# Systematic review of triploidy among parasitic worms.

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## Abstract

Parasitic worms have significant medical, veterinary, and economic importance. Numerous studies have therefore addressed various aspects of parasitic worms' biology. In contrast, the ploidy of parasitic worms remains comparatively understudied, despite a few known triploid species. Polyploidy is known to have phenotypic and genetic effects in animals, which can lead to changes at the evolutionary scale. The evolutionary consequences of polyploidy have been addressed in host-parasite systems; however, most studies have focused on the host perspective, with relatively few studies examining the parasitic side of the story. In this review, we provide available information on the distribution of triploidy among parasitic worms, along with information on such aspects as reproduction, origin of triploidy, and life history. Across 100 selected papers (out of 416 screened), triploidy was reported for 15 parasitic Platyhelminthes and 13 parasitic Nematoda. Most triploid species of parasitic worms (24 out of 28) were documented at the adult stage. Triploid lineages reported for the adult stage reproduce predominantly via parthenogenesis. Finally, we discuss the potential effects of ploidy variation for host-parasite dynamics and adaptation rates of parasitic worms. In particular, we discuss how parasitic worms adapt to their hosts despite potential constraints of asexuality. As well as whether triploid individuals outcompete diploid conspecifics when both ploidy levels coinfect the host, as could be expected if triploids have higher virulence.

**Keywords:** polyploidy; Platyhelminthes; Nematoda; host–parasite interactions; evolution of ploidy

# 1 Introduction

Parasitic worms have a significant impact on humans, livestock, and important crop cultures. It is estimated that a minimum of two billion people are infected by at least one parasitic worm, such as soil-transmitted helminths (Wright et al. 2018), flukes (Fürst et al. 2012, Wright et al. 2018), or tapeworms (Eichenberger et al. 2020, Scholz and Kuchta 2016). Nevertheless, the diseases they cause — helminthiasis — are severely understudied and many belong to the group of neglected tropical diseases. Geographically, cases of helminthiasis are not distributed evenly, as most human infections by helminths occur in low- and middle-income countries (James et al. 2018, Weatherhead, Hotez, and Mejia 2017). Helminthiases are particularly prevalent among children, which led to the launch of so-called Mass Drug Administration (MDA) programs that aim to provide chemotherapy to school-aged children (Majid, Kang, and Hotez 2019, Weatherhead, Hotez, and Mejia 2017). Helminths also impose a substantial economic burden on the livestock industry (€1.8 billion in Europe alone, (Charlier et al. 2020)) and plant food production ($80 billion worldwide, (Jones et al. 2013)). This has led to the widespread use of the anthelmintic drugs, which, unfortunately, resulted in the emergence of drug resistance to all classes of anthelmintics (Fissiha and Kinde 2021).

Given the importance of helminths and the emerging threat of drug resistance, numerous studies have examined various aspects of parasitic worms' biology, including distribution, epidemiology, and host-parasite interactions. However, one important aspect - worm ploidy - remains understudied. Ploidy is expected to play an important role in the evolution of host-parasite interactions and drug resistance, both of which are essential aspects of parasitic organisms. First, ploidy is hypothesised to affect host-parasite interaction by altering the number of antigens to be detected by hosts (M'Gonigle and Otto 2011). However, this effect was shown theoretically only in comparison of haploid and diploid pathogens, without any extrapolation to higher levels of ploidy. Second, theoretical studies suggest that polyploidy affects the rate of adaptation, as increased ploidy can lead to a higher number of beneficial mutations (Otto and Whitton 2000). Unfortunately, only a limited number of experimental studies test theoretical predictions or even consider the effect of polyploidy on host-parasite dynamics (King, Seppälä, and Neiman 2012), especially from the parasitic "point of view".

While little is known about the prevalence of polyploidy in parasitic worms — hence the reason for this study — parasitic worms with higher ploidy (mostly triploid) have already been observed, coexisting with their diploid conspecifics and congeners. The presence of such triploid parasitic species, usually reproducing through mitotic parthenogenesis, is interesting for several reasons. First, mitotic parthenogenesis means that oocytes are produced without recombination, and a new organism develops without fertilisation. Lack of recombination in parasitic worms contradicts theoretical models suggesting that recombination (associated with sexual reproduction) is beneficial for parasites under the strong selection they experience from their hosts (Salathé et al. 2008), as hosts can develop rapidly resistance against asexual lineages. Moreover, without recombination, asexual lineages are supposed to accumulate deleterious mutations and are therefore considered evolutionary "dead ends". On the other hand, resistance to anthelmintics can arise from multiple loci (Doyle et al. 2022), and the lack of recombination observed in several triploid parasitic worms can actually help preserve multigenic traits. Thus, one may hypothesize that anthelmintic resistance spreads faster in a population through asexual triploids, a hypothesis that is yet to be tested.

Second, triploidy can affect traits related to reproduction, physiology, and life history. For instance, comparison between diploid and polyploid individuals of *Daphnia pulex* and brine shrimps *Artemia parthenogenetica* has shown that polyploid individuals develop faster under harsher environments compared to diploid conspecifics (Dufresne and Hebert 1998, Zhang and King 1993). Extrapolated to parasites, this observation suggests that triploids can outcompete diploids coinfecting the same host due to higher virulence. Another comparison on free-living flatworms reported triploid individuals to produce 58% more offspring in comparison to tetraploids (D'souza, Storhas, and Michiels 2005). However, we still lack similar studies comparing different ploidy levels in terms of reproductive output and life-history traits in the context of host-parasite systems from the parasite perspective.

One of the first reviews mentioning polyploidy in animals was published in the context of parthenogenesis. For example, Suomalainen (1950) provides a list of parthenogenetic polyploids among insects, molluscs, and crustaceans. Suomalainen, Saura, and Lokki (1976) expanded the list of triploid parthenogenetic insects by including other orders. In 2000, Otto and Whitton (2000) reported triploidy and tetraploidy cases across insects and several vertebrate taxa. However, Otto and Whitton (2000) do not mention any groups of parasitic worms. A more recent study by Román-Palacios et al. (2021) provides estimates of polyploidy incidence among animals, including Platyhelminthes and Nematodes. However, because the main aim of the study was to compare chromosome counts between plants and animals, the authors did not specify whether the species included in the database are parasitic. Špakulová et al. (2011) have focused specifically on parasitic flatworms, reviewing karyotypes of Cestoda species. According to this study, seven species of Cestoda are either exclusively triploid or have triploid populations (Špakulová, Orosová, and Mackiewicz 2011). Triploidy has also been shown for several species of plant-parasitic root-knot nematodes (RKN), members of the *Meloidogyne* genus (Janssen et al. 2017), that are known for their noticeable economic impact, infecting essential crops (Jones et al. 2013).

Despite the obvious importance of triploidy in the evolution of drug resistance, no studies to date have investigated anthelmintic resistance in triploid parasitic worms. Thus, it is still to be investigated whether triploidy affects the evolution of resistance. Moreover, it is not clear how prevalent triploidy is among parasitic worms and what its physiological consequences are. Apart from the two overviews of triploidy in Cestoda and the RKN, information on the prevalence of triploidy across helminths is still missing.

To address this gap, we conducted a systematic review searching for all published cases of triploidy in parasitic worms. We aim to (1) provide data on the prevalence and distribution of triploidy, listing all reported cases among parasitic worms, (2) present information when available on relevant aspects of triploid parasitic worm biology, such as their origin, reproduction mode, coexistence with other ploidies, drug resistance, and observed physiological differences. We believe this review will shed light on the importance of ploidy and serve as a starting point for further helminth-related studies, especially those focused on drug resistance evolution or host-parasite interactions.

# 2 Materials and Methods

A systematic literature search was carried out on March 26, 2025, with the follow-up search on March 28, 2025 (see details below). We searched for articles published before the search dates on the Web of Science and Scopus platforms. The aim of the literature search was to find published English-language sources reporting triploidy in species from two animal phyla: Platyhelminthes (flatworms) and Nematoda (roundworms). For this, we used two sets of keywords. The first set covered terminology describing triploidy, such as "triploid*", "autotriploid*", and "allotriploid*". The second set included scientific and common names of main taxonomic groups from the two mentioned phyla (e.g., "cestod*", "trematod*", "nematod*"). See SI 1 for the complete list of search terms and search strings for each platform.

The initial search (conducted on March 26) included keywords covering all roundworms and flatworms with an emphasis on parasitic groups (such as cestodes and trematodes). The search returned 168 abstracts in Web of Science and 355 abstracts in Scopus. After removing duplicates, 396 abstracts remained. The second search run (conducted on March 28) included the same "triploidy" keyword set as the initial search, but only two keywords covering two taxonomic groups, "monogenea*" and "turbellaria*". The rationale for this decision is that the initial list of "taxonomic" keywords (which included the broad term "flatworm") did not specify a separate class of parasitic worms — Monogenea. The initial list of keywords did not specify any groups of free-living flatworms either. Although they are not considered a monophyletic group (Schockaert et al. 2008), we still decided to use the currently deprecated term "Turbellaria", specifically to address the older literature. The search resulted in 81 abstracts (21 in Web of Science, 60 in Scopus). After combining abstracts from both searches and checking for duplicates, the final number of abstracts was 416.

During the initial abstract screening, 143 papers were included for the full-text screening. A paper was marked as relevant if it was a published scientific material (an original paper, as well as a review) with an explicit report on triploidy of a species from the taxonomic groups defined above. See SI 2 for more details on the inclusion criteria for abstract screening and full-text reading. In total, 100 papers were marked as relevant and used for data extraction. Whenever possible, we extracted the species name, reproductive system and mode, origin of triploidy, other ploidy levels detected for a given species, and any potential benefits of triploidy compared to diploidy. See SI 3 for the PRISMA flow diagram. When any of this information was not reported for a given species in selected papers, we did an additional search. However, all the additional papers were not included in the primary dataset, but were cited in the Results section.

# 3 Results

We identified 121 cases of triploidy reported for Platyhelminthes and Nematoda in 100 articles. All these triploid cases have been reported in 52 species. Hereafter, by a triploid species we mean a species with populations that consist exclusively of triploid individuals or with a proportion of triploid individuals sampled at all life-cycle stages (i.e., eggs, larval stages, mature individuals).

In the following subsections, we focus on parasitic Nematoda and three parasitic classes of Platyhelminthes (Cestoda, Trematoda, and Monogenea). For each group, we provide the number of reported triploid species. For each species, we provide (when available) information on the origin of triploidy, the presence of other ploidy levels, and reproductive mode. Information on the phenotypic effects of triploidy includes any available information for a given species on the difference between triploids and individuals of other ploidy, as well as on potential drug resistance. See Table 1 for the complete list of triploid parasitic species within each taxonomic group. Figure 1 provides a summary for each taxonomic group on main aspects of triploid parasitic worm biology.

## 3.1 Triploidy among parasitic flatworms

We found 37 species of Platyhelminthes with reported triploidy, 22 of them are non-parasitic flatworms, and 15 species are parasitic. Parasitic triploid species belong to three classes: Cestoda (seven species), Trematoda (seven species), and Monogenea (one species).

### 3.1.1 Cestoda

**Reproduction**

All triploid species of Cestoda origin from hermaphroditic diploid state. Parthenogenesis, as a reproductive mode, was mentioned explicitly for four species out of seven. No information is available on reproductive mode for the next species: *Caryophyllaeus laticeps*, *Isoglaridacris bulbocirrus*, and *Spirometra mansonoides.* An additional search did not reveal any information. Apart from the parthenogenetic reproductive mode, three triploid species (*A. huronensis*, *D. latus*, and *G. catostomi*) were reported to have abnormal spermatogenesis.

**Origin of triploidy**

Suggestions for the origin of triploidy are available for three triploid species out of seven. *A. huronensis* is supposed to be of a hybrid origin (allopolyploidy) with another congeneric species, *A. tenuicollis*, as a potential candidate for an ancestral role (Špakulová et al. 2019). Two other species, *D. latus* (Orosová et al. 2021) and *G. catostomi* (Grey and Mackiewicz 1980, Oros et al. 2011), are assumed to have an autopolyploid origin. We did not find any data on *C. laticeps*, *I. bulbocirrus*, *S. erinaceieuropaei*, and *S. mansonoides.*

**Other ploidies**

*A. huronensis* is found to have exclusively triploid populations with no diploid lines (Oros et al. 2011). *S. erinaceieuropaei* triploid individuals are present along with diploid individuals in the same populations (Okino et al. 2017). Similar to *C. laticeps*, where a triploid individual was found in the same location as diploid individuals (Petkeviciute and Kuperman 1992). Both diploid and triploid populations were reported for *I. bulbocirrus.* However, it is unclear whether both ploidy levels occur within the same population. *G. catostomi* and *D. latus* can exist in both diploid and triploid state (see (Grey and Mackiewicz 1980) and (Radačovská, Čisovská Bazsalovicsová, and Králová-Hromadová 2022) respectively). However, individuals of different ploidy levels do not occur within the same population.

**Phenotypic effects of triploidy**

*Spirometra erinaceieuropaei* is the only species of triploid Cestoda which may be drug resistant (Bennett et al. 2014). The authors detected amino acids in $\beta$-tubulin genes of *S. erinaceieuropaei*, identical to those that are associated with resistance to benzimidazole in another Cestoda species, *Echinococcus multilocularis* (Bennett et al. 2014). At the same time, authors did not mention ploidy of the *S. erinaceieuropaei* sample, nor have they experimentally tested this alleged resistance. No information was found on the difference between triploid tapeworms and their diploid conspecifics.

### 3.1.2 Trematoda

#### Reproduction

Five species of trematodes with reported triploidy are hermaphrodites. Two species from the Schistosomatidae family (*Schistosoma mansoni* and *Schistosomatium douthitti*) are dioecious. Parthenogenesis, as a reproductive mode, was mentioned for four species out of seven. There is no explicit information about the reproductive mode of triploid individuals for *Ichthyocotylurus platycephalus* and *S. douthitti.* In case of *I. platycephalus*, the original paper concluded triploidy based on chromosomal preparations of the intramolluscan stage of the fluke. An additional search did not show any information about the reproductive mode. Despite this, we can suggest parthenogenetic reproduction, given that this species is hermaphroditic. It is worth mentioning that for *S. mansoni* triploidy was shown only for several cells at the intramolluscan stage of the parasite. No studies were found reporting triploidy in adults.

Triploidy of *S. douthitti* was shown on miracidial and cercarial embryos with XXY (a male) and XYY (a female) karyotypes. No adult triploid individuals were checked; therefore, no information is available about their reproductive mode. However, females of *S. douthitti* are known to produce eggs parthenogenetically.

Triploid *P. westermani* reproduces parthenogenetically and has abnormal spermatogenesis. At the same time, it was shown that non-reduced eggs (3n) of triploid individuals can fuse with reduced sperm (1n) from diploid individuals (Terasaki et al. 1996) when both ploidy forms co-infect a definitive host. Such fusion leads to the origin of tetraploid individuals, supporting the hypothesis that the tetraploid form of *P. westermani* has an autopolyploid origin. This finding may indicate a possibility for triploids to reproduce sexually when there are individuals with functional sperm.

#### Origin of triploidy

Limited information is available regarding the origin of triploidy among Trematoda. The most common way appears to be autotriploidisation. For example, one study shows that triploid individuals of *S. douthitti* originate from diploid conspecifics by fusion of a reduced sperm and an unreduced egg (Short and Menzel 1959). A similar conclusion could be made for triploidy of *S. mansoni.* Triploid individuals of this species were found in a lab-maintained population that was allegedly of diploid origin. This suggests a potential autotriploidisation event where an unreduced gamete fused with a reduced gamete (Hirai and LoVerde 1989). In case of *Allocreadium fasciatusi*, triploidy is supposed to appear as a result of the fusion of an unreduced gamete with a reduced gamete within one species as well (Ramanjaneyulu and Madhavi 1984). Origin of triploidy for *P. westermani* is not entirely clear (Blair 2024). It was suggested that different triploid populations of *P. westermani* might have multiple origins, following autopolyploidisation events (Saijuntha et al. 2016).

A hybrid origin was suggested only for a triploid line referred to in the literature as *Fasciola sp.*. The genetic structure of triploid *Fasciola sp.* individuals suggests that triploidisation followed two stages. First, an initial crossing between *F. hepatica* and *F. gigantica* produces a hybrid diploid. Then, a hybrid diploid backcrosses with either of the parental species and produces a triploid hybrid (Itagaki, Hayashi, and Ohari 2022).

#### Other ploidies

*A. fasciatusi* is the only reported species of Trematoda with exclusively triploid individuals (Ramanjaneyulu and Madhavi 1984). Triploid individuals of *Fasciola hepatica* were reported from one population only, where all sampled individuals possessed a triploid set of chromosomes (Fletcher et al. 2004). Other populations of *Fasciola hepatica* seem to have only diploid individuals. A hybrid line of *Fasciola sp.* occurs in both triploid and diploid forms, which are often present in the same populations. Moreover, both ploidy forms of *Fasciola sp.* are found along with both or either parental species.

*Ichthyocotylurus platycephalus* shows two ploidy forms, diploid and triploid, originating from the same population. *Paragonimus westermani* is present in three ploidy forms: diploid, triploid, and tetraploid. All three forms can occur sympatrically, while there are also areas where only one ploidy form is present (Kim et al. 2006). Both diploid and triploid individuals are shown for *S. mansoni*, which assumes that both ploidy forms may coexist. However, triploidy was reported only in a population maintained in a laboratory for several generations. In case of *S. douthitti*, diploid and triploid forms were found among the progeny of bisexual infection by diploid individuals.

**Phenotypic effects of triploidy**

Several studies have reported differences in life history traits between diploid and triploid individuals. For example, triploid individuals of *P. westermani* develop faster that diploids (Blair 2024). In addition, it was mentioned that triploid adult individuals, their metacercariae and eggs are larger compared to diploid individuals (Blair 2022). Triploid form of *P. westermani* is also more pathogenic than diploid form (Blair et al. 1997).

Diploid *F. hepatica* is known to be resistant to several anthelmintics, such as triclabendazole (TCBZ), albendazole (ABZ), and clorsulon (CLORS). Resistant individuals of *F. hepatica* were reported for several countries from Europe and South America, as well as from Australia and New Zealand. See Fairweather et al. (2020) for a review on resistance of *F. hepatica*. At the same time, triploid individuals of *F. hepatica* were isolated from a population susceptible to TCBZ (Fletcher et al. 2004).

Resistance of *P. westermani* to TCBZ was suspected in one medical case, where two courses of treatment with TCBZ did not treat a patient infected by *P. westermani* (Kyung et al. 2011). *S. mansoni* evolves resistance to praziquantel in experimental conditions (Wang, Wang, and Liang 2012). Observations from the field show few resistant isolates, but also several endemic populations with reduced susceptibility to praziquantel (Wang, Wang, and Liang 2012). At the same time, no studies show that resistance is linked to triploidy in either of the species.

### 3.1.3 Monogenea

One species of Monogenea, *Gyrodactylus salaris*, was reported to be triploid, the first triploid species in this genus. *G. salaris* is a hermaphrodite reproducing parthenogenetically. Ziętara et al. (2006) assumed that the triploid form originated from a diploid egg fertilised by a reduced sperm, which coincided with a switch to a rainbow trout host. Their study also suggested that *G. salaris* produces diploid offspring, which revert to sexual reproduction (Ziętara, Kuusela, and Lumme 2006). Diploid offspring are potentially produced via pseudogamous parthenogenesis, which involves the activation of a diploid egg by sperm from non-selfing hermaphrodites. However, there is no transfer of genetic material from sperm.

## 3.2 Triploidy among parasitic roundworms

Among Nematoda, 15 species are found to be triploid, with 13 of them parasitic. All triploid parasitic Nematoda species are dioecious.

**Reproduction**

Diploid individuals of *Haemonchus contortus* reproduce sexually. The reproductive mode of triploid individuals is not known because triploidy was detected at a larval stage post mortem (Doyle et al. 2018). No studies show triploidy at the adult stage.

Three triploid species of plant parasites from *Heterodera* genus (*H. lespedezae*, *H. sacchari*, and *H. trifolii*) reproduce parthenogenetically (Triantaphyllou and Hirschmann 1978). However, males, while rare and without details on their ploidy, can be found in populations (Triantaphyllou and Hirschmann 1978).

Triploidy was detected in nine species of RKN, members of the *Meloidogyne* genus. All triploid RKN species are reported to reproduce via mitotic parthenogenesis, in which an egg develops without meiosis (Janssen et al. 2017). Despite reproducing via mitotic parthenogenesis, studies have shown that males are present in triploid populations of RKN species. Males are reported, among others, for *M. africana* (Janssen et al. 2017), *M. inornata* (Carneiro et al. 2008), and *M. arenaria* (Cliff and Hirschmann 1985). In the case of *M. ardenensis*, males are not only present but also appear to be sexually active, as the spermathecae of triploid females from sampled populations were filled with sperm (Janssen et al. 2017). For two triploid species, *M. hapla* and *M. javanica*, it was shown that spermatozoa are able to enter an oocyte, but without further transfer of genetic material (Janssen et al. 2017). Males were also found together with triploid females in infected roots for *M. oryzae* (Mattos et al. 2018). However, this species reproduces exclusively parthenogenetically (Besnard et al. 2019). In addition, there is some evidence for genome reshuffling in *M. oryzae*, potentially, due to a few meiotic events soon after original polyploidisation (Besnard et al. 2019).

No information on males was found for triploid *M. incognita* and *M. enterolobii* from papers selected for the systematic review. However, it is known that *M. incognita* females can reverse sex into males (Papadopoulou and Traintaphyllou 1982).

Apart from parasitic nematodes, several free-living species of the genus *Panagrolaimus* are found to be exclusively triploid and reproducing parthenogenetically (Villegas et al. 2024). Eggs of triploid *Panagrolaimus* develop without sperm, with all offspring being females (Villegas et al. 2024).

## Origin of triploidy

Triploid individuals of *Haemonchus contortus* are highly likely to originate from an autotriploidization event, as triploid larvae were detected during the experimental infection by two lines of *H. contortus* (Doyle et al. 2018). Two potential mechanisms are proposed: (1) polyspermy, when an egg is fertilised by two sperm cells, or (2) fertilisation of a non-reduced egg. At the same time, it is not clear whether triploidy is prevalent in the field and whether triploid larvae are viable and fertile after reaching maturity (Doyle et al. 2018). However, an adult triploid female of *H. contortus* has been described earlier (Bremner 1954), which suggests that triploid individuals are at least able to reach maturity.

The origin of triploid species from the genus *Meloidogyne* is still under investigation. There are data available on the potential origin of the MIG complex that includes *M. incognita*, *M. javanica*, and *M. arenaria* (Schoonmaker et al. 2020). Initially, it was suggested that *M. incognita* is a double-hybrid between the ancestor of *M. floridensis* and another unknown species. (Lunt et al. 2014). Later, however, it was shown that *M. floridensis* rather belongs to MIG group (Schoonmaker et al. 2020). While all MIG species diverged from *M. hapla* with the following radiation (Schoonmaker et al. 2020).

In one study, triploid females of *M. hapla* resulted from a cross between diploid females and tetraploid males of the same species (Triantaphyllou 1991). Triploid females were able to produce normal-sized eggs. However, most of the eggs did not hatch (Triantaphyllou 1991), which raises uncertainty about whether triploidy in *M. hapla* is stable.

One study examines the genetic relatedness of two RKN species, triploid *M. oryzae* and diploid *M. graminicola*, suggesting that *M. graminicola* is a putative parent of *M. oryzae* (Besnard et al. 2019). We did not find information on the possible origin of other triploid RKN species. There was one study claiming that *M. enterolobii* has a hybrid origin. However, the paper was retracted by the authors due to contamination of sequencing data with another species (Koutsovoulos et al. 2025).

Free-living triploid species of *Panagrolaimus* are shown to be a monophyletic group that originates from a single triploidisation event (Schiffer et al. 2019, Villegas et al. 2024).

We did not find any information about the origin of triploidy for triploid species from the *Heterodera* genus.

## Other ploidies

Six RKN species are assumed to be exclusively triploid. These species are *M. africana*, *M. ardenensis*, *M. enterolobii*, *M. inornata*, *M. oryzae*, and *M. javanica.* The last species itself is rather a hypotriploid (or paleotriploid) with 43-46 chromosomes, which does not correspond to the full triple set (Cenis 1992, Schoonmaker et al. 2020). No information is available about the exclusivity of triploidy or the presence of other ploidies for *M. incognita.*

*M. arenaria* is shown to have a hybrid origin (Schoonmaker et al. 2020). Despite this, one study describes the presence of diploid individuals in one sampled population (Cliff and Hirschmann 1985).

Two stable ploidy lines are reported for *M. hapla*, diploid, and tetraploid. Triploid individuals appear due to outcrossing between diploids and tetraploids when both lineages co-infect the same plant (Triantaphyllou 1991). While its origin is plausible, triploidy does not seem to be stable given the low viability of eggs (Triantaphyllou 1991).

For *H. contortus*, seven individuals out of 41 progeny of a single female were identified as triploid at the larval stage (Doyle et al. 2018). Ploidy for other progeny was not specified. However, diploidy can be assumed, as the authors reported only triploidy among polyploid cases (Doyle et al. 2018).

## Phenotypic effects of triploidy

*H. contortus* shows resistance to anthelmintics from different families, such as benzimidazoles, imidazothiazoles, and macrocyclic lactones (Kotze and Prichard 2016). Triploid larvae of *H. contortus* were detected after co-infection with two genetically divergent strains, one fully susceptible and one resistant (Doyle et al. 2018). However, no information is available on whether triploid individuals inherited alleles responsible for resistance in *H. contortus.* Although not related to anthelmintic resistance, it is worth mentioning that studies have reported that triploid *M. enterolobii* overcomes the Mi-1 resistance gene in breeding cultivars (Santos, Abrantes, and Maleita 2019).

## 3.3 Non parasitic triploid species

Among 100 selected papers, we found information on triploidy in 24 non-parasitic flatworms and nematodes. Non-parasitic species of flatworms with triploid individuals belong to five genera: *Dolichoplana* - one species, *Dugesia* - 15 species, *Girardia* - three species, *Polycelis* - two species, *Schmidtea* - one species. Non-parasitic triploid flatworms reproduce parthenogenetically and by fission (splitting their body into two parts). In addition, some triploid species (e.g., *Dugesia ryukyuensis*) can reproduce sexually, switching reproductive modes seasonally (Nodono and Matsumoto 2022). Another species (*Schmidtea polychroa*) can produce fertile haploid sperm (D'souza and Michiels 2008). Among Nematoda, the only non-parasitic triploid species are *Caenorhabditis elegans* and members of the *Panagrolaimus* genus. *C. elegans* is the only reported triploid Nematoda species with an androdioecious reproductive system. See SI 4 for the full list of non-parasitic triploid species.

# 4 Discussion

In our systematic review we report 28 species of parasitic worms in which triploid individuals or populations have been detected. The number of known parasitic species with triploidy makes up only a tiny fraction of the total number of estimated species within each taxonomic group of parasitic worms. For example, Cestoda includes around 5'000 known species (Scholz and Kuchta 2022), and Trematoda includes at least 18'000 species (Kostadinova and Pérez-del-Olmo 2014). There are around 3'400 species of plant-parasitic nematodes (Singh, Hodda, and Ash 2013) and up to 28'000 estimated species of vertebrate-parasitic nematodes (Carlson et al. 2020).

The small number of known triploid species among parasitic worms, relative to their total number, could be explained by two main factors. The first, and very likely one, is a sampling bias and the lack of available information. Triploidy in animals, or polyploidy in the broader context, has been investigated over the last few decades, primarily from genetic and physiological perspectives (Choleva and Janko 2013, Small, Benfey, and Crawford 2022). However, parasitic worms were rarely present in reviews discussion polyploid animals. In addition, only a few studies have addressed the evolutionary and ecological consequences of polyploidy (but see (Wertheim, Beukeboom, and Zande 2013)), especially in the context of host-parasite interactions from a parasite perspective. The most recent overview of tapeworm cytogenetics (Špakulová, Orosová, and Mackiewicz 2011) provided karyological data for 115 species of parasitic worms. However, this study does not cover most of the species, because, as authors mentioned, only up to 2% of known Cestoda species were studied karyologically (Špakulová, Orosová, and Mackiewicz 2011). From our limited observation, triploid tapeworms make up around 6% of the total number of Cestoda species for which ploidy information is available. Can we then expect to have similar ratio of triploids out of the total number of tapeworm species?

The second explanation is the actual rarity of triploidy. There is a general perception that triploid animals are either rare or that triploid lines are "evolutionary dead-ends" (Mable 2004). Their populations are thus expected to be unstable and prone to dying out within a shorter time. However, such a perception may rely on assumptions that do not always hold. For example, connected with polyploidy, parthenogenesis and the consequent accumulation of deleterious mutations (see more in the following subsections).

Below, we focus on several aspects of triploid parasitic worms, including the origin of triploidy, reproduction, comparison with diploid conspecifics, and how these factors can affect host-parasite dynamics and adaptation rates, particularly in the context of drug resistance evolution.

## 4.1 Emergence of Triploidy

Origin of triploid parasitic worms can be broadly classified into two modes: hybrid origin (allotriploidy) and non-hybrid origin (autotriploidy). In the first case, a triploid lineage arises from hybridisation between two sexual diploid species. Autotriploids are formed from a mating within one diploid species. In both cases, triploidy may result from the fusion of either two or three gametes. When two gametes are involved, one is diploid (usually an ovum), the other is haploid (usually a spermatozoon). With three gametes, a haploid egg is fertilised by two sperm. See Choleva and Janko (2013) for an informative review of the mechanisms by which triploidy arises. While mechanisms describing the origin of triploidy are academically interesting, Soltis et al. (2010) raised an important question whether the mode of origin makes any evolutionary difference. This question can be formulated even more broadly: whether there is any difference between allo- and autotriploids that their origin mode can explain.

Choleva and Janko have reviewed scenarios of polyploidisation among animals, both allo- and autopolyploidy, with many examples illustrating each scenario Choleva and Janko (2013). However, it remains unclear which type of triploidy prevails in animals. This may be partly due to the challenges in identifying pathways to polyploidy, even in recently evolved lineages (Choleva and Janko 2013). As a result, the number of autopolyploids may be underestimated (Soltis et al. 2010).

On the other hand, studies of polyploidy in plants are more prevalent. For a long time in plant polyploidy studies, there was a traditional view that autopolyploids are rare and less fit than allopolyploids (discussed in (Soltis et al. 2010)). Contrary to this, Ramsey and Schemske (1998) have estimated that the rate of autopolyploid formation among flowering plants is higher than the rate of allopolyploid formation. This finding suggested that autopolyploids appear more common than previously thought. They have also stated that triploids play an important role in the formation of tetraploids among plants through the so-called "triploidy bridge" (Ramsey and Schemske 1998). Later, a literature review by Barker et al. (2016) revealed near parity between auto- and allopolyploids within plant genera. While such results clearly contrast with the traditional view on the rarity of autopolyploids, Barker et al. (2016) have concluded that allopolyploids do have an evolutionary advantage. Such a conclusion is based on the suggestion that autopolyploid plants should outnumber allopolyploids with at least a five-fold difference (Barker et al. 2016), which is not the case. At the same time, a recent meta-analysis showed that autopolyploid plants exhibit slightly greater resistance to some pathogenic groups than diploids and allopolyploids (Hagen and Mason 2024). However, the general finding states a lack of any consistent overall differences between di- and polyploids, as well as between the two types of polyploidy (Hagen and Mason 2024).

It is hypothesised that the reproductive system of original diploid lines can predispose triploids to be formed in a particular way. For example, many flatworm species (with several exceptions among Trematoda) are hermaphrodites with the potential for self-fertilisation. This raises an important question: Can we expect more cases of triploidy among hermaphrodites? We found data on the origin of triploidy for 10 species of flatworms. Only two of them have supposedly a hybrid origin, Cestoda species *Atractolytocestus huronensis* and Trematoda *Fasciola sp.* complex. On the other hand, most triploid nematodes are found within the RKN group, which includes exclusively dioecious species. Most RKN triploid species (five out of six) show a hybrid origin, resulting from a cross between two parental species.

A recent study on the dioecy-polyploidy association among plants revealed that polyploids are rare in genera where the majority of the species are dioecious (Osterman et al. 2024). The authors even suggested a reverse relationship, in which polyploidisation in hermaphrodites favours a transition to dioecy. However, the authors considered a species as a polyploid only if its chromosome count was typical of autopolyploids (Osterman et al. 2024). This may suggest that hermaphrodites do transit to polyploids more often than dioecious plants, but only through the non-hybrid pathway. Otto and Whitton formulated a similar idea for animals. They proposed that polyploidy should be more common, among others, in taxa with hermaphroditic or asexual reproduction (Otto and Whitton 2000). Again, this suggestion considers only potential autopolyploids. Thus, it is not yet clear whether allopolyploids are more common in taxa with predominantly dioecious species.

After their emergence, triploid animals can maintain reproductive connectivity with parental species, especially in cases of hybrid origin. One example is a hybrid species of the edible frog *Pelophylax esculentus* with triploid lines. Triploid individuals are fertile and, for reproduction, rely on gametes from one of the parental species (Biriuk et al. 2016). Among all triploid worm species we found, only one case resembles such a relationship - the triploid *Fasciola sp.* complex. Molecular studies revealed a potential scenario of hybrid *Fasciola* emergence. It was suggested that triploid lines have emerged via backcrossing between initial diploid hybrids and either parental species (reviewed in (Itagaki, Hayashi, and Ohari 2022)). An experimental crossing between *F. hepatica* and *F. gigantica* indicated that the first hybrid generation is fertile and can produce viable offspring (Itagaki et al. 2011). We did not find studies reporting whether backcrossing of *Fasciola* hybrids keeps occurring in natural populations. At the same time, the experimental study suggests that a reproductive connection between triploid *Fasciola* and parental species is possible during co-infection.

## 4.2 Reproduction of Triploids

Polyploidy in animals has long been associated with parthenogenesis (Suomalainen, Saura, and Lokki 1976, Suomalainen 1950). Our findings show that the association between triploidy (a specific case of polyploidy) and parthenogenesis holds across most triploid parasitic worms. An ability to reproduce sexually (along with parthenogenesis) has been suggested only for one species from our list of triploids - *P. westermani* when a host was coinfected by diploids and triploids (Terasaki et al. 1996). Triploid individuals, when coinfected with diploids, had sperm cells in their reproductive tracts. While no sperm was observed after infections of a host with several triploid metacercaria (Terasaki et al. 1996).

Given that triploidy is associated with parthenogenesis, the difference between triploids and diploids in terms of reproduction can be explained partially by the difference between asexuals and sexuals. Exploring such a difference between asexual triploids and sexual diploids could be useful in explaining (alleged) stability of some triploid lines. For example, triploid parthenogens can benefit from reduced costs associated with sex. The classic approach states that sexual reproduction imposes a twofold cost due to either the production of males or genome dilution (Maynard Smith 1971). Thus, parthenogens are likely to avoid any costs related to the production of males (for dioecious organisms) or the development of male gonads (for hermaphrodites).

Avoiding costs can explain why several triploid hermaphroditic species have abnormal testes or non-functional sperm (e.g., *D. latus* and *A. huronensis* from Cestoda (Bruňanská, Nebesářová, and Oros 2011, Orosová et al. 2021), or *Fasciola sp.,* from Trematoda (Itagaki, Hayashi, and Ohari 2022)). When a triploid line can reproduce without sperm, male gonads play no role. Thus, there is no need to invest in male gonads. At the same time, it remains unclear to what extent costs related to the production of male gonads (or individuals) contribute to the origin or stability of triploidy. We assume that any cost reduction follows triploidisation events, without playing a primary selective factor in establishing triploid lines. A similar idea was proposed by Lundmark and Saura (2006), stating that asexuality per se did not play a primary role in the success of asexual species over sexual ones. Our assumption is also supported by a few observations from the RKN species complex, where triploid species include both females and males, despite the predominant occurrence of mitotic parthenogenesis (e.g., *M. africana* (Janssen et al. 2017)). It should be mentioned, however, that *Meloidogyne* species seem to have environmental sex determination (for example, *M. hapla* and *M. incognita*, (Eisenback and Triantaphyllou 1991, Papadopoulou and Traintaphyllou 1982)). This observation suggests that the type of sex determination should be taken into account when comparing asexual parasitic worms with sexual ones.

Apart from the direct cost related to sex, parthenogens can have an advantage over sexual populations in populations with lower density. A recent study on the prevalence of *D. latus* in Alpine lakes shows that this species is usually found as a single plerocercoid per fish, a second intermediate host (Radačovská et al. 2020). This often leads to infection of a definitive host by a single worm (Bazsalovicsová et al. 2018, Orosová et al. 2021). Under such conditions, parthenogens can reproduce without relying on mating. In general, the probability of encounters between individuals (a proxy for population density) appears to play an important role in the transition to female-dominated parthenogenetic populations. Schwander et al. (2010) have developed an analytical model to investigate the conditions under which males are lost in populations with parthenogenetic females. They found that females dominate in a population under a low encounter rate and a medium-to-high proportion of eggs that develop without fertilisation (Schwander et al. 2010). However, this model implicitly assumes that sex is determined genetically, an assumption that cannot be applied to all parasitic worms, as mentioned earlier. Thus, it might be useful to investigate the spread of parthenogenesis in a population with environmental sex determination, in which males are present and fertile.

Discussion of cost comparison between sexuals and asexuals often includes recombination as a double-edged sword. Asexual triploid parasitic worms reproduce through mitotic parthenogenesis, in which an oocyte develops without meiosis and, consequently, without recombination. On the one hand, the lack of recombination is one of the reasons why parthenogenetic lineages are considered evolutionary dead-ends (Lodé 2013). In theory, deleterious mutations accumulate in the absence of recombination. This accumulation eventually limits the long-term persistence of asexual lineages, a phenomenon known as "Muller's ratchet" (Muller 1964). Thus, alternative mechanisms might be requred to sustaining asexuality. For example, Vogt (2017) has suggested that epigenetic mechanisms can increase phenotypic diversity within genetically identical clonal lines, thereby contributing to environmental adaptation. It is not clear, however, whether asexual triploid lines adapt such a mechanism.

On the other hand, recombination is assumed to be the most general cost of sex (in the short-term perspective), because it breaks up beneficial gene combinations (Lehtonen, Jennions, and Kokko 2012, Maynard Smith 1971). When, for example, heterozygosity confers higher fitness than homozygosity, asexual lineages maintain this difference by preserving the same level of heterozygosity (assuming a negligible mutational load). In contrast, already the first generation of sexuals will experience at least 50% heterozygosity decrease (Lewis 1987).

## 4.3 Comparison Between Diploids and Triploids

Stability of triploid parasitic species, or even their expansion, relies on the competitive advantages triploidy provides compared to diploidy. In their review, Otto and Whitton (2000) proposed a useful framework for comparing polyploids with diploids, splitting all effects into two categories: phenotypic and genetic. One of the most common phenotypic effects of polyploidy is increased cell size and, consequently, increased body size (see examples in (Otto and Whitton 2000) and (Choleva and Janko 2013)). These effects were shown for one species from our review - *P. westermani.* Triploid individuals have larger eggs, metacercariae, and adult body size compared to diploids (Blair 2024). In addition, triploid individuals of *P. westermani* reach maturity in two months in infected cats and dogs, while diploid flukes develop in almost two and a half months (Habe et al. 1996). All these life-history traits (while potentially associated with increased metabolic costs (Milosavljevic et al. 2024)) may provide selective advantages for triploids in competition with diploids for the host.

Furthermore, it has been hypothesised that polyploid animals better tolerate stressful environments (Van de Peer et al. 2021). Such a hypothesis has been tested experimentally with synthetic tetraploid *C. elegans.* Chauve et al. (2025) have shown that tetraploid individuals resist cold stress better than diploid conspecifics. Tertaploid individuals also produce more offspring under cold stress compared to diploid ones (Chauve et al. 2025). Irrespective of whether abiotic stressors limit the dispersal of triploid parasitic worms, the general ability to tolerate stress can be beneficial for triploids.

Genetic effects of triploidy can also provide a selective advantage over diploids. A theoretical model of Otto and Whitton (2000) showed that newly formed polyploids have an initial advantage of masking deleterious mutations. This advantage, however, diminishes later as mutational load in a stable state correlates with ploidy level (Otto 2007). In the same model, polyploids obtained beneficial mutations more often when the population was small, and mutations had partial dominance (Otto and Whitton 2000). While this model did not provide a parasitic perspective, it may be useful to apply a similar framework for comparing host-parasite dynamics between diploids and triploids.

## 4.4 The Effect of Triploidy on Host-Parasite Interaction

One aspect of polyploidy that, to the best of our knowledge, has been addressed quite rarely is parasitism. Namely, whether polyploidy of parasites affects the host-parasite dynamic. A few theoretical models have tested the effect of ploidy on the evolution of parasitism (M'Gonigle and Otto 2011, Nuismer and Otto 2004). However, they are limited to two ploidy levels only - haploidy and diploidy. The main conclusion of the mentioned models is that parasites benefit from being haploid as it limits an array of antigens that could be detected by a host (M'Gonigle and Otto 2011, Nuismer and Otto 2004). While diploidy is favoured among hosts as it helps to recognise a broader range of antigens (M'Gonigle and Otto 2011, Nuismer and Otto 2004). Applying this framework, can we expect triploids to be more easily detected by a host than diploid conspecifics? Which host recognition models (following description of Nuismer and Otto (2004)) will better detect triploids? Which role does the type of triploidy origin play in parasite recognition?

Sexual reproduction is expected to be maintained in systems with antagonistic interactions between hosts and parasites, a notion formulated as the Red Queen Hypothesis (Hamilton, Axelrod, and Tanese 1990, Ladle 1992). The main prediction of the Red Queen Hypothesis (that hosts increase recombination rate in the presence of coevolving virulent parasites) has been supported empirically in many systems (see examples in (Gibson and Fuentes 2015)). Theoretically, similar logic applies to parasites (Galvani, Coleman, and Ferguson 2003, Salathé et al. 2008), as they experience at least an equivalent level of selective pressure. A recent empirical study even shows that asexuality is less likely to arise on parasitic lineages of Nematoda compared to free-living ones (Gibson and Fuentes 2015). Thus, we see a potential contradiction to theoretical predictions, given examples when asexual triploids either expand their host range, as in *A. huronensis* (Špakulová et al. 2019), or overcome resistance against congenerics, as in *M. enterolobii* (Poullet et al. 2025). One should also not forget that parasitic worms can be infected by hyperparasites. For example, *Pasteuria penetrans* is an obligate parasite of phytonematodes that is used as a biocontrol agent (Mohan et al. 2020). As a result, asexual triploid parasitic worms experience simultaneous selective pressure from their hosts and their hyperparasites. Such contradictions open new prospects for further theoretical studies. One direction, for example, is to investigate conditions that allow asexual triploid lines to sustain themselves without recombination under selection from two sides.

## 4.5 Triploidy and Resistance

Triploid parasitic worms pose a noticeable threat to health and economy, which could intensify as drug resistance has been reported for all class of anthelmintics (Fissiha and Kinde 2021). We found several species reported to have triploid individuals in some populations, as well as cases of drug resistance. However, no data indicate that both are linked. At the same time, given examples of successful adaptation to new hosts, we should address questions related to anthelmintic resistance. One question of particular importance is whether triploid worms evolve resistance faster than diploids. What exactly can triploidy provide for resistance to evolve faster? As Doyle et al. (2018) stated, resistance to some anthelmintics has a multigenic nature. In this case, can we suppose that a lack of recombination will lead to a faster spread of a multigenic trait after its emergence? As was mentioned before, polyploids can receive more beneficial mutations under certain conditions. Would this factor play any role in the emergence of resistance? Given the importance of some triploid parasitic worms (e.g., members of RKN species), we see here a need to investigate the effect of polyploidy on the evolution of drug resistance. Theoretical models can serve as a first step, identifying which parameters should be considered in subsequent experimental studies.

# 5 Conclusion

Polyploidy in animals has received noticeable attention with the development of, broadly speaking, molecular methods, as polyploidy has been detected in a wider selection of taxa. Thanks to this, we have a general understanding of how often polyploidy appears among animals compared to plants. In addition, several studies have reported effects of polyploidy on genomics, as well as physiological and life history traits in animals. Partially due to such substantial progress, we can identify gaps in our understanding of the general effect of polyploidy on evolutionary dynamics and formulate new questions. For example, whether there are any consequences of triploidisation of parasitic worms on the host-parasite dynamic remains an open question. This is one of the aspects of polyploidy that was not investigated thoroughly before.

With this systematic review, we addressed two main aims. First, we wanted to attract attention to a parasitic aspect of triploidy (and polyploidy in general). Despite a perception that polyploid lineages are evolutionary "dead-ends", we have shown that some triploid species can have a noticeable effect on livestock health and crop production. Second, we aimed to collect and report available information on the distribution of triploidy, its origin, the reproduction of triploid lineages, and any phenotypic effects of triploidy. We believe that this information, as well as raised questions, will motivate further studies investigating various aspects of triploidy. Such as the effects of triploidy on parasite life history, host-parasite interactions, or the evolution of anthelminthic resistance. Any potential findings from these research areas may be of both academic and practical importance.

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# Authors' Contribution

Conceptualisation: VK and BT. Literature search and screening: VK. Synthesis and writing: VK and BT

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# Conflict of Interest

Authors declare no competing interests.

# Ethical Statement

Non-applicable

Table 1: List of species of parasitic worms from two classes – Platyhelminthes and Nematoda – with reported triploidy.

| **Species Name** | **Life Stage[a]** | **Definitive Host** | **Reproductive System[b]** | **Reproductive Mode[c]** | **Origin of Triploidy[d]** | **Other Ploidies[e]** | **Chromosome Number[f]** | **Method[g]** | **Reference** |
|---|---|---|---|---|---|---|---|---|---|
| **Platyhelminthes** | | | | | | | | | |
| **Cestoda** | | | | | | | | | |
| *Atractolytocestus huronensis* | Adult | Fish | Hermaphro | Partheno | Allo | No | 24 (8) | CC | [14, 62, 82, 112, 113] |
| *Caryophyllaeus laticeps* | Adult | Fish | Hermaphro | NI[h] | NI | 2n SP | 30 (10) | CC | [89, 113] |
| *Dibothriocephalus latus* | Adult | Humans | Hermaphro | Partheno | Auto | 2n OP | 27 (9) | CC | [83, 92, 93] |
| *Glaridacris catostomi* | Adult | Fish | Hermaphro | Partheno | Auto | 2n OP | 30 (10) | CC | [36, 113] |
| *Isoglaridacris bulbocirrus* | Adult | Fish | Hermaphro | NI | NI | 2n | 30 (10) | CC | [113] |
| *Spirometra erinaceieuropaei* | Adult | Mammals | Hermaphro | Partheno | NI | 2n SP | 27 (9) | CC | [81, 113] |
| *Spirometra mansonoides* | Adult | Mammals | Hermaphro | NI | NI | NI | 27 (9) | CC | [113] |
| **Monogenea** | | | | | | | | | |
| *Gyrodactylus salaris* | Adult | Fish | Hermaphro | Pseudogamous | Auto | NI | NI | AC | [132] |
| **Trematoda** | | | | | | | | | |
| *Allocreadium fasciatusi* | Adult | Fish | Hermaphro | Partheno | Auto | NI | 21 (7) | CC | [94] |
| *Fasciola hepatica* | Adult | Mammals | Hermaphro | Partheno | Auto | 2n OP | 30 (10) | CC | [6, 26, 40] |
| *Fasciola sp.* | Adult | Mammals | Hermaphro | Partheno | Allo | 2n SP | 30 (10) | CC | [46, 48–50, 80, 117–120] |
| *Ichthyocotylurus platycephalus* | Larvae | Fish | Hermaphro | NI | NI | 2n SP | 30 (10) | CC | [114] |
| *Paragonimus westermani* | Adult | Mammals | Hermaphro | Partheno, Sex | Auto | 2n+4n SP | 33 (11) | CC | [1–3, 10, 26, 41–43, 45, 51, 55, 57, 58, 88, 100, 107, 121] |
| *Schistosoma mansoni* | Larvae | Mammals | Dioecious | NI | Auto | 2n SP | 24 (8) | CC | [44] |
| *Schistosomatium douthitti* | Larvae | Mammals | Dioecious | NI | Auto | 2n SP | 21 (7) | CC | [108] |
| **Nematoda** | | | | | | | | | |

*Continued on next page*

**(continued)**

| Species Name | Life Stage[a] | Definitive Host | Reproductive System[b] | Reproductive Mode[c] | Origin of Triploidy[d] | Other Ploidies[e] | Chromosome Number[f] | Method[g] | Reference |
|---|---|---|---|---|---|---|---|---|---|
| *Haemonchus contortus* | Larvae | Mammals | Dioecious | NI | Auto | 2n SP | 18 (6) | WGS | [24] |
| *Heterodera lespedezae* | Adult | Plants | Dioecious | Partheno | NI | NI | 27 (9) | CC | [122] |
| *Heterodera sacchari* | Adult | Plants | Dioecious | Partheno | NI | NI | 27 (9) | CC | [53] |
| *Heterodera trifolii* | Adult | Plants | Dioecious | Partheno | NI | NI | 26-35 (9) | CC | [122] |
| *Meloidogyne africana* | Adult | Plants | Dioecious | Partheno | Allo | No | 21 (9) | CC | [53] |
| *Meloidogyne ardenensis* | Adult | Plants | Dioecious | Partheno | NI | No | 51-54 (17-18) | CC | [53] |
| *Meloidogyne arenaria* | Adult | Plants | Dioecious | Partheno | Allo | 2n SP | 51-56 (17-18) | CC | [21, 53, 105] |
| *Meloidogyne enterolobii* | Adult | Plants | Dioecious | Partheno | NI | No | NI | WGS | [90] |
| *Meloidogyne hapla* | Adult | Plants | Dioecious | Partheno | Auto | 2n+4n SP | (13-17) | CC | [123] |
| *Meloidogyne incognita* | Adult | Plants | Dioecious | Partheno | Allo | NI | NI | WGS | [69, 105] |
| *Meloidogyne inornata* | Adult | Plants | Dioecious | Partheno | NI | No | 54-58 (18-19) | CC | [53] |
| *Meloidogyne javanica* | Adult | Plants | Dioecious | Partheno | Allo | No | 44 | CC | [105] |
| *Meloidogyne oryzae* | Adult | Plants | Dioecious | Partheno | Allo | No | 54 (18) | WGS | [8, 53] |

**Notes**

[a] Life stage at which triploidy was detected. Adult — triploidy was detected at the adult stage; Larvae — triploidy was reported at a larval stage in any of the intermediate hosts.

[b] Hermaphro — adult individuals are hermaphroditic; Dioecious — adult individuals are dioecious (gonochoric).

[c] Reported reproductive mode of triploids. Partheno — triploid individuals reproduce through parthenogenesis; Pseudogamous — a triploid egg is activated by sperm without incorporating sperm genetic material; Sex — a triploid egg can fuse with haploid sperm to produce a zygote.

[d] Proposed origin of triploidy. Allo — allotriploidy, the hybrid origin of triploidy; Auto — autotriploidy, triploidy origins within one diploid species.

[e] No — a species is supposed to be exclusively triploid; 2n — both triploidy and diploids are reported with no information whether both are from the same population; 2n OP — diploids are present in other populations; 2n SP — diploids are present in the same population with triploids; 2n+4n SP — diploids and tetraploids are reported in the same population with triploids.

[f] A triploid chromosome count (a haploid chromosome count).

[g] A method how triploidy was confirmed for this species. AC - allele counting; CC - chromosome count; WGS - whole-genome sequencing.

[h] NI indicates that no information was found.

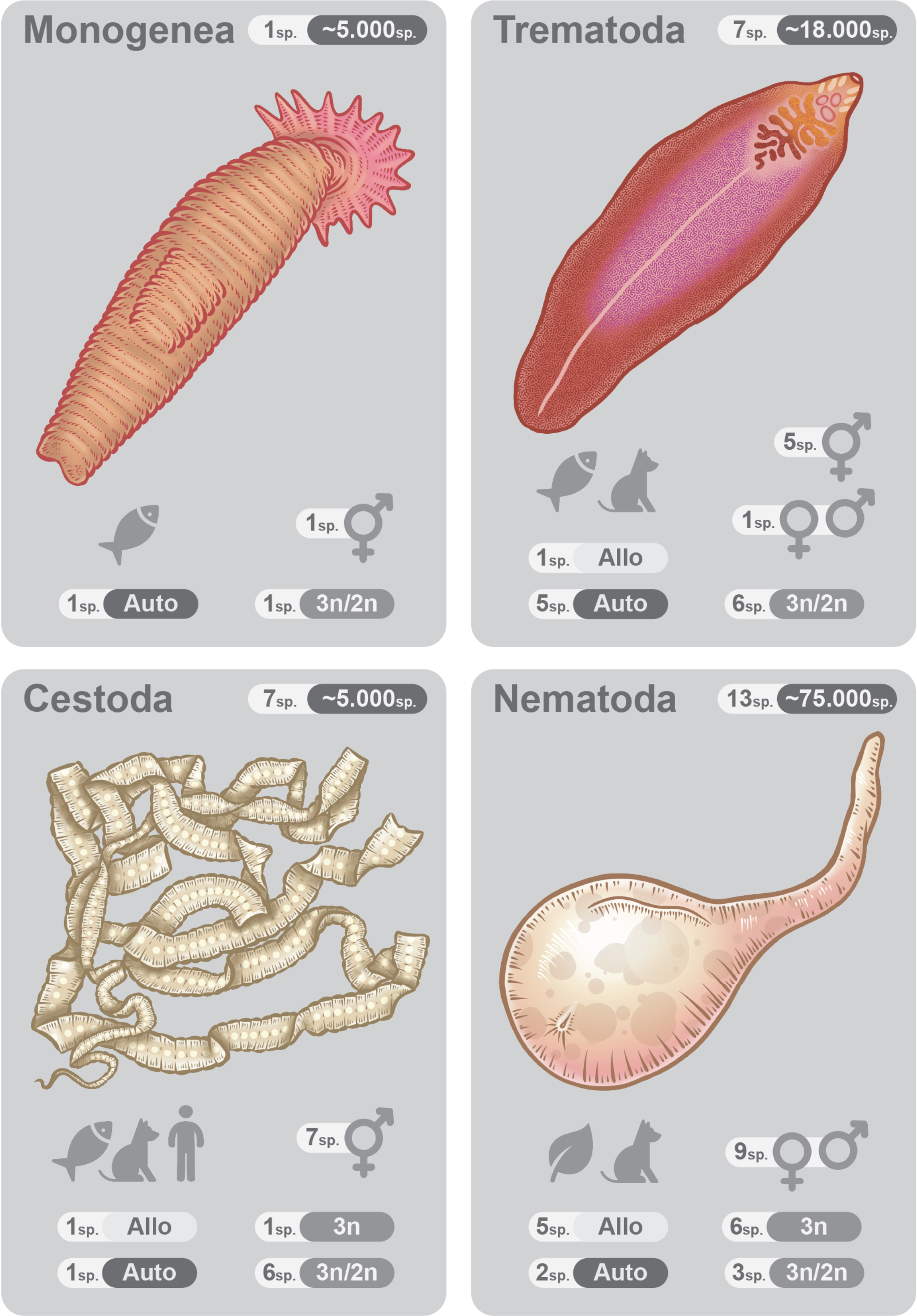

Figure 1: Summary of the main findings for each taxonomic group of parasitic worms included in the systematic review. Numbers at the top-right indicate the number of triploid species (white background) and the estimate of the total number of species. Icons at the bottom-left represent definitive hosts — fish, mammals (a dog), humans, and plants (a leaf). Auto - number of triploid species with alleged autotriploid origin. Allo - number of triploid species with alleged allotriploid origin. The hermaphrodite sign shows the number of hermaphrodite species. Venus and Mars signs show the number of dioecious species. 3n - a species is exclusively triploid. 3n/2n - both triploid and diploid populations can be found. Note that information on origin, reproductive system, and ploidy levels was available for not all triploid species.

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