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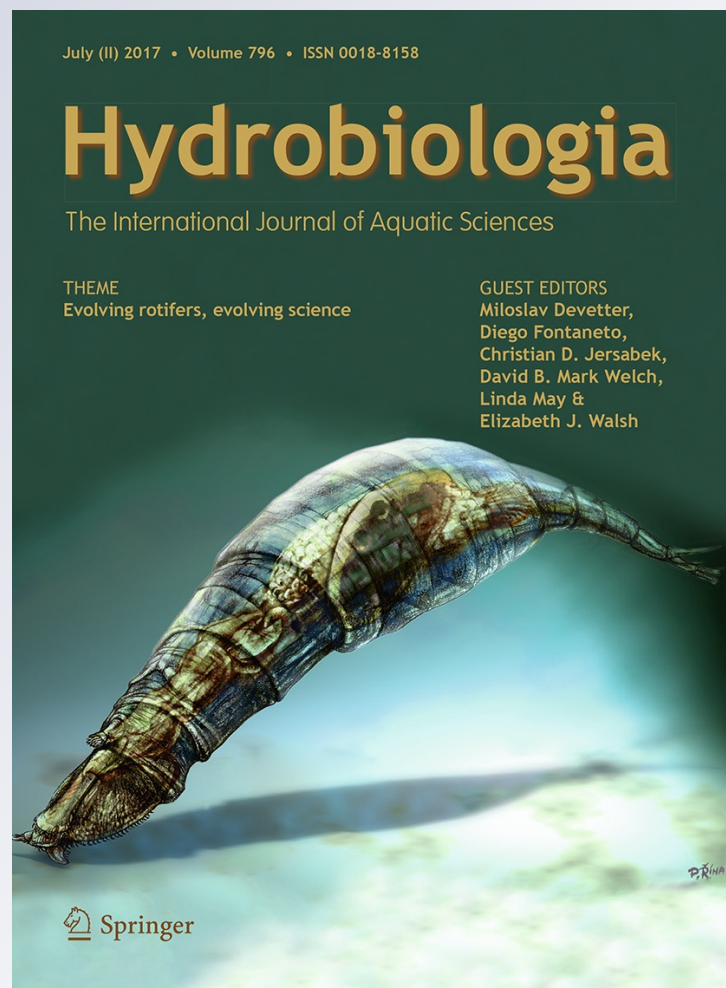
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A metadata approach to documenting sex in phylum Rotifera: diapausing embryos, males, and hatchlings from sediments

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Abstract We present a survey of the literature documenting sexuality in monogonont rotifers, including reports of diapausing embryos (DEs), males, and/or hatchlings from dry sediments. Of 30 families, 27 possess species with documented occurrences of sex. Information on DEs is lacking in 41 genera. Of ~300 species with evidence of sexuality (~20% of ~1500 monogononts), only 172 had direct observations of DEs; in the others, DE production was inferred from observations of males and/or hatchlings. DEs are sufficiently widespread to affirm that their presence is plesiomorphic, however few DE characteristics show a phylogenetic signature. They differ widely in

volume ($\sim 0.11\text{--}100 \times 10^5 \mu\text{m}^3$) and have a varied surface morphology (smooth to highly structured and ornamented). Some species retain DEs within their bodies; others carry them, deposit them on or attach them to surfaces, or release them free into the water. To better understand the evolutionary forces that influence monogonont sexuality and DE biology, a more comprehensive and uniform reporting scheme is needed. To enhance information dissemination, we propose that new and existing data on sex in monogonont rotifers (DEs, males, and hatchlings from dry sediments) be placed in an Internet-based repository.

Keywords Egg volume · Meta-analysis · Monogononta · Morphology · Phylogenetic distribution · Resting eggs · Survey

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Introduction

In monogonont rotifers, induction of sexuality initiates production of mictic females. These produce haploid males or, if the mictic female is fertilized, one or more diapausing embryos (DEs) (Gilbert, 1974; Gilbert & Williamson, 1983; Gilbert, 2004b; Wallace et al., 2015). Traditionally referred to as resting eggs (Rutner-Kolisko, 1974) or cysts (Snell and Janssen, 1995), DEs are embryos that have suspended any further development after several nuclear divisions (Gilbert, 1974; Boschetti et al., 2011).

DE production is a critical aspect of the life cycle because it increases the genetic diversity of populations (Gómez and Carvalho, 2000; Gómez, 2005). Because some DEs can remain dormant in sediments for decades, it also provides an egg bank for future repopulation thus providing an avenue for dispersal in time (Hairston Jr., 1996; Schröder 2001; Brendonck & De Meester, 2003; Gómez, 2005; Segers & De Smet, 2008; Epp et al., 2010; Chittapun, 2011; Michaloudi et al., 2012; Nielsen et al., 2012; Smith & Snell, 2012). In this regard, DEs represent a latent community that has the potential for immediate colonization when favorable conditions arise (Hairston et al., 2000; García-Roger et al., 2008; Battauz et al., 2014). In addition, DEs are agents of dispersal in space via hydrochory, zoochory, and anemochory (Rousset, 1909; Cáceres & Soluk 2002; Bailey et al., 2003, 2005a, b; Vanschoenwinkel et al., 2008).

Overall the importance of sex and concomitant production of DEs to the life history of monogononts is widely recognized and has been the focus of considerable study, including several comprehensive reviews (Gilbert, 1974, 1977; Pourriot & Snell, 1983; Lubzens et al., 2001; Ricci, 2001; Gilbert & Schröder, 2004; Schröder, 2005; Wallace et al., 2006).

Investigations have explored the evolution of sexuality and the biology of DEs in rotifers from a wide range of perspectives (Table 1). Yet, in spite of a rich literature on the subject, we still know very little about the diversity of monogonont sexuality and production of DEs, or of the functional significance of their morphology in the evolution of rotifers. Here we report a synoptic survey of monogonont sexuality by cataloging unambiguous records of DEs, the presence of males in the species, and/or hatchlings from rehydrated dried sediments. This information will be useful for framing future research into the evolution of sexuality, for refining phylogenies, and for systematizing morphological features for studies of functional ecology.

Methods

Our review of rotifer sexuality included more than 130 published reports from the primary and secondary literature (Supplemental Table 1), plus personal observations from colleagues and ourselves. Although comprehensive, this review is not exhaustive.

A species was deemed to be capable of sexuality if at least one of the following simple criteria were established: a DE, a male, or a hatchling from dried sediments had been reported. We used two equations to estimate DE volume for which we had relevant size data. These were: $4/3\pi r^3$ for spherical shapes and $4/3\pi r_1 r_2^2$ for oviform shapes, where r_1 = length of the longest axis (i.e., length) and r_2 is the length of the shortest axis (i.e., width).

Results

Distribution of sexual reproduction

In general, literature on monogonont sexuality is scant. For example, some reports state only “resting egg known” or “male reported”, or they provide incomplete descriptions (e.g., “resting egg spiny”). Often, relevant information is buried within the text of a much broader publication (Edmondson, 1940; Wallace, 1977). In contrast, some authors have noted that they have been unable to find evidence of sexuality in certain species using statements such as “males ... have not been observed” or “male unknown”—e.g., Stemberger (1976) for *Notholca laurentiae* Stemberger, 1976 and *Notholca michiganensis* Stemberger, 1976; and Luo et al. (2012) for *Notholca dongtingensis* Zhuge, Kutikova & Sudzuki, 1998. However, lack of information on male occurrence does not necessarily mean that sexuality does not occur in a species. Sexuality may last for only a few weeks during a growing season, so male production can be missed if samples are not collected during this period.

Despite limitations, there is much that we can learn from a survey of the literature (Supplemental Table 1). For example, of 30 monogonont families, we found documentary evidence of sexuality in 27 of them. To our knowledge, sexuality has not been reported in three rare, monospecific taxa: Birgeidae Haring & Myers, 1924, Clariidae Kutikova, Markevich & Spiridonov, 1990, and Cotylegaleatidae De Smet, 2007. Of 113 monogonont genera, we found evidence of sexuality in 72 (63.7%), with the remainder being *Anchitadina*, *Atrochus*, *Balatro*, *Beauchampia*, *Birgea*, *Claria*, *Cotylegaleata*, *Dicranophoroides*, *Dipleuchlanis*, *Diplois*, *Donneria*, *Dorystoma*, *Drilophaga*, *Elosa*, *Erignatha*, *Glaciera*, *Harringia*, *Inflatana*, *Kostea*, *Macrochaetus*, *Mikrocodides*, *Myersinella*,

Table 1 Summary of key information on monogonont sexuality and diapausing embryos in rotifers

Topic	Comments	Selected references
Sexuality		
Induction	Induction of sexuality varies in monogononts	Gilbert (1977), Gilbert (2004b), Snell et al. (2006), and Schröder & Walsh (2010)
Periodicity and frequency	Great variability within clones and among species	Aparici et al. (2001, 2002), and Smith & Snell (2012)
Loss of sex	Sexual reproduction is sometimes lost in long-term, stable cultures or unusually stable habitats	Bennett & Boraas (1989), Serra & Snell (2009), Stelzer et al. (2010), Scheuerl et al. (2011), and Pajdak-Stós et al. (2014)
Amphoteric females	One female produces both amictic and mictic eggs	Champ & Pourriot (1977), King & Snell (1977), Ruttner-Kolisko (1977), Snell & King (1977), Nogrady & Segers (2002), and Rico-Martínez & Walsh (2013)
Diapausing embryos		
General morphology	Shape varies from spherical to ovoid; surface varies from smooth to ornamented with plates, chambers, and spines	Documented herein: see Supplemental Table 1
Ultrastructure and biochemistry	Multilayered; trehalose, chitin, and late embryogenesis abundant proteins (LEA) are present; lipids	Piavaux (1970), Wurdak et al. (1977), Munuswamy et al. (1996), Caprioli et al. (2004), Gilbert (2004a), 2010), and Jones et al. (2012)
Development and genetic controls	No apparent phylogenetic signature of the stage at which development is arrested: nuclei no. <30 to 40–60 or more	Gilbert (1974), Boschetti et al. (2011), and Denekamp et al. (2009)
	Stem females of <i>Polyarthra</i> lack characteristic paddles (apterous)	Gilbert & Schröder (2004)
	Three classes of dormancy genes (antioxidation, heat shock proteins, and LEA) are present in <i>B. plicatilis</i>	Denekamp et al. (2009)
Asexual diapause	Induction via food limitation: potentially a strategy to spread risk	Gilbert & Schreiber (1995), and Gilbert & Schreiber (1998)
Sediments		
DE density and diversity	Different habitats and depths exhibit varying densities of DEs	Snell et al. 1983, Duggan et al. (2002), Albritton & White 2004, and García-Roger et al. (2008)
Hatching phenology	Hatching not uniform; phenology affects clonal and community structure	May (1987), King & Zhang (1993), Hairston et al. (2000), Langley et al. (2001), Albritton & White (2004), and Gaikwad et al. (2008); authors pers. obs.
Egg bank dynamics	Monogononts are suitable for testing bet-hedging theory	García-Roger et al. (2008), and García-Roger et al. (2014)
Paleoecology	Community structure and evidence of historic successional events	Hairston Jr. (1996), Van Geel (1998), Brendonck & De Meester (2003), Epp et al. (2010), and Battauz et al. (2014)

Paracolurella, *Parententrum*, *Pentatrocha*, *Pleurata*, *Pleurotrochopsis*, *Proalinopsis*, *Pseudoeuchlanis*, *Pseudoharringia*, *Pseudoploesoma*, *Pulchritia*, *Rous-seletia*, *Squatinella*, *Streptognatha*, *Taphrocampa*, *Tripleuchlanis*, *Tylotrocha*, *Wigrella*, *Wolga*, and *Wulfertia*. Of a total of 299 species where sexuality has been observed, 172 species had documented evidence of DEs and, of those, size information was

available for only 141. Lack of evidence of sexuality in some of these taxa may be related to the fact that many have not been studied sufficiently, in either field populations or laboratory cultures.

Clearly there is uncertainty associated with these summary statistics. Moreover, as the celebrated astronomer and science educator Carl Sagan reminded us “The absence of evidence is not the

evidence of absence.” Thus, we cannot be sure that those species for which there is no evidence of bisexuality are actually lacking that ability; it may have simply not been reported (Gilbert, 1977). Nevertheless, DEs are sufficiently widespread to posit that their presence is plesiomorphic. Indeed, DEs are probably much more widespread than published data supports. For example, populations of species that live in northern temperate lakes that freeze over during the winter probably restart from DE hatchlings in the spring.

Induction of sexuality

The parthenogenetic life cycle of monogononts has been well documented and need not be reviewed here (Wallace, 2002; Gilbert, 2004b; Wallace et al., 2006; Gilbert, 2007; Wallace et al., 2015). However, we do not have a thorough understanding of the diversity of factors that initiate sexuality or break DE dormancy within many monogononts. This is because most prior work focused on model species such as the species complexes of *Brachionus calyciflorus* Pallas, 1766 and *Brachionus plicatilis* O.F. Müller, 1786. Nonetheless, research recognizes the importance of prenatal food levels (Rumengan et al., 1998; Gilbert, 2010) and lipid energy reserves in DE production and viability (Gilbert, 2004a; Gilbert & Schröder, 2004). Also, research has begun to provide insights into the molecular controls of sexuality (Snell et al., 2006; Snell, 2011), including the identification of dormancy genes (Denekamp et al., 2009).

Periodicity and frequency

We are beginning to understand more about the timing of sexuality, how it can be modeled, and how it relates to habitat characteristics (e.g., Angulo et al., 2004; Gilbert & Schröder, 2004; Serra et al., 2004; Alver & Hagiwara, 2007; Serra et al., 2008; Gilbert, 2010; Gabaldón et al., 2015). For instance, Carmona et al. (2011) and Serra et al. (2011) explored sex initiation thresholds in *Brachionus manjavacas* Fontaneto, Giordani, Melone & Serra, 2007 using modeling approaches. Additionally, in a long-term experiment (>84 generations) populations experiencing treatment mimicking an ephemeral habitat evolved to produce greater numbers of diapausing embryos, maintained

higher frequencies of sexual females, and more readily induced mixis than a treatment simulating a permanent habitat (Smith & Snell, 2012).

Loss of sex

Under certain conditions, sex may be lost. Serra & Snell (2009) reviewed much of what is known about the loss of sex prior to 2009 and Stelzer et al. (2010) investigated potential mechanisms accounting for the loss. For instance, in multi-generational laboratory selection experiments *B. calyciflorus* can lose the ability to induce sexual reproduction (Bennett & Boraas, 1988; Fussmann et al., 2003; Stelzer et al., 2010; Scheuerl et al., 2011). Similarly there are reports of obligate asexual lineages of *Brachionus urceolaris* Müller, 1773 (Buchner, 1987), *Lecane inermis* (Bryce, 1892) (Pajdak-Stós et al., 2014), and *Epiphanes hawaiiensis* Schröder & Walsh (2010) (EJW, pers. obs.). In the latter two species, obligatorily asexual isolates were found in permanent habitats with little environmental variation (e.g., sewage treatment plants, and a permanent, high elevation lake in Hawaii, respectively).

Amphoterics and pseudosexual DEs

Amphoteric females produce eggs by simultaneous oogenesis via meiosis (male ova) and mitosis (female ova): i.e., a female carries both male and female offspring (Gilbert, 1974; King & Snell, 1977; Nogrady & Segers, 2002). For example, Ruttner-Kolisko (1977) reported a population of *Asplanchna priodonta* Gosse, 1850, where the females were carrying a male embryo and a DE or a female embryo and a DE. Also Rico-Martínez & Walsh (2013) confirmed reports by Champ & Pourriot (1977) of amphoterics in the sessile rotifer *Sinantharina socialis* (Linnaeus, 1756). By following the development of 12 females for 10 days after birth, they found that 25% produced both amictic and mictic eggs, while none produced DEs during the observation period. While amphoteric production appears to be rare it is likely to be plesiomorphic based on the fact that it is present in both Ploima and Gnesiotrocha. The cytological, genetic, and ecological consequences of amphoteric reproduction have yet to be fully explored. The same may be said for the production of diapausing amictic eggs (pseudosexual embryos) (Table 1). Gilbert &

Schreiber (1995, 1998) have examined this topic, but as the embryos are not produced sexually the topic lies outside the scope of this review.

Morphology of diapausing embryos

There is nothing unusual about the shape of DEs; in general they are either spheroids or ovoids, although some have slightly irregular variations on those forms. For example, DEs within the genera *Encentrum* and *Filinia* are often slightly flattened on one side. In contrast, there is wide variation in DE sizes ($n = 141$); the mean estimated volume was $\sim 6.8 \times 10^5 \mu\text{m}^3$, but their volumes span approximately three orders of magnitude (0.11×10^5 – $97.4 \times 10^5 \mu\text{m}^3$). The overall size distribution is clearly skewed towards smaller volumes, with $\sim 45\%$ of DE volumes being less than $2 \times 10^5 \mu\text{m}^3$ and $\sim 80\%$ being less than $10 \times 10^5 \mu\text{m}^3$ (Fig. 1). However, the analysis of DE size is complicated as the sizes of DEs collected from natural sediments vary with depth in the sediment (Snell et al., 1983; Brendonck & De Meester, 2003). Moreover, it is also known that there can be considerable clonal variation in DE volumes. For example, Liu & Niu (2010) found that DE volumes in clones of *B. calyciflorus* varied by up to 30%.

With the limited dataset presented here, it is difficult to identify a strong phylogenetic signature

in DE volume with any certainty. However, there are some notable patterns. For example, members of the Asplanchnidae (*Asplanchna*, $n = 6$ and *Asplanchnopus*, $n = 1$) have estimated DE volumes of greater than $15.5 \times 10^5 \mu\text{m}^3$. On the other hand, *Proalides subtilis* Rodewald, 1940 (Epiphanidae) and *Asciaporrrecta arcellicola* De Smet, 2006 (Asciaporrrectidae) have the smallest estimated volumes in our database: $0.11 \mu\text{m}^3$ and $0.16 \times 10^5 \mu\text{m}^3$, respectively.

The surface features of DEs also appear to vary considerably. This variability is seen within a species under different magnifications, as well as across species and genera. For example, some DEs appear to have a smooth surface, but closer examination using Transmission Electron Microscopy reveals a rugose surface at a scale of $\sim 1 \mu\text{m}$. This can be seen in *Asplanchna sieboldii* (Leydig, 1854) and other *Asplanchna* species (Gilbert & Wurdak, 1978; Wurdak et al., 1977), *B. plicatilis* sensu lato (Munuswamy et al., 1996), and *Brachionus rotundiformis* Tschugunoff, 1921 (Mills, 2006). Some species possess spiral ridges that resemble lines of elevation on a topographical map: e.g., *Conochilopsis causeyae* (Vidrine et al., 1985), *Conochilus natans* (Seligo, 1900), *Floscularia conifera* (Hudson, 1886), *Octotrocha speciosa* Thorpe, 1893, and *Ptygura pilula* (Cubitt, 1872). Other surface features include float chambers (*Filinia*), labyrinth-like walls (*Keratella valga*)

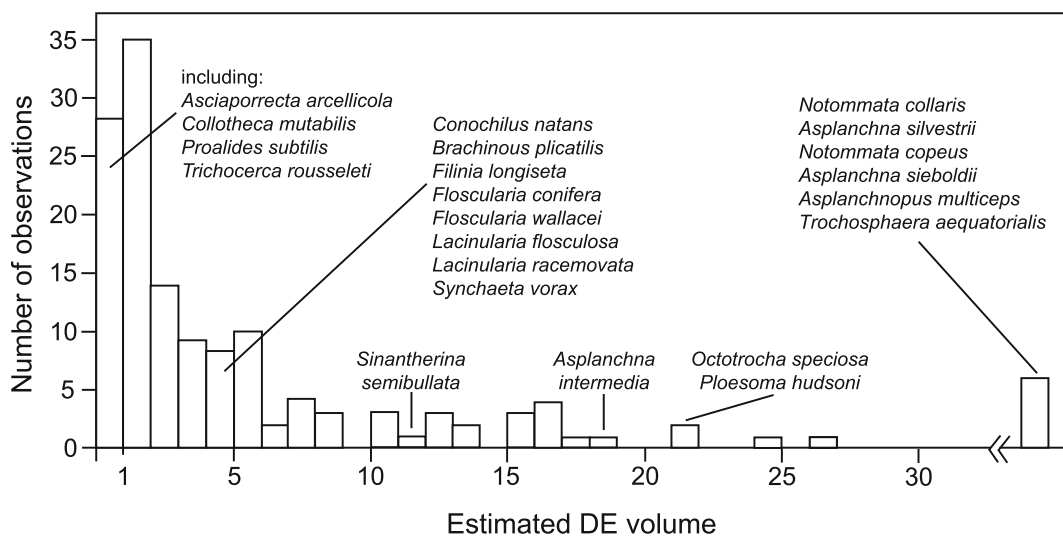


Fig. 1 Distribution of estimated volumes ($\times 10^5 \mu\text{m}^3$) of diapausing embryos of monogonont rotifers uncovered in our literature search. Mean volume ~ 6.8 ; minimum volume: *Asciaporrrecta arcellicola* (~ 0.11); largest estimated volumes:

Notommata collaris (32.5), *Asplanchna silvestrii* (38.8), *Notommata copeus* (39.0), *Asplanchna sieboldii* (45.1), *Asplanchnopus multiceps* (65.0), and *Trochosphaera aequatorialis* (97.4)

(Ehrenberg, 1834), and long projections (*Proales parasita* (Ehrenberg, 1838) and *Trochosphaera aequatorialis* Semper, 1872). The DEs of *Collotheca*, *Polyarthra*, and *Trochosphaera* have spines or spurs, while *Scaridium longicaudum* (Müller, 1786) has thin, hair-like projections.

In addition, the DE surface is not uniform among species within the same genus. For instance, *Epiphanes macroura* (Barrois & Daday, 1894) has minute hair-like projections, *Epiphanes daphnicola* (Thompson, 1892) has flattened granules, and *E. hawaiiensis* possesses a smooth surface. Unfortunately, comparison is difficult as there is no uniformity in terms used to describe DE surface features. For example, imprecise terminology such as bumps, corrugated, plates, reticulate, spurs, and wrinkled are often used to describe DE wall conformation (Koste, 1971; Wurdak et al., 1977; Wurdak et al., 1978; Mills, 2006).

Deposition of DEs

Positioning of the mature DE by the female varies greatly. Many species simply release them into the water, using gas-filled chambers to keep them afloat; such species include those from the genera *Filinia* and *Horaella* (Nogrady & Segers, 2002). However, even the DEs of species without obvious floatation chambers (e.g., *B. plicatilis*, *B. rotundiformis*) are known to float under certain circumstances (Hagiwara, 1996). Other species simply release their DEs into the water (e.g., *Notholca*), deposit them on surfaces [e.g., *Asplanchnopus*, *Epiphanes*, *Euchlanis* (Ruttner-Kolisko, 1974)], or retain their DEs within the body of the female [e.g., *Asplanchna*, *Hexarthra*, *Trochosphaera aequatorialis* Semper, 1872 and *Lecane* (Segers, 1995; Nogrady & Segers, 2002)]. In *Sinantherina ariprepes* Edmondson, 1939 and *Sinantherina socialis* (Linnaeus, 1758), DEs break out of the oviduct and slide into the elongated foot of the animal (Edmondson, 1940). *Rhinoglena* also retains the embryo within the body where it remains until the death of the adult (Ruttner-Kolisko, 1974). Even in closely related species variation in the deposition of their DEs is noteworthy. For example, of two clones within the cryptic species complex of *B. plicatilis*, one (SPO) keeps its DEs within the body, while the other (CU) holds them close to its body with a thin thread (Serrano et al., 1989), as does *Brachionus*

rotundiformis Tschugunoff, 1921. *Kellicottia* and *Keratella* carry their DEs close to their bodies, but *Pompholyx sulcata* Hudson, 1885 holds its DEs a bit further away from the body on short stalk. Sessile species tend to deposit their DEs into their extracorporeal tubes: e.g., *Collotheca*, *Floscularia*, *Ocotrocha*, *Ptygura*, and *Stephanoceros* (Koste, 1978). Members of Conochilidae do this too, but the DEs appear to be held for only a short time (Koste, 1978; RLW, pers. obs.). It is likely that the mode of deposition of diapausing eggs will have direct consequences for their dispersal and hatching success; as such, this aspect of their biology should not be ignored.

Dispersal of DEs

Rotifer DEs fall well below the ubiquity-biogeography transition point of $\leq 1000 \mu\text{m}$, so it seems likely that they are cosmopolitan in their dispersal (Weisse, 2006). Indeed, since first proposed by Rousselet (1909), cosmopolitanism has been the dominant construct in this context for most of the last century. This is the so-called Baas Becking principle or the ubiquitous hypothesis (de Wit & Bouvier, 2006). Although some rotifers do seem to have a marked biogeographical distribution (Dumont, 1983; Segers, 2001, 2003, 2008), the small size of their DEs provides a strong argument for their ready dispersal via anemochory (wind), hydrochory (water), and zoochory (animal). Jenkins & Underwood (1998), Cáceres & Soluk (2002), Frisch et al. (2007), and Altermatt et al. (2011), among other researchers, have explored these topics.

A field of study about which we know even less is the potential for anthropogenic dispersal. However, there is ample evidence of dispersal via sediments in the ballast water of ships (Bailey et al., 2003, 2004, 2005a, b; Briski et al., 2010). Species that have been hatched successfully from ballast sediments include *Asplanchna girodi* Guerne, 1888, *Brachionus budapestinensis* Daday, 1885, *B. calyciflorus*, *Filinia* spp., and *Ploesoma* spp. Other species that may have been dispersed by human transport of DEs include *Kellicottia bostoniensis* (Rousselet, 1908) (Armeno et al., 1968; Eloranta, 1988), *Brachionus havanaensis* Rousselet, 1911 and *Keratella americana* Carlin, 1943 (Segers, 2001), and *Lecane* spp. (Segers, 1996).

Egg banks in sediments and factors influencing their hatching success

Of course, DEs are critical to the re-establishment of rotifer communities that have endured drought (Nielsen et al., 2000; Jenkins & Boulton, 2003; Gaikwad et al., 2008), water level fluctuations (Albritton & White, 2004), periods of salinization (Nielsen et al., 2012), or other unfavorable environmental conditions (see Walsh et al., 2014). However, DE densities in sediments vary widely; indeed literature reports indicated that the densities range from only a few up to many more than 300 DEs cm⁻³ of sediment (Snell et al., 1983; Shiel et al., 2001; Duggan et al., 2002).

Hatching success of DEs deteriorates over time, with those found at greater depth being older and less likely to hatch than those from closer to the surface (García-Roger et al., 2006). However, that pattern did not hold for DEs of *Brachionus* sp. hatching from sediments in a Rhode Island (USA) estuary (Marcus et al., 1994). Dehydration also affects DE viability, especially in temporary waters (Chittapun et al., 2005; 2009; Walsh et al., 2014), and the littoral zone of larger water bodies (Albritton & White, 2004). In general, DEs of pelagic species are less likely to survive dehydration than those of littoral species (Langley et al., 2001; Albritton & White, 2004) or species that are found in temporary, desert ponds (EJW, pers. obs.). Other factors that affect survival of DEs in dry sediments include salinity, temperature, and UV light (Walsh et al., 2014). The practice of post harvest, stubble burning in Thai paddy fields also reduces DE hatching success (Chittapun, 2011). Beside sediment age, other factors such as condition of the mictic female and preservation conditions in the sediment are important to DE survival (Chittapun et al., 2005; Schröder, 2005).

While temperature (May, 1987; Duggan et al., 2002) and light (Kim et al., 2015) are known to be important factors in hatching, to our knowledge there have been few studies assessing hatching requirements across taxonomic lines (e.g., see Chittapun et al., 2005; Jones et al., 2012). Another aspect of the sediment egg bank about which we have little information is the importance of bioturbation in either burying DEs deeper or bringing them to the surface where they may be exposed to more favorable hatching conditions (see Wallace et al., 2006 for a brief review).

Methods for enumeration and extraction of DEs from sediments

The successful extraction, identification, and enumeration of DEs in sediments can be difficult to achieve (Snell et al., 1983). Many methods have been used with varying degrees of success, including induction of hatching (Balompapuerng et al., 1997; Pourriot & Snell, 1983; May, 1986; Hagiwara & Hino, 1989; Marcus et al., 1994; Albritton & White, 2004; Gilbert & Schröder, 2004; Chittapun, 2011; Battauz et al., 2014; Walsh et al., 2014). However, estimates of richness derived from rigorous sampling regimes may not be congruent with that from sediment hatching (Langley et al., 2001; Duggan et al., 2002). Other methods that have been employed to isolate DEs include flotation (Snell et al., 1983; Duggan et al., 2002) and manual isolation (Nipkow, 1961; Bogoslovsky, 1963; García-Roger et al., 2006).

Surface features of DEs may be very similar thus identification of specimens isolated from sediments is probably impossible or at least unreliable (Ruttner-Kolisko, 1974; Pourriot & Snell, 1983). Thus, the best way to build a species list is to induce hatching so that the hatchlings can be identified using standard keys.

Emergence traps have been used with good success for in situ assessment of DE hatching in lakes (Hairston et al., 2000) and the ballast tanks of ships (Bailey et al., 2005b), but this technique has not been widely adopted. Unfortunately the horizontal distribution of DEs in sediments has not been sufficiently examined. Nevertheless, we do know that DE density can vary spatially among sampling stations in a single habitat (Snell et al., 1983), a phenomenon that may be attributed to uneven sedimentation throughout a basin (Lehman, 1975; Brendonck & De Meester, 2003).

Another consideration is that the DEs of some species are notoriously difficult to hatch under laboratory conditions. For example, many researchers have attempted to hatch DEs of *Euchlanis dilatata* Ehrenberg, 1830 with very limited success. Only those from ephemeral pools seem to readily hatch under standard lab conditions (EJW, pers. obs.).

Paleoecology

While rehydration of sediments of >50 years old have yielded viable hatchlings, there are only a few reports of DEs from sediments that might qualify as fossils.

Mills (2006) cited the work of Manca and colleagues who found resting eggs in sediments >10,000 ybp from two Italian lakes; also Ruttner-Kolisko (1974) shows microphotographs of DEs of *Filinia* and *Polyarthra* that are reported to have been collected from “early post-glacial sediments.” However, without a comprehensive catalog of rotifer DE morphology, paleolimnological uses of DEs will be limited (Ruttner-Kolisko, 1974).

Hatchlings: stem females

Hatchlings from the DEs of species from the genera *Filinia* and *Polyarthra* do not possess the setae (bristles) or paddles, respectively, that characterize later generations: see for example the discussions of Ruttner-Kolisko (1974) and Luo et al. (2012). These stem females form the so-called aptera generation in *Polyarthra*, which, in the past, was nominated as a separate genus *Anarthra* (Hood, 1895). Two important questions may be posited about these forms including the following. (1) What are the epigenetic controls that block the initial production of bristles/paddles and how are these controls relaxed in subsequent generations? (2) Are the musculature, innervation, & swimming dynamics the same among these forms?

Another variation in stem female life history is their response to mictic signals. It has been assumed that, after hatching, females reproduce by parthenogenesis for several generations before becoming sufficiently sensitive to their mictic signal to initiate sex. For example, Schröder & Gilbert (2004) report that amictic females of several species are less responsive to mictic signals than later generations, with the greatest response coming after five generations. These researchers report that this delay in response varies among species and within strains. However, females of *Hexarthra* sp. populations from ephemeral rock pools of the Chihuahuan desert deviate from this classic pattern. Schröder et al. (2007) showed that, within 2 days of rains refilling these temporary pools, up to 85% of the females were sexual. In culture, 7–46% of hatchlings from rehydrated sediments were sexual and DEs were formed within 1.5 days at 30 °C.

Discussion

To our knowledge this is the first work since Wesenberg-Lund (1930) to attempt to compile data on

monogonont sexuality, with an emphasis on the occurrence of DEs. Unfortunately, our study was hindered by a scant, scattered, and incomplete literature. Thus, we encourage researchers to pay closer attention to DE morphology (size, shape, surface features), induction of sexuality, hatching conditions, and deposition, as well as the presence of amphoteric females and the production of pseudosexual diapausing embryos. However, to accomplish a uniform way of collecting data, we need to standardize the recording of DE size (maximum length and width) and shape, and develop a clear terminology for describing their surface features.

We acknowledge that our compilation of species that show evidence of sexual reproduction (Supplemental Table 1) is a preliminary step along the path to a better understanding of monogonont sexuality. Therefore, we recommend the development of a readily accessible database that documents observations of DEs, the unequivocal presence of males, and/or hatchlings from dry sediments. One way to accomplish this would be to construct a repository for new information as it becomes available. Ultimately, we envision this repository to exist as an electronic platform, perhaps as an expansion of an existing Internet-based catalog such as the *Rotifer World Catalog* (Jersabek & Leitner, 2015). Alternatively, it could be linked to a project such as the Freshwater Information Platform or maintained as an independent site. We suggest that a database on rotifer DEs should provide basic information including, but not limited to, the following: taxonomy (including naming authority), evidence of sex (DEs, presences of males, and/or hatchlings from sediments), DE morphology (measurements, surface features, mode of deposition), and environmental information at the time and place of collection (e.g., collection date, location and habitat, basic physical and chemical features of the site). Whenever possible, photographic documentation of the DEs should be included.

While we have too little information about DE characteristics to postulate specific phylogenetic signatures, monogonont DEs offer a wealth of opportunities to refine our taxonomic resolution of species and for formulating and testing hypotheses about adaptation to changing environments and ecological resilience. With a better understanding of monogonont DEs, researchers will be able to explore a wide range of research topics such as intraspecific variation in

morphology, life history patterns, developmental and hatching controls, biogeography and phylogeography, and paleolimnology.

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