

An Evolutionary diversity of the Flatworm group



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Abstract

Flatworms are a great model system for examining how variations in reproductive ecology across species are mirrored in the physiological and molecular specifics of how reproduction is accomplished since they demonstrate enormous variety in their reproductive biology. In this review, I focus on five significant "lifestyle choices" (i.e., alternate evolutionary/developmental outcomes) that, taken together, account for a large portion of flatworm sexual diversity. I start with the choices of (i) whether to be free-living or parasitic; (ii) whether to reproduce asexually or sexually; and (iii) whether to be gonochoristic (separate-sexed) or hermaphroditic. I next look at two further choices related to hermaphroditism: (iv) the balance of investment into the male vs female sex function and (v) outcrossing versus selfing (sex allocation). Collectively, these lifestyle decisions establish the fundamental guidelines for reproduction, but as I emphasise in the second section of the review, sexual selection, along with the related phenomena of sperm competition and sexual conflict, has a significant impact on flatworm reproduction as well. But how exactly this works out is greatly influenced by the specific reproductive techniques that each species has chosen to use.

1.1. Introduction

Around 20,000 documented species of watery, mostly tiny, soft-bodied, acoelomate animals with bilateral symmetry and dorso-ventral flattening make up the phylum Platyhelminthes (Hyman, 1951; Ruppert et al., 2004). Due to their extraordinary capacity for regeneration (Egger et al., 2007; Gentile et al., 2011) supported by a pluripotent stem cell system of "neoblasts" (Peter et al., 2004; Ladurner et al., 2008; Aboobaker, 2011; Baguna, 2012; Rink, 2013), several

members of the phylum have long piqued the interest of developmental biologists. Its inclusion of significant parasites, such as human pathogens like blood flukes that cause schistosomiasis and tapeworms that cause alveolar echinococcosis, cystic echinococcosis, and neurocysticercosis, makes the phylum of significant medical and veterinary importance (Olson et al., 2012).

The complexity and diversity of flatworms' reproductive systems—previously discussed in Hyman, 1951; Henley, 1974; and Tyler, 1999—is a notable characteristic I hope to examine in this review. This diversity has been divided up into five main categories that might be looked of as "lifestyle options." To start, while some flatworms live in the wild, others have adapted a parasitic lifestyle. In addition, certain flatworms can reproduce both sexually and asexually; some can even do both. Third, whereas some flatworms are hermaphroditic and can display both sex functions at different stages of their lives, either sequentially or simultaneously, others are gonochoristic (i.e., "dioecious," where individuals are either male or female). Wiley Online Library, Indian Council of Medical Research. Wiley Online Library's Terms and Conditions are available at (<https://onlinelibrary.wiley.com/terms-and-conditions>). OA publications are subject to the terms of the relevant Creative Commons License. Fourth, adopting a hermaphroditic lifestyle gives the option to choose between self-fertilization or outcrossing as a method of reproduction. Finally, hermaphrodites must choose how to allocate their resources between their male and female sex functions (also known as "sex allocation"). Flatworms are an appealing model for examining the multiple sexual lifestyle transitions and their underlying biological mechanisms since all of these options exist within the same phylum and because different species or groups exhibit highly diverse combinations of these qualities.

1.2. LIFESTYLE CHOICES AFFECTING FLATWORM REPRODUCTION

➤ Free-Living Versus Parasitism

Traditional flatworm taxonomy divided the Platyhelminthes into three parasitic groups—Cestoda, Trematoda, and Monogenea—plus one free-living group, the Turbellaria. However, molecular phylogenetic analyses unequivocally show that Turbellaria is paraphyletic. Thus, the parasitic lifestyle is a derived state in flatworms, and all parasitic flatworms belong to the Rhabditophora, which now includes all Platyhelminthes with the exception of the Catenulida (Egger et al., 2015). This group is called Neodermata (Fig. 1). In turn, the Neodermata is made up of the three wholly parasitic monophyletic groups Cestoda (tapeworms), Trematoda (flukes), and Monogenea, the latter of which is now thought to be a sister group to the other two based on recent molecular evidence (Egger et al., 2015; see also Laumer et al., 2015a,b). The Rhabditophora contains groups of free-living flatworms that include the most primitive Macrostomorpha as well as Lecithoepitheliata, Polycladida, Rhabdocoela, Proseriata, Tricladida, and Bothrioplanida, according to the same transcriptomic-phylogenomic research.

Together with the triclads, they make form the newly named Acentrostomata, which is currently regarded to be the sister group to the parasitic Neodermata. It is still debatable whether or not to include the free-living Acoels in the phylum Platyhelminthes given their evolutionary location (see Egger et al., 2009). Acoels should now be categorised as deuterostomes (Philippe et al., 2011) or hold a more basal position within the Bilateria (Srivastava et al., 2014; Telford and Copley, 2016), according to recent molecular phylogenetic evidence. In either case, they are outside of the Protostome clade and therefore far removed from flatworms, so they are not further considered here.

1.3. Sexual Versus Asexual Reproduction

As I just stated, some parasitic flatworms, like *S. mansoni*, combine asexual reproduction with sexual reproduction at different stages of their life cycles, taking advantage of the advantages of being able to quickly multiply within the intermediate host while maintaining the genetic "shuffling" made possible by sex (Agrawal, 2006). Among the flatworms that are free-living, some only reproduce sexually, while others do so asexually (reviewed in Henley, 1974). Others have the ability to alternate between sexual and asexual reproduction based on their surroundings. When conditions are favourable (warmer), for instance, individuals of the triclad flatworm *Dugesia ryukyuensis* reproduce asexually; nevertheless, when conditions are unfavourable (colder), they can transition to sexual reproduction (Kobayashi and Hoshi, 2011). Such a pattern supports the idea that sex is preferred in harsher and more unpredictable environmental situations, because having genetically varied offspring may increase the likelihood of producing at least some people that are better adapted to and can therefore survive these conditions (Williams, 1975). By giving sexually mature worms of a different species, asexual individuals can also be experimentally induced to stop fission and start sexual reproduction. Research has focused on identifying the sex-inducing signals provided by this stimulus (Kobayashi and Hoshi, 2002; Hoshi et al., 2003; Ishizuka et al., 2007; Kobayashi and Hoshi, 2011).

Different environmental conditions may occasionally encourage the evolution of asexual (parthenogenetic) lineages deriving from sexual predecessors; if the advantages and disadvantages of these two opposing methods balance out, both types may be able to endure in sympatry. The freshwater triclad *Schmidtea polychroa*, in which both diploid sexual and polyploid (often triploid) parthenogenetic forms coexist, has been particularly well studied in terms of the occurrence and evolutionary implications of parthenogenetic reproduction

(Weinzierl et al., 1999). The evolutionary mystery of predominant sex is represented by the possibility that a parthenogenetic mutant could have a significant transmission advantage over sexual forms (Agrawal, 2006; Lehtonen and Kokko, 2014). We can predict that a parthenogenetic mutant may spread in hermaphrodites, and more specifically in *S. polychroa*, if it can reduce male allocation and convert these resources into higher fecundity through the female sex function, and/or if a retained male sex function in parthenogens enables the transmission of genes for parthenogenesis to sexual individuals in the population (Weinzierl et al., 1999). The latter is conceivable in *S. polychroa* because parthenogenetic individuals need to receive allosperm to drive egg development, but this sperm does not contribute genetic material to the zygote (Weinzierl et al., 1999). Parthenogenesis is sperm-dependent (also known as "pseudogamous"). Both hypotheses are supported by the facts, which show that parthenogens have higher fecundity and less male allocation, and that triploid (and presumably parthenogenetic) offspring frequently develop from diploid sexual moms (Weinzierl et al., 1998, 1999).

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