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# Crafoord Days 2015

5–7 MAY IN STOCKHOLM AND LUND, SWEDEN



## The Crafoord Prize in Biosciences 2015

## Abstracts

## Programmes



RICHARD LEWONTIN AND TOMOKO OHTA CRAFOORD LAUREATS IN BIOSCIENCES 2015

## 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 SEK 6 million.

The Crafoord Prize is awarded by the Royal Swedish Academy of Sciences.

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## The Crafoord Laurates in Biosciences 2015



RICHARD LEWONTIN, HARVARD UNIVERSITY, CAMBRIDGE, MA, USA

TOMOKO OHTA, NATIONAL INSTITUTE OF GENETICS, MISHIMA, JAPAN

Richard Lewontin, US citizen. Born 1929 in New York, USA. Ph.D. 1954 from Columbia University, NY, USA. Emeritus Professor at Harvard University, MA, USA and Tomoko Ohta, Japanese citizen. Born 1933 in Miyoshi, Japan. Ph.D. 1967 from North Carolina State University, NC, USA. Emeritus Professor at the National Institute of Genetics, Mishima, Japan. "for their pioneering analyses and fundamental contributions to the understanding of genetic polymorphism".



#### INTRODUCTION TO THE CRAFOORD PRIZE IN BIOSCIENCES 2015

## Understanding genetic variation of populations

Nowadays, it may seem obvious that our genetic makeup is as unique as our fingerprints, but this was a startling contradiction to the prevailing theories when it was discovered in the 1960s. This new understanding, and the new theories it gave rise to, have provided science with a more accurate picture of genetic variation and natural selection. Crucial contributions to this body of knowledge were generated by this year's Crafoord Laureates, **Richard Lewontin** and **Tomoko Ohta**.



Anyone who has watched forensic experts in television series, hunting for traces of DNA, knows that each individual has his or her own unique set of genes. If our DNA wasn't as unique as our fingerprints, genetic traces could never be used to link a murderer to a crime.

However, until the 1960s, the view of genetic variation was entirely different: biologists believed that most individuals in a population were fairly similar, genetically speaking. This must, they assumed, be the result of natural selection, where every genetic variant that was less beneficial was eliminated.

This was why Richard Lewontin's discovery of the actual situation, made when he was working at the University of Chicago in the 1960s, was so revolutionary. Lewontin used a method that separated proteins based on their molecular characteristics, obtaining very surprising results: the genetic variation between individuals in a population was many times greater than expected.



#### INTRODUCTION TO THE CRAFOORD PRIZE IN BIOSCIENCES 2015

The results were published in *Genetics* in 1966 and aroused a great deal of attention. The first analysis used fruit flies, but the pattern was repeated in every species that the researchers examined: they all demonstrated a significant and unexpected genetic variation, appearing to contradict the principles of natural selection.

A theory of neutral mutations was put forward, in which gene variants that neither improve nor worsen an individual's fitness are created. This theory seemed to explain the significant variation discovered by the researchers. However, geneticist Tomoko Ohta from the National Institute of Genetics in Japan, believed that such a simple division into three types of mutations - good, neutral and harmful – did not reflect reality's true complexity. In actual fact, almost all mutations in genes that affect the encoded proteins are somewhat harmful, but the effect of this is so small that these gene variants can remain in the population. They can thus be considered nearly neutral. Ohta also showed that the size of a population is decisive for the effectiveness of natural selection: the smaller the population, the greater the effect of chance, and natural selection will function more poorly. Ohta presented this theory in the scientific journal Nature in 1973.

After these early and revolutionary publications, both Lewontin and Ohta have continued to study genetic variation and have, over a number of decades, made sizable contributions to the continuing development of knowledge in the field. Richard Lewontin and Tomoko Ohta are awarded the Crafoord Prize for basic research of great general significance. However, it is also possible to provide reallife examples of the applied knowledge of genetic variation:

- In ecology and conservation, it has led to a better understanding of population structure and genetic vulnerability among threatened populations. Another result has been new methods for estimating the size of natural populations using the DNA analysis of animal spoor, such as scat.
- In systematic biology, knowledge of genetic variation has resulted in new opportunities for understanding relationships between and within species.
- Thanks to knowledge of genetic variation, it is now possible to determine close relationships between individuals using DNA analysis. This has had a great impact on evolutionary ecology, such as its use in paternity analyses. It has been shown that in many species the females mate with more than one male, so that the offspring in one litter are often half-siblings.
- Additionally, knowledge of genetic variation has naturally been very important in the field of medicine. It lays the foundation for the extensive research being conducted into genetic risk factors for various diseases, but also for the increased focus on individuallyadapted treatments on the basis on the patient's genetics.

## ABSTRACTS Crafoord Days 2015

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#### ABSTRACTS

### Genotype to phenotype link and near-neutrality in evolution

TOMOKO OHTA, CRAFOORD LAUREATE, NATIONAL INSTITUTE OF GENETICS, MISHIMA, JAPAN

Incorporation of recent knowledge on genomics and epigenetics into evolutionary theory is needed. Prevalence of nearly neutral changes in protein evolution has now gained much support. Here recent progress on dynamics of protein structure and function is presented in relation to epigenetics, and how such dynamics is connected to the nearly neutral evolution and to phenotypic changes is discussed. Another subject is the gene expression diversity. For organismal development, particularly for morphological changes, modification of gene regulatory systems is important. In these systems, not only transcription factor-DNA binding for gene expression, but also numerous interacting processes such as DNA methylation and histone modifications work. Phenotype reflects all such mechanisms and resulting systems are often robust and plastic. Here selforganizing property may also be important. Effects of individual mutations are often very small and become nearly neutral.

- Ohta, T. (1973) Slightly deleterious mutant substitutions in evolution. Nature 2246,96–98.
- Ohta, T. (2002) Near-neutrality in evolution of genes and gene regulation. Proc Natl Acad Sci USA 99, 16134–16137.
- Ohta, T. (2011) Near-neutrality, robustness and epigenetics. Genome Biol Evol 3, 1034–1038.

#### ABSTRACTS

### Why population genetics is so important in modern biology

DEBORAH CHARLESWORTH, UNIVERSITY OF EDINBURGH, UK

Evolution consists of changes in the genetic make-up of populations and species. During the evolution of an inter-species difference, genetic variants must spread within species, and these changes are the focus of population genetics. For many years, theoretical work was far ahead of biologists' ability to integrate it with empirical data. Its value was not widely appreciated in biology, despite the development of understanding of selected and neutral variants, random mating and structured populations, and of the effects of genetic linkage, and of variants that are closely enough linked in genomes that associations exist between them. When molecular variability was discovered, this quantitative understanding quickly led to molecular evolutionary tools with applications throughout biology. Biologists interested in organismal functions can use the approach of combining inter-species difference data with data on variability within species, to recognise conserved versus changed DNA sequences and infer likely functional sequences, and estimate how much the differences between species were changes favoured by natural selection, versus changes that natural selection failed to prevent. Candidates for genes under recent or current selection can be detected (Ferrer-Admetlla et al., 2014), including ones of interest to ecologists that suggest adaptation to local environmental

differences (Beaumont & Balding, 2004). Associations between variants (Slatkin, 2008) are used to genetically map mutations casing human diseases and variants affecting other characteristics in humans and other organisms, including pathogens, and plant and animal breeders us them to predict responses to selection (Donnelly, 2008). With molecular markers, renewed study is possible of interesting, but previously inaccessible, evolutionary questions. I will outline examples of productive crossfertilisation and information flow between functional and molecular evolutionary research in today's biology.

Beaumont MA, Balding DJ. 2004. Identifying adaptive genetic divergence among populations from genome scans. Molecular Ecology 13: 969–980.

Donnelly P. 2008. Progress and challenges in genome-wide association studies in humans. Nature 456: 728–731.

Ferrer-Admetlla A, Liang M, Korneliussen T, Nielsen R. 2014. On detecting incomplete soft or hard selective sweeps using haplotype structure. Molecular Biology and Evolution 31: 1275–1291.

Slatkin M. 2008. Linkage disequilibrium — understanding the evolutionary past and mapping the medical future. Nature Reviews Genetics 9: 477.

## *From mutation to macroevolution: connecting genetic variation to the generation of biodiversity*

LINDELL BROMHAM, AUSTRALIAN NATIONAL UNIVERSITY, CANBERRA, AUSTRALIA

A new view is emerging of the interplay between mutation at the genomic level, substitution at the population level, and diversification at the lineage level1. Traditionally, these aspects of the evolutionary process have been the focus of different biological disciplines, with geneticists and biochemists investigating mutation, population biologists and ecologists studying population level processes, and palaeontologists and systematists revealing patterns of biodiversity. But molecular phylogenetic analysis offers the chance to examine all of these levels in the same comparative framework2. These analyses reveal that species characteristics can shape mutation rates, population size can drive different rates of genomic evolution, and rate of genomic change can influence the generation of biodiversity3, 4. Molecular phylogenetic analyses link change at the genomic level to species characteristics and biodiversity generation, highlighting the continuity of processes of mutation (generation of variation), microevolution (population divergence) and macroevolution (lineage diversification).

- Bromham L, Hua X, Lanfear R, Cowman P (2015) Exploring the relationships between mutation rates, life history, genome size, environment and species richness in flowering plants. Am Nat http://www.jstor.org/ stable/10.1086/680052.
- Bromham L (2009) Why do species vary in their rate of molecular evolution? Biol Lett 5:401-4.
- Bromham L (2011) The genome as a life-history character: why rate of molecular evolution varies between mammal species. Phil Trans Roy Soc B 366(1577):2503-13.
- Lanfear R, Ho SYW, Love D, Bromham L (2010) Mutation rate influences diversification rate in birds. Proc natl Acad Sci USA 107(47):20423-8.

## The use of genetic variation to conserve natural populations: From allozymes to genomes

FRED ALLENDORF, UNIVERSITY OF MONTANA, MISSOULA, MT, USA

The detection of molecular genetic variation in natural populations began with two pioneering papers in 1966 (Harris 1966; Hubby and Lewontin 1966). By 1984, the amount and distribution of genetic variation had been described in over 1,100 species, ranging from E. coli to blue whales using enzyme electrophoresis (Nevo et al. 1984). Understanding the relative amount and distribution of genetic variation within species is fundamentally important information in designing management plans to preserve species. In the short time since then, we have gone from describing genetic variation at a few tens of enzyme loci to the sequencing of complete genomes of individuals in wild species. Today the application of genomics has come to play an important role in conservation. For example, the description of genome wide patterns of homozygosity has allowed the estimation of individual inbreeding coefficients and the detection of inbreeding depression as never before possible. I will present an overview of the current applications of genetics and genomics to conservation of species and ecosystems (Allendorf et al. 2010).

- Allendorf, F. W., P. A. Hohenlohe, and G. Luikart. 2010. Genomics and the future of conservation genetics. Nature Reviews Genetics 11:697–709.
- Harris, H. 1966. Enzyme polymorphism in man. Proceedings of the Royal Society B: Biological Sciences 164:298–310.
- Hubby, J. L., and R. C. Lewontin. 1966. A molecular approach to the study of genic heterozygosity in natural populations. 1. The number of alleles at different loci in Drosophila pseudoobscura. Genetics 54:577-594.
- Nevo, E., A. Bailes, and R. Ben-Shlomo. 1984. The evolutionary significance of genetic diversity: ecological, demographic and life history correlates. Pp. 13–213 in S. Levin, ed. Lecture Notes in Biomathe matics. Vol. 53: Evolutionary Dynamics of Genetic Diversity, G.S. Mani (ed.). Springer-Verlag, Berlin.

## The quantity and role of nearly neutral mutations in the evolutionary process

ADAM EYRE-WALKER, UNIVERSITY OF SUSSEX, BRIGHTON, UK

In a series of ground-breaking papers in the early 1970's Tomoko Ohta introduced the concept of nearly neutral mutations <sup>1</sup>, mutations whose effects were subject to the effects of both random genetic drift and selection, and whose fate was determined by the effective population size. There is now considerable evidence that such a category of mutations exists.

In my talk I will describe two methods by which the proportion of mutations that are nearly neutral can be estimated. In the first we have used the distribution of allele frequencies in a smaple of DNA sequences, to estimate the distribution of fitness effects of new mutations<sup>2</sup>. In the second method we infer the distribution by considering the relationship between the effectiveness of selection as a function of the effective population across a genome. Both methods yield similar conclusions; the distribution of fitness effects is such that changes in the effective population size lead to moderate changes in the proportion of mutations that are effectively neutral. but a substantial fraction of the mutations segregating in a population are nearly neutral.

I will discuss some of the implications of these results for understanding the molecular clock and levels of diversity. In particular I will consider whether near neutrality can explain why levels of genetic diversity at the molecular level are relatively constant across species of very different population sizes, an observation partly discovered by and then highlighted by Dick Lewontin in his book "The genetic basis of evolutionary change"<sup>3</sup>.

- 1 Ohta, T. (1973) Slightly deleterious mutant substitutions in evolution. Nature 246, 96–98.
- 2 Eyre-Walker, A., Woolfit, M. & Phelps, T. (2006) The distribution of fitness effects of new deleterious amino acid mutations in humans. Genetics 173, 891–900.
- <sup>3</sup> Lewontn, R. (1974) The genetic basis of evolutionary change. New York: Columbia University Press.

### *The impact of mating system and polyploidy on plant genomic variation*

TANJA SLOTTE, STOCKHOLM UNIVERSITY, SWEDEN

Mating system shifts and whole genome duplication constitute two major evolutionary transitions in plants. Recent macroevolutionary analyses suggest that both polyploidy and transitions from outcrossing to self-fertilization are associated with reduced net diversification rates, but the underlying ecological and evolutionary mechanisms remain unclear (Wright et al 2013). While theory predicts that both selffertilization and whole genome duplication should be associated with a reduced efficacy of natural selection, it remains unclear how rapidly these effects can be detected. Here, we have investigated the early demographic and selective consequences of polyploidy and mating system shifts in the crucifer genus Capsella. We use genomic data to infer the timing and mode of mating system shifts and polyploidy, and assess their impact on patterns of polymorphism at different classes of sites. Our results suggest that in this genus, both polyploidy and mating system shifts have occurred relatively recently, ~100-300 kya, and were associated with reductions in the effective population size (Slotte et al 2013; Douglas et al 2015). Despite the recency of these shifts, signals of relaxed purifying selection are detectable in polymorphism data. Population genetic simulations suggest that both mating system shifts, demographic history and increased gene redundancy in polyploids contribute to the pattern of relaxed selection. Our results indicate that both selfing and polyploidy are associated with relaxation of selection against weakly deleterious mutations, which might contribute to the reduced net diversification rates associated with these major evolutionary transitions.

Wright SI, Kalisz S, Slotte T. 2013. Evolutionary consequences of self-fertilization in plants. Proceedings of the Royal Society Series B Biological Sciences 280:20130133.

Slotte T, Hazzouri KM, Ågren JA, Koenig D, Maumus F, Guo Y, Steige K, Platts AE, Escobar JS, Newman LK, Wang W, Mandakova T, Vello E, Smith SM, Steffen J, Takuno S, Brandvain Y, Coop G, Andolfatto P, Hu TT, Blanchette M, Clark RM, Quesneville H, Nordborg M, Gaut BS, Lysak MA, Jenkins J, Grimwood J, Prochnick S, Shu S, Rokhsar D, Schmutz J, Weigel D, Wright SI. 2013. The Capsella rubella genome and the genomic consequences of rapid mating system evolution. Nature Genetics 45:831–835.

Douglas GM, Gos G, Steige KA, Salcedo A, Holm K, Josephs EB, Arunkumar R, Ågren JA, Hazzouri K, Wang W, Platts AE, Williamson RJ, Neuffer B, Lascoux M, Slotte T, Wright SI. 2015. Hybrid origins and the earliest stages of diploidization in the highly successful recent polyploid Capsella bursa-pastoris. Proceedings of the National Academy of Sciences of the USA. In press.

### The genomics of adaptation and speciation

JOCHEN WOLF, UPPSALA UNIVERSITY, SWEDEN

The view of species as entities amenable to evolutionary change elaborated by Charles Darwin laid the conceptual foundation for our current understanding of how biodiversity can be generated. Initially marred by a rudimental understanding of hereditary principles, evolutionists gained appreciation of the mechanistic underpinnings of adaptation and speciation following the merger of Mendelian genetic principles with Darwinian evolution. By the late 20th century theoretical and empirical evolutionary genetic research, including important contributions by this year's laureates, a mature framework had been developed to investigate the genetic basis of species diversification. Spurred by

a recent revolution in nano-sequencing technology speciation genetic research has become increasingly open to nonmodel organisms. Genome-wide processes can now be investigated at unprecedented resolution in essentially any eco-evolutionary model species of interest. This development has expanded speciation research beyond the traditional boundaries and unveils the genetic basis of speciation from manifold perspectives and at various stages of the splitting process. In this talk I will give a micro-evolutionary perspective on recent work trying to unravel the genetic underpinnings of adaptation and speciation. PROGRAMME Prize Lectures & Prize Symposium

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## Overview programme Crafoord Days 2015

Tuesday 5 May

PRIZE SYMPOSIUM IN BIOSCIENCES

## Genetic variation in natural populations

Lectures by TOMOKO OHTA and invited speakers.

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

Registration at www.crafoordprize.se or http://kva.se

Wednesday 6 May

#### PRIZE AWARD CEREMONY

#### In the presence of H.M. King Carl XVI Gustaf and H.M. Queen Silvia of Sweden.

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

Registration at www.crafoordprize.se or http://kva.se

Thursday 7 May

#### THE CRAFOORD PRIZE LECTURES

Held by the Crafoord Laureate **TOMOKO OHTA** and Bengt Olle Bengtsson, Department of Biology, Lund University.

BLÅ HALLEN, EKOLOGIHUSET LUND UNIVERSITY, SÖLVEGATAN 37, LUND

No registration.

16.20-17.15

09.00-17.00

15.30-17.40

## Detailed programme



#### THE CRAFOORD PRIZE IN BIOSCIENCES 2015

PRIZE SYMPOSIUM IN BIOSCIENCES

### Genetic variation in natural populations

09.00-17.00

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

## Tuesday 5 May

Open to the public and free of charge. Seating is limited. Registration is required and must be made before 29 April 2015 at http://kva.se/crafoordsymp2015

09.00	Opening address	<i>Staffan Normark</i> , Permanent Secretary of the Royal Swedish Academy of Sciences
09.05	Introduction to the Crafoord Prize symposium	<i>Hans Ellegren</i> , the Crafoord Prize Committee and Uppsala University, Sweden
09.15	Genotype to phenotype link and near-neutrality in evolution	CRAFOORD LAUREATE 2015 TOMOKO OHTA, Crafoord Laureate, Natio- nal Institute of Genetics, Mishima, Japan
10.00	Break with refreshments	
10.30	Why population genetics is so important in modern biology	<i>Deborah Charlesworth</i> , University of Edinburgh, UK
11.15	From mutation to macroevolution: Connecting genetic variation to the generation of biodiversity	<i>Lindell Bromham</i> , Australian National University, Canberra, Australia
12.00	Lunch	(Included for registered participants)
13.30	The use of genetic variation to conserve natural populations: From allozymes to genomes	<i>Fred Allendorf</i> , University of Montana, Missoula, MT, USA
14.15	The quantity and role of nearly neutral mutations in the evolutionary process	<i>Adam Eyre-Walker,</i> University of Sussex, Brighton, UK
15.00	Break with refreshments	
15.30	The impact of mating system and polyploidy on plant genomic variation	<i>Tanja Slotte</i> , Stockholm University, Sweden
16.15	The genomics of adaptation and speciation	Jochen Wolf, Uppsala University, Sweden
18.00	End of the symposium	



### THE CRAFOORD PRIZE IN BIOSCIENCES 2015

PRIZE LECTURE IN BIOSCIENCES

## Progress of the near-neutrality concept in evolution

#### 15.30-17.40

BLÅ HALLEN, EKOLOGIHUSET, LUND UNIVERSITY, SÖLVEGATAN 37, LUND

Open to the public and free of charge. No registration. Seating is limited. For more information please visit http://kva.se/CrafoordLecture2015

## Thursday 7 May

Moderator: Ove Eriksson, Chairman of the Prize Committee

15.30	Welcome and practical information	<i>Ove Eriksson</i> , Chairman of the Prize Committee
15.35	Taking genetic variation seriously. An appreciation of Richard Lewontin's and Tomoko Ohta's contributions.	<i>Bengt Olle Bengtsson</i> , Lund University, Sweden
16.05	THE CRAFOORD PRIZE LECTURE 2015: Progress of the near-neutrality concept in evolution	CRAFOORD LAUREATE 2015 TOMOKO OHTA, Crafoord Laureate, Natio- nal Institute of Genetics, Mishima, Japan
16.35	Break with refreshments	
16.55	Opposing selection pressures in males and females as a form of near-neutrality	Jessica Abbott, Lund University, Sweden
17.15	Genomics and the basis of evolutionary change	<i>Magnus Nordborg</i> , Gregor Mendel Institute of Molecular Plant Biology, Vienna, Austria
17.35	Closing remarks	<i>Ove Eriksson</i> , Chairman of the Prize Committee
17.40	End of day	

## Anna-Greta and Holger 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 the University of Lund.

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 the University of Lund.

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.





HOLGER AND ANNA-GRETA CRAFOORD

#### THE ROYAL SWEDISH ACADEMY OF SCIENCES

is an independent, nongovernmental organization whose aim is to promote the sciences and strengthen their influence in society. Traditionally, the Academy takes a special responsibility for the natural sciences and mathematics, and strives to increase exchanges between various disciplines.

The activities of the Academy are aimed mainly at

- spreading knowledge of discoveries and problems in current research
- providing support for young researchers
- rewarding outstanding contributions in research
- stimulating interest in mathematics and the natural sciences in schools
- spreading scientific and popular-scientific information in various forms
- offering unique research environments
- maintaining contact with foreign academies, learned societies and other international scientific organisations
- representing the sciences in society
- carrying out independent analyses and evaluations based on scientific grounds on issues of importance for society

**THE ACADEMY HAS** has about 450 Swedish members and 175 foreign members. The Swedish members are active within Classes and committees. They initiate investigations, responses to government proposals, conferences and seminars. Once a month, the Academy holds a General Meeting, with a connected public lecture.

**THE ACADEMY'S OWN INSTITUTES** offer unique research environments for botany, ecological economics, the history of science and mathematics.

#### IN ADDITION TO THE CRAFOORD PRIZE, the

Academy annually awards a number of prizes, the best known of which are the Nobel Prizes in Physics and Chemistry and the Sveriges Riksbank Prize in Economic Sciences in Memory of Alfred Nobel. Others are the Söderberg Prize and the Göran Gustafsson Prize. The latter are awarded to outstanding young researchers and are a combination of a personal prize and a research grant. The Academy also supports researchers through scholarships and mentoring programmes, and is engaged in appointing many promising young researchers to long-term positions that are financed by foundations.

#### THROUGH ITS VARIOUS COMMITTEES, the

Academy also works for the development of a society based on scientific grounds. Great interest in environmental and educational issues has resulted in a wide variety of Academy activities in these areas.



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