CHAPTER 6-1
ONYCHOPHORA

TABLE OF CONTENTS

Phylum Onychophora (Velvet Worms) 6-1-2
Feeding Habits 6-1-3
Moisture and Light Relations 6-1-4
Mating and Reproduction 6-1-5
Mimics? 6-1-8
Summary 6-1-8
Acknowledgments 6-1-8
Literature Cited 6-1-8

CHAPTER 6-1 ONYCHOPHORA

Figure 1. ***Euperipatus rowelli***, a velvet worm that is being cultured on ***Sphagnum***. Photo by Andras Keszei, with permission.

Phylum Onychophora (Velvet Worms)

Onyches is the Greek word for claws and ***pherein*** means to carry, *i.e.*, claw bearers. The phylum Onychophora (Figure 1) derives its name from the pair of retractable, chitinous claws on each foot (Figure 2-Figure 3). It is interesting that the mandibles (jaws), deep within the throat, resemble these claws. This is a phylum of wormlike creatures, 0.5-20 cm long, closely related to the arthropods and tardigrades, classified into a super group known as the Panarthropoda (Wikipedia 2010). These functionally segmented animals have antennae (Figure 4), tiny eyes (Figure 4), many paired legs (Figure 2; Figure 6), and slime glands, but they lack the chitinous exoskeleton of the arthropods. Because of their legs, they more closely resemble caterpillars, but the fleshy antennae distinctly set them apart. And they are not jointed in the same way as arthropods. Their slow movements are not unlike those of caterpillars.

Figure 2. ***Euperipatus rowelli***, revealing the feet with chitinous claws. Note the two bluish slime glands beneath the antennae and the barely visible mouth in the center of the head.. Photo by Andras Keszei, with permission.

Figure 3. Close view of foot and claws of ***Euperipatus rowelli***. Photo by Andras Keszei, with permission.

Figure 4. ***Euperipatoides rowelli*** showing antennae with tiny eyes near their bases. Photo by Andras Keszei, with permission.

The phylum is rare. This is in part due to the restricted ranges of the species and their very narrow and restricted habitat needs. But part is due to industrialization and the loss of suitable habitat. Only eleven species have been studied in detail, and three of those are critically endangered or in one case possibly extinct (Wikipedia 2010).

They are circumtropical, but are most common in the Southern Hemisphere tropics, where they prey on small insects. Because of their sensitivity to drying out, they are most common in humid forests such as the tropical rainforests, where mosses seem to be an important part of their habitat (Figure 5) (Onychophora 2005). On the other hand, Brues (1948) reported that Dr. P. J. Darlington collected a specimen of ***Paraperipatus*** in the Bismarck range of New Guinea in moss at 10,000 ft. (3048 m), which is above timberline. ***Epiperipatus biolleyi*** (Figure 6) is often associated with mosses, especially in the early stages of succession (Brinck 1956; Ruhberg 1985; Mayer 2006). Mayer and Harzsch (2007) collected this species from mosses in Costa Rica for their study of the nervous system. The onycophorans use the moss as cover to protect them from the radiation.

Figure 5. ***Peripatus*** sp. amid mosses on a rock. Photo by Robbin Moran, with permission.

Figure 6. ***Epiperipatus biolleyi***. Photo by Georg Mayer, Creative Commons license of BMC.

Feeding Habits

These are slow walkers (1 cm s^{-1}) (Monge-Nájera *et al*. 1993) and thus cannot realistically use aggression for protection or capture. They sense their prey by air movements caused by the movement of the prey; they are nearly blind. To catch their prey, they squirt a sticky slime, generally about 1 cm, but up to 30 cm from the onychophoran (Read & Hughes 1987; Wikipedia 2010; BBC 2010). The glue dries very quickly and immobilizes the prey. For larger prey, they may target the limbs, immobilizing them with the glue-like slime. This slime comprises up to 11% of the dry weight of the velvet worm and is 90% water. Its constituents include mostly collagen proteins. It also includes sugars, lipids, and nonylphenol, a surfactant known only in the Onychophora. This makes a super glue, and the nature of the lipid and nonylphenol suggests that these two substances may be used to prevent the organism from being glued by its own secretions by stopping or slowing the drying process. Haritos *et al*. (2010) examined the mechanism in ***Euparipatoides rowelli*** (Figure 4) and proposed that when the slime is expelled from the gland, evaporative water loss triggers a "glass transition change in the protein solution, resulting in adhesive and enmeshing thread formation, assisted by cross-linking of the complementary charged and hydrophobic regions of the protein." That is, this species, and probably other onychophorans, uses disordered proteins rather than the structured silk-like proteins used by some other kinds of invertebrate predators. The large percentage of body mass accounted for by this substance is

somewhat balanced by the organism's behavior of eating and reusing the dried slime of its prey (Read & Hughes 1987; Wikipedia 2010; BBC 2010). It requires 24 days to replenish the supply provided by the repository (Read & Hughes 1987). This glue also seems to be their only form of defense.

Moisture and Light Relations

The Onychophora have a covering of α chitin that seems to do little to prevent desiccation, forcing them to live in areas with high humidity – mosses and leaf litter of rainforests (Wikipedia 2010). Their sensitivity to desiccation is counteracted by having their activity primarily at night or in rainy weather (Monge-Nájera *et al*. 1993). And at least some also prefer soil that has been covered by moss, most likely because that soil has a higher moisture content. When suddenly exposed to light and its drying effects, they may roll into a ball like some isopods, forming a position that conserves moisture (Figure 7).

Figure 7. ***Euperipatoides rowelli*** enrolled after being exposed from its log habitat. Photo by Andras Keszei, with permission.

It appears that desiccation is not the only problem for exposed onychophorans. ***Epiperipatus biolleyi*** (Figure 6) is phototactic and hides from direct sunlight, avoiding light in the range of 470-600 nm (Monge-Nájera *et al*. (1993).

Monge-Nájera *et al*. (1993) reported that the field preference of the onychophoran ***Epiperipatus biolleyi*** (Figure 6) was either the moss-substrate interface or in burrows in the soil. Using a series of experiments, Monge-Nájera *et al*. demonstrated the preference of the ***E. biolleyi*** for bryophytes over grass (Figure 10). The researchers covered half a Petri dish with the thallose liverwort ***Marchantia polymorpha*** (Figure 8) and half with blades of grass. When subjected to light, nearly 80% of the animals curled up under the bryophytes within a mean time of 189 seconds (n=9). The ones on soil continued searching by inserting their antennae and head among soil particles, but they never came to rest or made any burrow (Figure 10). The researchers suggested that in nature these animals may be limited to areas where there are suitable burrows or cover such as bryophytes that provide cover similar to that in a burrow. It appears that ***Macroperipatus torquatus*** (Figure 9) has a similar restriction (Read 1985) to such habitats.

Figure 8. ***Marchantia polymorpha***. James K. Lindsey, with permission.

Figure 9. ***Macroperipatus torquatus***, shown here crossing young bryophytes, used the liverwort ***Marchantia polymorpha*** as cover from light in the lab. Photo by Mr. Spanky, through Creative Commons.

Moisture, as well as light, were most likely driving forces in these experiments. Monge-Nájera *et al*. (1993) measured the humidity in the two vegetation choices (Figure 10) by drying them to a constant weight. Moisture was significantly higher in the bryophyte portions (bryophytes: 84.2±3.4, 76.5-87.9%; grass: 71.1±4.4, 66.8-80.0%) using Mann-Whitney U with $p<0.001$ and 10 replicates.

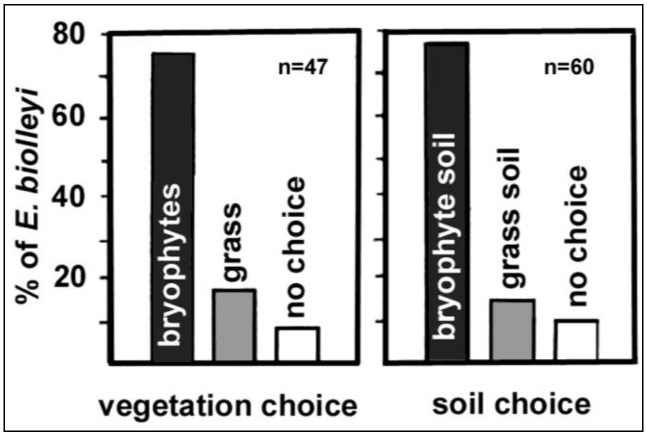

Figure 10. Comparison of percentage of ***Epiperipatus biolleyi*** in bryophyte cover vs grass blade cover (**left**) and on soil from under bryophytes vs soil from under grass (**right**) in 8 cm diameter Petri plates. These onychophorans were 5 cm long, so some straddled the two areas, having no clear choice. Modified from Monge-Nájera *et al*. 1993.

The onychophorans most likely also use the mosses as cover to avoid predators, which include the Clay-colored Robin (***Turdus grayi***; Figure 11) and Hemprich's Coral Snake (***Micrurus hemprichii***; Figure 12) (Monge-Nájera *et al*. 1993).

Figure 11. Clay-colored Robin, ***Turdus grayi***, a predator on onycophorans. Photo by Amado Demesa, through Creative Commons.

Figure 12. Yellow-banded Coral Snake, ***Micrurus hemprichii***, a predator on onycophorans. Photo by Rich Hoyer, through Creative Commons.

Mating and Reproduction

Finding suitable habitat or finding a mate requires considerable time for such slow-moving creatures and puts them at risk of desiccation. Thus, an efficient system for locating their habitat increases their chances for survival. Eliott *et al*. (1993) demonstrated for the first time in onychophorans, using ***Cephalofovea tomahmontis***, that the crural glands at the bases of the legs in males produce a pheromone that attracts females of the same species. It appears that pheromone-producing glands not only help in locating males, but may also prevent desiccation in females seeking new locations.

Peat moss is a typical substrate for culturing ***Euperipatus rowelli*** (Figure 13) (Barclay *et al*. 2000; Reinhard & Rowell 2005; Haritos *et al*. 2010; Andras Keszei, pers. comm. 7 March 2013). Keszei finds that ***Sphagnum*** (Figure 15) is the only suitable substrate he has found for culturing these onychophorans because it prevents mold while keeping them moist. This is perhaps due to the antibiotic properties of ***Sphagnum***. He says that this species does not normally live among the ***Sphagnum*** [they live in decaying logs, including *Eucalyptus* (Figure 14)], but that he has collected them from less than 100 m away and considers ***Sphagnum*** as a possible hunting ground for them.

Figure 13. ***Euperipatus rowelli*** being cultured on peatmoss, a medium that helps to limit fungal infection. Photo by Andras Keszei, with permission.

Figure 14. ***Euperipatus rowelli*** on decaying wood in NSW where they live in habitats ranging from rainforest to dry sclerophyll forests in decomposing logs. Photo by Andras Keszei, with permission.

Figure 15. ***Sphagnum cristatum***, a suitable substrate for culturing onycophorans. Photo by Janice Glime.

Eggs of at least some species are laid under mosses (Mayer & Tait 2009). On Mt. Macedon, Victoria, Australia, Mayer and Tait found ***Ooperipatellus insignis*** (see Figure 16) in leaf litter and under moss.

Figure 16. ***Ooperipatellus viridimaculatus*** on moss. Photo by Chris Morse, through Creative Commons.

Barclay *et al*. (2000) demonstrated that in ***Euperipatoides rowelli*** (Figure 13-Figure 19), males are the first dispersers. They secrete a pheromone that attracts both males and females of the same species. Thus, when these males disperse to decomposing logs, the females are able to locate this suitable habitat with a much lower water loss and expenditure of energy. It would be interesting to know if such a pheromone signal is equally used and effective among those onychophorans dwelling among bryophytes.

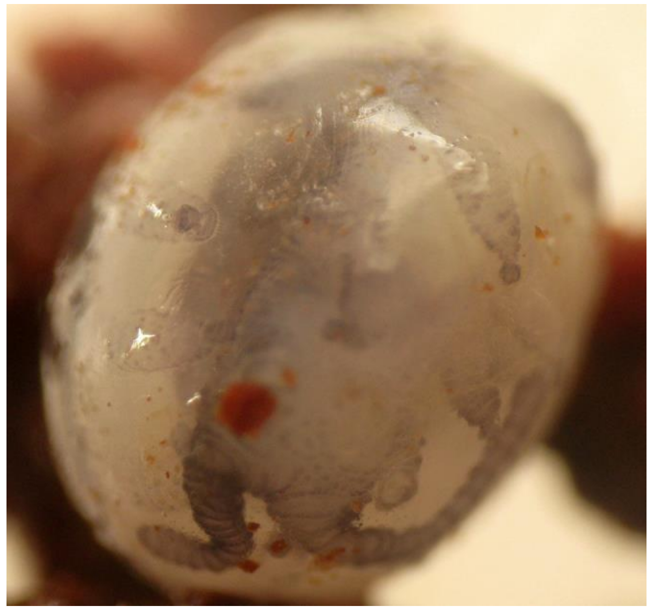

Figure 17. Oviviparous egg of ***Euperipatoides rowelli*** at time of "birth." Photo by Andras Keszei, with permission.

Figure 18. Newborn ***Euperipatoides rowelli***. Photo by Andras Keszei, with permission.

Figure 19. ***Euperipatus rowelli*** baby that has not yet developed its pigmentation. Photo by Andras Keszei, with permission.

Figure 20. ***Euperipatoides kanangrensis***. Photo by Martin Smith through Wikimedia Commons.

Like most of the onychophorans, ***Euperipatoides rowelli*** (Figure 1-Figure 2, Figure 7) is secretive. However, Reinhard and Rowell (2005) suggest that their behavior is nevertheless complex. They form aggregations as large as 15, comprised of females, males, and young. The female is dominant, and despite collective hunting, the dominant female eats first – alone. Behavior of aggressive dominant and passive-subordinate establishes a hierarchy. This structured group will defend its log aggressively against any invasion by onychophorans from another location.

Monge-Nájera and Alfaro (1995) hypothesized that onychophorans might find mosses because of some odor contributed by the mosses. However, when they provided them with filter paper with water on one end and macerated moss on the other end, the onychophorans showed no preference. Furthermore, while the preference of this species for moist habitats was greater than for dry habitats in Costa Rica, more specific preferences were not clear. Habitats included sandy soil, under moss, in and under logs, under stones, and in soil of crevices.

Reproduction is sexual in all but ***Epiperipatus imthurmi***, a species lacking males and using **parthenogenesis** (reproduction from an unfertilized egg) instead (Wikipedia 2010). Interestingly, the females are typically fertilized only once during their lives. If they are fertilized before the egg cells are mature, the sperm will be stored in a special reservoir. Sperm are released from their packets when amoebocytes from the female's blood collect inside the deposition site and decompose the packets. The young may be born live or laid as eggs, depending on the species.

Birds and rodents prey on the velvet worms. Their foraging activities may account for some of the disturbances to the mossy habitat.

Peripatoides novaezelandiae (Figure 21-Figure 23) is the most common peripatus species in New Zealand (Ryan 2012). I have not been able to verify that it lives among mosses, but it is commonly cultured on ***Sphagnum*** (Figure 15). However, a discussion on YouTube indicated that one of the posters photographed this species on ***Sphagnum***, and he stated that he photographed it in a culture that used the moss where it had been found.

Figure 21. ***Peripatoides novaezelandiae*** on moss. Photo by Paddy Ryan, with permission.

Figure 22. ***Peripatoides novaezelandiae*** showing feet. Photo by Paddy Ryan, with permission.

Figure 23. ***Peripatoides novaezelandiae*** on liverwort. These are likely traversed in search of food and soil beneath them is often sought to avoid dehydration. Photo by Paddy Ryan, with permission.

Mimics?

In the cloud forests of Ecuador, an onycophoran and a lepidopteran mimic live in the arboreal bryosphere (Zitani *et al*. 2018). The onycophorans are unable to close their many traheal spiracles and thus lose water easily. Therefore, bryophytes may serve as a moist habitat to maintain the moisture of the onycophorans. They are nocturnal and hav limited dispersal, further conserving thir moisture. In these arboreal moss cushions, they cohabit with annelids, molluscs, curstaceans, millipedes, centipedes, arachnids, and insects. But in one of the mosses samples there was a caterpillar that resembled th onycophoran in size, shape, and coloration. Is it really a mimic, or are both addapted by cryptic coloration to the same habitat? Is one of them unfit for would-be predators?

Summary

Among the bryophyte inhabitants are members of the relatively rare phylum Onychophora. Little is known about their behavior, but it appears that bryophytes are important in maintaining moisture in the soil beneath them where onychophorans may live. It is likely that we will discover that many more species make use of the bryophytes in some capacity.

Sphagnum is an important culture medium for onychophorans because they do not develop fungal infections when it is used.

Acknowledgments

I appreciate the helpful comments and images of Andras Keszei that have greatly enhanced the clarity of this chapter. Bernard Goffinet kindly sent me the article on the Onychophoran by Zitani *et al*.

Literature Cited

Barclay, S. D., Rowell, D. M., and Ash, J. E. 2000. Pheromonally mediated colonization patterns in the velvet worm *Euperipatoides rowelli* (Onychophora). J. Zool. 250: 437-446.

BBC. 2010. Life in the Undergrowth documentary series, 24 January 2010. Accessed 3 July 2013 at <http://wn.com/onychophora?upload_time=all_time&orderby=published>.

Brinck, P. 1956. Onychophora: A review of the South African species, with a discussion on the significance of the geographical distribution of the group. In: Hanstrom, B., Brinck, P., and Rubedeck, G. (eds.). South African Animal Life. Results of the Lund University Expedition 1950-1951. No. 4. Almquist and Wiksell, Uppsala, Sweden, pp. 7-32.

Brues, C. T. 1948. The distribution of Onychophora in New Guinea and neighboring islands. Psyche 55: 181-182.

Eliott, S., Tait, N. N., and Briscof, D. A. 1993. A pheromonal function for the crural glands of the onychophoran *Cephalofovea tomahmontis* (Onychophora: Peripatopsidae). J. Zool. 231: 1-9.

Haritos, V. S., Niranjane, A., Weisman, S., Trueman, H. E., Sriskantha, A., and Sutherland, T. D. 2010. Harnessing disorder: Onychophorans use highly unstructured proteins, not silks, for prey capture. Proc. Royal Soc. B 277: 3255-3263.

Mayer, G. 2006. Structure and development of onychophoran eyes: What is the ancestral visual organ in arthropods? Origin and Evolution of Arthropod Visual Systems (Part I). Arthropod Struc. Dev. 35: 231-245.

Mayer, G. and Harzsch, S. 2007. Immunolocalization of serotonin in Onychophora argues against segmental ganglia being an ancestral feature of arthropods. BMC Evolutionary Biology 7: 118 doi:10.1186/1471-2148-7-118.

Mayer, G. and Tait, N. N. 2009. Position and development of oocytes in velvet worms shed light on the evolution of the ovary in Onychophora and Arthropoda. Zool. J. Linn. Soc. London 157: 17-33.

Monge-Nájera, J. and Alfaro, J. P. 1995. Geographic variation of habitats in Costa Rican velvet worms (Onychophora: Peripatidae). Biogeographica 7: 97-108.

Monge-Nájera, J., Barrientos, Z., and Aguilar, F. 1993. Behavior of *Epiperipatus biolleyi* (Onychophora: Peripatidae) under laboratory conditions. Rev. Biol. Trop. 41: 689-696.

Onychophora. 2005. Updated 24 April 2005. Onychophora. Accessed 4 July 2011 at <http://www.peripatus.gen.nz/taxa/arthropoda/onychophora.html>.

Read, V. M. St. J. 1985. The ecology of *Macroperipatus torquatus* (Kennel) with special reference to feeding and a taxonomic review. Ph.D. Thesis, University College of North Wales, Bangor.

Read, V. M. St. J. and Hughes, R. N. 1987. Feeding behaviour and prey choice in *Macroperipatus torquatus* (Onychophora). Proc. Royal Soc. Lond. B 230: 483-506.

Reinhard, J. and Rowell, D. M. 2005. Social behaviour in an Australian velvet worm, *Euperipatoides rowelli* (Onychophora: Peripatopsidae). J. Zool. 267: 1-7.

Ruhberg, H. 1985. Die Peripatopsidae (Onychophora). Systematik, Ökologie, Chorologie und phylogenetische Aspekte. Zoologica 137: 1-183.

Ryan, Paddy. 2012. *Peripatus* - Walking worms, Te Ara - the Encyclopedia of New Zealand. Updated 21 September 2012 . Accessed 3 July 2013 at <http://www.TeAra.govt.nz/en/photograph/13243/peripatoides-novaezelandiae>.

Wikipedia. 2010. Onychophora. Last updated 23 September 2010. Accessed 11 October 2010 at <http://en.wikipedia.org/wiki/Onychophora>.

Zitani, N. M., Thorn, R. G., Hoyle, M., Schulz, J. M., Steipe, T., Bohorquez Ruiz, Y., Sarquis-Adamson, Y., and Wishart, A. E. 2018. An Onychophoran and its putative Lepidopteran mimic in the arboreal bryosphere of an Ecuadorian cloud forest. Amer. Entomol. 64: 94-101.