THE Crafoord PRIZE

Crafoord *Days* 2023

8–11 MAY IN LUND AND STOCKHOLM, SWEDEN

PHOTO: UBC, PAUL JOSEPH

DOLPH SCHLUTER

The Crafoord *Prize* in Biosciences

Abstracts and Programme

Anna-Greta and Holger Crafoord Fund

THE FUND WAS ESTABLISHED in 1980 by a donation to the Royal Swedish Academy of Sciences from Anna-Greta and Holger Crafoord. The Crafoord Prize was awarded for the first time in 1982. The purpose of the fund is to promote basic scientific research worldwide in the following disciplines:

- Mathematics
- Astronomy
- Geosciences
- Biosciences (with particular emphasis on Ecology)
- Polyarthritis (e.g. rheumatoid arthritis)

Support to research takes the form of an international prize awarded annually to outstanding scientists and of research grants to individuals or institutions in Sweden. Both awards and grants are made according to the following order:

year 1: Mathematics and Astronomy
year 2: Geosciences
year 3: Biosciences (with particular emphasis on Ecology)
year 4: Mathematics and Astronomy
etc.

The Prize in Polyarthritis is awarded only when the Academy's Class for medical sciences has shown that scientific progress in this field has been such that an award is justified.

Part of the fund is reserved for appropriate research projects at the Academy's institutes. The Crafoord Prize presently amounts to 6 million Swedish krona.

The Crafoord Prize is awarded in partnership between the Royal Swedish Academy of Sciences and the Crafoord Foundation in Lund. The Academy is responsible for selecting the Crafoord Laureates.

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The Crafoord Laureate in Biosciences 2023

PHOTO: UBC, PAUL JOSEPH

DOLPH SCHLUTER

Dolph Schluter, University of British Columbia, Canada,
"for fundamental contributions to the understanding of adaptive radiation and ecological speciation".

The Crafoord *Prize* in Biosciences 2023

Studies of how new species arise are rewarded with the Crafoord Prize

It all started on the Galapagos Islands; under the supervision of Rosemary and Peter Grant, **Dolph Schluter** studied the same type of finches that had interested Charles Darwin in the 1830s. Originally, this interest focused on a species of finch that had migrated from South America. Once the birds had adapted to the islands' various habitats, they diversified into more than a dozen different species, due to a process called adaptive radiation.

The main differences between the finches were their beaks. Surprisingly, Dolph Schluter also found that two species that lived on the same island sometimes displayed greater variation in beak size and shape than between the same two species living on different islands. Beak size and shape played a decisive role in the types of seeds the birds ate, so individuals that no longer needed to compete for the same food source had greater chances of surviving and breeding.

Ecological speciation is the name given to the evolution of species through natural selection, rather than by accumulation of chance mutations. Dolph Schluter asked whether this process could be repeated in other species in similar circumstances. To find the answer, he decided to look more closely at a small fish, the stickleback, which lives in the ocean, but also migrates up to freshwater lakes in British Columbia, Canada, among other places.

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And yes, the same thing happened over and over again in several different lake systems. The sticklebacks adapted to the freshwater environment and acquired different traits to those they had in a marine environment. Gradually, differences arose between the sticklebacks in the same lake, with some living at the bottom while others explored the free water mass. After generations of adaptation to their different habitats, their differences were so great that the two types no longer mated.

Dolph Schluter continued introducing marine sticklebacks to freshwater ponds, so that he and his colleagues could, in real time and in detail, track the genetic changes in the fish. Natural selection means that the fish with traits that are important for their survival are more likely to reproduce.

ABSTRACTS

Crafoord *Days* 2023

The evolution of phenotypic incompatibilities during speciation

CRAFOORD LAUREATE **DOLPH SCHLUTER**, UNIVERSITY OF BRITISH COLUMBIA, CANADA

What are the genes that underlie the origin of species? Dobzhansky questioned whether reproductive isolation accumulated via changes at genes underlying ordinary phenotypic differences between the species, or whether it evolved via a separate category of genetic changes evolving under special conditions. Since then, mapped genes underlying hybrid incompatibilities between species have often been found to be unrelated to phenotypic differences between species. Instead, we used stickleback to investigate how phenotypic differences between species lead to reduced hybrid fitness, and attempt to estimate the contributions of their underlying genes to reproductive isolation. In contrast to directly mapped genes, the fitness effect of the genes underlying hybrid phenotypic incompatibilities depend on the ecological environment. Surprisingly, most genetic differences predate the origin of modern stickleback species.

"Mate first, ask questions later": On the process of speciation in the Fungi

HANNA JOHANNESSON, THE ROYAL SWEDISH ACADEMY OF SCIENCES, SWEDEN

Speciation is one of the most fundamental processes of biology, being the force by which biodiversity is generated. Recent estimates, based on high-throughput sequencing methods, suggest that as many as 5.1 million fungal species exist. Understanding the speciation process in this highly diverse group of organisms is of both fundamental and applied importance – as fungi includes agricultural pathogens, emerging human diseases, and are important for industry and biotechnology. Just as in all sexual eukaryotes, the life cycle of a sexually reproducing fungus includes the alternation between a haploid and a diploid phase: the haploid phase ends with nuclear fusion, and the diploid returns to haploidy by meiosis. A specific feature of sexual reproduction in fungi is, however, that there is an extended phase between cell fusion (i.e. mating) and nuclear fusion. In this phase of the life cycle, the fungus discriminates self from non-self; a universal trait necessary for fundamental processes such as multicellular growth, detection of pathogens and choice of mating partners. Hence, the fungi mate first and ask questions later. In my talk, I will go through recent advances in the study of fungal speciation, and also specifically highlight recent work from our group suggesting that pleiotropic effects of recognition of vegetative and sexual compatibility can result in speciation in fungi.

Parallel speciation and the role of chromosomal rearrangements

KERSTIN JOHANNESSON, UNIVERSITY OF GOTHENBURG, SWEDEN

When evolution repeatedly causes the evolution of similar adaptations either in parallel from the same starting conditions, or by convergence from different starting conditions, this strongly suggests that natural selection is the main driver. Under divergent selection, gene flow can still oppose local adaptation by swamping a locally adapted population by introducing suboptimal genetic variation from another area that breaks down locally adapted gene complexes. However, the architecture of the genome can prevent this, for example, by favouring chromosomal rearrangements such as inversions (flipped parts of the chromosome).

In species of marine snails that live in a highly heterogeneous shore environment formation of locally adapted morphs (ecotypes) show how chromosomal inversions create internal barriers to genetic exchange between ecotype and support local adaptation on extremely small geographic scales. The studies me and colleagues have done on the west coast of Sweden, in UK and in Spain show that in the snail species *Littorina saxatilis* the same inversions are shared among geographically separated areas and contain genes coding for traits that are involved in parallel evolution of different ecotypes that are partially, or more or less completely, reproductively isolated. Some inversions are more involved in local adaptation along an environmental gradient from crab predation to heavy wave action favouring thick shells in one end and thin shells and large foot in the other end, while other inversions are responsible for adaptation over a low-shore vs high-shore environmental axis of temperature and dessicational stress.

Overall, this system shows interesting interactions between ecological and evolutionary factors shaping local adaptation, reproductive isolation and, eventually, speciation.

Parallelism and persistence during stickleback divergence

ANDREW MACCOLL, UNIVERSITY OF NOTTINGHAM, UK

Evolutionary parallelism, the occurrence of similar phenotypes in separate populations experiencing similar environments, is a striking phenomenon that provides strong evidence of the workings of natural selection. It has commonly been assumed to result from *in situ* adaptation. However, parallelism can evolve in different ways. For example, phenotypes might evolve repeatedly, completely *de novo* or from reassembly of standing genetic variation from a shared common ancestor. In contrast, phenotypes might evolve only once, but persist within lineages that disperse from their place of origin to locations where they are well-suited to the environment. These alternatives are especially hard to discern when different phenotypes co-occur geographically, because gene flow between them might tend to erase the genetic signal of their ancestry. The persistence of differences between divergent lineages, even in the face of gene flow, has sometimes been overlooked, when considering examples of parallelism, in favour of the assumption that divergence evolves *in situ*. Here I examine the extent of parallelism in the adaptive radiation of three-spined stickleback. At an intercontinental scale there is limited, but significant parallelism. At more local scales parallelism increases, but so too does evidence that this is driven by the large scale dispersal of lineages. In British Columbia, genomic and geological evidence suggests benthic stickleback may have a single origin. In the Atlantic, two contrasting ecotypes are found sympatrically in several, different, saltwater locations. Genomic data suggest that these arose as a long-distance dispersal of divergent lineages from allopatric glacial refugia. The ecotypes appear to have different adaptive proclivities. The persistence of lineages as suites of coadapted traits maintained by strong selection may have important consequences for evolution and speciation that are sometimes forgotten.

The causes and consequences of parallel speciation in plants

DANIEL ORTIZ-BARRIENTOS, UNIVERSITY OF QUEENSLAND, AUSTRALIA

In the natural world, we often observe repeated patterns where unrelated species independently evolve similar traits. This includes the uncanny similarity of wing patterns found in different butterfly species and the widespread occurrence of similar Mediterranean plant communities. Determinism plays a critical role in shaping the course of evolution. In this talk, I explore the concept of replicated speciation in plants, where natural selection drives the emergence of populations that can adapt to new environments by sacrificing their ability to interbreed with their ancestors but not with each other. Unlike animals, plants seem to undergo speciation between populations with replicated phenotypes using different molecular mechanisms. This suggests a fundamental difference in how traits evolve in sessile versus mobile organisms and highlights how natural selection gives rise to new species on our planet.

Genetics and the origin of stickleback species

CATHERINE PEICHEL, UNIVERSITY OF BERN, SWITZERLAND

Since the time of Darwin, much progress has been made in understanding the ecological and evolutionary forces that lead to the formation of new species. However, understanding the genetic basis of speciation has been impeded by the fact that species are, by definition, reproductively isolated from each other. To circumvent this issue, it is possible to study very young pairs of species, in which reproductive isolation is not yet complete. Threespine sticklebacks (*Gasterosteus aculeatus*) are a particularly compelling model system for genetic studies of the early stages of speciation, as pairs of stickleback populations have adapted to divergent, but overlapping habitats. These "species pairs" are morphologically and behaviorally distinct from each other and exhibit reproductive isolation in the wild. Most of the isolating barriers between them are behavioral or environmentally dependent, and these species pairs can be crossed in the lab to generate viable and fertile hybrids, enabling genetic studies of the phenotypic traits that contribute to reproductive isolation. I will discuss our genetic mapping studies of different isolating barriers between stickleback species pairs, which have provided surprising insights into the genetic architecture that underlies the formation of new species.

Hybrid speciation and genome stabilization in Passer sparrows

ANNA RUNEMARK, LUND UNIVERSITY, SWEDEN

Sequencing of entire genomes from closely related species has shown that phylogenetic trees are more reticulated than previously thought. Hybridization is now recognized as an important evolutionary force, providing new combinations that selection can act on, facilitating adaptation. When divergent lineages hybridize, incompatible combinations of alleles that have developed in these different lineages may result in low fitness in the individuals carrying them. How hybrid genomes are purged of such low fitness combinations and stabilize, and how the novel phenotypes that are visible to selection arise are two key challenges to address to understand hybridization derived novel variation. We use repeated hybridization events between house sparrows *Passer domesticus* and Spanish sparrows *P. hispaniolensis* on four Mediterranean islands, resulting in four lineages of the hybrid Italian sparrow *P. italiae* to address these questions. We show that island populations on Crete, Corsica, Sicily and Malta have different genomic compositions, ranging from 25 per cent to 75 per cent house sparrow contribution. We use this variation to identify alleles that are consistently fixed for one of the parental species. We uncover a highly significant enrichment of house sparrow mitonuclear sites and DNA-repair alleles. This is consistent with prior evidence suggesting that mitonuclear incompatibilities are important for reproductive isolation between these *Passer* taxa. Finally, recent research has suggested that combinations of divergent regulatory elements may result in novel patterns of gene expression in hybrids. We test this hypothesis through comparing patterns of gene expression in the gonads of the hybrid Italian sparrow to that of the parental species, and find that gene expression is highly transgressive in testis but not ovary. In our current research, we address if transgressive sorting of regulatory elements could be key for understanding how phenotypic novelty may arise from hybridization.

PROGRAMME

Crafoord *Days* 2023

Detailed programme

THE CRAFOORD PRIZE LECTURE IN BIOSCIENCES 2023

The Crafoord *Prize* Lecture in Biosciences

10:30
LUX, HELGONAVÄGEN 3, LUND

Open to the public and free of charge. Seating is limited.
For registration and further information visit:
www.kva.se/crafoordprizelecture2023

Monday 8 May

10:30	Registration and coffee	
11:00	Presentation of the Crafoord *Prize* and the Crafoord Laureate	Ove Eriksson, Chair of the Crafoord Prize Committee in Biosciences, the Royal Swedish Academy of Sciences
11:10	*The Origin of Modern Species*	CRAFOORD LAUREATE 2023 Dolph Schluter, University of British Columbia, Canada
11:45	Questions from the audience	
12:00	LUNCH	Lunch is served outside the lecture hall and is included for registered participants

Detailed programme

THE CRAFOORD PRIZE SYMPOSIUM IN BIOSCIENCES 2023

How do species originate?

09:00

BEIJERSALEN,
THE ROYAL SWEDISH ACADEMY OF SCIENCES,
LILLA FRESCATIVÄGEN 4A, STOCKHOLM

Open to the public and free of charge. Seating is limited.
For registration and further information visit:
www.kva.se/crafoordprizesymposium2023

Wednesday 10 May

09:00	Registration	
	MORNING SESSION	CHAIR: **Siv Andersson**, Member of the Crafoord Prize Committee in Biosciences
09:20	Opening address	**Hans Ellegren**, Secretary General, the Royal Swedish Academy of Sciences
09:25	Introduction of the Crafoord Laureate	**Ove Eriksson**, Chair of the Crafoord Prize Committee in Biosciences
09:30	*The evolution of phenotypic incompatibilities during speciation*	**CRAFOORD LAUREATE 2023** **Dolph Schluter**, University of British Columbia, Canada
10:20	COFFEE BREAK	
10:40	*Genetics and the origin of stickleback species*	**Catherine Peichel**, University of Bern, Switzerland
11:20	*Parallelism and persistence during stickleback divergence*	**Andrew MacColl**, University of Nottingham, UK
12:00	LUNCH	(Included for registered participants)
	AFTERNOON SESSION	CHAIR: **Sören Nylin**, Member of the Royal Swedish Academy of Sciences
13:20	*Parallel speciation and the role of chromosomal rearrangements*	**Kerstin Johannesson**, University of Gothenburg, Sweden
14:00	*The causes and consequences of parallel speciation in plants*	**Daniel Ortiz-Barrientos**, University of Queensland, Australia
14:40	COFFEE BREAK	
15:10	*"Mate first, ask questions later": On the process of speciation in the Fungi*	**Hanna Johannesson**, The Royal Swedish Academy of Sciences, Sweden
15:50	*Hybrid speciation and genome stabilization in Passer sparrows*	**Anna Runemark**, Lund University, Sweden
16:30	Closing remarks	**Ove Eriksson**, Chair of the Crafoord Prize Committee in Biosciences

Anna-Greta and Holger Crafoord

HOLGER AND ANNA-GRETA CRAFOORD

Holger Crafoord (1908–1982) was prominent in Swedish industry and commerce. He began his career with AB Åkerlund & Rausing and devoted a larger part of his working life to this company. In 1964, Holger Crafoord founded Gambro AB in Lund, Sweden, where the technique of manufacturing the artificial kidney was developed. This remarkable dialyser soon became world famous. Since then, a series of medical instruments has been introduced on the world market by Gambro.

In 1980, Holger Crafoord founded the Crafoord Foundation, which annually contributes greatly to the Anna-Greta and Holger Crafoord Fund.

Holger Crafoord became an honorary doctor of economics in 1972 and in 1976 an honorary doctor of medicine at Lund University.

Anna-Greta Crafoord (1914–1994) took, as Holger Crafoord's wife, part in the development of Gambro AB. Through generous donations and a strong commitment in the society around her, she contributed to the scientific and cultural life. In 1986 she founded the Anna-Greta Crafoord foundation for rheumatological research and in 1987 Anna-Greta Crafoord became an honorary doctor of medicine at Lund University.

Over the years, the Crafoords have furthered both science and culture in many ways and it is noteworthy that research in the natural sciences has received an important measure of support from the Anna-Greta and Holger Crafoord Fund.

THE ROYAL SWEDISH ACADEMY OF SCIENCES was founded in 1739 and is an independent non-governmental organisation, whose overall objective is to promote the sciences and strengthen their influence in society. The Academy has a particular responsibility for natural science and mathematics, but its work strives to increase interaction between different disciplines. The activities of the Royal Swedish Academy of Sciences primarily focus on:

- being a voice of science in society and influencing research policy (policy for science)
- providing a scientific basis for public debate and decision-making (science for policy)
- recognizing outstanding contributions to research
- being a meeting place for science, within and across subject boundaries
- providing support for young researchers
- stimulating interest in mathematics and natural science in school
- disseminating knowledge to the public
- mediating international scientific contacts
- preserving scientific heritage

THE ACADEMY has around 480 Swedish and 175 foreign members who are active in classes, committees and working groups. They initiate enquiries, consultation documents, conferences and seminars. The Academy has General Meetings a number of times each year.

THE ACADEMY´S institutes offer unique research environments in ecological economics, botany, the history of science and mathematics.

Every year, the Academy awards a number of prizes and rewards. The best known are the Nobel Prizes in Physics and Chemistry and the Sveriges Riksbank Prize in Economic Science in Memory of Alfred Nobel (the Prize in Economic Sciences). Other major prizes are the Crafoord Prize, Sjöberg Prize, Göran Gustafsson Prizes, Söderberg Prize and the Tobias Prize. The Göran Gustafsson Prizes are awarded to outstanding young researchers and are a combination of a personal prize and research funding. Since 2012, the Academy of Sciences has been one of the academies involved in implementing the Wallenberg Academy Fellows career programme, which provide long-term funding to the most promising young researchers. As well as a comprehensive range of scholarships, the Academy is also involved in appointments to research posts in a number of programmes funded by external foundations.

Through its working groups and committees, the Academy also works to promote sustainable, science-based societal development in the area of energy and the environment, among others. Issues relating to education and conditions for teachers are another major interest. The Academy regularly organises lectures and workshops on various scientific topics for teachers and students. In the 1990s, the Academy and the Royal Swedish Academy of Engineering Sciences founded one of Sweden's biggest school development programmes, NTA – Naturvetenskap och teknik för alla (Science and Technology for all).

THE CRAFOORD PRIZE IS AWARDED IN PARTNERSHIP BETWEEN THE ROYAL SWEDISH ACADEMY OF SCIENCES AND THE CRAFOORD FOUN- DATION IN LUND. THE ACADEMY IS RESPONSIBLE FOR SELECTING THE CRAFOORD LAUREATES

WWW.CRAFOORDPRIZE.SE

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