**Bioinformatics in drug discovery & Development  
not being updated  
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**Overviews  & introductions** [**Bioinformatics**](http://www.genomicglossaries.com/content/chapterinfosourcestext.asp#bioinfo)[**cheminformatics**](http://www.genomicglossaries.com/content/chapterchemogenomics.asp#chem info jrnls)[**Molecular Medicine informatics**](http://www.genomicglossaries.com/content/chapterinfosourcestext.asp#med info)

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**Bioinformatics** is inextricably intertwined with the biological, chemical and medical resources in all the other sections.

**What is Bioinformatics?** Many definitions, difficult to reach agreement on.

The field of science in which biology, computer science, and information technology merge into a single discipline. The ultimate goal of the field is to enable the discovery of new biological insights as well as to create a global perspective from which unifying principles in biology can be discerned. There are three important sub- disciplines within bioinformatics: the development of **new algorithms and statistics** with which to assess relationships among members of large data sets; the **analysis and** [**interpretation**](http://www.ncbi.nlm.nih.gov/Education/Bioinformatics/dataanal.html)of various [**types of data**](http://www.ncbi.nlm.nih.gov/Education/Bioinformatics/datatypes.html) including nucleotide and amino acid sequences, protein domains, and protein structures; and the development and implementation of tools that enable efficient access and management of different types of information. "Education" NCBI, 2003 http://www.ncbi.nlm.nih.gov/Education/index.html

The definition of bioinformatics is not universally agreed upon. Generally speaking, we define it as the creation and development of advanced information and computational technologies for problems in biology, most commonly molecular biology (but increasingly in other areas of biology). As such, it deals with methods for storing, retrieving and analyzing biological data, such as nucleic acid (DNA/ RNA) and protein sequences, structures, functions, pathways and genetic interactions.  Some people construe bioinformatics more narrowly, and include only those issues dealing with the management of genome project sequencing data. Others construe bioinformatics more broadly and include all areas of **computational biology**, including population modeling and numerical simulations. Russ Altman "What is bioinformatics?" Stanford Univ. 2002 http://smi-web.stanford.edu/people/altman/bioinformatics.html

Roughly, bioinformatics describes any use of computers to handle biological information. In practice the definition used by most people is narrower; bioinformatics to them is a synonym for "computational molecular biology" - the use of computers to characterise the molecular components of living things. Damian Counsell, bioinformatics.org FAQ <http://bioinformatics.org/faq/#whatIsBioinformatics>

Conceptualizing biology in terms of molecules (in the sense of physical- chemistry) and then applying "informatics" techniques (derived from disciplines such as applied math, CS [computer science] and statistics to understand and organize the information associated with these molecules on a large- scale. Mark Gerstein "What is Bioinformatics?" MB&B 474b3, 2001  
<http://bioinfo.mbb.yale.edu/what-is-it.html>

Research, development, or application of computational tools and approaches for expanding the use of biological, medical, behavioral or health data, including those to acquire, store, organize, archive, analyze, or visualize such data.  NIH, BISTIC Biomedical Information Science and Technology Initiative, 2005   <http://www.bisti.nih.gov/>

[**More bioinformatics definitions**](http://www.genomicglossaries.com/content/chapternotes.asp#bioinfo defs)  **More** [**bioinformatics**](http://www.genomicglossaries.com/content/chapterinfosourcestext.asp#informatics terminology) **terminology**

**Computational biology**A field of biology concerned with the development of techniques for the collection and manipulation of biological data, and the use of such data to make biological discoveries or predictions. This field encompasses all computational methods and theories applicable to MOLECULAR BIOLOGY and areas of computer-based techniques for solving biological problems including manipulation of models and datasets. [MeSH, 1997] Computational biology maps to bioinformatics in PubMed.

***Computational biology FAQ***, Robert D. Phair, US, 2000 <http://www.bioinformaticsservices.com/bis/resources/faq/faq.html>

I find that people use "computational biology" when discussing that subset of bioinformatics (in the broadest sense) closest to the field of classical general biology.  Computational biologists interest themselves more with evolutionary, population and theoretical biology rather than cell and molecular biomedicine. It is inevitable that molecular biology is profoundly important in computational biology, but it is certainly not what computational biology is all about ... Richard Durbin, Head of Informatics at the Wellcome Trust Sanger Institute, expressed an interesting opinion on this distinction in an interview on this distinction:  "I do not think all biological computing is bioinformatics, e.g. mathematical modelling is not bioinformatics, even when connected with biology- related problems. In my opinion, bioinformatics has to do with management and the subsequent use of biological information, particular genetic information."  [Damian Counsell, bioinformatics.org FAQ, 2001] [https://bioinformatics.org/faq/#definitionOfCompbiol](http://bioinformatics.org/faq/#definitionOfCompbiol)

**Bioinformatics Overviews & introductions**  
NCBI, NLM, NIH: **Science Primer** <http://www.ncbi.nlm.nih.gov/About/primer/index.html> Bioinformatics and molecular modeling

**Very very very short introduction to protein bioinformatics**, Patricia Babbitt et. al., 57 pages <http://baygenomics.ucsf.edu/education/workshop1/lectures/w1.color2.pdf>

**What is Informatics?  
Informatics according to the OED**[translation Russian *informatika* from information SEE –ICS.] (See quotation 1967) Cf. *information science* 1967 *FID News Bull. XVii 73/2 Informatics* is the discipline of science which investigates the structure and properties (not specific content) of scientific information, as well as the regularities of scientific information activity, its theory, history, methodology and organization. Oxford English Dictionary Oxford English Dictionary, 2nd edition.

**According to NIH's Office of Rare Diseases**  
The study of the application of computer and statistical techniques to the management of information. In genome projects, informatics includes the development of methods to search databases quickly, to analyse DNA sequence information, and to predict protein sequence and structure from DNA sequence data. ORD Office of Rare Diseases, NIH glossary.  [http://ord.aspensys.com/asp/resources/glossary\_f-m.asp#I](http://rarediseases.info.nih.gov/RareDiseaseList.aspx)

It is interesting that the OED definition specified domain independent information, while the ORD NIH definition is very domain specific. While "ontologies" offer the hope of cross domain interoperability, much effort is still being devoted to facilitating communication within domains. While the pharmaceutical research is increasingly interdisciplinary and NIH has come out with new initiatives such as the NIH Road map http://nihroadmap.nih.gov/index.asp  there are still many obstacles to truly interdisciplinary research.

**from the Dept. of Biopharmaceutical Sciences, UCSF Bioinformatic** and experimental analysis of protein superfamilies for understanding protein structure- function relationships and developing strategies for protein engineering. Using superfamily analysis to understand how protein sequence and structure determine protein function. Our computational approach begins with identifying the sets of divergently related proteins that comprise enzyme superfamilies and then attempts to correlate their conserved and variable structural features to similarities and differences in their functions.

This work also requires the development of new tools in protein bioinformatics to identify and evaluate distant relationships and to distinguish those elements of structure that provide common function from those that determine specificity. Designed to take advantage of the huge volumes of data coming out of the genome projects, this approach provides a much more contextual picture of the structure- function paradigm than can be achieved by studying a single protein at a time. This work has been successfully applied to such problems as the prediction of function for unknown reading frames and elucidation of enzyme mechanisms. Patricia Babbitt, Dept. of Biopharmaceutical Sciences, Univ. of California San Francisco, US http://www.ucsf.edu/dbps/faculty/pages/babbitt.html

**Introductions to protein bioinformatics**

**Protein bioinformatics**  
Some/ many? of the above definitions specifically include proteins.

**[Protein] Structural bioinformatics**Involves the process of determining a protein's three- dimensional structure using comparative primary sequence **alignment**, secondary and tertiary structure prediction methods, **homology modeling**, and crystallographic diffraction pattern analyses. Currently, there is no reliable *de novo* predictive method for protein 3D- structure determination. Over the past half- century, protein structure has been determined by purifying a protein, crystallizing it, then bombarding it with X-rays. The **X-ray diffraction** pattern from the bombardment is recorded electronically and analyzed using software that creates a rough draft of the 3D structure. Biological scientists and crystallographers then tweak and manipulate the rough draft considerably. The resulting spatial coordinate file can be examined using modeling- structure software to study the gross and subtle features of the protein's structure. Christopher Smith "Bioinformatics, Genomics, and Proteomics"  Scientist 14[23]:26, Nov. 27, 2000   
<http://the-scientist.com/yr2000/nov/profile_001127.html>

**See also** [**systems bioinformatics**](http://www.genomicglossaries.com/content/chapterinfosourcestext.asp#sysbio)

**What are cheminformatics, chemoinformatics, chemi- informatics?** The terminology is even less standardized here.

Google hits for:  
cheminformatics about 16,300 hits Dec. 11, 2003 about 168,000 Oct. 14, 2005  
chemoinformatics about 8,670 Dec. 11, 2003, about 85,300 Oct. 14, 2005  
"chemical informatics" about  3,300 Dec. 11, 2003, about  2,100,000 Oct. 14, 2005  
chemiinformatics  about 35 Dec. 11, 2003; about 168 Oct. 14, 2005

**Cheminformatics definitions  
Cheminformatics: Going by the literature**  
Mixing of information technology and management to transform data into information and information into knowledge for the intended purpose of making better decisions faster in the arena of drug lead identification and optimization. . In Chemoinformatics there are really only two [primary] questions: 1.) what to test next and 2.) what to make next. The main processes within drug discovery are lead identification, where a lead is something that has activity in the low micromolar range, and lead optimization, which is the process of transforming a lead into a drug candidate. Frank Brown, "Chemoinformatics: What is it and How does it Impact Drug Discovery" Annual Reports in Medicinal Chemistry 33: 375-384, 1998

Increasingly incorporates "compound registration into databases, including library enumeration; access to primary and secondary scientific literature; QSAR Quantitative Structure Activity Relationships) and similar tools for relating activity to structure; physical and chemical property calculations; chemical structure and property databases, chemical library design and analysis; structure- based design and statistical methods. Because these techniques have traditionally been considered the realms of scientists from different disciplines, differences in computer systems and terminology provide a barrier to effective communication. This is probably the single most challenging problem that chemoinformatics must solve. M Hann and R Green "Chemoinformatics  a new name for an old problem?" Current Opinion in Chemical Biology 3:379- 383, 1999

Many people view chemoinformatics as an extension of chemical information, which is a well established concept covering many areas that employ chemical structures, data storage and computational methods, such as compound registration databases, on- line chemical literature, SAR analysis and molecule- property calculation. Timothy Ritchie "Chemoinformatics; manipulating chemical information to facilitate decision- making in drug discovery" Drug Discovery Today 6(16) : 813- 814, Aug. 2001

**Chemical informatics**Variously known as chemoinformatics, cheminformatics, or even chemiinformatics, chemical informatics is the application of computer technology to chemistry in all of its manifestations. Much of the current use of cheminformatics techniques is in the drug industry. Indeed, one definition of chemical informatics is "the mixing of information resources to transform data into information and information into knowledge, for the intended purpose of making decisions faster in the arena of drug lead identification and optimization." Now chemical informatics is being applied to problems across the full range of chemistry.  Gary D. Wiggins, "What is Chemical Informatics?"  Indiana Univ., US, 2006  http://www.chembiogrid.org/resources/whatis.html

**Cheminformatics overviews & introductions**  
**25 Years of Research in Cheminformatics:** A Portrait of the Research Group of Prof. Johann Gasteiger, Computer Chemie Centrum and Institute of Organic Chemistry, Univ. of Erlangen- Nurnberg, 2001 <http://www2.chemie.uni-erlangen.de/presentations/symposium/torvs_e.pdf>

**Cheminformatics and beyond**Drug discovery and development is in the midst of a critical transition, from a discipline dominated by empirical tests and brute force to one in which biological and chemical structural knowledge are exploited intelligently, using computational assistance. Cheminformatics, the combination of chemical synthesis, biological screening, and data mining approaches used to guide drug discovery and development, cheminformatic tools that allow for the rational selection of designed compounds with drug- like properties from an almost infinite number of synthetic possibilities, building smarter focused libraries for virtual and high- throughput screening and the exploitation of previously obtained discovery data to guide lead optimization efforts are all important.

There are many sources of chemical data; registered chemical structures with stereochemistry, synthesis records, spectral data including NMR Nuclear Magnetic Resonance, purity determinations, not to mention the volume of data generated by HTS High Throughput Screening, SAR Structure Activity Relationship studies and the calculation of physiochemical  properties. Accessibility, manipulation, and data mining of chemical information translates to knowledge for smarter drug development. Chemoinformatic tools for storage, design and mining of chemical databases/ information have had success in lead identification and optimization. Chemoinformatics is about presenting and integrating a vast and complex array of information so that people who make the decisions in drug discovery can make better choices (relatively) quickly and easily.

**Molecular modeling and systems biology**Many people include these concepts under chemical informatics.

**Molecular modeling:**   
A technique for the investigation of molecular structures and properties using computational chemistry and graphical visualization techniques in order to provide a plausible three- dimensional representation under a given set of circumstances. IUPAC Medicinal Chemistry

***in silico*:** Literally "in the computer" (as contrasted with *"in vitro"* (in glass) or *"in vivo"* (in life). Can be used to screen out compounds which are not **druggable**.

In a white paper I wrote for the European Commission in 1988 I advocated the funding of genome programs, and in particular the use of computers. In this endeavour I coined "in silico" following "*in vitro*" and "*in vivo*" I think that the first public use of the word is in the following paper: A. Danchin, C. Médigue, O. Gascuel, H. Soldano, A. Hénaut, [From data banks to data bases.](http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&list_uids=1784830&dopt=Abstract) Res. Microbiol. (1991) 142: 913- 916.  You can find a developed account of this story in my book [The Delphic Boat](http://www.hup.harvard.edu/catalog/DANDEL.html), Harvard University Press, 2003, personal communication Antoine Danchin, Institute Pasteur, 2003

**Mapping and modeling networks and pathways**The experimental task of mapping genetic **regulatory networks** using genetic footprinting and [**yeast] two- hybrid** techniques is well underway, and the kinetics of these networks is being generated at an astounding rate. ... If the promise of the genome projects and the structural genomics effort is to be fully realized, then predictive simulation methods must be developed to make sense of this emerging experimental data.

There are three bottlenecks in the numerical analysis of biochemical reaction networks. The first is the **multiple time scales** involved. Since the time between biochemical reactions decreases exponentially with the total probability of a reaction per unit time, the number of computational steps to simulate a unit of biological time increases roughly exponentially as reactions are added to the system or rate constants are increased. The second bottleneck derives from the **necessity to collect sufficient statistics** from many runs of the Monte- Carlo simulation to predict the phenomenon of interest. The third bottleneck is a practical one of **model building and testing**: hypothesis exploration, sensitivity analyses, and back calculations, will also be computationally intensive. Lawrence Berkeley Lab "Advanced Computational Structural Genomics" Glossary, c. 1999

**more on** [**Networks and pathways**](http://www.genomicglossaries.com/content/chapternotes.asp#networks and pathways)**Systems biology**There are two opinions on what *systems biology* is supposed to be. One group sees *systems biology* as another level of combining data from different levels (like DNA, RNA and protein level) (see [Leroy] HOOD). Another group wants to combine classical molecular and cell biology with systems theory and focus on the new forms of behavior that emerge when systems of genes and proteins are studied in a wholistic way. For this they need data from all those different levels as well, of course. That is why they see *systems biology* as a cooperative effort, with systems theory providing a theoretical framework and a new view on things for biologists, along with lots of experience with complex systems, and biology providing in-depth knowledge of the field of application as well as practical handling experience. This data is the basis for developing the kind of detailed models that are necessary for such studies of systemic properties and behavior. For both groups, the goal is to reach a new level of understanding of biological systems often referred to as 'systems level' understanding. A glossary for Systems Biology, Systems Biology Group, Stuttgart [http://www.sysbio.de/projects/glossary/SYSTEMS\_BIOLOGY.shtml#systems\_biology](http://www.sysbio.de/projects/glossary/SYSTEMS_BIOLOGY.shtml/ohttp:/www.sysbio.de/projects/glossary/SYSTEMS_BIOLOGY.shtml#systems_biology)

**Institute for Systems Biology,** Seattle WA <http://www.systemsbiology.org/> Lee Hood's group.

**Systems bioinformatics**With the completion of the Human Genome Project, the scientific community is now faced with the even greater challenge of analyzing the resulting data from this and other large- scale genome projects to better understand the networks underlying biological function. Second International Computational Systems Bioinformatics Conference To be Held August 11-14, 2003 at Stanford University, IEEE CS Bioinformatics Technical Chair via BizWire <http://quickstart.clari.net/qs_se/webnews/wed/bx/Bca-ieee-cs_csb2003.RMsB_DuP.html>

**Drug discovery and development informatics**  
**Pharmainformatics**  
The multidisciplinary informatics needs of the pharmaceutical industry (HTS High Throughput Screening data, Computational Chemistry, Combinatorial Chemistry, ADME Informatics, Cheminformatics, Toxicology, Metabolic Modeling, Bioinformatics in Drug Discovery and Metabolism etc. information access and communication between various departments like the development and discovery.  Yahoo Groups Pharmainformatics <http://health.groups.yahoo.com/group/pharmainformatics/>

**Pharmaceutical bioinformatics**Bioinformatics and structure- aided drug design are really part of the same continuum. Bioinformatics offers a means to get to a structure through sequence; while structure- aided drug design offers a means to get to a drug through structure. We plan to combine innovative computational techniques with biochemical and structural expertise to bring bioinformatics and structure- aided drug design even closer together. In particular, we intend to blend computational chemistry with computational biology to create software that will aid protein chemists in understanding, evaluating and predicting the structure, function and activity of medically and industrially important proteins. My laboratory is currently involved in three "bioinformatics" projects. These include: (1) the development of novel methods to identify remote sequence/ structure relationships; (2) the creation of a compact, relational database with advanced bioinformatics functionality; and (3) the development of novel methods for predicting and evaluating protein secondary and tertiary structure. David Wishart, Wishart Pharmaceutical Research Group, Univ. of Alberta, Canada  <http://redpoll.pharmacy.ualberta.ca/projects/bioinfo.html>

**Research informatics**The explosion of genomic information, from sequences and gene expression to **SNPs** and protein structures, is of limited value for pharmaceutical researchers without powerful software capable of interpretation and comparisons. Data mining, multiple location data sharing, and computational enhancements of biological and chemistry projects, as well as integration of these efforts need various approaches for overcoming the problems of legacy information systems, the very different language and perspectives of chemists and biologists, and the organizational issues of compartmentalization and **information silos**.

**Laboratory informatics**The specialized application of information technology to maximize laboratory operations. Laboratory informatics encompasses data acquisition, data processing, laboratory information management system (LIMS), laboratory automation, scientific data management (including data analysis and long- term archiving), and electronic laboratory notebooks. Focus is on the application of this technology in analytical, production, and R&D laboratories.  Graduate Programs: Laboratory Informatics, Indiana Univ. School of Informatics, US  http://www.informatics.iupui.edu/Academics/graduate/laboratory\_informatics/index.php

**Toxicoinformatics**[**Toxicogenomics**](http://www.genomicglossaries.com/content/chaptergenomictext.asp#tox gen)

**Toxicoinformatics**An emerging scientific discipline that integrates approaches from multidisciplinary fields of bioinformatics, chemoinformatics, computational toxicology, informatics technologies and physiologically- based pharmacokinetic modeling with the objective of knowledge discovery and the elucidation of mechanisms of toxicity. NCTR's Center for Toxicoinformatics, National Center for Toxicological Research, FDA, 2003  <http://www.fda.gov/nctr/science/centers/toxicoinformatics/>

In the end, successfully moving research from the laboratory into the clinic is the ultimate **target validation**. While new technologies may be helpful and/or necessary, the challenges of scaling, automating (both for cost effectiveness and reproducibility) standardizing and simplifying are equally, if not more important.

**Medical Bioinformatics**Covers **haplotyping, genotyping** and **population genomics**, gene expression profiling, particularly for use in diagnosis, prognosis and therapeutic stratification of patients. Most of this work is being done first in oncology.

***Medical informatics***  
Medical informatics has many different contexts.

The field of information science concerned with the analysis and dissemination of medical data through the application of computers to various aspects of health care and medicine. [MeSH 1987]

Medical informatics has to do with all aspects of understanding and promoting the effective organization, analysis, management, and use of information in health care. While the field of medical informatics shares the general scope of these interests with some other health care specialties and disciplines, medical informatics has developed its own areas of emphasis and approaches that have set it apart from other disciplines and specialties. For one, a common thread through medical informatics has been the emphasis on technology as an integral tool to help organize, analyze, manage, and use information. In addition, as professionals involved at the intersection of information and technology and health care, those in medical informatics have historically tended to be engaged in the research, development, and evaluation side of things, and in studying and teaching the theoretical and methodological underpinnings of data applications in health care. However, today medical informatics also counts among its profession many whose activities are focussed on dimensions that include the administration and everyday collection and use of information in health care.  FAQ, American Medical Informatics Association, 2003 http://www.amia.org/about/faqs/f7.html

**Health information data**Includes Clinical data captured during the process of diagnosis and treatment. Epidemiological databases , that aggregate data about a population. Demographic data used to identify and communicate with and about an individual. Financial data derived from the care process or aggregated for an organization or population. Research data gathered as a part of care and used for research or gathered for specific research purposes in **clinical trials**. Reference data that interacts with the care of the individual or with the healthcare deliver systems, like a formulary, protocol, care plan, clinical alerts or reminders, etc. Coded data that is translated into a standard nomenclature or classification so that it may be aggregated, analyzed, and compared.  Health Information Management; Professional definitions, Committees on Professional Development, American Health Information Management Association, 1999, 2000 http://www.ahima.org/infocenter/definitions/HIMprofessionaldefinition.htm

**Public health informatics**The systematic application of information and computer sciences to public health practice, research, and learning. It is the discipline that integrates public health with information technology. The development of this field and dissemination of informatics knowledge and expertise to public health professionals is the key to unlocking the potential of information systems to improve the health of the nation. [www.nlm.nih.gov/pubs/cbm/phi2001.html](http://www.nlm.nih.gov/pubs/cbm/phi2001.html)  [MeSH 2003]

[Emerging medical informatics specialties](http://www.genomicglossaries.com/content/chapternotes.asp#emerging)

**Social informatics**An important and often ignored piece of the puzzle. A serviceable working conception of "social informatics" is that it identifies a body of research that examines the social aspects of computerization. A more formal definition is "the interdisciplinary study of the design, uses and consequences of information technologies that takes into account their interaction with institutional and cultural contexts." ... Social informatics has been a subject of systematic analytical and critical research for the last 25 years. Unfortunately, social informatics studies are scattered in the journals of several different fields, including computer science, information systems, information science and some social sciences. Each of these fields uses somewhat different nomenclature. This diversity of communication outlets and specialized terminologies makes it hard for many non- specialists (and even specialists) to locate important studies. Rob Kling, What is social informatics and why does  it matter? D-Lib 5(1): Jan. 1999 <http://www.dlib.org/dlib/january99/kling/01kling.html>

**Deuterostomes** (taxonomic term: **Deuterostomia**; from the Greek: "second mouth") are a superphylum of [animals](http://en.wikipedia.org/wiki/Animal). They are a [subtaxon](http://en.wikipedia.org/wiki/Taxon) of the [Bilateria](http://en.wikipedia.org/wiki/Bilateria) branch of the subregnum [Eumetazoa](http://en.wikipedia.org/wiki/Eumetazoa), and are opposed to the [protostomes](http://en.wikipedia.org/wiki/Protostome). Deuterostomes are distinguished by their [embryonic development](http://en.wikipedia.org/wiki/Embryonic_development); in deuterostomes, the first opening (the [blastopore](http://en.wikipedia.org/wiki/Blastopore)) becomes the [anus](http://en.wikipedia.org/wiki/Anus), while in protostomes it becomes the [mouth](http://en.wikipedia.org/wiki/Mouth). Deuterostomes are also known as **enterocoelomates** because their [coelom](http://en.wikipedia.org/wiki/Coelom) develops through [enterocoely](http://en.wikipedia.org/wiki/Enterocoely).

There are four extant phyla of deuterostomes:

* Phylum [Chordata](http://en.wikipedia.org/wiki/Chordata) ([vertebrates](http://en.wikipedia.org/wiki/Vertebrate) and their kin)
* Phylum [Echinodermata](http://en.wikipedia.org/wiki/Echinodermata) ([sea stars](http://en.wikipedia.org/wiki/Sea_star), [sea urchins](http://en.wikipedia.org/wiki/Sea_urchin), [sea cucumbers](http://en.wikipedia.org/wiki/Holothuroidea), etc.)
* Phylum [Hemichordata](http://en.wikipedia.org/wiki/Hemichordata) ([acorn worms](http://en.wikipedia.org/wiki/Acorn_Worm) and possibly [graptolites](http://en.wikipedia.org/wiki/Graptolite))
* Phylum [Xenoturbellida](http://en.wikipedia.org/wiki/Xenoturbellida) (2 species of worm-like animals)

Superphylum Deuterostomia was redefined in 1995 based on molecular sequence analyses when the lophophorates were removed from it and combined with other protostome animals to form superphylum [Lophotrochozoa](http://en.wikipedia.org/wiki/Lophotrochozoa).[[1]](http://en.wikipedia.org/wiki/Deuterostome#cite_note-0) The phylum [Chaetognatha](http://en.wikipedia.org/wiki/Chaetognatha) (arrow worms) may also belong here. Extinct groups may include the phylum [Vetulicolia](http://en.wikipedia.org/wiki/Vetulicolia). Echinodermata, Hemichordata and Xenoturbellida form the clade [Ambulacraria](http://en.wikipedia.org/wiki/Ambulacraria).[[2]](http://en.wikipedia.org/wiki/Deuterostome#cite_note-1)

In both deuterostomes and protostomes, a zygote first develops into a hollow ball of cells, called a [blastula](http://en.wikipedia.org/wiki/Blastula). In deuterostomes, the early divisions occur parallel or perpendicular to the polar axis. This is called [radial cleavage](http://en.wikipedia.org/wiki/Radial_cleavage), and also occurs in certain protostomes, such as the [lophophorates](http://en.wikipedia.org/wiki/Lophophorate). Most deuterostomes display [indeterminate cleavage](http://en.wikipedia.org/wiki/Indeterminate_cleavage), in which the developmental fate of the cells in the developing embryo are not determined by the identity of the parent cell. Thus if the first four cells are separated, each cell is capable of forming a complete small larva, and if a cell is removed from the blastula the other cells will compensate.

In deuterostomes the [mesoderm](http://en.wikipedia.org/wiki/Germ_layer#Mesoderm) forms as evaginations of the developed gut that pinch off, forming the [coelom](http://en.wikipedia.org/wiki/Body_cavity). This is called [enterocoely](http://en.wikipedia.org/wiki/Enterocoely).

Both the Hemichordata and Chordata have [gill slits](http://en.wikipedia.org/wiki/Gill_slit), and primitive fossil echinoderms also show signs of gill slits. A hollow nerve cord is found in all chordates, including [tunicates](http://en.wikipedia.org/wiki/Tunicate) (in the larval stage). Some hemichordates also have a tubular nerve cord. In the early embryonic stage it looks like the hollow nerve cord of chordates. Because of the degenerated nervous system of echinoderms, it is not possible to discern much about their ancestors in this matter, but based on different facts it is quite possible that all the present deuterostomes evolved from a common ancestor that had gill slits, a hollow nerve cord and a segmented body. It could have resembled the small group of Cambrian deuterostomes named [Vetulicolia](http://en.wikipedia.org/wiki/Vetulicolia).

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| --- |
| **Contents**   [[hide](http://en.wikipedia.org/wiki/Deuterostome)]   * [1 Formation of mouth and anus](http://en.wikipedia.org/wiki/Deuterostome#Formation_of_mouth_and_anus) * [2 Origins](http://en.wikipedia.org/wiki/Deuterostome#Origins) * [3 References](http://en.wikipedia.org/wiki/Deuterostome#References) * [4 External links](http://en.wikipedia.org/wiki/Deuterostome#External_links) |

**[**[**edit**](http://en.wikipedia.org/w/index.php?title=Deuterostome&action=edit&section=1)**] Formation of mouth and anus**

All chordates, such as birds and mammals, are deuterostomes. Shown here is a [Barred Owl](http://en.wikipedia.org/wiki/Barred_Owl).

*Main article:* [*Embryological origins of the mouth and anus*](http://en.wikipedia.org/wiki/Embryological_origins_of_the_mouth_and_anus)

The defining characteristic of the dueterostome is the fact that the blastopore (the opening at the bottom of the forming gastrula) is turned into the anus, whereas in protosomes the blastopore becomes the mouth. The deuterostome mouth develops at the opposite end of the embryo from the blastopore and a digestive tract develops in the middle connecting the two.

**[**[**edit**](http://en.wikipedia.org/w/index.php?title=Deuterostome&action=edit&section=2)**] Origins**

The majority of animals more complex than [jellyfish](http://en.wikipedia.org/wiki/Jellyfish) and other [Cnidarians](http://en.wikipedia.org/wiki/Cnidarians) are split into two groups, the [protostomes](http://en.wikipedia.org/wiki/Protostome) and deuterostomes. Chordates (which include all the vertebrates) are deuterostomes.[[3]](http://en.wikipedia.org/wiki/Deuterostome#cite_note-Erwin20002-2) It seems very likely that [555](http://toolserver.org/~verisimilus/Timeline/Timeline.php?Ma=555) million years old [*Kimberella*](http://en.wikipedia.org/wiki/Kimberella) was a member of the protostomes.[[4]](http://en.wikipedia.org/wiki/Deuterostome#cite_note-Fedonkin2007-3)[[5]](http://en.wikipedia.org/wiki/Deuterostome#cite_note-Butterfield2006-4) If so, this means that the protostome and deuterostome lineages must have split some time before *Kimberella* appeared — at least [558](http://toolserver.org/~verisimilus/Timeline/Timeline.php?Ma=558) million years ago, and hence well before the start of the Cambrian [542](http://toolserver.org/~verisimilus/Timeline/Timeline.php?Ma=542) million years ago.[[3]](http://en.wikipedia.org/wiki/Deuterostome#cite_note-Erwin20002-2) The [Ediacaran](http://en.wikipedia.org/wiki/Ediacaran) fossil [*Ernietta*](http://en.wikipedia.org/wiki/Ernietta), from about [549 to 543](http://toolserver.org/~verisimilus/Timeline/Timeline.php?Ma=549–543) million years ago, may represent a deuterostome animal.[[6]](http://en.wikipedia.org/wiki/Deuterostome#cite_note-5)

Fossils of one major deuterostome group, the [echinoderms](http://en.wikipedia.org/wiki/Echinoderm) (whose modern members include [sea stars](http://en.wikipedia.org/wiki/Sea_star), [sea urchins](http://en.wikipedia.org/wiki/Sea_urchin) and [crinoids](http://en.wikipedia.org/wiki/Crinoid)) are quite common from the start of the Cambrian, [542](http://toolserver.org/~verisimilus/Timeline/Timeline.php?Ma=542) million years ago.[[7]](http://en.wikipedia.org/wiki/Deuterostome#cite_note-Bengtson2004-6) The Mid [Cambrian](http://en.wikipedia.org/wiki/Cambrian) fossil [*Rhabdotubus johanssoni*](http://en.wikipedia.org/wiki/Rhabdotubus_johanssoni) has been interpreted as a [pterobranch](http://en.wikipedia.org/wiki/Pterobranch) hemichordate.[[8]](http://en.wikipedia.org/wiki/Deuterostome#cite_note-7) Opinions differ about whether the [Chengjiang fauna](http://en.wikipedia.org/wiki/Chengjiang_fauna) fossil [*Yunnanozoon*](http://en.wikipedia.org/wiki/Yunnanozoon), from the earlier Cambrian, was a hemichordate or chordate.[[9]](http://en.wikipedia.org/wiki/Deuterostome#cite_note-ChenHangLi1996-8)[[10]](http://en.wikipedia.org/wiki/Deuterostome#cite_note-ChenHangLi1999-9) Another Chenjiang fossil, [*Haikouella lanceolata*](http://en.wikipedia.org/wiki/Haikouella_lanceolata), also from the Chengjiang fauna, is interpreted as a chordate and possibly a craniate, as it shows signs of a heart, arteries, gill filaments, a tail, a neural chord with a brain at the front end, and possibly eyes — although it also had short tentacles round its mouth.[[10]](http://en.wikipedia.org/wiki/Deuterostome#cite_note-ChenHangLi1999-9) [*Haikouichthys*](http://en.wikipedia.org/wiki/Haikouichthys) and [*Myllokunmingia*](http://en.wikipedia.org/wiki/Myllokunmingia), also from the Chenjiang fauna, are regarded as [fish](http://en.wikipedia.org/wiki/Fish).[[11]](http://en.wikipedia.org/wiki/Deuterostome#cite_note-10)[[12]](http://en.wikipedia.org/wiki/Deuterostome#cite_note-11) [*Pikaia*](http://en.wikipedia.org/wiki/Pikaia), discovered much earlier but from the Mid Cambrian [Burgess Shale](http://en.wikipedia.org/wiki/Burgess_Shale), is also regarded as a primitive chordate.[[13]](http://en.wikipedia.org/wiki/Deuterostome#cite_note-12) On the other hand fossils of early chordates are very rare, since non-vertebrate chordates have no bones or teeth, and none have been reported for the rest of the Cambrian.

**Protostome**

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**Protostomia** (from [Greek](http://en.wikipedia.org/wiki/Greek_language) meaning "mouth first") are a [clade](http://en.wikipedia.org/wiki/Clade) of [animals](http://en.wikipedia.org/wiki/Animal). Together with the [deuterostomes](http://en.wikipedia.org/wiki/Deuterostome) and a few smaller [phyla](http://en.wikipedia.org/wiki/Phylum), they make up the [Bilateria](http://en.wikipedia.org/wiki/Bilateria), mostly comprising animals with [bilateral symmetry](http://en.wikipedia.org/wiki/Symmetry_(biology)#Bilateral_symmetry) and [three](http://en.wikipedia.org/wiki/Triploblastic) [germ layers](http://en.wikipedia.org/wiki/Germ_layer). The major distinctions between [deuterostomes](http://en.wikipedia.org/wiki/Deuterostome) and protostomes are found in [embryonic development](http://en.wikipedia.org/wiki/Embryonic_development).

In animals at least as complex as [earthworms](http://en.wikipedia.org/wiki/Earthworms), the [embryo](http://en.wikipedia.org/wiki/Embryo) forms a dent on one side, the [blastopore](http://en.wikipedia.org/wiki/Blastopore), which deepens to become the [archenteron](http://en.wikipedia.org/wiki/Archenteron), the first phase in the growth of the [gut](http://en.wikipedia.org/wiki/Gut_(zoology)). In [deuterostomes](http://en.wikipedia.org/wiki/Deuterostome), the original dent becomes the anus while the gut eventually tunnels through to make another opening, which forms the mouth. The protostomes were so named because it used to be thought that in their embryos the dent formed the mouth while the anus was formed later, at the opening made by the other end of the gut. More recent research, however, shows that in protostomes the edges of the dent close up in the middle, leaving openings at the ends which become the mouth and anus.[[1]](http://en.wikipedia.org/wiki/Protostome#cite_note-0) However, this idea has been challenged, because the [Acoelomorpha](http://en.wikipedia.org/wiki/Acoelomorpha), a group which forms a sister group to the rest of the bilaterian animals, have a single mouth which leads into a blind gut (with no anus). The genes employed in the embryonic construction of this mouth are the same as those expressed around the protostome mouth, [[2]](http://en.wikipedia.org/wiki/Protostome#cite_note-Hejnol2008-1)

There are other significant differences between the protostome and deuterostome patterns of development:

* Most protostomes are schizocoelomates, meaning a solid mass of the embryonic [mesoderm](http://en.wikipedia.org/wiki/Mesoderm) splits to form a [coelom](http://en.wikipedia.org/wiki/Coelom). A few, such as [Priapulids](http://en.wikipedia.org/wiki/Priapulid), have no coelom, but they may have descended from schizocoelomate ancestors. On the other hand all known deuterostomes are [enterocoelous](http://en.wikipedia.org/wiki/Enterocoely), meaning that the coelom is formed from longitudinal pouches of the [archenteron](http://en.wikipedia.org/wiki/Archenteron) which then become separate cavities.
* Within the Protostomes a number of phyla undergo what is known as [spiral cleavage](http://en.wikipedia.org/wiki/Spiral_cleavage) which is determinate, meaning that the fate of the cells is determined as they are formed. This is in contrast to deuterostomes which have [radial cleavage](http://en.wikipedia.org/wiki/Radial_cleavage) that is indeterminate.

Current molecular data suggest that protostome animals can be divided into three major groups:

* [Ecdysozoa](http://en.wikipedia.org/wiki/Ecdysozoa), e.g. [arthropods](http://en.wikipedia.org/wiki/Arthropod), [nematodes](http://en.wikipedia.org/wiki/Nematode)
* [Platyzoa](http://en.wikipedia.org/wiki/Platyzoa), e.g. [platyhelminthes](http://en.wikipedia.org/wiki/Platyhelminthes), [rotifers](http://en.wikipedia.org/wiki/Rotifer)
* [Lophotrochozoa](http://en.wikipedia.org/wiki/Lophotrochozoa), e.g. [molluscs](http://en.wikipedia.org/wiki/Mollusc), [annelids](http://en.wikipedia.org/wiki/Annelid)

as well as a number of minor taxa of basal or ambiguous affinity.

# Gill

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*For other uses, see* [*Gill (disambiguation)*](http://en.wikipedia.org/wiki/Gill_(disambiguation))*.*

[](http://en.wikipedia.org/wiki/File:Hermit_Crab_Gills.jpg)

[Caribbean hermit crabs](http://en.wikipedia.org/wiki/Caribbean_hermit_crab) have modified gills that allow them to live in humid conditions

A **gill** is a [respiratory organ](http://en.wikipedia.org/wiki/Respiration_organ) found in many [aquatic](http://en.wikipedia.org/wiki/Aquatic_ecosystem) organisms that extracts dissolved [oxygen](http://en.wikipedia.org/wiki/Oxygen) from [water](http://en.wikipedia.org/wiki/Water), afterward excreting [carbon dioxide](http://en.wikipedia.org/wiki/Carbon_dioxide). The gills of some species such as [hermit crabs](http://en.wikipedia.org/wiki/Hermit_crabs) have adapted to allow respiration on land provided they are kept moist. The microscopic structure of a gill presents a large [surface area](http://en.wikipedia.org/wiki/Surface_area) to the external environment.

Many microscopic aquatic animals, and some that are larger but inactive, can absorb adequate oxygen through the entire surface of their bodies, and so can respire adequately without a gill. However, more complex or more active aquatic organisms usually require a gill or gills.[*[citation needed](http://en.wikipedia.org/wiki/Wikipedia:Citation_needed" \o "Wikipedia:Citation needed)*]

Gills usually consist of thin filaments of tissue, branches, or slender tufted [processes](http://en.wikipedia.org/wiki/Process_(anatomy)) that have a highly folded surface to increase surface area. A high surface area is crucial to the [gas exchange](http://en.wikipedia.org/wiki/Gas_exchange) of aquatic organisms as water contains only 1/20 the dissolved oxygen that air does.[*[citation needed](http://en.wikipedia.org/wiki/Wikipedia:Citation_needed" \o "Wikipedia:Citation needed)*]

With the exception of some aquatic [insects](http://en.wikipedia.org/wiki/Insect), the filaments and lamellae (folds) contain [blood](http://en.wikipedia.org/wiki/Blood) or [coelomic](http://en.wikipedia.org/wiki/Body_cavity) fluid, from which gases are exchanged through the thin walls. The blood carries oxygen to other parts of the body. Carbon dioxide passes from the blood through the thin gill tissue into the water. Gills or gill-like organs, located in different parts of the body, are found in various groups of aquatic animals, including [mollusks](http://en.wikipedia.org/wiki/Mollusk), [crustaceans](http://en.wikipedia.org/wiki/Crustacean), insects, fish, and [amphibians](http://en.wikipedia.org/wiki/Amphibian).

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| --- |
| Contents  [[hide](http://en.wikipedia.org/wiki/Gill)]   * [1 Invertebrate gills](http://en.wikipedia.org/wiki/Gill#Invertebrate_gills)   + [1.1 Physical gills](http://en.wikipedia.org/wiki/Gill#Physical_gills) * [2 Vertebrate gills](http://en.wikipedia.org/wiki/Gill#Vertebrate_gills)   + [2.1 Cartilaginous fish](http://en.wikipedia.org/wiki/Gill#Cartilaginous_fish)   + [2.2 Bony fish](http://en.wikipedia.org/wiki/Gill#Bony_fish)   + [2.3 Other vertebrates](http://en.wikipedia.org/wiki/Gill#Other_vertebrates)   + [2.4 Branchia](http://en.wikipedia.org/wiki/Gill#Branchia) * [3 See also](http://en.wikipedia.org/wiki/Gill#See_also) * [4 References](http://en.wikipedia.org/wiki/Gill#References) |

## [[edit](http://en.wikipedia.org/w/index.php?title=Gill&action=edit&section=1)] Invertebrate gills

[](http://en.wikipedia.org/wiki/File:Pleurobranchaea_meckelii.jpg)

A live individual of the sea [slug](http://en.wikipedia.org/wiki/Slug) [*Pleurobranchaea meckelii*](http://en.wikipedia.org/wiki/Pleurobranchaea_meckelii). The gill (or ctenidium) is visible in this view of the right-hand side of the animal

Respiration in the [Echinodermata](http://en.wikipedia.org/wiki/Echinodermata) (includes [starfish](http://en.wikipedia.org/wiki/Starfish) and [sea urchins](http://en.wikipedia.org/wiki/Sea_urchin)) is carried out using a very primitive version of gills called papulae. These thin protuberances on the surface of the body contain [diverticula](http://en.wikipedia.org/wiki/Diverticulum) of the [water vascular system](http://en.wikipedia.org/wiki/Water_vascular_system). [Crustaceans](http://en.wikipedia.org/wiki/Crustacean), [molluscs](http://en.wikipedia.org/wiki/Mollusc), and some insects have gills that are tufted or plate-like structures at the surface of the body.[*[citation needed](http://en.wikipedia.org/wiki/Wikipedia:Citation_needed" \o "Wikipedia:Citation needed)*]

The gills of other insects are tracheal, and also include both thin plates and tufted structures, and, in the [larval](http://en.wikipedia.org/wiki/Larva) [dragon fly](http://en.wikipedia.org/wiki/Dragon_fly), the wall of the caudal end of the [alimentary tract](http://en.wikipedia.org/wiki/Gastrointestinal_tract) ([rectum](http://en.wikipedia.org/wiki/Rectum)) is richly supplied with tracheae as a rectal gill. Water pumped into and out of the rectum provides oxygen to the closed tracheae. [Aquatic insects](http://en.wikipedia.org/wiki/Aquatic_insects) use a [tracheal](http://en.wikipedia.org/wiki/Invertebrate_trachea) gill, which contains air tubes. The oxygen in these tubes is renewed through the gills.[*[citation needed](http://en.wikipedia.org/wiki/Wikipedia:Citation_needed" \o "Wikipedia:Citation needed)*]

### [[edit](http://en.wikipedia.org/w/index.php?title=Gill&action=edit&section=2)] Physical gills

**Physical gills** are a type of structural adaptation common among some types of aquatic insects, which holds atmospheric oxygen in an area with small openings called [spiracles](http://en.wikipedia.org/wiki/Spiracle). The structure (often called a [plastron](http://en.wikipedia.org/wiki/Plastron)) typically consists of dense patches of [hydrophobic](http://en.wikipedia.org/wiki/Hydrophobic) [setae](http://en.wikipedia.org/wiki/Setae) on the body, which prevent water entry into the spiracles. The physical properties of the interface between the trapped air bubble and surrounding water accomplish gas exchange through the spiracles, almost as if the insect were in atmospheric air. [Carbon dioxide](http://en.wikipedia.org/wiki/Carbon_dioxide) diffuses into the surrounding water due to its high [solubility](http://en.wikipedia.org/wiki/Solubility), while oxygen diffuses into bubbles as the concentration within the bubble has been reduced by [respiration](http://en.wikipedia.org/wiki/Respiration_(physiology)), and nitrogen also diffuses out as its tension has been increased. Oxygen diffuses into the bubble at a higher rate than Nitrogen diffuses out. However, water surrounding the insect can become oxygen-depleted if there is no [water movement](http://en.wikipedia.org/w/index.php?title=Water_movement&action=edit&redlink=1), so many aquatic insects in still water actively direct a flow of water over their bodies.[*[citation needed](http://en.wikipedia.org/wiki/Wikipedia:Citation_needed" \o "Wikipedia:Citation needed)*]

The physical gill mechanism allows aquatic insects with plastrons to remain constantly submerged. Examples include many [beetles](http://en.wikipedia.org/wiki/Beetle) in the family [Elmidae](http://en.wikipedia.org/w/index.php?title=Elmidae&action=edit&redlink=1), aquatic [weevils](http://en.wikipedia.org/wiki/Weevil), and [true bugs](http://en.wikipedia.org/wiki/True_bug) in the family [Aphelocheiridae](http://en.wikipedia.org/w/index.php?title=Aphelocheiridae&action=edit&redlink=1).[[*citation needed*](http://en.wikipedia.org/wiki/Wikipedia:Citation_needed)]

## [[edit](http://en.wikipedia.org/w/index.php?title=Gill&action=edit&section=3)] Vertebrate gills

[](http://en.wikipedia.org/wiki/File:Carp_gill_defect.jpg)

The red gills of this [common carp](http://en.wikipedia.org/wiki/Common_carp) are visible as a result of a [gill flap](http://en.wikipedia.org/wiki/Operculum_(fish)) [birth defect](http://en.wikipedia.org/wiki/Birth_defect).

[](http://en.wikipedia.org/wiki/File:FreshwaterFishGill400x7.jpg)

Freshwater Fish Gills magnified 400 times

The gills of [vertebrates](http://en.wikipedia.org/wiki/Vertebrate) typically develop in the walls of the [pharynx](http://en.wikipedia.org/wiki/Pharynx), along a series of gill slits opening to the exterior. Most species employ a [countercurrent exchange](http://en.wikipedia.org/wiki/Countercurrent_exchange) system to enhance the diffusion of substances in and out of the gill, with blood and water flowing in opposite directions to each other. The gills are composed of comb-like filaments, the **gill lamellae**, which help increase their surface area for oxygen exchange.[[1]](http://en.wikipedia.org/wiki/Gill#cite_note-0)

When a fish breathes, it draws in a mouthful of water at regular intervals. Then it draws the sides of its throat together, forcing the water through the gill openings, so that it passes over the gills to the outside. Fish gill slits may be the evolutionary ancestors of the [tonsils](http://en.wikipedia.org/wiki/Tonsil), [thymus gland](http://en.wikipedia.org/wiki/Thymus_gland), and [Eustachian tubes](http://en.wikipedia.org/wiki/Eustachian_tube), as well as many other structures derived from the embryonic [branchial pouches](http://en.wikipedia.org/wiki/Branchial_pouch).[[*citation needed*](http://en.wikipedia.org/wiki/Wikipedia:Citation_needed)]

### [[edit](http://en.wikipedia.org/w/index.php?title=Gill&action=edit&section=4)] Cartilaginous fish

[Sharks](http://en.wikipedia.org/wiki/Shark) and [rays](http://en.wikipedia.org/wiki/Ray_(fish)) typically have five pairs of gill slits that open directly to the outside of the body, though some more primitive sharks have six or seven pairs. Adjacent slits are separated by a [cartilaginous](http://en.wikipedia.org/wiki/Cartilage) gill arch from which projects a long sheet-like [septum](http://en.wikipedia.org/wiki/Septum), partly supported by a further piece of cartilage called the **gill ray**. The individual lamellae of the gills lie on either side of the septum. The base of the arch may also support [gill rakers](http://en.wikipedia.org/wiki/Gill_raker), small projecting elements that help to filter food from the water.[[2]](http://en.wikipedia.org/wiki/Gill#cite_note-VB-1)

A smaller opening, the [spiracle](http://en.wikipedia.org/wiki/Spiracle), lies in front of the first [gill slit](http://en.wikipedia.org/wiki/Gill_slit). This bears a small **pseudobranch** that resembles a gill in structure, but only receives blood already oxygenated by the true gills.[[2]](http://en.wikipedia.org/wiki/Gill#cite_note-VB-1) The spiracle is thought to be [homologous](http://en.wikipedia.org/wiki/Homology_(biology)) to the ear opening in higher vertebrates.[[3]](http://en.wikipedia.org/wiki/Gill#cite_note-2)

Most sharks rely on ram ventilation, forcing water into the mouth and over the gills by rapidly swimming forward. In slow-moving or bottom dwelling species, especially among skates and rays, the spiracle may be enlarged, and the fish breathes by sucking water through this opening, instead of through the mouth.[[2]](http://en.wikipedia.org/wiki/Gill#cite_note-VB-1)

[Chimaeras](http://en.wikipedia.org/wiki/Chimaera) differ from other cartilagenous fish, having lost both the spiracle and the fifth gill slit. The remaining slits are covered by an [operculum](http://en.wikipedia.org/wiki/Operculum_(fish)), developed from the septum of the gill arch in front of the first gill.[[2]](http://en.wikipedia.org/wiki/Gill#cite_note-VB-1)

### [[edit](http://en.wikipedia.org/w/index.php?title=Gill&action=edit&section=5)] Bony fish

[](http://en.wikipedia.org/wiki/File:Tuna_Gills_in_Situ_cut.jpg)

The red gills inside a detached [tuna](http://en.wikipedia.org/wiki/Tuna) head (viewed from behind)

In [bony fish](http://en.wikipedia.org/wiki/Osteichthyes), the gills lie in a branchial chamber covered by a bony operculum. The great majority of bony fish species have five pairs of gills, although a few have lost some over the course of evolution. The operculum can be important in adjusting the pressure of water inside of the pharynx to allow proper ventilation of the gills, so that bony fish do not have to rely on ram ventilation (and hence near constant motion) to breathe. Valves inside the mouth keep the water from escaping.[[2]](http://en.wikipedia.org/wiki/Gill#cite_note-VB-1)

The gill arches of bony fish typically have no septum, so that the gills alone project from the arch, supported by individual gill rays. Some species retain gill rakers. Though all but the most primitive bony fish lack a spiracle, the pseudobranch associated with it often remains, being located at the base of the operculum. This is, however, often greatly reduced, consisting of a small mass of cells without any remaining gill-like structure.[[2]](http://en.wikipedia.org/wiki/Gill#cite_note-VB-1)

Marine [teleosts](http://en.wikipedia.org/wiki/Teleost) also use gills to excrete [electrolytes](http://en.wikipedia.org/wiki/Electrolyte). The gills' large surface area tends to create a problem for fish that seek to regulate the [osmolarity](http://en.wikipedia.org/wiki/Osmolarity) of their internal fluids. Saltwater is less dilute than these internal fluids, so saltwater fish lose large quantities of water osmotically through their gills. To regain the water, they drink large amounts of [seawater](http://en.wikipedia.org/wiki/Seawater) and excrete the [salt](http://en.wikipedia.org/wiki/Salt). Freshwater is more dilute than the internal fluids of fish, however, so freshwater fish gain water [osmotically](http://en.wikipedia.org/wiki/Osmosis) through their gills.[[2]](http://en.wikipedia.org/wiki/Gill#cite_note-VB-1)

### [[edit](http://en.wikipedia.org/w/index.php?title=Gill&action=edit&section=6)] Other vertebrates

[](http://en.wikipedia.org/wiki/File:Smooth_Newt_larva_(aka).jpg)

An [Alpine newt](http://en.wikipedia.org/wiki/Alpine_newt) larva showing the external gills, which flare just behind the head

[Lampreys](http://en.wikipedia.org/wiki/Lamprey) and [hagfish](http://en.wikipedia.org/wiki/Hagfish) do not have gill slits as such. Instead, the gills are contained in spherical pouches, with a circular opening to the outside. Like the gill slits of higher fish, each pouch contains two gills. In some cases, the openings may be fused together, effectively forming an operculum. Lampreys have seven pairs of pouches, while hagfishes may have six to fourteen, depending on the species. In the hagfish, the pouches connect with the pharynx internally. In adult lampreys, a separate respiratory tube develops beneath the pharynx proper, separating food and water from respiration by closing a valve at its anterior end.[[2]](http://en.wikipedia.org/wiki/Gill#cite_note-VB-1)

[Tadpoles](http://en.wikipedia.org/wiki/Tadpole) of [amphibians](http://en.wikipedia.org/wiki/Amphibian) have from three to five gill slits that don't contain actual gills. There is usually no spiracle or true operculum, though many species have an operculum-like structure. Instead of internal gills, they develop three feathery external gills that grow from the outer surface of the gill arches. Sometimes adults retain these, but they usually disappear at [metamorphosis](http://en.wikipedia.org/wiki/Metamorphosis). [Lungfish](http://en.wikipedia.org/wiki/Lungfish) larvae also have external gills, as does the primitive [ray-finned fish](http://en.wikipedia.org/wiki/Actinopterygii) [*Polypterus*](http://en.wikipedia.org/wiki/Polypterus), though the latter has a structure different than amphibians.[[2]](http://en.wikipedia.org/wiki/Gill#cite_note-VB-1)

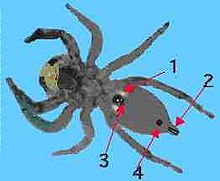
### [[edit](http://en.wikipedia.org/w/index.php?title=Gill&action=edit&section=7)] Branchia

**Branchia** (pl. **branchiæ**) is the [Ancient Greek](http://en.wikipedia.org/wiki/Ancient_Greek) naturalists' name for gills. [Galen](http://en.wikipedia.org/wiki/Galen) observed that fish had multitudes of openings (foramina), big enough to admit gases, but too fine to give passage to water. [Pliny the Elder](http://en.wikipedia.org/wiki/Pliny_the_Elder) held that fish respired by their gills, but observed that [Aristotle](http://en.wikipedia.org/wiki/Aristotle) was of another opinion.[[4]](http://en.wikipedia.org/wiki/Gill#cite_note-3) The word *branchia* comes from the [Greek](http://en.wikipedia.org/wiki/Greek_language) βράγχια, "gills", plural of βράγχιον (in singular, meaning a [fin](http://en.wikipedia.org/wiki/Fin)).[[5]](http://en.wikipedia.org/wiki/Gill#cite_note-4)

# Book lung

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[](http://en.wikipedia.org/wiki/File:Spin_vent_diag.jpg)

In this spider diagram, the book lung is labelled 1.

Spider [book lungs](http://en.wikipedia.org/wiki/Book_lungs) (cross section)

A **book lung** is a type of [respiration organ](http://en.wikipedia.org/wiki/Respiration_organ) used for atmospheric gas exchange and is found in [arachnids](http://en.wikipedia.org/wiki/Arachnid), such as [scorpions](http://en.wikipedia.org/wiki/Scorpion) and [spiders](http://en.wikipedia.org/wiki/Spider). Each of these organs is found inside a ventral abdominal cavity and connects with the surroundings through a small opening. Book lungs are not related to the [lungs](http://en.wikipedia.org/wiki/Lungs) of modern land-dwelling [vertebrates](http://en.wikipedia.org/wiki/Vertebrate). Their name describes their structure. Stacks of alternating air pockets and hemolymph-filled tissue give them an appearance similar to a "folded" book.[[1]](http://en.wikipedia.org/wiki/Book_lung#cite_note-rain-0) Their number varies from just one pair in most spiders to four pairs in scorpions. Sometimes the book lungs can be absent and the gas exchange is performed by the thin walls inside the cavity instead, with its surface area increased by branching into the body as thin tubes called [tracheae](http://en.wikipedia.org/wiki/Invertebrate_trachea). It is possible that the tracheae have evolved directly from the book lungs, because in some spiders the tracheae have a small number of greatly elongated chambers. Many [arachnids](http://en.wikipedia.org/wiki/Arachnid), like [mites](http://en.wikipedia.org/wiki/Mite) and harvestmen ([Opiliones](http://en.wikipedia.org/wiki/Opiliones" \o "Opiliones)), have no traces of book lungs and breathe through tracheae or through their body surface only.

The unfolded "pages" (plates) of the book lung are filled with [hemolymph](http://en.wikipedia.org/wiki/Hemolymph) (the [arthropod](http://en.wikipedia.org/wiki/Arthropod) [blood](http://en.wikipedia.org/wiki/Blood)). The folds maximize the surface exposed to [air](http://en.wikipedia.org/wiki/Air), and thereby maximize the amount of [gas](http://en.wikipedia.org/wiki/Gas) exchanged with the environment. In most [species](http://en.wikipedia.org/wiki/Species), no motion of the plates is required to facilitate this kind of [respiration](http://en.wikipedia.org/wiki/Respiration_(physiology)).

The oldest book lungs have been recovered from extinct [trigonotarbid](http://en.wikipedia.org/wiki/Trigonotarbid) arachnids preserved in the 410-million-year-old [Rhynie chert](http://en.wikipedia.org/wiki/Rhynie_chert) of Scotland. These [Devonian](http://en.wikipedia.org/wiki/Devonian) fossil lungs are almost indistinguishable from the lungs of modern arachnids.[[2]](http://en.wikipedia.org/wiki/Book_lung#cite_note-1)

The absence or presence of book lungs divides the Arachnida into two main groups, the pulmonate arachnids (book lungs present; [scorpions](http://en.wikipedia.org/wiki/Scorpion) and the [Tetrapulmonata](http://en.wikipedia.org/wiki/Tetrapulmonata); [whip scorpions](http://en.wikipedia.org/wiki/Whip_scorpion), [Schizomida](http://en.wikipedia.org/wiki/Schizomida), [Amblypygi](http://en.wikipedia.org/wiki/Amblypygi), and [spiders](http://en.wikipedia.org/wiki/Spider)), and the apulmonate arachnids (book lungs absent; [microwhip scorpions](http://en.wikipedia.org/wiki/Microwhip_scorpion), [harvestmen](http://en.wikipedia.org/wiki/Harvestmen), [Acarina](http://en.wikipedia.org/wiki/Acarina), [pseudoscorpions](http://en.wikipedia.org/wiki/Pseudoscorpion), [Ricinulei](http://en.wikipedia.org/wiki/Ricinulei) and [sunspiders](http://en.wikipedia.org/wiki/Solifugae)). One of the long-running controversies in arachnid evolution is whether the book lung evolved once in the arachnid common ancestor,[[3]](http://en.wikipedia.org/wiki/Book_lung" \l "cite_note-2) or whether it evolved in multiple groups of arachnids in parallel as they came onto land.

## [[edit](http://en.wikipedia.org/w/index.php?title=Book_lung&action=edit&section=1)] Book gills

[](http://en.wikipedia.org/wiki/File:Horseshoe_crab_female.jpg)

Underside of a female [horseshoe crab](http://en.wikipedia.org/wiki/Horseshoe_crab) showing the legs and book gills.

Scientists think book lungs evolved from book [gills](http://en.wikipedia.org/wiki/Gill). Although they have a similar book-like structure, they are found in different locations. Book gills are found externally while book lungs are found internally.[[4]](http://en.wikipedia.org/wiki/Book_lung#cite_note-3) Book gills are still found in [horseshoe crabs](http://en.wikipedia.org/wiki/Horseshoe_crab) which have five pairs of them, the flap in front of them being the genital operculum which lacks gills. Book gills are flap-like appendages that effect gas exchange within water and seem to have their origin as modified legs. On the inside of each appendage there are attached over 100 thin leaf-like membranes called *lamellae* which appear as pages in a book, and are the areas of the gill where gas exchange takes place. These appendages move with rhythmic movements to drive blood in and out of the lamellae and to circulate water over them. Respiration being their main purpose, they can also be used for swimming in young individuals. If they are kept moist, the horseshoe crab can live on land for many hours.

# Invertebrate trachea

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The **invertebrate trachea** refers to the open [respiratory system](http://en.wikipedia.org/wiki/Respiratory_system) composed of [spiracles](http://en.wikipedia.org/wiki/Spiracles), tracheae, and [tracheoles](http://en.wikipedia.org/wiki/Tracheole) that [terrestrial](http://en.wikipedia.org/wiki/Terrestrial_animal) [arthropods](http://en.wikipedia.org/wiki/Arthropod) have to transport [metabolic](http://en.wikipedia.org/wiki/Metabolism) [gases](http://en.wikipedia.org/wiki/Gas) to and from tissues.

The distribution of spiracles can vary greatly among the many [orders](http://en.wikipedia.org/wiki/Order_(biology)) of [insects](http://en.wikipedia.org/wiki/Insect), but in general each segment of the body can have no more than one pair of spiracles, each of which connects to an atrium and has a relatively large tracheal tube behind it. The tracheae are invaginations of the cuticular [exoskeleton](http://en.wikipedia.org/wiki/Exoskeleton) that branch ([anastomose](http://en.wikipedia.org/wiki/Anastomosis" \o "Anastomosis)) throughout the body with diameters from only a few micrometres up to 0.8 mm. The smallest tubes, tracheoles, penetrate cells and serve as sites of [diffusion](http://en.wikipedia.org/wiki/Diffusion) for [water](http://en.wikipedia.org/wiki/Water), [oxygen](http://en.wikipedia.org/wiki/Oxygen), and [carbon dioxide](http://en.wikipedia.org/wiki/Carbon_dioxide). Gas may be conducted through the respiratory system by means of active [ventilation](http://en.wikipedia.org/wiki/Ventilation_(physiology)) or passive [diffusion](http://en.wikipedia.org/wiki/Diffusion). Unlike [vertebrates](http://en.wikipedia.org/wiki/Vertebrates), insects do not generally carry [oxygen](http://en.wikipedia.org/wiki/Oxygen) in their [haemolymph](http://en.wikipedia.org/wiki/Hemolymph). This is one of the factors that may limit their size.

A tracheal tube may contain ridge-like circumferential rings of [taenidia](http://en.wikipedia.org/wiki/Taenidia) in various [geometries](http://en.wikipedia.org/wiki/Geometry) such as loops or [helices](http://en.wikipedia.org/wiki/Helix). In the [head](http://en.wikipedia.org/wiki/Head), [thorax](http://en.wikipedia.org/wiki/Thorax), or [abdomen](http://en.wikipedia.org/wiki/Abdomen), tracheae may also be connected to air sacs. Many insects, such as [grasshoppers](http://en.wikipedia.org/wiki/Grasshopper) and [bees](http://en.wikipedia.org/wiki/Bee), which actively pump the air sacs in their abdomen, are able to control the flow of air through their body. In some aquatic insects, the tracheae exchange gas through the body wall directly, in the form of a [gill](http://en.wikipedia.org/wiki/Gill). Note that despite being internal, the tracheae of arthropods are shed during moulting ([ecdysis](http://en.wikipedia.org/wiki/Ecdysis" \o "Ecdysis)).

Some terrestrial [woodlice](http://en.wikipedia.org/wiki/Woodlice) have evolved [pseudotrachea](http://en.wikipedia.org/w/index.php?title=Pseudotrachea&action=edit&redlink=1), also called [*corpora allata*](http://en.wikipedia.org/wiki/Corpus_allatum) (singular: *corpus allatum*), which is made up of air tubes that delivers oxygen to their [haemolymph](http://en.wikipedia.org/wiki/Hemolymph); a similar system has been found in some [caterpillars](http://en.wikipedia.org/wiki/Caterpillar).

# Reproductive isolation

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| --- | --- |
|  | It has been suggested that [*Isolating mechanisms*](http://en.wikipedia.org/wiki/Isolating_mechanisms) be [merged](http://en.wikipedia.org/wiki/Wikipedia:Merging) into this article or section. ([Discuss](http://en.wikipedia.org/wiki/Talk:Reproductive_isolation)) *Proposed since January 2010.* |

The **mechanisms of reproductive isolation** or **hybridization barriers** are a collection of mechanisms, [behaviors](http://en.wikipedia.org/wiki/Animal_behavior) and [physiological processes](http://en.wikipedia.org/wiki/Physiology) that prevent the members of two different [species](http://en.wikipedia.org/wiki/Species) that cross or mate from producing [offspring](http://en.wikipedia.org/wiki/Offspring), or which ensure that any offspring that may be produced is not fertile. These barriers maintain the integrity of a species over time, reducing or directly impeding [gene flow](http://en.wikipedia.org/wiki/Gene_flow) between individuals of different species, allowing the conservation of each species’ characteristics.[[1]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-T.Baker-0)[[2]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Barton-1)[[3]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Strickberger-2)[[4]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-FUTUYMA-3)

The mechanisms of reproductive isolation have been classified in a number of ways. [citation needed] Zoologist [Ernst Mayr](http://en.wikipedia.org/wiki/Ernst_Mayr) classified the mechanisms of reproductive isolation in two broad categories: those that act before [fertilization](http://en.wikipedia.org/wiki/Fertilization) (or before [mating](http://en.wikipedia.org/wiki/Mating) in the case of [animals](http://en.wikipedia.org/wiki/Animal), which are called pre-copulatory) and those that act after.[[5]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Mayr-4) These have also been termed pre-zygotic and post-zygotic mechanisms. The different mechanisms of reproductive isolation are [genetically](http://en.wikipedia.org/wiki/Genetics) controlled and it has been demonstrated experimentally that they can evolve in species whose geographic distribution overlaps ([sympatric speciation](http://en.wikipedia.org/wiki/Sympatric_speciation)) or as the result of adaptive divergence that accompanies [allopatric speciation](http://en.wikipedia.org/wiki/Allopatric_speciation).

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| Contents  [[hide](http://en.wikipedia.org/wiki/Reproductive_isolation)]   * [1 Isolation mechanisms that occur before breeding or copulation (pre-zygotic isolation)](http://en.wikipedia.org/wiki/Reproductive_isolation#Isolation_mechanisms_that_occur_before_breeding_or_copulation_.28pre-zygotic_isolation.29)   + [1.1 Temporal or habitat isolation](http://en.wikipedia.org/wiki/Reproductive_isolation#Temporal_or_habitat_isolation)   + [1.2 Sexual isolation by behavior or conduct](http://en.wikipedia.org/wiki/Reproductive_isolation#Sexual_isolation_by_behavior_or_conduct)   + [1.3 Mechanical isolation](http://en.wikipedia.org/wiki/Reproductive_isolation#Mechanical_isolation)   + [1.4 Gametic Isolation](http://en.wikipedia.org/wiki/Reproductive_isolation#Gametic_Isolation) * [2 Isolation mechanisms that occur after breeding or copulation (post-zygotic isolation)](http://en.wikipedia.org/wiki/Reproductive_isolation#Isolation_mechanisms_that_occur_after_breeding_or_copulation_.28post-zygotic_isolation.29)   + [2.1 Zygote mortality and non-viability of hybrids](http://en.wikipedia.org/wiki/Reproductive_isolation#Zygote_mortality_and_non-viability_of_hybrids)   + [2.2 Hybrid sterility](http://en.wikipedia.org/wiki/Reproductive_isolation#Hybrid_sterility) * [3 Multiple mechanisms](http://en.wikipedia.org/wiki/Reproductive_isolation#Multiple_mechanisms) * [4 Hybrid gender: Haldane's Rule](http://en.wikipedia.org/wiki/Reproductive_isolation#Hybrid_gender:_Haldane.27s_Rule) * [5 The genetics of reproductive isolation barriers](http://en.wikipedia.org/wiki/Reproductive_isolation#The_genetics_of_reproductive_isolation_barriers)   + [5.1 Pre-copulatory isolation mechanisms in animals](http://en.wikipedia.org/wiki/Reproductive_isolation#Pre-copulatory_isolation_mechanisms_in_animals)   + [5.2 Post copulation or fertilization isolation mechanisms in animals](http://en.wikipedia.org/wiki/Reproductive_isolation#Post_copulation_or_fertilization_isolation_mechanisms_in_animals)   + [5.3 Post copulation or fertilization isolation mechanisms in plants](http://en.wikipedia.org/wiki/Reproductive_isolation#Post_copulation_or_fertilization_isolation_mechanisms_in_plants)   + [5.4 Incompatibility caused by microorganisms](http://en.wikipedia.org/wiki/Reproductive_isolation#Incompatibility_caused_by_microorganisms) * [6 Selection for reproductive isolation](http://en.wikipedia.org/wiki/Reproductive_isolation#Selection_for_reproductive_isolation) * [7 See also](http://en.wikipedia.org/wiki/Reproductive_isolation#See_also) * [8 Notes](http://en.wikipedia.org/wiki/Reproductive_isolation#Notes) * [9 Bibliography](http://en.wikipedia.org/wiki/Reproductive_isolation#Bibliography) * [10 References](http://en.wikipedia.org/wiki/Reproductive_isolation#References) |

## [[edit](http://en.wikipedia.org/w/index.php?title=Reproductive_isolation&action=edit&section=1)] Isolation mechanisms that occur before breeding or copulation (pre-zygotic isolation)

Pre-zygotic isolation mechanisms are the most economic in terms of the [biological efficiency](http://en.wikipedia.org/wiki/Natural_selection) of a population, as resources are not wasted on the production of a descendent that is weak, non-viable or sterile.

### [[edit](http://en.wikipedia.org/w/index.php?title=Reproductive_isolation&action=edit&section=2)] Temporal or habitat isolation

Any of the factors that prevent potentially fertile individuals from meeting will reproductively isolate the members of distinct species. The types of barriers that can cause this isolation include: different [habitats](http://en.wikipedia.org/wiki/Habitat), physical barriers, and a difference in the time of [sexual maturity](http://en.wikipedia.org/wiki/Sexual_maturity) or flowering.[[6]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Levine-5)[[7]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Wiens-6) When factors change, especially physical barriers, often, species will branch off.

An example of the ecological or habitat differences that impede the meeting of potential pairs occurs in two fish species of the family [*Gasterosteidae*](http://en.wikipedia.org/wiki/Gasterosteidae) (sticklebacks). One species lives all year round in fresh water, mainly in small streams. The other species lives in the sea during winter, but in spring and summer individuals migrate to river estuaries to reproduce. The members of the two populations are reproductively isolated due to their adaptations to distinct salt concentrations.[[6]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Levine-5) An example of reproductive isolation due to differences in the mating season are found in the toad species [*Bufo americanus*](http://en.wikipedia.org/wiki/Bufo_americanus) and [*Bufo fowleri*](http://en.wikipedia.org/wiki/Bufo_fowleri) . The members of these species can be successfully crossed in the laboratory producing healthy, fertile hybrids. However, mating does not occur in the wild even though the geographical distribution of the two species overlaps. The reason for the absence of inter-species mating is that *B. americanus* mates in early summer and *B. fowleri* in late summer.[[6]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Levine-5) Certain plant species, such as [*Tradescantia canaliculata*](http://en.wikipedia.org/w/index.php?title=Tradescantia_canaliculata&action=edit&redlink=1) and [*T. subaspera*](http://en.wikipedia.org/w/index.php?title=Tradescantia_subaspera&action=edit&redlink=1), are sympatric throughout their geographic distribution yet they are reproductively isolated as they flower at different times of the year. In addition, one species grows in sunny areas and the other in deeply shaded areas.[[3]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Strickberger-2)[[7]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Wiens-6)

### [[edit](http://en.wikipedia.org/w/index.php?title=Reproductive_isolation&action=edit&section=3)] Sexual isolation by behavior or conduct

The different [mating](http://en.wikipedia.org/wiki/Mating) rituals of animal species creates extremely powerful reproductive barriers, termed sexual or behavior isolation, that isolate apparently similar species in the majority of the groups of the animal kingdom. In [dioecious](http://en.wikipedia.org/wiki/Dioecious) species, males and females have to search for a partner, be in proximity to each other, carry out the complex mating rituals and finally copulate or release their gametes into the environment in order to breed. [[8]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Wu1995-7) [[9]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-West-eberhard1983-8) [[10]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Mendelson2003-9)

The songs of birds, insects and many other animals are part of a ritual to attract potential partners of their own species. The song presents specific patterns recognizable only by members of the same species, and therefore represents a mechanism of reproductive isolation. This recording is the song of a species of [cicada](http://en.wikipedia.org/wiki/Cicada), recorded in Lower Hutt, [New Zealand](http://en.wikipedia.org/wiki/New_Zealand) on 15th February 2006.

Mating dances, the songs of males to attract females or the mutual grooming of pairs, are all examples of typical courtship behavior that allows both recognition and reproductive isolation. This is because each of the stages of courtship depend on the behavior of the partner. The male will only move onto the second stage of the exhibition if the female shows certain responses in her behavior. He will only pass onto the third stage when she displays a second key behavior. The behaviors of both interlink, are synchronized in time and lead finally to copulation or the liberation of gametes into the environment. No animal that is not physiologically suitable for fertilization can complete this demanding chain of behavior. In fact, the smallest difference in the courting patterns of two species is enough to prevent mating (for example, a specific song pattern acts as an isolation mechanism in distinct species of grasshopper of the genus [*Chorthippus*](http://en.wikipedia.org/wiki/Chorthippus).[[11]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Perdeck1958-10)). Even where there are minimal morphological differences between species, differences in behavior can be enough to prevent mating. For example, [*Drosophila melanogaster*](http://en.wikipedia.org/wiki/Drosophila_melanogaster) and [*D. simulans*](http://en.wikipedia.org/wiki/Drosophila_simulans) which are considered twin species due to their morphological similarity, do not mate even if they are kept together in a laboratory.[[3]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Strickberger-2)[[12]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-pc-11) [*Drosophila ananassae*](http://en.wikipedia.org/w/index.php?title=Drosophila_ananassae&action=edit&redlink=1) and *D. pallidosa* are twin species from [Melanesia](http://en.wikipedia.org/wiki/Melanesia). In the wild they rarely produce hybrids, although in the laboratory it is possible to produce fertile offspring. Studies of their sexual behavior show that the males court the females of both species but the females show a marked preference for mating with males of their own species. A different regulator region has been found on Chromosome II of both species that affects the selection behavior of the females.[[12]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-pc-11)

[Pheromones](http://en.wikipedia.org/wiki/Pheromones) play an important role in the sexual isolation of insect species.[[13]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Coyne1994-12) These compounds serve to identify individuals of the same species and of the same or different sex. Evaporated molecules of [volatile](http://en.wikipedia.org/wiki/Volatile_organic_compound) pheromones can serve as a wide-reaching chemical signal. In other cases, pheromones may be detected only at a short distance or by contact.

In species of the *melanogaster* group of *Drosophila*, the pheromones of the females are mixtures of different compounds, there is a clear dimorphism in the type and/or quantity of compounds present for each sex. In addition, there are differences in the quantity and quality of constituent compounds between related species, it is assumed that the pheromones serve to distinguish between individuals of each species. An example of the role of pheromones in sexual isolation is found in 'corn borers' in the genus [*Ostrinia*](http://en.wikipedia.org/wiki/Ostrinia). There are two twin species in Europe that occasionally cross. The females of both species produce pheromones that contain a volatile compound which has two [isomers](http://en.wikipedia.org/wiki/Isomer), E and Z; 99% of the compound produced by the females of one species is in the E isomer form, while the females of the other produce 99% isomer Z. The production of the compound is controlled by just one [locus](http://en.wikipedia.org/wiki/Locus_(genetics)) and the [interspecific hybrid](http://en.wikipedia.org/wiki/Hybrid_(biology)) produces an equal mix of the two isomers. The males, for their part, almost exclusively detect the isomer emitted by the females of their species, such that the hybridization although possible is scarce. The perception of the males is controlled by one [gene](http://en.wikipedia.org/wiki/Gene), distinct from the one for the production of isomers, the [heterozygous](http://en.wikipedia.org/wiki/Heterozygous) males show a moderate response to the odour of either type. In this case, just 2 'loci' produce the effect of ethological isolation between species that are genetically very similar.[[12]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-pc-11)

Sexual isolation between two species can be asymmetrical. This can happen when the mating that produces descendants only allows one of the two species to function as the female progenitor and the other as the male, while the reciprocal cross does not occur. For instance, half of the [wolves](http://en.wikipedia.org/wiki/Wolf) tested in the [Great Lakes](http://en.wikipedia.org/wiki/Great_Lakes) area of [America](http://en.wikipedia.org/wiki/United_States) show [mitochondrial DNA](http://en.wikipedia.org/wiki/Mitochondrial_DNA) sequences of [coyotes](http://en.wikipedia.org/wiki/Coyote). While mitochondrial DNA from wolves is never found in coyote populations. This probably reflects an asymmetry in inter-species mating due to the difference in size of the two species as male wolves take advantage of their greater size in order to mate with female coyotes, while female wolves and male coyotes do not mate[[14]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-LEHMAN-13) [[a]](http://en.wikipedia.org/wiki/Reproductive_isolation#endnote_Anone).

### [[edit](http://en.wikipedia.org/w/index.php?title=Reproductive_isolation&action=edit&section=4)] Mechanical isolation

[](http://en.wikipedia.org/wiki/File:Flores.gif)

The [flowers](http://en.wikipedia.org/wiki/Flower) of many species of [*Angiosperm*](http://en.wikipedia.org/wiki/Angiosperm) have evolved to attract and reward a single or a few pollinator species (insects, birds, mammals). Their wide diversity of form, colour, fragrance and presence of nectar is, in many cases, the result of [coevolution](http://en.wikipedia.org/wiki/Coevolution) with the pollinator species. This dependency on its pollinator species also acts as a reproductive isolation barrier.

Mating pairs may not be able to couple successfully if their genitals are not compatible. The relationship between the reproductive isolation of species and the form of their genital organs was signaled for the first time in 1844 by the French [entomologist](http://en.wikipedia.org/wiki/Entomologist) [Léon Dufour](http://en.wikipedia.org/wiki/L%C3%A9on_Jean_Marie_Dufour). Insects' rigid carapaces act in a manner analogous to a lock and key, as they will only allow mating between individuals with complementary structures, that is, males and females of the same species (termed *co-specifics*).

Evolution has led to the development of genital organs with increasingly complex and divergent characteristics, which will cause mechanical isolation between species. Certain characteristics of the genital organs will often have converted them into mechanisms of isolation. However, numerous studies show that organs that are anatomically very different can be functionally compatible, indicating that other factors also determine the form of these complicated structures.[[15]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-patc-14)

Mechanical isolation also occurs in plants and this is related to the adaptation and [coevolution](http://en.wikipedia.org/wiki/Coevolution) of each species in the attraction of a certain type of pollinator (where [pollination](http://en.wikipedia.org/wiki/Pollination) is [zoophilic](http://en.wikipedia.org/wiki/Zoophilia)) through a collection of [morphophysiological](http://en.wikipedia.org/wiki/Morphology_(biology)) characteristics of the flowers (called [floral syndrome](http://en.wikipedia.org/w/index.php?title=Floral_syndrome&action=edit&redlink=1)), in such a way that the transport of [pollen](http://en.wikipedia.org/wiki/Pollen) to other species does not occur.[[16]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Grant1994-15)

### [[edit](http://en.wikipedia.org/w/index.php?title=Reproductive_isolation&action=edit&section=5)] Gametic Isolation

The synchronous [spawning](http://en.wikipedia.org/wiki/Spawn_(biology)) of many species of coral in marine [reefs](http://en.wikipedia.org/wiki/Reefs) means that inter-species hybridization can take place as the gametes of hundreds of individuals of tens of species are liberated into the same water at the same time. Approximately a third of all the possible crosses between species are compatible, in the sense that the gametes will fuse and lead to individual hybrids. This hybridization apparently plays a fundamental role in the evolution of coral species.[[17]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-RAWSON-16) However, the other two-thirds of possible crosses are incompatible. It has been observed that in [sea urchins](http://en.wikipedia.org/wiki/Sea_urchin) of the genus [*Strongylocentrotus*](http://en.wikipedia.org/wiki/Strongylocentrotus) the concentration of [spermatocytes](http://en.wikipedia.org/wiki/Spermatocyte) that allow 100% fertilization of the ovules of the same species is only able to fertilize 1.5% of the ovules of other species. This inability to produce hybrid offspring, despite the fact that the gametes are found at the same time and in the same place, is due to a phenomenon known as *gamete incompatibility*, which is often found between marine invertebrates, and whose physiological causes are not fully understood.[[18]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-autogenerated1-17)[[19]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Harper-18)

In some [*Drosophila*](http://en.wikipedia.org/wiki/Drosophila) crosses, the swelling of the female's [vagina](http://en.wikipedia.org/wiki/Vagina) has been noted following insemination. This has the effect of consequently, preventing the fertilization of the ovule by sperm of a different species.[[20]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-autogenerated2-19)

In plants the pollen grains of a species can germinate in the [stigma](http://en.wikipedia.org/wiki/Gynoecium) and grow in the [style](http://en.wikipedia.org/wiki/Gynoecium) of other species. However, the growth of the pollen tubes may be detained at some point between the stigma and the ovules, in such a way that fertilization does not take place. This mechanism of reproductive isolation is common in the [Angiosperms](http://en.wikipedia.org/wiki/Angiosperms) and is called *cross-incompatibility* or *incongruence*.[[21]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Sala-20)[[22]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Hogenboom1975-21) A relationship exists between self-incompatibility and the phenomenon of cross-incompatibility. In general crosses between individuals of a self-compatible species (SC) with individuals of a self-incompatible (SI) species give hybrid offspring. On the other hand, a reciprocal cross (SI x SC) will not produce offspring, because the pollen tubes will not reach the ovules. This is known as *unilateral incompatibility*, which also occurs when two SC or two SI species are crossed.[[23]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Hadley-22)

[](http://en.wikipedia.org/wiki/File:Reef0484.jpg)

In [coral reefs](http://en.wikipedia.org/wiki/Coral_reefs), *gamete incompatibility* prevents the formation of numerous inter-species hybrids.

## [[edit](http://en.wikipedia.org/w/index.php?title=Reproductive_isolation&action=edit&section=6)] Isolation mechanisms that occur after breeding or copulation (post-zygotic isolation)

A number of mechanisms which act after fertilisation preventing successful inter-population crossing are discussed below.

### [[edit](http://en.wikipedia.org/w/index.php?title=Reproductive_isolation&action=edit&section=7)] Zygote mortality and non-viability of hybrids

A type of incompatibility that is found as often in plants as in animals occurs when the [ovule](http://en.wikipedia.org/wiki/Ovule) is fertilized but the [zygote](http://en.wikipedia.org/wiki/Zygote) does not develop, or it develops and the resulting individual has a reduced viability.[[3]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Strickberger-2) This is the case for crosses between species of the [frog](http://en.wikipedia.org/wiki/Frog) genus, where widely differing results are observed depending of the species involved. In some crosses there is no segmentation of the zygote (or it may be that the hybrid is extremely non-viable and changes occur from the first [mitosis](http://en.wikipedia.org/wiki/Mitosis)). In others, normal segmentation occurs in the [blastula](http://en.wikipedia.org/wiki/Blastula) but [gastrulation](http://en.wikipedia.org/wiki/Gastrulation) fails. Finally, in other crosses, the initial stages are normal but errors occur in the final phases of [embryo development](http://en.wikipedia.org/wiki/Embryo_development). This indicates differentiation of the embryo development genes (or gene complexes) in these species and these differences determine the non-viability of the hybrids.[[24]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Moore-23)

Similar results are observed in mosquitos of the [Culex](http://en.wikipedia.org/wiki/Culex) genus, but the differences are seen between [reciprocal crosses](http://en.wikipedia.org/wiki/Reciprocal_cross), from which it is concluded that the same effect occurs in the interaction between the genes of the [cell nucleus](http://en.wikipedia.org/wiki/Cell_nucleus) (inherited from both parents) as occurs in the genes of the [cytoplasmic organelles](http://en.wikipedia.org/w/index.php?title=Cytoplasmic_organelles&action=edit&redlink=1) which are inherited solely from the female progenitor through the cytoplasm of the ovule.[[3]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Strickberger-2)

In Angiosperms, the successful development of the embryo depends on the normal functioning of its [endosperm](http://en.wikipedia.org/wiki/Endosperm).[[25]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Brink1947-24)

The failure of endosperm development and its subsequent abortion has been observed in many interploidal crosses (that is, those between populations with a particular degree of intra or interspecific [ploidy](http://en.wikipedia.org/wiki/Ploidy),[[25]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Brink1947-24) [[26]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Woodell1961-25)[[27]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Valentine1963-26) [[28]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Valentine1960-27) [[29]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Marks1966-28) and in certain crosses in species with the same level of ploidy.[[29]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Marks1966-28)[[30]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Nishiyama1979-29) [[31]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Nishiyama1984-30) The collapse of the [endosperm](http://en.wikipedia.org/wiki/Endosperm), and the subsequent abortion of the hybrid embryo is one of the most common post-fertilization reproductive isolation mechanism found in [angiosperms](http://en.wikipedia.org/wiki/Angiosperms).

### [[edit](http://en.wikipedia.org/w/index.php?title=Reproductive_isolation&action=edit&section=8)] Hybrid sterility

[](http://en.wikipedia.org/wiki/File:Maultier_grau.jpg)

[Mules](http://en.wikipedia.org/wiki/Mule) are hybrids with interspecific sterility.

[](http://en.wikipedia.org/wiki/File:Polarbrown-1.jpg)

A hybrid between a polar bear and a brown bear, Rothschild Museum, Tring.

A hybrid has normal viability but is deficient in terms of reproduction or is sterile. This is demonstrated by the [mule](http://en.wikipedia.org/wiki/Mule) and in many other well known hybrids. In all of these cases sterility is due to the interaction between the genes of the two species involved; to chromosomal imbalances due to the different number of chromosomes in the parent species; or to nucleus-cytoplasmic interactions such as in the case of *Culex* described above.[[3]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Strickberger-2)

[Hinnies](http://en.wikipedia.org/wiki/Hinny) and mules are [hybrids](http://en.wikipedia.org/wiki/Hybrid_(biology)) resulting from a cross between a [horse](http://en.wikipedia.org/wiki/Horse) and an [ass](http://en.wikipedia.org/wiki/Equus_asinus) or between a mare and a donkey, respectively. These animals are nearly always sterile due to the difference in the number of chromosomes between the two parent species. Both horses and donkeys belong to the genus [*Equus*](http://en.wikipedia.org/wiki/Equus_(genus)), but *Equus caballus* has 64 chromosomes, while *Equus asinus* only has 62. A cross will produce offspring (mule or hinny) with 63 chromosomes, that will not form pairs, which means that they do not divide in a balanced manner during [meiosis](http://en.wikipedia.org/wiki/Meiosis). It is curious that they can cross with each other but the mule and the hinny are actually animals created by humans, as in the wild the species ignore each other and do not cross. In order to obtain mules or hinnies it is necessary to train the progenitors to accept copulation between the species or create them through [artificial insemination](http://en.wikipedia.org/wiki/Artificial_insemination).

The sterility of many of the interspecific hybrids among the [angiosperms](http://en.wikipedia.org/wiki/Angiosperms) is a widely recognised and studied phenomenon. [[32]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Stebbins1958-31) There are a variety of causes that can determine the interspecific sterility of hybrids in plants, these may be genetic, related to the genomes or the interaction between nuclear and cytoplasmic factors, as will be discussed in the corresponding section. Nevertheless, it should be pointed out that - on the contrary to the situation in animals - hybridization in plants is a stimulus for the creation of new species. [[33]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Anderson1954-32) Indeed, although the hybrid may be sterile it can continue to multiply in the wild through the mechanisms of [asexual reproduction](http://en.wikipedia.org/wiki/Asexual_reproduction), be they [vegetative propagation](http://en.wikipedia.org/wiki/Vegetative_propagation) or [apomixis](http://en.wikipedia.org/wiki/Apomixis) or the production of seeds. [[34]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-33) [[35]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Campbell1996-34) Indeed, interspecific hybridization can be associated with [polyploidia](http://en.wikipedia.org/wiki/Polyploidy) and, in this way, the origin of new species that are called [allopolyploids](http://en.wikipedia.org/wiki/Allopolyploid). [*Rosa canina*](http://en.wikipedia.org/wiki/Rosa_canina), for example, is the result of multiple hybridizations.[[36]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Ritz2005-35) or there is a type of [wheat](http://en.wikipedia.org/wiki/Wheat) that is an allohexaploid that contains the genomes of three different species.[[37]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Stebbins1971-36)

## [[edit](http://en.wikipedia.org/w/index.php?title=Reproductive_isolation&action=edit&section=9)] Multiple mechanisms

In general, the barriers that separate species do not consist of just one mechanism. The twin species of *Drosophila*, *D. pseuoobscura* and *D. persimilis*, are isolated from each other by habitat (*persimilis* generally lives in colder regions at higher altitudes), by the timing of the mating season (*persimilis* is generally more active in the morning and *pseuoobscura* at night) and by behavior during mating (the females of both species prefer the males of their respective species). In this way, although the distribution of these species overlaps in wide areas of the west of the [United States of America](http://en.wikipedia.org/wiki/United_States_of_America), these isolation mechanisms are sufficient to keep the species separated. Such that, only a few fertile females have been found amongst the other species among the thousands that have been analyzed. However, when hybrids are produced between both species, the [gene flow](http://en.wikipedia.org/wiki/Gene_flow) between the two will continue to be impeded as the hybrid males are sterile. Also, and in contrast with the great vigor shown by the sterile males, the descendants of the backcrosses of the hybrid females with the parent species are weak and notoriously non-viable. This last mechanism restricts even more the genetic interchange between the two species of fly in the wild.[[3]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Strickberger-2)

## [[edit](http://en.wikipedia.org/w/index.php?title=Reproductive_isolation&action=edit&section=10)] Hybrid gender: Haldane's Rule

[Haldane's Rule](http://en.wikipedia.org/wiki/Haldane%27s_Rule) states that when one of the two sexes is absent in interspecific hybrids between two specific species, then the gender that is not produced, is rare or is sterile is the [heterozygous](http://en.wikipedia.org/wiki/Heterozygous) (or heterogametic) sex. [[38]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Haldane-37) In mammals, at least, there is growing evidence to suggest that this is due to high rates of mutation of the genes determining masculinity in the [Y chromosome](http://en.wikipedia.org/wiki/Y_chromosome). [[38]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Haldane-37) [[39]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Short-38) [[40]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Wu1993-39)

It has been suggested that Haldane's Rule simply reflects the fact that the male gender is more sensitive than the female when the sex-determining genes are included in a hybrid genome. But there are also organisms in which the heterozygous sex is the female: [birds](http://en.wikipedia.org/wiki/Birds) and [butterflies](http://en.wikipedia.org/wiki/Butterflies) and the law is followed in these organisms. Therefore, it is not a problem related to sexual development, nor with the sex chromosomes. Haldane proposed that the stability of hybrid individual development requires the full gene complement of each parent species, so that the hybrid of the heterozygous sex is unbalanced (i.e. missing at least one chromosome from each of the parental species). For example, the hybrid male obtained by crossing *D. melanogaster* females with *D. simulans* males, which is non-viable, lacks the X chromosome of *D. simulans*.[[12]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-pc-11)

## [[edit](http://en.wikipedia.org/w/index.php?title=Reproductive_isolation&action=edit&section=11)] The genetics of reproductive isolation barriers

### [[edit](http://en.wikipedia.org/w/index.php?title=Reproductive_isolation&action=edit&section=12)] Pre-copulatory isolation mechanisms in animals

The genetics of [ethological](http://en.wikipedia.org/wiki/Ethological) isolation barriers will be discussed first. Pre-copulatory isolation occurs when the genes necessary for the sexual reproduction of one species differ from the equivalent genes of another species, such that if a male of species A and a female of species B are placed together they are unable to copulate. Study of the genetics involved in this reproductive barrier tries to identify the genes that govern distinct sexual behaviors in the two species. The males of *Drosophila melanogaster* and those of *D. simulans* conduct an elaborate courtship with their respective females, which are different for each species, but the differences between the species are more quantitative than qualitative. In fact the *simulans* males are able to hybridize with the *melanogaster* females. Although there are lines of the latter species that can easily cross there are others that are hardly able to. Using this difference, it is possible to assess the minimum number of genes involved in pre-copulatory isolation between the *melanogaster* and *simulans* species and their chromosomal location.[[12]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-pc-11)

In experiments, flies of the *D. melanogaster* line, which hybridizes readily with *simulans*, were crossed with another line that it does not hybridize with, or rarely. The females of the segregated populations obtained by this cross were placed next to *simulans* males and the percentage of hybridization was recorded, which is a measure of the degree of reproductive isolation. It was concluded from this experiment that 3 of the 8 chromosomes of the [haploid](http://en.wikipedia.org/wiki/Haploid) complement of *D. melanogaster* carry at least one gene that affects isolation, such that substituting one chromosome from a line of low isolation with another of high isolation reduces the hybridization frequency. In addition, interactions between chromosomes are detected so that certain combinations of the chromosomes have a multiplying effect.[[12]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-pc-11) Cross incompatibility or incongruence in plants is also determined by major genes that are not associated at the [self-incompatibility](http://en.wikipedia.org/wiki/Self-incompatibility) *S locus*.[[41]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Mutschler1994-40)[[42]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Hogenboom1973-41)[[43]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Ascher1986-42)

### [[edit](http://en.wikipedia.org/w/index.php?title=Reproductive_isolation&action=edit&section=13)] Post copulation or fertilization isolation mechanisms in animals

Reproductive isolation between species appears, in certain cases, a long time after fertilization and the formation of the zygote, as happens - for example - in the twin species [*Drosophila pavani*](http://en.wikipedia.org/w/index.php?title=Drosophila_pavani&action=edit&redlink=1) and [*D. gaucha*](http://en.wikipedia.org/w/index.php?title=Drosophila_gaucha&action=edit&redlink=1). The hybrids between both species are not sterile, in the sense that they produce viable gametes, ovules and spermatozoa. However, they cannot produce offspring as the sperm of the hybrid male do not survive in the semen receptors of the females, be they hybrids or from the parent lines. In the same way, the sperm of the males of the two parent species do not survive in the reproductive tract of the hybrid female.[[12]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-pc-11) This type of post copulatory isolation appears as the most efficient system for maintaining reproductive isolation in many species.[[44]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Templeton1981-43)

In fact, the development of a zygote into an adult is a complex and delicate process of interactions between genes and the environment that must be carried out precisely, and if there is any alteration in the usual process, caused by the absence of a necessary gene or the presence of a different one, it can arrest the normal development causing the non-viability of the hybrid or its sterility. It should be borne in mind that half of the chromosomes and genes of a hybrid are from one species and the other half come from the other. If the two species are genetically different, there is little possibility that the genes from both will act harmoniously in the hybrid. From this perspective, only a few genes would be required in order to bring about post copulatory isolation, as opposed to the situation described previously for pre-copulatory isolation.[[12]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-pc-11)[[45]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Wu1994-44)

In many species where pre-copulatory reproductive isolation does not exist, hybrids are produced but they are of only one sex. This is the case for the hybridization between females of *Drosophila simulans* and *Drosophila melanogaster* males: the hybridized females die early in their development so that only males are seen among the offspring. However, populations of *D. simulans* have been recorded with genes that permit the development of adult hybrid females, that is, the viability of the females is “rescued”. It is assumed that the normal activity of these [speciation](http://en.wikipedia.org/wiki/Speciation) genes is to “inhibit” the expression of the genes that allow the growth of the hybrid. There will also be regulator genes.[[12]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-pc-11)

A number of these genes have been found in the *melanogaster* species group. The first to be discovered was “Lhr” (Lethal hybrid rescue) located in Chromosome II of *D. simulans*. This [dominant allele](http://en.wikipedia.org/wiki/Dominant_allele) allows the development of hybrid females from the cross between *simulans* females and *melanogaster* males.[[46]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Watanabe1979-45) A different gene, also located on Chromosome II of *D. simulans* is “Shfr” that also allows the development of female hybrids, its activity being dependent on the temperature at which [development](http://en.wikipedia.org/w/index.php?title=Embryogenesis_in_Drosophila&action=edit&redlink=1) occurs.[[47]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Carracedo2000-46) Other similar genes have been located in distinct populations of species of this group. In short, only a few genes are needed for an effective post copulatory isolation barrier mediated through the non-viability of the hybrids.

As important as identifying an isolation gene is knowing its function. The *Hmr* gene, linked to the X chromosome and implicated in the viability of male hybrids between *D. melanogaster* and *D. simulans*, is a gene from the [proto-oncogene](http://en.wikipedia.org/wiki/Proto-oncogene) family [*myb*](http://en.wikipedia.org/wiki/MYB_(gene)), that codes for a transcriptional regulator. Two variants of this gene function perfectly well in each separate species, but in the hybrid they do not function correctly, possibly due to the different genetic background of each species. Examination of the allele sequence of the two species shows that change of direction substitutions are more abundant than [synonymous substitutions](http://en.wikipedia.org/wiki/Synonymous_substitution), suggesting that this gene has been subject to intense natural selection.[[48]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Hutter1990-47)

The [Dobzhansky](http://en.wikipedia.org/wiki/Theodosius_Dobzhansky)-Muller model proposes that reproductive incompatibilities between species are caused by the interaction of the genes of the respective species. It has been demonstrated recently that *Lhr* has functionally diverged in *D. simulans* and will interact with *Hmr* which, in turn, has functionally diverged in *D. melanogaster* to cause the lethality of the male hybrids. *Lhr* is located in a heterochromatic region of the genome and its sequence has diverged between these two species in a manner consistent with the mechanisms of positive selection. [[49]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Brideau2006-48) An important unanswered question is whether the genes detected correspond to old genes that initiated the speciation favoring hybrid non-viability, or are modern genes that have appear post-speciation by mutation, that are not shared by the different populations and that suppress the effect of the primitive non-viability genes. The *OdsH* (abbreviation of *Odysseus*) gene causes partial sterility in the hybrid between *Drosophila simulans* and a related species, *D. mauritiana*, which is only encountered on [Mauritius](http://en.wikipedia.org/wiki/Mauritius), and is of recent origin. This gene shows [monophyly](http://en.wikipedia.org/wiki/Monophyly) in both species and also has been subject to natural selection. It is thought that it is a gene that intervenes in the initial stages of speciation, while other genes that differentiate the two species show [polyphyly](http://en.wikipedia.org/wiki/Polyphyly). *Odsh* originated by duplication in the genome of *Drosophila* and has evolved at very high rates in *D. mauritania*, while its [paralogue](http://en.wikipedia.org/wiki/Paralogue), *unc-4*, is nearly identical between the species of the group *melanogaster*. [[50]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Ting2004-49) [[51]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Nei1998-50) [[52]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Sun2004-51) [[53]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Ting2000-52) Seemingly, all these cases illustrate the manner in which speciation mechanisms originated in nature, therefore they are collectively known as “speciation genes”, or possibly, gene sequences with a normal function within the populations of a species that diverge rapidly in response to positive selection thereby forming reproductive isolation barriers with other species. In general, all these genes have functions in the transcriptional [regulation](http://en.wikipedia.org/wiki/Regulation) of other genes. [[54]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Orr2005-53)

The *Nup96* gene is another example of the evolution of the genes implicated in post-copulatory isolation. It regulates the production of one of the approximately 30 proteins required to form a [nuclear pore](http://en.wikipedia.org/wiki/Nuclear_pore). In each of the *simulans* groups of *Drosophila* the protein from this gene interacts with the protein from another, as yet undiscovered, gene on the X chromosome in order to form a functioning pore. However, in a hybrid the pore that is formed is defective and causes sterility. The differences in the sequences of *Nup96* have been subject to adaptive selection, similar to the other examples of *speciation genes* described above. [[55]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Presgraves2003-54) [[56]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Barbash2007-55)

Post-copulatory isolation can also arise between chromosomally differentiated populations due to [chromosomal translocations](http://en.wikipedia.org/wiki/Chromosomal_translocation) and [inversions](http://en.wikipedia.org/wiki/Chromosomal_inversion). [[57]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Noor2001-56) If, for example, a reciprocal translocation is fixed in a population, the hybrid produced between this population and one that does not carry the translocation will not have a complete [meiosis](http://en.wikipedia.org/wiki/Meiosis). This will result in the production of unequal gametes containing unequal numbers of chromosomes with a reduced fertility. In certain cases, complete translocations exist that involve more than two chromosomes, so that the meiosis of the hybrids is irregular and their fertility is zero or nearly zero. [[58]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Rieseberg2001-57) Inversions can also give rise to abnormal gametes in heterozygous individuals but this effect has little importance compared to translocations. [[57]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Noor2001-56) An example of chromosomal changes causing sterility in hybrids comes from the study of [*Drosophila nasuta*](http://en.wikipedia.org/w/index.php?title=Drosophila_nasuta&action=edit&redlink=1) and [*D. albomicans*](http://en.wikipedia.org/w/index.php?title=Drosophila_albomicans&action=edit&redlink=1) which are twin species from the Indo-Pacific region. There is no sexual isolation between them and the F1 hybrid is fertile. However, the F2 hybrids are relatively infertile and leave few descendants which have a skewed ratio of the sexes. The reason is that the X chromosome of *albomicans* is translocated and linked to an [autosome](http://en.wikipedia.org/wiki/Autosome) which causes abnormal meiosis in hybrids. [Robertsonian translocations](http://en.wikipedia.org/wiki/Robertsonian_translocation) are variations in the numbers of chromosomes that arise from either: the fusion of two [acrocentric](http://en.wikipedia.org/wiki/Centromere) chromosomes into a single chromosome with two arms, causing a reduction in the haploid number, or conversely; or the fission of one chromosome into two acrocentric chromosomes, in this case increasing the haploid number. The hybrids of two populations with differing numbers of chromosomes can experience a certain loss of fertility, and therefore a poor adaptation, because of irregular meiosis.

### [[edit](http://en.wikipedia.org/w/index.php?title=Reproductive_isolation&action=edit&section=14)] Post copulation or fertilization isolation mechanisms in plants

In plants, hybrids often suffer from an autoimmune syndrome known as hybrid necrosis. In the hybirds, specific gene products contributed by one of the parents may be inappropriately recognized as foreign and pathogenic, and thus trigger pervasive cell death throughout the plant.[[59]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-pmid17404584-58) In at least one case, a pathogen receptor, encoded by the most variable gene family in plants, was identified as being responsible for hybrid necrosis.[[60]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-pmid17803357-59)

### [[edit](http://en.wikipedia.org/w/index.php?title=Reproductive_isolation&action=edit&section=15)] Incompatibility caused by microorganisms

In addition to the genetic causes of reproductive isolation between species there is another factor that can cause of post zygotic isolation: the presence of [microorganisms](http://en.wikipedia.org/wiki/Microorganism) in the cytoplasm of certain species. The presence of these organisms in a species and their absence in another causes the non-viability of the corresponding hybrid. For example, in the semi-species of the group *D. paulistorum* the hybrid females are fertile but the males are sterile, this is due to the presence of a [mycoplasma](http://en.wikipedia.org/wiki/Mycoplasma) in the cytoplasm which alters [spermatogenesis](http://en.wikipedia.org/wiki/Spermatogenesis) leading to sterility. It is interesting that incompatibility or isolation can also arise at an intraspecific level. Populations of *D. simulans* have been studied that show hybrid sterility according to the direction of the cross. The factor determining sterility has been found to be the presence or absence of a microorganism [*Wolbachia*](http://en.wikipedia.org/wiki/Wolbachia) and the populations tolerance or susceptibility to these organisms. This inter population incompatibility can be eliminated in the laboratory through the administration of a specific [antibiotic](http://en.wikipedia.org/wiki/Antibiotic) to kill the microorganism. Similar situations are known in a number of insects, as around 15% of species show infections caused by this [symbiont](http://en.wikipedia.org/wiki/Symbiosis). It has been suggested that, in some cases, the speciation process has taken place because of the incompatibility caused by this bacteria. Two [wasp](http://en.wikipedia.org/wiki/Wasp) species [*Nasonia giraulti*](http://en.wikipedia.org/w/index.php?title=Nasonia_giraulti&action=edit&redlink=1) and *N. longicornis* carry two different strains of *Wolbachia*. Crosses between an infected population and one free from infection produces a nearly total reproductive isolation between the semi-species. However, if both species are free from the bacteria or both are treated with antibiotics there is no reproductive barrier. [[61]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Breeuwer1990-60) [[62]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Bordenstein2001-61) *Wolbachia* also induces incompatibility due to the weakness of the hybrids in populations of spider mites (*[Tetranychus urticae](http://en.wikipedia.org/wiki/Tetranychus_urticae" \o "Tetranychus urticae)*, ,[[63]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Vala2000-62) between [*Drosophila recens*](http://en.wikipedia.org/w/index.php?title=Drosophila_recens&action=edit&redlink=1) and *D. subquinaria* [[64]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Shoemaker1999-63) and between species of [*Diabrotica*](http://en.wikipedia.org/wiki/Diabrotica) (beetle) and [*Gryllus*](http://en.wikipedia.org/wiki/Gryllus) (cricket). [[65]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Giordano1997-64)

## [[edit](http://en.wikipedia.org/w/index.php?title=Reproductive_isolation&action=edit&section=16)] Selection for reproductive isolation

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| **Selection for reproductive isolation between two *Drosophila* species.**[[66]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Koop-65) | |
| **Generation** | **Percentage of hybrids** |
| 1 | 49 |
| 2 | 17,6 |
| 3 | 3,3 |
| 4 | 1,0 |
| 5 | 1,4 |
| 10 | 0,6 |

In 1950 [K. F. Koopman](http://en.wikipedia.org/w/index.php?title=K._F._Koopman&action=edit&redlink=1) reported results from experiments designed to examine the hypothesis that [selection](http://en.wikipedia.org/wiki/Artificial_selection) can increase reproductive isolation between populations. He used *D. pseudoobscura* and *D. persimilis* in these experiments. When the flies of these species are kept at 16°C approximately a third of the matings are interspecific. In the experiment equal numbers of males and females of both species were placed in containers suitable for their survival and reproduction. The progeny of each generation were examined in order to determine if there were any interspecific hybrids. These hybrids were then eliminated. An equal number of males and females of the resulting progeny were then chosen to act as progenitors of the next generation. As the hybrids were destroyed in each generation the flies that solely mated with members of their own species produced more surviving descendants than the flies that mated solely with individuals of the other species. In the table to the right it can be seen that for each generation the number of hybrids continuously decreased up to the tenth generation when hardly any interspecific hybrids were produced. [[66]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Koop-65) It is evident that selection against the hybrids was very effective in increasing reproductive isolation between these species. From the third generation, the proportions of the hybrids were less than 5%. This confirmed that selection acts to reinforce the reproductive isolation of two genetically divergent populations if the hybrids formed by these species are less well adapted than their parents.

These discoveries allowed certain assumptions to be made regarding the origin of reproductive isolation mechanisms in nature. Namely, if selection reinforces the degree of reproductive isolation that exists between two species due to the poor adaptive value of the hybrids, it is expected that the populations of two species located in the same area will show a greater reproductive isolation than populations that are geographically separated. This mechanism for “reinforcing” hybridization barriers in sympatric populations is called the "[Wallace Effect](http://en.wikipedia.org/w/index.php?title=Wallace_Effect&action=edit&redlink=1)", as it was first proposed by [Alfred Russell Wallace](http://en.wikipedia.org/wiki/Alfred_Russell_Wallace) at the end of the 19th century, and it has been experimentally demonstrated in both plants and animals. [[67]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-66) [[68]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Sawyer1981-67) [[69]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Gillespie1991-68) [[70]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Bush1975-69) [[71]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Silvertown2005-70) [[72]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Antonovics2006-71)

The sexual isolation between [*Drosophila miranda*](http://en.wikipedia.org/w/index.php?title=Drosophila_miranda&action=edit&redlink=1) and *D. pseudoobscura*, for example, is more or less pronounced according to the geographic origin of the flies being studied. Flies from regions where the distribution of the species is superimposed show a greater sexual isolation than exists between populations originating in distant regions.

Reproductive isolation mechanisms can be a consequence of allopatric speciation. A population of *Drosophila* was divided into sub populations that were selected to adapt to different food types. After a number of generations the two sub populations were mixed again. It was observed that the subsequent matings occurred between individuals belonging to the same adapted group.[[73]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Dodd-72)

On the other hand, interspecific hybridization barriers can also arise as a result of the adaptive divergence that accompanies [allopatric speciation](http://en.wikipedia.org/wiki/Allopatric_speciation). This mechanism has been experimentally proved by an experiment carried out by [Diane Dodd](http://en.wikipedia.org/w/index.php?title=Diane_Dodd&action=edit&redlink=1) on *D. pseudoobscura*. A single population of flies was divided into two, with one of the populations fed with [starch](http://en.wikipedia.org/wiki/Starch)-based food and the other with [maltose](http://en.wikipedia.org/wiki/Maltose)-based food. This meant that each sub population was adapted to each food type over a number of generations. After the populations had diverged over many generations, the groups were again mixed; it was observed that the flies would mate only with others from their adapted population. This indicates that the mechanisms of reproductive isolation can arise even though the interspecific hybrids are not selected against. [[73]](http://en.wikipedia.org/wiki/Reproductive_isolation#cite_note-Dodd-72)

## [[edit](http://en.wikipedia.org/w/index.php?title=Reproductive_isolation&action=edit&section=17)] See also