

Why are there so many species of arthropods?

The great species richness within the arthropods as a group is fertile ground for discussion concerning the mechanisms that underlie speciation. Although allopatric and sympatric speciation are regularly used as explanations, they are actually too general to solve the speciation controversy. In this essay we focus on selfish elements that dwell within the arthropods and which may play important roles in diversification. We discuss the roles of *Wolbachia* and other bacteria, transposable elements, B-chromosomes, meiotic drive and Medea genes. In a table we show their abundance across taxa and species and their potential distribution within the arthropods. We also plea for more research into selfish elements and suggest a method through which more light may be shed on the role that selfish elements have played and are playing in speciation.

Entomologische berichten 62(1): 20-23.

Keywords: speciation mechanism, selfish elements, *Wolbachia*

Introduction

People have long wondered where the enormous species richness in arthropods came from. One explanation is that God must have been in an exceptionally creative mood when he designed the arthropod species, or as J.B.S. Haldane phrased it: "[God must have had] an inordinate fondness for beetles" (Hutchinson 1959). However, empirical information to test this creationism-based hypothesis is non-existing. For this we would have to rely on descriptive data coming from taxa that have evolved through selection (for more appealing details) and thoughtful drift (such as the unselective conservation of details or written narratives). Two current evolution-based hypotheses are that arthropods tend to speciate more often than other clades, or that they have lower extinction rates.

Until the early 1980's speciation was considered to be induced by geographic separation of two populations (allopatric speciation) or, more controversial, by assortative mating e.g. according to body size or shape (sympatric speciation). Given enough time for disruptive selection to do its work, viable or fertile offspring will not be produced when

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the former single species is crossed. In this view, speciation depends solely on the availability of separate niches and arthropods speciate more often because more niches are available to them. However, this niche-argument could be reversed: arthropods may occupy many niches because they are more prone to speciation.

As the reverse argument shows, the mechanisms of allopatric and sympatric speciation are too general and probably not sufficient to explain the enormous diversity within the arthropods group. Much resolution is lost when speciation is termed allopatric or sympatric, as more complex forces might have shaped the speciation event. For example, a parasitic and phytophagous lifestyle has been associated with a higher rate of speciation (Mitter et al. 1988; Dowton & Austin 1995). This association might be missed when strictly geography or assortative mating is considered.

In this essay we argue that selfish elements (SE's) may be important factors in arthropod speciation. These elements, ranging from cytoplasmic bacteria to transposable elements, dwell within the cell of an organism. They favour their own spread over their hosts and seem to persist more often in arthropods than in other clades, since they were mainly found in arthropods in the last twenty years (see also table 1). To induce speciation they must first be able to invade a population through manipulation of their hosts' reproduction such that they distort the pattern of their own transmission from Mendelian segregation. Subsequently, hybrid offspring (between 'carriers' and 'non carriers'), if produced at all, must at least suffer from reduced fitness so that differentially invaded populations become isolated. Below we describe SE's that have been discovered in arthropods and the effects they have on their host (see also Box 1).

The cytoplasmic endosymbiont *Wolbachia* is probably the best known and possibly the most widespread SE in arthropods. *Wolbachia* uses a wide variety of mechanisms to distort the hosts' reproduction, including parthenogenesis induction, male killing, feminisation and cytoplasmic incompatibility (CI; for a review see Stouthamer et al. 1999). As for all SE's, the involvement of *Wolbachia* in speciation is controversial. Recently, Bordenstein et al. (2001) showed that *Wolbachia* is the only post-mating barrier between two sister species of the parasitoid wasp *Nasonia* spec.. This indicates that *Wolbachia* may have played the pivotal role in the early days of *Nasonia* speciation. However, the two species are allopatric, which hampers assessment of the real influence of *Wolbachia* on diversification.

This summer another bacterium has raised the attention of the journal Science: a previously undescribed flavobacterium induces a haploid parthenogenetic phenotype in the mite *Brevipalpus phoenicis* (Weeks et al. 2001). Almost simultaneously a similar bacterium was discovered in a parasitoid wasp where it also induces parthenogenesis (Weeks, personal communication). This newly described bacterium is potentially widespread, especially since researchers have often looked specifically for *Wolbachia* to explain sex ratio distortions.

Transposable elements (TE's) are genetic elements that move through the genome either by a "cut and paste" mechanism or by making (multiple) copies of themselves that subsequently integrate into the hosts' genome. There are two ways in which TE's could contribute to speciation. The first is through gonadal dysgenesis; for example the P or I element in *Drosophila* causes lowered fitness in hybrids from matings between carrying and non-carrying populations (for a review see Kidwell & Lisch 1997). The second and possibly more general pathway is through the elevation of mutation rates and inversions, causing different populations to evolve faster. TE's are not only found in arthropods, they also make up a large part of the human genome and they were in fact first discovered in plants in the 1940's by Barbara McClintock. In arthropods however they seem to be very common (Robertson 1993).

Paternal Sex Ratio

The Paternal Sex Ratio (PSR) chromosome, which up to now has only been shown in *Nasonia vitripennis* and *Trichogramma kaykai*, is a B-chromosome (i.e. a supernumerary chromosome) and is transmitted to the egg through sperm. In the egg it causes the destruction of the paternal chromosomes with the exception of itself. These eggs develop as males (due to haplo-diploid sex determination). If the frequency becomes too high the population carrying it goes

Table 1. Arthropods and their selfish elements. *Geleedpotigen en hun zelfzuchtige elementen.*

selfish elements	potential abundance	taxa	species	phenotype ²	references ³
<i>Wolbachia</i> ¹	possibly 19% of all insect species according to Werren & Windsor 2000	Isopoda	<i>Armadillidium vulgare</i>	feminisation	Rigaud & Juchault 1992
		Acari	<i>Tetranychus urticae</i>	CI	Breeuwer 1997
		Hymenoptera	<i>Metaseiulus occidentalis</i>	CI	Johanowicz & Hoy 1998
			<i>Nasonia</i> sp.	CI	Breeuwer & Werren 1990
		Diptera	<i>Trichogramma</i> sp.	parthenogenesis	Schilthuisen & Stouthamer 1997
			<i>Drosophila</i> sp.	CI	Binnington & Hoffmann 1989
		Coleoptera	<i>Aedes albopictus</i>	CI	Dobson et al. 2001
			<i>Adalia bipunctata</i>	MK	Hurst et al. 1999
		Lepidoptera	<i>Acraea encedon</i>	MK	Hurst et al. 1999
			<i>Ostrinia scapularis</i>	feminisation	Fujii et al. 2001
		Thysanoptera	<i>Ephestia kuehniella</i>	CI	Sasaki & Ishikawa 1999
<i>Franklinothrips vespiformis</i>	parthenogenesis		Arakaki et al. 2001		
"New" Flavobacterium	previously overlooked, potentially widespread	Acari	<i>Brevipalpus phoenicis</i>	haploid feminisation	Weeks et al. 2001
Transposable elements	most likely all higher organisms	Hymenoptera	Parasitic wasp	parthenogenesis	Weeks, personal communication
		Most likely all arthropods		possible death or fitness decrease in hybrids carrying elements of different numbers or at different locations in the genome	Robertson 1993
PSR	too little known	Hymenoptera	<i>Nasonia vitripennis</i>	paternal chromosome destruction	Werren 1991
			<i>Trichogramma kaykai</i>	paternal chromosome destruction	Stouthamer et al. 2001
Meiotic drive	too little known	Diptera	<i>Drosophila</i> sp.	fitness decrease in <i>D. quinaria</i> hybrids	Jaenike 1996, 1999
			<i>Cyrtodiopsis dalmanni</i>	-	Presgraves et al. 1997
Medea genes	too little known		<i>Tribolium castaneum</i>	death of hybrid offspring	Beeman et al. 1992

¹ CI = cytoplasmic incompatibility; MK = male killing.

² Most references represent only one example of research into a particular selfish element.

³ Note that for *Wolbachia* only some examples are given in order to get a 'feel' for its abundance.

Box 1. Glossary

Assortative mating Mating preferences of a population or species depending on certain phenotypes.

Balancer genes Genes that suppress or counter the action of other genes, so that the net result is neutral when both are present in a genome.

Cytoplasmic incompatibility (CI) Probably the most common phenotype of *Wolbachia*. CI is expressed through crosses between infected males and uninfected females, or females infected with a different strain of *Wolbachia*. The phenotype is expressed in the progeny of the crosses and depends on the sex-determining system. In diploids the phenotype is characterized by reduced hatchability, in haplo-diploids by strong male-biased sex ratios.

Diploid Carrying two sets of homologous chromosomes. 'Normally' diploid arthropods develop from fertilized eggs.

Feminisation *Wolbachia* infected diploid males are turned into fully functional females.

Gonadal dysgenesis The incomplete differentiation of the gonad into an ovary or a testis.

Haplo-diploid Many arthropod species are composed of haploid and diploid individuals. In such a sex determination system, unfertilized eggs develop into males (haploids) and fertilized eggs develop into females (diploids).

Haploid Carrying only one set of chromosomes, as normally observed in a gamete of a diploid organism after meiosis. 'Normally' haploid arthropods develop from unfertilized eggs.

Haploid feminisation First-ever case reported by Weeks et al. (2001) of a higher organism that is fully haploid. Infected eggs develop into haploid females when eggs are cured from their selfish element (SE) through antibiotics they develop into haploid males.

Male killing A phenotype induced by *Wolbachia* where infected haploid males are killed during embryogenesis.

Parthenogenesis Diploid females producing females without mating. When the phenotype is induced by a SE, e.g. a microbial parasite, the infected organism can be cured from the parasite through high temperature rearing or antibiotics. Cured females might still produce males which, depending on the evolutionary time scale that parthenogenesis entered the species, may still be functional.

extinct. Extinction may be evaded through balancer genes in the autosomes that suppress the PSR phenotype (Beukeboom & Werren 1993). Recently, Stouthamer et al. (2001) proposed that PSR could possibly function as an opposing force of *Wolbachia* in *Trichogramma kaykai*.

Meiotic drive

During meiosis, so-called meiotic drive genes force the chromosome on which they lie to be inherited by more than half of their offspring. It is often found that drive exists between the sex chromosomes. This is normally associated with repression genes that are population specific or species specific (Jaenike 1996, 1999). Meiotic drive is therefore often discovered when crosses between different populations result in hybrid progeny having a lower fitness than either parent.

Medea genes

Maternal effect dominant embryonic arrest (Medea) genes cause loss of viability in back-crosses after hybridisation, because offspring not carrying the Medea gene cannot survive if the mother does have the gene. Medea was first discovered in the red flour beetle *Tribolium castaneum* and it has been suggested to play a role in reproductive isolation (Beeman et al. 1992).

Endnotes

Considering the literature over the last decade, it seemed to us that SE's are more frequently discovered in arthropods. However, these examples of SE's might reflect a bias of current research in arthropods and not tell us anything about the frequency in other clades. A way to substantiate our argument on the frequency of speciation would for example be to perform a sister-clade comparison as described in Mitter et al. (1988). This might tell us if having SE's makes a clade more prone to speciation. However, it is questionable whether enough data are available at this stage or whether we would be able to find genera that do not have any SE's at all, which is a prerequisite for such a comparison. A second critical point that goes for all SE's is that it has not been shown irrefutably that they can cause speciation.

In the first paragraph we joyfully referred to God and silently imagined her or him completing the Herculean task of putting on the segments and legs of a Diplopoda (millipedes). We must admit, however, that so far even scientific research has not shown the mechanisms that underlie the species richness of the arthropods.

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Samenvatting

Waarom zijn er zoveel soorten geleedpotigen?

Het grote aantal soorten binnen de geleedpotigen is vaak reden tot discussie omtrent de mechanismen die een rol spelen bij soortvorming. Soortvorming wordt vaak in twee typen onderverdeeld: allopatrische en sympatrische. Bij allopatrische soortvorming zijn twee populaties geografisch van elkaar gescheiden en door versturende selectie gaan ze genetisch van elkaar verschillen. Bij sympatrische soortvorming paren individuen selectief met elkaar omdat ze bepaalde (fenotypische) karaktertrekken in elkaar waarderen ('assortative mating'). Verschillende populaties kunnen daardoor sexueel van elkaar worden geïsoleerd terwijl ze wel in elkaars omgeving voorkomen (sympatrisch). Vaak wordt iets allopatrisch of sympatrisch genoemd terwijl de verantwoordelijke krachten voor soortvorming veel complexer zijn. Als gevolg hiervan dreigen de werkelijke patronen van soortvorming verhuld te blijven. In dit essay gaan we in op eigenzinnige elementen die in cellen van vele geleedpotigen leven en een belangrijke rol blijken te spelen bij soortvorming. Om soortvorming te genereren moet een eigenzinnig element in staat zijn de reproductie van z'n gastheer te beïnvloeden, zodat het element aan meer dan de helft van de nakomelingen wordt doorgegeven. Met andere woorden: de segregatie van het element wijkt af van de normale Mendeliaanse genetica, waarin chromosomen in een verhouding van 1:1 aan de volgende generatie worden doorgegeven. We beschrijven de rol van *Wolbachia* en een recent ontdekte bacterie, 'transposable' elementen, B-chromosomen, 'meiotic drive' en Medea-genen. In de tabel beschrijven we de potentiële verspreiding en het voorkomen van de elementen binnen taxa en soorten van de geleedpotigen. We pleiten voor meer onderzoek naar eigenzinnige elementen en stellen een methode van onderzoek voor om meer duidelijkheid te scheppen met betrekking tot eigenzinnige elementen en de rol die ze hebben gespeeld en spelen in soortvorming.