Evolution of sex-determining mechanisms in a wild population of *Armadillidium vulgare* Latr. (Crustacea, Isopoda): competition between two feminizing parasitic sex factors

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Sex determination in A, violgare may be under the control of two maternally transmitted parasitic sex factors (PSF) that reverse genetic males $\{ZZ\}$ into functional neo-females. The first PSF is a Wolbochia-like bacterium $\{F\}$ and the other $\{f\}$ is probably a sequence of the F bacterial DNA unstably integrated into the host genome. In the Niort population (France), where these two PSF are mixed, the frequency of neo-females harbouring f increased over a period of 23 years, at the expense of neo-females harbouring F. As the maternal transmission to offspring is higher for F than for f, the evolution of the F/f ratio disagrees with theoretical models involving a cytoplasmic factor. We show that an autosomal masculinizing gene $\{M\}$ allows a high rate of paternal transmission of f, which could explain the spread of this factor in the population.

Keywords: endocytobiote, masculinizing gene, maternal and paternal transmission, sex factor, sex ratio.

Introduction

Abnormal sex ratios (different from 1 d:1 V), due to sex determining mechanisms that are very different to homo-heterogamety, are known in gonochoric animals (L. D. Hurst, unpublished results). In two orders of Crustacea, parasitic sex factors (PSF) override sex factors carried by heterochromosomes. The term 'parasitic' must be understood in its broader sense, i.e. as defined by Dogiel (1964), 'organisms which use other living organism as their environment and relinquish to their host the task of regulating their relationships with the external environment'. This term has been extended to DNA sequences by Hickey (1982), in a model for the origin of sex.

In both Amphipoda Gammans duebeni and Orchestia gammarellus, PSF are related to Protozoa, and their main effect is to transform genetic males into functional neo-females (Bulnheim, 1978; Ginsburger-Vogel et al., 1980).

The most studied example of sex determination by PSF is the terrestrial Isopoda Armadillidium vulgare (pill-bug). In this crustacean, it has been shown experimentally that sex is determined by a male homogamety (ZZ) and a female heterogamety (WZ) (Juchault &

Legrand, 1972). However, in most populations, female sex is under the control of two distinct PSF, whose effects are very close (review in Juchault & Legrand, 1989). The first is a symbiotic feminizing Wolbachialike bacterium (F) carried by females (Rigaud et al., 1991b). Bacteria are located in the cytoplasm of the host cells, especially in oocytes, and are only transmitted maternally. Their main effect is to reverse genetic males (ZZ) into functional neo-females (ZZ+F), or sometimes into intersexes. These intersexes are of two types: on the one hand female intersexes (iF), which have a female physiology but possess small male external characters, and, on the other, male intersexes (iM), which are sterile and possess developed male external characters. The second PSF (named f) has the same feminizing properties and also reverses genetic males into neo-females (ZZ + f). No iF or iM intersexes are produced in progenies of such neo-females. While f is primarily maternally transmitted, paternal transmission has occasionally been observed. Moreover, a f transmission by neo-males (= ZZ + f neo-females experimentally reversed into functional males) has been reported (Legrand & Juchault, 1984). The precise nature of f remains unknown, but experimental data suggest that it might

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Evolution of Sex Determining Mechanisms James J. Bull, 1983 **Evolution of Sex Determining Mechanisms James J.** Bull, 1983 Classical sex determining mechanisms Male and female heterogamety 2 factor systems Multiple factor systems Genetics of sex development and the nature of sex factors A combinatorial enumeration of sex determining mechanisms 2 factor and multiple factor systems Evolution in multiple factor systems Evolution of the heterogametic mechanism of sex determination Polyfactorial sex determination Environmental sex determination ESD Evolution of environmental sex determination Uniparental males arrhenotoky Haplo diploidy and paternal genome loss Advantages of producing uniparental males Cytoplasmic sex determination A parental mechanism of sex determination maternal monogeny Sex chromosome evolution Characteristics of sex chromosomes extreme X Y heteromorphism Slight X Y heteromorphism and evidence of a transition Evolution of sex chromosome differences models and theory **Evolution of Sex Determining Mechanisms** James J. Bull, 1983 The Evolution of Sex Determination Leo Beukeboom, Nicolas Perrin, 2014-06-12 Sexual reproduction is a fundamental aspect of life It is defined by the occurrence of meiosis and the fusion of two gametes of different sexes or mating types Sex determination mechanisms are responsible for the sexual fate and development of sexual characteristics in an organism be it a unicellular alga a plant or an animal In many cases sex determination is genetic males and females have different alleles or different genes that specify their sexual morphology In animals this is often accompanied by chromosomal differences In other cases sex may be determined by environmental e q temperature or social variables e q the size of an organism relative to other members of its population Surprisingly sex determination mechanisms are not evolutionarily conserved but are bewilderingly diverse and appear to have had rapid turnover rates during evolution Evolutionary biologists continue to seek a solution to this conundrum What drives the surprising dynamics of such a fundamental process that always leads to the same outcome two sex types male and female The answer is complex but the ongoing genomic revolution has already greatly increased our knowledge of sex determination systems and sex chromosomes in recent years This novel book presents and synthesizes our current understanding and clearly shows that sex determination evolution will remain a dynamic field of future research The Evolution of Sex Determination is an advanced research level text suitable for graduate students and researchers in genetics developmental biology and evolution The Evolution of Sex Determination Leo W. Beukeboom, Nicolas Perrin, 2014 Sexual reproduction is a fundamental aspect of life It is defined by the occurrence of meiosis and the fusion of two gametes of different sexes or mating types Sex determination mechanisms are responsible for the sexual fate and development of sexual characteristics in an organism be it a unicellular alga a plant or an animal In many cases sex determination is genetic males and females have different alleles or different genes that specify their sexual morphology In animals this is often accompanied by chromosomal differences In other cases sex may be determined by environmental e g temperature or social variables e g the size of an organism relative to other members of its

population Surprisingly sex determination mechanisms are not evolutionarily conserved but are bewilderingly diverse and appear to have had rapid turnover rates during evolution Evolutionary biologists continue to seek a solution to this conundrum What drives the surprising dynamics of such a fundamental process that always leads to the same outcome two sex types male and female The answer is complex but the ongoing genomic revolution has already greatly increased our knowledge of sex determination systems and sex chromosomes in recent years This novel book presents and synthesizes our current understanding and clearly shows that sex determination evolution will remain a dynamic field of future research The Evolution of Sex Determination is an advanced research level text suitable for graduate students and researchers in genetics developmental biology and evolution Evolution of Sex-determining Mechanisms Irma Virginia Lagomarsino, 1990 Genetics and Biology of Sex Determination Derek J. Chadwick, Jamie A. Goode, 2002-04-26 Nature employs a wide variety of sex determining mechanisms and it is only comparatively recently that the tools have become available for these to be explored at the cellular and molecular levels A major landmark was the discovery in 1990 of the SRY gene and the subsequent demonstration of its key role in triggering male sex determination in transgenic mice This book reviews and discusses our current understanding of the molecular genetic pathways of sex determination with special emphasis on vertebrates It features comparisons with other modes of sex determination consideration of the biology of sexual development and discussion of the evolution of sex determining mechanisms By bringing together an international and interdisciplinary group of experts who study many different aspects of the problem the book highlights much new and exciting work in this area and serves to identify and stimulate promising new research directions **Theoretical Studies** on Sex Ratio Evolution Samuel Karlin, Sabin Lessard, 2020-03-31 This book deals with a key area of population genetics the ratio of the sexes in a population or the allocation of resources to male versus female reproductive function Samuel Karlin and Sabin Lessard establish the formal theoretical aspects of the evolution of sex ratio within the constraints of genetic mechanisms of sex determination Their results generalize and unify existing work on the topic strengthening previous conceptions in some cases and in other instances offering new directions of research There are two main approaches to understanding the causes and effects of sex ratio One approach focuses on the optimization and adaptive functions of sex allocation while the other emphasizes the consequences of genetic sex determination mechanisms In discussing the utility of these two approaches Professors Karlin and Lessard examine the principal sex determining mechanisms and facts involved in sex ratio representations the various genetic and environmental factors that contribute to adaptive sex expression and the evolution of sex determining systems and controls From a population genetic perspective the authors derive evolutionary properties in support of the high incidence of 1 1 sex ratio in natural populations and investigate the conditions that can explain the occurrence of biased sex ratio Genes and Mechanisms in Vertebrate Sex Determination Gerd Scherer, Michael Schmid, 2013-04-17 Following an opening chapter by the late Susumu Ohno on paralogues of sex

determining genes the five best studied genes essential for early mammalian gonadal development are portrayed in detail SF 1 and WT1 and their roles in early events in gonadal development SRY and SOX9 in testis determination and the anti testis gene DAX 1 Subsequent chapters look at the roles of these genes in sex determination in marsupial mammals birds reptiles amphibians and fish and review the different sex determining mechanisms genetic and environmental that operate in these different vertebrate classes Two insights emerge one that the same basic set of genes appears to operate during early gonadal development in all vertebrates despite the differences in mechanisms the other that sex determination in vertebrates results from a complex network of regulatory interactions and not from a simple hierarchical cascade of gene actions

Molecular-Genetic Mechanisms of Sex Determination in Animals Aleksandr F. Smirnov, A. V. Trukhina, Gender sex is a set of morphological and physiological characteristics of the organism underlying sexual reproduction the essence of which is reduced to fertilization i e the fusion of male and female gametes gametes zygote which develops into a new organism Sexual reproduction of a species is considered as one of the mechanisms of its homeostasis Thanks to this mechanism numerous species have an evolutionary advantage In the book two authors will discuss the types of genetic sex determination and differentiation mostly in multicellular animal organisms Sex determination is both genetic and environmental process the sex of an individual being established through an alternative physiological solution There are two main postulated mechanisms of sex determination genetic GSD Genetical Sex Determination and environmental ESD Environmental Sex Determination

Evolution of Sex-determining Mechanisms in Reptiles Alexander E. Ouinn, 2008 **Polyploidy and Genome Evolution** Pamela Soltis, Douglas E. Soltis, 2012-10-03 Polyploidy whole genome duplication WGD is a fundamental driver of biodiversity with significant consequences for genome structure organization and evolution Once considered a speciation process common only in plants polyploidy is now recognized to have played a major role in the structure gene content and evolution of most eukaryotic genomes In fact the diversity of eukaryotes seems closely tied to multiple WGDs Polyploidy generates new genomic interactions initially resulting in genomic and transcriptomic shock that must be resolved in a new polyploid lineage This process essentially acts as a reset button resulting in genomic changes that may ultimately promote adaptive speciation This book brings together for the first time the conceptual and theoretical underpinnings of polyploid genome evolution with syntheses of the patterns and processes of genome evolution in diverse polyploid groups Because polyploidy is most common and best studied in plants the book emphasizes plant models but recent studies of vertebrates and fungi are providing fresh perspectives on factors that allow polyploid speciation and shape polyploid genomes The emerging paradigm is that polyploidy through alterations in genome structure and gene regulation generates genetic and phenotypic novelty that manifests itself at the chromosomal physiological and organismal levels with long term ecological and evolutionary Mechanisms Driving Karyotype Evolution and Genomic Architecture Aurora Ruiz-Herrera, Marta consequences Farré-Belmonte, 2021-08-31 Understanding of the origin of species and their adaptability to new environments is one of the

main questions in biology This is fueled by the ongoing debate on species concepts and facilitated by the availability of an unprecedented large number of genomic resources Genomes are organized into chromosomes where significant variations in number and morphology are observed among species due to large scale structural variants such as inversions translocations fusions and fissions This genomic reshuffling provides in the long term new chromosomal forms on which natural selection can act upon contributing to the origin of biodiversity This book contains mainly articles reviews and an opinion piece that explore numerous aspects of genome plasticity among taxa that will help in understanding the dynamics of genome composition the evolutionary relationships between species and in the long run speciation The Princeton Guide to Evolution David A. Baum, Douglas J. Futuyma, Hopi E. Hoekstra, Richard E. Lenski, Allen J. Moore, Catherine L. Peichel, Dolph Schluter, Michael C. Whitlock, 2017-03-21 The essential one volume reference to evolution The Princeton Guide to Evolution is a comprehensive concise and authoritative reference to the major subjects and key concepts in evolutionary biology from genes to mass extinctions Edited by a distinguished team of evolutionary biologists with contributions from leading researchers the guide contains some 100 clear accurate and up to date articles on the most important topics in seven major areas phylogenetics and the history of life selection and adaptation evolutionary processes genes genomes and phenotypes speciation and macroevolution evolution of behavior society and humans and evolution and modern society Complete with more than 100 illustrations including eight pages in color glossaries of key terms suggestions for further reading on each topic and an index this is an essential volume for undergraduate and graduate students scientists in related fields and anyone else with a serious interest in evolution Explains key topics in some 100 concise and authoritative articles written by a team of leading evolutionary biologists Contains more than 100 illustrations including eight pages in color Each article includes an outline glossary bibliography and cross references Covers phylogenetics and the history of life selection and adaptation evolutionary processes genes genomes and phenotypes speciation and macroevolution evolution of behavior society and humans and evolution and modern society **Progress in Mosquito Research**, 2016-08-25 Progress in Mosquito Research provides readers with the latest interdisciplinary reviews on the topic It is an essential reference source for invertebrate physiologists neurobiologists entomologists zoologists and insect chemists with Volume 51 focusing on recent progress in mosquito research Presents a comprehensive overview of recent progress in mosquito science Written by leaders in their respective areas of mosquito research Ideal resource for invertebrate physiologists neurobiologists entomologists zoologists **Insect Symbiosis, Volume 3** Kostas Bourtzis, Thomas A. Miller, 2008-10-28 The associations and insect chemists between insects and microorganisms while pervasive and of paramount ecological importance have been relatively poorly understood The third book in this set Insect Symbiosis Volume 3 complements the previous volumes in exploring this somewhat uncharted territory Like its predecessors Volume 3 illustrates how symbiosis resear Genetics and Genomics of Cucurbitaceae Rebecca Grumet, Nurit Katzir, Jordi Garcia-Mas, 2017-10-13 This book provides an overview of the current state of knowledge of the genetics and genomics of the agriculturally important Cucurbitaceae plant family which includes crops such as watermelon melon cucumber summer and winter squashes pumpkins and gourds Recent years have resulted in tremendous increases in our knowledge of these species due to large scale genomic and transcriptomic studies and production of draft genomes for the four major species Citrullus lanatus Cucumis melo Cucumis sativus and Cucurbita spp This text examines genetic resources and structural and functional genomics for each species group and across species groups In addition it explores genomic informed understanding and commonalities in cucurbit biology with respect to vegetative growth floral development and sex expression fruit growth and development and important fruit quality traits

Encyclopedia of Genetics Eric C.R. Reeve, 2014-01-14 The Encyclopedia includes 125 entries beginning with the origins of genetics including historical background on the work of Gregor Mendel and Charles Darwin and progressing to the structure of DNA and modern theories such as selfish genes All branches of genetics are covered including the genetics of bacteria viruses insects animals and plants as well as humans Important topical issues such as the human genome project bioethics the law and genetics genetic disorders GM crops and the use of transgenic animals for food and pharmaceutical products are fully surveyed A section on techniques and biotechnology includes modern methods of analysis from DNA fingerprinting to the new science of bioinformatics The articles all written by specialists are largely non mathematical and progress from general concepts to deeper understanding Each essay is fully referenced with suggestions for further reading The text is supplemented by extensive illustrations tables and a color plate section The Encyclopedia of Genetics will be a valuable companion for all those working or studying in the various fields of genetical research and a fascinating reference for all readers with a basic background in biology Also includes color inserts Strickberger's Evolution Brian Keith Hall, Benedikt Hallgrímsson, Monroe W. Strickberger, 2014 The fifth Edition of Strickberger's Evolution is updated with the latest data and updates from the field The authors took care to carefully modify the chapter order in an effort to provide a more clear and student friendly presentation of course material The original scope and theme of this popular text remains as it continues to present an overview of prevailing evidence and theories about evolution by discussing how the world and its organisms arose and changed over time New boxed features concentrating on modern and exciting research in the field are included throughout the text New and Key Features of the Fifth Edition New Full color design and art program Maintains the student friendly engaging writing style for which it is known A reorganized chapter order provides a more clear and accessible presentation of course material Chapters on the evolution of biodiversity are now found on the text s website Access to the companion website is included with every new copy of the text New boxed features highlight new and exciting research in the field **On Epigenetics and Evolution** Carlos M. Guerrero-Bosagna, 2024-06-25 The emergence of genomic variability is a fundamental process in evolution that has been the focus of recent high profile scientific debates with a particular focus on epigenetic modifications shown to influence genomic variability Epigenetics and Evolution a new

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