

CHAPTER 5-2

TARDIGRADE REPRODUCTION

AND FOOD

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CHAPTER 5-2

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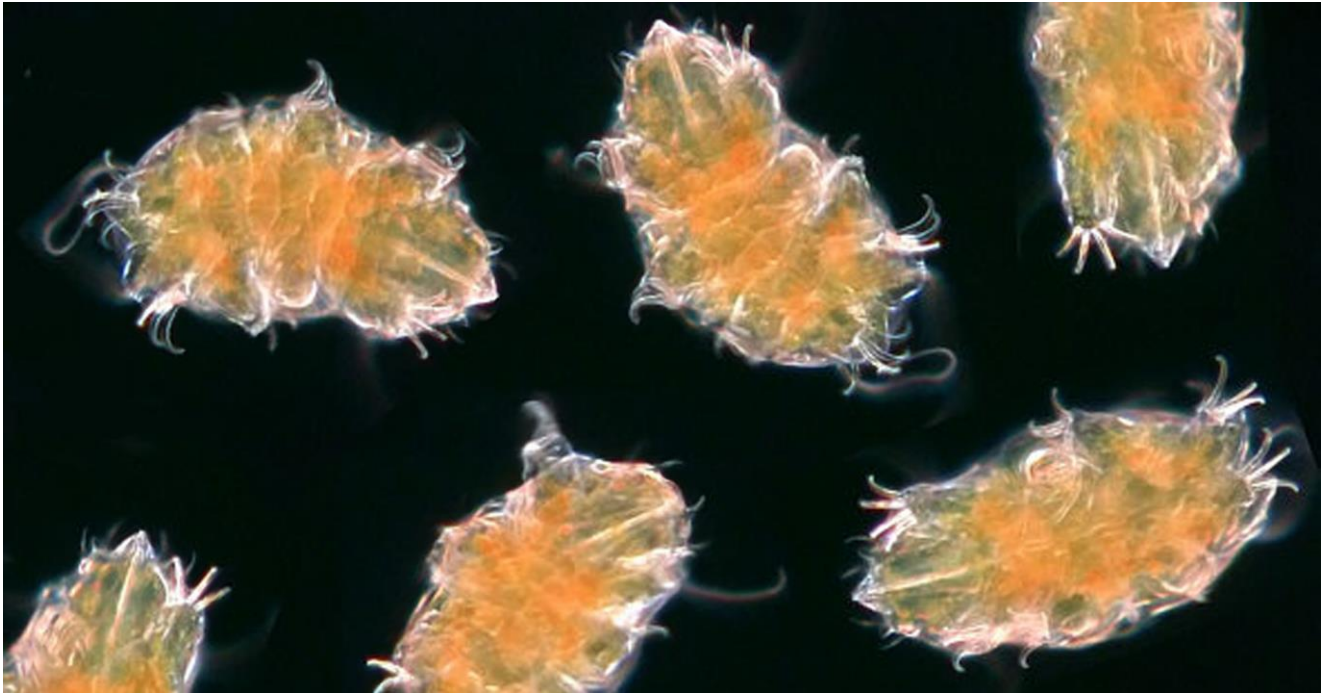


Figure 1. *Echiniscus*, a parthenogenetic genus with at least 146 described species (Guidetti & Bertolani 2005). This genus is common on bryophytes and reproduces there. Photo by Martin Mach, with permission.

Life Cycle and Reproductive Strategies

One means by which organisms survive in such changeable habitats as bryophytes is by progressing to a different life cycle stage to wait out the storm – or lack of one. Tardigrades are especially adept at this, as seen in Chapter 5-1 (diapause and cryptobiosis). In tardigrades, diapause and cryptobiosis can occur at any time and developmental stage. Here we will look at reproduction and its role in further providing an escape route, at least for the species, if not the individual, an even that often occurs on bryophytes (Figure 1).

Hofmann (1987) considers that tardigrades must be able to reproduce quickly and in sufficient numbers when conditions are favorable because their life style is one of intermittent activity and inactivity, the latter in either a state of dormancy or cryptobiosis. This constraint of brief reproductive periods and the necessity for a few individuals to have sufficient offspring makes them **r-strategists**. They lack a defined carrying capacity and the population density is dependent upon the length of time since establishment in that location.

Life history of tardigrades can differ among species, presumably providing somewhat different adaptive strategies. For example, *Paramacrobiotus tonollii* (Figure 2) requires 16 days for its embryonic development whereas

Macrobiotus sapiens requires only 12 days (Lemloh *et al.* 2011). *Paramacrobiotus tonollii* is larger than *M. sapiens* but the latter has a longer life span of 83 days.

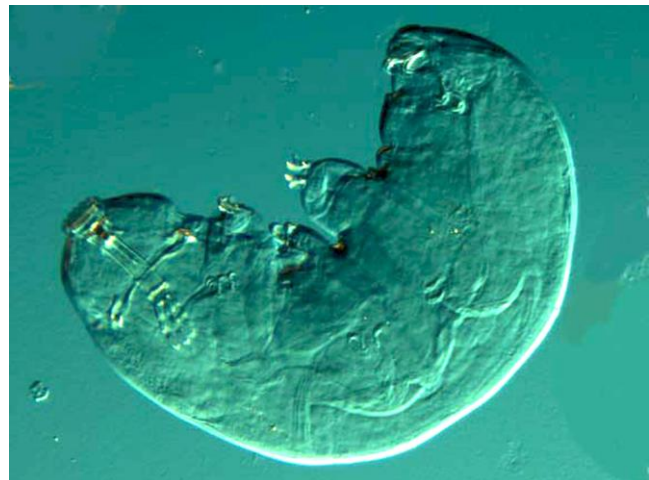


Figure 2. *Paramacrobiotus tonollii*. Photo by Paul Bartels, with permission.

Reproductive Strategies and Habitat

Reproductive mechanisms do differ among tardigrades in different habitats (Bertolani 2001). Those living among bryophytes, as well as those of freshwater, leaf litter, and soil, commonly are **parthenogenetic** (Figure 1), or more rarely **hermaphrodites** that self-fertilize. Marine species, on the other hand, have separate sexes. Bertolani hypothesized that organisms living in isolated and unstable habitats (including bryophytes) have evolved **cryptobiosis**, **parthenogenesis**, **self-fertilization**, and **passive dispersal**, benefitting them in their challenging living conditions.

Passive wind dispersal of tardigrades with mosses is already known and may be their primary dispersal strategy (Pilato 1979). As is common among many mosses, those tardigrades that have **parthenogenesis** (equivalent to vegetative reproduction in mosses, *i.e.* reproduction without males) do not also have self-fertilization. These reproductive strategies, as in bryophytes, permit tardigrades to reproduce when only one individual, or its egg (Figure 3), arrives to colonize a new location.

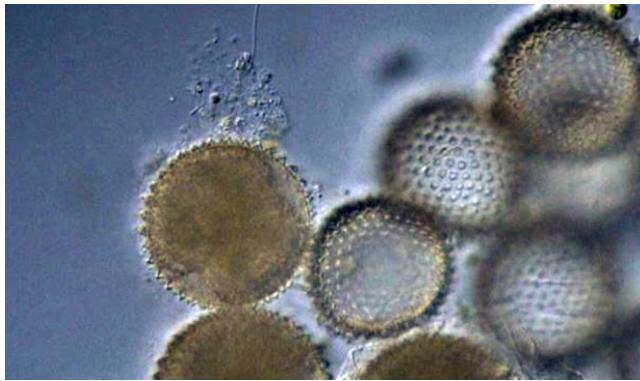


Figure 3. Eggs of a species of *Dactylobiotus*. The clustering of eggs may be beneficial in protecting each other, but their inherent resistance to almost everything suggests that is probably not important. Photo by Yuuji Tsukii, with permission.

Dispersal in tardigrades seems independent of the tardigrade because it is passive dispersal. But Bertolani *et al.* (1990) considered that the differences in distribution and frequency of members of the genus *Ramazzottius* relate to their differences in reproductive modes. In their study of *Ramazzottius* species on bryophytes and lichens, they found that the sex ratio was strongly influenced by the type of reproduction, but also differed when samples were collected from tree trunks and limited rocky areas versus extensive rocky outcrops. Bertolani *et al.* found that bryophyte-dwelling *Ramazzottius* tardigrades from tree trunks or slightly rocky areas exhibited parthenogenesis and absence of male tardigrades. Among the rocky outcrops, there were always at least some males, although some parthenogenesis still occurred. Males are only useful if there is sufficient opportunity for contact with females. Perhaps the rocky outcrops provided less of a labyrinth and permitted the needed contact? Eggs provide light-weight, windborne propagules to disperse the species (Figure 3).

[To clarify for botanists, some references tend to use the term egg for the zygote and sometimes even the developing organism (embryo) until it has hatched, like the hatching of a bird egg. Since I found the term egg used in my references, I shall use egg here as well.]

Eggs

Depending on the species, there are two ways tardigrade eggs (including embryos) may be deposited. Some lay free eggs on their substrate (Figure 3), but others deposit them in the shed **exuvia** of a molt (Mach: The Water Bear; Figure 4).

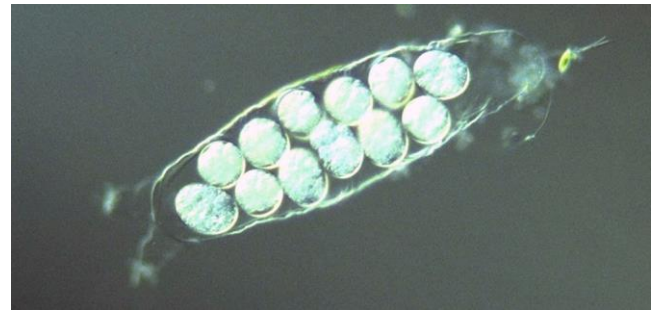


Figure 4. A number of eggs can develop within one shed **exuvia**, as shown here for *Hysibius* sp. Photo by Yuuji Tsukii, with permission.

Macrobiotus hufelandi (Figure 5) has two sexes – males do exist (Figure 5) (Mach 2010). It is one of the species having free eggs (Figure 6). Eggs deposited outside the exuviae generally have decorative processes (Figure 7) (Mach 2010). Kinchin (1994) suggests that the functions of the egg processes include anchorage of the egg to a substrate or a transporting medium, defensive structure against being eaten by other animals, water reservoir which slows down the desiccation process, and regulation of gas exchange between egg and environment.

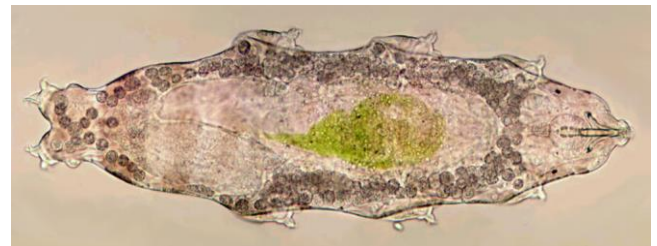


Figure 5. *Macrobiotus hufelandi* male. Photo by Martin Mach, with permission.



Figure 6. Egg of *Macrobiotus hufelandi*, demonstrating the decorative processes on this free-egg deposit. Photo by Martin Mach, with permission.

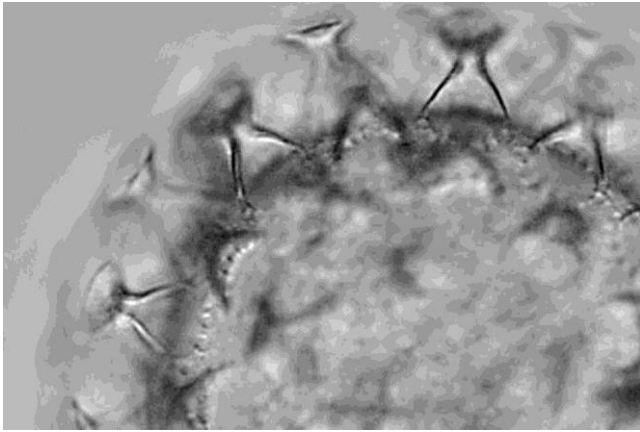


Figure 7. Egg of *Macrobiotus* sp., demonstrating the highly decorative surface that is typical of eggs laid free of the organism. Photo by Martin Mach, with permission.

When healthy adult tardigrades discard their outer covering, many taxa deposit eggs in these shed **exuviae** (outer "skins") (Figure 8-Figure 11) (Bertolani *et al.* 2009). The eggs may be few or many (up to 30-40) and may differ even within the same species, as can be seen for *Milnesium tardigradum* in Figure 9-Figure 11 (Altiero *et al.* 2006). The number of eggs depends on the species, but also on the nutritional status of the individual female (Mach: The Water Bear). And it seems that some bears may even ingest their own eggs to improve their nutritional status.

Egg development is poorly known. In *Paramacrobiotus* [= *Macrobiotus*] *richtersi* (Figure 12) it can be prolonged to 90 days or more if the eggs undergo desiccation and become resting eggs (Altiero *et al.* 2009). The non-resting (**subitaneous**) eggs may hatch in as little as 30-40 days.



Figure 8. These eggs reside in the shed exuvial "armor" of the parent and permit the tardigrade species to survive winter and desiccation. Photo by Martin Mach, with permission.

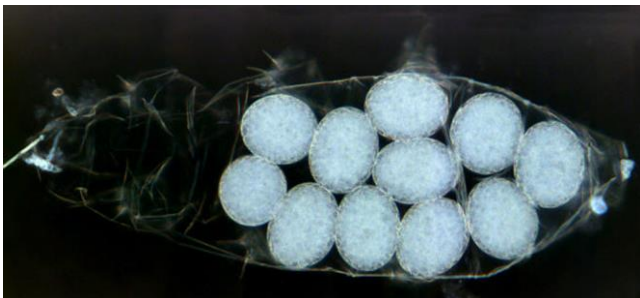


Figure 9. Individual of *Milnesium tardigradum* with eleven eggs in the shed exuvia. Photo by Martin Mach, with permission.



Figure 10. Individual of *Milnesium tardigradum* with only three large eggs in the exuvia. Photo by Martin Mach, with permission.

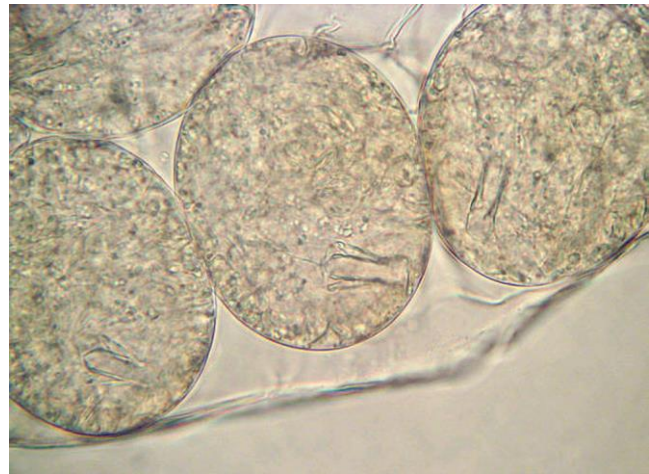


Figure 11. Developed eggs of *Milnesium tardigradum* with the buccal apparatus visible, indicating nearness to maturity. Photo by Martin Mach, with permission.



Figure 12. *Paramacrobiotus richtersi*. Photo from Science Photo Library, through Creative Commons.

The eggs generally develop within the exuvia until the fully-formed tardigrade is ready to leave the egg, as shown here for individuals in the genus *Echiniscus* (Figure 13-Figure 19), requiring several weeks for completion (Mach: The Water Bear). The eggs are able to survive the same drying conditions as the adult; development stops during that dry state. The young tardigrades resemble the adults (Figure 20-Figure 23), but are smaller, requiring a series of molts as they grow. Growth occurs by cell enlargement rather than by addition of cells. Since the eggs often remain in the exuvia until they hatch (Figure 21), size would tend to reduce wind-dispersal of the pollen-grain-sized eggs except when they are dispersed along with a substrate such as mosses.



Figure 13. *Echiniscus* adult. Photo by Martin Mach, with permission.



Figure 14. *Echiniscus* exuvia with eggs (embryos) after first division. Photo by Martin Mach, with permission.



Figure 15. *Echiniscus* embryo after two divisions. Photo by Martin Mach, with permission.



Figure 16. Multicellular *Echiniscus* embryo. Photo by Martin Mach, with permission.

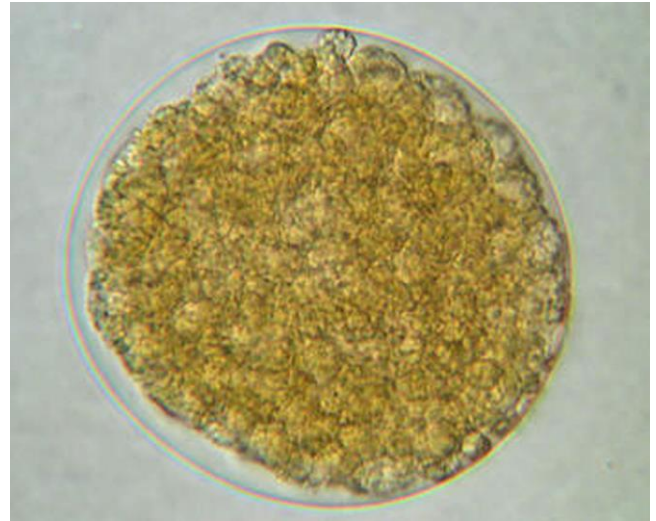


Figure 17. Morula stage in the embryo development of *Echiniscus*. Photo by Martin Mach, with permission.



Figure 18. This mature "egg" of *Echiniscus* can be found among bryophytes, and its smooth surface is typical of eggs that are kept within the exuvia. Note the buccal apparatus that signifies its late developmental stage. Photo by Martin Mach, with permission.

In soil-dwelling *Paramacrobiotus richtersi* (Figure 12; also a known bryophyte dweller), temperature played a role in rate of development, survival rate, body growth, and generation time (Figure 24; Hohberg 2006). On the other hand, hatching time, first to fourth molts, and maturation time were dependent upon body size alone.

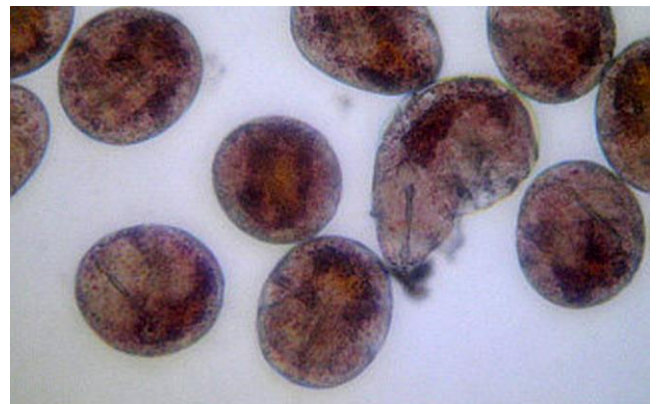


Figure 19. *Echiniscus* hatching from its eggs. Photo by Martin Mach, with permission.

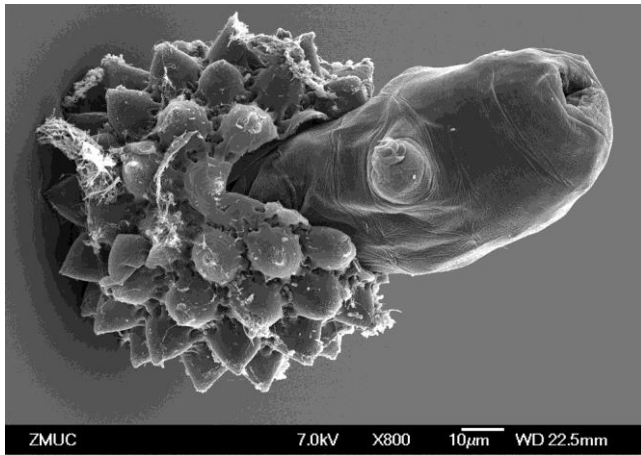


Figure 20. Moss-dweller *Macrobiotus derkai* hatching from a free "egg." Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

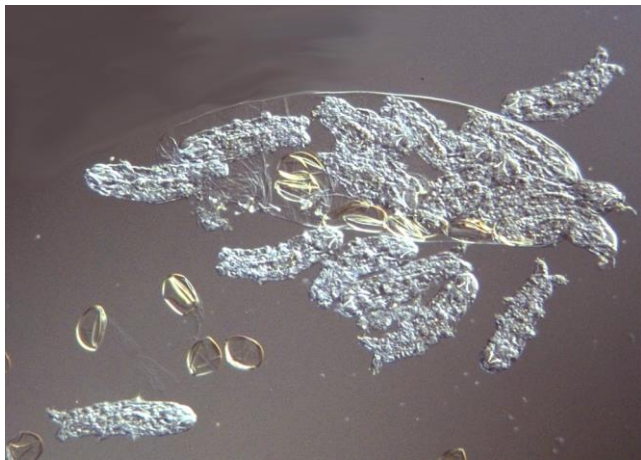


Figure 21. Despite the large number of eggs/embryos, it appears that most of them are successful in hatching into young tardigrades, as seen here for a species of *Hypsibius*. Photo by Yuuji Tsukii, with permission.



Figure 22. *Echiniscus* young and old. Note the long "hairs" extending from the body, giving the genus its name. Photo by Martin Mach, with permission.



Figure 23. *Echiniscus* young. Photo by Martin Mach, with permission.

Some tardigrades have found another safe site for their eggs. They can use the capsule of a moss as an egg depository (Mach: The Water Bear; Figure 25-Figure 26).

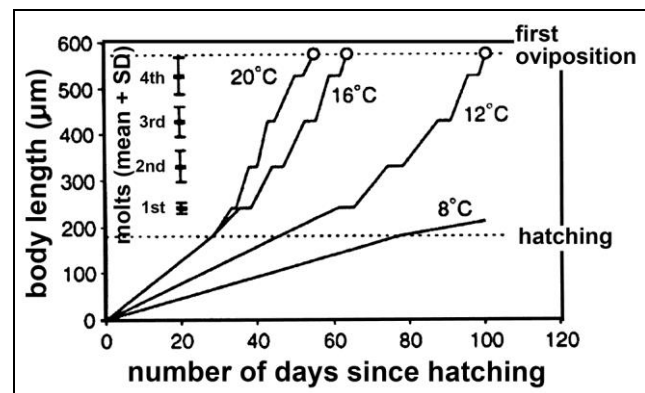


Figure 24. Effects of temperature on the development of *Paramacrobrius richtersi* (Figure 12), starting with the day the tardigrades hatched. Body lengths are for hatching and first oviposition only. Redrawn from Hohberg (2006).

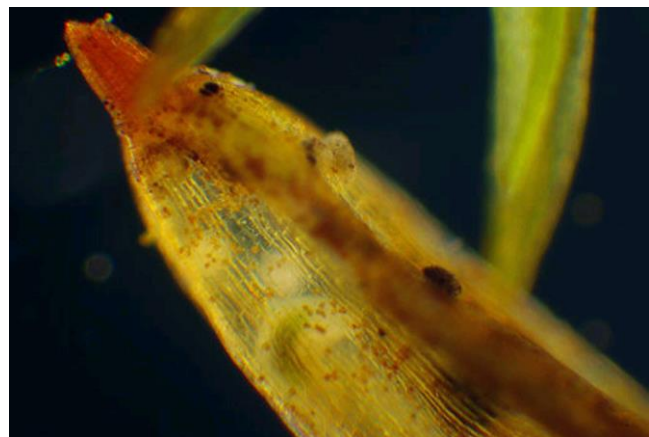


Figure 25. Moss capsule with tardigrade (with green gut) and two white eggs. Photo by Martin Mach, with permission.

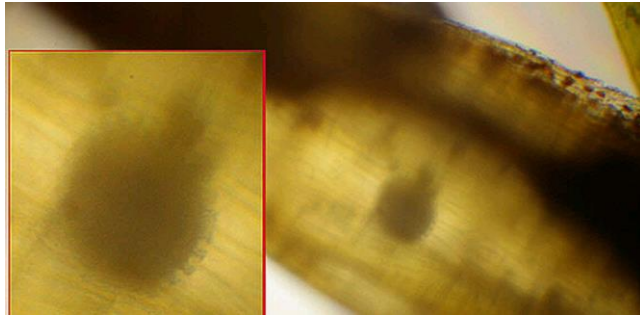


Figure 26. This egg is protected by a moss capsule. Based on the decorations on the eggs, they appear to be close to *Macrobiotus hufelandi*. Photos by Martin Mach, with permission.

Molting

Like its relatives in the Arthropoda, the tardigrade must **molt** (Figure 27-Figure 35). This process usually requires 5-10 days and occurs several times throughout its life (Walz 1982), including after sexual maturity while the body is still increasing in size (Nelson 1982). During molting, the old cuticle, claws, and lining of the fore- and hindgut are shed (Figure 28), causing a stage known as the **simplex** stage (Figure 35). Lacking its sclerified parts of the buccal-pharyngeal apparatus, the tardigrade cannot feed. It appears that tardigrades molt 4-12 times during their 3-30 months of active lives (Nelson 2002).



Figure 27. *Milnesium tardigradum* as it recedes from its cuticle in preparation for molting. Note the dark brown eggs that will soon be left behind. Photo by Martin Mach, with permission.



Figure 28. *Milnesium tardigradum* emerging from its exuvia during molting, leaving its claws, eggs, and various other parts behind. Photo by Martin Mach, with permission.

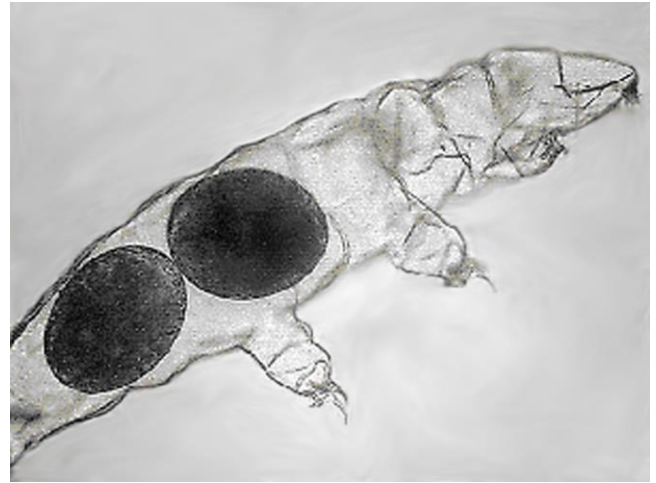


Figure 29. Eggs in the shed exuvia of *Milnesium tardigradum*. Photo by Martin Mach, with permission.



Figure 30. *Milnesium tardigradum* eggs in its shed exuvia. Photo by Martin Mach, with permission.

Cyclomorphosis

It appears that **cyclomorphosis** (annual cycle of morphological change) occurs in tardigrades, although it has been demonstrated in only a few species. It has been documented in the marine species *Halobiotus crispae* (Kristensen 1982; Halberg *et al.* 2009). Likewise, Dastych (1993) demonstrated cyclomorphosis in a cryoconite-dwelling species of *Hypsibius* (Figure 31), and in a bryophyte dweller. Furthermore, Rebecchi and Bertolani (1994) did demonstrate it for one species in the genus *Bertolanius* [= *Amphibolus*] (Figure 33), which does have moss-dwelling species.

Kristensen (1982) studied the marine *Halobiotus crispae* cycle and found two morphs. In winter there is a **pseudosimplex** stage that hibernates and is sexually immature. These winter forms gather in large **aggregations** in protected areas where the aggregations increase chances for survival of the freezing temperatures. The population experiences synchronous development of gonads, hence all reaching sexual maturity and breeding simultaneously. But the cycle for other taxa and habitats, including bryophytes, remains to be explored (Nelson 2002).

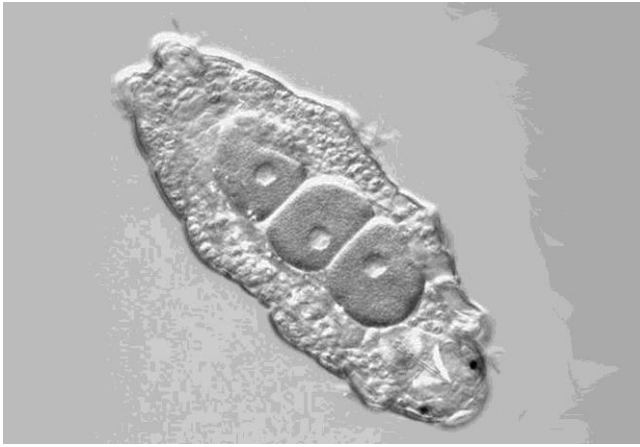


Figure 32. *Hypsibius dujardini* with 3 oocytes. Photo by Willow Gabriel, through EOL Creative Commons.

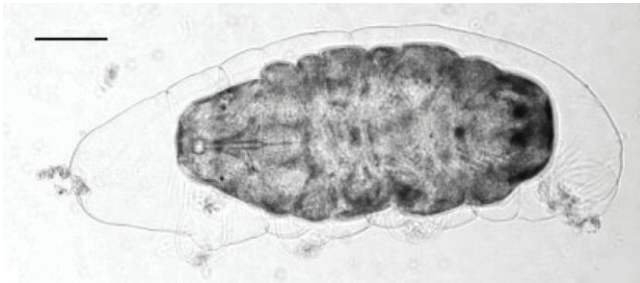


Figure 33. *Bertolanius volubilis* cuticle with a type A cyst inside. Photo by Roberto Bertolani, with permission.



Figure 34. *Ramazzottius oberhaeuseri* completing its molt out of its old cuticle. The emerging organism will remain in this **simplex** stage until it rebuilds its cuticular parts. Photo by Martin Mach, with permission.

Bryophytes as Food Reservoirs

Bryophyte-dwelling tardigrades include both bryophyte-eating tardigrades and those with a variety of other feeding strategies, including carnivory. The tardigrade has a specially adapted pair of **stylets** (Figure 49) and a muscular pharynx (Figure 50-Figure 52) that produces a suction into the gut, permitting the tardigrade to suck fluids from the interior of a bryophyte or algal cell (Figure 53) or even small animals such as rotifers (Figure 54) and nematodes [Tardigrada (Water Bears) 2005]. In the family Echiniscidae (Figure 36), a common family on

bryophytes, the stylet may be very long, permitting penetration of the thick cellulose walls of bryophytes. For example, *Echiniscus testudo* (Figure 37) feeds primarily on bryophytes (Morgan 1977). *Diphascon* (Figure 52), also a bryophyte dweller, has a flexible buccal tube with spiral rings resembling the extension on a vacuum cleaner. Small bryophyte dwellers may subsist on diatoms and bacteria that live epiphytically among the bryophytes [Bartels 2005; Tardigrada (Water Bears) 2005].



Figure 35. *Pseudobiotus* sp. shedding its cuticular exuvia and leaving its eggs/embryos behind. Photo by Paul Davison, with permission.



Figure 36. *Echiniscus perviridis* with green color, most likely due to its vegetarian diet. *Echiniscus testudo* is known to feed primarily on bryophytes. Photo by Łukasz Kaczmarek, with permission.



Figure 37. *Echiniscus testudo* tun. Photo by Power & Syred through Creative Commons.

Schill *et al.* (2011) consider the bryophytes to be a "rich food supply for both carnivorous and herbivorous species." These food sources include nematodes, rotifers, plant cells, algae (Figure 38), yeast, and bacteria, and for some, bryophytes. Schill and coworkers conducted a genetic tracer study (*rbcL*) on the guts of tardigrade species from various sites in Europe that demonstrated the presence of mosses from the **Erpodiaceae** [*Aulacopilum hodgkinsoniae*, *Venturiella sinensis* (Figure 39)] and **Pottiaceae** [*Syntrichia* (= *Tortula*) *obtusissima* (Figure 40)] in the guts of field-collected *Macrobiotus sapiens*, **Grimmiaceae** [*Grimmia elongata* (Figure 41), *Coscinodon cribrosus* (Figure 42), *Schistidium strictum* (Figure 43)] from *Macrobiotus persimilis* and *Echiniscus granulatus*, and the green alga *Trebouxia* (Figure 44) from *Richtersius coronifer* (Figure 38). For *Macrobiotus sapiens* they found no *rbcL* sequence demonstrating presence of the families **Pottiaceae** or **Orthotrichaceae**. It appears that *Macrobiotus sapiens* will only eat these latter two moss families when **Grimmiaceae** is not available, or that others had been digested completely before samples were extracted. The small tardigrade stylet makes it difficult for them to obtain cell contents from the moss genera *Polytrichum* (Figure 45), *Dicranum* (Figure 46), *Leucobryum* (Figure 47), and *Racomitrium* (Figure 48). Digestion in tardigrades is aided by the gut pH, with the foregut having an acidic environment and the midgut having a basic environment (Marcus 1928).

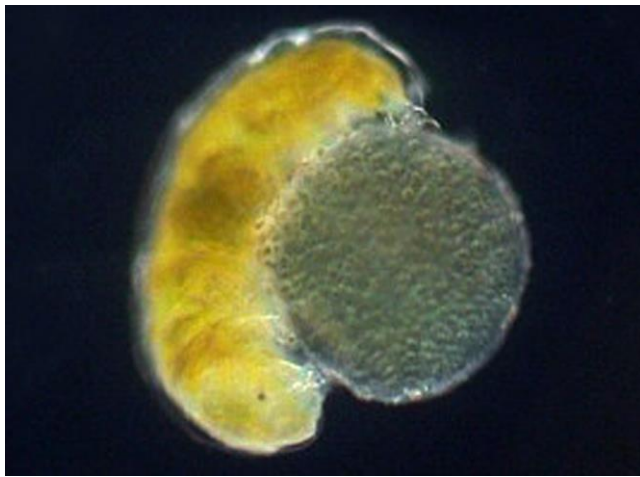


Figure 38. *Richtersius coronifer*, clinging to an algal cell. Photo by Martin Mach, with permission.



Figure 39. *Venturiella sinensis*, a moss eaten by *Macrobiotus sapiens*. Photo from Digital Museum, Hiroshima University, with permission, with permission.



Figure 40. *Syntrichia obtusissima* showing hair points. Photo by Claudio Delgadillo, with permission.



Figure 41. *Grimmia elongata*, a moss eaten by *Macrobiotus persimilis* and *Echiniscus granulatus*. Photo by Michael Lüth, with permission.

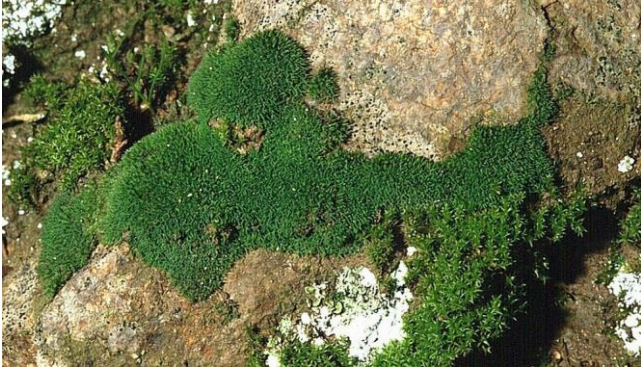


Figure 42. *Coscinodon cribrus*, a moss that is suitable habitat and food for *Macrobiotus persimilis* and *Echiniscus granulatus*. Photo by Michael Lüth, with permission.



Figure 43. *Schistidium strictum*, a moss that is eaten by *Macrobiotus persimilis* and *Echiniscus granulatus*. Photo by Jan-Peter Frahm, with permission.



Figure 44. *Trebouxia*, a lichen symbiont that appeared in the guts of field collected *Macrobiotus persimilis* and *Echiniscus granulatus*. Photo by Yuuki Tsukii, with permission.



Figure 45. *Polytrichum commune*, a moss with thick leaves that make feeding by tardigrades difficult. Photo by Michael Lüth, with permission.



Figure 46. *Dicranum scoparium*, a moss with leaves that seem to make feeding by tardigrades difficult. Photo by Janice Glime.



Figure 47. *Leucobryum glaucum*, showing thick leaves that make tardigrade feeding difficult. Photo by James K. Lindsey, with permission.



Figure 48. *Racomitrium macounii* ssp. *macounii*, a moss with leaves that seem to make feeding by tardigrades difficult, in Europe. Photo by Michael Lüth, with permission.

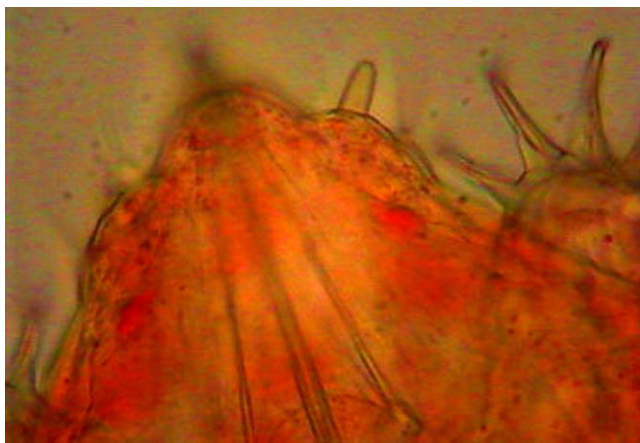


Figure 49. *Echiniscus* with the stylets protruding (out of focus). Photo by Martin Mach, with permission.

Tardigrades even consume smaller tardigrades. Larger species such as those of *Macrobiotus* (Figure 5) and *Milnesium* (Figure 9, Figure 51) consume smaller members such as *Diphascion* (Figure 52) and *Hypsibius* (Figure 64), as exhibited by remains of claws and buccal apparatus (Figure 57) in the gut (Nelson 2002). Large carnivorous Eutardigrada such as *Paramacrobiotus richtersi* (Figure 12), *Milnesium tardigradum* (Figure 9, Figure 10, Figure 51, Figure 54), and *Bertolanius*

nebulosus are widespread in many habitats, including bryophytes [Tardigrada (Water Bears) 2005]. They eat nematodes, rotifers, and smaller tardigrades, but still use the stylet to suck out cell contents. Suzuki (2003) reared *Milnesium tardigradum* from the moss *Bryum argenteum* (Figure 55), using only rotifers [*Lecane inermis*, common in wet *Sphagnum* (Miller 1931)] as food.



Figure 50. This tardigrade has the stylets withdrawn into its head. The pharynx is in the center behind the stylets. Photo by Paul Davison, with permission.



Figure 51. "Head" region of *Milnesium tardigradum* showing the pharynx. Photo by Martin Mach, with permission.

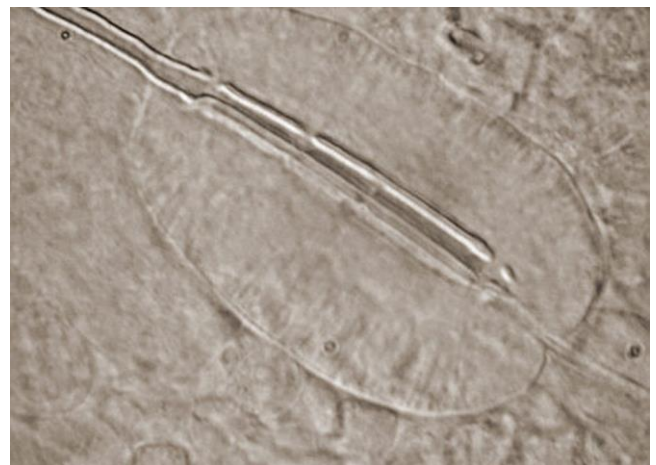


Figure 52. Pharynx (oval) of *Diphascion*, the organ that produces the suction for the stylets. Photo by Martin Mach, with permission.

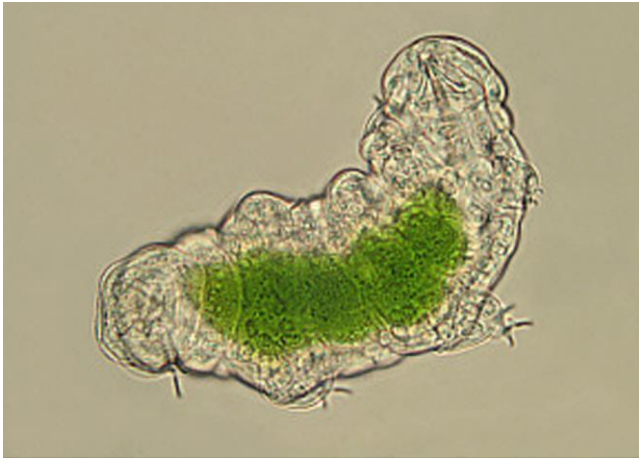


Figure 53. The green in this tardigrade is likely to be algae or moss. Photo by Paul Davison, with permission.

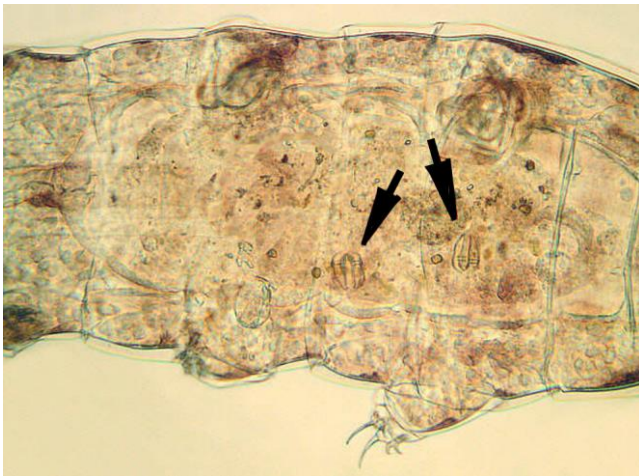


Figure 54. *Milnesium* with the mastax of rotifers visible in the gut (black arrows). Photo by Martin Mach, with permission.



Figure 55. *Bryum argenteum*, a moss known to house *Milnesium tardigradum*. Photo by Michael Lüth, with permission.

Suren (1988) attempted to determine the importance of bryophytes as food vs. simply substrate by using artificial mosses in high alpine New Zealand streams. When artificial structures were used, similar communities of invertebrates developed, but tardigrades appeared to be affected negatively by the absence of the bryophytes, a

difference Suren interpreted to reflect a loss of bryophytes as a food source. It seems to be one of the few animals specifically adapted to obtaining the good stuff from the insides of the cells of bryophytes. Its stylets (Figure 49-Figure 50) serve as a miniature needle and straw to puncture the cell and suck the nutrients from it. The pharynx (Figure 52) serves as a pump to draw fluids in through the stylets (Tardigrades, Bears of the Moss).

It appears that eating bryophytes requires more than just the equipment to suck the good stuff out of the cell. The excretory system seems also to be altered. Węglarska (1990) found that in four genera of tardigrades, those that live among bryophytes have larger excretory organs relative to body size than do the freshwater species. The purpose of this added size remains a mystery.

Ramazzotti and Maucci (1983) suggested that excretion probably occurs in four ways in tardigrades. At molting it occurs through the salivary glands. Likewise, when the cuticle is shed it removes accumulated excretory granules. It can occur through the wall of the midgut. And in the eutardigrades, it occurs through excretory glands. There is no study to determine how these various mechanisms might relate to a diet of bryophytes.

Role in Food Web

As seen above, tardigrades typically are either plant eaters or are carnivorous (Garey *et al.* 2008), including protozoa, nematodes, and rotifers (Figure 54), but also consume bacteria and fungi (Kinchin 1988). As noted in the earlier chapter on nematodes, they can be predators on nematodes that live in the same clump of moss (Sánchez-Moreno *et al.* 2008), making them important consumers and often the top carnivore.

Both *Paramacrobiotus* [= *Macrobiotus*] *richtersi* (Figure 12) and *Macrobiotus harmsworthi* (Figure 56-Figure 57) caused significant declines in the nematode populations, thus regulating the food web. In fact, a single *P. richtersi* dined on an average of 61 nematodes in a day! Unlike many of the slow-walking water bears, these carnivorous water bears are able to move swiftly to attack and devour their prey (Kristensen & Sørensen 2005).

Davison (2005) reports that tardigrades lumber across the substrate, swinging their heads back and forth in search of food. When he offered them nematodes and rotifers, the tardigrades made no attempt to eat them. When he offered them a larger choice, the annelid *Lumbriculus* sp., a genus with known members that inhabit mosses, he found that they immediately approached it and began eating it.

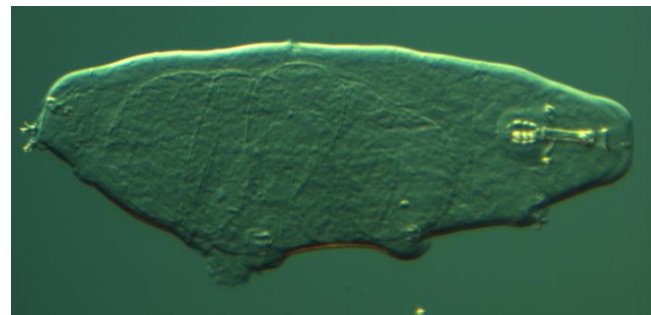


Figure 56. *Macrobiotus harmsworthi*, a nematode predator. Photo by Paul J. Bartels, with permission.

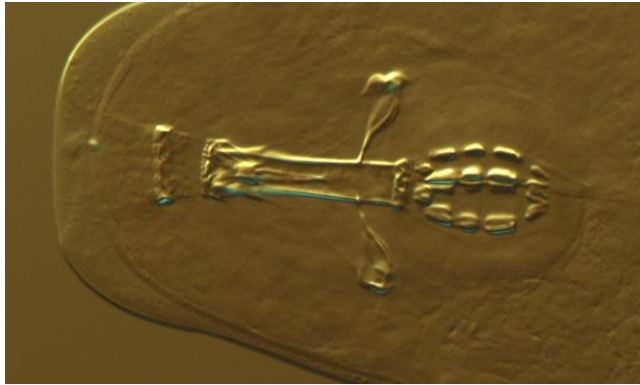


Figure 57. *Macrobotus harmsworthi* buccal apparatus. Photo by Paul Bartels, with permission.

Tardigrade specialists have assumed that the **buccal apparatus** (Figure 58-Figure 60) indicates characteristics of the food, but no studies exist on the relationships of buccal apparati among the limnoterrestrial taxa (Nelson 2002).

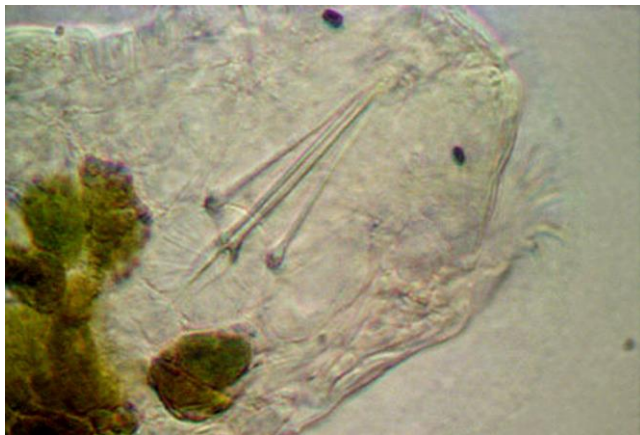


Figure 58. The three "filaments" and pharynx are the buccal apparatus of this *Echiniscoides sigismundi*. The **pharynx** resembles a pair of kidneys in contact with the three filaments. The outer two filaments are the stylets; the inner one is the buccal tube. The gut contains algal or plant material that has been ingested by this tidal zone species. Photo by Martin Mach, with permission.



Figure 59. The three "filaments" and oval behind them are the buccal apparatus of *Paramacrobotus* [=*Macrobotus*] *areolatus*. The bulbous oval to the right of the three filaments (stylets and buccal tube) is the pharynx. Photo by Martin Mach, with permission.



Figure 60. *Dactylobiotus dispar* has a buccal apparatus similar to that of *Paramacrobotus areolatus*. Photo by Martin Mach, with permission.

But tardigrades can have their predators too. Snails that live among the moss leaves could enjoy a meal of tardigrades (Fox 1966). The land snail *Bulimulus guadalupensis* (Figure 61) from Puerto Rico had evidence that all life cycle stages of the tardigrade *Echiniscus molluscorum* (see Figure 62) live in its feces (Fox & Garcia-Moll 1962). It is not clear if these passed unharmed through the gut or if they took advantage of the feces as a food source after defecation. It is even possible that eggs passed through the gut and hatched in the feces.



Figure 61. The land snail *Bulimulus guadalupensis* is a known predator on moss-dwelling tardigrades. Photo by Gary Rosenberg at <www.discoverlife.org>.

Tardigrades have smaller predators as well. The fungus *Ballocephala pedicellata* (Figure 63) is known from the tardigrades *Hypsibius dujardini* (Figure 64) and *Diphyscon pingue* complex (Figure 65) living in the moss *Atrichum angustatum* (Figure 66) (Pohlad & Bernard 1978). In this study, tardigrades with the fungus were only

present in January and February in the collecting area in southeastern USA.

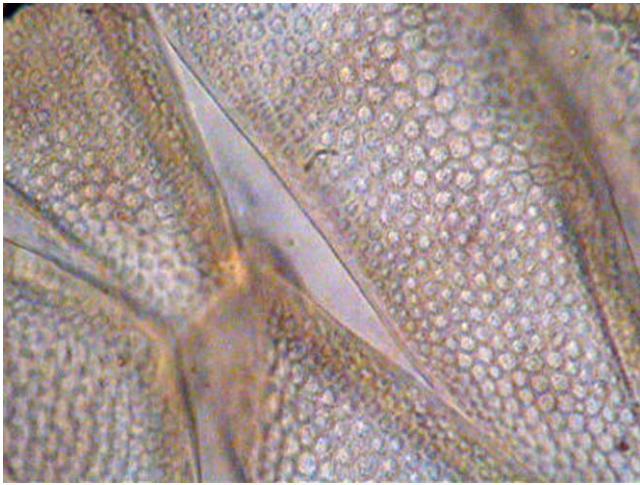


Figure 62. Armor of *Echiniscus* sp. Material such as this is easy to identify in the feces of predators. Photo by Martin Mach, with permission.



Figure 63. *Ballocephala sphaerospora* zygospores in a tardigrade. Photo by George Barron, with permission.



Figure 64. *Hypsibius dujardini*, a host for the fungus *Ballocephala pedicellata*. Photo from Rpgch Wikimedia Commons.



Figure 65. *Diphascos pingue*. Photo by Michael Collins, with permission.



Figure 66. *Atrichum angustatum*, a habitat for tardigrades, and in winter, their parasitic fungus *Ballocephala pedicellata*. Photo by Michael Lüth, with permission.

Summary

Life cycle stages often provide a means of surviving changes in the environment. Bryophyte-dwelling tardigrades are usually **parthenogenetic**. They rarely are **hermaphrodites**, and parthenogenetic individuals do not self-fertilize.

Tardigrade species may either lay free eggs or deposit them inside the exuvia as it is shed. External eggs are usually highly decorated, whereas those laid inside the exuvia tend toward smooth. The number of eggs varies up to 40, with the number depending on the species and nutritional status. Time required for development of the fertilized egg may be up to 90 days. Variability in development time permits **bet-hedging**. Temperature affects development rate, survival rate, and body growth, as well as affecting generation time. Young tardigrades resemble the adults and continue to grow by cell enlargement. Molting permits the tardigrade to expand its size and requires 5-10 days during which the tardigrade cannot eat and is less protected. Some species have more than one morph, where the winter morph may form aggregations that enhance survival of freezing conditions.

Tardigrades consume algae, bryophytes, fungi, protozoa, nematodes, rotifers, and smaller tardigrades. In many cases this is accomplished using a **stylet** that forms a straw for sucking cell contents. They suck in their prey with the pair of stylets, with the muscular pharynx producing suction. For whatever reason, bryophyte dwellers also have larger excretory organs than do tardigrades of other substrata.

They play an important role in regulating the food web of bryophytes in some circumstances. Tardigrades are subject to predation by snails and even larger tardigrades. Fungi may extract nutrition from them.

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