

to assume that the ecology of the Kem Kem was more similar to a modern ecosystem (we just have not found enough prey species yet for the large dinosaurs, whose numbers we might be overestimating anyway) than try to re-write the ecological rule book based on really quite inadequate fossil evidence.

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Social Evolution: War of the Worms

The discovery of a non-reproductive soldier caste in a clonally reproducing trematode greatly extends the taxonomic distribution of eusociality and reaffirms the importance of relatedness in the evolution of reproductive altruism.

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There is great variability in degrees of sociality within the animal kingdom. The most elaborate forms are found in species such as ants and termites, where division of labour is associated with a caste system in which queens monopolize reproduction and workers do all the other colony tasks, such as brood care and foraging. In recent years, the presence of specialized reproductive and non-reproductive castes has been uncovered in several other arthropods, including gall-forming aphids [1], thrips [2] and snapping shrimps [3]. A new study [4] now greatly extends the taxonomic range of these eusocial systems by describing the occurrence of specialised reproductive and soldier morphs in the parasitic trematodes or fluke worms.

Trematodes have a complicated lifecycle involving several distinct stages and several hosts (Figure 1). *Himasthla* sp. B infects the California horn snail, *Cerithidea californica*, as its second intermediate. Once in the host, the parasite exhibits repeated clonal reproduction of rediae, which then produce more of themselves or give rise to dispersive offspring (cercariae). All these individuals are clones of the diploid larvae that infected the host. While studying trematodes in marine snails, Hechinger *et al.* [4] observed that rediae occurred in two distinct morphological forms (Figure 2). The

larger, or primary, morph is that of the reproductive rediae already described in the literature. The other, secondary, morph is much smaller and more mobile, with relatively larger mouthparts. Importantly, the two morphs differ greatly in their reproductive abilities. While 96% of the

reproductive rediae contain embryos and/or dispersive cercariae, none of the smaller morphs show any sign of reproduction. Moreover, detailed censuses showed that the smaller morph is unable to undergo a transition to the much larger reproductive morph, thus indicating that it is fully sterile.

There are also important behavioural differences between the two forms. The larger, primary morphs are almost all located in the visceral mass of the host, mainly in the region of the gonads. The smaller form is distributed more widely throughout the host, but primarily within the mantle, which is the

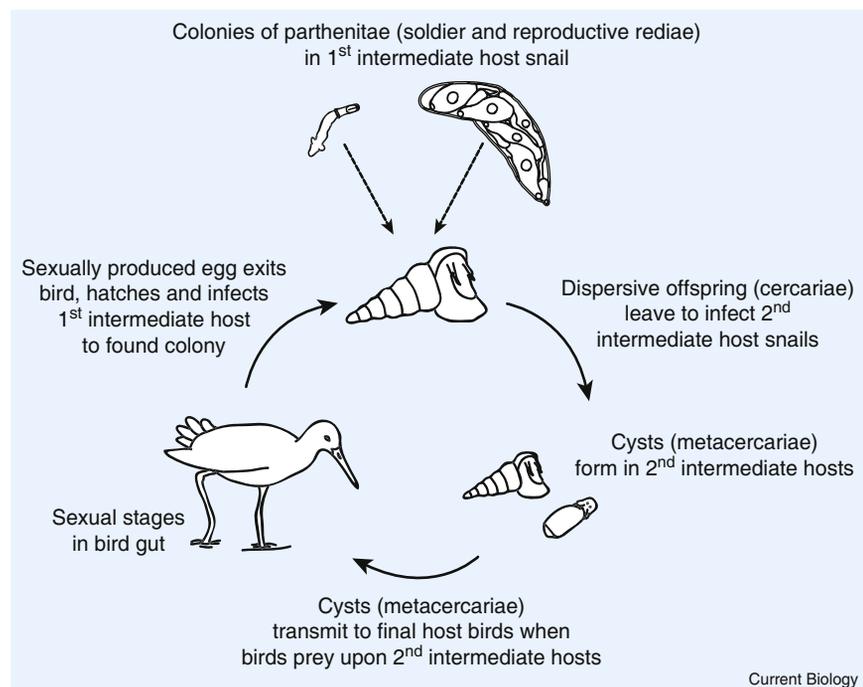


Figure 1. The complex life cycle of the trematode *Himasthla* sp. B.

As illustrated, the life cycle of the trematode *Himasthla* sp. B involves several sequential forms and three hosts. (Courtesy of Ryan Hechinger; reproduced with permission from [4].)



Figure 2. The large, primary reproductive morph and smaller, soldier morph of the rediae of the trematode *Himasthla* sp. B.

The free-swimming dispersal form (cercariae) can be seen developing within the larger primary morph. (Courtesy of Ryan Hechinger; reproduced with permission from [4].)

main point of entry for trematodes and the region furthest from the gonadal region. Behavioural trials supported the view that these differences in distribution are associated with the smaller morphs having a defensive function. *In vitro* trials showed that the reproductive morph only rarely attacked heterospecific trematodes and conspecifics collected from other infected snails. By contrast, the smaller morph invariably attacked individuals of the six species of trematodes that were tested, as well as attacking foreign conspecifics. On the basis of these morphological and behavioural differences, and the absence of reproduction in the smaller morph, Hechinger *et al.* [4] concluded that these two forms of rediae represent permanent physically and behaviourally distinct castes: a large reproductive caste and a smaller soldier caste.

The finding of a caste system associated with reproductive division of labour in a completely new taxonomic group is significant for understanding the selective forces promoting the evolution of reproductive altruism. One key

ecological factor thought to promote the evolution of eusociality is the 'fortress-defence model' [5], according to which offspring may be selected to remain at the natal site and help parents to raise additional offspring if the natal site represents a delimited food source that is defensible. This is the case for gall-forming aphids and wood-nesting termites. It is also the case for these trematodes, which defend the host, in which they live and on which they feed, from either heterospecific or conspecific invaders.

The second and related factor known to be necessary for the evolution of reproductive altruism is relatedness. Theory predicts that altruistic behaviours decreasing the lifetime reproductive success of an organism can evolve only when it increases the lifetime reproductive success of related individuals [6,7]. In line with this argument, the evolution of eusociality in Hymenoptera occurred in groups typically headed by one singly-mated female [8]. Thus, the workers help their mother to rear highly related siblings. Similarly, among snapping shrimps, most colony members are full siblings,

suggesting that they are the offspring of a single breeding pair [9]. High relatedness as a result of inbreeding is also at the origin of the evolution of eusociality among gall-forming thrips [2]. Finally, the evolution of a soldier caste in gall-forming aphids and polyembryonic wasps both occurred in groups of clonal individuals [10]. The discovery of a specialized non-reproductive soldier morph in clonal groups of trematodes demonstrates further the importance of high relatedness in the evolution of eusociality.

The discovery of eusociality in trematodes is interesting because the group is taxonomically very rich and diverse, with at least 20,000 species encompassing a wide variety of life-histories and ecologies. The presence of a soldier caste is already suspected in several other species of trematodes [4]. Determining how widespread is the emergence of a soldier caste, how many independent origins have occurred, and under what conditions, will contribute significantly to our understanding of the selective forces promoting eusociality.

Hechinger *et al.* [4] also experimentally demonstrated that the soldier morphs of these fluke worms are able to recognise kin, attacking conspecifics from other clones, but never members of their own clone. The conditions leading to the evolution and maintenance of kin recognition in animals remain poorly understood [11]. It is found among clonal wasp larvae [12], but is absent in most of the gall-forming aphids [13,14]. The trematodes present an opportunity to explore this question within a new and very diverse group.

The discovery of eusociality in fluke worms is somewhat surprising given the extensive research on these organisms [15]. Although undescribed, the trematode *Himasthla* sp. B has been extensively studied for 65 years [4]. The presence of reproductive division of labour may have been overlooked because research has focused largely on issues related to their importance as parasites and sources of disease. This raises the intriguing possibility that eusociality might be much more common than generally realized. This study, together with other recent findings of eusocial systems outside the Hymenoptera, will hopefully provide an incentive for

other scientists to search for similar phenomena within their study system.

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