periods they experience [18] and the atmospheric conditions (humidity, insolation, etc.) that affect them. Obviously, long term residents of frequently drying habitats can tolerate drying. But those that live in perennially wet habitats, such as lakes or rivers, may be less tolerant or completely intolerant of drying. Because of the expected adaptive differences between morphovariants, no universal procedure might be suitable to test all species for drying survival under uniform

laboratory conditions. The relevant question is whether a morphovariant can survive the drying of its own habitat rather than an artificial test. This question can be answered easily by removing naturally dried samples from the habitat of the morphovariant and then monitoring the rehydrated samples in the laboratory [17].

Discussion

I suspect that many clusters of morphovariants (exemplified by cluster Z in Fig. 1) can be resolved into species by careful morphological scrutiny and comparison with other species. To facilitate species comparisons and prevent future taxonomic problems, all new morphospecies descriptions should include information on all of the traits discussed here even if they are not diagnostic. The list of traits given here is not final; future work may discover new taxonomically significant traits. For example, there may be differences at the level of species or genera in numbers and arrangements of muscles, as there are in some genera of monogonont rotifers [19], and of glands in the feet (see above). Any deviation from the usual morphology and consistent idiosyncrasies in behavior observed in the specimens of a morphovariant would be significant and should be documented and presented. At the same time, potential intraspecific variability of morphological traits should be taken into account.

I will end with a final recommendation. Anyone preparing the description of a new bdelloid species should keep in mind this question: is this description detailed and accurate enough to allow others to make a reasonably confident determination that their specimen is or is not the one I am describing?

Acknowledgements

I thank Robert L. Wallace for a "friendly" review that improved the manuscript. I dedicate this paper to the memory of the late Eric Hollowday whom I had the fortune to meet in person in the 1990s and who contributed to my studies of bdelloid rotifers by sending me copies of articles from the Journal of the Quekett Microscopical Club and other old publications that were at that time not yet available on the internet.

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