

## SEXUAL DIMORPHISM IN *BRACHIONUS PLICATILIS* (ROTIFERA): EVOLUTIONARY AND ADAPTIVE SIGNIFICANCE

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The Metazoa include a number of very successful taxa with primarily parthenogenetic reproduction interrupted only occasionally by sexual reproduction (i.e., Cladocera, Rotifera, Aphididae). One of the major aquatic groups with such characteristics is the phylum Rotifera. In the monogonont rotifers, which dominate among the modern Rotifera, amictic females predominate but mictic females are occasionally produced in response to specific environmental stimuli (Gilbert, 1963, 1974; Ruttner-Kolisko, 1974; Pourriot and Rougier, 1977). Both amictic and mictic females are diploid. Mictic females produce haploid eggs through meiosis of the oocytes. These haploid eggs develop into males if they are unfertilized (Jones and Gilbert, 1976), but are also capable of becoming diploid resting eggs if they are fertilized. Actually the resting eggs are partially developed embryos in an arrested state of development (Wurdak et al., 1978). As the males increase in number and fertilize an increasing percentage of the mictic females, the production of new males in the population declines and the balance shifts towards the production of resting eggs.

Rotifer resting eggs represent the outcome of genetic recombination and are thus thought to be responsible for some degree of phenotypic diversity in the subsequent generation of parthenogenetic females (Pejler, 1956; Williams and Mitton, 1973; Williams, 1975). The value of this increased diversity is uncertain. Ruttner-Kolisko (1974) discusses several deviations from the typical pattern of heterogony in the rotifers including instances of parthenogenetic resting egg production and concludes that the biological importance of

the mictic phase lies in the production of the resting eggs rather than an increased genetic variety. The validity of this conclusion can be questioned in view of the apparent evolutionary feasibility of parthenogenetic resting egg production as a superior alternative to sexual resting egg production if recombination were not important. The predominance of sexual resting egg production thus implies that the recombination is important.

Male rotifers are small, short-lived and very active. These factors have led some authors to describe them as "free-swimming packets of sperm" (Ruttner-Kolisko, 1974), or "... not much more than a sperm sac surrounded by protoplasm and a cuticle, and having an anterior tuft of cilia" (Pennak, 1978). Males possess several adaptations for contacting mictic females—one of these is their very high rate of activity. As expressed by Hudson and Gosse (1889), "This strangely furnished creature leads a brief life of restless energy, now darting from place to place, so swiftly that the eye can scarcely follow it, and now whirling round as if anchored by its curved foot and penis." The behavioral dichotomy between the sexes allows the larger female to devote time and energy almost exclusively to feeding and egg production, whereas the males do not feed at all and devote all of their time to finding mictic females. In fact males of most species lack a functional digestive system (Hudson and Gosse, 1889; Ruttner-Kolisko, 1974; Gilbert, 1977; Pennak, 1978).

In the present study we examine the complex of adaptations including sporadic sexuality, extreme morphological and behavioral dichotomy between the sexes, and production of the resting eggs from

the standpoint of energetics in the species *Brachionus plicatilis* (Müller), a common monogonont rotifer of fresh and brackish water environments. We then compare life histories and morphologies of a wide range of rotifers in light of the metabolic data and draw some general conclusions concerning the patterns of adaptation and evolution in the Rotifera.

## MATERIALS AND METHODS

### *Culture Procedures*

*Brachionus plicatilis* was cultured in artificial Woods Hole sea water (Cavanaugh, 1956) which had been diluted to 100 m-osmoles and buffered to pH 8.0 (Epp and Winston, 1978). Females were fed bacteria-free *Haematococcus* sp. obtained originally from the Indiana University algal collections. Females were cultured in Stender dishes (diameter, 50 mm) at 24 C with a light cycle of 12L:12D.

High population densities, which others have found to be an effective stimulus for mictic female production in the genus *Brachionus*, did not induce sexuality in our population (Gilbert, 1963; Hino and Hirano, 1976; Pourriot and Rougier, 1977). The appearance of mictic females and the subsequent production of males were finally induced by removal of the cultures from the environmental chambers for 24 h. The stimulus may therefore have been the sudden change either in photoperiod or in temperature. Ruttner-Kolisko (1964) has previously shown that the production of mictic females may be triggered by "temperature shock" (i.e., a brief alteration in temperature).

Mictic females were isolated in the depressions of glass spot plates and returned to the environmental chambers. Spot plates were maintained in a water-saturated atmosphere to prevent evaporation from the depressions. After hatching from the mictic eggs, the males were isolated in other depressions containing several experimental media.

### *Activity Measurements*

Activity measurements were made in a Stender dish attached to a thermocouple

which served as a temperature control. This arrangement allowed us to maintain the temperature at  $24 \pm 0.5$  C throughout an experiment. A grid (1-mm squares) was placed under the dish and the depth of the water in the chamber was adjusted to 1 mm.

An experimental animal was placed in the dish for an equilibration period of 5 min prior to the activity measurement. The number of squares the animal entered during the subsequent 2 min was then recorded along with the number of stops and the total time the animal remained stationary. Since the emphasis of the experiment was on the energetic cost of movement, the trial was discarded if the stationary time exceeded 25% of the total time of the trial. The initial 5 min equilibration period was frequently extended to allow the animals to move from the side of the dish because of the difficulty of viewing rotifers near the glass wall. When an animal approached within 2 mm of the side, the trial was discarded.

### *Respiratory Measurements*

Straight-necked Cartesian divers with gas volumes of less than  $1 \mu\text{l}$  were used to determine the oxygen consumption of individual male and female rotifers as described by Epp and Winston (1978). Respiratory determinations lasted between 2 and 3 h and the results were converted to standard temperature and pressure. An oxy-caloric coefficient of  $4.8 \text{ Kcal l}^{-1}$  oxygen was then used to convert oxygen consumption to its caloric coefficient (Brody, 1945). Because metabolism was measured on unrestrained animals and activity was not enforced, the measurements were considered to represent "routine" metabolism (Prosser, 1973).

### *Size Determination*

Rotifers were lightly anesthetized with tricaine methanesulphonate and body dimensions were determined with an ocular micrometer at  $400\times$ . The simplified length:volume equation for *Brachionus* (Bottrell et al., 1976) was used for the females as follows:  $V = 0.13 a^3$  (the equa-

TABLE 1. *Body dimensions and caloric values of the male and female Brachionus plicatilis. Standard deviations are given with the means.*

	Length ( $\mu\text{m}$ )	N	Width ( $\mu\text{m}$ )	Volume (nl)	Dry wt. ( $\mu\text{g}$ )	Caloric value (Kcal)
Female	237 $\pm$ 13	5	170	1.77	0.195	10.89 $\times$ 10 <sup>-7</sup>
Male	113 $\pm$ 3	5	92	0.29	0.031	1.75 $\times$ 10 <sup>-7</sup>
Amictic egg	128 $\pm$ 1	8	105	0.90	0.096	5.50 $\times$ 10 <sup>-7</sup>
Mictic egg	98 $\pm$ 4	11	77	0.30	0.033	1.85 $\times$ 10 <sup>-7</sup>

tion includes a 10% allowance for the volume of the foot), where  $a$  is the length in  $\mu\text{m}$  excluding the foot and  $V$  is the volume in nl (nanoliters, 10<sup>-9</sup> l). The males were more elliptical than the females so the simplified equation of Bottrell et al. for *Gastropus* was used ( $V = 0.29 a^3$ ). Volumes were converted to wet weight assuming a specific gravity of 1.0. Dry weight was considered to be 11% of the wet weight (Sitaramaiah, 1976) and this was converted to calories with a conversion factor of 5.6 Kcal g<sup>-1</sup> (Winberg, 1971).

### RESULTS

The dimensions and caloric equivalents of the male, female, amictic egg, and mictic egg are shown in Table 1. The males are approximately half as long as the females and have total weights and caloric values 16% those of the females. The caloric value of the mictic egg is 35% of the caloric value of the amictic egg.

The depth of the water in the activity test chamber (1 mm) effectively limited the movement of the animals to the horizontal plane. The degree of movement can therefore be expressed as mm traveled minute<sup>-1</sup>. The rate of movement of the males is significantly greater than that of the females (84  $\pm$  9 versus 46  $\pm$  11 mm min<sup>-1</sup>;  $t = 13.7$ ,  $P < .001$ ). Activities also differ on a relative basis (number of body

lengths traveled per unit time). While the absolute activity of the males is approximately 80% greater than that of the females, the relative activity is nearly 300% greater (747 versus 198 body lengths min<sup>-1</sup>).

The absolute oxygen consumption of the females is approximately four times higher than that of the males (Table 2). When the oxygen consumption is converted to  $QO_2$  (ml O<sub>2</sub> g dry wt<sup>-1</sup>hr<sup>-1</sup>), however, we see that the energy expenditure per unit protoplasm is somewhat greater in the males.

A decrease in the relative metabolic rate ( $QO_2$ ) with increasing size has been recognized since the latter part of the nineteenth century (Rubner, 1883) and the subject has been considered in a number of reviews (Hemmingsen, 1950, 1960; Zeuthen, 1953, 1971). The relationship can be expressed by the equation  $Y = aX^b$ , with  $Y$  representing the oxygen consumption per individual and  $X$  the weight of the individual (symbols after Brody, 1945). The constant  $b$  is usually near 0.75 for interspecific comparisons at body weights greater than 40 mg wet weight (Zeuthen, 1953). Our own unpublished work with freshwater zooplankton indicates that metabolism does regress at a similar rate with increasing size at weights below 40 mg provided that the increase in

TABLE 2. *Oxygen consumption and caloric requirements for male and female Brachionus plicatilis. (24 C).  $QO_2$  and percent body weight (B.W.) are based on the weights given in Table 1.  $N = 30$  (females) and 9 (males).*

	$\mu\text{l O}_2 \times 10^{-4} \text{ind}^{-1} \text{hr}^{-1}$	Kcal hr <sup>-1</sup>	Kcal day <sup>-1</sup>	$QO_2$ (ml O <sub>2</sub> g <sup>-1</sup> hr <sup>-1</sup> )	% B.W. day <sup>-1</sup>
Female	21.6 $\pm$ 3.4	10.4 $\times$ 10 <sup>-9</sup>	248 $\times$ 10 <sup>-9</sup>	11.1	23
Male	4.9 $\pm$ 1.2	2.4 $\times$ 10 <sup>-9</sup>	56 $\times$ 10 <sup>-9</sup>	15.6	32

size does not involve a significant change in body form. The equation  $Y = aX^b$  with a  $b$  value of 0.75 was therefore used in the present study to determine the value of the constant  $a$  for both the male and female rotifers.

The value of  $a$  is 0.37 for the males and 0.41 for the females. Thus when the standard metabolic adjustment is made for size using a  $b$  value of 0.75, the males have a slightly lower  $QO_2$  than the females. This is counterintuitive, since the males are much more active and would thus be expected to have a higher  $QO_2$  when the adjustment for size is made. This apparent anomaly may be explained by the absence of the digestive tract in the male and the corresponding reduction in the metabolic cost of maintenance due to the greater simplicity of the male. Because of its more limited range of functions, the male can focus a greater percent of the routine metabolic rate on activity and thus reduce the total size-adjusted metabolic rate.

The power required to move the rotifers at the observed velocities was estimated from the following equation (after Campbell, 1977):  $P = C_d A \rho u^3$ , where  $P$  is the power in watts,  $u$  is the velocity in m/s,  $C_d$  is the drag coefficient,  $A$  is the cross-sectional area perpendicular to movement ( $m^2$ ) and  $\rho$  is the fluid density ( $10^3 kg/m^3$ ). The coefficient of drag was estimated as 0.46, which is the drag coefficient of a cylinder with the major axis parallel to the flow and with  $1 < L/D < 2$  (Campbell, 1977). Power in watts was subsequently multiplied by 0.861 to obtain  $Kcal\ hr^{-1}$  (Weast, 1966). The computation does not include any inefficiencies that might occur in the transfer of power from the propelling mechanism to the moving body, hence we will refer to  $P$  as the "theoretical power."

The theoretical power ( $P$ ) computed in this manner is 67% greater for the males than the females (Table 3) because the males move faster. If the males were the same size as the female, however, the energy expenditure for motion would be over three times as great as that of the normal small-size male. The small size of the male

TABLE 3. The caloric cost of movement (theoretical power,  $P$ , see text) in the male and female of *Brachionus plicatilis*. The % of the routine metabolic rate (R.M.R.) accounted for by the theoretical power is based on the metabolic rate data given in Table 2.

	$P$ , Kcal $hr^{-1} \times 10^{-15}$	% of R.M.R.
Female	4.32	0.00004
Male	7.21	0.00031
Hypothetical male*	24.60	0.00105

\* An animal having the same activity as the male but the size of a typical female.

thus partially offsets the higher power requirements related to its higher activity. The theoretical power for both males and females is extremely low relative to the routine metabolic rate, however (Table 3). The theoretical power is higher in relation to routine metabolic rate in males than in females (Table 3).

In a final experiment, 50 males were placed in four different test media with varying concentrations of dissolved organic material. One of these media was merely the diluted artificial sea water that was used as a general culture medium for the females. The other three media were 1) soil extract (James, 1974), 2) rotifer culture water from which the bacteria, algae and other rotifers had been removed by filtration, and 3) a water extract of homogenized *Haematococcus* sp. No changes in longevity were detected under the different conditions, suggesting that dissolved organic material does not nourish and thus extend the lifespan of the males. The lifespan for all the males was between 24 and 36 h. Pennak (1978) has suggested that the males of most species live for two to three days and Ruttner-Kolisko (1974) has estimated the average lifespan as a few hours up to two days depending on the degree of morphological reduction. Recently, Snell (1977) has estimated the lifespan of male *Asplanchna* at 1.74 days, which is approximately 50% that of the female.

## DISCUSSION

### *Metabolism, Size, and Locomotion*

Based on a caloric requirement of  $56 \times 10^{-9}$  Kcal  $day^{-1}$  (Table 2), and the ob-

served lifespan (24–36 h), the males of this study would use between 32 and 48% of their total body energy stores during their brief existence (24 C). The male is endowed with a fixed supply of energy at birth and the lifespan of the animal is obviously limited by this initial endowment because it does not feed or take up nutrients from the medium.

Selective pressures have undoubtedly favored females that supply their male offspring with only the minimal energy required to achieve reproductive success so that the number of males produced per unit time can be maximized (see also Gilbert, 1977). Recently Pourriot (1973) has shown that the number of eggs laid per unit time is greater in mictic females than in amictic females, but the total number of eggs produced is the same because of the shorter lifespan of the mictic females. The adaptive value of the small mictic egg may thus arise as much from the advantage of a quick response to the environmental stimuli as from the advantage of producing many eggs per unit time.

The extremely low theoretical power requirements for movement are surprising. There is some uncertainty in the calculations, particularly with regard to the drag coefficient, but no realistic drag coefficient would substantially raise the estimates of theoretical power. Vlymen (1970) suggests a drag coefficient of 0.85 for copepods instead of 0.46 as used for the rotifers in this study, but this would still yield theoretical power requirements equal to only  $57 \times 10^{-5}\%$  (male) and  $9 \times 10^{-5}\%$  (female) of the routine metabolic rate.

The difference between the active metabolic rate and the standard metabolic rate (i.e., resting metabolic rate: Prosser, 1973) has been shown to be considerable in all animals for which direct measurements have been made, including a number of small invertebrates (Krogh, 1941; Hanegan and Heath, 1970; Prosser, 1973). Direct measurements of the energetic cost of movement in aquatic microinvertebrates has thus far proven to be impossible, however (see Vlymen, 1970). The

great difference between active and standard metabolic rates in those organisms on which it has been possible to make direct measurements indicates that the energetic cost of movement is substantial, and it seems likely that this is also true for the rotifers and other microinvertebrates on which direct measurements have not yet been made. The present study has shown, however, that the energy required to move a rotifer at normal velocities, disregarding inefficiencies in the propelling mechanism, is extremely small. Together these facts suggest that the efficiency of locomotion, which can be expressed as follows, is extremely low:

$$\text{Locomotion Efficiency} = \frac{\left( \begin{array}{l} \text{Theoretical power required} \\ \text{to move a rotifer-size body} \end{array} \right)}{\left( \begin{array}{l} \text{Active Metabolic Rate} \\ - \text{Standard Metabolic Rate} \end{array} \right)} \times 100$$

Low locomotor efficiency implies that the locomotor organelles are extremely inefficient in translating metabolic energy into motion. This may be a major reason why the rotifers are one of the few groups of actively swimming metazoans to rely solely on ciliary movement for locomotion and may set severe size and habitat limitations on metazoans that move by cilia. Further exploration of this possibility by more extensive comparison of active and standard metabolic rates and power requirements for locomotion could be very revealing with regard to the evolution of the metazoa.

#### *Evolutionary Sequences*

Logical evolutionary sequences by which the small males with high activity and degenerate digestive systems could have developed are limited. It is very likely that small size evolved first or at least in conjunction with high activity. An increase in activity without a corresponding reduction in size would have greatly increased the energy required for movement in the male (Table 3, actual male versus hypothetical male). The most probable reason for the original reduction in size would be the selective advantage of producing more males per unit time. Once the

smaller size was established, the increase in activity could have followed without expenditure of a prohibitive amount of energy.

Degeneration of the digestive system probably evolved most recently. If it had occurred before a reduction in size, the greatly shortened lifespan, which is a necessary counterpart of life without food, would have caused serious disadvantages because of the necessarily lower activity of the larger organism. By the same token, degeneration of the digestive system without an increase in swimming speed would be disadvantageous.

The most likely evolutionary scheme would thus call for a reduction in size of males due to the advantages of producing more males per unit time. The reduction in size would in turn allow an increase in activity without a prohibitive increase in energy expenditure. With a greater efficiency of sexual contact due to the higher activity, the male digestive system would have lost its adaptive value in extending the lifespan and would be lost to minimize metabolic maintenance costs or to reduce body size further. The present study supports this concept since the size-adjusted metabolic rate of the male is 10% less than that of the female despite the much higher activity of the male and the correspondingly greater relative expenditure of energy on movement.

The evolutionary scheme presented here is also supported by the morphology of the rotifer genera *Proales* and *Rhinoglena*. In these genera, the males are somewhat smaller than the females and the digestive systems are fully developed and functional (Hyman, 1951; Ruttner-Kolisko, 1974). This is consistent with our belief that a reduction in the size of the males without the loss of the digestive system is feasible, but the reverse is not.

#### *A Rotifer Phylogeny*

Since the genera *Proales* and *Rhinoglena* appear to antedate the other Monogononta for the reasons given above, they provide, together with the information on metabolism, size and locomotion

which have been given, a key to the understanding of the evolution of the three major divisions of the Rotifera (Seisonidea, Bdelloidea and Monogononta). An evolutionary scheme based in part on the evolution of the reduced male and in part on the traditional evidence used in rotifer phylogeny (trophus morphology, number of ovaries, coronal morphology) is presented in Figure 1.

As shown in Figure 1, the Seisonidea probably diverged quite early from the main rotifer line and have retained such presumed primitive characteristics as the absence of sexual dimorphism, the paired gonads, and a lack of vitellarium (Hyman, 1951; Hutchinson, 1967). The unique trophi (fulcrate type), reduced corona, and general aberrant appearance of this group are probably the result of the parasitic (Hyman, 1951) or commensal (Pennak, 1978) existence of the group.

The Bdelloidea have retained paired ovaries, which indicates their early separation from the Monogononta. Their long evolutionary independence from the Monogononta is further illustrated by their specialized trophi (ramate type) and "wheel" type of corona (De Beauchamp, 1907, 1908, 1909). The loss of the males in the bdelloids is probably the result of selective pressures similar to those which led to the domination of parthenogenesis in the Monogononta. The complete loss of the male in the bdelloids probably occurred after the separation from the Monogononta, since most of the Monogononta have males (Hyman, 1951; Ruttner-Kolisko, 1974). If the male had been lost prior to the separation of the two lines, the presence of the monogonontid male would have necessitated its reappearance, which seems less likely than the alternative (see Williams, 1975).

Monogononta, which has been the most successful class of modern rotifers, branches in several major directions as shown in Figure 1. The Brachionidae probably branched from the main monogonont stem soon after its separation from the Bdelloidea, since *Rhinoglena* retains the primitive jaw (Hyman, 1951) and only

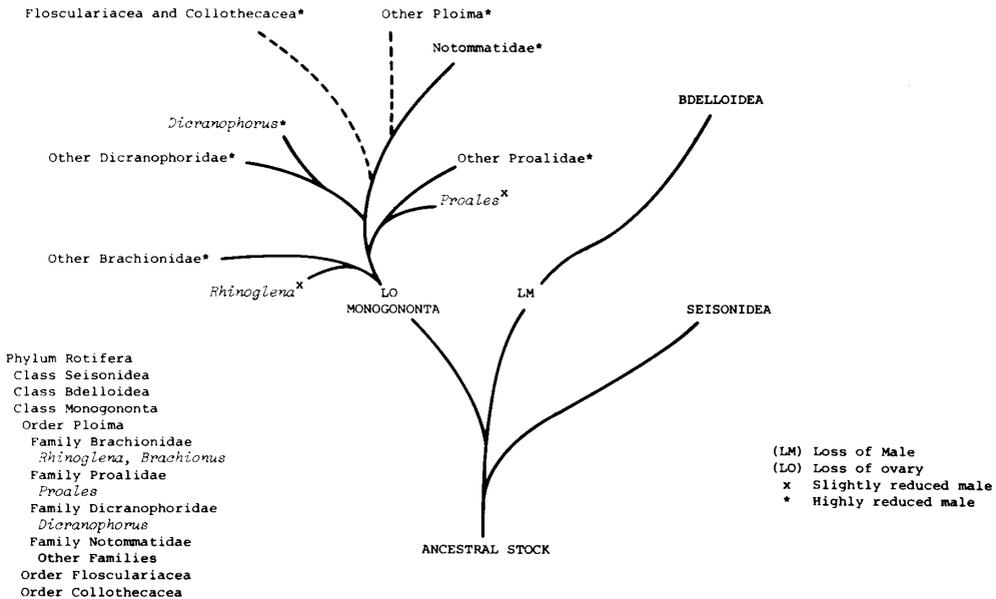


FIG. 1. Evolutionary scheme for the three major groups of Rotifera (Bdelloidea, Seisonidea and Monogononta) based on size of male and morphology according to the evolutionary sequences proposed in the text. The classification presented in the lower left is after Remane (1929–1931) as modified by Edmondson (1959). The positions of 15 advanced families of Ploima are uncertain and these are not shown.

slightly reduced male, and because of the similarity between the corona of *Rhinoglena* and that of the Bdelloidea. *Proales* seems most closely related to the brachionid *Rhinoglena* because of its retention of the maleate jaw and the primitive nephridia (De Beauchamp, 1965). For these reasons we have placed the proalid branch nearer the ancestral Monogononta than *Dicranophorus* even though *Dicranophorus* has retained the ancestral creeping mode of existence (Remane, 1929–1931; Pejler, 1956).

De Beauchamp (1907) suggests that the corona of *Dicranophorus* closely resembles the ancestral corona and also points out the similarity between the coronas of *Dicranophorus*, *Rhinoglena*, and the bdelloids (De Beauchamp, 1965). While *Dicranophorus* has retained the primitive corona, the genus shows considerable evolution of the trophi.

Characteristics such as the virgate (Harring and Myers, 1921) or modified maleate (Pennak, 1978) jaw link *Proales* with the notommatid rotifers (Remane,

1929–1931; Hyman, 1951). Consequently the reduction of the males in both the notommatid and brachionid rotifers is probably the result of convergent evolutionary processes, since the apparent ancestral representatives of these lines have nearly full-size males. The common selective pressures responsible for the reduction of the size of males may be associated with the freshwater environment, since the rotifers with no males or with the most reduced males are predominately freshwater groups (Bdelloidea and most Monogononta). Rotifers showing the least reduction in the size of the males include the Seisonidea, the primitive brachionids (*Rhinoglena*), and the primitive proalids (*Proales*). The Seisonidea are exclusively marine and the genera *Proales* and *Rhinoglena* have several brackish or marine representatives (Hyman, 1951; De Beauchamp, 1965; Remane and Schlieper, 1971; Ruttner-Kolisko, 1974).

The brackish and marine associations of the more primitive groups suggest a marine origin for the immediate ancestors

of the modern Rotifera, which are commonly assumed to have originated in fresh water. A marine origin consistent with recent work on the osmotic regulating process in *Brachionus plicatilis* showing that this species, which inhabits waters of high salinity, is incapable of regulating hyposmotically (Epp and Winston, 1977). Most other animals of freshwater origin that are capable of living in saline environments have well-developed powers of hyposmotic regulation.

The flame bulbs of the Rotifera could be considered to indicate freshwater ancestry if they are only osmoregulatory, but in marine forms flame bulbs probably function as nitrogen-excreting and ionic-regulating organs, or as a means of maintaining the hydrostatic skeleton. This would account for the presence of functional flame bulbs in contemporary marine rotifers, which would not otherwise be expected.

The modern Rotifera have achieved their greatest success in the freshwater environment despite their apparent origin in and continued associations with the marine environments. It may be significant in this connection that the marine environment is inhabited by a large number of larvae similar in size and environmental requirements to the Rotifera, whereas the freshwater environment generally lacks such forms. The adaptive radiation of the Rotifera in the freshwater environment may thus be due to a lack of competition comparable to that of typical marine environments. The reduction or loss of males is an adjunct of the freshwater radiation and may well be one of the factors allowing the extensive radiation of the Rotifera in freshwater environments.

#### SUMMARY

The metabolic rates, rates of movement, and theoretical energetic costs of movement for males and females of a sexually dimorphic rotifer (*Brachionus plicatilis*) are quantified. The small nonfeeding males, which are produced only occasionally between parthenogenetic generations, are short-lived but three

times more active than the females. Although active metabolism is known to be much higher than standard metabolism in invertebrates generally, the relative theoretical power requirements for movement of *Brachionus plicatilis* are extremely low for both males and females (ca.  $10^{-4}\%$  of routine metabolism), suggesting that the efficiency of the locomotor organelles (cilia) in moving the organisms is extremely low. This has wide implications for the evolution of small metazoans.

The relative cost of movement in a male *B. plicatilis* the size of a normal female would be several times higher than for a normal small-size male, suggesting that energy consumption makes small size a necessary adjunct of higher activity. We hypothesize that small males first appeared in response to selective pressures favoring production of a large number of males per unit time in conjunction with the environmental stimuli triggering sexuality. Once established, small size made feasible an increase in activity, which in turn allowed the sexual functions to be performed so quickly that the digestive system was superfluous and was lost. This suggests, in conjunction with some morphological features commonly used in classification, a new phylogeny of the Rotifera based on the degree of reduction in body size and on the morphology of the digestive system in the male. The new phylogeny gives evidence that the most primitive existing forms share marine affinities or high salinity tolerance, indicating a marine origin for the modern Rotifera. The more successful radiation of the Rotifera in the freshwater environment may be due to the absence in fresh water of small invertebrate larval forms similar in morphology to the rotifers.

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## LITERATURE CITED

- DE BEAUCHAMP, P. 1907. Morphologie et variations de l'appareil rotateur dans la série des Rotifères. Arch. Zool. Exp. 6:1-29.
- . 1908. Sur l'interprétation morphologique et la valeur phylogénique du mastax des Rotifères. Compt. Rend. 2:649-652.
- . 1909. Recherches sur les Rotifères: les formations tégumentaires et l'appareil digestif. Arch. Zool. Exp. 10:1-410.
- . 1965. Rotifères. In Grassé (ed.), *Traité de Zoologie*. Libraires de l'Académie de Médecine, Paris, 4:1226-1379.
- BOTTRELL, H. H., A. DUNCAN, Z. M. GLIWICZ, E. GRYGIEREK, A. HERZIG, A. HILLBRICHT-ILKOWSKA, H. KURASAWA, P. LARSSON, AND T. WEGLENSKA. 1977. A review of some of the problems in zooplankton production studies. *Norw. J. Zool.* 24: 419-456.
- BRODY, S. 1945. Bioenergetics and Growth, with Special Reference to the Efficiency Complex in Domestic Animals. Reinhold, N. Y. 1023 p.
- CAMPBELL, G. S. 1977. *An Introduction to Environmental Biophysics*. Springer-Verlag, N. Y. 159 p.
- CAVANAUGH, G. M. 1956. Formula and methods V of the Marine Biological Laboratory Chemical Room. Marine Biological Laboratory. Woods Hole, Mass. 86 p.
- EDMONDSON, W. T. 1959. Ward and Wipple, *Freshwater Biology*, sec. ed. Wiley, N. Y. 1248 p.
- EPP, R. W., AND P. W. WINSTON. 1977. Osmotic regulation in the brackish water rotifer, *Brachionus plicatilis* (Müller). *J. Exp. Biol.* 68:151-156.
- . 1978. The effects of salinity and pH on the oxygen consumption and activity of *Brachionus plicatilis* (Rotatoria). *Comp. Biochem. Physiol.* 59:9-12.
- GILBERT, J. J. 1963. Mictic female production in the rotifer *Brachionus calyciflorus*. *J. Exp. Zool.* 153:113-124.
- . 1974. Dormancy in rotifers. *Trans. Amer. Micros. Soc.* 83:490-513.
- . 1977. Defenses of males against cannibalism in the rotifer *Asplanchna*: Size, shape and failure to elicit tactile feeding responses. *Ecology* 58:1128-1135.
- HANEGAN, J. L., AND J. E. HEATH. 1970. Activity patterns and energetics of *Cecropia* moth. *J. Exp. Biol.* 53:611-627.
- HARRING, H. K., AND F. J. MYERS. 1921. The rotifer fauna of Wisconsin. *Trans. Wisc. Acad. Sci. Arts and Lett.* 20:553-662.
- HEMMINGSSEN, A. M. 1950. The relation of standard (basal) energy metabolism to total fresh weight of living organisms. *Rept. Steno. Mem. Hosp. and Nord. Insulin Lab.* 4:7-58.
- . 1960. Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Rept. Steno. Mem. Hosp. and Nord. Insulin Lab.* 7:110.
- HINO, A., AND R. HIRANO. 1976. Ecological studies on the mechanism of bisexual reproduction in the rotifer *Brachionus plicatilis*-I. General aspects of bisexual reproduction inducing factors. *Nippon Suisan Gak. Shi.* 42:1065-1192.
- HUDSON, C. T., AND P. H. GOSSE. 1889. *The Rotifera; or Wheel Animalcules*, Vol. 1. Longmans, London. 128 p.
- HUTCHINSON, G. E. 1967. *A Treatise on Limnology*. Vol. 2. Introduction to Lake Biology and the Limnoplankton. Wiley, N. Y. 1115 p.
- HYMAN, L. H. 1951. *The Invertebrates*. Vol. III. Acanthocephala, Aschelminthes, and the Entoprocta; the Pseudocoelomate Bilateria. McGraw-Hill, N. Y. 572 p.
- JAMES, D. E. 1974. *Culturing Algae*. Carolina Biological Supply, Burlington, N. C. 23 p.
- JONES, P. A., AND J. J. GILBERT. 1976. Male haploidy in rotifers: relative DNA content of nuclei from male and female *Asplanchna*. *J. Exp. Zool.* 198:281-285.
- KROGH, A. 1941. *Comparative Physiology of Respiratory Mechanisms*. Univ. of Pennsylvania Press. 172 p.
- PEJLER, B. 1956. On variation and evolution in planktonic Rotatoria. *Zoo. Bidr. Uppsala.* 32:1-66.
- PENNAK, R. W. 1978. *Freshwater Invertebrates of the United States*, 2nd ed. Wiley, N. Y. 803 p.
- POURRIOT, R. 1973. Recherches sur la biologie des Rotifères III. Fécondité et durée de vie comparées chez les femelles amictiques et mictiques de quelques espèces. *Ann. Limnol.* 9:241-258.
- POURRIOT, R., AND C. ROUGIER. 1977. Effets de la densité de population et du groupement sur la reproduction de *Brachionus calyciflorus* (Pallas) (Rotifère). *Ann. Limnol.* 13:101-114.
- PROSSER, C. L. 1973. *Comparative Animal Physiology*. Saunders, Philadelphia. 966 p.
- REMANE, A. 1929-1931. *Rotatorien. Klassen und Ordnungen des Tier-Reichs*, H. G. Bonn (ed.). 4 Bd, II Abt, 1 Buch: *Lief 1-4:1-576*. Akademische Verlagsgesellschaft, Leipzig.
- REMANE, A., AND C. SCHLIEPER. 1971. *Biology of Brackish Water*, 2nd ed. Wiley, N. Y. 372 p.
- RUBNER, M. 1883. Über den Einfluss der Körpergrösse auf Stoff- und Kraft-Wechsel. *Z. Biol.* 19:535-562.
- RUTTNER-KOLISKO, A. 1974. *Plankton Rotifers*. E. Schweizerbart'sche, Stuttgart. 146 p.
- . 1964. Über die labile Periode im Fortpflanzungszyklus der Rädertiere. *Internat. Rev. Hydrobiol.* 49:473-482.
- SITARAMAIAH, P. 1967. Water, nitrogen and caloric value of freshwater organisms. *J. Cons. Int. Expl. Mer.* 31:72-130.
- SNELL, T. W. 1977. Lifespan of male rotifers. *Arch. Hydrobiol. Beihefte. Ergebnisse der Limnol.* 8:65-66.
- VLYMEN, W. J. 1970. Energy expenditure of swimming copepods. *Limnol. Oceanogr.* 15:348-356.
- WEAST, R. C. 1966. *Handbook of Chemistry and Physics*. 47th ed. Chemical Rubber Co., Cleveland. 175 p.
- WILLIAMS, G. C. 1975. *Sex and Evolution*. Princeton Univ. Press, Princeton. 200 p.

- WILLIAMS, G. C., AND J. B. MITTON. 1973. Why reproduce sexually? *J. Theor. Biol.* 39:545-554.
- WINBERG, G. G. 1971. *Methods for the Estimation of Production of Aquatic Animals*. Academic Press, London. 173 p.
- WURDAK, E. S., J. J. GILBERT, AND R. JAGELS. 1978. Fine structure of the resting eggs of the rotifers *Brachionus calyciflorus* and *Asplanchna sieboldi*. *Trans. Amer. Micros. Soc.* 97:49-73.
- ZEUTHEN, E. 1953. Oxygen uptake as related to body size in organisms. *Quart. Rev. Biol.* 28:1-12.
- . 1971. Rate of living as related to body size in organisms. *Pol. Arch. Hydrobiol.* 17:21-30.